

ENCYCLOPEDIA OF THE WORLD'S BIOMES



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Library of Congress Cataloging-in-Publication Data

A catalog record for this book is available from the Library of Congress

British Library Cataloguing-in-Publication Data

A catalogue record for this book is available from the British Library

ISBN 978-0-12-816096-1

For information on all publications visit our website
at <http://store.elsevier.com>



Publisher: Oliver Walter
Acquisition Editor: Priscilla Braglia
Senior Content Project Manager: Richard Berryman
Associate Content Project Manager: Gayathri S
Designer: Matthew Limbert

ACKNOWLEDGMENTS AND DEDICATIONS

The idea for this encyclopedia came from conversations with scientists and managers who wanted to see a treatise on ecosystems and biomes. We then embarked on the *Encyclopedia of the World's Biomes* not to redefine and reclassify biomes but to highlight groups of similar ecosystems using existing biome classifications and how humans have shaped and interacted with these ecosystems.

Although this work is approximately 300 articles, we knew at the outset we could not cover all the amazing places on Earth. It is simply too broad, so we tried to provide some of the highlights for you and encourage you to keep looking for more.

The *Encyclopedia of the World's Biomes* is dedicated to the courage of Greta Thunberg.

Mike Goldstein
Dominick DellaSala
Lowell Suring
Mark J. Costello
Scott Elias
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Figure 5 Roads vs roadless
Figure 8 Island biogeography of Shallow water marine Organisms
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Figure 2 Island biogeography of Shallow water marine Organisms
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Perspectives on Terrestrial Biomes: The International Vegetation Classification

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Abstract

Despite the widespread use of the term biome, systematic, multi-scaled biome classifications are hard to come by. This may be in part because biomes represent large-scale ecosystems, and the complexity of ecological and biotic factors makes it hard to classify them at these large scales. In addition, humans play a large role in shaping biomes, such that both natural and anthropogenic biomes need to be treated. Here we introduce the International Vegetation Classification (IVC), based on the EcoVeg approach, as a useful, multi-scaled and comprehensive terrestrial classification that can inform biome concepts. We rely on vegetation as a primary criterion (typical of many approaches to biome concepts) while noting that ecoregional and functional approaches add additional valuable perspectives. The IVC uses an 8-level hierarchy for both natural and cultural vegetation. For natural vegetation, the IVC includes three upper (formation) levels, three mid (physiognomic-biogeographic-floristic) levels and two lower (floristic) levels. The IVC is most advanced in North and South America, but we describe a number of other major vegetation classifications with similar approaches that allow for a collaborative approach to describing ecosystems across the globe at all scales. The IVC provides a consistent thematic framework to support broad-scale vegetation mapping, inventory and assessment, including applications to both the IUCN Red List of Ecosystems and NatureServe Conservation Status Assessment protocols. The classification approach meets the need for a dynamic, 8-level catalogue of types for all existing vegetation, including large-scale ecosystems or biomes. The open, peer-review model allows for ongoing improvement by ecologists, while always providing comprehensive versions for users.

Biomes, Ecosystems and Vegetation

After several decades of contributions, in 2005 the 26th volume of the *Ecosystems of the World* series was completed (<https://www.elsevier.com/books/book-series/ecosystems-of-the-world>). Remarkable in its scope, the purpose of the series was “to describe the structure and functioning of all major types of ecosystems, whether aquatic or terrestrial, natural or subject to human influence—in some cases virtually man-made (like greenhouses, fishponds, or intensive animal production).” Most important for our purposes here, the subjects covered by *Ecosystems of The World* are divided by “ecosystem types or biomes.” Which raises the question as to the parallels between those volumes and the types covered in the *Encyclopedia of World Biomes*. To do so requires some decisions as to whether ecosystems and biomes are the same thing and how they are classified. Here we introduce the International Vegetation Classification (IVC) as one tool for understanding the range of variability of large biome-scale terrestrial ecosystems on land and aquatic margins. But to do that we first need to explore the relationship of ecosystem to biome.

Although many authors have offered definitions of an ecosystem, Keith et al. (2013) note that most encapsulate four essential elements implicit in Tansley's (1935) original concept: (i) a biotic complex or assemblage of species; (ii) an associated abiotic environment or complex; (iii) the interactions within and between those complexes; and (iv) a physical space in which these operate. Thus, ecosystems are defined by a degree of uniqueness in composition, structure and processes (involving the biota and the environment) and a spatial boundary. We follow Keith et al. (2013) in noting that terms such as “ecological communities,” “ecological systems,” “natural communities,” “habitats,” “biotopes,” and “vegetation types” are often applied as operational synonyms of “ecosystem types” for the purposes of classifying ecosystems.

For Tansley (1935), the biome was essentially an expression of a large-scale ecosystem: “The fundamental concept appropriate to the biome considered together with all the effective inorganic factors of its environment is the ecosystem” (Tansley, 1935). And, for terrestrial biomes “vegetation is of primary importance,” a criterion that is still currently maintained for almost all biome classifications (Moncrieff et al., 2016; Mucina, 2018). This in part stems from its role in primary production and as an “engineer” in many terrestrial and shallow aquatic ecosystems, but also from descriptive convenience—the structural and compositional features of vegetation are readily observed, and therefore useful descriptive tools. Thus, for our purposes, biomes are large-scale ecosystems, and vegetation has historically been the most productive way to describe and classify them. That said, animals, soils and other ecosystem components need to be addressed to fully understand the key processes and interactions of the biome.

Because ecosystems range across multiple spatial and temporal scales, a classification of ecosystems will be most valuable when they can operate across those scales (i.e., a biome-scale classification of ecosystems is not enough). Given the complexity of dealing with ecosystems, and a multitude of purposes, it's not surprising that ecologists have devised various classification systems. Three common ones are ecological site classifications, ecoregional classifications, and vegetation classifications (Fig. 1). They can be used separately or together to classify ecosystems, depending on the need. For example, WWF ecoregions (Dinerstein et al., 2017) can be

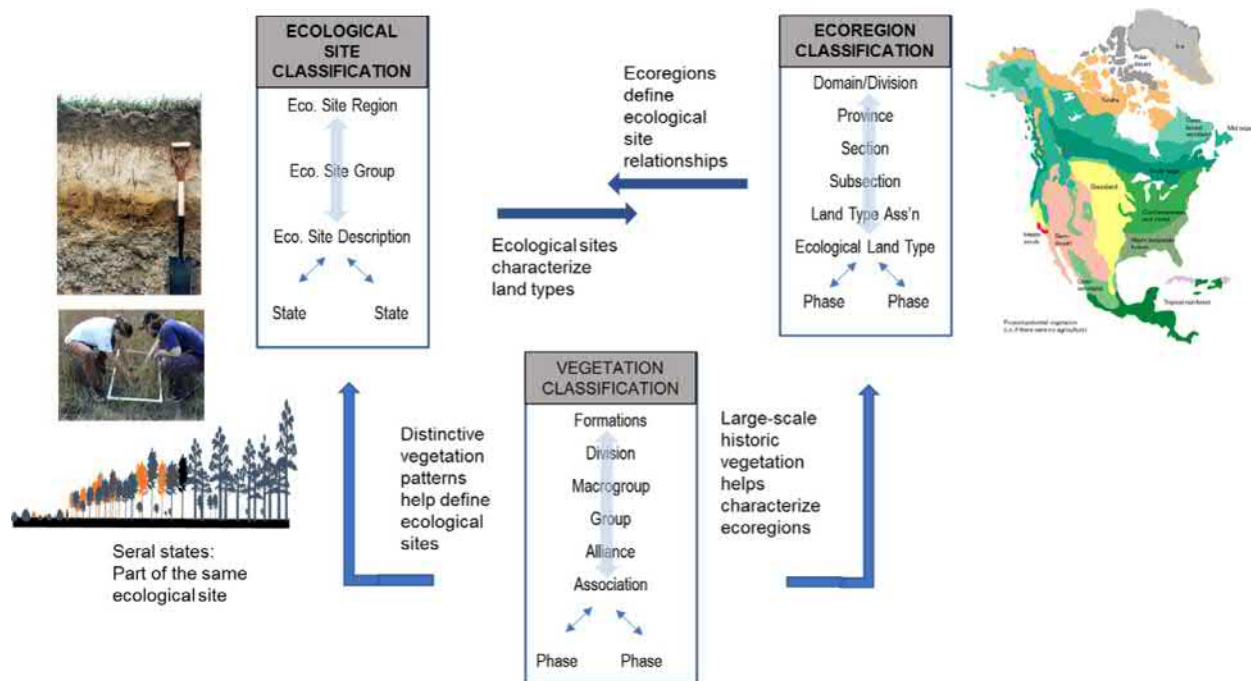


Fig. 1 Some commonly used, and complementary, approaches to classifying ecosystems, including large-scale ecosystems or biomes. Each approach can be used on its own or in collaboration with others to define ecosystems, including large-scale ecosystem or biomes.

used as a regional, spatially explicit, biome-scale classification, or it can be used in conjunction with the IVC to describe variation in ecosystem types found within and across ecoregions (Dixon et al., 2014).

To meet the need of characterizing the earth's terrestrial ecosystems, and to address critical conservation and resource management needs, biome-scale classifications should encompass both natural and cultural ecosystems. Indeed, the scope of the ecosystem concept can be applied to interweave these two together, without subsuming one into the other, to include both human and natural processes and disturbances within what are termed "social-ecological systems;" namely, linked systems of people and nature (Berkes and Folke, 1998). Finally, ecosystem classifications will also need to consider all three realms of ecosystems (terrestrial, freshwater, and marine), a task underway by an IUCN working group (Keith et al., 2019). Here we restrict ourselves to terrestrial biomes.

Why Include an IVC Perspective on Biomes?

In much of the literature, there is a considerable overlap and confusion between the concepts of biome, bioregion, ecosystem, and ecoregion among others, likely due to the plurality of meanings included in the word biome. The confusion is notable due to the mixture of definition, criteria, and hierarchical levels between concepts and terminology that place different emphasis on different definitional features, such as ecoregions, ecosystems, ecological systems, ecological divisions, biomes, ecozones, formations, bioregions, etc. A classification for biomes should lead us toward a parsimonious methodological and nomenclatural standardization able to explain and predict causally the distribution and global characteristics of the biomes based on a set of criteria or quantifiable variables. The classification should describe the diversity and dynamics of terrestrial ecosystems, span the full range of spatial and geographic scales across the globe, and provide knowledge of reference conditions and current states of ecosystems required to make decisions about conservation and resource management. There are imperatives to predict terrestrial ecosystem responses to alternative scenarios of environmental change and to develop an evidence base for adaptive management that seeks to reduce risks of ecosystem degradation and collapse. Assessing these risks, diagnosing their causes and designing management solutions to abate them depends critically on a basic understanding of the ecological processes and mechanisms that drive ecosystem change (Keith et al., 2013).

Despite these needs, there are few options for a comprehensive, operational, multi-scaled ecosystem classification, one that can scale down from large-scale biome patterns to finer-scale vegetation (plant community) patterns, or vice-versa. The IVC is currently unique in providing both global and continental biome-scaled ecosystem types that can be further resolved into regional to local ecosystem types (Faber-Langendoen et al., 2018). Collaboration with colleagues is needed to fully extend its application across the globe, in conjunction with other global, regional and national efforts. Still, although vegetation provides the primary basis for the IVC approach to classifying biomes, it is only part of what is needed to fully describe the key processes and interactions that govern biomes. Thus, the IVC and other such classifications are best seen as facilitators of the larger goal of understanding how ecosystems work.

Scaling ecosystems across the globe will always have limitations, given the wide diversity of species, growth forms, regions and ecological factors. We can look for some rough correlation between levels of ecological organization and spatial and temporal scales, but there are no universal rules. The IVC seeks to do this largely from a structural-compositional based perspective, interpreted and segmented along ecological gradients. More work is needed to develop models that integrate the IVC patterns with ecological processes, though recent mapping efforts in the Americas and Africa holds promise (Sayre et al., 2013; Ferrer-Paris et al., 2018).

Before describing the IVC in detail, we note that discrete classification of biomes is not always a goal, particularly when continuous attributes (such as NDVI) of an ecosystem or biome can describe certain functions or processes (Higgins et al., 2016).

Overview of the International Vegetation Classification

IVC and the EcoVeg Approach

The primary purpose of the IVC is to provide a consistent, systematic, and authoritative description and classification of terrestrial ecosystems, based primarily on vegetation patterns and their relationships with ecological, biogeographic, dynamic, and human processes. The IVC is based on the EcoVeg approach, as summarized in Faber-Langendoen et al. (2014, 2016, 2018). Briefly, the IVC was developed by NatureServe, in collaboration with partners of the US National Vegetation Classification (USNVC), including US federal agencies and the Ecological Society of America (FGDC, 2008), Canadian NVC (Baldwin and Meades, 2008) and others. The IVC is used widely by states, provinces and countries in the Americas that are part of the NatureServe Network. Initially, the IVC and USNVC partners adopted a strongly physiognomic approach for the upper levels, with floristic units nested below; in 2008, they supported the development and implementation of the EcoVeg approach for the USNVC (FGDC, 2008). The approach builds on the traditional physiognomic-floristic-ecological classifications that have been developed over many years (Faber-Langendoen et al., 2014). These perspectives also share a central philosophy with floristic-ecological approaches, such as the Braun-Blanquet approach (Westhoff and van der Maarel, 1973), and the biogeoclimatic approach (MacKenzie and Meidinger, 2018); namely, that vegetation types should be constructed in the context of ecological, dynamic, and biogeographic considerations. The EcoVeg approach integrates these considerations for all vegetation types at multiple thematic scales.

Guiding Principles

The IVC used the guiding principles from the EcoVeg approach, briefly summarized here (see Faber-Langendoen et al., 2014 for more details):

1. The classification is based on *existing vegetation* types, defined as the plant cover—including floristic composition and abundance and vegetation structure—documented at a specific location and time, under specified ecological conditions, and preferably described at an optimal time(s) during the growing season. Thus, as applied to biomes, we do not address potential natural vegetation, though the IVC does address historic patterns of vegetation that existed at time periods in the past.
2. Vegetation types are characterized by *full floristic* and *growth form (physiognomic)* composition, which together express *ecological* and *biogeographical* relations.
3. Vegetation characteristics can be described as a function of both *natural* and *cultural (or anthropogenic)* processes.
4. Characterizing and describing vegetation types is best accomplished using *plot data*, including both floristic and environmental site data, which are collected and compiled using *systematic protocols and survey techniques*.
5. Vegetation types can be defined using a *number of differentiating criteria*, depending on the level, including diagnostic, constant and dominant species, dominant and diagnostic growth forms, and compositional similarity (Table 1). The most useful criteria are those that express *environmental* and *biogeographical relationships* that clearly distinguish types. These criteria should be defined for application in the field or lab, so that *recognizable and unambiguous field characteristics* are provided to ensure consistent identification using keys and other tools. Types are defined both extensively (e.g., a full list of types is developed within each level of the hierarchy, a list of plots is attributed to each type, range maps are provided, etc.) and intensively (e.g., concise differentiating criteria are provided for each type, including diagnostic and dominant species, growth forms, environmental site factors and biogeography).
6. Classification and field recognition of vegetation types creates a conceptual framework of vegetation pattern and process that provides a foundation for multiple applications, e.g., *vegetation mapping, monitoring, modeling*.
7. Differentiating criteria for vegetation types can be arranged *hierarchically*, from *upper levels* primarily based on general growth forms, to *middle levels* based on specific growth forms and floristics that includes suites of general and regional combinations of characteristic species, to *lower levels* based primarily on gradients in floristics and ecology. At all levels, existing vegetation provides the primary criteria for definitions and descriptions within the hierarchy, but the hierarchical organization may be based on the existing ecological and biogeographical relations expressed by the vegetation.

Table 1 Brief summary of criteria for natural and cultural vegetation (for fuller description and references, see Faber-Langendoen et al. (2014)).

Criteria	Natural Vegetation	Cultural Vegetation
Growth forms	Growth form criteria include (1) diagnostic combinations of growth forms, (2) dominant growth forms, singly or in combination; and (3) vertical and horizontal structure of growth forms. Growth forms are based on structural types (e.g., tree), leaf form (e.g., broad-leaved macrophyll), relative plant and leaf size, and seasonal activity pattern (e.g., summergreen)	Growth form criteria include (1) diagnostic patterns of growth forms, (2) dominant growth forms, singly or in combination, and (3) vertical and horizontal structure of growth forms.
Floristics	Floristic composition is summarized by the “ <i>characteristic species combinations</i> ” (or diagnostic combination of species), including (a) diagnostic species (character and differential species), (b) constant species, (c) dominant species; all linked to growth forms and structure above	Floristic (crop or managed species) criteria include: (1) diagnostic combinations of species/crop or managed types, (2) dominant species, reflecting similar agricultural or developed vegetation patterns, (3) vertical and horizontal structure of species. Together these criteria are evaluated in a human management context
Compositional similarity	Compositional similarity is defined as a measure of the similarity in the presence and/or abundance of plant species between two or more plots or types. At middle scales of vegetation pattern, where plots increasingly lack overlap in species composition, but occupy similar ecological and biogeographical space, compositional similarity is assessed using suites of diagnostic species and growth forms related to biogeographic patterns. Large scale compositional similarity is captured in the distinct pool of species found in different biogeographic regions	Not applicable
Ecological context	Criteria for ecological context include (1) biogeography (from large-scale biogeographic regions to regional biogeographic and biogeoclimatic zones), (2) climate (macro, <i>meso</i> , and microclimates), (3) disturbances (natural and cultural disturbances, and successional patterns), and (4) topo-edaphic factors, including the topographic features of elevation, slope and aspect, as well as edaphic factors, such as pH, moisture, nutrients, and texture	Criteria for ecological context include (1) climate (macro, meso, and microclimate), though human management activities often compensate for many of the climatic effects, (2) effects of human activities (e.g., plowing, mowing), and (3) topo-edaphic factors, including creation of ponds, plowing, modifications of pH, moisture, nutrients, and texture. Because many crop species are planted and maintained outside their provenance, biogeography is rarely considered in the description of cultural types

8. An integrated hierarchy of vegetation types is best established by considering *each level as both independent and inter-connected* in a *nested* relationship; i.e., criteria selected to differentiate levels in the hierarchy are sufficient to define and distinguish types of a particular level, thereby preventing it from being arbitrarily defined by the level immediately above or below in the hierarchy. Thus, for the development of vegetation types, the EcoVeg approach is both “top-down” and “bottom-up.”

Classification protocols for the IVC are fully described in Faber-Langendoen et al. (2018).

Natural and Cultural Vegetation

The IVC describes and classifies both natural and cultural vegetation. Thus, it can be used to describe large-scale anthropogenic biomes, such as cropland, hay meadows and pasture, and plantations (Ellis and Ramankutty, 2008), as well as natural biomes, such as native forests, grasslands, deserts and wetlands. *Cultural vegetation* possesses a distinctive structure and composition that is determined by the response to human intervention, such as (1) regularly spaced herbaceous vegetation with substantial cover of bare soil for significant periods of the year (usually determined by tillage, chemical treatment, or agricultural flooding), (2) vegetation consisting of highly-manipulated growth forms or structures rarely found under natural plant development (usually determined by mechanical pruning, frequent mowing, clipping, etc.), and (3) vegetation composed of species not native to the area that have been intentionally introduced to the site by humans and that would not persist without active management by humans (e.g., lawns, golf courses, plantations, arboreta). The drivers of cultural vegetation are largely human, and thus intertwined with cultural, historical and socioeconomic aspects that make it difficult to generalize patterns.

By contrast, *Natural and semi-natural vegetation* is composed predominantly of spontaneously growing sets of plant species with composition shaped by both abiotic (site) and biotic processes; these are vegetation types whose species composition is primarily determined by non-human ecological processes (Westhoff and van der Maarel, 1973). Within natural and semi-natural vegetation there is a spectrum of human activities (e.g., logging, livestock grazing, fire, introduced pathogens), but “ruderal vegetation” represents the most human-influenced natural vegetation. We define ruderal vegetation as “vegetation found on human-disturbed sites that may not have apparent recent historical natural analogs, and whose current composition and structure is not a function of continuous cultivation by humans and includes a broadly distinctive characteristic species combination, whether tree, shrub or herb dominated. The vegetation is often composed of invasive species, whether exotic or native, that typically have expanded in extent and abundance due to the human disturbances” (from Faber-Langendoen et al. 2014). The term “novel ecosystem” has been applied to this kind of vegetation. For example, forests found on abandoned farm fields in the northeastern United States contain both invasive exotic trees (e.g., *Acer platanoides*, *Robinia pseudoacacia*) and generalist native trees (e.g., *Acer rubrum*), as well as invasive shrubs and herbs (e.g., *Rhamnus cathartica*, *Alliaria petiolata*). Both the vegetation and ecological processes associated with these forests are distinct from more natural forests. Inclusion of both native and weedy vegetation within “natural vegetation” is perhaps akin to many botanical manuals that treat both native and naturalized species within their scope; yet these manuals exclude the multitude of cultivated species found in lawns, gardens, farm fields and plantations.

Classification of natural and semi-natural vegetation

Growth forms and floristic characteristics that reflect ecological and biogeographical variables are the primary properties of natural vegetation, and the dominant and diagnostic combinations of these properties are used to define all units of the hierarchy (Faber-Langendoen et al., 2014) (Table 1).

The growth form types provided in Faber-Langendoen et al. (2014, 2016), are used to characterize IVC types at broader scales. Six general growth form types (tree, shrub, herb, nonvascular, epiphyte, liana) are further subdivided into 29 specific growth form types (e.g., broad-leaved evergreen tree, succulent shrub, sclerophyllous shrub, and lichen) that are diagnostic for large-scale biomes, such as tropical rainforest, desert, or cliffs. At lower levels, the characteristic species combination (or diagnostic species combination) is considered a strong indicator of bioclimatic, biogeographic, geo-edaphic, and successional conditions.

The classification hierarchy for natural ecosystems consists of eight levels that are aggregated into three groupings: upper levels (L1–L3), middle levels (L4–L6), and lower levels (L7–L8) (Table 2a). The criteria outlined in the previous section are used to develop descriptions of each unit in the hierarchy, following a standard template.

Classification of cultural vegetation

The criteria for classifying cultural vegetation include growth forms, floristics, and ecological setting (Table 2b). The criteria largely correspond to that of natural vegetation, except that compositional similarity is not used, given the typical mono- or mixed dominance of many cultural vegetation types.

As with natural vegetation, the hierarchy consists of eight levels that are aggregated into three sets, but growth forms and structure play a greater role for classifying cultural vegetation. The criteria outlined in the previous section are used to develop descriptions of each unit in the hierarchy, with the utility and relevance of the criteria varying by level.

Supporting Infrastructure and Peer Review

The classification is maintained through a coordinating body that oversees the recognition and integration of new and revised vegetation types through a peer-review process. The goal of the process is to maintain a standard set of recognized vegetation types

Table 2a Hierarchical classification for natural vegetation, with example.

Natural vegetation	Example
<i>Upper levels</i>	
1—Formation Class	Scientific Name: Mesomorphic Shrub & Herb Vegetation Colloquial Name: Shrubland & Grassland
2—Formation Subclass	Scientific Name: Temperate & Boreal Shrub & Herb Vegetation Colloquial Name: Temperate & Boreal Grassland & Shrubland
3—Formation	Scientific Name: Temperate Shrub & Herb Vegetation Colloquial Name: Temperate Grassland & Shrubland
<i>Mid levels</i>	
4—Division	Scientific Name: <i>Andropogon—Stipa—Bouteloua</i> Grassland & Shrubland Division Colloquial Name: Central North American Grassland & Shrubland
5—Macrogroup	Scientific Name: <i>Andropogon gerardii—Schizachyrium scoparium—Sorghastrum nutans</i> Grassland & Shrubland Macrogroup Colloquial Name: Central Lowlands Tallgrass Prairie
6—Group	Scientific Name: <i>Andropogon gerardii—Sporobolus heterolepis</i> Grassland Group Colloquial Name: Central Tallgrass Prairie
<i>Lower levels</i>	
7—Alliance	Scientific Name: <i>Andropogon gerardii—Sorghastrum nutans—Coreopsis palmata</i> Grassland Alliance Colloquial Name: Central Mesic Tallgrass Prairie
8—Association	Scientific Name: <i>Andropogon gerardii—Sorghastrum nutans—(Sporobolus heterolepis)—Liatris spp.—Ratibida pinnata</i> Grassland Colloquial Name: Midwest Mesic Loam Tallgrass Prairie

Adapted from FGDC (Federal Geographic Data Committee) (2008) *National vegetation classification standard, Version 2*, FGDC-STD-005-2008. Reston, VA: Vegetation Subcommittee, US Geological Survey.

Table 2b Hierarchical classification for cultural vegetation, with example.

Cultural vegetation	Example
<i>Upper levels</i>	
1—Cultural Class	Anthromorphic Vegetation
2—Cultural Subclass	Herbaceous Agricultural Vegetation
3—Cultural Formation	Row & Close Grain Crop
4—Cultural Subformation	Graminoid Row Crop
<i>Mid levels</i>	
5—Cultural Group	Tropical & Temperate Corn Crop
6—Cultural Subgroup	Corn Crop
<i>Lower levels</i>	
7—Cultural Type	Maize Corn
8—Cultural Subtype	Corn for Silage

Adapted from FGDC (Federal Geographic Data Committee) (2008) *National vegetation classification standard, Version 2*, FGDC-STD-005-2008. Reston, VA: Vegetation Subcommittee, US Geological Survey.

that represents the current best understanding of the universe of terrestrial ecosystems, based on vegetation and ecological characteristics.

NatureServe maintains the IVC, working in collaboration with international partners, such as the International Union for Conservation of Nature (IUCN), and with national partners, especially the USNVC (FGDC, 2008), Canadian NVC (Baldwin and Meades, 2008), Bolivian NVC (based on Navarro, 2011), among others. A future goal is to establish a formal international review panel that would oversee collaboration around national and international classifications (see section below “The IVC as the Basis for a Collaborative Framework Among Various Continental-National Approaches”). Revisions are based on quantitative plot-based analyses, literature review, and expert panel review. NatureServe staff maintain the IVC content and share the data with 82 member programs (US states, Canadian provinces and territories, and several Latin American countries). Information on the IVC for the Americas is available on the web at <http://natureserve.org/explorer> [see also below “Current Status of the IVC”].

Biome-Scale Levels of the IVC

We here describe the vegetation type levels most relevant to characterizing biome-scale ecosystems. Definitions and concepts are from Faber-Langendoen et al. (2014, 2016).

Formations: Global Biomes/Ecosystems

The upper levels of the IVC are based on the *formation*, a prominent concept throughout the history of vegetation classification. The formation is physiognomic-structural in character with supplementary ecological information and defined by dominance of a given growth form in the uppermost stratum of the community, or by a combination of dominant growth forms (Whittaker, 1975). These formations have been widely used to define biomes; as Moncrieff et al. (2016) state “Biomes refer to globally convergent vegetation formations similar in structure and function, explicitly ignoring floristic differences.” In the IVC, the two most relevant formation levels that correspond to many global biome concepts are formation subclass and formation (Table 3):

- *Formation Subclass (L2)*: defined by combinations of general dominant and diagnostic growth forms that reflect global macroclimatic factors driven primarily by latitude and continental position, or that reflect overriding substrate or aquatic conditions. Some biome classifications (e.g., the Walter scheme summarized by Mucina, 2018) distinguish between those formations determined largely by macroclimatic drivers (the so-called zonal biomes) from those determined by macro-hydrological and lithological factors (the so-called azonal biomes). We include the interactions of these factors along with natural disturbance processes in shaping the formation (Bond et al., 2005).
- *Formation (L3)*: defined by combinations of dominant and diagnostic growth forms that reflect global macroclimatic conditions as modified by altitude, seasonality of precipitation (e.g., bioclimate types such as pluvial, pluviseasonal, xeric, desertic), substrates, and hydrologic conditions (cf. “formation-type” and “biome-type” of Whittaker, 1975). Here again, the vegetation patterns reflect the interactions of these factors.

A complete list of IVC subclasses and formations is provided in Table 4.

Table 3 Comparison of various natural biome (large-scale ecosystem) classification approaches.

Biome scale	International Vegetation Classification	IUCN 2019 (Keith et al., 2019)	Terrestrial Ecoregions of the World (Dinerstein et al., 2017)
Purpose	Catalogue of ecosystem diversity at multiple scales relevant to conservation and management.	Ecosystem risk assessment and management, and natural asset accounting	Biogeography and spatial conservation planning
Global biome I	Formation Subclass (L2) ● Tropical Grassland, Savanna & Shrubland	Biomes ● Savannas & grasslands	Biome/Major Habitat Type ● Tropical and subtropical grasslands, savannas, and shrublands
Global biome II (“formation-type” and “biome-type” of Whittaker (1975))	Formation (L3) Combinations of dominant and diagnostic growth forms that reflect global macroclimatic conditions as modified by altitude, seasonality of precipitation, substrates, and hydrologic conditions. ● Tropical Lowland Grassland, Savanna & Shrubland	Ecosystem functional groups ● Pyric tussock savannas	–
Continental Biome (“formation” and “biome” of Whittaker (1975); Subzonobiome/ Azonal Biome subdivisions of Mucina (2018))	Division (L4) Combinations of dominant and diagnostic growth forms and a broad set of diagnostic plant species that reflect biogeographical differences in composition and continental differences in mesoclimate, geology, substrates, hydrology, and disturbance regimes. ● Brazilian-Parana Lowland Grassland, Savanna & Shrubland	Biogeographic ecotypes (in development)	Biogeographic Realm ● Neotropical
Regional (biome of Mucina (2018))	Macrogroup (L5) Moderate sets of diagnostic plant species and diagnostic growth forms that reflect biogeographical differences in composition and sub-continental to regional differences in mesoclimate, geology, substrates, hydrology, and disturbance regimes. ● Cerrado Savanna	Ecosystem types (L5) (in development)	Ecoregion ● Cerrado

The similarities in scaling biomes is not meant to imply that the units are necessarily equivalent. Levels of the IVC and other systems are only shown in relation to biome-scale patterns. Biome scale terms are adapted from Mucina (2018). IVC information from Faber-Langendoen et al. (2014), IUCN 2019 from Keith et al. (2019), Terrestrial Ecoregions of the World from Dinerstein et al. (2017). Bulleted lines provide an example of a type developed within each level for each classification approach.

Table 4 Formations (~global biomes) of the International Vegetation Classification.

<i>Level 2—Formation Subclass</i>	<i>Level 3—Formation (Wetland and aquatic formations marked with *)</i>
1.A. Tropical Forest & Woodland	1.A.1. Tropical Dry Forest & Woodland 1.A.2. Tropical Lowland Humid Forest 1.A.3. Tropical Montane Humid Forest 1.A.4. Tropical Flooded & Swamp Forest* 1.A.5. Mangrove*
1.B. Temperate & Boreal Forest & Woodland	1.B.1. Warm Temperate Forest & Woodland 1.B.2. Cool Temperate Forest & Woodland 1.B.3. Temperate Flooded & Swamp Forest* 1.B.4. Boreal Forest & Woodland 1.B.5. Boreal Flooded & Swamp Forest*
2.A. Tropical Grassland, Savanna & Shrubland	2.A.1. Tropical Lowland Grassland, Savanna & Shrubland 2.A.2. Tropical Montane Grassland & Shrubland 2.A.3. Tropical Scrub & Herb Coastal Vegetation
2.B. Temperate & Boreal Grassland & Shrubland	2.B.1. Mediterranean Scrub & Grassland 2.B.2. Temperate Grassland & Shrubland 2.B.3. Boreal Grassland & Shrubland 2.B.4. Temperate to Polar Scrub & Herb Coastal Vegetation
2.C. Shrub & Herb Wetland	2.C.1. Tropical Bog & Fen* 2.C.2. Temperate to Polar Bog & Fen* 2.C.3. Tropical Freshwater Marsh, Wet Meadow & Shrubland* 2.C.4. Temperate to Polar Freshwater Marsh, Wet Meadow & Shrubland* 2.C.5. Salt Marsh*
3.A. Warm Desert & Semi-Desert Woodland, Scrub & Grassland	3.A.1. Tropical Thorn Woodland 3.A.2. Warm Desert & Semi-Desert Scrub & Grassland
3.B. Cool Semi-Desert Scrub & Grassland	3.B.1. Cool Semi-Desert Scrub & Grassland
4.A. Tropical High Montane Scrub & Grassland	4.A.1. Tropical High Montane Scrub & Grassland
4.B. Temperate to Polar Alpine & Tundra Vegetation	4.B.1. Temperate & Boreal Alpine Dwarf-shrub & Grassland 4.B.2. Polar Tundra & Barrens
5.A. Saltwater Aquatic Vegetation	5.A.1. Floating & Suspended Macroalgae Saltwater Vegetation* 5.A.2. Benthic Macroalgae Saltwater Vegetation* 5.A.3. Benthic Vascular Saltwater Vegetation* 5.A.4. Benthic Lichen Saltwater Vegetation*
5.B. Freshwater Aquatic Vegetation	5.B.1. Tropical Freshwater Aquatic Vegetation* 5.B.2. Temperate to Polar Freshwater Aquatic Vegetation*
6.A. Tropical Open Rock Vegetation	6.A.1. Tropical Cliff, Scree & Other Rock Vegetation
6.B. Temperate & Boreal Open Rock Vegetation	6.B.1. Temperate & Boreal Cliff, Scree & Other Rock Vegetation
7.A. Woody Agricultural Vegetation	7.A.1. Woody Horticultural Crop 7.A.2. Forest Plantation & Agroforestry 7.A.3. Woody Wetland Horticultural Crop*
7.B. Herbaceous Agricultural Vegetation	7.B.1. Row & Close Grain Crop 7.B.2. Pasture & Hay Field Crop 7.B.3. Herbaceous Horticultural Crop 7.B.4. Fallow Field & Weed Vegetation 7.B.5. Herbaceous Wetland Crop*
7.C. Herbaceous & Woody Developed Vegetation	7.C.1. Lawn, Garden & Recreational Vegetation 7.C.2. Other Developed Vegetation 7.C.3. Developed Wetland Vegetation*
7.D. Agricultural & Developed Aquatic Vegetation	7.D.1. Agricultural Aquatic Vegetation* 7.D.2. Developed Aquatic Vegetation*

There are 13 natural and 4 cultural formation subclasses (Level 2; see also global biome I in Table 3) and 37 natural and 13 cultural formations (Level 3, see also global biome II in Table 3). * indicates a wetland formation.

Adapted from Faber-Langendoen D, Keeler-Wolf T, Meidinger D, et al. (2016) *Classification and description of world formation types*. Gen. Tech. Rep. RMRS-GTR-346. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Divisions: Continental Biomes/Ecosystems

Moving from global biomes to continental biomes introduces the role of large-scale species pools, broadly distinct growth form types, and their biogeographic patterns, as defined by the Division level (Table 3).

- *Division (L4)* is defined as the combinations of dominant and diagnostic growth forms and a broad set of diagnostic plant species that reflect biogeographic differences in composition and continental differences in mesoclimate, geology, substrates,

hydrology, and disturbance regimes. Whereas the formation level (L3) is more strictly physiognomic, the division level includes both physiognomic and floristic criteria. The term “Division” was adopted from the Braun-Blanquet approach, which proposed it as a level above the “class” (Westhoff and van der Maarel, 1973).

In many respects, the division concept is also equivalent to the term “biome,” but as a continental or regional biogeographic concept. For example, the “Nama-Karoo” biome of South Africa is largely equivalent to a division.

With the introduction of the division concept and floristic criteria, the upper level formation (global biome) types can be subdivided by continental scale biogeographic species pools. Thus, the Tropical Lowland Humid Forest formation is divided into several South American divisions (Amazonian Lowland Humid Forest, Brazilian-Parana Lowland Humid Forest) and African-Madagascan divisions (Guineo-Congolian Evergreen & Semi-Evergreen Rainforest, and Malagasy Evergreen & Semi-Evergreen Rain Forest) (see also Tropical Dry Forest example in Fig. 2). Typically, suites of diagnostic (character) species are selected that are restricted to a division type, along with the dominant species that express the dominant growth forms. In turn, from the bottom-up, shared growth forms among division types, which reflect a set of shared climatic and edaphic factors, lead to their placement within the same formation (though the level of convergence should not be overstated, cf. Moncrieff et al., 2016).

Macrogroup: Regional Ecosystems

Continental biomes may be further subdivided by a suite of species, growth forms and structure that reflect regional climate, substrate, disturbance and biogeographic patterns. These factors play into the definition of the macrogroup level (Table 3).

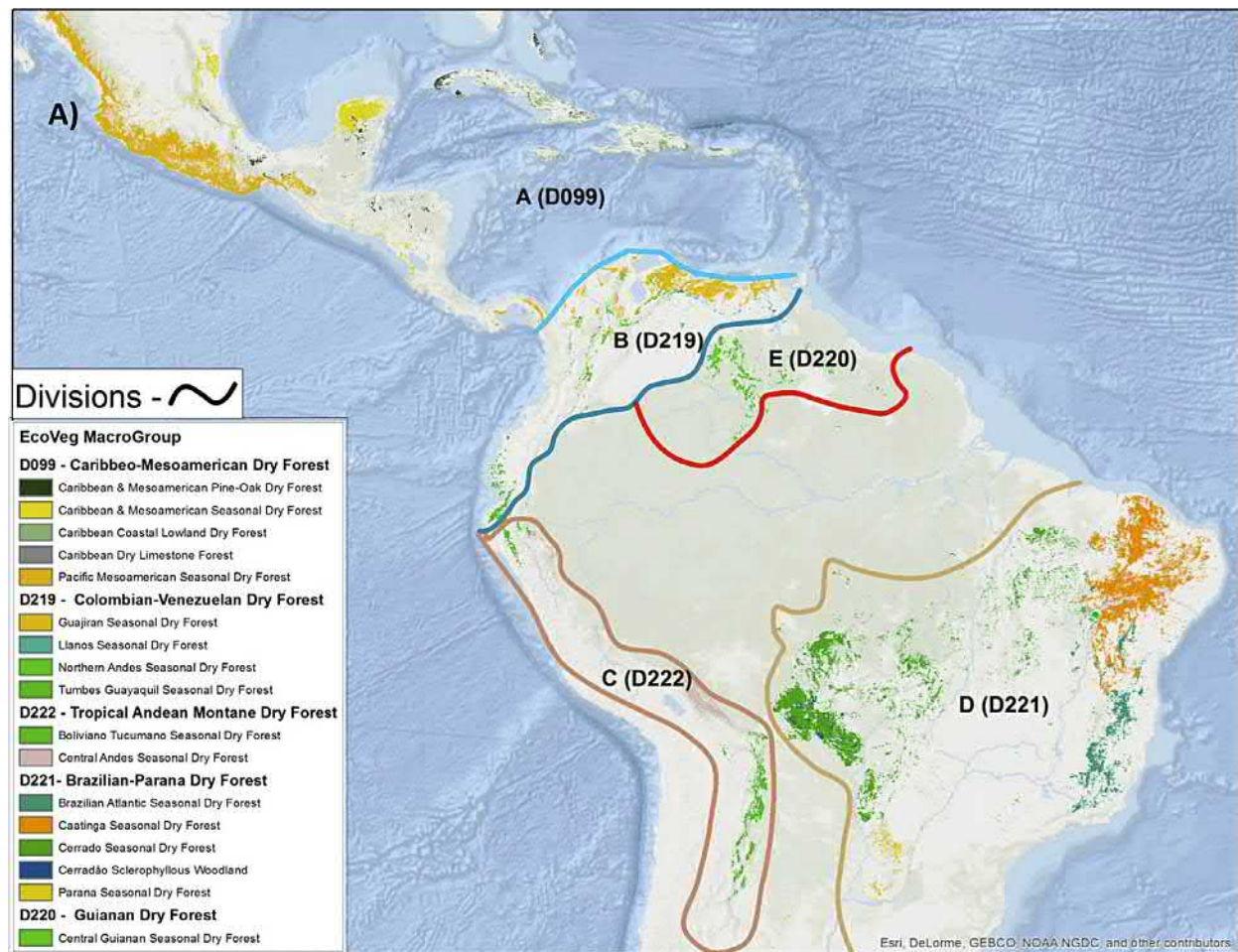


Fig. 2 Division and macrogroup types for Tropical Dry Forest & Woodland formation (International Vegetation Classification) in the neotropics. The number after each letter is a database code for the IVC division (see Faber-Langendoen et al., 2018, Supplement S4). Faber-Langendoen D, Baldwin K, Keeler-Wolf T, et al. (2018) The EcoVeg Approach in North America: U.S., Canadian, and International Vegetation Classifications. *Phytocoenologia* 48: 215-237, www.borntraeger-cramer.de/journals/phyto; Comer PJ, Hak JC, Josse C and Smyth R (2020) Long-term loss in extent and current protection of terrestrial ecosystem diversity in the temperate and tropical America. *PLOS One* (in press).

- *Macrogroup (L5)* is defined by moderate sets of diagnostic plant species and diagnostic growth forms that reflect biogeographic differences in composition and sub-continental to regional differences in mesoclimate, geology, substrates, hydrology, and disturbance regimes.

A macrogroup type typically contains a moderately large set (dozens) of strongly diagnostic species that share a broadly similar physiognomy and ecology in response to continental, sub-continental, or regional differences in ecological factors (Table 3). Thus, the macrogroup expresses the floristic, growth form and regional ecological factors that separate vegetation types within a division. For example, in South America, the Amazonian Lowland Humid Forest division contains seven macrogroups based on species changes that reflect regional climate and elevational gradients: Central Amazon Humid Forest, Northern Amazon Humid Forest, Southern Amazon Humid Forest, Southwestern Amazon Lowland Humid Forest, Southwestern Amazon Subandean Humid Forest, Western Amazon Lowland Humid Forest, Western Amazon Subandean Humid Forest. Similarly, the Californian Scrub & Grassland Division is based on both a variety of distinct species and distinct growth form patterns, e.g., California Chaparral and the California Coastal Scrub. These macrogroup types are probably scaled at a level finer than most biome classifications, and they are perhaps better seen as the key level below biome that facilitates understanding the variation within a continental biome.

The macrogroup is similar to the “class” level of the Braun-Blanquet approach (Westhoff and van der Maarel, 1973), opening up the possibility of assembling the European vegetation types within continental biomes or divisions of the IVC (see section below “The IVC as the Basis for a Collaborative Framework Among Various Continental-National Approaches”).

Comparison of IVC Biome-Scale Levels With Other Global Classifications

In previous publications, we demonstrated that our formations have many parallels with other large-scale vegetation or biome concepts, both in concept and in number of types (Faber-Langendoen et al., 2014, Appendix D). Here we focus specifically on current classifications that are multi-scaled and biome-like in their approach, global in scope, and “operational” (having a user group that is actively developing, refining and applying type concepts through database descriptions and maps) (Table 3).

Each of the three major classifications in Table 3 are structured to meet different purposes. The Terrestrial Ecoregions of the World (Dinerstein et al., 2017) emphasizes biogeography and spatial conservation planning; the IUCN approach (Keith et al., 2019) is designed for ecosystem risk assessment and management, as well as natural capital accounting; it also provides a framework for synthesis across terrestrial, freshwater and marine realms; the IVC provides a catalogue of terrestrial ecosystem diversity focused on vegetation traits and ecological relationships at multiple scales relevant to conservation and resource management. All three bring in biome concepts adapted to their purpose. Thus, they offer complementary attributes; as an ensemble, they are a potentially powerful toolbox.

The IVC as the Basis for a Collaborative Framework Among Various Continental-National Approaches

The IVC is global in scope, with comprehensive descriptions for all natural and cultural formations (L2, L3) (Faber-Langendoen et al., 2016). At the division level, only natural grasslands have been completely assessed across the earth (Dixon et al., 2014), but all natural types are comprehensively developed down to macrogroup across the Americas (Table 5) and for Africa (Sayre et al., 2013).

Table 5 Current degree of completeness for natural vegetation types within the Americas.

Level	IVC North America (Canada, US)	IVC Latin America	IVC Americas	IVC global
Class	6	6	6	6
Subclass	11	13	13	13
Formation	27	29	34	36
Division	57	121	140	(est. 447) ^b
Macrogroup	156	292	375	(est. 1196) ^b
Group	410	~728 ^a	1059 ¹	TBD
Alliance	TBD	TBD	TBD	TBD
Association	TBD	TBD	TBD	TBD

Number of types for each level of the hierarchy are shown for the United States, Canada, and across the Americas, as of Sep. 1, 2016. The IVC-Americas includes all units currently reported by NatureServe for Canada, continental US (excluding Hawaii and the territories of American Samoa, Guam, and Mariana Islands), Caribbean (including Puerto Rico and Virgin Islands), Central America, and South America.

^aBased on 617 Ecological System types for South America (Josse et al., 2003). Ecological System types are typically equivalent to or somewhat finer than IVC groups.

^bIVC units for the Americas cover 31.1% of the globe, excluding Antarctica. Multiplying the Americas numbers by 3.19 provides a global estimate, because division and macrogroup types in the Americas are almost entirely restricted to the Americas, apart from the circum-Arctic types.

Adapted from Table 1 in Faber-Langendoen D, Baldwin K, Keeler-Wolf T, et al. (2018) The EcoVeg Approach in North America: U.S., Canadian, and International Vegetation Classifications. *Phytocoenologia* 48: 215–237.

Fine-scale types are only available in North America and parts of Latin America. Cultural types have only been developed at lower levels for North American forest plantations. Currently all macrogroup types in the Americas are listed in Faber-Langendoen et al. (2018) and are published on NatureServe Explorer (natureserve.org/explorer).

Despite the incompleteness of the IVC per se at mid and lower levels, there are opportunities for completing a global view of vegetation types across all scales through a collaborative effort with comparable classifications. In this section, we highlight a number of important national or continental efforts that have strong similarities to the IVC.

South America

In South America concepts for IVC group types are approximated through a crosswalk to the closely related “terrestrial ecological system” types developed by NatureServe (Josse et al., 2003; Faber-Langendoen et al., 2018). These terrestrial ecological systems are mid-scale types based on aggregating associations or local vegetation types using spatial-ecological relationships. These types can then be aggregated to the macrogroup scale. The approach to mapping these types corresponds to the process described for Africa (see below).

Bolivia

Bolivian types are being described using the EcoVeg approach. The full integration of the vegetation types proposed for Bolivia (Navarro, 2011) into the IVC system is well underway through a collaboration with NatureServe (Table 6).

Africa

Terrestrial ecosystems and vegetation of Africa were classified and mapped as part of a larger effort and global protocol (GEOSS, the Global Earth Observation System of Systems), which includes an activity to map terrestrial ecosystems of the earth in a standardized, robust, and practical manner, and at the finest possible spatial resolution (Sayre et al., 2013). To model the potential distribution of ecosystems, new continental datasets for several key physical environment data layers (including coastline, landforms, surficial lithology, and bioclimate) were developed at spatial and classification resolutions finer than existing similar data layers. Multi-scale ecosystems were classified and mapped using the IVC in an increasingly detailed hierarchical framework, from class, subclass, formation, and division to macrogroup. A total of 157 macrogroup types were mapped, each with multiple, repeating occurrences on the landscape.

Europe

Europe has a long tradition of vegetation classification using the “Braun-Blanquet approach” (Westhoff and van der Maarel, 1973). In an effort to harmonize the many national and regional classifications developed over the last century, the IAVS Working Group European Vegetation Survey established the “European Vegetation Classification Committee” to maintain and update a standard classification of European vegetation, taking the “EuroVegChecklist” (Mucina et al., 2016) as a baseline (<http://euroveg.org/evc-committee>). This standard classification includes the phytosociological class, order and alliance level. A harmonization with the

Table 6 Application of International Vegetation Classification to Bolivian forest and xeromorphic woodland vegetation (Navarro, 2011).

<i>Formation (L3)</i> <i>Global biome</i>	<i>Division (L4)</i> <i>Continental biome</i>	<i>Macrogroup (L5)</i> <i>Regional</i>
1.A. Tropical Forest	1.A.1.Ek. Brazilian-Parana Dry Forest	M872. Cerradão Sclerophyllous Woodland
1.A.1. Tropical Seasonally Dry Forest	1.A.1.El. Tropical Andean Montane Dry Forest	M570. Cerrado Seasonal Dry Forest
		M573. Northern Andes Seasonal Dry Forest
		M574. Central Andes Seasonal Dry Forest
1.A. Tropical Forest	1.A.2.Ej. Amazonian Lowland Humid Forest	M590. Southwestern Amazon Lowland Humid Forest
1.A.2. Tropical Lowland Humid Forest		1.A.2.Ek. Brazilian-Parana Lowland Humid Forest
1.A. Tropical Forest	1.A.3.Ej. Tropical Andean Montane Humid Forest	M612. Bolivian-Tucuman Montane & Upper Montane Humid Forest
1.A.3. Tropical Montane Humid Forest		M610. Central Andean (Yungas) Montane & Upper Montane Humid Forest
	1.A.4.El. Amazonian Swamp & Flooded Forest	1.A.4.El. Amazonian Swamp & Flooded Forest
1.A. Tropical Forest		
1.A.4. Tropical Flooded & Swamp Forest	3.A.1.Ec. Interandean Valley Xeromorphic Scrub & Woodland	M769. Central Andes Xeromorphic Scrub & Woodland
3.A. Warm Desert & Semi-Desert Woodland, Scrub & Grassland		M770. Boliviano-Tucumano Xeromorphic Scrub & Woodland
3.A.1. Tropical Thorn Woodland	3.A.1.Ed. Chaco Xeromorphic Scrub & Woodland	M771. Northwestern Chaco Xeromorphic Scrub Woodland

Table 7 Application of International Vegetation Classification to European forest vegetation.**Formation 1.B.1. Warm Temperate Forest & Woodland**

Division: Mediterranean Basin Warm Temperate Sclerophyllous Forest & Scrub

Quercetea ilicis

Division: Macaronesian Warm Temperate Forest and Scrub

*Pruno lusitanicae-Lauretea azoricae**Lauro azoricae-Juniperetea brevifoliae**Cytiso-Pinetea canariensis***Formation 1.B.2. Cool Temperate Forest & Woodland**

Division: Western Eurasian Cool Temperate Forest

*Carpino-Fagetea sylvaticae**Quercetea pubescentis**Quercetea robori-petraeae**Crataego-Prunetea**Lonicero-Rubetea plicati**Robinietea**Salicetea arenariae**Brachypodio pinnati-Betuletea pendulae**Pyrolo-Pinetea sylvestris**Junipero-Pinetea sylvestris**Erico-Pinetea***Formation 1.B.3. Temperate Flooded & Swamp Forest**

Division: Mediterranean Flooded & Swamp Forest & Scrub

Nerio-Tamaricetea

Division: Western Eurasian Flooded and Swamp Forest & Scrub

*Alno glutinosae-Populetea albae**Salicetea purpureae**Alnetea glutinosae**Franguletea***Formation 1.B.4. Boreal Forest & Woodland**

Division: Western Eurasian Boreal Forest & Woodland [includes temperate high montane]

Vaccinio-Piceetea

Division: Western Eurasian Temperate-Subalpine & Subarctic Woodland & Krummholz

*Roso pendulinae-Pinetea mugo**Betulo carpaticae-Alnetea viridis***Formation 1.B.5. Boreal Flooded & Swamp Forest**Boreal flooded and swamp forests are currently included in the class *Vaccinio-Piceetea* (but see discussion of *Vaccinio uliginosi-Pinetea*, a boreal swamp forest class, in [Mucina et al., 2016](#))

A provisional assignment of Braun-Blanquet classes ([Mucina et al., 2016](#)) is made to draft division units and grouped into IVC formation (Wolfgang Willner). In the European tradition, vegetation dominated by medium or tall shrubs with cover >25% (typically >60%), as well as krummholz, is included in the Forest and Woodland formations. In fact, they are not even separated at the class (macrogroup) level in many cases.

upper and middle levels of the IVC seems feasible but has not been done so far (See example in [Table 7](#)). In accordance with the phytosociological tradition, cultural vegetation in the strict sense is not considered in the classification. However, spontaneous species assemblages in strongly anthropogenic habitats (e.g., weed communities in arable land) are included alongside natural and semi-natural vegetation, since these communities are mainly composed by species native in Europe and adjacent regions and have co-evolved with human agriculture since neolithic times.

China

The China Vegetation Classification System (China-VCS) was developed based on the “phytocoenological-ecological” approach dating back to 1960 ([Guo et al., 2018](#)). The main principles for vegetation classification include vegetation physiognomy and structure, dominant species, floristic composition, and environmental attributes. This classification system for natural/semi-natural vegetation has eight hierarchical levels: Association < Association-group < Subformation < Formation < Formation-group < Vegetation-subtype < Vegetation-type < Vegetation-type-group ([Table 8a](#); [Guo et al., 2018](#)). Compared with EcoVeg, both approaches use similar principles and criteria for the assignment of vegetation types, including major growth forms (physiognomy) and vegetation structure, species composition or floristics, and ecological context ([Guo et al., 2018](#); [Faber-Langendoen et al., 2018](#)). Physiognomy plays a predominant role at upper levels and floristics at lower levels in both classification systems. Floristic definitions of types at lower levels in the EcoVeg approach are based on “characteristic species combinations,” which include diagnostic, constant, and dominant species ([Faber-Langendoen et al., 2018](#)). However, lower levels in the China-VCS emphasize dominant species in multiple strata, based on species’ relative abundances (or importance values). The association, formation, and vegetation-subtype levels of the China-VCS are somewhat similar to the association, alliance, and division levels of

Table 8 The Chinese Vegetation Classification System and its relation to the International Vegetation Classification.

(a) Hierarchy level of China Vegetation Classification System

Levels	Units	Definitions	Examples
Upper	Vegetation-type-group	It is the uppermost unit and is defined based on the comprehensive ecological conditions and the physiognomy of vegetation. The unit generally reflects the main continental biomes (zonal vegetation) and the main azonal vegetation.	Forest
	Vegetation-type	It is the main upper class unit in the same vegetation-type-group, which is the assemblage of the plant communities with the dominant species in the dominant stratum sharing same or very similar life form (or growth form).	Deciduous needle leaved forest
	Vegetation-subtype	It is classified mainly based on the differences in ecological conditions of the same vegetation-type, e.g., altitude, temperature, substrates, and hydrologic conditions.	Cold temperate deciduous needle leaved forest
Middle	Formation-group	It is the assemblage of the formations, of which the dominants have very similar growth form and ecological habits and belong to the same taxonomic genus.	Larch forest (<i>Larix</i> forest)
	Formation	It is the main middle class unit under one vegetation-type or vegetation-subtype, which is the assemblage of the plant communities with the same dominant species in the dominant stratum.	<i>Larix gmelinii</i> forest
	Subformation	It is an auxiliary class unit below formation. Some species with wide ecological amplitudes may dominate in plant communities occurring in obviously different ecological habitats, but the difference is not large enough to assign the communities into different vegetation-types or vegetation-subtypes. It is not necessary for most formations to be classified into subformations.	–
Lower	Association-group	It is the assemblage of communities with the same dominant species in the dominant stratum and in a second stratum, which share similar structure and ecological conditions.	<i>Larix gmelinii</i> - <i>Ledum palustre</i> forest
	Association	It is the basic class unit, which is the assemblage of the communities with same or very close properties, such as the same dominants in all strata or synusiaes, very similar overall species composition and structure, and very similar ecological conditions.	<i>Larix gmelinii</i> - <i>Ledum palustre</i> - <i>Vaccinium vitis-idaea</i> - <i>Sphagnum squarrosum</i> forest

(b) Crosswalk Table for Chinese Vegetation Classification System and the International Vegetation Classification

China-VCS	IVC—EcoVeg
Vegetation-type-group	Formation class
Vegetation-type	Formation subclass
	Formation
Vegetation-subtype	Formation
	Division
Formation-group	Macrogroup
	Group
Formation	Alliance
Subformation	
Association-group	Association
Association	

EcoVeg, respectively (Table 8b). In the China-VCS, the formation is defined as “the assemblage of the plant communities with the same dominant species in the dominant stratum within one vegetation-type or vegetation-subtype” (Guo et al., 2018), while the higher-level classification is based on the dominant growth form and community physiognomy. To date, seven vegetation-type-groups, 40 vegetation-types and 93 vegetation-subtypes have been described in the China-VCS (Guo et al., 2018), while formations and associations are still not completely verified. Therefore, it is practical to use the IVC to describe regional biomes in China, with a crosswalk between China-VCS and EcoVeg.

Australia and New Zealand

Vegetation classifications and maps have been developed largely independently across eight Australian states and territories and New Zealand, due to historical legacies related to separate jurisdictional responsibilities for land management. Specht (1970) developed a factorial vegetation classification scheme with arbitrary quantitative thresholds based on dominant growth form, height and projective foliage cover of the tallest stratum, which became an important unifying influence on jurisdictional classification and mapping. Although a useful framework for mapping by remote sensing, its application to floristic classification was problematic due to structural variability of vegetation somewhat independent of floristic patterns. A variation of Specht's

scheme was subsequently used to attempt a synthesis within a National Vegetation Information System (NVIS), but jurisdictional inconsistencies in classification and spatial edge-matching have limited its usefulness. These are gradually being resolved, but the major groupings cut across natural ecological patterns. The most recent synthesis of Australian vegetation describes 16 physiognomically defined vegetation formations across the continent, with each of these resolved into a number of subclasses (Keith, 2017). Within an Australian context, many of these units are potentially referable to L3 (formation), L4 (division) and L5 (macrogroup) units of the IVC.

For New Zealand, Singers and Rogers (2014) define 140 terrestrial ecosystem units based on vegetation–biophysical relationships represented by dominant plant species, bioclimatic zones and azonal edaphic environments. These should be examined in relation to L4 (division) to L8 (association) levels of the IVC.

Applications of IVC for Conservation

We briefly note several recent applications of the IVC approach:

1. *Assessing ecosystems at risk*: There is a growing need for comprehensive approaches to assessing ecosystems at risk in order to address multiple levels of biodiversity in conservation planning and ecosystem services. A variety of methodologies have been developed in various nations and continents (e.g., NatureServe’s approach documented by Master et al., 2012), but the IUCN Red List of Ecosystem provides a global framework (Keith et al., 2013). Similarly, a number of ecosystem classifications can be used for red listing of terrestrial ecosystems, but the IVC typology provides guidance on a consistent scaling of those assessments. Current applications of ecosystem red listing in the Americas include a macrogroup scale assessment of all tropical and temperate forests across the Americas (Ferrer-Paris et al., 2018) and an ecological system assessment in temperate and tropical North America (Comer et al., 2020).
2. *Key Biodiversity Areas*: International conservation organizations have developed a methodology for identifying Key Biodiversity Areas (KBAs) (IUCN, 2016), including criteria for protection of at-risk ecosystems. In the KBA guidance, IVC macrogroups and equivalently units are noted as a suitable level for defining ecosystem types. When units such as these are categorized as “at-risk” through the Red List of Ecosystem process (see above), they can contribute to the identification of KBA sites.
3. *Analyses of protected status of regional ecosystem types*: As part of a “coarser filter” approach to protection of biodiversity, conservation planners seek to ensure that all major ecosystems are represented in protected areas. Belote et al. (2017) recently used the USNVC at the group scale and above to identify ecosystems that are currently under-represented in the existing protected area system. A comprehensive assessment of the current protection status of all macrogroups across the Americas has also been completed (Comer et al., 2020).

Conclusions

The basic structure of the IVC approach to classifying terrestrial biomes has strong similarities at the highest levels (IVC formation) to that of the Encyclopedia’s major sections (Table 9). The IVC develops a systematic approach to the full diversity of biomes around the globe, guided by large-scale patterns of vegetation, biogeography and ecology; whereas, the Encyclopedia takes more of an illustrative approach, listing the most prominent structural and biogeographic types. Because of its systematic approach, the IVC both describes the full range of ecosystems and contributes to systematic assessments of their rarity and protection status. But beyond the perspective of classification, the Encyclopedia provides a wide range of topics relevant to understanding how biomes function, including processes, threats, ecosystem services, animal life, and conservation, among others. Thus, the diversity of biome types provided by the IVC complements the diversity of biome topics provide in the Encyclopedia.

Table 9 Comparison of IVC formation class types (see also Table 4) and the major biome types used for the Encyclopedia.

<i>IVC formation class types</i>	<i>Encyclopedia: Major Sections</i>
1. Forest & Woodland	Forests
2.A. Tropical Grassland, Savanna & Shrubland	Grasslands and Shrublands
2.B. Temperate & Boreal Grassland & Shrubland	
3. Desert & Semi-Desert Vegetation	Deserts
4.A. Tropical High Montane Scrub & Grassland	Mountains (alpine systems)
4.B.1 Temperate & Boreal Alpine Dwarf-shrub & Grassland	
4.B.2. Polar Tundra & Barrens	Ice Sheets and Polar Deserts
5.B. Freshwater Aquatic Vegetation	Freshwater/Ponds
6. Open Rock Vegetation	—
7. Anthromorphic Vegetation	Anthromes
—	Islands and Atolls

Equivalencies are approximate.

Acknowledgments

The development of the IVC and the EcoVeg approach would not have been possible without support to the “Hierarchy Revisions Working Group” from the USNVC partners, namely, the Ecological Society of America Vegetation Classification Panel, NatureServe, and federal government agencies, especially the US Forest Service (lead agency and chair of FGDC), the US Geological Survey, the US National Park Service, and the US Bureau of Land Management.

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Freshwater Biome of the World

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Abstract

Of the Earth's three major biomes or realms, freshwater is the smallest, dwarfed in size and extent by terrestrial and marine realms. It has also been the most exposed to human exploitation, resulting in higher declines of biodiversity compared to other realms, primarily because of human reliance on fresh water and invasive species. Major sub-biomes in the freshwater realm can be grouped into seven categories: rivers and streams, lakes (salt, freshwater, oases and springs), palustrine wetlands (swamps, marshes, and floodplains), transitional waters (including estuarine and coastal lagoons), brackish tidal systems (deltas, intertidal forests, saltmarshes), subterranean water bodies and artificial wetlands (dams, rice paddies, aquaculture, canals and channels). A range of key freshwater characteristics, including the hydrological regime, water quality, and influences from terrestrial and marine drivers, form unique ecosystems around the world, providing for diverse species but ones which share many functional traits, reflected in convergent evolution. Direct or indirect appropriation of water resources (consumption, agriculture, and hydro-electricity) and disposal of waste water has devastated many of the world's freshwater ecosystems. Their protection demands identification of sustainable and cost-effective management of hydrological regimes and inflows, including protection and restoration of flows for the environment as well as management of invasive species, stopping habitat destruction and pollution.

Introduction

The freshwater realm is the smallest of the world's three major realms, but well behind terrestrial and marine realms in effective conservation management. Seasonal wetlands may only represent about 6% of the world's land surface but most of these (89%) are not in protected areas or identified as wetlands of international importance under the Ramsar Convention (Finlayson et al., 2011), recognized for their global importance (Reis et al., 2017). Ecosystems dependent on fresh water are also among the most biodiverse on Earth, providing habitats for many invertebrate, plant, fish, frog, reptile, bird and mammal species (Dudgeon et al., 2006). They are also critical for many terrestrial organisms which depend on water for drinking, dispersal and transport of nutrients (Kingsford et al., 2006). Their vulnerability to anthropogenic change primarily reflects humanity's fundamental dependence on these ecosystems for existence. Without fresh water, humans would not survive. These ecosystems provide many essential ecosystem services including drinking water, building materials, food, fiber, areas of significant cultural importance, and recreation (Mitsch and Gosselink, 2000; Kingsford et al., 2016). Despite relatively new technologies such as desalinization, most of our water still comes from surface or subsurface freshwater ecosystems. Unsurprisingly, we built many of our cities on the banks of rivers where there was a dependable supply of fresh water. This dependency has also made freshwater ecosystems among the world's most exploited, and consequently the most threatened (Dudgeon et al., 2006; Vörösmarty et al., 2010; Reis et al., 2017).

The freshwater realm extends well beyond the world's rivers and lakes to include floodplains, estuaries, saline lakes, coastal inlets, including fjords, and lagoons, springs and oases, geothermal springs, subterranean (e.g. karsts), and artificial ecosystems. All of these ecosystems are influenced by fresh water as a major driver, although this influence varies and interacts with other drivers to shape types of habitats and niches for different organisms. Ecosystems influenced by fresh water occur all over the world, in all biogeographic ecoregions, from the tundra, temperate areas, tropics, subtropics, and deserts (Olson et al., 2001; Abell et al., 2008).

There are freshwater ecosystems on the highest mountains and the lowest points in the landscape (e.g. Sea of Galilee, ~210 m below sea level).

The Biome concept has a long and versatile history in ecology. It has been adapted to diverse applications describing ecosystem functionality and biogeographical patterns, usually at large spatial scales (Mucina, 2019). The *Encyclopedia of the World's Biomes* recognizes freshwater environments as a single biome. Other applications of the concept recognize multiple biomes within the Freshwater realm. In this chapter, we follow IUCN's Global Ecosystem Typology (<https://iucnrle.org/about-rle/ongoing-initiatives/global-ecosystem-typology/>) to emphasize the diversity of ecological processes and biota across the full range of freshwater ecosystems. We recognize seven units (here termed "sub-biomes"), differentiated by major abiotic drivers that shape structure, function and composition. These sub-biomes are reasonably well established although often not explicitly linked to abiotic drivers (e.g. Kingsford et al., 2004). They include rivers and streams (lentic environments), lakes (freshwater lakes, salt lakes, springs, oases, geothermal springs), palustrine wetlands (floodplains or swamps), transitional wetlands (estuaries, coastal lagoons and inlets), brackish tidal systems (deltas, intertidal forests, saltmarshes), subterranean rivers and lakes and artificial ecosystems (e.g. dams, canals) (Table 1). Each of these sub-biomes is influenced by varying major abiotic drivers which determines their taxonomic structure and function. Importantly, these subbiomes are similarly structured around the world. Sometimes abiotic influences may vary. For example, temporary lakes in desert regions will vary considerably compared to permanent lakes in temperate regions of the world. Also, some lakes and rivers are affected by major seasonal changes such as freezing. But the major drivers will often be similar, varying in the type of hydrological regime (e.g. flow volume and frequency and duration of flooding).

There is one practical advantage to categorizing these freshwater-dependant sub-biomes in this way: the conservation management strategies are clear for reversing degradation processes as they are usually dependent on a particular abiotic factor (e.g. flow regime). Given available data, it is also possible to quantitatively determine their potential risk of collapse (Keith et al., 2013), allowing for regional and global assessments. This can prioritize a range of management options which extend from the local, regional, national and international. There are also a range of protection measures for ecosystems dependent on fresh water. Some of these are the same as for other realms, including protected areas and their management. Others are relevant to freshwater ecosystems include identification and legal designation of wetlands of international importance, under the Ramsar Convention, promoting wise use. Also, the scale of protection is critical, given that fresh water flows often originate high up in the catchment. There are also a range of international migratory bird agreements which focus on waterbirds dependent on ecosystems supplied by fresh water. These include flyway agreements and bilateral agreements. Most importantly for most freshwater ecosystems, there is a dependency on water management, often river management, required at the catchment or watershed scale, which includes management and protection of flow and flooding regimes.

In this chapter, we describe the major freshwater sub-biomes and their ecosystems, which depend on a unique hydrology and other interacting abiotic and biotic drivers that determine their particular structure, function and characteristic biota around the world. We also identify potential conservation management options for these complex ecosystems.

Different Freshwater Sub-Biomes

We describe each of the seven major freshwater sub-biomes separately, including different ecosystems categorized within each sub-biome (Table 1, Fig. 1), their distribution, major drivers, adapted biota and their threats.

Rivers and Streams

Rivers and streams carry water from upper catchments to join other rivers or flow out to sea or sometimes wetlands for endorheic river basins (Fig. 1, Table 1). As flowing bodies of fresh water, they are primarily defined by their linear structure, size and flow regimes, with a range of longitudinal, lateral and within river processes governing their ecology (Vannote et al., 1980; Junk et al., 1989; Thorp and Delong, 1994). Flow regimes depend on rainfall patterns in the stream catchment, which vary from year-round (e.g. Danube River, Sabie River, South Africa, Fig. 2) to seasonal (e.g. Tapi River, India) and episodic (Cooper Creek, Australia), as well as the geomorphology, position of a stream reach and size of the catchment (Table 1, Fig. 1). Africa's Nile River is the world's longest river at 6690 km, with a catchment area of 2.97 million km² while the Amazon River has the world's largest catchment area of >6.1 million km² (Holeman, 1968) and a river length of 6296 km (Holeman, 1968). Forty-six of the world's longest rivers are >2000 km and distributed across all continents (Holeman, 1968).

Rivers and streams can be separated into upland and lowland ecosystems (Fig. 1). Upland rivers and streams drain mountainous areas, with high topographic relief, at high rates of flow and provide for a range of habitats that reflect this, including rapids, riffles and waterfalls. Some rivers in the northern and southern hemisphere may freeze during the winter, limiting productivity and movements of organisms. Upland rivers drive high sediment and erosion processes when they flow, providing a range of ecological niches for organisms adapted to fast-flowing river environments, including micro-organisms, invertebrates, fish, reptiles (e.g. turtles) and some birds (e.g. dippers, *Cinclus* spp.).

Lowland rivers at low elevations with relatively simple topographic relief are usually much larger (width and depth) than their upland counterparts, carrying considerably larger volumes of water provided by a network of upland rivers and streams from upstream in the catchment. Lowland rivers generally have lower stream velocities, with increased turbidity (due to sediment) and higher temperatures than upland rivers. Their large size provides habitats for a range of small and large organisms including

Table 1 Major freshwater sub-biomes, their major abiotic drivers, characteristic biota and opportunities for conservation management. The sub-biomes described here are based on “biomes” defined within IUCN’s Global Ecosystem Typology (<https://iucnrl.org/about-rle/ongoing-initiatives/global-ecosystem-typology/>).

<i>Sub-biome</i>	<i>Description</i>	<i>Abiotic drivers</i>	<i>Characteristic biota</i>
Rivers and streams	Rivers and creeks which may be permanent, seasonal or intermittent, extending from mountains to the sea and including tributaries and distributaries, across all parts of the world. They can be separated into upland and lowland rivers, with perennial, seasonal or episodic flow regimes as well as some which go through a freeze-thaw cycle.	Flow is critical and varies with whether rivers are lowland or upland and climate (perennial, seasonal, episodic) resulting in significant variations in flow regimes. Turbidity and depth tend to be higher in lowland rivers and streams.	These vary depending on the flow regime and whether the river is upland or lowland. Upland biota are adapted to high flow rates and limited productivity while lowland biotic communities are often more complex, given the variety of different habitats. Where freezing affects rivers, biota are adapted to coping with these conditions.
Lakes	Salt and freshwater lakes which vary enormously in size, flooding regime (perennial, seasonal, episodic) and water quality (e.g. salt) across the world. Some also go through a freeze-thaw cycle. They also include small groundwater fed ecosystems such as springs and oases and geothermal springs.	Water is generally still but flooding regimes can be highly variable, with many lakes also affected by freezing. Area, depth, connectivity and water quality (e.g. salinity) all drive composition, structure and functions of lakes.	Biota are highly dependent on lake size and other drivers, with adaptations to flooding regime, salinity and freezing the most prominent, depending on the type of lake. Plants, invertebrates and vertebrates and other biota are adapted to these regimes.
Palustrine wetlands	These are distributed around the world and include floodplains, marshes, swamps, tropical and subtropical flooded and peat forests, bogs and fens. Variation is highly dependent on different flooding regimes, areas and structural complexity.	Flooding regime is critical, varying from permanent, seasonal to episodic, depending on the location of the wetland. Shallow depth and water quality as well as the size of the wetland are also primary drivers of complexity and type of system.	During wet phases, obligate aquatic organisms colonize these systems but they also support a wide range of amphibious plants and also terrestrial animals reliant on the productivity and drinking water, particularly in arid landscapes.
Transitional waters	Estuarine waters; permanent waters of estuaries and estuarine systems of deltas; intertidal marshes, includes salt-marshes, salt meadows, saltings, raised salt marshes, tidal brackish and freshwater marshes; intertidal forested wetlands, includes mangrove swamps, nipa swamps, tidal freshwater swamp forests and; brackish to saline lagoons and marshes with one or more relatively narrow connections with the sea.	These systems are determined by freshwater flow regime and their interaction with tidal systems. These are reflected in salinity, light, temperature and depth gradients. The variation in flow regimes	Biota are often adapted to brackish systems, sometimes with obligate parts of their life cycle tied to freshwater (e.g. fish breeding). The areas are important breeding sites for many organisms.
Brackish tidal systems	These include coastal deltas, intertidal forests and shrublands and coastal saltmarshes. They predominantly occur in the tropical regions of the world where there are significant freshwater ecosystems, including large rivers.	There is an interaction of freshwater inputs, tidal regime and terrestrial inputs in these systems. They interact in different ways to create spatio-temporal complex and dynamic, and often large ecosystems with many different niches. In particular, there is a strong salinity gradient reflecting these different drivers.	They support tidal forests, particularly mangroves and also saltmarshes. Depending on the size of these ecosystems they can support freshwater, marine and terrestrial organisms which can exploit the range of habitats created, across the different salinity gradients.
Subterranean rivers and wetlands	These include freshwater ecosystems underground or groundwater ecosystems. They include karst wetlands and cave systems as well as underground rivers.	Flow regime which may vary from lentic to lotic are important in determining characteristics of nutrient and flow processes as well as biotic interactions. Lack of light is the most important and determining factor. Low oxygen and scarce nutrients are also critical.	Organisms are generally adapted to the lack of light, with no eyes and lack of pigmentation (e.g. blind cave fish). They also have slow growth rates. Food-webs are truncated at the top, with few or no predators.

Table 1 Major freshwater sub-biomes, their major abiotic drivers, characteristic biota and opportunities for conservation management. The sub-biomes described here are based on “biomes” defined within IUCN’s Global Ecosystem Typology (<https://iucnrl.org/about-rle/ongoing-initiatives/global-ecosystem-typology/>).—cont’d

Sub-biome	Description	Abiotic drivers	Characteristic biota
Artificial wetlands	Water storage areas, including reservoirs, barrages, hydro-electric dams, impoundments; ponds, including farm ponds, stock ponds, small tanks; aquaculture ponds, fish ponds, shrimp ponds; salt exploitation, salt pans, salines; excavations; gravel pits, borrows pits, mining pools; wastewater treatment, including sewage farms, settling ponds, oxidation basins; irrigated land and irrigation channels, including rice fields, canals, ditches; seasonally flooded arable land, farm land and; canals, also includes water pipes and subterranean canals	Extreme variation in the hydrological regimes as well as nutrient loading, determined by the desired function, which in turn governs which species are able to exploit these systems.	Relatively low biodiversity, dependant on the hydrological character and physical attributes of structures. May offer refuge to species in times of low resource availability, namely droughts. Can influence transportation of individuals, assisting in colonization of both native and invasive species.

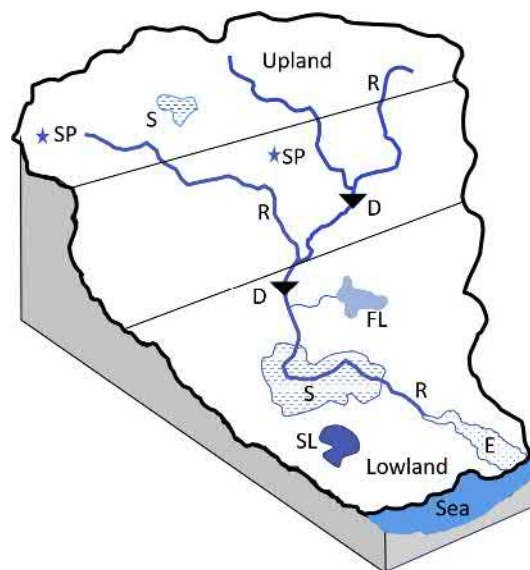


Fig. 1 Conceptual diagram of a river catchment, depicting rivers (R, upland and lowland) connecting a swamp (S) or floodplain, freshwater lake (FL) and estuary (E), with constructed dams (D) and isolated wetlands including springs (SP), salt lake (SL) and a swamp (S).

aquatic macrophytes, algae, plankton, waterbirds (e.g. waders, piscivores), reptiles (e.g. crocodiles) and mammals (e.g. otters, platypuses, dolphins).

Rivers and streams provide critical ecosystem services contributing to many global economies including agriculture, water supply, power generation, trade, transport and fisheries. Around the world 2 billion people rely directly on rivers for their drinking water, and 25% of the world’s food production depends on irrigation from rivers (Opperman et al., 2018). As a result of such major dependencies, rivers are threatened by related direct and indirect human activities. These include four major groups of threats: hydrological (water extraction, dams, changes to natural flow regimes, alteration of flooding regimes), physical (sediment extraction, channel alterations), pollution (water contamination, changes to water quality) and biological (loss/alteration to habitats, species’ invasions) (Dudgeon et al., 2006; Kingsford et al., 2016; Chiu et al., 2017). Climate change effects often compound these impacts (Balcombe et al., 2011).

Lakes

Lakes are enclosed still water areas, either freshwater or saline, found all over the world. They usually have inflowing and outflowing rivers or streams which maintain lake water levels. They vary enormously in size, depth, hydrological connectivity, permanence and water chemistry, reflecting their location and climate which drive flow and flooding regimes. Large permanent freshwater lakes (> 100 km²) are often connected to one or more rivers, with complex shorelines, varying depths and mosaics of habitat. Large



Fig. 2 Sabie River, a perennial river flowing through Kruger National Park, South Africa. Photo R.T. Kingsford.

permanent lakes are typically found in humid temperate and tropical regions, on large land masses (e.g. Great Lakes, North America, Lake Victoria, Africa, Qinghai Lake, China).

Similarly, small permanent freshwater lakes of up to 100 km² occur in humid temperate and tropical regions. They may be hydrologically isolated from streams or rivers, relying on local rainfall and small streams. Freeze-thaw freshwater lakes, predominantly in high latitudes and altitudes in the Northern Hemisphere and South America, freeze for at least 4–5 months of the year, over the late autumn, winter and early spring. During such periods, productivity is limited, given relatively poor exchange of nutrients, low flow and light combined with low temperatures. Small permanent lakes, which freeze, vary considerably in area and depth, and usually thaw in spring, increasing productivity for different organisms. Permanent lakes provide a perennial aquatic habitat which varies in relation to these seasonal drivers and inflows, providing habitats for a range of obligate aquatic organisms. This can lead to some of the world's most amazing biodiversity, with incredible examples of adaptive radiation (e.g. cichlid fish in Lake Malawi, (Albertson et al., 1999)). Lake Baikal in Russia is the deepest (~1.6 km) and holding the most water (23,000 km³) of any lake in the world, providing niches for more than 2660 animal and 1000 plant species (Timoshkin et al., 2016).

Artesian springs and oases are groundwater supplied wetlands, which are ecologically similar to small permanent lakes. They occur in dry, arid regions of southern Africa, the Sahara and Middle East, central Eurasia, southwest of North America and Australia. Their permanent water provides critical habitat for a range of biota, with high levels of endemism due to their hydrological isolation. Simple food webs are driven by autotrophs (e.g. aquatic algae and floating vascular plants) and macrophytes providing food for invertebrates (e.g. crustaceans, molluscs, arachnids, insects) and small-bodied fish. Geothermal pools and hot springs (e.g. Grand Prismatic Spring, Yellowstone National Park, USA, Fig. 3), mud pots and geysers also have their permanent water or moisture maintained by groundwater. Temperatures (>44 °C) are high and the water may be acidic (pH 2–4) or alkaline (pH 7–11) with high mineral content levels, resulting from the permanent interaction of groundwater with magma and hot igneous rocks. Geothermal pools occur in volcanically active areas at all latitudes. Their environments are hostile to most organisms and so they have low diversity of biota, which are highly specialized for extreme temperatures and water quality. They include bacteria and archaea, cyanobacteria, diatoms, filamentous algae, macrophytes and invertebrate detritivores (e.g. dipterans and coleopterans).

Seasonal freshwater lakes are typically small (<5 km²) and shallow (<1 m deep). Filling and drying patterns are driven by seasonal weather patterns of rainfall, inflow and evapotranspiration. They occur in sub-humid temperate and wet/dry tropical regions in monsoonal and Mediterranean climates where there are clear seasonal rainfall patterns. Where rainfall patterns are highly variable and episodic, there are many temporary freshwater lakes, filled by local rainfall, and episodic rivers and streams. They are shallow but may be large (>100 km²), occurring in semi-arid and arid regions of Africa, Americas, Asia and Australia. Seasonal freshwater lakes provide non-permanent wetland habitat for a range of biota that include those that are resident with coping strategies for dry periods (e.g. burrowing frogs (Lee and Mercer, 1967), zooplankton (Panarelli et al., 2008), and those that inhabit the wetland when water is available (e.g. fish (Kushlan, 1976) and waterbirds (Kingsford et al., 2010)).

Salt lakes receive flows from rivers or creeks but they seldom have outflows and so salts and minerals concentrate, as water evaporates. Permanent salt lakes can be large (>100 km²) and sometimes deep (>2 m). They are restricted to semi-arid climates, with high evaporation but reliable inflows, occurring in Africa, Eurasia (e.g. Caspian Sea) and western parts of North and South America (e.g. Great Salt Lake). Temporary salt lakes typically have short periods of inundation and long intervening dry periods in arid and



Fig. 3 Grand Prismatic Spring, geothermal pool in Yellowstone National Park, relies on high temperature groundwater. Photo K. Brandis.

semi-arid regions of Africa, Eurasia, Australia, North and South America. They can very large (e.g. Kati Thanda-Lake Eyre, Australia, 9500 km², Makgagikgadi Pan, Botswana, 4920 km²) and are typically shallow. High salinity of salt lakes and their temporary nature means they only provide habitat for specifically adapted organisms, although they can be highly productive. These organisms include specialized invertebrates (Williams, 1998) that can provide critical food resources for waterbirds (e.g. flamingos *Phoenicopterus* spp., Fig. 4) and Wilson's Phalaropes *Phalaropus tricolor*) (Senner et al., 2018).

Lakes also provide important ecosystem services to a range of human communities, including water for domestic, industrial and agricultural use, and food resources (Brönmark and Hansson, 2002) but this dependency also threatens lake ecosystems. Anthropogenic threats to lakes are similar to those affecting rivers, including alterations to flows, affecting inflows and outflows, pollution, infilling (land reclamation), invasive species and exploitation of resources (e.g. fish, waterbirds) (Kozhova and Silow, 1998; Brunsberg and Blomqvist, 2001; Senner et al., 2018). In addition to these threats, there are the pressures from increasing global populations and demands for freshwater and climate change impacts (Folke et al., 2004; Dudgeon et al., 2006).



Fig. 4 Flamingos are specialist animals living on salt lakes, such as Lake Nakuru in Kenya. Photo R.T. Kingsford.

Palustrine Wetlands

Palustrine wetlands are vegetated, non-riverine wetlands, moving between wet and dry phases, depending on the flooding regime. They are the interface between terrestrial and freshwater ecosystems and include tropical flooded forests and peat forests, subtropical/temperate forested wetlands, permanent marshes, seasonal floodplain marshes (Fig. 3), episodic arid floodplains, boreal, temperate and montane peat bogs, and boreal and temperate fens. They can be among the most extensive and biodiverse ecosystems on Earth, not only providing water for dependent organisms but also providing a source of high biodiversity, food and water for a large component of terrestrial biodiversity (e.g. Okavango Delta, Botswana, Fig. 5). They primarily occur where lowland rivers spread out across low elevation lands. Most large rivers have extensive floodplains, except where these have been developed, particularly in the Northern Hemisphere (Kingsford et al., 2016). Flooding regimes of these freshwater ecosystems are critical with the flood pulse providing the key input of productivity (Junk et al., 1989) but this can vary depending on the nature of river flows which supply these floodplains and are sometimes highly episodic and unpredictable (Walker et al., 1995).

Flooding regimes in these wetlands can vary from permanent shallow standing water or near-surface water tables, to seasonally high-water tables to episodic inundation with long inter-annual dry periods, dependent on highly variable flooding regimes of dryland rivers (Puckridge et al., 1998; Young and Kingsford, 2006). Filling of these wetlands can occur via episodic or seasonal high rainfall resulting in overbank river flows, or the maintenance of high-water tables providing abundant water through groundwater seeps or free-standing water (e.g. permanent marshes).

The availability of water plays a key role in determining productivity of these wetlands, often more productive compared to the surrounding landscape. Palustrine wetlands have complex food-web structures driven by primary producers such as zooplankton and macrophytes, supplying a range of high order vertebrates, including fish, birds, reptiles and mammal species. The productivity of these palustrine wetlands also make them important breeding sites for species such as waterbirds, some breeding in large colonies (Frederick and Ogden, 2001). The level of biodiversity and its responses largely depends on the size and complexity of the floodplain, swamp or forest.

Floodplain wetlands have supported large groups of people with their food and resources for building and maintaining settlements, including fish and reeds for buildings (Lemly et al., 2000). They also provide a plentiful supply of fresh water. In addition, congregation of terrestrial animals in such highly productive environments can also be a source of food for different communities and more recently for tourism. Many of the major wetlands of the world that attract high levels of tourism are large palustrine wetlands, including the Camargue (Europe), Florida Everglades (North America), Kakadu Wetlands (Australia), Mekong Delta (Asia), Okavango Delta (Africa, Fig. 5) and the Pantanal (South America, Fig. 6). Palustrine wetlands can also provide important ecosystem services through pollutant removal from water runoff (Reinelt and Horner, 1995).

Threats to palustrine wetlands include a wide range anthropogenic impacts: pollution, drainage and/or filling, conversion of use (e.g. to agricultural land, urbanization) (Reinelt et al., 1998), livestock grazing, water extraction, resource extraction (e.g. peat) (Graf



Fig. 5 Okavango Delta, Botswana, is an extensive flooding swamp system providing habitat for significant biodiversity. Photo R.T. Kingsford.



Fig. 6 Pantanal wetland floodplains have extremely high densities of waterbirds during the dry season as prey concentrates. Photo R.T. Kingsford.

et al., 2012). These have impacted on the biota that rely on these wetlands, including alterations to vegetation (van der Valk, 2013), reduced taxonomic richness in invertebrates as a result of changes to water quality (Campbell et al., 2009), and reduced waterbird breeding (Kingsford and Thomas, 2004).

Transitional Waters

Transitional waters include many coastal ecosystems around the world, where the major drivers originate from both marine and freshwater sources, including riverine estuaries and bays, coastal inlets or fjords, and intermittently closed and open lagoons and lakes. Different tidal and freshwater regimes interact seasonally with geomorphology to create diverse niches which vary in salinity, light, depth and nutrient regimes for survival and recruitment of a wide range of adapted biota.

Estuaries and bays are the tidal mouths of rivers where marine and freshwater mix, distributed through the world, although rarely found on arid or polar coasts. Some are permanently open while others are intermittently open. Permanently open riverine estuaries and bays vary over time reflecting differences in geomorphology, freshwater inflows, tides and seasonality of climate. Estuaries support highly productive communities of arthropods, molluscs, fish, and birds (Alongi, 2009) and are often fringed by a mosaic of mangroves, salt marshes, intertidal areas and muddy and sandy shores. They support complex food-webs composed of planktonic and benthic invertebrates, fish, waterbirds, seabirds, mammals and reptiles.

Deepwater coastal inlets are glacier formed semi-confined aquatic systems open to oceans. They are found mainly at higher latitudes including along the coast of Alaska, Norway, Scotland, Denmark and Greenland but also in Chile, New Zealand and Antarctica. Norway's coastline is estimated to have 1200 fjords (Gregory, 1913). Freshwater inputs are predominantly seasonal when snow and ice melt. Deepwater coastal inlets are characteristically steep sided with deep water and limited light penetration. Fjords in Norway and New Zealand support deep-water coral reefs which are high in biodiversity (Hovland, 2008).

Intermittently closed and open lagoons and lakes are highly dynamic with their status changing with a combination of tidal ranges, freshwater inflow volumes, and sedimentation (McSweeney et al., 2018). An estimated 3% of the world's estuaries are intermittently open, mostly in Australian, South Africa and Mexico (McSweeney et al., 2017). Estuarine ecosystems, which constantly experience variations in environmental factors (e.g. salinity, dissolved oxygen, water depth), are typically characterized by a restricted number of species well adapted to the variable conditions (Pasquaud et al., 2015). These include tolerances to wide ranges in salinity e.g. fish (Whitfield et al., 1981), seagrass (Koch et al., 2007) and mangroves (Parida and Jha, 2010).

Transitional waters are declining at alarming rates around the world (Hopkinson et al., 2019), destroyed by onsite developments (Bilkovic and Roggero, 2008; Newton et al., 2014) and declining freshwater resources from the catchment. Diversions of freshwater inputs increase salinity, altering available niches to suit more saline-tolerant species (Schlacher and Wooldridge, 1996; Zampatti et al., 2010). The high productivity of transitional waters has made them a focus for human exploitation, particularly for food resources, driving their degradation around the world (McHugh, 1976). Urbanization and exploitation for aquaculture have also had significant impacts, driving long-term declines in biota. Global annual loss of mangroves areas is estimated to be 3–5 times greater than the global deforestation rate (Spalding, 2010), estimated at annual loss of 1.1% between 1990 and 2000 (FAO, 2017).

Brackish Tidal Systems

Brackish tidal sub-biomes are the intersection of marine, terrestrial and freshwater processes, forming unique, complex and highly productive taxonomic diversity and functions, sometimes over large areas (Triest et al., 2018). They include deltas, intertidal forests and shrublands and saltmarshes. River mouths represent dispersal points of river-derived sediments (Wright, 1977), driving the formation of deltas (e.g. Ganges–Brahmaputra, Nile, Yellow River deltas), continuously changing through interactions with fluvial, tidal and wave processes (Dalrymple et al., 1992), with varying degrees of dominance (Ellison, 2019), but also affected by terrestrial processes. River deltas comprise subaerial and subaqueous areas, the former extending along the delta plain into low-lying floodplains influenced by tidal and/or saline intrusions and the latter extending onto the continental shelf where unloading or nutrients and sedimentation occur (Bianchi and Allison, 2009). This complex mosaic and dynamic, over extensive areas, provides niches supporting high taxonomic and functional diversity for both resident and migratory species (Kelin et al., 2005; Barendregt et al., 2009; Campbell, 2012; Visser et al., 2019).

Many intertidal forests and shrublands include mangroves. These represent a diverse group of tropical tree species with physiological and morphological adaptations for intertidal environments, loosely zoned to seaward, central, and landward zones (Polidoro et al., 2014; Ellison, 2019). Globally, mangroves cover about 150,000 km², a third in the South East Asia (Spalding, 2010). Mangroves offer many services, including the protection of shorelines from erosion by providing a physical barrier to waves, enabling deposition, and building of peat (Gedan et al., 2011). Mangrove forests can be highly productive, supporting rich communities of arthropods, molluscs, fish, and birds (Alongi, 2009), with sesarmid and fiddler crabs functioning as key ecosystem engineers (Kristensen, 2008).

Coastal saltmarshes replace mangroves in mid to high latitudes, with an estimated global saltmarsh area at about 54,950 km² (Mcowen et al., 2017). They can be characterized as a subset category of tidal marshes (Daiber, 1986), defined by vegetated intertidal communities, dominated by herbs, grasses, and low shrubs bordering saline waters, subject to flooding by saline waters as a result of fluctuations in water levels in surrounding waterbodies (Adam, 1993). As a result, organic and inorganic resources from marine and terrestrial sources, they are among the highly productive ecosystems of the world. Species' richness of saltmarshes tends to increase from tropical to temperate latitudes (Bridgewater and Cresswell, 2003; Saintilan, 2009). Saltmarshes are dominated by benthic invertebrates, including snails, crabs and bivalves and offer important habitat for fish, including both resident and marine transient species (Visser et al., 2019). Saltmarshes also provide important habitat for many avian species for breeding, feeding and roosting (Spencer et al., 2009). Benthic algae and bacteria are prolific on sediments in associations with emergent vegetation, with distinct communities structured by biophysical attributes (Sullivan and Currin, 2002).

Brackish tidal systems have historically supported considerable human development (Day Jr et al., 2007; Renaud et al., 2013), continuing to provide critical ecosystem services (Vörösmarty et al., 2004; Bianchi and Allison, 2009; Hopkins et al., 2018). This has made them vulnerable to on-site exploitation as well as impacted by declining freshwater inputs and increasing pollution from riverine catchments. Many of the world's large deltaic systems are collapsing due to up-stream water resource developments which capture water, sediment, reducing accretion, and increasingly exacerbated by sea level rise (Blum and Roberts, 2009; Syvitski et al., 2009; Vörösmarty et al., 2009; Tessler et al., 2015). Deltaic areas provide extremely productive terrestrial and marine habitats and resources such as fishing, agriculture and livestock, driving extensive land conversion and degradation (Stanley and Warne, 1993; Memon, 2005; Li et al., 2017). There is also evidence that pollutants, including heavy metals are increasing in their concentration in some deltas (Fu et al., 2003; Bai et al., 2012).

Subterranean

Freshwater underground ecosystems or aquifers are extensive, paralleling and even surpassing freshwater surface ecosystems (Culver and Pipan, 2019). Subterranean water accounts for ~30% of global fresh water, compared to ~0.26% in lakes and reservoirs, with slow renewal rates of ~1400 years (Shiklomanov and Rodda, 2004). Underground streams and pools have few to limited internal sources of energy and nutrients, relying predominantly on surface connected streams for input (Culver and Pipan, 2019) and are heavily influenced by the geomorphology and surface climate. They have low biological productivity, devoid of photosynthesis and primary producers, dominated by heterotrophs (bacteria, archaea, fungi, and protista) (Culver and Pipan, 2019). The lack of light has resulted in a convergent evolution of species (troglomorphy) sharing morphological characteristics such as the lack of pigment and eyes, and elongated appendages with high levels of endemism (Pipan and Culver, 2012). Estimating the diversity of global subterranean species is difficult, with currently 20,000 described species of stygobionts and trogllobionts (Culver and Pipan, 2019). In more connected subterranean pools and rivers, transient vertebrates such as fish and salamanders may occur. In contrast, aquifers and hyporheic zones of saturated sediments beneath rivers and lakes, offer little connectivity with surface water, supporting a limited trophic structure, comprised almost exclusively of heterotrophic microbes and invertebrates (Gibert and Deharveng, 2002).

Aquifers hold 25 times more fresh water compared to above ground water in lakes and rivers (Shiklomanov and Rodda, 2004), making up to 98% of the earth's fresh water and providing the primary drinking water source between 1.5 and 3 billion people (Kundzewicz and Doell, 2009) and approximately 40% of global freshwater use for agriculture (Döll et al., 2012). Ground water also provide critical support for humans during periods of droughts (Castle et al., 2014). As a result, many of the world's ground-water ecosystems are under considerable pressure from extraction. In one assessment, 21 of the world's 37 largest aquifers were found to be depleted at unsustainable rates (Richey et al., 2015). More so, depletion of ground water and impoundment of fresh

waters by dams has significantly accelerated sea level rise (Wada et al., 2012), threatening billions of humans living in coastal regions. Groundwater ecosystems are also threatened by pollution, originating from mining activities (Lei et al., 2010; Shakoor et al., 2017), including fracking (Mooney, 2011).

Artificial Wetlands

Artificial wetlands, either entirely or partially modified human-engineered waterbodies, are ubiquitous around the world (Downing et al., 2006; Ellis and Ramankutty, 2008). They include large reservoirs (Fig. 7), ponds (e.g. small dams, sewage ponds, garden ponds, stormwater treatment ponds, and mining pits), rice paddies, freshwater aquaculture, artificial waterways, including surface and subterranean canals and pipes (Table 1). Large reservoirs (> 1–5 ha; (Biggs et al., 2017)) are formed by impounding river flows with dam walls (e.g. Hume Dam on the River Murray in Australia, Fig. 7), with 7320 recorded dams and associated reservoirs globally and a cumulative storage capacity of 6864 km³ around the world (Lehner et al., 2011). The ecology of reservoirs varies considerably, reflecting their uses for releases and diversions, and affected by geomorphology and upstream land uses, delivering nutrients, predominantly phosphorus and nitrogen, as well as suspended sediments (Bremigan et al., 2008). Primary productivity is generally low to moderate, restricted to the euphotic zone (limnetic and littoral zones), with relatively simple trophic networks. Species diversity is highest in the shallow littoral zones, supporting benthic algae, macroinvertebrates, fish, waterbirds, aquatic reptiles, aquatic macrophytes and terrestrial or amphibious vertebrates.

There are hundreds of millions of small artificial dams or ponds (Verpoorter et al., 2014) and estimated 16.7 million reservoirs (> 0.01 ha) with a storage capacity of > 8000 km³ (Lehner et al., 2011), making up 10–30% of global standing water area (Downing et al., 2006). Their productivity varies with nutrient profile and input, from extremely high in wastewater treatment ponds to very low in toxic mining and excavation pits, determining the taxonomic and functional biodiversity, mediated by connectivity to other waterbodies, vegetation and the catchment (Chester and Robson, 2013). Ecosystem function and diversity are also dependent on flooding and drying and depth but they can support a range of species including macrophytes, macroinvertebrates, crayfish, frogs, fish and waterbirds.

Rice paddies are a significant artificial freshwater aquatic ecosystem, making up as much as 12.3% of global crop area and 1.3% of global land area (1,982,841 km²), producing almost 9% of global food production (FAOSTAT, 2019), and accounting for 25%–33% of the world's developed freshwater resources (Bouman, 2009). They occur on transformed floodplains but also on terraced hillsides. Temporary waters combined with intensive management force simple trophic networks, dominated by cultivated macrophytes as well as other autotrophs but also supporting opportunistic species such as invertebrates, zooplankton, insects, frog, fish and waterbirds.



Fig. 7 Hume Dam on the River Murray in southeastern Australia, regulates flows in the river to provide water to agricultural communities (irrigation) and towns downstream, reducing flows to dependent wetlands and groundwater ecosystems. Photo R.T. Kingsford.

Related freshwater aquaculture ecosystems are also widespread. In 2017, 48.4 t of aquaculture production (43% of global production) was produced from freshwater habitats, including fish farms, ponds and tanks (FAO, 2019). Construction of freshwater aquafarms is accelerating (Ottinger et al., 2018; Ren et al., 2018) as global marine fish stock are depleting (Goldburg and Naylor, 2005), particularly through conversion of coastal wetlands, lakes and lagoons. Freshwater aquaculture is heavily dependent on external inputs of feed, energy and chemicals for sustaining primarily fish or crustaceans, affecting water quality and quantity in connected habitats (Troell et al., 2014; Ottinger et al., 2016). These freshwater aquaculture ecosystems support a simple trophic structure, with few non-target primary producers and secondary consumers, including some amphibian and bird species (Kloskowski and Nieoczym, 2015).

Linear artificial waterways are globally ubiquitous, including channels for navigation, flood protection (including stormwater drains), and irrigation canals or ditches. Channelized waterways exceed 500,000 km while constructed canals extend for 63,000 km (Gleick et al., 2001). In the United States agricultural lands, ditches occupy > 112,000 km² (U.S. Department of Agriculture, 2018), more than 300,000 km in the Netherlands (Verdonshot et al., 2012) and about 600,000 km in the United Kingdom, significantly larger than the total stream network (Maltby et al., 2011). There are also artificial subterranean canals and water pipes throughout the world. For supply of drinking and irrigation water, rapid flow rates and turbulence dominate waters that are generally low in nutrients, with development of microbial biofilms on internal pipe surfaces (Douterelo et al., 2013). Contrastingly, urban stormwater and sewage pipes and canals have relatively slower flows with low turbulence and low water quality, given high levels of contaminants (Nilsen et al., 2019). The functions and biota of these artificial waterways are highly variable and dependent on flow, sediment base, substrate, and catchment scale inputs (Meybeck, 2003; Chester and Robson, 2013; Biggs et al., 2017). They generally have low taxonomic biodiversity with simple functional relationships, although can sometimes providing refuge, breeding grounds, and dispersal routes between habitats (Chester and Robson, 2013; Harvolk et al., 2014; Biggs et al., 2017).

Clearly these artificial freshwater ecosystems are established primarily to provide ecosystem services in the form of drinking water, water for agriculture, generation of hydroelectricity as well as providing food and fiber. But nearly all threaten natural freshwater ecosystems principally by removing or fundamentally changing the hydrological regime which sustains these natural ecosystems (Kingsford, 2000). When not managed well, degradation ensues, including destruction of habitat, loss of productivity from agricultural areas, with increasing salinity and pollution. Other examples include low level flooding of rice paddies which can produce anoxic soil conditions and emissions by methanogenic archaea, accounting for more than 10% of total methane flux in the atmosphere (Ehhalt et al., 2001; Sass and Cicerone, 2002) as well as increased transmission of diseases such as the avian influenza virus (Gilbert et al., 2017). Also, fish farms are generally considered detrimental to native fish biodiversity when released into natural freshwater habitats (Bezerra et al., 2019) as well as depleting native fish stocks for fish feed (Goldburg and Naylor, 2005).

Conservation Management

Direct and indirect human development has destroyed or degraded many of the world's freshwater ecosystems, well over half and up to 90% in some regions of the world (Junk et al., 2013; Davidson, 2014). Extensive natural freshwater ecosystems have disappeared and continue to be destroyed with ongoing appropriation of freshwater resources for human communities. This makes conservation management particularly challenging, given increasing human population growth and so much of our food, fiber and building materials dependent on use of fresh water. Until this fundamental challenge is appropriately addressed by reducing human demand on freshwater resources, the freshwater biome will continue to degrade and more water dependent species will be lost and many of those terrestrial species dependent on fresh water. There will also be significant impacts on dependent ecosystem services. As well, the human footprint in terms of establishing urban communities has destroyed many freshwater ecosystems around the world. For example, 10.9% of estimated global population resided in low-elevation coastal zone in 2000 (Neumann et al., 2015), resulting in destruction of many coastal ecosystems. In addition, establishment of large-scale agriculture also continues to destroy many freshwater ecosystems around the world (Zhang et al., 2010).

There are some critical measures which must be taken to halt the loss of freshwater ecosystems due to human activities around the world. These include focusing on the demand for fresh water and limiting the human footprint, particularly urban, mining and agricultural, on natural freshwater ecosystems (Butler et al., 2015; Dodds, 2019). Demand for appropriation of more fresh water can only be met through recycling of water in large urban communities, improved capture and use of water within urban communities, and desalination (Vörösmarty et al., 2010). Further, there is an urgent need to improve efficiencies with which irrigated plants receive water so that the impact on diverting water from surface and groundwater freshwater ecosystems is reduced (Howell, 2001; De Pascale et al., 2011). This does not mean increasing the area of irrigation but rather making the most of the water currently diverted and even allowing for returning water to freshwater ecosystems for restoration. In addition, further destruction of freshwater ecosystems by urbanization, mining and agriculture must be avoided. Such measures require political will (Chhatre and Saberwal, 2005), only accomplished through public discourse and knowledge (Cooke et al., 2013), which also needs to be founded on an improved understanding of the scale of loss of freshwater ecosystems and our dependencies on these systems for ecosystem services.

There are a range of policy and management mechanisms which are important for implementing improved conservation management of freshwater ecosystems (Amezaga et al., 2002; Kim, 2010; Clare and Creed, 2014). The traditional conservation approaches primarily hinge on protection of areas of freshwater ecosystems (Saunders et al., 2002). These primarily focus on the primary approach of gazetted and management of freshwater areas as protected areas within National Parks or other reserves.

Similarly, identification of such areas as wetlands of international importance under the Ramsar Convention represents a similar approach where areas of land including important freshwater ecosystems are identified and there is a focus on their sustainable management (Gardner and Davidson, 2011). Unfortunately, such management may not be effective unless there is a strong focus on also protecting the flow and flooding regimes to these systems. This primarily means stopping further loss of the sustaining flow and flooding regimes which are often impacted by diversions of water to urban communities or irrigated agriculture. Until both the area of the freshwater ecosystem and its supply of water are protected, there will be inadequate long-term conservation management.

There are also a range of broad policies related to protecting specific aquatic animals and plants which may be threatened by extinction (i.e., IUCN Red-listed species) (Rodrigues et al., 2006). These may address the protection of fresh water inflows. There are also various migratory species agreements which are critical for long-term conservation of different species, particularly bird species (Runge et al., 2014; Runge et al., 2017). Long term protection fundamentally relies on protection of habitats from human incursions around the world (Murray et al., 2014; Murray and Fuller, 2015).

Restoration of freshwater ecosystems can occur with a focus on restoring flows and natural flooding regimes. This may not only mean protection of the current flows but also restoration of more flows, sometimes termed environmental flows (Arthington, 2012; Acreman et al., 2014). These also inevitably need to be managed to determine the range of influences on long-term trajectories of restoration for the ecosystems and overall effectiveness (Thompson et al., 2018).

Conclusions

There are a range of diverse natural freshwater ecosystems in the freshwater realm, dependent on unique hydrological regimes. These include rivers and streams, lakes (freshwater and salt lakes, oases, springs, and ponds), palustrine wetlands (floodplains, swamps and marshes) transitional waters (coastal inlets and fjords and estuaries), brackish tidal systems (deltas, intertidal forests and shrublands, saltmarshes) and subterranean freshwater ecosystems. These provide a tremendous diversity of habitats and make up some of the Earth's most spectacular ecosystems for biodiversity. Unfortunately, much of this diversity has been lost over human history, largely because of our dependence on fresh water for our livelihoods, directly for drinking but also for much of our food, fiber, energy and building. The freshwater realm and the different sub-biomes and ecosystems are under increasing pressure, driving high rates of loss of freshwater ecosystems, their species and the essential ecosystem services they support. Management at the catchment scale is important, focusing on the protection of natural flow and flooding regimes. The dire status of freshwater ecosystems will not change without significant alteration of human behaviour in terms of reducing demand on freshwater resources and protecting these important habitats.

Acknowledgments

This work was supported by the Centre for Ecosystem Science, UNSW Sydney and the Australian Research Council, under Linkage projects LP180100159 and LP170101143.

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World Terrestrial Ecosystems

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Published by Elsevier Inc.

Acknowledgments

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Abstract

As the source providing units for several goods and services required for human survival (e.g. food, fuel, fiber, water provision and purification, etc.) ecosystems must be sustainably managed. This will require a globally comprehensive and detailed understanding of the distribution of ecosystems on Earth. While there have been several attempts to partition the planet into large ecologically meaningful areas (ecoregions), a high spatial resolution map of Earth's terrestrial ecosystems at the on-the-ground occurrences (patch) level has heretofore been lacking. A new, high resolution (250 m) map of data-derived World Terrestrial Ecosystems is characterized, and its utility for assessing policy-mandated ecosystem conservation targets is described.

There are many controlling influences which determine the distribution of species on the planet, including environmental heterogeneity (e.g. climate and geomorphology), evolutionary history, species relationships, dispersal dynamics, and the history and spatial patterns of natural and human-caused environmental disturbances. With a focus on understanding these drivers, biogeography is broadly understood as the study of why species are distributed where they are, a question which was of interest to Charles Darwin and Alfred Russel Wallace in the mid-1800s. Ecosystems geography is a similar but newer discipline that focuses on where ecosystems occur, and the drivers that control their distributions (Bailey, 2009). Ecosystems are understood as biological communities interacting with each other and with their physical environment (Odum 1953) and have been defined and mapped from a variety of perspectives related to both structural (e.g. canopy structure) and functional (e.g. photosynthesis) properties. Zhao and Costello (this volume) define ecosystems as enduring, spatially bounded environments where biological relationships (e.g. trophic levels) and energy interactions (e.g. evapotranspiration) are more similar within than with other ecosystems.

Ecosystems are multiscalar, and have been mapped at a variety of scales ranging from local to global. Common geographies for which ecosystem maps are developed include sites, nations, regions (including ecoregions), continents, and the planet. Terrestrial ecoregions are understood as macro-scale ecosystems and are defined as "relatively large units of land containing a distinct assemblage of natural communities and species" (Olson et al., 2001).

Understanding the distributions and condition of Earth's ecosystems is increasingly important as they provide humans with a number of goods and services (e.g. food, fiber, fuel, water quality and quantity, carbon sequestration, flood control, etc.) necessary for our survival. In order to continue providing these services, ecosystems need to be well-managed, and for many "endangered" ecosystems (Keith et al., 2013) a conservation focus is encouraged. The importance of conserving ecosystems is reflected in two major intergovernmental policy instruments: (1) Aichi Target 11, which establishes a 17% protection goal for all terrestrial ecosystems on the planet (www.cbd.int/sp/targets/), and (2) the UN Sustainable Development Goals (SDGs, and in particular SDG 6 (freshwater), SDG 14 (coastal and marine) and SDG 15 (terrestrial)) which call for the conservation of Earth's ecosystems (<https://sustainabledevelopment.un.org/sdgs>). A map of the distribution of these ecosystems and an analysis of their conservation status is essential for understanding progress toward these goals.

Given the importance of knowing what ecosystems exist on the planet, where they are located, and what condition they are in, a standardized (reproducible), data-derived, globally comprehensive, and high spatial resolution map of the distribution of earth's ecosystems is needed. Existing ecoregion maps (e.g. Bailey, 2009; Dinerstein et al., 2017) generally describe large, ecologically meaningful areas, and are often used in global conservation priority setting analyses. These ecoregion-scale maps do not, however, characterize the on-the-ground distributions of finer scale terrestrial ecosystems at the occurrence level.

A new map of World Terrestrial Ecosystems (Sayre et al., 2020) was recently produced at a 250 m spatial resolution based on an integration of climate regime, landforms, and vegetation/land cover. The map was developed using United Nations Food and Agriculture Organization (FAO) and Intergovernmental Panel on Climate Change (IPCC) criteria for ecological zones and climate regions. The World Terrestrial Ecosystems are depicted in Fig. 1. A legend block for the World Terrestrial Ecosystems is included in Fig. 2.

The World Terrestrial Ecosystems were developed from a spatial integration of several input layers. A World Temperature Domains (Polar, Boreal, Cool Temperate, Warm Temperate, Subtropical, and Tropical) layer was developed by analyzing



Fig. 1 World Terrestrial Ecosystems mapped at a 250 m spatial resolution. There are 431 ecosystems at the globally aggregated level, and 1778 ecosystems when segregated by biogeographic realms (Nearctic, Neotropical, Palearctic, Afrotropical, Indomalayan, Australasian, Oceania). Each ecosystem is a unique combination of climate regime, landform type, and vegetation assemblage/land cover. From Sayre R, Karagulle D, Frye C, Boucher T, Wolff N, Breyer S, Wright D, Martin M, Butler K, Van Graafeiland K, Touval J, Sotomayor L, McGowan J, Game E, and Possingham H (2020) An assessment of the representation of ecosystems in global protected areas using new maps of World Climate Regions and World Ecosystems. *Global Ecology and Conservation* 21(2020): e00860. <https://doi.org/10.1016/j.gecco.2019.e00860>.

temperature data from thousands of meteorological stations over a 30-year record of observations. A World Moisture Domains layer (Moist, Dry, and Desertic) was similarly developed from precipitation observations. The World Temperature Domains (6) layer was integrated with the World Moisture Domains (3) layer to produce 18 World Climate Regions. The 18 World Climate Regions were then unioned with a World Landforms (Plains, Hills, Mountains, and Tablelands) layer to produce a 72 class integrated climate/terrain layer. Finally, the 72 climate/terrain classes were integrated with a World Vegetation/Landcover layer (Forestlands, Shrublands, Grasslands, Bare Areas, Croplands, Water, Snow and Ice, and Settlements). The combination of 72 climate/terrain types with 8 vegetation/land cover types produces 576 possible combinations of World Terrestrial Ecosystems, of which 431 were realized (e.g. while tropical moist plains with snow and ice is a possible combination, it does not exist). The full methodological details and input layer descriptions are found in Sayre et al. (2020).

The conservation status of the World Terrestrial Ecosystems has also been identified from a global gap analysis of the representation of the ecosystems in protected areas. The gap analysis was an evaluation of the area of each ecosystem which was contained within a protected area in order to assess the ecosystem's conservation status against a protection goal (gap in protection). The gap analysis was conducted using all protected areas from the World Database on Protected Areas (WDPA; <https://www.protectedplanet.net>). The gap analysis was repeated using a subset of the WDPA polygons with only IUCN management category I-IV included to emphasize only those parks with a strict conservation management focus. As would be expected, using all protected areas in the gap analysis resulted in relatively increased conservation status for many ecosystems. However, when considering only strictly conserved protected areas (IUCN management category I-IV), few ecosystems approach the 17% protection goal as specified in Aichi Target 11 (www.cbd.int/sp/targets/). The true management effectiveness of all protected areas is still unknown, and until it is known, gap analyses based on IUCN management category and other criteria are best understood as approximations in need of refinement. More details on the gap analysis methods and results are found in Sayre et al. (2020).

The new World Terrestrial Ecosystems represent a mapping of the unique combinations of climate regime, landform and major vegetation assemblages/land cover types. As such they represent an ecosystem structure-based mapping approach, i.e. they are derived from a mapping and subsequent integration of the major abiotic and biotic structural elements of ecosystems. We recognize that there are other approaches to conceptualizing and mapping terrestrial ecosystems based on their functional properties (e.g. nutrient cycling, trophic relationships, etc.), but a globally comprehensive, high resolution, data-derived map of ecosystems based on most ecosystem functional properties does not yet exist (although productivity is a notable exception). A classification (list and description) of global ecosystems based on functional properties is in development by the IUCN Red List of Ecosystems community (Keith et al., 2013).

Faber-Langendoen et al. (this volume) describe global vegetation assemblages based on considerations of vegetation physiognomy (structure) and composition. The World Terrestrial Ecosystems resource is not a vegetation classification, but it does

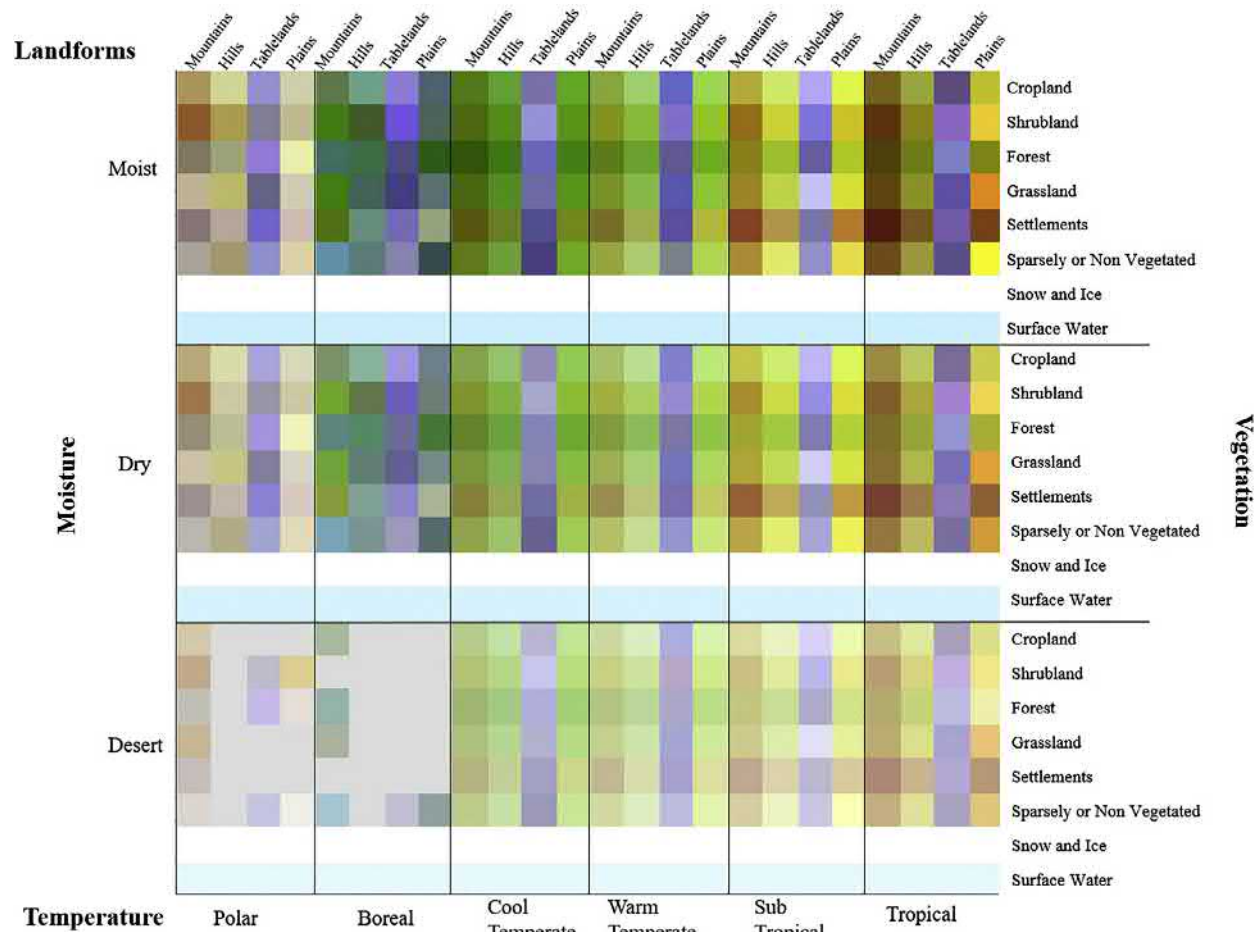


Fig. 2 Legend block for the map of World Terrestrial Ecosystems in Fig. 1, above. This graphic describes the color assignments for the 431 ecosystems. The legend block is not intended for distinguishing between similar ecosystems, which would have similar color assignments. Rather, the legend block is intended to allow users to understand ecosystems as all possible combinations that result from the combination of the climate regions (temperature and moisture), landform type, and vegetation assemblage/land cover type. From Sayre R, Karagulle D, Frye C, Boucher T, Wolff N, Breyer S, Wright D, Martin M, Butler K, Van Graafeiland K, Touval J, Sotomayor L, McGowan J, Game E, and Possingham H (2020) An assessment of the representation of ecosystems in global protected areas using new maps of World Climate Regions and World Ecosystems. *Global Ecology and Conservation* 21(2020): e00860. <https://doi.org/10.1016/j.gecco.2019.e00860>.

incorporate a biome-level vegetation assemblage classifier (i.e. forestlands, shrublands, grasslands, and sparsely- or non-vegetated natural areas), reporting either non-vegetated natural land cover (water, snow and ice) or converted land cover types (croplands, settlements) where natural vegetation is lacking. An assessment of the conceptual and spatial concordance between the EcoVeg units (Faber-Langendoen et al., this volume) and the World Terrestrial Ecosystems (Sayre et al., 2020) would be interesting and is encouraged along the lines of future work.

In conclusion, terrestrial ecosystems have been rigorously mapped from data at a 250 m spatial resolution based on climate, landform, and vegetation. This new characterization supports an understanding of the types and locations of the terrestrial ecosystems on Earth. Such an understanding is required to assess progress toward Aichi and SDG ecosystem conservation targets. The resource is intended to be useful for other applications as well, including ecosystem valuation and accounting, ecosystem-based inventory and management, and greenhouse gas modeling.

Acknowledgments

The authors would like to acknowledge the helpful reviews of Kate Ritzel, Tabitha King, and Ray Zhang from the U.S. Geological Survey. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

See also: Marine Ecosystems of the World; Tropical, Temperate, and Mediterranean Grasslands of the World.

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Islands and Atolls of the World

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Abstract

The Islands and Atolls Section of the Encyclopedia of the World's Biomes covers unique examples of islands, atolls, and archipelagos across the world. The section is unique in that it contains all of the physical and biological elements traditionally described as biomes in other sections, plus aspects of island biogeography. The papers in the Islands and Atolls Section represent a broad mix of island biogeography, ecology, conservation, and management.

Overview—Islands and Atolls

The Encyclopedia of the World's Biomes takes a broad look at the Earth's biogeographic zones, roughly broken into water, land, and human systems. Water includes oceans (one blue planet), freshwater (the oasis of life), ice sheets and polar deserts (ice of life), and islands and atolls (life in and surrounded by water). Terrestrial includes deserts (life in the extremes), forests (trees of life), and shrublands and grasslands (sea of plants). Human systems includes the geographic distribution of anthromes as well as the sustainable stewardship of the anthrome biosphere. This piece on anthromes helps tie together this work with our previous Encyclopedia of the Anthropocene ([DellaSala and Goldstein, 2018](#)). It also helps us think about the imperiled ecosystems and species of the world.

The Islands and Atolls Section does not follow traditional biome nomenclature. We realize it is unusual to hear that *Islands* are a biome unto themselves. We do not want that to be confusing. An *Island Biome*, while different than the traditional delineation of a biome, is distinct because it delivers to the reader an overview of the uniqueness of islands, atolls, and archipelagos across the world. The section roughly breaks out into an overview of the islands and atolls of the world, a revisit of the theory of island biogeography, a look at some interesting and unique regional examples, and aspects of development, management, and conservation.

Cross-Reference to Papers in the Islands and Atolls Section

1. Islands and Atolls of the World (Goldstein, 2020, this paper)
2. Global Islands ([Martin et al., 2020](#))
3. Island Biogeography Revisited ([Helmus and Behm, 2020](#))
4. How Consideration of Islands Has Inspired Mainstream Ecology: Links Between the Theory of Island Biogeography and Some Other Key Theories ([Warren et al., 2020](#))
5. Island Biogeography of Marine Shallow-water Organisms ([Hachich et al., 2020](#))
6. The Effect of Sea Level Rise on Islands and Atolls ([Miller, 2020](#))
7. Arctic Ocean Islands ([Gaston, 2020](#))
8. The Azores Archipelago: Biodiversity Erosion and Conservation Biogeography ([Borges et al., 2020](#))
9. Climate Change and Biodiversity Conservation in the Caribbean Islands ([Gould et al., 2020](#))
10. An Overview of the Socio-ecological System of Cays and Islets in the US Caribbean and Their Vulnerability to Climate Change ([Murry et al., 2020](#))
11. Physical Geography of the Hawaiian Islands ([Harrington et al., 2020a](#))
12. Hawaiian Islands Coastal Ecosystems: Past, Present, and Future ([Kim et al., 2020](#))
13. Physical Geography of the Mariana Archipelago ([Harrington et al., 2020b](#))
14. Coastal Strand and Mangrove Swamps of the Mariana Islands ([Plentovich et al., 2020](#))
15. Galapagos Island Biodiversity ([Elias, 2020](#))
16. The Island Biogeography of Wallacea and Krakatoa Island ([Yuni and Yuda, 2020](#))
17. Biogeography and Chemical Risks on Islands ([Ito et al., 2020](#))
18. Collaborative Conservation in the Madrean Sky Islands ([Sittig et al., 2020](#))

Summary of the Section's Papers

The section begins with an overview of global islands (Sayre et al., 2018; Martin et al., 2020). This paper displays a new map (Fig. 1) of the islands of the world using high resolution satellite imagery, classifying islands as continental mainland, islands $> 1 \text{ km}^2$, and islands $< 1 \text{ km}^2$ (Table 1). The new high-resolution islands data are intended to support coastal ecosystem mapping efforts and assessments of threatened island biodiversity, among other applications. This chapter summarizes the global island mapping approach and results and provides a new perspective on the size distribution of the islands, atolls, and archipelagos of the world.

Helmus and Behm (2020) discuss how island biogeography is determined by three processes: immigration, evolution, and extinction (Fig. 2). They further discuss how human impacts have become increasingly more important to island biogeography through human population expansion, species introductions resulting in rapid evolutionary change to native island species, and subsequent island extinctions.

Warren et al. (2020) provides links between the Theory of Island Biogeography and other key theories in ecology. They include modifications to “Core” Island Biogeography Theory and show the role the Theory plays in inspiring other quantitative theories that are at least as broad in relevance. The Island Biome, or islands surrounded by water is an obvious choice to study the effects of area and isolation on species richness. Island boundaries frequently provide longstanding limits to the distributions of species or populations. As discussed by Warren et al. (2020), and as we see in other papers in this section (Hawaii, for example, as summarized by Kim et al., 2020), islands provide particularly striking examples of rapid change in selection gradients following the arrival of new immigrants.

Through the perspective of shallow-water organisms, Hachich et al. (2020) explored island biogeography in the marine realm. Their goal was to provide an overview of processes and patterns related to marine shallow-water island biogeography. They formulated predictions of expected functional island biogeography patterns, regarding the effects of environmental filtering, selective extinction or neutral mechanisms. When put together, the data show patterns of speciation and endemism in marine shallow-water organisms in oceanic islands. For example, patterns of neo and paleo-endemism of reef fish are plotted in a global map (Fig. 3), and variations of marine shallow-water endemism with islands age, area, and isolation are shown for reef fishes and marine gastropods (Fig. 4).

Miller (2020) provides an overview of the social, ecologic, and economic impacts of sea level rise, a topic that is discussed across this section. Global sea level rise disproportionately effects the livelihood and ecosystem health of the nations and people residing on islands and atolls. Islands and atolls of the Western Pacific are the most threatened due to regional intensities of sea level rise, increasing intensity of storm events with associated storm surge, vulnerability of coral-based islands to erosion, and genetic and species vulnerability of biological communities due to their relative isolation (Fig. 5). The increasing loss of islands and atolls has resulted in an imminent loss of island cultures, species extinctions and ecosystems. Murry et al. (2020) show future scenarios in the Caribbean based on the combination of drought and sea level rise (Fig. 6).

Mitigating the effects of sea level rise are discussed, both from the global and local perspective, and suggest global mitigation actions will require a profound shift in the way we live over the next 100 years. Communities are considering options including

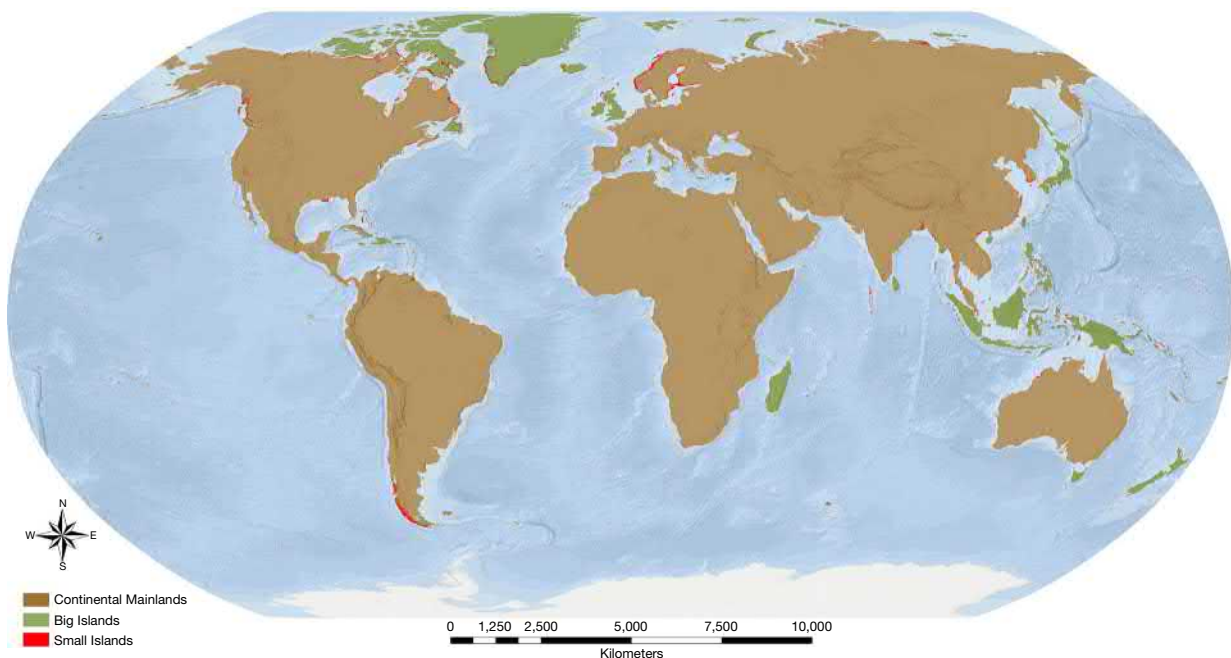


Fig. 1 Map of global islands (Sayre et al., 2018; Martin et al., 2020). Continental mainlands are depicted in brown, islands bigger than 1 km^2 (big islands) are depicted in green, and islands smaller than 1 km^2 (small islands) are depicted in red. Small islands, not visible at this coarse resolution and page size have been rendered visible through visual exaggeration using increased point sizes for feature symbols.

Table 1 Number, area, and coastline length for islands in three size classes (Sayre et al., 2018; Martin et al., 2020).

Landmass type	Number of polygons	Area (km ²)	Length of coastline (km)
Continental mainlands	5	125,129,046	813,467
Big Islands > 1 km ²	21,818	9,938,964	1,304,762
Small Islands ≤ 1 km ²	318,868	20,589	321,774

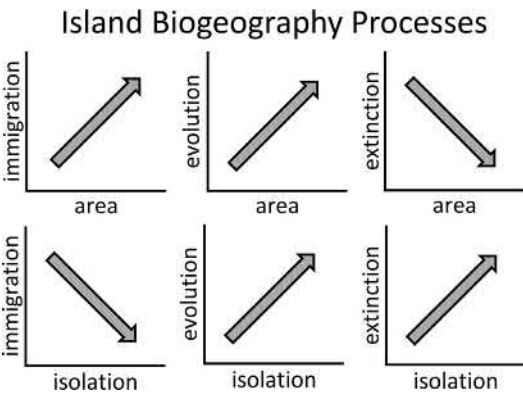


Fig. 2 Island biodiversity is determined by three fundamental biogeographic processes: immigration, evolution, and extinction (Helmus and Behm, 2020). These three processes vary with island area and isolation from source pools of immigrants. Arrows depict the relationship direction in these three processes, which vary with island area and isolation from source pools of immigrants.

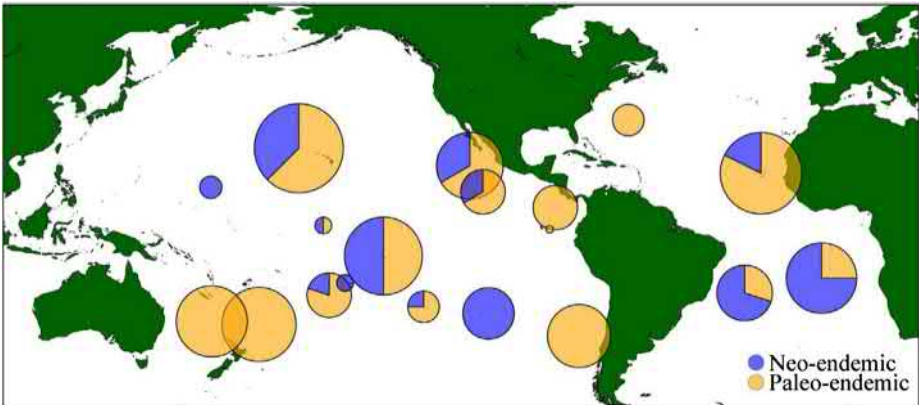


Fig. 3 The proportion of reef fish endemic species found in different oceanic islands across the marine biogeography regions. Circle sizes indicate the proportion of the assemblage made up by endemic species. Colors show the different types of endemism (neo or paleo) observed in oceanic islands (Hachich et al., 2020).

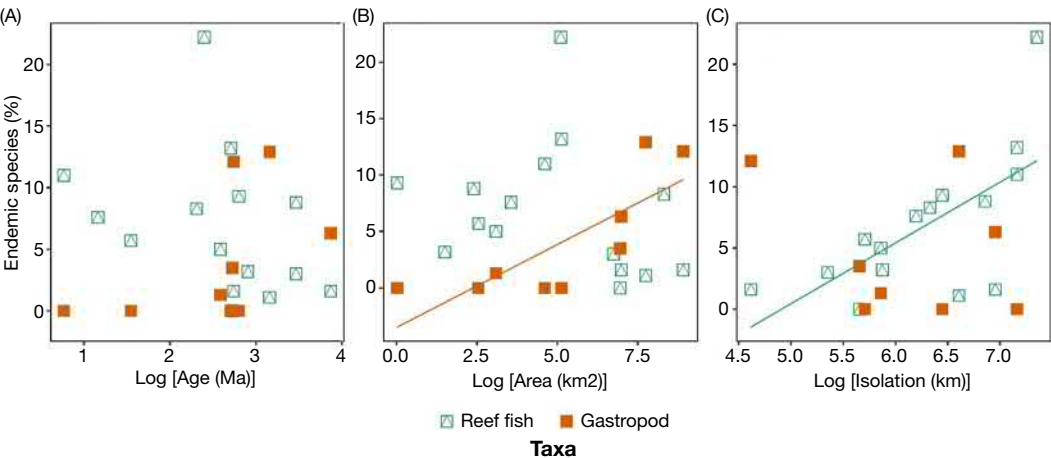


Fig. 4 The variation of marine shallow-water endemism with islands (A) age, (B) area and (C) isolation for reef fish and marine gastropod. Only significant ($p < 0.05$) regression lines are presented (Hachich et al., 2020).



Fig. 5 Sea level rise in the Solomon Islands in combination with increasing storm surge has made communities and ecosystems highly vulnerable to erosion and inundation (Miller, 2020) (from <https://www.newstalk.com/news/as-sea-levels-rise-in-the-pacific-five-of-the-solomon-islands-have-disappeared-598805>, accessed 20 January 2020).

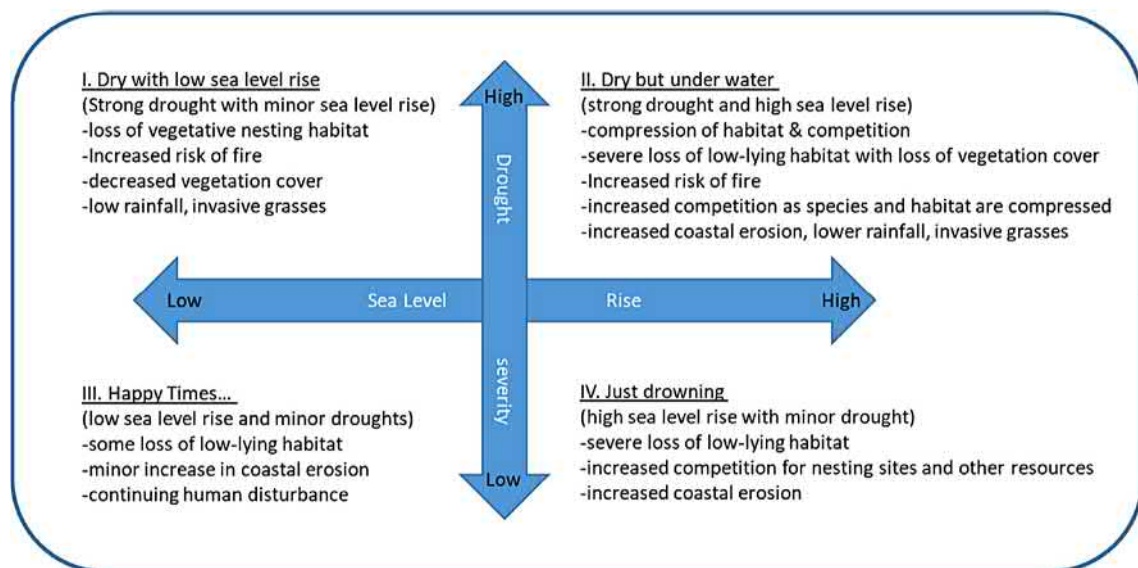


Fig. 6 Current projections in the Caribbean, for example, highlight extensive drought, extreme sea level rise, and more frequent and intense hurricanes. Four potential future scenarios are shown for the Caribbean, based on low to high sea level rise and small to large increases in drought (Murry et al., 2020).

building walls, moving to higher ground, and transfer off island to higher mainland areas. As sea water intrudes, area is lost or inhabitable and emigration must occur. The loss of heritage and culture is happening within a human lifetime.

The archipelagos of the high Arctic (Fig. 7) are some of the remotest places on Earth, where climates are extreme and change only slowly, given the dynamics of the Arctic Ocean. Gaston (2020) describes the physical biogeography of the Arctic islands and how these islands are home to specialized Arctic plants and animals, characteristic of the Pleistocene period, many of which will be severely challenged by global warming. They are likely to provide the last refugia for many High Arctic endemics, such as gyrfalcon (*Falco rusticolus*) and muskox (*Ovibos moschatus*), as well as many Pleistocene plants. Consequently, colonization by low Arctic and Boreal species may adversely impact many of these species.

Isolated in the North Atlantic Ocean, the Azores Islands are home to a unique biodiversity. Land-use changes, fragmentation, the introduction of exotic invasive species and climate change all act to threaten the persistence of species on these islands (Fig. 8). Effective conservation strategies should be based on a deep knowledge of species abundance, trends, and distributions, that can be obtained from long term monitoring schemes like the ones implemented there (Borges et al., 2020).

Gould et al. (2020) and Murry et al. (2020) each tackle aspects of climate change in the Caribbean. Gould describes the importance of coastal areas to the economic, cultural, and natural resource base of island societies, noting that sea level rise, storm surge, and the salinization of coastal soils have tremendous consequences to consider when planning for the future. Green infrastructure

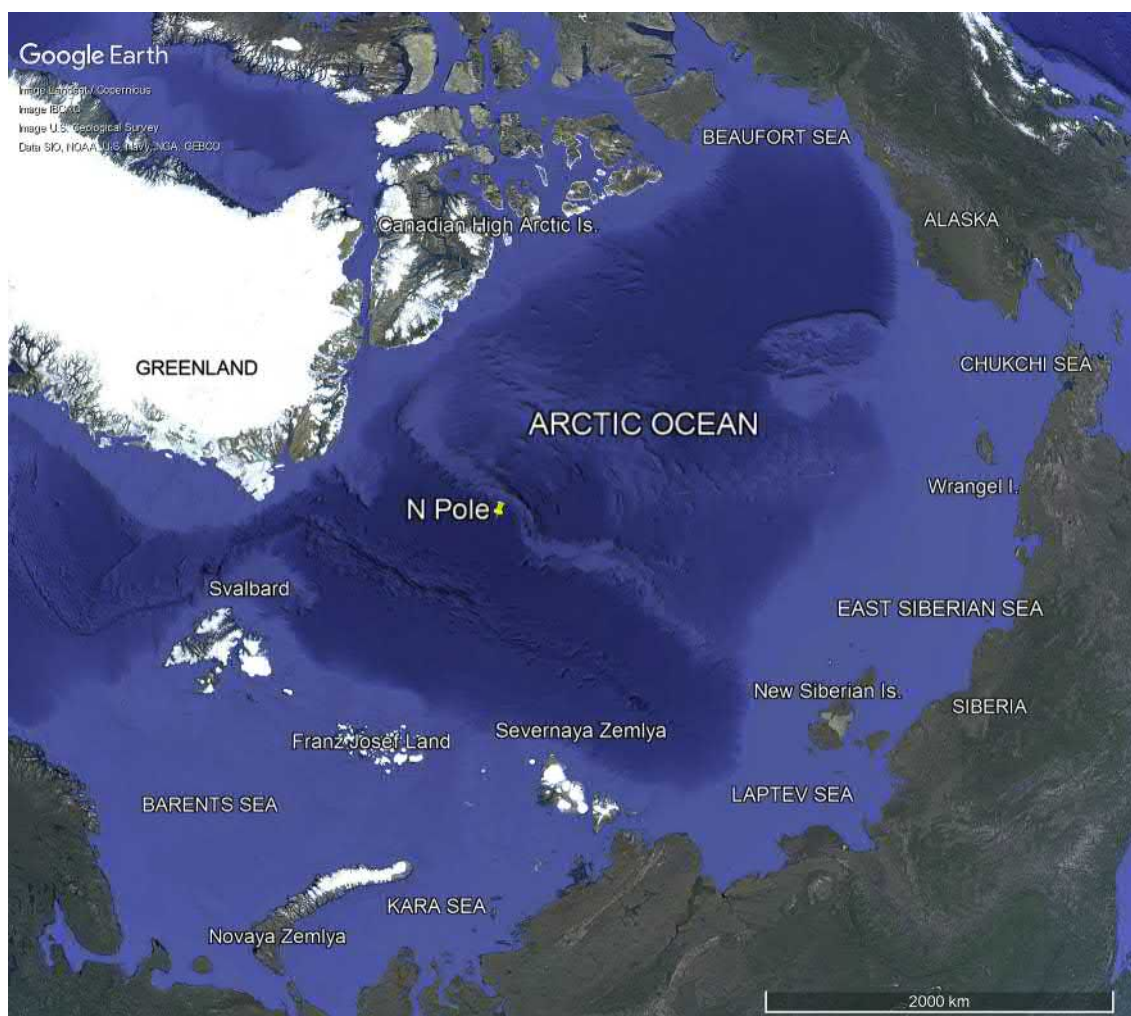


Fig. 7 Islands of the Canadian Arctic Archipelago (Gaston, 2020).



Fig. 8 The mosaic of human modified habitats at mid and low elevation (Terceira Island, Azores), with dominance of pastures for cattle grazing, surrounded by the exotic tree species, *Cryptomeria japonica*. Photo credit: P.A.V. Borges.



Fig. 9 Known locally as Elfin Woodland, these cloud forests in the Luquillo Mountains of Northeastern Puerto Rico lie within the El Yunque National Forest and Luquillo Experimental Forests. They harbor a high percentage of endemic species across many taxonomic groups (Gould et al., 2020). Photo credit: G. González.

can play an important role as both a buffer to sea level changes and a resource and habitat for wildlife. Habitat protection for rare and endemic species in the Caribbean is particularly important as the cloud forests of the upper mountains because the highest concentration of endemics, are also most vulnerable to a warming and drying climate (Fig. 9).

Murry et al. (2020) details how cays and islets can provide habitat and safe haven from anthropogenic impacts for many species of concern including many resident and migratory seabirds, shorebirds, endemic reptiles, and plants. The challenge, they contend, is that management is limited by insufficient resources, capacity, and a mixture of ownership (US Federal, Commonwealth, Territorial, non-profit organizations, and private), making regional planning a challenge (e.g., Fig. 10). Like most island systems, the dominant short- and long-term threats are invasive species. In addition, recreational and commercial uses by humans, as well as marine debris and accumulations from harmful algal blooms, also pose a significant threat. In the longer term, the cays ecosystems and fauna are



Fig. 10 The challenge of managing for people and biodiversity, as shown through recreational boat use of Cayo de Barca, Jobos Bay National Estuarine Research Reserve, Puerto Rico (Murry et al., 2020). Photo credit: E. Rodríguez.

expected to show high exposure and sensitivity with limited adaptive capacity, depending on the type of island, to the impacts of climate change. This can be countered by using a strategic adaptive approach to utilize projections of future conditions for decision making.

As described by [Harrington et al. \(2020a\)](#), the Hawaiian archipelago is the most isolated landmass in the world, approximately 3846 km from California and 6196 km from Japan. These islands range from small atolls in the northwest of the archipelago, to high volcanic islands in the southeast, and contain a range of ecosystems due to variations in elevation, topography, substrate,

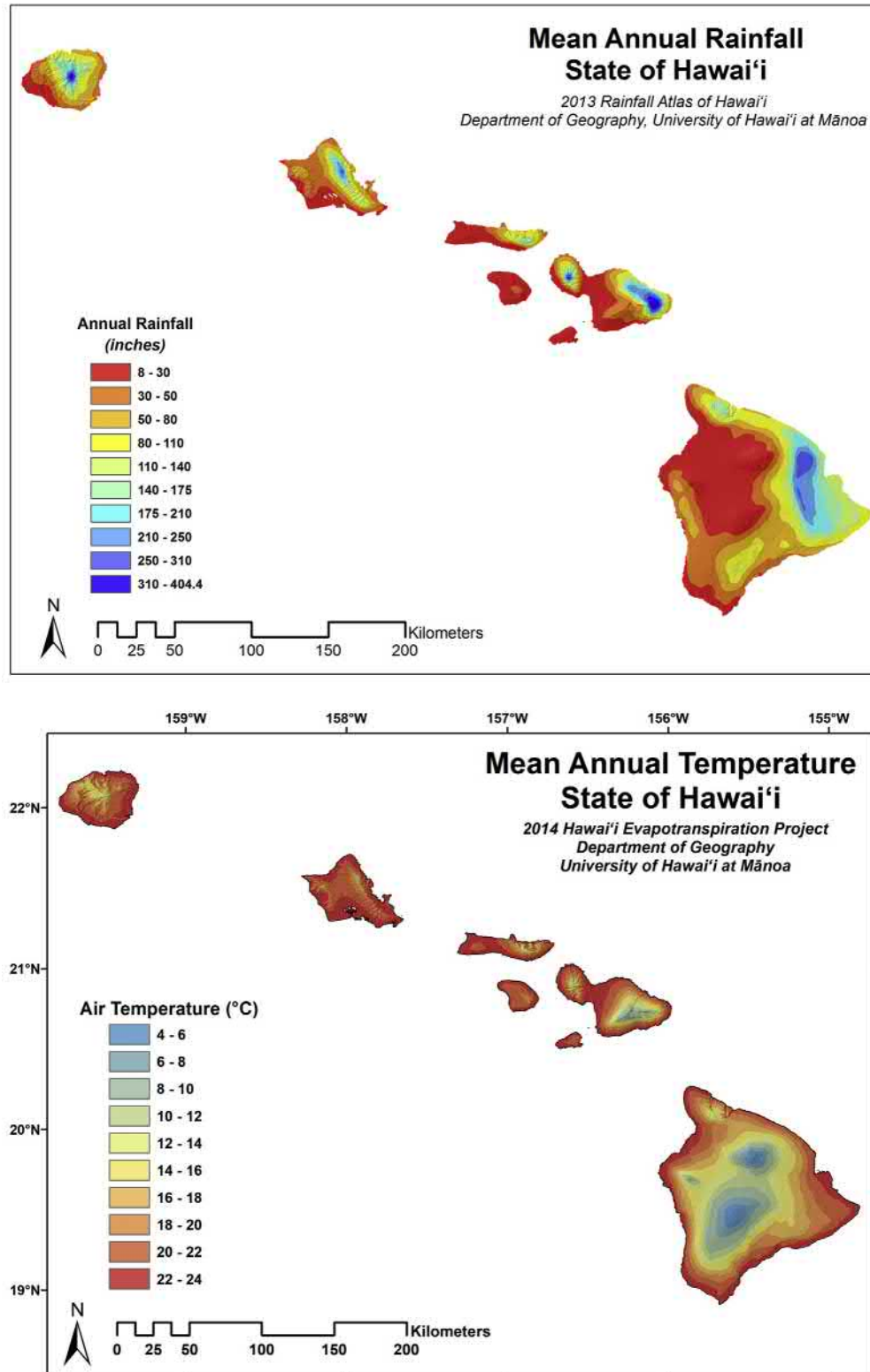


Fig. 11 Mean annual air temperature and precipitation across the main Hawaiian Islands (Harrington et al., 2020a).

hydrology, wind, and precipitation patterns (e.g., Fig. 11). Hawaiian coastal ecosystems were highly intact native coastal communities prior to human contact. These became heavily impacted post human contact and now require protection and restoration by local conservation and community groups for continued survival of native coastal species (Kim et al., 2020). Two coastal ecosystem sub-types occur in the archipelago and are defined by moisture regime: coastal dry and coastal wet-mesic sub-types. Coastal ecosystems were historically more resilient to stochastic events because they had more continuous populations of native flora with a higher faunal diversity. Currently, coastal ecosystems are in decline due to factors such as conversion pressure from expanding development and agriculture and the introduction of invasive species. The future of these communities will be based on the effectiveness of collaborative management of these coastal ecosystems.

Harrington et al. (2020b), describe the 15 islands (the largest of which is Guam) and various small islets of the Mariana Archipelago, which is famous for the Marianas Trench, the deepest location known on earth. The vast majority of the archipelago's land area is concentrated in the larger, southern main islands of Saipan, Tinian, Rota, and Guam. Plentovich et al. (2020) describe the status, stressors, and future viability of coastal strand and mangrove swamps of the Marianas. Of particular interest is their descriptions of the current conditions as they relate to future scenarios based on items of social interest, conservation values, laws and biosecurity, and long-term planning (Fig. 12).

The biodiversity of the Galapagos Islands (Elias, 2020) has a rich and storied history in ecology, famous for the basis of thought that Charles Darwin (Fig. 13) developed from his visit there in his youth. Current conservation efforts in the Galapagos relate strongly to ecotourism, and biosecurity measures seek to prevent the spread of terrestrial and marine invasive species.

Yuni and Yuda (2020) discuss the remarkable degree of endemism in Wallacea, a region that consists of three distinct island groups, Sulawesi, Lesser Sunda, and Moluccas (Fig. 14). They describe the geologically young islands of Sulawesi, with flora and fauna that evolved independently and high avian biodiversity of the Moluccas region, with 83 endemic species out of the nearly 600 species known. They also describe the dramatic Krakatoa Island, whose violent 1883 eruption, and subsequent eruptions has provided opportunities for long term ecological research on tropical island biogeography and succession.

Ito et al. (2020) describe another topic that transcends many islands, atolls, and archipelagos, a transported landscape. Ancestors of the Marshall Islands brought domestic plants and animals such as pigs, dogs, chickens, taro, breadfruit, and bananas from their original lands, and this became known as the portmanteau biota. In Majuro, the transported landscape has continued throughout the 2000 year human history. Parts of the Marshall Islands, such as Bikini Atoll and Eniwetok Atoll, have experienced adverse anthropological impacts such as nuclear testing conducted after World War II (resulting in food chain effects that led to iodine deficiency in humans, as in Fig. 15), and heavy metal contamination from industrial waste.

Not all islands are marine, however, and this volume has one unique article on a collaborative landscape conservation effort to conserve the Madrean Sky Islands (Sittig et al., 2020). In the Madrean Sky Islands (Fig. 16), deserts meet mountains in a patchwork



Fig. 12 Coastal development along the western coast of Saipan near the town of Garapan (Plentovich et al., 2020). Photo credit: R. Walker.



Fig. 13 Charles Darwin, aged 40. Lithograph by T. H. Maguire, 1849. Photo courtesy of Wellcome Collection.

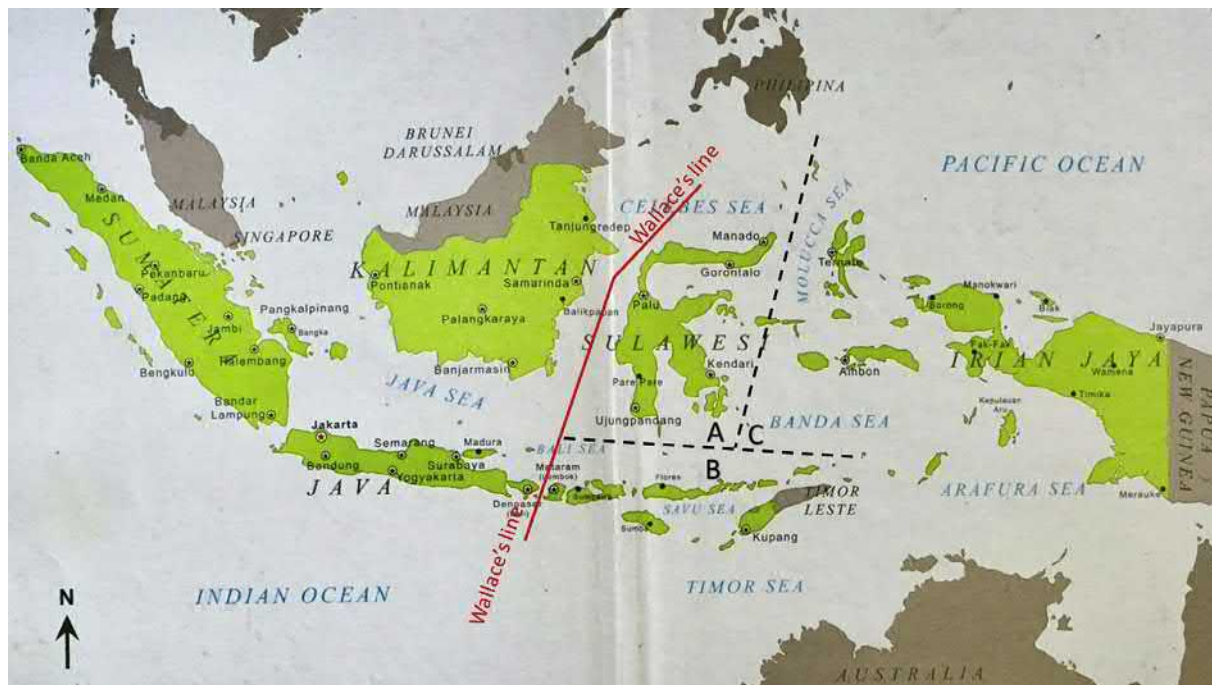


Fig. 14 Wallace's Line, drawn in 1859 by Alfred Russel Wallace, is a transitional zone separating the ecozones of Asia and Australia (Yuni and Yada, 2020).

of multiple biomes including desert, scrub, grassland, woodland, and forest. The Sky Islands of the United States and Mexico contain a unique ecology of rarity and endemism, whose geography spans international borders, whose social values are different than the surrounding areas, and where stressors and threats to the ecological health islands create many challenges. The article provides an example of work by multiple agencies, organizations, and individuals to overcome physical and social boundaries

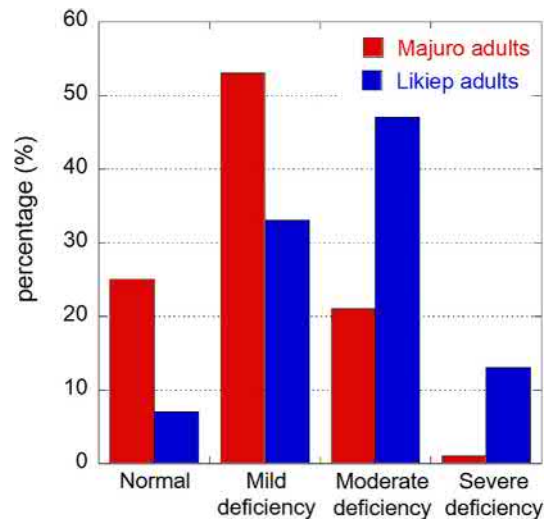


Fig. 15 Urinary iodine excretion in the Majuro and Likiep Atolls (Ito et al., 2020).



Fig. 16 The mountain ranges of the Madrean Sky Island ecoregion of the United States and Mexico (Sittig et al., 2020). Photo credit: Sky Island Alliance.



Fig. 17 By kayak, in 2019, Tongass National Forest—Sitka Ranger District staff and volunteers removed over 600 pounds of trash and recyclables from 12 beaches in the West Chichagof-Yakobi Wilderness Area. The haul included many Japanese plastic bottles which may have arrived in the wake of the 2011 Honshu tsunami. Photo credit: Voices of the Wilderness Artist in Residence, Cecil Howell.

to conserve natural resources. It describes challenges, lessons learned, and available tools and resources to the Madrean Landscape Conservation Design in order to inform and provide connections to conservation work elsewhere.

It became quickly apparent that although the authors would cover a great deal in this section, we could not cover everything. For example, although invasive species and biosecurity were discussed among many papers, no single treatise on invasive species and eradication is found here. Another topic that is similarly addressed among many papers is one of coastal pollution. As part of a recent monitoring trip to a Wilderness Area near where I live, volunteers picked up and packed into kayaks 580 pounds of non-recyclable plastic and six contractor bags of recyclable plastic and aluminum (Fig. 17). They cleaned a short stretch of shoreline including 12 beaches. Trash issues on islands, atolls, archipelagos, as well as in freshwater and across oceans, are an ever growing concern worthy of mention here.

Summary

The papers in the Islands and Atolls section take a new look at the distribution of global islands, revisit island biogeography, describe some geographic areas in great depth, and discuss complex histories, the potential effects of sea level rise and storm surges, and uncertain futures. The papers here provide an overview of complex and rich biogeography of the *Islands and Atolls of the World*.

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Global Islands

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Abstract

A new map of global islands at a high spatial resolution (30 m) has been produced from a semi-automated interpretation of 2014 satellite imagery. The data are available in the public domain. The islands were classified by size into continental mainlands (5), big islands $> 1 \text{ km}^2$ (21,818), and small islands $\leq 1 \text{ km}^2$ (318,868). The new high-resolution islands data are intended to support coastal ecosystem mapping efforts and assessments of threatened island biodiversity, among other applications. This chapter summarizes the global island mapping approach and results.

Islands vary greatly in shape, size, and composition, from small, virtually lifeless rocky outcrops to continental-scale landmasses teeming with life. If an island is simply defined as an area of land surrounded by water on all sides, then all the landmasses on Earth are considered islands, regardless of size. Due to their geographic isolation, islands often have high levels of endemism ([Whittaker and Fernández-Palacios, 2007](#)) and are often considered as important candidates for biodiversity conservation efforts, especially since extinctions and other biodiversity losses on islands are disproportionately more rapid ([Spatz et al., 2017](#)). It is therefore important to understand exactly how many islands there are on Earth, where they are located, how big they are, what biodiversity they contain, and what condition their ecosystems are in.

Many attempts have been made throughout history to map and characterize Earth's islands, but a definitive characterization is still lacking. With the help of increasingly high-resolution satellite imagery and geographic information system (GIS) processing, our understanding of global island geography has improved. A new map of global islands ([Sayre et al., 2018, 2019](#)) was recently created from 30 m spatial resolution, 2014 composite Landsat satellite imagery. The islands data were produced by the U.S. Geological Survey (USGS) and Esri under a commission from the intergovernmental Group on Earth Observations (GEO) to produce standardized, global ecological coastal units.

The GEO is a consortium of over 100 nations, which seeks to leverage the use of Earth observations to help solve societal challenges ([GEO, 2005](#)). One of GEO's initiatives is the development of a standardized, robust, and practical map of global ecosystems for terrestrial, freshwater, and coastal/marine environments ([Sayre et al., 2007](#)). The USGS is the designated federal agency implementing the GEO initiatives in a public/private partnership with Esri. Terrestrial ecosystem distributions were delineated using a structure-based mapping approach, where ecosystems were produced from the integration of data on climate regime, landforms, substrate, and land cover ([Sayre et al., 2014](#)). Subsequently, oceanic marine ecosystems were systematically mapped into volumetric regions based on ocean physical and chemical characteristics ([Sayre et al., 2017](#)). The resolution of the marine ecosystem mapping effort was sufficient for the open ocean but did not accurately characterize the coastal zone and its associated ecosystems. The USGS/Esri team therefore decided to develop an additional map for global coastal ecosystems.

For coastal ecosystem mapping, globally-consistent, high-resolution global shoreline vector data were needed. Annual composite 2014 Landsat satellite imagery was classified into two feature classes, land and ocean, using a semi-automated approach. An analyst manually identified thousands of training points from all of the planet's coastlines by visual inspection. These points were then used in a computer-based classification to delineate a new global shoreline vector. Antarctica was not included in the analysis, in part due to the difficulty in separating ice features from land features. During the automated classification step, a minimum mapping unit of four contiguous 30 m Landsat pixels was used, so islands smaller than the 3600 m^2 threshold were not identified and were therefore not included in the new global islands resource. A full description of the image-based island extraction methodology can be found in [Sayre et al. \(2018\)](#).

The resulting dataset contains 340,691 polygons, five of which represent the five continental mainlands of North America, South America, Africa, Eurasia, and Australia. North and South America were algorithmically separated by the Panama Canal, and Eurasia and Africa were similarly separated by the Suez Canal. For the remaining polygons, those larger than 1 km^2 are attributed as "big islands" and those smaller than 1 km^2 are attributed as "small islands." The new map of global islands is depicted in [Fig. 1](#), and the results from the size class analysis are presented in [Table 1](#).

Since this new set of island features was derived from primary interpretation of satellite imagery, the polygons initially lacked attribute information. Island name was considered the priority attribute field for development, and a three-phase island naming

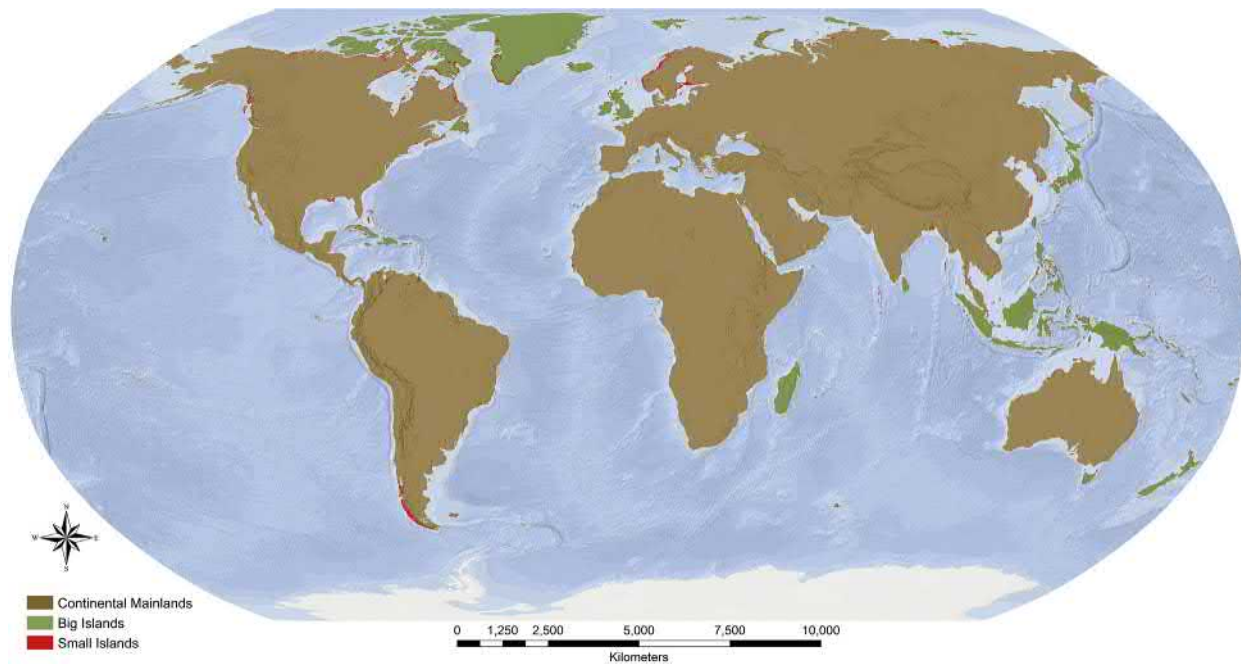


Fig. 1 Map of global islands. Continental mainlands are depicted in brown, islands bigger than 1 km² (big islands) are depicted in green, and islands smaller than 1 km² (small islands) are depicted in red. Note that the small islands, normally not visible at this map scale, are depicted here with exaggerated symbology (heavier outlines) to permit visualization.

Table 1 Number, total collective area, and coastline length for islands in three size classes.

Landmass type	Number of polygons	Area (km ²)	Length of coastline (km)
Continental mainlands	5	125,129,046	813,467
Islands > 1 km ²	21,818	9,938,964	1,304,762
Islands ≤ 1 km ²	318,868	20,589	321,774

Reproduced from Sayre R, Noble S, Hamann S, Smith R, Wright D, Breyer S, Butler K, Van Graafeiland K, Frye C, Karagulle D, Hopkins D, Stephens D, Kelly K, Basher Z, Burton D, Cress J, Atkins K, Van Sistine D, Friesen B, Allee R, Allen T, Aniello P, Asaad I, Costello M, Goodin K, Harris P, Kavanaugh M, Lillis H, Manca E, Muller-Karger F, Nyberg B, Parsons R, Saarinen J, Steiner J, and Reed A (2018) A new 30 meter resolution global shoreline vector and associated global islands database for the development of standardized ecological coastal units. *Journal of Operational Oceanography* 12: S47–S56. <https://doi.org/10.1080/1755876X.2018.1529714>.

process was initiated. The first phase was to manually name the 1000 largest islands in the United Nations Environment Programme (UNEP) Islands Directory (Dahl, 1991). Esri's WorldImage Basemap®, Open Street Map®, and Google Maps® were used as sources of information to manually identify names for these 1000 largest islands. While naming these islands, an additional ~2000 islands were opportunistically named and labeled because it was expedient to do so while zoomed in on a particular map extent with clusters of islands. At the end of this phase, 3156 big islands and 686 small islands were named. This process was considered accurate but very time-intensive.

For more efficient name attribution, an automated approach was used for phase 2. The island polygons were intersected with the GeoNames data, which are freely available point-based data containing geographical place-names for a variety of features including islands (<https://www.geonames.org/>). The phase 2 effort to match island polygon centroids with GeoNames data points resulted in the naming of an additional 5340 big islands and 12,253 small islands. While the automated naming approach was successful in assigning thousands of island names, over 60% of the big island polygons and 99% of the small island polygons still lacked name attributes at the end of phase 2.

During phase 3, the naming of small islands was discontinued due to the enormity of the effort, which would have required manually identifying names for the remaining ~305,000 small islands. For the remaining ~13,000 big islands, a return to the manual naming approach was implemented, again using Esri's WorldImage Basemap®, Open Street Map®, and Google Maps® as the source information for island names.

While developing name attributes, several conventions were used. First, only the proper noun, in English, was considered, and the descriptor "island" was not used. For example, the polygon representing Hilton Head Island in South Carolina, USA, was given a name attribute of "Hilton Head," not "Hilton Head Island." At times, this rule was sometimes difficult to enforce especially with non-English names, and exceptions to the convention were made. For example, for Isla Saona, a Dominican Republic island, the

English equivalent would be Saona Island, which would then be attributed as Saona. However, the island is universally referred to as Isla Saona, by English speakers and non-English speakers, so the name was therefore attributed as Isla Saona. For the same reason, the name Isle of Man was retained as is.

Only the 26 letters of the English alphabet (ISO basic Latin alphabet) were used. Diacritical marks, like accents, cedillas, tildes, and umlauts, were eliminated such that all names have been reduced to the simplest possible English language formulation. The attribute "UNNAMED" was given to island polygons when a name was lacking or not available in English, but it is recognized that there are very few islands on the planet that are, in reality, unnamed. Many fluvial islands, difficult to identify in the first place due to frequent change in their size, shape, and location, were also attributed as UNNAMED.

For easy access to and visualization of the integrated global coastal data, a web-based query and exploration tool called the Global Islands Explorer (<https://rmgsc.cr.usgs.gov/gie>) was developed. This tool allows anyone with access to the internet to zoom in on any island of interest and inspect its shoreline polygon on top of a number of backdrops (as in Fig. 2). The full set of polygons in the global island dataset is also available for download at the Global Islands Explorer website.

Future work and new collaborations are in development to improve the Global Islands data. Existing linework is being inspected for accuracy and needed improvement, and the potential for additional attribution is being evaluated using data from the UNEP World Conservation Monitoring Centre (WCMC) as well as a set of ~3000 islands that have been extensively characterized through invasive species and biodiversity conservation work (Spatz et al., 2017). The WCMC resource includes additional island polygons for islands smaller than the 3600 m² minimum mapping unit that are being added to the Global Islands resource.

In conclusion, a new set of some 340,000 global islands has been objectively and transparently developed and is freely accessible in the public domain as GIS polygon features. The resource facilitates an understanding of global island geography. Work is underway to improve the resource in terms of adding additional islands, improving linework, and enriching attribution.

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.



Fig. 2 Island polygons for St. Thomas, U.S. Virgin Islands, and surrounding islets. Island polygons for islands with an area $> 1 \text{ km}^2$ are shown with green outlines, and islands with an area $\leq 1 \text{ km}^2$ are shown with red/orange coastlines. The island polygons are shown on top of satellite imagery, where the fit of the shoreline linework to the shoreline discernible in the imagery can be visually inspected

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Island Biogeography Revisited

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Abstract

For centuries, naturalists have been intrigued by islands. Patterns in island biodiversity are the basis for fundamental theories in ecology such as island biogeography theory (IBT). Under this theory, the biodiversity of islands is a function of three processes: immigration, evolution and extinction. Immigration from source pools and subsequent evolution adds biodiversity to islands. Evolution allows immigrants to adapt to island habitats and evolve into new species. In contrast, extinction subtracts species. In a natural context, these three processes are a function of island area and isolation. Larger islands have more immigration, more evolution, and less extinction and thus more biodiversity than smaller islands. Isolated islands have more evolution, but less immigration and higher extinction resulting in lower biodiversity than proximate islands. Understanding how geography influences these three processes is the focus of IBT. Here, we review the history of island biogeographic study, discuss main themes of IBT, and place IBT in the context of the Anthropocene where humans are greatly impacting island immigration, evolution and extinction.

What Is Island Biogeography?

Biogeography is the study of the processes that determine the spatial and temporal distributions of organisms and their attributes across the earth (Lomolino et al., 2017). Biogeography focuses on understanding the geological, environmental, and historic factors that determine where biodiversity is and how it is different among regions. Geographic regions are defined by physical characteristics such as mountains, climate, or water. The boundaries among regions are not always well defined and can be broad gradients that are a mix of physical characteristics between neighboring regions. However, the boundaries of islands are well delineated because they are surrounded by water making them one of the most distinct type of region.

Island biogeography is the geographic study of the terrestrial, aquatic, and marine biodiversity of islands. Island biogeography is in part determined by island type. There are two natural types of islands: “continental” and “oceanic.” Continental islands reside on the continental shelf and were once connected to the continental mainland. They are often proximate to the continental mainland and as a result have many organismal groups in common with the mainland. Continental islands can be large in area such as Madagascar and Cuba. In contrast, oceanic islands are small, reside on the oceanic crust, and are mostly volcanic in origin. Atoll islands are coral reefs that have grown on top of submerged oceanic islands. Oceanic islands are often found distant from the mainland, and as a result, they are naturally isolated from the mainland and have only those species that are able to disperse long distances overwater (Helmus and Behm, 2018).

Today, island biogeography must be revisited to account for a third type of island: “artificial.” Artificial islands are made by draining water from seafloors or from pilling dredged sediment and sand onto seafloors and submerged coral reefs, which can have substantial impacts to marine species (e.g., de Groot, 1979). Artificial islands can vary considerably in their isolation from the mainland, but both continental and oceanic islands tend to be larger than artificial islands. Little is known about the biodiversity of artificial islands, but most of the species are likely introduced by humans.

History of Island Biogeography

For centuries, naturalists have studied island biogeography (Lomolino et al., 2004). Carl Linnaeus (1707–78) speculated that oceans once covered the earth except for a tall mountain range that formed an island close to the equator where all species on earth were created to match different altitudinal environments on the island. As water receded, the immutable species spread to fill earth’s different environments. In opposition to Linnaeus’s speculation, his contemporary Georges-Louis Leclerc Comte de Buffon (1707–88) amassed volumes of information on species distributions and found that regions with similar climate and environments

do not have the same plants and animals—as they would in Linnaeus’s argument—instead they have distinct plants and animals indicating that species change. This concept became known as Buffon’s law and was reaffirmed by other naturalists such as Joseph Banks (1743–1820) and Johann Reinhold Forster (1729–98) who circumnavigated the globe with James Cook cataloging geographically distinct species while comparing islands and the mainland. Forster was one of the first to describe positive species-area and negative species-isolation relationships; that is, the tendency of the number of species to increase as island area increases and decrease as island isolation from the mainland increases (Forster, 1778). The documentation of all these patterns led to the realization that life evolves in response to geographic and environmental factors.

Charles Darwin (1809–82) and Alfred Russel Wallace (1823–1913) independently conceived the theory of evolution by natural selection by observing island biodiversity. As evidence for evolution, Darwin argued that island species were more taxonomically similar to species on the closest continent even if the environment of that continent was different from the island. He wrote: “. . . there is a considerable degree of resemblance in the volcanic nature of the soil, in climate, height, and size of the islands, between the Galapagos and Cape de Verde Archipelago: but what an entire and absolute difference in their inhabitants! The inhabitants of the Cape de Verde Islands are related to those of Africa, like those of the Galapagos to America. I believe this grand fact can receive no sort of explanation on the ordinary view of independent creation” (Darwin, 1859). Alfred Russel Wallace independently devised the theory of evolution based in part on his work in Malay Archipelago. He identified a taxonomic divide located in the Malay Archipelago that delineates species derived from Southeast Asia vs. Australia due to past land connections when sea level was lower (Wallace, 1860). His book *Island Life* (Wallace, 1880) was the first comprehensive volume on island biogeography. It included a worldwide survey of island species and distinguished the two classes of islands, oceanic and continental, and how they differ in isolation. He argued that because oceanic islands are isolated from the mainland, they are colonized only infrequently by species that can immigrate over water. In contrast, continental islands are less isolated because they were once connected to the mainland and as a result have more species that are related to those of the mainland including species that did not need to colonize over water (e.g., large mammals).

Immigration, Evolution, Extinction

These early naturalists identified three fundamental processes that determine island biogeography: immigration, evolution and extinction (Lomolino et al., 2009). Species immigrate to islands by dispersing, often overwater, with some species groups more likely to disperse than other species groups (e.g., birds vs. frogs). Because the species that have immigrated to islands are often isolated from their source populations, island species evolve both by adapting to island life and randomly diverging from their source population (genetic bottleneck and drift). Finally, species naturally go extinct from islands as geography and the environment change.

Nearly a century after the early naturalists’ fundamental work on island biogeography and evolution, Robert H. MacArthur and Edward O. Wilson formulated a theory of island biogeography (IBT) based on immigration, evolution, and extinction and how they are determined by island area and isolation (MacArthur and Wilson, 1963; MacArthur and Wilson, 1967; Wilson, 1969). According to the theory, the biodiversity on an island is determined by immigration to the island followed by evolutionary adaptation to the island and subsequent extinction of that biodiversity. For simplicity, the measure of biodiversity often used is species richness (i.e., number of species). Immigration increases island species richness, and evolution, if it leads to vicariant speciation (i.e., the splitting of one species into two species), also increases species richness. Extinction of species from the island reduces species richness. Under IBT, the rates of these processes are determined by island area and isolation (Fig. 1). While other geographic and environmental factors such as island elevation, latitude, age, and habitat heterogeneity certainly influence island biodiversity; area and isolation are

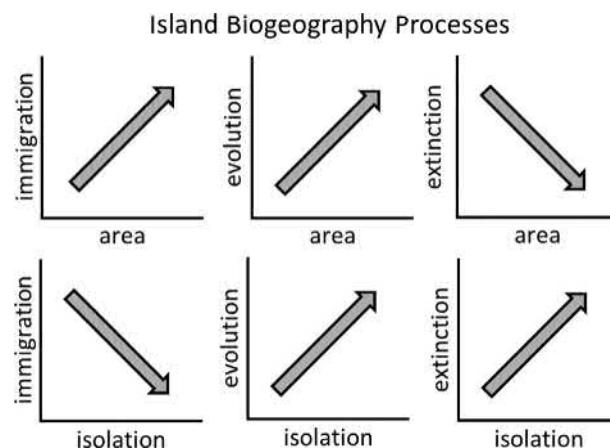


Fig. 1 Island biodiversity is determined by three fundamental biogeographic processes: immigration, evolution, and extinction. These three processes vary with island area and isolation from source pools of immigrants. Arrows depict relationship direction.

still considered the most important explanatory factors (Whitehead and Jones, 1969; Heaney, 2007; Whittaker et al., 2008; Warren et al., 2015).

Island Area and Isolation

Island area is typically defined as the amount of two-dimensional terrestrial surface area, and it affects all three biogeographic processes. Larger islands have more immigration because larger islands are a larger target for dispersing individuals to land. Larger islands have more resources, habitats and space for populations to evolve and speciate. Similarly, extinction is lower on larger islands because there are more resources and space for populations to grow large and be less prone to stochastic extinction events (Fig. 1).

Island isolation is defined by an island's distance from potential sources of colonists. Common metrics of isolation range from simple metrics of just the distance to the nearest continent, or more complex metrics that include distances to larger islands, island groups, or prevailing currents (Weigelt and Kreft, 2013). Like area, island isolation affects all three biogeographic rates (Fig. 1). The primary influence of isolation is on immigration rates whereby isolated islands tend to have lower immigration than proximate islands. Evolution is also higher on more isolated islands because colonists are isolated from gene flow from the source population and thus evolve independently (Heaney, 2000; Pinheiro et al., 2017). Extinction is also higher on isolated islands because populations on isolated islands cannot be rescued from extinction by immigration from source populations (Brown and Kordic-Brown, 1977).

According to IBT, the maximum number of species that an island can contain is called its saturation point. This point is determined by island area and the number of species in the species pool; that is, the total number of species that could potentially colonize the islands. Due to speciation and extinction occurring in source areas, island species pools are not static. In the extreme case, all species from the pool can immigrate to and establish on an island, but this is never the case in nature. The saturation points of islands are determined by island area with larger islands having higher saturation points than smaller islands because larger islands have higher immigration, higher evolution that leads to vicariant speciation, and lower extinction.

Island isolation determines how close an island of a given size is to its saturation because isolated islands have lower immigration and higher extinction. When the effects of area and isolation on the three rates are in balance, then the island is said to have reached its equilibrium point. In the Anthropocene, humans are modifying immigration, evolution and extinction and shifting island equilibrium points.

Immigration Is Higher Due to Human Introductions

The rate at which nonnative, exotic (i.e., alien) species are being introduced to islands is increasing. The richness of birds, mammals, lizards, plants and invertebrates have all greatly increased on islands (Sax et al., 2002; Dawson et al., 2017). Exotic species have been introduced both intentionally and unintentionally by humans to islands for centuries, but today due to global trade, exotic immigration rate is currently the highest ever seen, and the species that are immigrating are coming from long distances.

By introducing exotic species at higher rates, humans are essentially decreasing island isolation (Helmus et al., 2014; Moser et al., 2018). For example, while the richness of native anole lizards in the Caribbean is lower on isolated islands, the richness of exotic anoles is higher on isolated islands. This is expected according to IBT because isolated islands should be farther from their saturation point and can thus gain more species than less-isolated islands closer to their saturation points when immigration rate increases. Human introduction of anole species has essentially increased anole immigration rate. Today, instead of geographic isolation limiting exotic immigration, it is economic isolation. Economic isolation is measured as the degree that islands are connected to human trade such as shipping traffic. In the Caribbean, islands that are the least connected by shipping trade have the lowest immigration rates of exotic anole species (Helmus et al., 2014).

By introducing exotic species from long distances, humans have expanded the potential species pool of immigrants (Seebens et al., 2018). In the past, species mostly immigrated to islands from the nearest mainland or from nearby islands. For example, the Caribbean has many native gecko lizard species found across all the islands. Like most Caribbean reptiles, most native gecko species of the Caribbean are derived from South America (Hedges, 2006). Today, the Caribbean has been colonized by several exotic gecko species, many from tropical Asia, Africa and the Mediterranean. The long-distance immigration of the exotic geckos began during European colonialism that moved many people and products among hemispheres essentially expanding the species pool of geckos for Caribbean islands (Perella and Behm *in review*).

Evolution in Response to Human Impacts

Human impacts are a strong selective force acting on native island biodiversity. Humans alter species interactions by introducing species and altering habitats by removing native vegetation, building structures and transforming landscapes. If native species can evolve in response to these impacts, then they are less prone to extinction. However, island species are considered to have less

adaptive genetic variation than mainland species thus reducing their potential for evolution (Frankham, 1997). Regardless, native species on islands have been shown to adapt to human impacts.

Introduced species are a major force that drives evolution on islands (Mooney and Cleland, 2001; Strauss et al., 2006). For example, the mosquito *Culex quinquefasciatus* is a vector for avian malaria (*Plasmodium relictum*). Both were introduced to the Hawaiian Islands in the 1800s (Atkinson and LaPointe, 2009). The introduction of this disease greatly decreased native bird populations particularly Hawaiian honeycreepers, but this decrease acted as a selective force driving resistance to the disease in amakihi honeycreepers (Foster et al., 2007). Other examples of evolution of native island species in response to introduced species include native island plants that have evolved resistance to introduced herbivores (Vourc'h et al., 2001) and lizards that evolved different behavior and morphology in response to the introduction of lizard competitors and predators (Losos et al., 2006; Stuart et al., 2014). Introduced species also evolve following introductions to islands. For example, introduced plants have evolved reduced dispersal ability on islands similar to the reduced dispersal ability seen in native island plants (Cody and Overton, 1996) and introduced plants often adapt to novel island habitats (e.g., Dlugosch and Parker, 2008). Similarly, introduced lizards adapt their morphology in response to the novel habitats provided by islands (Herrel et al., 2008).

While introduced species can adapt to island habitats, resident island species also adapt to human alterations to their habitat. Urbanization is a strong selective force on islands (Johnson and Munshi-South, 2017). For example, *Anolis cristatellus* lizards on Puerto Rico naturally perch and climb on trees, but in developed areas of the island, lizard phenotypes have shifted to be better adapted to perch on human structures such as tiled walls (Winchell et al., 2018). *Aedes albopictus* mosquito populations in urban areas on Réunion Island are genetically differentiated from forested areas; urban areas provide human hosts and larval development sites that are different from unpopulated and undeveloped forested areas (Delatte et al., 2013).

We hypothesize that evolution of native island species in response to human impacts should be higher on larger islands and lower on isolated islands. The rationale for this hypothesis is on how area and isolation naturally affect island biodiversity. Larger islands have species with larger population sizes, thus species on large islands on average should have more phenotypic and genetic variation on which evolution can act and have more refuge from human impacts that provide time for adaptations. In contrast, smaller islands have smaller populations with less variability and less refugia from human impacts especially if those impacts are island wide. Isolated islands have low native biodiversity derived from few immigration events that can cause genetic bottlenecks that reduce adaptive genetic variation. Further, the biodiversity on isolated islands has often evolved in the absence of intense predation, herbivory and disease. Antipredator and other defenses are energetically costly and are lost from island populations released from such antagonistic interactions; a process termed the evolution of island-tameness. As a result, the ability to withstand and adapt to human impacts such as introduced predators before going extinct should be lowest on isolated islands. While the influence of island area and isolation on evolution in the Anthropocene has not been well studied, one example exists. Populations of Aegean wall lizards (*Podarcis erhardii*) across the Greek Cyclades are more tame on small and isolated islands that do not have introduced predators, while those with predators are less tame (Brock et al., 2015).

Human-Caused Extinction Is Higher on Islands

Islands make up only about 5% of the total land area on earth, yet over 60% of all known human-caused extinctions come from islands (Tershy et al., 2015). Island species are more threatened with extinction than mainland species, and much of this extinction is due to invasive predators such as cats and rats (Blackburn et al., 2004; Medina et al., 2011; Spatz et al., 2017). Island extinctions have been occurring throughout human history. For example, one of the best-known extinctions is the dodo bird once found only on the island of Mauritius. This bird was large and unafraid of humans and did not have natural defenses to predators. As a result, when Europeans colonized the island, they drove it to extinction through hunting and by introducing mammals such as cats and rats that fed on dodo eggs and chicks (Fuller, 2004). Bird extinctions on islands have been high. Polynesian colonization of the Hawaiian Islands precipitated the extinctions of several bird species due to introduced mammals, hunting, and deforestation, but then European colonization brought a second round of bird extinctions (Boyer, 2008). Similarly, extinction on Madagascar had been in two phases. First, prehistoric human colonization coincided with the extinction of giant lemurs and other megafauna, and today, resource extraction and illegal deforestation and hunting are causing Madagascar to have one of the highest extinction rates on earth (Burney, 2004; Perez et al., 2005; Jones et al., 2019).

The effect of island isolation on extinction is clear. Isolated islands have higher Anthropocene extinction rates than less isolated islands. This is thought to be due to genetic bottlenecks, island tameness, and increased island endemism that increases extinction susceptibility on isolated islands. In contrast, the effect of area on extinction rate is less clear. Smaller islands naturally are theorized to have higher extinction rates, and many small islands have seen high extinction rates. However, because larger islands have more endemic species and more people, larger islands also can have very high extinction rates. This unclear effect of area on extinction may be due to when extinction rate is determined, in the past or in the present. For example, birds that have already gone extinct disproportionately come from small islands, but birds that are threatened with extinction currently are more likely to be found on larger islands (Blackburn et al., 2004).

Island Biogeography Revisited for the Anthropocene

Like past biogeographers who built upon the research of early naturalists, today's researchers of island biogeography build upon vast amounts of published data. Many of the studies on island biogeography in the Anthropocene aggregate large data sets (e.g., Blackburn et al., 2004; Helmus et al., 2014; Moser et al., 2018; Silva-Rocha et al., 2019). These studies have identified three major trends that make it necessary to revisit island biogeography. First, island equilibrium points are increasing in the Anthropocene. While extinctions on islands are high, the number of introduced species on average is much greater than the number of extinct native species. Second, island evolutionary history is being obscured in the Anthropocene. Area and isolation created measurable evolutionary signatures on island biota, but native species are adapting to human impacts and introduced species are from new evolutionarily distinct species pools. Finally, economic geography has become more important than physical geography in determining island biogeography. The economic isolation of islands now determines immigration rates more than geographic isolation, while the level of development and habitat loss for agriculture and resource extraction that an island undergoes determines extinction rates. We do not know exactly what island biodiversity will look like in the Anthropocene, but what is clear is that it will differ from the natural biogeography of the past.

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Island Biogeography of Marine Shallow-Water Organisms

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Abstract

Marine shallow-water habitats include reefs, sand beaches, kelp forests, estuaries, and others, which have a high biological and economic importance. The study of island biogeography has uncovered the processes shaping species distribution patterns and have recently expanded to encompass the marine realm. In this article we provide an overview about marine shallow-water island biogeography. We explore the taxonomic and functional marine island biogeography, considering islands area, isolation, and geological age, as well as scale and taxon-dependency. We then discuss endemism patterns and speciation in remote marine systems and conclude with a discussion about methods of studying island biogeography in such habitats.

Introduction

Marine shallow-water habitats are normally considered as those within the neritic zone (littoral and sublittoral), typically extending to the edge of the shelf. In continental shelves this can reach as down as 200 m depth, although the shelf-break in islands generally occurs on shallower depths (Lalli and Parsons, 1997). These shallow-water habitats include reefs (rocky, biogenic or artificial), sand beaches, kelp forests, and estuaries (including marshes and mangroves; Fig. 1). The latter, although brackish, is closely associated with the sea and can be considered the most productive of the marine systems (Hemingson and Bellwood, 2018).

These marine shallow-water habitats have high biological and economic importance. For instance, marine shallow-water habitats are occupied or visited by 34 of the 35 extant animal phyla, and half of them are exclusively marine (Carr et al., 2003). Notwithstanding, they provide services as coastline protection, food production, nitrogen fixation, carbon dioxide sink, within others (Moberg and Folke, 1999; Holmlund and Hammer, 1999). But, besides its importance, the comprehension of most of these systems remains poor when compared to terrestrial and freshwater systems (Field et al., 2008).

Island biogeography, as a science that studies biodiversity distribution through the globe, has advanced our knowledge about the processes shaping species distribution patterns, and how physical and biological aspects of islands and species interfere on such patterns. The theories of island biogeography were initially built upon terrestrial island systems and have been extended to marine systems more recently (Hachich et al., 2015; Pinheiro et al., 2017; Ávila et al., 2019).

In this article we explore marine island biogeography through the perspective of shallow-water organisms. Our overall goal was to provide an overview of processes and patterns related to marine shallow-water island biogeography, considering taxonomic and functional biodiversity, as well as scale and taxon-dependency. We start by briefly presenting the most prominent island biogeography theories. This sets a theoretical background for the discussion of differences between terrestrial and marine island biogeography. We then present the state of art for taxonomic marine island biogeography, considering species-area, species-isolation and species-age patterns, as well as the applicability of more complex models on explaining marine shallow-water species richness distribution. The next section includes the discussion about marine island biogeography related to the functional component of diversity. We then proceed giving more emphasis to speciation and endemism patterns in marine systems, and finish with a brief discussion about methods of studying island biogeography in such habitats. Although reefs are by

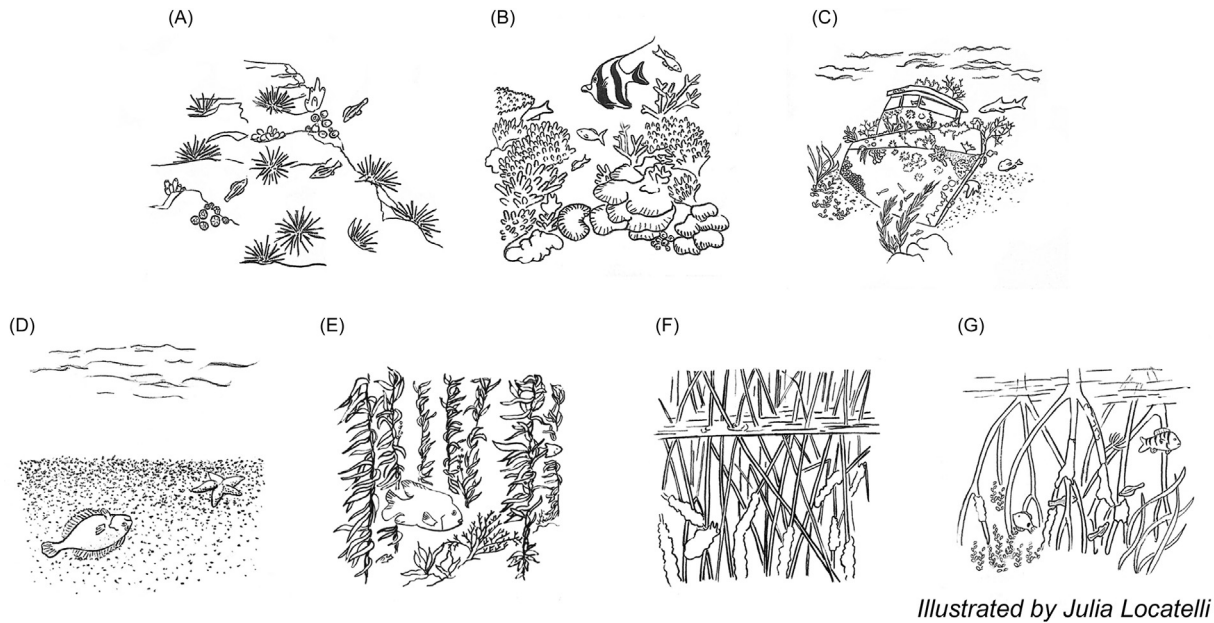


Fig. 1 Marine shallow-water habitats: (A) rocky reef, (B) coral reef (biogenic), (C) artificial reef, (D) sand beach, (E) kelp forest, (F) marsh, (G) mangrove. Illustrated by Julia Locatelli.

far the most well studied marine shallow-water habitats, as are reef fish, gastropod and seaweed the most well studied marine shallow-water groups, examples on other shallow-water habitats and taxa were brought to light whenever as possible.

Classical Theories of Island Biogeography: Predicted Patterns

The Theory of Island Biogeography (IBT) predicts a variation of species richness with island area and isolation ([MacArthur and Wilson, 1967](#)). According to the IBT, the species–area relationship (SAR) is due to larger habitat heterogeneity, that results on lower extinction rates and therefore, higher species richness maintenance. At the same time, such richness is expected to decrease as a function of island isolation, due to reduced immigration rates.

Further studies of island biogeography also pointed for an increase in species richness with island geological age due to longer times for species accumulation either by arrival of new immigrants or arise of a new species by speciation ([Rosenzweig, 1995](#)). The General Dynamic Theory of Oceanic Island Biogeography (GDM; [Whittaker et al., 2008](#)) also included island age as an important factor for predicting islands species richness, combined with island area. The explanation for the GDM also relies into the interaction between immigration, speciation and extinction rates. According to the GDM, species richness would increase linearly with island area, but would vary as a unimodal function of island age, due to the variation of habitat heterogeneity in the life cycle of an oceanic island. Such islands, which are mainly volcanic, tend to increase in area and height in their youth, due initially to volcanic activity and latter to erosion (that also increases habitat heterogeneity). An advanced stage of erosion leads to loss of habitats—increasing extinction rates—and, in older stages, the disappearance of the island, turning into an atoll or seamount, sinking into the sea.

Besides the influence of island area, age and isolation in species richness, it is also expected for those environmental variables to affect the level of endemism in islands. In the terrestrial realm, bigger islands are expected to show increased numbers of endemics, given the possibility of diversification driven by sympatric and ecological speciation—a process known as adaptive radiation. Older islands are also expected to show increased levels of endemism, due to longer times for cladogenesis. Notwithstanding, isolated islands shall exhibit increased percentage of endemic species as well, due to reduced gene flow.

The processes that influence biodiversity distributions on terrestrial and marine realms—i.e. immigration, speciation and extinction—although the same, interact differently and vary differently with such island physical features (area, isolation and age), leading to differences on island biogeography patterns.

Island Biogeography Patterns and Process of Marine Shallow-Water Organisms

Understanding island biogeography patterns for marine shallow-water organisms is key for the conservation of marine systems. For example, the richness patterns of reef fishes, corals, marine snails and lobsters are concordant across the globe and such richness is mainly concentrated in islands, with a predominance of their centers of endemism in the most isolated ones ([Roberts et al., 2002](#); [Tittensor et al., 2010](#); [Fig. 2](#)).

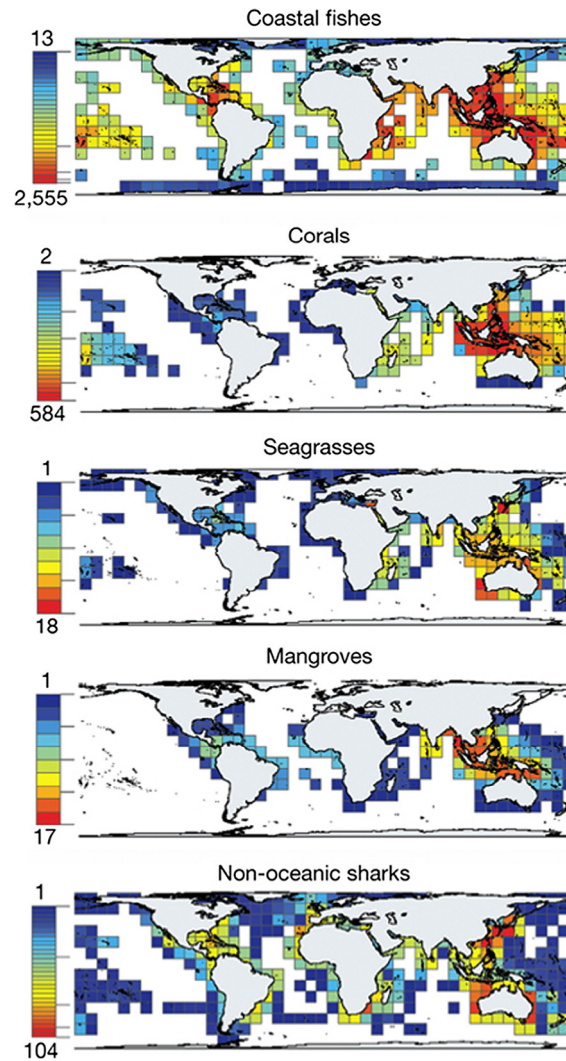


Fig. 2 Distribution of different marine shallow-water taxa across the globe. For seagrasses and mangroves only plant species were considered. Figure from Tittensor, D. P., Mora, C., Jetz, W., et al. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**, 1098–1103.

Yet, although the term biodiversity was originally related to the number of biological species units solely (Wilson and Peter, 1988), on a broader concept, biodiversity could embrace any variety of life. Moreover, the study of the diversity of species ecological traits and evolutionary history contributes to elucidate the processes shaping the distribution of the marine shallow-water biota in islands (Cavender-Bares et al., 2009). For this reason, we discuss herein the island biogeography patterns relying not only on taxonomic metrics of biodiversity but also on a functional approach.

Taxonomic Approach

The taxonomic approach for community ecology is based on the species as the lower measurable unit of biodiversity. The most classical island biogeography theories, briefly presented above, were developed upon this concept.

Species–area relationship

With regards to the most accepted biogeography pattern—the species–area relationship (SAR)—an increase of species richness with area is observed as a multiscale general pattern in both terrestrial and marine systems. For shallow-water marine organisms, the SAR was already detected with multiple taxa, on multiple geographical regions and over multiple spatial scales. This fact strengthens the statement as the SAR being “one of community ecology’s few genuine laws” (Schoener, 1976). Although few variations were shown, the power-model seems to be the best to explain SAR in both marine and terrestrial systems (Hachich et al., 2015; Triantis et al., 2012).

On a global scale, evidences of SAR were observed for reef fish (Parravicini et al., 2013; Pérez-Ruzafa et al., 2005), molluscs and echinoderms (Pérez-Ruzafa et al., 2005). On an oceanic scale, an increase of species richness with area was evident in the Atlantic Ocean for reef fishes, gastropods, seaweeds (Fig. 3; Hachich et al., 2015, 2016) and echinoderms (Ávila et al., 2018), and for reef fishes and corals in the Indo-Pacific Ocean (Bellwood and Hughes, 2001).

At the scale of a biogeographic region, the SAR was evident for reef fishes in the Caribbean (Sandin et al., 2008), and for sponges in the Eastern Atlantic (Xavier and Van Soest, 2012). The variation in seaweeds species richness between islands in the same archipelago, in the Lusitanian Macaronesia region, that comprises Azores, Madeira, the Salvage and Canary Islands, also varied in function of islands area (Tuya and Haroun, 2009), and the patterns found were consistent when considering red, green and brown algae separately or the three groups together. At smaller scales, the SAR was also evident in marine systems; the richness of decapod crustaceans associated with coral in the Gulf of Panama increases in function of coral heads sizes (Abele and Patton, 1976), and the richness of sessile and mobile marine invertebrates increased with boulders sizes in New South Wales (McGuinness, 1984).

The main explanation for SAR is equivalent for terrestrial and marine systems: bigger islands are expected to hold greater habitat variability and maintain larger populations, experiencing lower extinction rates and sustaining higher species richness. The target effect explanation, in which larger islands are more prone to be reached by chance by a propagule, has also been evoked for marine island biogeography (Velasquez et al., 2018), although its effect can be only marginal (Ávila et al., 2018). However, the hypothesis of higher speciation rates on larger islands, seems not to be so important for marine organisms. Their larger dispersal capacity hamper intra-island allopatric speciation, so in situ cladogenesis is low. A study of endemic reef fish in the seamounts and islands

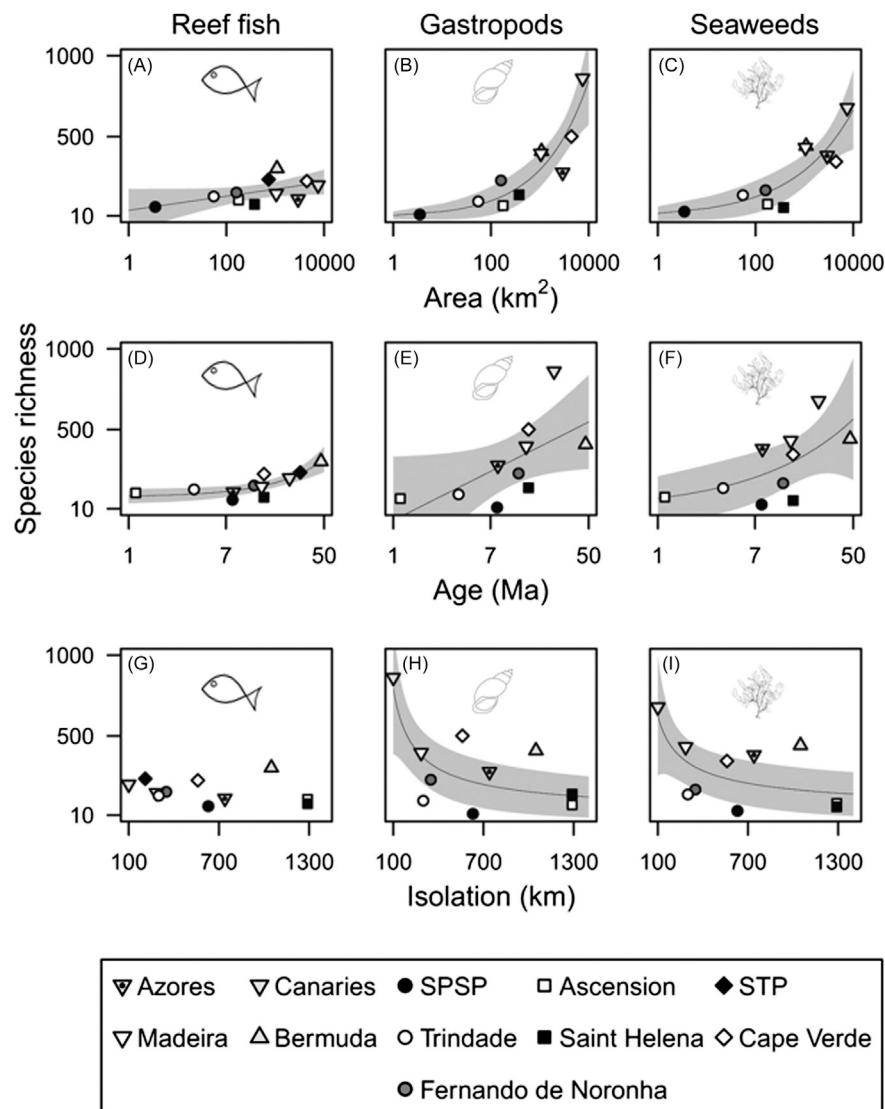


Fig. 3 Variation of marine shallow-water species richness with islands area (A–C), age (D–F) and isolation (G–I) for 11 oceanic islands in the Atlantic Ocean. Figure from Hachich N. F., Bonsall M. B., Arraut E. M., et al. (2016). Marine island biogeography. Response to comment on ‘island biogeography: Patterns of marine shallow-water organisms’. *Journal of Biogeography* **43**, 2517–2519.

of the Vitória-Trindade Chain (VTC), South-western Atlantic, showed evidences that speciation rates increased with the accumulation of species with low dispersal capacity, that suffered differentiation after immigration (Pinheiro et al., 2017). Speciation of marine shallow-water organisms in islands will be deeper discussed below.

Species–isolation relationship

The distribution of either marine or terrestrial organisms are influenced by geographical barriers, whose permeability is felt distinctively between the two realms. The seas represent a semipermeable matrix for the immigration of species to islands and the dispersion of organisms from one island to the other. For marine organisms such matrix is much easier to transpose than for terrestrial ones, mainly due to their resistance to water and salt. A study showed that terrestrial plants, which dispersal is within the widest from terrestrial groups, disperse one to two orders of magnitude less than sedentary marine species (Kinlan and Gaines, 2003).

Most marine shallow-water organisms, although sedentary when adults, have a planktotrophic larvae or other planktonic propagule stage on its life cycle. This capacity to live or even feed or photosynthesize while floating in the water surface favors dispersal through ocean currents (Thorson, 1949). Those marine organisms without a planktonic stage can have their dispersal facilitated through rafting. This is especially important for small-sized organisms that have the ability of attaching to migratory animals (e.g. birds or sea turtles) or drifting substrates (e.g. trunks or seaweeds). Rafting was shown to be an important mean of dispersal to marine shallow-water organisms through biogeographic barriers (Luiz et al., 2011). An overview on this subject pointed out for 946 species of marine invertebrates with clues of rafting (Table 1; Thiel and Gutow, 2005). The colonization of the reef fish *Chromis limbata* in the southern brazilian coast was probably a consequence of rafting of specimens from the Macaronesian region through the Atlantic Ocean—although other hypotheses are also discussed (Anderson et al., 2017), and the dispersal of the seastar *Patiriella exigua* is also suggested to occur via rafting on macroalgae (Waters and Roy, 2004).

Such wide dispersal capacity has implications to marine island biogeography. The IBT postulates that species richness is expected to decrease in function of island isolation due to reduced immigration rates. Although small coastal islands present higher diversity of reef fish species than larger oceanic islands (Pinheiro et al., 2015), for marine shallow-water groups, the species–isolation relationship seems to be not universal, but highly scale- and taxon-dependent (Fig. 3G–I). For example, in oceanic islands of the Atlantic Ocean the species-isolation pattern was detected for gastropods and seaweeds, but not for reef fishes (Fig. 3; Hachich et al., 2016) and echinoderms (Ávila et al., 2018). However, even for gastropods and seaweeds, the role of isolation on bounding species richness in the Atlantic islands seems to be secondary, as island area was by far the best model on explaining such richness variation (Hachich et al., 2015, 2016). On the other hand, at a smaller spatial scale, across the Lusitanian Macaronesia, seaweeds species richness decreases with distance from mainland when considering green, red or brown algae together or separately (Tuya and Haroun, 2009). Such variations in the influence of island isolation within marine shallow-water groups are also due to variations in species dispersal capacity. It was shown that while seaweeds dispersal ranges from few meters to 5 km, reef fish dispersal ranges from few to several hundreds of kilometers, and, finally, the dispersal of marine invertebrates varies from tens of meters to hundreds of kilometers (Fig. 4; Kinlan and Gaines, 2003).

Studies on large spatial-scale showed contrasting conclusions about the influence of isolation on reef fish species richness (Mora et al., 2003; Parravicini et al., 2013; Jacquet et al., 2017). The differences between these studies were their study area and the isolation metric used. Mora et al. (2003) included only the Indo-Pacific and showed a strong influence of the distance from the Coral Triangle (biodiversity center) on species richness. The two other studies spanned worldwide. Parravicini et al. (2013) found an extremely weak influence of isolation on reef fish species richness and used two measures of connectivity: (i) the relative proximity of each site to patches of reef fish habitat, using a nearest neighbor approach, and (ii) the distance of the site from the mid-domain, relative to the domain size. Finally, although Jacquet et al. (2017) showed a significant decrease of reef fishes with isolation ($p < 0.05$), they also showed that their isolation measure (based on nearest neighbor approach) was negatively correlated with reef area.

Those results highlight an important issue when investigating the influence of isolation on biodiversity, that is the measure of isolation used. Not only the distance to species sources and present ocean currents can influence connectivity between marine

Table 1 Number of species with evidence of rafting dispersal per marine invertebrate taxon.

<i>Taxon</i>	<i>Number of spp.</i>
Porifera	3
Cnidaria	131
Annelida	81
Mollusca	186
Arthropoda	398
Echinodermata	40
Ectoprocta	96
Chordata	11
Total	946

Data from Thiel, M., and Gutow, L. (2005). The ecology of rafting in the marine environment. II. The rafting organisms and community. *Oceanography and Marine Biology: An Annual Review* 43, 279–418.

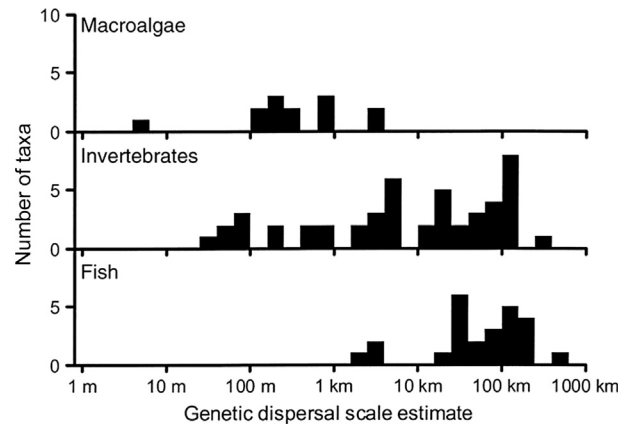


Fig. 4 Mean genetic dispersal distance estimates for marine benthic macroalgae (513 spp.), sessile and sedentary invertebrates (548 spp.) and demersal fish (525 spp.). Reproduced from Kinlan, B. P. and Gaines, S. D. (2003). Propagule dispersal in marine and terrestrial environments: A community perspective. *Ecology* **84**, 2007–2020.

habitats. Past ocean currents, presence of stepping-stones (islands and seamounts), sea level variation and distance to Quaternary coral reef refugia are other variables to be considered when studying marine shallow-water distributional patterns (Pellissier et al., 2014; Brown and Lomolino, 2006). The high species richness found in Trindade Island, for instance, is related to the presence of a seamount chain between the island and the continental coast, which was exposed during the low sea-level periods of the Pleistocene (Pinheiro et al., 2017; check the methodological caveat section for more examples).

Species–age relationship

The age of an island has also been shown to influence marine shallow-water species richness (although studies on marine species–age relationship are scarce). In a large-scale analysis of oceanic islands in the Atlantic, the species richness of seaweeds, gastropods and reef fishes were strongly correlated with islands geological age (Fig. 3). Moreover, when islands area, age and isolation were considered, age showed to be the best predictor of reef fish richness—although it was the worst predictor for seaweeds, reinforcing the taxon-dependency in marine shallow-water island biogeography patterns (Hachich et al., 2015). Still, the richness of epibiont species on pumice rafts also showed an influence of pumices age—measured as numbers of days since eruption (Velasquez et al., 2018).

The explanations for the marine shallow-water species-age patterns are equivalent for those of terrestrial biota, such as longer time for species accumulation by immigration and speciation (Hachich et al., 2015; Whittaker and Fernandez-Palacios, 2007). Moreover, the increase of island area through time (Whittaker et al., 2008; Ávila et al., 2019) can also intensify the relationship between islands age and species richness and will lie upon the life cycle of an oceanic island.

Multivariables models for species richness

The present geographical distribution of biodiversity in islands is expected to be a result of ecological, evolutionary and historical forces acting in different timescales. The GDM, explained above, is an attempt to incorporate to the IBT those processes operating in large timescales, and therefore, includes on a single model, island area and age as species richness predictors (Whittaker et al., 2008).

Although tests of this model proved it to be adequate for the terrestrial biota, it seems not to be satisfactory on explaining marine shallow-water biodiversity. For example, the GDM did not explain the richness variation of reef fish, gastropod, seaweed and echinoderm species in the Atlantic better than when considering only area or age as predictors variables alone (Hachich et al., 2015; Ávila et al., 2018).

To discuss the applicability of GDM to the marine realm with assertion, additional tests would be needed, including other taxa, biogeographic regions or spatial scales. Anyway, due to differences on the impact of island ontogeny on terrestrial and marine habitats, adaptations for the GDM model to embrace marine organisms are indeed necessary and are already being suggested. The main adaptation regards the influence of time in marine habitat area. As cited before, the GDM assumes that the erosion of islands enhances habitats heterogeneity on an initial stage, but drastically reduces it on advanced stages of erosion (Whittaker et al., 2008). However, longer times of erosion are needed for islands to reach a stage in which marine habitat heterogeneity starts to decrease, and so the species richness (Fig. 5). In fact, the seamount stage, achieved when islands are extremely old, is the one with greater marine area availability—but not necessarily the higher marine shallow-water species richness (Hachich et al., 2015; Pinheiro et al., 2017; Ávila et al., 2019).

The Vitória-Trindade Chain Model (VTCM; Pinheiro et al., 2017) and the Sea-Level Sensitive dynamic model (SLS; Ávila et al., 2019) are both models that comprise the effect of island ontogeny into marine systems processes, and show differences of predicted immigration, extinction and speciation rates if compared to the GDM. Those, in turn, result in differences on the estimated species richness and the system carrying capacity (Fig. 5). Notwithstanding, the SLS also comprises a more complex relationship of marine

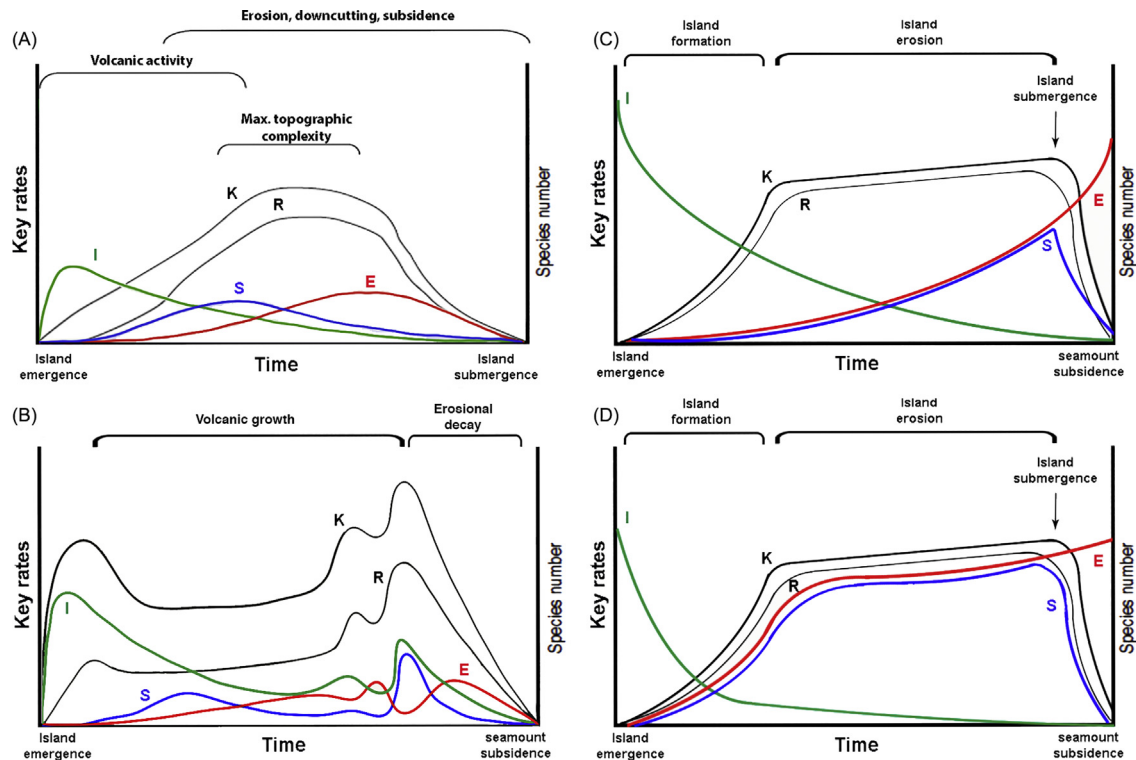


Fig. 5 Graphical representation of Immigration (I, green lines), Extinction (E, red lines) and Speciation (S, blue lines) rates of (A) the General Dynamic Model (GDM) of oceanic island biogeography; (B) the Sea-Level Sensitive (SLS) model of marine island biogeography; and (C, D) the Vitória-Trindade Chain general dynamic model (VTCM) of oceanic island biogeography for marine species, in which (C) immigration, extinction and speciation rates are only related with time (evolutionary history of the island—geological timescale) or (D) immigration, extinction and speciation rates are occurring in an ecological scale, strongly related to richness. For all models, K (black bold line) is the potential carrying capacity measured in species number, and R (black line) is the realized species richness. Adapted from Whittaker R. J., Triantis K. A., and Ladle R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* **35**, 977–994; Pinheiro, H. T., Bernardi, G., Simon, T., et al. (2017). Island biogeography of marine organisms. *Nature* **82**, 82–86. and Ávila, S. P., Melo, C., Berning, B., et al. (2019). Towards a 'sea-level sensitive' dynamic model: Impact of island ontogeny and glacio-eustasy on global patterns of marine island biogeography. *Biological Reviews of the Cambridge Philosophical Society* **94**, 1116–1142.

habitat heterogeneity and time, due to sea-level changes during glacial periods (Fig. 5; Ávila et al., 2019). Although neither the VTCM nor the SLS make predictions on how species richness must vary with islands features (such as area, age or isolation), they give important insights for the discussion of immigration, extinction and speciation rates of marine biota in islands (Fig. 5).

Functional Approach on Island Biogeography

The studies on biodiversity distribution patterns through time and space have originally considered only species richness as a measure of biodiversity (Gotelli and Colwell, 2001). The theories of island biogeography, for example, deal mainly with species counts. However, the foreseen equilibrium between immigration, extinction and (for some models) speciation rates, although predicts a stable species richness to be held by an island, also predicts a constant species turnover (MacArthur and Wilson, 1967; Whittaker et al., 2008). Little is known whether other biodiversity components than species richness would also remain constant or would vary through this turnover.

On relying on species richness solely, these theories consider species as being equivalent, disregarding their intrinsic features. Species phenotypic traits have been related to potential ecological functions played in the ecosystems (Mouchet et al., 2010). Such traits can be classified by morphological, behavioral and trophic characteristics (Mouillot et al., 2014). Through the combination of them—for example, body size, diet, and grouping behavior—it is possible to classify species on functional groups and, therefore, infer the community's functional richness.

Island systems show singular environmental features that could lead to nonrandom processes over its biota composition. Mechanisms like environmental filtering and competitive exclusion can favor functional traits by selective extinction (Si et al., 2017) or immigration (on the perspective of regional processes). The selective extinction or immigration caused by environmental filters would result on a higher functional similarity, that is, a functional clustering, while the selective extinction caused by competitive exclusion would result on lower functional similarity, that is, a functional overdispersion (Cavender-Bares et al., 2009; Si et al., 2017; Fig. 6).

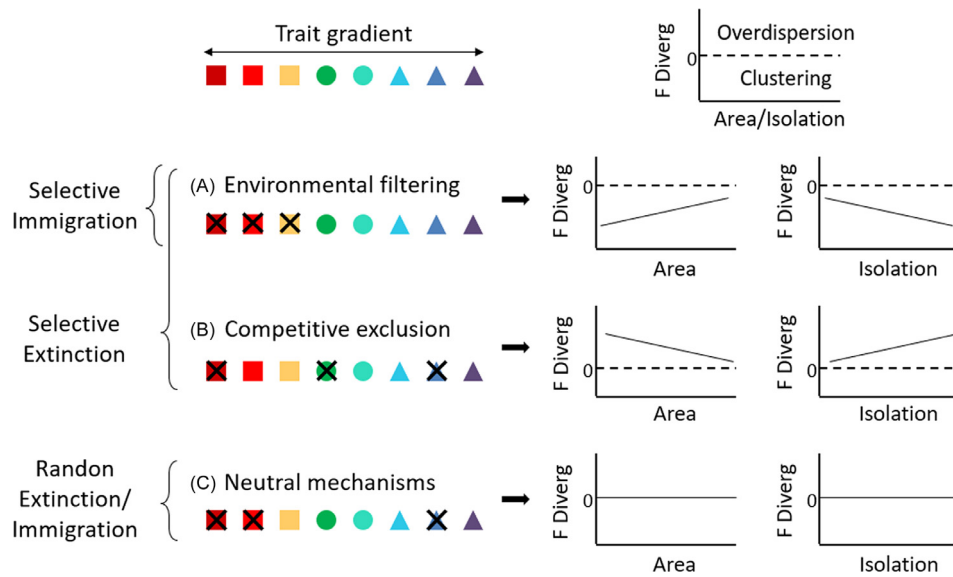


Fig. 6 Expected functional island biogeography patterns. The color and shape of symbols express the similarity in functional traits, where shape represents a categorical trait value and color a continuous trait value. F Diverg is a hypothetical measure of functional divergence between species. (A) Regional environmental conditions would cause a selective immigration, preventing the arrival of species with (or without) certain functional traits. Similarly, local environmental conditions would cause a selective extinction, eliminating species whose traits are unfavorable to these conditions. These selective immigration or extinction as result of environmental filtering would cause a clustering on the functional space and is expected to be more intense on smaller and more isolated islands, intensifying the clustering pattern with reducing area and increasing isolation. (B) Local competitive exclusion would cause a selective extinction, eliminating ecologically similar species and causing a functional overdispersion. This overdispersion intensity would decrease with islands area and increase with island isolation, due to the reduced habitat heterogeneity and rescue effect, respectively. (C) On the prevalence of neutral processes, there would be no selective immigration or extinction, so these processes would be random, and no patterns of varying functional overdispersion or clustering with islands area or isolation would be observed. Adapted from Si, X., Cadotte, M. W., Zeng, D., et al. (2017). Functional and phylogenetic structure of island bird communities. *Journal of Animal Ecology* **86**, 532–542.

On the assumption of an increasing habitat complexity with area, the effects of environmental filtering or competitive exclusion are expected to be more prominent on smaller islands. Given that, on the presence of local environmental filters, smaller islands would show even more functional clustering than bigger islands. In the same way, on the advent of competitive exclusion, the functional overdispersion will be stronger on smaller than on bigger islands (Fig. 6).

The IBT also predicts isolated islands to have lower immigration rates and, consequently, show reduced species richness (MacArthur and Wilson, 1967). Again, no assertions were made whether these immigration events are random regarding species functional traits (Whittaker et al., 2014). The challenges to achieve a remote island are tougher, as there is more chance for facing physical and environmental barriers in the way. Therefore, affected by regional environmental filtering, isolated islands would show even higher functional clustering than more connected ones (Fig. 6). Moreover, on the assumption of a reduced rescue effect on more isolated islands, the outcomes of competitive exclusion would be more intense, as the species are not receiving inputs of individuals from source communities, that could soften the extinction rates. Therefore, the functional overdispersion would increase with island isolation (Si et al., 2017; Fig. 6).

Finally, regarding island age, Borregaard et al. (2017) included a functional approach to the original General Dynamic Model of Oceanic Island Biogeography (GDM), but, again, focusing on terrestrial systems. According to them, young islands, on an initial stage of colonization, would hold a reduced pool of functional traits. These traits variability would increase with speciation events while the island is increasing in habitat heterogeneity. However, on its most advanced stage, habitat loss caused by excessive erosion would imply into lower niche availability, causing selective extinction of species with specialized traits and, also, intensifying extinction rates of those with similar traits—as a result of stronger competition between ecologically similar species (Borregaard et al., 2017).

Functional island biogeography for marine shallow-water species

To our knowledge, there are no studies relating marine shallow-water functional richness to islands features, although a few studies relates single marine shallow-water biota traits to islands area and isolation. Jacquet et al. (2017) proposed two process-based models including the functional component of biodiversity into the IBT. The Allometric Theory of Island Biogeography (ATIB) treats mainly of the variation on species body-size with island area and isolation, while the Allometric and Trophic Theory of Island Biogeography (ATTIB) emphasizes the importance of species trophic level together with body size (Jacquet et al., 2017).

On what concerns selective immigration, it is known that species dispersal ability influences their immigration capacity, so that weak dispersers would be almost absent in remote islands. In marine systems, functional traits like pelagic larval duration (PLD),

species body size, grouping behavior and nocturnal activity have been related to dispersal capacity (Reaka, 1980; Shanks et al., 2003; Mora et al., 2003; Luiz et al., 2013; Stier et al., 2014). For instance, larger coral-dwelling mantis shrimp species show a wider longitudinal span (Reaka, 1980). Likewise, a study on reef fish distributions through 134 tropical reefs across the globe showed an increase of species mean body size with isolation (Fig. 7B; Jacquet et al., 2017). Reef fish body size was also showed to be a predictor of their capacity to cross both the Mid-Atlantic and the Amazon-Orinoco Plume barriers in the Atlantic Ocean, mainly due to the faster growth rate of large species, which reduces the risk of predation while dispersing (Luiz et al., 2011). Still, reef fish species recorded in oceanic islands of the southwestern Atlantic are positively related to rafting use, great depth ranges and large body sizes, while their endemism is mainly related to small body sizes (Pinheiro et al., 2018). Exceptions for that would be for cases

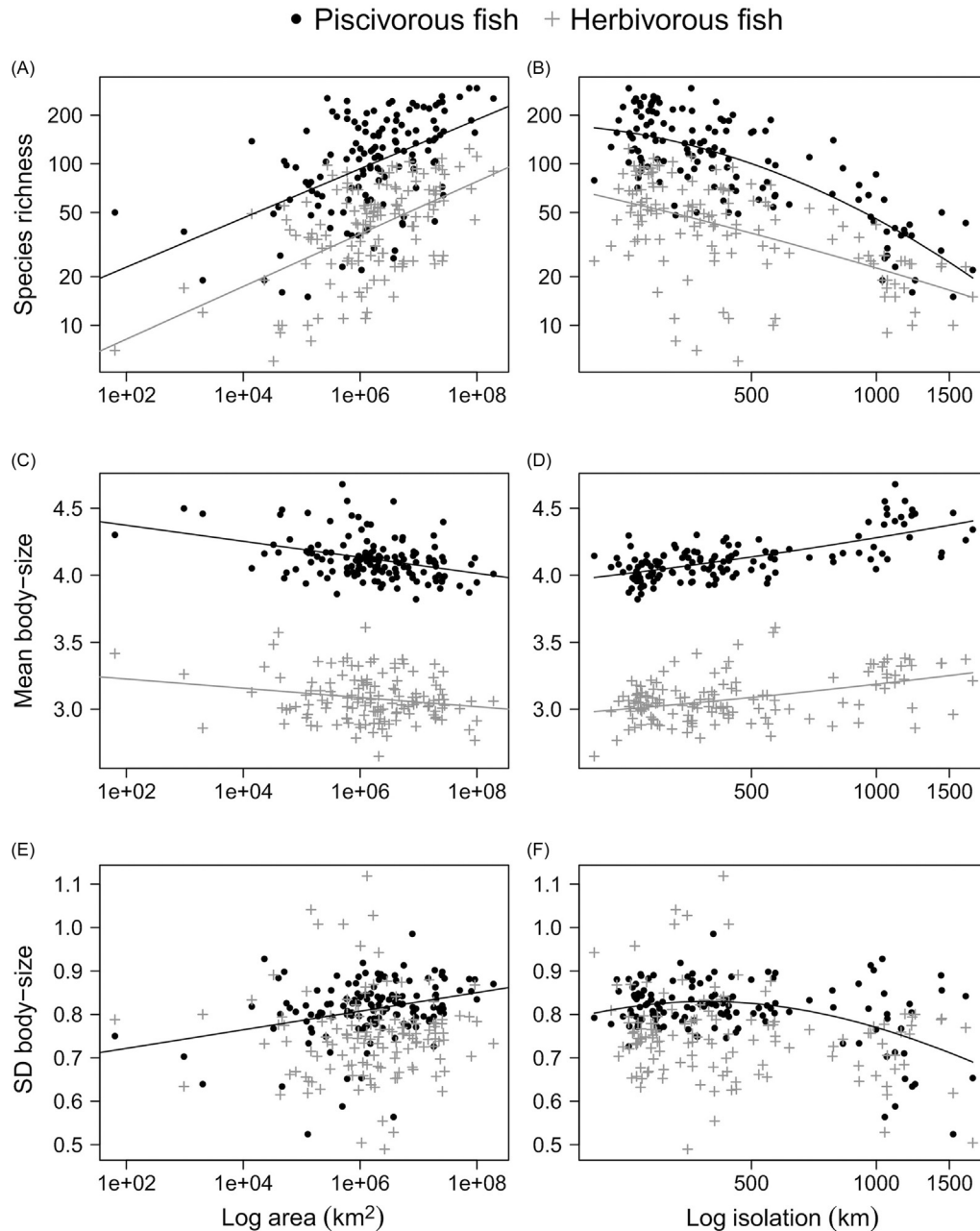


Fig. 7 Relationship between body sizes and reef area and isolation for piscivorous (black circles) and herbivorous (gray crosses) reef fish on 134 tropical reefs across the world. The lines illustrate significant ($p < 0.05$) relationships between the variables. Piscivorous and herbivorous mean body size (A) decreased with area and (B) increased with isolation. (C) The standard deviation (SD) of body size increased with area only when piscivorous fish were considered, showing that larger areas hold a greater variability of piscivorous fish body size. Figure from Jacquet, C., Mouillot, D., Kulbicki, M. and Gravel, D. (2017). Extensions of Island Biogeography Theory predict the scaling of functional trait composition with habitat area and isolation. *Ecology Letters* **20**, 135–146.

such as the VTC, in which an evolutionary path toward reduced reef fish dispersal capacity was followed through an anagenesis speciation process (Pinheiro et al., 2017), as a relationship between species evolutionary age and dispersion capacity was evident.

On what concerns selective extinction, species with generalist diets are expected to be less vulnerable to extinction than others with restricted diets, especially on smaller islands, in which resources are more limited. Although Jacquet et al. (2017) found no differences between piscivorous and herbivorous fish species-area and species-isolation patterns on islands (Fig. 7A–D), they verified a higher prevalence of extreme reef fish body sizes on larger areas only when piscivorous fish were considered (Fig. 7E). That is, while larger islands show variable sizes of piscivorous species, the smaller islands show a prevalence of fish species with intermediate mean body sizes. The explanation for this pattern relies on the relationship between the species body size, trophic group and extinction and immigration rates of this taxon. Reef fish intermediate-sized species are less susceptible to extinction than those with extreme body sizes, due either to their more generalist diet, when compared to smaller species, or to the maintenance of higher population densities, when compared to larger species (Jacquet et al., 2017). Therefore, the piscivorous fish, on being more specialist and therefore even more susceptible to extinction (if compared to herbivorous species), presented a pattern of increasing size standard deviation with island area (Fig. 7E).

Therefore, when comparing the ATIB and ATTIB, the latter, by also including the species trophic level as an important functional trait, was shown to be a better model than the ATIB (that included only species body size) on explaining reef fish distributions across the globe (Jacquet et al., 2017). However, although either the ATIB and ATTIB give important insights to functional island biogeography, generalizations to other marine shallow-water groups must bear in mind taxa specificity on the relationship between body size, trophic level and extinction and colonization rates (Jacquet et al., 2017).

On what concerns island age, although no tests on the GDM functional approach were done to marine biota yet, we would expect that adaptations equivalent to those proposed for taxonomic marine shallow-water GDM would be necessary, due to the increased marine shallow-water habitat area of islands on advanced erosion phases.

Speciation and Endemism Patterns in Marine Shallow-Water Habitats

Speciation is an evolutionary process that consists in the formation of one or more descendent species from an ancestral one (Mayr, 1947). Despite the advances in the knowledge about the origins of the terrestrial biodiversity, the understanding of how new species arise in marine habitats is still poorly known (Bowen et al., 2013). Major differences are related to the few opportunities for geographical isolation in a circumglobal aquatic medium, where few obvious physical barriers are present and for which most organisms have a pelagic larvae stage with a high dispersal potential. Anyway, an average of 42% of “endemism” can be seen within each marine realm—benthic molluscs and arthropods contribute the most for this endemism—so that major biogeographic barriers constrain species distribution worldwide (Costello et al., 2017). But, in general, many marine populations are genetically connected among different ocean basins, as it is the case for many pelagic and bathypelagic fish species (Gaither et al., 2016), the brown algae *Dictyota ciliolata* and *D. crenulata*, among other species that display a circumtropical distribution (Tronholm et al., 2012). Therefore, the combination of few physical barriers and high dispersal capacity reduces opportunities for allopatric speciation—classical model where populations become isolated due to the rise of physical barriers and end up in different evolutionary paths (Rocha et al., 2005). However, since many marine habitats (e.g. reefs, estuaries, kelp forests, sand beaches) shelter high biodiversity levels—some of them comparable to the highly diverse rainforests—the generalization that speciation must be rare in taxa with high dispersal capacity is inaccurate (Rocha et al., 2005; Pinheiro et al., 2017; Delrieu-Trottin et al., 2019).

Speciation in marine systems has been explored in biodiversity hotspots—e.g., Coral Triangle in the Indo-Pacific and the Caribbean—where richness levels are explained by three main hypotheses (Bowen et al., 2013). The first considers biodiversity hotspots as “Centers of origin,” where intensive competition among species would promote the emergence of new species (Briggs, 2003). According to this hypothesis, species originated in the biodiversity center could colonize marginal provinces and evolve in different species (Bowen et al., 2013). The second hypothesis, known as “Center of accumulation,” suggests that new species arise in peripheral areas, such as oceanic islands and archipelagos, and then colonize and accumulate in biodiversity hotspots, with the aid of prevailing currents (Kool et al., 2011). Some cases involve a biodiversity feedback process, where species migrate from biodiversity hotspots, evolve in a different species in the periphery, and finally colonize back the original province (Bowen et al., 2013). For instance, the Ember parrotfish (*Scarus rubroviolaceus*) and the Yellow tang (*Zebrasoma flavescens*) occur in the Indo-Pacific region, however population genetic data indicates that their ancestral lineage had first colonized and evolved in Hawaii, spreading back to the central Pacific later (Eble et al., 2011; Fitzpatrick et al., 2011). Finally, the “Center of overlap” hypothesis suggests that the high species richness observed in biodiversity hotspots is the result of different communities overlap, which were previously divided by historical events, such as changes in the sea level (Gaither and Rocha, 2013; Pinheiro et al., 2017) and movements of tectonic plates (Leprieur et al., 2016). In the Atlantic Ocean and in the Coral Triangle, low sea-levels intensified biogeographic barriers for marine organisms due to land exposing, reducing gene flow and driving allopatric speciation (Rocha et al., 2005; Floeter et al., 2008; Gaither and Rocha, 2013). In higher sea level stands, species expanded their distribution and overlapped in the biodiversity hotspot. However, sea-level oscillations played different roles on driving speciation, depending on the availability of shallow habitats. In the VTC, southwestern Atlantic, for example, low-stand sea levels, instead to promoting vicariance, allowed dispersal from mainland to the arising seamounts (Pinheiro et al., 2017), similarly to the effect of low sea levels in improving terrestrial connectivity. In summary, the Center of origin hypothesis involves speciation without complete geographic isolation—i.e., parapatric and sympatric speciation—while the Center of accumulation and the Center of Overlap hypotheses include some level of vicariance and isolation—i.e., allopatric or peripatric speciation. These hypotheses put oceanic islands in

opposing roles in what concerns marine shallow water biodiversity, since for the Center of origin model, islands are evolutionary dead ends for some species, whereas in the Center of accumulation and Center of overlap, islands are cradles of biodiversity (Bowen et al., 2013).

On contrasting terrestrial and marine realms, endemism is much more common on land than in the sea, again, due to the high dispersal capacity of marine organisms, allowing a greater connectivity between populations and, therefore, reducing extinction and speciation rates (Pinheiro et al., 2017; Ávila et al., 2019). For example, endemism levels for reef fish in the Atlantic Ocean, even considering its most isolated oceanic islands (Ascension and Saint Helena), varied from 0% to 13.2% (Hachich et al., 2015; Floeter et al., 2008). Conversely, in the Atlantic islands, the endemism of terrestrial plants—group within the ones with higher dispersal ability in land—ranged from 7.2% to 40% (Whittaker et al., 2008; Emerson and Oromí, 2005).

Another interesting contrast between the terrestrial and marine biotas is that isolated archipelagos are functionally “islands” for most marine species. Speciation within islands in a given archipelago is commonplace for terrestrial species, while in the sea it can be very uncommon. For example, while the speciation of tortoises and finches in the different islands of the Galapagos is well known (Román-Palacios and Wiens, 2018), endemic reef fishes there are spread over the entire archipelago (Bernardi et al., 2014). Despite the relatively lower rate of endemic shallow-water species in the ocean, there are 18 marine centers of endemism, which together, embrace > 50% of the world’s restricted-range species of fishes, corals, snails and lobsters (Fig. 8). Such centers are mainly composed by groups of islands that, although distributed across all the oceans, prevail in the Indo-Pacific region (Roberts et al., 2002).

Endemism relies into specific spatial and temporal boundaries. Geographic or ecological characteristics allow the delimitation of an area that encompass the distribution of an endemic species, while the evolutionary history of a species allows its classification as a new or an old endemic (Anderson, 1994). Neoendemic species would occupy a restricted area due to their recent origin, while paleoendemism would be the remnants of a more widespread ancestral species (Tedesco et al., 2012). In practical terms, paleoendemic species could be distinguished from neoendemism as the formers display deep divergence times from their sister species together with signals of distribution contraction (Cowman et al., 2017). Oceanic islands appear to harbor a combination of paleo and neoendemic species (Fig. 9; Cowman et al., 2017; Pinheiro et al., 2017; Delrieu-Trottin et al., 2019). The marine gastropod genus *Conus*, for instance, suffered an explosive radiation in Cape Verde during the last few million years, resulting in > 40 neoendemic species in the archipelago (Duda and Rolán, 2005; note that this within-archipelago speciation is an exception for marine organisms). On the other hand, the Trindade parrotfish *Sparisoma rocha* and the wrasse *Halichoeres rubrovirens* had their ancestral lineages extinct from the continental coast, only remaining in the VTC, that serves as a museum for these old lineages (Pinheiro et al., 2017). However, most endemic fishes of the VTC are indeed neoendemism (Fig. 9), with limited dispersal potential, which colonized the most distant islands when the sea-level was lower than today, exposing seamounts that acted as stepping stones. The sea-level rise created a vicariant barrier and contributed to speciation (Pinheiro et al., 2017). Therefore, the speciation scenario in the VTC follows the premises of the IBT, where good dispersers colonize distant islands first, and weak dispersers later. These good dispersers evolve by parapatric and ecological speciation, while the weak dispersers, if do not get extinct, evolve by allopatric or peripatric speciation. In the most extreme example of island isolation, the Easter Island shows one of the highest endemism levels of marine species in the world, with nearly 22% for reef fishes (Randall and Cea, 2011). The evolutionary history of Easter Island endemics also shows a majority of neoendemism with restrict geographic range, together with a few wide distributed older endemics (Delrieu-Trottin et al., 2019).

Our knowledge about the drivers of marine endemism patterns is still in its infancy, and few information is available regarding the variation of marine shallow-water endemism with islands area, age and isolation. The GDM foresees for the proportion of endemism the same trend behavior as for the variation on species richness with area and age. That is, endemism would increase linearly with area and as a unimodal function of age (Whittaker et al., 2008). Although this has been observed for terrestrial organisms (Whittaker et al., 2008; Cameron et al., 2012; Triantis et al., 2015), the GDM is not a good model for marine gastropod and reef fish endemism in the Atlantic (Hachich et al., 2015; Ávila et al., 2018). In fact, among the two groups, only gastropod shows an increase of endemism with area (Fig. 10B). Moreover, it seems to be no relation at all between reef fish and gastropod endemism with island age (Fig. 10A; Hachich et al., 2015; Ávila et al., 2018). Finally, only reef fish endemism varied with island isolation (positive relationship; Fig. 10C). Despite its high dispersal ability, reef fishes exhibit a high auto-recruitment, especially for endemic species (Robertson, 2001), which can also influence endemism spatial patterns.

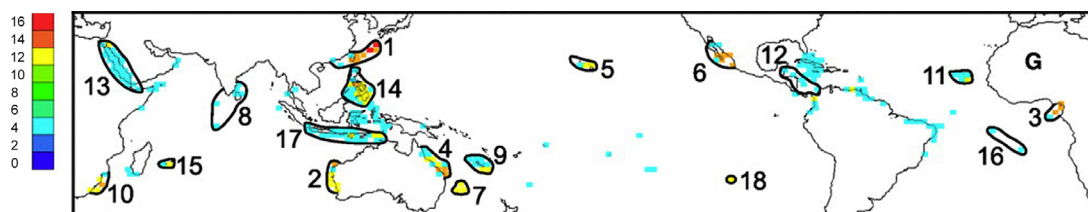


Fig. 8 The 18 multitaxa centers of marine endemism, considering fishes, corals, snails and lobsters. Figure from Roberts, C. M., McClean, C. J., Veron, J. E. N, et al. (2002). Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* **295**, 1280–1284.

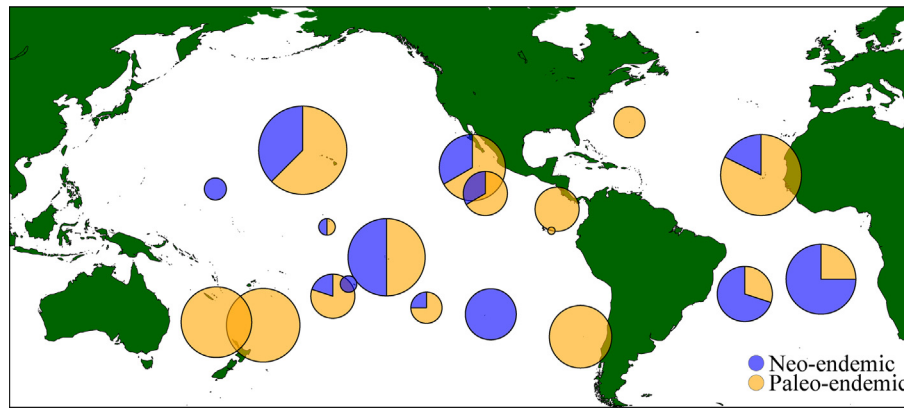


Fig. 9 Proportion of reef fish endemic species found in different oceanic islands across the marine biogeography regions. Size of circles indicates the proportion of the assemblage made up by endemic species. Colors show the different types of endemism observed in oceanic islands: neo-endemics (blue, ≤ 2.6 Ma), paleo-endemics (orange, > 2.6 Ma). Data was extracted from Cowman P. F., Parravicini V., Kulbicki M., and Floeter S. R. (2017). The biogeography of tropical reef fishes: Endemism and provinciality through time. *Biological Reviews* **92**, 2112–2130; Pinheiro, H. T., Bernardi, G., Simon, T., et al. (2017). Island biogeography of marine organisms. *Nature* **82**, 82–86, and Delrieu-Trottin, E., Brosseau-Acquaviva, L., Mona, S., et al. (2019). Understanding the origin of the most isolated endemic reef fish fauna of the Indo-Pacific: Coral reef fishes of Rapa Nui. *Journal of Biogeography*. doi:10.1111/jbi.13531.

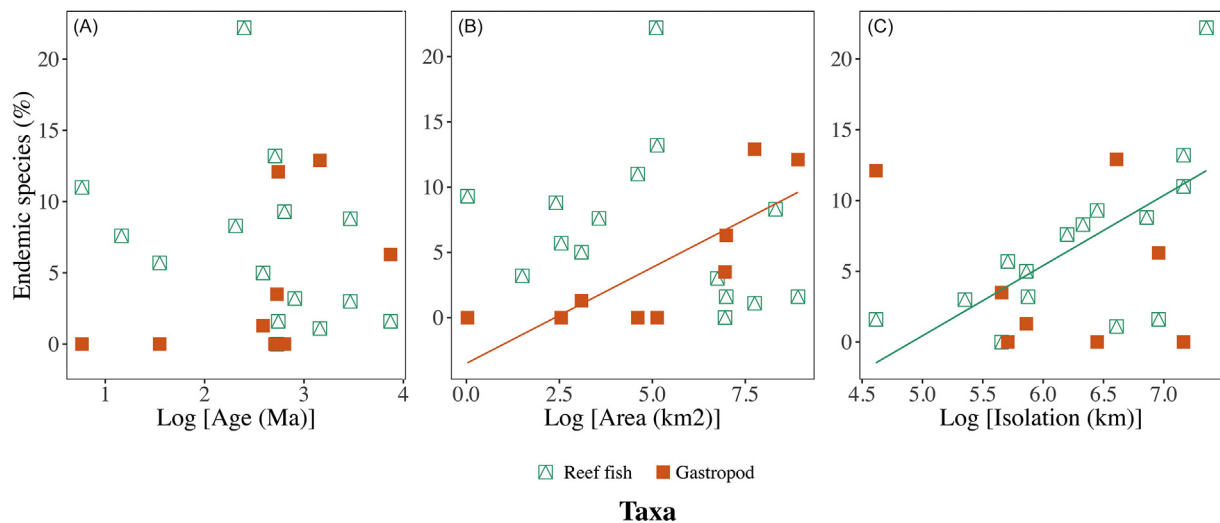


Fig. 10 Variation of marine shallow-water endemism with islands (A) age, (B) area and (C) isolation for reef fish and marine gastropod. Reef fish data are from 15 islands in the Atlantic and Tropical Eastern Pacific plus Easter Island (compiled from Robertson, 2001, Floeter et al., 2008, and Hachich et al., 2015). Gastropod data are from eight island in the Atlantic Ocean (obtained from Ávila et al., 2018). Only significant ($p < 0.05$) regressions lines were presented.

Methodological Caveats for Marine Shallow-Water Island Biogeography

The study of marine habitats, for those that are used to study the terrestrial biota, would be, in some ways, equivalent as looking to the world on an upside-down vision. Thus, adaptations to conventional research methods developed based on terrestrial studies are needed. Regarding island biogeography, except for the VTCM (Pinheiro et al., 2017), SLS (Ávila et al., 2019) and the ATIB and ATTIB (Jacquet et al., 2017), that were specially (and recently) designed for the marine biota, other theories and amends were conceived based on the terrestrial realm. Therefore, attention is required when bringing island biogeography to the marine sphere, either related to the measures of islands features—such as area, age and isolation—or to the limits to line off marine communities.

A first point of concern is related to island definition. For marine shallow-water organisms, depending on the scale of analysis, even a shipwreck or a small group of rocks can be treated as an island. On the other hand, for large spatial scale analysis, given the higher dispersal capacity of most of these organisms, a whole archipelago could be treated as a single island—in the sense that its component islands and islets show great within-island biota affinities. For sure such island definition must bear in mind taxon features specificity and the component of biodiversity being analyzed, as little is known about the distribution of functional groups within-islands in archipelagos.

When accounting for island area, although some authors have considered the emerged island area or coastal perimeter as a proxy for the real habitat area available for marine shallow water organisms (e.g. Tuya and Haroun, 2009), islands shallow shelf area would be, by far, a better unit of measure. The slope of an island aid on determining the availability of shallow shelf habitats, so that steeper surfaces imply in smaller areas. The terrain steep above and below water are not necessarily equivalent, especially for old islands on a high degree of erosion, which display a higher shallow water area compared to emerged area (Ávila et al., 2019). The shallow shelf surface of marine systems can be obtained by bathymetry from nautical charts or satellite data.

Another concern related to island area is that glacial periods were shown to have impacted the slope of islands terrain and their habitat variability directly, by selectively wiping out substrates such as beach sand (Ávila et al., 2019). And because islands shelf-break are generally shallower than continental ones, sea-level reduction would have hugely impacted their total available shallow area during glacial periods. Given that, also the past shallow shelf surface availability could have influenced the actual islands biodiversity, particularly when considering their functional diversity.

Another important discussion is about down to which depth to consider as shallow. Traditionally, shallow-water habitats are those down to depths of 200 m, just before the continental slope (Lalli and Parsons, 1997). However, authors have defined different depths for shallow-water organisms, even when the same taxon is being considered. For instance, although sponge richness increases with depth (Alcolado, 1994), depths limits from 10 to 30 m have been applied for sponge shallow-water studies (Longakit et al., 2007; Lim et al., 2012; Hadi et al., 2018; Ávila et al., 2011). On a quick literature overview, maximum depths delimitations for shallow-water organisms varied from 6 to 200 m deep (Sangil et al., 2018; Ávila et al., 2011; Edgar et al., 2004; Villaça and Pitombo, 1997; Flórez et al., 2018; Floeter et al., 2008), and a few papers did not even use a depth limitation. Whether this definition should rely on an arbitrary depth limit or be related to each taxon ecology, a standardization for the phrase, or at least a better definition in each paper—based on scientific arguments—would allow better grounded syntheses and multiple studies comparisons. For instance, there are evidences of a high malacofauna turnover about the 50 m isobath (Ávila et al., 2019) and the 30 m depth isobath was showed to be a transitional zone between reef fish shallow and deep species composition (Brokovich et al., 2008).

Measuring island isolation as a geographical parameter, is not that challenging, although measuring the real isolation between communities can be tricky, especially when considering marine organisms. Originally, the IBT has been measuring island isolation as the distance from mainland or even the distance to the nearest larger suitable habitat. These isolation measures rely on the source-sink dynamic model (Pulliam, 1988), in which larger areas, with high quality habitats, serve as source of species to smaller areas (impoverish habitats), such as islands. The distance from a hotspot can also be used as a measure of isolation, based on the “Center of origin” hypothesis on marine shallow-water biodiversity. However, especially when considering the “Center of accumulation” or “Center of overlap” hypotheses, in which islands are cradles of biodiversity, more complex measures of isolation, that consider the mosaic of suitable habitats in which the island is located, needs to be applied.

Finally, islands age measures are tricky to determine, mainly because islands can span long periods of formation—eastern Azores islands, for example, show rock fragments dated between 0.95 and 8.12 millions of year from the present (Abdel-Monem et al., 1975). The oldest age in which an island has reached a certain shallow water depth (again, depending on shallow-water definition) would be a reasonable estimate of the availability for colonization. Technology has advanced toward facilitating access to many of these data, so that IBT studies is expected to improve in accuracy and quality.

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How Consideration of Islands Has Inspired Mainstream Ecology: Links Between the Theory of Island Biogeography and Some Other Key Theories

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Abstract

The passing of the 50th anniversary of the theory of island biogeography (IBT) has helped spur a new wave of interest in the biology of islands. Despite the longstanding acclaim of [MacArthur and Wilson's \(1963, 1967\)](#) theory, the breadth of its influence in mainstream ecology today is easily overlooked. Here we summarize some of the main links between IBT and subsequent developments in ecology. These include not only modifications to the core model to incorporate greater biological complexity, but also the role of IBT in inspiring two other quantitative theories that are at least as broad in relevance—metapopulation theory and ecological neutral theory. Using habitat fragmentation and life-history evolution as examples, we also argue that a significant legacy of IBT has been in shaping and unifying ecological schools of thought.

Recent years have seen a surge in interest in island biology and island biogeography theory (IBT; [Losos and Ricklefs, 2010](#); [Santos et al., 2016](#); [Patino et al., 2017](#); [Whittaker et al., 2017](#)), partly motivated by the 40th and 50th anniversaries of the Core IBT model ([MacArthur and Wilson, 1963](#)) and the monograph that expanded on this model with related ideas ([MacArthur and Wilson, 1967](#)). We were involved in one such initiative, a working group on island biogeography funded by the Centre for the Synthesis and Analysis of Biodiversity (CESAB). A major output of the group was a collective perspective on how key attributes of islands surrounded by water provide prospects for improving our understanding of the ecology and evolution of biological communities in general ([Warren et al., 2015](#); see Box 1 for a detailed distinction of IBT and Core IBT). In the process of organizing our ideas, interesting issues arose that were tangential to this aim. One example is that over the decades since 1967, IBT has inspired numerous ecological theories and schools of thought. Although IBT is focussed on islands surrounded by water, even in the opening pages of the 1967 monograph, MacArthur and Wilson emphasized that such island biomes are an extreme example of fragmented or insular environments (isolated by geography or ecology) that are common worldwide. Consistent with this view, not only has IBT proven relevant to a wide variety of insular environments that are not islands surrounded by water (e.g., [Brown, 1971](#); [Drake et al., 2002](#); [Wagner et al., 2014](#)), but it also has links to important ecological theories and concepts, the implications of which stretch far beyond such islands.

Here we highlight some of the main links between IBT and subsequent developments in ecology and conservation biology.

The elegance of Core IBT stands in its ability to model complex phenomena with few parameters. Diversity dynamics on an island incorporate a simple birth and death process in which births represent species arriving through immigration and deaths represent local (i.e., island-wide) extinctions; Core IBT predicts that diversity will tend toward a “dynamic equilibrium” in which these processes are balanced. These ideas predict considerable variation in local community composition due to the stochasticity of immigration and local extinction, and the time taken to reach equilibrium (see also [Warren et al., 2015](#), Box 6, for related situations with unattained equilibria). Nonetheless, Core IBT provides a highly deterministic perspective on species richness based on the assumption that the rates of immigration and extinction are determined by the geographic context: near islands have a higher rate of immigration than far islands, and small islands have a higher rate of extinction than large islands. Accordingly, other things being equal, diversity should be highest on islands that are large and close to the mainland, and lowest on islands that are small and far.

The “island biome” (islands surrounded by water) is an obvious choice for studying the effects of area and isolation on species richness since insularity is acute; an island’s boundaries frequently provide longstanding limits to the distributions of species or populations (see [Warren et al., 2015](#) for further discussion, including key attributes of islands). Nonetheless, in addition to the predominance of other insular and fragmented environments worldwide, small habitat islands are among those most easily studied and manipulated. Such practical constraints are reflected in the range of systems in which the equilibrium predictions of Core IBT have been tested ([Schoener, 2010](#)), which include fragmented crops and intertidal habitats, as well as islands surrounded by water. Application of Core IBT to insular systems that are not “true islands” arguably reached an extreme in the design of protected areas, such as the debate over whether a single large, or several small, reserves is better for ensuring the persistence of species (“SLOSS” for short). Problems with this approach include the fact that Core IBT does not generate clear predictions in this matter ([Simberloff and Abele, 1982](#)), and also that for habitat islands, unlike “true islands”, an organism’s ability to inhabit, or disperse through, the intervening matrix is a critical factor. In the end, ecologists concluded that Core IBT provides only limited practical lessons for conservation managers ([Soulé and Simberloff, 1986](#)). Nonetheless, by forcing decision makers to think about population turnover within habitat fragments, as well as the influence of fragment size and isolation on colonization and extinction, a highly diversified field of fragmentation research can be traced back to Core IBT ([Laurence, 2010](#)).

A more direct example of the relevance to IBT of insular systems that are not “true islands” comes from an extension to the Core IBT model to improve its ability to predict species diversity. At low isolation, the frequent arrival of propagules protects insular populations from extinction. This “rescue effect” was first demonstrated empirically for arthropods on isolated plants (thistles; Brown and Kodric-Brown, 1977). Other examples of modifications to Core IBT include adding the effect of island habitat heterogeneity on colonization and extinction dynamics (e.g., Johnson et al., 1968; Whitehead and Jones, 1969; Kadmon and Allouche, 2007), as well as the effects of changes in the physical geography of islands over time (Whittaker et al., 2008). Recent developments have extended this legacy by showing how, without adding much complexity to the original model, species interactions could easily be incorporated with important consequences for the shape of the species-area relationship (Gravel et al., 2011) or even for the number of trophic levels expected in fragmented systems (Holt et al., 1999; Calcagno et al., 2011). For example, predator-prey interactions may slow down species accumulation with area, while mutualistic interactions may accelerate it. Realizing such multitrophic extensions to Core IBT was key in the development of recent theories of community assembly and codistribution in isolated habitats (Cazelles et al., 2015, 2016). Furthermore, some of the main parameters of Core IBT have sometimes been modified to provide new interpretations, as in Wright’s (1983) replacing area with available energy to develop a species-energy theory.

Another important extension of IBT was to consider the dynamics of populations on multiple islands (metapopulations) connected by movements of individuals. Although IBT and metapopulation theory (Levins, 1969, 1970) were not formally connected initially, their relationship can be traced back to an agreement among their authors to work on complementary questions, MacArthur and Wilson’s being “how many species does an island contain?” and Levins’ being “how many islands does a species occupy?” (R. Levins, pers. comm., 2013). This initial plan included the authors coming together later for a study of continental biogeography, although this was never realized (R. Levins, pers. comm., 2013). Current thinking in metapopulation ecology does fit the Core ITB perspective perfectly once changes in scale and geography are incorporated (Hanski, 2010). Core IBT becomes a metapopulation model when one excludes the mainland with its permanent source populations of each species and considers migration among multiple islands (e.g., Mouquet and Loreau, 2002). Although Levins’ (1969, 1970) original model focussed on a single species, and “islands” (habitat patches) that did not differ in size or accessibility, numerous later developments have relaxed these simplifying assumptions (Hanski, 2001, 2010). Furthermore, it is clear that much heritage of both IBT and metapopulation theory has percolated into today’s study of spatial ecology from metacommunities (Leibold et al., 2004; Leibold and Miller, 2004; Logue et al., 2011; Massol et al., 2011) to metaecosystems (Loreau et al., 2003; Gravel et al., 2011; Massol et al., 2011; Leibold and Chase, 2017).

Neutral biodiversity theory (Bell, 2001; Hubbell, 2001) is perhaps the most striking example of an unexpected legacy of IBT. MacArthur and Wilson apparently did not intend for IBT to be thought of as “neutral” at the species level (that is, species treated as ecologically equivalent). The concave functional forms for immigration and extinction rates in Core IBT were partially motivated by potential ecological differences between species (differences in propensity for immigration and extinction; MacArthur and Wilson, 1963; for further discussion see Gilpin and Armstrong, 1981; Schoener, 2010). From a strictly technical perspective, however, species in the classic IBT model are not labeled with their ecological identities. Rather, they are all treated as identical, and the model is thus neutral at the species level regardless of the ideas that motivated it.

The better-known form of neutral theory is one in which individuals (not species) are ecologically equivalent (Hubbell, 1979, 1997), and even the earliest work on such models (Caswell, 1976) notes the similarities with IBT. Later development of “The Unified Neutral Theory of Biodiversity and Biogeography” (Hubbell, 2001) caused a wave of interest in neutral models and further added to the legacy of MacArthur and Wilson as an inspiration for them. In particular, the unified neutral theory incorporates an explicit distinction between the local community and metacommunity, with both maintained at dynamic equilibria. Individual-based neutral theory has since accurately predicted a range of ecological data both in mainstream ecology and in the more specific domain of island biogeography (Bell, 2001; Chave, 2004; Alonso et al., 2006). Although neutral theory is also faced with contrary data (e.g., Ricklefs, 2003, 2006; McGill et al., 2006), it is widely viewed as a useful model to compare with empirical data, highlighting key roles for dispersal limitation, speciation, and ecological drift (Jabot and Chave, 2011; Rosindell et al., 2011, 2012).

While the influence of IBT in ecology is predominantly linked to Core IBT, it is important to note that the legacy also extends to other elements of the 1967 monograph. For example, the penultimate section predicts evolutionary changes following island colonization. MacArthur and Wilson (1967) reasoned that, upon first arriving on an island, a species’ population density is much lower relative to the carrying capacity of the environment than it was at its mainland source. They argued that selection on such newly-arriving immigrants should initially favor adaptations that produce high rates of population growth, even if resources are used inefficiently. They envisaged a contrasting situation for species in the mainland source for which population density is already at the environmental limit; in such source populations, selection should favor the ability to survive and reproduce with limited resources (i.e., efficient resource use). Borrowing notation from standard population models, they coined the terms *r*-selection and *K*-selection for these alternative regimes, respectively. They also argued that once a colonist attains its maximum population size on an island, it will tend to experience a switch back toward a *K*-selection regime (and indeed one that is stronger than on the mainland, due to a temporally more stable climate). MacArthur and Wilson’s (1967) ideas were further developed by Pianka (1970) to make explicit predictions for how individual life-history traits would evolve in response to *r*- and *K*-selection, forming the basis of what became known as life-history strategies. However, the *r*- and *K*-selection paradigm has since been criticized on numerous grounds, in particular that it has been applied in the absence of data on population dynamics, oversimplifies the process of natural selection, and is unable to make precise predictions about phenotypic change (see Reznick et al., 2002 for a review, and more recent related paradigms). Despite such shortcomings, the *r*- and *K*-selection paradigm has been useful in defining fitness under

density-dependent population regulation (Roff, 1992), and retains considerable popularity (e.g., Saether et al., 2016). Furthermore, consistent with the low species diversity of small and remote islands predicted by Core IBT, such islands provide particularly striking examples of rapid change in selection gradients following the arrival of new immigrants (e.g., Losos et al., 2004, 2006).

IBT is a major component of the foundation of modern ecology. Even though our working group included participants with a range of profiles, including island evolutionary biologists and ecological theoreticians, the number of important links with other ecological theories and schools of thought took many of us by surprise. From an ecological perspective, IBT has left a legacy that has (i) forced ecologists to connect local processes to regional patterns and (ii) enabled theoretical ecologists to propose simple models that capture a significant portion of ecological complexity on a biogeographic scale.

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The Effect of Sea Level Rise on Islands and Atolls

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Abstract

Islands and atolls are on the forefront of climate change, with sea level rise having some of the most immediate and profound impacts to the people and their surrounding environment. Since the industrial era of the late 1800s and particularly following World War II, global prosperity and the energy demands to meet growing economies has resulted in increasing emissions and accumulation of greenhouse gasses in our atmosphere. Greenhouse gasses such as CO₂ from the combustion of fossil fuels have allowed for the retention of radiative heat, which has resulted in increasing atmosphere and ocean temperatures above pre-industrial levels. Increasing temperatures, especially in the last 20 years, have resulted in the loss of ice from large ice sheets and receding glaciers, and an increase in the intensity of tropical cyclones with high storm surge events. The combined loss of ice and thermal expansion of sea water causing sea levels to rise, and storm surge events that flood and erode islands and atolls, have resulted in the first documentation of islands lost to sea level rise. The loss of islands and atolls constitute socioeconomic, cultural and environmental impacts that are a consequence of global economies, which cannot be mitigated at the local level alone. Global efforts have been central to establishing predictions and recommendations for reducing greenhouse gas emissions to levels that would slow the progression of climate change and allow time for economies to adjust to cleaner energy sources. Shifts in energy sources and increasing efficiencies however will require an unprecedented global-scale shift in the way we live. Central to this will be shifts to more renewable energy sources and efficiencies such as wind and solar power, both of which require technical advances to be applied more widely around the world.

Introduction

We have all seen how global climate change influences the way we live and think about our planet. For most, this has been in our experiencing unseasonal weather patterns, and in our changing attitudes and lifestyles to reduce our footprint on the environment. For those living on islands and atolls, the implications of climate change have a much more direct and impending result. Increasing emissions of greenhouse gasses in the last century have resulted in increasing atmospheric and ocean temperatures, resulting in more extreme weather events including tropical cyclones and sea level rise that together threaten the existence of these communities and the surrounding ecosystems. Islands and atolls are unique in many ways, with their relative isolation having endemic species and biodiversity, which are often central to the livelihood and culture of the people that live there. This isolation also imposes a reduced capacity for communities and organisms to adapt, especially in a time of rapid climate change and sea level rise. In fact, islands and atolls are on the forefront of this change, with the highest levels of biodiversity loss and first extinction of a species of mammal (Bramble Cay melomys, *Melomys rubicola*) due to climate change, and the displacement of whole communities and cultures from island systems, as seen in Micronesia and the Solomon Islands of the Western Pacific.

The concept of human-induced climate change was seeded in 19th century geological and paleoclimate sciences and by mathematicians and physicists, where it was first recognized that the earth's climate in the past was not static, and that the emission of hydrocarbons (major greenhouse gasses) into the atmosphere would eventually cause warming. Despite this early discovery, it was only until the 1970s when scientists and the public began to be concerned, with a general consensus by the global scientific community in the late 1980s with the establishment of the first Intergovernmental Panel on Climate Change (IPCC; <https://www.ipcc.ch/>; accessed 13Aug 2019). What would seem to be a slow progression of science leading up to recognizing climate change was and still is a result of the complexity of our earth and climate, and the progression of science and technology to monitor it with. Since the 1990s, advances in satellite imagery, ground-based measurements and computers have allowed for a near-continuous monitoring earth's temperature, ice coverage, and changing weather patterns that can influence sea level rise.

This article dives into the causes and effects of climate change and sea level rise, and how this is impacting islands and atolls now and into the future. This article will present and discuss the physical dynamics of climate change and sea level rise, and how sea level rise is impacting island communities and the surrounding natural ecosystems from which they depend on for culture, subsistence

and economic prosperity. Finally, we will discuss what is being done to reverse climate change, from international agreements to reduce emissions to taking steps to reduce other sources contributing to global warming.

Climate Change and Sea Level Rise

Climate Change

The causes of climate change is a story of global economic prosperity, especially in the last 70 years following World War 2 with increasing energy demands feeding a growing global economy. Increased emissions of greenhouse gases has predominantly come from electricity generation, agriculture, industry and transportation, much of which comes in the form of carbon dioxide (CO_2), and to a lesser extent methane and nitrous oxide (agriculture and forest practices), and fluorinated gasses (industrial processes, refrigeration). Greenhouse gasses in the atmosphere cause warming by trapping radiant heat from the earth that would otherwise be lost to space, with the continued buildup of greenhouse gasses over time causing, on average, a continued warming of the earth's atmosphere and warming of oceans that absorb this heat (Fig. 1).

Over the last century, total CO_2 emissions have risen by over an order of magnitude, with an estimated 68% increase over the last 20 years alone (Fig. 2). Over this same time span, global average temperature anomalies (temperatures above the global average) have increased by nearly 60%, with ocean temperatures responding with an average increase in the anomaly of 57% (Fig. 3). To put this into perspective, from the recording of temperature records since the 1880s and backward over 2000 years of reconstructed temperature records, the earth has never been warmer than the last 20 years. With continued emissions of greenhouse gasses at the current rate and continued ocean warming, current knowledge and application of climate models projects regions such as the Arctic to be completely free of ice by 2060 (2014 National Climate Assessment, <https://nca2014.globalchange.gov/report>). This rapid increase has been attributed in-part to another dynamic of global warming, in which the loss of sea and land ice has removed the reflective properties of the surface, with the sun's heat being more absorbed by darker, less reflective surfaces of the oceans and land. This is causing a type of positive feedback of loss of ice due to warming, which causes more absorbance of the sun's rays and further warming.

Sea Level Rise

The link between atmospheric and ocean warming to sea level rise first brings to mind the contribution of water from the loss of large ice sheets in polar regions, Greenland, and receding glaciers, adding volume to oceans. Indeed, these freshwater pools constitute upwards of 68% of earth's surface freshwater, which if completely melted would cause sea level to rise by 70 m (230 ft), virtually inundating most low lying atolls and islands (citation?). Another significant but less known contributor to sea level rise is through the thermal expansion of seawater, which is a function of the water's density and temperature. As global atmospheric temperatures rise and heat is absorbed by the oceans, sea temperatures rise and seawater expands. To what extent thermal expansion contributes to sea level rise however is much more complex and is debated, in part because of the dynamics of ocean mixing across

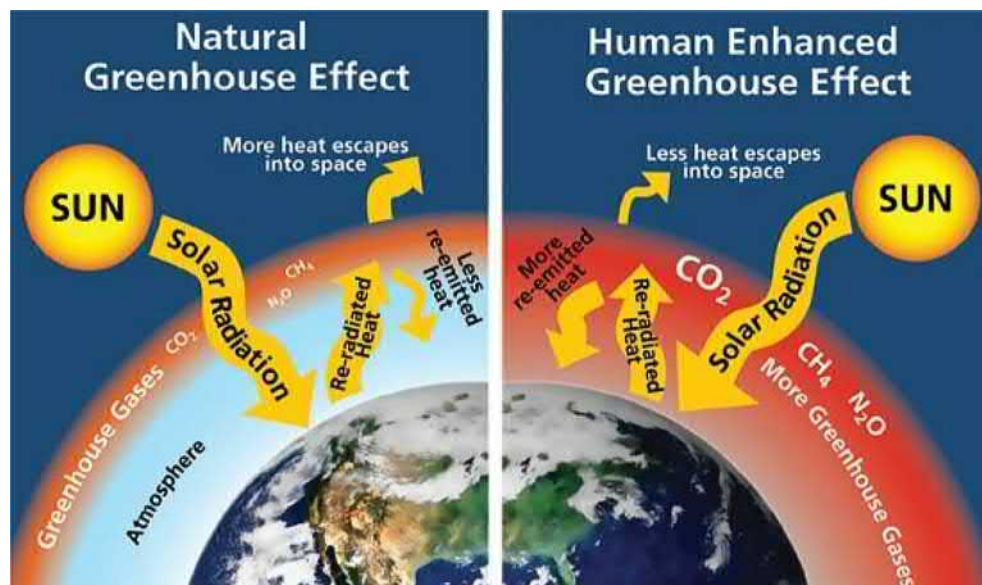


Fig. 1 Schematic of how greenhouse gasses effect global warming, with natural conditions (left) having a greater proportion of solar radiation escaping to space relative to the scenario of higher levels of greenhouse gasses (right) that insulate re-radiated heat from escaping the atmosphere (<https://www.c2es.org/content/climate-basics-for-kids/>).

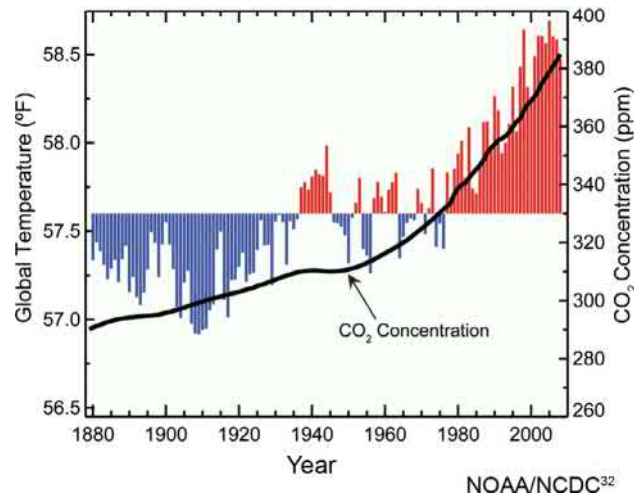


Fig. 2 Trend in global mean temperature anomalies (°F) and CO₂ concentrations (parts per million) from 1880 to present (<https://www.zmescience.com/science/news-science/co2-mid-century-unprecedented/>).

the globe and differences in pressure and temperature with depth, and our inability to measure this complexity. It is therefore understandable that there have been some differences in results from researchers trying to measure and predict sea level rise contributions from thermal expansion and ice melt. Limits in our use of land and satellite-based measures and how to interpret the data are central to these differences, but the main message from nearly all studies is that both ice loss and thermal expansion are significant contributors to the dynamics of sea level rise. Deciphering this will require further advancements in the tools we use to measure and model ocean systems.

With sea level rise occurring at an estimated 3 mm/year (Fig. 4), it has been predicted that mean sea levels will start to impact islands and coastal zones by the mid-century. However, the first signs of sea level rise to islands and atolls are being observed now through tropical cyclones (hurricanes and typhoons), which can push water toward the shore by the force of the winds moving cyclonically around the storm, a phenomenon called “storm surge.” There can also be an added increase in water height due to the low pressure associated with storm surge, but this is minimal relative to the piling of water to land from winds. Islands and atolls already experiencing elevated sea levels are thus immediately threatened by storm surge and waves, which in some cases can be over 20 ft above local average sea heights. In 2005, within the Gulf of Mexico the category-5 hurricane Katrina carried a storm surge of between 24 and 28 ft, covering 90 miles of the coastline consisting of islands and low-elevation coastal areas. The impacts of storm surge cover immediate flooding, erosion and loss of lands. Somewhat unique to islands and atolls and particularly from porous coral lands, the intrusion of seawater from storm surge can contaminate groundwater, making the island uninhabitable to humans and wildlife.

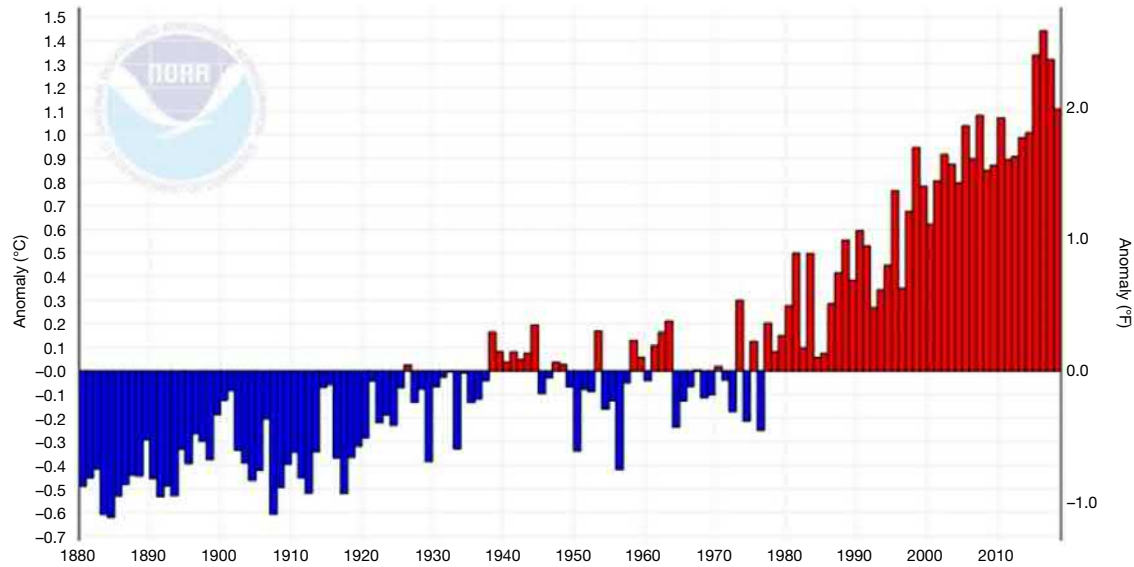
Regional Effects of Sea Level Rise

Sea level rise is a global issue, but the distribution and impact of sea level rise is not evenly distributed across oceans due to differences in ocean-atmospheric interactions, and the elevation and geological makeup of the land. The greatest increases in sea level rise and impacts to islands and atolls have been first seen in the western tropical Pacific and Indo-Pacific regions which contain most of the world’s low-lying islands and atolls (Fig. 5). The western Pacific is observed to have some of the greatest increases in sea level rise due to El Niño-related piling of water toward the western Pacific from sustained trade winds. The combination of low lying islands and atolls, many of which are no higher than 4 m and their geological makeup of coral has made this region the most prone to erosion and inundation (Figs. 6 and 7). As a result, the south Pacific and Indo-Pacific islands have been the sentinels of sea level rise, expressing the first scientific confirmation of islands lost due to rising seas and erosion in the Solomon Islands (Micronesia). Under the IPCC Special Report on Emission Scenarios, one of the scenarios predicted an annual increase of 3–4 mm-year with an increase of between 0.22 and 0.44 m in the 2090s to 1990 levels, which would cause further erosion and inundation of the world’s most vulnerable region to sea level rise. As we will see later in this article, this has led to some of the first occurrence of island communities to plan for eventual loss of their islands.

Ecological Impacts

Islands and atolls are of the most ecologically vulnerable to sea level rise due to their susceptibility to erosion and inundation, and their relative isolation of unique habitats, species, and communities. We have all heard of the large flightless Dodo bird (*Raphus*

Global Land Temperature Anomalies, January-December



Global Ocean Temperature Anomalies, January-December

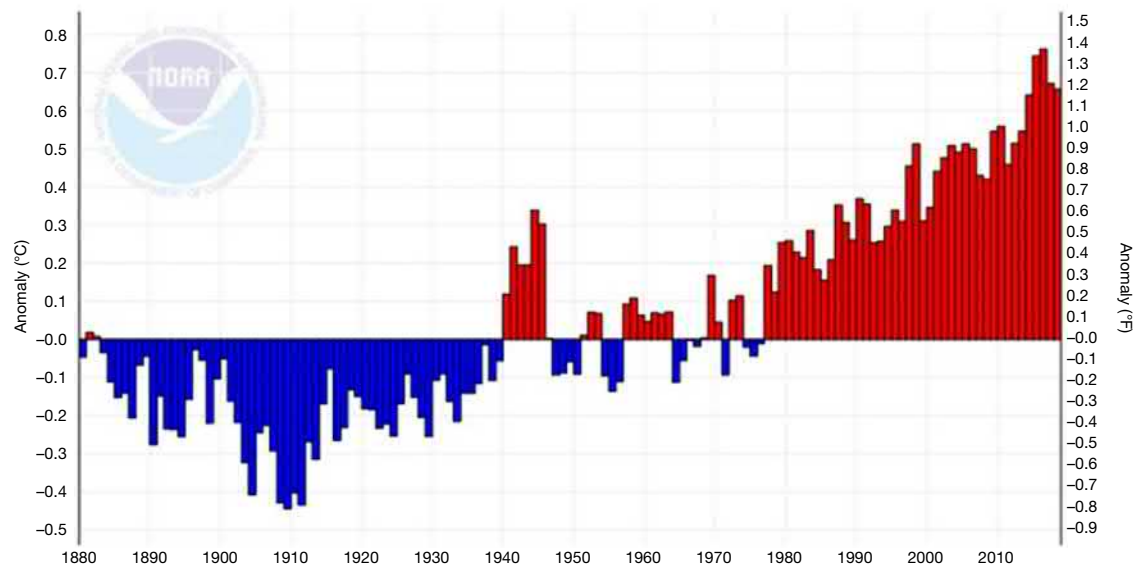


Fig. 3 Annual global land (top) and ocean (bottom) temperature anomalies from 1880 to 2019 (<https://www.ncdc.noaa.gov/cag/global/time-series/globe/ocean/1/1/1999-2019>).

cucullatus) of the islands east of Madagascar in the Indian Ocean, a species that went extinct due to overharvest and the introduction of invasive species (Citation). Although climate change didn't play a role in its demise, the Dodo is probably the most iconic animal representative of the vulnerability of island species to extinction. In fact, of the 724 recorded animal extinctions in the last 400 years, about half were island species (Citation). As islands and atolls are the most susceptible to sea level rise, they are the first indicators of measuring biodiversity loss, both the species that reside on land and those that reside in nearshore waters.

Marine aquatic species that rely on islands and atolls predominantly rely on habitats within shallow reef flats (within atolls) and coral reefs. Corals are bioengineers of their environment, growing hard substrate around islands that act as a barrier to erosion from sea level rise and storm events, and providing a rich diversity of habitats from which species have evolved to rely on for food and cover. In a recent study (Perry et al., 2018), researchers measured the vertical growth rate of corals to assess the threat of sea level rise to coral reefs, and they found that coral growth will not be able to keep up with current rates of increasing sea levels. Moreover, corresponding increasing ocean temperatures may further impede growth due to heat-related stress and coral bleaching. The implications of this include the potential loss of coral reefs and their rich biological communities, and the increase in loss of land due to exposure to waves and erosion. The effects to more shallow water reef and sand flat communities that are characteristic within atolls

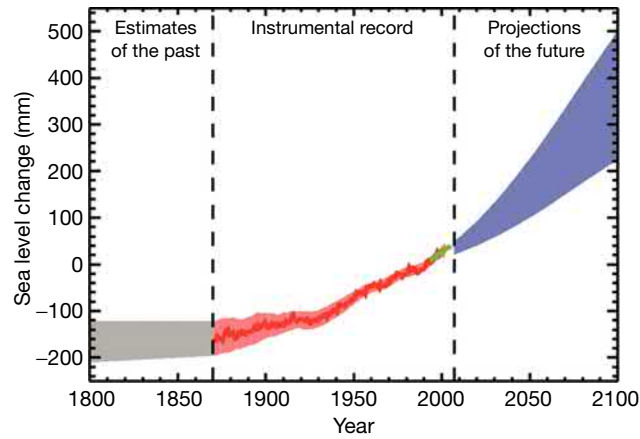


Fig. 4 Global sea level change (mm) from past estimates, direct measures and future predictions (https://archive.ipcc.ch/publications_and_data/ar4/wg1/en/faq-5-1-figure-1.html).

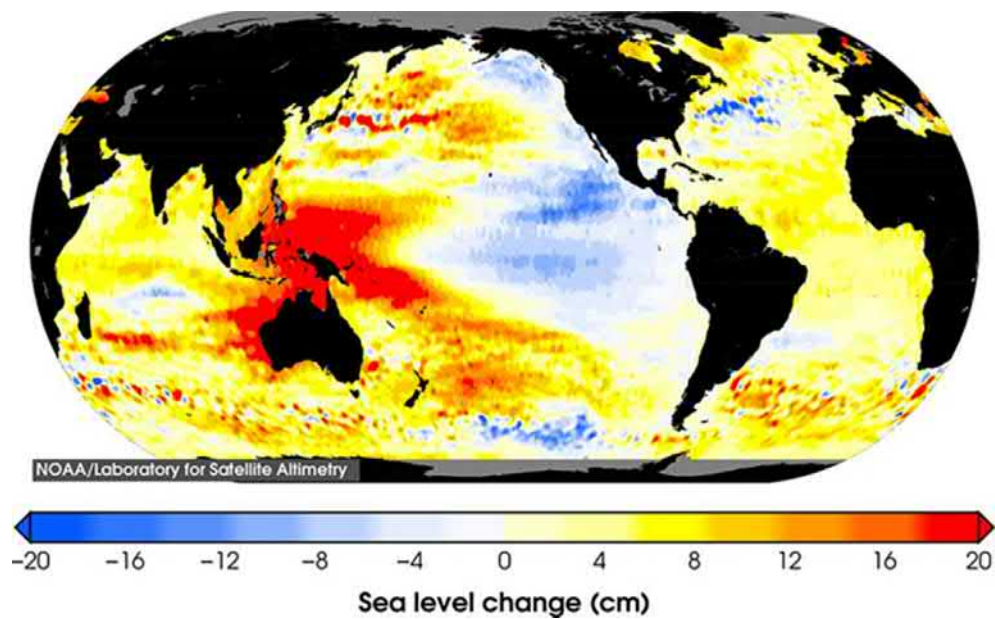


Fig. 5 Global sea level anomalies from average sea level height (cm), showing the regions with greatest increases in sea levels within the Western Pacific (<https://oceanservice.noaa.gov/facts/globalsl.html>).



Fig. 6 Abaiang Atoll, Republic of Kiribati, showing part of the atoll's lagoon and low-lying island ring and the susceptibility to erosion and sea level rise (<http://simondonner.blogspot.com/2013/05/kiribatis-battle-against-sea-level-rise.html>).



Fig. 7 Sea level rise in the Solomon Islands. The combination of sea level rise and increasing storm surge has made communities and ecosystems highly vulnerable to erosion and inundation (<https://www.newstalk.com/news/as-sea-levels-rise-in-the-pacific-five-of-the-solomon-islands-have-disappeared-598805>).

are not well known, due in part to these habitats being less studied. But the dependence of inner-atoll species on these shallow water habitats undoubtedly place them under direct threat of sea level rise because of the very nature of shallow waters being vulnerable to erosion and the eventual loss of low-lying atolls.

Of all species related to islands and atolls, the most susceptible to extinction from sea level rise spend at least part of their life on land. Islands are home to 20% of the world's bird, plant and reptile species, a number of which are endemic and not found anywhere else in the world. Many species of birds use islands as rest areas, foraging grounds and nesting and rearing, all of which are critical to their long-term survival. Sea turtles such as the green (*Chelonia mydas*) and leatherback (*Dermochelys coriacea*), although aquatic, rely on sandy beach habitats for nesting that are directly threatened by storm surge and increasing sea levels. Terrestrial plants and animals such as endemic invertebrates (insects, snails, and crabs), birds and mammals are constrained to their limited land habitats, the loss of which can account for significant impacts to the genetic integrity at the population and species level. As islands disappear, the loss of extant populations and their genetic diversity can reduce connectivity between populations on other islands, reducing their resiliency to persist in a changing climate. Ultimately, the loss of species can undermine whole ecosystems and the very web of life that island nations depend upon for subsistence and economic prosperity.

Socioeconomic and Cultural Impacts

As islands and atolls are on the forefront of climate change and sea level rise, so are the socioeconomic and cultural impacts that are embedded within communities and whole island nations. Islands and atolls are commonly isolated, with communities having a high proportion of their livelihood based on subsistence living and economies that are tied to nearshore resources and tourism. Most of the urban and rural communities of the western tropical Pacific islands, as well as other island systems around the world rely on healthy nearshore ecosystems as a major (>50%) source of food-protein from fish and invertebrates, the diminishing of which would undermine food security and economic opportunities in fisheries. In terms of tourism, the loss of coral reefs and beach habitats would undermine diving/snorkeling and sport fishing which are core to destination tourism in island economies. For example, the island nations of Fiji, Vanuatu, Kiribati which are of the most threatened to sea level rise receive between 20% and 40% contributions to their total economies (citation?). Aside from the loss of healthy ecosystems for subsistence and economic prosperity, the loss of potable freshwater from saltwater intrusion and climate-driven droughts, and increasing intensity of storm events have also been realized as major threats to the future of island and atoll communities.

One of the more eye-opening responses to early stage sea level rise to island and atoll communities has been the recent consideration of having open-access migration of people from threatened island and atoll nations (e.g., Tuvalu and Kiribati) to other countries such as Australia and New Zealand. This "climate refugee" scheme (is there a citation for this?) has not been to empty island nations but to preemptively address a potential rush to leave islands to other regions in the future, and to make these nations more sustainable, economically and environmentally given projections in population rise. The potential loss of islands and atolls to rising sea levels however leave few other options for life on the islands. Some have proposed alternative measures such as building walls and barriers to protect from erosion and intrusion, which have their own set of environmental impacts to reefs and species that need specific nearshore habitats, such as sea turtles, shore birds, fish, and invertebrates. For example, in Indonesia, there is a plan to build a giant sea wall, build a water reservoir and reclaim land in order to save the world's fastest sinking city (https://en.wikipedia.org/wiki/Giant_Sea_Wall_Jakarta, accessed 13 Aug 2019). The ultimate loss of islands or inhabitability due to sea water intrusion leave

no other options other than moving people off island. In this case the migration of people to distant lands would constitute not only an economic loss but more critically the loss of heritage and cultures that have evolved with the islands for thousands of years.

Mitigation

The causes of climate change and sea level rise has had a disproportionate effect on island communities due to the sources coming from more developed and populated regions of the world. As a result, addressing the progression of climate change will require a global effort to make unprecedented changes in the way we live. As the center for scientific knowledge, synthesis, and guidance on climate change, the IPCC has used global temperatures as reference points to preindustrial era levels, with our current state being approximately 1°C (XF) above values from the mid-1800s. From this, the IPCC has set future gas emissions and carbon budgets to estimate how much greenhouse gas levels would need to be reduced to reach threshold levels of between 1.5 °C and 2 °C. Based on their 2014 report, in order to avoid global temperatures to exceed the 2 °C threshold, greenhouse gas emissions in 2050 will have to be 40–70% lower than what they were in 2010 (IPCC, 2014). This reduction would not remove effects of warming and sea level rise, but would lessen future impacts and allow time to adjust economies and society to alternative energy sources. This reduction will require unprecedented changes in the way we live, encompassing shifts toward nonhydrocarbon energy sources, and major shifts in nearly every aspect of society including industry, housing, and transportation.

As a global issue, nations are coming together to agree on policies to reduce greenhouse gas emissions based on the 1.5 °C and 2 °C threshold levels set by the IPCC. Central to this has been the Paris Agreement (<https://unfccc.int/process-and-meetings/the-paris-agreement/the-paris-agreement>, accessed 13 Aug 2019), which was signed in 2016 to bring nations together to address greenhouse gas emissions mitigation, adaptation, and finance. Proposed measures of mitigation have pushed for nations' to shift to cleaner alternative energy sources and to increase efficiencies. However, of the 31 main economies on the Paris Agreement, to date only 7 have at least met the ≤ 2 °C threshold, with 9 at < 3 °C, and 15 at < 4 – $4 +$ °C. China and the United States which comprise 40% of the world's emissions are currently at the < 4 and $4 +$ °C threshold, respectively. The primary shifts in energy to work toward lowering emissions and ultimately the 1.5–2 °C level have been wind, solar and hydropower (and somewhat controversial use of nuclear power). Wind and solar power can be highly effective however they are limited by areas/regions with sustained conditions to provide a constant source of energy. Both of these options also require the capacity to store energy, and future technology in battery capacity is critical to making wind and solar power more amenable to regions across the world. Hydropower can be generated a number of ways, either through dams or tidal and wave generation. Of these, dams can have a profound environmental impact on river and riparian systems, altering habitats and restricting migration of fish and other organisms that rely on unimpeded waterways to survive.

At the local level of islands and atolls, the options for adapting to climate change and sea level rise are few. Proposals for the placement of barriers to reduce erosion and walls to hold back flooding are fraught with environmental impacts, such as the destruction of essential habitat for many species that use the nearshore and shoreline habitats around islands. Other proposals to raise land and building homes on stilts have also been considered, the results of which would only be a short-term fix to a problem that will continue into the future if emissions are not substantially reduced. For all of the above options, the economic cost of building barriers or elevating lands and structures also make it nearly cost-prohibitive. As discussed earlier, with the progression of sea level rise the only option will be the migration of populations to higher lands.

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Arctic Ocean Islands

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Abstract

The Island archipelagos of the Arctic Ocean support the most extreme examples of Arctic-adapted plant and animal communities. Compared with much of the planet, they have seen relatively little human disturbance. Their current faunas and floras have been strongly influenced by the degree of isolation of the different island groups and by Pleistocene glaciations and post-Pleistocene sea-level changes. Faunal interchange with adjacent continents has been modified by the annual connection via winter sea-ice. Current trends towards warmer temperatures and shorter sea-ice seasons in the Arctic may eventually result in the loss of seasonal ice-bridges, isolating some archipelagos and preventing colonization by southern faunal elements. Understanding and protecting these islands is the key to preserving the current remnants of the Pleistocene fauna and flora.

Introduction

The Arctic Ocean, along with the adjacent Kara, Barents, Laptev, East Siberian, Chukchi and Beaufort seas, and circumscribed by the northern extremities of Greenland and the Eurasian and North America continents, contains several important island groups. The largest of these are Svalbard (Norway), Novaya Zemlya, Franz Josef Land (*Zemlya Frantsa-Iosifa*), Severnaya Zemlya, the New Siberian Islands (*Novosibirskiye Ostrova*), and the comparatively isolated Wrangel Island, along with its small companion, Herald Island, all in Russia, and the Canadian Arctic Archipelago (Fig. 1). The Canadian islands include some very large ones situated close to the North American mainland (e.g., Baffin, Victoria, Banks islands) which are ecologically indistinguishable from the adjacent mainland. Consequently, for this review, I deal only with the Queen Elizabeth Islands to the north of the Parry Channel—Viscount Melville Sound—M'Clure Strait waterway at about 74°N (Fig. 2). These islands are more comparable, ecologically, to the other Arctic Ocean archipelagos than those farther south. For some purposes, I will discuss the Palearctic islands in two groups: (1) the islands of the Barents and Kara seas (Fig. 3), which experienced only brief and limited connections to continental Eurasia during the last glaciation and (2) the East Siberian Sea islands (Fig. 4), which for most of the last glaciation stood within a broad coastal plain extending hundreds of kilometers north of the current coast of Siberia.

Pleistocene and Holocene Histories

All of the islands under consideration were strongly affected by events during the last ice age (Pleistocene) and especially by the last glacial advance (Wisconsinan/Weichselian) and by postglacial (Holocene) events, especially sea-level changes. Many of the islands

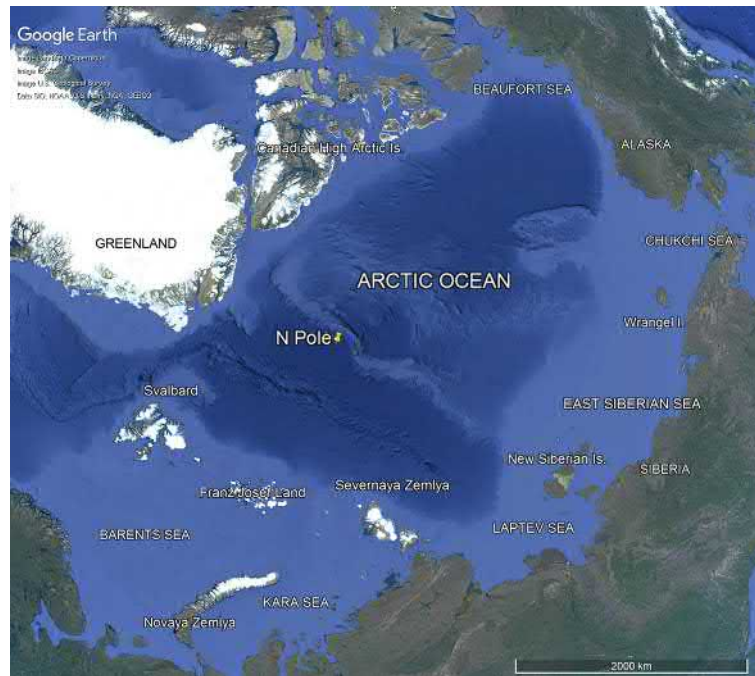


Fig. 1 The Arctic Ocean and the surrounding archipelagos and islands (Google Earth Pro, 2018).



Fig. 2 Islands of the Canadian Arctic Archipelago, north of the Parry Channel—Viscount Melville Sound—M'Clure Strait waterway (Google Earth Pro, 2018).

were entirely, or almost entirely covered by ice at the peak of glacial periods and consequently their terrestrial ecosystems tend to be very young, dating from the period of Wisconsinan deglaciation ~10,000 years ago. The only exceptions were Wrangel Island and parts of the New Siberian Islands and the northwesternmost of Canadian high Arctic islands, none of which was glaciated. As well, the reduced sea-levels of the glacial period exposed large areas of additional land around all of the archipelagos, especially Severnaya Zemlya and the islands of the East Siberian Sea, all of which had long-lasting land connections to the mainland of Asia during Pleistocene sea-level minima (Tolmachev, 1970; Formana et al., 2004; Jakobsson et al., 2012). These low-lying areas would have supported additional periglacial land which would have been home to a continental fauna and flora, components of which later became marooned after postglacial sea-levels rose (Andreev et al., 2009). Remnants of Pleistocene ice sheets remain on Devon, Ellesmere and Axel Heiberg islands, in Canada, on all the major islands of Svalbard and in Franz Josef Land, Novaya Zemlya and



Fig. 3 Islands of the Barents and Kara seas (Google Earth Pro, 2018).



Fig. 4 Islands of the East Siberian Sea (Google Earth Pro, 2018).

Severnaya Zemlya in Russia. Isostatic uplift, following the decay of major ice sheets, has affected most of the islands previously glaciated, leading to the creation of extensive raised beaches (Fig. 5).

Terrestrial Ecosystems

Flora

The vegetation of all the Arctic Ocean islands consists predominantly of graminoid and prostrate dwarf shrub tundra (G1 and G2, CAV Team, 2003) and lichen and moss-dominated cryptogam barrens (B1, B2). All these communities are characterized by plants of very short stature. The archipelagos fall within seven floristic provinces (clockwise from Wrangel I.): West Chukotka (Wrangel I.), Yana-Kolyma (E Siberian Is.), Taimyr (Severnaya Zemlya), Polar Ural (Novaya Zemlya), Svalbard-Franz Josef, Ellesmere-N Greenland (Ellesmere and Axel Heiberg islands and eastern Devon I.), Central Canadian Arctic (western Queen Elizabeth Is.). Provinces are defined on the basis of taxonomic affinities resulting from post-Pleistocene colonization processes, but the genera involved show much overlap (Daniëls et al., 2013). The most diverse and widespread families are Caryophyllaceae, Cruciferae, Cyperaceae, and Saxifragaceae and the most diverse genera *Carex*, *Draba*, and *Saxifraga*. There is a relatively low incidence of



Fig. 5 Raised beach deposits behind shorelines near Resolute Bay, Nunavut, Canada (Google Earth Pro, 2018).

endemism, presumably because of the relatively short time since deglaciation. Significantly, highest endemism is found at the unglaciated Wrangel Island, where 35 vascular plants endemic to the Arctic are present (33% of all Arctic endemics; Daniëls *et al.*, 2013). Wrangel Island also has a greater total diversity of vascular plants (315 species) than either Ellesmere Island, in Canada (199 species), or Svalbard (211 species), both considerably larger (Cf. Petrovskii and Yurtsev, 1970).

Vegetation throughout the Arctic Ocean archipelagos is very sparse, and few plants grow above 200 m altitude, apart from prostrate mosses and lichens. Above ground plant biomass is predominantly less than 50 g m^{-2} (CAV Team, 2003). Soils throughout are underlain by permafrost, impeding drainage and encouraging the creation of tundra polygons and bogs (Fig. 6), but as most precipitation falls as snow, there are few permanent watercourses. Many of the islands experience little rainfall and are regarded as polar deserts. Vegetation is frequently restricted to seasonal drainage channels (Fig. 7). The main factors controlling plant growth and the consequent vegetation communities in the high Arctic are summarized by Aiken *et al.* (2018):

- "Climate, which imposes a major temperature-based zonation, modified by local climates or microclimates;
- Drainage, which controls the summer water regime and has some effect on frost action;
- Nutrients, that are in limited supply in most arctic soils;
- Local soil type, which, along with climate and drainage, influences soil stability and fertility;
- Snow cover, which controls the duration of the growing season."



Fig. 6 Ice-wedge polygons on lowland tundra, Wrangel Island (Google Earth Pro, 2018).



Fig. 7 Braided drainage with vegetation concentrated along drainage channels, Khuzny Island, Novaya Zemlya (Google Earth Pro, 2018).

Despite the generally very low productivity of terrestrial biomes on the archipelagos, small areas exist where local conditions of moisture and soil types combine to create much lushier areas, sometimes termed “high Arctic oases” (Edlund and Alt, 1989). Examples in the Canadian islands include Polar Bear Pass on Bathurst Island (Sheard and Geale, 1983; Fig. 8), Lake Hazen on northern Ellesmere Island (Fig. 9), and Truelove Lowland, on Devon Island (Bliss, 1977; Fig. 10, Cf. Fig. 11) and. These areas typically support a much higher density of grazing mammals, hence also of wolves, than areas of lower productivity.

Oceanography

All the island archipelagos fall within Arctic waters, but the southeastern coasts of the Canadian islands and the west coast of Svalbard are affected by milder waters originating from the North Atlantic (Tang et al., 2004; Wassmann et al., 2006). To a small extent this is also true of Wrangel Island, where a plume of warm water, originating from the Bering Sea, moves westwards towards the east coast (Ahlén and Garrison, 1984). The waters surrounding all archipelagos are currently 100% covered by sea ice in winter



Fig. 8 Polar Bear Pass on Bathurst Island, a “high Arctic oasis” with a concentration of ungulates, loons, shorebirds, jaegers and snowy owls (Nettleship and Smith, 1975).



Fig. 9 Lake Hazen, a glacier-fed lake on northern Ellesmere Island (Google Earth Pro, 2018).



Fig. 10 Truelove lowlands and lowlands near Cape Sparbo, two “high Arctic oases” on the northeast coast of Devon Island (Cf. Fig. 11; Google Earth Pro, 2018).

but break up along the west coast of Svalbard occurs in May and in June in Baffin Bay and Lancaster Sound, south and east of Devon Island, and in the Kara Strait, south of Novaya Zemlya. Break-up in waters surrounding the other island groups occurs in July or later and in some years sea ice remains year-round adjacent to parts of Franz Josef and Severnaya Zemlya, giving these archipelagos very cool summers.

Terrestrial Vertebrates

The terrestrial vertebrate fauna of the various archipelagos largely reflects their isolation from continental landmasses. Both Wrangel Island and the New Siberian Islands were connected to the Asian mainland during periods of low sea levels which persisted into the postglacial period, so that they supported a diverse fauna including woolly mammoth, wild horses and musk oxen (Boeskorov,



Fig. 11 North-central Devon Island—dry upland area with low moisture and little vegetation (Google Earth Pro, 2018).

2004). The birds and mammals of the Canadian islands, with a maximum water barrier of 48 km separating them from the North American mainland (Gaston et al., 2012), are similar to those of mainland North American Arctic ecosystems, while those of the other archipelagos vary in their diversity, with Svalbard and Franz Josef Land, the most isolated groups, being the most depauperate. Svalbard supports only 15 species of nonmarine birds, compared to 36 species in the Canadian islands (Ganter and Gaston, 2013). Moreover, there are no wholly freshwater fishes in Svalbard (anadromous Arctic Char *Salvelinus* sp. is present).

Mammals

Arctic fox and polar bear occur on all the Arctic archipelagos. Traveling and living on the sea-ice, as they do in winter, they are capable of reaching all land masses in the Arctic ocean. Otherwise, all of the archipelagos have supported at least one species of terrestrial mammal (Fig. 12), but the most isolated (Svalbard, Franz Josef) support only reindeer/caribou *Rangifer tarandus* (reindeer

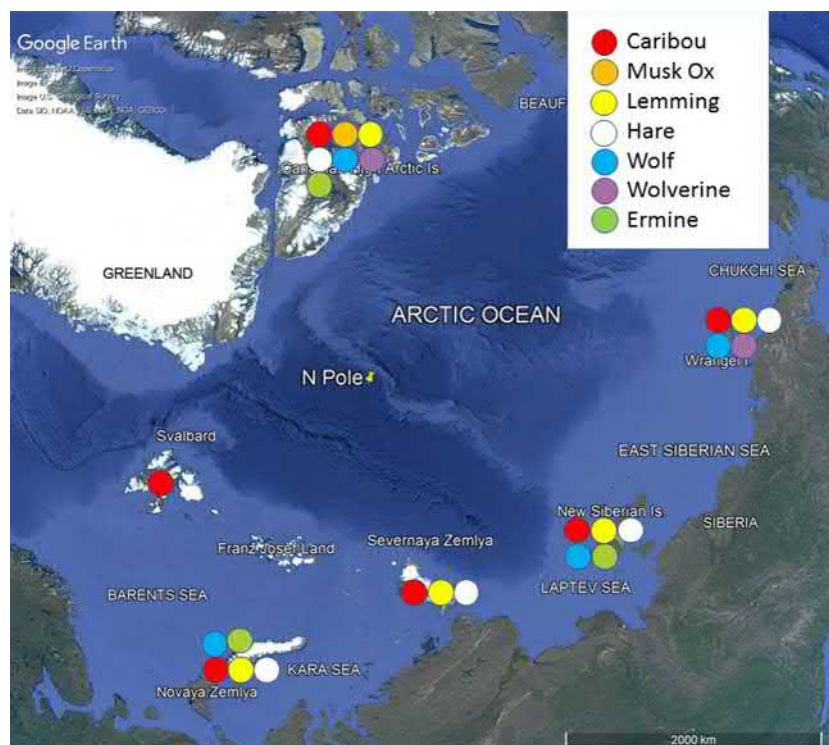


Fig. 12 Distribution of terrestrial mammals on Arctic Ocean archipelagos (data from Gaston et al., 2012).

became extinct on Franz Josef more than a millennium ago (Zale et al., 1994). Within the Canadian Arctic, caribou routinely move across sea ice over distances of up to at least 84 km (Miller et al., 2005). This suggests that herds on Novaya Zemlya, Severnaya Zemlya and the New Siberian Islands should be capable of interchange with Siberian mainland populations. Wrangel Island (140 km from the Siberian mainland), Franz Josef (367 km from Novaya Zemlya) and Svalbard (220 km from Franz Josef, and 640 km from mainland Norway) may be outside the normal over-ice dispersal range for caribou. Populations on those archipelagos, only one of which persisted into historic times, may have colonized those islands during the Pleistocene when lower sea-levels would have reduced over-ice distances. The current isolation of Svalbard caribou is emphasized by their low genetic diversity (Cronin et al., 2006).

Diversity of mammals is greatest on the islands of the Canadian archipelago, where all the “Arctic specialists” can be found. It is the only group of islands supporting Musk Ox *Ovibos moschatus* and the Arctic hare *Lepus arcticus* is found on most islands, whereas its congener in Eurasia, the mountain hare *Lepus timidus* only reaches the southernmost islands of Severnaya Zemlya, Novaya Zemlya and New Siberian Islands. Lemmings, *Dicrostonyx* and *Lemmus* spp., are found on all the larger islands in the Canadian Archipelago, on Novaya Zemlya, Severnaya Zemlya, the New Siberian Islands and Wrangel Island, but not on Franz Josef or Svalbard, presumably because of their isolation (Fig. 5).

Among carnivores, wolf *Canis lupus* is found on most of larger Canadian islands, except the westernmost, where caribou are also rare, and on all the Russian archipelagos except Franz Josef, although only an occasional visitor on Severnaya Zemlya (Gaston et al., 2012). The ermine *Mustela erminea* occurs on all the larger islands where lemmings occur, while the wolverine *Gulo gulo*, although very sparse, has been recorded on several of the Canadian islands, but is absent from the Palearctic archipelagos apart from Wrangel Island (Fig. 12).

Birds

Being able to fly allows birds to readily colonize distant islands so that their distribution is less affected by the periodic availability of land connections. Many high Arctic species have circumpolar distributions, (e.g., red-throated loon *Gavia stellata*, willow and rock ptarmigan *Lagopus lagopus*, *L. mutus*, gyrfalcon *Falco rusticolus*, snow bunting *Plectrophenax nivalis*, Lapland longspur *Calcarius lapponicus*). However, geese and shorebirds tend to be confined either to the Nearctic (e.g., Ross's goose *Anser rossii*, semipalmated, white-rumped, western and Baird's sandpipers *Calidris pusilla*, *C. fuscicollis*, *C. mauri*, *C. bairdii*, or the Palearctic (e.g., pink footed, bean and barnacle geese *Anser brachyrhynchus*, *A. fabalis*, *Branta leucopsis*, dotterel *Charadrius morinellus*), little and red-necked stints *Calidris minuta*, *C. ruficollis*, curlew sandpiper *C. ferruginea*).

In contrast with terrestrial mammals, diversity of waterfowl and seabirds among the Arctic Ocean islands, is highest on Svalbard, the most remote archipelago (Figs. 13 and 14), perhaps because of lack of terrestrial predators and competitors. The reverse is true of rodent-eating birds because most Arctic raptors depend on lemmings to provision their young and consequently most are absent from Svalbard and Franz Josef (Fig. 15). Shorebirds diversity is fairly similar among archipelagos (Fig. 16), with the exception of

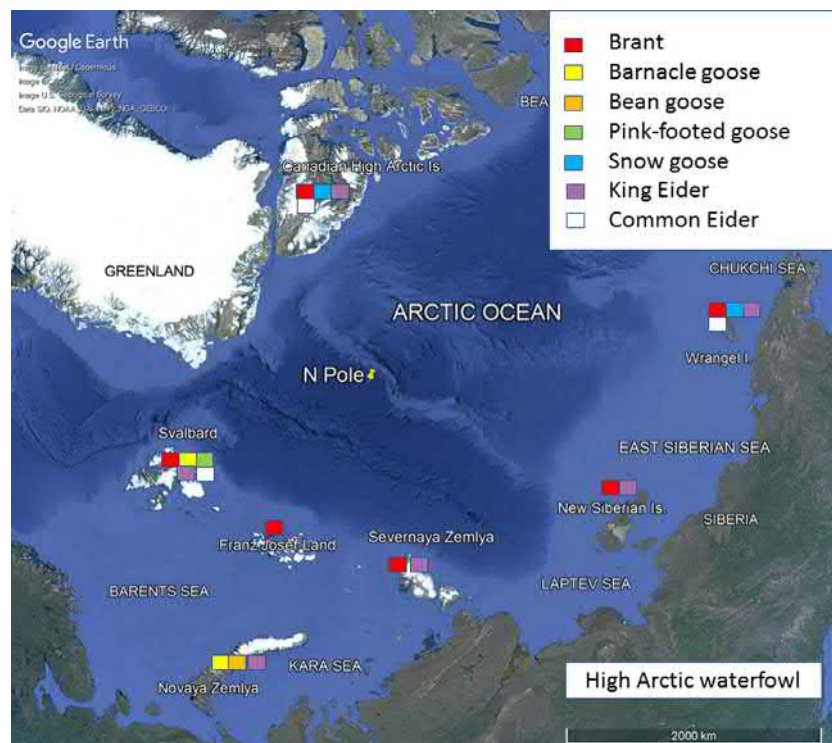


Fig. 13 Distribution of breeding waterfowl among Arctic Ocean archipelagos. Data from Portenko (1972), Cramp (1977, 1982, 1983, 1985), De Korte et al. (1995), and Ganter and Gaston (2013).

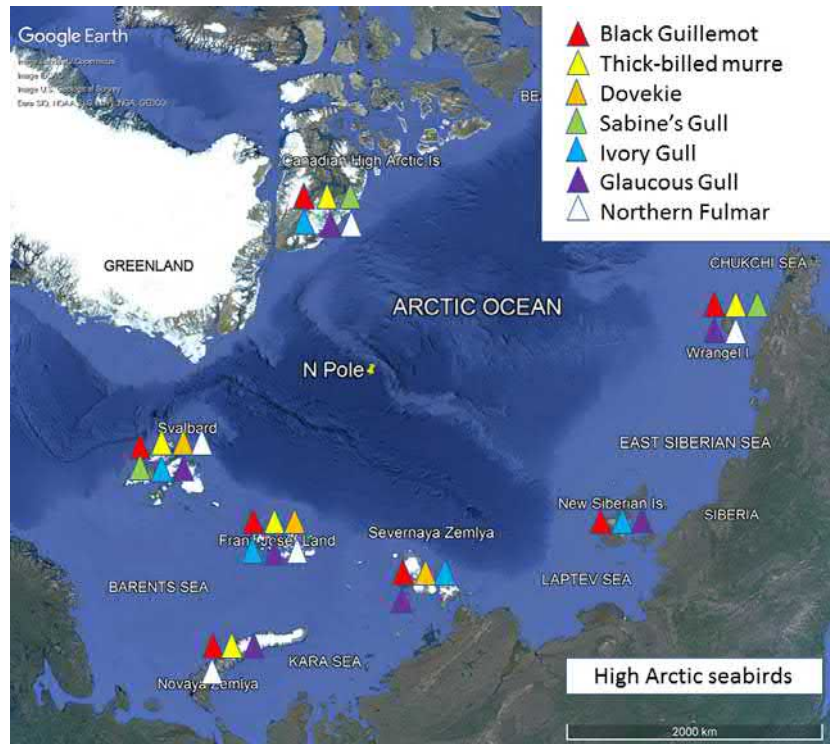


Fig. 14 Distribution of breeding seabirds among Arctic Ocean archipelagos. Data from Portenko (1972), Cramp (1977, 1982, 1983, 1985), De Korte et al. (1995), and Ganter and Gaston (2013).

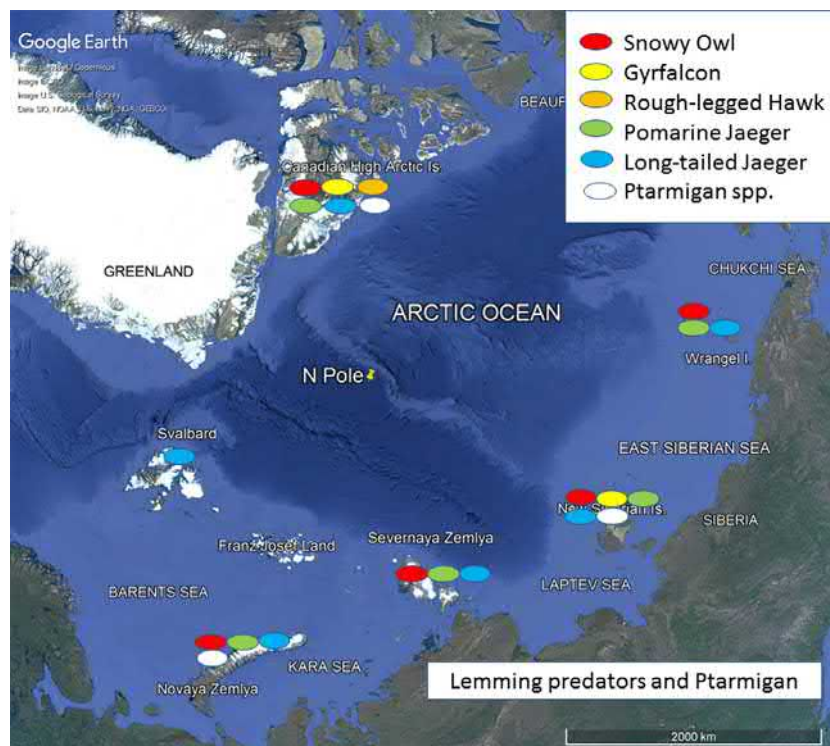


Fig. 15 Distribution of breeding raptors and ptarmigan among Arctic Ocean archipelagos.

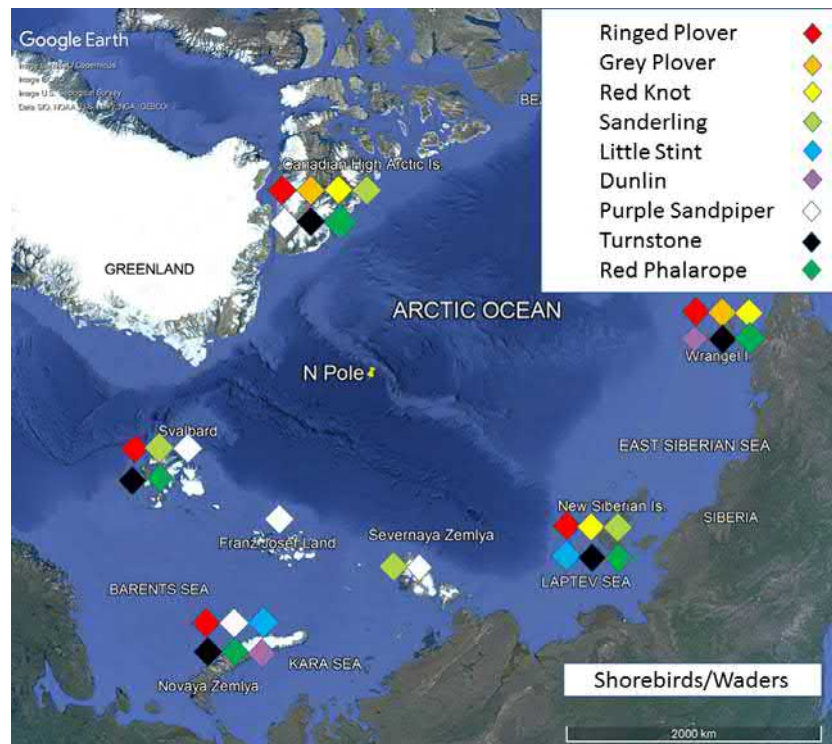


Fig. 16 Distribution of breeding shorebirds/waders among Arctic Ocean archipelagos. Data from Portenko (1972), Cramp (1977, 1982, 1983, 1985), De Korte et al. (1995), and Ganter and Gaston (2013).

Franz Josef, where only a single species breeds (purple sandpiper *Calidris maritima*). Shorebird diversity may relate principally to the extent of suitable habitat—for most species lowland wet tundra with sedge meadows—rather than to isolation.

Marine Ecosystems

Mammals

The islands of the Arctic ocean play an important role in marine ecosystems by providing breeding and hauling out opportunities for marine birds and mammals. Among mammals, the Arctic Ocean islands are particularly significant for polar bears *Ursus maritimus* and walrus *Odobenus rosmarus* which are found on all the archipelagos, although walrus are absent from the western and northern Queen Elizabeth Islands.

Walrus haul out on sea-ice when it is present, but once the seasonal ice has gone, they haul out on shore in dense aggregations which can number thousands of animals. They persist in areas of extensive winter ice cover by exploiting polynyas—areas of water kept open by strong currents and upwellings, but some populations are migratory, particularly the Pacific subspecies (*O. r. divergens*), which commutes between winter in the Bering Sea and summer in the Arctic Ocean, when large numbers occur at Wrangel Island (Aug–Oct; Fay, 1982). Despite this very large biomass of marine animals coming on land periodically, walrus have little impact on terrestrial ecosystems. Their droppings are deposited very close to the high-water mark and are mostly washed into the sea. They may provide prey for polar bears and carcasses, either killed by bears or other causes, may provide food for scavengers, such as ravens and gulls.

In contrast, polar bears may have significant impacts on terrestrial ecosystems. While ashore in summer, after the retreat of sea ice, they feed on grasses and forbs, as well as on birds' eggs and nestlings, on lemmings and caribou and on freshwater fishes. They frequently congregate in the vicinity of walrus haul-outs and kill smaller animals, especially dependent pups. Females frequently dig maternity dens on shore, in persistent snow drifts, usually within a few kilometers of the coast (Stirling, 1988).

The existence of the Arctic Ocean islands extends enormously the area of the Arctic Ocean accessible to both walrus and polar bears. The islands give access to haul-out and denning sites and, with their indented coastlines, provide excellent habitat for ringed seals *Pusa hispida*, the primary prey of the polar bear, as well as creating the type of narrow straits through which tidal currents maintain year-round polynya necessary for overwintering walrus.

Seabirds

Some species of seabird breed in dense colonies which not only provide opportunities for land-based predators, but also affect the local terrestrial ecosystems by importing large quantities of marine nutrients (Fig. 17) into the terrestrial environment (Klimowicz et al., 1997; Jónsdóttir, 2005; Zwolicki et al., 2013). The most common species breeding on the Arctic Ocean islands are the northern fulmar *Fulmarus glacialis*, thick-billed murre *Uria lomvia*, black-legged kittiwake *Rissa tridactyla*, dovekie *Alle alle*, and black guillemot *Cepphus grylle*. The murre and kittiwake normally breed on very steep coastal cliffs. Consequently, much of their droppings wash into the sea. However, dried feces, along with discarded food remains, are frequently blown up the cliffs by strong winds and are deposited in a zone which may be up to a kilometer wide inland from the cliff edge. Enrichment of the vegetation in this zone is clearly apparent at many colonies (e.g., Gaston and Donaldson, 1996). The effects of dovekie manuring can be more extensive, because their colonies are often situated some kilometers inland and the effects of manuring are found over the intervening area (Zwolicki et al., 2013). Similar effects can be seen on small islands where dense aggregations of common eider *Somateria molissima* breed.

Biogeography

The Arctic Ocean archipelagos share many physical characteristics related to their harsh climates and remoteness and many plants and animals occurring in the high Arctic archipelagos have circumpolar distributions. In the case of less widespread taxa, the flora and fauna of the Eurasian archipelagos are dominated by plants and animals of Palearctic affinities, whereas those of the North American sector include a greater proportion of organisms with Nearctic affinities. This division is more striking when we consider birds than for other organisms, perhaps because most Palearctic migrants winter in Asia or Africa, whereas most Nearctic migrants winter in the Americas. Some birds in the eastern Canadian high Arctic, however, move eastwards in fall to winter in Europe and Africa, migrations which presumably mirror the pathways by which they colonized the high Arctic after the last glaciation.

Human Influence

Human history in the Arctic Ocean islands goes back to mid-Holocene times on the New Siberian Islands, at Wrangel Island and at some (perhaps all) of the Canadian islands (Sutherland, 1980), including Ellesmere (Schledermann, 1978), Axel Heiberg, Devon and Cornwallis islands. However, Svalbard and Franz Josef Land probably were not accessed by people before being discovered by modern Europeans some time after 1000 CE (Chochorowski, 1991). Perhaps because of a general deterioration of climate during



Fig. 17 Freshwater ponds at the base on the Northern Fulmar colony at Cape Vera, Devon Island. The bright green margins show the effects of nutrient enrichment by the Northern Fulmar colony on the cliffs just inland of the ponds. Photo: Mark Mallory.

the last millennium, compared with the earlier Holocene, native people were absent from all of the archipelagos, other than Novaya Zemlya, by the time the islands were discovered by medieval and later whalers and explorers.

In the New Siberian Islands, evidence of Mesolithic hunters has been found on Zhokov Island (77 km²), in the northern part of the archipelago. A site dated at 7900 BP suggests that the hunters killed caribou and polar bears (Pitul'ko, 1993). By that period sea levels were similar to the present day, so these people had the technology to cross substantial water barriers: Zhokov is more than 100 km from Novaya Sibir Island, the easternmost of the larger East Siberian Islands and 38 km from the nearest potential “stepping stone” island.

Discovery of the Arctic archipelagos by Europeans may have begun with contact between Vikings and Inuit on Ellesmere Island, some time after 1200 CE (Schledermann, 1980). Vikings may well have discovered Svalbard, as well, but the discovery is generally attributed to the Dutch explorer Willem Barentsz who saw the islands in 1596. Thereafter the archipelago was used as a base for whaling (mostly Bowhead *Balaena mysticetus*) until stocks were more or less exhausted in the early 18th century (Woodby and Botkin, 1993). Surprisingly, considering the extent of activities on Svalbard, the Franz Josef archipelago was not discovered until the late 19th century, although it is possible that walrus hunters were familiar with it earlier. The Canadian high Arctic group was first sighted by William Baffin, who saw both Devon and Ellesmere islands, searching for the Northwest Passage in 1616. The islands were not seen again by Europeans until the renewal of attempts to find the Northwest Passage in the 19th century. Unlike the other island groups, New Siberian Islands were discovered by land and ice crossing in 1712 by a Cossack company. Herald Island, adjacent to Wrangel Island, was sighted in 1849 but the first people to land were probably the crew of USRC Corwin in 1881 and Severnaya Zemlya was the last archipelago to be discovered, by Russian icebreakers in 1913 (Wikipedia, 2018).

The archipelagos of the Arctic Ocean comprise some of the remotest and most physically challenging places on earth. The combination of high latitude, proximity to the frigid waters of the Arctic Ocean and the presence, in many places, of mountains and remnant ice-caps, combine to make these some of the coldest places with permanent settlements. Recent permanent habitation on the archipelagos, excluding military installations and weather stations, occur on the Canadian islands, on Svalbard and on Yuzhny Island (the southern island of Novaya Zemlya). The population in the Canadian islands comprises two small Inuit communities: Resolute Bay on Cornwallis Island (~200 people, Fig. 18), and Grise Fiord on the south coast of Ellesmere Island (~120 people, Fig. 19). There are five permanently occupied settlements on Spitzbergen, the largest island of the Svalbard archipelago, with the main town, Longyearbyen (Fig. 20), supporting a permanent population of about 2000 people and four other settlements currently occupied year-round, of which two are mines and one is the research facility of Ny-Ålesund, on the shore of Kongsfjorden. They support an additional 500 people year-round. In Novaya Zemlya, there are several settlements on Yuzhny Island (the southern large island), most near the southern end, with the largest town, Belushya Guba (Fig. 21), supporting about 2000 people and with several hundred more resident in the other hamlets.

The coldest settlements are the Canadian villages, which are Canada's northernmost settlements. They experience only 3 months when the mean daily temperature exceeds 0°C; the mean maximum temperature in July is only 7°C and the maxima in January–March are below –30°C. The monthly mean minimum and maximum temperatures at Longyearbyen are –21°C and –13°C (Feb) and +3°C and +7°C (Jul) and at Belushya Guba, –19°C and –11°C (Feb) and +3°C and +12°C (Jul). These two towns are among the warmest places in the Arctic Ocean islands.



Fig. 18 The settlement of Resolute Bay, Cornwallis Island, Qikiqtaaluk Region, Nunavut. The airport and associated logistics base of Polar Continental Shelf Project is 5 km northwest of the village (Google Earth Pro, 2018).



Fig. 19 Grise Fiord, Ellesmere Island, a small community in the Canadian high Arctic (Google Earth Pro, 2018).



Fig. 20 Longyearbyen, Spitzbergen, the largest settlement in Svalbard (Google Earth Pro, 2018).

In addition to the permanent settlements, temporary camps come and go throughout the islands, weather stations exist on all the archipelagos (e.g., Eureka, Canada; [Fig. 22](#)) and minor military facilities exist in the Canadian islands, as well as on all of the Russian archipelagos, but not on Svalbard, which has been declared a demilitarized zone ([Koivurova and Holienčin, 2017](#)). Novaya Zemlya, a former nuclear weapons test site, still supports substantial permanent military bases. Recently, Russia has enlarged military facilities on Alexandra Land, Franz Josef, stationing year-round, combat-ready troops there ([RFE, 2015](#)).

Conservation

The Arctic being among the most remote places on Earth does not confer immunity from human activities that threaten ecosystem maintenance. Because existing terrestrial ecosystems on the Arctic Ocean islands have very low productivity, they will take a long to



Fig. 21 Belushya Guba, Yuzhny Island, the main town of Novaya Zemlya (Google Earth Pro, 2018).



Fig. 22 Weather station at Eureka, Ellesmere island * (Google Earth Pro, 2018).

recover, once disturbed. Potential sources of disturbance include tourism, oil and gas exploration and exploitation, facilities relating to transportation, especially those relating to the northern Sea route along the Siberian coast, and increased militarization in the wake of increasing East–West tension.

Resource Extraction

Coal mining has been ongoing in Svalbard since the late 19th century and has been the major force in creating a permanent human population there. Russian interests continue to mine coal, although activity is less than in the 20th century. A small amount of mining has been carried out in the Canadian islands, with the Polaris mine on Little Cornwallis Island producing more than 20 million tons of zinc over 21 years. It closed in 2002. As of 2018, a new lead-zinc mine is being developed on Yuzhny Island, Novaya Zemlya by the ARMZ Uranium Holding Co. and is due to begin production in 2023 (Staalesen, 2018).

Mining affects the environment through the related disturbance, as well as disruption of drainage patterns. Vegetation characteristics and schedules of snowmelt can be noticeably altered by road dust (e.g., Auerbach et al., 1997), but a Canadian study found few negative effects of mining activities on birds within 1 km of the mine footprint (Smith et al., 2005). Some birds of prey nest on rock faces or infrastructure from mining activities and appear resilient to moderate levels of human disturbance

(Swem Jr., 1996). Indeed, some birds of prey may benefit from the artificial lighting, food subsidies and nesting substrate offered by resource extraction infrastructure. Further study is needed to better understand the effects of disturbance and habitat degradation related to mining at local and regional scales.

Potential oil and gas reserves have been identified on or close to all the arctic archipelagos (Meneley, 2008, Craighill, 2015, Klett, 2017, Marex, 2017, Nilsen, 2017). Widespread oil and gas exploration took place in the Queen Elizabeth Islands of Canada from 1968 to 1987 (Meneley, 2008), but despite the discovery of 17 oil or gas fields, no commercial exploitation has ensued. Although exploration was proposed in Baffin Bay, southeast of Devon Island, permission was withheld by Government of Canada on environmental grounds (Davidson, 1981) and the area has subsequently been given protection as part of the Tallurutiup Imanga National Marine Conservation Area (Doyle, 2017). Exploration is currently ongoing in the Barents, Kara and Laptev seas, but to date the only commercial production, in the southern Barents Sea, is far from Svalbard. No commercial wells have been developed on land in any of the islands, but the development of adjacent shelf seas looks very likely.

Oil and gas exploration on land, like mineral exploitation, can significantly degrade both terrestrial and aquatic habitats. The shallow wetlands of the Arctic are sensitive to disturbance of hydrology: Oil and gas extraction can induce subsidence, seismic exploration can lead to channelization and disruption of water flow patterns, and infrastructure and road dust can affect snow melt and permafrost (Jorgensen et al., 2010). Despite technological advancements in seismic exploration, these activities continue to significantly degrade tundra habitats (Kemper and Macdonald, 2009). In addition, industrial activities can lead to locally enriched populations of predators, indirectly impacting local breeding birds (Liebezeit et al., 2009). Birds such as ivory gull and gyrfalcon are known to be affected by low-level aircraft over-flights, such as those associated with oil and mineral exploration (Platt, 1977; Mallory et al., 2008). These and other secondary effects greatly expand the area impacted by resource extraction activities.

Tourism and Other Human Disturbance

Ecotourism is increasing in the Arctic, and human visits to colonies and important breeding areas for birds are increasingly frequent. Disturbance from aircraft, cruise ships, boats, and humans can affect the reproductive success of birds by causing eggs or chicks to fall from breeding ledges on cliffs (e.g., for Thick-billed Murres: Curry and Murphy, 1995) or by leaving eggs vulnerable to predators when parents temporarily desert their nests (e.g., eiders and murres). Likewise, terrestrial mammals may be forced to leave foraging areas. Disturbance of wildlife by aircraft, ships and other vehicles is becoming an increasingly important concern among northern wildlife managers and residents.

Pollution

Most of the harmful pollutants that are released in large quantities at lower latitudes, such as agricultural pesticides, are not used in the Arctic. Industrial chemicals, such as Polychlorinated Biphenyls (PCBs), may be released near communities and development sites, but the effects are usually localized. However, within the Arctic, a substantial risk of pollution comes from chemicals transported over long distances, entering into Arctic environments through atmospheric deposition, ocean currents, and river outlets (e.g., Macdonald et al., 2000; Braune et al., 2005). Through the process of bio-magnification as they ascend the food chain, some pollutants threaten species at the top of the food chain, such as marine mammals, seabirds and especially polar bears (Norstrom et al., 1998).

Some industrial chemicals, such as PCBs, have been regulated since the 1980s but others, such as flame retardants (PBDEs) that are used in computers, car parts and upholstery were not controlled until after 2000. The presence of these compounds in Arctic wildlife is decreasing (Braune et al., 2015a, b), but heavy metals such as mercury and cadmium remain a concern for some species (e.g., Provencher et al., 2014; Braune et al., 2014) and the pathways by which they enter arctic systems are not well understood (Macdonald et al., 2000). In the case of mercury occurring in the Arctic, the most likely source is East Asia, transported by upper atmosphere winds and deposited with precipitation (Braune et al., 2014). Future changes to food webs may affect contaminant exposure, as species adjust their diets and feed higher or lower on the food chain (Braune et al., 2015a). Data exist for only a handful of Arctic species, but the effects of pollutants on arctic wildlife are potentially widespread.

As shipping through the Arctic increases, birds in marine habitats face an increasing risk from chronic oil pollution and accidental spills. Chronic pollution can lead to oiling of individual birds, but may also threaten birds indirectly, through food chain effects (Wiese and Robertson, 2004). Some species, including Common and King Eiders, forage on benthic invertebrates where hydrocarbons may reach dangerous levels (Meador et al., 1995). The risks to wildlife from accidental oil spills are substantial everywhere but are greatest in the Arctic where cold water temperatures, ice cover and periods of darkness limit the dispersal and decomposition of oil and complicate clean-up options (Arctic Council, 2009). When birds or marine mammals concentrate in one place, such as when the entire Canadian population of Pacific common eiders stages in the Southeast Beaufort Sea while on spring migration, risks may extend to whole populations.

Military Installations

Because military arrangements are not usually subject to any local political control, the enforcement of environmental regulations for military bases is more difficult than making the equivalent arrangements for civilian developments. The northern island of

Novaya Zemlya, used from 1955 to 1990 for nuclear explosion testing, is still largely under military control. The proliferation of military installations in the high Arctic archipelagos is likely to complicate any future actions for ecosystem protection.

Protected Areas

Currently, the amount of land area within the Arctic archipelagos covered by Protected Areas (International Union for the Conservation of Nature (IUCN) protection categories I-IV) is much higher than in the Arctic as a whole (Huntington, 2013). Both Wrangel Island and Franz Josef Land are completely protected: Franz Josef as part of the Russian Arctic National Park, which also includes northern Novaya Zemlya, amounting to 7% of that archipelago, and Wrangel Island is a State Nature Reserve. Svalbard contains several Protected Areas, amounting to 65% of the land area, while in the Canadian archipelago two National Parks amount to 10% of the total land area. Neither Severnaya Zemlya nor the New Siberian Islands have protection at this level at present, but the area protected for all archipelagos combined is approximately 110,000 km², 17% of the total land area, which compares with 11% for the entire area defined as Arctic by the Convention on Arctic flora and Fauna (Huntington, 2013).

Climate Change and the Future of the High Arctic Fauna and Flora

Global warming is especially acute in the Arctic, where air temperatures have risen two to three times as fast as those elsewhere on Earth over the past 30 years (Pachauri and Reisinger, 2007). Arctic glaciers in Greenland and the Canadian islands are in rapid retreat (Rignot and Kanagaratnam, 2006; White and Copland, 2018a, b). Advances in the timing of Arctic spring sea ice break-up (Parkinson and Cavalieri, 2008), and substantial increases in both summer and winter air temperatures at many Arctic stations (Tedesco et al., 2009), are well documented. Arctic-adapted plants and animals may be affected directly, through susceptibility to elevated temperatures and other climatic changes (e.g., Gaston et al., 2002 found heat and water stress caused avian mortality in warm years in northern Hudson Bay, while Anctil et al., 2014 showed that higher rainfall increased nestling mortality of Arctic-breeding Peregrine Falcons *Falco peregrinus*). For most organisms, however, indirect effects, through changes in ecosystem structure (e.g., reduced prey, increased predation, competition, parasitism and disease) are likely to have a greater impact (Ganter and Gaston, 2013).

Although climate change poses a threat to all the world's ecosystems, those of the high Arctic are especially vulnerable because, being limited to the northern fringes of the continents, they have no way to find refuge as distributions shift northwards. However, the high Arctic islands, especially those beyond the swimming range of terrestrial vertebrates (all of those dealt with here), provide a special case where some of the potential effects of climate change may be delayed. Southern predators, of which mammals such as *Lynx lynx* spp., red fox *Vulpes vulpes* and various Mustelidae (*Martes*, *Mustela*, *Neovison*, etc.) have the greatest potential for disrupting current ecosystems, may not be able to spread across water barriers. Once seasonal ice cover disappears, they will not be able to access these remote islands unless inadvertently imported by people (Gaston et al., 2012). In this context, increasing tourism, development and military activity pose a real threat to biosecurity and ecosystem integrity.

The most distant archipelagos (Svalbard, Franz Josef) are likely to see only slow and selective immigration of southern plants and insects (Coulson et al., 2002), especially those taxa with low dispersal capabilities (e.g., plants with heavy seeds, nonflying animals). Moreover, the fact that these islands will continue to be surrounded by cool seas will prevent them from experiencing extreme temperatures characteristic of continental land-masses. Consequently, they may provide us with the best opportunity available for protecting the characteristic Arctic fauna and flora.

Unless we decide to deliberately introduce absent species to Svalbard and other remote islands, our best option for the defense of the high Arctic flora and fauna will be in the Canadian archipelago. These islands are the most extensive and have the widest range of native plants and animals among the Arctic Ocean archipelagos. Placing a "cordon sanitaire" around them, by rigorous exclusion of potential southern invasive species, may provide the best opportunity to allow the biotic communities of the high Arctic to persist in the face of climate warming. To achieve this goal, awareness of the risk from species invasions and the development of systems for inspection of ships, aircraft and cargoes arriving in the high Arctic islands will be necessary. The time for action is now.

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The Azores Archipelago: Biodiversity Erosion and Conservation Biogeography

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Abstract

The Azores is an isolated archipelago that is home to a unique biodiversity. However, their native biotas are being affected by different drivers of global change, mainly by land-use changes and fragmentation, introduction of exotic invasive species and climatic changes. The combined effects of these factors lead to changes in habitats structure and composition, the spread of exotic fauna and flora, and the impoverishment of native endemic species. Most of the Azorean endemic species were recently assessed for IUCN and a large fraction of the endemic arthropods have a status of conservation concern, including Critically Endangered, Endangered and Vulnerable species, which confirms an ongoing process of extinction debt that most probably will lead to the extinction of many species. One important step for designing and implementing conservation strategies that mitigate these impacts is having a deep knowledge of changes on abundance and range-size contraction and expansion. A long-term monitoring strategy is already in place in the Azores, but future actions should include implementing a “Global Island Monitoring Scheme” for the long-term coordinated survey and monitoring of native island biotas.

The Azores Archipelago

The Azores archipelago, lying on the North Atlantic Ocean, (39°43′23″N [Corvo]—36°55′43″N [Santa Maria]; 24°46′15″W [Formigas islets]—31°16′24″W [Monchique Islet—Flores]) is composed of nine islands and some islets, aligned along a WNW-ESE direction (Fig. 1). These islands are organized in three groups: the western group, including Corvo and Flores islands; the central group including Faial, Pico, Graciosa, São Jorge and Terceira islands; and the eastern group including São Miguel and Santa Maria islands, plus the Formigas islets (Fig. 1). The Azores archipelago is rather isolated, being far away from both Europe (1641 km) and North America (2985 km) continents, with Madeira archipelago being the nearest land (965 km). Within the archipelago, Pico and Faial islands are the less isolated (circa 6 km from each other). Regarding islands’ area, São Miguel is the largest island (745 km²) and Corvo is the smallest (17 km²). Pico reaches the highest altitude (2350 m abs) while five of the other islands have elevations around 1000 m asl and Graciosa island presents the lowest altitude (405 m asl) (Table 1).

All islands are oceanic of recent volcanic origin, but unlike for Hawaii or the Canary Islands, the age of the Azores is still under debate. According to França et al. (2003) (citing several authors) the oldest known geological ages of the Azores islands range from 8.12 Ma (Santa Maria) to 0.3 Ma (Pico). However, a recent study by Ramalho et al. (2017) supports a complex evolutionary history of Santa Maria, with a first emergence 6–5.8 Ma, followed by subsidence from 5.3 to 4.1 Ma, and a subsequent renewed volcanic activity (4.1–2.8 Ma) and an uplift (from 3.5 Ma to the present). Other recent studies also give younger ages than initially thought for the islands of Terceira, São Miguel and Graciosa (Hildenbrand et al., 2014; Larrea et al., 2014; Sibrant et al., 2015).

According to the Köppen Climate Classification (based on the period from 1971 to 2000), the prevalent climate in the Azores is temperate, with no dry seasons and mild summers (Cfb). Nevertheless, climate ranges from temperate, with hot and dry summers (Csa) (e.g., coastal areas of Faial and Graciosa, the west of Pico, the south and east coast of Terceira, part of the southern coast of São Miguel and west of Santa Maria) to the Tundra climate (ET) of Pico Mountain (above 1600 m). Santa Maria and Graciosa are the driest islands and the prevalent climate in these islands is temperate with dry and warm summers (Csa and Csb) (Agência Estatal de

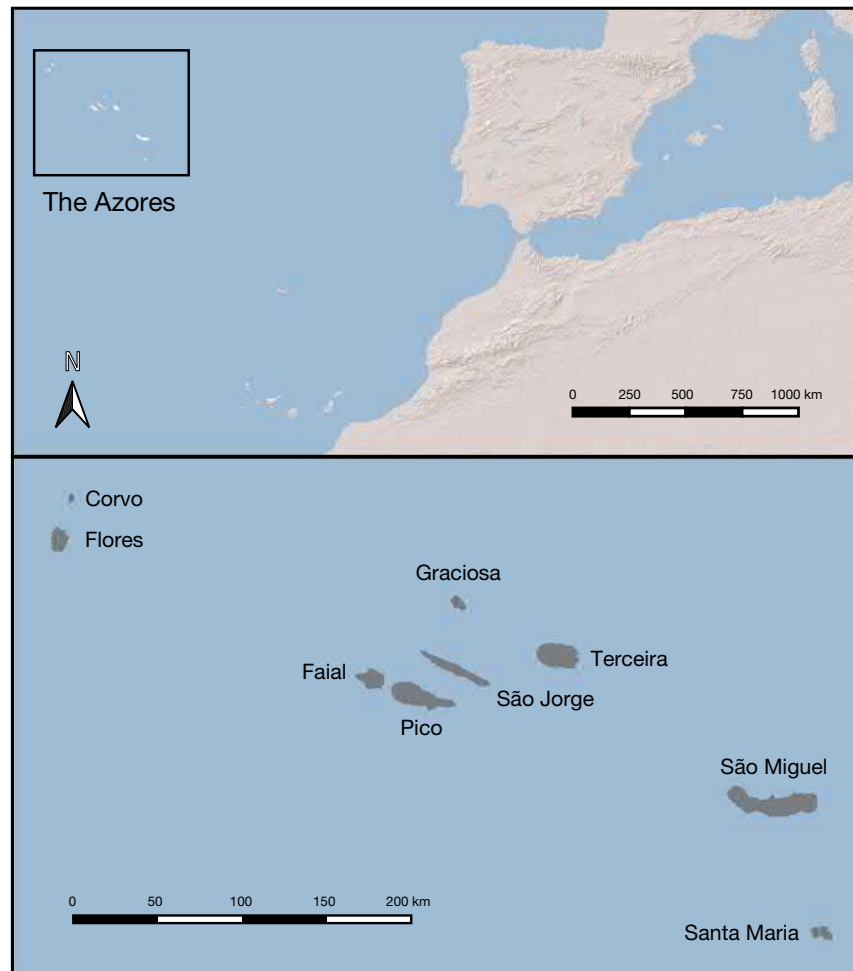


Fig. 1 Location of Azores in the Atlantic (*top*) and the nine islands (*bottom*).

Table 1 Geographic and climatic characteristics of the Azores.

<i>Island</i>	<i>Area (km²)</i>	<i>Maximum altitude (m asl)</i>	<i>Total annual rainfall (mm)</i>	<i>Mean annual temperature (°C)</i>
Santa Maria	97	587	775	17.5
São Miguel	745	1105	1027	17.3
Terceira	400	1021	1126	16.7
Graciosa	61	405	845	17.2
São Jorge	244	1053	974	17.3
Pico	445	2350	974	17.3
Faial	173	1043	974	17.3
Flores	141	911	1716	17.0
Corvo	17	720	1145	17.5

Geological age refers to the oldest known reference (see text for more details). Total annual precipitation and average annual temperature refer to periods of 13 years for Graciosa, 20 years for Corvo and Flores and 30 years for the remaining islands. For Pico and São Jorge there is no data available, so the same values of the neighboring island of Faial are considered. *Note:* Most geographical features are reported according to Forjaz et al. (2004). Climatic data are according to IPMA (Portuguese Institute of the Sea and Atmosphere) from weather stations located at: Santa Maria-Aeroporto (100 m asl), São Miguel-Ponta Delgada (35 m asl), Terceira-Angra do Heroísmo (74 m asl), Graciosa-Santa Cruz (27 m asl), Faial-Horta (60 m asl), Corvo-Village (28 m asl), Flores-Aeroporto (34 m asl), (<http://www.climaat.angra.uac.pt/>).

Meteorología & Instituto de Meteorologia, 2011). At low elevation, the total annual rainfall ranges from 775 mm/year in Santa Maria (Eastern group), to 1716 mm/year in Flores (Western group) (cf. Table 1). However, in the central higher elevation areas of many islands, climate models estimate that rainfall may reach more than 4000 mm/year. At low elevations, the range in mean annual temperature is low (between 16.7°C and 17.5°C). Nevertheless, mean annual temperature may go as low as 10.8°C (at 900 m asl), or 6.2°C (at 2000 m asl) (Azevedo et al., 2004; Elias et al., 2016).

The most recent checklist of Azorean biota includes a total of 6112 terrestrial species and 6164 subspecies, including 452 endemic *taxa* (Borges et al., 2010a). Humans have introduced many species, especially vascular plants, where introduced species reach more than three quarters of the total number of species. However, the percentage of endemism for vascular plants, if only indigenous species (native and endemic) are considered, is one of the highest in Macaronesia (35% in Azores, 20% in Madeira, 39% in Canaries, 23% in Cabo Verde; Gabriel et al., 2014).

At the time Azores was first discovered by humans (15th century), the archipelago was mainly covered by forests (Frutuoso, 1978, 1981, 1987). Considering the work of Elías et al. (2016), it is possible to draw a picture of the potential vegetation of the islands by this time. Many flat coastal areas may have been covered by *Erica-Morella* woodlands, while *Picconia-Morella* forests should have dominated the lowlands, up to 300 m asl. Lowland and sub montane forests (the Azorean Laurel forests, dominated by *Laurus azorica*) probably covered more than two thirds of the islands, from 300 m to 600 asl. Above the *Laurus* forests, between 600 m and 1000 asl, *Juniperus-Ilex* forests and *Juniperus* woodlands would have covered most of the areas. In the higher areas, *Calluna-Juniperus* scrublands would cover mountain ridges and *Calluna-Erica* scrublands and *Calluna* scrublands would occupy Pico Mountain, above 1200 m asl as they do today. In the midst of these vascular species, larger or smaller areas of peat bogs would occur (cf. Allorge and Allorge, 1946).

Unfortunately, native habitats have been subject to remarkable modification and disturbance since human colonization, and natural vegetation became almost extinct at low and middle elevations (Table 2) (see Fig. 2). Nowadays, native vegetation is found mainly above 500 m asl and most of the remaining forests are montane cloud forests, surviving mainly in Terceira (Fig. 3), Pico and Flores islands. These unique habitats are rich in endemic species including most of the 452 known endemics. For instance, based on the most detailed inventories of Azorean forests, the 20 most pristine native forest areas include 23 out of the known 26 Azorean endemic spiders and 43 out of the 78 endemic beetles (Borges et al., 2005a, 2010a; Ribeiro et al., 2005). The Azores are also the only archipelago in Macaronesia with large peat formations.

The Azores are a Portuguese autonomous region with a Parliament located on Faial Island and the main political institutions located in São Miguel, Terceira and also Faial islands. Human population in the archipelago is ca. 242,000 (Table 2). São Miguel Island is, by far, the most populated island, followed by Terceira (cf. Table 2). The economy was traditionally dominated by fisheries and agriculture (especially dairy-cattle products such as milk and cheese), but in the last decade, tourism is becoming one of the main drivers of Azorean economy.

Drivers of Biodiversity Erosion

According to the Millennium Ecosystem Assessment (MEA, 2003), drivers of change are “any natural or human-induced factor that directly or indirectly causes a change in an ecosystem. A direct driver unequivocally influences ecosystem processes. An indirect driver operates more diffusely by altering one or more direct drivers.” (MEA, 2003, p. 49). Physical and biological drivers are considered direct drivers, while demographic, economical, sociopolitical, cultural and religious, scientific and technological factors, are considered indirect drivers of change (Nelson et al., 2006). The Azores have suffered the long-term effects of many human impacts that have shaped its current diversity. Below we address some of the most important ones.

Table 2 Present-day human population size and native vegetation cover in the Azores archipelago.

Island group	Island	Estimated present-day human population size	Present-day native vegetation cover (%)	Present-day native forest cover (%)
Oriental group	Santa Maria	5578	7.8	0.1
	São Miguel	131,609	8.7	0.4
Central group	Terceira	55,833	14.2	5.9
	Graciosa	4780	0.4	0.0
	São Jorge	9674	14.7	1.2
	Pico	14,806	13.7	2.1
	Faial	15,063	9.4	1.3
Occidental group	Flores	3995	32.9	11.1
	Corvo	425	51.3	0.0
	Azores	241,763	12.8	2.5

Sources: SREA - Serviço Regional de Estatística dos Açores (2016). Demografia. Azores: Angra do Heroísmo; DROTRH – Direção Regional do Ordenamento do Território e Recursos Hídricos (2007). Carta de Ocupação do Solo dos Açores - Relatório. Azores: Ponta Delgada; Gaspar, C., Gaston, K. J., Borges, P. A. V. and Cardoso, P. (2011). Selection of priority areas for arthropod conservation in the Azores archipelago. *Journal of Insect Conservation* 15: 671–684.



Fig. 2 The mosaic of human modified habitats at mid and low elevation, with dominance of pastures for cattle grazing surrounded by an exotic tree, *Cryptomeria japonica* (Credit: Paulo A. V. Borges).



Fig. 3 The dense native *Juniperus-Ilex* forests in Terceira Island. Trees are covered with a dense carpet of mosses (Credit: Paulo A. V. Borges).

Habitat Changes

Native Azorean habitats have a long history of natural changes, that were mainly induced by volcanic eruptions and the Pleistocene climatic changes (Rull et al., 2017). However, human-induced changes have played a dramatic role in shaping the current biodiversity of the Azores (Rull et al., 2017). Historical records show that Portuguese sailors discovered and explored the Azores from the early XV century. However, it has been suggested that humans could have settled in the Azores prior to the official discovery of the archipelago (e.g., Connor et al., 2012; Gabriel et al., 2015; Rull et al., 2017). If that was the case, those settlements were temporary, since there are no historic accounts of human presence in the islands by Portuguese sailors and settlers.

The most eastern islands, Santa Maria and São Miguel, were the first to be discovered by Diogo de Silves around 1427. After that, all the remaining islands were sequentially discovered and populated by the Portuguese. The availability of drinking water sources

facilitated the colonization, but the main reported challenge was the progression of settlers due to the complex orography of the islands, furthermore covered with dense forests (e.g., Frutuoso, 1978, 1981, 1987). It is noteworthy that the Portuguese settlers were wise in many decisions regarding land occupation, for instance using lava fields for wine production, better soils for agriculture and wheat, and grasslands in the highest elevations (Silveira, 2013). However, human pressure was not innocuous and there is evidence that by 1700 most of the land below 300 m elevation was already transformed, and that by 1850, native vegetation was mostly restricted to areas above 500 m. In fact, the temporal sequence of native forest destruction followed the conic shape of these volcanic islands (e.g., Silveira, 2013).

In modern times, the most dramatic changes occurred during the two World Wars, with deforestation occurring at mid and higher elevations due to the need of wood as energy source. Thus, by 1950, a major enterprise was performed to reforest mid elevation areas with the exotic fast-growing tree, *Cryptomeria japonica*, already used in the islands since the XIX century. Additional deforestation of native forests occurred between 1970 and 1990 for the implantation of high elevation semi-natural pastures and additional *Cryptomeria japonica* plantations (Fig. 4).

A more recent period of intense changes occurred between 1980 and 2000, with the mechanization of agriculture boosted by European agricultural policies, and the creation of large areas of intensive pasture monocultures at high elevations (e.g., in Terceira, Pico and Flores islands). These changes implied, for instance, that from 1998 to 2013 Pico Island suffered an increase of 3% of the surface occupied by intensive pastures (Gil et al., 2018). The consequences of these changes for biodiversity are not completely known, but the richness of species from different taxonomic groups (e.g., bryophytes, ferns, arthropods) decreases from forests to grasslands, while semi-natural pastures have more complex vegetation that benefit phytophagous insects and spider diversity (Borges and Brown, 2001). All these indicators provide indirect evidence of the loss of biodiversity that occurs in intensive managed grasslands. Paradoxically, there is a strong predominance of intensive pastures and maize in areas theoretically unsuitable for this purpose in Terceira Island, boosted by the recent expansion (2001–11) of pasture intensification to areas more suitable for forests (Reis and Dentinho, 2015).

Azorean urban areas are mostly located in coastal areas. Indeed, many Azorean cities are close or within coastal biodiversity hotspots, producing impacts on the coastal biota (Bertocci et al., 2017). The increasing pressure of urbanization led to the destruction and degradation of many coastal habitats, and almost to the extinction of its original ecosystems (Elias et al., 2016). Many species currently persist in much reduced patches of coastal habitats, notably some invertebrates (Borges et al., 2018b) and plants, such as the emblematic *Azorina vidalii*. Together with the development of agriculture and urbanization came an increase in the transport networks that has been growing in the Azores during the last 50 years. This too is a driver of the degradation and fragmentation of native habitats, fostering the spread of invasive species, particularly impacting pristine native forests at mid to high elevation and cave ecosystems highly disturbed by new routes (Borges et al., 2012).

As a consequence of these major human changes, pristine native forests are currently restricted to less than 5% of the Azores area, being completely absent in Graciosa and Corvo islands and with larger and most well preserved areas occurring mainly in Terceira, Pico and Flores islands (Gaspar et al., 2011).



Fig. 4 The monoculture of the industrial plantation of *Cryptomeria japonica* in Azores (Credit: Paulo A. V. Borges).

The consequences of these land-use changes in Azorean biodiversity were investigated for some taxonomic groups, namely arthropods (e.g., Borges et al., 2008; Cardoso et al., 2009; Florencio et al., 2015, 2016; Rigal et al., 2018) and vascular plants (Marcelino et al., 2013). In both groups, exotic species tend to proliferate and indigenous species to decline with increasing anthropogenic disturbance and management intensity. In general, the fragmentation of the Azorean landscape and the prevalence of human modified habitats have promoted the expansion of soil epigeal exotic species adapted to native habitats. However, the same does not apply to the arboreal canopy arthropod communities, still dominated by endemic and native non-endemic arthropods, suggesting that native forest canopies are still acting as physical barriers to the colonization by exotic fauna (Florencio et al., 2016).

Several anthropogenic habitats are now the dominant land cover in the Azores, and therefore some of these habitats (e.g., semi-natural pastures, exotic forests and intensive pastures) surround many native forest fragments. Consequently, source-sink dynamics in Azorean arthropod communities constitute an important ecological process that operates at both spatial (Borges et al., 2008; Cardoso et al., 2009) and temporal scales (Matthews et al., 2019). Indeed, many species common in a given habitat are frequently being observed as pseudo-rare or tourists in other habitats (Borges et al., 2008). However, true rare endemic species (i.e., species with restricted distribution, low abundance and/or high habitat specialization) are also important in the native habitats and many of them are threatened (Borges et al., 2017a). Because of the lack of source-sink dynamics at the archipelago scale, Single Island Endemics (SIEs), i.e., endemic species restricted to only one island, are those under more severe threat.

Regarding vascular plants, Marcelino et al. (2013) observed that endemic and native non-endemic species could occur with some frequency in anthropogenic habitats. However, there is no empirical evidence that indicates that those populations are sustainable or contributing for the long-term survival of those species. Although some bryophyte species are present in different ecosystems, the highest richness is found inside native forests and near humid zones, while urban areas include only a small proportion of the mosses and liverworts that occur in the Azores (Gabriel and Bates, 2005; Gabriel et al., 2011).

Intense land-use change dynamics can also have an impact on species abundance, as demonstrated by studies on the Azorean arthropod communities; in native habitats, communities tend to approach a log-normal distribution (i.e., those in equilibrium), with some species being common, many species having intermediate abundance and many being rare species. In more disturbed habitats, like exotic forests and highly transformed pastures, communities are dominated by a few common species and many rare species, following a logseries distribution instead (Matthews et al., 2014b).

The extent of the impacts of land-use changes on insect pollinators was recently investigated with surprising results. Picanço et al. (2017) showed that Azorean flower-visiting insect communities are highly simplified across an entire disturbance gradient, with little difference between habitats. These results have two potential outcomes: (1) endemic and native insect pollinator successfully adapted to new anthropogenic habitats and are providing essential ecosystem services in agro-ecosystems; (2) in the absence of strong exotic competitors, indigenous flower-visiting insects expand their range, also facilitating the expansion of a large number of exotic plant species.

Cryptomeria japonica plantations are one of the most important anthropogenic habitats in the Azores. This gymnosperm was planted massively in the archipelago in the mid-20th century, and the impact of these plantations was positive to a certain point, because they mitigated soil erosion, improved water retention and served as a wind protection for cattle in pastures. However, the negative impacts are considerable since, depending on the compass of plantation, there is almost no understory vegetation and the arthropod fauna is very poor (Cardoso et al., 2009). In a recent study, Ferreira et al. (2017) showed that, contrary to expectations, the replacement of native forests by *Cryptomeria japonica* plantations did not affect litter decomposition in Azorean streams. However, these authors observed some changes in aquatic hyphomycete communities arriving from *Cryptomeria japonica* forest, suggesting that there is the need to create a riparian buffer of native vegetation in *C. japonica* plantations.

The clearing of native vegetation for the creation of anthropic habitats have already led to the extinction of many species (Alcover et al., 2015; Terzopoulou et al., 2015; Rando et al., 2017) and to the prediction of alarming future extinctions in extant habitats (Triantis et al., 2010), with direct consequences for the structure and functioning of many ecosystems. For some taxa like ground-beetles, the communities in Azorean native forest are unbalanced with the current absence of species of intermediate abundance, and the dominance of few species, some of them exotic (Boeiro et al., 2018), which is possibly a consequence of massive extinctions of large bodied species (Terzopoulou et al., 2015).

Habitat changes and biodiversity loss on Azores are still occurring today, not only because of land use changes, but also due to the spread of invasive species and climatic changes (see below).

Human Induced Climate Changes

Climate variation has been always an important driver of natural changes in the Azorean biota (Norder et al., 2019). However, human-induced habitat changes were of overwhelming importance in shaping Azorean ecosystems in the last 600 years of human occupation (Connor et al., 2012; Silveira, 2013). Current research in Azores indicates all Azorean islands lost precipitation below 500 m in the last 20 years (Eduardo Brito Azevedo, Pers. Comm.). The number of dry summers are also increasing with impacts at all elevations, but mostly at lower altitude. Moreover, despite no changes in total precipitation, there is a marked concentration of pluviometry in shorter periods. The expectations for the next decades are the intensification of these changes that will tend to be more important also at high elevations, and in particular islands with few remnants of native vegetation (Corvo, Graciosa, and Santa Maria islands).

The recent and future impacts of human-induced climatic changes on island biodiversity are now well recognized (Harter et al., 2015; Ferreira et al., 2016; Patiño et al., 2016). The most common responses to climatic changes are shifts in latitudinal and elevational ranges (Harter et al., 2015), which in Azores will have a huge impact on the long-term sustainability of many endemic hyper-humid forest adapted species of bryophytes (Ferreira et al., 2016; Patiño et al., 2016), arthropods and vascular plants (Ferreira et al., 2016). Indeed, many of those species will endure a reduction of their range size and, in some cases, current protected areas will not be effective tools for their long-term protection (Ferreira et al., 2019). Taking into consideration that more than half of the extant native forest-dependent arthropod endemic species might eventually be driven to extinction due to a process of extinction debt, related to major past and current land-use changes, fragmentation and forest loss (Triantis et al., 2010), the combination of these factors with climatic changes might be dramatic for the diverse endemic arthropods. It is worth reinforcing that the volcanic origin of the islands tends to create conic volumes; thus the upper elevations have much less area than the lower ones, which restricts even further the ability of species to colonize and survive on the remaining fragments with adequate climatic conditions.

Predictions based on climatic modeling, data on habitat fragmentation and information about species dispersal limitations, further forecast strong reductions (up to 94%) of important native forest areas for functional connectivity of fragmented populations of six endemic insects in Terceira Island (Aparício et al., 2018). The fact that many specialized ground-beetles (Borges et al., 2006) and bryophytes (Gabriel and Bates, 2005) are dependent of hyper humid conditions in high elevation native forests, make these species particularly vulnerable to potential changes in relative humidity. Indeed, the luxuriant bryophyte and fern communities of the high elevation native forests will be highly impacted if the number and intensity of droughts increase in Azores, as predicted by most climatic models (Patiño et al., 2016). The impacts for the forest structure are difficult to envisage, but important ecosystem services related with nutrient cycling and water retention may be highly impacted.

Exotic Species and Invasive Alien Species

Invasive Alien Species (IAS) are currently the major driver of biodiversity erosion in Azores. The fact that a large proportion of Azorean terrestrial seed plants (around 70%) and arthropods (around 45%) are exotic (Borges et al., 2005b), created an opportunity for a large number of them becoming invasive species, spreading not only in the native forest habitats, but also in freshwater and urban ecosystems (see more below). The success of exotic and invasive species in the Azores is related with several factors:

- (a) the Azorean native flora and fauna are species poor (Triantis et al., 2012), which creates the ecological opportunity for newcomers to settle down. According to Darwin's naturalization hypothesis, newcomers are more likely to become invaders when close related species are missing, a trend that is known to occur in the Azorean flora (Schaefer et al., 2011a).
- (b) the lack of natural enemies in Azorean native biota, which creates an "enemy free space";
- (c) the Azorean temperate mild climate, favoring the successful adaptation by species with wide ecological features and tolerances;
- (d) the fact that native pollinators may be visiting and pollinating exotic plants (Picanço et al., 2017), while native birds help in the dispersal of seeds of some IAS plants, which enhances the success of exotic and IAS plants in Azores;
- (e) the long coexistence between pasture grasses and maize, and their close taxonomic relationship (both are grasses), which host several exotic insects and insect pests, allowing these ecosystems to behave as a stepping stone in the invasion of native habitats;
- (f) the role of urban parks and gardens as a source of exotic ornamental species, which include a vast number of species, many of which have escaped to the wild (Bogas, 2003; Gabriel, 2019).

The high diversity of exotic species present in the Azorean Islands is reflected also by their dominance in many habitats, particularly in anthropogenic habitats (Cardoso et al., 2009; Schaefer et al., 2011a; Marcelino et al., 2013), but also, to some extent, in native forest, such as in the case of soil arthropods, particularly Collembola (Cicconardi et al., 2017). Noteworthy, an invasive earthworm species was even successful in colonize and establish in hostile conditions in volcanic soil on São Miguel (Azores) (Cunha et al., 2011).

Notwithstanding, the canopies of Azorean native forests still hold some level of resistance to the spread of exotic arthropods (Borges et al., 2008; Florencio et al., 2016), which may be related with the difficulty of exotic species to adapt to the architecture and micro-habitats of Azorean tree canopy. However, paradoxically, exotic species enlarged the ecological functional space in Azorean ecosystems, as exotic species differ in their functional profile from indigenous species in all studied land-uses (Rigal et al., 2018). Therefore, exotic species may contribute positively to the maintenance of some ecosystem functions in Azorean agro-ecosystems.

Exotic arthropod species are already well integrated in epigeal habitats, such that they are well mixed with native species when plotting the abundance of each species with their-occupancy (Rigal et al., 2013). However, it is also important to recognize that in Azorean native forests, introduced exotic species have lower densities, less spatial variance in these densities, and occupy fewer sites than native non-endemic and endemic species (Gaston et al., 2006; Borges et al., 2008). The high diversity of exotic arthropod species in native forest was observed mostly in sites located on the edge of still well preserved forest patches in Terceira (Borges et al., 2006). However, in many Azorean Islands the application of an Index of Biotic Integrity that incorporates several diversity metrics (Gaspar et al., 2011), shows that exotic arthropod species are having enormous impacts particularly on small fragments of native forest.

Concerning freshwater environments, Raposeiro et al. (2017b) showed that fish exotic predators introduced in Azores were the most important factor affecting the chironomid fly assemblages in lakes from S. Miguel Island. The presence of fish also affects other macroinvertebrates on permanent ponds in Terceira Island (Florencio and Lamelas-López, 2016).

In the last decades, the impact of IAS seed plants was particularly dramatic on Azorean native forests, forming dominant stands, altering the three-dimensional structure of native forests, sometimes replacing them entirely (see e.g., [Hortal et al., 2010](#) for a study with *Pittosporum undulatum* impacts). Based on an observation of invasion patterns of IAS plants in Azores, [Hanski \(2016\)](#) named this process as “A Green Tsunami,” since IAS plants are occupying large fractions of native forest. However, the impact of invasive plants on the structure and composition of soil biota in Azores remains to be empirically investigated.

It is currently established that IAS mammals, particularly rats and feral cats, were the drivers of extinction of many endemic birds in the Azores ([Alcover et al., 2015](#); [Rando et al., 2017](#)) and are still severely affecting populations of breeding birds, through predation on eggs, nestlings, and adults ([Monteiro et al., 1996](#); [Hervías et al., 2013](#)). In addition, rats are vectors or reservoirs of *Leptospirosis* spp., constituting a major threat to Azorean farmers’ health, including fatal human cases ([Collares-Pereira et al., 2000](#); [Esteves et al., 2014](#)).

In urban environments, in addition to rats and some common nuisance invertebrates (e.g., cockroaches, ants), four species of termites were recently identified in the archipelago, and three of them are promoting major economic impacts in Terceira, São Miguel and Faial islands ([Austin et al., 2012](#); [Guerreiro et al., 2014](#); [Duarte et al., 2018](#)). Particularly relevant is the impact of the drywood termite *Cryptotermes brevis*, for which the control measures in place are inefficient and the estimated costs for the future in terms of building treatments of rebuilding are in order of 1406 million euros ([Guerreiro et al., 2014](#)). More successful may be the control of the two subterranean termites for which there are some projects to eradicate the current two hotspots in Praia da Vitória (Terceira Island) and Horta (Faial Island).

In Macaronesia, one important initiative related to IAS, was the creation of the TOP100 Macaronesian IAS ([Silva et al., 2008](#)), a list that includes the most dangerous invasive species to Macaronesian native species and habitats. Most of the 100 IAS species identified include seed plants and vertebrates, but there are also some invertebrates. In due time, most of these species were included in a legal diploma (Annex IX of Regional Legislative Decree n.º 15/2012/A from 2 April), that aims to protect Azorean biodiversity.

Pollution and Contamination

The Azorean economy is currently dominated by dairy cattle production based on intensive permanent or semi-permanent pastures. These human activities difficult water infiltration and retention in the subsoil, and constitute a source of water pollution due to the use of fertilizers ([Borges et al., 2009](#)). Maize-pasture rotation is now widespread at both low and mid elevations, both farming systems serving only for dairy-cattle feeding. The massive use of chemicals for fertilization led to a continuous nutrient enrichment and pollution of all Azorean lakes and small temporary and permanent ponds (e.g., eutrophication and presence of nitrates in freshwater) ([Dentinho et al., 2008](#); [Cruz et al., 2015](#)), and are still polluting soils and freshwater with immense unmeasured impacts on biodiversity. For instance, high chlorophyll-*a* concentrations in water created unfavorable conditions for macroinvertebrates in permanent ponds from Terceira Island (Lamelas-López pers. comm). Moreover, changes in the chlorophyll-*a* concentrations can affect leaf litter decomposition in Azorean lakes, with potential consequences for nutrient cycling ([Raposeiro et al., 2017a](#)).

Fertilizers also have negative impacts on the arthropod communities in agricultural lands. [Santos et al. \(2005\)](#) studied both arthropod pests and their natural enemies in fruit orchards in Terceira Island, and found that the toxicity and frequency of use of pesticides had a negative effect on all arthropod groups, particularly on those that control pest species (i.e., spiders and parasitoids). Recent studies investigating the impact of agriculture practices on soil pollution (accumulation of trace metals in soil matrix) and microbial activity showed that agriculture intensification affected the soil microbial activities by decreasing the abundance of microbial biomass, with a consequent impact in organic matter decomposition and nutrient cycling ([Parelho et al., 2016](#)).

Indirect Drivers of Biodiversity Erosion

The processes leading to biodiversity erosion are not entirely dependent on physical and biological drivers. The role of indirect drivers should also be acknowledged, as both facilitators and hinderers of conservation and management of biodiversity.

In spite of the ongoing biodiversity crisis (e.g., [Cardinale et al., 2012](#); [Dobbs et al., 2014](#)), and the difficulties in halting it (e.g., [Sharman and Mlambo, 2012](#)), there are evidences that a new environmental paradigm is settling across the world ([Dunlap et al., 2000](#)), with human population showing a broad concern towards biodiversity and ecosystems preservation. The Azorean people are no exception. [Silva and Gabriel \(2009\)](#), studying a sample of 600 persons, stratified by island (São Miguel and Terceira) and place of residence (urban or rural), have shown that Azoreans generally endorsed the values of the New Environmental Paradigm, especially in what refers to the existence of other species (“Plants and animals have as much right as humans to exist”; 95,5% agreement). A favorable perspective towards biodiversity was also found among 1528 students (12–18 years old) from all the islands of the archipelago, who chose “Species protection” as the top investment area among 20 different themes, including the protection of groundwater or fire prevention ([Gabriel et al., 2012](#)).

There appears to be a contradiction between these shared perspectives supporting biodiversity, and the behaviors regarding land-use changes, exotic invasive species and contamination of the soils. This contradiction, or gap, between attitudes, values, beliefs, norms and pro-environmental behaviors has often been reported (e.g., [Kollmuss and Agyeman, 2002](#)) and different factors may help to explain it, including human perception, time scale and complexity inherent to ecological systems. For instance, the Azores are mostly perceived as “natural” for both residents and tourists ([Arroz et al., 2018](#)), while many invasive species occupy large areas in all the islands. On the other hand, the pace of ecological destruction (slow and gradual) is difficult to perceive at human scale and

ecosystems tend to be complex, with intricate relationships, for instance, the increased levels of nitrogen on the soil, may hinder the growth of bacterial films inside caves (Riquelme et al., 2015). Besides, emotional non-investment on environmental matters may lead to lack of knowledge and awareness and resistance against non-conforming information (people want to protect plant species—including invasive plant species), while a number of emotional reactions, such as apathy, denial and rational distancing may deter the preservation of natural ecosystems, thus leading to biodiversity erosion.

Conservation Biogeography

The design and establishment of proper conservation actions needs to be based on adequate data on the distribution, abundance and biology of the species and habitat characteristics intended to preserve. In Azores, the BALA project (1999–2004) is an exemplary case in which occurrence and abundance data were gathered using standardized sampling techniques in the soil and canopy of 100 plots in seven Azorean Islands, to respond to multiple community ecology and macroecological questions (see review in Borges et al., 2011). Similar efforts for other taxa in Azores are absent, but some approximate cases are: (i) the studies of the impact of anthropogenic disturbance in several islands on both vascular plants (Marcelino et al., 2013) and arthropods (Cardoso et al., 2009; Florencio et al., 2015, 2016), and (ii) the role of elevation on the diversity of Azorean bryophytes (Henriques et al., 2017b) and vascular plants (Coelho et al., 2016; Henriques et al., 2017c).

These large scale surveys have allowed addressing several biodiversity shortfalls for these islands (Cardoso et al., 2011; Hortal et al., 2015) in a systematic way, contributing also for the design of conservation policies in Azores. The best example is the TOP100 management priority species for the European archipelagos of the Macaronesian region (Azores, Madeira, and the Canary Islands) (Martín et al., 2010), and the ranking of Azorean protected areas based on a Biotic Integrity Index (Gaspar et al., 2011).

Research performed in the Azores in the last decades has also led to advances towards solving the “Linnean shortfall” (i.e., the need to describe the unknown species and revise the taxonomy of groups of species poorly known). For instance, 24 out of the known 26 endemic Azorean spiders have been described since 1989 (Borges and Wunderlich, 2008; Crespo et al., 2013, 2014) and a comprehensive checklist of Azorean terrestrial and marine biota is available (Borges et al., 2010a). However, despite the high rate of taxonomic descriptions in the last decades, many species are awaiting discovery and taxonomic description (Lobo and Borges, 2010; Schaefer et al., 2011b), and for some taxonomic groups this knowledge is still quite poor (e.g., Fungi, Lichens, Acari, Diptera, Hymenoptera; see Borges et al., 2010a). The Azorean Biodiversity Portal E-infrastructure (<http://azoresbiportal.uac.pt/>; Borges et al., 2010b), has been of great relevance to support the continuous exposure of Azorean biota to potential taxonomic revisions, contributing also to a public awareness on the relevance of Azorean biodiversity.

In addition to taxonomy, two very important sources of data are needed for proper conservation, the knowledge on the distribution and abundances of species (i.e., the so-called the Wallacean and Prestonian shortfalls, respectively; Cardoso et al., 2011; Hortal et al., 2015). In Azores, the study of the distribution of species at different spatial scales has been properly dealt in important initiatives already mentioned above for arthropods (the BALA project; Borges et al., 2006, 2011), vascular plants (Marcelino et al., 2013; Elias et al., 2016) and bryophytes (Gabriel and Bates, 2005; Aranda et al., 2011). The spatial variation of species abundances (Prestonian shortfall) was studied in detail only for Azorean arthropods in both native forests (Gaston et al., 2006) and other land-uses (Rigal et al., 2013). Evidence indicates that there is a positive relationship between species distributions and their relative abundances, and that exotic species are already well integrated in the native forest floor communities. However, exotic species tend to occur in less number of sites and have lower mean abundances (Gaston et al., 2006). One interesting future research avenue will be to investigate whether species incidence data (presence/absence) could be used to predict the spatial abundance of species. Jiménez-Valverde et al. (2009) found that this is possible but only for some few widespread exotic spiders in Terceira Island, which difficult the use of species distribution models (SDMs) as surrogates of detailed species abundances in space.

Arthropods were also used to study other important abundance metrics, which helped understanding the impact of seasonal variations on species relative abundances (Borges et al., 2017b), the spatial scaling properties of species abundance distributions (Borda-de-Água et al., 2017), the relevance of a species relative abundance metric (GAMBIN model) in the study of species relative abundances (SADs) (Matthews et al., 2014a, 2014b), and its application in biogeographical studies (Fattorini et al., 2016).

In terms of conservation management, the detailed knowledge of species abundances allowed the ranking of protected areas in Azores based on arthropod data (Borges et al., 2005a; Gaspar et al., 2011). Based on these studies the Azorean government created news protected areas and the legislation on species and habitats was improved (RAA, 2012).

Probably of high relevance is all the species distribution data digitized in the AZOREAN BIODIVERSITY PORTAL initiative (Borges et al., 2010a,b) at a 500 × 500 m grid, that allowed performing the IUCN assessments (red listing) for bryophytes, vascular plants and arthropods in Azores in the last 3 years. This data also led to other kind of spatial research responding to both ecological (Henriques et al., 2016), evolutionary (Steinbauer et al., 2016) and conservation questions related with reserve selection (Fattorini et al., 2012; Vergílio et al., 2016) and the impact of climatic changes in Azorean flora and fauna (Ferreira et al., 2016; Patiño et al., 2016).

For the first time in Azores, a long-term monitoring program is in place since 2012, to investigate the impact of climatic changes on the distribution and abundance of arthropods from the native forest (Borges et al., 2017b; Matthews et al., 2019).

The Hutchinsonian and Raunkiaeran shortfalls were originally coined by Mokany and Ferrier (2011) and Hortal et al. (2015) respectively. The Hutchinsonian shortfall relates to the lack of knowledge about the life history (and biotic tolerances), whereas the Raunkiaeran shortfall relates to species functional traits, and both shortfalls hamper proper biodiversity conservation. In many cases,

we lack also complete information on species interactions with other species (Eltonian shortfall). Advances in these critical fields about the knowledge of species biology are only now being tentatively filled with the creation of functional traits databases for bryophytes (Henriques et al., 2017a,d), vascular plants (Schaefer et al., 2011a; Heleno and Vargas, 2015), and arthropods (Whittaker et al., 2014; Rigal et al., 2018).

Present Answers and Future Prospects

Azorean Islands constitute unparalleled natural laboratories for testing the impact of global changes on biodiversity. A high proportion of endemic species are restricted to small fragments of native forests, and with few exceptions (e.g., canopy arthropods; Florencio et al., 2016) they are sensitive to biotic disturbance such as invasions, land-use changes and climatic changes. This creates the perfect setting to test the response of ecological communities to disturbance, and its effects on ecosystem processes. Investigating the spatial replacement of species (i.e., turnover) and richness difference components of beta time, Matthews et al. (2019) showed that exotic arthropod species have high temporal beta turnover than native species, which is due to source-sink dynamics related with the surrounding anthropogenic habitats.

Exotic species often alter ecological processes (Simberloff et al., 2013) and cause severe biodiversity loss. Nevertheless, these species may also provide ecosystem services: exotic arthropods can contribute to important ecological functions in agroecosystems (Rigal et al., 2018) and exotic plants can increase microbial activity (Vilà et al., 2011), introduced natural enemies can control pests (Heimpel and Mills, 2017), or provide ecological “insurance” after the decline of native species (Weissmann and Schaefer, 2017). Understanding the impact of invasive species is particularly important on islands, because of their unique biodiversity and vulnerability (Patiño et al., 2017).

According to Aparício et al. (2018) ensuring the creation of corridors between native vegetation areas should be a priority as an adaptation response to climate change effects in Azores. One important step for designing and implementing conservation strategies that mitigate these impacts is having a deep knowledge of changes on abundance and range-size contraction and expansion. A long-term monitoring strategy is already in place in the Azores, but future actions should include implementing a “Global Island Monitoring Scheme” for the long-term coordinated survey and monitoring of native island forest biota (Borges et al., 2018a).

Acknowledgments

PAVB and RG were partly supported by the project FCT MACDIV—FCT-PTDC/BIABIC/0054/2014. Open access was funded by Project AZORESBIOPORTAL—PORBIOTA (ACORES-01-0145-FEDER-000072). AMCS was supported by a Juan de la Cierva Fellowship (IJCI-2014-19,502) funded by the Spanish “Ministerio de Ciencia, Innovación y Universidades.”

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<http://islandlab.uac.pt/>—“Island Lab”.

<http://www.maisg.com/>—“IUCN SSC Mid-Atlantic Islands Invertebrate Specialist Group”.

Climate Change and Biodiversity Conservation in the Caribbean Islands

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Published by Elsevier Inc.

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Abstract

Given the important role of climate on species distributions, climate change is expected to have effects on biodiversity conservation. Biodiversity on the Caribbean Islands is characterized by a broad range of distributions, from cosmopolitan species to many rare and endemic species that occupy limited geographic areas. Species most vulnerable to climate change include rare and endemic species in wet upper mountain cloud forests and species in restricted coastal habitats vulnerable to warming oceans and sea level rise. Tropical montane cloud forests harbor endemic and endangered species from many taxa. Rising temperatures, reduced precipitation, decreasing relative humidity, and increasing intensity of hurricanes all present conservation challenges for protecting these species as migration upward to favorable climates is not possible. Coastal habitats are local biodiversity hotspots throughout the Caribbean. Rising and warming seas change conditions by increasing salinity of landward habitats, increasing the likelihood of coral bleaching, and increasing storm surge effects throughout the coastal zone. The high density of people and coastal infrastructure in the Caribbean Islands creates scenarios that limit potential landward migration of species and habitats in response to changing coastal conditions and present challenges in prioritizing land use and conservation.

Introduction

The Caribbean has been widely recognized as a biodiversity hotspot (Myers et al., 2000; Roberts et al., 2002; Mittermeier et al., 2004; Shi et al., 2005). The region encompasses 2.75 million square kilometers and includes over 7000 islands and cays. The islands of the Caribbean form an arc running from the Yucatan peninsula of Mexico extending east and south to the northeastern coast of South America (Fig. 1). Principle island groups include the Greater and Lesser Antilles, the Bahamas, Cayman Islands, and Turks and Caicos Islands. There are 13 sovereign island nations and 12 territories with ties to Europe and the United States. The majority of the Caribbean Islands are relatively small, only 13 have an area over 1000 km². The terrestrial land area of the Caribbean Islands is ca. 230,000 km² and nearly 87% of this is in the five largest islands of Cuba, Hispaniola, Jamaica, Puerto Rico, and Trinidad. Together these have a land area of over 200,000 km². Key components to the biodiversity of the Caribbean include the high level of endemism on individual islands or island groups, the diversity of habitats, a long history of human introduction of species, and the tropical climate of the region.

The coastal and marine ecosystems are extremely important to the cultural, economic, and ecological fabric of Caribbean societies. Near shore environments of coral reefs, seagrass beds, beaches, mangroves, rocky shorelines, and estuaries create a matrix of habitats that are some of the most biologically diverse on earth. Coral reefs anchor the marine end of the ridge to reef continuum. They serve as a living barrier that attenuates the wave energy of storms on green and gray shoreline infrastructure. They are sensitive to both ocean warming and acidification and vulnerable to climate change wherever they occur. The Caribbean includes nearly 8% of the world's coral reefs (Bryant et al., 1998), which covers about 26,000 km² (Burke et al., 2004). Seagrass beds and mangroves cover about 66,000 km² and 11,560 km² respectively (Miloslavich et al., 2010). Over 12,000 species have been reported to occur in marine habitats in the Caribbean, dominated by mollusks, crustaceans, and fish (Miloslavich et al., 2010).

A complex matrix of terrestrial habitats influenced by climate, substrates, topography, and land use history supports a reported flora of 12,847 native and introduced species (Acevedo Rodríguez and Strong, 2008; Lugo et al., 2012), with a native flora of ca. 11,000 species (Acevedo-Rodríguez and Strong, 2007) including nearly 8000 endemic vascular plant species (Francisco-Ortega et al., 2007). Terrestrial vertebrates have been reported to include 1342 species, including 564 bird, 520 reptile, 189 amphibian, and 69 mammal species (Anadón-Irizarry et al., 2012). Vertebrate faunal diversity includes high levels of endemic species and genera as a result of speciation on islands and distinctive and isolated habitats such as the upper mountain cloud forests, fragmented

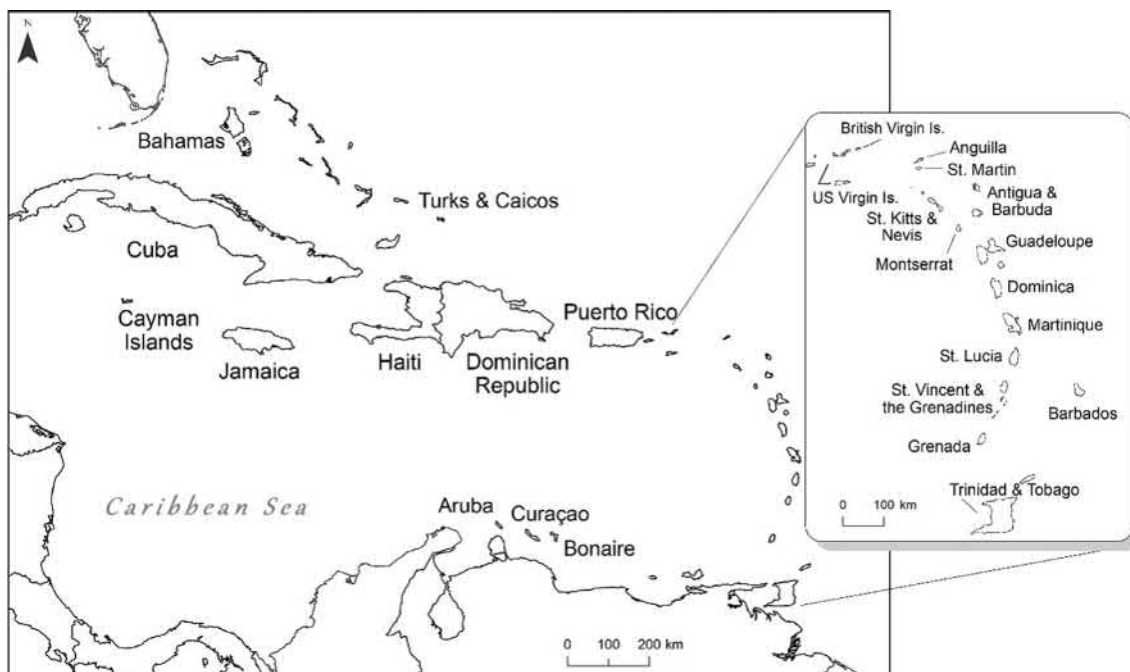


Fig. 1 The Insular Caribbean. From: González, G. and Heartsill-Scalley, T. (2016). Building a collaborative network to understand regional forest dynamics and advance forestry initiatives in the Caribbean. *Caribbean Naturalist*. Special Issue No. 1:245-256.

subtropical dry forests, and thousands of small dry islands and rocky cays. Less well documented but species rich groups of lichenized and other fungi, insects, spiders, and snails also show high levels of endemism due to insular isolation and the rich matrix of Caribbean Island habitats. In Puerto Rico alone over 1180 species of lichens have been recognized (Mercado-Díaz, 2009), with new endemic genera recently described (Mercado-Díaz et al., 2013; Mercado-Díaz et al., 2014) and estimates that the real lichen diversity of the island may reach about 2000 species—nearly 50% of the current checklist for North America (Mercado-Díaz et al., 2015). Fontenla (2003) reports endemism in butterflies of over 35% on the island of Hispaniola, and over 12% among the reported 1011 butterfly species for the Caribbean. The high degree of endemism and rarity across a wide range of taxa have implications as to the vulnerability of species to climate change.

Climate Change

Historically, the Caribbean region has experienced relatively stable seasonal rainfall patterns, moderate annual temperature fluctuations, and a variety of extreme weather events, such as tropical storms, hurricanes, and droughts. Variations in climate over the last 10,000 years have included drier conditions at the end of the last deglaciation (10–7 KY BP), wetter conditions in the early Holocene persisting over 4 k years, and a return to drier conditions in the late Holocene (Hodell et al., 1991). These changes are correlated with orbitally induced variations in seasonal insolation. However, the Caribbean climate is changing due to new atmospheric conditions in the Anthropocene, and is projected to be increasingly variable as levels of greenhouse gasses in the atmosphere increase. Climate change parameters affecting biodiversity in the Caribbean islands include the patterns of precipitation, increasing day and night time air temperatures, increasing sea surface temperature and acidity, sea level rise, and the predictability, frequency, and intensity of extreme climate events such as hurricanes and drought.

Rainfall

Caribbean islands typically experience a dry season from November through April and a wet season from May through October (Granger, 1985; Oliver, 2005; Taylor and Alfaro, 2005; Karmalkar et al., 2013). A characteristic of the Caribbean climate is what is known as the midsummer drought (MSD) (Magaña et al., 1999), which is a dry period (not necessarily a drought) during the wet season resulting in a bimodal cycle of precipitation. The timing and duration of the MSD varies across the Caribbean from early June in parts of the eastern Caribbean to late July around Cuba and the Bahamas, to non-existent in some eastern islands (Magaña et al., 1999; Curtis and Gamble, 2008; Gamble et al., 2008; Karmalkar et al., 2013). The timing, duration, and existence of the MSD in the Caribbean is important ecologically and as measures for modeling and downscaling projected climate for the Caribbean (Stoner et al., 2013; Hayhoe, 2013; Ryu and Hayhoe, 2014). The amount of rainfall varies considerably from drier northern to wetter

southern islands, and mountainous topography interacting with the northeasterly trade winds creates steep gradients in rainfall over short distances on many islands (Granger, 1985; Sobel et al., 2011; Daly et al., 2003). These gradients drive many patterns in species distributions, ecosystem functions, and biodiversity in the Caribbean (Gould et al., 2006; González et al., 2013). Recent downscaling efforts (Bowden et al., 2018; Bhardwaj et al., 2018) are providing projected climate data at fine scales and allowing researchers to model potential effects on crops and ecosystems (Fain et al., 2018; Khalyani et al., 2016). An analysis of the potential effects of climate change on 200 plant species in Puerto Rico suggests that environmental suitability are projected to increase for low-altitude dry and warm climate species while it decreased for the high-altitude colder and wet climate species (Khalyani et al., 2019) (Fig. 2).

Air Temperature

Rising temperatures have been manifested as both increasing night time minimum temperatures and as a higher frequency of extreme heat days (Van Beusekom et al., 2015; Gould et al., 2018). Climate projections indicate these trends will likely continue and accelerate (Khalyani et al., 2016; Bhardwaj et al., 2018). Projections of more hot dry days, longer periods without rain, and warming night time temperatures have implications for direct and indirect effects on species (Khalyani et al., 2016). There are a number of endemic species adapted to the cool, wet, cloudy climates of the higher mountains in Puerto Rico, Jamaica, Hispaniola, and Cuba. Many species from several taxa will likely be adversely affected as rainfall decreases, temperature rises, and relative humidity drops below threshold levels for the formation of cloud forests in the Caribbean (Gould et al., 2018; Miller et al., 2018; Helmer et al., 2019) (Fig. 3). Secondary effects of rising temperatures and reduced rainfall include changes in the phenology of fruiting, flowering, and leaf fall that have effects on habitat conditions, nutrient cycling, plant reproductive fitness, and animal populations (PRCCC, 2013; Gould et al., 2018). Additionally, unusually dry vegetation increases the risk of fire (Monmany et al., 2017; Van Beusekom et al., 2018a).

Sea Surface Temperature

Ocean surface waters have warmed globally by about 0.13 °F (0.07 °C) per decade between 1900 and 2016 (Jewett and Romanou, 2017). From 1955 to 2016 the waters of the northeast Caribbean increased at a rate of 0.23 °F (0.13 °C) per decade, and over the last two decades, the sea surface warming rate has reached 0.43 °F (0.24 °C) per decade (Boyer et al., 2013; Gould et al., 2018) (Fig. 4). One of the responses to ocean warming is bleaching of adult coral colonies. Prolonged or severe periods of high temperatures and extended coral bleaching can result in colony death. In 2005, a mass bleaching event, driven by 12 weeks of temperatures above the normal local seasonal maximum, affected the entire Caribbean region, resulting in the loss of 40–80% of the coral cover in the region (Donner et al., 2007; Selig et al., 2013; Gould et al., 2018) (Fig. 5).

Sea Level Rise

Since the middle of 20th century, relative sea levels have risen by about 0.08 in. (2 mm) per year on average along the coasts of Puerto Rico and the United States Virgin Islands. However, rates have been slowly accelerating since the early 2000s with an acceleration by a factor of about three starting in 2010–11. This recent acceleration agrees with what has been observed along the

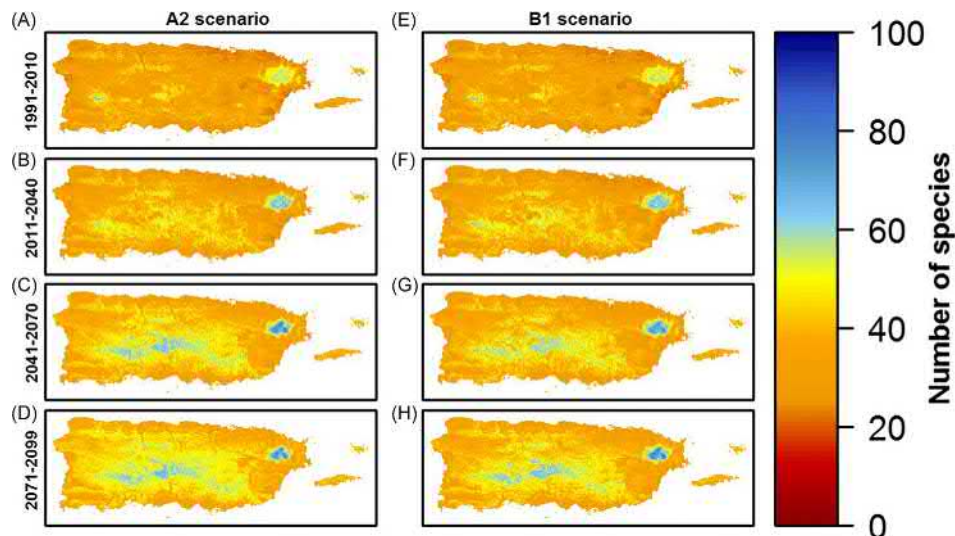


Fig. 2 Changes in the number of tree species as calculated from using the Spatially Explicit Species Assemblage Modeling framework (Guisan and Rahbek, 2011) for future periods under high (A–D) and low (E–H) carbon emission scenarios. From: Khalyani, A. H., Gould, W. A., Falkowski, M. J., Muscarella, R., Uriarte, M. and Yousef, F. (2019). Climate change increases potential plant species richness on Puerto Rican uplands. *Climatic Change* 16(2):587.



Fig. 3 Cloud forests in the Luquillo Mountains of Northeastern Puerto Rico. Known locally as Elfin Woodland, these forests lie within the El Yunque National Forest and Luquillo Experimental Forests. They harbor a high percentage of endemic species from many taxonomic groups (Gould et al., 2006; González et al., 2013). Photo credit: Grizelle González, USDA Forest Service International Institute of Tropical Forestry.

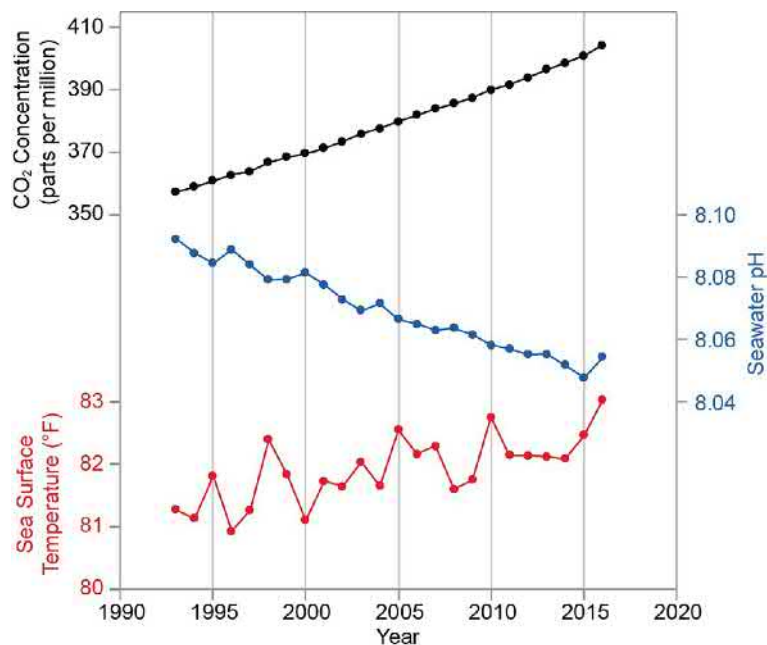


Fig. 4 Annual time series from 1993 to 2016 of atmospheric carbon dioxide (CO₂; black line), sea surface temperature (red line), and seawater pH (blue line) for the Caribbean region. (Gould et al., 2018; <https://nca2018.globalchange.gov/chapter/20#fig-20-5>.)

southeastern U.S. seaboard, and rates of global and regional relative sea level rise are projected to continue to increase substantially this century, largely dependent on the amount of future greenhouse gas emissions. Relative sea levels are projected to rise by about 0.8, 1.2, or 2.8 ft in low, intermediate or high emissions scenarios, respectively, by 2050 across the region compared to levels in 2000 and by about 1.6, 3.6, or 10.2 ft, respectively, by 2100 (Zervas, 2009; Sweet et al., 2017; Gould et al., 2018) (Fig. 6).

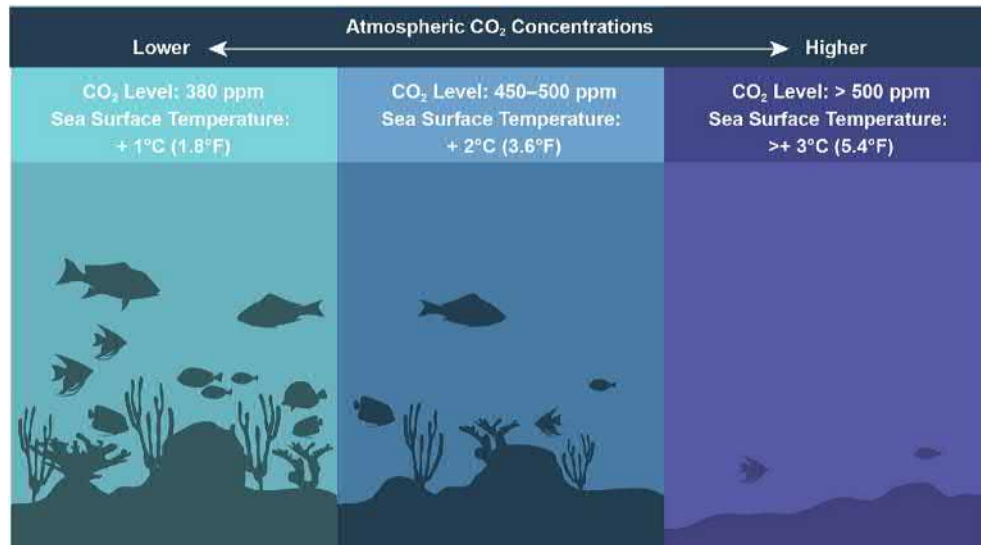


Fig. 5 Coral reefs are sensitive to sea surface temperatures. The condition of coral reefs has a big effect on biodiversity as so many species depend on healthy reef. The severity of effects increases as CO₂ levels and sea surface temperatures rise. If conditions stabilized with concentrations of atmospheric CO₂ at 380 ppm (parts per million), coral would continue to be carbonate accreting, meaning reefs would still form and have corals. At 450–500 ppm, reef erosion could exceed calcification, meaning that reef structure is likely to erode and coral cover is likely to decline dramatically. Beyond 500 ppm, corals are not expected to survive. (Gould et al. 2018; <https://nca2018.globalchange.gov/chapter/20#fig-20-6>).

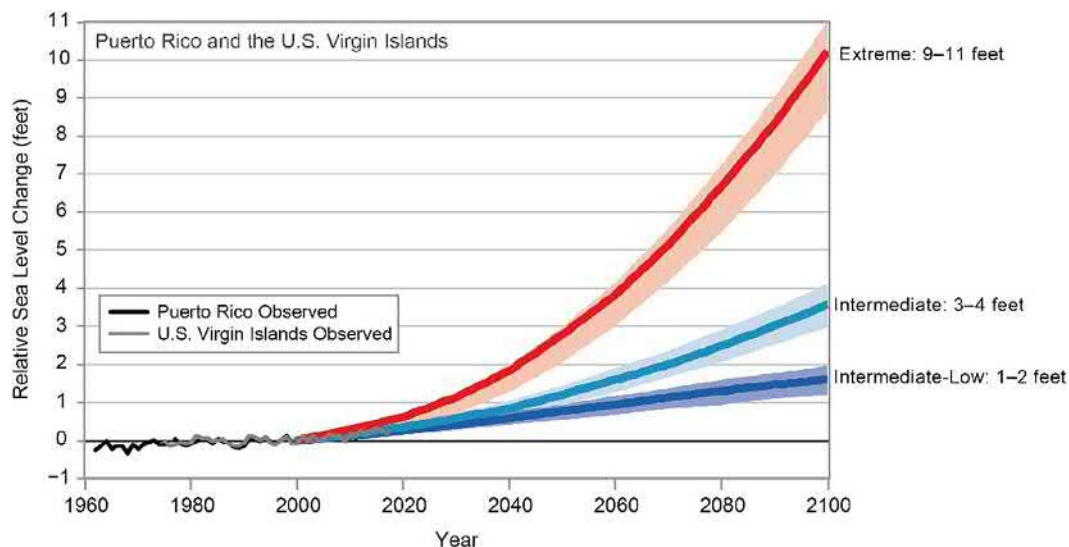


Fig. 6 Sea level rise trends in Puerto Rico and the U.S. Virgin Islands for the period 1962–2017. Projections are shown under three different scenarios of intermediate-low (1–2 ft), intermediate (3–4 ft), and extreme (9–11 ft) sea level rise. (Gould et al. 2018; <https://nca2018.globalchange.gov/chapter/20#fig-20-6>).

Biodiversity and Conservation

Protected area networks are a widely adopted strategy for conserving biodiversity and to mitigate the adverse effects of climate change (Dudley et al., 2010; Naughton-Treves et al., 2005). About 20% of the land base of the insular Caribbean is designated as protected area (UNEP-WCMC and IUCN, 2019). In this region, islands vary in the degree of protection from less than 5% on the island of Barbados to 60–70% on the islands of Guadeloupe and Martinique (Table 1). However, under new and changing climate conditions, species are shifting their distribution ranges, which means protected areas today may not be effective in the near future (Bustamante et al., 2018; Armsworth et al., 2018).

Island geography, sea level rise, and development can limit options for species migrations. As an example, in recent decades in Puerto Rico residential development increased adjacent to most of the island's protected areas, limiting capacity to expand and

Table 1 Relative and actual amount of marine and terrestrial protected areas for Caribbean Island.

	Terrestrial			Marine		
	Area protected (km ²)	Total area (km ²)	Percent	Area protected (km ²)	Total area (km ²)	Percent
Cuba	18,481	111,643	16.6	15,819	365,756	4.3
Hispaniola (DR)	12,727	48,510	26.2	48,625	270,774	18.0
Hispaniola (Haiti)	1954	27,390	7.1	1813	123,867	1.5
Bahamas	4930	13,458	36.6	47,355	597,705	7.9
Jamaica	1760	11,059	15.9	1860	246,488	0.8
Puerto Rico ^a	1356	9041	16.0	3078	176,163	1.8
Trinidad and Tobago	1595	5213	30.5	37	75,798	0.1
Guadeloupe	1170	1679	69.7	90,958	91,039	99.9
Martinique ^b	706.64	1150	61.4	47,916	47,644	100.0
Turks and Caicos	452	1018	44.4	150	154,242	0.1
Dominica	168	766	22.0	10	28,749	0.0
Antigua and Barbuda	85	455	18.6	197	108,492	0.2
Curacao	71	451	15.8	12	30,535	0.0
Barbados	6	444	1.3	10	185,020	0.0
Saint Vincent and Grenadines	92	410	22.4	80	36,511	0.2
US Virgin Islands	52	376	13.8	306	36,030	0.9
Grenada	37	374	9.8	23	26,282	0.1
Bonaire, Sint Eustatius, Saba	92	323	28.4	2756	25,112	11.0
Cayman Islands	31	289	10.8	93	119,605	0.1
Saint Kitts and Nevis	62	271	22.9	408	10,263	4.0
Aruba	36	189	18.9	0	25,214	0.0
British Virgin Islands	16	176	9.1	3	80,529	0.0
Montserrat	11	101	11.1	0	7628	0.0
Saint Martin/Sint Maarten	8	96	8.3	1074	1567	68.5
Anguilla	6	86	7.3	32	92,654	0.0
Saint Barthélemy	5	25	20.4	4244	4318	98.3
Total	45,909.64	234,993	21.7	266,859	2,967,985	16.1

^aPuerto Rico values based on Castro-Prieto et al., 2019.

^bMartinique estimates based on information from the Critical Ecosystems Partnership Fund (CEPF, 2010).

From UNEP-WCMC and IUCN. (2019). Protected planet: The world database on protected areas (WDPA)/database on other effective area-based conservation measures [On-line], September 2019, Cambridge, UK: UNEP-WCMC and IUCN. Available at: www.protectedplanet.net. except where noted.^{a,b}

adapt to new climatic conditions (Castro-Prieto et al., 2017, Fig. 7). Within montane protected areas, limited ability for upward migration along elevational climatic gradients increases the vulnerability of upper montane species. For example, as climate changes, climate constrained infectious disease may be driving changes in amphibian species ranges within natural areas. Analyses of historical records and recent frog acoustic samplings in the protected El Yunque National Forest (EYNF) in the Luquillo Mountains of Northeastern Puerto Rico suggest shifts in anuran distributions, where incidence of disease moves upward, and low elevation areas have lost at least six anuran species in the last 25 years (Campos-Cerqueira and Aide, 2017). Similarly, in a study of bird distributions along the elevational and climatic gradient in these mountains, most of the bird species studied (72%) did not present elevational shifts in their ranges but there is evidence of a significant upward shift in the range of eight species (Campos-Cerqueira et al., 2017).

Sea level rise affects terrestrial habitats through salinization of coastal wetlands and aquifers, through increased rates of erosion, and through inundation. These represent changes in habitat characteristics important in governing species distributions and biodiversity. Potentially, marine habitats can shift landward or increase in growth to adapt to rising seas, and terrestrial species can migrate landward to accommodate new salinity gradients. However, the coastal zones throughout the Caribbean are where most people live and build roads, airports, hospitals, hotels, and power plants. Infrastructure represents a significant barrier to the landward migration of species adapting to sea level rise (Yu et al., 2019). The conflicts between development and natural resource protection will only increase as natural areas are reduced by sea level rise and coasts are hardened to protect infrastructure and mitigate erosion (Fig. 8).

In addition to shifting climate means affecting species distributions, extreme climate events such as high temperatures, hurricanes, droughts, and flooding are all projected to increase with a warming climate, and species distributions will be affected (Van Beusekom et al., 2018b; Wunderle, 2018; Lloyd et al., 2019; Khalyani et al., 2019; Helmer et al., 2019). Extreme events can increase mortality rates and, under new climatic regimes, promote shifts in the distribution of habitats and species.

Protected areas are one of several mechanisms that can support biodiversity conservation in what has been described by Castro-Prieto et al. (2019) as an integrated system for the conservation of nature (Fig. 9). This includes recognizing four mechanisms in addition to protected area networks, i.e., the role of laws and regulations that protect species, habitats, and ecosystems;

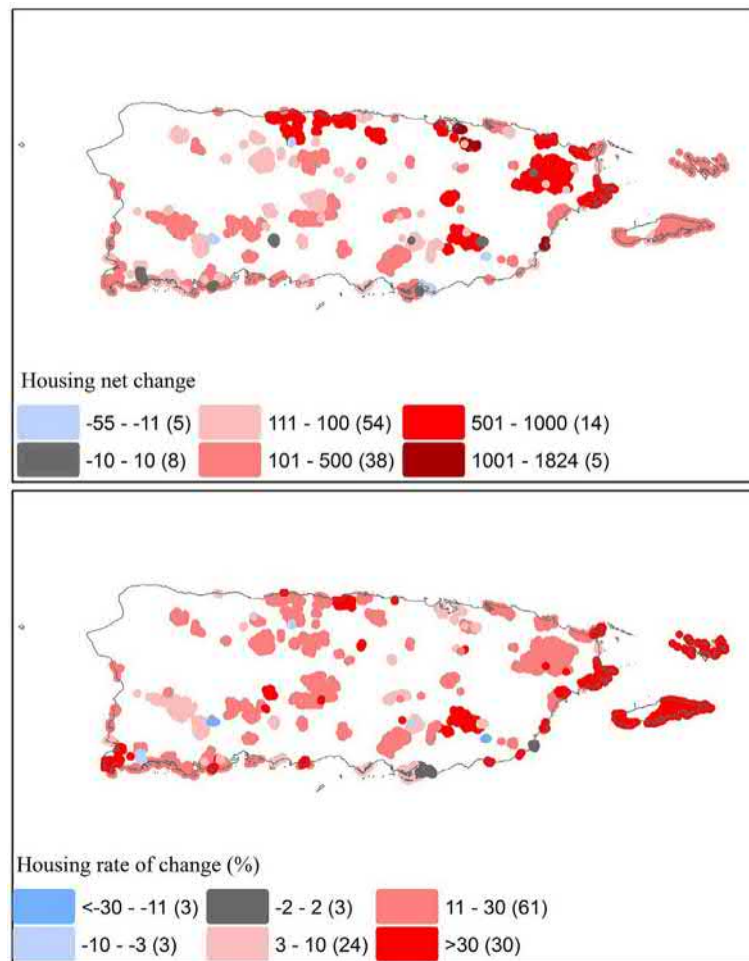


Fig. 7 Housing net change and the rate of change within 1-km of the protected areas in Puerto Rico (Castro-Prieto et al., 2017).



Fig. 8 Hawksbill turtle nest near Humacao, Puerto Rico, hemmed in by housing development and subject to hurricane damages from nearby infrastructure. Photo credit Carlos E. Díez González.

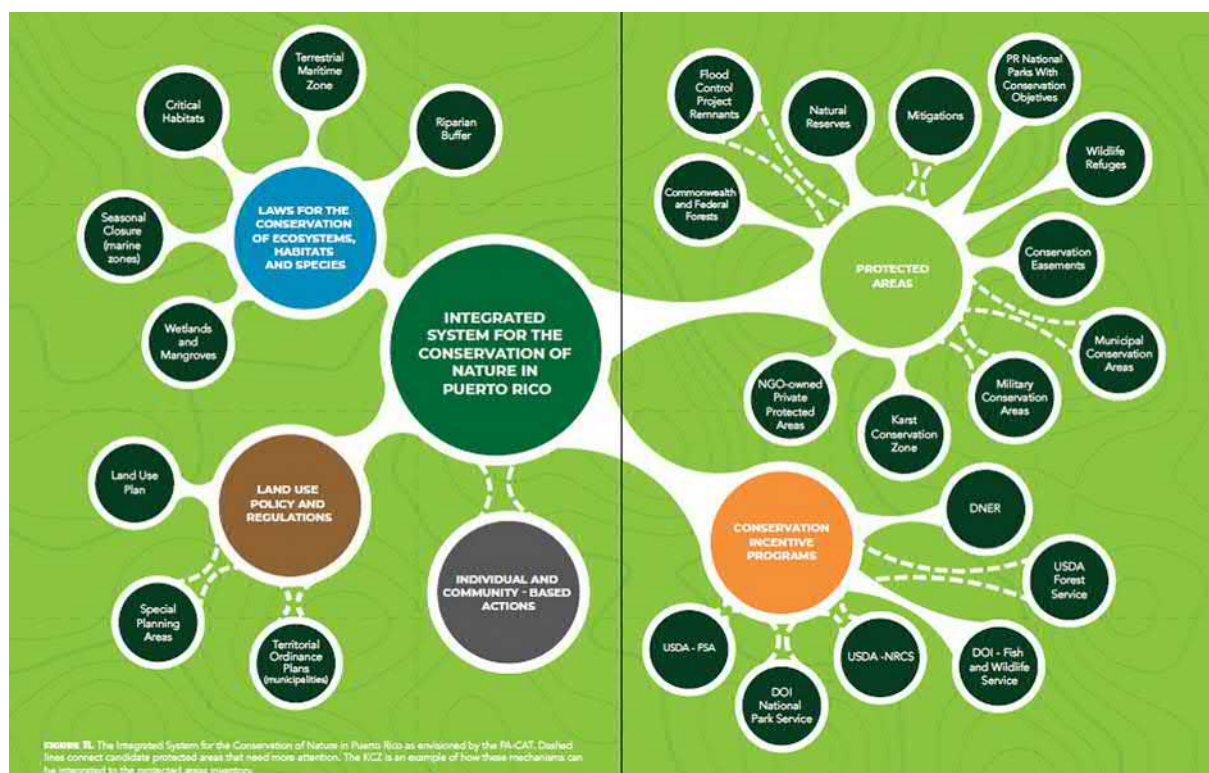


Fig. 9 An envisioned integrated system for the conservation of nature in Puerto Rico, which includes the protected areas and other land conservation mechanisms available in the island.

land use policies and regulations; incentive programs; and individual and community based actions. This integrated approach is important considering the magnitude of climate change effects and the recognition that management and effectiveness of biodiversity protection within protected area networks varies widely (Kairo et al., 2003; Visconti et al., 2019). Research is ongoing as to how well protected areas accomplish different aspects of biodiversity conservation, particularly in light of climate change (Rincón-Díaz et al., 2018; Armsworth et al., 2018; Maharaja et al., 2019). The integrated approach also recognized that biodiversity is a component not only of wildlands and protected areas, but also of working lands. Climate change has effects on biodiversity relevant to food security and agriculture. For example, forecasts based on long-term honey yield records and bioclimatic variables suggest a reduction on average yield and in areas suitable for honey production in Puerto Rico under multiple scenarios of climate change (Delgado et al., 2012). Additionally, projected climate trends suggest that increases in mean temperature and decreases in precipitation could result in the reduction of highly suitable growth conditions for *Coffea arabica* in this century (Fain et al., 2018). Balancing food security, conservation and economic development while dealing with climate risks is an ongoing issue across the Caribbean Region (Knowles et al., 2015; Gould et al., 2017; Gould et al., 2018).

Conclusions

The nature of governance of natural resources is particularly diverse in the Caribbean. Support for conservation and climate related research and adaptation practices from North American, Latin American, and European research institutes, governmental agencies, Universities, and local and global conservation organizations is extensive if not always coordinated (Gould et al., 2018, Fig. 10). Working across boundaries can be one way to reduce climate change vulnerabilities. As an example, an inter-agency effort allowed the development of a comprehensive protected areas database and the quantification and mapping of other conservation mechanisms that contribute to a larger picture of land conservation in Puerto Rico (Castro-Prieto et al., 2019).

Climate change risks are increasing and effects are being experienced by natural resource managers in the Caribbean. Islands don't have much space for large protected areas or for shifting and expanding their current boundaries. Targeted mechanisms can make the best use of resources—i.e., protecting those rare habitats from disturbance or implementing management to maintain some kind of condition will help maintain species of interest and biodiversity. There is a long history of information on climate and conservation research in the Caribbean. However, it is not always used for planning and management applications. Efforts to deliver

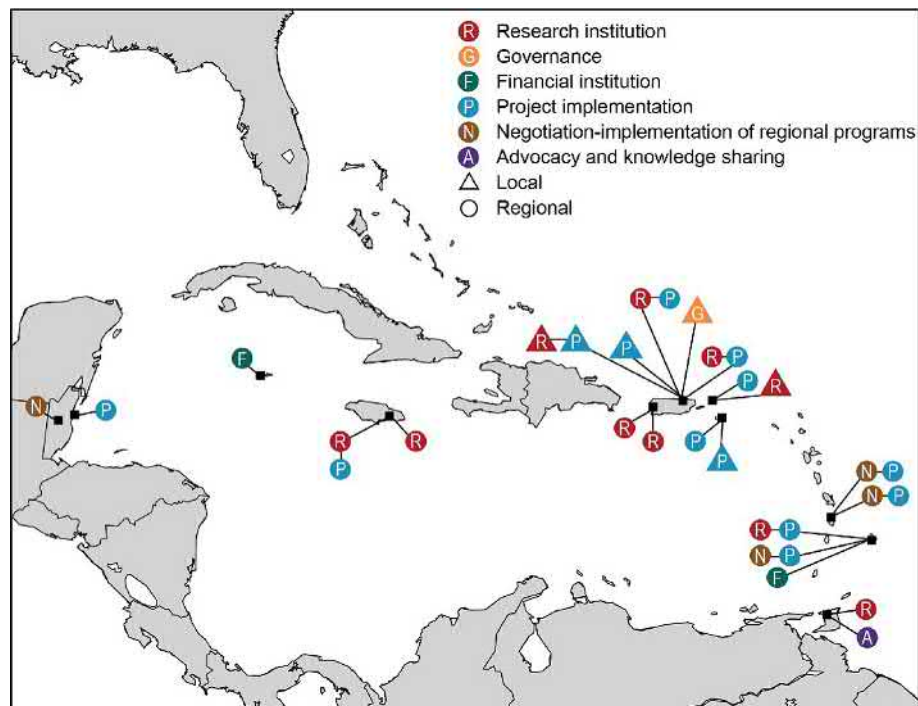


Fig. 10 Location of selected organizations working on climate risk assessment and management in the Caribbean region. Regional efforts to address climate challenges include the implementation of adaptation measures to reduce natural, social, and economic vulnerabilities, and actions to reduce greenhouse gas emissions (Gould et al., 2018; <http://nca2018.globalchange.gov/chapter/20#fig-20-18>).

science-based knowledge to agencies, universities, institutions and land managers dealing with vulnerable species and habitats will help organizations to act fast and adapt to climate change and weather variability. Regional and locally based vulnerability assessments focused on effects on biodiversity, modeling of projected climate change effects species that provide key ecological/and agricultural services, and assessing the effectiveness of adaptive practices are important components to reduce vulnerability to climate change. Actions that reduce the vulnerability to future risks include preparing for disturbance with nurseries and mitigation methods. Integrating species of interest with infrastructure in coastal and agricultural or working lands. Aligning best practices with mechanisms, incentives, and education of conservation practices in working lands that integrate biodiversity (e.g., multi-story cropping, alley cropping, corridors) (Álvarez-Berríos et al., 2018). Monitoring and managing to reduce cumulative effects. Collaborating internationally to share capacity, regional vulnerability assessments, and knowledge. Enjoying what we have—value and appreciation are key to conservation. Research needs include better quantifying values provided by nature, additional area covered by downscaling climate data, and modeling linking downscaling to species distributions, ecosystem services, and climate vulnerabilities.

Given the high level of biodiversity throughout the Caribbean, it is not easy to prioritize what is most at risk. Two priority areas from an example in Puerto Rico are found across the Caribbean (Fig. 11). They include wet mountain tops and cloud forests, and the marine and terrestrial coastal zone. The high number of endemics in island cloud forests, and the lack of ability to migrate from mountain tops, makes this a key habitat in the conservation of biodiversity. Additionally, species adapted to the coastal zones throughout the Caribbean are subject to multiple stressors of warming oceans, acidifying oceans, rising seas, and increasing constraints of development and infrastructure. Coastal species are often more cosmopolitan than cloud forest species, with relatively fewer endemics. However, coastal habitats tend to be local biodiversity hotspots due to the matrix of marine, wetland, and upland habitats. Sea level rise and salinization often trap coastal habitats between rising seas and infrastructure, limiting capacity for inward migration, and putting coastal biodiversity at risk and a priority for biodiversity conservation.

Acknowledgments

Thanks to Edgardo González and Sandra Soto Bayó for figure on habitats in Puerto Rico vulnerable to climate change. Thanks to Carlos E. Díez González for turtle and coastal erosion photographs. Thanks to Olga Ramos for figure identifying the Insular Caribbean. All research at the USDA Forest Service International Institute of Tropical Forestry is done in collaboration with the University of Puerto Rico.

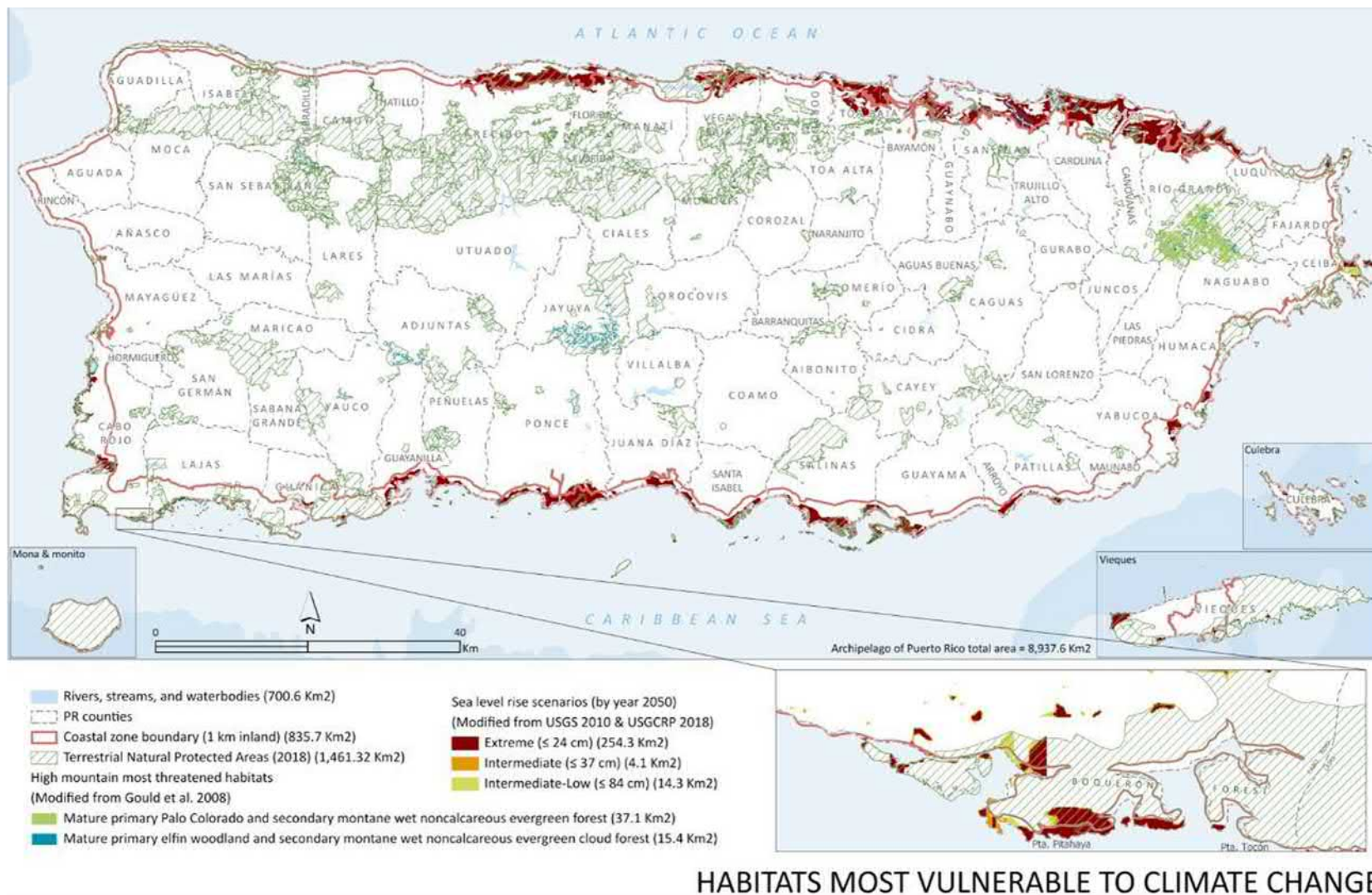


Fig. 11 Habitats in Puerto Rico most vulnerable to climate change as identified by resource managers. Coastal areas and high elevation ecosystems are some of the vulnerable environments where effects might have significant natural and physical results.

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An Overview of the Socio-Ecological System of Cays and Islets in the US Caribbean and Their Vulnerability to Climate Change

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Published by Elsevier Inc.

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Abstract

The offshore cays around the main islands of Puerto Rico, St. Thomas, St. John, and St. Croix are largely uninhabited and provide habitat for threatened, endangered, at-risk, and species of greatest conservation need including many resident and migratory species of seabirds, shorebirds, endemic reptiles, and plants. Management is limited by insufficient resources, capacity, and a mixture of ownership (federal, Commonwealth, Territorial, private NGO, and private), making regional planning a challenge. Invasive species are the dominant short- and long-term threats to these systems including invasive plants that alter habitat conditions and invasive mammals (e.g., mice, rats, goats) that kill native fauna and degrade habitats. Recreational and commercial uses by humans, as well as marine debris and accumulations from harmful algal blooms, pose a significant threat to crucial habitats and key conservation species, especially in the coastal zone. In the longer term, the cays ecosystems and fauna are expected to show high exposure and sensitivity with limited adaptive capacity, depending on the type of island, to the impacts of climate change. Current projections highlight substantially altered rainfall patterns and extensive drought, as well as extreme sea level rise (beyond 3 m by 2100 under the worst scenarios) and more frequent or intense hurricanes. The impacts of sea level and precipitation in particular were used to develop future scenarios to compare and contrast effects on focal species and coastal habitats. The scenarios and impacts were then used to suggest potential adaptation strategies.

Introduction

There are over 750 offshore islands within the U.S. Caribbean surrounding the main islands of Puerto Rico and U.S. Virgin Islands (USVI) of St. Thomas, St. Croix, and St. John (Fig. 1A and B). The diversity of these islands is influenced by geology, location (windward, leeward), adjacent ocean bathymetry, proximity to a larger land mass, elevation/topography, size, accessibility, and historical use. The terms island (*isla*), islet (*islote*), cay (*cayo*), and rock (*roca*, *peñón*, *piedra*) often prefix island names interchangeably but there appears to be no exact criteria for their use. An islet can refer to any small island, whereas interestingly, the word cay (or *cayo* in Spanish) in Puerto Rico often refers to a small, low island or bank composed of sand and coral fragments, whereas in the USVI

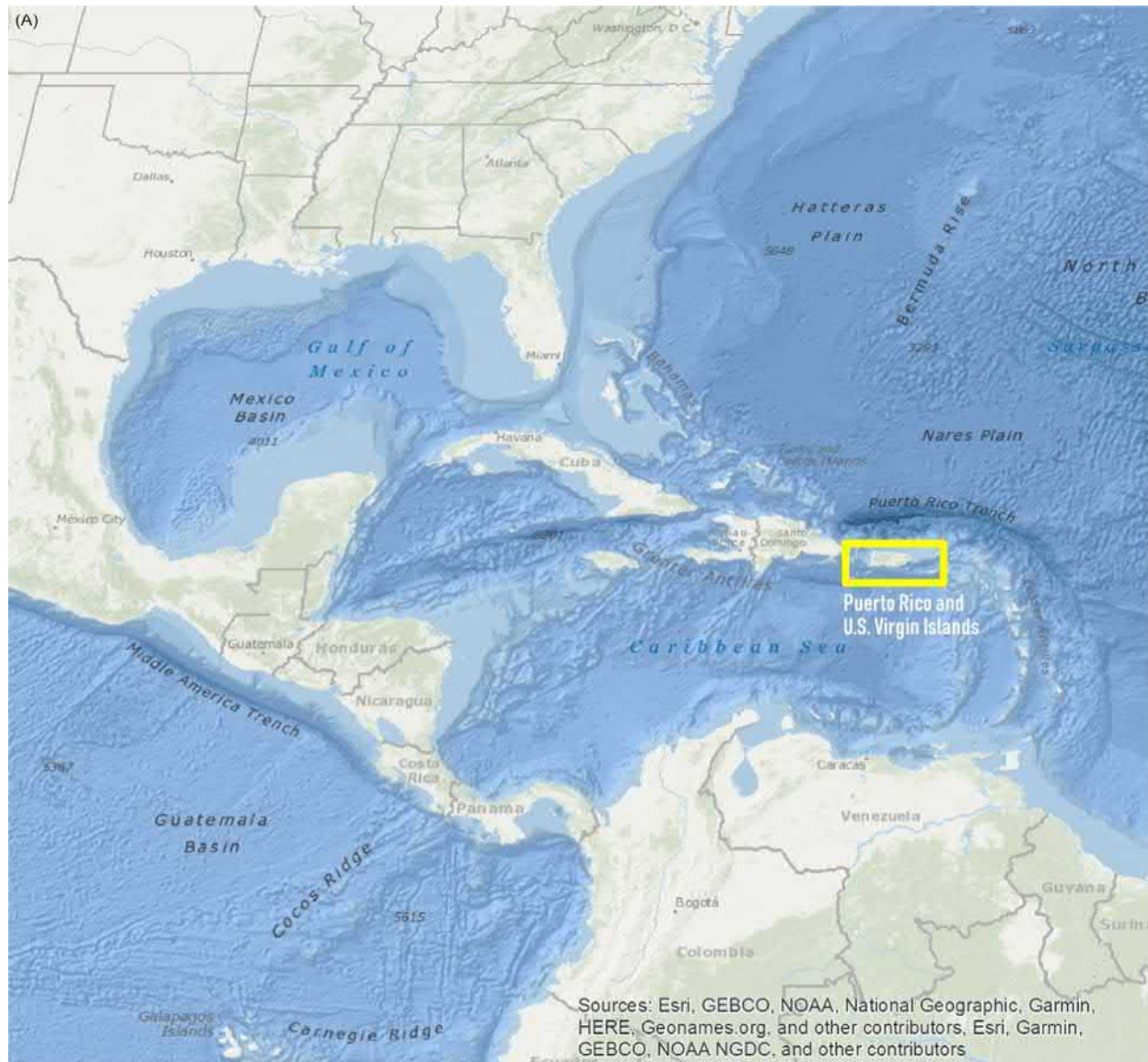


Fig. 1 (A) Regional map of the Caribbean framed by southern North American, Central America, and northern South America to provide reference for the location of the U.S. Caribbean, i.e., Puerto Rico and the U.S. Virgin Islands. (B) Map of the primary cays of the U.S. Caribbean mentioned in the text.

cays more commonly refer to the larger higher vegetated islands. Islands within the U.S. Caribbean can be classified into four types based on their formation or composition: (1) sand and coral cays; (2) mangrove cays; (3) volcanic and volcanoclastic; and (4) limestone. Each type is described in detail below.

Although some cays have been developed for human use, the majority are largely uninhabited and support many species, including some that are threatened, endangered, or endemic. In addition to providing wildlife refugia, the offshore islands are also important to society. Humans use the terrestrial and aquatic areas surrounding the islands for tourism, recreation, the extraction of resources (mining, fishing and forestry) and to market their scenic value. The excessive uses over time and high demand for the limited space on these islands has resulted in far reaching impacts such as invasive species (especially mammals such as rats, mice, mongoose, deer, feral cats, pigs, and goats, but also reptiles such as common iguanas, as well as non-native invasive plants) and anthropogenic disturbances due to direct use or plastic pollution reaching the cays.

There has been an extensive, and highly controversial, history of U.S. military use or lease for bombing practices from 1939 to 1975 within the Culebra Island archipelago and Desecheo Island (García-Muñoz, 1991, CINWRC-PR, 2011) and Monito Island. Additionally, the eastern end of Vieques Island, and many of the adjacent cays were used for various military practices (including bombing) from the 1940s to 2003.

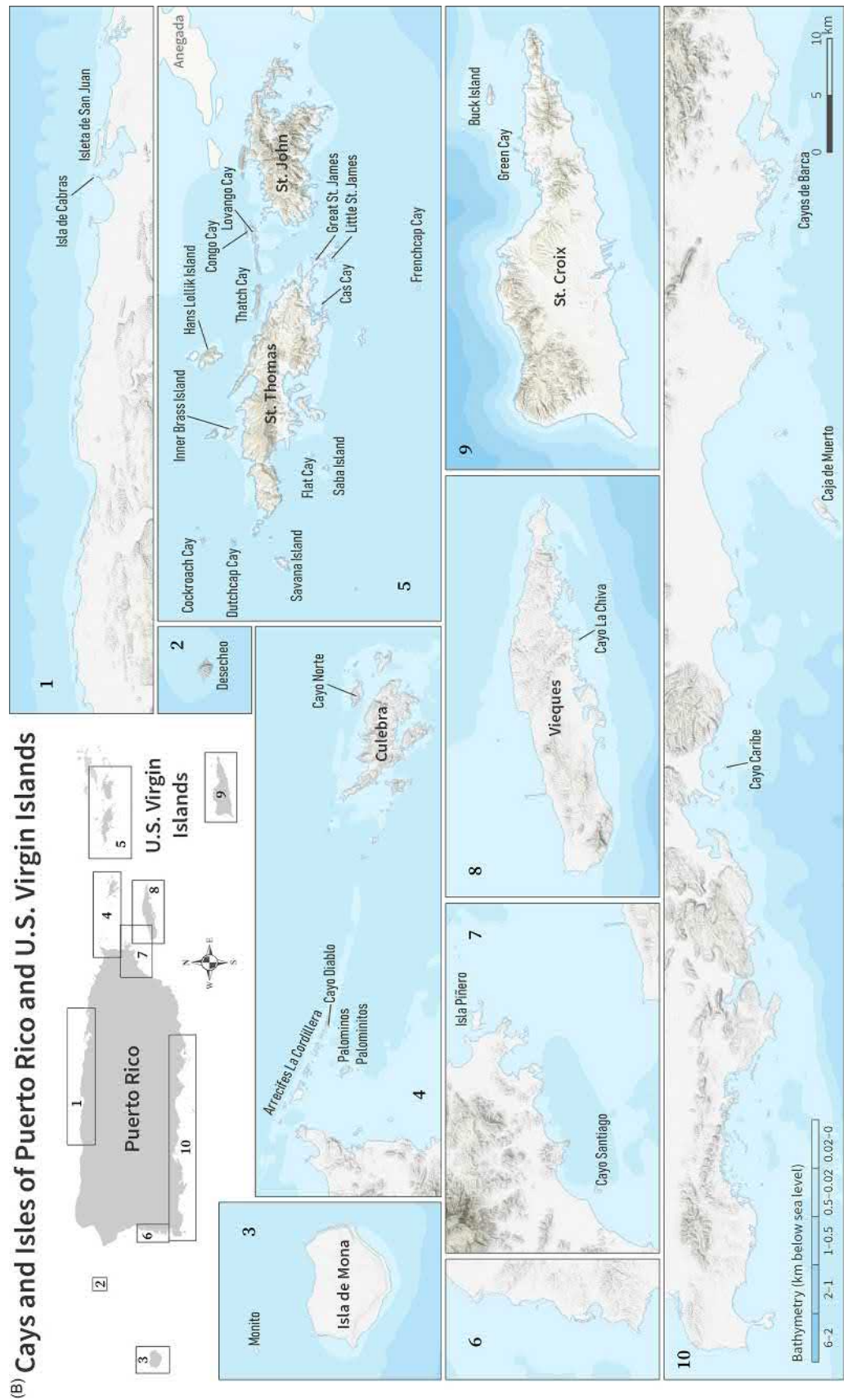


Fig. 1 (continued).

Potential impacts stemming from the effects of the current climate crisis include sea level rise, projected increases in the intensity and duration of droughts, warming air and water temperatures, intense coral bleaching and disease, ocean acidification, saltwater intrusion, and increased intensity and frequency of tropical storms and hurricanes (Gould et al., 2018). The species and habitats that sustain island ecosystems are highly vulnerable to the combined effects of these impacts.

Effective conservation and adaptation of these island systems will require a regional approach. However, the ownership, legal status, and use of cays and islets in the U.S. Caribbean is highly complex making regional planning challenging. Most of the larger islands are located within marine managed areas (MMAs) (Schärer-Umpierre et al., 2014). These are designated as Natural Reserves or Wildlife Sanctuaries administered by Puerto Rico Department of Natural and Environmental Resources (PR-DNER) (e.g., Mona, Monito, Caja de Muertos, Fig. 1) and the U.S. Virgin Islands Department of Planning and Natural Resources (USVI-DPNR), National Wildlife Refuges (NWR) administered by the U.S. Fish and Wildlife Service (USFWS) (e.g., Desecheo, in Puerto Rico, Navassa between Haiti and Jamaica, and Green Cay and Buck Island in the USVI), national parks administered by the U.S. National Park Service (NPS) (e.g., Buck Island Reef National Monument off St. Croix and several cays around St. John in the USVI), and one National Estuarine Research Reserve. In addition, several Natural Reserves (NR) and their marine extensions (e.g., Northeast Ecological Corridor, Arrecifes de la Cordillera; La Parguera; Mona and Monito Islands and Jobos Bay), and the Culebra NWR incorporate multiple islets and cays. While not formally protected, several Critical Wildlife Areas also incorporate multiple islets including the Fajardo coastline and mangroves and adjacent cays within the Punta Petrona NR (Ventosa-Febles, 2005). In Puerto Rico some islands are privately owned including Cayo Norte off Culebra and Isla Palominos and Palominitos in Arrecifes de la Cordillera NR. Private islands are more common in the USVI, with approximately a quarter of the territory's islands in private ownership. Of 57 identified cays, 29 belong to the Virgin Islands government, 14 are wholly private, three are partially private, co-owned with an NGO or Federal entity, eight are US government owned, and three are uncertain. Notable privately-owned islands in USVI include Hans Lollik, Thatch, Great and Little St. James, and Lovango, the latter two being relatively very developed. Interestingly, there is a man-made island of fascinating origin and evolution and Box 1 provides more detail on this interesting situation. Overall, the mixture of ownership creates political and logistical challenges in developing regional management plans for species that cross political boundaries and similarly adds complexity to climate adaptation planning.

Island Type Descriptions

Sand and coral cays: Many of the small cays along the south coast of Puerto Rico have developed over surfacing coral reefs (Fig. 2). The emergent portions are created by the effects of high wave energy accumulating fragments of coral skeletons, principally Elkhorn coral (*Acropora palmata*), (Glynn et al., 1964). These emergent parts of the cays are called ramparts (Hernandez-Avila et al., 1977; Williams et al., 1999). Lower energy sites have cays composed mostly of sand, vegetation, and detritus in addition to the Elkhorn ramparts. Over time, the sediment may stabilize as beach-rock forms (cemented at water level by precipitated calcium carbonate), and the cay becomes vegetated. These islands are dynamic systems, and their shape changes considerably due to accretion and erosion during storms. Many cays are associated with a variety of fringing, patch, bank, and shelf-edge coral reefs. Cays on fringing reefs are the most common and are found throughout the northeast, east, and southern shelf of Puerto Rico. One of the best examples is Arrecifes de la Cordillera Natural Reserve (ACNR), a chain of small, low-elevation cays, rocky islets, and coral reefs stretching between Fajardo and Culebra along a shallow, submarine ridge approximately 29 km long. Some of these cays comprise oolitic (sedimentary rock formed from ooids, spherical grains of concentric layers) eolianite (rock formed by compaction and cementing of particles that have been deposited by the wind) deposits similar to those found in the Bahamas (Kaye, 1959). The rocky islets are the top of ancient dunes that were cemented by calcite. Vegetation associations on these cays include evergreen littoral forest, dry evergreen brush, rocky shores, mangroves, and sandy beach. Sand/coral cays are rare in the USVI.

Mangrove cays: Many cays along the south coast of Puerto Rico are associated predominantly with mangroves (Pittman et al., 2010). These form through a successional process originating with red mangroves (*Rhizophora mangle*) colonizing seagrass beds dominated by turtle grass (*Thalassia testudinum*) on submerged marine sands and may go through a coral reef stage. Vegetation diversity, structure, and biomass of these cays are influenced by differences in soil salinity, frequency of tidal over-wash, wave intensity, and nutrient input. Two notable mangrove cay clusters in Puerto Rico occur in La Parguera Natural Reserve (LPNR) in the southwest and at Jobos Bay National Estuarine Research Reserve (JBNERR) in the southeast (e.g., Cayos Caribe, Cayos de Barca, see Fig. 3) in Puerto Rico. The mangrove islands in LPNR have formed along fringing reefs, some of which lie up to four km from the Puerto Rico shoreline. The cays in JBNERR stretch more than five km along fringing reefs, separated by deep drainage channels (Morelock et al., 1977). Most are covered by mangroves, but some larger cays contain small areas of evergreen littoral woodland and/or secondary vegetation and hypersaline lagoons. In the USVI mangrove cays are uncommon with only a single named cay (Cas Cay) and a few islets within the Mangrove Lagoon on the southeastern side St. Thomas.

Volcanic islands: The volcanic islands are represented by Desecheo Island to the west and Culebra Island to the east of Puerto Rico and most of the islands within the northern USVI (St. Thomas and St. John, Fig. 4). The Puerto Rican Bank archipelago comprises the large islands and over 100 smaller satellite islands, separated from each other in the late Holocene era by eustatic (due to glacial melting) sea level rise (5.3–2.5 million years before present). The islands are dominantly andesite lava, lava breccia, and tuffs (Banks, 1962; Veve and Taggart, 1996). The largest of the cays contain small patches of deciduous, semi-evergreen forest, while the smaller cays are largely steep-walled rocky platforms covered by grasses and shrubs or bare rock (Figs. 4B and 5A–C). Desecheo

Box 1 Ruth Cay, USVI: Industrial destruction turns into endangered species habitat.

Ruth Island is a low-lying man-made cay off the south central coast of St. Croix, U.S Virgin Islands (Fig. B1.1). The 13 hectare island was created in 1965 through deposition of dredge spoil from construction of a shipping channel through Krause Lagoon, a large mangrove system that was effectively destroyed by this action and associated industrialization. Yet the tiny island has grown in ecological value over the decades to become a critical resource for declining species.



Fig. B1.1 Ruth Island. Credit: Google Earth <https://earth.google.com/web/>, accessed June 2019.

The island is comprised of shell and coral rubble and sand with patches of woodland, coastal scrub, and bare rubble habitats (Fig. B1.2). A salt pond has developed on the southeastern corner, surrounded by mangroves planted during mitigation efforts in the 1970s to compensate for the loss of Krause Lagoon (Lewis and Haines, 1980). Habitats on the islands are continuously undergoing vegetation succession, allowing shrublands to become dense. The wetland and woody habitats are used by a number of birds, including White-cheeked Pintails (*Anas bahamensis*) and White-crowned Pigeons (*Patagioenas leucocephala*, Fig. B1.3) that nest in high numbers on this island (55–95 pairs; McNair, 2008). Due to historical hunting pressure combined with habitat loss and non-native mammalian predators, both of these species have been designated as territorial Species of Greatest Conservation Need.



Fig. B1.2 Ruth Island St Croix. Credit: R. Platenberg.

In 1990, 10 federally listed St. Croix Ground Lizards (*Pholidoscelis polops*, **Fig. B1.3**) were released on the island in a bid to expand the distribution of this critically endangered species (McNair and Mackay, 2005). Subsequent population estimates indicated an increase in individuals to 60 in 2003, and a 10-fold increase between 2003 and 2008 (McNair and Mackay, 2005; Geographic Consulting, 2011). This tiny population represents an important species refugia, being one of only four extant populations of this species.



Fig. B1.3 White crowned pigeon and St Croix Ground Lizard. Credit: R. Platenberg.



Fig. 2 Cayo San Cristobal south of Puerto Rico is an example of a sand and coral cay. Credit: HJR Reefscaping.

Island is primarily fragmented volcanic rocks of early Tertiary origin (Seiders et al., 1972) that is dominated by sub-tropical dry forest and is fringed by some of the healthiest coral reefs in the region (García-Sais et al., 2003).

Limestone islands: Situated in the Mona passage to the west of Puerto Rico are Mona (5500 ha) and Monito (14.5 ha) Islands and exemplify limestone islands (**Fig. 6A** and **B**); although Anegada Island in the British Virgin Islands, far to the east, is another important and very old limestone island. Mona Island is the largest offshore island in Puerto Rican waters (**Fig. 1B**). Both Mona and



Fig. 3 Cayo Caribe south of Puerto Rico is an example of a mangrove cay. Credit: HJR Reefscaping.



Fig. 4 (A) Geological interestingness associated with volcanic origin of most of the islands east of Puerto Rico, Grass Cay, St Thomas, USVI. (B) Many volcanic cays rise sharply from the sea providing safe nesting habitat for seabirds but restricting access for monitoring. Cockroach Cay, St. Thomas, USVI. (A) Credit: R. Platenberg and (B) Credit: R. Platenberg.

Monito have been separated from the main island of Puerto Rico far longer than the Culebra islands have been. Mona is a Mio-Pliocene tectonically uplifted carbonate limestone plateau (meseta) (Morelock et al., 2002; Renken et al., 2002; Frank et al. 1998; Seiders et al., 1972). This isolation has led to several endemic species, including an orchid, amphibians and reptiles such as the Mona Iguana (*Cyclura stejnegeri*) (Fig. 6C). Mona Island is dominated by sub-tropical dry forest and is fringed by well-developed coral reefs (García-Sais et al., 2003).



Fig. 5 Coastal shrub and woodland, (A) Dog, (B) Flanagan, and (C) Dutchcap Cays, St. Thomas. Credit: R. Platenberg.

Ecological Value of Cays

Because of their isolation, offshore islands provide valuable refuges for flora and fauna where threats from human persecution, habitat degradation, and climate change are either lacking or evident but with the chance of being more manageable than on the mainland. For example, the largest hawksbill (*Eretmochelys imbricata*) and green (*Chelonia mydas*) sea turtle rookeries in Puerto Rico are on Mona Island and Vieques Island respectively, and leatherbacks (*Dermochelys coriacea*) nest on several of the cays off St. Thomas. Endemic species occur on the larger, more isolated islands (Mona Fig. 6A and B; Monito, Desecheo) and many of these species are also designated as threatened under the US Endangered Species Act or local regulations. Other species such as white-crowned pigeon (*Patagioenas leucocephala*; see Box 1), brown pelican (*Pelecanus occidentalis*), other seabirds, and various shorebirds regularly nest or roost on offshore islets and cays. Coastal wetlands on cays provide habitat for a variety of migratory shorebirds and water birds, along with a variety of invertebrates. Several larger cays off the north shore of St. Thomas have cliff caves and fissures that are occupied by the Antillean Fruit-eating Bat (*Brachyphylla cavernarum*), while Mona and Monito Islands were mined for bat guano during the 19th century (Frank, 1998). Many reptile species that have been extirpated from human-inhabited islands maintain remnant population on these cays, such as the Puerto Rican racer *Borikenophis portoricensis*, the federally endangered St. Croix Ground Lizard (*Pholidoscelis polops*, see Box 1), and the endemic skinks *Spondylurus* spp. Amphibians and many land birds are also absent from most of these islands due to reduced habitat complexity. In a few cases, species threatened on the mainland have been translocated to offshore islets to safeguard populations (e.g., Virgin Islands boa, see Box 2).

Seabirds are an important component of marine biodiversity as they play significant regulatory roles and enhance primary productivity in local marine, intertidal, and terrestrial environments. Cays and islets are critical breeding sites for seabirds because of the reduced predation pressure and ease of access to foraging grounds. Eighteen species of seabirds breed on at least 37 offshore islands or island clusters in Puerto Rican waters (Fig. 7A). The major seabird nesting areas in the USVI are found on about 25 of the most remote or rugged cays off St. Thomas and St. John, where their eggs and offspring are less vulnerable to predators than on the

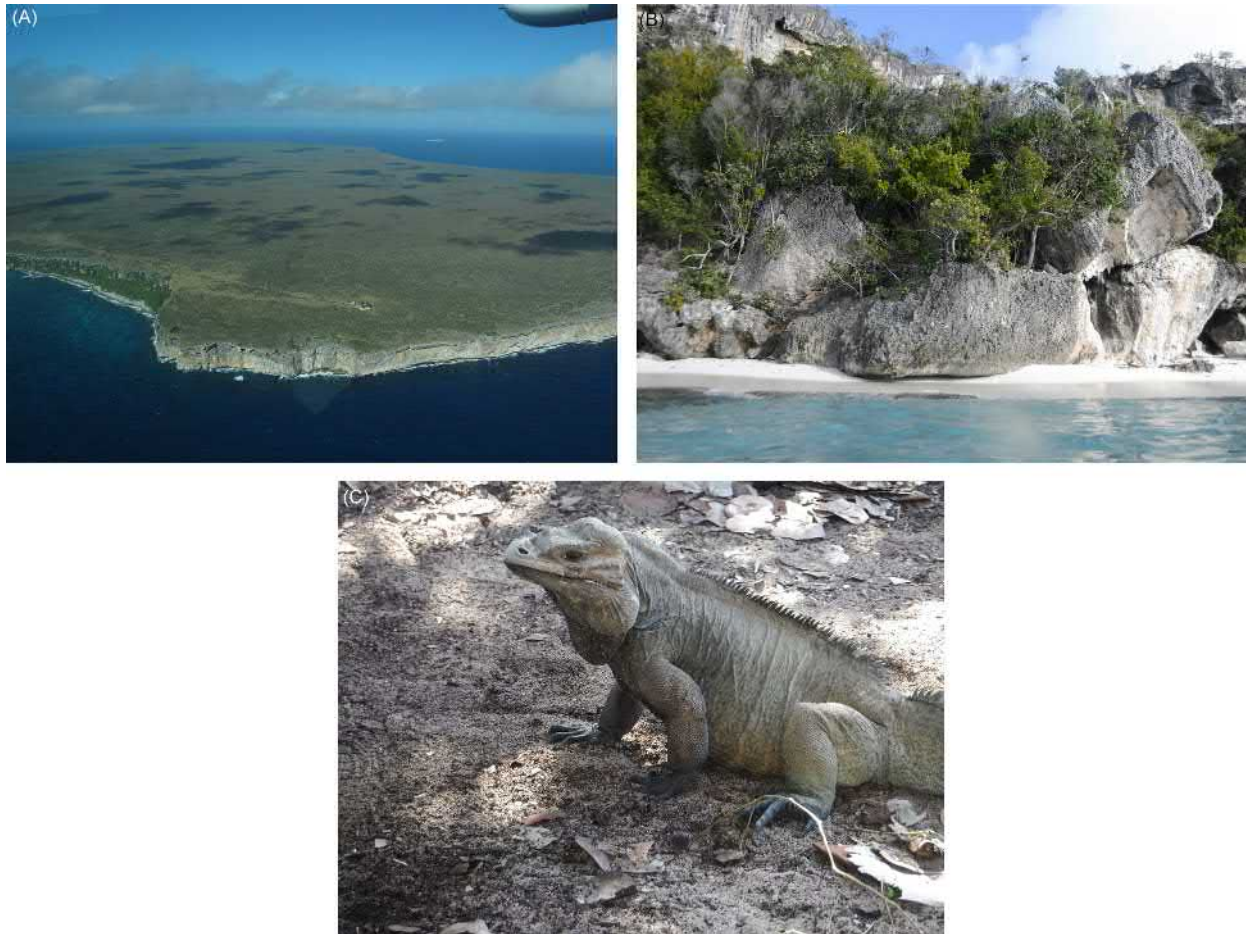


Fig. 6 (A) Aerial view of Mona Island, its steep cliffs rising out of the ocean and seemingly flat surface belies a rugged environment home to many endemic species. (B) Limestone cliffs, caves, white sand beach, and dry scrub habitat of Mona Island. (C) The endemic Mona Iguana (*Cyclura cornuta stejnegeri*). (A) Credit: M. García-Bermúdez, (B), Credit: B. Murry and (C) Credit: Molly Ramsey.

major islands (Pierce, 1996; Fig. 4B). The species composition of breeding seabirds varies among the cays depending upon the availability of nest sites. For example, Flat Cay and Saba Island harbor active rookeries of gulls and terns, Cockroach Cay (Fig. 4B) and Dutchcap Cay host colonies of boobies (Fig. 7B and C) and tropicbirds, and Congo Cay, Dutchcap Cay, Buck Island (St. Croix), and Green Cay (St. Croix) support nesting pelicans. Many species exhibit high site fidelity and can be found in the same sites year after year, while some species, such as the federally protected Roseate Tern (*Sterna dougallii*) utilize a complex of islands by selecting different sites on an annual basis. Except for some terns, most seabirds nest at the same colony year after year, and rarely form new colonies. These patterns in the multiple uses of islands by key species have significant management and adaptation implications as new methods may be needed to facilitate colony formation on islands with greater resilience to sea level rise, drought, and other stressors.

Offshore islands also provide valuable stopover sites and wintering grounds for Nearctic and Neotropical birds migrating along the Atlantic Flyway. They are likely to be the first landfall site that migrants encounter (Wallace et al., 1996), and function as refuges for migrants during tropical storms and hurricanes. Larger islands such as Mona can support over-wintering migrants. As the spread of invasive species and frequency of weather disruptions increases, offshore islands may become increasingly important to migratory species.

Social Value of Cays

In addition to the ecological importance of supporting high levels of unique biodiversity, the islands surrounding Puerto Rico and USVI also have social, economic, and cultural value. Their position on the coast can dissipate wave and storm energy reducing impacts to coastal communities on nearby islands. The ecosystems associated with cays and islands also provide nursery habitats for commercially important fish and invertebrates that support local artisanal and recreational fisheries. Danylchuk (2015) used acoustic tracking to define preferred shoals for bonefish and the associated recreational catch-and-release fishery around Culebra, Puerto Rico. The study shows how this depth-associated recreational fishery, of commercial importance for fishing guides and

Box 2 Case Study: Virgin Islands Tree Boa

The Puerto Rican Bank is found within the Caribbean Region, which is considered a biodiversity hotspot (Cincotta and Engelman, 2000; Helmer et al., 2002; Myers et al., 2000). This geological area encompasses the island of Puerto Rico (excluding Mona Island) and its offshore cays, the U. S. Virgin Islands (but not Saint Croix), the British Virgin Islands, and more than 180 associated small islets and cays (Heatwole and MacKenzie, 1967; Thomas, 1999), islands harbor a high percentage of endemic species and have suffered a high percentage of extinctions (Island Conservation, 2014). This unfortunate condition has promoted the implementation of diverse single species conservation initiatives aimed mainly at vertebrate species.

The endangered Virgin Islands tree boa (Fig. B2.1; Federal Register, 1970, 35:16047), *Chilabothrus granti* (Rodríguez-Robles et al., 2015), presents a disjunct distribution on the islands of the Puerto Rican Bank (Nellis et al. 1983; Mayer, 2012). Its patchiness in occupancy has been explained by pre-historical (eustatic) changes in sea level and more recently by anthropogenic disturbances (deforestation, invasive species) that have caused the population's extirpation within the species' original range (Nellis et al., 1983; Tolson, 1996). Due to its risk of extinction, a recovery project started in the mid 1980s to release captive bred offspring of founders from wild populations in Puerto Rico (Cayo Diablo) and St. Thomas and to reintroduce them to two cays near each respective locality. After twenty years, it was classified as "highly successful" due to the establishment of the two new and sustainable wild populations on protected lands (Tolson et al., 2008). To accomplish this milestone, several phases had to be completed:



Fig. B2.1 The Endangered Virgin Islands tree boa is an example of one of many threatened and endangered species that find refuge on the largely uninhabited cays of the Puerto Rican Bank, but are vulnerable to sea level rise in the long-term, invasive species and development in the short-term. Credit: M. García-Bermúdez.

1. Pre-evaluation and selection of cays according to habitat condition, presence of invasive cats, rats, and abundance of boa prey
2. Eradication of rats
3. Capture of wild boas to establish an ex situ captive breeding program
4. Release of captive born individuals in the wild
5. Long-term monitoring of released individuals for survivability and population growth

It was assumed that the translocation of Virgin Island tree boas to cays after eradicating the invasive species in Puerto Rico and the USVI, respectively, had safeguarded its recovery. However, the threats related to climate change, particularly sea level rise turned all these efforts into a stopgap action because the recipient cays are relatively low in relation to current sea level and will be impacted negatively by the projected increments in sea level and catastrophic events—hurricanes and droughts (PRCCC, 2013). Furthermore, during a recent post Hurricane Maria survey, no boas were found, and rats have recolonized the Puerto Rican cay (Island Conservation, 2018). These threats acting individually or in synergy will exacerbate the risk of extinction of the species and other components of the Caribbean biota. Therefore, a landscape approach to the recovery of these species addressing common threats (i.e., invasive species and sea level rise) to protect them is timely and urgent.

associated businesses, could be affected by sea level rise. Changes in the ecological value of these small islands, shoals, and cays can impact tourism, recreational fisheries, and the economies of coastal communities.

Historically there was extensive mining of guano, agriculture, and forestry practices on many of the region's islands. An interesting use of cays can be found at Santiago Cay off the east coast of Puerto Rico where primate research spanning over 70 years has been ongoing by the Caribbean Primate Research Center of the University of Puerto Rico. Islands also provide extensive recreational opportunities such as second homes, boating, fishing, snorkeling and scuba diving, surfing, and simply gathering to relax and barbeque (Fig. 8). Significant tourism has been developed in some of the nearshore cays with high visitation rates, local fishing charters and dive operators generating income to multiple sectors of the local economy. However, recreational use of cays can also be highly damaging to the ecological integrity of the cays and surrounding marine habitats (e.g., coral reefs and seagrass beds), representing a clear and present conflict of use.



Fig. 7 (A) Nesting habitat of seabirds at Media Luna Cay, La Parguera, Puerto Rico. Birds include least tern and brown noddy. (B) Masked booby nest on a St. Thomas cay. (C) Brown booby pair on nest, Kalkun Cay, St Thomas. (A) Credit: J. Vargas, (B) Credit: R. Platenberg, and (C) Credit: R. Platenberg.



Fig. 8 Recreational boat use of Cayo de Barca, Jobos Bay National Estuarine Research Reserve, Puerto Rico. Credit: E. Rodriguez.

In response, the PR-DNER administered a program of installation and maintenance of mooring buoys since 2004. The objective of the program is to reduce anchor damage on seagrass meadows and coral reefs. High-use and high-risk areas were assessed via aerial surveys to increase the effectiveness of placement of the mooring buoys (Fig. 8). The program successfully installed over

300 buoys (Rodríguez-Robles et al., 2015). Over time, patterns of boater use of different anchoring areas and degree of acceptance of the mooring buoys by the boaters as an alternative to anchoring can be detected through the photos.

Recreational boat use tends to peak during holidays and the most popular and high-risk locations tend to be nearby long-term docking facilities and on islands with sandy beaches. All the high use areas are associated with damages and diminished habitat quality to local corals and seagrasses and the intensity of use makes it logistically impossible to supply enough moorings (Rodríguez-Robles et al., 2015). Further, there has been a recent shift in use (2005–12 compared to 1998–2004) toward cays closer to the coast and docking areas (e.g., yacht clubs) that appears to be driven by rising fuel costs (Rodríguez-Robles et al., 2015). Thus, until economics and behaviors change, cays nearer the main island and their surrounding marine habitats are especially vulnerable to anthropogenic damage.

A similar mooring installation program was also initiated in the USVI, although the social usage patterns are different. USVI cays do not experience the high-level congregation on weekends and holidays that PR cays do; USVI cays are more exposed to ocean current, have smaller beaches or none at all, and many require technical skills to access. Rather, visitation is focused on fishing and diving activities. Historically the seabird colonies were plundered for egg collection and in response VI-DPNR installed “no entry” signage and a requirement for visitation permits for access beyond the beach and this activity has largely ended. Some locals still access the cays to hunt non-native goats that were placed decades or centuries ago as an emergency food resource. Goats and rats have been removed from the cays with important seabird nesting colonies, but goats and rats still remain on many privately-owned cays.

The accumulation of plastics carried by currents and winds towards mangrove and coastal zones of small islands is significant. These plastics are associated with the habitat degradation and direct risk of entanglement with sea turtles and seabirds that come to shore. Ingestion of the plastics that float near the islands by chicks increases their mortality, although the extent of this impact has not been assessed. Recent accumulations of large quantities of sargassum algae have been impacting the nearshore and coastal communities of islands in the US Caribbean. The weight of the algae can overcome the sea turtles that inhabit nearshore areas drowning them. Hatchling sea turtles are also affected by the sargassum accumulations off sea turtle nesting beaches increasing their mortality as they try to reach the sea. Marine organisms also perish due to the anoxic conditions that are created when the seaweed decompose, and bacteria consume most of the dissolved oxygen.

Beyond recreational use, the US military utilized many of the islands off the eastern coast of Puerto Rico (between Puerto Rico and St. Thomas), including Vieques and Culebra with sizable human populations (and very popular tourist destinations), for target shooting and bombing practice. This practice, which ended in 1975 in Culebra, and in 2003 in Vieques, due largely to public anger and objections, has left a legacy of habitat damage, pollution, and potentially live munitions within the terrestrial and shallow near-shore aquatic zones (McCaffrey, 2018). The majority of the lands were subsequently transferred from US military possession to the U.S. Fish and Wildlife Service National Refuge System. To protect human safety many areas are closed to access, although Cayo La Chiva in Vieques will be opened to public access following completion of the cleanup. Although environmental clean-up has been on-going and slow, social discontentment remains strong. Cleaning-up potentially live munitions requires acre by acre forest removal. To date, reforestation has been lacking, such that “cleaned” areas tend to be quickly colonized by invasive plant and vertebrate species. Management of vertebrate invasive species has also been largely lacking. Thus, although from a conservation perspective these lands are under protected status with reduced human access (due to safety risks), the ecological value of these lands is compromised due to the impacts of invasive species. Military activity on Monito and Desecheo Islands off the west coast devastated seabird colonies; these islands remain off limits to humans due to the risks associated with unexploded ordnance.

Climate Change Effects

Cays are at risk from climate change due to drought, rising sea levels, more intense and frequent storms, and potential natural and anthropogenic limits to inward (upslope) migration (Powell et al. 2017; Costanza et al., 2016). The resources on cays are sensitive to these influences because of the relatively small area and typically unique species assemblages. The most recent downscaled climate projections (Bowden et al. 2018; Gould et al., 2018) suggest changes in regional precipitation patterns and specifically longer and more intense droughts by mid-century (see also Murry et al., 2019 for coastal wetlands). Many organisms are adapted for xeric conditions, however extended drought, combined with increasing sea levels, storm surges, saltwater intrusion, and increased sea spray readily impacts native vegetation, paving the way for robust invasive species or loss of vegetation, with subsequent habitat-related impacts to native fauna.

Cays within the US Caribbean are not static features in time and space but change in shape, habitat, and ecological value in response to sea level, waves, currents, hurricanes, sediment inputs, and invasive species. Bush et al. (2014) provided an evaluation of historical shoreline change for a few of the cays around Puerto Rico. It is important to understand both global sea level trends, as well as local trends. Local tide gauges provide better estimates of sea level rise, and thus better insights into the long-term vulnerability of cays in response to local conditions, that we use to analyze low profile cays and their respective biological systems or habitats. Regardless, the vulnerability of cays is dependent on the ability of their elevation and habitats to keep pace with rates of sea level rise. For example, cays located in regions of tectonic uplift or subsidence can potentially minimize or exacerbate the impacts of long-term global sea level rise. Local, or relative, sea level rise rates do not necessarily match those of eustatic global dynamics.

Physical damage to the structure and transport of the loose or cemented coral carbonate skeletons is likely to increase due to stronger or more frequent hurricanes coupled with low rates of coral growth due to coral mortality and the net eroding effect of

increased ocean acidification. These erosion processes especially impact sand and coral cays. The physical action of the waves during high energy events such as hurricanes, storms, and swells increase substrates for coral re-colonization and coral fragmentation and redistribute coral rubble to low-lying areas creating space for islands to grow. These extreme events can also cause a high transport of sediments causing burial of benthic substrates and transporting material from shallow to deeper areas or vice versa. It has been suggested that reefs periodically disturbed by storms of intermediate intensity will increase growth rates and long-term calcification (Highsmith et al., 1980). However, it is certain that the ocean acidification caused by anthropogenic activities will increase in accord with atmospheric CO₂ emissions. Ocean acidification decreases the availability of the carbonate ion, CO₃²⁻ (the principal building block of most marine skeletal material), adversely affecting calcification and increasing dissolution processes. This leads to slow growth rates and malformed and less dense carbonate shells and skeletons (Cohen et al., 2009). As a result, species that undergo calcification may become displaced by species that do not. This will likely continue deteriorating reef conditions and cause ecological regime shifts from coral to algal reefs (Anthony et al., 2011). A decline in calcifying species (e.g., corals, crustose coralline algae, calcareous green algae) will affect the sediment budget available to island's shores, increase the potential for shore erosion, decrease the potential for carbonate island formation, and decrease beach and reef-based tourism and economic activity.

The combination of physical erosion, dissolution, and bioerosion processes in shallow reef habitats accelerate the loss of calcium carbonate sediments and decrease the stability of the reef skeletal framework (Eyre et al., 2014), potentially leading to a collapse of reef structures (Hoegh-Guldberg et al., 2007). Future acidification effects will not act independently from other global and local environmental pressures such as sedimentation. Such effects could compromise reef resiliency and increase vulnerability of certain types of islands in the face of other acute threats, such as thermal-stress, outbreak diseases, and rising sea level (Silverman et al., 2009).

It is estimated that coral reefs reduce the wave energy by an average of 97% (Ferrario et al., 2014) with most of the energy being absorbed at the shallower point (reef crest). In order for coral reefs to continue to provide coastal protection to low lying keys, corals will need to grow upward rapidly enough to keep pace with the rising sea level (Sheppard et al. 2005). If upward growth and reef complexity decrease due to ocean acidification, the reef will slowly "sink" as water depth increases and the wave energy reaching the shores behind those reefs will increase (Alvarez-Filip et al. 2009; Sheppard et al. 2005). In the case of the islands described herein, this will make coastal areas increasingly more vulnerable to the action of waves and storm surge with associated effects on the tourism sector, fisheries, and coastal infrastructure (Table 1).

Cay ramparts associated with high wave energy reefs are almost completely composed of Elkhorn coral as noted previously (Williams et al., 1999). If the live Elkhorn colonies that are the source of cay ramparts disappear, cays will be impacted in two ways: (1) they will receive more direct wave energy that is not dampened by the live corals, and (2) they may eventually erode away if no new pieces of coral skeletons are available to maintain accretion processes. Skeletons of Elkhorn coral form loose plate ramparts up to 4.5 m above sea level on cays exposed to high wave energy (Hernandez-Avila et al., 1977). This may protect the cays from wave-generated erosion and allow coral rubble and sand to accumulate on the cay. These ramparts also serve an ecologically important function as nesting habitat for many seabirds (e.g., least tern *Sternula antillarum*, brown noddies *Anous stolidus*).

Elkhorn coral once formed dense, high profile, monospecific stands in shallow depths (1–5 m) of the fore-reef zone and was abundant throughout the tropical Western Atlantic. In the 1970s and 1980s, Elkhorn coral experienced precipitous declines in abundance throughout its range, estimated at greater than 97% loss (NMFS 2014; Schärer et al., 2008). Data suggest that the decline in Elkhorn coral populations throughout Puerto Rico is primarily the result of disease and predation (Nemeth et al., 2014). Other threats to corals such as elevated seawater temperatures, overfishing, pollution, and ocean acidification are credible and potentially significant impediments to recovery of this species. In the past, storm damaged thickets have regenerated between major storms and thus produce the skeletal coral materials to replenish the cay ramparts during subsequent storms (Williams et al., 1999). The Elkhorn coral thickets also absorbed routine wave energy and protected the cays. Elkhorn coral abundance has significantly reduced the coral's ability to replenish cays and protect them from wave energy.

Climate Change Vulnerability

Climate change impacts, such as sea-level rise, storm surges, and drought could lead to a reduction in the size and number of low-lying islands while others that are morphologically resilient are expected to persist. Because the main islands of the US Virgin Islands have an extensive human footprint, they have relatively low conservation value; as such, the surrounding, largely uninhabited cays have been a focus of conservation efforts for decades. In contrast, until recently, the evaluation of small cays around Puerto Rico, their description, and ecologic importance have not received the attention that they deserve. Except for coral reefs, cays developed on coral rubble, sand shoals, and mangrove patches have received less attention. However, it is recognized that sea level rise and associated impacts are expected to negatively impact the ecological, societal, and economic benefits cays provide. Therefore, assessing the response of cays' shorelines to these stressors is critical for developing sound coastal management and land use planning guidelines for small islands (Bush et al., 2014; see Box 3).

Understanding the vulnerability of coastal areas is critical as this is the area where multiple stressors have the greatest opportunity to converge and where the greatest vulnerabilities lie (Gould et al., 2018). Toward that end, members of our writing team participated in a Climate Adaptation workshop to begin conceiving a long-term regional cays management plan in recognition that the species of greatest conservation interest span many jurisdictional management boundaries and occupy cays that individually range from low to very high vulnerability (based mainly on elevation). For this exercise two primary drivers were considered in scenarios

Table 1 Vulnerability of specific classes of biological targets to two specific drivers: sea level rise and extended droughts.

Climate driver	Targets	Climate-related impacts and vulnerabilities			Non-climate stressors	Relative vulnerability
		Exposure ^a	Sensitivity ^b	Adaptive capacity ^c		
Sea level rise	Sandy beaches and dunes	Extreme: at impact front	Extreme: change to aquatic habitat	Low: depending on island topography and accretion; habitat migration limited	Human recreation/disturbance	High
	Coastal shrub	Extreme: at impact front	Moderate-extreme: reduction in suitable area and salt spray	Low-moderate: depending on island topography; habitat migration limited	Human recreation/disturbance; invasive species (e.g., goats)	Moderate-high
	Rocky shores	Extreme: at impact front	Low-moderate: sand accretion could change to beach	Low-moderate: depending on island topography and accretion; habitat migration limited	Limited	Low-moderate
	Seabirds	Moderate-extreme: depending on specific microhabitat use	Moderate: depending on degree of habitat specificity	High: ability to alter habitat use (e.g., move upslope) or change islands	Invasive species; human recreation/disturbance; open ocean conditions	Moderate
	Endemic lizards	Moderate-extreme: many islands are low-lying	High: reduction in habitat space	Low: inability to colonize new islands without human intervention	(prey abundance, plastics)	High
	Endemic plants	Moderate-extreme: depending on specific microhabitat use	Moderate-extreme: reduction in habitat space and salt spray	Low-moderate: depending on mode of seed dispersal and degree of habitat specificity		Moderate-High
Extended droughts	Sandy beaches and dunes	Low	Low: dune plant desiccation	High: limited impacts	Human recreation/disturbance	Low
	Coastal shrub	Moderate	Moderate: shrub zone plant desiccation	Moderate: seed banking, selection toward drought resistance	Human recreation/disturbance; invasive species (e.g., goats)	Moderate
	Rocky shores	Low	None	High: limited impacts	Limited	Low
	Seabirds	Low-moderate: may experience some habitat changes	Low-moderate: not dependent on rain and moisture, but may experience habitat changes	Moderate: flexible nesting behavior; ability to move to more suitable islands, but drought likely to be regional	Invasive species; human recreation/disturbance; open ocean conditions (prey abundance, plastics)	Low-moderate
	Endemic lizards	Moderate: may experience some habitat changes	Low-moderate: dry adapted, but may experience changes in habitat and prey availability	Low-moderate: Behavioral responses to dryness, habitat, and prey changes		Moderate
	Endemic plants	High: water dependent to varying degrees	Low (cactus) to high: will depend on physiology	Low-moderate: depending on physiology and seed dispersal and dormancy		Low-high

This is not intended to be exhaustive nor overtly specific, but to serve as an example of the thought processes involved in assessing climate vulnerabilities. More precise vulnerabilities can be identified when considering specific species. Consideration is also paid to non-climate stressors that may have additive or synergistic effects.

^aExposure is defined by Stein et al. (2014) as the amount of change in climate and associated impacts the target species or system is likely to experience.

^bSensitivity is related to the affect or response of a species or target system to specific changes in climate variables or secondary effects.

^cAdaptive capacity refers to a species or system's ability to accommodate or cope with climate-associated changes.

Modeled after materials derived from: Stein, B.A., Glick, P., Edelson, N., and Staudt, A. (eds.). (2014). *Climate-smart conservation: Putting adaptation principles into practice*. National Wildlife Federation, Washington, D.C.

that were deemed independent and potentially synergistic, sea level rise and drought (Table 1). Specific habitat and species targets were identified, and we assessed their respective (and specific) exposure, sensitivity, and adaptive potential to the climate-related drivers (defined in Table 1). Importantly, we also considered non-climate stressors that will inevitably affect the vulnerability of the targets. Invasive species represented the greatest current and future threat and will likely be exacerbated by climate related impacts. We found that habitats tended to be more vulnerable to sea level rise than to droughts and sandy beaches and dunes more vulnerable than rocky shorelines (Table 1). Target species (seabirds, nesting sea turtles, lizards, and native plants) tended to also show greater vulnerability to sea level rise (through loss of habitat and habitat changes) than to drought.

A key step in developing a climate-smart adaptation plan is visualizing and defining a suite of potential future scenarios (Stein et al., 2014). Comparing and contrasting two climate change related impacts, namely sea level rise and drought, postulates four

Box 3 Case Study: Habitat Vulnerability Assessment of Small Oceanic Cays of Puerto Rico and U.S. Virgin Islands

Previous research conducted by [Bush et al. \(2014\)](#) between 2010 and 2013 focused on the assessment of coastal vulnerability and forecasted shoreline changes and land loss by application of three methods: (1) the simple slope/retreat model based on existing estimates of rates of sea-level rise; (2) historical shoreline change using t-sheets, aerial photographs, LiDAR, and satellite imagery, and extrapolation of those changes into the future; and (3) a coastal vulnerability index (CVI). The first approach presumes that the dominant control on coastal regression is the offshore/onshore long profile of the area of interest and the second approach presupposes that the shoreline change trends of the recent past will continue. Based on [Bush et al. \(2014\)](#), reliable data is available for both approaches; however, a more broad-based prediction can be made by applying a CVI. The CVI approach has been highly used in the United States and Canada but was applied in Puerto Rico and USVI for the first time to small islands in 2010. [Bush et al. \(2014\)](#) also employed the recently developed AMBUR (Analyzing Moving Boundaries Using R) software with the hazard-vulnerability assessment tool (AMBUR-HVA) to assess shoreline vulnerability for cays using geologic/geomorphologic data ([Bush et al. 2014](#); [Jackson et al., 2012](#)) (**Fig. B3.1**).



Fig. B3.1 High resolution UAV imagery of Caribe Cay, Peñuelas, Puerto Rico and inset showing submerged colonies of the threatened Elkhorn coral *Acropora palmata* in the fore reef area. Credit: HJR Reefscaping.

Since 2014, the USFWS Coastal Program has supported the collection of ecological information at landscape and seascape scales for cays around Puerto Rico and the USVI. The purpose is to determine population and/or habitat metrics that are more effective in assessing the sustainability of species and their habitats and to develop species/habitat vulnerability models that may be linked to existing and widely used geophysical models. This information will be used to assess species'

vulnerability to coastal hazards (erosion, inundation, and coastal exposure), climate change effects, as well as the need for habitat restoration and/or enhancement, and to identify and implement best management strategies. This initiative will be providing managers critical information: potential habitat loss in the context of spatial (i.e., sea, shoreline, cays and/or inland), temporal (e.g., 1 year, 10 years, 50 years, 100 years), and severity (i.e., low, medium, high risk) of these hazards. When complete this project is expected to provide the basis for developing assessment methods that would potentially be widely applicable to many coastal settings in the Southeastern U.S. and the Caribbean.

A multi-agency effort was initiated to establish a baseline for determining the vulnerability to climate change of small oceanic cays in the U.S. Caribbean. In 2013, local and federal natural resources agencies in collaboration with academic, private, and non-governmental organizations defined a series of research questions and management concerns that should be addressed in priority areas of interest. These concerns refer mainly to the potential loss of important habitats and the impacts upon the biodiversity and threatened or endangered species, particularly in areas where the marine and terrestrial environments interact in dynamic ways. The multi-disciplinary team identified criteria to rank study areas and chose 16 cays for this study spanning waters of Puerto Rico and the US Virgin Islands.

An ecosystem-based approach was devised to collect data on the marine, coastal, and terrestrial environments, allowing for the compilation of detailed data on habitat characteristics and species' composition on each cay. This information will be analyzed to determine habitat connectivity, patterns of habitat use (nesting, breeding, feeding, etc.), the location of critical habitats, incidence of habitat loss, and potential impacts to species' distributions. Detailed aerial ortho-photo mosaics, visual censuses, and underwater surveys near the shorelines are being conducted to evaluate the vulnerability of cays to climate change (Fig. 6). Preliminary results revealed the distribution of critical habitats for several threatened and endangered species such as the Virgin Island tree boa, St. Croix ground lizard, elkhorn and staghorn coral, and mountainous star coral on and around the cays. Data suggest that in some areas (1) inundation, (2) erosion, and (3) changes in vegetation are impacting the habitat quality and stability of cays and that preliminary model output (AMBUR-HVA-Cays, <http://ambur.r-forge.r-project.org/>) suggests fetch or coastal openness to wind/wave exposure is also a major factor influencing vulnerability.

potential future scenarios (Fig. 9); ranging from minor impacts from minimal sea level and minor increases in drought (lower left) to large increases in sea level rise and extended severe droughts (upper right).

The scenarios allow managers to prepare for a range of future conditions and prioritize actions to facilitate system adaptation (Table 2). All of the scenarios are nested within warmer ocean and air temperatures and continuing threats from invasive species and the impacts of human uses. Under the scenario of lowest impacts (lower left) managers can anticipate minor coastal erosion and instead focus attention on human disturbance and invasive species, whereas at the opposite extreme (upper right) where droughts and sea level rise are both high, managers will need to face increased threats of fire, loss of habitat space, potentially loss of low-lying islands, and severe habitat modification. Each scenario demands a separate suite of management actions to maximize resource allocation on the most likely threats. In the worst-case scenario this may include translocation of rare species from low-lying cays to higher elevation cays, facilitating habitat migration, and reducing non-climate stressors and threats (Table 2).

In conclusion, we continue to gather data on species and habitat distributions as well as climate, human, and ecological threats. The main goal must remain the implementation of conservation initiatives aimed at higher elevation habitats and species resilience to safeguard the long-term existence of these globally unique ecosystems.

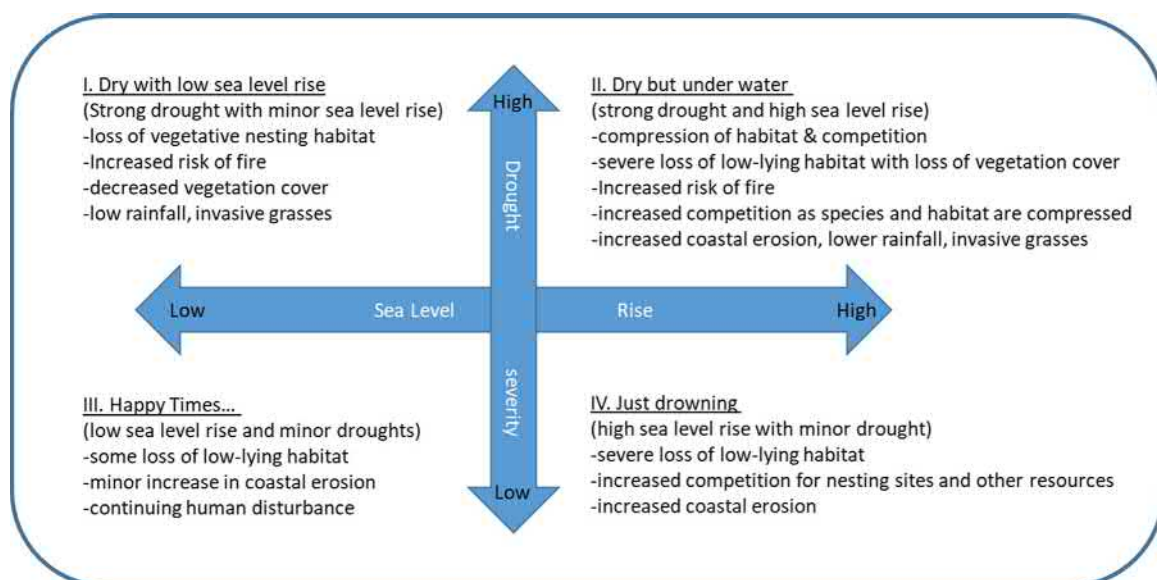


Fig. 9 Four potential future scenarios based on low to high sea level rise and small to large increase in drought.

Table 2 Potential management actions toward climate resilience on Caribbean cays.

<i>Conservation goal:</i> Maintain or increase the population of endemic and native species and their associated habitats in the offshore islands of the Puerto Rican Bank and St. Croix through the end of the century	
Key vulnerabilities: Sea level rise and droughts	
Proposed action	Linkage of action to climate change
Coastal zone restoration: sand dunes, forests, implement living shorelines, facilitate habitat migration	Habitat loss from rising sea levels and drought
Artificial/engineered structures: e.g., breeding platforms, islands, shading breeding areas, oyster bars, desalinization and irrigation	Addresses negative impacts of drought and habitat loss
Captive propagation and breeding programs: for population supplementation plus genetic diversity	Supports evolutionary potential and mortality associated with extreme events
Move populations: Translocations of vulnerable species populations to less vulnerable islands (higher and bigger), use of enclosures and supplemental feeding/care to improve success, improve seabird attraction techniques	Response to sea level rise and loss of islands and habitat loss from drought
Invasive species elimination and prevention: continue to improve and implement biosecurity measures and eradication	Reduction of non-climate stressors and exotics that may benefit from climate change
Improve seabird foraging success: fish aggregation devices (FADs) to congregate prey fish and protective fisheries regulations, e.g., nursery areas, no-take zones	Reduction of non-climate stressors
Restore degraded habitats: e.g., bombed islands, by using drought tolerant species	Non-climate stressors and drought response
Human dimensions: “adopt a skink” or “adopt an island” program, visitor centers and education with sacrificial populations for public interaction	Non-climate stressors
Restricted human use areas: controlled access beached, target priority areas; conservation easements and other incentives	Non-climate stressors and avoid climate-driven habitat loss

Acknowledgments

The authors wish to acknowledge the on-going efforts of the Puerto Rico Climate Change Council (PR-CCC) and specifically the 2016 Puerto Rico Climate Vulnerability Assessment where an earlier version of this work was published. Permission to republish the expanded version here was given by Ernesto Diaz, Director of the PR-CCC. We also acknowledge Martha Prada and Kurt Grove who participated in that original version. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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Physical Geography of the Hawaiian Islands

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Published by Elsevier Inc.

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Abstract

The Hawaiian archipelago consists of an expansive chain of islands situated almost in the center of the Pacific Ocean, formed by the northwest movement of the Pacific tectonic plate over a volcanic hotspot where magma rises through the earth's mantle until it erupts through the seafloor. These islands range from small atolls in the northwest of the archipelago, to high volcanic islands in the southeast of the archipelago. The Hawaiian archipelago has an abundant range of biomes due to extreme variations in elevation, and variations in wind and rain patterns, topography, substrate, and hydrology. The archipelago's remote location in the vast Pacific Ocean also contributes to its physical geography. Each island and atoll has unique physical and biological features. Here we focus on the physical features of the Hawaiian archipelago.

Geography

The Hawaiian archipelago is the most isolated landmass in the world: approximately 2390 miles (mi) (3846 kilometers (km)) from California and approximately 3850 mi (6196 km) from Japan. The entire archipelago consists of approximately 132 islands, including 8 larger, younger islands (the "main islands"—the islands of Hawai'i, Maui, Kaho'olawe, Moloka'i, Lāna'i, O'ahu, and Kaua'i), and numerous smaller islands, islets, atolls, reefs, and shoals, stretching 1603 mi (2580 km) on a southeast-northwest line across the middle of the Pacific Ocean, between 150°48' and 178°20'W longitude, and 18°56' to 28°22'N latitude (Juvik and Juvik, 1998, p. xiii; Walker, 1999, p. 21) (Fig. 1). The archipelago has the same general latitude as Hong Kong and Mexico City (Juvik and Juvik, 1998, p. xiii). More than 99% of the land area is concentrated within the eight main islands located in the southeastern quarter of the chain (Walker, 1999, p. 21).

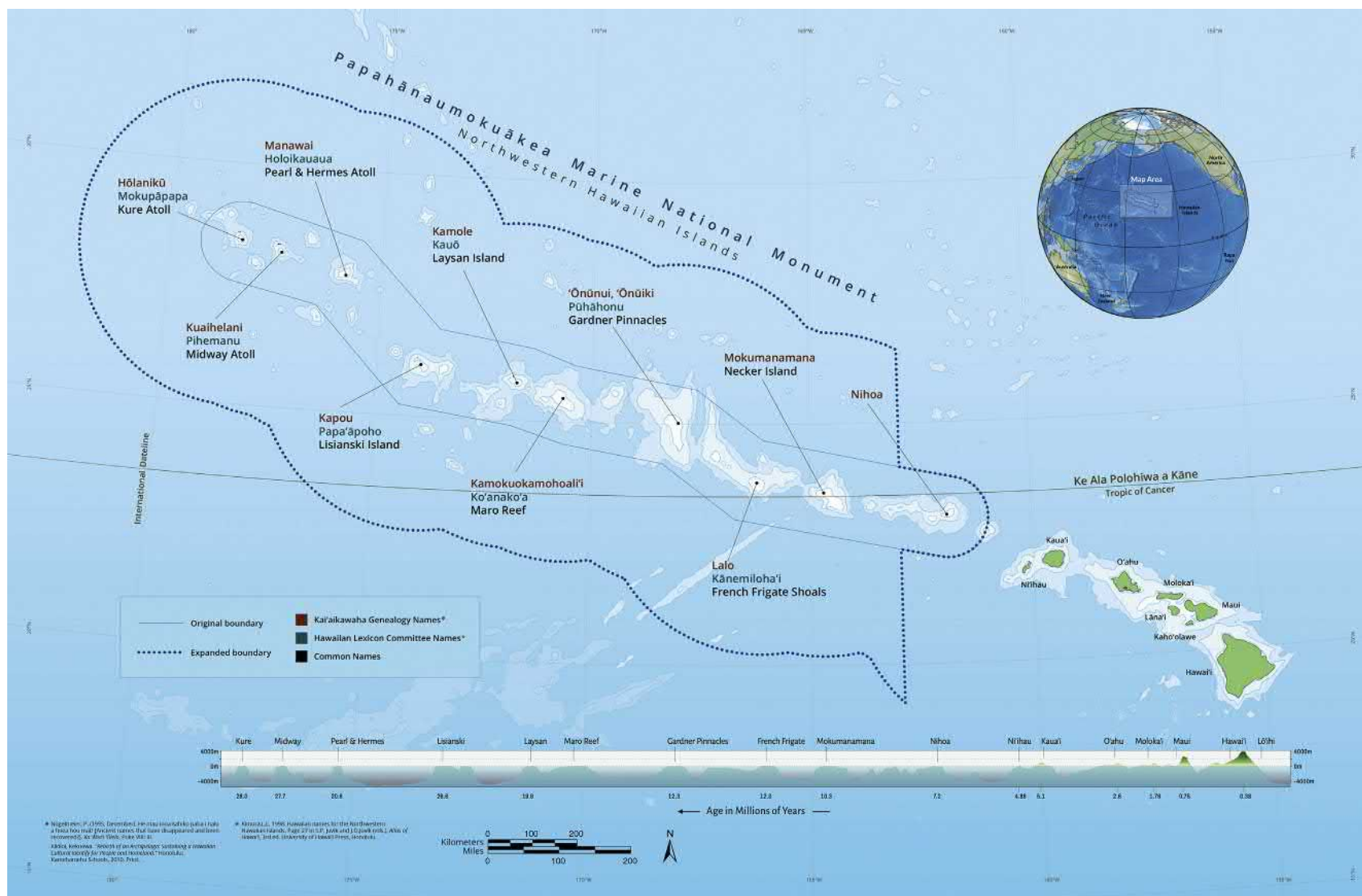


Fig. 1 Map of the Hawaiian archipelago including the main and northwestern islands. Source: <https://www.papahānaumokuākea.gov/>.

Geology

The main Hawaiian islands consists of eight main islands (Fig. 1; first eight entries in Table 1) that are substantially younger and larger than the long chain of older, eroded islands and atolls referred to as the Northwestern Hawaiian islands (NWHI). All of these islands were formed as the Pacific plate passed over a volcanic upwelling or accumulation of magma located in a transition zone located west of Hawaii Island (Fig. 2). Most of the world's active volcanoes are located at the edges of tectonic plates, such as observed with the Pacific "ring of fire;" however, some volcanoes are formed when magma rises up through a tectonic plate (Skilbeck and Whitehead 1978, pp. 499; 501; Clague, 1998, p. 37). These mid-plate volcanic areas are referred to as volcanic "hotspots." The creation of the Hawaiian archipelago has occurred over the last approximately 40 million years and is an ongoing process (Clague, 1998, p. 37; Cao et al., 2011, pp. 1068–1067). The Pacific plate is currently moving northwestward at about 4 inches (in) (9 centimeters (cm)) per year (Clague, 1998, p. 38). Each island was formed from eruptions of one or more undersea shield volcanoes which eventually grew to thousands of feet above sea level. Most of the islands formed over several hundred thousand years with several million years passing before activity ended and the volcano became extinct (Clague, 1998, pp. 38–39) (Fig. 2). As the islands increase in age they are carried northwest on the continental plate away from the hotspot. Clague and Sherrod (2014, p. 97) eloquently wrote:

As the Pacific Plate of the Earth's lithosphere moves slowly northwestward over the Hawaiian hotspot, volcanoes are successively born above it, evolve as they drift away from it, and eventually die and subside beneath the ocean surface.

Table 1 Geological summary and general characteristics of the Hawaiian archipelago.

Island (south to north)	Features and attributes						
	Emergent area <i>mi</i> ² (<i>km</i> ²)	Highest elevation <i>ft</i> (<i>m</i>)	Highest point	Coral reef or Atoll area (if applicable) <i>ac</i> (<i>ha</i>) ^a	Volcanic activity	Population (2010–15)	Surface water features
Hawai'i	4028 (10,430)	13,803 (4207.2)	Mauna Kea	25,946 (10,500)	Active	185,079	Bogs, streams, rivers, wetlands
Maui	727.2 (1883)	10,023 (3055)	Haleakalā	25,452 (10,300)	Dormant	154,834	Bogs, streams, wetlands
Kaho'olawe	44.59 (115.5)	1483 (452)	Pu'u Moaulanui	1320 (3262)	No	0	Seeps only
Lāna'i	140.5 (364)	3366 (1026)	Lanai Hale	6425 (2600)	No	3102	Ephemeral stream; seeps
Moloka'i	260 (670)	4961 (1512)	Kamakou	11,700 (28,911)	No	7345	Bogs, streams, wetlands
O'ahu	596.7 (1545)	4003 (1220)	Mt. Ka'ala	28,500 (70,425)	No	976,372	Bogs, streams, rivers, wetlands
Ni'ihau	69.5 (180)	1250 (381)	Mt. Paniau	24,389 (9870)	No	170	Ephemeral stream; seeps
Kaua'i	562.3 (1456)	5243 (1598)	Kawaikini	41,267 (16,700)	No	65,689	Bogs, streams, rivers, wetlands
Nihoa ^b	171 <i>ac</i> (69 <i>ha</i>)	892 (272)	Miller's Peak	142,000 (57,465)	No	0	Seeps only
Mokumanamana (Necker) ^b	45.2 <i>ac</i> (18.28 <i>ha</i>)	277 (84)	NA	385,000 (155,803)	No	0	Seeps only
Lalo (French Frigate Shoals) ^b	61.5 <i>ac</i> (25 <i>ha</i>)	120 (37)	La Perouse Pinnacle	232,000 (93,887)	No	0	Ephemeral seeps
Ōnūnui (Gardner Pinnacles) ^b	6 <i>acres</i> (2.4 <i>ha</i>)	170 (52)	Gardner Pinnacles	604,000 (244,430)	No	0	Ephemeral seeps
Kamole (Laysan)	1.6 (4.1)	50 (15)	NA	145,334 (58,8414)	No	0	Saline lake
Kapou (Lisianski) ^b	384 <i>ac</i> (156 <i>ha</i>)	40 (12)	NA	241,916 (97,900)	No	0	NA
Manawai (Pearl and Hermes) ^b	80 <i>ac</i> (32 <i>ha</i>)	3 (1)	NA	194,000 (78,509)	No	0	NA
Kuaihelani (Midway)	2.4 (6.2)	49.2 (15)	Water Tower Hill	85,929 (34,774)	No	40	NA
Hōlanikū (Kure) ^b	218 <i>ac</i> (88 <i>ha</i>)	20 (6)	Green Island	80,000 (32,375)	No	0	NA

^aFor the eight main islands, defined as "total coral reef and hard bottom" (BAE Systems, 2007); for the northwestern Hawaiian Islands, undefined (Juvik and Juvik, 1998, pp. 24; 304).

^bSize depicted in acres/hectares.

Currently located above the most active area of the hotspot, the island of Hawai'i is the youngest island in the chain and is still experiencing frequent, geologically-recent volcanic activity. Kilauea, the youngest of the island's five volcanoes, has been erupting continuously since 1983. Lō'ihi Seamount, located 3200 feet (ft) (975 meters (m)) below sea level and 19 mi (29 km) southeast of the coast of Hawai'i, is destined to emerge as a new island within the next 200,000 years (Clague, 1998, pp. 45–46). Located approximately 32 mi (51 km) from the hotspot toward the northwest lies Maui, the second oldest island. Essentially the entire eastern side of the island is composed of Halaekalā volcano, a dormant shield volcano. Although Halaekalā's last eruption was in 1790, its long eruption history and recent activity indicate it will erupt again in the future (U.S. Geological Survey 2018 'Volcano Hazards Program' <https://volcanoes.usgs.gov/volcanoes/haleakala/>).

Substratum

The soils of the Hawaiian archipelago originate as basaltic lavas characterized by relatively low levels of silica, but rich in iron, magnesia, and lime (compared to substrates in other volcanic regions). Mueller-Dombois and Fosberg (1998, p. 472) divided Hawai'i soils into three broad classes: (a) undeveloped or geomorphologically recent soil substrates, (b) well-developed soils in humid climates, and (c) well-developed soils in seasonal or dry climates. Armstrong (1983, p. 45) attributes the variety of soils to differences in: (1) the length of time to which they have been exposed to weathering, (2) the materials from which they have formed, (3) drainage conditions, (4) the variety and abundance of plants and animals that live in and on them, and (5) rainfall and temperature conditions to which the soils are exposed (Armstrong, 1983, p. 45). The soils in Hawai'i weather relatively quickly due to the year-round warm temperatures resulting from the tropical climate (Juvik and Juvik, 1998, pp. 92–93).

Climate

Climate in the Hawaiian archipelago is characterized by mild and equable temperatures year-round (Fig. 3), low to moderate humidity, persistence of northeasterly trade winds, phenomenal differences in rainfall within short distances, and infrequent hurricanes and severe storms (Wagner et al., 1999, p. 36). Most areas in the Hawaiian archipelago experience only two seasons. Warmer and drier "summer" weather occurs primarily between May and September, when the sun is more or less directly overhead and the trade winds most persistent (Giambelluca and Schroeder, 1998, p. 49; Wagner et al., 1999, p. 36). Slightly cooler and wetter "winter" weather occurs primarily between October and April, when the sun is in the south and the trade winds are often interrupted by other winds and by intervals of widespread cloud cover and rainfall (Mueller-Dombois and Fosberg, 1998, p. 464; Wagner et al., 1999, p. 36). However, winter blizzards, ice, and snow are not uncommon on the arid high-elevation peaks of the volcanoes Mauna Kea and Mauna Loa on the island of Hawai'i, and Haleakalā on the island of Maui.

Hawai'i's steep and rugged mountains significantly influence its weather and climate (Mueller-Dombois and Fosberg, 1998, p. 464). The tremendous variety of peaks, valleys, ridges, and broad slopes, provides Hawai'i with a climate greatly different from the surrounding ocean as well as nearly innumerable micro-climatic variety within the islands (Giambelluca and Schroeder, 1998, p. 54; Wagner et al., 1999, pp. 37; 43). Depending upon their elevation, the mountains obstruct, deflect, and accelerate the flow of air, and due to a low inversion layer and moisture-laden trade winds, create a rainfall pattern known as orographic effect that produces predictable and substantial precipitation on several of the main islands (Figs. 4–6). The orographic effects occur when warm, moist air encounters steep ridges and mountains, rises, then cools as it reaches the inversion layer forming clouds and rainfall. Conversely, the

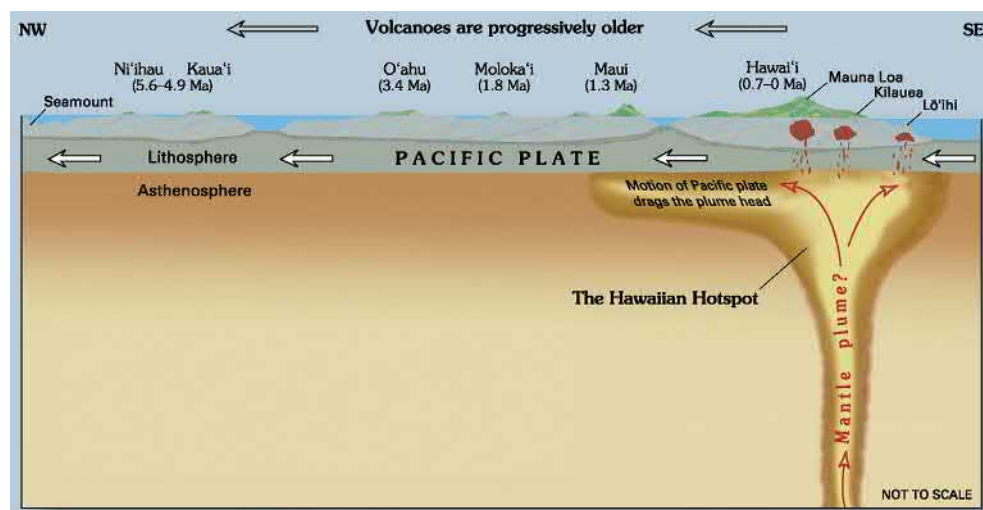


Fig. 2 Formation of the Hawaiian archipelago. Source: Simkin, T., Tilling, R.I., Vogt, P.R., Kirby, S.H., Kimberly, Paul, and Stewart, D.B. (2006). This dynamic planet map: World map of volcanoes, earthquakes, impact craters, and plate tectonics: US. Geological Survey geologic investigations series map I-2800 (<https://pubs.usgs.gov/imap/2800>).

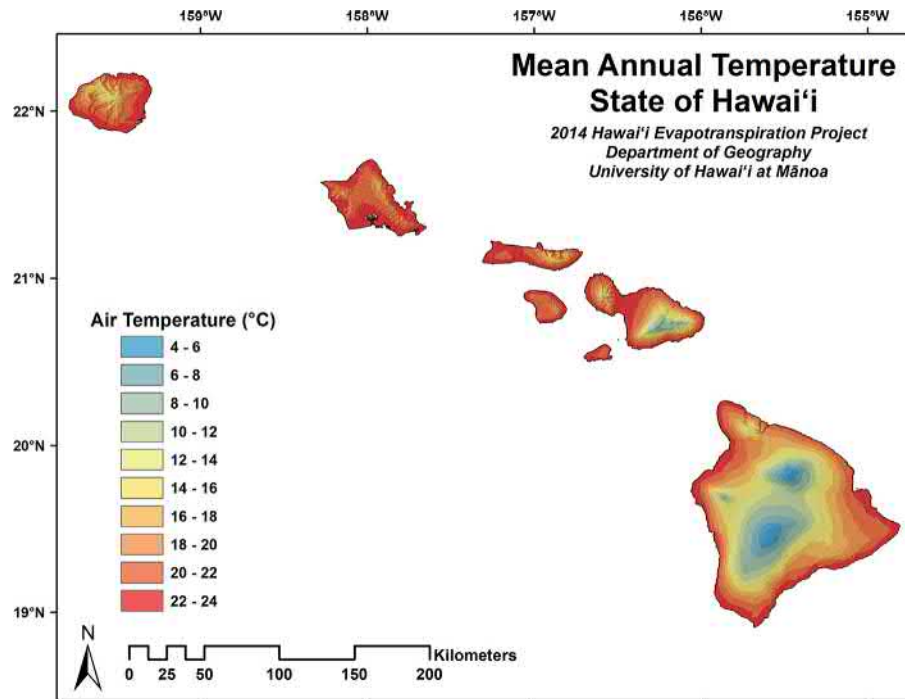


Fig. 3 Mean annual air temperature across the main Hawaiian islands (excluding Niihau). Source: Giambelluca, T.W., X. Shuai, M.L. Barnes, R.J. Alliss, R.J. Longman, T. Miura, Q. Chen, A.G. Frazier, R.G. Mudd, L. Cuo, and A.D. Businger. (2014). *Evapotranspiration of Hawai'i*. Final report submitted to the U.S. Army Corps of Engineers—Honolulu District, and the Commission on Water Resource Management, State of Hawai'i.

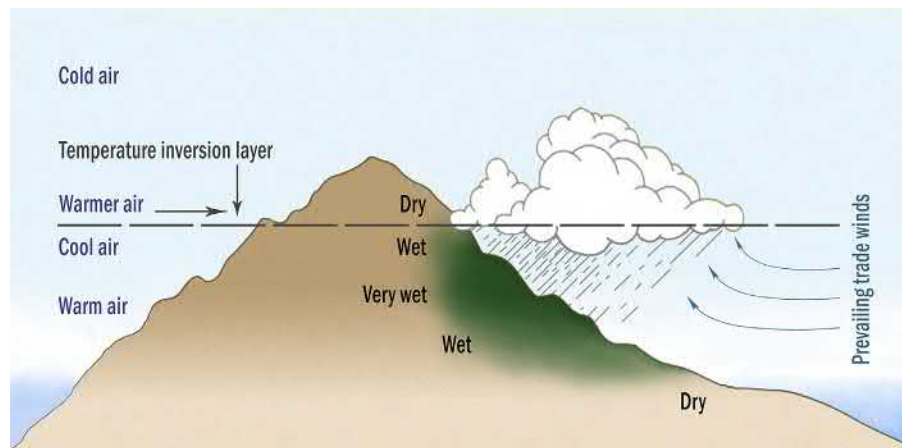


Fig. 4 This figure shows moist trade winds blowing toward and being forced upward on an island with a mountain that rises in elevation above the inversion layer. The rising air cools and condenses into rainfall which falls on the windward side of an island below the inversion layer (this example is similar to the specific orographic effects observed on the island of Hawai'i).

surrounding lowland and leeward areas tend to be sunny and dry. Air above the inversion layer warms again creating arid environment at high elevations (i.e., Mauna Kea, Mauna Loa, and Haleakalā). In places sheltered by terrain, local air movements are significantly different from winds in exposed localities, adding to the complexity and abundance of micro-climates. Since temperature decreases with elevation by about three degrees per one-thousand feet, Hawai'i's mountains, which extend from sea level to nearly 14,000 ft. (4267 m), contain a climatic range from the tropic to the sub-Arctic (Price, 1983, p. 59–61; Juvik and Juvik, 1998, pp. 121–127).

Rainfall

Annual mean rainfall ranges from 8 in (204 millimeters (mm)) near the dry, alpine summit of Mauna Kea to 400+ in (10,271+ mm) on the windward slopes of the tallest mountains on Kaua'i and Maui (Giambelluca et al., 2013, pp. 313–316) (Fig. 7). Comparatively, the surrounding ocean and most lowland areas of the islands receive an average of 20 in (500 mm)

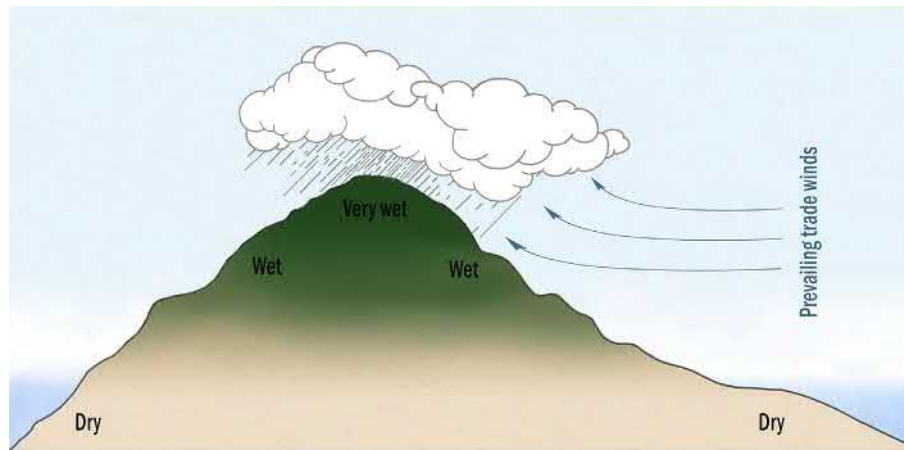


Fig. 5 This figure shows moist trade winds blowing toward an island with a mountain that rises gradually in elevation below the inversion layer. In this case where the mountain summit is below the level of the inversion layer, it receives a maximum amount of rainfall, which falls on both the leeward and windward sides of the summit (this example is similar to the specific orographic effects observed on the island of Maui.).

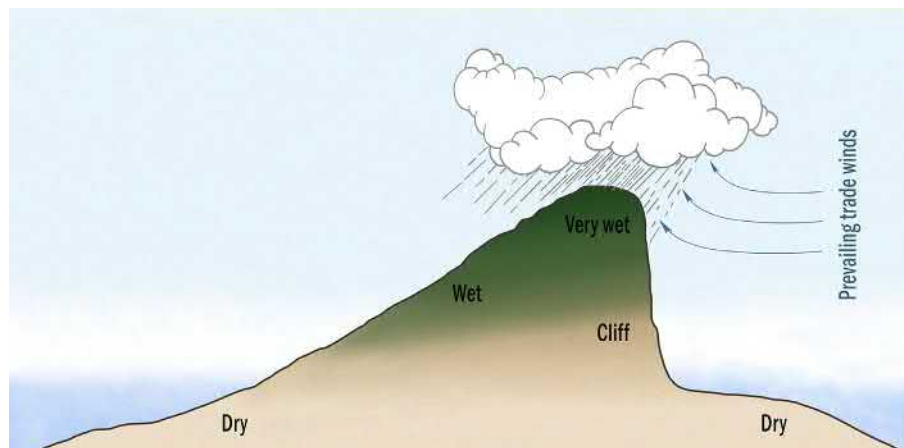


Fig. 6 This figure shows moist trade winds blowing toward an island with a mountain that rises steeply and abruptly in elevation below the inversion layer. When trade winds are confronted by a steep cliff such as in this example, they rise upward rapidly, with the larger amount of rainfall occurring on the leeward side of the summit (this example is similar to the specific orographic effects observed on the windward side of the islands of Moloka'i and O'ahu.).

annually. As noted above ([Fig. 4](#)), this variability is created principally by orographic rainfall. When the moisture-laden trade winds encounter the high-elevation Hawaiian islands, they are forced to either pass around the mountain or rise up above it. As trade winds rise up the volcanic peaks, or remnants thereof, the air cools causing its water vapor to condense into visible clouds, and under persistent rising and cooling conditions, rainfall ([Wagner et al., 1999, p. 40](#)). The trade wind inversion creates a ceiling-like phenomenon that inhibits the further rising of the moist, warm air causing an accumulation of clouds and rain below it, and dry conditions above it ([Giambelluca and Schroeder, 1998, p. 53](#)). During the daytime and summer months, the tops of the higher Hawaiian mountains are almost constantly obscured by a band of clouds produced in this fashion ([Wagner et al., 1999, p. 38](#)). Persistent conditions promoting or inhibiting rising air are responsible for many of the differences in climate across the Hawaiian islands ([Giambelluca and Schroeder, 1998, p. 52](#)).

Trade Winds and Kona Storms

The Hawaiian archipelago experiences relatively consistent northeasterly trade winds throughout the year that originate from the North Pacific anticyclone, located northeast of the islands ([Giambelluca and Schroeder, 1998, p. 53](#)). However, the trade winds are more persistent in summer than in winter (frequencies average 90% and 50% respectively), and stronger in the afternoon than at night ([Wagner et al., 1999, p. 38](#)). They may blow continuously for long periods of time, particularly in the summer, but at times they remain absent for weeks ([Giambelluca and Schroeder, 1998, p. 53](#); [Wagner et al., 1999, p. 38](#)). Between October and April, Hawai'i may come under the influence of another type of low-pressure system that develops in the subtropics at high

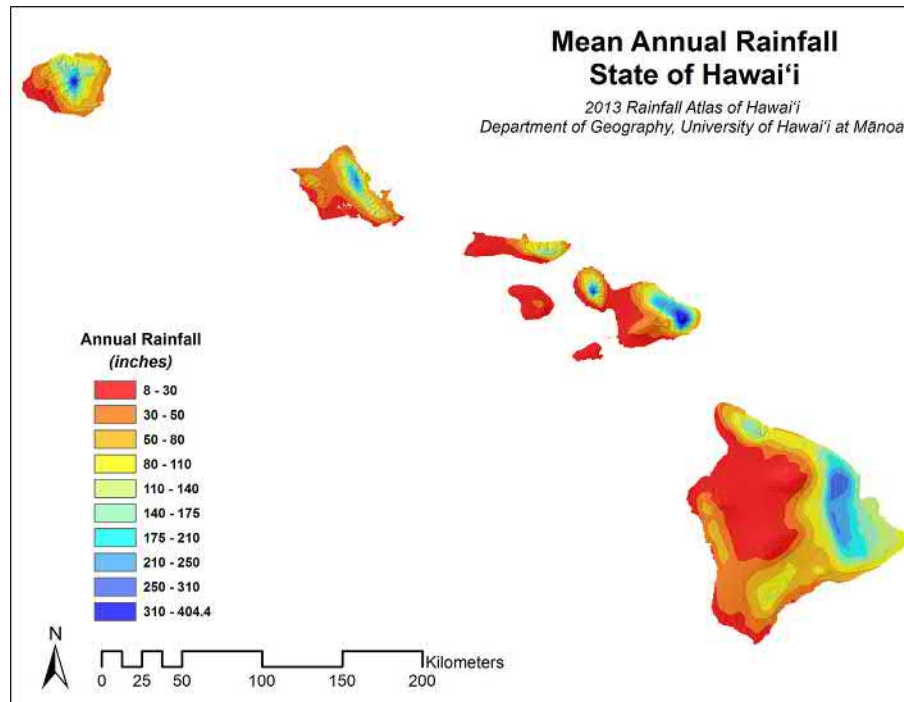


Fig. 7 Mean annual rainfall across the main Hawaiian islands (excluding Ni'ihau). Source: Giambelluca, T.W., Q. Chen, A.G. Frazier, J.P. Price, Y.-L. Chen, P.-S. Chu, J.K. Eischeid, and D.M. Delparte. (2013). Online rainfall atlas of Hawai'i. *Bulletin of the American Meteorological Society* 94, 313–316, <https://doi.org/10.1175/BAMS-D-11-00228.1>.

altitudes and gradually extends toward the surface, sometimes forming west of Hawai'i (Giambelluca and Schroeder, 1998, p. 53). This type of system brings moist, southerly winds and rain, what is termed Kona storms (Kona meaning "leeward") (Giambelluca and Schroeder, 1998, p. 53; Mueller-Dombois and Fosberg, 1998, p. 466; Wagner et al., 1999, p. 38) (Fig. 8). Occasionally, the islands receive southwesterly winds preceding strong northerly winds that follow cold fronts. In the absence of trade winds and Kona storms, winds may be light or variable which results in ocean-land temperature and pressure differences that generate local diurnal variations in wind (Giambelluca and Schroeder, 1998, 59; Wagner et al., 1999, p. 38). Such diurnal heating and cooling of islands results in onshore sea breezes during the day and offshore land breezes at night (Wagner et al., 1999, p. 38).

Hydrology

In addition to rainfall, the primary factor driving the complexity and diversity of hydrological conditions observed in Hawai'i is the highly permeable nature of the islands' volcanic substrates, an attribute particularly prevalent on the younger islands of Hawai'i and



Fig. 8 Trade and Kona wind patterns on the island of Hawai'i. Modified from U.S. Geological Survey; map base layers from ESRI. "World Elevation3D/Terrain3D" [basemap]. Scale not given. "Terrain 3D". Mar 13, 2019. <https://www.arcgis.com/home/item.html?id=7029fb60158543ad845c7e1527af11e4>. (April 5, 2019); ESRI. "World Hillshade" [basemap]. Scale not given. "World Hillshade". Mar 13, 2019. <https://www.arcgis.com/home/item.html?id=1b243539f4514b6ba35e7d995890db1d>. (April 5, 2019).

Maui (Juvik and Juvik, 1998, p. 89). To illustrate, the southern half of the island of Hawai'i from Hilo to Kohala lacks a single stream or river which reaches the coastline, over 220 mi (354 km) in all, despite some upslope areas receiving hundreds of inches of rainfall annually (Stearns, 1985, p. 291). However, substrate permeability varies considerably and in some rift zones of the mountains of the main islands, very hard, dense, and highly impermeable dike rock formations capture and hold large volumes of groundwater. This trapped groundwater slowly percolates through the rock horizontally toward areas of greater permeability including geologic faults and down-thrusts, or where rivers have carved channels through the dike formations (Stearns, 1985, pp. 294–298; Carlquist, 1992, p. 59; Polhemus, 2007, pp. 238–240).

Hawaiian Archipelago: Island Descriptions

Hawai'i

The island of Hawai'i, the largest, highest, and youngest of the main Hawaiian islands, is also the easternmost and southernmost island in the chain. It is located approximately 32 mi (51 km) from its nearest neighboring island, Maui. At 4038 square miles (mi²) (10,458 square kilometers (km²)), it comprises approximately two-thirds of the land area of the State of Hawai'i, making it Hawai'i's largest island, giving rise to its common name, the "Big Island." Five large shield volcanoes compose the island: Mauna Kea at 13,796 feet (ft) (4205 m) and Kohala at 5480 ft. (1670 m), both extinct, post shield stage, volcanoes; Hualalai at 8270 ft. (2520 m), the third most active volcano in the archipelago; and Mauna Loa (13,677 ft. (4169 m)) and Kilauea (4093 ft. (1248 m)), the second and first most active volcanoes in the archipelago, respectively (McDonald et al., 1990, pp. 345–379; USFWS 1994 (59 FR 10305, 1994); U.S. Geological Survey 2018 "Volcano Hazards Program" <https://volcanoes.usgs.gov>; Rubin 2018 "Hawaii Center for Volcanology" <http://www.soest.hawaii.edu/GG/hcv.html>). The island of Hawai'i includes a greater range of climatic zones than any other island in the State, with the highest and lowest temperatures, and several ecosystems ranging from coastal to alpine (Juvik and Juvik, 1998, p. 22; Wagner et al., 1999, p. 38, The Nature Conservancy of Hawai'i (TNCH) 2007 "Hawai'i High Islands" <http://www.hawaiieregionplan.info/>). The windward slopes receive the most rainfall, but orographic effects cause drier conditions to prevail in the leeward saddle area and in high elevation areas. The west or "leeward" side of the island (Kona), is in the rain shadow of the mountains, but does receive convection-driven rainfall in the afternoons resulting in annual rainfall ranging between 50 and 100 in (1270–2540 mm), capable of supporting mesic forest (Mitchell et al., 2005, pp. 6-71–6-91; Hawai'i Department of Land and Natural Resources, 2015, pp. 6-83–6-101).

Maui-Nui

The islands of Maui-Nui include Moloka'i, Lāna'i, Maui, and Kaho'olawe. During the last Ice Age about 21,000 years ago when sea levels were approximately 459 feet (ft) (140 meters (m)) below their present level, these four islands were connected by a broad lowland plain and unified as a single island (Nullet et al., 1998, p. 64; Ziegler, 2002, p. 22).

Maui Nui: Maui

The island of Maui (729 mi² (1888 km²)) is the second largest of the main Hawaiian islands (Juvik and Juvik, 1998, p. 14), and is located 32 mi (51 km) northwest of Hawai'i and 8 mi (13 km) from its nearest neighbor island, Kaho'olawe. Maui arose from two shield volcanoes resulting in formation of the west Maui mountains, which are about 1.3 million years old, and the east Maui mountains (Haleakalā volcano), about 750,000 years old (Juvik and Juvik, 1998, p. 14). These two mountain ranges are connected by the central Maui isthmus. The highest point on west Maui is Pu'u Kukui at 5788 ft. (1764 m) which receives 400 in (10,160 mm) rainfall per year (Juvik and Juvik, 1998, p. 14; Wagner et al., 1999, p. 41). East Maui's Haleakalā volcano last erupted only 200 years ago and is considered dormant (Juvik and Juvik, 1998, p. 14). Higher in elevation (10,023 ft. (3055 m)), Haleakalā is geologically younger and lacks the diverse vegetation of the older west Maui mountains. Annual rainfall on Haleakalā is about 35 in (890 mm) at the highest elevations, above the trade wind inversion, resulting in a dry cinder desert at the higher elevations (Giambelluca and Schroeder in Juvik and Juvik, 1998, p. 55). Lower elevations on windward east Maui receive as much as 404 in (10,262 mm) of annual rainfall (Giambelluca et al., 2013, p. 1).

Maui Nui: Kaho'olawe

Located 8 mi (13 km) southwest of the island of Maui, Kaho'olawe (45 mi² (116 km²)) is the smallest of the main Hawaiian islands and formed from a single shield volcano (Clague in Juvik and Juvik, 1998, p. 42; Juvik and Juvik, 1998, pp. 7–16). Its maximum elevation is 1476 ft. (450 m) at the summit of Pu'u 'O Moa'ula Nui (Juvik and Juvik, 1998, pp. 15–16). Because Kaho'olawe is located in the rain shadow of Haleakalā and is too low in elevation to experience orographic rainfall, it is relatively arid, receiving no more than 25 in (635 mm) of rainfall annually (Juvik and Juvik, 1998, p. 16; Mitchell et al., 2005, pp. 6–66).

Maui Nui: Lāna'i

Located 10 mi (17 km) south of Moloka'i and 9 mi (16 km) west of Maui, the island of Lāna'i (140 mi² (364 km²)) is the sixth largest of the main Hawaiian islands. Formed from a single shield volcano, its highest elevation is Lāna'ihale at 3366 ft. (1027 m). Due in part to a rain shadow cast by the west Maui mountains (Clague, 1998, p. 42), annual rainfall on the summit

ranges between 30 and 40 in (762 and 1016 mm). Annual rainfall is much less, ranging between 10 and 20 in (254 and 508 mm) over the lower elevation portions of the island (Giambelluca and Schroeder, 1998, p. 56).

Maui Nui: Moloka'i

Located 10 mi (17 km) north of Lāna'i and 10 mi (17 km) northwest of Maui, the island of Moloka'i (260 mi² (673 km²)), is the fifth largest of the main Hawaiian islands. The island is formed from three shield volcanoes, resulting in the east and west Moloka'i mountains and the Kalaupapa Peninsula (Juvik and Juvik, 1998, pp. 11–13). The taller and larger east Moloka'i mountain rises 4970 ft. (1514 m) above sea level and comprises roughly 50% of the island's area (Juvik and Juvik, 1998, pp. 11). Precipitous cliffs line the windward coast and deep valleys dissect the southern coastline. Annual rainfall on the windward side of the island ranges between 75 and 150 in (1905 and 3810 mm) (Giambelluca and Schroeder, 1998, p. 50). In contrast, the lower elevation, plain-like western half of the island is characterized by flat, rolling terrain that receives annual rainfall ranging between 15 and 30 in (381 and 762 mm).

O'ahu

Located 28 mi (46 km) west of Moloka'i, the island of O'ahu (600 mi² (1557 km²)) is the third oldest, third largest, and most populated of the main Hawaiian islands (Foote et al., 1972, p. 19; Juvik and Juvik, 1998, p. 7). The island is composed of two mountain ranges, the western Wai'anae range and the eastern Ko'olau range with a central plateau connecting them. These two mountain ranges formed from two separate shield volcanoes that ceased volcanic activity sometime between 1 and 2 million years ago. These mountain ranges are oriented perpendicular to the trade winds, creating distinctive leeward and windward climates due to the orographic effect. The arid Wai'anae range is located in the rain shadow of the Ko'olau range which receives most of the orographic rainfall (Juvik and Juvik, 1998, p. 7; Wagner et al., 1999, p. 39). The highest elevation on O'ahu occurs at the Mt. Ka'ala summit in the Wai'anae mountains (4025 ft., 1225 m) (Wagner et al., 1999, pp. 39–41). Rainfall on the island ranges from less than 20 in (500 mm) to more than 250 in (6350 mm) per year.

Kaua'i

Located approximately 76 mi (122 km) northwest of O'ahu, the island of Kaua'i (552 mi² (1430 km²)) is the oldest and northernmost of the main Hawaiian islands (Foote et al., 1972, p. 3). Kaua'i's highest elevation is Kawaikini Peak at 5148 ft. (1569 m), and the island's summit region is one of the most consistently wet areas on earth, receiving over 400 in (10,160 mm) of annual rainfall. Over 5 million years in age, erosion has created dramatic canyons and valleys across the island, notably Waimea Canyon and the rugged cliff lines on the Nā Pali Coast. In the past, Kaua'i has been severely affected by hurricanes, most recently by Hurricane Iniki in 1992 (U.S. Department of Commerce, 1993).

Ni'ihau

The island of Ni'ihau (69.5 mi² (180 km²)) is slightly younger than, and located 19 mi (31 km) southwest of, Kaua'i. Formed from a single shield volcano, it has unique geographic features including a low, flat plain with intermittent lakes. Ni'ihau is relatively arid, receiving 20–40 in (508–1016 mm) of annual rainfall, because it lies in the rain shadow of Kaua'i and lacks the elevation needed to create orographic rainfall (Stearns and MacDonald, 1947, p. 31). However, Kona storms provide some rainfall during the season of Kona winds. Although only 1280 ft. (390 m) at its highest elevation, Ni'ihau's northern coast includes precipitous sea cliffs. The geologically-related, but separate islet, of Lehua Island is a crescent-shaped tuff (ash) cone 284 ac (115 ha), that lies 0.7 mi (1.1 km) north of Ni'ihau, (Juvik and Juvik, 1998, pp. 3–6). Ka'ula Island 158 ac (64 ha), also known as Ka'ula Rock, is a small, crescent-shaped tuff cone, 550 ft. (167 m) high, and lies southwest of Ni'ihau.

Northwestern Hawaiian Islands

The Northwestern Hawaiian islands are located northwest of the inhabited main Hawaiian islands and consist of ten islands and atolls that span approximately 1200 mi (2000 km) beginning with the island of Nihoa to the southeast and extending to Kure atoll at the northwestern end. The islands were formed approximately 7–30 million years ago, as tall shield volcanoes over the same volcanic hotspot that formed the Emperor seamounts to the north and the main Hawaiian islands to the south (Clague and Dalrymple, 1989, p. 5). As the Pacific Plate moved north and later northwest over the hot spot, volcanic eruptions built up islands in a linear chain. The isolated land masses gradually eroded and subsided, beginning as high islands in the south, to become small atolls and seamounts north of 29°N Latitude (Fig. 1). In various stages of erosion, the Northwestern Hawaiian islands include an evolution from rocky basaltic islands surrounded by atolls or reefs such as Nihoa, Mokumanamana (Necker), Ōnūnui (Gardner Pinnacles), and Lalo (French Frigate Shoals), to the low sandy islands and atolls found to the north, including Kamole (Laysan), Kapou (Lisianski), Manawai (Pearl and Hermes), Kuaihelani (Midway), and Hōlanikū (Kure Atoll). Beyond Hōlanikū (Kure Atoll), the islands have completely subsided as the plate carries them forward into waters too cool for the formation of coral reefs to keep pace with the natural subsidence and erosion process (Fig. 9).

An important aspect of the Hawaiian cultural revival is the awareness that in numerous instances traditional place names either were replaced with foreign names or the Hawaiian names were misspelled to the degree that their meanings were changed.

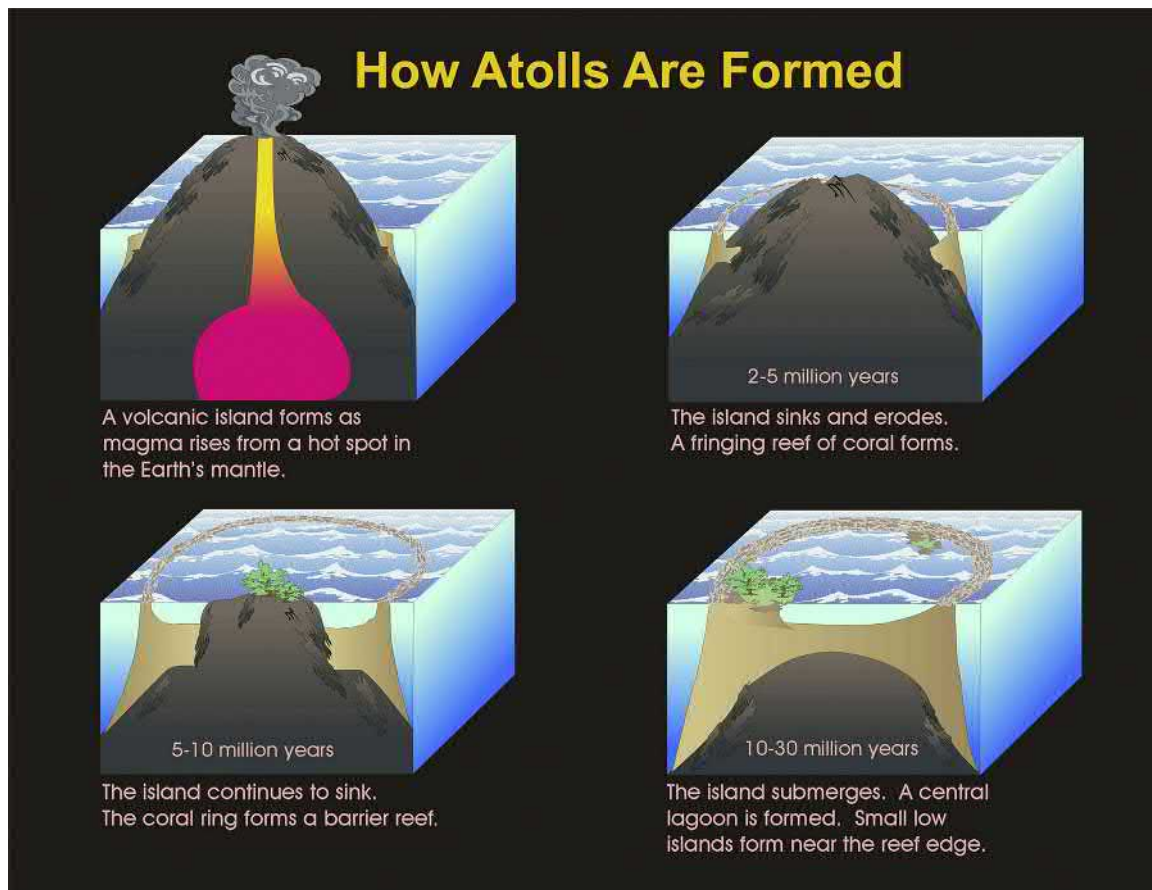


Fig. 9 How Volcanic Islands change to Atolls over time.

Consequently, the Hawaiian Lexicon Committee first published names for the NWHI in 1998, and then again in 2007. The new official name of Papahānaumokuākea was chosen to denote all of the northwestern islands and atolls. [Kikiloi \(2010, entire\)](#), updated the Hawaiian names for the NWHI based on 19th century Hawaiian language documents which we include here ([Table 2](#)).

Nihoa

Located 150 mi (240 km) northwest of the island of Kauaʻi, Nihoa is the tallest of 10 islands and atolls in the NWHI and is 0.27 mi² (0.6 km²) in land area ([Juvik and Juvik, 1998, pp. 24; 304](#)). The island has two peaks, Miller's Peak (892 ft. (272 m)) in the west and Tanager Peak (850 ft. (259 m)) in the east. The surface of the island slopes southward with an average decline of 23°. Although there are no permanent streams on the island, ephemeral streams have carved six major south flowing drainage valleys across the island. Hydrology includes three small water seeps, all located at the bottom of drainage valleys ([Evenhuis and Eldredge, 2004, pp. 27–28](#)).

Mokumanamana (Necker Island)

Located approximately 155 mi (249 km) northwest of Nihoa and lying north of the Tropic of Cancer, Necker is approximately 0.06 mi² (0.16 km²) in land area ([Juvik and Juvik, 1998, pp. 24; 304](#)). Composed of small peaks and intervening swales, Necker is the last

Table 2 List of known Hawaiian names for the Northwestern Hawaiian Islands^a

Island name (Armstrong, 1983, p. 29)	Hawaiian name (Juvik and Juvik, 1998, p. 27)	Hawaiian name (Kikiloi, 2010, p. 87–88)
Nihoa	Nihoa	Nihoa, Nihoa-Kuhikuhipu'uone, Moku Manu
Necker	Mokumanamana	Mokumanamana, Kamokumanamana, Hā'ena
French Frigate Shoals	Mokupāpapa	Lalo, Kānemiloha'i
Gardner Pinnacles	Puhāhōnu	'Ōnūnui, 'Ōnūiki
Maro Reef	Nalukakala	Kamokuokamohoali'i, Ko'anako'a
Laysan Island	Kauō	Kamole
Lisianski Island	Papa'āpoho	Kapou
Pearl and Hermes Atoll	Holoikauaua	Manawai
Midway Atoll	Pihemanu	Kuaihelani
Kure Atoll	Kānemiloha'i	Hōlanikū, Mokupāpapa

^aUnavailable or unknown if not listed.

remnants of an old, stream-eroded basaltic island. The edges of its individual islets are defined by steep sea cliffs with bases featuring wave-cut benches a few meters above sea level. Hydrology includes a few small seeps (Evenhuis and Eldredge, 2004, pp. 30–31).

Kānemiloha'i (French Frigate Shoals)

Located approximately 85 mi (137 km) northwest of Necker Island, French Frigate Shoals is the largest atoll in the NWHI in the form of an 18 mi (28.9 km) long crescent (Juvik and Juvik, 1998, pp. 24; 304). An estimated 12.3 million years old (Clague, 1998, p. 38), the shoals consist of 67 acres (0.27 km²) of total emergent rocky pinnacle and sand islands surrounded by approximately 230,000 acres (931 km²) of coral reef habitat. A combination of sand, rubble, nonliving coral substrate, and crustose coral-line algae occurs in the windward and exposed lagoon areas. The lagoon is unusual in that it contains two exposed volcanic pinnacles representing the last vestiges of the high island from which the atoll developed. The three small sand islets continually change size, shift position or disappear and reappear.

Pūhāhonu (Gardner Pinnacles)

Located approximately 108 mi (174 km) northwest of French Frigate Shoals, Gardner Pinnacles is the northernmost island in the chain with emergent portions of volcanic origin. These two basaltic peaks estimated at 15.8 million years in age (Clague, 1998, p. 38) are similar in size to the pinnacles of French Frigate Shoals, measuring approximately 180 feet (54.8 m) in height with a diameter of 590 ft. (179.8 m) (Juvik and Juvik, 1998, pp. 24; 304). These remnant volcanic pinnacles are surrounded by approximately 600,000 acres (2428 km²) of coral reef, most of which is in waters 60 feet (18.3 m) or deeper.

Kō'anakō'a, Nalukākala (Maro Reef)

Located between Gardner Pinnacle and Laysan Island, Maro Reef is a largely submerged open atoll 19.7 million years in age (Clague, 1998, p. 38). Less than one acre (4046.8 m²) of land is emergent, when during very low tide, a small coral outcrop of a former island breaks the surface of the water. The shallow water reef system is extensive, covering nearly a half-million acres (2023 km²) (Juvik and Juvik, 1998, p. 24), making Maro the largest coral reef in the region. Because its outermost reefs absorb the majority of the energy from the open ocean swells, the innermost reticulated reefs and aggregated patch reefs are sheltered and exhibit several characteristics of a true lagoon.

Kauō (Laysan Island)

Located approximately 342 mi (550 km) northwest of Gardner Pinnacles, Laysan is a raised atoll estimated at 20.7 million years in age (Clague, 1998, p. 38). With a maximum elevation of approximately 50 ft. (15 m) above sea level, it has a land area of approximately 1023 acres (4.14 km²), surrounded by 100,000 acres (405 km²) of coral reef (Juvik and Juvik, 1998, pp. 24; 304). Most of the reef lies in deeper waters with a small, shallow-water reef area in a bay off the southwest side of the island. Laysan's ring of sandy dunes surround a shallow depression of about 200 acres (0.8 km²) that contains a mix of hypersaline water and mud flats, a feature unique within the Hawaiian Archipelago and rare within the Pacific region. This hypersaline lake changes in size depending on variations in rainfall.

Lisianski (Papa'āpoho) and Neva Shoal

Located approximately 112 mi (180 km) northwest of Laysan, Lisianski Island is another raised atoll, estimated at 23.4-million years in age (Clague, 1998, p. 38). Rising to 40 ft. (12.1 m) above sea level, it includes approximately 400 acres (1.6 km²) of emergent land (Juvik and Juvik, 1998, pp. 24; 304). This island measures approximately 1.2 miles (1.9 km) in width and consists of an elevated rim surrounding a broad central depression, which unlike Laysan, does not enclose an interior saline lake. An extensive platform-like coral reef, called Neva Shoals, surrounds the island and totals more than 290,000 acres (1.74 km²). This reef covers approximately 60% of the lagoon/atoll's substrate.

Holoikauaia (Pearl and Hermes Atoll)

Located approximately 257 mi (414 km) northwest of Lisianski, Pearl and Hermes Atoll is a large atoll with several small islets, forming 96 acres (0.38 km²) of emergent land surrounded by more than 300,000 acres (1214 km²) of coral reef (Juvik and Juvik, 1998, p. 304). Estimated at 26.8 million years in age (Clague, 1998, p. 38), the atoll is 20 miles (32 km) across and 12 miles (19.3 km) wide (Juvik and Juvik, 1998, p. 24). Unlike Lisianski and Laysan to the southeast, Pearl and Hermes Atoll is a true atoll, fringed with shoals, permanent emergent islands, and ephemeral sandy islets.

Pihemanu (Midway Atoll)

Located approximately 15 mi (24 km) northwest of Pearl and Hermes, Midway Atoll consists of three sandy islets totaling 1464 acres (5.9 km²) in terrestrial area and lying within a large, elliptical barrier reef measuring approximately 5 miles (8 km) in diameter. The three islets include, Sand measuring 1117 ac (4.56 km²), Eastern measuring 337 ac (1.36 km²), and Spit, measuring 13 ac (0.05 km²) (Juvik and Juvik, 1998, pp. 24; 304). Estimated at 28.7 million years in age (Clague, 1998, p. 38), the atoll is surrounded by more than 88,500 acres (356 km²) of coral reefs. Core samples taken by the U.S. Geological Survey found solid basaltic rock 180 ft (54.8 m) beneath Sand Island and 1240 ft (377.9 m) beneath the northern reef.

Mokupāpapa (Kure Atoll)

Located approximately 55 mi (89 km) northwest of Midway Atoll, Kure is the most northwestern island in the Hawaiian chain and occupies a singular position at the “Darwin Point,” which is the northern extent of coral reef development, beyond which coral growth cannot keep pace with the rate of geological subsidence (Grigg, 1982, p. 29). Estimated at 29.8 million years of age (Clague, 1998, p. 38), Kure Atoll is circular in shape, with a coral reef measuring approximately 6 mi (9.6 km) in diameter and enclosing a lagoon. Two islets consisting of over 200 ac (0.91 km²) of emergent land are flanked by almost 80,000 acres (324 km²) of coral reef within the lagoon (Juvik and Juvik, 1998, pp. 24; 304). An outer reef forms a nearly complete circular barrier around the lagoon, with the exception of passages to the southwest. Of the two enclosed islets, the only perennially permanent land is found on the crescent-shaped Green Island, which rises to 20 ft. (6.1 m) above sea level and is located near the fringing reef in the southeastern quadrant of the lagoon. Currently, The coral around Kure is still growing, slightly faster than the island is subsiding. North of Kure, where growth rates are even slower, the drowned Emperor Seamounts foretell the future of Kure and all of the Hawaiian Archipelago. As Kure Atoll continues its slow migration atop the Pacific Plate, it too will eventually slip below the surface.

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Hawaiian Islands Coastal Ecosystems: Past, Present, and Future

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Published by Elsevier Inc.

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Abstract

We provide an overview of the coastal ecosystem of the Hawaiian archipelago and describe the ecological factors that have influenced the ecosystem in the past, present, and future. Coastal ecosystems found throughout the Hawaiian archipelago are subject to oceanic influences such as winds, salt-spray, and wave energy. Two coastal ecosystem sub-types occur in the archipelago and are defined by moisture regime: coastal dry and coastal wet-mesic sub-types. Limited information exists about what coastal ecosystems and their associated ecological communities looked like prior to human-contact. The assumption is that coastal ecosystems were historically more resilient to stochastic events because they had more continuous populations of native flora with a higher faunal diversity. Currently, coastal ecosystems are in decline due to factors such as conversion pressure from expanding development and agriculture and the introduction of invasive species. We analyzed four scenarios for a foreseeable future of coastal ecosystems with varying levels of change in Conservation Management Parameters: conservation values, laws and biosecurity, and development or conservation planning. We anticipate that coastal ecosystems will continue to decline unless significant management change occurs.

Introduction

The Hawaiian archipelago in the Pacific Ocean is more than 3200 km from the nearest continental land mass with extreme variations in elevation, wind, rain, topography, substrate, and hydrology. These variations create unique ecosystems across the archipelago. We provide an overview of the coastal ecosystem in Hawai'i and describe the ecological factors that have influenced it over time. Please see the chapter on *Physical Geography of the Hawaiian Islands* for a full description of the unique geography, geology, climate, hydrology and descriptions of the islands in the Hawaiian archipelago.

Description

Defining Hawaiian Islands Coastal Ecosystems

Coastal ecosystems are defined as near-shore areas impacted by the ocean. Bound by ocean on one side, these ecosystems generally range within 100 m of the high tide, and up to 300 m in elevation. This limit is determined by the effect of seawater on the substratum and plant rooting zone; the limit of spray kill; and the limit of formations such as sand dunes, elevated coral outcrops, and marine terraces, which are created largely through shoreline processes (e.g., inundation or exposure to salt water and onshore flow of 'ehukai salt mist, strong winds, movement of sand by winds, and brackish basal groundwater; see [Richmond and Mueller-Dombois, 1972](#); [Gagné and Cuddihy, 1999](#); [Warshauer et al., 2009](#)) and sometimes extends farther inland if strong prevailing onshore winds drive these processes into the lowland zone ([TNCH, 2009](#)).

Coastal ecosystems are found on all of the main Hawaiian Islands (Hawai'i, Maui, Moloka'i, Kaho'olawe, Lāna'i, O'ahu, Kaua'i, and Ni'ihau) and offshore islets. The highest species diversity occurs in the least populated and undeveloped coastal areas on the main Hawaiian Islands. These ecosystems also occur on the islands and atolls within the islands in the Northwestern Hawaiian Islands (NWHI or Papahānaumokuākea).

The coastal substrate consists of well-drained talus (the pile of rocks that accumulate at the base of a cliff, chute, or slopes), calcareous (limestone) slopes, and dunes. This ecosystem can be dry (less than 1200 mm annual rainfall), mesic (1200–2500 mm), and wet (more than 2500 mm). The vegetation community within these dry and wet-mesic ecosystems consist of herblands, sedgelands, grasslands, shrublands, mixed communities, and forests ([Table 1](#) and described below).

Pre-human Condition

Information about native vegetation in Hawai'i prior to the arrival of humans is limited. Our assumptions are based on existing vegetation, remnants in disturbed areas, patterns of climate and substrates, and a few fossilized remains ([Cuddihy and Stone, 1990](#)). Coastal ecosystems were found on all islands in the archipelago in a continuous ring, only interrupted by stretches of recent lava flows or unstable cliff faces ([Jacobi and Warshauer, 2017](#)). Native flora and fauna existing today are likely remnants of larger, more extensive past populations of flora and fauna ([Gagné and Cuddihy, 1999](#)). What is now an island or atoll within the Northwestern Hawaiian Islands was likely a high elevation island with a varying array of vegetation communities that do not currently exist. For example, typical high island tree species such as loulou (*Pritchardia* sp.) and 'iliahī (sandalwood, *Santalum ellipticum*) on the coral island of Kamole (Laysan) might have been the remnant of a more expansive vegetation community present at one time on a higher elevation island form ([Mueller-Dombois and Fosberg, 1998](#)) ([Fig. 1](#)).

Vegetation on rocky shores were low growing and mat forming species in areas closest to the ocean ([Warshauer et al., 2009](#)), or stunted due to strong winds (e.g., tree species grew to shrub forms) ([Gagné and Cuddihy, 1999](#)). Taller plants grew farther inland or where accumulated soil was locally available ([Warshauer et al., 2009](#)). A range of conditions at other sites allowed for species diversity within coastal communities ([Warshauer et al., 2009](#)). We assume that healthy, functioning coastal ecosystems unaltered by humans had the ability to provide natural protective buffers for inland ecosystems ([Fig. 2](#)).

Dry Hawaiian coastal ecosystems historically occurred on all coral atolls and high island remnants of the NWHI, and along the coastlines of all the main islands ([Gagné and Cuddihy, 1999](#)). They were likely more extensive on the drier leeward sides of larger

Table 1 Categories and sub-units of Hawaiian coastal systems and dominant plant species and vegetation type were used to classify habitat sub-units based on their elevation and moisture regimes within the coastal boundaries.

Coastal communities		
Coastal dry communities	Coastal dry herblands	<i>Nama</i> Herbland
		'Akulikuli (<i>Sesuvium</i>) Herbland
	Coastal dry grasslands	'Aki'aki (<i>Sporobolus</i>) Grassland
		Kāwelu (<i>Eragrostis</i>) Grassland
		<i>Lepturus</i> Grassland
	Coastal dry mixed communities	'Ilima (<i>Sida</i>) Mixed Shrub and Grassland
	Coastal dry shrublands	Naupaka Kahakai (<i>Scaevola</i>) Shrubland
		'Ilima (<i>Sida</i>) Shrubland
		Ma'o (<i>Gossypium</i>) Shrubland
		Hinahina/Kīpūkai (<i>Heliotropium</i>) Shrubland
		'Iliahialo'e (<i>Santalum</i>) Shrubland
		Coastal Cliff Mixed Shrubland
		'Āweoweo (<i>Chenopodium</i>) Coastal Shrubland
		Naio (<i>Myoporum</i>) Shrubland
Coastal wet-mesic communities	Coastal mesic forest	Hala (<i>Pandanus</i>) Forest
		Loulu (<i>Pritchardia</i>) Coastal Forest

Adapted from Gagné WC and Cuddihy LW (1999) Vegetation. In: Wagner WL, Herbst DR, and Sohmer SH (eds.) *Manual of the Flowering Plants of Hawai'i*, pp. 45–114. Honolulu: University of Hawai'i Press, Bishop Museum Press.



Fig. 1 Nihoa Island, a high island in the Northwestern Hawaiian Islands.



Fig. 2 Low growing and mat forming shrubs at Ka'ena Point on the island of O'ahu.

islands and on all sides of the smaller, arid islands and atolls in the Hawaiian archipelago (Gagné and Cuddihy, 1999; Landfire, 2016). Certain plants such as naupaka kahakai (*Scaevola taccada*) were able to utilize the brackish groundwater to grow year-round (Gagné and Cuddihy, 1999). Other typical coastal dry vegetation consisted of 'ōhai (*Sesbania tomentosa*), 'aki'a (*Wikstroemia uva-ursi*), naio (*Myoporum sandwicense*), pōpolo, 'akoko (*Chamaesyce celasroides*), 'ewa hinahina (*Achyranthes splendens* var. *rotundata*), pā'ū o Hi'iaka (*Jacquemontia ovalifolia* subsp. *sandwicensis*), and 'ilima (*Sida fallax*) (see Table 2) (Fig. 3).

Wet coastal ecosystems in Hawai'i included nutrient-rich flood plains, marshes, lowland riparian, fresh groundwater, and permanent stream areas. These included the coastal wet forests and the coastal mesic forests (see Table 3) (Fig. 4).

Hawaiian vertebrate species such as honu (Hawaiian green sea turtle, *Chelonia mydas*), honu 'ea (hawksbill turtle, *Eretmochelys imbricata*), and 'ilioholoholoikauaua (Hawaiian monk seal, *Monachus schauinslandi*) frequented coastlines where the offshore waters provide an abundance of limu and reef protection from predatory shark species. 'Ōpe'ape'a (Hawaiian hoary bat, *Lasiurus cinereus semotus*) foraged along the coasts searching for insect prey. Nesting seabirds left their young in sandy or rocky burrows to forage in the prey rich sources offshore. Other seabirds used the edge of the vegetation line to lay their eggs away from the high tide. Other native birds (e.g., finches (Family: Fringillidae), millerbirds (Family: Acrocephalidae), large flightless birds (Family: Anatidae), and various migratory shorebirds) used the native vegetation to build their nests and forage for food sources within the coastal

Table 2 Historic and current condition of coastal dry communities.

	Historic condition	Current condition
Coastal dry herblands	Coastal dry herblands occurred in rocky areas, on coralline surfaces, and on mudflats adjacent to lagoons, marshes, and anchialine pools on coralline or basaltic surfaces; from 0 to 5 m elevation; with an annual rainfall from less than 250 mm to more than 1000 mm (Gagné and Cuddihy, 1999). Dominant herb species included hinahina kahakai (<i>Nama sandwicensis</i>) and 'Akulikuli (<i>Sesuvium portulacastrum</i>) (Gagné and Cuddihy, 1999). Other herbaceous plants consisted of pā'ū o Hi'iaka and 'ohelo kai (<i>Lycium sandwicense</i>) (Gagné and Cuddihy, 1999).	Nama and 'akulikuli dry herbland communities currently occur only where human disturbance is minimized and along coastal bluffs and cliffs where there are rocky areas and coral surfaces (Gagné and Cuddihy, 1999, p. 55). Some of these native communities have been replaced by the non-native slender sea-purslane (<i>Sesuvium maritimum</i>).
Coastal dry grasslands	Coastal dry grasslands typically occurred in leeward areas, at sea level to 300 m elevation with an annual rainfall from 250 to 1000 mm, on variety of substrates of well-drained calcareous sand to newly vegetated volcanic flows (Gagné and Cuddihy, 1999). The plant communities were often subject to summer drought and "brown off" (with the exception of 'aki'aki (<i>Sporobolus virginicus</i>) and kāwelu (<i>Eragrostis variabilis</i>) (Gagné and Cuddihy, 1999). 'Aki'aki, kāwelu, and <i>Lepturus repens</i> were the dominant grasses.	Native coastal dry grasslands are limited to a few coastal dunes on which human disturbance has been minimized (Gagné and Cuddihy, 1999, p. 57). 'Aki'aki grasslands have been converted to kiawe forest communities. Nonnative weeds remain the primary threat to 'aki'aki, kāwelu, and <i>Lepturus</i> grassland communities (Gagné and Cuddihy, 1999, p. 58). 'Aki'aki is often the only native understory species beneath kiawe. Otherwise, the understories are dominated by nonnative drought-resistant grasses and herbs, particularly buffelgrass (<i>Cenchrus ciliaris</i>) fingergrass (<i>Chloris</i> spp.), and guinea grass.
Coastal dry mixed communities	Coastal dry mixed communities occurred on talus slopes or on shallow, rocky, weathered clay soils, especially in leeward areas with an annual rainfall of less than 500 mm, often subject to winter storm salt spray (Gagné and Cuddihy, 1999). 'Ilima was the dominant plant species.	'Ilima mixed shrub and grassland communities are still found, however, fingergrass now occurs with 'ilima as a dominant hybrid community in this coastal dry habitat. Additionally, in drier sites on the main Hawaiian Islands these communities have usually been replaced by kiawe, koa haole, Christmas berry or klu (<i>Acacia farnesiana</i>). Protection by isolation, especially from feral herbivores provides some protection to the native mixed community.
Coastal dry shrublands	Coastal dry shrubland communities occurred mostly on flat, rocky sites in open, widespread coastal areas below 300 m with an annual rainfall of less than 500 mm; small shrubs in this community were subject to harsh environmental conditions (e.g., highly seasonal precipitation, large temperature fluctuations, and intense solar radiation) (Gagné and Cuddihy, 1999). Naupaka kahakai (<i>Scaevola taccada</i>), 'ilima, ma'o, hinahina/kipūkai (<i>Heliotropium anomalum</i> var. <i>argenteum</i>)/ (<i>H. curassavicum</i>), and 'iliahialo'e (<i>Santalum ellipticum</i>) were dominant species. Coastal cliff mixed shrubland, another sub-habitat of the coastal dry shrublands, consisted of a mix of 'ilima, nehe (<i>Lipochaeta</i> spp.), 'akoko (<i>Euphorbia degeneri</i>), kāwelu, <i>Schiedea globosa</i> , and 'ānaunau (<i>Lepidium bidentatum</i> var. <i>o-waihiense</i>) species); 'Āweoweo (<i>Chenopodium oahuense</i>) and, pua kala (<i>Argemone glauca</i>), naio.	Native coastal dry shrubland communities occur where they are not subjected to grazing. Abandoned grazing lands along coastlines are extensive thickets of koa haole shrublands. Christmas berry and kiawe forest are also components of these shrublands, the latter community prevailing especially where kiawe is able to tap brackish groundwater. Currently predominantly native dry shrublands consist of mostly nonnatives. Naupaka kahakai shrubland occurring on dunes can be mixed with invasive species such as Indian fleabane (<i>Pluchea indica</i>), sourbush (<i>Pluchea carolinensis</i>) and Christmas berry; on raised coral can be found with stinking passionflower (<i>Passiflora foetida</i>); and on basalt cliffs can be found with sweet acacia (<i>Acacia farnesiana</i>). 'Ilima, ma'o, and hinahina/kipūkai, and 'a'ali'i shrublands occur on a few locations in the main Hawaiian Islands. Although severely disturbed by roads, trails, and nonnative weeds and only represented by a single natural occurrence at Makapu'u on O'ahu, 'iliahialo'e shrubland remains a native-dominated community (Gagné and Cuddihy, 1999). Coastal cliff mixed shrublands grade into nonnative dominated communities from the top to bottom of cliff bases. Native species are not large components of these communities.

Table 2 Historic and current condition of coastal dry communities.—cont'd

	Historic condition	Current condition
		Most of the native coastal dry shrublands that remain are being destroyed by urbanization, off-road vehicle activity, arson, grazing, and encroachment by nonnative plant species. 'Ilima, 'āweoweo, and naupaka kahakai shrublands occur on federally protected lands in the NWHI; naupaka kahakai shrublands are fairly dominant in certain coastal areas of the main Hawaiian Islands. Coastal cliff mixed shrublands also have some natural barriers (steepness of cliff slopes) which make it impossible for nonnative ungulates and predators to access, but is almost ubiquitously disturbed by nonnative plants. Although several of these communities occur within the State's Ka'ena Point Natural Area Reserve on O'ahu, they have not yet received protective management. Ma'o, hinahina/kipūkai, 'iliahialo'e, and naio shrub lands remain unprotected. The coastal dry shrubland is often delineated at the inland boundary by nonnative lowland shrubs and trees (klu, kiawe, koa haole, and Christmas berry) where the degree of salt spray, is minimal. No extant intact naio shrublands currently exist; only remnant scattered clumps of naio occur in the lowlands of O'ahu, such as on the Mokulē'ia side of Ka'ena Point, where they have not been impacted by agriculture or fire and subsequently replaced by nonnative shrublands or forests. On Laysan, this vegetational association was an important element until it was destroyed by introduced rabbits in the early 1900s and replaced by shrublands of Indian fleabane. 'Āweoweo coastal shrublands have since been reintroduced on Lisianski and Laysan.
Coastal dry forests	Coastal dry forests occurred in gently sloping and level lowlands, in areas where there was sufficient soil (Gagné and Cuddihy, 1999). Ground cover consisting of 'aki'aki extended inland beneath taller tree species such as wiliwili (<i>Erythrina sandwicensis</i>), 'ohe makai (<i>Reynoldsia sandwicensis</i>), and loulou (<i>Pritchardia</i> spp.). Typical plants in this community included 'ilima and nehe. Vegetation in the semi-arid conditions on the leeward coasts were able to utilize brackish water found under talus and alluvial substrates.	Additionally, wiliwili, 'ohe makai, and hoary abutilon have been replaced with invasive species such as lantana (<i>Lantana camara</i>), klu, Christmas berry, koa haole, or kiawe (the latter being the current dominant species in the coastal dry forest). Because kiawe is able to utilize brackish groundwater at great depths it thrives in the semi-arid conditions along this coastal habitat type. Logwood (<i>Haematoxylum campechianum</i>) is locally quite abundant and may be codominant with kiawe on the south Kona coast of Hawai'i Island.

Adapted from Gagné WC and Cuddihy LW (1999) Vegetation. In: Wagner WL, Herbst DR, and Sohmer SH (eds.) *Manual of the Flowering Plants of Hawai'i*, pp. 45–114. Honolulu: University of Hawai'i Press, Bishop Museum Press.

ecosystem. Native insects such as the yellow-faced bee (*Hylaeus* spp.) used the branches of native vegetation to build their nests. In short, these coastal areas were vibrant, diverse ecological communities that could sustain the ecological processes within the ecosystem.

Coastal Ecosystem Viability

We suspect that species viability in coastal ecosystems depended on maintaining multiple, distributed (or redundant) populations of sufficient quality and size to be resilient to change, and with a species richness and representative of a genetic range to survive across their ecological environment over time. The distribution of the coastal ecosystems in the Hawaiian archipelago likely provided the redundancy, which allowed the ecosystem to withstand stochastic events (like volcanic eruptions or hurricanes) on portions of the habitat.

We assume the ecosystem viability of coastal communities before pre-human contact were very resilient, redundant, and well represented and occurred in a continuous ring on all the islands, only restricted by elevation, rainfall, and ocean influences. Because they were widely distributed, it is believed their ability to recover from catastrophic events was more likely. These communities tolerated natural disturbances and any changes or variations to the environment.

Current Condition

Hawaiian coastal ecosystems have been transformed either intentionally (e.g., ornamental or food crops, human residences or hotels, other development such as harbors, jetties, and piers) or inadvertently (e.g., examples plus climate) by humans. Non-



Fig. 3 'Ōhai and naupaka on the island of O'ahu.

Table 3 Historic and current condition of coastal wet-mesic communities.

	<i>Historic condition</i>	<i>Current condition</i>
Coastal wet forests	Coastal wet forests were likely a widespread community which occurred on the windward coastlines (Gagné and Cuddihy, 1999). 'Ōhi'a (<i>Metrosideros polymorpha</i>) and lama (<i>Diospyros sandwicensis</i>) were likely widespread on the windward coasts (Gagné and Cuddihy, 1999).	'Ōhi'a/lama wet forests no longer exist as a primary dominant community type in the coastal habitat. The wet coastal forests that exist today are mangrove swamps consisting of American mangrove (<i>Rhizophora mangle</i>) and oriental mangrove (<i>Bruguiera gymnorhiza</i>).
Coastal mesic forests	Coastal mesic forests occurred on sandy coastlines, wetter lower slopes, valley bottoms, land shelves, and cliff bases from 0 to 493 ft. (150 m) elevation in areas with an annual rainfall of 71–150 in (1800–3800 mm) (Gagné and Cuddihy, 1999). Loulu were the dominant tree species in the coastal wet-mesic habitat.	Both hala and loulu coastal mesic forests are rare. Hala forests are now uncommon but still occur in areas not excessively altered by humans, e.g., example on the Nā Pali coast trail on the island of Kaua'i. Fairly intact hala forest are also found along the Puna coastline on Hawai'i Island but have since been covered by current (2018) lava flows. Only one extant population of loulu coastal forest currently remains on the island of Nihoa. This last loulu forest community is unique in that it is not subject to invasive mammalian seed predators. Common ironwood (<i>Casuarina equisetifolia</i>) which is considered an invasive tree, is another coastal mesic forest community. This community has the capability to grow in monospecific stands due to its aggressiveness in its nitrogen-fixing capability, ability to utilize brackish groundwater, and ability to exclude understory growth with its allelopathic leaves. Coconut (<i>Cocos nucifera</i>) trees introduced to Hawai'i by early Polynesian settlers are found along coastal beaches, sometimes in dense monotypic stands. Other areas that were once consisting of hala dominated species were farmed and subsequently abandoned by the ancient Hawaiians. These habitats have become dominated by common guava (<i>Psidium guajava</i>), strawberry guava (<i>P. cattleianum</i>), or black bamboo (<i>Phyllostachys nigra</i>), or by Polynesian introductions such as kamani (<i>Calophyllum inophyllum</i>), kukui (<i>Aleurites moluccana</i>), hau (<i>Hibiscus tiliaceus</i>), and tree heliotrope (<i>Tournefortia argentea</i>).



Fig. 4 Loulu coastal forest on the island of Nihoa.

native species may become naturalized or outcompete native species. For example, strawberry guava (*Psidium cattleianum*), a Brazilian native tree species, grows from sea level to 4000 ft in elevation (USFS, 2016). Strawberry guava competes with native species, fragments native habitat systems, alters water cycling of Hawaiian watersheds, and promotes secondary invasive species.

Ironwood (*Casuarina equisetifolia*) is an invasive species that is capable of fixing nitrogen and therefore, may alter the soil chemistry (Smith, 1992). It grows rapidly, forms exclusive stands, and its fallen branchlets produce allelopathic chemicals (Smith, 1992). In the NWHI, naupaka, a sand stabilizer of these islands, cannot tolerate the heavy shade from ironwood, thus has suffered from the gradual encroachment and eventual replacement by the invasive species (Smith, 1992). These low lying coastal islands are therefore more susceptible to erosive processes (Smith, 1992).

Koa haole (*Leucaena leucocephala*) is an aggressive pest due to its effective dispersal and potential for rapid population increase (Wester, 1992). Its ability to vigorously resprout and establish by seed after fire exhibits its ability to exploit new sites and shift the ecological systems (Smith and Tunison, 1992).

Coastal dry communities

Coastal dry communities have been inundated or replaced by invasive species such as pickleweed (*Batis maritima*), kiawe (*Prosopis pallida*), koa haole (*Leucaena leucocephala*), Christmas berry (*Schinus terebinthifolius*), sourbush (*Pluchea carolinensis*), guinea grass (*Megathyrsus maximus*). Native species are no longer dominant in the coastal dry forest (Gagné and Cuddihy, 1999); rather, the systems are made up of invasive plants as listed above and in Table 2.

Coastal wet-mesic communities

Coastal wet-mesic communities are represented by forests, generally restricted to the windward side due to the availability of rainfall, and in the NWHI and offshore islets (e.g., loulu valleys on Nihoa, ironwood stands on Midway, loulu on sea cliffs offshore of Moloka'i). Relative to other communities in the coastal system the coastal wet-mesic communities are relatively species-poor, but this may be a result of human alteration (Gagné and Cuddihy, 1999). Coastal mesic and wet forests have been significantly reduced to invasive dominated communities (see Table 3) (Figs. 5–8).

Current Biotic Components of Coastal Ecosystems

The honu, honu 'ea, and 'Ōlīoholoholoikauaua continue to use coastal areas, however, we speculate in less numbers than historic times. 'Ōpe'ape'a continue to forage in and off these habitats. Seabirds (Families: Sulidae, Fregatidae, Diomedidae, Procellariidae, Hydrobatidae, Laridae, Phaethontidae) are abundant on the NWHI. Honeycreepers and millerbirds continue to breed in coastal shrub communities in the NWHI. Flightless herbivorous birds, such as the moa nalo, are extinct. Native bees (*Hylaeus* spp.) may be found in remnant coastal communities in the main Hawaiian Islands and NWHI. Current threats to native species include introduced plants, mammals (rodents and ungulates), insects that negatively impact the native biota within the main Hawaiian Islands and NWHI in these coastal ecosystems (see below for discussion).

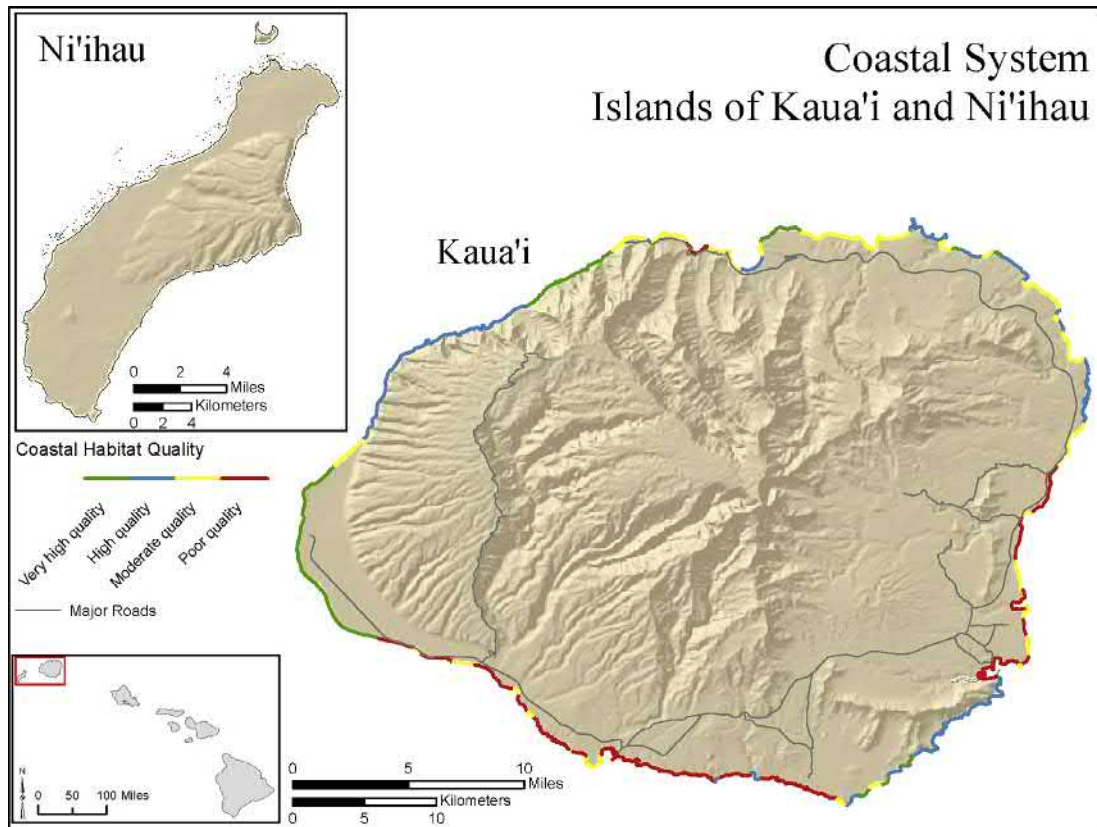


Fig. 5 Coastal ecosystem quality on the islands of Kaua'i and Nii'hau. From Reeves MK and Amidon F (2018) Habitat status assessment methods—Hawai'i, current condition summaries, August 2018. *Technical Report from United States Fish and Wildlife Service*, 439 pp. Honolulu, HI: Pacific Islands Fish and Wildlife Office.

Stressors

Development

Human development modified coastal ecosystems (Warshauer et al., 2009). Structures and sand hardening altered the hydrodynamics and water flow, wave regime, sediment dynamics, grain size, and depositional processes (Fletcher et al., 1997; Miles et al., 2001; Runyan and Griggs, 2003; Martin et al., 2005; Dugan et al., 2011). Beach hardening projects, including placement of seawalls, jetties, sandbags, and hardened structures, reduce coastal ecosystems, leading to the loss of coastal strand. These activities often result in sand compaction, erosion, and additional sedimentation in near-shore ecosystems, resulting in negative indirect effects to the ecological community and the ecosystem. Often, these increase erosion in adjacent areas and the potential for a cascading series of other beach stabilization projects (Fletcher, 2010; Coastal Geology Group, 2016).

When not managed, public access and recreation degrades or eliminates native communities. Vehicular access from tours, individual recreational access, and use of All Terrain Vehicles (ATV's) increases erosion and damages communities by crushing and breaking of native communities.

Ecosystem destruction and modification by urbanization and land use conversion lead to the direct fragmentation of coastal ecosystems and reduce native dominated coastal communities (Warshauer et al., 2009). Fragmentation decreases the total area of the ecosystem and native communities, reduces the diversity and composition of communities found in the ecosystem, and therefore reduces its resiliency (Figs. 9 and 10).

Biosecurity

Four agencies are responsible for inspection of goods arriving in Hawai'i. The Hawai'i Department of Agriculture (HDOA) inspects domestic cargo and vessels and focuses on pests of concern to Hawai'i, especially insects or plant diseases not yet known to be present in the State. The US Department of Homeland Security-Customs and Border Protection (CBP) is responsible for inspecting commercial, private, and military vessels and aircraft and related cargo and passengers arriving from foreign locations. They focus on a wide range of quarantine issues involving non-propagative plant materials (processed and unprocessed); wooden packing materials, timber, and products; internationally regulated commercial species under the Convention in International Trade in Endangered Species (CITES); federally listed noxious seeds and plants; soil; and pests of concern to the greater United States, such as

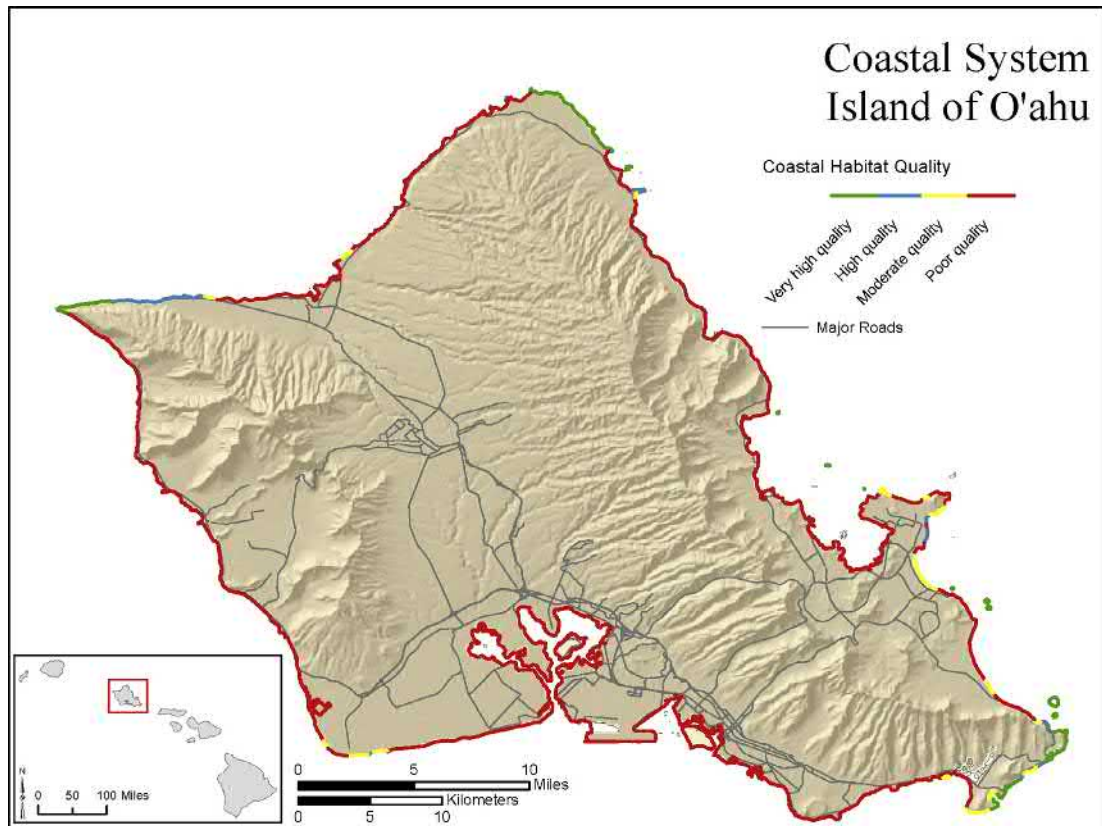


Fig. 6 Coastal ecosystem quality on the island of O'ahu. From Reeves MK and Amidon F (2018) *Habitat status assessment methods—Hawai'i, current condition summaries, August 2018. Technical Report from United States Fish and Wildlife Service*, 439 pp. Honolulu, HI: Pacific Islands Fish and Wildlife Office.

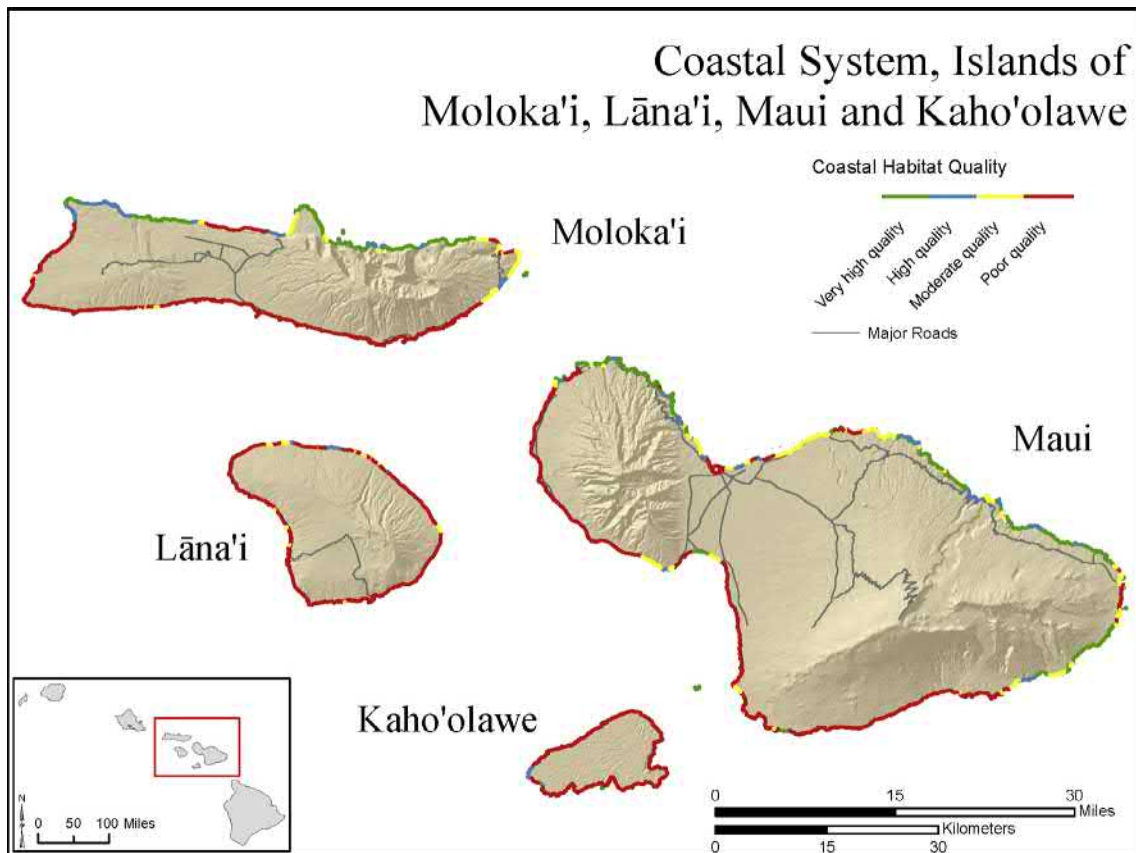


Fig. 7 Coastal ecosystem quality on the islands of Moloka'i, Lāna'i, Maui, and Kaho'olawe. From Reeves MK and Amidon F (2018) *Habitat status assessment methods—Hawai'i, current condition summaries, August 2018. Technical Report from United States Fish and Wildlife Service*, 439 pp. Honolulu, HI: Pacific Islands Fish and Wildlife Office.

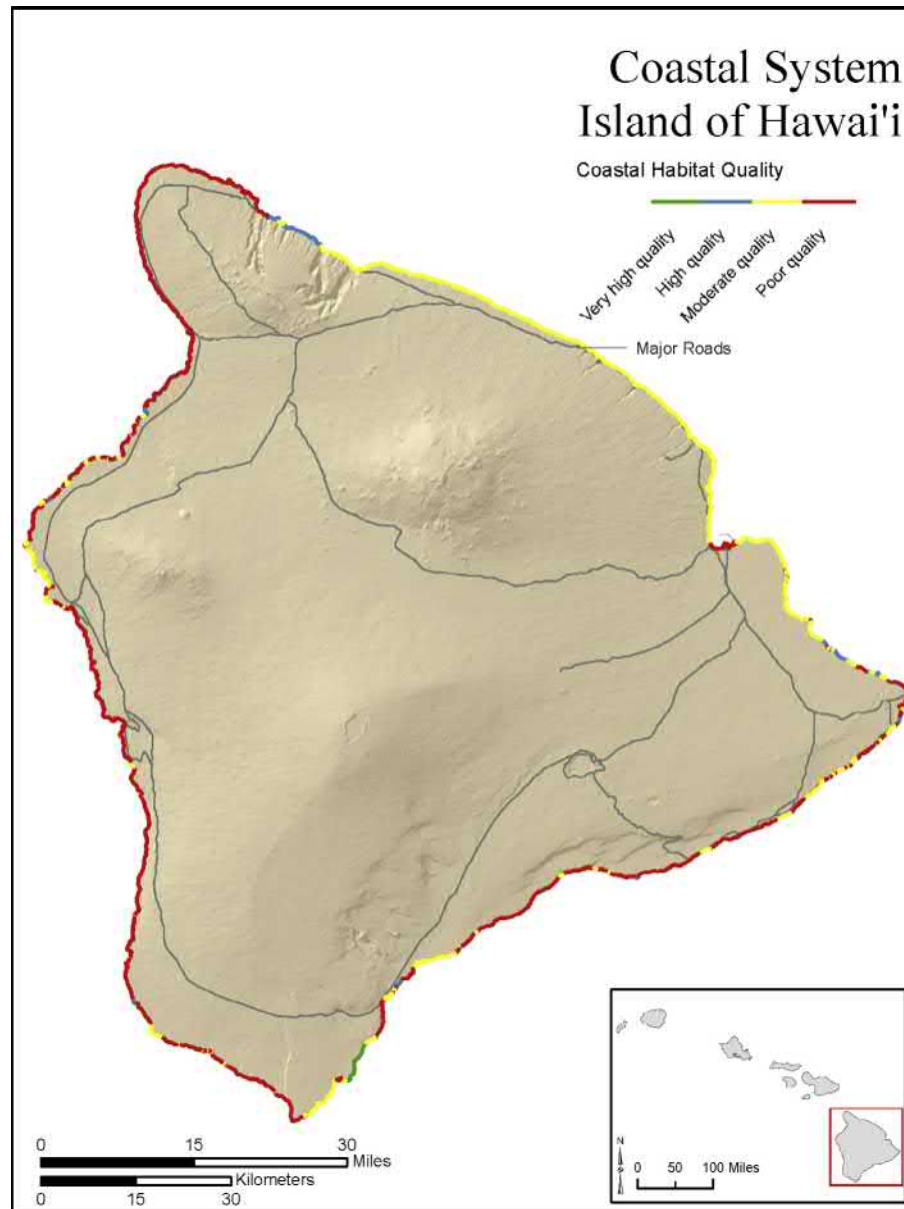


Fig. 8 Coastal ecosystem quality on the island of Hawai'i. From Reeves MK and Amidon F (2018) *Habitat status assessment methods—Hawai'i, current condition summaries*, August 2018. *Technical Report from United States Fish and Wildlife Service*, 439 pp. Honolulu, HI: Pacific Islands Fish and Wildlife Office.

pests of mainland US forests and agriculture. The US Department of Agriculture-Animal and Plant Health Inspection Service-Plant Protection and Quarantine (PPQ) inspects propagative plant material, provides identification services for arriving plants and pests, conducts pest risk assessments, trains CBP personnel, conducts permitting and preclearance inspections for products originating in foreign countries, and maintains a pest database that, again, has a focus on pests of wide concern across the United States. The USFWS inspects arriving wildlife products, enforces the injurious wildlife provisions of the Lacey Act (18 U.S.C. 42; 16 U.S.C. 3371 *et seq.*), and prosecutes CITES violations.

The State of Hawai'i's unique biosecurity needs are not recognized by Federal import regulations. Under the PPQ's commodity risk assessments for plant pests, regulations are based on species considered threats to the mainland United States and do not address many species that could be pests in Hawai'i. Interstate commerce provides the pathway for invasive species and commodities infested with non-federal quarantine pests to enter Hawai'i. Pests of quarantine concern for Hawai'i may be intercepted at ports in Hawai'i by Federal agents but are not always acted on by them because these pests are not regulated under Federal mandates. Hence, Federal protection against pest species of concern to Hawai'i has historically been inadequate. It is possible for the USDA to grant Hawai'i protective exemptions under the "Special Local Needs Rule," when clear and comprehensive arguments for both agricultural and conservation issues are provided; however, this exemption procedure operates on a case-by-case basis



Fig. 9 Public parking lot and road at Ka'ena Point Natural Area Reserve entrance.



Fig. 10 ATV and off road trails with nonnative species.

and is extremely time-consuming to satisfy. Therefore, that avenue may only provide minimal protection against the large diversity of foreign pests that threaten Hawai'i.

Adequate staffing, facilities, and equipment for Federal and State pest inspectors and identifiers in Hawai'i devoted to invasive species interdiction are critical biosecurity gaps. State laws have recently been passed that allow the HDOA to collect fees for quarantine inspection of freight entering Hawai'i (e.g., Act 36 (2011) H.R.S. 150A–5.3). Legislation enacted in 2011 (H.B. 1568) requires commercial harbors and airports in Hawai'i to provide biosecurity and to facilitate cargo inspections. As described above, the introduction of new pests to the State of Hawai'i is a significant risk to coastal ecosystems.

Invasive animals

Introduced animals have impacted coastal native vegetation and native fauna. Impacts to native species and ecosystems accelerated following the arrival of Captain James Cook in 1778. This expedition and subsequent explorers intentionally introduced European pigs, goats and other livestock for food sources for seagoing explorers (Tomich, 1986; Loope, 1998). The mild climate of the islands and lack of predators led to the successful establishment of large populations of ungulates.

In these systems, ungulates disturb the soil, destroying vegetative cover and native vegetation. They create open areas conducive to further invasion by invasive plants.

Dogs, cats, and mongoose also affect coastal ecosystems: dogs trample plants; mongoose opportunistically eat insect pollinators, fruits, and native plants; and cats spread the parasite, *Toxoplasma gondii*, in feces that affect 'iliholoakauaua.

Three species of introduced rats, Polynesian rat (*Rattus exulans*), black rat (*Rattus rattus*), and Norway rat (*Rattus norvegicus*), impact the coastal communities within the ecosystem. Omnivorous rats eat fleshy fruits, seeds, flowers, stems, leaves, and roots (Atkinson and Atkinson, 2000), strip bark and cut small branches (twig cutting) in search of moisture and nutrients, and seriously affect the vigor and regeneration of vegetation (Abe and Umeno, 2011; Nelson, 2012). In the Hawaiian Islands, rats may consume as much as 90% of seeds produced by some native plants, and in some cases prevent regeneration of species completely (Cuddihy and Stone, 1990). Hawaiian plants are particularly susceptible to rat predation because the successful reproduction is affected (Cuddihy and Stone, 1990). Given their impacts on native vegetation, rats have the potential to significantly alter coastal communities.

The introduced house mouse (*Mus musculus*) is most common in lowland ecosystems and abundant over a wide range of vegetation types (Cuddihy and Stone, 1990). Mice have been documented eating insects, grass seeds, fruits (Kami, 1966), and may disrupt plant pollination through destruction of larvae of pollinators (Cole et al., 2000; Cuddihy and Stone, 1990).

Invasive insects

Sometimes when invasive invertebrates feed on or defoliate native plants, the ranges of the native plants are reduced. For example, the erythrina gall wasp (*Quadrastichus erythrinae*) is an invasive invertebrate that impacts wiliwili trees (*Erythrina sandwicensis*). The gall wasp was first discovered on O'ahu in 2005 and subsequently spread to other main Hawaiian Islands (Heu et al., 2008). Like other gall-forming wasps, they insert eggs into young leaf and stem tissue. Larvae develop and eventually cut exit holes to emerge as adults. Heavily galled plants result in a loss of growth and vigor, while severe infestations lead to defoliation and death (Heu et al., 2008; Yang et al., 2004). As a destructive pest on native wiliwili trees, this wasp impacts coastal communities (by what? Please make this clear).

The black twig borer (*Xylosandrus compactus*), first discovered on O'ahu in 1961, has become widespread throughout the main Hawaiian Islands (Nelson and Davis, 1972). Black twig borers tunnel into woody twigs or branches to lay their eggs. This excavation and the introduction of pathogens damages the host. Severe infestation can kill host plants, including large trees (Tenbrink and Hara, 2007; Nelson and Davis, 1972). Black twig borers have also infested invasive understory shrub species (koa haole and Christmas berry (*Schinus terebinthifolia*)) (Nelson and Davis, 1972).

Naio thrips (*Klambothrips myopori*) was first detected on Hawai'i Island in 2008, attacking the native naio (HDLNR et al., 2013). Thrips feed on the host plant's foliage, resulting in leaf distortion and galls. Heavy infestations lead to leaf curling, dieback, defoliation, and mortality (HDLNR et al., 2013). These trips also impacts native insect herbivores and pollinators that rely on naio for food and/or habitat (HDLNR et al., 2013).

Invasive ants (Family Formicidae) including the big-headed ant (*Pheidole megacephala*), yellow crazy ant (*Anoplolepis gracilipes*), *Solenopsis papuana*, *S. geminata*, longhorn crazy ant (*Paratrechina longicornis*), *Tetramorium bicarinatum*, *T. simillimum*, bicolored trailing ant (*Monomorium floricola*), ghost ant (*Tapinoma melanocephalum*), *Cardiocondyla kagutsuchi*, *C. venustula*, and little red fire ants (*Solenopsis geminate*) compete with and displace native invertebrates for nectar food and nesting resources (Howarth, 1985; Hopper et al., 1996; Holway et al., 2002; Daly and Magnacca, 2003; Lach, 2008).

Gray bird grasshopper (*Schistocerca nitens*) has the potential to completely defoliate the native vegetation and has been documented on the island of Nihoa (Latchininsky, 2006, 2008; Plentovich et al., 2015). *S. nitens* feeds on broad-leaved plants and avoid grasses (Latchininsky, 2006; Plentovich et al., 2015). *S. nitens* outbreaks in 2002 and 2004 on the island of Nihoa posed a major threat to the vegetation (Gilmartin, 2005), especially to endangered plants (Plentovich et al., 2015).

Invasive plants

The historic flora consisted of approximately 1000 taxa, 89% of which were endemic. Over 800 plant taxa have been introduced, and nearly 100 of these are considered pests (Smith, 1985; Cuddihy and Stone, 1990; Gagné and Cuddihy, 1999). Some plants were brought for food or cultural reasons and are well established along coastlines (Cuddihy and Stone, 1990). Plantation owners and the territorial government of Hawai'i introduced nonnative trees for reforestation to protect water resources. Ranchers intentionally introduced pasture grasses and other nonnative plants for agriculture, and sometimes inadvertently introduced weeds. Other plants were brought for horticultural value (Scott et al., 1986; Cuddihy and Stone, 1990). Invasive plants compete for resources; modifying the availability of light; altering soil-water regimes; modifying nutrient cycling processes; altering fire characteristics of native ecosystems; lead to incursions of fire-tolerant nonnative plant species; and indirectly inhibit the growth requirement of native species (e.g., ironwood). Nonnative tree species constitute the greatest threat within coastal strand communities, especially if they can disperse readily and form dense thickets above native vegetation (Warshauer et al., 2009).

Fire

Although the number and size of wildfires have increased on the main Hawaiian Islands; their occurrences are unpredictable (Gima, 1998; County of Maui, 2009; Hamilton, 2009; Honolulu Advertiser, 2010; Pacific Disaster Center, 2011). Fires may create open ecosystems for invasive plants to exploit (D'Antonio and Vitousek, 1992). For example, Fountain grass (*Pennisetum setaceum*) is a fire-adapted nonnative plant that produces a high fuel load that increases fire intensity; the species regenerates quickly after

fire and establishes rapidly in burned areas (Fujioka and Fujii 1980 in Cuddihy and Stone, 1990; D'Antonio and Vitousek, 1992; Tunison et al., 2002).

Storms

Hurricanes exacerbate the impacts of other threats. By destroying native vegetation, hurricanes open tree canopy, modify the availability of light, and create disturbed areas conducive to invasion by invasive plants (Asner and Goldstein, 1997; Harrington et al., 1997). Major tsunamis occur worldwide about once every 10 years, on average, and almost 60% of those occur in the Pacific Ocean (Pacific Tsunami Warning Center, 2009). In 2011, a tsunami caused by an earthquake in Japan swept over Kuaihelani's Eastern Island and Hōlanikū's Green Island, where it inundated plants, spread plastic debris, as it traveled inland and had devastating effects to the native biota (Leary, 2011).

Flooding and erosion

In the open sea near Hawai'i, rainfall averages 630–760 mm per year, and some places may receive up to 15 times this amount, depending on topography (Wagner et al., 1999). Rain may fall at rates of 76 mm per hour and reach 1000 mm in 24 h, and the flash floods bring sediments down streams and narrow gulches; which may damage, destroy, or eliminate one or more isolated occurrences of native plants that persist in low numbers and limited geographic range due to invasive plants (Wagner et al., 1999). This compromises the redundancy and resilience of the ecosystem.

Sea level rise

According to the Intergovernmental Panel on Climate Change, the oceans are now absorbing more than 90% of the heat added to the Earth's climate ecosystem (Bindoff et al., 2013 and Rhein et al., 2013 as cited in Bindoff et al., 2019). Since 1961, this absorption has caused average global ocean temperatures to increase, seawater to expand, and sea-levels to rise. Melting ice-sheets, ice caps, and alpine glaciers also influence ocean levels. Analysis of the historical record indicates ocean surface temperature in Hawai'i has been increasing over the past century, and accelerated since the 1970s (Fletcher, 2010). Although coastal ecosystems will likely move inland as sea-level rises, low elevation islands are predicted to completely become affected by increased erosion and exposed to marine inundation (Fletcher, 2010).

Interactive conservation actions

Impacts from stressors are addressed through active management (e.g., predator and invasive species control, fencing, outplanting, etc.), land protections, laws and regulations, and education and outreach. These approaches are implemented by state and federal government agencies, private organizations, and non-government organizations (NGOs) (Table 4). Given that land ownership of this ecosystem is spread among these parties, partnerships are also formed to manage the ecosystem collectively. Many of the organizations and agencies that contribute to the protection and management of coastal areas are described in Table 4. The laws and regulations governing the work in Hawai'i may be found in Table 5.

Summary of Interactions

The two most significant stressors of coastal ecosystems are the conversion/fragmentation of land due to development pressure, and the ongoing impact of invasive species. The laws, regulations, land protection, and management actions are not currently enough to prevent the overall decline of native coastal ecosystems. The rate of native coastal ecosystem decline is associated with development pressure (e.g., O'ahu, Maui, Kaua'i, and Hawai'i). In these areas the fragmentation reduces resiliency, and the systems are unable to withstand normal stochastic events. Throughout coastal ecosystems, invasive animals and plants outcompete native species, resulting in invasive-dominated coastal communities.

Future Scenarios

Three conservation management parameters (CMPs) will drive the condition of coastal ecosystems into the future. These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are as follows:

- (1) *Conservation Values*: stakeholder involvement and public opinion determine the formulation, implementation and funding of natural resource conservation.
- (2) *Laws and Biosecurity*: national, state, county, and city regulations are the means by which natural resource conservation and biosecurity are implemented. (e.g., hunting regulations, Clean Water Act, Endangered Species Act, local laws, etc.).
- (3) *Development or Conservation Planning*: planning for development, protection, or both will result in losses or gains in natural resource conservation or biosecurity and implementation of these plans are key.

Table 4 Conservation efforts of multiple organizations and agencies.

<i>Protected area</i>	<i>Location information</i>	<i>Landowner/manager</i>	<i>Protected acreage (ac)</i>	<i>Conservation importance</i>
Hono O Nā Pali NAR:	Kaua'i	Hawai'i Department of Land and Natural Resources (DLNR)	These cliffs are dominated by common coastal plants such as kāwelu (<i>Eragrostis variabilis</i>), 'āhinahina (<i>Artemisia australis</i>), 'akoko, nehe, ko'oko'olau, 'ilima (<i>Sida fallax</i>), and akoko (<i>Chamaesyce celastroides</i>)	Lowland coastal systems containing steep cliffs characterized by plants found in drier areas
Ka'ena Point NAR	O'ahu	DLNR	A nesting area for the Laysan albatross and rest area for 'ilioholoholoikaua	Protection of coastal dry shrublands and rare coastal plants.
Oloku'i NAR	Moloka'i	DLNR	The reserve encompasses the mountain plateau to sea cliffs and is one of the very few areas undisturbed by feral ungulates	Protection of coastal dry grasslands
'Ahihi-Kina'u NAR	Maui	DLNR	The area contains examples of pioneer vegetation that serve as systems for rare plants, insects, and birds	Protection of coastal dry shrublands, coastal mesic communities
Manuka NAR	Hawai'i Island	DLNR	Unit extends from 600 ft. (183 m) in elevation down to the coastal boundary Low goat damage found in the coastal regions (State of Hawai'i 2018).	Protection of coastal dry shrubland ('ilima dominated) and lowland dry grasslands (pili)
Pu'u O Umi NAR	Hawai'i Island	DLNR		This reserve contains dry coastal sea cliffs, coastal dry shrublands and grasslands.
Haleakalā National Park, Kīpahulu District	Maui	National Park Service (NPS)	Located on the east side of Maui, the Kīpahulu District protects an intact ahupua'a (traditional native Hawaiian land division)	Protection of native coastal strand of hala and naupaka communities
Kalaupapa National Historical Park	Moloka'i	NPS	The park's boundary extends for a quarter mile offshore and includes 2000 acres of ocean, two small offshore islands, and wet shorelines. The offshore islands of 'Ōkala and Huelo support coastal mesic system for loulou and the endemic pua'ala (<i>Brighamia rockii</i>). On the ground management such as invasive plant control, fencing, and ungulate removal are conducted.	
The Ala Kahakai National Historic Trail, Kaloko-Honokōhau National Historical Park, Pu'ukoholā Heiau National Historic Site, Pu'uhonua o Hōnaunau National Historical Park,	Hawai'i	National Park Service (NPS)		Although the main purpose of these parks are cultural and public use, the coastal system management conservation actions exist to maintain the processes and native strand system that allow these areas to persist.
'Āpua Point, Keauhou, Halapē, and Ka'aha	Hawai'i	NPS	Coastal areas within the NPS's Hawai'i Volcanoes National Park that span approximately 20 miles across the coastline.	Contains dry coastal herblands, grasslands, and shrublands. Actions to conserve the coastal system in the park include endangered species monitoring and recovery, system restoration, nonnative plant and animal management, and fire ecology.

Table 4 Conservation efforts of multiple organizations and agencies.—cont'd

<i>Protected area</i>	<i>Location information</i>	<i>Landowner/manager</i>	<i>Protected acreage (ac)</i>	<i>Conservation importance</i>
Kiholo bay	Hawai'i	The Nature Conservancy (TNC) of Hawai'i	7 ac (3 ha)	Contains a vital interface between land and coastal waters, providing system for native flora and fauna.
Mo'omomi Preserve	Moloka'i	TNC managed in partnership with DLNR through the Natural Area Partnership Program.	Preserve is 921 acres (373 ha)	Sand dunes and beach system. Portions of the preserve dunes are lithified (sand dunes that become solidified) and are distinct in geological appearance and native strand.
Kamehame beach	Hawai'i	TNC	20 ac (8 ha)	Protection of nesting habitat for honu 'ea. System consists of naupaka with other coastal plants like 'aki'a, naio, and pā'u o Hi'iaka.
Akoakoa	Hawai'i	Kamehameha Schools	Three acre (1 ha)	Coastal bluff located along the Kohala; managed for ungulates and invasive plants; restoration of common native plants.
Koholālele	Hawai'i	Kamehameha Schools		Coastal bluff along Hāmākua coast; restoration of native, food, and canoe plants.
Kahanu Preserve	Maui	National Tropical Botanical Garden (NTBG)	122 ac (49 ha) unit	Contains the last remaining coastal wet forests in Hawai'i (dominated by hala trees); preserve is located in a key part of the larger coastal wet forest adjacent to Kahanu Garden and Pi'ilanihale Heiau.
Lāwai Kai	Kaua'i	NTBG	80 ac (32 ha)	The garden is situated next to Lāwa'i bay, important habitat for honu.
Coastal systems protected by conservation easements at Keopuka, South Kona, and Kaiholena, Kohala.	Hawai'i	Hawaiian Islands Land Trust (HILT)	More than 277.5 ac (112 ha)	These lands are conserved for shoreline and open space.
Conservation easement at Maka'ala, Hana; Hawea, Kapalua; and Papa'ula, Wailuku; Kipahulu; Kaulahao; and Hana Kakio II as well as fee ownership at the Waihe'e	Maui	HILT	More than 467.63 ac (189 ha)	For the protection of coastal dunes
Purchase of Honolulu/Lipoa	Maui	HILT	Over 244 ac (99 ha)	To preserve coastal system.
Coastal system protected by conservation easement at Pohaku Pili	Moloka'i	HILT	over 76 ac (31 ha)	To preserve coastal system.
Wainiha and Kahili Beach Preserves are owned by HILT	Kaua'i	HILT	Over 18 ac (7 ha)	Protection of coastal system
Conservation easement at Waikalua	Kaua'i	HILT	Over 18 ac (7 ha)	Protection of coastal system
Coastal system protected by the assistance of HILT at Kahili Beach and Hanalei/Black Pot Beach Park Expansion.	Kaua'i	HILT	Approximately 3.7 ac (1.5 ha)	Protection of coastal system
Assisted with the purchase and conservation of Awāwamalu (Ka 'Iwi Coast) and the North Shore.	O'ahu	HILT	Over 812 ac (329 ha)	Protection of coastal system

Table 5 Hawai'i laws and regulations related to conservation.

<i>Title</i>	<i>Year implemented</i>	<i>Authority</i>	<i>Intent/purpose</i>
Endangered Species Act	1973	Federal (USFWS and NMFS)	Protects critically imperiled species from extinction
50 CFR 16	1974	Federal	Implements the Lacey Act (18 USC 42), which prohibits importation of injurious species
Convention on International Trade in Endangered Species	1975	International	Ensures that international trade in specimens of wild animals and plants does not threaten the survival of the species in the wild
Executive Order 11987	1977	Federal	Charges Executive agencies with restricting the introduction of exotic species into the natural ecosystems on federal lands; and encourages States to do the same
Hawai'i Administrative Rules, Title 4, Subtitle 6, Chapters 68 and 70	1981	Hawai'i (Department of Agriculture)	Rules/amendments for noxious weeds, plant and non-domestic animal quarantine, plant import, and bromeliad import
Executive Order 13112	1999	Federal	Requires that a Council of Departments dealing with invasive species be created to prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause
HRS 194-2	2002	Hawai'i (Department of Land and Natural Resources)	Establishes Hawai'i Invasive Species Council (HISC)
Act 85	2003	Hawai'i (HISC)	Conveys statutory authority to HISC to continue to coordinate approaches among the various State and Federal initiatives for the prevention and control of invasive species
HRS Chapter 205A for Coastal Zone Management	2006	Hawai'i (DLNR)	To preserve, protect, and where possible, to restore the natural resources of the coastal zone of Hawai'i
Act 36 (2011) HRS 150A-5.3	2011	Hawai'i (DOA)	Imposes a fee for the inspection, quarantine, and eradication of invasive species contained in any freight brought into the State
HB 1568	2011	Hawai'i (DOA)	Requires commercial harbors and airports in Hawai'i to provide biosecurity and to facilitate cargo inspections
HRS 174C Hawai'i State Water Code	2013	Hawai'i (CWRM)	Establishes Commission on Water Resource Management and Water Resource Management Fund
Executive Order 13751	2016	Federal	To prevent the introduction of invasive species and provide for their control, and to minimize the economic, plant, animal, ecological, and human health impacts that invasive species cause (amends EO 13112)
7 CFR 360.200	2018	Federal	Designates certain plants as noxious weeds

The year 2035 is the extent of the “foreseeable future,” and is based on the projected divergence of IPCC Representative Concentration Pathway (RCP) climate change scenarios (van Vuuren et al., 2011a,b). The foreseeable future scenarios considered in this ecosystem assessment are explained below.

Future Scenario One

Scenario One is the status quo, and considered to be the most likely future scenario, and serves as a “baseline” for comparing the future scenarios. There is no change in the implementation of the three CMPs between 2018 and 2035. The current rate of change in land cover will continue through the foreseeable future. Human populations and residential, commercial, and agricultural land development will likely continue to expand, causing ecosystem stressors to continue to increase. It is also probable that Coastal Dry: Herblands, Grasslands, Shrublands, Mixed Communities; and Coastal Wet-Mesic Forests will continue to decline in extent, quality, and function. Native vegetation will continue to give way to an invasive dominated landscape. Resorts and residential communities along coastlines will expand. As development pressure continues, the remaining coastlines will become more fragmented and will be less resilient to stochastic events.

The conditions of each coastal sub-type will continue to slowly decline in Scenario One. Coastal areas will continue to decline in extent and function due to impacts from feral ungulates. High priority invasive weed species, such as koa haole and Christmas berry will expand along coastlines and form monotypic stands. Under a continuation of current bio-security laws, it is likely that new pathogens, diseases, and invasive plant and animal species will be introduced to coastal ecosystems. Erosion will increase, particularly along coastal bluffs, cliffs, and areas prone to strong wave energy. Drought and fire will marginalize the coastal strand. Sea level will rise approximately 1.5 mm per year or more (Coastal Geology Group, 2008) and low lying islands in the NWHI (Laysan, Lisianski, Pearl and Hermes, Midway, French Frigate Shoals, and Kure) will be vulnerable to wave-driven flooding or submersion.

Future Scenario Two

A slight increase in the CMPs marginally improves conservation management. Conservation Agencies and stakeholders work with increased but limited resources to slow or stop the degradation of landscape areas. Although the human population increases, development does not substantially increase. A slightly improved biosecurity effort reduces invasive species but some plant diseases but increases are still expected. The small increased support of natural resource management does not alter wildfire frequency or intensity much beyond Scenario One.

The CMP-supported conservation does not prevent, mitigate, or reverse the impacts of climate change-related stressors. Coastal Dry Herblands, Grasslands, and Shrublands, Mixed Communities, and Coastal Wet-Mesic Forests will continue to show a decline in extent, quality, and function. An increase in invasive plants and feral ungulates dominate the landscape. As development continues with the construction of resorts and residential communities, coastal ecosystems decrease in area. However, slight growth in natural resource conservation and biosecurity results in conservation easements. Agencies slightly increase management efforts by strategically fencing areas which protect bio-diversity in native coastal systems. Sea level rise impacts coastal zones as in Scenario One.

Future Scenario Three

There is a small to moderate decrease in conservation actions in the CMPs that relaxes biosecurity controls, resulting in reduced conservation efforts. An expanding human population requires increased land use for agriculture and development. Economic development outpaces conservation. Nonnative plants and recreation areas will expand. Feral ungulate populations will grow. Wildfire will increase. Coastal Dry Herblands, Grasslands, and Shrublands, Mixed Communities; and Coastal Wet-Mesic Forests will be severely reduced in extent, quality, and function. With extensive localized management, some native plant species may persist in park-like settings or in areas where land development is not possible. The value of current conservation easements and protected areas will diminish and sales of protected lands by private companies and NGO's could expand and facilitate development. As fragmentation increases in these coastal ecosystems, an invasive-dominated ecosystem will occur.

Future Scenario Four

There is a moderate to large increase in conservation actions in the CMPs that substantially improves conservation through a robust effort to engage stakeholders to identify and prioritize landscapes needed for conservation and restoration. The needs of an expanding human population are addressed through more efficient land use governance based on redevelopment rather than development of undeveloped areas. Modern and novel agricultural practices focus on those that do not affect existing natural areas or areas needed for native ecosystem restoration. Substantially improved biosecurity regulations decrease introductions of invasive species and plant diseases. These improved land management actions result in the decreased extent and frequency of wildfire. Climate change-related stressors continue but resiliency increases.

See also: Physical Geography of the Hawaiian Islands.

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Physical Geography of the Mariana Archipelago

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Published by Elsevier Inc.

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Abstract

The Mariana archipelago consists of an island arc formed as the Pacific plate converges with the Philippine plate in a subduction zone where the older, more dense Pacific plate sinks and moves underneath the Philippine plate creating the deepest location known on earth—the Marianas Trench. The islands in the north part of the arc are younger, active volcanoes, whereas the older islands in the south are volcanic remnants that have layers of limestone from a time when they were once below sea level. The Mariana archipelago has two distinct seasons, wet, and dry. The climate is mild; however, the archipelago is prone to typhoons. Because the Mariana archipelago has no elevation extremes, it does not host a wide variety of biomes. Here we focus on the physical features of the Mariana archipelago.

Geography

The Mariana archipelago consists of 15 main islands and various small islets spanning a north-south distance of 553 miles (mi) (890 kilometers (km)) in the western Pacific Ocean between latitudes 21° and 13°N and longitudes 144° and 146°E. The vast majority of the archipelago's land area is concentrated in the larger, southern main islands, including Saipan, Tinian, Rota, and Guam.

Geology

The islands within the Mariana archipelago vary in age between 5 million years in the north and 50 million years in the south. The archipelago was formed by the ongoing collision of the Pacific and Philippine tectonic plates at the Mariana Trench, which resulted in both uplifting and volcanic activity creating a chain of mountains protruding from the sea floor (Fig. 2) (Raulerson and Rinehart 1992, p. 3; Vigil and Tilling, 2006, entire). Primarily volcanic in origin, the northern portion of the archipelago (north of Farallon de Medinilla) includes both relatively active volcanic islands (Anatahan, Pagan, and Uracas) as well dormant volcanic islands (Agrihan, Alamagan, Asuncion, Guguan, Maug, and Sarigan). The geologically more complex, limestone and volcanic southern islands, including Aguiguan, Guam (with the adjacent Cocos Island), Rota, Saipan, and Tinian, have been historically and regularly

inhabited by humans. All of the other islands in the archipelago are currently uninhabited, although some, including Agrihan, Agui-guan, Alamagan, Anatahan, Pagan, and Sarigan have been historically inhabited by the Chamorro, and are still visited on occasion (Fig. 1).

Substratum

The complex substratum of the older southern islands is comprised of plateaus of ancient limestone seabed pushed up with the tectonic plate, rolling volcanic hills and mountains, and more relatively recent coral limestone formations (Ohba 1994, p. 14; Mueller-Dombois and Fosberg, 1998, p. 241; Carruth, 2003, p. 3; Gingerich, 2003, p. 1; Taborosi, 2004, pp. 8–13; Berger et al., 2005, p. 9). The younger northern islands, largely composed of black volcanic basalts, are typical cone-shaped stratovolcanoes (steep, many-layered volcanoes characterized by periodic, explosive eruptions) with steep slopes and often eroded with deep ravines (Ohba, 1994, p. 14; Mueller-Dombois and Fosberg, 1998, p. 241). As noted above, many of the northern islands (Anatahan, Pagan, and Uracas) remain volcanically active. Areas of exposed weathered volcanic substratum can be found on the southern islands, particularly in the middle of Saipan and on the southern half of Guam (Mueller-Dombois and Fosberg, 1998, p. 241). Extensive cave formations also occur within the karst topography of the southern islands of Saipan, Agui-guan, Rota, and Guam (Taborosi et al., 2003, pp. 1). Some northern islands also exhibit limited cave systems including lava tubes and related crevices.

Hydrology

The ultimate source of all freshwater in the Mariana archipelago is rainwater (Carruth, 2003, p. 2; Gingerich, 2003, p. 1; Falkland et al., 1991, p. 6). Some rainwater escapes to the atmosphere by evaporation and transpiration, some flows directly to the sea in streams, and some moves downward through the soil and rock to ground-water reservoirs and then into springs and seeps that discharge into streams or directly into the sea (Ward et al., 1965, p. H6). The occurrence of groundwater resources in small islands is a function of geomorphology, size, geology, and other factors. The larger the island, the more likely it will have a fresh

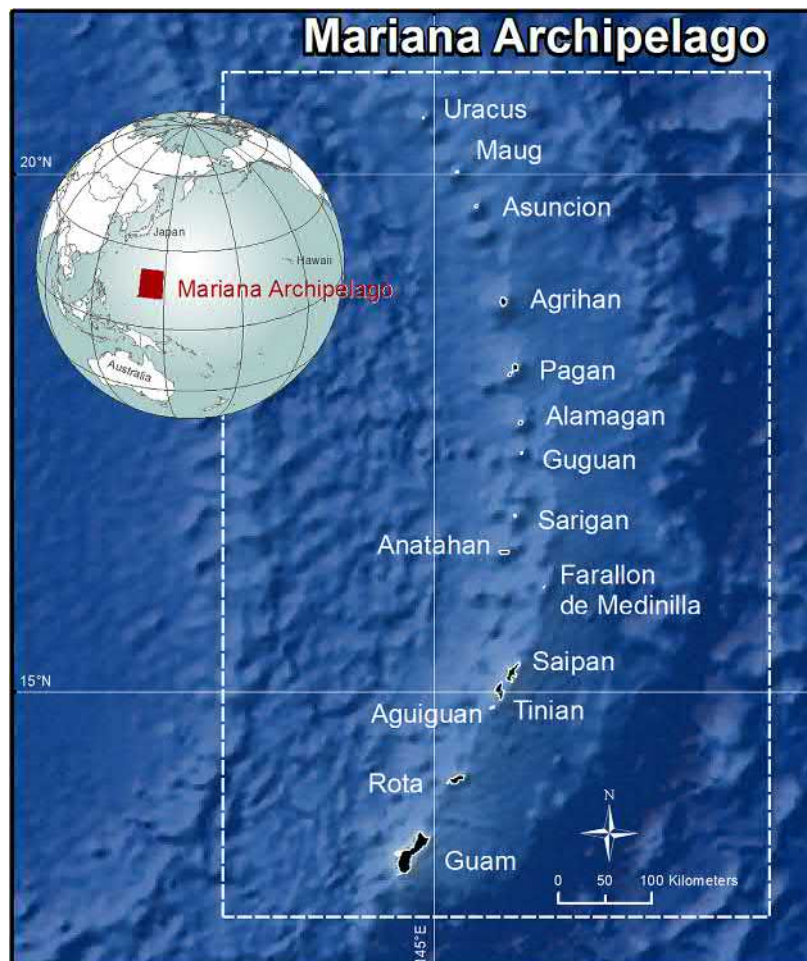
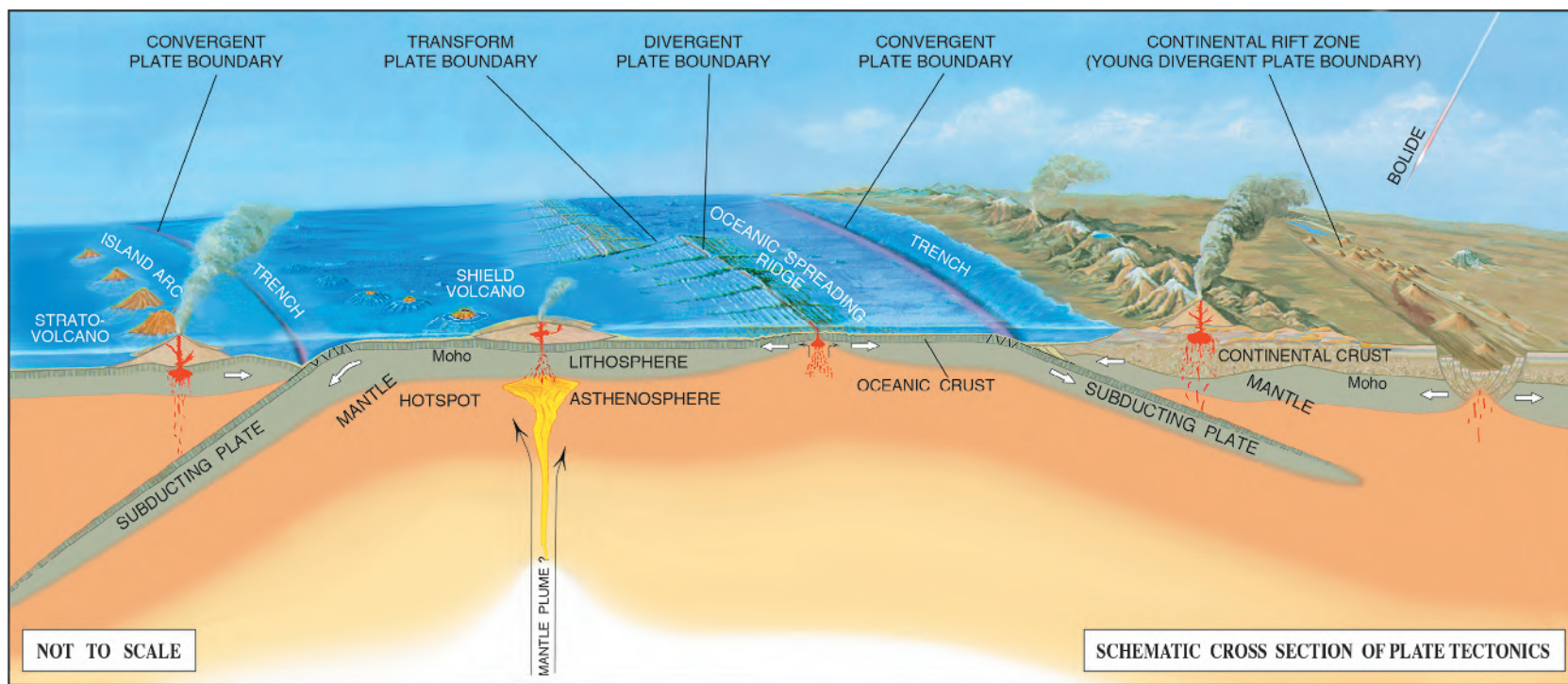


Fig. 1 Map of the Mariana archipelago. U.S. Fish and Wildlife, Pacific Islands Fish and Wildlife Office, U.S. Fish and Wildlife Service.



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Fig. 2 Formation of the Mariana archipelago. From Vigil, J.F. and R. Tilling. (2006). Schematic cross section of plate tectonics. In: Simkin, T., Tilling, R.I., Vogt, P.R., Kirby, S.H., Kimberly, P. and Stewart, D.B. (eds.). *This dynamic planet: World maps of volcanoes, earthquakes, impact craters, and plate tectonics. Geological investigations Map I-2800: the dynamic planet*. Image: U.S. Geological Survey.

groundwater body (Falkland et al., 1991, p. 41). Similarly, a more circular island will have more opportunity for developing groundwater than an elongated island of similar size (Falkland et al., 1991, p. 41). The flow in streams and the recharge and discharge of groundwater differ greatly with locality depending on the character of the rock (Ward et al., 1965, p. H6).

The highest volume of rainwater is captured on the older, southern islands, due to their abundance of limestone substratum which has much greater permeability than the predominant volcanic substratum of the northern islands. However, limestone varies in permeability due to geologic age, formation, and general character and distribution (Ward et al., 1965, p. H5; Carruth, 2003, p. 4). Due to its permeability, limestone substratum does not support surface water, whereas the less permeable volcanic substratum supports surface water (Falkland et al., 1991, p. 6). The permeable limestone allows rain to percolate into the ground instead of flowing on the surface (Taborosi, 2004, p. 15). Driven by gravity, the water moves underground through air-filled fractures, voids, and conduits, and enlarges and connects them by dissolution (Taborosi, 2004, p. 15). It reaches the groundwater level and a fresh groundwater body known as the freshwater lens is formed (Taborosi, 2004, p. 15) (Fig. 3). Groundwater discharge in volcanic terrane areas is mostly at seeps and springs dispersed along the streams (Ward et al., 1965, p. H6). Watersheds or drainage basins occur in such areas. As the rainfall decreases at the end of the wet season, streamflow on volcanic terrane recedes rapidly to the low flow maintained by the slow discharge of groundwater from the volcanic rock (Ward et al., 1965, p. H7). The absence of rainfall for only three or four weeks can cause a serious shortage in streamflow in some volcanic rock areas (Ward et al., 1965, p. H7). For example, there are no surface rivers on the northern part of Guam which is composed primarily of limestone, and numerous rivers and streams in the south due to its volcanic substratum. However, as with other small islands, river discharge rates in southern Guam fluctuate depending on rainfall volume and distribution over the year (Falkland et al., 1991, p. 7).

The freshwater lens floats on saltwater and is separated from the saltwater by a transition zone of brackish water. This freshwater lens sits just below the lowest water table (Gingerich, 2003, p. 2). The freshwater, brackish water, and saltwater are all part of the freshwater-lens system. Salinity in a freshwater-lens system is gradational, from an upper freshwater core through the underlying transition zone to saltwater. Minor perched systems can exist above the lowest water table. Groundwater flows from areas of high water level to areas of low water level, which in general, is from the interior of the island to the coast. A summary of the geological and hydrological features of the Mariana archipelago are provided in Table 1.

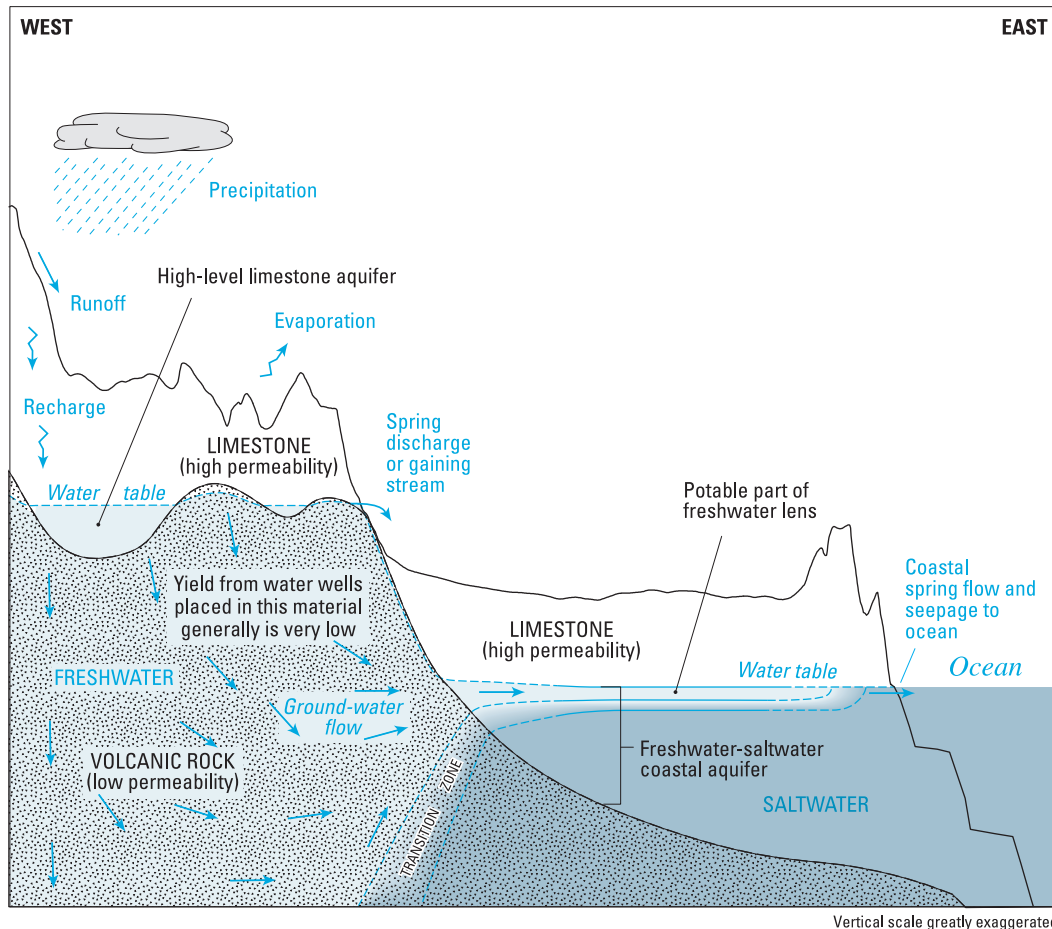


Fig. 3 Example of hydrologic cycle on the southern islands in the Mariana archipelago: rain water percolates through the limestone into a freshwater lens on eastern Saipan. From Carruth, R.L. (2003). Ground-water resources of Saipan, Commonwealth of the Northern Mariana Islands. U.S. Geological Survey Water-Resources Investigations Report 03-4178, p. 3, U.S. Geological Survey.

Table 1 Geological and hydrological summary of the Mariana archipelago.

Island (south to north)	Features and attributes				
	Emergent area mi^2 (km^2)	Highest elev. ft. (m)	Highest point	Volcanic activity	Surface water features
1 Guam	210 (540)	1334 (407)	Mount Lamlam	No	Streams, rivers, wetlands
2 Rota	33 (85.4)	1611 (491)	Mount Manira	No	Streams, wetlands
3 Aguiguan	2.74 (7.1)	515 (157)	Alutom	No	Seeps
4 Tinian	39 (101)	613 (187)	Mount Kastiyu	No	Wetland
5 Saipan	44.5 (115.38)	1555 (474)	Mount Tapochau	No	Streams, wetlands
6 FDM	0.33 (0.85)	266 (81)	NA	No	Ephemeral seeps
7 Anatahan	12 (31.2)	2582 (787)	NA	2008	Ephemeral streams, seeps
8 Sarigan	1.92 (4.97)	1801 (549)	NA	Holocene	Ephemeral streams, seeps
9 Guguan	1.5 (3.87)	988 (301)	NA	1883	Ephemeral streams, seeps
10 Alamagan	4.29 (11.11)	2441 (744)	Alamagan	870 CE	Ephemeral streams, seeps
11 Pagan	18.24 (47.24)	1900 (579)	Mount Pagan	2012	Lakes, ephemeral streams, seeps
12 Agrihan	16.8 (43.51)	3166 (965)	Mount Agrihan	1917	Ephemeral streams, seeps
13 Asuncion	2.82 (7.31)	2923 (891)	NA	1906	Ephemeral streams, seeps
14 Maug	0.82 (2.13)	745 (227)	North Island	$\geq 1500\text{s}$	Ephemeral seeps
15 Uracas	0.98 (2.5)	1047 (319)	NA	1967	Ephemeral seeps

Climate

The relatively low elevation (the highest point in the archipelago occurring on the island of Agrihan at 3166 ft. (965 m), juxtaposed with the close proximity to the equator and shallow seas to the west, insulate the Mariana archipelago from seasonal variation in weather creating one of the most stable climates in the world. According to the Koeppen Climate Classification, the entire archipelago is classified as Af, which refers to an equatorial or equatorial and fully humid climate, also sometimes referred to as tropical rainforest climate or tropical wet climate. Another key climate driver in the region is the pronounced annual monsoon season in the region which results in a distinct wet and dry season lasting 3–4 months each.

Temperature, Rainfall, and Monsoon Season

Despite a small number of weather stations in the Mariana archipelago, resulting in limited available meteorological data, the climate in the Mariana archipelago is uniquely stable, in particular with temperature as highs and lows range between 86°F and 73°F (30–22.8°C). However, due to the monsoon season in the western Pacific, the Mariana archipelago exhibits a notably wetter season from July through October, and a drier season from November through June, with April characteristically being the driest month of the year (Ohba, 1994, p. 16; Mueller-Dombois and Fosberg, 1998, p. 241) (Figs. 4 and 5).

Precipitation within the archipelago averages 96 in (218 cm) per year, dependent in part on elevation. Although none of the islands receive rainfall as a result of an orographic effect (mountains forcing moist air to rise and lose their moisture as rain), some of the tallest peaks experience more frequent cloud cover and slightly cooler temperatures. This is particularly true for the northern island summits of Anatahan, Alamagan, Pagan, and Sarigan (Dahl, 1980, pp. 22, 64; Ohba, 1994, pp. 18, 41, 48). The Mariana archipelago receives relatively constant trade winds most of the year, however during the summer months, storms and typhoons originating from the southeast and east occur frequently and typically pass by the archipelago on their journey to shallower seas to the east. An average of at least one typhoon per year impacts the Mariana archipelago (Mueller-Dombois and Fosberg, 1998, p. 241; Japan Meteorological Agency, 2019), and category 5 typhoons are not uncommon (Fig. 6).

Mariana Archipelago: Island Descriptions

Guam

Guam is located in the northwestern Pacific Ocean, 1200 mi (1930 km) east of the Philippines, 3500 mi (5632 km) west of the Hawaiian islands, and 54 mi (87 km) south of Rota. It is the largest and southernmost island of the Mariana archipelago with a land-mass of 216 mi^2 (mi^2) (560 square kilometers (km^2))—comparable in area to the Hawaiian island of Molokai. It is nearly 31 mi (50 km) long and from 4 to 9 mi (7–15 km) wide with a peak elevation of 1332 ft. (406 m) at Mt. Lamlam (Mueller-Dombois and Fosberg, 1998, p. 269).

The northern and southern regions of the island show marked contrast due to their geologic origin. The northern region is an extensive, upraised, terraced, limestone plateau or “mesa” between 300 and 600 ft. (90 and 180 m) above sea level interrupted by a few low hills, of which two (Mataguac and Mt. Santa Rosa) are volcanic in nature, while others are exclusively coralline limestone (e.g., Barrigada Hill and Ritidian Point) (Stone, 1970, p. 12). The southern region is primarily composed of volcanic mountains

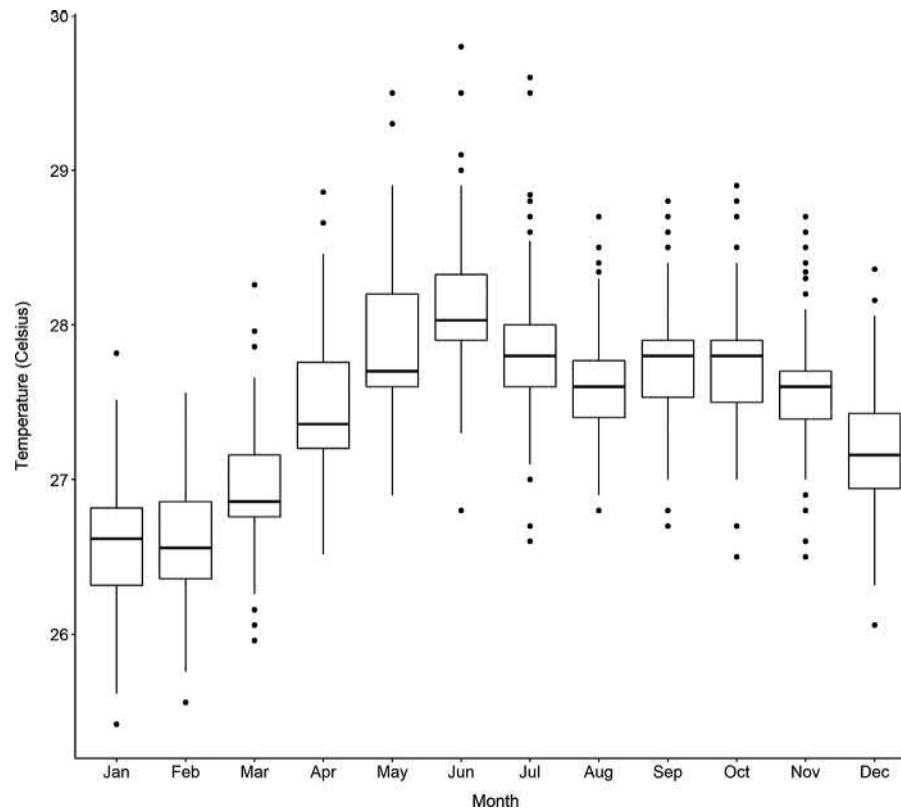


Fig. 4 Seasonal temperature in the Mariana archipelago. Data extracted from Harris, I., Jones, P. D., Osborn, T. J. and Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations—CRU TS3.10: The Climatic Research Unit (CRU) Time Series (TS) Version 3.10 Dataset. *International Journal of Climatology* **34** (3), 623–642, doi: 10.1002/joc3711; updated from previous version of CRU TS3.xx (most recent use in CCKP: TS3.24). U.S. Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office.

with several areas capped by a layer of limestone (Stone, 1970, p. 12). Within the Mariana archipelago, Guam contains the most extensive stream and drainage systems, particularly in the southern Talofofo Region (Stone, 1970, p. 13; Mueller-Dombois and Fosberg, 1998, p. 269). Fairly extensive wetland areas are found on the southern coasts as well and at Agana Swamp located in the middle of the island.

Rota

Located approximately 36 mi (58 km) northeast of Guam and 47 mi (76 km) southwest of Aguiguan, Rota is the fourth largest island in the Mariana archipelago, measuring 33 mi² (96 km²) (Mueller-Dombois and Fosberg, 1998, p. 265; CNMI-SWARS, 2010, p. 6). Rota consists primarily of terraced limestone surrounding a volcanic core that protrudes from the topmost plateau, known as Mount Sabana or Mount Manira, which is also the highest point on the island at 1611 ft. (491 m) (Mueller-Dombois and Fosberg, 1998, p. 265).

Aguiguan

Located approximately 47 mi (76 km) north of Rota and 7 mi (9 km) south of Tinian, Aguiguan is a small uninhabited island measuring 7 mi² (18 km²) with a peak elevation of 515 ft. (157 m) at Mt. Alutom (CNMI-SWARS, 2010, p. 6). Aguiguan is also known as “Goat Island” due to the presence of a fluctuating, but often large, feral goat population (Engbring et al., 1986, p. 8; Liske-Clark, 2015, p. 4–10). Geologically, Aguiguan is entirely limestone with very steep cliffs fringing most the island making access difficult (Engbring et al., 1986, p. 36). Hydrology on the island consists of a few freshwater seeps (Engbring et al., 1986, p. 8).

Tinian

Located approximately 7 mi (9 km) north of Aguiguan and 3 mi (5 km) southeast of Saipan, Tinian is the third largest island in the Mariana archipelago, measuring 40 mi² (101 km²) with a peak elevation of 613 ft. (187 m) at Mount Kastiyu (Engbring et al., 1986, p. 5). The geology is predominantly limestone with raised plateaus and ridges and low-lying plains (Stafford et al., 2005, p. 15; Engbring et al., 1986, p. 5). Tinian lacks streams but has two small wetland areas, Hagoi Marsh and Marpo Swamp (Engbring et al., 1986, p. 5).

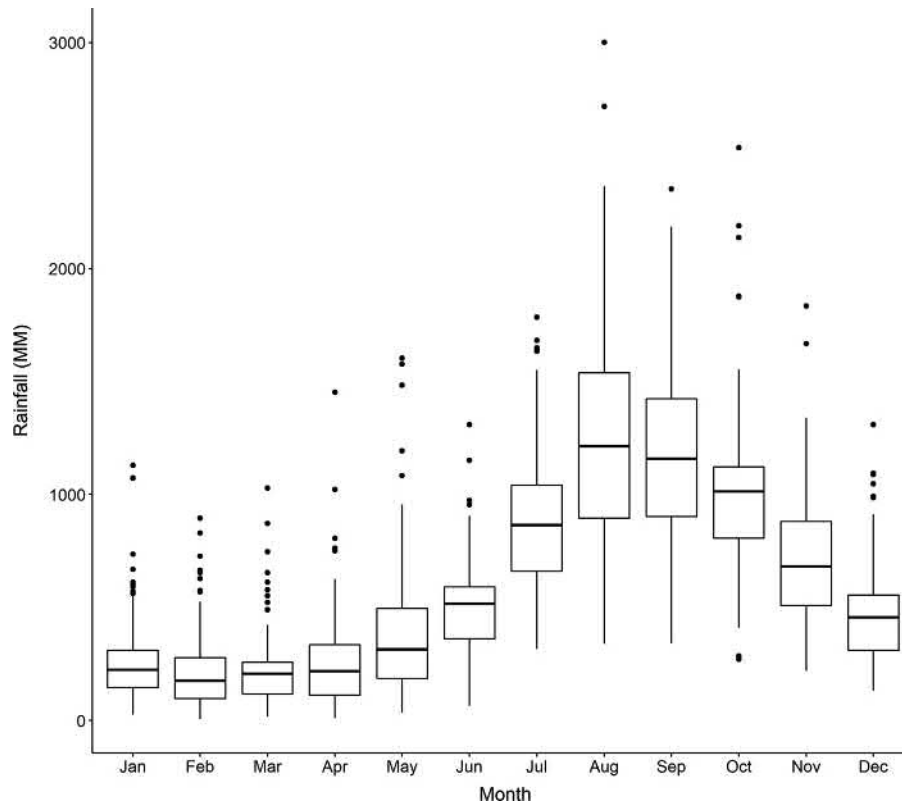


Fig. 5 Seasonal rainfall in the Mariana archipelago. Data extracted from Harris, I., Jones, P. D., Osborn, T. J. and Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations—CRU TS3.10: The Climatic Research Unit (CRU) Time Series (TS) Version 3.10 Dataset. *International Journal of Climatology* **34** (3), 623–642, doi: 10.1002/joc3711; updated from previous version of CRU TS3.xx (most recent use in CCKP: TS3.24). U.S. Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office.

Saipan

Located approximately 3 mi (4.5 km) northeast of Tinian and 52 mi (83 km) south of Farallon de Medinilla, Saipan is the second largest of the Mariana archipelago, measuring 44 mi² (115 km²) with a peak elevation of 1555 ft. (474 m) on Mt. Tapochau (Mueller-Dombois and Fosberg, 1998, p. 256). Geologically, the island is comprised primarily of terraced limestone peaks and intrusions of exposed volcanic ridges and slopes (Mueller-Dombois and Fosberg, 1998, p. 256). Small streams occur on the volcanic portions of the island as well as numerous wetlands of various size in the coastal areas.

Farallon de Medinilla

Located approximately 52 mi (83 km) northeast of Saipan and 33 mi (53 km) south of Anatahan, Farallon de Medinilla (FDM) is a small, uninhabited, limestone and volcanic island measuring less than 1 mi² (3 km²) with a peak elevation of 1047 ft. (319 m) (Lusk et al., 2000, pp. 1; CNMI-SWARS, 2010, p. 6). The island is mostly flat, but ringed by steep sea cliffs which make access by boat difficult. The island was used as a bombing target and a bomb disposal site for over three decades by the US Navy, and as a result, much of FDM is rocky and barren with the exception of some grass and shrubs. Hydrology on the island consists of ephemeral seeps.

Anatahan

Located approximately 33 mi (53 km) northwest of FDM and 23 mi (37 km) south of Sarigan, Anatahan is an active volcanic island measuring 12 mi² (31 km²) in land area with a peak elevation of 2582 ft. (788 m) (Mueller-Dombois and Fosberg, 1998, p. 252; CNMI-SWARS, 2010, p. 6). Notable physical features of Anatahan include two active volcanoes with an east to west trending summit depression formed by overlapping summit craters (Berger et al., 2005, p. 11). The largest caldera measures 1.5 by 2 mi (2 by 3 km) wide. Between 2003 and 2008, Anatahan erupted several times, with the largest eruption occurring in 2008, covering the island with at least 6 ft. (2 m) of volcanic ash and destroying an estimated 98% of its forest and savanna habitats (Berger et al., 2005, p. 11; Kessler, 2011, p. 321, 323). Hydrology on the island consists of ephemeral streams and seeps.

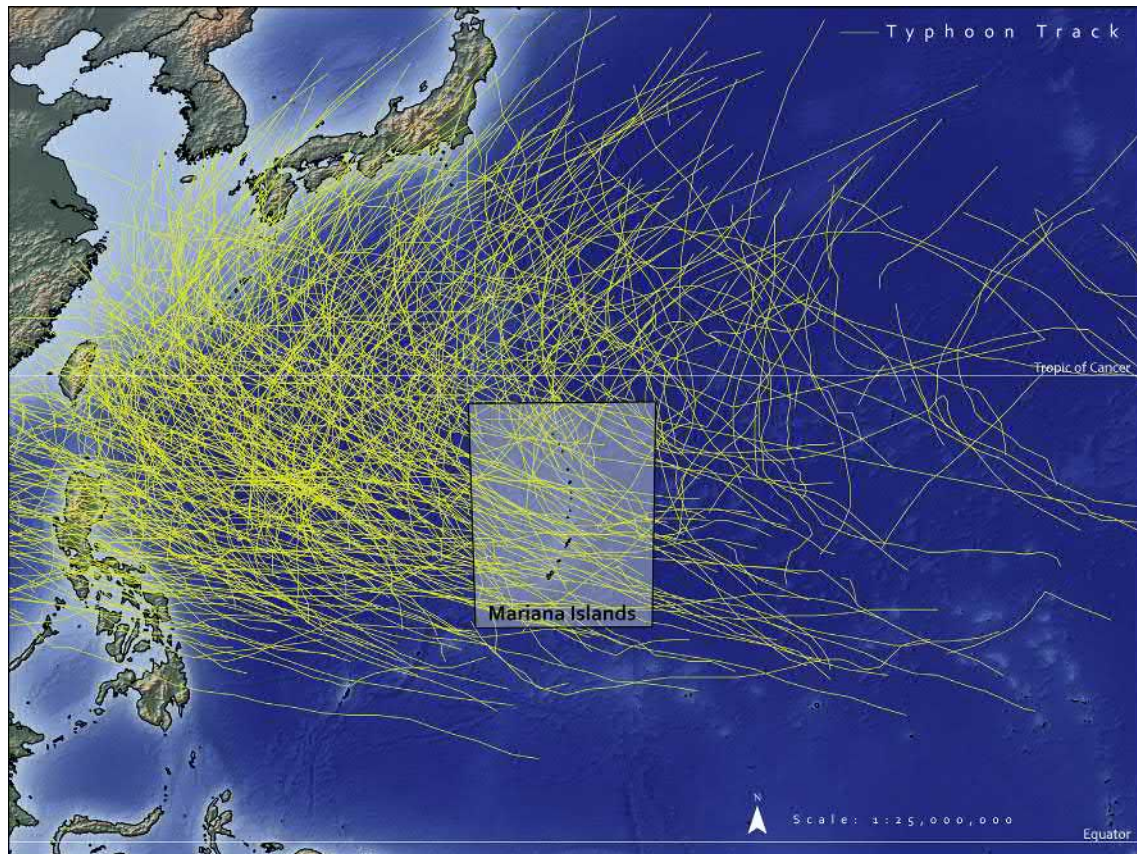


Fig. 6 Typhoon tracks passing near the Mariana archipelago since from 1901 through 2018. Data extracted from Japan Meteorological Agency, (2019). <https://www.jma.go.jp/jma/indexe.html>—U.S. Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office.

Sarigan

Located approximately 23 mi (37 km) northeast of Anatahan and 40 mi (64 km) south of Guguan, Sarigan is a roughly triangular-shaped, volcanic island measuring 2 mi² (5 km²) with a peak elevation of 1801 ft. (549 m) (CNMI-SWARS, 2010, p. 6). Sarigan consists of a low truncated volcanic cone with a 2460 ft. (750 m) wide summit crater containing a small ash cone. Other notable physical features of Sarigan include irregular shorelines with steep cliffs created by old lava flows (Berger et al., 2005, p. 12). Although currently uninhabited, the island is believed to have once been inhabited by the Chamorro people (Russell, 1998, p. 86). Hydrology on the island consists of ephemeral streams and seeps.

Guguan

Located approximately 19 mi (30 km) south of Alamagan and 40 mi (64 km) northeast of Sarigan, Guguan is an active volcanic island measuring a total of 2 mi² (4 km²) with a peak elevation of 988 ft. (301 m) (Ohba, 1994, p. 16). Its north side consists of an active volcano devoid of vegetation due to relatively recent activity and its south side consists of an older eroded volcano covered with dense native forest (Berger et al., 2005, p. 42; Amidon et al., 2011, p. 8). Other notable physical features of Guguan include steep cliffs along the shoreline and moist to wet ravines (Ohba, 1994, p. 16; Cruz et al., 2000, pp. 3–5, 9; Amidon et al., 2011, p. 8, 2017, pp. 20, 38). Hydrology on the island consists of ephemeral streams and seeps.

Alamagan

Located approximately 18 mi (29 km) north of Guguan and 30 mi (48 km) south of Pagan, Alamagan is an active volcanic island, measuring 4 mi² (11 km²) with a peak elevation of 2441 ft. (744 m) at Mt. Alamagan (Ohba, 1994, p. 16). Alamagan is the emergent summit of a large stratovolcano with a 1148 ft. (350 m) deep summit crater at the center of the island (Berger et al., 2005, p. 12). Most of the historically recent eruptions have been violently explosive (Berger et al., 2005, p. 12). Native forest occurs in mid-elevation ravines (Ohba, 1994, p. 16). Hydrology on the island consists of ephemeral streams and seeps.

Pagan

Located approximately 30 mi (48 km) north of Alamagan and 42 mi (68 km) south of Agrihan, Pagan is the fifth largest island in the Mariana archipelago and the largest of the northern islands with a total land area of 19 mi² (48 km²) (Ohba, 1994, p. 17). Pagan consists of four merged volcanoes, Mt. Pagan in the north, connected by a narrow isthmus to an unnamed complex of three older volcanoes in the south (Ohba, 1994, p. 17). The highest point on the island is Mt. Pagan, which rises 1870 ft. (570 m) above sea level. Mt. Pagan is among the most active volcanoes in the Mariana archipelago (Schils, 2010, p. 2). Mt. Pagan's last major eruption occurred in 1981 (Banks et al., 1981, p. 225); however, according to U.S. Geological Survey's Volcano Hazards Program, Mt. Pagan's most recent eruption occurred in 2012. Hydrology on the islands consists of two lakes on the flanks of Mt. Pagan and numerous ephemeral streams and seeps.

Agrihan

Located approximately 39 mi (63 km) north of Pagan and 64 mi (102 km) south of Asuncion, the island of Agrihan is an almost perfectly round, active volcanic cone (Ohba, 1994, p. 17) measuring 16.8 mi² (43.5 km²). With a peak elevation of 3166 ft. (965 m), it is the tallest island in the archipelago. Hydrology on the island consists of ephemeral streams and seeps.

Asuncion

Located approximately 62 mi (100 km) north of Agrihan and 23 mi (37 km) southeast of Maug, Asuncion is an active volcanic island measuring 3 mi² (7 km²) with a peak elevation of 2923 ft. (891 m) (Ohba, 1994, p. 18; Mueller-Dombois and Fosberg, 1998, p. 245). The long interval since Asuncion's last confirmed eruption in 1906, in conjunction with its high summit often enclosed by clouds, affords this cone-shaped island with densely forested slopes with diverse vegetation (Ohba, 1994, p. 18). Hydrology on the island consists of ephemeral streams and seeps.

Maug

Located approximately 24 mi (39 km) north of Asuncion and 43 mi (70 km) south of Uracas, Maug consists of three small volcanic islets, East Island, West Island, and North Island. The collective area of the three islets measures 0.8 mi² (2 km²) with a peak elevation of 745 ft. (227 m) on North Island (Ohba, 1994, p. 18; Mueller-Dombois and Fosberg, 1998, p. 244). The three islets are the emergent portions of a largely submerged volcano with a central lagoon (Ohba, 1994, p. 18; Mueller-Dombois and Fosberg, 1998, p. 244). Hydrology on these islets consists of ephemeral seeps.

Uracas

Located approximately 43 mi (70 km) south of Maug, Uracas (also known as Farallon de Pajaros), is the northernmost island of the Mariana archipelago. The island is an active volcano measuring 0.9 mi² (2 km²) with a peak elevation of 1180 ft. (334 m) (Ohba, 1994, p. 18). Hydrology on the island consists of ephemeral seeps.

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Coastal Strand and Mangrove Swamps of the Mariana Islands

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Published by Elsevier Inc.

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Abstract

This article represents a status assessment of the Mariana Islands coastal ecotype, including the status, stressors, and future viability. The coastal ecotype in the Mariana Islands is composed of two sub-types: coastal strand and mangrove swamps. Coastal strand is present on portions of the perimeter of all islands in the archipelago but is more extensive on the older and larger southern islands (i.e., Guam, Rota, Tinian and Saipan), while mangrove swamps are limited to Guam and Saipan. Coastal strand and mangrove swamps are generally limited to a narrow zone above high tide and below the line of influence of shoreline processes such as periodic salt-water inundation, eroding winds, salt spray, and groundwater influx. Invasive species degrade and fragment coastal areas and disrupt mutualistic relationships among biota. Sea level rise and increased storm frequency exacerbate this. Typhoons, drought, sedimentation, erosion and pollution also degrade coastal systems.

Introduction

The 15 main islands and associated small islets of the Mariana archipelago hereby referred to as Marianas, stretch north to south for 890 km in the western Pacific Ocean. The archipelago extends from Uracas (also known as Farallón de Pájaros) located at 20.5°N, 144.9°E south to the island of Guam located at 13.4°N, 144.8°E; all are of volcanic origin. The older and larger islands in the south are composed of elevated coral limestone and weathered basalt (Mueller-Dombois and Fosberg, 1998). The vast majority of the land area is concentrated in these large southern islands, specifically Guam, Rota, Tinian and Saipan. The younger islands to the north are composed of black basalts and some have active volcanoes (Ohba, 1994). The tropical climate has little temperature variation (e.g., monthly averages are 24 °C–27 °C) and distinct wet (July–October) and dry (November–June) seasons (Mueller-Dombois and Fosberg, 1998). Precipitation averages 2000–2500 mm/year (Mueller-Dombois and Fosberg, 1998). This document will describe the terrestrial coastal ecotype of the Marianas with a focus on factors that have influenced the systems in the past and what to expect in the future.

Geology

The Marianas are of volcanic origin but their geology varies based on the age of the island. The older and generally larger islands in the south, from Guam to Farallon de Medinilla, contain extensive areas of uplifted limestone and have a terraced appearance with large plateaus and steep cliffs (Mueller-Dombois and Fosberg, 1998). The limestone substrate weathered over time to produce

shallow, fertile soils that are high in calcium (Donnegan et al., 2011). The younger northern islands, from Anatahan to Uracas, are cone-shaped stratovolcanoes (i.e., steep, many-layered volcanoes characterized by periodic, explosive eruptions) comprised mostly of hardened lava, tephra, and volcanic ash (Mueller-Dombois and Fosberg, 1998; Ohba, 1994). Some of the islands remain volcanically active with periodic, explosive eruptions (e.g., Uracas in 1967; Pagan in 1981; Anatahan in 2003) (Venzke, 2013). Most beaches are made of calcareous sand, composed of pulverized fragments of the skeletons or shells of corals, calcareous algae, foraminifera, and mollusks (Mueller-Dombois and Fosberg, 1998). Volcanic sand exists near the young volcanoes of the northern islands and a few river mouths in southern Guam (Mueller-Dombois and Fosberg, 1998). The coastal ecotype is heavily influenced by movement of sediments such as sand and silt that are transported by waves and currents from the ocean, wind and rainfall, and rivers, which flush sediment from upland areas (Maanan and Robin, 2015). Therefore, fluctuations in sediment transport, especially those related to excess erosion and/or deposition can result in functional changes in coastal habitats, including changes in species composition and distribution (Levin et al., 2011).

Coastal Ecotype Description

The Mariana coastal ecotype generally is limited to a narrow zone above the high-tide level and below the line of influence of shoreline processes such as periodic salt-water inundation, eroding wind, salt spray and movement of groundwater (Falanruw et al., 1989; Mueller-Dombois and Fosberg, 1998). These processes sculpt the bare sand, muddy sand, rocks, bench platforms (narrow erosional platform cut into limestone or volcanic rock) and/or karst (landscape formed by the dissolution of soluble limestone rock) that make up the substrate in coastal areas. The coastal ecotype is present along portions of the coastlines of all islands and islets in the Marianas (Amidon et al., 2017; Ohba, 1994).

In the Marianas, two vegetation communities are present in the coastal system: coastal strand and mangrove swamp. The flora of both tends to be halophytic and plants often have fleshy leaves; an adaptation to reduce evaporation accelerated by the direct sunlight and/or strong winds present in this system (Fosberg, 1960). Although the coastal ecotype is present on all islands and islets in the Marianas, it is more extensive on the older and larger islands in the south (i.e., Guam, Rota, Saipan, and Tinian). Mangroves are only present on Guam and Saipan (Amidon et al., 2017). On the southern islands, all coastal habitat makes up no more than 2% of any island area (Amidon and Reeves, 2018). Sea level variation, typhoon frequency, and coastal disturbance by humans are drivers of the distribution of the coastal ecotype (Fosberg, 1960). Features within the ocean (e.g., coral reefs) bordering one side of this ecotype help protect from storm surge and other erosional forces (Fig. 1).

The coastal strand is a community of flowering plants, creeping vines and salt-tolerant grasses and is found above the high-tide line and sometimes between other inland ecotypes such as atoll and limestone forest (Falanruw et al., 1989). Coastal strand vegetation is adapted to well-drained soils and exposed shoreline conditions that include salt water and spray, strong winds, and direct sunlight, which increase evaporation rates (Fosberg, 1960). Coastal strand species are well adapted to maximize pollination services via insects. Seeds are light and buoyant to be easily dispersed by wind, ocean currents, or carried on the plumage or inside the gut of birds; contributing to wide distributions (Heatwole et al., 1981). This strategy also enhances the ability to recolonize suitable substrate after catastrophic or stochastic events (Table 1).

Mangrove swamps (mangroves) are limited to Guam and Saipan and found in estuarine-tidal flats and in coastal swamps at the mouths of small rivers (Moore et al., 1977; Stone, 1970). Mangroves provide sediment stabilization in estuaries, protection from storms, maintenance of water quality and spawning grounds and nutrients for a variety of fish and shellfish (Raulerson and



Fig. 1 Coastal strand vegetation at As Matmos Point, Rota dominated by the shrub *Scaevola taccada*. Photo: USFWS.

Table 1 Common plant species found in the coastal strand subtype of the coastal system in the Mariana archipelago (Stone, 1970; Raulerson and Rinehart, 1991; Asakura et al., 1994; Mueller-Dombois and Fosberg, 1998).

Species name	Chamorro or common name	Vegetation type
<i>Barringtonia asiatica</i>	Fishkill tree, putting, ghuul	Tree
<i>Bikkia tetrandra</i>	Torchwood, gausali	Shrub
<i>Casuarina equisetifolia</i>	Ironwood, gagu, gago	Tree
<i>Cassytha filiformis</i>	Love vine	Vine
<i>Cordia subcordata</i>	Niyoron, aliw	Tree
<i>Heliotropium foertherianum</i>	Velvet leaf, hunik, hunek, hunig, tchel	Tree
<i>Hibiscus tiliaceus</i>	Sea-hibiscus, corkwood, pago	Tree
<i>Hernandia nymphaeifolia</i>	Lantern tree	Tree
<i>Ipomoea pes-caprae</i>	Alaahi tasi, beach morning glory	Vine
<i>Lepturus repens</i>	Bunchgrass	Grass
<i>Mammea odorata</i>	Chapok, chopag	Tree
<i>Ochrosia mariannensis</i>	Lipstick tree, lengit	Tree
<i>Pandanus tectorius</i>	Kafu, fatsao	Tree
<i>Pemphis acidula</i>	Nigas, engi	Shrub
<i>Scaevola taccada</i>	Half flower, fan flower, nanaso, lanasa, liat	Small tree/shrub
<i>Sesuvium portulacastrum</i>	Chara	Herb
<i>Sporobolus virginicus</i>	Seashore rushgrass	Grass
<i>Thuarea involuta</i>	Las-aga, kuroiwa grass	Grass
<i>Thespesia populnea</i>	Rosewood	Small tree
<i>Vigna marina</i>	Beach pea	Vine

Table 2 Primary flora species found in the mangrove swamp subtype of the coastal system in the Mariana Islands archipelago (Stone, 1970; Falanruw et al., 1989).

Species name	Chamorro or common name	Vegetation type
<i>Acrostichum aureum</i>	Langayao	Fern
<i>Avicennia marina</i>	Gray mangrove, white mangrove	Tree
<i>Acrostichum aureum</i>	Mangrove fern, golden leather fern	Fern
<i>Barringtonia racemosa</i>	Langasát or langaasag	Tree
<i>Bruguiera gymnorrhiza</i>	Manglan lahi	Tree
<i>Heritiera littoralis</i>	Ufa-halomtano	Tree
<i>Hibiscus tiliaceus</i>	Sea hibiscus	Shrub
<i>Lumnitzera littorea</i>	Nana or red-flowered mangrove	Tree
<i>Nypa fruticans</i>	Nipa or mangrove palm	Tree
<i>Rhizophora apiculata</i>	Mangle hembra	Tree
<i>Rhizophora mucronata</i>	Red mangrove	Tree
<i>Rhizophora stylosa</i>	Stilted mangrove	Tree
<i>Xylocarpus granatum</i>	Mangrove cannonball	Tree
<i>Xylocarpus moluccensis</i>	Mangrove cannonball	Tree

Rinehart, 1991; Woodroffe, 1987; Selvam, 2007). In the Marianas, the mangrove swamp subtype has a fraction of species compared to mangroves elsewhere in the tropics (Fosberg, 1960); however, there is evidence that they are similarly productive as a function of detritus per unit area (Woodroffe, 1987). The seeds of the mangroves are torpedo-shaped propagules allowing them to either float to new habitat or establish in the water or mud beneath parent trees to create dense mangrove forests (Fosberg, 1960) (Table 2).

The viability of coastal strand and mangroves depends on maintaining multiple and distributed locations (redundant) of sufficient quality and size (resilient) with species richness and genetic diversity to be maintained across its ecological environment (representative) over time. The phrase “ecologically healthy” refers to functions affecting biodiversity, productivity, biochemical cycles, and evolutionary processes that are linked to the climatic and geologic conditions in the region (Borja et al., 2008). The ecologically healthy, or viable, coastal ecotype that existed throughout the Marianas prior to human contact likely maintained natural connections between system components. Native biota that was historically characteristic of Mariana coastal strand and mangroves filled environmental niches necessary to sustain the habitat (Fig. 2).

The coastal ecotype occurs in a narrow band around portions of islands. Although it was likely more abundant and diverse before human arrival and subsequent alteration and development of coastal areas, the coastal ecotype is still common and considered moderately redundant. The mangrove subtype has a more constricted range and only occurs on two islands in the archipelago (i.e., Guam and Saipan), thus this subtype has low redundancy.



Fig. 2 Example of a mangrove swamp with aerial roots visible at Cabras Marina, Guam. Photo: USFWS.

Resilience is defined as the amount of disturbance that the system can absorb without a change in structure and composition (Carpenter et al., 2001). Disturbance in coastal strand and mangrove habitats include natural forces such as typhoons and sea level change. Due to well drained soils in the coastal strand, salt water tolerance, and highly adapted flora and fauna (avian dispersal, floating seeds, and root systems) in coastal strand and mangroves, “healthy” coastal habitats have an increased capacity (high resiliency) to recover from natural stochastic events.

Representation relates to the variety of system types and variety of species within subtypes. The coastal strand subtype is relatively speciose and occurs on a wider range of islands within the archipelago compared to the mangrove subtype. The mangrove subtype’s restricted range means it is more poorly represented than coastal strand.

The primary driving factor for maintaining representation and redundancy for coastal strand and mangroves is related to dispersal and connectivity. Connectivity refers to the ability of plants and animals to move between habitat patches on the landscape (Tischendorf and Fahrig, 2000). Wind and water, specifically the ocean, is essential for dispersal to distant sites, though some propagules utilize birds for natural dispersal in aquatic systems. Seabirds and migratory birds which may consume or otherwise carry propagules, contribute to connectivity between coastal habitats at small to large scales (i.e., regional to inter-continental) while transiting between feeding, breeding, and non-breeding areas (Buelow and Sheaves, 2015).

Pre-Human Condition

Information about native vegetation in the Marianas prior to the arrival of humans is limited. Accurate descriptions of coastal vegetation communities during this period requires information from the fossil record and observations of the composition of relatively undisturbed, intact coastal systems. Prior to human colonization, the coastal system in the Marianas was present on every island in the archipelago (Fosberg, 1960; Ohba, 1994) and was heavily influenced by changes in sea level (Woodroffe, 1987). Pacific sea level declines during the late Holocene caused profound coastline changes. Around 3000–4000 years ago, the drop in sea level exposed extensive low tide platforms. Erosion, typhoons, and volcanic eruptions also influenced the physical coastline.

Prior to human colonization, coastal strand and mangrove swamps were more speciose overall and thus more resilient. The dominant species varied across the archipelago as dictated by geomorphology. Similar to today, mangrove swamps in the Marianas were less speciose relative to coastal strand (Fosberg, 1960). Thus, prior to human contact, the Marianas coastal ecotype was highly resilient and had medium (strand) and low (mangroves) levels of redundancy and representation (Table 3). As we see today, coastal

Table 3 Levels of resiliency, redundancy, and representation for coastal strand and mangrove swamp subtypes of the coastal ecotype that existed in the Mariana Island Archipelago prior to human contact.

<i>Habitat type</i>	<i>Resiliency</i>	<i>Redundancy</i>	<i>Representation</i>
Coastal strand	High	Medium	Medium
Mangroves	High	Low	Low

strand was diverse and widespread across the islands, and was better represented and had greater redundancy than the mangrove subtype, which had lower species diversity and was limited in distribution to Guam and Saipan (Fosberg, 1960; Falanruw et al., 1989).

Current Condition

Rapid human settlement of the central Pacific including the Marianas 2500–3500 years ago (Nunn, 1990) caused widespread alteration of coastal areas (Athens and Ward, 2004). The development of coastal plains as sea level fell since the last interglacial period may have made coastlines more attractive for human settlers. The human occupation of the Marianas resulted in coastal land use, development and accidental or intentional introduction of invasive species, which altered much of the vegetation across the islands so drastically that pristine habitats are rare (Spoehr, 1957; Athens and Ward, 2004). Over time, the distribution and species composition of coastal strand and mangroves changed substantially to include a variety of introduced biota that are capable of affecting species distribution, diversity and abundance (Reddy, 2011). Invasive plants [e.g., *Cuscuta campestris* (dodder) and *Antigonon leptopus* (chain of love)] and animals [e.g., feral ungulates, *Rattus* spp., invasive ants (Family Formicidae)] are present in coastal areas and can have profound effects on ecosystems (Table 4) (Kessler, 2011; Raulerson and Rinehart, 1991; Wiewel et al., 2009).

Some of the more dominant coastal strand species today include: *Pemphis acidula* (often pitted in limestone of windward coasts), *Heliotropium foertherianum* and *Casuarina equisetifolia*, which are found in loamy areas; and *Scaevola taccada* and *Ipomoea pes-caprae* which are found on sandy beaches (Table 1). Coconut palms (*Cocos nucifera*) were present in sediment cores over 4000 years ago prior to human colonization so are native to the Marianas (Athens and Ward, 2004). Coconut palms have gradually become more common as they were planted widely and many islands now contain nearly monotypic stands (Asakura et al., 1994). In many areas, native species still dominate coastal strand, primarily because the abiotic conditions (i.e., salt spray and inundation, wind and sun exposure) are harsh and limit colonization by other species.

In southern Guam, there was likely an increase of mangrove vegetation within the last 1000 years based on pollen cores in the area (Amesbury, 1999). Currently the largest concentrations exist along the eastern shores of Apra Harbor and smaller areas in Merizo and Inarajan. Guam's mangroves are dominated by *Rhizophora apiculata* but are composed of a variety of species that existed

Table 4 Primary invasive species in the Marianas coastal habitats.

Common name	Scientific name	Primary species affected	How invasive affects the ecotype	Where present	References
Ants	<i>Anoplolepis gracilipes</i> , <i>Wasmannia auropunctata</i>	Prey on native fauna, affect plant distribution via mutualisms and direct seed predation	Changes in distribution, abundance and diversity of biota	Pagan, Guam	Plentovich et al. (2018), Raymundo and Miller (2012), and Wetterer and Porter (2003)
Brown tree snake (BTS)	<i>Boiga irregularis</i>	Prey on fauna including birds and reptiles	Absence of bird dispersers, so reduced vegetation dispersal and reduced germination success	Guam	Savidge (1987) and Rodda and Savidge (2007)
Coconut rhinoceros beetle (CRB)	<i>Oryctes thinocerosrhinoveros</i>	Coconut palms	Loss of vegetation	Guam Rota	CNAS (2016) and Marshall and Moore (2016)
Vines (Ivy Gourd, Bitter Melon, Mile-a-Minute, Mikania, Woodrose, Chain of Love)	<i>Coccinia grandis</i> , <i>Momordica charantia</i> , <i>Mikania scandens</i> , <i>Mikania micrantha</i> , <i>Merremia tuberosa</i> , <i>Antigonon leptopus</i>	Native vegetation	Aggressively block sunlight and compete for water with native plants, smothering them altogether	Saipan, Tinian, Guam	PIER (2018)
Ungulates (goats, pigs, deer)	<i>Capra hircus</i> , <i>Sus scrofa</i> , <i>Rusa marianna</i>	Native vegetation	Dig up soils, facilitating erosion and sedimentation input, prevent survival of seedlings, consume or otherwise destroy natural resources	Guam, Aguiguan, Tinian, Rota, Anatahan, Pagan, Agrigan	Kessler (2011), Liske-Clark (2015) and Rubinoff and Holland (2018)
Rodents	<i>Mus musculus</i> , <i>Rattus</i> . Cf. <i>diardii</i> , <i>R. exulens</i> , <i>R. norvegicus</i> , <i>R. rattus</i> , <i>Suncus murinus</i>	Native biota; prey on native and nonnative biota, including birds and plant	Depredate and compete with native fauna, impede plant survival by eating seeds	All Islands	Steadman (1999), Liske-Clark (2015) and Wiewel et al. (2009)

historically. *Rhizophora* no longer occurs on Saipan; instead it has been replaced by another species in the Rhizophoraceae, *Bruguiera gymnorrhiza* (Moore et al., 1977). *Heritiera littoralis* and *Xylocarpus moluccensis* are also common in Saipan's mangroves (Falanruw et al., 1989).

Currently, coastal habitat makes up less than 2% of any island within the Marianas (Amidon and Reeves, 2018). Coastal areas were mapped on the larger, older southern islands where it composes 953 acres on Guam, 373 acres on Rota, 468 acres on Saipan, and 636 on Tinian. Coastal areas are not mapped on most of the northern islands. Of the 373 acres of coastal habitat on Guam, mangrove swamps account for 182 acres. Of the 468 acres of coastal habitat on Saipan, mangroves only account for 2 acres that occur near the American Memorial Park. The stressors below affect the ecotypes resilience, redundancy and representation.

Stressors

Climate Change

Predicted climate changes such as increased precipitation, sea level rise, and increased typhoon intensity will have significant effects on coastal systems in the Marianas. Global temperatures have increased over the past century and the rate accelerated in the mid-20th century (Pachauri et al., 2014). These increased temperatures correlate with carbon dioxide emissions, which have increased more since 1970 than in prior periods (Pachauri et al., 2014). The oceans are absorbing more than 80% of the heat added to the Earth's climate system (Griggs and Noguer, 2002) causing average global ocean temperatures to increase and thermal expansion of the sea. Thermal expansion combined with melting ice (e.g., alpine glaciers, ice-sheets and ice caps) will result in global sea level changes. Some coastal systems may be able to migrate inland as sea level rises if there is time and space; however, this may not be possible where heavy coastline development exists. Typhoons cause significant disturbance in these areas and increased intensity and frequency will reduce recovery time and will likely have significant negative effects on these systems in the foreseeable future.

Development

Economic development has and continues to affect the coastal ecotype in the Marianas. Coastal development includes the construction of buildings [e.g., hotels, residential homes, and facilities associated with providing necessities (e.g., fresh water, sewage treatment, etc.) to these buildings], marine structures (e.g., bulkheads, seawalls, breakwaters, jetties, and piers), recreational sites (e.g., parks, lookouts, harbors, etc.), and sand hardening that has occurred as a result of development. These structures can alter the substrate, hydrology, and resources required by native coastal communities (Agardy and Alder, 2005). Additionally, development of coastal areas increases the potential for invasion by nonnative species (see section **Invasive Species** below). For example, many invasive species such as invasive ants and brown tree snake can be transported in building materials, equipment, and soil (Hulme, 2009). Coastal development contributes to fragmentation of naturally occurring communities. The fragmentation of ecotypes decreases the total area and reduces the abundance, diversity and composition of communities found in the system, thereby reducing the system's resiliency, or ability to withstand stochastic events including typhoons and storm surge.

Development across the Marianas is correlated with population size. Guam and Saipan are the most populous and developed islands and therefore face the largest threat from development in the foreseeable future (Fig. 3). Coastal habitat on other islands,



Fig. 3 Coastal development along the western coast of Saipan near the town of Garapan. Photo: R. Walker.

including Tinian and Rota also experienced a decrease in total area due to development projects such as casinos and/or upscale hotels and military training facilities (Pacific Engineering Group, and Services, and Chris Hart, and Partners, Inc., 2018). World War II caused substantial impacts to natural resources of the Marianas. Post World War II, there was a large increase in development, including rebuilding Apra Harbor in Guam. Military operations and bases have continued to expand since that time and include the use of one of the northern islands, Farallon de Medinilla, for training exercises (Guampedia, 2018).

Tourism also contributes to development and thus a loss of coastal systems. In 2003, Guam and the Commonwealth of the Northern Mariana Islands (CNMI) were identified as two of thirteen most developed small island international destinations characterized by visitor density (McElroy, 2003). The inhospitable coastal geomorphology and topography naturally limit development in some areas.

Invasive Species

Oceanic islands such as the Marianas are known to be especially vulnerable to species introductions, which have caused significant, detrimental effects in coastal systems (Table 4) (Vitousek, 1988). Invasive generalist predators such as rats and invasive ants cause cascading effects in ecosystems (O'Dowd et al., 2003; Wiewel et al., 2009). Rats (*Rattus* sp.), which are not native to the Marianas, have detrimental effects in coastal systems by directly (e.g., eating plant seeds and flowers) and indirectly (e.g., reducing populations of other seed predators and dispersers such as birds and invertebrates) altering the distribution, diversity and abundance of plants (Rankin et al., 2018; Steadman, 1999; Wiewel et al., 2009). Currently three or more rat species are present in the archipelago (Wiewel et al., 2009). Invasive ants are another generalist predator that threatens coastal systems by displacing native invertebrates and vertebrates via predation and/or competition (O'Dowd et al., 2003; Plentovich et al., 2018; Wetterer and Porter, 2003). Additionally, ants farm sap-sucking insects (e.g., scales and aphids), which can cause defoliation of plant species. Little fire ant is currently only present on Guam, but its small size allows it to spread easily in soils, especially those in potted plants (Raymundo and Miller, 2012). The yellow crazy ant is present on Pagan and is spread primarily in cargo and soils. Little fire ant and yellow crazy ants pose significant risks to biodiversity in coastal areas in the Marianas.

In addition to the species above, the brown tree snake, other invasive invertebrates (e.g., coconut rhinoceros beetle), feral ungulates, and a variety of invasive plants cause significant and catastrophic degradation in coastal systems (Table 4). Biosecurity measures and monitoring are not adequate to prevent spread, or to determine the true extent of invasive species at this time. In addition, other invasive species are likely present but their presence and effects have not yet been determined.

Pollution

Various pollutants including oils, untreated sewage, human-generated trash, Polychlorinated biphenyls (PCBs), heavy metals, plastic marine debris and sediments negatively affect coastal systems in the Marianas, especially the populated southern islands. Oil from spills, run-off, and land-based waste adversely affects aquatic organisms at all trophic levels including primary producers, echinoderms, mollusks and seabirds (Li et al., 2016). Sewage run-off is a significant problem in the southern islands where there is a link between sewage-derived nitrogen pollution and coral disease severity (Redding et al., 2013). PCBs and heavy metals are present in harbor sediments and marine organisms on Guam and interfere with normal development and behavior (Denton et al., 2005, 2006). Marine debris including discarded fishing gear and plastics is widespread in the Marianas and has negative effects on coastal systems. Plastics form a thin layer on shells, sand and other debris and sink in water resulting in the inability to transfer nutrients and gases between water and sediments. Fauna using coastal systems, like sea turtles and seabirds, can become entangled in and ingest plastic and other debris causing harm and sometimes death (Wilcox et al., 2015).

Sedimentation/Erosion

Excess sediment deposition and erosion can change native plant and animal communities by destabilizing substrates, damaging or destroying individual plants, and altering hydrological patterns. In Guam, limited vegetation due to wildfires results in an increase in erosion and sedimentation, negatively affecting downstream areas and coral reefs (Golabi et al., 2005). These coral reefs provide coastal protection by dissipating wave energy, which could damage coastal areas (Pickard et al., 1990). Excess sediment from fires, vegetation clearing, and erosion upland of the coast overload coastal vegetation and fill stream estuaries where mangroves may be growing (Golabi et al., 2005).

Typhoons

The Marianas lie in a typhoon belt and regularly experience typhoons. Typhoons cause variety of impacts to vegetation including pruned or downed vegetation from intense wind, defoliation and damage from wind, heavy rain and salt spray, and mortality by salt-water inundation in low-lying areas (Fosberg, 1960; Kerr, 2000).

The stressors described above decrease ecotype range and diversity, and increase fragmentation relative to its prehuman condition. Climate change, development, erosion, and increased typhoon frequency contributed to permanent losses of native coastal communities and increased fragmentation, which has reduced resilience and redundancy of both the coastal strand and mangrove subtypes. Loss of mutualistic relationships and declines and/or extirpations of native species associated with species introductions

reduced species diversity and therefore representation in both subtypes. This will be exacerbated as the system degrades and becomes more and more vulnerable to species introduction. Species declines, permanent loss of habitat due to development and climate change, and the break-down of mutualistic relationships means the coastal system may not be able to recover and future restoration options are limited. Decreases in resiliency, representation, and redundancy translate into a loss of viability for the coastal ecotype.

Conservation Opportunities

Impacts from stressors may be addressed through laws and regulations, land protections, education, outreach, and/or various management approaches such as on-the-ground management (e.g., predator and invasive species control). These approaches are implemented by government agencies (territory, commonwealth and federal), private organizations or individuals, and non-governmental organizations. Given that land ownership of this system is spread among these parties, partnerships are sometimes formed to manage the system collectively. The following conservation efforts provide direct and indirect benefits to the coastal habitat as well as other habitats and ecosystems.

Guam Coastal and Estuarine Land Conservation Program Plan

A draft 2008 Guam Coastal and Estuarine Land Conservation Program Plan was written with the intention to protect important coastal and estuarine areas that have significant conservation and ecological values with consideration given to the degree of threat of loss, ecological significance and potential for effective management ([Guam Coastal Management Program, 2008](#)).

Cleanup Activities

Cleanup activities are limited to the Guam, Rota, Saipan and Tinian and are typically volunteer based. Both Guam and the CNMI participate in the annual Ocean Conservancy's annual beach clean-up in September. Volunteers collect garbage off beaches, strand, and other coastal areas. In 2014, the CNMI event had nearly 1400 volunteers collect over 19,600 pounds of trash. These efforts engage the public to care about local resources and improve the health of the coastal habitat ([Micronesia Challenge, 2018](#)).

The Guam National Wildlife Refuge hosts a beach clean-up on the first Saturday of each month to remove debris from the Refuge's coastline. In fiscal year 2017, over 195 volunteers removed 1304 pounds of trash from the beaches ([United States Fish and Wildlife Service, 2018](#)). The National Park Service hosts beach clean-ups on the second Saturday of each month at both its Guam and Saipan locations (<https://www.nps.gov>).

Erosion Control

Efforts to combat erosion have increased recently as a way to protect coral reefs and may indirectly improve the coastal habitat. Public education campaigns have periodically been enacted to educate outdoor enthusiasts of how their activities affect habitat. National Oceanic and Atmospheric Administration (NOAA) Coastal Management Program has committed resources to the conservation of Guam's Manell-Geus Habitat Focus Area by replanting upland areas and restoring native vegetation to the lower riverine areas. By focusing on stopping erosion in savanna areas, NOAA hopes to improve the health of the coastal habitat and ocean waters downstream. Long-term plans include establishment of a monitoring plan to detect changes in the health of the mangrove forests in this area ([National Oceanic and Atmospheric Administration \(NOAA\), 2014](#)).

On Saipan, the Laolao Bay watershed is being improved by revegetating badlands damaged by fire and illegal land clearings as well as conducting grassroots education campaigns. The intent is to restore the upland vegetation, which would result in reduced sediment in the watershed, ultimately improving the quality of coastal habitat and marine waters.

Invasive Species Management and Control Activities

Conservation efforts to control, interdict and mitigate the effects of terrestrial invasive species in the Marianas are limited. With a few exceptions (e.g., Brown tree snake and Coconut Rhinoceros beetle), the effects and extent of invasions are not well studied. Prevention of invasive species through biosecurity measures is essential in limiting risk to habitats and species of the Marianas. Both the CNMI and Guam have biosecurity mechanisms as part of their overall port programs. A major biosecurity focus within the Marianas is preventing the spread of brown tree snake (BTS) to the CNMI from Guam. In this regard, federal agencies support local capacity in Guam and the CNMI. On Guam, there are extensive efforts to keep BTS out of the transportation chain, effectively reducing the potential for BTS to be accidentally transported from the island. In the CNMI, there are efforts to ensure that high-risk cargo and craft arriving from Guam are inspected to reduce risks of BTS accidentally arriving and establishing.

The University of Guam and the Northern Marianas College provide research and extension services to support invasive species management, as do the various soil and water conservation districts. Activities include Coconut Rhinoceros Beetle monitoring and management and research programs. Similarly, both the CNMI and Guam have government offices and staff that support pest species and natural resource management and conservation and restoration efforts. The U.S. Department of Defense has active

natural resource programs on military lands, which included full time staff and various projects such as BTS management, feral ungulate control, habitat restoration and fencing control.

The Coconut Rhinoceros Beetle was first detected on Guam 2007 in an area totaling less than 1000 acres and eradication was attempted but failed. The Guam Coconut Rhinoceros Beetle Eradication Project was a joint effort involving the U.S. Department of Agriculture, the Guam Department of Agriculture and the University of Guam and U.S. Forest Service. Quarantine, biocontrol, sanitation, trapping, and chemical control of Coconut Rhinoceros Beetle were used unsuccessfully and the species is now found throughout Guam (A. Moore personal Communication 5/17/2018).

The National Park Service conducts vegetation management and has partnered with U.S. Fish and Wildlife Service on Guam on a project (Guam Recovery Actions for the Mariana eight-spot butterfly, tree snails, and a rare vine) to translocate species into the national park.

Interactions of Stressors, Conservation Actions, Protected Designations and Laws and Regulations

Of the stressors described above, the two most significant drivers of the current condition of coastal systems are (1) conversion/fragmentation of land due to development, and (2) the ongoing effects of invasive species. These stressors, which reduce resiliency, representation, and redundancy in the coastal system, are significant and ongoing, act in concert with other stressors, and are expected to continue or increase in magnitude and intensity into the future without effective management actions. Although laws, regulations, land protection, and conservation actions benefit coastal systems, these protections have not prevented an overall decline in native coastal systems.

The rate of native coastal system decline is highest on those islands with the largest human population (i.e., Guam and Saipan). Development within coastal systems is concentrated in Guam around Tumon Bay, Hagatna, and Apra Harbor and in Saipan in Garapan and Chalan Kanoa (Figs. 3 and 4). The plant and animal species found here have experienced reductions in numbers of populations and individuals and development contributes to fragmentation thus decreasing habitat connectivity. Mangroves have had additional protection through legislation and therefore have not faced similar threats from development. Throughout the archipelago, increased levels of restoration and conservation efforts such as invasive species management, restoration of badlands, and a reduction in the level of development have the potential to maintain the current native status or even reverse ongoing degradation occurring for these habitats.

Future Scenarios

The condition of the Marianas coastal ecotype in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are as follows:

- (1) *Conservation Values*: stakeholder involvement and public opinion determine the formulation, implementation and funding of natural resource conservation within laws and development plans.
- (2) *Laws and Biosecurity*: national, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented. (e.g., hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.).
- (3) *Development or Conservation Planning*: national, state, county, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

These conservation management parameters are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The year 2035 is the extent of the “foreseeable future,” and is based on the projected divergence of IPCC Representative Concentration Pathway (RCP) climate change scenarios (van Vuuren et al., 2011a,b). The four foreseeable future scenarios considered in this habitat assessment are:

Future Scenario One

Scenario One is considered the most likely future scenario, and serves as a “baseline.” There is no change in the implementation of the three CMPs between 2018 and 2035. A continuing current rate of change in land cover through this foreseeable future results in a slow but continuous change in the habitat. An expanding human population and increased development and general land use on all inhabited islands is anticipated (Table 5), and therefore habitat stressors are expected to increase at a small annual rate. The largest increases in development are expected on Saipan and Guam, where the largest human populations reside, with smaller increases on Rota and Tinian (Table 5). On average, the percentage of land developed for residential, commercial, and agricultural purposes within 100 m of the coastline on the four southern islands is expected to increase by 3% from 2016 to 2035.

The rate of sea level rise in relation to increased global temperatures has risen from about 0.1 in. (2.5 mm) per year in the 1990s to about 0.13 in. (3.4 mm) per year today (Legeais et al., 2018). As these trends continue, it is not likely to result in discernible changes to coastal communities within the Marianas in the next 15 years. Climate related stressors, such as drought and increased storm strength will further stress and degrade communities.

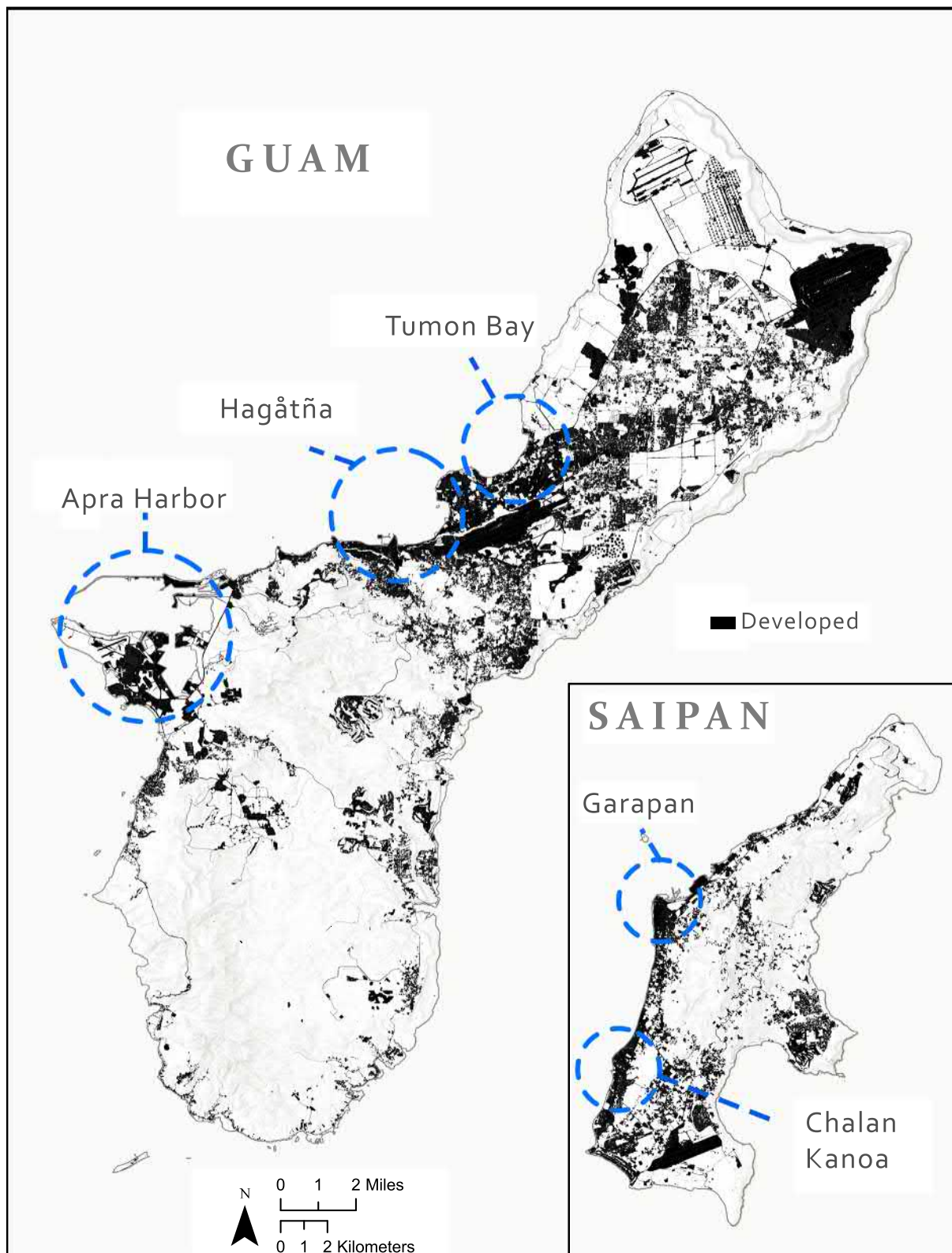


Fig. 4 Developed areas on Guam and Saipan defined as highly influenced by continuous human activities (e.g., impermeable human-made surfaces, landscaped areas, active cropland areas, roads, towns, parks, golf courses, airstrips, and military facilities, [Reeves and Amidon, 2018](#)).

Table 5 Current and future (2035) estimates of acreages of land classified as developed within the coastal zones (≤ 100 m from coastline) of the four main inhabited Mariana Islands.

<i>Island</i>	<i>Current^a</i>	<i>2035</i>	<i>Change</i>
Guam	455 (23.5%)	496 (25.7%)	+ 41 (2.2%)
Rota	37 (7.3%)	43 (8.6%)	+ 6 (1.3%)
Tinian	25 (4.5%)	31 (5.6%)	+ 6 (1.1%)
Saipan	173 (22.6%)	231 (30.1%)	+ 58 (7.5%)

All acreages are in hectares.

^aEstimates for Guam, Tinian, and Saipan are 2016 and Rota is 2014.

Data from Amidon F and Reeves M (2018) *Mariana Islands rates of change*. Technical Report 13. Honolulu, HI: U.S. Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office.

Based on the analysis of the status quo scenario, we expect species declines, permanent loss, degradation and fragmentation of the coastal system due to development, invasive species spread and climate change, and continued loss and disruptions of mutualistic relationships. The coastal strand will be more directly affected by development than mangroves. Both subtypes will be less able to recover from stochastic events (i.e., less resilient), less speciose and diverse (i.e., less represented), and less represented across the landscape.

Future Scenario Two

Under Scenario Two, conservation agencies and stakeholders work with increased but limited resources to slow or stop the degradation of landscape areas. Although there is an expanding human population, development is not expected to increase substantially. A slightly improved biosecurity effort will reduce the rate of introduction of new invasive species and plant diseases but increases in the number and range of invasive species are still expected. Highly destructive invasive species, such as ungulates, rats, yellow crazy ant, little fire ant and coconut rhinoceros beetle are likely to persist or expand along coastlines where they will depredate, displace or degrade the coastal system. The slight improvement of natural resource conservation could result in the increased stewardship and protection of coastal areas. This could expand and protect more coastal systems potentially increasing their resilience to stochastic events and perturbations. The small increase in the CMPs associated with conservation planning and conservation values will not prevent, mitigate, or reverse the impacts of climate change-related stressors and is not expected to greatly alter wildfire frequency and intensity.

Future Scenario Three

Under Scenario Three, all natural resource management actions in the CMPs are set aside in deference to land use for economic development. An expanding human population requires increased land use for agriculture and development with no encumbrance from natural resource management. Biosecurity controls are significantly weakened leading to an increase in the number and spread of invasive species and new plant diseases. Combined together, these factors will result in substantial increases in wildfire frequency. The substantial loss of CMP supported conservation may locally aggravate the impacts of climate change-related stressors. Under this scenario, the coastal system will decline substantially in extent, quality and function through the foreseeable future. Already fragmented coastal vegetation will be completely lost. Areas that cannot support development become the only areas of free-living native species.

Future Scenario Four

Under Scenario Four an overt and robust, active, ongoing effort is made to engage partners and stakeholders in identifying and prioritizing landscape areas needed for the conservation of native habitats and ecosystems, and to actively restore and expand these habitats and ecosystems. Active and well-supported natural resource management begins to restore and expand these habitats and ecosystems. The needs of an expanding human population are addressed through more efficient land use governance based on redevelopment rather than development of undeveloped areas. Substantially improved biosecurity regulations decrease the rate of introductions of invasive species and plant diseases. Established invasive species will continue to spread but at a decreased rate relative to previous scenarios. These improved land management actions result in decreased wildfire frequency and extent. The substantial increase in CMP supported conservation may locally mitigate the effects of climate change-related stressors, but climate-related changes are expected in the near future. The coastal subtypes would be larger and less fragmented and could potentially disperse naturally into new areas. The larger and relatively intact systems would be more resilient to perturbations, better represented in term of species diversity and more redundant across the landscape relative to previous scenarios.

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Galápagos Island Biodiversity

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Abstract

The Galápagos Islands are a living laboratory for evolutionary biologists, biogeographers and ecologists. Many of the organisms floated or flew to the islands subsequently radiated into groups of endemic species, thereby increasing the biodiversity of the islands. But the Galápagos biota are an odd mixture of plants and animals, with many reptiles, but no amphibians; many bird species, but almost no mammals. The peculiarities of the Galápagos wildlife intrigued the young Charles Darwin, starting him on an intellectual journey that eventually produced his theory of survival of the fittest and evolution. The colonization of the islands by humans brought ecological disturbances of ever-increasing intensity until the Ecuadoran government began to take steps to ensure conservation of the islands' unique biota. The focus of much of the current conservation efforts is the prevention of the entry and spread of invasive species, both on land and in the sea.

Introduction

The Galápagos Islands include 19 islands and more than 42 islets. The total land surface of the archipelago adds up to about 8000 km². The islands straddle the Equator, extending north and south of this by about 1° of latitude. Located approximately 1000 km west of the South American mainland, the islands range from about 89–92°W longitude. Stretching over a 320-km diameter, the Galápagos Islands encompass 50,000 km² of ocean surface. The islands are perched atop an oceanic plateau called the Galápagos Platform. The ocean waters over the platform are relatively shallow, with depths of 360–900 m.

The [World Wildlife Fund \(2019\)](#) categorizes the Galápagos as Neotropical desert and xeric shrubland, as summarized below. The climate of the Galápagos varies little between islands. Seasonal differences are largely the result of the effects of multiple water currents. The 'misty' season lasts from about May to December, and results from the effects of the cold Humboldt Current (a cold, low-salinity ocean current that flows north along the western coast of South America, then arcs westward past the Galápagos Islands). This season is characterized by cool temperatures, mist and drizzle known as "gaura" that accumulates on the highlands of larger islands. The hot and wet season prevails from about December to May, under the influence of the warm Cromwell or Panama current. This season is characterized by heavier rainfall and warmer temperatures with March reaching as high as 30 °C with the islands receiving as much as 80 mm of rainfall.

A major driver of Galápagos climate is the periodic occurrence of El Niño events. On average, El Niño events affect the central Pacific region every 2–7 years. During El Niño years, the upwelling of the cold Humboldt Current is overwhelmed by strong warm water currents. The Humboldt Current normally provides nutrient rich waters with plankton that are the basis for the Galápagos marine food chain. El Niño events have strong negative effects on the birds, reptiles and mammals that rely on the marine environment for food, because the warm waters are much less productive. Although marine-dependent creatures suffer losses during El Niño years, land-based organisms often thrive, as increased rainfall supports unusually rich growth of vegetation.

The Galápagos archipelago is best known for its large array of endemic species. These plants, invertebrates and vertebrate species have evolved over time due to isolated island life. Endemism rates are high in all groups of organisms on these islands from lichens, flowering plants, insects and land snails to finches, giant tortoises, iguanas and rats.

Human History of the Islands

The Galápagos Islands were apparently not discovered by native South Americans in prehistoric times. The first known landing on the Galápagos was by Friar Tomás de Berlanga (1487–1551) who was a Spanish priest who traveled to the New World and eventually became the fourth Bishop of Panama (Fig. 1). In 1535, he was on route to Peru to settle a dispute between Francisco Pizarro and Diego de Almagro over division of conquered Inca territory. His ship was becalmed off the coast of northern South America, and strong currents carried him out to the Galápagos Islands where he landed on March 10, 1535. Thus, he is credited with bringing the Galápagos Islands to the world's attention. Because of Friar Tomás' letters, early maps of the coast of South America began to include the Galápagos Islands. The earliest of these is a vellum chart, thought to be from the 1530s. The islands then appear in Gerard Mercator's world map of 1569. Based on his letters, Friar Tomás did not enjoy his brief time on the Galápagos. The islands appeared inhospitable to humans, with the lack of water being critical. Other Spanish explorers visited, but most found the islands waterless, somewhat uninteresting, and very difficult to live in. They were seen as having little more to offer than giant tortoises as a food source. However, the strategic location of the islands (near the west coast of South America, but not too close) made them an ideal location as a haven for English pirates of the 17th century who sought to attack Spanish ships laden with precious metals. By the late 18th century the islands were being used as a land base for whaling operations in the Pacific, first by the British, then by the Americans. Colonists from Ecuador began settlements on Floreana in the 1830s, and the islands were annexed by Ecuador in 1832. The colony failed by 1852, as the colonists had used up the available resources by that time. Several additional attempts were made to colonize the islands by the Ecuadorans in the latter half of the 19th century.

Darwin and the Voyage of the *Beagle*

The most important biological investigations of the Galápagos Islands began almost by accident, when Charles Darwin (Fig. 2) landed there in 1835. In 1831, Darwin, then aged 22, convinced Captain Robert Fitzroy to let him join a charting voyage around South America on the *H. M. S. Beagle* (Fig. 3) as ship's naturalist. When setting off from England for a 5-year voyage, Darwin had little ambition for groundbreaking scientific research. On September 17, 1835 on the return route across the Pacific, the *Beagle* arrived at the Galápagos Islands, starting with San Cristóbal. Darwin went ashore there (September 17–22), then went on to visit Floreana (September 24–27), Isabela (September 29 to October 2) and finally spent time on Santiago (October 8–17). While the



Fig. 1 Statue of Friar Tomás de Berlanga in Berlanga de Duero, Spain.

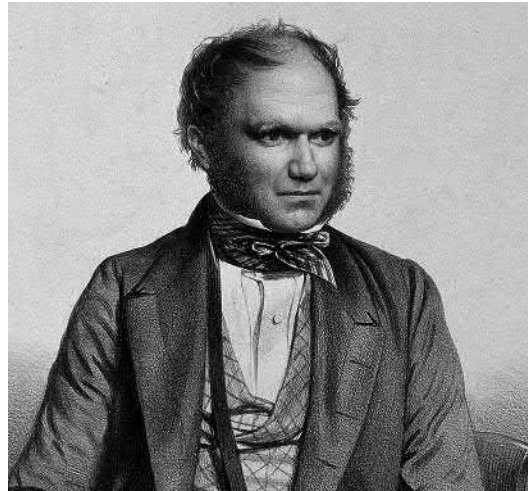


Fig. 2 Charles Darwin, aged 40. Lithograph by T. H. Maguire, 1849. Courtesy of Wellcome Collection. CC BY.



Fig. 3 HMS Beagle. Oil painting by Fran Camós, used with permission.

rest of the crew of the *Beagle* updated Admiralty charts of the archipelago, Darwin collected geological and biological specimens on the islands.

At the time of his visit, Darwin had not yet developed the ideas he presented later. Upon his return to England, he began to realize the full significance of the differences among Galápagos species, particularly based on his observations of the different species of Galápagos mockingbirds on various islands, as well as the differences between the giant tortoises of the different islands. Having failed to label all of the localities where he had taken specimens in his own collections, Darwin went to his crewmates from the *Beagle*, asking to see the specimens that they had collected, to track down inter-island variations among birds, plants, and other species. Darwin was curious about how life had first come to these islands. Most of the species he observed on the Galápagos were endemic to the islands, yet they all showed relationships with species from the Americas. He reasoned that the ancestors of Galápagos species must have been accidental colonists from Central and South America that proceeded to diverge from their ancestral stocks after arriving in the Galápagos. His visits to multiple islands in the archipelago turned out to be critical to the development of his ideas, because he discovered evidence suggesting that evolution was proceeding independently on each island, producing at least some unique species. Darwin spent the next 24 years developing his ideas about natural selection before

publishing his book, 'On the Origin of Species'. He described this book as "one long argument" that stemmed from his five-week visit to the Galápagos Islands and attempted to include all life on earth. As the basis of evolutionary theory, this book changed the course of the life sciences, and linked Darwin inextricably with the Galápagos.

Galápagos Environments

The Galápagos Islands remain a living laboratory for evolutionary biologists. The islands are separated from the mainland of South America by almost 1000 km. So, as Darwin surmised, every species that lives on the Galápagos today is descended from a migrant species that arrived there from some other part of the world. Since the geologic history of the islands is well known, evolutionary biologists can measure the time available for a founding population of organisms to evolve daughter species on a given island or islands. For this reason, the Galápagos Islands are quite probably the most studied archipelago in the world. The Galápagos also have a unique set of environmental conditions that set them apart from other island groups. The archipelago straddles the Equator (Fig. 4) and the islands are surrounded by the cool Humboldt Current. The waters of this current are about 9 °C colder than a surrounding tropical water near the equator. The cold water holds more dissolved oxygen and upwelling of the current along the coast brings nutrients to the surface. This nutrient rich water supports abundant phytoplankton which are the basis of thriving marine ecosystem. The Cromwell is a warm current that flows along the Equator. It upwells at the Galápagos, carrying nutrient-rich waters to the surface. The convergence of these warm and cold currents at the Galápagos produces a unique mix of tropical and temperate environments; these are reflected in the unusual plants and animals that inhabit them, another unique biological feature of the Galápagos.

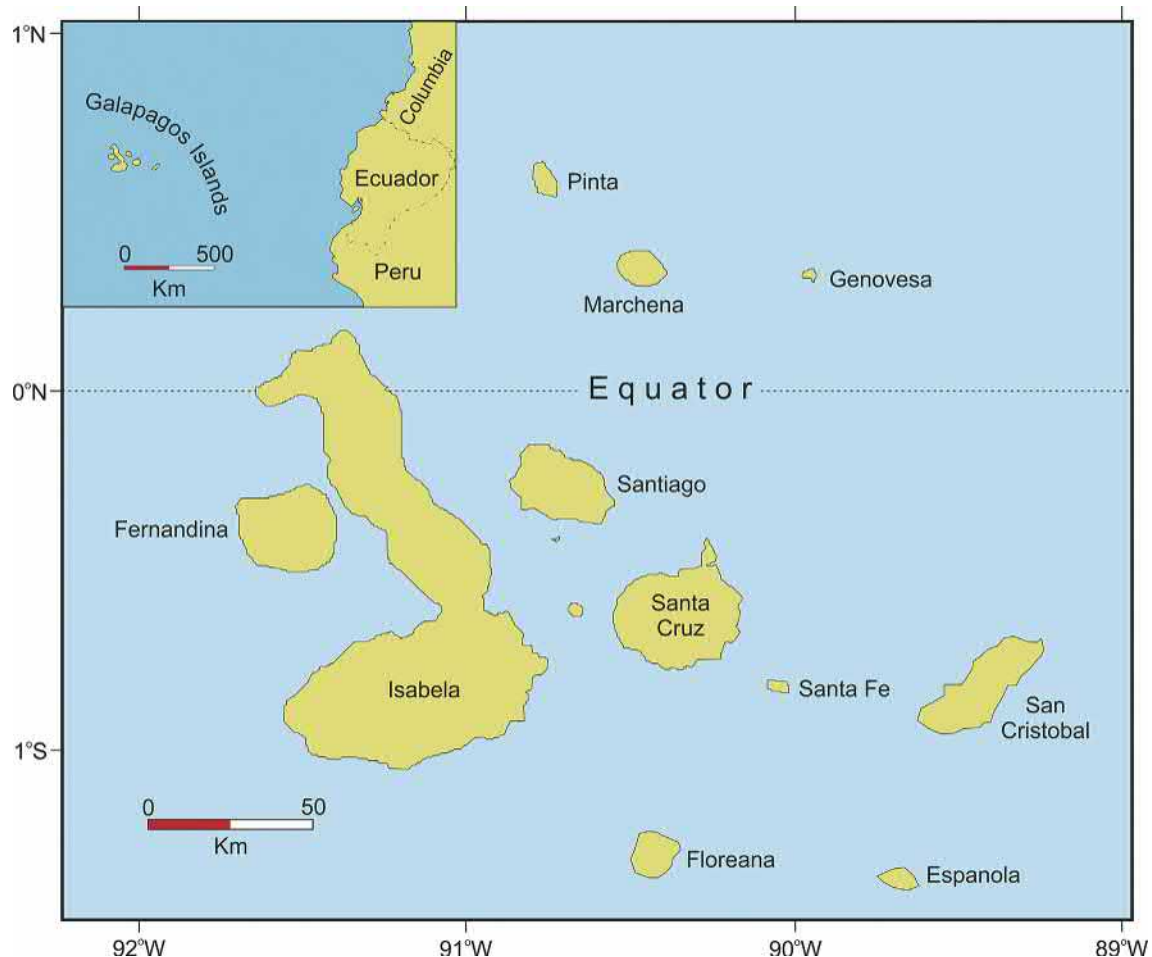


Fig. 4 Map of the Galápagos Islands.

Vegetation Zones

According to [Levin et al. \(2015\)](#), the flora of the Galápagos includes 1544 species of flowering plants including 241 endemic species. Most of the surfaces of these islands are covered by arid, semi-desert xerophytic (dry-adapted) vegetation. Only the upper elevations of the volcanoes are sufficiently high to receive more rainfall than the lowlands. Lush, tropical vegetation clothes these mountain tops. The island vegetation zones begin at sea level with a littoral zone, then upslope to the lowland arid zone, then further up into the mountain top humid zone of those islands with tall volcanoes.

The littoral zone is a narrow band of arid shoreline. The vegetation consists of salt-tolerant and xerophilous vegetation ([Fig. 5](#)). Stands of several mangrove species grow along calm lagoons. Common shrubs include Galápagos leatherleaf (*Maytenus octogona*)

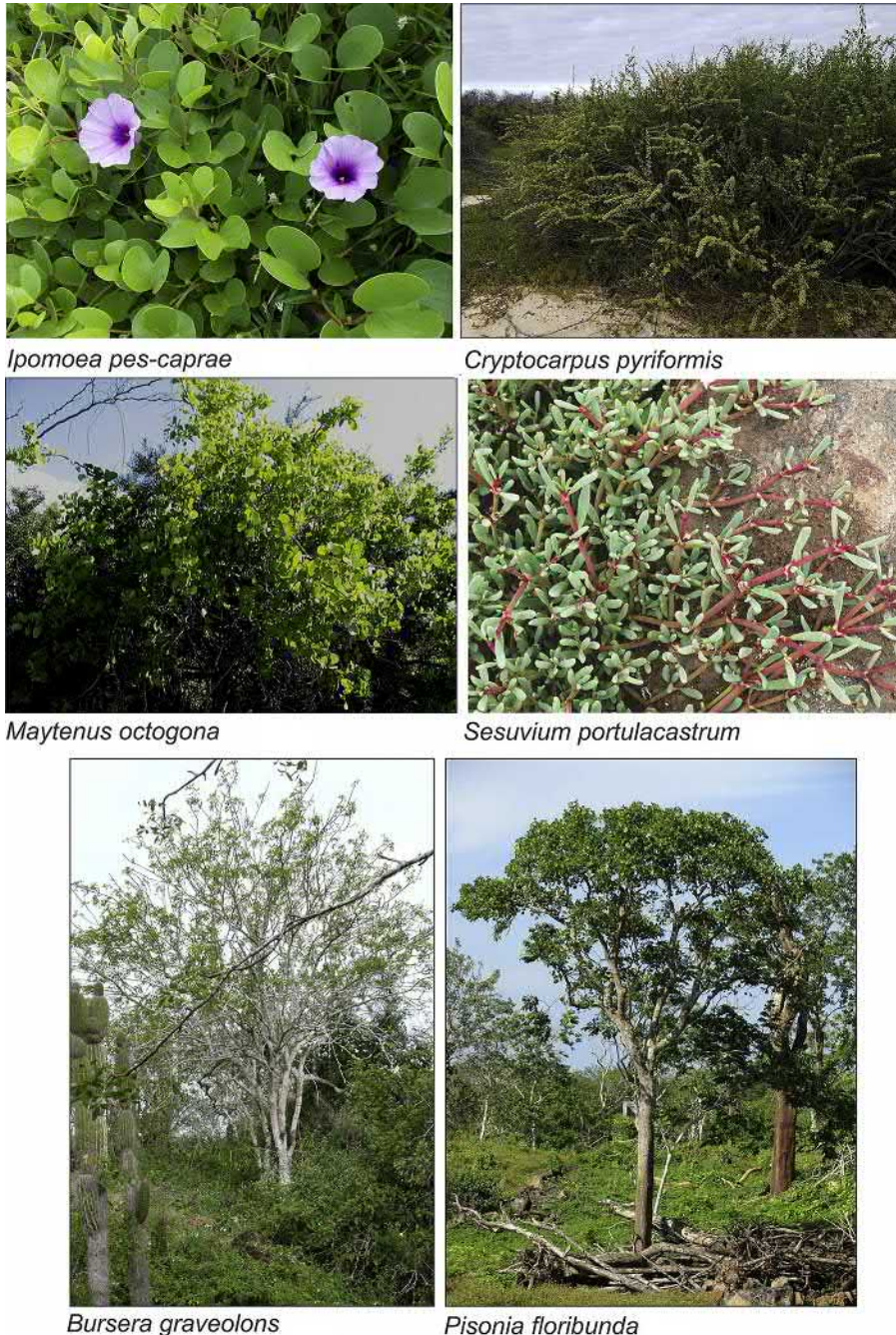


Fig. 5 Plant species growing in the littoral and arid zones. Photo of *Cryptocarpus pyriformis* by Michael Hogan, CC BY-SA 4.0; photo of *Maytenus octogona* on Santa Cruz Island by David Stang, CCA-Share Alike 4.0 International; photo of *Sesuvium portulacastrum* on North Seymour Island by Haplochromis, Creative CCA Share Alike 3.0 Unported; photo of *Ipomoea pes-caprae* by Primejyothi, CCA-Share Alike 3.0 Unported; photo of *Bursera graveolens* from Creative Commons; photo of *Pisonia floribunda*, courtesy of the Charles Darwin Foundation.

and saltbush (*Cryptocarpus pyriformis*). Herbaceous plants that grow along the beach include shoreline purslane (*Sesuvium portulacastrum*), Galápagos carpet weed (*S. edmonstonei*), and beach morning glory (*Ipomoea pes-caprae*), which helps stabilize coastal dunes.

The arid zone, immediately inland from the littoral zone, is the most extensive ecoregion of the Galápagos. The arid zone ranges from 80 to 200 m in elevation. It covers some small islands entirely. Arid zone plant communities (Fig. 5) are the most diverse on the islands. As the name suggests, the arid zone is populated by drought tolerant, xerophytic plants, including cacti, trees, shrubs and herbaceous plants. The most well-known tree is the palo santo (*Bursera graveolens*). Other trees in this zone include the guayabillo (*Psidium galapageium*) and paga paga (*Pisonia floribunda*). Since cacti thrive in arid environments, quite a number of species grow in the arid zone, including the endemic genus *Jasminocereus* and the lava cactus (*Brachycereus nesioticus*). Other examples of endemic cacti include the prickly pear cacti *Opuntia echios* and *O. helleri*. The woody shrubs of the arid zone form the lower levels of the vegetative layers in this zone such as the endemic *Castela galapageia*, *Lecocarpus pinnatifidus* and other species of the genus *Lecocarpus*. Herbaceous plants have also adapted to this arid zone, including several endemic varieties of Galápagos tomatoes (*Lycopersicon cheesmanii*), passionflower (*Passiflora foetida*), and species of the endemic genera *Tiquilia* and *Chamaesyce*.

The humid zone (Fig. 6) lies above the arid zone on islands that have volcanic peaks above 300 m. There is also a transition zone between the arid and humid zones. This transition zone is an ecotone, supporting a mixture of plant species from both adjacent



Fig. 6 Plant species growing in the humid zone. *Pisonia floribunda* photo by Charles Darwin Foundation; *Miconia robinsoniana* photo by Bruce Marcot, US Forest Service; *Psidium galapageium* photo from Creative Commons; *Zanthoxylum fagara* photo by Wikipedia Creative Commons; *Scalesia* trees photo by Galápagos Conservation Trust.

zones. These include pega pega (*Pisonia floribunda*), Galápagos guava (*Psidium galapageium*) and Scalesia trees. Garúa fogs maintain this humid zone during the dry season. They form during the night and last well into the next day, depositing moisture that acts as a shield against plant desiccation in these high elevation areas. Garúa is a Spanish word meaning drizzle or mist. Along the Pacific coast of South America (Peru and Chile) and on the Galápagos Islands, Garúa is the moist cold fog that blankets the coasts, especially during the winter. Within the humid zone the following elevational layers of vegetation are found. They are lush and tropical as a result of increased moisture. From 300 to 500 m elevation, Scalesia trees are dominant, reaching 5–15 m in height. There are 20 different species of *Scalesia*, the plant kingdom's version of Darwin's finches. From 500 to 600 m elevation, wild lime (*Zanthoxylum fagara*) is most abundant. Shrubs replace trees above 600 m, as seen on Santa Cruz and San Cristóbal islands. Galápagos miconia (*Miconia robinsoniana*) is a shrub that grows 3–4 m tall at 600–700 m above sea level, where it is dominant. Sadly, this endemic shrub is nearly extinct because of the impacts of agriculture and livestock grazing (World Wildlife Fund, 2019).

Above 900 m, the vegetation has been described as a fern-sedge zone. In place of shrubs there are ferns, sedges, grasses, and Sphagnum mosses. The only tall plant on this mountain top zone is the Galápagos tree fern, *Cyathea weatherbyana*. A moisture loving plant, it grows where pools of water accumulate, such as collapsed lava tubes, potholes and other cracks and crevices.

Geologic Setting

As described by White and Burdick (2019), these oceanic islands are of volcanic origin and have been building for the past 4 to 5 million years. The Galápagos Islands are located on the Nazca tectonic plate. This tectonic plate is drifting eastward over the Galápagos hot spot. Hot spots are volcanic regions thought to be fed by underlying mantle that is anomalously hot compared with its surroundings. The volcanic history of the Galápagos hot spot can be traced by the two adjacent submarine ridges: the Cocos and Carnegie ridges. The Cocos ridge extends northeast from the Galápagos Islands and subducts beneath Costa Rica. The Carnegie ridge extends eastward from the islands and subducts beneath Ecuador. With the exception of the largest island, Isabela, each major island consists of a single large volcano. Isabela was formed from the combination of five volcanoes (Fig. 7).

Most of the islands have a distinctive conical shape associated with volcanic action. The mountainous islands have been formed through continuing eruption, building layer upon layer. Due to this volcanic formation, the islands are characterized by many steep slopes, with heights ranging from a few meters to more than 1600 m above sea level. Two distinct types of volcanoes occur in the Galápagos. In the west, on the islands of Isabela and Fernandina, large volcanoes with an “inverted soup-bowl” morphology and deep calderas occur. In the east, smaller shield volcanos formed with more gentle slopes (Galápagos Conservancy, 2019b). La Cumbre is an example of a shield volcano on Fernandina Island (Fig. 8).

The difference between these two types of volcanoes is apparently due to the difference in lithospheric thickness beneath them. The emergence of the Galápagos Islands from the Pacific is only the most recent series of events in the history of volcano building from the ocean floor, which may extend back 12–15 million years. Some of the islands are anchored more than 3000 m below the surface, on the Pacific Ocean floor. Earthquakes are common, as are other volcanic characteristics such as crater lakes and parasitic vents flanked by lava flows marking the summits. Other volcanic landscape features include fumaroles, lava tubes, sulfur fields and a variety of pumice, ash, and tuff ejected from the volcanoes.



Fig. 7 Satellite photo of the main Galápagos Islands, showing the location of volcanoes. Note the presence of five volcanoes on Isabela Island. Photo courtesy of NASA Jet Propulsion Laboratory.



Fig. 8 La Cumbre is a shield volcano on Fernandina Island in the Galápagos Islands. La Cumbre is also the youngest volcano in the Galápagos Islands. Photo courtesy of NASA.

Among the Galápagos Islands there are 21 emergent volcanoes of which 13 are considered active. Unlike the Hawaiian Islands, these volcanoes do not form a linear chain. However, the oldest volcanoes tend to be located in the southeastern area of the archipelago. The oldest islands in the Galápagos are South Plaza (just east of Santa Cruz Island) at 4.2 million years, and Española at 3.2 million years. These dates correspond to the time when these islands first rose above sea level. Determining the age of the islands is made possible through a method called potassium-argon dating, which can be used to estimate the age of volcanic rocks (basalts).

Historic eruptions have occurred on many of the Galápagos volcanoes, including Fernandina, Volcán Wolf, Alcedo, Sierra Negra, Cerro Azul, Santiago, Pinta, Floreana, and Marchena. Eruptions in the recent geologic past (the last 10,000 years) have also occurred on Volcan Darwin, Volcan Ecuador, Genovesa, San Cristobal, and Santa Cruz. A number of submarine volcanoes have also been active in this time. It is quite unusual for a mantle plume to produce so many simultaneous active volcanoes.

Island Biogeography and Biodiversity

How and when were the Galápagos Islands colonized by plants and animals? These islands are situated in the Pacific Ocean 900 km west of the coast of South America. Unraveling the biological history of these isolated islands presents a formidable challenge for biogeographers. Darwin's explanation for the biotic colonization of the islands focused on the ability of organisms to disperse over barriers from their centers of origin. He later speculated (Darwin, 1871: 363) that there might have been a land bridge connecting the islands to the South American continent. However, subsequent examinations of the regional marine geology, combined with the volcanic origins of the Galápagos, rendered such land bridge theories untenable.

Evolutionary biologists are fascinated by island ecosystems because of the clarity with which the species that inhabit them illustrate evolutionary processes. For this reason, as well as a world-changing historic visit by Charles Darwin, the Galápagos Islands are quite arguably the best-studied archipelago in the world.

As discussed by the Galápagos Conservancy (2019c), when considering the diversity of species that inhabit the Galápagos Islands, it is important to note the unbalanced nature of the flora and fauna, compared with continental species diversity. For instance, there are many native reptile species, but no amphibians; there is an abundance of land and sea bird species, but few native mammals. Plants with large flowers and big seeds are absent while grasses and ferns abound. It is likely that the ancestors of present-day Galápagos animals that had the ability to swim some distances, such as sea lions (*Zalophus wolfebaeki*), sea turtles (*Chelonia mydas*), and penguins (*Spheniscus mendiculus*) swam to the islands with the help of ocean currents. Non-swimming migrants, such as reptiles and small mammals such as rice rats (*Aegialomys galapagoensis*) were likely carried to the islands from the South or Central American mainland on rafts of plant debris. Most of these rafts would have sunk before reaching the Galápagos, but it would have only taken a handful of successful rafts washing ashore to explain the present reptile diversity in Galápagos. This "raft" theory of arrival also explains why there are no native amphibians, few mammals, and many reptiles in the Galápagos Islands—reptiles are the best adapted to deal with the harsh salty and sunny conditions of weeks at sea. Coastal plants, such as the mangroves and saltbushes of Galápagos, have seeds that are salt tolerant, and those seeds are also likely to have arrived by sea. Amphibians are too

prone to desiccation to survive weeks on the open ocean. Wind is thought to have played a major role in transporting spores of the ferns, mosses, and lichens to the Galápagos Islands. Vascular plants with heavier seeds are quite scarce in the Galápagos because those seeds would have had a more difficult time traveling by wind, except plants with plumed seeds designed for wind transport. This explains why members of the dandelion family (Compositae) are found throughout the Galápagos. Wind also likely transported small invertebrates to the islands, as well as a few species of weaker-flying land birds and two species of bats. Not surprisingly, only a tiny fraction of the South American bird fauna became established on the islands. However, sea birds are generally excellent fliers over long distances, so they simply flew to the islands. Birds likely brought with them hitch-hiking plant seeds or propagules that were attached to their feathers or feet, or even in their guts.

Migration Routes to the Galápagos

As described by Grehan (2001), three principal migration track patterns or routes connect the Galápagos with three sources of origin for the islands' biota: The Eastern Pacific, the Caribbean, and the Pacific basin. The Eastern Pacific track has been identified through species with distributions that connect the Galápagos with North and South America, bypassing Central America. The ancient migration routes of the ancestors of the species found today in both the Galápagos and Caribbean islands follow a track along the Caribbean/Cocos/Nazca plate boundary. Distributions shared between the Galápagos, America, and eastern Asia/Australasia represent a Pacific basin track. Clues concerning the origins of the Galápagos biota can be found by examination of sister species relationships between mainland and Galápagos taxa (Table 1).

East Pacific tracks

This group of Galápagos species are found today in either North or South America, but not in most of Central America. The dispersal mechanisms for this group of species include both passive (e.g. flightless weevils) and active (e.g. wasps) dispersal methods. The shortest migration route in this group connects the Galápagos Islands to Peru and Ecuador. In many cases, the migrant population of species that made it to the Galápagos has genetically diverged from the mainland population. When the island population evolves into a separate (although closely related) species, this is called *allopatric speciation*. This is a mode of speciation that occurs when populations of a species become isolated from each other to an extent that prevents gene flow between those two populations.

There are many examples of organisms that followed the East Pacific track migration route. The flightless weevil genus *Galapaganus* includes five Galápagos species and three species living in Ecuador and Peru. The wasp *Tachysphex galapagensis* has a sister species on the mainland, *T. peruanus* (Fig. 9). These wasps link the Galápagos with Peru. Likewise, the Galápagos snake *Alsophis biserialis* is linked with its sister species *A. elegans* in Peru and southern Ecuador. Further south a sister species relationship connects the Galápagos snake *Pilodrya hoodensis* with its Chilean relative *P. chamissonis*. The lizard genus *Microlophus* includes at least three Galápagos species and 14 mainland species, ranging between Ecuador and northern Chile. The single species of the plant group Solanaceae (nightshade family) that became established in the Galápagos is related to 82 species of the family found throughout Peru and Chile.

Table 1 List of Galápagos species with sister species elsewhere.

Taxon	Galápagos species	Relatives elsewhere
<i>Porifera</i>		
Sponge genus <i>Rhabderemia</i>	<i>R. destituta</i>	<i>R. mona</i> in Puerto Rico
<i>Insects</i>		
Weevil genus <i>Galapaganus</i>	10 flightless species	5 species in Peru and Ecuador
Wasp genus <i>Tachysphex</i>	<i>T. galapagensis</i>	<i>T. peruanus</i> in Peru
Rove beetle genus <i>Rothium</i>	2 species	4 species on Pacific coast of Mexico, Peru, Ecuador
Moth genus <i>Oxydia</i>	<i>O. lignata</i>	<i>O. hoguei</i> on Cocos Island
Shore fly genus <i>Paracanace</i>	2 species	6 species in Caribbean, Panama and Brazil
Flower beetle genus <i>Ablechrus</i>	<i>A. flavipes</i>	8 species in Cuba, Mexico, Guatemala, Panama, Venezuela
<i>Reptiles</i>		
Snake genus <i>Alsophis</i>	<i>A. biserialis</i>	<i>A. elegans</i> in Peru and Southern Ecuador
Snake genus <i>Antillophus</i>	2 species	<i>A. andreae</i> in Cuba; <i>A. parvifrons</i> in Hispaniola
Snake genus <i>Pilodrya</i>	<i>P. hoodensis</i>	<i>P. chamissonis</i> in Chile
Lizard genus <i>Microlophus</i>	At least 3 species	14 species from Ecuador to N. Chile
Lizard genus <i>Phyllodactylus</i>	8 species	7 species in Puerto Rico, Venezuela and Columbia
<i>Flowering plants</i>		
Plant genus <i>Lycium</i>	18 species	70–80 species in the Americas
Plant genus <i>Nolana</i>	<i>N. galapagensis</i>	17 species in Peru and Chile
Plant genus <i>Gossypium</i>	<i>G. klotzschianum</i>	<i>G. davidsoni</i> in Baja California, Mexico
Plant genus <i>Galvezia</i>	<i>G. leucantha</i>	8 species in S. California, Mexico, Ecuador, Peru

Data from Grehan, J. (2001). Biogeography and evolution of the Galapagos: Integration of the biological and geological evidence. *Biological Journal of the Linnean Society* **74**, 267–287.

*Galapaganus femoratus* beetle*Desis* spider*Tachysphex* wasp*Oxydia* moth*Tornatellides* land snail

Fig. 9 Invertebrate species indigenous to the Galápagos Islands. *Tornatellides* snail, photo by Shinichiro Wada, Tohoku University; *Galapaganus femoratus* beetle photo Creative commons; *Tachysphex pompiliiformis* wasp photo by Ian Tew, Creative Commons; *Desis* spider photo by Magriet B, Creative Commons CC BY-NC 4.0; *Oxydia* moth photo by Charles J. Sharp, Creative commons CC BY-SA 4.0.

Examples of species that followed the Caribbean track include the lizards in the genus *Phyllodactylus*. These lizards have close relatives in Columbia, Venezuela and Puerto Rico. Note how this track bypasses Central America. This Caribbean connection via North and South America also characterizes the distribution pattern of the plant genus *Lycium* where the Galápagos species, *L. minimum*, fills a geographic gap west of Central America that complements the Caribbean distribution to the east. This interrelationship between East Pacific and Caribbean distributions may also apply to the Galápagos finches (Fig. 10). Assuming the designation of *Tiaris obscura* as the nearest mainland relative is correct, then this bird group follows a Galápagos–South America track. The genera *Tiaris* and the Caribbean *Melanospiza* form the Galápagos finch sister group. This relationship extends the East Pacific track to include the Caribbean basin.

A northern track is represented by sister species of the cotton plants *Gossypium klotzschianum* and *G. davidsonii* linking the Galápagos with Baja California. A similar link occurs for the sister genus relationship of the foxglove genus *Gambelia* in California and Mexico and *Galvezia* in the Galápagos. The track for *Galvezia* comprises Galápagos, Ecuador and Peru.

Caribbean connections with the Galápagos which involve Central America are also quite common. The Galápagos species of *Oxydia* moths may be closely related to species of *Oxydia* on Cocos Island and to a species on the Caribbean island of Guadalupe.



Fig. 10 Eleven of the seventeen species of Darwin's Finches endemic to the Galápagos. Photos courtesy of the Charles Darwin Foundation.

A subgenus of the shore-fly genus *Paracanace* forms a track between Galápagos, Panama and Brazil, but not Cocos Island. The track of the soft-winged flower beetle *Ablechrus* also connects the Galápagos, Central America and the Caribbean.

Pacific tracks

Although many Galápagos organisms are most closely related to species on the American mainlands, there are also biogeographic relationships that link the Galápagos biota to the Pacific basin. For instance, the land snail genus *Tornatellides* is confined to the Pacific basin, and its presence on the Galápagos represents its easternmost locality. The shoreline spider genus *Desis* is found throughout much of the Indian and Pacific Ocean basins, with 13 species known from the ocean shores of East Africa, India, Australia, New Guinea, and Japan. The easternmost species is *D. galapagoensis* from the Galápagos. How did organisms cross from the western to the eastern Pacific? The tectonic history of the eastern Pacific provides the best available evidence of direct contact between the Galápagos hotspot and proposed former Pacific–Caribbean island arcs. Tectonic plate movements transported island arcs eastward, across the ancient Pacific basin. When these island arcs moved over the hotspot beneath the Galápagos, it would have been possible for island arc biota to disperse onto the volcanic landscape.

DNA Evidence

Genetic analysis is shedding new light on the biogeographic history of the Galápagos. A study by [Sequeira et al. \(2000\)](#) examined 15 species in the afore-mentioned weevil genus *Galapaganus* that are distributed on coastal Peru and Ecuador and include 10 flightless species endemic to the Galápagos islands. Genetic samples were obtained from seven species from the oldest Galápagos islands: San Cristóbal, Española, Floreana, and Santa Cruz. Based on genetic mutation evidence, the oldest species, *G. galapagoensis* on the oldest island, San Cristóbal, diverged from the remaining species in the Galápagos about 7.2 Ma. This estimate exceeds the geological ages of the extant emerged islands. However, this study is not a fluke, as dating of endemic Galápagos iguanas, geckos and lizards by genetic mutation rates produced very similar results. An apparent explanation for the disparity between geological and genetic timeframes is that about 7 Ma there were islands in the Galápagos region that subsequently sank under the surface of the ocean. These islands may have been the ones initially colonized by the ancestors of these organisms. This hypothesis has gained support from the recent geological research that identified 11-Myr-old sunken islands, south-east of the present location of the archipelago.

[Torres-Carvajal et al. \(2016\)](#) took a fresh look at the biogeography of the leaf-toed geckos (*Phyllodactylus*) endemic to the Galápagos Islands by analyzing DNA. Previous workers had proposed a scenario in which there were three separate colonization events for this group. The DNA study supported the three colonization scenario with an early colonization that included most species of *Phyllodactylus*, occurring 5.5 and 13.8 Ma, followed by a second independent colonization of *P. darwini* 3.03 Ma ago. A third colonization to Wolf Island by *P. gilberti*, occurred 690 ka. As with many other Galápagos organisms, the Pacific coast of South America seems to be the source for the founders of the Galápagos leaf-toed geckos.

Biogeographic Modeling

[Funk and Burns \(2018\)](#) studied the geographic origins of Darwin's finches through biogeographic modeling. Darwin's finches are considered a classic example of an adaptive radiation and have been the focus of numerous studies over the last 50 years. Few studies, however, have attempted to investigate the biogeographic origins of these birds. Biogeographic models run using eight regions suggest Darwin's finches arose from an ancestor in a long-distance dispersal event from the Caribbean Islands as opposed to the geographically closer mainland South America. However, models run using only five areas suggest equal probability between a Caribbean and a mainland South America origin to Darwin's finches. This study suggests equal probability for a Caribbean origin to Darwin's finches as a South American mainland origin. Overall, the Caribbean Islands appear especially important for the initial diversification of this group of birds, with many small-island restricted species diversifying early in the radiation. Colonization success was likely coupled with high dispersal ability and highly variable bill morphology to exploit vacant niche space ([Table 2](#)).

Origins of Galápagos Insects

According to [Peck \(2006\)](#), there are almost 2000 species of insects and 350 species of other terrestrial arthropods on the Galápagos Islands. Of the 376 native beetle species, there are 266 endemic species and 110 indigenous species with populations outside the Galápagos. Most beetle colonization was probably passive—either through the air as 'aerial plankton' or by sea-surface transport (rafting on oceanic flotsam) from Mexico, Central or South America. However, unlike plants and vertebrates, beetle colonization of the Galápagos has not led to much speciation. The average for the native beetle fauna is about 1.35 species per colonizing ancestor. Factors suppressing beetle speciation on the Galápagos include the lack of habitat diversity on the islands and the geological youth of the islands.

One example of beetle colonization on these islands is the rove beetle genus *Rothium*. A study by [Frank and Ahm \(2011\)](#) examined this group of beetles that are strictly marine coastal inhabitants. Their habitat includes the shore area that falls between the low and high tides. They are found on rocky headlands, specifically on rocks with algae, and in tidal pools. Four species of *Rothium* are found along the Pacific coasts of Mexico, Peru, Ecuador. Two species are found only in the Galápagos: *R. littoralis* and *R. ashlocki*. Presumably these evolved from an ancestor closely related to a mainland species from South America.

Vertebrate Fauna of the Islands

The islands are home to 8 native species of mammals, 27 species of reptiles, 45 species of birds, and 11 species of fish, making a total of 91 native species of vertebrates on and around the islands ([Table 3](#)). Of these 91 species, 11 are listed by the IUCN as 'Endangered,' 7 are 'Vulnerable,' and 4 are 'Critically endangered.' This means that one-quarter of the vertebrate species of the islands are seriously threatened. This short review focuses on just two groups of animals that are unique to the Galápagos Islands: the giant tortoises and the iguanas.

Giant tortoises

The native vertebrate fauna of the Galápagos is limited to reptiles, birds and mammals. Descriptions of these animals are provided by the [Galápagos Conservancy \(2019d\)](#). Probably the most famous of these animals is the giant tortoise (*Chelonoidis nigra* complex). Giant tortoises once lived on most of the continents of the world, but all were driven to extinction except the Galápagos tortoises and the giant tortoises of the Aldabra Atoll in the Indian Ocean. The Galápagos Islands were named for their giant tortoises; the old Spanish word *galapago* meant saddle, a term used to describe the shape of their shells. The closest living relative of the Galápagos giant

Table 2 Distribution, characteristics and diet of Darwin's Finches.

Species	Common name	Distribution	Physical characteristics	Diet
<i>Geospiza acutirostris</i>	Genovesa ground finch	Only on Genovesa	Small, sharply pointed beak	Arthropods in trees, small seeds
<i>G. conirostris</i>	Española cactus finch	Restricted to Española, Genovesa, Darwin and Wolf Islands (not where common cactus finch lives)	Resembles the small, fine-beaked common cactus finch	Main food source is prickly-pear cactus <i>Opuntia</i>
<i>G. difficilis</i>	Sharp-beaked ground finch	Fernandina, Santiago, Pinta, Genovesa, Darwin and Wolf Islands	Medium length, sharply pointed beak	Seeds, insects and flowers
<i>G. fortis</i>	Medium ground finch	All but the northern islands	Short, stout beak	Main food source is seeds
<i>G. fuliginosa</i>	Small ground finch	On most of the islands	Short, stout beak	Small seeds and skin parasites iguanas and giant tortoises
<i>G. magnirostris</i>	Large ground finch	Found on most islands, but absent from southeastern islands	Largest species of group; very stout beak	Uses beak to crack open nuts
<i>G. propinqua</i>	Genovesa cactus finch	Only on Genovesa	Thick, long and robust beak	<i>Opuntia</i> cactus pulp, flowers, fruits and insects
<i>G. scandens</i>	Common cactus finch	On the main islands	Large, crow-like beak	<i>Opuntia</i> cactus seeds, flowers, insects
<i>G. septentrionalis</i>	Vampire ground finch	Only on Wolf and Darwin Islands	Small, sharply pointed beak	Wet season: seeds, insects; dry season: takes blood of nesting seabirds
<i>Camarhynchus heliobates</i>	Mangrove finch	Fernandina and Isabela - now missing from Fernandina	Medium size beak	Arthropods and plant matter in mangroves
<i>C. pallidus</i>	Woodpecker finch	Isabela, Santa Cruz, San Cristobal, Fernandina, Santiago, and Penzón	Long stout beak	Picks insects from tree cracks and crevices, also eats seeds
<i>C. pauper</i>	Medium tree finch	Only on Floreana Island	Intermediate sized, stout beak	Arthropods
<i>C. parvulus</i>	Small tree finch	On all the main islands	Short conical beak	Arthropods
<i>C. psittacula</i>	Large tree finch	On all the main islands except Española, Genovesa	Largest of the tree-finches; with heavy, parrot like beak	Takes arthropods by pecking through tree bark
<i>Certhidea olivacea</i>	Green warbler-finch	Santiago, Rábida, Pinzón, Isabela, Fernandina, and Santa Cruz	Short, sharp beak	Catches insect on the wing
<i>C. fusca</i>	Gray warbler-finch	Darwin, Wolf, Española, Santa Fe, San Cristobal, Pinta, Floreana	Smallest of Darwin's finches; short sharp beak	Insects
<i>Platyspiza crassirostris</i>	Vegetarian finch	San Cristóbal, Santa Cruz, Floreana, Isabela, Marchena, Santiago, Pinta and Fernandina	Broad, stout beak	Plant buds, leaves, flowers and fruit

Data from Charles Darwin Foundation. (2019). Galapagos species checklist. <https://www.darwinfoundation.org/en/datazone/checklist?species=5093> and Cornell List of Neotropical Birds (2019) <https://neotropical.birds.cornell.edu/Species-Account/nb/home>.

tortoise is the South American Chaco tortoise, but this small tortoise is not thought to be the direct ancestor of the Galápagos tortoises. The first tortoises arrived on the Galápagos 2–3 million years ago, probably by drifting across from the South American coast on vegetation rafts or on their own. The fossil evidence shows that they were already large animals before arriving in Galápagos. They began by colonizing the eastern islands of Española and San Cristóbal, then they dispersed throughout the archipelago, eventually establishing at least 15 separate populations on 10 of the largest Islands.

There are two main morphological forms of Galápagos tortoises, the more primitive domed carapace and the saddle-backed carapace (Fig. 11). Domed tortoises tend to be much larger. They inhabit the larger islands that have humid highlands where forage is generally abundant and easily available. Saddle-backed tortoises evolved on the arid islands and are adapted to survive on little food and water during the frequent droughts. The front of their shell angles upward, allowing the tortoise to extend its head to reach taller plants, such as cactus pads.

One of the giant tortoise's most unusual adaptations, its ability to survive without food or water for up to a year, became the indirect cause of its demise. Pirates, whalers and fur sealers discovered that they could have fresh meat on board their ships by keeping live giant tortoises on board, hence massive exploitation of the species began. Within 200 years, between 100,000 and 200,000 tortoises had been taken by sailors for their meat. Three species have been extinct for some time, and a fourth species (*Chelonoidis abingdonii*) lost its last member, Lonesome George in 2012. It is estimated that 20,000–25,000 wild tortoises live on the islands today. They represent 11 living species. The conservation status of these 11 tortoise species are Vulnerable, Endangered, and Critically Endangered (Table 4) (Galápagos Conservancy, 2019e).

Table 3 Vertebrate animal species of the Galápagos Islands.

<i>Species</i>	<i>Common name</i>	<i>IUCN status</i>
Mammals		
<i>Arctocephalus galapagoensis</i>	Galápagos fur seal	Endangered
<i>Aegialomys galapagoensis</i>	Galápagos rice rat	Vulnerable
<i>Zalophus wolfebaeki</i>	Galápagos sea lion	Endangered
<i>Neorhynchus cinereus</i>	Hoary bat	Least concern
<i>Lasiurus borealis brachyotis</i>	Galápagos red bat	Least concern
<i>Tursiops truncatus</i>	Bottle Nosed Dolphin	Least concern
<i>Mesoplodon densirostris</i>	Blainville's beaked whale	Data deficient
<i>Ziphius cavirostris</i>	Cuvier's beaked whale	Least concern
Reptiles		
<i>Chelonoidis nigra</i> complex	Galápagos tortoise	Endangered
<i>Chelonia mydas</i>	Green sea turtle	Endangered
<i>Amblyrhynchus cristatus</i>	Marine iguana	Vulnerable
<i>Conolophus subcristatus</i>	Galápagos land iguana	Vulnerable
<i>Microlophus albemarlensis</i>	Galápagos lava lizard	Least concern
<i>M. bivittatus</i>	San Cristóbal lava lizard	Near threatened
<i>M. delanonis</i>	Española lava lizard	Data deficient
<i>M. duncanensis</i>	Pinzón lava lizard	Not threatened
<i>M. grayii</i>	Floreana lava lizard	Not threatened
<i>M. habelii</i>	Marchena lava lizard	Least concern
<i>M. indefatigabilis</i>	Santa Cruz lava lizard	Least concern
<i>M. pacificus</i>	Common Pacific iguana	Least concern
<i>Pseudalsophis biserialis</i>	Eastern Galápagos racer	Near threatened
<i>P. darwini</i>	Darwin's racer	Least concern
<i>P. dorsalis</i>	Central Galápagos racer	Near threatened
<i>P. elegans</i>	Elegant racer	Data deficient
<i>P. hephaestus</i>	Santiago racer	Near threatened
<i>P. hoodensis</i>	Española racer	Near threatened
<i>P. occidentalis</i>	Western Galápagos racer	Least concern
<i>P. slevini</i>	Pinzón racer	Vulnerable
<i>P. steindachneri</i>	Painted racer	Endangered
<i>P. thomasi</i>	Thomas' Racer	Near threatened
<i>Phyllodactylus bauri</i>	Baur's leaf-toed gecko	Data deficient
<i>P. galapagoensis</i>	Galápagos leaf-toed gecko	Near threatened
<i>P. gilbati</i>	Wenman leaf-toed gecko	Data deficient
<i>P. leei</i>	San Cristóbal leaf-toed gecko	Near threatened
<i>P. tuberculatus</i>	Tuberculated leaf-toed gecko	Least concern
Birds		
<i>Phoenicopiterus ruber</i>	American flamingo	Least concern
<i>Setophaga petechia</i>	Yellow warbler	Least concern
<i>Sula nebulosa</i>	Blue-footed booby (marine)	Least concern
<i>Sula sula</i>	Red-footed booby (marine)	Least concern
<i>Sula granti</i>	Nazca booby (marine)	Least concern
<i>Anous stolidus</i>	Brown noddy (marine)	Least concern
<i>A. alba</i>	Great egret	Least concern
<i>Pelecanus occidentalis</i>	Brown pelican (marine)	Least concern
<i>Bubulcus ibis</i>	Cattle egret	Least concern
17 species of <i>Geospiza</i> , other genera	Darwin's finches	Two critically endangered
<i>Phalacrocorax harrisi</i>	Galápagos cormorant (marine)	Vulnerable
<i>Zenaidura macroura</i>	Galápagos dove	Least concern
<i>Myiarchus magnirostris</i>	Galápagos flycatcher	Least concern
<i>Puffinus subalaris</i>	Galápagos shearwater (marine)	Least concern
<i>Progne subis</i>	Galápagos martin	Endangered
<i>Buteo galapagoensis</i>	Galápagos hawk	Vulnerable
<i>Spheniscus mendiculus</i>	Galápagos penguin (marine)	Endangered
<i>Ardea herodias</i>	Great blue heron	Least concern
<i>Fregata minor</i>	Great frigatebird (marine)	Least concern
<i>Leucophaea fuliginosa</i>	Lava gull	Vulnerable
<i>Butorides sundevalli</i>	Galápagos heron	Data deficient
<i>B. striata</i>	Striated heron	Least concern
<i>Fregata magnificens</i>	Magnificent frigatebird (marine)	Least concern

Table 3 (Continued)

Species	Common name	IUCN status
<i>Pandion haliaetus</i>	Western osprey	Least concern
<i>Falco peregrinus</i>	Peregrine falcon	Least concern
<i>Phaethon aethereus</i>	Red-billed tropicbird (marine)	Least concern
<i>Creagrurus furcatus</i>	Swallow-tailed gull (marine)	Least concern
<i>Phoebastria irrorata</i>	Galápagos albatross (marine)	Critically endangered
<i>Nyctanassa violacea</i>	Yellow-crowned night heron	Least concern
<i>Mimus parvulus</i>	Galápagos mockingbird	Least concern
<i>M. macdonaldi</i>	Hood mockingbird	Vulnerable
<i>M. trifasciatus</i>	Floreana mockingbird	Endangered
<i>M. melanotis</i>	San Cristóbal mockingbird	Endangered
<i>Lateralus spilonota</i>	Galápagos rail	Vulnerable
Fish		
<i>Azurina eupalama</i>	Galápagos damsel	Critically endangered
<i>Sphyrna lewini</i>	Scalloped hammerhead shark	Endangered
<i>Triaenodon obesus</i>	Whitetip reef shark	Near threatened
<i>Ogcocephalus darwini</i>	Galápagos batfish	Endangered
<i>Aetobatus narinari</i>	Spotted eagle ray	Near threatened
<i>Rhinoptera steindachneri</i>	Pacific cownose ray	Near threatened
<i>Prionurus laticlavus</i>	Razor surgeonfish	Least concern
<i>Holacanthus passer</i>	King angelfish	Least concern
<i>Abudefduf saxatilis</i>	Galápagos reef fish	Least concern
<i>Rhincodon typus</i>	Whale shark	Endangered
<i>Carcharhinus galapagensis</i>	Galápagos shark	Near threatened

Data from Charles Darwin Foundation (2019). Galápagos species checklist. <https://www.darwinfoundation.org/en/datazone/checklist?species=5093>.

Galápagos iguanas

Galápagos iguanas are thought to have a common ancestor that arrived on the islands from the South American continent, floating on rafts of vegetation. Land and marine iguanas diverged about 10.5 million years ago. Genetic evidence suggests that the pink iguana (*Conolophus marthae*), diverged from the other land iguanas approximately 5.7 million years ago, before the current islands existed. The divergence between the two yellowish iguanas is fairly recent.

There are three species of land iguana found in the Galápagos Islands. The well-known yellowish land iguanas include *Conolophus subcristatus* (Fig. 11), native to six islands, and *Conolophus pallidus*, found only on the island of Santa Fe. A third species of land iguana (*Conolophus marthae*), the pink iguana, is found only on Wolf Volcano at the northern end of Isabela Island. It has a pinkish head, and pinkish and black body and legs, often with black stripes. This recently discovered species is morphologically, behaviorally, and genetically distinguished from the other two.

Land iguanas are more than 1 m long and may weigh up to 13 kg (30 lbs). They live in the arid zone of the Islands, and as ectotherms (animals whose regulation of body temperature depends on external sources, such as sunlight or a heated rock surface) they must warm their bodies in the mornings before they can fully function. They must avoid overheating from midday sun by resting in the shade of cacti, rocks, trees or other vegetation. At night they sleep in underground burrows to conserve their body heat. They eat low-growing plants and shrubs, fallen fruit and cactus pads. The moisture from these plants provides the iguanas the moisture they need to survive long droughts.

Land iguanas can live for more than 50 years. A census taken in 1959 found healthy, stable land iguana populations. In 1975, populations on two different islands were almost destroyed in <6 months by feral dog packs. Unlike tortoises, adult iguanas are not predator-proof. Saving them meant removing them from their natural habitat until dogs were eliminated. A breeding and rearing center was quickly established, but it was not large enough for all the adults. So, 38 Santa Cruz iguanas were released on the small islets of Venecia off the northwest coast of Santa Cruz. This population thrived, and the breeding program continues today. Many of the offspring have been repatriated to Santa Cruz and southern Isabela following the removal of feral dogs from the islands. The land iguana breeding and rearing program has been considered a complete success.

The marine iguana (*Amblyrhynchus cristatus*, Fig. 11) is the only sea-going lizard in the world. This extraordinary animal lives on land but feeds on seaweed. It finds its food on exposed rocks, in subtidal areas, and in shallow ocean waters. The iguanas dive as deep as 30 m and may spend up to 1 hour underwater. When diving 7 m or deeper, they often remain submerged for 15–30 min. However, these lizards are also ectotherms, so they cannot expose themselves to cold sea water for longer periods. They must climb out onto the shore to warm up. These iguanas have a short, blunt nose, adapted to feeding on algae growing on rocks. Unlike other lizards, their flattened tail propels the iguanas through the water while their legs hang at their sides. Iguanas have a gland to help them rid themselves of excess salt, consumed along with the algae. This gland is connected to their nostrils.

Marine iguanas are found throughout the islands in concentrations of up to 2700 individuals per km in some areas. The total population is estimated between 200,000 and 300,000. Changes in ocean currents associated with El Niño events cause the greatest

*Pseudalsophis biserialis**Pseudalsophis slevini**Phyllodactylus andysabini**Microlophus albemarlensis**Conolophus subcristatus**Amblyrhynchus cristatus**Chelonoidis nigra**Chelonoidis phantasticus*

Fig. 11 Reptile species indigenous to the Galápagos Islands. Illustrations of *Pseudalsophis biserialis* and *Pseudalsophis slevini* by Jose Vieira; *Microlophus albemarlensis* photo by Charles A. Sharp, CC BY-SA 4.0; photo of *Conolophus subcristatus* by Peter Wilton CCA 2.0; *Amblyrhynchus cristatus* photo by Ryan Fenton CC BY-SA 2.0; *Chelonoidis nigra* photo by Matthew Field, CC BY-SA 3.0; *Chelonoidis phantasticus* photo by Fallschirmjäger CC BY-SA 4.0.

mortality in marine iguanas, with up to 70% dying in some populations in the great 1982–83 El Niño. El Niño causes changes in water temperatures that directly affect marine life around the islands. Upwelling from the Equatorial Undercurrent is reduced during El Niño events. This reduces the food supply in the near-surface waters.

Conservation Issues

All remote islands are biologically fragile. The few species that manage to become established on such islands give rise to many endemic species that fill the empty ecological niches. Over millions of years, healthy, functional island ecosystems are formed. Then, sooner or later, people arrive. People invariably damage the natural ecosystems of the lands they enter, but human impacts on

Table 4 Status of giant tortoise species of the Galápagos.

Species	Common name	Distribution	Status
<i>Chelonoidis abingdonii</i>	Abingdon Island tortoise	Abingdon Island	Extinct in 2012
<i>C. becki</i>	Wolf Island tortoise	N Isabella and Wolf islands	Vulnerable
<i>C. chathamensis</i>	Chatham Island tortoise	NE San Cristobal Island	Endangered
<i>C. darwini</i>	James Island tortoise	Santiago Island	Critically endangered
<i>C. duncanensis</i>	Duncan Island tortoise	SW Pinzón Island	Vulnerable
<i>C. guentheri</i>	Sierra Negra tortoise	Isabela Island	Critically endangered
<i>C. hoodensis</i>	Hood Island tortoise	Española Island	Critically endangered
<i>C. microphyes</i>	Volcán Darwin tortoise	Isabela Island	Endangered
<i>C. nigra</i>	Floreana Island tortoise	Isabela Island	Extinct by 1846
<i>C. phantasticus</i>	Fernandina Island tortoise	Fernandina Island	Probably extinct
<i>C. porteri</i>	Indefatigable Island tortoise	Santa Cruz Island	Critically Endangered
<i>C. vandenburghi</i>	Volcán Alcedo tortoise	Isabela Island	Vulnerable
<i>C. vicina</i>	Iguana Cove tortoise	Isabela Island	Endangered

Data from Galápagos Conservancy. (2019e). Giant tortoise restoration. <https://www.galapagos.org/conservation/our-work/tortoise-restoration/>.

remote islands are far more devastating. The indigenous fauna is exposed to the depredations of predators they have never seen before. Endemic species are particularly vulnerable to extinction because once the native populations are gone, there is no other source of these organisms to re-colonize the island.

It is instructive to compare the history of human colonization of the Hawaiian Islands with that of the Galápagos. In the Hawaiian Islands, the eggs of ground-nesting birds were eaten by rats that arrived with the Polynesians, and many species were driven to extinction. On the Galápagos Islands, the giant tortoises fell prey to sailors who killed them in their thousands and drove many species to extinction. In Hawaii the lowland ecosystems were essentially destroyed as the native vegetation was replaced by agricultural crops, while the highlands were left virtually undisturbed. Ignoring the arid lowlands of the Galápagos, the colonists cut down forests on the highland regions of Floreana to create pastures and plant crops, including citrus. The lowlands of the Galápagos Islands are simply too arid to support agriculture, as demonstrated by multiple failed attempts by Ecuadoran immigrants to introduce farming to the islands in the 19th century. The early 19th century colonists unwittingly wrought more havoc with island ecosystems by the importation of goats, pigs, cattle and donkeys to the islands. The Polynesian colonists imported only three domesticated animals to the Hawaiian Islands: dogs, chickens and pigs. As previously mentioned, they also accidentally introduced rats to the islands.

As discussed by The Galápagos Conservancy (2019a), human impacts have resulted in substantial ecosystem damage on the islands. These impacts include major reductions in populations of fur seals, giant tortoises, groupers, lobsters, sea cucumbers, and whales. Human modifications of ecosystems have been greatest on the colonized islands of Floreana, Santa Cruz, San Cristobal, Baltra, and Isabela. The other easily accessible islands have also suffered ecological damage. These include Santiago, Española, Pinta and Pinzón. Some of the most important ecological disturbance on the Galápagos has come from the introduction of more than 1400 species of plants and animals.

History of protection of the islands

Government actions to preserve Galápagos ecosystems began in 1934, when the government of Ecuador adopted a decree to protect key species, regulate collections, and control visiting yachts. A 1936 the US government backed this law by mandating confiscation of all Galápagos animals taken in violation of the Ecuadorian law. That same year, the Ecuadorian government declared the Galápagos Islands a national reserve and established a national Scientific Commission to design strategies for the conservation of the islands. In 1959 the Ecuadorian government passed a law making all the Galápagos Islands a national park, except for those areas owned by existing colonists. The new law also banned the capture of species, such as iguanas and tortoises, and made port captains responsible for implementing the new rules. Then in 1969, another Ecuadoran legislation defined the borders of the National Park and gave legal status to the National Park Service as a conservation organization.

Marine biosecurity

Campbell et al. (2015) discussed a series of actions to protect the native marine biota of the Galápagos. Their recommendations stem from the results of two workshops on the topic of marine biosecurity in the Galápagos Islands (GI). These recommendations include the following:

- (1) Establish a baseline of known marine introduced species currently in the GI. Baseline studies enable prevention of new species and allow conservation authorities to make reliable response decisions when new organisms are found.
- (2) Encourage dive and tourism operators to help watch for non-native species. Outreach and education materials should highlight risks and harmful behaviors. Previous community surveillance has helped reef monitoring programs to provide early warning for pests such as the Crown of Thorns starfish.
- (3) Conduct baseline evaluations of Ecuadoran seaports, to interdict exotic species before they leave port and sail to the GI.

- (4) Establish a regulatory framework to prevent invasive species entering the Galápagos Islands in ship's ballast water. All vessels carrying ballast water into the Galápagos Islands should either undertake ballast water exchange at sea in compliance with the IMO Guidelines, or not discharge while in the Galápagos Islands.
- (5) Require vessels to have their hulls properly maintained, to prevent invasive species entering Galápagos Islands waters on ship's hulls.
- (6) Stop allowing international cruise vessels entering Galápagos waters. This has been accomplished by cruise ship passengers transferring to smaller tourist boats (16–100 passengers) outside of Galápagos Islands marine park waters. These smaller boats are based in the Galápagos Islands and are used for tourist island-hopping trips.

Galápagos Islands tourism began in earnest within the last few decades. The number of available tourist sites has increased from 35 land-based sites in 1983 to 169 marine sites in 2014. This has greatly increased the connectivity between islands. Most tourists today visit the Galápagos Islands ports of Santa Cruz and San Cristobal on their way to multi-day excursions on live-aboard cruise vessels. Tourists now fly in and then join cruises or stay on land. Island based tourism is also expanding with many inter-island day trips now available for land-based tourists. There is now so much tourism in the Galápagos Islands that the visitors are in danger of loving the islands to death. According to statistics from Galápagos National Park, the number of visitors to the islands increased by 39% between 2007 and 2016, from 161,000 to 225,000. The land-based portion of those tourists jumped 92% from 79,000 to 152,000. One reason for this rapid growth has been the increasing availability of hotels on the islands. In 2006 there were 65 hotels on the islands. In 2017, that number increased to 317. In 2018, a group of 35 tour operators group sent a letter to Ecuador's tourism minister to express their concern about the rising impacts of land-based tourism in the Galápagos Islands. The onslaught of tourists has the potential to harm its much-photographed landscapes and beaches as well as wildlife such as giant tortoises, sea lions and iguanas (Fig. 12). The letter asked the minister to limit and more carefully regulate land tourism.



Fig. 12 Top: The tank vessel *Jessica* ran hard aground in the Galápagos archipelago January 16, 2001, spilling about 200,000 gal of oil into a pristine environment known for unique wildlife and aquatic species. Photo by US Coast Guard; Center: Plastic and other debris constantly floats onto Galápagos beaches. A cleanup program collected 2.2 tons of refuse, including 8000 plastic bottles. Photo courtesy of ibanplastic.com; Bottom: A group of tourists surround a sea lion pup on a Galápagos beach. Photo courtesy of eturboneews.com.

Conclusions

The Galápagos Islands are a living laboratory for evolutionary biologists, biogeographers and ecologists. As with all isolated island groups, the native biota are descendants of a handful of species that flew, swam, or drifted on debris rafts onto the shores of the islands, thousands or even millions of years ago. Many of these founding organisms radiated into groups of endemic species, thereby increasing the biodiversity of the islands. But the Galápagos biota are an odd mixture of plants and animals. There are many native reptile species, but no amphibians; there is an abundance of bird species, but few native mammals. Plants with large flowers and big seeds are absent while grasses and ferns abound. The peculiarities of the Galápagos wildlife intrigued the young Charles Darwin, starting him on an intellectual journey that eventually produced his theory of survival of the fittest and evolution. The colonization of the islands by humans brought ecological disturbances of ever-increasing intensity until the Ecuadoran government began to take steps to ensure conservation of the islands' unique biota. The focus of much of the current conservation efforts is the prevention of the entry and spread of invasive species, both on land and in the sea.

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The Island Biogeography of Wallacea and Krakatoa Island

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Abstract

Wallacea is remarkable for a high degree of endemism. This region consists of three distinct island groups, namely Sulawesi, Lesser Sunda, and Moluccas. As the biggest island in this region, Sulawesi has several distinct forest types that provide habitat for the high number of endemic mammals and birds. Lesser Sunda Islands also has a unique biodiversity; most of its islands were very young geologically and have never been connected to a landmass. Therefore, their flora and fauna evolved independently. Similarly, the Moluccas region has high avian biodiversity, that is, provides home for 579 avifauna species, in which 83 species are endemic to the region. The other island described in this article is Krakatoa Island which is located between the islands of Sumatra and Java in the Republic of Indonesia. Its eruption in 1883 was one of the most violent volcanic events of modern history. This eruption has provided opportunities for long term ecological research on tropical island biogeography and succession. Krakatoa has also been an excellent site for biogeography studies.

Wallacea

Introduction

Alfred Russel Wallace, an explorer and naturalist, was born in 1823 in Usk, Monmouthshire. Summarized from his book *The Malay Archipelago*, he provided a view that the Indonesian Archipelago was inhabited by two distinct faunas, one in the east and one in the west. Based on the distribution of birds, he placed the boundary between Lombok and Bali and between Borneo and Sulawesi. The line that Wallace drew came to be known as Wallace's Line (Fig. 1). This line separates the Asian dominated avifauna of the Greater Sundas (Borneo, Sumatra, Java and Bali) from the Australasian-dominated avifauna of Papua and Wallacea (Sulawesi, Lesser Sunda, and Moluccas).

Wallacea region is known as a distinct island group in Eastern Indonesia (Fig. 1) including Sulawesi (A), Lesser Sunda (B), and Moluccas islands (C). Sulawesi is the largest island within this region, while the Lesser Sunda (Nusa Tenggara) and the Moluccas (Maluku) consist of many small to medium-sized islands. As reported by Burung Indonesia (2014), the largest island, Sulawesi, contributes the largest forest cover (56%) of Wallacea's forest, while the Moluccas and Lesser Sunda have only 24% and 19%, respectively. Evergreen and semi-evergreen forests dominates in Sulawesi and the Moluccas. According to Whitten et al. (1987), forests in Wallacea region is represented by some species of dipterocarps, including *Anisoptera* spp., *Hopea* spp., *Shorea assamica*, and *Vatica* spp. Distinctive ebonies (*Diospyros* spp.) were common in dense clumps in the lowland forests. Meanwhile, Monsoon forest (typically dominated by *Pterocarpus indicus*, also contain the remaining stands of Sandalwood *Santalum album*) dominates in Lesser Sundas.

According to the Köppen-Geiger climate classification, the predominant climate in Sulawesi can be described as the tropical rainforest climate (Af) (En.climate-data, 2018). Besides that, the Sulawesi region has several other different climates. The Central and Southeast region of Sulawesi share similar climate types, namely the oceanic climate (Cfb), the tropical monsoon climate (Am), and the tropical savanna climate (Aw). West Sulawesi has also the oceanic climate (Cfb) and tropical monsoon climate (Am). The Gorontalo region experiences the tropical monsoon climate (Am). Among those regions, North Sulawesi has only the tropical rainforest climate (Af). There is significant rainfall throughout the year in North Sulawesi, even though during the driest month.

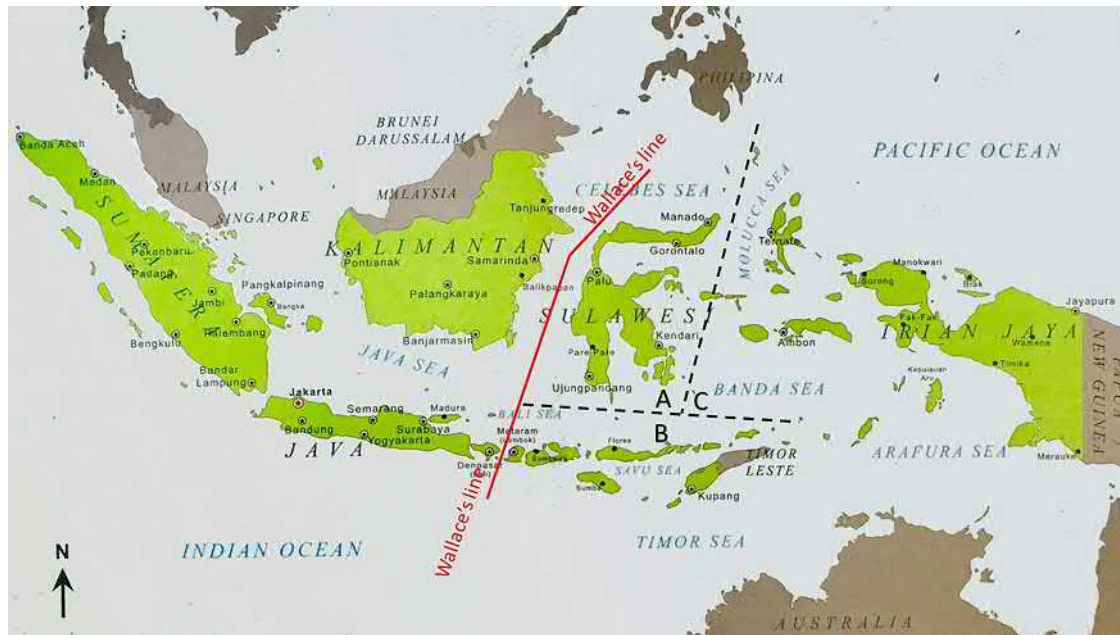


Fig. 1 Wallace's line and group of islands within Wallace region.

The climates of the Lesser Sunda Islands (Nusa Tenggara) are dominated by the tropical savanna climate (Aw) and the tropical monsoon climate (Am). Only a few regions experience the oceanic (Cfb) and the tropical rainforest climate (Af). The Subtropical highland oceanic climate (Cwb) covers only a small region in East Nusa Tenggara. In Moluccas (Maluku), the tropical rain forest climate (Af) predominantly covers the region, followed by the tropical savanna climate (Aw), the tropical monsoon climate (Am) and the oceanic climate (Cfb). Whereas the North Moluccas region only experience two climates, which are the tropical savanna climate (Aw) and the tropical monsoon climate (Am).

Biodiversity

Biodiversity in Wallacea region is very unique, and contains many endemic species. The drivers of speciation within this region include isolation, periodic connection to the Australian and New Guinean land masses, and the complex patterns of tectonic movement and volcanic activity, splitting and re-forming islands (Burung Indonesia, 2014). Table 1 below presents the summary of biodiversity of Wallacea. Examples of Wallacea's fauna are shown in Figs. 2 and 3. The brief review of each main island groups then is described in the following section.

Sulawesi Island

The Wallacea region is home to many endemic species. Sulawesi has the highest endemism because of its long isolation from Asia and Australia, and it has several distinct forest types that provide habitat for a high number of endemic mammals and birds (Whitten et al., 1987). Summarized from Simay et al. (2009), Burung Indonesia (2014) and IUCN (2018), Sulawesi is home to at least 103 endemic species (Table 2), comprised of 4 species from the plant kingdom and 99 species from the animal kingdom. Those from the animal kingdom are four species of butterflies, three species of crustaceans, three species of fishes, four species of amphibians, three species of reptiles, 27 species of birds, and 55 species of mammals. Whereas the endemic plant species are three species of Magnoliopsida and one species of Liliopsida.

Lesser Sunda Islands

The Lesser Sunda Islands (Indonesian: Kepulauan Nusa Tenggara) consist of a group of islands situated north of the Australian continent. The main Lesser Sunda Islands, from west to east, are Lombok, Sumbawa, Sumba, Flores, Alor Archipelago, Wetar, and Timor. Most of those islands belong to the territory of the Republic of Indonesia, except for the eastern part of Timor Island which belongs to the state of Timor Leste.

Most islands of the Lesser Sunda Islands group are very young geologically (1–15 million years old) and have never been connected to a landmass, which means that their flora and fauna evolved independently (De Lang, 2011). It is widely known that the largest lizard in the world, the Komodo Dragon *Varanus komodoensis*, is endemic to this region (Fig. 4). Specifically, the Komodo Dragon inhabits the Komodo Island, Rinca, Gili Motang, Gili Dasami, and Flores (Ciofi et al., 2007). One of the world's rarest turtle namely the Rote Snake-necked Turtle *Chelodina mccordi* is also endemic in this region (specifically in Rote Island), and this species was listed in Appendix II CITES in 2004 (Endarwin et al., 2005).

Table 1 Summary of biodiversity lives in Wallacea region

<i>Taxa</i>	<i>Number of species</i>	<i>Number of endemic species</i>	<i>Examples of the endemic species</i>
Mammals	222 (terrestrial)	127 (57%)	Babirusa <i>Babirusa</i> sp. Anoa <i>Bubalus depressicornis</i> , <i>B. quarlesi</i> . Tarsiers <i>Tarsius</i> sp. Timor Deer <i>Rusa timorensis</i> (Fig. 2)
Birds	711	274 (40%)	Yellow-crested Cockatoo <i>Cacatua sulphurea</i> Flores Hawk-eagle <i>Nisaetus floris</i> Flores Crow <i>Corvus florensis</i> Maleo <i>Macrocephalon maleo</i> (Fig. 3) Timor Imperial Pigeon <i>Ducula cineracea</i> Wetar Ground-dove <i>Gallicolumba hoedtii</i> Timor Green-pigeon <i>Treron psittaceus</i> Komodo Dragon <i>Varanus komodoensis</i> (Fig. 4)
Reptiles	222	99 (44%)	Sulawesian Tortoise <i>Indotestudo forstenii</i> Flores Blind Snake <i>Typhlops schmutzi</i>
Amphibians	48	33 (65%)	Djikoro Wart Frog <i>Limnonectes arathooni</i> Lombok Cross Frog <i>Oreophryne monticola</i>
Freshwater fishes	250	50 (20%)	Duckbilled bunting <i>Adrianichthys kruyti</i> Popta's Bunting <i>Xenopoecilus poptae</i>
Vascular plants	~10,000	15%	Sandalwood <i>Santalum album</i> Eaglewood <i>Aquilaria cumingiana</i> Pitcher plants <i>Nepenthes</i> spp.
Insects (Lepidoptera and Odonata)	–	40	Murphy's Crow <i>Euploea caespes</i> Wallace's Golden Birdwing <i>Ornithoptera Croesus</i> <i>Protosticta rozendalorum</i> <i>Procordulia lompopatang</i>
Freshwater mollusks	NA	NA	<i>Tylomelania kruiemeli</i> <i>Miratesta celebensis</i>

Summarized from Simay et al. (2009), Burung Indonesia (2014) and IUCN (2018).

De Lang (2011) revealed that 29 terrestrial and semi-aquatic snake species were known to inhabit the Lesser Sunda Islands (Nusa Tenggara). Of these, eight were endemic to the area: *Boiga hoeseli*, *Coelognathus subradiatus*, *Dendrelaphis inornatus*, *Stegonotus florensis*, *Cylindrophis opisthorhodus*, *Broghammerus timoriensis*, *Liasis mackloti* and *Typhlops schmutzi*. Insular endemism was only found at the subspecific level, including *Liasis mackloti dunni* (Wetar Island), *Liasis mackloti savuensis* (Sawu Island), *Ramphotyphlops polygrammicus brongersmai* (Sumba Island), *Ramphotyphlops polygrammicus elberti* (Lombok Island) and *Ramphotyphlops polygrammicus florensis* (Flores Island).

The Lesser Sunda Islands also contains high avian biodiversity. For example, 266 avifauna species were found on Lombok Island, 267 in Sumbawa, 292 in Sumba, 335 in Flores, 242 in Komodo, and 323 in West Timor (Avibase Data, 2018). In late 2017, one new avifauna species from family Meliphagidae was found in Lesser Sunda Islands, namely *Myzomela irianawidodoae*. This species is endemic to Rote Island, and was named after the current First Lady of Indonesia Mrs. Iriana Widodo. Another endemic species in this region is the Rinjani Scops Owl *Otus jolandae* (Fig. 5), which was first described by Sangster et al. (2013).

Molucca Islands

The Molucca Islands (Indonesian: Kepulauan Maluku) is situated in the Banda Sea. The major islands are Halmahera, Buru, Ambon, Seram, Ternate, Tidore, and Aru. This region has attracted the interests of many scientists across the past centuries, that is, Georg Eberhard Rumphius (Botanist, *Herbarium Amboinense* published in 1741), Alfred Russel Wallace (Naturalist, *The Malay Archipelago* published in 1890). This region is known from the past as the *Spice Islands of Indonesia*, since it was the world's original source of nutmeg *Myristica fragrans* and clove *Syzygium aromaticum*; a title that contributed to the start of European Colonialism in the region. Sago Palm *Metroxylon sagu* can also be found in several locations in Molucca since it is the source of the staple food for the local community (Sasaoka et al., 2014). Recent data revealed that Molucca has about 97 vascular plants in 53 genera and 34 families, with *Ecua moluccensis* as one of the endemic vascular plant species (Terrestrial-Biozones, 2018).

The Moluccas region has high avian biodiversity. From the Avibase data record (2018), it is known that the Moluccas region provides home for 579 avifauna species, of which 83 avifauna species are endemic to the region. The largest island in this region, Halmahera, play an important role in providing habitat for 25 of 27 of the endemic bird species in North Molucca (Burung Indonesia, 2018). One example is at the Aketajawe-Lolobata National Park, where 55 bird species from 25 families inhabit this conservation area (Arini and Kinho, 2014). Seventeen of these species were identified as endemic to Maluku and Halmahera Islands, namely the Rufous-bellied Triller *Lalage aurea*, Cinnamon-bellied Imperial Pigeon *Ducula basilica*, Scarlet-breasted Fruit Dove *Ptilinopus bernsteinii*, Grey-headed Fruit Dove *P. hyogaster*, Blue-capped Fruit Dove *P. monacha*, Azure Dollarbird *Eurystomus azureus*, Long-billed Crow *Corvus validus*, Paradise-crow *Lycocorax pyrrhopterus*, Wallace's Standardwing *Semioptera wallacei*,



Fig. 2 Timor Deer *Cervus timorensis* foraging on Komodo Island, Komodo National Park. Photo by L.P.E.K. Yuni (2016).



Fig. 3 Maleo birds *Macrocephalon maleo* and their underground nest at the Bogani Nani Wartabone National Park, Sulawesi. Photo by I.P. Yuda (2018).

White-streaked Friarbird *Melitograis gilolensis*, Dusky Friarbird *Philemon fuscicapillus*, Ivory-breasted Pitta *pitta maxima*, Chattering Lory *Lorius garrulus*, White Cockatoo *Cacatua alba*, Moluccan Hanging Parrot *Loriculus amabilis*, Seram Golden Bulbul *Ixos affinis*, Cream-throated White-eye *Zosterops atriceps*. Among those, the White Cockatoo and the Wallace's Standardwing are listed in IUCN Red List,

Table 2 List of some endemic species in Sulawesi Island

Category	English name	Species name	Status	Habitat
Insects Lepidoptera	The Sulawesi pied crow butterfly	<i>Euploea eupator</i>	LC	Terrestrial
Insects Lepidoptera	The Sulawesi striped blue crow butterfly	<i>Euploea configurata</i>	LC	Terrestrial
Insects Lepidoptera	Sulawesi tree-nymph	<i>Atrophaneura palu</i>	DD	Terrestrial
Insects Lepidoptera	Palu swallowtail	<i>Idea tambusisiana</i>	VU	Terrestrial
Arthropods Malacostraca	Harlequin Shrimp Sulawesi	<i>Caridina woltereckae</i>	EN	Wetlands (inland)—Towuti Lake
Arthropoda Malacostraca	Caridina Sulawesi Shrimp	<i>Caridina sulawesi</i>	LC	Wetlands (inland)
Arthropoda Malacostraca	Sulawesi Cardinal Shrimp	<i>Caridina dennerli</i>	CR	Wetlands (inland)—Matano Lake
Vertebrates Pisces	Sulawesi Coelacanth	<i>Latimeria manadoensis</i>	VU	Marine neritic
Vertebrates Pisces	Sulawesi Anchovy	<i>Stolephorus teguhi</i>	DD	Marine neritic
Vertebrates Pisces	Celebes Flathead	<i>Thysanophrys celebica</i>	LC	Marine neritic
Vertebrates Amphibia	Celebes Toad	<i>Ingerophrynus celebensis</i>	LC	Artificial/Aquatic and Marine, Wetlands (inland), Artificial/ Terrestrial, Forest
Vertebrates Amphibia	Celebes Oriental frog	<i>Occidozyga celebensis</i>	LC	Artificial/Aquatic and Marine, Wetlands (inland), Artificial/Terrestrial
Vertebrates Amphibia	Celebes cross frog	<i>Oreophryne celebensis</i>	VU	Forest
Vertebrates Amphibia	Celebes flying frog	<i>Rhacophorus edentulus</i>	LC	Wetlands (inland), forest
Vertebrates Reptilia	Sulawesi forest turtle	<i>Leucocephalon yuwonoi</i>	CR	Stream/river
Vertebrates Reptilia	Celebes tortoise	<i>Indotestudo forstenii</i>	EN	Forest
Vertebrates Reptilia	Rat snakes	<i>Ptyas dipsas</i>	DD	Forest
Vertebrates Aves	Sulawesi Goshawk	<i>Accipiter griseiceps</i>	LC	Forest, savanna
Vertebrates Aves	Sulawesi Serpent-eagle	<i>Spilornis rufipectus</i>	LC	Artificial/terrestrial, savanna, forest
Vertebrates Aves	Sulawesi honey buzzard	<i>Pernis celebensis</i>	LC	Forest
Vertebrates Aves	Sulawesi Hawk-eagle	<i>Nisaetus lanceolatus</i>	LC	Forest
Vertebrates Aves	Sulawesi Dwarf-kingfisher	<i>Ceyx fallax</i>	NT	Forest
Vertebrates Aves	Sulawesi Lilac kingfisher	<i>Cittura cyanotis</i>	LC	Forest
Vertebrates Aves	Sulawesi Masked-owl	<i>Tyto rosenbergii</i>	LC	Shrubland, artificial, terrestrial, grassland
Vertebrates Aves	Sulawesi Scoops-owl	<i>Otus manadensis</i>	LC	Forest
Vertebrates Aves	Sulawesi Nightjar	<i>Caprimulgus celebensis</i>	LC	Forest, shrubland
Vertebrates Aves	Knobbed Hornbill	<i>Rhyticeros cassidix</i>	VU	Forest
Vertebrates Aves	Sulawesi Hornbill	<i>Penelopides exarhatus</i>	VU	Forest
Vertebrates Aves	Sulawesi Hanging-parrot	<i>Loriculus stigmatus</i>	LC	Artificial/terrestrial, forest, shrubland
Vertebrates Aves	Sulawesi Thrush	<i>Cataponera turdoides</i>	LC	Forest

(Continued)

Table 2 (Continued)

Category	English name	Species name	Status	Habitat
Vertebrates Aves	Sulawesi Myzomela	<i>Myzomela chloroptera</i>	LC	Forest
Vertebrates Aves	Sulawesi Cuckoo	<i>Cuculus crassirostris</i>	LC	Forest
Vertebrates Aves	Sulawesi Pygmy woodpecker	<i>Picoides temminckii</i>	LC	Artificial, terrestrial, savanna, forest
Vertebrates Aves	Sulawesi leaf-warbler	<i>Phylloscopus sarasinorum</i>	LC	Forest
Vertebrates Aves	Sulawesi cicadabird	<i>Edolisoma morio</i>	LC	Artificial, terrestrial, forest
Vertebrates Aves	Sulawesi myna	<i>Basilornis celebensis</i>	LC	Savanna, forest, artificial/terrestrial
Vertebrates Aves	Sulawesi Babbler	<i>Trichastoma celebensis</i>	LC	Forest, shrubland, artificial/terrestrial, savanna
Vertebrates Aves	Sulawesi Pitta	<i>Erythropitta celebensis</i>	LC	Forest, wetlands (inland), shrubland, artificial/terrestrial
Vertebrates Aves	Sulawesi drongo	<i>Dicrurus montanus</i>	LC	Forest
Vertebrates Aves	Black-ringed white-eye	<i>Zosterops anomalus</i>	LC	Artificial/terrestrial, forest, shrubland
Vertebrates Aves	Henna-tailed jungle-flycatcher	<i>Cyornis colonus</i>	NT	Forest
Vertebrates Aves	Sulawesi blue fly-catcher	<i>Cyornis omissus</i>	LC	Forest, shrubland
Vertebrates Aves	Sulawesi woodcock	<i>Scolopax celebensis</i>	NT	Forest
Vertebrates Aves	Sulawesi ground-dove	<i>Gallicolumba tristigmata</i>	LC	Forest
Vertebrates Mammals	Sulawesi fruit bat	<i>Acerodon celebensis</i>	VU	Artificial/terrestrial, forest
Vertebrates Mammals	Bear cuscus	<i>Ailurops ursinus</i>	VU	Artificial/terrestrial, forest
Vertebrates Mammals	Sulawesi babirusa	<i>Babrousa celebensis</i>	VU	Wetland (inlands), Forest
Vertebrates Mammals	Lesser naked bat	<i>Cheiromeles parvidens</i>	LC	Artificial/terrestrial, caves and subterranean habitat (non-aquatic), forest
Vertebrates Mammals	Sulawesi shrew	<i>Crocidura lea</i>	LC	Forest
Vertebrates Mammals	Sulawesi tiny shrew	<i>Crocidura levicula</i>	LC	Artificial/terrestrial, forest
Vertebrates Mammals	Sulawesi white-handed shrew	<i>Crocidura rhoditis</i>	LC	Forest
Vertebrates Mammals	Sulawesi shrew mouse	<i>Crunomys celebensis</i>	DD	Forest
Vertebrates Mammals	Luzon shrew mouse	<i>Crunomys fallax</i>	DD	Forest
Vertebrates Mammals	Mindanao shrew mouse	<i>Crunomys melanius</i>	VU	Artificial/terrestrial, forest
Vertebrates Mammals	Katanglad shrew mouse	<i>Crunomys suncoides</i>	DD	Forest
Vertebrates Mammals	Sulawesi naked-backed fruit bat	<i>Dobsonia exoleta</i>	LC	Artificial/terrestrial, caves and subterranean habitat (non-aquatic), forest
Vertebrates Mammals	Central Sulawesi Echiotrix	<i>Echiotrix centrosa</i>	VU	Forest
Vertebrates Mammals	Northern Sulawesi Echiotrix	<i>Echiotrix leucura</i>	EN	Forest (Manado)
Vertebrates Mammals	Sulawesi soft-furred rat	<i>Eropeplus canus</i>	VU	Forest
Vertebrates Mammals	Lowland Sulawesi Haeromys	<i>Haeromys minahassae</i>	VU	Forest
Vertebrates Mammals	Sulawesi harpy fruit bat	<i>Harpyionycteris celebensis</i>	VU	Artificial/terrestrial, forest

Table 2 (Continued)

Category	English name	Species name	Status	Habitat
Vertebrates Mammals	Montane long-nosed squirrel	<i>Hyosciurus henrichi</i>	LC	Forest
Vertebrates Mammals	Lowland long-nosed squirrel	<i>Hyosciurus ileile</i>	VU	Shrub-land, forest, artificial/terrestrial
Vertebrates Mammals	Celebes crested macaque	<i>Macaca nigra</i>	CR	Artificial/terrestrial, forest
Vertebrates Mammals	Booted Macaca	<i>Macaca ochreata</i>	VU	Forest
Vertebrates Mammals	Sulawesi Civet	<i>Macrogalidia musschenbroekii</i>	VU	Grassland, forest, artificial/terrestrial, shrub-land
Vertebrates Mammals	Dollman's Sulawesi Maxomys	<i>Maxomys dollmani</i>	DD	Forest
Vertebrates Mammals	Hellwald's Sulawesi Maxomys	<i>Maxomys hellwaldii</i>	LC	Forest
Vertebrates Mammals	Musschenbroek's Sulawesi Maxomys	<i>Maxomys musschenbroekii</i>	LC	Forest, shrubland, artificial/terrestrial
Vertebrates Mammals	Watts's Sulawesi Maxomys	<i>Maxomys watti</i>	EN	Forest
Vertebrates Mammals	Diurnal Sulawesi shrew rat	<i>Melasmothrix naso</i>	DD	Forest
Vertebrates Mammals	Sulawesi free-tailed bat	<i>Mops sarasinorum</i>	DD	Forest, artificial/terrestrial
Vertebrates Mammals	Giant Sulawesi rat	<i>Paruromys dominator</i>	LC	Forest
Vertebrates Mammals	Secretive dwarf squirrel	<i>Prosciurillus abstrusus</i>	DD	Forest
Vertebrates Mammals	Whitish dwarf squirrel	<i>Prosciurillus leucomus</i>	DD	Forest
Vertebrates Mammals	Celebes dwarf squirrel	<i>Prosciurillus murinus</i>	DD	Forest
Vertebrates Mammals	Sanghir Squirrel	<i>Prosciurillus rosenbergii</i>	LC	Artificial/terrestrial, forest
Vertebrates Mammals	Weber's Sulawesi dwarf squirrel	<i>Prosciurillus weberi</i>	DD	Forest
Vertebrates Mammals	Hoffmann's Sulawesi rat	<i>Rattus hoffmanni</i>	LC	Shrublands, forest, artificial/terrestrial
Vertebrates Mammals	Lampobatang Sulawesi rat	<i>Rattus mollicomulus</i>	VU	Forest
Vertebrates Mammals	Sulawesi Horseshoe bat	<i>Rhinolophus celebensis</i>	LC	Caves and subterranean habitat (non-aquatic), forest
Vertebrates Mammals	Sulawesi rousette	<i>Rousettus celebensis</i>	LC	Artificial/terrestrial, caves and subterranean habitat, forest
Vertebrates Mammals	Sulawesi giant squirrel	<i>Rubisciurus rubriventer</i>	VU	Artificial/terrestrial, forest
Vertebrates Mammals	Sulawesi yellow house bat	<i>Scotophilus celebensis</i>	DD	Forest
Vertebrates Mammals	Sommer's Sulawesi rat	<i>Sommeromys macrorhinos</i>	DD	Forest
Vertebrates Mammals	Small Sulawesi cuscus	<i>Strigocuscus celebensis</i>	VU	Forest
Vertebrates Mammals	Wallace's stripe-faced fruit bat	<i>Styloctenium wallacei</i>	NT	Artificial/terrestrial, forest
Vertebrates Mammals	Sulawesi warty pig	<i>Sus celebensis</i>	NT	Forest, wetlands (inland), artificial/terrestrial, artificial/aquatic, marine, grassland
Vertebrates Mammals	Southeastern Mountain Taeromys	<i>Taeromys arcuatus</i>	LC	Artificial/terrestrial, forest
Vertebrates Mammals	Greater Taeromys	<i>Taeromys callitrichus</i>	DD	Forest
Vertebrates Mammals	Long-tailed Taeromys	<i>Taeromys celebensis</i>	LC	Forest

(Continued)

Table 2 (Continued)

Category	English name	Species name	Status	Habitat
Vertebrates Mammals	Central Mountain Taeromys	<i>Taeromys hamatus</i>	DD	Forest
Vertebrates Mammals	Small-eared Taeromys	<i>Taeromys microbullatus</i>	DD	Forest
Vertebrates Mammals	Reddish-furred Taeromys	<i>Taeromys punicans</i>	DD	Forest
Vertebrates Mammals	Northeastern Mountain Taeromys	<i>Taeromys taerae</i>	VU	Forest
Vertebrates Mammals	Pygmy Tarsier	<i>Tarsius pumilus</i>	DD	Forest
Vertebrates Mammals	Spectral Tarsier	<i>Tarsius Tarsier</i>	VU	Artificial/terrestrial, forest
Vertebrates Mammals	Long-tailed Sulawesi Shrew rat	<i>Tateomys macrocercus</i>	DD	Forest
Vertebrates Mammals	Tate's Sulawesi Shrew rat	<i>Tateomys rhinogradoides</i>	DD	Forest
Plants Magnoliopsida	–	<i>Pterospermum celebicum</i>	LC	Forest
Plants Magnoliopsida	–	<i>Magnolia sulawesiana</i>	EN	Forest
Plants Magnoliopsida	–	<i>Diospyros celebica</i>	–	–
Plants Liliopsida	–	<i>Halophila sulawesii</i>	DD	–

Summarized from Simay et al. (2009), Burung Indonesia (2014) and IUCN (2018).

Note: LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; DD, data deficient.



Fig. 4 Komodo Dragon *Varanus komodoensis* feeding on a buffalo carcass at Wae Waso Savannah, Komodo National Park. Photo by M. Azmi (2018).

as well as in Appendix II CITES (IUCN, 2018). Due to its notable endemism, Halmahera and its adjacent islands (i.e., Morotai, Bacan, Obi, etc.) are recognized as the World's 10th Endemic Bird Area (EBA) by BirdLife International; it is well known as the Northern Maluku Endemic Bird Area (Stattersfield et al., 1998).



Fig. 5 Rinjani Scops Owl *Otus jolandae* perched on branches at Kerandangan Natural Park, Lombok Island. Photo by M. Fathurrozi (left) and W. Amin (right) in 2018.

Threats to Wallace Biodiversity and Conservation Efforts

It has been described above that Wallacea region provides home for numerous endemic species. However, some concerns need to be addressed in order to preserve the unique biodiversity of the region. There are several threats to biodiversity in Wallace region (Irham, 2012; Arini and Kinho, 2014; Gillespie et al., 2015; Riyanto et al., 2017; IUCN, 2018). Some terrestrial animals were hunted or trapped for food (i.e., Sulawesi Giant Squirrel, Sulawesi Fruit Bat) or as treatment for ailments (i.e., Sulawesi Hornbill) or traded as pets (i.e., White Cockatoo, Wallace's Standardwing). Similarly, aquatic animals were also fished and harvested as food sources (i.e., Harlequin Shrimp Sulawesi, Sulawesi Forest Turtle). Furthermore, logging/wood harvest or deforestation cause major threats to biodiversity in the Wallace region (i.e., to both Herpetofauna and Avifauna). Human activities, such as residential and commercial development, energy production, mining activity, or the modification of natural systems, such as water resource management, also threaten biodiversity in the region (i.e., Harlequin Shrimp in Sulawesi). Other threats to the endemic species include the invasion of non-native alien species and diseases (i.e., Nile perch towards Caridina Shrimp). Considering these problems, conservation efforts/program are urgently implemented within this region. Since resources are limited for this region, conservation programs often compete with other priorities that provide more economic benefits for people in the Wallacea region (Burung Indonesia, 2014).

One approach conducted by the Indonesian Government was to ratify key international ecological conventions. For example, the Indonesian Government ratified the Ramsar Convention (Convention on Wetlands of International Importance especially in Waterfowl) in 1991, which resulted in the establishment of seven Ramsar sites in Indonesia, including Aopa Watumohai Peat Swamp National Park in South East Sulawesi region. The Indonesian government also ratified the United Nations' Convention on Biological Diversity by issuing the Indonesia Constitution Number 5 year 1994 (link: <https://pih.kemlu.go.id/files/UUU-594.pdf>), also ratified the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) by issuing the Presidential Decree Number 43 year 1978 (link: <https://surajis.files.wordpress.com/2015/06/keppres-no-43-tahun-1978-tentang-ratifikasi-cites.pdf>).

The establishment of conservation areas in Indonesia, including within the Wallacea region, reflects the strong commitment of the Indonesian government to preserve their valuable biodiversity. Indonesia has established 521 conservation areas, including 221 nature reserves, 75 wildlife reserves, 50 national parks, 115 nature recreational parks, 13 game hunting reserves, and 23 grand forest parks (FORCLIME, 2017). Among those, Sulawesi Island has 21 nature reserves, 17 wildlife reserves, and 8 national parks. The Lesser Sunda Islands region contains 13 nature reserves, 5 wildlife reserves, and 6 national parks (one example is presented in Fig. 6), and the Moluccas Islands contain 18 nature reserves, 5 wildlife reserves, and 2 national parks.

Krakatoa

Introduction

The island of Krakatoa (or Indonesian: Krakatau) is in the Sunda Strait between the islands of Sumatra and Java and is part of the Republic of Indonesia. This recent volcano group consists of four islands, namely Rakata, Sertung, Panjang, and Anak Krakatau. The first three islands are the remaining formation of Mt. Krakatau's ancient caldera. Meanwhile, Rakata Island is a volcano that grew together with the Danan and the Perbuatan (Self and Rampino, 1981; Winchester, 2003). Its eruptions in 1883 were some of the most violent volcanic events of modern history. The sounds of the explosions were heard in Sri Lanka (formerly Ceylon, in southern



Fig. 6 Kelimutu National Park. Photo by L.P.E.K. Yuni (2016).

India), Myanmar (formerly Burma), Manila (the Philippines), Doreh in Geelving Bay (New Guinea), and in Perth (Australia). It was estimated that the sound was transmitted over one-fifteenth of the surface of the earth, at a radius of about 3333 km—if a circle is drawn from Krakatau (Verbeek, 1884). The explosion was followed by a massive tsunami of which the most destructive wave was estimated at about 30–41 m in height (Metzger, 1884). Villages and towns near Krakatau, in both Sumatra and Java, were destroyed or seriously damaged; 36,417 (Metzger reported 32,635 killed by the eruption through November 1883 (2)) people were killed and thousands were injured (Winchester, 2003). The Volcanic Explosivity Index (VIE) of the 1883 eruption was 6, and rock materials were ejected across approximately 25 km³. Two-thirds of the island of Krakatau was destroyed.

Post 1883 Eruption: Current Activity

The 1883 eruption nearly wiped out two-thirds of Krakatau. Since 1927, a number of submarine eruptions have formed a new island in the original location. The island known as *Gunung Anak Krakatau* ("The Child of Krakatau") appeared in 1929, and has continued to grow at an average growth rate of approximately about four meters of height per year.

In 2000, the volume of the mountain body was estimated 5.52 km³. If Anak Krakatau's growth in height and volume remain consistent, then its volume in 2020 will be bigger than the volume of Rakata, Danan and Perburuan prior to the 1883 eruption (Sutawijaya, 2006). Since 1927, 45 series of eruptions have been confirmed, lasting between 3 and 12 months, and the VIEs varied from 1 to 3 (Global Volcanism Program, 2013). The eruption in 1952 destroyed the vegetation of Anak Krakatau Island (Thornton et al., 1988).

Anak Krakatau has continuously erupted since June 2018, with a massive eruption (Fig. 7) recorded in December 2018 (PVMBC, 2018b). On 22 December 2018, the eruption caused tsunami waves that wiped out the coastal areas of Banten (West Java) and Lampung (Southern Sumatra). At least 426 peoples were reported killed and thousands were injured due to the tsunami (BNPB, 2018). Due to these eruptions, the height of Anak Krakatau decreased to about 110 m asl (formerly was 338 m asl) since it lost about 150–180 million m³ of its volume (PVMBC, 2018a).

Biological Studies

Krakatau has attracted the interest of many biologists since the 1883 eruption. This eruption provided opportunities to research long term ecological succession in the tropics and explore the facets of island biogeography. For example, after the biota of Krakatau was totally destroyed, floral recolonization has been studied since 1886; this was initiated by Professor Treub of Buitenzorg, who visited the island 3 years after the eruption (Hill, 1937). Meanwhile the study of the faunal recolonization started in approximately 1908 (Thornton et al., 1988). Further intensive studies on the recolonization process from 1919 through 1933 were conducted by (Dammerman, 1922, 1948) and (Docters van Leeuwen, 1936).

There were no field surveys in the islands during the Asia-Pacific War (Yamane, 2013). In 1979, a two phase program called the Krakatoa Centenary Expedition was launched by British scientists to comprehensively survey the area just 100 years after the



Fig. 7 An aerial view of Anak Krakatau volcano during an eruption on 23 December 2010. Scientists say that the volcano is now only about one-quarter of its size after its eruption and collapse (Nurul Hidayat/ Bisnis Indonesia).

catastrophic 1883 eruption (Thornton and Rosengren, 1988). Animal field surveys resumed by Japanese and Australian team in the 1980s (Yamane, 2013).

Various study topics have been carried out in the islands, included recolonization (Thornton et al., 1988; Whittaker et al., 1989; New, 2015), development of flora and vegetation succession (Hill, 1937; Whittaker et al., 1989; Partomihardjo et al., 2004), forest dynamics (Whittaker et al., 1989), plant-animal interactions (Whittaker and Jones, 1994; Whittaker and Turner, 1994), the relevance of island biogeography theories (Thornton et al., 1988, 1990, 2002; Bush and Whittaker, 1993; Yukawa et al., 2000; Zabka and Netwig, 2002), and the consequences of colonization on genetic diversity (Barber et al., 2002; Parrish, 2002; Zavodna et al., 2005).

Biogeography and Biodiversity

The Krakatau Islands have been an excellent site for biogeography studies for the following reasons: (1) well known starting points of re-colonization, (2) very little human influence during the period of re-colonization, (3) well defined sources of colonization from Sumatra and Java, and (4) a well-documented biological history (Zabka and Netwig, 2002). MacArthur and Wilson (1967) tested their equilibrium model of immigration and extinction processes using their rate of recolonization by bird and vascular plants in the Krakatau Islands. They used bird data through 1933 and concluded that the resident terrestrial bird species on Rakata and Sertung had approached equilibrium, while the vascular plant species were still increasing. More recent studies using additional data on vertebrates collected from 1889 through 1986 revealed that vertebrate colonization and species turn-over in the islands has continued (Thornton et al., 1988). This study also reported that the actual number of vertebrate species was 9 terrestrial reptiles, 36 resident terrestrial birds and 15 species of bats. Among of them were recent colonizers: Malay False Vampire Bat *Megaderma spasma*, the insectivorous Whiskered Bat *Myotis muricola*, the Large Fruit Bat *Pteropus vampyrus*, and the Tokay *Gekko gecko* and King Gekko *monarchus*.

Zabka and Netwig (2002) found 44 Salticid (spider) species in the islands. However, they revealed that there was no correlation between area and species diversity. Even though the smallest island, Anak Krakatau had the richest species diversity of spider (28 species), compare to Rakata (22 species), Panjang (20 species) and Sertung (16 species).

The other islands in the Sunda Strait, such as Sebesi, Sertung and Panaitan, played important roles as stepping stones for colonization of the Krakatau Islands from Sumatra and Java. Sebesi Island acted as stepping stone for the colonization of butterflies (Yukawa et al., 2000). However other studies suggested that Sebesi Island had a little role as a stepping stone for colonization of terrestrial birds, reptiles, bats, land molluscs or plants (Thornton et al., 2002).

Acknowledgments

The authors acknowledge generous contribution from Muhammad Azmi of Komodo Survival Program for his Komodo Dragon photo. Great appreciation is also extended to Wahyudi Amin of Kerandangan Natural Park at Lombok Island, as well as Muhammad

Fathurrozi of Biology Study Program, Faculty of Mathematic and Natural Sciences, Udayana University for their Rinjani Scops Owl photos. The authors would also like to thank Nurul Hidayat and Bisnis Indonesia for their generosity allowing us to use their aerial photo of Krakatoa eruption in December 2018.

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Biogeography and Chemical Risks on Islands

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Abstract

The Marshall Islands consist of 29 low altitude atolls comprising corals and foraminifera sand, which makes them vulnerable to natural disasters and climate change. The large amount of precipitation sustains the island's biodiversity (Whitehead and Jones, 1969; Yamaguchi et al., 2009). Majuro, the capital city of the Marshall Islands, has one of the longest human resident histories of all atolls worldwide, for more than 2000 years (Yamaguchi et al., 2009). Across the islands, the portmanteau biota of pigs, dogs, chickens, taro, and breadfruit were transported from European ancestors (Crosby, 1986). However, World War II left the islands covered with radioactive chemicals and heavy metals, the bioaccumulation of which has had adverse effects on plants, animals, and humans inhabiting the islands (Odum, 1971). Adverse effects of chemicals may be found in water, air, and food. Proper risk management is needed to handle these substances of war and modernization.

Introduction

Many coral reef islands exist worldwide. Coral reefs are divided into three groups, namely, fringing reef, barrier reef, and atoll. In the case of atolls, carbonate platforms have grown on sinking volcanic edifices (Darwin, 1842) and comprised an annular reef rim surrounding a central lagoon (Woodroffe et al., 1999) (Fig. 1). About 500 atolls are present around the world, most of which are located in the equatorial Pacific Ocean, which has a circumtropical climate zone (e.g., Fujita et al., 2009; Yasukochi et al., 2014).

The Marshall Islands consist of 29 atolls and five small coral islands that are spread over 1300 km east–west and 1500 km north–south and scattered irregularly in two vaguely defined chains that are named Ralik and Radak (Ratak) for the northwest to the south-east groups, respectively (Thomas, 1989; Yamaguchi et al., 2009). The total land area in the Marshall Island republic is ~181 km, and the total area including lagoons is about 11,664 km (Thomas, 1989).

Among atolls and islands, namely, Utrok, Kwajalein, Maloelap, and Majuro, radiocarbon dating of carbide was reported as 2000 years cal BP, which corresponds to the earliest age of settlement area on the high islands in East Micronesia (Yamaguchi et al., 2009).

Sea-level fluctuations in the Holocene triggered the formation of reef islands (Dickinson, 2003). As the sea levels rose, corals grew vertically to the surface of the sea so zooxanthellae could carry on photosynthesis; after the sea level stabilized around 2000 BC, the corals continued to grow laterally; this period lasted for about 2000 years (Fig. 2) (Dickinson, 2003). After the

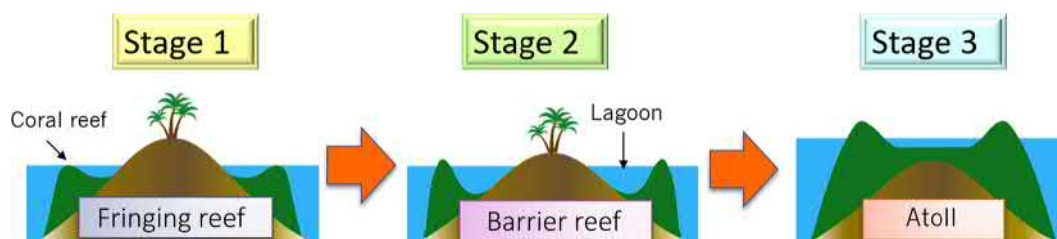


Fig. 1 Developing stage of coral reef islands. Depending on the coral development and the degree of volcano subsidence, each stage is called fringing reef, barrier reef, and atoll.

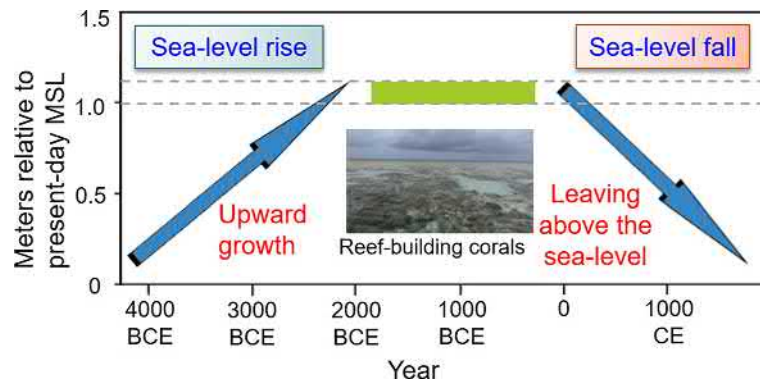


Fig. 2 Reconstructed sea-level curve for the late Holocene in the Marshall Islands. Vertical green bar indicates the elevation differences between the present-day mean sea level (MSL) and modern microatolls. Data from Kayanne H, Yasukochi T, Yamaguchi T, Yamano H, and Yoneda M (2011) Rapid settlement of Majuro Atoll, Central Pacific, following its emergence at 2000 years CalBP. *Geophysical Research Letters* 38: L20405; Kench PS, Owen SD, and Ford MR (2014) Evidence for coral island formation during rising sea level in the Central Pacific Ocean. *Geophysical Research Letters* 41: 820–827.

late Holocene, the tropical Pacific sea level fell, exposing the mid-Holocene reef flats, and they now stand well above sea level (Dickinson, 2003, 2004). The “close-over date” signifies when the seawater surface at high tide falls below the top of the coral, triggering coral land formation; this close-over date in the Marshall Islands (Table 1) was reported to be 700 AD (Dickinson, 2009). The magnitude of highstand in the Marshall Islands and Kiribati was updated by Kayanne et al. (2011), Kench et al. (2014), and Yamano et al. (2017). Yamano et al. (2017) pointed out issues with dating samples based mainly on cemented coral rubble deposits, and they encouraged a re-examination of the timing and magnitude of the late Holocene sea-level high stand at Tuvalu, which suggested 2.3–2.4 m above the present sea level (Schofield, 1977; Dickinson, 1999, 2009) (Table 1).

Islands began to form after reef flats emerged above the sea level and wave energy was reduced (Yasukochi et al., 2014). Unconsolidated calcareous bioclastic sands and gravels (Fig. 3) deposited on the reef flats (e.g., Perry et al., 2011; Yasukochi et al., 2014).

After the core islets emerged, the earliest islanders established habitations at around 2000 BP in Laura on the Majuro Atoll (Yamaguchi et al., 2005, 2009) (see “Portmanteau Biota” section).

The Marshall Islands are geographically isolated from mainland (Yamaguchi et al., 2009). Their isolation from continental species pools increased endemism and also made these island ecosystems hypersensitive to the introduction of exotic species. Human transport (accidentally or intentionally, called the “transported landscape”) of portmanteau biota from Europe altered natural landscapes (e.g., Crosby, 1986; McNeill, 1994; Yamaguchi et al., 2009) (see “Portmanteau Biota” section).

In this review, we discuss the biogeography, unique history, and ecosystems of the Marshall Islands, and how the chemical risks have arisen as modern issues.

Biodiversity Trends of Flora

The flora of the Marshall Islands is divided into tropical forests, cultivation lands, and seagrass areas. The tropical forest area is divided into indigenous and planted flora.

Mixed broadleaf forest is the most popular and obvious type of vegetation in undisturbed areas in the Marshall Islands; typical broadleaf forest of *Tournefortia argentea*, *Guettarda speciosa*, *Pisonia grandis*, *Pandanus tectorius*, *Allophylus timoriensis*, *Cordia subcordata*, *Hernandia sonora*, and other less common species was observed in the inner land (Thomas, 1989). The Marshall Islands spread from the Taongi Atoll at lat. 14°41'N south to the Ebon Atoll at lat. 4°30'N, resulting in varied annual precipitation throughout the islands (see “Required Conditions for Biodiversity” section).

Table 1 Highstand magnitude, tidal range, and cross over date according to the data from Dickinson (2009)

Island	Highstand magnitude (m)	Tidal range (m)	Crossover date (CE)
Marshall Islands	1.1 ^a	1.6	700
Kiribati–Tungaru chain	1.0 ^b	1.5	1000
Tuvalu	2.3	1.6	1100
Tokelau	1.8	1.0	1000
Northern Cook Islands	1.1	0.6	900
Northern Tuamotu Archipelago	1.0	0.3	900

The data of highstand magnitude in Marshall Island^a and Kiribati^b were acquired from Kayanne et al. (2011), Kench et al. (2014), and Yamano et al. (2017), respectively.

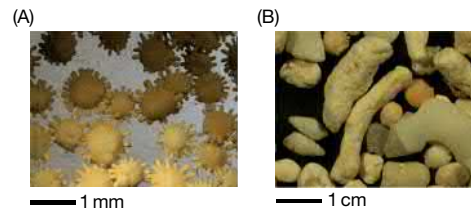


Fig. 3 Calcareous bioclastic materials, which constitute the sediment of coral reef islands. (A) Foraminifera (*Calcarina* spp.) and (B) Coral gravels and shells.

Mangrove vegetation exists in some of the areas of heaviest rain, such as Jaluit, Arno, and Ailinglapalap Atolls in the south (Thomas, 1989). Northward mangrove basins, especially *Bruguiera*, are situated in low and wet inland areas; in some cases, the Marshallese planted the propagules of *Bruguiera*, forming dense, pure stands; however, they did not spread in areas that have no connection with the sea (Thomas, 1989).

In some cases, indigenous plants survived as windbreaks. The windward sides of the islands are left more or less intact to protect the coconut plantations and taro pits from salt spray, providing a reservoir of natural diversity and food and copra production (Thomas, 1989).

Among cultivated trees, coconut and breadfruit were significant in pre-European traditional subsistence (Rappaport, 1963). People preserved breadfruit into a semifermented paste called “Bwiro,” which is still produced in quantity and regarded as a succulent addition to the post-breadfruit season diet (Dye, 1987). Traditional pit cultivation is also popular in the Marshall Islands. Phytogeographical studies indicated that similar to banana and breadfruit trees, wet taro can be cultivated on atolls where the mean annual precipitation is more than 2000 mm (e.g., Stoddart, 1992; Fosberg, 1984; Yamaguchi et al., 2009). The pits for taro cultivation are dug in the interiors of the large islands (Yamaguchi et al., 2009). Pits are filled with decomposing vegetable matter, such as *Colocasia* and *Cyrtosperma*, and the most edible taro genera, sugar cane, and a few plants useful as food and medicines are planted (Thomas, 1989).

The cultivation of aroid crops on atolls was limited to areas of low salinity, as well as sites modified by excavation for composting (Rappaport, 1963). The transformed areas were generally small, although primary productivity in taro pits was probably higher than that in any unmodified portion of the ecosystem (Rappaport, 1963). Among the root crops, tubers of *Cyrtosperma*, cultivated for its edible corm, have the highest carbohydrate content per unit among the aroids and are able to hold up against high water levels or flooding (Yamaguchi et al., 2009). This species is adaptable to a fluctuating water table (Lambert, 1982), explaining why *Cyrtosperma* has been the main aroid grown across the Marshall Island atolls (Yamaguchi et al., 2009). However, in Majuro, *Cyrtosperma* pits have been abandoned. The introduction of pigs led to a decrease in *Cyrtosperma* and *Tacca leontopetaloides* because of the animals’ rooting (Dye, 1987).

The copra tree industry has grown since the Germans first occupied the atoll in 1885 (Rappaport, 1963) and supports some aspects of the atoll’s economy (Riley, 1987; Kai, 2006). The present flora of the atoll began with the German occupation in the Marshall Islands in 1888, with the large increase in coconut plantations (Dye, 1987).

Sea grasses are rare in the Marshall Islands; only two stands of *Thalassia hemprichii* and *Cymodocea rotundata* are found in the shallow water of Ujelang, Ailinglapalap, and Majuro Atolls (Thomas, 1989). In particular, *C. rotundata* has flourished on lagoon shoals around the central part of the Laura Island in Majuro. *Halimeda* spp., a calcareous green alga with flake-like segments, constitutes the most abundant sediments of the lagoon (Thomas, 1989).

Biodiversity Trends of Fauna

The natural diversity of the Marshall Islands is higher than the dry northern atolls (Thomas, 1989). Marine and forest animals received commercial attention in the 19th century; for example, a remarkable market existed for sea cucumbers (Class: Holothuroidea) in China (McNeill, 1994).

For island-specific biota, nonisland creatures often become a threat. For example, accidentally introduced rats onto the uninhabited Taongi Atoll from support boats, visiting yachts, and fishing birds quickly decimated native bird populations (Thomas, 1989). Pigs, fowl, dogs and cats, transported from other continents, are abundant on the atoll today (see “Portmanteau Biota” section).

Regarding the characteristics and habitats of birds, we summarize the reports of Thomas (1989) and Hatheway (1953).

Birds are the most remarkable group of terrestrial animals in the Marshall Islands (Thomas, 1989). Three major feeding habitat categories of seabirds in the Marshalls are coastal (beaches, reefs, and lagoons), offshore (near islands or atolls), and pelagic; ranges may overlap or may vary by season (Thomas, 1989).

Seventy resident bird species (31 seabird species and 39 land and fresh water birds) have been recorded in the Marshall Islands (Thomas, 1989). Migrant shorebirds, such as white terns (*Gygis alba*) and noddies (*Anous sp.*), are usually found away from human activity. With no human habitation and few visitors, the northern Ralik Island chain has become an important breeding place for these species (Thomas, 1989).

Large numbers of great frigate birds (*Fregata minor*) and red-footed boobies (*Sula sula*) were observed on the atoll; red-footed boobies are the dominant nesting species, with an estimated 500–1000 individuals on Bikar, 250 on Jabwelo, and 150 on Almaní (Thomas, 1989). The groves of *Pisonia* trees serve as rookeries for numerous fish-eating seabirds on sandy soils near the lagoon (Hatheway, 1953). Destruction of *Pisonia* forests leads to a decrease in bird populations here (Thomas, 1989).

Hatheway (1953) reported that birds appeared to prefer branches of the *Pisonia* to those of any other trees; for example, the tops of large *Pisonia* trees on Arno Atoll were always crowded with flocks of roosting and nesting seabirds. The fruits of *P. grandis* are glutinous and adhere to the feathers of wide-ranging seabirds, which roost and nest in its branches (Hatheway, 1953). The presence or absence of local phosphate deposits in the interiors of many islands is probably not a coincidence (e.g., Hatheway, 1953; Mulder and Ellis, 2010; Ito et al., 2018a). Large flocks of roosting seabirds enrich the soil with their droppings (Dye, 1987). The droppings of these birds would eventually result in the formation of phosphatic rock, as observed on the Takleb Island; present local deposits of phosphatic rock may well coincide with former *Pisonia* groves (Hatheway, 1953). The islets, Takelib and Nami had been traditionally reserved as “bird islets” until 1876 and have expensive deposits of phosphatic rock underlying shallow humic topsoil (Dye, 1987).

However, when sea birds on coral atolls were driven out by human settlements, the soils could no longer be replenished with the phosphate and nitrate contents of guano (Fosberg, 1953; Hatheway, 1953). Fosberg (1953) pointed out that another possible cause of the loss of additional phosphate from island ecosystems could be the export of large quantities of phosphorous-rich copra.

The Marshall Islands are also famous for coconut crab (*Birgus latro*), endangered Hawksbill turtles (*Eretmochelys imbricata*), and threatened green turtles (*Chelonia mydas*) (Thomas, 1989; IUCN, 1982, 1983). The nearshore habitats support various species of fish, of which diversity is similar between the northern and southern Marshalls (Randall and Randall, 1987). Small skinks (*Scincella lateralis*), geckos (*Gekkonidae*), insects, and Polynesian rats (*Rattus exulans*) are found across the islands. Polynesian rats are common on Bikar and Jabwelo (Thomas, 1989).

Nostoc is a bacterial species that can fix nitrogen serving as a nutrient source for pioneer ecosystems on atolls, of which abundant colonies appear on coral sand flats and also on the flat exposure of lithified limestone after rain or heavy dew, drying black when exposed to the sun (Thomas, 1989).

Portmanteau Biota

The ancestors of the inhabitants of islands brought pigs, dogs, chickens, taro, breadfruit, and bananas from their original lands and recreated the scenery of their homes in their new landscapes; thus, a “transported landscape” has been created by these “portmanteau biota” (Anderson, 1952; Crosby, 1986; McNeill, 1994; Yamaguchi et al., 2009), as explained below.

Most people in Micronesia, including in the Marshall Islands, speak a language belonging to Nuclear Micronesian, one of the proto-Oceanic subgroups closely correlated with the eastward expansion of the Lapita cultural complex (Yamaguchi et al., 2009). Lapita peoples practiced distinctive irrigation in Melanesia, and cultivated root vegetables, *Colocasia* and *Cyrtosperma*, in natural squashy swales located at the back of the beach terraces where their homes are also located (Kirch and Hunt, 1997; Kirch and Lepofsky, 1993).

The islands where they moved were targets of environmental disasters of one sort or another, such as drought, cyclone, tsunami, volcanic eruption, and flood (McNeill, 1994). Faced with these disasters, island settlers tried to turn their new homes into familiar and manageable landscapes (McNeill, 1994). They created suitable “transported landscapes” (Anderson, 1952) to the best of their abilities by importing what Crosby had called a “portmanteau biota” (Crosby, 1986). When people first encountered the strange environment of the isolated atolls, they brought seed tubers and the knowledge to cultivate swamp taro in hydromorphic terrain (Yamaguchi et al., 2009). This landscape has continued for about 2000 years, one of the longest human histories in atolls (Yamaguchi et al., 2009).

“Portmanteau biota” also caused an ecological homogenization based on a small number of widely distributed species (McNeill, 1994). For example, the Polynesian portmanteau biota consisted dominantly of three or four animals, such as rat, dog, chicken, and pig, and several edible plants, such as coconut, taro, and breadfruit, that have been widespread over the Pacific (McNeill, 1994).

Regular or even sporadic interisland voyages triggered the spread of countless species, including parasites, insects, rodents, and other small land predators, and weeds and other plants whose seeds could be accidentally lodged and transported in canoes (Murdoch, 1963). These species are transplanted to islands, where their respective ecological niches were either unoccupied or occupied by weak autochthonous forms and where the forms they preyed on were unprotected and vulnerable. Therefore, introduced species repeatedly wreaked havoc on the native fauna and flora, extinguishing native species prior to documentation of their range and distribution (Murdoch, 1963).

Indigenous flora primarily survived in unoccupied areas (Murdoch, 1963), although some species survived under or within plantations (Rappaport, 1963). Even when exotic forms were not rejected, some were established less easily and less extensively than others (Rappaport, 1963). The establishment of introduced root crops, such as taro-like plants, generally required painstaking cultivation (Rappaport, 1963). Breadfruit cultivation was possible but limited by calcareous soil (Catala, 1957) and by the sensitivity of the trees to salt water spray or inundation (Fosberg, 1953). Some animals, such as rats, established readily (Rappaport, 1963).

The portmanteau biota has a second phase. The initial arrival of Europeans and their portmanteau biota was a disaster for lowland organisms and soils across the islands (Fosberg, 1992; McNeill, 1994). Many native species became extinct, and others

found their domains reduced by the onset of the invaders (Fosberg, 1992). For European residents, transporting exotic species, such as pineapple, pumpkin, potato, and cattle, as well as pet dogs and cats, became a way of life (Yamaguchi et al., 2009).

Humans are also an exotic biotic element in island ecosystems (Rappaport, 1963) with population density increasing over the last several decades (Spennemann, 1992). Currently greater than 20,000 people live in Majuro (Osawa et al., 2010). The population center moved to the east end of the atoll after World War II (Xue, 2001). This east area called Djarrit-Uliga-Delap (D.U.D) is composed of three islets. D.U.D contains 70% of the total population of Majuro (Spennemann, 1992). The remaining 6500 people live in less urbanized areas on the north and west sides, in Laura, Calalen, and Jelto.

Thomas (1989) suggested that increasing development activities would lead to the overexploitation of resources, the destruction of habitats, loss of key species, and breakdown of natural systems that have come before the environmental disasters that have occurred in other parts of the world. Severe soil erosion is an example of damage caused by development activities and is attributed to poor land use practices and forest exploitation; reefs and beaches are destroyed or degraded by siltation and dredging construction materials; lagoons are contaminated by urban wastes; and fisheries are depleted because of overexploitation and illegal fishing practices (Thomas, 1989).

Many species are threatened with extinction due to exploitation and environmental pollution. Here, the rate of species loss is high due partly to the small and isolated nature of the island habitats; in most cases, the lost species and their habitats are irreplaceable to biological diversity in the national, regional, and global viewpoints (Thomas, 1989). Intensive urbanization of the population, as seen in D.U.D (Xue, 2001), leads to overfishing and loss of marine biodiversity (Thomas, 1989).

Required Conditions for Biodiversity

Several factors contribute to terrestrial biodiversity, such as atoll size, height above sea level, vulnerability to sea-level rise and storms, precipitation, insufficient groundwater, and distance from mainland (Wiens, 1962; Niering, 1963; Whitehead and Jones, 1969; Stoddart, 1992; Yamaguchi et al., 2009).

In general, in atolls, transportation across open water and accessibility to land is difficult. Simberloff (1974) suggested that even the simplest equilibrium model indicates that distant islands ought to have fewer species than near islands, and small islands ought to have fewer species than large ones. Thus, the biota of an island chain reflects the biotic diversity of the source region, the island size, and the distance from the source (Whitehead and Jones, 1969).

The annual and seasonal precipitation differs across the Marshall Islands due to the trade-winds zone extending from west to east and the north to south gradient of increasing rainfall (Thomas, 1989; Yamaguchi et al., 2009). The northern atolls, such as Taongi, have an effectively semi-arid climate, with 750–1000 mm annual precipitation, whereas, the southern atolls, such as the Majuro and the Ebon, have 3700–5000 mm annual perception because they are within the equatorial high rainfall belt (Thomas, 1989). This range of precipitation is shown in Fig. 4 (Stoddart, 1992).

Rainwater soaks into the underground (up to ~20 m) because of the highly permeable coarse and porous sand made of unconsolidated bioclastic sands, such as foraminifera and coral gravel (e.g., Perry et al., 2011; Yasukochi et al., 2014). Subsequently, the rainwater floats on the seawater, and this floated water has a convex lens-like appearance and is called the “freshwater lens” (Hamlin and Anthony, 1987; Anthony et al., 1989). The gradient of this lens affects plant biodiversity, as influenced by local precipitation (Yamaguchi et al., 2009).

Laura in Majuro Atoll is famous for its large freshwater lens, which is as large as 182 ha (e.g., Hamlin and Anthony, 1987; Anthony et al., 1989; Yamaguchi et al., 2009). The survey in Laura revealed that the upper fine sand unit is about 25 m thick on the lagoon ward edge and 16 m even inland; this thickness and relatively low permeability prevents salty seawater from mixing upward with the freshwater (Underwood et al., 1992). Yamaguchi et al. (2009) indicated that one of the essential ingredients for human habitation seems to be the potential for cultivating wet taro in agricultural pits maintained by sufficient freshwater resources.

The increase in the number of species will not be significant unless the island size is large enough to maintain a freshwater lens (Whitehead and Jones, 1969). A larger island also provides crop protection from sea salt spray. Fresh ground water, which is

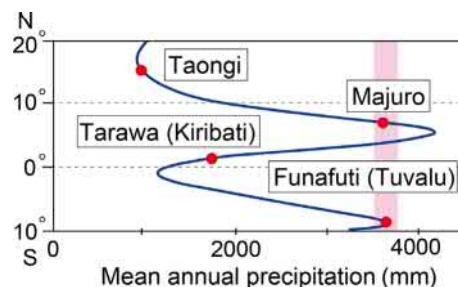


Fig. 4 Annual average precipitation in major atolls. Modified from Stoddart DR (1992) Biogeography of the tropical Pacific. *Pacific Science* 44: 276–293.

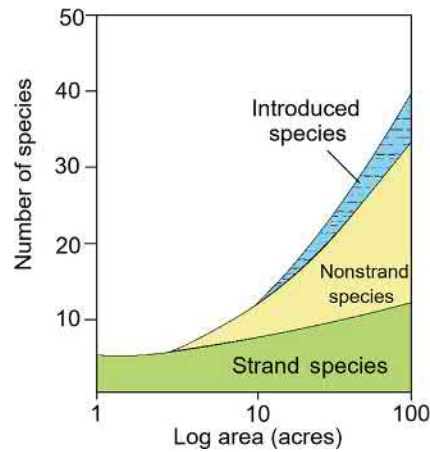


Fig. 5 Correlation between the number of species and island size. Modified from Whitehead DR and Jones CE (1969) Small islands and the equilibrium theory of insular biogeography. *Evolution* 23: 171–179.

essential for the growth of staple cultigens, was limited to only a few of the atoll's many islands (Dye, 1987). At least 1.4 ha is needed to store rainwater in the freshwater lens to allow a variety of salt-intolerant species to be established (Whitehead and Jones, 1969). Fig. 5 shows that a correlation exists between island size and (i) total number of species, (ii) strand species, (iii) nonstrand species, and (iv) introduced species. The number of species increases around 1.4 ha. The total number of this species available in the "species pool" is low; seldom more than 20–25 have been observed for any atoll system (Whitehead and Jones, 1969).

Nonstrand species that have low resistance to salt water are normally absent from the small islets (Whitehead and Jones, 1969). Nonstrand species can be established only when the islands are large enough to maintain water and possess high ecological diversity; they increase rapidly when the islets are sufficiently large to hold a freshwater reservoir, and introduced species also start to appear on islands that are large and diverse enough to be useful to man for both agriculture and habitation (Whitehead and Jones, 1969).

The area–diversity curve could be highly exaggerated by the introduced species, suggesting that the islands have been deeply affected by humans through habitation, maintenance of taro, breadfruit, and coconuts, and by the events of World War II (Whitehead and Jones, 1969).

The oligotrophic and the high pH of calcareous sand can also limit vegetation diversity. Fig. 6 depicts the depth profiles of major elements calcium (Ca) and magnesium (Mg), trace elements aluminum (Al), phosphorous (P), and iron (Fe), showing that Ca concentration remained almost constant and had the highest concentration among all elements (Ito et al., 2018a). The concentrations of Al, P, and Fe increased toward the surface in the three islands in Majuro; however, the concentration was markedly low in the rhizosphere. Among these trace elements, only P was found in high concentrations (Ito et al., 2018a), which likely originated from bird feces (e.g., Mulder and Ellis, 2010; Ito et al., 2018a).

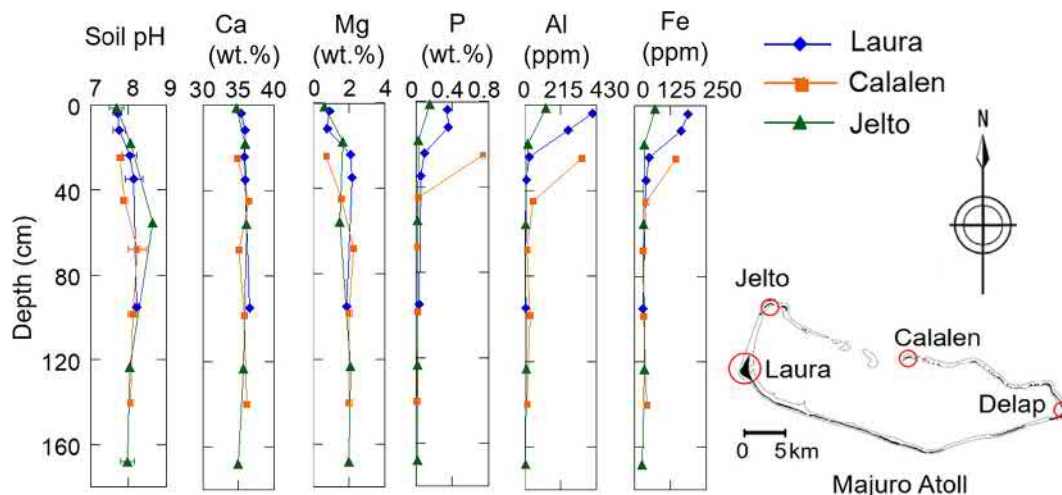


Fig. 6 Soil pH and concentration of elements in the sediment of the Majuro Atoll. Data from Ito L, Omori T, Yoneda M, Yamaguchi T, Kobayashi R, and Takahashi Y (2018a) Origin and migration of trace elements in the surface sediments of Majuro Atoll, Marshall Islands. *Chemosphere* 202: 65–75; Ito L, Yamaguchi T, Kobayashi R, Terada Y, and Takahashi Y (2018b) Influence of acidification on carbonate sediments of Majuro Atoll, Marshall Islands. *Chemistry Letters* 47: 566–569.

The surface layer pH was neutral and soil acidification was observed (Ito et al., 2018b). Overall soil pH ranged from 8 to 9. This high pH lowers the solubility of the low concentrations of Fe (e.g., Lindsay and Schwab, 1982); plant diversity is limited under this oligotrophic environment with high soil pH.

Chemical Risks

Adverse anthropological impacts in the form of chemicals (e.g., Tokai et al., 2002) have become points of concern. A rare element can become a biological concern if it forms a highly toxic metallic compound (e.g., Itai et al., 2014) or a radioactive isotope (e.g., Takahashi et al., 2017). Heavy metal contamination occurs from industrial products dumped directly into the environment without proper waste treatment plants; this problem has become a big issue on Funafuti in Tuvalu, where the population density is high, modernization is progressing, but garbage disposal technology is poor (Fujita et al., 2013, 2014). On the other hand, the ground-water contamination has stemmed from heavy metal co-precipitate on apatite formed by the chemical reaction occurring at the surface of calcareous foraminifera sand from the phosphorous from bird feces in Majuro Atoll (Ito et al., 2018a).

Other chemical risks related to residual radioactive nuclides have still remained because of the nuclear tests conducted after World War II around Bikini and Eniwetok Atolls.

Nuclear testing released a remarkable quantity of radioactive nuclides to the environment starting in 1946 when the United States set off a bomb at Bikini Atoll. The first hydrogen bomb test called Operation Greenhouse was conducted in 1952 on the neighboring Eniwetok Atoll (McNeill, 1994). Jackson (1969) reported that the tests killed off the rat population of the atoll. Most fission products in nuclear weapon tests involve elements, such as radioactive strontium (Sr) or cesium (Cs), that are not essential for life and have been added to the biosphere on a global scale (Odum, 1963, 1971).

These radioactive isotopes are concentrated in the food chain and eventually incorporated into the biomass (Odum, 1971). Organisms generally tend to accumulate nutrients, so concentrations within the biomass often exceed the concentration in the immediate physical environment (Odum, 1963). Among radioactive materials, the risk of fission product ^{90}Sr , which is particularly dangerous to man and other vertebrates, was enumerated by Odum (1963, 1971) as follows:

- (i) Global reach: ^{90}Sr is a common component of atomic fallout and atomic wastes worldwide.
- (ii) Long half-life: ^{90}Sr loses its radioactivity slowly (in technical terms, it has a half-life of 28 years) in contrast to many fission products that decay to harmless levels in a few hours or days.
- (iii) Similarity with Ca: ^{90}Sr behaves chemically like Ca, an abundant and biologically important element, and ^{90}Sr follows natural (nonradioactive) strontium and calcium into biogeochemical cycles.
- (iv) Easy absorption: ^{90}Sr is taken up by plants more readily than most fall-out materials directly via foliage absorption, soil, and water.
- (v) Bioaccumulation for fatal parts: when taken in with food by man and vertebrates, ^{90}Sr becomes concentrated and retained by the bone in close proximity to blood-making tissue in the bone marrow, which is rapid dividing cell area and especially sensitive to radiation damage; as such, mammals are considerably sensitive to low doses of ^{90}Sr (Gambino and Lindberg, 1964; Golley et al., 1965).

For example, ^{90}Sr from fall out assimilates into humans and animals readily through the grazing food chain in ecosystems, where precipitation is large (Odum, 1963). Also, a large proportion of fallout will enter food chains in nutrient-poor environments (Odum, 1971). The Marshall Islands, which have geological properties that meet these two conditions, requires further care and concern given the risks of these radioactive materials.

Radionuclides that enter marine food chains are rather strikingly different from those that enter terrestrial food chains (Palumbo, 1961). For example, soluble fission products, such as ^{90}Sr and ^{137}Cs , were found in the highest amounts in land plants and animals, whereas two types of elements shown below transfer in the highest amount to marine organisms; (i) ones that are induced by neutron bombardment and form strong complexes with organic matter such as cobalt (Co)-60, Fe-59, zinc (Zn)-65, and manganese (Mn)-54, and (ii) those that are present in particulate or colloidal form (cerium-144, praseodymium-144, zirconium-95, and rhodium-106) (Odum, 1971).

The effects of low-level chronic doses are difficult to measure because of the long-term genetic and somatic effects that may be involved (Odum, 1971). Before the first atomic tests, residents evacuated, and many returned early in the 1970s after the official safety declaration; however, they were re-evacuated from the islands when this declaration was doubted in the late 1970s, and the islanders' health status became a controversial issue (McNeill, 1994). From 1993 to 1997, medical and epidemiological studies were conducted via the Marshall Islands Nationwide Thyroid Disease Study. Takahashi et al. (1997, 1999) found that people who lived in Majuro in the 1950s and later had the highest prevalence of thyroid nodules, and a significant proportion of the Marshallese population suffers from moderate iodine deficiency based on the World Health Organization (WHO) criteria on inorganic iodine (World Health Organization, 1994). As a result of urine examination, 22% of the 309 adults in Majuro Atoll (184 females, median age of 50 years; 125 males, median age of 43 years) met the WHO criteria of moderate iodine deficiency and 1% of them met the criteria of severe deficiency, whereas a high ratio of the deficiency was observed in additional smaller groups (53 adults) in the Likiep Atoll, where lifestyles are based on traditional ways, such as fishing and traditional food-gathering practice; 48% showed moderate iodine deficiency and 13% adults showed severe iodine deficiency (Takahashi et al., 1999) (Fig. 7).

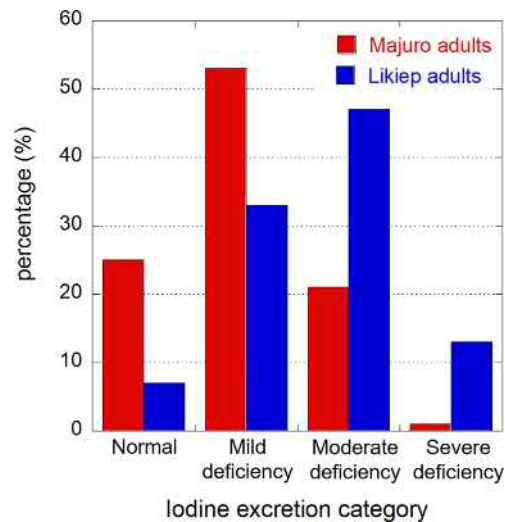


Fig. 7 Percentage of adults classified in each category of urinary iodine excretion in the Majuro and Likiep Atolls. Based on the data of Takahashi T, Fujimori K, Simon SL, Bechtner G, Edwards R, and Trott KR (1999) Thyroid nodules, thyroid function and dietary iodine in the Marshall Islands. *International Journal of Epidemiology* 28: 742–749.

These results and the dietary review in the Marshall Islands (Dignan et al., 1994) suggest that fish is the main source of dietary iodine; traditional lifestyle may cause iodine deficiency because the Marshallese should consume more than 130 mg of iodine only by fish, which would amply cover the requirement of the body (Takahashi et al., 1999) and should be related to the food chain and bio-accumulation. Although the moderate degree of iodine deficiency of the Marshallese is not severe enough to cause any clinical or biochemical signs of thyroid hormone disorder, they may have suffered from iodine deficiency for a long time (Takahashi et al., 1999).

Radioactive chemical risk has remained even after more than 50 years that bomb tests have been conducted and remains as one of the major problems in the Marshall Islands. Thus, “radioactive wastes must be anticipated, monitored and controlled” (Odum, 1971).

Conclusions

The Marshall Islands were formed via sea-level fluctuations in the late Holocene (Dickinson, 2003). The ancestors of the islands, the Lapita people, had come soon after the emergence of the islands (e.g., Kirch and Hunt, 1997; Kirch and Lepofsky, 1993; Kayanne et al., 2011). In the case of Majuro in the Marshall Islands, the “transported landscape” has lasted for ~2000 years (Yamaguchi et al., 2009) with abundant rainfall and sufficient land area (1.4 ha or more) to provide a high-quality freshwater lens (e.g., Whitehead and Jones, 1969; Stoddart, 1992). These important factors contributed to the sustainability of life on the islands. Introduced pigs, chickens, and dogs and cultivated plants, such as taro, breadfruit, and bananas, support people (Yamaguchi et al., 2009). These “portmanteau biota” had been transported from the original lands of the ancestors (e.g., Crosby, 1986; McNeill, 1994). Thus, many flora and fauna have flourished on the Marshall Islands with conditioned natural environment, and we can even encounter the endangered species, such as green turtles (*C. mydas*) (Thomas, 1989). However, the Marshall Islands faced severe chemical risks after World War II because of a number of nuclear bomb tests and the heavy metals in industrial products (e.g., McNeill, 1994; Fujita et al., 2014). Given that the islands have no facilities to treat these chemicals, people on the islands have had to face the risks associated with accumulated radioactive chemicals and heavy metals (e.g., Odum, 1971; Fujita et al., 2014; Ito, 2018). These chemicals have bioaccumulated in food sources (Odum, 1963, 1971). The risks posed by these chemicals are understudied.

Acknowledgments

I am grateful for the Marshall Islands Environmental Protection Authority (RMIEPA) and the staffs in Majuro and Japan who have cooperated on the fieldwork related to my study and this review. This work was supported by the Environment Research and Technology Development Fund (S17-1(2)) of the Environmental Restoration and Conservation Agency of Japan, and Grants-in-Aid for scientific research from the Ministry of Education, Culture, Sports, Science and Technology of Japan (18H04134).

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Collaborative Conservation in the Madrean Sky Islands

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Abstract

In the Madrean Sky Islands, deserts meet mountains in a patchwork of multiple biomes including desertscrub, grassland, woodland, and forest. The Sky Islands comprise the Madrean Archipelago, one of Conservation International's 35 Global Biodiversity Hotspots, and contain over 7000 species of plants and animals (Desert Landscape Conservation Cooperative 2019). This unique landscape faces complex threats and stressors, including longer and more extreme droughts, spatial and temporal changes in precipitation, increased groundwater withdrawal, invasive species, changing fire regimes, and expanding human communities. A collaborative group, the Madrean Transboundary Watersheds Landscape Conservation Design (Madrean LCD), has developed for the purpose of integrating social values with ecological goals to promote resilience in the Sky Islands. This article describes the Madrean Sky Islands and the process, lessons learned, and ongoing conservation priorities of the Madrean LCD.

The Madrean Sky Islands: Where Deserts Meet Mountains

Sky Islands are characterized by mountain "islands" surrounded by desert or grassland "seas." The Madrean Sky Islands comprise the ecoregion surrounding the Madrean Archipelago, a chain of mountains that connects the temperate Rocky Mountains to the north and the tropical Sierra Madre Occidental in the south. These 65 isolated mountains vary between 915 and 3300 m in elevation, rising out of the Sonoran Desert, Chihuahuan Desert, and Great Plains grasslands (Sky Island Alliance, 2019a). Higher elevations receive more precipitation than lower elevations, with some mountaintops receiving four times the annual rainfall of their

surrounding basins ([Banister et al., 2014](#)). Each mountain provides multiple environments where plants, animals and habitats connect and blend together—not in a single biome, but in a patchwork of biomes that vary according to elevation and aspect. In the Madrean Sky Islands, deserts meet mountains, jaguars meet black bears, and cacti meet cottonwood trees ([Sky Island Alliance, 2019a](#)) (Figs. 1 and 2).

Ecology of the Sky Islands

Biodiversity

The Madrean Sky Islands contain some of the most rugged and remote lands in the American Southwest, and feature some of the highest levels of biodiversity in the world ([Sky Island Alliance, 2019a,b](#)). The Madrean Archipelago ecoregion has been recognized as one of 35 Global Biodiversity Hotspots by Conservation International, and more than 7000 species of plants and animals, including over half the bird species in North America, can be found here ([Desert Landscape Conservation Cooperative, 2016](#)) (Figs. 3 and 4).

Biomes

The Madrean ecoregion is comprised of convergences of biomes and transition zones. At the base of the Madrean Sky Islands are warm, arid desert and scrubland dominated by cacti, succulents, and shrubs. Progressing up a mountain, grassland, woodland, pine forest, mixed conifer forest, and sub-alpine forest can be found, as well as wetter areas such as riparian forests and wetlands ([Debano, 1999](#)). Each Sky Island mountain is a vertically integrated succession of ecosystems that support the inhabitation and migration of a great and unique variety of species; the ability of organisms to migrate vertically as temperatures increase makes the Sky Islands important climate refugia ([Misztal et al., 2016](#)) (Figs. 5 and 6).

Riparian Ecosystems

In addition to the mountains that dot the Madrean ecoregion, a distinguishing landscape feature is the ribbons of streambeds that flow down mountains and through desert basins. Water may be present at the surface of these streambeds year-round, but many watercourses in the Sky Islands have only ephemeral flows. Water is also available at springs and wetlands, or cienegas ([Sky Island Action, 2008](#)). Regardless of whether surface water is present, areas where groundwater is close to the surface (i.e., riparian zones) are strikingly different from the surrounding drylands. Large trees such as cottonwood, willow, sycamore, and ash, as well as various shrubs, forbs, grasses, algae, and micro-organisms, are prevalent in riparian zones but in no other Sky Island communities. The dense vegetation stabilizes streambanks, slowing erosional processes and providing places for seed banks. The shade, litter, bark, and seeds from dense riparian vegetation support wildlife, which find respite in riparian areas from the warmer uplands. Riparian zones support a great variety and diversity of organisms; for example, the 230-km stretch of the San Pedro River alone contains more native vertebrate species than Yellowstone National Park ([Sky Island Alliance, 2019a,b](#)). Riparian areas also serve as corridors for migration or dispersal of numerous plant and animal species, as well as water, nutrients, and sediment. Riparian zones are a critical conservation resource in the Sky Islands ([Fig. 7](#)).



Fig. 1 The Madrean Archipelago, as viewed from the northern aspect of the Santa Catalina Mountains of southeastern Arizona, United States.



Fig. 2 The mountain ranges of the Madrean Sky Island ecoregion of the United States and Mexico (Sky Island Alliance, 2019b).



Fig. 3 Each Sky Island mountain is different, and their biota are largely impacted by elevation. For example, peaks of the Santa Rita Mountains, at approximately 280 m, are sub-alpine environments; while peaks of the Drought Mountains, at approximately 250 m, feature woodland communities.



Fig. 4 The Dragoon Mountains of southeast Arizona, United States contrast in elevation and geology (and therefore ecology) from the Santa Rita Mountains, only approximately 48 km (30 miles) away.



Fig. 5 Sonoran Desertscrub communities occur at low elevations surrounding Sky Island mountains.

Connectivity

Another asset of the Sky Islands for supporting major ecological functions is the connectivity of wildlife habitat. Many species migrate vertically within individual mountain ranges (including among and between riparian zones) to accommodate daily and seasonal environmental variations, while other species move between ranges. Animals such as mountain lion, jaguar, and bighorn sheep move frequently across ranges in pursuit of food or mates, and the absence of barriers between ranges allows populations to flourish. In addition, pollinators such as butterflies and bats migrate through the Sky Islands, and require habitat and forage to serve their function. It is important that wildlife corridors are considered in planning for infrastructure projects, urban development, and other human uses.

Geography and Human Uses

Human Communities

The Madrean Sky Islands span four states in the United States and Mexico, covering a patchwork of protected and unprotected public and private lands; and are interspersed by the cities of Tucson, Sierra Vista, and Nogales, Arizona; Silver City, New Mexico;



Fig. 6 Oak Woodland (foreground) transitions to Mixed Conifer Forest (background) in the Santa Rita Mountains.



Fig. 7 Winter precipitation in 2019 contributed to high surface flows in riparian zones of the Santa Catalina Mountains.

and Nogales, Hermosillo, and Magdalena, Sonora. In the United States, the majority of Sky Island mountain ranges are part of the Coronado National Forest, which hosts the greatest number of threatened and endangered species of any United States National Forest ([Sky Island Alliance, 2019a,b](#)). In Mexico, the Sky Island mountains and low desert valleys are largely a mixture of private ranches, *ejidos* (communal land used for agriculture), and *Reserva Forestal Nacional* (National forest reserves) ([Sky Island Alliance, 2019a,b](#)).

Human Use

Because they are so diverse, the Sky Islands have supported various human uses throughout history. Humans have continuously inhabited and farmed some areas since as early as 10,000 BCE, and one of the most advanced ancient irrigation systems in North America was built in the Santa Cruz River valley ([Potteiger, 2017](#)). Modern irrigation systems and long growing seasons have

supported extensive farming in the region (Banister et al., 2014). The grasslands between mountains have also supported centuries of ranching, and much of the Sky Island grasslands are still being utilized today for cattle production (Mizstal et al. 2017). Mining is another common industry that has sporadically supported towns and camps throughout the region (Banister et al., 2014). The Sky Islands have also become increasingly important for outdoor recreation; the variety of climates they offer support hiking, horseback riding, camping, birding, and other activities year-round (Coronado National Forest Recreation, 2019). The southernmost ski resort in the United States is located in the Santa Catalina mountains of southern Arizona, the top of which periodically receives enough winter snow for skiing, and the bottom of which is surrounded by Sonoran desertscrub as well as the Tucson metro area (Fig. 8).

Stressors and Threats in the Sky Islands

Between human uses and environmental factors, the Sky Islands face complex threats, including longer and more extreme droughts, spatial and temporal changes in precipitation, increased groundwater withdrawal, invasive species, more frequent and intense fire events, and expanding human communities (Misztal et al., 2016). Many of these threats are interrelated; for example, warming temperatures, decreasing water availability, and the spread of invasive species have caused ranchers to change their cattle rotations and farmers to alter their crops and growing practices. Urban development areas have altered hydrologic flows, water quality, and riparian systems. Decades of fire suppression, hotter temperatures, encroachment of invasive species, and drought have combined to create fuel conditions that support more severe wildfires (Patterson, 2016). Because of the diverse ecological communities that intersect in the Sky Islands, it is especially important to understand human, biological, geological, hydrological, and climatological relationships when managing issues and threats (Fig. 9).

Collaborative Conservation in the Sky Islands

The Need for Large-Landscape Conservation

With a multitude of environmental and social factors impacting the Sky Islands, conservation issues are manifested at much larger scales than those of individual management areas (Comer et al., 2013; Garfin et al., 2014). It is imperative to address these issues at the scale of large landscapes because they transcend existing jurisdictions and institutions (McKinney et al., 2010). Responding to these stressors requires coordinated planning and action at a scale that is relevant to ecological and evolutionary processes. To support conservation at the appropriate scale for effective results, a network of 22 Landscape Conservation Cooperatives (LCCs) was established by the US Department of Interior in 2010 to build systematic large-landscape conservation networks (Jacobson and Robertson, 2012). These LCCs were designed to facilitate collaboration across jurisdictional boundaries, developing shared conservation priorities and science needs, and creating strategies to be implemented through partnerships (National Academies of Sciences, Engineering, and Medicine, 2016).



Fig. 8 The grasslands surrounding Dripping Rock Mountains are used for livestock grazing.



Fig. 9 This photo depicts two interacting stressors on Sky Islands: invasive species and human development. Grasses such as Lehmann's Lovegrass (*Eragrostis lehmanniana*) have invaded Sonoran Desertscrub ecosystems. When the invasive grasses carry fire to these communities, they endanger species such as Saguaro cactus (*Carnegiea gigantea*) that are not fire-adapted. This location, the Santa Catalina Mountains, is surrounded by the city of Tucson, Arizona, which brings many recreationalists who can easily transport seeds of invasive species. However, with proper management, public education, and collaboration, the negative effects of human presence can be minimized.

Landscape Conservation Design

One of the primary ways to achieve the goals of LCCs was through the collaborative development of Landscape Conservation Designs (LCDs). LCDs are groups that involve the integration of societal values with ecological goals to describe where conservation can best be applied to support a resilient landscape. They adopt an iterative, collaborative, and holistic process to create strategic and spatial products that provide information, analytical tools, maps, and strategies to achieve landscape goals collectively held among partners (Desert Landscape Conservation Cooperative, 2016). In 2016, the Madrean Transboundary Watersheds LCD (Madrean LCD) was formed to support the resiliency of the Sky Islands across their diverse watersheds in the face of complex stressors.

Madrean Watersheds Landscape Conservation Design: Process, Outcomes, and Products

Process Summary

Genuine partner-driven collaboration is a foundational aspect of the Madrean LCD. From the outset, the effort has been based on partner priorities and management realities (rather than top-down directives). The LCD process, has included establishing a shared vision and goals; gathering existing plans, projects and data; identifying high-priority challenges and stressors; discussing actions and strategies for supporting climate resiliency; and iteratively engaging partners in developing tools that support their efforts.

Shared Values and Goals, Information Gathering, and Challenges

Preliminary discussions related to the Madrean LCD began in late 2015 with initial gatherings of partners from agencies, organizations, and institutions of the United States and Mexico in a series of bi-national workshops in Tucson, Arizona, Aguascalientes, Mexico and Alpine, Texas. In total, these gatherings were attended by over 140 participants from 45 different agencies and organizations (Desert Landscape Conservation Cooperative, Alpine Workshop Report 2016). In this preliminary stage, partners worked to identify shared values, pressing challenges, and stressors across the landscape, as well as gather relevant existing plans and information. These workshops built the foundation for Madrean LCD priorities and products.

Establishment of the Coordinating Team

As a central point for communication and guidance for the LCD, the Madrean Watersheds Coordinating Team was created in early 2016, comprising agencies, organizations and researchers from across the region. This team's role is to provide overall guidance and

direction for the design and implementation of the LCD process, and to help ensure the effort remains relevant to on-the-ground conservation and restoration actions. These partners are supported by a Core Team of staff of Sky Island Alliance (a local non-profit organization), the US Fish and Wildlife Service, and Southwest Decision Resources (facilitation and collaboration specialists). The Coordinating Team meets regularly to share information on partner activities, guide the development of collaborative tools, and plan workshops.

Collaborative Vision, Management Strategies, and Priority Ecosystems

After laying the foundational groundwork, the Madrean LCD effort was kicked off more broadly with Madrean Partner Workshop One in Tucson, Arizona in 2016. At this important gathering, more than 90 partners worked to develop shared goals and objectives, key management questions, and information gaps. Participants also identified locally relevant management strategies that are or can be used to help achieve shared goals.

An important outcome of this gathering was the shared development of the Madrean Watersheds Vision and Shared Goals for biodiversity, connectivity and socio-ecological services, each listed below:

Madrean Watersheds Vision

The Transboundary Madrean Watersheds initiative is a large-landscape, international effort to maintain and enhance the interconnected system of mountains, grasslands, deserts and waters that supports species diversity, promotes healthy watersheds, and maintains the overall ecosystem integrity that enriches the lives of human communities.

Shared Goals

Biodiversity: Transboundary Madrean watersheds are a haven for the unique diversity of native and endemic species.

Connectivity: Enhanced linkages connect the diverse life zones of Sky Island ecosystems, from valley bottoms to mountain tops, from southern Sonora to the Gila River in Arizona, enabling persistence of migratory wildlife and allowing for the possible future shift of species and ecosystems in a changing climate.

Socio-Ecological Services: Healthy watersheds, functioning ecosystems and cultural resources deliver highly valued benefits to human communities.

Additionally, workshop participants agreed on a list of priority ecosystems within the LCD geography, and they began work on developing appropriate indicators to assess landscape health and determine priority conservation actions in grasslands, Madrean evergreen woodlands, and streams. Biodiversity and connectivity were suggested as cross-ecosystems priorities.

Selection of Indicators of Landscape Health

In 2017, partners of the Madrean LCD began the important process of identifying key ecological and social indicators for the agreed upon priority ecosystems. The indicators will help assess both current and future ecosystem conditions, and provide a baseline and ongoing mechanism to detect changes that result from collaborative management actions. Madrean LCD partners developed criteria for these indicators, and met in February 2017 to evaluate a range of suggested options. Indicators selected were spatially based, ecologically and socially relevant, relevant to management and conservation goals of partner organizations, and able to guide the placement of conservation and restoration activities (*Madrean Landscape Conservation Design, 2018*, Madrean Watersheds Landscape Conservation Design: Developing Indicators and Analysis Methods to Assess Ecosystem Integrity at the Watershed, Core, and Corridor Scales). Since the preliminary list of indicators was developed, Madrean LCD partners have worked to determine whether appropriate data was available for those indicators, and then to locate and compile this information.

Formation of Topical Teams

Since priority ecosystems and preliminary indicators of landscape health were identified, sub-teams have been convened to gather resources related to those topics. A data team comprised of the Arizona Remote Sensing Center, Sky Island Alliance, and Coordinating Team members gathered data related to ecosystem indicators. Practitioners with interest and experience in Biodiversity and Connectivity met to develop geospatial products for supporting planning and decision making related to those topics. These teams communicate regularly with the Coordinating Team to ensure the relevance of data and tools.

Development of Tools and Products

The Madrean LCD partners are developing products to promote resilience of the ecoregion. These tools are being developed collaboratively, and are publicly accessible. Updating and improving these tools will be an ongoing priority for the Madrean LCD. The resources being developed include the following:

- A watershed and landscape-scale indicator assessment: A geospatial depiction of the indicators of landscape health selected by the Madrean LCD. This tool will be utilized to monitor trends over time, as well as to support geographic prioritization of conservation actions.

- A map of wildlife corridors in the Madrean Sky Islands: A combination of the work of multiple partners who have studied and ground-truthed corridors for different species, this map will show corridors important for the use of multiple species in the Sky Islands.
- An interactive list of management strategies specific to the region: An online index of what managers are doing to promote a resilient Sky Islands landscape, providing context and guidance for when and where those strategies can be effective.
- The Collaborative Conservation Adaptation Strategies Toolbox (CCAST): This interactive website provides case studies on management strategies prioritized for the Madrean Watersheds and other LCDs, along with resources to support implementing these strategies on a larger scale. The tool is fully functional online at: <https://www.arcgis.com/apps/Cascade/index.html?appid=01245fcb9dec43938996e18b53f0f14>.
- Support of sub-watershed-scale conservation collaboratives: The Madrean Watersheds supported the development of local efforts, including the Lower San Pedro Collaborative and the Santa Cruz Watershed Collaborative, which align partners in gathering resources and planning for the sustainability of those respective watersheds. The LCD intends to support more local collaboratives through designing and adapting products at scales applicable to local groups, as well as participating in an effort to connect watershed collaboratives in the state of Arizona.

Lessons Learned From the Madrean LCD

Overview

The partners of the Madrean LCD have learned and applied various lessons throughout the process. Although the lessons are too numerous to include in one article, some key insights that may be applicable to other collaborative conservation efforts are described below.

Establishing a Foundation

While many partners are eager to implement on-the-ground activities, establishing shared goals and priorities at the outset of a collaborative effort is critical. In the Madrean LCD, early meetings and workshops focused on listing and connecting existing work and developing shared priorities, rather than immediately developing products. Although applicable products have taken years to create, they are informed by specific, priority needs identified by program partners. Maintaining transparent and consistent communication between participants in the ever-changing efforts and priorities has been instrumental in the success of the collaborative, and Madrean LCD partners are aware of the importance of continuously listening to the needs of partners and adapting collaborative priorities accordingly. Building upon existing efforts to create relevant products requires time and thorough communication, but time is ultimately saved by avoiding duplication, and by identifying and integrating ongoing work in the region.

Maintaining Momentum at Multiple Scales

As a landscape-scale collaborative, a key question to answer is when to establish overarching goals and planning priorities versus conducting local, smaller-scale work. Madrean LCD partners have learned the importance of operating at multiple scales simultaneously to maintain momentum. The Madrean LCD connects and leverages the abilities of individual partner organizations conducting local work while establishing larger-scale priorities and values through the Coordinating Team and workshops. If on-the-ground work is not being used to illustrate the relevance of the collaborative, the development of more abstract concepts such as overarching goals and priority ecosystems can lose momentum. The foundational concept of structuring the collaborative to support concurrent work at multiple scales can be applied to any large-landscape conservation collaborative.

Diversifying Funding Sources

One lesson learned regarding funding of the Madrean LCD occurred when the founding initiative, the Desert Landscape Conservation Cooperative, was discontinued. In 2017, the US government announced that federal funding would be eliminated for Landscape Conservation Cooperatives, removing the main support for the Madrean LCD by the end of 2019. However, Madrean LCD partners considered the effort an important priority, and are working on creative solutions, specifically a shared funding structure in which multiple partners contribute funding and staff time to support coordination and other ongoing needs. Through the sudden loss of the primary funding source, the Madrean LCD partners have learned that a diverse support base not only reduces risk, but also encourages a sense of ownership and agency among partners of the collaborative.

Participating Across Borders

A major challenge for the Madrean LCD has been maintaining close partnerships across the international border. The LCD was originally intended to have equal participation from the United States and Mexico; the potential to strengthen

international relationships was a main reason for establishing this collaborative. However, the fact that strong relationships only existed between a few Mexican and American organizations has made it difficult to continue engaging partners from both nations, especially as staff changes occur. Also, there are few contiguous geospatial data sources that span both countries of the Sky Islands, so there are currently few landscape indicators that can be monitored and analyzed throughout the entire Madrean LCD region. In addition, in-person gatherings are challenging; the language barrier slows technical conversations that require translation, and it is difficult for government employees of both nations to obtain permission and funding to travel across international lines.

Although it has been difficult to keep partners from both nations in discussion, multiple conservation goals and challenges are common to Mexican and American communities that unify the effort. Given that the steps to build relationships across nations can be slow, the Madrean LCD has learned that making a concerted effort to include and empower all communities and organizations involved is a critical part of the collaborative process, and it is more beneficial to put effort into building and maintaining relationships than losing participants and having to re-engage them later in the process.

Institutionalizing Partner Engagement

One strategy for keeping relationships strong across jurisdictions of the Madrean LCD has been institutionalizing organizational participation. As staff of partner organizations have come and gone, it has been important for participating organizations to send a new representative—particularly in the case of government agencies, which generally experience more participant turnover than landowners or non-governmental organizations. Strategies for institutionalizing organizational participation include investing decision makers and land managers early in the process so that they understand its relevance and benefits; listing participant organizations in written documents of the collaborative to encourage a sense of belonging; and consistently gathering feedback from partner organizations to assure the tools and outcomes are directly useful.

What's Next for Collaborative Conservation in the Sky Islands?

Based on the work to date, lessons learned, and current partner needs, the Madrean LCD plans to continue as a fully functioning collaborative supported by multiple partner organizations that provide resources to local watershed collaboratives and scale up initiatives and priorities currently conducted at smaller scales. The Madrean LCD will host a workshop in 2019 to convene partners working on critical issues and identify collaborative projects for the short- and long-term. Madrean LCD partners will also apply the indicators of landscape health and the connectivity map to prioritize areas for conservation action. Madrean LCD partners have re-affirmed the importance of strengthening binational relationships, cultivating place-based connections and environmental stewardship, and integrating science and policy (Madrean Landscape Conservation Design, Synthesis of Partner Input 2018). Utilizing this approach, the Madrean LCD will continue as a robust partnership to promote collaborative efforts for ecosystem resilience in the years to come.

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Overview of Mountains (Alpine Systems): Life at the Top

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Abstract

The alpine biome is the life zone above the climatic treeline in mountains. It is the only biome that has a global distribution, although its elevation varies with latitude. The alpine is treeless by definition; its vegetation is composed of plants that grow close to the ground, including grasses, sedges, rushes, herbs, dwarf shrubs and cushion plants. The alpine biome covers about 3.3 million km² or 26% of the global mountain area. The alpine regions of the world support over 10,000 flowering plant species. This article provides an overview of the articles in the alpine section of the encyclopedia, including description and discussion of the alpine regions of North America, South America, Africa, Europe, Asia, and Oceania. The world's alpine ecosystems are extremely vulnerable to the current human-caused changes, including rising temperatures, livestock grazing, air pollution encroaching from urban centers, invasive species, declining levels of meltwater, and other anthropogenic disturbances is putting alpine biota under a great deal of stress. As with all the other biomes of the world, we need to be taking steps to ameliorate these disturbances, before it is too late.

Introduction

How is the alpine biome defined? As reviewed by Körner (this volume), the alpine biome is the life zone above the climatic treeline in mountains. It is the only biome that has a global distribution, although its elevation varies with latitude. The alpine is treeless by definition; its vegetation is composed of plants that grow close to the ground, including grasses, sedges, rushes, herbs, dwarf shrubs and cushion plants. Cryptogams (mosses, lichens, and liverworts) play an important role in some alpine regions. Generally, flowering plant diversity in the alpine is far greater than that of cryptogams, even though the latter group dominates the ground cover of some habitats. For instance, in the Himalaya alpine flowering plants comprise 87% of the flora (1585 species), while mosses, liverworts and lichens represent 13% (244 species).

The alpine biome covers about 3.3 million km² or 26% of the global mountain area. The alpine regions of the world support over 10,000 flowering plant species in 2000 genera, representing 100 families.

The productivity of alpine ecosystems is limited by the short duration of favorable daytime periods and a nutrient cycle slowed by frozen soils. The alpine biome is largely confined to the Holarctic region, with only tiny alpine land areas in Africa, Australia and Oceania. The alpine regions and the treeless Arctic lowlands, also covered by short stature plant communities, are often lumped under the term "tundra." However, Arctic tundra lacks the characteristic features of the alpine landscape. Alpine topography is rugged, creating high habitat diversity. Alpine ecosystems generally clothe steep terrain, Arctic tundra often grows on flat lands and hill country, and is often dominated by peatland (mires, fens), which are rare in mountains. Hence the term "tundra" is best not applied to the alpine biome, and the term "alpine tundra" has been avoided by the authors of this section of the encyclopedia.

Climatic Controls of High Elevation Treelines

Körner (this volume) also reviewed the climatic controls of the treeline elevations around the world. The worldwide position of treeline roughly corresponds with the 6 °C seasonal mean temperature isotherm. Below this temperature trees are unable to build new cells and tissues. In regions of extremely cold climate, such as the subpolar latitudes or at high mountain elevations, trees disappear from the landscape and only small plants can survive on the land above the limit of trees. Trees at high elevations are exposed to the lower temperatures and higher wind speeds found 2 m and more above the surface, while small plants profit from the warmth near the ground. At treeline, the windward side of trees is blasted by ice crystals through the winter, eventually creating a "flag tree"



Fig. 1 Engelmann spruce growing at treeline, Colorado Front Range. Note the lack of branches on the windward side of the tree. Englemann spruce at treeline Colorado, courtesy of Creative Commons.

with branches only on the leeward side of the tree (Fig. 1). Tree species that live in the forest-alpine ecotone also adopt a krummholz growth form, in which the plant is dwarfed, standing only a little taller than the surrounding herbaceous vegetation. The term “krummholz” is German for “twisted wood.” Above the forest-alpine boundary, tree islands may be found in some alpine regions (Fig. 2). These patches of krummholz are weather-driven specimens of deformed treeline species adrift in the alpine community



Fig. 2 Above: Diagram of a krummholz tree island, showing the effects of wind. Below: A tree island on Niwot Ridge, Front Range, Colorado. Above modified from Holtmeier, F. K. and Broll, G. (2017b). Feedback effects of clonal groups and tree clusters on site conditions at the treeline: Implications for treeline dynamics. *Climate Research* **73**, 85–96, photo courtesy of Tim Seastedt.

(Holtmeier and Broll, 2017b). This phenomenon is unique to conifers employing adventitious root growth. Tree islands are generally triangular in shape, with the point of the triangle hugging the ground as it faces into the wind, and the leeward base of the triangle reaching a meter or more in height. Tree islands are often up to five meters in length. They may start as detached segments of treeline individuals or have their genesis from seeds germinating in acceptable microclimates. Tree islands slowly migrate across alpine landscapes, always in the leeward direction. Growth takes place on the downwind side through the spread of adventitious roots. The roots take advantage of the snow-derived moisture that accumulates on the leeward side of the island, as well as alpine loess that collects in the eddy behind the island. Meanwhile, the upwind side of the island is slowly killed by the erosive effects of the wind. The migration rate of tree islands has been measured by radiocarbon dating of wood samples from the windward and leeward edges of islands in the Colorado alpine. The average migration rate was measured at 0.9–1.9 cm per year in this study (Benedict, 1984).

If global warming continues at its current pace, ecologists predict that mountain treelines will shift upslope, thus reducing the areal extent of alpine biomes.

Regional Studies

North America

As reviewed by Malanson (this volume), the alpine biome of North America is responding to a variety of ongoing anthropogenic environmental changes. These include changes in climate, nitrogen deposition, invasive species, and local human activity. The environmental factors that influence treeline elevations at the global, regional and landscape scale are discussed by Holtmeier and Broll (2017a) and are shown in Fig. 3. Terrestrial ecosystems are more affected by climate change and local human disturbances, while aquatic ecosystems are more greatly affected by nitrogen deposition and invasive species. Alpine vegetation varies over short distances and, because it is found in a wide variety of microclimates, responses to climate change may be habitat specific. Warmer climates speed up snowmelt in the alpine, lengthening the growing season by days or weeks. This might seem to be to the advantage of alpine plants, but these species have evolved in colder climatic regimes with short summers. Jump starting their period of summer activity leads to changes in the timing of biological events, or their *phenology*. For plants, these biological events include the timing of sprouting, flowering, setting seeds, and dying back for the winter. The relationships between flowering plants and pollinating insects in the alpine (as elsewhere) have been established through millennia of interactions. If a species of plant has traditionally blossomed between July 1 and 10, then the corresponding pollinators will show up on those dates. If, however, the timing of blossoming moves up by 10 days, then the insect pollinators will arrive too late. These kinds of relationships between alpine biota are likely to be greatly disturbed by warming climates.

High elevation vegetation response to climate change is also profoundly affected by snow persistence. Snow affects alpine plants through thermal protection, water provision, effect on atmospheric deposition, and determination of the length of the growing season. Higher temperatures are likely to reduce snow persistence. This will change the seasonality of alpine plants. Zhu et al. (2019) note that increasing temperatures in arctic and alpine regions will likely lead to fewer days of snowpack cover of landscapes. Many alpine plants and animals rely on winter snow cover to insulate them from bitterly cold air temperatures. The number of winter days without alpine snow cover in the mid-latitude highlands of the Northern Hemisphere are predicted to increase by 10 days per year in the next few decades. Thus, counterintuitively, warmer alpine winter temperatures will lead to increased exposure of sub-nivean organisms to bare ground in winter.

As discussed by Schoville and Rovito (this volume), North American alpine habitats harbor an exceptional number of plant species, as well as high levels of endemism in several distinct biomes. These include the cloud forest biome, subalpine biome and alpine biome found at high elevations in tropical and temperate mountains. The alpine zones of tropical North America (including Mexico) have more diverse floras and faunas than alpine regions in the mid- and high-latitudes. This trend is also seen in alpine mammalian faunal diversity. The Sierra Madre del Sur (16–19°N) is home to 245 species of mammals; the Sierra Madre Occidental (24–30°N) has 217 species of mammals; the Pacific Coast Range (38–58°N) has 208 mammal species. The least diverse mammal fauna is found in the Brooks Range of Arctic Alaska (67–69°N), with just 48 species of mammals. Similar latitudinal trends in species diversity hold true for alpine plants in North America.

What are the environmental factors that govern these patterns of diversity? As reviewed by Seastedt (this volume), at the landscape level, moisture and temperature regime are the dominant factors. At smaller spatial scales the biotic characteristics of plants come into play. Resource availability at the microhabitat level plays an important role in alpine species composition. Another factor that influences species diversity and composition in alpine regions is the environmental history of the mountains. South of the Arctic, alpine regions form habitat islands, surrounded by a “sea” of montane forests. During Pleistocene glaciations, treeline elevations descended by 1000 m or more, creating much larger alpine areas, albeit many of these highlands were covered by glaciers. During these intervals, alpine “islands” became “peninsulas,” allowing the migration of alpine species along these high mountain corridors (Fig. 4). The current flora and fauna of any alpine region are thus not stable communities over the long-term. Instead they represent the mixture of alpine species that became established during the last glaciation, when movements between alpine regions were greatly facilitated by the alpine connections that existed. Sadly, the North American alpine ecosystems that have waxed and waned through millennia may soon be exterminated. Climate models predict that the cold climate associated with the alpine biome will eventually cease to exist in the continental United States, given the current trends in climate change.

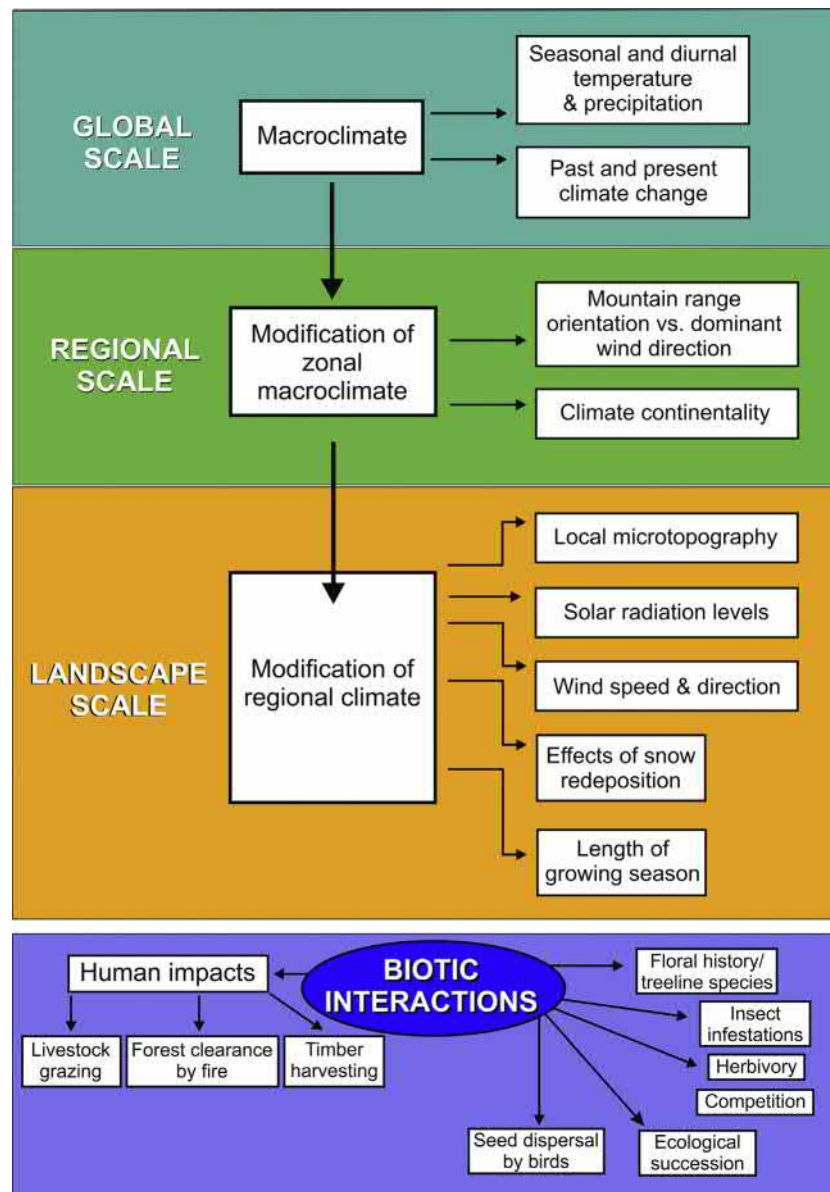


Fig. 3 Diagram illustrating the environmental factors (abiotic and biotic) that affect the altitudinal treeline at the global, regional and local landscape scales. Treeline elevation flow chart—heavily modified from Holtmeier, F. K. and Broll, G. (2017a). Treelines—Approaches at different scales. *Sustainability* 9: 808. <https://doi.org/10.3390/su9050808>.

South America

The alpine regions of South America are found along the tops of the Andes, the longest mountain chain in the world. Because the Andes span a huge range of latitudes, from 11°N in Colombia to 55°S in Chile, they support a wide variety of alpine habitats, ranging from sub-Antarctic alpine regions in southern Patagonia, through high-altitude alpine environments in the tropical latitudes to the north. As reviewed by Anthelme and Peyre (this volume), alpine biodiversity of the Andes is the richest in the world. It displays remarkable patterns of endemism, species radiations and morphological/physiological adaptations. Mountain building (orogeny) of the Andes began in the Early Jurassic and has continued to the present day. As the mountains slowly rose from the plains, new niches were formed that became available for colonization by both temperate and tropical species. These alpine ecosystems of the Andes are highly vulnerable to the combined effects of climate and land use changes. Extinction is already occurring at alarming rates in many plant groups. New threats, such as the introduction of invasive species and the creation of no-analog communities through new climatic regimes, will directly impact the biodiversity of the Andes alpine regions. The following regional summaries follow a north-south transect along the Andes.

Hofstede and LLambí examine the plant diversity in Páramo communities, found in the high mountains of the neotropical region. The páramo landscape consists of natural grasslands above treeline (3000–3500 m asl) and below glaciers

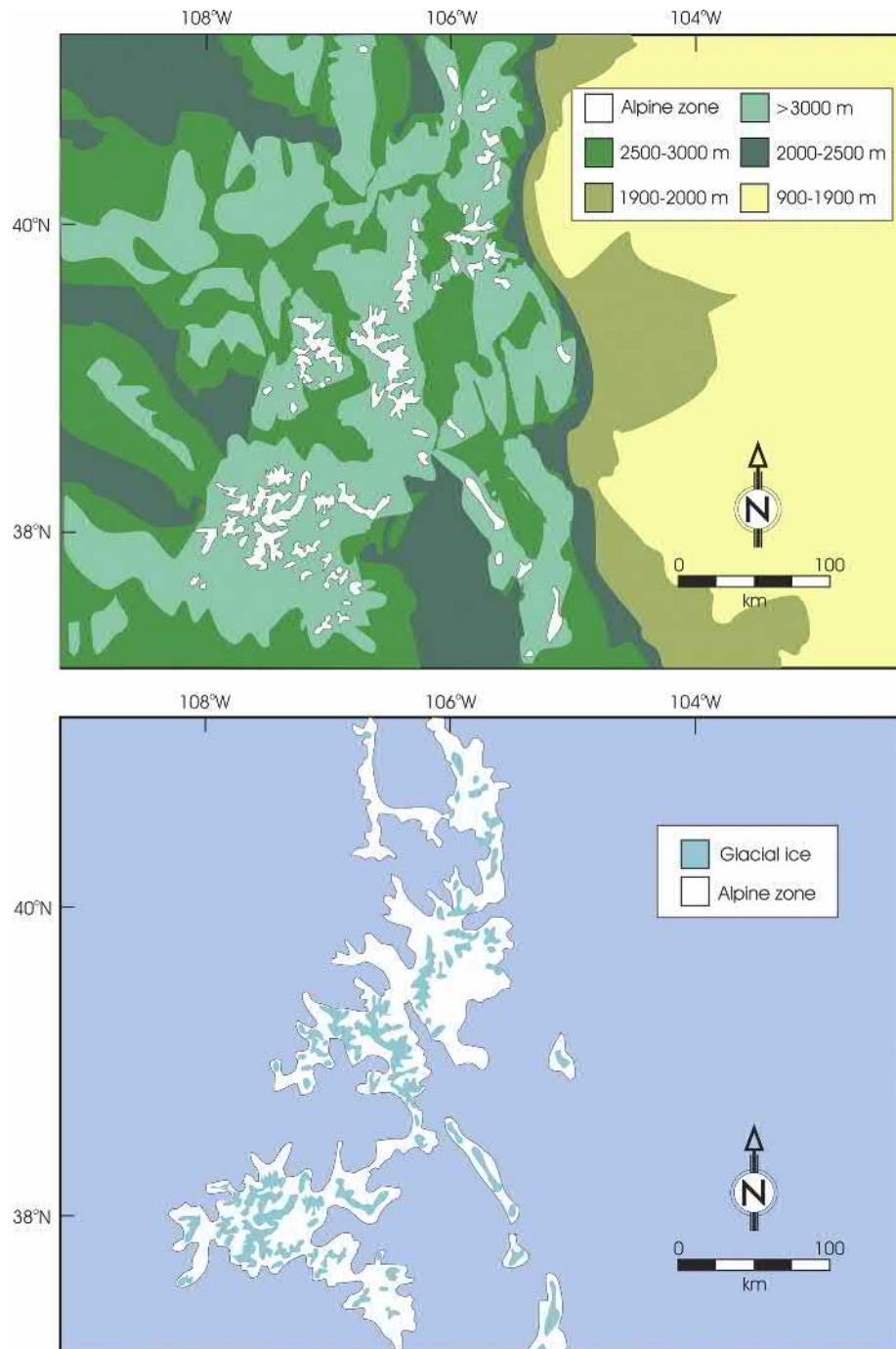


Fig. 4 Above: Map of the modern vegetation zones of Colorado, showing the isolated patches of alpine vegetation (*white*) surrounded by subalpine forests (*light green*). Below: Reconstruction of the extent of alpine tundra during the height of the last glacialiation, ca. 21,000 years ago. Note how most of the alpine regions have coalesced, allowing biotic interchange.

(4500–5000 m asl). This ecosystem covers $\sim 35,000 \text{ km}^2$ and extends across the tops of the Andes in Venezuela, Colombia, Ecuador, and northern Peru (Fig. 5). In addition, small patches of Páramo occur in Costa Rica and Panama. Thus, the Páramo forms an ecological archipelago, spread along the highest parts of the northern Andes. One of the characteristics of Páramo is that it is subjected to large daily temperature fluctuations. Mist cover alternates with high levels of solar radiation. Páramo plant species have developed unique adaptive strategies to cope with these extreme environments. These species show high levels of endemism. In fact, the Páramo has the highest alpine plant diversity in the world. A comparison of 19th century vegetation records with recent vegetation surveys of the Chimborazo volcano, Ecuador, suggest there has been an upward migration of many plant species associated with temperature warming. It is predicted by ecologists that ensuing climate change will cause the loss and fragmentation of

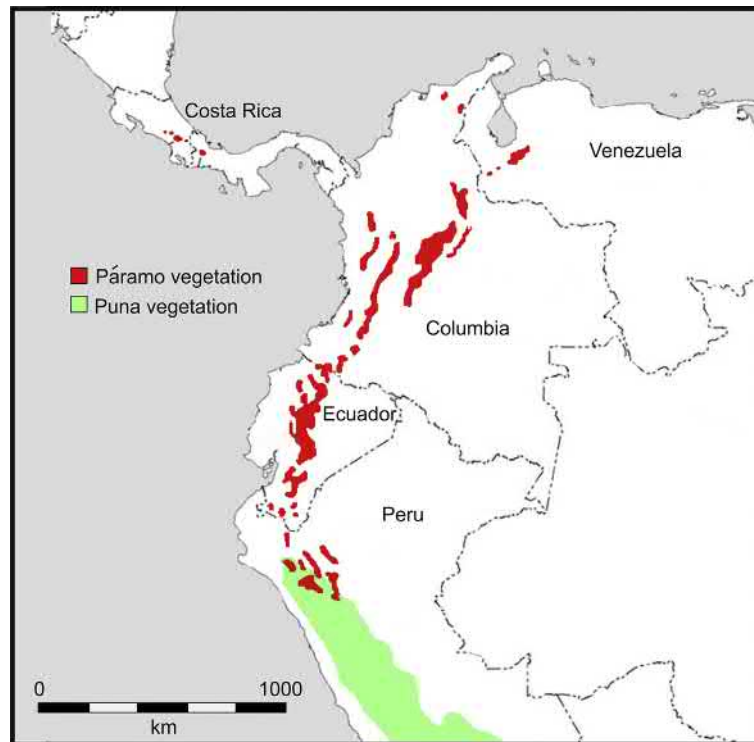


Fig. 5 Map of northwestern South America, showing locations of Páramo vegetation (in red) and the northern part of the Puna region (in green). Modified from Kappelle, M. and Horn, S. P. (2017). The Páramo ecosystem of Costa Rica's highlands. In: Kappelle, M. (ed.), *Costa Rican ecosystems*, pp. 492–523. Chicago: University of Chicago Press.

páramo habitat, exacerbating the risk of extinction of alpine species. However, more long-term, comparative field monitoring is essential to document the effects of climate change on high elevation páramo plant communities.

The Puna biome includes three subregions: High Andean Puna, Wet Puna, and wet montane grassland, as described by [Worldwildlife.org](https://www.worldwildlife.org/species-and-ecosystems/puna) (2019a,b). The High Andean Puna is found from 4200 to 5000 m asl. The area has highly contrasting diurnal temperatures, with summer warmth during the day and winter cold at night. As in the Páramo, the extreme daily temperature oscillations have been a selective force in the adaptation of plants to this environment. The Puna vegetation faces nightly freezes throughout the year. The annual precipitation at high elevations is < 700 mm, falling as snow and hail.

The Wet Puna is located on the Altiplano, from 3700 to 4200 m asl. The Wet Puna ecoregion is predominantly a high elevation grassland, ranging along the alpine regions of most of Peru to northern Bolivia. Treeline in the Wet Puna region lies at 3500 m asl. The regional vegetation includes bunchgrass communities, wetlands, small shrubs and trees, and herbaceous plants.

The precipitation regime in the Altiplano falls along a north-south divide. Northern regions (surrounding Lake Titicaca) have eight wet months, whereas southern regions have only one to two wet months per year. The wet montane grasslands are found in the eastern part of the Puna, from 3800 to 4200 m asl. Many endemic plant genera have centers of diversity in the Wet Puna, including *Culcitium*, *Perezia*, and *Polylepis*. Other endemic genera include *Alpaminia*, *Weberbaueria*, and *Mniodes*.

The Dry Puna ecoregion is found in parts of Argentina, Bolivia and Chile. The region lies 3500–5000 m asl. Like the Wet Puna, the Dry Puna experiences highly contrasting diurnal temperatures. The northern part of the ecoregion has temperatures ranging from 8 °C to 11 °C, and temperatures in the southern area are even lower. Annual precipitation in the Dry Puna is extremely variable, ranging from 51 to 406 mm.

At elevations over 4000 m asl, the vegetation is dominated by cushion bogs includes floating submerged cushion plants. Large cushions are formed by *Distichia muscoides*, *Oxychloe andina* and *Plantago rigida*. Other genera include *Gentiana*, *Hypsela*, *Isoetes*, *Lilaeopsis*, *Ourisia*, and *Scirpus*. Well-drained areas are home to other cushion plants, such as *Azorella compacta* (Fig. 6) and *Werneria aretioides*. The vegetation changes from east to west in the Dry Puna, from shrubland steppe with dry-adapted shrubs such as *Adesmia* (Fig. 6) *Nassauvia lagascae* (Fig. 6), *Baccharis*, *Fabiana*, and *Senecio* to grassy steppe with *Calamagrostis*, *Festuca*, and *Stipa*. The western slopes of the Andes in this region are extremely arid, forming the Atacama Desert, where the average annual precipitation is 15 mm, and in some years, there is no precipitation.

The entire Andean Puna has been greatly impacted by centuries of livestock grazing, burning, firewood collection and clearance for cultivation. Camelids, goats and sheep degrade the herbaceous vegetation, interfering with parts of their life cycles.

Ezcurra and Gavini review the alpine plant diversity of the mountains in the temperate latitudes of South America. The alpine ecosystems of this region fall south of the Puna region (Fig. 7) and extend to the tip of South America. The dry temperate Andes



Fig. 6 Plants of the alpine regions of the Andes. *Azorella compacta* courtesy of Creative Commons; *Nassauvia lagascae* by Patricio Novoa Quezada; *Oxalis erythrorhiza* by Jane McGary; *Calceolaria uniflora* by Liam Quinn; *Adesmia pinifolia* by Franz Zaver; *Chuquiraga jussieu* Paul Molina Abril; *Pappostipa humilis* by Hernan Tolosa. Photo of *Nassauvia lagascae* by Patricio Novoa Quezada, Photo of *Oxalis erythrorhiza* by Jane McGary, Photo of *Calceolaria uniflora* by Liam Quinn, Photo of *Pappostipa humilis* by Hernan Tolosa contacted by Facebook Messenger, Photo of *Adesmia pinifolia* by Franz Zaver/Creative commons, Photo of *Chuquiraga* by Paul Molina Abril contacted via ResearchGate.

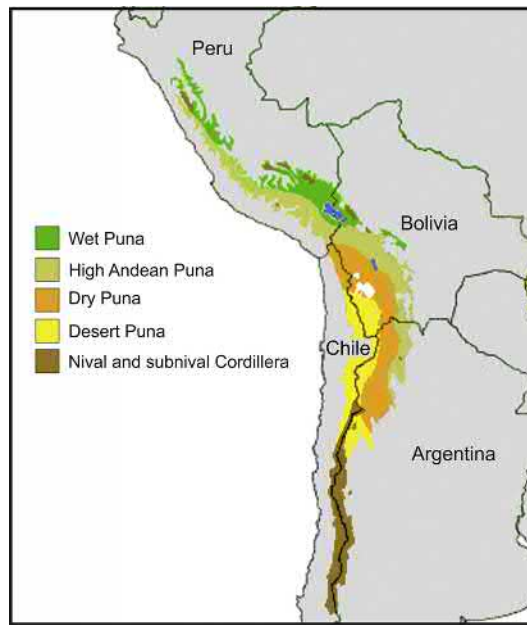


Fig. 7 Map of western South America, showing the various types of Puna vegetation along the Andes. Western S America veg map—Creative Commons, public domain.

(30°–37°S) reach elevations > 5000 m and are arid or semiarid. The alpine zone in this region lies above 3000 m and is bounded by xeric woods, matorral, and steppe. Further south, the wet temperate Andes (37°–55°S) are not as tall (< 3000 m elevation) but receive more precipitation. These alpine areas are surrounded by *Nothofagus* forest or krummholz. As in other parts of the world, treeline descends with latitude. It occurs about 2000 m above sea level (asl) in the north, ranging down to about 500 m in the south. The species diversity of vegetation in the temperate Andes is greatest at intermediate elevations, with decreasing species richness both towards treeline and toward mountain tops. Ezcurra and Gavini attribute the higher levels of plant diversity at middle elevations mainly to the positive effects of plant-plant interactions, especially the nursing of seedlings of various plant species by surrounding cushion plants. While this phenomenon is not unique to this region, it plays a vital role here because the harsh diurnal temperature and moisture fluctuations restrict seedling establishment, unless the seedlings sprout in the buffered environment provided by cushion plants.

The arid Patagonian region of Argentina is an important area for conservation due to the high levels of endemism. However, the natural vegetation cover of this region has been highly degraded as a result of human activities. Ecological rehabilitation strategies have been implemented to recover certain areas. One effort to restore native grasslands was a multi-year replanting of native species, including a perennial grass, *Pappostipa humilis* (Fig. 6). This, and another species (*P. speciosa*) were tested as possible “nurse species” that might help nurture seedlings of other native plants, in order to restore as much of the natural vegetation as possible (González and Pérez, 2017).

The mammal fauna of the Andes, as described by Novillo et al. (this volume), includes 200 species from 10 orders and 27 families. The greatest species richness is concentrated in two different areas: the ecotone between the Puna and the Yungas Montane forest, and the southern Páramo. The mammal fauna of the Andes consists of a combination of endemic alpine taxa, species whose main distribution is in the alpine, and species that are more broadly distributed, and only marginally reach high elevations. Rodent species represent almost 70% of all Andean mammals, followed by bats and carnivores, which account for 8% and 5% respectively. Andean mammals face several conservation threats, associated mainly with habitat loss or transformation, climate change and invasive species introduction. Among Andean species, near 20% have some degree of conservation concern, while 15% are considered data deficient.

Sevillano-Ríos et al. (this volume) review the environmental threats facing the bird species inhabiting the High Andes (> 2500 m asl). Altogether, the High Andes habitats host 945 species, composed of both resident and migratory species, generalists, and highly specialized, endemic birds. This level of bird faunal diversity is almost as great as that of the entire United States. Many are specialized, mountain-top species, adapted to live within narrow elevational ranges and climatic conditions. This climatic limitation makes them particularly vulnerable to climate change. Many endemic mountaintop species could become extirpated (locally extinct) or die out completely because of global change. The decoupling of species-habitat and other ecological relationships that could arise from shifting vegetation zones may be particularly serious for highly specialized birds of the Páramo, *Polylepis* forests, and wetlands.

Africa

Most high-elevation African mountains are isolated peaks or small groups of high mountains, separated into discrete island-like archipelagos. Many of these high elevation regions are remote, difficult to access, and thus far poorly studied.

Brown and du Preez (this volume) review the alpine vegetation of the temperate latitudes in Africa. The cluster of mountains in East Africa and the Chimanimani Mountains in Zimbabwe are separated by the broad Zambezi valley, and the latter is separated from the South African cluster by the Limpopo valley. The vegetation of the high African mountains consists of various elevational belts. The upper most belt (>3600 m asl), absent in southern Africa, is the Afroalpine ecoregion, with vegetation cover of bryophytes, tussock grasses, giant lobelias (*Lobelia* spp.) and senecios (*Dendrosenecio* spp.) (Fig. 8). A sub-Alpine belt (between 2800 and 3600 m) is characterized by sclerophyllous genera such as *Erica*, *Philippia*, *Cliffortia*, and *Passerina*. These plants have leaves that are evergreen, hard, thick, leathery, and usually small. These adaptations conserve water in the plant. Lower down an undifferentiated Afromontane vegetation belt (1800–2800 m) consists of indigenous forests, shrublands, moist grasslands and wetlands.

Carbutt (this volume) points out that the Afroalpine region is a center of plant endemism. About 81% of its plant species and four plant genera are unique to this region. But unlike the highly endemic flora of the Andes, the Afroalpine flora is species-poor with about 300–680 vascular plant species known from the various mountains. The most iconic plants of the Afroalpine region are the giant *Lobelia* and *Dendrosenecio*. These are well adapted to the strong diurnal-nocturnal temperature ranges experienced throughout the year. Some alpine shrub species thrive on the thin soils between rocky outcrops. *Protea kilimandscharica* (Fig. 8)

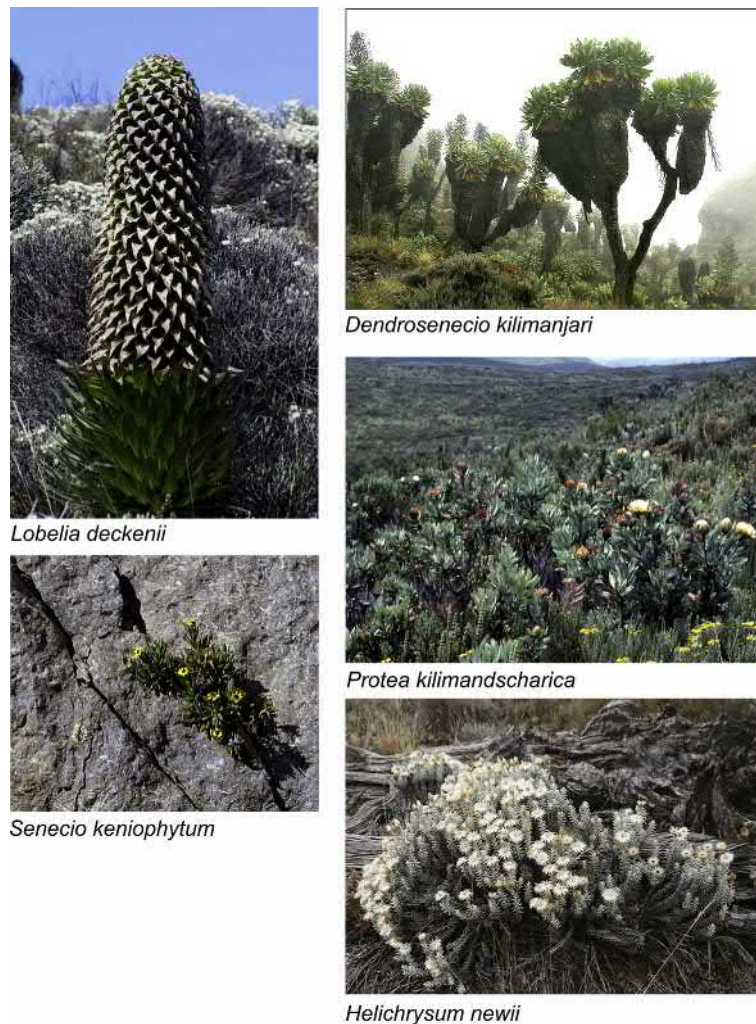


Fig. 8 Plants of the Afroalpine regions. *Lobelia deckenii* by Robert David Siegel, MD, PhD, Stanford University; *Dendrosenecio kilimanjari* by Carol Spears, Creative Commons; *Senecio keniophytum* by Mehmet Karatay, Creative Commons; *Protea kilimandscharica* by John Forlong, Creative Commons; *Helichrysum newii* by Mitchpa1094, Creative commons. Photo of giant African Lobelia by Robert Siegel (siegelr@stanford.edu) credit: Robert David Siegel, MD, PhD, Stanford University, Photo of *Dendrosenecio kilimanjari* by Carol Spears—Creative Commons, Photo of *Protea kilimandscharica* by John Forlong—Creative commons (queried), Photo of *Senecio keniophytum* by Mehmet Karatay, Creative Commons, Photo of *Helichrysum newii* by Mitchpa 1984 licensed under CC BY 2.0.

is found in this habitat, as described from Mount Kenya. The dwarf shrub *Helichrysum newii* (Fig. 8) thrives above treeline on Mount Kilimanjaro, especially near the rim of the ancient volcano.

The ecology of the Afroalpine ecoregions near the equator is reviewed by de Deus Vidal and Clark (this volume). This zone is isolated on mountaintops over 3200 m asl, and is found on 14 scattered mountains, covering 4525 km². This alpine region harbors between 515 and 521 species of flowering plants, 52 fern species, and >277 moss species. Endemism levels are around 35% for flowering plants and are 30% for mosses. Typical plant communities include tussock- and shrub-dominated grasslands and alpine bogs or fens, in which are embedded communities of Giant Lobelias and particularly Giant Groundsels (*Dendrosenecio*). Due to the difficulty of exploration in some of these mountains and the limitation of the available literature, this ecosystem needs more systematic research.

Töpfer and Gedeon (this volume) give an account of the alpine bird fauna of Africa. The Afroalpine bird fauna is small, particularly in relation to the Afromontane regions downslope from the alpine, where species diversity is far greater. In fact, there are no bird species unique to the Afroalpine. Rather, the alpine birds are a small subset of the Afromontane community. The Afroalpine bird fauna is comprised of four groups: (1) obligate biome-confined breeding residents (Ruddy Shelduck, Golden Eagle, and Red-billed Cough), (2) regular biome-affiliated residents (Thekla Lark, Brown Warbler, and Ankoher Serin), (3) facultative biome-affiliated residents (six species of tropical birds), (4) opportunistic residents and visitors (36 species of a variety of lowland habitats). To an even greater extent than with Afroalpine botanical studies, Afroalpine ornithology has only recently begun to assess the bird fauna of these habitat islands. Especially on a smaller geographic scale, information on regional or local differences between alpine bird communities remains fragmentary. Only 47 bird taxa are more-or-less confined to the Afroalpine.

Of the 25 nonpasserine bird taxa found in the Afroalpine, 17 are raptors, including owls. Of the 22 passerine taxa, five are seed-eaters that belong to just two genera (*Serinus* and *Crithagra*). Some of these birds deserve a closer look by ecologists, as they play important roles in the Afroalpine, even though they might not be found there exclusively.

The Afroalpine mammal fauna has been reviewed by Pillay and Joshi (this volume). Their definition of the Afroalpine zone is much broader than the other authors in this volume, as they consider the Afroalpine zone to be areas above 1800 m asl. Within this broader range of habitats, there are 109 mammal species in 10 orders. Endemic species account for 60% of the fauna and 38% are currently of conservation concern. As elsewhere, rodents constitute the majority of these mammals (53%). These small mammals display a variety of adaptations that reduce their exposure to lethal temperatures. As with bird studies, Afroalpine mammals are poorly studied in many of the representative countries because of their inaccessibility, the small number of field biologists and a lack of consistent field surveys.

Small mammals in the Afroalpine must cope with below freezing nighttime temperatures, year-round. Several rodents show behavioral, morphological and physiological adaptations to cold. For instance, to avoid lethal temperatures in the Bale mountains, some rodents are diurnal, rather than the typical nocturnal behavior pattern. This diurnal activity pattern is found in five species of Afroalpine rats. Some seek shelter in shrubs and rocky outcrops, which provide some protection from the freezing temperatures of the open valley habitats where they forage. Temperatures below ground remain more or less constant at a soil depth of 50 cm and even in shallower burrows. Thus, many small Afroalpine mammals avoid cold temperatures by nesting belowground.

Climate warming will likely cause Afro-alpine endemics to become very restricted in an already confined environment, with some species—especially those most obvious flagship giants adapted to the diurnal freeze-thaw cycle—being most at extinction risk. In addition, many high-elevation ecosystems in Africa are threatened by anthropogenic influences, of which overgrazing by domesticated animals tops the list. It is expected that because of their low competitive ability, alpine species will decrease in number while species from the lower-lying areas, better adapted to warmer conditions, will increase in number. Other human-caused threats include various land use changes such as massive deforestation and heavy agricultural intensification. These disturbances are already directly affecting even the fragile upper habitats of African mountains. A total of 38% of Afroalpine mammals are currently endangered, a number that is likely to increase in future. These mammals face a range of threats, most notably habitat destruction through human expansion and activity and ultimately global climate change.

Asia

The Asian mountain system consists of a series of mountain ranges and plateaus around Tibet (including the Pamir, Kunlun and Tien Shan Mountains). Mountains and highlands with alpine life zones extend to southern Asia along the Hindu Kush, Karakoram, Himalaya, and isolated peaks in Borneo, Sumatra, Lombok and New Guinea. Western Asian mountain ranges include the Urals, mountain ranges around the Iran Plateau, the Trans-Caucasian and Pontic Mountains, and some peaks on the Arabian Peninsula. In northern Asia, alpine ecoregions occur in the Altai, Sayan, Changai, East Siberian and Kamchatkan mountains with the transition from alpine to arctic habitats, as well as some ranges Eastern and Southern China, Taiwan, Korea, and Japan (Schickhoff and Mal, this volume).

Negi and Mukherjee (this volume) review the climate change impacts in the Himalayan mountain ecosystems. They note the significant absence of long-term climate observations and ecological data collection throughout the Himalayas, particularly in the alpine regions. The average annual temperature over the Asian land mass, including the Himalayas, is predicted to increase by about 3 °C by the 2050s and about 5 °C by the 2080s (IPCC, 2007), and average annual precipitation will increase by 10–30% by the 2080s (IPCC, 2007). Satellite imagery suggests that the margins of almost two-thirds of the glaciers in the Himalaya have retreated in recent decades. For example, in Central Himalayan region of Nepal, glacial margins are retreating by as much as 10 m/year (Fig. 9). According to the International Commission for Snow and Ice, glaciers in the Himalayas are receding faster



Fig. 9 Photo of the eastern terminus of Imja Lake where it meets Imja Glacier, Nepal, by Daniel Alton Byers, Creative Commons. The margins of this glacier are retreating by as much as 10 m/year. Photo of Imja Glacier, Nepal by Daniel Alton Byers, Creative Commons.

than in any other part of the world. If the present rate continues, they will probably disappear by 2035. Snow cover is another critical environmental aspect of Asian highlands. The snow-covered area of Asian mountains has significantly declined, especially since the 1960s. Snow-cover duration in the greater Himalayan region has decreased by 30 days per year in recent decades.

The alpine plant diversity of the temperate mountains of Asia is described by Sridith (this volume). Their article focuses on the alpine regions of the Himalayas and the Tibetan Plateau. This vegetation is characterized by dwarf shrubs with rhododendron growing in krummholz form at the forest-tundra ecotone. Alpine grassland is also rather common from the tree line up to the snow line. There is a high diversity of herbaceous vascular plants including some selected grasses and sedges, and this vegetation is more-or-less protected from livestock grazing because of steep slopes (angles over 45°) (Baniya, 2010). However, even the vegetation on the steepest slopes is not immune to the effects of climate change. The melting of glaciers is leading to changes in surface and groundwater hydrology of the Himalayas. This, in turn, is causing habitat and species loss.

As discussed by Schickhoff and Mal (this volume), climate change in the Himalayas is causing upslope expansion of subalpine species, changes in treeline dynamics, phenological shifts, and changes in primary production. The introduction of invasive species is increasing and is facilitated by warming climates.

The alpine regions of tropical Asia are confined to high mountaintops on islands. The New Guinea alpine zone, as discussed by Hope (this volume) lies above 3750 m asl. This is the highest, largest and wettest such region on any tropical island. The modern alpine consists of habitat islands spread over 1400 km with considerable variations in biodiversity between the individual mountain areas. The use of fire by native peoples has expanded open areas of vegetation near treeline over the past several thousand years. The alpine is threatened by increased warming and potential invasion by emergent shrubs but is unlikely to disappear, provided that wet conditions continue to prevail. With few exceptions, land management depends on local populations; widespread fires during El Niño-induced dry phases point to continuing human impacts linked to drought events.

New Zealand and Polynesia

As discussed by Lord (this volume), New Zealand harbors the most significant alpine ecosystems in the Southern Hemisphere outside of South America. Because of its long-term isolation, the alpine biota of New Zealand has high levels of endemism. Treeline in New Zealand varies from 1400 m asl in central North Island (39°S) to 900 m in south-western South Island (46°S). The elevational tree limit in New Zealand is dominated by evergreen *Nothofagus* trees. New Zealand's alpine areas are geologically recent and tectonically highly active, which has led to allopatric speciation and many poorly understood species complexes among plants, invertebrates and reptiles. In the alpine region, over 90% of plants are endemic. New Zealand's alpine biota has had to adapt to climatic unpredictability. This adaptability may buffer the effects of future climate change on New Zealand's alpine biota. The greatest threats to New Zealand alpine ecosystems are invasion by introduced pest species, most notably cold tolerant conifers, ungulates and rodents. In much of South Island, low diversity southern beech forest gives way abruptly to a low alpine zone of tall grassland dominated by the near endemic tussock genus *Chionochloa*. In central South Island, the alpine vegetation also consists of tall tussock grassland. The dominance of tall tussock-forming grasses and large-leaved, evergreen herbaceous plants in New Zealand's low alpine ecosystems differentiate them from temperate alpine areas of the Northern Hemisphere. Instead, these ecosystems more closely

resemble alpine ecosystems of tropical high mountains such as those of Africa that experience extreme temperature variations during diurnal cycles year-round.

The climate of the alpine zone in New Zealand and Hawaii is cold, and precipitation levels are highly variable. Mean annual alpine temperatures range from -6.9°C to 8.2°C in New Zealand and from 3.6°C to 10°C in Hawaii. New Zealand is subject to westerly winds in the mid-latitudes, while Hawaii is subject to the northeast trade winds in the tropics. The perpendicular orientation of the mountains to the prevailing moisture-laden winds results in extremely wet windward areas, amounting to over 10,000 mm per year on both the western slopes in New Zealand and the eastern slopes in Hawaii. In stark contrast to the wet windward regions, the dry leeward regions lie in rain shadows where precipitation can be as little as 500 mm per year in New Zealand and 200 mm per year in Hawaii.

Alpine ecosystems in the Pacific Islands are isolated and are also characterized by high levels of endemism, as discussed by Frazier and Brewington (this volume). Only Hawaii and New Zealand have mountains sufficiently tall to contain substantial alpine environments. In the alpine and subalpine ecosystems of Hawaii, 84% of plant species are endemic. About 11% of the land area of both island groups is located above treeline. The treeline of Mauna Kea is located about 2900 m asl. The treelines of Mauna Loa and Haleakalā are at least 450 m lower than on Mauna Kea, which may be due to soil-dependent factors. On the northeastern slope of Haleakalā, treeline occurs around 2100 m asl. Treeline elevation varies elsewhere in Hawaii. In most localities, native subalpine cloud forest gives way to alpine shrublands, herbs, and tussock grasslands that form a fog-drip community. Alpine desert conditions exist on Maui and Hawaii Island above about 3000 m asl.

These alpine ecosystems are threatened by invasion of exotic species, climate change, and human impacts. Both New Zealand and Hawaii have experienced strong warming at higher elevations, and future projections indicate that these warming trends will continue. For Hawaii, future projections of temperature indicate that the greatest warming will occur at the highest elevations. Projections range from 3.5°C to 5°C warmer temperatures by 2100. Glacial retreat has been noted in the Southern Alps of New Zealand, with 34% ice volume lost since 1977, and climate models predict that New Zealand as a whole may lose 88% of its ice volume by 2100. Similarly, snowfall on Hawaii's mountain peaks is projected to almost entirely disappear by 2100.

Current Human Impacts on Alpine Ecosystems

As we have seen, alpine ecosystems account for only a small percentage of terrestrial habitats yet, along with adjacent mountain systems, they provide water resources to nearly half of the world's human population. Approximately 20% of humans live in or near mountain areas, making it inherently important to understand current impacts on these systems. Cryosphere changes in the alpine include the melting of permanently frozen ground (permafrost), decline in snow cover duration and area, rapid retreat of glacial margins and thinning and water loss in alpine glaciers, with a total loss of 18% of glacier area occurring across > 900 alpine glaciers between 1985 and 1999 alone. Regional climate models project increases in alpine temperatures, combined with decreases in winter precipitation falling as snow and an increase in winter precipitation falling as rain. These coupled changes in temperature



Fig. 10 Photo of cattle grazing an alpine meadow in Switzerland. Photo of cattle grazing in Alps. Creative commons.

and precipitation will influence snow cover persistence and the timing of snowmelt which, in turn, will impact growing season length, productivity, and biogeochemical cycling in alpine systems worldwide. Most climate models predict an advance in the timing of alpine flowering in response to an advance in snowmelt timing. Alpine plant community composition has also shifted in recent decades, likely in response to warming. More than one-third of 125 plant species in the Alps have migrated at least 100 m higher than their historical lower elevation limits in recent decades, with simultaneous increases in abundance at their upper elevation limit that now experiences warmer temperatures. However, alpine plant response to increasing temperatures is often more complex than this. Many of the responses observed or predicted in alpine systems will be the result of complex, oftentimes interactive, processes. As discussed by Walsh and Gigu  t-Covex (this volume), the history of human disturbance of alpine landscapes in Europe extends back to 7000 years ago in the Neolithic Period. Livestock grazing has changed the species composition of Alpine vegetation over several millennia (Fig. 10).

In New Zealand and the Pacific islands, climate change, human-driven environmental degradation, and land use change have facilitated species invasions, to which these isolated alpine ecosystems are particularly vulnerable. The first known mammalian predator to arrive in New Zealand and Hawaii was the Polynesian rat around 800 years ago, but the vast majority of pests accompanied the European settlement of New Zealand and Hawaii in the 1800s, feral populations of red deer and rabbits have exerted significant pressure on New Zealand's alpine grasslands, while grazing livestock, especially sheep, also influence vegetation cover and species composition. Grazing livestock, including pigs, cattle, and goats, have severely affected Hawaiian alpine ecosystems, particularly in grassland-dominated areas. This has coincided with soil erosion and non-native plant invasions that have further reduced alpine plant community regeneration. Both New Zealand and Hawaii are far removed from mainland regions, so invasive species have been brought, either accidentally or deliberately. Hawaii has been called the poster child for invasive species. The Bishop Museum in Hawaii estimates that >5000 species of plants and animals occur in the Hawaiian Islands, including >1300 introduced vascular plant species.

Conclusions

The collection of articles on alpine ecosystems provides an excellent overview for each region. It is striking that these articles have so many themes in common. One would think that the nature of alpine regions in high-latitude North America or Asia would have little in common with the nature of alpine regions at the top of tropical islands, but this is not the case. Virtually all the alpine regions reviewed in the Alpine section of this encyclopedia share some common characteristics:

- (1) Most alpine regions represent habitat islands, isolated from each other by intervening valley systems that are impassable barriers to migration of many alpine taxa. This isolation makes alpine biota vulnerable to extinction in the face of severe environmental change, because recruitment of alpine biota from other habitat islands can only happen during glacial intervals.
- (2) There is a relatively high level of endemism in the flora and fauna. If enough populations of endemic species are driven to extinction, the whole species will die out, as there are no other regions from which new populations can be recruited.
- (3) Most of the fauna and flora of alpine regions are highly adapted to the severe physical environments in which they live. Because of this high level of adaptation, they are bound to suffer extirpations and extinctions when the climate becomes too warm. They already live on mountain tops, so there is no higher ground on which to seek cooler temperatures.
- (4) Global warming is amplified in many alpine regions of the world, exacerbating the pace and intensity of environmental change. This warming affects alpine communities in many ways, including changes in phenology of individual species, disturbance of species interactions, and invasion of more warm-adapted species from lower elevations.
- (5) Glaciers are decreasing in volume and their margins are retreating in most high mountain regions. Snow cover is shallower and is persisting fewer days per year. These changes are of such great magnitude that alpine glaciers may disappear within the next century. The decline of mountain snow and ice is causing hydrological changes that begin in the alpine zone (where soils can become desiccated) and continue downslope to the ocean. Melt water from alpine glaciers and snow fields is currently used for drinking, irrigation and hydroelectric power for about 1.5 billion people.
- (6) Many cultures around the world have tried to graze animals on the herbaceous vegetation of the high country. This invariably causes alpine habitat disturbance or destruction. Livestock grazing also facilitates the establishment of invasive species in the alpine, as it weakens the natural vegetation communities.

The take-home message here is that the world's alpine ecosystems are extremely tough when it comes to withstanding long, cold winters, but extremely vulnerable to the current human-caused changes because they have never before been exposed to them. The combination of rising temperatures, livestock grazing, air pollution encroaching from urban centers, invasive species, declining levels of meltwater, and other anthropogenic disturbances is putting alpine biota under a great deal of stress. As with all the other biomes of the world, we need to be taking steps to ameliorate these disturbances, before it is too late.

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Patterns and Controls on the Productivity and Plant Diversity of Alpine Ecosystems

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Abstract

The productivity and diversity of alpine ecosystems are two subjects that have attracted the attention of researchers for decades, but these characteristics have often been studied separately and at different spatial and temporal scales. Here, the relationships and causal mechanisms that appear to relate these two very different properties of ecosystems are presented. Recent studies confirm that at landscape-level scales controls are governed by moisture and energy, while at the smaller spatial scales the biotic characteristics that interact with resource availability are seen as important. These controls are now being influenced by directional environmental change drivers that will alter spatial relationships of alpine biota with other ecosystems and will both increase and decrease productivity and diversity within and among alpine areas.

Introduction

The alpine is renowned for its topography, biotic exuberances in summer, and extreme cold and wind in winter. The latter two features have perhaps been its salvation. While alpine regions can be found adjacent to large human populations, humans have not been able to dominate and transform these natural areas as has occurred in many other terrestrial ecosystems, at least not until recently. The isolation and topographic features of these islands in the sky have led to the evolution of biotic communities that are locally diverse and sculpted by multiple resource limitations. The time since the establishment of these communities varies from “just emerged from the Pleistocene ice” to sites that have been unglaciated for millennia and have a long evolutionary history of biotic interactions. The site heterogeneity and variation in time since establishment that characterize alpine areas are accompanied by a litany of stressors, including its short growing season, high levels of ultraviolet radiation, low soil fertility, and frequent freeze-thaw events that can occur during the growing season. Collectively these have resulted in the evolution of plant species possessing remarkable adaptations to these stressors (Körner, 2003). However, these communities must now experience climatic conditions and atmospheric chemistry drivers that have not been experienced since pre-Pleistocene times, if at all. This article summarizes recent findings that have attempted to clarify, elucidate, and advance new knowledge of these charismatic ecosystems and their adaptabilities and vulnerabilities in the emerging Anthropocene.

Is Alpine Tundra the Same as Arctic Tundra?

High elevation areas are often studied alongside high latitude areas. Both systems were identified and combined into a single study unit during the emergence of “big science,” the International Biological Program, during the 1960s (Worthington, 1975). Summaries and descriptions of these two similar-but-different systems are often combined in books (e.g., Chapin, 1995; Wielgolaski, 1975) and in volumes that discuss ‘the tundra biome’ as well as in journals (e.g., Arctic, Antarctic, and Alpine Research). A small to moderate percentage of plant species are shared between these two biomes (c.f., Billings, 1973; Cooper, 1989), and the low average temperatures and short growing seasons of both regions have affected vegetation structure and life-forms in similar ways. Both systems exhibit large variations in community types ranging from rock-covered lichens through wetland bogs, resulting in multiple combinations of vascular and nonvascular plant communities. The one common denominator is the lack of trees (or the presence of tree species with prostrate shrub growth-forms). Alpine ecosystems also evolved independently in tropical regions, and the major differences between arctic and alpine systems include the higher diurnal variation in temperature and irradiance experienced in the

alpine (Hedberg, 1997) and the relative importance of topography in controlling factors such as soil moisture and growing season length (Billings, 1973).

Alpine Plant Communities

Alpine ecosystems are composed of herbaceous plant communities found at elevations where soils are generally too cold to allow for forest growth (Körner and Paulsen, 2004). These communities are usually dominated by graminoid (= grasses + sedges + rushes) or forb (= nonwoody dicots) landscapes, although some woody species such as dwarf trees (krummholz), willows and other shrubs may also occur. Factors controlling the lower elevational limits of these meadows are a combination of temperature, moisture, wind, domestic grazing, and disturbances such as avalanches (Malanson et al., 2007; Bourgeron et al., 2015).

Alpine regions have held our interest in part because of their visual appeal, a factor related in part to the fact that flowering species often appear to dominate the landscape, and these alpine environments are often renowned for their floral displays. The forbs generally play a more dominant role in plant community structure than in other nonwoody communities such as grasslands and savannas. The abundance of forbs results in some alpine areas being referred to as “herbfields” (Chambers, 1995), however, dominance by forbs is often limited to small areas, and grasses and sedges usually dominate the dry, mesic, and wet meadows of alpine landscapes (Billings and Mooney, 1968). Still, the abundance of forbs in some alpine areas argues that mechanisms that contribute to the dominance of graminoid species in warmer climates not dominated by woody species are less effective in the alpine. Understanding these mechanisms remains a research focus.

Measuring Plant Diversity and Productivity in the Alpine

Plant diversity studies rely on the ability to identify species from a potentially large regional pool of vascular plants. To obtain statistical measures of species abundances, a sample area and sample size must be chosen. The standard sample unit can range from a fraction of a square meter to well over 100 m², with smaller plot areas usually selected in order to quantify differences due to community type or resulting from experimental manipulations. The point-intercept procedure (Fig. 1) is perhaps the most commonly used method to quantify alpine plant species and community characteristics. Point-intercept data can be used to estimate species number per plot (richness), amount of cover per species per plot, relative plant cover. These data can also be used to calculate species evenness and species diversity, which along with richness are the standard units of plant community ecology. Differences in plot size and in the way that various investigators have measured or calculated these variables limits the ability to conduct absolute comparisons among studies. However, the patterns and trends resulting from these measurements made across landscapes or experimental manipulations can be summarized.



Fig. 1 Plot plant species richness is often determined with point-intercept techniques, shown here, which can quantify the number of species as well as the amount of cover of alpine tundra plant species in small plots. A NEON (National Ecological Observatory Network) tower designed to measure carbon exchange and used to calculate GPP (gross primary productivity) for a large swath of tundra is seen in the background. Photo of Niwot Ridge, Colorado, taken by author.

Measurement of net plant production (NPP) requires measurements of the fates of the products of photosynthesis, both aboveground (ANPP) and belowground (BNPP). Historically, ANPP in the alpine was measured by clipping all aboveground live biomass down to the soil surface. Comparisons of these amounts were then made across various resource gradients, community types or treatments such as grazing or fertilizer additions (Bowman and Fisk, 2001). This technique assumes a strong correlation between the sample, usually harvested to represent peak biomass, and actual aboveground net primary production. In reality the estimate is affected by losses of biomass prior to collection or the failure to include additional production following the harvest. Losses due to aboveground herbivores and pathogens are often not included or assumed to be negligible. This low-tech method has been superseded by more sophisticated techniques, but the information gained relative to time and effort usually justifies the method.

Belowground estimates of plant materials produced per year are difficult to measure for multiple reasons, including the fact that live roots are often difficult to separate from dead roots that were produced in a previous year. Further, plants can produce large amounts of root exudates (Huo et al., 2017), allocate biomass produced by photosynthesis to mycorrhizal fungi (Marschner, 2012) as well as contribute a fraction of growth to root herbivores (Seastedt and Murray, 2008). Those contributions of NPP are rarely known or measured. While most aboveground growth of herbaceous species turns over (senesces) every year, a fraction of roots are longer-lived, meaning that belowground harvests do not represent annual production. Instead, root growth has been approximated by root ingrowth techniques (Fisk et al., 1998) or isotopic measurements (Smit et al., 2013), both of which are difficult to perform and time consuming.

Körner (2003) identified an important caveat about measurements of primary productivity in the alpine. A portion of what is included in an estimate of ANPP is allocation from stored materials accumulated in one or more previous years. Since alpine vegetation is dominated by perennial species, this contribution is potentially larger than in other herbaceous communities containing more annual species. This contribution, in addition to transfers to herbivores, and belowground transfers to root exudation and mycorrhizae mean that using biomass as a proxy for ANPP or NPP is problematic and arguably could be an over- or underestimate in any year. One might assume that underestimation is the rule (due primarily to losses to exudates and mycorrhizae), but in at least some years overestimates are possible.

More recently, a potentially much more precise, albeit large spatial scale estimate of gross primary production (GPP, the total amount of carbon fixed by plants per unit area per year prior to subtracting plant respiration costs) has been made possible through the use of carbon flux towers (e.g., Knowles et al., 2015; Fig. 1). These towers measure near-instantaneous changes in the downward and upward movements of carbon dioxide and, in doing so, can estimate net removal of carbon from the atmosphere into the plants during the growing season, and losses of carbon to respiration from all sources during periods when photosynthesis does not occur. Net primary production, in turn can be estimated as a fraction of GPP. Carbon flux towers are expensive to install and run, and the areas as well as the accuracy of measurements can be influenced by topography. As such, flux towers in alpine areas are few. However, given the large microsite heterogeneity in soils and plant resources found in the alpine (c.f., Körner, 2003), estimates from small sample areas come with very large variances and uncertainty of averages remains large without a major sampling effort. Both methods remain useful for addressing various questions, but the flux towers ultimately should provide the required knowledge of carbon flux and carbon sequestration in the alpine.

Patterns of Plant Diversity and Richness in Alpine Habitats

Alpine ecosystems occur in both the southern and northern hemispheres. Both are under fairly similar climatic constraints, but the separate evolutionary paths of different floras and faunas have generated some spectacular differences in alpine community composition. With the exception of a few plants (termed “bipolar arctic-alpine” by Billings and Mooney, 1968), these systems are biotically distinct. While the mechanisms that explain patterns in plant productivity and local diversity are suggested to hold for both hemispheres, one should expect some unique patterns generated by biotic communities that have evolved under unique resource and climatic constraints.

Factors affecting the numbers of species and their relative abundances within alpine areas have been a topic of interest for decades (Grabherr et al., 1995). Plant richness is often correlated with the long-term history and size of the local to regional amounts of areas composing alpine zones (Nagy and Grabherr, 2009). For example, numbers of species appear relatively low in isolated alpine regions such as in New Zealand (Mark and Dickinson, 1997) and in tropical Africa (Hedberg, 1997). The size and composition of the regional pool of plants and the time these have had to evolve and adapt to alpine climatic conditions clearly are important in determining the richness of alpine sites.

Our knowledge base of the alpine systems is also a function of geography. Studies of the patterns and controls on alpine plant diversity are relatively common for Europe where an entire volume has been dedicated to the subject (Nagy et al., 2003). That work has been updated with a volume on alpine biology that reviewed alpine habitats on most continents (Nagy and Grabherr, 2009). In North America, syntheses are fewer and are often site-specific (Bowman and Seastedt, 2001; Williams et al., 2015). A modest number of northern Eurasian studies were available and summarized several decades ago (Wielgolaski, 1975), but information accessible to English readers on alpine areas in China and Mongolia have only become common in the last two decades (c.f., Feng et al., 2006; Wang et al., 2013; Dong and Sherman, 2015).

Among the fairly safe generalities about the patterns of plant diversity in the alpine is that that lichens and bryophytes increase in richness with latitude while vascular plant richness declines (Virtanen et al., 2003). There is also strong support to show that soils with higher pH, which contains higher plant-usable cations and less soluble aluminum, have higher local and regional richness

values (Körner, 2003; Virtanen et al., 2003; Gasarch and Seastedt, 2015a). High local species richness is found in drier zones of the alpine. Marini et al. (2007) found alpine species richness to be highly positively related to the presence of “small stress-related species” which tend to be found in drier portions of the alpine. For example, in the Tatra Mountains, Czortek et al., (2018) found averages of over 40 species in dry meadow plots, compared to 20 or less species in plots located in wetlands and snowbeds. These trends are very similar to a dry to wet meadow gradient found in the Colorado Rockies (Bowman and Swatling-Holcomb, 2018) and elsewhere.

Effects of grazing on alpine richness and productivity have the potential to produce the same curvilinear response documented for many grasslands, that is, responses can be positive, neutral, or negative depending upon the intensity and frequency of grazing. If light to moderate grazing reduces the abundance of dominant species, then some increase in plant evenness and diversity is expected, and local richness may also increase. In contrast, heavy grazing and especially long-term moderate to heavy grazing will reduce both richness and productivity (Lu et al., 2017). Overgrazing has occurred in the past in most alpine systems and these grazing legacy effects may still be influencing observed patterns. Similar to abuses caused by road building and trampling, long-term overgrazing damage involves erosion and soil loss. Even smaller herbivores, such as gophers, can have this effect (Sherrod and Seastedt, 2001). Passive revegetation in the alpine (e.g., natural reseeding from adjacent areas), particularly in drier areas, is extremely slow (Ebersole, 2002), so legacy effects of overgrazing on current communities may be significant. Changes in grazing intensity and frequency may also interact with climate changes, enhancing or reducing the more diverse and productive habits found in the alpine (Wang et al., 2012). However, grazing could also prove to be a useful alpine management tool under some scenarios.

The Productivity of Alpine Ecosystems

The amount of carbon fixed into plant biomass per unit area per unit time (NPP) in alpine areas has been measured and reported numerous times since an original global summary by Lieth and Whittaker (1975). Aboveground values for vascular plants can range from zero to over 500 g m⁻² of mass with ranges of 100–300 g m⁻² being most common (Bowman and Fisk, 2001). Belowground production likely exceeds that of aboveground production (Fisk et al., 1998; Körner, 2003) and in some communities is likely more than double aboveground production. Understanding carbon dynamics of the alpine in an era of climate change is clearly a current concern. Most studies to date, however, have focused on the variability of NPP observed across the alpine tundra and the factors that control this variation.

The primary controls on plant productivity are the three potentially orthogonal resources: solar energy, nutrients, and water. Temperature might be considered a secondary control and can control the availability of water by converting plant-available water to ice or water vapor, and can also impose strong constraints on plant functioning via controls on enzyme structure and efficiencies. However, in the alpine, environmental controls interact with one another as well as with the biota, and the result of this produces often complex, localized patterns in plant productivity.

As discussed earlier, alpine regions can include areas that remained ice-free during the last glaciation, such as the 180,000-year-old surfaces found on Niwot Ridge (Bowman and Seastedt, 2001). Older surfaces have the potential to have mature soils that can accrue and store plant nutrients. At the opposite extreme are areas just now emerging from retreating glaciers or soils just now forming in what were nival (above the alpine) zones, producing clear nutrient limitations to plant species presence and abundances (Bueno de Mesquita et al., 2017; Castle et al., 2017). Accompanying this fact are the often substantial topographical constraints of slope and aspect that influence soil formation and fertility. Since soils hold both water and nutrients, generalizations about water and nutrient limitation in the alpine usually require site-specific qualifications, and the extent of soil limitations can vary from none to extreme.

The sensitivity of alpine vegetation to nutrient additions has been studied for many decades (e.g., Wielgolaski, 1975). In that study, vegetation was shown to increase by 4.6-fold after 2 years of a large addition of macro (nitrogen (N) phosphorus (P) and potassium (K)) and micro nutrients (magnesium (Mg) sulfur (S) and boron (B)). Of interest was the finding that the mixed fertilizer outperformed N fertilizer (as nitrate) by a factor of about three. Clearly, the vegetation in that study area experienced multiple nutrient limitations. More recently, scientists working at a global network of sites used a nutrient factorial experiment to identify those nutrients limiting to productivity. The general findings are that N and P, but not K or micronutrients, tend to limit productivity of grasslands, including the alpine (Fay et al., 2015). In alpine soils that have been recently exposed due to receding glaciers, P has been found to be more limiting to plant growth than N (Darcy et al. 2018). The relative magnitude of the response to nutrients is often a site (soil) characteristic, but alpine systems are generally sensitive to both N and P additions, and these additions affect both productivity and plant community composition (Fig. 2; Theodose and Bowman, 1997; Gasarch and Seastedt, 2015a).

How Resource Availability Sculpt the Diversity and Productivity of the Alpine

Integrating multiple resource limitations improves our understanding of the patterns of diversity and productivity seen on the alpine. The alpine topography is capable of generating a plethora of energy and moisture gradients and range in values that, from a vascular plant's perspective, vastly exceed an individual species' tolerance constraints. Changes in energy and water gradients though time generate nutrient and soil acidity gradients that also affect plant community diversity. However, one gets a sense



Fig. 2 A 2×2 m nitrogen + phosphorus plot in a dry meadow alpine located at Niwot Ridge, Colorado. This plot has been fertilized every other year for over 20 years. The dashed line borders have been added to better identify boundaries. The surrounding meadow is dominated by a sedge, *Kobresia myosuroides*, which has now been largely replaced in the plot with a variety of forbs and other graminoid species. Overall plot richness as well as diversity has increased in this plot, but responses to nutrients in other plots and in different moisture regimes can vary. Photo by author.

that water and energy are the primary factors, just as they appear to be in structuring the global diversity of vascular plant species (Kreft and Jetz, 2007). In the alpine, however, the fact that a large percentage of precipitation falls as snow confounds water-energy gradients even further (Billings, 1973). At one extreme the wind-scoured uplands remove most snow before the moisture can penetrate the soil. The soil surfaces of these wind-scoured areas receive substantially more solar energy inputs than surfaces beneath snowdrifts. By amplifying precipitation and light input differences, the topography of the alpine generates water-limited to light-limited (integrated solar radiation over the growing season) gradients that in turn affect soil development and generate plant diversity gradients. Snowfields can, on occasion, last beyond the annual growing season, thereby inhibiting all plant growth in that year. This likely explains, in part, why such a high fraction of alpine species are perennial rather than annual or biennial species.

When the consequences of the topography-climate interaction are expressed in terms of effect on alpine productivity, a curvilinear pattern across the tundra landscape is generated (Fig. 3). This figure might benefit from a third dimension that would explicitly recognize nutrient limitation, such that higher availability of N, P, and in some sites, certain micronutrients, would enhance NPP values. An empirical validation of this model is shown here by summarizing nine years of ANPP from a set of approximately 80 plots measured annually at Niwot Ridge, Colorado (Niwot LTER, 2019; Fig. 4). The production gradient goes from low production endpoints, fellfield or snow bed communities, to the increasing ANPP gradient generated by dry, moist, and wet meadow sites. Wet meadow sites can become free of snow after dry meadow sites, but due to runoff subsidies of water from upland

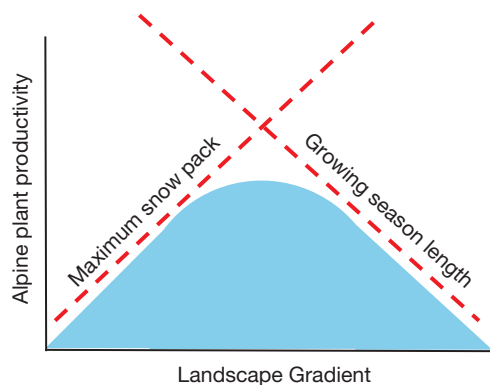


Fig. 3 Generalized model of site productivity (values in blue) as a function of light availability and snowpack. Extremely windblown sites have maximum light but minimum soil volume, fertility, and water. Snow bed communities, created by massive snowdrifts, have very limited growing seasons and following high snow pack winters may not melt out during the current growing season.

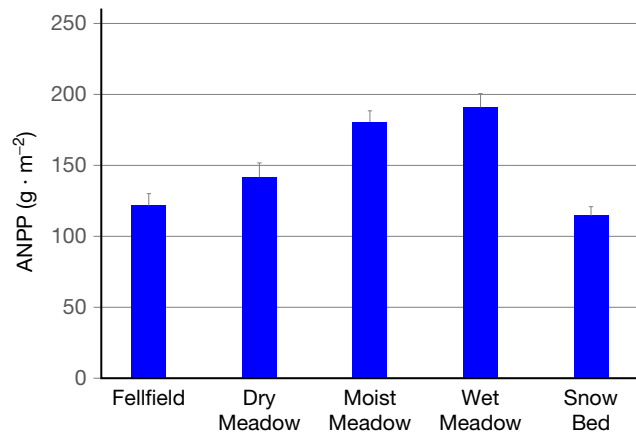


Fig. 4 Aboveground net primary productivity, estimated by aboveground biomass, measured over 9 years at Niwot Ridge, Colorado. Standard errors of the annual mean values are shown.

sites, these do not dry out during the summer as early as dry meadow sites. Hence, growing season duration can be affected by water as well as light availability.

The Relationship Between Diversity and Productivity of the Alpine

Demonstrating a beneficial relationship between diversity and ecosystem services has been somewhat of a Holy Grail mission of ecologists, and one that's been generally successful after decades of study (Isbell et al., 2011; Grace et al., 2016). At the entire biome or alpine community level scale, plant diversity usually correlates with ecosystem services such as plant productivity or carbon sequestration. However, when examined at smaller spatial scales, different patterns exist because of the varying strength of the biotic-abiotic interactions that influence diversity across local resource gradients. If, as suggested here, these gradients are both steep and large, we should expect patterns not seen in more homogenous environments.

Multivariate analyses, path analysis, and structural equation modeling are important tools to understanding both species diversity and productivity characteristics of alpine ecosystems (c.f., Kikvidze et al., 2005; Yuan et al., 2016). However, in applying these tools or attempting to generalize from site findings, the recognition that "context matters" needs to be acknowledged. Often a single variable or mechanism is touted as *the* factor affecting the pattern of interest. Clearly this is the exception rather than the rule in ecology (Belovsky et al., 2004), and this is particularly true when discussing patterns of diversity and productivity of the alpine tundra.

The concept that diversity might be a dominant factor affecting plant productivity in the alpine is intriguing. Since we know productivity declines with increasing elevation or latitude and richness also declines with increasing elevation or latitude, we should expect a positive correlation between productivity and plant species richness or diversity at a scale that includes all alpine sites (Fig. 5). This is correlation, not causation, and only indicates that whatever has a positive effect on diversity may also have a positive effect on productivity. At smaller spatial scales such as the site level, plant responses are dominated by the combination of resource

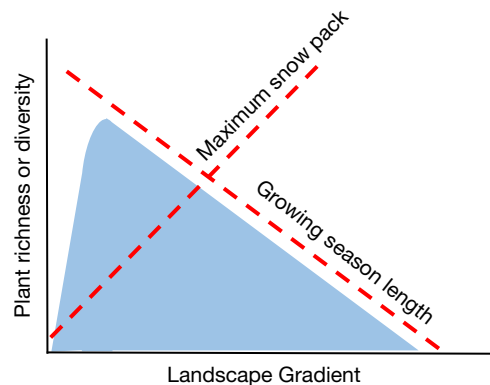


Fig. 5 Plant richness or plant diversity (values in blue) as a function of light and snow pack. The generalized model follows that of productivity except that maximum richness and diversity occurs in fellfield or dry meadow communities where positive species interactions such as facilitation and reduced competition among neighbors may outweigh negative interactions caused by absolute resource limitation.

availability, resource heterogeneity, and the diversity of plant growth strategies used to exploit resource availability. Using the same plot data shown in Fig. 4 to produce a richness-ANPP curve, a nonsignificant, negative relationship exists between productivity and plot richness, a response similar to that shown for site B in Fig. 5. As described earlier, at this site the highest species richness in plots is found in fellfield or dry meadow sites and declines from dry to wet plots. Here, as elsewhere, richness declines to lowest levels where rock cover and winds preclude water availability (e.g., Kikvidze et al., 2005). This produces a skewed version of the conceptual model that described production (Fig. 6). Such a response can be generated, as suggested by Marini et al. (2007), by an abundance of small species adapted to the dry and wind-scoured areas of the alpine, by changes in how the plants affect other plant species across a resource gradient, or both of these alpine species characteristics.

Kikvidze et al. (2005) and Bowman and Swatling-Holcomb (2018) demonstrated that plant species interactions consistent with concepts of facilitation or competition are not uniform across resource gradients in alpine communities. Those authors noted that net positive interactions tended to be more common in low resource, low production areas such as fellfields and dry meadows. They noted that certain species function as facilitators, and those plants may occur only in a subset of alpine communities. Conversely, the competitive characteristics of individual species can also vary across habitats that have relative large resource gradients. Certain species, such as the clover, *Trifolium dasyphyllum*, a plant associated with nitrogen fixation and found only in drier habitats, increase the plant diversity in their immediate surroundings (Thomas and Bowman, 1998). The strength of negative and positive feedbacks produced by the dominant forb *Geum rossii* can vary across the resource gradients that it inhabits (Bowman and Swatling-Holcomb, 2018). In contrast, the alpine grass *Deschampsia cespitosa*, a species with relatively large growth capabilities in the alpine, exhibits strong competitive effects and can suppress species diversity (Suding et al., 2008) but tends to occur only in the more productive habitats. Thus, plant traits influence local richness, and the tendency for negative interactions in more resource-rich areas appears to be a common trait across herbaceous communities (Grace et al., 2016).

Abiotic factors can also contribute to facilitation of species. Rocks can contribute to the fitness of alpine species in wind-scoured areas by reducing wind damage and potentially providing snow cover and additional moisture in leeward areas. Such sites are also important for plant recruitment and community development in primary succession following deglaciation (Jumpponen et al., 1999). Unlike nurse plants, rocks will not subsequently compete with neighbors for resources, so while the interactions between species can be transitory over a growing season, the abiotic-biotic interaction within a single area remains fixed. However, similar to alpine plants switching from positive to neutral to negative feedbacks, a rock in a wet, sheltered area clearly does not function in a similar manner to one found in a fellfield. Thus, both biotic and abiotic factors can influence the abundances and diversity of neighboring plant species, and the intensity and outcomes (+, 0, –) of these factors can vary across the alpine landscape.

The Alpine in the Anthropocene: Anticipated Changes in the Coming Decades

Among the human-generated factors we classify as threats to alpine communities are the introduction of invasive species, changes in atmospheric inputs including such materials as dust, nutrients, and organic and inorganic pollutants, climate warming, and changes in the seasonality and amounts of precipitation. The well-documented warming trends for most alpine areas are arguably driving plant species uphill and potentially off the tops of the mountains. However, consistent with the finding that alpine diversity and productivity are controlled by multiple factors and the interactions among these factors, we should anticipate that predicted changes for the alpine will be strongly modified by site-specific responses.

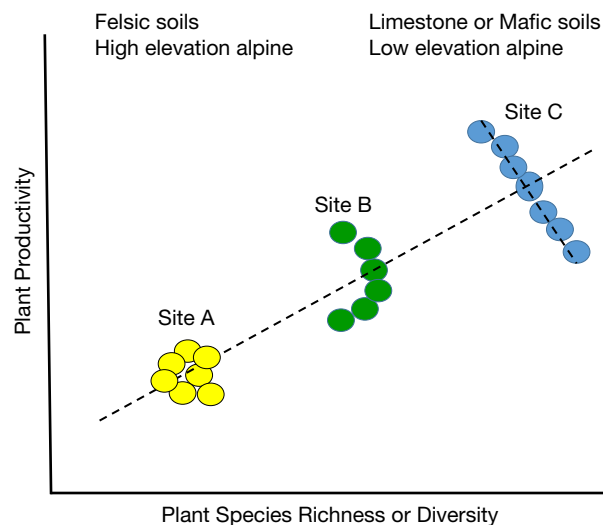


Fig. 6 The regional and site-specific relationships proposed for alpine productivity in relation to alpine species richness or diversity. In the lowest productive sites (Site A), there is little to no relationship between these variables. Under more fertile soils or more benign climates, alpine the relationship becomes curvilinear or negative as competition for light in the most productive plots reduces local richness (Sites B, C).

Introduced plant species are now appearing in the alpine where they were not found decades ago (McDougall et al., 2005). The concern here is species displacement, species extirpations, and the loss of desirable ecosystem services such as carbon sequestration provided by those species. As noted by Alexander et al. (2016), the numbers of nonnative species already present or seen as current potential invaders is relatively modest compared to warmer ecosystems, but with warming, invasive species already established at lower elevations may indeed move upslope into alpine areas. Management practices to discourage both undesirable native and introduced species may be feasible, given that cold-adapted invasive species have, to date at least, been few. However, management also must deal with the changing baseline in human land use practices, climate and atmospheric chemistry drivers.

Human-caused acid rain, a major concern particularly towards the end of the last century, affected soil acidity (Krug and Frink, 1983), a known control on alpine plant richness and diversity. This threat was replaced with somewhat similar concerns for N deposition in alpine communities (Bowman et al., 2015). When atmospheric N deposition accumulates in ecosystems, there is a propensity for soils to also become more acidic, even if the precipitation itself is not strongly acidic. While sites may increase in productivity from the fertilization effect of plant-available N, the acidification process may subsequently produce longer-term, negative effects on plant growth and have negative and long-term effects on plant diversity (Bowman et al., 2018).

Nitrogen fertilizer studies tend to show that graminoids benefit more from N additions than forbs (e.g., Theodose and Bowman, 1997; Gasarch and Seastedt, 2015b). This is believed to be due, in part, to the very conservative growth strategies possessed by alpine forbs. Forbs exhibit “preformation of tissues” and produce embryonic structures that do not emerge as aboveground foliage for 3 years (Diggle, 2002). Thus, when a large nutrient source is added, growth is limited to the number of structures created in previous, potentially low-nutrient years. Graminoids, in contrast, can be more opportunistic and produce more tissue that become leaves and stems in a current growing season. Thus, this rapid growth response can contribute to greater competition and suppress forbs under high resource availability. Of some interest, however, is that additions of both N and P may slowly increase dominance by at least a subset of forbs in some areas of the alpine, suggesting a more important role of P in the structure of alpine communities (Venterink, 2011; Darcy et al., 2018).

Enhanced dust deposition resulting from droughts and inappropriate human management of low elevation, semiarid and arid regions also is affecting alpine communities found at considerable distances from these sources (Steltzer et al., 2009). While there is reason to believe this dust contains materials that buffer acidity and add soil nutrients to alpine communities, the material also affects seasonal snow dynamics by greatly reducing snow albedo and speeding melt-off (Neff et al., 2008). Enhanced dust deposition therefore is an amplifier of climate warming effects.

In a warming world, plants adapted to the colder conditions of the Pleistocene and Holocene can be expected to decline in abundance (Theurillat and Guisan, 2001). Cold-adapted species are at risk (Gottfried et al., 2012) and low-statured plants may be more vulnerable than others (Bjorkman et al., 2018). Climate warming is allowing trees to move uphill in some areas (Leonelli et al., 2011; Rixen et al., 2014), and community sensitivity to change can be a function of elevation (Rosbakh et al., 2014). In alpine regions with both warming and ample precipitation, upward movement of more temperate- or boreal-zone species is a reasonable expectation (Boutin et al., 2017). However, wind, water or winter temperature limitations may preclude that activity in at least some areas (Harsch et al., 2009; le Roux et al., 2013; Moyes et al., 2013). Meanwhile, there is strong evidence that alpine vegetation is moving up in elevation (e.g., Chen et al., 2011), limited now by a combination of soil development, nutrients, and microbial processes (Bueno de Mesquita et al., 2017). Between these endpoints, dynamic changes in vegetation composition and productivity are underway due to a combination of climate and atmospheric chemistry impacts (Bueno de Mesquita et al., 2018). Documenting these changes usually requires the collection of multiple decades of data; measurements over shorter periods have found that vascular plant communities at individual sites or mountain ranges show some resilience to climate change (Gottfried et al., 2012; Spasojevic et al., 2013; Vanneste et al., 2017).

At a landscape scale, there is reason to believe that climate warming will have a neutral to positive effect on alpine plant richness (Sommer et al., 2010; Wehn et al., 2014). A major unknown involves how the seasonality and amounts of precipitation will change in association with warming trends. Regional warming can result in more high-elevation precipitation deposition (Williams et al., 2015), but a higher percentage of that moisture falls as rain rather than snow, and surfaces can have higher evapotranspiration rates. Without the snow cover, the freeze-thaw patterns and phenology of plant growth can be affected, and dry-downs during the growing season could also affect plant phenology (Ernakovich et al., 2014). Under this scenario, Sommer et al. (2010) identify concerns where species reductions are possible, especially when species well adapted to cold and low nutrient conditions must compete with generalists better adapted to warmer, higher nutrient conditions. In North American alpine and arctic areas, “shrublandification,” the process whereby willows or other shrubs can successfully invade herbaceous systems such as alpine meadows, has been identified as problematic (Kudo et al., 2011; Myers-Smith et al., 2011; Formica et al., 2014).

The fate of alpine regions in the 21st century remains uncertain, but observations to date allow for some predictions. What happens if we impose directional warming on the productivity and diversity patterns shown in Figs. 3 and 6? One concludes that some of the species and some of the communities within the alpine would benefit while some would be harmed. The directional drivers could certainly push these communities uphill, provided higher ground exists and can provide areas for vegetation colonization. As growing season length is affected by temperatures, water, snow duration, and irradiance, communities will change. Concurrent effects of atmospheric N and dust deposition, in conjunction with an adjacent, regional pool of plant species able to exploit new conditions, will add further confounding effects. Finally, all of these variables will be amplified or attenuated by existing soil fertility status. The large and steep resource gradients and local heterogeneity in soils and plant community composition suggest that the alpine will remain both a bellwether for change and excellent outdoor laboratory to study factors controlling vegetation change for some time to come.

Acknowledgements

Comments and suggestions from Cliff Bueno de Mesquita, William Bowman and Katharine Suding contributed to this article and are appreciated. Research at Niwot Ridge Colorado has provided a “model alpine system” used to illustrate ideas presented here, and studies at this site have been continuously supported by the National Science Foundation since 1980. Recent researchers that contributed ideas, training, and results for this study include Eve Beaury, Amy Concilio, Eve Gasarch, Vanessa Haggans, Hope Humphries, and Jane Smith. Data used here for the figures are available at the Niwot Ridge Long-Term Ecological Research (LTER) site: <https://portal.lternet.edu/nis/home.jsp> and <http://niwot.colorado.edu/data>.

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Climatic Controls of the Global High Elevation Treelines

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Abstract

The term “treeline” refers to the natural high elevation or polar limit of tree growth, irrespective of the tree species. Thus, the treeline is a limit of the life form tree, with trees defined as single stemmed, upright woody species taller than an adult person. This life form boundary occurs globally wherever the seasonal mean temperature declines to c. 6 °C and the length of the growing season is at least 3 months. The position of this treeline isotherm is near sea level in the Arctic and can exceed 4000 m in the subtropics and tropics. It commonly is higher in drier and lower at more humid conditions. Human land use (logging, pastoralism) or disturbances (fire, erosion, avalanches) can cause trees to be absent from the climatic treeline. The reason why trees reach a thermal limit, beyond which alpine or arctic, small stature plants do well, has to do with the coupling of tree crowns to atmospheric circulation, while small plants profit from solar heating near the ground.

The Life Form Concept

Biologists have developed two ways to categorize the overwhelming diversity of organismal life: (1) the concept of genetic similarity or relatedness, which yields species, genera, families etc. and (2) the concept of life form, that is grouping the species into morphological categories, which in the case of plants, yields herbs, shrubs, lianas, or trees. This contribution is on the *life form trees*, irrespective of the species or other taxonomic unit to which a tree belongs. Before a tree species has grown to tree size, it passes through the stages of seed, seedling, sapling and the term “tree” applies only after it clearly exceeds the size of shrubs. Thus, a tree is an upright, single stemmed woody plant that has become taller than an adult person. This way, the shoots and leaves experience temperatures that a weather station might measure 2 m above the ground. Experts talk about “aerodynamic coupling to the atmosphere.” In contrast, small stature plants, including tree seedlings, thrive close to the ground, where the climatic conditions can be quite different from those in the free air at 2 m above the ground. It can be much warmer when the sun is out, and such small stature vegetation is sheltered from free air circulation (wind). Hence, low stature plant communities are partly decoupled aerodynamically from the climatic conditions at 2 m height. This distinction is central to the following assessment of the treeline phenomenon.

Definition of Treeline

When the climate becomes very cold, as happens at high, sub-polar latitudes or at high elevations in mountains, trees disappear from the landscape and only small plants can thrive on the land beyond the limit of trees (because they profit from the warmth near the ground). Under undisturbed, natural conditions and provided there is soil and sufficient moisture, trees can grow till they reach a low temperature limit, and the line connecting the most northern or the highest elevation groups of tree individuals is called the *climatic treeline* (Körner, 2012). The upper limit of the closed montane forest is the forest line (called timberline in the older literature), and the position of uppermost isolated saplings, often distorted (see below), is the tree species line, exceeded only by scattered seedlings in sheltered microhabitats that may be found several hundred meters above the treeline. The entire transition zone from the montane forest to the highest elevation saplings is called the *treeline ecotone*. This ecotone may be narrow (sharp tree-line) or gradual and/or fragmented, depending on regeneration stage, disturbance regimes and topography.

If there is insufficient water, as in mountains of hot deserts, or if soil is missing (bare rock), plants cannot grow and there is also no climatic treeline. Under conditions that are so cold that trees approach their range limit, the minimum required annual precipitation for tree growth is 250 mm (Paulsen and Körner, 2014). Most commonly, precipitation is higher than 250 mm in such high elevation or polar regions so that drought does not prevent tree growth (but it may slow tree growth). Under such conditions, the range limit of trees is set by temperature (see below). Wherever mountains are sufficiently high and receive more than 250 mm of

precipitation, a natural climatic treeline is formed (Fig. 1). The elevation of the treeline can be close to sea level in the Arctic, it may be at 2000 m asl in cool temperate zone mountains, or it may occur around 4000 m elevation near the equator. The highest locations of groups of tree-size individuals are found in the dry continental mountains of Bolivia and Tibet (4800–4900 m elevation).

Yet, it is not elevation as such that is important, but the air temperature that is associated with elevation. The record high elevation treelines mentioned above reflect regional climatic anomalies (a very high position of the treeline isotherm; see below). On average, air temperature declines by 0.55 degree per hundred meters of elevation. So, treeline elevation rises progressively from geographical high latitude (the arctic treeline) to the tropics. There is no Southern Hemisphere polar treeline at sea level, because the continents do not reach far enough into high southern latitudes to reach the critically low temperature for tree growth. The southern tip of South America lies at 56°S, a latitude far too warm to prevent tree growth.

Treeline is a global phenomenon (Fig. 1). At least 100 tree species belonging to different plant families are able to grow at tree-line. In the Northern Hemisphere treeline is composed mostly of species belonging to the Pinaceae (conifers such as pines, spruces, larches, firs or junipers), Betulaceae (birch and alder), or the genus *Sorbus* (rowan, family Rosaceae). In the Southern Hemisphere these are Nothofagaceae (southern beeches) or Myrtaceae (eucalypts). In the subtropics a prominent genus in the Andes is *Polylepis* (Rosaceae). In the tropics there is a wide spectrum of taxa that reach treeline. Examples are *Schima* sp. in Theaceae (SE Asia) and Ericaceae (Africa). There are also isolated island regions with high mountains such as Hawaii where no native treeline forming taxa exist (they never made it to Hawaii), but when continental treeline taxa are brought in, they do well and find a limit at the same low temperatures as are found in their native habitats. In some regions, humans have eradicated taxa that would normally form a tree-line, such as happened to *Abies alba* (white fir) in the Italian Apennine. In this case, trees are absent from the potential treeline, and the locally available tree species form a tree species limit set by their specific cold tolerance. An example of this is the tree species limit of *Fagus sylvatica* (European beech) in the mountains of southern Italy. This limit does not fall at climatic treeline.

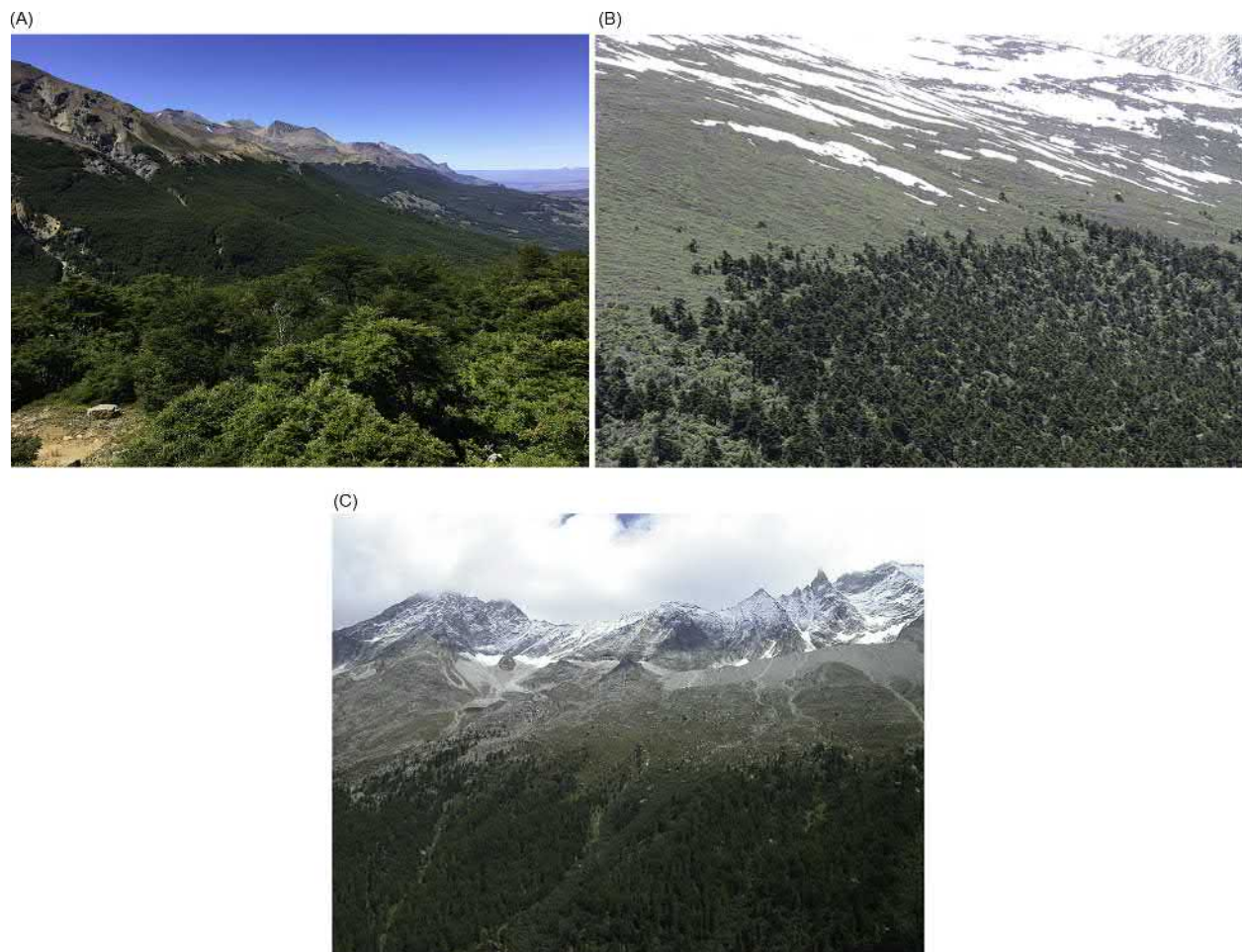


Fig. 1 Examples of high elevation treelines. (A) The *Nothofagus pumilio* (southern beech) treeline at 1200 m elevation in Patagonia follows sharply the treeline isotherm of air temperature. (B) The treeline in the Baima Mountains of northern Yunnan, China, at 4300 m, is composed of *Abies georgei* (fir) and *Rhododendron*. (C) The treeline in the central Alps of Switzerland at 2300 m, composed of *Pinus cembra*, is fragmented by avalanches and century long pastoralism. Note the avalanche track is filled with *Alnus viridis* krummholz, that tolerates heavy snow loads.



Fig. 2 Where soils are missing, trees cannot grow, irrespective of elevation. In such cases, trees are absent from the climatic treeline as is the case in this example from Kinabalu in Borneo, where *Schima brevifolia*-dominated patches of forest reach only 3700 m elevation, 100–150 m below the climatic tree limit.

These examples of artificial treelines is a central problem in the treeline debate: a treeline can only be defined on the basis of biological principles (see below). In regions where humans cut or burned trees, where avalanches wiped out stretches high montane forest, where soil has been eroded to the bedrock surface (Fig. 2), and where no taxa are regionally available that are physiologically fit to grow at the climatic treeline, then there is no visible treeline in the mountain landscape. The treeline concept loses its meaning, when the next-best forest edge is termed treeline. This means that the actual presence of trees is often a poor indicator of the line at which the tree life form reaches a natural low temperature limit. Trees may be absent from the treeline for many reasons. A treeline concept founded in biological principles must refer to “potential treeline,” a line where trees could grow if they were “allowed” to (hence are not cut, burnt or find substrate to root in). It makes no sense, scientifically, to address any high elevation or high latitude forest edge as a treeline, if the local disturbance regime is not known. This also means that treelines cannot become “depressed,” but they will follow the regional climatic regime (the treeline isotherm), provided trees had not been removed from the line by disturbance.

What Determines Undisturbed Treeline Position?

Because the alpine belt above the potential treeline is defined by the natural absence, of (trees), the treeline defines the biogeographic boundary between the montane and the alpine belt. The montane belt remains naturally forested as long as moisture permits. Because this prominent vegetation boundary is formed so consistently around the globe, the question arises concerning the identity of the common driver of treeline position. Given that geology, patterns of precipitation and atmospheric pressure differ considerably between subarctic treelines near sea level and treelines at 4800–4900 m elevation in Tibet or Bolivia, a critically low temperature remains the only remaining factor common to all undisturbed treelines. This was confirmed first by scaling air temperature from nearest weather stations to treeline elevation (Körner, 1998), and was refined later by obtaining temperature records from sites at treeline at various latitudes (Körner and Paulsen, 2004), and finally, by correlating treeline position as seen from satellites with a climatic envelope of treelines modeled from temperature and precipitation data derived from a climate data base for across the globe (Paulsen and Körner, 2014). It turned out that natural, climatic treelines are established where the mean air temperature during the growing season is around 6 °C, irrespective of whether the growing season lasts 3 months (the minimum length required for tree growth), or 12 months in the equatorial tropics. This hints at a direct impact of low temperature rather than an influence of season length. Further, the influence must be a gradual action of temperature on metabolism and growth, because low temperature extremes (absolute minimum temperature, freezing damage) vary so much across the globe that the treeline pattern we observe in nature could never be established.

The knowledge of a region’s growing season’s mean temperature allows the prediction of regional treeline elevations. The only other condition affecting treeline is that the growing season must not be shorter than 3 months, as defined by the number of days per year with a daily mean temperature of at least 1 °C (Paulsen and Körner, 2014). The precision of this prediction is 10 m of

elevation in oceanic islands such as New Zealand (very stable and predictable isotherms) and 78 m of elevation across all mountains of the world. This error term is largely related to the limited reliability of climatic data for remote mountain areas. Thus, the low temperature treeline is the best defined (and most predictable) biogeographic boundary globally, and it can serve as a reference line for other climatic vegetation boundaries at lower elevations (Körner et al., 2011, 2017). The predictive power of climatic data for treeline position can also be used to locate the position of the treeline isotherm (and thus the lower edge of the alpine life zone) in regions that had become entirely deforested (Noroozi and Körner, 2018).

Why is the Climatic Treeline Where it is?

A conclusive biological explanation for the position of tree limit at the 6 °C isotherm of seasonal mean temperature is not yet available, however there are several factors that can be ruled out, whereas others hold promise. As mentioned above, freezing tolerance can be ruled out, given that the global pattern of treeline position does not match a common freezing regime. The rate of photosynthetic carbon acquisition (CO₂ uptake) can be ruled out, because at 6 °C, leaves of cold-adapted trees reach 50–70% of their maximum rate, and still acquire carbon at a rate of about 30% at 0 °C. Trees cannot grow in freezing temperatures, that is they cannot build new cells and differentiate tissues (e.g. Rossi et al., 2007; Alvarez-Uria and Körner, 2007). Because of that discrepancy between the high rates of photosynthesis (sugar production) and the poor ability to invest these sugars into new structural growth, trees at treeline accumulate rather more reserves (e.g. starch) compared to trees at lower elevations, and there is no indication whatsoever that treeline trees are lacking in carbohydrates (Hoch and Körner, 2012; Fajardo et al., 2012). So, the most likely mechanism through which tree life is constrained when it gets cold is the lack of ability to produce new tissue, both through the cambium (tree ring formation) and apical meristems (length growth of shoots).

It had also been discussed whether cold soils at high elevation could constrain the nutrient cycle and cause trees at treeline to grow so slowly that decay exceeds new growth and thus, sets a tree limit. However, trees at treeline are not generally found to suffer from malnutrition (Birmann and Körner, 2009; Mayor et al., 2017), and such a constraint would also equally affect shrubs above treeline. Moreover, soil nutrient provision also depends on bedrock quality, weathering, topography and moisture regime, none of which are tied to an isotherm. Hence, soil driven tree limits would never follow a globally uniform temperature limit, but reflect local soil conditions, which is not the pattern seen across the mountains of the world. It is a truism that all plants in the wild do not exhibit optimal growth in terms of nutrition, that is, they do not achieve a maximum growth rate that would be possible when fertilizer were added. Indeed, trees growing close to treeline are no different from any other trees in that soil nutrients constrain growth, and thus, they do grow faster when nutrients are added (Möhl et al., 2019). Yet, this growth stimulation does not mitigate the impact of low temperature that sets the ultimate elevational limit to tree distribution. When trees grow at their absolute thermal limit, the addition of nutrients cannot alleviate the thermal growth constraint (Hoch, 2013). Quite clearly, nutrients do not set the position of the treeline (Mayor et al., 2017), although they do constrain the rate of tree growth.

Thermal growth constraints are not tree-specific, but hold for all cold-adapted plants. However, as tree saplings grow to heights above the low stature ground vegetation, which is able to trap solar heat, they experience the free atmospheric air temperature and cannot “produce” their own warmer microclimate as alpine plants do by forming dense low stature stands (Fig. 3). In essence, it is the exposure to ambient air temperature that puts the tree life form on a losing track when it gets cold, whereas low stature alpine plants can decouple from the temperature of the free atmosphere and “engineer” their own, milder microclimate near the ground. This explains why trees are hit first when it gets cold along elevational or latitudinal gradients (see first section). Paradoxically, life conditions are clearly better (warmer) for alpine dwarf shrubs and heathland above the treeline than for treeline trees

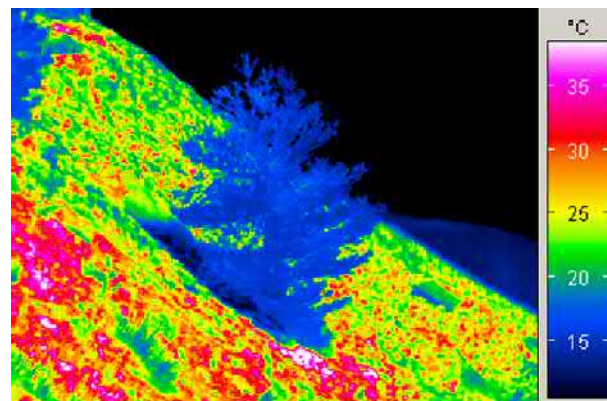


Fig. 3 Trees experience a colder environment than do low stature plants, as illustrated by this thermal image. Low stature vegetation accumulates heat under solar radiation, but the crown temperature of trees at treeline is essentially the same as the air temperature 2 m above the surface.

(Körner, 2007). Thus we see that the treeline phenomenon is related to tree architecture, the open nature of which does not permit significant departures from air temperature. This also explains why undisturbed treelines follow isolines of elevation across often rough mountain terrain like the shore line of an alpine lake.

Krummholz

The treeline is rarely abrupt. Trees gradually get shorter until no upright growth is possible and the tree limit is reached. Beyond treeline, one may find deformed, shrub-shaped trees (so called “krummholz”) that profit from self-shelter and moderate heat accumulation among the dense thicket of branchlets. Such shrubby tree individuals can even form clones with layering branches that build adventitious roots (Körner, 2012). Should the climate warm, these shrubby individuals could become upright trees. In contrast to such deformed trees, there are also genetic krummholz species. These are taxa that exhibit a life form intermediate between tree and shrub. Such krummholz taxa can exert severe competition to tree recruitment and can even become so dominant that trees become suppressed in the treeline ecotone (Fig. 4). Examples are *Pinus mugo* and *Alnus viridis* (European mountains), *Pinus pumila* (Japan), and many species of *Rhododendron* in SE Asia.

Tree Recruitment

In all cases, there must be a successful tree seedling before there can be a tree. It commonly requires thousands of seeds and hundreds of tree seedlings to produce one mature tree, a rule that holds for any forest, including those at their high elevation limit. The early life stage is particularly vulnerable in all organisms. The randomness of the environment adds to the lottery of early tree life. Safe and unsafe recruitment niches, snow mold, disturbances by animal browsing, trampling and erosion, top soil desiccation and seed bed overheating, ground frost, etc. keep most seedlings from becoming a tree. It is thus important to ascertain the degree to which early life stage success can have an influence on treeline position and whether the risks discussed above are higher at treeline than elsewhere. While the globally consistent treeline isotherm would not provide much leeway for a site-specific recruitment success, recruitment dynamics in the treeline ecotone are likely to contribute to the shape of treelines at the scale of several tenths of meters of elevation. Likewise, periodic seedling success will influence the state of tree demography (age structure) in the uppermost montane tree assemblages.

From the previous sections it is clear that tree seedlings in treeless patches within and above the treeline ecotone experience warmer conditions than these individuals will eventually experience when they have grown above the shelter of grasses and dwarf shrubs close to the ground, as they enter the sapling life stage. This explains why tree seedlings can be found far above treeline (Fig. 5). So, the direct physiological influence of low temperature is the least likely factor to constrain tree seedlings. Success of seedlings at and above treeline appears to relate to a trade-off between becoming out-competed by dense, low stature alpine vegetation on the one hand (e.g. Angulo et al., 2019), and the risks of life on bare spots (no shelter) on the other hand. On open ground, small seedlings are at great risk of becoming overheated. They are also subject to top soil dehydration, combined with the deleterious effects of intense solar radiation (Cui and Smith, 1991; Germino and Smith, 1999; Bader et al., 2007). Such risks are likely to be even greater for tree seedlings at low elevation, compared to those at treeline. Also, wind-swept mountain ridges are bad places for seedlings to recruit without shelter (McIntire et al., 2016; Renard et al., 2016). Even in the tropics open terrain above treeline exerts a risk of damage by ground frost in clear nights (Rehm and Feeley, 2015).

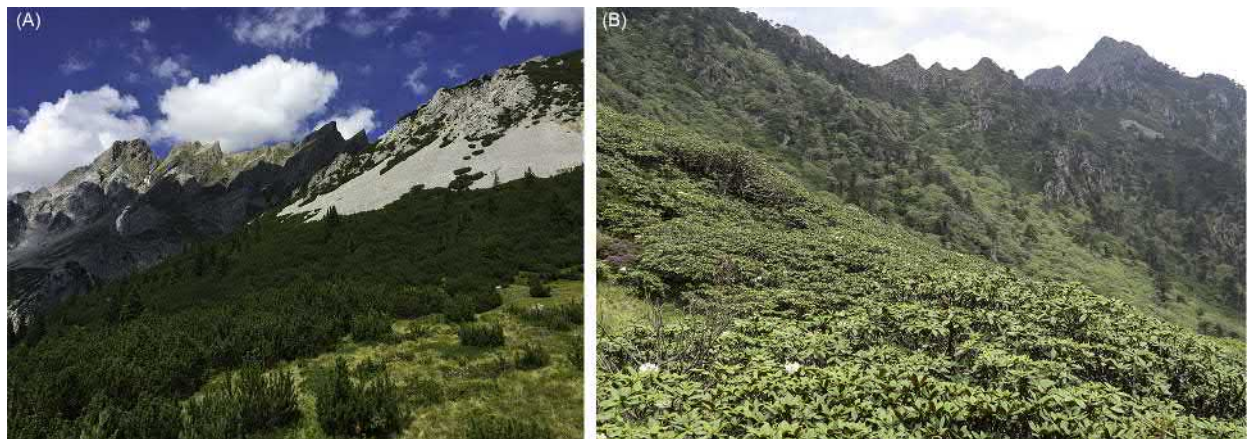


Fig. 4 Examples of genotypic “krummholz” species that may suppress and replace trees in the treeline ecotone. (A) *Pinus mugo* at 2000 m in the Austrian Alps with scattered *Picea abies* individuals. (B) Vast *Rhododendron* thickets out compete *Abies georgei* in Northern Yunnan, China. Deformed individuals of otherwise treeline taxa may also form krummholz above the treeline.

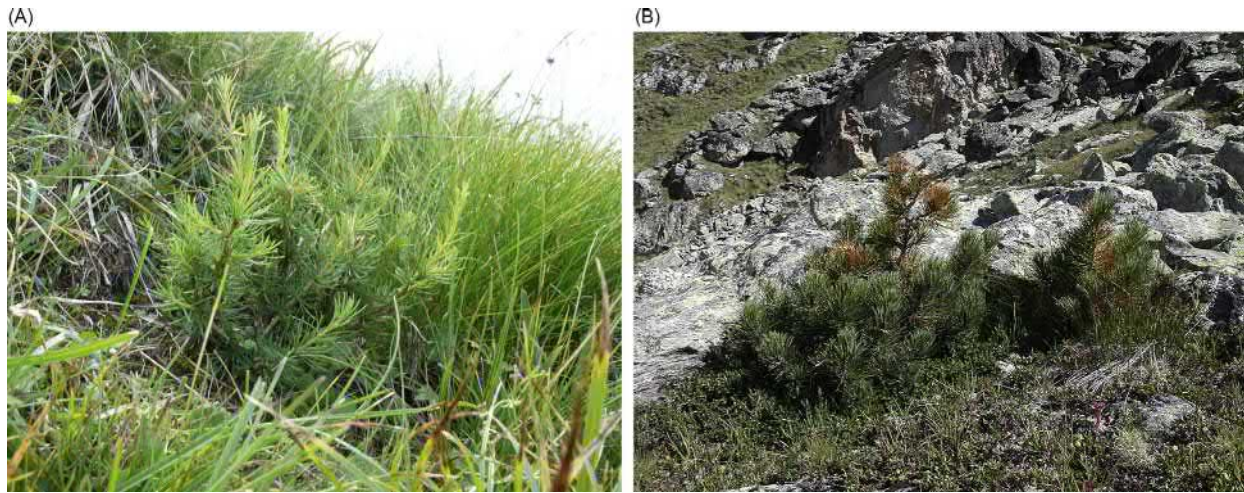


Fig. 5 Tree seedlings far above treeline profit from shelter among small stature alpine plants and rocks. Temperatures are much warmer close to the ground compared to a tree canopy, causing seedlings to be less constrained by low temperature than fully-grown trees. Once shoots protrude from the warm boundary layer they become damaged. The examples shown here are from the Swiss central Alps at 100 m (*Larix decidua*) to 400 m (*Pinus cembra*) above treeline.

Because tree recruitment is commonly not continuous but occurs in waves supported by mass fruiting events, combined with several favorable follow-up seasons, a seedling census at one point in time may not be representative of the long-term situation. The maintenance of treeline may require only one or two successful recruitment waves in a century. Because of the resulting demographic bias, one may find treelines in various stages of regeneration or mortality, reflecting the legacy of events that may date back more than 100 years. Disturbance regimes such as avalanches, fire, wind break, pastoralism or wild animal browsing cycles complicate the interpretation of tree demography at any one point in time. As is often the case in ecology, things that look simple from a great distance and at large scales become quite complicated at finer scales of time and space. Recruitment—related processes are thus likely to affect the small scale appearance and demography of the treeline ecotone (Holtmeier, 2003; Bader et al., 2007), but will hardly affect its climate—driven elevational position as long as no disturbance regimes come into play.

Future Treelines

Given the tight coupling of treeline position with temperature, treeline elevation has changed in response to past climates and it will continue to do so in the future (Körner, 2012). Warmer climates will cause treeline trees to grow faster, a trend already evidenced for recent decades (Paulsen et al., 2000; Rolland et al., 1998), and treelines will move upslope. But given the stochastic nature of recruitment, this is not likely to be a continuous process, but rather episodic, varying with topography and disturbance regimes (Holtmeier and Broll, 2005). Since treeline trees are not commonly carbon limited (Hoch and Körner, 2012) the rise of atmospheric CO₂ concentration itself is unlikely to facilitate a general further stimulation of tree growth. However depending on local settings, species and life stage, and concurrent warming, a transitory CO₂ fertilization effect may come into action. For instance, a CO₂ enrichment experiment with sapling-sized trees at treeline in the Swiss Alps revealed that *Pinus uncinata* is entirely unresponsive to a CO₂ enriched atmosphere (555 ppm CO₂), whereas *Larix decidua* took advantage from such a step change in CO₂ concentration during the early part of the 9 year experiment. This was particularly the case during warm years, which could affect the competitive interaction between species (Dawes et al., 2011). A warmer climate could also increase the intensity and duration of insect outbreaks such as the larch bud moth (Baltensweiler et al., 2008). Since treelines are affected by land use around the globe, changing land use practices are likely to supersede climate change effects in many mountain regions. Land use pressure (and incurred fire frequency) can devastate upper montane forests (Hemp, 2005), and land use abandonment may cause undesirable, rapid shrub encroachment in formerly cleared land that prevents tree recruitment at treeline (Hiltbrunner et al., 2014).

Summary

The tree life form suffers aerodynamically from its tall and open architecture when the weather gets cold. This is the reason why trees find a low temperature limit at lower elevation (and lower latitude) than low stature alpine (arctic) vegetation. Because of their exposure to the free atmospheric circulation, the high elevation tree limit follows a line (the treeline), once a critical air temperature is reached, a pattern that is not seen in low stature vegetation, the distribution of which is more strongly shaped by topography than by elevation. Trees are not physiologically inferior to alpine plants, but they experience harsher climatic conditions once they grow

taller than the shelter provided by grasses and shrubs (or rock fields) within the treeline ecotone. The action of low temperature impacts tissue growth directly (the meristems) rather than photosynthetic carbon acquisition, and freezing tolerance provides no explanation of treeline position at a global scale. Recruitment can be severely constrained when seedbed shelter is lacking. Because the position of undisturbed treelines is set by temperature, climatic warming will inevitably cause treelines to move upslope, yet the dynamics of this process depend on stochastic events, and thus will vary from place to place.

See also: Alpine Plant Diversity in Temperate Mountains of Asia.

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Nature of Alpine Ecosystems in Tropical Mountains of South America

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Abstract

The three grass-dominated mountain top formations in South America are the Puna, the Páramos and the Campos de altitude. The first two span a wide latitudinal range in the Andes, while the Campos de Altitude are found in relicts in the higher areas of the Brazilian Atlantic forest. They are all dominated by C3 tussock grasses and harbor high levels of endemism. Remarkably, they share a number of grass genera despite the geographical distance between the Andes and the Atlantic forest. All these alpine grasslands also harbor iconic fauna and provide key ecosystem services. Moreover, they share a history of intense human-induced disturbance, which has resulted in high degradation and fragmentation rates. Climate change is exacerbating the threats to these ecosystems because they are systems driven by specific adaptations and narrow niches of species, thus small environmental changes can cause a re-assemblage of species communities and increase fragmentation. Lastly, they remain poorly studied compared to other grasslands ecosystems, and we identify the main knowledge gaps that should be urgently addressed if we aim to conserve these precious systems.

Introduction

Tropical grasslands are estimated to occupy about 15 million km², a similar area to that of tropical forests (Olson et al., 1983). However, they are often misclassified as woodland or savannas (Hall and Scurlock, 1991) or as degraded systems (Parr et al., 2014). Moreover, much of their original extent has been converted to crops, mixed farming and artificial pastures.

South America is one of the continents in which the study of grasslands has been most neglected. While the continent is well renowned for its vast biodiversity, this is often associated with its tropical and subtropical moist rainforests - particularly the Amazon. However, South America harbors 11 of the world's 14 biomes defined by Dinerstein et al. (2017) including an extensive variety of grassland ecosystems, such as the llanos and open savannas.

This paper reviews some of the most iconic yet perhaps most neglected ecosystems: the tropical alpine grasslands in the Andes and the Atlantic forest: the Puna, Páramos and Campos de altitude—the three grass-dominated mountain top formations in South America.

Mountains of South America and Their Grasslands

The Andes is the primary mountain range in South America and harbors the largest number of endemic plant and animal species in the world (Myers et al., 2000). The Andes provide a wide range of ecosystem services to about 100 million people living in both high-altitude areas and in the neighboring lowlands (Buytaert et al., 2011). Tussock grasslands span the entire tropical Andes at elevations above 3000 m asl and are termed either Puna or Páramo depending on their location and species composition, as reviewed in the next section. Humans have co-existed with these natural grasslands in the Andes since pre-Inca times (Ellenberg,

1979) but anthropogenic pressure has significantly increased in the last century (Spehn et al., 2006). For example, in the Northern Andes, changes in agricultural practices have caused extensive ecosystem degradation (Sarmiento et al., 2003), and intensive grazing and burning have caused several native species to disappear (Premauer, 2004). Human transformation of landscapes is also affecting the hydrological regulation capacity of the alpine regions in the Andes (Podwojewski et al., 2002; Crespo et al., 2010).

Besides the Andes, the Atlantic Forest along the coast of South-Eastern Brazil contains the Serra do Mar and Serra da Mantiqueira mountain ranges comprising the Campos de altitude (Highland grasslands) above an elevation of 1500–1800 m. The Atlantic forest also has exceptional levels of endemism, with an average of 50% and regionally up to 95% endemic species (Morellato and Haddad, 2000). However, this ecosystem has been reduced to only 7–14% of its original extent (Ribeiro et al., 2009). The Campos de altitude are azonal formations above 1500/1800 m within the Atlantic forest, containing a mosaic of shrubs, bunch-grasses, bamboo and a sparse herb understorey (Safford, 1999a,b). They are often compared to the Andean Parámos and despite their small extent, their patchy assemblages and the mounting threats, biodiversity is exceptionally high (Safford, 1999a,b) (Fig. 1).

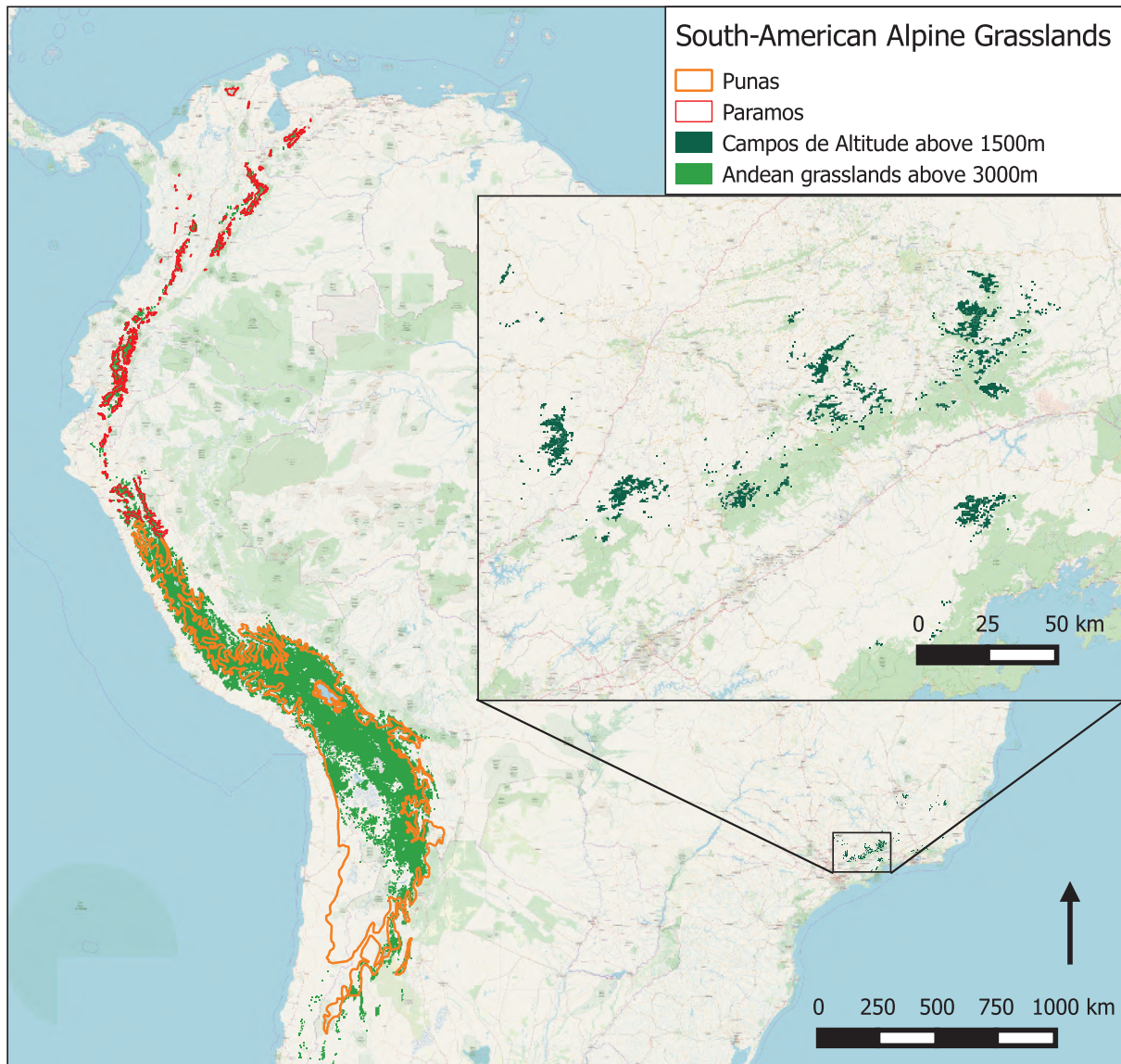


Fig. 1 Map of the alpine grasslands of South-America according to the definition adopted in this review and overlaid with the outlines of the Myers eco-regions of the Puna and Parámos (Myers et al., 2000). Map produced from MODIS Land Cover Map (classes 7, 9 and 10 for Parámos and Puna grasslands; classes 9 and 10 for Campos de altitude) masked with the SRTM Digital Elevation Model based on an elevation above 3000 m asl for the Andes and above 1500 m asl for Campos de altitude.

Grasslands

Types of Tropical Alpine Grasslands and Their Ecology

We define alpine tropical South American grasslands as intertropical ecosystems dominated by herbs and shrubs found between the tropics of Cancer and Capricorn at elevations above 3000 m asl in regions near the equator, and above 1500 m asl in higher latitudes. According to this definition, South America contains three major tropical alpine grassland regions: the equatorial *Parámos*, the wet and dry *Punas* in the Andes, and the *Campos de altitude* in South-Eastern Brazil. Some authors argue that, due to their intertropical position, the term ‘alpine’ in the Andean context should be replaced by the term ‘tropical andine’ (Lauer, 2018) but, in order to include the *Campos de altitude*, we retain the use of the term ‘alpine.’

Due to their distinct climate and topographic conditions, all three types of alpine grasslands harbor exceptional levels of biodiversity and endemism. The ecological peculiarities of each grassland region are discussed below, with reference to their climate, geology and soil, vegetation (vegetation belts, dominant taxonomic groups and lifeforms, adaptations) and faunal.

Parámos

“*Parámos*” comes from the ancient Spanish word for “an elevated, barren, treeless plateau” (Ramsay, 1992) and is used for ecological formations dominated by grasslands found in the tropical high mountains of all continents; the Andean *Parámos* is by far the most extensive of these, spanning the Northern Andes between Colombia, Venezuela, Ecuador and Northern Peru (Lauer, 2018).

Climate

The *Parámo* climate is tropic-alpine with high diurnal temperature oscillations and relatively low annual variation in temperature, which converges into a temperate climate with more seasonality towards the South (Ramsay, 1992). Despite the North-South variation, the main axis of environmental variation is East-West causing distinct zonation and occurrence of *Parámos*: in the western Andes the *Parámos* extend from 10° North to 10° South, and in the Eastern Andes from 10° North to 30° South (Ramsay, 1992). This large longitudinal extension of the *Parámos* across the Andes results in different exposures to the circulation patterns of the atmosphere, creating large variations in precipitation from 2000–5000 mm (Lauer, 2018). Nonetheless, the *Parámos* are remarkably drier than the cloud forests below (Lauer, 2018). In proximity to the Equator, rainfall at high elevations is infrequent due to the oscillation of the Intertropical Front (Fittkau, 1969). As one moves South, rainfall becomes more seasonal (Ramsay, 1992). This rainfall seasonality is a critical factor for occurrence and character of *Parámos*, with a 3-month dry-period in Colombia, and 4–6 month dry-period in Venezuela. Frost is prevalent in the *Parámos*, with the number of days of frost increasing sharply around 3300 m at the boundary to the montane forests below. At the upper *Parámos* limit between 4500 and 4700 m asl, up to 100 frost days per year can occur (Ramsay, 1992).

Geology and soil

Parámo soils are mostly dark, acidic, rocky and poorly developed. Inorganic nutrient content is low and high organic content can be only found in the upper horizon. However, varying factors like topography, geological history and altitude result in local variation of soil properties (Ramsay, 1992).

Vegetation

Parámo vegetation is at least four million years old and the long duration of its evolution has given rise to 30 endemic genera out of 300 (10%) (Van der Hammen, 1988). In the Colombian *Parámos*, half of the genera are of either tropical or neotropical origin, while in the Ecuadorian *Parámos*, the lower temperatures and lower humidity favor temperate taxa such as the *Compositae* and *Poaceae* families (Ramsay, 1992).

The *Parámos* occupy the vegetation belt between the upper limit of the montane cloud forest and the snow-line occurring at 4700–4800 m asl (Hess, 2017). Elevation is the main driver for *Parámo* vegetation, and this results in an internal vertical structure with three main *Parámo* vegetation belts: the sub-*Parámo*, the grass *Parámo* and supra-*Parámo*. The shrubby sub-*Parámo* sits above the upper Andean forest between 3500 and 4100 m asl and contains scattered forest fragments and trees. Above the sub-*Parámo* lies the grass *Parámo*, dominated by tussock grasses. Immediately below the snowline, at about 4100 m, the grass *Parámo* converges into the supra-*Parámo*, dominated by mat-forming and cushion plants (Lauer, 2018). Within the vegetation belts, especially in the grass-*Parámo*, local environmental variables and human-induced disturbances cause compositional discontinuities leading to a patchy mosaic of species composition and vegetation structure (Valencia et al., 2019).

The majority of *Parámo* vegetation is dominated by tussocks. Other accompanying growth forms include acaulescent rosettes, upright shrubs, prostrate shrubs, erect herbs and prostrate herbs and, at higher elevations, cushions. Plant species in the *Parámos* exhibit adaptations to the harsh climate and to human-induced disturbances. Many *Parámo* communities contain plants that resprout vigorously following fires and regenerate from below-ground plant parts, as well as from within the tussock bases (Ramsay, 1992). Burning generally creates cyclical patterns of community development and the establishment of some species (such as *Lupinus* cf. *pubescens*) relies on burning. Ultimately, the severity of a fire, established through measures such as the interval length since the last burn, determines the degree of survival. Another adaptation is the resistance to low night-time temperatures evolved by a number of plants, which is largely determined by the growth form (Ramsay, 1992).

Fauna

The main mammals in the Páramos are deer (*Odocoileus virginianus*), and several large predators such as the puma (*Felis concolor*), spectacled bear (*Tremarctos ornatus*) and the Andean fox (*Dusicyon culpacus*). Smaller mammals include rabbits (*Sylvilagus brasiliensis*) and numerous small rodents.

Large bird species include Carrion-feeders like the Condor (*Vultur gryphus*) and large birds of prey. The Páramos provide habitat to 12 species of hummingbirds (*Trochilidae*), the Cordillera Snipe (*Chubbia jamesoni*) and, in the lakes, to ducks and teals, along with populations of introduced trout (*Salmo gairdnerii* and *S. trutta*).

Puna

Westwards and in rain shadow areas, Páramos are progressively replaced by Puna grasslands, a drier vegetation type situated above 3400 m, extending from northern Peru to northern Argentina (Alba Mejía, 2008). The Puna spans over an area of more than 10° longitude and is up to 300 km wide, covering the east and west flanks of the Andes, resulting in different Puna sub-regions, shaped by different levels of humidity: the wet Puna, the dry Puna and the central Puna. The wet Puna spans across the Andean mountains of Peru and eastern Bolivia, while the dry Puna lies in southwestern Peru and north-western Bolivia. The Central Puna grasslands are located on the west-Andean flanks in Southern Peru and East of the Bolivian dry Puna, with an intermediate climate and subsequent unique species assemblages that distinguish it from the dry and wet Puna.

Climate

The wet Puna is characterized by a semi-dry climate with precipitation varying between 500 and 700 mm per year from North to South and annual average temperatures ranging from 5 to 7 °C. The dry Puna receives even lower precipitation, between 250 and 500 mm per year. Average annual temperatures vary from cold to temperate, in a range of <0 and 15 °C (Pulgar Vidal, 2014). At higher elevations, the central Puna has an oligothermic climate with large diurnal temperature ranges and an annual precipitation of less than 700 mm, mostly in the form of hail and snow.

Geology and soil

Most of the Puna ecoregion rests on 6–8 million year old Tertiary and Quaternary volcanic bedrock from the formation of the Andes, with glacial landforms such as moraines present throughout (Whitmore, 1997). The Puna Ecoregion contains Lake Titicaca, the highest lake in the world at 3800 m asl, and an extended salt plain.

Vegetation

Puna vegetation is broadly grouped into the central Andean Puna, wet Puna and dry Puna. The central and wet Puna are dominated by bunchgrass communities, wetlands, small shrubs and trees, and herbaceous plants with a high number of endemic species.

The wet Puna occurs between 3700 and 4200 m asl in the Altiplano and is vegetated by grasses and shrubs. Sedges and rushes dominate wet areas with genera such as *Carex*, *Juncus*, *Oreobolus* and *Scirpus* below 4000 m asl and floating submerged cushion plants above 4000 m asl (Whitmore, 1997). Montane grasslands can be found between 3800 and 4200 m asl in deep glacial valleys, under a greater precipitation regime than that of the wet Puna.

The Central Andean Puna lies between 4200 and 5000 m asl and is vegetated by grasses with prostrate and roseate growth forms, such as *Festuca*, *Stipa ichu*, and *Calamagrostis*. Dry Puna is characterized by xerophytic vegetation and patchy distributions. Harsh conditions of aridity and thin atmosphere, coupled with strong natural disturbances like droughts and frosts, create vegetative adaptations such as particular leaf shapes, very slow growth, stunted forms and high resin content. The genera *Calamagrostis*, *Agrostis* and *Festuca* are common here (Hess, 2017).

Besides these major Puna vegetation belts, there are also azonal formations ('bofedales') with wet grasslands in peat bogs, fens and reed beds vegetated by *Juncaceae*, *Cyperaceae*, and *Asteraceae*. The salt plains feature halophytic shrubs and low herbaceous grasses of *Muhlenbergia* and *Distichlis humilis* (Alba Mejía 2008).

The Puna regions harbor an exceptionally high number of species. Alba Mejía (2008) recorded a total of 1500 plant species, with floristic similarities to the Parámo and Jalca and about 40 Puna-endemic genera. According to Davis et al. (1994) there are 1000–1500 vascular plants on the Peruvian side of the wet Puna alone. Endemic species of the ecoregion are the supu-tola (*Diplostephium tovari*) and the mullu-mullu (*Ribes brachybotrys*).

Fauna

Andean camelids of the Puna include the vicuña (*Vicugna vicugna*), llama (*Lama glama*), guanaco (*Lama guanacoe*), and alpaca (*Lama pacos*). Predators include the puma (*Felis concolor*), and the Andean fox (*Pseudalopex culpaeus*) which prey on rodents like the chinchilla (*Chinchilla brevicaudata*), the Puna mouse (*Punomys lemmings*) and the vizcacha (*Lagidium* sp.).

The dry Puna ecoregion harbors a rich endemic avifauna and many critically endangered species such as the Ash-breasted tit-tyrant (*Anairetes alpinus*) and the critically threatened royal cinclodes (*Cinclodes aricomae*). The suri (*Pterocnemia pennata*) is an emblematic Puna bird species. Puna herbivores have strong incisors to feed on the hard, silicon-rich plant tissues, and they exhibit special skins or plumage as an adaptation to low temperatures and strong winds.

Brazilian Campos de altitude

The Campos de altitude (Highland Grasslands) are found at an elevation above 1500 or 1800 m asl, inserted in the mountain ranges of the Serra da Mantiqueira, Serra do Caparaó and Serra do Mar of the Brazilian Atlantic rainforest biome in South-Eastern Brazil.

Due to their position on mountaintops, they can be regarded as isolated patches or habitat islands within a forested landscape, with different climate conditions than the surrounding Atlantic Forest.

They are distinct from the quartzite Campos Rupestre, located further inland at somewhat lower elevations in a continental climate in Mantiqueira, Espinhaço and associated mountain ranges in central Brazil (Fernandes, 2016). Due to its occurrence above 900 m asl, the Campos Rupestre can be regarded as montane grasslands, mainly shaped by edaphic factors, and are thus not examined in-depth in this article about alpine grasslands. However, their conservation importance should not be underestimated, with a richness of 6000 plant species and some families reaching up to 80–90% endemism (Fernandes, 2016) within an area of only 26,418 km². For the sake of completeness, some additional campos can also be found on Amazonian mountains between 1600 and 2900 m asl. These “Campos de altitude da Amazônia” are dominated by shrubs and herbs such as *Melastomataceae*, *Poaceae*, *Bromeliaceae* (Martinelli, 2007).

Climate

The region has a mean annual temperature of 12 °C, with cool summers and moderately cold winters with frequent frost. The climate in the Campos de altitude is oceanic, and seasonality of rainfall, frost and temperature is high. In the rainy season from November to March, monthly precipitation can exceed 400 mm, while monthly mean temperatures lay between 11 and 13 °C. During the dry season in May–August, monthly precipitation can be as little as 30 mm and monthly mean temperatures are 7–8 °C with 10–15 frost days per month. Thus, summer droughts paired with frost are a main stressor for vegetation but can partially be offset by orographic fog (Safford, 1999a,b). Mean diurnal temperature range is 7 °C. Safford (1999a,b) concludes that the Campos de altitude are climatically similar to the Páramos de Costa Rica, resulting in physiognomic similarities, even though seasonal climatic differences are up to four times greater in the Campos de altitude. The high climatic seasonality results in a high intra- and interspecific diversity of eco-physiological behavior (Scarano, 2002).

Geology and soil

Campos de altitude are found on igneous and metamorphic substrates, mostly of Precambrian age such as granite rocks or Nepheline-syenite (Alves and Kolbek, 2010). Soils are highly acidic and nutrient-poor with soil types ranging from deep, organic mulls, moderately lateritic clays to rare moors (Safford, 1999a,b). Morphological formations include plateaus with rolling, rounded hilltops, deeply dissected stream courses headed in steep amphitheaters, inselberg landscapes, large expanses of bare rock and often high cliffs (Safford, 1999a,b).

Vegetation

Major vegetation associations include (1) grasslands with dispersed shrubs dominated by dwarf bamboo and pampas grass, (2) hydric associations with reed and sedges, and (3) dwarf tree associations and rocky slopes, cliffs and summits with herbs and grasses (Safford, 1999a,b). Due to the low elevational range of just 700 m, vegetation belts are not clearly distinguishable and vegetation is mostly controlled by local topography, the drainage network, and the distribution of soil types (Safford, 1999a,b).

Vegetation consists of a mosaic of graminoids such as tall-stemmed bunchgrasses (*Cortaderia*, *Calamagrostis*, *Andropogon*), sclerophyllus shrubs (especially species of *Baccharis*, *Vernonia*, various *Eupatorieae*, *Tibouchina*, *Leandra*, and *Myrtaceae*) and short stunted trees (e.g. *Escallonia*, *Weinmannia*, *Rapanea*, *Symplocos*, *Maytenus*, *Roupala*) and bamboo (*Chusquea* spp.) with a sparse understory of herbs and pteridophytes. Common families are, in order, *Asteraceae*, *Polypodiaceae* sensu lato, *Melastomataceae*, *Orchidaceae*, *Poaceae*, *Lamiaceae*, *Lycopodiaceae*, *Cyperaceae*, *Ericaceae*, and *Rubiaceae* (Safford, 1999a,b).

In the lower Campos de altitude, close to treeline, the grasslands co-exist with azonal vegetation types such as stands of elfin or Araucaria forest, wetlands and peat bogs (Safford, 1999a,b). The modern vegetation structure is also shaped by anthropogenic fires and grazing (Safford, 1999a,b).

Floristic endemism is high; estimates range from 25%–33% endemic species (Iganci et al., 2011). These high numbers of endemics suggest that the vegetation is quite old, at least since the Late Pleistocene (Behling, 1997), and not solely the product of recent human disturbances. The vegetation shows strong floristic similarities to equatorial alpine formations of the Andean and Central American Cordillera despite aerial disjunctions (Safford, 1999a,b).

Ecosystem Services of Alpine Grasslands

The biodiversity and ecosystem functioning of alpine grasslands provides a multitude of ecosystem services that promote human wellbeing. These services include the provision of fresh surface water, food, fiber, fuel and genetic resources; regulating services such as pollination, seed dispersal, climate regulation; hazard and erosion control; and water purification. Moreover, grasslands support primary production, habitat provision, nutrient and water cycling and soil formation, as well as providing cultural services, such as education, recreation and spiritual values (Peart, 2008).

For example, the Páramos and the Puna are key in sustaining the lives of millions of people, by providing essential ecosystem services such as water for urban use, irrigation and hydropower generation. Moreover, the soils and vegetation promote carbon storage and sequestration (IUCN and WCPA, n.d.).

Grassland biodiversity, such as that of the Campos de altitude, safeguards these ecosystem services, but the impacts of climate change on biodiversity might negatively affect the ecological flows and ecosystem services that grasslands provide for human well-being (Díaz et al., 2015).

Conservation of Alpine Grasslands

Threats

Human use and disturbance

As opposed to other continents, human settlement and seats of political power in South America were historically concentrated in the mountains, with habitation by ancient peoples well before the establishment of the Inca Empire in the 15th Century (Mathieu, 2013). This long history of human occupation and use of the mountains has led to constant human encroachment and resulting threats to the alpine grassland environments.

Peart (2008) identified common threats to temperate grasslands of South America, which include the Páramos and Punas due to their elevated position and thus temperate resemblance. These threats include: 1. Livestock grazing, 2. Conversion/clearing for forest plantations and crop production, 3. Mining and energy production (precious metals, coal, oil/gas, and electricity), 4. Urban and infrastructural expansion, 5. Altered fire regimes, 6. Inadequate hydrological management, 7. Lack of protection of biological resources and poor management of protected areas, 8. Exploitation of species through collection for fuel and medicinal plants, illegal hunting/poaching.

Peart (2008) points out that these drivers of grassland change are modified by climate change and that the interplay of human encroachment with climate change might lead to structural landscape changes through habitat loss, fragmentation, loss of diversity and integrity degradation, and even desertification of temperate grasslands.

These general threats vary between the three grassland regions due to the different environmental biotic and abiotic conditions and due to differing human legacies, discussed below.

Páramos

The predominantly wet climatic conditions of the Páramos are unfavorable to livestock and agriculture, resulting in low human populations. Nonetheless, there are ancient Inca and pre-Inca roads, terraces and houses (Lægaard, 1992). Despite the low level of habitation, human influence is pervasive. Past human communities in the high Andes were generally characterized by self-sufficient subsistence farming due to isolation, combined with access to a broad resource base (Ramsay, 1992). During colonial times, mining penetrated the Páramos. In dry years, occasional burning takes place (Lægaard, 1992). However, extensive burning, cultivation, and grazing only began with the arrival of European settlers (Sarmiento, 1986). Burning has increased in recent times. The aim is to alter the nutritional value of the 'pajonal' tussocks, by removing choking dead leaves, thereby stimulating the growth of succulent new shoots (Ramsay, 1992).

Nowadays, dispersed stock raising, mining, and extraction of firewood and canes are taking place (Alba Mejía, 2008). Recently, the Páramos have been exposed to high levels of grazing (Molinillo and Monasterio, 1997), agricultural expansion and intensification (Suárez and Medina, 2001) resulting in high ecosystem degradation (Sarmiento, 2000). Shrubs are collected for fuel, resulting in overutilization and degradation of the ecosystem (Ramsay, 1992).

Overgrazing results in a decrease of species richness, changes in soil properties, an increase of bare surfaces, and the risk of water channeling and wind erosion (Podwojewski et al., 2002).

The Páramos are already susceptible to natural fragmentation due to the rugged topography and associated microclimates. The alpine location, coupled with the transitional climate between low and high areas, dry and wet, makes the Páramos highly vulnerable to climate change and desiccation, which interplays with fragmentation, deforestation, mining and other anthropogenic impacts (Alba Mejía, 2008). Moreover, wildlife hunting and killing by farmers across the Páramo has caused, and is still causing, faunal declines across all animal groups (Ramsay, 1992).

Punas

The Punas have experienced human influence for millennia, causing huge changes in the natural vegetation. Puna regions some of the most modified areas in Peru and Bolivia.

Human habitation is highest in the humid and eastern Punas. All of the Puna is grazed in some form or other by sheep, alpaca and llamas, with cattle, horses, donkeys and pigs disrupting the completion of life cycles for many plants, resulting in degradation (Alba Mejía, 2008).

The central Puna region is also cultivated with tubers and grains. The grazing regime undergoes seasonal patterns, with migration of the herds to the humid 'bofedales' during the dry season and grazing shifts to the extensive grasslands/shrublands during wetter seasons. Fire is used as a management tool to establish grazing areas. The combination of extensive grazing with fire threatens natural meadows, shrublands and woodlands, and particularly the edges of wetlands and moist habitats grazed in the dry season. Some Puna regions have also been strongly affected by mining, urban development and waste disposal (Alba Mejía, 2008).

Campos de altitude

The fate of the island-like Campos de altitude is strongly determined by the surrounding Atlantic Forest biome, which acts as a buffer to maintain local climate and avoid species invasions (Martinelli, 1989). Therefore, current deforestation and savannization of the Atlantic Forest biome will likely have negative effects on the Campos de altitude as well (Scarano et al., 2016).

Since large parts of the Campos de altitude are within protected areas, anthropogenic fires and grazing are mostly excluded. However, there is an evident increase in the frequency of fires, with largely unknown origin and causes (Aximoff and de Carvalho Rodrigues, 2011).

Climate change

Mountain ecosystems are especially vulnerable to climate change due to (1) the very specific adaptations and narrow niches of species, which mean that even small environmental changes can cause a re-assemblage of species communities and (2) the limited and small extent of mountain ecosystems and the tendency towards fragmentation, coupled with physical barriers hindering species migrations to and from other mountain ecosystems (Grabherr et al., 2003).

Much research has been conducted on how altitudinal vegetation and ecotones in mountains, and especially treelines, change with increased temperatures (Harsch et al., 2009; Malanson et al., 2011; Körner, 1998; Körner and Paulsen, 2004). The treeline is the transition zone between closed forest and alpine grasslands, and marks the lower boundary for alpine grassland ecosystems (Fadrique et al., 2018). Treeline shifts determine the potential areal extent of alpine grasslands.

There are generally two contrasting trends of altitudinal shifts of mountain ecosystems in response to global warming. As temperatures increase, species migrate upslope to match their thermal niches, or they shift downslope due to land-use legacies and anthropogenic suppression of tree growth (Feeley and Rehm, 2015). Upslope shifts have been witnessed across the world. Morueta-Holme et al. (2015) found an upslope migration of vegetation zones on the Ecuadorian Mount Chimborazo of up to 400 m since Alexander von Humboldt visited in 1805.

Fadrique et al. (2018) assessed the directional shifts of mountain forest ecosystems in the tropical Andes biodiversity hotspot and witnessed a process called thermophilization, i.e. the change in composition towards greater abundances of lowland species. However, the rates of compositional change are variable, due to different warming rates and varying community composition along ecotones, such as treelines (Fadrique et al., 2018). Beyond that, individual responses of plants will likely differ substantially (Löffler et al., 2011).

Upslope migration can be limited by low dispersal capabilities of alpine species, fragmentation, isolation and the lack of migration routes, so that in many cases, upwards movement lags behind temperature increases (Löffler et al., 2011). Extinctions of mountain-top species take place when their upslope migration is hindered by the physical lack of land at higher elevations. In the short term, warming experiments for mountain ecosystems reveal changes in plant growth and reproduction, phenology, vegetation structure and assemblage composition, while longer-term experiments show an increase in species homogeneity (Löffler et al., 2011).

Climate warming has the potential benefits for vegetation, such as the prolongation of the growing season, but these seeming advantages may well be overridden by negative effects on growth and reproduction caused by, for instance, increased frost damage or reduced snowpack (Inouye, 2008; Wipf et al., 2006). In the Páramos, upslope migration of treeline is reduced because of the difficulty of tree seedling establishment at high elevations caused by night frosts, fires and extreme radiation (Löffler et al., 2011).

The opposite trend of downslope shifts of vegetation zones and alpine ecotones can be caused by land use changes. For example, the high-elevation 'pajonal' grasslands of Mount Chimborazo expanded their distribution several hundred meters downslope, driven by forest clearing, cattle grazing and fire (Feeley and Rehm, 2015). A similar effect is known for treelines in the Andes. In areas used for cattle grazing and fires, treeline is much less likely to migrate upwards than in protected areas (Lutz et al., 2013).

Consequently, the alpine biota of South America is expected to undergo large ecological changes. In particular, the fauna will likely suffer from modifications in host-plant interactions, food availability, habitat quality and predator/parasite abundance (Löffler et al., 2011).

Climate Change Forecasts

Under the multitude of global change drivers, alpine grassland species will either adapt, move or go extinct (Hofstede et al., 2014). High Andean Tropical ecosystems are expected to face exceptionally strong warming effects and associated ecosystem changes during the 21st century because of their elevation (Bradley et al., 2006), as exemplified through projections for vertebrate species turnover rates of up to 90% for low to mid-high emission scenarios (Scarano et al., 2016).

However, responses of tropical mountain ecosystems to climate change will certainly be variable. Tovar et al. (2013) assessed Andean ecosystems under different climate scenarios and found that not all biomes move in the same direction and at the same degree, such that for 2050, 75–83% of biomes will stay stable, 4–8% will change significantly, and 13–17% do not show consensus in models.

The Páramos will most likely be affected by modifications in precipitation regime, relative humidity, and higher levels of solar radiation. In addition, changes in climate will drive the expansion of agriculture and livestock into higher elevations (Araújo and Rahbek, 2006; Hofstede et al., 2014). Cuesta-Camacho et al. (2008) estimate that around 35% of the 102 bird species and 60% of the assessed 125 plant species in the Páramos will either go extinct or become critically endangered until 2080. These scenarios of

species losses or threats are due mostly to the poor dispersal capabilities of alpine species. Moreover, climate change will impact Páramos' plant biodiversity through an increase in diseases and plagues, replacement through invasive species, and negative effects of increased radiation on plant structures (Hofstede et al., 2014). As vegetation belts move upwards under global warming, the Campos de altitude will experience a loss of available habitat, especially for plants (Spehn and Körner, 2005; Scarano et al., 2016).

Knowledge Gaps

Mountain ecosystems such as the Campos de altitude remain poorly studied, and there is a need to establish long-term ecological monitoring sites to track the effects of climate change on species and ecosystems (Scarano et al., 2016), especially since compositional change is not necessarily heterogenous across elevations (Fadrique et al., 2018).

With many studies focussing on forest ecosystems, the plasticity of grassland species in the face of increased temperatures and reduced humidity remains largely unstudied (Scarano et al., 2016). While most mountain climate change studies focus on shifts in vegetation zones, we know far too little about the responses of ecosystem functions like carbon sequestration and water provision. Ecosystem responses are multifaceted and include habitat reductions, species and population changes, alterations in phenology, plant-animal interactions, and trophic cascades. Furthermore, complex interactions complicate predictions on ecosystem changes for alpine grasslands (Scarano et al., 2016).

For the Páramos, central uncertainties include the lack of knowledge for species dispersal under different degrees of human alteration, the manner in which genetic diversity of populations respond to climate change, and how diversity generally will help in promoting adaptation (Fadrique et al., 2018; Hofstede et al., 2014).

Conservation Status

In comparison to large forest ecosystems such as the Amazon, alpine tropical grasslands are relatively neglected by conservationists and need to be recognized as valuable ecosystems and conservation units. The Campos de altitude, for instance, is not even represented within the Dinerstein et al. (2017) ecoregion framework.

In terms of raw numbers, the Páramos have a comparatively high proportion of protection of 43%, while only 18% of the Puna is protected (Michelson, 2008). However, high levels of protection must also be seen in the light of the simplicity of establishing protected areas in high and remote places, when there is little competition with human needs (Watson et al., 2014).

Recent years have seen the establishment of several international programs, such as the Alpine Convention (Austria), the Centre for Mountain studies (UK) and the International Mountain Society (Switzerland), concerned with the evaluation and protection of mountain biodiversity. However, most of the programs focus on mountain ecosystems of Europe, North America and Asia (Martinelli, 2007). Recently, organizations like the Temperate Grasslands Conservation Initiative, which included the Páramos and Puna, have been created to serve as the centre point for international communications and collaboration for the improved conservation and protection of the world's indigenous temperate grasslands. Despite the existence of conservation initiatives, on the ground implementation of alpine grassland conservation still falls short. In the Puna, for instance, a major problem is the lack of management effectiveness in protected areas, and the low representation of the wet Puna ecoregion, where only 6% of the ecosystem is protected (IUCN and WCPA, n.d.).

The relatively tiny Campos de altitude cover 350 m² on four disjunct mountain ranges, and are, to a large degree, part of some of the oldest protected areas of Latin America, yet until recently, management plans were non-existent or not enforced (Safford, 1999a,b). The largest remnants of the Campos de altitude are found in Itatiaia National Park, with 50 km² on the Itatiaia Plateau. Despite the protection of the Campos de altitude in four national parks, large distances of 50–150 km between the protected areas are a serious problem for species migration (Safford, 1999a,b). On top of that, most protected areas either lack specific conservation and management plans or the policies fail to account of the peculiarities of mountain environments, resulting in degradation even within the protected area boundaries. Thus, conservation planning must consider the distinct communities and biotic zones, particularly in regard to elevation (Martinelli, 2007).

Conclusion

The high levels of biodiversity, endemism, evolutionary significance and unique species assemblages make the South American alpine grasslands some of the most diverse and valuable ecosystems worldwide. The mountaintop grasslands serve as relict places and refugia for highland species and also provide a multitude of ecosystem services, thus meriting protection from an eco-centric and anthropocentric point of view.

Alpine grasslands are facing multidimensional threats, especially degradation, climate change and insufficient protection and management. Many of the threats are interlinked and have to be understood holistically, from an ecosystem perspective, to scrutinize how environmental change will affect the biosphere, hydrosphere, pedosphere and cryosphere of the alpine grasslands.

Historically, the ecology of grasslands has mostly been neglected and overlooked. Nowadays, in the light of growing environmental pressures, there is an essential need to recognize grasslands as valuable ecosystems in their own right to guarantee maximum protection, such as by including them into ecosystem/biome categorizations and by embedding grassland restoration and protection into carbon-sequestration programs like REDD.

Ultimately, any restoration proposals and protection measures should account for the unique ecology of alpine grasslands and be adaptive to fast-changing environmental drivers, in order to guarantee the continued existence of those unique ecosystems.

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Nature of Alpine Ecosystems in Tropical Mountains of Africa

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Abstract

Volcanic episodes linked to the East African Rift System gave rise to the Ethiopian highlands and most of the isolated mountain peaks in Kenya, Tanzania and Uganda, collectively referred to as the Afroalpine region. These highly disjunct high elevation enclaves or “sky islands” (3500–4500 m a.s.l.) are thought to have been colonized by plant taxa during the Plio-Pleistocene whose distributions expanded further during dry cycles in the Holocene. Phylogeographic studies suggest mostly a northern hemisphere origin from Holarctic ancestors. This Afroalpine region is recognized as a regional center of plant endemism with c. 81% of its plant species and four plant genera found nowhere else in the world. It is generally species-poor with no more than 300–680 vascular plant taxa recorded across the various mountains. It has an estimated total area of 3500–5000 km² linked exclusively to the alpine belt. The major Afroalpine vegetation types are open *Dendrosenecio* woodland, Afroalpine scrub, *Carex* and *Scirpus*-dominated bogs, and tussock-forming temperate grasslands. The most iconic plants of the Afroalpine region are the giant life-forms of *Lobelia* and *Dendrosenecio*, well adapted to strong diurnal-nocturnal temperature ranges repeated throughout the year. Levels of protection vary from mountain to mountain and from country to country, whilst anthropogenic pressures are high, mostly due to heavy grazing pressure from livestock farming and regular fire.

Introduction

Volcanic episodes linked to the East African Rift System, culminating in the Eastern and Western Rift branches, gave rise to the highlands of Ethiopia and most of the isolated mountain peaks in Kenya, Tanzania, and Uganda during the Miocene to late Pliocene (Baker et al., 1972; Griffiths, 1993). These highly disjunct enclaves or “sky islands” are scattered throughout equatorial eastern and north-eastern African mountains (Fig. 1) between latitudes 14°N and 6°S, and longitudes 25°E and 40°E (Hedberg, 1994; Wesche et al., 2008a). Together they comprise what has been termed the “Afroalpine” region, named in part after the global “alpine” concept—pre-Indo-Germanic for “steep slopes” or “high mountains” (Körner et al., 2006)—which reached Africa by the 19th century (e.g., Engler, 1892, 1904). By no means, however, was a systematic relationship with the alpine flora of the European Alps implied (Killick, 1963; Herbst and Roberts, 1974). Hauman (1933, 1955) added the prefix “afro” to assert an African context, a tradition reinforced by Monod (1957) and Hedberg (1961, 1964) amidst criticism by others (e.g., Boughey, 1955).

Flora and Vegetation

“Flora” refers to the plant species composition of a particular region or habitat, listed according to a taxonomic hierarchy. “Vegetation” is a broader term, referring to the particular assemblages of plants in a particular region or habitat grouped by their general structural appearance. Studies relating to vegetation zonation—the natural “layering”/stratification of vegetation communities along an elevation gradient—have had a major bearing on understanding the vegetation of the Afroalpine region. The vegetation of the broader tropical African highlands is partitioned into alpine, ericaceous subalpine scrub-forest and montane forest belts, the latter capped with stands of bamboo and *Hagenia-Hypericum* (Hedberg, 1951, 1955). The zonation studies not only relate to the partitioning of distinctive vegetation belts within a landscape (e.g., Richards, 1963; Hall, 1973; Bussmann, 2006), but also relate to elevational zonation gradients within a single vegetation type such as forest (e.g., Hamilton and Perrott, 1981; Hemp, 2006a). These vegetation belts are more sharply delineated than the high elevation vegetation of southern Africa (Hedberg, 1997), probably due to steeper altitudinal gradients in the Afrotropics. However, during the Last Glacial Maximum (LGM), much of Africa’s high mountains were glaciated and vegetation belts descended to lower elevations by as much as 1000 m (Coetzee, 1964; Bonnefille

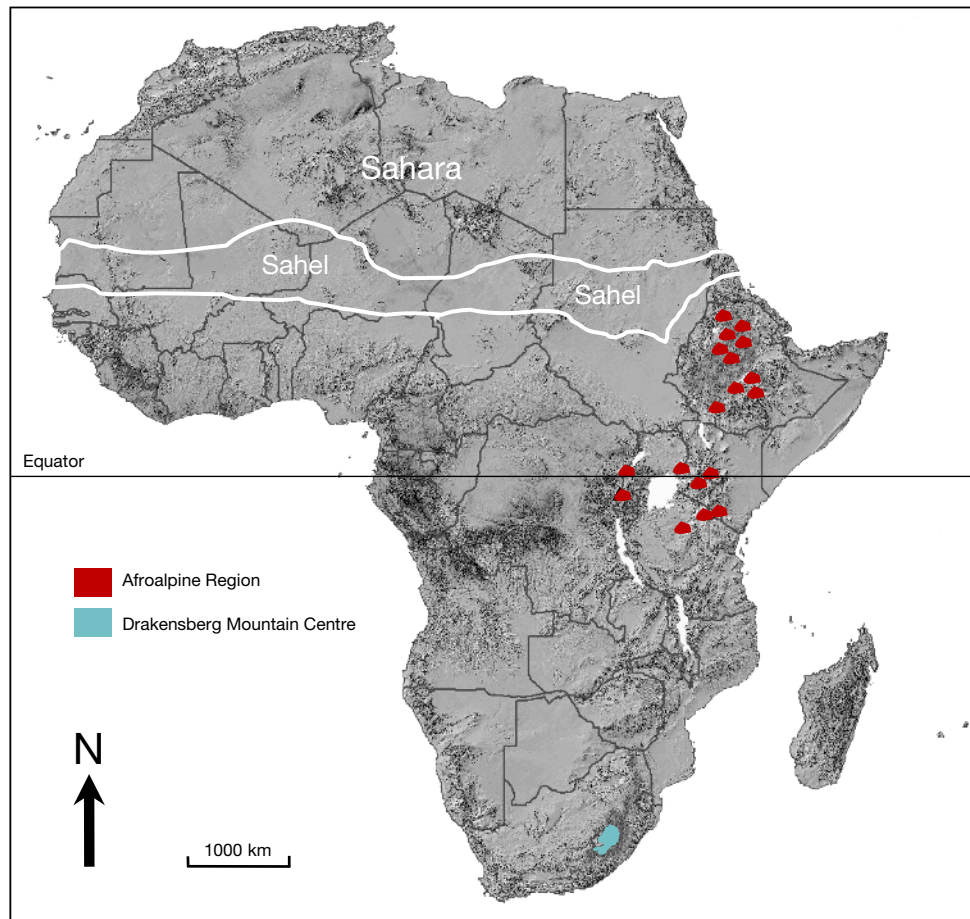


Fig. 1 Approximate location of the Afroalpine “sky islands” in tropical Africa, stretching from the Simen Mtns in northern Ethiopia to Mt. Hanang in Tanzania. Mt. Cameroon in West African is an active volcano and therefore not well representative of the Afroalpine region. Africa’s only other alpine system is located further south in the Drakensberg Mountain Centre. Adapted from Carbutt, C. and Edwards, T. J. (2015). Reconciling ecological and phytogeographical spatial boundaries to clarify the limits of the montane and alpine regions of sub-Saharan Africa. *South African Journal of Botany* **98**, 64–75, with permission.

and Riollot, 1988; Olago, 2001). The Afroalpine region therefore occupied a considerably larger area during the LGM when the climate was cooler and drier (Ehrlich et al., 2007), estimated by Chala et al. (2017) at eight times greater than at present. During the LGM, most of the Afroalpine enclaves of the Ethiopian highlands were interconnected except across the Great Rift Valley whereas the alpine habitats on isolated mountains of East Africa remained disconnected (Chala et al., 2017).

Strictly speaking, the Afroalpine flora and vegetation is restricted to the alpine belt, essentially the area above the upper treeline ecotone of the ericaceous belt, ranging from a lower limit of 3550–4100 m a.s.l. to an upper limit of 4500 m a.s.l. where continuous vegetation cover is absent (Wesche et al., 2008a; Gehrke and Linder, 2014). Kiage and Liu (2006) erroneously placed the alpine belt below the ericaceous belt. The alpine belt in tropical Africa has an estimated total area of 3500–5000 km² (Hedberg, 1994; Gehrke and Linder, 2014). The Afroalpine flora is generally species-poor, comprising no more than some 300–350 vascular plant species (Hedberg, 1994), although a more ancient African volcano such as Mount Elgon has a comparatively richer flora (680 vascular plant species) (Wesche, 2002). The major Afroalpine vegetation types are open *Dendrosenecio* woodland, Afroalpine (*Alchemilla* and *Helichrysum*) scrub, *Carex* and *Scirpus*-dominated bogs, and tussock-forming temperate grasslands dominated by the grass genera *Avena*, *Festuca*, *Koeleria*, and *Poa* (Hedberg, 1994; Wesche et al., 2008a). No doubt the most iconic plants of the Afroalpine region are the giant life-forms of *Lobelia* (Fig. 2) and *Dendrosenecio*, the latter referred to as “giant groundsels” (Hedberg, 1994). The alpine belt is regarded as treeless despite the unorthodox occurrence of these taxa—they rarely aggregate in dense concentrations and are sometimes regarded as giant herbs rather than trees. The closely affiliated upper-montane (subalpine) communities include ericaceous scrub dominated by *Cliffortia*, *Erica*, *Hypericum* and *Stoebe*, and grasslands dominated by *Andropogon*, *Exothea*, and *Sporobolus* (Hedberg, 1964; Wesche et al., 2008a). Knapp (1973) showed a clear distinction between upper-montane and alpine grasslands. Grimshaw (2001) proposed combining the alpine and ericaceous belts to form the “altimontane” belt but the inclusion of the term “montane” is contradictory in this context, given the conceptual inclusion of the alpine belt.

Wesche et al. (2008a) gave an overview of detailed vegetation surveys of the larger northern Rift Mountains spanning the last two decades, but noted knowledge gaps from the Albertine Rift and Ethiopia, and from a vegetation type perspective, knowledge of the

temperate grasslands above the treeline is limited. The majority of Ethiopian alpine vegetation studies have focused on the Great Rift escarpment of northern Ethiopia (Aynekulu et al., 2012) and the Bale Mountains towards the south (Assefa et al., 2011; Tallents and Macdonald, 2011). The latter region contains the largest and most intact expanse of Afroalpine vegetation on the Sanetti Plateau (Fig. 2) (Yalden, 1983; Brooks et al., 2004).



Fig. 2 Typical Afroalpine landscapes and vegetation: (A and B). The most expansive area of Afroalpine vegetation occurs on the Sanetti Plateau, Bale Highlands, Ethiopia; (C and D). One of the iconic giant life-forms of *Lobelia*, *L. rhynchoptalum*. Adapted from Carbutt, C. and Edwards, T.J. (2015). Reconciling ecological and phytogeographical spatial boundaries to clarify the limits of the montane and alpine regions of sub-Saharan Africa. *South African Journal of Botany* **98**, 64–75, with permission.

High Elevation Treeline

The correct partitioning of the Afroalpine region from the closely associated lower-lying Afromontane region (and associated flora and vegetation) hinges in part on the explicit understanding that the “treeline” is a thermal boundary separating the alpine and montane belts (Körner et al., 2011; Körner, 2012). The treeline (or treeline ecotone) in tropical Africa occurs between 3550–4100 m a.s.l. (Hedberg, 1951; Jacob et al., 2014), grading into alpine scrub at higher elevations and montane forest at lower elevations. This treeline is essentially the upper extent of the ericaceous belt (Hedberg, 1951; Wesche et al., 2000), comprising dense stands of shrubs or small trees such as *Erica arborea* and *E. trimera* (Hedberg, 1997; Gizaw et al., 2013), although small groves of both species also occur as outposts in Afroalpine grasslands (Wesche et al., 2000). The most well developed and intact ericaceous belt is located in the Rwenzori Mountains, most likely because it is an exceptionally high rainfall region (Wesche et al., 2000). The ericaceous belt is the best placement for the treeline in tropical Africa given Körner’s (2003, 2012) definition of the natural upper-climatic treeline includes the uppermost pockets of trees above the forest line. This treeline is not always easy discernable as it can grade seamlessly into montane forest, and is a dynamic boundary that expands and contracts depending on the prevailing environmental conditions. Therefore, the “climate-elevation,” or more recently the “isothermal” control model of treelines (Körner, 2003, 2012), must also be tempered with smaller-scale disturbance drivers in the Afrotropics such as regular dry season fire and grazing (Wesche et al., 2000; Fetene et al., 2006; Wesche, 2006), as well as climate change and associated warming and drying events (Hemp, 2005). The harsh soil surface microclimate at the alpine-treeline boundary is thought to limit seed recruitment of treeline-forming species (Wesche et al., 2008b). Fire and anthropo-zoogenic impacts (especially burning practices to remove woody vegetation for livestock grazing) are believed to stabilize the treeline, preventing treeline advancement to higher elevations predicted to occur as a result of climate change (Jacob et al., 2014; Johansson and Granström, 2014).

Climate-Induced Adaptive Ecophysiology

The climate of the high elevation Afrotropics is characterized by significant daily temperature oscillations that occur throughout the year (Hedberg, 1964; Sarmiento, 1986; Fetene et al., 1998). For example, in the Rwenzori Mountains, daily temperatures range between -5°C and 20°C over a 24 h period in the alpine and nival zones (Eggermont et al., 2009). These ecological constraints are reflected in adaptive syndromes such as the giant life-forms of *Lobelia* (Fig. 2) and *Dendrosenecio* (Hedberg, 1964; Mabblerley, 1986). Such Afroalpine plant life forms are convergent with *Espeletia* and *Puya* in the Andean Páramo where similar conditions prevail (Meinzer and Goldstein, 1986; Ramsay, 2014). Pachycaulous (thick-stemmed) architecture, incorporating large caulescent leaf rosettes (a radiating arrangement of spreading leaves supported by an above-ground stem) that protect the developing shoot apex, and marcescent leaves (dead leaves remaining on the stem after they senesce) which insulate the stem, are believed to limit cold injury when night-time temperatures drop well below freezing (Hedberg, 1964; Meinzer and Goldstein, 1986; Fetene et al., 1998). Warm daytime temperatures probably release adequate soil nutrients to sustain these large plants (Hedberg, 1964).

Socio-Ecological Drivers

The major vegetation types constituting the alpine (and upper-montane) communities are subject to seral changes under different fire and grazing regimes (Johansson and Granström, 2014), with grasslands usually replacing woody vegetation under high fire frequency and intensity due to periodic droughts every 7–10 years (Hemp, 2006b; Wesche, 2006; Abera and Kinahan, 2011). Periodic droughts also result in desiccation stress and are thought to impact seedling establishment (Wesche, 2003). Such disturbances from fire disrupt competitive dominance and increase available habitat for less competitive alpine plants, thereby preventing treeline ascent and increasing the Afroalpine flora’s resilience to global warming (Johansson et al., 2018). Human impacts on Afroalpine vegetation during the Holocene may have been relatively minor (Umer et al., 2007), although Nyssen et al. (2004) suggest anthropogenic impacts dating back to at least 5000–4800 years BP. More dramatic changes have been detected over the past 40 years (Kidane et al., 2012). The United Nations Reducing Emissions from Deforestation and Forest Degradation (REDD⁺) program (e.g., Watson et al., 2013), which incentivizes developing countries to keep their forests standing, is believed to be a threat to traditional fire management practices in the Afroalpine region because it aims to increase carbon storage through fire suppression (Johansson et al., 2018).

Phytogeography and Endemism

The Afroalpine region is recognized as a regional center of plant endemism with c. 81% of its plant species and four plant genera found nowhere else in the world (Hedberg, 1961, 1964). Not only is this home to a unique assemblage of plant life. A number of animal species, such as the Big-headed African Mole-rat (*Tachyoryctes macrocephalus*), Blue-winged Goose (*Cyanochen cyanoptera*), Ethiopian Highland or Starck’s Hare (*Lepus starcki*), Ethiopian Wolf (*Canis simensis*), Gelada (*Theropithecus gelada*), and Walia Ibex (*Capra waliae*) are largely endemic to this unique ecosystem (Wesche et al., 2008a; Sillero-Zubiri et al., 2011). The evolution of endemics is attributed to steady adaptive responses to the environment (Hedberg, 1964, 1986) characterized by periods of

Table 1 Breakdown of the phytogeographical elements highlighting the complex derivation of the Afroalpine flora of tropical Africa. More recent studies suggest a greater affiliation with the temperate floras of the Northern Hemisphere

Element	Number of taxa	Percentage of total (%)
Pantemperate (subcosmopolitan)	87	33
Endemic Afromontane ^a	82	32
Northern Hemisphere (Boreal)	34	13
Southern African ^b	25	10
Mediterranean	18	7
Himalayan (Siwalik)	8	3
Southern Hemisphere	6	2
Σ	260	100

^aEndemic Afromontane element includes the endemic Afroalpine element.

^bSouthern African element comprises the South African and Cape elements.

Adapted from Hedberg, O. (1961). The phytogeographical position of the Afroalpine flora. *Recent Advances in Botany* **1**, 914–919; Hedberg, O. (1965). Afroalpine flora elements. *Webbia* **19**, 519–529. Used from Carbutt, C. and Edwards, T. J. (2015). Reconciling ecological and phytogeographical spatial boundaries to clarify the limits of the montane and alpine regions of sub-Saharan Africa. *South African Journal of Botany* **98**, 64–75, with permission.

isolation from other high mountain temperate biotas (Hedberg, 1969) and persistence in isolated small refugia during glacial cycles (Gizaw et al., 2013; Masao et al., 2013). This has resulted in low levels of genetic diversity and bottlenecks (Masao et al., 2013) followed by alternating stochastic episodes of intermountain gene flow (Wondimu et al., 2014). The nonendemic element of the Afroalpine flora appears more closely affiliated with the temperate floras of the Northern Hemisphere than the flora of its adjacent lowlands or of the Southern Hemisphere (Table 1). It is therefore regarded by Linder (2014) as a “northern temperate flora.” Collectively, its “Tropic-alpine” flora is regarded as Africa’s youngest (Linder, 2014) and is thought to have colonized the Afroalpine region during the Plio-Pleistocene (Gehrke and Linder, 2014) and expanded during dry cycles in the Holocene (4500 years BP; Umer et al., 2007). Although elements of the Afroalpine flora are relatively recent colonizers (e.g., Gizaw et al., 2013; Wondimu et al., 2017), the actual time of colonization and mechanisms of speciation remain poorly understood (Gizaw, 2012). Other elements are believed to be Tertiary relicts (e.g., Gizaw, 2012).

Several Afroalpine species colonized Africa from Asia during the Pleistocene via the coastal mountain ranges of the Arabian Peninsula (Koch et al., 2006; Eggermont et al., 2009). One proposal is that the African mountains were almost devoid of vegetation above the treeline until land contact was established between the African and European plates in the Middle Miocene about 18 Ma BP, and again in 13 Ma BP, facilitating the migration of temperate plant genera into Africa’s high elevation regions (Eggermont et al., 2009). A number of other taxa entered Africa from this northern track. Examples derived from Holarctic ancestors include *Trifolium* (Ellison et al., 2006), *Arabis alpina* (Koch et al., 2006), *Cardamine* (Carlsen et al., 2007), *Lychnis* (Popp et al., 2008), *Alchemilla*, *Carex*, and *Ranunculus* (Gehrke and Linder, 2009), *Dianthus* (Valente et al., 2010), and *Scabiosa* (Carlson et al., 2012). Thus repetitive episodes of immigration from the Northern Hemisphere, in combination with in situ radiation, have heavily influenced the composition of the high elevation floras of sub-Saharan Africa, making the Holarctic the most important source of lineage recruitment (McGuire and Kron, 2005; Gehrke and Linder, 2009; Eggermont et al., 2009). A lesser but still significant influence is a southern or “Cape” origin with clades such as *Disa*, *Irideae* p.p., *Moraea*, *Passerina*, *Pentastichis*, and *Restionaceae* migrating northwards along mountain corridors into tropical Africa. This southern track is thought to have facilitated at least 18 unidirectional radiation events (Linder, 2003; Galley and Linder, 2006; Gehrke and Linder, 2009). A wide range of phylogenetic patterns suggest highly individualistic responses to Pleistocene climatic oscillations and therefore different phylogeographic histories (Masao et al., 2013).

Conclusion

Finding a home for the placement of the Afroalpine flora in African phytogeography has been an ongoing dilemma. White (1978) included it in the broader Afromontane phytochorion (a phytochorion, in phytogeography, is a geographic area with a relatively uniform composition of plant species). White’s (1978) delineation of the Afromontane phytochorion should rather, however, only reflect the distribution of a montane flora and vegetation linked to the montane belt located below the treeline (Carbutt and Edwards, 2015), and which is more closely related to lowland forests (Hedberg, 1994; Linder, 2014). This would then, correctly, exclude the alpine belt of the Afroalpine region characterized by a distinct assemblage of plant (and animal) taxa in terms of life-forms, species composition and high species endemism (Hedberg, 1961) and having unique extra-African affinities (Linder, 2014). The historical inclusion of the Afroalpine region as part of the broader Afromontane framework (e.g., White, 1978) therefore reflects the lack of alignment between the phytogeographical and ecological contexts of this phytochorion (Carbutt and Edwards, 2015). When the Afroalpine flora is included as part of the “endemic Afromontane element,” levels of endemism change significantly from 81% to 32% (Table 1) due to the incorporation of a larger number of Afromontane species in a larger floristic region with disproportionately fewer endemics.

Final Thoughts

Africa's only other alpine system, located in the Drakensberg Mountain Center in southern Africa (Carbutt and Edwards, 2015), is also characterized by numerous endemic plants (Carbutt and Edwards, 2006). Unfortunately in the past it has also been referred to as "Afroalpine" (e.g., Killick, 1978) but this attribution fails on both floristic and ecological grounds (Carbutt and Edwards, 2015). Another misapplied term is "tundra" (e.g., Killick, 1997), a term that should not be applied to alpine environments (Körner, 2001, 2003), including those of tropical and southern Africa. Although there are various types of tundra, the term is most commonly associated with the Arctic and Antarctic regions characterized by subsoil permafrost. The Afroalpine landscape has also been referred to as "moorland" (e.g., Mekonnen et al., 2011), which generally refers to upland areas of open, uncultivated land dominated by heather on acidic soils, or "steppe" (e.g., Sillero-Zubiri et al., 2011), more generally applied to the extensive tree-less landscapes of Eurasia.

Much of the Afroalpine region is under various forms of formal protection, ranging from 30% in Ethiopia to almost 100% in East Africa (Wesche et al., 2008a). Few of these areas, however, are free from human impact. Poaching, poverty, political instability, high livestock grazing pressure, lack of security, limited budgets and regular anthropogenic fires all pose significant challenges, although fires do maintain grassland diversity and vegetation mosaics (Wesche et al., 2008a; Johansson and Granström, 2014). One hopes that this biologically and culturally diverse and unique region will receive more attention from conservationists, politicians, and researchers.

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Nature of Alpine Ecosystems in the Tropical Mountains of Asia

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Abstract

The Asian tropics are a zone of plate collision that has led to relatively young mountains across the region. Surprisingly, the highest areas where above-treeline habitats are found are all on islands rather than mainland tropical Asia. Isolated ranges in Taiwan and Borneo have a few peaks reaching 4000 m while there are extensive areas on 50 peaks above this elevation in Papua (Indonesia) and Papua New Guinea. The Taiwanese mountains experience seasonal weather, but the equatorial mountains have mild rainfall seasonality and stable temperatures. Depending on rock type and steepness, above-treeline shrublands and grasslands occur above ca. 3700 m with the highest tree lines occurring on limestone around 4100 m elevation. The generally wet and cloudy environments limit temperature variations and lead to widespread organic soils and mire communities. Disturbance is limited as agriculture is not possible but currently some areas are exposed to increasing tourism and erosion.

Introduction

Tropical Asia is an active plate collision zone between the northward-drifting Australian plate and plates in the Pacific and Asian mainland. The area is accordingly mountainous and structured by shear zones and volcanism. The mainland south of the Tropic of Cancer (23.5°N) has many widely separated ranges (Table 1) but the summits lie at or below near 3000 m so are forested to their summits, except where the vegetation has been disturbed.

True alpine environments, with an estimated extent of around 3375 km², are only found on some high tropical mountains that occur on the islands lying between the continents of Asia and Australia, including central Taiwan, the Malaysian portion of the island of Borneo, the Indonesian archipelago and the island of New Guinea (both Papua New Guinea and Papua province, Indonesia) (Prentice et al., 2011). The highest point in this region is Puncak Jaya (Mt Carstensz) (4954 m) in New Guinea (Papua or Irian Jaya, Indonesia). This is the highest mountain on any island in the world. Significant peaks on other islands include the schist mountain Yushan (3952 m) in central Taiwan, the granitic Mount Kinabalu (4101 m) on Borneo and several peaks in Sumatra, Java, Lombok, and Sulawesi which exceed 3400 m. (Fig. 1 and Table 2).

The only extensive alpine habitats in the Asian tropics lie just south of the equator and extend for 1200 km along the island of New Guinea (Prentice et al., 2011; Hope, 2014). The New Guinea high mountains cover a latitudinal range from about 3°S to 8°S, with lower outliers to the west in the Bird's Head peninsula and to the east in New Britain. Fifty peaks exceed 3750 m and the area above 3600 m is 3350 km² (Hope, 2014) (Fig. 2). (Wikipedia:https://en.wikipedia.org/wiki/List_of_highest_mountains_of_New_Guinea).

Alpine Environments in the Asian Tropics

The true alpine biome is a zone above the climatic treeline, which, in the equatorial areas, correlates with a mean annual temp of 7.1 °C according to Körner (2012). Above the alpine is a nival zone, now restricted to Mt. Jaya and rapidly disappearing (Prentice and Hope, 2007). Summits are places with extreme conditions such as rock substrates, high exposure and rapid temperature changes so that, on isolated summits, treelines are often pushed down below the regional treeline elevation, reflecting local alpine conditions. In the Asian tropics the treeless zone includes low heaths, grasslands with scattered emergent shrubs, herb fields, mires and a variety of scree and cliff specialist vegetation.

Climate: The Asian tropical mountains are probably the most humid on Earth, surrounded by warm seas that are a major source of latent heat. Only the Amazonian slopes of the eastern Andes can match this level of humidity, and there is a substantial surplus of precipitation over evaporation in the summit areas, in contrast to African mountains such as Mount Kenya or those in the Trade wind belt such as Mauna Kea, Hawai'i. Yushan in Taiwan has seasonal cold temperatures, with a reliable snow cover from December

Table 1 Tropical mountains on mainland Asia.

Country	Peak	Summit elevation m	Latitude N
India (Kerala)	Anamudi (Ghats)	2695	10° 8.1'
Sri Lanka (Central)	Pidurutalagala	2524	6° 59.8
Myanmar (Chin)	Nat Ma Taung	3070	21° 11.9'
China (Yunnan)	Yanyanpao	2990	23° 21.2'
Vietnam	Fansipan	3143	22° 15.9'
Laos	Phou Bia	2830	18° 56.7'

**Fig. 1** Tropical Asia.**Table 2** Tropical mountains above 3400 m on islands.

Country	Mountain	Elevation m	Location
Taiwan	Yushan	3952	23°28'12"N 120°57'26"E
Malaysia (Sabah)	Kinabalu	4101	6°5'N 116°33'E
Indonesia (Sumatra)	Tanpa Nama (Leseur)	3466	3°44'29"N 97°9'18"E
Indonesia (Sumatra)	Kerinci	3805	1°41'48"S 101°15'56"E
Indonesia (Java)	Semeru	3677	8°6'28.8"S 112°55'12.0"E
Indonesia (Java)	Slamet	3428	7°14'21"S 109°13'12"E
Indonesia (Lombok)	Rinjani	3727	8°24'52"S 116°27'35"E
Indonesia (Sulawesi)	Rantemario/Latimojong	3478	3°23'06"S 120°01'27"E

to March, but the other alpine areas are equatorial so have constant insolation and reliable rainfall with few moisture deficit months (Fig. 3).

The central ranges of New Guinea intercept the southeast trade winds as well as monsoonal (Intertropical Convergence Zone) moisture from the north. The high rainfall convergence zone is > 1200 km north-south in the western Pacific and it usually overlies at least northern New Guinea throughout the year. Unlike Trade wind systems which are only 2–3000 m deep, the ICTZ is sufficiently deep to affect all Asian mountains. Thus, there are no extreme aspect or altitudinal differences in precipitation, in contrast to the rain shadow effects seen in the equatorial Andes or Hawai'i. In New Guinea, there is a pronounced precipitation maximum at mid- elevations (Prentice and Hope, 2007). However, rainfall totals there are so high (6000–12,000 mm per annum), and diurnal convective activity so intense, that any reduction in rainfall with elevation does not lead to moisture deficits longer than a few days at the summits in most years. Summit rainfall is estimated at ca. 2500–4000 mm pa for the main cordillera but is possibly less along the Owen Stanley Range in eastern PNG (around 8°S). Cloud-lie from mid-morning is a feature of most summit areas. Radiation levels under cloud have been shown to be quite low. Photosynthesis requires a minimum amount of solar radiation, and

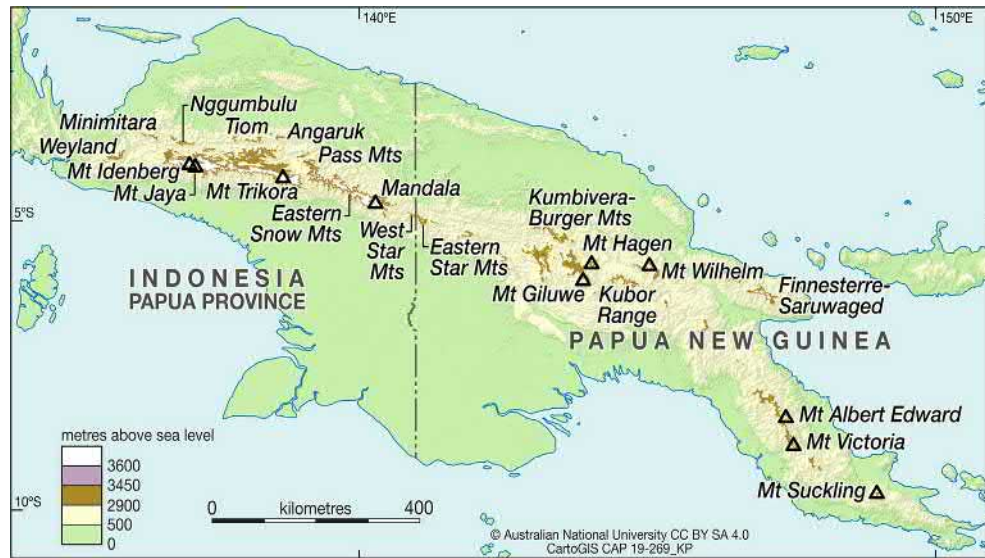


Fig. 2 High elevation areas in New Guinea.



Fig. 3 Glaciers above the alpine in the Meren Valley Mt. Jaya. This photo was taken in 1972 and almost all ice in this photo has since melted.

adaptations by reptiles to overcome low ambient temperatures such as sun-basking will be of little use under cloudy conditions (Green and Stein, 2015). Pindaunde on Mount Wilhelm receives < 25% of the possible hours of sunshine because of almost permanent cloud cover (Hnatiuk et al., 1976) and in the same area alpine plants receive only one-third of the solar radiation of plants in the lowlands (Körner, 2012). This results in higher growing temperatures and more insolation on eastern slopes that experience morning sun than on western slopes or shaded areas, which may explain some vegetation patterning (Smith, 1977). The treeline lies at about the 7.1 °C mean annual temperature for all tropical sites (Körner, 2012).

There are a variety of seasonal precipitation maxima, and in eastern New Guinea a distinctly drier season of 2–3 months occurs from June–September. The very wet conditions reduce the diurnal temperature range by comparison with less humid areas of the Andes and Africa. Hence there is no analogue in this region to the “Afro-alpine” or Páramo zone where there are plant adaptations to severe frost.

However, El Niño events can lead to drought periods of several weeks’ duration every few decades, as occurred in 1972, 1984, 1997–98 and 2003. Kitayama (1996) notes the occurrence of air subsidence and extensive aridity associated with El Niño episodes in the alpine zone of Mount Kinabalu. He points out that high elevations of tropical mountains may be more sensitive to drought

than temperate mountains due to high diffusion coefficients and a high radiation load (Leuschner, 2000). In New Guinea, during El Niño droughts, heavy frosts caused tree deaths in the upper montane forest and crop losses down to 1500 m (Ballard, 2000).

While ground frost occurs on a high proportion of nights above 3750 m, temperatures below -5°C are rarely encountered. Surface temperatures in the intense sunlight can often exceed 30°C for a few hours in the morning. Between-year variability can be more extreme than within-year variation, which for Mount Wilhelm is the lowest so far reported of any of the tropical mountains (Körner, 2012: p. 45).

Wind is not a major factor in the tropics although locations on the mountains can be subject to high windiness due to funneling of katabatic flows. Typical wind pruning of heaths and better development of shrubs behind obstacles can occur but feldmark (severely restricted plant growth) is very rare.

Edaphic controls: Soils of the alpine range from extensive bare rock and screes, moraines and till sheets (lithosols) to deep clays and peats. Mt. Kinabalu has striking granite sheets exposed by unloading and vegetation is highly restricted by this (Fig. 4).

The underlying geology influences the formation of soil and growing conditions. For example, treeline woody vegetation reaches higher elevations on limestone than on impervious substrates such as basalt. This appears to reflect better drainage as most alpine soils are wet and prone to waterlogging. Glacial action also creates larger moraines and till sheets on some types of rocks which provide habitat for seedling establishment. On all substrates, organic debris and moss and lichen mounds develop into peat soils which are resistant to erosion by rain that sluices the rocky slopes. Peats are generally acidic and prone to waterlogging. Recent morainal debris formed by limestone gravels has a pH of 8.5 and is free-draining. This develops moss mats within 15–20 years that have pH levels of 4.5 and present new plant colonization sites (Hope, 1976; Fig. 5).

Disturbance: The alpine zone experiences numerous freeze-thaw cycles throughout the year and needle ice commonly disturbs exposed soils. Natural fires are rare but in frequently visited areas human-lit fires are widespread and can affect closed shrublands and grasslands. These are especially marked during El Niño drought episodes and fragment the treeline, for example at Mt. Giluwe, PNG. On longer timescales, frequent earthquakes destabilize slopes and many mountains were affected by neoglaciation (Little Ice Age) which increased snow lie and expanded glaciers between 1650 and 1850. Ice and snow retreat over the past century has exposed fresh ground that supports successional open herb or moss dominated communities despite minimal soil development.

Volcanic activity strongly limits ecological succession and the combination of loose ejecta and ground frosts make it very difficult for plants to colonize. Mt. Kerinci is an active volcano that has an extremely bare summit zone for these reasons (Ohsawa et al., 1985) (Fig. 6).

Main Vegetation Communities Above Treeline

The tropical Asian alpine vegetation communities are low shrublands and grasslands on medium to deep well-drained soils, open dwarf shrublands on shallow stony soils and several mire communities, including fens and moss and graminoid-dominated herb fields. The vegetation of the Taiwanese mountains differs from the mountains to the south and west because the flora is derived from China and lacks the strong Australian-sub Antarctic element found on the more equatorial islands. However, the main vegetation communities are similar structurally although wetlands are absent from the steep summit area.



Fig. 4 Granite summit plateau of Mt. Kinabalu, Malaysia.



Fig. 5 Dwarf shrub heath and open moss heath at 4400 m in the Meren Valley on Mt. Jaya. The mosses and scattered *Epilobium* tufts occupy a very young moraine while the shrubs lie outside the recent ice margin.



Fig. 6 Summit area of Mt. Kerinci, consisting of recent ash and debris from the crater.

The upper limit of the subalpine forest is generally a low dense forest formed by gymnosperms (in New Guinea podocarps such as *Dacrycarpus compactus*, on Kinabalu by *Dacrycarpus kinabaluensis* and *Phyllocladus hypophyllus* and on Yushan by the conifer *Abies kawakami*). Tree rhododendrons and other trees such as *Rapanea* (Mysinaceae), *Quintinia* (Paracryphiaceae) or *Schima* (Theaceae) often contribute. Isolated trees or patches of forest may extend above the forest limit, often as small stands of tall shrubland in sheltered places.

Heath and Open Dwarf Shrublands

The alpine climate inhibits woody plant growth (Körner, 2003). Shrubs are often low to the ground and set into graminoid communities. Heaths made of larger shrubs often reflect edaphic controls that limit tree growth, as on Mt. Kinabalu above 3300 m where soils are shallow or absent (Kitayama, 1992; Wong and Chan, 2015) (Fig. 7).



Fig. 7 Xeromorphic scrub vegetation at 3300 m on Mount Kinabalu. The shrubland is dominated by species with leptophyll leaves (up to 25 mm² in size) such as *Leptospermum recurvum*, *Rhododendron ericoides*, *Styphelia suaveolens* and *Gaultheria* species, with *Carex* and *Belvisia* species on rocky patches.

In New Guinea, alpine shrublands similar to the Kinabalu heath community grow to 0.7–1.5 m in height, and are dominated by *Coprosma* species such as *C. brassii* and *C. novoguineensis* with *Styphelia suaveolens*, various *Rhododendron* species (e.g., *R. versteegii*, *R. gaultherifolium*, *R. womersleyi*) and *Tasmannia piperita*. These tall heaths do not reach the highest elevation but exceed 4000 m on Mt. Jaya (Hope, 1976, 1980; Johns et al., 2006). On Yushan a tall heath of *Juniperus squamata* and *J. formosum* occupies the deeper soils.

At higher elevations, shrubs contribute to a formation called Dwarf Shrub Heath by Wade and McVean (1969). Small rounded shrubs of *Styphelia suaveolens*, *Trochocarpa decockii*, *Drapetes ericoides*, several species of *Tetramolopium* and of *Parahebe* occur on deeper, well drained soils interspersed with mosses and grasses.

The formation has variable floristics across the isolated peaks of New Guinea. Species that are prominent on one mountain are absent or rare on others. For example, the blue-flowered *Veronica tubata* (Plantaginaceae) is known from the Saruwaget Range and Mt. Wilhelm, while the alpine fern *Polystichum* (*Papuapteris*) *lineare* occurs on Mt. Albert Edward, Mt. Wilhelm and Mt. Giluwe (Hope, 2014).

On more exposed and higher slopes, a very open heath occurs with a carpet of mosses such as *Rhacomitrium* and *Campylopus* spp. and low (< 30 cm) small shrubs of *Tetramolopium* spp. and grasses such as *Poa nivicola* (Mangen, 1993). Small herbs such as *Cerastium papuanum* and *Epilobium detznerianum* grow in the moss cushions. Plant growth is excluded on bare ground, because the bare gravels are strongly frost-heaved.

The summit plateau of Mt. Kinabalu (Fig. 4) is largely bare rock, but small shrubs of *Rhododendron ericoides*, *Styphelia suaveolens*, and *Leptospermum recurvum* with sedges such as *Oreobolus ambiguus* and *Centrolepis philippinensis* and tussocks of *Deschampsia flexuosa* grow in crevices so a form of dwarf heath is probably present there, termed *Styphelia suaveolens*—*Trigonotis borneensis* heath by Smith (1980). Numerous species are shared with New Guinea or are closely related to New Guinea species, for example *Agrostis reinwardtii*, *Danthonia oreoboloides*, *Poa papuana*, and *Drapetes ericoides*.

Grasslands and Herb Fields

A common type of alpine grassland is dominated by robust tussocks of *Deschampsia klossii* that grow to 60 cm high. This grassland usually occurs on deeper soils on slopes and along the banks of streams. At high elevation, the grass is viviparous, with seeds sprouting on the parent plant. Other grasses include *Anthoxanthum redolens* and *Poa nivicola* and gaps in the tussocks have a rich mat of *Poa* spp., *Cerastium* sp., *Geranium monticola* and *Epilobium detznerianum*.

Short alpine grassland, with small tussocks of *Poa erectifolia* and *P. lamii*, dominates Mt. Albert Edward, but similarly structured grasslands with other dominants occur on other mountains (Fig. 8). Small tussock and tuft grasses that include *Deyeuxia brassii*, occur with scattered low shrubs of *Coprosma*, *Vaccinium*, and *Rhododendron* species.

Astelia alpina alpine herb field is widespread with *Astelia* cushions forming large stands on some mountains, such as the Star Mountains and Mt. Giluwe (Fig. 9). Small cushion plants, including *Centrolepis philippinensis*, *Potentilla brassii*, *Oreomyrrhis pumila*, and *Danthonia oreoboloides* and *Oreobolus pumilio* and occasional grasses are often important. Such cushions extend into waterlogged areas, forming a cushion bog. This bog type is notably more common in the Snow Mountains of Papua than in PNG.



Fig. 8 Short alpine grasslands at 3990 m dominated by *Poa* and *Danthonia* species, Mt. Wilhelm. Shrubs are *Coprosma* sp.

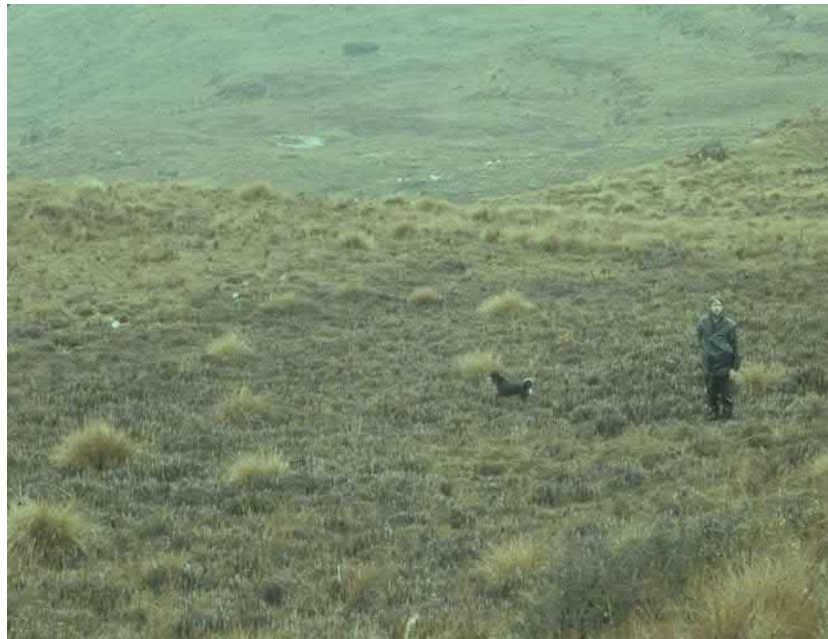


Fig. 9 *Astelia alpina* herb field and *Gleichenia vulcanica* fernland. The large tussocks are *Deschampsia klossii* on Mt. Giluwe, PNG.

Alpine moss lands. Structurally these communities, dominated by a carpet of mosses, resemble boreal moss communities. On waterlogged or inundated sites *Ranunculus* spp. are interspersed with the mosses (Fig. 10), but on stable screes a complex of mosses with small cushions of *Cerastium*, *Potentilla* or *Oreobolus* support small tuft grasses that grow in the moss.

On drier sites such as moraine and rock surfaces, mosses form a discontinuous carpet with scattered herbs such as *Epilobium* and *Plantago* and small grasses (Fig. 11). Small shrubs of *Styphelia suaveolens* may also be present, as noted by Mangen (1993) on Mt. Trikora.

Wade and McVean identified these moss lands as wet or dry tundra. However, alpine grasslands and open heaths occur at the same elevation on more mature soils. Hence these moss lands are probably time-limited and will eventually give way to alpine grasslands or grass-dominated bog. The mosses cover the ground and quickly reduce the pH on calcareous sites, providing an acid organic substrate (Hope, 1976).



Fig. 10 Alpine moss land with *Ranunculus* sp. in the Yellow Valley on Mt. Jaya at 4450 m altitude.



Fig. 11 These *Rhacomitrium* moss lands on Mt. Wilhelm summit at 4420 m are developing in an area that was probably covered by firn (granular snow) prior to 1860.

Wetlands

Sedges dominate several types of alpine fen with varying degrees of inundation. *Carpha alpina* fen is characteristic of less wet sites with robust small tussocks (Fig. 12). *Carex gaudichaudiana* dominates pond edge fen with *Isolepis crassiuscula* in semi-permanent shallow ponds. *Uncinia riparia* also forms a closed sedge land on Mt. Trikora (Mangen, 1993). Related fens extend through the alpine of Australia to the sub-Antarctic, possibly reflecting the role of migratory birds in spreading wetland plants.

Elements of these New Guinean alpine communities reach Mt. Kinabalu and indeed Mauna Loa in Hawaii has related *Styphelia*, *Anthoxanthum*, *Festuca*, and *Coprosma* species. Yushan has a Himalayan element including *Gentiana* spp. and *Rhododendron pseudochrysanthum*. These genera have radiated in the New Guinea mountains, presumably reflecting the newness of high mountain



Fig. 12 Fringing fen of *Carpha alpina* and *Astelia* around a tarn, Mt. Victoria, PNG.

environments in New Guinea. This also explains the high level of southern temperate taxa such as *Astelia* and *Poa* that have migrated to the region.

Fauna

In Taiwan, voles (*Microtus kikuchii*) are common in high elevation meadows and help to spread their main food grass, *Yushania nii-takayamensis* (Yeh et al., 2012). Elsewhere, rat species are major herbivores in alpine grasslands. Mt. Kinabalu hosts four mammal species in the summit area—the Summit Rat (*Rattus baluensis*), the Kinabalu Shrew (*Crocidura baluensis*), the short-tailed Gymnure (*Hylomys suillus*) and the mountain squirrel (*Callosciurus baluensis*) (Wong and Chan, 2015). The Blackbird (*Turdus poliocephalus*) is common there and also in the New Guinea alpine, where rats such as *Rattus niobe* and *R. giluwensis* live in alpine grasslands. The Glacier Rat (*R. richardsonii*) occurs up to the highest elevations in rocky terrain. Remains of the 3 kg Giant New Guinea Rat (*Mallomys istapantap*) have also been collected at 4430 m elevation on Mt. Jaya (Hope et al., 1976) even though it is thought to be largely folivorous (leaf-eating). Marsupials are present, though they are found only occasionally in the alpine zone. The bandicoot *Microperoryctes longicauda* is an insectivore closely resembling the shrews of Kinabalu. Wild dogs (*Canis lupus*) introduced to New Guinea about 3500 years ago, are quite common in the alpine zone and reflect the high density of rodents.

Birds such as the Blackbird, Glossy Swiftlets (*Collocalia esculenta*), the island thrush, (*Turdus poliocephalus*), the alpine robin (*Petroica archboldi*) and the New Guinea pipit (*Anthus gutturalis*) exploit a sparse insect population in the alpine. Alpine lakes are also visited by Salvadori's Teal (*Anas waiguensis*) and other water birds that feed on invertebrates and water plants. A feature of tropical high mountains is a rain-out of dead insects and even lowland bird species brought up by powerful updrafts, adding to the food resources of predators and scavengers in the summit zone (Schodde et al., 1975).

Human Usage

The tropical high mountains are cold, cloudy and wet, so do not provide an opportunity for agriculture. Prior to modern tourism, the alpine received infrequent visitors. In some cases, such as Kinabalu, the peaks were considered sacred and so were not visited. In western New Guinea there are tracks traversing the range and crossing the alpine zone (Fig. 13). Hunting takes place in the alpine and subalpine grasslands. A rock shelter in the alpine of Mt. Jaya at 4200 m has a basal age of 6200 cal years BP (Hope et al., 1976). It is likely that people have exploited the alpine throughout the Holocene as vegetation histories show the presence of fire from 12,000 years ago in some areas (Fairbairn et al., 2006). However, mountains such as Mt. Wilhelm and Mt. Giluwe experienced forest disruption quite recently with clearance due to fire over the last several centuries (Corlett, 1984; Hope unpublished). This may reflect increasing human populations at lower elevations who exerted pressure to exploit the mountains for mammals and birds. This use of the mountains for transit and hunting continues to the present though may be reducing in some areas.



Fig. 13 This grassland area of the snow mountains near Mt. Trikora has been burnt over the past 11,000 years.

This long history explains some of the mosaic of subalpine forest and grasslands, together with a fragmentation of the treeline in some mountain areas such as Mt. Albert Edward and Mt. Jaya. Many grassland and herb field species have expanded into lower elevation niches as the subalpine forests retreated and were replaced by grasslands.

Over the past 50 years tourism has expanded greatly, such that permits to ascend Yushan and Kinabalu have had to be limited. Thousands of visitors follow the most popular tracks. New Guinea is a far less popular tourist destination, although guided tours of Mount Wilhelm take place and other mountains such as Mt. Giluwe and Mt. Trikora are accessible from nearby towns. Mount Jaya attracts numerous climbing expeditions, as it is one of the seven world summits, the highest point in Oceania.

The summit of Mount Albert Edward has microwave facilities serviced by helicopter and similar facilities have been abandoned on Mt. Wilhelm and Mt. Giluwe. Mining on Mt. Jaya has removed several km² of alpine habitat due to the mining of gold and copper at Grasberg and the dumping of tailings up to 4200 m.

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Alpine Ecosystems in Temperate Mountains of North America

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Abstract

The temperate zone mountains of North America contain alpine ecosystems whose distinctive plant and animal communities are adapted to the cold temperatures, winter snow cover, short growing seasons, and high winds found in the steep rocky terrain at high elevations. Although 3% of the land area is alpine, the alpine zone contains 4% of the world's flora and is therefore richer in biodiversity than expected. At the landscape scale (>100 m), wind and snow interact with landforms to form mesotopographic gradients along hillslopes. Snow redistributed by winds produces long-lasting snowdrifts on lee slopes, which increase water availability downslope, but also affect the timing and length of the growing season for plants. Along the gradient, cushion plant-dominated vegetation occurs on exposed ridgetops, followed by dry sedge meadows or dwarf-shrub heaths in less exposed positions below the ridge, moist meadows or heaths in early-melting midslope positions, late-melting snowbed vegetation, and wet meadows or bogs in valleys. Alpine plant adaptations to the harsh environmental conditions include short stature, cold tolerance, long lifespans, and vegetative reproduction. Animals cope with winter conditions by living in sheltered environments under snow and talus, hibernating, or migrating. The American pika, a potential sentinel species for climate change, is intolerant of warm temperatures and depends on winter snow cover. On Niwot Ridge in Colorado, minimum temperatures and precipitation are increasing, but declining precipitation has also been observed in the western US. Climate change and atmospheric deposition of nitrogen are likely to contribute to shifts in ecosystem properties and plant and animal species distributions, such as shrub encroachment into herbaceous communities.

Introduction

The mountains of North America are home to alpine ecosystems whose distinctive plant and animal communities are adapted to the cold temperatures, snow, and wind found in the steep rocky terrain at high elevations (Fig. 1). Alpine ecosystems occupy 3% of the land surface worldwide but contain 4% of the world's flora, and are therefore richer in than expected (Körner, 2003). In addition to this important contribution to global biodiversity, alpine ecosystems are valued for their aesthetic beauty and recreation opportunities. They also influence the quality and quantity of water and nutrients delivered to downslope areas, and may be sensitive indicators of global change factors such as climate and air pollution.

Plants in alpine ecosystems survive the harsh climate by hugging the ground (up to a few decimeters in height) and using the intense solar radiation during the growing season to produce vividly colored flowers in meadows and among low shrubs. Cushion plants (low compact herbaceous plants) and lichens may be found in the most severe conditions on exposed ridge tops and summits. Characteristic alpine plant growth forms are shown in Fig. 2. Year-round animal residents of the alpine zone of North America include pikas, marmots, ptarmigan, pipits, and rosy finches. Larger herbivores such as bighorn sheep, mountain goats, deer, elk, and moose may be seasonal visitors, along with many other birds and mammals (Armstrong et al., 2001).



Fig. 1 Alpine landscape on Niwot Ridge in the Colorado Front Range of the Rocky Mountains, a National Science Foundation-sponsored Long Term Ecological Research site.



Fig. 2 Alpine plant growth forms. (Upper left) graminoid (*Carex heteroneura*); (upper right) forb (herbaceous flowering plant; *Anemone occidentalis*); (bottom left) dwarf shrub (*Salix nivalis*); and (bottom right) cushion plant (*Silene acaulis*).

Alpine ecosystems are found above treeline and below the permanent snow line, if one is present (Billings, 2000). Many mountains in North America have alpine vegetation growing from treeline all the way to the summit. Others have snow lines or nival zones above the alpine zone where plant growth is limited except in protected areas (Nagy and Grabherr, 2009).



Fig. 3 Krummholz trees and alpine vegetation at treeline on Niwot Ridge.

The transition from the taller crowns of forest trees to the diminutive stature of alpine vegetation is an obvious landscape feature of high mountains (**Fig. 3**). The tree “line” is actually part of a zone of transition or ecotone from closed canopy forests to open alpine ecosystems. At treeline, upright trees occur as patches that alternate with patches of herbaceous vegetation ([Bourgeron et al., 2015](#)). Alpine vegetation may also occur below treeline where disturbances such as avalanches have removed trees. In addition, dwarf trees (krummholz) may be found in protected locations above treeline. The ecotone is porous in nature because the factors that define the lower limits of alpine species are not necessarily those that limit the upward distribution of trees. Temperature, precipitation, and wind are all factors that influence the location of treeline and therefore the lower limit of the alpine zone. The elevation at which the average temperature during the growing season is 6 °C or lower roughly corresponds to this lower limit ([Körner and Paulsen, 2004](#)).

Alpine ecosystems are often referred to as alpine “tundra”, which implies a similarity with arctic tundra ([Billings, 2000](#)). Although both types have similar physiognomy, and alpine areas generally share species in common with the arctic zone, important differences exist in environmental conditions. Both ecosystem types have low temperatures during the growing season. However, alpine environments have greater solar radiation intensity, wind, snow cover, and topographic heterogeneity, but shorter daylength, and less permafrost compared to arctic systems ([Körner, 2003](#)).

Temperate Zone Mountains

The temperate zone limits in North America, for the purposes of this article, are those described by [Nagy and Grabherr \(2009\)](#). Their categorization was based on a combination of existing climate life zone classifications that use temperature and precipitation together with broad vegetation classes to delineate zones. The temperate zone is located between the more northerly boreal zone of Canada and Alaska and the subtropical zone of the southeastern and southwestern United States.

On the east coast of North America, the highest peaks in the northern Appalachian Mountains have limited alpine zones, such as the Adirondack Mountains in New York, the Presidential Range in New Hampshire, and Mt. Katahdin in Maine. Temperate zone mountains with alpine ecosystems include the two great western Cordilleras, the Coastal Cordillera and the Rocky Mountains (**Fig. 4**). Alpine environments in the Coastal Cordillera are found in the Coast Mountains of British Columbia and the Cascade Mountains in the Pacific Northwest (**Fig. 4A**). Alpine ecosystems in the Rockies occur in southern British Columbia and Alberta and in the western United States from Idaho and Montana to New Mexico (**Fig. 4B–D**). The Great Basin contains several isolated mountain ranges with alpine ecosystems.

The elevation of treeline (the lower limit of the alpine zone) varies among North American temperate zone mountain ranges, depending on overall height and prevailing climate conditions. Treeline in the northern Appalachian Mountains ranges from 1300 to 1600 m ([Carlson et al., 2011](#)). In the Cascade Mountains treeline occurs at about 2000 m ([Nagy and Grabherr, 2009](#)), and in the Rocky Mountains, treeline decreases from south to north. For example, on Wheeler Peak, New Mexico, it occurs at about 3700 m ([Baker, 1983](#)), whereas on Niwot Ridge in the Colorado Front Range, it is located at about 3500 m, and in Glacier National Park it ranges from about 1800 to 2100 m.

The tectonic age of temperate mountain ranges decreases from east to west. The relatively old Appalachian Mountains arose in the Cambrian to the Pennsylvanian, the Rockies in the upper Cretaceous to Oligocene, and the Coastal Cordillera in the Pliocene to

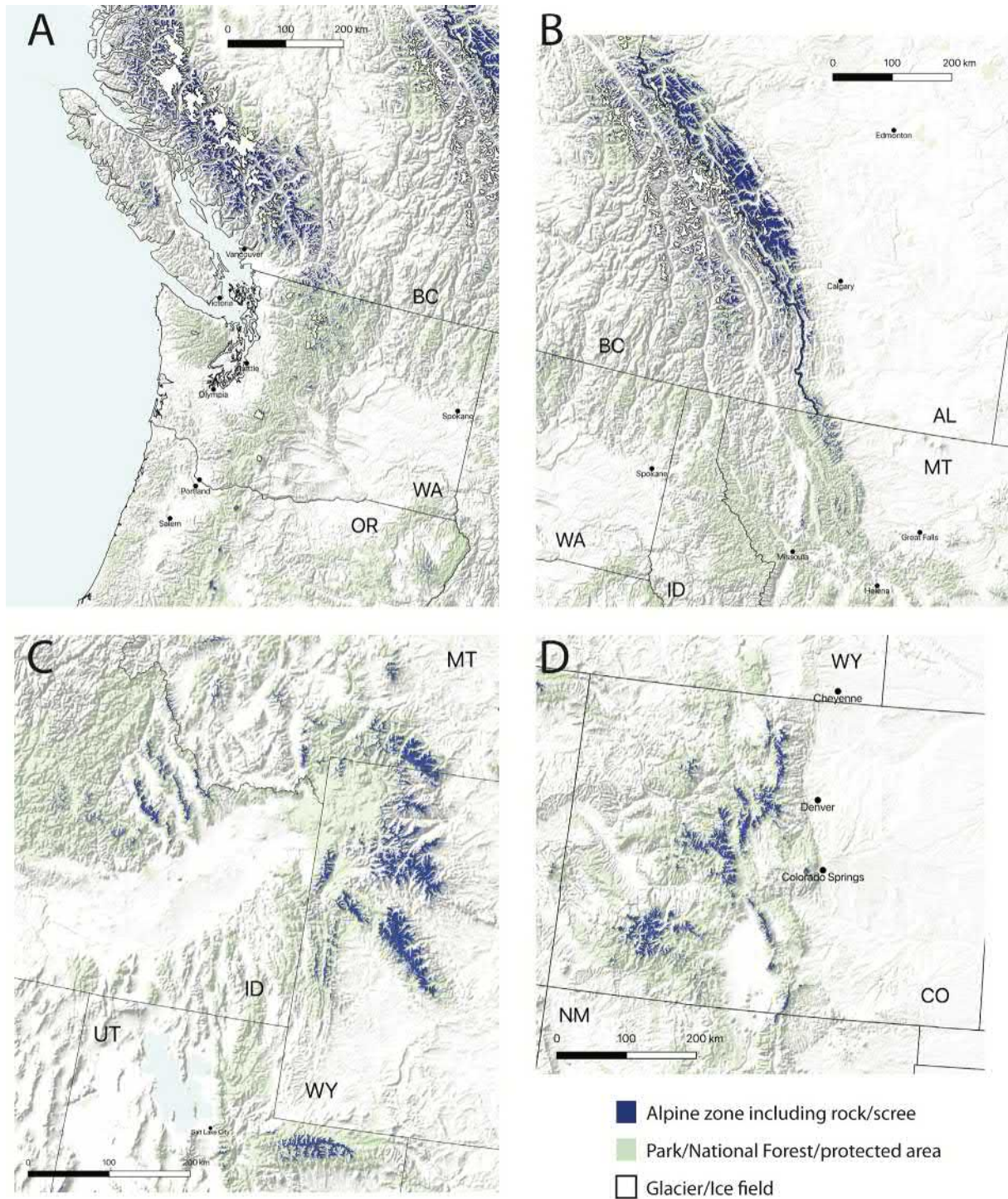


Fig. 4 Alpine areas in the temperate zone of North America, as defined by the GAP/LANDFIRE National Terrestrial Ecosystems project for the continental United States (US Geological Survey Gap Analysis Project 20,160,513, 2011, <https://doi.org/10.5066/F7ZS2TM0>) and the Canadian National Vegetation Classification. United States national, state, and local parks; other protected areas; and National Forests. Parks, ecological reserves, and protected areas in British Columbia and Alberta are parks and protected areas managed for important conservation values. Canadian glaciated area polygons derived from DCW (Digital Chart of the World). (A) Coast Range and Cascade Mountains, (B) Northern Rocky Mountains, (C) Central Rocky Mountains, and (D) Southern Rocky Mountains. Northern Appalachian and Great Basin alpine zones not shown due to small areal extents.

Pleistocene (Billings, 2000). Pleistocene glaciation affected mountains throughout the temperate zone. Continental ice sheets covered mountains in the northeastern and northwestern mountain ranges, whereas local ice caps and glaciers shaped interior western ranges south of the ice sheets. Extensive reshuffling of biotic distributions occurred during this period (Elias, 2001).

Environmental Factors

Climate

Cold temperatures, winter snow cover, short growing seasons, and high winds characterize alpine environments in temperate North America. Temperature decreases with increasing elevation, but the extent differs with latitude, atmospheric circulation pattern, and geographic position on the North American continent and may also be altered locally by wind, slope, and aspect (Nagy and Grabherr, 2009). Aboveground air temperatures do not necessarily reflect temperatures at the soil surface or in the canopies of plants, which may be much higher due to absorption of solar radiation and the high aerodynamic resistance of short-statured alpine plants (Billings, 2000). These differences depend on weather, time of year, time of day, and individual plant species characteristics (Körner, 2003). In addition, diurnal fluctuations in temperature may be quite large, exposing plants and animals to the stresses of temperature extremes over short time periods (Nagy and Grabherr, 2009).

An important factor that distinguishes the temperate zone of North America from other North American life zones is continentality, an increase in the range of temperatures in interior versus coastal areas (Nagy and Grabherr, 2009). Mountain ranges in the northeastern and northwestern temperate zone experience a greater degree of maritime influence on climate, which moderates temperature extremes compared to those occurring in the continental interior, that is the Rocky Mountain and Great Basin ranges. In the North Cascades, climate regimes shift from maritime to continental going from west to east. As a consequence of this shift, western North Cascade plant community types are more closely related to those in other west coast ranges, but eastern types have a greater resemblance to Rocky Mountain communities (Douglas and Bliss, 1977).

The amount of solar radiation received at a particular location in the alpine zone depends on elevation, slope, aspect, latitude, and position of the sun, creating microtopographic insolation gradients (Nagy and Grabherr, 2009). Incoming solar radiation increases with increasing elevation, especially in the UV range (Billings, 2000). However, cloudiness may also increase with elevation, attenuating the amount of solar radiation actually available to plants for photosynthesis (Körner, 2003). Cloud cover in the form of wet fog is a particularly important environmental feature of the alpine zone of the northern Appalachian Mountains on north and west-facing slopes, and is a contributing factor to the presence of a large number of Arctic plant species in the alpine ecosystem (Bliss, 1963).

Temperate zone mountain ranges are generally characterized by an abundance of winter snow (Nagy and Grabherr, 2009). Precipitation regimes vary both among and within mountain ranges due to geographic position, degree of continentality, and prevailing atmospheric circulation patterns. Although temperature regimes in the alpine zones of Mount Washington, New Hampshire, and Niwot Ridge, Colorado are similar (cool, short growing seasons), the north Appalachian Mountains experience a fairly even distribution of precipitation throughout the year, making summer drought unlikely (Billings, 2000). In contrast, 75% of annual precipitation occurs as snow in the southern Rockies (Greenland and Losleben, 2001), resulting in drier summers where precipitation occurs in the form of convective thunderstorms.

Geomorphology and Soils

Physical disturbances to plant and animal habitats range in size and intensity in alpine ecosystems as a result of the high topographic relief. Mass movement events can occur over short time scales, for example, snow or rock avalanches, or can take a longer time to manifest, for example, development of scree and talus slopes or glaciers (Nagy and Grabherr, 2009). Some small mammal species inhabit scree and talus slope habitats, such as pikas (*Ochotona princeps*), marmots (*Marmota flaviventris*), and deer mice (*Peromyscus maniculatus*) (Armstrong et al., 2001). Rocky slopes are sparsely occupied by plants, but provide habitat for some species, for example, *Saxifraga* and *Draba* species (Walker et al., 2001).

Alpine soils are cold and, depending on topographic position, range from dry to wet (Billings, 2000). The harsh climate limits the amount of chemical weathering, but intensive freeze-thaw cycles may break rock down (Seastedt, 2001). In soils containing moisture, rock and gravel may be brought to the surface, producing patterned ground features such as stone nets, stripes, and circles, as well as solifluction lobes. At a fine scale, frost churning produces needle ice, frost boils, and frost creep, which can be disruptive to plants. However, plant communities with a complete ground cover can provide insulation against frost disturbance (Körner, 2004).

Soil development is a function of position in the landscape, with the least developed soils occurring in both windblown and snow accumulation areas because insufficient biotic-related weathering takes place (Seastedt et al., 2004). Although overall nutrient levels tend to be low in alpine soils, they vary spatially. Nitrogen increases from dry to moist to wet meadows (Suding et al., 2015).

Mesotopographic and Microtopographic Gradients

In the alpine zone, topography, wind, and snow combine to determine the conditions under which plants and animals live. At the landscape scale (> 100 m), wind and snow interact with landforms to form mesotopographic gradients along hillslopes (Fig. 5). The mesotopographic model developed by Billings (2000) has been used to explain plant and animal distributions in a number



Fig. 5 Mesotopographic-scale snowdrifts in the Saddle site on Niwot Ridge. Foreground, windward slope; background, lee slope.

of temperate zone alpine sites (see below). Ridgetops, midslopes, and bottom slopes differ in the amount of snow cover and its duration. Snow falling on mountains may be blown from windward-facing slopes by strong winds and redeposited on leeward-facing slopes, leading to the accumulation of long-lasting snowdrifts on these slopes (Fig. 5). Snow drifts increase water availability downslope and provide protection from wind, cold temperatures, and frost effects, but also constrain the timing and length of the growing season for plants. On Niwot Ridge, the growing season on a windswept ridgetop with little snow accumulation was 109 days, but was only 52 days for a wet meadow area with a late-lying snowpack (May and Webber, 1982). Soil moisture varies across the mesotopographic gradient as a function of snowpack and meltwater supply, with the lowest soil moisture values at the top of ridges and the highest values at the foot of slopes where meltwater accumulates (Walker et al., 2001). The landscape continuum model developed by Seastedt et al. (2004) couples the mesotopographic approach with an emphasis on transport processes as organizing agents of ecosystems. Transport of materials occurs by means of wind, water, avalanches, and landslides. For example, alpine areas at the bottom of slopes receive water and nutrient inputs from upslope areas.

Alpine ecosystems are affected by microtopographic differences at spatial scales less than 10 m (Suding et al., 2015). Mosaics of microhabitats occur as a result of features like small depressions, rocks, and plants themselves. Microdrifts of snow accumulate in the lee of rocks and plants (Fig. 6). Small-scale heterogeneity in slope and aspect generates variation in solar radiation; other microhabitat factors include wind protection, soil temperature, and soil nutrients. These factors are the same as those influencing biotic distributions at the landscape scale (Suding et al., 2015). Micro-environmental mosaics constrain the biota and are in turn altered by biotic processes. The combination of meso- and microtopographic gradients in alpine landscapes produces transitions between plant, animal, and microbial communities (beta diversity) over short horizontal distances within the larger landscape-level gradients.

Biodiversity

Vegetation

The applicability of the mesotopographic concept for understanding alpine vegetation patterns has been demonstrated for several North American temperate zone locations. A common topography/snow/meltwater gradient consists of cushion plant-dominated vegetation on exposed ridgetops, followed by dry sedge meadows or dwarf-shrub heaths in less exposed positions below the ridge, moist meadows or heaths in early-melting midslope positions, late-melting snowbed vegetation, and wet meadows or bogs in valleys (Billings, 2000).

Alpine vegetation patterns at Niwot Ridge in the southern Rocky Mountains have been explained as resulting from a mesotopographic gradient in snow (Fig. 7) (Walker et al., 2001). Fellfield communities occur in the most windswept, exposed positions where plant cover is sparse and cushion plant life forms dominate. Characteristic fellfield species are cushion plants such as *Silene acaulis* (moss campion) and *Minuartia obtusiloba* (twinflower sandwort), the mat-forming plant *Trifolium dasyphyllum* (alpine clover), and *Carex rupestris* (curly sedge). This rocky, dry habitat is blown free of snow in the winter. Just below ridgetops on windward slopes, dry meadow communities have little winter snow cover and are dominated by a sedge species, *Kobresia myosuroides* (Bellardi bog sedge), which forms dense turfs. *Kobresia* is unable to survive the harsh winter conditions in fellfields. It also appears to require



Fig. 6 Microtopographic-scale snowdrifts. (Top) Niwot Ridge and (bottom) Beartooth Plateau, Montana.

a long snow-free period in spring and fall and does not survive in habitats where snow cover routinely develops early. The club moss *Selaginella densa* (Rocky Mountain spikemoss) is also abundant in dry meadows. Another sedge species, *Carex elynoides* (blackroot sedge), occupies a smaller areal extent than *Kobresia* on relatively dry south slopes. This species is more abundant in other Rocky Mountain locations that lack *Kobresia*. Moist meadow communities occur on lower slopes where snow cover is moderate but melts relatively early in the growing season and soil moisture is abundant. The dominant species in this community type are a grass species, *Deschampsia cespitosa* (hairgrass), and a forb (herbaceous flowering plant), *Geum rossii* (Ross' avens), which is also present in most other communities. Late-lying snowbanks on lee slopes are the locations of snowbed communities, characterized by *Sibbaldia procumbens* (a forb, creeping sibbaldia), and *Carex pyrenaica* (Pyrenean sedge). These habitats have a very short growing season, and soil moisture disappears rapidly following snowmelt, producing sparse vegetation. Wet meadow communities occur downslope from snowbeds, where meltwater provides abundant soil moisture during most of the growing season. *Carex scopulorum* (mountain sedge), and *Caltha leptosepala* (a forb, white marsh marigold) are the dominant species. The shrub community type has a fairly continuous cover of *Salix* (willow) species, and is found in protected areas near the bottom of the slope.

Baker (1983) studied alpine community types in the Sangre de Cristo Mountains of New Mexico along a mesotopographic gradient similar to Niwot's. The species composition of most communities resembled those occurring on Niwot, but also included some community types that were not equivalent, such as a *Festuca thurberi*-dominated community on very steep southeast-facing slopes.

Billings and his associates conducted research at several western United States temperate alpine sites and related vegetation mosaic patterns to mesotopographic snow gradients (Billings, 2000).

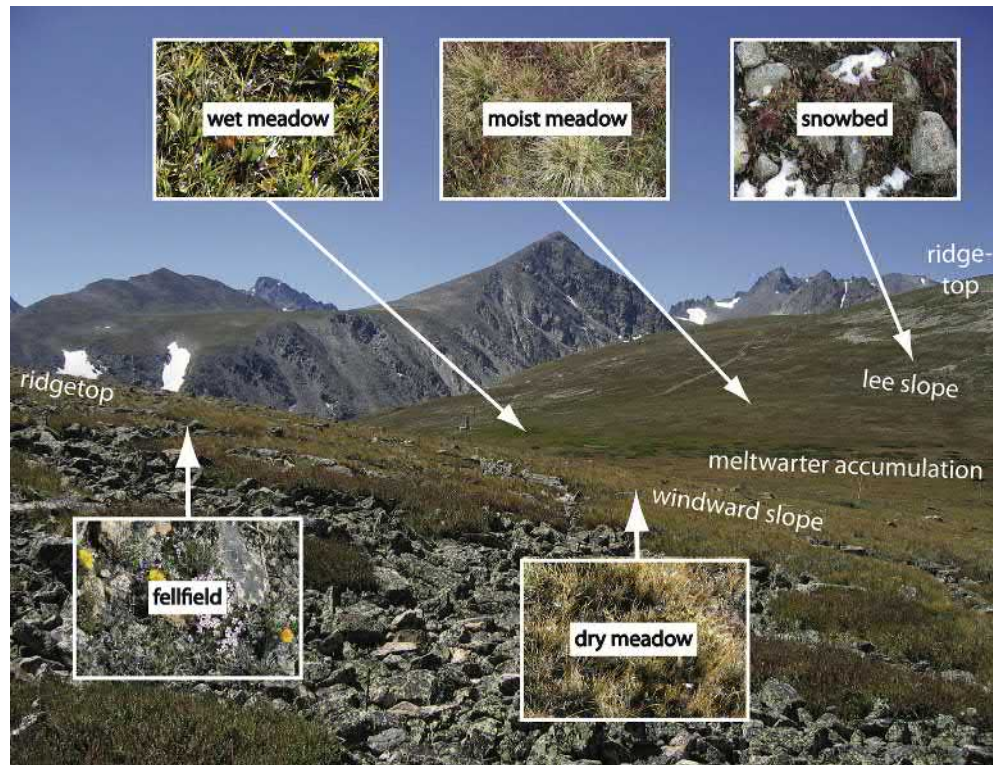


Fig. 7 Hillslope positions along a mesotopographic gradient and associated plant community types in the Saddle site on Niwot Ridge, elevation ~3520 m. Fellfield occurs on windswept ridgetops, dry meadow on windward slopes with low winter snow cover, wet meadow at the bottom of slopes in areas of meltwater accumulation, moist meadow on lower slopes with moderate snow cover, and snowbed on lee slopes with late-melting deep snow.

Plant communities occurred along a steep snow cover/soil moisture/wind gradient in the Medicine Bow Mountains of Wyoming, about 100 km north of Niwot Ridge. The Medicine Bow communities were similar to those found at Niwot, with the notable exception that Niwot's dominant dry meadow species, *Kobresia myosuroides*, was absent. At a windward location below the ridgetop, the rocky slope was sparsely vegetated with an open fellfield community rather than a sedge-dominated turf.

On the broad expanses of alpine vegetation on the Beartooth Plateau of Wyoming and Montana, [Johnson and Billings \(1962\)](#) found that plant communities were structured similarly to those of Niwot along a snow mesotopographic gradient. As in the Medicine Bow Range, the characteristic Niwot dry meadow community did not occur. However, a species with similar habitat requirements, *Carex elynoides* (blackroot sedge), was present in dry environments. A possible contributing factor to the low abundance of *Kobresia myosuroides* on the Plateau was a smut found on 15% of plants that were examined. As at Niwot, microtopographic differences in snow accumulation produced a mosaic of microhabitats within major vegetation types. Soil frost activity was an important driver of geomorphic processes on the Beartooth Plateau. Frost-churned peat hummocks ([Billings, 2000](#)), disturbed *Deschampsia* meadows, producing fine-scale vegetation heterogeneity. Taller hummocks, which melted out earlier than lower ones, were dominated by *Deschampsia cespitosa* and *Carex scopulorum*. *Juncus drummondii* completely covered some lower hummocks, but only occurred on the sides of higher ones. The intervening troughs contained *Caltha leptosepala*, *Juncus* (rush), and *Salix* species. On the relatively gentle slopes that occurred on the Plateau, plant community boundaries were not distinct, grading into a continuum.

In the North Cascades, the mesotopographic gradient followed the general pattern outlined by [Billings \(2000\)](#). Mosaics of plant communities were more common in the western North Cascades as a result of more complex topography and greater snowfall, whereas community transitions were more gradual on the gentler eastern slopes, which have a drier environment ([Douglas and Bliss, 1977](#)). The dominant species in the vegetation types differed in eastern versus western alpine ecosystems. The western North Cascades showed greater affinity to other west coast ranges but the eastern North Cascades were more closely related to the Rocky Mountains and southern Yukon and Alaska.

[Bliss \(1963\)](#) described vegetation-environmental relationships in the Presidential Range of the Northern Appalachians, in which plant community types were associated with two rather than one mesotopographic gradient. A snow accumulation/wind gradient ranged from a *Diapensia*-dominated community on ridgetops with little snow cover, to well-drained heath-rush, early-melting heath, and late-melting snowbed in deep depressions. Bog and streamside communities occurred at protected lower elevation sites. The second gradient in atmospheric moisture ranged from fog-adapted sedge meadow on high elevation north and west facing slopes, to sedge-heath, sedge-rush-heath, and heath-rush, culminating with heath, the least foggy community in the gradient.

The dominant sedge in the alpine zone was *Carex bigelowii* (Bigelow's sedge). *Juncus trifidus* (highland rush), *Sibbaldiopsis tridentata* (shrubby fivefingers, an evergreen forb), and *Minuartia groenlandica* (Greenland stitchwort, a cushion) were also abundant. As in the Cascades and other northwest locations, ericaceous dwarf shrubs, such as *Diapensia lapponica* (pincushion plant) and *Vaccinium vitis-idaea* (lingonberry), were important components of the flora in contrast to the southern Rocky Mountains where they are not represented, probably due to a drier environment.

Plant Species

Plant species richness decreases with increasing elevation on mountains, but because alpine plants are small and microtopographic heterogeneity provides a diverse mosaic of habitats, a small patch of ground may contain many alpine species. In fact, species richness is higher per unit area than in almost any other herbaceous vegetation type (Bowman, 2000). Abrupt changes in species composition may also occur across relatively short distances (< 10 m). Alpine plants are generally long-lived perennials that tolerate low temperatures and nutrient availability, have low growth rates and short stature, and reproduce primarily by vegetative means, although seedling recruitment occurs on disturbances (Walker et al., 2001). They can be categorized by type of growth form. Fig. 2 shows four of the most important growth forms in the temperate alpine zone of North America.

Alpine plants have adapted to the short growing season by preforming leaf and flower buds one or more years in advance, which allows plants to leaf out as soon as conditions permit in the spring. In some species, this growth occurs under snow before meltout. They invest less biomass in stems and more biomass in roots than lower elevation plants, resulting in a high root to shoot ratio. These adaptations are conservative strategies that enable survival in a harsh environment (Gasarch and Seastedt, 2015). However, they also constrain potential responses to changing conditions (Bowman, 2000).

Vertebrate Species

Few vertebrates are restricted solely to alpine habitats, but a number of species are visitors over varying periods of time. In a survey of vertebrates in the alpine zone of the Cascades and northern Rocky Mountains, species richness was lowest in alpine ecosystems (46 species), but the set of species occurring in the alpine zone had low overlap with those in other ecosystems, making a significant contribution to vertebrate diversity (Raphael et al., 2002). Vertebrates occurring in alpine ecosystems were also found to occupy greater elevation ranges and more plant community types than those in other ecosystems.

The white-tailed ptarmigan (*Lagopus leucurus*) is a year-round resident in the Colorado alpine zone, but some ptarmigan winter in the subalpine zone. Bird species other than ptarmigan that breed in the alpine zone of Colorado are the horned lark (*Eremophila alpestris*), the American pipit (*Anthus rubescens*), the white-crowned sparrow (*Zonotrichia leucophrys*), and the brown-capped rosy finch (*Leucosticte arctoa*) (Armstrong et al., 2001). In the Columbia River Basin, four bird species are listed as occurring solely in alpine habitat. They consist of the white-tailed ptarmigan, American pipit, black rosy finch (*Leucosticte arctoa*), and gray-crowned rosy finch (*Leucosticte tephrocotis*) (Raphael et al., 2002). A number of other bird species occupy alpine habitats seasonally or migrate through these areas. American robins (*Turdus migratorius*) and mountain bluebirds (*Sialia currucoides*) are common summer visitors to the alpine zone.

Small mammal species that are commonly found year-round in temperate North American alpine ecosystems include pikas, northern pocket gophers (*Thomomys talpoides*), marmots, and snowshoe hares (*Lepus americanus*), as well as species of weasels, squirrels, chipmunks, mice, voles, and shrews. Marmots survive the winter by hibernating, accumulating fat reserves during the growing season. Pikas and other small mammals such as pocket gophers and voles cache food for later consumption, but only pikas store enormous "haypiles" (~30 kg for a < 200 g animal).

American pikas are charismatic small mammals inhabiting the alpine zone where they occupy talus and boulder fields but also occur in lower elevation rocky habitats (Erb et al., 2011). They have widely been considered a sentinel species for the effects of climate change because of their low tolerance for warm temperatures and dependence on winter snow cover for survival in alpine habitats. Pikas are non-hibernators, collecting and caching food for the winter in haypiles that largely consist of forbs, especially *Geum rossii* in Colorado, whereas their summer diet consists mainly of graminoids. They may be affected by reductions in forb biomass and lack of snow cover in the winter, for example during drought years. Secondary compounds in *Geum* may act as preservatives of forage stored in haypiles (Dearing, 2001).

The northern pocket gopher is a small burrowing mammal with fur-lined cheek pouches that has been described as a "keystone species" because of its substantial effects on biogeochemical and geomorphic processes (Seastedt, 2001). Pocket gophers bring excavated soil to the surface to produce soil heaps or "gopher mounds", which bury existing plants (Sherrod et al., 2005). On Niwot Ridge and elsewhere, pocket gopher activity is highest in moist meadow communities, but also occurs in other communities such as those dominated by *Carex elynoides*. Higher species richness on mounds may contribute to maintaining biodiversity in the communities gophers inhabit. Abandoned gopher tunnel systems may degenerate into areas of miniature terracettes, a widespread kind of small terrace with riser and tread features (Nagy and Grabherr, 2009).

Large herbivores that are widespread in the temperate alpine zone include bighorn sheep (*Ovis canadensis*), elk (*Cervus canadensis*), and moose (*Alces alces*). Large carnivores, such as wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) have been extirpated from many locations in the continental United States, and with the exception of some national parks, these are now restricted to northern regions of the temperate zone.

All alpine ecosystems are grazed, whether by the native fauna or introduced animal species (Körner, 2003). Alpine plant species produce secondary compounds as a defense against herbivory, such as tannins, which had the highest values in *Geum rossii* on Niwot Ridge (Dearing, 2001). Some aspects of plant herbivory appear to promote the expansion of graminoids, such as a preference for forbs by some herbivores, and deposition of nutrients in urine and feces, both of which favor graminoids. However, other species such as elk prefer graminoids to forbs; these opposing preferences may balance each other.

Anthropogenic Impacts

Following European settlement, grazing and mining in temperate zone mountains caused large-scale disturbances whose effects on alpine ecosystems have been long lasting. Many thousands of domestic sheep were pastured on alpine vegetation during the late 1800s and early 1900s throughout the Rocky Mountains and Great Basin (Billings, 2000). During the past 50 or more years, live-stock grazing on public lands generally has been either closely regulated or phased out, but the impacts of previous grazing may continue to affect the abundance and species composition of the vegetation in alpine ecosystems (Nagy and Grabherr, 2009). On Niwot Ridge, willow shrubs (*Salix* species) were found to have expanded more than 400% over 62 years, primarily by clonal growth (Formica et al., 2014). In 1949, when the US Forest Service halted sheep grazing on the Ridge, rangers recorded the alpine vegetation as degraded with few willows. Experiments conducted in the alpine zone have shown that increased nitrogen and temperatures facilitate willow growth; both are anthropogenic impact factors (see below) that may lead to increased woody encroachment in alpine ecosystems.

Alpine ecosystems can take decades to recover from damage incurred by recreational use. The results of pedestrian trampling on alpine vegetation were examined over a 42-year period in Rocky Mountain National Park, Colorado (Willard et al., 2007). Trampling had occurred in an alpine dry meadow site for 26 years before sampling was initiated. The trajectory of recovery illustrates the difficulty of reestablishing vegetative cover once it has been degraded, especially for dry meadow dominated by *Kobresia myosuroides*, which can only recolonize by vegetative growth from the remaining individuals. Although plants colonized and spread during some periods of time, two decades after the start of sampling recovery was severely set back due to unchecked soil erosion and several years of heavy snow accumulation. It is now thought that at least a century will be required for this vegetation to fully recover.

In recent years, ski area development has dramatically increased in the United States and elsewhere. The expansion and maintenance of ski resorts and ski runs impacts high elevation habitats, which are vulnerable to erosion and recover slowly after disturbances to the vegetation (Martin, 2015). Climate warming is likely to lead to upward shifts in the elevations that have snow suitable for skiing, increasing the use of alpine environments.

Global Change Effects

Nitrogen Deposition

Human activities such as burning fossil fuels and the use of inorganic nitrogen as a fertilizer generate emissions of atmospheric nitrogen that have important impacts on the biosphere.

Nitrogen deposition from anthropogenic sources doubled in the United States between 1961 and 1997 (Bobbink et al., 2010). Atmospheric nitrogen deposited in the alpine zone is an important factor in both the northeast and western regions of the temperate zone. On Niwot Ridge, the deposition rate has been measured at 6 kg N ha^{-1} . This rate is higher than the critical load estimated to affect sensitive plant species (4 kg N ha^{-1}) but lower than the critical load that indicates alpine community response (10 kg N ha^{-1}) (Bowman et al., 2015).

An increase in the supply of nitrogen affects plant production as well as plant and microbial species composition. In the alpine zone of Colorado, the community that is most susceptible to the influence of increased nitrogen is moist meadow, because it is dominated by both a nitrogen-limited species, *Deschampsia cespitosa*, and a nitrogen-insensitive species, *Geum rossii*. The addition of nitrogen to the system results in competitive displacement of *Geum* by *Deschampsia*. A positive feedback to nitrogen inputs can develop that increases nitrogen export from the community, due to net nitrogen mineralization rates that are up to 10 times higher in soils occupied by *Deschampsia* than *Geum*. This disparity produces microscale heterogeneity in nutrient distributions. However, increased nitrogen deposition could overwhelm this heterogeneity, resulting in changes to plant communities such as a decline in *Kobresia* abundance in dry meadows and an increase in *Deschampsia* in moist and wet meadows (Bowman et al., 2015).

Climate Change

Climate change is affecting alpine communities throughout the world; this may arguably be the greatest threat to their biodiversity (Erb et al., 2011). Warming temperatures would be expected to potentially have profound effects in a cold-limited environment. In the alpine zone at Niwot Ridge, minimum temperatures have been increasing since the 1950s (McGuire et al., 2012). The potential consequences of precipitation changes are great for alpine ecosystems due to the importance of snow as a primary driver of ecosystem response. In addition, meltwater from mountain snowpacks in the western United States is critical for maintaining downstream water supplies for human use. At Niwot Ridge, precipitation substantially increased from the 1950s to 2010 in the alpine zone, occurring primarily in winter and early spring (Kittel et al., 2015). In contrast to the results for Niwot Ridge, significant

declining trends in snowpack were found at many monitoring sites in the western United States. Declines extended across all months, states, and climates, but were largest in spring, in the Pacific states, and in locations with a mild winter climate (Mote et al., 2018).

The physiological adaptations of alpine species to cold environments, as well as their geographic constraints, may leave them especially vulnerable to climate warming (Erb et al., 2011). The American pika has disappeared from locations that were previously inhabited. This loss has been attributed to climate warming. However, a recent comprehensive survey of pika habitat in the Great Basin found pikas living in habitats they were not previously known to occupy, including warmer, drier sites as well as wetter, colder sites (Millar et al., 2018), leading to the conclusion that they can tolerate a wider range of conditions than previously thought, and suggesting that other factors in addition to climate may control pika distributions.

Conservation

Many alpine areas in temperate North America have at least some degree of protection from development. Fig. 3 shows overlap of the temperate North American alpine zone with extents of parks, other protected areas and National Forests, as an indication of the extent of protected areas, since National Forest lands include wilderness areas, but also lands that are managed for multiple use where conservation may not be assured. Due to the iconic status of scenic mountain peaks, alpine ecosystems are often well represented in parks and wilderness areas compared with lowland ecosystems. However, the popularity of many areas leads to heavy recreational use, as described above, especially in mountains easily accessible from major metropolitan areas.

Malanson et al. (2009) proposed actions that could be taken to mitigate the effects of climate change on alpine vegetation with the goal of preserving biodiversity. Direct actions include reducing non-climate stressors such as controlling the spread of invasive species, since climate itself cannot be controlled, and realigning the boundaries of reserves to encompass areas where species might be expected to be able to persist under climate change.

Conclusions

The plant, animal, and microbial species in alpine ecosystems of the North American temperate zone that are present today are those that have passed through a strong filtering process imposed by the severe environment, including cold temperatures, wind, snow cover, and short growing seasons. Biodiversity is enhanced by spatial heterogeneity in the form of repeatable landscape elements that provide a variety of habitats at meso- and microtopographic scales. However, anthropogenic impacts to alpine environments are testing the resilience of these valued ecosystems. Loss of biodiversity is a potential outcome as ecosystem properties and sensitive species distributions shift in response to climate change, nitrogen deposition, and human use.

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Alpine Plant Diversity in Temperate Mountains of South America

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Abstract

The temperate Andes are climatically, topographically and floristically very diverse. The dry temperate Andes (30°–37°S) reach elevations > 5000 m and are arid or semiarid. The wet temperate Andes (37°–55°S) rarely reach 3000 m elevation and receive higher annual precipitation. Although alpine vegetation of the temperate Andes is generally found in areas with growing season temperatures below 9°C, the effect of latitude and the north-to-south and east-to-west precipitation gradients result in differences in species composition and treeline elevation. Alpine areas of the dry temperate Andes are generally found above 3000 m and are bounded by xeric woods, matorral, and steppe. In contrast, the alpine areas of the wet temperate Andes are surrounded by *Nothofagus* forest or *krummholz*, and in this region, the treeline descends with latitude from ca. 2000 m in the north to ca. 500 m in the south. At the local scale, abiotic factors such as precipitation, elevation, aspect, and related temperature differences are the major determinants of floristic variation and species richness in alpine regions of the temperate Andes. On a larger scale, at different latitudes with different precipitation, species richness increases in the southernmost wettest sites. In all sites, the number of species is higher at intermediate elevations, with decreasing species richness toward the extremes. The higher levels of plant diversity at middle elevations are related principally to the effects of positive plant-plant interactions. Therefore, patterns of diversity in the high temperate Andes can be attributed to abiotic (mostly climatic) variables, but also to biotic interactions, for instance, owed to nursing cushion plants. Biotic interactions can play an important role as evolutionary drivers of alpine plant diversity, challenging the assumption that only large-scale abiotic phenomena such as climate, geomorphology and historical processes regulate alpine plant diversity.

Introduction

Mountains provide opportunities for adaptive evolution by increasing spatial heterogeneity of the landscape and thus generating a wide variety of environments. They also produce complex climatic gradients, promoting speciation through phenotypic divergence. In addition, they affect the migration of organisms and the distribution of species since mountain ranges can act as both biological corridors and ecological barriers (Antonelli et al., 2018; Luebert and Weigend, 2014). As a result, mountains host a large proportion of the biological diversity on earth (Barthlott et al., 2007; Antonelli et al., 2018).

The Andes are the longest mountain chain in the world. From approximately 11°N to 55°S, they traverse > 7000 km, crossing the Equator, the tropic of Capricorn, and reaching the southernmost tip of South America. Their great north-south extension coincides with remarkable variations in climate, from wet to hyperarid and from tropical to temperate. However, the higher elevations of many of its cordilleras, with numerous mountains reaching > 5000 m, result in the presence of a long strip of more-or-less continuous, open, cold terrain along the west of South America, above the lower forests or shrublands. This high Andean terrain has served as both a bridge and a barrier in the evolutionary history of many plant lineages from the New World, and currently contains a unique, rich and diverse flora (Luebert and Weigend, 2014).

The beauty and distinctive characteristics of the alpine flora of the Andes has attracted botanists since the early 19th century. The botanical expedition of Humboldt and Bonpland to Central and South America, that included the ascent to Volcán Chimborazo in Ecuador, resulted in the first descriptions of high-elevation plant communities of the tropical Andes in their *Tableau Physique des Andes et Pays Voisines* (Humboldt and Bonpland, 1805). Some decades later, Weddell (1857) published *Chloris andina: essai d'une flore de la région alpine des Cordillères de l'Amérique du Sud*, in two volumes of rigorous descriptions and beautiful illustrations of plants of Andean high elevations, thus initiating the study of alpine plant diversity of the Andes, both tropical and temperate.

In recent times, a renewed interest in the origin, characteristics and determinants of floral diversity of the Andes has produced several studies on alpine plant diversity of the mountains of South America. Although the tropical Andes are well known for high levels of diversity and endemism of their mountain floras, the alpine flora of the temperate Andes has been less well-studied. Even though the levels of richness and endemism of the temperate alpine Andes are probably less than those of the tropical Andes (e.g., Barthlott et al., 2007), the unique traits and probable antiquity of the flora of the former makes them especially important (Luebert and Weigend, 2014). Here we describe the characteristics of the high elevation flora of the temperate Andes and the main patterns and determinants of alpine plant diversity in this region.

Physical Setting

The Andes are divided into Northern, Central and Southern sectors that are biogeographically differentiated (Luebert and Weigend, 2014). The alpine areas of these sectors mostly comprise the high elevation Páramo (in Colombia, Ecuador and northern Peru), the elevated Puna altiplano (in southern Peru, northern Chile, southwestern Bolivia and northwestern Argentina), and the extra-tropical high-Andean portion corresponding to temperate latitudes (in central and southern Chile and Argentina), respectively (Cabrera and Willink, 1980; Olson et al., 2001). In this article, the temperate Andes are defined as the portion extending south of the Puna to the tip of South America, i.e., approximately from 30°S to 55°S. This extratropical southern portion of the Andes is also delimited to the north by a climatic and biogeographic barrier, the hyperarid Atacama Desert, which occupies an area from 18°S to 30°S in western South America (Arroyo et al., 1988; Squeo et al., 1994; Luebert and Weigend, 2014).

This southern area of the Andes is climatically, topographically and floristically very diverse (Fig. 1). Because of the climate, the temperate Andes can be divided into a northern, drier area from 30°S to approx. 37°S, in latitudes that mostly have a semiarid, temperate Mediterranean climate (the dry temperate Andes sensu Lliboutry, 1998), and a southern, more humid region from approx. 37°S to 55°S, in latitudes of mostly humid temperate oceanic climate (the wet temperate Andes sensu Lliboutry, 1998). These two areas also have different topography (Fig. 1A). The dry temperate Andes (DTA) are higher and less dissected by glacial features. They include the highest mountains of South America, such as Mount Aconcagua (6960 m) and Mount Tupungato (6800 m). The wet temperate Andes (WTA) are lower and are more dissected by glacially-carved landscapes at these higher latitudes. From the Great Patagonian Glaciation (GPG, ca. 1 Ma BP) to the last glacial maximum (LGM, ca. 25 ka BP), the WTA were repeatedly covered by continuous ice sheets from 37°S to 56°S (Rabassa et al., 2011). Currently, they are traversed by many lakes of glacial origin, and contain three important ice fields (Patagonian North, Patagonian South, and Cordillera Darwin; Lliboutry, 1998). Their mountains generally do not surpass 2500 m, with only a few peaks attaining ca. 4000 m, such as Mount Valentín (3910 m), Volcán

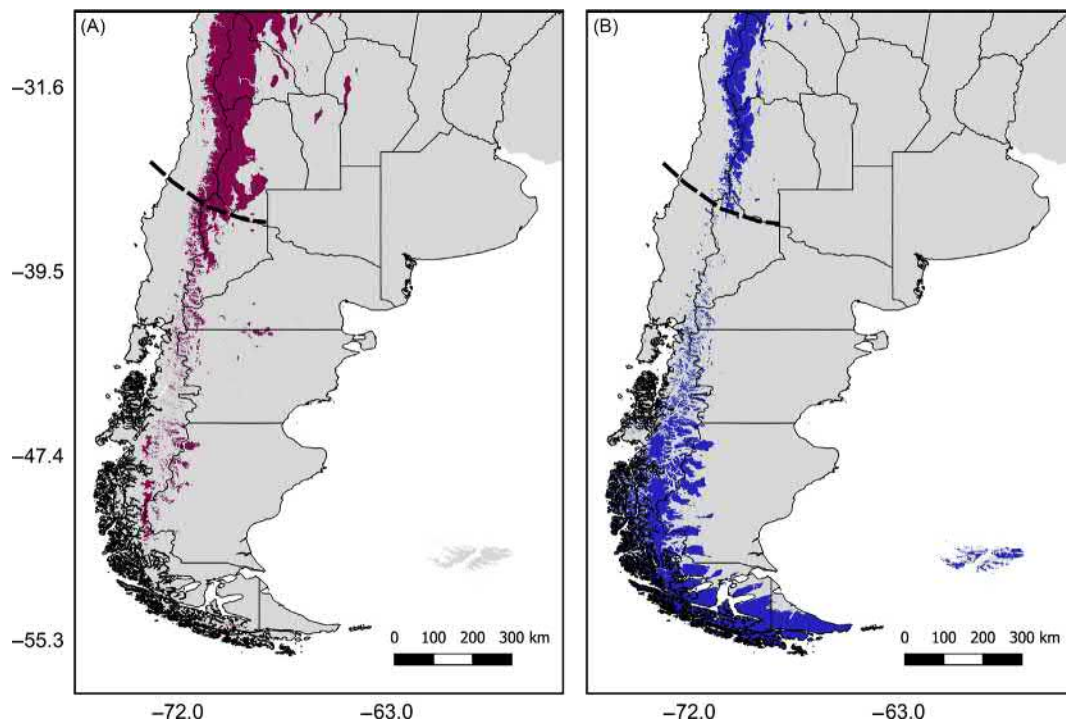


Fig. 1 Alpine areas of the temperate Andes. Map of southern South America indicating the regions (A) that exceed 2000 m asl, (B) that present a mean temperature during the growing season of $< 9.5^{\circ}\text{C}$. The dashed line separates the DTA (dry temperate Andes) in the north from the WTA (wet temperate Andes) in the south.

Lanín (3776 m) and Mount San Lorenzo (3706 m). Even though the mountains of the WTA are generally lower in altitude than those of the DTA, their higher latitude fosters open, treeless alpine environments on mountaintops.

The DTA, found from San Juan to northern Neuquén provinces of Argentina and from the regions of Coquimbo to Maule in Chile, are formed by several parallel ranges. From west to east, these include the Cordillera Principal, the Cordillera Frontal, and the Precordillera (Taylor, 1991). The WTA, from northern Neuquén in Argentina and bordering areas of Chile to Tierra del Fuego, consist mostly of the Patagonian Andes (Taylor, 1991). Some mountains higher than 2000 m are also found on the Patagonian sierras and mesetas to the east (Fig. 1A), but these and other elevated ranges of temperate southern South America, such as the Cordillera de la Costa in western Chile and the Sierras Pampeanas in central Argentina, are not included in this chapter. In general, these highlands do not attain >2000 m in elevation, and do not have a conspicuous alpine flora (e.g., Martínez et al., 2017).

Climatic Variation

The climate of the dry temperate Andes is arid or semiarid. The elevated part of this region corresponds with the Southern Andean Steppe Ecoregion (Olson et al., 2001; Ezcurra, 2001). Snowstorms, hailstorms and frosts are frequent year-round in these high montane regions. Precipitation in the central and southern regions falls mostly in winter, driven by winds from the Pacific, whereas in the northeast part of the DTA the precipitation pattern is affected by winds from the Atlantic and tends to fall in summer. Mean annual precipitation varies from north to south, from approximately 200 to 800 mm, and increases with elevation. For example, mean annual precipitation and mean annual temperature in Puente del Inca at 2720 m in Mendoza (in the central part of the region) is 342 mm and 7.4°C respectively (Cabrera, 1976). Precipitation levels tend to decrease from west to east, especially in the center and south of the dry temperate Andes.

Further south, the climate of the wet temperate Andes is generally wetter. The region corresponds with the Maule, Valdivian and Magellanic subpolar forest ecoregions (Olson et al., 2001). Strong, humid winds blow from the Pacific year-round, especially in winter and spring, resulting in high levels of rainfall. The highest precipitation levels are found between about 40°S and 44°S, and decrease toward the South. For instance, the average annual precipitation is >3000 mm in Peulla at the latitude of Mount Tronador (approx. 41°S), while it is <1000 mm in the mountains near Ushuaia (approx. 55°S). In addition, the southern Andes intercept the humid westerlies that blow from the Pacific Ocean, producing a rain-shadow effect that results in a steep west-east precipitation gradient. Therefore, annual precipitation levels in alpine areas also vary from west to east, e.g., from >3000 mm to the west of Mount Tronador (71°53'W), to approx. 1000 mm near Mount Meta (71°24'W), i.e., within <50 km distance (Ferreira et al., 1998a). At this latitude, temperatures at 1955 m in Mount Catedral vary from a mean of 8°C in the summer months to a mean of -2.8°C in the winter months (Wardle et al., 2001). In the wet temperate Andes, temperature decreases with elevation but also with latitude in a complex way, with a lapse rate of approximately 0.6°C/100 m altitude and 0.8°C/degree of latitude, as seen in other mountains (Wardle et al., 2001).

Due to climatic distinctions and the difference in composition of the alpine floras of the DTA and the WTA, they have been classified as belonging to two different phytogeographic districts of the high-Andean biogeographic Province (*Provincia Altoandina*: Cabrera, 1976, Cabrera and Willink, 1980). The *Cuyano* district (in reference to the region of Cuyo, which comprises the provinces of Mendoza, San Juan and San Luis of central Argentina) corresponds with the DTA, and the *Austral* district with the WTA (Cabrera, 1976). In recent biogeographical regionalization of the Andean Region, the former is included as Cuyan High Andean province (Morrone and Ezcurra, 2016), but the latter is not differentiated from the southern biogeographic provinces of the Maule, Valdivian and Magellanic forests. This is probably due to the smaller area occupied by alpine vegetation in the WTA, forming isolated islands restricted to mountaintops surrounded by forest.

Limits of the Alpine Vegetation in the Temperate Andes

Alpine vegetation is mostly defined as that found above treeline on mountains, so in arid areas devoid of forests it is difficult to establish the limits between alpine and subalpine vegetation. In these cases, alpine vegetation is characterized by plant communities without large woody plants (i.e., <3 m, Körner, 1998) that generally coincide with areas with average temperature of the growing season lower than 6.5°C (Körner, 1998; Mark et al., 2001; Körner and Paulsen, 2004). In the Southern Hemisphere, treelines of broad-leaved species such as *Nothofagus* (Nothofagaceae) or *Kageneckia* (Rosaceae), have been found at lower elevations than conifers in the Northern Hemisphere (Wardle et al., 2001; Piper et al., 2006). This has generally been attributed to the idiosyncratic characteristics of these genera, which apparently have different thermal requirements than Northern Hemisphere treeline genera such as *Pinus* (Mark et al., 2001; Körner and Paulsen, 2004; Piper et al., 2006). In New Zealand (Wardle, 1965) and South America (Ezcurra & Gavini pers. obs.), specimens of the exotic *Pinus contorta* from North America can spread to elevations that are higher than the natural *Nothofagus* treelines. Therefore, alpine areas of the temperate Andes can be considered to generally correspond with high altitude areas that have growing season temperatures below ca. 9.5°C (Körner and Paulsen, 2004, Gavini, unpublished, but see Mark et al., 2001 for the latitude of Tierra del Fuego). The area between this line and that of permanent snow is the region considered here as the alpine (Fig. 1B).

Vegetation of the Dry Temperate Andes

The high-Andean vegetation on the Chilean side of the dry temperate Andes is generally found above the mesic forest remnants of *Nothofagus macrocarpa*, *N. pumilio* (Nothofagaceae) and/or *Austrocedrus chilensis* (Cupressaceae), or above more xeric Mediterranean matorral with small trees of *Kageneckia angustifolia*. There is an altitudinal zonation with a lower belt dominated by large shrubs, an intermediate belt represented by small shrubs, tussock grasses and cushion plants, and a high, subnival, desert belt with small forbs, rosettes and small-sized grasses. These belts have been given different names, mostly Sub-Andean, Lower Andean and High Andean, or *Piso Subandino*, *Piso Andino Inferior*, and *Piso Andino Superior* (e.g., Squeo et al., 1994; Muñoz-Schick et al., 2000). At the latitude of Santiago, Chile, shrubs such as *Chusquea oppositifolia* and *Nassauvia axillaris* are representative of the lower belt (approx. 2000–2700 m), cushion plants such as *Azorella madreporica* and *Laretia acaulis* characterize the intermediate belt (approx. 2700–3300 m), and *Nassauvia lagascae*, *Oxalis erythrorhiza*, *Nassauvia pinnigera* and *Moschopsis leyboldii* occur in the high Andean desert (approx. 3300–3900 m). There are also areas with tussock grasses of the genus *Pappostipa* termed “coironales,” generally growing in places with less pronounced slopes (Muñoz-Schick et al., 2000). In humid or wet sites, species-rich bog communities termed “*vegas*” develop, dominated by Juncaceae, Cyperaceae and grasses. These latter areas can become overgrazed by domestic livestock, especially goats that are taken to these sites in summer (Chiapella and Ezcurra, 1999).

At different latitudes on the Argentinian side, the high Andean plant communities of the DTA grow above the Monte desert vegetation dominated by *Larrea* species (e.g., Méndez, 2004) or above the Patagonian steppe (Chiapella and Ezcurra, 1999). These communities vary in relation to elevation, humidity, continentality, slope angle, slope aspect and soil type. This is the reason why vegetation belts cannot be clearly delimited here (e.g., Chiapella and Ezcurra, 1999; Méndez, 2004; Méndez et al., 2006). However, the pattern is somewhat similar to that of the Chilean side, with three vegetation belts that are given different names, generally a lower belt of tussock grasses, mostly of *Pappostipa*, together with large shrubs of *Adesmia*, *Mulinum*, *Nassauvia* and *Chusquea* at lower elevations (approx. 1900–2700 m). This belt has sometimes been described as “*región de la leña amarilla*” due to the yellow color of the branches of *Adesmia pinifolia*, a conspicuous large shrub that sometimes grows taller than 2 m in the area. At intermediate elevations (approx. 2700–3300 m), small shrubs and cushion plants dominate, e.g., *Oxalis*, *Junellia*, *Adesmia*, *Laretia* and *Azorella*. This belt has been described as “*región de la llareta*,” the common name given to dense woody cushion plants in the area. On the highest belt (approx. 3300–4500 m), especially adapted perennial forbs of genera such as *Senecio*, *Nassauvia*, *Chaetanthera*, *Draba*, *Barneoudia*, *Leucheria*, and *Moschopsis* withstand the extreme insolation, wind and cold found on the denuded, rocky terrain or on unstable scree slopes. In areas with wet soils and near streams, Cyperaceae and Juncaceae dominate, with some genera forming dense and hard cushions such as *Oxychloe* and *Patosia*, together with beautiful large-flowered forbs such as *Mimulus*, *Euphrasia* and *Senecio* species. In these wet environments, bryophytes are also frequent (e.g., Méndez et al., 2006).

Vegetation of the Wet Temperate Andes

The WTA are characterized by the presence of *Nothofagus*-dominated forests on their slopes. These forests, composed of *N. pumilio* at tree-line (or *N. antarctica* in tree-lines of the most arid and extreme situations) reach approximately 2200 m elevation in northern Neuquén and Bío Bío (37°S), but only attain 500–600 m elevation in Tierra del Fuego (approx. 55°S), as latitude increases (Mark et al., 2001; Wardle et al., 2001). Near treeline, these tree species form prostrate *krummholz*. Above these forests, alpine vegetation appears on mountaintops in the archipelago of open terrain.

Altitudinal zonation is not clear in the WTA. The lower alpine belt is generally characterized by a relatively high cover of small shrubs such as *Gaultheria pumila*, *Empetrum rubrum* and *Baccharis magellanica* (Roig, 1998; Ferreyra et al., 1998a; Mark et al., 2001). The strong precipitation gradient from west to east results in important differences in humidity and duration of snow-cover in different mountains that result in marked differences in plant composition and species richness (Ferreyra et al., 1998a,b). Studies on mountains along precipitation gradients at different latitudes of the WTA have shown an increase of richness from west to east and from higher to lower latitudes (Arroyo et al., 1989; Ferreyra et al., 1998a; López-Angulo et al., 2018). In addition, on a given mountain, the altitude, wind exposure, slope, and aspect contribute to determine different levels of species richness, vegetation-cover and life-form spectra. The temperature gradient determined by altitude, and the humidity gradient determined by solar radiation and wind exposure that relate to slope aspect produce marked differences in community composition and richness on mountains (Ferreyra et al., 1998a; Mark et al., 2001).

At the latitude of Nahuel Huapi National Park, Argentina, in the northern WTA, a rich alpine flora has been recorded, with > 230 species (Ferreyra et al., 1998b). The western sector with higher precipitation harbors fewer alpine species (~149) than the drier eastern sector (~220). Lower species richness in mountains with higher precipitation has also been observed in the southern WTA. In Sierra de los Baguales, Chile, 349 species were recorded for alpine and subalpine vegetation, varying from 252 species of plants on Mount Santa Lucía in the east to just 53 species on Mount Daudet in the west (Arroyo et al., 1989). These differences have been attributed to a shorter growing season in the west, due to a longer duration of the snow-cover and the higher levels of precipitation, and also to historical effects that persist from the last glaciation (Arroyo et al., 1989; Ferreyra et al., 1998b).

Plant communities along the margins of streams and in wet meadows (termed *mallines* in this area) are dominated by Cyperaceae and Juncaceae (e.g., *Carex*, *Oreobolus*, *Marsippospermum*), mixed with bryophytes and forbs with showy flowers of genera such

as *Calandrinia*, *Caltha*, *Senecio* or *Primula*. Some dwarf shrubs such as *Azorella lycopodioides* form dense cushions on these wet soils. The diversity of the alpine plant communities of these wet places, together with that of drier sites, contributes to the overall high species richness of the alpine areas of the eastern mountains of the wet temperate Andes.

Diversity of Life Forms

Plants of the high montane regions of the temperate Andes have considerable adaptations to the particularly diverse, harsh environments. During the winter the plants remain covered by snow for many months, and during the summer they can withstand extreme cold, heat, wind, and desiccation within a single day. The main life forms of alpine plants of the temperate Andes are perennial forbs (Fig. 2), tussock grasses, cushions and shrubs (Fig. 3). Annual herbs are very rare, and only appear in the lower sub-Andean belt of the DTA (Squeo et al., 1994). At higher elevations, many plants grow close to the ground and form flat cushions or dense mats that withstand the wind and cold temperatures (e.g., *Oreopolus glacialis*, *Oxalis erythrorhiza*, *Azorella monantha*). Perennial forbs can form rosettes that can be wide and flat (e.g., *Pachylaena atriplicifolia*, *Gamocarpha scapigera*, *G. ventosa*) or more or less cylindrical and vertical (e.g., *Nassauvia revoluta*, *Chaetanthera spathulifolia*, *Viola columnaris*), and frequently have deep rhizomes or taproots and fleshy leaves (Fig. 2). These latter plants sometimes mimic the shape of stones, probably as an anti-herbivory defense, but are very conspicuous in flower. The rigid, cylindrical growth-form is probably an adaptation to the deposition of sand and ash from frequent volcanic eruptions throughout the Cenozoic. Rocks, as well as tussock grasses and cushion plants (Fig. 3), protect softer and smaller forbs from the cold and the wind, and in some cases rich associations of different species are formed (Cavieres et al., 1998; Nuñez et al., 1999). Forbs such as *Chaetanthera spheroidalis* (Asteraceae) and *Moschopsis leyboldii* (Calyceae) in the DTA, or *Senecio portalesianus* (Asteraceae) and *Nassauvia lagascae* in the WTA, reach the highest elevations (Squeo et al., 1994; Chiappella and Ezcurra, 1999; Ferreyra et al., 1998b; Mark et al., 2001).

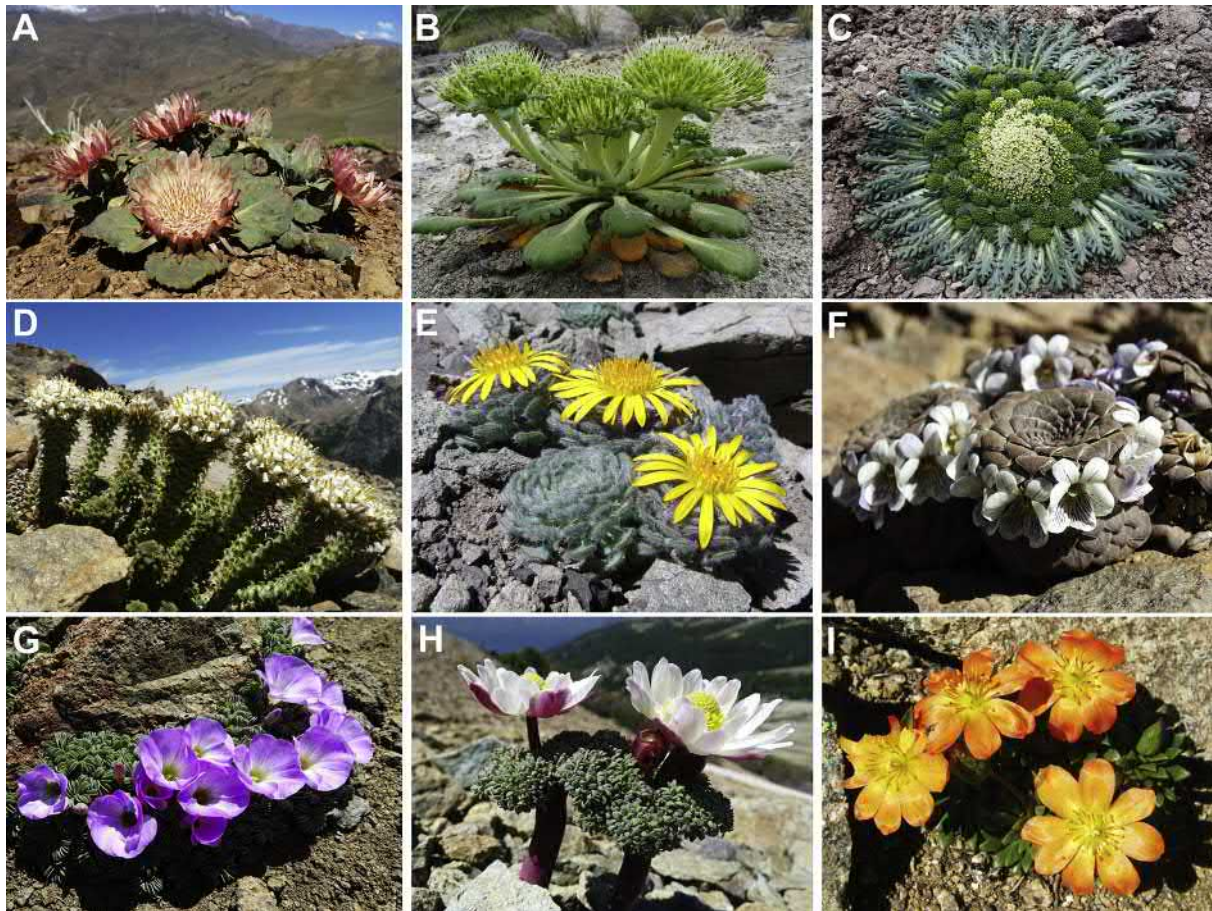


Fig. 2 Types of perennial forbs of the temperate Andes. Flat rosettes (A) *Pachylaena atriplicifolia*, (B) *Gamocarpha scapigera*, (C) *Gamocarpha ventosa*; cylindrical rosettes, (D) *Nassauvia revoluta*, (E) *Chaetanthera spathulifolia*, (F) *Viola* aff. *Columnaris*; other forbs (G) *Oxalis adenophylla*, (H) *Callianthemoides semiverticillatus*, (I) *Calandrinia caespitosa*. Photographs by Marcela Ferreyra, used with permission.

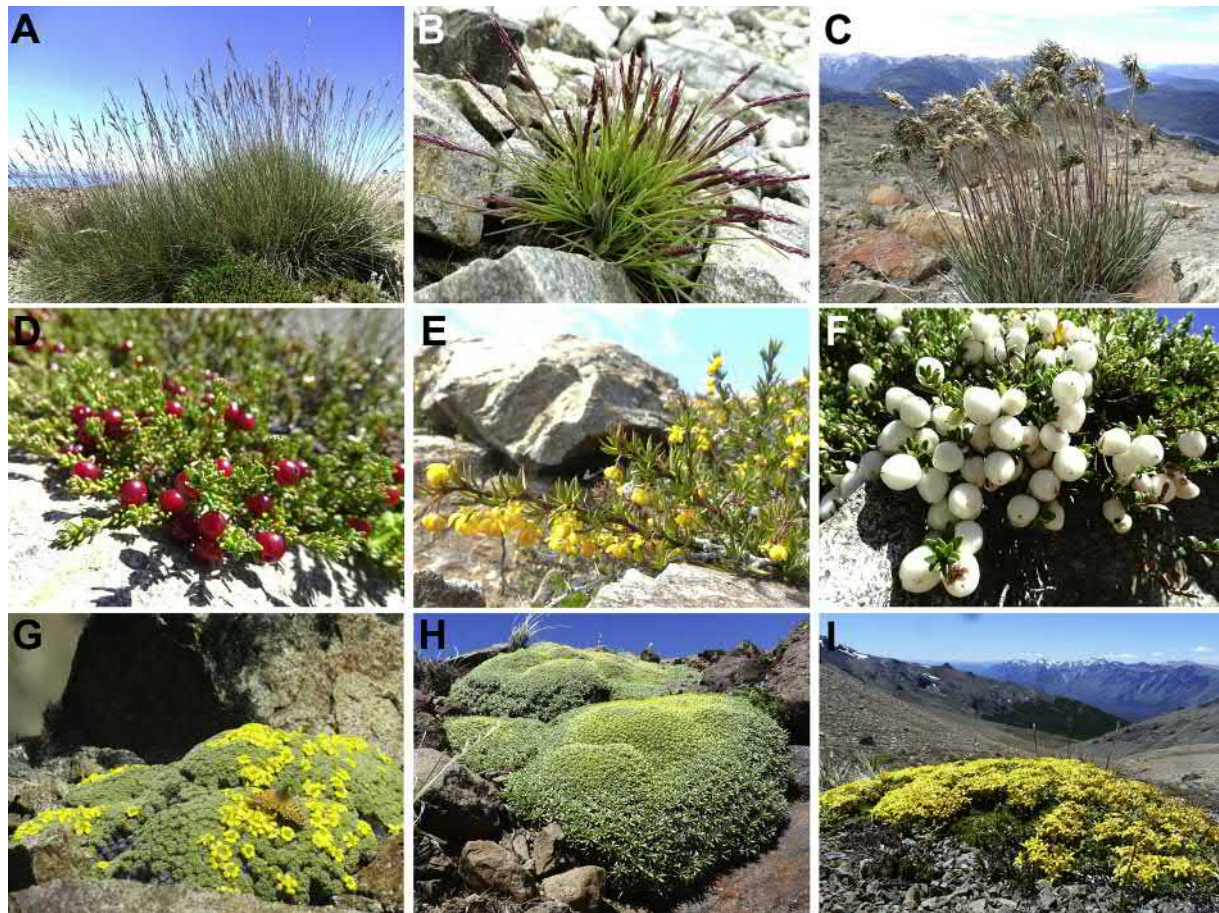


Fig. 3 Additional plant life-forms of alpine regions of the temperate Andes. Grasses (A) *Festuca pallescens*, (B) *Deyeuxia erythrostachya*, (C) *Poa obvallata*; shrubs (D) *Empetrum rubrum*, (E) *Berberis empetrifolia*, (F) *Gaultheria pumila*; cushions (G) *Oxalis erythrorhiza*, (H) *Azorella monantha*, (I) *Oreopolus glacialis*. Photographs by Marcela Ferreyra and Sabrina Gavini, used with permission.

Abiotic Determinants of Alpine Plant Diversity of the Temperate Andes

Climate is an important determinant of large-scale biodiversity patterns. Mean annual temperature and precipitation have been shown to be the two most important predictors of species richness in mountains at global and regional scales (Antonelli et al., 2018). Both low temperatures and aridity can be limiting factors in mountain environments. In the DTA, species richness increases toward the south with the increasing winter precipitation (Arroyo et al., 1988; Squeo et al., 1994). On the other hand, richness and plant cover have been observed to more-or-less peak at middle alpine elevations, where conditions are intermediately dry and cold, especially in the north of this region that receives summer precipitation (Arroyo et al., 1988).

In the WTA, steep climatic gradients are generated over short distances. The strong precipitation gradient determined by the rain-shadow effect of the Southern Andes on the westerlies, together with the temperature gradients produced by elevation and slope aspect, result in a mosaic of environments, i.e., relatively wet and warm, wet and cold, dry and warm, and dry and cold. These can be observed in different parts of a mountain, and among different mountains at the same latitude. For example, on three mountains along a west-east transect at 41°S in Nahuel Huapi National Park, Argentina, in the north of the WTA (Mounts Tronador, Lopez, and Meta), annual precipitation varies from ca. 3000 mm in the west to <1000 mm in the east. The relationship between environmental and floristic variation was analyzed in the alpine areas of these mountains using ordination methods (Ferreyra et al., 1998a). In order of importance, longitude, elevation and aspect were the major determinants of floristic variation, resulting in two main vegetation gradients. The first gradient is related to moisture availability, primarily determined by precipitation (related to longitude) and secondarily to variation in wind exposure (west vs. east aspect). The second gradient is related to variation in temperature, primarily determined by elevation, and secondarily by differences in insolation (north vs. south aspect). The great climatic heterogeneity found in this alpine area correlates with an exceptionally high species richness. Average richness within 10 × 10 m plots varied from 9 to 21 species, with higher richness in the relatively drier plant communities with less snow and a longer growing season (Ferreyra et al., 1998a). In 20 surveyed mountains of Nahuel Huapi National Park, a total of 232 alpine species, representing 111 genera and 48 families of vascular plants, have been identified (Ferreyra et al., 1998b). The region of Nahuel Huapi corresponds

to latitudes with the highest precipitation levels of the whole temperate Andes, and the steep precipitation gradient within the National Park results in exceptional regional environmental variation and related plant diversity.

A study of alpine vegetation in higher latitudes, i.e., in the southernmost WTA in the Martial Mountains near the city of Ushuaia (approx. 55°S) found only 80 species (Mark et al., 2001), i.e., a much smaller number. In this area, high-Andean vegetation occurs above *Nothofagus pumilio* forests and *N. antarctica* krummholz with the treeline at ca. 600 m and mean annual precipitation about 600 mm. Here also, major determinants of floristic variation were elevation, aspect, and related temperature (Mark et al., 2001). Species richness decreased significantly with elevation, and was generally higher on the warmer north aspects. Of all the alpine life forms, chamaephytes, i.e., dwarf shrubs, especially the cushion form, were shown to increase in importance with elevation, except at the highest elevations (Mark et al., 2001). A recent large-scale study of plant richness variation at different latitudes in the temperate Andes has provided important insights into the determinants of high mountain plant diversity in this region (López-Angulo et al., 2018). Alpine plant communities were surveyed at three sites, at two latitudes of the DTA with Mediterranean climate and a more- or- less marked summer drought (at 33°S and 35°S), and at a higher latitude in the WTA where drought is negligible, and temperatures are lower (at 51°S). The first two sites of the DTA have treelines of *Kageneckia angustifolia* at 2200 m, and of *Nothofagus antarctica* and *Austrocedrus chilensis* at 1700 m, respectively, with annual precipitation of about 900 mm. The southernmost site has a treeline of *Nothofagus pumilio* at 500 m and annual precipitation of 900–1000 mm. At each site, environmental (standardized elevation, slope, and aspect) and soil characteristics, species richness and cover, and plant-plant interactions were determined at different scales (20 × 20 m plots, 2.4 × 2.4 m quadrats, and 30 × 30 cm cells).

This study showed that species richness ranged from 12 to 50 species per plot, with a mean of 25 species, and was highest in the southernmost, wetter site, whereas beta-diversity among plots (i.e., differences between sites in species assemblages) was lowest there. In all sites, the number of species was higher toward intermediate elevations above treeline, with decreased richness toward the lower and upper alpine limits, while beta-diversity was found to decrease monotonically with elevation. The decrease in richness in the DTA in relation to the WTA, contrary to the well-documented latitudinal decline in species richness toward the poles, was attributed to the intense summer drought found in the DTA that does not exist in the WTA (López-Angulo et al., 2018). The unimodal increase in richness with alpine elevation in all three latitudes of the temperate Andes, i.e., higher values at middle elevations above treeline (Fig. 4), was related principally to the effect and prevalence of positive plant-plant interactions at intermediate elevations (López-Angulo et al., 2018). Therefore, patterns of diversity in the temperate Andes can be attributed to large-scale abiotic (climatic) variables, as well as to smaller-scale biotic interactions.

Biotic Determinants of Alpine Plant Diversity of the Temperate Andes

Biotic interactions, more commonly known as the role of cooccurring species, can also be important drivers of biodiversity. Competition, predator–prey and symbiotic relationships are all classic examples of different types of interactions between living organisms. Particularly, biotic interactions are the effects that one organism have on another, whether these effects are negative or positive. However, the outcome and the magnitude of those effects are known to strongly depend on the environmental conditions (Callaway et al., 2002). This environment-dependence of biotic interactions has been formalized as the “Stress Gradient Hypothesis” (Bertness and Callaway, 1994). This hypothesis postulates that under more benign conditions, negative interactions (i.e., competition) prevail, whereas under high environmental stress and disturbance conditions, positive interactions become more frequent

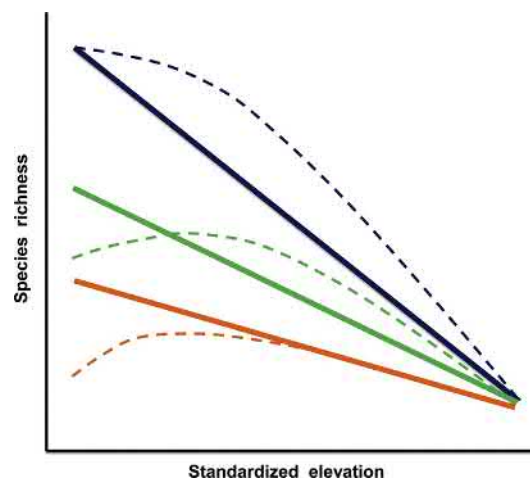


Fig. 4 Relationship between species richness and elevation across different latitudes of the temperate Andes. Species richness along an altitudinal gradient in the wet temperate Andes (blue) and in two latitudes of the dry temperate Andes: with shorter dry season (green) and longer dry season (orange). Solid lines when the main environmental stressor is low temperature; dotted lines when summer drought (orange), facilitation (blue), or both mechanisms (green) act to modulate the original monotonic pattern. Modified from López-Angulo et al., 2018.

and important (Bertness and Callaway, 1994; Callaway et al., 2002). In the latter context, positive interactions are usually referred as “facilitation” since, in general, one organism or species receives benefits and the other is neither harmed nor benefited.

Alpine ecosystems represent highly stressful environments for organisms. For instance, plants must cope with extremely low temperatures, short growing seasons, excessive radiation levels, strong winds, nutrient-poor soils, unstable substrates as a result of local avalanches, and the runoff associated with melting snow (Körner, 2003). Cushion plants are, however, one of the life-forms best adapted to these severe high mountain ecosystems. In particular, the short stature and compact shape of cushion plants allows them to decrease the wind abrasion, buffer the extreme temperatures, and soils below cushions usually retain more water and nutrients than the surrounding bare ground (Arredondo-Núñez et al., 2009). In this way, cushion plants modify the suitability of the abiotic environment. This is the reason that cushion plants are widely recognized as “nurse plants”. Nurse plants are organisms that facilitate the establishment, growth and/or survival of other less-stress tolerant organisms by offering microhabitats more favorable than the surrounding environment (Callaway, 2007). Indeed, several studies have reported the presence of other species of plants growing within cushion plant patches. This process is the classic type of facilitation in which the positive effects of neighbors buffer others from the stressful conditions.

Facilitation is a highly ubiquitous phenomenon that occurs in all alpine regions of the world (Cavieres et al., 2016), and high-Andean communities are no exception. Numerous small-scale observational and experimental studies performed in the Andes have revealed the importance of cushion plants on alpine plant diversity. For instance, in the Patagonian Andes, Nuñez et al. (1999) showed that patches dominated by cushions of *Mulinum leptacanthum* (Apiaceae) and *Oreopolus glacialis* (Rubiaceae) harbor a greater number of species than patches without cushion plants. Consistently, studies in the alpine communities of central Chile found that between 30 and 50% of plant species grow more frequently inside cushions than outside of them (e.g., Cavieres et al., 1998, 2002, 2006; Badano et al., 2002; Arroyo et al., 2003; see Arredondo-Núñez et al., 2009). Furthermore, the dependence of several plant species to the presence of cushion plants typically increases with the elevation, because environmental stresses also increase. Nonetheless, as indicated by some empirical studies, this is not always the case (e.g., Cavieres et al., 2006; Cavieres and Badano, 2009), suggesting that it is not yet clear how facilitation varies through gradients of environmental stress.

In South America, mainly in the Andes of Chile, much research has been performed on the so called “genetic” cushion plant species. These are species that, regardless of environmental conditions, always adopt the cushion life-form. Notable species include *Bolax gummifera*, *Laretia acaulis*, *Azorella monantha* and *Azorella madreporica* (Apiaceae). These are all well-studied species of cushion plants in the Chilean Andes (e.g., Cavieres and Badano, 2009; Arredondo-Núñez et al., 2009). *Mulinum leptacanthum* and *Oreopolus glacialis* are the most common and well known cushion plants from the Argentinian Andes (Nuñez et al., 1999). Hence, broadly speaking, species of Apiaceae (Umbelliferae) seem to be the most common cushion plants across the southern Andes (Fig. 5). However, far less attention has been given to species that we define here as “facultative” cushion plants. In contrast to the aforementioned cushion plants, these plants are herbs, tussocks, or prostrate shrubs whose life-forms occasionally shift to cushion-like patches, a change that could be driven by the extreme environmental conditions. Accordingly, these facultative cushion plants can also act as nurse plants. Some examples from the Argentinian Andes are *Acaena* (Rosaceae), *Senecio* (Asteraceae) and *Gaultheria* (Ericaceae) (Fig. 5).

Most studies have assessed the facilitative effects of Angiosperm cushion plant species, even though the ecological role as a nurse plant is not necessarily exclusive to this taxonomic group. In fact, bryophytes may excel as nurse plants. Particularly, mosses are the dominant ground cover in a wide array of ecosystems, especially in those developing under extreme cold-humid environments such as alpine ice-melting forelands (Fig. 6). Consequently, mosses may influence the performance and distribution of other plants. Like many vascular plants with a cushion growth form, mosses can provide better microhabitats than the surrounding environment by increasing soil moisture and nutrients, by also reducing the frost damage experienced by seedlings and plant roots, and buffering the extreme temperatures that affect the surrounding bare ground (Carlsson and Callaghan, 1991; Gold and Bliss, 1995; Groeneveld and Rochefort, 2005; Groeneveld et al., 2007; Roberts et al., 2009). Hence, the microenvironment provided by mosses can also enhance the establishment, growth and/or survival of other plant species (Carlsson and Callaghan, 1991; Groeneveld et al., 2007; Casanova-Katny and Cavieres, 2012). Consistent with some studies done in the Polar tundra, recent research performed in alpine ice-melting forelands in the northern Patagonian Andes showed that several species of vascular plants settle and grow within species of cushion-forming mosses (Gavini, unpublished), like *Philonotis esquelensis* (Bartramiaceae), *Bryum pseudotriquetrum* (Bryaceae), and *Bartramia patens* (Bartramiaceae) (Fig. 6). Therefore, moss-cushion patches can sustain higher species richness and plant abundance in comparison with bare ground and rocky areas, a similar pattern as that found for angiosperm cushion-plant species.

Origin of the Alpine Flora of the Temperate Andes

Alpine floras generally originate from a mix of local ancient Tertiary elements, immigrants from several sources, and new evolutionary lineages (e.g., Körner, 2003). Andean orogeny is considered one of the most important drivers in the development of plant diversity in South America. A recent work compared available phylogenetic studies and divergence time estimates for plant lineages that may have diversified in response to Andean orogeny. Divergence time estimates indicate that most high-elevation lineages originated and diversified during or after the major phases of Andean uplift (Mid-Miocene to Pliocene). As expected, Andean mid-elevation lineages tend to be older than high-elevation groups (Luebert and Weigend, 2014), suggesting a relatively modern origin for the much of high Andean flora.

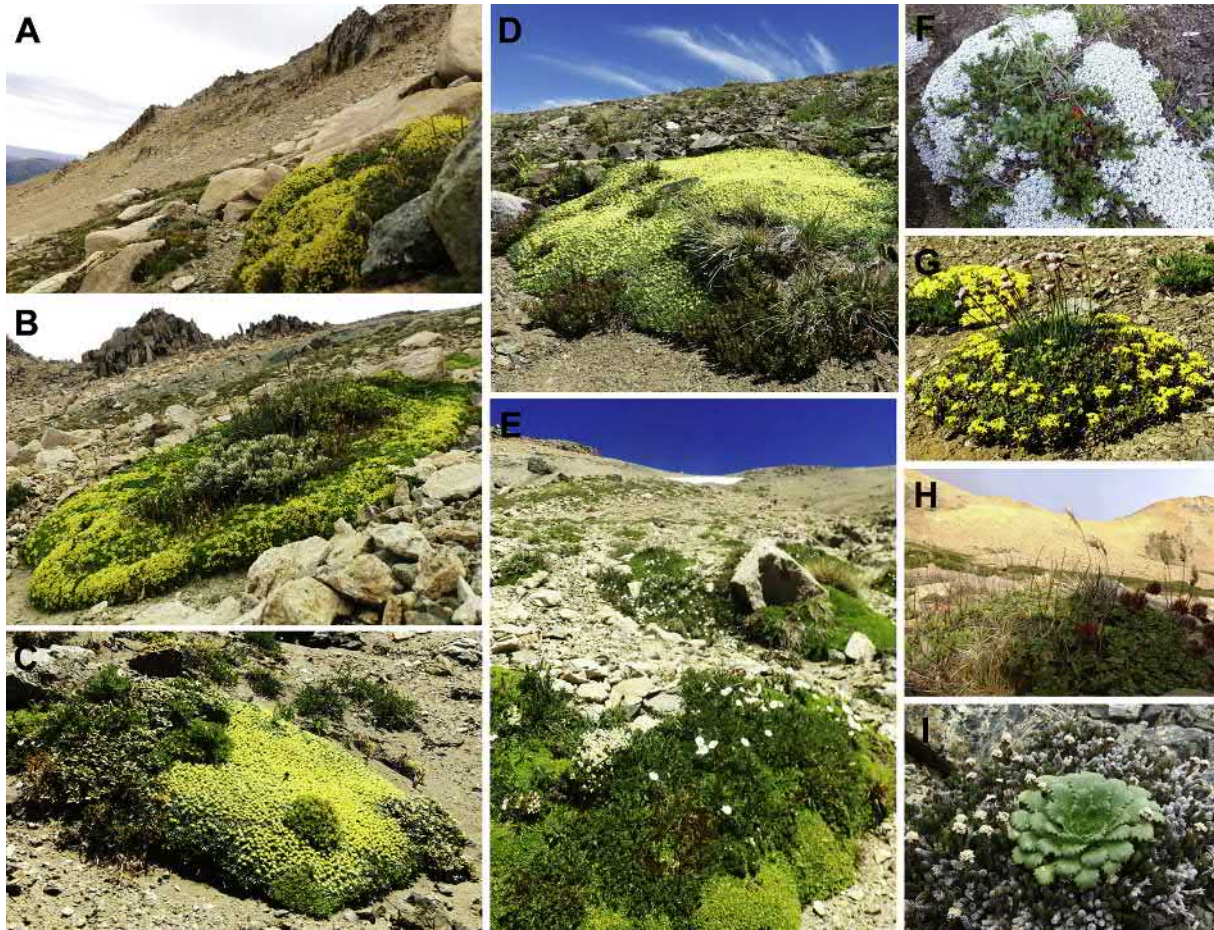


Fig. 5 Angiosperm cushion plants facilitating other species of angiosperms. (A and B) *Mulinum leptacanthum*, (C and D) *Azorella monantha*, (E) *Azorella lycopodioides*, (F) *Belloa chilensis*, (G) *Oreopolis glacialis*. Non-cushion species that can eventually form cushion plant patches, potentially leading to the nursing of other species, (H) *Acaena macrocephala*, (I) *Nassauvia pygmaea*. (Note several species found growing inside cushion patches). Photographs by Sabrina Gavini.

Dispersal along the Andes has been shown to occur in either north or south directions, mostly after the Andean uplift (Luebert and Weigend, 2014). However, Doan (2003) proposed a general south-to-north diversification pattern for plants and animals based on the earlier uplift of the Southern Andes in the early Miocene. In fact, evidence of this has been found for several plant genera, including *Azorella*, *Chuquiraga*, *Oreobolus*, *Ourisia* and *Perezia* (Luebert and Weigend, 2014 and lit cit. there). Work based on Miocene fossils (Palazzesi et al., 2012) also reconstructed a northward displacement of an originally south-temperate floristic element, coinciding with climatic cooling, eastern Patagonian aridization and Andean uplift. This northward displacement of various lineages of southern South American plants during the colonization of the Andes was likely the result of niche conservatism. Limited climatic tolerances to decreasing temperatures probably led to northern shifts of distributions, as species tracked their fundamental climate niches through space (Palazzesi et al., 2012). Therefore, the temperate Andes and other high-latitude elevated areas of southern South America appear to have been important in the origin of alpine floras of lower latitudes of the continent. The close relationship between the floras of Patagonia, the High Andes, and the Puna has long been observed (Cabrera, 1978). Nevertheless, the history of the high Andean flora is complex and plant diversification surely has been driven by a variety of processes, including Andean orogeny, but also environmental changes and biotic interactions (Luebert and Weigend, 2014).

Current Conservation Status

Alpine regions of the temperate Andes have several more-or-less protected areas throughout their entire length, so there has been relatively little anthropogenic habitat loss to affect biodiversity conservation. The alpine areas are not seriously threatened by habitat conversion, even though some high-Andean species have traditionally been used as medicine, as fodder, and for fuel (Squeo et al., 1994; Chiapella and Ezcurra, 1999; Méndez et al., 2006). However, mining activities and a marked increase in ecotourism and

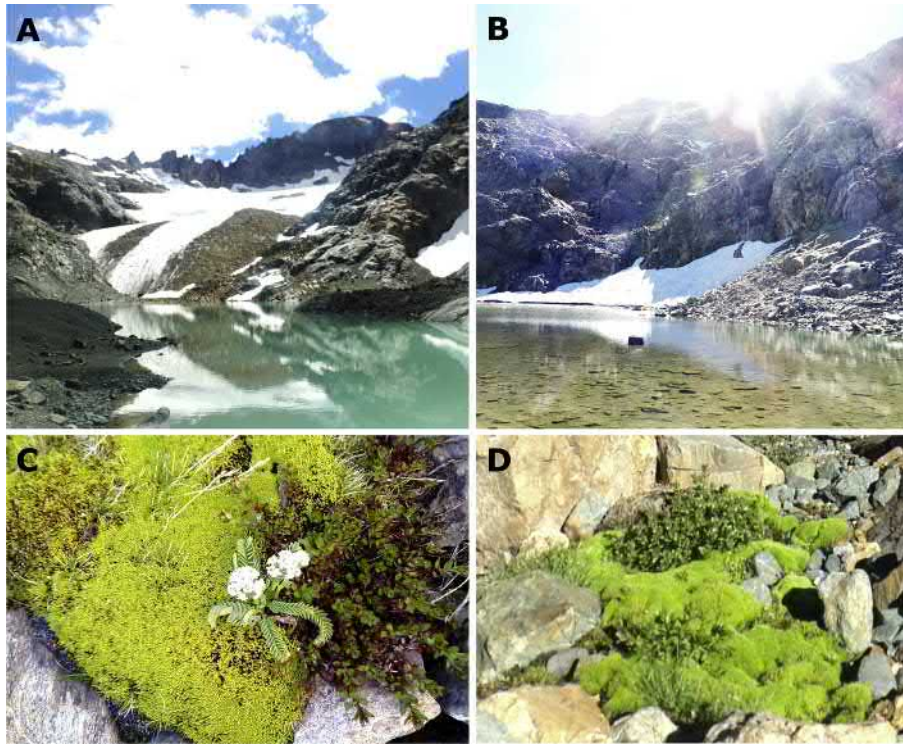


Fig. 6 Mosses forming cushions facilitating other species. Alpine ice-melting communities (A) Cerro Hielo Azul (Chubut, Argentina) and (B) Cerro Lopez (Rio Negro, Argentina) where (C, D) moss-cushion patches can be found facilitating angiosperm species. Photographs by Sabrina Gavini.

mountain sports such as climbing or skiing can be observed on several major mountains of the region. These human disturbances may cause problems, such as introductions of exotic species, littering, erosion, sewage disposal and the cutting of woody vegetation for fires. Protected mountain areas with limited prior human use are quite vulnerable to the invasion of exotic plant species because of their popularity as mountaineer destinations (Barros and Pickering, 2014). Burning of shrubs for fuel is common among local herdsmen (Squeo et al., 1994) and is probably an activity that started in ancient times, surely performed by native hunters and gatherers before European settlement. But if this activity increases it could affect the vegetation of the region (e.g., Chiapella and Ezcurra, 1999; Méndez et al., 2006). Although the vegetation is also probably adapted to grazing by native camelids such as vicuñas (*Vicugna vicugna*) and guanacos (*Lama guanicoe*), the relatively recent introduction of exotic ungulates, especially goats (Squeo et al., 1994) and pack animals (Barros and Pickering, 2014), can also have an important impact, especially in the fragile humid ecosystems (Chiapella and Ezcurra, 1999; Méndez et al., 2006; Barros and Pickering, 2014).

Conclusions

Many biogeographic studies have shown a decreasing trend in species richness with latitude and elevation at large scales, which can be attributed in part to space availability, biotic processes, and past evolutionary history, but mostly to an increase in climatic harshness due to temperature decrease (e.g., McCain and Grytnes, 2010). Additionally, the latitudinal and altitudinal temperature gradient can interact with precipitation gradients, resulting in unexpected patterns. In general, climate models predict a decrease in diversity with elevation on humid mountains, and a unimodal diversity pattern on arid-based mountains (Arroyo et al., 1988; McCain and Grytnes, 2010). In addition, at finer scales, other abiotic factors can alter large-scale patterns, such as aspect or slope that determine differences in solar radiation and snow duration, as well as soil characteristics (e.g., Ferreyra et al., 1998a; Mark et al., 2001). All these abiotic factors have been shown to be important determinants of alpine plant diversity in the temperate Andes.

In recent years, several tools have been developed to help quantify and analyze the magnitude of facilitative interactions, e.g., to assess for the effects of cushion plants at the species or community-level (Cavieres and Badano, 2009; Cavieres et al., 2016). Despite current knowledge, more research is needed to unravel the potential ecological and long term evolutionary consequences of biotic interactions in alpine ecosystems. For instance, it has recently been found that biotic interactions can play an important role as evolutionary drivers of alpine plant diversity (Gavini et al., 2019). In particular, both negative (i.e., competition) and positive (i.e., facilitation) interactions can be equally important ecological forces in promoting diversification of alpine plant lineages world-wide, challenging the assumption that only large-scale abiotic phenomena like climate, geomorphology and historical

processes (Körner, 2003) regulate alpine plant diversity. In sum, there is an overwhelming body of evidence indicating that biodiversity in the extreme-cold alpine environments of the temperate Andes is also sustained through biotic interactions, mainly owed to the nurse effect exerted by several unrelated lineages of plants.

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Nature of Alpine Ecosystems in Temperate Mountains of New Zealand

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Abstract

New Zealand harbors the most significant alpine ecosystems in the Southern Hemisphere outside of South America, with a biota characterized by high levels of endemism. However, NZ's alpine areas are geologically recent and tectonically highly active, which has led to allopatric speciation and many poorly understood species complexes among plants, invertebrates and reptiles. NZ's alpine biota has had to adapt to climatic unpredictability so possibly may be less affected by future climate change. The greatest threats to NZ alpine ecosystems are invasion by introduced pest species, most notably cold tolerant conifers, ungulates, and rodents.

Origin of the New Zealand Alpine Zone

New Zealand is a long, narrow, topographically diverse archipelago with 58% of the landmass above 250 m altitude and 22% of the largest island, South Island, above 1000 m altitude (Salinger, 1988). The three main islands, North, South and Stewart, cover a latitudinal range from 34.42°S at the northernmost tip of North Island to 47.28°S at the southernmost point of Stewart Island. Alpine ecosystems, defined as the regions between actual or reconstructed timberline and permanent snow line, cover c. 30,000 km², or approximately 11% of New Zealand (Halloy and Mark, 2003). These alpine areas owe their existence to New Zealand's position on the boundary of the Pacific and Australian plates. The Kaikoura orogeny, which commenced c. 25 million years ago, uplifted a spine of mountains along this plate boundary, with a single Alpine slip fault (Fig. 1) bounding their western edge through the central South Island (Fitzsimons and Veit, 2001). Named the Southern Alps for their resemblance to the European Alps, these mountains support the largest area of alpine ecosystems in New Zealand. However, these alpine areas are geologically young, resulting from accelerated uplift over the last 5 million years, combined with a cooling climate (Heenan and McGlone, 2012). Rates of uplift of the Southern Alps are still high, 5–8 mm/year, but are counteracted by high rates of erosion associated with easily fractured basement sedimentary greywacke, earthquake-triggered landslides and extremely high orographic precipitation (Fitzsimons and Veit, 2001). Due to these high rates of erosion, New Zealand's alpine areas do not reach the heights of Northern Hemisphere temperate mountains, for example the highest peak, Aoraki/Mt. Cook (Fig. 2) is only 3724 m above sea level (2014 survey), having lost 40 m since 1991 from rockfall and slips (Sirguey, 2014). Alpine areas in New Zealand's North Island are also geologically young but much smaller in extent, with some ranges relating to North Island fault systems (Fig. 1). The largest alpine areas in North Island are associated with the Taupo volcanic complex, which commenced andesitic activity c. 2 million years ago and is the most frequently active and productive silicic volcanic system on Earth (Wilson et al., 1995). Alpine vegetation also occurs sporadically at lower-than-expected altitudes on infertile or water-logged soils exposed to harsh winds, for example Mt. Moehau (892 m) in northeastern North Island (Fig. 1) and at sea-level in Stewart Island.

Habitat Types

The alpine zone commences at lower altitudes in New Zealand compared with similar northern latitudes as a result of New Zealand's strongly oceanic climate. Tree species grow to more than 4500 m at c. 35°N latitude in Tibet and to over 3000 m at c. 47°N (Miehe et al., 2007). In contrast, treeline in New Zealand varies from 1400 m in central North Island (39°S) to 900 m in south-western South Island (46°S) (Mark and Dickinson, 1997). In much of South Island, low diversity southern beech forest (family Nothofagaceae) gives way abruptly to a low alpine zone of tall grassland dominated by the near endemic tussock (bunchgrass) genus *Chionochloa* (Poaceae; Fig. 3). In parts of the country lacking southern beeches, such as the "beech gap" in central South Island, and Mt. Taranaki, western North Island, southern conifers (family Podocarpaceae) and tall subalpine shrubs in the Asteraceae and Ericaceae families grade into tall tussock grassland (Mark, 2012; Cieraad and McGlone, 2014; Wardle, 2008). The

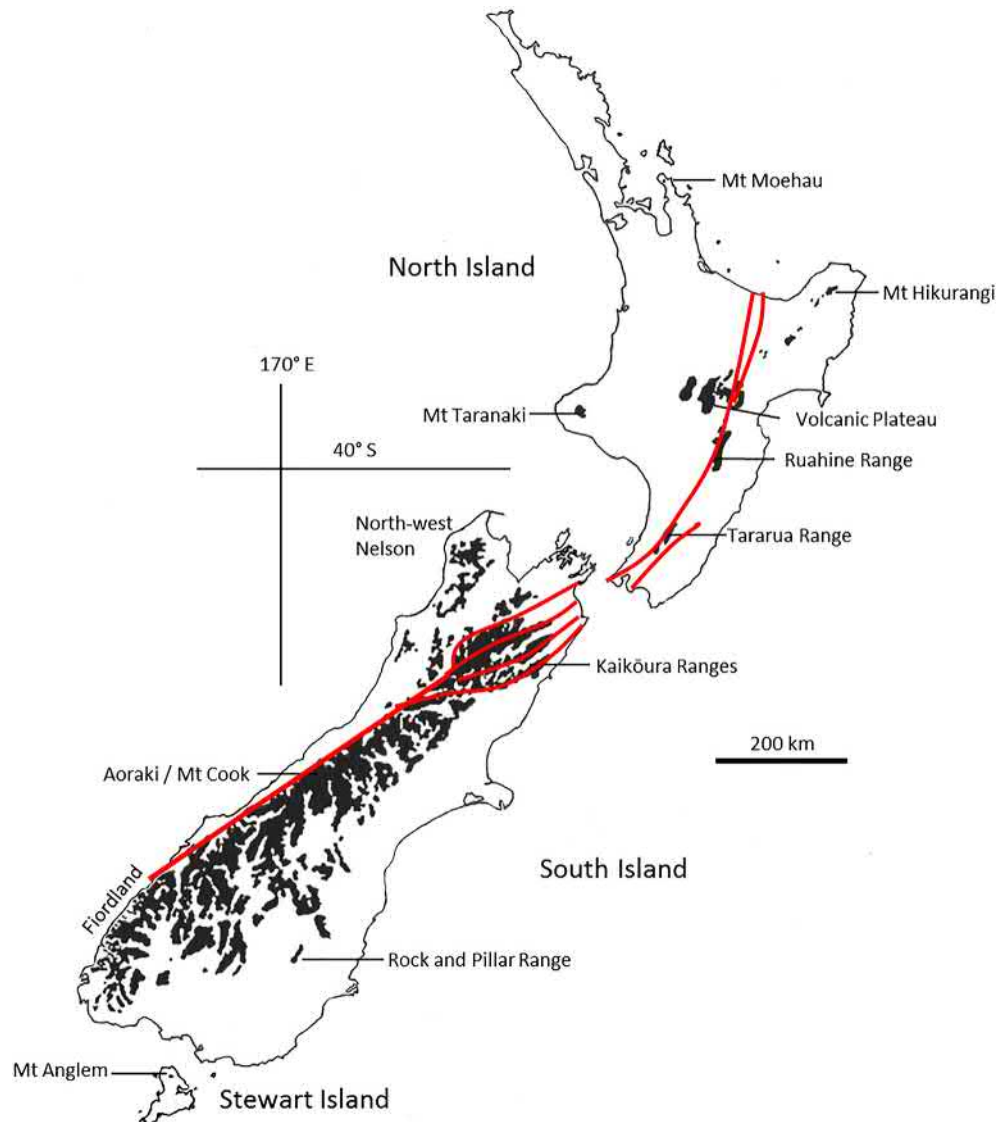


Fig. 1 New Zealand alpine regions, showing major fault lines and key locations mentioned in the text. Alpine areas based on Fisher, F.J.F. (1965). The alpine *Ranunculi* of New Zealand. *Bulletin, New Zealand Department of Scientific and Industrial Research* **165**, 1–192. Fault lines follow GNS Science www.gns.cri.nz/.../Major-Faults-in-New-Zealand.

dominance of tall tussock-forming grasses and large-leaved, evergreen herbaceous plants in New Zealand's low alpine ecosystems differentiate them from temperate alpine areas of the Northern Hemisphere. Instead, these ecosystems more closely resemble alpine ecosystems of tropical high mountains that, like New Zealand, can experience as much temperature variation during diurnal cycles as between seasons (Mark et al., 2000).

The distribution of habitat types in the alpine zone most commonly relates to slope stability, soil development and winter snow cover (Mark and Dickinson, 1997; Lord et al., 2018). Due to the youth of New Zealand's mountains and the highly dynamic tectonic environment, soils are generally weakly developed, and highly mobile areas of rocky talus, or "scree," as they are known locally, are common in the steep, fractured mountains of central South Island (Figs. 2 and 4). These scree environments are home to a specialist set of plants from a range of families that produce robust, long lived roots that grow downslope, and are often attached only loosely to small aboveground rosettes (Dawson, 1988). These plants are often highly cryptic, at least to human eyes (Fig. 5). On stable rock, the sparse vegetation features a number of spectacular hummock-forming plants in the Asteraceae family, known locally as "vegetable sheep." This growth form has parallels with the giant *Azorella* cushions of high altitude South American deserts which have been shown to buffer internal tissue temperatures against extreme diurnal temperature fluctuations (Kleier and Rundel, 2009).

Below permanent snow line, which decreases from 2400 m in central North Island to 2000 m in southern South Island (Mark and Dickinson, 1997), winter snow depth and length of snow cover is strongly affected by the interaction between topography and prevailing wind flow. Snow tends to be deposited by cold, wet, south-westerly weather systems and redistributed during gusty,



Fig. 2 Aoraki/Mt. Cook, with Hooker Glacier in the middle distance and Mueller Glacier moraine in the foreground, Canterbury.

north-westerly anticyclonic periods, leading to marked west-east gradients in rain and snow fall, especially across central and southern South Island. Annual precipitation exceeds 4 m for exposed mountains in the North Island and can exceed 10 m on the western slopes of the Southern Alps. Isolated alpine ranges in the rain shadow-affected eastern South Island, such as Rock and Pillar Range (Fig. 1), are significantly drier but still receive more than 1000 mm annual precipitation. On these ranges, redistribution of snow results in a largely snow-free summit plateau, while late-lying snow banks up to 7 m deep accumulate in eastern (leeward) gullies (Fig. 6), and in some seasons do not thaw completely in summer (Lord et al., 2018). The timing of snowmelt is critically important to flowering phenology in these snowbanks, with many species forming floral apices in autumn, enabling rapid flowering in spring even as the snow is receding (Mark, 1970). This marked variation in snow depth and duration, combined with strong winds (averaging more than 6 m/s, and gusting up to 17.4 m/s), and frequent frosts year round, leads to a vegetation gradient from summit cushionfield, dominated by lichens and ground-hugging dwarf shrubs and herbs, through grassy herbfield on leeward slopes under moderate snow cover, to highly speciose snowbank communities in wet, leeward gullies (Lord et al., 2018; Bliss and Mark, 1974).

Flora and Fauna

The vascular flora of New Zealand's alpine ecosystems (species which occur above timberline, regardless of whether they are restricted to alpine areas) currently consists of more than 750 species, subspecies, and varieties (Table 1) representing as much as 30% of the native flora of New Zealand. While about 93% of alpine plant species are endemic to New Zealand, plant endemism is very low at the genus level, with many genera shared with Australia, South America, and South Africa (Mark, 2012). Many species, or their close relatives, also occur in cold, wet infertile areas at lower altitudes, suggesting colonization of the newly uplifted alpine areas by preexisting lineages (Heenan and McGlone, 2012), followed by allopatric speciation on mountain ranges isolated during Pleistocene interglacials (Winkworth et al., 2005). Molecular studies in speciose alpine genera (e.g., the *Veronica* complex (*Hebe*, *Parahebe*, *Chionohebe*, *Hebejebbie*), *Myosotis*, *Ranunculus*, *Chionochoa*) show rapid morphological diversification in the last 1–3 million years, but low genetic differentiation, leading to poor phylogenetic resolution for many genera, hybridizing or



Fig. 3 *Chionochloa* tussock grassland, Dunstan Range, Otago.

intergrading species complexes and a high prevalence of polyploids (Murray and Lange, 2011; Pirie et al., 2010; Lockhart et al., 2001; Winkworth et al., 2005; Wagstaff and Garnock-Jones, 1998; Meudt et al., 2015). Speciation in some groups is related to edaphic specialization; the endemic alpine rockcresses, *Pachycladon* (Brassicaceae), show a pattern of basal generalist species and radiation of specialists on particular rock types (Heenan and Mitchell, 2003). Species diversity also differs markedly between alpine regions, with high levels of endemism in the so-called “endemism centers” of the south-west and north-west of South Island, but lower levels in central South Island and North Island alpine ecosystems (McGlone, 1985). A number of alpine plant taxa also show disjunct distributions between South Island endemism centers (Clarke et al., 2018). In North Island this low level of endemism is likely related to frequent volcanic activity (McGlone, 1985). However, the central South Island endemism gap may be more a product of elevated rates of speciation in the more topographically and geological diverse “endemism centers” rather than climatic or tectonic factors (McGlone et al., 2001; Clarke et al., 2018). For example, *Chionochloa* tussocks (Poaceae) show greatest species richness and regional endemism in south-west South Island (5/14 taxa endemic) followed by north-west South Island (3/10 taxa endemic), with many taxa occurring in specialized habitats or on uncommon rock types. Only two of seven species found on North Island are region endemics and the species found in central and eastern South Island are all widespread, but represented by geographically distinct subspecies (Pirie et al., 2010; Edgar and Connor, 2000).

Invertebrate biodiversity is exceptionally high in New Zealand alpine ecosystems, with c. 40% of invertebrate species in the New Zealand Biological Region found in alpine areas and more than 90% of them endemic to New Zealand (Mark, 2012). Many groups show considerable geographic variation and are poorly resolved taxonomically. Unlike northern temperate alpine areas, New Zealand has no native social bees. Instead, small (4–10 mm long), solitary bees in the families Colletidae and Halictidae are found throughout the mountains (Donovan, 2007). There are relatively few butterfly species in New Zealand, although a recent revision indicates considerable allopatric speciation in what were once thought to be single, widespread montane/alpine species (Patrick and Patrick, 2012). Moths, on the other hand, are exceptionally diverse and common in New Zealand, with well over 1650 species, c. 85% of which are endemic (Hoare et al., 2011). Moth diversity is especially high in South Island alpine regions with many taxa yet to be formally described (Mark, 2012; Hoare et al., 2011), and many knowledge gaps concerning host plant relationships (Buxton et al., 2018). Coleoptera are also diverse and common in New Zealand alpine ecosystems, with large, day-active chafer beetles (Scarabaeidae) and weevils (Curculionidae) being particularly conspicuous (Mark, 2012). One of the most spectacular groups of alpine insects are giant (20–80 mm long), flightless Orthopterans in the family Anostostomatidae, known as weta. Two genera in particular, *Deinacrida* and *Hemideina* (Fig. 7), have speciated extensively in South Island montane and alpine environments, following



Fig. 4 Rock talus and scree habitats, Canterbury.

mountain uplift over the last 5 million years (Pratt et al., 2008). Orthopterans in the grasshopper family Acrididae are also speciose and abundant components of alpine ecosystems. Twelve of the 15 species described by Bigelow (1967) are found in alpine grassland and scree habitats. More recent work has indicated several of the most widespread species are in fact unresolved species complexes (Trewick and Morris, 2008). Considerable color variation exists within these species complexes that may at least partly relate to crypsis (Fig. 8).

The alpine avifauna of New Zealand, as with the country as a whole, has suffered numerous extinctions since the arrival of humans (Holdaway, 1989). Subfossil remains indicate that three species of flightless moa (Dinornithiformes) were a component of alpine ecosystems (Worthy, 1990) along with extinct coot and raptor species (Holdaway, 1989). The now critically endangered flightless parrot, Kakapo (*Strigops habroptilis*), was also present in pre-human alpine ecosystems, but is now restricted to managed populations on predator-free islands (Powlesland et al., 2006). While a range of birds, including seabirds such as Black-backed gull (*Larus dominicanus*), utilize alpine areas during summer, the nationally endangered Hutton's shearwater (*Puffinus huttoni*) is the only seabird globally to breed exclusively in an alpine environment, and only the kea (*Nestor notabilis*), and the rock wren (*Xenicus gilviventris*) are true alpine specialists, occurring exclusively in the Southern Alps of South Island (Gaze, 2013; Kemp, 2013). The only naturally occurring wild population of the flightless South Island Takahe is in a low alpine valley in Fiordland, where it feeds on the tiller bases of *Chionochloa* during summer and fern roots below timberline during winter. However, as for Kakapo, subfossil remains indicate that Takahe were once also widespread at lower altitudes (Maxwell, 2013).

New Zealand's only native land mammals, bats, are not known to venture above timberline; the only other vertebrates, apart from birds, that naturally occur in alpine areas of New Zealand are lizards. Four of New Zealand's six lizard genera, approximately a third of currently known gecko species and a quarter of skink species, are found in alpine and montane habitats (Hare et al., 2016). Intensive field survey efforts in South Island mountains since the 1990s have revealed considerably more lizard diversity than previously thought with many more species undoubtedly yet to be discovered (Mark, 2012; Hitchmough et al., 2016). The recently described gecko genus, *Mokopiriakau*, is possibly the most specialist alpine group with several undescribed entities restricted to single mountain ranges. Likewise the common gecko complex, genus *Woodworthia*, contains a number of undescribed, apparently geographically restricted entities (Hitchmough et al., 2016), also suggesting a role for allopatric speciation.



Fig. 5 *Ranunculus haastii* on scree slope, Mt. Kyeburn, Otago.



Fig. 6 Late spring snow distribution on eastern (leeward) slopes, Rock and Pillar Range. Shrub belt represents approximate location of original treeline which has been affected by fire and grazing.

Table 1 New Zealand alpine species richness in major taxonomic groups

<i>Taxonomic group</i>	<i>Taxonomic subgroup</i>	<i>Number of alpine taxa</i>	<i>Important groups</i>
Non vascular flora	Algae	?	
	Bryophytes	c. 400 species	
	Lichens	c. 100 genera	<i>Usnea, Umbilicaria, Rhizocarpon</i>
Vascular flora	Conifers	3 species	
	Eudicots	597 species	Asteraceae (<i>Celmisia</i>), Ericaceae (<i>Dracophyllum</i>), Apiaceae (<i>Aciphylla</i>), Plantaginaceae (<i>Veronica</i>)
	Monocots	165 species	Poaceae (<i>Poa, Chionochloa</i>)
	Ferns and Allies	17 species	
Fungi	Fungi	?	
Invertebrates	Butterflies	23+ species	<i>Argyrophenga, Lysaena</i>
	Moths	200+ species	Crambidae, Geometridae, Noctuidae
	Orthoptera	23+ species	<i>Sigaes, Deinacrida</i>
	Coleoptera	abundant	
	Diptera	abundant	Tipulidae, Calliphoridae, Syrphidae, Tachinidae
	Apoidea (bees)	12 species	Colletidae, Halictidae
	Other Hymenoptera	?	
	Blattodea	11+ species	<i>Celatoblatta</i>
	Aranadae	abundant	
	birds	21 species	
Vertebrates	reptiles	20+ species	

**Fig. 7** A female alpine stone weta, *Hemideina maori*, body length c. 80 mm.

Pollination Biology

The New Zealand alpine flora is remarkable for the prevalence of white flowers (**Fig. 9**), estimated as 78% of large-flowered species by [Cockayne \(1928\)](#), but more accurately around 62% of biotically pollinated species (Lord unpublished data). Unpigmented flowers that appear white to humans, and do not reflect UV, dominate even in groups such as *Veronica*, forget-me-nots (*Myosotis*) and gentians (*Gentianella*) known for their blue-purple flowers elsewhere ([Lloyd, 1985](#); [Campbell et al., 2010](#)). In Northern Hemisphere alpine and arctic regions, blue and purple flower colors are associated with pollination by social bees ([Eidesen et al., 2017](#); [Ishii et al., 2018](#)). As there are no native social bees in New Zealand, the high frequency of white flowers in alpine ecosystems has been linked to the abundance of flower-visiting Diptera ([Ishii et al., 2018](#)). However, New Zealand subantarctic islands that lack even solitary bees, support endemic blue *Veronica* and *Myosotis* species and pink-purple *Gentianella* species ([Lord et al., 2013](#); [Lloyd, 1985](#)). Furthermore, native flies can show color discrimination behavior, whereas native solitary bees often show a preference for white flowers ([Campbell et al., 2010, 2012](#); [McGimpsey and Lord, 2015](#)). While less abundant than flies, solitary bees can be many times more effective pollinators, so may have had a role in the evolution of flower color in the New Zealand alpine ([Bischoff et al., 2013a,b](#)). It is, however, still unclear whether selection by legitimate pollinators is the main, or only, driver of loss of floral pigments

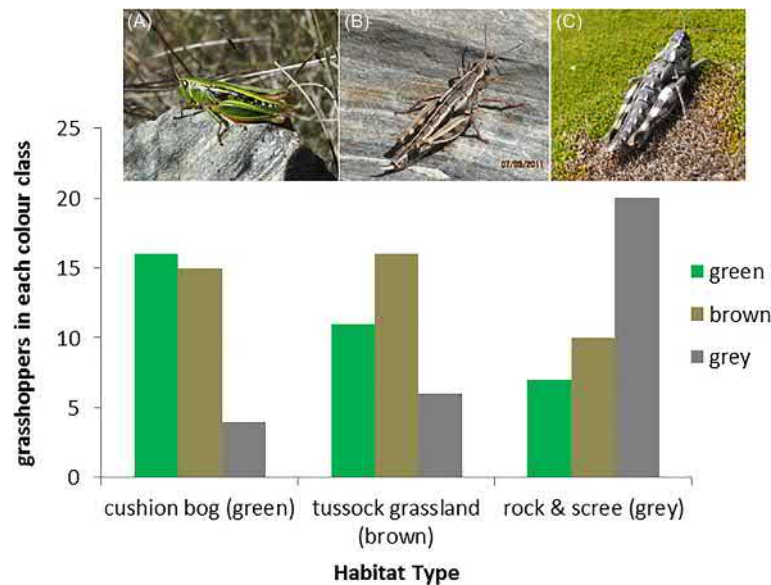


Fig. 8 Number of grasshoppers (*Sigaus australis* complex; Acrididae) of each of three broad color morphs encountered during a 5 min walk through three different alpine habitat types, Remarkables Range, New Zealand. Images show: *Green* (A) and *brown* (B) morphs on rock, and *gray* morph (C) on cushion bog vegetation. Redrawn from Richardson, E. (2011). *Warm or well obscured: Microhabitat selection in the New Zealand alpine grasshopper Sigaus australis*, Postgraduate Diploma in Science Dissertation, University of Otago, New Zealand.

in New Zealand alpine plants. The low fertility of New Zealand's raw, highly leached alpine soils may make pigments costly to produce; pigment expression in flowers, where it does occur, may be more associated with the benefits of anthocyanin production in stressful environments (Campbell et al., 2012). For example, blue coloration due to cyanidin production in the grassland harebell *Wahlenbergia albomarginata* (Campanulaceae) increases with altitude, cold temperatures and drought (Sawrey, 2012; Sawrey and Lord, unpublished data).

Mast-Flowering

Trophic interactions in New Zealand's alpine ecosystems are strongly influenced by large scale variation in productivity driven by mast-flowering species. Mast-flowering or mast-seeding is the phenomenon of synchronized mass reproduction within a species at supra-annual intervals, with intervening years of little or no seed output, and is especially prevalent in the New Zealand flora (Schauber et al., 2002). Alpine snow tussocks in the genus *Chionochloa* include some of the most extreme mast-flowering species in the world; synchronized mast-flowering of co-occurring *Chionochloa* species significantly reduces the proportion of seeds lost to specialist native dipteran and lepidopteran seed predators (Kelly et al., 2000). This pulse in resources also stimulates population increases in introduced mice which switch diet from invertebrates to *Chionochloa* seeds in heavy mast years (Wilson and Lee, 2010). The giant speargrasses (*Aciphylla* species, Apiaceae) also exhibit mast-flowering behavior (Young, 2006; Campbell, 1981), and may play a critical role in the population dynamics of associated flower- and leaf-feeding invertebrates. For example, native flightless speargrass weevils (*Lyperobius* species, Curculionidae: Molytinae) are host specific to Apiaceae, predominantly *Aciphylla*, and show extensive allopatric speciation in alpine areas of South Island. Larvae feed on *Aciphylla* roots, but the adults, which can live 2–3 years, feed on leaves and inflorescences (Craw, 1999). Several *Celmisia* species and other alpine Asteraceae also show mast-flowering behavior (Kelly et al., 2013; Campbell, 1981; Mark, 1970). While levels of seed predation by dipteran larvae do not appear to differ between mast-flowering and regular flowering *Celmisia* species (Spence, 1990), common flower visitors to Asteraceae and *Aciphylla*, such as hoverflies (e.g., *Allograpta* spp., *Platycheirus* spp., Syrphidae), increase significantly in abundance in a heavy mast-flowering year (Miller et al., 2018).

Principal Anthropogenic Stressors and Trends

New Zealand was the last landmass of significant size to be colonized by humans, so there arguably is a much clearer picture of human impacts on alpine ecosystems here, than anywhere else in the world. Ancestors of the indigenous Māori people voyaged from Polynesia around 800 years ago. The high mountains of the new homeland, Aotearoa, came to feature strongly in stories of creation and shaping of the land in both North Island/Te Ika o Maui (Te Ahukaramū, 2006) and South Island/ Te Wai Pounamu/Te Waka o Aoraki (Anon, 2004; Waaka, 2016). Seasonal "mahinga kai" expeditions to inland and alpine areas were not



Fig. 9 A montage of common southern New Zealand alpine plants illustrating the abundance of small white flowers.

only vital for food gathering, but also expressed connection to ancestral beings, kinship, and guardianship of the land (Phillips et al., 2016). In addition to hunting and harvesting activities, the Southern Alps were also crossed by east coast South Island iwi (tribes) in order to obtain the prized pounamu stone (jade) from west coast rivers, that was then traded throughout the country (Brailsford, 1996), hence one of the Maori names for South Island—Te Wai Pounamu. Along the way, expeditioners made use of alpine plants such as tussock grasses and Tikumu (mainly *Celmisia semicordata*) for clothing and insulation (Lord et al., 2010; White and Lord, 2012). Widespread fires were a feature of this period of human exploration (McWethy et al., 2010). These fires likely spread into alpine areas, removing the natural timberline forest in rainshadow-affected eastern South Island. This allowed *Chionochloa* tussock grasses and other alpine species to extend to lower altitudes leading to the formation of extensive tall grasslands in central eastern South Island below climatic timberline (McGlone, 2001).

European explorers did not discover New Zealand until Abel Tasman sighted what was probably the Southern Alps in 1642 (Wilson, 2005). Systematic European colonization of New Zealand from the mid-1800s brought widespread pastoral farming to inland montane and alpine grasslands of South Island, which came to be known as the “High Country.” While much of this land remained in the ownership of the Crown (NZ Government), High Country pastoral leases with perpetual right of renewal gave farmers exclusive grazing rights. Sheep in particular were allowed to freely range to high altitudes over summer periods, initially grazing exclusively on native species. *Chionochloa* tussocks, the structural dominants of alpine grassland show high levels of natural leaf abscission with limited ability to tolerate the browsing style of mammals (Antonelli et al., 2011; Mills et al., 1989). Thus the period of exploitative pastoralism that followed in the mid-late 1800s lead to rapid depletion of palatable native grasses and herbs (O’Connor, 1982). From the 1800s until the 1980s fire was used as a farm management tool to remove plant litter and stimulate new palatable growth of long lived *Chionochloa* tussocks. However, High Country “burn-offs” have become rare in recent times following a reassessment of their impact. Fire stimulates *Chionochloa* tussocks to flower which depletes available growing points, but can be tolerated if occasional or during damp conditions (Payton and Pearce, 2009). However, if fires are frequent or combined with grazing they lead to significant reduction in biomass and ultimate death of these keystone species (Mark, 1994). On some mountain ranges the replacement of tall tussock grassland by shorter unpalatable grasses or cushion plants is thought to be due to intensive burning and grazing (Mark, 1994; Mark and Dickinson, 1997).

Following concerns over declining productivity of high country grasslands, the 1950s saw the start of widespread over-sowing with introduced grasses and legumes (Allan and Chapman, 1989), and along with them the accidental spread of pastoral weeds. While this had little effect on high alpine ecosystems, a subset of these species, particularly *Agrostis capillaris*, *Trifolium repens*, and *Hieracium* species, are now widespread in low alpine ecosystems, particularly in anthropogenic habitats such as road verges, walking tracks and around buildings. Away from human disturbances and in the absence of grazing by introduced mammals, most introduced herbaceous plants seem unlikely to competitively exclude native plants. However, aggressively invasive *Hieracium* species, which can reach the high alpine, are found in areas that have never been grazed by domestic stock; their presence could instead be facilitated by naturalized mammals such as Himalayan Thar (Steer and Norton, 2013). Even though most introduced plants may not be directly competing with native plants, introduced species with open-access flowers such as *Achillea millefolium* and *Hypochaeris radicata* (both Asteraceae), can be highly attractive to native alpine bees and flies, leading to indirect negative effects on native plant reproduction via reduced pollinator services and stigma clogging (Miller et al., 2018). Introduced legumes with long tubular flowers such as *Trifolium repens* and *Lotus corniculatus*, are not attractive to native bees and flies whose tongues are too short to access the nectar (Iwasaki et al., 2018). The spread of these species in New Zealand alpine ecosystems has only been made possible by the availability of introduced long-tongued honey bees (*Apis mellifera*) and bumble bees (*Bombus* species) to act as pollinators; *B. terrestris*, especially, is well-established in alpine areas foraging up to 2500 m (Donovan, 2007). However, due to different foraging preferences and nesting requirements, *B. terrestris* does not appear to compete directly with native solitary bees (Iwasaki et al., 2018).

New Zealand has more introduced plant species than there are native plant species (Wilton and Breitwieser, 2000), and 31 species of naturalized introduced mammals (Parkes and Murphy, 2003). However, relatively few of these have become established in alpine areas, especially away from human activities (Mark and Dickinson, 1997; Mark, 2012). Mice and hares can be more abundant in alpine grassland compared with montane forest, and mice appear to have a significant impact on alpine invertebrates, especially weta (Wilson et al., 2006). Rats are largely restricted to lower altitudes by a combination of food availability and temperature. However, they may be able to invade upslope during mild winters (Christie et al., 2016). Ungulates introduced by European colonists for hunting, particularly Red Deer (*Cervus elaphus*), Chamois (*Rupicapra rupicapra*), and Himalayan Thar (*Hemitragus jemlahicus*), have formed large self-sustaining populations in South Island mountains and can significantly damage vegetation by trampling and heavy browsing (Cruz et al., 2017).

The most serious threat to New Zealand’s alpine ecosystems from introduced plants is posed by the spread of Northern Hemisphere conifers. *Pinus* species introduced for timber were noted to be forming wild populations as early as the late 1800s (Froude, 2011b). Despite this, significant areas of infestation were not recorded until the 1940s, possibly coinciding with changing farming practices (Froude, 2011a). Currently more than 25 introduced conifers have formed self-sustaining populations in the wild (Froude, 2011b) and some species such as *Pinus contorta* have greater frost tolerances than native timberline trees (Wardle, 1985). The ability of these species to withstand the stressors of alpine environments has enabled them to readily invade alpine grassland ecosystems well above natural timberline (Cieraad and McGlone, 2014). In 2007 wilding conifers were estimated to threaten 805,000 ha of eastern South Island, with spread most prevalent in inland montane basins and ranges, including alpine areas (Froude, 2011a). The conversion of these alpine grassland ecosystems into exotic coniferous forests is undoubtedly leading to the loss of native alpine species.

Tourism is New Zealand’s largest industry in terms of foreign exchange earnings and the number of international visitors per annum is expected to exceed the size of the resident population by the year 2024 (Driver, 2018). Popular alpine areas are heavily used for sight-seeing, tramping/hiking and skiing. For example, view points for the highest peak, Aoraki/Mt. Cook, now attract more 1 million visitors per year, putting severe strain on current facilities (Littlewood, 2019). The number of visitors to Franz Joseph

Glacier reached 750,000 over the 2017/2018 season and 130,000 visitors attempted the Tongariro Alpine Crossing in central North Island in the same season (Driver, 2018). The New Zealand ski industry has a target of 2 million skier days by 2020 (Jamieson, 2018), placing considerable pressure on the alpine areas utilized, especially in terms of water consumption for snow making and solid waste disposal (Reiser, 2002).

Changing Climatic Conditions

New Zealand has a distinctly oceanic climate with cool summers and mild winters. This leads to an extended growing season at high altitudes. However, summers are not predictably warm and frosts can occur at any time of the year (McGlone et al., 2010; Lord et al., 2018). Winter snow cover is also not predictable and in low alpine ecosystems soils go through freeze-thaw cycles leading to frost heave and subsequent surface feature sorting such as solifluction terraces, rock nets, and plowing boulders (Mark and Dickinson, 1997; Bliss and Mark, 1974; Grab et al., 2008). Climatic variation between years in New Zealand alpine ecosystems is also affected by the El Niño-Southern Oscillation system of linked changes in sea temperature and atmospheric pressure across central and eastern Pacific. Under El Niño summer conditions the west-east rainfall gradient across the Southern Alps becomes exaggerated, leading to heavier than normal precipitation on western areas and drought in eastern alpine areas. El Niño also increases the frequency of southerly airflows in winter, bringing more snow and colder temperatures to much of New Zealand. La Niña has less impact on New Zealand, but is typically associated with warmer temperatures (NIWA, 2019b). New Zealand alpine invertebrates, like other Southern Hemisphere invertebrates, are commonly freezing-tolerant, able to survive internal ice formation (Sinclair et al., 2003; Sinclair and Chown, 2005). These species can go through freeze-thaw cycles on a daily basis, allowing for winter activity should conditions be favorable (Sinclair, 2001; Ramløv, 1999). Similarly, New Zealand herbaceous alpine plants show higher growing season frost tolerances than equivalent Northern Hemisphere species (Bannister et al., 2005). The lack of a predictably warm growing season is thought to explain why the New Zealand native flora as a whole, and the alpine flora in particular contain very few obligate annual species (Lloyd, 1985).

Climate change scenarios for New Zealand based on IPCC 5th assessment models predict temperature increases of +0.7 to +1.0 °C by 2040 and up to +3.0 °C by 2090. This warming trend is predicted to be greatest at higher elevations, with regional climate models suggesting that maximum daily temperatures in the Southern Alps could rise by more than 4 °C by 2100 (NIWA, 2019a; Hendriks and Hreinsson, 2010). As a result, large decreases in snow cover are predicted at high altitudes and in southern regions of South Island (NIWA, 2019a). The duration and depth of seasonal snow is expected to decrease at all elevations but to be especially marked below 1000 m altitude (Hendriks and Hreinsson, 2010). In line with global trends, the New Zealand land-mass has warmed by 0.9 °C in the last century (Mullan et al., 2008), three of the last 5 years have been among the hottest on record for New Zealand, and a third of the ice volume in the New Zealand alpine has been lost in the last 40 years (NIWA, 2019a). However, between 1983 and 2008, when the vast majority of the world's glaciers were shrinking, at least 58 New Zealand glaciers increased in size, most likely due to regional cooling (Mackintosh et al., 2017). This effect was glacier specific and short-lived, e.g., while Franz Josef glacier on South Island's west coast regained at least half of the mass lost in the first half of the 20th century, the Tasman glacier on the eastern side of Aoraki/Mt. Cook continued to retreat. Since 2011 Franz Josef glacier has retreated by 1.5 km, quite possibly linked to warmer temperatures in the Tasman Sea to the west of New Zealand (Mackintosh et al., 2017), which were 6 °C warmer than average in 2018 (NIWA, 2019a). Despite these trends, New Zealand tree lines do not appear to have responded to warming temperatures as much as predicted, with only modest sapling establishment above adult tree line in monitored plots (Wardle, 2008). However, altitudinal increases in treeline seem to be more rapid in diffuse treelines as opposed to the abrupt treelines dominated by southern beech species, suggesting factors other than temperature are important (Harsch, 2010).

As New Zealand alpine species already show adaptations to unpredictable climatic conditions, it is difficult to assess how climate change per se will affect species distributions. The frost tolerances of snowbank species indicate that although these species normally overwinter under snow, they would be able to tolerate increased exposure to winter conditions (Bannister et al., 2005). In a reciprocal transplant experiment on the Rock and Pillar Range, snowbank turfs moved to areas of reduced snow cover showed slow changes in species composition even after 7 years, but the fruticose lichen *Thamnolia vermicularis* showed rapid colonization of newly available snow free areas (Lord et al., 2018). This study concluded that drought during the growing season may be more important to species survival than reduced seasonal snow. The impacts of upward-migrating woody natives and pest species may be of greatest concern for New Zealand alpine ecosystems under a changing climate (McGlone et al., 2010). Introduced small mammals that show intermittent use of alpine areas could have a greater impact under warmer climatic conditions (Christie et al., 2016). Mice in particular, by consuming large numbers of invertebrates and seeds, may limit the ability of native species to migrate successfully with their climatic niches. Assuming the position of treeline is temperature dependent, and given an latitudinal lapse rate of 0.6 °C/100 m, a 3 °C warming scenario could raise New Zealand treelines by 500 m, reducing the area available for alpine plants and resulting in the loss of c. 80% of current alpine "islands" (Halloy and Mark, 2003). As only 0.03% of the total area above treeline is higher than the highest recorded vascular plants, species displaced by upward-migrating woody species would have limited areas in which to expand (Halloy and Mark, 2003). Two alpine summit sites in South Island have been established to measure climate changes and altitudinal migration of species (Mark et al., 2006) as part of the Global Observation Research Initiative in Alpine Environments (GLORIA; Grabherr et al., 2000), and have been regularly surveyed since 2001 (Mt Burns) and 2004 (Mt Pisa). However, it is by no means clear that simple changes in altitudinal range will be observed, or even should be expected, for New Zealand alpine species as has been reported elsewhere (Grabherr et al., 2010), given the topographic and climatic variability of the New Zealand alpine environment; minimal response or counter-intuitive outcomes are possible (McGlone et al., 2010).

Conservation Strategies

New Zealand has the highest proportion in the OECD (Organization for Economic Cooperation and Development) of land area protected for conservation purposes and almost 98% of the land area above permanent snowline and 94% of alpine areas in the Southern Alps have legal protection for conservation (Anon, 2010). However, c. 18% of mountain areas with indigenous plant cover in central and southern North Island, Taranaki and north-eastern South Island, and more than 60% of mountain and hill country areas with indigenous plant cover in south-eastern South Island, still lack legal protection (Anon, 2010). In the last 20 years the amount of alpine land legally protected for conservation purposes has increased significantly as an outcome of High Country Tenure Review. This voluntary government-run process gives pastoral lessees the opportunity to purchase some of their leasehold land, often the lower altitude portions, in exchange for relinquishing rights to other, often higher altitude, parts of their lease, and has led to the formation of high country conservation areas, and improved public access and recreation in South Island alpine areas.

The New Zealand Department of Conservation (DoC) is the government entity responsible for managing the national conservation estate. Activities not only include pest and weed control but also rare species management. The New Zealand Threat Classification System (Townsend et al., 2008) determines the risk of extinction of species and changes in status over time, allowing for species to be prioritized for intervention. Many alpine species are highly range-restricted so feature on threatened species lists, for example 16 of the more than 40 *Myosotis* species in New Zealand are considered threatened due to very small ranges (Meudt et al., 2015). However, because the alpine environment is well represented in the conservation estate, management of alpine species is of less concern than lower altitude species threatened by habitat loss or introduced species. Even so, despite legal protection, a number of alpine species remain on threatened species lists and have continued to decline. For example the iconic alpine parrot, *Nestor notabilis*, kea, was reassessed in 2016 as Nationally Endangered because populations number only 1000–5000 mature individuals, with an ongoing predicted decline of 50–70% over 10 years or three generations (Robertson et al., 2017).

Conclusions

The alpine ecosystems of New Zealand are the most significant in the Southern Hemisphere apart from South America. Due to New Zealand's geographic isolation and geological history, recent rapid speciation has produced a high diversity of endemic taxa, many of which are yet to be described. While global climate change may not have as much impact on alpine species in New Zealand as elsewhere, the combined threats posed by invasion plants and animals, and anthropogenic pressures are significant. Thus the future security of New Zealand's alpine ecosystems depends largely on government commitment to large scale control of high impact pests such as introduced conifers and browsing mammals, as well as ensuring that the regulations that control alpine activities prioritize biological conservation over economic development.

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Climate Change Impacts in the Himalayan Mountain Ecosystems

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Abstract

The evidence of global temperature rise is now widely accepted. On average the global temperature rose by 0.74 °C over the last hundred years (1906–2005), with more than half of this rise, i.e., 0.44 °C reportedly occurred in the last 25 years. Subsequently, the number of extreme precipitation events—like heavy rainfall and severe storms—appears to have increased. According to the fourth assessment report of the Intergovernmental Panel on Climate Change (IPCC, 2007) “most of the observed increase in globally averaged temperatures since the mid 20th century is very likely due to the observed increase in anthropogenic greenhouse gas concentrations.” Such changes in climate have already started affecting biological systems worldwide. Significant upward shift of plant species have already been reported from many parts of the globe due to warming. Several studies have detected effects of climate change on species distribution, the storage of carbon in plants and soils, and the timing of life history events of animals and plants. The change in climate will also affect the livelihoods and food security of the regional inhabitants who depend on the natural resources of high mountains. This article presents an overview of impacts of climate change in Himalayan mountains on agriculture and forest ecosystems based on literature review and some anecdotal evidence.

Introduction: Climate Change in the Himalaya

In the next few decades, the mountains of the world are predicted to continue warming at an alarming rate. During the last few decades, the Himalayas have experienced approximately two to three times greater atmospheric temperature warming than the global average (Xu et al., 2009). Temperature trends in most Himalayan regions substantially exceed the global mean trend of 0.85 °C (between 1880 and 2012), with winter season temperature trends being generally higher than those of other seasons (Schickhoff et al., 2015). The greatest average increase, 0.07 °C/year is observed in winter, whereas the least increase, 0.03 °C/year in summer (Shrestha et al., 2012); and the warming rate increases with altitude, peaking between 4800 and 6200 m altitudes (Singh et al., 2011). The IPCC predicts that average annual mean temperature over the Asian land mass, including the Himalayas, will increase by about 3 °C by the 2050s and about 5 °C by the 2080s (IPCC, 2007), and average annual precipitation will increase by 10–30% by the 2080s (IPCC, 2007). Satellite imagery suggests almost 67% of the glaciers in the Himalaya have retreated. For example, in Nepal (Central Himalaya) glacial margins are retreating by as much as 10 m/year (Ageta and Kadota, 1992). It has been stated that in the face of climate change (CC) most ecosystems and landscapes will be impacted through changes in species composition, productivity and biodiversity. Thus, the magnitude of potential response of the climate-sensitive Himalayan region needs to be better understood. As glacier margins recede, and snowlines move upwards, river flow rates are likely to change. Furthermore, an alteration in water flow regime may lead to a plethora of social issues, endanger biological communities, impact forestry and agriculture-based livelihoods and affect the overall well-being of the people.

Dimri and Dash (2012) reported that the Western Himalayan region shows a warming trend of 0.2–0.4 °C/decade. Consistent warming signature over IHR, more than the global average, was reported by the north-western Himalaya by Bhutiyani et al. (2007) for the last century. Dash et al. (2012) reported that warming over north-east India was around 0.2 °C/decade during 1971–2005. Similarly, warming rate of Nepal Central Himalaya during 1977–2002 was also reported to be 0.6 °C/decade by Shrestha and Aryal (2011). Moreover, statistically significant projected warming rate of 0.23–0.52 °C/decade was reported by Dimri et al. (2018) for minimum and maximum air temperatures under RCP 4.5 and 8.5 by 2099. Recently, Singh (2019), based on 32 yrs. observed data between 1980 and 2012 for a central Himalayan site Mukteshwar (an IMD station in Uttarakhand), showed that annual average maximum and minimum air temperature (observed at 2 m height) were significantly (P -value < .05) increasing (0.01 and 0.02 °C/decade). These studies indicate that the Himalayan region is probably warming at rates higher than the global average.

In the Indian Himalayan Region (IHR), the rainfall processes of both summer monsoon seasons and winter western disturbances are significantly modulated by the complex terrains through terrain-induced changes in the convection process, vapor flux, cloud water content and wind distribution. Subsequently, significant rainfall variability due to complex terrain and increasing temperature may lead to excessive landslides, induced disasters, and increased flooding of rivers and rivulets. Therefore, many reports have been published on the long-term changes in rainfall over different stations of IHR with various degrees of change, for

example positive trends (i.e., increasing seasonal and/annual mean of rainfall) in the rainfall pattern for some local regions, as reported by Sharma et al. (2000) for Kosi basin in Nepal and by Kumar et al. (2005) for Himachal Pradesh, India. Similarly, negative rainfall trends are reported by Singh and Sen-Roy (2002) for Beas basin and Kumar and Jain (2010) for Qazigund and Kukarnag of Kashmir. No significant changes in rainfall were reported by Archer and Fowler (2004) for the upper Indus basin, for the Jhelum river basin of Pakistan (Khan, 2001), and for the Almora and Nainital towns of Uttarakhand state, India (Joshi et al., 2013). Kumar et al. (2008) reported that the annual rainfall has decreased by 3.91 mm in 11 years. between 1991 and 2001 in the Alaknanda valley of Garhwal Himalaya, and the mean annual temperature has increased by 0.15 °C, in 40 years. between 1960 and 2000. A spatial analysis of the summer monsoon rainfall trend over IHR by Mukherjee et al. (2014) further reveals that both monsoon *strong* and *weak* phases are decreasing for the entire Himalayan region with seasonal average rainfall trend is decreasing for the eastern Himalayan states. However, a dominant cycle of ~ 2.7 years of high frequency of extreme rainfall events over the IHR was reported by Mukherjee et al. (2014). Moreover, it was reported that projected rainfall amount is expected to increase by 0.75 mm/day over the northwest Himalaya, whereas the flood plain of Assam is expected to receive less rainfall during 2020–70 (Mukherjee et al., 2017).

Climate change has emerged as a major issue across the globe. The mountain regions, including the Himalaya, are particularly vulnerable to CC on two main counts: (i) warming trends are higher in the region, and (ii) the impacts are magnified by the sharp change in altitude over small distances. However, we still lack sufficient climatological data for much of the Himalayan region. In particular, good data are needed for the Himalayan region to assess the current situation of CC impacts, and to make reliable predictions that can be used as a basis for planning. In spite of global attention, CC research is still in its infancy in the Himalayan mountains. As such there is a paucity of long-term climate data in the region and the available data has been collected without any uniform instrumentation and methodology, hence, the magnitude of observed data and data quality is uncertain. Limited studies are available which may demonstrate the impact of CC on mountain ecosystems.

Impacts on Food Production Systems and Livelihoods

Agriculture is the mainstay of mountain people in the western Himalayan region. Mountain agriculture is mostly rain-fed (~85%), and dependent upon biomass energy (fodder for livestock, manuring leaves, fuelwood, wood for agricultural implements, wild edibles etc.) derived from the surrounding forests. The small holdings (size >1 ha of majority of people) distributed over rugged terrain have low agricultural productivity (~1 t/ha), yet it is a rich repository of agro-biodiversity and the region is resilient to crop diseases. For example, in Uttarakhand, over 40 different crops and hundreds of cultivars comprising cereals, millets, pseudo-cereals, pulses and tuber crops are cultivated (Maikhuri et al., 2001). Mixed cropping of 12 crops (Baranaja) is another best example of rich agri-diversity of the region. These crops are adapted to the local environmental conditions and withstand the environmental risks and other natural hazards and thus have contributed to the food and nutritional security of the hill farmers for many generations. However, in recent decades the area planted with traditional crops has drastically decreased (>60%), and many of the crop species are on the brink of extinction, such as *Panicum miliaceum*, *Glycine* spp., *Setaria italica*, *Hibiscus sabdarffia*, *Vigna* spp., and *Perilla frutescens*, to name a few (Negi and Joshi, 1996). The irrigation systems (locally called as guls), have been severely damaged with the rainfall becoming erratic and springs are drying. Similarly, a comparison of climate data reveals the negative impact of CC on fruit yields, as reported in the Kullu valley (Himachal Pradesh). This is apparently the result of decreased rainfall by about 7 cm, decreased snowfall about 12 cm, and an increase in the mean minimum and maximum temperatures by 0.25–1 °C (Vishvakarma et al., 2003). Also, it has been reported that apple cultivation has shifted to higher altitudes and that apple yields from orchards at lower altitudes have declined due to inadequate and delayed snow fall. The temperature at lower altitudes is also rising due to CC. Alterations in the floral diversity due to land use and land cover change and extinction of local cultivars has also negatively affected the population of pollinators (native bees) in the region resulting in inadequate pollination and decline in apple productivity (Partap and Partap, 2003). The farmers are now compelled to rent colonies of honey bees for pollinating the apple orchards, and devise short-term solutions until the “polliniser” trees in their orchards begin flowering.

Some of the documented impacts on mountain food production systems linked with CC in the Himalayan region are (Negi et al., 2012): (i) reduced availability of water for irrigation; (ii) extreme drought events and shifts in the rainfall regime, resulting in failure of crop germination and fruit set; (iii) invasion of weeds (e.g., *Lantana*, *Parthenium*, *Eupatorium*) in the croplands; (iv) increased frequency of insect-pest attacks; and (v) decline in crop yield. These factors have led to loss in agri-diversity and change in crops and cropping patterns in the Western Himalayan region, leading to abandonment of crop fields and out-migration of people.

Impacts on Biodiversity and Forest Ecosystems

Among global mountains, the Himalayan region is most prominent on account of the height of its mountains and the length of the range. The Himalayas represent one of the 36 “Global Biodiversity Hotspots” (https://en.wikipedia.org/wiki/Biodiversity_hotspot). The richness of endemic species with restricted distribution and life support values (goods and services) of these hotspots is highly vulnerable under the changing climate scenarios (Palni and Rawal, 2013). Vegetation patterns (distribution, structure and ecology of forests) across the globe are controlled mainly by climate. Several climate-vegetation studies have shown that certain climatic

regimes are associated with particular plant communities. The Fourth Assessment Report of IPCC (2001) concluded that forest ecosystems could be seriously impacted by future CC. Even with global warming of 1–2 °C, much less than the most recent projections of warming during this century (IPCC, 2001), most ecosystems will be impacted through changes in species composition, productivity and biodiversity (Leemans and Eickhout, 2004). It has been demonstrated that upward movement of plants will take place in a warming world (Kelly and Goulden, 2008). In a recent study the expansion and upward movement of *Rhododendron campanulatum* along an altitudinal transect (3511–3665 m asl) running from the upper forest limit to the treeline and beyond in Uttarakhand was estimated at 1.4 m/year (Singh et al., 2018) due to rising temperatures (0.11 °C/year in the past two decades) (Table 1). Studies in the western Himalayas have recorded an upward shift of treeline species of 19 and 14 m over 10 years on south- and north-facing slopes, respectively (Dubey et al., 2003). Due to increase in temperatures, change in vegetation, rapid deforestation and scarcity of drinking water, habitat destruction and ecological corridor fragmentation may lead to extinction of wild flora and fauna. In some high altitude regions, the biodiversity is being lost or endangered because of land degradation and the over- use of resources. For instance, in 1995, about 10% of the known species in the Himalayas were listed as threatened.

The impact of atmospheric warming is clearly observed in the changing phenology of plant life in the region, in particular, the timing of the onset of growth of plants, particularly flowering in this region. Phenological studies in Kumaun Himalayan forests (Sal, Pine, and Oak forests) has revealed the mean date of leafing and flowering has advanced by 1–2 weeks within a period of 30 years (1985–2015) due to the increase in temperature (0.005 °C/year) and decline in rainfall (3.3 mm/year) over the years (Singh and Negi, 2016). In these species a rise in temperature and water stress may advance seed maturation, which might breakdown the synchrony between monsoon rains and seed germination, thus reducing forest regeneration, and the species diversity of forests. The flowering and fruiting at the wrong time, in advance or after the appropriate season, may lead to failure in finding pollinators, failure to match demands of growing offspring with temporal peaks in food resources, or failure by a pollinator to find pollen and nectar, or of a flower to be pollinated. Climatologists believe that even with global warming of 1–2 °C, much less than the most recent projections of warming during this century, most ecosystems and landscapes will be impacted through changes in species composition, productivity and biodiversity (Leemans and Eickhout, 2004). It is expected that with the CC, scenario of the forests, both in terms of structure and functioning, is likely to change substantially. In the case of many dominant forest species of the region, such as sal (*Shorea robusta*), tilonj oak (*Quercus floribunda*) and kharsu oak (*Q. semecarpifolia*) seed maturation and seed germination have traditionally coincided with monsoon rainfall. In wet conditions these species show vivipary (germination of seeds while they are still on trees). A rise in temperature and water stress may advance seed maturation, which might result in the breakdown of synchrony between monsoon rains and seed germination of these species (Singh, 2014).

In the western Himalayan mountains, early flowering in several members of Rosaceae (e.g., *Pyrus*, *Prunus* spp.) and *Rhododendrons* has often been linked with global warming. Earlier onset of flowering in *Rhododendron* about two weeks as compared to the past has been reported in Kumaun Himalaya. A Generalized Additive Model (GAM) using real-time field observations (2009–11) and herbarium records (1893–2003, Hooker 1949) predicted 88–97 days early flowering over the last 100 years in *Rhododendron arboreum* due to a rise in annual mean maximum temperature in Western Himalaya (Gaira et al., 2014). Ranjitkar et al. (2014) has reported that tree *Rhododendron* might expand its distributional range in response to global warming under the recent trend of rising winter-spring temperature (Xu et al., 2009). Telwala et al. (2014) reported range shifts of 87% of the 124 endemic species as a consequence of winter warming in the alpine zone of the Sikkim Himalaya, using historical climatic and taxonomic data from 1849 to 50 and 2007–10. Similarly, significantly ($P < .01$) earlier flowering was recorded for 11 alpine/sub-alpine and 12 temperate high-value medicinal herbs, in response to increasing winter temperature. Alpine species confined to the tops of low-lying mountains face the risk of extinction as their habitats are likely to be taken over by the forests. Literature reports indicate that climatic conditions are more useful “predictors” than the calendar dates. For example, photosynthesis is an important parameter that is affected by changing temperature, CO₂ and light conditions. However, many of these studies suffer from the lack of long-term meteorological data to establish a clear-cut relationship with CC and there is a pressing need for observational climatic data in the region.

Forests are also the source of NTFPs (including medicinal plants). The oak forests (*Quercus* spp.), native of the cool temperate climate of the region, are the storehouse of biodiversity, non-timber forest products (NTFPs), and a variety of medicinal plants. For example, *Morchella esculenta* (an edible fungi), found in the oak-conifer forests of this region, is collected by the local people. On average, each household collects about 1.5 kg dry wt. every year which is sold for 5000 rupees, or \$72 US per kg. Another

Table 1 Atmospheric temperature recorded for Tungnath (Uttarakhand, Western Himalaya) by various workers.

Year of measurement	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Growing season mean (Jul–Sept.)
1985–86	6.3	11.1	15.9	14.4	12.9	7.4	5.6	–	–	11.6
1985–86	–	–	–	12.3	12.0	9.0	7.2	–	–	11.1
1990–97	–	10.0	12.0	10.0	9.0	8.0	7.0	–	–	9.0
2008–10	7.0	8.0	11.0	12.0	11.5	9.0	7.0	4.0	1.0	10.8
2017	6.7	8.09	10.2	11.7	11.7	10.1	6.4	2.6	–	11.2
2017 (day time)	–	–	12.8	13.9	16.0	15.8	13.2	–	–	15.2

(–), data not available.

From: P Singh, V. Arya, G.C.S. Negi & S.P. Singh, 2018. Expansion of *Rhododendron campanulatum* krummholz in the treeline ecotone in Tungnath, Garhwal Himalaya. Tropical Ecology 59(2): 287–295, 2018.

example is *Myrica esculenta* fruits. These are collected by local people from the forests that are sold in the nearby markets. The spread of invasive, exotic and alien spp. (e.g., *Lantana*, *Eupatorium*, and *Parthenium* spp.) in the natural forests of this region has also been linked with CC. These have a competitive impact on the native flora. Increased incidences of forest fire are another prominent change that is linked with CC. The frequency, size, intensity, seasonality, and type of fires depend on weather and climate in addition to forest structure and composition. A comparison of air temperatures during the fire season for the 2 years 1994 (no fire event) and 1995 (large fire events) in Binsar Wildlife Sanctuary, Western Himalaya showed that in 1995 the air temperature was higher (Sharma and Rikhari, 1997). It is expected that with the increase in drought cycles and concomitant increase in forest fires, the NTFPs derived from oak (*Quercus* spp.) forests will decline. Apart from the direct benefits accrued from these forests the ecosystem services generated by these forests would also alter. Singh (2007) has estimated the carbon stocks of the forests of Uttarakhand Himalaya at 264 million tons. Inevitably, any change in the forest (distribution, density and species composition) under CC would immensely influence economies like forestry, agriculture, livestock husbandry, NTFPs, medicinal plants and many others. The ability of species to respond to climate change will depend on their being able to “track” shifting climatic zones and colonize new territory or to adapt their physiology and seasonal behavior to changing conditions.

Impact of Climate Change on People

The impacts of CC on the socio-economic conditions of people living in the Himalaya can be observed in agriculture, livestock, forestry, tourism, fishery, as well as human health (Sharma et al., 2009). However, specific knowledge and data on the impacts of CC on human well-being in the Himalaya is limited. Regional inhabitants depend heavily on forest resources, therefore the consequences of biodiversity loss from CC are likely to be the worst in case of the poor and marginalized people who depend almost exclusively on natural resources. This region is characterized by poverty, poor infrastructure (roads, electricity, water supply, education and health care services, communication, and irrigation), and other indicators of underdevelopment, making the Himalayan inhabitants more vulnerable to CC because their capacity to adapt is quite low. Signatures of the impacts of CC on human health are now becoming apparent through changes in the ranges of disease vectors (e.g., mosquitoes), water-borne pathogens, water quality, air quality, food availability and quality (McMichael et al., 2003) and malnutrition from crop failures (Patz et al., 2005). With a rise in surface temperature and changes in rainfall patterns, the distribution of vector mosquito species may change (Patz and Martens, 1996). Malaria mosquitoes have recently been observed at high altitudes in the region (Eriksson et al., 2008). Huge quantities of municipal waste produced in the mountain towns is further compounding the problem of emission, sanitation and associated health hazards. Another health hazard is posed due to burning of pine forests that give rise to smoke containing sulfur dioxide, benzopyrene, carbon monoxide, nitrogen oxides, polycyclic hydrocarbons and albeitic acid. These gases alone or along-with carbon could be the responsible factors for lung injury with fibrosis (Rison et al., 2000). Aerosols have been shown to contribute to global warming. Based on per unit AOD increase at Mohal-Kullu (Himachal Pradesh, Western Himalaya), temperature rise due to radiative forcing from aerosols in the atmosphere was calculated as high as 0.95 °C per day during summer (April–July) and as low as 0.51 °C per day during winter (December, January–March) (Guleria et al., 2001). Climate change will increase the incidence of diarrheal diseases from deteriorating water quality, as well as increases in infectious diseases and the frequency of cardio-respiratory diseases from the build-up of high concentrations of air pollutants such as nitrogen dioxide (NO₂), lower tropospheric and ground-level ozone, and air-borne particles in large urban areas.

Issues for Future Action

In the current context of changing climatic regime, it is imperative that a proper assessment of long-term changes in the climate parameters be made on a variety of spatio-temporal scales across the different landscapes in the Himalayan region so that sector-wise targeted adaptation and mitigation practices and policies can be framed. However, such detailed assessment of long-term changes in regional climate parameters is greatly impeded by the lack of sufficient data. The IHR, in addition to Nepal and Bhutan contain significant numbers of unique, climate sensitive bio-diversity hotspots and socio-cultural diversity. However, as discussed above, this region lacks sufficient climate data. This lack of data causes the Himalayan region to be under reported in most climate change studies (Singh et al., 2011; IPCC-AR5, 2014). However, scientific interest in quantifying long-term changes in climatological parameters of the IHR, particularly rainfall and surface air temperature, has grown in the last decade. Also, the lack of systematic information on the impact of CC on Himalayan biological systems is widely recognized. Likewise, the need for the development of a Himalayan database among ecologists at the global level has also been highlighted. Therefore, strong initiatives are required not only to utilize but to further strengthen existing databases on Himalayan ecosystems so as to enhance our ecological understanding of CC impacts. This is the only way to properly address issues of conservation and management of Himalayan ecosystems at the local and regional level.

Acknowledgments

Authors are thankful to Dr. R.S. Rawal, Director of the Institute for providing necessary facilities to write this article.

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Plant Adaptations to Alpine Environments

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Abstract

The alpine biome is the life zone above the climatic treeline in mountains. It is the only biome that has a global distribution, with its elevation varying with latitude. Being naturally treeless by definition, its vegetation is composed of small stature plants belonging to the life form graminoids (grasses, sedges, and rushes), herbs, dwarf shrubs and cushion plants covering c. 3.55 Million km² or 21.5% of the global mountain area of 16.5 Million km². Driven by the combination of small, compact plant stature and topography effects (exposure, direction to the sun and shelter) the actual climate experienced by these plants and the animals and microbes associated with them is much warmer (heated by the sun) than one would expect from weather station data. This physical manipulation of an otherwise harsh climate explains much of the physiology observed in alpine plant taxa. Because nights are cool, and—at extratropical latitudes—as the growing season gets increasingly short the productivity of alpine ecosystems is limited by the duration of favorable daytime periods and the slow nutrient cycle. Alpine plants are well adapted to the life conditions they experience, and counter wide spread belief, are not particularly stressed. Because topographic diversity provides escapes from unpleasant habitat conditions over very short distances, the alpine biome and its biodiversity are not particularly vulnerable to climatic change, but rather represent refugia that deserve protection.

The Alpine Biome

In the scientific literature the term alpine refers to the land above the low temperature limit of tree growth, the natural high elevation treeline (see treeline Chapters). Hence, by definition, the alpine life zone is treeless. When trees had been cut or burnt locally, or are absent for other reasons (avalanches, lack of soil, etc.), the treeline is not visible in the landscape, with the montane forest replaced by a low stature vegetation (e.g., meadows, hay fields). This sometimes “alpine looking” substitute vegetation does not belong to that alpine life zone but belongs to the montane life zone. Note the difference between the general term mountain for elevated and rugged land (see below), and the term montane that refers to the upper part of mountains that could be forested but may not bear any trees for disturbance reasons or lack of soil or water. These distinctions are important because they place that alpine life zone in a specific elevational belt that is characterized by climate and not by elevation. In other words, the alpine life zone is confined to a high elevation temperature regime that does not support tree growth. Note, in English, “elevation” applies to elevated land, while “altitude” refers to the height above ground in the free atmosphere; [McVicar and Körner, 2013](#)).

Defined that way, the alpine life zone occurs globally where mountains are sufficiently high ([Fig. 1](#)). The alpine biome is thus the only biome that has a global distribution across all continents (except Antarctica) and it occurs across all latitudes—though at varying elevations. Its common environmental determinants are a lower limit set by the climatic treeline (see above) and the ultimate low temperature limit for plant life, the upper range limit of the alpine biome. That uppermost, often very fragmented part of the alpine world is often addressed as “nival,” because it occurs above the lower limit of potentially permanent snow fields or glaciers. Readers are invited to “visit” the alpine biome across the globe at www.alpandino.org, an open access electronic course that introduces life and life conditions in alpine ecosystems around the world.

The common biological features of the alpine biome are plants of small (commonly less than 0.5 m) size that form shrub land near treeline, followed upslope by graminoid communities and open, fragmented alpine (and nival) vegetation with isolated plants at highest elevations. The term graminoid is employed here because it includes similar life forms that belong to several plant families such as grasses (Poaceae), sedges (Cyperaceae), and rushes (Juncaceae). Although these plants may look like grasses to a lay person, they belong to very different groups of plant species (see life forms below). The commonly small size (stature) of alpine plants has substantial beneficial effects on the actual climate experienced by these plants and the animals and microbes associated with them (the so-called microclimate, see below) and it has implications for sensitivity to disturbance (e.g., grazing, fire, and wind).

How large is the global fraction of land that belongs to the alpine biome? To answer this question, we must first define the term “mountain,” with the alpine biome a subunit of the global mountain area. Mountains are not defined by elevation but by the ruggedness of the landscape. The plains of the short grass prairie at 2000 m elevation are not mountains, but steep coastal ranges



Fig. 1 The alpine biome. Examples from different latitudes (from top left to bottom right): (1) arctic-alpine (Sweden, 69°N, 1100 m), (2) temperate-alpine and nival (Swiss Alps, Rhone glacier, 47°N, 2200–3500 m), (3) temperate-alpine grassland (Austrian Alps, Hohe Tauern, 47°N, 2300 m), (4) temperate-alpine heathland (Chile, Cerro Castillo, 46°S, 1300 m), (5) semiarid tropical-alpine (Bolivia, Sajama, 19°S, 4800 m), (6) humid tropical-alpine (Bolivia, Sajama, 19°S, 4300 m).

with summits only a few hundred meters above sea level are clearly mountains. A 200 m span of elevation over a distance of c. 2.5 km comes very close to what most people consider a mountain. Using that threshold in a 30'' gridded global digital elevation model, the resulting global mountain area is 16.5 million km², 78.5% of which belong to the montane belt (i.e., potentially forested; Körner et al., 2011).

When the alpine fraction is defined as land above the treeline isotherm (at least 94 days with a seasonal temperature of 6.4°C and the season defined as any day with a daily mean temperature >0.9°C (the outcome of a global statistical analysis by Paulsen and Körner, 2014), the total alpine land area amounts to 3.55 million km², which represents 21.5% of the global mountain area (including a 3.2% nival fraction) or 2.6% of all land area outside Antarctica. The geo-statistics shown in Table 1 are restricted to discrete mountains one can identify on a map (83.3% of all rugged terrain). Done this way, the global alpine area is almost the same (3.3 million km², 24% of all mountain area) because the remaining rugged terrain has hardly any alpine land). The alpine biome is not distributed equally on all continents, but is largely confined to Eurasia and the Americas, with only tiny alpine land areas in Africa, Australia and Oceania (Table 1). These statistics do not include the treeless Arctic lowlands, also covered by short stature plant communities that are often subsumed under the term tundra or Arctic semi-desert, both lacking the characteristic features of the alpine landscape, its ruggedness and thus, high habitat diversity. Not surprisingly these arctic ecosystems are much poorer in plant species. While the total alpine flora may comprise about 10,000 species of flowering plants (Körner, 1995), the entirety of these lowland Arctic systems hosts about one seventh as many flowering plant species (Chapin and Körner, 1994). While steepness of terrain is a typical feature of alpine ecosystems, many Arctic systems cover flat lands and hill country, often dominated by

Table 1 The global alpine biome: land cover statistics (Körner et al., 2011, 2017)

Region	Nival belt (km ²)	Upper alpine (km ²)	Lower alpine (km ²)	Total alpine (km ²) (%Mt) ^a	Total mountain (km ²) (% of global) ^b
Africa	43	85	963	1091 (1.5)	706,257 (5.1)
Asia	196,031	420,559	1,356,970	1,973,560 (26.0)	7,600,456 (55.2)
Australia	0	0	1010	1010 (1.4)	74,747 (0.5)
Europe	58,401	34,845	63,721	156,967 (20.0)	784,679 (5.7)
Greenland	71,000	7668	3030	81,698 (99.8)	81,844 (0.6)
N-America	106,870	167,467	424,972	699,309 (28.1)	2,490,842 (18.1)
S-America	27,952	70,351	292,615	390,918 (20.0)	1,956,280 (14.2)
Oceania	450	241	3371	4062 (6.3)	64,754 (0.5)
Total	460,747	701,216	2,146,652	3,308,615 (24.0)	13,759,859 (100)

^aAlpine land area fraction (in %) of the total mountain area in the region.

^bContribution of the regional (continental) mountain area to the global mountain area. Note the 13.76 million km² of mountain terrain includes only the area of discrete ca. 1060 mountain ranges with a name (83.4% of all mountain terrain, mountain polygons, Körner et al., 2017). An additional c. 2.7 million km² of rugged terrain that falls in the mountain category is distributed diffusely across the globe and commonly has no alpine belt (many, very small mountains). With this terrain added, the global mountain area rises to c. 16.5 million km² (100%) outside Antarctica (Körner et al., 2011).

peatland (mires, fens), which are rare in mountains. Hence the term “tundra” is best not applied to the alpine biome (Billings, 1988). However, subarctic mountains do also have alpine ecosystem (arctic-alpine ecosystems; Fig. 1).

Because of the wide latitudinal range across which alpine ecosystems occur, their elevational position varies greatly. While alpine life conditions can be found a few hundred meters above sea level in the subarctic, similarly cool conditions can be found at 4000–5000 m elevation near the equator, although with a longer (often year-round) growing season. The highest location of flowering plants is found in the Himalayas at ca. 6300 m elevation (Körner, 2003), but this is not the coldest place on earth with flowering plants (angiosperms), which was actually discovered in the temperate zone at 4505 m elevation in the Swiss Alps (Körner, 2011). So elevation as such is not a suitable factor to describe the alpine biome. What matters is the climate that is associated with elevation.

Life Forms of Plants That Shape the Alpine Ecosystem

A life form is a category of plant architecture, irrespective of the taxonomic, phylogenetic association. The assembly of plant life forms shapes the nature of biomes. As explained above, the alpine biome is characterized by the absence of tree life forms, but also lacks tall shrubs and lianas, all typically stretching high into the air, and thus forced to “take over” ambient air temperature. Not so the typical alpine life forms described below (Fig. 2).

Alpine herbs are commonly those with leaves forming a rosette attached to the ground, represent the most diverse alpine life form. They commonly fill the space between graminoid tussocks. Most of these herbs spread by below ground rhizomes or runners, hence form clonal systems as well. Alpine herbs also belong to the highest elevation taxa, reaching far into the nival belt. However, most alpine biomes also host some tall herb taxa, which are mostly confined to sheltered, nutrient-rich locations.

The graminoid life form (see above) covers the core of the alpine landscape in most parts of the world (often addressed as alpine grassland or heathland). Most commonly, these graminoids form so-called tussocks, that is, tufts of tillers confined to a common (clonal) root stock. The buds for the next growing season are below ground (1–3 cm), and thus, can hardly become damaged by trampling, grazing, fire or freezing.

Dwarf shrubs are commonly not taller than 50 cm, with taller individuals confined to lower elevation when the montane forest is absent. At higher elevation, these woody species can become prostrate and form dense carpets, closely attached to the ground. The buds for next season's growth are above ground. Layering stems produce adventitious roots permitting these plants to form large clonal systems (vegetative spreading).

Cushion plants represent the most compact life form. These plants occupy raw or eroded terrain, and they trap the annual plant debris (leaf litter) inside often dome shaped canopies. Thus, the benefit of this life form is a closed nutrient cycle at the price of slow growth, and thus, low competitiveness.

In addition, alpine biomes are rich in so-called cryptogams, that is, mosses (bryophytes) and lichens (a symbiosis of fungi and algae). Many of these tolerate periodic desiccation, and thus can grow without roots, even on bare rock. A special feature are so-called cryptogram crusts that may cover large areas of otherwise bare land and prevent substrate erosion. They pioneer soil formation, for instance, in glacier forefields (Table 1).



Fig. 2 Typical life forms of plants in the alpine biome (from top left to bottom right). Rosette forming herbs: (1) *Alstroemeria spatulata*, Portillo, 2850 m, Chile; (2) *Gentiana algida* and *Pedicularis* sp., Tibet 4600 m, China. Graminoids: (3) *Carex curvula*, Swiss Alps, 2500 m; (4) *Kobresia* (syn. *Carex*) *pygmaea*, Tibet 4600 m. Cushion plants: (5) *Dracophyllum muscoides*, Old Man range, 1650 m, New Zealand; (6) *Saxifraga biflora*, Swiss Alps, 2500 m. Dwarf shrubs: (7) prostrate *Loiseleuria* (syn. *Kalmia*) *procumbens*, Swiss Alps, 2450 m; (8) *Rhododendron*-shrub at the low edge of the alpine belt at treeline, Yunnan, 4300 m, China.

Alpine Life Conditions

Given that the alpine biome is confined to certain climatic conditions (not suitable for tree growth) rather than elevation as such, the question arises: What are the common factors that separate the climate of the alpine biome from biomes at lower elevation. There are actually only a few factors that change with elevation in a common manner, globally. These include the reduction of atmospheric pressure (and the partial pressures of oxygen and CO₂) by about 10% per km of altitude and the associated drop in atmospheric temperature between 0.5 and 0.6 K per 100 m (Kelvin is the preferred unit to refer to temperature differences to avoid confusion with temperature in °C; [McVicar and Körner, 2013](#)). Also clear sky solar radiation and the fraction of UV-radiation increase with elevation, but not the dose of solar radiation as such, because cloudiness often increases with elevation. Neither wind speed nor precipitation change in a consistent way with altitude across the world's mountains ([Körner, 2003](#)). There are alpine deserts above the convective cloud layer in some (tropical and subtropical) regions, and mountains belong to the least windy parts of the globe, except for exposed summits and ridges.

Alpinists often find the alpine environment harsh. However, this is a very human perspective. First, a mountaineer experiences atmospheric conditions between 1 and 1.8 m above the ground, and second, evolution did not select humans for alpine life. The environment experienced by alpine organisms is very different from that experienced by an alpinist or that a weather station might report. Hence, it is not appropriate to apply weather station data to explain alpine life conditions (Körner and Hiltbrunner, 2018).

Aerodynamics are key to understanding alpine plant life and the functioning of the alpine biome. Because alpine plants are “small by design” (genotypically), they would not grow much taller, even if brought to lower elevations. They are evolutionary dwarfs. As such, they can engineer their microenvironment in a way that is much warmer than that recorded by a weather station. Roughly half of the solar radiation belongs to the long wave spectrum (warmth) and even part of the short wave spectrum (light) becomes converted to warmth once absorbed by a structure. So any sun-exposed surface will warm up. This heat is dissipated to the air surrounding this structure. In tall structures (e.g., a tree) that heat would be blown away by wind. In dense, low stature plant communities, this heat exchange is delayed. This explains why alpine plants operate at surprisingly warm temperatures during the day (see discussion below). In fact, it has been shown that their photosynthetic metabolism is adjusted to the same high temperatures as experienced by plants of low elevation. Under bright weather conditions during the growing season, compact alpine plants may warm up to 30°C. Inflorescences may also heat up substantially above air temperature (Fig. 3).

Yet, without solar radiation, that is during the night and during the cold season under snow (winter) in seasonal climates (outside the tropics), alpine plants do experience cold conditions. Snow cover plays a key role in controlling life conditions in winter. Without snow protection, alpine plants may experience (and have to tolerate) temperatures down to −30°C, while under an insulating snowpack, temperatures rarely drop below 0°C. Not surprisingly, snow distribution is a key driver of plant species distribution (Spasojevic et al., 2013). Snow distribution, in addition to wind and solar radiation during the growing season, strongly interacts with topography. Therefore alpine landscapes are characterized by a mosaic of rather contrasting life conditions over short distances.

A single alpine slope may provide locations with seasonal mean temperatures for growing plant tissues at 2500 m elevation that differ by 10 K, thus they differ as much as air temperatures differ over 1700 m of elevation (if a decline of temperature by 0.6 degree per 100 m of elevation is assumed; Scherrer and Körner, 2009). For this reason, alpine landscapes are relatively safe havens for vegetation when the climate changes, because organisms can find suitable habitats over a few meters’ distance (Scherrer and Körner, 2011).

Alpine soils are often poor in nutrients, with a high fraction of nutrients trapped in soil organic matter, a nutrient fraction not available to plants. Alpine soils are often peaty or highly leached and quite acidic. For that reason highly specialized mycorrhizae symbiosis is essential, and these fungi are present even at the highest places where plants occur (Oehl and Körner, 2014). These fungi are essential to make soil nutrients available to alpine plants (Theodose and Bowman, 1997). In regions with a short growing season, this general shortage of soil nutrients is somewhat mitigated by the fact that soil microorganisms continue mineralizing plant debris over the long winter so that at flushing after snowmelt there is a short peak of high nutrient availability, including those nutrients which had accumulated in snow and become available with melt water. In such seasonal climates alpine plants must be specialized to capitalize on such nutrient peaks. In tropical alpine environments, the “endless” season, can somewhat compensate for the slow microbial nutrient provision.

Alpine Plant Life

How specialized are alpine plants to cope with alpine life conditions? From a physiological perspective, less than one would expect. Since plants photosynthesize only during light hours, the warm canopy conditions described above explain why CO₂ uptake

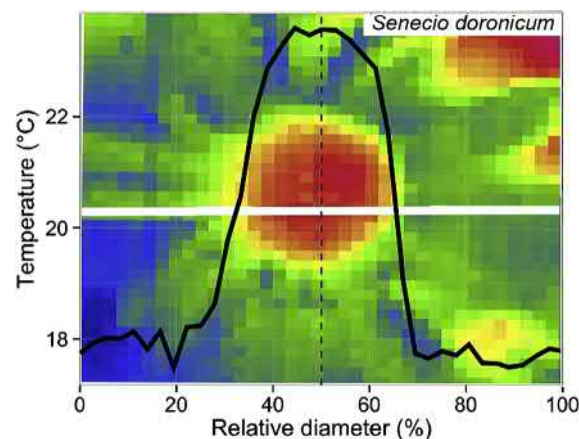


Fig. 3 The temperature in an alpine inflorescence under sunny weather conditions. Note the heated center where ovaries are located and where seeds will develop (Dietrich and Körner, 2014).

reaches a peak at roughly the same temperatures as in their lowland relatives (Körner, 2003). There is sound evidence that strong solar radiation does no harm to alpine plants, including UV-radiation (Lütz, 2012). Freezing tolerance is so high during the dormant season that winter is not an issue. Frost events can damage leaves and flowers during the growing season, yet the flora of the alpine biome is well adapted to cope with such events (Taschler and Neuner, 2004; Larcher et al., 2010; Ladinig et al., 2013). Since most alpine plant species grow clonally and thus live very long (potentially millennia), they do not depend on regular sexual reproduction, hence episodic losses of inflorescences or premature seeds are not fatal to them.

In contrast to photosynthesis (carbon uptake during the day) the investment of carbon into growing tissues is constrained by low temperatures, particularly during the night. Yet alpine plants can build new cells at substantial rates when temperatures are as low as 5°C, a temperature at which lowland plants (or crops) would scarcely grow. Alpine plants may even grow very slowly down to 0°C, but they take no advantage for growth from tissue temperatures above 15°C, as lowland plants do (Nagelmüller et al., 2017). Alpine plants thus utilize the short warm periods for growth, requiring very rapid development in cases where the season is very short. This calls for an adapted phenology, that is the seasonal succession of developmental events such as leaf expansion, flowering, fruiting, and controlled senescence and dormancy transition. However, there is a high diversity in alpine phenology, with some species ready to flower even before snow disappears and others flowering only very late in an otherwise short summer. Seed maturation must complement these rhythms of life. This life event shows a great deal of flexibility in alpine plants (e.g., Molau, 1993; Wagner et al., 2010).

The Alpine Biome Under Global Change

With its global occurrence, the alpine biome is particularly interesting for monitoring the influences of environmental changes at a large scale. Yet there are some misconceptions associated with the potential hazards of global warming on alpine ecosystems. Because of the central role of topography for shaping actual life conditions and because of the evolutionary adjustment to these many microclimatic niches in an alpine landscape, the alpine biome is possibly the safest of all biomes when the climate changes (Scherrer and Körner, 2011). Nowhere else can organisms escape from “unpleasant” locations faster and over shorter distances than in topographically structured alpine terrain. So there is little evidence that alpine ecosystems and alpine organisms are particularly vulnerable to climatic warming.

This does not mean that at a local scale a finely tuned interplay between plant and animal activity may easily escape from climate change driven running “out-of-phase.” Yet, at a scale of a few km² such problems will become greatly moderated by topographic diversity. Perhaps the most damaging change will be a shortening of snow duration for plants and animals that require snow protection. So changes in precipitation, especially in snowfall, are likely to have greater impacts than changes in temperature as such. At a global scale, there is a trend for increasing precipitation with increasing atmospheric temperature. So regionally snow pack may even increase (particularly at very high elevation) despite climate warming. There may be more frequent summer drought in some areas, the effect of which will depend on season length and soil depth. With a short season and deep soils, temperate, and subarctic alpine ecosystems are unlikely to experience fatal drought during dry episodes. However, Mediterranean alpine ecosystems might be impacted. There is evidence that the arrival of new species on high mountain summits has increased in recent years in the temperate zone, but it has decreased in the Mediterranean (Pauli et al., 2012; Gottfried et al., 2012). Mobile animals (birds and insects) respond faster than plants (Roth et al., 2014).

Less widely acknowledged are changes of global dimensions such as the steady rise in atmospheric CO₂ concentrations (a potential driver of photosynthesis) and atmospheric nitrogen deposition (a fertilizer). Because growth in alpine plants is (a) intrinsically slow, (b) limited by low temperature, and (c) strongly limited by the availability of a broad spectrum of soil nutrients, it is not surprising that in situ exposure to elevated concentrations of CO₂ over several growing seasons has no stimulating effect on plant growth (Körner et al., 1997; Inauen et al., 2012). So alpine plants do not seem to be carbon limited at the current atmospheric CO₂ concentrations.

In contrast, the addition of soluble nitrogen compounds is potentially very harmful, because freely available nitrogen is known to shift the competitive balance among species, with fast growing, “trivial” species outcompeting slow growing rare species (Bobbink et al., 2010). A trivialization of the flora during recent years had been documented for the Swiss forelands of the Alps (Roth et al., 2013). Although atmospheric loading with soluble nitrogen compounds from fossil burning had been reduced by employing catalysers in cars, emissions from intense agriculture has increased in many areas at the same time. While high mountain terrain is commonly less loaded, these nitrogen-limited ecosystems are particularly sensitive to N additions and depositions as low as 5–10 kg N ha⁻¹ a⁻¹ were found to exert significant changes (hence surpass what is considered a critical load; Bobbink et al., 2010).

At a global scale, land use and land transformation are possibly the most severe facets of global change in the alpine biome. With herding and fire, many high ecosystems become over-utilized and destroyed in some parts of the world, and under-used or rapidly abandoned in other parts. Although the most severe impacts occur in the upper montane (often deforested) belt, these activities reach into the lower part of the alpine biome, and once land becomes scarce at lower elevations the herders move to the alpine proper. Millennia of land use continues to impact many high elevation and alpine ecosystems globally (e.g., Noroozi and Körner, 2018; Monteiro and Körner, 2013; Miehe et al., 2019). These direct impacts on the alpine biome can be mitigated or reverted at local or regional scale, while the global atmospheric changes are beyond the reach of local stakeholders.

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Plant Diversity in Páramo—Neotropical High Mountain Humid Grasslands

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Abstract

The páramo landscape consists of natural grasslands above the closed forest line (generally at 3000–3500 m asl—above sea level) and below the glaciers (4500–5000 m asl), where these are present. They cover ~35,000 km² extending across Venezuela, Colombia, Ecuador, and northern Peru and a number of small patches between Costa Rica and Panamá. They constitute an ecological archipelago, distributed along the highest parts of the northern Andes. The vegetation is subjected to large daily temperature fluctuations, and mist cover alternates with high solar irradiation. Therefore, organisms have developed unique adaptive strategies to cope with abiotic conditions in this extreme environment, leading to important processes of speciation and evolutionary convergence. This has resulted in high endemism and a remarkable plant diversity, the highest among all alpine landscapes in the world (Fig. 1).

Páramos provide a range of ecosystem services that created a large social basis for its conservation, especially for water regulation. However, human activities, including agriculture, cattle grazing and mining, impact their capacity to provide benefits for the wider society. The current configuration and diversity of páramo cannot be assessed without considering its coexistence, positively and negatively, with human society. This situation is even more dynamic considering the yet little understood impact of global climate change. High mountain ecosystems are among the most exposed and vulnerable in the world to the effects of global warming and páramo is no exception. However, there is still a large knowledge gap about the actual effects on local temperature regimes and precipitation patterns and therefore, the associated impact on the ecosystem, its vegetation and society remain little understood.

Introduction: Description and Distribution of Páramo

The highest parts of the wet perhumid northern tropical Andes consist of fragile landscapes characterized by a high biodiversity (Körner and Spehn, 2002; Price, 2006). These ecosystems include alpine páramo grasslands and humid montane cloud forests, which originally covered large tracts in Venezuela, Colombia, Ecuador, and Peru. The páramo landscape consists of natural grasslands above the closed forest line and below the glaciers, where these are present. They cover ~35,000 km² extending across Venezuela, Colombia, Ecuador, and northern Peru (11° North to 8° South), and a number of small patches (less than 20,000 ha in total) between Costa Rica and Panamá (Fig. 2, Cuesta et al., 2014; Hofstede et al., 2003, 2014a,b; Llambí and Cuesta, 2014; Luteyn, 1999).

The South American páramos constitute an ecological archipelago, distributed along the highest parts of the northern Andes. In this insular environment, landscape diversity is high, because the Andes are relatively young in geological history, molded both by volcanic and glacial/periglacial activity, and distributed along wide elevation and latitudinal gradients. The vegetation is subjected to large daily temperature fluctuations, and mist cover alternates with high solar irradiation. Therefore, organisms have developed unique adaptive strategies to cope with abiotic conditions in this extreme environment (Azócar and Rada, 2006; Rada, 2016), leading to important processes of speciation and evolutionary convergence (Cuatrecasas, 1958; Hedberg and Hedberg, 1979; Monasterio and Sarmiento, 1991; Van der Hammen and Cleef, 1986). This has resulted in a high level of endemism and remarkable plant diversity. It is well documented that this tropical alpine zone is the richest in terms of plant diversity among all alpine landscapes in the world (Smith and Cleef, 1988; Cuesta et al., 2017). The páramo also exhibits an outstanding functional plant diversity (Llambí et al., 2014), reflected in a wide range of plant growth-forms including giant rosettes, sclerophyllous shrubs, tussock grasses, nongraminoid herbs, cushion plants and acaulescent rosettes (Hedberg and Hedberg, 1979; Ramsay and Oxley, 1997).

Páramo is of high social and economic importance, because it provides important ecosystem services, particularly the regulation of water for human consumption and irrigation (Buytaert et al., 2006; Buytaert and de Bièvre, 2012). While these ecosystem services helped to create a social basis for its conservation (Llambí et al., 2005; Sarmiento et al., 2017), other uses of páramo, including agriculture, cattle grazing and mining, affect their capacity to provide benefits to the wider society. Inhabitants of these regions reflect complex cultural and socio-economic conditions. While intensive potato-farming is present in easily accessible páramo around major population centers, many and more remote communities are made up of indigenous peoples and mestizo farmers that rely almost entirely on the natural resources of páramo, principally for agricultural production (Cuesta et al., 2012a,b; Ange-Jaramillo et al., 2002;

Hofstede, 2011; Sarmiento et al., 2017). All of these human uses have developed in a haphazard way, and are steadily affecting more areas. The current ecological conditions and biological diversity of páramo cannot be assessed without considering its coexistence, positively and negatively, with human society. This situation is even more dynamic because of the still poorly understood impacts of global climate change. High mountain ecosystems are among the most exposed and vulnerable to the effects of global warming and páramo is no exception (Castaño-Urbe, 2002; Cuesta et al., 2008; Tovar et al., 2013; Vuille et al., 2018). However, there is still a large knowledge gap concerning the actual effects of global change on páramo temperature regimes and precipitation patterns (Tovar et al., 2013; Ramirez-Villegas et al., 2014; Morueta-Holme et al., 2015).

Biogeography

The heterogeneity of the páramo landscape reflects the diverse abiotic, biotic, and anthropogenic processes (Llambí and Cuesta, 2014). The Northern Andes consists of three (northern portion) and two (central portion) *Cordilleras* (mountain ranges), divided by inter-Andean valleys. Climatic processes, such as the humid currents from the Amazon basin and the Equatorial Tropical Pacific (Humboldt), drier currents from the Caribbean and the Southern Tropical Pacific (Nazca), cloud cover and main wind directions give rise to more-or-less humid slopes and valleys, determining the characteristics of each of páramo zone (Rivera and Rodríguez, 2011). Present-day geological (vulcanism, glaciation) and geographical aspects (geomorphology, drainage, soils) determine different types of páramo, even at the local scale. Biogeography (origin, distribution, connectivity, and radiation) is another aspect that determines biodiversity and the classification of different páramos (Jørgensen and Ulloa, 1994). Finally, the type and degree of human intervention is an additional factor that determines the actual structure and functioning of páramo.

Different authors have proposed different classifications of páramo types, depending on geographical distribution, altitudinal zonation, vegetation physiognomy, climatic regime, and conservation status. The best known is the one proposed by Cuatrecasas (1958), based on a division into altitudinal belts: subpáramo (the lower, shrub-determined zone, understood as a transition between the mountain forest and open páramo, Fig. 3), páramo proper or grass-páramo (the typical páramo landscape, dominated by tussock grasses and giant rosettes, Fig. 1) and the highest-elevation super-páramo (a more open vegetation without full soil coverage and a high abundance of prostrate shrubs and herbs, cushions, lycopodia and lichens, Fig. 4).

Climatic processes are the basis for a bioclimatic classification of dry páramo, semi-humid, humid, very humid, super humid, and pluvial páramo (Rangel, 2000). The World Wildlife Foundation (WWF) proposed an ecoregional classification, distinguishing four different páramo ecosystems on the basis of their geographic situation on the Andean mountain ranges (Cordillera de Mérida páramo, Sierra Nevada de Santa Marta páramo, Cordillera Central páramo and Northern Andes páramo (Dinerstein et al., 1995). These bioclimatic and biogeographic classifications were combined by Josse et al. (2009) to devise a more detailed ecosystem classification at the scale of the Northern and Central Andes (from Bolivia to Venezuela). Within their Northern Andes phytoregion, three exclusive páramo macrogroups were identified. These were further subdivided into six ecosystems for páramo proper, three páramo wetland ecosystems and one ecosystem for superpáramo. This classification included the traditionally considered subpáramo or shrub páramo within the macrogroup of humid high Andean forests and shrublands.



Fig. 1 Páramo proper (or grass páramo) vegetation with stem rosettes (*Espeletia hartwegiana*) and tussock grass (*Calamagrostis effusa*). In the background, shrub dominated sub-páramo and high Andean forest (Los Nevados National Park, Colombia; 3600 m asl).

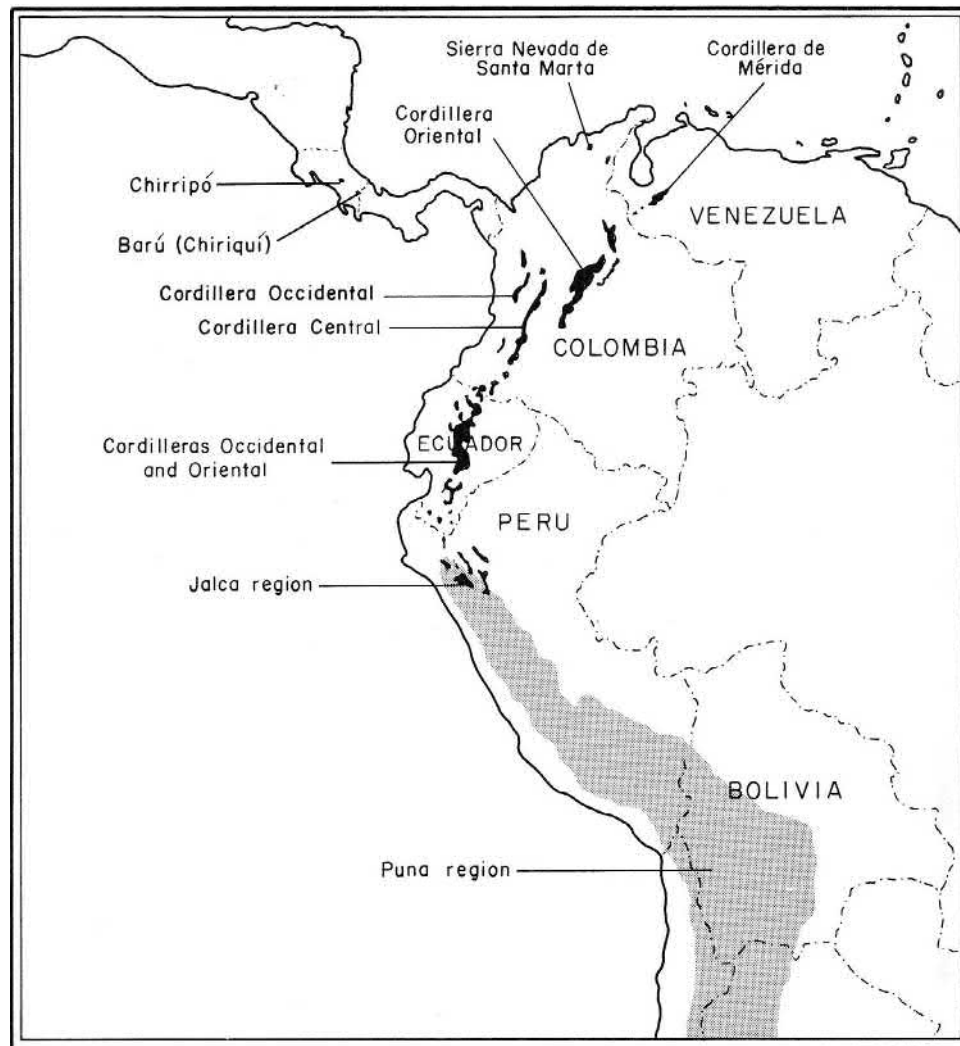


Fig. 2 Extension of páramo (black areas) in South and Central America. Taken from Luteyn J. L. (1999). *Páramos: a checklist of plant diversity, geographical distribution, and botanical literature*. Memoirs of the New York Botanical Garden; vol. 84. New York: NYBG.

Other authors used social and land use characteristics to describe different páramo types. Using a socio-ecosystem approach, [Monasterio and Molinillo \(2003\)](#) redefined the classic altitudinal zonation by Cuatrecasas, using a combination of natural and cultural characteristics. Their *piso andino* (or Andean belt) corresponds to the high mountain forest and lower páramo life zone and is characterized by highly productive crops (Andean tubers, fresh vegetables, flowers, etc.) that replace the natural páramo systems, especially in flat and more fertile areas. The *piso altiandino* (or high Andean belt) corresponds to the páramo proper belt where the upper agricultural limit is found, with an alternating system of crop planting and fallow lands which promotes successional processes leading to ecosystem regeneration. This area is naturally covered by tussock grasses and stem rosettes. Above the crop line, the only anthropogenic land use is extensive livestock grazing. At higher elevations they defined the *piso periglacial* (periglacial belt), where frequent night frost events impede agricultural activity and where the vegetation types are called the desert páramo and periglacial desert. Finally, [Hofstede et al. \(2002\)](#) proposed a categorization for health status of tussock-grass dominated páramo, describing five classes (from “poor” to “excellent” health condition) based on flora, fauna, and soil characteristics that, combined with social indicators, helped to determine the degree of disturbance.

Geological History

Páramo is a relatively young ecosystem; it might even be considered the youngest of all Andean ecosystems ([Castaño-Urbe, 2002](#); [Van der Hammen and Cleef, 1986](#)). The history of neotropical vegetation begins ~100 million years ago (Ma), when the South American continent separated from Gondwana. The uplift of the Andes initiated 40 Ma and during the Miocene, 10 Ma, the mountain range started to take its current shape and individual mountain massifs were connected, allowing for migration of plants from



Fig. 3 Lower elevation páramo (sub-páramo) dominated by shrubs and low trees (Sangay National Park, Ecuador; 3600 m asl).



Fig. 4 Higher elevation páramo (super-páramo) dominated by herbs, ground rosettes and cryptogams (Pichincha volcano, Ecuador; 4300 m asl).

the Southern (colder) mountain environments to the North. Also around that time, South America became connected to North America through the Panama Isthmus. After this, during the Miocene, several Holarctic taxa entered South America and the Andes continued to arise (Gentry, 1982). During the Pliocene, between ~ 5 and 2.5 Ma, there was abundant volcanic activity, at which time elevations above the treeline came into being. Only then the Andean range reached its current elevation, with relatively large areas covered by open vegetation above the continuous forest line (Morales et al., 2007). The landscapes above treeline connected with Northern and Southern temperate zones, creating the environment in which the current páramo vegetation could evolve.

The upper Andean forest and páramo belts evolved more or less simultaneously during this period and in the Early Pleistocene (4–2 Ma), and an early páramo vegetation (proto-páramo) developed. The early tropical biogeographical elements were species from lower (forest) environments that became adapted to the environment at higher elevation. The largest diversity of these elements is found in the Northeastern-most extension of the Northern Andes, the Cordillera de Mérida, near the Venezuela-Colombia border, which is geologically the oldest part of the Northern Andes. Some typical páramo genera like *Espeletia* have their centers of speciation here (Pouchon et al., 2018). Other genera migrated from the more temperate regions to the north and south,



Fig. 5 Indigenous páramo inhabitants (Chimborazo, Ecuador).



Fig. 6 Cattle grazing has transformed stem rosette and tussock grass dominated páramo proper in a compact, short mat of ground covering grass (Tolima, Colombia).

giving rise to an early vegetation of Poaceae, Cyperaceae, Asteraceae, and Ericaceae, among others (Van der Hammen and Cleef, 1986). During this time, genera of north temperate origin (*Alnus*, *Quercus*) also entered the Andean forest, signaling the next phase in connectivity between the Northern and Tropical cool biomes (0.3 Ma; Luteyn, 1999).

During the Pleistocene, glacial periods alternated with interglacial periods, with some severe cold periods. At that time there were numerous changes in the proportions of landscape cover between páramo and forest elements, although the páramo flora was already well established and probably dominated. There was a cold and wet period during which the last glaciation reached its maximum advance (42,000–25,000 BP), during which the glaciers and forest may have been connected at elevations between 2200 and 2700 m asl and the páramo belt must have been narrow and wet (Van der Hammen and Cleef, 1986). In contrast to this, between 21,000 and 14,000 BP there was a very cold but dry period. At that time glaciation was not so extensive, and the páramo belt was broad and covered most of the area above 2000 m asl. (Luteyn, 1999). At the beginning of the Holocene (13,000 BP) the climate became warmer and forest limits rose to elevations even higher than today. At that time, the páramo became restricted to the highest parts of the Andean mountain range. Finally, at about 2900 BP there was a remarkable climatic cooling that marked the last downward movement of the forest and páramo belts to their present-day positions (Wille et al., 2002). This series of past climatic changes and associated lowering and rising altitudinal belts and the narrowing and widening of areas occupied by páramo, caused páramo patches to be connected and separated repeatedly (Flantua and Hooghiemstra, 2018). It is expected that during colder periods, in which páramo occupied larger areas, the connectivity resulted in the rapid expansion of species over the Andes, while



Fig. 7 Potato cultivation and grazing of fields in fallow has transformed the páramo landscape in a mosaic of different levels of intervention that, in this case, led to low biodiversity and clear signs of land degradation (Guerrero, Colombia).

during warmer periods, many páramo areas were isolated from each other, resulting in species radiation. A spectacular example of this process involved the stem rosettes of the *Espeletia* complex, which is the fastest adaptive radiation recorded for plants (Díazgranados and Barber, 2017; Hofstede et al., 2014a,b; Madriñán et al., 2013; Pouchon et al. 2018). Therefore, the present páramo flora has many tropical as well as boreal elements, with genera that are relatively common (Sklenář et al., 2005) but with an extremely high level of species endemism (Luteyn, 1992).

Connectivity and Isolation

The historic rhythm of connectivity and isolation of different páramo regions contributed to species distribution and radiation (Van der Hammen and Cleef, 1986; Flantua and Hooghiemstra, 2018). Nowadays, páramo forms an ecological archipelago, distributed along the highest parts of the northern Andes, like a “chain of pearls” (Balslev, 2001). In total, it occupies $\sim 35,000 \text{ km}^2$ (Llambí and Cuesta, 2014). The northernmost páramo areas are the isolated complex at the Sierra Nevada de Santa Marta, in Colombia, and the small areas on top of the Talamanca mountain range in Costa Rica. Due to their isolation, both have a specific flora and fauna. The páramos in the Colombian Western Cordillera form isolated small patches that might have been connected in the past.

In the North of the Andean corridor is a large connected páramo complex in the Mérida Cordillera in Venezuela. From Tamá (the transborder páramo between Colombia and Venezuela) down to the Sumapaz massif south of Bogotá, there is a large and, in many areas, connected complex that covers the Colombian eastern Cordillera. The Central Cordillera, its southern continuation in the Colombian Massif, and the entire Ecuadorian Cordillera are of volcanic origin, resulting in a large mountain range of diverse maximum elevations. There are large, but separated complexes of páramo in the Colombian Nevados, the páramo of Las Hermosas, the páramo of the Colombian Massif and the Southernmost páramos, connected to the North Ecuadorian páramos of Carchi and Nariño. Within the Ecuadorian volcanic mountain ranges, the largest connected complex of páramos are found, covering the entire Eastern, or Cordillera Real, from the Cayambe Volcano down to the Sangay National park, only interrupted by the Ambato river valley. In the Ecuadorian Western Cordillera large but separated páramos complexes are found around the Cotacachi, Pichincha, Ilinizas, and Chimborazo volcanoes. In Southern Ecuador, where the Andes are older, and consist of heavily glaciated metamorphic geology, a large separated páramo complex is found west of the city of Cuenca (El Cajas). The Southernmost páramo extension is again a connected, but very narrow páramo covering the lower and wet páramo of the Cordillera de Sabanilla down to the Valley of Huancabamba (Hofstede et al., 2014a,b). The latter is generally considered as the biogeographical limit between the Northern and the Central Andes (Jorgensen and Ulloa Ulloa, 1994). South of the Huancabamba valley, a similar, but more seasonal ecosystem continues, locally known as Jalca.

The present pattern of connectivity and separation is being affected by human impact. In several areas the páramo has disappeared after transformation to productive grassland, potato fields or industrial pine plantations. This artificial separation has caused interruption of natural larger páramo complexes. On the other hand, large scale burning of páramo and Andean forest caused a downward movement of páramo vegetation, covering areas that were naturally covered by Andean forest (Ellenberg, 1979; Laegaard, 1992). This artificial lowering of the forest line caused an extension of the páramo biome (“paramisation”) and therefore

greater connectivity in certain areas. Normally, these areas are used for extensive animal husbandry that includes repeated burning. Therefore, the larger páramo extension through “paramisation,” and its associated connectivity, provide little possibility for native flora to expand and disperse to other areas and the most valued páramo plant and animal species disappear from these new páramo extensions (Hofstede et al., 2002).

The geological history of the Andes determined the origin of the páramo flora. The early uplift of the Andes (40 Ma) happened in a tropical environment without any connection with area of cooler climate. Therefore, the first elements of the páramo flora evolved from tropical ancestors. The result of this history is a páramo flora that, in terms of genera, consists of 7% páramo elements (genera endemic to the ecosystem), 34% Neotropical, 9% Austral-antarctic, 11% Holarctic, 21% broad temperate, 10% broad tropical, and 8% cosmopolitan. This means that, ~45% of all genera are of temperate origin and 45% are of Neotropical origin (Van der Hammen and Cleef, 1986).

The páramo endemic genera most likely originated in the Pliocene, while the immigrant genera would have arrived during the late Pliocene and Pleistocene. The characteristic caulescent rosette genus *Espeletia* originated in tree-like *Espeletiinae*, and it speciated during the Pleistocene to more than 150 extant species, the fastest adaptive radiation recorded for plants (Diazgranados and Barber, 2017; Morales et al., 2007; Pouchon et al., 2018; Van der Hammen and Cleef, 1986). The taxonomic group *Espeletiinae* was originally formed in the Venezuelan Andes (close to the border with Colombia), where the *frailejones* group (*Espeletia*-*Espeletiinae*) has a large number of endemic species. This is the oldest geological formation that harbors páramo and is the center of diversification and expansion (Cuatrecasas 1958; Pouchon et al., 2018; Smith and Koch, 1935). *Espeletia* is the largest evolutionary and adaptation “success” in the occupation of the most extreme environments (in terms of climatic conditions): its diversity in terms of form and function permitted *Espeletia* to occupy a wide range of habitats. It currently occupies habitats in all different páramo types between Venezuela and the North of Ecuador (Cuatrecasas 1958; Van der Hammen and Cleef 1986; Monasterio and Sarmiento 1991; Rada, 2016). Moreover, giant rosettes of the *Espeletia* complex have been shown to act as ecosystem engineers in the harsh superpáramo environments, improving local microhabitat conditions (including marked increases in soil organic matter), and having a positive-facilitation effect on the cover and species richness of many other páramo plants (Mora et al., 2018).

Plant Richness and Endemism

According to Luteyn’s (1999) checklist of páramo plants, there are approximately 3400 species of vascular plants and 1300 of nonvascular plants in the entire páramo biome. Sklenář et al. (2005) reports 3595 species of vascular plants in 127 families and 540 genera, 14 of which are endemic to the Northern Andes. Rangel (2000) estimated that the total number of páramo vascular plant species is at least 4700. The relatively large difference between these total numbers of species can be explained by different concepts of the split between Andean forest and páramo species or, in other words, where to place the virtual division line in the Andean forest—subpáramo ecotone.

The most species-rich families (including their approximate numbers of genera and species) are Asteraceae (100 genera and 710 species), Orchidaceae (57 genera and 580 species), Poaceae (40 genera and 150 species), Melastomataceae (12 genera and 110 species), and Bromeliaceae (7 genera and 100 species). Genera with the highest number of species (approximate numbers) are *Epidendrum* (Orchidaceae; 105 species), *Espeletia* (Asteraceae; 80 species), *Pleurothallis* (Orchidaceae; 80 species), *Diplostephium* (Asteraceae; 75 species), *Miconia* (Melastomataceae; 65 species), *Hypericum* (Hypericaceae; 55 species), *Monticalia* (Asteraceae; 55 species) y *Baccharis* (Asteraceae; 55 species) (Cuatrecasas, 1958; Luteyn, 1999; Rangel, 2000; Sklenář et al., 2005; Van der Hammen and Cleef, 1986). This list indicates that the taxa characteristic of the open, grassland-dominated páramo vegetation are included (Poaceae, Asteraceae, *Espeletia*, *Hypericum*), but most are taxa typical of the lower, shrub-dominated páramo (Orchidaceae, Melastomataceae Bromeliaceae, *Baccharis*). This reflects the trend that species richness generally decreases with increasing elevation. The highest species diversity is found between 3000 and 3400 m asl; above 4000 m asl, the number of species decreases (Beltrán et al., 2009; Cuesta et al., 2017).

The number of genera endemic to the páramo ecosystem is relatively low, but endemism at species level is very high (Luteyn, 1992; estimated at 60%, again depending on where the virtual division-line between Andean forest and páramo is placed). This is explained by the relatively young geological age of páramo. Specific endemism for the total area is high, but even higher for geographically isolated areas, like many of the páramo communities in Colombia and the Ecuadorian Western Cordillera (Luteyn, 1999). Also, endemism increases with increasing altitude and superpáramo has few species, but many are not found anywhere else in the world (Sklenář, 2000). The high and singular biodiversity is related to the diversity of ecological conditions created by a complex topography and glacial geomorphology (Llambí and Cuesta, 2014) resulting in a large number of different vegetation associations, each of which has its own species assembly (Rangel, 2000).

Rangel (2000) mentions 118 families, 567 genera, and 3380 species, just in Colombia. For the Ecuadorian páramo, a total of 1524 species of vascular plants have been reported, which is half the number of Colombian species in a similar-sized area. This can be attributed to lower degree of isolation of the Ecuadorian páramo complexes and their greater distance from the origin of radiation of páramo species in Venezuela-NE Colombia (Beltrán et al., 2009; León-Yáñez, 2011). In Ecuador, 628 species are endemic to the páramos which represents 15% of the total flora endemic to Ecuador. In addition, 75% of the species that are endemic to Ecuadorian páramos are considered endangered and only 48% of them are in protected areas (León-Yáñez, 2011). The Venezuelan páramo has 1420 species in an area five times smaller than that of Colombia or Ecuador (Briceño and Morillo, 2002). Two reasons explain the high species richness and endemism here: first, the Mérida Cordillera has high habitat

diversity with contrasting habitats and landscapes where cryothermic deserts mingle with wetlands. Second, this region is the center of diversification for páramo flora (Rodríguez and Rojas-Suárez, 1995; Pouchon et al., 2018). Due to its closeness to the Southern Andean region, the páramo flora of Perú is characterized by species associations that differ from those of other Andean countries. Besides typical páramo grass and grass-like genera (*Calamagrostis*, *Festuca*, *Stipa*, *Carex*), there are more taxa of southern origin, such as *Cortaderia*, *Chuquiraga* and shrubs in the Podocarpaceae (Novoa et al., 2011). In one single páramo complex in the Northern Peru (Pacaipampa) 116 vascular plant species were found, 51 of which are endemic to the area (Cuesta et al., 2012b, 2017). In Costa Rica, more than 350 species of vascular plants were identified, in addition to 230 bryophytes and 215 lichens (Kappelle, 2003).

Impact of Human Activities on Páramo Plant Diversity

Páramo has been used by people ever since the early days of human occupation of the South American continent (10,000 years BP). Although during most of this time, use was very low in intensity, due to the long interaction between people and páramo, the natural ecosystem has been altered and cultural diversity coexists with natural diversity; therefore, páramo should be interpreted as a socio-ecosystem. The history of human occupation of páramo has very different characteristics over time: during prehispanic times páramo was only used for communication, occasional hunting-gathering and water harvesting. During Spanish colonial times, it began to be used intensively for large-scale sheep grazing and wheat cultivation for export to Europe. After the agricultural reforms of the mid-20th Century, large *haciendas* were split up, and land use was diversified and the previously marginalized indigenous groups and displaced farmers chose páramo as permanent habitat for living and farming (González and Cárdenas, 1995; Hofstede et al., 2014a,b; Reyes, 1995; Molano, 2010; Monasterio, 1980; Recharte and Gearheard, 2001; Fig. 5). Originally, small scale land-use was developed at the lowest elevations and was of low impact; in fact, the existence of small-scale farming communities who benefitted from the use of the natural ecosystems added to overall landscape diversity and created a socio-ecosystem of coexistence that fostered large cultural and biological diversity (Maldonado and De Bievre, 2011). However, due to different social changes, such as marginalization, environmental degradation, climate change, and political initiatives, such as agricultural reform, the human communities encroached on the Páramo, and natural grasslands became increasingly transformed to agricultural fields. Even more damaging has been the intensive use of páramo for large scale, industrialized potato cultivation, mostly financed by city-based companies and landowners (Machado et al., 2010; Monasterio and Molinillo, 2003; Sarmiento et al., 2017).

The result of the history of human occupation is that nowadays, there are different levels of intensity of páramo use, depending on the region. Meanwhile, there are also still large areas of páramo with very little human impact because they are too wet, too inhospitable, or lack easy access. In total, 35% of páramo is included in protected areas (Hofstede et al., 2014a,b). The different land use types and intensities in this landscape result in a mosaic of different habitats, caused by high levels of patchiness of landscape elements. In some areas, this impact of land use contributes to the landscape diversity, but in others it constitutes the main threat to its existence (Hofstede, 2001; Monasterio and Molinillo, 2003).

The main agricultural activities affecting páramo vegetation are cattle grazing (Fig. 6) and its associated burning, and potato growing (Fig. 7). The impact of grazing on the ecosystem depends on the type of animal and its stocking rate. Páramo evolved without a high biomass of large herbivores and therefore, its vegetation is not adapted to grazing. Some growth forms, such as tussock grasses and ground rosettes, are able to tolerate moderate levels of grazing but others, particularly introduced stoloniferous species such as *Holcus lanatus* and *Pennisetum clandestinum*, tolerate grazing and trampling much better. Therefore, with higher grazing densities, these plants tend to increase in the landscape. Other native páramo species, particularly shrubs and endemic super-paramo herbs, are intolerant to grazing and trampling and tend to decrease their abundance or disappear. As a result, grazing affects the structure (more open, less tall) and composition of the vegetation (more creeping, stoloniferous, more exotic species and less shrubs and endemic herbs; Verweij, 1995; Molinillo and Monasterio, 1997, 2006).

In many regions, it is impossible to consider grazing independently from burning (except in the Venezuelan páramos, where burning is not a practice associated with cattle management). In most areas where páramo is used for cattle grazing, farmers tend to burn the tall tussock grass vegetation to provide the cattle with better access to regrowth (Hofstede, 1995; Vargas et al., 2002). These fires affect different species differently: some species tolerate moderate intensity and frequency of fires, such as tussock grass, creeping herbs and shrubs, but others are strongly affected, such as most woody plants and several native herbs. Therefore, with repeated fires the vegetation structure and composition changes (Laegaard, 1992; Verweij, 1995). The combination of grazing and burning has a synergistic effect. Research has identified areas with low grazing intensity and burning frequency, where the total number of species is higher than in natural páramo areas. However, when the species composition is considered, it becomes evident that several typical páramo species have disappeared from burnt and grazed areas, while new species (mostly exotics) have appeared. In areas of high grazing and burning intensity the number of species decreases, but vegetation cover is also less complete, contributing to soil erosion (Hofstede, 2001; Poulenard et al., 2004; Verweij, 1995).

Potato cultivation is widespread in several páramo regions, up to 4000 m asl. In most cases, cultivation is being rotated with animal husbandry: after 2 or 3 crops, the area is left for recovery, sowing grass for grazing. Traditionally, the fallow time was up to 20 years. However, recently, this has become as short as 3–5 years (Sarmiento and Llambí, 2011). Also, improved technologies and climate change have opened more páramo areas for potato cultivation (Morales et al., 2007). For cultivation, the entire natural vegetation cover is removed. Subsequent recovery of the natural vegetation after agricultural use depends on the length rotation time and on the style of land management. If the cultivated plots are large, rotation is short and during the fallow interval the landscape is used for dairy cattle, feeding on exotic grasses. Under these circumstances there is little chance of natural vegetation recovery.

On the other hand, in Venezuela several studies have analyzed semi-traditional system of páramo cultivation, with low intensity, varied crops and long fallow periods. This has resulted in a stable and acceptable level of restoration of nutrient cycling and plant diversity (Abadín et al., 2002; Llambí et al., 2003; Llambí and Sarmiento, 1998; Sarmiento et al., 2003; Sarmiento and Llambí, 2011). These studies showed that, contrary to the general belief that high Andean ecosystems are highly vulnerable, with low resilience, in fact with long fallow intervals (more than a decade) páramo does recover a considerable proportion of its plant species and plant community structure. However, some species will never recolonize the previously used parcels and alpha biodiversity is lower than before land use (Sarmiento et al., 2002, 2003).

High mountain ecosystems are generally considered among the most vulnerable to the effects of climate change. The aspects of climate change that potentially have an effect on páramo vegetation are increased temperatures, changes in precipitation regimes and higher irradiation. This can have an effect on the position of altitudinal belts, causing the disappearance of species that do not tolerate the new environment, combined with the appearance of species that better tolerate the new conditions. The new environmental conditions also favor increased human land use, with upslope shifts in agriculture, affecting the vegetation (Araujo and Rahbek, 2006; Anderson et al., 2011; Cuesta et al., 2012a). The upward movement of altitudinal belts, deforestation and agricultural activity at higher areas, in combination with the phenomenon of “paramisation” (fire-induced lowering the forest line) has caused that currently, in most high mountain areas it is impossible to identify the natural upper forest line (Hofstede et al., 2014a,b; Llambí et al., 2014).

At the species level, there are three responses to climate change: migration, adaptation or local extinction. An interaction between the three can be expected in mountain areas: an accelerated upslope migration of vegetation belts can result in immediate local extinction as well as impacts on phenology and physiology of species (Buytaert et al., 2010; Cuesta et al., 2012b; Parmesan and Yohe, 2003; Tovar et al., 2013). It is assumed that high mountain plant species are particularly sensitive to climate change because they have specific adaptations to extreme climatic conditions. If these conditions change, their developed adaptation gives them less competitive advantage. Also, mountain ecosystems have a limited range; their populations are fragmented, and species have many barriers to migrate to other areas (Bendix et al., 2013; Grabherr et al., 2010). If the patterns of climate change effects on vegetation in the páramo are similar to those observed in other mountain regions in the world (Peñuelas and Boada, 2003; Pauli et al., 2007; Sanz-Elorza et al., 2003), the species related to the highest-elevation vegetation belt (superpáramo) should be the most threatened (Buytaert et al., 2006; Cuesta et al., 2017).

Based on species distribution and climate models, it was estimated that ~60% of all páramo plant species will have populations heavily reduced or become extinct by 2080 (Cuesta et al., 2008, 2012b). However, as these same authors admit, it is risky to make estimates of extinction patterns based on future climate and vegetation distribution models, considering there is a high difference between different warming scenarios and there is little knowledge on the actual response of species to changing climatic conditions (Buytaert et al., 2010). To fill this knowledge gap, there is a wide network of GLORIA sites in the Tropical Andes (Cuesta et al., 2012b, 2017).

A recent study comparing historical vegetation records made by Humboldt during the 19th century with recent surveys of the vegetation of the Chimborazo volcano, suggest there has been an upward migration of many plant species associated with temperature warming (Morueta-Holme et al., 2015). Similar conclusions have been derived for Carabidae beetles based on more recent diachronic studies (Moret et al., 2016). So far, the few available empirical and theoretical studies from the paramos reinforce the idea that the loss and fragmentation of habitat exacerbate the risk of extinction of mountain species due to climate change (Larsen et al., 2011). However, more long-term, comparative field monitoring is essential to document the effects of climate change on high elevation páramo plant communities. Ongoing surveys within the system of permanent plots established in high mountain summits during the last decade by the GLORIA-Andes network will undoubtedly make an important contribution towards this goal (Cuesta et al., 2012b, 2017).

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Afro-Alpine Plant Diversity in the Tropical Mountains of Africa

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Glossary

Afro-alpine Zone A vegetation zone situated between the Giant Heath Forest and Nival Zones to the highest mountains in tropical Africa, characterized by strong diurnal variation in temperature.

Fromontane The phytogeographic “catch-all” for the archipelago-like moist upland vegetation scattered in sub-Saharan African and characterized by montane forests and grasslands rich in local and regional endemism.

Bio-temperature The mean value of daily mean temperature above 0°C divided by 365.

Ecotone An intermediate zone between two different ecological communities.

Endemic A taxon unique to a defined area; confined to a certain area.

General dynamic model A model that links the geomorphological life cycle of volcanic oceanic islands (from original emergence to submersion) to that of island species richness and endemism (through colonization, speciation and extinction).

Giant Groundsel The genus *Dendrosenecio* (Asteraceae), endemic to the tropical African mountains, and found at high elevation regions (>2500 m) in the Giant Heath and Afro-alpine Zones—typically the “flagship” genus of the Afro-alpine Zone although the genus is not endemic to this Zone.

Giant Lobelia A subset of the genus *Lobelia* (Campanulaceae) that have attained giant proportions, occurring in moderate to high elevations (>1300 m) in tropical Africa, Oceania and southeast Asia.

Páramos The Andean tropical alpine equivalent to the Afro-alpine, and characterized by giant forms similar to those in the Afro-alpine (although unrelated genetically); occurs from 2800 to 4700 m elevation.

Phylogenetics The study of the evolutionary history and relationships among individuals or groups of organisms.

Phytogeography The study of the geographic distribution of plant species and explanations thereof.

Speciation The biological process by which new species develop.

Species complex A group of species with unclear taxonomic boundaries, often due to intergrading morphological characteristics.

Tropical Alpine Zone The highest elevation regions within the tropics but below the Nival Zone; usually between 3200 and 4500 m elevation.

Abstract

The Afro-alpine Zone is a fragmented vegetation type that occurs above 3200 m elevation on 14 scattered mountains and covers some 4525 km² in tropical Africa. Defined by the strong diurnal climate of “summer every day and winter every night,” the Afro-alpine Zone is typified by a unique flora characterized by Giant Groundsel and Giant Lobelia species. The Afro-alpine Zone is mostly concentrated in the eastern region of the continent, with a single western occurrence on Mount Cameroon. It is estimated that the Afro-alpine region harbors between 515 and 521 species of flowering plants, 52 fern species, and >277 moss species, with endemism levels around 35% for flowering plants and 30% for mosses. This represents moderate diversity and richness compared to other tropical alpine areas such as the Páramos of the South American Andes and the highlands of New Guinea. Typical plant communities in the Afro-alpine are tussock- and shrub-dominated grasslands and alpine bogs or fens, in which are embedded communities of Giant Lobelias and particularly Giant Groundsels. Biogeographically, the evolution of Afro-alpine diversity appears to be driven by age, size, and the geographical proximity of the mountains to each other, similar to the processes described by the General Dynamic Model for oceanic islands but overall much more complex. Due to the difficulty of exploration in some of these mountains and the limitation and biases of the available literature, there is work to be done in terms of finalizing data on the Afro-alpine biotic composition and determining its underlying biogeographic history. Understanding these processes may provide important insights on the conservation of these unique habitats, which are especially threatened by immediate human activities (e.g., overuse of fire) and anthropogenic-driven climatic change.

The Afro-Alpine Zone on Tropical African Mountains

Introduction

The unique vegetation found above the forests on the highest mountains of tropical Africa has held a strong fascination for botanists and plant geographers for over a century (Engler, 1892; Grimshaw, 2001; Eggermont et al., 2009). The focus of this attraction has been the unique diversity in this Afro-alpine Zone (Hedberg, 1957; White, 1983; Plate 1), the similarities in plant form and function to other tropical alpine regions of the world (e.g., the Páramo of the Andes; Hedberg, 1970, 1992; Sklenář et al., 2011; Anthelme et al., 2014), and the phytogeographical “conundrum” of how a similar Afro-alpine flora evolved on different host mountains, despite the occurrence of large distances of unsuitable habitats separating them (Hedberg, 1957; Gehrke and Linder, 2014; Chala et al., 2017, etc.). Modern methods in ecology and biogeography have largely resolved these questions (e.g., Gehrke and Linder, 2009; Linder, 2014; Gehrke et al., 2016; Kandziara et al., 2016; Chala et al., 2017). Nevertheless, the fascination of this unique habitat in Africa, its species composition, and its charismatic giant species (Kandziara et al., 2016), remains strong.

Alpine vegetation in tropical Africa—generally referred to as the tropical Afro-alpine Zone and defined by strong diurnal temperature variation, as opposed to seasonal climate variation (Hedberg, 1951; Hauman, 1955; White, 1983)—is confined to the highest mountains in eastern Africa: Mounts Elgon, Kenya, Kilimanjaro and Meru; the Aberdare, Ruwenzori, Simien and Bale mountains; and the Virunga volcanoes (Sklenář et al., 2011); and one in western Africa: Mount Cameroon (Gehrke and Linder, 2014; Fig. 1; Table 1; Plate 1). Gehrke and Linder (2014) include the Cherangani Hills and the Loolmalasin, Hanang, and Imatong mountains (eastern Africa) in their Afro-alpine circumscription—although these would be considered marginal by other authors (e.g., Hedberg, 1951). In addition, scattered tropical alpine elements (and more extensive sub-alpine vegetation) can be found as far south as South Africa and on Madagascar and Réunion Islands, but none of those can be considered true tropical alpine environments (Gehrke and Linder, 2014). Carbutt and Edwards (2015) have argued for a temperate Austro-alpine definition for the Maloti-Drakensberg (part of Linder’s, 2014 Austro-temperate flora, and separated from Killick’s, 1978 Afro-alpine definition), given that this alpine area is ecologically and physiognomically distinct from the tropical Afro-alpine, notably due to strong seasonal rather than diurnal temperature variation. Separation of the African tropical montane (i.e., Afromontane sensu White, 1983) and tropical alpine (i.e., tropical Afro-alpine sensu Hedberg, 1951) is also supported by multiple-genera phylogenetic reconstruction (Linder, 2014).

The Afro-alpine Zone represents the smallest and youngest phytogeographical region in Africa (Hedberg, 1951; Linder, 2014). As is the case in African mountain floristics and phytosociology, debate continues around this vegetation’s best circumscription in the Afromontane phytogeographical concept conceived by White (1978, 1983). Nonetheless, we consider it pragmatic to follow Hedberg’s (1951) definition of this Zone on the “roof of Africa.” In tropical African mountains, the concept of “Zone” and “vegetation type” is largely synonymous in that these free-standing mountains of high relative elevation allow for clear bands of vegetation that are more or less discrete from one another (although ecotonal transitions are always present; Hedberg, 1951; Bussmann, 2006). The generalized order of sequence of these Zones, from lowest to highest elevation, is: Lowland Rainforest, Montane Forest (including Bamboo Forest and Cloud Forest), Giant Heath Forest, Afro-alpine, and Nival (Hedberg, 1951; Niemelä and Pellikka, 2004; Bussmann, 2006; Fig. 2). Following Hedberg (1951), the Afro-alpine Zone is bounded by the Giant Heath Forest Zone below and the Nival Zone above, in an envelope of ca. 3200/3500–5000 m. Grimshaw (2001) argues for the inclusion of the Giant Heath Zone into the Afro-alpine Zone, but we confine ourselves to Hedberg’s (1951) more discrete definition that separates the two (although the lower elevation limit of Afro-alpine varies according to authors, e.g., Hedberg 3500 m; Gehrke and Linder 3200–3600/3800 m).

African mountain building resulting in elevations high enough to support alpine vegetation has been in progress since the Eocene (Fig. 3), mostly from repeated volcanic activity and uplift events associated with the East African Rift System and the



Plate 1 Tropical African alpine (Afro-alpine) landscapes. (A) Batu Summit, Bale Mountains (Ethiopia), c.4000 m, with *Lobelia rhynchopetalum* (Campanulaceae; erect plant on left) and *Alchemilla haumanii* (Rosaceae; dominant gray shrub); (B) Freshfield Pass, Ruwenzori (Uganda), c.4600 m, with *Dendrosenecio adnivalis* (Asteraceae); (C) Alpine moorland, Mount Cameroon (Cameroon), c.3800 m, dominated by mosses and *Pentaschistis mannii* (Poaceae); (D) *Dendrosenecio keniodendron* community in alpine tussock moorland, Mount Kenya (Kenya); (E) *Alchemilla argyrophylla* thickets, Mount Elgon (Uganda), c.4000 m, with *Dendrosenecio elgonensis* in the background; (F) Tarn on Mount Elgon (Uganda), c.3800 m, surrounded by *Dendrosenecio elgonensis*. Photographs: Peter Linder (A and B), Berit Gehrke (C), Tara Hetz (D), Ralph Clark (E and F).

Cameroon volcanic line (Burke, 2001; Schlüter, 1997; Tsafack et al., 2009). The result is 14 scattered, high-elevation mountains in eastern Africa and one in western Africa that supports isolated Afro-alpine habitats, with these host mountains being 40 million years (the Bale and Simien Mountains) to less than one million years old (Mount Meru), or still volcanically active (Mount Cameroon) (Table 1). Of the 14 host mountains, only the Ethiopian Highlands (Bale and Simien mountains), Mount Elgon, and the Imatong date from late Eocene, with most of the other mountains (at least in terms of factors allowing them to reach current elevations) being younger (Schlüter, 1997; Gehrke and Linder, 2014).

From Hedberg's (1951) stricter definition of a lower limit of 3500 m to Gehrke and Linder's (2014) laxer lower limit of 3200 m, the scattered tropical Afro-alpine fragments together cover between 3500 and 4525 km². According to Gehrke and Linder (2014), the largest Afro-alpine areas occur in the Ethiopian Highlands (2200 km²), with the Bale Mountains hosting the largest single component (1200 km²); the Cherangani Hills, the Hanang, the Imatong, and the Loolmalasin mountains have the smallest area components, each less than five square kilometers (Gehrke and Linder, 2014; Table 1). It is interesting to note that there is only a weak correlation between Afro-alpine surface area and the summit elevation of the host mountains (Fig. 4). This is indicative that absolute elevation is not as important as the surface area present within the suitable climatic belt and suggests that the climatic envelope suitable for the Afro-alpine evolution has been increasing relative to the host mountain elevation since the Miocene.

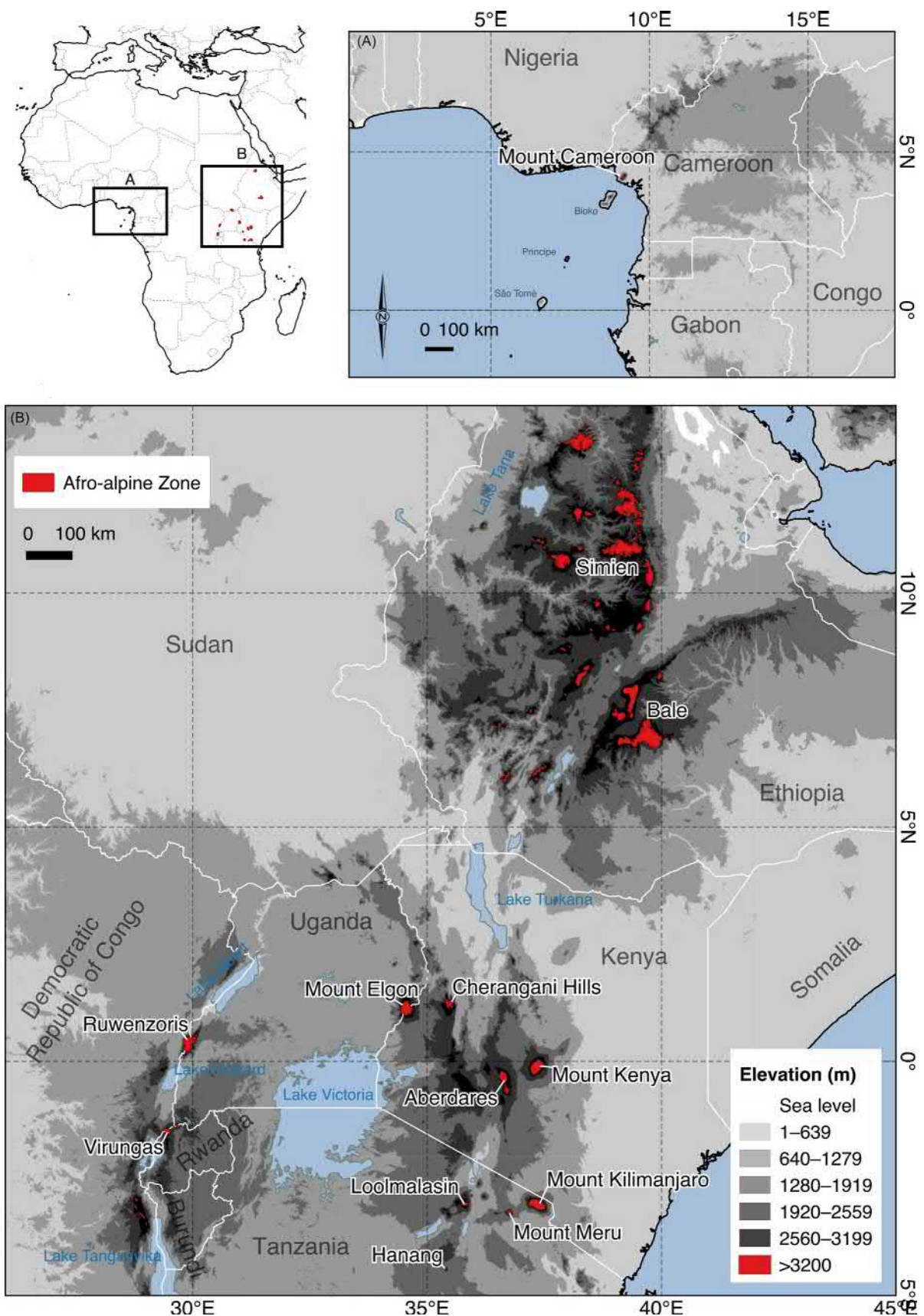


Fig. 1 The Afro-alpine Zone in tropical Africa. (A) Eastern Africa; (B) Western Africa. Based on Gehrke, B. and Linder, H. P. (2014). Species richness, endemism and species composition in the tropical Afroalpine flora. *Alpine Botany* **124**, 165–177.

Table 1 The 14 tropical African mountains hosting Afro-alpine vegetation, indicating the approximate Afro-alpine extent on each, their summit elevation, and the approximate ages of their orogenies (in millions of years, Mya)

Host Mountain	Afro-alpine area (km ²)	Summit elevation (m)	Age (Mya)	Country location
Bale	1200	4377	7–40	Ethiopia
Simien	1000	4533	26–40	Ethiopia
Mount Kenya	600	5199	2.5–5	Kenya
Ruwenzoris	500	5109	3–8	Democratic Republic of the Congo (DRC), Uganda
Mount Elgon	450	4321	12–23	Kenya, Uganda
Mount Kilimanjaro	420	5895	1–2.5	Tanzania
Aberdares	280	3995	5–6.5	Kenya
Mount Meru	20	4566	0.06–2	Tanzania
Virungas	20	4506	0.2–12.6	DRC, Rwanda, Uganda
Mount Cameroon	15	4100	0–25	Cameroon
Cherangani Hills	>5	3369	2–3	Kenya
Hanang	>5	3417	0.2–2.1	Tanzania
Imatong	>5	3187	10–25	South Sudan
Loolmalasin	>5	3682	1.4–1.9	Tanzania
Total: 4525 km²		Average: 4304 m		Countries: 8
Average: 323 km² per mountain				

Adapted from Gehrke, B. and Linder, H. P. (2014). Species richness, endemism and species composition in the tropical Afroalpine flora. *Alpine Botany* **124**, 165–177.

Floristic Diversity

Data availability and constraints

Different elevational bounds, and therefore spatial delimitations of the Afro-alpine Zone by different authors have resulted in numerous different floristic statistics for Afro-alpine diversity (Gehrke and Linder, 2014). The most recent and comprehensive assessment of floristic diversity is Gehrke and Linder's (2014) work on flowering species diversity and distributions in the Afro-alpine Zone, and is the first such synthesis following Hedberg's (1957) much earlier work. On-going and unpublished work (e.g., Abdi, 2013; Wekesa, 2015) will require a further revision of Gehrke and Linder's (2014) work in future.

As with any spatially defined entity, "species accounting" is always in flux, with tallies changing as continued work in relatively poorly botanized areas are targeted for further exploration. Additionally, new records come to light, the taxonomies of species' complexes are untangled, and herbarium records become easier to access in a digitized world. Even Gehrke and Linder's (2014) work shows conflicting figures, and how they arrived at their figures (especially for endemic tallies) is not completely clear. Despite the above, we know more about plant diversity in the Afro-alpine than before, thanks largely to Gehrke and Linder (2014).

Although some non-Spermatophyte plants—like ferns, mosses and liverworts—and organisms like lichens are ecologically important components in the Afro-alpine (Pócs, 1991; Eggermont et al., 2009; Wekesa, 2015) and range in elevation into the Nival Zone, they did not form part of Gehrke and Linder's (2014) work, which focused on flowering plants. Gathering such non-Spermatophyte data for the Afro-alpine would require similar methods used by Gehrke and Linder (2014) for flowering plants, as most relevant data remain embedded in national and regional flora publications or incidental records. Although it primarily presents an interesting opportunity for future work, a brief window into this diversity is provided.

While Gehrke and Linder (2014) provide the most comprehensive figures for flowering plant diversity, Hemp (2002) provides the most comprehensive overview of available fern data. Although his data are confined to Mount Kilimanjaro and regional comparisons to past works, Hemp (2002) states that this mountain has the highest fern diversity in eastern Africa, and therefore gives us some indication of fern diversity in the Afro-alpine. Although most moss collecting on tropical African mountains has been in Montane Forests, Bizot et al. (1978), Pócs (1991), and Wekesa (2015) provide an insightful sample of moss diversity in the Afro-alpine. We have not considered liverworts and lesser-known lichens in this contribution, other than incidental notes, for instance from Pócs (1991).

Flowering plant diversity in the Afro-alpine

According to Gehrke and Linder (2014) the number of Afro-alpine flowering plant species, in its liberal sense (i.e., above 3200 m) is considered to be between 515 and 521 species (representing 50 families and 191 genera), versus 155 species (representing 29 families and 70 genera) in its stricter sense (i.e., above 3600 m) (Table 2). The best-represented families above 3200 m are Asteraceae (comprising 26% of the Afro-alpine flora), followed by Poaceae (11%), Fabaceae and Rosaceae (both 5%); above 3600 m this becomes Asteraceae (28%), Poaceae (21%), and Rosaceae (8.5%). The most species-rich genera (above both 3200 and 3600 m) are (in numerical order): *Senecio*, *Alchemilla*, *Dendrosenecio*, *Lobelia* and *Helichrysum* (Plates 2 and 3); *Festuca* and *Suertia* become more important proportionally in the flora above 3600 m. The highest elevation recorded for an Afro-alpine flowering species is *Helichrysum newii*, at 5670 m on Mount Kilimanjaro (Willis, 2000).

Gehrke and Linder (2014) determined four mountain clusters in the Afro-alpine based on floristic similarity (Table 2). The South-eastern East African Mountain Cluster (comprising Mounts Elgon, Kenya, Kilimanjaro, Meru, the Cherangani Hills, Hanang,

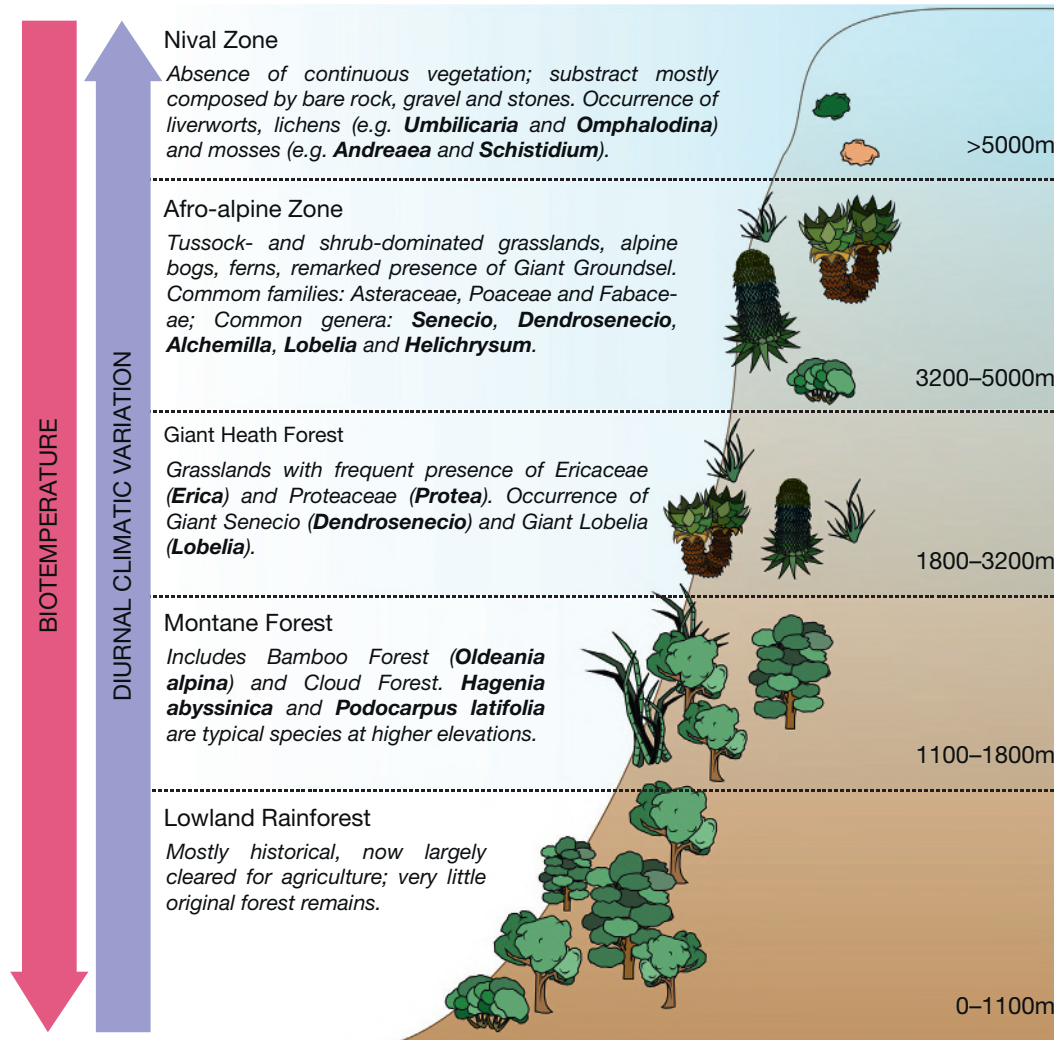


Fig. 2 Schematic of the Vegetation Zones in tropical African mountains. Based on Bussmann, R. W. (2006). Vegetation zonation and nomenclature of African mountains—an overview. *Lyonia* 11, 41–66.

Loolmalasin and the Aberdares) has the highest species diversity, harboring 363 species. The West African Mountain Cluster (comprising Mount Cameroon) has the lowest species diversity, with 51 species. The Western East African Mountain Cluster (comprising the Virungas and Ruwenzoris) has 339 species, and the Northern East African Mountain Cluster (comprising the Imatong and the Ethiopian highlands) has 306 species. Floristically, the West African Mountain Cluster is sufficiently distinct from the remainder of the Afro-alpine to be considered its own sub-region within the Afro-alpine (Gehrke and Linder, 2014, confirming Smith and Cleef, 1988). Hedberg (1964) suggested that the Ethiopian component (most of Gehrke and Linder's, 2014 Northern East African Mountain Cluster) should be its own subgroup due to the absence of *Dendrosenecio* and most shrubby *Alchemilla*, and the unique presence of *Primula* and *Rosa*, although these differences are not enough to statistically alter Gehrke and Linder's (2014) analysis (further fieldwork, aligned with phylogenetically weighted approaches and standardized field methods in the generally poorly explored Ethiopian Highlands, may change this however).

Of the individual mountain ranges, the Bale Mountains (in south-eastern Ethiopia) have the highest Afro-alpine species diversity (at 274 species; Fig. 5; Table 2), while Loolmalasin has the lowest (at 30 species). Other high diversity highlands are Mounts Elgon (273 species) and Kenya (269 species), the Aberdares (262 species), the Simien Mountains (238 species), and Mount Kilimanjaro (227 species). It is surprising that the Ruwenzoris score much lower (at 167 species) than the Virungas (with 180 species), and that Mount Meru (116 species) has substantially fewer species (111 fewer species) than its larger neighbor, Mount Kilimanjaro. Unsurprisingly, therefore, species diversity is proportional to Afro-alpine area (Fig. 6). In contrast, small mountains may host notable species richness. For example the Virungas harbor 180 species despite having only a 20 km² alpine area, while the neighboring, much larger (500 km²) Ruwenzoris are home to only 167 species. Mount Elgon, despite having only 450 km² of Afro-alpine area, has the second highest species richness (273 species)—a level of richness comparable to that of the massive 1200 km² alpine area of Bale (274 species).

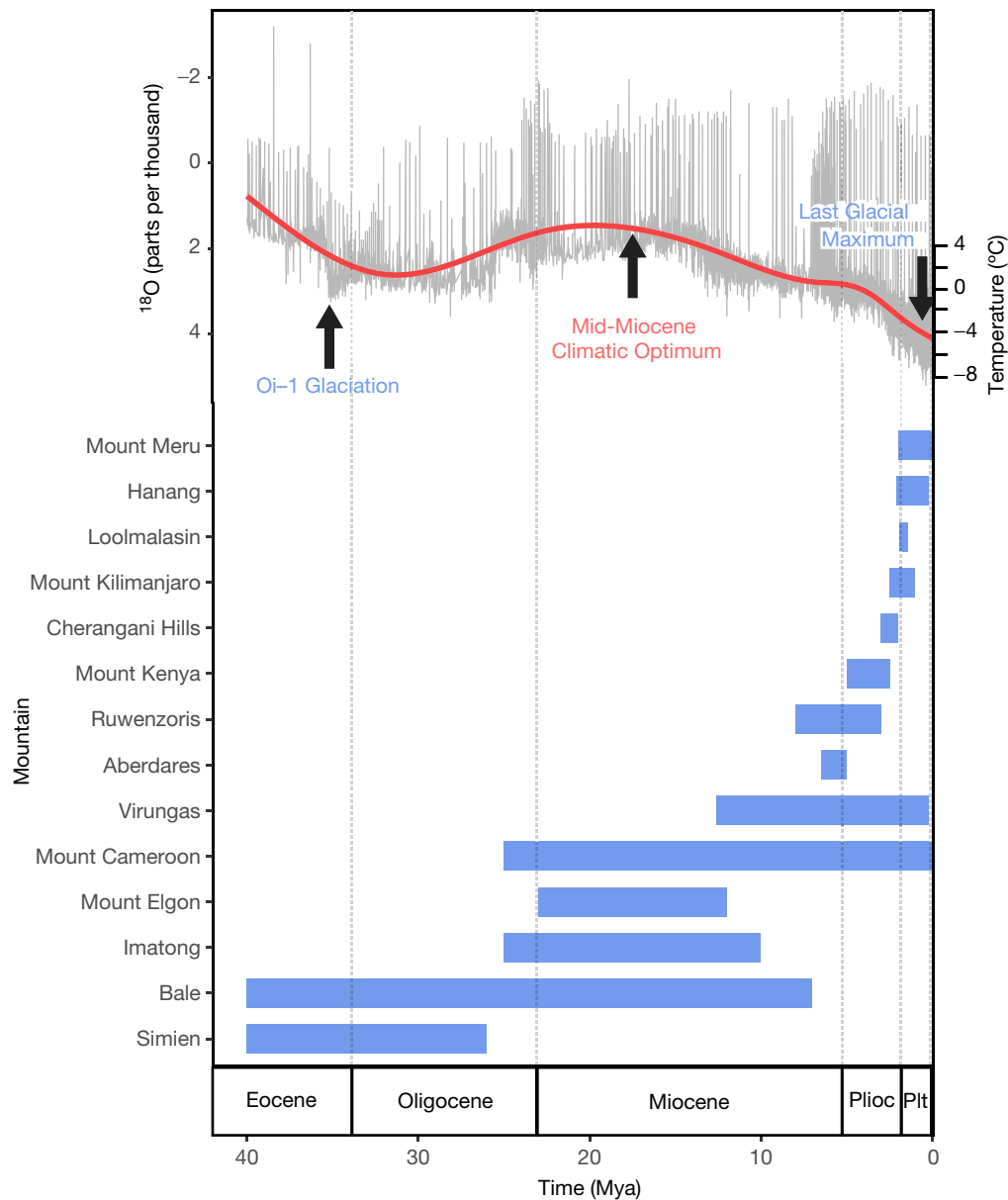


Fig. 3 Orogeny of the 14 Afro-alpine host mountains in tropical Africa (data from Burke, K. (2001). Origin of the Cameroon Line of volcano-capped swells. *The Journal of Geology* **109**, 349–362; Schlüter, T. (1997). *Geology of East Africa*. Berlin: Borntraeger; and Tsafack, J.-P. F., Wandji, P., Bardintzeff, J.-M., Bellon, H. and Guillon, H. (2009). The Mount Cameroon stratovolcano (Cameroon Volcanic Line Central Africa): Petrology, geochemistry, isotope and age data. *Geochemistry, Mineralogy and Petrology* **47**, 65–78) and main climatic events since the Eocene. $\delta^{18}\text{O}$ = oxygen isotope found in biologic sedimentary record, in parts per million (adapted from Zachos, J., Pagani, M., Sloan, L., Thomas, E. and Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Mya to present. *Science* **292**, 686–693 and Veizer, J., Ala, D., Azmy, K., Bruckschen, P., Buhl, D., Bruhn, F., Carden, G. A. F., Diener, A., Ebner, S., Godderis, Y., Jasper, T., Korte, C., Pawellek, F., Podlaha, O. and Strauss, H. (1999). $87\text{Sr}/86\text{Sr}$, $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ evolution of Phanerozoic seawater. *Chemical Geology* **161**, 59–88) Plioc: Pliocene; Plt: Pleistocene; Holocene (0.011 Mya–present) not displayed due to figure size.

Fern diversity in the Afro-alpine

Although Africa is relatively fern species-poor, the Afromontane region sensu White (1978) is one of the richer fern enclaves on the continent (Liu et al., 2016). In this Afromontane sensu lato, fern diversity is highest within the Montane Forest Zone (Hemp, 2002), although those occurring in the Afro-alpine perhaps show more interesting macro-scale distribution patterns with associated biogeographical interest (Aldasoro et al., 2004). Ferns are recognized as having varying elevation distributions on different mountains in tropical Africa, and species elevation limits vary from one mountain to another (Hemp, 2002), making it more challenging to define a particular Afro-alpine fern flora. Sampling deficiency is almost certainly a strong factor, with records (distribution and elevational) currently being ad hoc rather than representing a reliable elevation continuum across the Afro-alpine (only Wekesa, 2015 did this, for Mount Kenya). Nevertheless, the fern flora of the Afro-alpine is biogeographically

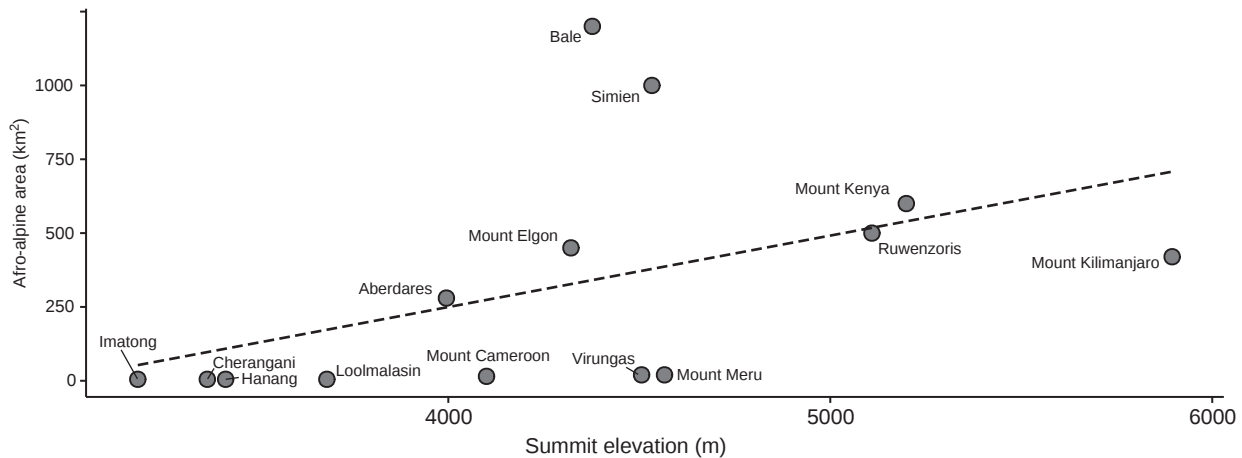


Fig. 4 The relationship between surface area and summit elevation in the Afro-alpine Zone of tropical Africa.

Table 2 Patterns of flowering plant species diversity and endemism in the Afro-alpine Zone of tropical African mountains

Site	Plant diversity	Endemics
Afro-alpine sensu lato (>3200 m)	515–521 (av. of 518 = 100%)	168–184 (32–36)
Afro-alpine sensu stricto (>3600 m)	155 (30)	155 (30)
Northern East African Mountain Cluster	306 (59)	85–90 (16–17)
Bale	274 (53)	6–11 (1–2)
Simien	238 (46)	22–24 (4–5)
Imatong	65 (13)	0 (0)
South-eastern East African Mountain Cluster	363 (70)	54–97 (10–19)
Mount Elgon	273 (53)	15–17 (3)
Mount Kenya	269 (52)	6–8 (1–2)
Aberdares	262 (51)	7 (1)
Mount Kilimanjaro	227 (53)	7 (1)
Mount Meru	116 (22)	0 (0)
Cherangani Hills	87 (17)	1 (0)
Hanang	63 (12)	0 (0)
Loolmalasin	30 (6)	0 (0)
Western East African Mountain Cluster	339 (65)	31–54 (6–10)
Virungas	180 (35)	8–9 (2)
Ruwenzoris	167 (32)	10–11 (2)
West African Mountain Cluster (=Mount Cameroon)	51 (10)	0–1 (0)

Given the conflicting data available for Endemics, both lower and upper figures available are provided. For both Plant Diversity and Endemism, percentage of the Afro-alpine flora (i.e., occurring >3200 m) is indicated in parentheses.

Adapted from Gehrke, B. and Linder, H. P. (2014). Species richness, endemism and species composition in the tropical Afroalpine flora. *Alpine Botany* **124**, 165–177.

fascinating, having strong links to the temperate montane grasslands of southern Africa (as many as 70% shared species) and the sub-Antarctic islands (Jacobsen and Jacobsen, 1989; Aldasoro et al., 2004).

Hemp (2002) provided the most data for considering an Afro-alpine fern flora, based on extensive work on Mount Kilimanjaro and comparisons with previous work in the region by Pichi Sermolli (1983, 1985), Johns (1991) and Faden (1994). Accordingly, it appears that there are at least 52 Afro-alpine fern species (34 from 3200 m upwards, dropping to only 18 species above 3600 m). The robustness of Hemp's (2002) work is evident when compared Jacobsen and Jacobsen (1989), who only record 26 species above 3200 m and eight species above 3600 m (from the Kenyan highlands and Albertine rift mountains). The record for the highest elevation fern is *Cystopteris fragilis* at 4750 m (Willis, 2000), followed by *Huperzia saururus* at 4575 m (Jacobsen and Jacobsen, 1989).

Moss diversity in the Afro-alpine

According to Geffert et al. (2013), the eastern African mountains are a global center of moss diversity, mirroring a global trend wherein mountains play a much more important role in driving moss diversity and endemism than does latitude. Spence and Pócs (1989) recorded 277 moss species from the Afro-alpine in eastern Africa. From Bizot et al. (1978), some 72 species are present at or above 4000 m, with *Andreaea mildbraedii* reaching 5000 m (Bizot et al., 1978) and *Schistidium apocarpum* reaching 5050 m (Spence and Pócs, 1989). On Mount Kenya the mosses *Grimmia* (forming "moss balls"; Hedberg, 1964; Pócs, 1991) and *Andreaea* occur at



Plate 2 Characteristic genera of the Afro-alpine include *Senecio* and *Euryops* (both Asteraceae), *Alchemilla* (Rosaceae) and *Swertia* (Gentianaceae). (A) *Senecio purpureus*, a wide-spread species in the Afro-alpine and temperate Afro-austral grasslands—here on Mount Cameroon (Cameroon), c.3800 m; (B) *Euryops brownei*, endemic to the Aberdares, Cherangani Hills and Mounts Elgon, Kenya and Meru—here on Mount Elgon (Uganda), c.3800 m; (C) *Alchemilla argyrophylla*, a widespread species in the Afro-alpine, here on Mount Elgon (Uganda), c.4000 m; (D) *Swertia subnivalis*, Mount Elgon (Uganda), c.3800 m. Photographs: Berit Gehrke (A), Ralph Clark (B–D).

higher elevations (4600–4800 m) than any of the vascular plants on that mountain (Wekesa, 2015). Pócs (1991) indicates that *Dendrosenecio* communities, alpine tussock grassland/shrub land and rocky cliffs are the most important Afro-alpine habitats for mosses (as well as for liverworts and lichens). Willis (2000), for example, noted that 40 moss species could occur on one *Dendrosenecio* plant in Mount Kilimanjaro's Afro-alpine Zone. As is the case for ferns, moss species distributions show intriguing connections to the temperate mountains of southern Africa, the southern hemisphere in general (e.g., *Bryum laevigatum*), and the sub-Antarctic (Bizot et al., 1978; Pócs, 2004). Within the Afro-alpine Zone, the floristic relationship between the moss flora of Mounts Kilimanjaro and Kenya is stronger than between any other mountains (Pócs, 1991).

Comments on liverwort and lichen diversity in the Afro-alpine

According to Pócs (1991), at least 25 liverwort species occur on Mount Kilimanjaro's Afro-alpine Zone above 3200 m, 19 of which extend above 3600 m; *Marsupella africana* reaches 4200 m (Pócs, 1991). Eggermont et al. (2009) indicate that *Umbilicaria* and *Usnea* lichens dominate in the Nival Zone of the Ruwenzoris, and Pócs (1991) recorded *Omphalodina melanophthalma* and *Umbilicaria aprina* at 5400 m on Mount Kilimanjaro. Just as with flowering plants, distribution patterns of Afro-alpine ferns and mosses, liverworts and lichens have complex and interesting biogeographical relationships within the Afro-alpine and beyond, notably with the high Asian mountains (Pócs, 1991).



Plate 3 Everlastings (*Helichrysum*, Asteraceae) are typical of the Afro-alpine Zone. (A) *Helichrysum stuhlmannii*, widespread in the Afro-alpine, here on the Bale Mountains (Ethiopia); (B) *Helichrysum* sp., in bud on Mount Cameroon (Cameroon), c.3600 m; (C) *Helichrysum* cf. *formosissimum*, in flower on Mount Elgon (Uganda), c.3800 m; (D) *Helichrysum* cf. *meyer-johannis*, Mount Elgon (Uganda), c.3800 m; (E) Alpine grassland dominated by *Helichrysum stuhlmannii*, Mount Elgon (Uganda), c.3800 m. Photographs: Peter Linder (A), Berit Gehrke (B), Ralph Clark (C–E).

Endemism

Data sources and constraints

As for flowering plant diversity, Gehrke and Linder (2014) provide the most recent synthesis of flowering plant endemism in the Afro-alpine. Unfortunately however, this work provides confusing results that are difficult to interpret in relation to elevation (above 3200/3600 m), as is their grouping of four mountain clusters, versus consideration of individual mountains (e.g. their “single mountain endemics” concept). There are also discrepancies between the figures in the tables, text and supplementary material that make firm endemism figures difficult to discern.

Although Aldasoro et al. (2004) indicates that the mountains of eastern and western Africa host significant fern endemism, actual data on Afro-alpine fern endemism was difficult to source. As for diversity, it may be that a careful mining of regional literature will yield accurate estimates of levels of Afro-alpine fern endemism and associated patterns; as a result we have excluded ferns from this component. Pócs (1991) provided the most detail on probable moss endemism for the Afro-alpine, although these

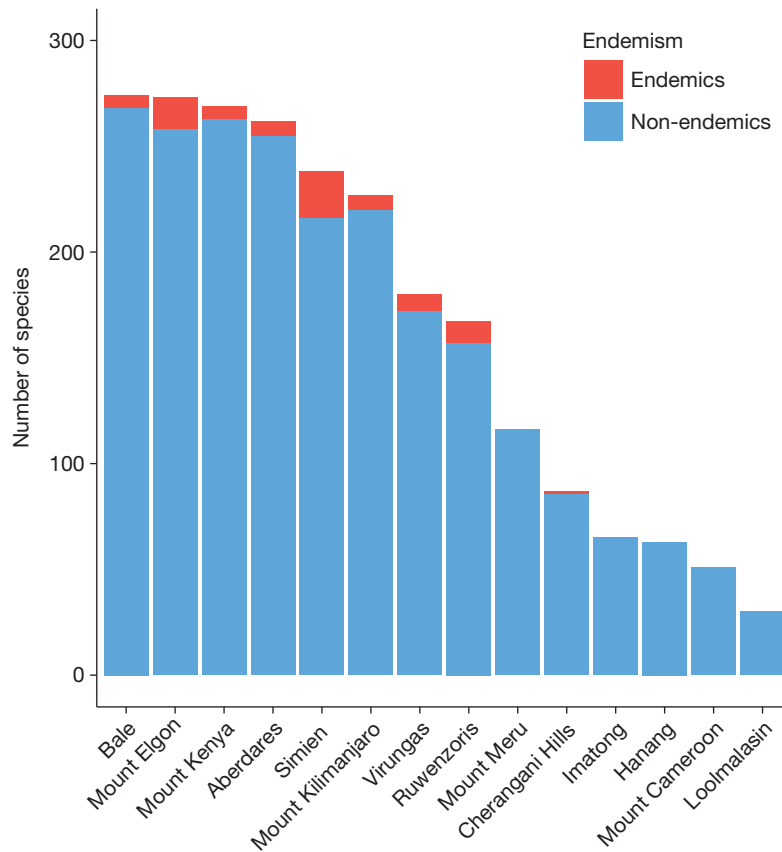


Fig. 5 Plant species richness and endemism as distributed in the Afro-alpine Zone of tropical Africa.

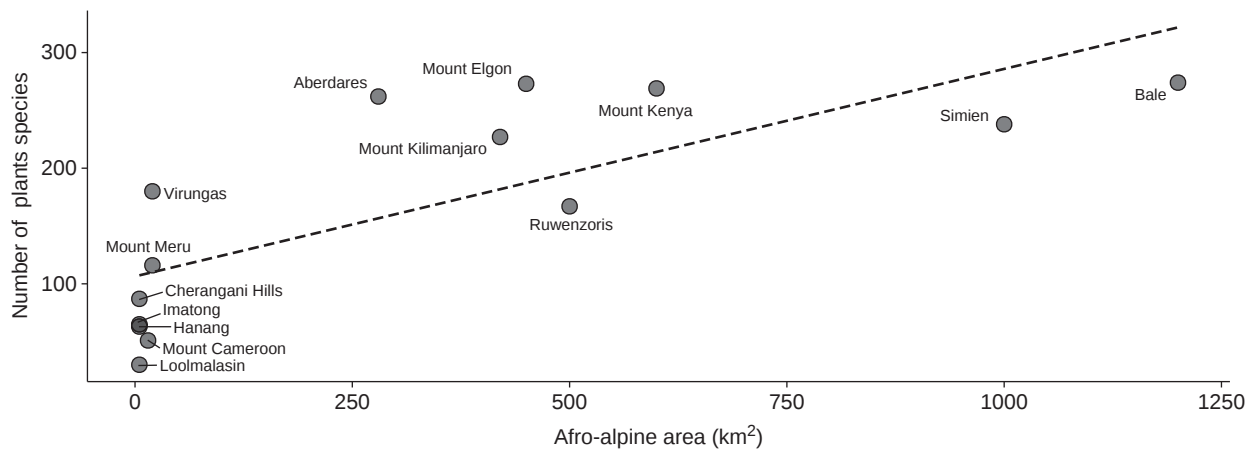


Fig. 6 Species-area curve for Afro-alpine plant richness in the tropical African mountains.

data are still scanty. As for ferns, data on lichen endemism is unavailable at present without a dedicated data gathering process, and lichens are therefore also excluded.

Flowering plants

Gehrke and Linder (2014) indicated that 168–184 flowering plant species could be considered Afro-alpine endemics (i.e., presumably confined to regions above 3200 m), comprising 32%–36% of the Afro-alpine flowering plant flora above 3200 m (Table 2). This compares to Hedberg’s (1951, 1969) stricter lower limit of 3500 m and associated 81% endemism.

Because of the ambiguous results in Gehrke and Linder (2014), it is not possible to state with confidence the patterns of endemism in terms of their four mountain clusters (Table 2). If we take their highest figures, the *South-eastern East African Mountain*

Cluster has the highest recorded endemism (97), and the *Western African Mountain Cluster* the lowest (one); the *Northern East African Mountain Cluster* (90) is a close second, followed by the *Western East African Mountain Cluster* (54). However, if we take their lower limits, the *Northern East African Mountain Cluster* has the highest level of endemism (85), followed by the *South-eastern East African Mountain Cluster* (54). Of the individual mountain ranges, the Simien has the highest number of local endemics (22–24), and Mount Meru, Hanang, and Loolmalasin the least, with no Afro-alpine endemics on any of them. Mount Elgon, the Ruwenzoris and Bale Mountains follow the Simien Mountains in local endemism, with 15–17, 10–11 and 6–11 endemic species each. All other mountains host endemics in single figures, that is, the Virungas (eight to nine), the Aberdares and Mount Kilimanjaro (seven each), Mount Kenya (six to eight), and the Cherangani Hills and Mount Cameroon (one each). If we consider the extent of the Afro-alpine Zone on each mountain, and therefore highest level of endemic richness per unit area, the Virungas—despite having only 20 km² of alpine area—are the richest in endemic species (eight to nine endemic species), richer than host mountains with much larger Afro-alpine areas, like Mount Kenya and Mount Kilimanjaro (Fig. 7).

Mount Cameroon (i.e., the *West African Mountain Cluster*) is worth a special mention. Based on their liberal and strict delimitations of 3200 m and 3600 m, Gehrke and Linder (2014) considered there to be only one Afro-alpine endemic on Mount Cameroon, although this solitary shield volcano seems to host up to 19 moorland and grassland–forest interface endemics (Maitland, 1932; Cheek et al., 1996; Linder et al., 2010). As this grassland extends down to ca. 2600 m, most of the grassland endemics fall outside Gehrke and Linder's (2014) definitions of "Afro-alpine endemic" (liberal or strict). However, based on Maitland's (1932) descriptions of alpine communities and more recent work by Cheek et al. (1996), two species (*Helichrysum mannii* and *Pentameris pictigluma* var. *mannii*) would qualify as true Afro-alpine endemics from Mount Cameroon, apparently being confined to elevations above 3600 m. Smith and Cleef (1988), for example used 2985 m as the lower limit for data from Mount Cameroon for their global tropical alpine analysis. Mount Meru also deserves mention in that—although Gehrke and Linder (2014) consider it to have no Afro-alpine endemics—Afro-alpine-associated endemics certainly occur there (Knox, 2005).

Some notable Afro-alpine endemics among the flowering plants are the Giant Lobelias *Lobelia* species and Giant Groundsels *Dendrosenecio* species (Mabberley, 1974, 1975; Givnish, 2010; Plates 4–7). These giant forms have attracted much research attention from physiognomic, ecological, taxonomic, and phylogeographical perspectives (Hedberg, 1969; Zhao et al., 2016, etc.). The taxonomies of these two genera are particularly complex, and have motivated a reasonable debate as to species delimitations (Knox and Palmer, 1995, 1998) and therefore endemism tallies. While *Dendrosenecio* is absent from Mount Cameroon, *Lobelia* (*L. columnaris*) is present, representing a ubiquitous "giant genus" in the entire Afro-alpine. Currently, 11 species (and 11 subspecies!) of *Dendrosenecio* are recognized (Table 3). Only three of these species can be said to be true Afro-alpine endemics (as per Gehrke and Linder's, 2014 definition). Eight species are considered near-endemics, with none exclusively below the Afro-alpine Zone. For the 12 species of Giant *Lobelia* currently recognized (Table 4), only two are true Afro-alpine endemics, six are near-endemics, and the remaining four do not extend above the Montane or Giant Heath Zones into the Afro-alpine Zone. Gehrke and Linder (2014) note another four *Lobelia* species that occur in the Afro-alpine Zone that are not giant species.

Mosses and liverwort endemism in the Afro-alpine

Pócs (1991) indicated that there are 83 species of moss endemic to the Afro-alpine. Endemism is evident on single mountains, such as the 12 mosses and liverworts endemic to Mount Kilimanjaro, eight of which occur in the Afro-alpine Zone and nine extend into the Nival Zone (Pócs, 1991). According to Pócs (1991), there are at least 20 species of liverwort endemic to the Afro-alpine Zone.

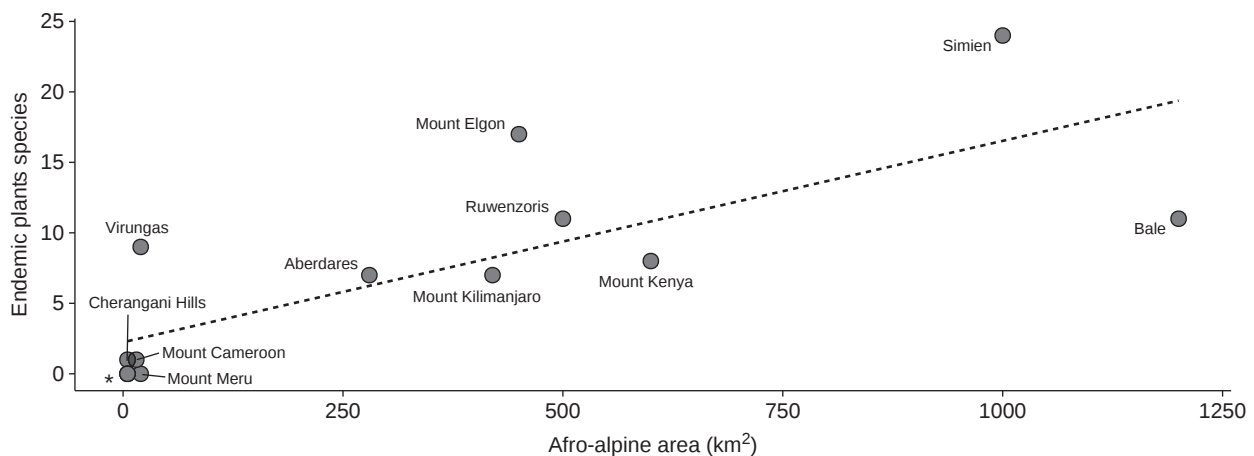


Fig. 7 Species-area curve for Afro-alpine endemics in the tropical African mountains. Data from Gehrke, B. and Linder, H. P. (2014). Species richness, endemism and species composition in the tropical Afroalpine flora. *Alpine Botany* 124, 165–177.



Plate 4 Giant forms of *Lobelia* (Campanulaceae) are typical in tropical African mountains, as they are in other tropical areas such as Oceania, with only a few occurring in the Afro-alpine in tropical Africa. (A) *L. columnaris*, a forest species endemic to Mount Cameroon and the Bamenda Highlands (Cameroon, Nigeria); (B) *L. giberroa*, a common and widespread eastern Afromontane forest species; (C) *L. stuhlmannii*, in the Ruwenzoris (Uganda); (D) *L. aberdarica*, endemic to Mount Elgon, the Aberdares and Cherangani Hills (Kenya, Uganda), here on Mount Elgon at c.3200 m; (E) *L. wolastonii*, a colony in the Ruwenzoris (Uganda). Photographs: Berit Gehrke (A), Peter Linder (B, C, E), Ralph Clark (D).

Characteristic Species and Communities

There are very distinct plant communities within the Afro-alpine Zone (Hedberg, 1964; Niemelä and Pellikka, 2004) and several primary plant communities can be recognized, notably extensive tussock- and shrub-dominated grasslands and alpine bogs or fens (Rejmankova and Rejmanek, 1995; Willis, 2000; Niemelä and Pellikka, 2004). The areal extent, structure, and species composition of these communities varies from mountain to mountain. There is, for instance, much more alpine bog on the Ruwenzoris than on the mountains east of the Rift Valley (Rejmankova and Rejmanek, 1995). Sparse to dense communities of Giant Groundsel and Giant *Lobelia* occur in both tussock grassland/shrub land and alpine bogs.

Tussock grasslands are dominated by tufted grasses of the genera *Agrostis*, *Andropogon*, *Descampsia*, *Festuca*, *Koeleria*, *Pentameris*, and *Poa*. Shrubs are represented particularly by *Alchemilla* and *Helichrysum* (Plates 1–3), with notable others including *Euryops* and *Erica* (Plates 2 and 8). Such grassland and shrub-land is relatively rich in both diversity and Afro-alpine endemic species, with



Plate 5 Giant Lobelia (cont.). (A) *L. telekii*, endemic to Mounts Elgon and Kenya and the Aberdares (Uganda, Kenya); (B) *L. deckenii* subsp. *elgonensis*, on Mount Elgon (with *Dendrosenecio elgonensis* in background); (C) *L. deckenii* subsp. *bequaertii*, in the Ruwenzoris (Uganda). Photographs: Ralph Clark (A and B), Peter Linder (C).

interesting biogeographical connections, such as with the “Cape Flora” of far southern South Africa (Weimarck, 1941; Hedberg, 1970, 1986; Linder, 2014). The most characteristic genera in alpine bogs are *Carex* sedges; mosses such as *Meesia*, *Scapania*, *Sematophyllum*, and *Sphagnum* (Rejmankova and Rejmanek, 1995); various *Luzula*, *Ranunculus*, and—prominently—*Lobelia* and *Dendrosenecio* (Pócs, 1991; Plates 4–7).

Drivers of Plant Diversity and Endemism in the Afro-Alpine

Hedberg (1969, 1970, 1986) compared the widely scattered Afro-alpine Zone components to the extreme isolation experienced by many oceanic islands. In fact, he considered this level of isolation to be even stronger than that experienced on oceanic islands, due to the absence of ocean currents that would transport propagules (Hedberg, 1969, 1970). We know, however, that many agents of dispersal must have operated in creating this unique flora on the roof of Africa (Hedberg, 1970; Chala et al., 2017). This is born out by the array of genetic relationships the Afro-alpine flora shares with most of the world (Gehrke and Linder, 2009; Gehrke and Linder, 2014; Chala et al., 2017). The idea of the Afro-alpine Zone comprising the ultimate “sky islands” and, therefore, amenable to test hypothesis in terms of the General Dynamic Model of Whittaker et al. (2008), has been most comprehensively attempted by



Plate 6 The Giant Groundsels comprise the genus *Dendrosenecio* (Asteraceae), endemic to the tropical African mountains, with most species occurring in the Giant Heath and Afro-alpine Zones. (A) *D. elgonensis*, endemic to Mount Elgon (Uganda), 3000–4300 m; (B) *D. adnivalis*, endemic to the Ruwenzoris and Virungas (Uganda, Rwanda, Burundi and the Democratic Republic of the Congo); (C) *D. kilimanjari*, endemic to Mount Kilimanjaro (Tanzania); (D) *D. keniensis*, endemic to Mount Kenya (Kenya); (E) Old *D. adnivalis* community, in the Ruwenzoris. Photographs: Ralph Clark (A), Christopher Gardner (B), Nigel Forshaw (C), Tara Hetz (D), Peter Linder (E).

Gehrke and Linder (2014). This—and subsequent work (e.g., Kandziora et al., 2016; Zhao et al., 2016; Chala et al., 2017, etc.) has shown that there is surprising connectivity between individual Afro-alpine communities, as indicated by the evidence of shared species and complex phylogeographic patterns. This, in turn, suggests multiple dispersal and colonization events.

Plant diversity and endemism in the Afro-alpine Zone appears to be driven primarily by age, size, and geographical proximity of the host mountains to one another (Gehrke and Linder, 2014). The ages of the host mountains appear to be the most important factor in determining plant richness and diversity, as older mountains have had more time to accumulate diversity, both through colonization and in situ speciation (Gehrke and Linder, 2014). Converse to this, mountains that are senescent are often more eroded, and may have thus lost many Afro-alpine elements through loss of elevation and loss of topographic complexity (sensu



Plate 7 Giant Groundsels (cont.). (A) *D. battiscombei*, endemic to Mount Kenya and the Aberdares (Kenya); (B) *D. keniodendron*, endemic to Mount Kenya (Kenya); (C) *D. erici-rosenii*, endemic to the Ruwenzoris, Virungas and Mitumbas (Uganda, Rwanda, Burundi and the Democratic Republic of the Congo); (D) *D. adnivalis*, endemic to the Ruwenzoris and Virungas (Uganda, Rwanda, Burundi and the Democratic Republic of the Congo). Photographs: Mike Loomis (A), Tara Hetz (B), Christopher Gardner (C and D).

Whittaker et al., 2008 for mature oceanic islands). An example is the Cherangani Hills, and to some extent the Aberdares (Gehrke and Linder, 2014), which only just retain some Afro-alpine elements. Isolation is a strong driver of higher endemism but generally favors lower species diversity (Chala et al., 2017). However, the most isolated Afro-alpine area (Mount Cameroon) does not show either high levels of diversity or endemism, as a result of the recent age of the higher elevations of the mountain. Here there are still periodic volcanic eruptions that cause local extinctions (Cheek et al., 1996; Gehrke and Linder, 2014).

While in broad terms the age, size, and proximity of mountains hosting Afro-alpine vegetation might have the most explanatory power (Gehrke and Linder, 2014), intra-specific patterns of genetic structuring suggest that much more dynamic biogeographical histories led to the creation of these Afro-alpine communities (Chala et al., 2017). Ruggedness most certainly plays a role in enhancing fine-scale habitat heterogeneity (Whittaker et al., 2008), which has been suggested as an important feature determining

Table 3 Summary of Giant Groundsel (*Dendrosenecio*) in the Afro-alpine Zone

Species	Distribution	Elevation range (m)	E/NE/N
<i>D. adnivalis</i> (Stapf) E.B. Knox (with subspp. <i>adnivalis</i> , <i>friesiorum</i> & var. <i>petiolatus</i>)	Ruwenzoris, Virungas	3600–4250	E
<i>D. battiscombei</i> (R.E.Fr. and T.C.E.Fr.) E.B. Knox	Aberdares, Mount Kenya	2950–4000	NE
<i>D. brassiciformis</i> (R.E.Fr. and T.C.E.Fr.) Mabb.	Aberdares	2950–3950	NE
<i>D. cheranganiensis</i> (Cotton and Blakelock) E.B. Knox (with subspp. <i>cherangiensis</i> , <i>dalei</i>)	Cherangani Hills	2600–3400	NE
<i>D. elgonensis</i> (T.C.E.Fr.) E.B. Knox (with subspp. <i>barbatipes</i> , <i>elgonensis</i>)	Mount Elgon	2750–4200	NE
<i>D. erici-rosenii</i> (R.E.Fr. and T.C.E.Fr.) E.B. Knox (with subspp. <i>alticola</i> , <i>erici-rosenii</i>)	Rwenzoris, Virungas, Mitumbas	2750–4200	NE
<i>D. johnstonii</i> (Oliv.) B. Nord.	Mount Kilimanjaro	2750–3350	NE
<i>D. keniensis</i> (Baker f.) Mabb.	Mount Kenya	3300–4275	E
<i>D. keniodendron</i> (R.E.Fr. and T.C.E.Fr.) B. Nord.	Mount Kenya	3650–4350	E
<i>D. kilimanjari</i> E.B. Knox (with subspp. <i>cottonii</i> , <i>kilimanjari</i>)	Mount Kilimanjaro	3000–3800	NE
<i>D. meruensis</i> (Cotton and Blakelock) E.B. Knox	Mount Meru	2850–3350	NE

Elevation ranges provided here are conservative compared to some other sources, and an attempt at combining all available elevation records has not been made. E = Afro-alpine Endemic (i.e., restricted to >3200 m elevation), NE = Afro-alpine Near-endemic (i.e., also occurs <3200 m), N = Not an Afro-alpine species (i.e., only <3200 m). Based on data from Knox, E. B. (2005). *Dendrosenecio*. In: Beentje, H. J., Jeffrey, C. and Hind, D. J. N. (eds.). *Flora of tropical east Africa: Compositae part 3*. pp. 547–548. London: Kew Royal Botanic Gardens. and Gehrke, B. and Linder, H. P. (2014). Species richness, endemism and species composition in the tropical Afroalpine flora. *Alpine Botany* **124**, 165–177.

Table 4 Summary of Giant Lobelia (*Lobelia* spp.) in the Afro-alpine Zone

Species	Distribution	Elevation range (m)	E/NE/N
<i>L. aberdarica</i> R.E.Fr. and T.C.E.Fr.	Aberdares, Cherangani Hills, Mount Elgon	1800–3500	NE
<i>L. bambuseti</i> R.E.Fr. and T.C.E.Fr.	Aberdares, Mount Kenya	2750–2900	NE
<i>L. cheranganiensis</i> Thulin	Cherangani Hills	3050–3300	NE
<i>L. columnaris</i> Hook.f.	Bamenda Highlands, Mount Cameroon	(900–)1380–2550	N
<i>L. deckenii</i> (Asch.) Hemsl. (including subspp. <i>bequaertii</i> , <i>burtii</i> , <i>deckenii</i> , <i>elgonensis</i> , <i>incipiens</i> , <i>keniensis</i> , <i>sattimae</i>)	Ruwenzoris, Mounts Elgon, Kenya, Kilimanjaro	2440–4300	NE
<i>L. giberroa</i> Hemsl. (including subspp. <i>giberroa</i> , <i>squarrosa</i>)	Aberdares, Ruwenzoris, Virungas, Mounts Elgon, Kenya, Kilimanjaro; Ngorongoro, Uluguru, Utshungwe ranges (Tanzania)	1500–3000	N
<i>L. mildbraedii</i> Engl.	Ruwenzoris, Virungas. Also on numerous mountains in Malawi, Burundi and Tanzania	1900–3500	NE
<i>L. rhynchopetalum</i> (Hochst. ex A. Rich.) Hemsl.	Bale and Simien Mountains	3000–4350	NE
<i>L. stricklandiae</i> Gilliland	Widespread in the eastern Afromontane (from Zimbabwe to Tanzania) and in Angola	1500–1950	N
<i>Lobelia stuhlmannii</i> Schweinf. ex Stuhl.	Ruwenzoris, Virungas	3300–3600	E
<i>L. telekii</i> Schweinf.	Aberdares, Mounts Elgon and Kenya	2950–4550	NE
<i>L. wollastonii</i> Baker f.	Ruwenzoris, Virungas	3350–4250	E

Elevation ranges provided here are conservative compared to some other sources, and an attempt at combining all available elevation records has not been made. E, Afro-alpine endemic (i.e., restricted to >3200 m elevation), NE, Afro-alpine near-endemic (i.e., also occurs <3200 m); N, Not an Afro-alpine species (i.e., only <3200 m). Based on data from Bruce, E. A. (1934). The giant lobelias of East Africa. *Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew)* **1934**, 61–88; Mabberley, D. J. (1974). The pachycaul Lobelias of Africa and St. Helena. *Kew Bulletin* **29**, 535–584; Linder, H. P. and Gehrke, B. (2006). Common plants of the Rwenzori, particularly the upper zones. Version 2, 15 June 2006. Institute for Systematic Botany, University of Zurich; Gehrke, B. and Linder, H. P. (2014). Species richness, endemism and species composition in the tropical Afroalpine flora. *Alpine Botany* **124**, 165–177 and the African Plant Database (Conservatoire et Jardin Botaniques de la Ville de Genève and South African National Biodiversity Institute (2019). African Plant Database (version 3.4.0). Retrieved April 2019. <http://www.ville-ge.ch/musinfo/bd/cjb/africa/>).

species richness in Afro-alpine environments (Gehrke and Linder, 2014)—especially in non-Spermatophytes. Geological stability of the host mountain is also an important factor, for instance long time periods of dormancy on volcanic mountains are required for colonization and speciation. Following the General Dynamic Model, it is expected that intermediate-aged landscapes present higher terrain ruggedness than either much younger or much older ones. In Afro-alpine environments, however, older (Bale and Simien), intermediate (Mount Elgon), and recently (Mount Kenya, Aberdares, and Mount Kilimanjaro) formed mountains present similar species richness. Factors such as elevational descent of vegetation zones during cooler periods (e.g., the Last Glacial Maximum), repeat dispersal and colonization events for the same species, the historical presence of grassland corridors, and unexpected evidence of an ability of Afro-alpine species to cross seemingly permanent barriers (such as the Turkana lowlands), all point to an intriguing and complex biogeographical history (Masao et al., 2013; Wondimu et al., 2014; Chala et al., 2017). This suggests that



Plate 8 Heaths or Heathers (*Erica*, Ericaceae) is a typical Afro-alpine genus with links to both the “Cape” flora of southern Africa and the temperate flora of Europe. (A) *Erica silvatica*, Mount Cameroon (Cameroon), c.3600 m; (B) *Erica silvatica*, Mount Elgon (Uganda), c.3800 m; (C) *Erica mannii* subsp. *mannii*, Mount Cameroon (Cameroon), c.3600 m. Photographs: Berit Gehrke (A and C), Ralph Clark (B).

the historical biogeography of the tropical alpine in Africa is more complex than a simple application of the General Dynamic Model.

Global Comparisons

When compared in a species-area relationship to other tropical alpine regions in the world (i.e., the Páramo, the highlands of New Guinea, and Oceania; Gehrke and Linder, 2014; Costin et al., 1979; Pickering et al., 2008; Sklenář et al., 2011; Royen, 1979; Fig. 8), the Afro-alpine Zone is relatively species-poor (for flowering plants) and the Páramo is the most species diverse (Smith and Cleef, 1988; Sklenář et al., 2011). Gehrke and Linder (2014) note that even when accounting for area (i.e., richness) the Afro-alpine is still species-poor (Smith and Cleef, 1988). However, the lack of detailed data for some mountains may skew this, and intensive botanical collecting efforts in the more poorly documented Afro-alpine areas may increase both the overall species tally as well as that of level of endemism (although this would require an intensive effort). Interestingly, although gymnosperms are locally dominant in Afromontane forests (i.e., *Podocarpus*), they do not occur in the Afro-alpine. However, they are present in southeastern Asian tropical alpine habitats (Smith and Cleef, 1988).

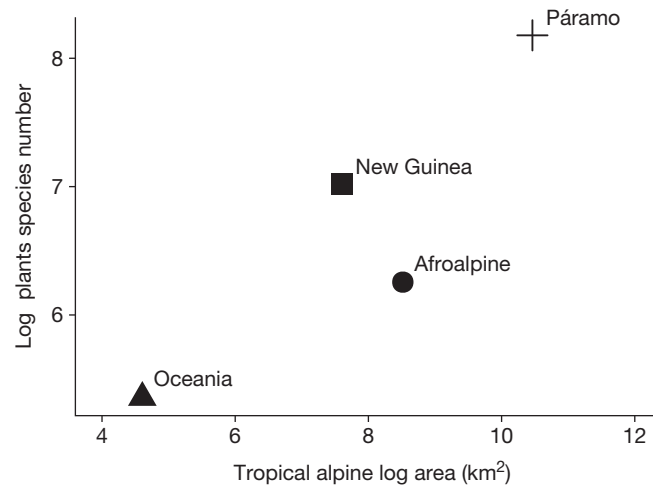


Fig. 8 Species-area curve for four tropical alpine areas globally.

Much has been made of the convergent evolution in the giant growth forms in the Afro-alpine (Giant Groundsel and Giant Lobelia), Páramo (Frailejones *Espeletia*), and vegetation of high elevations in the Hawai'i archipelago (Silverswords *Argyroxiphium* and *Lobelia* sect. *Galeatella*), with remarkably similar forms in unrelated groups present in the tropical alpine (Hedberg and Hedberg, 1979; Antonelli, 2009; Givnish, 2010). Unlike the other tropical alpine giant groups globally, Giant Lobelias are not confined to the tropical alpine and also occur at lower elevations on the same mountains as their alpine relatives (Givnish, 2010).

Future Research Needs

The Delimitation Problem

The traditional delimitation around defining the Afro-alpine based on elevation, while pragmatic in many ways, needs to be reassessed. Both Mounts Cameroon and Meru show a pattern in which grassland (potentially Afro-alpine) occurs below 3200 m, hosting numerous typically Afro-alpine-like endemics (e.g., *Dendrosenecio meruensis*) that scarcely occur in the Giant Heath or Montane Forest Zones. It is worth noting that Smith and Cleef (1988) used different lower elevations for different mountains in their global comparison of tropical alpine floras, and Gehrke and Linder (2014) attempted to accommodate the effect of latitude on vegetation zones in their synopsis. Also, Hedberg (1970) indicated that many typical Afro-alpine-associated species occur well below the Afro-alpine lower limit, some as low as 1000 m. Admittedly, the situation becomes more confusing when large-scale transformation of Giant Heathland (e.g., from over-use of fire; Wesche et al., 2000; Hemp, 2005), artificially transforms such woody habitats into alpine-like environments (Friis and Demissew, 2001). Nevertheless, a climatic-based spatial delimitation of the Afro-alpine may be more practical than just an elevational one, as the relative elevation, overall bulk, ruggedness and resulting local climate of each mountain/mountain block may result in Afro-alpine vegetation being favored at different elevations on individual mountains.

The Holdridge life zone system (where "alpine" is defined as the mean bio-temperature being between 1.5°C and 3°C; Holdridge, 1947), or Köppen climate classification (where the Alpine Zone is defined as no month in the year having a mean temperature above 10°C), may be more appropriate in defining the Afro-alpine Zone. The Holdridge system is considered to be better suited to tropical vegetation and does not consider elevation as a primary factor. While mostly applied in the deciduous fruit and nut industry (Luedeling and Brown, 2011; Luedeling, 2012), the positive chill unit (PCU) concept (Linville, 1990; Schulze and Maharaj, 2007) could be explored as a method for defining strictly Afro-alpine endemics, based on accumulated 24 h minimum temperatures essential for survival and or reproduction of such species. There does not appear to be any literature on using the PCU concept in the tropical alpine (although it has been proposed for the Austro-alpine in southern Africa; van Wyk and Smith, 2001). In addition, the PCU concept may be a useful empirical measure of how individual Afro-alpine endemics might be (or are already being) affected by climate change, and what the actual temperature thresholds for functional extinction are.

The Continued Need for Comprehensive Fieldwork, Data Inventory, and Taxonomic Investigation

Grimshaw (2001, p. 954) noted that the Afro-alpine flora—despite a century of investigation—is still a flora "worthy of any research effort." Despite the small areal extent of the Afro-alpine, its high elevation, fragmented distribution, and rugged topography render it relatively difficult to thoroughly explore. Ethiopia, in particular, still requires extensive fieldwork to accurately determine the floristic composition of its Afro-alpine fragments (Puff and Nemomissa, 2005), notably in the Amba Alagi, Mount Gurage, Welel, Choqa, and Guna areas (Gehrke and Linder, 2014). Better-sampled mountains are also not exempt, including (somewhat

surprisingly) the charismatic Ruwenzoris, along with the Virungas and Mount Meru (Gehrke and Linder, 2014)—the latter a “stone’s throw” from the very intensely studied Mount Kilimanjaro. Some plant groups are particularly poorly documented, notably non-Spermatophytes (e.g., Wekesa, 2015). Focused collecting of such groups will no doubt greatly improve our diversity and biogeographical knowledge of these species in the Afro-alpine (and Nival Zone). In particular, the ecosystems services value of mosses and liverworts in the Afro-alpine (Pócs, 1991) makes them very important for further distributional, taxonomic, and ecological study. Geffert et al. (2013) indicated that although the eastern African mountains are a center of species richness and diversity globally for mosses, inventories and taxonomic revisions for such tropical areas are far from complete (compared to e.g., Europe). Pócs (1991) also affirmed that the lichen knowledge of the Afro-alpine is still poor.

Despite the overall low species diversity of the Afro-alpine, the taxonomy of many species and species complexes remains unresolved (Wondimu et al., 2017). Consequently, Wondimu et al. (2017) strongly urge continued field-work in the Afro-alpine to target localized populations representing the array of complex taxa in particular genera. Such collecting and resulting analyses (morphological, phylogenetic, etc.) will assist in delimiting species circumscriptions more clearly and further refine our understanding of the biogeographical history of the Afro-alpine. Revised taxonomic circumscriptions may also result in more robust diversity and endemism tallies.

Climate Change and Conservation

A large appeal of the Afro-alpine is the charismatic giant growth forms present, notably of *Lobelia* and *Dendrosenecio*. Using the Ethiopian Afro-alpine endemic *Lobelia rhynchopetalum* as a model, Chala et al. (2016) indicate that drastic habitat envelope contraction for Afro-alpine species is likely to occur with global warming. The implication is that Afro-alpine endemics may become very restricted in an already confined environment, with some species—especially those most obvious flagship giants adapted to the diurnal freeze-thaw cycle—being most at extinction risk (Chala et al., 2016). Long-term monitoring sites in the Afro-alpine and Nival Zones may be able to track the change of vegetation in response to climate change.

Immediate anthropogenic impacts usually outpace the impacts from climate change, and are often more of an immediate concern in terms of African mountains. *Dendrosenecio* plants, for instance, are vulnerable to frequent grass fires caused by hikers and honey gatherers (Niemelä and Pellikka, 2004).

Acknowledgments

We thank Peter Linder for his valuable comments on the text. Berit Gehrke, Christopher Gardner, Mike Loomis, Nigel Forshaw, Peter Linder, and Tara Hetz and are thanked for generous permissions to use their photographs. Quentin Luke assisted with identifications of *Swertia* and *Helichrysum* for Plates 2 and 3.

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Alpine Vegetation of Temperate Mountains of Southern Africa

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Abstract

Southern Africa is characterized by a rich diversity of plant species and habitats with high levels of endemism. This region comprises nine biomes with a large number of vegetation types. One of these vegetation types is located on the high-lying mountains of the Drakensberg and is classified as being sub-Alpine vegetation. This sensitive ecosystem is described as a center of endemism and consists of unique plant species adapted to the relatively harsh environments.

Introduction

Alpine vegetation is found throughout the world on higher-lying mountains normally above 3000 m.a.s.l. Alpine vegetation grows in relatively harsh environmental conditions with extreme temperature and rainfall variations. The vegetation is characterized by the dominance of short grasses with meadows. Typical alpine vegetation is associated with the Alps in Europe, Andes in South America, Himalayas in South-east Asia, the Rockies in North America and the vegetation on the highest mountains of tropical East Africa (Aberdare Mountain, Mt. Ruwenzori, the Virunga Volcanos, Mt. Elgon, Mt. Kenia, Mt. Meru and Kilimanjaro).

Unlike the Andes and Rocky mountain ranges, most of the high- elevation African mountains occur as discrete island-like archipelagos. The continuum between the East African cluster and the Chimanimani Mountains in Zimbabwe is separated by the broad Zambezi valley, while the latter is separated from the South African cluster by the Limpopo valley (Fig. 1).

According to Van As et al. (2012) the vegetation of the slopes of high African mountains can be zoned into various elevational belts. The upper most belt (> 3600 m), which is absent in southern Africa, is dominated by Afroalpine vegetation comprising bryophytes, tussock grasses, giant lobelias (*Lobelia* spp.) and senecios (*Dendrosenecio* spp.). A sub-Alpine belt (between 2800 and 3600 m) is characterized by the dominance of various species of sclerophyllous genera such as *Erica*, *Philippia*, *Cliffortia* and *Passerina*. Lower down an undifferentiated Afromontane vegetation belt (1800–2800 m) occurs which consists of indigenous forests, shrublands, moist grasslands and wetlands. Although the vegetation of the East African mountains shows affinity with that of the higher mountains of southern Africa, there are also various differences in terms of species composition. According to White (1983) this affinity can be ascribed to the fact that where latitude compensates for elevation, as in the case of southern Africa, vegetation zones with Afromontane affinities occur at lower elevations.

The highest mountains in southern Africa span the western boundary of the KwaZulu-Natal Province to the southern high plateau of Lesotho and are known as the Maluti-Drakensberg range. This area is also described as the Drakensberg Alpine Center (DAC) of endemism (Van Wyk and Smith, 2001). The area is approximately 40,000 km² and occurs mostly above 1800 m above sea level. The Drakensberg Mountain range of South Africa is regarded as the southernmost point of the Afromontane region with alpine -like vegetation (Killick, 1997). The elevations of the highest peaks range between 2500 and 3480 m above sea level.

Geologically these mountains consist of basaltic rocks that were deposited over softer sandstone and shale layers, due to thick lava flows. The magma or molten rock flowed onto the area through a complex system of cracks or fissures, creating these mountains. Volcanic basalts are estimated to be up to 1.5 km thick (McCarthy and Rubidge, 2005). The chemical composition of the basalt is not homogeneous, resulting in some areas being less resistant to weathering. Thus, the opportunity for erosion was greater in certain sections than others. Whereas the basalts of the cap layers were brittle, underground crystallization of the lavas in cracks and fissures resulted in the formation of hard blue dolerite dykes and sills (Fig. 2).

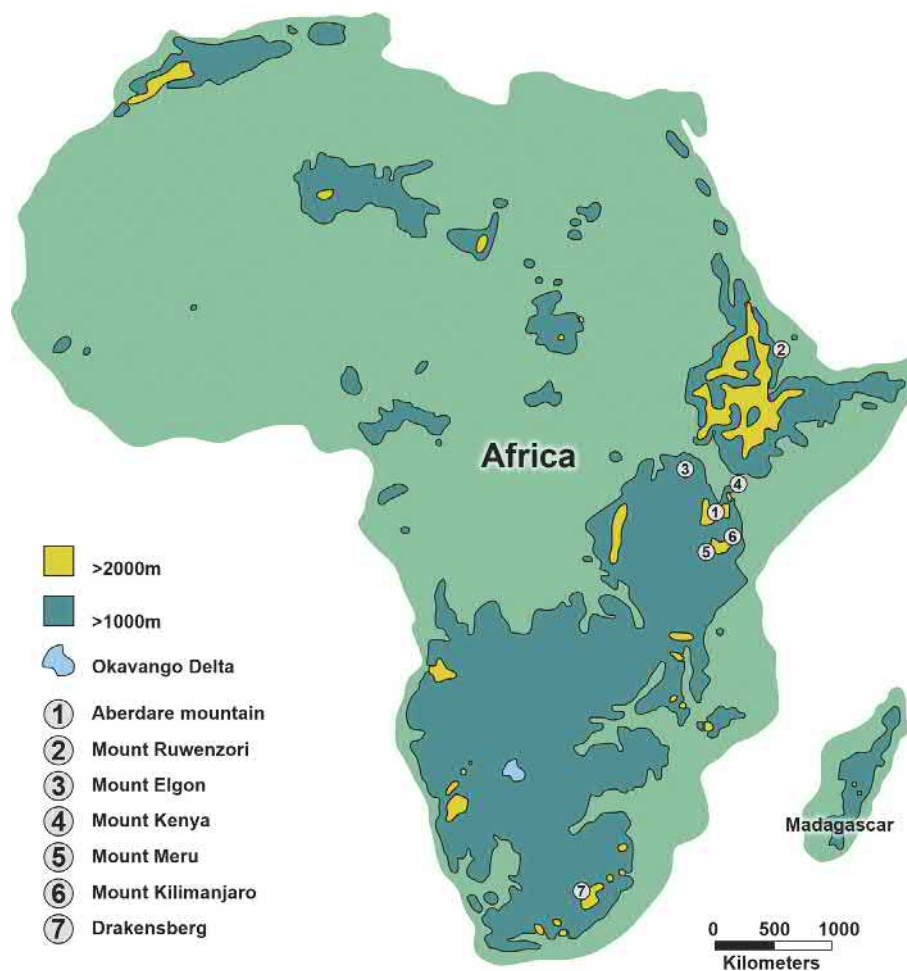


Fig. 1 Location of the high-elevation mountains of southern and eastern Africa. Adapted from Van As, J., Du Preez, P.J., Brown, L.R. and Smit N. (2012). *The story of life and the environment: An African perspective*. Cape Town: Struik.

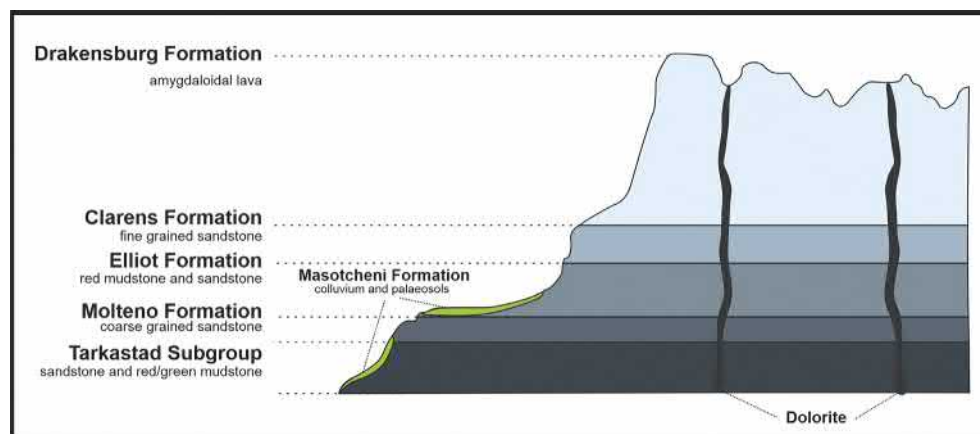


Fig. 2 Geology of the Drakensberg region. Adapted from Ezemvelo KwaZulu-Natal Wildlife. (2012). uKhahlamba Drakensberg Park World Heritage Site: Integrated Management Plan Version 1.0. Pietermaritzburg, KZN Wildlife.

Typical Plant Species of the Southern African Vegetation Belts

The vegetation of these areas consists of herbaceous vegetation that is dominated by mostly short grasses and forbs. Due to the cold temperatures, woody plants are normally absent. Where they are present, they are mostly scandent (short growth form with a spreading nature) or medium-sized shrubs in ravines or more protected rocky areas. In some ravines tall Afromontane forests are present (Fig. 3). The vegetation is divided into two groups:

Afromontane Vegetation Belt (1800–2800 m)

This belt includes three main vegetation types, namely Forests (restricted to sheltered ravines), open and closed shrublands, moist grasslands and wetlands. The following genera are typical for the forests: *Podocarpus*, *Curtisae*, *Rapanea*, *Chionanthus*, *Ocotea*, *Pittosporum*, *Ptaeroxylon*, *Prunus*, *Ilex*, *Halleria*, *Maytenus*, *Apodytes*, *Kiggelaria*, *Nuxia*, *Scolopia* and *Xymalos*. In the shrublands *Halleria*, *Buddleja*, *Leucosidea*, *Protea*, *Metalasia*, *Cliffortia*, *Metalasia*, *Greyia*, *Kiggelaria*, *Ilex*, *Muraltia*, *Erioccephalus*, and *Helichrysum* are typical genera present. Common genera for the shrublands, moist grassland and wetlands include *Protea*, *Leucosidea*, *Cussonia*, *Buddleja*, *Themeda*, *Rendlia*, *Phragmites*, *Festuca*, *Andropogon*, *Agrostis*, *Gunnera*, *Ficinia*, *Rumex*, *Ranunculus*, *Lobelia*, *Centella* and *Juncus*.

Sub-Alpine Belt (2800–3600 m)

The vegetation of these areas occurs on steep slopes and rolling plateaus and is characterized by treeless alpine vegetation consisting of grasses, scandent shrubs and herbaceous plants (Fig. 4). These areas include peaks such as Cathedral Peak, the inner and outer Horns and the Pyramid (Killick, 2012). Two main vegetation types can be distinguished, namely upland vegetation and peatlands/mires. The upland vegetation consists of species belonging to the following genera: *Passerina*, *Cliffortia*, *Erica*, *Philippia*, *Merxmuellera*, *Festuca*, *Koeleria*, *Bromus*, *Brachiaria*, *Festuca*, *Catalepis*, *Pentaschistis*, *Helichrysum*, *Ursinia*, *Lotononis*, *Crassula*, *Monsonia*, *Xerophyta*, *Psammotropha*, *Eumorphia*, *Pentameris*, *Thesium*. On the steep slopes the grasslands dominate, while the dwarf shrubs are more prominent on the crests and high plateau areas. The peatlands/mires include hydrophilic species belonging to the genera *Haplocarpa*, *Andropogon*, *Cotula*, *Isolepis*, *Ranunculus*, *Pentameris*, *Hypoxis*, *Limosella*, *Athrixia*, *Poa*, and *Trifolium*.

Mucina and Rutherford (2006) state that many of the genera of this belt show affinity with East African mountains (e.g. *Festuca*, *Koeleria*, *Merxmuellera* etc.). These areas consist of species-rich grasslands as well as short shrub-dominated vegetation with several

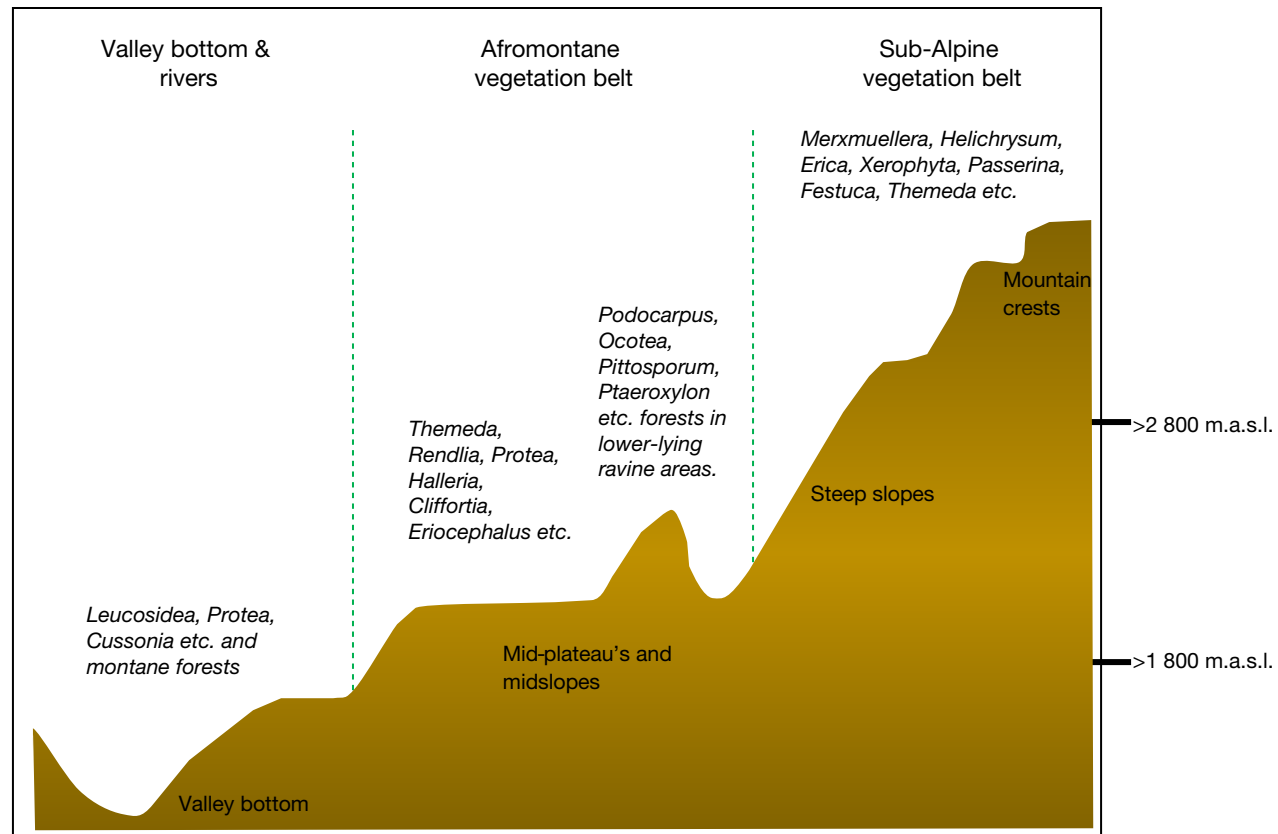


Fig. 3 Typical broad vegetation belts of the higher-lying mountains of southern Africa.



Fig. 4 Typical steep slopes, rolling plateaus and ravines of the Sub-Alpine vegetation belt of the Drakensberg region of southern Africa. Photo: LR Brown.

forb species. The grass *Merxmüllera disticha* and cushion plants, e.g. *Helichrysum sessilioides* and *H. praecurrens*, the latter forming low mats, are common in these areas. Other grasses that are prominent in this alpine belt include *Festuca caprina* and *Pentaschistis oreodoxa*. The “alpine everlasting” (*Helichrysum trilineatum*) as well as the dwarf shrub *Erica thodei* are common species that have adapted to surviving in this harsh environment.

Environmental and Ecological Drivers

Landscape and Climate

Mountains as prominent landscape features have a high habitat diversity characterized by high elevations, moderate to steep slopes and deep ravines, causing sharp climatic and ecological gradients. The peaks and slopes of mountains undergo a continuous process of erosion. On high elevation mountains, freeze-thaw events are the principal agents of rock weathering as well as soil heaving. Due to temperature fluctuations, rocks expand and contract, thereby causing small sections of rocks to be continually broken off. This is referred to as rock exfoliation (Van As et al., 2012). These series of changes, also referred to as periglacial processes, are normally slow and affect the soil structure that in turn affects the habitat of plant and animal species (Knight et al., 2018). Together with rock exfoliation, water erosion on the steep slopes causes the formation of gullies, ravines and valleys (Van As et al., 2012).

The different mountain ranges in southern Africa vary greatly in environmental conditions due to differences in longitude, topography, size, elevation, and aspect, as well as their distance from oceans. Mountain topography and aspect varies between areas, thereby creating micro-environments that may considerably differ from regional macroclimatic conditions. These micro-environments provide different habitats suitable for various plant and animal species. The sheltered environments normally have a higher rock cover, lower temperatures and lower evaporation rates. As a result, these protected areas normally have more nutritious soil, better moisture retention and a lush vegetation than unprotected areas (Van As et al., 2012). Due to habitat diversity, the vegetation of the Afromontane belt is structurally mixed and therefore not specific to any major physiognomic category (White, 1983).

Elevation has a significant effect on most climatic variables. Generally, an increase in elevation results in increased rainfall but decreases in temperature. Rainfall is regarded as a major driver of South African vegetation. Precipitation increases with elevation, which can be ascribed to the combination of rainfall and condensation from fog. In addition, the high mountain ranges also act as barriers that influence the flow of moist air-masses. Contributing to the variation in rainfall is the rain-shadow effect (Fig. 5). Most mountain ranges in southern Africa are situated along a north-south axis and intercept cool moist air drifting inland from the oceans. As a result, some slopes become wetter and others drier. This is referred to as the rain-shadow effect, and results in the vegetation on the drier slopes being dominated by dry woodland, savannah or karroid shrubland, whereas the wetter slopes are clothed in lowland forest (Van As et al., 2012). Although the average rainfall for these areas is approximately 1000 mm per annum, the wetter areas can receive as much as 1600 mm while the drier areas as low as 500 mm (Sene et al., 1998).

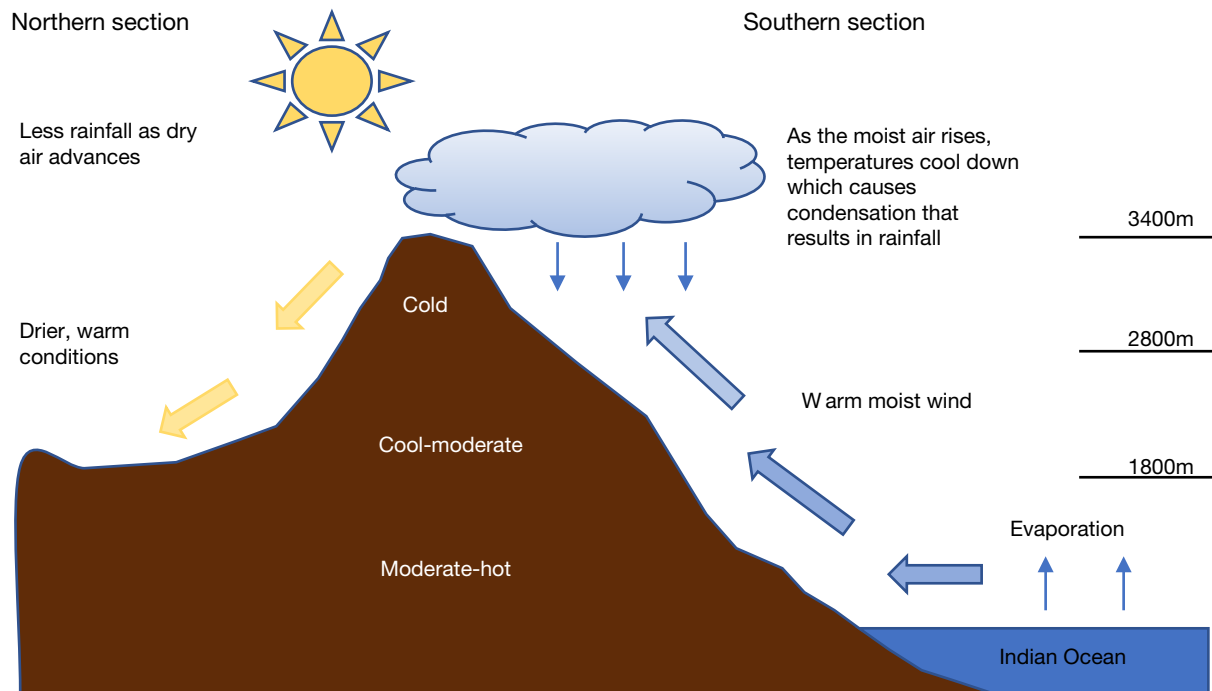


Fig. 5 Illustration of the rainshadow effect resulting in the southern mountain slopes being cooler and moister than the northern slopes.

Average temperature for these high lying areas (wet and dry) is 13°C and ranges between – 8 and 32°C. Throughout the year, cool daytime temperatures prevail. Frost and snow are common during winter with occurrence increasing with elevation (Mucina and Rutherford, 2006). Frost seldom penetrates more than 3–5 cm, resulting in only finer substrates being subjected to cryoturbation (Archibald, 1995). The many bare rock surfaces of these mountains contribute to pronounced daily temperature fluctuations with temperatures dropping below freezing at night and rising more than 15° during the day (Smith and Young, 1987). These temperature fluctuations, as well as temperature extremes, are responsible for the specific plant species composition. Only species that can adapt and survive these conditions are established here. Fog forms frequently throughout the year. In some areas the cold temperatures and snow negate the effects of high rainfall, resulting in drier environmental conditions than expected.

Wind

The frequency, magnitude and duration of the local wind regime at high elevations can influence plant growth and structure of vegetation (Gardiner et al., 2016). High wind speeds cool the leaf surfaces of plants, reducing the leaf- to- air vapor pressure deficit between the plant and the environment, which results in reduced transpiration and evaporation (Dixon and Grace, 1984). In some cases, the cool air can also lead to leaf mortality. Alpine plants are adapted to survive in these cold and windy conditions due to various morphological adaptations. According to Fitzgerald and Kirkpatrick (2017) graminoids, cushion plants and shrubs display a morphological response to wind by growing in the direction the most frequent damaging winds are blowing. Wind also plays an important role in seed dispersal of alpine plants. Tackenberg and Stöcklin (2009) found that alpine vegetation is dispersed over long distances due to the more intense vertical turbulence of alpine habitats.

Fire

Fire affects the general landscape of the ecosystem. According to O'Connor and Bredenkamp (1997) fire is vital in the maintenance of the structural and textural patterns of the vegetation. Fires are naturally caused by lightning strikes and, in rare instances, by rock falls (Van As et al., 2012). Sparks from hardened falling rocks (as a result of earth tremors, animal or human activity), causes veld fires when the dislodged rock strikes a spark on a boulder covered with highly flammable grass material (Edwards, 1984; Simons, 2017). Fire is a natural ecological factor in the grasslands and savannah of southern Africa. The Drakensberg region consists mostly of grasslands with the fynbos-alpine heath-like vegetation on mountain crests and plateaus. The vegetation composition and structure are maintained as a result of the climate and the role that fire plays in this high-elevation ecosystem. According to Granger (1976) and De Villiers and O'Connor (2010) the anthropogenic exclusion of fire from this ecosystem has resulted in a shift from grassland to thicket. Natural fires used to occur throughout the region, but with the development of high-elevation farming,

including the erecting of fences around farms and other properties, fires were kept out of these ecosystems. This resulted in changes in plant species composition and structure. Together with climate, fire is one of the most important ecological drivers responsible for maintaining the structure and composition of the vegetation on the high-lying mountains of southern Africa.

Animals

Generally, the mountain fauna is less distinctive than the vegetation, however, all of these species have adapted to these variable and harsh climatic conditions that persist in the area. One such species, the bearded vulture (*Gypaetus barbatus*) occurs in the high-elevation mountains of Drakensberg. This vulture is adapted to the cold conditions due to a downy insulating layer beneath its feathers. The strong winds prevailing at these high elevations allow them to effortlessly soar for most of the day in search of food (Van As et al., 2012).

Insects and other invertebrates are poikilotherms, meaning that their body temperatures are influenced and dependent on that of the surrounding environment (Clusella-Trullas et al., 2008). According to Chapman (2002) alpine insects are often dark since that allows them to absorb more solar radiation than light-colored ones. All the insect species of the alpine regions are also frost tolerant and can therefore endure the temperature extremes.

Likewise, poikilothermic reptiles, including lizards, are adapted to these cold conditions and make use of solar radiation to warm themselves in this cold climate.

The ice rat (*Otomys sloggetti*) is a natural mammalian inhabitant of high-elevation vegetation and is endemic to the southern African Alpine zone (Du Preez and Brown, 2011). Ice rats (Fig. 6) are diurnal, herbivorous, burrow-dwelling rodents that are adapted to these cold and wet conditions. During the day the rats forage and warm themselves on the rocks; during the night they move into their burrows where they huddle together for warmth and are thus protected against the cold night temperatures and strong winds.

Adaptations of Vegetation

The extreme environmental conditions present on mountains have a major impact upon organisms which live in these areas. The extremely low temperatures above and below ground, and long periods of low light intensity, have a major influence on plants and animals. Furthermore, strong, desiccating winds, snowstorms and permafrost conditions, where soils are permanently frozen except for the upper few centimeters, contribute to limit the survivors of these conditions to a well-adapted plants and animals. Due to these harsh environmental conditions the vegetation comprises low-growing, dwarfish plants.

The cold temperatures and shallow soil occurring in these areas are only suitable for smaller plants. Freeze-thaw cycles put further stress on plants. These plants contain cryoprotectants in their cellular cytoplasm to lower its freezing point. Cryoprotectants are solutes such as glycerol, glucose, fructose and other compounds that act as antifreeze to prevent the water in the cellular fluids forming ice crystals that may puncture cellular membranes (Daubenmire, 1974; Van As et al., 2012). Many plants living in these extreme environments do not shed their dead leaves. These marcescent leaves insulate the stem and branches, protecting them against the cold. Other plants such as *Helichrysum* spp. have a low, cushion-like growth form to survive the fierce cold winds on exposed habitats. The leaves of some rosette plants fold inwards at night, protecting the meristematic tissue and buds from



Fig. 6 The ice rat (*Otomys sloggetti*) basking in the sun on the Drakensberg. Photo: LR Brown.

extremely low temperatures and cold, desiccating winds (Daubenmire, 1974; Van As et al., 2012). The small or needle-like leaves of some plants not only protect them against cold temperatures, but also serve to reduce the amount of water lost to the environment via transpiration.

Although these mountain areas generally have high precipitation, the clear skies expose the vegetation to more direct sunlight than plants at lower elevations, resulting in a more rapid loss of water. Moss species in particular are well adapted to handle dry conditions. They do not have a proper cuticle and readily lose water from the cytoplasm and become desiccated as external ice is formed. Thus, they are poikilohydric, meaning that the intracellular water content drops as the water availability in the habitat drops. This mechanism prevents the formation of large ice crystals inside the cells (Daubenmire, 1974). Other water loss protection measures of plants include pubescent leaves. These densely packed trichomes help prevent moisture loss in dry climates and also isolate leaves from low air temperatures. Some plants have leathery or thick fleshy leaves with sunken stomata to protect them against excessive water loss.

The dominant grasses and dwarf shrubs are short in structure and generally well-adapted to survive in cold temperatures. These plants have thin leaves to protect them against cold temperatures and water loss and they grow quickly to produce seed during the short growing season. The location of their meristematic tissues close to the ground not only prevents damage of these tissues against grazing and fire, but more importantly against cold temperatures. Most of the grasses occurring at these high elevations and cold temperatures, are C3 plants. These plants are well-adapted to cold temperatures and they produce a higher percentage of crude proteins than C4 grasses, though their rate of translocation of the end-products is very low. Although it was previously believed that the lower CO₂ concentrations at high elevation are responsible for C3 photosynthesis, the latest research shows that these lower photosynthetic rates are due to cold temperatures (Wittmer et al., 2010).

The wetlands of these areas are also characterized by the presence of a variety of plant species. Typical wetland plants found at lower elevations cannot cope well with the cold conditions of high-elevation wetlands and are therefore absent from these peatlands.

Biodiversity and Conservation Importance

The natural environment of these high-elevation areas is very important from a biodiversity perspective. According to Mukwada et al. (2016) the mountain ecosystems in South Africa are biologically unique with a high biodiversity, species richness and ecosystem complexity. These areas act as important sites of plant refugia and as migration routes for various animal species (Brand et al., 2011).

Due to the high precipitation of these areas they are referred to as the water factories of South Africa. The presence of a large number of high-elevation wetlands not only purifies the water, but most importantly acts as water reservoirs that slowly release the water into river systems. The Maluti-Drakensberg region supplies water to the rivers (Orange River as well as the Vaal River catchment systems) of the lower-lying areas of South Africa and is regarded as the most important water catchment area for southern Africa, in particular Lesotho and South Africa.

High-elevation mountains are regarded as centers of evolution for flowering plants (Hörandl and Emadzade, 2011). Although species richness generally decreases with elevation the DAC is regarded as a plant diversity 'hotspot' with a diversity of plant species showing affinity to vegetation of the south-eastern Cape as well as that of mountains further north in Africa. Due to the harsh environmental conditions and large number of micro-habitats, these areas are normally high in endemic species (Nagy and Grabherr, 2009). There are approximately 2520 flowering plant species, of which 334 are endemic and 594 near-endemic to this area (Ezemvelo KwaZulu-Natal Wildlife, 2012). That means that nearly 37% of all plant species present are endemic/near-endemic (Fig. 7). The variety in landscape, ranging from steep slopes with shallow soil to protected ravines with deeper soil as well as the various plateau terraces, creates many micro-habitats that provide suitable conditions for a variety of plant species. The Drakensberg Mountains have only 20 vascular plant species in common with the high-elevation flora of east and northeast Africa. This can be ascribed to the unique ecological conditions of the Drakensberg region (Davis et al., 1994).

These areas are also characterized by the presence of a large number of peatlands. Peatlands are unique in terms of species composition and age, with the peat-forming process taking place over thousands of years (Du Preez and Brown, 2011). It is estimated that peat grows at an average of 1 mm per year. These peatlands provide habitat for a large number of plant and animal species some of them rare or endangered.

Approximately 250 different bird species have been identified within the Drakensberg Mountain area. One species (mountain pipit—*Anthus hoeschi*) is endemic while another six species are near-endemic to this ecoregion. Three globally-threatened bird species, namely the southern bald ibis (*Geronticus calvus*), Cape vulture (*Gyps coprotheres*) and the wintering lesser kestrel (*Falco naumanni*) also occur in this high-elevation region (Hilton-Taylor, 2000). Three endemic river frogs as well as three endemic lizards are found in this ecoregion. In terms of invertebrates, a recent study identified 61 different species, of which between 18% and 36% are endemic to the DAC (Amstrong and Brand, 2012).

The large number of endemic animal and plant species indicate this area to be of high conservation importance. The various animal species, especially the reptiles and invertebrates, are also strongly associated with the different plant communities of the area. According to Brand et al. (2011) these areas provide ecosystem services in acting as enormous carbon sinks and also play a role in climate amelioration.

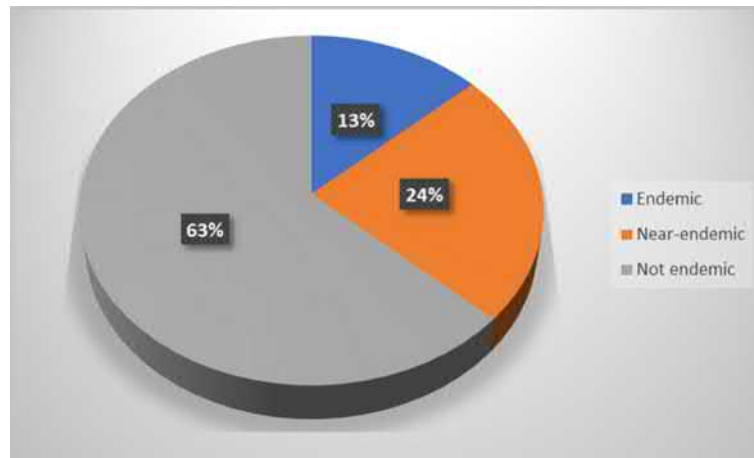


Fig. 7 Endemic species of the Drakensberg region.

Threats to the Ecosystem

Due to the harsh climatic conditions that prevail, these areas are not highly productive. Furthermore, these ecosystems are not resilient and do not cope well with disturbances. People living in these areas utilize the vegetation mostly for the seasonal grazing of their livestock and in some cases the establishment of small agricultural fields. Areas that are heavily grazed cause degradation of the land that leads to the destruction of the native plants and animals of these areas. Many of these high-elevation ecosystems in South Africa are threatened by anthropogenic influences, of which overgrazing by domesticated animals forms the largest threat. In the country of Lesotho, the local people living in these high-elevation areas are dependent on these areas for their livelihood. Since this high-alpine vegetation comprises mostly sour grasses (meaning low productivity and palatability) the local herdsmen are highly dependent on the more palatable grasses occurring alongside and in the peatlands in summer (Du Preez and Brown, 2011). The livestock industry is a vital component of the economic and social structure of the people living in these areas. Unfortunately, many of the high-alpine grasslands and peatlands are overgrazed, due to mismanagement and incorrect grazing practices. This has caused large scale degradation of not only the grassland ecosystems, but also the peatlands in Lesotho (Du Preez and Brown, 2011). Large scale erosion has taken place in some areas, while species composition has been altered as a result of the overutilization (Fig. 8). It is therefore important that not only the needs of the people in the areas should be addressed, but most importantly that sustainable management plans are established and implemented to ensure the conservation of these sensitive ecosystems.

Towards the Future

Alpine plants are potentially susceptible to climate change in terms of species composition and structure. Unfortunately, there few detailed studies have been done on the sub-alpine belt vegetation of southern Africa, due to the difficulty in accessing these areas as well as difficulty in obtaining funding for such studies. Whereas various long-term resampling studies have been done on the European Alps that allow for some comparisons in species changes over time, very little information is available on the vegetation of these areas in southern Africa. It is, however, predicted that where these areas are currently dominated by C3 grasses, the number of species will decline and the extent of alpine areas will become smaller over time (Mucina and Rutherford, 2006). Other studies predict that there will be an elevational ascent of many grasses, forbs and low shrubs. It is expected that because of their low competitive ability, alpine species will decrease in number while species from the lower-lying areas, better adapted to warmer conditions, will increase in number. Rosbakh (2013) states that montane and subalpine species will decrease in number due to climate change. Knight et al. (2018) consider that rapid climate warming of these high-elevation mountains has already reduced the efficiency of periglacial processes, which in turn may result in a change in soil structure and micro-habitats, thereby affecting the vegetation composition and structure, as well as that of the associated animals. Various ecological, physical and anthropogenic processes influence the vegetation of these high-lying mountains in southern Africa (Fig. 9). As discussed previously, these different processes are all interlinked, thus a change in only one of these processes will result in a change of the ecosystem that will affect the plant and animal species present in these areas.

This alpine ecosystem in southern Africa is not currently under threat in terms of anthropogenic pressures, mainly due to large sections being conserved in the uKhahlamba Drakensberg Park and smaller conservation areas (Mucina and Rutherford, 2006).



Fig. 8 Large scale erosion of the high-elevation peatlands of the Drakensberg regions of Lesotho, due to incorrect grazing practices. Photo: LR Brown.

Although many areas are negatively affected by overgrazing, large sections are still natural. It is, however, important that these high ecosystem service areas are constantly monitored to detect any negative effects or signs of degradation. It is equally important that the local people depending on these areas for their livelihood are involved in any decision-making exercises to ensure sustainable utilization and conservation of these ecologically sensitive areas. By implementing long-term research and monitoring studies, more information on the vegetation and resilience of this ecosystem would become available. This could assist current and future generations to make scientifically defensible decisions on the management and conservation of these areas.

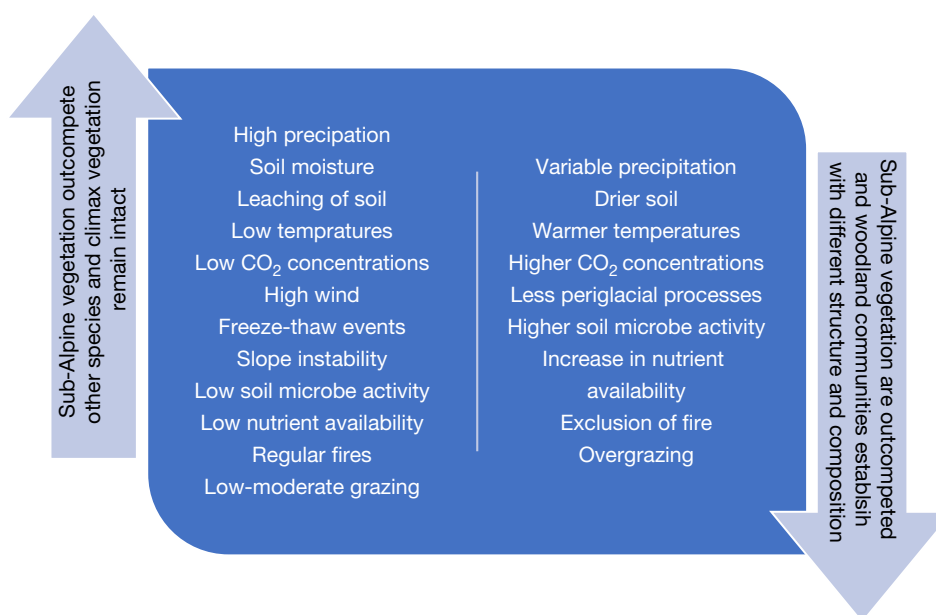


Fig. 9 Physical, anthropogenic and ecological processes that affect the plant species composition and structure of the southern African Sub-Alpine vegetation belt.

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Alpine Plant Diversity in Temperate Mountains of Asia

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Abstract

The Alpine zone of the temperate mountains of Asia is found mostly in the Himalayas. In addition, some alpine areas occur in the Tibetan Plateau. These areas are located at the junction of two major biogeographic realms: the Indo-Malayan and the Palearctic. The period of plant growth is severely limited by low growing season temperatures and a very short frost-free period. The Alpine vegetation of the temperate mountains of Asia is characterized by dwarf shrubs growing close to the ground. Three main vegetation types are recognized in the Alpine Zone of the Himalayas: alpine grassland, *Juniperus* scrub community, and *Rhododendron* krummholz community.

Location, Distribution and Ecological Condition

The Alpine zone of the temperate mountains of Asia is found mostly in the Himalayas. In addition, some alpine areas occur in the Tibetan Plateau (Hong et al., 1999) as well as selected high mountain regions of the temperate region of Asia such as Mount Fuji in Japan (Nakamura and Krestov, 2007). The cold climate of the alpine zone in temperate mountains is caused by adiabatic air cooling, so that it resembles polar climate. However, few studies have been made on the alpine vegetation plant diversity in temperate mountains of Asia. Most studies on the diversity of Alpine plants in the temperate region of Asia come from the Himalayas. The Himalayan range dates back to ca. 40–45 million years, and includes the highest mountain of the world. This range separates the Tibetan Plateau from the Indian subcontinent. Moreover, these areas are located at the junction of two major biogeographic realms: the Indo-Malayan and the Palearctic. The region is characterized by mountains of simple slopes separated by deep river gorges and valleys. These mountain regions consist of a number of unique habitats, ranging from tropical jungles in the south to alpine zones in the north, due to the variation in topography and climate (Jamtsho and Sridith, 2015). The ecological condition of the Alpine zone of the temperate mountains of Asia similar to the alpine zones of other mountain ranges of the world, characterized by harsh climate with cold temperatures, high winds and abundant winter snow. The period of plant growth is severely limited by low growing season temperatures and a very short frost-free period (Pojar and Stewart, 1991).

Plant Diversity

Like the vegetation of other alpine regions of the world, the Alpine vegetation of the temperate mountains of Asia is characterized by dwarf shrubs growing close to the ground. Most of the alpine is treeless, but in the ecotone with the upper forest zone there are trees growing in krummholz form (Pojar and Stewart, 1991). According to a case study in the Eastern Bhutan Himalayas (Jamtsho and Sridith, 2015), three main vegetation types are recognized in the Alpine Zone of the Himalayas, as follows:

I. *Alpine grassland* (Fig. 1): This type of vegetation is rather common above the tree line up to the snow line (Tshuchida, 1991; Jamtsho and Sridith, 2015). It has a high diversity of herbaceous vascular plants including some selected grasses and sedges such as *Arundinella hookeri* Munro ex Keng, *Eragrostis nigra* Nees ex Steud. as well as *Juncus* spp. This fragile natural mountain meadow is mostly adorned by the luxurious growth of *Potentilla coriandrifolia* D. Don, *Bistorta* sp., *Cyananthus macrocalyx* subsp. *Spathulifolius* (Nannf.) K. K. Shrestha and shrubby *Rhododendron setosum* D. Don. The alpine soil is characteristically poor in nutrients and easily degraded by climate change, herbivore grazing, human activities, and rodents (Wen et al. 2010). The growth of herbaceous plants in the alpine community of the Himalaya is well supported because the steep slopes have curtailed most anthropogenic disturbances, such as animal husbandry Himalayan slopes are typically steep (angles over 45 degree) preventing easy access for grazing livestock. There are also no signs of environmental impacts by rodents. In the Bhutan Himalaya at Merak (Jamtsho and Sridith, 2015), it has been found that human intervention in the succession of natural alpine environment is comparatively low because of the lack of livestock grazing.

II. *Juniperus Scrub Community* (Fig. 2): This is a small community forming above treeline. It is mainly composed of dwarf *Juniperus recurva* Buch. -Ham. ex D. Don and *J. squamata* Buch. -Ham. ex D. Don. It forms rather scattered vegetation in the areas between the alpine grassland and the krummholz in the Himalayas. *Gentiana* spp. and dwarf *Rhododendron nivale* Hook. f. are some other common species found in this community (Jamtsho and Sridith, 2015).

III. *Rhododendron Krummholz Community* (Fig. 3): *Rhododendron* krummholz is another type of community forming above tree-line with a rich growth of bryophytes at the ground level. Krummholz is the dwarf, crooked and contorted trees that form small



Fig. 1 Alpine Grassland, Sakteng Wildlife Sanctuary, Trashigang district, Eastern Bhutan Himalayas. Photo: Karma Jamtsho.



Fig. 2 *Juniperus* Scrub community, Sakteng Wildlife Sanctuary, Trashigang district, Eastern Bhutan Himalayas. Photo: Karma Jamtsho.

clumps shaped by the wind. It is a mixed vegetation comprised of isolated patches of *Rhododendron* spp. Open grounds, gaps, and margins of such communities usually have a high diversity of herbaceous vascular plants, including *Potentilla saundersiana* var. *caespitosa* (Lehm.) Th. Wolf, various *Primula* spp., *Bergenia purpurascens* (Hook. f. & Thomson) Engl., *Oxygraphis endlicheri* (Walp.) Bennet & Sum. (Jamtsho and Sridith, 2015). The *Rhododendron* krummholz of the Alpine in the temperate zone of the Himalayas provides a microclimate that allows different plant species to co-exist. Therefore, this community also has rich diversity of herbaceous plants along with rigorous growth of *Rhododendron* spp. themselves. This community includes *Bistorta griffithii* (Hook.f.) Grierson (Polygonaceae), *Potentilla saundersiana* var. *caespitosa* (Lehm.) Th. Wolf (Rosaceae), *Bergenia purpurascens* (Hook.f. & Thomson) Engl.



Fig. 3 The *Rhododendron* Krummholz community, Sakteng Wildlife Sanctuary, Trashigang district, Eastern Bhutan Himalayas. Photo: Karma Jamtsho.

(Saxifragaceae), which generally flower in June. The same niche includes species of the same families that draw the same nutrients, including *Rheum acuminatum* Hook. f. & Thomson, *Potentilla fruticosa* var. *arbuscula* (D. Don) Maxim., and *Saxifraga hispidula* D. Don. These species flower in August approximately within the gap of 8 months. However, this plant community is damaged by animal grazing. Palatable plants are consumed, and unpalatable plants are trampled (Jamtsho and Sridith, 2015) (Table 1).

Table 1 Selected vascular plant species of the Alpine zone of the Temperate Himalayas.

Family	Species	Alpine tundra grassland	Juniperus scrub	Rhododendron Krummholz
<i>Eudicots</i>				
Asteraceae	<i>Anaphalis nepalensis</i> var. <i>monocephala</i> (DC.) Hand. -Mazz.	+		
	<i>Cremanthodium reniforme</i> (DC.) Benth.			+
	<i>Saussurea gossypiphora</i> D. Don.	++		
	<i>Soroseris hookeriana</i> Stebbins	++		
Berberidaceae	<i>Berberis angulosa</i> Wall. ex Hook.f. & Thomson		++	
Campanulaceae	<i>Cyananthus macrocalyx</i> subsp. <i>spathulifolius</i> (Nannf.) K. K. Shrestha	++++++	+++	+++
Caryophyllaceae	<i>Arenaria densissima</i> Wall.	++		
Celastraceae	<i>Parnassia laxmannii</i> Pall. ex Schult.			++
Diapensiaceae	<i>Diapensia himalaica</i> Hook.f. & Thomson	++++		
Ericaceae	<i>Cassiope selaginoides</i> Hook.f. & Thomson		+++	
	<i>Gaultheria trichophylla</i> Royle.		++	
	<i>Gaultheria pyrolloides</i> Hook.f. & Thomson ex Miq.		++	
	<i>Rhododendron anthopogon</i> var. <i>haemonium</i> (Balf. f. & R. E. Cooper) Cowan & Davidian		++	
	<i>Rhododendron campanulatum</i> subsp. <i>aeruginosum</i> (Hook. f.) D.F. Chamb.		++++	+++++
	<i>Rhododendron bhutanense</i> D.G. Long & Bowes Lyon		++	
	<i>Rhododendron setosum</i> D. Don	+++++++	+++++	++++
	<i>Rhododendron fulgens</i> Hook.f.		++	

(Continued)

Table 1 Selected vascular plant species of the Alpine zone of the Temperate Himalayas.—cont'd

Family	Species	Alpine tundra grassland	Juniperus scrub	Rhododendron Krummholz
Gentianaceae	<i>Gentiana prostrata</i> var. <i>karelinii</i> (Griseb.) Kusn.	++		
	<i>Swertia assamensis</i> Harry Sm.			+++++
Polygonaceae	<i>Bistorta griffithii</i> (Hook.f.) Grierson		+	+
	<i>Bistorta macrophylla</i> (D.Don) Soják		+	
	<i>Bistorta vacciniifolia</i> Greene		+++	
	<i>Rheum acuminatum</i> Hook.f. & Thomson			++
	<i>Persicaria nepalensis</i> (Meisn.) Miyabe	+++		
Primulaceae	<i>Primula dickieana</i> Watt, J. Linn. Soc.			++
	<i>Primula capitata</i> Hook.			++
	<i>Primula gambeliana</i> Watt			++
	<i>Primula glabra</i> Klatt			++
	<i>Primula deuteranana</i> Craib		++	
	<i>Primula primulina</i> Spreng.			++
Ranunculaceae	<i>Oxygraphis endlicheri</i> (Walp.) Bennet & Sum. Chandra		++	
Rosaceae	<i>Potentilla fruticosa</i> var. <i>arbuscula</i> (D. Don) Maxim.			+++++
	<i>Potentilla coriandrifolia</i> D. Don	+	++	++++
	<i>Potentilla saundersiana</i> var. <i>caespitosa</i> (Lehm.) Th. Wolf		++	
	<i>Potentilla microphylla</i> D. Don	+++++		
Saxifragaceae	<i>Bergenia purpurascens</i> (Hook.f. & Thomson) Engl.	++	++	++
	<i>Saxifraga hispidula</i> D.Don			+
Scrophulariaceae	<i>Oreosolen wattii</i> Hook. f.	++		
<i>Monocots</i>				
Juncaceae	<i>Juncus</i> sp.	+		
Liliaceae	<i>Lloydia flavonutans</i> Hara		++	
Poaceae	<i>Arundinella hookeri</i> Munro ex Keng	+		
	<i>Eragrostis nigra</i> Nees ex Steud.	+		
<i>Gymnosperms</i>				
Cupressaceae	<i>Juniperus recurva</i> Buch.-Ham. ex D.Don	+	+++++	+++
	<i>Juniperus squamata</i> Buch.-Ham. ex D.Don		+++++	++
Pinaceae	<i>Abies densa</i> Griff.		++	

Modified from Jamtsho K and Sridith K (2015) Exploring the Patterns of Alpine Vegetation of Eastern Bhutan: A case study from the Merak Himalaya, *SpringerPlus* 4: 304.

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Nature of Alpine Soils

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Abstract

Alpine soils, like alpine biota, have evolved under extremely cold climates. Snow cover has been a vital element of alpine ecology. The length and timing of the growing season are other essential aspects of the alpine. These climate-driven aspects of alpine environments are changing at a pace otherwise found only in the Arctic. Scientists can predict some of the likely effects of long-term warming on alpine soils and vegetation, but ecological relationships are often far more complex than we currently understand, especially in regions as remote and difficult to study as the tops of high mountains. What other unforeseen breakdowns in alpine ecological relationships will occur in the coming decades? We can only watch and wait to see what happens.

Introduction

Soils in the alpine regions of the world are generally thin, rocky, and frozen year-round. They are thin in part because they are young. Most alpine regions were covered by glacial ice during the last ice age, and today's soils have accumulated and developed only since that ice melted away. They are rocky because they lie in or near the paths of rock slides, rock fall areas adjacent to frost-shattered cliffs. The alpine landscape is also typically littered with rock debris left over from high-altitude glacial deposits. These rocks, ranging from pebbles to boulders, have become incorporated into postglacial alpine soils. However, the deposition of rocks is also an ongoing process in many alpine landscapes. The soils are frozen year-round because much of the alpine zone experiences a climate in which the average annual temperature is -2°C or colder. Anyone who has attempted to dig an alpine soil pit can testify that just a few cm below the surface is a rock-hard permafrost zone. One would think that alpine soils are too poor to support much vegetation, but this is far from the case. As [Körner \(2003\)](#) explains, alpine plants draw water and mineral resources from soils that are different in many ways from those at lower altitudes. There are a large variety of alpine soil types that change from one kind to another over very short distances. These soils range from alpine sand dunes to peat bogs, from shallow soils typical of steep alpine slopes to the much deeper soils of some alpine meadows. Alpine plant communities follow these below-ground patterns, so that soils and plant distributions are closely linked. This brief account of the nature of alpine soils aims to introduce their principal features and point toward threats to alpine soils from global warming.

Alpine Soil Characteristics

As mentioned above, alpine soils have unique characteristics. Many forces that shape alpine soils are associated with the cold climate regime of the high mountains. The climate data from Mount Evans, Colorado provides a typical example of North American alpine temperature regimes. Average winter high temperatures range from -11°C to -3°C between January and April. Average

winter low temperatures range from -22°C to -16°C , and never get above freezing, even in the summer. The climate data from the Matterhorn provides a typical example of high elevation temperature regimes in the Swiss Alps. Average winter high temperatures range from -11°C to -7°C between January and April. Average winter low temperatures range from -16°C to -8°C , and remain below freezing throughout the year.

Large Scale Processes and Landforms

Butler et al. (2009) described geomorphic patterns and processes that shape alpine landforms and soils, using research from Glacier National Park, Montana as the basis for their observations. At large scales (e.g., across valleys), the alpine landscape is shaped by avalanches, debris flows, landslides, and rock fall. Talus deposits that accumulate beneath rock falls may descend well below treeline (Fig. 1).

Medium Scale Processes and Landforms

At a medium scale, some alpine surfaces do not support vegetation except mosses and lichens. Examples of these inhospitable areas include talus deposits, avalanche boulder tongues, and solifluction lobes. These lobes (Fig. 2) are composed of alternating “treads” and “risers,” as are found on stairs. Turf-banked terrace risers are difficult sites for seedling penetration because of the dense covering of alpine vegetation, such as *Dryas octopetala*. Solifluction treads are equally difficult sites for seedling establishment because of their exposure to wind and drying, which makes the soil impenetrable to seeds.

Fine Scale Processes and Landforms

Fine-scale processes such as frost heaving and churning are inimical to the survival of most alpine plants, whereas other processes such as turf exfoliation may facilitate seedling establishment by creating microsites that are less compacted, more penetrable by seeds, and are sources of moisture retention. Turf exfoliation is process active in periglacial areas in which frost heaving destroys continuous ground vegetation cover by removing the soil exposed along small terrace fronts. On their leeward side, boulders resting on an alpine surface offer shelter to young plants where the microclimate might otherwise be too harsh for their survival. Needle-ice pans are ovoid to circular depressions 1–6 m in diameter with a steep scarp 20–40 cm high, affected by exfoliation. The pans may originate from animal trampling and hoof disruption of the turf surface. The surface of pans frequently show well-developed frost sorting and fine-scale patterned ground.



Fig. 1 Talus slope, Cascade Mountains, Washington State, by Laurel Fan (deceased, 2016).



Fig. 2 Solifluction lobes on mountain slope near Nome, Alaska. Photo courtesy of Oak Ridge National Laboratories.

Soil Formation

Alpine soils have been described by Schmid et al. (2019). Alpine soils near treeline in Glacier National Park (GNP), Montana, have traditionally been considered to be shallow, Lithic Cryochrepts with minimal horizon development. Cryochrepts are cold-climate soils lacking in development at both the surface and sub-surface levels (Fig. 3). These soils are thin but with well-developed O2 horizons and stony to very stony sandy loam to sand A, B, and C horizons.

Schmid et al. (2019) described the typical soils characterizing seven types of alpine microenvironments. These environments range from dry windblown sites to wet meadows and semi-permanent snow pack localities. Thus, topographic site conditions are the most important factor in alpine soil development because they control both snow cover and loess distribution, which in turn influence the rate of soil development.

Sources of Soil Materials

Soil development in more temperate climates involves considerable chemical weathering. But in high-mountain soils, the chemical reactions associated with chemical weathering have been considered by soil scientists to be inhibited by very cold temperatures, often to the point of non-occurrence. The general perception of weathering in alpine soils has been that mechanical processes predominate, with “freeze-thaw” weathering as the primary agent. However, contrary to this temperature-inhibited model, several recent studies have shown that chemical weathering does occur in cold alpine regions, and that the process is mainly controlled by moisture availability. Furthermore, since weathering rates decrease over time, the availability of fresh mineral surfaces derived from physical erosion influences or determines chemical weathering rates (Egli et al., 2014).

Alpine soil formation rates have been estimated at about 320–450 tons per km² per year. Using a method called the known surface age and soil thickness approach, Egli et al. (2014) used age constraints based on dated surfaces (e.g. moraines) to estimate soil formation rates by relating soil profile thickness to surface age. Their results show alpine soil formation easily reaches rates of up to 800–2000 tons per km² per year. Previous alpine soil studies have shown that particularly young soils intensively weather, even under continuous seasonal snowpack. These findings cast doubt on the concept of ‘temperature-controlled’ soil development in alpine regions.

As discussed by Körner (2003), there are four principal sources of accumulation of fine mineral substrates in alpine terrain: (1) local erosion of parent rock, (2) movements of sediments by gravity (on and below slopes), (3) sedimentation by water or snow (avalanches etc.), and (4) sedimentation by wind. Because of the presence of permafrost in alpine soils, cryogenic processes play a role in deposition from all four sources. The coarse matrix into which finer sediments fill is created by landslides, glacial deposits, scree accumulation or solid rock weathering. In this coarse matrix, fine sediments accumulate from the bottom up, only slowly reaching the soil surface.

The accumulation of fine particles by eolian deposition is a particularly important component of alpine soil formation. Dust deposition is enhanced in the alpine zone, especially in younger mountain ranges, which include nearly all the large mountain ranges of the world. As discussed above, physical weathering of rocks in the alpine provides a steady source of newly eroded sediments. The erosion of surfaces by alpine glaciers generates large quantities of silt. Thus, in glaciated mountains, this silt is a particularly significant dust source. Mountain winds stir this dust up and redeposit it over alpine landscapes. It accumulates in



Fig. 3 Alpine soil profile from Slovenia, courtesy of Agricultural Institute of Slovenia. Note the shallow organic horizon near the surface, underlain by mineral soils.

topographic depressions and on vegetation. A steady supply of loess (wind-blown silt) causes alpine soil profiles to contain large fractions of very fine grain sizes.

Permafrost and Periglacial Features

Most alpine soils are in permafrost. In summer, a relatively shallow active layer thaws, providing a suitable substrate for alpine vegetation. However, the roots of alpine plants are shallow, because they cannot penetrate the permanently frozen ground beneath the active layer. Alpine permafrost may consist of solid rock with ice-filled joints, fine grained soils containing segregation ice, ice-supersaturated gravels, where not all particles are in contact, or dirty ice with some dispersed solid particles distributed within the ice (Harris et al., 2009). Segregation ice forms as discrete layers or lenses of ice develop in freezing mineral or organic soils, as a result of the migration and subsequent freezing of pore water.

Cryoturbation

As discussed by Pollard (2018), cryoturbation, or frost heaving, involves soil movements due to frost action. Frost heave is the upward movement of soil and rock due to frost action (Fig. 4). It occurs where climates are so cold that freezing temperatures propagate below the ground surface. If there is enough soil water and the soils are frost-susceptible, the cold soils cause ice lens formation. Water migrates from nearby unfrozen soils toward the ice lens by capillary action. This type of enhanced ice formation is called ice segregation.

Cryoturbation causes the mixing of materials from various soils horizons down to bedrock due to freezing and thawing. The extent of cryoturbation in alpine soils varies considerably. It is much more common on exposed sites than in sheltered sites such as alpine valleys (Fig. 5). In the autumn, cold nights cause alpine soils to freeze, and relatively warm days melt the frozen soils. These freeze/thaw cycles generate lenses of ice that form when meltwater penetrates down in the soil. As this freeze/thaw process continues, the soil in the active layer gradually loses moisture. This water percolates down to the permafrost boundary. The dried,



Fig. 4 Frost-heaved mounds in alpine area below Mugi Hill on Mount Kenya. Photo by Mehmet Karatay, Creative Commons Attribution-Share Alike 3.0 Unported license.



Fig. 5 Alternating patches of vegetated and frost-disturbed ground, Trail Ridge, Rocky Mountain National Park. Photo courtesy of the Niwot Ridge Long Term Ecological Research program, University of Colorado.

frost-heaved soil at the surface forms granular structures. Separation of coarse from fine soil materials produces distinctive patterned ground in various alpine soils.

Frost boils are one expression of alpine cryoturbation. These are small circular mounds of fresh soil material formed by soil upheaval and needle ice formation (Fig. 6) in frost-disturbed ground.

One might think that such highly disturbed substrates would be unsuitable for plant seedling establishment, but this turns out not to be the case. Frost boils have been found to provide “safe sites” for recruitment because these bare patches have reduced competition from other plants for space, light, and nutrients, and so they take advantage of the gap in the vegetation cover. In a study of alpine seedling establishment in and around frost boils, Sutton et al. (2006) found that the optimal location for seedling establishment is at the frost boil’s edge, and seedlings decreased near the center where the level of disturbance is at a maximum.

Because of the highly variable topography and parent material of alpine soils, there are a variety of different soil textures and soil water is unevenly distributed. These variable features, plus the movement of soil water as soils freeze, create differential frost heaving and the preferential heaving of objects buried in the soil. Fine-grained soils may move by frost action during the thawing phase. This combined with the frost heaving during freezing produces a convection-like system that contributes to the formation of various forms of patterned ground (Fig. 7), as well as the downslope creep of sediments on slopes.



Fig. 6 Needle ice pushing up soil. Photo by Thomas Bresson - Glaçons, CC BY 2.0, <https://commons.wikimedia.org/w/index.php?curid=5592822>.

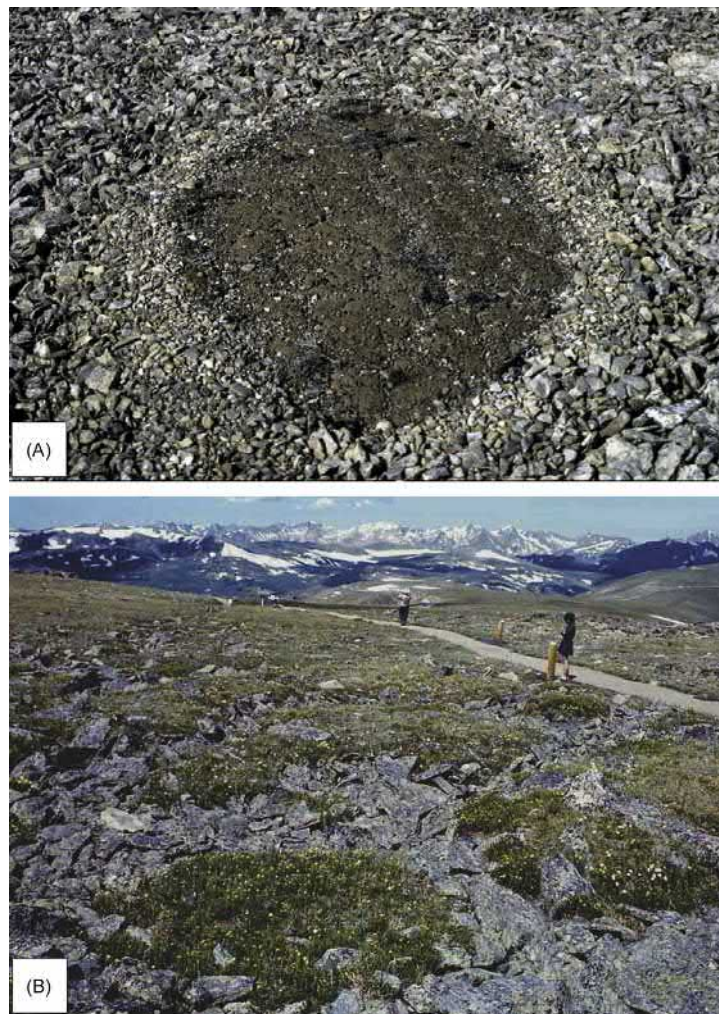


Fig. 7 Sorted stone circles. (A) Fine-grained circle; (B) coarse-grained circle. Photos from Pollard, W. (2018). Periglacial processes in glacial environments. In J. Menzies and J. J. M. van der Meer (eds.), *Past glacial environments*, pp. 537–564. Amsterdam: Elsevier.

Patterned Ground

Patterned ground may be seen where there is a ground surface showing an ordered, more-or-less symmetrical, morphological pattern of ground. Patterned ground associated with cryoturbation is common in alpine regions where there is intensive frost action. In permafrost regions it is limited to the active layer. The patterns include sorted and non-sorted circles, polygons, nets, stripes, and steps.

Solifluction

Frost action on slopes also results in the development of large lobes that slowly migrate downslope, a process called solifluction. In permafrost regions, this process is differentiated by the attribution of the name “gelifluction.” Gelifluction is prominent in alpine regions where snow falls during 6–8 months of the year. Solifluction is a form of slow, creep-based mass movement of waterlogged soils that reflects the combined effect of gravity and freeze/thaw activity on gentle to moderate slopes in periglacial environments. Repeated freeze/thaw of slope sediments results in the incremental downslope displacement of materials by a process called frost creep. Surface displacement rates in gelifluction range from several millimeters to several tens of millimeters per year. In a study of gelifluction in the Tianshan Mountains of China, [Gengnian et al. \(1995\)](#) found the mean surface rate of movement to be 11.14 cm per year, but that not all parts of the lobes move at the same speed. The leading edge of the Tianshan gelifluction lobes moved at a rate of 1.86 cm per year. The rate of movement at the center of the lobes (3.1 cm per year) was greater than at the sides (0.86 cm per year).

Nivation

Nivation is the erosion of the ground beneath and at the sides of a snow bank, mainly as a result of alternate freezing and thawing. Since snow banks tend to form in the same alpine localities year after year (the leeward side of boulders, topographic depressions), the repeated erosion eventually creates a nivation hollow ([Fig. 8](#)). This is a self-perpetuating process, as seasonal or perennial snow cover causes erosion that deepens existing hollows, in which more snow is likely to accumulate in the future.

Impacts of Climate Change

Global change is already bringing higher temperatures to alpine regions around the world. Mountain temperatures are increasing far more quickly than the global average, at a rate closer to that of the Arctic ([MRI EDW Working Group, 2015](#)). Accelerated mountain warming may be due to loss of albedo. Mountain peaks are losing their highly reflective blankets of snow and ice that return much of the sun’s radiation back to space. Instead, darker-colored ground absorbs heat, amplifying the heat-trapping effect of greenhouse gas pollution.



Fig. 8 Nivation hollow in the Cairngorm Mountains, Scotland. Photo by Ash Green, used with permission.

Snow Cover

As discussed by [Edwards et al. \(2007\)](#), one of the vulnerabilities of alpine ecosystems is their reliance on snow cover for much of the year. Various aspects of the relationships between alpine soils and plants that experience seasonal snow cover are susceptible to major perturbations if the snow cover duration and thickness decline because of climatic warming. In particular, the number, frequency and duration of freeze/thaw events influence the nature of nutrient and carbon cycling. Freeze/thaw events disrupt soil structure and act as a selective anti-microbial agent. Soil microclimate is particularly important in alpine ecosystems, responding to changes in water movement and nutrient cycling that are affected by larger scale increases in temperature and changes in precipitation ([Winkler et al., 2019](#)). With declines in snowpack brought on by climate change, alterations are expected in soil N availability, soil organic matter and water holding capacity, soil pH, and even soil texture, all of which may lead to both direct and indirect effects on alpine flora.

Winter temperatures beneath alpine snowpack are substantially warmer than the adjacent air temperatures. A study of temperatures beneath snowbanks in Svalbard showed that temperatures beneath 30 cm of snow remained extremely stable and did not fall below -2°C , even though air temperatures above the snow dropped as low as -24°C ([Convey et al., 2015](#)). This subnivean habitat is vitally important to a host of organisms. Subnivean temperatures influence the kinetics of microbially mediated metabolic and transformation processes. Edwards et al. identified three key snowpack periods based on the length and general significance of contrasting physical conditions. These included a pre- and post-snowpack period likely to experience freeze/thaw conditions with a relatively stable middle period of continuous snow cover. As discussed by [Winkler et al. \(2019\)](#), changes in the timing of snowmelt will dictate changes in growing season length and seasonal soil dry-down rates. They will also create differences in soil nutrients including nitrogen and phosphorous as well as soil pH levels.

Permafrost Degradation

Experimental warming-induced degradation of permafrost in an alpine meadow on the Tibetan Plateau caused an exponential decrease in soil organic matter, which made the soil more gravelly and coarse ([Winkler et al., 2019](#)). Furthermore, soils at colder, high-elevation sites shifted further toward coarser soil textures than warmer, low-elevation alpine sites. Declines in organic matter and coarser soil texture reduce water-holding capacity, which is expected to have consequences for alpine plant communities. These studies also showed that warming increased soil respiration rates only when adequate soil moisture was available.

Alpine Soil Changes

As we have seen, the warming of alpine soils is predicted to bring increased nitrogen availability through greater efficiency of soil microbe decomposers. The increased availability of nitrogen will likely enhance plant growth and reproduction. However, this may be offset by decreased available moisture where summer rainfall is insufficient to maintain soil moisture through a longer, warmer growing season.

Alpine soils can contain more labile soil organic matter than soils from lower elevations because of the slower decomposition and biochemical transformation at colder temperatures.

As discussed by [Pellissier and Rasmann \(2018\)](#), in cold alpine regions, rates of organic matter decomposition from soil organisms decrease with elevation, while organic matter and carbon storage increases. These features of alpine soils will necessarily change under a warmer climatic regime. In future, rates of organic matter decomposition will increase, while organic matter and carbon storage decrease. Soil carbon stocks will decline because warmer soils increase soil respiration.

The loss of soil organic matter will likely bring about a coarsening of alpine soils, as shown in the study of warmed soils on the Tibetan Plateau ([Winkler et al., 2019](#)). They also observed that soils at colder, high-elevation sites on the plateau shifted further toward coarser soil textures than warmer soils in low-elevation alpine sites. Finally, coarse-grained soils retain less water than soils with strong fine-grained components. This decreased ability to hold water will compound the problem discussed above, wherein longer summers and declining snowpack will tend to dry alpine soils, regardless of the predicted decline in soil water retention capability.

Conclusions

Alpine soils, like alpine biota, have evolved under extremely cold climates. Snow cover has been a vital element of alpine ecology. The length and timing of the growing season are other essential aspects of the alpine. Mathematical modeling and limited field observations combine to predict some of the likely effects of long-term warming on alpine soils and vegetation, as discussed here. But ecological relationships are often far more complex than we currently understand, especially in regions as remote and difficult to study as the tops of high mountains. What other unforeseen breakdowns in alpine ecological relationships will occur in the coming decades? We can only watch and wait to see what happens. But just as the alpine flora and fauna cannot migrate to colder environments because they already live on the tops of mountains, so also alpine soils will have no colder place to develop in the face of climatic warming. In other words, the whole alpine ecosystem is endangered by global change, from the bottom up.

See also: Contemporary Human Impacts on Alpine Ecosystems: The Direct and Indirect Effects of Human-Induced Climate Change and Land Use.

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Cold Adaptations of Alpine Insects

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Abstract

This article deals with insect adaptations for life in the alpine zone, primarily in the middle and high latitudes. Their behavioral adaptations are mainly focused on seeking shelter from winter air temperatures. Their physical adaptations include small body size and dark-colored exoskeleton. Most alpine insects are flightless. Their physiological adaptations include freeze resistance, freeze tolerance, and cryoprotective dehydration. Their enzymes are geared to work at low temperatures. Because alpine vegetation is often sparse and grows slowly, plant-feeding species represent a very small proportion of the insect fauna. Many alpine insects are predators or scavengers that rely on arthropods from lower elevations for their food. These insects and spiders are blown up onto the alpine landscape by upslope winds. The life history adaptations of alpine insects include multi-year life spans, especially of larvae and adults, as well as adaptations in their phenology: the timing of periodic events in their life cycle.

Introduction

Insects, like other invertebrate animals, cannot regulate their own body temperatures except by behavioral means such as basking in the sun or burrowing in the soil. In regions such as the tropics, where temperatures are generally both warm and stable throughout the year, this aspect of insect physiology puts little or no environmental stress on insects. However, seasonality and cold temperatures increase in the higher latitudes and at high elevations, and winter air temperatures become lethal to insects in the alpine regions. This article deals primarily with insect adaptations for life in the rarified air of those mountaintops.

Insects have many ways of dealing with cold climates. Surprisingly, the one adaptation that is utilized by very few alpine insects is migration to lower elevations during winter. Nearly all alpine insects and other invertebrates remain there throughout the year. Their behavioral adaptations are mainly focused on seeking shelter from winter air temperatures. Their physical adaptations include small body size and dark-colored exoskeleton. Their physiological adaptations include freeze resistance, freeze tolerance, and cryoprotective dehydration. Their life history adaptations include multi-year life spans, especially of larvae and adults, as well as adaptations in their phenology: the timing of periodic events in their life cycle. Each of these topics are discussed in some detail, below, after a brief discourse on the natural history of alpine insects.

Alpine Insect Life

There are important differences between Arctic insects and those living at high altitude, because the environmental characteristics of these regions are quite different, in spite of their similarities of cold temperature regime (Mani, 1968). Atmospheric pressure decreases with altitude. In the alpine zone above treeline, atmospheric pressure is only 40–60% of that at sea level. Low atmospheric pressure has a wide range of effects on alpine environments. The thin air is highly transparent to incoming solar radiation (insolation). However, the air holds less heat than the denser air closer to sea level, so the alpine climate is cold. The thin air also holds less moisture, making alpine air quite dry. The lack of moisture also reduces the greenhouse effect, which leads to large differences between daytime and night time temperatures. The cold air temperatures cause most of the alpine precipitation to fall as snow. The thin air also does a poor job of screening out ultraviolet radiation, so UV levels are high in the alpine. The aridity of the air leads to greater rates of moisture evaporation from exposed surfaces. This causes rapid desiccation of soft-bodied invertebrates. The

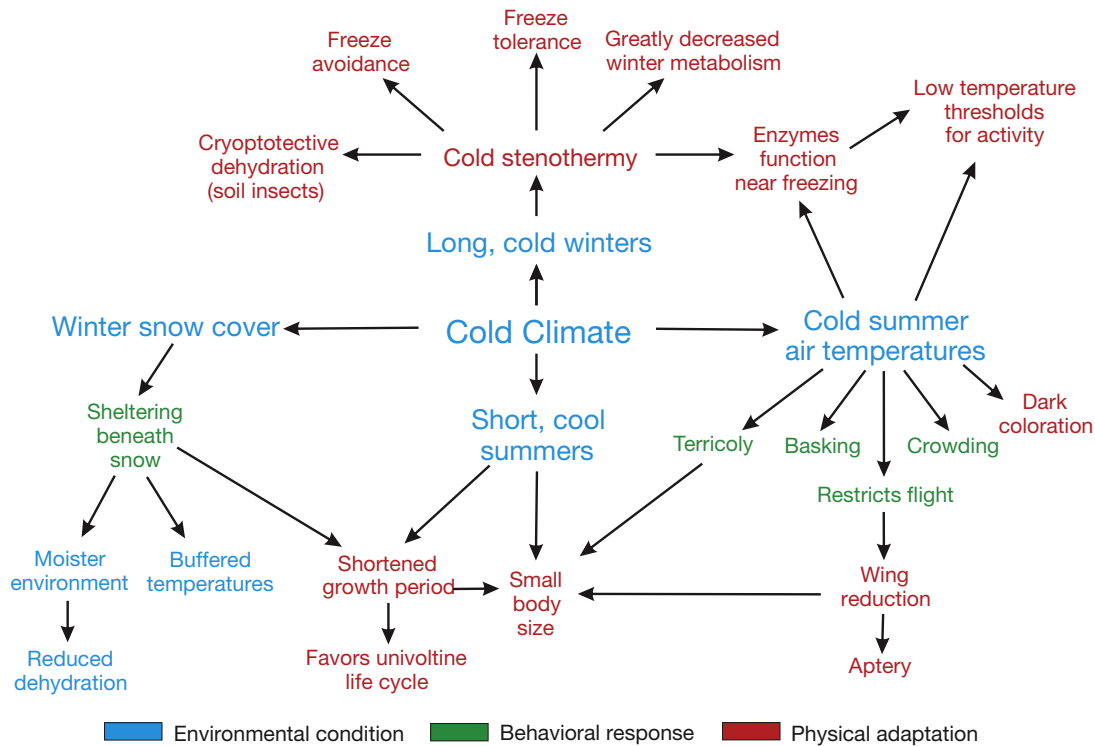


Fig. 1 The ecological importance of cold climate for alpine insects. After Mani, M.S. (1968). Ecology and biogeography of high altitude insects. The Hague: Dr. W. Junk Publishers.

high levels of insolation also cause rapid heating of insect bodies in the summer. Mani (1968) argues that the cold temperatures of the alpine regions are crucial to the survival of high altitude insects, as the cold air keeps insects from overheating in the intense sunshine. It also tends to counteract the aridity of the region and it slows the rate of moisture evaporation from exposed surfaces.

The ecological importance of cold climate is summarized in Fig. 1. Cold temperatures drive both behavioral responses and physical adaptations in alpine insects. The alpine regions are generally inhospitable to insects and other invertebrates. The winters are very long and incredibly cold, with potentially lethal air temperatures persisting for several months of the year. Summers are short, and the length of the growing season decreases with elevation. The growing season in high elevations above treeline average 50–60 days. The highest peaks have only sparse, intermittent plant cover. Thus, the diversity of plant feeding insects is low here.

Because of the thin air, summer daytime temperatures in the alpine vary greatly, depending on location. As shown in Fig. 2, the temperature on a rock surface exposed to the sun may be 30 °C, while the temperature in the shade may be –5 °C. At the same time, the temperature in a pocket of air just beneath a stone is considerably buffered (7 °C) (Mani, 1968). In order to maintain a more-or-less stable internal temperature, alpine insects must continually select suitable microhabitats.

Alpine Insect Life Cycles

Danks (2006) discussed the ability of cold-adapted insects to accelerate the development of their life stages in regions with short growing seasons, such as the alpine. Faster development is assisted by more rapid metabolism (at a given temperature), by reducing the amount of heat required for development, by low threshold temperatures for development, by adaptations of structure or color to assist heat gains, and in several other ways. The average temperature threshold for development in insects is about 10 or 11 °C. Some species from cold habitats such as the alpine have much lower developmental thresholds. For example, winter crane flies of the genus *Trichocera* develop at temperatures as low as –1.5 °C and cold stream stoneflies develop in water that is only 1 to 2 °C. Many alpine species are active at temperatures below freezing.

In winter, almost all alpine insects enter an essentially inactive state called diapause. This is a form of developmental arrest in insects that allows them to survive frigid winter conditions. Some cold-adapted insect species are capable of entering diapause several times. This adaptation facilitates their survival for several years in cold regions where this may be required for the completion of development.

A few groups of plant-feeding insects thrive in alpine environments, including leafhoppers, and grasshoppers. High-altitude grasshoppers rely on an extended life span to overcome the rigors of the climate. Most low altitude grasshoppers overwinter in the egg stage. These eggs hatch in spring, then rapidly proceed through the immature stages (nymphs) and become adults within a few weeks. But the maturation process requires warmth, and that is in short supply in the alpine. Lower elevation hoppers become

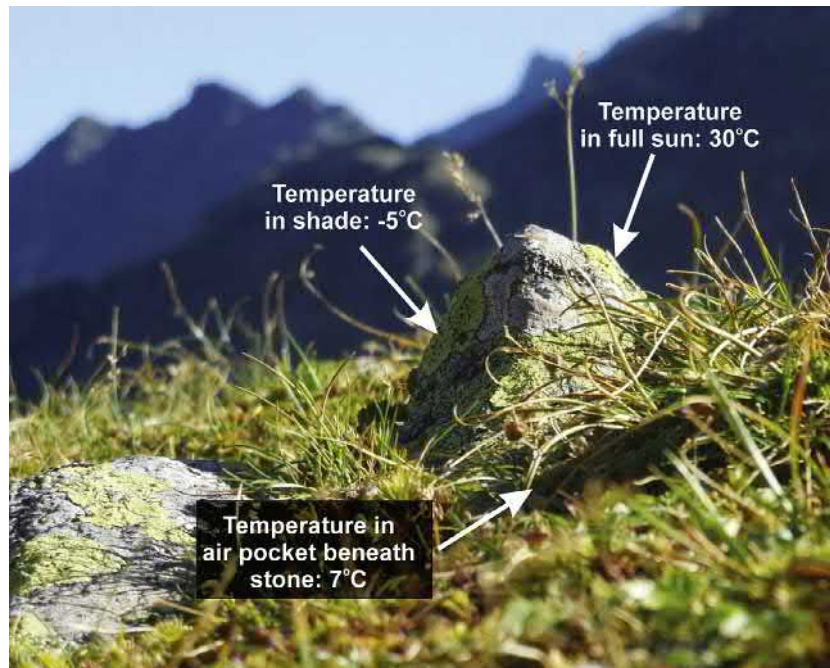


Fig. 2 Differences in temperature in alpine microclimates. The shady side of a rock may be 25 °C colder than the side exposed to the sun. The temperature in an air pocket beneath the rock is buffered.

adults in as little as 30 days, but this process can take almost twice as long at high elevations. High altitude grasshoppers often overwinter as nymphs. This strategy gives them an early start on the maturation process when warm weather arrives in the alpine. Some alpine species stretch their life cycles into more than 1 year, passing the first winter in the egg stage and a second winter as a nymph. Adults also occasionally survive the winter. Late developing species commonly survive until the first severe frost while adults of early developing species may die in mid-summer.

Aquatic alpine insects have a number of adaptations to cope with cold climate and short growing season, as discussed by [Danks \(2007\)](#). These include the use of widely available foods, increased food range, prolonged development (including development lasting more than 1 year per generation), programmed life cycles with diapause and other responses to environmental cues, often enforcing a strict univoltine life cycle and staggered development. Univoltine insects are those that lay just one batch of eggs per year. The response of alpine aquatic insects to the onset of winter conditions may be met by diapause as well as by movement to terrestrial habitats, to less severe aquatic habitats, or to different parts of the same habitat, and by construction of shelters.

Alpine streams are characterized by high solar radiation, year-round low air and water temperatures, scarce vegetation, and a short snow-free season. Many alpine streams drain glaciers at the tops of their catchments. [Schütz and Füreder \(2018\)](#) examined the growth and development of alpine midges (family Chironomidae) in a highly glaciated headwater stream in the Austrian Alps. Water temperature at the site closest to the glacier ranged from 1.1 °C in mid-August to 0.3 °C in early October. Only a few highly adapted midge larvae (genus *Diamesa*) live in these extreme conditions. The study showed that larval size and volume increases in close proximity to the glacier. These are the coldest stream waters of the alpine zone, but they contain higher levels of benthic organic matter toward the glacier. Because these midge larvae are some of the most cold-adapted in the world, they can take advantage of the increased food availability in highly glaciated alpine headwaters. The harsh conditions in these environments (low temperatures, high turbidity and flow dynamics) apparently exclude most midge taxa, but favor these highly adapted species, when their essential needs (food quality and quantity) are guaranteed.

Melanism and Reduced Body Size

Most alpine insects are darker in color and smaller in size than species that live at lower elevations. In species that have ranges that span many life zones, there are often population differences, with alpine specimens being the darkest in coloration and smallest in size. Melanism is an adaptive response that makes the most of limited solar warming in cold regions. Absorption of solar energy by the exoskeleton warms the insect's internal organs, facilitating activity at lower temperatures. As shown in [Fig. 3](#), there are various factors that stimulate the development of dark pigments on insect exoskeletons. Among these are the high levels of ultraviolet radiation and solar radiation of high elevations. High levels of pigmentation protect insects from UV damage to internal tissues. Darker bodies absorb more heat from the insolation, a critical aspect for high-altitude insects living in perpetually cold conditions. However, dark surfaces not only absorb solar energy more effectively, they also lose energy more readily. Alpine insects must try to gain more heat during the day than they lose at night, as their bodies emit infrared radiation back into the atmosphere.

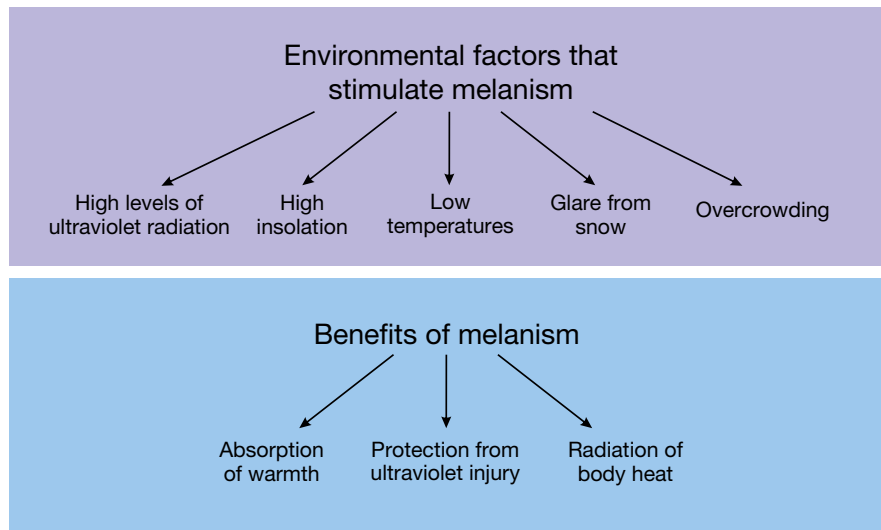


Fig. 3 Above: environmental factors that stimulate melanism in alpine insects; below: benefits of melanism to alpine insects. Concepts from Mani (1968).

A notable example of increased melanism with elevation can be seen in specimens of the butterfly *Parnassius clodius*. This species ranges widely throughout western North America. High elevation populations, found in alpine meadows, have broad dark bands on both the forewings and hindwings, as well as large red spots on the hind wings (Fig. 4A). Its lower elevation populations, found in montane meadows, have a white ground color on the wings, rather narrow dark bands on the forewings, and small red spots on the hind wings (Fig. 4B).

Orthoptera, the insect group that encompasses grasshoppers and bush crickets, includes a particularly large number of species that are color polymorphic with a marked green-brown polymorphism being particularly widespread. It has repeatedly been reported that orthopterans raised under cool conditions are darker than those raised under warm conditions. Valverde and Schielzeth (2015) tested for the effects of background color and ambient temperature on the occurrence of color morph switches (green to brown or brown to green) and developmental darkening in the alpine dwelling club-legged grasshopper *Gomphocerus sibiricus*. Their results indicate that melanin, a multipurpose pigment responsible for dark coloration, seems to be strategically allocated according to environmental conditions. Unlike other grasshoppers, the species is apparently unable to switch color morphs (green/brown) during development. Thus it appears that this darker form is determined genetically, or very early in development.

Most alpine insects have smaller bodies than low elevation species, as discussed by Mani (1968). He noted that species of the ground beetle genus *Bembidion* that live from 2500 to 3000 m elevation range in size from 8 to 13 mm in length. Species that live from 3000 to 4000 m in the Himalayas are 5–8 mm long, while species that live above 5000 m range from 2 to 4 mm in length. As discussed below, the vast majority of alpine beetles are flightless. The reduction in size, or total absence of wings, is associated with smaller body size in beetles at all elevations. The cold climate and lengthy period of diapause of alpine insects slows down the process of insect metamorphosis, limiting the time for growth and development of the various life stages to a few short weeks

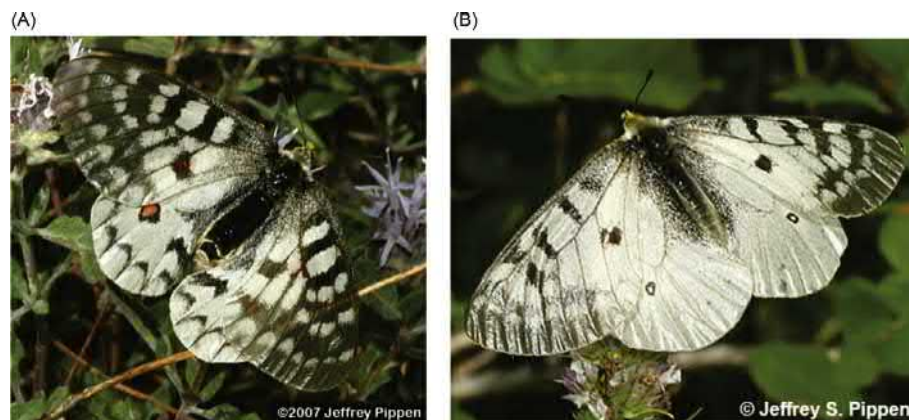


Fig. 4 Differing levels of melanism expressed in different populations of the butterfly *Parnassius clodius*. (A) Note the broad dark bands on both the forewings and hindwings, as well as large red spots on the hind wings of a specimen from an alpine population; (B) note the poorly developed dark bands and small spots on the hind wings of a specimen from a low elevation population. Photos by Jeff Pippen, used by permission.

of summer. This limitation is also thought to put selective pressure favoring reduced body size of alpine insects. Small body size also allows alpine insects to shelter in nooks and crannies where the microclimate is most suitable.

Many alpine insects are clothed in scales, bristles, and hairs (setae) that provide some measure of insulation from cold air by trapping small pockets of air around their bodies. This is especially important for insects that spend time on snowfields, where chilling would otherwise be fatal. Some of these insects also have a waxy coating on their bodies that helps prevent desiccation.

Brachyptery

Brachypterous insects have very reduced wings, so that they are unable to fly. This is a common feature of some alpine insect groups. Apterous insects have no wings, so are likewise flightless. [Darlington \(1943\)](#) noted early on that alpine beetles (especially the family Carabidae, or ground beetles) are mostly flightless. There are several reasons why brachyptery is an advantage to alpine insects. First, the alpine regions are the windiest regions of the world, often experiencing hurricane-force winds. In such conditions, wings are a handicap, not an advantage. Alpine insects live on patches of treeless mountaintops, surrounded by montane forests. From an ecological perspective, the alpine regions are considered habitat ‘islands,’ surrounded by a ‘sea’ of lower-elevation forests, where alpine insects do not belong. The flightless habit of alpine insects, such as beetles, keeps them from being blown off the mountain tops, down to lower elevations. This is not the case for some important alpine insect groups, such as butterflies and moths (Lepidoptera) and flies (Diptera), but even these flying insects tend to stay very close to the ground in the alpine. [Table 1](#) shows the percentage composition of apterous and flightless species in some important alpine insect orders and families in the northwest Himalayan region. [Hiramatsu and Usio \(2018\)](#) studied the species composition of ground beetles in a mountain wildlife reserve in Japan. They identified 23 taxa living in the subalpine and alpine zones of Mount Hakusan. Of these, 12 were apterous, and 7 were brachypterous. Further downslope, the ground beetle fauna of a nearby grassland contained about 75% macropterous (fully-winged) species ([Fig. 5](#)).

Table 1 Percentage composition of apterous and flightless species in some important alpine insect orders and families in the northwest Himalaya.

Order or family	Percentage of apterous species	Percentage of flightless species
Orthoptera (grasshoppers, katydids, crickets)	70	25
Dermaptera (earwigs, pincer bugs)	100	0
Heteroptera (true bugs)	56	?
Hymenoptera (ants, wasps and bees)	40	10
Coleoptera: Carabidae (ground beetles)	90	10
Coleoptera: Staphylinidae (rove beetles)	–	100
Coleoptera: Tenebrionidae (darkling beetles)	100	–
Coleoptera: Chrysomelidae (leaf beetles)	86	12
Coleoptera: Curculionidae (weevils or snout beetles)	75	25

After Mani, M.S. (1968). Ecology and biogeography of high altitude insects. The Hague: Dr. W. Junk Publishers.

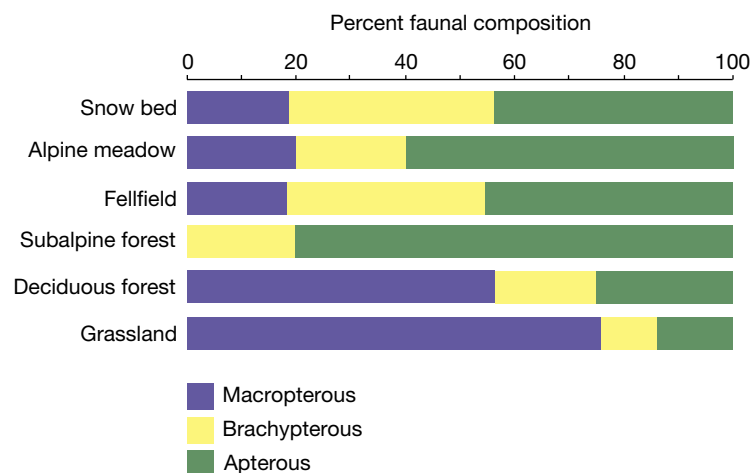


Fig. 5 Percent composition of macropterous, brachypterous and apterous specimens of ground beetles collected by [Hiramatsu and Usio \(2018\)](#) from different habitats on Mount Hakusan, Japan.

Behavioral Adaptations

Temperature thresholds for development and activity are commonly very low in alpine species. Relatively low summer temperatures are offset by development at low temperatures, by selection of warm habitats and microhabitats, and in adults by thermoregulation and modified mating activity. As mentioned above, those alpine insects that do fly generally fly very close to the ground, where heat reflected from the soil creates a warm microhabitat. Resting adult insects often select particularly warm sites, such as locations with dark surfaces, as well as inside the heads of flowers that have a parabolic shape to trap solar energy. Basking in the sunshine is an important behavior for flying insects, as they need to warm their flight muscles before they can fly.

Aquatic insects in alpine ponds and streams have some interesting behavioral adaptations to bitterly cold winter temperatures (Fig. 6) as discussed by Danks (2007). A few species move during winter to resist anoxia beneath ice. High stream flow rates and ice scour take place in spring. These environmental threats may be withstood or avoided by wintering in less severe habitats, penetrating the substrates of streams and ponds, or by delaying activity until after peak flow. However, the growing season is so short in the alpine that many species become active as early as possible in the spring. This trait is enhanced in some pond habitats by choosing overwintering sites that warm up first in spring.

As discussed above, larvae of the midge genus *Diamesa* are adapted to live in the coldest of alpine streams where the spring/summer melt brings dangerously high water volumes and scouring ice. As discussed by Danks (2007), most other midge and other aquatic larvae develop lower in the channel during winter and so avoid the disturbances of summer. Alpine streams fed by melting snowbanks and rainfall are warmer and much less turbid than those fed by glaciers, with peak flows in spring. The diversity of aquatic insect species increases with distance downstream from mountain tops. Streams that are fed at least partially by groundwater tend to have more constant temperature and flow, and chemical characteristics that depend on the water sources. Alpine streams that serve as lake outlets provide yet another set of habitats. Different habitats within streams differ in hydrology, especially the major spring peak from melting ice and snow, but they also differ in warming and cooling rates as well as heat accumulation. In alpine aquatic habitats, key climatic elements influencing the insect fauna arise from seasonality and variability. Food supply is also important.

In most aquatic alpine habitats options for heat gain by immature stages are limited, and therefore site selection plays a key role in ponds. In cold regions, mosquito larvae tend to aggregate in the warmest places in the pools where they develop, preferring sunny to shaded locations and even adjusting their depth to select places closer to the preferred temperature. Chosen sunny sites can be as much as 6 °C or 7 °C warmer at the same time of day than other parts of the same pond that are cooled by permafrost and lack insolation. Many species from cool streams are cold stenotherms that are active at low temperatures. Eggs of stoneflies (Plecoptera) are cold adapted, and many larval stoneflies develop at very low temperatures. Some larval mayflies (Ephemeroptera) and caddisflies (Trichoptera) are active at temperatures below 0.5 °C. Many rapidly developing species are small, a trait that reduces requirements of heat as well as food.

Crowding—the massing together of large numbers of insects—is a well-known behavior of insects on mountain tops (Mani, 1968). The frequency and intensity of crowding increases with elevation in high mountain regions. This makes sense ecologically, because the number of suitable insect habitats likewise decreases with elevation. So high alpine insects are found crowded together in the few microhabitats where they can survive the environmental extremes of high mountains. It is interesting to note that many

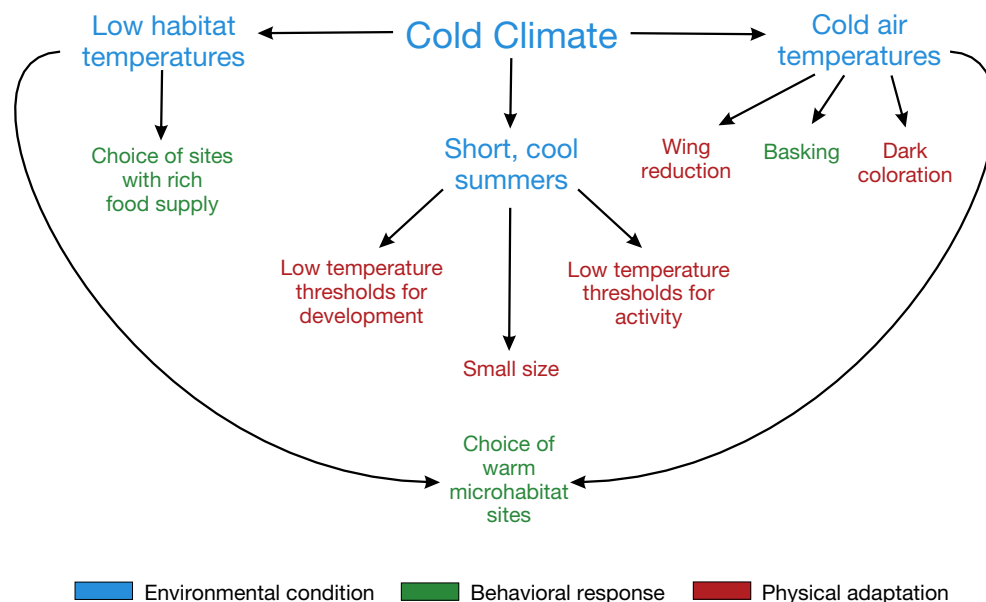


Fig. 6 Flow chart illustrating alpine aquatic insect adaptations.

different species of arthropods, often from quite different taxonomic groups, are found crowded together in isolated pockets of alpine landscapes. The author has often seen several different predatory ground beetles, rove beetles and spiders, sheltering under the same stone in alpine meadows in the Colorado Rockies. This overcrowding into numerous isolated groups slows growth rates, limits body size, structure and color (favoring melanism) (Mani, 1968).

Dietary Adaptations

The short growing season and cold climate lead to a paucity of food resources in the high alpine. For aquatic insects, all of the normal food sources insects tend to be reduced. First, terrestrial vegetation surrounding aquatic habitats is less rich and diverse in the alpine, limiting allochthonous (from outside sources) inputs of litter (Danks, 2007). In particular, trees are absent in the alpine zone, reducing the autumn pulse of deciduous leaves that characterize temperate habitats. Decaying leaves in streams supply the coarse particulate organic matter on which many stream insects depend. Second, other organisms that serve as food for predatory insects are reduced these in cold, unproductive habitats. Third, cold conditions slow the growth of periphyton in streams, thereby limiting autochthonous (indigenous) food. Periphyton consists of the freshwater organisms attached to or clinging to plants and other objects projecting above the bottom sediments, including algae and cyanobacteria. Plankton growth in many lakes is likewise inhibited by low temperatures and low nutrient levels.

Alpine vegetation cover is sparse in many places. It grows slowly and never more than a few cm above the ground. Food for phytophagous insects is thus in relatively short supply. Because of this, the normal trophic system, or ecological pyramid, is turned upside down. In other ecosystems, the phytophagous species are most diverse and abundant while predatory species are relatively few and rare on the landscape. In the alpine, plant-feeding species represent a very small proportion of insect species. Mani (1968) reported that only 3% of insect species in the high alpine regions of the northwest Himalaya are phytophagous. The rest either feed on various kinds of organic debris, or carrion, or they are active predators. Predaceous groups, such as the ground beetles (Carabidae), rove beetles (Staphylinidae), mosquitoes (Culcidae) and various families of biting flies are well-represented in alpine insect faunas, while plant feeding groups, such as leaf beetles (Chrysomelidae), weevils (Curculionidae) and grasshoppers (Orthoptera) are far less diverse here. Alpine terrestrial predators and scavengers rely heavily on allochthonous insects for their food. This topic is discussed by Mani (1968). This exotic food source consists of plants and animals carried aloft by wind onto alpine snowbanks. This includes microscopic food, such as pollen grains and spores, as well as larger plant materials, such as seeds and leaves. Montane and lower elevation insects, spiders and other arthropods are an important food source for scavengers and predators. Many insects take flight on warm summer days, either in search of food or as part of mating behavior. Spiders launch themselves on long strings of silk that catch the wind. Once airborne, these insects and other arthropods are frequently caught in strong upslope winds. When they reach high altitudes, the cold air causes them to fold their wings. Some of these insects land on snowbanks, where their bodies are chilled to the point of immobility and eventual death. Alpine predators and scavengers run out onto the snow to feed on these moribund insects.

One of the more interesting groups of predators operating at high elevations are ground beetles in the genus *Nebria* (Fig. 7). Some species of *Nebria* live near snow banks that persist through the summer months, and at night they hunt other insects that have become trapped on the snow surface. The *Nebria* beetles that live in the alpine zone are physiologically adapted to function at temperatures near freezing, and they have very long legs that help keep their bodies raised off of the surface of the snow, to avoid chilling. Presumably they hunt on snowfields at night to avoid predation by birds.

Arthropods that are active at lower elevations in autumn form another important source of food for alpine scavengers, even though the later are usually forced to enter diapause by early September. Organisms that fall on alpine snowbanks in the autumn remain frozen in the snow until the spring thaw. Then their frozen carcasses thaw out of the snow layers. Some of these are deposited on the ground adjacent to retreating snowbanks, where they provide an important food source for terrestrial predators and scavengers that are just coming out of their winter diapause. Other frozen carcasses form part of the flotsam carried from melting snowbanks into alpine streams and ponds, where they provide food for aquatic predators and scavengers. The top of the food chain on alpine snowbanks includes birds that hunt for insects on the snow surface, as well as predaceous insects, such as ground beetles and rove beetles that hunt the insect scavengers searching for food on the snow.

Selection of Overwintering Sites

All alpine arthropods on land or in shallow waters are exposed to freezing temperatures for much of the year. Nevertheless, even in permafrost areas, insects take shelter under winter snow that insulates them from air temperatures that are far lower. Although alpine ridge tops are typically blown free of snow in winter, good protection beneath snow is available in other alpine habitats, such as snowbanks in depressions and on the lee side of hills. Bottom sediments in alpine ponds are likewise considerably warmer than the air. A study of temperatures beneath snowbanks in Svalbard showed that temperatures beneath just 30 cm of snow remained extremely stable and did not fall below -2°C , even though air temperatures above the snow dropped as low as -24°C (Convey et al., 2015). These stable, near-freezing environments beneath the snow allow some alpine insects and other arthropods to remain active during the winter. Slatyer et al. (2017) studied the sub-nivean arthropod fauna of the Australian alpine region, and found individuals from 18 arthropod orders that were active beneath the snow during winter. These arthropods included springtails (Collembola), spiders (Araneae), mites (Acari) and beetles (Coleoptera). These groups accounted for 95–98% of the individuals collected.

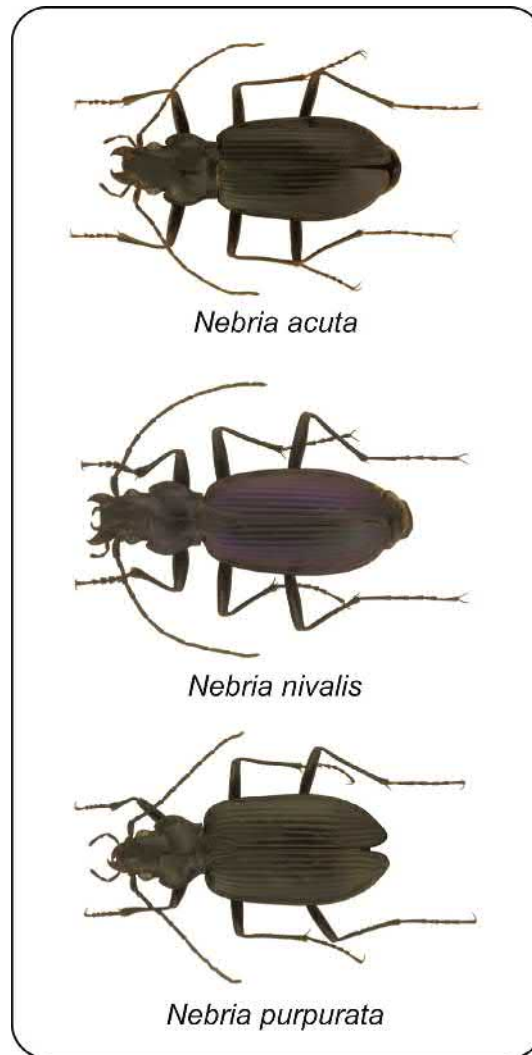


Fig. 7 Photographs of three species of alpine predatory beetles in the genus *Nebria*. Photos courtesy of Mackenzie Flight.

Survival and winter activity beneath the shelter of snow in alpine ecosystems apparently facilitates the multi-year life history of some cold-adapted beetles. Hågvar et al. (2017) studied the ground beetle fauna living beneath winter snow in an alpine region of southern Norway. They documented a two-year life cycle for three common alpine species of ground beetles: *Nebria nivalis*, *N. rufescens*, and *Patrobus septentrionis*. The extended life cycle was facilitated by the simultaneous hibernation of larvae and adults under the snow. Furthermore, both larvae and adults of *P. septentrionis* showed considerable activity through the winter months, beneath the snow. This study indicates that some individuals may hibernate a second time and thus experience two egg-laying seasons. The ability of these beetle species to be active under snow was found to be one of the critical aspects of their ecological requirements.

Paradoxically, warm winters are actually more hazardous for alpine insects than cold ones. Boychuk et al. (2015) point out that repeated freeze–thaw cycles are more common in mountain habitats during unusually warm winters, and that mild winters often lack the significant snowfall levels of colder winters (Fig. 8). Insulation beneath snow cover is especially important in spring and autumn, when early accumulation or late melt of snow cover can extend the period during which environmental temperatures are buffered. In contrast, reduced snow pack exposes overwintering insects to extreme low air temperatures in the spring and autumn, especially because these are seasons when insect cold tolerance may be inadequate for survival.

Some alpine stream insects survive temperatures below freezing as overwintering eggs, including some black flies and mayflies. Some aquatic insect eggs, such as those of the dragonfly genus *Lestes*, survive temperatures below -20°C , and as low as -28°C in *Lestes congener*, although snow cover is also necessary for winter survival (Danks, 2007). In some caddisflies that live in temporary pools, the gelatinous egg matrix resists freezing and drying and perhaps even provides freeze-tolerance to the eggs. However, in frozen streams, the eggs of the stonefly *Arcynopteryx compacta*, although encased in ice, overwinter down to -29°C . This is not accomplished through freezing, but by supercooling through loss of up to two-thirds of the normal water content (see desiccation tolerance, below).

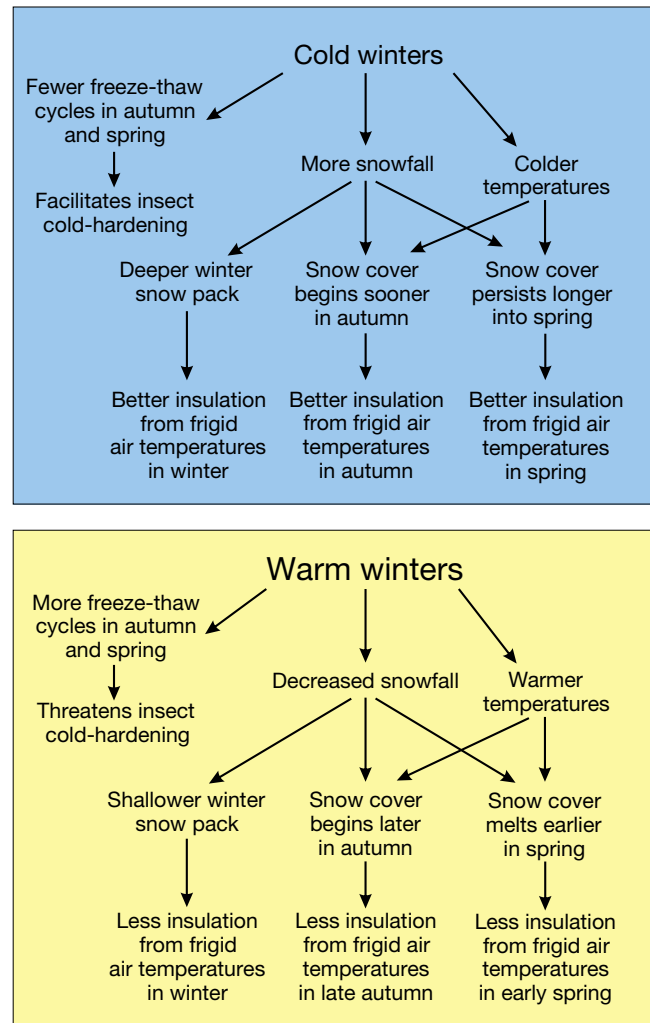


Fig. 8 Flow charts tracing the environmental impacts on alpine insects during cold and warm winters, respectively, based on concepts from Boychuk et al. (2015).

Cold-Temperature Physiology

Alpine insects are able to function at temperatures near freezing because of a set of physiological adaptations. Their body chemistry is geared to function at temperatures near or below freezing. In cold-acclimated beetles, motor nerve fibers show six different activity types, compared with only two types in warm-acclimated beetles. The metabolism of alpine insects in cold temperatures functions at rates similar to those of temperate-zone insects living in moderate temperatures. Cold-adapted insects have evolved 'cold-adapted' enzymes that facilitate chemical reactions at low temperatures (Georlette et al., 2004). Enzymes are organic catalysts, and the package of enzymes in cold-adapted insects have a high catalytic efficiency. However, this efficiency comes at a price: their effectiveness breaks down at higher temperatures. One might be tempted to think that cold-adapted alpine insects would thrive in the kind of warm temperatures experienced at lower elevations, but this is not the case. Because cold-adapted metabolism is facilitated by enzymes that work *only* at low temperatures, alpine insects exposed to temperatures above about 15–20 °C often die because of metabolic failure. Specifically, the weak stability of these enzymes, at even moderate temperatures, causes them to become ineffective and even break down (Georlette et al., 2004). Cold-adapted insects produce enzymes that have a specific activity at low temperatures that is up to tenfold higher than the enzymes in warm-adapted insects. This is the principal physiological adaptation to cold at the enzyme level. It compensates for the otherwise inhibitory effect of low temperatures on chemical reaction rates, providing alpine insects with sufficient metabolic activity to carry out their life cycles in frigid temperatures.

Recent studies have examined the unique aspects of metabolic regulation and cell preservation that facilitate natural cold hardiness. Because cold-hardy insects seek shelter beneath the surface (i.e., underneath snow cover, in frozen mud, under piles of plant debris), their access to atmospheric oxygen becomes limited. Furthermore, insects living in alpine regions survive the winter either in their egg stage, or as overwintering larvae or adults that undergo diapause. Insect metabolism requires oxygen, but because environmental oxygen is limited or unavailable to overwintering insects buried beneath the surface, they must be able to cope

with anoxia. Oxygen requirements fall as insect metabolic rates slow during diapause. Winter survival of cold-adapted insects is enhanced by active suppression of energy-expensive cell functions, including mitochondrial activity. However, survival in oxygen-poor or oxygen-starved environments does not include the suppression of all biochemical functions. There is up-regulation of the hypoxia inducible factor, HIF-1, to coordinate responses that provide hypoxia protection and prevent loss of hemolymph flow to vital organs. This involves increased cellular response to molecular stimulus due to an increase in the number of receptors on the cell surface. Overall, the studies summarized by Storey and Storey (2010) show that cold hardy insect species use a suite of dynamic responses to modulate cellular metabolism in response to seasonal, low temperature, and freeze/thaw cues.

Acclimation and Cooling Rates

The difference between summer and winter temperatures is quite large in many alpine regions. On exposed surfaces, temperatures can vary by as much as 50 °C between seasons. Most alpine insects acclimatize to the cold in the weeks just before winter (Everatt et al., 2015). They prepare themselves physiologically and improve their low temperature tolerance. As autumn progresses, insects use environmental signals such as shortening day lengths and gradually decreasing temperatures to trigger seasonal cold-hardening adaptations. These mechanisms include dramatic changes in biochemistry, cell function and gene expression that permit improved cell function and viability at low temperature (Teets and Denlinger, 2013). Rapid cold hardening mechanisms include dramatic changes in biochemistry, cell function and gene expression that provide improved cell function and viability at low temperature.

The connection between cold-hardiness and gene expression has been investigated for stick insects (Phasmatodea) in New Zealand by Dunning et al. (2013). Of the New Zealand stick insect fauna, only one species of the genus *Micrarchus* is found exclusively at high elevations. This species inhabits the mountain ranges of north-west South Island, which regularly experience sub-zero temperatures throughout the year. All life stages of this species overwinter. Prior to this study, nothing was known about cold tolerance in stick insects. Likewise, very little was known about the genes underpinning their cold tolerance. The authors identified the following about cold-responsive genes.

- (1) The *snd1* gene encodes a complex, six-domain, multifunctional protein with many biological functions. Rapid cold-hardening in *Drosophila* reduces apoptosis and lowers caspase-3-like protein levels, and the authors speculate that elevated expression of *snd1* in the cold-adapted species of *Micrarchus* may be associated with this process. It is possible that *snd1* expression is part of a general stress response in *Micrarchus*, rather than being specifically cold-related.
- (2) Increased expression of the PAHA1 gene in this species of *Micrarchus* might be associated with stabilization or the refolding of proteins that were denatured by cold-shock treatment, or to stabilize structural peptides in anticipation of future cold exposures.

Rapid transitions from summer to winter can leave alpine insects unprepared. If they fail to achieve cold-hardiness in time, the survival of freeze-tolerant species is threatened. Such quick seasonal transitions also raise the supercooling point of freeze-avoiding species, and reduce the capacity of these animals to survive chilling injuries. However, many alpine insects have developed a survival mechanism that allows them to cope with rapid temperature drops. This is called rapid cold hardening. This response allows insects to adjust quickly to falling temperatures within a few days or less. However, relatively little is known about the physiological mechanisms that lie behind rapid cold hardening.

Freeze Tolerance and Freeze Avoidance

Insects have evolved various adaptations to cold, from avoidance of freezing temperatures to tolerance to freezing. These topics are covered in-depth in Denlinger and Lee (2010). The ability to acclimatize to cold conditions is determined by natural selection for cold adaptation. There are two physiological mechanisms by which cold-adapted insects survive freezing temperatures. The first of these is freeze-avoidance; the other is freeze tolerance. Freeze-avoiding insects can be separated into four different groups (Everatt et al., 2015). These include true freeze-avoiding taxa, for which their lower lethal temperature equals the supercooling point. There is also a group of chill-tolerant taxa that show minimal pre-freeze mortality, as well as chill-susceptible taxa that die well above their supercooling points. Finally, there are opportunistic survival taxa that are unable to survive below their developmental threshold.

For small invertebrates, tolerance to temperature extremes is not a necessary adaptation to alpine environments. Instead, the capacity to maintain activity at low temperatures (c. 0 °C) and avoid or tolerate freezing should determine a species' ability to persist in these areas (Mani, 1968). Further, Sinclair et al. (2003) suggested that the mechanisms by which individuals survive sub-zero temperatures are, at least in part, a reflection of the predictability of their environment; freeze tolerance (survival of internal ice formation) predominates in unpredictably cold environments, while freeze avoidance (depression of the freezing point, with ice formation lethal) is more common in predictable, moderately cold environments.

Insects that exhibit resistance to freezing temperatures are able to occupy extremely cold regions. Most cold hardy insects develop freeze avoidance mechanisms because the indiscriminate formation of ice inside the body is lethal. The development of ice nucleators and antifreeze proteins are of critical importance for cold-hardy insect survival in winter. They survive at low temperatures by removing ice nucleating agents from their body fluids that could potentially cause spontaneous internal freezing.

They also accumulate low molecular weight compounds (glycerol or other polyols) in such high concentrations that their bodies remain unfrozen, even at temperatures as low as -40°C to -60°C . Thus, they overwinter in a super-cooled state, stabilized by the production of internal antifreeze compounds. Supercooling is principally achieved via three processes, and is biochemically simpler than freeze tolerance. The first is the removal of ice nucleating agents. Another method of prohibiting ice formation inside freeze-avoiding insects is the accumulation of antifreeze proteins, as well as the production of polyols (organic compounds with multiple hydroxyl groups), sugars and amino acids. Together, these chemical compounds serve both to protect insects from freezing and to enhance their metabolic functions at lower temperatures.

Supercooling points (SCP, nucleation temperature, or crystallization temperature) of insects and other terrestrial arthropods vary greatly, from -2°C to -100°C or lower (Duman et al., 2010). Supercooling is affected by a number of factors, including the volume and water content of the organism, and the ability of the body surface to prevent inoculative freezing by external ice. Freeze-tolerant species often exhibit high SCPs (above -10°C) and have selected for extracellular ice nucleators, while freeze-avoiding insects generally have selected against ice nucleators and for antifreezes, allowing them to supercool below ambient temperatures to which they are exposed over the winter. Protein ice nucleators limit supercooling by organizing water into an ice-like structure, the embryo crystal that promotes freezing at a temperature higher than that where ice would otherwise form. Experiments have shown that this strategy lowers the supercooling point of bodily fluids by up to 20°C in some insects (Everatt et al., 2015).

Freeze-tolerance is another vital survival mechanism for insects subject to long-term exposure to sub-freezing temperatures. This tolerance allows insects to survive through the use of selective internal ice formation. This induced freezing takes place at temperatures just below the freezing point of water (-3° to -10°C) (Everatt et al., 2015), in a controlled manner that minimizes cell damage. Experiments have shown that this strategy lowers the supercooling point of bodily fluids by up to 20°C in some insects. The vast majority of freeze-tolerant insects restrict ice formation to internal body compartments outside their vital organs. This is chiefly done through the accumulation of ice-nucleating agents, including specialized proteins, food particles, crystalloid compounds and even microorganisms. All of these act as locations of water molecule aggregation. By accumulating these agents in the hemolymph (insect blood) and gut, as well as in other tissues, ice formation is encouraged to take place outside of cells. At near-freezing temperatures, ice crystal growth is relatively slow, allowing time for water to be released from cells and join the newly formed ice crystals. Cellular fluids (cytoplasm) therefore become more concentrated and cell walls are less susceptible splitting open because of water freezing inside them.

Freeze-tolerant insects also produce antifreeze proteins and/or antifreeze glycolipids. These compounds stop the expansion of large ice crystals and instead promote the growth of many small crystals that do less damage to tissues. However, these compounds cannot prevent all cellular damage from ice, so freeze-tolerant insects also accumulate additional antifreeze compounds, such as polyhydric alcohols, glycerol, sorbitol and trehalose. Within the cell, these compounds stabilize proteins and membranes, and prevent tissue freezing.

Nevertheless, freeze tolerance poses many challenges to the insect. Freezing can cause cellular dehydration and mechanical damage. As discussed above, existence at temperatures below 0°C greatly inhibits metabolic processes. While freeze-tolerant insects accumulate many potentially protective molecules, the mechanisms underlying freeze tolerance have not yet been fully explored (Toxopeus and Sinclair, 2018). It is thought that freeze-tolerant insects survive the winter by controlling the quality and quantity of ice that forms in their bodies, by preventing or repairing cell damage, by managing biochemical processes while frozen and while thawing, and by restoring their physiological processes after their bodies have thawed (Toxopeus and Sinclair, 2018).

Several species of insects combine both freeze-tolerance and freeze-resistance. Insects of this kind are able to super-cool and at the same time be tolerant to freezing. The molecular basis of this combination of properties remains unknown.

New Zealand has extensive alpine and subalpine habitats where insects are exposed to freezing temperatures. Studies of cold tolerance in New Zealand insects have centered on an alpine Weta (*Hemideina maori*), the world's largest freeze-tolerant insect, and an alpine cockroach (*Celatoblatta quinque maculata*). Both of these insects are moderately freeze-tolerant and have ice nucleating agents in their hemolymph and guts (Wharton, 2011). *H. maori* has been shown to survive with 82% of its body water turning to ice at -5°C . It has been shown that *C. quinque maculata* survives the 28 freeze/thaw events per month that occur during winter in New Zealand's Rock and Pillar Range and that it survives what would appear to be lethal freezing events. The evidence suggests that the lower temperature limit for survival of this cockroach is set by the accumulation of a critical amount of damage in its most sensitive tissues (Wharton, 2011, and references therein).

Alpine insects generally do not feed over winter and hence must rely on stored energy to fuel their metabolism over winter. Most overwintering insects end winter with substantially lower levels of lipids than they had in summer, which suggests that lipids are a primary source of overwintering fuel. Diapause brings on depressed metabolic rates over winter, so the consumption of lipids is more likely to take place in the autumn and spring, when temperatures are higher but insects remain dormant. For freeze-tolerant insects (which withstand internal ice), Sinclair and Marshall (2018) speculate that impaired oxygen delivery limits lipid oxidation when ice forms inside insect exoskeletons. Acetylated triacylglycerols remain liquid at low temperatures and interact with water molecules, suggesting a possible role in cryoprotection. Similarly, antifreeze glycolipids may play an important role in structuring water and ice during overwintering. Lipids are certainly an important component of insect overwintering energetics, but this aspect of insect physiology remains poorly understood.

Desiccation Tolerance

An ability to tolerate water loss is crucial for the survival of some alpine insects, although this adaptation is more commonly found in polar insects. Anti-desiccation adaptations have a good deal in common with freeze-avoidance, including the production of polyols and sugars. Soil-dwelling insects and many immature stages of above-ground species spend most of their time in the soil. These must cope with soil ice during winter. Most of these insects have only two options for survival: either tolerate internal freezing or dehydrate. In frozen soil, there is a strong tendency for ice outside the insects' bodies to draw the liquid water out of their bodies, causing desiccation of tissues (Holmstrup, 2015). A cold tolerance mechanism that retards this process is called cryoprotective dehydration (CPD). Utilization of this protective mechanism requires an insect to withstand substantial dehydration of its bodily fluids. However, CPD is essentially a freeze-avoidance strategy, and the associated physiological traits are essentially the same as those found in freeze tolerance. Dehydration virtually eliminates the risk of tissue ice formation, ensuring survival in frozen soils. Thus, winter survival of soil-dwelling invertebrates depends more on dehydration than on supercooling. However, cryoprotective dehydration can be slow, so some supercooling capacity is needed in its initial phases (Sørensen and Holmstrup, 2011).

Conclusions

The ability of insects to live in extremely cold alpine environments is truly remarkable, and involves every aspect of their lives, from timing of events in their annual life cycles to their behavior patterns and their internal physiology. Most of these adaptations are encoded in their DNA, and geneticists are only now starting to unravel the location and function of genes that control the processes described in this article. In the vernacular, we would say that alpine insects are *hard wired* to live where they do. However, these very adaptations to cold make alpine insects and other invertebrates extremely vulnerable to global warming. As temperatures rise, the native alpine fauna will suffer and decline. As they are already living at such high elevations, there are no higher elevations available for immigration. The rising temperatures will cause decreased fitness in cold-hardy insects, and they will also be forced to compete with more warm-adapted insects, invading from lower elevations. Likewise, changes in the composition of high altitude plant communities, a phenomenon already documented in many alpine regions, will disturb the balance of alpine ecosystems, including long-established plant-insect interactions. The cold-hardiness of alpine insects, their greatest asset for survival in previous millennia, may very well become their greatest liability in the coming decades.

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Alpine Insect Distribution Patterns

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Abstract

Alpine insects are a remarkable group of organisms, not just surviving the frigid climates and short summers of the alpine zone, but actually thriving there. They do this through a series of physiological and behavioral adaptations. These cold-adaptations make it virtually impossible for alpine-dwelling insects to migrate out of their mountain top habitat islands today. However, the DNA, modern and fossil evidence show us that alpine insects have shifted their distributions in the past. The cold glacial periods of the Pleistocene offered these insects the opportunity to disperse into lowland regions. The Pleistocene glacial intervals were times of massive population expansion of cold-adapted insects, down from the mountain tops and out into the periglacial environments of the lowland regions that existed in reasonably close proximity to continental ice sheets and mountain glacial systems.

Introduction

To the casual observer, the sight of insects on mountain tops on a summer's day may seem serendipitous. Indeed, it might seem that these insects were carried upslope by the almost-constant winds of the alpine zone, and that they are doomed to expire when the first cold snap hits the high country. However, a more systematic study of alpine insects reveals that most of them are permanent residents there, not accidental transplants. As are their counterparts in the Polar Regions, these insects are highly adapted to cold temperatures and a short growing season. Alpine insect adaptations are discussed elsewhere in this volume. The point of this article is to review what is known about the distribution of alpine insects, past and present.

Just as in the Arctic, alpine-zone insects are dominated by predators and scavengers. Plant productivity is generally low in these regions. In the alpine, soils are shallow and poorly developed, temperatures are cold, and the growing season is quite short. These factors limit plant productivity and the diversity and abundance of alpine phytophages. Unlike the Arctic fauna, many alpine predators and scavengers rely on arthropod prey (mainly spiders and flying insects) that are transported up to the alpine zone from the mountain forests, below. Many montane and subalpine insects are caught in upslope winds on summer days, and end up on alpine snowfields, where they die of hypothermia. These dead and dying insects form the principal prey for various alpine insects, especially predatory beetles.

The diversity of Arctic insects decreases with latitude, so that the low Arctic has far more diversity of species than polar desert regions of the far north. So also does the diversity and abundance of alpine insects regions decrease with elevation. This is partly due to differences in the richness of vegetation. Lower alpine slopes tend to be gentler than high alpine slopes, which are often steep. The former landscapes tend to have richer, better developed soils that support a greater variety and abundance of alpine vegetation. The latter landscapes range from poorly vegetated to bare rock surfaces and snowfields. The insect diversity of alpine meadows is thus greater than the diversity of rocky peaks (Table 1).

There is a high degree of endemism in alpine insect species. Endemism refers to a species that is restricted to a particular geographic region as a result of factors such as isolation or in response to abiotic conditions. In the case of alpine insects, both conditions apply, i.e., species living in the alpine are geographically isolated from species in other regions, and they are highly adapted to the rather severe abiotic conditions of cold climate, short growing season, high winds, rocky substrates, and other abiotic factors. Mani (1968) has documented the percentage of endemic species in the major orders of Himalayan insects, as follows: Hemiptera—65%; Coleoptera—60%; Hymenoptera—47%; Lepidoptera (butterflies only)—45%. Thus the overall average for all groups is 54% endemic species. Such an accounting has not been done for other mountain ranges, but the proportion of endemics is probably somewhat similar.

Attempts to reconstruct the origins and past movements of alpine insects that are based solely on their modern distributions are like trying to understand a very lengthy novel by reading only the final page. Human lifetimes are simply too short to allow us to observe distributional shifts of organisms at any meaningful timescale. For instance, some cold-adapted insect species have populations both in the Arctic and in alpine regions further south. Presumably at some time in the past there was an original population of such species, but where did that species originate—in the Arctic or on top of some mid-latitude mountain range? Moreover, when did such cold-adapted species arise, and what have been their distributional shifts through time? Biogeographic and genetic studies suggest that dispersal, rather than ecological divergence from low elevation species, is the principal factor governing the biogeography of alpine species (Schoville and Rovito, 2019). Since these dispersal events must have taken place during the Pleistocene, we

Table 1 Arthropod species diversity in percent composition of alpine faunas as a function of elevation in various mountain ranges

Region and taxonomic groups	Altitude range (m above sea level)	Percentage of species
Tatra Mountains, Poland Lepidoptera	900–1545	74
	1545–1789	16
	1960–2350	8
	2350–2662	2
Western Himalayan Mountains (NW India, Pakistan) Lepidoptera	1500–1600	30
	1600–2800	20
	2800–3000	20
	3000–4100	10
	4100–4300	10
The Alps (France, Switzerland, Italy, and Austria) Hydracarina (water mites)	1800–2000	37
	2000–2200	28
	2200–2400	20
	2400–2600	13
	2600–2800	2
Pamir Mountains, Tajikistan, and Kyrgyzstan Orthoptera, Dermaptera, Hemiptera, and Coleoptera	1850–2800	43
	2800–3400	24
	3400–3800	17
	3800–4400	15
	> 4400	1
Eastern Himalayan Mountains of NE India, China, Nepal, Bhutan Orthoptera, Hemiptera, Coleoptera, Lepidoptera	2500–3000	15
	3000–3600	13
	3600–4000	24
	4000–4500	9
	4500–5000	28
	5000–5400	8
	5400–5800	3

Data from Mani, M. S. (1968). *Ecology and biogeography of high altitude insects*. The Hague: Dr. W. Junk N.V. Publishers.

must look to the fossil record to piece together the history of alpine insect biogeographic patterns. The modern insect data cannot answer these questions, although the analysis of modern and ancient DNA is starting to shed new light.

Since about the 1930s, zoogeographers have discussed the means by which alpine insects and other organisms survived Pleistocene glaciations—times when their modern mountaintop habitats were generally glaciated. Specifically, it has long been debated whether high alpine taxa survived ice ages in situ on small ice-free islands of habitat, called nunataks, or whether survival during glaciations was restricted to regions of lower elevation, so called “massifs de refuge” that existed beyond glacial limits.

As Mani (1968) noted, the ecological specializations that characterize alpine insects severely restrict their means of dispersal from one mountain range to another. As discussed below, it appears that the cold climates associated with Pleistocene glaciations played a dominant role in the dispersal of these insects across the lowlands that separate mountain ranges. Today these lowlands are far too hot in the summer to be crossed by the extremely cold-adapted insects that live in alpine habitats. These insects are nearly all inactive during winter (another cold-region adaptation), so their potential dispersal is limited to the summer season. Furthermore, many alpine insect species are brachypterous—they lack usable flight wings. There are several reasons why brachyptery is an advantage to alpine insects. First, the alpine regions are some of the windiest regions of the world, often experiencing hurricane-force winds. In such conditions, wings are a handicap, not an advantage. Alpine insects live on patches of treeless mountaintops, surrounded by montane forests. From an ecological perspective, the alpine regions are considered habitat “islands,” surrounded by a “sea” of lower-elevation forests, where alpine insects do not belong. The flightless habit of alpine insects keeps them from being blown off the mountain tops, down to lower elevations. The exception to this is the alpine butterflies and moths (Lepidoptera) and the flies (Diptera). But even these insects that are capable of flight are not adapted to spend the weeks or months that it might take them to traverse inhospitable lowland regions, on their way to new alpine regions. Most of the alpine Lepidoptera species rely on specific host plants for nectar. Many of these plants are found only in the alpine regions.

DNA Evidence

A study of the modern DNA of populations of the cold-adapted ground beetle *Amara alpina* has helped elucidate its Pleistocene history in North America. This species currently has populations throughout the North American Arctic, Greenland, northern Siberia,

the Rocky Mountains and the northern Appalachians. Reiss et al. (1999) analyzed mitochondrial DNA from 22 North American populations of *A. alpina*. They found that populations from Alaska and the Yukon (the former region of Eastern Beringia that was a refuge for Arctic biota in the Pleistocene) were the most genetically diverse, which agrees with the idea that this region was continuously inhabited by this species throughout the Pleistocene. Canadian Arctic regions east of Beringia were colonized by populations from Beringia, but only after the last deglaciation, which took place in arctic Canada only about 6000 years ago. The genotypes of these more eastern Arctic populations are a subset of the Beringian types. Finally, at least two ancestral haplotypes existed in the populations living in the southern refugium from which the Rockies and Appalachian populations were founded. The fossil record of *A. alpina* from the lower 48 states of the United States includes populations living near the margins of continental ice sheets during the Last glaciation. The more westerly of these populations managed to survive postglacial warming of the lowlands by shifting to the alpine zone of the Rockies. The more easterly of these populations managed to survive postglacial warming of the lowlands by shifting to the alpine zone of the northern Appalachians, such as Mount Washington, New Hampshire, and Katahdin, Maine.

DNA evidence from a different region has also dealt a blow to the nunatak hypothesis. This comes from a study of modern ground beetles in the Alps. Lohse et al. (2010) studied the local radiation of high alpine carabid beetles (genus *Trechus*) in the Orobanchian Alps, Northern Italy. Geologic evidence indicates that the summits along the northern flank of this mountain range were surrounded by an ice sheet, leaving the highest peaks as nunataks during the Last Glacial Maximum (LGM), and that the southern flanks of the range remained unglaciated. Lohse et al. analyzed both MtDNA and nuclear DNA samples from 12 beetle populations. They estimated the ancestral location states in the gene trees, which in turn were used to infer the most likely order of recolonization under a model of sequential founder events from a *massif de refuge* from the mitochondrial data. They found that only three of the *Trechus* populations presented genetic evidence that was incompatible with LGM survival in a *massif de refuge*, and that both mitochondrial and nuclear data support separate refugial origins for populations on the western and eastern ends of the northern ridge. Finally, the mitochondrial evidence suggests the persistence of *Trechus* populations on the northern ridge for part of the last ice age.

A study of the mitochondrial DNA (MtDNA) of the alpine butterflies in the *Parnassius phoebus* complex by Todisco et al. (2012) provides fascinating insights into the Pleistocene and Holocene history of these cold-adapted insects. This species complex is unique in the genus *Parnassius* because of its Holarctic distribution. Scattered populations occur in high elevations of the Alps, the northern Urals and in central and eastern Siberia, as well as on mountaintops of western North America from Alaska to California and Colorado (Fig. 1). Butterfly taxonomists recognize five species in this group (Fig. 2), based on their external morphology, ecological requirements, and geographic isolation.

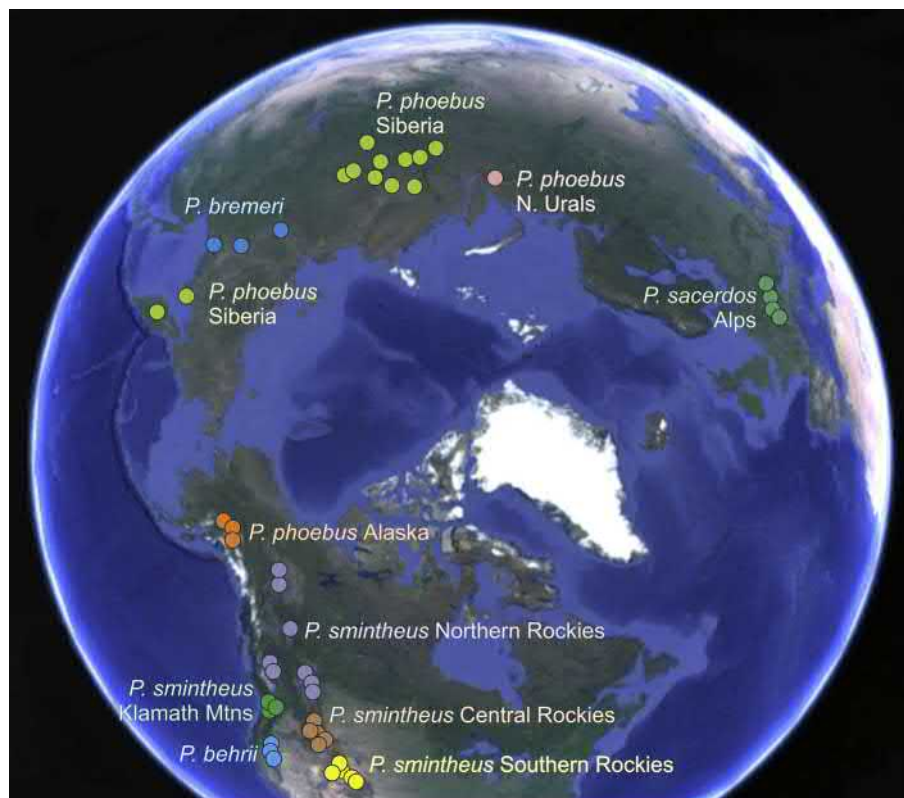


Fig. 1 Modern distribution maps of alpine butterflies in the *Parnassius phoebus* complex. Data from Todisco V, Gratton P, Zakharov EV, et al. (2012). Mitochondrial phylogeography of the Holarctic *Parnassius phoebus* complex supports a recent refugial model for alpine butterflies. *Journal of Biogeography* 39, 1058–1072.



Parnassius phoebus



Parnassius smintheus



Parnassius behrii



Parnassius bremeri



Parnassius clodius



Parnassius sacerdos

Fig. 2 Photographs of the species in the *Parnassius phoebus* complex and *P. clodius*, a western North American species. Photo of *Parnassius phoebus* by Thomas Neubauer; photo of *P. smintheus* provided by the Butterfly and Moth Information Network; photo of *P. behrii* by Elise Larsen; photo of *P. bremeri* by Andrei Proplyetkin; photo of *P. clodius* by Jeffrey Pippen; photo of *P. sacerdos* by Klaas van Haeringen. All photos used by permission of the authors.

The genetic evidence suggests that there are two distinct clades within this group of butterflies: a North American clade and a Eurasian-Alaskan clade. A clade is by definition monophyletic, including one ancestor and all its descendants. Based on the MtDNA evidence, the estimated time to the most recent common ancestor of the North American clade was less than 125,000 years ago (125 ka). The estimated time to the most recent common ancestor of the Eurasian-Alaskan clade was less than 80 ka. [Todisco et al. \(2012\)](#) argue that the mtDNA data are consistent with range expansions across each of the two continents during the Last glaciation (ca. 30,000–11,000 years ago). They also concluded that significant gene flow between the various populations ended during the Holocene. The authors proposed that this *Parnassius* species complex may serve as a model for Holarctic alpine invertebrates that have moderate dispersal abilities in that its genetic structure at a continental scale reflects extensive connectivity during the most recent glaciation. Butterflies leave essentially no fossil record, except for the occasional caterpillar mandible. However, the fossil beetle record supports this butterfly genetic model of alpine insect distribution pattern. While the modern populations of alpine beetle species are restricted to isolated habitat islands on mountaintops, their Late Pleistocene fossil record demonstrates that they spread throughout many lowland regions during glacial times. This promoted the extensive genetic connectivity—mixing of the gene pools of today's alpine species during lengthy glacial intervals.

Another phenomenon indicated by the *Parnassius* butterfly MtDNA study is that samples of *P. smintheus* from Yukon and British Columbia share their haplotypes with samples from the northern United States (Washington and Montana). This indicates that this species expanded northwards following the retreat of glaciers after the LGM, starting about 19,000 years ago. The North American ice sheets therefore acted as a massive geographical barrier between *P. smintheus* and *P. phoebus* during the last glacial period. This

phenomenon has also been observed in the fossil beetle record from the lower 48 states of the United States. As discussed below, populations of cold-adapted beetles lived at low elevations south of the Laurentide and Cordilleran Ice Sheets during the Last glaciation. These ice sheets formed an insurmountable physical barrier between arctic and mid-latitude populations of many cold-adapted species. When deglaciation began, some species were able to disperse northward along the edge of the retreating ice. However, most cold-adapted species either retreated to mountain-top regions as they became ice-free, or if this mode of dispersal was geographically untenable, then some species simply were extirpated from the middle latitudes of North America. These postglacial mountain refuges include the alpine zones of the Sierras, Cascades, Rockies, and northern Appalachians. The Rocky Mountains have the best-documented Late Pleistocene and Holocene insect fossil record, so they form the basis of much of what follows.

Fossil Beetle Evidence—North America

The mountain tops of the Rockies form an archipelago of alpine habitat islands, stretching from the Arctic tundra of Canada south to the highlands of New Mexico. As such, these habitat islands have provided a series of migration corridors for cold-adapted biota, with the Great Plains on the east and various deserts and other arid regions on the west. As shown in Fig. 3, the most mountainous state of the Rockies, Colorado, has hundreds of relatively small alpine patches, many of which are isolated from other patches by 20 km or more. However, during the last glaciation, the alpine zone expanded downslope to about 3000 m elevation, covering what is now subalpine forest. The dark green areas seen on the map represent the current subalpine zone, but during the last glaciation those forests likewise shifted downslope by around 1000 m. Much of the expanded alpine regions were glaciated during the LGM, but the Southern Rockies were too dry to support many large glaciers. Thus the available alpine habitat for cold-adapted insects expanded during the last glaciation. As predicted by the butterfly MtDNA results, populations of alpine insects in the Rockies that had previously been isolated from each other during interglacial warm periods would have been able to spread into much larger areas during glacial cold periods, as their alpine habitat expanded.

Thousands of analyzed Quaternary beetle assemblages (summarized in Elias, 2010) have demonstrated that beetles (and probably many other groups of insects that lack substantial fossil records) shift their geographic ranges in response to climatic oscillations. Evidence for large-scale range shifts of this kind has been found in fossil assemblages from Europe (Coope, 1973), Australia (Porch et al., 2009), New Zealand (Marra, 2003), and North America (Elias, 1991). There is scant fossil evidence of insect extinctions due to Pleistocene glaciations, even in the more sedentary insect groups (Coope, 1978). In the Arctic, where permafrost deposits have yielded insect exoskeletal fossil assemblages dating back to the Pliocene, the vast majority of identified species represent extant taxa (Elias and Matthews, 2002).

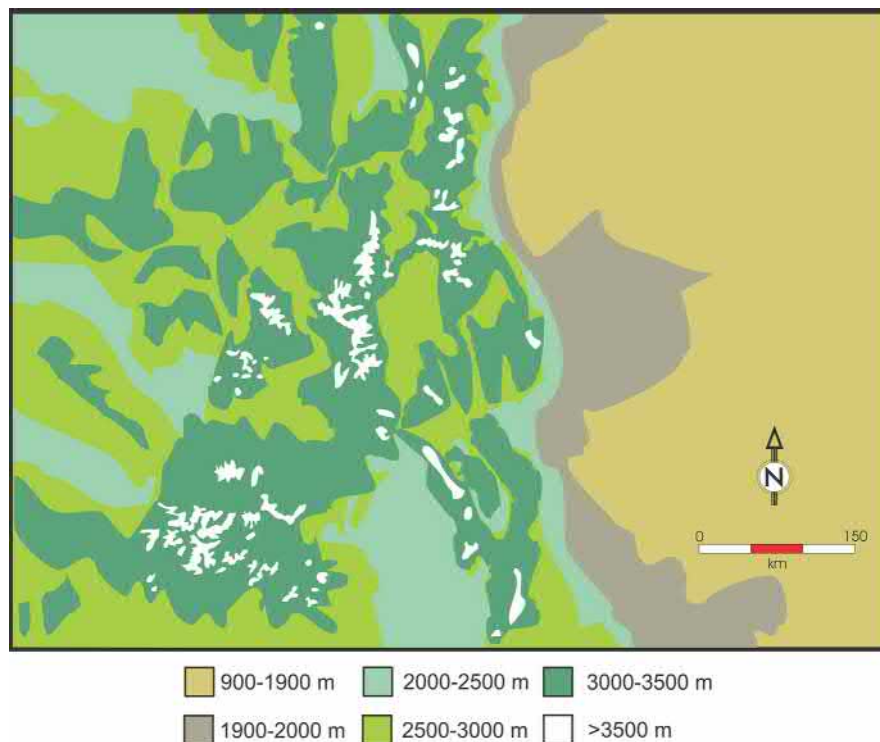


Fig. 3 Map of the current alpine zone in Colorado (*white areas*) and the presumed extent of the alpine and glaciated zone in Colorado during the LGM (*dark green areas*).

The last 2.6 million years (the Quaternary) represent an interval of time during which climates of the temperate and high latitudes have oscillated frequently, and on large scales. Insect migrations in response to these climatic oscillations have not been deliberate acts to move away from unsuitable environments. Rather, as typical r-selected biota, insects generally have large numbers of offspring, and most of these offspring move away from their point of origin, to minimize competition with other members of the local population. This habit of fanning out in all directions ensures that species survive environmental changes, climatic, and otherwise. Those individuals that happen to migrate to regions that still fall within the suitable environmental envelope of their species will survive such changes. Even if only a small percentage of a population lands in a suitable habitat, their rapid reproduction and large numbers of offspring ensure that the species itself survives the environmental change. Over Quaternary time scales, this phenomenon has made virtual globe-trotters of some beetle species (Elias, 2015).

The Rocky Mountains are an ideal region to test the competing hypotheses on the regional survival of alpine insects during glaciations, for two reasons. First, the chain of Rocky Mountain ranges extends from the edge of the Arctic tundra in Canada to the edge of the Chihuahuan Desert in New Mexico, facilitating comparisons along a 4800 km corridor of highlands. Second, organic deposits from sites in the Rockies and from adjacent lowland areas have provided good fossil evidence of the distributional shifts of beetles in response to Late Pleistocene glaciation.

The author has studied 122 fossil insect assemblages from 13 sites, ranging from northern Montana to southern Colorado (Elias, 2015). More than 90% of the identifiable fragments of insect exoskeleton preserved in these organic deposits come from beetles, or Coleoptera. Beetles are the largest order of insects, and their exoskeletons are more heavily reinforced with chitin than those of most other insect orders. The results of these studies reveal a variety of insect responses to the last glaciation.

Roughly three-quarters of the 200 beetle species identified from the Rocky Mountain regional faunal assemblages apparently remained in this region during the Last glaciation. It appears that nearly all these species shifted their ranges downslope, thereby escaping mountain glaciers. Thus far we have found no fossil evidence for survival of any beetle species on nunataks—bare peaks that rose above regional glaciers and ice sheets in the Rockies. The other 45 species (23%) found in Rockies fossil assemblages have become regionally extirpated. In other words, they are apparently no longer resident in this region, although they persist elsewhere. None of the 200 species in the fossil assemblages has gone extinct. Roughly half of the extirpated species found in fossil assemblages from the LGM are found today in either the arctic or the boreo-arctic regions of Canada and Alaska.

The oldest fauna discussed here, dated to the LGM (21,700 year BP), is from the Lamb Spring site, situated in the foothills west of Denver, Colorado. This fauna included the regionally extirpated species of water scavenger beetle *Helophorus splendidus*. This species is found today only along the shores of the Arctic Ocean of Canada, west of Hudson Bay (Fig. 4). The populations that lived south of the Laurentide and Cordilleran Ice Sheets may have died out completely toward the end of the last glaciation. If that is the case, then the modern Arctic populations may be derived from populations that survived the LGM in Eastern Beringia—the unglaciated lowlands of Alaska and the Yukon. However, the lack of any known modern populations in the Beringian region strongly suggests that small populations of *H. splendidus* followed the retreating margins of the continental ice sheets as they moved northward through the last 18,000 years. Based on the climatic conditions at the modern collecting localities for *H. splendidus*, it is adapted to live where mean July temperatures (Tmax) are 8°C–10°C, and where mean January temperatures (Tmin) are –34°C to –28°C. This means that this beetle is adapted to the extremely cold temperatures found only in Arctic and alpine regions today.

This scenario of beetle populations following the retreating margins of ice sheets has also been suggested for the postglacial history of another member of this genus, *Helophorus arcticus* (Morgan, 1989). Interestingly, this LGM fauna from Lamb Spring contains several species of beetles now found in the alpine regions of Colorado. This strongly suggests that alpine insects shifted downslope during the Last glaciation, which supports the *massif de refuge* hypothesis over the nunatak hypothesis.

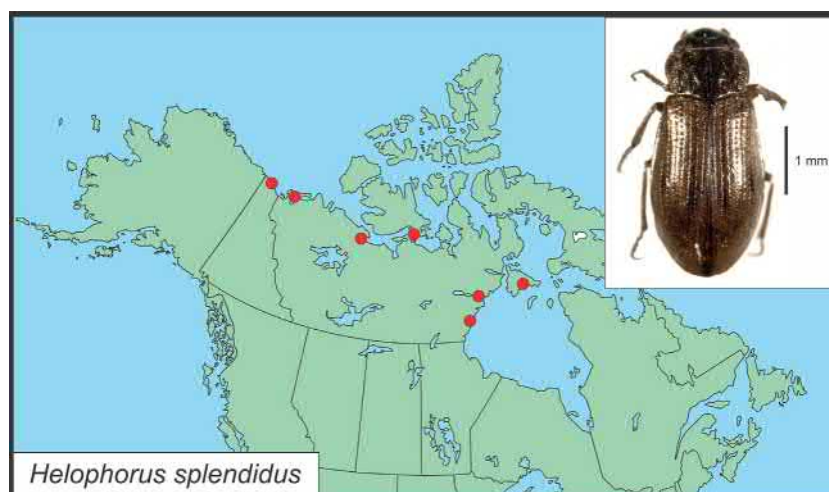


Fig. 4 Modern distribution of the cold-adapted water scavenger beetle *Helophorus splendidus*. Inset: photo of *H. splendidus*, courtesy of Creative Commons.

The younger of the two faunas from Lamb Spring, directly dated to 17,600 year BP, includes the rove beetles *Olophrum rotundicolle*, *Tachinus elongatus*, and *Gymnusa atra*. *Olophrum rotundicolle* is a boreo-arctic species that ranges south along the Appalachian chain but is not known from the Rocky Mountains today (Campbell, 1983). It was found in fossil assemblages from the Colorado Rockies that are as young as the last thousand years but is apparently not present in the Rocky Mountain region today. *Tachinus elongatus* is a boreo-montane species, with modern populations extending south along the Rocky Mountains to the Medicine Bow Mountains of southern Wyoming (Campbell, 1973). The southern edge of its modern range is only about 100–200 km north of the sites from which it has been found in Colorado. It persisted in Colorado until at least 2000 years ago; its last fossil record is from a site in Rocky Mountain National Park.

The Late Glacial interval began about 17,000 year BP in the Rocky Mountains, and ended about 11,600 year BP. By that time, the margins of mountain glaciers and ice caps were rapidly retreating upslope, exposing subalpine and then alpine landscapes for the first time in about 18,000 years. Not surprisingly, the trees of the subalpine forest did not become established at the modern treeline elevations until about 1500 years later, as soil development and primary succession had to take place before the trees could reach their elevational limits (Elias, 1985).

The extirpated species found in Late Glacial beetle faunas from the Rockies include the ground beetle *Bembidion sulcipenne hyperboroides*, the carrion beetle *Thanatophilus trituberculatus*, the water scavenger beetles *Helophorus alternatus*, *H. sempervarians*, and *H. splendidus*, the rove beetles *Olophrum boreale*, *O. rotundicolle*, *Stenus hyperboreus*, and *Holoboreaphilus nordenskiöldi* (Fig. 5). *Bembidion sulcipenne hyperboroides* is known today only from the boreo-arctic regions of northwest Canada and Alaska (Lindroth, 1963). It was found in the faunal assemblage from Marias Pass, Montana, dated at 13,400 year BP. This locality is about 1800 km southeast of the southern limit of its modern range in northern British Columbia. The carrion beetle *Thanatophilus trituberculatus* was also found in this assemblage, and is likewise found today only in the boreo-arctic regions of North America (Anderson and Peck, 1985). The rove beetles *Stenus hyperboreus* and *Holoboreaphilus nordenskiöldi* are both cold-adapted species. The former species is found today in the boreo-arctic regions of North America. It was part of the 15,000-year old fauna from a site in the central Colorado Rockies. *Holoboreaphilus nordenskiöldi* is an arctic species today. Its modern range includes the arctic coastal regions of North America and Siberia, as well as alpine tundra localities in Alaska and the Yukon (Campbell, 1978). This species was also part of the Late Glacial assemblage from Marias Pass, Montana.

The water scavenger beetles discussed above have very different modern distributions. *Helophorus alternatus* is found today only in the highlands of California and Oregon (Smetana, 1985). This species was found in central Colorado Rockies assemblages ranging from 16,000–15,000 year BP. On the other hand, *Helophorus sempervarians* is a boreo-arctic species today, with no known populations in the western United States. Finally, *Helophorus splendidus* is an arctic species, as discussed above. Its youngest occurrence in Rocky Mountain fossil assemblages also comes from the 15,000-year old assemblage in the Colorado Rockies.

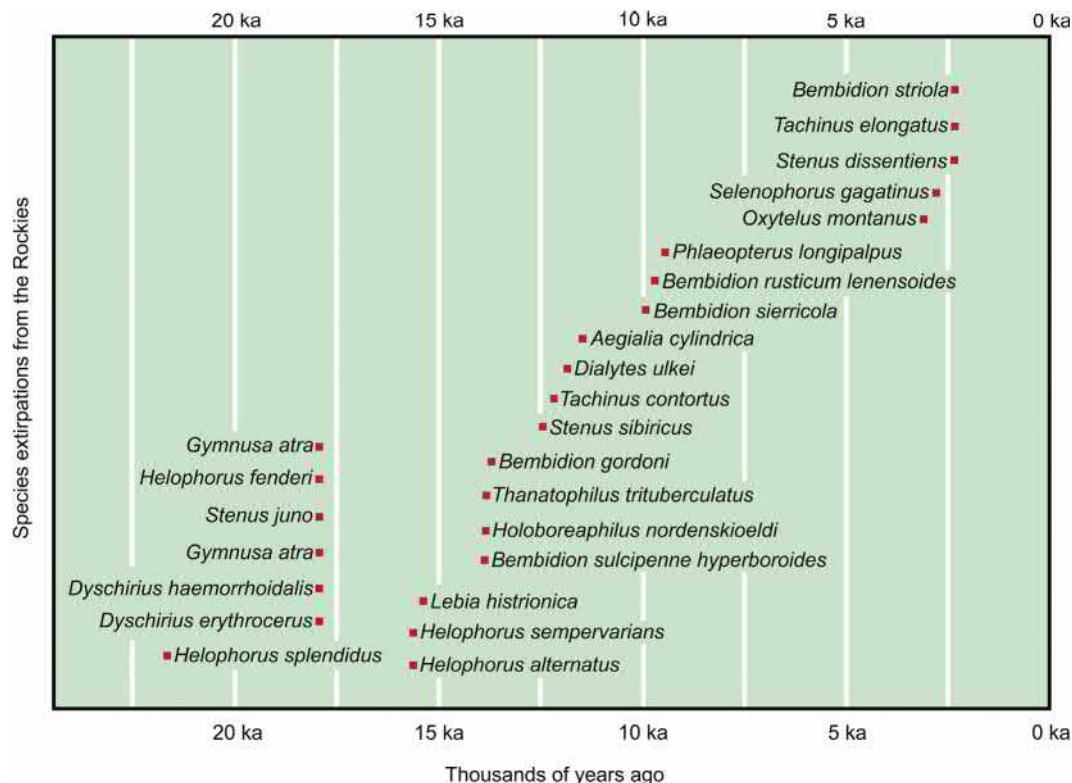


Fig. 5 Rocky Mountain beetle species extirpation chronology since the Last glaciation.

The modern ranges of the regionally extirpated species found in Late Glacial faunas from the Rockies are mostly in the arctic and boreo-arctic regions (Table 2). However, about a quarter of the species are found today only in the Pacific Northwest (PNW) region, with the remainder being found today either in the alpine regions of the mountain ranges of New England (i.e., the Presidential Range of New Hampshire and Mt. Katahdin, Maine), or in the Northern Rockies. Interestingly, while the migration corridors between the Rockies and the PNW region remained open for beetles after the Late Glacial interval, migration between eastern North America and the Rockies appears to have stopped in the early Holocene, about 11,000 years ago.

The early Holocene interval is taken here to mean 11,500–5000 years ago. The extirpated species found in early Holocene beetle faunas from the Rockies include the ground beetles *Bembidion rusticum lenensoides* and *B. sierricola*, and the rove beetles *Phlaeopterus longipalpus* and *Stenus sibiricus*. *Bembidion rusticum lenensoides* is found today in the western boreo-arctic region, much like *B. sulcipenne hyperboroides*. It was found in a fossil assemblage dated 9000 year BP from the San Juan Mountains of southern Colorado. *Bembidion sierricola* is known today only from the mountain ranges of the Pacific coast. Its last appearance in Rocky Mountain fossil assemblages was also at 9000 cal years BP in Southern Colorado. Unfortunately, no fossil beetle research has been carried out in any California highlands, so we know nothing of the beetle faunal history of this region.

The rove beetle *Phlaeopterus longipalpus* is an alpine snowfield species, known today from the high mountains of the PNW region, extending southeast to Utah (Hatch, 1957). It was found in fossil assemblages from a high-altitude site in northern Colorado, in assemblages ranging from 10,000–1500 year BP. Thus, it would seem that its extirpation from the Southern Rockies has been quite recent. *Stenus sibiricus* is known today only from the Arctic (Campbell and Davies, 1991). Its fossil remains were found in a sequence of assemblages ranging from 11,000–9000 years old from a high-altitude site in central Colorado.

Table 2 Modern and Late Pleistocene ranges of alpine beetle species from North America

Species	Modern North American range	Late Pleistocene records
Family Carabidae		
<i>Carabus taedatus</i>	Arctic; alpine of western mountains	Wisconsin, Minnesota: Late glacial; AB: Late Holocene
<i>Nebria arkansana</i>	Alpine of the Rocky Mountains	Colorado: Mid-Holocene
<i>Nebria gyllenhali</i>	Arctic; alpine of eastern and western mountains	Alberta: Late Holocene
<i>Pterostichus pinguedineus</i>	Arctic; alpine of eastern mountains	Pennsylvania: Late glacial
<i>Pterostichus surgens</i>	Alpine of the Rocky Mountains	Colorado: LGM, Early Holocene
<i>Stereocerus haematopus</i>	Arctic; alpine of Eastern mountains and Wyoming	Quebec: Late glacial
<i>Amara alpina</i>	Arctic; alpine of eastern and western mountains	Quebec: Late glacial; Colorado: Late glacial and Early Holocene
<i>Trichocellus cognatus</i>	Arctic; alpine of eastern and western mountains	Quebec: Early Holocene
<i>Trichocellus mannerheimi</i>	Arctic; alpine of Colorado	Colorado: Early to mid-Holocene
<i>Cymindis unicolor</i>	Alpine of eastern and western mountains	Wisconsin: Late glacial; Minnesota: Late glacial; Quebec: Late glacial; Michigan: Late glacial
Family Staphylinidae		
<i>Tachinus angustatus</i>	Alpine of western mountains	Colorado: MIS5b
<i>Tachinus elongatus</i>	Boreo-arctic; alpine of Colorado, New Hampshire, Wyoming	Pennsylvania: LGM; Quebec: Early Holocene; Colorado: MIS 5c and 5b, Late glacial and Early Holocene
<i>Tachyporus nimicola</i>	Alpine of New Hampshire, New York, Colorado	Colorado: MIS 5b and 5c, Early Holocene
<i>Phlaeopterus filicornis</i>	Alpine of Sierra Nevada	Colorado: Early and mid-Holocene
<i>Acidota quadrata</i>	Arctic; alpine of New Hampshire, Colorado, Montana	Wisconsin: Late glacial; Ontario: Early Holocene; Pennsylvania: LGM and Late glacial; North Dakota: Early Holocene; Colorado: Early Holocene, mid-Holocene and Late Holocene
<i>Olophrum boreale</i>	Boreo-arctic; alpine of Montana, Wyoming, Utah	New York: Early Holocene; Pennsylvania: Early Holocene; Ontario: Late glacial; North Dakota: Early Holocene; Colorado: MIS 5a, Late glacial and Early Holocene; Washington: MIS 3, MIS 2
<i>Olophrum rotundicollis</i>	Boreo-arctic; alpine of Colorado	Nova Scotia: Late glacial; New York: Late glacial and Early Holocene; North Dakota: Early Holocene; Minnesota: Late glacial; Ontario: Late glacial; Colorado: Late glacial, Early and Late Holocene
<i>Eucnecusum brachypterum</i>	Arctic; alpine of eastern mountains	New York: Late glacial and Early Holocene; Colorado: MIS 5a and 5c
<i>Eucnecusum tenue</i>	Boreo-arctic; alpine of Colorado, Utah	Wisconsin: Late glacial; North Dakota: Early Holocene; New York: Late glacial; Ontario: Late glacial; Colorado: MIS 5a, Early and Late Holocene
<i>Eucnecusum brunescens</i>	Boreo-arctic; alpine of Colorado	Ontario: Late glacial; Colorado: MIS 5a, Late glacial, Early Holocene, Mid-Holocene and Late Holocene
Family Silphidae		
<i>Thanatophilus coloradensis</i>	Boreo-alpine in the Rocky Mountains, British Columbia	Colorado: MIS 5e and 5b

The latter half of the Holocene saw climatic cooling in the Rocky Mountain region, especially in the last 3000 years, when both summer and winter temperature averages dropped below modern levels (Elias, 1996). *Bembidion striola* is confined today to the Pacific coastal mountain ranges (Lindroth, 1963). Its last known occurrence in the Rockies was at 2000 year BP at a site in Rocky Mountain National Park (RMNP), Colorado. The last known occurrence of *Oxytelus montanus* was at 2000 year BP, also in RMNP. This species is found today in the PNW region. Perhaps the most surprising aspect of the late Holocene faunas is that so many species were extirpated so recently from the Rockies. Of the 45 species known to have been extirpated from this region in the last 125,000 years, eight died out regionally within the last few thousand years. This speaks to the dynamism of insect migration. Each species is constantly attempting to become established in new regions. There are no stable insect communities, in any meaningful sense of the term. Perhaps the factor driving the disappearance of so many species from the Southern Rockies to the PNW region was a change in precipitation. If the extirpated species are adapted to wetter climatic conditions than those available in the Southern Rockies today, then only their PNW populations would have survived, as the PNW region is considerably wetter than the Southern Rockies.

A number of cold-adapted beetle species that live today in the alpine regions of the northern Appalachian Mountains, such as the Presidential Range in New England and Mount Katahdin in Maine, have Late Pleistocene fossil records from lowland regions of eastern and central North America. For instance, the ground beetle *Pterostichus pinguedineus* is known today from the Arctic and from the alpine of the northern Appalachians, but fossil specimens have been identified from a lowland site in Pennsylvania, dating to the Late glacial interval. It would appear that eastern lowland populations retreated to the northern Appalachians at the beginning of the Holocene. Likewise the rove beetle *Eucnecusum brachypterum*, a species commonly found in fossil assemblages from cold intervals in Europe and North America, has a modern North American distribution limited to the Arctic, and to the alpine zone of the northern Appalachians. Its relative, *Eucnecusum brunnescens*, is another cold adapted species. Fossils have been found that date to the Late glacial interval in southern Ontario and to the both the Late glacial and Holocene in Colorado. Today it is found in the Colorado alpine and in the boreo-arctic regions of North America. Presumably the populations that lived just south of the Laurentide Ice Sheet in Ontario migrated north as the ice margin retreated, becoming established in the cold boreo-arctic regions of Canada during the Holocene. Similarly, *Eucnecusum tenue* lived during the Last glaciation in regions south of the Laurentide Ice Sheet, as attested by fossil localities in Wisconsin, North Dakota and New York. It also lived in the Rocky Mountain region, downslope from mountain glaciers during the Last glaciation. The mid-western and eastern glacial populations presumably followed the retreating margins of the Laurentide Ice Sheet, and have become established in the boreo-arctic regions of Canada during the Holocene. The glacial-age populations in Colorado migrated upslope to the alpine zone in the Holocene.

Fossil Beetle Evidence—Europe

A similar story of alpine insect advances and retreats in the face of glacial-interglacial cycles can be seen in the fossil beetle record from sites in Europe. Quite a number of these cold-adapted beetle species live today either in the Arctic, or in both the Arctic and alpine regions of Europe. But the Late Pleistocene fossil record of these species clearly demonstrates that they came down out of the high mountains of Europe, and onto the adjacent lowlands during glacial intervals. Such beetle species were the dominant elements in glacial-age assemblages from Britain, the Netherlands, Germany, France, and other countries in Europe. For example, *Diacheila polita* is an arctic ground beetle with a Holarctic distribution today. Fossils of this species have been commonly found in British fossil records as well as in glacial assemblages from Eastern Europe and in North America, south of the last glacial ice sheets. In modern Eurasia, *D. polita* is found only in arctic regions from the Kola Peninsula eastward. In North America, it is found today only in arctic and subarctic regions of Alaska and the Yukon Territory, with isolated populations on alpine tundra in the Alaska Range.

As discussed above, *Amara alpina* is an arctic and alpine species today, with populations extending south along mountains in Scandinavia. It is the northernmost ground beetle in the Arctic fauna, ranging north to northernmost Greenland, Ellesmere Island in Canada, and northernmost Siberia. Fossils of *A. alpina* have been found in several European lowland sites from cold-interval assemblages. Interestingly, this species was present as far south as northern Italy during the Last glaciation, but it does not inhabit the Alps today. The most likely reason for this is that *A. alpina* is both cold-adapted and dry-adapted, and the climate of the Alps is probably too wet for this species.

An alpine water beetle, *Helophorus glacialis*, was found in Swedish, British, French, and Swiss lowland fossil assemblages from the Last glaciation. Today this species is confined to mountain top ponds in the Pyrenees, Alps, Scandinavian Alps, and some isolated mountain tops in smaller mountain ranges of Europe. Another cold-adapted species of this genus, *Helophorus lapponicus*, was widespread in Western Europe during the cold phases of the last glaciation, but its modern distribution reflects the species' retreat to the northern regions in Scandinavia and mountainous regions as far south as Spain. Angus (1983) captured modern specimens of this species from Sweden and Spain. He brought them into his laboratory and observed that the two populations successfully interbred, despite their genetic isolation of the two populations during the last 11,000 years.

The pill beetle (Byrrhidae), *Syncalyptra cyclolepidia* apparently lived throughout much of lowland Europe during the last glaciation. It has been found in British fossil faunas as well as from glacial-age assemblages near the end of the last glaciation in northern Switzerland. Today this moss-feeding beetle occupies arctic and alpine regions of Scandinavia, and has isolated populations in the Alps of Austria. Why did it not also relocate to the highlands of the Swiss Alps? We will probably never know the answer, but its

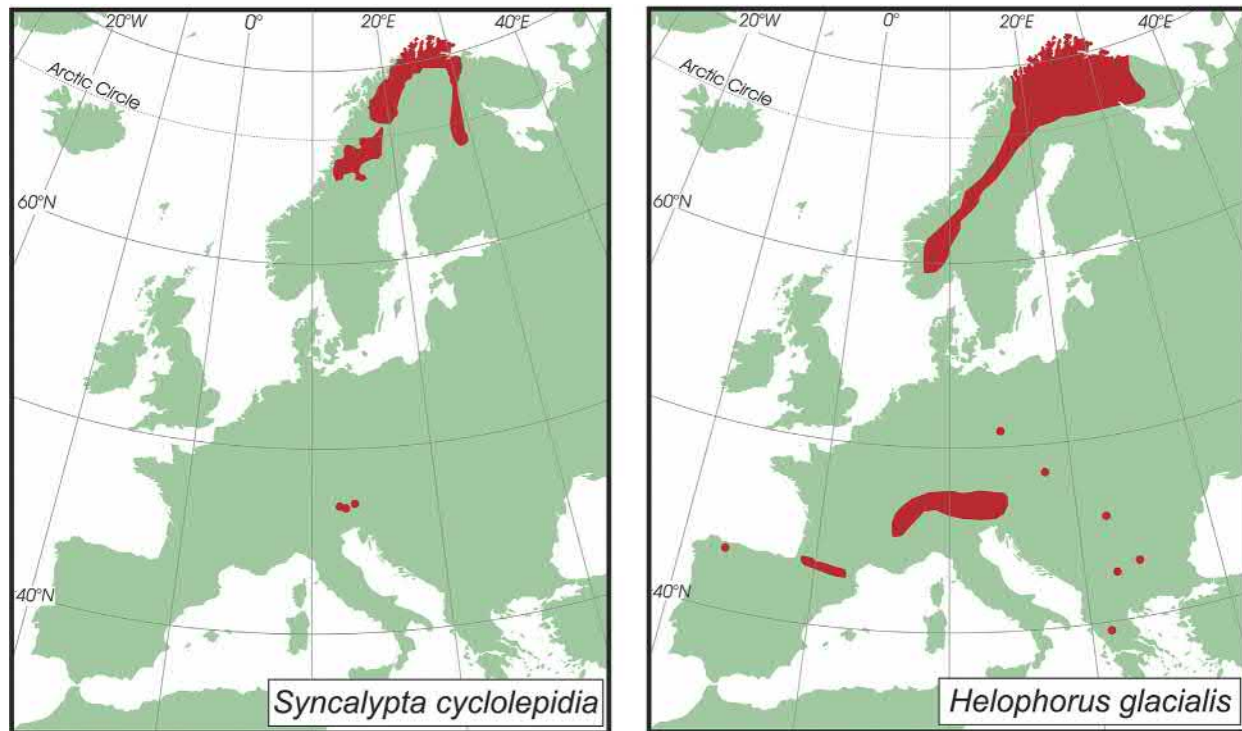


Fig. 6 Modern European distributions of *Syncalyptra cyclolepidia* and *Helophorus glacialis*.

absence from modern day Switzerland demonstrates the somewhat serendipitous nature of insect species migration in response to rapid, large-scale climate change. No species operates in a vacuum. Perhaps other species of pill beetles that lived within reasonable proximity to the Alps toward the end of the Last glaciation had a slight competitive advantage over *S. cyclolepidia*. A checklist of Swiss Coleoptera lists five species of Byrrhidae currently living there. The pill beetle species that lives at high altitude is *Byrrhus pilula*. Like *S. cyclolepidia* (and almost all other Byrrhidae), *B. pilula* feeds on mosses. According to the fossil record, from 125,000–12,000 years ago, *B. pilula* lived in England. But this species has a much broader thermal tolerance than *S. cyclolepidia*. *B. pilula* can be found today in mossy habitats from sea level to the snowfields of the Alps. Perhaps its broad thermal tolerance gave it a competitive advantage over *S. cyclolepidia* at the end of the Last glaciation.

The water scavenger beetle *Helophorus glacialis* was likewise widespread on periglacial landscapes of the European lowlands during the Last glaciation. But unlike *S. cyclolepidia*, *H. glacialis* managed to become established in many of the alpine regions of Europe, from the Pyrenees and Alps to the Tatra and Carpathian Mountains of Central Europe, and south to the Pindus Mountains of Greece (Fig. 6).

Conclusions

Alpine insects are a remarkable group of organisms, not just surviving the frigid climates and short summers of the alpine zone, but actually thriving there. They do this through a series of physiological and behavioral adaptations. This package of cold-adaptations makes it virtually impossible for nearly all alpine-dwelling insects to migrate out of their mountain top habitat islands in an attempt to colonize other alpine regions. However, the DNA, modern and fossil evidence combine to show us that alpine insects have shifted their distributions in the past. The fossil evidence clearly indicates that the cold glacial periods of the Pleistocene offered these insects the opportunity to disperse into lowland regions, where they survived in what must have been far larger populations than those of today on mountain top habitat islands. From the standpoint of cold-adapted insect biogeography, the current and previous warm interglacial periods have been times of population decline and forced retreat to mountain tops. In contrast to this, the glacial intervals of the Pleistocene were times of massive population expansion, down from the mountain tops and out into the periglacial environments of the lowland regions that existed in reasonably close proximity to continental ice sheets and mountain glacial systems. Over the last 2.6 million years, these glacial intervals have dominated Earth history. In fact, cold periods account for upwards of 90% of the Pleistocene epoch, while warm periods represent just 10%. In other words, from a long-term perspective, cold glacial conditions have been the norm for the past 2.6 million years, while warm interglacial conditions have been the exception.

See also: Cold Adaptations of Alpine Insects.

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Alpine Mammals of South America

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Abstract

The alpine environment of the Andes encompasses a vast and continuous extension of regions above tree line, in which three main ecoregions are identified: Paramo (north), Puna and Altiplano (center) and Southern Andes (South). Along this region, 200 species of mammals are found; these belong to 10 orders and 27 families. Greater species richness is concentrated in two different areas, one at the ecotone between the Puna and the Yungas Montane forest, and the other within the southern portion of the Paramo. Both regions share species that are endemic or have their main distribution in the alpine or are broadly distributed species that only marginally reach high elevations.

Rodent species represent almost 70% of all Andean mammals, followed by bats and carnivores, which account for 8% and 5% respectively. Bats are only marginally present in the high Andes, whereas rodents encompass >40% of their range along the high Andes.

Andean mammals face several conservation threats, related mainly with habitat loss or transformation, climate change and invasive species introduction. Among Andean species, near 20% have some degree of conservation concern, while 15% are considered data deficient.

Introduction

The South American Andes extend over a north-south length of 8500 km, and are the world's longest mountain chain, with an elevation range from 700 to 7000 m asl. Within this region, three major geographical units can be identified: The Northern, the Central, and the Southern Andes (Sempere et al., 2008). Between the NA and CA, there is a transition zone termed "Amotape-Huancabamba". Its geography and topography provide an excellent scenario for the study and understanding of species distribution and biodiversity patterns.

The Andean uplift played an important role in the historical diversification of the Neotropical biota. It served as a source of new high elevation habitats (Young et al., 2007). It acted as a vicariant barrier, by promoting isolation of lowland organisms on either side of the mountains. It also represented a N-S corridor for several species (Patterson et al., 2012) and it generated a heterogeneous mosaic of habitats and micro-habitats (montane and inter montane valleys) where colonization and differentiation could occur. All these features contributed to the high diversity and endemism of this region (Novillo and Ojeda, 2012; Ceballos and Ehrlich, 2006; Maestri and Patterson, 2016).

The alpine environment of the Andes encompasses a vast and continuous extension of regions above tree line (Fig. 1A). To the north, this environment tends to be wetter and fragmented (Peru to Venezuela), where they are called "páramos." From southern Peru to central Argentina, the high-elevation communities are termed "puna" and the portion that extends across western Bolivia is

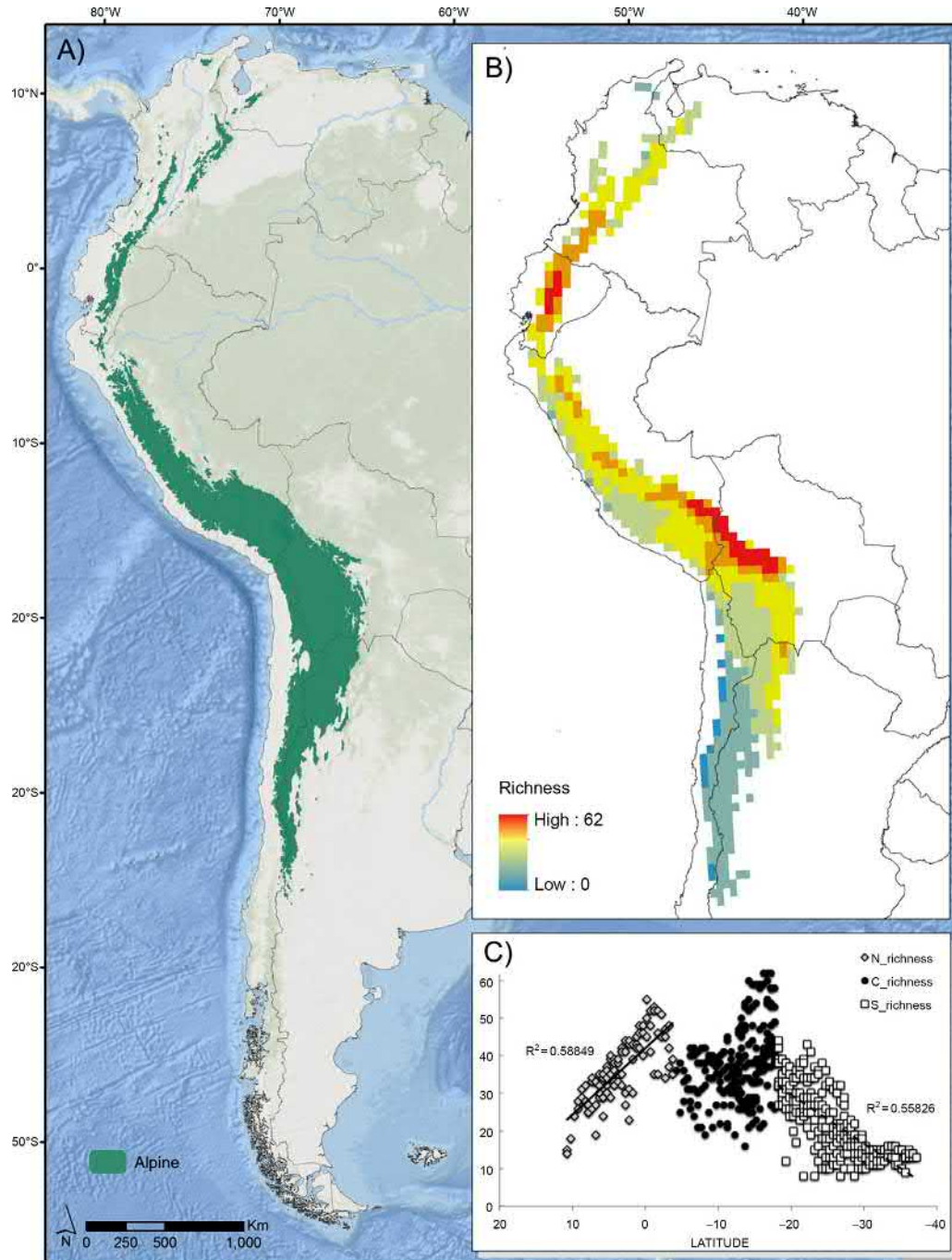


Fig. 1 (A) Alpine region along the Andes. (B) Alpine mammals richness. (C) Relationship between richness and latitude, using Alpine mammals separated into three groups: (1) N_richness—northern group (above the Amotape-Huancabamba depression); (2) C_richness—central group; (3) S_richness—southern group (below 20°S).

called “Altiplano”; both regions constitute a continuous arid province. The transitional communities above 3000 m in central Peru are known as “jalca”. Finally, the Southern Andes include the remaining Andean zones south of 29°S. Here, elevations tend to decrease from North to South (Pankhurst and Herve, 2007).

The Páramo comprises a number of neotropical high altitude grassland ecosystems, mainly in the upper parts of the Northern Andes. Its vegetation is mainly dominated by tussock grasses, dwarf shrubs, cushion plants and other forms of vegetation adapted to the cold, wind and intense ultra-violet radiation found at high altitudes. This region houses some rare and large species of mammals, such as the spectacled bear (*Tremarctos ornatus*), the mountain tapir (*Tapirus pinchaque*) and the white-tailed deer

(*Odocoileus virginianus*) (Kattan et al., 2004). Several large mammals of the Paramos are susceptible of local extinction or are characterized as endangered (Díaz et al., 1997). Additionally some studies have been done on Páramo rabbits (*Sylvilagus brasiliensis andinus*), and on the diversity and distribution of small mammals (Kattan et al., 2004). The Northern Andes are considered a hotspot for restricted-range species (those 25% of species with the smallest ranges), which places a high conservation status on this region (Ceballos and Ehrlich, 2006). In general, the Paramos are inhabited by almost 25 mammal species, most of which are rodents (Díaz et al., 1997).

Puna and Altiplano are the most arid portion of the alpine environment and they are also considered the oldest. These regions are considered a mixture of heterogeneous habitats, with marked zonal vegetation.

The biogeographical history of several species supports the antiquity of the Altiplano. Among the South American Camelids, the Vicugna shows a demographic expansion associated with the last major glacial event of the Pleistocene, an indication of former refugia (Marín et al., 2008). Also, the Guanacos show that the Puna and Altiplano acted as a geographic barrier between populations of the Northwest (Sechura and Atacama desert) and the Southeast (South from Bolivia) (Marín et al., 2008). Rodents also show the same pattern; Phyllotine rodents exhibit ancestral character states and basal positions on phylogenies, whereas lowland taxa tend to exhibit derived characters (Spotorno et al., 2001).

Several parallel ranges shape the Southern Andes: the Cordillera Principal, Cordillera Frontal and the Pre-cordillera. The highest elevational limits of the vegetation in this area are found at approximately 5000 m asl in the north and 3000 m in the south. The vertical relief is extremely abrupt and some of the highest peaks of the Andes occur in its northern portion. In the south, elevations generally decrease to <3000 m, but high volcanoes are frequent. Permanent snow, ice caps and glaciers are found in the summits of these elevations. The Southern Alpine Andes are rich in endemic plants (Luebert and Weigend, 2014), though this does not hold true for mammals. Most mammal species have large geographic ranges, extending north into the Puna and eastward into the Monte Desert and Patagonia (Novillo and Ojeda, 2012). Some endemic or near-endemic mammals are small ground living species, such as the rodents of the genus *Euneomys* and *Abrothrix andina* (Ojeda et al., 2015b).

Although it is commonly considered that cold-adapted ecosystems such as high mountain ranges are robust and change slowly compared to other ecosystems. However, they are especially sensitive to threats associated with climate change and land use changes (Nogués-Bravo et al., 2007, 2008).

The purpose of this contribution is to characterize the composition, distribution and conservation of the high Andean range mammal fauna.

Distribution Patterns

Along the Andes we registered 200 species of mammals, representing 10 orders and 27 families (Table 1). Species richness was higher at the ecotone between the Puna and the Yungas Montane forest, and within the southern portion of the Paramo (Fig. 1B). Below 20°S, there is a clear and sharp monotonic decreasing pattern, which also is shown in an East–West richness decline (Fig. 1B). When richness is evaluated along a north south transect, it is clear that richness decreases with increasing latitude from the Equator, both to the north and to the south from 20°S (Fig. 1C). The central and southern regions show an east to west decrease in species richness; meanwhile the northern region shows the opposite trend.

Rodents represent almost 70% of all Andean mammals, followed by bats and carnivores, which account for 8 and 5% respectively (Fig. 2A). Mean distributional range of all mammalian orders identified from the Andes accounted for less than half % of their overall ranges as a whole (Fig. 2B). A total of 19% of species can be considered regionally restricted or endemic (alpine range > 70%, 39 species). Indeed, most of the species have broad distributions that include the alpine environment to some extent, in some cases just marginally (see section Order Accounts).

Andean environments are potentially threatened by several anthropogenic factors, such as climate change and land use change, among others. Therefore, we expect that conservation concerns of several alpine species will increase in future. Among endangered species are the emblematic species, mountain tapir (*Tapirus pinchaque*), the only alpine representative of the order Perissodactyla, almost 20% carnivores, 5% of Chiroptera and 5% of Rodentia. If conservation categories such as ‘near threatened’ or ‘vulnerable’ are included, 40% of carnivores, 15% of Chiroptera and Didelphimorphia, 50% of Paucituberculata and 15% of rodents found in the alpine Andes are included as species of conservation concern (Fig. 2C). Additionally, several mammal orders have a high proportion of species whose conservation status is poorly known, including almost 50% of Cingulata, 15% of Didelphimorphia and 20% of rodents. These are categorized as “data deficient” (Fig. 2C).

Order Accounts

Ungulates (Order Cetartiodactyla)

The order is represented by two families (Camelidae and Cervidae), which encompass six genera and eight species (Fig. 3A). Among them only three registered >50% of their ranges along the Alpine Andes, and the rest registered <30% (Fig. 3B). Of these, 30% of camelids and 80% of the cervids are considered vulnerable of extinction (Fig. 3C).

Table 1 Alpine mammal species.

Order	Family	Genus	Species	IUCN	% alpine range	
Carnivora	Canidae	Lycalopex	<i>Pseudalopex culpaeus</i>	LC	34	
	Felidae	Leopardus	<i>Leopardus colocolo</i>	NT	19	
			<i>Leopardus jacobita</i>	EN	74	
			<i>Puma concolor</i>	LC	5	
		Mephitidae	Conepatus	<i>Conepatus chinga</i>	LC	14
	Mustelidae	Galictis	<i>Galictis cuja</i>	LC	6	
		Mustela	<i>Mustela frenata</i>	LC	5	
	Procyonidae	Nasua	<i>Nasua narica</i>	LC	11	
		Nasuella	<i>Nasuella meridensis</i>	EN	16	
			<i>Nasuella olivacea</i>	NT	21	
		Ursidae	Tremarctos	<i>Tremarctos ornatus</i>	VU	19
	Cetartiodactyla	Camelidae	Lama	<i>Lama guanicoe</i>	LC	19
			Vicugna	<i>Vicugna vicugna</i>	LC	87
Cervidae		Hippocamelus	<i>Hippocamelus antisensis</i>	VU	96	
		Mazama	<i>Mazama bricenii</i>	VU	18	
			<i>Mazama chunyi</i>	VU	20	
		<i>Mazama rufina</i>	VU	25		
		Odocoileus	<i>Odocoileus virginianus</i>	LC	4	
		Pudu	<i>Pudu mephistopheles</i>	VU	51	
Chiroptera		Molossidae	Mormopterus	<i>Mormopterus kalinowskii</i>	LC	39
				<i>Mormopterus phrudus</i>	VU	75
	Tadarida		<i>Tadarida brasiliensis</i>	LC	12	
	Phyllostomidae	Anoura	<i>Anoura geoffroyi</i>	LC	6	
		Artibeus	<i>Artibeus fraterculus</i>	LC	27	
		Chiroderma	<i>Chiroderma salvini</i>	LC	14	
		Lonchophylla	<i>Lonchophylla hesperia</i>	NT	23	
		Platyrrhinus	<i>Platyrrhinus dorsalis</i>	LC	7	
			<i>Platyrrhinus nigellus</i>	LC	44	
			<i>Sturnira aratathomasi</i>	LC	9	
		<i>Sturnira luisi</i>	LC	10		
		<i>Sturnira magna</i>	LC	16		
	Vespertilionidae	Eptesicus	<i>Eptesicus andinus</i>	LC	16	
		Histiotus	<i>Histiotus macrotus</i>	LC	44	
			<i>Histiotus montanus</i>	LC	12	
		Myotis	<i>Myotis atacamensis</i>	EN	20	
			<i>Myotis dinellii</i>	LC	9	
			<i>Myotis keaysi</i>	LC	12	
			<i>Myotis oxyotus</i>	LC	19	
Cingulata	Dasypodidae	Chaetophractus	<i>Chaetophractus vellerosus</i>	LC	21	
		Dasypus	<i>Dasypus pilosus</i>	DD	46	
Didelphimorphia	Didelphidae	Didelphis	<i>Didelphis pernigra</i>	LC	32	
		Gracilinanus	<i>Gracilinanus aceramarcae</i>	LC	54	
			<i>Gracilinanus dryas</i>	LC	12	
		Marmosops	<i>Marmosops juninensis</i>	VU	22	
	Monodelphis	<i>Monodelphis osgoodi</i>	LC	29		
		Thylamys	<i>Thylamys pallidior</i>	LC	30	
		<i>Thylamys venustus</i>	DD	18		
	Eulipotyphla	Soricidae	Cryptotis	<i>Cryptotis brachyonyx</i>	DD	6
<i>Cryptotis equatoris</i>				LC	58	
<i>Cryptotis meridensis</i>				LC	18	
<i>Cryptotis montivaga</i>				LC	61	
<i>Cryptotis peruviansis</i>				DD	20	
<i>Cryptotis squamipes</i>				LC	26	
<i>Cryptotis tamensis</i>				LC	30	
<i>Cryptotis thomasi</i>				LC	26	
				<i>Sylvilagus brasiliensis</i>	LC	1
Lagomorpha				Leporidae	Sylvilagus	<i>Sylvilagus brasiliensis</i>
Paucituberculata	Caenolestidae	Caenolestes	<i>Caenolestes caniventer</i>	NT	34	
			<i>Caenolestes convelatus</i>	VU	16	
			<i>Caenolestes fuliginosus</i>	LC	28	
				Lestoros	<i>Lestoros inca</i>	LC
Perissodactyla	Tapiridae	Tapirus	<i>Tapirus pinchaque</i>	EN	41	

Table 1 (Continued)

Order	Family	Genus	Species	IUCN	% alpine range
Rodentia	Abrocomidae	Abrocoma	<i>Abrocoma bennettii</i>	LC	19
			<i>Abrocoma cinerea</i>	LC	83
			<i>Abrocoma famatina</i>	DD	46
			<i>Abrocoma shistacea</i>	LC	16
			<i>Abrocoma vaccarum</i>	DD	100
	Caviidae	Cuscomys	<i>Cuscomys ashaninka</i>	DD	77
		Cavia	<i>Cavia patzelti</i>	DD	43
			<i>Cavia tschudii</i>	LC	56
			<i>Galea comes</i>	DD	66
		Microcavia	<i>Microcavia niata</i>	LC	98
	Chinchillidae	Chinchilla	<i>Microcavia shiptoni</i>	NT	65
			<i>Chinchilla chinchilla</i>	EN	89
		Lagidium	<i>Lagidium ahuacaense</i>	DD	7
	Cricetidae	Abrothrix	<i>Lagidium viscacia</i>	LC	46
			<i>Abrothrix andina</i>	LC	89
			<i>Abrothrix illutea</i>	NT	24
			<i>Abrothrix jelskii</i>	LC	94
		Aegialomys	<i>Aegialomys xantheolus</i>	LC	15
		Aepeomys	<i>Aepeomys lugens</i>	LC	26
		Akodon	<i>Akodon affinis</i>	LC	20
			<i>Akodon albiventer</i>	LC	96
			<i>Akodon boliviensis</i>	LC	84
			<i>Akodon fumeus</i>	LC	27
			<i>Akodon kofordi</i>	LC	34
			<i>Akodon lutescens</i>	LC	56
			<i>Akodon mimus</i>	LC	69
			<i>Akodon mollis</i>	LC	33
			<i>Akodon siberiae</i>	NT	27
			<i>Akodon simulator</i>	LC	6
			<i>Akodon spegazzinii</i>	LC	21
			<i>Akodon subfuscus</i>	LC	79
			<i>Akodon surdus</i>	VU	43
			<i>Akodon torques</i>	LC	37
			<i>Akodon varius</i>	DD	16
		Andinomys	<i>Andinomys edax</i>	LC	68
		Anotomys	<i>Anotomys leander</i>	VU	68
		Auliscomys	<i>Auliscomys boliviensis</i>	LC	88
			<i>Auliscomys pictus</i>	LC	95
			<i>Auliscomys sublimis</i>	LC	98
			<i>Calomys boliviae</i>	LC	9
		Calomys	<i>Calomys lepidus</i>	LC	91
			<i>Calomys musculus</i>	LC	7
			<i>Calomys sorellus</i>	LC	92
			<i>Chibchanomys orcesi</i>	DD	54
		Chilomys	<i>Chilomys instans</i>	LC	29
		Chinchillula	<i>Chinchillula sahamae</i>	LC	99
		Eligmodontia	<i>Eligmodontia puerulus</i>	LC	93
		Euneomys	<i>Euneomys mordax</i>	LC	17
		Galenomys	<i>Galenomys garleppi</i>	DD	100
		Graomys	<i>Graomys edithae</i>	DD	16
		Ichthyomys	<i>Ichthyomys hydrobates</i>	NT	19
			<i>Ichthyomys stolzmanni</i>	DD	39
		Microryzomys	<i>Microryzomys altissimus</i>	LC	54
			<i>Microryzomys minutus</i>	LC	27
		Necromys	<i>Necromys amoenus</i>	LC	83
			<i>Necromys lactens</i>	LC	21
			<i>Necromys punctulatus</i>	DD	39
		Neomicroxus	<i>Akodon bogotensis</i>	LC	30
			<i>Akodon latebricola</i>	VU	68
		Neotomys	<i>Neotomys ebriosus</i>	LC	92

(Continued)

Table 1 (Continued)

Order	Family	Genus	Species	IUCN	% alpine range
		Nephelomys	Nephelomys latigularis	LC	28
			<i>Nephelomys meridensis</i>	LC	19
		Neusticomys	<i>Neusticomys monticolus</i>	LC	40
			<i>Neusticomys mussoi</i>	EN	12
		Oligoryzomys	<i>Oligoryzomys andinus</i>	LC	76
			<i>Oligoryzomys arenalis</i>	LC	11
			<i>Oligoryzomys destructor</i>	LC	29
			<i>Oligoryzomys griseolus</i>	LC	29
		Oxymycterus	<i>Oxymycterus hiska</i>	LC	13
			<i>Oxymycterus paramensis</i>	LC	38
		Phyllotis	<i>Phyllotis andium</i>	LC	42
			<i>Phyllotis anitae</i>	DD	30
			<i>Phyllotis caprinus</i>	LC	63
			<i>Phyllotis definitus</i>	EN	80
			<i>Phyllotis haggardi</i>	LC	61
			<i>Phyllotis limatus</i>	LC	10
			<i>Phyllotis magister</i>	LC	79
			<i>Phyllotis osgoodi</i>	DD	84
			<i>Phyllotis osilae</i>	LC	88
			<i>Phyllotis wolffsohni</i>	LC	29
			<i>Phyllotis xanthopygus</i>	LC	50
		Punomys	<i>Punomys kofordi</i>	VU	100
			<i>Punomys lemminus</i>	VU	100
		Reithrodontomys	<i>Reithrodontomys mexicanus</i>	LC	24
		Rhipidomys	<i>Rhipidomys caucensis</i>	DD	12
			<i>Rhipidomys fulviventer</i>	LC	24
			<i>Rhipidomys venustus</i>	LC	30
		Sigmodon	<i>Sigmodon inopinatus</i>	VU	76
		Thomasomys	<i>Thomasomys apeco</i>	VU	52
			<i>Thomasomys aureus</i>	LC	28
			<i>Thomasomys baeops</i>	LC	43
			<i>Thomasomys caudivarius</i>	LC	32
			<i>Thomasomys cinereiventer</i>	LC	24
			<i>Thomasomys cinereus</i>	LC	28
			<i>Thomasomys cinnamomeus</i>	LC	70
			<i>Thomasomys daphne</i>	LC	26
			<i>Thomasomys eleusis</i>	LC	14
			<i>Thomasomys erro</i>	LC	78
			<i>Thomasomys gracilis</i>	NT	25
			<i>Thomasomys hudsoni</i>	DD	44
			<i>Thomasomys hylophilus</i>	EN	8
			<i>Thomasomys incanus</i>	VU	58
			<i>Thomasomys ischyrius</i>	VU	31
			<i>Thomasomys kalinowskii</i>	VU	46
			<i>Thomasomys ladewi</i>	LC	52
			<i>Thomasomys laniger</i>	LC	21
			<i>Thomasomys macrotis</i>	VU	57
			<i>Thomasomys monochromos</i>	EN	38
			<i>Thomasomys niveipes</i>	LC	35
			<i>Thomasomys notatus</i>	LC	41
			<i>Thomasomys onkiro</i>	VU	12
			<i>Thomasomys oreas</i>	LC	31
			<i>Thomasomys paramorum</i>	LC	57
			<i>Thomasomys praetor</i>	DD	46
			<i>Thomasomys pyrrhonotus</i>	VU	10
			<i>Thomasomys rosalinda</i>	DD	40
			<i>Thomasomys silvestris</i>	LC	68
			<i>Thomasomys taczanowskii</i>	LC	29
			<i>Thomasomys ucucha</i>	VU	84
			<i>Thomasomys vestitus</i>	LC	38
			<i>Thomasomys vulcani</i>	DD	52

Table 1 (Continued)

Order	Family	Genus	Species	IUCN	% alpine range
	Ctenomyidae	Ctenomys	<i>Ctenomys frater</i>	LC	29
			<i>Ctenomys fulvus</i>	LC	83
			<i>Ctenomys knighti</i>	DD	34
			<i>Ctenomys leucodon</i>	LC	100
			<i>Ctenomys lewisi</i>	LC	63
			<i>Ctenomys opimus</i>	LC	99
			<i>Ctenomys peruanus</i>	LC	100
			<i>Ctenomys saltarius</i>	DD	33
			<i>Ctenomys scagliai</i>	DD	22
			<i>Ctenomys tulduco</i>	DD	22
	Cuniculidae	Cuniculus	<i>Cuniculus taczanowskii</i>	NT	14
	Echimyidae	Dactylomys	<i>Dactylomys peruanus</i>	DD	9
		Olallamys	<i>Olallamys albicauda</i>	DD	16
	Erethizontidae	Coendou	<i>Coendou quichua</i>	DD	8
			<i>Coendou rufescens</i>	LC	11
	Octodontidae	Octodontomys	<i>Octodontomys gliroides</i>	LC	66
	Sciuridae	Sciurus	<i>Sciurus pucheranii</i>	DD	13

Taxonomy, conservation status and % of their total range along the high Andes.

EN, endangered; LC, least concern; NT, near threaten; VU, vulnerable. IUCN red list categories. DD, data deficient.

Family Camelidae

South American Camelids encompass four species “Llama and Alpaca” (both domestic) and “Guanaco and Vicuña” (wild), all widely distributed in South America. Wild camelids form social groups that live in family groups, groups of bachelors and solitary individuals (Young and Franklin, 2004). Their mating system is polygynous for defense of resources, in which adult males defend territories of high forage quality and low predator density (Young and Franklin, 2004).

Camelids are intimately connected with Andean culture. At present, human use activities such as live capture and shearing could play an important role in the conservation of these species and their habitat (Carmanchahi et al., 2014).

The Guanaco (*Lama guanicoe*) ranges from northern Peru (8°30' S) to southern Tierra del Fuego (55°S), and from sea level up to 4857 m asl (Baldi et al., 2016). Historically, this species experienced significant population decline (Wheeler, 2012), and now its populations can be considered stable, mainly along its southern distribution (Schroeder et al., 2014). Guanaco habitat is characterized by seasonal climates in regions with low plant productivity. They are considered the largest (widely distributed) endemic herbivore of South-America, due to their anatomy, behavior and physiology (Puig et al., 2014; Ovejero et al., 2016).

Vicuñas (*Vicugna vicugna*) are restricted to fragmented areas of high elevation between 9°S and 29°S latitude in the Andes (Wheeler, 2012; and reference therein). DNA data suggest that their current distribution is the result of a westward expansion associated with glacial events during the Late Pleistocene 14–12,000 years ago (Wheeler, 2012).

Vicuña habitats include shallow wetlands “Vegas”, halophytic plant communities, steppes, prairies, and rolling shrub steppes (tolares) (Arzamendia and Vila, 2014). Vegas are intensively used by Vicuñas, given that they are obligate drinkers (Franklin, 2011). Water availability influences daily activity patterns, while in the night Vicuñas move to hillsides to avoid predation from pumas (Donadio and Buskirk, 2016). The Vicuña is considered a generalist herbivore that behaves as a facultative grazer that can also include shrubs in its diet (Mosca Torres and Puig, 2012; Mosca Torres et al., 2015).

Family Cervidae

Latin America has largest deer diversity in the world, with seven genera and 18 species thus far described (Wemmer, 1998). The alpine environment has 7 species in 4 genera (*Hippocamelus*, *Mazama*, *Odocoileus* and *Pudu*).

The genus *Hippocamelus* comprises two species, the “Taruka” (*Hippocamelus antisensis*), and the “Huemul” (*Hippocamelus bisulcus*). Taruka distribution extends through the highlands of the Andes from Peru to NE Chile (Barrio, 2013; Barrio et al., 2017), while the Huemul is endemic to Chile and Argentina (Vila et al., 2006). Both species’ distributions are fragmented with populations isolated from each other (Corti et al., 2011) and there is evidence of a decreasing population trend (Barrio et al., 2017; Flueck and Smith-Flueck, 2006). Tarukas are found between 2000 and 5000 m asl in rock outcrops within grassland vegetation and nearby water sources. Meanwhile, Huemul ranges from sea level up to 3000 m elevation, and is found mainly at the forest edge (*Nothofagus* spp.). Predation can be a major limiting factor and may even threaten species population viability (Elbroch and Wittmer, 2013). Several factors have been hypothesized to explain these species’ populations failure to recover (cattle, exotic trees, irrational forestry, exotic animals, illegal hunting, diseases, dogs, reduced numbers, loss of winter range) (Flueck and Smith-Flueck, 2006).

The genus *Mazama* has been the focus of a broad taxonomic debate. DNA studies suggest that this genus is polyphyletic (Gutiérrez et al., 2017). Three species of *Mazama* are found in the alpine Andes: *Mazama bricenii*, *Mazama chunyi* and *Mazama rufina*.

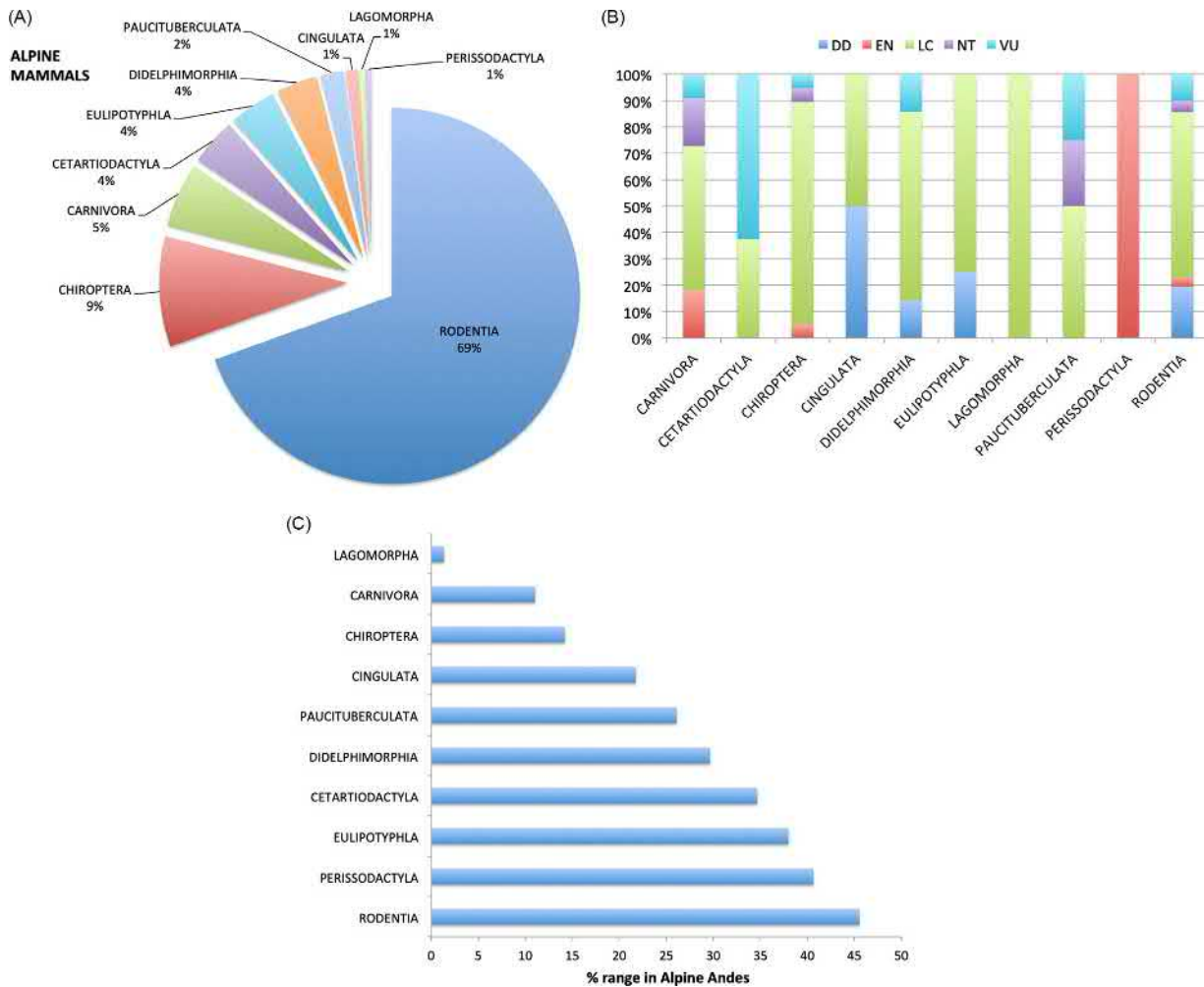


Fig. 2 (A) Percentage of High Andean mammals by Order. (B) Conservation status, percentage of species in each IUCN red list category. (C) Percentage of the species range encompass along the alpine region.

The ecology and general biology of the genus *Mazama* is unknown, although they seem to be solitary, active day and night, and with a browser/frugivore diet. In general, these species exhibit a decreasing population trend and are in need of further research.

Mazama bricenii "Mérida Brocket" is patchily distributed along the high Andes (1000–3500 m asl) in northern Colombia and western Venezuela, mainly along montane forests and in the Paramo (Lizcano and Alvarez, 2016). *Mazama chunyi* "Peruvian Dwarf Brocket" inhabits the highlands of southern Peru and northern Bolivia. Its current distribution and abundance need to be further assessed (Rumíz and Pardo, 2010). *Mazama rufina* "Dwarf Red Brocket" is found along the montane forest and the Paramos of Colombia, Ecuador and Peru, between 1500 and 3500 m asl.

Odocoileus virginianus "White tailed Deer" is a broadly distributed species that extends along the North and South American continents (Smith, 1991). In South America eight subspecies have been described, (Smith, 1991; Moscarella et al., 2003), among which 3 are present at the high Andes: (1) *O. v. goudotii* (Highlands Andes of Venezuela, Colombia, Ecuador and Northern Peru); (2) *O. v. ustus* (Andean region of Ecuador and Colombia); (3) and *O. v. peruvianus* (Peru and Bolivia, excluding amazon region) (Smith, 1991). South American populations are declining (Gallina and López-Arevalo, 2016), and conservation of the Andean subspecies is strongly suggested (Moscarella et al., 2003). White tailed deer diet is seasonal, and it can be considered as an opportunistic forager in the Paramos.

Pudu mephistopheles "Northern Pudu" is the only species of the genus present in the high Andes. Its range is fragmented, and it inhabits the montane forests and Paramos of Colombia, Ecuador and Peru. There is evidence of a high degree of isolation between populations (Loyola et al., 2010). Northern Pudu was intensively exploited from the 1950s to early 1980s. However, the current threats are mainly habitat conversion and predation by domestic dogs.

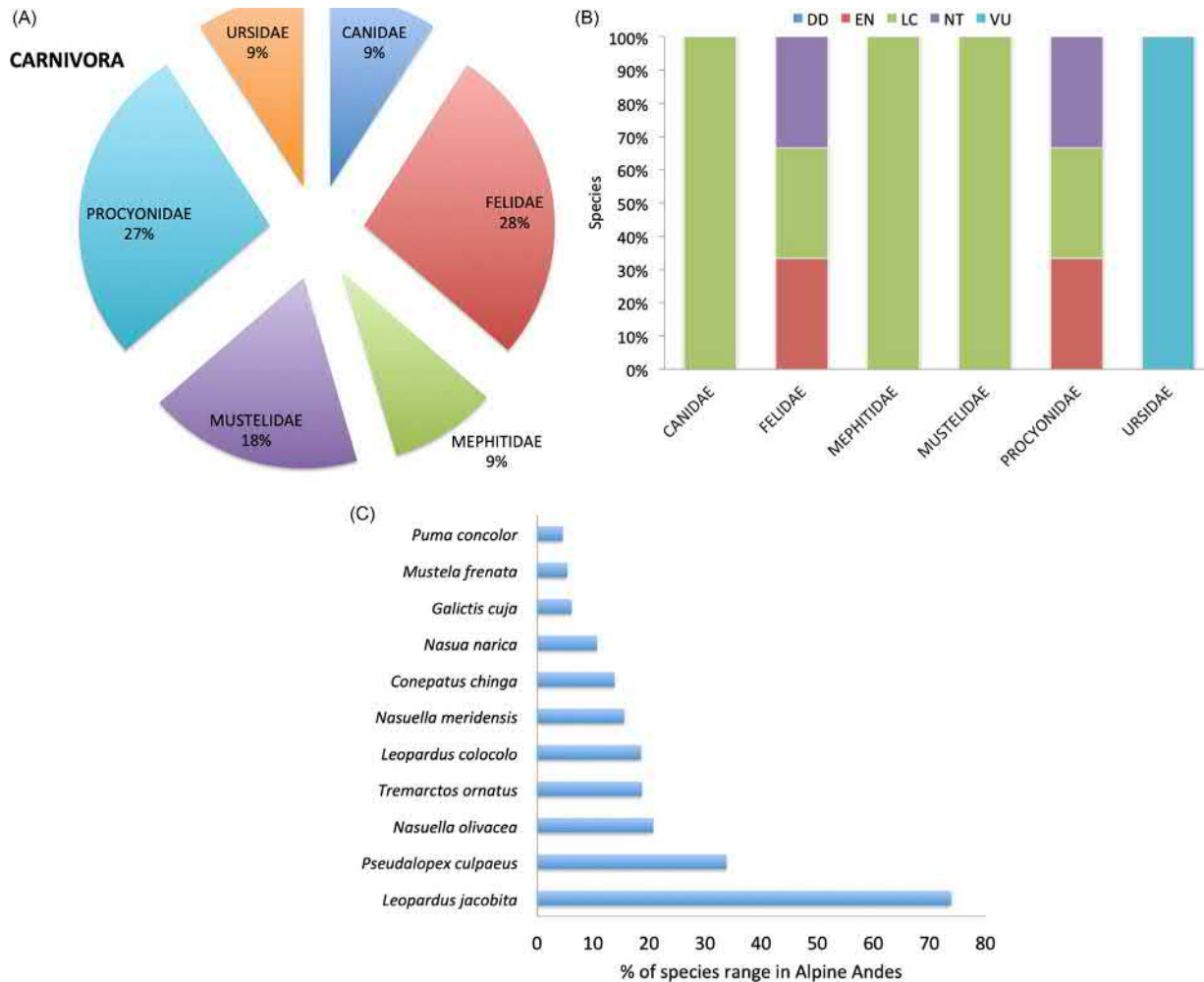


Fig. 3 (A) Percentage of High Andean carnivores by family. (B) Conservation status, percentage of species in each IUCN red list category. (C) Percentage of the species range encompass along the alpine region.

Carnivores (Order Carnivora)

Six carnivore families are found along the high Andes, comprising 10 genera and 11 species (Fig. 4A). Among them, Felidae (28% of the species) and Procyonidae (27%) are the best-represented. The Andean cat is the only carnivore that can be considered as endemic to the high Andes, with most of its range confined to high elevations (Fig. 4B). In general, most carnivores have only 15 to 20% of their ranges in the Andes (Fig. 4B). The families Felidae and Procyonidae have 30% of their species categorized as endangered, with another 30% considered vulnerable (Fig. 4C). The only bear (family Ursidae) found in the high Andes is the Andean Bear (*Tremarctos ornatus*); this species is categorized as vulnerable.

The family Canidae is represented by the “Culpeo” (*Lycalopex culpaeus*), which have a broad distribution throughout South America, from sea level to 4800 m asl (Ramírez-Chaves et al., 2013). Its population trend is stable, but culpeos are been persecuted throughout their range due to human conflicts (Lucherini and Merino, 2008). Also there is evidence for negative effects with coexistence with the puma (Travaini et al., 2007).

The family Felidae is represented in the Andes only by the “Pampas cat” (*Leopardus colocolo*), the “Andean cat” (*Leopardus jacobita*) and the “Puma or cougar” (*Puma concolor*). The pampas cat has a broad distribution in South America. Along the Andes, populations seem to be stable and may even reach high densities (0.74–0.78 individuals/km²), mainly along productive habitat patches (Lucherini et al., 2016). In the high Andes this cat’s diet includes mountain viscacha and small rodents (Napolitano et al., 2008; Fajardo et al., 2014).

The Andean cat has a patchy distribution in the Andes, restricted to rocky habitats above 3600 m (Argentina, Bolivia, Chile and Peru) (Cossios and Angers, 2007; Novaro et al., 2010; Reppucci et al., 2011). Genetic studies confirm two isolated populations that can be considered as “Evolutionary Significant Units” (ESUs); also these studies confirm that the species has very low genetic

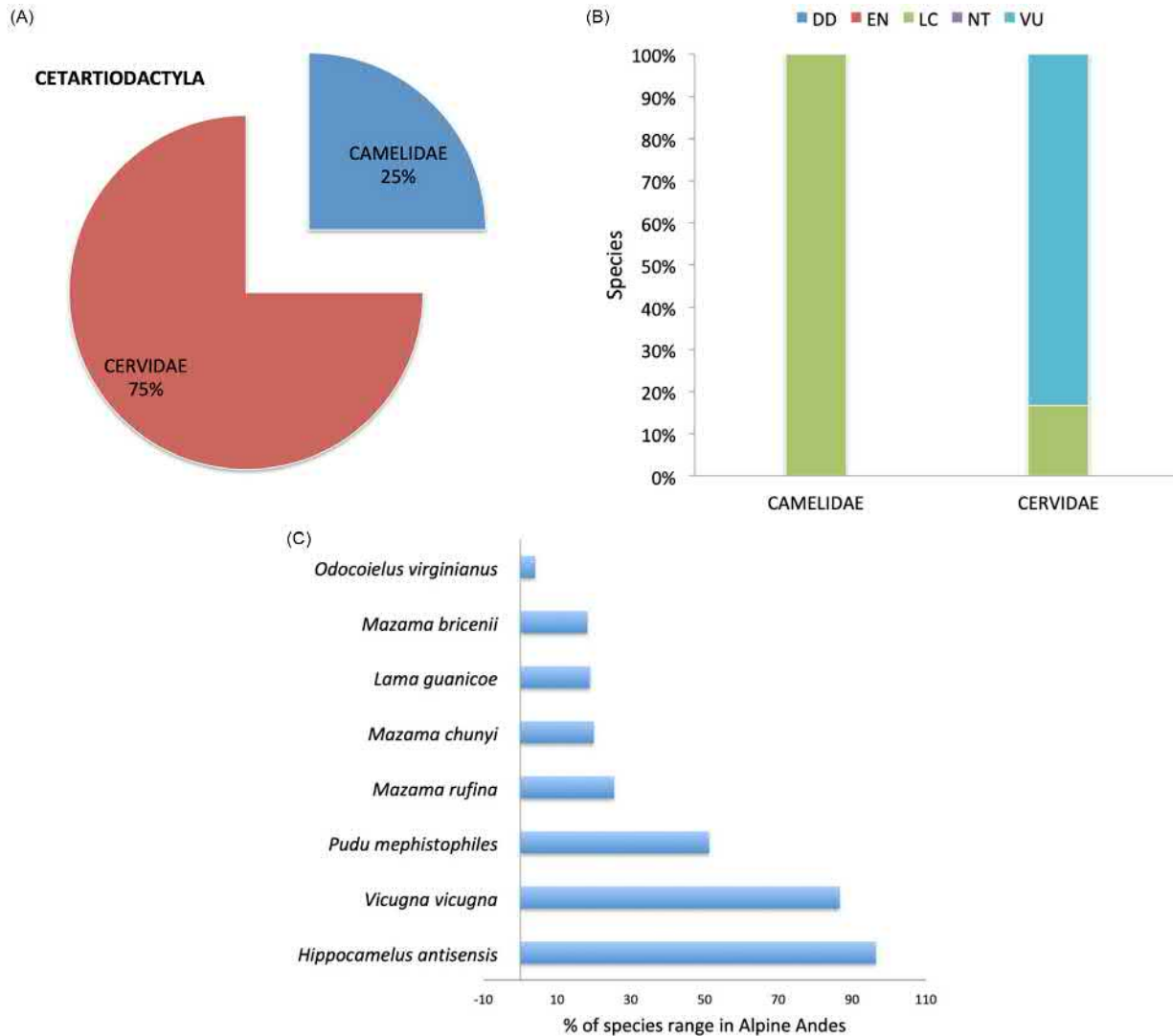


Fig. 4 (A) Percentage of High Andean ungulates by family. (B) Conservation status, percentage of species in each IUCN red list category. (C) Percentage of the species range encompass along the alpine region.

diversity (Cossíos et al., 2012). The Andes cat may be considered as a habitat and diet specialist, with high proportions of rodents and mountain viscachas (*Lagidium spp.*) in its diet (Napolitano et al., 2008; Marino et al., 2010).

The puma is the largest carnivore of the region, with a broad distribution throughout the Americas. Due to conflicts with humans, pumas can be considered near threatened in specific places and have been categorized as least concern with a decreasing population trend by IUCN (Nielsen et al., 2015).

Ranges of several of these species overlap along the Andes (Lucherini et al., 2009), which may be leading to intraguild competition and a high degree of dietary overlap (Lucherini et al., 2008; Donadio and Buskirk, 2016). Evidence suggests a negative effect of competition among carnivores that may impact the most endangered species (Lucherini and Luengos Vidal, 2003; Napolitano et al., 2008). This competition among predators leads to ecological segregation by temporal partitioning (Lucherini et al., 2009).

The Procyonid family, “Coatis” extend along the northern Andes, from Northern Peru to Venezuela and display restricted or limited distributions (Helgen et al., 2009; González-Maya et al., 2011). The two species of *Nasuella* (*olivacea* and *meridensis*) were previously considered to be one, and the genus *Nasua* seems not to be monophyletic (Helgen et al., 2009). All three species of alpine procyonids exhibit decreasing population trends, mainly due to habitat loss (Helgen et al., 2009). There is little reliable information about their distribution, ecology, and biology (Balaguera-Reina et al., 2009). In general, the species are omnivorous, eating predominantly invertebrates and fruit (Rodríguez-Bolaños et al., 2000). Coatis are gregarious, with a complex social organization (Rodríguez-Bolaños et al., 2000).

The Molinas hog-nosed skunk, the only representative of Mephitidae family, has a broad distribution, from southern Peru to Chile and Argentina (Emmons et al., 2016). In general it is a common species with average densities of 3 individuals/km. It is a

nocturnal and solitary, with a generalist diet (Donadio et al., 2004). It is categorized as least concern by IUCN, but is currently showing a decreasing population trend (Emmons et al., 2016).

Mustelids are represented by the Lesser grison and Long-tailed weasel. Both are considered as least concern for conservation (Helgen and Schiaffini, 2016; Helgen and Reid, 2016). The former is a broadly distributed species (from Southern Peru to Argentina and Chile), which is frequently found near water and open habitats (Poo-Muñoz et al., 2014). It is relatively rare in most habitats. Its diet consists of small and medium-sized vertebrates, with a predominance of introduced lagomorphs and native rodents. Lesser grisons are active during the day, but also at dusk and may also be nocturnal. The long-tailed weasel tends to be solitary or to live in small groups. It has the greatest geographical range among mustelids of the Western Hemisphere and inhabits a wide array of habitats and elevations (Sheffield and Thomas, 1997). Mismatch analyses suggest a longer genetic stability of long-tailed weasel lineages in southern versus northern habitats (Harding and Dragoo, 2012).

The spectacled or Andean bear is the only extant representative of the Ursidae in South America (Kattan et al., 2004). Its geographic distribution extends along the tropical Andes from Venezuela to Bolivia-Argentina and it occupies a variety of ecosystems (García-Rangel, 2012). Its range is severely fragmented (mostly in the northern part); this entails conservation problems for the species, including isolated and small populations, habitat loss, altitudinal movement limitations, etc. (Troya et al., 2004). Andean bears are omnivorous, though the meat proportion of their diet is rather low (Troya et al., 2004). Populations are on the decline mainly due to habitat loss and fragmentation (Kattan et al., 2004; García-Rangel, 2012). Conservation actions are mainly focused on the preservation or development of habitat corridors for the species (Yerena and García-Rangel, 2010).

Bats (Order Chiroptera)

Chiroptera are the second most speciose order of mammals. Along the high Andes we registered 3 families, 11 genera and 19 species of bats (Fig. 5A), which in general encompass <20% of their ranges along the high Andes (Fig. 5B). Little information about habitat, activity patterns and general ecology is available for Andean bats. The Incan mastiff bat (*Mormopterus phrudus*) has most of its range (75%) in the high Andes, although this species is only known from the type locality in Cusco, Peru. There are few records of bat species above 3500 m, with the probable exception of *Histiotus montanus* (Handley Jr. and Gardner, 2008). Conservation status among Andean bats reveals that, among the family Vespertilionidae, 12% of the species are considered endangered, 10% of Phyllostomidae are near threatened and 30% of Molossidae are categorized as vulnerable (Fig. 5C). The Andean bat community is characterized by reduced species richness and little endemism (Mena et al., 2011).

Armadillos (Order Cingulata)

This order includes only the family Dasypodidae, commonly known as “armadillos or quirquinchos”. We found two genera that reach the high Andes region, each represented by a single species. The screaming hairy armadillo (*Chaetophractus vellerosus*) is distributed in the center and south of Bolivia (Tarifa and Romero-Muñoz, 2009), west of Paraguay and north of Argentina (Abba and Superina, 2010), generally in arid and semi-arid environments. The subspecies *C. v. vellerosus*, present in the Puna of Bolivia and Argentina, occurs at altitudes from sea level to 4600 m asl, and almost 20% of its distribution falls within the high Andes. It is considered, as least concern for conservation and its population trend is stable. However, this species is heavily hunted and its habitat has been intensively transformed (Superina et al., 2014). Its diet is omnivorous and it constructs burrows for refuge (Abba and Cassini, 2008). The hairy long-nosed armadillo (*Dasypus pilosus*) has been recorded only from the southwestern Peruvian Andes, and its distribution probably reaches the high Andean environment (Superina et al., 2014). Both morphology and invertebrate ecology support the hypothesis that *Dasypus pilosus* likely bases its diet on soft-bodied invertebrates. More studies are necessary to clarify its ecology and distribution (Superina and Loughry, 2015).

Opossums (Order Didelphimorphia)

This order includes the majority of the living American marsupials (Gardner, 2008). All of them are included in the family Didelphinae. Six species occur in the Andes, representing four genera. Most of them reach the margins of high elevations, mainly due to its arboreal habits and ecophysiological aspects (Fig. 6A). The Andean white eared opossum (*Didelphis pernigra*) is found along the Andes from northwestern Venezuela and Colombia to the north of Argentina (rare along the Puna and Paramo environment). *Gracilinanus aceramarcae* has a narrow distributional range, with a significant proportion of its range in the high Andes (Fig. 6B). It has been found in the Cordillera Vilcabamba at 3350 m, in a mixed habitat consisting of pajonales, sphagnum bogs, mixed-species forest, and Polylepis forest on a “blocky” limestone substrate (Voss et al., 2005). The Wood-sprite Opossum (*Gracilinanus dryas*) is known from the Andes of Venezuela and Colombia, mainly in montane wet forest at elevations from 2300 to 4000 m asl. This species is not endangered but its population trend is decreasing (Pérez-Hernandez et al., 2016). Osgood’s Short-tailed Opossum (*Monodelphis osgoodi*) is found in the eastern Andes in Perú and Bolivia from 1400 to 3500 m asl. Most records are from the montane forest; its presence on alpine regions is peripheral. This species is the least arboreal; its diet consists of insects, seeds and fruits (Nowak, 1999). Two species in the genus *Thylamys*, *T. venustus* and *T. pallidior* range into the high Andes. Both species have broad ranges in Argentina, Chile, Bolivia and Peru (Solari, 2003). The genus is in need of extensive taxonomic revision (Braun et al., 2005). Little information is available about *T. venustus*, so it is considered as data deficient in terms of conservation (Fig. 6B).

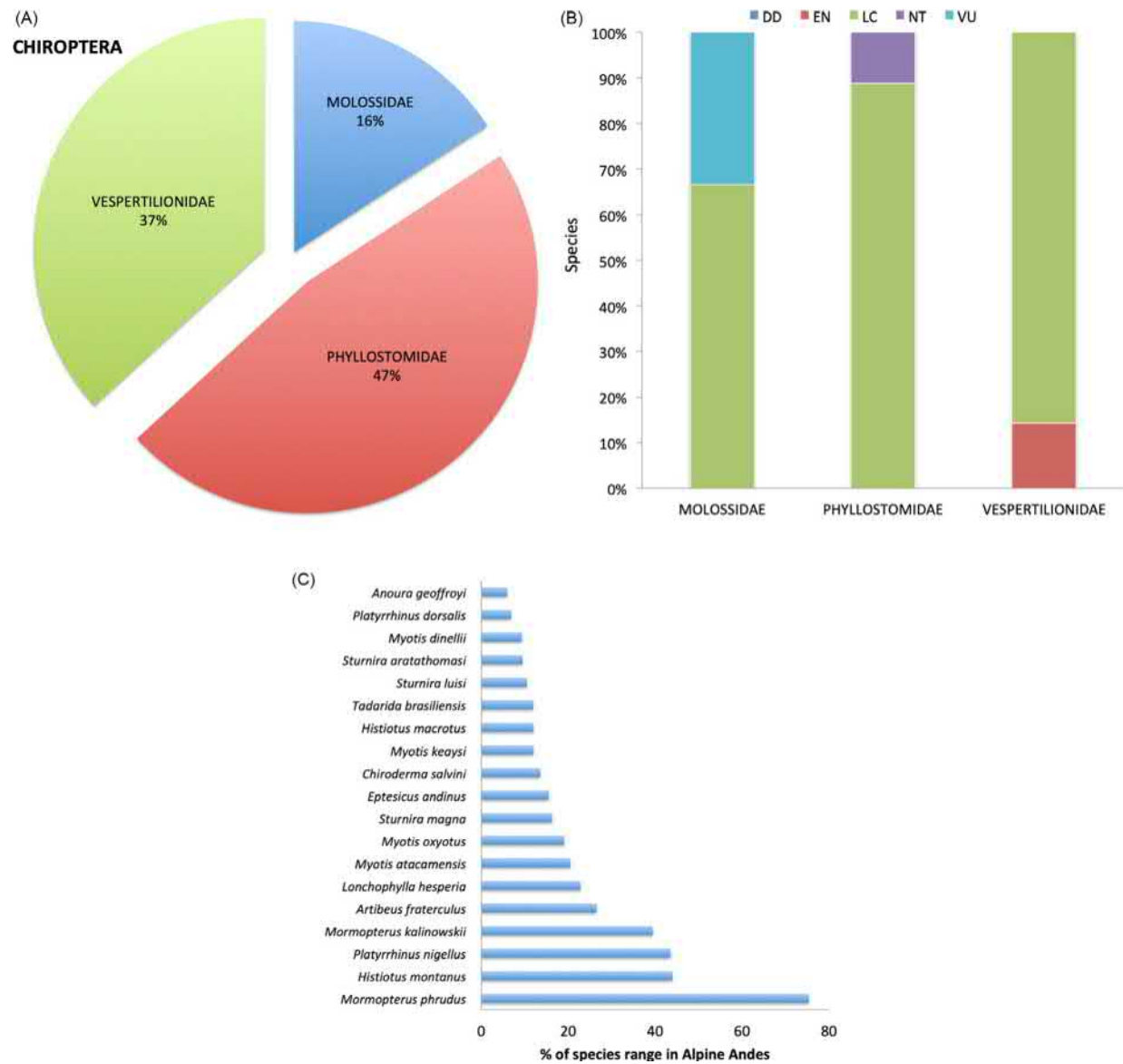


Fig. 5 (A) Percentage of High Andean bats by family. (B) Conservation status, percentage of species in each IUCN red list category. (C) Percentage of the species range encompass along the alpine region.

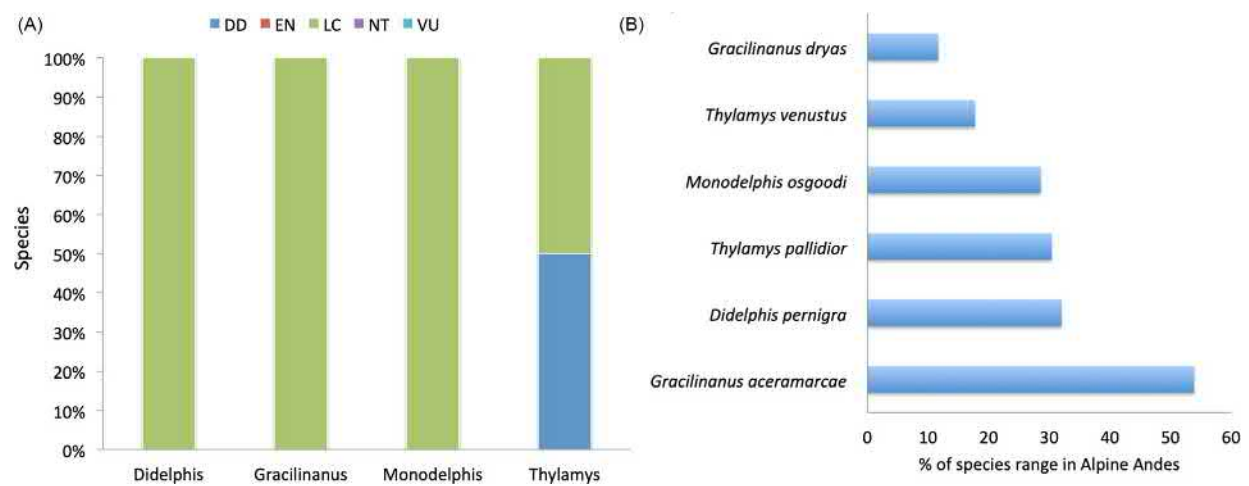


Fig. 6 Order Cingulata. (A) Conservation status, percentage of species in each IUCN red list category. (B) Percentage of the species range encompass along the alpine region.

Shrews (Order Eulipotyphla)

Andean shrews are represented by the family Soricidae and the genus *Cryptotis*, which encompass 8 species. Their range extends from Venezuela to Peru north of the Huancabamba depression (Woodman and Péfaur, 2008). *Cryptotis* is known only from elevations above 1200 m in a variety of habitat types (Lower and Montane Forest, Paramo, and in disturbed forest and pasture lands). Taxonomic treatments of the genus *Cryptotis* partition the species among four informal species groups. Most South American shrews are members of the *C. thomasi*-group, which is distinguished by a number of derived characters. Among this group, *C. equatorius* and *C. motivaga* comprise >50% of their ranges along high Andes (Fig. 7). In general, most of the species are distributed along the lower and montane forests and extend only marginally over the Paramo (Woodman and Díaz de Pascual, 2004). There is no clear conservation concern among shrews, although there is little information about their natural history. *C. peruvensis* is considered as data deficient, mainly as it is only known from two specimens (Vivar et al., 1997).

Shrew Opossums (Order Paucituberculata)

This order is represented by one family (Caenolestidae), which comprises 3 genera, known only from South America. We list only two genera (*Caenolestes* and *Lestoros*) and 4 species that reaches high Andes elevations, and whose geographic range extends discontinuously from western Venezuela to Bolivia (Timm and Patterson, 2008; Patterson, 2015). All species registered <40% of their ranges along the Andes (Fig. 8A), generally they inhabit montane forest, near streams or water courses, and may reach the high

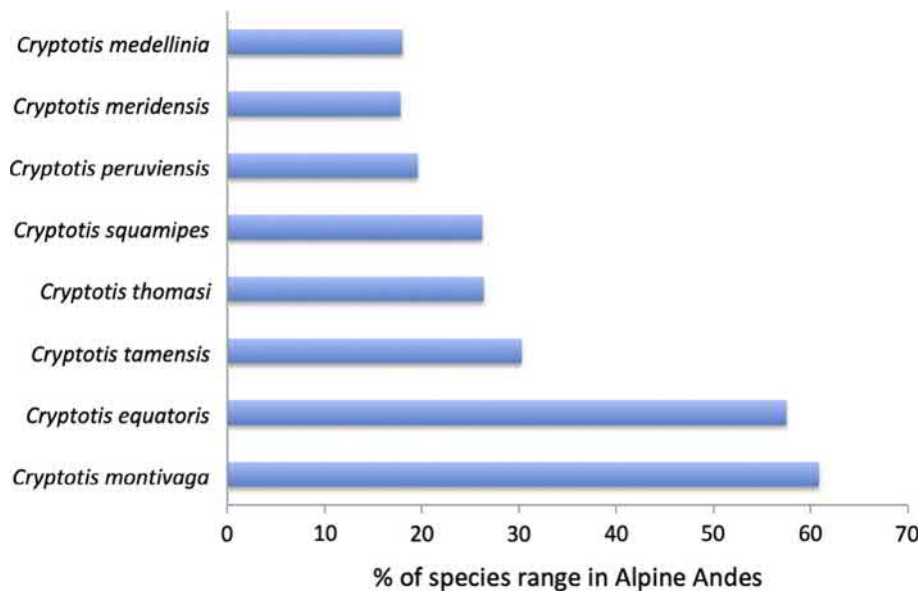


Fig. 7 Order Eulipotyphla. Percentage of the species range encompass along the alpine region.

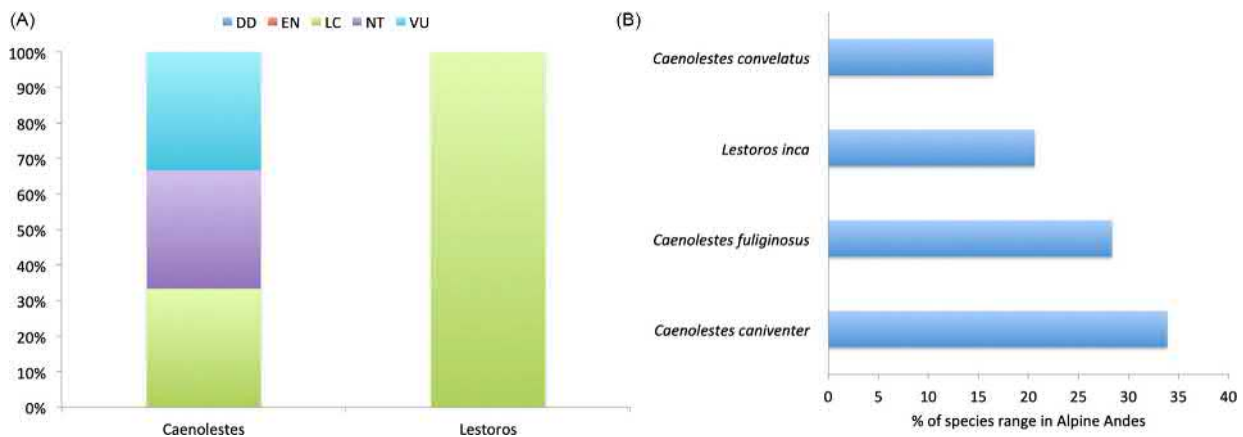


Fig. 8 Order Paucituberculata. (A) Conservation status, percentage of species in each IUCN red list category. (B) Percentage of the species range encompass along the alpine region.

elevations only marginally (Timm and Patterson, 2008; Patterson, 2015). Shrew opossums are mostly nocturnal, feeding on earthworms, flatworms, and several arthropods, both as larvae and adults (Patterson, 2015). *C. caniventer* and *C. convelatus* registered some conservation concerns, meanwhile *C. fuliginosus* and *Lestoros inca* are considered of least concern (Fig. 8B). Land transformation for agricultural purposes is among the mayor threats (Solari and Martínez-Cerón, 2015).

Páramo Rabbit (Order Lagomorpha)

The Páramo Rabbit, *Sylvilagus brasiliensis* has been classified as the subspecies *S. b. meridensis*, which inhabits all Venezuelan and Colombian páramos (Durant, 1983); and *S. B. andinus* is present at high elevations in Ecuador (Diersing and Wilson, 2017). Population density along Venezuela Páramos was estimated at 2.85 rabbits per ha. (Durant, 1983) and in Ecuador it ranged from 23 to 92 individuals/ha. Abundance is strongly associated with vegetation structure (García et al., 2016), since higher complexity and higher diversity of the vegetation leads to more possible refuges for rabbits to avoid predators and greater diversity of diet items. The size and abundance of rabbits make them an important Páramo prey species (García et al., 2016), therefore its presence and abundance are important for community structure (Durant, 1983). The Páramo rabbit has several adaptations that improve its survival at high elevations. It has a set of morpho-physiological specializations, including heavier fur with longer hairs, a longer gestation period, a reduction in the number of teats and in the number of offspring per litter, and strong territoriality (Díaz et al., 1997).

Mountain Tapir (Order Perissodactyla)

The mountain tapir is known from Andean region of Colombia, Ecuador and Northern Peru, above 1400–4700 m asl. Its population is heavily fragmented, therefore leading to a genetic bottleneck effect (Downer, 1997, 2001). Also this species displays several attributes (slow reproduction rate, large home range, solitary nature) that make it particularly vulnerable (Downer, 1997). Human activities, such as hunting, farming, mining and habitat conversion are among the major conservation threats (Lizcano et al., 2002). Also there is a great concern about the effects of climate change on mountain tapir populations (Ortega-Andrade et al., 2015).

Rodents (Order Rodentia)

Rodents comprise more than half of all Neotropical mammal species (Maestri and Patterson, 2016), and occupy most terrestrial environments (Lacher et al., 2016). They are separated into two groups: “caviomorphs or sigmodontines”, which have greater diversity (Patton et al., 2015; Upham and Patterson, 2015; Ojeda et al., 2015a, 2016). Previous studies showed that the Andes support high levels of species richness and turnover of rodents (Amori et al., 2013; Maestri and Patterson, 2016). Rodents encompass almost 70% of the mammals present at the Andes (Fig. 1A) and are the only small mammals that inhabit elevations above 4000 m. The family Cricetidae embraces almost 80% of all the Andean rodents (108 species); meanwhile the other families are represented by no >10% (Fig. 9A). Fifteen out of 44 genera are considered endemic to the Andean region, with >70% of their ranges constrained to this region (Fig. 9B). Around 50% of the species in the Andes are categorized as least concern, 15% are considered data deficient and 14% conveyed some conservation issue.

Among families, Chinchillidae constitute a high proportion of endangered species, while Caviidae and Cuniculidae contain species categorized as near threatened (Fig. 9C). Most families contain species for which conservation information is scarce; there are therefore categorized as data deficient. Among the family Cricetidae almost 5% of the species are considered endangered and almost 10% are considered vulnerable (Fig. 9C).

Caviomorph rodents radiated in the Neotropics and now occupy a wide spectrum of landscapes, elevations, and habitats here (Ojeda et al., 2016; Upham and Patterson, 2015). The Ctenomyidae and Chinchillidae are mostly distributed in temperate regions. Tuco-tucos (Ctenomyidae) have a wide distribution from southern Peru to Tierra del Fuego, and from Andean Puna to the Atlantic coast (Upham and Patterson, 2015), several species show restricted distributional ranges and some are known only from the type locality (Ojeda et al., 2016). On the other hand Chinchillas extend from the central Andes to southern Patagonia. Specifically, the genera *Chinchilla* and *Lagidim* are restricted to Altiplano and Puna environments (Valladares et al., 2014; Ojeda et al., 2015a, 2016). The main threats for Chinchilla populations are mining exploitation and commercial hunting for the fur trade (Valladares et al., 2014).

The distribution patterns of the families Octodontidae and Abrocomidae extend along the arid Andes (Upham and Patterson, 2015). Among Octodontids, the mountain degu (*Octodontomys gliroides*) lives in dry Andean zones of northern Chile, Bolivia and northwest Argentina, mostly in rocky areas with herbaceous vegetation (Verzi et al., 2015). On the other hand, the chinchilla rats (Abrocomidae) show restricted and non- overlapping ranges along the southern Andes (Woods and Kilpatrick, 2005). The family Caviidae shows the broadest distribution among caviomorphs and includes most major biomes. The highest species density occurs in the dry south-central Andes, in the Cerrado and Caatinga ecoregions (Ojeda et al., 2015a).

The Echimyidae, Erethizontidae and Sciuridae are mainly found in tropical forests, with high diversity along the Yungas and in Amazonia. Most species occupy arboreal habits and may reach the Alpine region marginally, mostly in the Páramos of Colombia and Venezuela (Ojeda et al., 2016; Upham and Patterson, 2015).

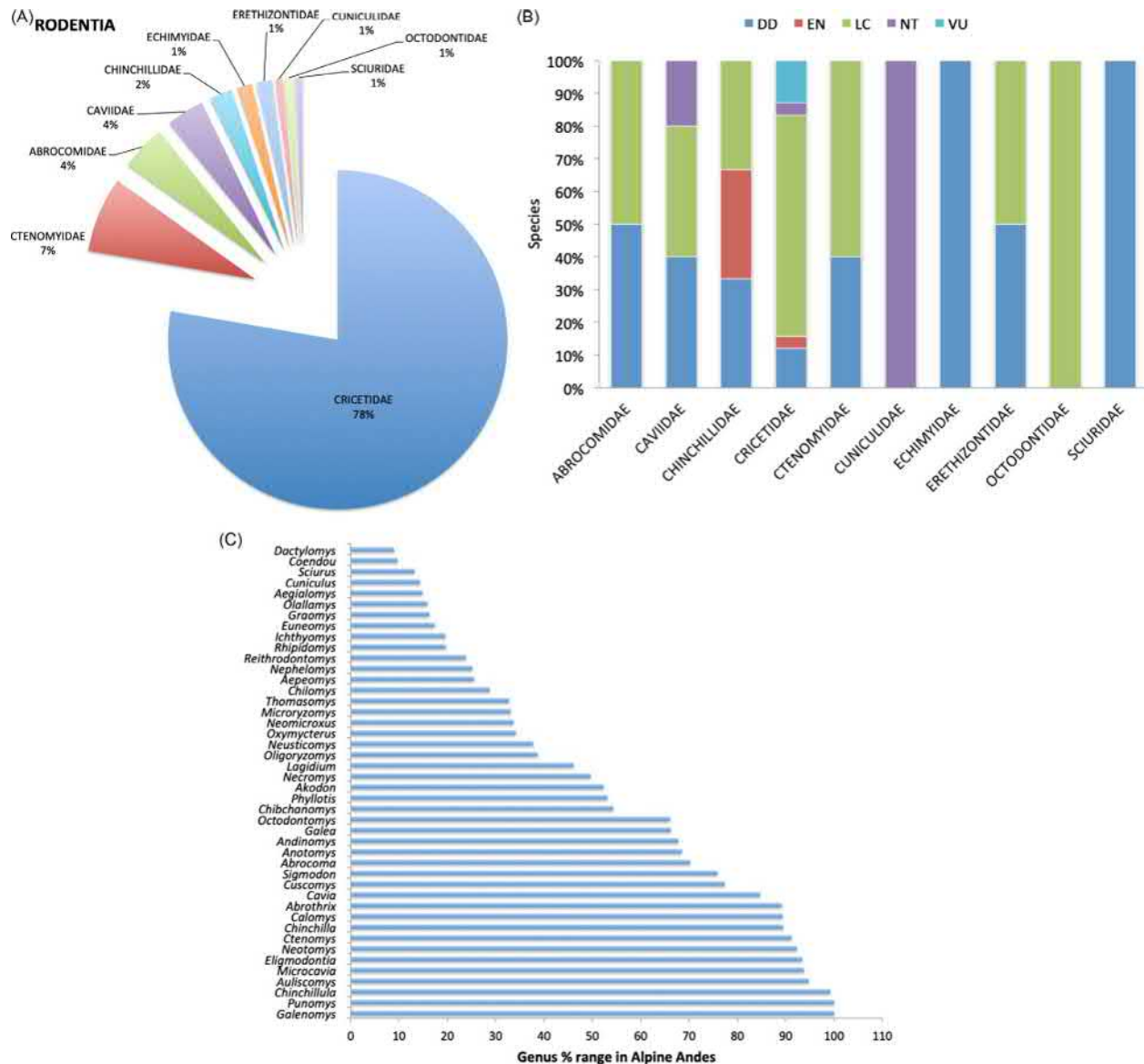


Fig. 9 (A) Percentage of High Andean rodents by family. (B) Conservation status, percentage of species in each IUCN red list category. (C) Percentage of the species range encompass along the alpine region.

The geographic distribution of the family Cuniculidae extends from central Mexico to northern Argentina (Ojeda et al., 2015a). Species density is highest in the tropical Andes region (Ojeda et al., 2015a; Upham and Patterson, 2015). Only the Mountain Paca (*C. taczanowskii*) is found in the high Andes of Peru, Ecuador, Colombia, and Venezuela (Woods and Kilpatrick, 2005), between elevations of 2000 and 3500 m asl. This species is considered as near- threatened due to habitat destruction, invasive species and hunting pressure (Zapata-Ríos and Branch, 2016).

Among cricetid rodents, some genera are mainly Andean in distribution (*Chinchillula*, *Auliscomys*, *Punomys*, among others) and others with broad distributions in other ecoregions that extend into the Andes (*Akodon*, *Oligoryzomys*, *Oxymycterus*, etc.) (Patton et al., 2015). Half of the genera present in the high Andes area have >50% of their ranges in this region (Fig. 10A). Almost 70% of these species are considered as least concern, while 10% are poorly known and categorized as data deficient, plus 20% that have some level of conservation issues (Fig. 10B).

Alpine rats and mice's ranges confirm that the Huancabamba depression separates two different groups: a northern and a southern one (Fig. 10C). The Central Andes was recognized as an important area for sigmodontines differentiation (Novillo and Ojeda, 2012; Maestri and Patterson, 2016; and reference therein). Therefore the Puna and the Altiplano are considered to harbor high species endemism (Ojeda et al., 2000).

Concluding Remarks

One of South-America's most vexing and polarizing challenges is how best to manage public lands established for multiple uses such as natural resource extraction, wildlife, and recreation. The intersection between energy development and biological conservation affords opportunities both to gather knowledge and to implement findings about how to mitigate impacts to wildlife, without neglecting local and regional development. Among all species registered in the Andes, 32% of rodents, 25% of ungulates and 5% of bats and carnivores can be considered endemics, with >70% of their ranges found in the Alpine region. Most of these species show adaptations to harsh climate (low temperatures and oxygen pressure) (Ostojic et al., 2002); and are habitat specialists confined to a specific habitat type (Andean cats, mountain vizcachas, vicuñas, among others).

As the footprint of human development continues to expand globally into regions that have historically supported abundant wildlife resources, there will be even more pressing needs for long-term data collection, in conjunction with baseline data, to examine changes in life history parameters and behavioral processes. Mountains are fragile environments (Díaz et al., 2003), which are strongly affected by climate change and several anthropogenic pressures (Young, 2009). Mountain regions are highly sensitive to climate change, and show above average warming, in comparison to global means during the 20th century (IPCC, 2014; Nogués-Bravo et al., 2007). Therefore, under this scenario elevational shifting of climatic belts is expected to occur, with concomitant effects on biodiversity. Species are expected to shift their distributions upslope in response to warming; however, there may no longer be appropriate habitat on mountain summits, leading to a high likelihood of Alpine species extinction (Oppenheimer et al., 2014). For example, regions of highest mammals richness (southern Paramo and the Puna/Altiplano, Fig. 1) will experience a temperatures rise up to 5°C (IPCC, 2014; Baez et al., 2016). This future scenario may lead to an upward shift of tree limit, reducing the alpine environment area, and constraining the suitable environment of several species. There is evidence of mountain species extinctions due to severe range contraction among endemic species (Parmesan, 2006) and that species from tropical latitudes are unlikely to evolve physiological tolerances to heat increase, being more affected by climate change (Araújo et al., 2013.). Among rodents, high Andean species show that animals from mid- and high elevations reduced their activity under high temperatures; this behavior decreases animal foraging and reproducing time, leading to fitness reduction (Sassi et al., 2015).

Conflicts between humans and wildlife occur when the interests and objectives of human activities, such as extensive and intensive livestock farming, agriculture and extractive activities do not take into account the native flora or fauna of the landscape, much less its functional diversity in a perspective of conservation of ecosystem services. Anthropogenic activities such as land change use for farming (small and large scale agriculture), oil and gas prospecting, invasive species introduction (feral dogs), and city expansion, are among the major threats to biodiversity (Zapata-Ríos and Branch, 2016; Salvador et al., 2014). Such unplanned activities represent a key challenge for society because their negative impacts can affect food security (wildlife damaging crops), the sustainability of ecosystems (over-exploitation of available resources) and biodiversity (human dimension as an agent of stress, loss of habitat and functional diversity, displacement of native species by exotic species). Thus, the sum of the effects of human activities can threaten the integrity of ecosystems on which both biodiversity (fauna and flora) and agriculture and livestock depend, i.e. whether the species that provide key ecosystem services (nutrient cycling, pollination, etc.)

In summary Alpine environments are fragile, vulnerable and lack the required resilience to withstand future changes (Gonzalez et al., 2010). They are inhabited by cold adapted species in most cases with restrictions to migrate, or adapt to new scenarios. Therefore these regions should be a top priority when studying the effects of climate change (Dirnböck et al., 2011; Laurance et al., 2011) and among conservation actions.

Appendix: Supplementary Material

Supplementary material related to this chapter can be found on the accompanying CD or online at <https://doi.org/10.1016/B978-0-12-409548-9.11907-4>.

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Alpine Mammals of Africa

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Abstract

The African alpine (Afroalpine) zone is poorly defined and generally considered part of the wider Afromontane region. We consider the Afroalpine zone as areas exceeding 1800 m elevation. These zones occur as isolated pockets, stretching across large parts of tropical and sub-tropical Africa. Afroalpine habitats are isolated on mountain tops, supporting fragmented and unique vegetation types. Afroalpine mammals are represented by 10 orders, currently comprising 109 species, 60% of which are endemic. Of concern is that 38% are endangered, a number that is likely to increase in future. Rodents comprise 53% of the Afroalpine mammal species and are generally better studied than other groups. Some are specialists occupying a narrow altitudinal range while others are generalists, occupying a wider range of elevations. Afroalpine rodents show a range of adaptations to their habitats to minimize exposure to lethal temperatures. We present two case studies, one of the non-specialist ice rat, whose success depends on behavioral and morphological adaptations, and the other of the charismatic Ethiopian wolf, whose specialized diet and habitat use makes it vulnerable to extinction. Afromontane mammals face a range of threats, most notably habitat destruction through human expansion and activity and ultimately global climate change.

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Definition and Distribution of African Alpine (Afroalpine) Region

The word alpine conjures up visions of sparkling snowy slopes in temperate regions of Europe, from where the term originates. However, 'alpine' can also refer to regions occurring in other parts of the world, in particular to vegetation above the altitudinal tree line. Africa's alpine zones, known as the Afroalpine, are extensive and span temperate, tropical and equatorial regions of sub-Saharan Africa. Yet, while the term Afroalpine appears sporadically in the literature, historically there has been little consensus about what constitutes Africa's alpine region, as discussed below.

The term Afroalpine was coined by [Hauman \(1955\)](#) to refer to species-poor floristic areas, characterized by giant rosette life forms occurring in the East African tropical high mountains of > 3000 m elevation. Generally, Afroalpine habitats are characterized by short and sparse vegetation, as seen in the Ethiopian highlands ([Sillero-Zubiri and Gottelli, 1994](#)) and the southern African Drakensberg ([Schwaibold and Pillay, 2010](#)). The uppermost regions of these mountains act as refugia for unique flora with patchy distribution, characterized by the occurrence of plants such as giant *Senecio*, giant *Lobelia*, shrubby *Alchemilla*, and containing representatives of many genera not seen in the lowlands of tropical Africa. These plants are present on the high mountains of Ethiopia, with a few species extending to the Yemen, Cameroon, south tropical Africa, and South Africa ([Hedberg, 1961](#)). In southern Africa,

Coetzee (1967) coined the term Austro-afroalpine to distinguish the ecological belt in Lesotho and the Drakensberg Mountains in Southern Africa from the one recognized by Hauman (1955) in East Africa. The term subalpine has also been used in the Austro-afroalpine context in Southern Africa, but the term has not been applied consistently. For example, Thode (1894, cited in Killick, 1978) described the uppermost region between 2130 and 3050 m elevation of the South African Drakensberg, as subalpine. In contrast, Killick (1963) and Edwards (1967) used this term for the vegetation between 1830 and 1980 m and 2865–2895 m elevations respectively. Jacot Guillarmod (1971) described the subalpine belt in Lesotho as that lying between 2290 and 2900 m elevation. Coetzee (1967) rejected the idea of a subalpine region due to the lack of tall coniferous trees above the montane forests, which is typical of the European Alps, and proposed that the upper level of the montane forest represents the tree line and the vegetation above this level constitutes the Austro-afroalpine belt.

The contentious issues of the definition of the Afroalpine zone appear to center around geographic context (i.e. country and elevation) and floral composition. For the purposes of our review, we adopted a broader, more pragmatic view of Afroalpine regions as those occurring above 1800 m elevation, thereby casting a wider net to capture the mammal biodiversity. This approach combines the Afroalpine with upper elevations of most Afromontane areas (see <https://en.wikipedia.org/wiki/Afromontane>), and thus we consider largely Afromontane mammals in our appraisal, unless the literature specifically mentions Afroalpine mammals. In addition, we sometimes considered mammals at lower elevations if there was a likelihood that their distribution might breach the 1800 m cut-off.

The Afroalpine area as defined here comprises six disjunct zones (Fig. 1), occurring in western, eastern and southern Africa. In West Africa, the Afroalpine zone occurs along the Cameroon Highlands. In East Africa, the distribution of these zones follows a chain of isolated mountain peaks and plateaus, stretching from Ethiopia in the north to Zimbabwe and the Drakensberg mountain range in South Africa in the south. This distribution follows the Western, Eastern and Southern Rift and includes the following countries: Uganda, Rwanda, Burundi, Democratic Republic of the Congo, Kenya, Tanzania, and Zimbabwe. The mountains and plateaus are

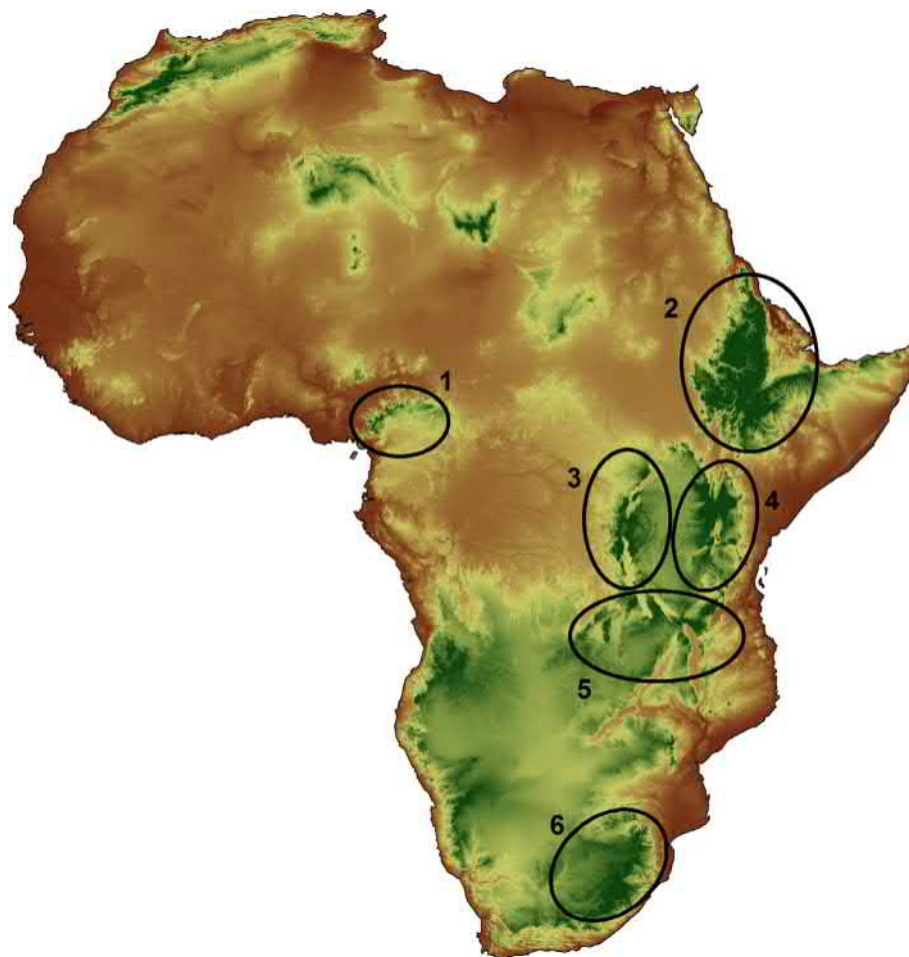


Fig. 1 Afroalpine distribution. 1. Cameroon highlands, 2. Ethiopian highlands, 3. Western Rift, 4. Eastern Rift, 5. Southern Rift and Eastern Highlands, 6. Drakensberg/Maluti. Produced using Arcmap 10.3 by Jolene Fisher; University of the Witwatersrand, Johannesburg; adapted from Andrew Z. Colvin 2016. Own work based on satellite image from Nasa Image: Topography of africa.jpg and original creator Ulanwp., CC BY-SA 4.0, <https://commons.wikimedia.org/w/index.php?curid=54035829>.

separated by lower savannas and woodlands (White, 1983). Aptly stated by Kingdon (1989), the mountains represent “Africa’s Galapagos islands” with each mountain and plateau existing as a habitat island, supporting a characteristic fauna and flora.

Several biological phenomena are generally associated with changes in elevation and this is also true of the Afromontane areas. For example, the climate becomes more temperate and alpine, with seasonal or regular frost, low rainfall and snow at the highest elevations (Happold and Happold, 1989). Snow is even permanent at the higher reaches of equatorial Mount Kilimanjaro (Willis, 2000). Distinct altitudinal zones are apparent, with different plant and animal assemblages. In addition to elevation, several other factors contribute to the formation of different vegetation zones, such as latitude, aspect and the location of the mountain. For example, while Afroalpine grassland can occur as low as 1500 m above sea level in the Drakensberg region, it occurs only above 3800–4000 m elevation in the equatorial mountains of East Africa (Hamilton, 1982). This is because the effects of latitude and elevation are inter-related, and thus climatic conditions at higher elevations are similar to the conditions at lower elevations further away from the equator.

The unique geographical contexts of latitude and elevation are the primary drivers of the evolution of a plethora of endemic animal and plant species, particularly in the Afromontane ecosystem. While there are ample studies documenting the flora in relation to zonation in African mountains (Hedberg, 1957; White, 1981, 1983; Killick, 1978), studies on vertebrates are limited in the literature and are often only anecdotal reports. Nonetheless, small terrestrial mammals at high elevations on African mountains have been comparatively well studied, for example in Mount Ruwenzori, Mount Cameroon, Mount Kahuzi, Mount Elgon (Clausnitzer, 2001), Mount Kenya (Moreau, 1945), Mount Kilimanjaro (Grimshaw et al., 1995), Drakensberg (Rowe-Rowe and Meester, 1982; Perrin and Carranza, 2000), and the Maluti Mountains (Hinze and Pillay, 2006).

African Alpine Mammals

Afroalpine habitats are poorly studied in many of the representative countries because of their inaccessibility, the small number of field biologists and a lack of consistent field surveys. There have been some recent attempts to conduct small mammal studies in West Africa by personnel at the Natural History Museum in Paris (Christiane Denys pers. com) and there have been sporadic studies by field biologists in Kenya. Several long-term studies have been conducted in the Bale Mountains in Ethiopia. In Southern Africa, studies in the South African and Lesotho Drakensberg are routinely conducted by biologists from both countries (details below).

Based on historical and current studies, 10 orders of mammals occur in Afromontane areas, including Rodentia (58), Insectivora (27), Carnivora (7), Cetartiodactyla (6), Primates (5), Hyracoidea (2), Chiroptera (1), Lagomorpha (1), Macroscelidea (1) and Tubulidentata (1). At the time of this writing, we identified 109 mammal species, representing 20 families (Table 1). We expect these numbers to change as better sampling is undertaken and better systematic assessments appear in the literature in future (Christiane Denys pers. com).

Of the 109 species, 60% (65) are endemic, mostly to Ethiopia (29) and the Cameroon (16). About 38% of the mammals are of conservation concern, including 3 critically endangered, 16 endangered and 22 vulnerable/threatened. Most (60; 55%) are of least concern and we could not find the status of 7% (8) of mammal species (IUCN, 2017). Specifically, of the endemic species, a staggering 57% (37) are of conservation concern (mostly those from Ethiopia and Cameroon; IUCN, 2017). Three large mammals are endangered, including the Walia ibex *Capra ibex waliae*, Mountain Nyala *Tragelaphus buxtoni* and the Ethiopian wolf *Canis simensis*, all from Ethiopia. The remaining species belong to the orders Rodentia and Insectivora.

Rodents

As evident from Tables 1, 53% of the species are rodents, the most speciose mammal order globally. Most (35, 60%) of these are endemic. This high rodent endemism reflects the unique geological and biogeographic history, topography, variation in climatic conditions and a wide range of vegetation types in disjunct mountain ranges, promoting high biodiversity and endemism in countries with Afroalpine habitats (Yalden and Largen, 1992; Bekele, 1996; Clausnitzer, 2003). Generally, the distribution and abundance of rodent species are influenced by various environmental factors, such as vegetation, climatic conditions, disease, predation, life history strategies and human encroachment (Marino, 2003; Fitzherbert et al., 2007). For example, in the Bale Mountains, a higher density of rodents occurs in *Alchemilla* meadows and rocky grasslands and lower densities occur in the *Helichrysum* heaths and *Artemisia* grasslands (Marino, 2003), showing the influence of vegetation on life history biology.

Some Afroalpine rodents inhabit a narrow elevational range, including many of the Ethiopian endemic species listed in Table 1, whereas others are elevation generalists (Yihune, and Bekele, 2012). As expected, non-endemic rodent species are not restricted geographically and inhabit a wide range of montane habitats above 3000 m elevation and also occur at lower elevations. Examples include the four-striped mouse *Rhabdomys* spp., North-east African mole rat *Tachyoryctes splendens*, Northern groove-toothed rat *Otomys typus* and Abyssinian grass rat *Arvicanthis abyssinicus*, and the yellow-spotted brush-furred rat *Lophuromys flavopunctatus*. In particular, the ability of the yellow-spotted brush-furred rat to thrive in unfavorable habitats such as heathlands reflects its generalist nature (Yalden and Largen, 1992; Happold and Happold, 1992). Endemism is not related to ecological specialization, however. For example, some Ethiopian endemic rodent species are habitat specialists (e.g. grassland: Blick’s grass rat *Arvicanthis blicki*; Lovat’s climbing mouse *Dendromus lovati*; *Tachyoryctes macrocephalus*; shrubland: Nikolaus’s mouse *Megadendromus nikolausi*). Others are habitat generalists, such the Ethiopian narrow-headed rat *Stenocephalemys albocaudata* and Gray-tailed narrow-headed rat *Stenocephalemys griseicauda* that occupy grassland and shrubland.

Table 1 A current list of mammal species by order occupying Afro-montane habitats, including their endemism, ecological specialization and conservation status.

	Order	Species (common name)	Family	Endemism	Generalist/ Specialist	Conservation status	Reference(s)
1	Carnivora	<i>Canis simensis</i> (Ethiopian wolf)	Canidae	Endemic to Ethiopia	Specialist	Endangered	Sillero-Zubiri et al. (1997)
2	Carnivora	<i>Crocuta crocuta</i> (Spotted hyaena)	Hyaenidae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
3	Carnivora	<i>Genetta maculata</i> (Large spotted genet)	Viverridae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
4	Carnivora	<i>Herpestes ichneumon</i> (Egyptian mongoose)	Herpestidae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
5	Carnivora	<i>Leptailurus serval</i> (Serval)	Felidae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
6	Carnivora	<i>Lutra maculicollis</i> (Spotted-necked otter)	Mustelidae	Wide distribution	Specialist	Threatened	Perrin and Carranza (2000) and IUCN red list
7	Carnivora	<i>Panthera pardus</i> (Leopard)	Felidae	Wide distribution	Generalist	Vulnerable	Grimshaw et al. (1995)
8	Cetartiodactyla	<i>Capra ibex walie</i> (<i>Walia ibex</i>)	Bovidae	Endemic to Ethiopia	Generalist	Endangered	Brown (1969)
9	Cetartiodactyla	<i>Nesotragus moschatus</i> (Suni)	Bovidae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
10	Cetartiodactyla	<i>Sylvicapra grimmia</i> (Common duiker)	Bovidae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
11	Cetartiodactyla	<i>Syncerus caffer</i> (African buffalo)	Bovidae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
12	Cetartiodactyla	<i>Tragelaphus oryx</i> (Eland)	Bovidae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
13	Cetartiodactyla	<i>Tragelaphus buxtoni</i> (Mountain nyala)	Bovidae	Endemic to Ethiopia	Generalist	Endangered	Evangelista et al. (2007)
14	Chiroptera	<i>Myotis scotti</i> (Scott's mouse-eared bat)	Vespertilionidae	Endemic to Ethiopia	Specialist	Vulnerable	IUCN red list
15	Hyracoidea	<i>Dendrohyrax validus</i> (East tree hyrax)	Procaviidae	Endemic to Kenya/Tanzania	Specialist	Threatened	Grimshaw et al. (1995)
16	Hyracoidea	<i>Procavia capensis</i> (Rock hyrax)	Procaviidae	Wide distribution	Generalist	Least concern	IUCN red list
17	Insectivora	<i>Crocidura allea</i> (East African highland shrew)	Soricidae	Endemic to Kenya/Tanzania	Specialist	Vulnerable	Grimshaw et al. (1995)
18	Insectivora	<i>Crocidura baileyi</i> (Bailey's shrew)	Soricidae	Endemic to Ethiopia	Specialist?	Least concern	Yalden and Largen (1992) and IUCN red list
19	Insectivora	<i>Crocidura bottegoides</i> (Bale shrew)	Soricidae	Endemic to Ethiopia	Specialist	Endangered	Hutterer and Yalden (1990)
20	Insectivora	<i>Crocidura eisentrauti</i> (Eisentraut's shrew)	Soricidae	Endemic to Cameroon	Specialist	Vulnerable	Cronin et al. (2014)
21	Insectivora	<i>Crocidura glassi</i> (Glass's shrew)	Soricidae	Endemic to Ethiopia	Specialist	Vulnerable	IUCN red list
22	Insectivora	<i>Crocidura harena</i> (Harena shrew)	Soricidae	Endemic to Ethiopia	Specialist	Critically Endangered	Hutterer and Yalden (1990)
23	Insectivora	<i>Crocidura lucina</i> (Lucina's shrew)	Soricidae	Endemic to Ethiopia	Specialist	Vulnerable	IUCN red list
24	Insectivora	<i>Crocidura monax</i> (Kilimanjaro shrew)	Soricidae	Endemic to Tanzania	Specialist	—	Grimshaw et al. (1995)
25	Insectivora	<i>Crocidura montis</i> (Montane white-toothed shrew)	Soricidae	Wide distribution	Generalist	Least concern	Clausnitzer et al. (2003)
26	Insectivora	<i>Crocidura olivieri</i> (African giant musk shrew/Olivier's shrew)	Soricidae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
27	Insectivora	<i>Crocidura phaeura</i> (Guramba shrew)	Soricidae	Endemic to Ethiopia	Specialist	Endangered	IUCN red list
28	Insectivora	<i>Crocidura picea</i> (Cameroonian shrew)	Soricidae	Endemic to Cameroon	Specialist	Endangered	Cronin et al. (2014)
29	Insectivora	<i>Crocidura thalia</i> (Thalia's shrew)	Soricidae	Endemic to Ethiopia	Generalist	Least concern	IUCN red list
30	Insectivora	<i>Crocidura zaphiri</i> (Zaphir's shrew)	Soricidae	Endemic to Ethiopia	—	—	IUCN red list
31	Insectivora	<i>Myosorex babaulti</i> (Babault's mouse shrew)	Soricidae	Wide distribution	Specialist	Least concern	Kingdon (1981) and IUCN red list

32	Insectivora	<i>Myosorex blarina</i> (Montane mouse shrew)	Soricidae	Wide distribution (Congo, Uganda)	Specialist	Endangered	Kingdon (1981) and IUCN red list
33	Insectivora	<i>Myosorex eisentrauti</i> (Eisentraut's mouse shrew)	Soricidae	Endemic to Cameroon	Specialist	Critically Endangered	Cronin et al. (2014)
34	Insectivora	<i>Myosorex okuensis</i> (Oku mouse shrew)	Soricidae	Endemic to Cameroon	Specialist	Vulnerable?	Cronin et al. (2014) and IUCN red list
35	Insectivora	<i>Myosorex varius</i> (Forest shrew)	Soricidae	Wide distribution (Lesotho, South Africa, Swaziland)	Generalist	Least concern	Rowe-Rowe and Meester (1982)
36	Insectivora	<i>Myosorex zinki</i> (Kilimanjaro mouse shrew)	Soricidae	Endemic to Tanzania (Mt Kilimanjaro)	Generalist	Least concern	Stanley et al. (2011)
37	Insectivora	<i>Paracrocidura maxima</i> (Greater large-headed shrew/Greater shrew)	Soricidae	Endemic to Bwindi Impenetrable National Park, Uganda	Specialist	Least concern	Kasangaki et al. (2003)
38	Insectivora	<i>Scutisorex somereni</i> (Armored shrew)	Soricidae	Wide distribution	Specialist	Least concern	Churchfield et al. (2007)
39	Insectivora	<i>Sylvisorex camerunensis</i> (Cameroonian forest shrew)	Soricidae	Endemic to Cameroon	Specialist	Vulnerable	Cronin et al. (2014)
40	Insectivora	<i>Sylvisorex granti</i> (Grant's forest shrew)	Soricidae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
41	Insectivora	<i>Sylvisorex lunaris</i> (Crescent shrew/Moon forest shrew)	Soricidae	Endemic to Bwindi Impenetrable National Park, Uganda	Specialist	Threatened	Kasangaki et al. (2003) and IUCN red list
42	Insectivora	<i>Sylvisorex morio</i> (Mt. Cameroon forest shrew/Arrogant shrew)	Soricidae	Endemic to Cameroon	Specialist	Endangered	Cronin et al. (2014) and IUCN red list
43	Insectivora	<i>Sylvisorex vulcanorum</i> (Volcano shrew)	Soricidae	Endemic to Bwindi Impenetrable National Park, Uganda	Generalist	Least concern	Kasangaki et al. (2003)
44	Lagomorpha	<i>Lepus starcki</i> (Ethiopian highland hare)	Leporidae	Endemic to Ethiopia	Generalist	Least concern	IUCN red list
45	Macroscelidae	<i>Rhynchocyon udzungwensis</i> (Gray-faced sengi)	Macroscelidae	Endemic to Tanzania	Specialist	Vulnerable	Stanley et al. (2011) and Rovero et al. (2008)
46	Primates	<i>Cercopithecus mitis</i> (Blue monkey)	Cercopithecidae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
47	Primates	<i>Chlorocebus djamdjamensis</i> (Bale monkey)	Cercopithecidae	Endemic to Bale mountains, Ethiopia	Specialist	Vulnerable	Mekonnen et al. (2010)
48	Primates	<i>Colobus guereza</i> (Kilimanjaro black-and-white colobus)	Cercopithecidae	Endemic to Mt. Kilimanjaro and Mt. Meru	Generalist	Least concern	Grimshaw et al. (1995)
49	Primates	<i>Otolemur garnettii</i> (Garnett's greater galago)	Galagidae	Wide distribution (Kenya, Somalia, Tanzania)	Generalist	Least concern	Grimshaw et al. (1995)
50	Primates	<i>Theropithecus gelada</i> (Gelada baboon)	Cercopithecidae	Endemic to Ethiopia	Generalist	Least concern	IUCN red list
51	Rodentia	<i>Arvicanthis abyssinicus</i> (Abyssinian grass rat)	Muridae	Endemic to Ethiopia	Generalist	Least concern	Ashenafi et al. (2012)
52	Rodentia	<i>Arvicanthis blicki</i> (Blick's grass rat)	Muridae	Endemic to Ethiopia	Specialist	Threatened	IUCN red list
53	Rodentia	<i>Colomys goslingi</i> (African water rat/African wading rat)	Muridae	Wide distribution	Generalist	Least concern	Clausnitzer (2001)
54	Rodentia	<i>Cricetomys gambianus</i> (Gambian pouched rat)	Muridae	Wide distribution	Generalist	Least concern	Clausnitzer (2003)
55	Rodentia	<i>Dasymys incommutatus</i> (African marsh rat)	Muridae	Wide distribution	Generalist/Specialist	Least concern	Clausnitzer (2003)

(Continued)

Table 1 A current list of mammal species by order occupying Afro-montane habitats, including their endemism, ecological specialization and conservation status.—cont'd

	Order	Species (common name)	Family	Endemism	Generalist/ Specialist	Conservation status	Reference(s)
56	Rodentia	<i>Delanymys brooksi</i> (Delany's mouse/ Delany's swamp mouse)	Nesomyidae	Endemic to Bwindi Impenetrable National Park, Uganda	Specialist	Vulnerable	Kasangaki et al. (2003)
57	Rodentia	<i>Dendromus insignis</i> (Montane climbing mouse)	Nesomyidae	Wide distribution (DRC, Kenya, Rwanda, Uganda)	Generalist	Least concern	Grimshaw et al. (1995)
58	Rodentia	<i>Dendromus mesomelas</i> (Brant's climbing mouse)	Nesomyidae	Wide distribution	Generalist	Least concern	Yalden and Largen (1992)
59	Rodentia	<i>Dendromus mystacalis</i> (Chestnut climbing mouse)	Nesomyidae	Wide distribution	Generalist	Least concern	Yalden and Largen (1992)
60	Rodentia	<i>Dendromus lovati</i> (Lovat's climbing mouse)	Nesomyidae	Endemic to Ethiopia	Generalist	Least concern	IUCN red list
61	Rodentia	<i>Desmomys harringtoni</i> (Harrington's rat)	Muridae	Endemic to Ethiopia	Generalist	Least concern	IUCN red list
62	Rodentia	<i>Grammomys dolichurus</i> (Common thicket rat)	Muridae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
63	Rodentia	<i>Grammomys dryas</i> (Forest thicket rat)	Muridae	Endemic to Bwindi Impenetrable National Park, Uganda	Generalist	Least concern	Kasangaki et al. (2003)
64	Rodentia	<i>Graphiurus murinus</i> (African common dormouse)	Gliridae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
65	Rodentia	<i>Hylomyscus aeta</i> (Beaded wood mouse)	Muridae	Wide distribution	Generalist	Least concern	Beja et al. (2019)
66	Rodentia	<i>Hylomyscus denniae</i> (Montane wood mouse)	Muridae	Wide distribution	Generalist	Least concern?	Clausnitzer (2001) and IUCN red list
67	Rodentia	<i>Hylomyscus grandis</i> (Mt. Oku Hylomyscus)	Muridae	Endemic to Cameroon	Specialist	Endangered	Cronin et al. (2014)
68	Rodentia	<i>Hylomyscus vulcanorum</i> (Albertine Rift Wood Mouse)	Muridae	Endemic to Bwindi Impenetrable National Park, Uganda/Rwanda	Generalist	Least concern	Tuyisingize et al. (2013)
69	Rodentia	<i>Hystrix cristata</i> (Crested porcupine)	Hystriidae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
70	Rodentia	<i>Lamottemys okuensis</i> (Mt. Oku rat)	Muridae	Endemic to Cameroon	Specialist	Endangered	Cronin et al. (2014)
71	Rodentia	<i>Lemniscomys mittendorfi</i> (Mittendorf's Striped grass mouse)	Muridae	Endemic to Cameroon	Specialist	Least concern?	Cronin et al. (2014) and IUCN red list
72	Rodentia	<i>Lophuromys aquilus</i> (Gray brush- furred rat)	Muridae	Endemic to DRC	Specialist	—	Grimshaw et al. (1995)
73	Rodentia	<i>Lophuromys breviceaudus</i> (Short-tailed brush-furred rat)	Muridae	Endemic to Ethiopia	Specialist	Threatened	Kostin et al. (2018) and IUCN red list
74	Rodentia	<i>Lophuromys chrysopus</i> (Ethiopian forest brush-furred rat)	Muridae	Endemic to Ethiopia	Generalist	Least concern	Kostin et al. (2018)
75	Rodentia	<i>Lophuromys dieterleni</i> (Dieterlen's brush furred mouse)	Muridae	Endemic to Cameroon	Specialist	Endangered	Cronin et al. (2014)

76	Rodentia	<i>Lophuromys eisentrauti</i> (Eisentraut's brush furred mouse/ Mount Lefo Brush-furred)	Muridae	Endemic to Cameroon	Specialist	Critically Endangered	Cronin et al. (2014)
77	Rodentia	<i>Lophuromys flavopunctatus</i> (Yellow-spotted brush-furred rat)	Muridae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
78	Rodentia	<i>Lophuromys mediceauctatus</i> (Medium-tailed brush-furred rat)	Muridae	Wide distribution (DRC, Uganda, Rwanda)	Specialist	Vulnerable	Grimshaw et al. (1995)
79	Rodentia	<i>Lophuromys melanonyx</i> (Black-clawed brush-furred rat)	Muridae	Endemic to Ethiopia	Specialist	Vulnerable	IUCN red list
80	Rodentia	<i>Lophuromys rahmi</i> (Rahm's brush-furred rat)	Muridae	Endemic to Bwindi Impenetrable National Park, Uganda	Specialist	Threatened	Kasangaki et al. (2003)
81	Rodentia	<i>Lophuromys woosnami</i> (Woosnam's brush-furred rat)	Muridae	Endemic to Bwindi Impenetrable National Park, Uganda	Generalist	Least concern	Kasangaki et al. (2003)
82	Rodentia	<i>Megadendromus nikolausi</i> (Nikolaus's mouse)	Nesomyidae	Endemic to Ethiopia	Specialist	–	IUCN red list
83	Rodentia	<i>Muriculus imberbis</i> (Ethiopian striped mouse)	Muridae	Endemic to Ethiopia	Generalist	Least concern	IUCN red list
84	Rodentia	<i>Mus mahomet</i> (Mahomet mouse)	Muridae	Wide distribution	Generalist	Least concern	Yalden and Largen (1992)
85	Rodentia	<i>Mus musculoides</i> (Northern pygmy mouse)	Muridae	Wide distribution	Specialist	Least concern?	Grimshaw et al. (1995) and IUCN red list
86	Rodentia	<i>Mus triton</i> (Gray-bellied pygmy mouse)	Muridae	Wide distribution	Generalist	Least concern	Kasangaki et al. (2003)
87	Rodentia	<i>Otomys barbouri</i> (Barbour's vlei rat)	Muridae	Endemic to Mt. Elgon, Uganda	Specialist	Endangered	Clausnitzer (2001)
88	Rodentia	<i>Otomys burtoni</i> (Burton's vlei rat)	Muridae	Endemic to Cameroon	Specialist	Endangered	Cronin et al. (2014)
89	Rodentia	<i>Otomys occidentalis</i> (Western vlei rat)	Muridae	Endemic to Cameroon	Specialist	Vulnerable	Cronin et al. (2014)
90	Rodentia	<i>Otomys sloggetti</i> robertsi (Ice rat)	Muridae	Endemic to Drakensberg and Maluti mountains	Generalist	Least concern	Killick (1978)
91	Rodentia	<i>Otomys typus</i> (Northern groove-toothed rat)	Muridae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
92	Rodentia	<i>Paraxerus vexillarius</i> (Swynnerton's bush squirrel)	Sciuridae	Endemic to Tanzania	Specialist	Threatened	Grimshaw et al. (1995) and IUCN red list
93	Rodentia	<i>Pelomys rex</i> (Groove-toothed creek rat)	Muridae	–	–	–	Yalden et al. (1976)
94	Rodentia	<i>Praomys delectorum</i> (Delectable soft-furred rat)	Muridae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)
95	Rodentia	<i>Praomys hartwigi</i> (Hartwig's soft-furred mouse)	Muridae	Endemic to Cameroon	Specialist	Vulnerable	Cronin et al. (2014)
96	Rodentia	<i>Praomys jacksoni</i> (Jackson's soft-furred mouse)	Muridae	Wide distribution	Generalist	Least concern	Cronin et al. (2014)
97	Rodentia	<i>Praomys morio</i> (Cameroon soft-furred mouse)	Muridae	Endemic to Cameroon	Specialist	Endangered	Cronin et al. (2014)
98	Rodentia	<i>Praomys obscurus</i> (Gotel mountain soft-furred mouse)	Muridae	Endemic to Cameroon	Specialist	Endangered	Cronin et al. (2014)

(Continued)

Table 1 A current list of mammal species by order occupying Afro-montane habitats, including their endemism, ecological specialization and conservation status.—cont'd

	Order	Species (common name)	Family	Endemism	Generalist/ Specialist	Conservation status	Reference(s)
99	Rodentia	<i>Rhabdomys</i> spp. (Four-striped field mouse)	Muridae	Wide distribution	Generalist	Least concern	Happold and Happold (1989) and Rowe-Rowe and Meester (1982)
100	Rodentia	<i>Stenocephalemys albicauda</i> (Ethiopian narrow-headed rat)	Muridae	Endemic to Ethiopia	Generalist	Least concern	IUCN red list
101	Rodentia	<i>Stenocephalemys albipes</i> (Ethiopian white-footed mouse/White-footed stenocephalemys)	Muridae	Endemic to Ethiopia	Generalist	Least concern	IUCN red list
102	Rodentia	<i>Stenocephalemys griseicauda</i> (Gray-tailed narrow-headed rat)	Muridae	Endemic to Ethiopia	Generalist	Least concern	IUCN red list
103	Rodentia	<i>Stenocephalemys ruppi</i> (Rupp's mouse)	Muridae	Endemic to Ethiopia	Specialist	—	Van der Straeten and Dieterlen (1983) and IUCN red list
104	Rodentia	<i>Tachyoryctes daemon</i> (Mt Kilimanjaro mole rat)	Spalacidae	Endemic to Tanzania	Generalist	—	Grimshaw et al. (1995)
105	Rodentia	<i>Tachyoryctes macrocephalus</i> (Big-headed African mole rat/Giant mole rat)	Spalacidae	Endemic to Ethiopia	Specialist	Endangered	IUCN red list
106	Rodentia	<i>Tachyoryctes ruddi</i> (Rudd's African mole-rat)	Spalacidae	Endemic to Mt. Elgon, Uganda	Generalist	—	Clausnitzer (2001)
107	Rodentia	<i>Tachyoryctes splendens</i> (North-east African mole rat)	Spalacidae	Wide distribution	Generalist	Least concern	Yalden and Largen (1992) and Wilson and Reader (2005)
108	Rodentia	<i>Thamnomys venustus</i> (Charming thicket rat)	Muridae	Wide distribution (DRC, Uganda)	Specialist	Least concern	Plumptre et al. (2015)
109	Tubulidentata	<i>Orycteropus afer</i> (Aardvark)	Orycteropodidae	Wide distribution	Generalist	Least concern	Grimshaw et al. (1995)

—Indicates data deficient.

Data were obtained from original sources and/or the IUCN red list (<https://www.iucnredlist.org>) when the primary source was unavailable.

Adaptations to Afroalpine Life

Hedberg (1957) characterized Afroalpine climatic conditions as “winter every night and summer every day” (p. 10). Small mammals elsewhere cope with such variable diurnal conditions through diverse adaptations. For example, they could increase locomotion (Kauffmann et al., 2003), hibernate, enter torpor (McNab, 1974, 1983), have longer and denser fur, darker coloration and exhibit diurnal foraging behavior (Young and Evans, 1993) or display huddling behaviors (Gilbert et al., 2010). Since more is known about small Afroalpine mammals, particularly rodents, we focus on rodents for the most part hereafter.

The extremely low night temperatures experienced at high elevations impose constraints on the activity patterns of rodents generally, largely because of their small body size and greater heat loss (Cheviron et al., 2012). There is evidence that several Afroalpine rodents show behavioral, morphological and physiological adaptations to cold. To avoid lethal ambient temperatures in the Bale mountains, some rodents are diurnal, such as the yellow-spotted brush-furred rat, Abyssinian grass rat, Blick's grass rat, black-clawed brush-furred rat *L. melanonyx* and the Northern groove-toothed rat (Yalden, 1988; Sillero-Zubiri et al., 1995a). Utilizing protected nest sites, such as a burrow, can also provide thermoregulation benefits (Marino, 2003) for Afroalpine rodents. For example, the nocturnal yellow-spotted brush-furred rat and gray-tailed narrow-headed rat are found in areas dominated by shrubs and rocky boulders, which may provide protection against the lethal, subfreezing temperatures of their open valley habitats (Sillero-Zubiri et al., 1995b). The dense fur of the gray-tailed narrow-headed rat also confers a thermoregulatory advantage, enabling it to exploit many habitat types (Ashenafi et al., 2012). In addition, the comparatively large body and perhaps a slow metabolic rate of the Ethiopian narrow-headed rat enable it to utilize shallow burrows in areas where shallow soil or the danger of flooding exists (Ashenafi et al., 2012).

Soil depth is believed to limit the distribution of the giant mole rat in the Bale mountains, due to the thermoregulatory costs of burrowing. Despite large diurnal fluctuations in air temperature, the temperature remains more or less constant at a soil depth of 50 cm (Sillero-Zubiri et al., 1995a) and even in shallower burrows (Hinze et al., 2006). As such, small mammals can avoid harsh cold temperatures by nesting belowground (Sillero-Zubiri and Gottelli, 1995; Sillero-Zubiri et al., 1995a; Ashenafi et al., 2012), adopting a fossorial or semi-fossorial existence.

There are some other adaptations in Afroalpine rodents not related to thermoregulation. Stenocephaly, the narrowing of the interorbital area, reduces the distance between the eyes which become close-set and dorsally placed. In giant mole rats, stenocephaly enhances stereoscopic vision, enabling better detection of predators in its open short grass habitats (Yalden, 1975; Yalden and Lagen, 1992; Sumbera et al., 2018).

Case Study 1: African Ice Rat *Otomys sloggetti robertsi*

Ice rats are diurnal herbivores, endemic to the subalpine and alpine regions (>2000 m) of the Drakensberg and the Maluti mountains of southern Africa. They do not hibernate or enter torpor (Hinze et al., 2006). Laboratory experiments by Richter et al. (1997) highlighted three points demonstrating that ice rats are also poorly adapted physiologically to low temperatures. Firstly, their oxygen consumption (VO₂) decreases linearly with increasing temperature between 0.7 °C and 26.0 °C, with the zone of thermoneutrality occurring between 26 °C and 28 °C. Secondly, they can tolerate temperatures higher than those which are experienced in their habitat (e.g. 34 °C in contrast to natural range of 15–23 °C). Thirdly, their metabolic rate was higher than predicted, but thermal conductance was greater than expected, creating a % metabolic rate: % thermal conductance ratio of 0.87, which corresponds to values obtained for many arid/warm-adapted mammals. Richter et al. (1997) concluded that the metabolic rate and greater thermal conductance of ice rats did not appear to be sufficient to counteract the relatively high rate of heat loss at low temperatures. Moreover, their body temperature remained fairly constant even at low temperatures, which is energetically costly, as metabolic rates were almost twice as high at low temperatures than within its thermoneutral zone. Yet, they are locally abundant in Afroalpine habitats in Southern Africa, which warranted further intensive scientific research.

To cope with its challenging Afroalpine environment, ice rats have evolved morphological and behavioral adaptations. They possess a short tail and small ear pinnae to reduce heat loss (Richter et al., 1997). Their fur density of 1000 hairs per cm² potentially reduces heat loss through improved insulation. The fur density of other members of its family (Otomyinae) that live in arid regions is only one-fifth that of ice rats (Rymer et al., 2007). Compared to low elevation otomyines, ice rats have a larger small intestine, caecum, stomach volume and parts of the colon, which are possible adaptations for increased energy uptake and/or poor diet quality in alpine environments (Schwaibold and Pillay, 2003). Interesting seasonal sexual differences have also been observed, with females increasing dimensions of the stomach, small intestine length, caecum, and large intestine in summer. Such changes were absent in males. Morphological plasticity in females is apparently related to increased energy requirements during pregnancy and lactation, in response to poor quality vegetation and a shorter growing season in their alpine habitats (Schwaibold and Pillay, 2003).

Ice rats live in small colonies of 4 to 17 individuals, which collectively construct intricate belowground burrows. These burrows buffer extremes in aboveground temperatures throughout the year and provide opportunities for communal huddling belowground (Hinze et al., 2006). Moreover, their extensive interlinking tunnels provide underground access routes to aboveground feeding sites, thereby reducing exposure to adverse conditions (Hinze et al., 2006). Hinze and Pillay (2006) showed that ice rats have a bimodal diurnal activity profile aboveground in summer, retreating into their burrows during the middle of the day when ambient temperatures and solar radiation levels were at their highest. In contrast, in winter, a unimodal activity profile

was evident. They alter their behavioral profile seasonally by spending more time foraging and basking in winter and remaining belowground in their burrows for longer periods in summer (Schwaibold and Pillay, 2006). Basking, by drawing in the limbs closer to the body and pilo-erecting the fur (Fig. 2), reduces thermoregulatory costs for ice rats (Hinze and Pillay, 2006).

Case Study 2: The Ethiopian Wolf

The Ethiopian wolf *Canis simensis* (Fig. 3) is an Afroalpine specialist, endemic to the Ethiopian highlands above 3000 m (Gottelli and Sillero-Zubiri, 1992). Its diurnal habits and distinctive coat make it conspicuous. The species evolved in the geographically isolated Ethiopian massif, where it became highly adapted to prey on the abundant Afroalpine rodent fauna. Unlike other canids which have a broad diet breadth, its diet is mainly comprised of diurnal rodents, with the giant mole rat (Fig. 4) being the predominant prey (Gottelli and Sillero-Zubiri, 1992). The morphology of their skull reveals adaptations for catching rodents, such as a very elongated skull, long jaws and widely spaced teeth (mainly the premolars) (Clutton-Brock et al., 1976; Yalden and Lagen, 1992; Sillero-Zubiri and Gottelli, 1994). Unlike other pack-living wolf species, the Ethiopian wolf is a solitary forager. It is mainly because of these feeding specializations that they are now on the verge of extinction, as discussed below.

Threats to African Alpine Environment

Like most ecosystems on the planet, Afroalpine habitats are being negatively impacted by human activity and encroachment. Life here is threatened by a combination of serious threats related to loss of habitat and/or habitat change as a consequence of the combined effects of clearing land for farming and land degradation due to livestock grazing. Civil war in several African



Fig. 2 A basking ice rat, drawing in its limbs and pilo-erecting its fur. Courtesy of Neville Pillay.



Fig. 3 An Ethiopian wolf. Courtesy of Charles Sharp.



Fig. 4 A giant mole-rat. Note the close-set, dorsally placed eyes, a consequence of stenocephaly. Courtesy of Will Burrard-Lucas.

countries has also disturbed many Afroalpine habitats. Displaced people may seek refuge at high elevation, destroying natural habitats and supplementing their diets with bushmeat (Tefera, 2011). Ultimately, global climate change will exacerbate some of these already fragile refugia for many species (Tefera, 2011). The loss of biodiversity is likely to occur unabated for the foreseeable future.

The impacts of such environmental changes are not well documented for Afroalpine mammals. Some expected impacts of expanding human population and their livestock are linked to a variety of threats to wildlife. For example, the Northern groove-toothed rat is adapted to humid swamp grasslands in Ethiopia but is now absent in areas which are heavily grazed (Ashenafi et al., 2012). Similarly, an increase in human disturbance has negatively affected the genus *Otomys* (Monadjem, 1997, 1999). In Ethiopia, the mountain nyala and other antelopes compete directly with livestock for food and are usually absent from areas where livestock numbers are high (Brown, 1969).

Clearing of natural Afroalpine vegetation for farming is occurring at an alarming rate (Lemenih and Teketay, 2006; Bogaert et al., 2008; Skarbek, 2008). The Bale monkey *Chlorocebus djamdjamensis*, an arboreal primate endemic to the southern Ethiopian highlands, is susceptible to extinction because of the rapid clearance of bamboo forest; it feeds on the leaves and stems of a single bamboo species (Mekonnen et al., 2010). Consequently, crop raiding and hybridization with other *Chlorocebus* taxa might drive the Bale monkeys to extinction.

More is known about the charismatic Ethiopian wolf whose decline as a consequence of habitat loss and risk of persecution by people has been documented (Yalden and Largen, 1992). These apex predators face a barrage of other threats, including infection by rabies transmitted by domestic dogs (Sillero-Zubiri et al., 1996; Marino et al., 2006). There has also been a marked decline in its rodent prey base, particularly the giant mole rat, whose numbers have been diminishing because of overgrazing of its grassland habitats by domesticated animals (Ashenafi et al., 2012; Busby et al., 2006).

The impact of natural fires in Afroalpine regions has direct and indirect influences on small mammal populations. Some species, such as *Otomys* spp. and *Rhabdomys* spp. in the Afroalpine region of Mt. Elgon, Uganda, benefit from fire-induced habitat changes that turn ericaceous forests into grasslands; frequent fires lead to patchy grassland distribution which confers benefits to *Rhabdomys* spp. (Clausnitzer, 2001).

Fire can kill individuals or make an area uninhabitable due to loss of vegetation and cover (Fuller and Perrin, 2001; Abera and Kinahan, 2011). Humans also use fires to alter Afroalpine habitats. For example, to increase forage for their livestock, herders in Ethiopia and Uganda regularly burn large expanses of *Erica* plants prior to the spring rains to open the landscape and promote germination of vascular plants. Although this practice is presumed to be decades old, historical accounts (e.g. Hedberg, 1971) suggest that it was never as widespread or destructive as it has been in recent years (Wesche et al., 2000). The impact of such burning on mammals in this region is not known.

Little is known about how mammals themselves shape their Afroalpine habitats. In one exception, Mokotjomela et al. (2009) erected enclosure plots to investigate the single or combined effects foraging/burrowing of ice rat and foraging/trampling by domesticated livestock on the vegetation and soil characteristics in their alpine habitats, and whether these activities potentially influence soil erosion (Fig. 5). In this year-long study, ice rats appeared to be a greater contributor to vegetation change and soil movement than livestock. The impact of the species is apparently linked to increased population growth. Ice rat survival depends on the severity of the winters, with persistent low temperatures being detrimental for this physiologically poorly-adapted rodent. The winters have been comparatively mild in recent years, potentially related to global climate change, leading to better over-winter survival of ice rats (Mokotjomela et al., 2009; Pillay and Rymer, 2017). Thus, it is possible that ice rats could alter the ecological balance in the Drakensberg Mountains (Mokotjomela et al., 2009). Nonetheless, a 10-year study by Grab (2012) showed that the impact of ice rats might not be as dramatic because of the episodic spatial shift of ice colonies to new areas of greater foraging potential, allowing for the recovery of previously degraded areas.



Fig. 5 The impact of ice rat behavior on their habitat. Note the collapsed flooded burrow system. Courtesy of Stefan Grab.

Concluding Remarks

The Afroalpine zone represents isolated pockets on mountain tops, stretching over a vast geographic distance. Unsurprisingly, each Afroalpine zone has a unique set of mammalian species, comprised mainly of rodents. Some charismatic species have evolved on these isolated mountains, notably the Ethiopian wolf and giant mole rat. Afroalpine zones contain a large number of endemic mammal species, making them refugia for biodiversity. Thus, the future management of Afroalpine ecosystems are critical for the conservation of endemic species. We relied on the literature, our own experience and input from colleagues to describe Afroalpine mammal diversity. However, cataloguing the Afroalpine mammal diversity and its conservation requires continued focused fieldwork in many countries. Long-term sampling is needed to detect changes in population sizes and the vulnerability of species to extinction. Moreover, focused research on the adaptations of selected Afroalpine mammals, such the ice rat, will provide useful foundational knowledge and also highlight their plight under global climate change. Such research is critical but may prove challenging because Afroalpine zones are often remote and there is a dearth of field biologists working in these zones.

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Asian Alpine Mammals

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Abstract

This article discusses the mammalian wildlife of the alpine regions of Asia. These include about 76 species, ranging from small rodents to large ungulates and their predators. The wild mammals of these regions are a unique, irreplaceable biological resource that deserve our protection. Eight of these species are endangered and two are critically endangered. All highland mammals of Asia face threats from habitat degradation and loss, the impacts of domesticated ungulates, intrusion into formerly pristine highlands by farms, roads, and fences, impacts from hunting, and trapping and poisoning by poachers and herders. The common denominator here is the human population of the Asian highlands, which used to be extremely small and based solely on subsistence farming and herding. It has grown incredibly and now stands at about 40 million. People and wildlife are increasingly coming into contact as the wild spaces decrease, and the human populations grow. This causes conflict as wild animals destroy crops and kill livestock.

Introduction

The countries considered in this article include, from west to east, Uzbekistan, Afghanistan, Pakistan, Tajikistan, Kazakhstan, Kyrgyzstan, India, Nepal, Bhutan, China, southeastern Russia, and northern Myanmar (Fig. 1). These countries are home to numerous mountain ranges, including, from west to east, the Hindu Kush, Pamirs, Karakoram, Tien Shan, Kunlun Shan, the Altai Mountains, and the Hengduan Shan. The Greater Himalayan Range sweeps across northern India, Nepal, Bhutan, and southwest China. To the northeast of this range lies the Tibetan Plateau, the highest major plateau in the world, with average elevations of 5000 m. As shown in Fig. 1, these mountain ranges are extensively glaciated, especially in the eastern regions. The melting of winter snows and glacial ice feeds some of the most important river systems of the continent, including the Indus, the Brahmaputra, the Ganges, the Yangtze, the Yellow River, the Mekong, and the Irrawaddy.

Regional Environments

The alpine regions of Asia are generally inhospitable to vertebrate life. The winters are very long and incredibly cold, with potentially lethal air temperatures persisting for several months of the year. Summers are short, and the length of the growing season decreases with elevation. The growing season in high elevations above treeline average 50–60 days. The highest peaks have only sparse, intermittent plant cover. The short growing season and cold climate lead to a paucity of food resources in the high alpine. Thus, the diversity of plant feeding mammals is low here. Because of the thin air, summer daytime temperatures in the alpine vary greatly, depending on location.

The decrease in air temperature due to increasing elevation shapes many aspects of alpine climate. The temperature lapse rate (TLR) is mainly controlled by the topography and climatology of the region. Mean lapse rate in the Himalayas varies from 0.43°C per 100 m in January to 0.61°C per 100 m in April, with monsoon moisture associated with the lower lapse rates for the region

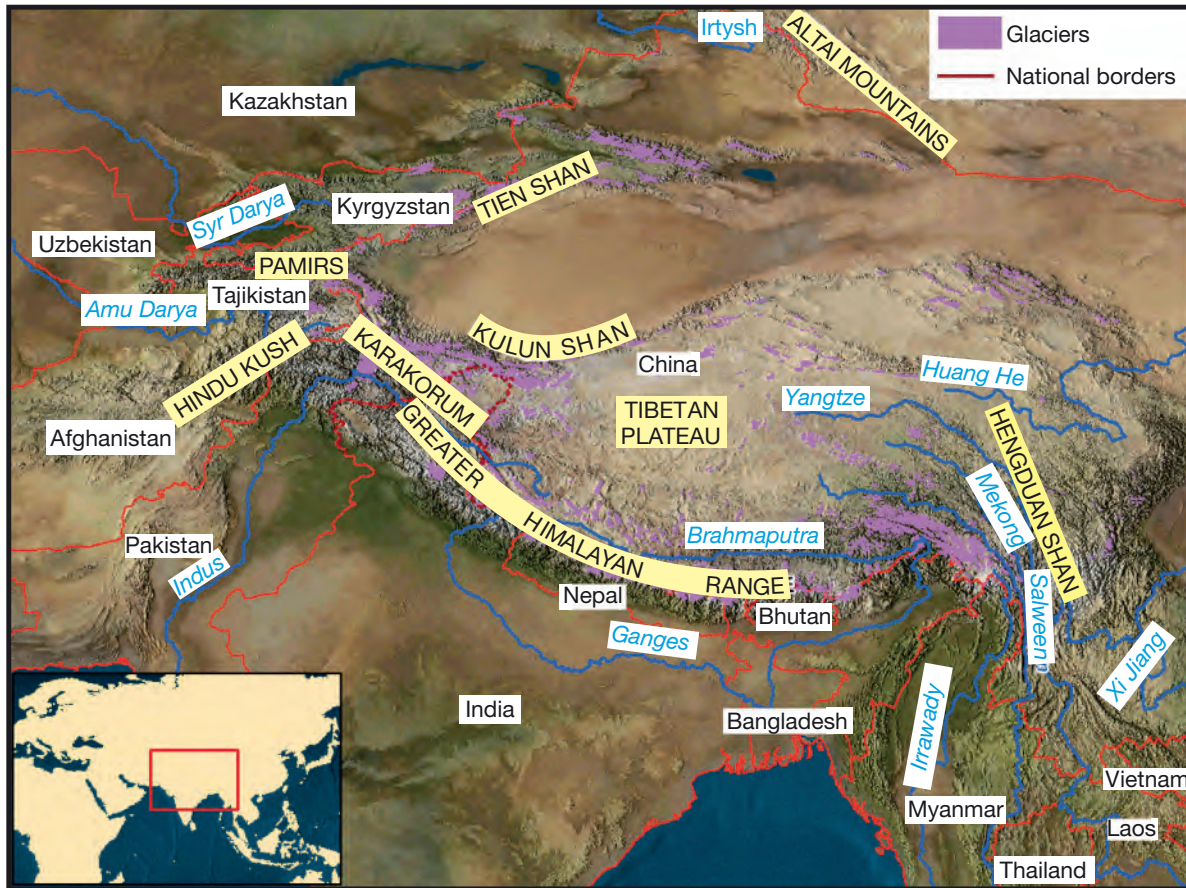


Fig. 1 Map of Asia, showing the countries and mountain ranges discussed in the text.

(Kattel et al., 2013). High mountains in the mid-latitudes of Asia have afternoon temperatures in the summer months that average only about 5–9°C, and many night time temperatures fall below freezing. A weather station at the base camp on Annapurna in the high Himalayas (4130 m above sea level) records minimum temperatures above freezing from May to early September. A weather station at 4794 m elevation on Mount Xixibangma in Tibet shows differences between monthly high and low temperatures of 12–14°C. Here, summer temperatures rise to 17°C, and winter temperatures fall as low as –18°C in February. The wettest, least windy sites are dominated by snow beds, which persist into late summer, leaving behind soils saturated with melt water for a few brief weeks before snowfall resumes.

The Karakoram Range is essentially a desert. The average annual precipitation does not exceed 100 mm. At elevations above 4900 m, precipitation always falls as snow. At heights between 3900 and 5700 m, summer temperatures are lower than 10°C. At elevations of about 5700 m, the average temperature during the warmest month is below freezing.

The climate of the Tien Shan Mountains features extensive areas of permafrost above 2750 m. The maintenance of permanently frozen ground requires average annual temperatures below 0°C for two or more years. The temperature in July at 3200 elevation in the inner Tien Shan averages 5°C, and frost is possible throughout the summer. Winter temperatures of –23°C are common in the alpine regions of the inner Tien Shan; in some localities, especially the Ak-Say valley, winter temperatures fall as low as –50°C.

Human Population of Asian Mountain Regions

The mountainous countries of mid-latitude Asia are home to over 3.3 billion people. This represents 43% of the global population. Of course, only a small fraction of these people live in the mountains of their respective countries, but it is clear that human populations in the mountainous regions of Asia have been growing steadily since the end of the Second World War. At that time, the total population of these Asian countries was 1.1 billion, just one-third of what it is today. Table 1 shows the current and 1945 populations of the eleven countries discussed in this article. Table 2 shows the current populations living in the mountain ranges of those countries. Increasing human populations in these Asiatic mountains pose multiple threats to high elevation mammal populations. These threats include over-hunting of large mammals, competition for grazing from domesticated animals, habitat dissection from roads, fences, farms, villages, and other man-made obstructions, and habitat loss due to changing land-use

Table 1 Human population of the mountainous countries of mid-latitude Asia

<i>Country</i>	<i>Area (km²)</i>	<i>2019 Population (millions)</i>	<i>1945 Population (millions)</i>
Uzbekistan	447,400	32.81	6.45
Afghanistan	652,237	37.21	12.6 (1954)
Pakistan	881,913	197	32.74
Tajikistan	143,100	9.24	1.51
Kazakhstan	2,725,000	18.54	6.44
India	3,287,000	1370	360.1 (1951)
Nepal	147,180	29.94	6.84
Bhutan	38,394	0.83	0.65 (1950)
China	9,597,000	1420	537.53
Myanmar	676,575	54.34	15.65
Russia	17,100,000	143.89	106.0

Table 2 Human population of the mountain ranges of mid-latitude Asia

<i>Mountain range</i>	<i>Area (km²)</i>	<i>2019 population (millions)</i>
Greater Himalayan range	660,000	50
Hindu Kush	232,000	210
Pamir	118,000	0.016
Karakoram mountains	22,600	0.815
Tien Shan mountains	2,592,000	4.1
Kunlun mountains	570,000	0.254
Hengduan mountains	360,000	0.250
Southern Altai mountains	328,000	0.612

practices. Because of population pressures, people are now living at higher elevations in these mountain ranges, and they are extending pastoral rangelands into formerly pristine alpine regions.

Mammals of the Asian Alpine

According to the most recent estimate (Burgin et al., 2018), there are 6400 species of mammals in the world today. Most of these live in the tropical regions, with Brazil ranking first among the nations for greatest number of mammal species (600). The number of mammal species (and most other groups of organisms) decreases towards the poles and with elevation in mountainous regions. This article deals with the mammalian fauna of the Asian alpine region. As shown in Table 3, this region is home to about 76 species of mammals. There is a high degree of endemism in the alpine mammal species of Asia. Endemism refers to a species that is restricted to a particular geographic region as a result of factors such as isolation or in response to abiotic conditions. In the case of alpine mammals, both conditions apply, that is, species living in the alpine are geographically isolated from species in other regions, and they are highly adapted to the rather severe abiotic conditions of cold climate, short growing season, high winds, rocky substrates, and other abiotic factors.

IUCN Classifications

The International Union for Conservation of Nature (IUCN) has established a set of standards to classify the conservation status of wildlife (Table 4). Classifications of more than 98,500 species of plants and animals have thus far been made. The information is made available through the IUCN Redlist web site. This site provides information about range, population size, habitat and ecology, use and/or trade, threats, and conservation actions that help inform conservation decisions by governments and international agencies. Fortunately, most mammal species of the Asian alpine regions are not immediately threatened with extinction, but a few species are critically endangered.

Small Mammals (Fig. 2)

Small mammals, such as voles, shrews, pikas and lemmings, have a very large surface-to-volume ratio. This causes them to lose a great deal of heat to the environment during the winter. Not surprisingly, then, the small mammals of the Asian alpine avoid exposure to winter air temperatures to the best of their ability. Most of them gain protection from winter air temperatures by tunneling beneath the snow. Snow provides excellent insulation from cold air temperatures.

Table 3 IUCN conservation status and ranges of alpine mammals in Asian countries/regions[illegible]

[illegible]

Table 4 Definitions of the IUCN species conservation classification system

<i>IUCN classifications</i>	<i>Definition</i>
Extinct (EX)	Beyond reasonable doubt that the species is no longer extant
Extinct in the wild (EW)	Survives only in captivity, cultivation and/or outside native range, as presumed after exhaustive surveys
Critically endangered (CR)	In a particularly and extremely critical state
Endangered (EN)	Very high risk of extinction in the wild
Vulnerable (VU)	Meets one of the five red list criteria and thus considered to be at high risk of unnatural (human-caused) extinction without further human intervention
Near threatened (NT)	Close to being at high risk of extinction in the near future
Least concern (LC)	Unlikely to become extinct in the near future
Data deficient (DD)	Insufficient information on the conservation status of a species

Information from IUCN (2019). The IUCN Red List of Threatened Species. Version 2019-1. <http://www.iucnredlist.org>.

A study of temperatures beneath snowbanks in Svalbard showed that temperatures beneath just 30 cm of snow remained extremely stable and did not fall below -2°C , even though air temperatures above the snow dropped as low as -24°C (Convey et al., 2015). These stable, near-freezing environments beneath the snow allow some small alpine mammals to remain active during the winter. Tunnels made by small mammals beneath the snow are not only substantially warmer than the air above, they also hold considerable moisture. This relatively warm, moist air helps small mammals avoid both the freezing and desiccation they would face on the surface. Johnsen et al. (2017) examined vole survival in mountain habitats and found that high elevation environments showed greater stability. They had lower temperatures, deeper snow, and longer lasting snow cover than those at low elevations. Thus, perhaps counterintuitively, mild winter conditions contributed to more vole fatalities. Cold conditions, with deep, stable snowpack, enhanced vole survival in high alpine environments, because of improved subnivean conditions.

Voles

The voles of the Asian alpine regions are incredibly diverse, with thirteen species representing six different genera (Table 3). Most of these species are not threatened by population declines or habitat loss, except for two: Royle's mountain vole (*Alticola roylei*) and the burrowing vole (*Hyperacrius fertilis*). These two species are in the "near threatened" category of the IUCN. Royle's mountain vole is decreasing in numbers, chiefly because of habitat loss and fragmentation due to grazing of domesticated animals in the alpine zone. The burrowing vole is threatened by habitat fragmentation, causing small populations to become isolated from each other. Many of the alpine voles of Asia store foods underground in order to survive the winter. For instance, the root vole (*Microtus oeconomus*) begins accumulating food in late September. They store their winter foods in previously excavated underground storerooms, and spend the winter underground, thus avoiding exposure to the extreme cold temperatures at the surface. Snow cover is apparently essential to vole survival in alpine winters. Johnsen et al. (2017) noted the differences in alpine vole survival related to the depth and stability of the snowpack. Vole populations living at high elevations having greater winter survival rates, because the lower temperatures, deeper snow, and longer lasting snow cover in the high country ensure that the voles have better, longer-lasting snow cover than those living at lower elevations.

Ground squirrels and marmots

Unlike some other alpine regions of the world, the Asian alpine is home to only one species of ground squirrel, the Alashan ground squirrel (*Spermophilus alashanicus*). This ground squirrel lives in China and Mongolia. It occupies a wide range of habitats, from the steppe zone and the foothills regions, up to alpine meadows. In China it can also be found in desert habitat. This ground squirrel falls in the "Least concern" category of the IUCN, as its population appears to be stable.

The marmots of the Asian alpine are quite diverse, with four extant species: the Altai marmot (*Marmota baibacina*), the Long-tailed marmot (*M. caudata*), the Himalayan marmot (*M. himalayana*), and the Mongolian marmot (*M. sibirica*). Marmots form part of snow leopard prey. All but the Mongolian marmot are categorized as "Least concern" by the IUCN. The Mongolian marmot is endangered. This is because the population is severely fragmented. *Marmota sibirica* is a social, colonial-living rodent that ranges widely throughout northern Asia. This marmot was once common in Mongolia, but hunting has fragmented its distribution, leading to an estimated 70% decline in population size during the 1990s. Since then, its numbers are believed to have declined even further. In Russia the species is rare and declining. Mongolian hunters kill these marmots for their meat and skins, which fetch high prices now that the species has become rare. The government of Mongolia set limits on the number of Mongolian marmots that could be taken by hunters. However, recent surveys estimate that actual numbers of skins sold exceed the hunting quotas by more than three times. Over 117,000 illegally traded marmot skins were confiscated in 2004. There has been an increase in hunting since the price of pelts increased and factors such as the improvement of roads is providing better access for hunters to find marmot colonies.

The Siberian marmot is often considered a keystone species because its burrows are an important resource for a variety of taxa, including carnivores (Murdoch et al., 2009). Keystone species are species on which other species in an ecosystem largely depend; if the keystone species were removed, the ecosystem would change drastically. Among the species that make use of these marmot burrows in steppe regions is the corsac fox (*Vulpes corsac*). Corsacs regularly make use of marmot burrows. The burrows are thus important resource for foxes, supporting the notion of the Mongolian marmot as a keystone species.



Cricetulus alticola
(Tibetan dwarf hamster)



Microtus gregalis
(Narrow-headed vole)



Alticola argentatus
(Silver Mountain vole)



Ochotona curzoniae
(Plateau pika)



Ochotona thibetana
(Moupin pika)



Ochotona hyperborea
(Northern pika)



Alticola roylei
(Royle's mountain vole)



Alticola stoliczkanus
(Stoliczka's mountain vole)



Marmota sibirica
(Mongolian marmot)



Marmota himalayana
(Himalayan marmot)



Lepus oiostolus
(Woolly hare)



Hemiechinus auritus
(Long-eared hedgehog)

Fig. 2 Photo plate of some of the small mammals of the Asian alpine regions. Photos of *Cricetulus alticola*, *Alticola roylei*, and *Alticola stoliczkanus* by used by permission of Geraldine Werhahn; photo of *Microtus gregalis* used by permission of Arthur Tiutenko; photo of *Hemiechinus auratus* used by permission of Guy Haimovitch. All other photos are in the public domain.

The Himalayan marmot (*Marmota himalayana*) is one of the largest marmots in the world, stoutly built with short legs and a small stubby tail. They weigh up to 9 kg and are up to 67 cm long. The Himalayan marmot is regarded as an ecosystem engineer because of the effect of its burrowing on soil fertility and plant diversity in the mountain ecosystems. Unfortunately, Himalayan marmots are considered pests in parts of the Asian highlands, and in some areas they are killed by farmers. Like the Mongolian

marmot, the Himalayan marmot is also killed for fur and meat. In affected areas, harvesting for illegal trade and lethal control are considered the major causes of decline of marmot populations.

A study of Himalayan marmot habitats by Chaudhary et al. (2017) found that this species most often lives between the upper treeline and the snowline of the highlands of Asia. The maximum number of marmots were observed at elevations above 4000 m. Steep slopes with loose soil are the preferred habitat of these marmots, due to ease in excavation of their burrows. This marmot lives in colonies and excavates deep burrows that colony members share during hibernation. Burrows are up to 10 m deep, depending on soil type. Where soil conditions are ideal on alluvial terraces, marmot colonies comprise up to 30 families, with up to 10 families living in an area of 1 km. This species feeds on plants growing in alpine meadows, in particular the soft parts of grasses.

Su and Liu (2000) studied the overwintering strategies of small herbivorous mammals inhabiting alpine areas of China (Fig. 3). Observations were concentrated on the five most common species: Himalayan marmot, plateau pika, Gansu pika, root vole, and plateau zokor. These animals use three main strategies to survive the winter. The Himalayan marmot was the only hibernator in this group. It hibernates from late September to the mid-April. It therefore did not need to store food for winter. The plateau zokor was the only subterranean rodent among the nonhibernators. It typically starts to store food for winter by the middle of September—the time when juveniles are able to leave their mothers to live separately. Food gathering ends in late October or early November when soils freeze, making further burrowing impossible. Root voles begin to store food in late September. They store winter foods in underground storerooms that have been dug previously, thus avoiding exposure to extreme cold temperatures. Gansu pikas collect and dry herbs (hay making) in late September. They harvest plants and cache them above ground at locations within 1 m of their burrow openings. Plateau pikas that live in meadows store large amounts of forage in hay piles, for later consumption. Interestingly, however, it appears that food limitation in the cold season is not an important factor influencing the mortality rate of pika (Qu et al., 2013).

Why did small herbivorous mammals in the alpine area adopt different wintering strategies? First, the high risk of predation may prevent small mammals from hibernating. Second, fat deposits are needed to survive during both hibernation and posthibernation activity that occurs before new food becomes available in the environment, so small-bodied species cannot afford to practice hibernation because they cannot store sufficient fat deposits to carry them through winter. These factors explain why the Himalayan marmot was the only hibernator in this study. Third, the life history and adaptations of these small mammals play a role in how they overwinter. For instance, the plateau zokor is a nonhibernating subterranean rodent; it lives on the underground parts of plants. If it does not excavate enough tunnels in the soil before winter begins, it will die from starvation because foraging by burrowing in frozen soils is impossible. Fourth, an animal's tolerance to cold, correlated to body size, determines its cold exposure limitations and thus its method of overwintering. This can be used to explain the differences of wintering strategies adopted by plateau pika, Gansu pika, Chinese zokor, and root vole. The differences in feeding strategies of these four small herbivores (Fig. 3) allow them to occupy overlapping territories without directly competing for food resources. The wintering strategies of these animals has been shaped by the long process of natural selection.

Hares and pikas

Only two species of hares are found in the Asian alpine, the woolly hare and the mountain hare. Both species are in the “Least concern” category. The woolly hare is found in China, India, and Nepal. The mountain hare ranges widely throughout northern Eurasia. The conservation status of the woolly hare in Tibet has been examined by Lu (2011). Woolly hares range up to 5500 m elevation in this region, representing the highest distribution of *Lepus* hares in the world. Human activities, mainly livestock grazing, are exerting heavy pressures upon the alpine grassland and meadow ecosystems in Tibet. As a result, natural vegetation has become heavily degraded. However, alpine shrub vegetation persists in protected valleys, allowing woolly hares to survive there. In contrast

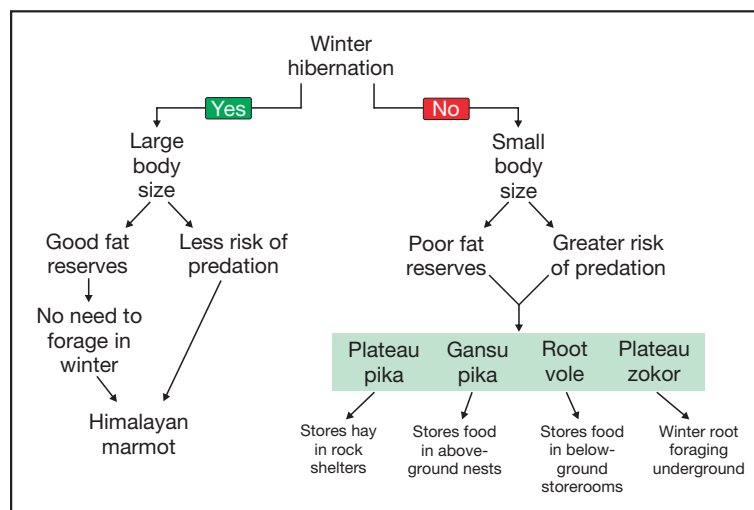


Fig. 3 Overwintering strategies of small herbivorous mammals inhabiting alpine areas of China. Data from Su, J., Liu, J. (2000). Overwinter of small herbivorous mammals inhabiting alpine area. *Acta Theriologica Sinica* 20, 186–192.

to the limited distribution of the woolly hare, the mountain hare ranges from the British Isles to northeastern Siberia, living in both forests and arctic and alpine regions. This species is notable for its fecundity. Adult females are able to give birth to up to 24 leverets (offspring) per year.

The highlands of Asia are the center of origin for pikas. Here they achieve their greatest species diversity: 18 species. Ten additional species live at lower elevations in Asia. By comparison, in North America there are only two species of pika. Of the 18 alpine pika species in Asia, 14 are considered “Least threatened,” one is “Data deficient,” and three are endangered. These include the silver pika (*Ochotona argentata*), the Ili pika (*Ochotona iliensis*), and Kozlov’s pika (*Ochotona koslowi*). According to the IUCN (2019), there are currently only three populations of the silver pika, all from the Ningxia Hui Autonomous Region of north-central China. Populations are declining because of habitat loss. The Ili Pika is endemic to the Xinjiang Autonomous Region of northwest China. It is known only from two spurs of the Tian Shan Mountains and the Ili pika has a highly fragmented distribution within this restricted geographic range. Population declines have been observed for several locations inhabited by this species. Upon its initial discovery in 2005, the Ili Pika was determined to occupy 14 locations: 12 in the north spur of the Tian Shan, two in the south spur. It currently occupies only four of these sites, none of which are in the south spur. Even in occupied localities, the population density is very low and apparently declining. According to Li and Smith (2005) the Ili pika also has a low rate of reproduction. Additionally, populations on its preferred habitat of cliff faces are highly fragmented. Increased temperatures, possibly due to global warming, and increased grazing pressure from domesticated yaks may have interacted with the normal population dynamics of the Ili pika to contribute to its recent dramatic decline.

According to the IUCN (2019), Koslov’s pika was found to be locally abundant as recently as 1999. However, recent surveys have documented severe declines in the number of extant populations as well as overall population density in the remaining studied populations. It is currently known from only ten locations, all in the Xinjiang Autonomous Region of northwest China. Like other pikas, this species reproduces only once a year, producing 4–8 young per litter.

The Plateau pika is considered by Smith and Foggin (1999) to be a keystone species in its habitat (Fig. 4). This is because it makes burrows that turn the soil and thus help soil mixing and aeration, enhanced soil water infiltration, and enhanced seed dispersal, all of which foster greater plant productivity, diversity and abundance. Jiang and Xia (1987) determined that the foraging of plateau pikas may play an important role in the stabilization of alpine meadow plant communities. This species’ old, abandoned burrows become the primary homes to a wide variety of small birds and lizards. It serves as the principal prey for nearly all of the plateau’s predator species. Thus, this pika makes a positive contribution to ecosystem-level dynamics. The burrows constructed by the plateau pika offer breeding habitat for many species. Hume’s ground jay (*Pseudopodoces humilis*) and several species of snow-finch (*Montifringilla adamsi*, *M. blanfordi*, *M. davidiana*, *M. ruficollis*, *M. taczanowski*) all nest mainly in the burrows excavated by this pika. Two species of lizards, including the snow lizard (*Phrynocephalus vlangalii*) and the multiocellated racerunner (*Eremas multiocellata*) use pika burrows for cover and as breeding sites. Taken altogether, the plateau pika serves to increase the biodiversity of the localities where it lives.

Most predators in the Asian alpine, especially on the Tibetan plateau, rely heavily on pikas for food. Pikas are not only the most abundant source of food for predators during the summer, but as pikas do not hibernate, they become almost the sole source of winter food for many predatory species. These predators include steppe polecat (*Mustela eversmanni*) weasels (*Mustela altaica*, *M. eversmanni*), foxes (*Vulpes ferrilata*, *V. vulpes*), and Pallas’s cat. All of these rely heavily on pikas for food. Many larger mammalian predators such as wolves, snow leopards, and brown bears also prey on animals as small as pikas. Snow leopards largely specialize on big game (Mallon et al., 2016), and pikas act only as a buffer species. However, pikas comprise over 50% of the diet of wolves in some areas, and brown bears appear to be particularly reliant on pikas for food. One study in the Chang Tang region found that pikas comprise almost 60% of brown bear diet. Most large predatory birds on the Tibetan plateau depend upon pikas as a food source, including golden eagles (*Aquila chrysaetos*), upland buzzards (*Buteo hemilasius*), saker falcons (*Falco cherrug*), goshawks (*Accipiter gentilis*), black kites (*Milvus migrans*), and little owls (*Athene noctua*).

Large Mammals (Fig. 5)

In contrast to the small mammals, the large mammals have a far smaller surface-to-volume ratio, so they lose much less internal metabolic heat to the environment. Many of these larger mammals remain active in the winter, such as the yak, chamois, wild sheep, ibex, deer, and their predators. Their exposure to low winter temperatures is not without cost, however. All of these animals lose weight through the cold months. Grazers must continue to forage for food throughout the year, in order to maintain the gut micro-organisms that are essential to their digestion. Snow conditions are critical to the health and survival of grazing mammals in the alpine. When snow cover is too deep, many grazers may starve before the end of the winter season.

Bovids, gazelles, and wild yaks

Of the fourteen species in this group of even-toed ungulates, four are considered “Vulnerable” and one is considered “Endangered” by the IUCN. Six other species are in the “Near threatened” category, making a total of 11 out of 14 species that are under some level of threat to their existence. There are multiple threats posed to these grazers. They have all been extensively hunted for their meat and hides. The horns of some species have been sought by trophy hunters. These grazers are also under threat from grazing competition from farm animals, especially the domesticated yak. According to the World Wildlife Fund (2019), habitat loss is also extensive in the Asian alpine regions. Over 75% of primeval Himalayan habitat has been destroyed or degraded. Fuelwood and fodder collection have damaged subalpine forests and alpine grasslands. In addition to wild grazers having to compete with domesticated animals for food, extensive livestock grazing in alpine meadows has permanently altered plant community composition.



Fig. 4 The Plateau pika is a keystone species in its habitat. Data from by Smith, A.T., Foggin, J.M. (1999). The plateau pika (*Ochotona curzoniae*) is a keystone species for biodiversity on the Tibetan plateau. *Animal Conservation* 2, 235–240.

In the past 100 years, the population of wild yaks has declined rapidly due to human activities (Table 5). There are four major anthropogenic activities that threaten the long-term survival of wild yaks (Shi et al., 2016). The first is excessive hunting. Poaching, including commercial poaching, has always been regarded as the most serious threat to wild yaks, especially for male yaks. Since the mid-1950s, highway construction has facilitated access of commercial poachers to wild yak's populations, increasing the hunting pressure and the threats to wild yaks. Between 1958 and 1961, a large team hunted wild yaks in the area of Yoniugou and elsewhere in Qinghai Province, China, that killed at least 40,000 mammals. To this day, the populations of wild yaks and other wildlife in these regions have not recovered. The extent of poaching has declined in recent decades. However, increasing numbers of human-wildlife conflicts due to resource competition has increased the extent of retaliatory killing. Owners of domesticated grazers (yak, horse, donkey, sheep, and goats) kill wild yaks that compete with their livestock for grazing access. In addition to causing human-wildlife conflict, competition for forage resources has led to habitat destruction and fragmentation, causing reduced gene flow between populations. Studies have found that wild yaks probably need larger ranges than other wild ungulates, with limited or no human disturbances. Roads are also a major obstacle to wild yak migration.



Bos mutus (Wild yak)



Hemitragus jemlahicus (Himalayan tahr)



Budorcas taxicolor (Takin)



Ovis ammon (Argali)



Naemorhedus griseus (Chinese goral)



Pseudois nayaur (Bharal)



Capra falconeri (Markhor)

Fig. 5 Photo plate of some of the ungulates of the Asian alpine regions. Photo of *Bos mutus* used by permission of George Schaller; photo of *Hemitragus jemlahicus* used by permission of Klaus Rodloff; photo of *Pseudois nayaur* used by permission of Brent Hoffman. All other photos are in the public domain.

Table 5 Estimated numbers of wild yaks in Chinese provinces

Province	Total area (km ²)	Estimated population size
Gansu	454,430	130
Qinghai	721,000	3200–3700
Tibet	1,202,369	7157–8761
Xijiang	1,660,000	10,000

Data from Shi, Q., Guo, Y., Engelhardt, S.C., Weladji, R.B., Zhou, Y., et al. (2016). Endangered wild yak (*Bos grunniens*) in the Tibetan plateau and adjacent regions: Population size, distribution, conservation perspectives and its relation to the domestic subspecies. *Journal for Nature Conservation* **32**, 35–43.

The dwarf blue sheep (*Pseudois nayaur schaeferi*) is a critically endangered subspecies of the blue sheep, found only in China (Upper Yangtze Gorge in west Sichuan and adjacent parts of Tibet and north Yunnan). The population has declined by more than 50% in the last 10 years. Although protected by the Chinese government, this sheep continues to be hunted by poachers. In fact, the hunters themselves report that the numbers of this subspecies had fallen drastically. Previously observed group size ranges of 10–36 animals have dropped to 3–6 animals in recent years.

The Himalayan tahr (*Hemitragus jemlahicus*) lives along the Himalayan range from northwest India through Nepal to Sikkim, and localities along the western Chinese border. This bovine inhabits steep rocky mountain sides, around the treeline and forest edges from 2500 to 4000 m. The species is considered to be declining, and it is assessed as Near Threatened on the IUCN Red List. The tahr is important prey for snow leopard populations in Nepal.

Cervids: Deer, elk, and moose

Numbers of both the alpine musk deer and Himalayan musk deer are declining rapidly because of the demand for their musk—a secretion from the caudal gland of male musk deer. Musk is used in fragrances and perfumes and in Chinese folk medicines. Data on musk purchased by local traditional Chinese medicine companies suggest dramatic declines in Chinese musk deer populations since the 1970s and 1980s. In protected areas of Nepal, musk deer numbers are reportedly increasing, with upwards of 2500 individuals in national parks. Outside of protected areas the species is declining.

Predators (Fig. 6)

Predators of the Asian alpine regions include the family Felidae (cats, lynx, tiger, and snow leopard), Canidae (wolves, foxes, jackals, and dhole), Mustelidae (badgers, weasels, and wolverine), and Ursidae (bears). Nine out of the fifteen species of predators are under some level of threat in Asia, according to the IUCN. As with the large mammals discussed above, habitat loss, over-hunting, and retaliatory killing have taken their toll on predator species' populations. An additional hazard to predators is the decline in numbers of their prey species.

Felidae (cats, lynx, tiger, and snow leopard)

The Chinese mountain cat is a small cat, about the size of the domesticated cat. It lives only in the Chinese provinces of Xinjiang, Qinghai, and Gansu. Its numbers are thought to be less than 10,000 individuals. Ironically, one the main causes of decline for this species is accidental killing through the use of poisons to control rodents. It is also suffering from trapping and hunting for the illegal fur trade. The IUCN lists it as "Vulnerable."

In the Asian highlands there is a subspecies of lynx known as the Tibetan lynx. While numbers of the Tibetan lynx are strong in China (more than 27,000), the species is considered "Vulnerable" further west in Uzbekistan. It is found along the northern slopes of the Himalayas, and has been reported from barren, rocky areas above the tree line, as well as in forested regions.

Pallas's cat is very wide ranging in Asian highlands, from Iran east to the mountains of China. Like the Chinese mountain cat, Pallas's cat is about the size of a domesticated cat. This cat is very secretive in habit. Pictures of Pallas's cat have only been taken within the last decade, through the use of camera trapping surveys. Pallas' cats are ambush hunters that stalk their prey using short vegetation and rocky terrain for cover. They also wait at entrances to burrows and pounce when their inhabitants exit. Pallas' cats prey mainly upon pikas and other small rodents, and birds. Populations of this species have declined because of habitat degradation, decline in prey numbers, and hunting. It is classified as Near Threatened by the IUCN.

The snow leopard is another cat that is rarely seen by people. These large cats are sparsely distributed over the mountainous regions of 12 countries in Central Asia. They take a wide variety of prey (Table 6), but their main prey animals are the large, wild ungulates that live in the snow leopard's range. Chetri et al. (2019) studied snow leopard populations in Nepal. The global snow leopard population size has been estimated between 4678 and 8745 individuals. However, this is only a rough estimate. To date, less than 2% of the global snow leopard distribution range has been sampled systematically, and surveys have often focused on prime habitats. They are extremely elusive and challenging to survey. However, new research, including camera trapping, is starting to indicate there may be more cats than previously thought.



Panthera uncia (Snow leopard)



Gulo gulo (Wolverine)



Otocolobus manul Pallas' cat



Mustela altaica (Mountain weasel)



Lynx lynx isabellinus (Tibetan lynx)



Canis aureus (Golden jackal)

Fig. 6 Photo plate of some of the predators of the Asian alpine regions. Photograph of *Gulo gulo* courtesy of Corel Corporation; photo of *Otocolobus manul* used by permission of Ben Williams, ISEC Canada; photo of *Mustela altaica* used by permission of Geraldine Werhahn; photo of *Lynx lynx* used by permission of Vladimir Motyčka; photo of *Canis aureus* used by permission of Carlo Galliani.

The main threats to the snow leopard are poaching, retaliatory killings due to livestock loss, declines in prey species numbers, degradation of habitat due to developmental activities (e.g., mining, dams, roads, railway lines, etc.) and global climate change. Blue sheep, Siberian ibex and Marco Polo sheep provide almost 50%–60% of the biomass consumed by the large carnivores of the Asian highlands, including the snow leopard, wolf, brown bear, and lynx. As discussed above, hunting of these alpine sheep is not only legal in countries such as Mongolia, Kyrgyzstan and Tajikistan, it is actively encouraged as a source of much-needed revenue.

Snow leopard pelts are very valuable, and even though killing snow leopards is illegal in the twelve Asian countries where it lives, this trade persists (Fig. 7). It is almost impossible to enforce the antipoaching laws in the snow leopard's remote mountain habitat. Snow leopard poaching in Russia was recently alleviated in several important areas. This was done through a concerted government effort to remove wire-snare from the landscape, and through the recruitment of former poachers as wildlife rangers in protected areas. Anti-poaching efforts in Tajikistan, Kyrgyzstan, and Kazakhstan have also been strengthened, thus addressing the main underlying threat that led to the drastic decline in numbers in several Central Asian states (Snow Leopard Trust, 2019).

Table 6 Species recorded in snow leopard diet

<i>Common name</i>	<i>Scientific name</i>
<i>Mammals</i>	
Siberian ibex	<i>Capra ibex</i>
Markhor	<i>Capra falconeri</i>
Blue sheep (bharal)	<i>Pseudois nayaur</i>
Himalayan tahr	<i>Hemitragus jemlahicus</i>
Argali wild sheep	<i>Ovis ammon</i>
Ladakh urial	<i>Ovis orientalis</i>
Elk (red deer)	<i>Cephus elaphus</i>
White-lipped deer	<i>Przewalskium albirostris</i>
Siberian roe deer	<i>Capreolus pygargus</i>
Musk deer	<i>Moschus</i> spp.
Moose	<i>Alces alces</i>
Goitered gazelle	<i>Gazella subgutturosa</i>
Wild ass	<i>Equus hemionus</i>
Wild boar	<i>Sus scrofa</i>
Wild camel	<i>Camelus ferus</i>
Himalayan marmot	<i>Marmota himalayana</i>
Altai marmot	<i>Marmota baibacina</i>
Long-tailed marmot	<i>Marmota caudata</i>
Menzbier's marmot	<i>Marmota mensbieri</i>
Red squirrel	<i>Sciurus vulgaris</i>
Tien Shan ground squirrel	<i>Sciurus relictus</i>
Royle's mountain vole	<i>Alticola roylei</i>
Pika	<i>Ochotona</i> spp.
Royle's pika	<i>Ochotona curzoniae</i>
Tolai hare	<i>Lepus tolai</i>
Arctic hare	<i>Lepus timidus</i>
Desert hare	<i>Lepus tibetanus</i>
Woolly hare	<i>Lepus oiostolus</i>
Red fox	<i>Vulpes vulpes</i>
Stone marten	<i>Martes foina</i>
Yellow-throated marten	<i>Martes flavigula</i>
Least weasel	<i>Mustela nivalis</i>
Common palm civet	<i>Paradoxurus hermaphroditus</i>
Eurasian badger	<i>Meles meles</i>
Brown bear	<i>Ursus arctos</i>
<i>Birds</i>	
Snowcock	<i>Tetraogallus</i> spp.
Rock ptarmigan	<i>Lagopus mutus</i>
Chukar	<i>Alectoris chukar</i>
Pheasants	Phasianidae spp.
Pigeons	Columbidae spp.

Data from Mallon, D., Harris, R.B., Wegge, P. (2016). Chapter 4: Snow leopard prey and diet. In: McCarthy, T., Mallon, D. (eds.), *Snow Leopards*, pp. 43–55. Amsterdam: Elsevier.

Canids (*wolves, foxes, jackals, and dhole*)

The Tibetan wolf (*Canis lupus chanco*) is a subspecies of the gray wolf (*Canis lupus*). The Tibetan wolves are distinct from their European and North American counterparts because of the coloration of their fur. Tibetan wolves have been hunted, trapped, and poisoned in the Asian highlands for many decades. Nevertheless, they remain an important predator in alpine ecosystems of the Himalaya and Tibetan Plateau. The efficiency of wolves in taking large prey animals and the increasing levels of encroachment of yaks, goats, sheep and other domesticated ungulates into the alpine means that conflict with livestock herders is inevitable. Wolf predation on livestock is very costly to the herder. For instance, when wolves kill a domesticated yak, the herder suffers a loss of almost \$1000. This may lead to retribution killings, even in countries where the wolf is legally protected, such as Nepal. Wolves that live in wildlife sanctuaries and preserves may receive protection, but as pack sizes increase, small groups wander away from the protected areas. Wolves in this region are listed as critically endangered in IUCN Red List.

Dholes are a kind of wild dog that is a generalist carnivore. Their favorite prey is the wild boar, followed by barking deer, musk deer, blue sheep, goral, and pika (Aryal et al., 2015). Like wolves, dholes have been systematically hunted, trapped, and poisoned throughout their range in the Asian high country, due to their preying on livestock. The IUCN reckons that there are only about 950–2200 dholes today. They fall into the “Endangered” category because of such small numbers. The subspecies known as the Ussuri dhole exists in small, isolated populations in Bhutan, China, India, and Nepal.

Tibetan sand foxes are native to the Ladakh plateau of northern India and to the Tibetan Plateau and adjacent regions of China. They primarily prey on Plateau pikas, and are known to cooperate in pika hunting with brown bears. The bears dig the pikas out of their burrows, and the foxes catch any pikas that manage to elude the bears. This fox has healthy populations, and considered “Least threatened” by the IUCN.

Family mustelidae (*weasels, wolverine, and badgers*)

The mountain or Altai weasel is a small, agile hunter that feeds primarily on pikas and voles. It hunts mainly at night. During the day it seeks shelter in rock crevices and the abandoned burrows of other animals, including the burrows of the animals it has killed. It ranges across Kazakhstan, northern India, Tibet, Mongolia, northeastern China, and southern Siberia. Overgrazing of alpine vegetation by cattle, goats, and sheep has caused declines in the voles and pikas, thereby threatening its food base. Reduction in the weasel’s prey has also been caused by the poisoning of pikas. Herders put out poison for pikas because they compete with livestock for alpine grasses and wild flowers. If a weasel scavenges a poisoned pika carcass, it may be killed by the same poison. Finally, Altai weasel numbers follow the fluctuations of their prey, especially voles, whose numbers vary by a factor of four to five times from year to year.

Multi-Country Conservation Efforts

There are many common threats to the wildlife of the Asian alpine regions, from voles and pikas to wild yaks and snow leopards. The common problems include habitat degradation and loss, the impacts of domesticated ungulates, intrusion into formerly pristine highlands by farms, roads, and fences, impacts from hunting, and trapping and poisoning by poachers and herders. The common denominator here is that human populations of the Asian highlands, which used to be extremely small and based solely on subsistence farming and herding, have grown incredibly. For instance, the human population of the Himalayan region tripled from 11 to 33 million between 1901 and 1981, with the rate of increase accelerating after 1951, and now stands at about 40 million.



Fig. 7 Photo of snow leopard skins being sold in a market in Tibet, used by permission of Brenda Turnidge.

People and wildlife are increasingly coming into contact as human populations grow. This causes conflict as wild animals destroy crops and kill livestock (World Wildlife Fund, 2019). What can be done to protect the remaining wildlife of the region?

One answer is the development of international cooperation among the Asian highland countries. A recent project is called the Kangchenjunga Landscape Conservation and Development Initiative (KLCDI). Stretching along the southern side of Mount Kangchenjunga, India, the Kangchenjunga Landscape (KL) is one of the six transboundary landscapes identified by the International Centre for Integrated Mountain Development (ICIMOD) in the Hindu Kush Himalayan (HKH) region. It covers an area of 25,081 km² and spreads across part of eastern Nepal, Sikkim, and West Bengal of India and the western and south-western parts of Bhutan (Fig. 8). At the heart of this landscape lies Mount Kangchenjunga (8586 m), the third highest peak in the world. This region sustains many of the vital Himalayan rivers and crucial watersheds. With 19 established protected areas, comprising 30% of

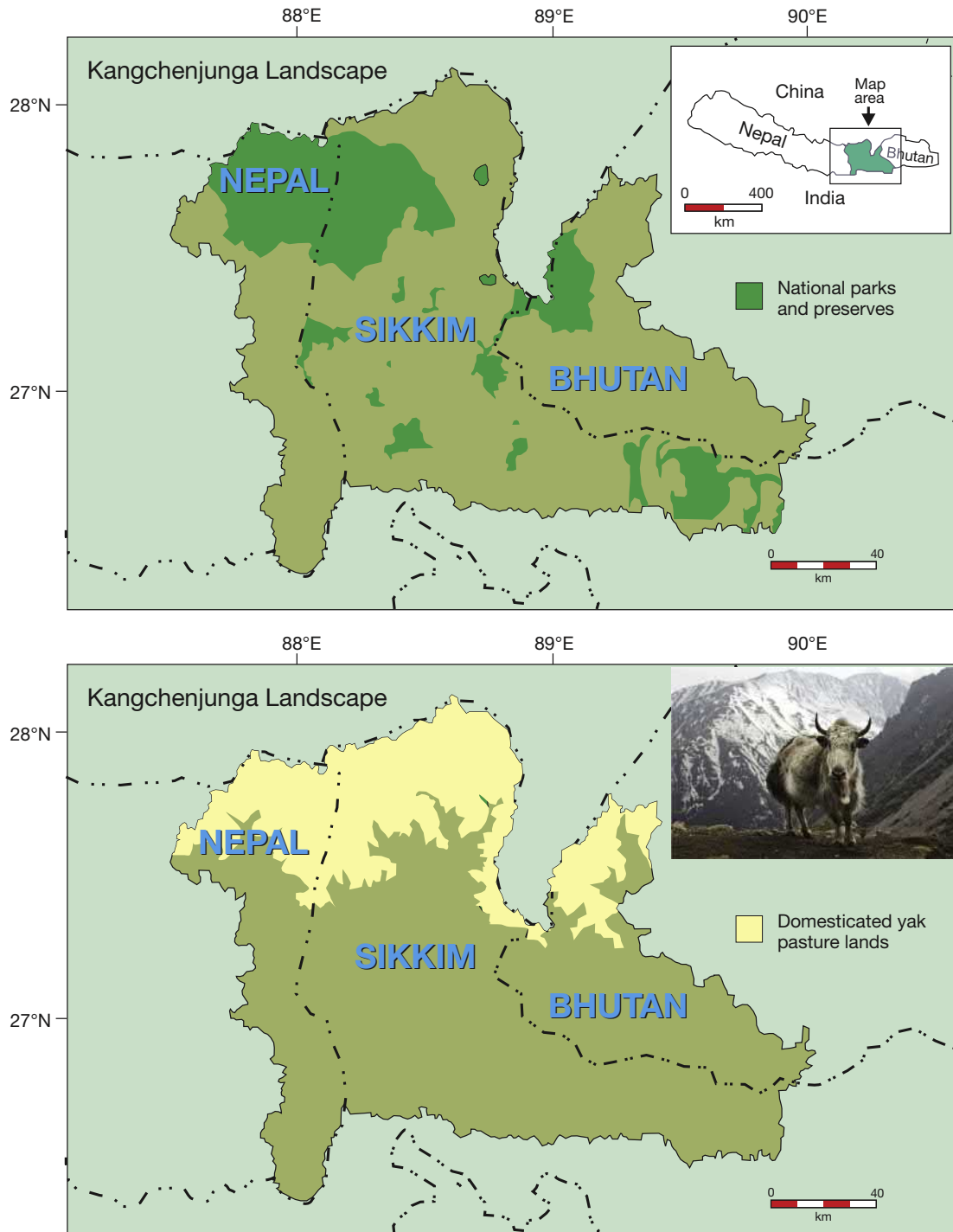


Fig. 8 Maps of eastern Nepal, Sikkim, and West Bengal of India and the western and south-western parts of Bhutan, showing the national parks and preserves that make up the Kangchenjunga Wildlife Preserve, showing national park and preserve regions (above) and the regions grazed by domesticated yaks (below). After Kangchenjunga Landscape Conservation and Development Initiative (2019). <http://www.icimod.org/kl>—KLCDI home page website.

the landscape, the KL contains more than 4500 plant species, more than 160 mammal species, 580 bird species, and 600 butterfly species. The landscape serves as a contiguous habitat for many umbrella and charismatic species including snow leopard, takin, Himalayan black bear, and Himalayan musk deer. It is also home to 7.2 million people (KLCDI, 2019).

From 2012 to 2015, the Kangchenjunga Landscape Conservation and Development Initiative (KLCDI) produced a feasibility study of trans-boundary initiatives, conservation and development strategies, and a regional cooperation framework. The implementation phase began in 2016. It has focused on common issues and opportunities such as community-based tourism, value chain developments for livestock and various cash crops, regional cooperation to minimize human wildlife conflict and illegal trade, the development of common research protocols and methods to promote science, policy, and practice interface.

More than 20% of the KL is rangeland, and animal husbandry is deeply embedded in the regional cultures and is the main source of livelihoods for the people of high elevations in Bhutan, Sikkim, and eastern Nepal. One of the most important aspects of the KLCDI has been to find ways to sustain this way of life while preserving or expanding vital wildlife habitat in this region.

The basic precepts of the KLCD initiative face the reality that the people who now live in the Asian highland regions are there to stay, and that they are not going to abandon their traditional way of life, which centers on livestock farming. Thus, the emphasis for wildlife conservation must be to preserve as much of the remaining wilderness as possible while developing ways to diversify the livelihoods of the people who live close by. Such initiatives must involve the cooperation of multiple nations, as the KLCD initiative has done.

The wild mammals of the Asian alpine are a unique, irreplaceable biological resource that deserve our protection. As of this writing, we stand on the cusp of major decisions concerning their conservation. If the peoples of the world, and more particularly the people who live and around the Asian highlands, make determined efforts to preserve this fauna, then it can survive. If conservation issues are ignored, postponed, or weakened because of political pressure, then large numbers of Asian alpine species will very likely become extinct within the next few decades.

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Alpine Birds of South America

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Abstract

In South America, “alpine birds” are those bird species inhabiting the High Andes (> 2500 masl). The study of this group has progressed from the inventories and catalogues of expeditions led by 19th-century European naturalists to ecological studies of their distribution, work which has enabled the production of country-specific field guides allowing for continued study by new generations of local researchers and amateurs alike. There are six predominant Andean ecosystems that alpine birds of South America inhabit: *Paramo*, *Puna*, high-Andean wetlands and water bodies, high-Andean forests, human-modified areas and glaciers. Here, we describe high-Andean bird diversity according to its distribution throughout these six ecosystems and discuss threats to bird populations and conservation approaches. Altogether, these habitats host a species-rich group of 945 species, composed of both resident and migratory species, generalists and also highly specialized, endemic birds. Because many are specialized, mountain-top species, adapted to live within narrow elevational ranges and climatic conditions, one of the greatest conservation concerns facing South American alpine birds is the threat posed by climate change. Although upslope migration appears to be a viable strategy for some species, there is also evidence that others, especially many endemic mountaintop species, could become locally extinct as a consequence of global change. The decoupling of species-habitat and other ecological relationships that could arise from altitudinal migration may be particularly serious for highly specialized birds of *Paramos*, *Polylepis* forests, and wetlands. Due to the high vulnerability of South American alpine birds to climate change, it is important to undertake actions for the conservation and restoration of the ecosystems on which they depend as habitat, ranging from legal protection to education.

Introduction

To speak about alpine birds of South America is to speak of the birds of the High Andes. Ranging from Venezuela to Patagonia, the Andes are recognized as the most latitudinally-extensive tropical mountain range in the world (Fig. 1) (Borsdorf and Stadel, 2015) and as one of the most biodiverse areas in the world (Myers et al., 2000). The complex topography, with altitudinal gradients exceeding 6000 m, shapes interactions among biotic, climatic and environmental factors, promotes high rates of speciation, and provides habitat for many species endemic to the Andes (Terborgh and Weske, 1975). Not only is within-site, or alpha, diversity high, but the Andes also has a high turnover of species (beta diversity) and ecosystems along elevational and altitudinal gradients (Borsdorf and Stadel, 2015). As one traverses elevational or latitudinal gradients, restricted-range, sister species are commonly encountered, as they replace each other. For these reasons, as many as 900 bird species can be encountered along some Andean elevation gradients, such as the Manu Road (300–3100 masl), Mayo Valley and Abra Patricia in Peru.

In this chapter, we discuss alpine birds of South America from an ecological perspective applied to conservation. After a brief introduction to the history of these studies, we define these alpine birds according to their relationship to six main high-elevation ecosystems. In each ecosystem, we explore general aspects of the associated bird community, highlighting what we consider the most relevant and interesting information for general knowledge and conservation. Finally, we discuss the conservation concerns of alpine birds of South America in the context of climate change.

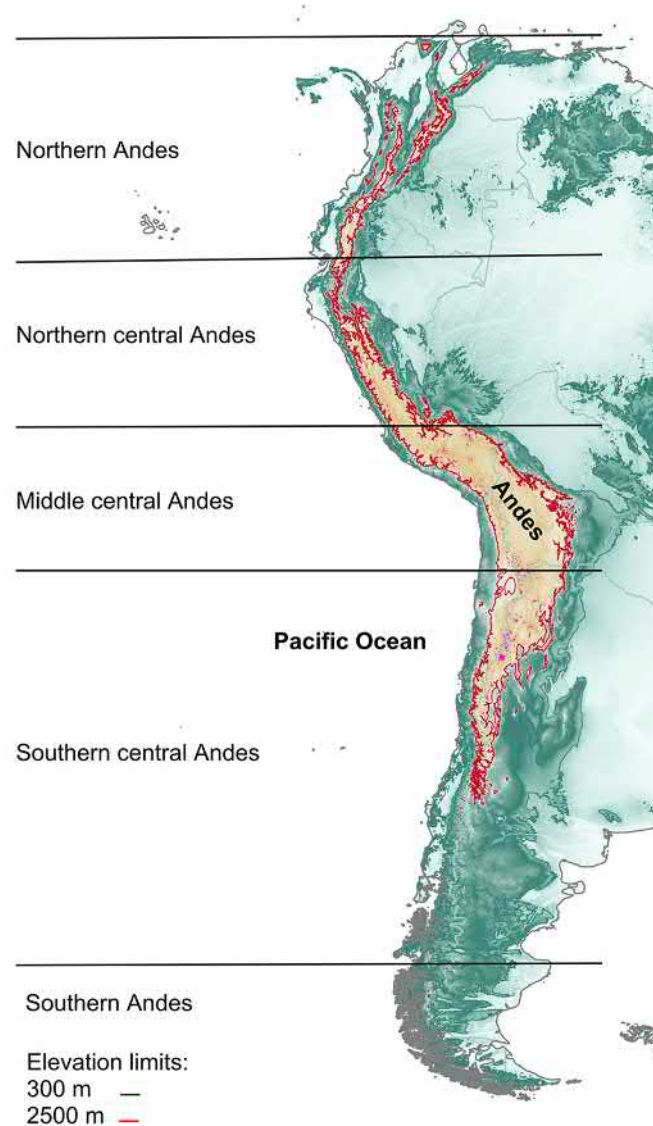


Fig. 1 Map of the Andes with the five main latitudinal regions. The red line define the bottom limit of the High Andes (2500 m). Based on Tanner, H. (1978). *Sudamerika*. Band 1: Andenstaaten. Braunschweig; Borsdorf, A. and Stadel, C. (2015). *The Andes: A geographical portrait*. Switzerland: Springer.

History of Alpine Birds of South America

The study of Alpine birds of South America began with the expeditions of European naturalists during the early 19th century. In 1802, German naturalist and explorer Alexander von Humboldt commenced the first expedition, in which he described and collected specimens across much of the northern Andes. His work includes iconic interpretations and illustrations of the pattern of replacement within plant and animal communities along the slopes of Ecuador's Chimborazo volcano. Later, French, Swiss and Polish naturalists collected thousands of bird specimens throughout the High Andes of Chile, Bolivia and Peru although these were not more thoroughly explored until the late 19th century and early 20th century. Thomas Oldfield and Perry O. Simmons, led some of the main expeditions, collecting a large number of specimens throughout the Andes of Ecuador, Peru, Bolivia and Argentina. Likewise, Frank Chapman and Melbourne Armstrong Carriker, Jr. collected and independently described several high-elevation bird species in the Santa Marta region and the three main ranges (Cordillera Occidental, Central and Oriental) of Colombia and the high mountains of Ecuador, Peru and Bolivia. Many of these species are recognized as endemic and highly specialized species to specific ecosystems (e.g., *Anairetes alpinus*) (Fjeldså and Krabbe, 1990). Other ornithologists that improved our knowledge of alpine bird diversity, including John Todd Zimmer (1889–1957), James Bond (1900–89), and Rodolphe Meyer de Schauensee (1901–84) working mainly in Ecuador, Peru and Bolivia.

During the second half of the 20th century and beyond, the most notable advances were made in the new ecological study of species distributions. Around 1969, François Vuilleumier (1938–2017) pioneered the ecological, evolutionary and biogeographical study of alpine birds and elucidated how mountains act as both as biogeographical barriers and as chains of “islands” that shape speciation processes similar to those occurring in archipelagos (Vuilleumier and Monasterio, 1986). At the same time, John Terborgh began intensive studies to understand how biotic, climatic and environmental factors explain high-elevation bird diversity along elevation gradients in Peru (Terborgh, 1977). Nevertheless, expeditions to unexplored high-elevation areas continued, improving our knowledge of distributions, sometimes describing new species, and allowing for the collection and study of bird vocalizations. For example, Maria and Hans-Wilhelm Koepcke described the White-cheeked Cotinga (*Zaratornis stresemanni*), an endemic frugivore and one of the few altitudinal migrants at high elevations. Ted Parker’s new and extensive song collection from along the entire Andes supplemented the knowledge of high-Andean birds. Collectively, this body of work became foundational papers for the understanding of alpine bird ecology worldwide.

An important milestone in the progress of South American Alpine ornithology was the development of field guides for amateur and professional ornithologists. In 1990, John Fjeldså and Niels Krabbe, based on their extensive experience in the High Andes, published the “Birds of the High Andes,” describing ~1100 bird species, including some previously unnamed species together with ~2000 illustrations, and information-rich distribution maps. More recently, the publication of several bird field guides by country, such as the Birds of Venezuela; Birds of Colombia; Birds of Ecuador; Birds of Peru; Birds of Bolivia and Birds of Chile has supported the development of a new generation of Latin American biologists, ecologists and ornithologists interested in the study and conservation of South American Alpine birds and the ecosystems they depend on.

Alpine Birds of South America and Their Ecosystems

For this chapter, we define “alpine bird” as a species that inhabits one or more high-elevation (>2500 masl) mountain ecosystems in South America (Fig. 1). According to the elevational ranges compiled by Quintero and Jetz (2018), 945 bird species (in 385 genera and 61 families) distributed throughout Venezuela, Colombia, Ecuador, Peru, Bolivia, Chile and Argentina, meet this definition (Supplementary Table 1 in the online version at <https://doi.org/10.1016/B978-0-12-409548-9.11806-8>). Because Andean ecosystems are shaped by different climatic regimes and topographic relief (Borsdorf and Stadel, 2015), they are useful biological and ecological units around which to organize our discussion of alpine birds of South America. Therefore, we focus this chapter on alpine bird diversity associated with six main ecosystems: *Paramo*, *Puna*, high-Andean wetlands and water bodies, high-Andean forests, areas modified by human activities, and glaciers. A summary of these species by country and the six ecosystems are included on the Supplementary Table 2 in the online version at <https://doi.org/10.1016/B978-0-12-409548-9.11806-8>.

Paramos

Paramo is a grassland-shrubland ecosystem found between ~3000–5000 masl from Venezuela to northern Peru (Fig. 3) in areas that are humid year-round, with >3000 mm of annual precipitation, and that lack strong seasonality (Rundel et al., 1994). *Paramo* is dominated by tussock grasses (primarily *Festuca* and *Calamagrostis* spp.) and rosette plants and is often distinguished by abundant stemmed rosette plants of *Espeletia* spp. (*frailejones*), which are missing from the central and southern Andes (Balslev and Luteyn, 1992). In their middle elevations, *Paramos* are also characterized by their deep, organic-rich humic or volcanic soils that hold large amounts of water (Balslev and Luteyn, 1992).

Although a number of studies have described avifauna associated with *Paramo*, the total number of species remains uncertain. Prior studies have reported anywhere from 32 to 40 species belonging to 15 families and 8 orders in Ecuador (Koenen and Gale, 2000), to 60 bird species, including 29 *Paramo* specialists, in Venezuela, Colombia and Ecuador, to 79 resident species and 67 occasional visitors or migrants in Venezuela (Diaz et al., 1997). At the higher end of species richness, Chaves and Arango (1998) reported 129 bird species, from 84 genera and 31 families, in the Colombian *Paramos*, whereas Krabbe et al. (2006) reported 155 bird species from Colombia.

Both resident and migratory species use *Paramo*. About 30 migratory species, including Lesser Yellowlegs (*Tringa flavipes*), Least Sandpiper (*Calidris minutilla*), and Killdeer (*Charadrius vociferus*), use the Andes as a migratory corridor and stopover in *Paramos* to rest or replenish fuel reserves. A wide range of resident species that reflect various foraging strategies and adaptations to high-elevation environments occur in *Paramo* (Diaz et al., 1997), with ground insectivores and hummingbirds being most numerous and distinct. The coloration and behavior of many *Paramo* birds reflects their environment and enables camouflage and avoidance of predators (e.g., ground nesting, skulking and obscure movements) (Fjeldså and Krabbe, 1990). Common residents include the *Paramo* Pipit (*Anthus bogotensis*); *Paramo* Tapaculo (*Scytalopus opacus*); *Paramo* Seedeater (*Catamenia homochroa*); Chestnut-winged Cinclodes (*Cinclodes albidiventris*), and Ash-colored Tapaculo (*Myornis senilis*), among others.

Hummingbirds have developed specific adaptations to exploit the *Paramo* resources. Snow (1983) observed that hummingbirds specialize on different species of *Frailejon* (*Espeletia* spp.) by using their unusually short beaks and long legs to perch and feed on the nectar and on insects that are often trapped in the water that accumulates in these plants. Hummingbirds also have respiratory adaptations that allow them to fly in hypoxic conditions (i.e., at high elevations) (Altshuler and Dudley, 2006). Many of these species are endemic to specific mountain ranges while others migrate seasonally to lower elevations during the dry season. Some endemic species include: the Ecuadorian Hillstar (*Oreotrochilus chimborazo*), Buffy Helmetcrest (*Oxygogon stubelii*),

Blue-bearded Helmetcrest (*Oxygogon cyanoaemus*), White-bearded Helmetcrest (*Oxygogon lindenii*), and Green-bearded Helmetcrest (*Oxygogon guerini*), whereas the Purple-backed Thornbill (*Ramphomicron microhynchum*), and Bronze-tailed Thornbill (*Chalcostigma heteropogon*) make seasonal altitudinal movements (Fig. 4). Resident hummingbirds in the *Paramo* include some widespread species like the Giant Hummingbird (*Patagona gigas*), Great Sapphirewing (*Pterophanes cyanopterus*), Black-tailed Trainbearer (*Lesbia victoriae*), and Green-tailed Trainbearer (*Lesbia nuna*). Despite being a relatively well-studied and charismatic group, new hummingbird species continue to be discovered. The Blue-throated Hillstar (*Oreotrochilus cyanoaemus*), for example, was recently described in a remote *Paramo* area of the southwestern Andes of Ecuador and listed as critically threatened, due to its restricted distribution, small population (<750 individuals), and vulnerability to ongoing threats (Sornoza-Molina et al., 2018).

Puna

Puna ecosystems are another grassland-shrubland ecosystem found between ~3000–5000 masl from Northern Peru to Chile and Argentina (Fig. 5). *Puna* is distinguished from *Paramo* by climatic regime and floristic composition (Rundel et al., 1994). *Puna* is found in areas with <2000 mm of annual precipitation and seasonally arid periods 3–6 months of the year (Troll, 1965). It is dominated by grasses and cushion plants (Rundel et al., 1994). Three types of *Puna* systems are defined by rainfall and seasonality: moist, dry, and desert (Troll, 1965; Baied and Wheeler, 1993).

Moist *Puna* covers most of the Peruvian and Bolivian high Andes, typically between 3700 and 5000 masl (Fig. 5) in areas with 400–2000 mm of annual precipitation and annual temperatures of 5–7°C. Humidity gradients along the Andes change with latitude, as do the distributions of *Puna* birds. In particular, the degree of distinction between the eastern and western slopes of the Andes increases with latitude, and species associated with more arid conditions are most likely to occur along the western slopes in the central and southern Andes (Fjeldsø and Krabbe, 1990). Some species may have extensive latitudinal ranges but extremely restricted elevational distributions. The moist *Puna* areas are mainly dominated by *Ichu* (*Stipa ichu*), other tussock grasses such as *Festuca dolichophylla* and *Calamagrostis* spp., with interspersed wetlands and stands of *Polylepis* trees or *Puya raimondii*. The complex topography is often mirrored by patterns of endemism and richness among the birds. Among the most representative genera are the Canasteros (*Asthenes* spp.), Ground-Tyrant (*Muscisaxicola* spp.), Miners (*Geositta* spp.) and Earthcreepers (*Upucerthia* spp.) (Fjeldsø and Irestedt, 2009) (Fig. 6).

The dry and saline *Puna* is located further south along highland plateaus between 3500 and 5000 masl in Chile, Bolivia and Argentina (Fig. 5). These areas receive 100–400 mm of annual precipitation and often have a large number of salt bodies locally called “salares” and areas dominated by Tola shrubs (*Parastrephia quadrangularis*) and the tussock grasslands of *Festuca orthophylla*. Birdlife is generally less diverse and numerous than moist *Puna* and common residents include Puna Tinamou (*Tinamotis pentlandii*), Andean Goose (*Oressochen melanopterus*), Puna Miner (*Geositta punensis*), Puna Canastero (*Asthenes sclateri*), Puna Ground-Tyrant (*Muscisaxicola juninensis*), Yellow-Finch Puna (*Sicalis lutea*).

Finally, the *Puna* desert, which is characterized by the near total lack of precipitation, extends to the southernmost zone of *Puna* distribution (Fig. 5). Vegetation communities are sparse and xerophytic, such as the cushion plants Yareta (*Azorella compacta*), Tola (*Baccharis incarum*) and Cardón de la Puna (*Echinopsis atacamensis*). There are few bird species here, with only ~20 species recorded, including five specialists. These are the Lesser Rhea (*Rhea pennata*), Tawny-throated Dotterel (*Oreopholus ruficollis*), Least Seedsnipe (*Thinocorus rumicivorus*), Gray-bellied Shrike-Tyrant (*Agriornis micropterus*), and Spot-billed Ground-Tyrant (*Muscisaxicola maculirostris*) (Vuilleumier, 1997).

High-Andean Wetlands

High-Andean wetlands include a rich assortment of peatlands, swamps, lagoons and lakes that are fed by rain and glaciers. Peatlands, peat bogs or *bofedales*, as they are locally called, are the bulk of high-Andean wetlands and are characterized by fertile and very moist soils that retain water year-round, and support cushion plants (*Distichia* spp., *Oxychloe* spp., *Plantago* spp.) that act as sponges for water storage and provide “oases” for migratory and resident birds (Weller, 1999; Fig. 7). In Peru 98 bird species—including 38 specialists—were recorded in Andean peatlands (Gibbons, 2012), although lower levels of species richness were reported for Bolivia (16 species, Naoki et al., 2014), Peru (34 species, Tellería et al., 2006), and Argentina (60 bird, Josens et al., 2017). That said, despite not being especially species rich, peatlands and other high-Andean wetlands support distinctive bird communities that include the Black-faced Ibis (*Theristicus melanopis*), Puna Ibis (*Plegadis ridgwayi*), Andean Negrito (*Lessonia oreas*), Gray-breasted Seedsnipe (*Thinocorus orbignyianus*), and Andean Lapwing (*Vanellus resplendens*) as well as many ducks (Anatidae), coots and rails (Rallidae) (Fig. 8).

One alarming projection is that 75% of Andean peatlands, systems that only comprise approximately 5% of the land in the High Andes, may disappear with climate change (Gibbons, 2012). As a consequence, some birds highly adapted to peatland habitats could become extinct (IUCN; BirdLife International, 2018). The White-bellied Cinclodes (*Cinclodes palliatus*) is one of these. This species is critically endangered (CR) (BirdLife International, 2018) given that its population of <250 individuals is restricted to elevations between 4400 and 5000 masl of the central Andes of Peru. Populations of this species are decreasing primarily because of peat extraction, overgrazing, mining, and water extraction for agriculture (BirdLife International, 2018). The Diademed Sandpiper-Plover (*Phegornis mitchellii*) is another species considered by the IUCN Red List as near-threatened (BirdLife International, 2018).

Lakes and lagoons are another important habitat for alpine birds (Fjelds , 1985). The Totora reed (*Schoenoplectus californicus*), in particular, provides food, refuge and breeding habitat for many birds including the Chilean Flamingo (*Phoenicopterus chilensis*), Andean Flamingo (*Phoenicoparrus andinus*), Andean Duck (*Oxyura ferruginea*), Yellow-billed Pintail (*Anas georgica*), Giant Coot (*Fulica gigantea*), and Slate-colored Coot (*Fulica ardesiaca*). One of the most interesting, but endangered, groups inhabiting wetlands, are grebes (Podicipedidae), which include several flightless species endemic to single lakes or regions. Examples include the Jun n Grebe (*Podiceps taczanowskii*) restricted to the Jun n Lake in Peru (4082.7 masl), the Titicaca Grebe (*Rollandia microptera*) restricted to Lake Titicaca between Peru and Bolivia (3812 masl), and the extinct Colombian Grebe (*Podiceps andinus*) that was recorded for the last time in the wetlands of Bogota (2600 masl) in 1977 (BirdLife International, 2018).

High-Elevation Forests

Although the classic definition of “alpine zones” specifies areas above treeline, the High Andes hosts trees above 2500 masl and even up to 5100 masl for some small patches of forest dominated by *Polylepis* trees (Purcell et al., 2004). In the northern and eastern slopes of the Central Andes, upper montane or cloud forest comprises areas of continuous forest cover up to 3000 masl, with mixed-species forest cover, epiphyte-rich canopies, and underbrush providing complex habitat for many bird species, some of which are not high-elevation specialists. In the southern regions and western slopes of the Central Andes, patches are sparser and are comprised of trees such as *Alnus acuminata*, *Escallonia* spp., and *Buddleja* spp. However, across the Andes above 3000 masl, it is the small forest islands comprised of *Polylepis* trees that contribute most uniquely to bird diversity in the alpine zone, providing important habitat for endemic, specialized, and vulnerable species.

Polylepis forest

Forests dominated by trees and shrubs of the genus *Polylepis* (Rosacea) are restricted to the High Andes and Cordoba Mountains of Argentina (Kessler and Schmidt-Lebuhn, 2006) (Fig. 2E–F; Fig. 9). *Polylepis* forest represents the upper elevational extent of forest in the world (~5100 m) (Purcell et al., 2004) and are a recognized center of avian diversity and endemism (Fjelds , 2002). Across the Andes, *Polylepis* forests are regularly used by 214 bird species, which include 31 endemic species, 27 IUCN red-listed species, and 23 specialists (Sevillano-R os et al., 2018) (Fig. 10). Not surprisingly, the fragmented distribution of *Polylepis* forests at local, regional and continental scales shapes the distribution of many specialized *Polylepis* birds, which are often restricted in population size and geographic extent (Lloyd, 2008; Sevillano-R os and Rodewald, 2017). Consequently, many birds associated with *Polylepis* are globally threatened (BirdLife International, 2018) and require deliberate conservation (Fuentealba and Sevillano, 2016).

In the Northern Andes, *Polylepis* forms small woodland patches above 3200 masl within the *Paramos* (Fandi o and Caro, 2009). Vegetative diversity is high in these humid zones, with species like *Frailejones* (*Espeletia* spp., *Coespeletia* spp.) and shrubs such as *Hypericum laricifolium*, *Weinmannia*, *Oreopanax*, *Myrsine*, *Miconia*, *Ageratina*, *Ribes*, *Monticalia*, *Tibouchina*, *Hesperomeles*, *Hypericum*, *Berberis*, and *Gynoxys baccharoides* (Fandi o and Caro, 2009). As an interesting contrast, the northern Andes region lacks avian



Fig. 2 Bird communities of six main high-Andean ecosystems covered here. The *Paramo*, restricted to the northern Andes (A); the *Puna* covering the major part of central Andes (B); lakes, lagoons (C) and wetlands (*bofedales* in Spanish) (D); high-elevation forest dominated by *Polylepis* trees (E–F); human-modified ecosystems (G) and glaciers, usually above 5000 m (B, C, H). Photos: Cristina Flores (A); Steven Sevillano-R os (B–H).

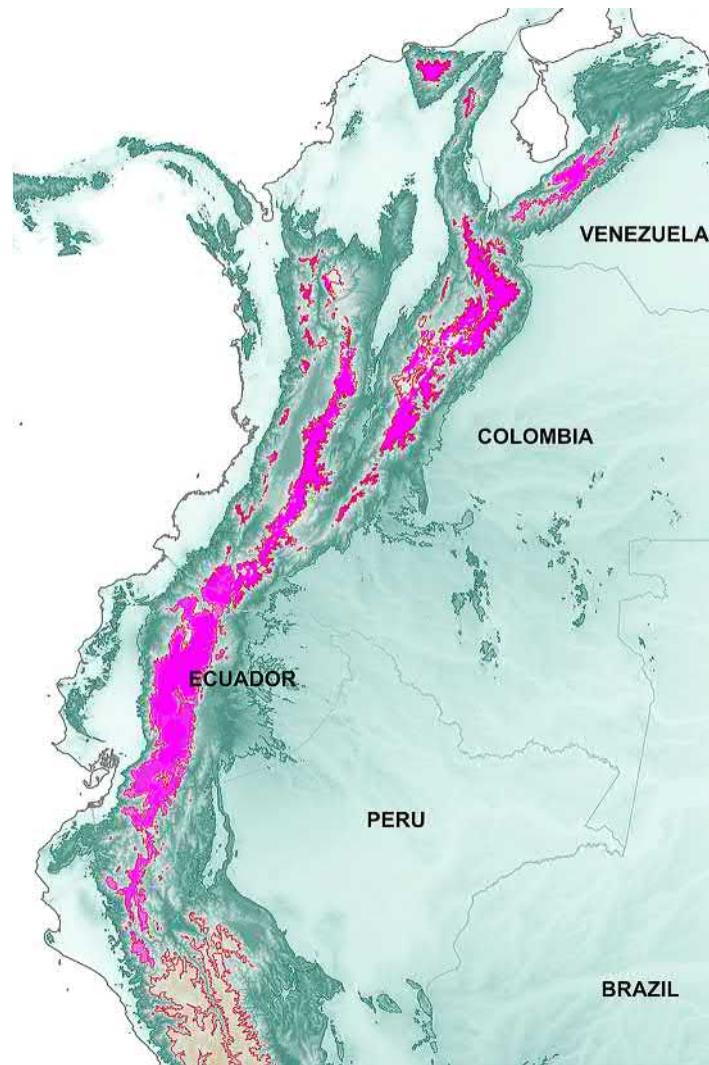


Fig. 3 Distribution map of the *Paramo* in Venezuela, Colombia Ecuador and northern Peru. Based on IAvH. (2012). *Cartografía de Páramos de Colombia Esc. 1:100.000. Proyecto: Actualización del Atlas de Páramos de Colombia. Convenio Interadministrativo de Asociación 11–103*, Instituto Humboldt y Ministerio de Ambiente y Desarrollo Sostenible. Bogotá, DC, Colombia; Cuesta, F., Sevink, J., Llambí, L. D., De Bièvre, B. and Posner, J. (2014). *Avances en investigación para la conservación de los páramos andinos*. Quito, Ecuador: CONDESAN.

specialists on *Polylepis* and most bird species in this habitat are also found in humid montane forests (Valderrama and Verhelst, 2009; Sevillano-Ríos et al., 2018). Nevertheless, some species of high conservation value, such as the globally-threatened Dusky Starfrontlet (*Coeligena orina*) (CR), depend of these forests (BirdLife International, 2018).

The northern and middle Central Andes contain the highest number of birds specialized on *Polylepis* within roughly three elevational zones. At lower elevations (~2500 masl), *Polylepis* borders cloud forest and, as such, shares many of the same species from groups like tanagers, flowerpiercers (Thraupidae) and hummingbirds, and even a few *Polylepis* specialists such as the Giant Conebill (*Conirostrum binghami*) (Vuilleumier, 1984). At intermediate elevations (3400–3800 masl), *Polylepis* starts to dominate mixed-forest stands of *Gynoxys*, *Buddleja*, *Baccharis*, *Senecio* and *Berberis* (Fjeldsâ, 1992; Kessler, 2006,) and bird communities become notably more diverse (Lloyd, 2008; Sevillano-Ríos and Rodewald, 2017). A recent study from *Polylepis* forests in Cordillera Blanca in the northern central Andes reported ~30–40 bird species, including a mix of generalists and specialists, such as the Tit-like Dacnis (*Xenodacnis parina*), Line-cheeked Spinetail (*Cranioleuca antisensis*); Baron's Spinetail (*C. baroni*) and Stripe-headed Antpitta (*Grallaria andicolus*) (Sevillano-Ríos and Rodewald, 2017; Fig. 11). At higher elevations (3800–4700 masl) the environments are increasingly cold but wet, with *Polylepis* forest forming islands on the moist *Puna* landscapes (Kessler, 2006). Incredibly, this is where the endemic and highly specialized Andean bird diversity peaks (Lloyd, 2008; Sevillano-Ríos and Rodewald, 2017; Sevillano-Ríos et al., 2018). Some of the most representative bird species include the Giant Conebill (*Conirostrum binghami*), Royal Cinclodes (*Cinclodes aricomae*), Tawny Tit-Spinetail (*Leptasthenura yanacensis*), White-browed Tit-Spinetail (*Leptasthenura xenothorax*), and the White-cheeked Cotinga (*Zaratornis stresemanni*) (Fig. 11).



Fig. 4 Hummingbirds associated to the *Paramo*: (A) Ecuadorian Hillstar (*Oreotrochilus chimborazo*); (B) Sparkling Violetear (*Colibri coruscans*); (C) Black-tailed Trainbearer (*Lesbia victoriae*); (D) Blue-mantled Thornbill (*Chalcostigma stanleyi*); (E) Shining Sunbeam (*Aglæactis cupripennis*); (F) Giant Hummingbird (*Patagona gigas*); (G) Buffy Helmetcrest (*Oxypogon stubelii*); (H) Purple-backed Thornbill (*Ramphomicron microrhynchum*). Photos: Rubi Shapiro (A); Steven Sevillano-Rios (B–F), Juan José Arango (G), Andrés García Ávila (H).

Finally, the southern Central Andes are increasingly cold and dry, with *Polylepis* forest forming islands on the dry and desert *Puna* landscapes at very high elevations (3800–5100 masl). Here, along with a decreasing degree of bird diversity, almost no *Polylepis* bird specialists are found. Yet, one endemic species, the Olrog's Cinclodes (*Cinclodes olrogi*), is associated with *Polylepis* at these latitudes (BirdLife International, 2018).

Human-Modified Areas

Human-modified or anthropogenic areas include cities, towns, crop fields, forest plantations and other areas modified by humans since the Andes were settled approximately 10,000 years ago (Rademaker et al., 2014). As is typical for these landscapes, certain bird species tolerate disturbances better than others and several have adapted quite well to living in human environments (Slabbekoorn and Peet, 2003). In many cases, they are species that modify their nesting behavior to use manmade materials and may feed on crops or even from the waste that is generated by man. In general, these are generalist and cosmopolitan species that are found throughout the Andes or are cosmopolitan throughout the Americas and benefit from the disturbances of the landscape. The city of Bogotá (2600 masl), for example, is one of the largest cities in the Andes and according to eBird, around 250 species have been registered within the city (eBird records in October 2018). Many of these observations have been made on the Monserrate hill (146 species), the Córdoba wetland (162 species) and La Florida Park (290 species). Quito (2850 masl), another large Andean city, has around 220 bird species while around 200 species were recorded in the city of Cuzco. On the other hand, crop fields and plantations of introduced trees like *Eucalyptus*, have strongly modified the Andean landscape and nowadays many bird species inhabit them. Some of the most common birds include the Rufous-collared Sparrow (*Zonotrichia capensis*), Chiguanco Thrush (*Turdus chiguanco*), Eared Dove (*Zenaida auriculata*), House Wren (*Troglodytes aedon*), Sparkling Violetear (*Colibri coruscans*), among many others (Fig. 12).

Glaciers

The lower limit of glaciers in the Andes occurs at approximately 5000 masl, and this represents the upper limit of the distribution of many bird species. However, recent observations (e.g., Hardy and Hardy, 2008; Hardy et al., 2018), indicate that in fact, some bird species can nest and feed directly on glaciers. Among these species are the White-winged Diuca-Finch (*Idioparus specularis*), Taczanowski's Ground-Tyrant (*Muscisaxicola griseus*), White-fronted Ground-Tyrant (*Muscisaxicola albifrons*), Plumbeous Sierra Finch (*Geospizopsis unicolor*), Rufous-bellied Seedsnipe (*Attagis gayi*), Gray-breasted Seedsnipe (*Thinocorus orbignyianus*), and some hummingbirds such as the Olivaceous Thornbill (*Chalcostigma olivaceum*).

The White-winged Diuca-Finch is the only bird species known to actively nest in the high Andean glaciers up to ~5400 masl (Hardy and Hardy, 2008; Hardy et al., 2018). In 2005, during a scientific expedition to the Quelccaya glacier, in Cuzco, Peru, Hardy and Hardy (2008) documented the first White-winged Diuca-Finch nest at these elevations. Subsequent observations from the



Fig. 5 Distribution map of the moist, dry-saline and desert Puna along Peru, Bolivia, Chile and Argentina. Based on Troll, C. (1965). Seasonal climates of the earth. In: Rodenwaldt, E., Juszat, H. J. (eds.) *Weltkarten zur Klimakunde / World maps of climatology*. Berlin, Heidelberg: Springer; Baied, C. A. and Wheeler, J. C. (1993). Evolution of high Andean puna ecosystems: Environment, climate, and culture change over the last 12,000 years in the Central Andes. *Mountain Research and Development*, 145–156; Ministerio del Ambiente del Peru. (2015). *Mapa nacional de cobertura vegetal : memoria descriptiva / Ministerio del Ambiente, Dirección General de Evaluación, Valoración y Financiamiento del Patrimonio Natural*. Lima: MINAM.



Fig. 6 Several puna birds tend to have dull colors, like gray (A and B) or brown (C) are adapted to live in open areas. Similarity in coloration can make some species can be difficult to distinguish from each other, like the Taczanowski's Ground-Tyrant (*Muscisaxicola griseus*) (A) from the Cinereous Ground-Tyrant (*Muscisaxicola cinereus*) (B). The Streak-throated Canastero (*Asthenes humilis*) (C) has light yellow streaks on dun brown that help it camouflage with the tussock grasses. Photos: Steven Sevillano-Rios.



Fig. 7 Distribution map of wetlands along the High Andes, including peatlands, swamps, *bofedales* (A) and lakes, lagoons and seasonal wetlands in Bolivia (B). Based on Ricaurte, L. F., Patiño, J. E., Arias, J. C., Acevedo, Ó., Restrepo, D., Jaramillo, Ú., Vélez, J. I. (2015). *La pluralidad del agua: tipos de humedales de Colombia; sistema de clasificación de humedales*. Colombia anfibio: un país de humedales, 116–133; Ministerio del Ambiente del Peru. (2015). *Mapa nacional de cobertura vegetal : memoria descriptiva / Ministerio del Ambiente, Dirección General de Evaluación, Valoración y Financiamiento del Patrimonio Natural*. Lima: MINAM; Digital Chart of the World available on Diva-GIS in Hijmans, R. J., Guarino, L., Bussink, C., Mathur, P., Cruz, M., Barrientes, I., and Rojas, E. (2004). Diva-Gis. Vsn. 5.0. A geographic information system for the analysis of species distribution data.

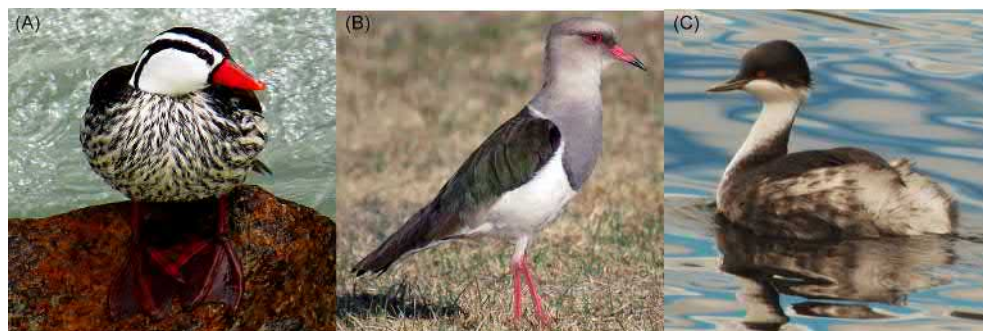


Fig. 8 Birds associated with high-Andean wetlands: Torrent Duck (*Merganetta armata*) (A); Andean Lapwing (*Vanellus resplendens*) (B); Junin Grebe (*Podiceps taczanowskii*) (C). Photos: Steven Sevillano-Rios (A), Nestor Ccacya Baca (B), Kevin Chumpitaz Trujillo (C).

Quelccaya glacier and the Vallunaraju mountain in Cordillera Blanca by [INAIGEM \(2017\)](#) provide further evidence of this behavior, which has been speculated to occur in many other glaciers along the Andes ([Hardy and Hardy, 2008](#)). More recently, [Hardy et al. \(2018\)](#) reported the results of a decade of study of the White-winged Diuca-Finch nesting biology in glaciers, suggesting that this species could be an obligate glacier-nester. Moreover, their results were also documented by a BBC documentary available online (see extra sources).

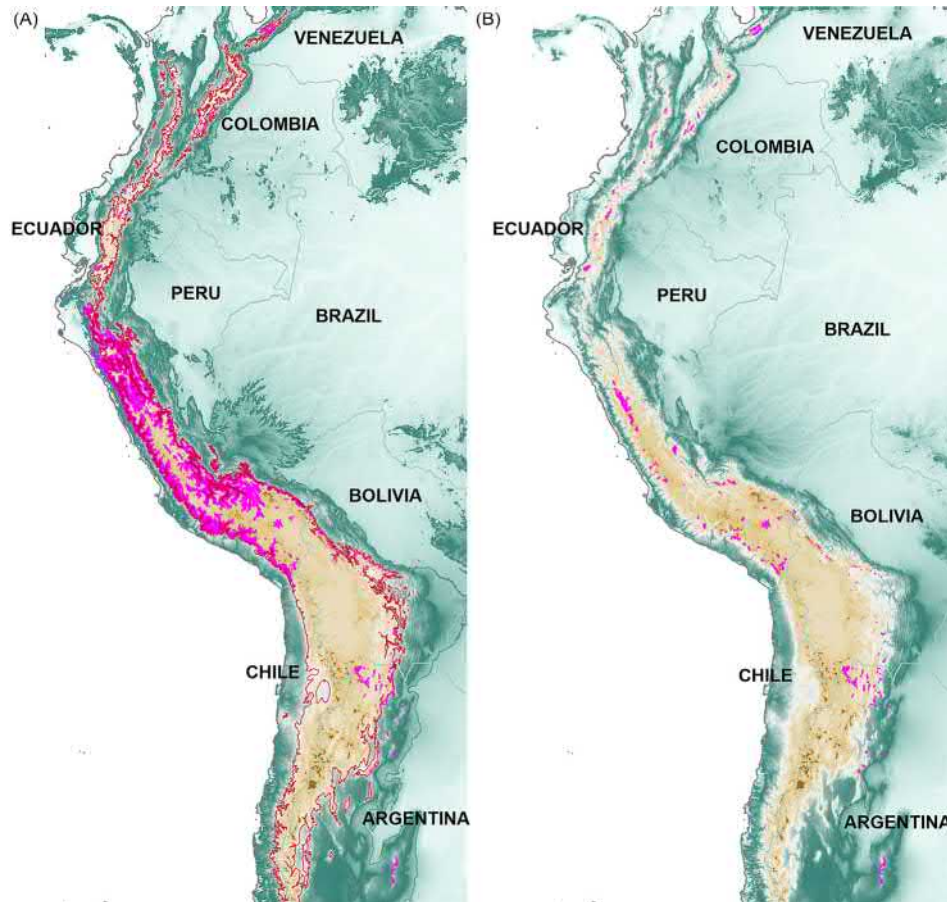


Fig. 9 Map of the distribution of all high-elevation forest, including mountain cloud forest, relict forest and shrubby areas (A). *Polyplepis* forests represent the most important high elevation relict forests (B). Based on Ministerio del Ambiente del Peru. (2015). *Mapa nacional de cobertura vegetal : memoria descriptiva / Ministerio del Ambiente, Dirección General de Evaluación, Valoración y Financiamiento del Patrimonio Natural*. Lima: MINAM; Arnal, H., Sampson, A., Navarro, G., Palomino, W., Ferreira, W., Romoleroux, K., Caro, D., Teich, I., Cuyckens, E., Antezana, C., Arrazola, S., Auca, C., Balderrama, J., Beck, S., Burneo, S., De la Barra, N., Bustamante, A., Fandino, Y., Ferro, G., Gomez, I., Guzman, G., Iglesias, J., Irazabal, J., Lozano, P., Mercado, M., Monsalve, A., Renison, D., Salgado, S. and Samochualpa, E. (2014). *Mapa Pan Andino de Bosques de Polyplepis prioritarios para Conservación*. American Bird Conservancy, The Plains, USA and Sevillano-Ríos, C.S., Rodewald, A.D. and Morales, L.V. (2018). *Ecología y conservación de las aves asociadas con Polyplepis: ¿qué sabemos de esta comunidad cada vez más vulnerable?*. *Ecología Austral*, 28, pp. 216–228.

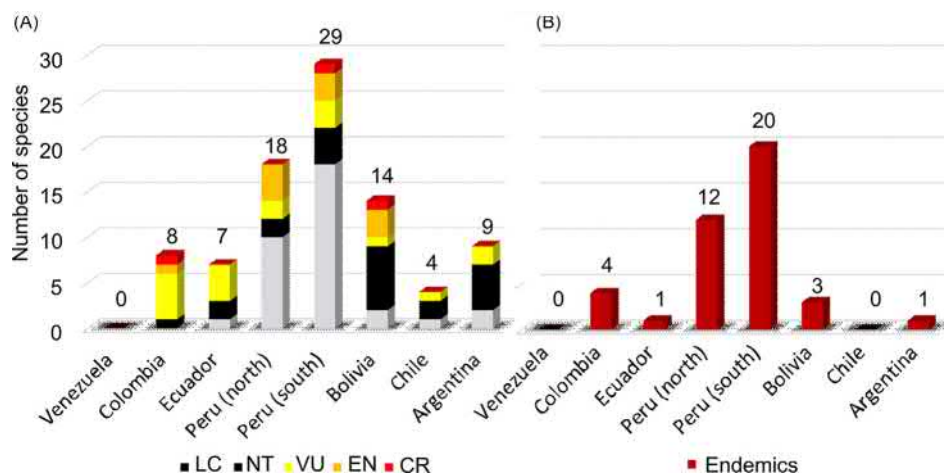


Fig. 10 Number of threatened (A) and endemic (B) bird species associated to *Polyplepis* forest by country. The threatened categories follow the IUCN Red List: CR: Critically Endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least Concern. Source: IUCN (2018). Red List of Threatened Species.



Fig. 11 Several bird species inhabiting high-elevation forest, some of which are considered *Polylepis* forest specialists: Stripe-headed Antpitta (*Grallaria andicola*) (A); Tit-like Dacnis (*Xenodacnis parina*) (B); Black-crested Tit-Tyrant (*Anairetes nigrocristatus*) (C); White-cheeked Cotinga (*Zaratornis stresemanni*) (D); Giant Conebill (*Conirostrum binghami*) (E); Ash-breasted Tit-Tyrant (*Anairetes alpinus*). Photos: Steven Sevillano-Rios.



Fig. 12 Some common birds usually found in anthropogenic areas like cities or towns: Eared Dove (*Zenaida auriculata*) (A); Vermilion Flycatcher, male (*Pyrocephalus rubinus*) (B); Rufous-collared Sparrow (*Zonotrichia capensis*) (C); Golden Grosbeak (*Pheucticus chrysogaster*). Photos: Steven Sevillano-Rios.

The Taczanowski's and the White-fronted Ground-Tyrants are two species that normally inhabit open areas of the *Puna* ecosystem during the day but seem to fly back to small ice-caves in the interior of the glaciers for roosting and spend the night there (Hardy et al., 2018). Moreover, recent observations (Hardy et al., 2018; unpublished data, Autoridad Nacional del Agua, Peru), have discovered them feeding on the glaciers, specifically feeding on insects that were trapped in small holes with a black matter called cryoconites. The same behavior has been recorded for the Olivaceous Thornbill (per. Obs., S. Sevillano-Rios.) in the Pastoruri glacier at 5200 m in Cordillera Blanca and according to Hardy et al., 2018, many more species could be depending of glaciers as an important habitat. Although the number of observations is still limited to anecdotal records, they open the possibility to develop serious studies on understanding why and how alpine birds use glaciers and if some would adapt to live at high elevations under future climate conditions when Andean glaciers disappear.

Vulnerability to Climate Change and Conservation

One of the greatest concerns arising from future climate scenarios is the eventual extinction of many species of flora and fauna, with those restricted to mountain ecosystems, like the high Andes, among the most vulnerable (Şekercioglu et al., 2012). Species will exhibit three alternative responses to climate change: 1) migrate to newly suitable habitat, 2) adapt in situ, or 3) go extinct (Habary et al., 2017). For high-Andean species, there are several reasons to be concerned about their capacity to migrate or adapt in response

to climate change. Many are adapted to live within very narrow climatic ranges with little temporal variability and, due to the complex Andean topography, these species have restricted ranges, low dispersal capabilities and small populations. These characteristics may make movement or in situ adaptation of such species slow, increasing their risk of extinction in the face of rapid climate change; species that do not move to other places or adapt fast enough to keep up with environmental and climatic changes are predicted to become extinct in the near future (Şekercioğlu et al., 2012).

Different species of flora and fauna have successfully moved upslope as a result of the global increase in temperature (see Parmesan and Yohe, 2003; Chen et al., 2011). However, the few studies that have examined upslope movement of Andean birds suggest that such migration may be slow and may not be a viable response for all species. A comparative study developed in Cerros del Cirá in Peru found that although climate change is certainly pushing bird species to modify their upper limit, 55 bird species moved an average of 49 m in a period of 41 years, far below the predicted migration distance (152 m) that would be required to keep up with predicted increase in temperature ($\sim 0.79^{\circ}\text{C}$) (Forero-Medina et al., 2011). More recently, Freeman et al. (2018) showed that after 32 years, the ranges of many mountain bird species in Cerro Pantiacolla, Peru, have shrunk, or their population sizes have decreased. Furthermore, they also found that many mountaintop species have already disappeared in response to climate change (Freeman et al., 2018). Therefore, although upslope migration is occurring and could perhaps be a viable strategy for some species, many mountaintop species may become extinct as a consequence of global change.

One implication of modifying species limits is that species-habitat relationships could also drastically change. For example, because it could take much longer for an entire plant community or ecosystem to migrate the same distance upslope than it does for animal species, this disconnect could generate a lack of suitable habitat at these new climatically suitable elevations. Consequently, this could cause a decoupling of ecological relationships, exacerbating mountain-top extinctions (Colwell et al., 2008). Moreover, modifying species limits could also modify interspecific relationships such as mutualism, competition, or predation. For example, the upslope migration of more competitive, generalist bird species could cause the displacement of subordinate species currently well-adapted to higher elevations; this appears to be the case in Cerro Pantiacolla (Freeman et al., 2018). This could likewise affect many endemic birds specialized to the *Paramos*, the *Polylepis* forests, peatlands or lakes (Freeman et al., 2018; Sevilano-Ríos et al., 2018).

Due to the high vulnerability of South American alpine birds to climate change, we believe that it is important to initiate actions for the conservation and restoration of the ecosystems on which they depend as habitat. Specifically, the following actions should be undertaken: 1) identify and legally protect a large number of priority areas, involving local human populations, together with NGOs, government agencies, and the academy, in the conservation and restoration process; 2) prioritize conservation and restoration of *Paramos*, *Puna*, forests, peatlands, lakes and lagoons located at the headwaters of watersheds because they are highly important and the most vulnerable to climate change; 3) avoid unnecessary destruction of biodiversity by reducing the levels of fire, logging, overgrazing and livestock on these areas (Morales et al., 2018). Instead, the development of more sustainable economic activities (e.g., ecotourism, agroforestry) should be encouraged; finally, 4) educate the public, including local people, visitors and students, but especially policy makers, ministry advisors and politicians who can help determine the effectiveness of the different conservation and restoration actions along the Andes.

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Relevant Websites

<http://www.pbs.org/kingdomssky/episodes/andes/>—Meet the Bird that Nests Inside Glaciers (02:50).

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Alpine Birds of Africa

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Abstract

Africa's alpine biome, the Afroalpine, extends between the treeline and the permanent snow line. The number of bird taxa recorded in the Afroalpine is relatively small, particularly in relation to the speciose subjacent Afromontane. By and large, the avifauna of the Afroalpine represents a greatly impoverished Afromontane community as opposed to its own distinct community, although a few taxa are more regularly encountered than others, including a small number of endemics. Although a limited number of 47 bird taxa populates the alpine belt, there are substantial differences in taxonomic composition between the Ethiopian highlands and the East African mountains. Depending on the strength of their association with the biome, these birds can be assigned to four groups: (1) obligate biome-confined breeding residents, (2) regular biome-affiliated residents, (3) facultative biome-affiliated residents, (4) opportunistic residents and visitors. Among the Afroalpine avifauna, there are interesting ecological aggregations of taxa that have been observed exploiting special food resources. Birds of prey form regionally speciose communities, as do seedeaters among the passerines. However, further research is needed to discern the spatial and temporal patterns of occurrence of Afroalpine birds and the biotic and abiotic triggers shaping their temporal and spatial distribution. We suggest systematic bird monitoring activities and a focus on biological key aspects (feeding, breeding, temporal and spatial movements) and on the effects of climate change.

Introduction

From the viewpoint of an ornithologist, the barren landscapes of high-elevation mountains can be fascinating. The alpine areas of African mountains offer an attractive, yet challenging setting for the observation of relatively species-poor communities. Accordingly, the number of systematic studies of the avifauna of the Afroalpine is low and long-term approaches usually only consider the more speciose biomes at lower elevations.

While it is unsurprising that species diversity in alpine regions around the globe is low, one might expect a more unique African alpine avifauna, considering the continent's species-rich birdlife. In fact, most of the birds found in these realms are not entirely confined to the alpine habitats of Africa's high-altitudinal belt but have strong links to the subjacent Afromontane, which harbors much more diverse avian communities. In the following, we compile the scattered information on African alpine birdlife, analyze underlying patterns of occurrences and discuss challenges for future research.

The African Alpine Biome

Geographic Delimitation

The Afroalpine biome covers only a small fraction of the African continent. Here, we define the Afroalpine as the high mountains of Sub-Saharan Africa, excluding the biogeographically distinct and much lower South-African mountains. As only the highest

elevations above the treeline are considered true alpine habitats, their geographic distribution is limited to a few prominent mountain ranges. By and large, these include the Ethiopian highlands, Mt. Kilimanjaro, Mt. Meru, Mt. Kenya, Mt. Elgon, Mt. Karisimbi, the Rwenzori Mts and Mt. Cameroon. However, the latter is also excluded from our considerations because its high-elevation ranges are mainly covered by montane grasslands constituting a different biome than that of the Afroalpine in the strict sense.

Characteristics

In a simplified ecological definition, the alpine biome as defined here is a high-elevation zone having low temperatures, a short growing season and low-nutrient soils that inhibit tree growth (Fig. 1). Following this definition, the alpine biome extends in variable breadth between the treeline and the permanent snow line, that is, above the montane and below the nival zone.

As with many other mountain regions in the world, a strict elevational delimitation of the Afroalpine is impossible. Treelines vary depending on exposure, slope inclination, solar radiation and other associated abiotic factors such as soil temperature and humidity, creating differences even within short distances on one mountain side (e.g., Hedberg, 1955; Coe, 1967; Uhlig, 1990; Busmann, 2006). During the last several million years, the position of the treeline in Africa has risen and fallen in connection with glaciation and deglaciation events. In East African mountains, the treeline has moved nearly 1000 m uphill since the end of the last glacial maximum, 15,000 years ago (Odada and Olago, 2005), likely influencing distribution and speciation patterns of birds (Moreau, 1966). Many authors include the Ericaceous belt in the Afroalpine despite local tree-like growth of some of these species (Walter and Breckle, 1984), while others do not (e.g., Hedberg, 1955; Coe, 1967; Wesche, 2002). As a consequence, the lower limits of the alpine zones are geographically variable and differ depending on conceptual conventions. Similarly, high-elevation grasslands are sometimes considered part of the Afroalpine as well: the biome is then regarded to consist of two sub-biomes, mountaintop grasslands/shrublands and moorlands (e.g., Dorst and Vuilleumier, 1986; Burgess et al., 2004). Again, here we restrict the Afroalpine only to the tundra-like habitats which largely correspond to the aforementioned “moorland” zone of Moreau (1966). However, this is not identical to the “Ericaceous moorland” zone of Coe (1967). This incongruence also causes different estimates of the extent of the Afroalpine, which is between 6000 km² (Dorst and Vuilleumier, 1986) and 50,700 km² (Burgess et al., 2004), depending on the respective delimitation. These regionally changing boundaries also define the upper limits of agricultural use (“agro-ecological belts”). The uppermost, infertile, zone (called “Werch” or “High Wurch” in Ethiopia) would be situated in the Afroalpine as defined here (Kingdon, 1990; Ritler, 2017).

There are characteristic climatic conditions in the Afroalpine, often including year-round nightly frosts and, during the dry season, warm sunshine by day that favors a characteristic high-elevation vegetation (Moreau, 1966; Brown et al., 1982). Besides sharing low primary productivity, biomass and species number between the arctic tundra and the Afroalpine (Müller, 1981; Lomolino et al., 2010), the atmospheric pressure of the relatively dry air of the Afroalpine is lower, while the insolation is higher, combined with a strongly latitude-correlated photoperiod in the high-elevation alpine biome (Cloudsley-Thompson, 1975). Water resources in Afroalpine regions may depend less on rainfall and more on mist (Walter and Breckle, 1984), and the characteristically low water availability during seasonal dryness clearly sets this biome apart from arctic tundra. Thus, the term “tundra,” maintained for historical reasons because of superficial morphological similarities, should only be applied to the lowland tundra proper of Northern latitudes, while the high-mountain landscapes of the African tropics should be termed “Afroalpine.” The term “páramo,”



Fig. 1 Afroalpine, tundra-like landscape (Bale Mts, Sanetti Plateau Ethiopia). Photo: T. Pröhl.

suggested as a global name for all tropical biota above the treeline (Monasterio and Vuilleumier, 1986) apparently has not gained wide acceptance.

Habitats

Locally different combinations of mountain relief and inclination, annual temperature profile and exposure, and bedrock type cause patchwork distributions of Afroalpine soil and vegetation. It is therefore obvious that habitats are not evenly distributed and that local environmental conditions shape the temporal appearance of habitats and the composition of its associated fauna (e.g., Coe, 1967; White, 1983).

Considering birdlife, there are characteristic habitats of the Afroalpine that are relevant for the occurrence of different taxa. The seasonal availability of water greatly affects the appearance of Afroalpine landscapes. Depending on regional rainfall patterns, moorlands, streams, and even small water bodies (tarns) are present during some periods (Fig. 2). They attract birds such as ducks, waders and cranes (cf. Table 1) to breed in the area. This temporary water supply also provides the basis for food resources including plant matter, nectar, insects and small mammals, from which birds, in particular songbirds and raptors, benefit. Other important habitat features that are present year-round are cliffs, rocky slopes and exposed rocks (Fig. 3). These are not only lookout perches and sources for invertebrate bird food but also provide shelter for nest building. Such rocky elements are often interspersed with varying low shrubby or grassy vegetation, causing small-scale habitat mosaic structures.

Finally, locally-specific interactions of abiotic landscape features, seasonally changing environmental conditions and the resulting biotic responses, lead to temporally different occurrences of bird communities in different geographical parts of the Afroalpine. Triggered by the changing availability of food resources and, to a lesser degree, of breeding opportunities, numerous bird taxa are absent from the area in periods of relative dryness. This is an important temporal aspect of Afroalpine bird communities and explains why these are not particularly species-rich and seasonally dynamic.

The Afroalpine Birdlife

Delimitation of Afroalpine Avifauna

The complexity of delimitating the Afroalpine might also be extended to the circumscription of associated bird communities. The inconsistent and instable climatic conditions of alpine habitats cause mosaic-like animal distribution patterns (Müller, 1981), which also holds true for Afroalpine birds (Moreau, 1966; Monasterio and Vuilleumier, 1986). Despite the fact that African mountains do harbor many bird taxa and among them often endemics with narrow elevational ranges, the wealth of these taxa is not exclusively confined to the Afroalpine. To classify these high mountain bird communities, the term “non-forest bird fauna” has also been used (Moreau, 1966; Monasterio and Vuilleumier, 1986). However, no formal distinction between the Afromontane and the Afroalpine has been agreed in this context. Moreover, the characteristic patchy distribution patterns of African mountain bird populations mainly reflect their predominantly Afromontane ranges. This might also have been the reason why the Afroalpine



Fig. 2 Moorlands, streams, and small water bodies (tarns) are at least seasonally present in the Afroalpine (Bale Mts, Sanetti Plateau Ethiopia). They provide food resources for many bird species and attract breeding by some of them. Photo: T. Pröhl.

Table 1 Important bird taxa found in the Afroalpine and their respective affiliation to the biome.

Group	Ethiopian highlands	East African mountains
1—Obligate biome-confined breeding residents	Ruddy Shelduck <i>Tadorna ferruginea</i> ^{a,b} Golden Eagle <i>Aquila chrysaetos</i> ^{a,b} Red-billed Chough <i>Pyrrhocorax pyrrhocorax</i> ^{a,b}	None
2—Regular biome-affiliated residents	Thekla Lark <i>Galerida theklae</i> (ssp. <i>huei</i>) ^b Brown Warbler <i>Sylvia lugens</i> (ssp. <i>griseiventris</i>) ^b Ankober Serin <i>Crithagra ankoberensis</i> ^b	None
3—Facultative biome-affiliated residents	Moorland Francolin <i>Francolinus psilolaemus</i> ^b Blue-winged Goose <i>Cyanochen cyanoptera</i> ^b Spot-breasted Plover <i>Vanellus melanocephalus</i> ^b	Elgon Francolin <i>Scleroptila elgonensis</i> ^c Moorland Chat <i>Pinarochroa sordida</i> ^d Red-tufted Sunbird <i>Nectarinia johnstoni</i> ^c
4a—Opportunistic residents and visitors (mainly Afromontane species)	Chestnut-naped Francolin <i>Pternistis castaneicollis</i> ^b Erckel's Francolin <i>Pternistis erckelli</i> ^b Yellow-billed Duck <i>Anas undulata</i> ^b White-collared Pigeon <i>Columba albitorques</i> ^b Rouget's Rail <i>Rougetius rougetii</i> ^b Wattled Crane <i>Bugeranus carunculatus</i> ^b Wattled Ibis <i>Bostrychia carunculatus</i> ^b African Snipe <i>Gallinago nigripennis</i> ^d Cape Eagle-Owl <i>Bubo capensis</i> ^d Bearded Vulture <i>Gypaetus barbatus</i> ^{a,d} Verreaux's Eagle <i>Aquila verreauxi</i> ^d Augur Buzzard <i>Buteo augur</i> ^d Thick-billed Raven <i>Corvus crassirostris</i> ^b Slender-billed Starling <i>Onychognathus tenuirostris</i> ^d White-billed Starling <i>Onychognathus albirostris</i> ^b Ethiopian Thrush <i>Psophocichla simensis</i> ^b Moorland Chat <i>Pinarochroa sordida</i> ^d Rusty-breasted Wheatear <i>Oenanthe frenata</i> ^b Tacaze Sunbird <i>Nectarinia tacaze</i> ^b Abyssinian Longclaw <i>Macronyx flavicollis</i> ^b Black-headed Siskin <i>Serinus nigriceps</i> ^b Brown-rumped Seedeater <i>Crithagra tristriata</i> ^b Streaky Seedeater <i>Crithagra striolata</i> ^d	African Black Duck <i>Anas sparsa</i> ^c Striped Flufftail <i>Sarothrura affinis</i> ^c African Snipe <i>Gallinago nigripennis</i> ^d Cape Eagle-Owl <i>Bubo capensis</i> ^d Bearded Vulture <i>Gypaetus barbatus</i> ^{a,d} Verreaux's Eagle <i>Aquila verreauxi</i> ^d Hunter's Cisticola <i>Cisticola hunteri</i> ^c Slender-billed Starling <i>Onychognathus tenuirostris</i> ^d Yellow-crowned Canary <i>Serinus flavivertex</i> ^c Streaky Seedeater <i>Crithagra striolata</i> ^d
4b—Opportunistic residents and visitors (widely distributed)	Tawny Eagle <i>Aquila rapax</i> ^{b,e} Steppe Eagle <i>Aquila nipalensis</i> ^{a,b} Pallid Harrier <i>Circus macrourus</i> ^{b,e} Lanner Falcon <i>Falco biarmicus</i> ^{a,d} Common Kestrel <i>Falco tinnunculus</i> ^{a,d} Cape Crow <i>Corvus capensis</i> ^b African Plain Martin <i>Riparia paludicola</i> ^d Red-throated Pipit <i>Anthus cervinus</i> ^b	Augur Buzzard <i>Buteo augur</i> ^d Lanner Falcon <i>Falco biarmicus</i> ^{a,d} Common Kestrel <i>Falco tinnunculus</i> ^{a,d} White-necked Raven <i>Corvus albicollis</i> ^c African Plain Martin <i>Riparia paludicola</i> ^d

^aTaxon occurring in Afrotropic and Palearctic.^bTaxon within biome in Ethiopian highlands only.^cTaxon within biome in East African mountains only.^dTaxon both in Ethiopian highlands and in East African mountains.^eTaxon occurring in Afrotropic, Palearctic, and Indomalaya.

Data compiled from personal observations and from Dorst, J. and Vuilleumier, F. (1986). Convergences in bird communities at high altitudes in the tropics (especially the Andes and Africa) and at temperate latitudes (Tibet). In: Vuilleumier, F. and Monasterio, M. (eds.) *High altitude tropical biogeography*, pp. 120–149. New York and Oxford: Oxford University Press. Taxonomy follows del Hoyo and Collar (2014, 2016).

avifauna has only rarely been given enough attention as a separate community. Instead, alpine regions of Africa were considered merely the topmost sub-region of a larger montane zone that extends the lowland zone uphill. Indeed, regular occurrences of certain birds in the Afroalpine are predominantly offshoots of more extensive montane ranges of the same species (Moreau, 1966). Consequently, there is no unique high-elevation avifauna characterizing the Afroalpine.

Birds of the Afroalpine

Here we present a preliminary compilation of avian taxa that have been recorded in the Afroalpine (Table 1). As of yet, our geographic comparisons and conclusions are provisional due to the relatively few studies that systematically assess Afroalpine bird-life, making bird faunal comparisons difficult (Moreau, 1966; Dowsett, 1986). Especially on a smaller geographic scale, information



Fig. 3 Important habitat features of the Afroalpine are cliffs, rocky slopes and exposed rocks, serving as lookout perches for birds and providing shelter for nest building (Bale Mts, Sanetti Plateau Ethiopia). Photo: T. Pröhl.

on regional or local differences between alpine bird communities is still fragmentary. Only a limited number of 47 bird taxa is more or less bound to the alpine belt (**Table 1**). Moreover, there are pronounced differences in occurrences between the Ethiopian highlands and the East African mountains. Depending on the strength of their association with the biome, these birds can be assigned to four groups:

Group 1—Obligate biome-confined breeding residents. These birds exclusively inhabit the Afromontane.

Group 2—Regular biome-affiliated residents. These birds predominantly inhabit the Afromontane.

Group 3—Facultative biome-affiliated residents. These birds have a substantial amount of their ranges in the Afromontane.

Group 4—Opportunistic residents and visitors. These birds are regularly, though opportunistically, found in the Afroalpine. Among them, two subgroups are apparent: Group 4a comprises taxa with largely Afromontane distributions. Group 4b with more widespread forms inhabiting several other biomes as well.

Obligate Biome-Confined Breeding Residents (Group 1)

Ruddy Shelduck (**Fig. 4**), Golden Eagle and Red-billed Chough are the only bird species that show a distinct confinement to the alpine biome in Africa. They are resident only in the Ethiopian highlands. In spite of that, none of these species is restricted to Africa. In fact, their occurrences in the Afroalpine represent distinct southern breeding populations of their much larger Palearctic ranges where, moreover, they are also found outside of alpine zones. Their habitat requirements are thus varied and regionally incongruent across their whole breeding range (see also [Moreau, 1966](#)). In Africa, they co-occur because of locally overlapping habitats in the relatively small-scaled Afroalpine zone, apparently without much interspecific interaction.

Regular Biome-Affiliated Residents (Group 2)

Thekla Lark (ssp. *huei*), Brown Warbler (ssp. *griseiventris*), and the Ankober Serin are possibly the only true African birds with a strong affiliation to the Afroalpine, although their habitat requirements and lifestyles are not identical. While the Brown Parisoma is quite variable in terms of food (insects, seeds) and foraging methods and strata (on ground and in/on vegetation), the Thekla Lark is bound to a more terrestrial lifestyle while sharing a similar diet. In contrast, the Ankober Serin is confined to a strict diet of grass seeds which is obtained in much rockier habitats than the other birds. Again, these three birds are solely resident in the Ethiopian highlands.

Facultative Biome-Affiliated Residents (Group 3)

This group, consisting only of Afrotropical bird taxa, is represented both in the Ethiopian highlands and the East African mountains. They harbor the same small number of three species each, but form very different bird communities. Taxonomically, only two francolin species (Moorland and Elgon Francolin) represent the same bird family in the two geographic areas, respectively, whereas the



Fig. 4 The Ruddy Shelduck is among the few bird species with a distinct confinement to the Afroalpine in Ethiopia, where it represents an isolated southern breeding population of a much larger Palearctic range. Photo: T. Pröhl.

other species either belong to waterfowl (Blue-winged Goose, **Fig. 5**) and waders (Spot-breasted Plover, **Fig. 6**) or to songbirds (Red-tufted Sunbird and Moorland Chat). Biogeographically, the Ethiopian Afroalpine community consists exclusively of species that are only to be found there, whereas the East African community shares one species with group 4 of the Ethiopian highlands (Moorland Chat). In terms of lifestyle, the species differ in their habitat preferences: the francolins are found in areas of denser vegetation that provides shelter, the goose and plovers have a certain affinity to (temporal) water bodies, and the songbirds exploit the invertebrate fauna or the nectar of different flowering plants.

Opportunistic Residents and Visitors (Group 4)

This group contains only such species that are to be expected to occur repeatedly in the Afroalpine, based on current knowledge. The group comprises the largest overall number of 36 species, and some of them occur in the Palearctic and Indomalayan region as well. They are likewise found both in the Ethiopian highlands and the East African mountains. Again, there are differences, not only in Ethiopia having the larger species number (31 vs. 15), but also in the composition of the respective bird communities. For example, there are no francolins in the alpine East African mountain regions while two duck species (Yellow-billed and African Black Duck) appear to replace each other geographically. There are ten species that are encountered in both geographic locations while 20 species are solely found in the Ethiopian highlands and 5 solely in the East African mountains. By far the largest part of this group's species have a mainly Afromontane distribution (group 4a with 27 species) whereas 13 species are more widespread (group 4b). Moreover, the Augur Buzzard is assigned to group 4a in the Ethiopian highlands but to group 4b in the East African mountains, while the Moorland Chat of group 4a in the Ethiopian highlands is found in group 3 of the East African mountain bird community. Noteworthy taxonomically is the occurrence of four seedeater species alone in group 4a, while subgroup 4b is of particular interest because it contains numerous raptor species (among them typical migratory visitors like the Pallid Harrier). As a consequence of the diversity of avian taxa involved, this group cannot be defined on grounds of specific shared habitat requirements.

Noteworthy Distributional Peculiarities

Of the 25 non-passerine taxa assigned to the Afroalpine, 17 are raptors (including owls). Of the 22 passerine taxa, five are seedeater species belonging to two genera (*Serinus* and *Crithagra*). Some of these birds are worth a closer look as they play important roles in the avifauna of the Afroalpine, even though they might not be found there exclusively.



Fig. 5 The Blue-winged Goose is a regular inhabitant of the Ethiopian alpine zones. It is suspected to leave these areas seasonally, possibly following the availability of food or water. Photo: T. Pröhl.



Fig. 6 The Spot-breasted Plover apparently follows a similar occurrence pattern like the Blue-winged Goose in Ethiopia's alpine region. Photo: T. Pröhl.

Birds of prey fulfill important ecological functions either as top predators or carrion feeders. The relatively large raptor community encountered in the Afroalpine reflects both their high trophic levels in the food chain and the exceptional conditions of the biome: the necessity to remove carrion from alpine habitats and plentiful food sources (particularly small mammals, but also other birds) explains the speciose composition of the Afroalpine raptor community and their exclusive utilization of food resources (Clouet et al., 1999; Rödel et al., 2002).

Among them, the Bearded Vulture (Fig. 7) is commonly associated with barren high-mountain habitats, but this is just one component of their lifestyle. Bearded Vultures are apex elements of food chains, consuming even the last skeletal remains of vertebrate carcasses. Traveling over broad geographic distances, Bearded Vultures are extremely flexible in terms of hunting and breeding habits, and they are not confined to alpine regions. Although they are very widely distributed over many mountainous habitats across Africa, Europe and Asia, they occupy a wide range of lowland areas if occasion requires. Thus, the Bearded Vulture is a prime example of a nomadic species that opportunistically uses resources in the Afroalpine without being bound to this biome exclusively.



Fig. 7 The Bearded Vulture is a prime example for a nomadic species that opportunistically uses resources in the Afroalpine without being bound to this biome exclusively. Photo: T. Pröhl.

The Augur Buzzard (**Fig. 8**) represents a comparable situation to the Moorland Chat in being assigned to two different groups, although in this case only the sub-grouping of group 4 is affected. This means that the Augur Buzzard is a much more range-restricted species in the Ethiopian highlands (group 4a), where it is a regular visitor, than it is in the East African mountains (group 4b) where it occurs over a substantially larger area beyond the montane and alpine zones of the mountain ranges. It has been suggested by [Moreau \(1966\)](#) that the Augur Buzzard is only a visitor to the Afroalpine because of its dependence on the mountain forests for nesting sites, which might also explain its different distribution patterns.

Among the songbirds of the Afroalpine, the corvids (**Fig. 9**) represent a particularly interesting group in regard to their ecology. Being generally opportunistic birds with a great deal of adaptability to different environmental conditions, it is not surprising to find four corvid species in the Afroalpine. Among them, the aforementioned Red-billed Chough comes closest to being a genuine alpine bird (group 1), whereas the other three species are opportunistic residents and visitors to the biome only (group 4). It is obvious that the latter three are separated from the chough by very different and less habitat-bound lifestyles, including a much closer affinity to



Fig. 8 The Augur Buzzard is only a visitor to the Afroalpine because it depends on the mountain forests for nesting sites. Photo: T. Pröhl.



Fig. 9 Like some other corvids, the Thick-billed Raven has a certain affinity to human settlements. Therefore, potential future distributional changes in connection with the spread of settlements should be monitored carefully. Photo: T. Pröhl.

human settlements. Therefore, an open eye should be kept on the dynamics of potential future distributional changes of these corvids in connection with the spread of settlements.

The small Moorland Chat (**Fig. 10**) has previously been mentioned as a typical element of the Afroalpine (Moreau, 1944; Moreau, 1966; Salt, 1954 in Franz, 1979). Its regular occurrence in the Afroalpine is remarkable since insectivorous bird species usually are underrepresented in alpine habitats, possibly because of the scarcity of appropriate food. In fact, the Moorland Chat shows different distributional patterns in different parts of Africa: while it is a resident with some degree of affiliation to alpine habitats in the east African mountains (Kilimanjaro: Moreau, 1944; Salt, 1954 in Franz, 1979; Mt. Kenya: Coe, 1967), it is probably much more of a common visitor to the Afroalpine of the Ethiopian highlands than a regular inhabitant (personal observations). In terms of its taxonomy, the Moorland Chat consists of numerous subspecies across Africa but their respective association with the Afroalpine biome has not been studied so far. In contrast, the Brown Warbler and the Thekla Lark are represented by particular



Fig. 10 The regular occurrence of the Moorland Chat in the Afroalpine is remarkable since in many alpine habitats insectivorous bird species usually are underrepresented. Beyond that, it is one of the biologically most fascinating, but poorly studied birds of the African mountains. Photo: T. Pröhl.

subspecies that have a known close affiliation with the biome. Such geographical and seasonal differences must be taken into account when generalizing about the Afroalpine avifauna, especially since quantitative data on the relative proportions of Afroalpine and Afromontane breeding populations are lacking.

The seedeater taxa (**Fig. 11**) have a special position among African finches because they are comparatively species-rich and tend to occupy only small ranges, leading to a high degree of intra-generic endemism. In the Afroalpine, there are five seedeater species. As in the corvids, there is one species (the Ankober Serin of group 2) that is more closely affiliated with the biome, in contrast to the remaining four which are opportunistic residents of the Afroalpine (group 4). Apparently resource competition prevented these birds from co-habiting the biome with other species: the Ankober Serin has an extremely specialized diet of very small grass seeds, a food source that is not available throughout the Afroalpine in sufficient quantities to sustain larger populations of different species.

Moreover, swifts (Apodidae) and swallows and martins (Hirundinidae, **Fig. 12**) that are frequently encountered foraging on the wing usually remain unassigned to the biome, particularly if evidence of breeding is not produced (but see [Coe \(1967\)](#) who



Fig. 11 The Black-headed Siskin is one of five seedeater taxa in the Afroalpine. Photo: T. Pröhl.



Fig. 12 The African Plain Martin belongs to the group of aerial insectivores that are frequently encountered foraging, but usually remain unassigned to the Afroalpine. Photo: T. Pröhl.

claimed to have found disused nests of Alpine Swifts *Tachymarptis melba* on Mt. Kenya). Their widespread geographic distribution and lack of specific association with the biome, however, do not render them characteristic elements of the Afroalpine. Nonetheless, although species identification poses another challenge, we expect more species to be found in the Afroalpine than are listed in **Table 1** if more attention was focused on these neglected groups. Similarly, cisticolas (Cisticolidae) are underrepresented in observation records of Afroalpine avifaunas, most likely because of their difficult identification. Some cisticolas are found in high-elevation moorland areas (cf. [Moreau, 1966](#)), and although there might not be many, they deserve the effort of careful identification.

Community Transition Patterns

Typically, the overlap between two adjacent habitats (ecotones) forms a particularly species-rich community ([Lomolino et al., 2010](#)). In contrast, the transition zone between the Afromontane and the Afroalpine is not characterized by an enhanced number of bird taxa. This finding has an interesting parallel in terrestrial invertebrate groups (e.g., Carabid beetles) which also do not constitute a separate community above the Ericaceous belt on Mt. Kilimanjaro but an impoverished set of montane communities ([Franz, 1979](#)). However, this similarity should not be overly generalized since beetles on Mt. Kenya and in the Ethiopian highlands do appear to form specific alpine communities ([Franz, 1979](#)). Moreover, soil invertebrates and even small mammals are much less mobile and often more specifically bound to local ecological conditions than birds. The huge species diversity of shrews on isolated African mountaintops is an example of such regional diversification as a result of adaptive radiations (e.g., [Stanley et al., 2015](#); [Lavrenchenko et al., 2016](#)). In contrast, the mobility of birds combined with their ability to quickly avoid unfavorable conditions, may have prevented them from forming distinct Afroalpine communities.

Additionally, the temporal patterns of presence and absence of Afroalpine birds are not well understood and the potential effect and extent of elevational migration in the Afroalpine has scarcely been studied. In particular, members of groups 2 and 3 may perform temporal elevational migrations, thus shifting their ranges between the Afroalpine and the Afromontane, either regularly or opportunistically. Such movements have been found in Afromontane birds ([Brown et al., 1982](#)) and are likely to take place in some Afroalpine taxa as well. For instance, there is evidence that at least some species of the Ethiopian alpine zones (e.g., Blue-winged Goose or Spot-breasted Plover) apparently leave these habitats, possibly following the availability of food or water (personal observation), while their whereabouts outside their well-documented highland occurrences are virtually unknown. Moreover, at least for the White-collared Pigeon a daily movement between high-elevation foraging sites and much lower roosting sites has been described ([Boswall and Demment, 1970](#)) but such patterns of movement are insufficiently known for other Afroalpine birds.

Another aspect of particular ecological interest is the close dependency of raptors on small mammal communities in the Ethiopian Bale Mountains. The exceptional species richness and abundance of small mammals in this area sustains a likewise unusually speciose raptor community that opportunistically exploits this food resource ([Colwell et al., 2008](#)). This might explain why there are so many raptors found among group 4.

The numerical difference between the Ethiopian and East African Afroalpine bird taxa differs from the finding of [Moreau \(1966\)](#), who already suspected his assessment to be biased because of the then less well-known Ethiopian avifauna. Although the situation has since changed, the biological information thus far collected remains comparatively poor and requires further focused study.

Comparison With Avifaunas of Other Alpine Biomes

In contrast to the arctic tundra and alpine tundra-like biomes on high-elevation mountains of the Palearctic, where broadly disjunct populations of the same bird species occur in climatically and structurally similar habitats as a result of a Post-Pleistocene separation of ranges (e.g., the Rock Ptarmigan *Lagopus mutus* with regular occurrences in the European Alps and in the Northern tundra proper), there is no such situation of separated lowland and highland distributions of birds to be found in Sub-Saharan Africa.

The Afroalpine shows both similarities and differences in comparison to other high mountain ranges on other continents (noteworthy are the European Alps, the American Cordillera, the Himalayas of Asia and the Southern Alps of New Zealand). Direct comparisons of alpine bird communities exist between African and South American mountains but usually do not focus on alpine zones alone (e.g., [Löffler, 1977](#); [Dorst and Vuilleumier, 1986](#); [Hanz et al., 2018](#)). Nonetheless, basic patterns of morphological, behavioral and functional aspects are remarkably similar, despite phylogenetic differences. Obviously, similar ecological conditions apparently influenced the combination of traits of both Old World and New World bird communities in a similar way, so that ecological counterparts can be identified among many avian feeding guilds between the mountain systems of the two continents ("intercontinental convergence," [Dorst and Vuilleumier, 1986](#)). This is particularly pronounced in passerines, namely in small insectivores and nectarivores as well as in small seed-eaters ([Dorst and Vuilleumier, 1986](#)). Moreover, the availability of food resources and the structure of the vegetation appear to be more important drivers for the diversification of avian communities than abiotic factors like temperature and precipitation ([Hanz et al., 2018](#)). However, since abiotic factors have a strong influence on the structure and composition of the Afroalpine landscape, its impoverished avifauna may reflect merely its ecological opportunism and resistance towards unfavorable conditions rather than representing a truly specialized alpine community ([Moreau, 1966](#)).

Conservation Aspects

In conservation practice, the Afroalpine usually plays a subordinate role, being either included in a broadly defined “Afrotropical Highlands” biome (Fishpool and Evans, 2001) or forming a sub-biome “Alpine moorland” of “Montane grasslands and shrublands” (Burgess et al., 2004). While these assignments are generally useful with respect to the protection of large-scaled geographic units, the Afroalpine as a mosaic of species range fringes needs particular attention as a sensitive indicator of upcoming ecological changes.

Considering the potential effects of ongoing climate change and particularly of global warming on the African continent (e.g., Hulme et al., 2005), biological responses could be substantial in mountain systems as uphill elevational shifts of communities, either in part or as a whole, are to be expected (BirdLife International and National Audubon Society, 2015; Freeman et al., 2018a). As a consequence, species composition and associated functional features of communities along elevational gradients might change drastically (Colwell et al., 2008; Corlett, 2011). Potential scenarios could be extreme, including the extinction of species at the highest elevations (“mountaintop extinction”; Colwell et al., 2008; Chala et al., 2016; Freeman et al., 2018b), thus possibly affecting Afroalpine birds directly. Moreover, upward movements of animal communities might become restricted by a much slower shift of treeline, decoupling biological interactions and destabilizing communities (Dehling et al., 2014). Regarding the bird communities found in the Afroalpine regions, effects are difficult to forecast as most of them do not affect this biome alone. Climate-induced changes to plant communities might at least indirectly influence the species-rich Afromontane bird communities (Vollstädt et al., 2017), and may subsequently affect Afroalpine birds as well.

Unfortunately, climate change is not the only threat to the Afroalpine biome. A growing human population and acute land use changes such as massive deforestation, heavy agricultural intensification and livestock overstocking already directly impact even the fragile upper habitats of African mountains (Messerli and Hurni, 1990; Burgess et al., 2004; BirdLife International, 2018). It is thus important to be able to identify and anticipate threats to the Afroalpine and its bird populations since geographically large-scaled protection assessments usually do not differentiate between effects in the Afromontane and in the Afroalpine.

Perspectives

Many of the birds taxa associated with the Afroalpine have not been adequately studied with respect to their actual affiliation with the biome. Systematic monitoring data do not exist and basic biological information is often fragmentary. Some birds appear to be just regular visitors while breeding is incompletely documented. Biological data on food and resource utilization in general is available only cursorily. Relevant comparisons between Afroalpine and Afromontane populations of the same species have so far not been made. Also, further research is required to understand the temporal mechanism and the potential triggers of (regular?) elevational movements of the birds inhabiting the Afroalpine. All this is of particular importance considering the intensified land use in African mountain systems against the backdrop of ongoing climate change. A prioritization of practical conservation measures is necessary to guarantee their effectiveness but can only be based on well-founded research. Thus, we suggest systematic bird monitoring activities that are accompanied by structured studies focusing on key aspects of the biology (feeding, breeding, seasonality) of Afroalpine birds.

Conclusions

The number of avian taxa recorded in the Afroalpine is relatively small, particularly considering the speciose subjacent elevational zone, the Afromontane. However, there is no specific Afroalpine bird community, although a few taxa are more regularly encountered there than others, including a small number of endemics. By and large, the avifauna of the Afroalpine merely represents a greatly impoverished Afromontane community rather than a distinct community of its own.

As a consequence, the transition zone between the Afromontane and the Afroalpine is not characterized by an enhanced number of bird taxa. This is in contrast to the typical effect found at many habitat edges (ecotones), where members of two adjacent zones form a particularly species-rich community.

Further research is needed to comprehend the patterns of occurrence of Afroalpine birds and the biotic and abiotic triggers shaping their temporal and spatial distribution. A wary eye has to be kept on the effects of climate change as habitats on high elevations might suffer severely under persistent global warming.

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Biogeography of South American Highlands

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Abstract

Alpine environments in South America occur essentially in the Andes, which extend along a latitudinal gradient between 11°N in Colombia and 55°S in Chile. The alpine biodiversity of the Andes is the richest in the world and it displays remarkable patterns of endemism, species radiations and morphological/physiological adaptations. In this article we aim at discussing the major biogeographical drivers of alpine biodiversity in the Andes and their consequent spatial patterns (i) in the past, (ii) at present, and (iii) in a near future under the influence of global change. Moreover, we briefly discuss the biogeography of smaller alpine environments in South America, that is, the Guayana highlands, Campos de Altitude and Tristan da Cunha Island. First, the evolution of the South American continent during the Mesozoic and Cenozoic greatly shaped biodiversity patterns in the Andes through mountain uplift and successive periods of geographic connectivity and isolation. Mountain building led to new niches that became available for colonization by both temperate and tropical species, while important topographic changes and the continental connection with North America provided either biotic corridors or sky islands. Second, Pleistocene glacial dynamics accelerated taxonomic diversification but also exacerbated extinction processes that substantially changed Andean biodiversity. Third, human activities have progressively influenced the structure and function of alpine ecosystems, leading to today's Andean biogeography. Current drivers of biodiversity distribution can be described at three spatial scales. At the continental scale, latitudinal shifts create strong variations in temperature seasonality, influencing, for example, snow cover duration and generating distinctive adaptations from the North to the South. At the regional scale, rain shadow effects, the Humboldt Current and trade winds combine with topographical and bedrock variations to create hotspots of endemism such as are found in the Sierra Nevada de Santa Marta (Colombia) or alpine deserts with specific life forms such as are found in the Central Andes. At the local scale, the spatial distribution of species is extended through habitat amelioration by nurse/engineering plants. These unique alpine ecosystems are highly vulnerable to the combined effects of climate and land use changes. High-Andean biota will undoubtedly respond to these changes by either adaptation, local/regional migration, or extinction. Extinction is already occurring at alarming rates in many taxonomic groups. Finally, we predict that new threats, such as biotic invasions and the creation of non-analog communities will directly affect biodiversity responses.

Introduction

By crossing the continent from one end to the other, the Andes are not only the largest mountain range in South America but also the longest continental mountain range in the world, spanning seven countries between latitudes 11°N in the Sierra Nevada de Santa Marta and 55°S in the Cordillera de Darwin. The Andes encompass large highland areas within and outside the tropics. In this article, we will refer to highlands as alpine environments *sensu lato*, whose ecosystems are constrained by low minimum temperature and are mostly located above the natural treeline (Körner, 2003). Alpine areas in the tropical Andes lie roughly between 3000 and 5000 m a.s.l. but they develop at sea level in boreal Patagonia, including outside the Andes. By hosting 38% of the immense Neotropical plant diversity (Antonelli and Sanmartín, 2011), the Andes are major contributors to South American

biodiversity. Spatial patterns of biodiversity include exceptional rates of endemism, very rapid species radiation rates (Madriñán et al., 2013) and the development of specific functional traits and life forms representing specific adaptations (Rundel et al., 1994). An outstanding example is the Páramo in the northern Andes, which is considered the most phytodiverse tropical-alpine province on Earth, with about 5000 plant species, 60% of which are endemic (Sklénář et al., 2014; Peyre et al., n.d.; Fig. 1).

To provide an overview of the biogeography of alpine Andean region and make exploratory scenarios for the future of the biodiversity, we divided this article into three sections: past, present and future. In each section we focus on the evolution of broad-scale spatial patterns of biodiversity and their biotic-abiotic drivers, and illustrate with diverse specific examples. We close the article by exploring the biogeographical features of the other, much smaller alpine environments of South America. Because of our experience as plant ecologist and phytogeographer, this contribution is centred on the biogeography of plants, without disregarding animals.

The Past

The geological and human histories of the Andes are greatly responsible for the substantial species diversification that happened through time on the South American continent, particularly their alpine environments. Among the most important factors that gave rise to Andean biodiversity and whose effects are sometimes difficult to disentangle are the mountain uplift itself, the presence of biogeographic barriers and migration routes, and extreme climatic fluctuations, followed by a posteriori anthropogenic remodeling (Fig. 2).

Andean Uplift and Altitudinal Migrations

The Andean uplift progressively allowed the creation, shaping and maintenance of a true Andean alpine belt with specific tropical alpine ecosystems. Regional subduction tectonics of the Pacific plates under the South American plate initiated in the Mesozoic (Jurassic-Cretaceous) and led to the initial uplift of the Central and Southern Andes, while draining the Amazonian sea that was covering most of central South America. The main orogeny of the northern, central and southern Andes took place during the Paleogene, especially Eocene and Oligocene (60–30 Myr). The northern Andes were geographically separated from the central Andes at the time by the Western Andean Portal (WAP), a relic of the Amazonian sea at $\sim 5^\circ\text{S}$ (Hooim et al., 2010). In the early Miocene (~ 23 Myr), the Pacific plates split, leading to a collision of the South American and Caribbean plates and resulting in an intensified uplift of the northern Andes. The mountain building of approximately 50% of the Andes consequently narrowed the Orinoco distal basin and allowed for a large watershed, the Pebas system, to occupy most of Amazonia (Hooim et al., 2010).

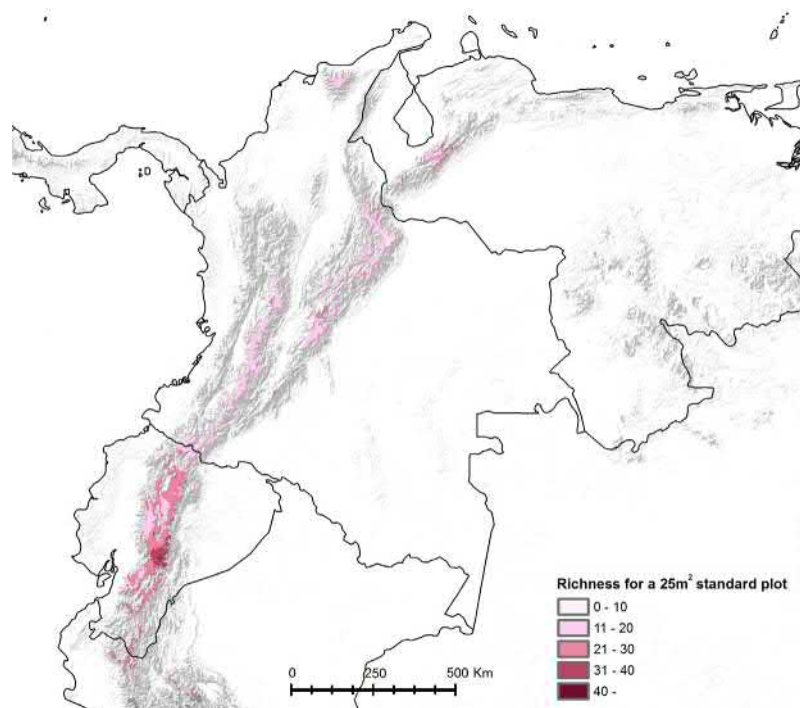


Fig. 1 Predicted local plant species richness across the Páramo biogeographical province, shown at a 30 arc-second (~ 1 km) resolution. The local richness predictions at plot scale were obtained using a Universal Kriging model, adjusting an environmental Generalized Least Squares model and spatial interpolations in form of an Ordinary Kriging model.

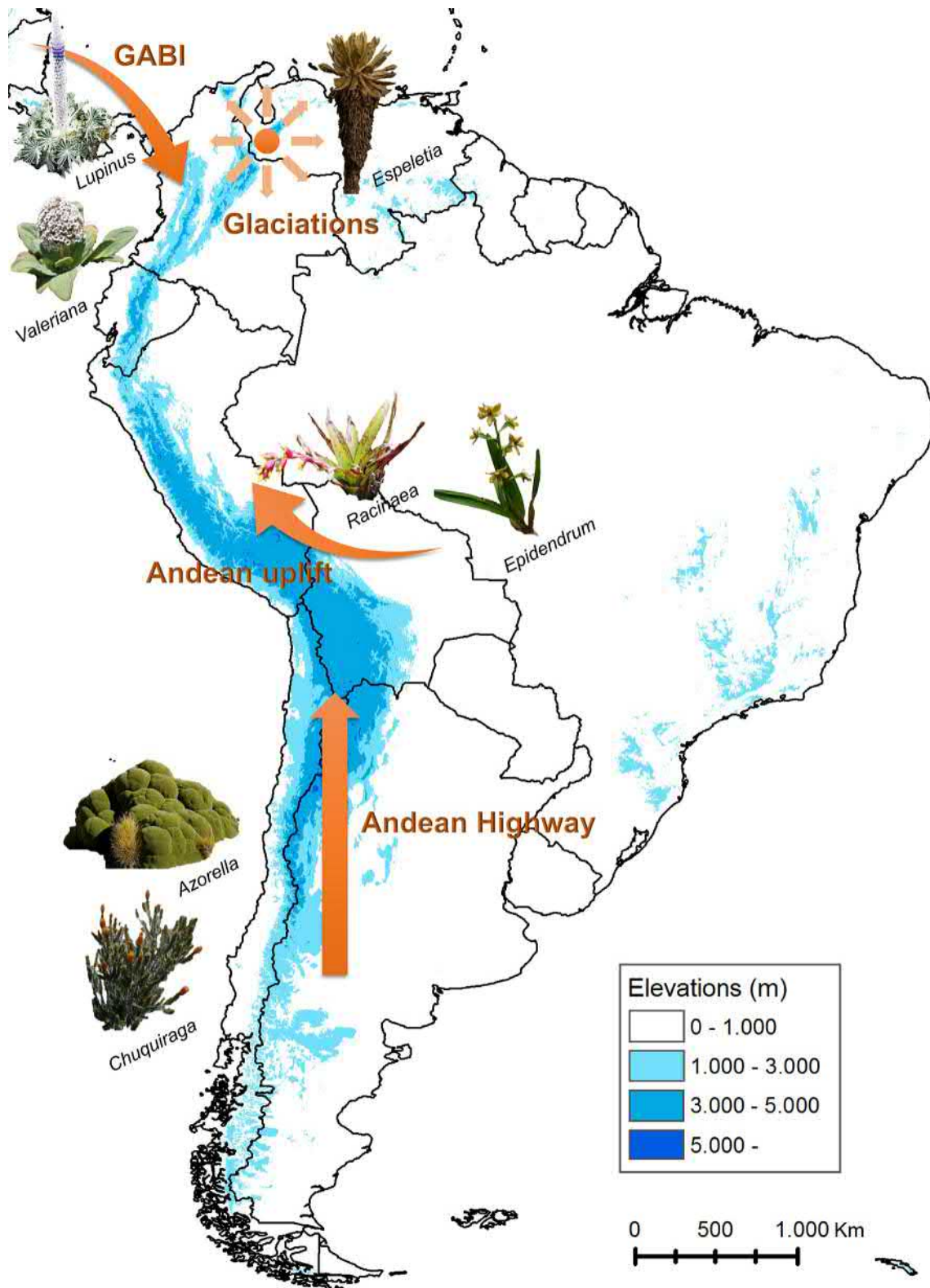


Fig. 2 Main events in high-Andean plant past biogeography: the Andean uplift allowing upheaval of species with adaptive capacity to the alpine environments; the Andean Highway migration route, which allowed north-south migrations along the cordilleras; the Great American Biotic Interchange (GABI) resulting in north-American taxa reaching and colonizing the Andes; the Glaciation dynamics that promoted diversification through rapid lower-upper movements of the treeline and snowline.

However, the most intense orogeny phase for the region came later, during the Mid-Miocene (~10 Myr) and early Pliocene (~4.5 Myr), with the Andes reaching 60% of their present elevation in this short period (Garziona et al., 2008). Finally, by the end of the Pliocene, the western Colombian cordillera emerged, completing the last significant uplift of the Andes.

With the Andean uplift, new topographic and environmental heterogeneity was created, leading Andean and outer-Andean species to adapt in different ways. In fact, the Andes form a strong barrier separating the lowland species from either the Pacific or Amazonian-Pampa sides. At the same time, the raising cordilleras created new niches and provided biotic temperate corridors, which allowed for mountainous species to disperse and radiate (Antonelli and Sanmartín, 2011), especially in the mostly continuous tropical Andes and to a lesser degree in the more isolated southern Andes. Finally, the highly diverse species pools of the lowlands, for example, from the Amazonian and Chocó biomes, contained many taxa with adaptive capacities that escaped these overly saturated lowland areas and dispersed to colonize alpine areas (Antonelli and Sanmartín, 2011). This pattern was observed for many taxa such as tropical bamboos and bromeliads (Sklenář et al., 2011; Fig. 2).

Geographic Isolation and Latitudinal Migration Routes

The WAP in northern Peru constituted one of the most important biogeographic barriers to alpine biodiversity during the Andean orogeny, because its low elevation at sea level and marine influence greatly limited species' dispersal. The WAP gradually closed ~12 Myr, allowing species to cross over from the south-central Andes to the northern Andes and back, hence creating the "Andean highway migration route" (Antonelli and Sanmartín, 2011). For example, *Azorella* is an Austral-Antarctic plant genus that used this path to colonize the newly available northern Andes from the south (Nicolas and Plunkett, 2012; Fig. 2). By the end of the Miocene, the Pebas system had drained and the Marañón River dug the narrow Huancabamba depression through the Andean cordillera in northern Peru, thereby creating a new biogeographical barrier to the dispersal of high elevation taxa, as observed for birds (Hazzi et al., 2018).

South America became an isolated continent during the Cretaceous and therefore independently developed a very ancient and largely endemic biota (Smith and Klicka, 2010). This isolation continued until the uplift of the Panama isthmus, which connected the continent to North America ~3 Myr ago, resulting in the Great American Biotic Interchange (GABI; Antonelli and Sanmartín, 2011). However, many high-elevation animals and plants may have crossed between the two continents before the final closing of the Panama Isthmus, probably through long distance-dispersal and island hopping, for example, the genus *Valeriana* in the Miocene (Bell and Donoghue, 2005). Biotic migrations greatly accelerated with the GABI (Hoon et al., 2010). For example, the Holarctic temperate genera *Lupinus* (Hughes and Eastwood, 2006) crossed the isthmus to colonize the northern Andes and radiate south, eventually reaching Patagonia. Other plant taxa with representation in the Neotropical lowlands and highlands such as *Pitcairnia* and *Tillandsia* successfully migrated and colonized Central America using the GABI (Givnish et al., 2014). An equal exchange of taxa occurred between the two continents, as observed for mammals, birds and plants, however, taxa moving to South America usually proved more successful than those that migrated in the opposite direction, resulting in important species accumulation in the South American lowlands and but also in alpine areas (Smith and Klicka, 2010). For example, for mammals, 50% of modern South American genera have North American origins, whereas only 10% the other way around (Marshall et al., 1982). Therefore, the Andean alpine belt became considerably species-enriched, especially regarding plants but also animals, thanks to these new latitudinal migration routes trespassing previous geographic barriers.

Glaciations and Taxonomic Diversification

By the end of the Pliocene, most of the Andes had reached their modern elevation and presented mountain forests topped by grass- and shrub-dominated alpine communities, precursors of the Puna and Páramo biogeographical provinces (Garziona et al., 2008). During the Pleistocene, species diversification amplified in the high Andes, mostly driven by glacial dynamics. In comparison with other continents, South America was generally less affected by ice cover and temperatures were generally only 5–10°C lower than today (Sandel et al., 2011). The Neotropics, especially the lowlands, acted as a biological refuge, enhancing species accumulation through niche conservatism and speciation time mechanisms. The Andes experienced ~20 glacial-interglacial cycles in the Pleistocene, consisting roughly of 90% glacial epochs and 10% interglacial epochs. These climatic cycles influenced and sped the differentiation of both alpine flora and fauna. For example, glaciations shaped the Páramo as the coolest and fastest evolving hotspot in the world (Madriñán et al., 2013).

During glacial epochs, the elevation belts shifted downslope greatly, down to 1000–1500 m for the northern Andes and increased considerably their surface area, for example, the Páramo increased by three times its modern size (Flantua and Hooghiemstra, 2018). Alpine species usually migrated downward and radiated through the continuous elevation belts, whereas extra-Andean species concentrated in lowland refugia. In contrast, during interglacial epochs, elevation belts gradually rose up and isolated the Páramo and the Puna, creating mountain biogeographic islands (Flantua and Hooghiemstra, 2018). At this time, the organisms that could keep up with climate change became isolated and speciated, contributing to the important endemism that is observed today (Hughes and Eastwood, 2006). In parallel, the contingent lowlands lost species that used this opportunity to further colonize mountain areas, as observed in birds (Hazzi et al., 2018). A good example of Pleistocene-induced diversification is the Asteraceae subtribe Espeletiinae, which appeared at the end of the Pliocene in Venezuela and radiated along the Colombian cordilleras, reaching Ecuador during the Pleistocene, speciating into about 60 species in the process (Fig. 2).

Human Influence

The first evidence of human presence in the Andes goes back to 15,000 year BP (Wheeler, 1984) with testimony of hunter-gatherer human behavior in the humid Puna of Central Peru. Occupation records for the dry Puna of the south-central Andes go back to around 10,000 year, and it is not until 6000 year that traces of domestication were encountered and showed the first signs of settling and grazing-agricultural activities (Wheeler, 1984). Such domestication occurred principally in the Central Andes and included animals, that is, llama and alpaca, and plants, that is, potato and quíñua. The expanding and increasing activities slowly caused environmental impacts; nonetheless, it is only in the case of broad-scale human migrations such as the Inca's through Bolivia, Peru and Ecuador that said impacts influenced the general alpine landscape and biogeography. For example, *Polylepis* forests were believed to dominate the treeline around 4000 m for most of the Pleistocene and the authors hypothesize that humans gradually deforested the treeline (Fjeldsø, 1992). In comparison with the central and later southern Andes, the northern Andes remained mostly unoccupied until Spanish colonization, with only scant evidence of nomad hunter-gatherer practices after AD 1200 and no important development of permanent settlements (Molinillo and Monasterio, 2002).

The Spanish colonization of the Andean countries in the 16th century brought many important environmental impacts on the alpine ecosystems and their species, especially in the relatively pristine northern Andes. The strictly controlled grazing and agricultural practices of pre-Colombian societies were quickly replaced by more extensive methods combined with the introduction of new crop and cattle species, for example, cow, sheep, and goat (Molinillo and Monasterio, 2002). The lower alpine elevations were usually used for crops, whereas higher elevations were used for unregulated grazing. Moreover, it was common to associate grazing areas with frequent burning of the existing biomass to create more palatable grasses for cattle, hence homogenizing large landscape areas (Hofstede et al., 2003). In parallel, settling land-owners progressively promoted new adapting grasses to increase the foraging quality, originally either local species from local lower elevations such as *Paspalum* and *Bromus*, or alien species, like *Pennisetum*, *Holcus*, and *Anthoxanthum* (Molinillo and Monasterio, 2002). The anthropogenic pressure kept increasing with time, with humans diversifying and accelerating their activities with the successive technological advances and agrarian reforms, especially in the second half of the 20th century (Hofstede et al., 2003). Each innovation of human practices intensified and expanded geographically, slowly replacing native, specialized species, selecting opportunistic species and allowing for aliens to intrude the alpine belt, while the landscapes became homogenized over broad-areas and fragmented in others. Therefore, the anthropogenic history of the Andean highlands has played a significant role in progressively shaping the spatial patterns of biodiversity found today, forming the basis of their future evolution.

The Present

Effects of Latitude (Continental Scale)

Several Andean biogeographical provinces have been described along the Andean latitudinal gradient, without focusing specifically on the alpine belt. We propose a simple and focused classification inspired from existing works (Fig. 3). The tropical Andes host two biogeographical provinces with strong dissimilarities in their environment and biodiversity (Cuesta et al., 2017): (i) the wet Páramo province with reduced seasonality in the northern Andes and (ii) the drier and more seasonal Puna located in the central Andes. Further south, the Mediterranean high Andes occur from 25°S (Antofagasta) to 39°S (Osorno) and are defined by a pronounced dry season and precipitation concentrated during the austral winter. This biogeographical province encompasses the Prepuna as defined by Morrone (2006) and includes an enlarged area of the Mediterranean Andean region as described by Rivas-Martínez et al. (2011). The southernmost province is Patagonia, which can itself be divided into temperate and boreal provinces. More pronounced seasonality to the South increasingly influences Patagonian biodiversity, with higher variations in photoperiod and reduced growing season for plants. Accordingly, although alpine vegetation is characterized by a high level of environmental homogeneity worldwide, especially due to low minimum temperatures (Körner, 2003), the extended latitudinal gradient shaping the Andes gives opportunities for living organisms to develop specific adaptations. We describe below some of the prominent effects of the Andean latitudinal gradient on the alpine biodiversity distribution in the Andes.

Temperature seasonality increases markedly with latitude, affecting patterns of alpine biodiversity. The latitudinal effect is almost nil close to the Equator while reaching maximum values in Patagonia, where it is responsible for long snow cover duration during winter. Conversely, at low latitude, daily temperature variations increase and generate diurnal freeze-thaw cycles because of the absence of protective snow cover at night (Rundel et al., 1994). The distribution of alpine biodiversity is strongly driven by the spatial and temporal distribution of snow cover, especially because of its ability to protect plants against cold temperatures at night. Accordingly, whereas most alpine plants share dwarf shapes and crucial investment in root structure, low-latitude climatic patterns promote specific adaptations to the absence of snowpack. This includes higher ratios between the plant's aerial and root biomasses with, for example, the development of giant alpine life forms (Rundel et al., 1994; Fig. 4). Other adaptations at low latitude include tolerance of temperatures that may drop as low as -20°C almost every night, through (i) the development of large, hemispheric cushions able to ameliorate microenvironments (e.g., *Azorella compacta* Phil.; Fig. 2) or (ii) the accumulation of soluble sugar in *Polylepis tarapacana* Phil. as a freezing avoidance mechanism, which also allows growth activity most of the year (supercooling; Rundel et al., 1994; Fig. 4).

Another latitudinal effect builds on a mismatch between the dry and the cold season outside versus inside the tropics, which represents the transition between the Puna and the Mediterranean high Andes (Fig. 3). Being sufficiently far from the equator, the

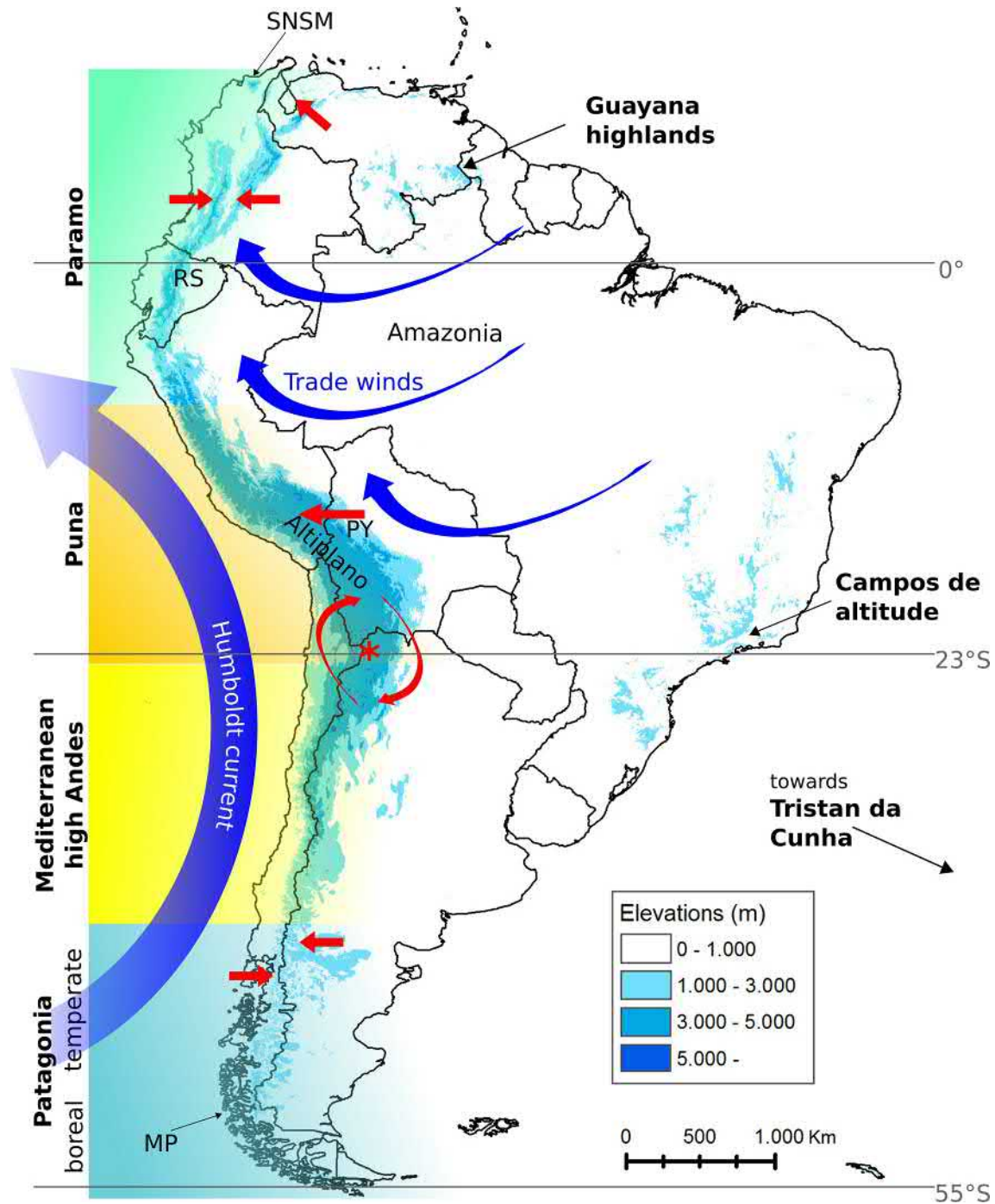


Fig. 3 Distribution of mountains and alpine biogeographical provinces in South America. SNSM: Sierra Nevada de Santa Marta; PY: Páramo Yungueño; MP: Magellanic Páramo; RS: Volcanoes Reventador and Sumaco. Red arrows indicate steep climatic variations: *: seasonal mismatch between precipitation and temperature above and below the Tropic of Capricorn (23°S); other arrows are examples of rainshadow effects at different latitudes along the Andean Cordillera, in relation with the effects of trade winds and the Humboldt Current.

Puna is significantly influenced by annual temperature variations. Whereas precipitations concentrate between November and March during the “warm” season (*Bolivian winter*), it experiences a cold season, which usually peaks in July and August and coincides with the lowest precipitation amounts. These cold, dry conditions create a stressful period for organisms, with the combined effects of minimum temperature and drought in the absence of protective snow cover. Outside the tropics (Mediterranean), this pattern changes, with precipitation falling during the cold season, mostly as snow. Interestingly, the disjunct distribution of the cushion peatland species *Patosia clandestina* (Phil.) Buchenau with significantly distinct leaf traits in these two provinces suggests that the

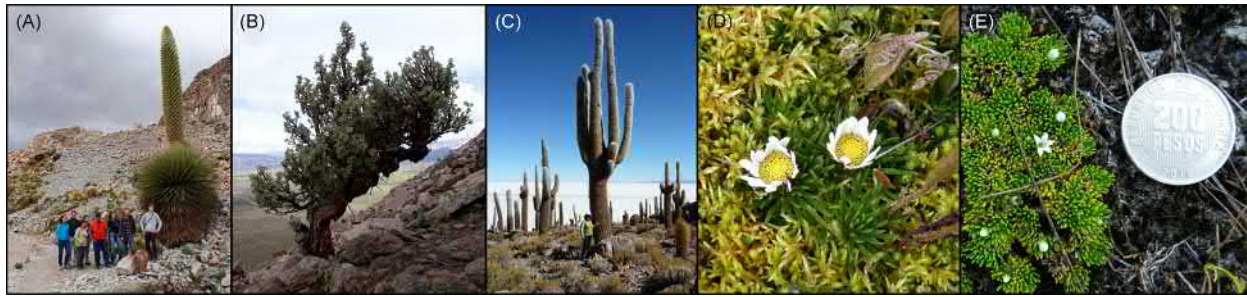


Fig. 4 Alpine plant sizes in the Andes. Giant life form is a specific adaptation likely due to the absence of durable snow cover in tropical alpine regions. (A) Giant basal rosette *Puya Raimondii* Harms, 4200 m a.s.l. (Puna). (B) *Polylepis tarapacana* Phil. tree, 4800 m (Puna). (C) Cactus *Trichocereus pasacana* Britton & Rose (F.A.C. Weber ex Rümpler) (Puna; up to 9 m, pers. obs.). See also *Espeletia occidentalis* A.C.Sm. in Fig. 6. Dwarf life forms develop in all alpine environments of the Andes. (D) *Xenophyllum humile* (Kunth) V.A.Funk, 3600 m (Páramo). (E) *Lysipomia muscoides* Hook.f., 3200 m (Páramo).

contrasting seasonality, combined with an important physiological barrier (alpine desert) may lead to speciation processes (unpublished data; Fig. 5).

The elevation of alpine environments in the Andes decreases steadily with increasing latitude, from 3000 to 5000 m near the equator to sea level in southern Patagonia. At higher elevations, UV radiation increases and atmospheric oxygen decreases, posing additional constraints for living organisms through tissue damage and reduced respiration. Moreover, elevation increases atmospheric aridity, both through reduced relative air humidity and a significantly lower amount of precipitation above 2000–3000 m, known as the inverted rainfall gradient (Nagy and Grabherr, 2009). To withstand these particular constraints, tropical alpine plants have developed specific adaptations. They include overrepresentation in the Páramo and the Puna of (i) small, microphyllous, perennial leaves to limit desiccation, (ii) dense hairiness in leaves, stems and flowers to avoid damage from UV radiation, desiccation, the effects of cold temperature, and to increase stomatal activity (Rundel et al., 1994), and (iii) nodding capitula to ensure floral development and protect them from the negative effects of precipitation (Sklénář, 1999; Fig. 6).

Effects of Regional Parameters

High Andean summits have been shown to generate rain shadow effects that give birth to strong climatic variations and influence species distribution. Rain shadow effects can occur in the presence of several sequential mountains, as in Colombia and in Venezuela, in the presence of a high Andean plateau located between two cordilleras, for example in Bolivia, or between two sides of a single mountain, as in Ecuador (Mount Chimborazo; Sklénář and Lægaard, 2003). In each case, topographical barriers reduce precipitation from the West (humid Pacific influence) or from the East, (humid Atlantic influence and/or humid Amazonian influence brought by trade winds; Fig. 3). In temperate Patagonia, annual precipitation levels decrease from 3000 mm to 500 mm in only 80 km from the East to West (Veblen et al., 2003). Rain shadow effects are easily detectable in the high mountains bordering Amazonia, with glacier fronts located at lower elevations on their eastern side than on their western side. In the Páramo province, the climatic variability attributable to rain shadow effects has had a significant influence on patterns of plant richness and species distribution into phytogeographical units (Peyre et al., n.d.).

The vicinity of Amazonia on the eastern flank of the Bolivian Andes has created extrazonal páramos in the Puna biogeographical province, which share a significant number of taxa with the Páramo biogeographical province in the northern Andes (Páramo Yungueño). Interestingly, the major influence exerted by neighboring ocean on the climate of south-western Patagonia (hyper-oceanic bioclimate sensu Rivas-Martínez et al., 2011) seem to have created other extrazonal páramos at latitudes of approximately

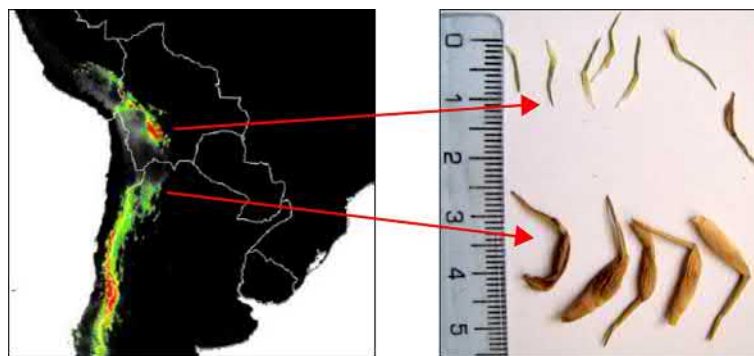


Fig. 5 Disjunct, potential distribution of the cushion peatland species *Patosia clandestina* within and outside the Tropics (left) with individual of each population displaying distinct leaf traits thought to source from seasonal mismatch (right).



Fig. 6 Common morphological adaptations of plants to high elevation in the tropical alpine Andes, not frequent at higher latitudes. (Left) Microphyllous, coriaceous leaves in *Chuquiraga jussieui* J.F.Gmel. (Rucu Pichincha, Ecuador, 4400 m). Centre: hairiness in the leaves and flowers of *Espeletia occidentalis* A.C.Sm. (páramo de Belmira, Colombia, 3100 m); see also *Lasiocephalus ovatus* Schltdl. in Fig. 8. (Right) Nodding capitula in *Senecio serratifolius* (Meyen & Walp.) Cuatrec. (Cordillera Real, Bolivia, 4860 m). The palm species *Ceroxylon parvifrons* (Engel) H.Wendl. also adapted to the tropical alpine climate (centre).

50°S (Magellanic Páramo; Morrone, 2006; Fig. 3). Characterizing the connections between the northern Andean Páramo, the Páramo Yungueño and the Magellanic Páramo constitute an interesting scientific perspective to better understand the biogeographical processes shaping the alpine biodiversity of the Andes.

Under the influence of the cold Humboldt marine current from the coasts of central Chile to southern Ecuador, precipitation coming from the Pacific Ocean is sharply reduced (Fig. 3). This regional pattern gives birth to arid alpine environments on the western side of the Andes, adding to climatic heterogeneity and contributing to the existence of the Puna and the Mediterranean high Andes. The rain shadow effects, combined at some places with the effects of the Humboldt current, have created alpine deserts, where species have adapted and created specific forms and strategies, not only to cope with atmospheric aridity but also with edaphic drought. Grass species such as *Festuca orthophylla* Pilg. (Puna), trees such as *Polylepis tarapacana* Phil. (Puna) and even the caulescent rosettes (*Coespeletia timotensis* (Cuatrec.) Cuatrec., Venezuelan Páramo) are examples of species that have adapted and developed spotted patterns so as to avoid root competition among individuals of their own species in alpine deserts. In parallel, cactus species (Cactaceae), are observed in the Puna up to 4500 m (*Cumulopuntia boliviana* (Salm-Dyck) F. Ritter and *Lobivia pentlandii* (Hook.) Britton & Rose; Meneses et al., 2015; see also Fig. 4).

Beside the climate, geo-edaphic conditions and the topography are important drivers of biodiversity patterns in the alpine provinces of the Andes. Apart from metamorphic and sedimentary bedrocks, the high Andes are partly made of volcanic bedrock. For example, most of the Ecuadorian páramos are found on volcanic substrates, which has been suggested to favor the development of high microendemism in carabid beetles (Moret, 2009). The volcanic soils of the páramos have also been shown to develop exceptional properties of water retention, generating hydromorphic ecosystems within specific assemblages of plants (Poulenard et al., 2003). From a topographical standpoint, the north and the extreme south of the Andes are particularly fragmented (Fig. 3), giving birth to an archipelago of alpine areas where patterns of speciation have been documented for several organisms (review in Anthelme et al., 2014b). This fragmentation has given birth to particularly uncommon vegetation patterns such the occurrence of a cold-adapted palm in the Páramo, up to 3600 m (*Ceroxylon parvifrons* (Engel) H. Wendl.; Sanín et al., 2016; Fig. 6) and microendemism in aquatic invertebrates developing in glacial-fed streams (Jacobsen and Dangles, 2017). Small alpine areas separated by large distances from main alpine areas have created alpine environments with outstanding endemism in plants, birds and invertebrates, as in the Sierra Nevada de Santa Marta, Colombia (Anthelme et al., 2014b; Fig. 3). In the Ecuadorian volcanoes Reventador and Sumaco, strong isolation and volcanic activity has led to early successional Páramo plant assemblages likely brought by long-distance dispersal (Løjtman and Molau, 1983). Conversely, the rest of the Andes, from the north of Peru southward, display an alpine continuum represented by the Andean Altiplano. These regions have developed fewer endemic species assemblages.

Biogenic Amelioration of Habitats (Local Scale)

Alpine environments have been shown to host plant communities strongly driven by positive interactions between plants through biogenic amelioration. This takes place at the local level, but it well prove to be as important as predictor of future plant diversity as the effects of climate change in alpine environments, as proven with several studies conducted in the Andes and other alpine environments (*stress-gradient hypothesis*; Cavieres et al., 2014). At the ecosystem scale, some cushion species generate high Andean peatlands. These are extensively distributed in the Andes from Colombia to Chile and Argentina and provide habitats for a significant number of associated plants along a wide altitudinal range, such as *Gentiana sedifolia* Kunth, *Oritrophium peruvianum* (Lam.) Cuatrec. and *Werneria pygmaea* Gillies ex Hook. & Arn., (Fig. 7). The presence of large cushion-forming plants in the Páramo provide carabid beetles with local refuges that partly explain the high rate of endemism found in the high tropical Andes (Moret, 2009). These examples attest to a significant impact of nurse plants in reducing biogeographical barriers for other plants and animals.



Fig. 7 The Engineer/nurse species *Distichia muscoides* Nees & Meyen (centre) creates alpine peatlands that host similar species on an extended latitudinal gradient, for example, *Gentiana sedifolia* Kunth: in Bolivia on the left, in Colombia on the right.

The Future

Tropical Andean mountains are classified as *highly vulnerable* by the Intergovernmental Panel on Climate Change (IPCC), this mostly due to their geographic position, elevation, environmental heterogeneity and high biodiversity in terms of species and ecosystems.

Global Change

Predicting the effects of climate change on biodiversity is particularly difficult in tropical mountain areas. However, most authors agree that temperatures will increase up to 3°C (± 1.5) in the most vulnerable areas such as the Andean Páramo. Higher temperature anomalies, that is, increases of 0.1–0.3°C have been observed in the tropical Andes during the second half of the 20th century (Buytaert et al., 2011). Overall, Andean areas at relatively low elevation and close to the cooling humid lowland hotspots (Amazonia, Chocó) are less likely to suffer drastic temperature changes than high elevation areas in drier climates. Higher levels of precipitation are predicted for the coming decades in the northern Andes, up to +300 mm/year, apart from the Caribbean-facing mountains which may receive less precipitation (Buytaert et al., 2011). Increased seasonality is predicted for the Central Andes, with an overall extension of dry periods. In addition, temporal, spatial and intensity changes in the Pacific Decadal Oscillation, El Niño Southern Oscillation, and position of the Inter-Tropical Convergence Zone, will undoubtedly affect Andean meso- and microclimates, especially regarding precipitation patterns. Finally, the retreat of glaciers is a predominant issue, with glaciers thinning between 0.6 and 1.2 m/year in the tropical Andes, usually faster in the northern Andes in comparison with central Andes (Rabatel et al., 2013). Moreover, anthropogenic responses to climate change are predicted to have an even greater impact than climate change itself. Human population and activities will increase, intensifying impacts in already-occupied regions and bringing impacts to areas currently unavailable, for example the raising of the agricultural frontier above 4200 m in the northern Andes (Hofstede et al., 2003).

Biodiversity Response

Because of the diversity and complexity of the alpine environments of the Andes, it is particularly challenging to maintain species, ecosystems and their ecological equilibrium in the future. Facing global change, species can adapt, migrate or go extinct. It is expected that many Andean species will adapt their life cycle or physiology, for example so they can handle more extreme climatic events and fluctuations as shown for plants (Sierra-Almeida and Cavieres, 2010). In addition, distribution, and richness patterns could drastically change, for example, frogs and toads are shifting to higher elevations in the Peruvian Puna (Seimon et al., 2007). Such migrations can be impaired near the mountaintops where available niches and dispersal deficiency become limiting factors (Peyre et al., 2018; Fig. 8). Increase in local extinction rates of species or communities, as well as changes in phenological patterns are also expected to occur. Some authors predicted an extinction rate of almost 60% of plants by 2080 for the northern Andes, but smaller-scale studies revised this rate to 10% for high-elevation plants in the alpine Ecuador by 2100, although this number is still very problematic due to the fact that most threatened species are endemics (Peyre et al., 2018). At the ecosystem and biome level, drastic changes regarding species distribution and assemblages could also occur. For example, it is expected that the alpine plant communities of Ecuador will suffer drastic changes in terms of species assemblages and richness decreases, especially along the Amazonian flank (Peyre et al., 2018). Changes at the community level can however be buffered by the maintenance of microclimatic and edaphic conditions, for example, nurse plants and their associated biota (Anthelme et al., 2014a).

Invasive Species and Non-Analog Communities

Invasive species represent a serious issue in most of the alpine belt of the Andes, but especially in the northern range. The invasive strategies of such species and whether they move or extend their ecological niche in the Páramo and the Puna remain

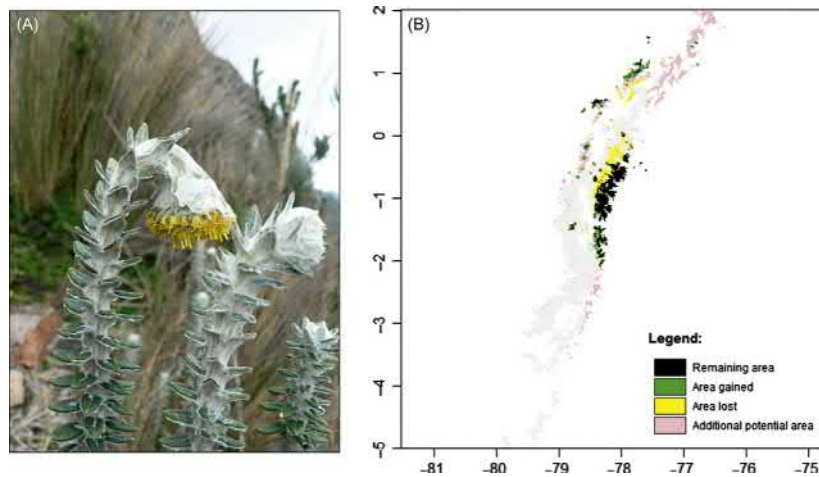


Fig. 8 Picture (A) and distribution changes (B) of *Lasiocephalus ovatus* (Asteraceae) in the Ecuadorian super-páramo belt (4000–5000 m) under the effect of Climate Change for the period 2010–2100 (under the BCCCSM1-1 global climate model). Colors indicate where the species has remained (black), expanded (green), retracted (yellow) and where it could possibly be but could not disperse by 2100 (pink).

understudied. Five main drivers are usually associated with invasions in high mountains: (1) pre-adaptation to abiotic conditions, (2) disturbances, (3) biotic resistance of local communities through strong interactions, (4) propagule pressure, and (5) capacity to create synergic interactions with local species (Pauchard et al., 2009). Given the harsh environmental conditions, most invasive species in the Andes are plants, for example the shrub *Ulex europaeus* L. and herb *Rumex acetosella* L. in the northern Andes, or the tree *Pinus contorta* Douglas ex Loudon and the herb *Taraxacum officinale* (L.) Weber ex F.H.Wigg. in the southern Andes. However, animals, especially invertebrates, can only intrude and proliferate in the alpine belt, for example Pterophoridae (plume moths) are invading and weakening Espeletiineae species in the Páramo (Salinas et al., 2013). Disease incidence and impacts are also favored by climate change, as illustrated by the spread of frog pathogens through species migration and community re-assemblages in the central Andes (Seimon et al., 2007). Finally, new alpine niches will become available, especially related to glacier melting, and these areas are prone to important invasions and formation of non-analog communities comprised mostly of opportunistic and invasive species (Walther, 2004).

Other Alpine Environments of South America

Guayana highlands (GH): also called Pantepuis, the GH are table mountains mainly distributed in the tropics of Venezuela, with several extensions in Brazil, Colombia and Guyana. These highlands reach a maximum elevation of 3014 m at Sierra de la Neblina (Fig. 3). From a morphological viewpoint, the (sub)alpine plants observed in the GH are relatively similar to their tropical Andean counterparts, and form a “páramoid” vegetation (Huber, 1994). However, their pronounced geographic isolation has given birth to a high degree of endemism at the species level whereas endemism at the genus level is relatively low as a result of substantial connections between the GH and the lowlands, as evidenced with shared taxa. Some important taxonomic/functional groups are shared with the Andes (e.g., Asteraceae stem rosettes), whereas other important groups such as the Poaceae are comparatively less represented (Rull and Vegas-Vilarrúbia, 2006). The absence of a dry season in the GH and their limited elevation may explain certain differences with their Andean counterparts, such as the presence of broadleaved meadows. Up to one-third of the GH endemic plants are expected to be under threat of extinction by 2100, under temperature increase scenarios of 2–4°C (Rull and Vegas-Vilarrúbia, 2006).

Campos de altitude: the Campos are cool-humid, highly fragmented Brazilian alpine areas developed between 1800 and 2000 m and 2890 m in the Serra do Mar, the Serra do Caparaó and the Serra da Mantiqueira, between latitudes 20 and 23°S (DeForest Safford, 2007; Fig. 3). Ecological similarities have been described between the Páramo and the Campos, based on a significant percentage of shared species. The Campos are floristically closer to the tropical Andes and other Brazilian highlands than they are to the adjacent lowlands, suggesting that their species are adapted to an alpine climate. A significant part of the Campos flora is of temperate origin and might therefore have migrated through ancient favorable habitats instead of recent long-dispersal processes (DeForest Safford, 2007).

Tristan da Cunha Island: located at latitude 37°5S in the Atlantic ocean and influenced by a hyper-oceanic, temperate climate, Tristan da Cunha is part of a group of three Brazilian islands, considered as some of the most isolated in the world. Tristan da Cunha is a volcano that reaches a maximum elevation of 2060 m. The top of the island supports an alpine desert because of exposure to persistently high winds and recurrent soil instability due to solifluction and frost-heaving (Wace and Holdgate, 1958). These particular conditions partly explain the dominance of bryophytes and lichens and the absence of vascular plants at high elevations.

Still, we hypothesize that pronounced isolation combined with recurrent volcanic activity has led to the absence of nurse/engineer plants, such as the Austral-Antarctic genus *Azorella*, which could potentially facilitate ecological succession and improve the environment for other organisms. The island's dominant plant species demonstrate (1) that long-distance dispersal may have been partly effective from Patagonia (*Empetrum nigrum* L.) and (2) that the human presence since 1810 has generated strong invasion patterns (*Rumex acetosella* L.; Wace and Holdgate, 1958). Also, closely related species of snails in Tristan da Cunha and the Azores islands suggest that long-distance dispersal has partly shaped the island's biodiversity by connecting two temperate environments separated by the intertropical zone (Gittenberger et al., 2006).

Conclusion

A large body of literature on the past, current and future distributions of alpine biodiversity of South America has been made progressively available, evidencing a large panel of patterns and mechanisms for different taxonomic groups. This article was an attempt to confront these contributions, with the aim to provide relevant explanation on the biodiversity patterns observed today and predict their changes in the future. The unprecedented extensions of latitudinal and elevation gradients shaping the Andes are major drivers of biodiversity variation since the formation of the South American continent. Threats include the increasing impacts of human activities through changing climate and land use intensification. We expect them to have a major influence on the future of alpine biodiversity in South America, through accelerated migrations, substantial adaptations and induced vulnerabilities due to increasing habitat destruction, anthropogenic biogeographical barriers, and invasions by introduced taxa. The specific resistance and resilience abilities of species and ecosystems will be crucial parameters to understand the future distribution of a unique and endemic biodiversity.

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Biogeography of North American Highlands

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Glossary

Adaptive radiation The rapid diversification of closely related species into distinct ecological niches.

Allopatric speciation The divergence of two geographically isolated species from a common ancestor.

Alpine biome A treeless habitat found at high elevation or high latitude, characterized by cold daily and annual temperatures, and tundra vegetation.

Biogeography The study of species distributions in space and time.

Cloud forest biome A subtropical or tropical evergreen montane forest with persistent cloud cover, characterized by relatively cool and wet conditions.

Ecological divergence The divergence of a lineage through time resulting in the occupation of a novel ecological niche.

Endemism The number of species found exclusively in a defined geographical area.

Evenness The total number of species (richness) weighted by the relative abundance of species found in a defined geographical area.

Föhn wind A warm, dry wind that first moves upslope to high elevations and then downslope on the leeward side of a mountain range, and is generated by a rain shadow (orographic) effect.

Highland Any mountainous region or elevated mountainous plateau.

Katabatic wind A cold, dry wind that moves downslope from higher elevations, and is generated by the force of gravity acting on high-density air.

Latitudinal diversity gradient A decline in global species richness from the equator to the poles.

Orogeny The geological process of crustal folding that causes mountain formation.

Orographic precipitation As warm, moist air moves up a mountain slope, it cools (adiabatic effect) and clouds form, eventually leading to precipitation on the windward side of the mountain. This leads to a rain shadow effect on the leeward side.

Parapatric speciation The divergence of two species in close geographical proximity (abutting geographical ranges) from a common ancestor.

Peripatric speciation Similar to allopatric isolation, in that there is divergence of two geographically isolated species from a common ancestor, but where one of the new species is formed as a small peripheral isolate of the more broadly distributed species.

Rain shadow A dry region on the leeward (downwind) side of a mountain, produced by the removal of moisture from air as it moves up and over the mountain slope.

Species richness The total number of species found in a defined geographical area.

Subalpine biome A transitional habitat, from closed woodland (timberline) to the upper elevation limit of trees (treeline), but encompassing forest, meadow, and bog habitats.

Sympatric speciation The divergence of two geographically co-occurring species from a common ancestor.

Windthrow A term in forestry used to describe trees that have been uprooted or broken by intense wind.

Abstract

North American highland habitats harbor exceptional species diversity, as well as high endemism in several distinct biomes. These include the cloud forest biome, subalpine biome and alpine biome found at high elevations in tropical and temperate mountains. Understanding the distribution of biodiversity in highland habitats, as well as the origin of endemic species, provides general insight into the evolutionary processes that generate new species. Major highland areas stretch from the Arctic Circle to the tropical southern border of Mexico, in a complex of old and young mountains. However, these highland areas are isolated from one another, and while highland species appear to be closely related across mountains, distinct endemic species are often found. Geological and paleoecological evidence suggests that past glacial climate fluctuations increased the connectivity of highland habitats, facilitating the movement of highland species during cool and wet climate episodes. Genetic studies of different plant and animal species have shown that the evolution of highland species has been rapid, with the distributional shifts from past climate change facilitating allopatric and peripatric speciation. Furthermore, in some rare cases, evolutionary divergence across steep ecological gradients found on mountain slopes has led to parapatric or sympatric speciation, with some lineages exhibiting adaptive radiation into novel ecological niches. Due to the wealth of biodiversity in these habitats, and the additional importance of highlands for the ecosystem services they provide to human communities, there is considerable concern about ongoing habitat destruction and climate change impacts on North American highlands.

Introduction to North American Mountain Regions

Highland habitats are of considerable interest in the study of biodiversity, as they not only contain high numbers of species, but reflect the outcomes of multiple processes that generate diversity (Steinbauer et al., 2016; Hoorn et al., 2013). This includes variation in environmental factors (climate, soils, elevation, etc.), geographical factors (riverine and montane barriers), and historical factors (geological and climatological change) that interact at a small spatial scale. Furthermore, these habitats are often insular in nature, functioning as “sky-islands” for the distinct montane biomes they contain relative to intervening low elevation habitats that act as natural barriers for highland species (Brown, 1971; Howell, 1947). Thus, highland habitats are often used by biologists as natural laboratories to disentangle the importance of different factors in generating and maintaining biodiversity (Badgley et al., 2017), as well as determining the factors that influence the distribution of species (the field of biogeography).

Beyond their importance to biodiversity studies, highland habitats provide a wealth of natural resources and ecosystem services (Egan and Price, 2017). These range from forest products, geological ores and game animals, to water storage, provision and filtration of water, carbon storage, and natural erosion of nutrient rich soils that enhance downstream agroecosystems. Additionally, they are often known for an array of natural features (waterfalls, soaring vistas, rock formations, pristine rivers, etc.), as well as indigenous cultures and ethnic diversity (Payne et al., 2017), which stimulate tourism and facilitate recreation. Thus, highland habitats are frequently managed by federal laws under some level of protection to ensure these resources are used sustainably for human benefit (Grêt-Regamey et al., 2012). In North America, protected areas in highland habitats exceed the 17% recommendation of the Convention on Biological Diversity (Aichi, Target 11), and therefore serve as important refuges for terrestrial biodiversity in general (Elsen et al., 2018).

North American highland habitats span the extent of the continent (Fig. 1) in what is known as the North American Cordillera. The North American Cordillera joins the American Cordillera in South America to form a nearly continuous string of mountain ranges running along the western side of the two continents. In North America, highland habitats range from the arctic north in the Brooks and Alaska Ranges to the tropical Sierra Madre del Sur in southern Mexico, and cross the entire continent from the Pacific Coast mountain ranges that are in western North America to the Appalachian Mountains and Sierra Madre Oriental in eastern North America. The physical geography of these mountains plays an important role in influencing the distribution of biomes and biogeographical patterns among mountain ranges. Most of these mountains are oriented north-south, which leads to variation in the elevational range of highland biomes and the distributional range of associated species across latitude. Additionally, North American highlands comprise multiple isolated mountains or mountain ranges (such as the Cascades volcanic chain, or the Southern, Central and Northern Rocky Mountains), which leads to high species turnover (local endemism) across isolated montane habitats. Furthermore, these mountains formed at different intervals of time (Coney, 1972), which further influences the biogeography of highland species.

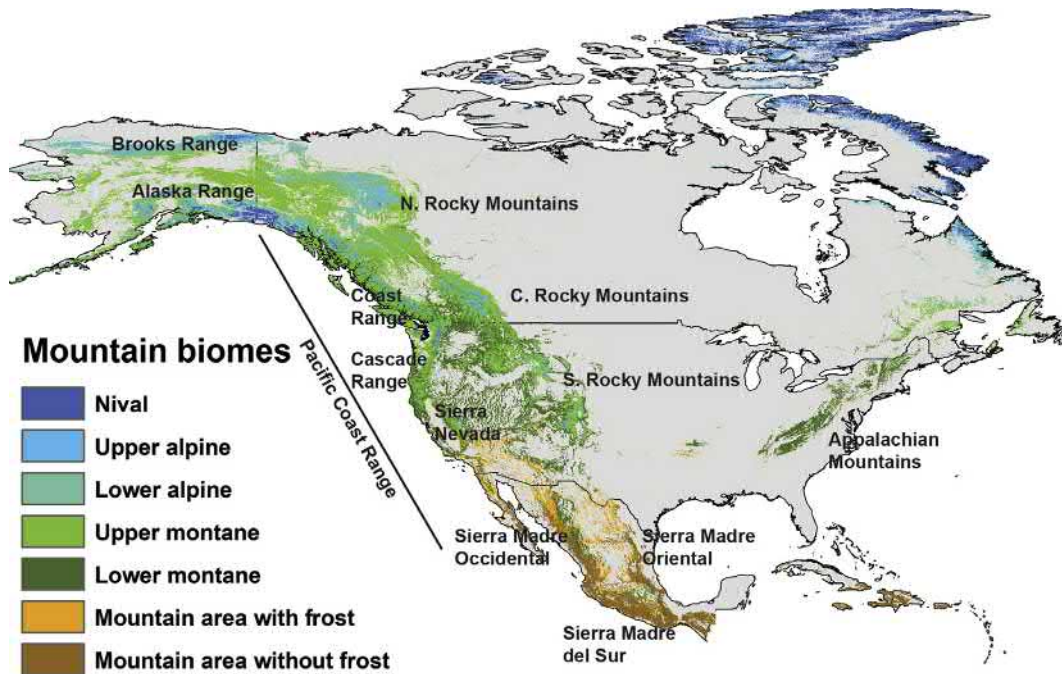


Fig. 1 Map of major highland areas and mountain biomes (Körner et al., 2017) in Canada, the United States and Mexico.

Major Highland Areas

Among the major North American mountain ranges, the Brooks Range is highest in latitude, sitting within the Arctic Circle in Alaska and Canada, where it began to form as early as ~145 million years ago (Mull et al., 1997). It spans nearly 1100 km in an east-west orientation, and its southern slope demarcates the northern limit of coniferous forest belts as they give way to arctic tundra. To the south, the Alaska Range in southeastern Alaska is one of the world's highest mountain ranges, with Denali surpassing all other mountain summits in North America with an elevation of 6190 m. The range stretches in an east-west orientation over 650 km and started forming ~144 million years ago (Ridgway et al., 2002) as part of tectonic plate collisions along the Alaska Range suture zone. It continues to experience frequent earthquakes as it overlays multiple active fault zones. With some of the harshest weather in the world (winds reaching 240 km per hour and temperatures as low as -70°C), it supports massive glaciers (>1100 m thick and >70 km long). The rapid loss of these glaciers due to climate warming appears to be a significant factor in the rise of sea level globally (Berthier et al., 2010).

The largest mountain range in North America is actually a complex of mountain ranges known as the Pacific Coast Range, which stretch 6100 km north-south along the edge of western North America in Canada, the United States, and Mexico. It includes the St. Elias Mountains in southeastern Alaska, the Canadian Coast Range, the Olympic Mountains of Washington state, the Oregon and California Coastal Ranges, the Peninsular Range in southern California and Baja California, and the Sierra Madre Occidental in Mexico. The mountains were initially formed by the accretion of island arc terranes (starting as early as ~325–350 million years ago), but significantly uplifted during the Laramide orogeny (~80 million years ago) that was initiated by subduction of the Farallon and Kula plates under the edge of the North American plate boundary as it moved slowly westward (Dickinson et al., 2009). The Pacific Coast Range encompasses a broad range of habitats, but perhaps the Sierra Madre Occidental is most distinctive (and therefore is treated separately below), with its species-rich pine-oak forests offset by desert and tropical deciduous forest at low elevations. Many of the mountain ranges within the Pacific Coast Range experienced differential rates of uplift through time, and subsequent volcanic activity. The Sierra Madre Occidental had several periods of uplift (in the Eocene, Oligocene, and Miocene), with the most recent volcanic activity occurring during the Pliocene in the Trans-Mexican Volcanic Belt in the south (Ferrari et al., 2007).

The youngest mountain range in North America is the Cascade Range, with most of the modern volcanoes forming less than 4 million years ago, and highest formed as recently as 100,000 years ago (Cheney, 2016). A complex of 20 major volcanoes spans 1100 km from southern British Columbia to northern California. The volcanic arc starting forming 37 million years ago as the Juan de Fuca plate began subducting under the North American Plate (McKenzie and Parker, 1967). The 12 largest volcanoes demonstrate a history of glaciation, and several support large modern glaciers. Coniferous forests dominate lower elevation habitats in most of the Cascade Range, although there is a strong rain shadow effect and habitats are typically dry to the east. The higher elevations support subalpine and alpine biomes.

The Sierra Nevada begins at the southern terminus of the Cascade Range in northern California and runs south for an additional 640 km south to the Transverse Range in southern California. Formed by the subduction of the Farallon plate and accretion of island arcs, the Sierra Nevada began uplifting 155 million years ago, and may have provided high elevation habitats throughout

its early history (House et al., 1998). Another period of uplift began 10–20 million years ago, associated with the crustal extension of the Basin and Range province, and continues to uplift the mountain range today (Huber, 1981). The range supports extensive contiguous habitat above 2500 m elevation, forming subalpine, and alpine biomes. Lower elevation habitats support coniferous forests, and a rain shadow effect to the east creates high desert habitat in the Great Basin.

Moving eastward into the interior of North America, the Rocky Mountain chain stretches 4800 km from northern British Columbia to New Mexico. It is a series of discontinuous mountain ranges of distinct origin, often grouped into the northern, central and southern Rocky Mountains. The modern mountain ranges were formed primarily during the Laramide orogeny (80–55 million years ago), though the Rocky Mountains overlay older mountains formed as early as 300 million years ago (English and Johnston, 2004; Dickinson et al., 1978). The mountains support substantial subalpine and alpine habitat throughout their extent, with coniferous forest largely dominating low elevation habitats. A strong rain shadow effect defines the Great Plains to the east of the Rocky Mountains, but it is also notable that the Great Basin to the west of the southern and Central Rocky Mountains is predominantly a high desert biome.

Continuing east, the Appalachian Mountains run north-south from southeastern Canada to the southeastern United States for approximately 2400 km. Most of the range is relatively low-lying, around 900 m in elevation, but the mountains in North Carolina reach over 2000 m in elevation. The Appalachian Mountains are an ancient mountain range, having formed 480 million years ago (Gibson, 1970) during plate tectonic activity associated with the formation of the supercontinent Pangaea. Periods of nearly complete erosion and subsequent uplift appear to have characterized its history through time, with a recent uplift in the mid-Miocene ~11–16 million years ago (Poag and Sevon, 1989). The Appalachian Mountains support a diverse set of biomes, including temperate rainforest and bogs, as well as a coniferous forest belt that extends to high elevations. Much of the low elevation habitat supports the deciduous broadleaf and mixed forest biome characteristic of the eastern United States and southeastern Canada.

Going south along the east coast of Mexico is the Sierra Madre Oriental, which is at the same longitude and formed from the same Laramide orogeny (80 million years ago) that uplifted the Rocky Mountains (Guzmán and de Csema, 1963; Fitz Diaz et al., 2017). It spans approximately 1000 km, from the Rio Grande in the state of Coahuila south to Hidalgo, where it meets the Trans-Mexican Volcanic Belt. With some summits reaching 3700 m elevation, the Sierra Madre Oriental supports a high diversity of endemic species found in a pine-oak forest biome and cloud forest. Lower elevation habitats are often xeric. The Mexican Plateau lies to the west of the Sierra Madre Oriental, averaging >1000 m in elevation, and is characterized by deserts and shrublands. The Gulf Coastal Plain lies to the east with subtropical to tropical forest and grasslands.

Farthest to the south, the Sierra Madre del Sur runs 1000 km west to east in southern Mexico, from the state of Michoacán through Guerrero to Oaxaca, ending at the lowland Isthmus of Tehuantepec. It starting forming as part of the Laramide orogeny (~80 million years ago), but most significant uplift occurred in the Late Paleocene to Miocene epochs (56–23 million years ago) as a result of interactions among the North American, Farallon, and Caribbean plates (Cerca et al., 2007). High elevation habitats (with summits reaching >3700 m elevation) support pine-oak forest and exceptional species endemism, while low elevations support tropical dry forest habitat.

Biotic Challenges and Biotic Zones in Highland Habitats

Katabatic and föhn winds can accelerate to hurricane force, rushing downslope over mountain backbones, to tear plants from the ground. Encountering a swath of full grown trees, uprooted alive and tossed again to the ground in a windthrow, draws a vivid image of the volatility and intensity of abiotic stresses in highland habitats. While harsh wind, rockslides and avalanches are among the abiotic factors influencing the distribution of life in highland habitats, they are relatively minor compared to the important roles of temperature, precipitation, solar radiation, and oxygen concentration. Temperatures decline with elevation, and low mean temperatures near mountain summits limit the annual productivity of plant life and activity of animal life. Additionally, high elevation habitats frequently experience broad daily temperature variation, which requires behavioral, physiological or morphological specialization to these environments. Precipitation is typically greater in highland habitats relative to low elevation habitats, though it often varies seasonally (and can be effectively drier in summer periods). Coupled with cooler temperatures, high elevation precipitation often forms frost or snow. In northern mountains, snow can persist for 9 months of the year, or in some cases never disappear, eventually compressing into glacial ice. This reduces annual growth opportunities, as many organisms wait for snow-free conditions to start growing. In southern tropical mountains, mid-elevation habitats experience nearly constant cloud cover at the level of the canopy trees, creating the misty wet cloud forest environment. This alters the spectral bandwidth of penetrating sunlight and the reduced light quality requires a corresponding shift in absorbance spectra of plants conducting photosynthesis (Reinhardt et al., 2010). Aside from cloud interference, the quality of sunlight shifts with elevation in mountain habitats as solar ultraviolet (UV) radiation generally increases (Blumthaler et al., 1997). UV radiation has been linked to DNA damage in plant and animal tissues, and biologically active pigments are often used to absorb or reflect harmful UV rays (Barnes et al., 1987; Sommaruga, 2001). Finally, atmospheric oxygen levels decline with higher elevation, roughly at a linear rate, such that oxygen levels are 50% of their value at sea level at 5500 m elevation (Peacock, 1998). Some animals and plants have evolved strategies to enhance oxygen uptake and limit hypoxia, such as the deer mouse which has altered globin molecules to have greater affinity for oxygen molecules (Storz et al., 2009).

This range of environmental conditions and physiological challenges has created unique habitats and patterns of biodiversity in highland areas. Low to mid-elevation highland habitats in North America encompass nearly the entire diversity of North American biomes. They are typically extensions of habitats in the immediate vicinity of the highlands, though it should be noted that

mountainous regions often influence these habitat types by capturing precipitation from air flow across the mountain (orographic precipitation) and producing rain shadows on the leeward side of the mountain that lead to desertification. Major components of low to mid-elevation montane habitats in North America include temperature deciduous and evergreen forests, tropical rainforest and dry forest, and Mediterranean forest, woodland, and scrub habitats. In contrast, high elevations give rise to several unique biomes that are only found in highland habitats, including cloud forest, subalpine forest, and alpine tundra and grasslands.

Cloud Forest Biome

In subtropical and tropical settings, highland environments can be characterized by a unique evergreen montane forest habitat known as the cloud forest biome. Clouds form at the level of the forest canopy and persist throughout the day, and across seasons, providing wet and cool conditions. A significant portion of the precipitation in this biome is created by the condensation of fog on plants, but the persistent cloud cover also reduces evapotranspiration. These saturated environments have reduced decomposition rates, reduced mineralization and increased soil acidity. Another consequence of steady cloud cover is reduced solar radiation, which limits the photosynthetic potential of plants. These abiotic factors provide unique challenges and opportunities to plant life in these environments. While plant species characteristic of cloud forests vary between regions, tree ferns, *Podocarpus*, and arbo-real bromeliads are often found in Mesoamerican cloud forests. In some high elevation cloud forests, particularly on more isolated mountains, elfin forest may occur, with stunted trees and extensive moss and epiphyte growth. Endemism of plant and animal life is exceptional in cloud forest habitats (Hamilton et al., 2012; Webster et al., 1995), even though they comprise less than 1% of the total area in global forest habitats.

Subalpine Biome

In many North American highland habitats, the upper elevational distribution of trees forms the subalpine biome. Coniferous fir, hemlock, spruce and pine trees are characteristic of many North American subalpine habitats. As they near their upper elevational limits ("treeline"), these windblown trees become dwarfed and twisted into krummholz forms, often growing horizontally across the ground and in clumps in response to wind. Subalpine habitats include the transition from closed "timberline" forest to this treeline. Subalpine biomes also include subalpine meadow and bog habitats, which are frequently irrigated throughout summer months by snowmelt from higher elevations and may have riparian areas with willow species. The climate is harsh in this biome, with heavy precipitation in the form of snowfall and low mean temperatures from early fall to late spring. The resulting growing season is short and restricted to summer months, and many subalpine species have evolved to be long-lived and to develop slowly. Subalpine and alpine communities often share species, but the subalpine habitats have a greater diversity of species, including montane species reaching their distributional limits (Billings, 1974).

Alpine Biome

Among the biomes encountered in highland habitats, the alpine biome is the smallest in overall area and the lowest in overall species diversity, but notable in having a distinct endemic fauna and flora (Stebbins and Major, 1965). It is characterized by treeless habitat, cold daily and annual temperatures (the annual mean temperature at which trees fail to grow is 1.5–3°C), heavy snowfall and short growing seasons, and often high elevations (in some cases reaching as high as 3000 or 4000 m above sea level). This biome is perhaps the most dynamic, having undergone dramatic climatic fluctuations, distributional shifts, and rapid community assembly subsequent to the last glacial maximum (Gillespie and Zehfuss, 2004; Woolfenden, 2003). This dynamic pattern has repeated over semi-regular time intervals during the climatic cycles of the Pliocene and Pleistocene epochs.

There are a variety of distinct habitat types within the alpine biome of North America. Perennial grasses, sedges and forbs frequently characterize the wind-swept areas and alpine meadows. These plants typically grow close to the ground and have more below-ground than above-ground biomass, which is important in storing energy over winter. While windswept habitats are relatively barren, alpine meadows have dense grass and forb vegetation, and also include prostrate shrubs. Alpine rock gardens form on well-draining slopes (often gravel beds or sandy soils) with cold-specialized succulents and cushion plants. These plants are compact and low-growing to avoid wind damage, and have thickened leaves, matted growth forms and tap roots to help extract and retain water in this dry microhabitat. The flowers of these plants are often large and showy relative to the plant size, and are attractive to a diverse set of insect pollinators.

North American Highland Habitats Through Time

Global climate has cooled dramatically since the Paleogene period (65–23 MYA), leading to expansion of polar ice, the development of continental and alpine glaciers, and a shift from tropical to temperate biomes at high latitudes (Gingerich, 2006). Although highland environments existed in many parts of the world during the Paleogene (Mani, 1968), it is unclear whether the abiotic conditions in these environments created the diversity of biomes found in modern mountains. In particular, the distinctive alpine biomes may not have characterized high elevation habitat Paleogene mountains, unless those mountains were much higher in the

past than at present. When did modern highland biomes develop in North America and what is the earliest age for the origins of endemic montane organisms?

Furthermore, how did subsequent climate change influence the distribution and connectivity of highland biomes through time? Fluctuations in past global climate, in the form of warming and cooling trends and shifts in global circulation and precipitation, are evident in a variety of global geological, chemical and paleontological records. Global cooling trends ("icehouse conditions") increased in frequency and severity from the Miocene and Pliocene into the Pleistocene, and a cyclical pattern of cooling and warming now characterizes long-term global climate (Lisiecki and Raymo, 2007). Alternating glacial (stadial) and interglacial (interstadial) periods are thought to be caused by orbital forcing (changes in the tilt of the Earth's axis; Hays et al., 1976), although there is debate about this relationship (reviewed in Lisiecki and Raymo, 2007). The highest resolution indicator of the frequency, duration and intensity of global temperature changes is dissolved oxygen isotopic variation preserved in Northern Hemisphere ice cores (Andersen et al., 2004; Jouzel et al., 1987) and the fossil remains of foraminifera preserved in oceanic sediments (Lisiecki and Raymo, 2005). The repeated global cooling trends observed in these records are highly correlated and nearly synchronous with the development of massive continental and alpine glaciers (Benson et al., 1997), as well as the timing of related landform transformation (Kaufman et al., 2004), sea-level depression (Herbert et al., 2001), and dramatic regional shifts in plant and animal distributions (Bradshaw, 1999). Global records have been combined and used to model atmospheric temperature over the last 5.3 million years (Lisiecki and Raymo, 2005), with high precision over the last 1 million years (Bintanja et al., 2005). This record is useful for identifying the timing, duration and intensity of worldwide glacial phases over the both Pliocene and Pleistocene epochs. However, it is not clear whether global temperature records from these sources translate into climate events at a regional scale in a given mountain range (Herbert et al., 2001, 2002). Some scientists have argued that the timing of glacier growth and retreat in highland habitats is offset from these global records by local circulation patterns (Bischoff and Cummins, 2001; Winograd et al., 1992; Winograd, 2002).

These glacial-interglacial transitions have had profound effects on animal and plant distributions (Comes and Kadereit, 1998; Hewitt, 1999; Bradshaw, 1999), as well as the physical geography of different regions. While many highland habitats in North America are currently isolated and environmental conditions limit the dispersal of highland organisms, these environments reorganized during glacial phases and connectivity to other mountains may have increased. While some authors have argued that glacial stage environments lead to the expansion of highland biomes (Chabot and Billings, 1972; DeChaine and Martin, 2004), it is not clear whether highland organisms went through population expansion or contraction during these episodes as they were displaced by glacial ice. By developing information on the timing and geographical extent of glaciations in highland habitats, it may be possible to constrain the temporal intervals of dispersal from other mountain ranges, as well as the intervals of potential population size changes in response to past climatic events.

While the geology of the North America has been studied since the 19th century, there continues to be debate about the paleoelevation of mountain ranges and how elevation has changed through time (Cecil et al., 2006; Mulch et al., 2006; Molnar and England, 1990). In this section, we review the literature on the timing of mountain building, estimates of paleoelevation in North America, and subsequent climate history for several key mountain ranges, in an attempt to provide age constraints on the origin of subalpine and alpine highland habitats.

Sierra Nevada Mountains

The Sierra Nevada began developing as a continental arc during the late Triassic period (Ducea, 2001), but the extent of uplift at that time remains unclear. Previous interpretations of sediment discharge and erosion, which implied a rapid uplift of the Sierra Nevada during the Miocene epoch, have been criticized due to concurrent glacial processes and their importance on measured rates of sediment discharge and erosion (Molnar and England, 1990). More recent attempts to infer the age and paleoelevation of the Sierra Nevada have relied on isotopic data from minerals and volcanic glass. These studies suggest that topographic surfaces similar to modern surfaces were present at least 60 million years ago (Cecil et al., 2006; House et al., 2001), and that a rain-shadow effect similar to the modern one has been in place over the last 12 million years (Mulch et al., 2008; Poage and Chamberlain, 2002). Thus, high elevation habitat has existed for at least 12 million years. The White Mountains of California, lying east and at one point connected to the Eastern Sierra Nevada, also reached high elevations in the period from 12 to 6 million years ago (Stockli et al., 2003). The Sierra Nevada continued to increase in relief from 10 to 3 million years ago, which is evident in increased incision rates in multiple river canyons (Stock et al., 2004).

While paleoelevation in the Sierra Nevada has been high since the Miocene, it is unclear whether these high elevations provided conditions suitable for highland organisms. While available data do not provide a clear upward bound for the appearance of cold climatic conditions at high elevations, extensive evidence of recent, repeated alpine glaciation in the Sierra Nevada is represented in a variety of geological features, including moraine deposits, erratic boulders, U-shaped valleys, and glacial sculpting (Guyton, 1998; Gillespie and Zehfuss, 2004). These geological features provide strong support for the existence and geographical extent of Pliocene-Pleistocene glacial events over the last 3 million years. Furthermore, the downstream drainage of glacial sediments ("rock-flour") and deposition of pollen in nearby lakes provide high resolution estimates of the onset, duration and retreat of alpine glaciers (Benson et al., 1997; Bischoff and Cummins, 2001), although these data are mostly limited to recent geologic history (<200,000 years B.P.).

There are slight differences from the global climate average, in terms of the timing and resolution of glacial activity, evident in recent paleorecords from the Sierra Nevada (Bischoff and Cummins, 2001; Gillespie and Zehfuss, 2004). Most importantly, these

data indicate repeated growth and recession of alpine glaciers during major glacial phases, suggesting that glacial environments were not stable and were influenced by local climate shifts. The importance of short-term distributional shifts has been well studied using plant pollen and macrofossil remains (Smith and Anderson, 1992; Woolfenden, 1996, 2003; Thompson and Anderson, 2000; Davis, 1999; Serceij and Adam, 1975), as well as fossilized midges (Porinchu et al., 2003, 2007). Highland species may have fluctuated in abundance and distribution during these short-term climate oscillations, and so the hypothesis of expanding highland habitats during glacial phases or long stable geographical distributions requires testing with further evidence.

Rocky Mountains

Similar patterns apply to the Rocky Mountains, but they are significantly different in having a much longer history of high elevation habitat. The uplift of the Rocky Mountains during the Laramide orogeny (80–55 million years ago) is thought to have generated considerable topographic relief (>2 km in elevation) that affected continental weather patterns (Bird, 1984; Dettman and Lohmann, 2000b). Some studies have suggested that paleoelevations were even higher (>4000 m on average), reaching elevations beyond those seen in the present day (Mulch et al., 2004). As recently as the Miocene (Wolfe et al., 1998), paleoelevations are thought to have remained near modern levels and could therefore have supported permanent snowfields (Dettman and Lohmann, 2000a; Norris et al., 1996). This would suggest that subalpine and alpine biomes were present in the Rocky Mountains for at least 23 million years, or perhaps even longer. However, the presence of permanent snow and such high elevations through time remains under debate (Fricke and Wing, 2004).

Appalachian Mountains

Reconstructed climates during the Paleozoic (255 million years ago) suggest the Appalachian Mountains may have been as high as 4500 m during its early history (Fluteau et al., 2001), providing significant relief that may have supported modern montane biomes. However, geological studies have demonstrated a long history of sediment erosion that is consistent with gradual decline in the elevation of the mountains through time (Gibson, 1970), with a lack of significant tectonic uplift for >100 million years. This suggests the mountains have lacked substantial high elevation habitat for some time, as they currently reach maximum elevations of 2000 m and erosion has proceeded at a rate of 27 mm per kyr (Gallen et al., 2013). Although more recent studies have shown that the Appalachian Mountains have gained elevation in subsequent periods, for example in the mid-Miocene (Poag and Sevon, 1989; Gallen et al., 2013), the elevational uplift only resulted in 100–150 m elevation gain (McKeon et al., 2014).

Biodiversity and Biogeography of North American Mountains

Biodiversity patterns are often quantified in terms of species richness (the number of species) and evenness (the richness weighted by the abundance of each species), although there are other measures that weigh functional diversity (accounting for ecological or morphological variation), phylogenetic diversity (accounting for the evolutionary distinctiveness of species), and endemism (the number of unique species found in that region). The highlands of North America are considered global biodiversity hotspots based on representation of distinct habitat types (Olson and Dinerstein, 1998), and many rank highly in terms of species richness and/or endemism (Pimm et al., 2014; Ricketts et al., 1999). Endemism is particularly high in unique biomes represented in mountain ranges, for example in the alpine flora of the Sierra Nevada (Rundel, 2011), or the birds of cloud forests of Mexico (Fjeldså et al., 2012). Southern mountain ranges, particularly the highlands of Mexico, are exceptionally rich in numbers of species compared to more northern highland areas in North America (Table 1). In part, this trend reflects the latitudinal diversity gradient, a well-known phenomenon of global biodiversity patterns where species richness exhibits a general trend towards decreasing species diversity toward the poles (Gaston, 2000).

Biogeography is the study of species distributions in space and time, and includes research on the evolutionary history and ecology of species. There are three main biogeographical sources for highland species in North American mountain regions. The first involves dispersal from a similar biome in a nearby mountain range. Under this model, species should be closely related among mountains, with evolutionary distance increasing with geographical distance and/or the age of mountains (Chabot and Billings, 1972; Kimball et al., 2004; Brown, 1971). The second model involves dispersal over long distances from similar biomes found in other parts of the world. For example, arctic and alpine environments are similar, and some plants and animals inhabit both biomes, in some cases stretching in distribution from Eurasia to North America (Billings, 1973; Packer, 1974). Such long range dispersal might be facilitated by climate fluctuations through time, when favorable conditions are episodic and allow dispersal over longer distances than currently seem possible. Third, highland species might have evolved from species inhabiting lower elevation habitats in the same mountain range, in a process of ecological diversification across different montane biomes. The retention of species in a particular highland area has been associated with the rate of past climate change and dispersal ability of species (Sandel et al., 2011), where those habitats undergoing the most change have lower diversity and poorer representation of low dispersal organisms. Once established in a given mountain range, lineages can evolve to have multiple endemic species as diversification occurs due to (1) multiple colonization events from an exogenous source, (2) geographical isolation within the mountain range (allopatric or peripatric speciation) due to geographical barriers or climate fluctuations, and/or (3) sympatric or parapatric speciation.

Table 1 Species richness in major North American highland areas

	<i>Conifers^a</i>	<i>Birds</i>	<i>Mammals</i>	<i>Reptiles</i>	<i>Amphibians</i>	<i>Fish</i>	<i>Butterflies</i>
Brooks Range	3	163	48	0	1	1	52
Alaska Range	6	195	66	0	2	14	58
Pacific Coast Range ^b	51	475	208	83	61	120	267
Cascades Range	33	350	143	25	37	33	157
Sierra Nevada	26 ^c	318	119	63	43	8	182
Rocky Mountains	31	438	169	71	29	11	274
Appalachian Mountains	24	309	83	63	100	43	181
Sierra Madre Occidental	39	574	217	224	64	154	734
Sierra Madre Oriental	41	539	151	167	51	?	728
Sierra Madre del Sur	32	766	245	301	159	?	1271

?, unknown.

^aFrom the Global Mountain Biodiversity Assessment, <http://www.mountainbiodiversity.org/explore>

^bIncludes the Canadian Coast Mountains, Coast Range of Oregon and California, and the Peninsular Range in southern California.

^cFrom Lanner (1999).

The Alpine Biome in North America

There is considerable evidence that alpine species have dispersed among mountain ranges in temperate North America during glacial climate fluctuations, and that their distributional patterns relate to habitat suitability and dispersal ability (Major and Bamberg, 1967). For example, highly dispersive alpine taxa moved between the Rocky Mountains and Sierra Nevada Mountains by crossing the Great Basin during glacial periods, including plants (Chabot and Billings, 1972; Kimball et al., 2004), mammals (Brown, 1971), birds and butterflies (Wilcox et al., 1986). Such distributional patterns have been supported with genetic studies of population and species relationships (Schoville and Roderick, 2009; Nice and Shapiro, 2001; Schultheis et al., 2012; Schoville et al., 2011). Less dispersive taxa do not show this pattern, instead showing relationships in a north-south orientation along the Sierra Nevada-Cascades Range, or the Rocky Mountains-Northern Cascades (Charlet, 2007; Fites-Kauffman et al., 2007; Galbreath et al., 2009; Shafer et al., 2010). For those taxa with extremely limited dispersal abilities, multiple alpine species have evolved within a mountain range as a consequence of glacial climate fluctuations and geological barriers (Schoville and Roderick, 2010; Rovito, 2010; Schoville et al., 2012). These studies suggest that dispersal, rather than ecological divergence from low elevation species, is the principal factor governing the biogeography of alpine species. However, there are a few notable cases where ecological divergence has occurred across montane and alpine biomes (Rovito, 2010; Rubidge et al., 2014), perhaps as a result of parapatric speciation. Very large mountain ranges, with extensive topographic variation, distinctively show such a pattern of extensive local species diversification (Xing and Ree, 2017). Some examples of species whose histories have been reconstructed using genetic data are shown in Fig. 2.

Broad-scale biogeographical studies have shown that alpine species are frequently closely related over vast distances (Mani, 1968), spanning isolated mountain ranges in the Northern Hemisphere (Kadereit et al., 2008; Hultén, 1937). As many of the diverse alpine species assemblages are products of recent species radiations (Hughes and Atchison, 2015), this raises the question of whether alpine lifeforms have arisen from a common source. One of the more interesting hypotheses suggests that uplift of the Himalayan Mountains and Tibetan Plateau (~40 million years ago; Renner, 2016), following the collision of the Indian subcontinent with the Asian continent 52–55 million years ago, may have led to the evolution of alpine specialists in many taxonomic groups (Favre et al., 2016). The emergence of high elevation habitats during a period of warm global temperatures would have isolated such species until global cooling events began, following the first Antarctic glaciation 34 million years ago. The onset of global climate cooling, and particularly the frequent and extensive glaciation events of the Pliocene and Pleistocene epochs (3 million years ago to the present), subsequently allowed dispersal to distant mountain ranges in Eurasia and across the Bering Land Bridge into North America (Zhang et al., 2014; Wang et al., 2016). However, a competing model is for the highland habitats in North America (i.e., the Rocky Mountains) to have served as a cradle for the evolution of alpine specialists during the Laramide orogeny (80–55 million years ago), with subsequent dispersal towards the mountains in Eurasia (Ebersbach et al., 2017). Both cases are supported by empirical data, and it remains possible that other early mountain ranges served as cradles for the evolution of alpine ecotypes.

Mexican Cloud Forests

Cloud forests occur at intermediate elevations in the Sierra Madre Oriental, northern highlands of Oaxaca, and in some portions of the Sierra Madre del Sur of Oaxaca, Mexico. They form a band between the tropical forest or pine forest below and the montane pine-oak forest above. Cloud forests contain a mix of north temperate floral elements, such as oaks (*Quercus*) and sweetgum (*Liquidambar*) and elements such as *Podocarpus* that originated in South America. Genetic and paleobotanical data show that *Podocarpus* has been present in Mexican forests since the Miocene, as has *Liquidambar* (Graham, 1999; Ornelas et al., 2010; Ruiz-Sánchez and Ornelas, 2014). In the north, cloud forests occur as sky islands on isolated mountains, such as in the emblematic El Cielo Biosphere Reserve, while their distribution becomes somewhat more continuous to the south. Their association with cloud formation confines

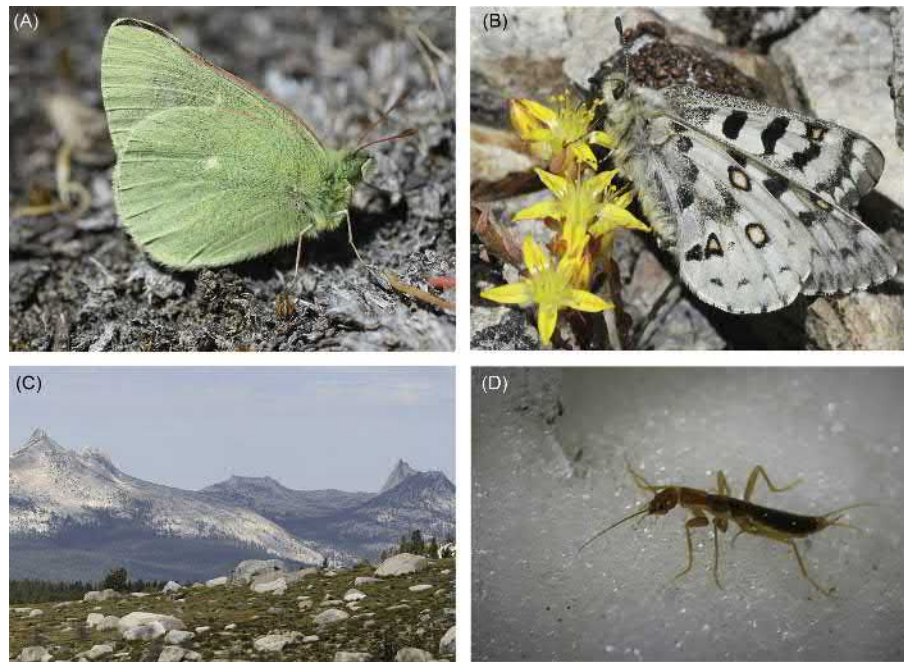


Fig. 2 The alpine biome is characterized by species that were able to disperse among mountain ranges during the last glacial period, as well as those with limited dispersal ability that diversified within mountain ranges. The butterflies (A) *Colias behrii* and (B) *Parnassius behrii* are recently derived endemic species in the Sierra Nevada, closely related to species found in the Rocky Mountains. (C) A view of alpine and treeline habitats in the Cathedral Range of Yosemite National Park. (D) Ice crawlers, *Grylloblatta* sp., are wingless insects that have diversified into a complex of 7–8 species in the Sierra Nevada.

them to a narrow elevational belt, which is broken in many places by lower elevation valleys with tropical or xeric vegetation. This elevational belt likely moved upward during interglacial periods and downward during glacial periods, resulting in expansions and contractions of cloud forest habitat. Such changes in cloud forest extent have resulted in demographic fluctuations within wide-ranging species including the Maquique tree fern, a typical cloud forest taxon (Ramírez-Barahona and Eguiarte, 2014). In other species, including some with relatively high dispersal capacity such as jays (*Aphelacoma*), glacial cycles have resulted in lineage divergence and cryptic allopatric speciation between cloud forests in different regions (Venkatraman et al., 2018). Because of their strong dependence on cloud water, different combinations of past temperature and precipitation changes could have resulted in less predictable patterns of distribution change compared to other vegetation types.

Cloud forest fragmentation and expansion in response to climatic changes have produced complex patterns of genetic diversity across wide-ranging species (Ornelas et al., 2010; Ramírez-Barahona and Eguiarte, 2013). Past distributional changes and fragmentation in cloud forest have likely resulted in repeated events of allopatric speciation in organisms with lower dispersal ability. This is especially likely in the case of organisms that make extensive use of arboreal bromeliads (strongly tied to cloud water deposition), which provide moist microenvironments during dry periods. Lungless salamanders (family Plethodontidae) are diverse in Mexican cloud forests (Fig. 3), and many species use arboreal bromeliads as daytime refugia (Wake, 1987). Most cloud forest salamander species are narrowly endemic to small regions or even single mountaintops, with sister species found in adjacent mountain ranges (Rovito et al., 2013; Rovito and Parra-Olea, 2015). In addition to the many likely cases of allopatric speciation in this group (Rovito, 2017), strong elevational gradients in the Sierra Madre Oriental, highlands of northern Oaxaca and other areas have provided opportunities for parapatric speciation between cloud forest and adjacent vegetation types. In the Sierra de Juárez of Oaxaca, for example, three pairs of sister species of salamanders occur, with one species found in bromeliads in the cloud forest and its sister species found at higher elevation in montane pine-oak forest. This pattern suggests that species formation, likely involving selection for bromeliad use in the cloud forest, could have led to parapatric speciation across the boundary between cloud forest and pine-oak forest over short timescales (Pleistocene) (Rovito and Parra-Olea, 2016; Rovito, 2017). Although less studied than vertebrates and vascular plants, cloud forest insects such as beetles of the family Passalidae have likely responded to distributional changes in cloud forest in similar ways to salamanders, with repeated events of dispersal and divergence between adjacent montane regions; such a pattern has been found in the cloud forests of Central America (MacVean and Schuster, 1981).

Conservation of North American Highlands

Mountain ranges are under considerable threat of habitat loss, habitat degradation, and climate change (Payne et al., 2017). Habitat loss and degradation result from resource extraction (forest products and mineral ores), agricultural intensification and residential



Fig. 3 Salamanders in the cloud forest biome of the Sierra Madre Oriental and highlands of Oaxaca have diversified among isolated forest patches. (A) Cloud forest habitat showing extensive growth of arboreal bromeliads and other epiphytes. (B) *Pseudoeurycea saltator*, a cloud forest endemic typically found in arboreal bromeliads. (C) *Thorius arboreus*, one of the smallest species of salamanders, reaches a maximum of 20 mm snout-vent length and is found in bromeliads in the cloud forest of the Sierra de Juárez, Oaxaca. (D) *Chiropterotriton cieloensis*, a salamander endemic to the cloud forests of the El Cielo Biosphere reserve in Tamaulipas, Mexico. El Cielo (a sky island) and nearby forest patches represent the northernmost extent of cloud forest habitat in North America.

development. While these land use changes primarily influence unprotected mountain habitats, even pristine mountain habitats in protected areas are undergoing dramatic changes due to global warming. Over the last century, U.S. national parks have seen a 1.0°C increase in average temperature (Gonzalez et al., 2018). In at least a third of all mountains globally, climate shifts are predicted to lead to declines in available habitat for montane biomes due to the reduction of surface area available at higher elevations on mountains (Elsen and Tingley, 2015). These changes not only result from temperature increases, but also from precipitation changes and the discordance between temperature and precipitation shifts (McCain and Colwell, 2011). This is alarming, as montane habitats not only protect high levels of biodiversity, but have also served as refuges for diverse species of biota during past climate change. Highland regions are also particularly rich in intraspecific genetic diversity (Stralberg et al., 2018). Importantly, changes to highland biomes are occurring rapidly and we still lack basic knowledge of the biodiversity of North American highlands, the function and value of their diverse ecosystem services, and the resiliency of montane ecosystems to ongoing change (Payne et al., 2017).

Among the North American highland biomes, Mexican cloud forest biomes are considered particularly vulnerable to global climate change (Still et al., 1999; Ponce-Reyes et al., 2012), and many of the species found in these habitats have limited physiological tolerance for temperature extremes or dry conditions outside the mean conditions of these habitats (Pounds et al., 1999; Nadkarni and Solano, 2002). These forests are also threatened by the deforestation of lower elevation tropical forests (Lawton et al., 2001), which reduce the cloud layer and raise temperatures in upland cloud forest habitat. Alpine and subalpine biomes, in contrast, may be more stable to shifting temperatures due to topographical complexity at local scales (Graae et al., 2018). For example, certain habitats such as mountain streams appear to be changing relatively slowly (Isaak et al., 2016). However, incremental temperature change may be less significant to these biomes than the threat of declining snowpack (Mote et al., 2005), which increases the exposure of alpine organisms to extreme temperature fluctuations (Choler, 2018), increases the aridity of these habitats, and raises the risk of fire (Camac et al., 2017), and alters mountain hydrology (e.g., heavy rainfall instead of snowfall increases flood events and erosion).

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Biogeography of the Mountain Ranges of South Asia

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Abstract

An understanding of the heterogeneity, or nonrandomness, in the distribution of species on Earth is one of the central goals in the ecological sciences and constitutes the collective science of Biogeography. This multidisciplinary branch of science incorporates elements from widely disparate disciplines such as biology, ecology, geography, remote sensing, physical and climate sciences and studies all aspects of the adaptations of an organism to its environment, considering systematically the origins, migrations and associations of living things. Mountain systems provide ideal ecological laboratories to understand the biogeography of plants and animals as they present a large variety of environmental conditions across their elevational gradients, thereby hosting a great variety of life forms over short distances. This is particularly true for the mountain systems of the tropics which harbor some of the world's finest biodiversity hotspots. In this article, we describe briefly the biogeography of the 12 major mountain ranges of South Asia, which together form the backbone of the economy and biodiversity heritage of their respective countries. These majestic mountains play a pivotal role in determining, regulating and even modifying overall climate system of continental Asia, including the middle-east and parts of Europe and Russia. These act as reservoirs of unparalleled natural resources, glaciers and rivers systems supporting a major fraction of the human population

in the continent. A deeper understanding of the biogeography and natural heritage of these mountains is critical to their science-based conservation and for sustainable development in these remote regions with fast depleting resources.

Introduction

Biogeography is the collective science that incorporates elements from widely disparate disciplines, with a unified aim towards understanding the distribution of plants and animals. It studies all aspects of the adaptations of an organism to its environment, systematically considering the origins, migrations and associations of living things. Hence, it aims to synthesize data from non-biological (geology, geography, climatology and meteorology) and biological (biology, taxonomy, genetics, and physiology) disciplines. Biogeographical relationships can be understood only from an ecological perspective which examines the interactions between an organism and its environment. While historic biogeography attempts to understand the role of historic climate and paleogeography in determining current species distributions, modern biogeography includes current anthropogenic pressures as a major environmental variable influencing the distribution of plants and animals (Fig. 1 and Table 1).

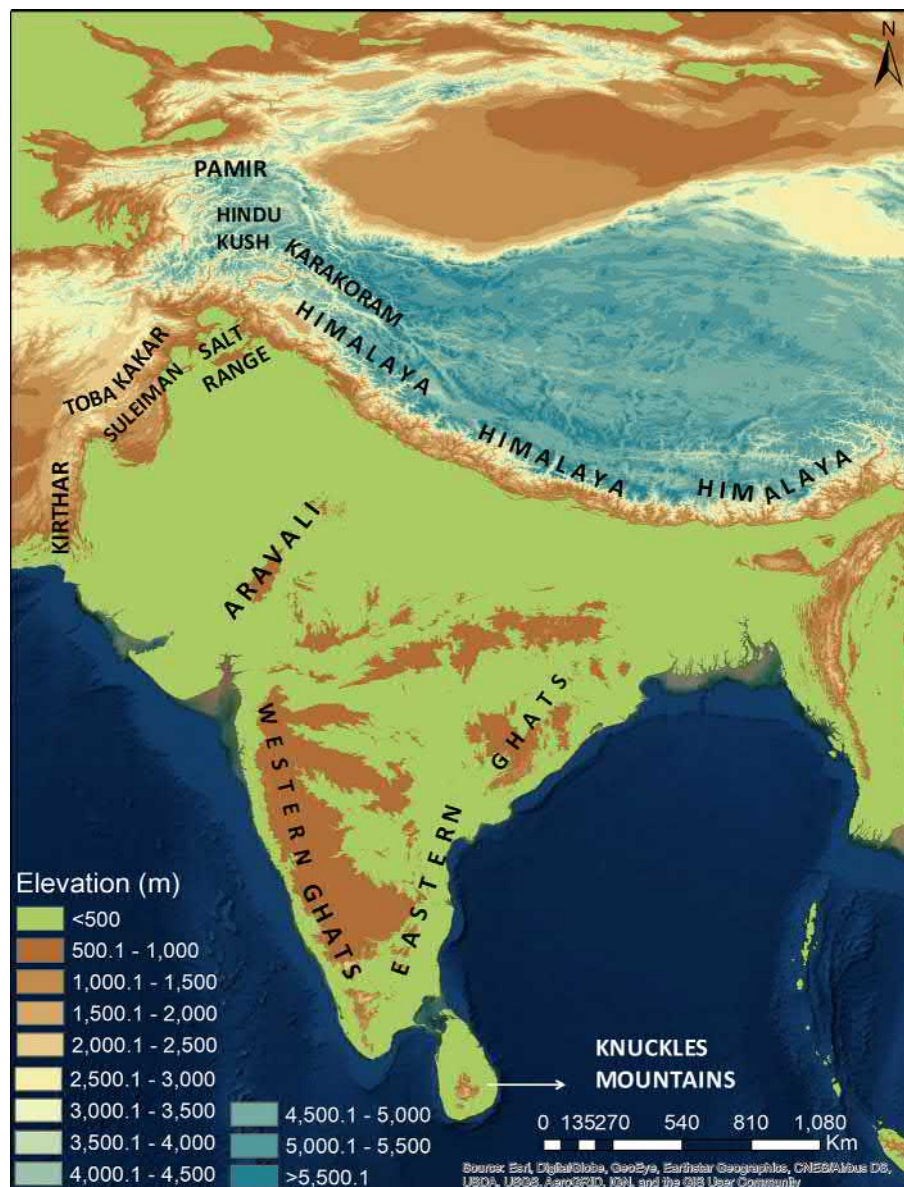


Fig. 1 A Digital Elevation Map of South Asia, representing the major mountain ranges in the region.

Table 1 Distribution and associated environments of the major mountain ranges of southern Asia.

<i>Name</i>	<i>Country</i>	<i>Highest peak</i>
Aravalli Range	India	Guru shikhar: 1722 m
Eastern Ghats	India	Arma konda: 1680 m
Himalaya	India, Nepal, Pakistan, China, Bhutan	Mount Everest: 8848 m
Hindu Kush	Afghanistan, Pakistan	Tirich Mir: 7708 m
Karakoram	Pakistan, china, India	K2: 8611 m
Kirthar	Pakistan	Barugh Hill: 2151 m
Knuckles Mountain Range	Sri Lanka	Gombaniya: 1906 m
Pamir	Afghanistan	Kongur Tagh: 7649 m
Salt Range	Pakistan	Sakesar: 1522 m
Sulaiman Mountains	Pakistan, Afghanistan	Loe Nekan: 3578 m
Toba Kakar	Afghanistan, Pakistan	Takh-i-Sulaiman: 3449 m
Western Ghats	India	Anamudi: 2695 m

The Aravallis, India

The word Aravalli originates as a composite of two Sanskrit words “*ara*” + “*vali*” which translates to “*line of peaks*.” The Aravalli Range diagonally bisects the State of Rajasthan into a western arid region and the eastern semi-arid zone (Roy, 1990). The western zone, the Thar, is continued into a chain of arid zones up to the great Sahara desert. The hilly Aravalli terrain experiences frequent drought due to poor and delayed monsoons, high summer temperatures and limited water resources. The Northern Aravalli range in Delhi and Haryana has humid subtropical climate and hot semi-arid climate with very hot summers and cool winters. The maximum daytime temperature during the summer varies between 40 and 46 °C. During winter, it ranges between 1.5 and 4 °C. The Central Aravalli range in Rajasthan has an arid and dry climate. The Southern part of the range in Gujarat has a tropical wet and dry climate.

Rivers and Drainage

Three major rivers and their tributaries flow from the Aravallis, namely the Chambal, Sahibi and Loni. The Chambal and Sahibi rivers are tributaries of the Yamuna, while the Loni River flows into the Rann of Kutch. The north-to-south flowing rivers originate from the western slopes of the Aravalli range in Rajasthan, pass through the southeastern portion of the Thar Desert, and end along the coast of Gujarat. West to north-west flowing rivers originate from the western slopes of the Aravalli range in Rajasthan, flow through semi-arid historical Shekhawati region and drain into southern Haryana.

Biodiversity

The natural vegetation of the area falls within the Northern Tropical Dry Deciduous Forest and Northern Tropical Thorn Forest types (Champion and Seth, 1968). The Aravalli Biodiversity Park has over 160 species of native plants. The following national parks, wildlife reserves, and forests lie in the Aravalli Range:

Delhi: Northern ridge biodiversity park, Yamuna biodiversity park, Neela Hauz biodiversity park, Sanjay Van, Sanjay Lake, Aravalli Biodiversity Park, Tilpath valley biodiversity park, Asola Bhatti Wildlife Sanctuary.

Haryana: Aravali Biodiversity Park, Madhogarh biodiversity park forest, Nuh Aravalli biodiversity park forest, Satnali biodiversity park forest, Tosham hills range biodiversity park, Masani barrage wildlife area, Matanhail wildlife area, Chhuchhakwas-Godhari wetland, Khaparwas Wildlife Sanctuary, Bhindawas Wildlife Sanctuary, Sarbashirpur, Sultanpur National Park, Bandhwari forest, Mangar Bani forest, The Lost Lake (Gurugram).

Rajasthan: Sariska Tiger Reserve, Ranthambore National Park, National Chambal Sanctuary, Phulwari ki Nal Wildlife Sanctuary, Sita Mata Wildlife Sanctuary, Todgarh-Raoli Sanctuary, Mount Abu Wildlife Sanctuary, Kumbhalgarh Wildlife Sanctuary, Bassi Wildlife Sanctuary, Jaisamand Wildlife Sanctuary.

Gujarat: Balaram Ambaji Wildlife Sanctuary, Jambughoda Wildlife Sanctuary, Jessore Sloth Bear Sanctuary.

The Eastern Ghats, India

The Eastern Ghats are a prominent topographic feature on the Indian Peninsula, comprising of a broken chain of hills that extend from Orissa to Tamil Nadu, crossing Andhra Pradesh and stretching from the southern tip of the peninsula to near Bhubaneswar. The range derives its name from the Hindi word *ghat*, which means “a series of mountains.” Eastern Ghats are spread over three states of India namely Orissa, Andhra Pradesh and Tamil Nadu. The Eastern Ghats can be broadly divided into Northern, Central

Table 2 Eastern Ghat classification.

<i>State</i>	<i>Division</i>	<i>District</i>	<i>Hill ranges</i>
Orissa	Northern Eastern Ghats	Pulbani, Kalahandi, Ganjam	Mahendragiri
Andhra Pradesh	Northern Eastern Ghats	Srikakulam East Godavari Vijayanagaram	Palakonda, Pathapatnam, Mandasa, Sompeta Addatigala, Rampachodavaram hills, and Bison hills Sal forest Manda forest, Peddakonda forest, Duggeru forest, Kurupam forest
Andhra Pradesh	Central part of Eastern Ghats	Visakhapatnam Krishna Kurnool Prakasam Mahaboobnagar Cuddapah Nellore Chittoor, Cuddapah	Galikonda hills, Sunkari metta, Anantagiri Kondapalli ranges Nallamala ranges Yerramala. Palakonda ranges Veligonda ranges Seshachalam, Lankamala Nagari, Kambakkam ranges.
Tamil Nadu	Southern Eastern Ghats	North Arcot South Arcot Salem Namakkal Dharmapuri Tiruchirapalli	Javadi hills Gingee hills Shevaroy hills, Kalrayan Kollimalai, Bodamalai, Nainamalai Melagiri hills Pachamailai

and Southern sectors (Table 2). Land use changes of the last 200 years have greatly altered the natural vegetation (Anupama et al. 2014).

The Eastern Ghats have a tropical monsoon climate. This region receives rainfall from both the South-West North-East monsoons. In the northern part, the annual rainfall ranges from 114.2 to 165 cm, indicating sub-humid climate, whereas in the central and southern parts, the mean annual rainfall ranges from 60 to 106 cm exhibiting semi-arid climate except in the hilly station peaks. Heavy winter rains coupled with 15 cyclonic storms per year typify the climate of the eastern portion, especially in the coastal plains. The mean temperatures in January range between 20 and 35 °C. The maximum temperature increases up to 46 °C during summer season. During the rainy season the relative humidity is quite high, up to 70–75%.

Rivers and Drainage

The major rivers are the Cauvery, Krishna, Godavari, and Mahanadi, whereas the minor rivers include the Bahuda, Vamsadhara, Nagavali, Indravati, Rushikulya, Sileru, Sabari, Gundlakamma, Poleru, Sagileru and Penna. All these rivers empty into the Bay of Bengal. The Godavari originates in Triambak near Nasik in the Western Ghats. The Vashista, Gautami, Tulya, Attreya and Bharadwaja rivers are branches of the Godavari river. It flows over a distance of 1465 km before reaching the Bay of Bengal. Godavari is also known as the “Ganges of the South” or “Dakshin Ganga.” It flows throughout the year in the south. The Cauvery River rises near Brahmagiri hills and is one of the biggest river systems of peninsular India. It flows over a distance of 805 km before reaching the Bay of Bengal.

Biodiversity

The common mammal species in Eastern Ghats are the Indian elephant, blackbuck, Asian palm civet, small Indian civet, Madras treeshrew, common grey mongoose, sambar deer, Indian crested porcupine, Indian bison, wild boar, common muntjac, Indian leopard, Bengal tiger, dhole, golden jackal, Indian giant squirrel, Indian hare, Asian house shrew, tufted grey langur, Indian flying fox, bonnet macaque, rhesus macaque, Bengal fox, smooth-coated otter, jungle cat, cheetal, Nilgai, Indian boar, striped hyena, Indian Wolf and the Indian mole-rat. The common avifauna include the Great Indian bustard, red-wattled lapwing, spot-billed pelican, blue peafowl, Indian pond heron, hoopoe, spotted owl, greater coucal, pied crested cuckoo, Oriental white ibis, Indian pitta, Indian paradise flycatcher, red-vented bulbul, red-whiskered bulbul, jungle babbler, painted stork, black-rumped flameback, brahminy kite, jungle myna, Indian spotted eagle, Indian vulture, and Malabar whistling thrush. The endemic fauna of the Eastern Ghats are the Jerdon's courser and grey slender loris. The rare geckos found here are the Indian golden gecko, granite rock gecko, Yercaud slender gecko. The other reptiles include Sharma's skink and snakes such as Gower's shieldtail snake, Shortt's shieldtail snake and the Nagarjun Sagar racer. In total, nearly 100 species of reptiles occur in the Eastern Ghats.

The Himalaya, Bhutan, China, India, Nepal, and Pakistan

The Himalaya constitutes an impressive crescent-shaped mountain range extending for over 2500 km from the south of the Indus Valley beyond Nanga Parbat in the west to Namcha Barwa in the east; spanning five countries (India, Pakistan, Nepal, China and

Bhutan). The word Himalaya means “abode of snow” in Sanskrit. Nine of the world’s 10 highest peaks are located here, including the tallest—Mt. Everest. The Himalaya contain the world’s third largest deposit of ice and snow on the planet, giving it a common name of “The Third Pole.” The Himalaya consist of four parallel mountain ranges: the Sivalik Hills on the south, the Lower Himalayan Range, the Great Himalaya, which is the highest and central range, and the Tibetan Himalaya on the north. The average summer temperature in the southern foothills is about 30 °C and the average winter temperature is around 18 °C. In the middle of the Himalayan valleys the average summer temperature is around 25 °C while the winters are really cold. And on the higher region of the middle Himalaya the summer temperature is recorded at around 15–18 °C while the winters are below freezing point. The climatic condition at region above 4880 m is below freezing and is permanently covered with snow. During the winter the snowfall is heavy while the summers are much more mild and temperate. The Himalayan Alpine climate varies according to the altitude. Local climate is also affected by topography: The leeward side of the mountains receive less rain while the well-exposed slopes receive heavy rainfall (Palazzi et al., 2013).

Rivers and Drainage

The Himalaya are drained by 19 major rivers, of which the Indus and the Brahmaputra are the largest, each having mountain catchment basins of about 260,000 km² in extent. Five of the 19 rivers, with a total catchment area of about 132,000 km², belong to the Indus system—the Jhelum, the Chenab, the Ravi, the Beas, and the Sutlej—and collectively define the vast region divided between Punjab state in India and Punjab province in Pakistan. Of the remaining rivers, nine belong to the Ganges system, and three belong to the Brahmaputra system. Glaciers also play an important role in draining the higher elevations and in feeding the Himalayan rivers.

Biodiversity

Stretched over an area of more than 4 million km², the region hosts parts of four Global Biodiversity Hotspots: the Himalaya Hotspot, the Indo-Burma Hotspot, the Mountains of South-West China Hotspot, and the Mountains of Central Asia Hotspot (Chettri et al., 2008). Of the estimated 10,000 species of plants in the Himalaya hotspot, about 3160 are endemic, as are 71 genera. Furthermore, five plant families are endemic to the region, the Tetracentraceae, Hamamelidaceae, Circaeasteraceae, Butomaceae and Stachyuraceae. The largest family of flowering plants in the hotspot is the Orchidaceae, with 750 species. Biogeographically, the Himalayan Mountain Range straddles a transition zone between the Palearctic and Indo-Malayan realms. Species from both realms are represented in the hotspot (Salick et al., 2009).

The Hindu Kush, Afghanistan and Pakistan

The Hindu Kush is part of the larger Hindu Kush Himalaya ranges, and spans Afghanistan and Pakistan, with few parts extending into Tajikistan and China. The Hindu Kush system stretches for around 966 km laterally, and its median width is around 240 km. It divides the valley of the Amu Darya to the north from the Indus River valley to the south. The eastern end of the Hindu Kush in the north merges with the Karakoram Range. Towards its southern end, it connects with the Spin Ghar Range near the Kabul River. Since the Hindu Kush separates one major climate zone of Asia from another, the range’s climate shows great variations. The mountains of Swat Kohistan are within the area of the rain-bearing summer monsoon winds, and most of the eastern Hindu Kush, as well as the Hindu Raj, rises up at the extreme western limit of monsoonal Asia. This region experiences rainy or snowy summers (from July to September) and dry winters. The central and western Hindu Kush, however, border the Mediterranean climatic zone, characterized by hot, dry summers and cold, wet or snowy winters (from December to early March).

Rivers and Drainage

Rivers that flow from the mountain system include the Helmand, the Hari and the Kabul River. The lower Sistan basin gets little rainfall (~50 mm per year) and the main source of water is the Helmand River which brings snow-melt water from the southern Hindu Kush. The smaller Khash, the Farah and the Arashkan (Harut) rivers bring water from the western Hindu Kush. The basin of these rivers serves waters the region west to Hindu Kush, but the flow in these rivers fluctuates severely and has been a historical problem for any settlement. Extreme and extended droughts have been common.

Biodiversity

Well-adapted species of wildlife are found throughout the mountains. The Siberian ibex, markhor (both wild goats), Marco Polo sheep, black bear, Himalayan brown bear and urial (another wild sheep) are common. Chitral valley wildlife shelter the rare snow leopard. The landscape is home to a considerable number of globally threatened mammal species, including the Himalayan lynx, blue sheep, wolf and musk deer as well as small mammals like the golden marmot. The rich birdlife of the mountains includes vultures, eagles, Tibetan snowcock, Himalayan snowcock and the bar-headed goose. The streams of the northern slope contain brown trout in abundance. From about 1300 to 2300 m, sclerophyllous forests are dominant with *Quercus* and *Olea* (wild olive);

from 2300 to 3300 m one finds coniferous forests with cedars, *Picea*, *Abies*, *Pinus*, and junipers. Steppe desert vegetation covers the landscape between 3300 and 3600 m.

Karakoram–Pamir, Afghanistan, India, and Pakistan

The *Karakoram Range* derives its name from the literal translation, “Black Gravel.” The range lies in the hinterland of Eurasia and is regarded as the central backbone of Tibet. It forms the second highest range of mountain systems in the world. This complex of mountain systems, spanning Central and South Asia, hosts the mighty Hindu Kush in the west, the Pamir to the northwest, Kunlun mountain ranges to the northeast and the Himalaya to the southeast. The convergence of several international borders (Pakistan, Afghanistan, China, Tajikistan and India) give this remote region a high geopolitical significance.

The climate of the region is characterized as semi-arid and continental in nature. The steep and long southern slopes are fed by monsoonal moisture from the Indian Ocean, but the shorter northern slopes are relatively dry. The lower and middle slopes are arid, with annual precipitation that rarely exceeds 100 mm. At higher elevations (>4900 m), snow is the only precipitation, however, snowfall in lower elevations is also not uncommon. At higher elevations (>5700 m), the average summer temperature remains sub-zero and elevations below that (3900–5700 m), mean summer temperature ranges between 0 and 10 °C. Rarefied air, intense insolation, harsh winds and considerable diurnal temperature ranges constitute the typical features of this region.

Rivers and Drainage

The northern boundary is drained by the Yarkand and Karakash rivers, while the southern boundary is drained by the Gilgit, Indus and Shyok rivers, separating it from the Himalaya range. The Karakoram itself serves as the watershed for the Indus (south) and Yarkhand (north) rivers. Seasonal thawing of huge glaciers supply water to river channels, often resulting in floods on the moister southern slope.

Biodiversity

Ranges of several ungulates, such as the Marco Polo sheep and the orargali, have shrunk to the point that breeding only occurs in the eastern Pamirs, with animals migrating to the western Karakorams. Wild sheep (*Ladakh urials*) thrive in the lower mountains of the east, while the rocky slopes are frequented by the Siberian ibex and the markhors. Large raptors like the Himalayan griffon, lammergeiers and golden eagles are also commonly spotted in the region.

Kirthar Mountains, Pakistan

Traversing along the western boundary of the Indian subcontinent, eastwards of Ornach Nal and Chaman, stands the Sulaiman and Kirthar mountain ranges in the country of Pakistan, in the Sindh and Balochistan provinces. The mountains span over 310 km towards the south from the Mula River (east-central Balochistan) to Cape Monze on the Arabian Sea, forming the demarcation between the lower Indus plains and Balochistan. Overall, the precipitation pattern of the region is very erratic, both spatially and temporally, with overall arid conditions. The discharge of streams and river oscillates rapidly between dry and peak flow levels. The sudden burst in flow results in heavy erosion, coupled with extreme and destructive flooding. Rain occurs mostly during summer monsoons in the months of June–September. The average temperature records ranges from 18.21 °C in January to 33.61 °C in May. Short-term climate data from Dureji, Balochistan, reflects an arid climate, with mean annual rainfall of 65 mm, along with an average monthly temperature range from 15 to 38.1 °C.

Rivers and Drainage

The primary drainage of the south Kirthar mountains are the Hab and Lyari rivers, while the northern part is drained by the Kolachi river, all draining into the Arabian sea.

Biodiversity

Kirthar National Park is one of the largest wildlife protection areas of Pakistan, housing an array of rare and indigenous flora and fauna within its extensive mountainous terrain. Mammals such as the Singh ibex (*Capra aegagrus*), Urial (*Ovis vignei*) and Chinkara (*Gazella bennettii*) are found here. Indian grey mongooses, hedgehogs and porcupine are among the other encountered species. The park also hosts several winter deciduous species of small trees and shrubs such as *Prosopis cineraria*, *Tamarix aphylla*, *Lycium shawii*, *Salvadora oleoides*, and *Ziziphus nummularia*. Summer rains aid in the growth of lush grasses and herbs from seeds that lie dormant in the winter soil. This summer bloom helps sustain wildlife and livestock populations.

Knuckles Mountain Range, Sri Lanka

The geography of Sri Lanka can be described as three massifs, running north to south. The Knuckles mountain range forms the northernly massif. This range forms the northern block of what is known as “Hill country” but is isolated by the Kandy plateau and the broad Dumbara valley, both to the south of the range. The range got its name from a series of stretched folds and peaks in the west which resemble the knuckles of a clenched fist.

The pattern of rainfall varies widely across the Knuckles mountains. It receives rainfall from both the southwest and northeast monsoons. The highlands and the western areas of the range are wet throughout the year and experience an annual rainfall of about 5000 mm, whereas the lower eastern slopes are not as wet, receiving an annual rainfall of 2500 mm. The area's mean annual temperature outside the massif is more than 26 °C, and this value falls to about 21 °C at elevations above 915 m and to about 18.5 °C at the highest elevations.

River and Drainage

The Knuckle Mountain Forest Range (KMFR) plays an important role as a watershed, housing more than 500 streams that is an origin point for many rivers and streams that drain East into the lower Mahaweli River system (Heen Ganga, Hasalaka Oya, and Maha Oya), southwest into the upper Mahaweli River system (Hulu Ganga), and northeast into the Amban Ganga River system (Kalu Ganga, and Teligam Oya). The KMFR catchments area contributes about 30% of water to the three reservoirs (Victoria, Rantamgala and Rantambe) of the Mahaweli River system.

Biodiversity

Typical patches of sub-montane forest are found at Cobert's Gap in Kelabokka. The Riverstone area and the trees in the sub-montane forest are stunted, much branched and aerodynamically shaped by strong winds. Approximately 1033 species of vascular plants are found, including 170 endemic species of woody trees (3% of which are nationally threatened) and several endemic flowering herbs. Also, it harbors 33% of all the flowering plant species of the island. Around 262 species of vertebrates have been recorded, of which around 69 are endemic and 60 are nationally endangered. There are several species of fish, amphibians and reptiles that are endemic to the Knuckles range. Out of 21 endemic species of birds of Sri Lanka, 14 are endemic to this specific region. Among the fauna, 5 species of amphibians, 6 species of mammals and 10 species of reptiles are threatened. The Knuckles range is inhabited by various mammals such as wild boar, spotted deer, giant squirrel, barking deer, purple faced leaf monkey, mongoose and porcupine. The endemic lizard species found at Knuckles range include the Crestless Lizard (*Calotes Leiocephalus*), Pigmy Lizard (*Cophotis ceylonica*), Kangaroo Lizard (*Otocryptus Wiegmanni*) and leaf nose lizard (*Ceratotheca Tennentii*).

Pamir Mountain Range, Afghanistan

The Pamir region, also known as the Gorno-Badakhshan, lies on an elevated plateau in the center of the mountainous Badakhshan region, in north-eastern Afghanistan and south-eastern Tajikistan. Although the exact extent of the Pamir range is debatable, most of it falls within the borders of Tajikistan, with some fringes extending into Afghanistan, China and Kyrgyzstan.

The eastern Pamirs rise from a high-elevation foundation, with the average elevation being a minimum of 6100 m. The climate of the Pamirs is typical of cold desert and semi-desert, characterized by extreme winters and warm, dry summers. The mean temperature during the former season ranges between 2 and 10 °C, while the annual average trends between 0 to –8 °C. Summer storms are a common feature in western valleys. Most wind activity and movement patterns are influenced by the Afghan winds from north-western Afghanistan. These winds intensify over ridges in the lower Pamirs, resulting in dust storms and frequent rainfall. The frigid winters limits growth of forests, with the climate made more hostile to trees by the presence of strong dry winds.

Rivers and Drainage

The primary drainages of the northern Hindu Kush-south western Pamir area originate within the Harirud fault, in a sharp and irregular drainage that divides them and the southern rivers of central Afghanistan. The rivers drain an arid region and join the Amu river. The rivers exhibit sharp knickpoints (a point in a river or channel where there is a sharp change in channel slope), cutting the main Hindu Kush range, while traversing the intramontane faults. The rivers draining southwestern Pamir show much higher gradients and flow north. These rivers are incised throughout their courses, except in their upper reaches where they flow on Quaternary glacial outwash.

The main Pamir mountains are drained predominantly by Pyandzh–Amu river and its tributaries. The river exhibits a gentle profile and show several incisions throughout its course, except on the central plateau and the lower Amu reaches. This is the only drainage for the main mountain system without much disruption. The right bank, however, houses many more tributaries and is responsible for draining most of the northern and central parts, flowing over major thrust lines. The rivers of the north Pamir mountains flow in a westward direction into the Kyzylsu and Vakhsh tributaries to the Amu. The primary river of the Trans- Alai

valley, the Kyzylsu–Surkhab–Vakhsh, exhibits a disruption in its middle and lower reaches and runs along the compression zone between North Pamir and Tien Shan.

Biodiversity

The Pamir shares a distinct ecological similarity with the Mediterranean type gravelly desert at lower elevations. With gradual elevational ascent, the community changes to thorny cushion plants, supported in an open steppe habitat. Further uphill, the higher steppe community supports abundant growth of needle grass and fescue grass. The higher elevations harbor alpine meadows. The upper limit of vegetation is typified by hardy perennial flora. The alpine flora of the Pamir shows high phytogeographical similarities to the Tibetan plateau.

The drier eastern Pamir harbors several avian species such as the brown-headed gull (*Larus brunnicephalus*), bar-headed goose (*Anser indicus*), two species of snow cock (*Tetraogallus himalayensis* and *T. tibetanus*). The Pamirs also are home to an array of mammals; some of the endangered encountered mammals include the brown bear (*Ursus arctos isabellinus*) and snow leopard (*Uncia uncia*). Several species of goat and wild sheep are also commonly encountered across the desert and tundra region, the most abundant being the Siberian Ibex (*Capra ibex sibirica*) and the Marco polo sheep (*Ovis ammon polii*).

The Salt Range, Pakistan

Salt Range is a series of hills and low mountains between the valleys of the Indus and Jhelum rivers, located in the northern part of the Punjab region of Pakistan. It derives its name from extensive deposits of rock salt that form one of the richest salt fields in the world. The range is approximately 300 km long from east to west, and its width ranges from 8 to 25 km. Its average height is 660 m and its highest altitude, at Sakesar mountain, is 1522 m.

The climate of the Salt Range is continental and arid, ranging from tropic to subtropic. Tropical air prevails during all seasons of the year except the cold winter months, when relatively cool polar air penetrates at the tail end of high-pressure systems (cyclones). During summer, precipitation is linked with the equatorial, moist, southwestern (Indian) monsoon, which reaches the limits of its occurrence in West Punjab but brings the largest amounts of precipitation (more than 50% annually).

Rivers and Drainage

To the west of the Indus river, the Jhelum runs south into the districts of Bannu and Dera Ismail Khan. It sinks gently towards the Potwar Plateau in the north. The salt range is divided into two parts:

1. Main Salt Range or Cis-Indus Salt range, lies east of river Indus
2. Trans-Indus Salt Range, lies to the west of river Indus

Part of the Central Salt Range has a wetland called “Uchhali Wetlands Complex” located in the Khushab District. It encompasses three lakes: the Uchhali Lake, the Khabbeki Lake and the Jahlar Lake. These lakes are mainly fed by local rainfall, small springs, seepage from adjacent irrigated land and run off from surrounding hills.

Biodiversity

The Salt Range is bestowed with a great diversity of habitats and has a correspondingly rich species diversity. Dominant trees are *Acacia modesta*, *Olea ferruginea*, *Tecomella undulata* and *Butea frondosa*, whereas dominant shrubs are *Dodonaea viscosa*, *Justicia adhatoda*, *Maytenus royleanus*, *Ziziphus nummularia* and *Buxus papillosa*. Over 60 palatable grass species have been recorded from the area, dominant among them are *Chrysopogon serrulatus*, *Heteropogon contortus*, *Dichanthium foveolatum*, *Cynodon dactylon*, and *Aristida mutabilis*.

A total of 138 bird species have been recorded, belonging to 13 orders and 48 families. Most of the birds are migratory and few are resident. The rose ringed parakeet, house crow, house sparrow, mynas, and bulbuls are common among the resident birds, while kingfisher, koel, rollers, and tree pie are increasingly rare. The Grey Francolin is widely associated with the drier regions of the Indus plains and has penetrated the salt range and agroforestry tracks of the Pothwar Plateau in the Punjab. Quail and Grey Partridge are found in large numbers as there are many places providing shelter for their breeding and other activities. The Red Turtle Dove is a summer visitor and the spotted dove is common. Rock Pigeon, Hill Pigeon, Snow Pigeon, Pale-backed Pigeon, Common Wood-Pigeon, Speckled Wood-Pigeon, Eurasian Turtle Dove, and other members of the same family are migratory summer visitors.

Sulaiman Mountains, Afghanistan and Pakistan

The Sulaiman mountains are a folded mountain belt which was formed by the collision of Indo-Pakistan and Eurasian plates. The range derives its name from the name of Prophet Solomon, who is said to have climbed this mountain. The Sulaiman range runs north in Loya Paktia and meets the Spin Ghar range northeast of Gardez in Paktia province. To the northwest, the Sulaimans merge

beyond Loya Paktia into the Koh-i-Baba range. To the east, the Sulaimans enter the districts of Dera Ghazi Khan in Punjab and Dera Ismail Khan in Khyber Pakhtunkhwa, and approaches the Indus River near Mithankot in the Rajanpur District of Punjab. The eastern slopes drop very quickly to the Indus River, but the mountain range drops gradually towards the west, in Kandahar southwest into Helmand and the Sistan Basin.

The climate of the area varies in terms of precipitation and temperature. Summer temperatures are hot (up to 35° C) while winters are cold, with temperature as low as -15° C. Also, there is a strong diurnal variation in temperature. Rainfall is mostly light (270–300 mm/year) and occurs in summers. Winter precipitation mostly falls as snow. The region lies on the path of passing western disturbances carrying moisture laden winds from the Mediterranean Sea. These winds provide moisture in winter.

River and Drainage

Two major rivers originate from the Sulaiman mountains. The Gomul river, which flows towards east into the Indus river, and the Dori river and various other small tributaries of the Arghandab river which flow south westward into the Helmand river.

Biodiversity

The Suleiman Range has the world's largest pure stand of Chilgoza forests and is home to the endangered Suleiman Markhor. It includes the Niazi Kot, Ghundai Kun, Lakai, Kachai and Ahmadi Dargah valley district. Two distinct forest types exist in the area: dry temperate forest and sub-tropical broad-leaved evergreen forest. The flora includes *Pinus gerardiana* (Chilgoza), *Pinus wallichiana* (Kail or Nashtar), *Olea ferruginea* (Showan), *Pistachio cabulica* (Ozgai), *Pistachio khinjuk* (Sharawan), *Prunus eburnea* (Wild Almond), *Perowskia abrotanoides* (Shinshab), *Salsola foetida* (Lani), *Daphne* spp. (Laghunrd), *Acacia modesta* (Phulai), *Artemisia maritime* (Jhau), *Ziziphus nummularia* (Karkanda), *Fraxinus zanthoxyloides* (Shang) and *Monothea buxifolia* (Gurgura).

Mammals found in the region include the Suleiman Markhor, Common leopard, Black bear, Fox, Wolf, Asiatic Steppe Cat, Hyena, Asiatic Jackals, Indian Crested Porcupine. Many snake species have also been reported from the area. The braid snake, *Platyceps* (formerly *Coluber*) *rhododracus* and *Agama* lizards. are common. Birds found in the region are the Eurasian Griffon Vulture, long legged buzzard, partridge, Chukor, Blue rock pigeon, Oriental turtle dove, Little swift, Kashmir roller, Greater shirt toed lark, crested lark, small skylark, Long billed pipit, Water pipit, Grey Headed yellow wagtail, rufous backed redstart, collared Indian bushchat, pied bushchat, Isabelline wheater, Eastern pied wheater, Indian robin, Blue rock thrush, Black throated thrush, Blyths reed warbler, Great tit, Himalayan tree creeper, Jungle crow, and Migratory house sparrow.

Toba Kakkar Range, Afghanistan and Pakistan

The Toba Kakkar range in the Zhob and Quetta-Pishin districts of Baluchistan forms the transboundary between Baluchistan and Afghanistan and the watershed between India and Central Asia. It descends towards the west and opposite Chaman, taking a sharp turn to the south west, continuing under the name of the Khwaja Amran and Sarlath. The Torghar Mountains experience dry cold winters (average mean temperature 4 °C) and warm summers (average mean temperature 26 °C). The area receives heavy snowfalls in winter and violent thunderstorms in summer. Total annual precipitation lies between 180 mm and 270 mm, making the region semi-desert.

Biodiversity

The Torghar hill of Toba Kakkar range is a semi desert landscape dominated by shrub steppe plant communities. In upland slopes, the vegetation that flourishes includes Bunchgrasses, forbs, wild almond (*Amygdalus brahmica*) trees, *Ephedra* sp., *Artemisia* sp., and other shrubs. However, in low lying area, plants such as *Cargana* sp. and *Tamarix* sp. grow at places where water is available. Trees are rare, but include juniper (*Juniperus macropoda*), wild pistachio trees (*Pistacia khinjuk*), and almond trees are scattered across the landscape. The mountains of northern Balochistan were rich biodiversity as recently as the 1950s, and had significant populations of Suleiman markhor, Afghan urial, leopards, Asiatic black bears (*Ursus thibetanus*), etc. Unchecked hunting led to regional extirpation of the leopard and black bear in the Torghar hills in the mid-1980s. By then, the total combined regional populations of markhor and urial were estimated at about 200 head. Today only small populations of the following species are found here: Suleiman markhor, Afghan urial, wolf, hyaena, fox, Pallas's cat, steppe wild cat and stone marten.

The Western Ghats, India

The Western Ghats (also known as the *Sahayadris*—"benevolent mountain") are a chain of continuous mountains that run along the west coast of peninsular India from Tamil Nadu through Kerala, Karnataka and Goa to Maharashtra. Older than the Himalaya mountains, the mountain chain of the Western Ghats represents geomorphic features of immense importance with unique biophysical and ecological processes. The site's high montane forest ecosystems influence the Indian monsoon weather pattern. Moderating the tropical climate of the region, the site presents one of the best examples of the monsoon system on the planet. It also has an

Table 3 Classification of the Eastern Ghats.

<i>Group</i>	<i>Reserve (Sub-region)</i>	<i>State</i>
Agasthyamalai Group	Kalakad-Mundanthurai Tiger Res.	Tamil Nadu
	Shendurney Wildlife Sanctuary	Kerala
	Neyyar Wildlife Sanctuary	Kerala
	Peppara Wildlife Sanctuary	Kerala
	Kulathupuzha Range Reserved Forest	Kerala
	Palode Range Reserved Forest	Kerala
Periyar Group	Periyar Tiger Reserve	Kerala
	Ranni Forest Division	Kerala
	Konni Forest Division	Kerala
	Achankovil Forest Division	Kerala
	Srivilliputtur Wildlife Tamil Sanctuary	Tamil Nadu
	Tirunelveli (North) Forest (part)	Tamil Nadu
Anamalai Group	Eravikulam National Park + extension	Kerala
	Grass Hills National Park	Tamil Nadu
	Karian Shola National Park	Tamil Nadu
	Parambikulam Wildlife Sanctuary	Kerala
	Chinnar Wildlife Sanctuary	Kerala
	Mankulam Range Forest	Kerala
Nilgiri Group	Mannavan Shola	Kerala
	Silent Valley National Park	Kerala
	Mukurti National Park	Tamil Nadu
	New Amarambalam Reserved Forest	Kerala
	Kalikavu Range Reserved Forest	Kerala
	Attapadi Reserved Forest	Kerala
Talacauvery Group	Pushpagiri Wildlife Sanctuary	Karnataka
	Brahmagiri Wildlife Sanctuary	Karnataka
	Talacauvery Wildlife Sanctuary	Karnataka
	Aralam Wildlife Sanctuary	Karnataka
	Padinalknad Reserved Forest	Karnataka
	Kerti Reserved Forest	Karnataka
Kudremukh Group	Kudremukh National Park	Karnataka
	Someshwara Wildlife Sanctuary	Karnataka
	Someshwara Reserved Forest	Karnataka
	Agumbe Reserved Forest	Karnataka
	Balahalli Reserved Forest	Karnataka
	Kas Plateau Reserved Forest	Maharashtra
Sahyadri Group	Koyna Wildlife Sanctuary	Maharashtra
	Chandoli National Park	Maharashtra
	Radhanagari Wildlife Sanctuary	Maharashtra

exceptionally high level of biological diversity and endemism and is recognized as one of the world's eight "hottest hotspots" of biological diversity. The Western Ghats cover approximately 795,315 ha and are divided into seven separate groups containing 39 reserves spread over 1250 km, listed below from south to north (**Table 3**).

The coast and lower foothills are humid and tropical; elevations above 1500 m in the north and the higher regions of the south are more temperate. The west side of the mountains intercepts the prevailing southwesterly monsoon winds between June and September when 65–80% of the rain falls. Most of the rest falls during the northeast monsoon between October and November. The rainfall on the west side averages 2000–3000 mm with local extremes up to 10,000 mm. The eastern slopes in the rain shadow receive an average of about 1000 mm near the crest. Average annual temperatures range from around 15 °C in the north to 35 °C in the south. At some high elevations temperatures touch 0 °C during the winter and frost is common.

Rivers and Drainage

A total of 81 rivers originate in the Western Ghats. There are two types of rivers: west flowing and east flowing. The water of west flowing rivers is discharged into the Arabian sea at a faster flow rate due to shorter distance and steeper landscapes. The rivers flowing eastwards are generally slow and merge with large rivers such as the Kaveri and Krishna. The west flowing rivers of the Western Ghats are the Periyar, Bharathappuzha, Netravati, Sharavathi, and Mandovi. Rivers that flow towards the east are the Godavari, Krishna and Kaveri.

Biodiversity

Agasthyamalai Group: Shendurney Wildlife Sanctuary has 951 vascular plant species, 309 being endemic to the Ghats, and 100 endangered species. Neyyar Wildlife Sanctuary has several threatened trees and 125 orchid species. The Kalakad-Mundanthurai Tiger Reserve shelters 43 mammals, 245 birds, 43 amphibians, 46 reptiles and 42 fish. Found in the sites of the group are the Asian elephant, tiger and gaur. There are also large populations of the endemic lion-tailed macaque (*Nilgiri langur*), the Nilgiri marten, the sloth bear and the Nilgiri tahr (Radhakrishnan and Rajmohana, 2012).

Periyar Group: 75% of the site is covered by tropical wet evergreen forest, 13% by moist deciduous forest. Eight vegetation types are present with 1651 vascular plant species—50% of Kerala's total. There are 77 species of Cyperaceae, 10 species of palm and 145 orchids. In the Periyar Tiger Reserve and adjoining sites 62 mammals, 330 birds, 27 amphibians, 45 reptiles, 38 fish and 160 butterflies are recorded, almost the highest overall count in the property.

Anamalai Group: There are six vegetation types and 297 grassland and 108 fungi species. Karian Shola is a separate, very small, mid-level rain forest park at 650–1000 m. In Eravikulam and Grass Hills National Parks there are 29 mammals, 132 birds, 20 amphibians and 101 species of butterflies. In addition to the flagship and local large mammals there are the Nilgiri marten and dusky palm squirrel (*Funambulus sublinea*). One thousand five hundred of the Western Ghats' population of over 2000 Nilgiri tahr (EN) are found here.

Nilgiri Group: This is one of the most important landscapes with a 6000 km² tropical evergreen forest in the southwest and dry euphorbia scrub in the southeast. There are five vegetation types dominated by tropical wet evergreen forest in the west and shola grassland in the hills; with 966 vascular plants, and 108 orchids. Alpine type flora includes the 12-yearly flowering blue flower after which the Nilgiris, the blue mountains, are named.

Talacauvery Group: The vegetation here is predominantly west coast dense tropical evergreen and semi-evergreen forest with shola grassland at high elevations. Seventy tree species are endemic to the Western Ghats. Brahmagiri Wildlife Sanctuary has undulating terrain with steep valleys and is similar in character with thickets of bamboo growing in formerly farmed areas.

Kudremukh Group: Kudremukh National Park has a large continuous forest of tropical evergreen forest below 300 m with deciduous forest and a wide expanse of grassland above 1000 m. Eighty-eight species are endemic to the Maharashtra Ghats. The number of animal species is very high: 33 mammals, 181 birds, 36 amphibians, 54 reptiles, 23 fish, 73 molluscs and 149 butterfly species are recorded.

Sahyadri Group: The Kas Forest region is called the plateau of flowers: it has 850 plant species including many ephemeral herbs and bulbs. Radhanagari Wildlife Sanctuary is the habitat of a large range of animals: 47 mammals, 264 birds, 20 amphibians, 59 reptiles, and 66 butterflies.

Summary

South Asia extends south from the main part of the continent to the *Indian Ocean*. The principal boundaries of South Asia are the Indian Ocean, the *Himalayas*, and Afghanistan. The *Arabian Sea* borders Pakistan and India to the west, and the *Bay of Bengal* borders India and Bangladesh to the east. The western boundary is the desert region where Pakistan shares a border with Iran. The majority of the South Asian landmass was formed from the land in the original Indian Plate. This action started about 70 million years ago and gave rise to the highest mountain ranges in the world.

The balancing of natural landscapes with human population growth is and will remain a primary issue in the realm's future. South Asia is highly populated, with about one-and-a-half billion people (Ebi et al., 2007).

The mountain ranges of South Asia form the backbone of their respective countries. They play a pivotal role, in providing natural resources. A large fraction of the human population depends directly or indirectly on these natural resources. Fresh water sources that originate from these mountains are unparalleled in terms of the population sizes they support.

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A History of Human Exploitation of Alpine Regions

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Abstract

Today, some still consider the higher elevations of the European Alps as mostly wild or “natural” landscapes; biomes that have to some extent avoided the consequences of human economic activities. This article explains how this notion is misplaced via an overview of the interplay of climate, topography and human activity. Offering a synthesis of recent research from across the alpine arc, this contribution considers how human-environment interactions have developed through the Holocene. The evidence employed here focusses on palaeoenvironmental archaeological evidence spanning the Alps, from Austria to France.

Introduction

The history of human exploitation of alpine regions is undeniably complex, but more importantly, it is a history that reveals the ability of people to exploit one of the most ecologically and geomorphologically, complex, demanding and unpredictable regions on the planet’s surface. In the 21st century, some still consider the high elevations of the Alps to be “natural” landscapes; these areas are the product of human activities that span the entire Holocene. Despite the difficulty of living and working in the mountains, these landscapes offer a wide variety of niches, and other resources, including minerals. Certain regions of the Alps have been critical nodal economic points in complex networks, linking the Alps to other regions across the wider continent. Here, we present a chronological overview of the important phases and trends of human-environment interactions in the Alps spanning the Holocene (see **Table 1** for a breakdown of archaeological periods and their dates). Geographically, we define the European Alps as stretching from the French Alps in the west to the Slovenian Alps in the east; running via the Swiss, Italian and Austrian Alps (**Fig. 1**).

Alpine Biomes—Regional Variation

The Alps are situated between two other significant biomes with concomitant climatic and ecological influences: zones with temperate broadleaf deciduous forest to the north and the Mediterranean biome to the south (**Quinn, 2008, p. 122**). Also, the spatial extent of the Köppen-Geiger climate zones has fluctuated with time, with the external alpine areas moving in and out of

Table 1 Archaeological chronological periods.

Age	Cultural period
After 568 AD	Middle Ages
375–568 AD	Migration Period
15 BC–375 AD	Roman Period
450–15 BC	Late Iron Age
800–450 BC	Early Iron Age
1350–800 BC	Late Bronze Age
1550–1350 BC	Middle Bronze Age
2200–1550 BC	Early Bronze Age
3700–2200 BC	Chalcolithic
5500–3700 BC	Neolithic
6500–5600 BC	Late Mesolithic
10,000–6500 BC	Early Mesolithic

N.B. There is some variation across the region; this table is a broad framework.

**Fig. 1** Map of the European Alps and the key zones referred to in the text.

the boreal and alpine climatic classification. The southern Alps in France and Italy are influenced by the Mediterranean climate especially with regards to hydrological activity (Wilhelm et al., 2012; Wilhelm et al., 2017). The natural timber and tree lines are higher here than other parts of the Alps. In the northern Swiss Alps, the potential timberline is 2000–2200 m, whereas the actual timberline is 1700–1900 m (Röpke et al., 2011). The maximum treeline in the central European Alps should be around 2500 m (Carnelli et al., 2004), while in the southern French Alps, charcoal studies suggest that the treeline was as high as 2700 m until about 5000 years ago (Talon, 2010). Further east, in the Austrian Alps, tree-ring series from subfossil logs also reveal that the timberline reached its highest level (> 2400 m asl.) during the Holocene Climatic Optimum, i.e., between 4000 and 2500 BC (Nicolussi et al., 2005). These regional variations have consequences for biome trajectories and how certain human activities have developed during the Holocene.

The spatial extent of glaciers influences the elevation of ecotone boundaries and ecological reproduction rates (pedogenesis and vegetation growth) in front of the glacier. The extension of permafrost zones, and then areas with shorter growing seasons, limited any activity that comprised the exploitation of vegetation, especially grazing. Glacier extent also influenced how people moved, lived and worked in and around alpine areas. Areas, such as the Schnidejoch, Lötschenpass, Tisenjoch, and Gemsbichl/Rieserferner glaciers were traversed during the Neolithic and Bronze Age, with archaeological materials now exposed as the ice retreats (Hafner, 2012).

Definition of vertical ecological zones

It is rare for any permanent settlement to exist above 2000 m. In the Alps, the highest parish or communes are Trepalle (Italy) at 2209 m, Juf (Switzerland) at 2126 m and Saint V  ran (France) at 2040 m. This contribution focusses on the development of human-environment interactions in the higher elevation zones, taken here as the zones above 1000 m. In turn, for each chronological period discussed below, we focus on the palaeoenvironmental and archaeological evidence for the montane zone (c. 500 m in the northern Alps and 1000 m in the southern Alps), and the sub-alpine and alpine zones (starting c. 1200 m in the northern Alps and 1700 m in the southern Alps) (Fig. 2). This upper limit of the sub-alpine and into the alpine zone is notionally the area that is only exploitable during the summer months, although there are certain activities, such as mining, that take place outside of the clement period. Today, the limit of forest/woodland (the treeline), tends to be situated at the start of the sub-alpine zone, with the alpine belt comprising shrubby and grassy vegetation. From an archaeological/anthropogenic perspective, these zones are important as they influence the development of some important activities, for example, hunting and pastoralism in the sub-alpine zones appear to have been concentrated in the areas between 1500 and 2300 m, zones where the forest, especially towards 2000 m, would have been more open and facilitated hunting and pastoral activities.

Defining mountain landscapes

The defining characteristic of mountainous areas is vertical zonation; the relationship between environments (climate, vegetation, soil) across the vertical zones, the types of activity that can take place therein and when (in which season) these activities can take place. These notions underpin the framework and models for much research in mountains. The reduction in temperature of 0.6  C for every 300 m climbed is a defining environmental variable in mountainous areas. Biogeographical models have influenced how we interrogate and interpret human-environment engagements in the Alps. The application of such models when assessing human colonization and life in high altitude zones is problematic. There are, however, simple, unavoidable biogeographical rules: at a general level, pedogenesis decreases with elevation, although there are variations dependent on microtopography, hydrology and local temperature variances (Poulenard and Podwojewski, 2006). Unsurprisingly, the number of different species of plants and animals also decreases. While the primary productivity of an alpine zone influences forms of hunting, gathering, farming, and pastoralism, with most of these activities typically taking place during the summer months, there are specific resources, especially minerals and ores that can be exploited all year round (Fig. 3).

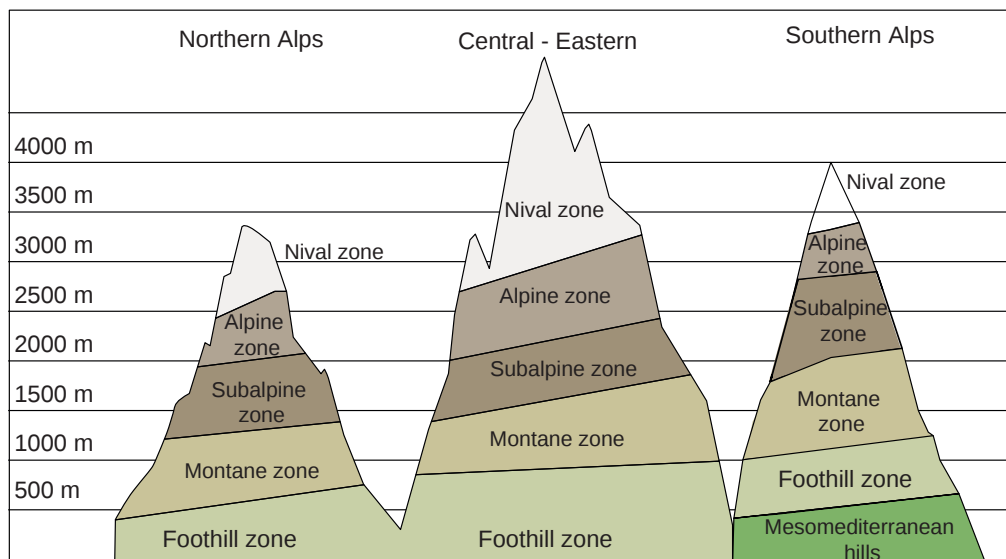


Fig. 2 The altitudinal zones across the European Alps. This contribution focusses on human-environment interactions across the montane and sub-alpine zones. Based on Pethrus (https://commons.wikimedia.org/wiki/File:Altitudinal_zones_of_Alps_mountains_Extended_diagram-fr.svg), text by K.J Walsh, <https://creativecommons.org/licenses/by-sa/4.0/legalcode>.

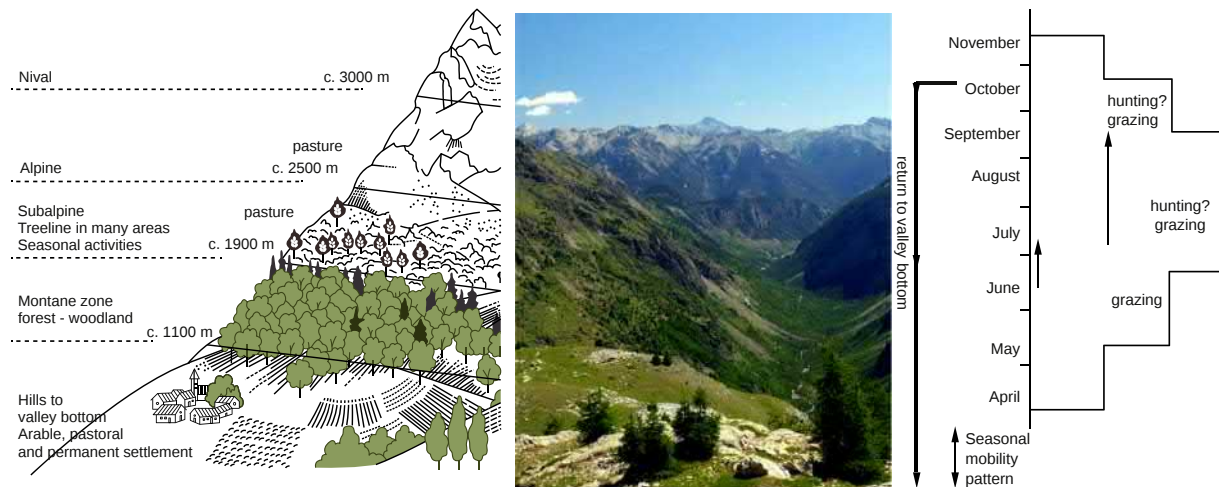


Fig. 3 The relationship between altitudinal zones and seasonal human activities is fundamental. For example, Mesolithic hunting and gathering would have taken place during the summer months. High-altitude grazing, as represented in the right-hand section of this figure, also takes place during the summer months. Detail of typical altitudinal zones with concomitant vegetation bands. Based on Mayoux, Ph. 2004, *Fleurs des Pyrénées* faciles à reconnaître, Rando Edsmiddle photo, K. Walsh.

The Holocene climate, environment and landscape

As with most regions, the Alps warmed rapidly from the start of the Holocene, as inferred from several proxies. Proxies from lake sediments in the Swiss and Austrian Alps, including beetle, cladoceran, chironomid, pollen and isotopic signatures of biogenic carbonates, reveal a rise of about 2.5–4°C during the transition to the Holocene (~9700 BC). There are variations in these records that are dependent on altitude (von Grafenstein et al., 1999; Lemdahl, 2000; Heiri and Lotter, 2003; Lotter et al., 2006). Beetle evidence from the Swiss Alps that suggests rapid warming at the end of the Younger Dryas and the start of the Pre-Boreal (von Grafenstein et al., 1999; Lemdahl, 2000; Heiri and Lotter, 2003) (Fig. 4). The increase in temperature during the transition to the Holocene resulted in significant changes in the altitudinal displacements of trees and other plants (ecotone movement) (Berthel et al., 2012). One of the most important corollaries of climate warming in the Alps was glacier contraction; fundamentally important as the newly exposed land surfaces were colonized by plants and animals, creating new niches potentially exploitable by hunter-gatherers (Le Roy et al., 2017). Treeline advance plays a fundamental role in the development of niches for all mammals; the treeline forms an ecotonal boundary, a zone where animals (including people) have access to different floral communities. In the central Swiss Alps, glacier retreat took place during the Mesolithic (8000–6000 BC) (Hormes et al., 2001). Similar phases of glacier retraction have also been identified in the Bernina Massif in the Swiss Alps (Joerin et al., 2006).

Mesolithic Activity

People moved into the high-elevation zones for hunting at the start of the Early Holocene. In the Venetian Pre-Alps, evidence derived from a palynological core from the Palughetto basin at c. 1000 m and archaeological sites between 1900 m and 2400 m demonstrate the presence of late Early Mesolithic peoples, hunting in forests (Avigliano et al., 2000). The development of bows and arrows may be an adaptation to forest hunting where medium-sized prey was targeted during the early Holocene (Tomka, 2013). Lithic artifacts in Trentino span the transition to the Holocene; deer were often hunted in this area, both for food and as a source of workable bone for tools (Bazzanella, 2001, 2005). Many of the Mesolithic (c. 6500 BC) sites were located at high elevation (between 1800 and 2300 m), with lower sites at c. 1000 m interpreted as intermediate camps on routes between valley bottoms and the high-elevation hunting grounds. In the western Swiss pre-Alps, rock shelters from 900 to 1200 m were occupied c. 9500 BC, while open-air sites are between 1400 and 1700 m (Crotti and Bullinger, 2008). Climatic amelioration brought denser forests, forcing hunters to become more mobile and to hunt in clearings. Mesolithic hunting sites above 2000 m show a preference for open ground where prey could be more easily spotted and killed.

It is difficult to demonstrate any significant impact of hunter-gatherers on alpine environments, although they may have cleared small areas of forest to attract prey, a process identified in some parts of Europe, including North Yorkshire (Simmons and Innes, 1996). Farming began in the Neolithic in the Alps, initiating human impacts on alpine environments.

Neolithic

Across the Alps, the valley bottoms were colonized and landscapes modified by early farmers. Pollen records and some sedimentary archives reflect the creation of new cultural niches (Smith, 2011). Forest was cleared, and arable land was developed. Farming gradually moved upslope to mid-high-elevation areas (Walsh et al., 2014). There was little human impact on the sub-alpine and alpine

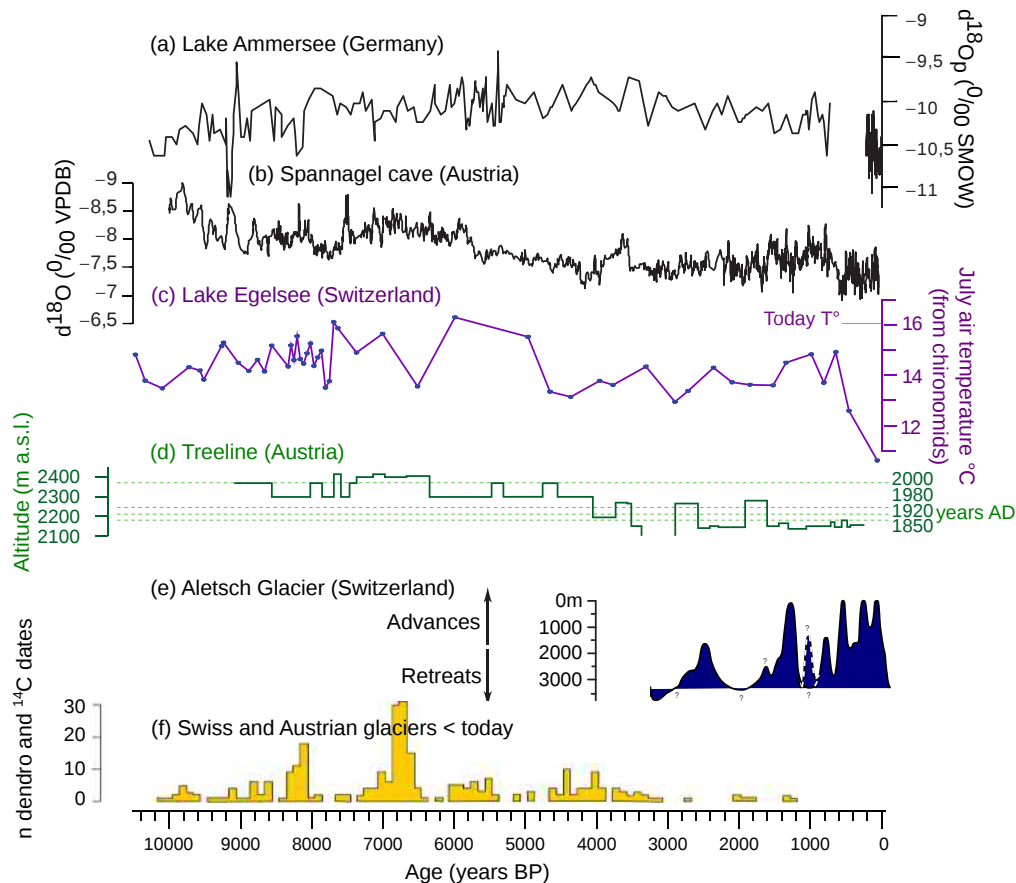


Fig. 4 Holocene climatic trends in the Alps. Oxygen isotopes on ostracod shells (A) from Lake Ammersee sediments can be used as proxy for mid-European (at the northern alpine front) past temperature (von Grafenstein et al., 1999). Oxygen isotopes from Spannagel speleothems (B) is a climatic proxy for Eastern Alps (Fohlmeister et al., 2013). The abrupt shift recorded from 6000 years ago may reflect higher precipitation. Chironomid community composition from Lake Egelsee in Central Northern Alps (C) is used to reconstruct past summer (July) temperature (Larocque-Tobler et al., 2010). The Treeline evolution in Austria (D), obtained from dendrochronological analyses from living trees and subfossil logs (Nicolussi et al., 2005), reflects a mix between climatic changes and anthropogenic activities (deforestation). Glacier fluctuations in Switzerland and Austria from dendrochronological and ^{14}C analyses ((E) Holzhauser et al., 2005, 2005; (F) Nicolussi and Patzelt, 2001; Joerin et al., 2006, Joerin et al., 2008; Kellerer-Pirklbauer et al., 2008; Nicolussi and Schluchter, 2012) (all figures redrawn by Giguët-Covex).

zones in the Neolithic, but people were moving into, and through these areas; Neolithic artifacts from the melting ice on the Schnidejoch Pass (2756 m) in Switzerland demonstrate human traffic across high alpine passes (Hafner and Schwörer, 2018).

Neolithic alpine valley farming focussed on wheat and barley with certain varieties of spring wheat growing as high as 2000 m in some areas of the Swiss Alps (Martin et al., 2008). However, there was little farming in the sub-alpine zone, and hunting and gathering remained important here (Binder and Centre de recherches archéologiques, 1991). At 1720 m in the French Alps, people gathered plants from their campsite, up to subalpine areas 400 m higher (Martin et al., 2012). In parts of the Swiss Alps, farming settlements were created during the sixth millennium BC (Della Casa et al., 2013; Jacquat and Della Casa, 2018). There is little evidence for human impact at high elevation at that time. However, the planting of nitrogen-loving agricultural crop species changed the soil chemistry of farmland.

Early human impact on the (sub)alpine zone and the development of pastoralism—The transition from the Neolithic to the Chalcolithic

First, we should explain the idiosyncrasies of archaeological chrono-typologies: the division of the past into periods founded on fundamental cultural and technological changes. The Chalcolithic is in some ways a hybrid period, one characterized by the continued use of Neolithic technologies (specific lithic tools and agricultural systems) and the start of copper extraction and working. This period broadly starts at c. 3500 BC. This period is of fundamental importance in the Alps as the development of mining and the intensification of pastoralism, have significant consequences for our landscapes.

An example of early high-elevation activity comes from the Italian central Alps. Here, archaeological and palaeoecological evidence demonstrates Neolithic activity at elevations between 1800 and 2300 m. The upper limit of this activity was probably at the upper limit of vegetation. The presence of Early Neolithic charcoal at the timberline in this region indicates human impact on the forest (Wick,

1994). Palaeoecological evidence from a lake at 2065 m near Schnidejoch suggests high altitude pastoralism by c. 4700 BC (Schwörer et al., 2014). In the Silvretta Alps, there is evidence for Middle Neolithic farming, although cereal pollen from c. 4200 BC and 3400 BC likely came from lower elevation farms. There is evidence for Neolithic occupation at high-altitude, from a shelter dated to c. 4300 BC. This corresponds with the contemporaneous presence of cereal pollen at 2170 m in the Lower Engadine. By c. 3600 BC open *Larix* meadows indicate pasture at 1590 m near Ardez. Pastoralism was significant in these areas by 2200 BC (Della-Casa et al., 2013; Dietre et al., 2014; Kothieringer et al., 2015). Moving west, to the northern French Alps, the first pastoral activities, as high as 2000 m, are tentatively dated to around 2900 BC. The clearance of *Pinus cembra* suggests the development of such activity, an increase in erosion, and the first record of cow DNA in sediments from Lake Anterne also support the suggestion that pastoral activity developed at this time (Giguet-Covex et al., 2014; Pansu et al., 2015). However, the lowering of the treeline and the increase in erosion might also be explained by the transition towards the Neoglacial Period, i.e., a colder and wetter period (Wanner et al., 2008). Still in the northern French Alps, but at lower elevation, Late Neolithic cow DNA has been identified in sediments sampled from Lake La Thuile (900 m asl, in the Massif des Bauges). Interestingly, this pastoral activity developed in a forested area as demonstrated by the presence of DNA from fir and alder (Bajard et al., 2017a,b; Giguet-Covex et al., 2019; Fig. 12).

Pollen evidence from the southern French Alps reveals human activity across the full range of elevations (Court-Picon, 2007; Walsh et al., 2014). It is apparent that Neolithic populations were farming the valley-bottoms, and that human impact on the high-elevation (sub-alpine and alpine zones) landscapes did not develop until the end of the Neolithic and Chalcolithic (Walsh and Mocci 2011).

Chalcolithic to Bronze Age

Pastoralism, lactase persistence and niche creation

At c. 2200 BC, the transition between the Middle and Late Holocene (Walker et al., 2012), we move into a phase of complex climatic oscillations that would have influenced the ecological characteristics of alpine biomes. This period comprised a “mélange” of climatic and societal changes (Roberts et al., 2011). During the Chalcolithic and Bronze Age (from c. 3000 to 1000 BC), alpine landscapes, especially the sub-alpine altitudinal belt, emerged as the product of a complex set of co-evolutionary processes. The increased exploitation of secondary products (milk-products, wool, traction) (Sherratt, 1981; Greenfield, 2010) intersected with the increase in lactase persistence in many humans across Europe (Shishlina, 2005; Leonardi et al., 2012). Lactase persistence is strongly correlated with pastoralism (Holden and Mace, 1997, 2002), although it seems likely that pastoralism was adopted before people developed the ability to digest milk (Leonardi et al., 2012). The intensification and extension of pastoralism that included high-altitude summering in the Alps was part of a process where a form of agriculture and landscape management was inextricably linked with the extension of the lactase persistence gene via increased consumption of dairy products (Gerbault et al., 2011).

From the late third to mid-second millennium BC palaeoenvironmental and archaeological evidence reveal a significant extension and intensification of human activity in the higher zones of the Alps. In the Austrian Central Alps, pastoral activity developed by 3000 BC (Schmidt et al., 2006, p. 502). In the Swiss central Alpine region at 1210 m, cattle farming increased throughout the Bronze Age, at the expense of sheep and goats (Bopp-Ito, 2012). Pasture creation per se is not required for sheep/goats as these animals can seek out food for themselves. However, cattle require better quality grass, so pasture creation and increasing cattle herds went hand in hand. Dairy farming and the use of cattle for traction became more important (Bopp-Ito, 2012).

Pollen evidence from the Central Austrian Alps records pastoral activity from the mid-second millennium onwards (mid-late Bronze Age) (Schmidt et al., 2002) and in the St Antönien Valley (Switzerland) at 1400–3000 m) from c. 1300 BC. A study from 2343 m in the Central Swiss Alps suggests forest opening from about 2700 BC (Tinner et al., 1996). In the Ötztal Alps, evidence for human impact at high elevations dates to the Middle Bronze Age. In the southern French Alps, the first stone-structures associated with pastoralism date to c. 2500 BC are found at elevations between 2100 and 2400 m (Fig. 5) (Walsh et al., 2005). Palynological evidence for the third and second millennia BC indicates an intensification of pastoral activities (Court-Picon et al., 2007; Mocci et al., 2009; Richer, 2009). On certain high elevation sites, fungal spores and nitrophilous plant pollen indicate Bronze Age pastoral activity in the immediate vicinities of these sites (Walsh et al., 2006) (Fig. 6). Moreover, charcoal evidence from the pollen cores, along with charcoal from sediments found within and around the archaeological sites, is indicative of woodland clearance designed to create more suitable pasture.

Mining as a driver of landscape change

Unsurprisingly, the activity that characterizes this period (the Bronze Age) is the development of copper mining. Miners would have used wood and timber in a variety of practices, including fire-setting for the extraction of copper ore (Bourgarit et al., 2008; Barge and Talon, 2012a,b). At a fen near Falkenstein (Schwaz, Tyrol, Austria), the lead scandium ratio increased during the Neolithic to Bronze Age transition; this combined with the increase in charcoal values from the Middle Bronze Age suggest increasing impact on this environment over time (Breitenlechner et al., 2010).

The intensification of agricultural activities in the Alps was often linked with the increase in mining activity. Miners required food, and new “wealth-producing” activities would have attracted people to the mineral and ore-bearing areas of the Alps. In the Montafon Valley in the Voralberg area of western Austria, human activities combining mining and farming are apparent from c. 3000 BC onwards. During the Early-Middle Bronze Age, people gradually extended their use of the landscape at higher altitudes. Non-arboreal pollen values for this period are equivalent to those of today. Crops exploited in the area included barley and emmer wheat (*Hordeum vulgare*, *Triticum dicoccum*) and spelt (*Triticum spelta*), with rare examples of Broomcorn millet (*Panicum*



Fig. 5 Bronze Age animal enclosure from the southern French Alps. Photo K. Walsh.



Fig. 6 (Left) Contemporary sheep enclosures and (right) frequently used pasture in the southern French Alps. Vegetation in these zones are dominated by nitrophilous species, *Rumex* and *Plantago*. Photos K. Walsh.

miliaceum) (Schmidl et al., 2005). In the Salzburg area, mining and pastoral activities contributed to changes in the landscape and an opening up of the forest (Breitenlechner et al., 2010, 2014). In the French Alps, high levels of copper in lake sediments from the Grandes Rousses Massif (c. 2400 m) reveal the impact of mining activities in the area (Guyard et al., 2007). Evidence for fire setting dated to 1750–1520 BC comes from the copper mine at Saint Véran and is dated to 1750–1520 BC (Fig. 7). *Pinus cembra* was the predominant choice for fire setting, with some larch and pubescent birch. Specific choices were made regarding the most suitable wood for the task (Barge and Talon, 2012a,b). The pyro-technologies associated with mining go beyond smelting; the production of ceramics, cooking, domestic heating, are also activities that required significant quantities of wood (Cattiglia and Rossi, 1995).



Fig. 7 The Copper mine at Saint Véran, French Alps. Photo K. Walsh.

The receding treeline

From the Late Neolithic onwards, the depression of the treeline with the replacement of trees by pasture occurred across the Alps. Although there was little human impact above 2000 m, Bronze Age people developed high elevation areas for their agro-pastoral system. At 2265 m in the northern Swiss Alps, the treeline descended during the Bronze Age. Multiple lines of evidence point to the critical role of people in these landscape changes (Lotter et al., 2006). This was part of a broader trend of opening the alpine landscape, as seen in southern Switzerland (Hofstetter et al., 2006). In western Austria, human impact on woodlands during the Middle Bronze Age was enough to alter the botanical composition of spruce-fir woodland. Charcoal analyses from an altitudinal transect (1700–2700 m) in the northern French Alps demonstrate that vegetation was increasingly disturbed by human impacts from the mid-Holocene onwards (Carcaillat and Brun, 2000). The treeline also descended in the central Eastern Alps at c. 2000 BC (Nicolussi et al., 2005). At high elevation in the southern French Alps, stone pine forests were gradually replaced with larch and spruce from the Neolithic to the Bronze Age (Ali et al., 2005). This change in forest composition was driven by fire events most likely set by people clearing areas for pasture (Fig. 8).

Mountain erosion dynamics

This period also saw increased erosion and landslides, at least in part caused by forest clearance and associated grazing and mining activities. Evidence of these geomorphic changes has been found in the Dolomites, the Maritime Alps, and the south-central Italian Alps (Borgatti and Soldati, 2010).

Landscape changes during this period also manifested themselves via changes in the geomorphic system; changes in part caused by the reduction of forest cover, associated grazing and mining activities, all played their roles. Also, the start and the Late Bronze Age (2200 and 1200 BC) witnessed periods of climate change. In the Dolomites, there was a significant increase in landslides during the Bronze Age; in fact, higher numbers of landslides than any subsequent period (Borgatti and Soldati, 2010). At Lac Petit at 2200 m in the Alpes-Maritimes, a phase of reduction in vegetation cover and significant erosion was centered on 2200 BC (Brisset et al., 2013). Pollen from species indicative of meadows suddenly spiked, and its correlation with a phase of substantial erosion suggests direct links between these processes. The proxies from Lake Ledro (southern-central Italian Alps) reveal a significant rise in the lake level at c. 2500 BC, a consequence of climate change and human activity, the period between 2200 and 1000 BC saw a significant increase in erosion (Magny et al., 2012; Simonneau et al., 2013). Undoubtedly, this was a consequence of the combined effects of climatic variations, but also the exposure of more extensive areas of soil after forest clearance by people. In the northern French Alps, around Lake Verney (2188 m, Petit St Bernard Pass), the combination of increased hydrological activity and the beginning of pastoral activities during the Bronze Age (2350 BC) also led to a change in vegetation cover and an increase in erosion, which disrupted the soil system (Bajard et al., 2017a,b). These human activities are considered as the roots of regressive soil evolution. Farther north, at Lake Anterne (2060 m), a tipping point, characterized by an increase in flood deposit thickness and frequency, as well as erosion of deep soil-horizons, was recorded from 1450 BC (Giguet-Covex et al., 2011 Fig. 12). The identification of low levels of sheep DNA and the significant increase in *Plantago* DNA contemporary with these sedimentological processes suggests a human-triggered erosion (Giguet-Covex et al., 2014; Pansu et al., 2015). However, these erosion processes were also probably amplified by a climatic degradation as suggested by the glaciers advances (Kuhlemann et al., 2008; Ivy-Ochs et al., 2009; Le Roy et al., 2015). In the western Swiss Alps, phases of higher landslide frequencies associated with human-triggered vegetation changes were also recorded during the Bronze Age (1700 BC) (Dapples et al., 2002).

Bronze Age 2400 - 1000 BC

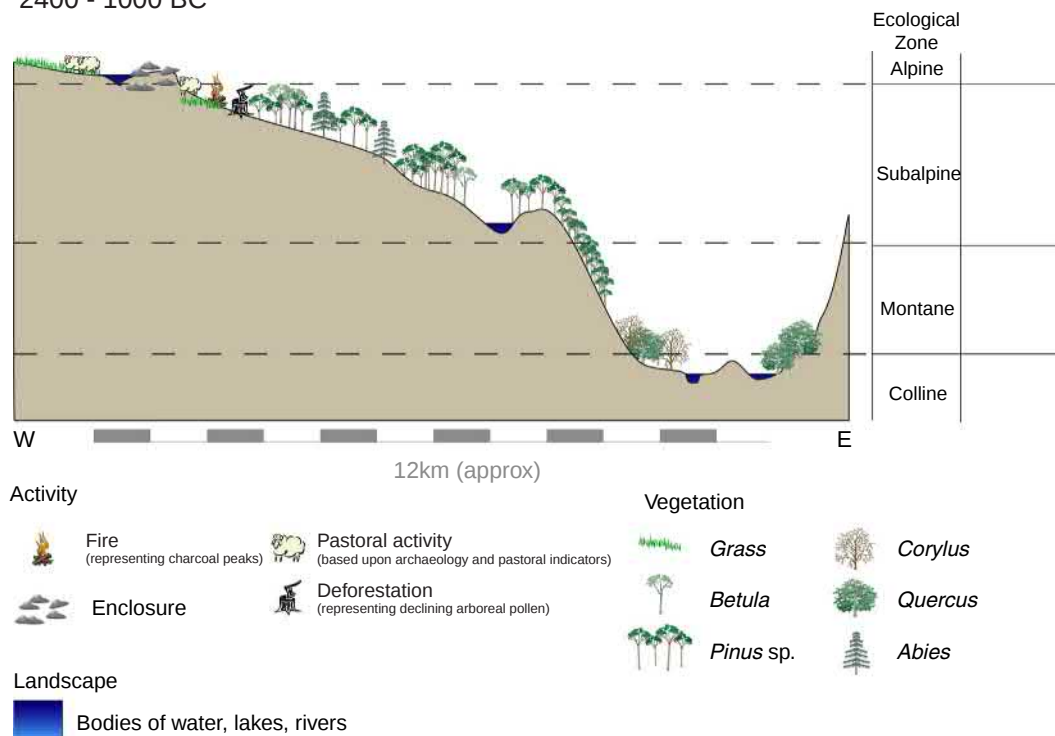


Fig. 8 Cartoon reconstruction of a typical altitudinal section dated to the Bronze Age. First opening of forest in the sub-alpine zone (via burning in many instances). Adapted, with permission, from Richer, S. (2009) *From pollen to people: the interaction between people and their environment in the mid- to high- altitudes of the southern French Alps*. University of York.

Iron Age

Climate

Much of the Iron Age (c. 800–200 BC) was characterized by climatic cooling (Fig. 4), and in many areas, increased precipitation (Van Geel et al., 1996). Alpine lake levels rose from 750 to 350 BC. Climatic cooling led to the advance of many glaciers (Holzhauser et al., 2005). These changes shortened the growing season. A reduction in farming activities is recognized in some records. Despite climatic deterioration, mining activities increased during the Early Iron Age. Therefore, many economic activities increased, causing increased environmental impacts (Anreiter et al., 2009).

Changes in pastoral systems and impact on the landscape

In the South Tyrol/Italian Alps, the early Iron Age (referred to as the Hallstatt period (c. 800–600 BC)) saw a decline in human activity, perhaps as a consequence of climatic deterioration. However, during the later Iron Age (La Tène Period—fifth to first centuries BC), pastoral activity increased (Putzer et al., 2016). In some areas of the Tyrol, this level of human activity was not seen again until the Middle Ages (Heiss et al., 2005). Research in the Eastern Alps reveals increased farming, reaching the higher elevations. The dominant crops were barley, emmer wheat and spelt (Schmidl et al., 2007).

The forest at a site in the Ötztal Alps started to disappear after 550 BC, and pollen from cereals and other food crops starts to appear. At the Lagaun, Schwarzboden, and Penaud mires (2180, 2150, and 2330 m respectively). A site situated at 2150 m shows evidence of forest clearance from about 850 BC, the area emerging as pasture. This pasture remained intact to the end of the Roman Period (Festi et al., 2014). There was significant erosion at the site from 950 to 550 BC, perhaps because of climatic deterioration. In the Italian central Alps, the practices that started in the Bronze Age continued, the evidence for an increase in grazing is mirrored by an increase in charcoal (suggesting burning) from the immediate area (Moe et al., 2007). In the Leventina Valley (southern Swiss Alps) the Iron Age did not see a significant increase in human activity (Jacquat and Della Casa, 2018), although a diagram from the Fimba Valley does show a late Iron Age peak in microcharcoal (Dietre et al., 2014). Moreover, the earliest evidence for dairy production is found in Engadine, from organic residue analyses on potteries dating to the early Iron Age (Carrer et al., 2016). In the central Swiss Alps, at Hinterburgsee (1515 m asl), the first signs of human-triggered forest clearing began at ~450 BC (Heiri and Lotter, 2003).

A regional erosion signal for the NW Alps from Lake Bourget (France) comprises a geochemical signature (K/Ti ratio) that suggests two phases of erosion with a sub-alpine origin, erosion that may well have been caused by pastoral activities (Arnaud et al., 2012). For the Late Iron Age, this assumption is supported by the detection of cow and sheep DNA associated with the

beginning of a new phase of erosion. This record coming from the sediments of Lake Anterne, part of the Lake Bourget catchment (Giguet-Covex et al., 2014). Also, in the Lake Bourget catchment, but at a lower altitude, pollen and DNA records from Lake La Thuile (874 m asl), reveal the presence of *Plantago* and *Rumex*, i.e., indicators of pastoral activity. At Lake Verney (2188 m asl.), in the Tarentaise area, sheep DNA is also present in sediments dating to the Late Iron Age (Bajard et al., 2017b). At Lake Anterne there is also an interesting intersection between the sedimentary DNA evidence and archaeological data where the Late Iron Age animal DNA signal seems to be contemporary with the first occupation of a cabin around the lake (data from P.J. Rey in Giguet-Covex et al., 2014). An enclosure found next to the cabin might also have been used during this period.

In the southern French Alps, regional climatic variations influenced alpine ecology and possibly, economic practices. Unlike the Bronze Age, there are very few archaeological structures at high elevation in the southern French Alps. Deforestation took place across all mountain zones. Plant species indicative of human activity fluctuated during this period (Walsh et al., 2014) (Fig. 9).

Mining and impact on alpine environments

The Early Iron Age saw witnessed the expansion of mining in the Alps. Mining brought a reduction in forest and woodland as well as soil and water pollution that damaged the environment of certain areas. However, the fossil record is too scattered to allow the identification of specific impacts. An increase in charcoal at 1120 m in the Austrian Tyrol, suggests increased mining in the area (Breitenlechner et al., 2010). Salt mining became important in Austria, with important mines at Hallstatt (Kern et al., 2009) (Figs. 10 and 11). Charcoal analysis from a copper mining area in the Tyrol suggests that Early Iron Age miners chose coniferous wood for fire-setting.

The Roman Period

The Roman period in the Alps witnessed a radical change in the way farmlands were organized; however, this did not significantly change the level of human impact on sub-alpine and alpine ecosystems. Some regions of the Alps witnessed an increase and others, a decline in human activity.

Climate

At the start of the Roman period (1st century BC to 1st century AD), the climate underwent relative warming (Fig. 4). Proxy data from 1791 m in Switzerland suggests that the period from 15 BC to AD 120 was characterized by moderately warm temperatures,

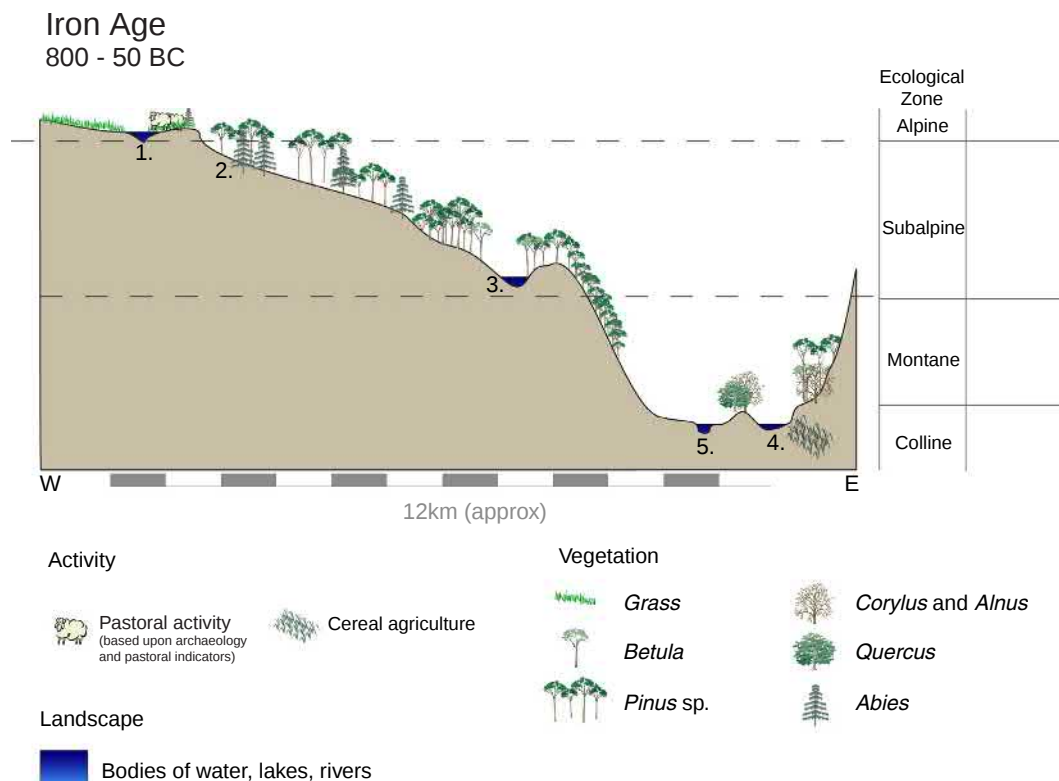


Fig. 9 Cartoon reconstruction of a typical altitudinal section dated to the Iron Age. A period characterized by variation in the level of human impact across the Alps, but relatively few examples of significant pastoral pressure on high altitudes. Adapted, with permission, from Richer, S. (2009) *From pollen to people: the interaction between people and their environment in the mid- to high- altitudes of the southern French Alps*. University of York.

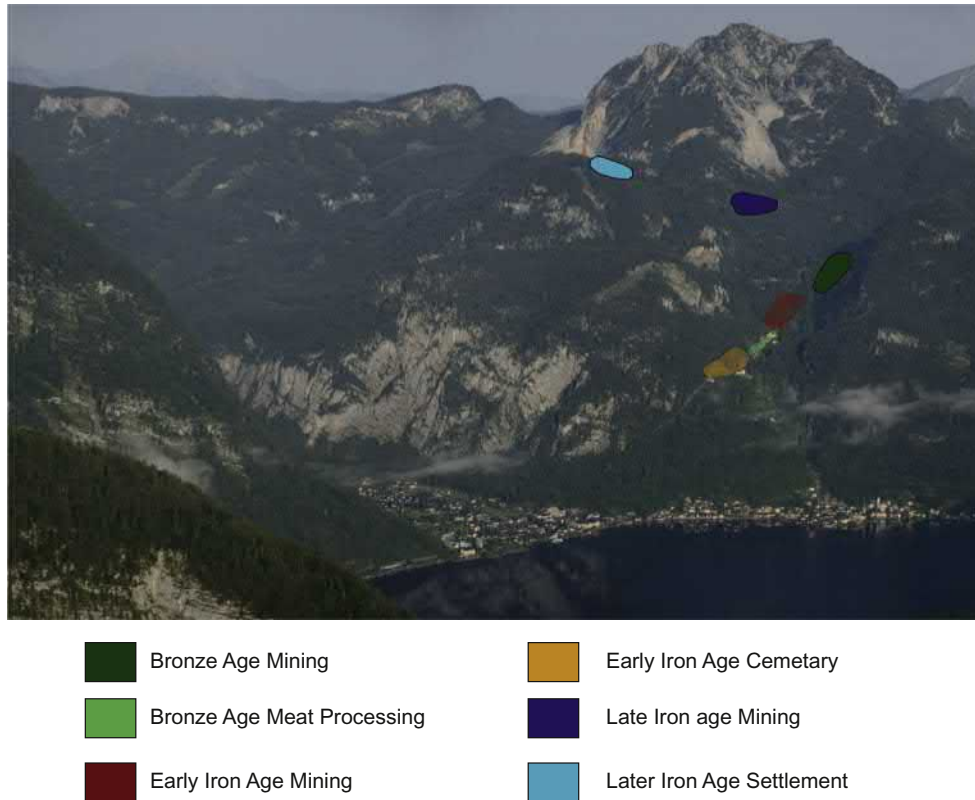


Fig. 10 The areas of past activities (especially salt mining) across the Hallstatt area. Photo Copyright: Daniel Brandner, zones based on Kern, A., Kowarik, K., Rausch, A. W. and Reschreiter, H. (2009). *Kingdom of Salt: 7000 Years of Hallstatt*. Vienna: Natural History Museum (Prähistorische Abteilung). Available at: <https://books.google.co.uk/books?id=8IM7SQAACAAJ>.



Fig. 11 Hallstatt, Austria. *Left*. View of extensive wood remains and mining waste' *Right*. Wooden staircase—Austria. Permission and copyright, NHM Wien.

with some temporal variability (Stewart et al., 2011). This Roman climatic optimum may have been critical in facilitating Rome's success, with Alpine mountain passes possibly remaining open for much of the year during the climatic optimum (Hyde, 1935). Glaciological data from the Swiss Alps indicates that some glaciers were less extensive than they are today (Holzhauser et al., 2005).

Changes in pastoralism and impact on the landscape

Pollen records from areas either side of the Alps suggest increased agricultural activity during the early Roman Period. However, the South Tyrol saw increases in arboreal pollen, suggesting the reestablishment of forest (Heiss et al., 2005). In some areas, such as in the Southern Swiss Alps, agricultural activity remained steady until the end of the Roman Period (Della Casa, 2018). High-elevation pastoralism persisted throughout the Roman Period in the South Tyrol/Italian Alps, while alpine regions forests were re-established (Heiss et al., 2005). In the Italian Alps, all elevational zones were exploited during the Iron Age, but the Roman Period saw woodland recovery (Moe et al., 2007).

Ancient DNA analyses from Roman Period sediments in alpine lakes in the French Alps reveals significant increase in the number of sheep and cattle pastured at c. 2000 m (Fig. 12) (Giguët-Covex et al., 2014; Bajard et al., 2017a,b) and even as high as 2443 m asl at the important Savine pass between France and Italy (Sabatier et al., 2017). These activities, which might reflect the development of a trade with Rome (Giguët-Covex et al., 2014), lead to significant increases in erosion and substantial degradation of the soil resources (Giguët-Covex et al., 2014; Pansu et al., 2015; Bajard et al., 2017a,b).

In the southern French Alps, there is little evidence to suggest a dramatic change in the “natural” environment during the Roman period. Palynological research at lower elevations suggests the development of a heterogeneous, mosaic landscape. Certain areas were heavily exploited while other areas saw the reestablishment of woodland (Fig. 13). Cultivated trees such as walnut, chestnut, and even olive emerge. Perhaps there was pasturing at lower elevations in woodland. In some higher areas, the reduction in woodland may well have been related to mining, based on an increase in lead in sedimentary records (Segard, 2009; Py et al., 2014). Perhaps relatively accessible high-elevation landscapes witnessed increased human activity, such as in southern French Alps where zones around the Lac de Lauzun were exploited for pasture (Ponel et al., 2011).

Mining

There is surprisingly little evidence for mining in the Tyrol during the Roman period (Breitenlechner et al., 2010). Roman period mining may have occurred in the southern French Alps, although the only evidence is the change in lead content and isotopic signature in a peat bog. In fact, woodland may well have re-established itself in the sub-alpine zone during the second half of this period (Py et al., 2014). Several lake sediment cores in the North Western Alps also revealed peaks in heavy metals, notably lead, possibly from mining (Arnaud et al., 2006; Guyard et al., 2007; Giguët-Covex et al., 2011; Thevenon et al., 2011; Bajard et al., 2017a). In the Alpes-Maritimes, there is also some archaeological evidence for mining (Morin et al., 2007).

Medieval to Post-Medieval Periods

Climate

Based on evidence from multiple paleoclimatic proxies, the medieval climatic history of the Alps includes three different phases. First, the Late Roman-Early Medieval climatic deterioration centered on fourth-fifth centuries, second, the climatic optimum of the eighth-ninth centuries, and finally the Little Ice Age between 14th and 19th centuries (Buntgen et al., 2011).

Changes in pastoral systems and environmental consequences

In the high-elevation areas of the northern Swiss Alps, the early medieval period saw the recovery of the forest after the fall of the Roman Empire. In some areas, it is clear that grazing also declined (Wick et al., 2003). During the High Medieval Ages, alpine farmers developed clearings as part of the summer-farming system. The presence of *Potentilla* pollen signals this activity. During the Little Ice Age, increased soil instability across alpine slopes probably contributed to decreased human activity and concomitant reforestation (Röpke et al., 2011). In other parts of the Swiss Alps, the start of the trajectory towards the modern landscape began in the High Medieval Period, with extensive forest clearance (Wick et al., 2003). In the Silvretta Massif (Switzerland/Austria), a significant increase in the quantities of microcharcoal reveals human impact. While an increase in coprophilous spores represents increased livestock grazing areas during Medieval and Modern Times (Dietre et al., 2014). Evidence from the sub-alpine zone of the southeastern Swiss Alps (c. 1800 m) suggests that the landscape was open, with much of the forest cleared, by c. 1450 AD (Gobet et al., 2003) (Fig. 14).

In the Italian Alps, proxy-data suggests a phase of reforestation during the 14th century, interpreted as a downturn in human activity caused by the Black Death, a phenomenon seen in many areas of the Alps. Human activity subsequently increased, with another downturn during the Little Ice Age (Joannin et al., 2014).

In the northern French Alps, from 1000 AD, intensive pastoral activities developed across the “Alpages” and Montane zone. Interestingly, lake sediment DNA analyses reveal a change in livestock farming practices with the decrease of sheep in favor of cowherds, probably related to the development of cheese production (Fig. 12) (Giguët-Covex et al., 2014; Bajard et al., 2017a,b). In the Montane zone cereal crops significantly increase from 450 AD and triggered a strong degradation of the soils (Bajard et al., 2017a,b). From 1000 AD, this soil erosion decreases with the development of a diverse culture of fruit trees, including (pears, walnuts, plum or cherries, and grapes). Grapevine disappears due to the colder conditions during the LIA (Fig. 12).

In the southern French Alps, human activity in the sub-alpine increased during the medieval period (Fig. 14). Mining from the 10th century onwards caused a continued impact on forests (Fig. 15). Mining communities required wood and timber in significant quantities (Py et al., 2013). The High Medieval Period also witnessed an increase in pastoral activities, and this contributed to changes in vegetation across the sub-alpine zone. Several Medieval stone structures have been found in these pastureslands (Fig. 16). This activity continued into the 17th century, with tree-cover only restabilizing itself in the last 150 years or so.

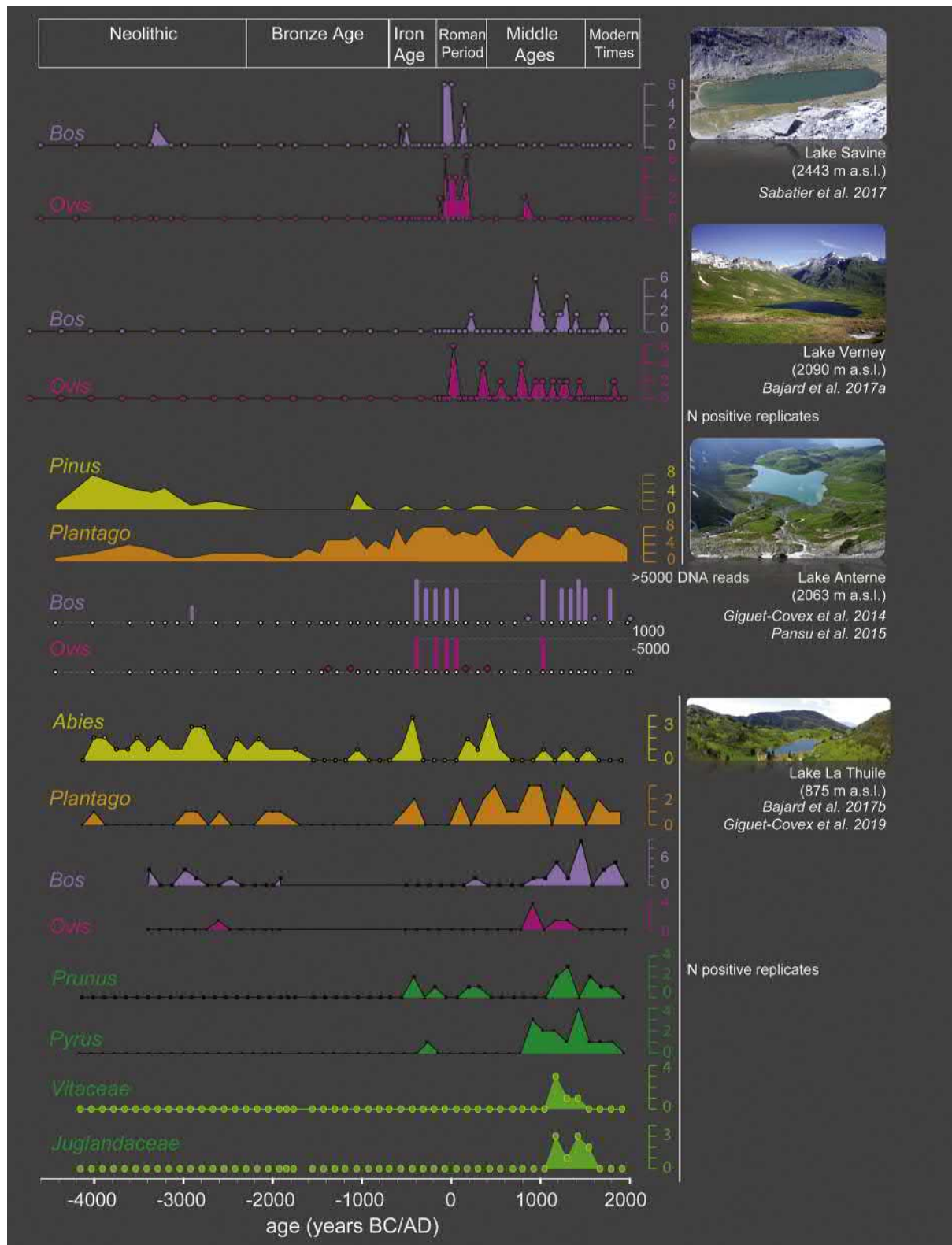


Fig. 12 Lake sediment DNA records from the northern French Alps. The DNA metabarcoding analyses provide the animal composition in the Alpagoes around the lakes Savine (Sabatier et al., 2017), Verney (Bajard et al., 2017b), Anterne (Giguët-Covex et al., 2014) and La Thuile (Bajard et al., 2017a) (from the top to the bottom figure). For lakes Anterne and La Thuile, selected plant DNA, i.e., showing the forest (*Pinus* and *Abies* sp.), pastoral (*Plantago* sp.) and fruit tree evolution (*Pyrus* sp., *Prunus* sp., *Vitaceae*, *Juglandaceae*) are also presented (Pansu et al., 2015; Bajard et al., 2017a).

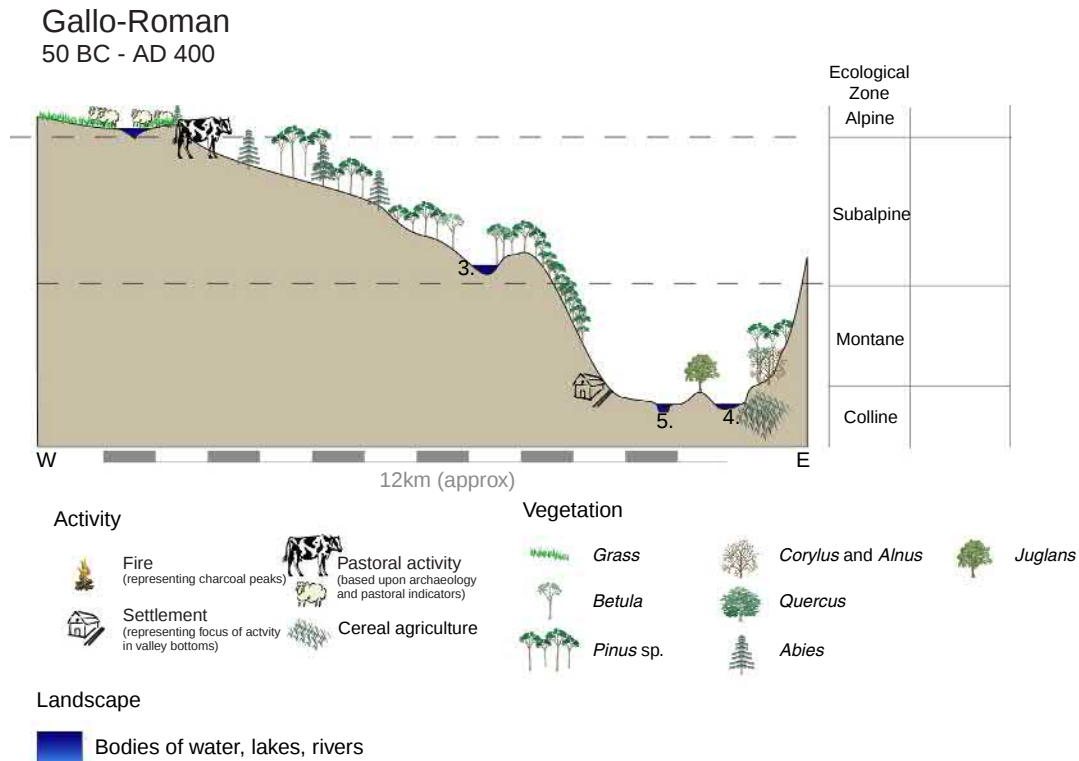


Fig. 13 Cartoon reconstruction of a typical altitudinal section dated to the Roman Period. Adapted, with permission, from Richer, S. (2009) *From pollen to people: the interaction between people and their environment in the mid- to high- altitudes of the southern French Alps*. University of York.

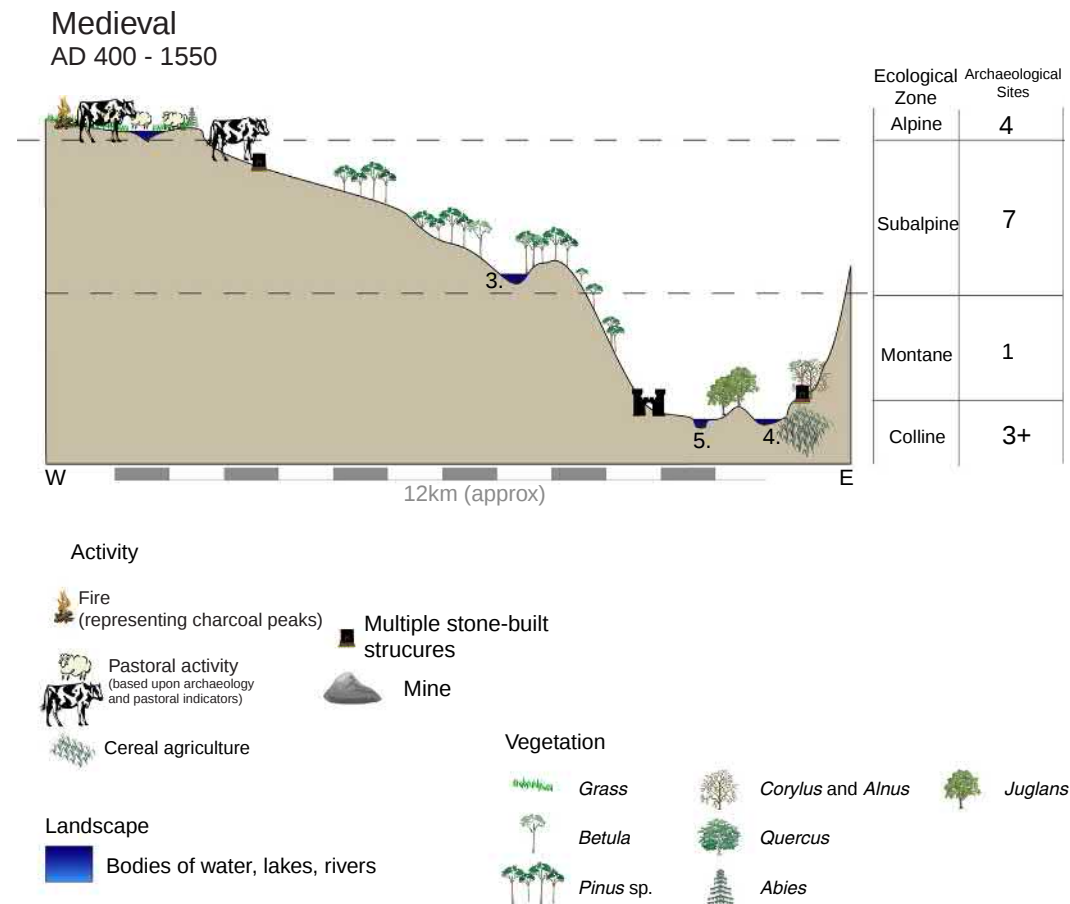


Fig. 14 Cartoon reconstruction of a typical altitudinal section dated to the Medieval Period. Adapted, with permission, from Richer, S. (2009) *From pollen to people: the interaction between people and their environment in the mid- to high- altitudes of the southern French Alps*. University of York.



Fig. 15 Entrance to a mined seam of silver bearing lead in the southern French Alps at 2000 m. Photo K. Walsh.



Fig. 16 Medieval and post-Medieval structures at c. 2200 m in the southern French Alps. (A) Sept-cabannes, Valgaudamar; (B) Plateau de Faravel. Photos K. Walsh.

During the 18th and 19th centuries, there was of course variation in landscape trajectories, although broad trends were common across many valleys. Mining was intense in those areas where minerals were present. Pastoral activity was at its most intense across much of the Alps, with forest often depleted, leading to environmental problems, especially erosion. In some French alpine regions, cheese-production, often linked to large collective dairies, became important (Rosenberg, 1988). Provençal transhumance increased during the 19th century with a concomitant increase in population. The impact on the landscape resulted in state-level laws and regulations, including the Forestry Code in France. This period of intense activity took place despite the Little Ice Age, a climatic phase that appears to have ended relatively quickly in the Alps, with glaciers starting to retreat from the mid-19th century; a consequence of temperature increases exacerbated by industrial black carbon (Painter et al., 2013).

Depopulation was common across many valleys during the 20th century, although long-distance transhumance, now coupled with tourism, started to develop (Rosenberg, 1988). New European regulations and the development of protected regional and national parks have helped conserve and promote the pastoral activities and the maintenance of rich meadows and traditional forms of agriculture (von Glasenapp and Thomson, 2011; Schermer et al., 2016). However, at the same time, ski resorts with all of their infrastructure requirements have had a significant impact on the ecology and geomorphology of many valleys (Arnaud-Fassetta et al., 2005; Barni et al., 2007; Patthey et al., 2008). What is clear, is that the heterogeneity of these 21st-century biomes is at a tipping-point along a complex trajectory whose origins lay with the first incursions of hunters and pastoralists many millennia ago.

Acknowledgments

We would like to thank Suzi Richer for allowing us to modify figures from her Ph.D. thesis, Kerstin Kowarik for obtaining images from the NHM, Wien, and images taken by Daniel Brandner.

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Contemporary Human Impacts on Alpine Ecosystems: The Direct and Indirect Effects of Human-Induced Climate Change and Land Use

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Abstract

Alpine ecosystems account for c. 3% of terrestrial habitats yet, along with adjacent mountain systems, provide water resources to nearly half of the world's human population. Approximately 20% of humans live in or near mountain areas, making it inherently important to understand contemporary impacts on these systems. Here, I review literature regarding contemporary and projected human impacts on alpine ecosystems, including the direct and indirect impacts of human-induced climate change on alpine plant, animal, and soil communities. I also discuss the influence of recreation and tourism, grazing, and other land use changes including the introduction of nonnative and invasive species in alpine systems. I conclude with management implications as well as future areas of research needed to better understand changes to these systems.

Changing Alpine Systems

Mid-latitude and polar alpine species are highly adapted to climatic factors that largely determine the biotic composition and distribution of plant and animal communities (Nagy and Grabherr, 2009). This includes low mean annual temperatures during a short summer growing season, limited moisture availability largely determined by snowmelt from winter precipitation, high levels of solar radiation, and large microclimatic variability across relatively short distances on the order of centimeters to meters (Körner 2003). Conversely, tropical alpine areas experience year-round growing season temperatures daily and are characterized by large diel temperature changes from day to night (Rundel, 1994; Buytaert et al., 2011).

Minimum temperatures have increased approximately 2 °C in alpine systems worldwide over the past three decades and have been accompanied, on average, by decreases in precipitation (Beniston et al., 1997). However, changes have varied as a function of regional climate controls (Beniston et al., 1997; Stocker et al., 2013). For example, high elevation sites in the Rocky Mountains of Colorado have experienced an increase in mean winter temperatures of 0.09 °C each decade since 1979, all of which were greater than changes observed across the entire state (Clow, 2010). At the same time, precipitation and snowpack have increased during spring months at high elevation sites (Mote et al., 2005). Additionally, recent climate warming has been attributed to major changes to alpine portions of the cryosphere including permafrost and glaciers (Paul et al., 2004; Liu and Chen, 2000). For example, major permafrost shifts have been observed on the Tibetan Plateau, including upward movements of 50–80 m. These changes have been observed in addition to range contractions as large as 1–2 km northward in the last few decades of the 20th century (Cheng and Wu, 2007). Cryosphere changes also include the rapid retreat of and water loss in alpine glaciers (Xu et al., 2009; Huss et al., 2010): a total loss of 18% of glacier area occurred across more than 900 alpine glaciers between 1985 and 1999 alone (Paul et al., 2004). Overall climatic changes in alpine systems have been characterized as having greater interannual variability than those observed in other systems around the globe (Beniston et al., 1997), leaving some to predict that alpine systems will experience some of the highest levels of warming globally while also showing responses to change before other terrestrial systems (Cannone et al., 2007).

Human impacts on future alpine climates are expected to be the direct result of increases in atmospheric concentrations of CO₂, which will lead to changes in temperature and precipitation (Winkler et al., 2019). A doubling of CO₂ will lead to increases in temperatures that are elevation-dependent and will lead to pronounced warming at higher elevations. If CO₂ concentrations triple, monthly rainfall may increase in alpine systems, though these changes will likely be small (up to 6% in one model; Burkhardt, 1999). However, regional models project decreases in winter precipitation falling as snow and an increase in winter precipitation falling as rain (Solomon et al., 2007). These coupled changes in temperature and precipitation will subsequently influence snowpack persistence and the timing of snowmelt, which, in turn, will impact growing season length, productivity, and biogeochemical cycling in alpine systems worldwide (Stewart, 2009; Winkler et al., 2016a).

Changes in alpine soils with respect to climate change will have substantial impacts on overall ecosystem performance since soils play an important role in structuring alpine vegetation (Körner, 2003). Soil microclimates, in particular, influence water movement

and nutrient cycling, and, as a result, species distributions and community composition (Graham et al., 2012). Given expected changes in snowmelt patterns, subsequent changes in soil properties and nutrient availability are also expected. Experimental warming on the Tibetan Plateau found that permafrost degraded with warming, accompanied by decreases in soil organic matter (Wang et al., 2006). Colder, higher-elevation alpine sites can have coarser soils and, as a result, less plant-available nitrogen (N) and higher soil pH than warmer, lower-elevation sites (Huber et al., 2007). Thus, climate warming has the potential to increase N availability as these higher elevation sites become warmer, thereby shifting ecosystem productivity (Brooks et al., 2011). Warming experiments have revealed distinct temperature effects on N cycling in alpine systems. Changes include increased N mineralization rates and net nitrification rates (Bai et al., 2013), increases in labile carbon and microbial biomass (Rui et al., 2011; Peng et al., 2016). Studies have also produced varying responses in overall soil N availability, including no change in available soil N (Wang et al., 2012) and increases in plant-available soil N with warming (Winkler et al., 2019). Overall, shifts in N availability may act as a feedback to plant responses but such changes are likely to vary by species, leading to shifts in community structure, diversity, and ecosystem productivity (Farrer et al., 2015; Alatalo et al., 2015).

Alpine Species Responses to Change

Alpine plant species are expected to respond to warming by growing taller as temperature limitations are alleviated (Walker et al., 2006). However, warmer temperatures are expected to influence snowmelt timing, which may negatively impact plant species by increasing their exposure to early-growing-season frost events (Wipf et al., 2009; Sierra-Almeida and Cavieres, 2010). These responses are also expected to vary by species (Sierra-Almeida et al., 2016). More complex phenological responses to warming are expected in alpine plants given the oftentimes tight coupling of seasonal growth initiation and duration to snowmelt (Winkler et al., 2018). As a result, most studies have found an advance in the timing of flowering in response to an advance in snowmelt timing (Steltzer et al., 2009). Similar phenological results have been observed in response to warming (Hovenden et al., 2008; Gimenez-Benavides et al., 2011).

However, whether temperature changes and snowmelt timing will be large enough to advance flowering remains unknown (Petraglia et al., 2014), and whether plants will be able to overcome the potential indirect effects of warming is also unresolved, including decreased available moisture and earlier senescence in response to advanced snowmelt and warmer growing season temperatures (Gimenez-Benavides et al., 2011; Ernakovich et al., 2014). Decreased stress under warmer temperatures may increase competition among plant species (Schöb et al., 2012). That said, some studies have found that facilitation among alpine plant species will remain an important process in a warming alpine environment (Cavieres and Sierra-Almeida, 2010; Anadon-Rosell et al., 2017). Additional research is needed to better understand plant-plant interactions in changing alpine systems.

Changes in alpine plant diversity, including those linked to recent climate warming, have generally found increases in alpine diversity over the past 25–100 years (e.g., Grabherr et al., 1995; Gigauri et al., 2013). At the same time, alpine plant community composition, though perhaps richer, has also shifted in recent decades and has likely done so in response to warming (Pauli et al., 2007). This matches predictions from experimental warming studies in alpine systems around the globe, though there is variability in how individual species or functional groups will respond (Kudo et al., 2010; Wahren et al., 2013). Long-term studies have in some cases revealed that recent warming explains a majority of the variation in changes in alpine species abundance (Soudzilovskaia et al., 2013). Some of these compositional shifts are likely the result of individual species migrating in response to historical climate change (Grabherr et al., 1995; Lenoir et al., 2008). For example, more than a third of 125 species have migrated at least 100 m higher than their previously reported upper range limits recorded 100 years ago (Frei et al., 2010). Some species have disappeared from their historical lower elevation limits with simultaneous increases in abundance at their upper-elevation limit that now experiences warmer temperatures (Klanderud and Birks, 2003). Such shifts have accelerated in recent decades (Rixen and Wipf, 2017) but have not been synchronous across species within a given community (Cannone et al., 2007). Additionally, alpine floral responses to warming can also be influenced by other climate changes including drought, wildfires, and nitrogen deposition (Lenoir et al., 2010; but see Williams et al., 2009). For example, plant responses to experimental warming in an alpine heathland in Australia revealed differential responses to warming in unburned areas resulting in increased forb and shrub cover and decreased grass cover, while warming in burned areas reduced grass and forb cover and facilitated a rapid expansion of shrub cover (Camac et al., 2015). These results highlight that many of the responses observed or predicted in alpine systems will be the result of complex, oftentimes interactive, processes.

Climate warming impacts have also been manifest in alpine animal species (e.g., Beaver et al., 2016; Rubidge et al., 2012). Perhaps the most well-documented changes have been to iconic pika species including the American pika, *Ochotona princeps*, which has experienced major range retractions with climate warming in recent decades (Mathewson et al., 2017; but see Millar and Westfall, 2010). Molecular evidence and ecological modeling show that recent demographic declines across all *O. princeps* lineages suggest that the species will experience declines in genetic diversity with continued climate warming (Galbreath et al., 2009). Alpine arthropod communities are also at risk due to climate change (Gobbi et al., 2006; Hågvær and Klanderud, 2009) and this has large implications since arthropods account for a large part of alpine fauna communities that are structured by strong climatic relationships (Edwards, 1987). However, alpine arthropod responses to warming can vary substantially by taxonomic order (Hågvær and Klanderud, 2009). For example, a snow removal experiment in Australia found that of the Collembola, Araneae, Acari, and Coleoptera orders that accounted for 95%–98% of the arthropod diversity at this site, Collembola was most sensitive to early-season snow removal and that both positive and negative responses were observed within the order (Slatyer et al., 2017). Furthermore,

changes in alpine plant species composition and cover can also have direct effects on faunal communities that depend on them, and vice versa (Rasmann et al., 2014).

Novel Species in the Alpine

Human-induced climate warming has also been linked to an increase in plant and animal invasions and encroachment in alpine systems around the globe (McDougall et al., 2005). This remains separate from the multitude of intentionally introduced non-native species in alpine systems around the globe (see grazing section below; Donald et al., 2001; Wilson and Lee, 2010). These unintended invasions include the fly *Rhagoletis completa* in Europe, which consumes alpine plants during the fly's larval stage (Aluja et al., 2011), the invasive dwarf bamboo *Sasa kurilensis* in northern Japan (Kudo et al., 2018), and a dandelion in the Chilean Andes (Molina-Montenegro et al., 2012). Invasions in alpine ecosystems have serious implications for native species because they can cause reductions in available resources, changes in productivity and cycling, as well as lead to pollinator disruption (McDougall et al., 2011; Kašák et al., 2015). It is possible that human transport has mediated some of these invasions (McDougall et al., 2005) but it is also likely that the amelioration of historically-harsh climatic conditions has allowed invasives to colonize alpine systems (Pauchard et al., 2009; Winkler et al., 2016b).

A similar framework of ameliorated microclimatic conditions has been used to understand shifts of the treeline ecotone into historically alpine-restricted zones (Kharuk et al., 2009; Kueppers et al., 2017). This line of investigation has also been used to document and understand woody encroachment above historic treeline elevations and into alpine areas that were previously grass- or forb-dominated (Brandt et al., 2013; Gartzia et al., 2014). While some studies have shown positive growth and establishment of tree seedlings above the traditional treeline (e.g., Danby and Hik, 2007) others have shown that warming can lead to decreased recruitment at and above treeline, likely owing to coupled soil moisture changes (Hofgaard et al., 2010; Kueppers et al., 2017). Together, these shifts in treeline and woody species abundance above treeline have serious implications with potential to disrupt carbon storage and nutrient cycling across the globe (Greenwood and Jump, 2014).

Grazing and Human Development Impacts on Alpine Systems

Livestock grazing is common in many alpine regions of Asia, Australia, Europe, and South America (Fig. 1; Nagy and Grabherr, 2009). Grazing can alter landscapes and can also influence alpine-species responses to climate change (Scherer and Pickering, 2005;



Fig. 1 Examples of the direct human impacts on alpine ecosystems, including cattle grazing (top left), a skier on the alpine slopes above a ski resort (top right), hikers and hiking trails (bottom left), and the basecamp in Nepal that marks the start of the climb up Mount Everest (bottom right).

Luo et al., 2010; Hope, 2014). Warming, combined with continued grazing in some of these alpine systems, may lead to declines in vegetation productivity and overall forage quality for livestock (Klein et al., 2007). There are also direct conservation issues related to humans controlling native alpine populations to increase forage value for livestock and other domesticated animals. Perhaps most notorious is the poisoning of the Plateau pika, *O. curzoniae*, that has led to major population declines while simultaneously opening more forage opportunities for livestock (Smith and Foggin, 1999). Animals introduced for grazing are not the only groups to negatively impact native alpine species. In the case of New Zealand's introduced, invasive stoat, *Mustela erminea*, the native and endangered takahe, *Porphyrio hochstetteri*, and rock wren, *Xenicus gilviventris* are at major risk of predation and potentially extinction (O'Donnell et al., 2017). A similar story holds for the introduced house mouse, *Mus musculus*, and its impacts on native alpine plant and arthropod species (Wilson and Lee, 2010).

Climate change impacts on alpine aquatic species including freshwater invertebrates and amphibians have been exacerbated by human development of dams, canals, and introduced species (often for recreational fishing; Bradley et al., 2006; Tiberti et al., 2014). These human-caused changes have resulted in drastic declines in frog, microcrustacean, and native macroinvertebrate abundances and diversity in alpine lakes in the Sierra Nevada of California (Bradford et al., 1998). Similar declines have been observed in the Italian Alps (Tiberti et al., 2014) and the Canadian Rocky Mountains (McNaught et al., 1999). However, evidence points at the potential for recovery when invasive fish have been removed from some of these same alpine lakes (Donald et al., 2001), providing sound management implications if conservation measures are prioritized. Conservation of freshwater insects in alpine lakes has been identified as a potential issue in response to hydraulic stress resulting from dams and canals used to control water resources (Rossaro et al., 2006). Given that more than half of the world's human populations depend on alpine and montane water resources (Viviroli et al., 2011), alpine freshwater invertebrates not only demonstrate the direct human impacts related to damming, canalization (Rossaro et al., 2006), and invasive species impacts (Magnea et al., 2013), but can also be utilized as indicators of environmental change in the rivers and lakes where they occur (Catalan et al., 2006).

Recreation and Tourism in Alpine Systems

Visitation to protected alpine areas is expected to increase as a direct response to climate change increasing periods of desirable weather for tourism (Fig. 1; Richardson and Loomis, 2005). This has serious management implications, as recreational activities have been shown to directly impact alpine floral (Pickering and Hill, 2007) and faunal communities to varying degrees (Monz et al., 2010; Negro et al., 2010). For example, a study in an undisturbed alpine zone in Tasmania found that trampling alpine plants led to declines in vegetation cover after an environmental threshold of 200 steps on a given point occurred (Whinam and Chilcott, 2003). The study also found that the threshold varied as a function of plant type, with woody shrubs and grasses susceptible to damage with fewer steps whereas alpine cushions were tolerant of up to 500 steps. Also, watersheds in the Himalaya have been shown to be negatively impacted by the increasing tourism in the area (Fig. 1; Nepal, 2003; Byers, 2005).

Alpine faunas have been shown to be equally susceptible to recreation impacts (Roland et al., 2007; Patthey et al., 2008). A global meta-analysis found that alpine birds were most susceptible to the negative impacts of winter recreation (i.e., skiing) and mammals and arthropods were also susceptible to a lesser extent (Fig. 1; Sato et al., 2013). Interestingly, this meta-analysis also identified a number of cases that showed no effect on faunal communities but an overall decline in animal species richness, abundance, and diversity was observed in ski resort areas (Sato et al., 2013). However, some research has modeled decisions tourists make and identified potential management practices that would minimize human-wildlife interactions in alpine systems (Coppes and Braunsch, 2013).

Conclusions and Future Directions

Humans are altering alpine systems worldwide through impacts related to grazing, development, and tourism, and also climate change. These perturbations are already pushing these ecosystems into novel states. With recent impacts on alpine floral and faunal diversity and distributions, new communities are emerging with clear, negative impacts on alpine species. Many of these responses are being driven by changes to the abiotic and microclimatic controls in these systems. For example, the loss of alpine glaciers will have dramatic effects on the flora and fauna of alpine environments, in addition to the human populations that depend on the resources they provide (Xu et al., 2009; Huss et al., 2010). Although these changes will likely have irreversible effects on many alpine species (Haeberli and Beniston, 1998), effective management efforts have the potential to mediate at least some responses to change and can curtail previous recreation and development impacts (Morrison and Pickering, 2013). However, the challenge of documenting changes that have already occurred in alpine systems and predicting future changes remains. Nonetheless, the global importance of alpine systems should outweigh the difficulties that may be necessary to overcome in order for managers and public and private stakeholders to effectively manage and conserve these valuable ecosystems.

Acknowledgments

This review was funded by the U.S. Geological Survey. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Ongoing Change in the Alpine Biome of North America

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Abstract

The alpine biome of North America is responding to ongoing changes in climate, nitrogen deposition, invasive species, and local human activity. The response to widespread climate change is complicated by heterogeneity in abiotic interactions and biotic interactions. Interactions across spatial scales and time lags limit understanding. The other three drivers are spatially concentrated. Terrestrial ecosystems are more affected by climate change and local human activities, while aquatic ecosystems bear the brunt of impact by nitrogen deposition and invasive species. Because of the heterogeneities and time lags, changes in biodiversity are likely to be limited to marginal ecosystems, and changes in carbon balance will be locally important but small relative to global flux. Water resources from alpine areas may change significantly, but due to the direct effects of climate, not through change in the biome.

Alpine Change

The alpine biome in North America is changing in response to four major forces of global environmental change: climate change, nitrogen flux, invasive species, and habitat destruction and deterioration. The alpine biome is climatically defined as high elevation zone where too little energy or heat exists to support trees but enough to prevent permanent snow and ice. The biome has varied terrestrial and aquatic ecosystems. The vegetation of terrestrial ecosystems are primarily alpine plant communities, which are dominated by forbs, sedges, and grasses and include a range of moss and lichen in addition to often prostrate shrubs and some “subligneous” plants (not quite forbs or woody but not strictly herbaceous). The terrestrial ecosystems are heterogeneous, with different plant communities within small areas that vary because of differences in soils and especially in water availability. The aquatic ecosystems are headwaters lakes, ponds, and streams and often freeze completely in winter. The aquatic ecosystems differ geographically but are simple in comparison to other aquatic realms. Alpine wetlands can be transitional between the two major types but are so often seasonal that they are more closely associated with terrestrial plant communities. Secondarily, the “alpine” can extend to where scant soil or water limit trees at high elevation.

All four forces of global change are affecting alpine ecosystems of North America. Their importance varies overall and among the different ecosystems. Climate change is by far the most general and most studied driver of change in the alpine biome of North America. Nitrogen flux is spatially concentrated, and where it occurs it is relatively more important in aquatic ecosystems. Invasive species are few but can be locally important. Habitat destruction and deterioration are isolated to the immediate corridors of the few roads and many trails.

Climate Change

Expected Responses

Because the alpine biome is primarily delimited by cold climates, it is expected to be affected by global warming. However, impacts are uncertain. Because climatic gradients are steep on mountain slopes plant biogeography is spatially compressed, and the shift in climatic habitat may be within the dispersal ranges of species. However, the alpine biome cannot move upwards, and in many cases, the terrain existing at the highest elevations has no soil. Moreover, an upward shift in alpine treeline would reduce the area of the alpine. Even allowing for the colonization of now-bare areas or increased densities, the total area should decrease because mountain peaks are generally conical. Along with upward movement, areas such as saddles or cols that joined higher alpine regions could become tree-covered, further isolating the remaining areas of alpine vegetation. Moreover, many alpine plant species do not have the adaptations required for long-distance dispersal (Morgan and Venn, 2017).

Also, alpine biome areas may experience elevation-dependent warming (EDW) (Pepin et al., 2015), which would accelerate climate change impacts. Based on the observations, EDW is a climatic phenomenon in which high elevation areas increase in temperature more than other landscapes, e.g., warming 1.8 times more than the global average in the northern Rocky Mountains (Pederson et al., 2010). Other long-term observations of snow and ice also reflect rapid temperature changes in North American mountains (Fountain et al., 2017).

The current area of the alpine could decrease within decades. At a coarse resolution, Diaz and Eischeid (2007) calculated that the cold climate associated with the alpine biome will no longer exist in the continental United States, given the current trends in climate change. The true area of the alpine biome is not known, however, because delineating boundaries in steep terrain has been difficult (although current remote sensing could rectify this). Additionally, the potential upslope advance of treeline carries considerable uncertainty. Components of alpine vegetation might shift upslope, but the alpine is not zonally divided by elevation. Instead, topographic variation at all scales creates differences in energy, water, and soil resources that determine the habitats within which different types of alpine vegetation exist. Therefore, a simple upward shift of alpine community types is not expected, and change could be in a variety of directions (Malanson and Fagre, 2013).

In a thorough review of the effects of climate change on alpine limnology, Redmond (2018) primarily reported on expectations and complications, and some of these occur through interaction with other factors of global change, most notably nitrogen deposition and invasive species. Her expectations are summarized in Fig. 1.

Observed Responses

Some of these responses may now be visible. Settele et al. (2014, 317), as part of the IPCC process, reported that"

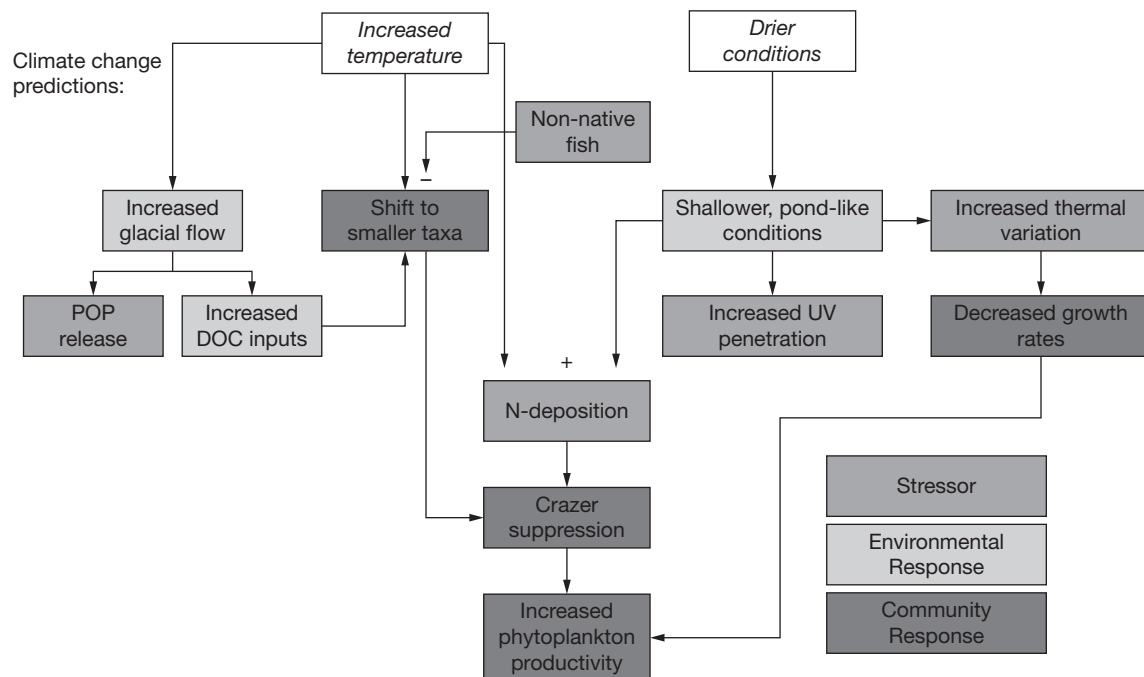


Fig. 1 Redmond's (2018) summary of the cumulative effects of climate change and other stressors on the function and community composition of alpine lakes. Redmond, L.E. (2018). Alpine limnology of the Rocky Mountains of Canada and the USA in the context of environmental change. *Environmental Reviews* 26, 231–238.

"There is high confidence that alpine systems are already showing a high sensitivity to ongoing climate change and will be highly vulnerable to change in the future."

Expectations led to the creation of alpine vegetation monitoring efforts. The most developed of these is the Global Observation Research Initiative in Alpine Environments network (GLORIA) (Grabherr et al., 2000). GLORIA was developed to extend the record from observations in the early 20th century and to extend similar types of observations across the globe to sites where a legacy of alpine vegetation data did not exist. GLORIA is a network of > 120 sites at which summit vegetation is monitored; summits are some of the harshest environments for plants and even slight warming might have distinct impacts in plant composition, phenology, and growth.

GLORIA includes sites in North America; 31 were established and four more proposed, but not all are continuing with the planned a 5-year schedule (Table 1). These observations are in their early stages and have not yet produced definitive results (e.g., in the Brooks Range, AK and in the Chic Chocs, Quebec; personal communication March 2019, J. Jorgensen and G. Fortin, respectively). In Glacier National Park, where some observations were made annually, the annual turnover in species composition was high (personal communication March 2019, D. Fagre), and 5-year change was substantial but not consistent in direction over 5 years (Malanson and Fagre, 2013).

More restricted monitoring has also yielded useful results. Lesica (2014) established plots for monitoring alpine vegetation change in Glacier National Park in 1988. Initial results of this project showed a shift toward drier vegetation types. Reporting observations through 2011, Lesica (2014) found declines in the cover of species with narrow, high-elevation distributions. However, absence of change predominated. For a broader study that included some of the same sites and again focused on species at the southern end of their ranges, Lesica and Crone (2017) reported decreases in populations for all six alpine dicots and three of six

Table 1 GLORIA projects underway or proposed (*) for North America. Note that some may no longer be operational (e.g., at Niwot Ridge, CO, vandals disrupted the project; personal communication, William Bowman)

State or province	Range or region	Year established or * possible	Surveys or baseline completed
Alaska	Brooks range	2007	2
	Selawik wildlife refuge	2007	2
	Blackberry Ridge, Juneau	2017	B
British Columbia	Canadian Coast Range	2006	1
	Vancouver Island	2006	1
	Northern Interior Mtns	2013	B
	Cariboo Mountains	2011	B
	Selkirk Mountains	*	
California	White Mtns, non-carbonates	2004	1
	White Mtns, carbonates	2005	1
	Dunderberg Peaks	2004	1
	Carson Range/Tahoe Basin	2008	1
	Mt Langley	2010	1
	Sweetwater Mtns	2011	B
	Death Valley NP	2013	B
Colorado	Great Sand Dunes NP	2009	1
	Rocky Mountain NP	2009	1
	San Juan Mtns	2006	1
	Niwot Ridge	2007	B
	Ruby Range	2008	B
	Mosquito Range	2016	1
Idaho	Lemhi Range	*	
Montana	Glacier NP	2003	2
	Pioneer and Pintlar Range	2008	2
Nevada	Great Basin NP	2008	1
New Hampshire	White Mountains	2014	B
New Mexico	Pecos Wilderness	2016	B
	Sangre de Cristo	*	
Oregon	Wallowa Mountains	2018	B
Quebec	Monts Chic-Chocs	2012	1
	Monts Groulx	2010	B
Wyoming	Absaroka-Beartooth Wilderness	2012	1
	Yellowstone NP	2011	1
	Selawik wildlife refuge	2007	2
	Blackberry Ridge, Juneau	2017	B
Yukon	Northern Rockies	*	

monocots (plus two increasing and one unchanged). They attributed the inertia of monocots to their root systems being more adaptable to periods of drought.

For longer time periods, resurveys of earlier plots, or at least the same slopes, have been informative. For 88 plots established on Niwot Ridge, CO, Spasojevic et al. (2013) resurveyed them six times in 20 years and found that community change could be substantial. The degree of change varied with the type of alpine plant community, and some were temporary. Danby et al. (2011) reported increased diversity and evenness in alpine vegetation in the Canadian Yukon over four decades. Changes differed among sites, particularly with aspect, with the least amount of increase in richness but the greatest change in composition occurring on southwest aspects. Still, the overall change was attributed to an observed increase in mean annual temperature during the period between observations.

Changes in growth, phenology, and/or carbon flux have been observed following climate change or experimental manipulation (e.g., of snow cover, with consequent warmer subsnow temperatures) (e.g., Walker et al., 1995, 1999). Both observational (Wagner and Reichegger, 1997) and experimental (Galen and Stanton, 1995) studies of climate effects on flowering and seed development have yielded significant results. Intensive study in the southern Rocky Mountains has highlighted damage from earlier flowering due to subsequent frost and has established the timing of snowmelt as an important driver that is affected by climate change (e.g., Inouye, 2008).

Complicating Factors

Factors that complicate alpine biome response to warming and separate expectations from observations include abiotic drivers, biotic interactions, and spatial and temporal scale issues.

Abiotic complications

Alpine vegetation is found across a broad range of moisture conditions, and differentiation of plant communities may be related to water availability (Malanson et al., 2012; Winkler et al., 2016) in addition to temperature gradients (Elmendorf et al., 2012). The moisture conditions are largely controlled by topography at multiple scales (ranging from orographic precipitation/rain shadow effects to microtopographic rills). Even the details of microtopography across a few centimeters affect species composition and diversity (e.g., Rose and Malanson, 2012). Moreover, the variation in alpine communities is often weakly correlated with other abiotic variables (Suding et al., 2015). Thus, alpine vegetation varies over short distances and, because it is found in a wide variety of microclimates, responses to climate change may be habitat specific.

High elevation vegetation response to climate change is also profoundly affected by snow persistence. Snow affects alpine plants through thermal protection, water provision, effect on atmospheric deposition, and determination of the length of the growing season. Upward shifts in snow cover could lead to threshold effects more profound than the causal temperature changes. Many western North American mountains are relatively arid. Increased future temperatures, without compensating increases in precipitation, will drive these landscapes to greater aridity and have out-sized impacts on the current mountain vegetation that may be existing near their drought tolerance limits. Greater aridity will make snow beds, springs and other wet areas more important to some plants and generally increase the variability in moisture across the mountain landscape. Reduced snow persistence will likely change seasonality for alpine plants, shortening the growing season and lowering plant productivity (Ernakovich et al., 2014). Vegetation vulnerability to increased aridity will also be manifest in wildfire as an agent of disturbance in alpine areas where it has been rare or not existed before.

An example complication is for change in water resources in the northern Rocky Mountains, United States. In this region, snow is often relatively dry when it falls and easily redistributed by wind, from windward, convex slopes to leeward, concave slopes. It accumulates in "snow beds" that persist into summer long after other snow has melted (and in some cases are year-round features). As elsewhere, snow bed vegetation, growing near these features, is adapted to this water source and could be classified as wetland vegetation in some instances. Snow beds can change with climate change. Warmer summer temperatures or less winter precipitation will reduce snow bed area. Smaller snow beds hold less water. Changes in local hydrology or changes in the predominant wind direction could also reduce snow beds. In this case, Local vegetation type will become dominated by species adapted to drier conditions. Although aspects of this example do not occur everywhere (and snow beds are common even where snowfall is not so dry), warmer temperatures not accompanied by increased precipitation would lead to similar expectations more generally, and any shift of climate could change the niches expressed on an alpine landscape.

Soil differences can also complicate alpine vegetation response to climate change. Soils may differentiate plant communities, and their plant-soil interactions may vary (Buri et al., 2017). However, organisms involved in these relations range from bacteria to bears, which vary locally and regionally. A number of experiments on Niwot Ridge have shown an association between fine sediments and types of alpine communities (e.g., Forbis et al., 2004; Sherrod et al., 2005). Perhaps most notable has been the rapidity of overall change in the ecosystem. At fine scales, the rates of biome response to climate change may be affected by the soils in the context of microtopography (Suding et al., 2015).

In aquatic systems, the abiotic complications of climate change identified by Redmond (2018) included the variation in thermal variability with water body size and depth and glacial influences, in addition to the variation in the drivers of increased temperature and increased dryness. In the often fish-less waters, effects on plankton can be significant. Phytoplankton are expected to increase in productivity, with consequences for water clarity. On a size gradient, smaller water bodies (ponds) are expected to respond differently to climate change than larger ones (lakes). Although lakes might appear better buffered by their size, warming and drying would move them in the direction of ponds, which have distinctly different zooplankton biota. Alpine lake zooplankton have

less tolerance for warmer conditions to which pond zooplankton are adapted. With drying, shallower lakes could have greater penetration of UV radiation, to which some zooplankton are sensitive. Melting glaciers also complicate the responses to climate change. Increase meltwater inflow can reduce some of the impact of warming and drying, but could also be a source of organic pollutants stored in past years. At some point the loss of this inflow altogether could trigger major shifts in the ecosystems.

Biotic complications

Biological interactions in the alpine are well-recognized. Although competition remains important (Theodose and Bowman, 1997), the role of neighboring plants in modifying microclimate is greater relative to lower-elevation biomes (e.g., Choler et al., 2001). The implications for long-term dynamics are uncertain. Soil microorganisms further complicate edaphic conditions and affect plant communities relative to climate (e.g., Bueno de Mesquita et al., 2016).

Species diversity is relatively high over small areas for the level of productivity, but intraspecific variation is also common. This variation means that responses to climate change can vary among and within species and across habitats. Temporally, changing phenology in relation to climate change exhibits complicating factors (Walker et al., 1995; Inouye, 2008). Some phenological responses are habitat-specific or species-specific—or even vary within species. The degree of interannual variability could significantly complicate response to climate change. Such changes have been observed when plots are regularly monitored.

Spatial complications

The relative isolation of the distribution of the alpine biome in the mountains will affect responses to climate change. Because of isolation, the turnover rate in the absence of climate change should be low, so that observations may be useful. In the far north, the alpine biome merges with the arctic biome and the degree of isolation is less.

Suding et al. (2015) found that assessment of community stability was scale-dependent. Energy and water resources vary at fine scales in alpine environments (e.g., Saunders and Bailey, 1994), as does disturbance (e.g., Johnson and Billings, 1962). Malanson and Fagre (2013) found that GLORIA single summit responses were small when considered within a continental scale context.

Over larger scales heterogeneity matters modestly. For two intensively sampled regions, the Indian Peaks Area, CO (IPA) and Glacier National Park, MT (GNP), the range of difference in alpine plant community composition between the two regions was matched by the range within each (Malanson et al., 2011). The source of this variation is in the details of topography at multiple scales. While substantial differences in temperature regimes exist within the alpine zone in any mountain range because of elevation, aspect often creates as great a difference, given the potential differences in insolation at high altitude. Local heterogeneity is found in many places given differences in albedo and vertical structure within alpine communities, and differences in soil moisture could be equally important in maintaining cooler temperatures in daytime and perhaps warmer temperatures at night. At the largest scales, the differences in species composition may not be strongly related to current climates (Malanson et al., 2015a).

The biotic climate-related complications highlighted by Redmond (2018) for aquatic systems depend on the initial taxa in a given lake or pond (which differ), complicated primary productivity, and varying trophic structures with differential growth rates.

Temporal complications

Temporally, the alpine biome may exhibit considerable inertia in relation to climate change because many species are long-lived perennials and with broad ecological tolerances. Yet the extreme alpine environment is such that ‘noise’ in the ecological ‘signal’ is created by interannual variability from establishment quickly followed by mortality. Alpine communities may thus have a slow response in some species, masked by ‘noise’ from others. It is this individualistic set of responses that poses one of the greatest challenges for scientists attempting to assess alpine tundra as a sentinel for climate change and its impacts. Efforts to identify communities for monitoring (mountain summits or wet-turf sites) may need to be supplemented by a focus on individual species.

The extent of the alpine biome may have been much greater 20,000 years ago than it is now (Harris, 2007). Following current theory and work from island biogeography and habitat fragmentation, as area decreases and isolation increases, alpine regions should be able to support fewer species, but with a time lag known as “extinction debt”, i.e., in the smaller and more isolated areas, some species are doomed to eventual extinction as the lower equilibrium number of species is approached.

The consequences of disequilibrium for the alpine biome are that species may not occupy the area where they would have maximum fitness given their adaptations and their relations with other species. At an extreme, species could appear to be randomly distributed within the constraints of their adaptations. In that case, the alpine biome may have been in disequilibrium with climate for millennia, and current observations of the presence and abundance of species in relation to climate will not be useful for predicting responses to climate change.

Lastly, climate change is not linear and gradual. Natural variability, including decadal scale cycles, can create pulses of change in temperature, precipitation, and prevailing winds. Alpine biome change can thus be episodic.

Nitrogen Flux

Nitrogen deposition in alpine ecosystems occurs in areas that are downwind of urban and agricultural sources (Bowman and Steltzer, 1998). In North America, these are primarily in the Sierra Nevada and the Front Range in Colorado, where upslope winds countervailing the regional dominant airflow affect alpine regions. Much of the nitrogen deposition in the alpine biome occurs in

winter snowpack, and runoff carries it directly into alpine lakes and streams; a minimal ability for alpine plants to absorb nitrogen also contributes to this flux. Thus, aquatic systems are most strongly affected.

In the terrestrial ecosystem, alpine grasses are likely to be favored at the expense of forbs, and a shift in the composition and diversity of plant communities is possible. Dominance of grasses would likely lead to a decrease in diversity.

In the aquatic ecosystems this flux has led to changes in the algae and possibly among microorganisms. Eventual acidification is possible. [Redmond \(2018\)](#) noted N-deposition as a primary stressor that could interact with higher temperatures and shallower ponds to affect grazer populations as well as primary productivity. Again, a notable impact would be a decrease in diversity.

Other chemicals originating from human activities also reach the alpine biome. These include lead and mercury among heavy metals and organochlorides such as PCBs ([Bowman et al., 2002](#)). Some of these become concentrated at higher trophic levels, e.g., in fish, and thus become a hazard to consumers such as eagles, bears, and humans. This concentration can be increased by warmer temperatures.

Invasive Species

Invasive species are a minor problem in the terrestrial ecosystems of the alpine biome. In the northwestern United States, [Parks et al. \(2005\)](#) categorized 92 species in three alpine regions by their ability to invade with or without disturbance. Of these potential 276 targets, only seven could invade without disturbance. Worldwide, [Alexander et al. \(2016\)](#) reported fewer than 200 nonnatives in alpine biomes. However, they noted that the problem is likely to increase. Occurrences, and impacts to the aesthetic resource, are spatially concentrated along trails and roads. Even then, most of that change in resource will be hard to recognize. Work on invasive and native congener dandelions suggests that the former may be able to spread their combined coverage as well as replace the latter to some degree ([Brock et al., 2005](#)).

In alpine lakes, many of which had no fish in the past because of their isolation, stocking of trout—many nonnative—has changed these ecosystems. In some cases, the introductions of nonnative species eliminated species of native trout. Even the introduction of native trout to previously fishless lakes has consequences for other organisms, such as amphibians ([Knapp et al., 2001](#)). [Redmond \(2018\)](#) noted that such introductions changed the size structure of aquatic organisms, which would affect the overall aquatic ecosystem response to climate change.

Habitat Destruction and Deterioration

Few roads and fewer land use transformations occur in the alpine biome of North America. However, [Bowman et al. \(2002\)](#) identified recreation as the most serious direct threat to alpine environments. Little of this intrusion is directly motorized, with few roads in the alpine biome, but these roads provide easy access to the many trails. Where roads and trails meet, crowds can form and localized trampling is a concern. In some national parks, hiker density in midsummer can be similar to a busy city sidewalk. [Willard and Marr \(1970\)](#) noted the susceptibility of wetter ecosystems to trampling in Rocky Mountain National Park, and in a follow-on report, [Willard et al. \(2007\)](#) reported some recovery but concluded that even without further impact complete recovery might take a century. Even far from roads, popular trails and peaks can be crowded in the summer. Alpinists affect the feeding activity of grizzly bears (other than as meals) ([White Jr et al., 1999](#)). Some of the more prominent recreational effects are the construction of ski facilities ([Richard and Côté, 2016](#)), but the active skiers might also impact animal behavior. The larger effect associated with trails is the introduction of exotic species.

People have also grazed livestock in limited areas of the alpine biome in North America. While controlled grazing, especially of sheep, has had impacts in subalpine meadows, grazing above treeline was rare simply because it was less accessible, less productive, and unnecessary. Overgrazing by native herbivores with denser populations due to the loss of predators can, however, have ecological effects, but these are uncertain. Herbivore trampling is a localized and perhaps temporary effect, and such grazing is decreasing as more of the alpine is devoted to recreation and wilderness.

Consequences of Change

Biodiversity

A primary concern for the impacts of change in the alpine biome of North America is the loss of species. Observations to date indicate that such losses are not yet occurring, but any period of increased rates of change and the possibility of extinction debts results in the potential for loss. Of particular concern is the high number of endemic species in the biome ([Malanson et al., 2015b](#)), for which local extinctions would be global extinctions. Because of the heterogeneity of habitat at even local scales, however, the losses of species may be restricted to those that are specialized in the extremes of this biome: the wettest, driest, warmest, or coldest places—if, in their locale, the climate becomes drier, wetter, colder, or warmer, respectively. Given the larger trends, species adapted to relatively warm conditions should have the opportunity to move upward unless limited by space while being replaced by nonalpine species. Those adapted to the coldest habitats may have no viable local places to move. Drier- and wetter- adapted species could be threatened, depending on the direction of change in precipitation. All potential changes are highly uncertain and will depend on local conditions.

Losses of biodiversity may also be seen at higher trophic levels. Although the animals that inhabit the alpine at least some of the time range from grizzly bears to butterflies, those that are specialized are most threatened. Perhaps the most iconic of these is the pika (*Ochotona princeps*). While the loss of alpine vegetation will reduce the habitat for pika, climate change can have direct impacts as well. Although pika can die from heat stress, they also may be stressed by low temperatures where protective snowpack has been reduced; both stresses can reduce populations and lead to local extinctions (Beever et al., 2010; Smith and Millar, 2018). Equally visible but quieter, populations of alpine butterflies may also be reduced by warmer temperatures and more extremes events (Buckley and Kingsolver, 2012; Roland and Matter, 2013). The effects of such losses on other species in food webs are unknown, but interactions will cascade into other biomes; e.g., alpine summer-resident army cutworm moths form a substantial portion of the calories consumed by grizzly bears (White et al., 1998).

Water

Mountains are important sources of water for human uses. Whereas climate change in alpine regions is beginning to have significant impacts on water resources, such as the loss of glaciers, changes in the alpine biome per se that will affect hydrology are likely to be minimal. The replacement of alpine vegetation by trees could increase snow local snow retention, but this change is likely to be small and slow.

Carbon Flux

The carbon balance of the alpine biome is becoming negative. Increased carbon sequestration as a consequence of rising treelines, and thus the replacement of lower carbon storing alpine landscapes with trees, would not be a major change. A calculation can be made, based on numbers from the alpine area in the coterminous United States of 1.1% (Lugo et al., 1999) and assuming 2% for Canada and Alaska, differences in carbon storage from Grafius and Malanson (2015), and the current emissions levels from the International Energy Agency (IEA, 2019):

• North American alpine area (1.6%)	$0.30 \times 10^6 \text{ km}^2$
• 10% change over 100 year, assumed	$0.03 \times 10^6 \text{ km}^2$
• Subalpine-alpine difference	2300 T km^{-2}
• Total 100-year difference	$69 \times 10^6 \text{ T}$
• 2018 USA energy-related emissions of carbon	$4.8 \times 10^9 \text{ T}$

The 100 year increase in carbon storage resulting from a replacement of 10% of alpine biome by alpine ecotone trees would be approximately 7% of the current *annual* energy-related emissions of carbon by the United States. Moreover, warming climate would lead to greater respiration, which could be increased in areas with nitrogen deposition; areas with less snow cover may be the most dynamic, with a net output of $2.3 \text{ T km}^{-2} \text{ year}^{-2}$ (Knowles et al., 2019). Assuming these areas cover 10% of the alpine biome, their output would be $3.5 \times 10^6 \text{ T year}^{-1}$, or five times the potential carbon sequestration by rising treelines over a century.

Aesthetics and Recreation

The alpine biome is an important destination for hikers. The athletic and aesthetic experiences remain for those able and willing to venture away from popular locations. For many, however, the experience is deteriorating. The biome per se is largely unchanged, but the consequences of more people in the most crowded locations will inevitably lead more people to hike and camp slightly farther into the biome; these in turn will add to habitat deterioration, invasive species, and changes in the populations and/or behavior of native species.

Summary

Unforeseen changes are always possible. Ferrarini et al. (2017) have shown novel climates can create novel complications in alpine biome. The interactions of the major forces of change remain speculative but worrisome. The alpine biome in North America in the future will remain a valuable resource, especially in the most remote areas, but no areas will remain unaffected by change.

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Current Changes in Alpine Ecosystems of Asia

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Abstract

Impacts of climatic and land use changes on alpine life zones of Asia are presented, reviewing the most current knowledge with a focus on cryospheric responses, biotic responses, and the alteration of land use patterns. Rates of climate warming in Asian mountain systems substantially exceed the global mean, leading to a significantly declining snow-covered area (SCA), to widespread decreases in area, length, and volume of glaciers, and to widespread permafrost degradation. Complex adaptations of mountain biota to novel combinations of bioclimatic and other site conditions are ongoing, including upslope expansion of distribution ranges, treeline dynamics, migration of invasive species, phenological shifts, and changes in primary production. These biotic responses will inevitably lead to modified structure, composition, and functioning of alpine ecosystems. Recently, globalization effects, socio-economic integration processes, and in some places new laws have enhanced modernization trends in montane and alpine land use that have resulted in outmigration and reduced land use intensity at higher elevations in many Asian mountain ranges, providing the chance of ecosystem recovery.

Introduction

The alpine life zone, covering 3% of the world's land area, is commonly defined as being located above the natural high elevation treeline or extending upslope from a boundary corresponding to the global thermal limit for treelines. Alpine areas, however, are of global significance owing to their controlling hydrological function, in particular regarding the flow of meltwater from glaciers and snowfields to the lowlands. Alpine ecosystems represent some of the few remaining wilderness areas of the globe, and encompass some of the most intriguing habitats both in terms of the human fascination with high mountain landscapes and of alpine biota's special adaptations to the harsh physical environment. At the same time, alpine ecosystems are fragile and less resilient since long periods of time may be needed for recovery from damage or excessive stress.

Alpine ecosystems of Asia extend over vast areas; they occur from the higher latitudes to the tropics. The mountain ranges and plateaus of mainland Asia constitute the largest mass of highlands in the world, including all 66 peaks exceeding 7000 m a.s.l. The core of the Asian mountain system is represented by the vast complex of mountain ranges and plateaus around Tibet (including Pamir, Kunlun and Tien Shan) from where mountains and highlands with alpine life zones extend to S and SE Asia (Hindu Kush, Karakoram, Himalaya, some peaks and high valleys on Borneo, Sumatra, Lombok and New Guinea), W Asia (the Urals, mountains around the Iran Plateau, Trans-Caucasian and Pontic Mountains, some peaks on the Arabian Peninsula), and N and E Asia (Altai, Sayan, Changai, E Siberian and Kamchatkan mountains with the transition from alpine to arctic habitats, some ranges and high valleys in E and S China, Taiwan, Korea, and Japan) (Fig. 1).

Alpine life zones are highly susceptible to global environmental change. As elsewhere on the globe, climatic and land use changes are the major drivers increasingly threatening the integrity of alpine ecosystems in Asia, affecting their capacity to provide goods and services (Fig. 2). Alpine regions everywhere in Asia are showing increasing evidence of climate change impacts on physical and biological systems. High elevation environments are in general considered to be among the most sensitive terrestrial systems to respond to climatic variations (Schickhoff, 2011). Observed changes of glaciers, snow cover, permafrost, hydrological conditions, and of the complex altitudinal zonation of vegetation and fauna indicate distinct vulnerabilities. In view of the goods and services mountains provide to about half of humanity, changes in alpine life zones are giving rise to great concern. In the case of water supply, the key function of mountains for humanity, global warming will cause a decline. This reduction of water resources will affect more than half of Asia's population. More than a billion people in Asia live in watersheds of rivers that have their sources in mountains.

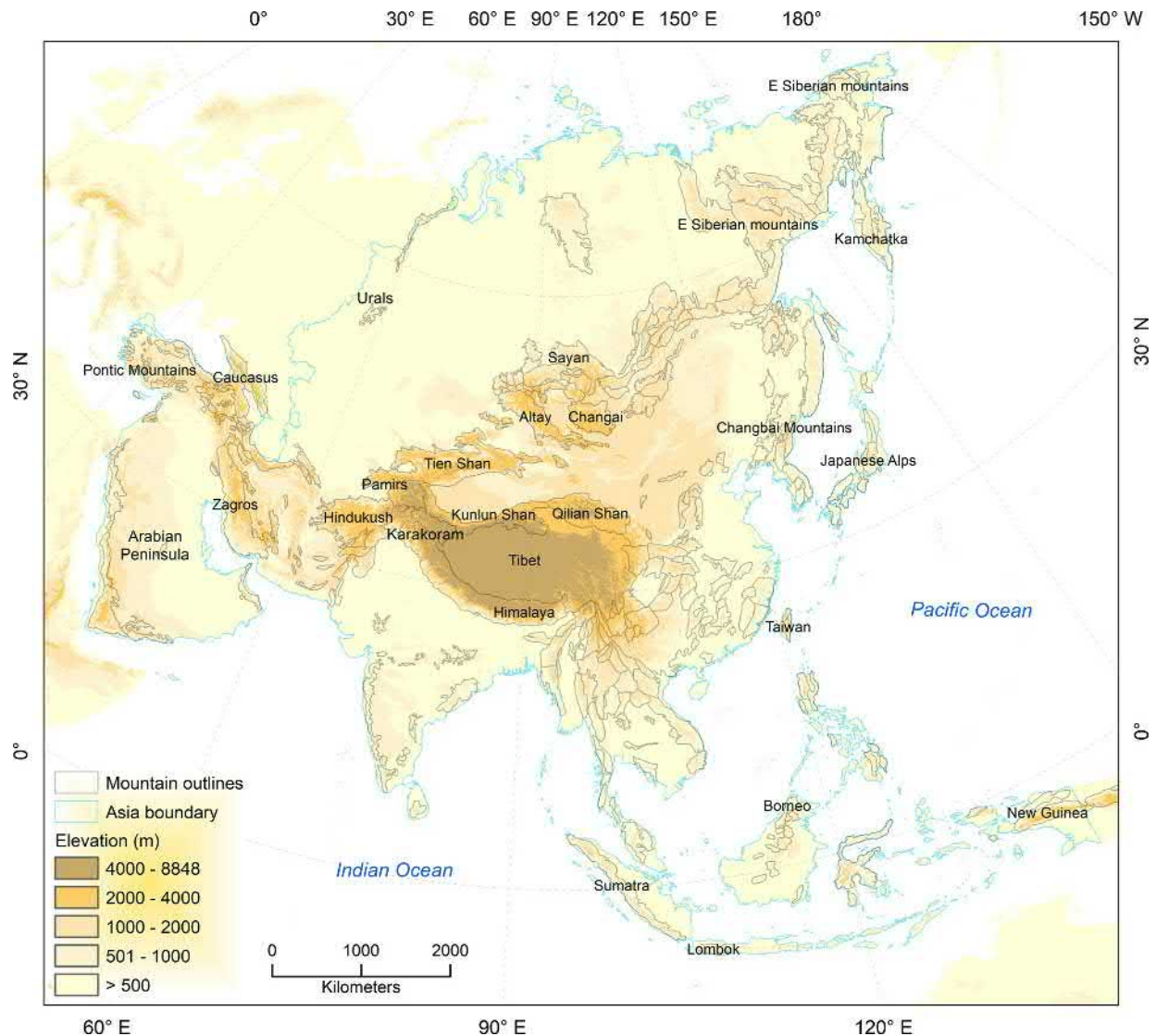


Fig. 1 Spatial distribution of mountains in Asia; mountain ranges with alpine life zones are highlighted. Mountain outlines adapted from Körner C, Jetz W, Paulsen J, Payne D, Rudmann-Maurer K, Spehn EM (2017) A global inventory of mountains for bio-geographical applications. *Alpine Botany* 127: 1–15; Background image from https://dds.cr.usgs.gov/srtm/version2_1/SRTM30/.

With regard to physical systems, current global warming has already left distinct traces in the cryosphere and hydrosphere. It is also a powerful stressor on alpine biota, inducing shifts in phenology, species distributions, and community structure as well as other ecosystem changes. Alpine environments in Asian countries are also significantly affected by changes in land use patterns caused by widespread socio-economic change. This chapter reviews the most current knowledge with respect to impacts of climatic and land use changes on alpine life zones of Asia.

Climate Change-Induced Effects in Alpine Life Zones of Asia

Climatic Changes

Global warming reached approximately 1 °C above pre-industrial values in 2017. The high latitudes of the Northern Hemisphere, in particular the northern Asian sector, show the largest increase in mean temperatures (Hoegh-Guldberg et al., 2018). Here, polar amplification leads to warming rates of more than 2 °C per 50 years. Warming trends and increasing temperature extremes have been observed across most of Asia over the past century (Hijioka et al., 2014). Warming trends have been particularly strong in the cold season (November–March). Since the middle of the 20th century, numbers of cold days and nights have generally decreased, whereas numbers of warm days and nights as well as heat wave frequencies have increased (Hijioka et al., 2014). Across Asia, the strongest extreme warming events are projected to occur in western and Central Asia (Hoegh-Guldberg et al., 2018).



Fig. 2 Ladakhi pastoralists let their goats and sheep graze at Lake Tso Moriri (4522 m); the integrity of alpine ecosystems in Asia is threatened by climatic changes and land use changes. Photo © Udo Schickhoff, September 23, 2018.

Temperature trends in most regions of Asian mountain systems substantially exceed the global mean trend since 1880, albeit with distinct patterns of spatial and seasonal differentiations, in particular in terms of vertical gradients. A general phenomenon, prevalent over most of Asian mountain regions, is the amplification of warming rates with increasing elevation, attributed mainly to changes in albedo and downward thermal radiation (Hasson et al., 2016). The amplification of warming with elevation will increase with higher greenhouse gas emission scenarios, subjecting alpine life zones of Asia to more extreme changes in habitat conditions than those of lower elevations (Schickhoff et al., 2016a).

Impacts on Physical Systems

Climate warming causes cascading effects on alpine physical systems, with some of the affected physical processes providing important feedbacks to the climate system. The above-average temperature trends in Asian mountains have inevitable consequences for cryospheric processes, such as substantial changes in snow cover, glaciers, permafrost, and related hydrological processes.

Snow cover is the largest and most important cryosphere component, affecting the global energy budget, water cycle and balance, river discharge regimes, soil moisture, vegetation, and water supply to diverse human activities, including irrigation-agriculture, hydroelectricity generation, industries, tourism, etc. The snow-covered area (SCA) in Asian mountains has significantly declined since the 1960s. The Hindu Kush Himalaya (HKH) and Tibetan regions show declines in snow accumulation rates (Bolch et al., 2019). However, westerly-dominated basins (Indus basin, NW Himalaya) show increases in winter SCA. In the Siberian region including Kamchatka, as well as in the Pamir, Alay, and Altai, the SCA has declined significantly over recent decades, while the Tien Shan and Kunlun show mixed trends (cf. Bormann et al., 2018). The trends of SCA are related to trends in snow cover duration (SCD), which has decreased in the HKH region, Tien Shan, Kunlun, Altai, and Kamchatka by up to 30 days per decade between 1982 and 2013 (Chen et al., 2016).

The mass balance of glaciers in Asia is negative in recent decades (Fig. 3), with some exceptions in the Karakoram, Pamir, western Kunlun, and Altun Shan. The average glacier area loss in the entire extended HKH region was estimated at 0.35% per year between 1970 and 2000; the rate increased to 0.42% per year between 2000 and 2010 (Bolch et al., 2019). Simultaneously, the glacier mass balance rate has increased from -0.26 (m w.e.⁻¹) (1970–2000) to -0.37 (m w.e.⁻¹) in 2000–10, with some regional variations and anomalies. There is a strong E-W gradient of glacier retreat, with average glacier area change rates of -0.81% a⁻¹ in the eastern Himalaya decreasing to -0.37 and -0.34% per year in the central and western Himalaya between 2000 and 2010. In contrast, glacier area changes in the Karakoram show a divergent pattern known as the “Karakoram anomaly.” Non-surge-type glaciers were relatively stable and surge-type glaciers showed large increases as well as decreases over the past decade. Accordingly, most Karakoram glaciers had a positive mass balance in recent decades.

Glacier terminus recession rates have been assessed to be highest in the eastern Himalaya, while a considerably lower glacier recession is observed in the central and western Himalaya, and partially a surging/advancement in the Karakoram (Azam et al., 2018). Recently, recession rates of large glaciers in the central and western Himalaya (Gangotri (Fig. 4); Milam; Bara Shigri) slowed, while glaciers of the NW Himalaya showed very low change rates or were relatively stable (Schmidt and Nüsser, 2012; Mal et al., 2019). Glacier recession has fragmented larger glaciers into smaller ones, resulting in a distinct increase in number and area of



Fig. 3 The margins of Himalayan glaciers are retreating at a fast rate, resulting in the recent formation of meltwater lakes as in the former snout area of Gangapurna glacier (3550 m), Nepal, which create a potential danger from glacial lake outburst floods. Photo © Udo Schickhoff, September 23, 2013.



Fig. 4 Reductions in the area and volume of large glaciers in the Himalaya like the Gangotri glacier (4050 m) will adversely affect the seasonal water supply of a large human population in the lowlands. Photo © Udo Schickhoff, May 6, 2007.

glacial lakes (fed by glacier meltwater; cf. Fig. 3) in recent decades (Krause et al., 2019). The average glacier area loss rate on the Tibetan plateau was slightly lower than in the Himalaya in recent decades, whereas the area shrinkage of glaciers in the Tien Shan, the Caucasus, the Urals, the Altai, and in Siberian mountains including Kamchatka has been considerably higher. Many glaciers in the Chinese part of the Tien Shan and in the Pamir Alay have disappeared.

Permafrost is another important component of the cryosphere, significantly influencing energy balance, terrain stability-related geophysical hazards, ground and subsurface hydrology, river sedimentation, infrastructure, etc. Permafrost degradation contributes to mountain slope destabilization and increased mass-movements and related hazards. Local studies on the Himalayan south slope

suggest widespread permafrost degradation and the rise of the lower limits of permafrost by several hundreds of meters since the 1970s (Fukui et al., 2007). Significant thermal degradation of permafrost has occurred on the Tibetan plateau, in Siberian and Mongolian high mountains and the Tien Shan. Climate change and anthropogenic activities, especially hydropower projects and irrigation, have significantly affected the hydrology in Asian mountains (river discharge, hydrological budgets) during the past century. River runoff in Central and South Asian river basins has decreased up to 30% in recent decades (Scott et al., 2019).

Biotic Responses

Alpine life zones of Asia are being subjected to some of the highest levels of warming globally. Respective biotic responses are increasingly observed, although our understanding of alpine Asian ecosystems remains profoundly deficient (Schickhoff et al., 2016a). Since many plants adjust sequences of phenological events to the rise in temperatures and to the advance in the timing of snowmelt, phenological shifts are considered to be sensitive indications of the response to climate warming. In general, species responses to climate change are driven by their capacity to persist in situ by altering fitness-related traits through phenotypic plasticity or genetic adaptation to novel stresses. However, plants at higher elevations have a low capacity to persist in situ since traits such as slow growth or dwarfism are genotypically determined, and phenotypic plasticity is constrained under harsh climatic conditions. A greater potential for high-elevation species to survive rapid anthropogenic climate change lies in distributional shifts to track preferred bioclimatic conditions. Predicted changes include the gradual transformation of species composition and community structure of resident communities, in particular in the alpine and nival zones. The magnitude and rate of climate change, as well as induced alterations of abiotic and biotic site conditions, will out-strip the adaptive capacity of many species, causing increased extinction risks and loss of biodiversity.

A recent assessment based on satellite-derived NDVI datasets indicates that the length of the growing season in the HKH has increased by 4.25 days per decade over the last five decades, in line with an overall greening trend in NDVI magnitude and an earlier green-up in most parts of the HKH region (Krishnan et al., 2019). Respective observations of shifts in species-specific phenological patterns indicate large-scale changes. Several *Rhododendron* and *Roscoea* species are currently flowering 3–4 weeks earlier than in previous decades (Xu et al., 2009). Telwala et al. (2013) provided evidence of warmth-driven elevational range shifts in 87% of 124 studied endemic plant species in alpine Sikkim over the last 150 years. Considering shifts of species' upper elevation limits of up to c. 1000 m, present-day plant assemblages and community structures are markedly different from those of the 19th century. In recent years, long-term research plots have been established within the Himalayan GLORIA (Global Observation Research Initiative in Alpine Environments) network to monitor details of species distribution patterns. The first resampling of plots in the eastern Himalaya (Hengduan Mountains) after 7 years showed that alpine plants on high-elevation summits increased in number of species, in frequency and in diversity, and that even endemic species showed population increases (Salick et al., 2019). Warming-induced upward migration of plants was recently also confirmed in the western Himalaya by Dolezal et al. (2016), who resurveyed outpost populations of subnival plants after ten years and found an extension of plant species elevational ranges of 120–180 m.

Treeline dynamics and elevational shifts in the HKH region mostly result from combined effects of land use change and climate change. Substantial treeline advances or shrub encroachments into alpine meadows in recent decades are mainly due to land use change. Near-natural treelines on north-facing slopes are krummholz treelines which show a rather low responsiveness to climate warming. The strong competitiveness of krummholz species such as *Rhododendron campanulatum* largely prevents the upslope migration of *Betula* and *Abies* spp. and other tree species (Schickhoff et al., 2015, 2016b). Nevertheless, increasing stand density as well as intense tree recruitment within treeline ecotones point to ongoing treeline dynamics (Schwab et al., 2016, 2017; Bürzle et al., 2018), resulting most likely in treeline advances in the medium- and long-term (Fig. 5). Moreover, modeling studies support the concept of climate change-induced upslope migration of treeline species (Bobrowski et al., 2017; Chhetri et al., 2018). Recent dendroecological studies at HKH treelines indicate a strong sensitivity of tree growth to pre-monsoon temperature and humidity conditions; moisture supply in the dry pre-monsoon season may become an effective control of future treeline dynamics (Schwab et al., 2018; Sigdel et al., 2018).

Recently deglaciated terrain represents another highly dynamic alpine habitat (Fig. 6). The surface area of deglaciated glacier forelands has been increasing considerably due to the ongoing recession of the vast majority of HKH glacial margins. Vegetation successions on glacier forelands have not been addressed in great detail so far. Some preliminary studies have been done on the colonization of glacier forelands by pioneer species (e.g., Mieke, 2015). Similar trends of climate change-induced biotic responses, summarized above for the HKH alpine regions, prevail in other Asian mountain systems and their alpine life zones. Recent positive trends in vegetation growth and productivity, shifts of phenological dates and of the upper limit of species distributions are widespread across Asian mountain ranges.

Effects of Land Use Changes in Alpine Life Zones of Asia

The mountains and highlands of Asia have been subjected to anthropogenic landscape transformation for millennia. Over many generations, mountain dwellers have developed sophisticated, complex resource utilization strategies for their sustenance, including a wide variety of farming and pastoral practices. Initially, mountain nomadism evolved as a strategy to sustain mountain-related livelihoods, often complementing or replacing subsistence hunting and gathering. After the establishment of permanent settlements and village lands, the combination of crop-farming and livestock-keeping evolved as the dominant basis of high mountain



Fig. 5 Himalayan fir (*Abies spectabilis*) sapling found at 4200 m, 100–150 m above the current treeline in Rolwaling Himal, Nepal, reflecting ongoing treeline dynamics. Photo © Udo Schickhoff, August 20, 2013.



Fig. 6 Recently deglaciated terrain provide dynamic habitats for primary succession, Annapurna Range, Manang, Nepal. Photo © Udo Schickhoff, September 22, 2013.

agriculture. Pastoral practices in alpine life zones have been increasingly integrated into more complex land use systems including *Alpwirtschaft* (combined or mixed mountain agriculture) and transhumance. In Asian mountains, however, nomadic pastoralism is still found in Siberia and Mongolia, in the Altai, Tien Shan, Pamir, parts of Tibet, the HKH region and in the Zagros. Developing sophisticated practices of combined mountain agriculture involved the clearance of mountain forests which have been increasingly converted to croplands. However, as long as mountain regions remained sparsely settled, human impacts on alpine life zones were negligible for many generations, and remote mountain ranges remained relatively undisturbed. In previous centuries, mountains provided a degree of isolation from the outside world for their permanent inhabitants and were often characterized by distinct inaccessibility resulting in more or less independent subsistence economies with limited trade and exchange relations with the plains or other mountain regions (Schickhoff, 2011).

In the past 200 years, the human populations of many Asian mountain ranges increased markedly, as did the intensification of land use. These changes accompanied the arrival of European colonialism in major mountain ranges. For instance, rapid landscape transformations in the Himalaya, i.e., large-scale deforestation and substantial changes in the distribution of forests and agricultural lands, occurred only after the British annexation of these regions in the 19th century. During the 20th century, the less-developed regions of the Asian highlands experienced high population growth, poverty, lack of economic opportunities, increased land use pressure, and increased integration into the economy of the lowlands. The primary sector had still been growing in importance, and local mountain farmers were often forced to intensify land use in response to internal (population growth) and external (lowland markets) drivers. Most of alpine Asia was subjected to increased pressure on grazing lands that adversely affected highland integrity and biodiversity (Fig. 7). Even the most distant and remote mountain regions were influenced by effects of globalization. Mountains in general have been affected by far-reaching socio-economic transformation processes, notably in the second half of the 20th century. In developed mountain regions (Japan, Taiwan, parts of China and Russia), these transformations have eventually led to the gradual abandonment of traditional land use. These changes took place concurrently with new types of exploitation of high mountain environments, such as tourism, mining, power generation or industrial-scale farming in favorable areas. However, the replacement of farming and herding by tourism is still confined to a few mountain ranges.

Recently, globalization effects and socio-economic integration into the larger world have brought modernization trends in mountain agriculture. Mountain farmers seek to improve their livelihood by combining alternative farming systems (e.g., agroforestry, cash crops), non-agrarian income (e.g., tourism), and migrant labor remittances, while taking full advantage of well-established access to lowland markets, provided by the newly developed road systems. Increasingly, mountain people are moving from remote locations to urban centers. This trend began in the late 20th century. Highland-lowland migration serves to alleviate population pressure on alpine ecosystems, and leads to a reduced land use intensity there. Reduced human pressure may allow ecosystem and biodiversity recovery of previously over-used alpine grazing lands. It also facilitates the introduction of new forms of land tenure, for instance the establishment of national parks and other protected areas whose number has considerably increased in recent decades.

In the vast HKH region, pastoral strategies are still critically important for sustaining livelihoods of a large human population (Kreutzmann, 2012). However, as elsewhere, alpine pastoralism is highly vulnerable to outside forces, such as social, economic and cultural changes. These changes have resulted in a significant decrease in highland livestock grazing. Labor out-migration is the most important driver of reduced alpine land use intensity. In Nepal, for instance, the migrant population is steadily increasing. Almost 500,000 workers left Nepal in 2014 to work in India and elsewhere, consequently, remittances (i.e., money sent home by Nepalese working abroad) now constitute more than 30% of the country's gross domestic product (Siddiqui et al., 2019). Animal husbandry in the HKH region has seen a general decline. Likewise, land abandonment and the decrease of traditional agricultural practices due to labor shortages are apparently more pronounced at higher elevations. Whereas the decline in grazing intensity in the Himalaya mainly results from modified strategies adopted by pastoralists, reduced high-elevation pasture utilization on the Tibetan Plateau as



Fig. 7 Livestock grazing is the predominant land use at higher elevations in Central Asia, large highland tracts have thus been subjected to overgrazing, Altai Mountains, western Mongolia. Photo © Udo Schickhoff, September 10, 2005.

well as in high mountain ranges of E and S China has been driven by Chinese government programs aimed at the transformation of the pastoral sector. These programs include human resettlement schemes and the forcing of nomadic peoples to live in permanent settlements, with the aim of modernization and the reduction of grazing pressure and ecological degradation. In recent decades, overgrazing was a major stressor on alpine ecosystems. Indeed, poor livestock management practices have resulted in the degradation of alpine grazinglands across the entire HKH region, in particular in drier parts and on the Tibetan Plateau (e.g., Baranova et al., 2016). The current overhaul of alpine pastoralism practices provides hope that pasturelands will no longer be grazed beyond their carrying capacity, and that formerly degraded rangelands will recover.

Since time immemorial, pastoralism has dominated alpine land use in the Pamir, Tien Shan, and Altai, playing a crucial role in Central Asian economies, societies, and cultures. In the former Soviet Central Asian Republics, pastoral traditions and strategies have undergone tremendous changes in the course of the 20th century, driven by strong external interventions. The first decades of the Soviet era were characterized by forced sedentarization and collectivization campaigns, resulting in intensification of pastoral land use and its integration into socialist agro-industrial production. The disintegration of the Soviet Union in 1991 and the subsequent political and economic upheavals forced regional inhabitants to develop different pastoral strategies, based on private ownership of livestock, subsistence farming, and little state interference in land use practices. Deindustrialization, the initial decline of national economies, and the disappearance of social safety net have led, among other things, to an increased dependency on grazingland resources. After three decades of post-Soviet transformation, an increased scope and diversity of pasture-related socio-ecological challenges can be observed. These include conflicts about access to pasture lands, utilization rivalries, insufficient management practices, and degradation processes (Borchardt et al., 2011; Dörre and Borchardt, 2012). These conflicts have arisen in spite of state efforts to decentralize governance and to establish community-based pasture management. The spatial pattern of pasture degradation has changed in recent decades. Grazing intensity on remote high elevation summer pastures has declined because farmers have abandoned the practice of seasonal livestock migration (Fig. 8). In contrast to this, winter pastures, located close to settlements, have been subjected to more intense grazing pressure with adverse effects on vegetation, plant functional traits, and soils such as lower species richness and diversity, lower biomass, decreased plant height and specific leaf area, lower organic matter content, and higher soil pH values (e.g., Hoppe et al., 2016).

The history of mobile pastoralists' land use strategies and livelihoods in alpine zones of Mongolian mountain ranges in the 20th century has many similarities to the former Soviet Central Asian Republics. The revival of pastoral nomadism in the early 1990s resulted in rapidly growing livestock populations, shifts in herd composition, and widespread degradation of rangelands, also at higher elevations. The ongoing establishment of community-based rangeland management—over 2000 formally organized herder groups formed since 1999—is a promising institutional innovation which should support the implementation of strategies leading to sustainable pastoral land use. Land use patterns and livelihoods of pastoralists in Russian mountain ranges (Siberia, the Urals) have been affected by the implementation of post-socialist land use policy in a similarly fundamental way, subjecting herders to socio-ecological challenges such as unequal allocation of grazingland and localized high grazing pressure.



Fig. 8 Grazing intensity on remote summer pastures in the Tien Shan has been decreasing recently due to declining seasonal livestock migration, Suusamyr valley, Kyrgyzstan. Photo © Udo Schickhoff, September 26, 2004.

In the Caucasus, post-socialist land reforms have resulted in outmigration, land abandonment, and increasing use of the land for recreational activities. By contrast, alpine ecosystems of Iran are increasingly threatened by increased grazing impact, even in protected areas. Overgrazing has also caused severe pasture degradation in the Pontic Mountains. Land use impacts on alpine life zones in New Guinea are considered to be relatively low, with the exception of some mining impacts on Mt. Jaya and recently developing ecotourism on Mt. Wilhelm. Increasingly adverse tourism impacts on the alpine environment are also to be observed on Mt. Kinabalu, Borneo.

Conclusions

This review illustrates the fundamental changes happening in the alpine ecosystems of Asia. Across most of Asia, snow cover is declining, glaciers are thinning, losing mass, and their margins are retreating. Permafrost is also degrading. Increasing cryospheric changes in coming decades will add to natural hazard risks, and affect seasonal water supply in Asian river systems, with potentially severe implications for agriculture, hydropower generation, and local water resource availability. This may lead to conflicts over water resources and threaten livelihoods and food security of millions of lowland people, in particular in South and East Asia. Biotic responses to climate change such as phenological shifts, changing species distributions, migration of invasive species, and changes in primary production will modify species compositions of communities and thus the structure and functioning of alpine ecosystems, threatening the provision of ecosystem services. Pastoralism is still widespread in alpine Asia, sustaining the livelihoods of a large human population. The recent trend of reduced land use intensity in many mountain ranges provides the chance for ecosystem recovery. However, establishing the kind of land use practices in high mountain regions that would safeguard human livelihoods while simultaneously maintaining ecological sustainability remains a considerable task. Such changes need to be embedded in the major challenge of mitigating negative effects of drivers of environmental and socioeconomic change in alpine Asia.

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Current Changes in Alpine Ecosystems of New Guinea

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Abstract

The New Guinea alpine zone above 3750 m elevation is the highest, largest and wettest such region on any tropical island. The modern alpine consists of islands of habitat spanning 1400 km with considerable variations in biodiversity between the individual mountain areas. During the Pleistocene glacial periods, a zone above 3400 m was affected by glaciation and alpine habitat was greatly expanded. With post-glacial warming the alpine contracted and shrublands colonized the lower alpine. Current climate warming has nearly removed the nival zone but tree lines have not yet noticeably advanced to higher elevations. Successional changes to mature, waterlogged, soils have been observed. The alpine is threatened by increased warming and potential invasion by emergent shrubs but is unlikely to disappear, provided that wet conditions continue to prevail.

Opening out of the tree line in the past is associated with fire that may reflect visits by people for hunting. Evidence for fire spans several millennia in some areas but is quite recent on other mountains or absent on more remote peaks. Some alpine mammals and birds have disappeared or suffered local extinctions. Changing cultural use of high elevations suggests that previously disturbed habitats may be recovering in some areas.

With few exceptions, land management depends on local populations; widespread fires during El Niño induced dry phases point to continuing human impacts linked to drought events. The alpine has not been greatly affected by modern development although a large mine on Mt. Jaya influences subalpine usage over a large area. Tourism is very minor and unlikely to expand while political problems affect both PNG and Papua province and infrastructure remains rudimentary. However, locally managed tourism on Mt. Wilhelm provides a good model for future development.

The Alpine across New Guinea

Alpine habitats in the great equatorial island of New Guinea occur above 3600–4100 m and cover approximately 3300 km² at present.

The alpine zone in New Guinea has been defined as: “a treeless zone bordering a transitional subalpine zone and along its higher altitudinal border limited by the last vascular plants” (van Royen, 1979, p. 22). However plants occur up to the highest points available and it is unlikely that a true limit to growth is reached. The tree line varies, being highest on limestone at up to 4050 m and lower on the shaded and waterlogged parts of volcanic and metamorphic mountains at 3650 m a.s.l. In most areas however, the natural tree line has been greatly disturbed, and open grasslands are extensive to below 3000 m a.s.l. (Fig. 1).

Some of these lower grasslands are regarded as subalpine as they support shrubs and tree ferns that are absent from the alpine. The subalpine forest is low (10–15 m) and variable, transitioning from taller complex forest (upper montane forest) around 2800–3000 m a.s.l. On some mountains it is reduced to scattered trees or small forest patches surrounded by grassland.

The New Guinea alpine is an example of islands within an island-numerous young isolated and fluctuating habitats with island-like characteristics of habitat, local endemism and active species radiations (Green and Stein, 2015). As such it is a remarkable laboratory for studying evolution and differential adaptation to climate change in conditions of relatively low past human impact. This article considers causes of change to the alpine vegetation but in doing so it emphasizes the paucity of knowledge currently available.

Successional Change

Mapping alpine tundra-like habitats as fixed vegetational units ignores the fact that these pioneer communities are usually developing into more complex communities with deeper and more productive soils. At high latitudes like the Arctic or sub-Antarctic, such successional changes are very slow due to extremely low winter temperatures and very short growing seasons when there is sufficient radiation for plant growth. Hence Arctic plant community boundaries may be fairly stable on timescales of decades to centuries. By contrast, at high elevations in the tropics, despite low mean daily temperatures, there is abundant radiation throughout



Fig. 1 *Poa erecta* tussock grassland and infilled glacial basins on the summit plateau of Mt. Albert Edward. Photo: M. Prebble (2008).

the year and plants can grow in microhabitats that may be quite warm for a few hours each day. Here successional change can be relatively rapid.

The potential rate of change can be estimated by comparing alpine grassland-low shrubland on well-developed soils with very open dwarf shrublands on fresh moraines. The young moraines have been exposed by ice retreat within the last century so the succession to open dwarf shrubland has presumably occurred within several decades. Current snow and ice retreat (Prentice et al., 2011) exposes fresh rock and till surfaces to a rapid succession by fungi, algae, lichens, bryophytes and vascular plants.

Similarly ponds and tarns are being invaded by a range of mosses, sedges and herbs to form fens. Open mosslands on flooded pans develop towards herbfields and cushion bog. The complex development of lichen, moss and liverwort associations on rock and scree surfaces have not been studied in New Guinea. Mangel (1993) describes cliff and scree cryptogam communities that develop rapidly in the misty humid environment. Fig. 2. The moss and lichen mats trap humic soils which are then invaded by grasses and small shrubs.



Fig. 2 Lichens and mosses colonizing a granodiorite slab at 4400 m, Mt. Wilhelm. The shrub is *Vaccinium amblyandrum*. Photo: G. Hope (2010).



Fig. 3 Ice algae communities on the now defunct Meren Glacier, 4420 m, Mt. Jaya. Photo: G. Hope (1971).

The loss of ice cover has caused specialized snow algae communities to disappear. These communities have only been described from Mt. Jaya (Kol and Peterson, 1976) and they consist of colonies of six species of green algae and a blue-green alga, *Nostoc fuscescens* var. *carstenszis*. The colonies of algae increase the absorption of sunlight and lead to localized melting and the development of blue englacial ponds ranging up to 10 m or so in diameter. Fig. 3 shows the ablation (melting) zone of the Meren Glacier in 1970 with well-developed ponds. These have now disappeared with the melting of the glacier.

Invasive Species

Invasive plant species are not well known from the New Guinean alpine and currently play little part in the alpine vegetation. Native shrubs from the subalpine such as the tall daisy, *Papuacalia versteegii* (Asteraceae), have been seen growing vegetatively in newly exposed till at 4250 m altitude on Mt. Jaya. Other readily dispersed taxa will potentially follow.

Some exotic composite weed species such as thistles and other weeds such as *Anagallis arvensis* invaded the subalpine after the 1998 fires and were still persisting in burnt grasslands on Mt. Giluwe in 2001. Hence these disturbances provide a route for invaders. European bulbs such as *Lilium* and grasses such as *Poa annua* are following track lines upwards on Mt. Wilhelm. Other introduced grasses, composites and *Lantana* are potential threats. Mt. Albert Edward supports a large pig population causing disturbance of large areas due to their seeking roots and worms in grassland. These overturned patches result in local erosion and damage from grass fires. Potential problems could arise from other introduced mammals such as rabbits.

Possible Impacts of Climate Change

The rapidly disappearing ice cover on the New Guinea alpine summits provides the clearest evidence for climate warming in the Asian tropics. Warming has been occurring for at least 110 years and probably since the Little Ice Age ended around 1850 BCE. In Papua province (Indonesia) the four highest areas supported glaciers or ice caps and ice extent is estimated to have been about 42 km² in 1907, mostly on Mt. Jaya (Carstensch). The ice cap on Mt. Trikora disappeared around 1942 (Hope et al., 1973) and on Idenberg and Mt. Mandala (Juliana) in the 1990s. The Carstensch icecaps have reduced to two small areas totaling about 0.6 km² in 2012 and are expected to be gone in the next few years (Prentice and Glidden, 2010; Lavers and Abbott, 2016), Fig. 4. The highest rate of retreat occurred during pronounced El Niño events in 1997–9 and 2008. The less cloudy conditions and lowered snowfall led to accelerated ablation and strongly negative mass balances (Prentice and Hope, 2007).

The warming trend indicated by these reductions in ice cover correlates with a mean temperature increase of 1 °C since 1880. Phenological changes have been noted in species in the alpine zone including flowering at higher elevations. However there are no systematic observations and many changes, such as increasing shrub cover, may be responses to changing disturbance regimes and not climate change. At lower elevations Bourke (2011) has identified significant changes in the ranges of economic plants over the past 30 years that point to temperature increases of 1 °C and lower frequencies of limiting conditions, such as frost.

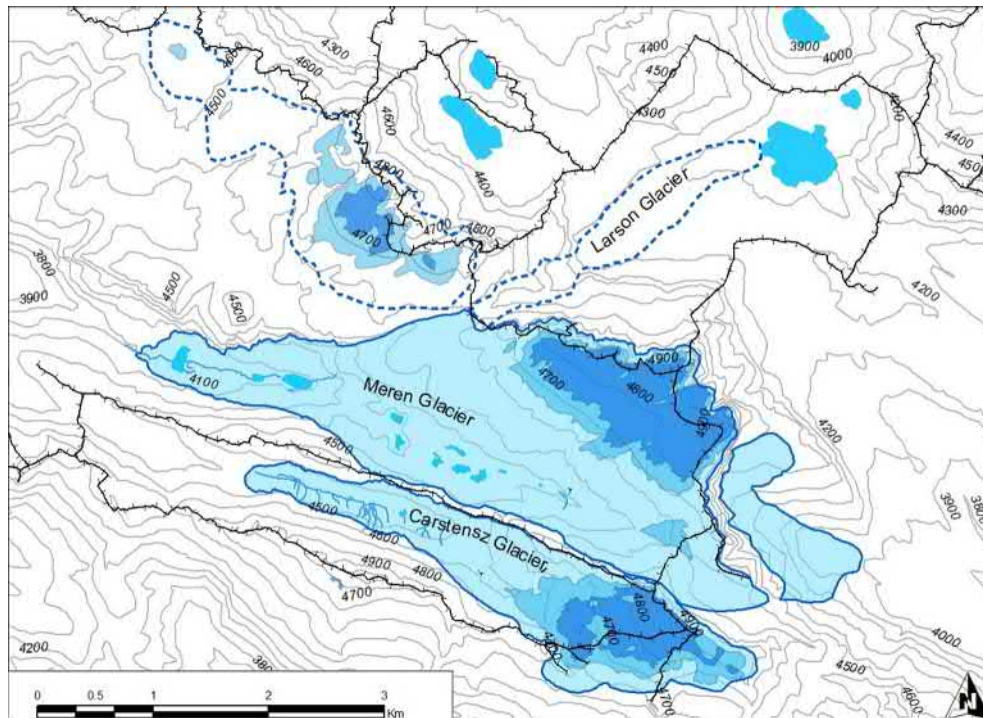


Fig. 4 Ice retreat on Mt. Jaya. The lighter blue and blue hatching indicates probable ice extent in 1850. Middle blue shows the extent in 1980 and the darkest blue the extent in 2000. Diagram by M.L. Prentice.

Few direct climate observations have been made in the alpine. Two dataloggers were buried at a depth of 10 cm at treeline on Mt. Wilhelm from 2007 to 2010 (**Fig. 5**). No warming trend was observed and the records displayed the least seasonal changes known for any tropical mountains (C. Korner and K. Green, pers. comm.; [Korner, 2012](#)). This may indicate that under moist and foggy conditions relatively little change is occurring at high elevation.



Fig. 5 Data logger site on Bogunaltobokwa Ridge at 3990 m on Mt. Wilhelm. The *Rapanea vaccinioides* trees have been stable for 40 years. Photo: G. Hope (2010).

A good reference climate station exists at the Ertzberg mine site at 3650 m on Mt. Jaya (Prentice and Hope, 2007). The rainfall data at this station identified the large impact of the 97–98 El Niño on the snowline at that time, which rose 100 m but then stabilized before retreating more slowly. This highlights that future climate impacts might follow increased and more severe drought events. These events include low cloud cover and a 30% reduction in rainfall for several months, with runs of weeks between significant rain events. During the El Niño, plants show signs of wilting and surface peats are dry. Mosses and lichens become crisp and may flake off while shallow ponds dry out and the sediments crack. Low humidity combines with low vapor pressure to dessicate plants and soils quickly. The clear skies result in very high levels of UV radiation which may bleach leaves and influence flowering. Since the flora is not adapted to drought, the effects of an El Niño event may be very disruptive, as suggested for Mt. Kinabalu by Kitayama (1996). Exposed ground provides habitat for colonizing herbs and lichens but is subject to frost-heaving and erosion.

Rising temperatures can be expected to result in changing plant altitudinal limits and community changes (Green and Stein, 2015). In the next few centuries there will be a reduction of rocky open habitats in the face of generalized warming which may result in increasing shrub cover and a rise in the tree line as frost-sensitive taxa migrate upwards. Raised CO₂ levels will encourage woody plants to invade grasslands. The evidence for this can be seen by comparing old photos with more recent ones in areas of little human impact. The effect is not marked to date and in many cases fire is maintaining or reducing shrub cover.

The Owen Stanley Range around 8° S in the southeast of New Guinea has a more-seasonal climate with a winter dry season. The ecology there may indicate a possible trajectory for the alpine vegetation in wetter alpine if drought events become more common. Mt. Albert Edward has a widespread low *Poa erectifolia* grassland across the summit plateau and heath areas are restricted to rocky outcrops (Fig. 1).

While paleoecological study (Hope, 2009) shows that the grassland has a very long history, its wide extent is due to fire that has prevented forest from becoming established at the highest limits. The predicted increase in shrubs is being prevented by widespread burning by both intentional fires and lightning-caused ignitions.

Disturbance: Fire, Development, Tourism

As treelines rose across the island when climates warmed after 15,000 year BP, in some areas burning by humans seems to have maintained open areas with alpine vegetation. In fact fire has continued to expand the available habitat for treeless subalpine vegetation throughout the last 9000 years (Hope and Haberle 2005). If major drought events increase in frequency then human ignited, and possibly natural, fires will alter the balance further. Large blanket peat areas (Hope, 2007) may dry out in droughts and are at risk of burning.

Agriculture is not practiced above 2800 m so the main traditional purposes for visiting alpine areas are for hunting (Fig. 6) and to traverse the range crests to reach settlements across the ranges. Animals sought at high elevation include the worm-eating monotreme, *Zaglossus bruijnii*, possums, birds such as the Snow Mountains quail and giant rodents like *Mallomys antap*. Traditionally parties of men would use high elevation huts or rockshelters for a week or two, returning to the village with a proportion of the game, including captured live animals, skins and feathers for ceremonial dress. Large quantities of wood were needed to support these camps and fires often escaped. A small kangaroo of the treeline, *Thylogale christensenii*, became extinct in the Papuan mountains around 3000 year BP (Flannery, 1992) and monotremes such as *Zaglossus* are now absent from the PNG highlands but still to be found in the subalpine of Papua and the Owen Stanley Ranges (Flannery, 1995). The bird of paradise with the highest elevation



Fig. 6 Copper ringtail possum captured in the Prinz Willem Range, Papua. This species has occupied alpine habitat as other fauna has been made extinct. Photo: Bren Weatherstone (1993).

range, *Macgregoria pulchella*, has a similar fragmented distribution that is probably the result of excessive hunting near large montane population centers. On Mt. Wilhelm fronds of an obligate ground fern, *Polystichum (Papuapteris) linearis*, is sought as bride price goods and for decoration.

With the arrival of modern states, alternative transport has reduced the use of tracks in the high country. For example, tracks crossing over Mt. Wilhelm from the upper Chimbu to Kerowagi are rarely used today, as lower elevation roads allow easier travel and old enmities that prevented free passage have relaxed. In a few instances the gradual loss of forest has been reversed. On the Kemabu Plateau north of Mt. Jaya, the vegetation is becoming more shrubby and overgrown while regeneration on stone pavements indicate an easing of the former destructive fire regime that destroyed the soil cover. This inferred reduction in human impact is supported by pollen data from Ijomba swamp which show increasing shrub and tree-fern cover after 2500 years ago when hunting may have lessened (Hope and Haberle 2005; Hope, 2014).

A new road is currently being built that traverses the alpine west of Mt. Trikora at 3800 m and connects the regional center of Wamena with Nduga. This road will likely replace a network of tracks that cross the range. The environment along the road will experience increased impact, but the general use of the high elevation away from the road may be reduced.

Different histories are known from other mountains such as Mt. Scorpio and Mt. Giluwe where grassland is still replacing subalpine forest due to fires lit by hunting parties (Fig. 7).

Some summits, such as Mt. Albert Edward, host radio telephone equipment serviced by helicopter but facilities on some other mountains (Mt. Giluwe, Mt. Ialabu, Mt. Wilhelm) have been abandoned as mobile phone technology expands.

There are exceptions to this scenario of relatively low human impact. The area near the Ertsberg and Grasberg copper-gold mines west of Mt. Jaya are impacted by a large open cut pit and extensive tipping of waste rock up to 4300 m elevation on formerly glaciated terrain. (Fig. 8). Mine spoil has buried the known habitat of an alpine community, *Euphrasia lamii-Tetramolopium distichum* herbfield, that was colonizing limestone screes and fans.

Mine workers from villages to the north now walk several days to and from the mine across the Kemabu Plateau. Mine workers also visit the ice area with consequent litter problems (Utteridge and Edwards, 2009). The mine is enclosed by the Lorentz National Park, a 25,056 km² reserve that extends 150 km from Mt. Jaya to Mt. Trikora across the largest high-elevation area on the island. The Park is not managed to any great extent at present and traditional uses such as hunting are continuing. The Park and many other high elevation areas were affected by widespread fire during the 1997–98 El Niño event.

Tourism to New Guinean mountains is quite minor in comparison with the massive popularity of mountains such as Mt. Kinabalu Malaysia. Numbers may even have reduced as the logistic difficulties and security problems in both Papua and PNG are perceived to have increased. An exception to the absence of tourism is Mt. Wilhelm, at 4509 m the highest mountain in PNG, where local groups are developing ecotourism along the Pindaunde valley, the most popular route to the summit from the road head at 2850 m. Lodges have been built with locally collected funds and official guides are employed. Tracks have been improved, funded from guide fees. Fuel for cooking is brought up to the subalpine and cutting the subalpine forest is discouraged. The area above 2900 m is national land but managed by the agreement of the local landowners. Visitor numbers are still relatively low, at a few hundred per year, but the enterprise provides a possible model for the management of other mountain areas. Gaining an income then provides incentives to maintain the vegetation and wildlife. The concentration on a single valley allows other valleys to remain



Fig. 7 Burnt grasslands at 3750 m on the summit plateau of Mt. Giluwe, PNG. Photo: M.L. Prentice (2002).



Fig. 8 The huge Grasberg mine on Mt. Jaya has removed several km² of alpine habitat, leaving a 1 km deep pit and placing overburden up to 4300 m. It has also disrupted traditional trackways across the mountains. Photomosaic Freeport McMoren (2010).



Fig. 9 Eroding track at 4250 m, Mt. Wilhelm. Photo: B. Pillans (2010).

unvisited because access is much more difficult. Visits are generally of short duration (2–4 days) so far. Track damage and some litter problems can be observed in the alpine but these could be readily fixed if visitation and hence income increase (Fig. 9).

A niche tourism market arises from the status of Mt. Jaya as the highest summit in Oceania leading to a market that caters for mountaineers keen to ascend the peak as one of the “Seven Summits.” Climbing the Carstensz Pyramid is the only one of the Seven Summits which specifically requires technical rock-climbing experience with routes of a difficulty up to 5.8. Expeditions are organized by trekking companies who can handle the visa and travel permit requirements. Groups fly into Sugapa, a small airstrip south of the mountain, and walk for 3 days to reach the alpine area. A popular recent alternative is a direct helicopter charter to the mountain. Benefits (and incentives for conservation) largely evaporate if centralized tourism companies based in towns take over the

activities and tourism management. This has been the tendency in ecotourism and climbing groups on Mt. Trikora and Mt. Jaya where the web largely promotes Jakarta-based firms and local attempts to provide services lose out to better organized and resourced firms with better market access and government connections.

Other mountains are occasionally visited and often publicized by web blogs. These include Mt. Victoria, Mt. Albert Edward, Saruwaged Mts, Mt. Giluwe and Mt. Scorpio in PNG and Mt. Mandala and Mt. Trikora in Papua. Very limited scientific research currently takes place on the New Guinea alpine but occasionally leads to new work on otherwise unvisited mountains such as Mt. Strong (Bishop Museum), Mt. Trikora (LIPI, Wamena) and the Finisterre Range (Lamont).

Discussion

The present status of both management and research on the subalpine and alpine of New Guinea is one of benign neglect. PNG lacks an organized reserve system while Papua has defined conservation areas and management aims but few resources to implement them. In general traditional resource use for the alpine continues unchanged. It seems likely that increasing montane populations and rising temperatures will cause subalpine forest to be cleared and crops such as potato and cabbage to expand to higher altitudes. The indirect effect of this will be to make the alpine more accessible, with risk to wildlife. However traditional use of the alpine has been minor and may now be declining as the population of montane villages becomes more oriented to town life. Over the past 40 years I have found it harder to find knowledgeable guides with the skills to work in the high regions, and many areas seem less visited, despite generally increasing highland populations.

Many isolated mountain areas across the island have never been studied and are rarely visited. Research is at the early stage of collecting and description in most cases. Offsetting this is the increasing maturity of local universities and research institutions, whose students and staff are undertaking research projects that may include alpine projects. In the longer term the magnificent landscapes will draw visitors and necessitate more targeted management.

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Current Changes in Alpine Ecosystems of Pacific Islands

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Abstract

Alpine ecosystems in the Pacific Islands are isolated and unique, characterized by high levels of endemism. Only Hawai'i and New Zealand have elevations high enough to contain substantial alpine climates, and about 11% of the land area of both island groups is located above treeline. Both of these volcanically active archipelagos are characterized by complex topography, with peaks over 3700 m. These alpine ecosystems have significant cultural, social, and economic value; however, they are threatened by invasion of exotic species, climate change, and human impacts. Nonnative ungulates reduce native shrubland and grassland cover, and threaten populations of endangered birds. Exotic plants alter water yields and increase fire risk, and increased recreational visitation to these remote areas facilitates the introduction of exotic plant seeds, pests, and pathogens. Both New Zealand and Hawai'i have experienced strong warming at higher elevations, and future projections indicate that these robust warming trends will continue. Glacial retreat has been noted in the Southern Alps, with 34% ice volume lost since 1977, and New Zealand may lose 88% of its ice volume by 2100. Snowfall on Hawai'i's mountain peaks is projected to almost entirely disappear by 2100. Changes are occurring rapidly, and additional monitoring and research are needed to conserve these uniquely sensitive, remote regions.

Introduction

Alpine ecosystems occur above the altitudinal limit of forests, known as the treeline. Complex mountainous topography leads to climates that change rapidly with elevation over short distances, resulting in steep gradients in vegetation and hydrology. Alpine ecosystems are often characterized as biodiversity “hotspots” and by high levels of endemism due to the isolation of species at high elevations (Beniston, 2003). On oceanic islands, geographic isolation has further contributed to the endemism found in these rare, unique alpine environments, and they are subject to markedly different oceanic-influenced climates than continental areas (Harter et al., 2015). Treelines here are also found at lower elevations than mainland treelines and are likely controlled by regional climatic factors (Irl et al., 2016).

Many studies have suggested that alpine ecosystems are among the most sensitive to climatic changes (e.g., Diaz et al., 2003), and growing evidence indicates that high mountain environments are warming faster than lower elevation areas (Pepin et al., 2015). This enhanced warming with elevation can accelerate the rate of change in mountain ecosystems, requiring species to respond by acclimating, adapting, moving, or facing extinction (Corlett and Westcott, 2013). For many alpine species, warming is expected to cause substantial range losses (Dullinger et al., 2012), and evidence indicates that many plant species will not be able to keep up with rapid changes in climate expected in the 21st century (Corlett and Westcott, 2013). For islands, the threat of climate change is even greater as native species are often poor competitors against introduced species, have limited potential to migrate because of the surrounding ocean, and for species at the highest elevations, migrating further upward is not possible (Harter et al., 2015). Climate change impacts on high islands can therefore result in a disproportionately high potential for global biodiversity loss.

Changes in high elevation ecosystems and the resources they provide can also be driven by numerous other factors, including overgrazing by livestock, invasion by nonnative species, land use change, and environmental stress from human activities (Beniston, 2003). Islands in particular are more vulnerable to anthropogenic impacts due to their limited land areas (Kier et al., 2009). Alpine ecosystems are susceptible to landslides, soil erosion, and loss of biodiversity and endemic species. Changes to these ecosystems impact the landscape, hydrological regimes, and water resources, with downstream impacts to the lowland areas and a wide range of socioeconomic consequences (Diaz et al., 2003).

In the Pacific Ocean, islands range in size from small low-lying coral atolls at sea level to large islands with volcanic peaks at 4200 m. Alpine ecosystems in the Pacific Islands are primarily concentrated in Hawai'i, New Zealand (Aotearoa), and Papua New Guinea. It should be noted, however, that Tahiti in French Polynesia (maximum elevation 2241 m) and Vanuatu (1879 m) contain some subalpine shrublands with low scrubby and herbaceous vegetation above the cloud forest on the highest peaks (Leuschner, 1996; Meyer et al., 2010). The Solomon Islands (2335 m) are forested to the summits with some local *Sphagnum* moss alpine bogs (Leuschner, 1996). Australia also contains approximately 11,500 km² of alpine and subalpine habitat concentrated mainly in the southeast of the continent and the island of Tasmania (Williams et al., 2008). For more information on alpine ecosystems of Australia, please refer to McDougall and Walsh (2007), Slatyer (2010), and Kirkpatrick (1983). This article focuses on characterizing current changes in alpine environments of Hawai'i and New Zealand. The section "High Elevation Ecosystems in Pacific Islands" describes the vegetation and climate of these ecosystems, while the "Current Changes" section describes current changes in these regions, followed by a "Concluding Remarks" section.

High Elevation Ecosystems in Pacific Islands

Geologic Setting

New Zealand's approximately 260,000 km² of land area today represents only 5% of a much larger, submerged continent known as Zealandia. New Zealand (Fig. 1) is a mountainous country located between 34° and 47°S latitude and 166° to 179°E longitude. Around 11% of the total land area is above the treeline (Halloy and Mark, 2003). The highest point above sea level is Aoraki/Mount Cook (3754 m) located in the Southern Alps on the South Island, and another 222 named peaks have elevations > 2300 m (Campbell et al., 2012). Alpine areas on the North Island are limited to a few peaks above treeline, and only the active stratovolcano Mount Ruapehu (2752 m) supports glaciers (Chinn, 2001). The Southern Alps were created by the collision of the Pacific and Australian plates, starting about 5 million years ago, and were extensively glaciated around 20,000 years ago during the Last Glacial Maximum. The Alpine Fault spans the length of the Southern Alps from north to south and regularly produces large earthquakes, which, along with erosion and tectonic activity, have shaped the unique mountain topography found today (Campbell et al., 2012). Active volcanic areas are confined to six areas: five in the North Island and one offshore to the northeast. From a geophysical standpoint, New Zealand possesses characteristics of both islands and continents, so it is not surprising that its remarkable biodiversity occurred as a result of both dispersal from nearby land masses and evolution from ancestors of Zealandia (Wallis and Trewick, 2009).

The Hawaiian archipelago lies in the center of the Pacific plate between 18° and 23°N latitude and 160° and 154°W longitude and was formed by volcanic activity as the plate slowly moved over a hotspot (Macdonald et al., 1983). The islands extend over 2400 km from Hawai'i Island in the southeast to Kure Atoll in the northwest, ranging in age from 0.5 to 28 million years. Hawai'i is nearly 4000 km from the nearest continent, and is one of the most isolated major archipelagos in the world. Eight main islands (Fig. 2) have a land area of 16,637 km² (Juvik and Juvik, 1998), of which Hawai'i Island is the largest and contains three of the four highest peaks: Mauna Kea (4205 m), Mauna Loa (4169 m), and Hualālai (2521 m). Mauna Loa and Hualālai are active shield volcanoes; Mauna Kea is a dormant shield volcano (Juvik and Juvik, 1998). To the west of Hawai'i Island is the island of Maui, whose tallest peak, Haleakalā (3055 m), is also an active shield volcano (Juvik and Juvik, 1998). These four peaks are home to all of Hawai'i's alpine and subalpine vegetation, and similar to New Zealand, Hawai'i's tropical alpine and subalpine regions comprise ~11% of the land area.

Climatology

The climates of Pacific Island highlands are subject to strong influences from the surrounding ocean, and precipitation patterns are predominantly driven by orographic processes. Interdecadal and decadal climate variability are driven by large-scale modes of variability, including the El Niño-Southern Oscillation (ENSO) (Frazier et al., 2018; Sturman and Wanner, 2001). New Zealand experiences westerly winds in the mid-latitudes, while Hawai'i is subject to northeast trade winds in the tropics, and the perpendicular orientation of the mountains to the prevailing moisture-laden winds results in extremely wet windward areas (over 10,000 mm year⁻¹ on both the western slopes in New Zealand and the eastern slopes in Hawai'i; Giambelluca et al., 2013; Hendriks et al., 2012). Extreme gradients characterize both archipelagos, with a stark contrast in the rain shadow of the dry leeward areas where precipitation can be as little as 500 mm year⁻¹ in New Zealand and ~200 mm year⁻¹ in Hawai'i (Giambelluca et al., 2013; Tait et al., 2006). Mean annual temperatures range from -6.9 to 8.2°C and from 3.6 to 10°C in alpine areas of New Zealand and Hawai'i, respectively (LENZ, 2010; Giambelluca et al., 2014). In New Zealand, cold fronts originating along the eastern side of the mountain range can cause sudden drops in temperature and increases in humidity, with damaging winds (Sturman and Wanner, 2001). Wind speeds exceeding 160 km h⁻¹ have been recorded at the higher elevations in New Zealand. New Zealand experiences extensive seasonal snow cover (Hendriks et al., 2012), while in Hawai'i, snow occasionally falls on the highest mountains, although no direct measurements of snow are currently recorded (Zhang et al., 2017). In Hawai'i, high elevation areas have some of the lowest evapotranspiration and rainfall rates, the lowest cloud frequency and relative humidity, and the highest solar radiation (Giambelluca et al., 2014). These climate patterns are largely driven by the presence of an atmospheric inversion layer around 2150 m, known as the Trade Wind Inversion (TWI), which caps cloud growth and produces extremely dry, sunny conditions above (Longman et al., 2015a). This sharp change in moisture availability, combined with extreme El Niño-induced drought events, is thought to drive the position of the treeline (Crausbay et al., 2014).

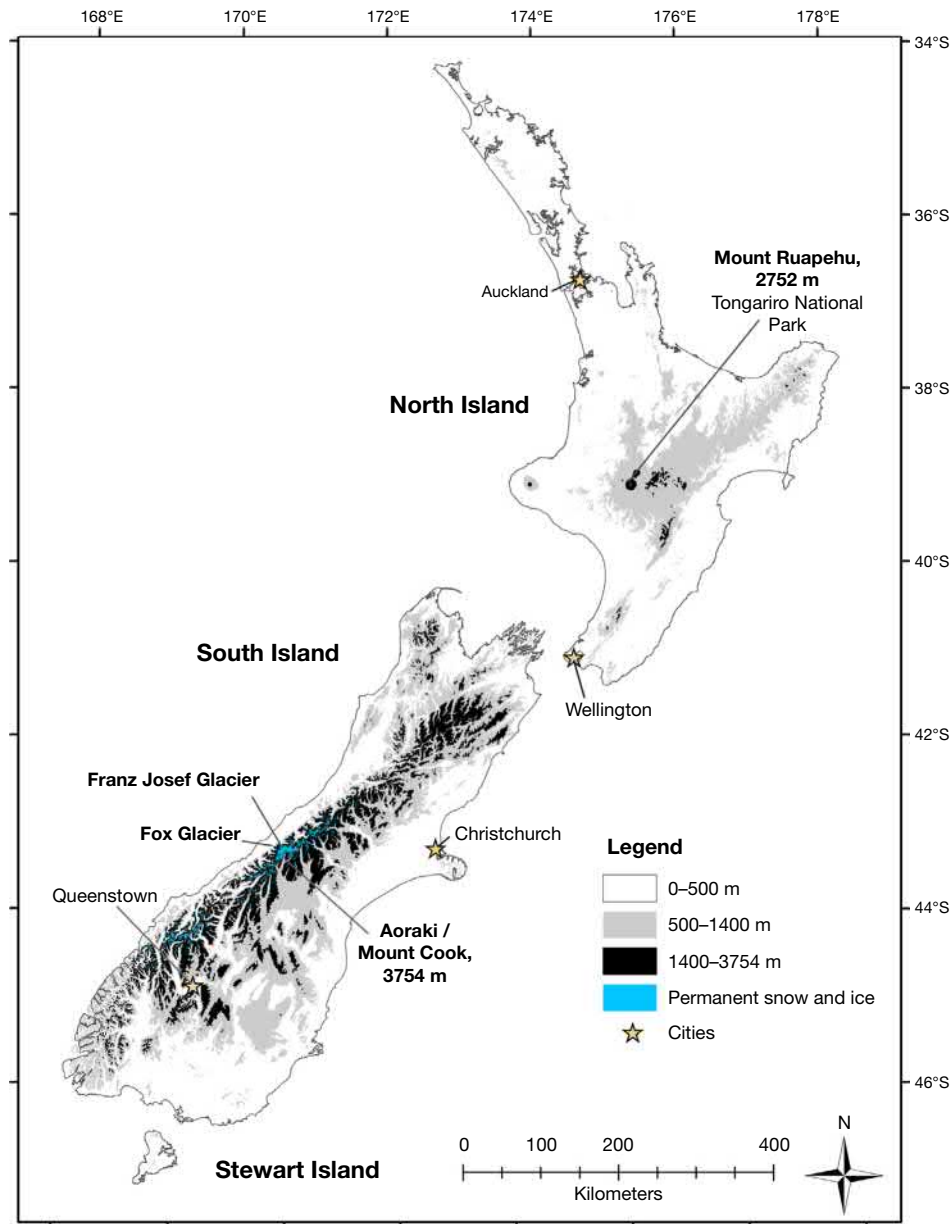


Fig. 1 Elevation zone map of New Zealand showing land above the approximate treeline elevation. Some individual summits and glaciers discussed in the text are labeled.

Ecological Zones and Plant Communities

Treelines in New Zealand occur within similar thermal ranges as in other sites worldwide (although at lower elevations; Cieraad et al., 2014). The high altitude tree limit in New Zealand's alpine regions is dominated by two species of evergreen *Nothofagus* trees ranging from ~1000 m in the southern part of the Southern Alps to ~1400 m on the North Island (Wardle, 2008). Above the treeline, the vegetation of the high mountains (Fig. 3) consists of a lower alpine zone dominated by shrubs and tall tussock grasslands and a high alpine zone dominated by dwarfed plant communities and grasslands (Mark et al., 2000). There are no native mammalian herbivores in this region. The snow tussock lands (*Chionochloa* spp.) in the southeastern South Island are known to intercept large amounts of fog that contribute substantially to the water yield from these uplands (Mark et al., 2013). Above the high alpine zone lies the permanent snowline, which is the lower limit of the nival zone (Mark et al., 2000). Areas of permanent snow are extensive along the central Southern Alps and in the southern part of the range (Fig. 1). Over 3000 glaciers have been identified, and as a result of the strong precipitation gradient they range in elevation from ~1600 m in elevation in the west to ~2500 m in the east (Chinn, 2001). Terminal alpine lakes are frequently present at the base of glaciers (Fig. 3A). Permafrost is found at the higher elevations in the central part of the range (Sattler et al., 2016).

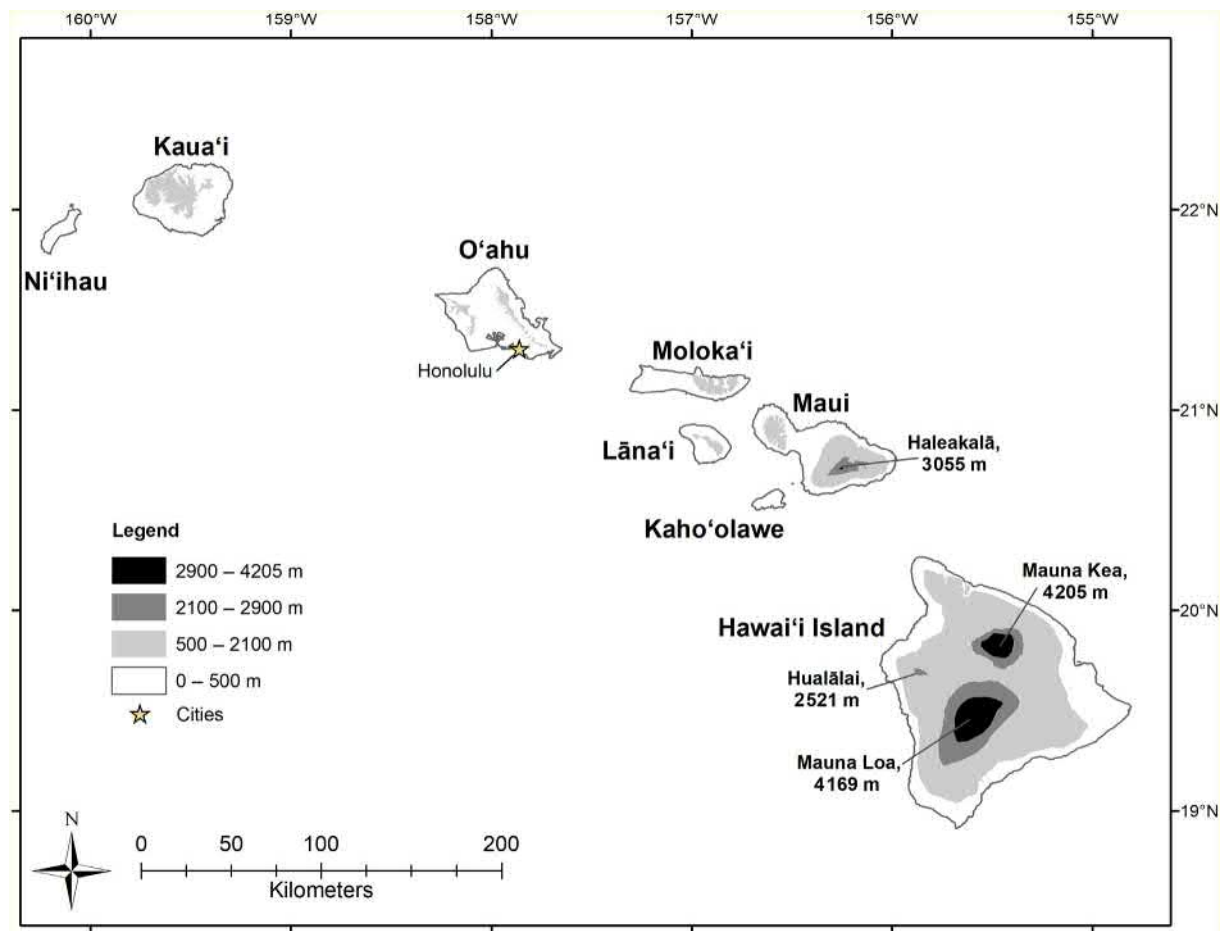


Fig. 2 Elevation zone map of the main Hawaiian Islands showing land above the approximate treeline elevations. Some individual summits discussed in the text are labeled.

In Hawai'i, between ~2000 and 3000 m are subalpine forests, woodlands, and shrublands. The treeline of Mauna Kea is typically defined as the upper extent of the māmane (*Sophora chrysophylla*) woodland and is located ~2900 m above sea level (Gerrish, 2013; Leuschner, 1996). The treelines of Mauna Loa and Haleakalā are at least 450 m lower than on Mauna Kea, which may be due to soil-dependent factors (Leuschner, 1996). Along parts of the northeastern slope of Haleakalā, the treeline occurs around 2100 m and is delineated by plantations of conifers that were introduced in the early 1900s. In other areas, treeline elevation varies and is made up of native subalpine cloud forest dominated by 'ōhi'a (*Metrosideros polymorpha*), which gives way to alpine shrublands, herbs, and tussock grasslands that form a fog-drip community of alpine scrub (Crausbay and Hotchkiss, 2010). Alpine desert conditions exist on Maui and Hawai'i Island above ~3000 m. These are dry and semibarren, with dwarf native shrubs dominated by pūkiawe (*Styphelia tameiameia*), 'ōhelo (*Vaccinium reticulatum*), 'āhinahina or Hawai'i silversword (*Argyroxiphium sandwicense*), and na'ena'e (*Dubautia* species). At the summits, eolian deserts (also called stone deserts, Fig. 3C) are populated with grasses, mosses, and lichens (Gerrish, 2013; Juvik and Juvik, 1998).

Mauna Kea was home to a 70 km² ice cap until 15,000 years ago, which left conspicuous, preserved moraines (Anslow et al., 2010). Despite mean annual temperatures well above freezing, perennial ice is present as permafrost inside two cinder cones on Mauna Kea and two lava tube ice caves on Mauna Loa (Schörghofer et al., 2018). Hawai'i's only alpine lake, Lake Waiau (3970 m) (Fig. 3D), is found in the Pu'u Waiau cinder cone on the slopes of Mauna Kea and is fed primarily by winter storms (Ehlmann et al., 2005), though there is concern over recent declining lake levels (Patrick and Kauahikaua, 2015). Pu'upōhaku pond (4000 m) is a nearby sporadic pond that was only recently recognized (Leopold et al., 2016). Given the porous nature of basaltic lava (which cannot hold water to form lakes), the causes of these permanent water bodies on Mauna Kea remain unknown.

Cultural Significance and Human Impacts

Globally, alpine environments are associated with cultural identity, spiritual practices and religious ceremonies, and the provision of ecosystem services such as food and water, natural hazards regulation, and tourism and recreation (Palomo, 2017). The mountains of New Zealand are immensely important to the Māori way of life and sense of place, with individual peaks seen as



Fig. 3 Alpine summits, glaciers, and lakes: (A) Mueller Glacier and Mount Cook, Aoraki/Mount Cook National Park, New Zealand; (B) Tongariro Alpine Crossing, Tongariro National Park, New Zealand; (C) Mauna Kea Summit, Hawai'i; (D) Lake Waiau, Mauna Kea, Hawai'i. Photo credits: (A) Vern (CC, Flickr); (B) Andrea Schaffer (CC, Flickr); (C) Laura Brewington; (D) Thomas Tunsch (CC, Flickr).

representations of ancestors (Pawson and Egli, 2001). Human impacts on the vegetation since the arrival of the Māori ~1000 years ago, however, have been pervasive. Fires in the region significantly altered the vegetation composition, allowing high-alpine plants to extend their ranges into low-alpine tussock grasslands (Halloy and Mark, 2003). European discovery and settlement of this region occurred in the 17th century (Pawson and Egli, 2001) and subsequent economic interests in the region included a brief gold rush, logging, coal mining, and agriculture (Balcar and Pearce, 1996), followed by a tourism boom in the late 20th century. Hiking, hunting, fishing, and skiing/snowboarding are permitted in many of the country's high elevation parks, nature reserves, and scenic areas, although special protected areas of high conservation value have been designated within them (Fig. 3B, Fig. 4A,B) (Mark et al., 2013). Today New Zealand's nature tourism industry generates 6% of the country's GDP and attracts upward of 3 million international visitors a year; only the dairy industry contributes more to the national economy (Stats, 2017). "Glacier Country" in the Southern Alps alone receives over 600,000 visitors a year between Franz Josef and Fox Glaciers (Purdie, 2013).

Native Hawaiian tradition states that deities reside in the high mountain summit areas of the archipelago, and Mauna Loa, Mauna Kea, and Haleakalā are therefore regarded as sacred places of great spiritual importance. The summit of Mauna Kea, the tallest point in Hawai'i, is extremely culturally significant as its peak is considered the *piko* (umbilical cord) of the Hawaiian spiritual world, connecting the Earth, heavens, and stars (Ho'akea, 2009). Lake Waiau is culturally significant to Native Hawaiians as a source of healing water used for ceremonies and worship (Ho'akea, 2009). Most of Hawai'i's alpine regions fall into various conservation zones, which have historically shielded them from development and other human impacts. Nevertheless, Haleakalā National Park on Maui is visited by 1–2 million people a year, established roadways and trail networks provide relatively easy access to all alpine sites, and the construction and operation of astronomical observatories—particularly those near the summit of Mauna Kea—have been the subject of debate for decades due to their impacts on native ecosystems and culturally important sites (Fig. 4C,D) (Hilberg et al., 2018).

Current Changes

Changes in Native and Invasive Species

In New Zealand's Southern Alps, extensive radiations of vertebrate and invertebrate alpine communities have been facilitated by the relatively recent tectonic activity and partial glaciation (Wallis and Trewick, 2009), most notably plants and some birds, such as the

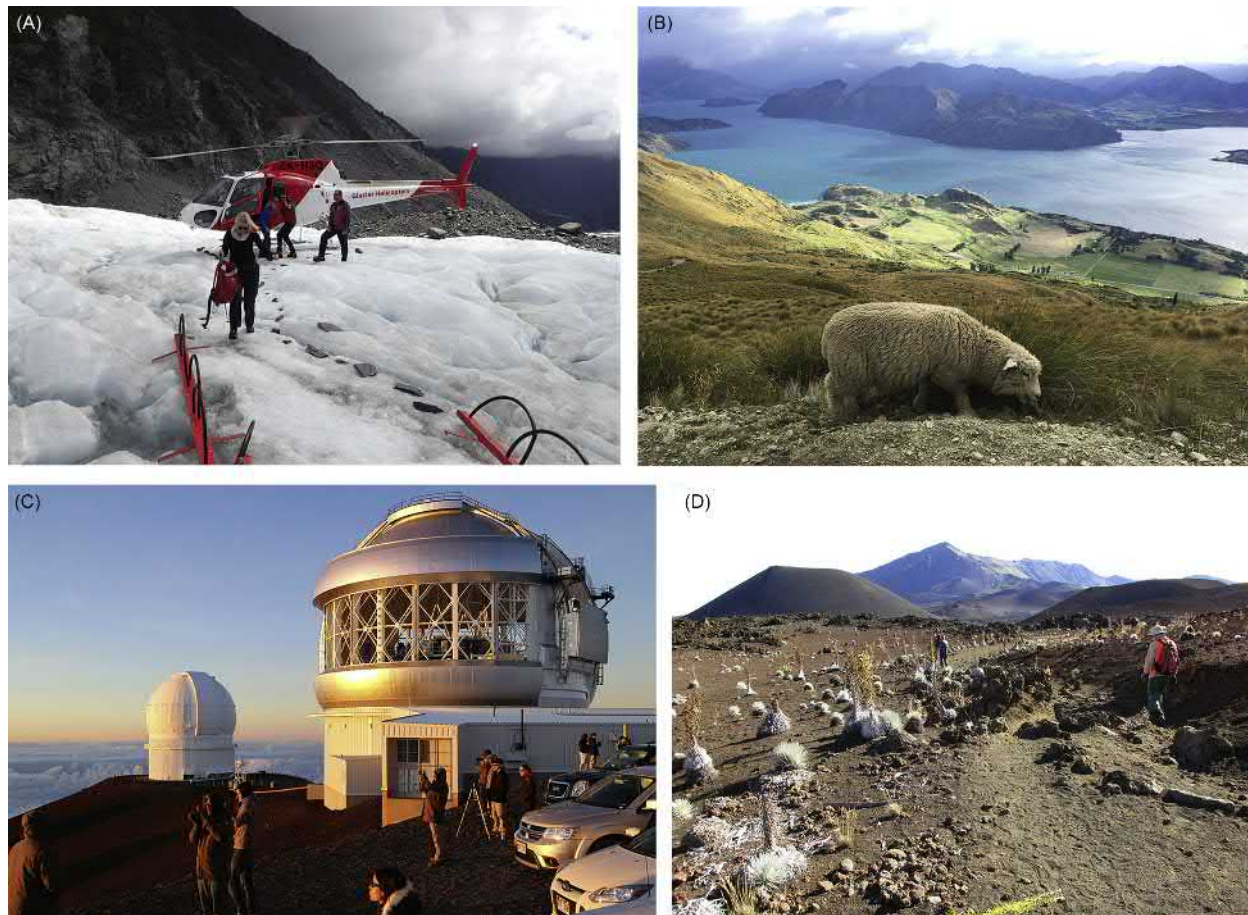


Fig. 4 Human interactions with alpine regions: (A) helicopter tourism operation, Fox Glacier, New Zealand; (B) grazing sheep near Wanaka, New Zealand; (C) tourism and astronomical observatories, Mauna Kea, Hawai'i; (D) popular hiking trails through Haleakalā crater, Maui, with many flowering silverswords. Photo credits: (A) Abby Frazier; (B) Laura Brewington; (C) Laura Brewington; (D) Forest & Kim Starr.

kea (*Nestor notabilis*) and rock wren (*Xenicus gilviventris*) (Fig. 5A,C). Like other oceanic islands, New Zealand has very high rates of endemism (around 30% of plants and 82% of animals; Gordon, 2013); many of the endemic birds are partially or completely flightless (e.g., South Island takahē (*Porphyrio hochstetteri*), Fig. 5B). In the alpine region, over 90% of plants are endemic (Halloy and Mark, 2003). O'Donnell et al. (2017) recently identified 24 native alpine bird species that are characteristic of the Southern Alps region, 17 of which are considered to be at risk. Cold-tolerant lizards (including geckos and skinks), invertebrates like the wētā (*Deinacrida* species) (Fig. 5D), cicadas, giant carnivorous land snails, butterflies, moths, giant wingless stoneflies, and freshwater fish are among the other indigenous biota found at these high altitudes (O'Donnell et al., 2017). The kea, the world's only alpine parrot, was the target of an official campaign from the late 1800s until 1971 to reduce their numbers due to attacks on farm animals (Young et al., 2012), and the New Zealand Department of Conservation (2017) estimates that there are fewer than 7000 today. During the growing season, kea feed extensively on fruiting plant species in the alpine region and as the only species that is known to fly long distances between mountains and ranges, they are significant contributors to alpine plant dispersal in New Zealand (Young et al., 2012).

In the alpine and subalpine ecosystems of Hawai'i, 84% of floristic species are endemic, with more species on Maui than Hawai'i Island despite a much smaller land area and elevational range (Price, 2004). One of the most iconic endemic alpine species, the Hawaiian silversword, is extremely vulnerable to warmer and drier conditions that have been experienced in recent decades (Krushelnycky et al., 2013). The Hawaiian alpine Wēkiu bug (*Nysius wekiuicola*), first discovered in 1979, is a rare endemic, flightless insect species found within a narrow elevation range (3415–4205 m) in the alpine stone desert zone of Mauna Kea that survives on wind-borne insect carcasses blown up from lower elevations (Stephenson et al., 2017). Seabirds, such as the 'ua'u (Hawaiian petrel, *Pterodroma sandwichensis*), are also observed throughout Hawai'i's alpine regions (Banko et al., 2001), and alpine grasslands and shrublands also provide habitat for the endangered state bird of Hawai'i, the nēnē (Hawaiian Goose, *Branta sandvicensis*) (Fig. 5E).

The Hawaiian Islands once had abundant endemic avian biota. Mosquito-borne avian pox and avian malaria, however, have resulted in widespread mortality of forest birds and a shift to higher elevations where colder temperatures inhibit mosquito reproduction (Liao et al., 2015). 'Ōma'o (*Myadestes obscurus*), one of only two remaining species of endemic solitary birds, have been



Fig. 5 Endemic alpine and subalpine fauna. New Zealand: (A) Kea; (B) Takahē; (C) Rock Wren; (D) Alpine Scree Wētā (*Deinacrida connectens*). Hawai'i: (E) Nēnē; (F) Palila. Photo credits: (A) Tomas Sobek (CC, Unsplash); (B) Larry Koester (CC, Flickr); (C) Francesco Veronesi (Wikimedia Commons); (D) Danilo Hegg; (E) Forest & Kim Starr; (F) Jack Jeffrey, USGS (Wikimedia Commons).

observed in the scrub alpine environments of Hawai'i Island where they are vulnerable to predation by cats and rats (Judge et al., 2012). They, like most of Hawai'i's native forest birds, have lost an enormous proportion of their native range (estimated 70%) due to land cover change and nonnative species invasions, impacts that are expected to be exacerbated by projected changes in climate (Fortini et al., 2015). The palila (*Loxioides bailleui*), a species of critically endangered Hawaiian honeycreeper (Fig. 5F), is almost entirely dependent on the endemic subalpine māmane tree for its food, and has experienced drastic range reductions due to browsing pressure from introduced ungulates that have degraded its habitat. This species is at high risk for extinction with the simultaneous threats of drought, wildfire, and invasive ungulates (Banko et al., 2014).

The alpine regions of the world are often viewed as being relatively resistant to biological invasions, due to their extreme climate and inaccessibility to humans (Pauchard et al., 2016). However, climate change, human-driven environmental degradation, and land use change facilitate species invasions, to which the isolated alpine ecosystems in the Pacific Islands are particularly vulnerable.

The first known mammalian predator to arrive to New Zealand was the Polynesian rat around 800 years ago, but the vast majority of pests were introduced after European settlement in the 1800s (Wallis and Trewick, 2009). Feral populations of red deer (*Cervus elaphus scoticus*) and rabbits (*Oryctolagus cuniculus*) exert significant pressure on New Zealand's alpine grasslands above the treeline, while grazing livestock (primarily sheep, *Ovis aries*) also influence the vegetation cover and species makeup. In particular, native tussocks have declined in favor of invasive herbs in areas with a long history of summer livestock grazing (Norton and Young, 2016). Significant reductions in red deer populations in the Southern Alps have led to the recovery of native shrublands and grasslands in both number and size, however, suggesting that long-term management practices and exclusion of ungulates from sensitive areas can lead to successful restoration (Tanentzap et al., 2009). Himalayan tahr (*Hemitragus jemlahicus*) (Fig. 6A) was introduced to New Zealand's Southern Alps in 1904 as a hunting resource, which reproduced rapidly and reduced native tussock plant species to bare ground. While some efforts to reduce their numbers have been made, the population has continued to increase with long-term impacts on native alpine grassland communities (Cruz et al., 2017). New Zealand's ground-dwelling native alpine birds are particularly susceptible to predation by invasive mammals, including feral cats, stoats, and mice, which have been primarily responsible for their decline (Weston et al., 2018). Alpine populations of endangered takahē and rock wren have been extensively reduced by stoats (*Mustela erminea*) (Fig. 6B) (O'Donnell et al., 2017). Almost half of the country's endemic birds have gone extinct, while limited remaining populations are more vulnerable to changes in climate, extreme events, and disease (Innes et al., 2010).

Invasive ungulates, including pigs, cattle, and goats, have also severely impacted Hawaiian alpine ecosystems at various times over the last 200 years, particularly above the TWI in grassland-dominated areas (Daehler, 2005). This has coincided with soil erosion and nonnative plant invasions that have further reduced alpine plant community regeneration (Daehler, 2005). While goat and cattle populations have been greatly reduced on Hawai'i Island, feral sheep and mouflon have not yet been eradicated. Goats were eradicated from Maui in 1989 but axis deer are increasing in number (Hess, 2016). Removal of ungulates from a subalpine region of East Maui resulted in significant increases in relative cover of native shrubs and ferns, and a decrease in alien grass cover (Hughes et al., 2014). Other invasive mammals, such as cats and mongooses, are rarely observed in Hawai'i's alpine locations, but are still a concern (Fig. 6D). Mice and rats, however, persist at all elevations and are especially abundant near food sources and visitor sites (Vanderwoude et al., 2015). Invasive social insects, such as the Argentine ant (*Linepithema humile*) that has been documented at Haleakalā National Park for the past 25 years (Hartley et al., 2010), have the potential to alter alpine native invertebrate communities and may enter new habitat ranges as the climate continues to warm, disturbing native ecosystems as well as visitor sites (Vanderwoude et al., 2015).



Fig. 6 Invasive Species: (A) Himalayan Tahr near Cameron Glacier, Canterbury, New Zealand; (B) Stoat, New Zealand; (C) *Pinus radiata* (Monterey pine) in the subalpine shrubland, Haleakalā, Maui; (D) National Park Service installing an 8 km long cat-proof fence to protect endangered Hawaiian petrel habitat on the slopes of Mauna Loa, Hawai'i, 2400–3000 m elevation. Photo credits: (A) Jake Osborne (CC, Flickr); (B) Soumyajit Nandy (Wikimedia Commons); (C) Abby Frazier; (D) NPS.

Transportation networks are a main driver species introductions to mountain systems (Alexander et al., 2016), and recreational tourist visitation to Haleakalā National Park, Mauna Kea, and Mauna Loa has facilitated the introduction of invasive plant seeds, pathogens, and insects into higher elevations in Hawai'i (Daehler, 2005). Backcountry huts in New Zealand have also been identified as important sites for invasion by nonnative plant species into remote alpine areas (Lloyd et al., 2006). The area around Lake Waiau on Mauna Kea experiences high levels of visitation via trail and has been invaded by common dandelion (*Taraxicum officinale*) and two species of beetle (*Agonum c.f. muelleri* and *Trechus obtusus*; Vanderwoude et al., 2015). Vegetation surveys along roadsides at Mauna Loa's upper elevations conducted 50 years apart (1958–2008) revealed a significant increase in the number of both native and invasive plant species. The reasons for the establishment of new species remain unclear, but are more likely due to increased human impacts and access than climate warming in this arid and sparsely vegetated environment (Juvik et al., 2011). On Mauna Kea, invasive grasses pose a serious threat to the ecosystems, both in terms of composition and fire risk (Banko et al., 2014), and introduced weeds are abundant in the alpine zone in New Zealand, including hawkweed (*Hieracium* species) (Steer and Norton, 2013). Conifers introduced to the windward slopes of Haleakalā as part of an early 20th century forestry initiative are moving into higher elevations and outcompeting native shrub species (Fig. 6C) (Pauchard et al., 2009). Introduced *Pinus contorta* (lodgepole pine) in New Zealand has also increased at high elevations by 180% over the past 20 years and is now found up to 270 m higher than previously established (Tomioolo et al., 2016). Planted *Pinus radiata* (Monterey pine) was found to reduce water yield by 43% compared to native snow tussock (Mark and Dickinson, 2008).

Observed Climate Changes and Impacts

Since 1900, New Zealand's mean annual temperatures have risen at a rate similar to the global mean, with most of the warming occurring after 1946 ($0.12\text{--}0.14^\circ\text{C decade}^{-1}$, 50-year trend ending in 2006, Dean and Stott, 2009). However, irregularities in observations and poor station coverage in alpine areas result in uncertainties in warming rates for high elevation areas (de Freitas et al., 2014). What is known, however, is that warming has reduced New Zealand's glacier volume since 1850 (Mark et al., 2006). In a recent glacier inventory, Chinn et al. (2012) found that the melting of the region's 12 largest glaciers accounts for 71% of total glacial volume loss in the last 30 years, while the melting of thousands of small- and medium-sized glaciers accounts for the remaining 29%. In total, ice volume in the Southern Alps has been reduced by 18.4 km^3 , or 34%, since 1977 (Chinn et al., 2012), and glacier retreat and reductions in snowfall have impacted tourism operations, with a shift to helicopter-oriented glacier tours (Purdie, 2013) and increased artificial snow-making for skiing and snowboarding (Hopkins, 2014). Despite the expectation that climate-induced warming will cause an upward shift in treeline in alpine locations worldwide, study of treeline areas dominated by *Nothofagus* (beech) in the Southern Alps has shown little response to recent temperature increases (Harsch et al., 2012). Precipitation over the past three decades has trended toward drier conditions on the west coast of the South Island, while wetter trends are found for the west coast (Salinger and Mullan, 1999).

Hawai'i's highest elevations have experienced rapid warming in the last four decades (Giambelluca et al., 2008). The Mauna Loa Slope Observatory (MLO) station, located at 3341 m elevation, has experienced a mean warming trend of $0.19^\circ\text{C decade}^{-1}$ between 1955 and 2016 (McKenzie et al., 2019). This strong warming trend has been linked to degradation of the permafrost on Mauna Kea, which has shrunk by an order of magnitude between 1973 and 2015 (Schorghofer et al., 2017). Based on historical accounts, snowfall used to be much more common on Mauna Kea, but in the modern climate snow occurs only a few times in winter and rarely in summer (Schorghofer et al., 2014). High elevation areas have experienced significant drying since 1920, particularly in the dry season (May to October; Frazier and Giambelluca, 2017). This is consistent with the observed increases in high elevation solar radiation and decreasing cloud cover since 1988, driven by changes in the TWI (Longman et al., 2015a). An abrupt shift in TWI in 1990 resulted in a 20% increase in mean TWI frequency, likely driven by increased intensity of Hadley Cell subsidence near the Hawaiian Islands (Longman et al., 2015a). This shift in TWI has been linked to ecological responses, such as the decline in the Haleakalā silversword population (Krushelnysky et al., 2016).

Future Projected Climate Changes

Alpine ecosystems may be the most affected by global climate change. Alpine climates are extremely complex due to the interactions between mountains and atmospheric circulation. A lack of high spatial and temporal resolution observations, coupled with the limitations of general circulation models (GCMs) in representing the complex terrain, restricts our understanding of these climates (Beniston et al., 1997). Representing complex topography on small islands in climate models is even more challenging, as the differences between land and ocean climates are stark. In Hawai'i, the entire state may fit into only a few grid cells in a GCM, and these coarse-resolution products are not able to simulate the complex processes that operate on relatively small scales (Elison Timm et al., 2015). To overcome these limitations in Hawai'i and New Zealand, various downscaling methods are employed to generate local- and regional-scale projections from the global models.

According to mid-range scenario projections for New Zealand's climate, by 2040, temperatures are expected to increase by 0.8°C , doubling again to 1.6°C by 2110, with the strongest warming over higher elevations. Rainfall will likely increase in the west and decrease in the east and north due to an increase in westerly winds; extreme daily wind speeds will be stronger, especially in the Southern Alps (Ministry for the Environment, 2018). Model projections for snowfall in popular ski destinations suggest dramatic cuts in the number of snow days averaged across all sites by 2040 (up to 24%, depending on the climate scenario) and catastrophic reductions (up to 68%) by 2100 (Hendrikx and Hreinsson, 2012). As in other glaciated areas of the world, New Zealand may lose

88% of ice volume by the end of the century, driven largely by reductions in snowfall (Shannon et al., 2019); by 2100 Franz Josef Glacier could lose 38% of its volume (Anderson et al., 2008). In addition to the gradual loss of alpine glaciers and permafrost as indicators of climate change, there may be a greater risk of landslides and rockfalls associated with short-term temperature extremes, although this has not been confirmed in New Zealand's Southern Alps (Allen and Huggel, 2013). Species-area modeling results show that a 3°C rise in temperatures could lead to a loss of 33%–50% of native alpine plant species, and > 100 new exotic species (Halloy and Mark, 2003). The loss of snow cover due to a warming climate may impact the frost-resistance of alpine plant species (Bannister et al., 2005). Reduced snow cover will likely result in more thermal stress for alpine cockroaches (*Celatoblatta quinque-maculata*) (Sinclair, 2001), while warmer temperatures are expected to reduce and displace populations of alpine grasshoppers (*Paprides nitidus*) (White and Sedcole, 1991). A recent transplant experiment found that some alpine plant communities had inherent resilience to altered snow cover, while novel biotic interactions such as herbivory and competition affected survival (Lord et al., 2018). In addition to warming, patterns of rainfall, wind, and snow cover as well as human disturbances and invasive species behavior will also change in complex ways, and there is still much that is unknown about the response of native species to these changes (Halloy and Mark, 2003).

For Hawai'i, future projections of temperature indicate robust warming statewide, with the greatest warming also at the highest elevations (projections range from 3.5°C to 5°C warmer temperatures by 2100; Elison Timm, 2017; Zhang et al., 2016). Future projections of rainfall are less certain. General patterns indicate that windward areas will become wetter or stay the same, while leeward areas will become drier by the late 21st century (Elison Timm et al., 2015; Zhang et al., 2016). TWI projections indicate a robust increase in the frequency of TWI days, from 82% to 91% on Hawai'i Island, and a decrease in mean base height (Zhang et al., 2016). End-of-century snowfall simulations indicate that snow will nearly disappear on the summits of Mauna Kea and Mauna Loa, with implications for the Hawaiian language name "Mauna Kea," which means "white mountain" (Zhang et al., 2017). As for the ecological impacts of these changes, very little is known about species- or community-level impacts of climate change on alpine ecosystems in Hawai'i. However, given the evidence for a moisture-driven treeline (e.g., Crausbay et al., 2014), a lower and more frequent TWI combined with an increase in El Niño event frequency could depress any upward movement, possibly resulting in downslope migration of the treeline.

Concluding Remarks

Climate change, introduced species, and human impacts have independent and interacting effects on alpine ecosystems globally. On the one hand, the harsher climate of alpine environments and reduced anthropogenic disturbance have historically prevented the establishment of nonnative biota (Alexander et al., 2016), but warming temperatures are alleviating those unfavorable conditions (Pauchard et al., 2016). Similarly, human influence can exacerbate the impacts of climate change while facilitating further introduction and establishment of introduced organisms into new ranges. Native species in these regions—especially those in low densities—may also lack adequate baseline information and are uniquely vulnerable to major threats such as global climate change and human impacts. Resource managers are therefore challenged with accommodating multiple-use natural areas (conservation, public hunting, tourism, cultural use, etc.) while monitoring and managing for ecosystem change with limited information.

The need to track changes in Pacific Island alpine environments is clear: they are rare, isolated (geographically and by elevation), and are uniquely sensitive to the threats posed by climate change, introduced species, and human impacts. Two field sites in the Southern Alps were recently incorporated into the Global Observation Research Initiative in Alpine Environments (GLORIA) project, which was founded in 2001 to monitor vegetation and climate in target high elevation regions worldwide (Mark et al., 2006). The Haleakalā Climate Network (HaleNet), established in 1988, monitors 13 climate variables at eight stations along two transects (windward and leeward) in Haleakalā National Park from 960 to 2990 m elevation (Longman et al., 2015b). The 30-plus years of data gathered here provide an invaluable monitoring dataset for the State of Hawai'i. Other alpine areas, however, are severely lacking climate information. Additional monitoring and research are needed to better understand the sensitivity of these diverse ecosystems to the simultaneous threats of climate change, invasion, and human-driven degradation.

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Deserts: Life in the Extremes

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Abstract

Deserts are biodiverse places where life thrives in the extremes. Deserts cover roughly one-third of the Earth's surface, exist on every continent and in hot (subtropical), cool coastal, and polar climates (the Arctic and Antarctica deserts are covered in the Polar Biome section). Eleven of the world's largest (> 50,000 km²) deserts are in Asia, 7 in Australia, 5 in North America, and 2 each in Africa and South America. Deserts are biodiverse places with many endemic life forms uniquely adapted to some of the most extreme terrestrial environments on Earth. Many species are threatened by agriculture and aquaculture, energy development, desertification, unabated collection of plants and seeds for horticulture and private ornamental collectors, livestock overgrazing, invasive plants, off highway vehicles, and climate change.

What Are Deserts and Where Are They Found?

With annual rainfall < 25 cm, deserts are dry for most of the year. Deserts cover roughly one-third of the Earth's surface, spanning polar, subtropical, temperate, and cold climates. Most of the world's subtropical-hot deserts occur from 20 to 35 degrees north and south of the equator with temperate deserts at mid latitudes. While there are different climatic classification schemes for grouping deserts (e.g., Köppen climate classification BWh, BWk, BWn; <https://www.britannica.com/science/Koppen-climate-classification>), in this section, we cover hot (subtropical), cool coastal, and cold winter deserts (Table 1, Fig. 1). Polar deserts (Arctic, Antarctica) are in the Polar Biome section. We focused on a reasonable representation of the Desert Biome globally with all articles following broad topical themes such as biodiversity, conservation importance, status, and management needs.

In general, the movement of air masses that rise and compress moisture over vast areas create dry conditions for deserts to persist. But not all deserts are in the dry interior of continents. Some like the Namib in Africa and Atacama in Chile are coastal; this generally is due to air masses lacking moisture associated with cold oceanic currents. In sum, 11 of the world's largest (> 50,000 km²) deserts occur in Asia, 7 in Australia, 5 in North America, and 2 each in Africa and South America (Table 1, Fig. 1). Smaller deserts, while important ecologically, are also covered in this section. For example, the Baja is addressed here, but could also have been placed in the larger Sonoran region. However, we kept the Sonora as a separate region because of the restricted distribution of Saguaro cactus (*Carnegiea gigantea*), the main indicator species found only in the United States.

Deserts Are Biodiverse Places

If you know where and when to look, deserts are teeming with life (<https://www.conservationmagazine.org/2015/03/deserts-teem-with-biodiversity-if-you-know-where-to-look>). While they are places often with very sparse vegetation, desert occupants are uniquely adapted to low moisture, extreme temperatures (e.g., hot in the day, cold at night; winter in places), and scarcity of resources (mainly water). There are numerous endemic plants (e.g., cacti of the Chihuahua, Sonoran, and Baja deserts) and many specialized animals (especially reptiles and invertebrates) that thrive under these conditions.

Witness the largest cactus in the United States, the Saguaro (Fig. 2). Its ridge-like "skin" (outer surface) is covered with a thick waxy layer that serves to reduce water loss from evapotranspiration. Remarkably, the surface contracts and expands with the availability of water. Thorny hard spines ("leaves") with reduced surface area prevent evaporative loss. To get at subsurface water, the Saguaro sends out a single tap root that descends like a giant straw to nearly 2 m. Additional root masses nearer the surface soak up rainfall during periodic monsoons.

Many desert animals are nocturnal, escaping extreme diurnal heat by burrowing into the soil or sand (e.g., numerous reptiles, rodents, and arthropods). Some take advantage of brief periods when water is available (e.g., monsoon and flash floods). Sonora desert toads (*Bufo alvarius*), for example, emerge from their summer burrows (or rodent holes) during wet periods to reproduce.

Table 1 World's largest deserts (>50,000 km²) grouped by regions.

Name	Type	Area (km ²)	Region
Saharan	Subtropical	> 9 million	North Africa
Kalahari	Subtropical	900,000	South Africa
Arabian	Subtropical	2.3 million	Western Asia
Gobi	Subtropical	1.3 million	Eastern Asia
Syrian	Subtropical	520,000	Western Asia
Karakum	Cold winter	350,000	Central Asia
Kyzylkun	Cold winter	300,000	Central Asia
Taklamakan	Cold winter	270,000	Central Asia
Thar	Subtropical	200,000	South Asia
Daht-e Margo	Subtropical	150,000	South Asia
Registan	Subtropical	146,000	South Asia
Dasht-e Kavir	Subtropical	77,000	South Asia
Dasht-e Kavir	Subtropical	52,000	Central Asia
Patagonian	Cold winter	620,000	South America
Atacama	Cool coastal	140,000	South America
Great Basin	Cold winter	492,000	Western North America
Chihuahuan	Subtropical	450,000	Western North America
Colorado Plateau	Cold winter	337,000	Western North America
Mojave	Subtropical	310,000	Western North America
Sonoran	Subtropical	124,000	Western North America
Great Victoria	Subtropical	348,750	Southwestern-Central Australia
Great Sandy	Subtropical	267,250	Northwestern Australia
Tanami	Subtropical	184,500	Northcentral Australia
Simpson	Subtropical	176,500	Northeastern-Central Australia
Gibson	Subtropical	156,000	Westcentral Australia
Little Sandy	Subtropical	111,500	Westcentral Australia
Strzelecki	Subtropical	80,250	Southcentral Australia

Source: https://en.wikipedia.org/wiki/List_of_deserts_by_area. For global map of these areas see <https://upload.wikimedia.org/wikipedia/commons/e/e2/Deserts.png>. For additional desert locations see <https://www.infoplease.com/world/world-geography/principal-deserts-world>.

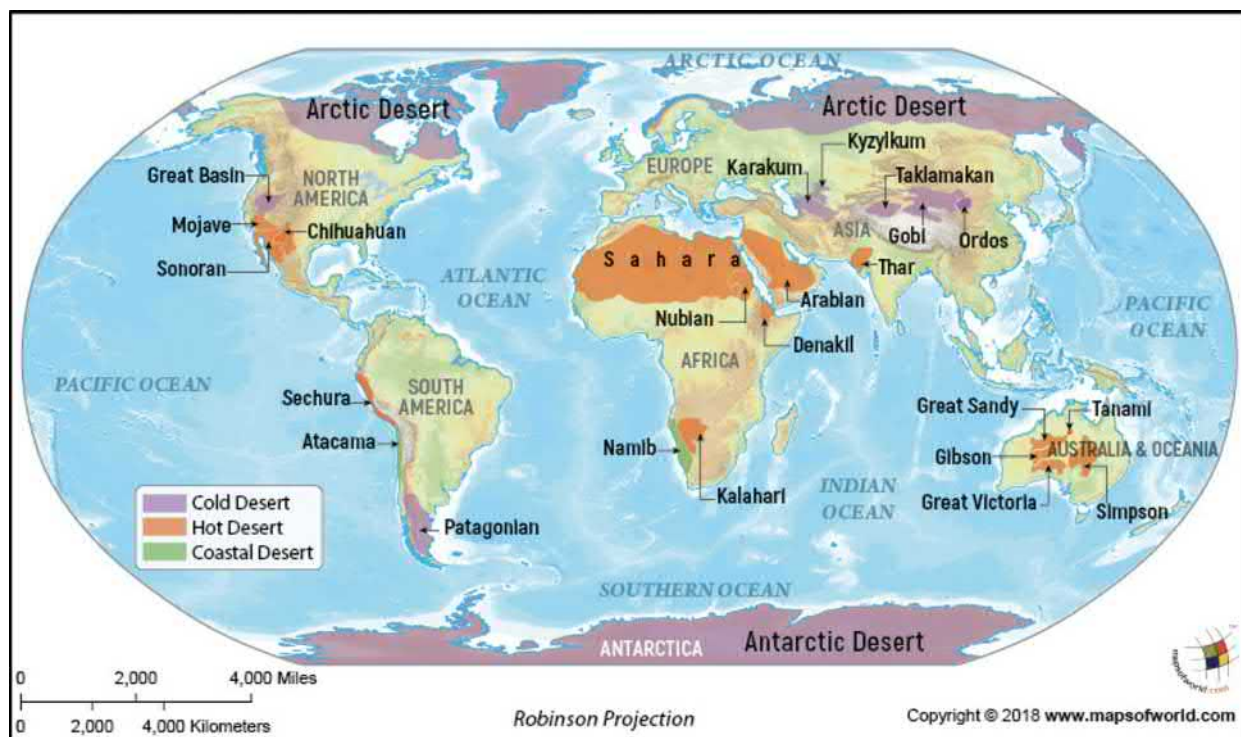


Fig. 1 Continental distribution of world's largest deserts (www.mapsofworld.com). Note: different datasources were used for **Table 1** and **Fig. 1** and thus there are differences in the table compared with the figure.



Fig. 2 Saguaro of the Sonora desert. Note the surface ridges on the Saguaro cactus (left of center) (photo: Julia Sittig with permission).



Fig. 3 The highly adaptable desert camel, Mauritania region (photo: with permission, JC Brito, this section).

Contrary to popular belief, the “hump” of the camel (e.g., *Camelus dromedaries*, **Fig. 3**) does not store water but rather is a reservoir for energy-rich fat important when food is scarce.

When and where water appears, the desert comes to life with a kaleidoscope of flowering plants (e.g., see great Atacama bloom of > 200 flowering plants—<https://www.nationalgeographic.com/news/2017/08/chile-atacama-desert-wildflower-super-bloom-video-spd/>; <https://www.thisischile.cl/the-desert-in-bloom-a-natural-wonder/?lang=en>) producing abundant nectar for a profusion of pollinators. Endemic species like the desert pupfish (*Cyprinodon* spp.) are restricted to rare desert oases (Quitobaquito springs). In other places, tiny rock ponds, called *gueltas* in Mauritania (Sahara-Sahel; northwest Africa), can be as small as 100 m² but function as localized biodiversity “hotspots” (Vale et al. 2015). Ephemeral ponds (**Fig. 4**) provide watering holes for thirsty animals and reproduction sites for insects and amphibians on a short-life cycle clock before the holes dry out.

Some deserts are also noted for their distinguishable sand dunes (**Fig. 5**). Carnivores such as the brown hyaena (*Hyaena brunnea*), also known as the strandwolf, are the rarest of hyaena species (listed as nearly threatened by IUCN red list citation) in African deserts (**Fig. 6**). The largest remaining population is in the southern Kalahari and coastal southwest Africa.



Fig. 4 Two images of “guelta” (pocket of water forming in drainage canals/waids) from Sahara region (photo: with permission, JC Britto, this section).

Benefits and Uses of Deserts

Deserts have historically provided homes for human settlements as they do today with >1 billion people that call deserts their homeland (<https://www.nationalgeographic.com/environment/habitats/deserts/>). According to the UN, nearly half of the world’s population in 2030 will be living in areas of high water stress under threat of climate change (https://www.un.org/en/events/desertification_decade/whynow.shtml).

This is critically important as most desert inhabitants live in developing countries in poor economic and social conditions exacerbated by land degradation and difficult access to water and food (<https://en.wikipedia.org/wiki/Desertification>) that will only intensify in a changing climate.

Notably, German particle physicist Gerhard Knies calculated that in 6 h, the world’s deserts receive more energy from the sun than humans consume in a year. An $\sim 21,000 \text{ km}^2$ stretch of Saharan desert—an area the size of Wales—could power all of Europe. With water present, deserts provide countless agricultural products. Some examples of crops grown include melons, apples, green onions, cucumbers, corn, peppers, radishes, carrots, cabbage, soybeans, pears, tomatoes, squash, spinach, date palms, and alfalfa (for livestock). Desert salts also contain important minerals such as gypsum, borates, nitrates, potassium and other salts exposed when water dries up. From a recreation standpoint, many desert canyons are known worldwide for their exceptional white-water rafting and hiking opportunities and for visiting archeology sites to learn about civilizations (Fig. 7A and B).



Fig. 5 (A) The vast southern Kalahari landscape showing parallel dunes and a dry riverbed (the Nossob) (photo: with permission, G. Mills, this section). (B) Morocco sand dunes (photo: with permission, JC Britto, this section).



Fig. 6 The brown hyaena is the most numerous large carnivore in this area but is rare globally (photo: with permission, G. Mills, this section).



Fig. 7 Recreational and educational desert values: (A) Private Grand Canyon raft trip with Diamond Peak in the background; (B) learning about the archeological findings at the Unkar Delta in the Grand Canyon, including houses, communities, and crops, as described by National Park Service archeologist Greg Woodall (photo: with permission, Michael I. Goldstein).

Conservation Status

Globally, deserts are under enormous pressures (Figs. 8, 9) from land conversion (agriculture and aquaculture, and more recently energy development), unabated collection of plants and seeds for horticulture and private ornamental collectors (e.g., cacti in the Americas), livestock overgrazing (Wuerthner this section), invasive plants (Rogers this section), and climate change (Goettsch et al. 2015). Alarming, 31% of the 1478 cacti evaluated by researchers are threatened with extinction (Goettsch et al. 2015). The entire Cactus family (endemic to the Americas) is on CITES Appendix II, with the most endangered species on Appendix I (<https://www.iucn.org/ssc-groups/plants-fungi/cactus-and-succulent-plants-specialist-group/cites-species>). As reported by IUCN, TRAFFIC North America estimates that between 1998 and June 2001 nearly 100,000 succulents, with an estimated value of \$3 million were taken from Texas and Mexico for the garden market in Arizona.

Many succulents are of interest to the horticulture industry (which artificially propagates them) because of their unusual growth forms and characteristics. They are used for food, fodder, fiber, shelter, medicines (e.g., *Aloe vera*, *Agave*, *Euphorbia* spp., *Dioscorea deltoidea*), oils and cosmetics (e.g., *Aloe*).

As far as grazing pressure in the high-altitude deserts like the Great Basin in North America (Fig. 8), the combination of alien species and more frequent novel fires have transformed much of the native vegetation resulting in extensive biodiversity losses

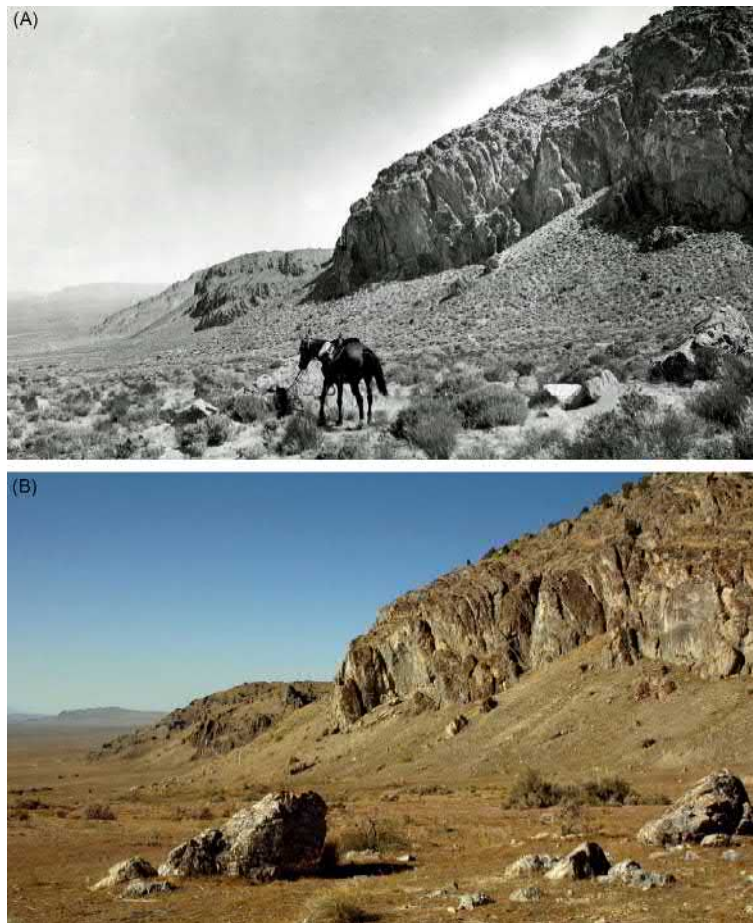


Fig. 8 Matched photographs (A and B) illustrate the loss of native vegetation common in deserts around the world. The first photo (A), taken in 1901 by geologist G. K. Gilbert shows Gilbert's horse Sally (public domain photo) beside a boulder in a salt desert shrubland typical of lower valleys across the Great Basin Desert of North America. The second photo (B), taken in 2008 (photo: with permission, G. Rogers, this section), shows the same location but with few remaining shrubs and only a thin thatch of summer-dried remains of invasive *Bromus tectorum* and other alien annual weeds.

(see Wuerthner this section). Notably, unusually severe fires in Sonora have been devastating to ancient Saguaro cactus that did not evolve with “crown” fires now more prevalent in the system due to the spread of exotic cheatgrass from livestock grazing.

The articles in this section provide a synopsis of the multitude of uses and threats (most are increasing) as summarized in Fig. 9.

Finally, desertification is an expanding threat to many desert systems world-wide that are being impacted by the loss of native plants and increased sandstorms from overgrazing, over farming, and climate change. Efforts are underway in the Gobi desert, for instance, to plant over a billion trees (China's “green wall”) to combat desertification (which is associated with rural poverty); however, this has had questionable results (see <https://www.motherjones.com/environment/2017/08/china-plants-billions-of-trees-in-the-desert/>). Some 119,139 km² of arable land turn to desert every year due to climate change and practices such as forest clear-cutting (<https://worldpreservationfoundation.org/environment/desertification/>, accessed September 6, 2019). Desertification threatens the livelihoods of > 1 billion people in 110 countries (https://www.un.org/en/events/desertification_decade/value.shtml, accessed September 4, 2019), representing an economic loss of US\$42 billion per year.

Conservation Needs

Popular perceptions of deserts are vast wastelands in post-apocalyptic scenarios that you just do not want to be stuck in. But the Desert Biome overall is highly complex; rich in species, rarity, and endemism; and is one of the most misunderstood biomes on the planet.

Deserts in fact are places where nature not only persists but thrives in temporal and spatial hot spots of biological activity. Much of the biodiversity is concentrated in vernal pools and is present during seasonal monsoons that trigger a kaleidoscope of flowering plants, pollinators, and many other species. Deserts are also highly threatened by a host of human activities conspiring with

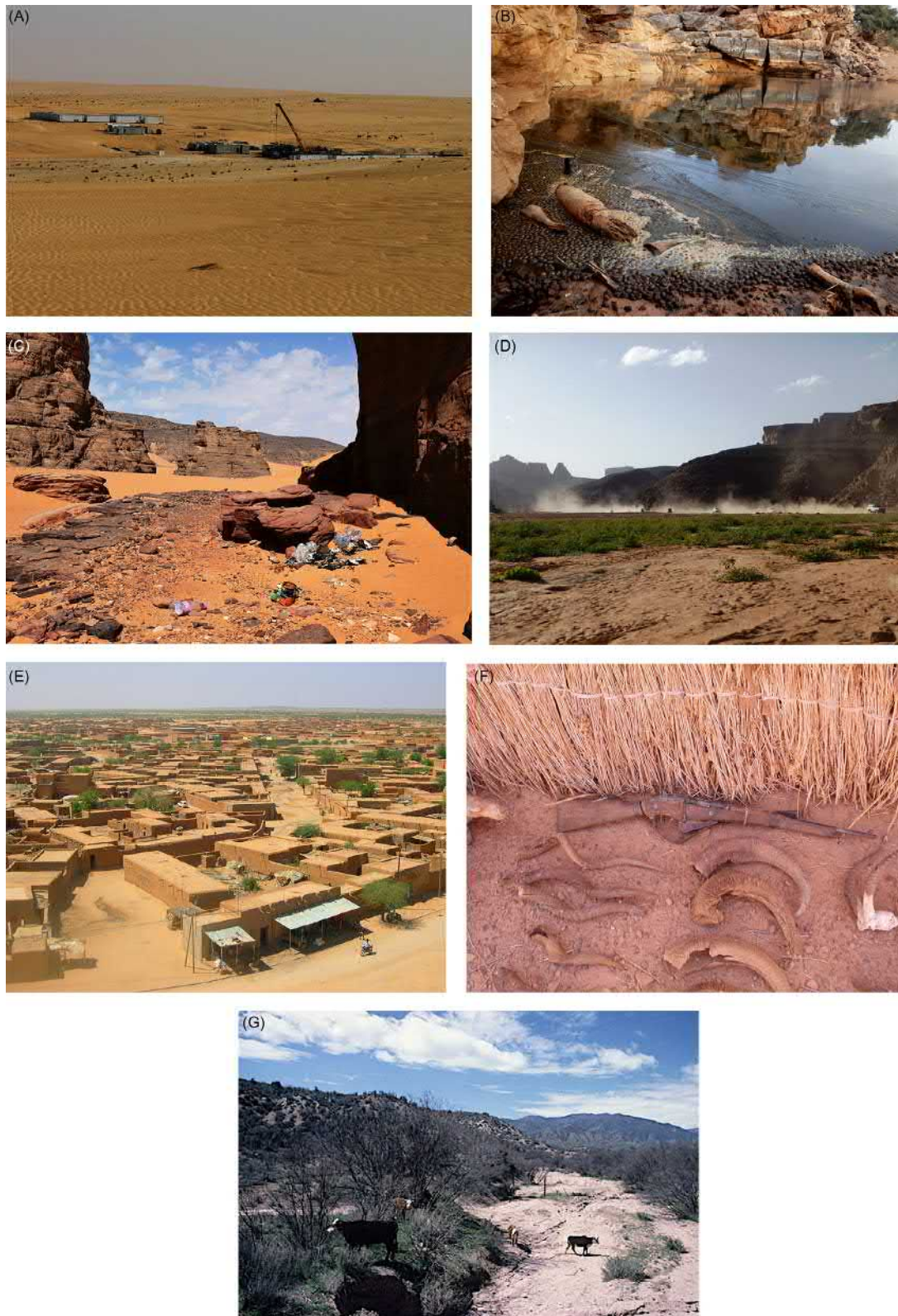


Fig. 9 Threats facing desert systems: (A) oil exploration in Niger; (B) eutrophication from livestock grazing in Mauritania; (C) garbage from excessive tourism in Algeria; (D) road impacts in Algeria; (E) large settlement in Niger; (F) poaching of white antelope *Addax nasomaculatus* and Barbary sheep *Ammotragus lervia* in Mauritania (photos: with permission, JC Brito, this section); and (G) livestock damage (changes in channel morphology, cut bank erosion, loss of native plants) in the Tonto National Forest, Arizona (photo: with permission, G. Wuerthner, this section).

unprecedented climate change that will push much of the biota past a threshold of where not even their unique adaptations will allow them to persist in the more extreme conditions (e.g., temperature/precipitation changes outside climate envelopes). The authors of this volume summarize the unique biodiversity values of their region, threats to persistence of desert features, and conservation needs. For example,

- Smith and Pettorelli (this section) provide a comprehensive introduction to desert ecosystems and conservation challenges.
- Rogers (this section) states that advanced planning and public support are essential for prevention and control of invasive weeds that are altering desert systems globally, creating vast weedy wastelands.
- Mills (this section) describes the arid Kalahari, containing the Kgalagadi Transfrontier Park, as the only functional large carnivore community in an African desert, and possibly anywhere else on earth.
- Santarém (this volume) outline the potential for and limitation of ecotourism in preserving the desert biome while supporting local cultures, traditional livelihoods and sustainable development goals.
- Brito and Pleguezuelos (this volume) discuss how the desert biome comprises highly adapted species, harboring about 25% of continental vertebrate species in places, and how increasing exploitation activities and climate change threaten biodiversity.
- Austin et al. (this volume) provide an overview of one of the most relatively intact high desert ecosystems on Earth, the Northern Great Basin United States, that is under threat from agriculture, livestock grazing, housing and energy development, altered fire regimes, invasives, and loss of riparian systems.
- Malakoutikhah and Hemami (this volume) discuss that despite the extraordinary biological diversity levels in deserts world-wide, only 9–11% of the biome is in protection status with ~7% in protected connected habitat status.
- Wuerthner (this volume) demonstrates how desert regions due to natural aridity, climate extremes, and limited vegetative production are especially vulnerable to impacts from domestic livestock production.
- Laverty (this volume) describes the unique biodiversity found in one of the world's oldest deserts, the Namib Desert, with a focus on the often-overlooked bat community that lives among desert-dwelling megafauna in the Namib's northern reaches.
- Briggs et al. (this volume) describe one of the most biologically diverse and endemic rich deserts, the Chihuahuan, that faces numerous threats requiring a coordinated binational response.
- Vale et al. (this volume) describe species distribution patterns in the Sahara-Sahel where α -diversity (local species number) follows general latitudinal gradients in species richness with high richness also along corridors and refugia while hotspots define β -diversity gradients. Isolated and residual wetlands constitute hotspots in need of conservation.
- Bradley and Colodner (this volume) provide an overview of the Sonoran Desert, one of the most distinctive ecoregions in the world, and its unique biota that are under threat from climate change, invasive species, livestock grazing, land conversion, and the US/Mexico border-wall.
- Nussear and Esque (this volume) discuss the biogeography of hottest and driest of the four North American deserts, the Mojave, its unique species, and conservation challenges in a changing climate with increasing land-use pressures.
- Vanderplank and Ezcurra (this volume) describe the biogeographical patterns and ecological processes that have resulted in high levels of endemism and rarity throughout the deserts of the world.
- Anderson (this volume) describes the potential conflicts and solutions between energy and arid ecosystems as the global quest to transition to renewable energy proceeds.

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<https://databasin.org/maps/7c6012cd4026493585483db7b56ff59c>—Biodiversity hot spots and WWF global 200 ecoregions.
<https://www.nationalgeographic.org/encyclopedia/desert/>—Desert. National Geographic.

Desert Biodiversity—World's Hot Spots/Globally Outstanding Biodiverse Deserts

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Abstract

The desert biome is usually perceived as bare and rather homogeneous area that exhibit relatively low diversity in comparison to other biomes. However, deserts are surprisingly rich, harboring about 25% of continental vertebrate species and comprising highly adapted and specialized species that are found nowhere else. They display high rates of endemism due to the adaptive processes of organisms to the extreme environmental conditions, as well as locally endangered hotspots of biodiversity. Biodiversity is distributed according to the extreme climatic conditions of deserts, and concentrates in mountains, suitable climatic corridors, and in the rare, generally small, and fragile wetlands. Geological events and palaeoclimatic oscillations largely drove the main evolutionary processes, acting over diversification and speciation events mainly through vicariance. Remarkable and unique adaptations for survival in the aridity, heat, and salinity conditions of deserts are found in species inhabiting these environments. Desert biodiversity is currently threatened by increasing human exploitation activities and climate change. Still, deserts classify as one of the last wild biomes on Earth, where implementing conservation actions would be most cost-effective. Long-term conservation of desert biodiversity requires appropriate policy instruments that promote conservation and sustainable use of natural resources. Raising environmental alertness and pride within local communities of the value and uniqueness of the desert wildlife is needed to pressure strong policy change.

Introduction

Deserts, defined by aridity index (average annual precipitation/potential evapo-transpiration) below 0.05, and arid regions, defined by aridity index between 0.05 and 0.20 (Ward, 2016), represent about 41% of the Earth's land surface and are inhabited by 2 billion people. They are distributed at 25–35 degrees latitude in both the northern and southern hemispheres, and cover six biogeographical realms, Afrotropics, Australasian, Indo-Malay, Nearctic, Neotropical, and Palearctic (UNEP, 2006). They are usually perceived by the general public as bare and rather homogeneous areas that exhibit relatively low diversity in comparison to other regions, which results in attracting less global research funding and scientific attention. However, deserts landscapes are rather diverse (Fig. 1): from flat deserts of rock and sand, such as the Sahara, to rocky mountains emerging from lowland sedimentary plains, as in Central Asia or North America (UNEP, 2006). The climatic variations during the Plio-Pleistocene period, with feedback mechanisms between rainfall reduction and vegetation cover, forced world's deserts to contract during cold glacial periods and to expand during the hot interglacial. The last humid period ended between 6 and 5000 years ago, leading to the current warming and aridity trend. These climate and land-cover oscillations have greatly shifted the extent and limits of world's deserts, and regulated biodiversity patterns and evolutionary processes (Brito et al., 2014). Deserts and arid regions are surprisingly rich, harboring about 25% of continental vertebrate species and comprising highly adapted and specialized species that are found nowhere else (Mace et al., 2005). Furthermore, they display high rates of endemism due to the adaptive processes of organisms to the extreme environmental conditions, as well as locally endangered hotspots of biodiversity (Davies et al., 2012; Murphy et al., 2012; Brito et al., 2014; Vale et al., 2015; Rossini et al., 2018). The extreme climatic conditions of these regions generate sharp landscape and ecological gradients that may be associated with the range limits of many species (Brito et al., 2014). These traits make deserts and arid regions excellent natural laboratories to examine the effects of extreme environments on the distribution of biodiversity patterns (Ward, 2016).

Although most deserts and arid regions still classify as one of the last wild biomes on Earth, they are increasingly threatened (UNEP, 2006; Davies et al., 2012), with negative consequences in the ecosystem services provided by these biomes, such as food, energy, water and livelihood security, as well as, the good physical and mental health of individuals and societies living there. Biodiversity is locally threatened by increasing human exploitation activities and progressive aridity conditions (UNEP, 2006; Brito et al., 2016, 2018). Presently, deserts contain some of the most endangered species in the world (Mace et al., 2005; Durant et al., 2014; Khalatbari et al., 2017), while together with arid lands supporting at the same time nearly a quarter of the world's population



Fig. 1 Landscape diversity across the Sahara-Sahel, the largest warm desert of the world. (A) Sand dunes (Nouakchott, Mauritania); (B) Mountains (Elmeki, Niger); (C) rock-pools (Touia, Algeria); (D) Coastal (Boujdour, Morocco). Photograph credits: José C. Brito.

and some of the most poor and vulnerable people (UNEP, 2006). Increasing poverty and frequency of conflicts have been associated with decline of local wildlife in desert biome (Brito et al., 2018). Furthermore, the magnitude and velocity of climate change in deserts and arid regions are predicted to be strong and fast (UNEP, 2006), which will likely cause biodiversity declines and the desert-adapted species may even be the most vulnerable ones with respect to other terrestrial biomes (Vale and Brito, 2015). Climate-related adversities are also likely to spark regional conflict and further biodiversity loss (Brito et al., 2018) associated to fast-growing human population rates and the ethnical fractioned societies that characterize many countries where deserts are found. These threats are causing growing international awareness for desert biodiversity (UNEP, 2006; Davies et al., 2012; Ward, 2016; Brito et al., 2018).

Biodiversity Research in Desert Biomes

Although deserts and arid regions are highly appealing for biodiversity and evolutionary research, their usual large size and remoteness, and in some cases long-term political instability, contribute substantially to a generalized lack of knowledge (Brito et al., 2014). The African Sahara and the deserts of Central Asia are particularly poorly studied. On the contrary, there are multiple institutions dedicated to desert research and/or research facilities implemented to welcome visitors and researchers in the deserts of North America, Australia, and Namibia. These include in North America the Desert Studies Center (California; <http://nsm.fullerton.edu/dsc/>), Desert Research Learning Center (Sonora; <https://www.nps.gov/im/sodn/drlc.htm>), Desert Research Unit (Arizona; <https://snre.arizona.edu/facilities/dru>) and the Desert Research Institute (Nevada; <http://www.dri.edu/>); in Australia the Desert Ecology Research Group (Sydney; <http://www.desertecology.edu.au/>) and Desert Knowledge Australia (<https://www.dka.com.au/>); and in Namibia the Desert Research Foundation (<http://www.drfn.org.na/>) and the Gobabeb Desert Research and Training Centre (<http://www.gobabebtrc.org/>). The 50 years of work being developed at Gobabeb have allowed gathering a remarkable body of knowledge on multiple subjects, from vegetation ecology to herptile diversity and distribution.

The research efforts in desert environments have increased exponentially over the last decades (Fig. 2). Research is now developed using contemporary tools and analytical processes, including molecular (DNA sequencing and genotyping) and

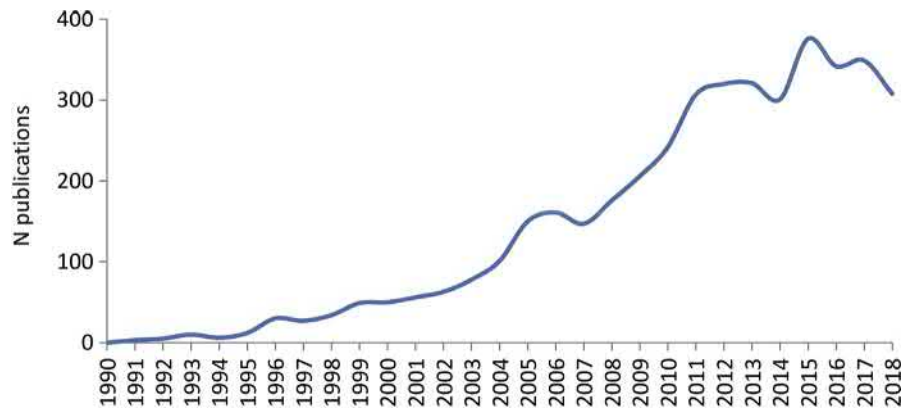


Fig. 2 Yearly evolution of the number of papers listed in ISI-Web of Science (assessed November 27, 2018) since 1990 with the keywords Desert* and Biodiversit*.

geomatic (Global Navigation Satellite Systems and Geographical Information Systems) tools. Together with broad sampling of taxa, a growing body of studies are starting to reveal and mapping patterns in the distribution of biodiversity, including local hotspots of biodiversity and cryptic diversity, as well as to provide insights on the evolutionary history of multiple taxa, including information on the causes, timing and patterns of radiation and divergence (Brito et al., 2014). Still, these studies are also revealing gaps on these topics and exposing severe threats to biodiversity conservation.

Desert Biodiversity in Numbers

Deserts and arid regions accumulate at least 7000 species of amphibians, reptiles, birds and mammals, of which about 1000 are endemics, distributed in 300 families (Mace et al., 2005). These estimates are remarkably close to the figures displayed by other biomes known to have high levels of species richness, such as tropical grasslands and tropical dry forests. The Sahara-Sahel alone gathers 1147 terrestrial vertebrates, of which 125 are endemics (Brito et al., 2016). Deserts and arid regions are home to 80% of the mammals, birds, and amphibians of North America, around 70% in Europe, Asia and North Africa, and 60% in sub-Saharan Africa and Latin America (Davies et al., 2012). They also support iconic plant groups, such as the cacti and succulents, trees such as Acacia and Baobab, and many of the world's grassland species.

While some deserts display low species richness per unit area, especially the hyper-arid areas of the Sahara, Central Asia or Central Australia, other areas exhibit relatively high levels of species richness, such as the African Sahel, Coastal Arabia or the North American grassland plains, or even exceptionally high number of species per unit area, such as the arid and dry sub-humid areas in the Andes (Davies et al., 2012; Ward, 2016). The African Sahara-Sahel, the Arabian Peninsula and Australian deserts have been shown to display a significant high number of reptiles, especially lizards, in comparison to other tetrapods. Some deserts are particularly rich in endemic phylogenetic lineages, such as the North American deserts for terrestrial mammals, or display high phylogenetic diversity in comparison to the observed species richness, such as the African Sahel for terrestrial birds.

Phylogeographic studies using molecular markers are uncovering additional cryptic diversity in multiple taxonomic groups across world's deserts (Murphy et al., 2012; Brito et al., 2014 and references therein; Silva et al., 2017; Šmíd et al., 2017; Gonçalves et al., 2018a,b; Velo-Antón et al., 2018). In some cases, molecular phylogenies are supporting the splitting of previously considered wide-ranging species (Murphy et al., 2013; Brito et al., 2014 and references therein; Šmíd et al., 2017). Taken together, these studies suggest that the diversity in deserts is still largely underestimated and they are changing completely the perceptions on biodiversity distribution patterns in deserts (Brito et al., 2014, 2016). The predominant idea that deserts accumulate few species with large distributions is being increasingly replaced by evidence showing that larger numbers of species are present and that in some cases they display narrower ranges, often limited to local hotspots of biodiversity (Murphy et al., 2013, 2015a; Vale et al., 2015; Rossini et al., 2018).

Biodiversity Patterns in Desert Biomes

The knowledge of biodiversity distribution in world's deserts is highly biased towards North America and Australia (Fig. 3). The availability of biodiversity distribution data in the Sahara-Sahel, the Horn of Africa, the Arabian Peninsula, and Central Asia is scarce in relation to other global deserts (and biomes). The central portions of these deserts are the most under-sampled areas, which is related to their restricted accessibility and in some cases to the occurrence of armed conflicts (Brito et al., 2014, 2018). For instance, the south of the Arabian Peninsula, the Irano-Anatolian region, and the Central Asian mountains have been shown to potentially display higher reptile richness than currently known and to represent knowledge gaps in the biodiversity distribution. In fact, there

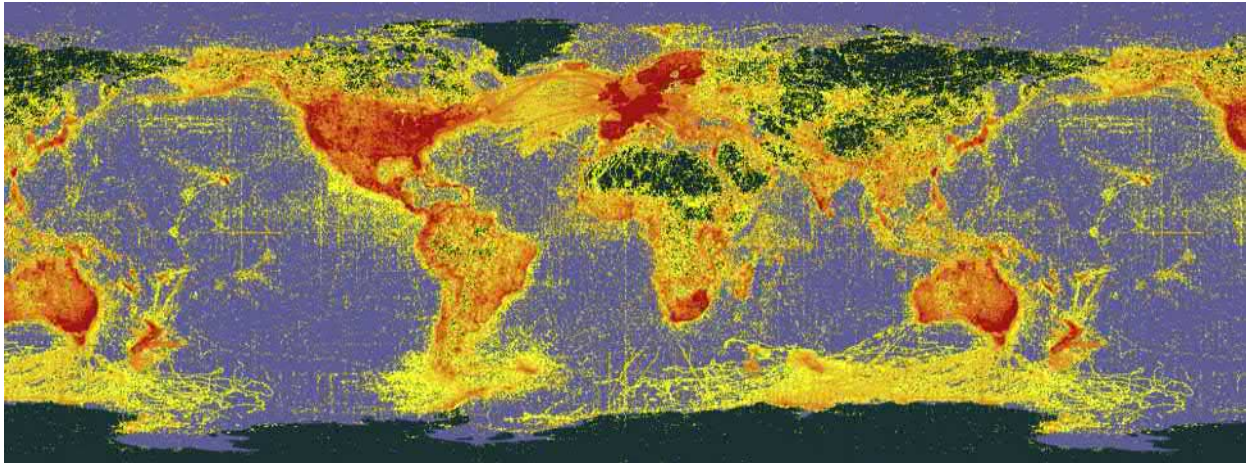


Fig. 3 Distribution of the 1,038,666,838 occurrence records (assessed in 27/11/2018) at the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>).

are very few comprehensive and recent distribution atlases available for desert biodiversity, which hampers the identification of regional biodiversity hotspots and optimized conservation planning.

Despite the broad knowledge gaps, multiple patterns emerge in the distribution of biodiversity in deserts and arid regions:

- (1) Biodiversity is not randomly distributed. For instance, the distribution of terrestrial vertebrates in the Sahara-Sahel is spatially structured and apparently it is related to environmental variation: ten biogroups (species assemblages with shared distributions) were identified and wide-range biogroups tend to overlap in specific climate regions (Brito et al., 2016). In Australia, five major *Acacia* biogeographical regions were identified and these match with other bioregionalization exercises. The differences in community composition of aquatic invertebrate communities in Western Australia are associated to the spatial configuration of the dendritic network and to the regional topographic complexity interplaying with local environmental conditions. A global comparison of the distributions of 5000 mammals showed that both high life-history trait diversity and phylogenetic beta diversity are found in deserts and arid regions, and that this diversity is probably related to the environmental heterogeneities of this biome.*****

The increasing use of ecological niche-based models is indicating that biodiversity distribution in deserts can be associated with multiple environmental factors (Brito et al., 2014 and references therein). The distribution of multiple species has been tightly linked to geographical variation in rainfall and temperature (Wilson and Pitts, 2012; Silva et al., 2017; Gonçalves et al., 2018a,b; Rossini et al., 2018; Velo-Antón et al., 2018). In the Australian arid zone, there is asynchronous demographic responses in fecundity, recruitment, and survival of reptiles to rainfall and temporal variability in temperature, during and prior to the breeding season. The geomorphic landform surface composition of the Mojave Desert was shown to be associated with habitat suitability in reptiles. Human activities have also been associated with the distribution, range contraction and population dynamics of large-sized mammals, such as cheetah and gazelles in Southwest Asia (Khalatbary et al., 2017);

- (2) Mountains in deserts constitute refugia for biodiversity particularly for aquatic and mesic species (Brito et al., 2014, 2016 and references therein), and supporting examples are found in multiple taxa (e.g., Šmíd et al., 2017; Gonçalves et al., 2018a). Given the general remote and inaccessible characters of mountains, they also tend to constitute major refugia for threatened large ungulates and carnivores (Brito et al., 2016, 2018). In the Sahara-Sahel, mountains accumulate a significant portion of the regional endemic species and contain many isolated populations of vertebrates of non-Saharan origin (Brito et al., 2016). These populations usually persist in isolated populations restricted to humid habitats and their surroundings and their presence has been associated with temporal distribution shifts linked to Plio-Pleistocene climate fluctuations (Brito et al., 2014 and references therein);
- (3) High biodiversity levels are found along ecological corridors. in deserts and arid regions. In some cases, these corridors are remnants of savannah-like habitats that covered deserts during past humid periods. In the Sahara-Sahel, those corridors have been hypothesized to follow a North-South axis, along the Atlantic and the Red Sea coastal areas, and the Central Sahara mountains (Brito et al., 2014). In the former regions, the mild climate influenced by the proximity of the sea is likely to be related with current high biodiversity levels observed (Gonçalves et al., 2018b; Velo-Antón et al., 2018). Dispersal corridors are linked to the occurrence of secondary contacts during the Pliocene between differentiated lineages of lizards in Australia;
- (4) Given the high aridity levels that characterize deserts high concentrations of species richness are found around the rare wetlands. Oases in sand-seas are crucial for plant, animal, and human subsistence and constitute refugia for multiple aquatic species around the most extreme arid areas (Fig. 4). The spring complexes of the Great Artesian Basin (GAB) in the arid and semiarid regions of eastern Australia constitute exceptional biodiversity hotspot, where 75 of the 326 spring complexes accumulate up to 96 species and subspecies of fishes, mollusks, crustaceans and plants endemic to these springs, and most of the endemics are limited to small and individual spring complexes (Rossini et al., 2018). Molecular studies done with



Fig. 4 Wetlands in deserts constitute local biodiversity hotspots. (A) Hamdoun rock-pool, Mauritania; (B) Umm al Maa lake, Libya; (C) Ounianga Serir lake, Chad; (D) Bilma oasis, Niger. Photograph credits: José C. Brito.

amphipods at the local scale in the Lake Eyre GAB show consistent patterns: pronounced genetic diversity was identified indicating that the levels of endemism in amphipods still need better estimation, many taxa (species and Evolutionarily Significant Units) have highly restricted distributions and are endemic to few springs (Murphy et al., 2013). Mountain rock pools have been identified as local biodiversity hotspots in Sahara-Sahel mountains (Brito et al., 2014 and references therein). Studies in Mauritania have uncovered a system of pools sparsely distributed in temporal riverbeds in mountains that allow the maintenance of rich communities, with many endemic species, and that act as refugia to relict Afro-tropical fauna (Vale et al., 2015). In 69 pools examined, with a mere aggregated extent of 43 ha, they hold about 32% and 78% of the total and endemic fishes, amphibians, reptiles and mammals of Mauritania, respectively. A spectacular example of the biodiversity value of these pools is the presence of crocodiles (*Crocodylus suchus*) in about 100 Mauritanian pools (Fig. 5). Dispersal events between specific pools during the rainy season have been recorded and these are likely related with the distribution of hydrographic basins, water availability patterns, and local human pressures, as well as with the patterns of population structuring found;

- (5) The vast empty-quarters (unpopulated areas) and dune massifs are crucial refugia for threatened species. In the Sahara-Sahel, although these regions exhibit overall low species richness, they accumulate most of the threatened taxa, including birds, large ungulates, and carnivores that suffered extreme declines in other regions because of direct persecution (Brito et al., 2014, 2016, 2018).

Evolutionary Processes in Desert Biomes

Current biodiversity patterns in deserts and arid regions are the result of millions of years of geological events and palaeoclimatic oscillations across Earth. The appearance of the first deserts certainly posed challenges to the survival of species dependent on humid habitats, but also opened up opportunities for diversification in species with tentative adaptations to arid environments. For instance, the increased aridity that followed the onset of the Sahara-Sahel presumably acted mainly as a North-South vicariant feature and it has been linked with diversification processes for several species and to allopatric effects (reviewed in Brito et al., 2014).

The palaeoclimatic oscillations have greatly shifted the climate and land-cover, and in consequence the limits of deserts. For instance, during the Last Glacial Maximum (LGM), the northern limits of world's deserts tended to be colder and more humid in

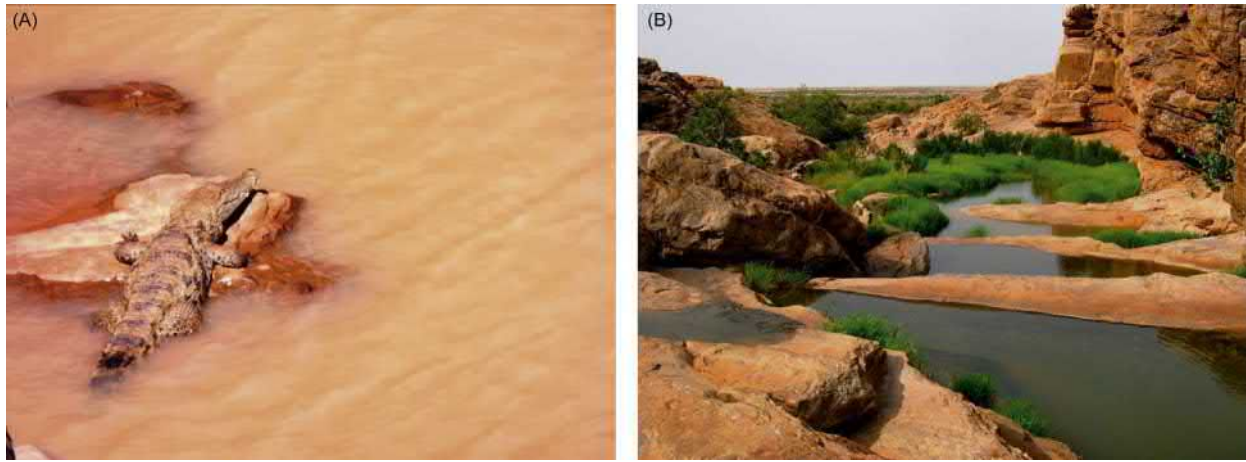


Fig. 5 West African crocodile (*Crocodylus suchus*) is one of the many Afro-tropical relicts persisting in isolated rock pools of Mauritania (A) adult crocodile basking in Tartêga; (B) habitat in mountain canyon, Garaouel. Photograph credits: (A) Frederico Santarém; (B) José C. Brito.

comparison to the present time, whereas the southern tropical limits were generally drier than in the present time (UNEP, 2006). In response to these climate characteristics of the LGM, the Mediterranean areas of North Africa became wetter and colder, while large dune systems developed along the southern Sahara-Sahel region and in the Thar Desert of India. The magnitude and extent of these range shifts in desert limits, as well as the onset age were distinct across the world's deserts. For instance, in Africa, the Namibe desert is very old (c.55 million year or even older; Ward, 2016) and its range has been rather stable throughout time. On the contrary, the Sahara is more recent (c.7 million year or even younger) and its range has largely shifted in result of rather frequent and intense oscillations between dry/humid periods, following cycles of approximately 100,000–20,000 years during the last million years. These differences in the temporal and spatial variation of desert onset and extent had dramatic consequences over biodiversity distribution patterns (Brito et al., 2014; Ward, 2016). For instance, there was a burst in the development of woodlands of pinyon pines, junipers, and oaks in the Chihuahuan Desert of North America during the late Pleistocene, while the increasing drier conditions in the tropical dry woodlands of central Mexico created the environmental conditions for the evolution of the rich cactus flora that characterizes the region today (UNEP, 2006).

Geological events and palaeoclimatic oscillations largely drive the main evolutionary processes, acting over diversification and speciation events. For instance, molecular dating indicates that the changing climate at the beginning of the Pliocene, from hot and dry to cold and humid, is likely responsible for increased speciation in *Hemidactylus* lizards in the Arabian Peninsula (Šmíd et al., 2017), and the Pleistocene climate oscillations where associated with range expansion and contraction in the velvet ant *Sphaerophthalma difficilis* that led to the formation of genetically distinct populations inhabiting distinct arid regions in the North American deserts (Wilson and Pitts, 2012). The main driver of speciation in the world's deserts is vicariance, when considering a neutral scenario where adaptation processes are discarded. During vicariant events, the geographical separation and isolation of a subpopulation from the original population results in the interruption of gene flow, which ultimately promotes divergence within the original species and differentiation as evolutionarily independent lineages or new species (Fig. 6). In the Sahara-Sahel, it has been shown that ecological traits and habitat requirements play a key role in the timing and nature of the vicariant effects (Brito et al., 2014). In xeric species, adapted to arid environments, the diversification events occurred during the humid periods, followed by range expansions during the dry periods (e.g., Velo-Antón et al., 2018). Conversely, in mesic species, adapted to arid conditions but requiring some level of moisture, the diversification events occurred under hyper-arid conditions when they suffered range contraction into suitable fragmented areas, such as rocky massifs and mountain ranges (e.g., Gonçalves et al., 2018a,b). During humid periods, mesic species may experience population expansions from areas of refugia. The cycles of population expansion during suitable climatic conditions and population contraction during harsh climate conditions have translated into opposing patterns: dispersal along corridors that facilitated gene flow and possibly secondary contact during suitable climatic periods (e.g., Gonçalves et al., 2018a; Velo-Antón et al., 2018), and divergence in the absence of gene flow in refugia and speciation (e.g., Šmíd et al., 2017; Gonçalves et al., 2018b) during unsuitable climatic periods.

Water-dependent species inhabiting deserts are particularly susceptible to climatic oscillations and to water availability. During wet periods, gene flow among populations occurs continuously along permanent or temporary rivers, and during the dry periods these species become extinct or isolated in small wetlands (oases and springs). As expected, divergence events occurred during hyper-arid periods. For instance, the formation of deserts around Lake Eyre in the early Pleistocene led to the hydrological isolation of spring complexes in the GAB and was associated with significant molecular divergence in hydrobiid freshwater snails of genus *Trochidrobina*, supporting the “trapped in desert springs” hypothesis for the diversification of intraspecific lineages in the Australian desert (Murphy et al., 2012). The effects of the dynamics of water availability in promoting diversification events of aquatic species are particular evident in the Lake Eyre, resulting in extraordinary levels of micro-endemism in chiltoniid amphipods: over 13 genetically divergent lineages were recognized as Evolutionarily Significant Units, all of which could be considered as separate

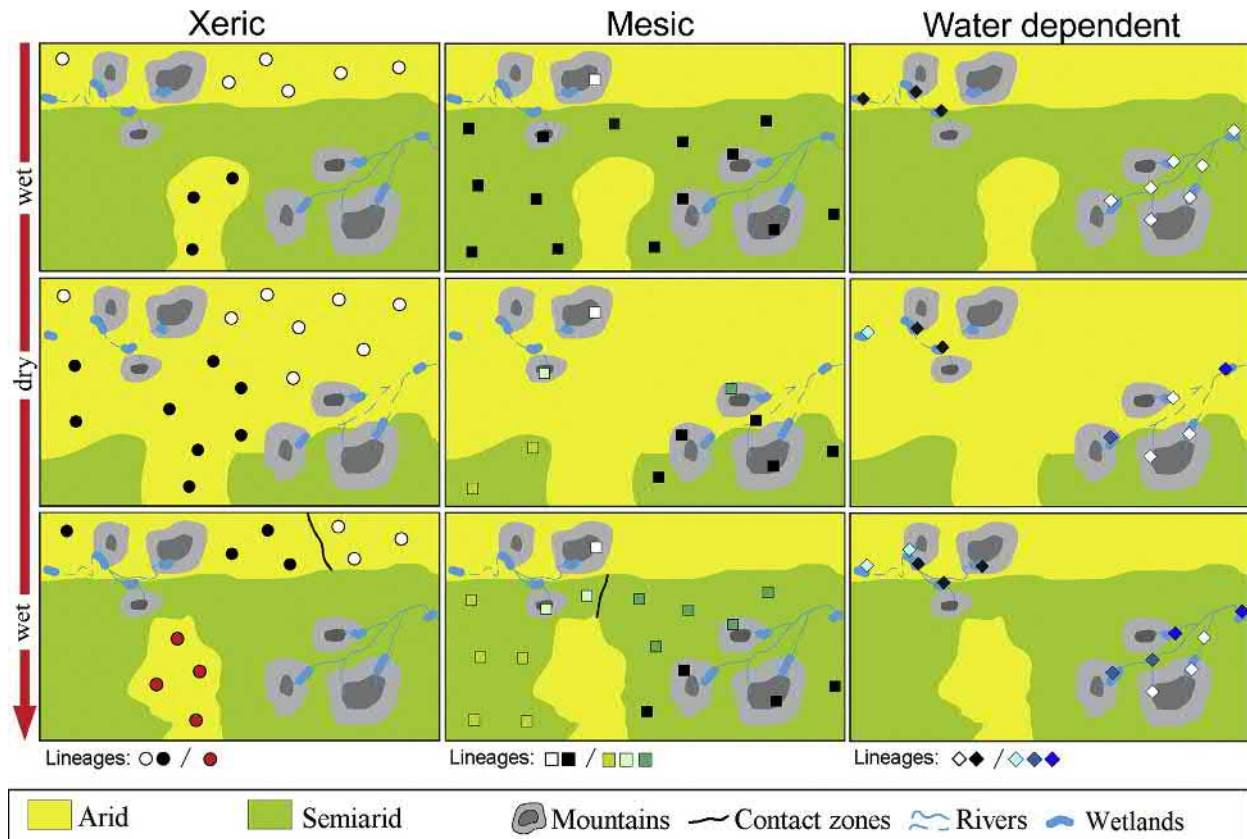


Fig. 6 Schematic representation of hypothetical diversification mechanisms through allopatric processes expected in three types of species: xeric (circles), mesic (squares) and water-dependent species (diamonds). Along the time-series of climatic cycles (from top to bottom), there is expansion of semiarid environments (green) during wet periods, alternated with expansion of arid environments (yellow) during dry periods. The cycles of range expansion-contraction promote the emergence of new lineages (colors) and subsequent contact zones between lineages (black lines). Adapted from Brito, J.C., Godinho, R., Martínez-Freiria, F., Pleguezuelos, J.M., Rebelo, H., Santos, X., Vale, C.G., Velo-Antón, G., Boratyński, Z., Carvalho, S.B., Ferreira, S., Gonçalves, D.V., Silva, T.L., Tarroso, P., Campos, J.C., Leite, J.V., Nogueira, J., Álvares, F., Sillero, N., Sow, A.S., Fahd, S., Crochet, P.-A. and Carranza, S. (2014). Unravelling biodiversity, evolution and threats to conservation in the Sahara-Sahel. *Biological Reviews* **89**, 215–231.

species (Murphy et al., 2013). Climatic oscillations also impacted the hydrological networks and consequently population connectivity, which might prompt vicariant processes, as suggested in Lake Chad and in the Nile River. Landscape connectivity of aquatic fauna in deserts, mostly in fishes and invertebrates in the deserts of Australia and North America, has been shown to decline with increasing geographic scale and to be highly dependent in species dispersal abilities and hydrological connectivity (Murphy et al., 2015b).

Refugia during harsh climatic conditions are pivotal for diversification events in world's deserts. Mountains and wetlands provide persistence areas during periods of unsuitable climatic conditions and then facilitate gene flow during suitable climatic conditions (reviewed in Brito et al., 2014). For instance, the Colorado Plateau and parts of the Great Basin Desert of North America were shown to be refugia during Pleistocene climate conditions for velvet ants, and many other taxa (Wilson and Pitts, 2012). In the case of long-term allopatric isolation in mountains during harsh climatic conditions, divergence and speciation events were observed in *Agama* lizards of the Sahara-Sahel (Gonçalves et al., 2018b) and the topographically complex mountains of southwestern Arabia were associated with a significant radiation in *Hemidactylus* geckos, by allowing multiple allopatric speciation events to occur in relatively small areas (Šmíd et al., 2017). During suitable climatic conditions, mountain populations are at the origin of several episodes of range expansion, promoting the occurrence of gene flow events between previously isolated populations. A spectacular example comes from the desert springs of the Lake Eyre of Australia, which work both as refugia for several endemic faunal groups (isopods, amphipods, ostracods, snails, and beetles) that diverged into multiple lineages before the formation of present-day deserts, and as evolutionary cradles of future biodiversity hotspots by allowing the diversification of novel endemic fauna during isolation periods (Murphy et al., 2015a).

Adaptations to Desert Biomes

Life originally evolved in water and water is the most fundamental element for the survival of almost all living organisms. The imposition of desert conditions forced plants and animals to deal with unpredictable spatial and temporal limitations in water and food resources, and extreme temperatures and solar radiation during the day. As such, organisms inhabiting the world's deserts have either developed unique adaptive features and/or behavioral adaptations to cope with the harsh environmental conditions. For instance, most of the desert-dwelling species tend to avoid exposure or activity during the hottest and driest parts of the day and year. An extreme and most effective way of dealing with harsh desert conditions is the evolution of ephemeral life-cycles, characterized by short-life cycles and resistant propagation forms, found in plants and many invertebrates, such as in the Tadpole shrimps of genus *Triops* (Fig. 7). Many annual plants are able to thrive in deserts by germinating immediately after the rainy season and completing their life-cycles before the onset of the dry season (Ward, 2016).

The most remarkable and unique adaptations for survival in the aridity, heat, and salinity conditions of deserts are found in xeric species, inhabiting the environments where water availability is most scarce (UNEP, 2006). In plants, these include deep root systems in trees and shrubs to exploit deep aquifers, and different gas exchanges levels (with less stomatal control of water loss), leaf shedding periods, and leaf sizes and positions to cope with droughts (Ward, 2016). In animals, these include morphological adaptations related to size and shape that enhance fitness by controlling heat gains or water losses. For instance, larger body size evolved as response to avoid over-heating by increased thermal inertia (when evaporative cooling is not possible) or elongated bodies, wedge-shaped heads and limb reductions evolved multiple times in sand-diving species, such as in the Sandfish of genus *Scincus* (Fig. 7; Brito et al., 2014; Ward, 2016). To minimize body contact with the burning ground surface and to allow to use and to travel fast across open and loose microhabitats, specialized mechanisms of locomotion evolved: the sidewinding locomotion in the case of the Horned vipers of genus *Cerastes* and the bipedalism in the case of small desert mammals, like the Jerboa of genus *Jaculus* (Fig. 7).

Physiological adaptations also evolved, allowing the survival under conditions of low water availability, high heat, or excessive salt. For instance, reduction of resting metabolic rate evolved multiple times allowing more efficient conservation of energy and water, and long retention time of fluid in the gastrointestinal tract has allowed the reduction of overall energy turnover and lowering



Fig. 7 Examples of animals with specific adaptations to the environmental conditions of deserts. (A) Tadpole shrimp (*Triops mauritanicus*), Mauritania; (B) Sandfish (*Scincus albifasciatus*), Mauritania; (C) Desert horned viper (*Cerastes cerastes*), Morocco; (D) Jerboa (*Jaculus* sp.), Mauritania. Photograph credits: José C. Brito.

the metabolic rate. In some extreme cases, particular adaptations to aridity evolved, allowing even large sized species to persist in environments without water availability, such as the case of the Addax (*Addax nasomaculatus*) inhabiting vast empty quarters of the Sahara desert.

Most of the world's deserts have originated in distinct time periods and have developed in relative isolation from each other (UNEP, 2006). As such, many of the life forms currently inhabiting deserts have evolved from different ancestral forms. The remarkable cases of convergent evolution of desert forms across the globe make desert prime natural laboratories to study and understand the processes behind the development of similar morphological forms and other adaptations derived from different ancestors. Presumably, convergent evolution of desert forms is consequence of the similarities in selection pressures placed on these organisms (Ward, 2016). There are multiple examples of convergent evolution in world deserts, from plants to animals (Table 1). The classic example of convergence is the succulent Cactaceae in the Americas and the Euphorbiaceae in Africa, as is the convergence of stem-succulent tree *Aloe* genus in South Africa and stem-succulent *Yucca* genus in North America (Ward, 2016). Another example is found among the sand-diving skinks, which find representatives across the world's deserts sharing striking morphological and behavioral adaptations.

Threats to Biodiversity in Desert Biomes

World deserts are currently threatened by the synergistic effects of two rather recent processes, the human penetration in this biome with exploitation purposes due to increasing demands and climatic change (UNEP, 2006; Davies et al., 2012; Brito et al., 2016, 2018; Ward, 2016). In general, the naturally stressed biota and water scarcity that characterize the desert biome poses environmental challenges to sustainable human development and natural resource use. Deserts do not regenerate quickly and human impacts can remain in this biome for decades. The combined pressures of exerted by urbanization and traffic, farming and overgrazing, water overexploitation and salinization, and natural resource extraction, is leading to the degradation of world's deserts (UNEP, 2006; Ward, 2016), with the addition that these are deprived of the native biodiversity.

The nomadic lifestyle was the only way humans had to survive in deserts for centuries. Housing and urban development are relatively recent and expanding processes in deserts, and are threatening habitats and unique vegetation communities. For instance, biodiversity decline in the coastal areas of the Arabian Peninsula is linked to development and urbanization, as well as to overexploitation of natural resources, both resulting from growing human population and lifestyle changes (Tourenq and Launay, 2008). Off-road recreational vehicles particularly impact the fragile arid areas, by soil compaction, accelerating water and wind erosion, vegetation destruction, or by the effect of vehicle noise on desert vertebrates (UNEP, 2006).

Farmland surface has increased dramatically in some deserts, causing habitat loss and fragmentation, and groundwater over-exploitation. These processes affected large portions of coastal areas of the Arabian Peninsula or the African Sahel. Grazing is a major

Table 1 Examples of convergent evolution in four world deserts

Guild	North America	Australia	North Africa	South Africa
Succulent plants	Cactacea <i>Yucca</i>		Euphorbiaceae	Euphorbiaceae <i>Aloe</i>
Bipedal rodent granivores	<i>Dipodomys</i>	<i>Notomys</i>	<i>Jaculus</i>	
Quadrupedal rodent granivores	<i>Chaetodipus</i> <i>Perognathus</i>		<i>Taterillus</i> <i>Pachyuromis</i> <i>Gerbillus</i> <i>Sekeetamys</i>	<i>Gerbillus</i> <i>Gerbillurus</i>
Small mammalian insectivores	<i>Onychomys</i> <i>Notiosorex</i>	<i>Antechinus</i> <i>Sminthopsis</i> <i>Antechinomys</i> <i>Onychogalea</i>	<i>Crocidura</i>	<i>Crocidura</i> <i>Elephantulus</i> <i>Macroscelides</i> <i>Pedetes</i>
Mid-size herbivores	<i>Lepus</i> <i>Sylvilagus</i>		<i>Lepus</i>	
Horned snakes	<i>Crotalus</i>		<i>Cerastes</i>	<i>Bitis</i>
Ant eating horny lizards	<i>Phrynosoma</i>	<i>Moloch</i>		
Open space, long-legged, sand-diving lizards	<i>Callisaurus</i> <i>Uma</i>	<i>Amphibolurus</i>	<i>Acanthodactylus</i>	<i>Gerrhosaurus</i> <i>Merops</i>
Sand-diving skinks	<i>Plestiodon</i>	<i>Eremiascincus</i> <i>Lerista</i>	<i>Chalcides</i> <i>Scincopus</i> <i>Scincus</i> <i>Trachylepis</i>	<i>Trachylepis</i>
Medium-sized, lizard-eating reptiles	<i>Crotaphytus</i>	<i>Varanus</i>	<i>Varanus</i>	

Despite these taxa have different phylogenetic origins and biogeographic histories, many share strikingly similar morphological traits.

Adapted and expanded from UNEP (2006). *Global deserts outlook*, Ezcurra, E. (ed.) Kenya: United Nations Environment Programme. <http://www.unep.org/geo/gdoutlook/> and Ward, D. (2016). *The biology of deserts* (2nd edn). Oxford: Oxford University Press.

cause of land degradation across the desert biome, especially at its margins. For example, excess of pastoral activity affected the threatened populations of Houbara Bustard, *Chlamydotis undulata*, in the north-western fringe of the Sahara, and cattle grazing and browsing have damaged sensitive desert scrubs and riparian habitats in the Chihuahuan Desert in Mexico (UNEP, 2006). Water overexploitation for human and livestock consumption threatens local fauna and flora (Fig. 8). For instance, fecal pollution, eutrophication and water shortage during the dry season are linked to increased pressure over fragile crocodile populations scattered in isolated mountains of the Sahara-Sahel (Brito et al., 2014). The extraordinary micro-endemism levels of the desert springs fed by the Australian GAB are threatened by groundwater use, with extraction partially exceeding recharge rates and drastically degrading the groundwater dependent ecosystem (Murphy et al., 2013). In the north-western margin of the Sahara, numerous water cisterns were built for watering livestock, which attract desert vertebrates (mainly reptiles and mammals) and act as unintentional death traps for them and changes the variety and quality of amphibian breeding sites, causing additional pressures over already scattered populations in desert habitats (García-Cardenete et al., 2014).

The exploitation of natural resources is growing across world's deserts, through industrial mining, oil and gas exploration, and recently by photovoltaic and wind power stations, and it is threatening the locally fragmented and remnant desert biodiversity. For example, the highest mountain system in Mauritania (Kediet ej Jill) and the surrounding rock outcrops are partially falling apart by the intense iron ore extraction, even before these habitats are scientifically explored. The projected growth in natural resources exploitation in world's deserts is likely to further threaten biodiversity. For instance, prospection for new oil sources in Niger was the major reason for population collapse of critically endangered Addax, *Addax nasomaculatus* (Fig. 8; Durant et al., 2014), and increasing mining activities in the Central Basin desert of Iran further threatens the last wild populations of the Asiatic cheetah, *Acinonyx jubatus venaticus* (Khalatbari et al., 2017).

Accessibility to world's deserts is growing and linear infrastructures are an increasingly common feature in most desert landscapes, mostly through roads but also by railways and pipelines. These features threaten local biodiversity by increasing vehicle-collision probability, modifying animal behavior, and by allowing the spreading of invasive species and the increasing human use of previously remote areas. For example, road collision is currently one of the most important threats to the critically small Asiatic cheetah populations in Iran (Khalatbari et al., 2017). The expansion of road networks and also the growing usage of

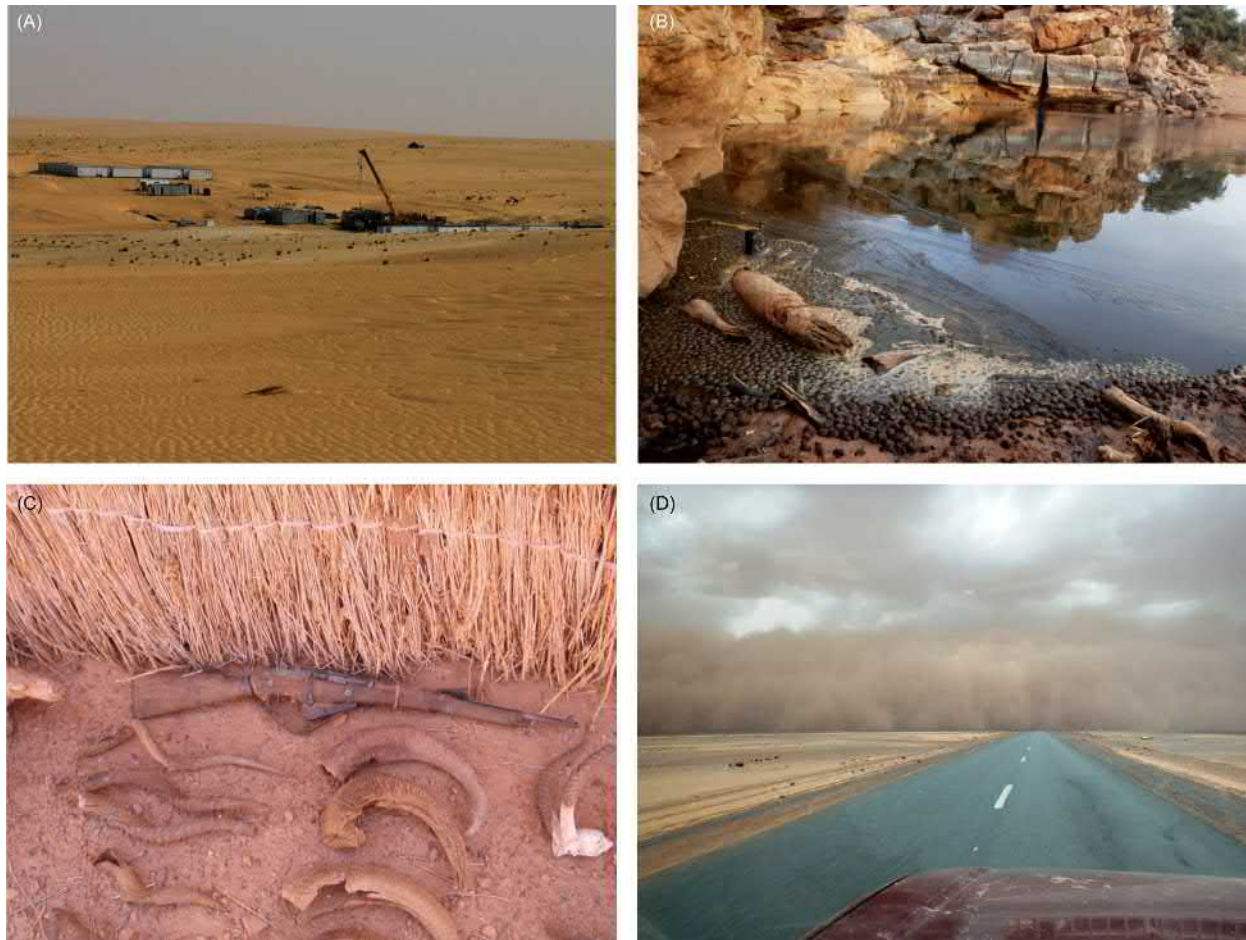


Fig. 8 Examples of threats in desert biomes. (A) Oil exploration, Niger; (B) fecal pollution and eutrophication of mountain rock pool, Mauritania; (C) overhunting and biological resource use, Mauritania; (D) increasing road network, Mauritania. Photograph credits: José C. Brito.

four-wheel-drive vehicles is increasing the accessibility to previously remote areas in most world deserts, which combined with the spreading of firearms, is amplifying the impacts of overhunting (Fig. 8). The negative synergistic combination of these factors has been associated with the decline in threatened fauna of the Sahara-Sahel, particularly in large body-sized vertebrates (Durant et al., 2014; Brito et al., 2018), a pattern also observed in the Arabian desert (Tourenq and Launay, 2008). The recent increase in global conflicts, particularly in deserts and arid regions, is further threatening already imperiled fauna. Within the Sahara-Sahel countries, the absolute number of conflicts has growth 565% over the last 20 years, and this trend was associated with the decline and in some cases with the massacre of large mammals, including the Addax, the Dorcas gazelle, *Gazella dorcas*, and the African savannah elephant, *Loxodonta africana* (Bruto et al., 2018).

Climate change will increase extinction rates of organisms in the future and is projected to be more severe in deserts in comparison to other biomes. Deserts experienced an overall increase in temperature of 0.5–2°C between 1976 and 2000, a much higher value than the average global temperature increase (0.45°C), which has been attributed to the higher atmospheric concentrations of greenhouse gases (UNEP, 2006). Current and future climate warming would affect the phenology and distribution of many species, and in synergistic combination with other human-induced threats in the desert biome, will probably lead to range contraction and species extinction. Given that desert-adapted species already live close to their physiological limits, they may be the most vulnerable ones, as suggested for the endemic vertebrates of the Sahara-Sahel (Vale and Brito, 2015). Ecological niche-based models projecting biodiversity distribution under climate-change scenarios predict dramatic losses of suitable climates with potential consequences in species diversity. For example, the Tassili n'Ajjer National Park of Algeria is predicted to lose about 50% of current mammal richness, with only about 10% species gain (reviewed in Brito et al., 2014). Climate warming may also favor range expansion of invasive organisms sensitive to low winter temperatures, as observed in invasive Neotropical plants in the North American deserts.

Biodiversity Conservation in Desert Biomes

Still there are good reasons for hope because most world deserts are among the last wilderness areas at global level that can still be considered mostly intact (UNEP, 2006; Davies et al., 2012), and where implementing conservation actions would be most cost-effective. Because of climatic constraints, more than the 90% of the tropical deserts of the world remain uncultivated, has rather low economic value, and the protection of these areas for biodiversity conservation is rather inexpensive (Durant et al., 2014). Area prioritization for biodiversity conservation begin to be available for some deserts organisms, such as the continental vertebrates of the Sahara-Sahel (Bruto et al., 2016), but these efforts needs to be extended to regional/national scales and for other world deserts. Reserve design targeting desert freshwater diversity needs to consider the effects of hydrology and species' ecology on population connectivity (Murphy et al., 2015b). The assessment of the conservation status under the IUCN Red List criteria is still poorly developed in desert-dwelling species, and needs to be extended to regional/national scales and for invertebrates in particular (Rossini et al., 2018).

The percentage of deserts and drylands that are formally designated as protected areas is gradually increasing, but the protected area coverage is below the 10% target of the Convention on Biological Biodiversity (UNEP, 2006; Davies et al., 2012). For instance, Niger declared the largest reserve of Africa for the protection of the Addax population, but local biodiversity hotspots with high endemism rates associated with rare perennial wetlands remain mostly unprotected, as are the cases of the mountains rock pools of Mauritania and the desert springs of the Australian GAB (Vale et al., 2015; Rossini et al., 2018). Deserts extending over developing countries, such as in the Sahara-Sahel, currently lack the resources and capacities and in some cases the commitment to make the strong structural changes needed to ensure sustainable natural resource management and social stability (Bruto et al., 2018). Changing the current status of poor governance, high corruption levels, low income, and lack of perspectives on social development and poor human rights enforcement that characterizes Sahara-Sahel countries remains a major societal challenge.

At the local scale, Community-based Natural Resource Management projects are building awareness of the environment and the cultural, economic and ecological importance of biodiversity and ecosystem services, as in the cases of the high Andes of Peru, Namibe desert or the Mongolian Gobi desert (Davies et al., 2012); these efforts need to be extended to other world's deserts. Actions directed at improving education and awareness on the local biodiversity can be a rewarding path to enhance desert conservation. Local communities have a good perception of the surrounding biodiversity, and stimulating collaboration with researchers, environmental managers and ecotourism agencies may be of cultural benefit for them, generate alternative income sources, and improve their understanding of the ecosystem services afforded by deserts (UNEP, 2006; Brito et al., 2014). Responsible ecotourism-based industry may provide alternative and better livelihoods to the local people, and is one of the ecosystem services provided by deserts that still remains unexplored.

Conservation actions directed at managing or restoring threatened populations of regionally extinct or threatened species are occurring in the world's deserts. For example, extensive conservation efforts were developed to save the two remaining natural populations of the Numbat, *Myrmecobius fasciatus*, in Australia, while conservation breeding and reintroduction programs have succeeded in establishing six populations in its former range (Davies et al., 2012). In Chad, concerted actions between local administrations, the environmental authorities of Abu-Dhabi, and the Sahara Conservation Fund (www.saharaconservation.org) allowed the recent reintroduction of the Scimitar oryx, *Oryx dammah*, in the Ouadi Rimé-Ouadi Achim Game Reserve, after decades of being considered extinct in the wild. Morocco is developing an ex situ breeding facility (M'cissi Reserve) of large ungulates (Oryx, Addax) and the Ostrich, *Struthio camelus*, to be reintroduced in the northwestern fringes of the Sahara, while captive breeding and

releasing programs of Houbara Bustard are being successful, although they are aimed at maintaining hunting activities, by falconry, on this large bird (UNEP, 2006). Reintroduction and restocking of wild species is a first step for the restoration of ecosystem function in deserts (Durant et al., 2014), but such operations require detailed decision processes and are costly, lengthy and logistically difficult, reinforcing that local extinction should be avoided whenever possible (Brito et al., 2018).

Management actions directed at conserving threatened species or restoring sites are developing across the world's deserts. Measures are being developed to reduce the accidental entrapment of desert organism in anthropogenic infrastructures by on-site, cost-effective management actions, such as the case of roadside fencing and animal underpasses forecasted for the Semnan-Mashhad highway (N44), stretching along the northern boundary of Touran Biosphere Reserve in Iran, where road collision is a major cause for population decline in Asiatic cheetah (Khalatbari et al., 2017). Dense wire mesh in the inlet and overflow slits of the modern water cisterns for watering livestock could prevent wild desert organisms from being caught, and simple ramps in the settling tanks could facilitate the escape of trapped species, while not restricting livestock from watering. For example, in the north-western fringe of the Sahara, this mitigation measure reduced 66% of amphibian and reptile mortality from trapping (Pleguezuelos et al., 2017). However, the management of desert spring in North America and Central Australia must include disturbance produced by livestock to maintain the native fish fauna, probably because a long history of disturbances by native mammals and aboriginal humans in these habitats.

Molecular-based studies are unraveling cryptic diversity and geographic structuring in genetic diversity across the world's deserts that should be preserved. For example, conservation of the threatened Cuvier's gazelle, *Gazella cuvieri*, in the northern Sahara should consider the preservation of the recent mountain and lowland ecotypes to maintain the overall adaptive potential of the species (Silva et al., 2017). In the desert springs of the Australian GAB, molecular studies have uncovered massive numbers of endemic forms in aquatic invertebrates (Murphy et al., 2013). The systematic status of these genetic demes and the evolutionary drivers of such diversity are mostly unknown (Brito et al., 2014). Molecular studies will likely continue to reveal additional biodiversity in the desert biome.

Long-term conservation of desert biodiversity requires appropriate policy instruments that promote conservation and sustainable use of natural resources. Strong commitments for change in global attitude towards nature and biodiversity conservation and regional stability are needed to drive societal change. Raising environmental alertness and pride within local communities of the value and uniqueness of the desert wildlife is needed to pressure strong policy change (Brito et al., 2018).

Acknowledgments

This study was developed under AGRIGEN-NORTE-01-0145-FEDER-000007, supported by Norte Portugal Regional Operational Programme (NORTE2020), under the PORTUGAL 2020 Partnership Agreement, through the European Regional Development Fund (ERDF). JCB is supported by Fundação para a Ciência e Tecnologia through contract IF/00459/2013.

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The Ecohydrology of Desert Environments: What Makes it Distinctive?

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Abstract

The global arid lands, or drylands, can be loosely-defined in terms of precipitation and evapo-transpiration, which characteristically result in semi-permanent water scarcity. This manifests itself in low soil moisture availability, ephemeral stream and river flow, and a plant cover that occupies only a part of the landscape. However, microphytic plants occupy many areas of otherwise bare soil where vascular plants are absent, and can confer some resistance to wind and water erosion. Dryland plants have developed some important adaptations to water scarcity, including the ability to capture rain and deliver it as stemflow to the soil around the base of the plant. There are also community-level adaptations that permit more abundant vegetation cover than might be expected in water-scarce environments. These include various kind of patchy vegetation, in which water is shed from bare areas and drains downslope to support localized groves of plants. A striking form of this adaptation that occurs in many parts of the global drylands is known as “tiger bush.” Drylands face ecohydrological change as global and regional climates change. A key issue that remains to be fully resolved is the extent to which dryland ecosystems are vulnerable to the effects of such change. In some ways that are discussed in this article, drylands may be seen as possessing some attributes that may in fact make them somewhat resilient to climate change.

Introduction

Drylands may be distinguished from other environments, landscapes, and ecosystems using a range of criteria. There can be no single definition of a dryland, owing to the great diversity of global dryland regions, some of which are dominated by sand, others by rock; some are semiarid whilst others are hyper-arid; some are fire-prone; many are affected to varying degrees by human occupation, resource extraction, or by the introduction of grazing or pest organisms (Canadell et al., 2007).

Dryland landscapes owe much of their fundamental character to water scarcity arising from a range of causes. Rock type may exacerbate aridity, as in karstic regions where rock solubility allows precipitation to pass into the deep groundwater relatively rapidly, leaving the surface dry as a “lithological desert.” Shallow soils, with limited capacity to store water between falls of rain, can locally also contribute to water scarcity and can increase the difficulty of sustaining plant growth. This effect is not distinctive of drylands, however, since even in humid areas, shallow soils can result in plant moisture stress akin to that occurring in deserts, if rainfall is low for an extended period and evapotranspirative demand is high.

Unsurprisingly, therefore, definitions of drylands by different authors are based on differing sets of “defining characteristics”; however, because of the essential character of water scarcity, most of these rely on one or more aspects of climate or hydrology that are considered to be distinctive of deserts. These include the idea that deserts are areas of “low and highly variable precipitation of generally small event sizes and particularly vulnerable to climate change” (Palmquist et al., 2016), or “regions with relatively low precipitation, long dry spells and frequent occurrence of water scarce conditions” (Wang et al., 2011), or areas characterized by “potential rates of ET greatly exceeding rainfall input” (Jenerette et al., 2012). D’Odorico and Porporato (2006) noted that “Drylands are drought-prone areas of the world in which rainfall is less than the potential evapotranspiration for the whole year or for part of it, and conditions of either permanent or seasonal soil water deficit occur. The obvious features of the rainfall regime are the low precipitation amounts and the high variability and unpredictability of precipitation, which occurs in a discrete number

of relatively infrequent events.” Thus, dryland ecosystems are in general water-controlled “with infrequent, discrete, and largely unpredictable water inputs” (Noy-Meir, 1973, 26).

From these few definitions, selected from a large number that have been used, we can assemble a list of proposed ecohydrologic characteristics of drylands:

- low and highly variable precipitation
- unpredictable precipitation
- small rainfall event sizes (depths)
- relatively infrequent rainfall events
- long dry spells with water-scarce conditions
- potential ET greatly exceeding rainfall input
- drought-prone
- permanent or seasonal soil water deficit
- vulnerable to climate change

Most of these proposed characteristics relate to the low and variable dryland rainfall, together with the resulting scarcity of soil moisture. However, as will be considered below, a knowledge of dryland rainfall is only the first step in understanding the availability of water to organisms and the occurrence of important ecosystem processes such as overland flow on dryland hillslopes and the ephemeral flow in desert streams and rivers. Many components of dryland landscapes and ecosystems affect both the distribution and availability of water that cannot be understood from a knowledge of the rainfall alone. For instance, desert trees, shrubs and grasses, and even microphytic plants, commonly exert an influence on hydrologic processes including interception and the partitioning of rainfall before water finally reaches the soil. Moreover, as we shall see, nonrainfall water can be vital in some drylands, where fog and dew become as ecologically-important as rainfall. Their occurrence may also be far more regular and predictable than dryland rainfall. The reader is referred to D’Odorico and Porporato (2006) for an account of dryland ecohydrology and to Nicholson (2011) for a general review of the climatology of dryland regions.

Why Are Drylands and Their Ecohydrology Globally Important?

Drylands are variously assessed as covering 30%–>40% of the global ice-free landsurface and therefore occupy a sufficiently large area to exert an influence on the continental albedo, landsurface temperatures, runoff from large regional drainage basins, chemical and physical weathering rates, and other components of the global land-atmosphere system. Low erosion rates in drylands (Perron, 2017) in turn affect regional tectonics, and hence, there is a feedback from tectonics to regional climate. Ahlström et al. (2015) investigated the importance of carbon sequestration or release in the globally extensive dryland ecosystems to fluctuations in the atmospheric CO₂ concentration. Whilst tropical forests dominate the global biomass sink for carbon, the semi-arid lands in the model of Ahlström et al. (2015) accounted for most (0.04 Pg C a⁻¹) of the time trend in net biome production (several Pg C per annum). They speculated that this was attributable to the encroachment of woody plants in semi-arid areas, reflected in the increased greening observed in satellite data. In the drylands of the Southwestern United States Brunelle et al. (2013) confirmed this trend, and observed that it paralleled the rising concentration of atmospheric CO₂ that unhelpfully for the confident attribution of causes, occurred concurrently with a period of intensification of grazing. D’Odorico et al. (2010) have shown that there can be a positive feedback between shrub growth (in *Larrea tridentata*) and microclimatic conditions that favor shrub growth, including a rise in minimum winter temperatures. In this way, relatively small changes in the external climate might result in significant ecosystem shifts, via regenerative change (positive feedback).

In many drylands, plant cover occurs in patches rather than as a continuous cover. It is hypothesized that this is a potentially metastable intermediate state between the full vegetation cover of humid regions and the virtually complete absence of vascular plant cover of the most hyper-arid regions. As a corollary, it is thought that landuse and climate change pose a risk of regime change or “catastrophic shifts,” involving a possible collapse of plant cover to bare desert. If this is so, then the drylands may be important to regional hydrology and influence regional and perhaps global climate, since vegetation is important to the hydrologic cycle interactions of the landsurface and the atmosphere. Using a coupled atmosphere-biosphere model, Snyder et al. (2004) explored this by removing in turn the vegetation cover in major biomes globally (including the tropical and boreal forests, temperate forests, savanna, and shrubland). Results showed varying effects on rainfall and temperature. Removal of the tropical forest vegetation reduced rainfall by 1.3 mm d⁻¹ (24%) over the entire biome. Loss of dry shrublands in Australia resulted in temperature increasing by 1.2°C in summer, and cooling by a slightly smaller amount in winter. Rainfall over much of dryland Australia also declined by 1–2 mm d⁻¹, attributed to lower concentrations of water vapor in the atmosphere, owing to the reduced moisture flux from plant transpiration. Findings such as these emphasize that rainfall in the drylands as elsewhere, is not solely an atmospheric phenomenon, but shows a strong dependence on the landsurface, and the extent to which vegetation there recycles and transpires moisture. Condensation of transpired water vapor in the atmosphere releases the latent heat of vaporization, and this is an important driver of convection within the atmosphere. The partitioning of solar radiation into sensible heat (H) and latent heat (LE) affects the strength of atmospheric uplift, the formation of cloud, and hence rainfall. Bare surfaces can exhibit a high albedo, which leaves a reduced net radiation at the surface, and a smaller capacity to warm the lower atmosphere and drive the convection that gives rise to rainfall.

There are many other ways in which the condition of the global drylands and their vegetation are linked to components of the broader Earth-system. One is via the transfer of dryland dust to the oceans, where the iron contained in the dust enhances the productivity of marine phytoplankton, which normally suffer iron limitation. The flux of dust is itself linked in part to the occurrence of drought, and decline in plant cover, in the drylands. The effects of the dust have global climate ramifications (Jickells et al., 2005), and, by forming overly-numerous condensation nuclei, may result in the inhibition of rainfall. Further consideration of the global dust flux from drylands and its environmental role is beyond the scope of this chapter, and is not considered further.

It is worth briefly recalling how the global drylands are involved in the inter-connected tectonics—erosion rates—climate interactions. Orogenic uplands may result in aridity downwind (the rainshadow effect), as exhibited in the Tibetan Plateau or the South American Altiplano. The dryness of these areas reduces river flows and erosion rates, and limits the ability of rivers to maintain their course across the rising uplands. Basins of internal drainage may result, such that sediment is not unloaded from the crust to allow ongoing uplift, but rather accumulates. This then feeds back to rates and mechanisms of orogenesis (Strecker et al., 2007), and to the occurrence of areas of higher rainfall related to orography.

Owing to its evident pivotal role, let us consider the nature of dryland rainfall in a little more detail.

Rainfall in Drylands

Rainfall in drylands, as in all environments, occurs in episodes—rainfall events—separated by rainless periods. Rainfall events in many climatic environments may be brief, lasting perhaps an hour or a few hours, or may extend over several days. Consequently, the tallying of daily rainfall amounts as a means of exploring the differences among, say, wet tropical and dryland rainfall climatologies, may not offer sufficient temporal resolution to explore the argument raised earlier that dryland rainfall is characteristically brief in occurrence. Many overviews of dryland rainfall consider primarily annual and seasonal amounts, and perhaps the kinds of intensities that occur (e.g. Williams and Lazarides, 1985). However, the arrival of rainfall over minutes to hours is especially important in the ecohydrology of drylands, because at other times, high evaporation rates mean that soils become dry and surface water does not occur.

Are the characteristics of rainfall events more critical to dryland ecohydrological processes than in other climates and biomes? Almost certainly, the answer is “yes.” Small amounts of rain are vulnerable to rapid evaporative loss following the rain, and therefore to generate important landscape-scale outcomes such as recharge to the groundwater system, or to cause desert streams to flow, commonly requires large events—at least tens of mm. Recharge may occur from the flow carried by river channels, especially through porous, sandy and gravelly channel sediments that are normally dry, or through the floors of desert lakes and playas (Fig. 1). Because the channels of dryland rivers are normally dry, there can be high rates of transmission loss—reaching 5%–10% discharge loss per km of flow—into the channel-margin sediments as the empty intergranular pore spaces there are filled. As a result, river flows may not arrive at the playas or other basins toward which they drain, except in large events that carry sufficient volume to survive the transmission losses. In humid climates, where there is often a permanent baseflow sustaining perennial streams, many of these processes do not occur; across whole landscapes, groundwater recharge frequently amounts to hundreds of mm a^{-1} . In drylands, sufficiently large rainfall events to cause river flow or groundwater recharge are uncommon, and rates of groundwater recharge are typically $< 1\text{--}2 \text{ mm a}^{-1}$, or perhaps just 1% of the rate seen in humid environments. In many dryland areas, recharge rates are lower still, at $\sim 0.1 \text{ mm a}^{-1}$. Large rainfall events are important to biological outcomes, also; they may be required in order to generate overbank flows capable



Fig. 1 The dry sandy bed of an ephemeral drylands stream (Fowlers Creek, western New South Wales, Australia). During the brief flows in this stream, water infiltrates into the bed and banks, later supporting the trees lining the channel during the long periods when it remains dry.

of supporting seedling establishment and tree growth along river corridors; they may also be associated with major episodes of flowering and seed production, and of breeding cycles of fish, birds, and amphibians along rivers and in ephemeral lakes. In turn, especially in semi-arid areas, vegetation may influence groundwater recharge, via soil macroporosity, concentrated stemflow, and other mechanisms. More recharge appears to occur beneath the trees of dry woodlands than in the open spaces between trees (Ilstedt et al., 2016). Ecologically-important ephemeral pools may be left in ephemeral stream channels once the flow has ceased, especially where the bed is locally rocky or less permeable than elsewhere. If shaded by overhanging trees, these pools can in some cases persist for week or months (Fig. 2).

It is useful in seeking to characterize rainfall events and their temporal characteristics, to adopt a formal definition of a rainfall event. This is most often done by defining a “minimum inter-event time” (MIT), the minimum number of rainless hours that must occur in order for subsequent rainfall to be identified as a new rainfall event. A wide range of MIT values has been used in published literature, ranging from 15 min to 24 h (Dunkerley, 2008); however, a value of 6 h is common, and is frequently adopted because it corresponds to the length of time needed for plant foliage to become dry after a rainfall event. The use of the MIT approach to delimit rainfall events means that long events can contain periods when rain ceases temporarily, but these cannot exceed the MIT, or else a new event is identified. Importantly for dryland rainfall, events can have durations of just a few minutes or tens of minutes, and they can begin and end at any time. Thus, a 17-min rainfall event might begin at 16:55 and end at 17:12. This makes the statistical properties of rainfall events more useful in describing brief showers than aggregated daily or hourly totals.

Are desert rainfall events distinct from those of wetter areas? Barbosa et al. (2018) examined rainfall events delineated using the MIT approach at hot semiarid and tropical wet climates in north-east Brazil. Their results are summarized in Table 1. The semiarid locations have longer, larger and more intense rainfall events than the wet tropical site.

The results from Brazil suggest that at the semiarid locations, rainfall events are larger, longer, and more intense than at the wet tropical location. The values change slightly if a different statistical measure is used, such as the median rather than the mean. In light of this, taken together with the smaller mean annual rainfalls at the semi-arid locations, it is evident that the annual rainfall could be delivered in a smaller total time there than at the wet tropical site. Using just the mean figures as an approximation, the rain durations (annual total/mean intensity) would be 48 h at Aiuaba, 48.5 h at São João do Cariri (both about 2 days), and 200.2 h at Guaraíra (more than 8 days). The data show how short the mean rainfall event is—only about an hour at all three locations.

In a similar study, Dunkerley (2018) compared rainfall events at Broken Hill, New South Wales, in the Australian drylands, with Millaa Millaa in the wet tropics of far northern Queensland, Australia (Table 2).

The results differed from those for Brazil (Table 1) except that the dryland site, as in Brazil, exhibited more intense rainfall events than the wet tropical site. Using the mean figures as before, at Broken Hill if rain fell at the mean event intensity, it would require 51 h to deliver the mean annual rainfall. At Millaa Millaa, this would take 1126 h (about 47 days). Again it is evident that the duration of rain is relatively brief at the dryland locations. These very approximate estimates can be compared with the actual figures for the total time occupied by rainfall events, which are on average 141 h a^{-1} (Fowlers Gap) and 2426 h a^{-1} (Millaa Millaa), so that mean annual aggregate rainfall event duration is on average more than $17 \times$ larger at wet tropical Millaa Millaa, than at the dryland site, Fowlers Gap.

To the descriptors of the rainfall climatology of deserts referred to previously, we could add the nature of the “rainfall event intensity profile”—that is, the pattern of rainfall intensity fluctuations during the course of the rainfall event, including any periods when the rainfall ceases temporarily. The intensity profile has been relatively neglected in studies of dryland rainfall climatology, but it is



Fig. 2 This pool of water accumulates in a low-lying section of the channel of an ephemeral stream that is normally dry (Fowlers Creek, western New South Wales, Australia). It is slowly lost to seepage and evaporation, but is an important water source for the trees lining the channel, as well as for local fauna.

Table 1 Rainfall at three locations in Brazil

<i>Rainfall characteristic</i>	<i>Aiuaba</i>	<i>São João do Cariri</i>	<i>Guaraíra</i>
Mean annual rainfall (mm)	560	460	1700
Mean event duration (h)	1.2	1.0	0.9
Mean event depth (mm)	10.8	8.38	5.95
Mean event rainfall rate (mm h ⁻¹)	11.64	9.49	8.49

Table 2 Rainfall at a dryland location and a wet tropical location in Australia

<i>Rainfall characteristic</i>	<i>Broken Hill, dryland NSW</i>	<i>Millaa Millaa, wet tropical Queensland</i>
Mean annual rainfall (mm)	~220	~2500
Mean event duration (h)	5.1	18.6
Mean event depth (mm)	10.2	21.3
Mean event rainfall rate (mm h ⁻¹)	4.3	2.22

important for several reasons. First, even if rain is continuous during an event, the intensity is likely to fluctuate, and the position of periods of intense rain in the course of the event affects the partitioning of the rainfall among surface ponding, infiltration, and overland flow (Dunkerley 2012). If, for instance, the most intense rain comes late in an event, then the soil surface will already have become wet, and a larger amount of the rain may be partitioned into overland flow. If the intense rain arrives early, before the soil has become wet, more of the rain may infiltrate. If rain ceases briefly during an event, then any surface ponding has a chance to infiltrate, renewing the depression storage capacity; likewise, plant foliage has a chance to dry, renewing the canopy interception storage capacity. In the water-scarce drylands, all of these effects are worthy of study and almost certainly have ecohydrological importance.

The analysis and description of temporal profiles is not yet standardized. Todisco (2014) for instance identified “first half storms” and “second half storms,” and found that for Masse (central Italy), “first half storms” dominated. Early analyses of temporal profiles divided storm durations into four equal-length segments, called “quartiles.”

What forms of intensity profile are found in drylands, as compared with, say, wet tropical locations? Where convective rain is important, driven by heat-driven uplift from hot soil surfaces in the late afternoon, early intensity peaks (first-quartile storms) would be expected. Once intense convective rain has commenced, the soil surface is rapidly cooled evaporatively, and the uplift and convergence of moist air is slowed; in this way, the intensity declines toward the later phases of a convective rainfall event. In nondesert environments, frontal, monsoonal, or orographic rain would not be expected to follow the same intensity profile. For Brazil, Barbosa et al. (2018) found largely constant intensity (“rectangular” event profile) for their wet coastal site. In contrast, Aiuaba, a semi-arid inland site, showed mostly early-peak (their “unimodal left-skewed” type). Dunkerley (2013) analyzed event profiles for dry and wet years at Fowlers Gap in dryland NSW, where there are large inter-annual fluctuations in rainfall linked to ENSO. He showed that in wet years, first quartile events were the most common, but that the largest share of the total rainfall was delivered in third quartile events. In contrast, in dry years the largest proportions of both events and rainfall were in first quartile events. This is potentially ecologically important, since first quartile events tend to promote infiltration, and so reduce moisture stress in dry years. Full details of rainfall event profiles, and their ecological significance, remain unexplored for many global drylands.

Interannual Variability in Rainfall, Including Drought, in Drylands

Marked variability in rainfall is a widely-cited characteristic of drylands; rain may occur with marked intermittency, and with long dry spells between falls. These dry spells may last for weeks to months; for Fowlers Gap, Dunkerley (2008) reported a mean waiting time between rainfall events (MIT = 6 h) of 83 h, but the longest dry spell extended for 2443 h (about 102 days).

Years of well below average rainfall, especially multiple successive years, may result in severe droughts in drylands. During drought conditions, soil moisture can fall to levels that cause mortality in plants, including long-lived taxa such as trees and woody shrubs. As a result of drought, vegetation cover may decline, and wind erosion can become dominant. In drought conditions in arid western NSW, the author has observed that abrasion by saltating sand can erode the biological soil crusts that help to stabilize silty soils against wind and water erosion, so exacerbating the effects of the drought. The rainfall record for the regional city of Broken Hill provides quantitative examples of the variation in annual rainfalls. In 1902 (a year included in the Federation drought of 1895–1902; Ummenhofer et al., 2009) Broken Hill recorded rainfall of 91 mm. In 1940, during the “World War II” drought, the yearly rainfall at Broken Hill fell to 57.4 mm, or just 22% of the long-term average annual rainfall at the Patton Street raingauge station, which is 260 mm (based on 122 years of record, 1889–2015). The wettest year, 1974 (838 mm) was nearly 15 × wetter than 1940. The coefficient of variation (CV) of the annual rainfall for this station is 0.45; for Australian dryland rainfall stations in the Lake Eyre Basin, McMahon et al. (2008) reported a maximum CV of 0.79 at Mungeranie. Overall, the CV was found to be ~60% larger than for other global dryland regions, in part related to the influence of ENSO. In even more arid locations, the CV may lie in the range 1–2, or even larger, and completely rainless years or runs of years may occur.

Taking a Longer-Term View of Dryland Rainfall

Historical, instrumental rainfall data only span a short period—perhaps 100 years in many cases, and often less. They can consequently not represent conditions through even millennial timescales, and it is well established that past climatic and hydrologic conditions are not the same as conditions experienced in the last 100 years or so. For instance, as noted above, parts of the Australian drylands have experienced several severe droughts in the 20th and early 21st centuries. However, instrumental records only began in Australia in the mid- to late-19th century, and it is therefore unclear whether the historical droughts were more or less severe, or long-lasting, than droughts of prior centuries. Various proxy records can be used in an attempt to extend the rainfall record and detect wet and dry periods prior to instrumental records.

Some recent examples illustrate this. Lough (2011) recorded luminescence in *Porites* corals from the Great Barrier Reef off the east coast of Australia, where coral growth is affected by major freshwater floods; this is recorded in the growth bands of the coral. The coral record was correlated with instrumental records and the relationship was then extended to earlier dates. Results showed details of rainfall from the late 1600s, including an extended drier period from the 1760s to 1850s, when interannual rainfall variability was reduced. Vance et al. (2015) examined ice core evidence from the Law Dome in East Antarctica, with dating done by layer counting. Accumulation rates of snow, and sea salt abundance in the ice, were recorded, and correlated with climatic conditions in Australia. Results suggested the occurrence of 8 Australian “megadroughts” lasting more than 5 years, including one drought which lasted for 39 years in the period 1174–1212 CE. The 12th century was found to be a long period of unprecedented dryness.

Results such as these, though relying on indirect proxy evidence, and attended by the challenges of calibration and verification, nonetheless suggest strongly that the variability of dryland rainfall known from the historic period does not reflect conditions through recent geological time. In particular, the occurrence of longer droughts than have occurred historically is a striking suggestion from the proxy studies. Future climate change may bring more frequent or more geographically-widespread droughts. In various parts of the world, rainfall exclusion experiments, using roofing placed temporarily above shrublands and other dryland vegetation communities, is being used to build an understanding of the possible effects of future droughts (e.g. Longepierre et al., 2014).

The Fate of Rainfall Near the Groundsurface: Canopy and Litter Interception and Stemflow

Rainfall in drylands may in large part arrive at the surface of bare soil, rock, sand, or alluvium (Fig. 3). However, even where the soil lacks vascular plant cover, rain may make first contact with microphytic plants such as lichens or mosses; cyanobacteria also colonize many dryland soil surfaces. These may cover extensive areas of soil and rock, and are generally referred to as “biological soil crusts” (Fig. 4). Where vascular plants—grasses, shrubs, and trees—are present, rainfall may initially contact the foliage, branches and stems of the plants, or else fallen organic litter of leaves, twigs, flower parts resting on the ground (Fig. 5). In all these situations, water is partly intercepted before it can reach the soil. From the interception stores it may be absorbed, evaporate, or splash, drip, or trickle down the plant to reach the soil as released throughfall or stemflow (also referred to as contact flow). Water may be lost to evaporation from the interception stores, even during rainfall, at rates of perhaps 0.4 mm h^{-1} , which is significant in relation to the common dryland rainfall intensities of just a few mm h^{-1} .

Experimental studies of dryland plants have investigated the amount of water intercepted or delivered to the base of a plant as stemflow. In China, stemflow in *Caragana korshinskii* amounted to 8% of the rainfall on average, and was delivered after a minimum



Fig. 3 A typical arid landscape in the drylands of Australia. Here, rocky ridges carry relatively little vegetation owing to their thin, stony soils. In contrast, on different lithologies in the valley, trees are able to survive, aided by runoff from the rocky hillslopes.



Fig. 4 A cyanobacteria crust that has colonized the surface of a loamy dryland soil. The image shows the typical structure of separate plates in the crust. In the foreground, the crust, which normally confers some erosion resistance to the soil, is being broken up and eroded, perhaps as a result of grazing stock.



Fig. 5 Scattered trees in the Australian drylands, showing the way in which such plants may alter their local micro-environment. The soil beneath each tree benefits from some shade, and the patches of litter visible in the photo increase the availability of soil organic matter. These favorable locations also support more abundant soil and decomposer organisms, and typically have higher infiltrability. Note that soil between the trees is largely devoid of vegetation.

of 2.2 mm of rain. [Yuan et al. \(2017\)](#) presented a lower estimate of 0.9 mm for this shrub, and a slightly higher value of 2.1 mm for *Salix psammophila*. Inter-specific differences relate to properties of the foliage and stems, including the architecture and inclination of the branches. The focused delivery of stemflow, with funneling ratios of up to ~ 90 , was found by Yang et al. to recharge relatively deep soil moisture. [Slatyer \(1959\)](#) reported that mulga trees (*Acacia aneura*) in central Australia also shed stemflow after as little as 2–3 mm of rain, and in many storms delivered about 40% of the rainfall over the projected canopy area. He stressed that the 100 L or so of stemflow delivered to the base of a tree in a rainfall of 15–20 mm amounted to an important water source for the plant in the dryland conditions of inland Australia. Working on mulga in south-west Queensland, [Pressland \(1973\)](#) found that 18% of gross precipitation was channeled as stemflow, though the proportion declined slightly in events of > 10 mm. This decline was attributed to an increase in stem and leaf drip, resulting in reduced contact flow. [Pressland \(1976\)](#) drew additional attention to the fate of the stemflow, noting that it had been observed to infiltrate within 50 cm of large trees, and 30 cm of small trees. In this way, he showed that the increase in effective depth of precipitation over the area around the base of the plants, where the stemflow is concentrated and within which it is absorbed, reached almost 200% of the open-field rainfall for a 10 mm rainfall over a small tree. Though very few plant taxa have been studied, the available evidence suggests that in drylands where many rainfall events are small, the funneling of stemflow boosts the delivery of water to the base of the plant, and supports deeper penetration of the wetting front in the soil beneath the plant. There, the stored water is available to support the plant during the potentially long waiting time until the next rain.

[Magliano et al. \(2019\)](#) present an overview of interception, throughfall and stemflow in the global drylands.

Fog and Dew in Drylands

The nocturnal cooling of the ground surface that occurs under the frequent clear-sky conditions of drylands is conducive to the formation of dew. Dry uplands adjoining warm oceans may be exposed to drifting fog and mist, or low cloud, from which plants may extract moisture. Dew and fog water are both forms of occult precipitation, and their ecological role, which has been studied in a number of drylands, is locally important. The water can be directly absorbed into the leaves of some plants, without having to enter the soil, and also supports biological soil crust organisms. Cacti of the American deserts accumulate dew, assisted by their spines. In the Negev, Hill et al. (2015) used environmental isotopes to establish that three taxa, *Salsola inermis*, *Artemisia sieberi* and *Haloxylon scoparium*, derived 56%, 63% and 46% of their water from dewfall, and concluded that dew was an important aid to plant survival in the water-scarce Negev. Soil may also take in water directly, by absorption, from the humidity of the lower atmosphere. Though this water may not be used by plants, it nonetheless become involved in evaporation, and hence in the overall energy balance and temperature regulation of the dryland surface. In addition to supporting plants, water absorbed from the atmosphere may facilitate microbial activity in the soil, which in turn affects ecosystem carbon cycling. All of this means that whilst rainfall is a limiting resource in drylands, nonrainfall sources of water may also be vital to some taxa.

Dryland Shrubs as “Ecosystem Engineers”

Owing to the limited availability of soil moisture, dryland plants typically form only a partial cover on the soil surface, and are characteristically arranged in patches, clumps, or groves (Fig. 6). Individually, and in these clusters, the plants produce changes in the soil (such as the concentration of stemflow water and materials dissolved in it), but also nutrients gathered by spreading root systems, that help to support the plants. Often, shrubs grow on small mounds of fine sand and silt, partly built of particles trapped from wind transport, and partly from particles splashed from the surrounding unvegetated soil by the beating action of rain. Once beneath the



Fig. 6 Plants in drylands are often scattered, forming an incomplete cover. This can be seen in these two images of scattered shrubs (*Cassia* spp.) growing on stony dryland soils (*upper* photo) and a plain carrying primarily scattered chenopod shrubs (*lower* photo). In the lower photo, some scattered tall shrubs (*Acacia* spp.) can be seen on the low ridge in the background.

shelter of a plant canopy, soil particles are less likely to be splashed out again, and so tend to accumulate. Clusters of plants also provide mutually beneficial effects such as sheltering from wind and shading from sun. However, these beneficial or “facilitative” effects are offset by competition among the plants for nutrients and especially for soil moisture. Because of the diverse effects of plants on the soil in their immediate vicinity, they are considered to be “ecosystem engineers”; often the outcome is the formation of favorable micro-habitats that can assist other plants to become established, as well as an enhanced ability to survive dry conditions (Segoli et al., 2008). The areas modified by plants have been referred to as “fertile islands” (Schlesinger et al., 1996).

The patchiness of dryland vegetation extends in spatial scale from individual plants surrounded by unvegetated soils, to clusters of plants a few m in size, to groves that may have dimensions of hundreds of meters. Where plants are clustered and facilitative and competitive effects arise, geometrically regular patterns may emerge, among the most striking of which are the contour-aligned groves known as “tiger bush” (Fig. 7). These patterns are hypothesized to be “emergent patterns” that arise from the plant interactions and the ways in which they alter the availability of soil moisture, especially the positive feedback in which the soils close to plants show higher infiltrability. This constitutes a positive feedback effect, in which groves become favorable habitats, and bare soil becomes a hostile habitat. The beating action of rain on bare soils can produce thin seals or crusts that limit the infiltrability of the soils, and encourage overland flow directed toward plants downslope. Large bare areas can support large groves of plants downslope; areas downslope of plant groves are likely to receive little overland flow, and hence tend to become bare. As these interactions occur through repeated cycles of rain, plant growth, and drought stress, the locations of plants becomes organized in a way that is ecohydrologically efficient, with bare areas adjoining groves of plants immediately downslope. The resulting emergent vegetation patterns such as tiger bush thus provide a form of adaptation to water scarcity that involves the action of many individual plants; they are community-level adaptations, rather than the individual adaptations seen in plants with specially-adapted leaves, root systems, or drought tolerance.

Let us consider the ecohydrologic operation of patterned vegetation a little further. Components of the vegetation mosaic that are unvegetated have low infiltrability, and are source areas for shallow Hortonian overland flow. This moves downslope to locations where the higher infiltrability of groves allows the water to be infiltrated to support plant growth. In this way, the groves of



Fig. 7 Community-level adaptations to water scarcity include these striking, contour-aligned grove and inter grove ecosystems, known as “tiger bush” because of the stripy appearance. The tiger bush landscapes shown are developed in Mitchell grass (*Astrabla* spp.) growing in the Broken Hill district of western New South Wales, Australia (upper photo) and in mulga (*Acacia* spp.) growing in the Alice Springs district of central Australia (lower photo).

plants receive both direct rainfall and the additional runoff water from upslope. The groves offer higher infiltrability owing to several effects of the plants and associated organisms (ants, termites): more biopores, better soil structure owing to the addition of organic matter, less raindrop impact crust development owing to shelter by the plant canopies and litter. Surface runoff is also slowed by the plants and litter and the greater surface roughness that results, allowing more opportunity time for infiltration. In this way, unvegetated and impervious intergroves may take in perhaps 50% of the incident rainfall, whilst groves take in 200%, depending on the relative widths of the intergroves and groves (the relative widths are known to vary with the dryness of the climate). Because of the concentration of water within the groves, the total biomass of vegetation that can be supported is increased by the tiger bush structure over what would be possible with a low but uniform vegetation cover of scattered, isolated plants.

Biological Soil Crusts and the Fate of Rainfall

Microphytic plants are able to colonize the uppermost millimeters of the soil surface in drylands, where their metabolism is supported by falls of rain too small to benefit vascular plants, as well as water extracted from fog and dew fall. Their presence confers erosional stability to the soils, but also affects the partitioning and disposition of rain arriving at the ground, including infiltration and water retention. [Lange et al. \(1994\)](#) investigated the water relations of lichen crusts in the Namib desert, where the annual rainfall is a mere 13 mm or so, falling on just 1–5 days per year. They showed that nocturnal respiration could begin as a result of moisture derived from fog or dew, and that water uptake by the biological soil crusts after heavy fog was 0.49–0.73 mm rain equivalent. These biological soil crust organisms are classified as “poikilohydrous,” having the capacity to exist in a dormant state once desiccated, but able to resume respiration once re-hydrated. Summed across all the rainfall events in a year, moss crusts in the Negev desert can intercept in total up to 5–7 mm of rain, but this does not significantly reduce soil wetting in larger rainfall events ([Kidron, 2014](#)). Other biological crusts are considered to enhance infiltration ([Eldridge and Greene, 1994](#)). There are undoubtedly variations in the ecohydrological role of the diverse forms of biocrusts in different environments. For a review, the reader is directed to [Weber et al. \(2016\)](#).

Dryland Responses to Climatic and Environmental Changes: Vulnerability and Resilience

Expansion of Arid and Semi-Arid Regions Globally

As we have seen, globally, the drylands cover 30% to > 40% of the ice-free land area (the range reflects the various ways in which dryland boundaries can be defined). However, climate change and variability, perhaps related to rising concentrations of CO₂ and other greenhouse gases in the atmosphere, together with feedback processes, involve an increase in global mean temperature. Global mean temperatures do not reveal significant regional differences in the pattern of climate warming, and the drylands are a notable instance of this. In fact, the drylands have exhibited the largest warming, accounting for more than half the continental warming ([Huang et al., 2017](#)). The warming in turn is associated with increasing ET losses from the landsurface in many but not all drylands, and hence in increasing values of the index of aridity (P/PET; P = precipitation, PET = potential evapotranspiration).

[Huang et al. \(2016\)](#) reported accelerating expansion of the global drylands. Using corrections to the Fifth Coupled Model Intercomparison Project (CMIP5), they showed that it was probable that drylands will expand to cover more than half of the global land area by the end of the 21st century. Exact figures depend upon which Representative Concentration Pathway (RCP) is used to project future CO₂ levels. Under RCP8.5, global dryland area would increase by 23%, but by a smaller 11% under the RCP4.5 scenario of reduced emissions, relative to the 1961–90 baseline area. Huang et al. speculate that the dryland expansion will reduce carbon sequestration there and so will contribute to further regional climate warming, posing risks to the sustainability of the affected drylands. Expansion of the semi-arid drylands, which cover the largest area of dryland globally (~ 15% of the land area), has been reported to have increased by 7% between the 1948–62 data and the 1990–2004 data ([Huang et al., 2016](#)).

Drought and Ecohydrology in the Global Drylands under Climate Change

Scenarios of the future warmer global climate forecast widespread increases in the risk of climatological drought ([Carrão et al., 2018](#)), though the change in risk is not uniform across the globe. However, knowledge of likely changes to P and PET are insufficient to estimate how the dryland ecosystems will respond. The response of plants to the additional atmospheric CO₂, which will make carbon more readily available, will be to need fewer stomata across which gas exchange can occur. If plants reduce stomatal numbers and/or stomatal conductance, this will have the associated effect of reducing plant water loss. Ordinarily, plants close their stomata in response to triggers in atmospheric humidity and temperature, in a way that protects the plant from desiccation. Reduced stomatal opening related to the additional atmospheric CO₂ is envisaged to compensate for much of the apparent increased aridity suggested by P/PET indexes, since PET does not correspond to actual ET when plants limit their transpiration ([Swann et al., 2016](#)). Uncertainty remains about the extent to which these ideas are generally applicable across the global drylands. Almost certainly, local ecosystem structure and floristics, especially the ability of different taxa to access limited soil water reserves during drought, depending on characteristics such as rooting depth, will result in considerable regional variation in the outcomes for dryland environments and organisms.

Drylands contain ecosystems that are frequently under stress, from nutrient scarcity, moisture shortage, or high temperatures and desiccation. Niches within the drylands, such as along the corridors of ephemeral dryland streams and rivers, or in the sheltered

micro-environment beneath stones, support distinctive local communities of organisms, from microbes to large trees. In this situation, a change in stress or resource availability can be expected to result in shifts in ecosystem composition or functioning. It is worth considering what changes have been seen in the global drylands during the historic era, and what changes might be expected in coming decades, in a warmer world with an invigorated hydrologic cycle.

Encroachment of Woody Plants in the Drylands

Over the last century or two, grasslands in many regions have been progressively experiencing increased occurrence of woody plants such as shrubs and trees. The ecological and environmental controls on the distribution of trees and grasses within savanna and other semi-arid landscapes are complex and still debated. However, fire is likely to be one of the key determinants of tree cover. It has been hypothesized that the rising levels of atmospheric CO₂ may be benefitting trees, contributing to the observed increase in woody plants. Grasses have a C3 metabolic pathway, whilst woody plants have the C4 pathway (Franks et al., 2014). There are several other hypotheses, including the reduced stomatal conductance mentioned above. This could allow the woody plants to access an additional water resource made available by reduced transpiration by grasses. Grazing effects may also be involved, with less palatable taxa expanding at the expense of preferred fodder species.

A trend to global greening has been observed in satellite data, and has been associated with a rise in global land evapotranspiration. The greening trend occurs even in the drylands. Changes in plant architecture are also occurring as growth conditions alter, affecting the leaf area index (LAI) and other properties. All of this is significant because the nature of the vegetation affects the global climate and hydrological cycle. For instance, it has been argued that reduced stomatal opening and associated reduced transpiration have had a detectable impact on global river flows, which may have increased through the 20th century in response.

Ecohydrological processes involve far more than transpiration, however. When woody plants encroach on formerly grassy drylands, other processes can be affected. These include the canopy interception of rainfall, the infiltrability of soils, the delivery of water as stemflow to locations close to the stems of plants, and, overall, possible changes in the pattern of soil moisture and of recharge to groundwater. These changes may then contribute to further changes in the vegetation, via feedback loops. Ecohydrology, especially during a period of climatic change, presents many complex challenges to understanding, and monitoring of ecosystem responses to environmental change will be required in coming decades in order to test the various hypotheses just outlined.

Collapse of Self-Organized Dryland Vegetation Systems

As noted earlier, many drylands contain mosaic vegetation patterns, exemplified by tiger bush. The origin and controls on these emergent patterns remain topics of research and debate. However, a number of authors have hypothesized that climate change, especially increasing aridity or drought occurrence, poses a risk to these landscapes. Mosaics are seen as an intermediate state between full vegetation cover and a completely bare surface, and vulnerable to moving toward a complete lack of vegetation in the face of more limited available soil moisture in a future warmer world. However, once again this is a complex issue that depends on local or regional climates of the future, as well as on the response of particular local plant taxa to those altered conditions. Presently, there is insufficient knowledge of many of these issues to be completely confident about the fate of emergent vegetation patterning in the drylands. It has been shown that isolated plants, lacking the facilitative effects of close neighboring plants, can nevertheless achieve higher water use efficiency; mechanisms such as this may confer resilience on patterned vegetation during any tendency to decline in plant cover.

Precipitation in a Future Warmer World

The climatic environment of drylands involves high rainfall intensities. An important issue is how these intensities might change in coming decades. As noted earlier, fog and dew can be critical moisture sources in drylands, and therefore it is also important to consider how the availability of these may change.

A warmer atmosphere can hold more water vapor, and according to the Clausius-Clapeyron relation, the capacity increases at 7% °C⁻¹. Given that this may result in more precipitable water in the atmosphere, it is likely that the intensity of rainfalls will increase in the future. In terms of ecosystem rainfall partitioning, this suggests that an increasing fraction of the rain in extreme events may be partitioned into overland flow, rather than into locally plant-available soil moisture. On the other hand, the occurrence of dew and fog may increase if the atmospheric water content rises. There have been many investigations of temporal trends in rainfall intensities, though primarily examining only statistics of daily or hourly values, rather than sub-hourly intensities. Some have found evidence of an historical decline in intensity, and some have detected increasing trends. In many cases, the pattern of change is geographically complex, with different areas exhibiting different trends or rates of change. As we saw earlier, subhourly rainfall characteristics are important in ecohydrology, perhaps more than they are in general climatology. This is because infiltration and water partitioning at the soil surface, interception in plant canopies, and the delivery of stemflow, are all known to be strongly influenced by rainfall intensity. Short-term rainfall intensities are often assessed over periods of 10–30 min, and related to the kinds of ecohydrologic processes just mentioned. Such studies require rainfall data having high temporal resolution.

The remaining uncertainty about many of the ecohydrological process, and of possible changes in them in a warmer world, provides a strong motivation for continuing our efforts to understand dryland ecohydrology, and for ongoing monitoring of the responses exhibited by dryland ecosystems to the changing hydroclimate of the coming decades.

Conclusions: Revisiting the Ecohydrologic Definition of “Desert”

Much of what was discussed above makes it clear that defining “deserts” in terms of ecohydrologic characteristics is not straightforward. Some desert locations show relatively high rainfall intensities, but not all do. However, even if particular desert locations have rain that is no more intense than other locations, the small annual rainfall of deserts means that the duration of rain must be less than elsewhere. If the duration of rain is less, then the duration of nonraining dry time must be larger, and as shown above, this can extend to months in some drylands. Consequently, we might expect to see plant characteristics that permit efficient harnessing of the limited water delivered in widely-spaced falls of rain. These characteristics might include low canopy interception losses and efficient stemflow funneling. In terms of dryland community structure, patchy growth of plants, and perhaps vegetation mosaics with runoff-runon systems, are beneficial characteristics that result in efficient harnessing of available water, and which would not be expected in humid environments where water is generally not a limiting resource. We can also recall the reliance on dew and fog that is seen in some deserts, and especially as a source of moisture for nonvascular plants. Again, whilst fog drip contributes significant amounts of water even in humid forested environments, its ecohydrological importance is greater in the drylands. Therefore, we can conclude that in many ways, our understanding of dryland and their distinctive ecohydrology is advanced by considering the nature and controls of ecohydrological processes such as interception, stemflow, and infiltration. It is clear that a knowledge of annual rainfall and its potential future variability, whilst informative at one level, is insufficient to predict the future of dryland ecosystems. These will certainly be affected by fire, drought, human landuse, and the abundance of CO₂ in the atmosphere, as well as by changes in temperature and in many aspects of rainfall. Consequently, process-based ecosystem and landscape models—supplemented by direct field observation in the drylands, with acquisition of parameterization and validation data—will be required in order to track and understand the changes in the extent and characteristics of the global drylands that may take place in coming decades.

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Desert Oasis Springs: Ecohydrology, Biocultural Diversity, Mythology, and Societal Implications

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Abstract

Desert oases function as centers and sources of dynamic cultural diversity. Despite their often small size, oases and other springs often contain tightly packed, highly interactive assemblages of upland and wetland obligate plants and animals. Springs function as keystone ecosystems, ecologically interactive points, and refugia within larger geographic areas and across long timescales. Desert oases provide crucial habitat for wild and domesticated biodiversity, and sources of economic well-being and inspiration for humans. In this article, we focus on the springs and oases of the Sonoran Desert in southwestern North America. With a long prehistory of human use and great intensification of exploitation for agriculture, recreation, and urbanization during historic times, Sonoran Desert oases and other springs throughout the world have become highly threatened. Oases have long held archetypal appeal as lush refugia for humans traveling through arid regions. However, these spatially limited, bioculturally rich island-like desert refugia are compelling to the human psyche, and have been mythologized in modern society. The “myth of the oasis” does not scale effectively to large urban settings, and this has set the stage for unrealistic expectations and demands on limited environmental resources in these harsh, arid regions. Nonetheless, this myth has inextricably permeated arid land urban society, creating overdrafts in water use and abstraction that portend ever more serious conflicts of an unsustainable future.

Introduction

Oases in arid lands are desert springs ecosystems that function as centers and sources of dynamic cultural diversity. The term comes from the Demotic Egyptian words *ouahe* or *wahe*, meaning “dwelling place.” As with all springs, oases are places where groundwater reaches the Earth’s surface, often creating lush wetland habitat that are occupied by many life forms, and which can function as ecologically highly interactive focal points in the surrounding landscapes. Aridland groundwater-dependent ecosystems (GDEs) often have orders of magnitude higher biological productivity and biodiversity compared to adjacent uplands. While this is the case for many springs types, oases are focal points for human evolution, culture, engagement, and association with arid landscapes (Kreamer et al., 2015; Stevens and Meretsky, 2008). The term oasis evokes an image of cultural context in which humans balance use and sustainability of scarce resources, creating a fine-scale, local refugial niche amidst inhospitable surroundings (Laureano, 2001). However, over the course of human cultural development and history, the concept, dream, and reality of the oasis have been extended to include desert cities, such as those in the Middle East and the American Southwest. Scaling up and extending the oasis concept to large urban settings sets the stage for unsustainable expectations and demands on limited environmental resources.

In this article, we focus on the biodiversity and consequences of human socioecology on oases in the Sonoran Desert in southwestern North America (Fig. 1). The Sonoran Desert covers roughly 260,000 km² in the southwestern United States and northern Sonora in Mexico. Springs distribution data in Mexico are not known to us, but nearly 1000 springs have been reported in the Sonoran Desert in Arizona and California, and if springs density is relatively consistent across the entire Sonoran Desert, we estimate that more than 2000 springs exist in the Sonoran Desert, a density of slightly less than 0.01 springs/km². These springs often are the only water sources in large areas, and vary tremendously in terms of their size, water quality, species diversity, ecological significance, structure, cultural history, contemporary use, and conservation status. Given the isolation and biocultural richness and importance of its springs, the Sonoran Desert is an ideal region in which to examine how regional ecohydrology influences oasis ecosystem form, function, conservation status, and roles in aridland societal development.

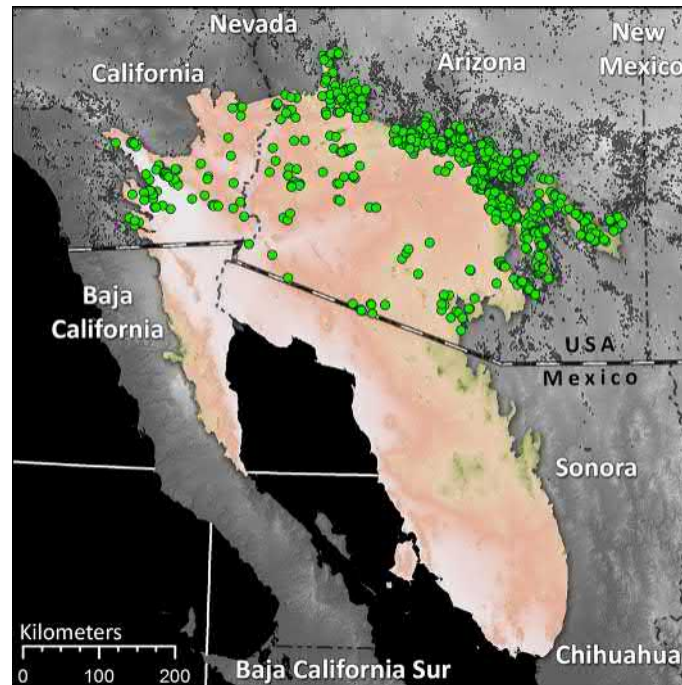


Fig. 1 The Sonoran Desert, including springs reported in the California, Arizona, and New Mexico portions of the desert. Map produced by J. Jenness (Museum of Northern Arizona Springs Stewardship Institute, Flagstaff), with base cover derived from <http://maps.tnc.org/files/shp/terr-ecoregions-TNC.zip>, and springs distribution data from MNA-SSI.

Characterization of Sonoran Desert Springs and Oases

Springs emerge in terrestrial and aquatic (including marine) environments. Springs can be perennial, seasonally ephemeral, or have periodic or erratic emergence intraannually and among years. Springs flow can be immeasurably small, or sufficiently large to create large wetlands, rivers, and even lakes. The largest reported springs ecosystem on Earth is reportedly Dumanli Spring in Turkey (mean flow = 5.03×10^4 L/s; [Karanjac and Günay, 1980](#)). Springs water can be cold, warm, or geothermally hot, and have low to very high concentrations of solutes, depending on the hydrogeology, flow path, and aquifer lithology.

Classification and definition of a clear lexicon are required for any field of scientific inquiry, and establishing those prerequisites is long overdue for the field of springs ecosystem ecology. Despite their often small size, springs ecosystems are enormously complex, each with particular groundwater flow paths that vary from a few hours for those near recharge areas, to millennia and long distances for aquifers with low hydraulic conductivity. Groundwater emergence onto the Earth's surface is usually driven by gravity, but also can be pushed by geologic processes or gas. Flow path and aquifer conditions can determine springs geochemistry, temperature, flow rates, and consistency, all of which may be extremely constant or highly variable and diverse.

Springs emergences generate aquatic, wetland, and riparian habitats that function in remarkably individualistic fashion, and even closely adjacent springs are rarely similar in all ecological details. Springs ecosystems often develop in complex landscapes, and usually are small, making them difficult or impossible to detect on aerial photographs or through remote sensing. However, some springs are so expansive they create hundreds of hectares of aquatic and wetland habitat. Springs and sometimes lakes create the headwater base flow of all streams and rivers in nonice-dominated landscapes on Earth.

In the Sonoran Desert, precipitation (including snowmelt) infiltrates aquifers through recharge zones, often at the base of mountains (mountain front recharge). Aquifers are formed by alluvial fill of unconsolidated sand and gravel in basins, permeable sedimentary rocks such as sandstones and limestones, and heavily fractured volcanic and crystalline rocks. Springs often form at the contact between an aquifer and an aquitard such as impermeable shales, mudstones, claystones, siltstones and dense crystalline rocks. Groundwater percolating through the higher permeability strata reaches the aquiclude or aquitard and flows along it horizontally, or nearly so until it emerges in a geologic fracture or fault on a canyon wall, a hillslope, or an escarpment edge. The high geologic and geomorphologic complexity of the Sonoran Desert allows for the emergence of thousands of springs, particularly from small aquifers on mountain flanks. The largest Sonoran Desert springs may be Blue Springs, a complex that emerges in the lower Little Colorado River, with an average flow of about 6.37×10^3 L/s. This perennial flow supports the highest abundance and diversity of native desert fish in the Southwest.

Variability in springs characteristics has proven to be a daunting challenge to hydrologists, who have argued without resolution for more than a century over potential ways to classify springs. Springs' enormous geomorphological and ecological diversity generates ecosystem complexity that transcends traditional discipline-based classification and requires collaborative engagement among

the fields of hydrology, ecology, and anthropology. Such collaboration is both difficult and rare, but without it, the recognition of springs and oases as focal sociocultural ecohydrological habitats has not occurred. This lack of consensus on springs classification has directly led to the ubiquitous, but largely ignored degradation and loss of these important ecosystems.

To address the challenge of springs classification, [Springer and Stevens \(2009\)](#) developed a comprehensive terrestrial springs classification system, describing 12 springs types, all but one of which occur in the Sonoran Desert ([Table 1](#); [Figs. 2-3](#)). Among these, many hillslope, helocrene, limnocrene, mound-form, gushets, and hanging gardens springs types have been extensively modified by humans, and qualify as oases. Hillslope springs, which allow the use of gravity to transport water across human-dominated landscapes are common water sources for desert oasis agricultural irrigation.

Adding greatly to the ecological complexity of springs is the cooccurrence within springs of as many as a dozen different geomorphic microhabitats, each of which is generated by discrete physical processes, and each supporting its own suite of species. These microhabitats can include bedrock surfaces, pools, channels, terraces, spray zones, and hyporheic zones below the channel floor, among others ([Springer and Stevens, 2009](#)).

Evolutionary Ecology and Diversity

Oases and other springs are complex ecosystems with diverse ecological and evolutionary processes and functions. In arid regions, such as the Sonoran Desert, springs often are differentially highly productive ecosystems located in areas of relatively low productivity. Despite their often small size, they contain tightly packed, highly interactive assemblages of both upland and wetland obligate plants and animals. Thus, springs function both as refugia and as keystone ecosystems—ecologically interactive points within larger geographic areas. Depending on their age, geomorphology, isolation, and specific environmental and biogeographic histories, some springs function as paelorefugia, supporting high levels of endemism because they provide environmental constancy through evolutionary time. Many species, including humans have survived episodes of glaciation and global warming, desertification, and shifting precipitation at, or by seeking out springs refugia ([Nekola, 1999](#); [Cuthbert and Ashley, 2014](#)).

Springs-dependent species are those that rely on springs habitat for at least one phase of their life histories. The processes of relictualization and adaptation have led to the evolution of a wide array of springs-endemic species that are closely adapted to thermal or physiochemical conditions at specific springs. Prominent among these springs-dependent taxa in the Sonoran Desert are aquatic springsnails (Hydrobiidae, especially the hyper-diverse genus *Pyrgulopsis*), dryopoid beetles (Dryopidae and Elmidae), pupfish (Cyprinodontidae), and many poorly-known or unstudied invertebrate taxa. Low-elevation, endemic springs plant species primarily include alkaline soil specialists, while potentially endemic springs riparian invertebrates have not received much scientific attention. Through relictualization, springs-dependent populations become even more restricted in distribution under harshening, adverse environmental conditions, but through adaptation those populations also may expand when environmental harshness relaxes.

One of the older springs complexes in the Sonoran Desert appears to be Montezuma Well in the Verde River in central Arizona ([Blinn, 2008](#)). This collapsed carbonate mound springs ecosystem forms a 120 m-wide pool that is 16 m deep, and lies in a kilometer-wide travertine paleosprings complex ([Fig. 4](#)). Its unithermal, carbonate- and arsenic-rich waters create a highly productive, fishless ecosystem that, due to the processes mentioned above, support at least five endemic springs-dependent invertebrate species and an endemic diatom, the highest concentration of unique species at a single point in North America, to our knowledge ([Fig. 5](#)).

Table 1 Springs classification system ([Springer and Stevens, 2009](#)).

<i>Spring type</i>	<i>Description</i>
Cave	Groundwater emerges in a cave system, typically in karstic aquifers with large conduits.
Exposure	Exposure of groundwater at the Earth's surface in a fracture or sinkhole.
Fountain	Focused groundwater flow forced out of the Earth by head pressure from a confined aquifer.
Geyser	Explosive flow of hot water from a confined aquifer (the only springs type not found in the Sonoran Desert).
Gushet	Discrete springs flow gushes from an escarpment or steep slope of perched, unconfined aquifers, often along fracture zones.
Hanging Garden	Water emerges from indistinct or multiple sources seeping from shallow, unconfined aquifers. These often form in canyons of layered sedimentary rocks, where underlying formations have been weathered back from a harder, impermeable layer above.
Helocrene	Groundwater emerges diffusely in a marshy, wet meadow or low gradient wetlands, often with indistinct or multiple sources seeping from shallow, unconfined aquifers.
Hillslope	Springs form from unconfined aquifers on a hillslope, often with indistinct or multiple sources of flow.
Hypocrene	Shallow buried springs where flow does not reach the surface, but is expressed through wetland vegetation. This is also a transitional state of springs that are being dewatered, either naturally or through anthropogenic groundwater withdrawal.
Limnocrene	Groundwater emerges in a pool, often with relatively uniform temperature and chemistry.
Mound Form	Groundwater creates a organic, mineralized (often carbonate or travertine) or ice (e.g., permafrost-zone pingos) mound.
Rheocrene	Flow from springs emerges into a stream channel.



Fig. 2 Lower Deer Creek Springs, a hillslope springs ecosystem along the Colorado River in central Grand Canyon. In northern Arizona, the Sonoran Desert extends into the Grand Canyon, upstream along the Colorado River. Photo by L.E. Stevens.



Fig. 3 Bug Spring Hanging Garden: A rare hanging garden springs type in the Sonoran Desert. Photo by L.E. Stevens.



Fig. 4 Montezuma Well, a collapsed carbonate mound oasis spring in central Arizona, supports at least six endemic springs-dependent species, and contains abundant prehistoric Sinagua Indian house and agricultural fields, including irrigation canals. Photo by L.E. Stevens.

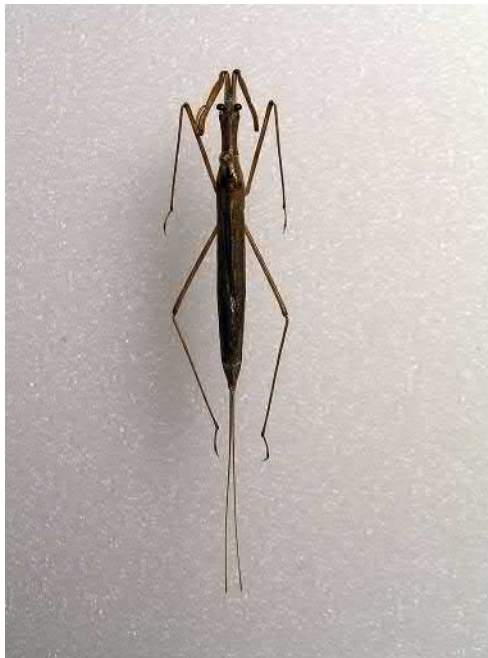


Fig. 5 Montezuma Well Water Scorpion—Hemiptera-Nepidae: *Ranatra montezuma* Polhemus 1976, one of several endemic invertebrates living only in the Montezuma Well oasis springs ecosystem, central Arizona. Photo by L.E. Stevens.

The composition of species assemblages at springs is shaped by topography, isolation from other similar springs, the size of the wetted area, environmental stochasticity, and the sequence, life history strategies, and genetic constitution of colonizing species. Old and environmentally constant springs ecosystems can function as paleorefugia, supporting a few to many endemic species, whereas highly variable or newly formed springs function as neorefugia, supporting widespread weedy species with long-distance dispersal mechanisms, including nonnative taxa. Nonintuitively, nonnative plant species richness is positively related to that of native species at springs. This is likely due to the elevated productivity of springs that, when disturbed by natural or anthropogenic mechanisms,

are quickly colonized by weedy species. Springs function as stepping stone refugia, serving as stop-over points for migrating or dispersing birds and mammals, as well as supporting unique combinations and assemblages of microbes, plants, and animals. Springs may support metapopulations, interconnecting sink and source populations that, with periodic connectivity, can maintain species over long time periods. Springs also are settings in which frequent connectivity through animal migration or human trade introduce complex suites of species that can survive and persist in the favorable oasis environment. These processes highlight the tension between isolation and episodic connectivity that characterize immigration, colonization, and extinction in springs ecosystems. The dueling ecological impacts of isolation and environmental connectivity can create highly stable and resilient springs habitats over time, but can render others fragile and highly susceptible to human-induced degradation (Fig. 6).

Indigenous Use of Springs Ecosystems

Springs have played an integral role in human ecology and evolution in arid zones throughout the world. Our hominin ancestors repeatedly retreated to springs in the Olduvai Gorge during dry phases (Cuthbert and Ashley, 2014). In the Sonoran Desert, springs ecosystems served as vital locations for prehistoric peoples and societies, and as such, have a long history of human management. Archeological investigations at relic springs sites in the Sonoran Desert reveal fossil and carbon evidence that early Clovis cultures used springs to ambush Pleistocene megafauna, such as mammoths, camels, and bison at the end of the last ice age 13,000 years ago (Haynes Jr, 2008). Springs at that time served as nuclei for hunter-gather cultures because of their concentrated water, plant, and animal food resources. Subsequently, and with the invention of agriculture, springs played an integral role in human settlement, cosmology, and transition to farming in the Sonoran Desert.

The complex topography of the Sonoran Desert gave rise to oasis cultures different than those of other drier, more formidable deserts. In the Sonoran Desert, annual rainfall varies from 3 to 20 in. with a distinct, bimodal precipitation regime of intense summer monsoons, and low-intensity winter storms. Elevations range from below sea level at points on the Baja California peninsula to over 3,050 m (10,000 ft) in the Sky Islands of the Sierra Madre and ranges of southeastern Arizona. Oases of the Sonoran Desert and Baja California peninsula are rugged and resemble the Old World desert oases of the Arabian Peninsula and North Africa, with lush green vegetation sharply contrasting the surrounding hyper-arid desert (Fig. 7). Sonoran Desert springs exhibit diverse habitats, including seeps, plunge pools, ciénegas, and narrow canyon streams, as well as ephemeral runoff-supported wetland and riparian ecosystems. Indigenous exploitation of these environments was as spatially and temporally diverse as the landscapes of their inhabitation.

Early prehistoric cultures of the Sonoran Desert practiced a type of proto-agriculture, encouraging, and later collecting seeds and actively irrigating plant species native to the region (Mabry, 2005). In southeastern Arizona, these species included goosefoot (*Chenopodium* spp.), amaranth (*Amaranthus* spp.), tansy mustard (*Descurainia* spp.), Indian rice grass (*Oryzopsis hymenoides*), dropseed grass (*Sporobolus* spp.), native tobacco (*Nicotiana* spp.), and possibly native cotton (*Gossypium* spp.) Archeological research dates



Fig. 6 Yellow Monkeyflower—Phrymaceae: *Erythranthe guttata* (Fisch. DC.) G.L. Nesom, northwestern corner of the Sonoran Desert in Spring Creek Canyon, Grand Canyon National Park, Arizona. Photo by Springs Stewardship Institute.



Fig. 7 San Borja oasis on the Baja California peninsula of Mexico. Note the date palms (*Phoenix dactylifera*) growing as an overstory species. Photo by R. de Grenade.

the use of these proto-crop complexes to 5,000–3,000 years before present (y.b.p.). Mesoamerican crop species arrived to the Sonoran Desert 4,500–2,500 y.b.p., either through migration or diffusion, including maize (popcorn) (*Zea mays*), pepo squash (*Cucurbita pepo*), common bean (*Phaseolus vulgaris*), bottle gourd (*Lagenaria siceraria*), and possibly domesticated cotton (*Gossypium hirsutum*). From 1,500 to 900 y.b.p. tropical cultivar complexes arrived in the region, including flour corn (*Zea mays*), jack bean (*Canavalia ensiformis*), cushaw squash (*Cucurbita mixta*), butternut squash (*Cucurbita moschata*), and domesticated tobacco (*Nicotiana rustica*). During that phase, archeological and historic records indicate that additional native Sonoran Desert plants were domesticated, including tepary bean (*Phaseolus acutifolius* var. *latifolius*), agave (*Agave* spp.), little barley (*Hordeum pusillum*), panic grass (*Panicum sonorum*), and devil's claw (*Proboscidea parviflora* var. *parviflora*).

The Santa Cruz River in Tucson, Arizona was a perennial stream, with a lush riparian environment created by a perched aquifer. Indigenous cultures managed the intermittent flow of this riparian system basin for almost four millennia. Excavations at the site of Las Capas, northwest of Tucson near the confluence of the Santa Cruz and Rillito Rivers, revealed 3,200-year old irrigation canals, with diversion channels and gridded gardens (Mabry, 2008). The later Hohokam culture (450 CE) reconstructed these irrigation systems, and also developed additional farming and water-management technologies to survive in the arid, highly variable climate of the Sonoran Desert. The Hohokam practiced floodwater farming on lower mountain slopes and arroyos, capturing and spreading ephemeral flows laden with nutrient-rich organic debris onto agricultural fields. They also directed overland sheet flow with simple rock berms to intercept and concentrate stormwater. They built small mounds of rocks to hold extra moisture for dispersed agave cultivation across hundreds of hectares of the lower mountain bajadas (Fish and Fish, 1992).

Likely descendants of the Hohokam, related O'odham tribes later inhabited the Sonoran Desert. The Tohono O'odham lived in the mountain foothills during the winter, and moved to farming camps or villages along desert washes in the summer. They employed a technique called *ak-chin*, or flood irrigation farming, diverting springs and ephemeral floodwaters during summer monsoon storms from small washes to floodplain fields. They planted cottonwood and willow trees in living fencerows to help slow, direct, and spread the nutrient-dense floodwaters over their fields. When the waters receded, they planted many different traditional crops, such as varieties of corn, beans and squash in the fertile, moist ground. These low-tech landscape strategies included shallow contour terracing created by placing lines of single stones, diversion walls, grids, and living fencerows—all methods of capturing limited water resources and creating a positive environmental niche in an arid environment to allow cultures to thrive for millennia in the harsh environment (Nabhan, 1983).

Rea (2008) describes how springs in the Sonoran Desert and US Southwest often are sites of legends, creation sagas, mythical creatures, and divine beings. In some creation beliefs, springs were not only sources of sustenance, but sources of life, where clans emerged from other dimensions to live on the Earth. Such springs were and remain keystone cultural foci, providing not only basic living resources, but a landscape connection to history and a sense of cultural reconnection and meaning for future generations. The famous water serpent emerges in many tribal cosmologies as the sacred guardian of springs. A persistent belief in Sonoran cultures today, the divine beings that occupy/create springs must be honored and respected to maintain the perpetuity of water and societal well-being. If the serpent is killed, the water and human culture will disappear.

Old World and New World Influences in Oasis Agriculture

Jesuit missionaries first arrived to the Sonoran Desert from central Mexico in the late 1600s, bringing with them a complex suite of Old World beliefs, agricultural practices, and species (Sheridan, 2004). In colonial fashion, these were injected into indigenous Mesoamerican land use practices and native plant assemblages to create novel socioecological systems. Jesuits and other Spanish colonizers implemented their own, larger canal irrigation systems, called *acequias*, from the Arabic *as-saqiyya*. The missionaries forced indigenous neophytes to dig an *acequia madre*, or “mother” ditch to intercept springs outflow. That canal delivered water to lateral ditches to irrigate fields and orchards. They lined some of the canals with rock or lime mortar, and in places created holding ponds to regulate the flow of water to the fields. Jesuit missionaries implemented these irrigation and farming systems as an integral part of their evangelizing colonization strategy. By controlling water supplies, the missions quickly became centers of *reducción*, concentrating and converting indigenous tribes to Catholic life and beliefs.

The Jesuits introduced a largely Mediterranean oasis crop repertoire that included species available in Europe, the Middle East, North Africa, and the Canary Islands, and several newly acquired species from the New World. They introduced perennial species, such as figs, grapes, olives, citrus, quince, peach, apricot, apple, pear, pomegranates, dates, and bananas, and annual crops such as wheat, corn, barley, beans, garbanzos, rice, cotton, watermelons, melons, squash, onions, beets, garlic, yams, tomatoes, lettuce, radishes, and peppers. They also brought domesticated livestock, including horses, burros, sheep, goats, and cattle. Using these strategies, the Jesuits established a succession of missions along river valleys, advancing northward through the Sonoran Desert.

On the hyper-arid and rugged Baja California peninsula, the shock of Jesuit missionary arrival and cultural transformation was more severe. The extreme topography of the central peninsula precluded subsistence agriculture, limiting indigenous lifeways there to nomadic, hunter-gathering practices. During their 70-year ecclesiastical reign on the peninsula (1697–1768), Jesuits enforced the *reducción* of the nomadic Pericú, Guaycura, and Cochimí peoples into sedentary, agrarian lives (Crosby, 1994). Cultural conversion was concentrated on isolated spring-fed oases, where they developed terraced fields and *acequia*-style irrigation systems. As elsewhere, the Jesuits introduced Old World crop and livestock species, as well as New World species from the North and South American mainlands. Those oases were changed into complex agroecological systems with livestock, stratified cropping, terraced fields, and canal systems. The crop repertoire within each oasis thus reflected cumulative geographies of agricultural and cultural colonization and dissemination.

Studies of Baja California oases reveal that as these ecosystems provide refugia for wild species, they also serve as in-situ crop refugia (de Grenade and Nabhan, 2013). Within 241 oasis *huertas* (field gardens) surveyed in the 2010/2011, a total of 89 species of perennial food crops, belonging to 64 genera and 36 families were recorded (Figs. 8–9). These included 21 perennial species introduced by Jesuit missionaries, as well as newer arrivals. Oasis *huertas*, which hold both native and introduced species of flora and fauna, are still managed as diverse agroecosystems. They are, in most cases, small-scale farming systems that integrate crop rotation, livestock, mixed annuals and perennials, and crop tiering. In many gardens, perennial fruit plants grow along the irrigation ditches and form hedgerows between fields, providing shade, windbreaks, and attraction for insectivores and pollinators. Fields are planted with forage crops, grains, legumes, and vegetable crops, or rows of perennial fruit crops, nopal (*Opuntia* spp.), or vine crops. Livestock, including cattle, burros, sheep and goats are grazed in the gardens



Fig. 8 Oasis *huerta* or field-garden in Comondú, Baja California peninsula, Mexico. Citrus, olive, sugar cane and date palms are visible in the *huerta*. Photo by R. de Grenade.



Fig. 9 Pomegranate from Santa Gertrudis oasis, Baja California, Mexico. Photo by R. de Grenade.

during fallow periods, or tethered to tall trees and palms and fed grass and herbaceous plants harvested by sickle. This fine-scale, mixed-method agriculture offers a defense against pest epidemics, drought, and floods and enables long-term viability of farms and farm families.

These biocultural oases exhibit species-packing and structural diversity; as [Rosenzweig \(1995\)](#) noted in wild systems, the more species that coexist in a particular space, the more niches they distinguish within that space. In oasis gardens, the more complex the garden structure, the more agriculture species are likely to be found. Agricultural space also is managed in temporally diverse methods, including multi-story cultivation systems, a careful mix of perennial and annual species, integrated livestock use, and alternate fallowing of terraces. Native fan palms (*Washingtonia* spp.) are the most characteristic keystone species of these oases, hosting numerous insect visitors and pollinators and providing shade, food, and habitat for resident amphibians, reptiles, birds and mammal species, as well as migratory or overwintering species ([Cornett, 2008](#)). Naturalized date palms (*Phoenix dactylifera*) now grow intermixed with native *Washingtonia* palms and have become a novel keystone species in the new guilds of wild, weedy, and domesticated species. In these ecosystems, the greatest agrobiodiversity and biodiversity often are associated with traditional land management approaches, where low-levels of mechanization are employed in cultivation. Small sections of fields are tilled for annual crops, while other sections are used to grow perennial fruit trees, vines, and forage crops. Fields with the lowest biodiversity are those that are abandoned and those that have been converted to industrial agricultural practices.

Biodiversity and agrobiodiversity within spring-fed desert oases distinctly reflect human cultural and political processes through time. Studies of two small oases in the Sonoran Desert, Quitovac, Mexico and Quitobaquito, Arizona, located within 25 miles of each other on each side of the United States-Mexican border, have shown how oasis flora has been differentially determined by Indigenous, colonial, industrial, and political forces. Elevated wild plant and avian diversity was recorded in Quitovac, where traditional Tohono O'odham and Spanish agricultural practices support a greater diversity of wild and domesticated crop species than at Quitobaquito in Arizona, where the supporting springs are now part of Oregon Pipe National Monument and isolated from continued farming and ranching practices ([Nabhan et al., 1982](#)). Surprisingly, this elevated biodiversity at Quitovac has persisted even though the springs and surrounding community have been heavily degraded by bulldozing, draining of the lagoon, groundwater extraction, gold mining, population growth, woodcutting, and grazing. Traditional cultural and farming practices support a mix of wild, weedy, and domesticated species assemblages. Anthropogenic forces, however may prove too intense as modern agriculture and industrial practices expand in the region and traditional practices wane.

Urban Up-Scaling the Myth of the Oasis

Oases throughout history have served as the intersections of cultural development and trans-continental and intercontinental trade routes. As a result of their abundant productivity, biological diversity, and general appeal, springs have become one of the most threatened ecosystems on Earth, particularly in arid regions. In the Sonoran Desert, this process began with overgrazing and intensification of agriculture, mining, and sophistication of groundwater extraction technology. Rapid agricultural expansion led to unsustainable rates of groundwater use that have been magnified as urban and suburban expansion supplants agriculture. Interbasin water transfer from the Colorado River via the Central Arizona Project facilitates ever higher rates of water use for agriculture, industry, and urbanization throughout the "sunbelt" of the Sonoran Desert. The tremendous growth of desert cities such as Phoenix, Tucson, Casa Grande, and the surrounding metropolitan areas have placed significant stress on water resources. The region's vast aquifers and thousands of springs have succumbed to rural and urban appropriation, agricultural uses, resource

extraction (e.g., for mining and livestock grazing), and recreation. Our ecological investigations in several landscapes in the Southwest revealed that often more than 90% of the springs in lowland landscapes have been ecologically impaired or destroyed by human activities, particularly groundwater depletion and pollution, and by under-informed livestock grazing and land management practices.

Oases in the Sonoran Desert were places of survival and divine significance for indigenous cultures. The oasis concept also has deep Judeo-Christian roots, and the Spanish and subsequent European colonists clearly understood the relationships between water, belief, and social dominion in arid regions. The concept of the oasis applies well to fine-scale agro-management of water sources, but does not scale-up appropriately to inform urban desert landscape development, which is erratically subject to both internal and external forces, with little emphasis on ecological sustainability. Nonetheless, the oasis has been transformed into a myth, the belief that desert lands can be “reclaimed” and transformed into vibrant, green urban spaces. The myth of the oasis has become a central water resource management paradigm behind water use policy and practice in the Southwest. The myth has become deeply embedded into the collective social unconscious, and continues to guide urban development in the Southwest.

Sonoran Desert cities are now heavily dependent on massive interbasin water transfers, and all face diminishing groundwater supplies. As with other desert urban cultures around the world, Sonoran cities generate conflict by bringing together divisive historical and societal beliefs about resource ownership, self-determination, trade, and cultural connectivity, often pitting urban and industrial expansion and values against rural lifeways and agriculture. Such conflicted societal spaces contain deep, inherent conflicts over water scarcity, and at best adopt short-term solutions that ignore potential future deficits and long-term resource management. The urban myth of the oasis clashes with need for each aridland community to recognize that a cornerstone of good governance in the desert is sustainability of water supplies and the ecological integrity of its landscape.

Human activities have greatly reduced the ecological integrity of many wetland, riparian, and springs ecosystems through competing exploitative uses, including groundwater pumping, diversions, fuel wood harvest, recreation, livestock grazing, mining, recreational use, and wildlife management. Many springs have been lost due to the construction of roads and buildings. Others have been depleted by expanding populations of invasive native and nonnative species. Invasive plants and animals often overwhelm native species, disturbing springs ecological integrity. These landscape-level impacts affect the springs source, but also may alter long-term water infiltration, flow, and emergence at distant sites.

At a landscape-scale, springs ecosystems serve as the canary in the coal mine of human-induced global change. As windows into aquifers, springs are some of the most sensitive indicators of climate change. Threats posed by climate change will profoundly affect springs, particularly through declining and faster-melting montane snowpacks, as well as through drought, wildfire, and changing precipitation regimes. These challenges alter ecosystem resilience and dynamics across spatial scale. Fragile but resilient, springs will be subject to heightened anthropogenic pressures; these pressures will elevate extinction risks of the many hundreds of springs-dependent species in the Sonoran Desert and throughout the world.

Assessment and understanding of the extent, duration, and consequences of human impacts on oases and other springs is now emerging (Stevens and Meretsky, 2008; Kreamer et al., 2015). Springs occupy such a miniscule proportion of the southwestern landscape that their demise has gone largely unnoticed. Springs may be part of larger water management systems that are highly altered for urban, mining, and agricultural use that involves complex systems of groundwater extraction and interbasin transfers, masking the fine-scale dynamics of springs and the remaining oases in relation to the landscapes in which they exist. The many external threats to these ecosystems points to the need for improved knowledge of their distribution (the quality of mapping data remains very poor in most landscapes), basic understanding of springs and oasis ecosystem ecology, and refined understanding of sustainable stewardship options.

Sonoran Desert Springs in the Future

Losing oases and springs constitutes a global environmental crisis. However, there are still opportunities for recovery of these ecosystems. If the supporting aquifer is not impaired (many montane aquifers are not), springs ecosystems can be rehabilitated and restored. Springs provide essential keystone ecosystem functions, and conserving small springs can provide cascading benefits on the surrounding landscape. The Museum of Northern Arizona Springs Stewardship Institute (www.springstewardshipinstitute.org) supports sustainable springs management and recovery by providing guidance to those interested in springs inventory, assessment, planning, stewardship, and monitoring. Mapping of springs locations and scientific study of springs ecosystems informs stewards and conservationists, policy makers, and the public. Rangeland health initiatives, rotational grazing and fencing of isolated springs has led to stabilization of some springs ecosystems. In urban spaces, sustainable water management practices such as storm-water detention basins, rainwater harvesting, and arid-adapted urban landscaping can create small oasis-like environments, even in areas where natural groundwater has been depleted. Formal measures, such as the Ramsar Convention list of Wetlands of International Importance, FAO's Globally Important Agricultural Heritage Systems, UNESCO's Man and Biosphere Programme and World Heritage sites, and the Global Geoparks Network have gained traction to help protect the natural and cultural assets of many oases. Intensive efforts at individual springs and water conservation at the landscape scale are critical to maintain the springs ecosystems and biodiversity of desert oases.

Conclusions

Desert oasis ecosystems harbor endemic native species assemblages as well as unique wild, weedy, and domesticated species complexes. Given the small land area that these spring-fed ecosystems occupy, their importance as quality habitat, migratory rest-stops, biodiversity, centers of agrobiodiversity, and economic value in arid regions is vastly underestimated. Desert oases and springs provide critical resources for wild and domesticated biodiversity, but are among the most threatened ecosystems on earth. Enhanced recognition of their importance, better understanding of their ecology and sociocultural significance, and improving stewardship practices are needed to sustain societal well-being and Earth's biodiversity. Oases have long held archetypal appeal as lush refugia for humans traveling through deserts. However, these spatially limited, bioculturally rich island-like refugia are compelling to the human psyche, and have been mythologized in modern society. Unfortunately, the "myth of the oasis" does not scale effectively to large urban settings, and this has set the stage for unrealistic expectations and demands on the limited environmental resources in these harsh, arid regions. Nonetheless, this myth has inextricably permeated aridland urban society, creating overdrafts in water use and abstraction that portend ever more serious conflicts in an unsustainable future. It is time to reconsider the myth of the oasis in relation to planning and management of urbanization in the desert Southwest to better ensure the sustainability of aridlands ecology and society. Is the oasis a suitable paradigm for urbanization of the desert, or is it, along with the dream of a cool July day in Phoenix, a perilous mirage?

Acknowledgments

We wish to express our gratitude to the University of Arizona Southwest Center and the Museum of Northern Arizona Springs Stewardship Institute for support in preparation of this article. The map was created by Jeff Jenness (MNA-SSI GIS Department), and Andrea Hazelton, Alek Mendoza, and Tierney Schipper of MNA-SSI provided welcome comments on earlier drafts.

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Desert Rarity, Endemism and Uniqueness

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Abstract

The high levels of rarity and endemism (geographically restricted species) seen in the deserts of the world are largely a result of their geographic distribution, landforms, evolutionary history and biotic interactions. Long histories of isolation and climatic change have resulted in suites of unique species, both young and old, in all major deserts. The biogeographic history of each desert is key to the processes and the evolution of its species, with key examples being latitudinal deserts, rainshadow deserts, sky islands within deserts, and fog deserts. Rainfall pulses and other evolutionary pressures have resulted in surprising levels of convergence between the deserts of the world, with plants and animals taking similar forms, but coming from very different lineages and origins. Excellent stewardship of our global deserts is of key importance to biodiversity conservation worldwide.

Global Distribution Patterns

Most deserts of the world are rich in rare and endemic species, largely due to their evolution in relative geographic isolation. The extraordinary variation in climate, size, age, and evolutionary history of the world's deserts have contributed to their biological uniqueness. To understand endemism and rarity in deserts, we must first look at global patterns of distribution, and then at the evolution and origin of deserts. The fragmented evolutionary history of the deserts of the world has been the driving force of their biological rarity, of adaptation to local conditions, and of specialization to isolated environments.

On a global scale, vegetation patterns (the building blocks of ecosystems) are determined by climate. Plant diversity is highest near the equator in tropical areas ([Kier et al., 2005](#)). [Qian \(1998\)](#) showed that globally, along the latitudinal gradient, generic richness shows a striking increase with decreasing latitude. However, recent research from [Jansson \(2003\)](#) indicates that global patterns in locally endemic taxa are caused by the amplitude of climatic change during peaks of Milankovitch oscillations (every 10–100,000 years). [Stebbins and Major \(1965\)](#) classify endemic species into two main types neoendemics (recently derived endemic taxa) and paleoendemics (relicts from ancient lineages). Neo-endemics may not yet have reached their potential climatic limits if they have not had adequate time to expand their ranges. These two categories of endemism can be difficult to separate without a large amount of inference, but they are significant when considering the modern day patterns of desert endemism. Smaller climatic shifts allow the survival of paleoendemics and diverging gene pools (neoendemics) are able to persist. Using change in mean annual temperature since the last glacial maximum, [Jansson \(2003\)](#) showed that areas which have experienced larger temperature changes have lower endemism in mammals, birds, reptiles, amphibians and vascular plants (robust to area, latitude, extent of former

glaciation and oceanic island syndrome). This research suggests that Rapoport's rule (species range increases with latitude) is a product of the increase in the amplitude of climatic oscillations as you move towards the poles.

The first true desert conditions in most of the world are thought to have originated during the Pliocene, 5–10 million years ago, and expanded gradually during the Pleistocene interglacials. The Namib Desert began to develop in the Early Oligocene as cold water from the Southern Ocean was able to penetrate northwards (Van Zinderen Bakker, 1975). The antiquity of this desert is well reflected in its endemic biota. Climate has changed significantly in the world's deserts since the late Pleistocene glacial period. The Last Glacial Maximum (LGM) was 25–17 thousand years ago, when large ice sheets dominated and the climate was cooler. During this time deserts moved towards the equator, shrinking in the mid-latitudes, where they were replaced by more temperate vegetation types. Many of our modern desert plants and animals took refuge in areas that are now dry subtropical forest. As the glaciers retreated (around 15 thousand years ago) the Holocene period began, which leads us right up to the current Anthropocene climate. Generally, the high-latitudinal edge of the world's desert was colder and wetter during the last glacial maximum but the tropical edge may actually have been drier than it is today. For example, in the late Pleistocene the Chihuahuan Desert of North America harbored woodlands of piñon pines, junipers, and oaks, while the tropical dry woodlands of central Mexico became drier, evolving the extremely rich cactus flora (endemism and diversity) that characterizes this region. Modern warm-desert vegetation in Western North America started becoming extensive < 12,000 years ago (Frenzel, 2005; Raven and Axelrod, 1978; Axelrod, 1978). Holocene climate brought a more intense monsoonal season in sub-tropical regions and deserts moved into the mid-latitudes.

Sky-Islands and Fog Deserts

Much of the endemism within our global deserts is found in isolated outcroppings or sky islands. This is most often the case in rugged and cool mountain ranges that are located within expansive desert plains. The refugial effect allowed the continued existence of species that were extirpated elsewhere. Their isolation for 15–20 thousand years has resulted in many unique genetic traits and new taxa. The biological effects of the LGM were more severe in the northern hemisphere and therefore the sky islands of the north are richest in relictual species. A similar phenomenon is also seen in areas where coastal moisture (fog) creates climatic refugia, allowing the continued existence and proliferation of ancient taxa.

In North America, the relictual "Madro-Tertiary" flora which originated in Mexico, moved north and then was largely extirpated, is well documented in the fossil record (Axelrod, 1950). In Africa, similar relictual ranges are found within the Saharan plains, and the Atlas Mountains in northern Morocco shelter rich pine (*Pinus*) and oak (*Quercus*) forests in a similar fashion. The mountain ranges of south-eastern Algeria and northern Niger harbor a number of endemic and rare Mediterranean species such as tarout (*Cupressus dupreziana*), wild olive (*Olea europaea*), and Saharan myrtle (*Myrtus communis*). The Tibesti Mountains in southern Libya are also home to a relictual flora from the Mediterranean and the tropics. Northern relicts are also present in the Somali Peninsula in the high mountains. In the tip of the Horn of Africa, the Somali Montane Woodlands depend on the marine layer and coastal moisture forming a refuge and center of endemism for plants and animals. The higher part of the ranges is home to species such as kadi (*Murraya koenigii*), mountain box (*Arctostaphylos uva-ursi*), Ethiopian pistachio (*Pistacia aethiopica*), and remnants of ancient juniper (*Juniperus*) forests. The high mountains of Yemen and Saudi Arabia also give shelter to a rich relict montane ecosystem. Coastal fog nearest the Red Sea creates a refugium for more than 170 endemic plants, and it is a critical refuge for a large number of endangered animals such as the Arabian leopard (*Panthera pardus nimr*) and the Hamadryas baboon (*Papio hamadryas*). On the Arabian Peninsula, the Al Hajar range forms a wall of mountains (< 3000 m) from the surrounding deserts, providing an important refuge for endemic and relict species of plants of Mediterranean and Indo-Iranian origin, often growing in the vicinity of tiyu (a carob relative) and other trees of African ancestry. The endemic Arabian tahr (*Arabitragus jayakari*), a type of wild goat, is still frequent in these precipitous slopes.

Along the Pacific coasts of Baja California, a fog refugium occurs where Mediterranean ecosystems give way to Sonoran Desert (Jennings et al., 2018; Vanderplank and Ezcurra, 2015; Vanderplank, 2013). Similar patterns can be seen in the extensive foggy deserts of Chile, particularly in the Copiapó region, for which the cactus *Copiapoa* is named. Some plants of the Chilean desert survive almost entirely on fog moisture, as do the desert camels or guanacos (*Lama guanicoe*) which are the famous inhabitants of the arid Atacama (Raedeke and Simonetti, 1988). The dunes of Namibia are home to many examples of tenebrionid beetle endemism. Species in the genus *Onymacris* have larvae that come to the surface at night and absorb water vapor through their rectal cavity, giving them unique adaptations to the most arid environments and allowing them to take advantage of fog moisture (Henschel and Seely, 2008).

Species Migrations and Biotic Considerations

Ackerly (2009a) introduces the concepts of synclimatic (with climate) migration, resulting in niche conservatism; and anticlimatic (not following climate) migration which often results in adaptive evolution. As such, species that moved with climate have conserved niches, species that did not move fast enough had to adapt. This of course results in ancient species that are very distinct (e.g., *Welwitschia* of the Namib desert), as well as more recently evolved desert endemics that have adapted on a climatic edge such as desert legumes that reach 60%–70% endemism in the central deserts of Baja California (Garcillan et al., 2010). Ackerly (2009a,b) points out that survival may be heavily dependent on biotic contexts and for those species not migrating with the climate it may be

the competition (or lack thereof) from new species arriving (or not) dictates whether a species survives the new regime (rather than it being wholly necessary to “adapt” to the new climate). In light of this, successful adaptive response may simply be driven by barriers to dispersal of other species.

Recent research on the biotic interactions between plants in the Tehuacan Valley has revealed that facilitation as a mutualism evolved between taxa from the quaternary (nurse plants) and taxa from the tertiary that were adapted to wetter conditions, but persist as a result of the nursing effects of more recently derived desert lineages (Valiente-Banuet et al., 2006). This is essentially a newer lineage (perhaps not endemic, certainly not rare) nurturing a paleoendemic in an inland desert. This facilitation prevented extinction during times of climatic change at the end of the tertiary, and facilitation is often provided by just a few keystone “nurse” species (Verdú and Valiente-Banuet, 2008). Surprisingly the generalist nurses are often the most abundant species in the community, providing strong resistance to extinction for the dependent species. These results indicate that biotic relationships between taxa not only have provided a mechanism for preserving biodiversity but also a mechanism for stabilizing selection through time (Valiente-Banuet et al., 2006). This facilitation also allows niche conservatism in ancient lineages and increases phylogenetic diversity in desert plant communities (Valiente-Banuet and Verdú, 2007). In closely related species, these facilitative mutualisms can turn into competition in times of stress of changing climate (Valiente-Banuet and Verdú, 2007; Verdú et al., 2010).

Rarity

Rarity is separate from endemism, a scarce plant having a wide range is essentially the complete opposite of a narrow endemic (i.e., endemics are not always rare, and vice versa), and this distinction relates to the differing habitats and distribution patterns of these plants (Mills and Schwartz, 2005). Kruckeberg and Rabinowitz (1985) give an excellent review of understanding of rarity and factors affecting narrow plant distributions, which are often considered the most threatened. There are seven broad types of rarity that vary with accordance to their degree of restriction, degree of habitat specificity, and local abundance—the most “rare” being both habitat specific and small range with a small population such as a species occupying an edaphic outcrop. Narrow endemics are most often members of distinctive communities or singular habitats, and as such, deserts are a rich breeding-ground for narrowly endemic species. An inability to exploit new habitats or to cope with anthropogenic change may be the most important general features associated with rarity (Cadotte and Lovett-Doust, 2002). Many desert species are considered “rare” simply because they are only seen above-ground following significant rainfall events—many ephemeral plants and geophytes, as well as several invertebrates which may only hatch *en masse* following specific climatic conditions. Scarcity is a dangerous strategy in arid environments since opportunities to reproduce are often highly restricted. Many animal species considered rare today in the world’s deserts have been pushed into this conservation status by anthropogenic impacts.

Desert Biogeography

Deserts are found throughout the world, and it is their biogeographic history that is critical to endemism and rarity. Deserts dominate in bands of arid land which run parallel to the equator, in both the northern and southern hemispheres, at 25–35 degrees latitude in each hemisphere (Fig. 1), forming the large, mid-latitude deserts approximately 2000–4000 km from the equatorial rainforests. In the northern hemisphere, the succession of mid-latitude subtropical deserts is formed by (1) the Nearctic, (3) the Palearctic, and (3) Indo-Malay. In the southern hemisphere, the chain is formed by (1) Neotropics, (2) the Afrotropics, and (3) the Australasian deserts (Allan et al., 1993; McGinnies et al., 1977; Pipes, 1998; Ricciuti, 1996).

Latitudinal Desert Belts

Solar radiation is highest nearest the equator, yet the tilt of earth’s axis (23.5 degrees) generates a zone of maximum solar interception that is to the north in the tropic of cancer half the year, and to the south in the tropic of Capricorn half the year. This creates a band of unstable air around the equator which in turn generates significant rainfall and is home to the equatorial rainforests. In the maximum solar interception regions (25–35 degrees north and south of the equator) the air is cooler and more stable, resulting in less precipitation, it is calm dry air that dominates. These are known as the “horse latitudes” and this is where our great deserts are located (Goudie and Wilkinson, 1977).

Continentality and Inland Deserts

Sometimes an arid desert is formed because of the enormity of a continental landmass. Atmospheric moisture comes primarily from the evaporation of our oceans and distance from the ocean can generate a considerable aridity gradient. As such, land-locked central areas of large continents may become deserts simply because the air reaching them is already dry. A good example of this is the Monte Desert in South America, as well as the Central Deserts of Australia and the Great Basin Desert of North America, but most especially in the Taklimakan and Gobi deserts of Central East Asia.

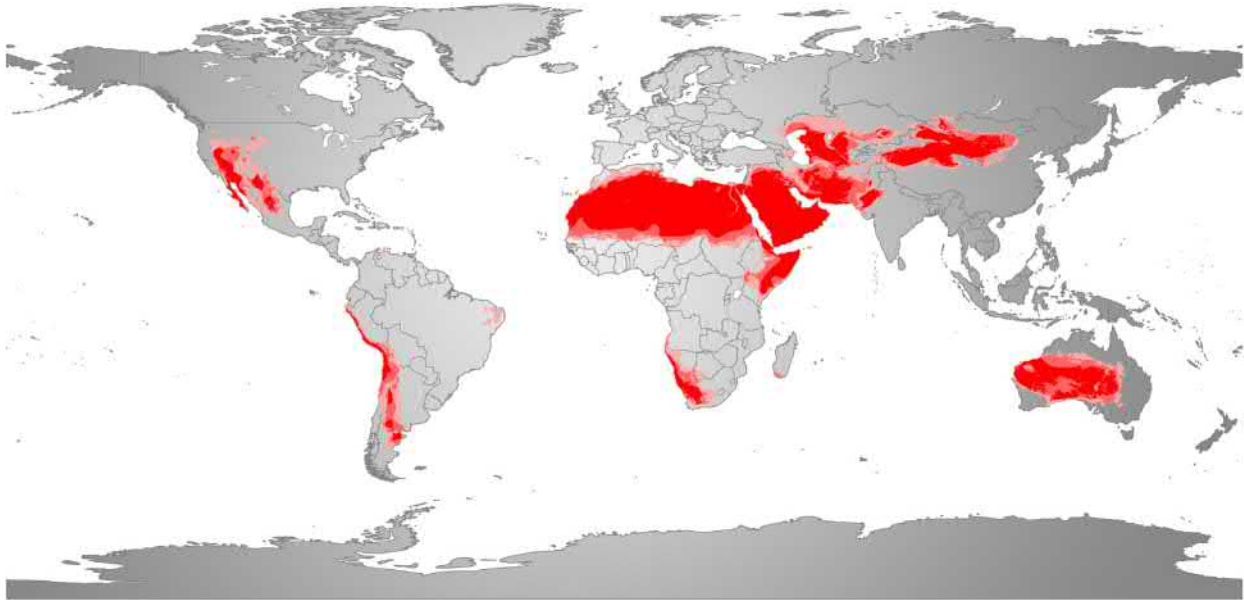


Fig. 1 The Desert Biome defined by three alternative criteria: (A) Arid regions of the planet as defined in the World Atlas of Desertification (UNEP, 1997); (B) global ecoregions of the world (Olson et al., 2001) that harbor desert vegetation; and (C) contiguous regions of extremely low vegetation cover derived from AVHRR satellite images of the world (USGS, 2005). The intensity of the red color indicates congruency between the three criteria: Areas in intense red correspond to regions where the three criteria coincide, areas in intermediate color highlight regions where two criteria coincide, and areas in pale red show areas where only one criterion operates.

Coastal Deserts and Fog Deserts

Despite the general latitudinal pattern of the world's deserts, only the western side of continents are normally occupied by deserts, while the eastern side tend to be more mesic. This is related to the circulation of our ocean currents. The pull is strongest at the equator that drives current to move in a clockwise direction in the northern hemisphere, and an anticlockwise direction in the southern hemisphere. As the surface waters move away from the continents, they pull cold, nutrient-rich water up to the surface, generating cool, stable air, often known as the "marine layer" or coastal fog. This very stable air can form some of the driest deserts on earth, such as the Atacama Desert, but also the Namib Desert, the Baja California Deserts, and the Coastal Desert of Morocco.

Rain Shadows and Tropical Deserts

Topographic considerations are also key to desert conditions. While the windward slopes of most tropical mountain ranges are covered by cloud forests, the leeward part, known as the "rain shadow" of the mountains, is covered by arid scrub. The rain shadow effect is largely responsible for many tropical arid lands that are found outside the mid-latitudinal ranges. Examples include the Sechura Desert in Peru and Ecuador, the Caatinga scrub in equatorial Brazil, or the Tehuacán Valley desert in southern Mexico, a hot-spot for cactus biodiversity. They are also responsible for some high-latitude cold deserts, such as Patagonia, and the deserts of Central Asia.

Desert Landforms

Deserts suffer much more wind erosion than any other environment. Additionally, if slopes are steep and when the rain does fall, they also experience very fast water erosion. Desert landscapes come in two categories: (1) "shield" deserts and (2) "mountain-and-basin" deserts (Cooke et al., 1992; Mabbutt, 1977) which alter their hydrology and carve their landscapes into new microhabitats for desert life.

Rainfall Pulses

Rainfall pulses are the central driving force structuring desert ecosystems and controlling the resource in highest demand. Plants and animals in desert regions have developed a plethora of adaptations to cope with the ephemeral abundance of water, in terms of their growth, population dynamics, and life cycles (Sher et al., 2004). Rainfall events often vary significantly from one pulse to the next, temporally (in terms of season), in size, intensity, duration, and dry interludes between pulses. Each desert organism is adapted to take advantage of these pulses, although often at different soil depths (triggered by different intensities and durations). Surface-

dweller are particularly excellent at taking advantage of brief and light pulses and endemism and rarity are seen in annual plants and short-lived (or *k*-selected) animals. More significant pulses sustain longer-lived species and the heterogeneity of pulses promotes species richness and biodiversity of desert ecosystems (Chesson et al., 2004). When rainfall is ample, desert annual wildflowers replenish their seedbanks, crustaceans, desert toads, and other amphibians reproduce exponentially before returning to their dry torpor, and granivorous rodents, such as North American kangaroo rats (*Dipodomys*), Australian hopping mice (*Notomys*), and African jerboas (*Jaculus*), can stock up their underground caches and larders, storing food for the long drought ahead.

Seasonality of rainfall pulses is extremely important and often affects which species are able to respond. Winter rainfall deserts tend to be found closer to Mediterranean and temperate ranges (higher latitudes) and summer rainfall deserts closer to the equator, with bimodal rainfall patterns in between. Seasonality affects which plants will germinate in bimodal deserts (Mulroy and Rundel, 1977). Unsurprisingly plants responding to winter rainfall tend to show more temperate affinities in their phylogeny and plants of summer rainfall have more tropical affinities. Plants that respond to winter rain are often faced with a very limited growth period because temperatures may not be conducive to the growth in winter months, and if they delay growth into the summer drought is imminent. This leaves just the spring months for plants to be productive, and as such, shifts the percentage of annual plants significantly up in the winter rainfall deserts (as compared to summer rainfall deserts). The rapid response of desert ephemerals often leads to highly synchronous blooms (including the famous “super-blooms” like that of 2019 in the California deserts). These plants survive dry periods (often many years of drought) as seeds or even in underground storage organs such as bulbs or tubers, and then must carry-out their life cycle very quickly in the short growing season. These species can afford to have aboveground structures that lack drought adaptation because they will be abscised or killed as the drought begins. As such, they can have large soft leaves and stomata, increasing their growth rate and providing significant resources to desert herbivores. Short generation times that dominate in desert environments are also subject to high evolutionary pressures and result in increased levels of speciation (Cutter and Gray, 2016). Monsoonal or summer rains, in contrast, provide water at a time when temperatures are ideal for plant growth and fast growth followed by a “hibernation period” which in plants results in drought-deciduousness as the dominant life-form and for animals an aestivation period (e.g., kangaroo rats and other members of the Heteromyidae). Fleshy trunks and extreme succulence are common in summer rainfall deserts, many of these plants having very shallow roots that cover a large surface area to capture even the slightest pulse.

Geographic Origins

The deserts of the world occur in six of the world’s large biogeographic domains, or eco-realms. A detailed description of each desert ecoregion within these realms can be found at National Geographic’s Wild World website (www.nationalgeographic.com/wildworld/terrestrial.html) and at the World Wildlife Fund’s terrestrial ecoregions website (<http://www.worldwildlife.org/science/ecoregions/biomes.cfm>). See further reading section for additional details (see EE papers) Enc Bio.

Afrotropic Realm: Deserts of East and Southern Africa

The Afrotropic deserts include four lowland desert ecoregions as well as eight coastal desert ecoregions including Arabia, Madagascar, Somalia, Namibia, and South Africa’s Succulent Karoo. They include 2.7 million square kilometers (10% protected), and they are home to charismatic macroflora such as *Welwitschia mirabilis*, with the greatest leaf longevity in the world, in the Namib desert, succulent-stemmed baobab trees (*Adansonia*), myrrh-trees (*Commiphora*), bottle-trees (*Pachypodium*), and kokerbooms (*Aloe dichotoma*). Southern Africa is home to 10% of the world’s flora, with 30% of the world’s fishmoths (Lepismatidae) are endemic therein. The deep red sands of the Arabian Desert are dominated by characteristic perennial plants such as *Calligonum comosum*, *Artemisia monosperma*, *Monsonia nivea*, and *Scrophularia deserti*; tussock grasses, *Panicum turgidum*, and other grasses are also abundant (Vesey-Fitzgerald, 1957). On the African continent, relictual species from wetter periods find refuge in the granitic inselbergs and ephemeral annual species dominate the dolerite ridges (Burke, 2003). Surprisingly the inselberg archipelago in the southern Namib Desert are not home to any endemic plant species, despite their aridity and isolation (Burke et al., 2002). However, high levels of endemism are found in plants, vertebrates, and invertebrates in Namibia’s escarpment region (Simmons et al., 1998).

The Succulent Karoo has three times as many endemics as the Sonoran Desert in one third of its area (Cowling et al., 1999), and is the world’s only plant biodiversity hotspot that is entirely found within the desert biome (Mittermeier et al., 1999) that boasts high levels of endemism for succulent plants, reptiles and invertebrates. The spatial isolation of rupicolous taxa (e.g., insects and reptiles) that are restricted to large coastal dune fields is hypothesized to have been key to speciation processes (Simmons et al., 1998). Areas of endemism and species richness in the succulent karoo do not overlap for mesic taxa, but show high overlap for succulent plants, insects, and arachnids (Simmons et al., 1998). Namaqualand is a winter-rainfall desert, with 40%–50% endemism in its flora, and narrow endemics in the northwestern parts of Namaqualand are significantly overrepresented in the Mesembryanthemaceae, Crassulaceae, and Asclepiadaceae (Cowling et al., 1999). Endemic plants are over-represented among succulent (dwarf and low) shrubs and, to a lesser extent, geophytes. Most endemic plant species in Namaqualand are neoendemics: mostly belonging to large genera and having many close relatives (Cowling et al., 1999). The Madagascan thorny desert thickets also have a unique and highly diverse flora and fauna, with high levels of localized endemism including the octopus tree (*Didierea madagascariensis*). The flora of Namibia includes at least 687 endemic plant species wholly within Namibia’s borders (17% of the flora), with two

centers of endemism therein: the Kaokoveld, and the Succulent Karoo. The Kaokoveld is home to 211 endemic species when the Angolan region is included, many of which are relics from the flora of northeast Africa. The succulent Karoo has around 380 endemic plants (including near-endemics) with high levels of recent speciation in the genus *Lithops* (Maggs et al., 1998).

Australasian Realm: Deserts of Australia

The deserts in the Australasian realm comprise 10 flat, lowland ecoregions in WWF's classification, covering some 3.6 million square kilometers (9% protected). All the arid eco-regions identified in Australia receive only sporadic rain and are sparsely vegetated. Endemism is particularly high in the mammals of the Australian deserts (excluding bats) (Keast, 1968). The Great Artesian Basin in central Australia has many desert springs that are home to very high levels of endemism in its amphipod populations (Murphy et al., 2013). Moisture-harvesting lizard the Australian thorny devil, *Moloch horridus*, (the only species in the genus, endemic to arid Western Australia) has special skin structures, comprising a micro-structured surface with capillary channels in between imbricate overlapping scales, which enable the lizard to collect water by capillarity and transport it to the mouth for ingestion (Comanns et al., 2016). The Gibson Desert, or stony desert is home to unique species such as the bloodwood or bleeding tree (*Corymbia opaca*), the mulga (*Acacia aneura*), and spinifex (*Triodia*) or Porcupine grass. Permanently wet areas for refugia and are home to a suite of relic-tual endemic ferns, reeds, and rushes. The Great Sandy-Tanami Desert is an extensive area of reddish sand plains (Ayers' Rock); while the Tirari Desert has vast sand dunes that harbor an abundant and diverse fauna, including locally endemic marsupials, lizards, frogs, and parrots.

Indo-Malay Realm: Deserts of India and Pakistan

The Indo-Malay region harbors two hot lowland deserts—the Indus Valley and the Thar—covering 0.26 million square kilometers (20% protected). The Thar desert is home to numerous species of reptiles, desert scorpions, mongoose (*Herpestes*), red fox (*Vulpes*), chinkara (*Gazella*), and falcons (*Falco*). Rare species such as the Indian Bustard, Blackbuck, and wild cat are disappearing in other parts of India but find refuge in the great desert. The area boasts 23 lizards and 25 different snakes. One of the most iconic species of conservation concern in the region is the Indian wild ass (*Equus hemionus khur*). The Thar desert is home to dominant plants such as *Halostachys caspica* on salty soils and *Aristida pennata* on sandy ones. Some of the endemic plant species of the Thar Desert are: *Caligonum polygonoides*, *Cenchrus biflorus*, *Acacia nilotica*, *Prosopis cineraria*, *Lasiurus indicus*, *Tecomella undulata*, *Citrullus colocynthis*, *Anogeissus pendula*, *Salvadora oleoides*, *Commiphora wightii*, *Haloxylon salicornicum*, *Capparis decidua*, *Suaeda fruticosa*, *Aerva pseudotomentosa*, *Crotalaria burhia*, and *Leptadenia pyrotechnica* (Khan et al., 2003). Around 45 plant species in the region are considered threatened or endangered (Khan et al., 2003). In the Indus Valley five large mammals are found: the Indian wolf, striped hyena, caracal, Indian leopard, and the urial (*Ovis orientalis punjabensis*) along with many rodents and other mammals. Meanwhile, the 190 species of bird in the desert include the red-necked falcon.

Nearctic Realm: Deserts of North America

The Nearctic deserts are formed by five lowland deserts including the Chihuahuan, Sonoran, and Mojave deserts and the coastal deserts of Baja California. They cover 1.7 million square kilometers (19% protected). The giant saguaro cactus (*Carnegiea gigantea*) is emblematic of the Sonoran Desert; and similar in appearance to the Cardón (*Pachycereus pringlei*) which dominates the Baja California deserts. The mostly arid peninsula of Baja California is home to more than 3500 species of plants, almost a quarter of which are endemic (Rebman et al., 2016). Major genera that dominate these deserts and exhibit high levels of endemism include *Agave*, *Fouquieria*, and *Bursera*. Around 1000 of the 3200 plant species in the Chihuahuan Desert are endemic. The Joshua tree (*Yucca brevifolia*) is the charismatic symbol of the Mojave Desert. Scorpion endemism is high in Baja California deserts, and very narrowly endemic desert pupfish are also found throughout the Nearctic deserts. Interestingly in the flora of Utah, most endemic plants are restricted to the low deserts of the state (Shultz, 1993). In California, Kraft et al. (2010) looked at the distribution of neoendemisms, which correlated poorly to climate and topography. They found the endemics of the western edge of deserts to be very young, with most endemism in habitats that have undergone post-pleistocene isolation or climatic change; with sky islands having wetter climates and the greatest temporal diversity of endemics.

Neotropic Realm: Deserts of South America

The Neotropic deserts include two lowland deserts a high-altitude inland desert (Central Andean Dry Puna), and the coastal deserts of Atacama and Sechura. They cover 1.1 million square kilometers (6% protected). These deserts form a long arid continuum that cover South America's "arid diagonal," starting from the Pacific Ocean in Peru, and running in a southeast direction to the Atlantic coast of northern Patagonia. The barren landscape of the Atacama Desert is one of the driest deserts on earth, sometimes going more than 20 years without rain (Armesto et al., 1993). On the coastal slopes above 600 m, plants and animals of the Atacama are entirely

dependent on the moisture provided by frequent fog (Armesto et al., 1993). However, on the coastal plains and canyons where fog is absent (between 26 and 30 degrees latitude), rainfall is the only moisture, and 40%–60% of the flora belongs to genera endemic to Chile (Armesto et al., 1993). The Monte, east of the Andes, is an open, low thorn-scrub harboring a characteristic endemic flora of zygophylls (family Zygophyllaceae). Many genera of invertebrates exhibit high endemism within the boundaries of the biogeographic province (Roig-Juñent et al., 2001). The Monte Desert is home to at least 180 endemic plants, mostly distributed in the most arid regions, with *Monttea aphylla* being endemic to the Monte and considered one of the species whose distribution most closely coincides with the proposed boundaries of the biogeographic province (Elías and Agesen, 2016). The dry Central Andean Puna carries tall tussocks of bunchgrass and a unique flora of high-altitude cushion plants.

Palaearctic Realm: Deserts of central Asia, the Middle East, and Northern Africa

The Palaearctic realm includes the largest set of deserts in the world including 21 lowland desert ecoregions that cover an immense corridor from the Atlantic coast of Morocco, to the Mediterranean coast of the Sahara, to the Gobi in Central Asia. The Palaearctic realm also harbors three coastal deserts (Atlantic Persian Gulf, and Red Sea), and in total covers 16 million square kilometers, 63% of all the deserts on the planet (9% protected). The great shield desert of the Sahara has immense dune fields for a third of its area. The deserts of sub-Saharan Africa show much more concentrated centers of endemism north of the equator, and the distribution of endemism bears no correlation to modern-day climate patterns (Linder, 2001). The deserts of the Middle East and Central Asia are all rain-shadow deserts, and the Sahara alone occupies 10% of the African continent. Vegetation is more diverse in the Western Sahara, with xerophytes and ephemeral plants in the open desert plains. Considering the hyper-arid conditions, the fauna of the Sahara is relatively rich, with 70 mammal species, 20 of them large; 90 species of resident birds, and around 100 species of reptiles. Central Asian Deserts are home to desert bulbs such as wild tulips (*Tulipa* spp.); and animals like wild Bactrian camels (*Camelus ferus*) and Asian wild asses (*Equus hemionus*). The Mesopotamian shrub desert is transitional between the deserts to the south and the steppes to the north. The whole eco-realm has evolved under continual grazing pressure and most plants are adapted to grazing pressure.

Convergence

The isolation of the great deserts of the different continents has driven outstanding examples of convergence, which are embodied by many examples from the arid-adapted plants (Figs. 2 and 3). Succulence, CAM (Crassulacean Acid Metabolism) photosynthesis,



Fig. 2 The Australian horny devils (*Moloch horridus*, shown in this picture taken in Alice Springs, Australia) are surprisingly similar the North American horned lizards (*Phrynosoma coronatum*, in Baja California) in both their feeding habits and their ecology. Their similarity, however, is due to convergent evolution in distant deserts, as they belong in different families and are taxonomically unrelated. Photo credits: Patricio Robles-Gil.



Fig. 3 Evolutionary convergence in desert plants' life-forms from different evolutionary origins. (1) *Sarcocaulouscent* (giant-stemmed) trees: (A) Baobab trees (*Adansonia digitata*, Malvaceae) in the Bandia Reserve, Senegal and (B) Elephant tree (*Bursera microphylla*, Burseraceae) in Baja California, Mexico. (2) *Succulent-leaved rosettes*: (C) Socotrine aloe (*Aloe perryi*, Asphodelaceae) in the island of Socotra, Yemen, and (D) desert agave (*Agave deserti*, Agavaceae) in Palm Canyon, California. (3) *Crassicaulescent* (succulent-stemmed) growth forms: (E) Candelabra tree (*Euphorbia candelabrum*, Euphorbiaceae) in Northern Tanzania, and (F) Senita cactus (*Pachycereus schottii*, Cactaceae) near La Paz, Baja California Sur, Mexico. (A) From Myriam Louviot Wikimedia Commons id = 2,717,945. (B) From Dick Culbert, Wikimedia Commons id = 50,051,571. (C) From Gerry & Bonni, Wikimedia Commons id = 38,582,139. (D) From Stan Shebs, Wikimedia Commons id = 195,444. (E) From Amante Darmanin, Wikimedia Commons id = 42,133,155.

and drought adaptations have evolved multiple times in these discreet regions. For example, cacti (Cactaceae) and euphorbs (Euphorbiaceae) have evolved very similar suites of characters, including spines, succulent bodies, leaflessness or highly ephemeral leaves, slow growth rates, high longevity, CAM photosynthesis and the presence of bumps on their surface. Convergence is also seen between different members of the Cactaceae such as the *Mammillaria* species of North American and the *Gymnocalycium* of South America. The family Aizoaceae, predominantly African in origin, including the living stones (*Lithops*) consists of succulents that bare remarkable resemblance to many of the Crassulaceae, primarily found in the Americas (e.g., stonecrops and *Sedum* species). Even woody-stemmed spiny shrubs can be seen to converge when we compare *Fouquieria* (Fouquieriaceae) from the Sonoran Desert with and *Didierea* (Didiereaceae) from Madagascar. Stem-succulent trees are a distinctive feature of tropical drylands. In addition to their water storage capacity, they often have photosynthetic bark, which can process internally respired CO₂ with almost no water loss at

all (Ávila-Lovera and Ezcurra, 2016). These trees include the Baobab (*Adansonia*) from Africa, and the *Burseras* of central America and the Caribbean. Other non-succulent trees with green photosynthetic stems include many of the legumes of the Baja California deserts (e.g., *Parkinsonia*), as well as *Colletia* from Argentina and South American deserts. Similar processes have occurred in the fauna, one example being the similarities between the hares or jackrabbits (*Lepus californicus*) of North America and the bilby (*Macrotis lagotis*), an endangered marsupial similar to a jackrabbit, with giant ears for temperature control in Australia. In 1976, Blair assessed convergence across vertebrates between the Monte Desert (Argentina) and the Sonoran Desert (USA). He found very low endemism in amphibians, but higher in reptiles. Highest of all are the levels of endemism in desert heterotherms (vertebrates which can control and adjust their body temperature), which reach 71% in the Monte and 61% in the Sonoran Desert (excluding Baja California). Mammals in contrast exhibit very low levels of endemism in both regions, and although the mammal fauna of Sonoran deserts is double that of the Monte, it has lower rates of endemism (Blair et al., 1976). *Ariocarpus agavoides* in Tamaulipas looks a lot like the rosetofilous agaves of central Mexico and there are almost endless examples of uniquely evolved taxa from distinct origins, sharing very similar morphologies and adaptations. Recent research indicates that convergence and trait conservatism can be very difficult to separate and are highly dependent on temporal scale (Ackerly, 2009a; Ackerly et al., 2010). Some examples of convergence can be seen in the disparate deserts of the world, yet in contrast to the high levels of endemism in many desert plants around the world, desert vines are surprisingly pantropical and the genera shared between the major deserts (Parsons, 2005).

Conclusion

Diverse processes have affected the evolution and origin of the incredible biodiversity of the world's deserts. The formation of the deserts themselves, climatic change through deep time, and biotic interactions have all shaped the biodiversity patterns that we see today, resulting in hotspots of endemic taxa which may be young or old, or both. These processes have resulted in key conservation targets, both in the deserts themselves, and the unique species found therein. Despite similar climatic conditions, isolation has resulted in the evolution of many similar life forms with highly divergent origins in arid lands around the globe. While deserts and their inhabitants may sometimes look similar, each represents a unique series of adaptations and an original solution to our shared challenge of life on planet earth. Excellent stewardship of our global deserts is essential to biodiversity conservation and the survival of many highly evolved plants and animals.

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Desert Biogeography: Sahara-Sahel Biodiversity Patterns

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Abstract

The common perception of the Desert biome is that it generally constitutes remote areas of low diversity. However, the world's largest warm desert, the Sahara, together with the neighboring arid Sahel exhibit high topographic and climate heterogeneity and have experienced strong climatic oscillations that have shaped land-cover and biodiversity distribution. This review summarizes the knowledge on the Sahara-Sahel biodiversity patterns based on the distribution of terrestrial vertebrate species richness (also called α -diversity) and species turnover or the change in species among sites (β -diversity). The distribution of β -diversity in the Sahara-Sahel follows the general latitudinal gradient, with higher percentage of species found in the southern Sahel region. This broad latitudinal gradient pattern is disrupted by higher number of species distributed along hypothesized ecological corridors and refugia. The distribution of β -diversity highlights the boundaries of the Sahara-Sahel hotspots of species richness. At local scale, recent studies have emphasized the natural value of isolated and residual wetlands (oases, lakes, and seasonal rivers) of high productivity, acting as refugia for relict populations. Among these wetlands, mountain rock-pools constitute local hotspots of biodiversity.

Introduction

Desert biomes are generally perceived as remote and uniform areas of low diversity when compared to other biomes. Yet they host unique assemblages of species, communities and ecological processes (Ward, 2016). Desert biomes exhibit high local diversity, often endemics, largely because organisms are capable of exploiting patches of high productivity (Ward, 2016). Deserts constitute perfect laboratories for biogeographic studies as species and communities are highly structured and are subject to strong climate control (Ward, 2016). In North Africa, the Sahara Desert and the arid Sahel exhibit unique features that distinguish them from other warm deserts and arid regions worldwide, which make them suitable for observing and understanding biogeographic patterns.

The Sahara is the largest warm desert in the world with land coverage of about 9 million km², and together with the arid region Sahel, they cover about 11 million km² (Fig. 1). Despite its large extent, the Sahara was recently formed. Evidences pointed for about 7 million years ago in Chad (Schuster et al., 2006; Zhang et al., 2014) or even more recently (2–3 million years ago) in western regions (Swezey, 2009). Around 7 million years ago, the African tectonic plate crashed relative to the Eurasian plate and the resulting closure of the Tethys Sea (the forerunner of the modern Mediterranean Sea) was associated with the earlier aridification of the Sahara Desert (Zhang et al., 2014). Since the Pliocene (5.3–2.5 Mya), the region experienced strong climatic oscillations with multiple dry-wet cycles (Le Houérou, 1997). For instance, around the mid-Holocene, the region experienced the last humid period being covered with extensive grassland vegetation, lakes and wetlands (Gasse, 2000; Kröpelin et al., 2008). This wet period finished between 6 and 5000 years ago with an increase of aridity, disappearance of mesic vegetation communities, decreased of lake levels, and the current onset of conditions were established (Foley et al., 2003; Holmes, 2008). The climate and land-cover oscillations have greatly shifted the limit between the Sahara and the Sahel with profound effects in the distribution of biodiversity patterns (Brito et al., 2014, and references within).

The Sahara-Sahel is characterized by high topographic heterogeneity, from salt pans below sea level to high-altitude peaks distributed along a system of mountains (UNEP, 2006; Fig. 1). The region displays strong environmental gradient and heterogeneity, mostly arranged in a latitudinal way (Fig. 2). There is considerable spatial variability in average annual temperature (from 8°C to 30.8°C) and precipitation (up to 1432 mm). The current location of the border between the Sahara and the Sahel overlaps with a biogeographic crossroad between the Palaearctic and Afro-tropical biogeographic realms (Dinerstein et al., 2017; Fig. 1), and with a transition zone between two major biomes—Deserts and Xeric Shrublands and Tropical and subtropical grasslands, savannas, and shrublands (Fig. 2). This biogeographic location resulted in a latitudinal variation in species distribution and increased local biodiversity (Brito et al., 2014, and references therein). Given the biogeographic location, the Sahara-Sahel is a perfect example of an area of high species replacement, holding a geographically structured assemblage of species, natural communities, and environmental conditions (Ecoregions, Dinerstein et al., 2017). Thus, it is highly suitable for studying biogeographic patterns. In this

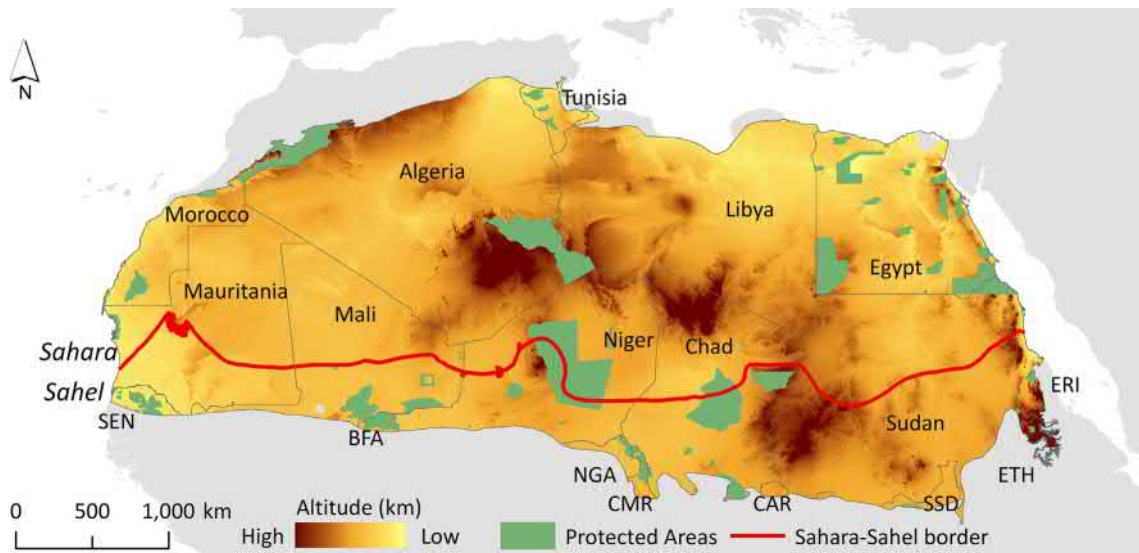


Fig. 1 The Sahara-Sahel. Limits of the Sahara-Sahel (Dinerstein et al., 2017), altitudinal variation, and distribution of protected areas. SEN: Senegal; BFA: Burkina-Faso; NGA: Nigeria; CMR: Cameroon; CAR: Central African Republic; ETH: Ethiopia; ERI: Eritrea.

context, uncovering distribution patterns of spatial structure of biodiversity focusing local species richness (also called α -diversity), species turnover, i.e., change in species among sites (β -diversity), and regional species diversity (γ -diversity) are fundamental for understanding the biogeography of the region. This chapter describes the major biogeographic patterns of biodiversity in the Sahara-Sahel region, focusing in these major components of diversity.

Biodiversity Distribution Patterns

The knowledge about biodiversity distribution patterns across the Sahara-Sahel is still poorly documented in comparison to other biomes, despite the increasing sampling efforts over the last decades (Brito et al., 2014, 2016). The geographic location in countries of low human development has hampered the allocation of funds for scientific studies (Durant et al., 2012; Brito et al., 2014). Moreover, field surveys and trans-border research has been also obstructed by the regional insecurity and armed conflicts (Brito et al., 2018). These constraints result in a large number of species whose knowledge on geographic distribution, population status and demographic trends are insufficient or lacking for assessing conservation status. For instance, ~17% of the Sahara-Sahel terrestrial endemics remain unevaluated (NE) and 15% are data deficient (DD) according to IUCN Red List (2018). Due to general remoteness and insecurity, large portions remain poorly surveyed and unexplored, such as northern-eastern Mauritania, northern Mali, south-western Algeria, or southern Libya (Brito et al., 2014).

From the available data about distribution patterns of terrestrial vertebrates (amphibians, reptiles, birds and mammals), the Sahara-Sahel biodiversity is spatially well-structured (Fig. 3). Overall, biodiversity distribution (α -diversity) in the Sahara-Sahel follows one of the oldest patterns in ecology and biogeography: the latitudinal diversity gradient (Brown and Lomolino, 1998). Thus, there is a latitudinal gradient in species richness, with high number of species restricted to the southern Sahel, followed by the lower Nile valley. The latitudinal distribution patterns are consistent with the distribution of biogroups, i.e., species assemblages with shared distributions, and functional groups, i.e., species assemblages with shared biological traits (Vale and Brito, 2015; Brito et al., 2016).

The broad latitudinal gradient is however disrupted by high percentage of species restricted to the central Sahara mountains and along the Nile river valley (Fig. 3). Furthermore, high levels of biodiversity are also distributed along rivers, and hypothesized ecological corridors and refugia in the Sahara-Sahel (Brito et al., 2014, and references within). For example, the coastal belt of the Atlantic Sahara, the mountains of the central Sahara, the Red Sea coast, and the Nile River valley are pointed as ecological corridors for terrestrial vertebrates (Brito et al., 2014). They follow North-South axis and are remnants of savannah-like habitats that covered the region during past humid periods (Brito et al., 2014). The mild climate influenced by the proximity of the sea in the Atlantic Sahara and Red Sea corridors also contribute to local high species richness (Brito et al., 2014; Gonçalves et al., 2018; Velo-Antón et al., 2018). Continental mountains support high α -diversity of endemic terrestrial vertebrate species, as well as a relatively high diversity of Afrotropical fishes and flora (Brito et al., 2014, and references within). Due to their geographic or environmental isolation, Sahara-Sahel mountains constitute refugia for biodiversity, particularly for aquatic and mesic species (Brito et al., 2014, 2016; Gonçalves et al., 2018 and references therein). Species with distinct biogeographic affinities are currently found in isolated suitable habitats, suggesting temporal distribution shifts during Plio-Pleistocene cycles (Dumont, 1982; Le Houérou, 1997; Drake et al., 2011) and former population connectivity during favorable conditions (Dumont, 1982; Drake et al., 2011).

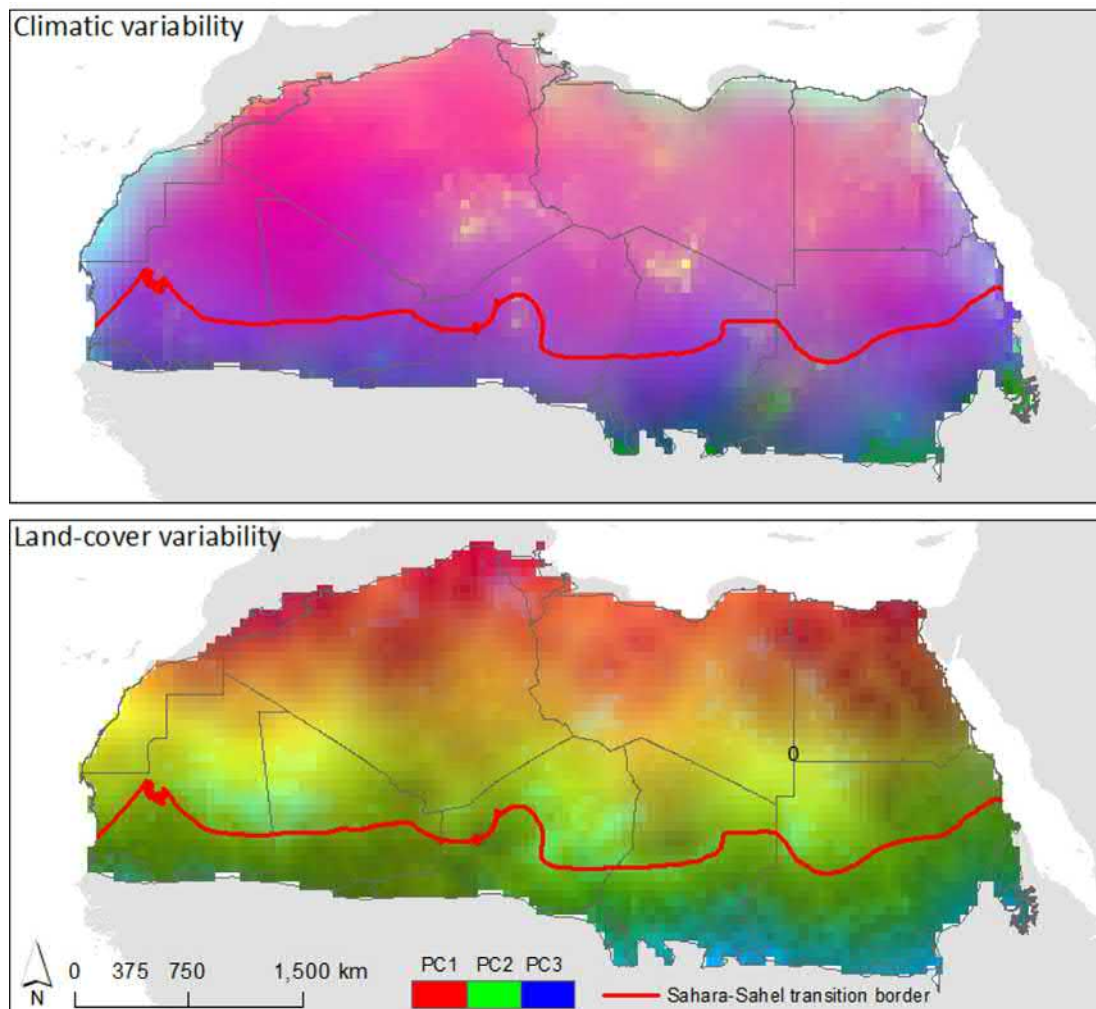


Fig. 2 Environmental variability in Sahara-Sahel derived by spatial principal component analysis (SPCA). *Top*: Composite map of current climate variability, where PC1 in red (52.5%): temperature seasonality (standard deviation $\times 100$), and temperature annual range; PC2 in green (24.5%): maximum temperature of warmest month and mean temperature of warmest quarter; and PC3 in blue (10.3%): annual mean temperature, minimum temperature of coldest month and precipitation of wettest month. *Bottom*: Composite map of land cover variability, where PC1 in red (43.3%): distance to open broadleaved deciduous forest/woodland, shrubland and herbaceous vegetation and grassland; PC2 in green (15%): distance to cropland, mosaic cropland and sparse vegetation or grassland and PC3 in blue (11%): distance to bare, rock and sandy areas.

The distribution of β -diversity in terrestrial vertebrates tends to disrupt the broad latitudinal gradient pattern observed for α -diversity (Fig. 3). While the hypothesized ecological corridors and refugia are identified by α -diversity patterns (i.e., high number of species observed), β -diversity highlights the boundaries within the Sahara-Sahel hotspots of species richness. High turnover is expected in transition areas between high and low species richness, and also abrupt shifts in assemblage composition. There is some overlap in the transition area between the Palaearctic and Afro-Tropical realms (Dinerstein et al., 2017) and high β -diversity, which reveals a turnover in species composition and richness in the area. High β -diversity of total species depicts the edge of hypothesized ecological corridors and refugia, such as the Atlantic Sahara, the Central Sahara mountains, the Red Sea coastal mountains, and the Nile river valley. The β -diversity in endemics, besides defining as well these ecological corridors and refugia, also highlights the vast empty quarters and dune massifs with low β -diversity values and overall low species diversity (Brito et al., 2014; Vale and Brito, 2015). The Sahara-Sahel mountains hold high levels of endemics, probably resulting from the refugia character of mountains during past climatic oscillations (Trape, 2009; Brito et al., 2014). Due to the mild conditions and high productivity, the Atlantic and the Red Sea coastal areas and the Nile river valley also hold high levels of Sahara-Sahel endemics (Brito et al., 2014, and references within).

The distribution of β -diversity patterns is inconsistent among taxonomic groups (Fig. 3). For instance, there are no amphibian communities in the deepest Sahara, due to generalized lack of water availability. The β -diversity patterns in reptiles are similar to those observed for mammals, particularly within the Sahara. Similarity is also observed to endemics, as most of endemic species of the Sahara-Sahel are constituted by reptiles and mammals (Fig. 3). Endemic lizards were located in the most arid and flat areas of the Sahara-Sahel (Vale and Brito, 2015). In birds, β -diversity follows different patterns and highlights the major migratory routes,

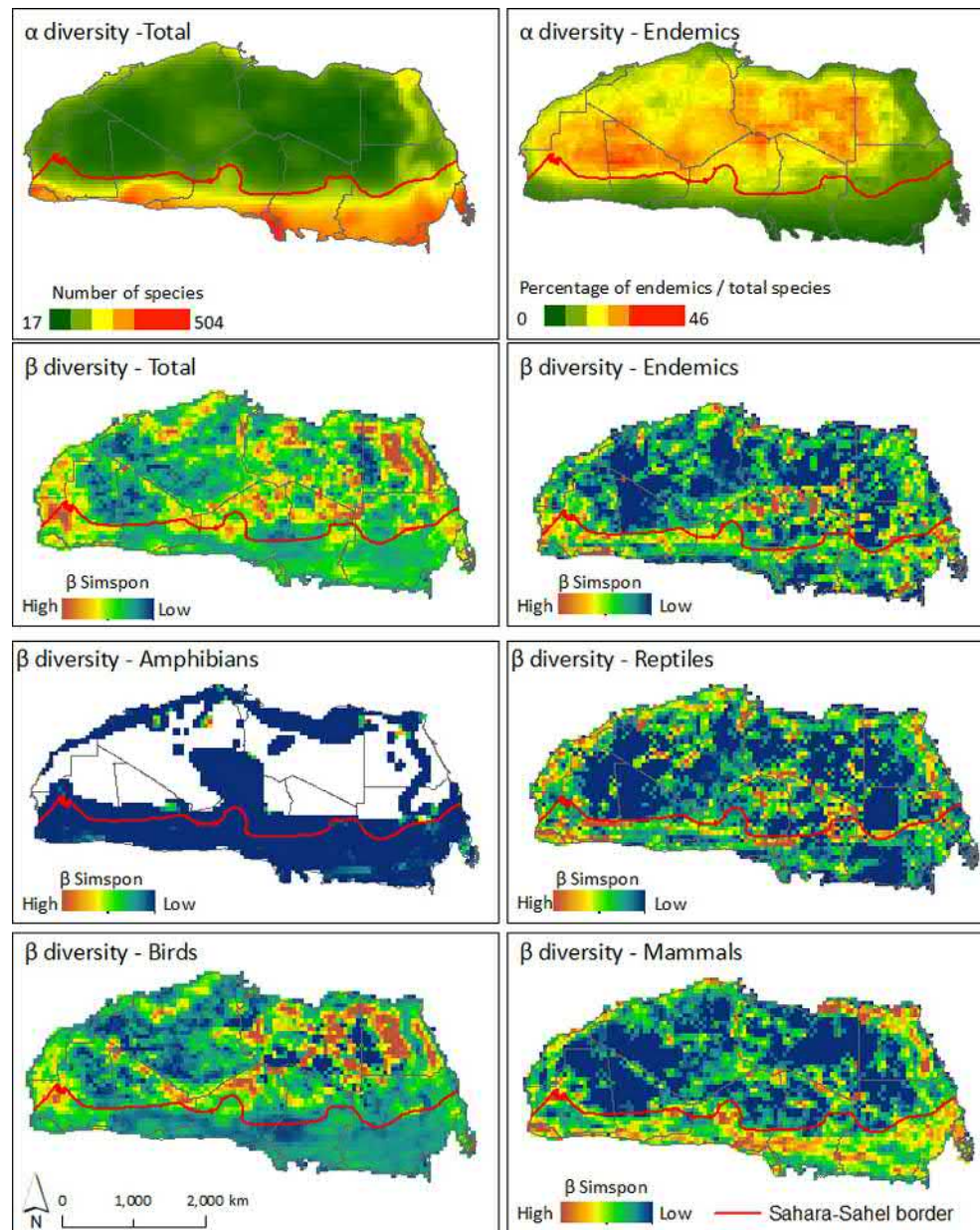


Fig. 3 Biodiversity distribution patterns of terrestrial vertebrates (amphibians, reptiles, birds and mammals) in the Sahara-Sahel. α -Diversity and β -diversity for total number of species and endemics, and β -diversity by taxonomic group. Species distribution polygons were retrieved from IUCN (2018). β -Diversity was quantified using the Simpson measure (β sim) which account for pure spatial species turnover (Baselga, 2010).

across the Libyan desert and following Western Nile river valley (Somveille et al., 2019). β -Diversity in mammals tends to follow the patterns observed for reptiles and endemics, highlighting the vast empty-quarters as important for small mammals (Vale and Brito, 2015) and for large-sized vertebrates, such as *Acinonyx jubatus*, *Addax nasomaculatus*, or *Chlamydotis undulata* (Brito et al., 2014, and references within).

At the local scale, isolated and residual wetlands (oases, lakes and seasonal rivers) surrounded by sandy areas act as refugia for relict populations and constitute suitable habitats where unique species have evolved (Brito et al., 2014, and references within, Trape, 2013). High levels of local diversity are found restricted to these humid habitats within corridors, such as the Atlantic Sahara-Sahel and mountain refugia. Located in the upstream of narrow valleys at the base of these mountains, mountain rock pools (locally known as *gueltas*) constitute micro-wetlands that allow the maintenance of rich communities, with many endemic species, and relict Afro-tropical fauna (Vale et al., 2015; Brito et al., 2014, and references within). A study of 69 *gueltas* (total area of about 43 ha) highlighted their natural value as local hotspots of biodiversity, since they hold about 32% and 78% of the total taxa analyzed and endemics of Mauritania, respectively (Vale et al., 2015). The number of species present in *gueltas* was found to be positively correlated with primary productivity, area of *gueltas*, and occurrence of permanent water (Vale et al., 2015). Studies in the Atlantic

Sahara corridor emphasized the existence of a network of seasonal rivers that acted as dispersal corridors. For example, these corridors allow gene flow between isolated populations of West African crocodile (*Crocodylus suchus*) in the mountains of Mauritania and southern populations in Mali and Senegal (Velo-Antón et al., 2014). The value of wetlands across the Sahara as refugia for relict tropical fauna is emphasized by the presence of these crocodiles, which persist as relict populations in Chad and Mauritania (Brito et al., 2014, and references within).

In the last decade, and despite the growing regional insecurity, increasing scientific efforts allowed the consolation of the Sahara-Sahel as natural laboratory for understanding biogeographic patterns. Insights on biodiversity distribution have emerged from increasing sampling effort of taxa and multidisciplinary scientific studies. The Sahara-Sahel is a perfect model to understand the effects of extreme climatic events on biodiversity distribution. The past climatic oscillations in the region have left an obvious signature in the distribution of alpha and beta diversity. Locally, small wetlands act as refugia for relict populations and constitute places where unique species evolve, constituting hotspots of biodiversity. The biogeographic patterns currently observed may provide also indications on potential outcomes of increasing aridity.

The conservation of Sahara-Sahel biodiversity has been yet neglected and overlooked by global assessments (Brito et al., 2014, 2016, 2018). The predicted increasing aridity associated with the escalating conflicts and social insecurity is expected to accelerate biodiversity decline (Brito et al., 2014, 2016, 2018; Vale and Brito, 2015). Desert adapted species living mostly in flat areas, where the predicted magnitude and velocity of climate change are higher, are the most vulnerable ones (Vale and Brito, 2015). Among those are the Sahara-Sahel iconic mega-fauna that have been experienced recent continuous decline due to unsustainable hunting pressure (Brito et al., 2018). Despite the design of protected areas outside areas of human activities, they are clearly insufficient and inefficient as they cross multiple political borders, requiring internationally coordinated efforts for implementation and management (Brito et al., 2016). This is particularly challenging as Sahara-Sahel range countries are developing nations, most ranked as Low Human Development and are largely underfunded for biodiversity conservation (Brito et al., 2018 and references within). As such, strategies for regional and optimized biodiversity conservation are still in need of development in the Sahara-Sahel. For instance, conservation efforts should engage from local governments to local communities in the safeguard of seasonal wetlands that sustain both human communities as well as biodiversity. Conservation actions and programs linking poverty reduction with biodiversity conservation are also in need of development. Increasing local awareness and pride within communities of the value and uniqueness of the Sahara-Sahel wildlife should be one of the first actions. Such approach would allow including biodiversity conservation and awareness into resilient peace strategies, under penalty of any other conservation measure failure (Brito et al., 2018).

Acknowledgments

This research was supported by the project Enabling Green E-science for the SKA Research Infrastructure (ENGAGE SKA), reference POCI-01-0145-FEDER-022217, funded by COMPETE 2020 and FCT, Portugal. CGV is supported by post-doctoral research fellow under the project. JCB is supported by Fundação para a Ciência e Tecnologia through contract FCT-DL57.

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The High Desert Biome: Flora, Fauna and Geology of the Northern Great Basin

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Abstract

The Great Basin of the western United States is the largest cold desert in North America. The region is most commonly defined by its hydrology, delineating an area more than 300,000 km² in size with no natural outlet to the ocean. This vast expanse of the North American interior west is dominated by the variable topography of the Basin and Range geologic province and encompasses a broad spectrum of both arid and semi-arid plants and animals. The Northern terminus of this closed basin system lies in the high desert ecological province of southeast Oregon. One of the healthiest and most intact ecosystems within the Great Basin, the Northern Great Basin boasts a fascinating diversity of native plant and animal communities and is a worldwide exemplar of the sagebrush steppe ecosystem. The biotic and abiotic components of this region make it a useful case study to examine the biodiversity of the high desert biome in North America. Here we discuss the role of geology in establishing the present day Northern Great Basin, the major plant communities and terrestrial vertebrates found there, and threats facing the region's natural systems.

The High Desert Biome

The Great Basin

The Great Basin of western North America contains some of the most topographically fragmented landscapes on the planet (Badgley et al., 2014). Characterized by the dramatic physiography of the Basin and Range geologic province, with broad temperature and elevation gradients (Chambers and Wisdom, 2009), the region supports a surprising diversity of arid and semi-arid flora and fauna, including some of North America's most recognizable species.

Defining the Great Basin's boundaries has traditionally depended on one of three sets of attributes—the region's flora, hydrology, or geology. The most common definition delineates a hydrographic region that sits between the Sierra Nevada and Cascade mountain ranges on the west, and the Rocky Mountains on the east (Fig. 1). Composed of a series of contiguous watersheds, the Great Basin spans over 300,000 km² across six western states and has no natural outlet to the ocean (Grayson, 2011).

Annual precipitation ranges widely from an average of approximately 5 cm in the lowest basin in Death Valley, California to over 100 cm on the high peaks of the Wasatch Mountains in Utah. The combination of dramatic shifts in both elevation and interannual



Fig. 1 The hydrographic Great Basin. Data sources: [USGS](#); [NOAA](#).

precipitation has played a critical role in shaping the ecology of the region and has produced a mixed composition of both grassland and desert species ([West, 1999](#)).

The Northern Great Basin

In the far northern reaches of the Great Basin lies the high desert ecological province of southeastern Oregon ([Anderson et al., 1998](#)). As with the larger Great Basin, this landscape is dominated by a series of north-south oriented fault block mountains separated by lowland basins ([Franklin and Dyness, 1988](#)), ranging in elevations from 1250 to 2965 m. Annual precipitation averages 25 cm across the region, fluctuating nearly 100 cm between the lowest basins and highest ranges ([Anderson et al., 1998](#)). Low and high temperatures during the growing season average 1°C and 20°C respectively ([Anderson et al., 1998](#)) and can vary dramatically throughout the year from extreme lows of −30°C to over 40°C during summer months.

We define the focal area of this paper as the northern portion of the hydrologic Great Basin in southeast Oregon, henceforth referred to as the Northern Great Basin ([Fig. 2](#)). The diversity of life and landform in this region provides a useful case study to examine the geology, plant communities and major classes of wildlife that inhabit the high desert biome of western North America.



Fig. 2 The Northern Great Basin. Data Sources: [USGS](#); [NOAA](#).

Geology

The geologic processes behind the Northern Great Basin's most prominent features have played a foundational role in shaping the region's biodiversity. Two major processes, volcanism and faulting, and how they have interacted with climate, are major drivers in landform development across the region. The resulting landscape creates a unique set of systems where diverse communities of organisms interact.

Geologic Provinces

The Northern Great Basin overlaps with three geologic provinces of Oregon: the High Lava Plains, Basin and Range, and the Owyhee Upland (**Fig. 3**). These provinces are located east of the Cascade mountain range, which blocks moist air from the Pacific Ocean and contributes to the region's arid climate. The High Lava Plains and Owyhee Upland provinces consist of mostly flat-lying volcanic deposits that give this part of the region its characteristic topography of vast, rolling plains of grasslands and sagebrush. The Basin and Range province, which dominates the Northern Great Basin, is the northwest extent of the much larger Basin and Range physiographic region that extends throughout much of the Great Basin and interior western United States. The Basin and Range is characterized by numerous, roughly parallel mountain ranges separated by flat valleys, or basins (**Fig. 4**). This topography creates abrupt changes in elevation over very short distances, resulting in arid desert valleys immediately adjacent to steep mountainous terrain. Each of these geologic provinces shares a similar geologic history that has been shaped by volcanic activity and faulting.

Volcanism

The Northern Great Basin is among the most active volcanic regions in the western United States. Nearly all of the rocks exposed in the region are volcanic in origin and geologically very young, ranging in age from about 17 million years old to just a few 1000 years old (**Fig. 3**). Between about 17 and 14 million years ago, massive eruptions of flood basalts occurred from numerous vents in

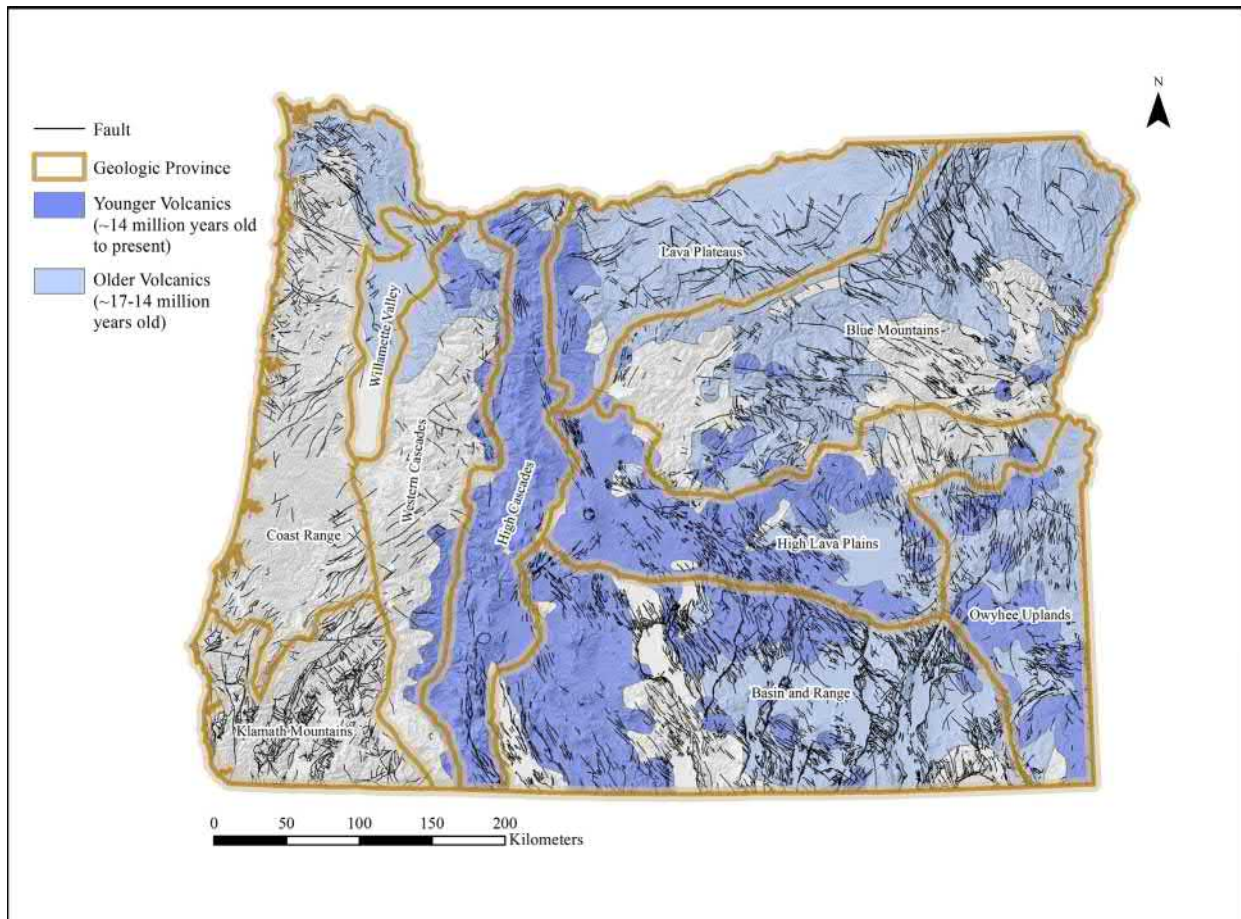


Fig. 3 Geologic provinces of Oregon (modified from Miller, M.B. (2014). *Roadside Geology of Oregon*. Missoula, MT: Mountain Press Publishing Company), volcanic deposits from ~17 million years ago to present (modified from Smith, R.L. and Luedke, R.G. (1984). Potentially Active Volcanic lineaments and loci in western conterminous United States. In: *Explosive Volcanism: Inception, Evolution, and Hazards*, 47–66), and Oregon faults. Data Sources: USGS; NOAA; Oregon Explorer.

a north-south alignment from northern Nevada to southeastern Washington (e.g., Zoback et al., 1994; Carlson and Hart, 1987; Hooper, 1997). The largest volumes of basalt erupted in the northern portions of this region, including the Columbia River Basalts (e.g., Tolan et al., 1989) and the Steens Basalts (e.g., Carlson and Hart, 1987) which together cover large portions of the Northern Great Basin. Near the southern boundary of the Northern Great Basin, eruptions of flood basalts were accompanied by large, highly explosive caldera-forming eruptions that produced silicic volcanic centers similar to those along the Snake River Plain in Idaho and the Yellowstone area (e.g., Conrad, 1984; Rytuba and McKee, 1984; Ekren et al., 1982). From about 14 million years ago to the present, volcanic activity has continued, creating numerous volcanic centers and lava flows (e.g., Hart et al., 1984; Jordan et al., 2004). Many of these young volcanic deposits and flows lack significant vegetation and soil development, creating stark volcanic landscapes that offer unique microclimates and habitats.

Fault Systems

In addition to active volcanism, the Northern Great Basin is also characterized by geologically young fault systems. These faults are caused by extension of the Earth's crust, which in turn is caused by the global forces of plate tectonics. Many of these faults were active prior to and concurrent with volcanic activity, offsetting the volcanic rocks described above. In the Northern Great Basin, fault systems trend northwest and north-northeast (Fig. 3). The north-northeast trending faults are part of the larger Basin and Range province and are tens of kilometers long and have offset the earth's surface by hundreds of meters to several kilometers (e.g., Donath, 1962; Walker and MacLeod, 1991; Pezzopane and Weldon, 1993; Crider, 2001). It is estimated that Basin and Range extension has stretched the Northern Great Basin by about 17% during the last 15 million years (Wells and Heller, 1988). In contrast to the north-northeast trending faults in the Basin and Range province, the High Lava Plains province is dominated by northwest trending faults. These occur as hundreds of short, parallel fault systems that cover a wide zone called the Brothers Fault Zone. These faults are a few kilometers long at most and have offset the surface by only a few tens of meters (e.g., Lawrence, 1976; Walker and



Fig. 4 Basin and range topography in the Northern Great Basin. Source: Photo by Jim Davis.

MacLeod, 1991). Short, northwest trending faults like those of the Brothers Fault Zone also occur within, and are contemporaneous with, the larger north-northeast trending faults of the Northern Great Basin's Basin and Range province (e.g., Crider, 2001; Donath, 1962; Pezzopane and Weldon, 1993). The contrast between the flat or rolling topography of the High Lava Plains province and the high relief of the Basin and Range province is in part a result of these two types of faults; shorter faults with less offset have created the subdued topography of the High Lava Plains, which grades southward into the steep mountain ranges and valleys created by longer faults with more offset.

Climate

During the last 2 million years changes in Earth's climate caused multiple ice ages, or glacial periods. During these periods, increased precipitation filled the enclosed valleys of the Northern Great Basin's Basin and Range, creating large lakes (e.g., Snyder et al., 1964; Orme, 2008). At the highest elevations, alpine glaciers formed and carved glacial cirques, arêtes, and U-shaped valleys in the layers of volcanic rock uplifted by Basin and Range faulting (e.g., Smith, 1927; Evans and Geisler, 2010). About 12,000 years ago the most recent glacial period ended as the climate became warmer and drier. Alpine glaciers disappeared and the extensive lakes throughout the Northern Great Basin evaporated, leaving behind much smaller, shallow alkaline lakes and dry playas common in the region today.

Plant Communities of the Northern Great Basin

The Northern Great Basin contains some of the most intact sagebrush steppe plant communities in North America (Connelly et al., 2004). Millions of acres of sagebrush cover the landscape providing critical habitat for species such as the greater sage-grouse (*Centrocercus urophasianus*), pygmy rabbit (*Brachylagus idahoensis*) and the Great Basin spadefoot toad (*Spea intermontana*). Within this shrub dominated expanse, several other notable plant communities contribute important roles to the regional ecology, including salt desert scrub, riparian area, and tree communities, often following elevation and edaphic changes (Shreve, 1942) (Fig. 5). Each of these plant communities has unique attributes and qualities that, in combination, contribute to the Northern Great Basin's diverse assemblage of life (Miller and Eddleman, 2000).

Sagebrush Steppe

The sagebrush steppe of the Northern Great Basin is defined by its high elevation shrub communities, hot dry summers, and cold wet winters (Miller and Eddleman, 2000; Pyke et al., 2015; West, 1999). Sagebrush (*Artemisia* spp.) are the dominate shrubs of the region and a keystone species, occurring across an array of ecological conditions (Fig. 6). There are over 20 species and subspecies of woody sagebrush, with 12 commonly found in the Northern Great Basin (Winward, 1980; Shreve, 1942). Of these, big sagebrush

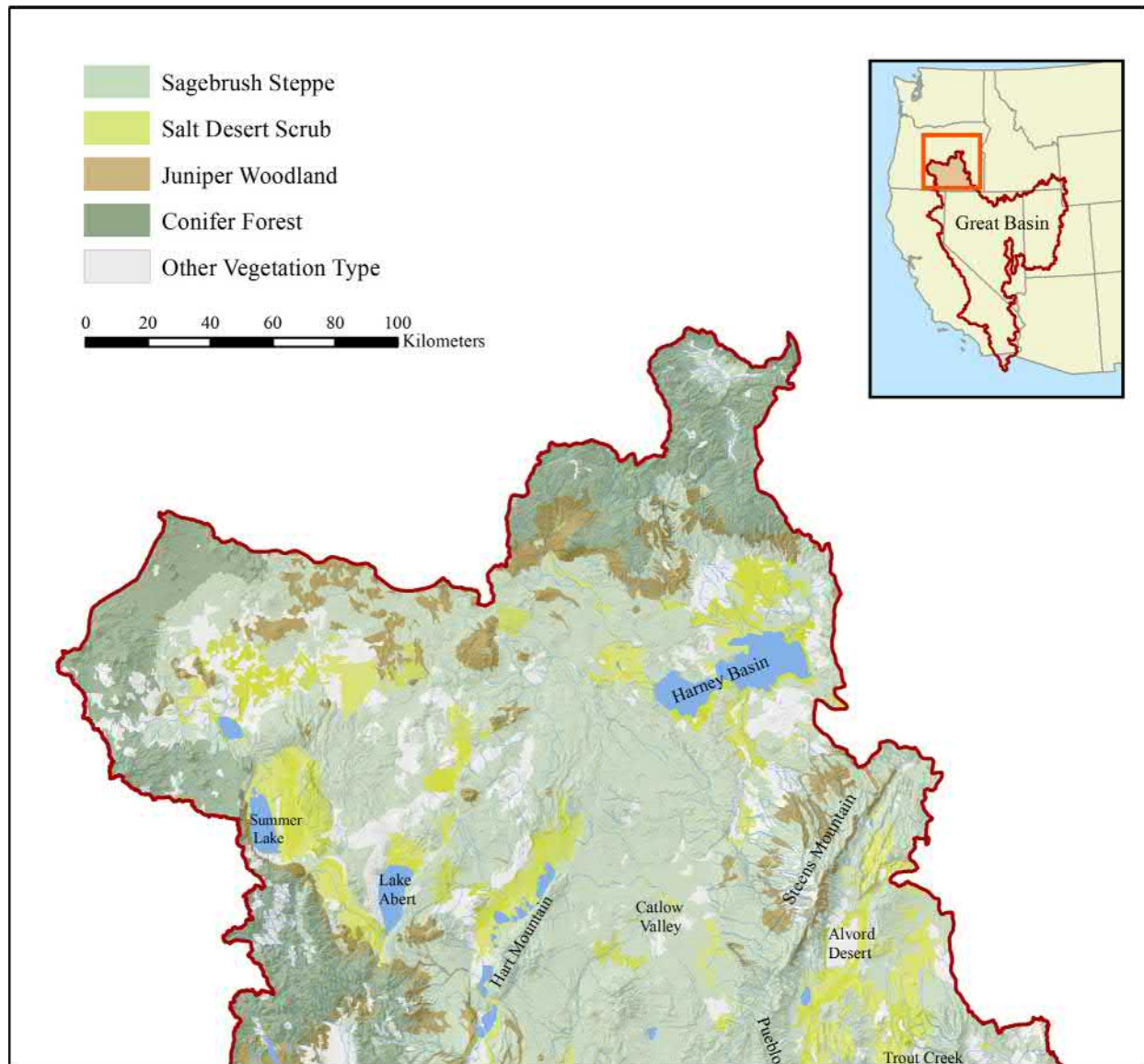


Fig. 5 Plant communities in the Northern Great Basin. Data Sources: USGS; NOAA; The Habitat Institute.

(*Artemisia tridentata*) and low sagebrush (*Artemisia arbuscula*) commonly occur and frame much of the ecology (Winward, 1980; Franklin and Dyrness, 1988; Miller and Eddleman, 2000). Numerous other shrub species are common within the sagebrush steppe, most notably rabbitbrush (*Chrysothamnus* spp.) and bitterbrush (*Purshia tridentata*) (Franklin and Dyrness, 1988).

Big sagebrush is the most widespread sagebrush species in the Northern Great Basin, with three commonly recognized subspecies (Winward, 1980). Of these subspecies, Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and mountain big sagebrush (*Artemisia tridentata vaseyana*) dominate, providing important wildlife habitat across the region from the edge of the lowland alkali flats to the high montane woodlands (Dealy et al., 1981; Miller and Eddleman, 2000; Pyke et al., 2015).

Wyoming big sagebrush is typical of more arid sites, generally below 1800 m, and is the most prominent of the big sagebrush subspecies (Winward, 1980). As a more drought tolerant sagebrush, it tends to support a lower abundance of understory plants, most notably forb species, when compared to mountain big sagebrush (Winward, 1980; Davies and Bates, 2010). In contrast, mountain big sagebrush generally occupies higher elevation foothills and mountain slopes between 1050 and 3000 m (Winward, 1980) where soils are deeper and moisture persists for longer periods throughout the year (Davies and Bates, 2010; Winward, 1980). The environmental conditions of these sites make mountain big sagebrush communities more productive (Davies and Bates, 2010; Winward, 1980), with it not uncommon to find several dozen species of forb in the understory (Miller and Eddleman, 2000; Winward, 1980). Big sagebrush communities play an essential role in the life histories of regional wildlife, constituting an important food source and creating essential cover for hiding and thermal refugia. The plant's evergreen leaves and year-round availability



Fig. 6 The sagebrush steppe in the Northern Great Basin. Sources: Photo by Jim Davis.

of crude protein make it valuable winter forage for numerous wildlife species, including the greater sage-grouse, mule deer and pronghorn (Welch and McArthur, 1979).

Low sagebrush, while not as common as big sagebrush, is found consistently throughout the Northern Great Basin between 1000 and 3300 m (Winward, 1980). It prefers areas with shallow, stony soils with poor drainage, often overlaying unfractured bedrock or an impermeable substrate (Franklin and Dyrness, 1988; Winward, 1980). Low sagebrush communities constitute important seasonal food sources for foraging wildlife, especially in the spring due to the early emergence of forage species (grasses and forbs) relative to surrounding plant communities (Dealy et al., 1981).

Understory

The native understory of the sagebrush steppe is a dynamic composition of perennial bunchgrasses, forbs, and biological soil crust (Miller and Eddleman, 2000). Depending on a variety of factors, the ratio between forbs, perennial grasses and shrubs can vary widely (Pyke et al., 2015).

Perennial bunchgrasses form the dominant component of the herbaceous understory and include species such as: bluebunch wheatgrass (*Pseudoroegneria spicata*), needle-and-thread grass (*Hesperostipa comata*), Thurber's needlegrass (*Achnatherum thurberianum*), Idaho fescue (*Festuca idahoensis*), bottlebrush squirreltail (*Elymus elymoides*), and Sandberg bluegrass (*Poa secunda*) (Dealy et al., 1981; Franklin and Dyrness, 1988; Winward, 1980). Forbs are a smaller percentage of the ground cover, however they display a far greater diversity with over 200 species having been documented in the sagebrush steppe (Miller and Eddleman, 2000; Miller et al., 2000). Biological soil crust, while sometimes overlooked, is a critical component of the sagebrush steppe understory. A complex mix of organisms including lichen, algae, fungi and cyanobacteria (Ponzetti and McCune, 2001), biological soil crust helps prevent soil erosion and establishment of non-native species, and contributes nitrogen and other minerals to adjacent plant species (Ponzetti and McCune, 2001).

Salt Desert Scrub

Salt desert scrub is characterized by halophytic plant communities that are well adapted to the lowland dry lake beds and alkali flats of the region's basins (Comstock and Ehleringer, 1992; Franklin and Dyrness, 1988). The saline soils of these sites create an environment that limits the presence of sagebrush, giving way to two other dominant shrub communities, shadscale (*Atriplex confertifolia*) and greasewood (*Sarcobatus vermiculatus*) (Comstock and Ehleringer, 1992; Dealy et al., 1981) (Fig. 7).

Often in close proximity to one another, shadscale and greasewood communities are typically distributed along elevational gradients (Shreve, 1942). Greasewood communities tend to occupy the lowest elevations where soil salinity and the water table are highest (Blaisdell and Holmgren, 1984; Comstock and Ehleringer, 1992; Dealy et al., 1981). In contrast, shadscale communities generally prefer moderately saline soils that are well-drained, often in more upland environments (Comstock and Ehleringer, 1992). Many of the plants in these communities have evolved interesting adaptations to live in the harsh alkali surroundings,



Fig. 7 Salt desert scrub plant community in the Northern Great Basin. Sources: Photo by Greg Burke.

such as elevated internal salt concentrations to allow for water absorption in the highly saline environment (Taylor, 1992). Other common shrubs associated with salt desert scrub include fourwing saltbush (*Atriplex canescens*), winterfat (*Krascheninnikovia lanata*), spiny hopsage (*Atriplex spinosa*), mormon tea (*Ephedra viridis*), rabbitbrush (*Chrysothamnus* spp.), and big sagebrush (*Artemisia tridentata*) (Dealy et al., 1981; Franklin and Dyrness, 1988; Kagan et al., 1999).

Riparian Areas

Riparian areas are the least abundant habitat in the Northern Great Basin, constituting less than 1% of the region's land surface (Dobkin et al., 1998). However, of the described terrestrial wildlife species that are found here, up to 80% depend on these unique zones during their lifetime (Thomas et al., 1979a). The outsized importance of riparian areas to the region's wildlife centers on the relative abundance of water, diversity of vegetation, and the stark contrast they form to the surrounding arid shrub communities (Fig. 8).

In the Northern Great Basin, riparian areas includes both lentic—lakes, ponds, seeps, bogs and meadows—and lotic systems—rivers, streams and springs (Thomas et al., 1979a). They are some of the most productive plant communities and provide complex structure and species diversity critical to resident and migratory wildlife. The often linear shapes of riparian areas allow them to cut through elevational gradients, connecting seasonal wildlife habitats and serving as migratory corridors (Dealy et al., 1981). Dramatic differences between the arid shrub steppe and riparian plant communities create conditions where wildlife species with broad ecological requirements interact (known as the edge effect) and make them hotspots for biological diversity (Thomas et al., 1979b).

Tree Communities

On the upper reaches of the Northern Great Basin's mountain ranges, sagebrush and shrubs often give way to tree dominant or co-dominant communities, most notably curleaf mountain mahogany (*Cercocarpus ledifolius*), aspen (*Populus tremuloides*), and juniper (*Juniperus occidentalis*). On the perimeter foothills and mountain ranges, coniferous forests are well established and even occur in a handful of isolated patches throughout the region (Anderson et al., 1998). While frequently limited in acreage, tree communities provide contrasting vertical cover from the surrounding low statured sagebrush steppe, and as a group play an especially important role in providing thermal and hiding cover for wildlife, most prominent being native ungulates such as elk (*Cervus elaphus canadensis*) and mule deer (*Odocoileus hemionus*) (Dealy et al., 1981).

Fauna of the Northern Great Basin

Hundreds of terrestrial vertebrate species rely on the Northern Great Basin's diverse habitats during their life histories. The semi-arid climate of much of the region has resulted in a mixed composition of both grassland and desert species (West, 1999). Some of the



Fig. 8 Riparian area in the Northern Great Basin. Sources: Photo by Greg Burke.

most visible species belong to the mammal, bird, reptile and amphibian groups, and together compose a core of the region's wildlife identity. Species from each of these vertebrate groups can be found here throughout the year, occupying habitats from the lowland basins to the high alpine ridge tops, utilizing a host of adaptations to survive within the region's harshest fringes.

Mammals

The complex climatic and topographic history of the Northern Great Basin has contributed to a high regional diversity of extant mammal species (Badgley et al., 2014). Classifications of Great Basin mammals have documented as many as 172 native species (Rowe and Matocq, 2014) and can differ widely depending on how the Great Basin is defined. Riddle et al. (2014) described a core group of 94 extant mammal species distributed across the Great Basin shrub-steppe. Nearly all of them can be found in the Northern Great Basin, including some of North America's most recognizable fauna such as the pronghorn, coyote, and mountain lion.

One group of mammals disproportionately contributes to the region's high mammalian diversity. Of the 94 core species described by Riddle et al. (2014), 45 species are rodents. The high diversity of rodents is largely attributed to the ability of these small mammals to finely subdivide their habitat along elevational gradients (Badgley et al., 2014). Rodents are found in all of the major habitats in the region, serving as prey for numerous predator species and acting as important seed dispersers for native plants.

Perhaps the most recognizable mammal in the Northern Great Basin is the pronghorn (*Antilocapra americana*) (Fig. 9). The only extant member of the family Antilocapridae, the pronghorn is the fastest land animal in North America, able to reach speeds up to nearly 100 km per hour. Considered a sagebrush obligate species (Rowland et al., 2006), pronghorn are well adapted to the extreme temperatures and low shrub communities characteristic of much of the Northern Great Basin (O'Gara, 2004). Unlike other North American wild ungulates, pronghorn do not rely on tall vegetation for hiding cover, preferring rolling topographies with a mix of grass and shrub species (Yoakum, 2004). Having evolved the largest eye relative to their size of any North American ungulate, the pronghorn instead relies on both its eyesight and speed to evade predators (O'Gara, 2004).

The sagebrush steppe is also critical habitat for numerous other mammal species. Like the pronghorn, the sagebrush vole (*Lemmiscus curtatus*) and pygmy rabbit (*Brachylagus idahoensis*) are both considered sagebrush obligate species, relying on intact blocks of sagebrush to survive (Rowland et al., 2006). Several other species of conservation concern similarly rely on the sagebrush steppe, including the kit fox (*Vulpes macrotis*), white-tailed jackrabbit (*Lepus townsendii*), Ord's kangaroo mouse (*Dipodomys ordii*), and Merriam's shrew (*Sorex merriami*) (Rowland et al., 2006).

The Northern Great Basin's often discrete riparian communities are disproportionately important for the majority of the region's mammal species. Recognized as the most critical wildlife habitat in the high desert, riparian areas have the potential to provide mammal species with all three components of habitat—food, shelter, and water (Thomas et al., 1979a). Species such as the North



Fig. 9 Pronghorn (*Antilocapra americana*). Sources: Photo by Greg Burke.

American beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), and the North American otter (*Lontra canadensis*) are completely dependent on riparian areas to survive (Thomas et al., 1979a).

At higher elevations, taller tree communities afford mule deer and elk the tall vegetation they require for security cover. Bighorn sheep (*Ovis canadensis*), while sometimes found in big sagebrush and tree communities, more often use the region's steep escarpments and cliff faces for cover and protection from predators (Van Dyke et al., 1983). Other species found in these communities include numerous bat species, bushy-tailed woodrat (*Neotoma cinerea*), and the mountain cottontail (*Sylvilagus nuttallii*).

Birds

Birds encompass the greatest variety of vertebrates in the Northern Great Basin. Approximately 390 bird species are known to have occurred in Northern Great Basin (Marshall et al., 2006). Of these, 200 species have been confirmed to breed there (Adamus et al., 2001), and as many as 96 species are sufficiently adapted to succeed as year-round residents (Marshall et al., 2006).

Sagebrush is the defining habitat of the Northern Great Basin. Thirty-seven bird species are extensively dependent on the sagebrush shrub steppe ecosystems in the region (Dobkin and Sauder, 2004). The sage thrasher (*Oreoscoptes montanus*), Brewer's sparrow (*Spizella breweri*), and sagebrush sparrow (*Artemisiospiza nevadensis*) are considered sagebrush obligates, and are completely dependent on sagebrush for breeding and brood-rearing (Patterson, 1952). However, only a single bird species, the greater sage-grouse (*Centrocercus urophasianus*), spends its entire life cycle in the sagebrush steppe habitat (i.e., as both a sagebrush obligate and endemic species) (Fig. 10). Furthermore, it is the only bird species that consumes sagebrush as a part of its diet (Girard, 1937; Griner, 1939; Batterson and Morse, 1948; Schroeder et al., 1999). The Northern Great Basin and its large expanses of intact sagebrush communities, is one of only a few remaining strongholds throughout the range of this magnificent bird.

The greater sage-grouse is a large bird, standing at approximately half a meter tall. This iconic species is legendary for its exotic mating ritual, where a group of up to 150 males gather in leks to attract females and attempt to mate. The display involves repeatedly inflating and popping two gular air sacs that can hold up to a gallon of air. The displays go on for hours in the early morning for up to 3 months during the spring. Female sage-grouse are highly selective in choosing a mate, and despite all the effort put on by multiple males, most mating is consummated by just one male (Patterson, 1952; Wiley, 1973).

Other habitats in the Northern Great Basin are equally important to supporting the region's bird communities. Lake Abert, a 15-mile long hypersaline body of water, supports vast quantities of brine shrimp and brine flies, providing a crucial stopover and feeding site along the Pacific Flyway. Under optimal conditions, up to 300,000 Wilson's phalaropes (*Phalaropus tricolor*), 20,000 eared grebes (*Podiceps nigricollis*) and 40,000 American avocets (*Recurvirostra americana*) will stop and gather at the lake in preparation for their southward migration in the fall. Similarly, snow (*Chen caerulescens*), Ross's (*Chen rossii*), and greater white-fronted (*Anser albifrons*) geese gather in the tens of thousands in the Harney Basin during their spring and fall migrations, utilizing critical networks of riparian plant communities.

On the high elevation slopes of fault block mountains such as the Steens, black rosy-finch (*Leucosticte atrata*) and golden eagle (*Aquila chrysaetos*) find refuge. Volcanic formations and rimrock cliffs provide nesting habitat for white-throated swift (*Aeronautes*



Fig. 10 A male Greater Sage-Grouse (*Centrocercus urophasianus*). Sources: Photo by Alan St. John.

saxatilis), Say's phoebe (*Sayornis saya*), prairie falcon (*Falco mexicanus*), rock wren (*Salpinctes obsoletus*), and canyon wren (*Catherpes mexicanus*) (Marshall et al., 2006). And in the region's woodland habitats, Townsend's solitaire (*Myadestes townsendi*), juniper titmouse (*Baeolophus ridgwayi*), and blue-gray gnatcatcher (*Poliophtila caerulea*) can be found (Littlefield, 1990).

Reptiles and Amphibians

While not as rich in species as the mammalian and avian communities, numerous amphibians and reptiles have evolved interesting adaptations to survive and prosper in the severe climate of the Northern Great Basin. As ectotherms, lizards and snakes do not need to constantly supply themselves with calories to produce metabolic heat, allowing them to survive on amazingly small amounts of nourishment in extremely arid environments. They are well represented in the Northern Great Basin. Amphibians, while limited in distribution and diversity due to the scarcity of water, are nevertheless represented by salamanders, frogs and toads. In total, 19 reptile species and 5 amphibian species occur in the region.

The relatively warmer salt desert scrub habitats of the Northern Great Basin contain higher concentrations of reptiles than the surrounding mountain ranges and sagebrush steppe. Typical of these communities is the long-nosed leopard lizard (*Gambelia wislizenii*), which can grow to 30 cm in length, and the equally large in size western whiptail (*Aspidoscelis tigris*). Characteristic of some species in extremely arid regions, the leopard lizard does not require water to survive and instead can obtain its moisture from food sources. This adaptation allows them to thrive in the lowland basins where rainfall can be as little as 12 cm a year. Also inhabiting salt desert scrub communities is the desert horned lizard (*Phrynosoma platyrhinos*), having evolved a spine-clad body and head to ward off coyotes and predatory snakes such as the striped whipsnake (*Masticophis taeniatus*) and racer (*Coluber constrictor*).

On adjacent lower foothills, often in the transition zones between the salt desert scrub and sagebrush steppe shrub lands, the diminutive side-blotched lizard (*Uta stansburiana*) and somewhat larger western fence lizard (*Sceloporus occidentalis*) can be found. Preying upon these two species is the larger Great Basin collared lizard (*Crotaphytus bicinctores*). This predatory reptile can attain a total length of 33 cm, and when startled, often runs on its hind legs much like bipedal dinosaurs once did.

In riparian environments, the distinct chorus of Pacific treefrogs (*Pseudacris regilla*) can often be heard. This small, ubiquitous species is polymorphic, featuring individuals within the same population that are green, tan, brown, gray, or rarely, blue. Other amphibians found in the lush vegetation of riparian communities include the larger Columbia spotted frog (*Rana luteiventris*), western toad (*Anaxyrus boreas*), and the long-toed salamanders (*Ambystoma macrodactylum*). Reptilian predators include the common garter snake (*Thamnophis sirtalis*) and western terrestrial garter snake (*Thamnophis elegans*).

Across nearly all habitats in the Northern Great Basin, several snake species are predominantly nocturnally active. During the peak daytime heat in the summer months, many reptiles stay hidden in cool subterranean retreats. As the sun sets and temperatures moderate, a host of species become active. Gopher Snakes (*Pituophis catenifer*) are usually the first to be out, along with Great Basin Rattlesnakes (*Crotalus oreganus lutosus*). Later, the Desert Night Snake (*Hypsiglena chlorophaea*) utilizes its cats-eye vertical pupils to seek out small lizards asleep in crevices. To subdue its prey, the Desert Night Snake utilizes a mild saliva venom that flows down grooves in the snake's enlarged rear teeth.

During summer precipitation events, a unique arid-adapted amphibian of the salt desert scrub and sagebrush steppe emerges. This is the Great Basin spadefoot (*Spea intermontana*), a small toad with a sharp-edged protrusion on the heel of each rear foot (Fig. 11). These nodules, or spades, are utilized to rapidly dig backwards into soil where the toad waits out surface dry spells, which can extend for over a year during prolonged droughts (Hovingh et al., 1985). In early springtime, male spadefoots attract females with their loud monotone chorus, breeding in temporary rain-pools and any other available shallow water. Well adapted to the



Fig. 11 Great Basin spadefoot (*Spea intermontana*). Sources: Photo by Alan St. John.

region's aridity, the resulting gelatinous egg clusters hatch in 2 or 3 days; and before the aquatic habitat evaporates, the tadpole larvae can transform into terrestrial adults within 2 weeks.

Ascending the Northern Great Basin's fault-block ranges, such as Hart Mountain and Steens Mountain, the surroundings change rapidly. The salt scrub of alkali flats gives way to slopes and level ridge-tops of sagebrush, bunchgrasses, juniper woodlands, and patches of mountain mahogany. Here can be found species such as the sagebrush lizard (*Sceloporus graciosus*), western skink (*Plestiodon skiltonianus*), and rubber boa (*Charina bottae*)—the most northerly-ranging true boa in the world (St. John, 2002).

Possibly the most iconic sagebrush steppe reptile in the Northern Great Basin is the endemic pygmy short-horned lizard (*Phrynosoma douglasii*) (Fig. 12). Sometimes wrongly called a horned toad, this lizard rarely grows to more than seven centimeters in total length. Recent field studies have disclosed that short-horned lizards routinely hibernate by burying in sand just ten to twelve centimeters below the surface, freezing solid for months at a time (Mathies and Martin, 2008). When the warmth of springtime arrives, the lizards thaw unharmed. Remarkable for an ectothermic reptile at the Northern Great Basin's latitude, the pygmy short-horned lizard has been recorded at nearly 2400 m elevation (Lahti et al., 2007), surviving in the stunted sagebrush and bunchgrass habitats of the region's mountain summits. In these rarefied zones that are snowbound for months on end, short-horned lizards spend the majority of the year in hibernation.

Threats to Biodiversity

The Northern Great Basin of today remains a stronghold of the sagebrush steppe and high desert ecosystems. However, the natural systems here and elsewhere in the Great Basin are among the most threatened in all of North America (Heinz III, 2002; Chambers



Fig. 12 Pygmy short-horned lizard (*Phrynosoma douglasii*). Sources: Photo by Alan St. John.

and Wisdom, 2009; Wisdom et al., 2005). Nearly two centuries of human caused impacts have resulted in landscape-scale fragmentation and degradation of some of the continent's most widespread ecosystems. Protecting relic landscapes from anthropogenic stressors is paramount to providing the greatest chance of maintaining the health of these systems.

More than 30 million hectares of the sagebrush steppe have been degraded, a staggering half of its historic range. Agriculture, livestock grazing, housing development, energy development, altered fire regimes, and a host of alterations to riparian systems, among other changes, have impacted native communities across the Great Basin and arid west. Threats posed by the proliferation of non-native plant species, specifically cheatgrass (*Bromus tectorum*), and the expansion of juniper into higher elevation shrub communities, are resulting in landscape scale impacts. Climate change, predicted to have the greatest impact on arid systems such as those of the Great Basin, is already being realized on the landscape (Chambers and Wisdom, 2009). Decreases in winter snowpack in the Great Basin are some of the greatest observed in the United States and are expected to continue, reducing spring runoff and water availability throughout the year (Chambers and Wisdom, 2009; Mote et al., 2005).

These changes are having far reaching negative consequences for the flora and fauna of the Great Basin and arid west. Over 350 plants and animals within the historic range of the sagebrush steppe have been identified as species of concern (Wisdom et al., 2005). Shrub communities, and their herbaceous understories, are being heavily impacted by cheatgrass leading to changes in hydrology, fire regimes and connectivity of wildlife habitat. In many place, riparian areas are no longer functioning properly, decreasing the availability of critical water sources for all life. The ripple effect of these impacts extend far beyond the arid west, creating barriers for migratory species and additional pinch points for birds moving along the chain of habitats known as the Pacific Flyway.

The multitude and complexity of these threats pose significant challenges to maintaining ecological processes and regional biodiversity, demanding creative solutions, robust partnerships and adequate resources to effectively combat them. Roughly two thirds of the Great Basin is public land, managed by the federal government of the United States. In the face of losing native plants, watershed function and native wildlife species, places with high biodiversity and healthy native communities should be prioritized for conservation management and protection through administrative and legislative actions. Safeguarding systems like those of the Northern Great Basin, with high levels of endemism and native species, will help maintain the unique biodiversity of the high desert biome in the face of an uncertain future.

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Shifting Winds in the Mongolian Gobi Desert: Nature and Traditions Face the Modern Era

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Abstract

The Mongolian Gobi Desert supports globally-significant biodiversity, and is part of the largest steppe ecosystem in the world that supports its historic wildlife assemblage, including long distance wildlife migrations, as well as traditional nomadic pastoralism. Like other development frontiers in arid lands, the wildlife and biodiversity of the region are threatened by the rapid growth of mining and related infrastructure. Globally, environmental licensing and mitigation face challenges in practice. Mitigation is typically a reactive process conducted on a site by site basis that does not account for the landscape context, or the cumulative impacts of multiple projects and regional biogeography. The Mongolian government has developed a national mitigation framework based on systematic conservation planning adapted to guide landscape-level mitigation. The framework balances development and conservation goals to designate new protected areas and guide offset design, and demonstrates that landscape-level mitigation based on stakeholder- and data-driven conservation planning is possible and practical.

Introduction

The Gobi Desert basin lies across southern Mongolia and northwestern China between the Mongolian Altai and Khangai mountains and the Himalayan Plateau (see map in [Fig. 1](#)). This region is a cold desert with a continental climate and long, cold winters. Average temperatures range from below -20°C in January to over 33°C in July ([Hijmans et al., 2005](#)). In the rain shadow of the Himalayas, precipitation ranges from less than 40 mm in extreme arid areas to over 200 mm in the Gobi-Altai mountains ([Hijmans et al., 2005](#)), and varies greatly interannually, with some areas not receiving any measurable precipitation for years at a time ([Vandendorj et al., 2015](#)).

The name “Gobi” comes from the Mongolia word “Govi” for a dry landscape with characteristic arid vegetation including palatable forage species (*Allium* and *Nitraria* spp.) and rare medicinal plants. Gobi desert vegetation is a mix of true desert, desert grasslands, and steppe. Despite the climate, the Mongolian portion of the Gobi Desert region supports globally-significant wild lands and wildlife, and is part of the largest steppe ecosystem in the world that supports its historic wildlife assemblage, including long distance wildlife migrations ([Batsaikhan et al., 2014](#)). Historically, this region was near the center of the Mongol Empire (c. 1206–1294) and has been crossed by human migrations and trade routes for 5000 years ([Hare, 2009](#)).

Arid lands, which include the semi-arid grasslands and deserts of the Gobi Desert region, cover a third of the world’s land mass ([Mortimore et al., 2009](#)) and support unique biodiversity and many endangered species ([Durant et al., 2012](#); [IUCN, 2011](#)). However, as much as 20% has experienced degradation ([Reynolds et al., 2007](#); [Safriel, 2006](#); [UNCCD, 1994](#)) and less than 10% of arid lands benefit from some form of protection ([Hoekstra et al., 2005](#)). Arid and semi-arid biomes are home to 20% of the world’s population, mostly subsistence farmers and pastoralists ([Mortimore et al., 2009](#)). The dry climate promotes the formation and concentration of important minerals and salts through the movement and evaporation of water. Half of the world’s copper and uranium and 75% of world oil reserves are in arid lands ([UNEP, 2006](#)).

Parts of the Mongolian Gobi Desert region have been identified as among the world’s largest and most intact (least converted) remaining wild areas ([Allan et al., 2017](#); [Kennedy et al., 2019](#)), and the human population density was very low historically and still is today ([ECJRC and CIESIN, 2015](#)). The Mongolian Gobi Desert currently supports more than 30 mammals, herptiles, and birds listed as nationally threatened or endangered ([Clark et al., 2006](#); [Terbish et al., 2006](#); [Gombobataar et al., 2011](#)), including the world’s largest remaining populations of Asiatic wild ass or khulan (*Equus hemionus*), wild Bactrian camel (*Camelus ferus*), Gobi brown bear (*Ursus arctos gobiensis*), Siberian ibex (*Capra sibirica*), Goitered gazelle (*Gazella subgutturosa*), and Mongolian gazelle



Fig. 1 Gobi Desert region as delineated by WWF (Olson et al. 2001) and Dash (2007). Basemap: ESRI (2019).

(*Procapra gutturosa*), (Kaczensky et al., 2015; Mallon, 2008a,b). The low mountain ranges also support one of the most stable and productive populations of Snow Leopards (*Panthera uncia*) in the global range (Sharma et al., 2014; Jackson et al., 2009).

The Mongolia steppes and desert grasslands also support traditional nomadic pastoralism that originated thousands of years ago. Mongolia nomadic pastoralists spend the winter at fixed households and shelters, and spend spring, summer, and autumn traveling between seasonal camps and pastures, though grazing practices and herd composition vary by geography and climate. In less productive desert grasslands, pastoralists typically visit as many as 10–15 seasonal pastures over the course of a year. In Mongolia, domestic livestock include horses, camels, yak, and cattle, though sheep and goats are the most numerous. Extreme winter weather events, sometimes coupled with summer drought, can cause catastrophic die-offs of livestock and wildlife. These weather events occur frequently enough to earn the name “dzud.” Dzud events take a variety of forms, including “white dzud”—deep snow reducing access to pasture forage, “black dzud”—extreme cold and no snow reducing forage and water availability, “storm dzud”—high winds and heavy snow, “iron dzud”—impenetrable ice covering pasture forage, “combined dzud”—deep snow and extreme cold, and “hoofed dzud”—out of season movements of many livestock to one pasture that eliminates forage with trampling and grazing (Begzsuren et al., 2004; Fernandez-Gimenez et al., 2011).

Though the Mongolian Gobi Steppe system still supports its historic wildlife and pastoral traditions, the wildlife and pastoral livelihoods face increasing threats and pressures following the transition from a soviet to market economy in 1990. Pastoral systems and grazing practices have changed in response (Fernandez-Gimenez and Batbuyan, 2004; Fernandez-Gimenez, 2001), and the number of livestock has nearly tripled, growing from 25 to over 66 million animals, in fewer, larger herds (National Statistical Office of Mongolia, 2018). This has resulted in overgrazing, particularly in areas near rural population centers and water sources (Stumpp et al., 2005), though estimates of the degree and extent of rangeland degradation vary (Jamsranjav et al., 2018; Addison et al., 2012).

These rapid changes have led to concerns about ecological tipping points, the loss of knowledge of traditional herding practices, and the loss of cultural identity (Fernandez-Gimenez et al., 2017).

A possibly more urgent threat to wildlife and biodiversity is the cumulative impacts of rapid growth of mining and related infrastructure (Suzuki, 2013; Batsaikhan et al., 2014). Mongolia is rich in mineral resources, and mineral exploration and extraction is increasing dramatically. In 2012, 14% of Mongolia's surface area and 24% of the Gobi study area was leased for mineral extraction or exploration (MMRE, 2012). Though the direct impacts of mining on land and water are significant and can reach far beyond the mine site, perhaps the most urgent threat to wildlife is created by transportation infrastructure and traffic to support mining operations that create barriers to movement (Nandintsetseg et al., 2019; Batsaikhan et al., 2014; Ito et al., 2013).

Development Frontiers and the Challenge of Mitigation

The trend of development in Mongolia is similar to other development frontiers around the world. Growing resource demands are pushing development to new frontiers in developing countries that support important biological diversity and have not seen this level or pace of infrastructure development. Impacts associated with development are the most significant anthropogenic drivers of biodiversity decline (Newbold et al., 2015), and an estimated 20% of the world's remaining natural lands are at risk of fragmentation from mining, energy, agriculture, and urban expansion (Oakleaf et al., 2015). Existing mechanisms for managing impacts and losses—environmental licensing, mitigation requirements, and conservation planning—fall short in practice, in part because development and conservation planning are typically independent, isolated processes (Kiesecker and Naugle, 2017).

Environmental licensing mechanisms such as Environmental Impact Assessment (EIA) and the mitigation hierarchy play a critical role in controlling the environmental impacts of development projects (McKenney and Kiesecker, 2010; Saenz et al., 2013). EIA laws require developers to assess impacts and submit mitigation plans to obtain a permit before construction and operation can begin, and EIA has been legally adopted in almost all countries in the world (Morgan, 2012). EIAs proactively examine the environmental impacts of planned developments, typically individual projects, with the goal of preventing or mitigating environmental damage through the application of the mitigation hierarchy: first avoid impacts, then minimize, then restore, and last compensate for residual impacts through offsets (McKenney and Kiesecker, 2010; BBOP, 2012; Ekstrom et al., 2015). To avoid impacts to rare or vulnerable biodiversity, measures are taken at the beginning, such as careful placement or timing of infrastructure construction and operation. For impacts that cannot be avoided, minimization measures are designed to reduce the duration, intensity, and/or extent. Restoration measures seek to rehabilitate degraded ecosystems after impacts. Finally, to compensate for remaining, residual impacts, biodiversity offsets are management interventions outside the impact area, such as protecting other areas where biodiversity loss is projected or restoration of similar, degraded habitat offsite (Kiesecker et al., 2009). Offsets have great potential as a source of funding to underwrite the costs of effective protection and management, given the appropriate sequence—avoid, minimize, and then offset—is followed.

However, effective mitigation faces challenges in practice. Mitigation efforts often skip the first, critical step in the mitigation hierarchy, avoidance (Clare et al., 2011; Villarroya et al., 2014; Phalan et al., 2018). EIAs are typically conducted on a project-by-project basis that does not consider the landscape context, or regional biogeography and cumulative impacts of multiple projects. Though consideration of the landscape context of impacts is a fundamental principle of effective mitigation (BBOP, 2012; Gardner et al., 2013; Pilgrim and Bennun, 2014; Ekstrom et al., 2015), little guidance exists for how to determine when and where impacts should be avoided or proceed (Kiesecker et al., 2010; McKenzie and Kiesecker, 2010). Offset design must also consider the landscape context to ensure ecological equivalence of the impact and offset, and to achieve “additionality,” (i.e., maximize conservation benefit by aligning with broader regional priorities and goals. Offset design must also account for the security or permanence of offset investments by considering risks and conflicts with future development).

Planning for Conservation and Mitigation in Mongolia

Mongolia established perhaps the world's longest continuously protected nature reserve, Bogd Khan, in 1778. Following transition from a Soviet economy to market economy, and in anticipation of mining boom, the government set an ambitious goal of protecting 30% of all natural habitats with a Master Plan for Protected Areas (Parliament of Mongolia, 1998, 2014) and published a Biodiversity Conservation Action Plan (MNE, 1996) that recommended designing a reserve network of strictly protected areas, national parks, and heritage areas. As of 2008, Mongolia had designated 74 national protected areas covering about 217,000 sq. km. or 14% of the country (MNET, 2008). The Nature Conservancy (TNC) established a Mongolia country program office in 2008 and has been working to apply the Development by Design strategy (Kiesecker et al., 2010) to balance development and conservation goals, with focus on landscape-level conservation planning to guide mitigation decisions, specifically regarding avoidance and offsets, and policy guidance to strengthen licensing and mitigation.

In 2013, following a pilot study in the Eastern Grasslands, TNC produced a landscape level conservation plan for the Mongolian Gobi region in collaboration with national and provincial governments, universities, and NGOs. This plan identified a set of priority conservation areas, referred to as a “portfolio,” that could maintain the biodiversity and ecological processes representative of the region given adequate protection and management as high quality core habitat within a larger landscape matrix that supports habitat use and movement. The portfolio was designed to (a) include national protected areas, (b) meet representation goals for the

amount and distribution of focal biodiversity elements—terrestrial ecosystems and threatened species—based on the government commitment to protect 30% of all natural habitats, and (c) optimize for ecological condition based on a spatial index of disturbance and cumulative anthropogenic impacts. Portfolio sites were delineated through site selection analysis with MARXAN spatial planning software (Ball et al., 2009). Spatial datasets were chosen and developed to address the scope and scale of conservation planning across the large, data-scarce Mongolian Gobi landscape (Heiner et al., 2013), and methods follow systematic conservation planning approaches (Margules and Pressey, 2000; Groves et al., 2002; Groves, 2003) adapted for landscape level mitigation (Kiesecker et al., 2010).

Portfolio design also considered conflict with planned mining. Where proposed portfolio sites and mineral exploration leases intersected, these conflict areas were reevaluated. Conflict areas with rare or vulnerable habitat, as defined by several criteria, were designated as areas of critical conservation significance where mining should be avoided. The other, remaining conflict areas were removed from the proposed portfolio and replaced with sites of similar ecosystem composition outside exploration leases. In this way, the portfolio design balanced tradeoffs between conservation and development goals based on the regional distributions of biodiversity values and development potential. The final portfolio consisted of 50 sites, covering 195,000 sq. km. or 37% of the Mongolian Gobi Desert study area, and contained at least 30% of the area distribution of all the focal ecosystem types.

New Protection and Avoidance Outcomes

After completion of the Gobi Desert conservation plan, 68,800sq. km. of new protected areas were designated based on the portfolio. With the establishment of these new protected areas, 160 exploration and application leases have been retired. The planning process was formally approved by the Mongolian Academy of Sciences in 2014 (MAS, 2014), establishing it as the basis for landscape level conservation planning and the national framework for implementing both the government protected area commitment and the mitigation hierarchy, specifically to determine areas to avoid development. Current legislation prohibits mining in national and local protected areas, and therefore protected area designation functions as a mechanism to implement avoidance (Mongolian Law on Mining, Parliament of Mongolia, 2016). Thus, the portfolio plays two roles: prioritizing new protected areas and implementing the mitigation hierarchy. The Mongolian Gobi Desert planning process was expanded to cover Mongolia and completed in 2017 to produce a national mitigation framework based on the conservation area portfolio and supporting datasets. Nationally, ~177,000 sq. km. of new protected areas have been established based on the national conservation portfolio and planning process.

Offset Outcomes

Offsets are a mechanism to ensure that environmental impacts of development are balanced by environmental gains with the overall aim of achieving a net neutral or positive outcome. Biodiversity offset design must overcome several methodological obstacles including how to ensure ecological equivalence to losses in terms of the ecological systems and/or species impacted, where to locate offsets relative to impacts, and how to minimize uncertainty and conflicts with future development (Kiesecker et al., 2009; Bull et al., 2013; Sochi and Kiesecker, 2016). The conservation portfolio and the supporting spatial datasets provide a mechanism to address these challenges by directing offsets to portfolio sites that can become protected areas. Designating these sites as protected areas maximizes biodiversity conservation benefits and long-term security, and also provides a mechanism to direct offset funds to restoration and management.

In 2012, the Mongolian Parliament amended the EIA law to require biodiversity offsets for all new development projects (Parliament of Mongolia, 2012). The law requires developers to calculate a minimum offset cost following specifications published by the Ministry of Environment, Green Development, and Tourism (MEGDT) that are based on the conservation portfolio and supporting datasets (MEGDT, 2014). The specifications define a method for calculating compensation according to impacts measured in terms of area, magnitude, duration, and four landscape conservation factors based on ecosystem composition, ecological condition, critical habitat designation, and proximity to portfolio sites. The four landscape conservation factors are designed to require higher compensation for impacts to rare and highly productive ecosystems, areas in good ecological condition, and/or near the portfolio sites, with the goal of steering development away from these areas. To support transparent and replicable implementation of this regulation, the MEGDT developed a Mitigation Design GIS Toolset to apply these specifications and made the conservation planning datasets publicly available through a web-based GIS application and a public GIS archive (TNC, 2016).

Additional Applications of Landscape Planning Framework

The datasets developed to support this framework have also been instrumental for implementing protection of riverine wetlands. At least 40% of the area of riverine wetlands in Mongolia may be degraded by heavy summer livestock use (Jamsranjav et al., 2018) and rivers are further threatened by wetland conversion and water withdrawals by mine operations. In 2009, Mongolia passed a law protecting water resources that prohibits mining near water sources (Parliament of Mongolia, 2009) but does not specify how to delineate these protection zones, and available maps and surveys are inconsistent. The terrestrial ecosystem classification developed

for the conservation plans includes a delineation of floodplains and riverine wetlands that has been the basis for formal protection and effective local implementation of the law in seven major river basins (WWF Mongolia, 2015).

Additional Challenges

Linear Infrastructure: Transportation infrastructure and traffic supporting mining operations create barriers to wildlife movement that are an urgent threat to the viability of wide ranging species including Mongolia's iconic plains ungulates (Ito et al., 2013; Batsaikhan et al., 2014; Wingard et al., 2014; Olson and van der Ree, 2015). Protected areas alone cannot effectively conserve the current populations of wide ranging species (Runge et al., 2014). Mitigation of impacts to movement and connectivity of wide ranging species is a difficult and urgent challenge, requiring improvements in both policy guidance and practical mitigation measures that include siting analysis, wildlife passage structures, and traffic curfews, all of which require more research as well as local studies to guide implementation. Mitigation measures for transportation are summarized by van der Ree et al. (2015). Climate change will likely require further shifts in ranges and habitat use and compound the threat of habitat loss, fragmentation, and movement barriers (Singh and Milner-Gulland, 2011).

Ground Water Management: In the Gobi Desert, water withdrawals to support mining operations could reduce groundwater supplies, affecting wells, springs, and vegetation productivity, and ultimately reducing water and forage for livestock and wildlife. In the Inner Mongolian grasslands of China, water withdrawal for coal mining has been identified as the dominant cause of loss of surface water (Tao et al., 2015). Because current understanding of the hydrology of this system is limited, it is difficult to estimate the amount, spatial extent or duration of mining-related ground water impacts.

Climate Change: Mongolia and Central Asia have been warming since the 1950s, at a faster rate than before over the last 1000 years (Chen et al., 2009; Davi et al., 2015), and producing hotter, more frequent droughts (Pederson et al., 2014; Batima et al., 2005). This trend is predicted to continue and cause declines in soil moisture and rangeland productivity (Angerer et al., 2008). Surface- and ground-water sources and stream flows have declined recently across Mongolia (MNET, 2009; Fassnacht et al., 2011). These changes to rangelands and water sources will have serious implications for wildlife, pastoralists, and economic development.

Conclusion

Mitigation frameworks and conservation planning are supported by large bodies of research and guiding principles, but both fall short in practice. Historically, mitigation has been a reactive process occurring at small spatial scales on a site-by-site basis and little guidance exists for regulatory authorities to decide when and where to avoid, minimize, or offset. Most landscape-level conservation plans do not produce tangible conservation actions (Prendergast et al., 1999; Knight et al., 2008). A root cause of these gaps in practice is that development and conservation planning are typically independent, isolated processes (Kiesecker and Naugle, 2017).

Like many other arid lands, the Mongolia Gobi Desert is a data-scarce landscape with globally significant biodiversity facing rapid development. Mongolia's national mitigation framework is designed to guide site level mitigation decisions with a landscape-scale information system, and move from a reactive, site by site approach to a proactive, regional vision that balances goals for development and conservation. This demonstrates that landscape-level mitigation based on stakeholder-driven and data-driven conservation planning is both possible and practical, and can provide a mechanism to fund conservation in proportion to development.

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Adaptations of Large Carnivores to the Arid Kalahari

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Abstract

Little is known about ecological interactions between large carnivores in arid landscapes. A review of the densities, diets and foraging ecology, as well as the relations between the large carnivores in the arid Kalahari, illustrates the way they have successfully adapted to arid conditions, and highlights some of the differences in these relationships with those in more mesic areas. Relative densities of the large carnivores are more even, community structure is different, with the inclusion of the brown hyena and the disappearance of the African wild dog. Resource partitioning is more acute and diet flexibility is shown. The relative contribution to animals killed by predation is more equitably shared by the predator community, and high rates of food loss by smaller carnivores to larger ones has not been recorded. More attention should be given to research and conservation of these species in arid areas.

Introduction

Adaptation is the evolutionary process whereby an organism is able to survive in a habitat. Because of the variety of habitats, and the ever-changing nature of ecosystems, organisms are forced to adapt to changes in order to survive through the process of natural selection. Most large African carnivores are widely distributed and able to adapt to different savannah regions, but they tend to disappear in more extreme habitats such as rain forests and deserts. The leopard (*Panthera pardus*) is the most widely distributed and adaptable large carnivore species, able to survive in almost all terrestrial habitats. The brown hyena (*Hyaena brunnea*) and its northern relative the striped hyena (*Hyaena hyaena*) are primarily found in arid regions.

Most studies of large African carnivores have taken place in areas that receive an average of 450 mm or more rainfall per annum. However, a substantial part of Africa (43%) covers more arid areas, where annual rainfall is below 350 mm, and where the biomass of herbivores is lower. This would be expected to have an impact on large carnivore impacts and relationships. For example, lower large carnivore densities would be likely because of the decrease in food biomass and availability, and this might affect the larger or more specialized species more than generalists. Dietary habits and resource partitioning might change and prey species not often utilized in more productive areas might become more important. Foraging behavior too could be different. The carnivores might have to move further to find food. Finally, behavioral interactions between the carnivores might vary and the impact they have on each other take on a different dynamic.

Globally dry land areas have been neglected by both scientists and conservationists, because of their relatively low productivity (Durant et al., 2012). Yet they are home to species that are adapted to harsh and highly variable environments. One arid area that has received more attention than most, particularly with regards to the large mammalian carnivore community, is the arid Kalahari, specifically the southern part of the Kgalagadi Transfrontier Park (KTP).

In this article I review ecological and behavioral adaptations of large carnivores to the southern arid Kalahari. I consider relative densities, aspects of their diet, feeding ecology and behavior, as well as interactions between the species; I show that some of the generally accepted principles of African large carnivore community dynamics are not applicable to arid regions.

The Arid Kalahari

The Kalahari is a large, sand filled basin stretching from 24°S to 1°N in the west of Africa. The arid Kalahari is in the extreme south of the region. The KTP (24°S and 27°S and 20°E and 22°E) covering 36,000 km² in South Africa and Botswana is situated here and is a well conserved ecosystem. In this region the sand is piled into vegetated linear or seif dunes fixed by vegetation (Fig. 1). Two riverbeds, the Nossob and the Auob, which only flow for short periods and distances during abnormally wet years run through the KTP.



Fig. 1 Leopard on Kalahari dune.

There is no naturally occurring permanent water, but boreholes have been introduced especially along the riverbeds, but also sporadically in the dunes and on some pans. However, the natural fauna of this area, including the large carnivores, are adapted to survive without surface water.

Average annual rainfall in the southern KTP ranges from 150 mm in the south-west to 250 mm in the north. The vegetation type is classified as Kalahari Duneveld and is predominantly shrubby grassland, except along the riverbeds and some adjacent areas where an open *Acacia erioloba* and *Acacia haematoxylon* tree savannah is found (Fig. 2). Ecological conditions dictate that herbivorous animals are generally thinly distributed and need to be mobile. Gemsbok (*Oryx gazella*), blue wildebeest (*Connochaetes taurinus*) (along the riverbeds), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*) and common ostrich (*Struthio camelus*) are sedentary species, whereas springbok (*Antidorcas marsupialis*), red hartebeest (*Alcelaphus buselaphus*), common eland (*Tragelaphus oryx*) and wildebeest (away from the riverbeds) are nomadic. These herbivores tend to concentrate along the riverbeds during the wet season and disperse in the dry season. Smaller herbivorous mammals such as Cape porcupine (*Hystrix africae australis*), hares (*Lepus* sp.) and springhares (*Pedetes capensis*) are widespread. Besides the large carnivores, mesocarnivores, such as black-backed jackal (*Canis mesomelas*), bat-eared fox (*Otocyon megalotis*), caracal (*Caracal caracal*) and African wild cat (*Felis silvestris*) are well represented (Mills and Mills, 2013).

Methods

The sand and sparse vegetation in the arid Kalahari provide unique conditions for tracking spoor over long distances with experienced Bushmen trackers. The sparse vegetation and open landscape also make it possible to visually follow habituated animals in



Fig. 2 Lions moving along the Auob riverbed.

a vehicle for long periods. These methods have been utilized by a number of researchers and have made it possible to compile accurate profiles of the diets of the large carnivores as well as revealing much about other ecological and behavioral adaptations of their life histories. The information used in this review for brown hyenas and spotted hyenas (*Crocuta crocuta*) are from Mills (1990), for cheetahs (*Acinonyx jubatus*) from Mills and Mills (2017), for lions (*Panthera leo*) from Eloff (1973, 1984) and for leopards from Bothma and le Riche (1984, 1986, 1990) and Bothma et al. (1997).

Results

Large Carnivore Densities

Unlike in moister African savannas where spotted hyena and lion tend to numerically and behaviorally dominate the large carnivore community, the relative densities of large carnivores in the arid Kalahari are generally lower but more even (Table 1). In fact the large carnivore that exists at the highest density, the brown hyena, is absent from the moister savannas. The wild dog (*Lycaon pictus*) is only sporadically seen in the KTP, and although it has been observed to occasionally breed successfully there, it is not known to have done so for the last 20 years (Mills and Mills, 2013). It is not dealt with here.

Diet and Prey Selection

Table 2 summarizes the diets of the five species in the arid Kalahari showing those species that make up 5% or more of their food. The two hyena species differ markedly in diet. The brown hyena has the widest diet of all the large carnivores, supplementing carrion of almost any origin, which makes up 69% of the diet, with wild fruits which make up 23% of the diet, especially the tsamma melon *Citrullus lanatus* and gemsbok cucumber *Acanthosicyos naudianus*. To a lesser extent it also eats reptiles, insects and birds eggs, especially ostrich eggs. Many feeding events involve picking up small items such as kill remains and wild fruits, consequently the species foragers solitarily although it breeds cooperatively. Hunting is almost irrelevant and contributes only about 2% of the biomass of its food. Although an accomplished and opportunistic scavenger, the spotted hyena is predominantly a hunter of gemsbok calves (Fig. 3) and wildebeest of all ages; kills contributing 65% of the biomass eaten. It tends to be the most specialized hunter in the arid Kalahari, with only two species making up 68% of kills.

The lion has a similar diet to the spotted hyena, although the two species tend to prey on different segments of the gemsbok population; adults in the case of lions, and calves in the case of spotted hyenas. This may be an example of resource partitioning as lions are better equipped to capture adult gemsbok than are spotted hyenas and so are able to dominate this food source.

The outstanding feature of the lion's diet is the preponderance of porcupines *Hystrix africaeaustralis* killed (Fig. 4), far more than has been recorded anywhere else (Hayward and Kerley, 2005). This is testimony to the low density of large herbivores in this arid

Table 1 Large carnivore densities (100 km²−¹) from the southern Kgalagadi Transfrontier Park

Lion	Leopard	Cheetah	Spotted hyena	Brown hyena
1.0	0.2	0.9	0.9	1.8

Data from Mills, M. G. L. 2015. Living near the edge: A review of the ecological relationships between large carnivores in the arid Kalahari. *African Journal of Wildlife Research* 45, 127–137.

Table 2 Diets of large carnivores from the southern Kgalagadi Transfrontier Park

	Lion	Leopard	Cheetah	Spotted hyena	Brown hyena
Number of kills/food items ^a	92	80	411	346 (65% ^b)	7794 (2% ^b)
Species making up >5% of the diet	Porcupine 34%	Porcupine 20%	Steenbok 36%	Gemsbok 50% (80% calves)	Wild fruits ^c 25%
	Gemsbok 26% (60% adults)	Gemsbok calves 19%	Hare 19%	Wildebeest 18%	
	Springbok 11%	Duiker 10%	Springbok 15%		
	Hartebeest 9%	Black-backed jackal 9%	Springhare 7%		
		Bat-eared fox 9%	Ostrich 7%		
		Steenbok 8%	Gemsbok calf 6%		
		Genet 6%			

^aFor spotted hyena carcasses fed on, for brown hyena food items eaten.

^b% Biomass killed.

^cTsamma and gemsbok cucumber.

Data from Mills, M. G. L. 2015. Living near the edge: A review of the ecological relationships between large carnivores in the arid Kalahari. *African Journal of Wildlife Research* 45, 127–137.



Fig. 3 Spotted hyena killing gemsbok calf.



Fig. 4 The remains of a porcupine killed by a lion as revealed from following spoor.

region and to the adaptability of the lion. The leopard also capitalizes on porcupines far more often in the arid Kalahari than anywhere else so far studied (Hayward et al., 2006a). However, in line with the leopard's reputation for killing carnivores, especially in less productive areas, small carnivores comprised 24% of its kills. These were the abundant and wide spread canids; black-backed jackal and bat-eared fox, which are killed in equal proportions, and the small-spotted genet *Genetta genetta*. Additionally, more typical antelope species were often utilized.

The cheetah's most important prey is the widespread steenbok, which does not feature in the leopard's diet to anything like the same extent. Other important prey for the cheetah are hares, springbok and springhare, and, for coalition males, gemsbok calves (Fig. 5) and adult ostrich. Most of these species are also not usually associated as important prey for cheetahs in other areas.

Whereas cheetah and leopard diets are similar in more mesic savannahs, only one species, steenbok, is represented in over 5% of their kills in the arid Kalahari. However, the steenbok is utilized four times more frequently by the cheetah than the leopard. The cheetah is well adapted to arid regions. Its ability to survive on small, cryptic and solitary species such as steenbok, hare and springhare is noteworthy and somewhat at odds to the conclusion of Hayward et al. (2006b) that it prefers to kill prey within a body mass range of 23–56 kg.

Although, the porcupine is less common in the arid Kalahari than other potential prey species of similar size such as steenbok, duiker, black-backed jackal and bat-eared fox (Mills 1990), it is less agile, albeit equipped with formidable defense structures through its quills. It is therefore easier for the more robust cats like lions and leopard to catch (the spotted hyena has also been observed killing it occasionally). The cheetah's small jaws and teeth, adaptations for speed, preclude its ability to kill a porcupine. The ubiquitous steenbok, on the other hand, is most vulnerable to the swift cheetah (Fig. 6), but less so to the other hunters. The reason for springbok being a less important prey than might be expected is because of their limited distribution, being almost exclusively confined to the river-beds.

Foraging Behavior

Table 3 summarizes aspects of the foraging behavior of the five species where known. Cheetahs were active for much less time than both hyena species, and while the hyenas are strongly nocturnal, the cheetah is mainly diurnal, although in the Kalahari more



Fig. 5 Cheetah males killing a gemsbok calf.



Fig. 6 Cheetah hunting steenbok.

Table 3 Aspects of foraging ecology and behavior of large carnivores from the southern Kgalagadi Transfrontier Park

	<i>Lion</i>	<i>Leopard</i>	<i>Cheetah</i>	<i>Spotted hyena</i>	<i>Brown hyena</i>
Mean %24 h active	?	?	10.3	31	42.6
Mean distance (km) moved/24 h	11.8	13.9	11.0	27.1	31.1
Mean distance moved (km) between meals	25.2	24.5	15.9	32.7	9.2
Mean amount of food available at each meal (kg)	58	22	15	59	1.7
% Chases successful	39 ($n = 148$)	18 ($n = 110$)	43 ($n = 730$)	35 ($n = 136$)	9 ($n = 70$)

Data from Mills, M. G. L. 2015. Living near the edge: A review of the ecological relationships between large carnivores in the arid Kalahari. *African Journal of Wildlife Research* 45, 127–137.

nocturnal than is often taken to be the case. There are no data on activity for lions and leopards from the arid Kalahari, because these studies relied solely on tracking spoor. However, they are predominantly nocturnal.

Because they are active for longer periods than the cheetah, and probably the other cats as well, hyenas are generally more mobile and cover longer distances over a 24 h period than cats. For the brown hyena this is an important adaptation for a scavenging strategy, where food items are often widely scattered and quite small, as they usually comprise remains only. Mobility for the spotted hyena is important because, not only does it scavenge about one third of its food, it is also the most selective hunter of the large carnivores in the arid Kalahari. Additionally, it has the challenge of having to locate gemsbok calves, which only make up approximately 10% of the relatively thinly dispersed gemsbok population, but on which it relies heavily for food. The cats make up for their limited mobility by being able to catch a larger range of prey than the spotted hyena (Table 2). Additionally, cats typically hunt by stealth, employing a sit and wait or ambush foraging strategy, followed by a stalk and a short chase, whereas the spotted hyena follows a widely foraging and cursorial hunting strategy of running down prey over quite long distances.

Estimations of the average size of a meal for each species were calculated by assuming that the average mass of food from a kill was three quarters of the average size of an adult female of the species, summing the total for all kills, and dividing that by the number of kills recorded. The average travel distances between meals of over 1 kg for all species varied and is related to the average size of the meals (Mills, 2015). The solitary foraging brown hyena tends to find several small meals per night, whereas the spotted hyena and the lion eat fewer, but substantially larger meals which they often share with conspecifics. The sometimes social cheetah (males in coalitions or females with several cubs) and the more solitary leopard eat intermediate sized meals, although leopards move nearly twice as far as cheetahs do between meals.

Lion, cheetah and spotted hyena hunting success was similar, but leopard hunting success was lower. This might be the reason for the longer distances moved by leopards, but overcome to an extent by the leopard's broader diet (it has the most prey species making up more than 5% of its diet from the smallest kill sample). On the other hand, the leopard appears to exist at the lowest density of the large carnivores in the area, and therefore may be the least well adapted species to this habitat. As hunting plays an insignificant role in the brown hyena's foraging behavior it was omitted from this analysis.

Interspecific Relations

Because of the relatively low densities of the large carnivores in the arid Kalahari, interactions between the species are comparatively rare, but that does not necessarily mean that they are trivial.

The spotted hyena and the lion are potentially serious competitors, as they have the largest measure of overlap in diet and activity regime. Interactions between lions and spotted hyenas in the study area, although infrequent, are intense. Some interactions lasted over an hour, especially when initiated by spotted hyenas, as was the case in 64% of all the interactions observed. Food loss to either species was however uncommon.

When spotted hyenas were the initiators of an interaction, the impression gained was that they were attempting to move the larger competitors away from the area, and were prepared to take risks to achieve this. It seems that in the KTP spotted hyena/lion interactions are not as one-sided as they are in a highly productive area like the Ngorongoro Crater, where lions are clearly dominant (Kruuk, 1972). Perhaps in this arid region, where food resources are thinly distributed, the loss or gain of a kill is a more significant event. The smaller spotted hyena has more to lose if lions steal a kill in the arid Kalahari than Ngorongoro and, therefore, is more prepared to take the risk of standing up to lions. In two instances lions killed a spotted hyena cub, but spotted hyenas killing lion cubs was never observed.

The comparatively low spotted hyena density results in few interactions between them and leopards and cheetahs which mean that these cats lose little food to the spotted hyena. The brown hyena may lose food to the spotted hyena through being displaced from a scavenged carcass, although occasionally the two species were observed to share a carcass, at least briefly. Away from food spotted hyenas may harass brown hyenas and even occasionally kill one. However, the brown hyena outnumbered the larger and dominant spotted hyena by about 2:1 in the KTP, so the detrimental effects of these interactions are localized, and mainly take place in the vicinity of spotted hyena dens.

The numerical dominance of the spotted hyena in most African ecosystems is diminished in the arid Kalahari, and the rarer brown hyena is better able to survive in an area where food resources, especially large ones, are scarce. However, the fact that even in the arid Kalahari the spotted hyena appears to impact on the brown hyena, at least locally in the vicinity of spotted hyena dens, may explain the limited distribution of the brown hyena and its exclusion from areas of higher rainfall where spotted hyenas reach much higher densities.

The brown hyena derives considerable benefit by scavenging from lion kills in the KTP. Not only were 43% of the carcasses of known origin scavenged by brown hyenas killed by lions, the amount of food gained was relatively high, as these were large ungulates. On the other hand, lions may attack and kill or maim a brown hyena, but this is rare. On balance, it would seem that the brown hyena gains more than it loses from the presence of the lion in the arid Kalahari. In the case of the leopard, neither species is influenced by the presence of the other, but the cheetah is an important contributor of food to the brown hyena, especially along the riverbeds where springbok remains are frequently scavenged (Fig. 7). However, only 6% of cheetah springbok kills observed were kleptoparasitised by a brown hyena, and mostly the hyenas ate the remains after the cheetahs had departed. The diurnal hunting behavior of the cheetah, especially females with cubs, and the nocturnal activity regime of the brown hyena is a major reason for this; an example where temporal activity partitioning is important.

The cheetah (together with the wild dog) is often considered to be the most vulnerable of the large African carnivores to competition with larger carnivores, especially the lion and spotted hyena. However, although predation on small cheetah cubs in the KTP is high, lions and spotted hyenas were not found to be the major culprits and a range of smaller carnivores including black-backed jackals and honey badgers *Mellivora capensis* were suspected. Furthermore, energetically the cheetah is better able to deal with kleptoparasitism than the wild dog and the incidence of kleptoparasitism for cheetahs in the KTP is low; only 6.1% of carcasses were stolen, with an average percentage loss of meat of 65% per kill. Direct killing of cheetah adults by other carnivores was also found to be low; only two instances were observed, both by leopards, and both cheetahs were probably injured beforehand.

Interspecific interactions between carnivores has been held up as a major cause of density differences between large and smaller species. In Africa, this has been especially well illustrated in the case of the wild dog. However, the relative densities of carnivores are also determined by other factors. The availability of resources, not just biomass of prey (Hayward et al., 2007), but also the structure of the prey community is crucial. Arid ecosystems have a dominance of smaller-sized herbivores, while the more mesic savannah



Fig. 7 Brown hyena scavenging the remains of a springbok kill stolen from a cheetah.

ecosystems are dominated by larger-bodied herbivores. When these are in short supply, it may even up the differences in relative densities between large and smaller carnivores.

Conclusion

A major difference between the dynamics of large carnivore communities in mesic compared to arid savannahs like the arid Kalahari, is that larger carnivores are not the numerically dominate species in the arid systems as they are in the more mesic systems. Furthermore, the wild dog seems to be the first species to disappear as aridity increases, and the brown (and in the north, the striped) hyena appears. In this arid area the generalist brown hyena is numerically the dominate species.

Resource partitioning appears to be more acute in arid systems. Where prey is less abundant, dietary selection becomes more finely tuned, and each species tends to concentrate on the prey species and foraging strategy it is best adapted to utilize. For example, the cheetah, because of its superior acceleration, and ability to successfully follow the rapid twist and turns of fleeing steenbok, is the major predator of this wide ranging and common species in the arid Kalahari. The brown hyena, with its ability to move long distances, is the chief scavenger, whereas the spotted hyena hunts more and scavenges less than it does in areas where the brown hyena is absent. At the same time, some species show flexibility in diet and are able to make use of prey that, although abundant in other systems, are not often killed, for example, porcupines by lions and leopards, and springhares by cheetahs.

Interspecific relations between carnivores in arid systems may also take on a different dynamic than in more mesic savannahs. Whereas in the latter the largest and numerically dominant carnivores contribute the major share of animals killed across a wide size range, this is more equitably shared by the predator community in arid areas. Additionally, high rates of food loss by smaller carnivores (e.g. the Ngorongoro Crater) where lions stole much food from spotted hyenas has not been recorded in the arid Kalahari. The relationship between the lion and the brown hyena in the arid Kalahari is also an unusual example of a smaller carnivore deriving considerable benefit from a larger one.

Clearly arid regions are important habitat for large carnivores. Their flexibility to adapt foraging behavior and the varied nature of the relationships between the species are aspects of functional biodiversity that need to be conserved. Because of the extent to which arid regions cover Africa, more attention should be given to research and conservation in these areas. As has been pointed out by (Durant et al., 2014), the restoration of desert ecosystems will not only benefit biodiversity, it may also help to mitigate against global climate change where it leads to increasing aridity.

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Conservation Strategies for Managing Threatened Species and Desert Landscapes: Experiences From a Biodiversity Offset Trust

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Abstract

The extreme of desert environments increases the challenges of conducting conservation activities for threatened species and biodiversity. The vast distances, inaccessibility, extreme temperatures, unpredictable weather, sparse population, time and costs all create a situation in which limited research or land management practice occur in many arid environments in Australia. In the Great Victoria Desert in Western Australia, a biodiversity offset trust was established to improve conservation outcomes for threatened species through research and landscape-scale on-ground land management practices. The costs and challenges associated with working in remote regions require conservation strategies that maximize available resources. We describe the conservation strategies employed by a small biodiversity offset trust to use funding, build partnerships and build knowledge to achieve positive conservation outcomes for two species, Sandhill Dunnart (*Sminthopsis psammophila*) and Malleefowl (*Leipoa ocellata*) in the Great Victoria Desert. These strategies are used as a means of overcoming the key challenges working in a remote arid region, lack of existing consolidated knowledge, expense and time of on-ground activities and lack of new knowledge.

Introduction

Achieving successful, sustainable conservation outcomes is challenging in vast, remote and sparsely populated areas (Jupp et al., 2015). The inaccessibility of remote deserts, lack of imperative, lack of resources, distance, time, weather extremes, climate variability and limited human resources create a situation in which understanding the biota of remote deserts in Western Australia is severely limited (Larson et al., 2009).

The Great Victoria Desert in Western Australia is one of the most remote and understudied regions in Australia (Fig. 1). Whilst knowledge of the biodiversity in the region is limited, the research which has been conducted demonstrates the region is an area of high biodiversity. There are over 1200 plant species recorded in the region, 51 of which are of conservation significance. There is one priority ecological community, which contains very high vertebrate diversity and unusual combinations of species (DBCA, 2017). The reptile diversity of the region is one of the highest in the world (Pianka, 1994). In terms of mammal and bird diversity, the area has a low diversity. There has been large loss of species, particularly mammals, from the region and a high proportion of the remaining species are threatened or vulnerable (Short and Smith, 1994; Woinarski et al., 2015).

The loss of species can be partially attributed to the lack of land management occurring across the region. Approximately 70% of the land tenure is unallocated crown land. This results in very limited funding available for government-led initiatives to take place on this land type. Approximately 25% of the land is Native Title, with Traditional Owners responsible for the land management practices. Government funding for the management of Native Title lands is also very limited. Increasingly Indigenous ranger positions are being funded by partnerships between Indigenous groups, environmental nongovernment groups and through the private sector to supplement government funding (Jupp et al., 2015). The remaining significant tenure in the Great Victoria Desert is Nature

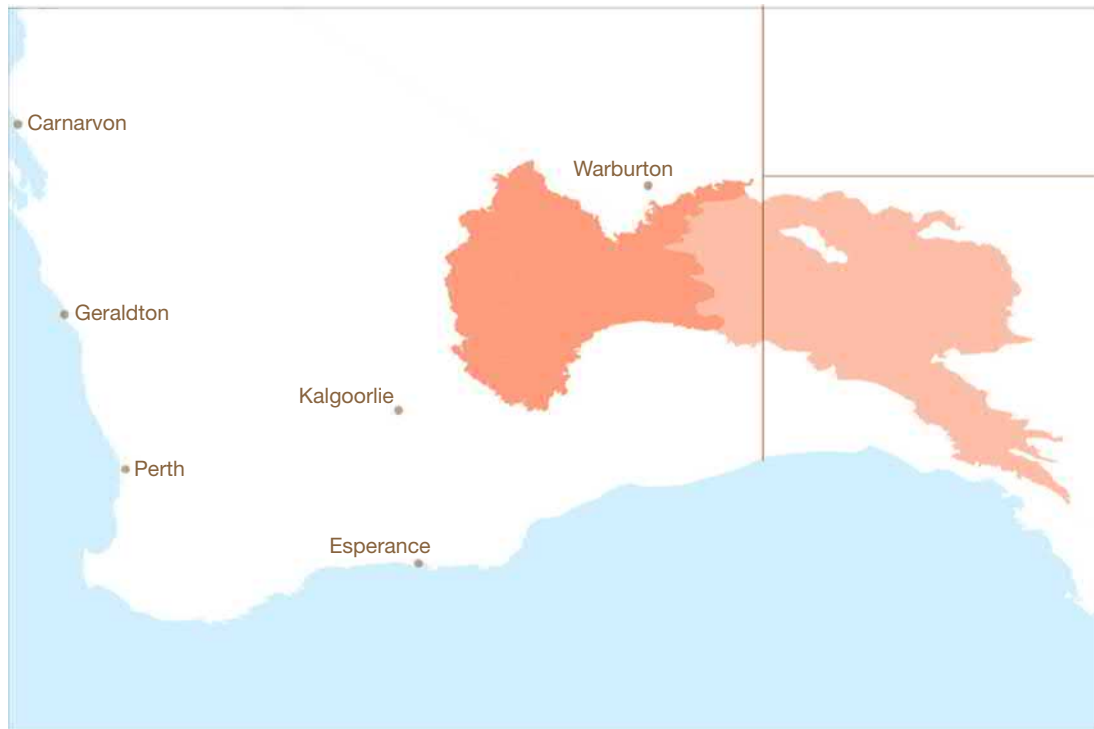


Fig. 1 The Great Victoria Desert. Dark orange shows the Western Australian focus area, the light orange shows the size of the desert, as it stretches across South Australia.

Reserves, vested with the Department of Biodiversity, Conservation and Attractions. As with the other land tenure types, government funding is limited for work on Nature Reserves.

Two operational mines exist in the region, they occupy a very small percentage of the land tenure. Like many mining operations, the mines have a small physical footprint but an intense impact in the vicinity of the footprint. One mine in the region, Tropicana Joint Venture, established the Great Victoria Desert Biodiversity Trust (the Trust) as a means of offsetting the potential impacts of the mine. Biodiversity offsets are intended to create a “no net loss” or “net gain” for the species or biodiversity impacted by a development (Calvet et al., 2015). In this case, the offset was set as part of an environmental assessment under the *Commonwealth Environment Protection and Biodiversity Conservation Act 1999* which requires that any offset deliver a conservation outcome that improves or at least maintains the viability of the aspect of the environment that is affected by the proposal (DSEWPC, 2012). The offset was required because of potential impacts on three threatened species.

The constraints to traditional offsets that faced the mine were lack of knowledge on the threatened species potentially impacted and lack of biodiversity knowledge in the region leading to uncertainty over how offset funds could be best utilized for positive conservation outcomes for the threatened species potentially impacted by the mine. The offset was principally an indirect one with the establishment and funding of a Trust fund. The Trust was established with an independent management board, to use pre-determined funding to conduct research and on-ground management for the conservation of threatened species, focussing on the Sandhill Dunnart (*Sminthopsis psammophila*) and Malleefowl (*Leipoa ocellata*), in the Great Victoria Desert (Figs. 2 and 3). The mandate of the Trust also acknowledged that activities need to consider biodiversity and threats at the landscape level and to employ Traditional Owners where possible to conduct land management activities.



Fig. 2 Sandhill Dunnart (*Sminthopsis psammophila*). Photo by Ray Lloyd.



Fig. 3 Malleefowl (*Leipoa ocellata*).

We outline the processes and strategic principles involved in achieving successful conservation strategies when working in a remote, inaccessible, sparsely populated region, with limited funding. Examples of the projects and activities initiated under these strategic conservation principles are also described. Key strategies include actively engaging with a variety of stakeholders in the region, building partnerships, building on foundational efforts and developing projects that meet multiple objectives. These techniques are recognized as important features of conservation and natural resource management in Australia (Fitzsimons et al., 2013).

Method

Stakeholder Engagement and Partnerships

Successful conservation activities should acknowledge that different groups and organizations have different strengths and understandings of threatened species and biodiversity in the region. Finding appropriate ways of engaging with these stakeholders and building partnerships to create a collaborative approach is critical to the success of projects in remote areas. Stakeholder engagement delivers multi-faceted benefits, not only do groups build new knowledge whilst building new relationships. It also increases stakeholder trust, ownership and ability to act. Meaningful engagement can lead to better quality decisions, reduce conflict, increase the likelihood of success for a project and reduce implementation costs through cost sharing or in-kind support (Sterling et al., 2017).

Experts in the field

Working in a region with limited stakeholders, limited and dispersed knowledge and limited funding necessitates working closely with all stakeholders to maximize the benefits and utilize the strengths and knowledge of different actors. In 2014 the Trust held a series of workshops on threatened species in the region. The aim of these workshops was to bring together experts who had knowledge of the threatened species and work conducted in this remote region. By bringing together key actors, the latest information was attained. As a group, experts were also able to discuss the gaps in their collective knowledge. By examining existing knowledge and knowledge gaps, the groups were able to determine the next key funding priorities for threatened species. Bringing together experts and reaching consensus on the next steps required gave the Trust a strong mandate for funding future projects.

Adaptive Management Partners

Whilst the threatened species in the region were the primary focus of these initial workshops, engagement continued at a broader landscape level concurrently. Threatened species exist within a broader landscape and whilst there many knowledge gaps for particular species, the broad level threats, effecting biodiversity and ecosystems in the region are also threatening processes for individual species. The principle threats are recognized as predation by introduced species particularly the feral cat, *Felis catus*, and the European Red Fox, *Vulpes vulpes*, and altered fire regimes (Woinarski et al., 2015). To address these broader landscape level threats, the Trust partnered with key land managers and stakeholders in the region. These groups included Traditional Owner groups, the Western Australian Department of Biodiversity, Conservation and Attractions, Rangelands Natural Resources Management, Greening Australia and Central Desert Native Title Services. These groups each brought an array of different knowledge of the region as well as different priorities in terms of the perceived threats to biodiversity. Over the course of three formal workshops, groups were able to work together through the Conservation Action Planning process to, as a group, assess which threats or assets were in immediate need for action and which threats or assets were of lower priority. Working through this process collectively, the group prioritized actions on known threats and also identified additional landscape threats. These threats included the likely loss of the unique Traditional Ecological Knowledge (TEK) and cultural knowledge in the region and the threat that buffel grass (*Cenchrus ciliaris*) invasions posed to biodiversity by fuelling large, intense bush fires. The result of this Adaptive Management Partnership was the successful funding of several projects including funding for a cultural and biodiversity trip by Traditional Owners, fire scar mapping projects and funding for buffel grass (*C. ciliaris*) management.

After the initial meetings and funding of projects, outputs from the partnership have slowed. Changes in personnel, lack of leadership and lack of direction has resulted in limited meeting of the “Adaptive Management Partners” as a formal group. The plan created by this process, whilst referenced by different groups, has not effectively been “owned” by any of the key stakeholders. Whilst the lack of ongoing structured meetings and lack of ownership of the plan may make the project appear unsuccessful, regular interactions still occur between different members of the group and therefore process has resulted in strong relationships between the organizations.

Mining and exploration operations

Mining and explorations operations in the Great Victoria Desert represent one of the few industries operating in the region. These operations have the potential to have a significant impact on biodiversity through direct disturbance to the environment and through the introduction of waste outputs (food/garbage, etc.). These impacts may increase the number of scavenger species (feral dogs, cats, foxes, mice and rats) in the area which in turn negatively impact on the biodiversity of the area (Sonter et al., 2018). Mining operations also come with a number of environmental regulatory conditions and the requirement to conduct environmental surveys to determine what species are present in a particular area. With limited other funding available, the surveys and data collected by these operations represent a key resource for understanding the biodiversity of the region. Working in partnership with mining and exploration industries has been a key component of understanding biodiversity in the region. The Trust has actively informed mining companies of its activities and worked with them to share knowledge and resources. The Tropicana Joint Venture, has provided a large amount of in-kind support to Trust funded activities by providing access to their village and facilities, food and equipment and use of transportation resources. This has allowed projects to be undertaken at a significantly reduced cost or in some instances, made possible projects that would have otherwise been logistically near impossible. Vimy Resources, another mining operation in the region, has actively shared their methods for camera trapping Sandhill Dunnarts including their process for refinement and improvement of standard camera trapping techniques. Partnering, knowledge sharing and in-kind support are vital contributors to achieving outcomes in a region as remote and inaccessible at the Great Victoria Desert.

Traditional Owners

Engagement and collaboration with Traditional Owners is a vital part of any environmental work undertaken in Australia. In the Great Victoria Desert, where the Traditional Owners are the only permanent residents on-country, this collaboration is even more vital. Traditional Owners have a unique knowledge of country and species. They also have an extremely long connection to the land and Elders are able to describe changes that have occurred in the landscape in terms of weather, plants and changes in animal populations. Valuing the knowledge and skills of Traditional Owners and integrating it with western science deepens the understanding of the land, species and changes that have been occurring over many millennia (Horstman and Wightman, 2001).

One project undertaken to support Traditional Owners involved facilitating Traditional Owners access to their sacred cultural sites. In this region, distance and lack of vehicle access has prevented many Traditional Owners from visiting their cultural sites of significance. This means that whilst Elders know the sites and their significance, they have not been able to pass this cultural knowledge onto younger generations. The inability to visit sites also means that the sites are not being protected from bushfire and their current status is unknown. The uncertainty over the sites results in lack of action in terms of management, as Elders and Traditional Owner Ranger teams are reluctant to conduct activities which may adversely impact on the sites. The Trust provided funding to allow Elders and Traditional Owner Ranger teams to access sites using helicopters. This allowed the Traditional Owners to visit sites in a relatively fast manner and pass on traditional knowledge to younger generations. The Indigenous Ranger teams also used technology to map the biodiversity of these cultural sites. Using iPads and an application called *Fulcrum* rangers were able to photograph sites, document species and conditions of the site and conduct biodiversity assessments of the areas.

The project met two primary objectives, facilitating the transfer of TEK and cultural knowledge as well documenting the sites and assessing the need for landscape management activities. Understanding the priorities for Traditional Owners and utilizing western science and technology alongside these priorities can create opportunities for comanagement in which all groups benefit (Zurba et al., 2012).

Collaborations and knowledge sharing

Whilst formal partnerships are essential for some projects, ongoing collaborations and knowledge sharing with any actors in the region is vital. With limited research being undertaken and limited on-ground work being conducted, maximizing the knowledge that anyone is conducting in the region is essential. Regular contact with organizations known to be working in the region is the most simple and direct means for knowledge sharing. Outside of known organizations, determining who is working in the region and where they are working is more challenging. The Trust reviews databases (e.g., TENGGRAPH from the Department of Mines and Petroleum) to see which companies hold tenements (mining and exploration) in the region. The Trust also hold workshops and invites a wide range of stakeholders to participate in knowledge sharing sessions, these workshops include regulatory agencies who may have a clearer picture of who is undertaking work and the type of work being conducted in the region.

Building on Existing Knowledge/Maximum Utility of Funds

Biodiversity conservation plan

In remote areas, where funding and access are limited, it is vital that existing knowledge of biodiversity is known and utilized. In the Great Victoria Desert, research has been conducted over a number of decades, across a variety of species and in a wide array of locations. As part of its mandate, the Trust completed a “biodiversity conservation plan for the Shield and Central regions of the GVD.” This document compiled the available information to create a baseline of knowledge for the region and is expected to evolve as more research and studies are undertaken in the region.

Desktop studies

In order to thoroughly investigate projects before funds are expended on costly on-ground activities, the Trust initiated a series of desk top studies on Sandhill Dunnart and Malleefowl and fire effects, considered to be one of the greatest threats facing these species. For the two threatened species, the Trust funded projects that focussed on examining all known location records, detailing the habitat preferences and determining which areas were suitable for the species. The Trust also funded research into the best methods for surveying for these species. These desktop studies have enabled the Trust to fund on-ground surveys using the best available techniques. These surveys have used the data to search locations in which the species have a high likelihood of being present as well as search locations which could re-shape knowledge of the species if the species were detected in habitat previously determined to be “unsuitable.”

Remote sensing

Intense fire is one of the critical threats facing the Great Victoria Desert. Whilst fire has always been part of the desert ecosystem, the scale and intensity of fire in the Great Victoria Desert has increased at a dramatic rate (Burrows and Chapman, 2018). The Sandhill Dunnart and Malleefowl habitation are principally associated with long unburnt areas (Davis et al., 2016; Moseby et al., 2016). Habitation typically occurs in habitats that are over 10 years unburnt (Moseby et al., 2016). In order to determine the locations of long unburnt areas, the Trust funded a project to detect the fire scars in the landscape for the last 20 years (from 2000 to present). This project has allowed stakeholders the ability to interrogate areas of the Great Victoria Desert for fire scars including recent fires. The accuracy of the fire scar data has been questioned however the datasets are likely to provide fire data at a broad level.

In the Great Victoria Desert, the fire landscape was thought to have changed when the Traditional Owners were removed from the region. To investigate fire patterns under traditional management versus contemporary fire regimes, with virtually no fire management, the Trust commissioned a project to examine the earliest available records of the region. The result was an analysis of photography from 1960/61, shortly after the removal of Traditional Owners from the region (Burrows and Chapman, 2018). The fire scar imagery in 1960/61 showed mean and maximum fire scars of 11.2 ha and 3953 ha respectively. The mean and maximum fire scar size over the 17-year study period (2000–17) was 3699 ha and 1,033,121 ha, respectively (Burrows and Chapman, 2018). The result of this study is the need for reinstating smaller, low intensity, mosaic fires in the landscape in order to increase biodiversity and attain vegetation of diverse ages.

Multipurpose On-ground Efforts

Camera studies

In order to investigate a large number of areas where research had not previously been conducted the Trust funded camera studies across large areas of the Great Victoria Desert. The locations were selected based on a design for testing Sandhill Dunnart habitat preference. The design was based on a number of variables but principally designed on habitat deemed “suitable,” “moderately suitable” and “unsuitable” for Sandhill Dunnarts. Twenty random locations across the Great Victoria Desert encompassing these three habitat preferences and cameras were set up for 30 days. The aim was to detect Sandhill Dunnarts but also what other species were present across the desert. The result was the detection of Sandhill Dunnarts at two possible locations and detection of a range of native and feral species.

Alongside the cameras the contractors also conducted searches to determine evidence of other species (tracks, nests, burrows, etc.). Significant numbers of other species were detected and the data are available for analysis by researchers seeking to interrogate it for timings, numbers and species and the correlations between them.

Pitfall trapping and long walks

To investigate the possible Sandhill Dunnart locations, detected in the camera studies, contractors conducted two trips to the locations. The first trip was to dig pitfall traps and place out arrays of cameras at these two sites. Habitat assessments were also conducted. During the second trip camera data was collected and pitfall traps were opened. Species captured in the pitfall traps were recorded each day for a week. During the day, contractors conducted “long walks” to detect Malleefowl in the region. Long walks are a technique recognized for detecting Malleefowl in arid areas, where distances between Malleefowl mounds are likely to be large. This technique allows large distances to be searched over a relatively short period of time. The walks were conducted in areas that previous desk top studies had deemed as “highly suitable” for Malleefowl. Combining multiple techniques when searching for a species allows for documenting a wide variety of species, whether through direct capture, camera detection or sightings or evidence of species.

Conclusion and Key Challenges

We highlighted a number of key challenges in working towards positive conservation outcomes in remote desert regions. Firstly, knowledge of biodiversity in desert regions can be dispersed among diverse experts and across decades in terms of research. Creating forums to bring together this expertise can work well in discrete events as a “knowledge capture” however building and sustainable long-term collaborative partnerships takes time, effort, resources and the ability to effectively engage stakeholders to take shared ownership of a project. Maintaining motivation and drive, when stakeholders are located in geographically distant locations, with limited resources and competing priorities, can lead to ebbs and flows in engagement. Regular interactions with stakeholders, through any available mode can help to maintain a relationship through periods when the project priorities are not that of individual stakeholders. The location of the Trust, in the capital city of Perth, is a potential constraint to achieving successful outcomes. Whilst several key stakeholders are also based in Perth, this makes the distance to the region and to actual land managers very large, limiting the amount of time Trust staff spend on-ground in the Great Victoria Desert. This is a barrier to building trust with on-ground land managers.

A second challenge to achieving positive conservation outcomes in remote desert regions is the distance away from population centers, creating large costs involved in the mobilization of any on-ground project. To minimize these costs, where possible, research can be conducted using desktop studies and remote sensing. This can allow researchers to access the best available information and help shape and define parameters for future on-ground projects. A positive is that this creates opportunity and motivation to engage with and utilize the Traditional Owners living on Country, which not only provides useful data but also helps establish positive working relationships and provides additional financial support for them to stay on Country.

Finally, the limited scientific biodiversity knowledge of many desert regions is a key challenge for creating positive conservation outcomes. This lack of knowledge necessitates that any on-ground activities that do occur should capture as much data as possible during the time in the field, including of non-target species. A key criterion the Trust now uses when considering funding projects is the nature and extent of opportunistic data collection that can be carried out. This issue of limited scientific biodiversity knowledge has bought the Trust’s attention to the need to collect the knowledge of the Traditional Owners living on Country.

The conservation strategies we outlined in this paper are the some of the initial strategies employed by the Trust to increase knowledge, build partnerships and commence on-ground research on threatened species and biodiversity in the region. The next steps for the Trust and its partners will be ensuring on-ground action that delivers conservation benefit to the threatened species and biodiversity of the region. Monitoring any on-ground action, evaluating the success of interventions and then adapting projects based on learnings are the key next steps for the Trust. Success will be measured not only by positive outcomes for the species and reductions in threats, but by the strength of partnerships, the trust among partners, utilizing appropriate technologies and desktop studies where appropriate and attempting to get the most multi-purpose knowledge gain from any on-ground activities. The extremes and challenges of the desert environment may mean that longer time frames are needed to achieve results but they can be achieved when holistic conservation strategies are employed.

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Desert Biogeography: Mojave

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Abstract

The Mojave Desert is a vast and diverse landscape in the southwestern United States, encompassing 127,689 km². This ecoregion is bordered by the colder and wetter Great Basin desert to the north, and the warmer and wetter Sonoran and Chihuahuan deserts to the south. Spanning from 86 m below sea level at Badwater Basin in Death Valley, California, to 3632 m at its highest mountains near Las Vegas, Nevada, the Mojave is the driest of the four North American deserts, in part due to the rain-shadow caused by the Transverse Ranges on its western edge. Extremes of moisture availability, temperature, physiographic variety, and soil diversity all are key in the formation of this unique landscape, and the divergence of its inhabitants over time. While the Mojave is often considered an intermediary with respect to the plants and animals that occupy the Great Basin and Sonoran Deserts, there are many species unique to the Mojave that aid in highlighting its unique characteristics. The Joshua Tree, Mojave Desert Tortoise, Mohave ground squirrel, and several species of fringe-toed lizards are all endemics to this ecoregion that have adapted to this austere environment. There is also a wide array of fishes and aquatic invertebrates that occupy the Mojave's sparse and discontinuous waterways and springs. Nearly all of these Mojave endemics are the subjects of conservation concern facing a rapidly changing environment driven by increasing human populations and land use, and a changing climate.

Introduction

The biogeography of the Mojave involves the interaction of geography, ecology, and physiology as shaped by the temporal changes of geology and climatic conditions. The Mojave is a broad desert landscape, with complex topography, and a harsh and unforgiving climate, both of which have a dynamic history of change during the assembly of the flora and fauna that inhabit the region. Vicariant events have isolated and rejoined the flora and fauna of the region, and allowed and facilitated the immigration of new species into the region. Thus, the Mojave flora and fauna are an assemblage composed of a combination of species that pre-date the region as a desert environment, and others that have migrated into it relatively recently. Below we describe the Mojave in a brief historical context of its location, its geological history, and the species that characterize its flora and fauna, including species unique to the Mojave. We discuss the conditions under which those species arrived in the Mojave, and the current challenges to their persistence.

Where Is the Mojave Desert?

The Mojave Desert ecoregion encompasses approximately 127,689 km² in the southwestern United States of America ranging from southern California—through southern Nevada to southwestern Utah, and northwestern Arizona (Fig. 1). This smallest of North American deserts, is often considered an intermediate between the Great Basin Desert immediately to the north and the Sonoran Desert to the south (MacMahon and National Audubon Society, 1985; Turner, 1994a). Encompassing Death Valley National Park (NP), the Mojave includes the lowest elevation site in North America ensuring infamy as the hottest and driest place in North America. This hot-temperate desert is typified by a basin and range topology with low broad valleys interspersed by abruptly rising mountain ranges that result from block fault dynamics.

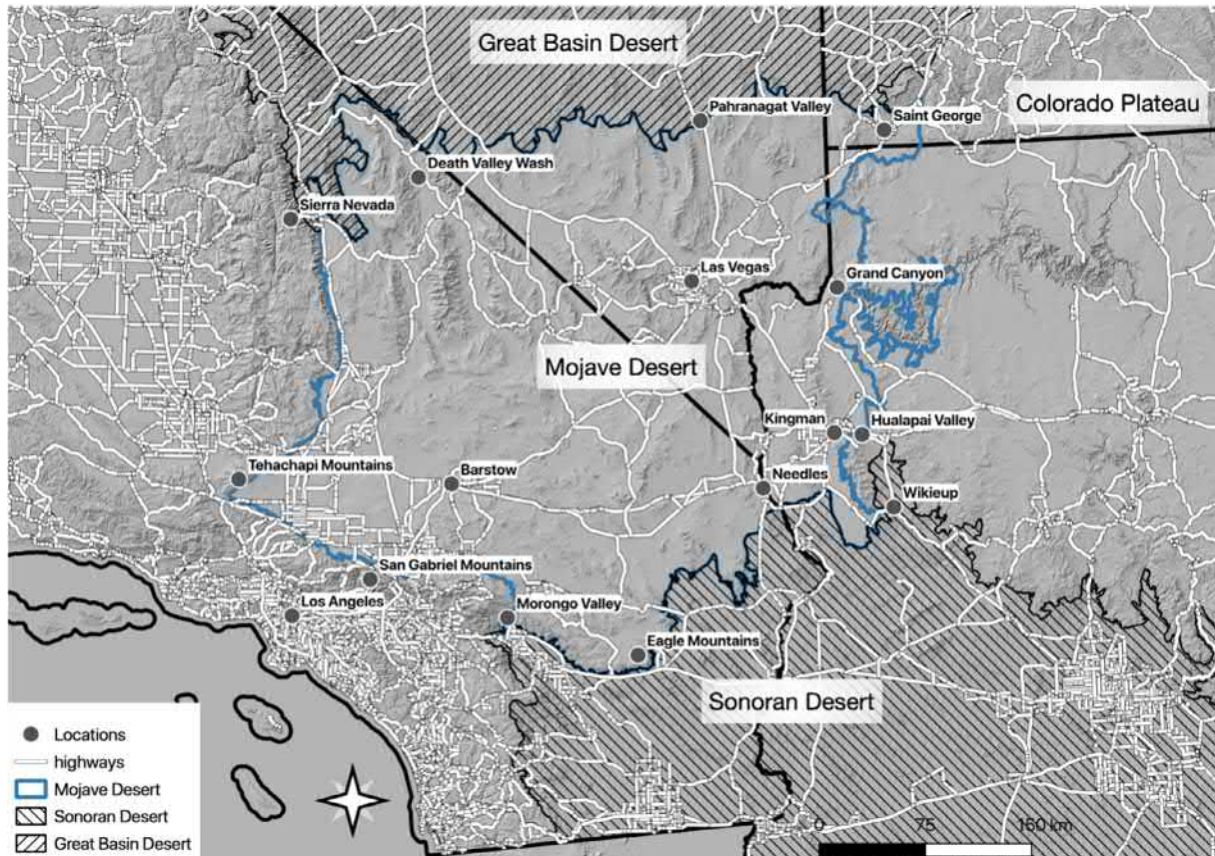


Fig. 1 The Mojave Desert and surrounding deserts, located in the southwestern United States.

The westernmost point in the Mojave occurs at the apex of a sideward-leaning 'V' at the convergence of the San Andreas, and Garlock Faults in southern California, at Tehachapi Pass between the San Gabriel Mountains in the Transverse Ranges and Tehachapi Mountains at the southern extent of the Sierra Nevada Range (Fig. 2). The northern boundary of the Mojave merges in a broad ecotone with the cooler/higher elevation Great Basin Desert (MacKay, 2013), from Death Valley Wash, California, through the Pahrangat Valley, Nevada, to St. George, Utah (Fig. 1). The ecotone undulates across the generally north-south oriented basins that commonly contain remnants of pluvial lakes, which have since dried, leaving behind saline lake bottoms (playas, Bowman, 2019), or extensive wash systems (now only intermittently wet). The Mojave is bounded by the Colorado Plateau in the northeast, southward to the mouth of the Grand Canyon, Arizona, and Hualapai Valley (Fig. 1). Along its southern boundary, the Mojave intergrades with the Sonoran Desert near Wikieup, Arizona, and then southwest toward Needles Arizona. Across the Colorado River, at Needles, California, the Mojave comes into contact with the Colorado Desert through the Eagle Mountains to the Morongo Valley, where it merges with the western mountain ranges (Fig. 1).

The Driest, Hottest, Place in North America

In California, prevailing winter atmospheric low pressure systems from the Pacific Ocean draw warm moist air from the south providing winter rains. However, before the winter storms reach the Mojave, the high mountains of the Pacific Cordillera draw moisture from the atmosphere due to orographic lift, creating a rain-shadow that renders the Mojave as the driest of the North American Deserts. The northwest extent of the desert, near Bishop, California is in the depth of this rain shadow, and what little precipitation occurs, is dominated by winter storms during October through May. Starting at -117° longitude, near Barstow, California and in the middle of the Mojave, a gradient toward bi-seasonal precipitation increases (Hereford et al., 2006) as summer storms of tropical origin move northward from the Gulf of California, and the Pacific from June through September. Isolated desert mountain ranges separated by deep valleys create localized orographic uplift that cools the moisture laden tropical flows resulting in highly variable and often violent summer storms. These summer storms add to the annual precipitation totals in the region that are low (regional mean 137 mm/yr) and range from 34 to 310 mm/yr (Hereford et al., 2006).

Mojave Desert precipitation is also highly variable among years and decades. This climate pattern is influenced by fluctuations in surface water temperatures in the Pacific Ocean known as the Southern Oscillation Index (SOI). Over the last century there have

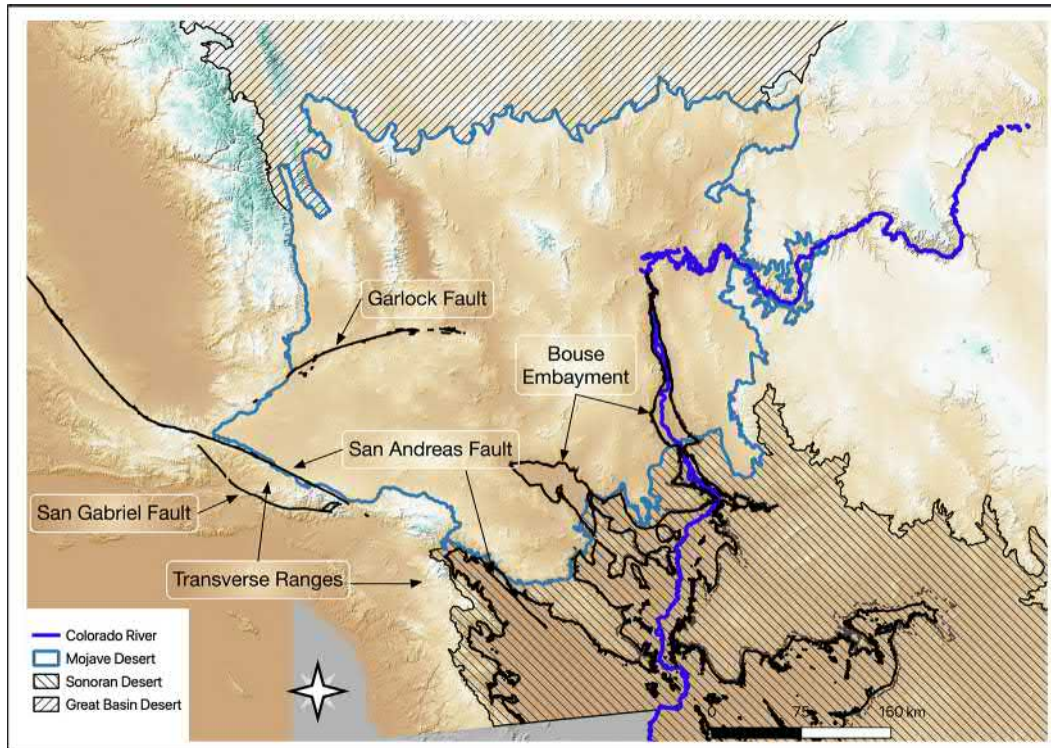


Fig. 2 Prominent Faults and vicariant features of the Mojave Desert.

been many extended periods of drought, including 1893–1904, 1940–75, and 1989–91 interspersed by wetter periods (Hereford et al., 2006). This pattern of dry and wet periods creates pulses of resource availability that are a driving force for plant and animal population dynamics across the Mojave, and other arid ecosystems (Schwinning et al., 2004), although these effects on animal populations are asynchronous, and extremely complex (Brown and Morgan Ernest, 2002; Greenville et al., 2016; Thibault et al., 2010).

Temperatures in the Mojave are notoriously extreme, but also highly variable—given the ranges of elevation encompassed by the Mojave (Redmond, 2009). Summer temperatures are highest in the lowest portions of Death Valley, where air temperatures in July can average in excess of 47 °C with soil surface temperatures of 62 °C, and average day and night temperatures can differ by ~ 29 °C (Redmond, 2009). Extreme temperatures in the western Mojave range between – 9 °C to 57 °C (Bai et al., 2010) and in the Northeastern Mojave have been reported to have similar extremes (– 19 °C to 46 °C; Beatley, 1974), while average air temperatures for the western Mojave range between – 0.5 °C to 38 °C, and average temperatures in the eastern Mojave are 2.2 °C and 40 °C (Germano et al., 1994). These extreme temperatures readily evaporate summer precipitation on the warmest days, creating stress on desert plants (Munson et al., 2015; Redmond, 2009). Average soil temperatures at –0.5 m are linearly related to elevation, and range between 12 °C and 30 °C (Bai et al., 2010). Temperatures in the Mojave have been increasing since the 1970s (Redmond, 2009), and these changes have resulted in differential persistence in perennial plant composition (Munson et al., 2015). With increasing temperatures, and reduced rainfall predicted in the future (Cayan et al., 2010), there may be yet unforeseen shifts in desert plant community composition (Munson et al., 2015), that may have cascading effects on the entire ecosystem.

Vegetation

Owing to the harsh environmental conditions, the Mojave Desert is a land nearly devoid of trees. The shrubby vegetation types in the Mojave are generally sparse, with vegetative cover between 45% and 15% or less over large expanses. Plant species distributions in the Mojave vary in association with climate, parent soil, soil texture, landscape position (correlated with hydrology, temperature, and particle size), biological interactions, and historical biogeography. The flora of the Mojave is diverse, with upwards of 2600 plant species in the desert within California alone (MacKay, 2013). Some of the plant species that typify the Mojave are shared with the other North American deserts (Turner, 1994a), and while there is greater overlap of growth forms and species with the Sonoran and Chihuahuan hot deserts, there is also overlap among species with the colder Great Basin Desert. Considering the area covered, the Mojave is largely dominated by a creosote/white bursage (*Larrea tridentata*/*Ambrosia dumosa*) scrub alliance—which is inter-mixed with other prominent flora (Barbour et al., 2007). This association is not unique to the Mojave and is largely shared with the Sonoran desert flora—except for the replacement of white bursage for triangle-leaf bursage (*Ambrosia deltoidea*). The southern

boundaries of the Mojave thus can be difficult to identify (Turner, 1994a). However, to the east of the Colorado River, the giant saguaro cactus (*Carnegiea gigantea*), indicates the ecotone with the Sonoran Desert, and west of the Colorado River, the smoke tree (*Psoralea argemone*) indicates the ecotone with the Colorado Desert.

At the northern boundaries of the Mojave and Great Basin desert, ecotones occur where stands of blackbrush (*Coleogyne ramosissima*), a prominent shrub in the upper elevations and northern regions of the Mojave, transitions to areas dominated by several species of Sagebrush (*Artemisia* spp.; Richardson and Meyer, 2012). Biogeographically, the plant communities of the Mojave are of recent origin, following major climatic changes during the Pleistocene and Holocene (Barbour et al., 2007; Koehler et al., 2005; Spaulding, 1991). Joshua trees (*Yucca brevifolia*, and *Yucca jaegeriana*) are endemic to the Mojave, and are thought to be among the most characteristic plants defining the Mojave (Lenz, 2007). These species are not distributed ubiquitously across the desert, but rather tend to be found in cooler/higher and more northerly upland habitats, in mixed Mojave desert scrub communities, and are largely absent from the lower elevation desert basins and southerly regions (Coville and Clark, 1893; Rowlands, 1978; Turner, 1994a). Vegetation in the desert typically occurs in zones driven by temperature, precipitation, and soil types, all of which covary with elevation (Merriam, 1890; Beatley, 1976).

Shrublands

Shrublands are comprised of several plant growth forms with widely dispersed perennial woody and herbaceous plants, succulents, geophytes, and annual plant species comprising the majority of land surface. Starting at the lowest elevations and from the playa edges, in closed basins, the Saltbush Scrub Community is most common due to the tolerance of its community members to higher salt content (halophytes). This community is typified by several species of saltbush (e.g., *Atriplex canescens*, *A. confertifolia*, and *A. polycarpa*), but also includes hop-sage (*Grayia spinosa*) and winter fat (*Krascheninnikovia lanata*), among others (MacKay, 2013; Turner, 1994a).

Upslope from the playa, are the extensive shrublands of the middle or upper bajada (a regional name for outwash plains composed of alluvial deposits, Bowman, 2019) where habitats typically have warmer temperatures, and plant associations vary widely depending on soil composition and depth, temperature, and precipitation patterns and amounts (Barbour et al., 2007). Creosote/bursage (*Larrea tridentata* and *Ambrosia dumosa*) are frequently dominant members of the plant community here, and alluvial slopes and fans comprise much of the Mojave landscape. This plant association co-occurs in four major plant alliances across a broad elevational gradient and topologies including bajadas, washes, toeslopes, hillsides, and rocky slopes (Barbour et al., 2007). Other plants associated with this vegetation alliance include many shrub species (e.g., brittlebush—*Encelia farinosa*, Anderson boxthorn—*Lycium andersonii*, saltbush species—*Atriplex* spp., joint-fir—*Ephedra nevadensis* and *E. californica*), cacti (beavertail prickly pear—*Opuntia basilaris*, Mojave mound cactus—*Echinocereus triglochidiatus*, and chollas—*Cylindropuntia* spp.), and yuccas (Mojave yucca—*Yucca schidigera*).

On the upper bajada creosote/bursage scrub communities can be more diverse (than lower elevation sites), coinciding with cooler temperatures, higher rainfall, and frequently shallower soils. This zone is frequently called “Mixed Mojave desert scrub,” and contains visually dominant yucca species. Yucca composition changes with elevation across this upland habitat, where Mojave yucca (*Yucca schidigera*) occurs in lower elevations, followed by a mix with Joshua trees (*Y. brevifolia* and *Y. jaegeriana*), and Banana yucca (*Y. baccata*) replacing other yuccas at higher elevations, where they are thought to compete for water resources (Yeaton et al., 1985). Localized areas can be densely populated in savannah-like communities described as “Joshua Tree woodlands.” These communities typically have an understory of creosote bush, cheesebush (*Hymenoclea salsola*), and jointfir (*Ephedra* spp.) among other species of Yucca (*Y. schidigera* and *Y. baccata*). Joshua tree woodlands typically transition into Blackbrush habitat at higher elevations. While the Joshua tree can dominate landscapes visually, their dominance has been said to be of stature only (Turner, 1994a), as they “contribute little in a quantitative sense” to vegetation abundance (Rowlands, 1978). However, Joshua tree stands can become quite dense, as seen in areas like Joshua Tree National Park and Mojave National Preserve in California, the Wee Thump Joshua Tree Wilderness Area in Nevada, the Grapevine Mesa Area of Critical Environmental Concern in Arizona, and Joshua tree Highway (along Hwy 93 from Wikieup to Wickenburg, Arizona).

Blackbrush shrublands and rare stands of sagebrush (*Artemisia* spp.—i.e., near bishop, CA; Spring Mountains, NV; and south of St. George, UT—Richardson and Meyer, 2012) represent the highest elevations/latitudes of shrublands in the Mojave desert biome—as they are tolerant of cooler temperatures, but are absent from higher elevation basins where low temperature extremes may limit their distribution (Turner, 1994b) and from areas of higher rainfall (Beatley, 1976). In such areas, low temperature extremes likely limit the presence of creosote bush (Beatley, 1974), and thus blackbrush can occur in near monocultures at upper elevations (Barbour et al., 2007). Mojave blackbrush communities also include jointfir (*Ephedra* spp.), Joshua tree, and spiny hopsage.

At higher elevations within the Mojave, with even cooler temperatures and more rainfall, conifer woodlands intermix with chaparral species at lower elevations, and pine forests to alpine habitats at upper elevations. The woodlands are characterized by juniper (*Juniperus* spp.) and piñon pine (*Pinus* spp.), with transitional interior chaparral species, for example, oaks (*Quercus* spp.), manzanita (*Arctostaphylos* spp.) and mountain mahogany (*Cercocarpus ledifolius*). While not common in the Mojave, several of the higher mountain ranges (e.g., the Spring and Sheep ranges within southern Nevada) include habitat transitioning to Mixed Conifers (e.g., ponderosa pines—*Pinus ponderosa*, white fir—*Abies concolor*) and even to bristlecone pine (*Pinus longaeva*; Charlet, 1996), and alpine habitats on the peaks of the highest ranges in Clark County, Nevada (Clokey, 1951). Similarly, Telescope Peak and the

Panamint and Argus ranges in Death Valley, CA have similar community types including pine woodlands, bristlecone pine, limber pines (*Pinus flexilis*) and other tree species (e.g., mountain mahogany, *Cercocarpus*; Barbour et al., 2007).

Riparian Habitat

The rare trees found in the Mojave generally only exist in riparian habitats, where surface water flows along major river systems (e.g., Colorado River, Virgin River, Muddy River, Amargosa River, and Mojave River), and rare desert oases where artesian springs spill out into the desert. Xeriparian habitats (also known locally as washes or arroyos) are more common than riparian habitats, and exist only where watercourses flow intermittently. Xeriparian trees (e.g., catclaw acacia—*Acacia greggii*, desert willow—*Chilopsis linearis*) are generally smaller than those found in riparian habitats. Both types of riparian habits also support a variety of shrubby and herbaceous plant species and are important as cover and food resources for a tremendous variety of wildlife including migrating birds.

Riparian habitats in the Mojave are among the rarest habitat type, but are high in diversity of plants as well as animal species, and these serve as vital habitat for many birds. Riparian areas are inhabited by several tree species (e.g., cottonwood (*Populus fremontii*), willow (*Salix* spp.), velvet ash (*Fraxinus velutina*), honey mesquite (*Prosopis glandulosa*) and screwbean mesquite (*P. pubescens*) that provide important habitat structure and shelter for nesting birds (Fleishman et al., 2003), and foraging habitat for several species of bats (Williams et al., 2006). Birds occupying riparian habitats are the subject of much conservation concern, including Yellow-Billed Cuckoo (*Coccyzus americanus*), Arizona Bell's Vireo (*Vireo bellii arizonae*), Le Conte's Thrasher (*Toxostoma lecontei*), Phainopepla (*Phainopepla nitens*), Costa's Hummingbird (*Calypte costae*), Southwestern Willow Flycatcher (*Empidonax traillii eximius*), and Yuma Ridgway's Rail (*Rallus obsoletus yumanensis*), among others (Austin, 1970).

Invasive plant species in desert riparian systems have been the source of much concern, among the most notorious are Salt Cedar (*Tamarix ramosissima*, and *T. athel*), which have invaded most of the riparian systems in the Mojave (Fleishman et al., 2003; Sogge et al., 2008). While this species displaces many of the native tree species, many bird species appear to use it effectively for their nesting and cover needs, and there is concern that the removal of structural function during restoration efforts may cause unwanted impacts to sensitive bird species (Fleishman et al., 2003; Sogge et al., 2008).

Mojave Desert Fauna

Mojave desert species are renowned for the variety of ways that they adapt to the harsh environmental conditions found there. Many desert animals avoid extremes of heat or cold by avoiding those conditions in subterranean or vegetative cover sites, and only being active for relatively short periods of time on a daily, seasonal, or annual basis. Desert tortoises vary their daily activity periods according to temperature windows that meet their physiological limits (Zimmerman et al., 1994). Mohave ground squirrels are active during a very short period of time during April through June each year, when they glean all of their nutritional needs, and reproduce (Best, 1995). The desert slender salamander (*Batrachoseps major aridus*) is active only during wet winter periods, and otherwise very difficult to find (Duncan and Esque, 1986). The silky flycatcher (*Phainopepla nitens*) is a bird that lays its eggs and raises its young beginning in later winter (February) when its host plant desert mistletoe (Chu and Walsberg, 1999) flowers and attracts nitrogen rich insects to feed its young, then they all leave the desert during the summer. There are also many anatomical and physiological means of coping with desert conditions. Jackrabbits (*Lepus californicus*) use evaporative cooling of their nasal area combined with vasoconstriction in their extravagantly long ears to assist in cooling their brains (Caputa et al., 1976). Kangaroo rats (*Dipodomys* spp.) have tortuous nasal passages causing the water vapor in their breath to condense in those passages reducing water loss (Schmidt-Nielsen and Schmidt-Nielsen, 1951). Some desert fishes exist in hypersaline desert hot springs (McClanahan et al., 1986). During cold desert nights, the herbivorous desert chuckwalla lizard (*Sauromalus ater*) maintains a high body temperature that is required by its symbiotic gut microflora by seeking out and hugging rocks that retain high temperatures deep into the night (Zimmerman and Tracy, 1989). Following is a description of some of the diverse groups of desert animals.

Although biologists have conducted biological surveys of the Mojave Desert since the late 19th century (Fisher et al., 1893), there is not a complete accounting of mammals present. Furthermore, most resident species occur across multiple desert biomes. However, recent surveys (using a combination of museum records, field censuses and literature reviews) of the five Mojave national parks (Death Valley NP, Joshua Tree NP, Manzanar NHA, and Mojave National Preserve, CA; Lake Mead NRA, NV) identified ~128 unique species of mammals potentially inhabiting the parks collectively, and average of 70 unique species within individual parks (Drost and Hart, 2008). The national parks represent a range of habitats that typify extant Mojave habitat types, and thus the species encountered there are likely to be an ample representation of mammal diversity in the Mojave. Herbivores and granivores include rodents such as the kangaroo rats (*Dipodomys* spp.), pocket mice (*Perognathus* spp.), pocket gophers (*Thomomys* spp.), woodrats (*Neotoma* spp.), lagomorphs (black-tailed jackrabbit—*Lepus californicus*, and desert cottontails—*Sylvilagus auduboni*), squirrels (*Ammospermophilus leucurus* and *Xerospermophilus mojaviensis*), and ungulates (desert bighorn—*Ovis canadensis nelsoni*, mule deer—*Odocoileus hemionus*, and pronghorn—*Antilocapra americana*). Insectivores include desert shrews (*Notiosorex crawfordi*) and bats (Vespertilionidae). Carnivores include western spotted skunk (*Spilogale gracilis*); kit fox (*Vulpes macrotis*); coyote (*Canis latrans*); American badger (*Taxidea taxus*); and mountain lion (*Puma concolor*).

Only a single avian species, LeConte's Thrasher (*Toxostoma lecontei*), is considered a Mojave specialist (Turner, 1994a), and it attracted the attention of ornithologists from the earliest explorations of the region due to its unexpected breadth in distribution and

niche (Fisher, 1893; Grinnell, 1933). Flight provides birds the opportunity to migrate seasonally to escape harsh northerly winter conditions, or inhospitable summer conditions locally, track resource fluctuations to breed in the most productive areas, or simply pass through from more northerly or southerly locations when resources are most abundant in the spring or fall. Resource-rich areas such as riparian areas, mesquite bosques, or urban islands of habitat can provide migrants important rich locations for cover and resource acquisition in an otherwise 'desert' of resource availability. Such locations are referred to as 'bird traps' because once known, these areas of elevated diversity and density during inclement conditions along migration routes can be visited by researchers or bird enthusiasts reliably to observe a diversity of species (Paxton et al., 2008). Representative Mojave Desert birds include: Black-throated Sparrow (*Amphispiza bilineata*); Rock Wren (*Salpinctes obsoletus*); Silky Flycatcher (*Phainopepla nitens*); Horned Lark (*Eremophila alpestris*); Loggerhead Shrike (*Lanius ludovicianus*); LeConte's Thrasher (*Toxostoma lecontei*); Common Poor Will (*Phalaenoptilus nuttallii*); House Finch (*Haemorhous mexicanus*); Roadrunner (*Geococcyx californianus*); Common Raven (*Corvus corax*); Turkey Vulture (*Cathartes aura*); Red-tailed Hawk (*Buteo jamaicensis*); Burrowing Owl (*Athene cunicularia*), and Golden Eagle (*Aquila chrysaetos*).

Reptiles are distributed across the landscape in a mosaic of habitats—some as generalists, such as side-blotched lizards (*Uta stansburiana*) found almost anywhere having shrubs, while others specialize on discrete habitats, which typically have lower connectivity at a landscape scale. For example, the Mojave Desert fringe-toed lizard (*Uma scoparia*) is a dune obligate species, and thus is limited to areas of extensive windblown sand dunes. Mojave fringe-toed lizards are found at Dumont dunes and Kelso dunes on California, and Big Dune in Nevada; and are present at >25 known currently isolated localities (Norris, 1958). While isolated to dunes, this species can be found in areas with Eolian sand substrates throughout the Mojave where drainages transport alluvium into lower areas where sand accumulates (Norris, 1958). There are also Sonoran species of fringed-toed lizards (e.g., the *U. notata* complex), occurring in the Lower Colorado Subdivision of the Sonoran Desert and south of the Mojave desert ecoregion. Recent genetic research indicates a distinct separation of these two related taxa with a Pleistocene origin of *U. scoparia*, without gene flow between them, despite their relative proximity compared to within species distances (Gottscho et al., 2014). Mountains uplifted along the San Andreas Fault during the Miocene are thought to have maintained vicariance between the two taxa, and the Pleistocene origin of *U. scoparia* is considered to be a founder effect, where colonization occurred with a small—one-time dispersal into the Mojave. Within the Mojave there is little genetic structure among populations of *U. scoparia* despite their geographic isolation, which may be due to their recent expansion within the Mojave (Gottscho et al., 2014). Similar patterns are seen in "island like" restricted fish and dune obligate insects in the Mojave, where divergence among populations lacks evidence of being driven by geographic processes, and is better explained with chance founder events (Van Dam and Matzke, 2016). A study of the flora on sand dunes was used to estimate the relative ages of the dunes (Pavlik, 1989). The migration of the dune flora indicate colonization of the dunes emanating from the valleys north of the Mojave (i.e., Mono Basin east of the Sierras, Fish Lake, and Big Smokey Valleys in west Central Nevada) southward along the east and west sides of Death Valley during the late Pleistocene/Early Holocene. Dune formation in Death Valley was later with mid- to late-Holocene dune formation and plant colonization northward into Panamint and Death Valleys (Pavlik, 1989).

Biogeography

The biogeography of the Mojave as we see it today is driven by the history of the topography, and climate, interacting with the flora and fauna of the region. The region has a broad elevational range from −86 m at the bottom of Death Valley, to Mt. Charleston in Clark County NV at 3632 m. Other high elevation ranges serving to create "sky island" habitats include Telescope Peak in the Panamint Range in Death Valley at 3367 m, and Hayford Peak in the Sheep Range in southern Nevada at 3021 m. The Mojave has a low number of endemic species, partially due to the climatic, rather than physical obstacles defining its borders to the north and south (Bell et al., 2010). Until recently only three terrestrial endemics were recognized; the Joshua tree, the Mohave ground squirrel (*Xerospermophilus mohavensis*), and the Mojave fringe-toed lizard (*Uma scoparia*; Bell et al., 2010), although genetic research continues to yield new species. Joshua trees are now recognized as two species (Lenz, 2007), and the Mojave desert tortoise *Gopherus agassizii* was recently recognized as a separate species unique to the Mojave, after being split from the Sonoran Desert Tortoise—*G. morafkai*, which inhabits the Sonoran Desert east of the Colorado River (Murphy et al., 2011). In addition, there are many aquatic species endemic to the Mojave associated with springs, and permanent and ephemeral water systems. For example, endemic fishes, most of which are rare and of conservation concern, include Tui Chub (*Gila* spp.), Dace (*Lepidomeda* spp., *Rhinichthys* spp., *Moapa coriacea*), Pupfish (*Cyprinodon* spp.), Suckers (*Catostomus* spp.), and Springfish (*Crenichthys* spp.), among others (Williams et al., 1985). There are also many endemic aquatic macroinvertebrates in hundreds of isolated spring systems throughout the Mojave where Springsnails (*Pyrgulopsis* spp.) have radiated under recent isolation (Hershler and Liu, 2008) and have become a recent conservation concern due to over apportionment of water resources, and draw down of aquifers (Hershler et al., 2014; Sada et al., 2005).

Speciation in the Mojave is thought to be a result of the recent assembly of many of its current inhabitants during the late Pleistocene, as species emigrated from refugia occupied during glacial advances, and when the region was inundated with pluvial lakes. Indeed, the Mojave flora is an admixture of species from the cooler Great Basin desert to the north, the Colorado Plateau to the northeast, and the warmer and wetter Sonoran desert to the south (Axelrod, 1983; Barbour et al., 2007; Turner, 1994a). Geological events in the Miocene separated species in the region much earlier, as the Sierra and Transverse Ranges experienced uplifting, and eventually caused rain shadows in the valleys to the east (Bell et al., 2010; Vandergast et al., 2013). The Transverse

Ranges rose along the San Gabriel fault 10 – 5 Mya, which stopped the drainage of the Mojave River in the west Mojave from flowing down the Cajon Pass and redirected it toward the interior of the basin toward Coyote Lake near what is now Barstow California. Uplift of the ranges also terminated the Mojave at Silver Lake/Death Valley north of what is now the town of Baker California (Cox et al., 2003). Evidence of that wetter period can be found in the shells of large extirpated bivalve species in the dry lake beds today. The large alluvial fans (bajadas, Bowman, 2019) that comprise much of the Mojave upland habitat resulted from erosion due to increased runoff from major deposits that were formed during the Pleistocene during wetter pluvial periods in the region (Cox et al., 2003). Additional soil deposition events occurred at the Pleistocene/Holocene boundary 9.4–10 kya which may have been due to increased storm cycles (Harvey et al. 1999; McDonald et al., 2003).

In addition to changing the hydric environment, the mountains bordering the western Mojave serve as vicariant boundaries that limit the dispersal of organisms, resulting in relatively distinct flora and fauna on either side of the Transverse Range (Fig. 2, Bell et al., 2010). Incursions of the Salton Trough in southern California during Pleistocene pluvial periods served as boundaries resulting in divergence in many mammal species between the Mojave and Sonoran deserts in California and Arizona (Hafner and Riddle, 2011). The inundation of currently upland habitats occurred when higher sea levels force the Sea of Cortez to surge northward along the Bouse Embayment. The Bouse Embayment is a low elevation geographic area following the Colorado River drainage for approximately 275 km (north of its current merger with the Sea of Cortez) during the late Pliocene some 6 to 5.3 Mya (Lucchitta, 1979, Fig. 2). These events corresponded more closely with species differentiation for nine of 12 species across broad taxonomic groups than did climatic fluctuations corresponding with Pleistocene glacial and pluvial periods (Wood et al., 2013). Only three of the 12 species had evidence of divergence only during the Pleistocene, while most showed evidence of differentiation related to both time periods (Wood et al., 2013). Similar divergence patterns in other species indicate that the Bouse Embayment was likely an important vicariance that led to allopatric/vicariant speciation, separating Mojave and Sonoran species during the Pliocene/Miocene (Hafner and Riddle, 2011). Species which are thought to have been separated in this way include the Mojave desert tortoise (Edwards et al., 2015; Murphy et al., 2011), western spotted skunk–*Spilogale gracilis*, (Ferguson et al., 2017), some species of pocket mice (*Perognathus* spp.) and kangaroo rats (*Dipodomys* spp.; Riddle, 1995). However, this mechanism was not sufficient to explain divergence in species of desert tarantula (*Aphonopelma* spp.)—other mechanisms, such as the inclusion of Miocene tectonics may warrant consideration (Graham et al., 2015).

In a recent study, most species also showed evidence of population expansions 100–200 kya, which is consistent with the re-invasion of species to the Mojave desert lowlands as the climate warmed and dried (Wood et al., 2013). Desert scorpion (Scorpionidae) divergence is also thought to be consistent with a post Pleistocene origin model (Graham et al., 2013). While the Mojave was once dominated by a Piñon/Juniper woodland, the climate fluctuations, and an eventual drying period resulted in a transition to the current creosote/bursage dominated landscape (Vandergast et al., 2013), but not beginning until around 23 kya, with evidence of *Larrea* becoming a dominant species in the Mojave approximately 7 kya (Turner, 1994a; Harvey et al., 1999; Vandergast et al., 2013). Given these relatively recent changes in climate and vegetation it is clear that some desert species may be exapted to desert habitats, such that they arrived in this desert environment with adaptive capacity, rather than evolving specialized adaptations to survive in harsh desert environments in situ, the desert tortoise among them (Morafka and Berry, 2002).

While the divergence mechanisms and the timing of separation are different among species (e.g., Graham et al., 2015), there are clear zones where species have separated and diversified along the boundaries of the Mojave Desert ecoregion. Recent research using a diverse group of species analyzed genetic divergence and diversity, and found strong separation of species along the Mojave/Sonoran boundary both west and east of the Colorado River (Vandergast et al., 2013). That study identified 10 evolutionary hot-spots where up to 17 species demonstrated high levels of genetic divergence within relatively local areas. Thus, while the vegetative boundaries between these adjacent deserts are gradual (Barbour et al., 2007; Turner, 1994a), there are sufficient environmental differences between the Mojave and Colorado (Sonoran) desert regions to yield genetic separation among species (Vandergast et al., 2013).

Species Connectivity

Some species are highly connected across the landscape of the Mojave Desert through the matrix of low elevation bajadas and basins, such as the Mojave desert tortoise, and exhibit a genetic pattern known as ‘isolation by distance’ (Hagerty et al., 2011), where individuals that are close together geographically share more genetic similarities and more recent ancestry than those that are farther apart. Because genetic connectivity is well characterized in the Mojave Desert Tortoise it provides a good illustration of patterns found in other widely distributed bajada/basin species.

Desert tortoise populations exhibit genetic structure that reflects geographic barriers at regional scales, but show low levels of differentiation across broader landscapes in the absence of those barriers, with gradual changes in genetics operating on a large gradient (Hagerty and Tracy, 2010). For example, three basal populations were identified in a north south orientation, where tortoises west of Death Valley, and south of the Ivanpah Valley, CA form a southern “California Cluster.” While tortoises in the Ivanpah, Mesquite, Amargosa and Las Vegas valleys form a “Las Vegas Cluster,” and populations North and East of the Pahranaagat Valley form a “Northern Mojave Cluster.” Each of these major valley systems are bounded by mountainous regions that tortoises do not traverse easily (Hagerty and Tracy, 2010). At a landscape scale, desert tortoise populations are well connected, and genetic distances (i.e., a measurement of differences in genetic composition within or between populations) generally correspond to straight line distances. However, where large geographic barriers (e.g., high and rugged mountain ranges) exist they reduce genetic connectivity around these barriers, and thus funnel connectivity through areas connected by more favorable habitat (Hagerty et al.,

2011). The open habitats of the west Mojave support generally well connected populations with lower pairwise genetic distance values, while comparisons among populations separated by barriers in the east Mojave tend to have higher differentiation (Hagerty et al., 2011). The Mojave Desert Tortoise as separated from its related taxon, the Sonoran Desert Tortoise (*G. morafkai*), 8 – 4 Mya when the Colorado river formed in the late Pliocene. Interestingly, the river channel has meandered broadly through time, apparently creating a pattern of “stepping stone” habitat for the species to cross the channel to Arizona habitat, and resulting in a secondary contact zone between the two species (Edwards et al., 2015). This exchange of individuals resulted in *G. agassizii* individuals becoming isolated on the eastern side of the Colorado River, where they have hybridized with *G. morafkai* near the Hualapai Mountains. The hybrid tortoises exhibit intermediate habitat preferences compared to either the Mojave Desert Tortoise or the Sonoran Desert tortoise. Mojave Desert Tortoise habitats consist largely of lower bajadas and upland slopes and typified by Mojave desertscrub, Mixed Mojave desertscrub or vegetation of the Lower Colorado River Subdivision of the Sonoran Desert; while the Sonoran desert tortoise is more commonly found in higher and rockier upland mountain slopes with higher perennial vegetation density and diversity of the Arizona Upland Subdivision of the Sonoran Desert (Edwards et al., 2015; Nussear and Tuberville, 2014).

Biogeographic Isolation and Landscape Connectivity

Much of the Mojave landscape consists of bajadas and uplands composed of alluvial fans ranging from 600 to 1200 m (Norris, 1958), emanating from a series of mountain ranges with a network of drainages leading to terminal dry lakes (playas). The topography of the west Mojave has far fewer mountains (excepting the Transverse Ranges at its western boundary), creating relatively broad and open landscape. As noted—few of the species of mammals, birds, reptiles or amphibians are unique to the Mojave, as most are found in the adjacent deserts as well (Pianka, 1967; Turner, 1994a). Brown (1971) tested the concepts of island biogeography (MacArthur and Wilson, 1963) on boreal mammals (those found elevations above approximately 2286 m along the montane/piñon/juniper border) of California, Nevada, and Utah, and found that isolated mountaintops functioned as “sky islands,” which exhibit low rates of connectivity relative to distance and island size. While Island-like habitat may exist for many species in the Mojave, it is far more the exception than the rule (indeed Brown only found three species in the Sheep range of Nevada, and one in the Panamint range of California that met his definition; Brown, 1971). Most terrestrial species in the Mojave exhibit higher levels of connectivity as they occupy a vast, interconnected matrix of bajadas and basin habitats.

The Anthropocene

Virtually every location within the Mojave has been influenced by the expansive growth of the human population. Studies of land change in the 11 western US states estimated that 13% of the western United States is covered by anthropogenic features, which are mostly agricultural lands, populated areas, and secondary roads (Leu et al., 2008). While the Mojave is largely not an agricultural area, the ecoregion has succumbed to explosive population growth over the last several decades (U.S. Census Bureau, 2010). For example, the Las Vegas Valley in Nevada is home to the largest metropolitan area in the Mojave, and has expanded from 16,414 people in 1940 to an estimated 2.2 million people today (U.S. Census Bureau, 2019). Urban areas, and their associated infrastructure across the landscape, are typically built near the valley floor (Leu et al., 2008); therefore primary and secondary roadways, utility transmission right-of-ways (gas, and electrical), pipelines, and railways traverse nearly every valley in the Mojave with their accompanying infrastructure and human encroachment. Most recently, burgeoning utility scale solar and wind generation facilities have increased habitat losses and fragmentation (Averill-Murray et al., 2012, 2013; BLM, 2016; Inman et al., 2013).

Human infrastructure is not the only anthropogenic influence important to desert species. The Mojave has more than a 100-year history of cattle and sheep grazing. Grazing has led to vegetative change, and changes to soil nutrients and structure (Morafka, 1982). Grazing has also led to the introduction of non-native plant species, which tend to establish in disturbed soils (Beatley, 1966). Red brome (*Bromus rubens* [*madritensis*]) is an especially aggressive Mediterranean grass thought to have been introduced as a result of livestock and crops imported to California during the Gold Rush in the late 1800s (Salo, 2005). The earliest records of red brome near the Mojave region are an arrival in Los Angeles as early as 1887, with records in the Las Vegas area by 1920, and widespread presence throughout the desert by 1960 (Salo, 2005). *Bromus* promotes wildfire spread by providing a fine, continuous, light, and therefore, fast burning fuel in the interstices between native shrubs (Beatley, 1966; Hereford et al., 2006). In recent decades the increased presence of *Bromus*, along with El Niño Southern Oscillation (ENSO) driven increases in winter precipitation (Hereford et al., 2006) have introduced a new threat to the Mojave in the form of wide-spread wildland fires, which have been increasing in size and frequency (Brooks and Esque, 2002; Brooks and Matchett, 2006). For example, in 2005 more than 300,000 acres of Mojave habitat was burned by wildfires, including 36,000 acres of critical habitat for the Desert tortoise (Nussear and Tuberville, 2014; Van Linn et al., 2013). Due to historically low fuel loads provided by predominant environmental conditions in Mojave shrublands, there was not a regular fire cycles in the desert, thus Mojave species are frequently not well adapted to survive wildfire (DeFalco et al., 2010; Esque et al., 2003; Van Linn et al., 2013). The removal of native perennial shrubs eliminates cover for animals and plants from the intense desert insolation and promotes further invasion of *Bromus* and other invasives, which can out-compete native annual species that provide forage for many desert animals (Beatley, 1966; Esque et al., 2014; Nussear and Tuberville, 2014). This can result in a grass/fire cycle that perpetuates this vegetative change resulting in a vegetative state change

(from shrubland to invasive/exotic annual grassland), promoting near monocultures of *Bromus*. The positive feedback loop has been termed a grass/fire cycle (D'Antonio and Vitousek, 1992; Van Linn et al., 2013).

Bromus can also have detrimental nutritional effects (Esque et al., 2014). For example, *Bromus* may impart increased susceptibility to disease, as it has a lower digestive efficiency relative to other potential forage species for desert tortoises, resulting in reduced nutritive value, and increased potential of a reduced immunocompetence (Tracy et al., 2005). There is also the potential for mechanical injury, as the sharp awns on *Bromus* seed can become impacted in the jaws of tortoises (Medica and Eckert, 2007) or damage the gastrointestinal—tracts (Drake et al., 2016; Esque et al., 2014). Together these combined impacts can result in reduction of health condition, growth rates, and survivorship, especially in juvenile animals, and ultimately may reduce population persistence and resilience (Drake et al., 2016) for this, and other native species.

Collectively, this incursion of the human footprint into wide expanses of habitat leads to expansive fragmentation and degradation (Nussenaar and Tuberville, 2014), which can not only influence many taxa, but can also lead to large-scale habitat alterations that change the vegetation composition and habitability of entire landscapes.

Conclusions

The Mojave is a vast area, rich in biodiversity. Its geological and climatic history have led to a diversity of habitats and radiation of species throughout the region. In the last 100 years, there has been an influx of people and associated disturbance in the forms of urbanization and associated infrastructure, habitat conversion to agriculture, and wide-ranging use of the desert for ranching and recreation. These multiple uses have brought with them habitat destruction, degradation, and fragmentation of the landscape that impact many desert dwelling species. Despite the resilience of many of its species, the Mojave desert ecosystem is fragile in nature, and can take centuries for soils and vegetation to recover from disturbance (Webb et al., 2009). While there are many conservation efforts focusing on restoration of desert habitats, they are no substitute for careful planning and management of this fragile ecosystem.

Acknowledgments

Our love and knowledge of the Mojave has been inspired and shaped by our mentors R. Bruce Bury, Philip A. Medica, and C. Richard Tracy. We thank them for instilling our curiosity about this vast desert, which has led to careers of exploring its inhabitants. KEN is supported in part by the National Fish and Wildlife Foundation (NFWF), and the Strategic Environmental Research and Development Program (SERDP), and the Clark County Desert Conservation program (CCDCP). TCE is supported by the USGS Energy Resources, Invasive Species, Wildlife programs.

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The Sonoran Desert

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Abstract

The Sonoran Desert has been identified as one of the most distinctive ecoregions in the world, recognized for its columnar cacti such as the saguaro and cardón. It is home to 130 mammal, 400+ bird, 100 endemic reptile, 750 bee, and nearly 2500 endemic plant species. This great variety of species and habitats is due to the desert's subtropical climate, wide-ranging topography, bimodal rainfall pattern, and location at the crossroads of several different ecoregions. Geologic processes shaped the landscape and created the Gulf of California, a biologically rich body of water that influences the region's climate. The desert's biota faces numerous challenges including increasing temperatures and changing rainfall patterns, loss of native vegetation from invasive species and livestock grazing, habitat fragmentation from transportation and border wall infrastructure, and loss of habitat and riparian areas due to human expansion and groundwater pumping. In the US, nearly 3.88 million hectares (9.58 million acres) is protected from development or other incursions, although other threats to the ecoregion are ongoing. In Mexico, nearly 1.5 million hectares (3.7 million acres) have been set aside as biosphere reserves and other protected areas. A large marine biosphere reserve in the northern Gulf of California has been unsuccessful at preventing the alarming population decline of the vaquita porpoise, which hovers on the brink of extinction.

A Unique Ecoregion

Spanning over 224,000 km² across two countries and four Mexican and US states, the Sonoran Desert encompasses a great variety of species and habitats. The area has been identified as one of the most distinctive ecoregions in the world based on analyses of species richness, species endemism, and global rarity of major habitat types (Olson and Dinerstein, 2002). The species list includes 130 mammals, 400+ birds, 100 endemic reptiles, 750 bees, and over 4000 plants, nearly 2500 of which are endemic to the Sonoran Desert (Nabhan, 2015a). This great biodiversity is due to the subtropical climate, varied geology, wide-ranging topography, and most importantly, rainfall that occurs in both the summer and winter, which supports a broad array of both warm and cool season flora. In fact, this desert has the greatest diversity of plant growth forms, or adaptive strategies evolved to survive high temperatures and drought, of any desert in the world (Nabhan, 2015b).

Geologic History

The contemporary desert Southwest landscape was formed by two main geological events that occurred over millions of years and involved the movement of tectonic plates. The first event occurred from approximately 200 to 50 million years ago, when the Farallon plate was subducted beneath the lighter North American Plate. This action compressed the North American plate, like pushing a rug up against a wall, forming the Rocky Mountains and the Sierra Madre Occidental, and causing much of the volcanic activity in the region.

The second event, starting at about 35 million years ago, occurred as the spreading center between the Pacific plate and the Farallon plate was also subducted beneath the North American plate. Because the Pacific plate was moving in a generally westerly direction, it pulled and stretched this portion of the North American plate along with it. This stretching caused the earth's crust to crack like the surface of a cooling pumpkin pie and formed huge valleys as sections dropped downward in what is called block faulting. The high ground between the valleys remains as today's mountain ranges, creating what is known as the Basin and Range province and the hundreds of isolated mountain ranges that extend from southern Oregon to central Mexico. At about 5.5 million years ago, this motion began pulling the Baja California peninsula away from the mainland of Mexico, eventually creating the Gulf of California. This motion continues today as the peninsula and areas in California west of the San Andreas fault continue moving northwest at a rate of about 5 cm a year (Scarborough and Brusca, 2015).

Defining the Ecoregion

The Sonoran Desert (Fig. 1) is at the crossroads of several different ecoregions and biotic communities that contribute to its incredible biodiversity. To the north, interior chaparral leads to the higher-elevation montane conifer forests of the Mogollon Rim. The west and east edges are bookended by the peninsular ranges of southern California and the grasslands and woodlands of the Sky Islands. Sinaloan thornscrub, the ancestral biome from which many Sonoran Desert plants and animals evolved, transitions into tropical deciduous forests further south (Van Devender and Brusca, 2015).

The Sonoran Desert is visually distinguished from other North American deserts by two life forms: legume trees such as the acacia, and large columnar cacti (Dimmitt, 2015). These cacti include the saguaro (*Carnegiea gigantea*) and the cardón (*Pachycereus pringlei*), the largest cactus in the world. Forrest Shreve first described and mapped the boundary of the desert in 1942 while working at the Carnegie Institution's Desert Laboratory in Tucson (Shreve, 1942). Being a botanist, he differentiated the deserts based on their floristic composition, physical appearance, and community structure of the dominant plant species. He subsequently refined his description of the Sonoran Desert and defined seven subregions that included the deserts of the Baja California peninsula (Shreve, 1951).

More recently, scientists have used a different approach to define the boundaries of the Sonoran Desert (Riddle et al., 2000). They used DNA to reconstruct the historic processes that are responsible for the contemporary geographic distribution of species in the desert. They found that the desert biota of the Baja California peninsula has a unique evolutionary history, as distinct as the other regional deserts, and proposed that it should be considered a separate desert, the Peninsular Desert, instead of a subdivision of the Sonoran Desert. This additional classification has not been met with wide acceptance (Hafner and Riddle, 2011), but for the purposes of this chapter we will discuss the Sonoran Desert and Baja Peninsular Desert as separate entities.

Vegetative Subdivisions of the Sonoran Desert

Desert plants are supremely adapted to their arid environment. To people from wetter parts of the planet, it may appear that they are just eking out an existence, but in fact, these plants could not survive in wetter places. They thrive in the desert. Their adaptations to aridity include succulence (the ability to store water in fleshy leaves, stems, and roots), extensive shallow root systems designed to absorb water from any rainfall, waxy coatings to prevent water loss from stems and leaves, small leaves to prevent overheating and limit water loss, and green stems which provide photosynthesis even when leaves are small or absent. Another strategy is drought-avoidance, as displayed by annual plants which complete their life cycles during brief wet seasons and then die after channeling all their energy into producing seeds (Dimmitt, 2015).

Lower Colorado River Valley

The largest, hottest and driest subdivision is found along the Lower Colorado River, and is second only to the Mohave Desert's Death Valley as the hottest and driest place in North America. Summer highs can exceed 120 F (48.5C), and humidity is often less than 10%. Annual rainfall in the driest areas is generally less than 75 mm, and it is not uncommon for some locations to go two or 3 years without rain. Even so, life exists here, and is abundant in the rare wet years (Dimmitt, 2015).

The landscape in this subdivision is dominated by broad flat basins interrupted by small rocky ranges. It includes the Gran Desierto de Altar, a 5700 km² sand sea, the only area one might recognize as stereotypical desert. The spectacular Pinacate volcanic field lies within this sub-region as well. The valleys are dominated by low shrubs, primarily creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*). These are the two most drought-tolerant plants in North America, but in the driest areas of



Fig. 1 Map of the Sonoran Desert and surrounding ecoregions by Curtis Bradley. Data Source: Ecoregions 2017 © Resolve.

this subdivision even they are restricted to drainages. Trees are found only in the larger washes. The mountains support a wider variety of shrubs and cacti, but the density is sparse. Columnar cacti are rare and restricted to drainages. Annual plants comprise well over half the flora (90% at the driest sites), and are abundant only in wet years (Dimmitt, 2015).

Arizona Upland

This northeastern section, mostly in south-central Arizona and northern Sonora, is the highest and coldest subdivision of the Sonoran Desert (Fig. 2). The terrain contains numerous mountain ranges, and the valleys are narrower than in the Lower Colorado River Valley subdivision. Trees are common on rocky slopes as well as drainages, and saguaros are found everywhere except the valley floors. This community is also called the saguaro-palo verde forest. It is the only subdivision that experiences frequent hard winter frosts, so many species of the lower elevation and more southerly subdivisions cannot survive here.

The Arizona Upland is home to a great variety of cacti, ranging from saguaros that can reach heights of 12 m to several tiny species less than 10 cm. There are tall columnar cacti, round cacti (barrels), jointed stick-like cacti (chollas), and cacti with flat



Fig. 2 Arizona Upland in the Tucson Mountains. Photo by Dug Schoellkopf.

pads (prickly pears). Other common plants found here are agaves (*Agave spp.*), yuccas (*Yucca spp.*), and legumes such as mesquite (*Prosopis spp.*), palo verde (*Parkinsonia spp.*), ironwood (*Olneya tesota*), and acacia (*Acacia spp.*). Low shrubs include white bursage, brittlebush (*Encelia farinosa*), jojoba (*Simmondsia chinensis*), ocotillos (*Fouquieria splendens*), and a variety of desert grasses.

Central Gulf Coast

The Central Gulf Coast subdivision occupies strips along both sides of the Gulf of California, and desert vegetation grows right to the seashore. Small shrubs are nearly absent; their shallow root systems and lack of water storage cannot sustain them through the extreme aridity here. Dominating the vegetation are large stem-succulents, particularly the massive cardón (**Fig. 3**) and trees such as palo verde, ocotillo, ironwood, elephant trees (*Bursera spp.*), and limberbush (*Jatropha spp.*), which are leafless most of the time. The average annual rainfall of less than 5 in (125 mm) occurs mostly in summer, though not dependably enough to call it a rainy season ([Dimmitt, 2015](#)).

Plains of Sonora

The Plains of Sonora, a small region of central Sonora, is similar to the Arizona Upland with denser vegetation (due to more rain and deeper, finer soils) and additional tropical species. Most of the subdivision has been converted to agriculture ([Dimmitt, 2015](#)).

Climate

Annual precipitation in the Sonoran Desert ranges from 50 to 400 mm (2–16") a year with substantial inter- and intra-annual variability in timing and quantity. Lower elevations near the Colorado River and Gulf of California receive the least amount of rain and higher elevations near the Sierra Madre Occidental receive the most. The desert is situated at 28–34° latitude which, combined with its location at the western edge of a large land mass, is in an area dominated by sinking, dry equatorial air and high pressure that serves to reroute incoming frontal storms. During the cooler winter months, from December to March, this high pressure breaks down and moisture from the Pacific Ocean arrives on the back of strong westerly winds. Much of this moisture is lost on the windward side of the peninsular mountain ranges of Southern California and Baja California, and never makes it to the desert. This rain shadow effect is caused when an air mass is forced up and over a mountain range, cooling it, and thus causing the moisture to precipitate out as rain or snow.

There are five seasons in the Sonoran Desert: fall, winter, spring, and two summer seasons. Fore-summer occurs in May and June and is characterized by cloudless, dry, sunny days with temperatures commonly exceeding 40 °C (104 °F). Monsoon season typically arrives in early July and is characterized by a shift in the wind patterns, increasing humidity, and chances for rain. The North American monsoon shares the basic characteristics of the Indian counterpart but lacks its duration and intensity. The event is created by several factors working in concert. A thermal low-pressure system forms near the Arizona and California border created by rising air from the intense solar heating of the Earth's surface. This pulls in low level moisture from the nearby warm waters of the Gulf of California. Secondly, a high pressure system develops over the Four Corners area where the US states of Arizona, New Mexico,



Fig. 3 Organ pipe cactus (*Stenocereus thurberi*) in foreground, cardón, and saguaro in background. Photo by Sky Jacobs.

Colorado, and Utah meet. The air cools over this higher elevation area, falling, and creating a counter clockwise air flow that draws in higher-level moisture from the Gulf of Mexico. These conditions can combine to produce intense but localized afternoon thunderstorms.

Representative Sonoran Desert Animals

Arthropods

Just as elsewhere in the world, arthropods comprise over 85% of the described animal species in the Sonoran Desert. They are the most important pollinators, and they aerate the soil, and decompose dead plants and animals. Arthropods are also some of the most important herbivores and prey in terrestrial food webs. The Sonoran Desert is a biodiversity hotspot for arthropods. Their great variety of adaptations to desert life, interesting behaviors, and critical ecological functions are fascinating. Each summer during monsoon season, two-legged entomologists swarm the region to study its six- and eight- legged residents.

The most famous/infamous arthropods in the Sonoran Desert are probably its black widow spiders (*Latrodectus hesperus*), tarantulas (*Aphonopelma* spp., **Fig. 4**), and scorpions. Most spiders are venomous, but only the black widow and brown recluse (*Loxosceles* spp.) have venom dangerous to people. The female black widow will sometimes eat the male after mating, thus the name “widow,” although this behavior is actually seen in many types of spiders. Tarantulas are 3 to 4 in. long and commonly seen during the summer rainy season when males leave their burrows to seek out females. They have an unusual defense mechanism: irritating barbed hairs that they can brush onto the mouth, nose or paws of a predator.

There are more than 30 species of scorpion in the region. They occur in a great variety of habitats, spending much of their time underground, under rocks or, as with bark scorpions, high above ground in trees or in rock crevices. Scorpions give birth to live young which quickly clamber on to their mother’s back to hitch a ride until their first molt. One of the most unusual traits of scorpions is that they fluoresce under ultraviolet light ([Lizotte, 2015](#)).

Many other arthropods are keystone ecological players in the Sonoran Desert. The region is home to more than 750 species of bees. They range in size from the world’s smallest bee, *Perdita minima*, measuring less than 2 mm, to carpenter bees (*Xylocopa* spp.),



Fig. 4 Arizona-Sonora Desert Museum. Photograph of tarantula by Howard Byrne III.

which are up to 40 mm long. Unlike most other groups of animals, bee diversity peaks in deserts and savannahs, rather than in rainforests. Most native Sonoran Desert bees are solitary, creating nests inside perfectly circular holes dug in the ground, although some make their nesting holes in dried stems or wood (Buchmann, 2015).

Birds

People flock from all over the world to catch a glimpse of both the diversity and distinctiveness of the Sonoran Desert's more than 400 bird species (Fig. 5). Some of the greatest stars are the dozen or so hummingbird species that live in or pass through the region. They include the smallest birds in the world and range from 7 to 13 cm. They have the most brilliant iridescent colors, the fastest wingbeats, and the most amazing flying acrobatics, with the ability to fly up, down, sideways, and backward.



Fig. 5 The cactus ferruginous pygmy-owl (*Glaucidium brasilianum*) was formerly common in the Arizona Upland subdivision but is now considered endangered in the United States due to habitat loss. Photograph by Sky Jacobs.

The greater roadrunner (*Geococcyx californianus*) is probably the most iconic desert bird. These birds can fly, but usually walk or run instead. In the open, they can reach speeds of 30 km per hour. A fierce predator, the roadrunner can catch snakes, lizards, rodents, small birds and insects. They prefer the open habitat of desert or pinyon/juniper.

Gambel's quail (*Callipepla gambelii*) are some of the most visible and audible birds in the Sonoran Desert. They spend most of their time on the ground and are commonly seen scurrying in groups from the cover of one sprawling mesquite to another. During spring and summer, one often sees young quail following their parents in a single file line of 10 or more brown fluff balls. They are common in desert scrub, thorn scrub and riparian areas (Kaufman, 2015).

Of the many hawks and eagles that inhabit the Sonoran Desert, Harris's hawks (*Parabuteo unicinctus*) are the only ones that live and hunt in social groups. They cooperate in defending their nest, and in flushing out prey during a hunt. Other common hawks are Cooper's hawks (*Accipiter cooperii*) and red-tailed hawks (*Buteo jamaicensis*). The American kestrel (*Falco sparverius*) is a familiar sight as well. This small falcon can reach great speeds chasing the large insects that make up most of its diet. Another bird in the falcon family, the crested caracara (*Caracara cheriway*), is a large, majestic, slow-flying bird that will catch live prey or eat carrion. It is mainly a tropical bird, common in the southern part of the Sonoran Desert, however its range is expanding northward into Arizona (Jennes, 2015). Many other birds inhabit the diverse landscape and soundscape of the Sonoran Desert, much too numerous to list here.

Mammals

Over 40 species of bat live in the Sonoran Desert Region. Bats are one of the most diverse groups of mammals and one of the most threatened. White nose syndrome, which has devastated bat populations in the northeast US, has not yet reached the Sonoran Desert. Bats keep insect populations in check and are important pollinators of many Sonoran Desert plants, including the iconic columnar cacti (Tyburec, 2015).

Sonoran Desert canids include coyotes (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and kit fox (*Vulpes macrotis*). Coyotes are found in all habitats, while gray foxes prefer rocky canyons and kit foxes like more open flats, with deeper soils for digging their dens. Coyotes appear prominently in the stories people have told about this region throughout time. All three desert dogs are omnivores, eating whatever they can find. Coyotes are mostly social animals, living in small family groups and filling the desert with their yips and howls whenever there is news to share, but especially at dusk. Gray foxes can climb, forage and sleep in trees, safe from many of their predators. Kit foxes are nocturnal and use their underground dens year-round. They can survive without free water, getting all the water they need from their food. The endangered Mexican gray wolf (*Canis lupus baileyi*) also lives in the region, in the mountains at the desert's edges.

Four wild cats make their homes in the Sonoran Desert region. The largest two, the jaguar (*Felis onca*) and mountain lion (*Felis concolor*), live mostly in the sky islands. Bobcats (*Felis rufus*) are common in many habitats, including people's back yards. Ocelots (*Felis pardalis*) are found in thorn scrub, oak woodland and riparian areas in Sonora, Mexico, and are rarely seen in the northern part of the Sonoran Desert.

Two distinctive, but rarely seen Sonoran Desert mammals are the ringtail (*Bassariscus astutus*; Fig. 6) and coati (*Nasua narica*). Both are related to raccoons in the procyonid family. Ringtails are squirrel-sized, with large eyes and a long fluffy ringed tail. They have excellent climbing abilities and are solitary and nocturnal. Coatis are social animals, living in large bands of up to 30 individuals in riparian areas or oak-sycamore canyons. They are longer and thinner than a raccoon with a longer snout ringed tails. They often walk with their tails erect. Both of these animals, like raccoons, are omnivores.

Other Sonoran Desert mammals are: desert bighorn sheep (*Ovis canadensis nelsoni*), Sonoran pronghorn (*Antilocapra americana sonoriensis*) and multiple species of skunks, badgers, deer, rabbits, and a variety of rodents, many with fascinating adaptations to the heat and aridity of the desert.

Fishes and Amphibians

"Desert fish" may sound an oxymoron, but fish are also found in the Sonoran Desert. Many washes that are dry today were once streams that ran at least intermittently. There are dozens of freshwater species native to the region, and even more that have been introduced. Native species include the small (5 cm) Gila topminnow (*Poeciliopsis occidentalis*) and the largest minnow in the region—the 1.8 m Colorado pikeminnow (*Ptychocheilus lucius*). At least two thirds of the native species are threatened or endangered due to loss of habitat and competition from nonnative species (Ivanyi and Marsh, 2015) including the Sonoyta or Quitobaquito pupfish (*Cyprinodon eremus*), which is found in one location on the Rio Sonoyta in Sonoran and at Quitobaquito Springs in Organ Pipe National Monument.

Sonoran Desert amphibians have evolved some ingenious methods to get and keep the water they need. For example, Couch's spadefoots (*Scaphiopus couchii*) burrow into moist soil and emerge to feed and breed only on rainy nights. They lay their eggs in temporary ponds, and they hatch and metamorphose in less than 2 weeks, hopefully before the pond has dried up. Similarly, the large (18 cm) Sonoran Desert toad (*Incilius alvarius*) spends most of the year in rodent or other underground burrows, emerging in the rainy season to mate and feed. Their tadpoles take longer to mature – 6 to 10 weeks, requiring larger or longer-lived ponds to complete the life cycle. Both types of amphibian are generally nocturnal (Ivanyi et al., 2015).



Fig. 6 Ringtail Photo by Paul and Joyce Berquist.

Reptiles

Sonoran Desert tortoises (*Gopherus morafkai*) are widespread throughout the region. They survive the heat of summer days and the cold of winter in a hibernation-like state in burrows, which they dig with strong, flattened, front legs. They extract water from the plants they eat and will drink free water if it's available. Their bladder has the capacity to store 40% of their body weight in water to get them through long dry spells. Gila monsters (*Heloderma suspectum*, **Fig. 7**) are one of only two medically significant venomous



Fig. 7 Gila monster. Photograph by Alex Kerstitch.

lizards in the world, the other being the beaded lizard found along the Pacific slopes of Mexico from Southern Sonora into Guatemala. The Gila monster is a large wide-bodied lizard, reaching about 45 cm in length and brightly bedecked in bands or a network of pink, red, or orange, contrasted with black—which is considered warning (aposematic) coloration (Ivanyi et al., 2015).

There is a great diversity of other lizards and snakes in the Sonoran Desert, reflecting not only the diversity of habitats, but the region's position adjacent to grasslands of the mid-continent and the tropics to the south. A species that is adapted to the Sonoran Desert is the Tucson shovel-nosed snake (*Chionactis annulata klauberi*), a non-venomous mimic of the Sonoran coral snake (Fig. 8). It has a specially adapted spade like snout that allows it to burrow or “swim” through sandy soils and preys on everything from beetle larvae to scorpions.

Arizona is home to at least 18 different varieties of rattlesnake and, if you add in those found in the state of Sonora and the Baja California peninsula, as well as species found on islands in the Gulf of California, this region easily rivals any other in rattlesnake diversity. Rattlesnake venom is a highly specialized mixture of enzymes that attacks blood, tissue, heart and nerves. They are most active in the warmer seasons, and mostly nocturnal in the summer. To aid seeing in the dark, they have a pair of unusual infrared-sensing organs that help them find prey, avoid predators, and navigate the challenging thermal landscape in which they live (Ivanyi et al., 2015).

Indigenous Peoples and Colonization

Humans have been living in Sonoran Desert for at least 13,000 years, shaping its ecosystems and biodiversity, just as the environment has shaped human cultures through time. Some scientists believe that Paleo-Indians contributed to the extinction of large megafauna that roamed North America during the Ice Age. Archeologists have documented changes in the abundance of various mammal species near early human settlements due to human consumption patterns. Hohokam people built extensive irrigation networks and cleared desert vegetation for fields and firewood. The Seri people on the Sonoran coast helped to expand the range of several species of reptiles during their travels. For at least 4000 years, Sonoran Desert peoples such as the O’odham, Cocopas, Yoemem, and Mayos (and their ancestral cultures) cultivated maize, tepary and pinto beans, gourds, squash, cotton, amaranth, devil’s claw, agaves, and many other plants, changing their abundance and distribution on the landscape (Sheridan, 2015).

With the arrival of Europeans in the 16th century, came the devastating dispersal of new diseases, which are estimated to have killed up to 95% of the indigenous population. Europeans also brought new plants and animals including winter wheat, fruit trees, mules, oxen, cattle, sheep, goats, and horses, which further changed the landscape and biodiversity. The discovery of silver and gold deposits in the late 17th century accelerated this trend. Ranching and mining settlements were developed. The railroad arrived in the 1880s, followed by cattle, copper, and cotton. Each did their part to remake portions of the Sonoran Desert. The widespread availability of air conditioners starting in the 1940s led to rapid urban growth in Arizona. Each successive wave of human settlement left its mark on the biome we call the Sonoran Desert, a process that continues today (Sheridan, 2015).



Fig. 8 The venomous Sonoran coral snake (*Micruroides euryxanthus*) is distinguished from its non-venomous shovel-nosed mimics by its black snout and thicker bands. Photograph by Sky Jacobs.

Threats to Biodiversity

Climate Change

Nearly all the world's biomes have experienced temperature increases over the last 50 years, and the Sonoran Desert is no exception. According to the Fourth National Climate Change assessment, the region has already seen a 0.89 °C (1.61 °F) increase in average annual temperature since the beginning of the 20th century. This is predicted to increase by an additional 2.7 to 4.8 °C (4.9–8.7 °F) by the end of this century under the lower (RCP4.5) and higher (RCP8.5) emissions scenarios, respectively (Wuebbles et al., 2017).

Changes in rainfall patterns have been equally significant (Fig. 9). Regions of the Sonoran Desert have experienced a 15% reduction in precipitation (USGCRP 2017), and a 19% reduction of flows has been observed on the Colorado River (Udall and Overpeck, 2017). Most models forecast less winter and spring rain and lower overall precipitation in the future. At the same time, rainfall intensity, or the amount of rain in a given period of time, is predicted to increase during summer thunderstorms because warmer air can hold more moisture. Summer rains typically produce localized precipitation that does not percolate into the soil as deeply as winter rains that originate from large Pacific Ocean frontal systems (MacMahon and Wagner, 1985).

These changes in climate are predicted to affect the distribution and abundance of many Sonoran Desert species. The hotter temperatures will mean a decrease in available soil moisture due to increased evapotranspiration. Plants with root systems that can tolerate water stress and can utilize summer versus winter precipitation will be favored. This change is being observed with the reduction of foothill paloverde (*Parkinsonia microphyllum*) and ocotillo (*Fouquieria splendens*) on south and west facing slopes (Munson et al., 2011). It is also predicted that many of the desert's plant species ranges will move up in elevation in response to climate change. A study on the Santa Catalina Mountains near Tucson found that 15 of 27 plant species already had shifted higher in elevation over a 49-year period (Brusca et al., 2013).

Invasive Species

An invasive species is defined by the U.S. Department of Agriculture as a species that is non-native to that ecosystem and whose introduction will cause economic or environmental harm. There are several invasive plants that pose a threat to the native plants of the Sonoran Desert either through competition or by changing the fire regime. Fast growing annuals such as red brome (*Bromus*

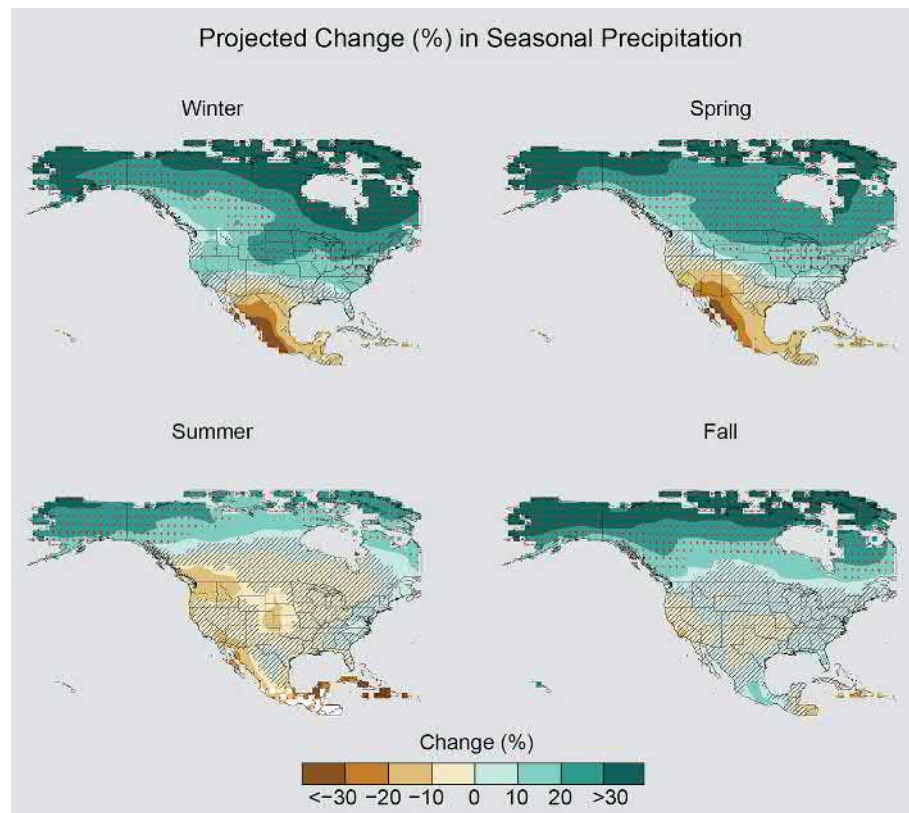


Fig. 9 Projected change (%) in total seasonal precipitation from CMIP5 simulations for 2070–99 relative to the 1976–2005 average. These are results for the higher scenario (RCP8.5). Stippling indicates large changes and hatching indicates small changes as compared to natural variations. Data source: World Climate Research Program's (WCRP's) Coupled Model Intercomparison Project. Figure source: NOAA NCEI - National Oceanic and Atmospheric Administration National Center for Environmental Information.

rubens), Arabian grass (*Schismus arabicus*), Sahara mustard (*Brassica tournefortii*), and cheatgrass (*Bromus tectorum*) outcompete native annuals. Perennials such as buffelgrass (*Pennisetum ciliare*), and fountain grass (*Pennisetum setaceum*) can grow large and dense enough to compete with native shrubs for light and nutrients (Dimmit and Fusari, 2015). Saltcedar (*Tamarix* spp.) is an invasive tree that displaces native trees in riparian areas that are habitat for many birds.

Buffelgrass, native to the savannas of Africa and India, has been planted in Sonora and Arizona since the 1950s to increase forage for cattle production (Brenner, 2011). In Sonora, buffelgrass cultivation boomed from government-subsidized programs to support the ranching industry. By 2002, nearly 1.6 million hectares of land in Sonora had been cleared and seeded with buffelgrass (Búrquez et al., 2002). In Arizona, its planting was promoted by the US department of Agriculture as a soil stabilizer and is now a common sight in disturbed areas, along roads, or in desert scrub covered slopes. It produces large amounts of seed in response to rain but its ability to withstand fire is what makes it a threat to the desert.

Native vegetation is not dense enough to support fires larger than a few hectares and plants such as the giant saguaro have not evolved with fire. Whereas a single fire can kill significant numbers of cacti and succulents, buffelgrass will quickly colonize these disturbed areas, repeat the fire cycle, and expand to form dense, single species stands. Once buffelgrass is established in an area it is extremely difficult to eradicate (Fig. 10).

Livestock Grazing

Domestic cattle are another invasive species that arrived in 1540 with the Spanish explorer Coronado and were subsequently promoted by the numerous missions in the region (Fleischner, 2010). By the late nineteenth century, large numbers of livestock roamed the Southwest and their overgrazing, combined with a severe drought, converted the majority of the desert grasslands into desert-like scrublands that persist today (Dimmit and Fusari, 2015) (Fig. 11). Livestock grazing is now permitted on 3.6 million hectares of the Sonoran Desert ecoregion and across 1 million square kilometers of public lands in the United States. Grazing has a far greater impact on ecosystem health than do all roads, timber harvest, and wildfires combined (Beschta et al., 2013).

Soil compaction from livestock grazing has severe effects on deserts soils and has been identified as an extensive problem on US public lands (FS and BLM, 1997). This is because the weight of a 450-kg cow will exert more than five times the compacting pressure of a bulldozer and significantly reduce the soil's ability to store water (Cowley, 2002). When the soil cannot store as much water due to compaction and reduction of plant cover due to overgrazing, increased runoff will occur during high-intensity rainfall events of the summer monsoons (Branson et al., 1981). The increased runoff causes erosion, loss of topsoil and the downcutting of stream-banks and washes commonly seen in western landscapes.

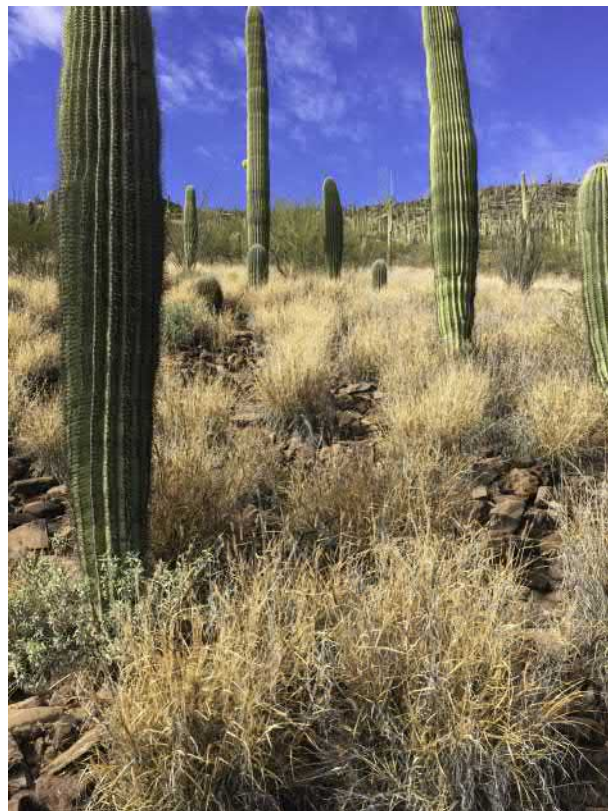


Fig. 10 Buffelgrass and saguaros on Tumamoc Hill in Tucson, Arizona. Photo by Curtis Bradley.



Fig. 11 Soil loss from cattle grazing in a mesquite bosque that once supported sacaton grass. Photo by Sky Jacobs.

Border Wall

Since the early 1990s, the U.S. government's border control efforts have been driven by a "prevention through deterrence" strategy—the concept that increased personnel and infrastructure will discourage undocumented immigration. This strategy was first implemented in heavily populated border areas such as San Diego and El Paso and shifted immigration, drug trafficking and other activities to more remote areas of the Sonoran Desert, causing extensive environmental damage and social disruption.

Border wall construction accelerated with the passage of the 2006 Secure Fence Act, which mandated more than 1287 km (800 miles) of border wall construction, and the REAL ID Act of 2005, which gave the secretary of Homeland Security the power to waive US environmental laws to expedite construction (**Fig. 12**). In total, Homeland Security has installed 570 km (354 miles) of primary border wall ("pedestrian fencing") as well as 482 km (300 miles) of vehicle fencing ([United States, 2017](#)).



Fig. 12 Border pedestrian fencing along Organ Pipe National Monument. Photo by National Park Service.

Border walls threaten the biological integrity of the borderlands through direct habitat destruction, fragmentation, and creation of barriers between wildlife populations. These barriers prevent essential movement and gene flow while facilitating increased vehicular traffic and human disturbance in previously undisturbed areas (ACE, 2001).

One of the species that would be affected by additional proposed border wall infrastructure is the Sonoran pronghorn, whose population has declined to fewer than 1000 animals. Pronghorn require immense open areas and must travel long distances in search of food and water. They are also particularly sensitive to disturbance from human activities. The proposed border wall would limit their ability to travel freely in search of food and water and would permanently separate the species' northern and southern populations, preventing dispersal and gene flow that are essential to their survival and recovery.

Several scientific studies demonstrate the impact the wall is having on animals of the Sonoran Desert. Flesch et al. (2010) examined two species, the cactus ferruginous pygmy owl and desert bighorn sheep, and found that these species along with others with similar movement abilities and spatial distributions may be affected by border development. McCallum et al. (2014) used camera traps to compare movements of people and wildlife between areas with and without border walls and found that both pumas and coatis were recorded in higher numbers in areas without walls. The authors found no difference in number of people detected between the two, suggesting that intermittent fencing in this area was not effective at deterring human migrants, but did affect wildlife populations.

Land Conversion and Loss of Riparian Habitat

Historically, the southwest deserts of North America were less populated, and less disturbed, than the rest of the continent due to the lack of water and extreme heat. This changed in the mid-20th century with the construction of large-scale irrigation projects bringing water from the Colorado River and the introduction of air conditioning. Since then cities and agricultural lands have grown rapidly and, as of 2014, over 2.9 million hectares (7.16 million acres) of Sonoran Desert in the United States had been converted to urban environments, agriculture, roads, or non-native scrublands.

Damming, diversion of rivers, and ground water pumping to satisfy the booming population have strongly altered riparian areas in the Sonoran Desert and much of the riparian forests have been lost due to changes in land usage (Zaimes, 2007). Persistent drought through the early 2000s has further dried riparian habitats, and climate change models predict continued drying. Riparian areas support more diverse plant and animal communities than the surrounding drier uplands. The impacts of disappearing rivers are most severe for aquatic species—fish, amphibians and some reptiles and arthropods, but many other animals rely on these waters for some part of their life cycle, or for a source of drinking water. Even intermittent streams support denser ribbons of vegetation through the desert, providing more diverse habitat for animals.

Conservation Status and Planning (Fig. 13)

Mexico

Land tenure in Mexico radically changed after the Mexican Revolution and with the land reforms of the Cárdenas presidency of 1934–40. The land reforms redistributed nearly 18 million hectares of expropriated private land into ejidos, or common property used for agriculture (Stoleson et al., 2005). In Sonora, most of the desert ejidos were barely able to produce a subsistence crop and were used for cattle grazing, where it is now the default land use. A 1992 amendment to the Mexican Constitution allowed these lands to be sold and has accelerated the pace of privatization. As of 2007, a majority of municipalities in Sonora were under private land tenure while the majority of Baja California lands remain in ejidos. Public land tenure only covers 4% of the entire nation (Bonilla-Moheno et al., 2013).

In 1993 two large biosphere reserves were established in northern Mexico, the Alto Golfo de California y Delta del Río Colorado and the El Pinacate y Gran Desierto de Altar. These reserves were created to protect endangered species both from the Gulf of California and the Colorado River estuary including the vaquita (*Phocoena sinus*), the totoaba (*Totoaba macdonaldi*), the desert pupfish (*Cyprinodon macularius*), and the Yuma clapper rail (*Rallus longirostris yumanensis*).

The vaquita is a small and elusive porpoise that occupies a limited range in the northernmost reaches of the Gulf of California and is considered the most endangered marine mammal in the world. Its population has plummeted due to entanglement in fishing gear, including in nets set for the totoaba, a large and endangered fish endemic to the Gulf. Totoaba swim bladders are illegally exported to Asia to make soup perceived to have medicinal properties. In 2011, a single bladder could reportedly sell for between \$2500 and \$10,000.

The high demand for totoaba has meant more vaquita drowning as bycatch and the population has plummeted from 567 individuals in 1997 to less than 20 in 2018. In response to international pressure, in 2015 Mexico announced a ban on gillnets, with exemptions for two fish species (curvina and sierra), in the Gulf to protect the vaquita. But the remoteness of the Gulf—ringed by high cliffs and dotted with hundreds of desolate islands—has made it challenging to police, particularly given the involvement of drug cartels in the illegal totoaba trade. Attempts to capture vaquita to establish a captive breeding program have so far failed. If drastic action is not taken soon this species will disappear forever.

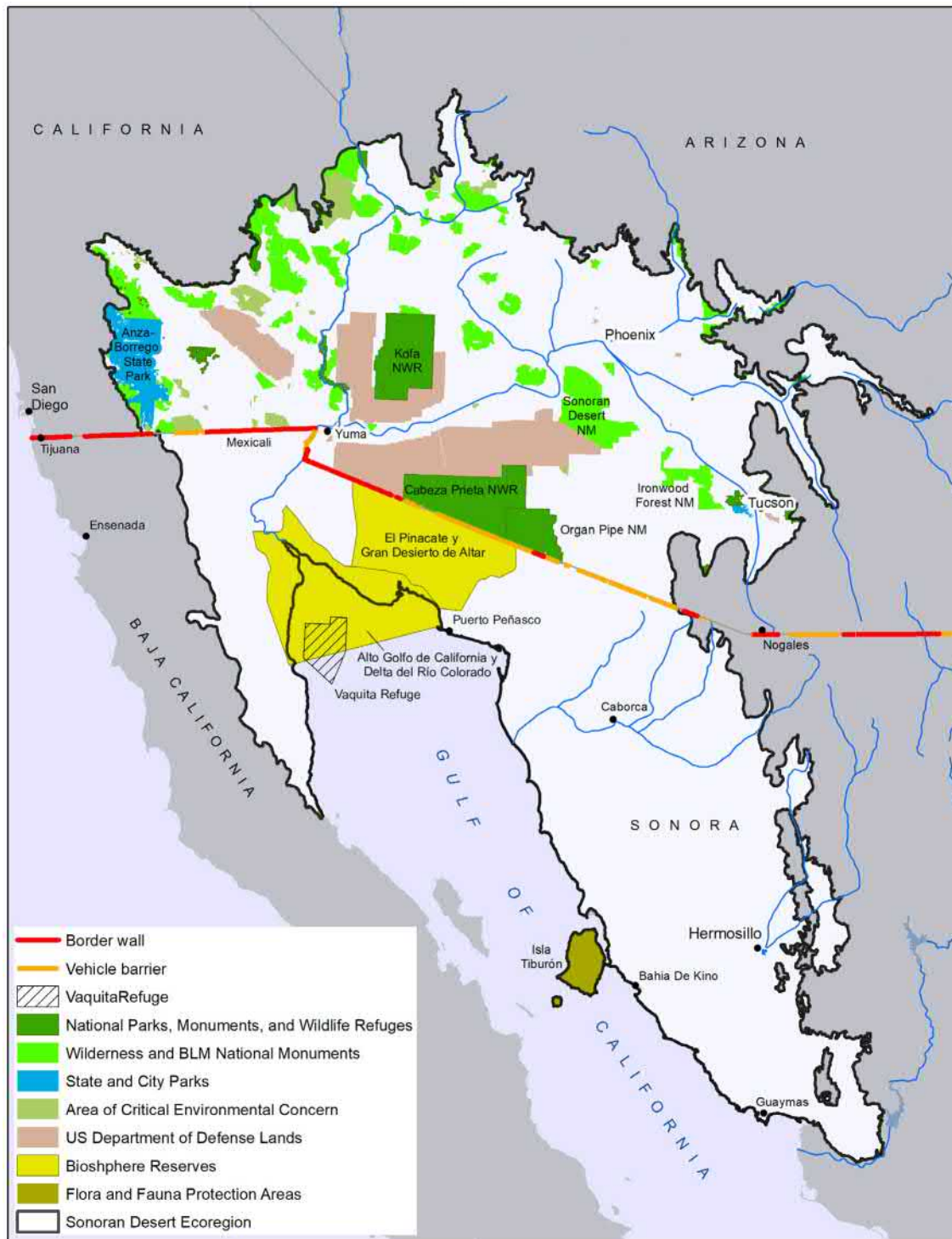


Fig. 13 Map of protected areas of the Sonoran Desert by Curtis Bradley. Data Sources: Ecoregions 2017 © Resolve (Sonoran Desert Ecoregion), Reveal from the Center for Investigative Reporting (Border Wall), World Database on Protected Areas, Protected Areas Database of the US (Protected Areas).

United States

Despite the significant population pressures in the United States, large tracts of Sonoran Desert are protected from human development because they are managed by the US federal government as either public lands: Bureau of Land Management, National Park Service, US Fish and Wildlife Service or military lands (Department of Defense).

Various US federal government agencies manage lands under different protocols to conserve resources. Congressionally designated wilderness areas are managed to minimize human imprint and prevent activities such as land conversion, road construction, power lines, pipelines, and off-road vehicle use. Wilderness areas and national monuments administered by the Bureau of Land Management typically allow cattle grazing within the desert. US Department of Defense lands are typically not thought of as protected areas but do provide valuable restrictions on human development, off-road vehicle use, and cattle grazing. National parks, monuments administered by the National Park Service, national wildlife refuges, and some state parks are managed to protect the flora and fauna of the Sonoran Desert and don't allow cattle grazing or other desert harming activities. Organ Pipe National Monument, Saguaro National Park, Anza-Borrego Desert State Park, and Tucson Mountain Park are excellent places to see the desert preserved in a relatively untouched state.

The future of the Sonoran Desert

The most critical threat to the flora and fauna of the Sonoran Desert is climate change, which is predicted to bring with it increasing temperatures and a shift in the timing and amounts of rainfall to the region. Although there is evidence that similar changes may have happened in the past and the desert has adapted accordingly, the rate of change was over millennia, not decades as is predicted under our current climate trajectory.

Unlike climate change, which needs to be addressed at a global scale, habitat destruction can be prevented if local governments and private citizens organize to protect the desert they love. An example of this can be found in southern Arizona with the Sonoran Desert Conservation Plan. This multispecies conservation plan has a goal of ensuring the long-term survival of Pima County's native biota through maintaining the habitat conditions and ecosystem functions necessary for their survival. It was developed over a 20-year process among diverse stakeholders that balanced the conservation and protection of cultural and natural resources with efforts to maintain an economically vigorous and fiscally responsible community. The plan requires continued citizen involvement to make sure it is implemented in a region that is experiencing some of the fastest population growth in the country. And while threats to the desert's biodiversity such as invasive species, the border wall, livestock grazing, and groundwater pumping are challenging, the result of inaction is equally severe with the vaquita serving as an example of when self-centered economic interests are allowed to rule our future.

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The Chihuahuan Desert: A Binational Conservation Response to Protect a Global Treasure

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Abstract

Occupying over 140,000 km² (54,000 mi²), the Chihuahuan Desert is the second largest desert in North America and includes much of the Mexican states of Chihuahua, Coahuila, Durango, Zacatecas and San Luis Potosi, as well as large parts of New Mexico and the Trans-Pecos region of Texas in the U.S. Of the arid ecoregions in the world, the Chihuahuan Desert ranks at the top with regard to plant diversity. This incredible ecoregion is also noted for its endemism, with over 670 species of plants and nearly half of its freshwater fish found nowhere else in the world. The Chihuahuan Desert faces a variety of threats, including habitat loss and fragmentation, climate change, changing wild fire regimes, and deterioration of its freshwater resources. We review these threats as well as the conservation response to them, which includes a diversity of public-private partnerships operating at regional to local scales. We conclude with a summary of conservation priorities for the future, which highlights the importance of a binational response that directly addresses the main drivers of decline, is based on lessons learned from past conservation efforts, expands natural resource monitoring, and builds on momentum of small scale conservation efforts for greater impact.

Introducing the Chihuahuan Desert

The Chihuahuan Desert is the most biologically diverse desert in the Western Hemisphere and one of the most diverse arid regions in the world (Cotera et al., 2004). From north to south, the ecoregion extends nearly 1500 km (932 miles), with its northern extent just south of Albuquerque, New Mexico to its southern extent in the Trans-Mexican Volcanic Belt, which lies just 250 km (155 miles) north of Mexico City. Occupying over 140,000 km² (54,000 mi²), the Chihuahuan Desert includes much of the states of the Chihuahua, Coahuila, Durango, Zacatecas and San Luis Potosi, as well as large parts of New Mexico and the Trans-Pecos region of Texas, making it the second largest desert in North America (Fig. 1).

The Chihuahuan Desert has hot summers and cool to cold, dry winters. The moisture sources that affect the Chihuahuan Desert's climate most are the Sea of Cortez and Gulf of Mexico. Surrounding mountain masses and the position of the desert in the center of the continent results in little frontal precipitation. As a result, the Chihuahuan Desert has a high percentage of its precipitation falling in the form of monsoonal rains during the summer months. With average annual precipitation typically ranging from 150 to 500 mm (6 to 20 in.), this desert has more rainfall than many warm desert ecoregions (Schmidt, 1979).

Distinctive habitat types in the Chihuahuan Desert include yucca woodlands, playas, gypsum dunes, and a diverse array of freshwater habitats. Isolated by the high mountains of the Sierra Madre Oriental, the Sierra Madre Occidental, and the Arizona-New Mexico Mountains, the portion of the Chihuahuan Desert of high Mexican Plateau is rich with endemic species, particularly plants and reptiles (Hernandez and Barcenas, 1995; Gómez-Hinostrosa and Hernández, 2000). For example, a recent study found endemic plants comprising 67 families, 263 genera, 671 species and 155 infraspecific taxa (73 subspecies, 79 varieties and 3 additional hybrids), making a total of 826 taxa (Villarreal-Quintanilla et al., 2017). These results align well with an earlier study that documented



Fig. 1 Location and extent of the Chihuahuan Desert ecoregion alongside two of its ‘sister’ North American deserts, the Mojave Desert and Sonoran Desert. The binational region of Big Bend (discussed later on in this article) is delineated by square. Map from the Desert Landscape Conservation Center.

over 1000 endemic plant taxa (Johnston, 1977). Highlands have significantly higher woody plant diversity than lowlands throughout the region, and physiography is a major control on woody plant diversity (Montaña, 1990; Gómez-Hinostrosa and Hernández, 2000; Poulos and Camp, 2010). Tall mountains and rugged topography provide habitat characteristics conducive to vertical stacking of biotic communities, which amplifies the biodiversity of the Chihuahuan Desert’s montane ecosystems.

Grasslands comprise a small part of the Chihuahuan Desert but are vital to the biological diversity of the ecoregion (PACP-Ch, 2011). Characteristic grasses of the Chihuahuan Desert are tobosa (*Pleuraphis mutica*) and black grama (*Bouteloua eriopoda*) but other common species include alkali sacaton (*Sporobolus airoides*), big alkali sacaton (*S. wrightii*), mesa dropseed (*S. flexuosus*), blue grama (*B. gracilis*), sideoats grama (*B. curtipendula*), hairy grama (*B. hirsuta*), slender grama (*B. filiformis*), chino grama (*B. brevistata*), spruce top grama (*B. chondrosioides*), bush muhly (*Muhlenbergia porteri*), several three awns (*Aristida* spp.), and fluff grass (*Dasyochloa pulchella*) (Johnston, 1977; Dinerstein et al., 2000).

Reptile diversity in the Chihuahuan Desert is impressive and well-documented (UTEP Museum, n.d.; Prival and Goode, 2014; Cruz-Elizalde et al., 2014). Two orders of reptiles occur in the Chihuahuan Desert: Testudines (turtles) (Fig. 2) and Squamata (lizards and snakes), with the latter order being particularly diverse. Seven families of lizards have been recorded in the Chihuahuan Desert region. The Gila Monster (*Heloderma suspectum*) is one of only two known poisonous lizards worldwide, though its range barely overlaps with the Chihuahuan Desert (touching the northwestern portion near the Arizona/New Mexico border) with most of its range is in the Sonoran Desert. The grand majority of snake species (suborder Serpentes) in the Chihuahuan Desert are in the family Colubridae, which are nonvenomous. In contrast, the coral snake (Family Elapidae) is venomous with two species occurring in the eastern and western fringes of the Chihuahuan Desert: the Eastern Coral Snake (*Micrurus fulvius*) and the Western Coral Snake (*Micrurus euryxanthus*). The more familiar venomous snakes in the region are the pit vipers (Family Viperidae), which includes five rattlesnakes. The name comes from the presence of a pit between the eyes and nostrils that contains receptors for infrared radiation (heat) that allow tracking of warm-blooded prey.

A striking number of endemic freshwater fish occur in the Chihuahuan Desert—nearly half of the species in the ecoregion are either endemic or of limited distribution. Most of these are relict pupfish (Cyprinodontidae), shiners (Cyprinidae), livebearers (Poeciliidae), and Mexican livebearers (Goodeidae) found in isolated springs in the closed basins of the region. One of the better-known aquatic basins is Cuatro Ciénegas in central Coahuila, but other significant areas of endemism include the Rio Nazas, Media Luna, the Guzman Basin (Miller, 1977; Minckley, 1984; Minckley et al., 1991), and the Pecos Plain. At least one undescribed species of



Fig. 2 Two turtle species of the Chihuahuan Desert biome that are of conservation concern: western painted turtle (*Chrysemys picta*) (lower) and the Big Bend slider (*Trachemys galgae*) (upper). Photo by John Karges, The Nature Conservancy.

trout (*Oncorhynchus* sp.) occurs in the Chihuahuan Desert ecoregion as an evolutionary isolate in headwater streams in the Sierra Madre Occidental (Hendrickson et al., 2006).

There are also far-ranging large mammals such as Carmen Mountain white-tailed deer (*Odocoileus virginianus carminis*), desert mule deer (*Odocoileus hemionus crooki*), bighorn sheep (*Ovis canadensis mexicana*), elk (*Cervus canadensis*), pronghorn (*Antilocapra americana mexicana*), black bear (*Ursus americanus*), mountain lion (*Puma concolor*), and, jaguar (*Panthera onca*) and, perhaps, some released Mexican wolves (*Canis lupus baileyi*). Over 350 bird species have been recorded in this region, and the river corridor serves as a major thoroughfare and/or stopover for birds (Brush, 2005) and other species (e.g., the Monarch butterfly) that migrate between the Americas.

Threats

Of the many threats that face the Chihuahuan Desert, several standouts seem particularly critical and will need to be addressed as part of a multisector, binational response in the future.

Habitat Loss and Fragmentation

Outright loss of habitat and habitat fragmentation throughout the Chihuahuan Desert has been driven by a variety of factors, including agriculture, urbanization, road construction, amongst others. The conversion of native grassland ecosystems to agriculture has been particularly severe. The rate of grassland conversion varies with location. In the central and northern valleys of the state of Chihuahua, analysis of satellite imagery and on-the-ground observations revealed that more than 69,000 ha (170,500 acres) were converted to agriculture between 2006 and 2011. This amounts to an expansion of the agricultural footprint in this region by an annual rate of 6.04% (Pool et al., 2014). If this continues unabated, it has been estimated that grassland habitat in central Chihuahua will disappear completely by 2025 (NABCI, 2016).

Climate Change

One of the few certainties regarding the effects of global climate change is that wet areas will tend to get wetter and dry areas will become drier. There is no more dramatic evidence of this phenomenon than the Chihuahuan Desert. From 1993 to 2005, after the relatively wet years of 1990–1991, the portion of the Chihuahuan Desert within the Rio Grande/Bravo (RGB) (this binational river is often referred to as the 'Rio Grande' in the U.S. and 'Rio Bravo' in Mexico. Hence, Rio Grande/Bravo (RGB)) watershed suffered the most extreme drought in 100 years. The drought not only undermined economic growth and severely stressed the natural environment, it fueled tensions between the US and Mexico over allocation of internationally shared waters (e.g., the Rio Grande/Rio Bravo, which constitutes the international border in the eastern half of the Chihuahuan Desert).

In an analysis of long-term climate data in the northern portion of the Chihuahua Desert, temperatures are projected to continue to increase throughout the 21st century and, depending on future emissions and other factors, the warming may accelerate

(McRoberts and Nielsen-Gammon, 2010). Average temperatures are expected to rise 2 °C–3 °C (3 °F–5 °F) by the middle of the 21st century (Nielsen-Gammon, 2008). When considering interannual variability, even cool years during the middle of the 21st century will be normal or above normal relative to current temperatures.

The effects of climate change on precipitation are much less predictable, with models suggesting a slight decrease in precipitation across much of the Chihuahuan Desert region in Texas. However, changes in precipitation are projected to be much smaller than the natural variability. For a given amount of precipitation, evaporation increases with increased temperatures and this will make future droughts even if rainfall stays the same. Additionally, increased evaporation will create dwindling water supplies and the projected increase in population will further decrease water. This is eye-opening forecast because the majority of precipitation falls during the warm season. Therefore, the availability of water will depend more and more on cool season precipitation, which is normally sparse in this region (McRoberts and Nielsen-Gammon, 2010).

Changes in precipitation and temperature affect biophysical and chemical processes with cascading impacts on all Chihuahuan Desert ecosystems, and with consummate effects on people and wildlife, alike. For example, warmer water temperatures, increased salinization, and low dissolved oxygen, such as are projected for the Rio Grande Basin (Llewellyn and Vaddey, 2013), may increase the likelihood that nonnative aquatic species will invade (Rahel and Olden, 2008; Bond et al., 2008). Longer, more severe droughts could decrease runoff and eliminate ephemeral lakes and spring pools, as well as drive perennial streams toward intermittent flow, and intermittent streams to ephemeral (Grimm et al., 1998; Garssen et al., 2014).

Changes in Wildfire Regimes

Fire regimes in the region have shifted dramatically over the past two centuries. Prior to Euro-American settlement, frequent, low-intensity surface fire prevailed across most of the dry woodlands and forests of this region (Sakulich and Taylor, 2007; Poulos et al., 2009; Poulos et al., 2013). Starting in the early 20th century, fire exclusion from livestock grazing and then active fire suppression led to a precipitous decline in fire frequency (Swetnam and Betancourt, 1990). Today, more than a century of mounting fuel loads in combination with intensified aridity have sparked a regional surge in catastrophic fires (Dennison et al., 2014; Westerling et al., 2006; Abatzoglou and Williams, 2016). Like the fire suppression era before it, this new fire regime is well outside the historic range of variation for most grassland, semiarid woodland and forest types in the American Southwest and has contributed to large-scale shifts in species composition and structure (Poulos et al., 2013).

Deterioration of Freshwater Ecosystems

Water is important in any context, but is particularly so in the Chihuahuan Desert, where access to sufficient water of sound quality is essential to people and native species, alike. Along the international border between Mexico and the U.S., the Binational Big Bend region of the Chihuahuan Desert is named after the characteristic “bend” in the RGB. Along this border region, the mainstem of the RGB, itself, and its second largest tributary, the Rio Conchos (Fig. 3) comprise the region’s ecological backbone, providing water, food and shelter for 5.5 million citizens as well as a grand diversity of wildlife. Portions of the RGB river system are estimated to be 150% over-allocated. For example, a study of water supply and demand in the lower RGB basin finds that there will be a 730.3 Mm³ (592,084 acre-feet per year (ac-ft/yr)) supply shortfall (demand minus supply) by 2060, with an additional 106.6 Mm³ (86,438 ac-ft/yr) added to that amount as a result of climate change impacts (BOR, 2013). Groundwater is faring no better; 43 of the Desert’s aquifers are overexploited as they are pumped to supply irrigated agriculture, whose footprint has expanded as more and more native grasslands are converted to cropland.

Although flow from the Rio Conchos rejuvenates the hydrology of the RGB through Big Bend, the river’s hydrograph is highly modified and reflects the impacts of impoundment, channelization, over-allocation of water, and fragmentation (Everitt, 1993). Along the RGB in Big Bend, declines in mean and peak stream flow, combined with a relatively unchanged sediment supply and the invasive giant cane (*Arundo donax*), which has established in dense, almost impenetrable stands along channel margins, have fostered aggradational processes (processes that increase surface elevation as a result of deposition of sediment) that bury high quality native aquatic and riparian habitat (Dean and Schmidt, 2013). Many small tributaries of the RGB system are not faring any better. For example, Terlingua Creek, whose watershed lies just north of the international border in Big Bend, was once a “bold running stream, studded with cottonwood timber and alive with beaver” (BIBE, historical archives). However, mining and agricultural activities during the late 19th and early 20th centuries precipitated the loss of these riparian forests and the many species that depend on them for their survival. Similar changes have occurred in many streams across the Chihuahuan Desert ecoregion.

Conservation Response

High species richness, large numbers of endemic species, and presence of globally rare habitats has identified the Chihuahuan Desert as one of a group of 200 high priority ecoregions worldwide (Olson and Dinerstein, 2002). The conservation response to protect the natural resources of this rich ecoregion ranges from global recognition to binational declarations and initiatives between Mexico and U.S. to smaller scale efforts conducted by a variety of public-private partnerships. Selected initiatives in each of these categories are presented below.



Fig. 3 Idealized map of the Rio Grande/Bravo (RGB) basin, which overlaps substantially with the Chihuahuan Desert biome and whose freshwater ecosystems are critical to sustaining this ecoregion's native species and citizens.

International

There are several international agreements associated with key parts of the Chihuahuan Desert that, in and of themselves, do not protect the areas they are associated with yet serve as rallying points for attracting a diverse governmental and nongovernmental conservation response. One such example is the Ramsar Convention of Wetlands, which is an international treaty (signed in the city of Ramsar, Iran in 1971) that supports the conservation and sustainable use of wetlands globally. In the Mexican portion of the Chihuahuan Desert, there are several important wetlands sites that are recognized by the Ramsar Convention, including: Laguna de Babicora, Rio San Pedro-Meoqui (Fig. 4), Laguna La Juanota, Humedales de Guachochi, Manantiales Geotermiales de Julimes, and the Área de Protección de Flora y Fauna Cuatrociénegas in the state of Coahuila.

Several binational declarations and benchmarks between the U.S. and Mexico underscore the importance of protecting the Chihuahuan Desert's treasured natural resources, particularly along the desert's greater binational region of Big Bend. Although nonbinding, these agreements serve to highlight the Chihuahuan Desert's border region as a binational conservation priority and have attracted a diversity of partnerships and funding that are helping to protect this key portion of the Chihuahuan Desert in the long-term. These binational declarations and benchmarks, include:

2000	Joint declaration signed by Bruce Babbitt (Secretary of State, U.S.) and Julia Carabias (Secretary of Environment, Mexico) '... to improve and conserve the natural resources of the Rio Grande/Río Bravo and associated habitats.'
2009	A joint declaration by the U.S. Secretary of the Interior Ken Salazar and Mexican Minister of Environment and Natural Resources Juan Elvira to conserve this region's important and diverse natural resources.
2010	Joint Statement from President Barack Obama and President Felipe Calderón that recognized the 'extraordinary biological diversity' of the Big Bend region, committing their respective agencies "to manage the region in a way that enhances security and protects these areas for wildlife preservation, ecosystem restoration, climate change adaptation, wildland fire management, and invasive species control."



Fig. 4 The declaration of the Meoqui wetland, which lies along the Rio San Pedro (a tributary of the Rio Conchos, which flows into the RGB at Big Bend), as a Ramsar site has spurred the formation of public-private partnerships and attracted outside funding that have greatly helped to protect this critical wetland site for people and wildlife in the long-term. Photo by Alfredo Rodríguez, WWF-Mexico, with permission.

National

Within the portion of the Chihuahuan Desert that lies in Mexico, the Mexican government has established a mosaic of eight protected natural areas that are managed by Comisión Nacional de Áreas Naturales Protegidas (CONANP) to protect key scenic and ecological values of the Chihuahuan Desert. The conservation focus of each of these areas differs with geography, biotic communities and the priorities of the people living in these areas. On the U.S. side of the Chihuahuan Desert, there are numerous conservation and recreation areas managed by the Forest Service, National Park Service, Fish and Wildlife Service, Bureau of Land Management as well as areas managed by the states of New Mexico and Texas. For example, across from the expanse of protected areas managed by Mexico in the Big Bend binational region, Big Bend National Park is bracketed by two natural areas managed by the Texas Parks and Wildlife Department: Big Bend Ranch State Park and Black Gap Wildlife Management Area. Together with the protected areas managed across the river by CONANP, the footprint of these protected areas covers over 13,000 ki^2 (5000 mi^2) (Fig. 5). The conservation importance of the RGB through the Chihuahuan Desert is further recognized by the river's designation as Wild and Scenic (managed by the National Park Service on U.S. side of the river) and Monumento Natural (managed by CONANP on the Mexican side of the river).

Local—Examples From the Field

Working with private landowners

Given the amount of land in the Chihuahuan Desert that is in private hands, collaboration between the private sector and the conservation community is key to protecting the Chihuahuan Desert. Two efforts are highlighted, below, to offer a taste of the plethora of community-based conservation work that is taking place in this remarkable ecoregion.

Working with ranchers to stem soil erosion in the upper Rio Conchos

Overgrazing, urban development, expansion of agricultural, road development, mining, amongst other human interferences have altered vegetation cover and accelerated soil erosion and loss from upper watershed surfaces (Rodríguez-Pineda et al., 2017). In Mexico, federal agencies, and such nongovernmental organizations like World Wildlife Fund, Mexico (WWF-Mexico), have worked collaboratively with private landowners to implement a variety of conservation efforts to stem soil erosion. For example, working with upland ranchers and farmers (those without irrigation rights), this collaborative public-private partnership constructed berms to slow soil loss on 10,230 ha (25,280 acres) of priority Chihuahuan Desert uplands between 2004 and 2010. A critical part of this effort is to provide ranchers, farmers and ejidatarios (members of communally managed lands known as Ejidos) education and training needed to maintain and expand upon these initial successes (Fig. 6).

Water harvesting with Raramuri communities

To engage local citizens in natural resource conservation efforts, the needs of local citizens need to be addressed, as well. Particularly with regard to economically compromised communities, citizens often do not have the luxury to involve themselves in long-term initiatives when efforts to maintain livelihood can be a day-to-day struggle. However, if projects can meet immediate socioeconomic

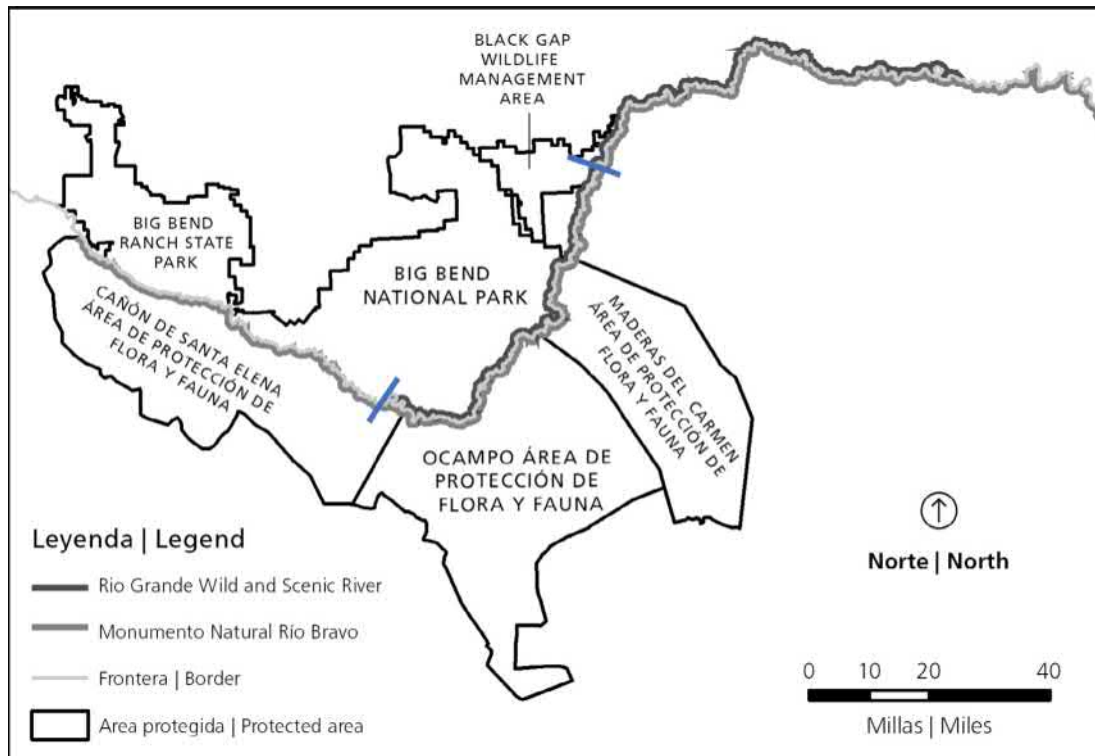


Fig. 5 Map of the binational Big Bend region of the Chihuahuan Desert, whose central feature is a core of protected areas on both sides of the international border that cover over 13,000 ki^2 (5000 mi^2). Binational restoration efforts have improved biophysical conditions along over 160 km of the RGB (the reach between the two hash marks). See 'Protecting Freshwater Ecosystems,' below. Map by Marie Landis, Big Bend National Park.



Fig. 6 Ranchers in the state of Chihuahua install berms along contour lines to increase water retention and stem soil loss. Photo by Day's Edge Productions.

needs, a foundation for longer term and more natural resource conservation focused efforts can be established. An example of this trajectory is an effort implemented by WWF-Mexico to install water harvesting projects (collecting water off of roof tops for family use and home gardens) in several Raramuri communities in the Sierra Tarahumara mountains of the southwestern portion of the state of Chihuahua. In and of itself, this effort has little to do with protecting Chihuahuan Desert natural resources and all to do with benefiting the well-being of the Raramuri communities. Yet, such community-based work is instrumental in fostering a variety of long-term grassland and forest restoration efforts in the subbasins that are part of the Raramuri lands. In addition, water harvesting efforts that began with Raramuri communities are now being replicated in other parts of the Chihuahuan Desert (Fig. 7). The bottom line: such community-based efforts are key to private engagement and toward expanding conservation efforts for greater impact.



Fig. 7 Community-based water harvesting projects such as this one in the community of Paseo de San Antonio (near the U.S.-Mexico international border) stemmed from work conducted with Raramuri communities and provides great incentive for larger community involvement in a range of conservation activities. Photo by Javier Ochoa-Espinosa (Área de Protección de Flora y Fauna Maderas del Carmen).

Understanding and managing changing fire regimes

Managers throughout the region agree that reducing the risk of destructive, uncharacteristically severe forest wildfires is a priority. Although the actions needed to mitigate this risk vary with location, the reduction of tree density and surface fuel loads is often put forward as central objectives (CEC, 2014). To accomplish these objectives, prescribed fire, forest thinning, and their combination are some of the few tools managers have to manage the surface and aerial fuel array in fire-adapted forests (Schwilk et al., 2009; Stephens et al., 2009).

Studies on the results of fuels hazard mitigation treatments have been carried out at a range of sites on the US portion of the Chihuahuan Desert, including the Guadalupe Mountains, Davis Mountains, and Big Bend National Park (Poulos and Gatewood, 2013; Poulos et al., 2019a,b). Results from these studies suggest that there are tradeoffs associated with carrying out either prescribed fire, forest thinning, or their combination. Resource managers throughout the region need more comprehensive information about the consequences of alternative management practices involving fire and mechanical/manual fuel reduction treatments in a range of upland sites in the Chihuahuan Desert. Work to this end is ongoing, and managers are continuing to experiment with fuel reduction activities at all of the aforementioned sites with the goal reducing management risk and uncertainty of catastrophic wildfire to the greatest degree possible.

Protecting freshwater ecosystems

Native fish conservation

In spite of being well-adapted, many native freshwater fish of the Chihuahuan Desert are threatened or endangered, often due to human actions that have altered streamflow and their natural habitat. There are several efforts that are specifically aimed at protecting the native freshwater fish of the Chihuahuan Desert. On the U.S. side of the ecoregion, stream restoration efforts have been conducted to benefit the threatened Pecos Bluntnose Shiner (*Notropis simus pecosensis*) (Hoagstrom et al., 2008) and to reintroduce the Rio Grande silvery minnow (*Hybognathus amarus*) (USFWS, 2010; Edwards, 2005). In Mexico, the waters of the Rio Conchos provide life to a great diversity of native freshwater fish, many of which are endemic (De la Maza-Benignos, 2009). In the upper part of basin, the Conchos Trout (*Oncorhynchus* sp.) is the only native Mexican trout known from an Atlantic drainage (Hendrickson et al., 2006). WWF-Mexico in collaboration with federal agencies and local communities are protecting the last known refuges of this species through a combination of watershed-based upland and bottomland conservation actions.

An essential part of this work is protecting the streamflow that the Conchos Trout and other native fish depend on for their survival. In pursuit of this goal, 10 sites in the Rio Conchos basin were selected as priorities to define federally mandated environmental flow prescriptions that will protect water needs of local citizens as well as native aquatic species, including the Conchos Trout. Although challenges to protecting streamflow for environmental purposes are formidable, progress is occurring. For example, the large irrigation district of Delicias is working to implement environmental flow prescriptions that will be sustainable for both irrigated agriculture and Rio Conchos trout.

One of the most threatened fish of the Chihuahuan Desert (possibly in the world) is the Julimes pupfish (*Cyprinodon julimes*). Rarely more than 5 cm (2 in.) long, the Julimes pupfish lives in hot-spring waters that reach 45.5 °C (114° F), earning it the title of the “hottest fish in the world.” The Julimes pupfish is endemic to the hot springs of the small municipality of Julimes, where

a population of several thousand fish—along with a tiny snail that is its main food source—survives in an area of about 745 square meters (8000 sq. ft) (De la Maza-Benignos, 2009) (Fig. 8). To protect the hottest fish in the world, a unique partnership developed between NGOs (Pronatura Noreste and WWF-Mexico), several private foundations, and management agencies. To date, this partnership has realized several key accomplishments that include: (i) restoring suitable habitat for the pupfish; (ii) having the hot springs nominated as a global Ramsar site; and (iii) working within the Mexican National Water Law of 1992 to establish and protect minimum flow requirements for the pupfish.

Binational effort to bring back the Rio Grande/Bravo in Big Bend

A centerpiece of the portion of the Rio Grande/Bravo (RGB) watershed that lies within the Chihuahuan Desert is the remote Big Bend binational area. Three protected areas in the U.S.—Big Bend National Park, Big Bend Ranch State Park, and Black Gap—and three in México—Cañón de Santa Elena, Ocampo and Maderas del Carmen—protect over 1 M hectares (over 3800 mile²) of relatively intact Chihuahuan desert habitat and a 290 km (180 miles) reach of the Rio Bravo (Fig. 5). With few road access points, this reach of the RGB that passes through this region is considered one of the great wilderness rivers in North America.

As noted previously, by the early 2000s, dense, almost impenetrable stands of giant cane have become established along many streams and rivers of the Chihuahuan Desert, including parts of the RGB in Big Bend. In response, a binational partnership that consists of federal and state land and water managers, nongovernmental organizations, private foundations, businesses, and river-side citizens designed and implemented a restoration program whose aim is to (i) significantly reduce the extent and dominance of giant cane along the Big Bend reach of the river; (ii) monitor results and conduct needed science; and (iii) work with land and water management agencies to improve water management that better reflects the needs of native stream ecosystems and the riverside communities along this critical binational river (Fig. 9). To date, the binational partnership has restored over 160 km (100 miles) of both sides of the Rio Grande/Rio Bravo in Big Bend.

Working with ranchers to protect key Rio Grande/Bravo tributaries

Restoring native aquatic and riparian habitat along tributaries of the RGB has become an important binational conservation priority. Given that many of these streams are on private lands, working with ranchers on solutions that will benefit them as well as the environment is essential. In Mexico, CONANP is working with local communities to bring back several key small tributaries of the RGB that have been degraded by mining, overgrazing, pollution, and introduction of nonnative species. The diverse conservation campaign that CONANP has launched includes environmental education (with particular attention on the importance of water and water harvesting strategies), scientific studies on current conditions and trends, and restoration and monitoring. An example of this response is restoration work along the streams of San Carlos and San Antonio streams, which are tributaries of the RGB and together drain an area of roughly 2000 sq. km (772 sq. miles). Restoration along these tributaries has centered on controlling nonnative plants and fish (e.g., saltcedar (*Tamarix* spp.) and the plains killfish (*Fundulus zebrinus*)), planting native riparian trees, and working with local communities to improve livestock management and waste water treatment. Similar work is also being conducted along tributaries in the U.S. portion of the Chihuahuan Desert.



Fig. 8 Visitors tour the Julimes hot springs. Ecotourism is a key component of this community-based effort to protect the Julimes pupfish in the long-term. Photo by Alfredo Rodríguez (WWF-Mexico).



Fig. 9 Prescribed burn of dense stands of giant cane along the Rio Grande/Bravo in the binational region of Big Bend (right). Binational efforts to improve conditions along the RGB have been conducted along over 160 km (100 miles) and demonstrate that stream restoration in complicated sociopolitical landscapes is not only possible but can produce substantial win-wins for people and the environment. Photo by Kelon Crawford, RGSSS.

Looking to the Future

The Chihuahuan Desert embodies the challenges of a new era in which the unsolved natural resource issues of the 20th century meet the 21st century's global challenges of security, development, and conservation. It is a place of clashing cultures, economic dynamism, political strife, and a natural environment under increasing pressure. It is also a place of rare opportunity, where a confluence of political will, scientific and policy advances, stakeholder engagement, and a unique mosaic of conservation efforts on both sides of the US/Mexico border have set the stage for adaptive watershed management that integrate social and ecological resilience to overcome water scarcity and support the development of a green economy. But the Chihuahuan Desert is a very big place. Where best to concentrate our efforts across this expansive ecoregion? Fortunately, social and political events, as well as the collective experiences from a range of past and on-going conservation efforts can help point us in the right direction. As we look to the future, key conservation priorities for the Chihuahuan Desert should include the following considerations:

- (1) *Stop the Bleeding!* Whether we are considering the Chihuahuan Desert's montane forests, desert scrublands, grasslands, or fresh water ecosystems, the first rule of conservation is the same: identify and eliminate (or reduce the impacts of) the main stressors that are causing ecosystem decline. Our ability to do this may be the most important fork in the conservation road. If the major stressors cannot be addressed, it is likely that we will be left working on the fringes, making only minor progress toward real improvement. On the other hand, if a main stressor is eliminated or its impacts are significantly reduced, there may be great potential for dramatic improvement of ecologic conditions at a much larger scale with consummate win-wins for people and wildlife.
- (2) *Scaling Up for Greater Impact:* There are parts of the Chihuahuan Desert where the pieces are in place for a much more ambitious effort to address the environmental, social and economic challenges at landscape scale. One good example is in the Big Bend region where binational restoration work along the RGB coupled with protected areas on both sides of the river (both sides of the international border) offer great opportunities for expansion. How such conservation/restoration expansion will be funded is a key question. One funding avenue that needs to be explored is how future conservation and restoration actions could be supported by binational ecotourism, which could increase under a regional strategy that aligns with conservation goals identified by agency managers and local communities. In general, ecotourism could be enhanced with greater attention to public outreach that emphasizes the importance of the Chihuahuan Desert as a stopover and/or destination location for such species as land bird migrants (Macías-Duarte et al., 2009; Finch and Yang, 2000) and the Monarch butterfly (Jepsen et al., 2015) that are appealing to the public and offer the potential of bringing in much needed conservation funding.
- (3) *Strengthen Support of Existing Federal and State Protected Areas:* As noted earlier, numerous state and federal protected lands are scattered throughout the Chihuahuan Desert. Regardless of where these protected areas occur and the entity that manages them, cuts in staff and resources over the years have left many in a precarious position that threatens their ability to realize their conservation mission and goals. Strengthening of federal (as well as state) conservation budgets on both sides of the border has to be a priority.
- (4) *Expand Public-Private Partnerships and Binational Collaboration:* With the above point made, it is also important to note that governments will not be able to address threats to the Chihuahuan Desert ecoregion on their own. Although diverse and numerous, the total area under federal or state protection is miniscule when compared to the entire footprint of the Chihuahuan Desert. Therefore, one of the keys to protecting the natural resources of the Chihuahuan Desert is alignment,

cooperation and collaboration between the conservation community, the private sector (communities, Ejidos, private land-owners, businesses, farmers, and ranchers), land and water managers, and academic institutes. Building off of momentum gained from public-private partnerships that have already been created and have a track record of conservation accomplishments is key. The diverse mix of agencies, organizations, institutes, businesses, and communities that are working together to protect the natural resources along the border region provides an example of what is needed for the future to protect the Chihuahuan Desert ecoregion as a whole.

- (5) *Protect Biodiversity Hotspots*: Biodiversity hotspots in the Chihuahuan Desert have been identified and should rise to the top as conservation priorities. These hotspots include:

- *Key mountain ranges*: Recent research has identified key mountain ranges in the Chihuahuan Desert that are characterized by high tree species richness—likely due to the complex topography that provides a wide-range of environmental conditions for tree growth—that warrant greater conservation attention owing to both the biodiversity they support and the threats they face (CEC, 2014; Villarreal-Quintanilla et al., 2017).
- *Grasslands*: Given the high percentage of private lands in this ecoregion, protecting intact grasslands and restoring damaged ones will hinge on partnerships with private landowners. In Mexico, more emphasis needs to be placed on working with ejidos (communal land holdings) and Mennonite communities that farm areas that were previously grassland, and/or adjacent to native grasslands. The goal has to be to find ways to manage the land that support the conservation of biodiversity while still meeting the land and food needs of citizens. Past work has identified several grassland dominated areas with particularly high plant diversity (Dinerstein et al., 2000).
- *Wetlands, Streams, and Springs*: Protecting the Chihuahuan Desert's fresh water ecosystems means protecting the water resources that sustain them. The saying, 'water is for fighting, whiskey is for drinking,' underscores the scramble for water between countries, states, agriculture and municipalities that is already occurring in the Chihuahuan Desert as the gap between water supply and demand continues to grow. The environment will be the inevitable loser if we are not able to protect and dedicate water for native ecosystems. Recent binational forums have identified a diversity of efforts already underway to improve management and protect flow for native species and riverside citizens (Briggs et al., 2018). But, more needs to be done to learn from these efforts for greater future impact.

In addition, protecting key wetland, stream, and spring complexes need to be a priority. For example, the wetland complexes in Cuatro Ciénegas has long been held up as a conservation priority. Although parts of this critical wetland complex lie within areas managed by CONANP, the battle over water will require strong public-private partnerships to protect water supplies needed to maintain these critical wetlands in the future.

- (6) *Expand Natural Resource Monitoring*: The uncertain future of the integrity of the Chihuahuan Desert ecosystem underscores the importance of generating baselines for monitoring changes in natural resource conditions of priority conservation targets. Conservation biologists, restoration ecologists, natural resources managers, and local land owners need benchmarks for documenting changes in ecosystem structure and function and for defining best management practices. Although much more needs to be done in this regard, there are on-going monitoring efforts that are documenting hydroecologic vital signs amongst diverse priority conservation areas on both sides of the US-Mexico Border. For example, a 149-plot monitoring network has been established that spans the range of key Chihuahuan Desert ecosystems to evaluate the health and integrity of the region based on photography and vegetation surveys (Poulos and Lozano-Cavazos, 2014). But, more needs to be done and greater attention needs to be given to collecting baseline information and monitoring changes in natural resource conditions and the threats that are driving change.

- (7) *Taking Stock of Past Conservation Efforts*: Numerous conservation efforts of different scales have been implemented by a variety of players across the Chihuahuan Desert ecoregion. The results of such efforts provide an opportunity to take stock and learn from them for future benefit. Pertinent questions, include: How well did these efforts meet their conservation/restoration objectives and what were the key lessons learned from them? What types of efforts and/or strategies and/or mix of entities were effective in meeting conservation objectives? Are the results of these efforts viable in the long-term? Selected examples of past or on-going conservation efforts that we should take stock of are highlighted, below:

- *Community-based conservation*: As mentioned previously, numerous community-based efforts have taken place in the Chihuahuan Desert (e.g., Raramuri communities highlighted, above) that offer a wealth of experience on involving municipalities, Ejidos, local communities, and the agricultural sector in conservation efforts that produces win-wins for people and the environment.
- *Restoration of RGB riverine ecosystems*: Key lessons learned from collaborative, binational work to bring back aquatic and riparian habitat along the RGB, include the importance of establishing: (i) Strong binational working relationships; (ii) Public-private partnerships; (iv) A mix of near-term tangible conservation objectives while longer term (more difficult) objectives are being pursued. Lessons learned from these initiatives are critical to protecting and bringing back freshwater ecosystems throughout the Chihuahuan Desert.
- *Work with ranchers and farmers*—On-going conservation work with both of these sectors demonstrates how important their involvement is to protecting the natural resources of the Chihuahuan Desert. Working with ranchers to improve livestock management, slow water and soil runoff, enhance recharge is central to improving grassland conditions in many parts of the Chihuahuan Desert. Working with farmers (as well as water managers) to conserve water and improve the flexibility of water management will be central to protecting drops for native freshwater ecosystems as well as the livelihoods of Chihuahuan Desert citizens.

- (8) Share the Good News and Keep the Momentum Going: Although the people and the natural resources of the Chihuahuan Desert face many challenges, there is much good news in the form successful conservation projects, partnerships, and binational initiatives. This 'good news' needs to be shared more broadly both within and outside the Chihuahuan Desert. Three examples of efforts conducted to enhance communication, coordination and collaboration toward key conservation goals in the Chihuahuan Desert are highlighted, below:
- A binational forum on water scarcity in the Rio Grande/Bravo basin, which took place in El Paso in 2017, brought together municipalities, farmers, scientists, natural resource and water experts, conservationists, water and land managers, and community leaders to identify strategies to address water scarcity. Priorities and next steps were identified (Briggs et al., 2018);
 - The International Boundary Water Commission and its sister agency in Mexico, la Comisión Internacional de Límites y Agua (CILA), routinely hold binational forums on water distribution and management as it relates to the water treaties between the U.S. and Mexico. These forums provide excellent opportunities to identify and move forward on solutions to water scarcity;
 - The Rio Grande/Bravo Climate Impacts & Outlook ('The Outlook') monthly newsletter that provides timely climate, weather, and impacts information to stakeholders, researchers, and other interested parties in the Rio Grande/Bravo Basin region of New Mexico, Texas, and Mexico. The Outlook is a product of the North American Climate Services Partnership (NACSP)—an innovative trilateral partnership between the U.S., Mexico and Canada.

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Biodiversity of Perennial Vegetation in the Desert Regions of Baja California and Baja California Sur, Mexico

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Abstract

The desert regions of central and southern Baja California, Mexico, are a subdivision of the Sonoran Desert, and this region has many special characteristics that make it unique in the world's deserts. Over a period of decades, the perennial vegetation of this desert region was mapped at an approximate scale of 5 km. The Baja peninsula has at least three general climate zones that affect the species composition of perennial vegetation. In Baja California (Norte), most of the precipitation occurs in winter, particularly west of the peninsular divide. This zone has vegetation assemblages with affinities to California chaparral. In Baja California Sur, summer precipitation, particularly related to tropical cyclones, prevails, and vegetation affinities to the Sonoran Desert are more apparent, particularly in the prevalence of leguminous trees. Mid-peninsula, and west of the peninsular divide, summer fog offers cooling and moisture to perennial vegetation. The maximum biodiversity of cacti and succulents was found in an area where the zones of predominantly winter rainfall, predominantly summer rainfall, and summer fog intersected. This zone could be unstable in the face of future climate change, particularly the incidence of summer fog in the desert areas.

Introduction

Biodiversity of perennial vegetation, and particularly of cacti and succulent, is important for many reasons to scientists and land managers in the deserts of the Western Hemisphere. Understanding where high biodiversity occurs is crucial to management plans as well as understanding the conditions under which these interesting species grow. Baja California, México (Fig. 1), has long been known as a biodiversity hotspot for cacti and succulent plants in North America (Rebman, 2001). Joseph (1985) referred to Cerro Colorado, a volcanic mountain east of San Ignacio (Fig. 2), as "Succulent Hill" because of the large number of species that occur there. According to Dimmitt et al. (2003, 2005), Cerro Colorado had the highest biodiversity of cacti and succulent plants in the Sonoran Desert and therefore presumably in North America.

The desert region of Baja California is segregated by a complex topography, the highlight of which is the peninsular divide, the mountain range that traverses the peninsula, generally occurring in its center (Fig. 1). The deserts south of Mexicali and east of the peninsular divide are considered a southerly extension of the Colorado Desert of southern California (referred to as the Lower Colorado Desert in Rebman and Roberts, 2012). Roughly south of San Quintín and west of the peninsular divide, extending to about the border with Baja California Sur, is the Central Desert, the middle of which is dominated by the Valle de los Cirios Biosphere Preserve. The Vizcaino Peninsula, from Bahía de los Tortugas on the west to San Ignacio on the east and southeast of the peninsular divide, has the Vizcaino Desert (Rebman and Roberts, 2012). The broad lowlands on the west coast around Ciudad Insurgentes are known as the Magdalena Plains, whereas east of the peninsular divide is the Central Gulf Coast region. Finally, the Cape Lowlands surround the Sierra la Laguna in the cape region between La Paz and Cabo San Lucas (Fig. 1). In slightly broader terms, the northern

* Deceased.

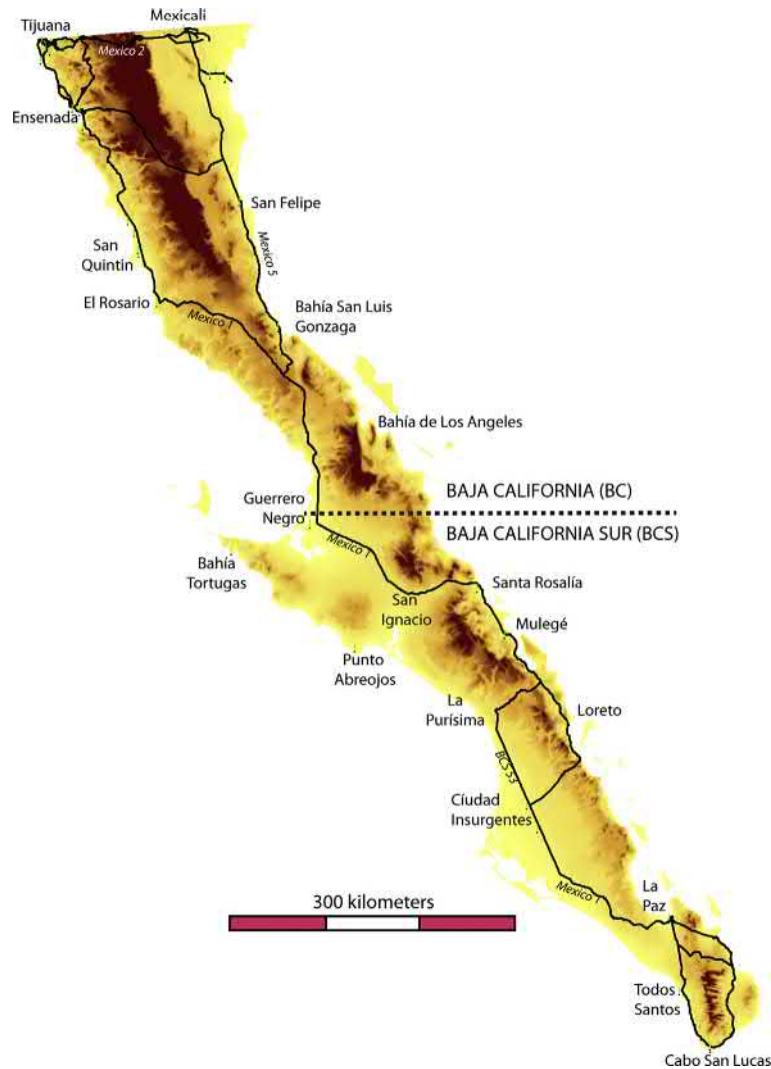


Fig. 1 Map of the Baja California peninsula showing major towns and the two states of Baja California (Norte) and Baja California Sur.

desert regions of Baja California have affinities to the California chaparral and Mojave Desert, whereas the southern desert regions have affinities to the Sonoran Desert and tropical deciduous forests of the western Mexican mainland.

As is the case in many deserts, the available floras are typically incomplete. [Wiggins \(1980\)](#) is the only flora with a mostly complete coverage at the time of publication. [Rebman and Roberts \(2012\)](#) discusses many common species in lay terms and, in some ways, is the most complete flora available for perennial vegetation but it lacks treatment of annuals and biennials, which are extremely important in the winter-rainfall regions of the northern peninsula. [Turner et al. \(1995\)](#) has considerable ecological detail and biogeography on common perennial species but is incomplete with respect to many uncommon perennials and all annuals and biennials.

Many investigators have discussed species distributions and biodiversity in Baja California. [Turner et al. \(1995\)](#) mapped many perennial plant, including cacti and succulents, in the Sonoran Desert, including Baja California. [Webb et al. \(2014\)](#) extended the work of [Turner et al. \(1995\)](#) by more accurately mapping the distribution of cirio (*Fouquieria columnaris*) in Baja California. Following [Gentry \(1978, 1982\)](#), [Webb and Starr \(2015\)](#) revised the genus *Agave* in Baja California and provided more accurate distribution maps to those given in Gentry's seminal work. Inspired by [Joseph \(1985\)](#) and [Dimmitt et al. \(2003, 2005\)](#), and extending the work of [Turner et al. \(1995\)](#) and [Webb and Turner \(2015\)](#) used higher spatial resolution mapping to evaluate areas of maximum biodiversity of cacti and succulent plants on the peninsula. Here, we revisit the work of [Webb and Turner \(2015\)](#) and also discuss the spatial biodiversity of non-succulent perennial vegetation.

Methods Used for Mapping Perennial Vegetation

[Webb and Turner \(2015\)](#) discuss the techniques they used to map perennial vegetation in Baja California. Whereas [Turner et al. \(1995\)](#) used an irregular grid spacing of approximately 8 km and lumped their data into blocks of 0.1° of latitude and longitude,



Fig. 2 Aerial view of Cerro Colorado, a volcanic hill east of San Ignacio, Baja California Sur, looking southwest towards the Picachos de Santa Clara in the center distance. Joseph (1985) referred to this locality as “Succulent Hill,” and Dimmitt et al. (2003, 2005) referred to this locality – the entire hill as well as some of the terrain off to the right – as having the highest succulent plant and cacti biodiversity in the Sonoran Desert.

Webb and Turner (2015) documented plant lists at approximately 3–5 km spacing with no data lumping. Although the same region was traversed, an improved network of roads and trails allowed greater access to the landscape and therefore more data. Webb and Turner (2015) had less resolution in southern Baja California Sur (Fig. 1), where the Sonoran Desert transitions into a thorn scrub in the Cape Region, because of extensive agricultural clearing and more difficult terrain in the Sierra de la Giganta. Most of the sampling points were north of the Llano de Magdalena around Ciudad Insurgentes (Fig. 1). Webb and Turner (2015) assembled a data set of 1573 observation points, each of which represented all species documented in an idealized area of 100-m radius with a measurement time of 0.5 to 1.0 h. Additional details are given in Webb and Turner (2015).

Biodiversity is the number of specific types of organisms per unit area. Because it has units of density, rules are required to define an area for comparison, what taxa are included, and the amount of time expended in the search for those taxa. Biodiversity is expected to increase logarithmically with both increasing area and increasing time expenditure; in other words, the rate of biodiversity increase slows as more area is added and as more time is used searching for species. Dimmitt et al. (2003) reported spending several days over multiple trips scouring all of Cerro Colorado, which they estimated had an area of 11 km². They found 44 species in that area over that time, including non-native species and some putative hybrids; in our smaller area and shorter acquisition time, we found 22 taxa.

Categorization of Taxa

Our analysis of biodiversity used rules based on generally accepted taxonomy of species, subspecies, and varieties of cacti and other succulent plants in Baja California (e.g., Rebman and Roberts, 2012). Wilder et al. (2008) discussed biodiversity in the islands on the Sonoran side of the Gulf of California and found that 16% of the perennial flora was comprised of succulent plants in the three categories of xerophytic succulents, semisucculents, and halophytic succulents. We chose a modified approach using the three categories of cacti, succulents, and other “species of interest,” as well as non-succulent perennial vegetation grouped more broadly.

Of 701 total perennial plant taxa that we mapped, 173 taxa (25%) were categorized into cacti, succulents, and other species. Wilder et al. (2008) included halophytes, but in Baja California succulent species within the Chenopodiaceae are not significant with distance from dry lakes, arroyos, or the coastlines. Taxa within the Cactaceae are the easiest group to define. Unlike Dimmitt et al. (2003), we did not attempt to categorize hybrids within the genera *Ferocactus* or *Cylindropuntia* but instead placed any unusual-looking individuals within the species that they most resembled. The definition of succulent plants is more complex. True succulents (e.g., *Euphorbia misera*, *Pedilanthus macrocarpa*) are easily categorized, but other species, such as *Acalypha californica*, are leaf succulents at best. Trees were typically classified as nonsucculents (e.g. legumes) or hemisucculents (Turner et al., 1995). Even though they were included in our species lists, we did not include non-native succulent species. A total of 72 taxa are included in the succulent category.

What is included within the category of “Other Species” is subject to debate, and we generally followed the definitions within Turner et al. (1995), Wilder et al. (2008), and Dimmitt et al. (2003) in establishing this group. For example, *Ficus petiolaris* is included within this group, as are the native palms (*Brahea armata*, *Washingtonia filifera*). The genus *Fouquieria* also is included

here, including *F. columnaris* (the iconic cirio), for reasons discussed in Webb et al. (2014); also see Nilsen et al. (1990) and Carlquist (2001). We had a total of 16 taxa in the “Other Species” category.

Because non-succulent species are rather numerous, we choose not to differentiate them in terms of life form other than to segregate leguminous trees from the remainder. We therefore discuss the biogeography of cacti and succulents with additional discussion of total species biogeography and the distribution of leguminous trees.

Biogeography of the Desert Vegetation in Baja California

Distribution of Agaves

Agaves are a major element of the succulent flora in Baja California, and their distribution is uneven along the peninsula. Webb and Starr (2015) revised the genus *Agave* in Baja California, including the two new species of *Agave turneri* (Webb and Salazar-Ceseña, 2011) and *A. azurea* (Webb and Starr, 2014). Webb and Starr (2015) mapped 23 taxa with 22 endemics and presented maps depicting the species distribution and the relationship among them on the peninsula. Several species are narrow endemics; for example, *Agave gigantensis* is restricted in its distribution to several mesas in the northern Sierra de la Giganta (Figs. 1 and 3), *A. azurea* only occurs in the Picachos de Santa Clara on the Vizcaino Peninsula (Fig. 4), and *A. turneri* only occurs in the Sierra Cucupá in north-eastern Baja California.

Two groups of species with very different ecological characteristics are important to biogeography in Baja California. The *Agave sobria* complex, which extends from the northern Sierra de la Giganta to the Cape region and sea level to approximately 1500 m, is primarily in the summer rainfall area outside of the fog-influenced area. As many as five forms of *A. sobria* occur, and some of these could be new species or subspecies. The *Agave shawii* complex of *A. shawii* ssp. *goldmaniana* and *A. shawii* ssp. *shawii* are distributed west of the peninsular divide. *Agave shawii* ssp. *shawii* occurs in the California chaparral in the coastal fog belt from the US-Mexico border to El Rosario (Fig. 1). *Agave shawii* ssp. *goldmaniana* occurs primarily in the region of summer fog, although inland from the coast, from El Rosario to the border with Baja California Sur, and is very common near Punta Prieta (Figs. 5 and 6). Neither species depends upon summer rainfall, and both could be sensitive to climate change that involves reduction in summer fog.

Ocotillos

Four of the eleven species of ocotillo (*Fouquieria* sp., Henrickson, 1972) occur in Baja California. Three species (*F. splendens*, *F. diguetii*, and *F. burragei*) have wand-like stems with only a short trunk. *Fouquieria splendens* is widespread in the Sonoran Desert of the United States and Mexico, and in Baja California it mostly occurs in the winter-rainfall areas of Baja California (Norte).



Fig. 3 This view to the southeast from the summit of Cerro el Potrero shows an arroyo leading to the Gulf of California in the northern Sierra de la Giganta in Baja California Sur. This region of predominantly summer rainfall has lower floral biodiversity, in part because of climate and because of the minimal soil in this volcanic terrain. Palo adán (*Fouquieria diguetii*) and maguey (*Agave gigantensis*) appear in the foreground of this view.



Fig. 4 This view shows Cerro del Gato in the Picachos de Santa Clara on the southern Vizcaino Peninsula in Baja California Sur. This site, the type locality for a new species of maguey (*Agave azurea*) has 19 species of cacti and other succulent plants, including red-flowered elephant tree (*Pachycormus discolor* ssp. *veatcheana*) in the midground, and chollas (*Cylindropuntia cholla* and *C. alcahes*) throughout the view. This region has frequent summer fog and rainfall, but its low elevation and isolation by the surrounding sandy plains of the Vizcaino Desert create lower biodiversity of cacti and succulent plants compared to more northerly and easterly sites.



Fig. 5 In the plains to the southeast of Punta Prieta, Baja California Norte, biodiversity is relatively low despite numerous endemic and iconic species. This view shows elephant tree (*Pachycormus discolor*) in the right midground and datillio (*Yucca valida*) in the left foreground to background. These species are most common in the winter-rainfall regions of Baja California.

Beginning in southern Baja California (Norte), and extending to the Cape Region (**Fig. 1**), *Fouquieria diguetii* is widespread in the desert vegetation and has limited overlap with *F. splendens* in the Valle de los Cirios. *Fouquieria burragei* is a narrow endemic in north-eastern Baja California Sur.

The cirio (*Fouquieria columnaris*) is an iconic species of the northern deserts of the Baja California peninsula in Mexico (**Fig. 7**). Cirio populations measured in the northern part of its range appear to be declining, and the maximum longevity of this species is about 300–400 years (Bullock et al., 2005; Escoto-Rodríguez and Bullock, 2002). Webb and Turner (2015) found that cirio ranges



Fig. 6 Although the area between Punta Prieta and El Crucero in Valle de los Cirios appears to be rich in cacti and other succulent plants, the biodiversity of succulent plants and cacti here is only moderate. Large cacti and other succulent plants include senita (*Lophocereus schottii*) at center, cardón (*Pachycereus pringlei*) in the right foreground and midground, elephant tree (*Pachycormus discolor*) at left center, ocotillo (*Fouquieria splendens*) in the right foreground, and chollas (*Cylindropuntia cactus* and *molesta*) throughout the view. Although summer fog commonly occurs here, this is a region of winter rainfall.



Fig. 7 A low hillslope east of El Rosario, Baja California Norte. This hillslope has a dense stand of cirios (*Fouquieria columnaris*) on the hillslope in the background with perennial vegetation typical of winter-rainfall regions in the foreground. Among that vegetation is Mojave yucca (*Yucca schidigera*), left foreground, and creosote bush (*Larrea tridentata*) in the right.

from southeast of San Quintín to Volcán las Tres Vírgenes (**Fig. 1**) and from near sea level to about 1500 m in the mountains of the central peninsular divide. Cirio typically occurs with *F. splendens* and in a few places also with *F. diguetii*, which increases the succulent plant biodiversity of those localities.

Of the ocotillos, cirio is the species most linked to climate. Most populations of grow where there is a strong Pacific maritime influence mostly east of the peninsular divide in the winter-rainfall region. While fog generally is a reliable aspect of summer climate, winter rainfall is highly variable (Bullock, 2003), and summer or early autumn rain is occasional but potentially large during incursions of hurricanes (Clark). Fog moderates temperatures, adds moisture, reduces evapotranspiration, and locally

encourages growth of *Tillandsia recurvata* and lichens on the branches and trunks of cirios. In other parts of its range, fog is unusual, rainfall is biseasonal, and temperatures are high during the summer months.

Biodiversity of Cacti and Succulent Plants

On average, cacti and succulent plants comprised 43% of the perennial vegetation in the 1573 sampling points in Baja California and Baja California Sur. Cardón (*Pachycereus pringlei*) occurred at 901 sites, the most of any species, followed by senita (*Lophocereus* [*Pachycereus*] *schottii*) at 898 sites. One or more cholla species (*Cylindropuntia*) occurred at 1190 localities (76% of sites), making one or more of the chollas the most commonly observed succulent plant or cacti in Baja California. The most commonly observed succulent was torote (*Bursera microphylla*) at 478 sites, followed by lomboy (*Jatropha cinerea*) at 392 sites; one or more species of torote (mostly *B. hindsiana* and *B. microphylla*) were observed at 550 sites (35%). One or more species of cacti and succulents were observed at 43% of the sites, emphasizing the importance of this group of plants to the perennial vegetation of Baja California's deserts.

Webb and Turner (2015) provide a list of the sites with the highest biodiversity of cacti and succulents in Baja California. The highest biodiversity (27) occurred at four sites in either the southern part of Baja California (Norte)—for example, Cañon de San Andrés north of Guerrero Negro—or just south of the border in Baja California Sur—for example, Paso de Oeste de Tres Virgenes (Fig. 8). Jointly, these sites have 49 species and are 55% similar in species composition (Webb and Turner, 2015). The only species common to all four sites are *Bursera microphylla*, bisnaga (*Ferocactus peninsulae* ssp. *vizcainoensis*), *Lophocereus schottii*, pincushion (*Mammillaria dioica*), *Pachycereus pringlei*, lady slippers (*Pedilanthus macrocarpus*), pitaya agria (*Stenocereus gummosus*), and pitaya dulce (*S. thurberi*) (Webb and Turner, 2015).

The area with the highest biodiversity of cacti and other succulent plants (≥ 25) is approximately L-shaped and spans the border on the west side of the peninsular divide in Baja California (Norte) and Baja California Sur (Fig. 9A). Despite claims made by Dimmitt et al. (2003, 2005), Cerro Colorado (Fig. 2) had a more modest 22 taxa. A smaller hill to the west of San Ignacio, Cerro las Mulas (Fig. 9B), had 25 taxa. The western slopes of the Sierra de San Francisco, west of Guerrero Negro and northwest of San Ignacio (Fig. 1), also had high biodiversity of cacti and succulent plants (Fig. 9C and D). Other sites with higher biodiversity occurred west and north of this mountain, indicating that Cerro Colorado is on the southeastern side of the region of high biodiversity in Baja California. Most of the sites are within the western foothills of the peninsular ranges at elevations of 100–600 m; the exceptions are Cañón de San Andrés and Mesa al Sur de San Gregorio Viejo at 33 and 874 m elevation, respectively.

The peninsular divide acts as blocking topography to certain types of storms and has a rain-shadow effect for winter precipitation, particularly in Baja California (Norte). On the other hand, tropical cyclones tracking up the Gulf of California during the summer and fall months may be at least somewhat blocked from tracking west owing to that same peninsular divide. As a result of these combined climatic effects, perennial vegetation generally is lower on the east side of the peninsular divide than on the west, but nonetheless complex vegetation associations occur (Fig. 10).

Although we believe we have found the zone of highest cacti and succulent plant biodiversity in Baja California, individual sites with high biodiversity are likely still undiscovered owing to access difficulties in rugged terrain. Highly diverse assemblages are



Fig. 8 Volcán de Las Tres Virgenes, which has a diverse flora of 27 cacti and other succulent plants on its west side. This view of a recent lava flow shows a mature elephant tree (*Pachycormus discolor*) on the right. This dormant volcano has the most southeasterly locality for cirio (*Fouquieria columnaris*) on its northwesterly flank (Webb et al. 2014).

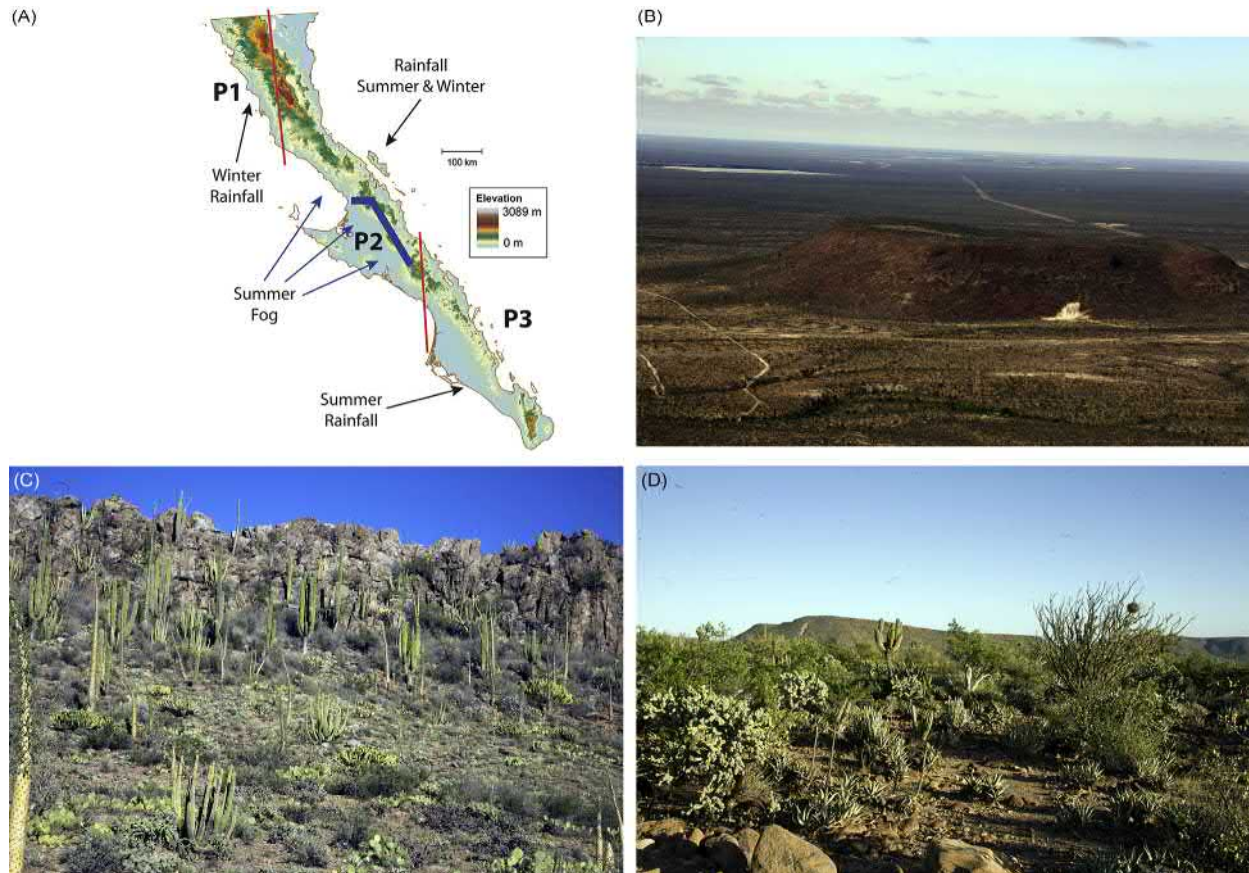


Fig. 9 (A) Climate zones of Baja California, Mexico (following Reyes et al. 1990 and Bullock 2003). The thick blue line represents the approximate zone of high biodiversity of cacti and other succulent plants. Summer fog occurs in most coastal areas of the Pacific Ocean but is most common in the desert areas in the west central part of the peninsula. (B) Aerial view looking west at Cerro Las Mulas, a small volcanic hill west of San Ignacio in Baja California Sur. The southeastern slopes of this hill had 27 species of cacti and other succulents, including some species known only from this locality. In contrast, the sandy plains in the distance have low biodiversity owing to unstable substrates. (C) Hillslopes on the west side of the Sierra de San Francisco have as many as 27 taxa of cacti and succulents, giving this area some of the highest floral biodiversity in Baja California. The plants on this slope include pitaya dulce (*Stenocereus thurberi*) and cardón (*Pachycereus pringlei*) throughout the view; candelabra cactus (*Myrtillocactus cochal*) on the midground slopes, and cirio (*Fouquieria columnaris*) in the left foreground. (D) This view on a mesa north of Miraflores in Baja California Sur shows a typically lush assemblage of cacti and succulents in this high biodiversity region. This mesa, west of the Sierra de San Francisco, typically has summer fog. Maguey (*Agave cerulata* ssp. *subcerulata*) appears in the foreground, cholla (*Cylindropuntia cholla*) appears in the left foreground, and palo adán (*Fouquieria diguetii*) with a ball of tillandsia (*Tillandsia recurvata*) in it appears at left center.

known to occur outside of the L-shaped region we documented (Fig. 9A) owing to the potential for favorable microsites. The Cape Region particularly the foothills of the Sierra la Laguna south of La Paz (Fig. 1), have biodiversity hotspots. We found 25 species of cacti and other succulent plants, including four species of *Bursera*, in a small area near Cabo Pulmo on the Gulf of California (Fig. 11). In this region of summer rainfall, particularly from tropical cyclones, the desert transitions into a tropical deciduous forest, and here the potential for high biodiversity switches from the west side of the peninsula to the drier east coast.

Substrate plays a complex but important role in the biodiversity of cacti and succulent plants. All of the sites with high biodiversity are in areas of complex geomorphology with mixtures of rocky substrate and bedrock. Sites with unstable substrates, such as sand dunes, playa margins, sandy plains, and arroyo margins, had low biodiversity. The site west of Volcán de Las Tres Virgenes (Fig. 8), is in a narrow canyon. Sites on the west slope of the Sierra de San Francisco (Fig. 9D) and north of Miraflores (Fig. 9C) are sloping with rocky substrate and bedrock ledges. At Cerro las Mulas (Fig. 9B), high biodiversity occurs where the toe of a volcanic hill transitions into a sandy plain. However, in a similar but more isolated valley to the south in the Picachos de Santa Clara (Fig. 4), biodiversity is lower. Biodiversity also is lower on homogeneous geomorphic surfaces, particularly sand sheets characteristic of the Vizcaino Desert north of Punta Prieta (Figs. 5 and 6).

Riparian Vegetation

Many riparian vegetation areas in Baja California are typical of what occurs in the Sonoran Desert of Arizona and Sonora, with numerous leguminous trees—mesquite (*Prosopis glandulosa*), palo verde (*Parkinsonia* sp.), and palo blanco (*Lysiloma candida*)—



Fig. 10 In Baja California Norte, east of the peninsular divide at Cuesta de la Ley, biodiversity remains relatively low despite some summer rainfall influence from the Gulf of California. In this view, lady's slipper (*Pedilanthus macrocarpus*) appear in the right and left foreground, torote (*Bursera microphylla*) is at the base of a cardón (*Pachycereus pringlei*) in the left foreground, and cholla (*Cylindropuntia alcahes*) occurs at center.



Fig. 11 Inland from Cabo Pulmo, on the Gulf of California coast southeast of La Paz, cacti and succulent plant biodiversity is high despite the fact that this is a summer rainfall area with little fog influence. Among the many species here are maguey (*Agave aurea*), four species of torote (*Bursera* sp.), four species of cholla (*Cylindropuntia* sp.), and pitaya dulce (*Stenocereus thurberi*).

lining ephemeral channels (Fig. 12). The dense overstory provides habitat for numerous other woody species, particularly wolfberry (*Lycium* sp.), graythorn (*Ziziphus obtusifolia*), and hackberry (*Celtis* sp.). What is unique about Baja California is the abundance of water, either in cienegas or perennial streams, and these reaches can support palms (Fig. 13). Besides the famous date palm orchards near towns such as San Ignacio, native palms occur in many places, most famously at Cataviña east of El Rosario (Fig. 1). Despite the high biomass of perennial vegetation, as well as the large ecosystem services provided by these riparian areas, their biodiversity—at least when the riparian zone is considered in isolation—is low. As will be shown, this changes in settings of riparian vegetation within a narrow bedrock canyon, particularly where summer fog is prevalent (see below).



Fig. 12 This view shows the central Sierra de la Gigante in Baja California Sur in the background and dense vegetation in Arroyo Agua Verde near the Gulf of California. The trees with white bark are palo blanco (*Lysiloma candida*), an endemic to Baja California, and several other leguminous trees and shrubs occur in this view with few cacti and succulents present.



Fig. 13 Palms, in this case California fan palm (*Washingtonia filifera*) and Mexican blue palm (*Brahea armata*), are locally common in areas with dependable water supply. Despite the unusual species present and the riparian setting, this site has low floral biodiversity.

Perennial Vegetation

As previously noted, the two most common perennial species we observed at sites in Baja California were cardón and senita, observed at 901 and 898 sites, respectively, or 57% of the sampling points. Creosote bush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*) were the most frequently encountered species, observed at 836 and 674 sites, respectively (53% and 43%). Of the 20 species most frequently encountered at sites in Baja California, half were cacti and succulents and the other half were non-succulents.



Fig. 14 At the northern edge of the desert in Baja California Norte, numerous species are crowded together in this region of highest winter rainfall in a transition to more chaparral vegetation to the north. Here, bracketing this laurel sumac (*Malosma laurina*) and cholla (*Cylindropuntia cholla*); pitaya agria (*Stenocereus gummosus*) occurs at center, and datillio (*Yucca valida*) and cardón (*Pachycereus pringlei*) occur in the right background.

Total perennial vegetation generally was highest at sites north of the boundary between Baja California (Norte) and Baja California Sur (Fig. 1). The highest number of perennial species observed in our sampling was 66 at Cañon de San Andrés and a mesa southeast of San Borja, in the zone of mixed summer and winter precipitation with summer fog (Fig. 9A), suggesting that biodiversity of perennial vegetation is somewhat controlled by the number of cacti and succulents observed. However, many of the sites are in diverse topography where ephemeral arroyos pass through bedrock canyons, such as Cañon de San Andrés. Other sites with high biodiversity of perennial vegetation are at higher elevation and represent a transition between the desert and the chaparral in the north (Fig. 14) or mesa tops at about the same elevation as the summer fog belt (Fig. 9C and D).

A total of 23 sites, mostly in Baja California (Norte) and mostly in middle-elevation sites, had 50 or more species of perennial plants. Unlike the high biodiversity of cacti and succulent plants, these sites have little in common geographically and are spread over a large range from west of Volcán de Las Tres Vírgenes (Fig. 8) to the northern edge of the desert northeast of El Rosario (Fig. 1). All of these sites are west of the peninsular divide. Low biodiversity sites, excluding barren areas, generally have 2–5 species and are much easier to characterize. Sandy plains, such as the Vizcaino Desert east of Guerrero Negro, tend to be dominated by halophytes such as Palmer's seaheath (*Frankenia palmeri*), and these sites only have 2–5 perennial species in general.

Climate and Perennial Plant Biodiversity

The standard explanation for high biodiversity, and especially high endemism, is geographic isolation over geologic time. This explanation might be useful for explaining unique plant assemblages over the entire peninsula of Baja California, but is not useful for discussing the geography of perennial plant biodiversity. In the desert regions of Baja California, climate and topography interact to produce biodiversity hotspots or to create low biodiversity zones. What is unique about this desert is the influence of summer fog and its influence on the cacti and succulent distribution.

The climate of Baja California is extremely variable seasonally and interannually (Bullock, 2003), which severely limits analysis that might link climatic and biodiversity. In general, the zone of high biodiversity of cacti and succulent plants occurs where precipitation is bimodal (Reyes Coca et al., 1990) and summer fog helps to increase relative humidity in summer and cool the desert. Proximity to the Pacific Ocean and on-shore winds are the most important characteristics of climate in the zone of high biodiversity. Summer fog is uncommon on the eastern side of the trans-peninsular ranges and the Gulf of California. The interaction of geography and fog, combined with two seasons of precipitation, determines where high biodiversity is to be expected.

The geography of persistent fog is difficult, perhaps even impossible, to quantify for Baja California, but in general the top of the maritime clouds in the central peninsula appears to be at an elevation of about 500 m, with dense fog occurring regularly at altitudes of about 250–500 m. This altitude ranges varies widely along the peninsula and through the seasons, but generally maritime-influenced species adapted to high humidity, such as lichens and the epiphytic tillandsia (*Tillandsia recurvata*), occur within this elevation band. The upper 500-m limit of maritime fog irregularly occurs in the foothills of the peninsular divide, creating

innumerable microclimates sustaining high biodiversity. Unlike along the coast, fog in the foothills of the peninsular divide may dissipate early in the day, modulating temperatures and increasing humidity but not greatly reducing solar insolation.

Although outliers exist, most high-biodiversity sites are between 300 and 600 m elevation on west- or southwest-facing sites where fog can accumulate in the morning hours on a regular basis. Cacti and succulent plant biodiversity at the sites of highest biodiversity are strongly influenced by fog. *Myrtillocactus cochal* and *Opuntia* sp., which generally occur in areas influenced by summer fog far to the north of the desert regions of Baja California, are notable at the high biodiversity sites (Webb and Turner, 2015). The presence of *Cochemia maritima* and *Echinocereus maritima*, as well as two *Dudleya* taxa, also attests to the maritime influence.

Species strongly affected by maritime fog occur with other desert species with wider climatic tolerances, such as *Pachycereus pringlei*, *Lophocereus schottii*, and the *Cylindropuntia*. Dimmitt et al. (2003, 2005) discussed how Cerro Colorado had a mixture of floral elements that represented a narrow local environment with species from both the northern and southern deserts. High biodiversity in essence is chance on either the scale we used or that of Dimmitt et al. (2003, 2005); random occurrences of taxa whose distributional centers lie long distances away aggregate to create highly diverse assemblages of cacti and other succulents.

Long-Term Threats to the Desert Vegetation of Baja California

Outside of the urban centers of Tijuana, Mexicali, and La Paz (Fig. 1), Baja California largely has largely a pastoral economy based on livestock grazing with some major centers of agricultural production. These centers—especially near San Quintín and Ciudad Insurgentes (Fig. 1)—are one of the biggest threats to the desert regions. These centers rely on groundwater pumping for irrigation and also benefit from summer fog to lower temperatures and evapotranspiration. It is uncertain whether large-scale agriculture would encroach further into the desert regions.

Although its climate historically has been highly variable, climate change is expected to strongly affect the peninsula. How climate change will alter cacti and succulent plant biography, or perennial plant distributions in general, is largely speculative. Within the extremely variable data (Bullock, 2003), it would appear that winter rainfall has decreased in the last few decades. Continued decrease could affect species composition at the northern edges of the desert (e.g., Fig. 14) and upper elevation limits of the desert along the peninsular divide. Information on the incidence of summer fog is lacking, but anecdotal information suggests that fog has also decreased, leading to higher summer temperatures and solar insolation in some areas. Incursions of tropical cyclones, especially hurricanes, are too episodic to reveal trends in their effects on summer rainfall and perennial plant biodiversity.

Climatic change may have a wide range of species-specific effects instead of changes at the assemblage level. Webb et al. (2014), discussing possible threats to the iconic cirio, suggested that its ability to grow over an extremely wide range of climatic conditions suggests that cirio may not be as heavily impacted as other endemic species with more-specific climatic requirements. Cardón is another species unlikely to be severely impacted by climate change. Species highly adapted to the fog-influenced coastal areas of Baja California, such as *Myrtillocactus*, *Dudleya*, some *Cochemia* and *Echinocereus*, and, of course, lichens and tillandsia, are likely to be the most negatively affected species over the short term.

Summary

The desert regions of Baja California, Mexico, are a subdivision of the Sonoran Desert, and this subdivision is noteworthy in particular for its abundance of cacti and succulent plants. We made species lists at 1573 points in the desert regions, mostly north of the Llano de Magdalena in Baja California Sur. Of 701 total perennial plant taxa that we mapped, 173 taxa (25%) were categorized into cacti, succulents, and other species and 43% of the total perennial vegetation at all sites were in this category. This vividly illustrates the importance of cacti and succulent plants in the flora of Baja California's deserts.

The biodiversity of perennial vegetation—particularly cacti and succulent plants—is controlled by the complex climate of the peninsula. Areas where only winter or only summer precipitation occur have lower biodiversity in general than does the area where summer and winter precipitation occur and particularly where summer fog cools the landscape. Climate change that shifts the summer fog belt could have a serious impact on biogeography of the peninsula. Other pressures on the desert landscape of Baja California include agricultural clearing in several important areas, urban development, and the possible decrease in winter precipitation in Baja California (Norte).

Acknowledgments

A large number of scientists and volunteers helped to collect plant lists in our company between 2001 and 2015. We especially thank Mario Salazar-Ceseña for his numerous contributions to this work, especially the collection of plant lists in the Sierra la Libertad.

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The Gibson, Great Sandy, and Little Sandy Deserts of Australia

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Abstract

The Great Sandy Desert (394,900 km²), Gibson Desert (156,300 km²), and Little Sandy Desert (110,900 km²) are three important desert regions within the much larger Australian Arid Zone which covers ~70% of the continent. The three adjoining deserts are characterized by very hot temperatures and low rainfall (averaging 250–350 mm per annum) which is highly variable from year to year, and strongly seasonal (summer-dominant). Sand-dune systems, sandstone mesas and rocky plains dominant the landscapes; the vast majority of these (92% by area) being covered by hummock grasslands (*Triodia* spp.) with scattered eucalypt trees (*Eucalyptus* and *Corymbia* spp.) and *Acacia* shrubs. Plant diversity is relatively high for deserts (over 2000 plant taxa known), with only two threatened plant species recognized to date. Diversity of reptiles and birds is also relatively high, but many small- to medium-sized mammals have been lost from these deserts or are near extinction. Despite the almost complete lack of vegetation clearing across these deserts, and the mostly good to excellent condition of the vegetation, there are still insidious threats to be managed, including widespread wildfires, feral animals and uncontrolled grazing, and weeds. Levels of protected land are well above-average globally (covering some 43% of the area), but are relatively low in terms of formal conservation estate (for instance only 7% for the Great Sandy Desert). Most (85%) of the protected lands across the three deserts comprise Indigenous Protected Areas which provides a means to effectively manage the threats and safeguard natural assets over large expanses of these deserts provided there is adequate and ongoing support given to the Aboriginal custodians.

Location and Introduction

Three large adjoining deserts spread from near the coast of north-west Western Australia to central Australia: the aptly named Great Sandy Desert, the remote Gibson Desert and the Little Sandy Desert (Fig. 1). In many respects these are classic Australian deserts of red sand dunes and rocky gibber plains covered by hummock grasses and sparse white-barked eucalypts and acacia shrubs. The boundaries used to delineate these deserts in this review are the bioregions of the same names (Fig. 1), as defined by Thackway and Cresswell (1997). Of these, the Great Sandy Desert (GSD) bioregion is by far the largest covering some 394,900 km², followed by Gibson Desert (GD; 156,300 km²) and Little Sandy Desert (LSD; 110,900 km²). The Great Victoria Desert, which is reviewed in this volume, lies immediately to the south (Fig. 1).

The three deserts mostly correspond to series of old sedimentary basins which have experienced occasional inundation by sea and extensive in-fill by sediments over millions of years, much of which have been consolidated into sandstone and other sedimentary rocks. Today they feature extensive sand dune systems and isolated rises and ranges with vegetation mostly comprising hummock grassland and *Acacia*-dominated shrublands. Rainfall is typically higher than deserts on other continents (ranging from 350 mm in the north to 250 mm in the south) but this is offset by extreme variability from year to year and very high

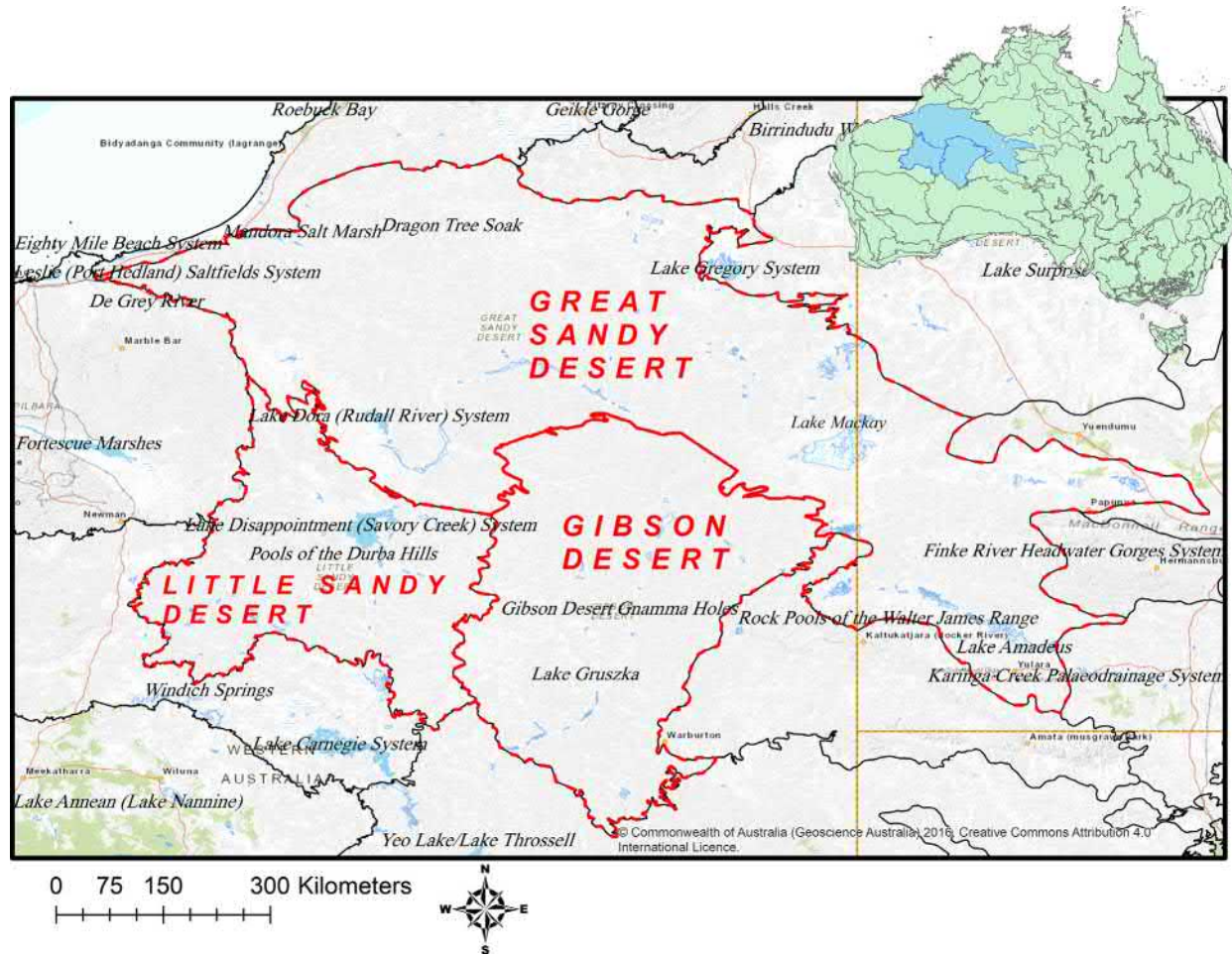


Fig. 1 Map of the three desert bioregions (Great Sandy Desert, Little Sandy Desert, and Gibson Desert) and major biophysical features including towns and geophysical features mentioned in the text. Inset shows Interim Biogeographic Regionalization for Australia (IBRA) regions across Australia with three desert bioregions shaded. Source of data: Department of the Environment (2012). *Interim Biogeographic Regionalisation for Australia*, vol. 7 (IBRA) [ESRI shapefile] Available from: <http://www.environment.gov.au/fed/catalog/main/home.page>.

temperatures and evaporation rates. Consequently the vegetation cover is typically open but not as sparse as many deserts on other continents and large wildfires can occur under the right conditions (Burrows et al., 1991; van Etten and Burrows, 2018).

Biophysical Environment

Current Climate

In contrast to the rest of Australia, the region has very sparse and temporally limited meteorological data with only four active weather stations either within or immediately adjacent to these deserts (Table 1). Climate graphs showing monthly averages of rainfall and maximum temperature are presented at Fig. 2, with annual averages shown in Table 1. Interpolation of these and other meteorological data show that mean annual rainfall is around 350 mm in the northern part of the GSD and broadly declines with distance south to an average of around 250 mm in the southern GD and LSD (Table 1; Beard and Webb, 1974). Median rainfall is some 30–40 mm lower than mean rainfall, mainly because a small number of extreme rainfall events (typically generated by tropical cyclones which regularly develop off the north-west coast of Australia and occasionally cross into these deserts) has skewed the mean rainfall. These cyclonic rainfall episodes can be responsible for 100–300 mm of rain over the course of a few days and are a major contributor to the very high to extreme interannual rainfall variability of these deserts (Table 1; van Etten, 2009). There is also strong evidence that rainfall in recent decades has been above long-term average (O'Donnell et al., 2015).

Rainfall is clearly biased to summer-autumn and again tropical cyclones (or remains thereof) play an important role here, but there is also some monsoonal influence especially in the northern part of the GSD (for instance, rainfall at Balgo is much more summer dominated than other weather station sites; Fig. 2), but otherwise thunderstorms are responsible for much of the rain in summer and autumn. Rainfall is possible in each month, but spring (August to October) are typically very dry (Fig. 2).

Table 1 Average and variability in rainfall at four available meteorological stations in or adjacent to the three desert regions.

Rainfall variable	Balgo	Telfer	Walungurru	Carnegie
No. of years	68	45	22	63
Location, region	Tanami Desert, near GSD	Western GSD	WA-NT border, GSD	Gascoyne region, near GD
Mean	356.4	370.9	293.9	242.2
Std dev	172.8	181.8	178.0	122.1
CV	48.5	49.0	60.6	50.4
Median	327.7	331	269.8	229.3
90th percentile	560.7	621.5	487.6	403.2
10th percentile	159.4	179.5	108.4	97.7
VI	1.22	1.34	1.40	1.33

CV, is coefficient of variability; VI, is variability index (calculated by 90th–10th percentile/median).

Data from Bureau of Meteorology, Australia (www.bom.gov.au/climate/data).

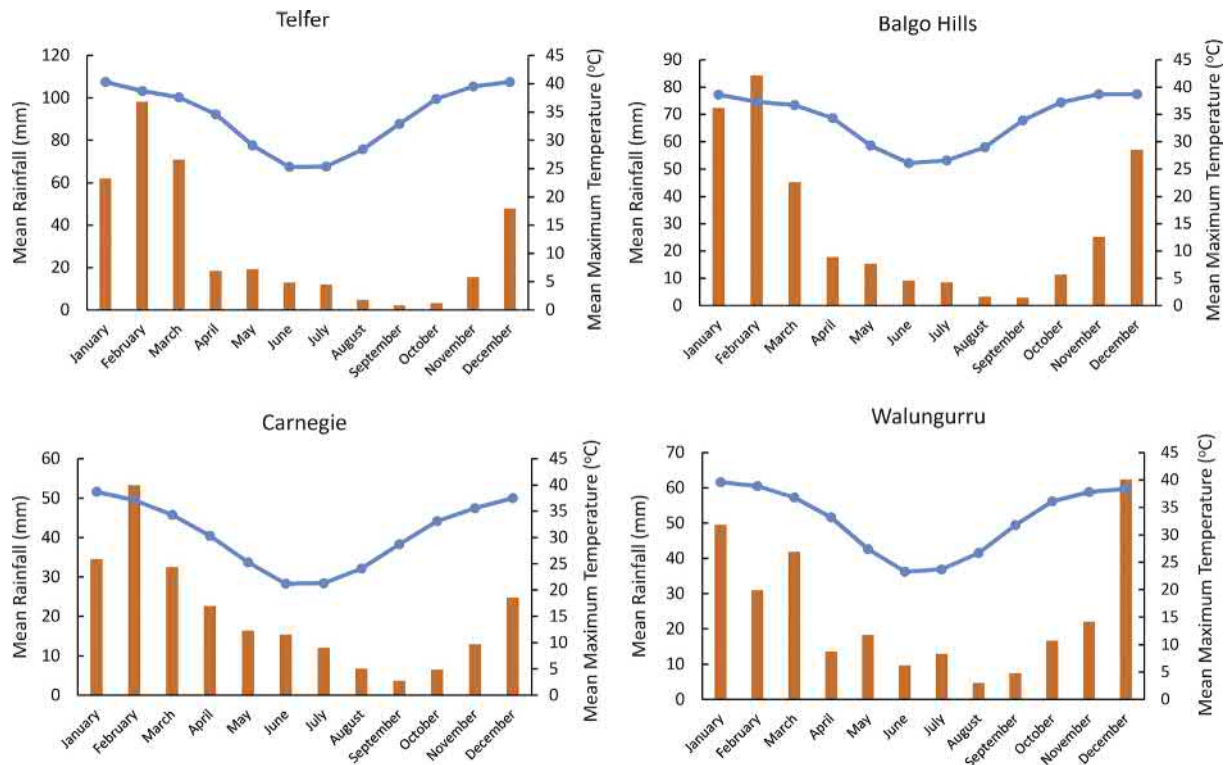


Fig. 2 Monthly means of maximum daily temperature (line) and rainfall (bars) for the four meteorological stations within or immediately adjacent to the three deserts (see Table 2 for locations and annual averages). Graphs constructed by author using data obtained from Bureau of Meteorology, Australia (www.bom.gov.au/climate/data).

Temperatures are typically very hot in summer (January–February daily maxima average almost 40 °C across the three deserts) and are mild in winter (maximum temperature averages 20–25 °C in July; Fig. 2). Occasional frosts can occur in winter away from the coast. Pan evaporation varies from 3600 to 4200 mm per year, which is some 10 times greater than annual rainfall and the highest in Australia (Beard and Webb, 1974).

Climate History

The aridity of the region gradually emerged over millions of years in response to the northward migration of the Australian continent into drier subtropical belts and progressive constriction of the Indonesian Throughflow as the Australian and Asian plates collided, which largely separated Pacific and Indian Ocean circulation and reduced transport of atmospheric moisture across north-west Australia (Christensen et al., 2017). This also corresponded to a time of general global cooling and drying. By the start of the Quaternary Period (~2.4 Ma) the transition from humid to arid climate was complete with seasonal (monsoonal) precipitation

due to orbital forcing now a feature (Pillans, 2018). Characteristic landform features of these desert regions, such as extensive dune fields, salt lakes and restricted drainage, also emerged at this time, although these became more widespread and well developed during glacial periods of the Quaternary (i.e., ice-ages) when the climate was even more arid (Fujioka and Chappell, 2010).

Geology and Landforms

Consistent with being old sedimentary basins, the geomorphology of the three desert regions comprises recent unconsolidated sediment (mostly wind-blown sand dunes and water-shifted alluvia) over thick sedimentary rocks (mostly sandstones). The GSD is dominated by Quaternary red sand dunefields overlying Jurassic and Cretaceous sandstones of the Canning and Amadeus Basins. In places the sandstones form gently undulating laterized uplands. In addition, calcrete and evaporite surfaces associated with occluded palaeo-drainage systems traverse the desert and now feature chains of salt lakes and salt pans (Fig. 1). In contrast, the LSD is dominated by stony hills, low ranges and plains with alluvial deposits in valleys, although the western side has extensive dune fields and sandstone ranges similar to that found in the GSD. The Gibson Desert is mostly covered in fairly uniform and most flat sandy-gravelly sandplain and lateritic “buckshot” gravel plains, with some sandstone mesas (laterized remnants) of again Jurassic and Cretaceous age. Quaternary alluvia associated with palaeo-drainage lines occur across all three deserts (Beard and Webb, 1974).

Vegetation

Major vegetation types for the three deserts were derived from the structural formations and vegetation descriptions of Beard et al. (2013) aided by interpretation from original vegetation maps and reports for the Great Sandy Desert (Beard and Webb, 1974), Pilbara (Beard, 1975), and Great Victoria Desert (Beard, 1974) map sheets. These major types of vegetation are described below (with recognized subtypes) and are mapped in Fig. 3.

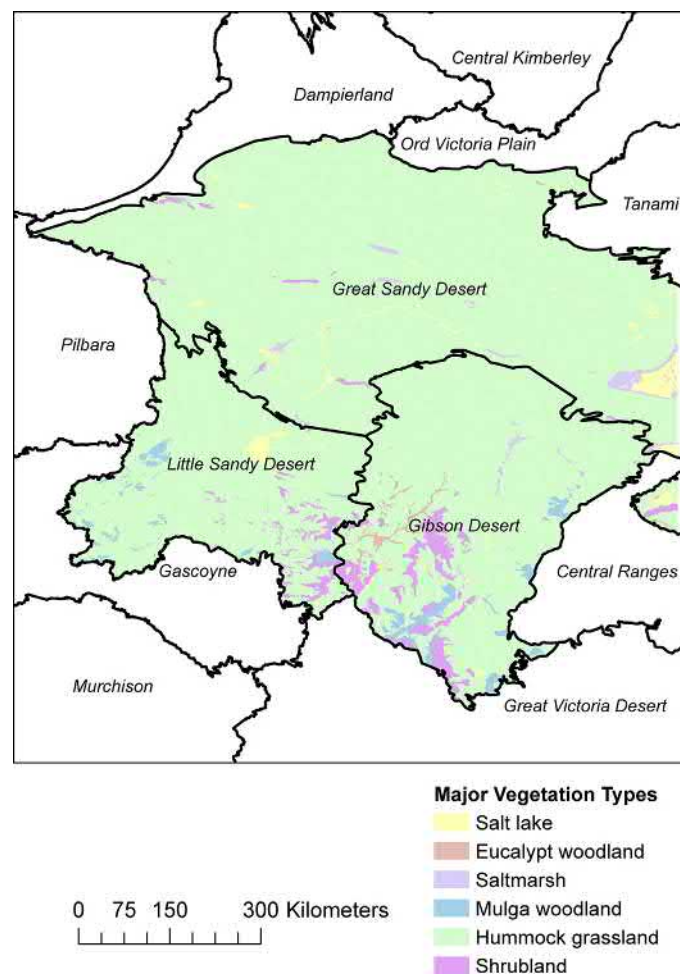


Fig. 3 Map of major vegetation types of the three deserts regions (available for Western Australia only). Map produced by author using data from Beard, J. S., Beeston, G. R., Harvey, J. M., Hopkins, A. J. M. and Shepherd, D. P. (2013). The vegetation of Western Australia at the 1: 3,000,000 scale. *Explanatory memoir, Conservation Science Western Australia* 9, 2013, 1–152.

Hummock grasslands

By far the most widespread vegetation type covering some 92% of the study area is hummock grassland which dominates the sandplains, dunes, and lateritic plains. These grasslands are dominated by the grass genus *Triodia*, commonly known as hummock grasses due to the distinct rounded mounds or “hummocks” these grasses form as they age, which is believed to be a graminoid lifeform unique to arid and semi-arid Australia. The grasses can be quite old (generally forming a ring with bare/dead center when they several decades old) and are colloquially known as “spinifex,” although this name is not preferred here given there is also a grass genus *Spinifex* common to coastal dunes. Sparse to very sparse trees and/or shrubs are common to these grasslands (so they are rarely pure grasslands), and in some situations patches of denser tree/shrub stands can develop to form a landscape mosaic with hummock grassland (but as the latter is typically more widespread in these areas, they are mapped here as hummock grassland). The composition and structure of these trees/shrubs define the subtypes as described below (termed tree or shrub steppe depending on which life-form is the most common emergent of the grasslands):

- (a) Tree steppe of desert walnut (*Owenia reticulata*) and bloodwoods (*Corymbia* spp. such as *C. chippendalei*, *C. opaca*, and *C. aspera*) common on dune systems in the northern part of the GSD;
- (b) Tree steppe of desert oak (*Allocasuarina decaisneana*) on dunes and sandplains of northern GD and eastern GSD;
- (c) Shrub steppe of mallee (various *Eucalyptus* spp. with multistemmed form 1–5 m high) often with sparse *Acacia* shrubs;
- (d) Shrub steppe dominated by *Acacia* spp. of various sizes and density (including *A. aneura* s.l., *A. pachyacra*, *A. ligulata*, *A. maitlandii*, and *A. dictyophleba*), but also *Grevillea* and *Hakea* spp.;
- (e) Shrub steppe of *Aluta maisonneuvei* (Myrtaceae) which develop as thickets of low shrubs within a broader mosaic of hummock grassland which likely develops in response to fire absence (Wright, 2018).

Shrubland

This vegetation type is dominated by shrubs 1–5 m tall with at least 30% cover and an open ground layer mostly comprising annual and perennial bunch grasses and forbs, especially after rain. Shrubland covers 3.1% of the deserts by area with three major subtypes:

- (a) Teatree scrub comprising dense stands of *Melaleuca* (mostly *M. lasiandra* and *M. glomerata*) in claypans of dune swales and adjacent to saltlakes receiving freshwater runoff (nonsaline); mostly found in western GSD;
- (b) Mulga shrubland or scrub dominated by *Acacia aneura* s.l. mixed with other *Acacia* species and commonly occurring on stony hills and plains in the GD (this vegetation is similar to Mulga woodlands as described below but differs in the dominance of shrubs rather than trees);
- (c) Mixed *Acacia* shrubland involving many *Acacia* species, such as *A. pachycarpa*, *A. monticola*, and *A. orthocarpa*, on rocky plains and lateritic outcrops.

Mulga woodland

These are woodlands dominated by mulga *Acacia aneura* s.l. trees (generally single-stemmed and 2–10 m high) predominantly found in southern parts of the LSD and GD (Fig. 3) mostly in alluvial soils of large drainage systems and red loams over hardpans. Mulga woodlands are the most common type of vegetation in the Gascoyne and Murchison bioregions to the south, but comprise only 1.5% by area of the three deserts. Mulga woodland is similar to mulga scrub described above but the latter is generally confined to shallow, rocky soils of uplands where the mulga is stunted and generally multistemmed.

Eucalypt woodland

Along the major ephemeral rivers and other major drainage lines throughout the deserts are fringing woodlands of relatively tall trees with a perennial tussock grass understorey. Common tree species include *Eucalyptus victrix*, *E. camaldulensis* and, occasionally, *Corymbia* species. An uncommon vegetation type (<1% by area).

Saltmarsh

This vegetation types develops around salt lakes and major saline drainage systems and is dominated by halophytes from the Chenopodiaceae family, particularly *Tecticornia* spp. (samphire), but also *Maireana* and *Atriplex* species. A sparse to mid-dense shrub layer of *Acacia* and *Melaleuca* develops at some sites. Comprises only 1.1% of the study area.

Salt lakes

Salt lakes of varying size develop in the lowest parts of landscapes where saline groundwater discharges to surface and salts accumulate via evaporation. Some of the large salt lakes of these deserts include Lake Disappointment and Lake Mackay, both of which occur at the lowest point of internal (endorheic) drainage basins. Salt lakes are predominantly bare but can develop sparse annual plant cover in some circumstances. They cover 1.9% of the study area.

Flora

There are over 2000 plant taxa (formerly described species, subspecies and varieties) known from these three deserts, with the most found in the GSD (1788 plant taxa), followed by LSD (1088 taxa), and Gibson Desert (760 taxa), based on Atlas of Living Australia

(ala.gov.au) records. Of these, only 320 plant taxa occur have been recorded in all three desert bioregions, suggesting reasonably high species turnover across these deserts. Common plant families (and genera) are Fabaceae (*Acacia*, *Senna*, *Swainsona*), Poaceae (*Triodia*, *Eragrostis*, *Eriachne*), Malvaceae (*Sida*, *Hibiscus*, *Corchorus*), Asteraceae (*Rhodanthe*, *Calotis*), Myrtaceae (*Eucalyptus*, *Melaleuca*, *Corymbia*), Chenopodiaceae (*Maireana*, *Tecticornia*, *Sclerolaena*), Scrophulariaceae (*Eremophila*), Goodeniaceae (*Goodenia*, *Scaevola*), and Amaranthaceae (*Ptilotus*). Just 35 alien plant species have been collected from these deserts, which is very low given the size of the area concerned; the most widespread and problematic of these is buffel grass *Cenchrus ciliaris* (syn. *Pennisetum ciliare*) which is known to modify fire regimes and fauna habitat where it dominates (Marshall et al., 2012). The number of collected plant taxa is generally lower compared to other Australian bioregions, but it is likely these deserts have been relatively under-collected given their remoteness and lack of large-scale land/resource development (which tends to facilitate biological surveys).

Just two listed threatened plant species are known from these deserts:

- (1) *Seringia exastia*, commonly known as “fringed fire-bush,” is a short-lived shrub typically only found after fire in hummock grasslands; its known distribution is restricted to north-western GSD and adjacent south Kimberley region and its current status is Critically Endangered under State (WA) and Federal legislation (Wilkins and Whitlock, 2016).
- (2) *Thryptomene wittweri*, a shrub from the family Myrtaceae, is listed as Vulnerable by State and Commonwealth governments; very uncommon and only known from western LSD, and northern Pilbara and Gascoyne bioregions.

In addition to these formally recognized threatened species, there are numerous “Priority” plant taxa, which represents those which are currently rare but poorly known due to inadequate data or survey effort. As of February 2019, there were 103 Priority taxa for these deserts of which 39 are Priority 1 (highest priority for future survey). It is therefore likely that more threatened flora will be identified in the future.

Two State-listed Threatened Ecological Communities (TECs) occur in these deserts: (1) the “Mandora Mounds” are small isolated biotic assemblages of organic springs and mounds of the Mandora Marshes located some 140 km south of Broome on the western edge of the GSD (Halse et al., 2005); and (2) “Dragon Tree Soak” being an classic example of a desert oasis in the western GSD supporting a unique vegetation of dense sedgeland with emergent dragon tree (*Sesbania formosa*) (Fig. 1). Both these TECs are classified as “Endangered” based on IUCN criteria and are mainly threatened by grazing and trampling by feral camels and cattle.

Fauna

These three deserts are noted for their richness of reptile species, particularly skinks (*Ctenotus* and *Lerista*), and also have a rich avian diversity (Pianka, 1981; Reid and Fleming, 1992). Mammal species are far fewer in number with many small- to medium-sized species of mammals having been lost from these deserts since European colonization; several of these are either completely extinct or now restricted to off-shore islands. The extinction of these arid zone mammals is an internationally recognized conservation disaster and is likely to have several interacting causes, including exotic predators (cats and foxes), changes in fire regimes and excessive grazing, particularly within refuge areas (Woinarski et al., 2015).

The main threatened mammals still found in the region (based on IUCN Red List) are the: (1) bilby *Macrotis lagotis* (IUCN: Vulnerable) with the dunefields of the LSD and GSD being the mainstay of its current distribution, which was once much wider (Cramer et al., 2016); and (2) black-footed rock wallaby *Petrogale lateralis* (Vulnerable) found scattered across central Australia including the GSD and GD, where it prefers rocky upland habitat. The region also includes captive populations of the mala or rufous hare wallaby (*Lagorchestes hirsutus*; IUCN: Vulnerable as a species complex) which was once widespread across central Australia but, until recently, persisted in the wild only on islands off the Western Australian coast. The loss has been mainly attributable to predation by cats and foxes. However the extant island populations are recognized as distinct subspecies compared to the mainland ones (Eldridge et al., 2019). A unnamed subspecies from mainland central Australia survived via captive breeding and translocations to safe sites, and has been recently re-introduced into predator-proof exclosures in national parks/reserves in its former range in the eastern GSD (including Uluru-KataTjuta NP, Wattaka NP, Newhaven PNP; Fig. 3). Other at risk mammals include: brush tail mulgara (*Dasymercus hillieri*); the Southern marsupial mole (*Notoryctes typhlops*); and the Northern marsupial mole (*Notoryctes caurinus*).

Threatened birds of the three desert regions include the elusive night parrot *Pezoporus occidentalis* (IUCN: Endangered) which was thought to be extinct but recently sighted in the LSD and likely to be elsewhere in region (Olsen, 2018). Its preferred habitat appears to be long unburnt hummock grassland. The princess parrot *Polytelis alexandrae* (IUCN: Near-threatened) is also known from these deserts. Other at risk birds include: Major Mitchell’s cockatoo (*Cacatua leadbeateri*); scarlet-chested parrot (*Neophema splendida*); slender-billed thornbill (*Acanthiza iredalei iredalei*); and the malleefowl, a ground-dwelling megapode found in the southern GD (Vulnerable; *Leipoa ocellata*).

Threatened reptiles of the deserts include the great desert skink *Liopholis kintorei* (formerly *Egernia kintorei*; Vulnerable) which is a large burrowing lizard now restricted to a small number of populations in sand-dune habitat across the eastern GSD, northern GD and Tanami Desert to the north (McAlpin, 2001). Other at risk reptiles include the snakes *Aspidites ramsayi* (woma python) and *Liasis olivaceus* (olive python).

Hydrology and Wetlands

The three desert regions are characterized by low rainfall, high evaporation rates and generally sandy soils, and therefore there are very few permanent surface-water features (the main exception being a small number of surface water seeps and springs).

However ephemeral streams and wetlands exist throughout, with these holding surface water following large deluges, which occur every 5–10 years, with major floods occurring once every 20 years on average, an event which leads to prolific breeding of many species of waterbirds (Halse et al., 2005). Most of the surface water drainage occurs within large endoheric (internal) drainage basins which typically terminate at large salt lakes, such as Lake Amadeus and Lake Mackay (Fig. 1), the latter being Australia's fourth largest lake system. The Rudall River is probably the only true example in the region of an arid zone river with near-permanent wetlands along its course, flowing from uplands to a major salt lake (Lake Dora) within the Great Sandy Desert. Elsewhere a series of interdunal ephemeral wetlands which are dominated by coolibah (*Eucalyptus victrix*) can be found following large rainfall deluges.

There are several recognized Wetlands of National Significance (and other significant aquatic systems) in these deserts (see Fig. 1 for localities):

- (1) Great Sandy Desert: Mandora Marsh; Dragon Tree Soak; Rock Pools of the Breaden Hills; Lake Dora and Rudall River; Lake Amadeus; and Lake Macdonald.
- (2) Little Sandy Desert: Rockholes and Pools of the Carnarvon Range (and other uplands); Saline lakes systems along paleo-drainage lines such as Lake Wilderness and Lake Disappointment; Riparian zone of Savory Creek; and permanent springs of the Durba Hills.
- (3) Gibson Desert: Lake Gruszka, a large (500 ha) seasonal/intermittent freshwater wooded lake; and the Gibson Desert Gnamma Holes, a series of "rock pools," with important ecological, historical and cultural values.

Cultural and Social Context

The three deserts are sparsely populated with most people living in small, isolated Aboriginal communities and settlements. These include Kintore (Walungurru in local language) in the eastern GSD with a population of 400–500, Kiwirrkura (population 200–250) in the northern GD, and three Martu communities (Parnngurr, population 60–80, Kunawarritji, population 100–120, and Punmu, population 90–120) in the LSD and western GSD. Telfer is a mining town in the GSD with around 500 people at any one time, although most mine employees now visit on a "fly-in-fly-out" basis.

The Aboriginal people of these deserts are part of a linguistically linked group known as the Western Desert Aboriginal People who were the last to live as permanent hunter-gatherers in Australia up until the 1980s. A group of nine people were the last to abandon their fully traditional lifestyle in the GSD in 1984. Although there has been consistent migration of desert Aboriginal people, much of it forced, into towns and cities of the region since the 1930s, in recent years small groups of indigenous people have moved back to their traditional country across these deserts, as part of what has come to be called the outstation movement.

Conservation and Management

Threats to Biodiversity

The area is predominantly intact with only minimal amounts of clearing native vegetation and conversion to other land uses. However there are still serious threats to the biota and ecosystems of the deserts from altered fire regimes, nonnative invasive species, altered hydrology, and climate change.

Hummock grasses are generally dense and highly flammable and so the predominance of hummock (spinifex) grassland over the three desert regions (Fig. 3) means vegetation fire is a common, widespread and regular occurrence, with the biota of these grasslands being largely adapted to withstand the effects of fire and/or able to regenerate or recolonize areas after fire (Nano et al., 2012; van Etten and Burrows, 2018). Burrows et al. (2009) studied spinifex fuel dynamics across several sites across the three desert regions and showed that fuel loads increased with time since fire, plateauing at about 10–12 t ha⁻¹ some 18–20 years after fire (van Etten and Burrows, 2018). Typical spinifex fire return intervals are 5–15 years, with fires more common and larger (in terms of area burnt) following wet years (Burrows et al., 1991; Greenville et al., 2009).

Analysis of black and white aerial photography of the GSD from the 1950s demonstrated that the spatial pattern of fires when Aboriginal people lived traditional lifestyles in this region comprised a complex arrangement of many small fires with intervening unburnt areas (Burrows and Christensen, 1990; Burrows et al., 2006). Following the cessation of traditional Aboriginal burning practices across much of these deserts, the fire regime changed from predominantly small, patchy cool-season fires to widespread, intense hot-season fires (Allan and Southgate, 2002; Zeanah et al., 2017). For example, over the period 2000–02, over 500,000 km² of hummock grassland was burnt by wildfire across Central and Western Deserts (Wright and Clarke, 2007), and single summer wildfires can exceed 200,000 ha, burning for several days to weeks (Allan and Southgate, 2002; Burrows et al., 2009). This "boom and bust" fire regime is now largely determined by rainfall which drives the rate of fuel accumulation (Griffin et al., 1983; Allan and Southgate, 2002; Greenville et al., 2009), with lightning now the dominant ignition source. This changed fire regime has been implicated in the decline of small to medium-sized mammals and some bird species, as well as the contraction of fire-sensitive plants, such as native cypress pine (*Callitris* spp.), and vegetation, such as mulga woodlands (Bowman et al., 2008; Ward et al., 2014). It is now accepted that fire sensitive plant species and vegetation were likely to have spread, and perhaps

even protected, under Aboriginal burning regimes, and are now threatened by large uncontrolled wildfires (Wright, 2018). Although Aboriginal burning practices are still practiced in some small areas, they have been recently reintroduced in others in the GSD and GD, and there is evidence that such burning has reduced the number and size of large wildfires (compared to areas without traditional burning; Bliege Bird et al., 2016).

Feral nonnative animals abound in the region and include camels, goats, rabbits, donkeys, and cats. Large herbivores such as camels put extensive pressure on vegetation where they gather, which leads to soil erosion, especially around water points (either natural springs or artificial water points), whilst browsers such as goats damage vegetation across a range of vegetation types (Brim Box et al., 2016). Feral cats (domestic cats, *Felis catus*, which have gone wild) are widespread in these deserts and are a major problem given their prey is mostly native animals, ranging from small mammals, reptiles, birds to invertebrates (Doherty et al., 2015), whilst another introduced predator, the red fox (*Vulpes vulpes*) occurs at relatively low densities throughout these deserts (Burrows et al., 2003).

Although not heavily utilized as yet, the abundant shallow groundwater systems in many parts of the deserts are a potential source of water for irrigated agriculture. Several current proposals to exploit groundwater resources in and adjacent to the western edge of the GSD, mostly involving center-pivot irrigation to produce fodder for cattle, pose an emerging threat to important wetlands in this area, including the Mandora Marshes.

Protected Areas and Land Tenure

Some 43% of the total area of the three desert regions comprise protected areas, with the Gibson Desert having the highest percentage of protected land (58% by area) and the GSD having the lowest (37%; Table 2). The remaining land tenure is mostly UCL (Unallocated Crown Land), ostensibly meaning public land held by the government but not yet allocated for a particular use or designation. There are also several pastoral leases around the edges of these desert, although several of these are not currently kept with domestic livestock (van Etten, 2013). Native title rights exist over the majority of land across the three deserts; this is land for which Aboriginal people have legally recognized rights and interests arising from their traditional laws and customs. Native title can coexist with other types of land tenure.

These proportions of protected land are much higher than many other regions in Australia and most other desert regions globally (Woodley et al., 2012). However, only a relatively small percentage of land is in the most secure IUCN Categories I-IV (National Parks, Nature Reserves, and other areas which are managed primarily for biodiversity conservation), especially for GSD (7% of total area) and GD (18%), which are below and at global benchmarks for levels of conservation-land reservation, respectively (Table 2). Examples of large National Parks (NPs) and Nature Reserves (NRs) include the globally iconic Uluru-Kata Tjuta NP in eastern GSD, Karlamilyi NP which straddles the LSD and GSD (second largest National Park in Australia, formerly known as Rudall River NP), and the Gibson Desert NR (Fig. 4). Newhaven Sanctuary in the north-east GSD is classed as a PNR (Private Nature Reserve) and is an example of a NGO-managed conservation reserve (in this case by Australian Wildlife Conservancy) funded mainly by philanthropy (262,200 ha).

The vast majority (85%) of protected areas across the three deserts are Indigenous Protected Areas (IPAs), a type of protected land recognized and partially funded by the Australian Government and formed by voluntarily agreements with local indigenous custodians. Although they cover a range of IUCN reservation categories, most IPAs are included in IUCN Category VI which allows for sustainable use of resources by the indigenous owners (including fishing and hunting; Table 2; Fig. 4). However some are classed as Category III, such as the very large Birriliburu IPA in the LSD and GD (6.6 million ha), or as Category II (e.g., most of Karajarri IPA; Fig. 4). This reflects the history of some of these areas where they include former conservation reserves

Table 2 Area (ha) of protected areas and other reserves in each of the three IBRA regions of NW Australian deserts divided into IUCN reservation categories as of 30 June 2016.

<i>IUCN category</i>	<i>Gibson Desert</i>	<i>Great Sandy Desert</i>	<i>Little Sandy Desert</i>
IA Strict nature reserve	1,845,737	17,733	–
II National park	–	2,804,855	514,038
III Natural monument or feature	1,097,678	–	4,736,103
I–IV Total	2,943,415	2,822,589	5,250,141
% IBRA	18.83	7.15	47.34
V protected landscape/seascape	–	16,797	–
VI protected area with sustainable use of natural resources	6,183,950	11,812,602	–
V–VI total	6,183,950	11,829,400	0
% IBRA	39.57	29.96	0.00
Total (all categories)	9,127,365	14,651,988	5,250,141
Bioregion area (ha)	15,628,918	39,486,135	11,089,857
% IBRA	58.40	37.11	47.34

Data obtained from Collaborative Australian Protected Areas Database (CAPAD) 2016, Commonwealth of Australia 2017.

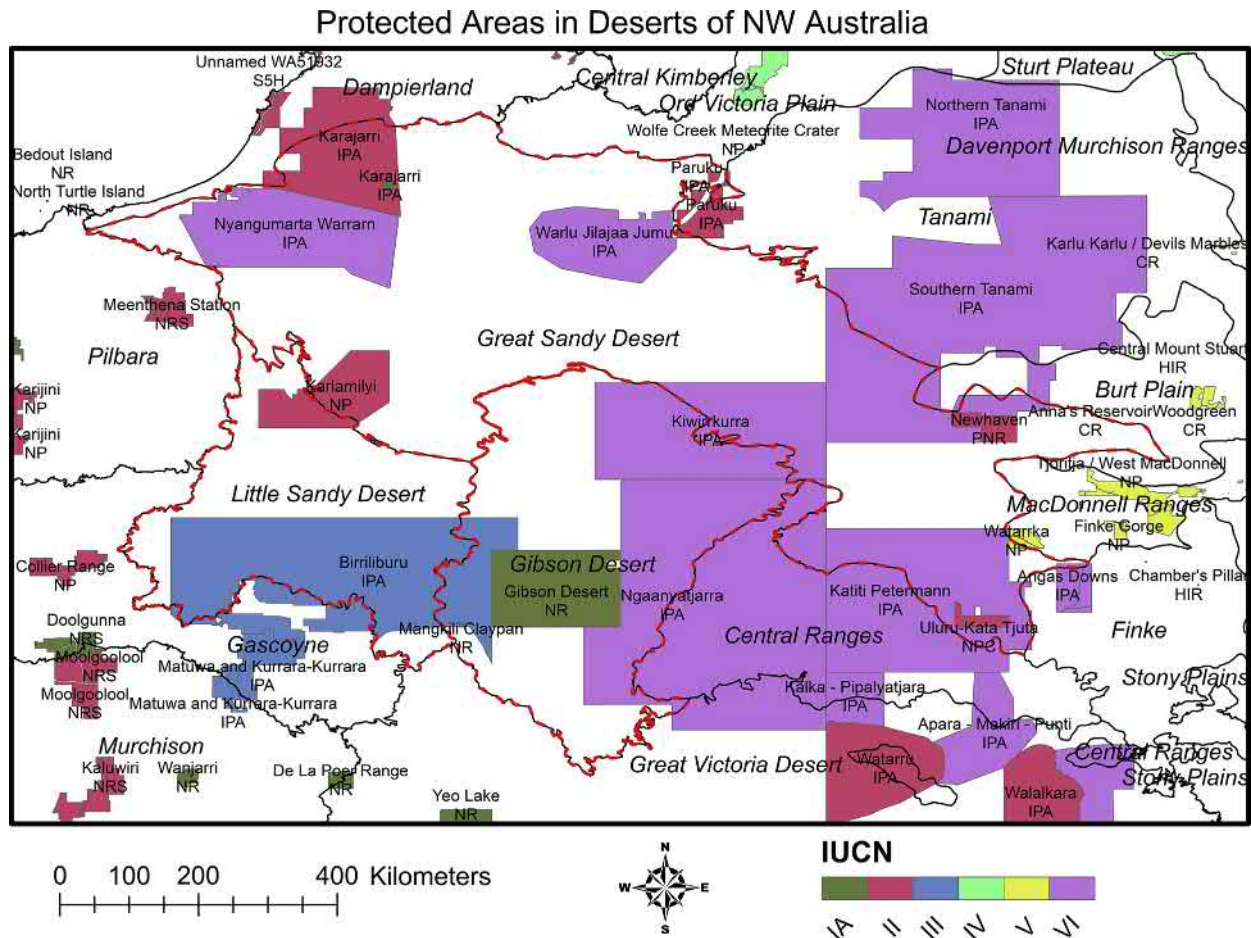


Fig. 4 Map of protected areas across the three desert bioregion classified by IUCN protected area category (see Table 2). Map produced by author using data from: Collaborative Australian Protected Areas Database (CAPAD) 2016, Commonwealth of Australia 2017.

which are now under co-management arrangements or other agreements with State conservation agencies. However, several IPAs are formally managed in accordance with more than one IUCN category (e.g., Birriliburu IPA is managed under both IUCN Categories III and VI to enable both traditional resource management and conservation of specific natural features in certain areas). The IUCN category reported and mapped for each IPA (Table 2; Fig. 4) should be that which applies to at least three-quarters of the protected area, the “75 per cent rule” (Woodley et al., 2012), but in reality may simply reflect what is reported to the Australian Government. IPAs generally have been successful in enhancing protection of biota and landscapes, providing land management services (both traditional and ecological) and enabling much-needed employment for Indigenous people (Ross et al., 2009). For example, the traditional owners of the Birriliburu IPA, the Martu people, undertake on-ground management actions to protect and preserve the flora and fauna of the region, which includes reinstating traditional burning patterns, monitoring threatened species and weed control, and they recently established an Indigenous ranger program employing locals from nearby communities (Jupp et al., 2016).

Summary and Conclusions

These three old desert regions of north-west Australia are characterized by similar physical features such as hot climate, highly variable rainfall, and extensive sand dunes, laterized uplands and rocky plains. They contain significant biotic features such as: (1) relatively rich plant diversity (over 2000 plant species); (2) highly threatened fauna, including medium-sized marsupials such as bilby and mala; (3) intact, near pristine vegetation; and (4) large ephemeral playa and other wetlands which burst into life with occasional flooding.

Although the proportion of land in the formal conservation estate (IUCN Categories I to IV) is below international benchmarks (for at least two of these deserts), large expanses of Indigenous Protected Areas effectively means that the natural assets are managed and protected over large expanses of land in these regions. Despite the lack of vegetation clearing and major human disturbances

across these deserts, and the mostly good to excellent condition of the vegetation, there are still insidious threats to be managed, including widespread wildfires, feral animals and uncontrolled grazing, and weeds. Therefore, providing adequate and ongoing support (guidance, finance, infrastructure, employment, etc.) to the Aboriginal custodians is critical to ensure the rich biodiversity values of these deserts are not diminished.

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Patagonian Desert

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Abstract

The Argentinian Patagonia is a vast area (790,000-km²) of southern South America between 36° and 55°S. Almost 90% of the area is arid, semiarid or dry- subhumid (drylands) and covers important and heterogeneous ecological zones that are determined primarily by climatic gradients and a highly complex geomorphology. That gives rise to different soils (mainly Aridisols, Entisols and Mollisols) and vegetation types (semideserts, shrub steppes, shrub-grass steppes, grass-shrub steppes and grass steppes). Grazing (mainly sheep) and, to a lesser extent, fires are the principal anthropogenic stress factors that have dramatically altered the structure and functioning of these ecosystems. Climatic models predict an increase in aridity for Patagonian drylands, which could accentuate the negative effects of overgrazing on ecosystem health and reduce the capability of Patagonian ecosystems to provide essential services such as forage production and carbon sequestration. The adjustment of grazing management practices could mitigate negative effects but requires routine monitoring of ecosystem structure and functioning, for which the MARAS system (Spanish acronym for 'Environmental Monitoring for Arid and Semi-Arid Regions') has been developed.

Patagonia

Patagonia is a vast area of southern Argentina and Chile (south of South America) between 36° and 55°S. The area covers important and heterogeneous ecological zones that are determined primarily by climatic gradients and a highly complex geomorphology that gives rise to different soils and vegetation types. The boundaries of this region, especially the northern limit, vary according to the criteria adopted, depending on whether it is a biogeographical or political-administrative. This chapter refers mainly to drylands of Argentinian Patagonia (excluding the Andean, humid region, dominated by temperate forests) an area of 790,000-km². We consider the Barrancas and Colorado rivers as the northern limit of this region (Fig. 1).

Climate

The center and western part of the region is dominated by air masses coming from the Pacific Ocean and influenced by the Andes mountains that impose a barrier for humid air masses. These winds ascend the western slope, discharging their humidity mainly in the Chilean sector. West of the Andes, in the Argentine sector, there is a rapid decrease in precipitation from 2000 mm year⁻¹ or more in some sectors of the Andes to less than 200 mm year⁻¹ in a 100-km distance. The seasonal displacement of the low- and

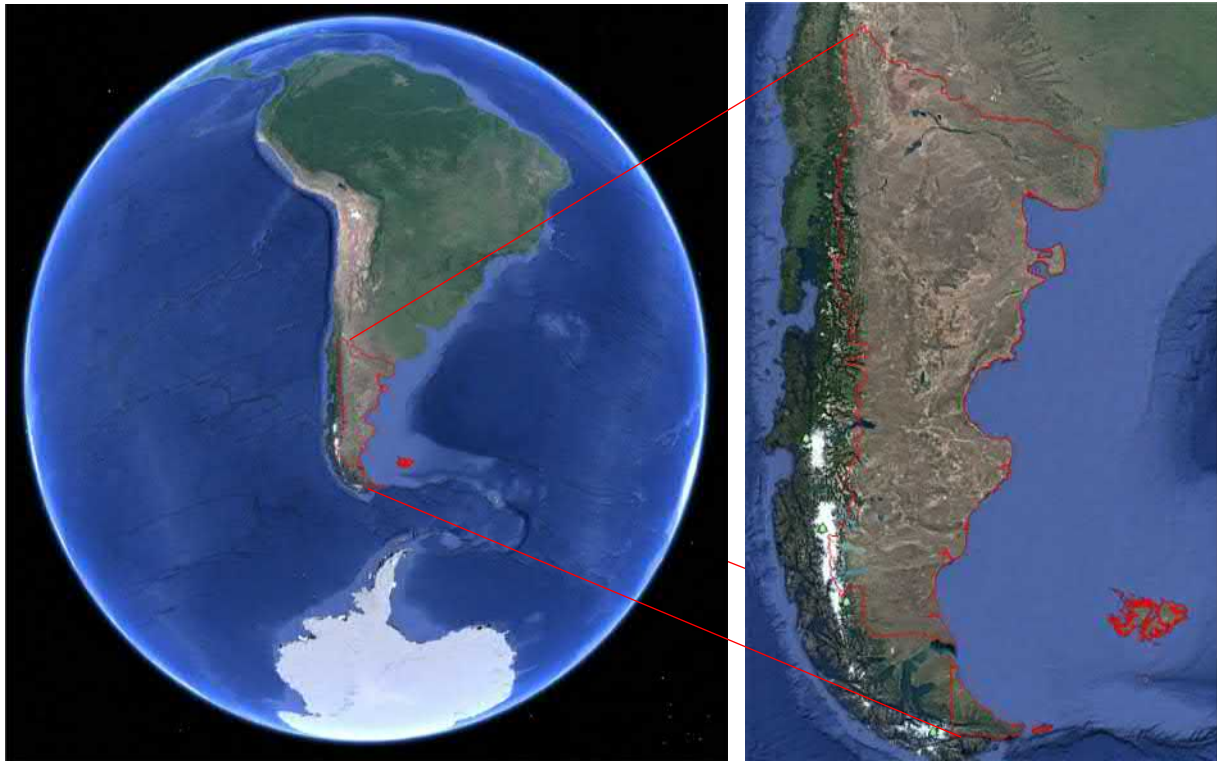


Fig. 1 Location of Argentinian Patagonia.

high-pressure systems and the equatorward ocean current determine the seasonal pattern of precipitation. During winter, precipitation increases over the region due to a higher intensity of the subpolar low, combined with the northward displacement of the Pacific high and higher ocean temperatures relative to the continent. The result is a clear winter-distribution pattern of precipitation over most of the area (Paruelo et al., 1998), with about 46% of precipitation concentrated in winter (Jobbágy et al., 1995) and a strong water deficit in summer. The northeastern and the southern parts of the region are additionally affected by air masses coming from the Atlantic Ocean and present more evenly distributed rainfall (Paruelo et al., 1998). Annual precipitation is <200 mm in 37.5% of the region, while 34.5% of the area shows 200 to 300 mm (this means that 72% of the Argentinian Patagonia has annual rainfall <300 mm). In small areas (3.2%) rainfall can be >1000 mm (Fig. 2). Most of the area (86.7%) may be considered a Dryland since its Aridity Index (rainfall/potential evapotranspiration relation) is <0.65. Within these Drylands, 32.7% is classified as arid, 51.3% as semiarid and 2.7% as dry subhumid (Fig. 3). Isotherms show a northeast to southwest distribution due to the effects of increasing latitude and altitude on temperature. Mean annual temperature ranges from 15 °C in the northeastern to 3 °C in the south (Fig. 4). Patagonia is located between the belt of high subtropical pressures and the area of low subpolar pressures, so it is fully included in the zone of circulation of the winds from the west of the Southern Hemisphere. Westerly winds are characterized not only by their persistence during the year but also by their intensity. Mean annual values of wind speed vary between 10 and 20 km h⁻¹ in the north of the region and between 20 and 30 km h⁻¹ in the center and south part of the region. According to these values, Patagonia is within 5% of the world's windiest lands (Fig. 5). The annual distribution of the wind speed shows a maximum between September and January and a minimum in winter (Paruelo et al., 1998).

Landscapes and Soils

The most characteristic landscapes of Patagonia drylands are the plateaus or *mesetas*. These plateaus decrease in elevation from the Andes towards the Atlantic coast and are usually covered by basalt rocks, the product of volcanic eruptions in the Cenozoic era, or by pebbles or *rodados patagónicos*: rounded rock fragments generated by erosion during water transport during events of snow and ice melting. Volcanic features, hills, plains and fluvial valleys are found between the plateaus. A series of rivers that flow from the Andes to the Atlantic, such as the Colorado, Negro, Chubut, Chico and Santa Cruz. The uplift of the Andes in the Miocene is, perhaps, the most significant event shaping the Patagonian landscapes because it imposed a barrier for moisture from the Pacific Ocean by the prevailing westerly winds. This produced a change in the climate of the Argentinian Patagonia, from moist in the west to arid and semi-arid eastward, creating conditions favorable to wind erosion (Paruelo et al., 2007), that transported large quantities of sediment from the eroding mountains toward the plains and plateaus farther east. These sediments have been the original material and shape the distinctive characteristics of the soils of Patagonian drylands. Nine of the twelve taxonomic soil orders included in the

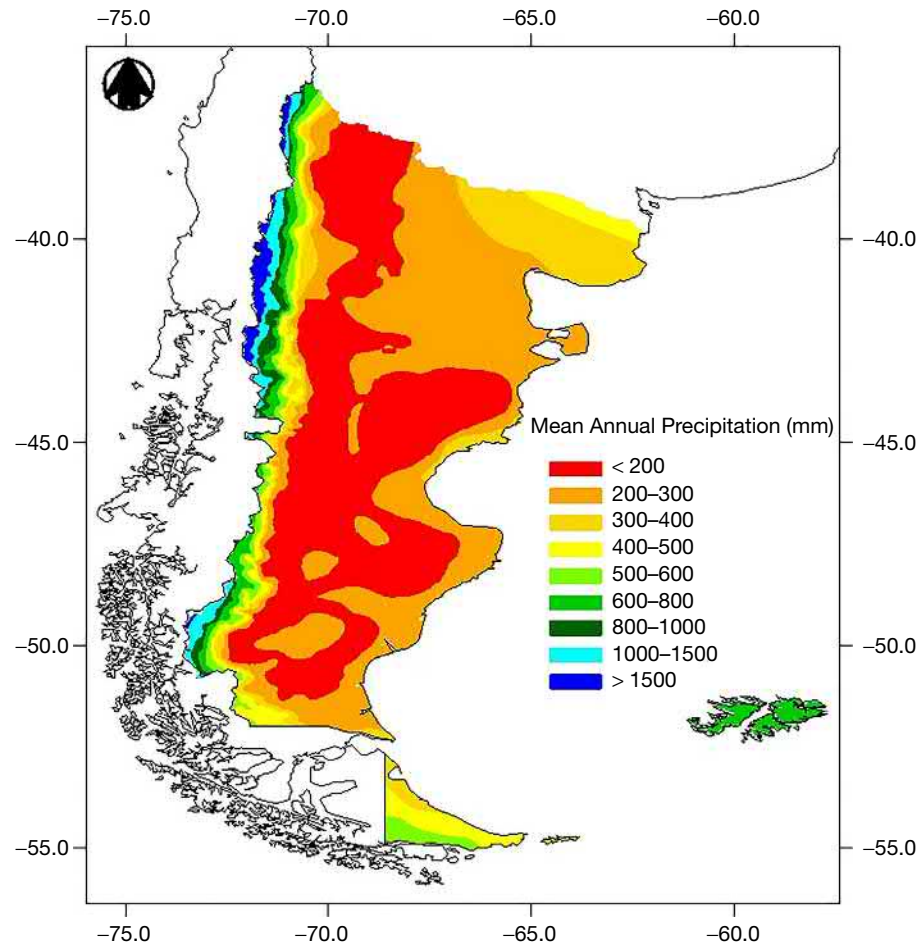


Fig. 2 Mean annual precipitation (Bianchi and Cravero, 2010) in the Argentinian Patagonia. Bianchi, A.R., and Cravero, S.A.C. (2010). Atlas climático digital de la República Argentina. Instituto Nacional de Tecnología Agropecuaria: Salta, Argentina.

U.S. Soil Taxonomy (Soil Survey Staff, 1999) are present in Patagonia (del Valle, 1998). Two of them are strongly dominant: Aridisols (50%), Entisols (22%). Water deficit is the major defining characteristic of Aridisols as they are soils of dry regions, mostly of deserts. Entisols are soils with little or no evidence of profile development. A series of volcanoes are located along the Andes mountains, especially on the Chilean side between 36° and 46° South, and 50 of them are active or have had an eruption in historical times (Besoaín, 1985). Predominant winds from the west have distributed volcanic material from Chile to the Andean-Patagonian region of Argentina, where soils derived from volcanic ash classified as Andisols (Soil Survey Staff, 1999) comprise 4 M ha or 5% of the region (del Valle, 1998). The marked gradient of precipitation in west-east direction has conditioned the evolution of these soils and generated differential properties (Colmet Daage et al., 1988; Gaitán and López, 2007). Mollisols occupy about 13% of the territory. They generally occur in a north-south belt in the occidental portion of the Patagonian region (del Valle, 1998), in the transition area between the humid sector of the Andes (with Andisols) and the extra-Andean drylands (dominated by Aridisols and Entisols).

Due to water redistribution, induced by the topography, wet meadows, locally known as *mallines* (a Native American word meaning muddy area) occupy the depressed portions of the landscape, such as the drainage lines between hills and plateaus (Fig. 6; Marcolín et al., 1978). Higher water availability in *mallines* leads to the development of azonal types of soils and plant communities (Gaitán et al., 2011b). These ecosystems occupy between 1.5 and 2.0% of the region's surface, and up to 8% in some areas (Mazzoni and Vazquez, 2000; Bran et al., 2004a). Water dynamics in these wetlands show a seasonal recharge of the soil profile in autumn–winter, followed by a progressive decrease in the level of the water table during spring, reaching its lowest value in summer (Cremona and Lanciotti, 1996). Soils of *mallines* are deep, loamy textured and with abundant organic matter.

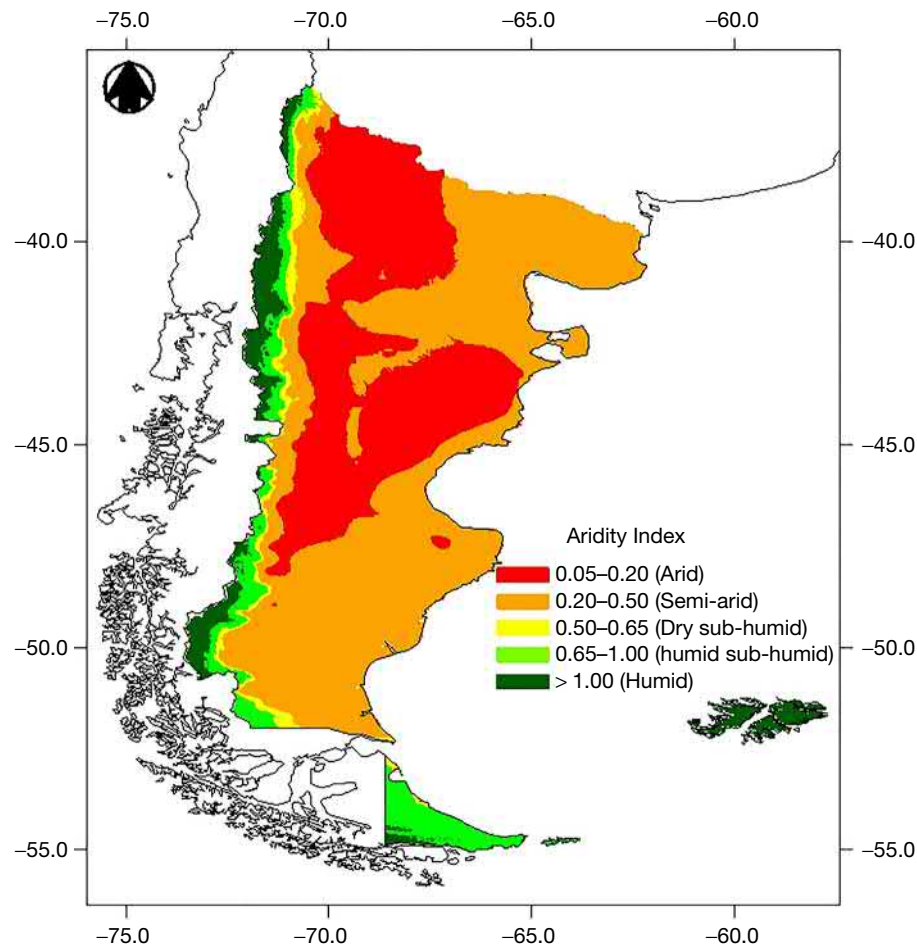


Fig. 3 Aridity Index (Precipitation/Potential Evapotranspiration relation) in the Argentinian Patagonia. Elaborated from Precipitation data from Bianchi, A.R., and Cravero, S.A.C. (2010). Atlas climático digital de la República Argentina. Instituto Nacional de Tecnología Agropecuaria: Salta, Argentina and Potential evapotranspiration data from Zomer, R.J., Trabucco, A., Bossio, D.A., van Straaten, O. and Verchot, L.V. (2008). Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture, Ecosystems and Environment* **126**, 67–80.

Vegetation: Description of the Main Plant Communities and Their Relationship With Climatic Gradients

The vegetation of Patagonia drylands includes diverse vegetal communities, that belong to two phytogeographic provinces (Patagonia and Monte) and a wide ecotone between both. It has developed under arid, semiarid and dry sub-humid climates that also show different thermal regimes according to the latitude and the altitude. Table 1 presents in a simplified way the Main Vegetation Units (MVU) and their relationship with these two climatic attributes (aridity index and mean annual temperature), and are delimited in the Fig. 7. Among these MVU, the changes in general are not abrupt, and intermediate vegetation types will be found accompanying the climatic gradients. Physiognomic and floristic variants will be also found according to the types of soil on which they develop, where depth, texture and alkalinity are the main determining factors. Management history also influences vegetation, as overgrazing has generated convergent effect with aridity. Species characteristic of drier environments increase in overgrazed areas, as noted by Gaitán et al. (2018) and this changes ecosystem attributes and function.

Phytogeographic Province: Patagonia

Following the criterion of aridity index, three groups of communities can be considered. In the dry subhumid, grass steppes dominate, in the semiarid the low shrub–grass steppes and in the arid low shrub steppes.

Grass Steppes

Grass steppes dominated by *Festuca pallescentis* (Fig. 8A) are found in the Andes foothills, that show also ecotones in the form of patches or mosaics with the deciduous forest (*Nothofagus pumilio* and *N. antarctica*). These steppes have been called Subandino District (Soriano, 1956; Golluscio et al., 1982). With some variants, they are also found further to the east in very high plateaus or

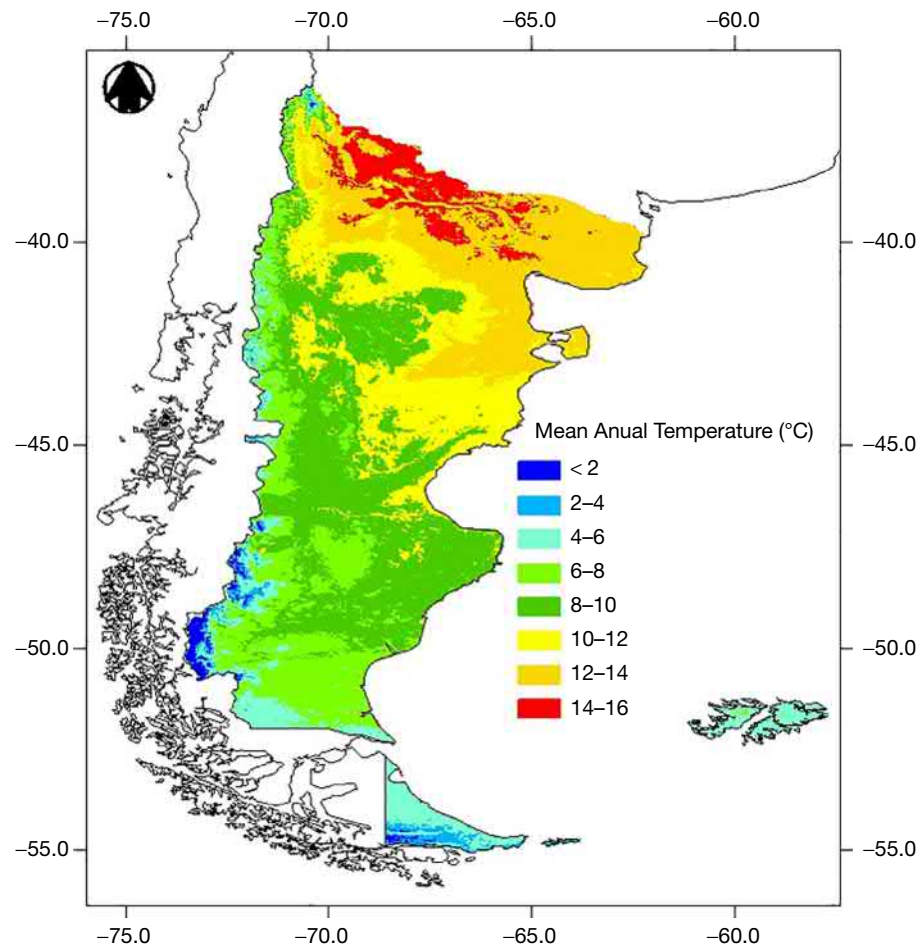


Fig. 4 Mean annual temperature (Gaitán et al., 2011a) in the Argentinean Patagonia. Gaitán, J.J., Raffo, F. and Umaña, F. (2011a). Estimación de la temperatura de la superficie terrestre mediante imágenes satelitales en el norte de la Patagonia. Comunicación Técnica N°32, Agrometeorología, INTA EEA Bariloche, 11 pp.

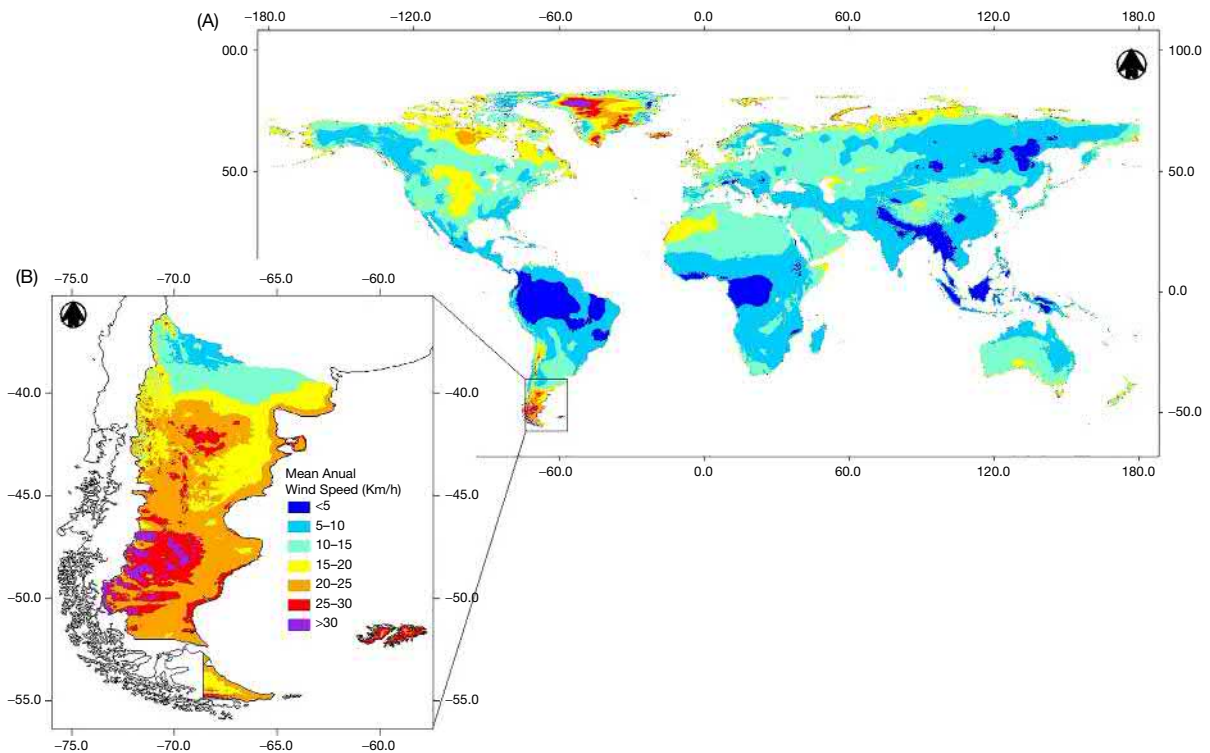


Fig. 5 Mean annual wind speed (Fick and Hijmans, 2017) in the world (A) and in the Argentinean Patagonia (B). Fick, S.E. and Hijmans, R.J. (2017). WorldClim 2: New 1 km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37, 4302-4315.

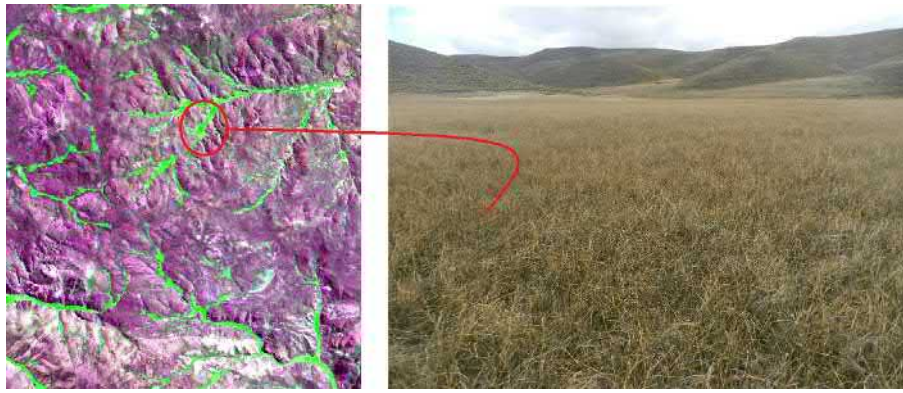


Fig. 6 Landsat satellite image showing wet meadows, locally known as *mallines*, occupy the drainage lines between hills.

Table 1 Summary of climatic conditions, dominant physiognomy and species of Main Vegetation Units in Argentinian Patagonia drylands.

Mean annual temperature	> 13 °C		10–13 °C	< 10 °C		
Aridity index	Semi-arid to Dry subhumid	Semi-arid	Semi-arid	Dry subhumid	Semi-arid	Arid
Main vegetation units	● Monte oriental	● Monte austral	● Ecotono ● Ecotono Chuquiraga avellanadae ● Ecotono Peninsula Valdez ● Payunia District	● Subandino District (DS) ● Magellanic Xeric District (DMX) ● Magellanic Humid District (DMH)	● Occidental District (DO) ● Golfo District (DG) ● Mata Negra District (MN)	● Central District
Dominant physiognomy	Medium to tall shrubs steppes with small scattered emergent trees	Medium shrubs steppes	Medium to low shrubs steppes	Grass steppe	Low shrub-grass steppes	Sub-shrubs steppes
Dominant species	<i>Larrea divaricata</i> , <i>Prosopis flexuosa</i> and <i>Geoffroea decorticans</i>	<i>Larrea</i> spp., <i>Monttea aphylla</i> , <i>Atriplex lampa</i>	<i>Larrea nitida</i> , <i>Schinus</i> sp., <i>Prosopis denudans</i>	<i>Festuca pallescens</i> (DS) <i>Festuca gracillima</i> (DMX and DMH)	<i>Mulinum spinosum</i> and <i>Adesmia volckmannii</i> (DO) <i>Mulinum spinosum</i> and <i>Trevoa patagónica</i> (DG) <i>Junellia tridens</i> (MN)	<i>Nassauvia glomerulosa</i> , <i>N. ulicina</i> y <i>Chuquiraga</i> spp.

hills (generally above 1200 m a.s.l.). The typical vegetation is a grass steppe with high vegetation cover (60–70%), dominated by *Festuca pallescens* and accompanied by *Rytidosperma* spp., *Lathyrus magellanicus* (Colluscio et al., 1982). Other frequent species are *Agrostis pyrogea*, *Senecio sericeonitens* and *Nassauvia aculeata*. Degradation caused by fire and overgrazing increases cover of shrub species such as *Mulinum spinosum*, *Acaena splendens* and *Senecio* spp. *Rumex acetosella* invasion is also frequent (Franzese and Ghermandi, 2012a).

Other grass steppes dominated by *Festuca gracillima* are found in the south near the Strait of Magellan (Magellanic District, León et al., 1998). Among the *F. gracillima* tussocks a rich stratum of short grasses and herbs such as *Poa spiciformis*, *Bromus setifolius*, *Rytidosperma virescens*, *Carex* spp., *Festuca magellanica*, *Hordeum* spp., *Phlaiophles biflora* and *Armeria maritima* develops. Dwarf shrubs such as *Nardophyllum bryoides*, *Nassauvia ulicina*, dominate degraded areas and in the more humid areas with acid soils the creeping shrub *Empetrum rubrum* becomes important. Other common dwarf shrubs are *Nassauvia fuegiana*, *Perezia recurvata* and *Ephedra frustillata*. The total vegetation cover varies on average between 60% and 80%. Oliva et al. (2001), differentiate two variants, one more xeric (Magellanic Xeric District) and the other more humid (Magellanic Humid District, Fig. 8B).

Low Shrub-Grass Steppes

Low shrub-grasslands steppes develop in the arid and semi-arid areas in a broad area east of the Andes known as Occidental District (Soriano, 1956; Fig. 9A). Vegetation has a cover of 40–60% and distributed almost proportionally between low shrubs (between 0.5 and 1.0 m in height) and tussock grasses, locally called *coirones*. Dominant shrubs are *Mulinum spinosum*, *Adesmia volckmannii*,

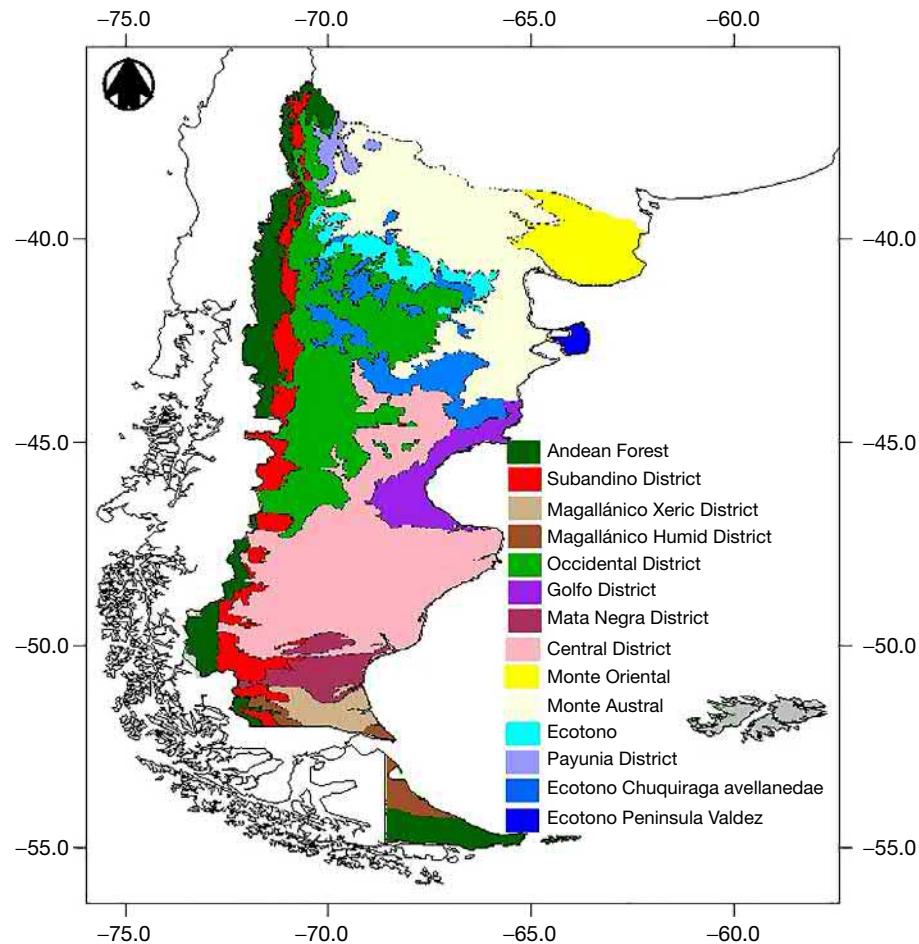


Fig. 7 Main vegetation units in Argentinian Patagonia. Modified from León, R., Bran, D., Collantes, M., Paruelo, J. and Soriano, A. (1998). Grandes unidades de vegetación de la Patagonia extra andina. *Ecología Austral* 8, 123–141.

Senecio spp. (mainly *S. bracteolatus* and *S. filaginoides*), *Berberis heterophylla* and *Tetraglochin alatum*. Among the grasses are *Pappostipa* spp. (mainly *P. speciosa*, *P. major* and *P. humilis*), *Poa ligularis* and *Festuca argentina*. The presence of a medium shrub layer is common in rocky soils such as mountain foothills and basaltic landslides where *Colliguaja integerrima* or *Retanilla patagonica* are frequently dominant. Another related shrubs formations are found in the coastal region of the Gulf of San Jorge (Golfo District; Soriano, 1956). They are also shrub-grass steppe with vegetation cover of 40–60%, but shrubs are higher (1.5–2.0 m high), mainly dominated by *Retanilla patagonica* and other shrubs such as *Colliguaja integerrima*, *Mulinum spinosum*, *Anartrophyllum rigidum*, *Lycium* spp., and *Prosopis denudans*. Common grasses are *Festuca argentina*, accompanied by *Poa spiciformis* and *Pappostipa* spp. In the south of continental Patagonia an additional shrub-grass steppe develops, dominated by low shrubs (0.5–1.0 m in height) of *Junellia tridens* (Mata Negra District; Fig. 9B). Other common shrubs are *Nardophyllum obtusifolium* and *Berberis heterophylla*, and grasses forming tussock such as *Festuca pallescens*, *F. gracillima*, *Pappostipa* spp., and *Jarava neai*, are also present. Short grasses such as *Poa spiciformis*, *Pappostipa ibari*, *Festuca pyrogea* and *Rytidosperma virescens* and dwarf shrubs of *Nassauvia glomerulosa* and *N. ulicina*, *Satureja darwinii* and *Ephedra frustillata* are also present in this diverse community.

Sub-Shrubs Steppes

Dwarf or creeping shrubs lower than 20 cm height are widespread in Patagonia. These steppes show low vegetation cover (20% or 30%) and were called Central district by Soriano (1956). Dominant species is the shrub *Nassauvia glomerulosa* but degraded areas include *Nassauvia ulicina* and *Chuquiraga aurea*. Erosion of shallow, duplex soils shows here clay layers and abundant erosion pavements. *Pappostipa* spp. are common grasses. Northern areas show higher, scattered shrubs of *Chuquiraga avellanedae*, *Senecio filaginoides* and *Lycium ameghinoi*. *Acantholippia seriphioides* is also common. Towards the south shrubs of *Junellia tridens*, *Anartrophyllum rigidum*, *Schinus* sp. and *Berberis heterophylla* are also common following drainage lines.

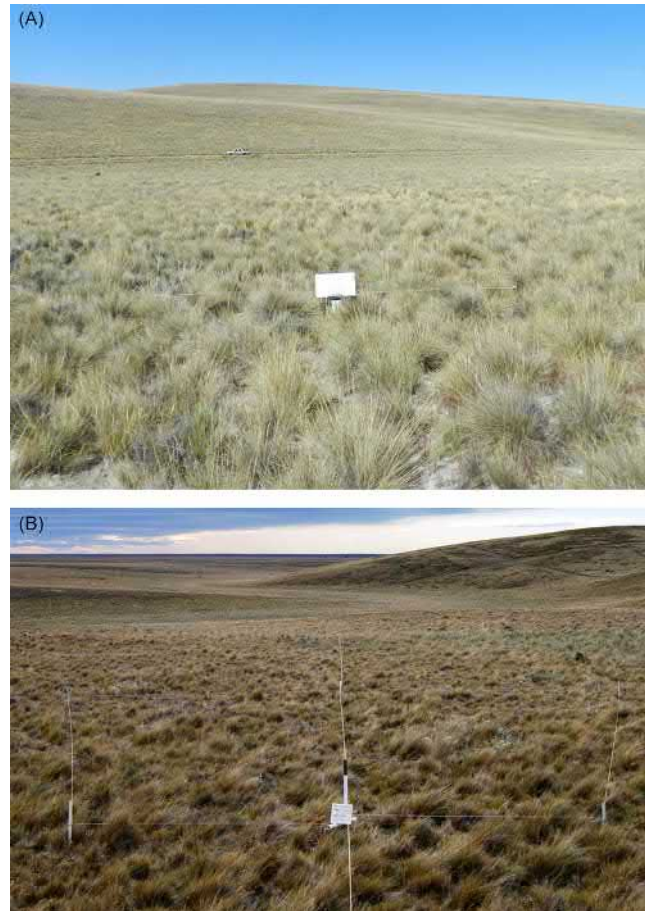


Fig. 8 Subandino district (A) and Magellanic Humid district (B).

Phytogeographic Province: Monte

In the northeastern part of Patagonia, where relatively higher latitudes are combined with relatively low altitudes, vegetation communities belong to the Monte Phytogeographic Province (Cabrerá, 1976), that extends east of the Andes mountains, from North of Argentina to Patagonia, and is characterized by the predominance of medium to tall shrub steppes, dominated by *Larrea* spp.

In the northeastern end of the region, these shrublands show different physiognomy and floristic composition and are classified as “Monte Oriental” (León et al., 1998; Fig. 10A). The genus *Prosopis* (mainly *P. flexuosa* and *P. alpataco*), is here dominant, and there are more C4 grasses such as *Pappophorum caespitosum*, *Setaria leucopila*, *Sporobolus cryptandras*, and *Trichloris crinita*. Total vegetation cover is relatively high (60–80%) and emergent tree layers of *P. flexuosa* (and very sporadically of *P. caldenia*) and patches of *Geoffroea decorticans* are common. Shrubs are dominant, and the most conspicuous species are *Larrea divaricata*, *Condalia microphylla*, *Chuquiraga erinacea* and *Prosopis alpataco*. Grasses are dominated by *Nassella tenuis* and *Piptochaetium napostaense*, *Nassella longiglumis*, *Jarava plumosa* and *Poa ligularis*, in addition to the C4 grasses mentioned above. The area endures recurring fires, which temporarily modify the physiognomy and the relative vegetation cover of grasses and shrubs (Bran et al., 2007).

The rest of the Monte in Patagonia (“Monte Austral”; León et al., 1998; Fig. 10B) is mostly under Semi-arid climate. Vegetation is mostly a shrub steppe that does not exceed 2 m in height, with a total vegetation cover close to 40%. The most frequent species is *Larrea divaricata*, accompanied by *L. cuneifolia* (which dominate in sites of greater edaphic aridity) and *L. nitida* (which becomes more abundant towards the ecotone with the Phytogeographic province of Patagonia). Other frequent tall shrubs are: *Monthea aphylla*, *Bougainvillea spinosa*, *Schinus* spp., *Lycium* spp. and *Prosopis alpataco*, and in the short sub-shrubs *Cassia aphylla* and *Acantholippia seriphioides*. Grass cover depends on grazing pressures, and the most common species are: *Nassella tenuis*, *Pappostipa speciosa*, *Jarava neaei* and *Poa ligularis*. Cover of *N. tenuis* varies greatly depending on the interannual variations of rainfall. In the relatively low positions with higher salinity-alkalinity soils, *Atriplex lampa* dominates, in mixed communities with *Larrea divaricata* and *Larrea cuneifolia*. Where salinity is high and soils have finer textures, *A. lampa* is accompanied or replaced by *Chuquiraga avellaneda*. *Suaeda divaricata* is frequently found on the margins of the salinas. In environments with significant sandy accumulations the dominant species is *Hyalis argentea*, accompanied by *Sporobolus rigens* and *Panicum urvilleanu*.

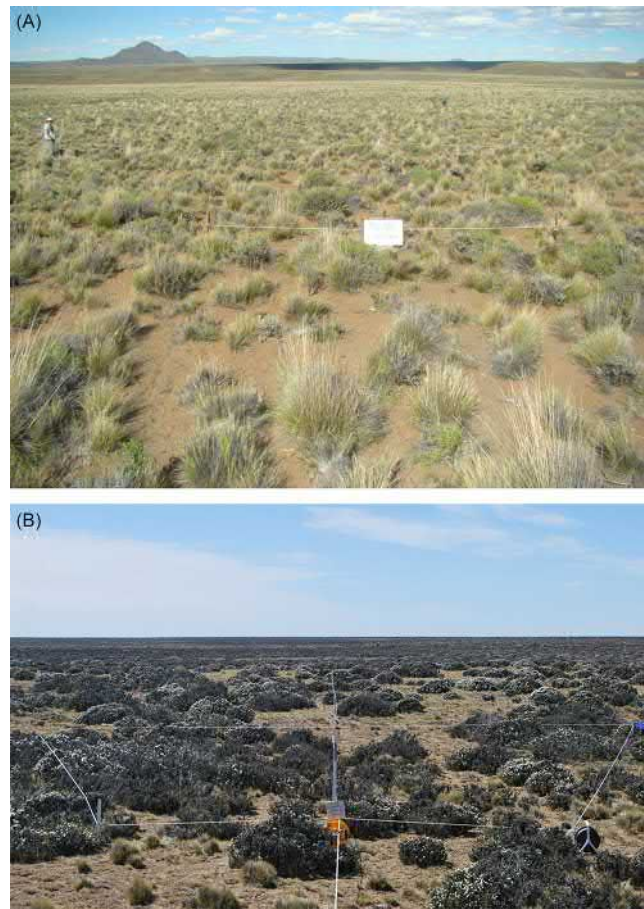


Fig. 9 Occidental district (A) and Mata Negra district (B).

Patagonia-Monte Ecotone

In the northeast of the region (approximately between 400 and 700 m a.s.l.) an ecotone between Patagonia and Monte (called Ecotono, León et al., 1998) is found with low to medium shrub steppes of *Schinus johnstonii*, *Prosopis denudans* and *Larrea nitida*, usually in “islands” that do not exceed 1.5 m in height, and with a total vegetation cover close to 40%. *Lycium chilense*, and *Junellia aspera* are also common. *Prosopidastrum globosum* is dominant in rocky soils such as those of the basaltic plateaus. Among the shrub “islands”, low shrubs and grasses dominate with *Grindelia chiloensis*, *Mulinum spinosum*, *Senecio filaginoides*, *Nassauvia axillaris* and *Acantholippia serphioides*. The grass stratum is generally poor and dominated by *Pappostipa humilis*, *P. speciosa*, *Jarava neaei* and *Nassella tenuis*. Within shrubs “islands” *Eremium erianthum* is common.

Towards the Northwest the ecotone has been described as the Payunia District (Cabrera, 1976), dominated by shrub steppes that do not exceed 2 m. height of *Ephedra ochreatea*, *Coliguaya integrerrima*, *Larrea nitida*, *Neosparton aphyllum* and *Schinus* spp. An intermediate stratum includes shrubs such as *Mulinum spinosum*, *Stillingia patagonica*, *Senecio* spp., *Grindelia chiloensis* and *Chuquiraga rosulata*.

Southern sector of the ecotone is dominated by *Chuquiraga avellanadae* (Called Ecotono *Chuquiraga avellanadae*; León et al., 1998), with an open high shrub stratum of *Lycium ameghinoi*, *L. chilense*, *Junellia ligustrina*, *Prosopis denudans* and *Schinus* sp. In the lower stratum there are *Acantholippia serphiodes*, *Nassauvia ulicina*, *Pleurophora patagonica*, and *Pappostipa humilis*.

Another interesting vegetation variant is present in the Valdez Peninsula, that shows a shrub steppe dominated by *Chuquiraga avellanadae*, *Chuquiraga erinacea* and *Condalia microphylla* (called Ecotono Península Valdez, León et al., 1998). *Lycium chilense*, *Schinus* sp., *Prosopidastrum globosum* and *Larrea nitida* are also frequent here. The most abundant grasses are *Nassella tenuis*, *Nassella longiglumis*, *Pappostipa speciosa*, and *Piptochaetium napostaense*. *Hyalis argentea* with *Sporobolus rigens* and *Panicum urvilleanum* dominate in very sandy soils.

Native Fauna

Animals native to Patagonia are closely related to those of Australia and New Zealand and in a more distant manner to those of South Africa and North America. Fauna of the Patagonian steppe forms two distinct groups associated with vegetation units of the

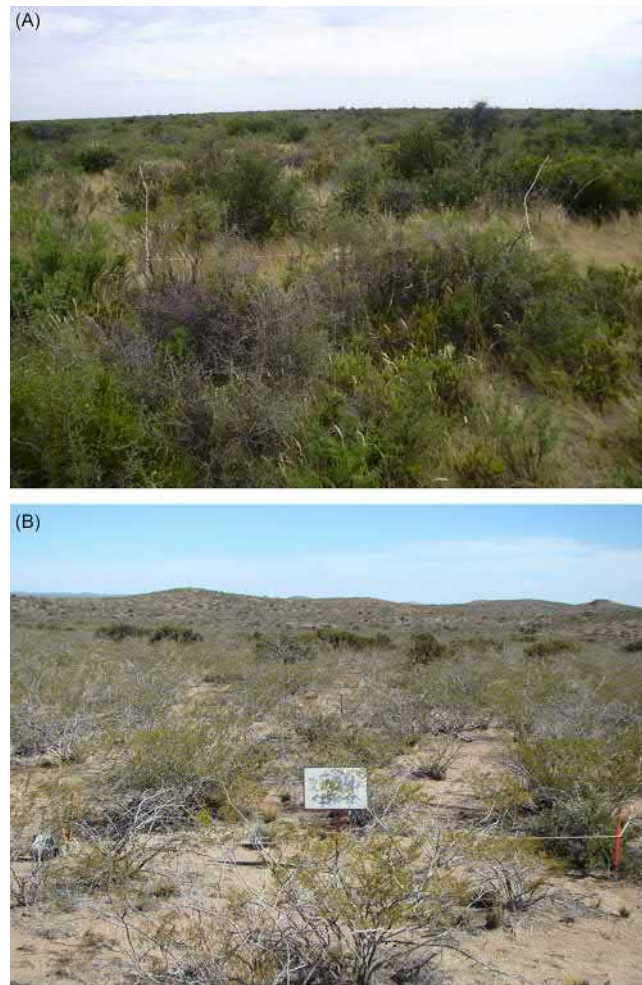


Fig. 10 Monte oriental (A) and Monte austral (B).

“Monte” in the north and “Patagonia” in the south, with numerous endemic taxa of great ecological importance (Bonino, 1994). Reptiles are especially abundant in the north, with 109 mostly endemic species, including lizards of genus *Liolaemus* and *Diplolaemus*, 18 species of snakes and a two earth turtles. Excluding marine animals, there are actually nine orders of mammals in the region, with 20 families, 58 genus and 90 species, 77 of which are native and 12 introduced. Some of them are rare endemic marsupials such as the Comadreja overa (*Didelphis* sp.), the Marmosa (*Thylamis* sp.), and the secretive Monito del Monte (*Dromiciops gliroides*). Nine species of Bats (*Histiolus* sp.) are present. The most abundant are rodents with digging habits, with 26 species of mice (*Akodon* sp. and others), Tuco-tucos (*Ctenomys* spp.), Cuises (*Microcavia*), and the “Patagonian hare” or Mara (*Dolichotis patagonum*). The only great herbivore of these steppes is an endemic camelid: the Guanaco (*Lama guanicoe*). Carnivores include the widespread Puma (*Felis concolor*), Gray and Red foxes (*Lycalopex culpaeus*), a Ferret (*Lyncodon patagonicus*), wild cats such as Montés (*Leopardus geoffroyi*) and Pajonal (*L.colocolo*) and Skunks (*Conepatus humboldtii*). Some introduced mammals have become dominant, including the European hare, rabbits, the American mink and the Canadian beaver. Bird life is abundant, with over 300 species (Narosky and Babarskas, 2000), although a great proportion of them are marine or restricted to the Andes. The steppes are habitats for running species such as Rheas or Choiques (*Pterocnemia pennata*), Martineta (*Eudromia elegans*), and Quiula, that is endemic of the region (*Tinamotis ingoufi*). Insectivorous birds such as Bandurrita (*Upucerthia dumetaria*), and Caminera Patagónica (*Geositta antarctica*) are mostly of walking habits and gray or brown plumaje. Wetlands in the desert harbor more eye-catching birds such as the endemic, threatened Macá Tobiano (*Podiceps gallardoi*), Gallineta Chica (*Rallus antarcticus*) or Pato Vapor (*Tachyeres patachonicus*). Anatidae family is more abundant and includes a number of Ducks, Black necked Swans (*Cygnus melancoryphus*) and Upland geese or Cauquen Común (*Chloephaga picta*) and Colorado (*Ch.rubidiceps*), this last one in severe retraction. North of the región and within the Monte vegetation a different suite of species includes Gallito Arena (*Teledromas fuscus*), Canastero Patagónico (*Asthenes patagónica*) and Caserote Pardo (*Pseudoseisura gutturalis*).

Principal Anthropogenic Stressors

Grazing

The influence of grazing in Patagonia has been matter of debate. [Milchunas et al. \(1992\)](#) used the region as an example of short evolutionary history of grazing, but guanacos, the only great herbivores present before colonization, had been grazing these cold semi deserts since the end of the Tertiary, 2 M years ago. [Cabrera and Yepes \(1960\)](#) estimated their populations at about 7 M at the end of 19th century, and [Lauenroth \(1998\)](#) considered that they may have been a significant factor in the evolution of apparent defense mechanisms in spiny shrubs and tough forage. Domestic herbivores were introduced in Patagonia close to 1880, and wild, mobile guanaco grazing was replaced with continuous sheep grazing at fixed, high stocking rates that were only possible after the introduction of fences and water holes in close to 11,000 great units or “*Estancias*.”

It is not possible to reconstruct past carrying capacities of rangelands during the early stages of colonization, but they can be compared to actual carrying capacity estimations based on primary productivity from 2000 to 2015 satellite images ([Oliva et al., 2018](#)). Analysis of historical stock in [Fig. 11](#) shows that sheep increased driving total grazing well over this threshold early in the past century and remained high during six decades. From 1978 onwards they decreased sharply and were only partially replaced by cattle, reducing total domestic stock numbers until they converged to estimated carrying capacity. The process was probably forced by low reproduction rates ([Golluscio et al., 1998](#)) that complicated replacement of stocks during disasters such as volcanic ash, drought or excess of snow ([Andrade et al., 2002](#)). Huge areas of central Patagonia were abandoned and *Estancias* reduced their flocks close at a minimum numbers compatible with commercial production, with great unrest for local livelihoods and the economy of rural towns ([Andrade et al., 2010](#)). Patagonian rangelands showed stability, as they endured over six decades of overgrazing, probably because they were dominated by long-lived perennials ([Oliva et al., 1998](#)). On the other hand, low resilience explains lack of recovery after drastic stock reductions late in the 20th century ([Gaitán et al., 2015](#)), probably because vegetation suffered transitions to shrublands with soil erosion ([Paruelo et al., 1993](#)), that affect close to one-third of the region ([del Valle et al., 1998](#)). Even though present domestic stock seems to have reached a balance with primary production, local misbalances still remain in place. Guanaco populations that were estimated at only 0.6 M in 1990 ([Bolkovic and Ramadori, 2006](#)) have recovered in the last two decades after great sheep destocking, and are now at a 2.2 M, a significant addition to grazing pressure ([Bay Gavuzzo et al., 2015](#)). In conclusion, overgrazing has severely affected soils and vegetation in the region. While sustainable stocking rates may stop degradation ([Oliva et al., 2012](#)), recovery processes of soil, productivity and diversity are very slow, and will probably require in the future joint management of native and domestic herbivores after decades of overuse ([Oliva et al., 2016](#)).

Fires

In many arid and semiarid ecosystems fire is a major ecological force, as in South Africa ([Bond et al., 2003](#)). Although fire seems to have played a lesser role in Patagonia, in some parts of the region fire has shaped vegetation patterns. Wildfires are frequent in two regions of North Patagonia, the Subandino District grass steppes and the eastern “Monte” shrublands ([Bran et al., 2004b](#)). In other areas of Patagonia, especially when vegetation cover is less than 50%, fires are not frequent, and probably in the south part (i.e. Magellanic District) climate conditions inhibit the development of fires.

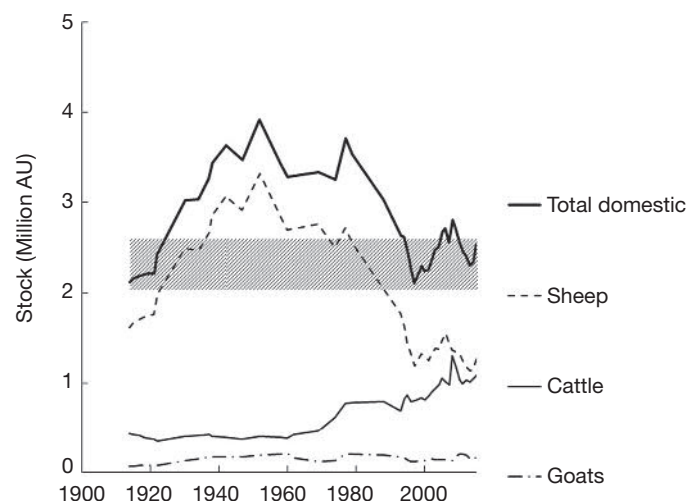


Fig. 11 Sheep, cattle, goat and total combined stock for Patagonia from 1914 to 2015 in Animal Units (1 AU = 1 cow/year). Shaded area represents carrying capacity ($\pm$ SD) in the 2000–15 period estimated from satellite images. Modified from Oliva, G., Paredes, P., Ferrante, D., Cepeda, C. and Rabinovich, J. (2018). Comparación entre receptividad y existencias ganaderas en La Patagonia. Una aproximación a escala regional. *Resumen VIII Congreso Nacional sobre Manejo de Pastizales Naturales-IV Congreso del Mercosur sobre Manejo de Pastizales Naturales*. 15 al 17 de mayo de 2018 Chamical, La Rioja.

In north-western Patagonia fires are relatively frequent and are influenced by ENSO events. [de Torres Curth et al. \(2008\)](#) studied fires in this region during 1984–2004 and registered only two fire seasons with large burned areas, and both were related to “La Niña” phenomena. [Oddi and Ghermandi \(2016\)](#) characterized the fire regime between 1973 and 2011 for a study area that covers 5,600 km² (40°16′ to 41°11′ South and 70°26′ to 71°01′ West), using a 1973–2011 time series of Landsat images. They determined a total burned area of 72,500 ha which represents 13% of the study area, in 88 different fires. The largest wildfire was of 21,477 ha and occurred in 1999, the year with the most extensive burned area (30,284 ha).

In Post-fire regeneration, the recovery of the original community prevails by persistence of resprouter species and by auto-replacement of species ([Ghermandi et al., 2004](#)), but some other processes that induce partial changes were observed, such as:

- The increase of shrub cover, mainly of *Senecio bracteolatus* ([Franzese et al., 2009](#)) and *Fabiana imbricata* ([Oddi et al., 2010](#); [de Torres Curth et al., 2012](#)).
- Changes in the relative cover between dominant tussock species, locally named “coirones” (*Pappostipa major* and *Festuca pallescens*). This is consequence of differences in post-fire survival (higher in *P. major*), post fire recruitment (lower in *F. pallescens*, due to little protection structures in seeds and lack of self-burial mechanisms compared to *P. major*), as well as changing competitive interactions during post fire regeneration, especially when there is an early post-fire grazing that led to a reduction in *F. pallescens* the more palatable species ([Gittins et al., 2011](#); [Franzese and Ghermandi, 2012b](#)).
- Weed invasion principally of *Rumex acetosella*. This exotic perennial herb invades the area between the “coirones,” and produced notable changes on the “intercoironal” vegetation ([Franzese and Ghermandi, 2012a](#)).
- The establishment of a community of fugitive species. These species that colonizes early from the seed bank have a short life, but are able to recharge the seed bank before the next disturbance and increase diversity. Due to this behavior this group of species, such as *Montiopsis polycarpoides*, *Boopis gracilis*, *Heliotropium paronychioides*, *Nicotiana linearis*, *Chenopodium scabraule* and *Descurainia pimpinellifolia*, was called the “phantom community” ([Ghermandi et al., 2004](#)).

In the “Monte” shrublands, wildfires can affect large areas. [Bran et al. \(2001\)](#) reported 720,000 ha burned during the 2000/01 summer. The biggest continuous polygon of burned areas covered more than 50% of this surface (365,000 ha). The fires could be seen in a Landsat image ([Fig. 12](#)).

Fire and grazing seem to affect the relationship between the dominant functional groups. [Kröpf et al. \(2015\)](#) developed a state and transition model for the eastern Monte with six stable states and 12 transitions, focused on the three most conspicuous layers: shrubs, grasses and biological crust. They concluded that the grass layer is most frequently affected by intensive and continuous grazing, which reduces the occurrence of fires and shifts the equilibrium toward the shrubs. The shrub layer is affected by large-scale disturbances (fire, mechanical clearing) which maintain the balance between grasses and shrubs in the system. History and intensity of these disturbances can explain the different vegetation structures observed in the region.

[Bran et al. \(2007\)](#) studied the effect of burn severity in the early post fire vegetation evolution and observed a faster recovery for vegetation cover in areas with lower burn severity. In sites with high burn severity seed banks were apparently destroyed. In all the cases the grass/shrub cover ratio was higher in burned than unburned areas. High burn severity also affected soil organic carbon concentration ([Gaitán et al., 2007](#)).

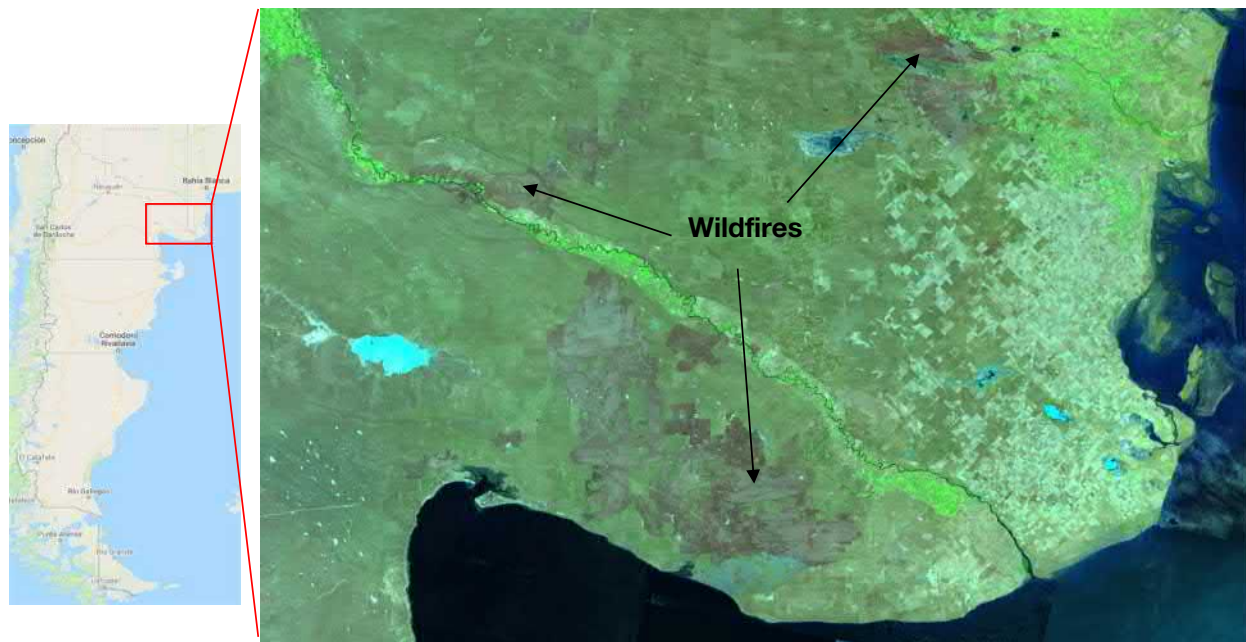


Fig. 12 Area affected by wildfires in the “Monte” shrublands, during the summer 2000/2001, seen in a Landsat 5 TM satellite image.

Global Climatic Change Effects

According to the Global Climate Models (GCMs), the expected changes in the climate during this century will not affect in the same way the broad Patagonian region. To evaluate the spatial variability of these changes, we used 17 MCGs presented in the 5th Report of the Intergovernmental Panel on Climate Change (IPCC, 2013), in two scenarios of greenhouse gas emissions (RCP4.5 and RCP 8.5) for the period 2061–80. These models show increases of the mean annual temperature of 2–3 °C in the south of the region and of 4–5 °C in the north in the RCP4.5 scenario. While in the RCP8.5 scenario the changes would be more accentuated: 4–5 °C in the south and 6–7 °C in the north. Mean annual precipitation in both scenarios is expected to decrease, except in the extreme north and south of the region, where increases of up to 10% are projected. Rainfall in Center and west areas is expected to decrease 10–20% (Fig. 13).

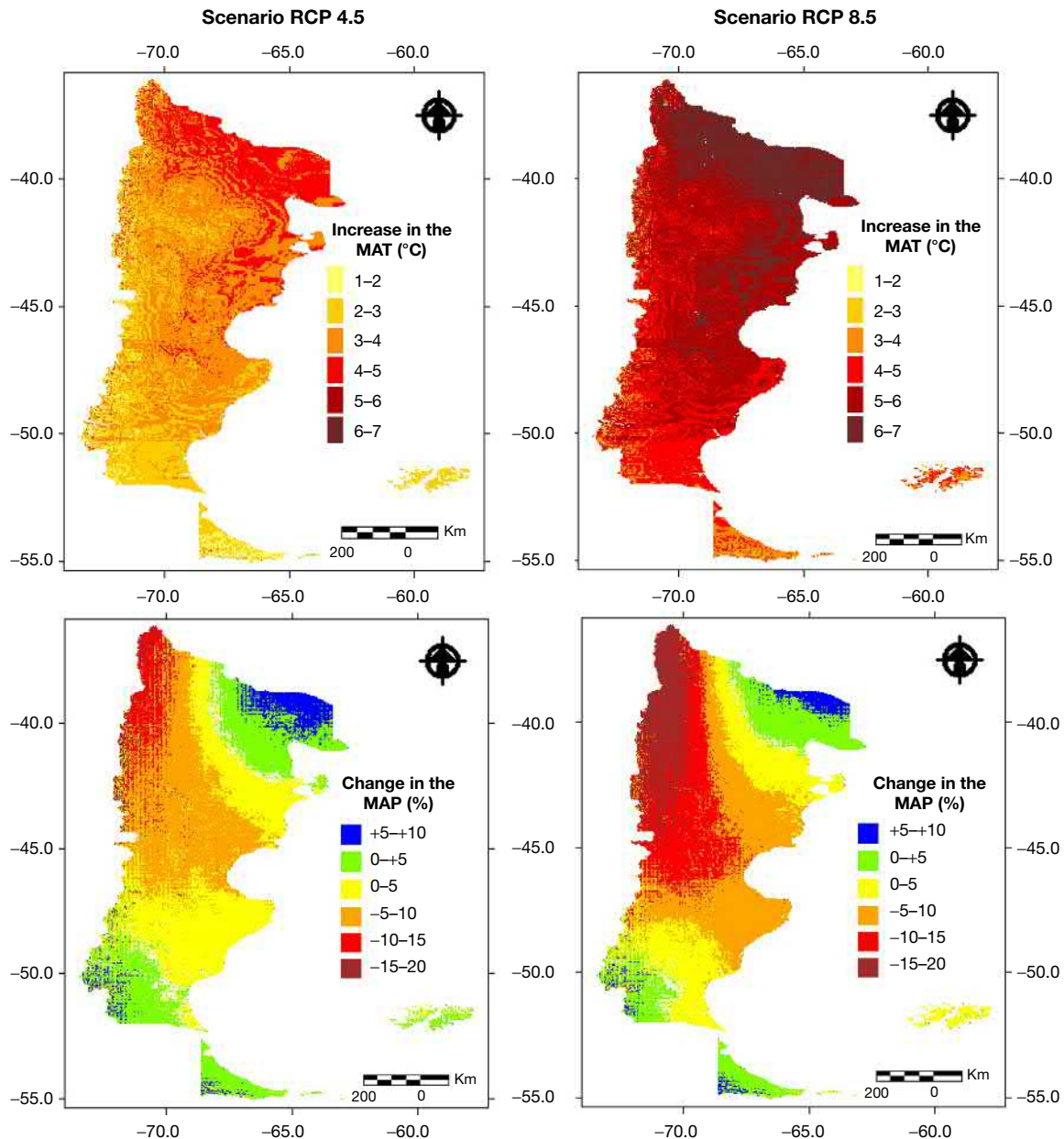


Fig. 13 Projected changes in mean annual temperature (MAT) and precipitation (MAP) for the period 2060–80 in two scenarios of greenhouse gas emissions (RCP4.5 and RCP 8.5) for the Argentinian Patagonian region. Based on the current climate (1950–2000) of WorldClim model (Hijmans et al., 2005, <http://www.worldclim.org/current>) and the average of the projections made by 17 Global Climate Models presented in the 5th Report of the Intergovernmental Panel on Climate Change (IPCC, 2013), available at: <http://www.worldclim.org/cmip5>.

Previous studies show that temperature has a negative relationship with grass cover and species richness and a positive relationship with shrub cover across Patagonian drylands (Gaitán et al., 2014a). In addition, temperature affects indirectly and negatively the aboveground net primary productivity (ANPP) of these ecosystems. Lower rainfall is related to lower grass cover, lower species richness and ANPP, and increasing shrub cover (Gaitán et al., 2014a, 2018). These studies suggest that projected increases in temperature and aridity will generate an impact on the structure and functioning of these ecosystems. The expected increases in temperature and aridity suggest an increase in shrub cover, a decrease in total grass cover (mainly in palatable grass species), and a reduction in species richness. In addition, climate change is expected to have direct and indirect effects (mediated by their effects on vegetation structure) on the functionality of these ecosystems. It is likely that ANPP and forage productivity will decrease in Patagonian drylands, and that these ecosystems will be less efficient in converting the precipitation into biomass. Soil functional processes, such as nutrient cycling, infiltration and stability in relation to erosion processes, would also be affected (Gaitán et al., 2018). The increase in temperature and the severity of droughts would also have a negative effect on the ANPP (Gaitán et al., 2014b).

Monitoring System

Long-term land monitoring technology is needed to track slow changes in drylands and evaluate biodiversity, biological invasions, local extinctions and physical or chemical soil variations including carbon storage. Consistent data sets are lacking because researchers and government agencies use multiple techniques to evaluate the same variables. The MARAS system (Spanish acronym for Environmental Monitoring Arid and Semi-arid Regions) is a network for long-term monitoring Patagonian drylands that use a standardized methodology that enable different research teams collaborate across wide geographical areas using a common open data-base (Oliva et al., 2019). This system was developed by INTA at the beginning of the 2000's with the purpose of establishing a regional long-term monitoring system capable of detecting the trend of the desertification process and provide early warnings that would aid management decisions that could slow down and reverse the problem.

Sites were uniform areas with dominant vegetation type and representative management (in sheep farms they were typically ewe paddocks), distant at least 500 m from water sources and roads. Wetlands or other azonal vegetation types were not sampled. The methodology for site evaluation was described in detail in manuals (Oliva et al., 2011), so here it will be briefly summarized: in each MARAS site a photographic pole was fixed and a 72-m central line was laid following the main resource flux direction (wind or water flow direction). Three poles were fixed at 8.5 m along this line, separated perpendicularly 2.5 m and two additional sets of three poles were set at 13.5 and 72 m separated by 6.5 m. Photos were obtained from photographic pole at 2 m height and positions of pole 1 and 9 were registered with GPS. Three 50-m transects were placed, two for vegetation and one for patch structure sampling and Landscape Functional Analysis sampling (Fig. 14).

Vegetation cover was estimated using the point intercept method (Müller-Dombois and Ellenberg, 1974). Along each transect, we recorded the type of ground surface (plant species, bare soil, rocks, cryptogams, standing dead or litter) every 20 cm (500 records per site). Patch structure was analyzed using gap-intercept method described in Herrick et al. (2005) along the soil line. Patches were defined as areas >10 cm that retained resources. They were mostly live plants but occasionally consisted of standing dead or decomposing litter fixed to the soil. Interpatches were areas >5 cm that lost resources, and mostly consisting of bare soil or desert pavement areas. A minimum of 25 and a maximum of 50 patch-interpatch pairs were recorded. With these data we calculate

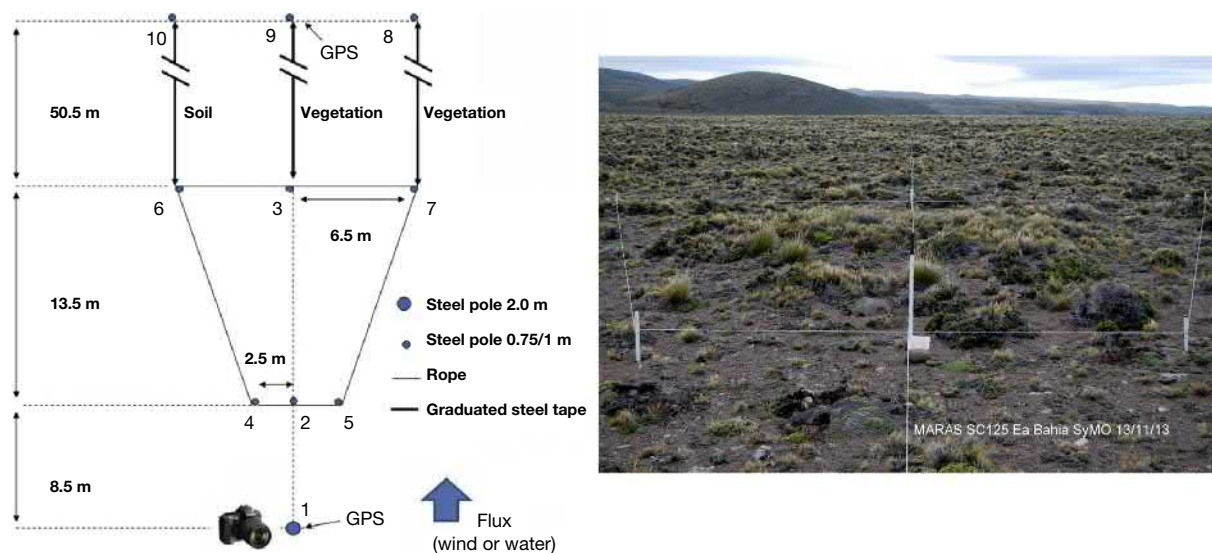


Fig. 14 Scheme of MARAS monitor and an example of a network site.

structural attributes of the vegetation: basal vegetation cover, average size (width, length and height) and density (number every 10 m) of the patches and average length of the interpatches. Landscape Functional Analysis (LFA) was estimated in plots outlined over the first 10 interpatches that exceeded 40 cm in length along the soil line. This was a modification of [Tongway and Hindley's \(2004\)](#) methodology, where plots were systematically placed at intervals along a line. Eleven soil surface indicators were visually rated using a scale proposed by [Tongway \(1994\)](#) that was modified to suit regional soil and vegetation. From these 11 indicators three LFA indexes were estimated: Stability, Infiltration and Nutrient Cycling. Composite superficial (0–10 cm depth) soil samples were obtained from patch and interpatch areas and tested for pH, electric conductivity, organic carbon, N and texture.

The MARAS network has 380 sites distributed across Patagonian drylands, which were installed and assessed between 2008 and 2017 ([Fig. 15](#)). The first evaluation of these sites allowed generating a baseline that has been recently published ([Oliva et al., 2019](#)) and this ground data has been combined with remotely sensed information ([Gaitán et al., 2013](#)), in order to extrapolate the data. As of 2013 the sites began to be resampled and currently (December 2018) 192 sites have a second evaluation after 69.6 ± 15.1 months of the first. [Fig. 16](#) shows an example of a site with two ground evaluations.

The MARAS network, where soil and vegetation indicators are evaluated in the field, together with climate data and satellite images, give way to a monitoring system that seems to have potential to detect change of biophysical traits of arid lands with a detail and precision that was not possible with multiple techniques and isolated data bases. This system that may be useful in other arid and semiarid areas of the world since it offers a structure to perform sampling, to store and share information between scientists of different countries and institutions ([Oliva et al., 2019](#)).

Conservation Strategies

Patagonian drylands are among the areas of lower human population density, and with less degree of artificialization and substitution of its ecosystems, and the name "Patagonia" evokes romantic images of a windy wilderness at the end of the Earth. But human activities, since the century 19th–20th transition, have forever altered the structure and composition of Patagonian

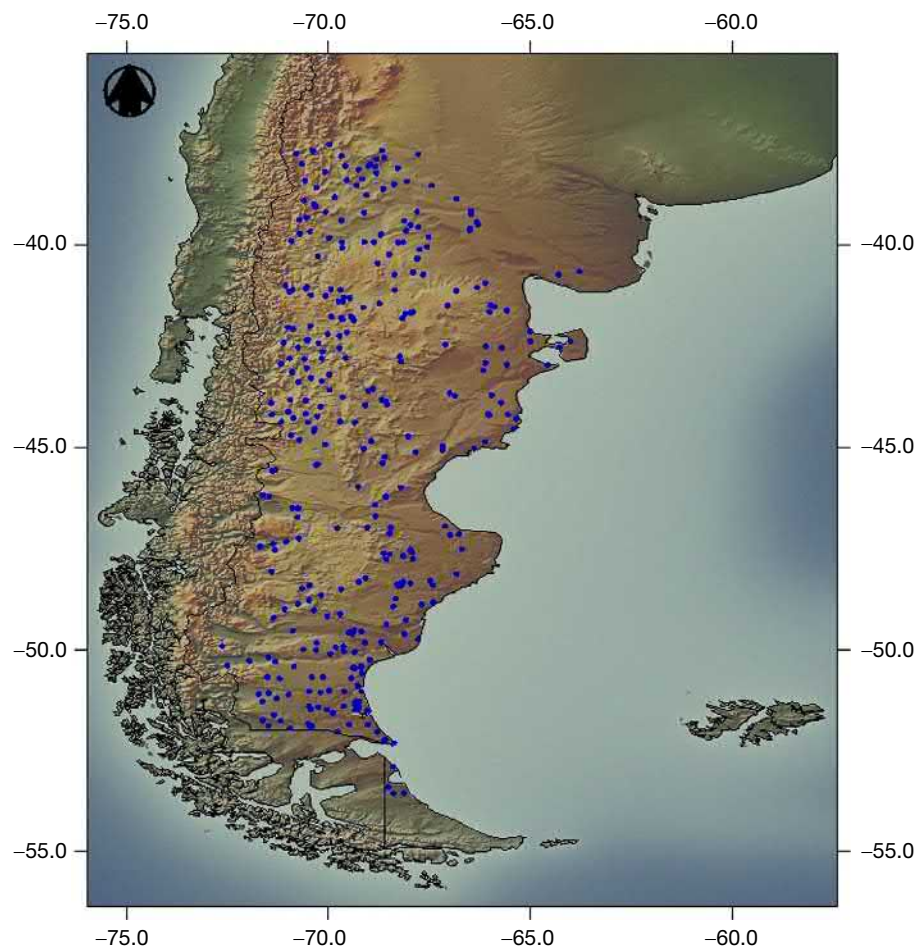


Fig. 15 Location of MARAS sites network.

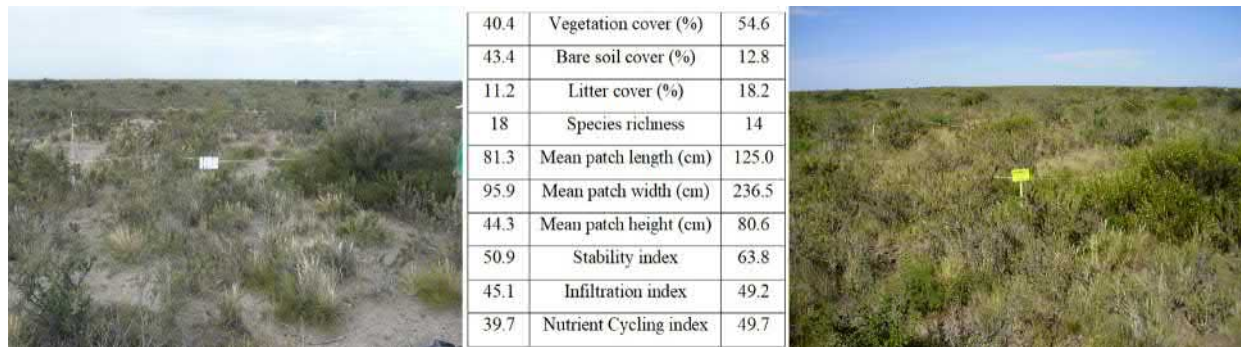


Fig. 16 Example of a MARAS network site with two ground evaluations: 12/15/2012 and 4/12/2017. The data of some structural and functional indicators of the ecosystem are shown.

wildlife and vegetation communities, and most of Patagonia is no longer truly wild (Walker et al., 2005). Vegetation and soils have been depredated mainly due to sheep and goat overgrazing, and 80% of its surface is affected by some degree of desertification (del Valle et al., 1998).

In Dinerstein et al. (1995) evaluation of the terrestrial eco-regions of Latin America, the Patagonian Steppe was classified as Vulnerable and of Maximum Regional Priority; and it was one of the 200 world ecosystems classified as priority for conservation (Olson and Dinerstein, 2002). They also consider that Patagonian drylands had not an adequate network of protected areas, with less than 1% of the area under strict protection category and several ecosystems without representation.

In recent years, efforts have been made to change this situation, identifying areas of importance for the conservation of biodiversity (Chehébar et al., 2013) and through creation of National Parks (Monte León coastal-marine National Park in 2004; Petrified Forests of Jaramillo National Park, in 2012; and Patagonia National Park, in 2015). Complementary initiatives aimed to achieving land sustainable management have been carried out, like the Project to Combat Desertification in Patagonia (INTA-GTZ, 1995) and the GEF PNUD ARG 07/G35 Project (Sustainable Management of Arid and Semiarid Systems for Desertification Control in Patagonia, Argentina. 2007–13). This last project provided the resources to install the MARAS environmental monitoring system of the Patagonian drylands.

Rangelands Evaluation for Sustainable Grazing Management

From the decade of 1990 the National Institute of Agricultural Technology of Argentina (INTA) developed a methodology applicable to livestock ranches in Patagonia in order to optimize production without compromising long-term rangelands health. This methodology basically consists in identifying the different types of environments present in a ranch, for which the interpretation and analysis of satellite images is carried out. In the field, vegetation composition, degradation state and forage productivity is estimated based on the cover of palatable species and their status. Animal stocking rate is adjusted according to consumable forage and estimated yearly animal consumption (Borrelli and Oliva, 2001; Elissalde et al., 2002; Siffredi, 2012).

With this forage allowance, animals consume approximately 30% of the total forage biomass, and no more than 50% of the biomass of the most palatable species for sheep. This residual level is considered necessary in order to allow for regeneration according to a practical rule in the rangelands management (Stoddart and Smith, 1955). In controlled grazing trials, rangelands that were under 10 years of animal stocking rate adjusted with this methodology maintained their diversity and increased their total vegetation cover and the cover of palatable grasses and herbs (Oliva et al., 1998).

Concluding Remarks

The Argentinian Patagonia is one of the world's largest rangelands in drylands with heterogeneous vegetation structure and comprehensive climatic variation. Grazing by domestic herbivores is the most widespread human use in the area. Over 100 years of grazing have induced strong changes in the structure of Patagonian ecosystems. Regional models of climate change for the next century predict an increase in arid conditions due to lower precipitation and higher temperatures in Patagonia. These climatic changes are likely to have a negative impact on the sustainability of Patagonian ecosystems due to their strong impact on vegetation structure and functioning. Appropriate management of livestock carrying capacity and the use of rotational grazing can offset or mitigate these negative effects of climate change. Finally, the use of long-term monitoring systems such as MARAS, which integrate field-based surveys, remote sensing, climatic data and a multivariate interpretative framework could be a useful tool to detect and provide range managers and government agencies with 'early warning' signals for the onset of desertification processes due to human use and/or climate change.

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The Namib Desert and Its Bats

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Abstract

While not typically thought of as having high biodiversity, deserts are home to many unique and endemic species adapted to arid environments. The Namib Desert, along the Atlantic Coast of southern Africa, is one of the world's oldest deserts and is unique in that it still harbors several megaherbivores. Often overlooked are the nocturnal, volant mammals in this desert—its bats. Here, I conduct the first intensive study of northern Namib bats using both mist nets and acoustic detectors. While bat species richness is typically maximized in wetter, warmer areas, the topographical and vegetative diversity of the Namib supports more species than otherwise expected. I conclude with the primary threats to biodiversity conservation and human-wildlife coexistence in the Namib Desert, including my findings from 86 semi-structured interviews with local pastoralists.

Desert Biodiversity

Deserts are often seen as relatively simple ecosystems characterized by low productivity and species richness (Noy-Meir, 1974; Seely and Louw, 1980; Polis, 1991). Rarely are they considered bastions of biodiversity. Nevertheless, these systems harbor a surprising number of unique species adapted to the harsh and highly variable desert environments that cover 17% of earth's terrestrial surface (Crawford, 1981; Polis, 1991; Durant et al., 2014).

Water plays an important role in structuring wildlife communities (Noy-Meir, 1974), particularly in deserts where precipitation totals—while low on average—show extreme inter-annual variation (von Wehrden et al., 2010). Desert mammal distributions and behaviors are strongly affected by daily water losses (e.g. well digging by elephants; Ramey et al., 2013), though some species are less dependent on access to bodies of water than others (e.g., giraffe; Fennessy, 2009). Many deserts contain rivers, which strongly differ from their mesic counterparts because desert rivers can be almost entirely subterranean or highly intermittent with no flows for years, yet continue to harbor remarkable biodiversity (Young and Kingsford, 2006). Surface water availability concentrates desert life, such that springs in arid landscapes are recognized as global biodiversity hotspots (Brown and Ernest, 2002; Bogan et al., 2014; Davis et al., 2017).

Global Patterns in Species Richness

Globally, species richness tends to decrease with distance from the equator, resulting in a latitudinal gradient in diversity (Hillebrand, 2004). One explanation for this pattern is the “time and area” hypothesis (Mittelbach et al., 2007), which states that the age of a community may enable proliferation of more diverse life forms (i.e., speciation). The tropics may have accumulated species over a longer time than temperate zones due to reduced impacts of the Pleistocene's glacial-interglacial cycles near the equator in comparison to higher latitudes (Stephens and Wiens, 2003). Some areas of the world outside the tropics, however, are also recognized to have a long history of climatic stability.

Among arid zones, the Namib along the Atlantic coast of southern Africa is considered to be one of the world's oldest deserts (Fig. 1). The Namib is a 50–150 km wide coastal desert stretching over 2000 km from the Rio Bentiaba (São Nicolau; 14°16' S; 12°22' E) in Angola across Namibia to the Olifants River in South Africa (31°42' S; 18°11' E) (Werger, 1978; Henschel and Lancaster, 2013). While the current ecological state of the Namib is thought to have developed during the Pleistocene Epoch at the start of the Benguela Upwelling System (Walter and Breckle, 1984), evidence from a geological review suggests that this desert was never more



Fig. 1 The Namib Desert meeting the Atlantic Ocean. Courtesy Emsie Verway.

humid than semi-arid for at least the last 55–80 million years (Ward et al., 1983). Perhaps owing to this antiquity and historical stability, the majority of Namibia's endemic and near-endemic flora and fauna are found in the Kaoko escarpment of the northern Namib Desert, which is considered to be the most important endemism hotspot for vertebrate taxa in Namibia and Angola (Simmons et al., 1998). The region has remained a relatively stable center for the evolution of desert species and adaptations to arid conditions.

An Overview of the Namib Desert

The Namib comprises several phytogeographic subdivisions (Jürgens et al., 1997). These include the northern Namib, central Namib plains, central Namib dunes including the Namib Sand Sea, and the southern Namib, which branches into the East Gariep Namib inland, and the northwestern Namaqualand Sandveld along the coast. Major geomorphic features include mountain ranges and river canyons in the north (Fig. 2), which give way to gravel plains interspersed with inselbergs and mountain outcrops (Seeley and Pallett, 2008).

Large sand dune systems (i.e., the Kunene Sand Sea, the Skeleton Coast dune field, and the central Namib Sand Sea) are found throughout areas of the desert, but particularly dominate the land forms in the southern and parts of the central Namib. The entire desert is characterized by high winds, extreme daytime temperatures, and almost negligible rainfall (Parker and Lawrence, 2001).

A key ecological driver of species diversity among these habitats is water availability. In parts of the Namib Desert, water occurs as frequent coastal fog (as many as 200 days per year in the central Namib; Schachtschneider and February, 2010). Additionally, a series of large ephemeral rivers cross the central and northern regions of Namib Desert from east to west. Wildlife depend on the water and vegetation resources in these ephemeral rivers (Jacobson and Jacobson, 2013). Surface flows in this region only occur during significant rainfall events within the catchment and rapidly conclude after rainfall ends due to the large evaporative losses found in the Namib Desert (i.e., evaporation rates reaching 200 times the mean annual rainfall in some areas; Fig. 3; Lancaster et al., 1984).

Permanent flowing rivers occur in the Namib on Namibia's northern and southern borders—the Kunene River to the north and the Orange River to the south—which harbor additional biodiversity not typically associated with deserts. For instance, the Kunene River is home to Nile crocodiles (*Crocodylus niloticus*) and Nile soft-shelled terrapins (*Trionyx triunguis*).

Namib Desert Biodiversity

Much of the published research on the biodiversity, climate, and geology of the Namib Desert has been conducted by researchers and affiliated scientists at the Gobabeb Research and Training Centre located at the ecotone in which the Namib Sand Sea meets the



Fig. 2 The mountainous terrain adjacent to the Hoanib River in the northern Namib Desert. Courtesy Emsie Verway.



Fig. 3 The Hoanib River in flood. Courtesy Emsie Verway.

central Namib gravel plains (Henschel and Lancaster, 2013). Because of this research station, much is known about this region's unique smaller fauna, including the Namaqua chameleon (*Chamaeleo namaquensis*; Fig. 4), the web-footed gecko (*Pachydactylus ran-gei*), the shovel-snouted lizard (*Meroles anchietae*), and the sidewinder or Peringuey's adder (*Bitis peringueyi*). Many of these species



Fig. 4 A Namaqua chameleon. Courtesy Emsie Verway.

or their prey, such as tenebrionid beetles, have adapted to collect fog water from the edges of the Namib's sand dunes, which are among the tallest linear dunes in the world (Bristow et al., 2000).

Further north of the Namib Sand Sea and Namib gravel plains, biologists have mainly focused on the large mammal and plant communities concentrated in the Namib's ephemeral river systems. Among the unique plants found in this region, the continuously-growing broadleaved evergreen welwitschia (*Welwitschia mirabilis*) is an endemic gymnosperm (Henschel et al., 2019). Individuals of this species are among the world's oldest living plants, with ages estimated up to 3000 years (Bornman et al., 1972). The northern Namib Desert is unique in that it is home to three desert-adapted megaherbivores (Viljoen, 1987), including the African elephant (*Loxodonta africana*), the Angolan giraffe (*Giraffa giraffa angolensis*; Fig. 5), and the world's largest population of free-ranging black rhinoceros (*Diceros bicornis*). Smaller herbivores include Hartmann's mountain zebra (*Equus zebra hartmannae*), greater kudu (*Tragelaphus strepsiceros*), gemsbok or oryx (*Oryx gazella*), springbok (*Antidorcas marsupialis*), and steenbok (*Raphicerus campestris*). Low densities of pastoralists and their livestock live among several large carnivores in this region (Lavery et al., 2019), including the African lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), caracal (*Caracal caracal*), spotted hyena (*Crocuta crocuta*), brown hyena (*Hyaena brunnea*), and black-backed jackal (*Canis mesomelas*). Other common species



Fig. 5 An Angolan giraffe in the northern Namib Desert. Courtesy Emsie Verway.

include the common ostrich (*Struthio camelus*) and Chacma baboon (*Papio ursinus*). While charismatic large mammals are relatively well-studied in the Namib Desert, little is known about many other species. Among those understudied are one of the most diverse and successful groups of mammals in deserts—bats (Carpenter, 1969).

Bat Natural History and Species Richness Patterns

Worldwide, bats comprise more than 20% of mammals (Simmons, 2006). The majority of bat species are insectivorous and play a major role in both the regulation of nocturnal insects and the movement of nutrients across landscapes, particularly from stream corridors to roost sites (Pierson, 1998). Relative to their body size, bats travel large distances (i.e., several kilometers per night) and consume vast quantities of insects (i.e., up to 100% of their body weight each night) (Kunz, 1982; Rainey et al., 1992). Despite their recognized importance in community ecology, many aspects of their basic biology, including interspecific interactions with closely and distantly related taxa, remain unknown due to the difficulties of studying nocturnal, volant organisms. Additionally, bats generally do not fit the demographic and reproductive trends for mammals of similar sizes. Most species give birth to only one pup a year and lead relatively long lives, while maintaining a high survival rate past the first year of life (Findley, 1993; Adams, 2003). From a conservation perspective, the longevity and low fecundity rates of bats should make their research a priority comparable to large mammals.

Across the globe, bat diversity is maximized in warm, wet environments and declines as temperature and water availability decrease (McCain, 2007). Bat species richness in southern Africa generally decreases as one moves from the more mesic eastern savannas to the arid western deserts (Andrews and O'Brien, 2000; Schoeman et al., 2013; Cooper-Bohannon et al., 2016; Herkt et al., 2016; Monadjem et al., 2018). While species richness is largely driven by aridity at the regional scale (Andrews and O'Brien, 2000), precipitation totals alone do not explain patterns in bat species richness in arid and semi-arid ecosystems, illustrating the need for ground-validation of species distribution models (Rebelo and Jones, 2010). In southern Africa, species richness drops to as low as four resident bat species in the Kalahari Desert, but rises to at least 11 resident species to the northwest in the more arid Namib Desert (Fig. 6). Monadjem et al. (2018) attribute this to greater availability of roosting sites (i.e., more abundant cliffs and caves) and habitat heterogeneity in the Namib Desert. Given its long history of aridity, bats found in the Namib Desert may show sufficient adaptations to water stress and thus species richness may depend more on other features found in the local environment (e.g., roost availability, habitat heterogeneity, elevational gradients). Indeed, at least one species of insectivorous bat can survive for 72 days without water in the Namib Desert (Neuweiler, 2000).

The natural history and ecology of many African bats remains poorly understood as large parts of Africa lack survey data (Guyton and Brook, 2015). Under these circumstances, discriminating knowledge gaps from true species absences is extremely challenging and impedes conservation efforts (Racey, 2013). To contribute to addressing these gaps, I sampled bat communities in the northern Namib Desert above bodies of water, where desert bats typically concentrate in higher numbers for access to water and/or food (Adams and Thibault, 2006). From 27 February 2016 to 4 April 2017, I used a combination of invasive (i.e., mist netting) and noninvasive methods (i.e., acoustic detectors) to identify species presence and activity levels. To the best of my knowledge, this research is the first exhaustive study on bats in the region beyond a few short-term museum collection trips (e.g., Shortridge, 1934). My goal was to not only document the diversity of bats in this region, but also understand how various biotic and abiotic factors contribute to their distributions.

Study Area

My research took place in the northern Namib Desert, specifically the Kunene Region of Namibia, with sites in or adjacent to Skelton Coast National Park (Fig. 7). I regularly surveyed bats over 25 permanent bodies of water located within the catchments of the Hoanib, Uniab, Koigab, and Huab Rivers—4 of the 12 major ephemeral rivers of Namibia (Jacobson et al., 1995). In total, my study area encompassed more than 24,000 km². While mean annual rainfall exceeds 300 mm in the eastern headwater regions within these catchments, it declines to near zero in the west where the rivers meet the Atlantic Ocean (Berger, 1997; Jacobson and Jacobson, 2013). The eastern and western edges of my particular study area receive on average approximately 100 and 30 mm of annual precipitation, respectively. Permanent surface water sources in this region consist of natural springs, artificial pools constructed for wildlife and/or livestock use, and short (≤ 3 km) running water stretches. During the wet season (January to April) rivers sustain aboveground flows for on average less than 20 days per year (Jacobson et al., 1995; Leggett et al., 2001; Jacobson and Jacobson, 2013).

Bats of the Northern Namib Desert

Using a combination of mist netting and acoustic sampling, I detected 19 species of bats in the northern Namib Desert over permanent bodies of water (unpublished data). This included two species in the family Pteropodidae—the Angolan epauletted fruit bat (*Epomophorus angolensis*) and the African straw-colored fruit bat (*Eidolon helvum*)—which feed on the fruits of trees in this region. These species are the largest that I encountered (weighing ~ 90 and 200 g, respectively) and are characterized by dog-like faces

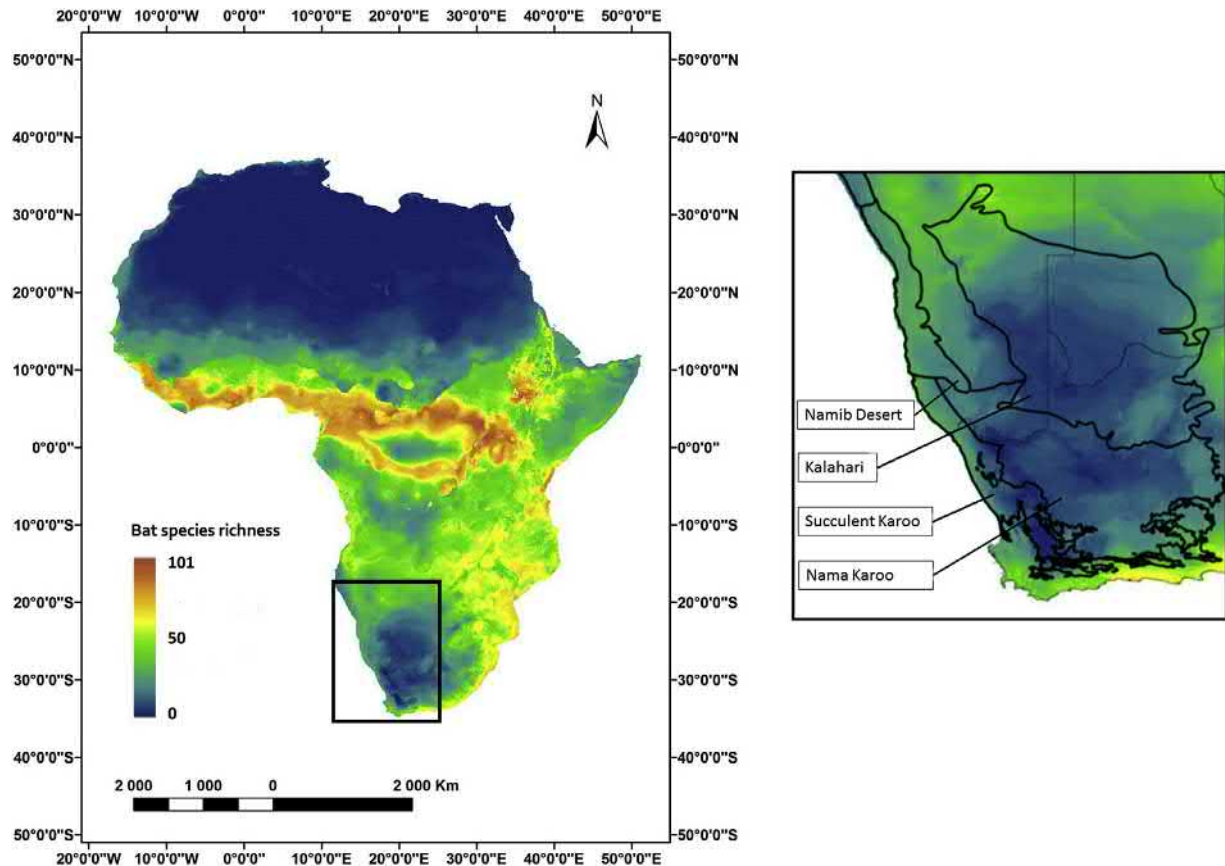


Fig. 6 Species richness patterns of bats in Africa based on potential distributions derived from niche modeling. Species richness declines east to west in southern Africa and is low in other arid zones of the continent, including the Sahara Desert in the north. The insert focuses on the species richness in arid southern Africa and highlights the spatial variability of bat diversity in this region. Reproduced with permission from Monadjem, A., Conenna, I., Taylor, P.J. and Schoeman, C. (2018). Species richness patterns and functional traits of the bat fauna of arid southern Africa. *Hystrix* **29**, 19–24.

and relatively large eyes. They do not echolocate to find their food, but instead orient by vision and sense of smell. While the Angolan epauletted fruit bat is endemic to the northern Namib Desert, the African straw-colored fruit bat is transient, only appearing during the early winter months (i.e., May and June) of my sampling period when strong winds blew in from the east.

The remaining 17 species that I detected were insectivorous species (Fig. 8). Two free-tailed bats (family Molossidae)—Roberts’s flat-headed bat (*Sauromys petrophilus*) and the Egyptian free-tailed bat (*Tadarida aegyptiaca*)—were the species most commonly captured in mist nets. Many free-tailed bats are characterized by a wrinkled upper lip, which gives them a bulldog-like appearance, and all have a tail that extends beyond the tail membrane (Monadjem et al., 2010). Long and pointed wings provide these species with swift, agile flight. They are open-air foragers with low echolocation frequencies sometimes audible to humans (i.e., any frequency ≥ 20 kHz). Roberts’s flat-headed bat has a flattened skull, allowing it to roost in narrow cracks and under slabs of exfoliating rock in small colonies (~ 10 individuals). The slightly larger Egyptian free-tailed bat similarly roosts under exfoliating rocks and crevices, but can also be found in caves, hollow trees, behind the bark of dead trees, and in buildings where they roost in larger colonies (dozens to hundreds). Both free-tailed species are permanent residents of the northern Namib Desert as they were captured and acoustically detected year-round, but at higher rates during the wet season when their insect prey is presumably more abundant.

Most of the species I captured or detected were in the Vespertilionidae family, also known as plain-faced or evening bats. These bats are characterized by a long tail fully enclosed within the tail membrane, plain noses without additional flaps of skin, and a conspicuous tragus, or specialized flap of skin in the ears of many insectivorous bats of variable shape and size. I captured two Vespertilionidae species that are endemic to the Namib Desert—the Angolan wing-gland bat (*Cistugo seabrae*) and the Namibian long-eared bat (*Laephotis namibensis*). The former was among the smallest species that I captured, weighing on average 3.5 g. Very little is known about the ecology of these species, but both are clutter-edge foragers who feed on insects in more vegetated environments. I physically captured and recorded five other species in the Vespertilionidae family that were all clutter-edge foragers, including the long-tailed serotine (*Eptesicus hottentotus*), the Cape serotine (*Neoromicia capensis*), the Zulu serotine (*Neoromicia zuluensis*), Schlieffen’s twilight bat (*Nycticeinops schlieffeni*), and the yellow-bellied house bat (*Scotophilus dinganii*). The long-tailed serotine roosts in small groups of two to four individuals in caves and rock crevices. The Cape serotine and Schlieffen’s

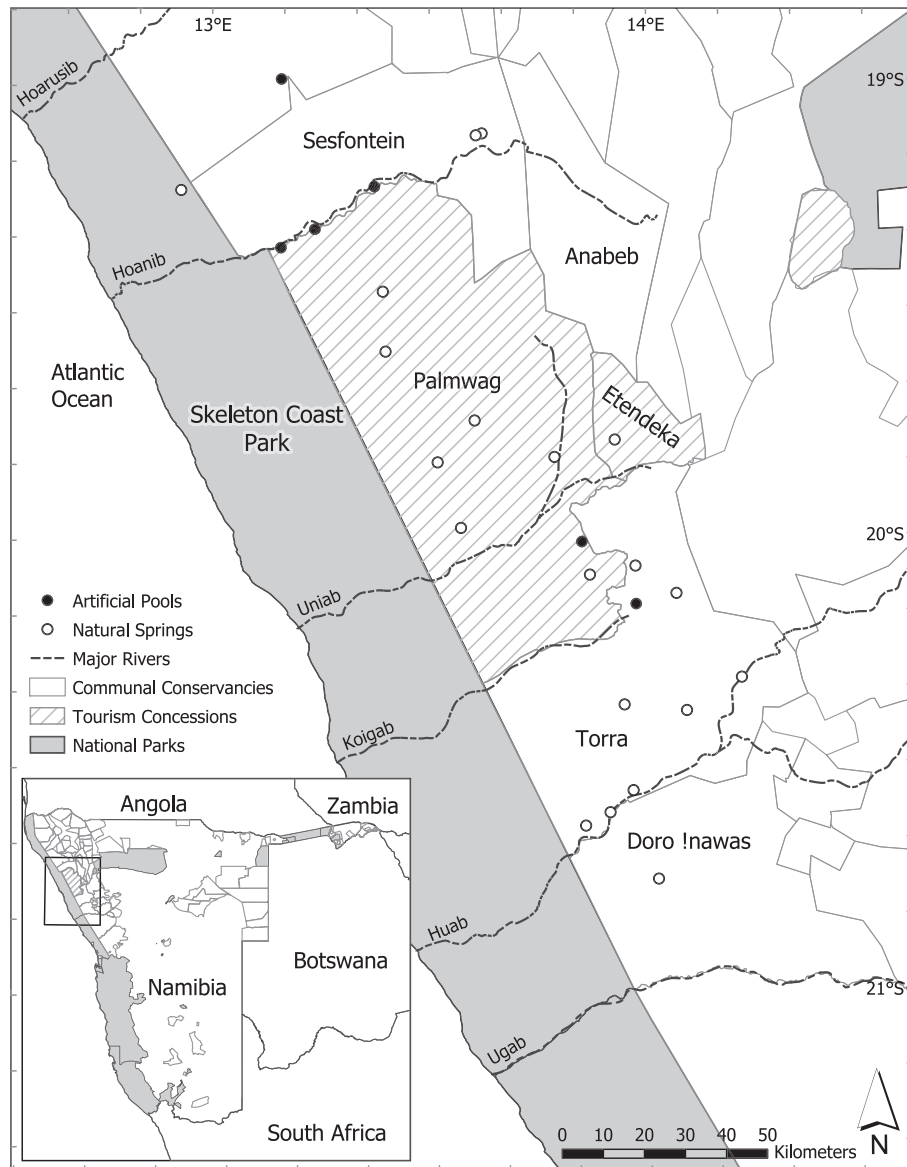


Fig. 7 Map of the 2016–2017 study area from which bats were sampled.

twilight bat roost under the bark of trees and under the roofs of houses, which explains why they were only detected at springs around human settlements (e.g., Sesfontein) in the northern Namib Desert. The Cape serotine is considered to be one of the most widespread species of bats in southern Africa (Monadjem et al., 2010). Little is known about the roosting behaviors of the Zulu serotine. The presence of the yellow-bellied house bat is often tied to the availability of trees as their roosts include tree hollows in addition to roofs of houses.

The remaining eight species physically captured or acoustically detected were cave-dwelling bats of the families Rhinolophidae, Hipposideridae, Nycteridae, and Miniopteridae. I physically captured two species of Miniopteridae—the greater long-fingered bat (*Miniopterus inflatus*) and the Natal long-fingered bat (*Miniopterus natalensis*). Species in the Miniopteridae family are characterized by an elongated bone toward the edge of their wings (i.e., the second phalanx of the third digit) that allows their wing to “bend” back onto itself, providing them with the common name of “bent-wing bats.” The long, narrow wings of these species help them efficiently fly in open areas, but they forage more in vegetated environments (i.e., clutter-edge foragers).

Unlike the other insectivorous bats described above, species in the families Nycteridae, Hipposideridae, and Rhinolophidae all produce echolocation pulses emitted through their noses (rather than through their mouths) to locate their prey and avoid obstacles at night. I captured and recorded one species of the family Nycteridae—the Egyptian slit-faced bat (*Nycteris thebaica*). The genus *Nycteris* is characterized by a T-shaped tail (i.e., the last vertebra of the tail is bifurcated at its tip). This species is a clutter forager with short, rounded wings that assist in slow, maneuverable flight. It flies low above the ground listening for prey on the surface



Fig. 8 A sample of the diversity of insectivorous bats captured in the northern Namib Desert.

with its large ears. Besides caves, the Egyptian slit-faced bat has also been found roosting in aardvark (*Orycteropus afer*) burrows, culverts under roads, and the trunks of large trees (Monadjem et al., 2010). Species in the family Nycteridae are often called “whispering bats” due to their soft, low-intensity, multi-harmonic echolocation calls, which prove difficult to record with acoustic detectors unless positioned at short distances.

I physically captured one species in the family Hipposideridae—Sundevall’s leaf-nosed bat (*Hipposideros coffer*)—but also infrequently recorded the striped leaf-nosed bat (*Hipposideros vittatus*). Both species have characteristic half-moon shaped noseleaves and highly maneuverable, broad wings. While the clutter-edge forager striped leaf-nosed bat is dependent on caves for roosting and breeding, the clutter forager Sundevall’s leaf-nosed bat utilizes sinkholes and cavities, including mines and culverts, in addition to caves for roosting habitats. Sundevall’s leaf-nosed bat had the highest frequency echolocation call recorded in the northern Namib Desert (i.e., a peak frequency of ~140 kHz).

Lastly, I recorded three species in the Rhinolophidae family—the Damara horseshoe bat (*Rhinolophus damarensis*), Dent’s horseshoe bat (*Rhinolophus denti*), and Rüppell’s horseshoe bat (*Rhinolophus fumigatus*). All three species are clutter foragers with broad wings and maneuverable flight. They have intricate noseleaves and produce distinct constant frequency echolocation calls. In addition to caves, these species roost in mines, road culverts, cavities and crevices in rock outcrops, and under thatched roofs. While these species are difficult to capture in mist nets (I only physically captured Rüppell’s horseshoe bat), they were frequently recorded over the bodies of water in my study area. The Damara horseshoe bat (*Rhinolophus damarensis*) is a near-endemic species to the Namib Desert.

Key Threats to Bats of the Northern Namib Desert

To assess threats to bats in this region, a translator and I conducted 86 semi-structured interviews of pastoralists across three conservancies in the northern Namib Desert. Among questions to assess for wildlife value orientations and the types and frequencies of interactions with wildlife in general (Lavery et al., 2019), I also inquired about bat presence and behaviors (unpublished data). Preliminary analyses of these data suggest that many respondents were aware of bats in their vicinity, but could not necessarily identify them in photographs. Interviews also indicated that bats are very infrequently killed in the region and are not consumed as food by local ethnic groups (i.e. Damara, Herero, Himba, and Riemvasmaker).

Our knowledge on the distributions and habitat requirements of bats in the Namib Desert is very restricted. Only three of the 19 species I detected in this study—the African straw-colored fruit bat, the Angolan epauletted fruit bat, and the striped leaf-nosed bat—are classified as near-threatened by the IUCN Red List of Threatened Species. The remaining species are classified as least concern although many aspects of their natural history remain unknown. It is believed that many Namib Desert bats live in rock crevices or caves and thus are unlikely to be affected by local pastoralists (Monadjem et al., 2010). Therefore, the greatest threats to bat conservation in the region likely include those related to water quality and availability (Fig. 9). The loss of or



Fig. 9 Kuidas Spring along the Huab River in the northern Namib Desert.

degradation to open water sources, such as a reduction in water quality, may be caused by increased use of these habitats by humans or livestock. Mining activity not only destroys potential bat roosting habitats, but can also pollute water sources with heavy metals that may bioaccumulate in bats (Korine et al., 2016). Given the extreme variation in annual precipitation in the Namib Desert, more research is needed to (1) confirm which species reside in the region or migrate through, (2) detail relative population trends or activity levels in this region over space and time, and (3) document the extent of bat distributions over the entirety of the Namib Desert.

Additional Threats to Namib Desert Biodiversity

As in any desert ecosystem, a major threat to people, livestock, and wildlife in the Namib Desert includes a drop in the water table due to groundwater extraction within ephemeral river catchments. The extensive water demands for mining operations, particularly for uranium, often fuels this problem (Lovegrove, 1993; Jacobson and Jacobson, 2013). Where water is used, roads, pipelines, and powerlines are constructed to access the source, damaging local habitat. The creation of desalination plants on the Atlantic coast to meet domestic and industrial water needs may reduce the current demand for groundwater extraction, but the energy requirements associated with desalination has limited its application in Namibia (Jacobson and Jacobson, 2013).

Although much of the western Namib Desert is protected and thus incurs little to no impacts of human settlements (Seeley and Pallett, 2008), off-road driving is a major threat to this region. The greatest impact of off-road driving occurs on the gravel plains where depressions left by vehicles can remain for more than 40 years. Lichens are especially sensitive to off-road driving as they grow extremely slowly and cannot repair damage quickly. This threat is largely caused by mining company vehicles on prospecting expeditions (Lovegrove, 1993), but self-drive tourists are increasingly contributing to this problem.

Climate change may exacerbate these problems as temperatures are predicted to increase and precipitation to decrease over the next 100 years (de Wit and Stankiewicz, 2006; Dai, 2011). With less rainfall, off-road tracks are less likely to be washed away and the water table will likely continue to lower. Population declines along the northern range limit of the quiver tree (*Aloidendron dichotomum*) in the Namib Desert suggests regional warming and drying has already begun, as this species is relatively tolerant of drought and climatic variation (Foden et al., 2007). While temperature increases combined with decreased rainfall should reduce any downstream flow of the Namib's ephemeral rivers, runoff patterns are also expected to change with predicted increases in rainfall intensity and potential responses of catchment vegetation (New et al., 2006; Jacobson and Jacobson, 2013).

History, Land Use, and Conservation Opportunities

Despite its isolation and low human population densities, wildlife populations in the northern Namib Desert declined over the early and mid-1900s due to expanding human settlements, war, intensive hunting and poaching, and drought (Viljoen, 1987;

Leggett et al., 2003). Since the early 1980s, conservation efforts have focused on northwestern Namibia, where wildlife populations have stabilized or increased since the country's independence in 1990 (Scanlon and Kull, 2009). Unlike most countries, Namibia's constitution explicitly safeguards biological diversity and essential ecological processes (Barnard et al., 1998). Wildlife populations have increased due to effective law enforcement, the creation of communal conservancies, and the shift in natural resource ownership from government entities to property owners. While much of the western Namib Desert is protected as national parks, parts of the coast are still actively mined with restricted public access.

The western reaches of the northern Namib Desert make up Skeleton Coast Park, while the desert to the east is primarily comprised of communal conservancies (i.e., land areas collectively managed by residents who have agreed to conserve and share their natural resources in a sustainable and economically beneficial manner; Shaw and Marker, 2010). Only established in Namibia after the 1996 Nature Conservation Amendment Act, conservancies are home to many ethnic groups (Laverty et al., 2019). Local pastoralists in the area rely on livestock for income, although ecotourism and trophy hunting are also increasingly important (Bandyopadhyay et al., 2004; Lindsey et al., 2007). Except for a veterinary fence built to restrict foot-and-mouth disease transfer, these conservancies are mostly unfenced, which permits free movement of wildlife and livestock in the desert (Rust and Marker, 2014). As in other areas in southern Africa using community-based natural resource management (CBNRM), these conservancies allow both consumptive and non-consumptive uses of wildlife, and have devolved management responsibility to local people (Van Schalkwyk et al., 2010).

To assess local conservation challenges and highlight potential means to address any problems, I analyzed additional data from the 86 semi-structured interviews of pastoralists described earlier (Laverty et al., 2019). Most respondents reported challenges related to subsistence needs, including human and livestock safety as well as reliable access to water. Over 90% of interviews mentioned carnivores killing livestock as a primary problem to living among wildlife. The most commonly reported suggestions to reduce conflicts with wildlife addressed this issue. Recommendations involved moving or reducing local predator populations, but not eliminating them entirely. Nearly 25% of interviews favored fencing predators within the conservancies, but away from human settlements. This would not only allow residents to retain the benefits that predators bring as tourist attractions, but would also provide pastoralists and their children the chance to still encounter these species. Using semi-structured interviews allows not only an assessment of the greatest perceived human-wildlife challenges in a region, but also the identification of potential management solutions most likely to be supported by local communities.

Conclusions

The Namib Desert is one of the world's oldest deserts, known for its geological variability and diverse arid-adapted biota. The northern reaches of the desert are home to African elephants, black rhinoceroses, and Angolan giraffes, which are some of the world's largest terrestrial mammals. It is also home to variety of small, understudied mammals, including at least 19 species of bats. My research in the northern Namib Desert highlighted the importance of waterholes as resources for this diverse community of desert-dwelling bats. Many aspects of the natural history of bats in this region remain unknown and require further investigation, but Namib Desert bat populations do not appear to be particularly threatened by humans at this time. Local pastoralist communities instead are largely concerned about carnivores threatening human and livestock wellbeing in addition to securing reliable access to water. Semi-structured interviews suggested that pastoralists generally tolerate living among local wildlife, but management of predator populations in particular may be necessary for long-term human-wildlife coexistence.

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Desert Conservation and Management: Biodiversity Loss

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Abstract

This article provides a comprehensive introduction to desert ecosystems and the many challenges their conservation poses to human societies. The first section focuses on highlighting the unique biodiversity capable to cope with the extreme environmental conditions that characterize deserts. We then briefly review current desert conservation policy and its effectiveness, describing some of the frameworks in place to protect desert ecosystems and the millions of people that depend upon them. The third section identifies the main anthropogenic threats to desert wildlife and discusses how climate change may substantially alter the functioning of these ecosystems. The final section details current and potential conservation strategies that may help secure this unique biodiversity in the near future.

What Are Deserts?

Deserts are a type of dryland, which are ecosystems characterized by a deficit in moisture: year on year, they lose more water via evaporation than they receive from rainfall (Table 1). In fact, annual rainfall provides on average <250 mm of water in deserts. Additionally, these ecosystems often experience extreme day and night temperatures, averaging 38 °C in the daytime and falling to −3.9 °C overnight. Deserts can be found all over the world: the world's largest desert is the polar desert of the Antarctic, which stretches over 14.2 million square kilometers. The largest hot desert is the Sahara Desert, which covers over 9 million square kilometers in Africa. Both the lowest and highest temperatures ever recorded on Earth were found in deserts: a record low of −89.2 °C has been measured in Antarctica, whereas a record high of 58 °C has been documented in the Sahara.

Deserts occur in a range of different climatic zones: subtropical, cool winter, cool coastal, and polar deserts (Fig. 1). Sub-tropical deserts, such as the Sahara, Mojave and Sonoran Deserts, are the hottest, characterized by high temperatures and warm soils. These deserts are usually found in sandy or rocky landscapes. Cool winter deserts have long dry summers and cold winters with low rainfall or snowfall. They are shielded from precipitation by neighboring high mountain ranges, such as the Himalayas (next to the Gobi) and the Andes (next to the Patagonian Desert). Coastal deserts, such as the Namib Desert and the Atacama, receive moisture from coastal fog blown in from the sea. In these deserts, plants have evolved adaptations to soak up the air moisture while a number of herbivorous animals primarily source their water from eating plants. Polar deserts, such as those found in Antarctica, receive very little precipitation and remain at very low temperatures all year round: there, the average temperature is between −10 °C and −60 °C.

Key ecological characteristics of deserts include their low productivity, sparse vegetation and minimal aquatic features. Trees are often absent, and shrubs provide incomplete ground cover. Although rainfall is generally the main limiting factor for ecosystem processes characterizing deserts, the availability of important nutrients such as nitrogen and phosphorus can also be low, further constraining primary productivity (Hadley and Szarek, 1981). Desert flora and fauna tend to be highly specialized, as the extreme conditions mean that only highly adapted species can withstand the characteristic high temperatures and long drought episodes. Some of these unique desert species can be important ecosystem engineers. For example, large shrubs and occasionally trees can create a unique shaded microhabitat for other species under which to grow. Termites aid the process of decomposition and allow

Table 1 Defining drylands by aridity (UNEP-WCMC, 2011). The aridity index is defined as the average annual precipitation divided by potential evapotranspiration

Aridity index	Level of aridity	Ecosystem	Percentage of global land AREA (%)	Locations
0.00–0.03	Hyper-arid	Desert	6.6	Sahara, Gobi, Atacama deserts
0.03–0.20	Arid	Semidesert	10.6	Australian and United States deserts
0.20–0.50	Semiarid	Grassland	15.2	Occur on outskirts of deserts
0.50–0.65	Dry-sub-humid	Rangelands	8.7	Occur on outskirts of grasslands

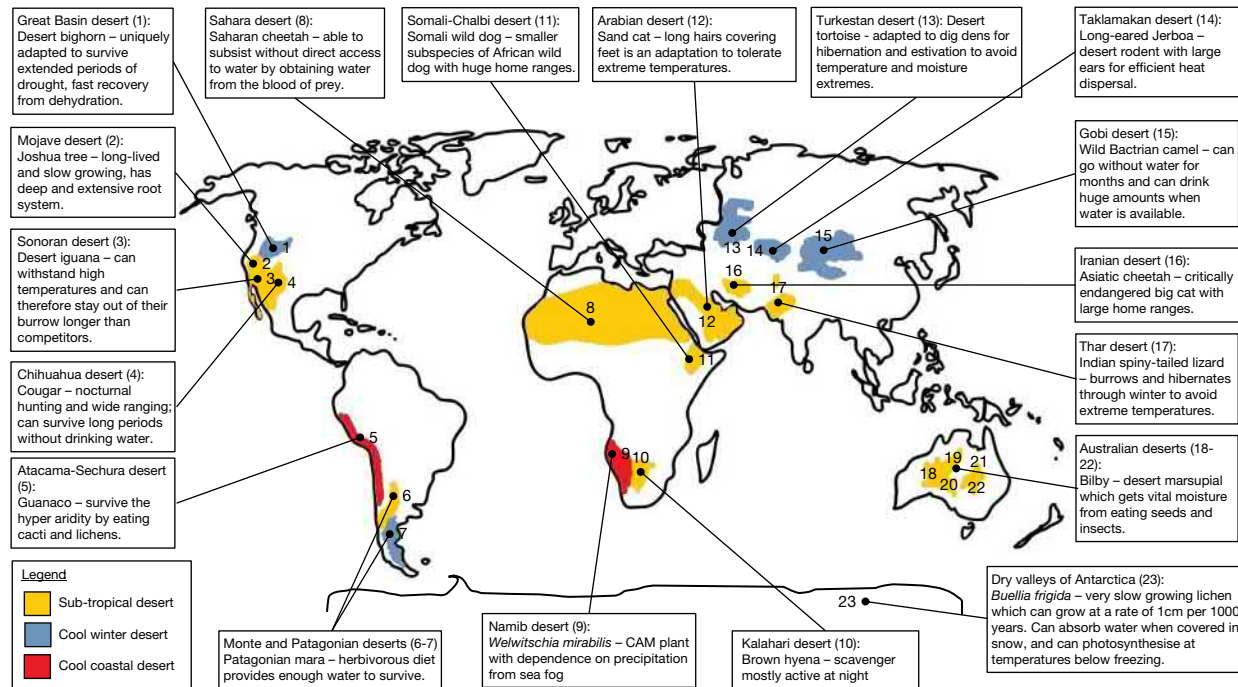


Fig. 1 World map providing examples of desert adapted species found in subtropical, cool winter and cool coastal deserts.

water to infiltrate the dry soil via the creation of micropores. Larger herbivores also control habitat structure by grazing and supporting seed dispersal, allowing other species to thrive in these seemingly hostile environments.

The main challenge faced by plants in deserts is obtaining and retaining water for photosynthesis. They generally limit water loss by reducing the size and number of stomata and by having waxy coatings and tiny leaves. But some plants (Crassulacean Acid Metabolism (CAM) plants) are also able to capture the carbon dioxide needed for photosynthesis by opening their stomata during the night, when temperatures are low and transpiration rates are slower, thereby reducing water loss. Other adaptations seen in desert plants include reduced leaf networks, such as cacti, as well as dormancy in seeds and delayed germination, which enable these plants to only reproduce and grow during the wetter periods of the year.

Lower densities of resources due to low productivity in deserts means animals often occur at lower densities and have much larger ranges than in other biomes (see e.g., [Belbachir et al., 2015](#)). Many desert animals gain enough moisture from their diet to survive the arid conditions, whereas some are able to make the most of sporadic water sources by drinking and storing large quantities in fat deposits (e.g., camels (*Camelus dromedarius*)). As well as finding enough water, limiting water loss is also an issue for animals in deserts as thermoregulation is often controlled by evaporative heat loss, like sweating or panting. In extreme temperatures, maintaining a safe body temperature is vital because hyper- or hypothermia can lead to organ failure and death. To avoid overheating, and therefore minimize the need to thermoregulate by evaporation, behavioral adaptations such as burrowing, nocturnal activity and shade-seeking are often seen in desert animals. Physiological adaptations such as long limbs or large ears can also reduce the need for evaporative cooling by providing larger body surface areas from which heat can be dissipated via radiation and convection. Some highly specialized mammals including camels and other ungulates can withstand large fluctuations in body temperature throughout the day: being able to modulate their body temperature to such an extent allow them to lessen the difference between body and air temperatures, thereby reducing the need for evaporative heat regulation ([Fuller et al., 2014](#)). Other unusual adaptations of desert wildlife include the ability to obtain drinking water from high-salt content water by secreting excess salt via salt glands, like in several species of iguana and birds. For a more in-depth introduction to desert environments, specially adapted species and the biology of the habitat, see *The Biology of Deserts – David Ward (2009)*.

Conserving and Protecting Deserts

Deserts are delicate and unique ecosystems with enormous value to wildlife and people. They are widely distributed—covering 17% of Earth's land mass—and host 25% of terrestrial vertebrate species, making them one of the richest biomes for terrestrial vertebrates ([Mace et al., 2005](#); [Millennium Ecosystem Assessment, 2005](#)). They are also rich in endemics as well as being home to some of the most endangered species in the world ([Davies et al., 2012](#)). Some of the species found in deserts are both evolutionarily and ecologically unique, giving them incredibly high conservation value because they represent a significant amount of unique evolutionary history (see www.edgeofexistence.org). However, the low productivity of deserts means that they tend to be overlooked in terms of

their conservation importance. For instance, the Saharan nations cover 43% of Africa's land mass yet only received 12% of Global Environment Facility funding allocated to Africa between 1991 and 2009 (Durant et al., 2012).

Deserts moreover support some of the most marginalized human populations in the world and provide key ecosystem services to 6% of the world's human population, many of whom are at immediate threat from rapid environmental change (Middleton et al., 2011). Traditionally, people in deserts live in hunter-gatherer communities or are pastoralists, surviving on the resources the environment provides. Often this requires a nomadic lifestyle with no permanent home base, which means that these people regularly cover large distances to secure access to water, food and material. Mobility is thus key for these communities to benefit from the ecosystem services provided by deserts.

Protecting deserts and the people in them is achieved through a number of policy frameworks. For example, the protection of deserts is a central tenant of the United Nations Convention to Combat Desertification (UNCCD). As indicated by its name, the convention primarily focuses on desertification, a type of land degradation in which a relatively dry area of land becomes increasingly arid, resulting in a loss of water bodies, vegetation and wildlife as well as widespread poverty. Desertification is thought to affect as much as one-sixth of the world's population, 70% of all drylands, and one-quarter of the total land area of the world. The current 2018–30 UNCCD framework aims to “*avoid, minimise and reverse desertification and land degradation and mitigate the effects of drought*” (<https://www.unccd.int/>). However, the UNCCD's visibility and capacity are presently relatively low, and the convention has received criticism for its lack of action (Conliffe, 2011; Tollefson and Gilbert, 2012). Together with the low level of funding targeting desert regions, achieving the 2018–30 UNCCD targets is therefore expected to be challenging. Interestingly, desertification has also been recognized as a pressing issue by the United Nations' Sustainable Development Goals (SDGs; <https://sustainabledevelopment.un.org/>), which broadly aim to encourage all nations to tackle poverty and protect the natural world into the future. SDG 15 of the 2030 Agenda, in particular, aims to “*protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss*.” Such a recognition could help catalyze conservation activities in deserts in the years to come.

The Convention on Biological Diversity (CBD) is another key policy framework for desert conservation, through its work on developing and supporting a comprehensive, effectively managed and sustainably funded global network of protected areas. Protected areas currently cover 13% of the world's dryland areas and can prevent desertification by protecting plant cover (UNEP-WCMC and IUCN, 2016; Dudley et al., 2015). However, protected area coverage is uneven among different types of drylands (Davies et al., 2012), and even in deserts affording good levels of protection (such as the Sahara), conservation priority areas have been thought to be inadequately captured by the current protected area network (Brito et al., 2016).

Other important policy instruments to safeguard deserts include regional treaties and acts, such as the Protocol on Environmental Protection to the Antarctic Treaty (The Madrid Protocol). Adopted in 1991, this protocol secured the designation of Antarctica as a natural reserve and the indefinite prohibition of mining in the area. Another interesting example is the California Desert Protection Acts (1994; 2010; 2017), which have explicitly acknowledged the importance of balancing the protection of the United States of America's (USA) unique desert landscapes for nature conservancy, recreation opportunities and development of renewable energy.

Principal Anthropogenic Threats to Desert Ecosystems

Human actions have a substantial impact on desert environments: in the Sahara-Sahel region, for example, anthropogenic actions are currently thought to represent the biggest threat to desert biodiversity (Brito et al., 2014). Until recently, illegal hunting of wildlife was the primary driver of extinction, but now resource extraction and habitat degradation due to increasing agricultural activities are becoming just as important (Newby et al., 2016). Overgrazing by livestock, unsustainable use of natural resources and conversion of natural habitat into pasture cause landscape fragmentation and lead to the destruction of valuable microhabitats. In addition, overexploitation of water resources reduces water quality, through, for example, fecal contamination and excessive eutrophication, and can lead to increased human-animal conflicts (Brito et al., 2014).

Despite the arid conditions, farming can occur in deserts. Often farmers will own livestock such as sheep, goats, cattle and camels; in many situations, farmers will have to move long distances to find suitable grazing areas and water sources for their livestock. Farming in deserts can yet impact ecosystem dynamics and cause problems for the uniquely adapted wildlife. In the Gobi Desert and throughout Patagonia and the Monte, livestock grazing is thought to affect the functioning of desert ecosystems by reducing resources for wild animals and by changing the accumulation of water in the soil, thereby promoting desertification (Ekernas et al., 2017; Bisigato and Laphitz, 2009). In addition, encroachment of agriculture and human settlement, perhaps in part due to the greening of deserts (see below), increases opportunities for human and wildlife interactions. This represents another substantial threat, which is on the increase in some deserts and is negatively affecting conservation and wildlife recovery (Newby et al., 2016). Higher levels of encroachment and human-wildlife conflicts have led to various calls for large-scale fencing. These calls have, however, been met with a certain amount of skepticism: in dryland ecosystems, animals and people indeed rely on wide-ranging mobility to access unpredictable and sporadic resources, and fences could prevent access to these resources (Durant et al., 2015). Dryland reserves often do not cover the entire extent of an animal's range, or do not include both dry or wet season ranges for migratory species (Fynn and Bonyongo, 2011). Fencing such reserves could thus disrupt access to widespread resources and seasonal migrations.

Increased human activities in deserts impact natural resource supplies, especially of water, and can increase the incidence of bushfires and disease transmissions (Newby et al., 2016). Over 70% of global water loss over recent decades is concentrated in five countries, all of which contain desert ecosystems within their national boundaries. There, water loss is thought to be primarily caused by anthropogenic actions, such as water course diversion (Pekel et al., 2016). Creating artificial water sources can lead to an unnatural spatial concentration of wildlife and livestock; these can then favor disease spread and lead to greater levels of human-wildlife conflicts, both of which ultimately potentially generating further biodiversity loss (Fig. 2; Owen et al., 2015).

Extractive activities (oil, gas, minerals) are also becoming more common in desert environments, leading among other things to the expansion of the local road networks and the construction of other new infrastructures. These developments tend to be associated with the destruction of rare habitats and frequently endanger threatened wildlife, such as the desert tortoise in the Mojave (Boarman and Sazaki, 2006) and the last wild addax population (*Addax nasomaculatus*) in Niger (Duncan et al., 2014). Rising global demand for minerals, in particular, has been causing an increase in mining activities in deserts around the world, contributing to environmental degradation in these ecosystems (Brito et al., 2014).

More roads in deserts also means that remote areas previously known to act as refuges are becoming more accessible to poachers. A number of studies have now established that roads are a significant problem for desert wildlife around the world: in the Gobi Desert for example, roads and trainlines to mining sites are dividing habitats and obstructing wide-ranging migrations (Ito et al., 2013). Road collisions are one of the main threats to Iranian desert cat populations such as the Asiatic cheetah (*Acinonyx jubatus venaticus*) and sand cat (*Felis margarita*) (Farhadinia et al., 2017; Ghadirian et al., 2016).

Drylands are primarily found in the most conflict-prone regions of the world, due in part to environmental degradation adversely affecting political and economic stability on many scales (Middleton et al., 2011). Sensitivity to conflict, together with poor governance and high corruption levels that characterize some of the countries hosting major deserts, has further contributed to desert biodiversity loss (Brito et al., 2018). In Niger, for example, oil companies and the army both ignored environmental and security regulations protecting the addax, which led to a significant decline in population size, an environmental crime that was left unpunished (Brito et al., 2018). Other reports of political corruption in Niger means that funds meant for conservation and combatting desertification have often been diverted to other uses (Usman and Adefalu, 2010). In many countries hosting desert ecosystems, conflict and political instability have promoted the circulation of firearms; used in combination with motorized vehicles, this drastic change from traditional hunting approaches can lead to unsustainable levels of offtake (Newby et al., 2016). Similarly, the use of firearms and associated danger to public safety has led to a reduced level of protection for both wildlife and the landscape, even in legally protected areas (Brito et al., 2018). The clear association between the population decline in elephants (*Loxodonta africana*) and Dorcas gazelle (*Gazella dorcas*) and the increased level of human conflicts in the Sahara-Sahel region is an example of how political instability can influence conservation outcomes (Brito et al., 2018). Similarly, illegal killings of animals were reported to accelerate 2–3 years after armed conflicts began in Libya and Mali, suggesting the organized crime and conflict had a negative effect on species conservation (Brito et al., 2018).

Table 2 describes the decline of the 14 large vertebrates typical of the Sahara-Sahel region, many of which are endemic to that part of the world. Four are now extinct in the wild and the majority have been lost from more than 90% of their Saharan range—all are now on the brink of extinction due to the combined impact of anthropogenic actions.

Deserts and Climate Change

Anthropogenic climate change is affecting biodiversity worldwide and deserts are among the places where climate change is happening at the highest speed (Loarie et al., 2009). In fact, many would argue that climate change is the dominant driver of



Fig. 2 Artificial waterpoint, and the subsequent damage to the surrounding environment, as seen from space. Image captured in the Ouadi Rime-Ouadi Achim Faunal Reserve, Chad, and obtained from Bing Maps (Microsoft 2014).

Table 2 Endangered megafauna of the Sahara-Sahel and their associated range loss.

Species	Current status (IUCN)	Range loss in Sahara (%)
Bubal hartebeest (<i>Alcelaphus buselaphus buselaphus</i>)	EX	100
Scimitar-horned oryx (<i>Oryx dammah</i>)	EW	100
Addax (<i>Addax nasomaculatus</i>)	CE	99
Dama gazelle (<i>Nanger dama</i>)	CE	99
Saharan cheetah (<i>Acinonyx jubatus hecki</i>)	CE	90
African wild dog (<i>Lycaon pictus</i>)	EN	100
Slender-horned gazelle (<i>Gazella leptoceros</i>)	EN	86
Cuvier's gazelle (<i>Gazella cuvieri</i>)	EN	66
Lion (<i>Panthera leo</i>)	VU	100
Dorcas gazelle (<i>Gazella dorcas</i>)	VU	86
Barbary sheep (<i>Ammotragus lervia</i>)	VU	77
Nubian ibex (<i>Copra nubiana</i>)	VU	10
Leopard (<i>Panthera pardus</i>)	NT	97
North African ostrich (<i>Struthio camelus camelus</i>)	LC	99.8
	(Saharan race not assessed)	

IUCN status: EX = Extinct, EW = Extinct in the wild, CE = Critically endangered, EN = Endangered, VU = Vulnerable, NT = Not threatened, LC = Least concern.

Adapted from Durant, S.M., Wachter, T., Bashir, S., Woodroffe, R., De Ornellas, P., Ransom, C., Newby, J., Abáigar, T., Abdelgadir, M., El Alqarny, H. and Baillie, J. (2014). Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. *Diversity and Distributions*, **20**(1), 114–122.

biodiversity change in tundra and deserts (Millennium Ecosystem Assessment, 2005). For example, anomalous increases in rainfall have stimulated the increase of vegetation and a re-greening of the Sahel, after decades of intense drought (Fig. 3; Brandt et al., 2014). There, woody vegetation cover has increased significantly since 2000, especially in areas undisturbed by humans (Brandt et al., 2016). In North America, changes in precipitation and temperature have increased the incidence of desert wildfires. There, increased abundance of invasive grasses, such as cheatgrass (*Bromus tectorum*), has provided perfect conditions for larger, longer-lasting and wider-spread fires which can ultimately impact the viability of threatened wildlife (Abatzoglou and Kolden, 2011). In cold deserts, thinning of ice caps, thawing of permafrost and retreat of glaciers have all contributed to increased rates of desertification. Thawing of ice and snow has indeed led to the depletion of the already sparse vegetation, opening the land to rapid erosion. The subsequent depletion of natural resources, such as water availability, has had severe impacts on local communities relying on ecosystem services for their survival. In addition, climatic volatility is increasing with climate change, impacting the frequency and severity of droughts and severe snowstorms, altogether resulting in devastation of livestock (Pragya, 2009). Critically, further thawing of permafrost is expected to result in a positive feedback loop, leading to more greenhouse gases being released into the atmosphere.

As exemplified above, changes in climatic conditions are impacting the distribution and occurrence of natural resources in deserts. In many situations, increased drought intensity, duration and frequency is expected to severely impact primary productivity and the availability of water, leading to declines in herbivore abundance (Duncan et al., 2012). Both the timing and the routes of species migrations are predicted to change as a result of altered food distribution and the spatiotemporal unpredictability of water availability, which could adversely affect the dynamics of migratory ungulate populations (Duncan et al., 2012).

The changing distribution and timing of resource availability is also expected to have a detrimental effect on the people living in desert environments. The United Nations Food and Agriculture Organization (FAO) reported that particularly high proportions of the rural poor are inhabiting drylands, where climate variability and vulnerability to droughts are the main drivers of poverty. In these areas, climate-related crop failures, food shortages and poor livestock condition can all exacerbate poverty levels (Middleton et al., 2011).



Fig. 3 Satellite imagery illustrating the greening of the Sahel (imagery from Google Earth: Landsat/Copernicus, December 1988 and December 2009).

Despite this sensitivity to changing climatic conditions, deserts actually have a huge potential to contribute to climate regulation—dryland environments indeed harbor an estimated one-third of terrestrial global carbon stock and could potentially sequester even more through improved land management (Trumper et al., 2008). This means that the conservation of deserts and those species displaying unique adaptations to drought and temperature extremes is an important endeavor in a world trying to adapt to climate change. Research into adaptive techniques focused on desert species could spearhead improvements in agriculture and human health, helping to prepare our world for the challenges ahead (Durant et al., 2014).

Conservation Strategies for Maintaining Deserts in an Increasingly Human-Dominated World (Anthromes)

The uniqueness of deserts, their outstanding biodiversity and the growing threats to their survival means they are of immediate conservation concern. Identifying conservation strategies that can address the challenges posed by rapidly changing environmental conditions is vital for the maintenance of deserts and their wildlife in the future. For these remote and inaccessible areas, new technologies could enable better monitoring, provide a better knowledge base and enable faster development of adaptive solutions to the threats described above.

Satellite remote sensing, in particular, has been shown to successfully support the identification and monitoring of anthropogenic threats to desert biodiversity, such as the detection of oil exploration activities (Duncan et al., 2014) and the creation of artificial water holes (Owen et al., 2015). Open access satellite imagery from Landsat and MODIS could prove vital for the success of conservation work as extractive activities continue to penetrate further into remote desert regions. Similarly, satellite remote sensing has been a key tool for broadening our understanding of desert ecosystem dynamics under changing climatic conditions. For example, the detection of the re-greening in the Sahel (as seen in Fig. 3; Brandt et al., 2014, 2016; Dardel et al., 2014). Because satellite remote sensing has been going on for decades, the technology also has potential to directly support environmental management decision making processes by assessing long-term trends in primary productivity, forest cover, habitat heterogeneity and threat levels within the landscape (Pettorelli et al., 2014). In Chad, for example, conservationists were able to use satellite imagery to assess the suitability of a given reserve for the reintroduction of the Scimitar-horned oryx (*Oryx dammah*) (Freemantle et al., 2013).

Camera traps are another useful remote sensing technology for the management and conservation of elusive desert wildlife. This tool, which collects on-the-ground information on species distribution, has proven particularly valuable for estimating population size, as well as for deriving information on behavior, health and species interactions. Camera traps were used to show that the critically endangered Saharan cheetah (*Acinonyx jubatus hecki*) survives in the harsh desert environments at much lower density than cheetahs in savannah environments; individuals were also found to be wider-ranging and more nocturnal (Fig. 4; Belbachir et al., 2015). The ecological knowledge gained on this particular species ultimately enables the development of a better, more targeted approach to its conservation.

Adopting a wide range of new technologies for monitoring deserts is only part of the solution to designing efficient conservation strategies for these ecosystems. Another important aspect is the relevant designation and efficient management of protected areas. Large protected areas have been suggested as a useful tool to mitigate the problem of rapid climate velocity in desert biomes (Loarie et al., 2009). By increasing the size of protected areas in the desert regions, connectivity of suitable habitat can be secured more effectively, while more space enables animals to migrate more easily as the climate changes. For protected areas to work, resources and funding are needed. Sporadic funding allocated to gazetting protected areas alone does not guarantee long-term sustainable conservation outcomes (Emerton et al., 2006). Effective management strategies, long-term planning and reliable, consistent funding are needed. It has been suggested that, in developing countries, lack of financial resources or management deficiencies (e.g., lack of skilled staff) are the main limitations to the effective management of protected areas. Collaboration between protected



Fig. 4 Camera trap image of a critically endangered Saharan cheetah, captured during a survey in Algeria.

areas is another means by which more productive and sustainable conservation can be enabled, providing a mechanism for sharing best management practice (Di Minin and Toivonen, 2015).

Well-managed protected areas not only can make a difference to the conservation of resident species, but they can also be used to support other conservation initiatives such as species translocations. Translocations can be used to enhance populations of locally threatened species or reintroduce species once found in these areas; they can also be used to introduce new species in new areas in cases where future suitable conditions are expected to be found primarily outside the historic distribution range. Translocated animals can be sourced either from neighboring areas or captive breeding programs. For instance, intercontinental collaborative captive breeding programs based in the United States, Europe and the Middle East are maintaining populations of threatened Sahelo-Saharan desert species as an insurance against extinction and are supporting reintroduction projects in North Africa (Newby et al., 2016). The first reintroduction program aiming to restore a sustainable, free-ranging population of over 500 Scimitar-horned oryx (IUCN: extinct in the wild) in a protected area in Chad began in 2016. A successful birth of a calf in September 2016 is likely to be the first scimitar-horned oryx calf to be born in the wild for over 30 years. The following year, a second phase of reintroduction released more individuals into the wild in what appears to be a very promising example of reintroduction in the wild.

The translocation of animals into protected areas is however not easy. The logistics of relocating animals and suitability of the environment in which they will be hosted both need to be determined during planning. In that respect, habitat destruction and weak no-take legislation in some of the target locations are pressures to consider before translocations (Newby et al., 2016). Areas where the animals are likely to migrate to, either during natural migrations or in response to climate change and other pressures, must also be appropriate and accessible to these animals. In addition, there are significant challenges associated with captive breeding such as retaining genetic diversity, risk of adaptation to captivity, expense, and disease risk (Newby et al., 2016). These challenges mean that translocation should be seen as a last resort solution, and all efforts should be put into avoiding species become extinct in the wild in the first place.

Protected areas can also be conducive for ecotourism, another valuable method to support conservation efforts in deserts within an increasingly human-dominated world. Ecotourism is defined as “responsible travel to natural areas that conserves the environment, sustains the wellbeing of local people and involves interpretation and education” (International Ecotourism Society, 2015). Ecotourism is expected to promote conservation by developing a local wildlife-based economy and by educating both tourists and local staff about the uniqueness, wonder and conservation value of deserts. It is the fastest growing segment of tourism, generating over US \$28 billion per year for developing countries (Kirkby et al., 2011). Successful ecotourism enterprises in deserts could be used to generate new funding streams to protect biodiversity and alleviate direct and indirect pressures to the ecosystems. Desert landscapes are advantageous for ecotourism development: they are often unaltered by human activity and offer tourists a large viewing range due to the sparsely vegetated areas (Santarém and Paiva, 2015). The endangered wildlife that inhabit deserts, as well as the unique geological features and unusual vegetation, are also likely to help attract specialized tourists (Santarém and Paiva, 2015). Ecotourism has been successfully used to promote conservation in American and Australian deserts (e.g. the Grand Canyon and Simpson Desert), where protected areas attract many visitors and are subsequently sufficiently funded and well-protected (Santarém and Paiva, 2015). Admittedly, in some countries, ecotourism is currently not a viable desert conservation option: in the Sahara and Arabic deserts, for example, the current lack of facilities to accommodate people, the poor transportation facilities and the high levels of insecurity (linked to wars, corruption and kidnappings; Brito et al., 2014) result in far fewer visitors and less income from ecotourism than could be achieved. As economies in those regions rebuild, the examples from the USA and Australia should act as a reminder that healthy deserts can foster economic growth and support development.

Conclusions

We described the fascinating and exceptional properties defining desert ecosystems. The extreme abiotic conditions that characterize deserts have resulted in the evolution of highly adapted and extremely unique animals and plants. We showed that people across the world depend upon these landscapes for subsistence, for recreation and for vital ecosystem services. These areas are now under serious threat both directly, through hunting, mining, warfare and economic development, and indirectly through climate change. Conservation action needs to be stepped up in these precious environments and we have outlined the ways in which this may be achieved. Technological advances and an increase in protected area coverage can support the conservation of these ecosystems; however, these efforts will only be successful if there is a real political will to conserve these landscapes and sufficient funding is directed towards their preservation.

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The Sahara Desert Hydroclimate and Expanse: Natural Variability and Climate Change

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Abstract

The Sahara Desert is the largest warm desert on the planet, with an area comparable to that of contiguous United States. It is a key element of the African climate system. 20th-Century trends in seasonal temperature and precipitation over the African continent are analyzed from observational data to characterize the seasonal footprints of hydroclimate change. Given the prominence of agricultural economies on the continent, a seasonal perspective was considered more pertinent than the annual-average typically used in desert characterization as the latter can mask off-setting but agriculturally-sensitive seasonal hydroclimate trends. Seasonal surface air temperature (SAT) trends show that heat stress has increased in several regions, including Sudan and Northern Africa where largest SAT trends occur in the warm season—in stark contrast with the seasonal structure of climate change over northern continents where the warming is most pronounced in winter. Precipitation trends are varied but notable declining trends are found in the countries along the Gulf of Guinea, especially in the source region of Niger river in West Africa, and in the Congo river basin. Rainfall over the African Great Lakes—one of the largest freshwater repositories—has, however, increased. The Sahara Desert is shown to have expanded over the 20th century, notably southward in summer, reflecting the retreat of the northern edge of the Sahel rainfall belt. Specific mechanisms for desert expansion are investigated.

Introduction

Climate change has footprints across the planet; however, certain regions are disproportionately affected. Africa is less responsible for the occurrence than any other continent (Fields, 2005) but more vulnerable to the effects of climate change due to its high population, low adaptive capacity, and multiple converging stressors (Fields, 2005 Busby et al., 2014 Niang et al., 2014). Africa is furthermore an interesting case study for climate change due to its unique climatological features. It is the only continent that has almost equal parts in the Southern and Northern Hemispheres and thus home to a wide variety of climate zones. It consists of the Sahara Desert and Sahel in northern Africa, the Namib/Kalahari Desert in southern Africa, tropical rainforest in Equatorial Africa, and grasslands and savanna in-between. The Sahara Desert is the largest warm desert on the planet, with an area comparable to that of contiguous United States. It is bounded to the south by the Sahel—the semiarid transition zone between approximately 10° and 20°N that receives most of its rainfall in summer. Not surprisingly, the Sahara Desert appears more expansive in winter than summer in satellite imagery. The prevalence of land-surface effects, internal climate variability, and hydroclimate sensitivity to global sea surface temperatures make the continent climatically complex (Hulme et al., 2001).

Global climate change often leads to the wet regions getting wetter and the dry ones drier (Chou et al., 2013), suggesting adverse impacts on deserts. The impact on the Sahara Desert is of great importance for the proximal countries in Northern Africa as well as for remote regions through the influence of Saharan dust on sea surface temperatures (SSTs) and Atlantic hurricane activity (Evan et al., 2016). Precipitation trends have been well-studied over the Sahel region which bounds the Sahara to the south. The drying trends over Sahel have been attributed to land-surface processes, including amplification of meteorological drought from biophysical (Charney, 1975) and surface hydrologic feedbacks (Nicholson, 2000), and to the increasing concentration of greenhouse gases and aerosol loading (e.g., Held et al., 2006). Regional and global patterns of SST anomalies have also been implicated (Folland et al., 1986 Giannini et al., 2003) as have sulfate aerosols in the Northern Hemisphere through their effect on Atlantic

SSTs (Biasutti and Giannini, 2006). The 1980s Sahel drought—the most intense episode of the 20th century—has been attributed to the circulation-change associated with Indian Ocean warming (Hagos and Cook, 2008), and the drought recovery linked to higher levels of greenhouse gases in the atmosphere (Dong and Sutton, 2015). Sahel rainfall has also been linked to variability in SSTs in the North Atlantic, the Atlantic Multidecadal Oscillation (AMO) (Mohino et al., 2011 Knight et al., 2006). This oscillation has a period of 50–80 years, with the cold AMO phase coincident with extended droughts over Sahel (Kavvada et al., 2013). Causes of surface temperature variability in this region are less well-established (Collins, 2011), although an amplified warming signal has been detected over the Sahara Desert in recent decades (Cook and Vizi, 2015 Vizi and Cook, 2017). The importance of agriculture in the African economies warrants a seasonally resolved analysis of hydroclimate variability and change over the continent. This article updates the findings of Thomas and Nigam (2018) from analysis of more extended observational records, especially precipitation's. It documents the regional structure of the century-long seasonal temperature and precipitation trends over the African continent, focusing on how these trends affect the Sahara Desert boundary and expanse. The data sets and analysis methods are described in “**Datasets and Analysis Method**” section. The seasonal climatology of near-surface air temperature (SAT) and precipitation over the African continent are outlined in “**Seasonal Climatology**” section to provide context for characterization of the century-long seasonal hydroclimate trends in “**Centennial Trends in Surface Air Temperature and Precipitation**” section. Expansion of the Sahara Desert over the 20th century is discussed in “**Change in Sahara Desert Expanse over 20th Century**” section, and the summer expansion mechanisms investigated in “**Sahara's Expanse: Variation and Potential Mechanisms**” section. Concluding remarks, including sensitivity of the desert expansion rate to the analysis period follow in “**Concluding Remarks**” section.

Datasets and Analysis Method

The study focuses on centennial trends rather than multidecadal variability (a more common analysis focus) of African hydroclimate. The analysis period begins in 1920, in order to focus on the relatively stable rain gauge network period (Nicholson, 2018, personal communication). Linear trends in temperature and precipitation are computed from least-squares fitting using seasonally-averaged data. To avoid confusion given Africa's expansive footprints in both hemispheres, seasons are referred using their boreal definition: Winter is the average of December, January and February (DJF), and so on.

Observational Datasets

Three independent analyses of the observed SAT are used in this study: The CRU-TS4.02 monthly analysis from the Climate Research Unit of the University of East Anglia (Harris et al., 2014) is available on a 0.5° continental grid for the January 1901–December 2017 period, from http://www.cru.uea.ac.uk/cru/data/hrg/cru_ts_4.02/. Berkeley Earth's monthly analysis of surface temperature anomalies relative to the 1951–80 climatology (Rohde et al., 2013) is available on a 1.0° grid for the period January 1850–December 2015; it is downloadable from <http://berkeleyearth.org/data/>. Finally, the NASA Goddard Institute for Space Studies (GISS) analysis of SAT anomalies relative to the 1951–80 baseline (Hansen et al., 2010) is available on a 2.0° land-ocean grid for the January 1880–September 2015 period from <http://www.esrl.noaa.gov/psd/data/gridded/data.gistemp.html>. The data sets are converted to a common 0.5° resolution using bilinear spatial interpolation.

The Global Precipitation Climatology Centre (GPCC; Becker et al., 2013) provides a monthly analysis of precipitation from quality-controlled rain gauge data; GPCC's Full Data Reanalysis Version 8 data is available on a 0.5° continental grid from January 1901–December 2016, from <http://www.esrl.noaa.gov/psd/data/gridded/data.gpcc.html#detail>. Sahel rainfall is defined as the area-averaged rainfall within 20°W–40°E and 10°N–20°N, following Held et al. (2006).

Several climate indices are used in the study: The Atlantic Multidecadal Oscillation (AMO; Enfield et al., 2001 Kavvada et al., 2013) index was computed as the linearly detrended seasonal SST anomaly over the North Atlantic (75°W–5°W, EQ–60°N), following Enfield et al. (2001); SST from the HadISSTv1.1 analysis (Rayner et al., 2003) was used. An additional marker of AMO variability was the principal component extracted from an extended empirical orthogonal function analysis of HadISSTv1.1 SST data (Guan and Nigam, 2009). The Pacific Decadal Oscillation (PDO) index was obtained from <http://jisao.washington.edu/data/pdo/> where it is defined as the leading principal component of monthly SST anomalies in the North Pacific basin (poleward of 20°N; Zhang et al., 1997).

Desert Expansion

Two methods are used to quantify desert expansion during the 1920–2016 period. In both methods, a precipitation threshold is chosen to define the desert boundary; two threshold values—100 mm/year (or 0.274 mm/day) and 150 mm/year (or 0.411 mm/day)—based on previous definitions of the annual-mean Sahara boundary (e.g., Tucker and Nicholson, 1999 Berman and Dewit, 1983) are used. Two thresholds were considered so that sensitivity of the desert-area trend to the desert definition can be assessed. Desert area is computed by taking an area sum after weighting each latitude-longitude grid-cell area by the cosine of its latitude; GrADS function “*asum*” was used. In the first method, referred to as the area-trend method, the desert area is computed each year in each of the four seasons and annually, with average rainfall less than 0.274 mm/day (0.411 mm/day) defining deserts. The 1920–2016 linear trend in the computed area characterizes desert expansion/contraction over the 20th century.

In the second method, referred to as the endpoint method, the precipitation climatology (P_{clim}) and the linear trend in precipitation (P_{trend}) over the 97-year record are first computed at each grid point, seasonally and annually. These are used to create two maps: Precipitation at the end (from the plus sign in the following expression) and at the beginning (from the minus sign) of the record,

$$P = P_{\text{clim}} \pm (P_{\text{trend}}) * 47 \text{ years}.$$

The desert extent is then mapped in these synthetic 1920 and 2016 precipitation distributions at the endpoints of the record based on the chosen threshold, with the difference yielding desert expansion over the time period.

In both methods, the desert area computation is restricted to North Africa (northward of 5°N) to preclude inclusion of the Namib/Kalahari Desert, and to the west of 43°E to avoid inclusion of the Horn of Africa.

Each method has its advantages: The area-trend method is conceptually simple but it does not reveal the desert advance/retreat regions. The endpoint method is slightly more complex but it easily outlines the desert advance/retreat regions. Both methods should yield similar results except, perhaps, when the analysis period is comparable to the embedded variability timescales—a condition met with AMO, especially when it is influential on regional hydroclimate. The aliasing of multidecadal variability into linear trends would be inevitable in this case but with the two methods having different exposure to aliasing from the inverted order of the area-computation and linear-trend operations.

To remove the influence of multidecadal variability in the precipitation record, seasonally stratified precipitation fields are regressed onto the seasonal AMO and Pacific Decadal Variability—North Pacific (PDV-NP) SST principal components (PCs, which are orthonormal) over the full period (1920–2016). The influence of these multidecadal variability modes is computed by multiplying their time-independent regression coefficients by their time-varying PC, seasonally. The influence is then subtracted from the precipitation record, and the desert expanse recomputed, as above.

Statistical Significance

Statistical significance of individual linear trends at the 95% confidence level was assessed using the “AdjSE+AdjDF” approach of [Santer et al. \(2000\)](#). This method employs an effective sample size based on the lag-1 autocorrelation coefficient of the regression residuals.

Seasonal Climatology

The seasonal cycle of rainfall over the African continent is shown in [Fig. 1](#). Rainfall is larger, not surprisingly, in the summer hemisphere: Over tropical West Africa, Sahel, and Ethiopia in boreal summer (JJA), and over the Congo and Zambezi basins in austral summer (DJF). The similarity of the March–May and September–November rainfall distributions—with equatorial Africa, especially Congo basin being the rainfall focus—reflects the similar insolation distribution over the continent at these times—from the Sun being overhead twice at the equator each year, during the vernal (late March) and autumnal (late September) equinox. The Sahara Desert is, however, drier in spring than it is in fall, and the Namib/Kalahari Desert likewise in its spring than fall. The strong latitudinal gradient in precipitation at the southern boundary of the Sahara is a notable feature in all seasons, with the movement of this gradient over time having implications for regional agricultural productivity.

The desert boundary, based on the seasonally averaged rainfall threshold of 0.274 mm/day (or 25 mm/season), is shown in thick black contours in [Fig. 1](#). The Sahara expanse is largest in boreal winter and smallest in boreal fall (see [Table 1](#)); the larger threshold (0.411 mm/day or 37.5 mm/season) yields the smallest expanse in summer; both analysis methods return the same seasons for maximum and minimum expanse (cf. [Table 1](#)). In winter, the dry region extends from ~10°N to ~30°N but in summer, the Sahel rainfall pushes Sahara’s southern edge closer to 20°N. Likewise, the Namib/Kalahari Desert in Southern Hemisphere Africa is most expansive in austral winter, consistent with the notion of the desert location under the descending branch of the meridionally overturning Hadley Circulation; the Hadley descent is most intense in each hemisphere’s winter (e.g., [Nigam and Chan, 2009](#)).

The seasonal distribution of climatological SAT is also shown in [Fig. 1](#), using red contours. The warmest temperatures are found in boreal summer when SAT exceeds 33 °C over western Saharan Africa. The coldest temperatures occur northward of the Atlas Mountains in Algeria and Morocco in boreal winter. A local minimum in SAT exists over Ethiopia in all four seasons due to the high elevation of the Ethiopian Highlands. The spring and fall distributions exhibit less similarity in SAT than in rainfall, especially over Sub-Saharan Africa where SAT is notably higher in boreal spring; likely, because of the preceding dry season (winter) and depleted soil moisture stores which would preclude latent disposition of increased spring insolation.

Centennial Trends in Surface Air Temperature and Precipitation

The 1920–2014 period linear trend, obtained by averaging the linear trend in three independent analyses of SAT observations, is shown in [Fig. 2](#). Notable features include:

- Larger trends over Northern Hemisphere Africa, in all seasons.

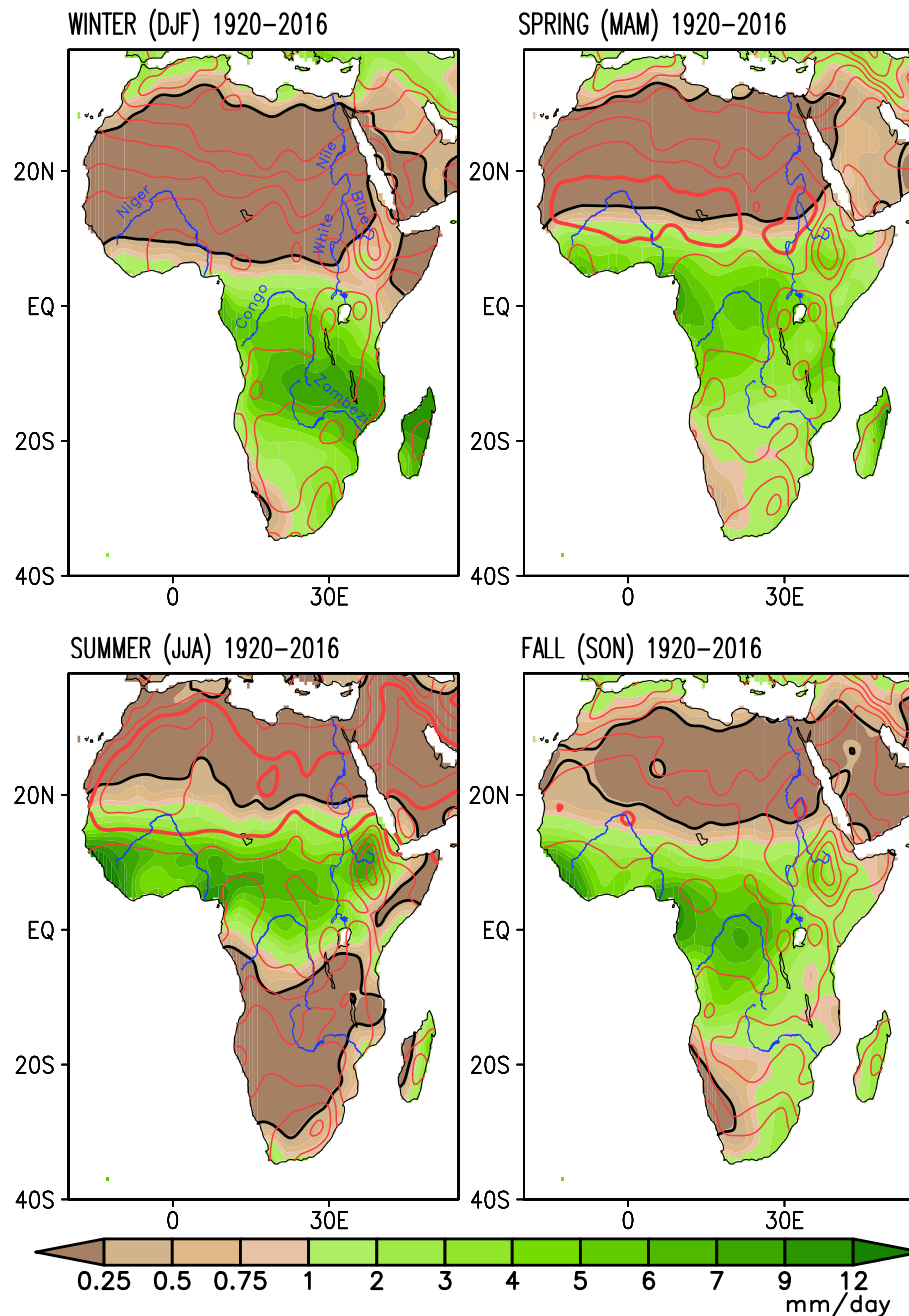


Fig. 1 Seasonally averaged precipitation (brown-green shading; mm/day) and surface air temperature (SAT; red contours; °C) for the period 1920–2016. Precipitation is from GPCP and SAT from the CRU-TS4.02 dataset. The non-uniform shading interval for precipitation is indicated through the color bar. Contour interval for SAT is 3.0 °C. Fields are shown after 9 applications of the 9-point smoother (*smth9*) in GrADS. Thick red contours indicate the 30 °C isotherm, while thick black ones mark the 0.274 mm/day precipitation isoline. Note, 0.274 mm/day is equivalent to 100 mm/year, a precipitation-based definition of the annual-mean Sahara Desert boundary (Tucker and Nicholson, 1999). Major rivers are shown in thin blue lines and labeled in the top-left panel.

- A regional maximum over Sudan, particularly, in spring when SAT trends are larger than 1.5 °C/century; interestingly, this is the Nile River basin.
- A pronounced seasonality in trends over North Africa, near Algeria and Tunisia. Trends here range from ~0.8 °C/century in winter to as much as 2.0 °C/century in summer.
- A comparatively muted seasonality in trends over Southern Hemisphere Africa except for Angola, Namibia, and Botswana where austral winter (JJA) warming is stronger than in other seasons.
- The similarity in boreal winter and fall SAT trends over much of the continent.

Table 1 Expansion of the Sahara Desert: seasonally and annually during 1920–2016, based on the movement of the 100 and 150 mm year^{−1} precipitation isolines.

	Threshold (mm/year)	Winter (DJF)	Spring (MAM)	Summer (JJA)	Fall (SON)	Annual mean
Climatological Sahara extent (km ²)	100	14,057,000 (13,084,000)	10,743,000 (10,093,000)	7,858,000 (6,528,000)	7,809,000 (6,577,000)	7,518,000 (6,920,000)
	150	14,855,000 (13,998,000)	11,556,000 (10,829,000)	8,628,000 (7,622,000)	8,910,000 (8,137,000)	8,591,000 (7,967,000)
Sahara Expansion (km ²)	100	602,000 (578,000)	461,000 (410,000)	241,000 (140,000)	150,000 (35,000)	212,000 (302,000)
	150	532,000 (576,000)	426,000 (355,000)	262,000 (202,000)	114,000 (240,000)	346,000 (391,000)
Sahara Expansion (% of seasonal (annual-mean) climatological area)	100	4.3%; 7.1% (4.4%; 8.4%)	4.3%; 6.1% (4.1%; 5.9%)	3.1%; 3.2% (2.1%; 2.0%)	1.9%; 2.0% (0.5%; 0.5%)	2.8% (4.4%)
	150	3.6%; 6.2% (4.1%; 7.2%)	3.7%; 5.0% (3.3%; 4.5%)	3.0%; 3.0% (2.7%; 2.6%)	1.3%; 1.3% (2.9%; 3.0%)	4.0% (4.9%)
Countries Affected (obtainable only from the endpoint method; the ones in bold are most impacted by the desert advance)		Libya, Egypt, Western Sahara, Central African Rep., Cameroon, Nigeria, Guinea, Cote D'Ivoire, Sierra Leone, Ghana, Togo, Benin	Sudan, Chad, Niger, Nigeria, Mali, Senegal	Mauritania, Western Sahara, Sudan	Western Sahara, Mauritania, Sudan	Egypt, Mauritania, Mali, Chad, Sudan

The expansion is computed using both area-trend and endpoint methods; endpoint values are in parentheses. The areal values are rounded off to the nearest 1000 km² (which is about 1/3 of the 0.5° grid cell area at the equator). DJF refers to boreal winter months (December, January, and February), and so on. The impacted countries are identifiable only from the endpoint method; the ones in boldface are the most impacted by desert advance.

The seasonality of SAT trends can potentially modulate the amplitude of the seasonal cycle of SAT in the recent period. An increasing amplitude can worsen heat stress, as over central-southern Sudan (to the west of the White Nile) where 20th century SAT trends are large, especially in spring when the SAT peaks climatologically as well (cf. Fig. 1)—leading to hotter springs and increased heat stress. Likewise, over Northern Africa, including Algeria, Tunisia, and Libya, SAT trends are largest in summer, the season of greatest climatological SAT. In both these regions, the SAT trends amplify the seasonal cycle of regional SAT, intensifying heat extremes.

The linear trend in seasonal precipitation over the 20th century (1920–2016) is shown in Fig. 3 against the backdrop of the climatological dry regions (brown hatched). The centennial trends show interesting variations, corroborating the importance of seasonal analysis. For example, over Kenya and Tanzania, declining rainfall trends are present in boreal spring while increasing ones are present in fall and winter, each with socioeconomic implications. An annual-mean perspective, where offsetting seasonal trends average out, is not particularly relevant in understanding the impact of climate change on a continent where the seasonal rhythm of rainfall is the pace maker.

The rainfall decline is notably intense—with no seasonal offsets—over tropical West Africa. The decline is broadly focused on the source region of the Niger river, extending across several Gulf of Guinea rim countries (Senegal, Gambia, Guinea-Bissau, Guinea, Sierra Leone, Liberia, and Cote d'Ivoire). The rainfall decline exceeds 1.0 mm/day/century here, i.e., a 10–25% decline in seasonal rainfall over the course of the 20th century. The boreal spring decline is most impressive, percent-wise, and must lead to an increasing delay in the build-up of Niger streamflow after the dry winter season.

Another region showing rainfall decline in all seasons is the Congo river basin, especially the part encompassing Angola and the Democratic Republic of the Congo. Rainfall decline here is impressive in the shoulder seasons (spring and fall), with trends exceeding 0.6 mm/day/century where seasonal rainfall is ~6.0 mm/day. The thick brown lines in Fig. 3 mark the climatological desert boundaries, facilitating a visual assessment of desert expansion/contraction over the 20th century—the focus of the next section.

The African Great Lakes, especially Victoria and Tanganyika, are one of the few regions on the continent exhibiting increasing 20th-century rainfall, mostly in austral spring and summer. This is interesting because of the proximity of this region to the source of the Nile river, and implications for streamflow in the downriver region.

Change in Sahara Desert Expanse Over 20th Century

The overlay of 20th-century precipitation trends on the climatological dry zones in Fig. 3 suggests that the Sahara Desert has expanded equatorward. The Sahara's extent has been investigated using vegetation-zone boundaries as markers of desert expanse and its interannual variation (Tucker et al., 1991 Tucker and Nicholson, 1999). Although interesting because of the implicit seasonal context, these studies analyzed short records such as the recent 10–17-year long satellite-era ones. Unfortunately, desert trends over such periods reveal little about the secular changes in Sahara because of the potential aliasing of decadal-multidecadal variability into short-period trends.

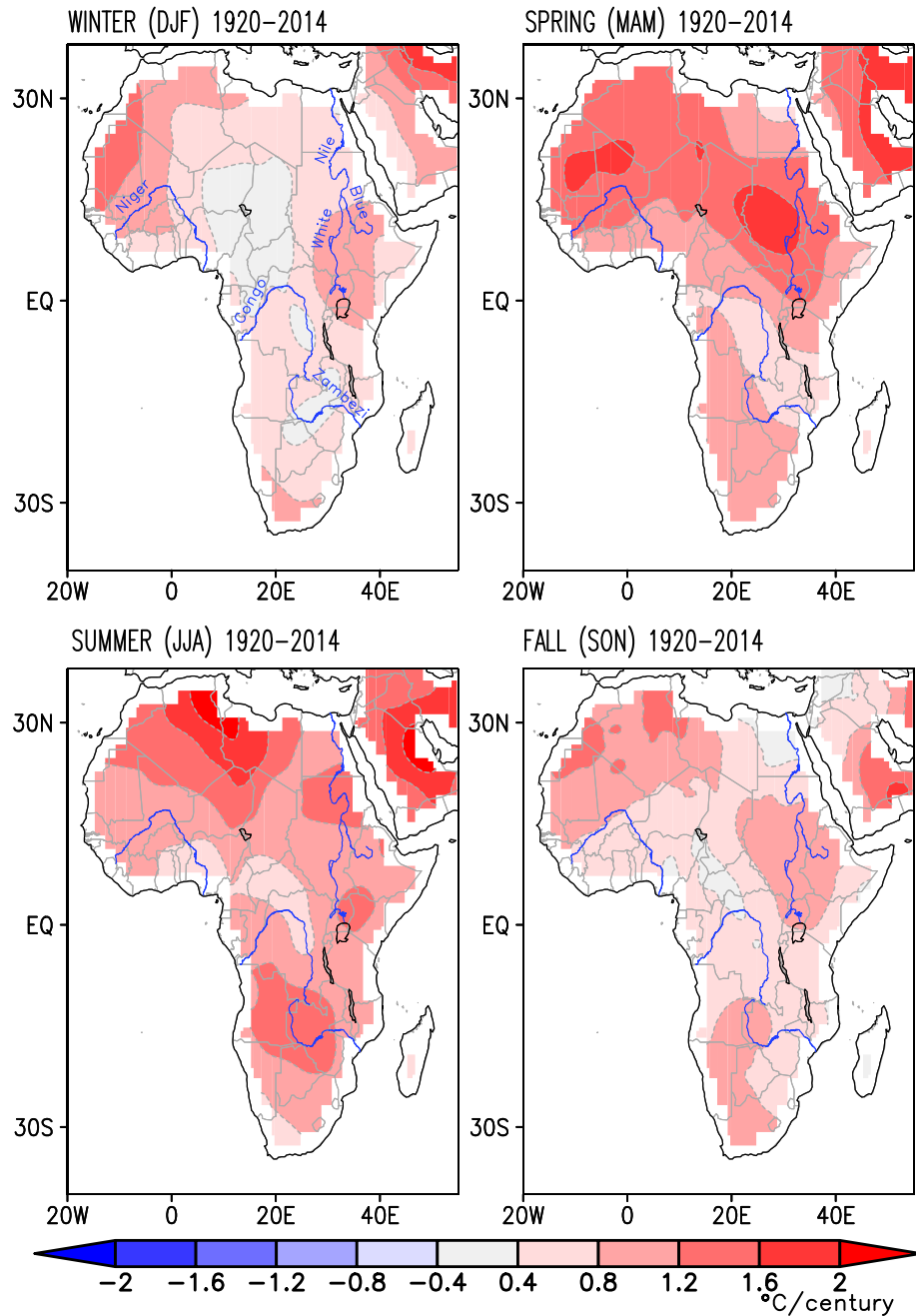


Fig. 2 Linear trends in near-surface air temperature (SAT) over the African continent during 1920–2014. Average of the trends in three independent SAT analyses—CRU TS4.02, Berkeley Earth, and NASA-GISS—is shown after each was interpolated to 0.5° resolution. Contour and shading are at $0.4^\circ\text{C}/\text{century}$ interval. Fields are shown after 9 applications of the 9-point smoother (*smth9*) in GRADS. Country boundaries are shown in thin gray and major rivers in thin blue lines.

Here, we use the precipitation rate to demarcate the desert region. The use of precipitation rather than vegetation allows analysis of a longer record notwithstanding the spatiotemporal sparseness of the precipitation record in the early 20th century. A direct relationship between precipitation and the vegetation index found in previous studies (Tucker and Nicholson, 1999; Tucker et al., 1991) supports such a strategy. In Fig. 3, a 100 mm/year (or 0.274 mm/day; one of the two thresholds discussed in “Desert Expansion” section) precipitation isohaline demarcates the deserts, seasonally. A light brown hatching of the regions where climatological precipitation is less than this value marks the desert expanse which is monitored using the two methods discussed in “Datasets and Analysis Method” section.

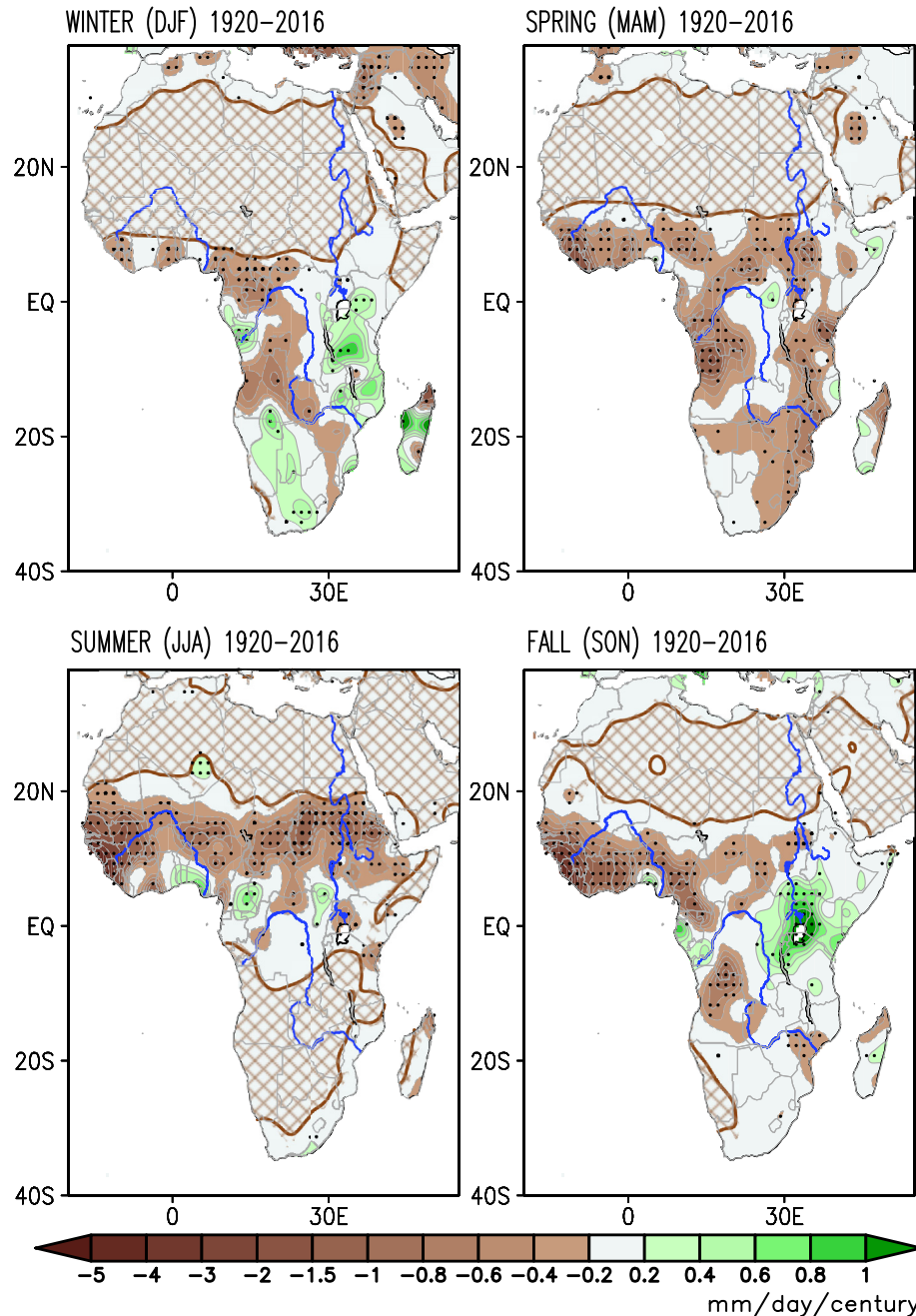


Fig. 3 Linear trends in seasonal precipitation over the African continent during 1920–2016, from the 0.5° resolution GPCP dataset v8, in units of mm/day/century. The non-uniform *contouring and shading* interval is indicated via the color bar. *Thick solid brown contours* mark the 0.274 mm/day climatological precipitation isoline, and brown hatching indicates regions where climatological precipitation is below 0.274 mm/day (or 100 mm/year)—a precipitation threshold used for defining the Sahara Desert. Fields are shown after 9 applications of the 9-point smoother (*smth9*) in GRADS. Trends significant at the 95% confidence level are denoted with *black dots*. Major rivers are shown in *thin blue lines* and country boundaries in *thin gray lines*.

Sahara's Advance

The 20th century change in Sahara Desert's seasonal (annual) extent is displayed in Fig. 4B; the change is estimated using the endpoint method. Brown shading, which represents the desert's advance over the century, shows modest northward creep in boreal winter albeit not uniformly across longitudes; northward expansion is seen in Egypt and Libya, while modest desert retreat is seen in Algeria. The desert has encroached equatorward as well in winter, with notable intrusions in Nigeria, Cameroon, and the Central African Republic.

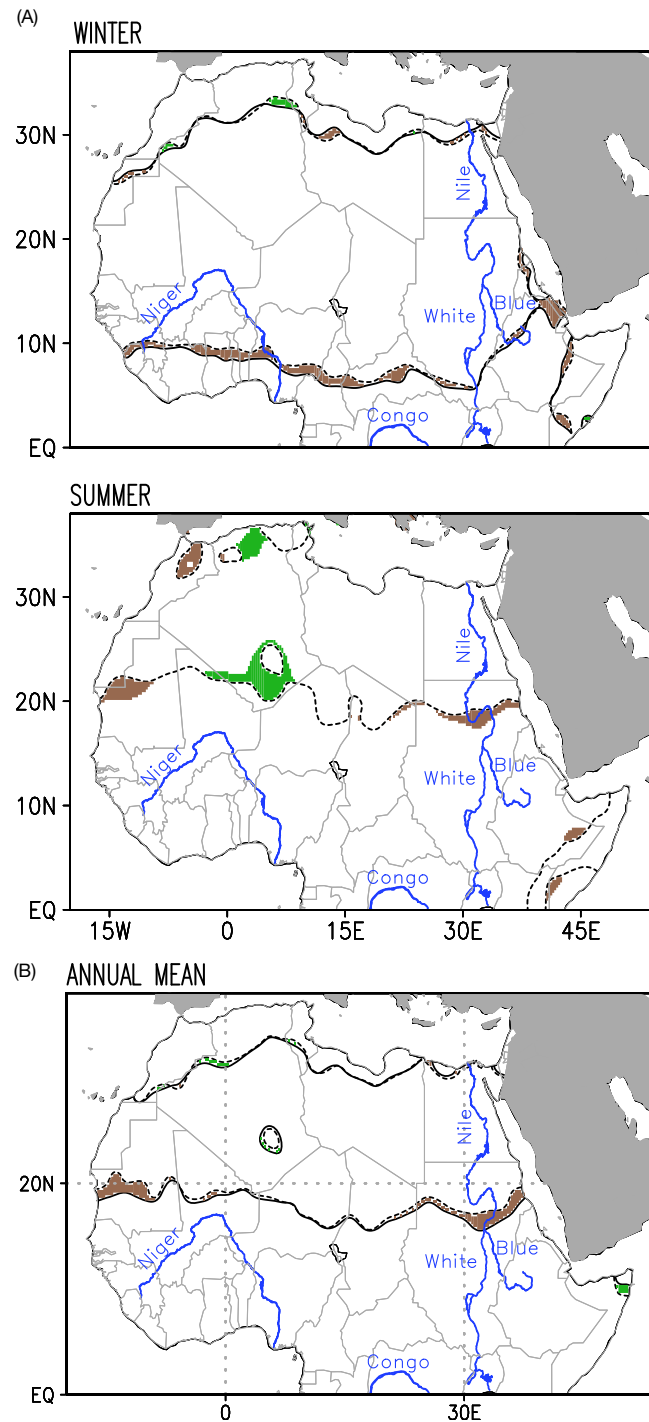


Fig. 4 (A) Advance/retreat of the Sahara Desert over the 1920–2016 period, *seasonally*. The *dashed (solid) brown lines* denote the 0.274 mm/day precipitation isolines in the synthetic 1920 (2016) precipitation map obtained from the endpoint analysis (cf. Section “**Datasets and Analysis Method**”). The *brown (green) shaded areas* denote desert advance (retreat). [Note, the observed precipitation distribution at the period endpoints cannot be directly used as it includes both interannual and decadal-multidecadal variability components and the sought-after linear trend.]. (B) Advance/retreat of the Sahara Desert over the 1920–2016 period, *annually*. Desert identification here is fully consistent with the canonical desert definition based on annual rainfall; a 100 mm/year threshold is used. Rest as in (A).

The centennial change in Sahara’s summer extent is primarily through the equatorward advance of its southern boundary (Fig. 4) which is climatologically located at $\sim 20^{\circ}\text{N}$ because of robust summer rainfall in the northern Tropics including the Sahel (EQ– 20°N ; cf. Fig. 1). Much as with the winter desert advance at the northern boundary, the southern advance is sectorally focused, with intrusions in Mauritania to the west and Sudan in the western sector, and desert retreat again seen in Algeria. The countries most impacted by the Sahara Desert’s seasonal and annual-mean advance are listed in Table 1.

The annual-mean desert advance (using the 100 mm/year threshold), displayed in Fig. 4B, provides context for the seasonal analysis and comports with canonical definitions of the desert based on annual-mean rainfall threshold (e.g., Tucker and Nicholson, 1999). The annual-mean advance shows primarily southward creep relative to the annual-mean desert boundaries.

Sahara's Expanse

A quantitative analysis of the centennial change in Sahara Desert's seasonal and annual-mean expanse is reported in Table 1. The primary analysis is based on the area-trend method but the endpoint method which generated Fig. 4 is also used with both desert definitions to assess the sensitivity of the desert expansion to analysis methods. The expansion has been largest (area-wise) in boreal winter (602,000 km², a 4.3% increase) and smallest in fall (150,000 km², a 1.9% increase) using the area-trend method with a 100 mm/year threshold. Estimates of desert expansion from the endpoint method (noted in parentheses in Table 1), with the same threshold, also yield maximum desert expansion in winter (578,000 km², a 4.4% increase) and a minimum in fall (35,000 km², a 0.5% increase).

The sensitivity of the desert expansion rate to the desert-defining precipitation-threshold is also reported in Table 1. A less stringent definition, based on a 150 mm/year threshold, leads to more expansive deserts—not surprisingly—but also smaller centennial expansions, indicating a tightening of the meridional precipitation gradient over the century. Percentages drop on both counts but Sahara's expansion remains robust with the largest expansion, as before, in boreal winter (532,000 km², a 3.6% increase). The weakest expansion again is in fall (114,000 km², a 1.3% increase). Results from the endpoint method using the larger threshold are qualitatively similar to those obtained with the lower one.

The sensitivity analysis indicates that while desert expansion and related area-percentage vary somewhat with the desert definition and analysis method, one can reasonably conclude that the Sahara Desert has grown larger, area-wise, more in winter than summer and fall. The countries bearing the brunt of the Sahara's southward advance in winter are the Gulf of Guinea rim countries, including Nigeria, Cameroon, and Central African Republic, and Mauritania and Sudan in summer (cf. Fig. 4B). Notable against these areas of desert advance (brown shading) over the northern continent are areas of green over Algeria in winter and summer, reflecting Sahara's retreat.

The expansion of the Sahara Desert is also analyzed using the conventional annual-rainfall based desert definition. Table 1 (last column) notes the findings from the area-trend and endpoint methods for both the 100 and 150 mm/year annual-rainfall thresholds. During 1920–2013, the Sahara expanded by over 212,000 km² (or ~2200 km²/year) based on the 100 mm/year definition, indicating a ~3% expansion over its climatological area (7,518,000 km²). The desert's southward creep is the major contributor to the expansion.

Sahara's Expanse: Variation and Potential Mechanisms

The Sahara Desert's expanse during the 1920–2016 period, and not just at its endpoints, is the focus of this section. The desert expanse in summer is plotted in Fig. 5, along with select indices of circulation and SST variability that can provide insights on causal mechanisms. The focus is on the summer season, when variations in the Sahara Desert's expanse arise mainly from the north-south movements of its southern boundary which borders the Sahel.

The summer expanse (solid black line) exhibits both an upward trend, highlighted by the linear fit (thin black straight line), as well as notable decadal-multidecadal variations. As areal changes result from the equatorward advance or poleward retreat of the desert's southern edge, Sahara's summer expanse should be inversely linked to Sahel rainfall (defined in "Observational Datasets" section) which is plotted with a dashed black line. The inverse relationship can be visually discerned: for example, the drying of the Sahel—a multidecadal decline in Sahel rainfall from the mid-1950s to the mid-1980s—is coincident with Sahara's expansion; the full-period correlation ($r = -0.78$) points to a strong inverse relationship. The anti-correlation allows tapping into extensive analyses of Sahel rainfall variability in the attribution of the summer waxing and waning of the Sahara Desert.

The Sahel rainfall has been linked to AMO variability among other processes, as noted in the introduction. To assess links between AMO and the Sahara's extent, two markers of AMO variability are plotted in Fig. 5 along with their correlations to Sahara's expanse and Sahel rainfall. The AMO SST principal component (dashed red line), obtained from an evolution-centric spatiotemporal analysis of seasonal SST anomalies in the 20th century (Guan and Nigam, 2009), shows higher correlations with both Sahara's expanse ($r = -0.49$) and Sahel rainfall ($r = 0.55$) in boreal summer.

Decadal SST variability in the Pacific basin, as typified by Pacific Decadal Oscillation (PDO; Mantua et al., 1997), is also linked with Sahel rainfall (Villamayor and Mohino, 2015; Nigam and Ruiz-Barradas, 2016) albeit not as strongly as the AMO. The PDO index, shown in Fig. 5 (solid blue line), is correlated with Sahel rainfall and Sahara's expanse at -0.34 and 0.27 , respectively. A contemporaneous statistical link between the PDO and Sahel rainfall seems more intriguing than the rainfall's link with the AMO because the AMO SST anomalies are proximal, with their tropical footprints offering potential mechanisms for their influence. In contrast, the PDO SST anomalies are distant and focused in the midlatitudes, disadvantaging them from the influence potential perspective, especially as only the tropical SST anomalies are generally viewed as influential on faraway regions. Interestingly, these disadvantages disappear once one recognizes that PDO is not without tropical links: Guan and Nigam (2008) showed the PDO counterpart in their spatiotemporal analysis (called Pacific Decadal Variability–North Pacific, or PDV-NP) to be linked with the

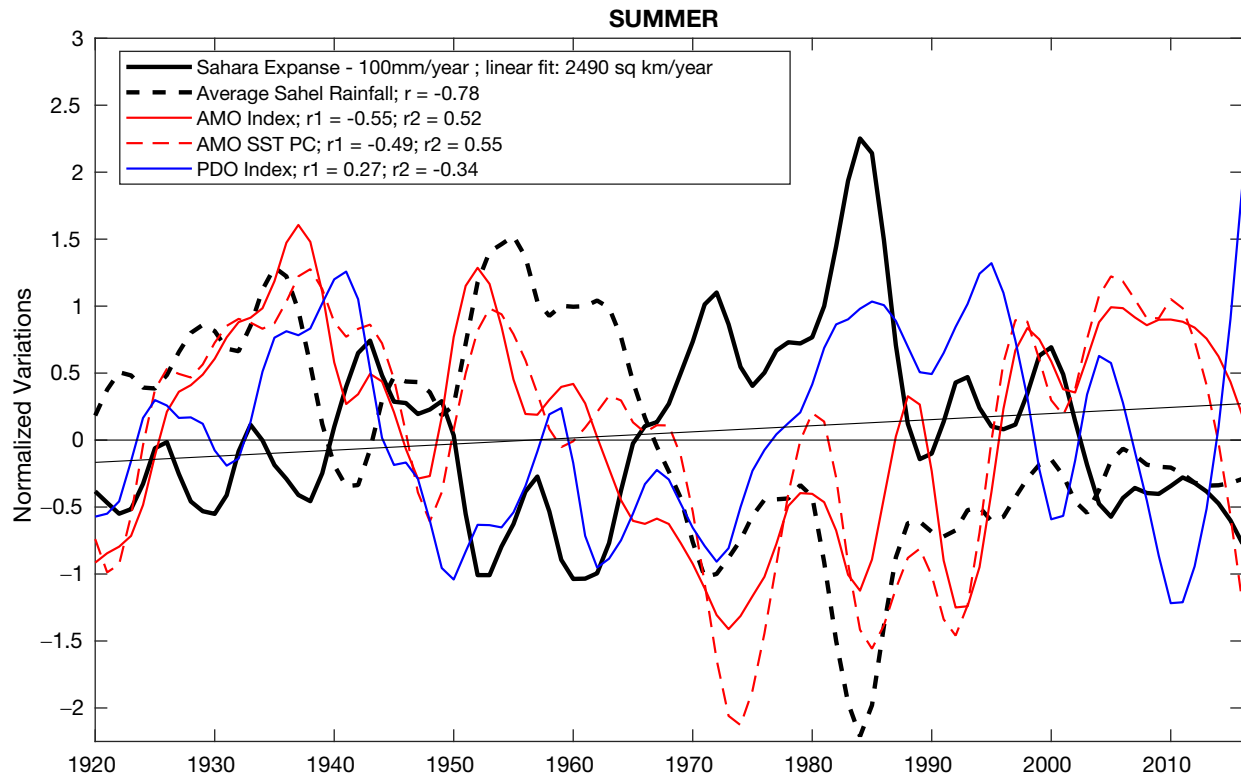


Fig. 5 Sahara Desert's expanse during 1920–2016. The boreal summer expanse is shown in the top using the *thick solid black line*. The *thin black straight line* is the linear fit to the desert expanse over the entire period—it is the basis of the area-trend analysis reported in [Table 1](#). Indices of sea surface temperature (SST) and rainfall variability with potential links to Sahara Desert's summer expanse are shown in the bottom panel, along with their correlation coefficients. For each index, r_1 (r_2) is the correlation between the index and Sahara expanse (Sahel rainfall). The Atlantic Multidecadal Oscillation (AMO) and Pacific Decadal Oscillation (PDO) are displayed using their common SST indices; an SST principal component (PC) based AMO index is also shown. The rainfall over Sahel is plotted as well. All time-series depict normalized anomalies after 10% Loess smoothing; the time-series for the latitude of the Northern Hemisphere (NH) subtropical jet was smoothed with a 20% Loess function. All time-series are normalized by their standard deviations; these are 703,903 km², 0.458 mm/day, 0.245, 1.005, and 0.977 for Sahara's summer expanse, Sahel's summer rainfall, AMO index, AMO PC, PDO index, respectively.

tropical Indian and Pacific basin SSTs. The PDO's modest influence on Sahel rainfall, if realized through its tropical Indian Ocean footprints, would be consistent with the findings of [Hagos and Cook \(2008\)](#).

Secular change is often characterized using the century-long linear trends in observational records, as for Sahara's expanse in [Fig. 5](#). The linear trend is however susceptible to the aliasing of multidecadal variability should the latter be prominently manifest in the record—the case in summer (cf. [Fig. 5](#)). The origin of the 95-year linear trend (referred as secular trend) in Sahara's summer expanse remains to be elucidated; the elucidation is challenging, especially, for an observational analysis. Trends on centennial and longer timescales can potentially result from the interaction of multidecadal variabilities (e.g., PDO and AMO) and, of course, from the increasing concentration of greenhouse gases and aerosol loading (e.g., [Held et al., 2006](#)) and the related secular change in SST distribution ([Nigam and Ruiz-Barradas, 2016](#); see their Fig. 23.6).

Concluding Remarks

The footprints of climate change over the African Continent are widely noted (e.g., [Niang et al., 2014](#)) but even region-specific descriptions seldom stray from the annual-mean displays of hydroclimate trends—and this over the African continent, where the seasonal waxing and waning of the Sahara Desert and the complementary expansion and retraction of Sahel rainfall rule the northern continent. Southern Hemisphere Africa is also no stranger to the munificence of the seasonal cycle which brings rainfall and life to vast stretches of the Namib/Kalahari Desert in austral summer. The utility of the seasonal perspective in climate change, i.e., seasonally-stratified centennial trends in precipitation and near-surface air temperature, for long-term water resource management cannot, of course, be overstated.

The centennial SAT trends are larger over the northern continent, especially in the northwestern sector and North Africa (Algeria and Libya) where they are often greater than 1.6 °C/century. The trends are furthermore pronounced in boreal summer, amplifying the regional seasonal cycle, i.e., making hot summers even hotter and exacerbating heat-related distress. Another focal point of large

SAT trends over north Africa is the region to the west of the White Nile (central-southern Sudan). For context, these SAT trends are not much smaller than the largest SAT trends over North America (e.g., Nigam et al., 2017, Fig. 1), that are manifest over western-central Canada in winter.

Centennial precipitation trends, especially the drying ones are notable over the tropical continent, i.e., in the region between the Sahara and the Namib/Kalahari deserts. River-basin wise, impressive drying trends are found in the source region of the Niger River from spring to fall, i.e., in the local rainy seasons; the decline is impressive because it represents a 10–25% decline in seasonal rainfall over the course of the 20th century. Another focal point of declining rainfall is the Congo River basin, and the Blue Nile source region around Lake Tana in Ethiopia; the latter in boreal summer—the peak rainfall season.

When viewed together, the key features of the centennial drying trends can be interpreted as the southward expansion of the Sahara Desert during boreal spring-to-fall, or alternatively, as the equatorward retreat of the northern edge of the Sahel rainfall belt. We show that the Sahara Desert has expanded over 1920–2016—by 2–4% depending on the season—using conservative estimates from the area-trend method. The southward expansion in summer is linked to the SST variability in the Atlantic and Pacific basins on multidecadal timescales, through Atlantic Multidecadal Oscillation (AMO) and Pacific Decadal Oscillation's (PDO) impact on Sahel rainfall. On centennial timescales, the summer expansion is related to aliased multidecadal variabilities and the increasing concentration of greenhouse gases and aerosol loading (e.g., Held et al., 2006).

The seasonally stratified analysis of hydroclimate trends—the focus of the study—was complemented by analyses of the annual-mean trends. The latter, more directly relatable to deserts in view of the canonical annual-rainfall based desert definition, also revealed expansion for the Sahara Desert over the 20th century (Table 1, Fig. 6). The rate is however sensitive to the analysis period, from exposure to the aliasing of multidecadal variability (e.g., AMO and PDO) and variability of the rain gauge network.

The aliasing of multidecadal variability in the linear trend in Sahara's annual-mean expanse is directly investigated during the relatively stable rain-gauge network period (1920-onwards) in Fig. 6. The AMO and PDO influences are removed from the precipitation record via linear regression. The annual-mean Sahara Desert expanse sans the multidecadal modes' influence is shown in Fig. 6 by the red curve. The AMO and PDO's influence is strong during the 1970s–90s when the red curve diverges from the black one; its contribution to the drying of the Sahel during the 1950s–80s is quite evident. The different linear trends of the two time series indicate that slightly more than half of the 2.8% increase in Sahara Desert's annual-mean expanse during 1920–2016 is attributable to multidecadal variability, and the remaining half to the rising greenhouse gas concentrations and aerosol loadings, and other factors.

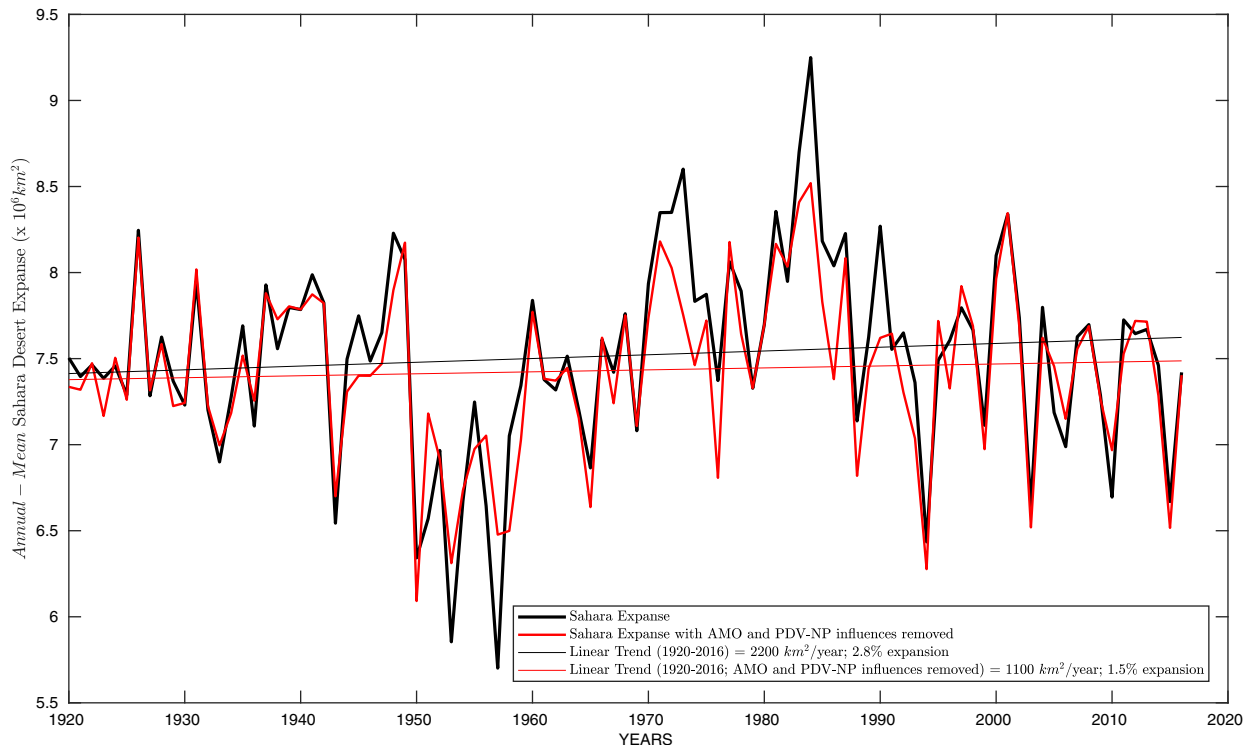


Fig. 6 Annual-mean Sahara Desert expanse (km^2 ; computed from the area-trend method). The linear trend is shown for 1920–2016 (thin black line); the value is noted in the legend. The red curve and the corresponding 1920–2016 linear trend (thin red line) track desert expanse after removal of the Atlantic Multidecadal Oscillation (AMO) and Pacific Decadal Oscillation's (PDO) influence from the precipitation data set. The area-expansion percentages are all computed using the 1920–2016 climatological desert expanse.

The Sahara Desert has expanded by 2–4% over 1920–2016. The southward desert creep is pronounced at both ends of the tropical continent—in Mauritania and Mali in western Africa and in Sudan at the eastern edge of the continent. A more reliable measure of the land-area lost to desert encroachment each year is, perhaps, obtained by distributing the annual lost area uniformly across longitudes, which leads to a southward desert creep of about 2/3 Km each year along the entire ~5000 Km width of the Sahara. Future desertification will depend upon the phases of related sea surface temperature variability as well as anthropogenic effects. Continued expansion of the Sahara Desert will likely have significant implications for agriculture, water resources, and food security in the proximal countries.

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Desert Conservation and Management: Biodiversity Threats From Invasive Weeds

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Abstract

Weeds are the first stage of recovery following disturbances that reduce perennial plants and biological soil crusts (BSCs). This normal weed function can change when people transport weeds to habitats outside their home range. Freed from their usual consumers and competitors, some of the transported weeds invade the new habitats and replace local plants. Diversity, productivity, and stability decline. As their abundance increases, the invaders' dried remains often provide fine fuel that increases ignition and spread of lightning and human caused fires. In some regions, desert fire frequency has increased beyond the recovery ability of native vegetation and BSCs. This creates new plant communities dominated by weeds sometimes with a few of the smaller, faster-growing members of the original plant community. Control of invasive weeds requires public participation, inventories, habitat protection, monitoring systems, prioritization of species and sites, and strong financial support.

Weeds Characteristics

Plants that disperse rapidly, mature quickly, and tolerated drought and full sunlight, can colonize disturbed sites and grow free of interference by plants from the predisturbance vegetation.

While some plants live long deliberate lives of hundreds or thousands of years, natural disturbances opened an alternate evolutionary pathway for weeds. Except for the spreading roots of a few species and some short-lived trees, most weeds live only 1 or 2 years. Even among those with long-lived roots, the parts we see, the shoots are short-lived.

Weeds' short lives and their preference for full sun does not allow them to compete with large, mat-forming, shade-casting, long-lived climax species of the desert grasslands, shrublands, woodlands, and forests. During the normal course of events, those species spread back into disturbed sites and replace the weeds. The long-lived plants persist until another catastrophe exposes the soil and allows the weeds to return.

In deserts, drought-tolerant weeds spread across upland slopes, and moisture-dependent invaders spread on the banks of streams and springs. Rabbitfootgrass (*Polypogon monspeliensis*) in Fig. 1, is a weed of moist habitats that invades along the banks of desert streams. However, weeds are the supreme opportunists, capable of rapid spread during brief benign periods. And many can reproduce at a broad range of sizes. When moisture is limited, summer cypress (*Kochia scoparia*) for example, can mature and produce a single spike of seeds at a height of three centimeters. When sufficient moisture is available, summer cypress can reach four meters in height and produce many seed laden spikes. Weeds that colonize stream banks can spread to upland habitats following periods of above average rainfall. They may seem to disappear when average conditions return, but many leave behind persistent propagules ready to continue advancing in future wet periods.



Fig. 1 Rabbitfootgrass (*Polypogon monspeliensis*). This moisture-loving grass probably originated in Europe, but it became a global cosmopolitan so early in human history its origin is uncertain. This one is growing beside the Agua Fria River, a small desert stream in central Arizona, United States. Rabbitfootgrass can spread through dry upland sites by following roadside ditches where it joins a diverse collection of invasive weeds.

Few weeds of the deserts grow well in the shade of other plants. In most instances, weed establishment requires disturbed habitats. Some invasive weeds might be capable of invading undisturbed natural vegetation, but determining this is difficult. Livestock grazing, food and fuel gathering, and farming have damaged ecosystems across the desert biome.

In their rapid response to vegetation destruction by construction, fires, floods, and foraging animals, weeds resemble human first responders. Weeds cover exposed soil and provide protection from erosion. Following geomorphic events such as landslides, weed roots and decaying parts bind sand and gravel and rebuild the soil.

However, when people disperse weeds beyond their normal range, problems can develop. Freed from home range predators and competitors, a few introduced weeds will invade local habitats and replace climax plants.

Dispersal

Animals, wind, water, and people walking, boating and driving serve as weed dispersal vectors. [Frenkel \(1970\)](#) once analyzed the debris traps of the drains at a car wash and found the propagules of over 400 species. Most weed propagules spread adhered to surfaces, moving through guts, or mixed with seeds of agricultural crops. However, people have planted many weeds to provide soil stabilization, produce food for livestock and people, serve as garden ornamentals, and more. On numerous occasions, introduced species have spread beyond their intended purpose, invading native vegetation with disastrous effects. For example, many nurseries sell Dalmatian toadflax (*Linaria dalmatica*) for flower gardens. Toadflax ([Fig. 2](#)) roots delve deep, persist for years, and may send up shoots outside flowerbeds. Controlling Toadflax is easy in small gardens and yards, but seeds often spread into native vegetation. Once established, the plant's deep root system has allowed it to become a permanent resident across thousands of hectares of arid shrub and woodlands.

Weed dispersal vectors deposit propagules along roads and fences, beneath the distal tips of tree and shrub branches, and on the margins of irrigated pastures and crops. Besides seeds, weed propagules include underground rhizomes, surface stolons, and vines. These organs can grow 10 m or more per year, but none of them attains the velocity achieved by the seeds of weeds whose seedpods explode when they become dry. These botanical cannons propel their seeds surprising distances. The bursting seedpods of creeping woodsorrel (*Oxalis corniculata*), a petite weed of stream banks and field margins, can shoot seeds over three meters.

Most introduced plants do not spread or even survive to form a persistent population. Some grow scattered among other plants and have limited impact. Some remain in small patches for years and then begin to spread. However, less than 10% of the hundreds of plant species people accidentally or intentionally introduce to the deserts will invade and replace native vegetation.

Fire

Fire was not important in deserts before invasive weeds arrived. Unlike plants of the temperate grasslands and semiarid evergreen woodlands and forests, desert plant cover is often too discontinuous for fires to spread. In fact, [Rogers and Steele \(1980\)](#) found almost no fire-tolerant traits among the dominant shrubs and trees of the Sonoran Desert. Introduced weeds that invaded the Great



Fig. 2 Dalmatian toadflax (*Linaria dalmatica*). This common horticultural flower, spreads by seeds and long-lived underground roots.

Basin Desert in the 19th century (Watson, 1871) provided a new source of fine fuel that facilitated ignition and spread of fires. These weeds became the most disruptive invasive species on Earth (Brooks et al., 2004). These weeds are more efficient than natives are at extracting moisture and nutrients from desert soils. They fill the gaps between perennial plants and give fires continuous fuel in which to spread. Over the past century, desert fires have decimated millions of hectares of desert vegetation. Figs. 3 and 4 illustrate the change from shrubland to grassland dominated by fire prone weeds (fireweeds) in the cool-climate Great Basin Desert. Fig. 5 illustrates the same change in the warm-climate Sonoran Desert.

Triangle bursage and brittlebush (*Ambrosia deltoidea* and *Encelia farinosa*) with an understory of the invasive annuals dominate rocky slopes. Before the 1974 fire tall saguaro and rounded paloverde and ironwood (*Olneya tesota*) in a matrix of shrubs covered and crowned the slopes and ridges.



Fig. 3 Cedar Mountains, United States, 1901. This photograph illustrates typical salt desert shrubland dominated by Shadscale (*Atriplex confertifolia*) at lower elevations of the Great Basin Desert. Photograph by G. K. Gilbert © U. S. Geological Survey Photograph Library (public domain).



Fig. 4 Cedar Mountains, United States 2008. Matching the scene in **Fig. 3**, this photograph taken September 1, 2008 shows that most of the shrubs are gone. The loss of plant cover is particularly striking on the slopes at the base of the cliffs. A dry thatch of cheatgrass (*Bromus tectorum*) and redstem filaree (*Erodium cicutarium*) covers the ground.



Fig. 5 Saguaro fire site, February 29, 2008. Two fires (1974 and 1987) transformed the saguaro-paloverde (*Carnegiea gigantea*-*Parkinsonia microphylla*) woodland of this Sonoran Desert site to an annual grassland dominated by the invasive annuals, red brome (*Bromus rubens*), redstem filaree (*Erodium cicutarium*), and more.

Biological Soil Crusts

Two groups of microorganisms are important constituents of desert ecosystems. Biological soil crusts (BSCs) composed of soil particles, cyanobacteria, algae, microfungi, lichens, and bryophytes form thin layers on exposed soil surfaces between desert plants. BSCs cover and stabilize the soil, capture nutrients, and retain moisture. They make up over 70% of the living ground cover in parts of the deserts. BSCs develop best with full sun exposure, and their cover increases as annual precipitation and vascular plant cover decrease. **Fig. 6** shows a common biological soil crust of the cool Great Basin Desert. Though the rough texture traps wind-blown seeds, few roots penetrate the crust's surface.



Fig. 6 Pinnated biological soil crust in a protected area of the Great Basin Desert. Such crusts allow desert soils to accumulate moisture and nutrients and they block invasive weeds. Livestock trampling can eliminate them.

Arbuscular mycorrhizal fungi (AMF) sheath and connect the roots of desert plants. AMF are obligate symbionts whose carbon nutrition depends on the photosynthetic success of their host plant. They benefit hosts by facilitating absorption of water, phosphorus and other micronutrients, and they can increase nodule formation by nitrogen-fixing bacteria.

Well-developed BSCs and AMF help prevent entry by invasive weeds. BSCs limit germination sites and AMF increase the success of native plants and can inhibit the growth of invasives (Vogelsang and Bever, 2009). Wheeled vehicles, livestock trampling, and fire can destroy BSC and AMF continuity. Like desert vascular plants (Rogers and Steele, 1980), BSCs, and AMF can take decades to recover (Root et al., 2017).

Invasive Weed Management

Early detection of new weeds is critical. In just a few years, invaders can form large colonies with many distant satellite populations. Rapid response measures must be ready to control or eradicate detected invaders before they can spread. Managers prepare treatment plans for invaders, establish schedules for repeated surveys, and enlist public help in finding and treating invaders. Detailed information for weed management is available online from the North American Invasive Species Management Association. The Center for Agriculture and Biosciences International (location) provides news and national weed control plans and policies indexed by subject and by location.

Strategic Concepts

Adaptive management

Numerous biological and environmental factors make weed growth so unpredictable that weed managers view all treatments except the most direct physical removal of weeds as experimental. They define the methods and study the results of each treatment to gain insights that allow shifting tactics to improve results.

Justification for invasive weed management

The field of Weed Science developed in response to the loss of crop yields because of weed invasions. Learning to measure the economic cost of wildland invasions has taken longer but is now well developed (Farber et al., 2006). De Groot et al. (2012) provide estimates of the monetary value of ecosystems and their services across global biomes, and Naylor (2000) discusses the reduction of ecosystem services by invasive species.

Prevention, regulation, and ecosystem maintenance

Weed management involves defense and target hardening. Defense requires policies and regulations to stop weed imports by people, livestock, and equipment. Target hardening requires landuse policies that maintain healthy native vegetation. Many regions have border inspection regulations in place to prevent entry of plants and diseases that invade farms and natural vegetation. Likewise, weed managers work with other landuse managers to promote public education and sustainable landuse. For example, the Play, Clean, Go program cited below in the List of Relevant Websites publicizes the invasive species problem and enlists citizen participation in curtailing weed spread.

Early detection, monitoring and response

Effective weed control requires rapid detection and response. The goal is to prevent maturation and seed production by potential invaders. It requires preliminary inventories and regular monitoring to discover new populations before they can spread. Because of the uncertain survival of new weeds, the first response to most species is establishing a monitoring schedule. This does not apply to weed species known to be invasive in similar sites.

Satellite populations

Weed populations grow by expanding their boundary and by long-distance dispersal to establish satellite populations. Since a single plant can produce thousands of seeds, tiny satellite populations of one or a few plants can serve as significant sources for further invasion. As the area of an infestation grows, the proportion of each plant's propagules falling among the plants within the occupied area will increase and the proportion falling outside the area will decline. Thus, the rate of expansion will decrease as the infested area grows. Because the rate of expansion is greater for small satellite populations, managers give treatment of satellite populations the highest priority.

Coordination with neighbors

Property boundaries do little to influence weed dispersal and establishment. Fences may stop the first wave of tumbleweeds, but they are not an effective barrier. Coordinating prevention, inventory, and control with neighboring agencies and private landowners is part of weed management planning.

Control versus eradication

Immediate eradication of invasive species is sometimes the most cost effective option. Annual costs to control weeds increases as new species arrive and existing species spread and establish satellite populations. Even though eradication of a widespread species is difficult and costly, it might be essential to preserve high-priority habitats. [Mack and Foster \(2009\)](#) found that eradication requires the following:

1. An effective prevention plan,
2. An exhaustive inventory,
3. Readily visible target species,
4. Accessible and easily inventoried and monitored terrain,
5. Target species with short-lived seed banks (3 years maximum),
6. Target species with small enough range that available resources are adequate for inventory, eradication, and monitoring,
7. Monitoring support well past the expected duration of the seed bank. Otherwise, seedlings and other individuals missed in inventories, treatments, and subsequent monitoring will produce new seed banks.
8. Guaranteed continuity of public and financial support.

Inventory

Inventories to discover and map invasive species rely on two approaches. The first is for areas of continuous weed cover. It produces vegetation maps made from sample observations and aerial photographs. The second method is for areas of scattered weed presence. It creates descriptions and small maps of weed occurrence. Continuous weed cover develops as repeated fires, floods, or overgrazing weaken and remove native vegetation. Scattered weed presence occurs around trees, along fences, and in patches of disturbed vegetation. Since some weed species become invasive after years of quiet residence, initial inventory maps and descriptions should include all known weed species. Managers can treat known invaders immediately and set monitoring schedules for other weeds.

Prioritizing Weed Species and Sites in Deserts

Prioritizing species

Prioritization equips weed managers for immediate response when known invaders appear. The practice begins with literature searches for information on the ecology, distribution, and control of each individual weed species. The information produced by the searches will provide a first approximation of the relevant characteristics and control treatments for species in, or likely to reach a management area. Critical considerations for prioritizing species include potential for arrival, establishment, spread, and

impact. Large invasive-species data sets are available from the Global Register of Introduced and Invasive Species and the Invasive Species Compendium hosted by the Center for Agriculture and Biosciences International. Internet links for these and other Internet information sources follow the references.

The ideal prioritization system integrates ecological knowledge of individual species with site conditions, and adjusts with monitoring information and observed results of treatments.

Prioritizing sites

Hobbs and Humphries (1995) proposed ranking sites for weed control based on two factors, ecosystem value and level of site disturbance. Protected parks, wilderness areas, and critical habitats such as desert streams (Fig. 7) have more ecosystem value and should receive the greatest weed-control effort.

The diagram below (Fig. 8) illustrates possible weed management responses for sites and species of varying priority.

Numbers in cells (not including the left column) indicate the recommended frequency in years for monitoring existing infestations. The “0” in the cells for highest and high priority sites and weeds show rapid response instead of monitoring. The seasonal timing of observations follows maturation of the weeds. The term “withdraw” indicates intervention to limit human disturbances. Sites in the cells at lower right are monitored to detect appearances by high-priority species. Depending on resources and proximity to high-value sites, managers might eradicate such species.

Treatment

Treatment tactics vary for each weed species and each site. They include pulling and cutting, chemical herbicides, releases of predatory insects and microorganisms imported from homelands, planting native species, prescribed fires, and combinations of these. Published information on individual weed responses to some treatments is often available, but for many weeds, results of treatments are unpredictable.

Restoration

Healthy native vegetation resists weed invasions. However, eradicating invasive weeds and preventing their return while aiding establishment of native species is difficult and expensive. Weeds often leave behind persistent propagules, changed soil chemistry,



Fig. 7 Damaged streambank. Water diversions, livestock, human travel and settlement, and floods disturb desert riparian habitats. The site in this photograph retains high value despite the impacts because it is a perennial stream with a relatively large willow-cottonwood riparian forest occupying the floodplain.

Prioritization for Species and Sites with Management Actions				
Weeds ⇨ Sites ⇩	Highest	High	Medium	Low
Highest (<1)	(0) Withdraw, eradicate, and restore.	(0) Withdraw, eradicate, and restore.	(2) Monitor, treat if expanding.	(3) Monitor, treat if expanding.
High (1)	(0) Withdraw, evaluate for eradication, & restoration.	(1) Withdraw, evaluate for eradication & restoration.	(2) Monitor, treat if expanding.	(3) Monitor, treat if expanding.
Medium (2)	(0) Withdraw, begin control treatment.	(2) Monitor, treat if expanding.	(3) Monitor.	(5) Monitor.
Low (3)	(1) Withdraw, begin control treatment.	(3) Monitor, treat if expanding.	(5) Monitor.	No Action.

Fig. 8 Priority sites and species. Numbers in the left column represent the minimum number of years between weed inventories. Highest-priority sites receive two or more visits each year because some species germinate throughout the growing season and others germinate during spring or during summer.

and depleted soil microorganism communities. Restoration costs are justified only for the highest priority sites. The Society for Ecological Restoration supplies information with examples and techniques on the organization's website.

Explaining Invasions

Eurasia has produced most of the invasive weeds found on other continents. The larger Eurasian deserts, with their broad connection to North Africa, their great environmental variability, and their long history of Old World human occupation and disturbance created pressures for Eurasian weeds to evolve better dispersal, establishment, growth, and reproduction abilities than the weeds of Africa, Australia, and the New World. For example, no North American weeds can match the overwhelming success of cheatgrass, redstem filaree, and others that have spread across the arid western US.

Weeds grow and spread in new habitats because they are free of their homeland predators and competitors. Casual and formal tests of this "escape hypothesis" have had mixed results, but most support the idea. For example, [Lucero \(2018\)](#) found granivorous rodents preferred seeds of native brome grass and left more seeds of the invaders to spread and germinate.

Predators, competitors, and environmental conditions restrain most introduced weeds. Those that spread after a period of stasis might do so because of environmental changes or because they have made genetic adaptations to the new conditions.

The most successful desert invaders are those that mature and dry by late spring or early summer and produce fire-tolerant seeds. As mentioned above, these fireweeds are spreading, and fueling destructive desert fires that are wiping out native shrubs and trees.

The Future

Disturbances of native vegetation and introductions of new weeds are increasing. As climate change intensifies, disturbances will multiply. The traits of invasive weeds that let them colonize new sites—their short lives, high mobility, rapid reproduction, and genetic adaptability—also equip them for success as weather and climate change. Without increased control efforts, a legacy of the Anthropocene will be weed dominance of the desert biome.

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Livestock Impacts on Deserts

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Abstract

Livestock production occurs in all deserts (except for polar deserts) worldwide. In many desert areas, it is the single most significant human impact. Livestock production includes the grazing of plants, but also all associated activities that occur to produce domestic animals. This consists of the dewatering rivers for irrigated forage crops, killing of predators and “pest” species, forage competition between native and domestic animals, soil compaction and erosion, changes in fire regimes, spread of alien plant species, loss of biodiversity and numerous other ecosystem effects.

Introduction

Worldwide some 3 billion hectares of land, including deserts, are grazed by domestic livestock and the majority suffer degradation and loss of biodiversity as a result (Carter et al., 2014).

Deserts are usually defined as arid or semi-arid landscapes often with high evapotranspiration rates, high rates of solar radiation and large daily and seasonal temperature range. These factors limit the plant and animal life that can survive in these environments, although there are many remarkable adaptations that species have developed to deal with these extreme conditions.

Many people associate the term desert with “hot” temperatures like the Saharan desert in Africa or the Sonoran Desert in Arizona and northern Mexico which are found where descending air creates dry zones. However, many other deserts are colder, often associated with the rain shadow effect of mountains. Cold deserts like those found in Central Asia (Gobi) or Great Basin in North America will often get snow cover for part of the year. The polar desert in Antarctica is the largest desert area in the world and is almost entirely snow-covered year-round.

No matter where they are found, all desert zones experience periods of acute shortages of precipitation and this has significant implications for the human ability to exploit the ecosystem with livestock grazing. Domestic livestock includes grazing animals such as cattle, sheep, goats, horses, donkeys, yaks, camels, and other species (Fig. 1).

Humans have traditionally used marginally productive landscapes and steeper terrain mountainous areas for livestock production, while better-watered landscapes and flatter terrain are reserved for crop production. Except for irrigated landscapes, most deserts have limited ability to support crop agriculture other than hay or pasture. Consequently, livestock grazing is often the dominant economic use.

With the exception, of the polar deserts, most of the world’s desert areas experience some amount of livestock grazing. Indeed, ungrazed reference points or refugia where livestock grazing has not occurred is difficult to find. (Note unless otherwise noted, when I use the term “grazing” I am referring to cropping by domestic livestock.)

Throughout the world’s deserts, there are many native herbivores. In North American deserts, native herbivores include insects like grasshopper (*Melanoplus* spp.), rodents like ground squirrels (*Spermophilus* spp.), pig-like javelina (*Tayassu tajacu*) to larger ungulates like mule deer (*Odocoileus hemionus*) or pronghorn antelope (*Antilocapra americana*). Herbivores like kangaroos (*Macropus*) are found in Australian deserts, while Asia and Africa have even more large native herbivores.

Though there are many native herbivores, it’s important to note that this does not necessarily mean those plant communities are adapted to exotic domestic livestock grazing. Exotic livestock do not utilize the landscape in the same way as native species. And



Fig. 1 Cattle and water tank in Mojave National Preserve, California.

even when a species might be “native” to a particular ecosystem, the tendency to maximize profits and animal production leads to excessive domestic animals that are above the ability of the landscape to support.

As a generalization, livestock grazing is one of the major human activities responsible for creating or expanding desert areas through the process of “desertification” (<https://www.env.go.jp/en/nature/desert/download/p2.pdf>, accessed 3-12-2019).

The vegetation in most deserts outside of the polar regions is characterized by grasses, shrubs, and scattered trees. Grasses and shrubs are the dominant forage utilized by domestic herbivores.

Aridity has its limitations on livestock production and tends to exaggerate the ecological impacts of livestock.

First, compared to other ecosystems, the lack of precipitation limits plant growth. Regarding primary productivity, desert ecosystems have some of the lowest primary productivity (rate at which energy is converted by photosynthetic and chemosynthetic autotrophs to organic substance) on earth. For instance, the United States (U.S.) General Accounting Office (GAO, 1991) concluded that “hot deserts are among the least productive grazing lands in the United States.” An appraisal conducted in 1984 by U.S. Bureau of Land Management (BLM) and the U.S. Forest Service found that more than 160 acres of land were sometimes required to support one cow for 1 month in southern New Mexico, Arizona, southwestern Utah, southeastern California, and most of Nevada (GAO, 1991).

One of the significant characteristics of desert landscapes is variable precipitation. Precipitation has a huge effect on plant growth. Drought conditions are more likely in desert regions and typically will last longer than in other ecosystems. Since much plant growth is dependent on the amount and timing of precipitation, prolonged drought can significantly reduce the annual plant biomass production and thus the forage to support livestock.

The cumulative impact of livestock is more than “grazing” or “browsing” (see below), rather these should include the collateral damage from livestock “production” (Wuerthner and Matteson, 2002). A 1994 U.S. Forest Service report concluded that livestock grazing was the 4th major cause of overall species endangerment and the 2nd major cause of plant endangerment (Belsky et al., 2002).

As the U.S. General Accounting Office (GAO, 1991) concluded in a report to Congress: “Current livestock grazing activity on BLM allotments in hot desert areas risks long-term environmental damage while not generating grazing fee revenues sufficient to provide for adequate management. GAO found evidence of damage occurring on BLM lands as well as evidence of livestock grazing’s adverse impacts on several wildlife species. Some damaged lands may take decades to recover if they recover at all.”

Among the well documented direct impacts of livestock production on desert ecosystems are the destruction of soil crust, damage to riparian areas, forage competition with native wildlife, the spread of invasive weeds, changes in plant community composition, and losses in carbon storage.

Other aspects of livestock production include disease transmission from livestock to native wildlife, water pollution, the killing of “pests” and predators to protect livestock, the dewatering of rivers for irrigation and the “capture” of springs and other water sources for livestock (Wuerthner and Matteson, 2002; Fleischer, 1994).

Not all species are negatively impacted by livestock production. For instance, brown-headed cowbirds (*Molothrus ater*), a nest parasite, increase with more domestic cattle. Sagebrush sparrow (*Artemisiospiza nevadensis*) likely “benefited” from the shift from grasslands to more shrublands in some cold desert ecosystems (Bock et al., 1993). However, in most cases, the species benefiting are wide-spread generalists, while those harmed by grazing tend to be rarer or those with special habitat needs.

As Bock et al. (1993) concluded in one research review “The problem with livestock across much of the West today is not with their presence, but with their ubiquity.” Those plants and animals, including neotropical migratory birds, intolerant of activities of domestic grazers have comparatively few places left to live.

Specific Livestock Impacts

Soil Crusts

One of the essential negative impacts from domestic livestock, particularly animals that are herded in tight groups, is the trampling of soil crusts. Soil crust is important components of arid to semi-arid ecosystems. Soil crusts are known by many names including biocrusts, cryptogamic, cryptobiotic, microbiotic, or microphytic crusts. Soil crust consists of cyan bacteria, fungi, lichens, mosses, and green algae and may consist up to 70% of the plant cover in some communities. Indeed, in many desert ecosystems, there are more species of soil crusts than vascular species (Fig. 2).

By covering the soil, biocrusts reduce wind and water erosion as well as act as a mulch helping to retain soil moisture. Many soil crusts can fix atmospheric nitrogen, so it's available to other plants. They also affect carbon storage, and influence plant germination and growth. Notably, nitrogen is one of the limiting factors in many desert areas. In some desert locations, nitrogen fixation by soil crust is often one of the most important sources of nitrogen (Evans and Belnap, 1999).

Crusts often play a critical role in soil productivity. Many biological soil crusts in western North America are dominated nitrogen-fixing cyanobacteria and lichens. Micro fungi also weave filaments through the top portions of the soil, holding the soil particles together.

While many desert vascular plants have adaptations to assist in germination such as self-burial mechanisms or rely on rodents for caching seeds, but unlike native species, many exotic species like cheatgrass (*Bromus tectorum*) lack such adaptations and can be inhibited from successful germination by intact soil crust.

Livestock grazing, by destroying soil crusts, also increases the occurrence of wildfire that is one of the major threats to sagebrush ecosystems, and wildlife like sage grouse (*Centrocercus minimus*).

Soil Compaction and Trampling

Trampling and compaction of soils is an unavoidable impact from domestic livestock. The destruction of soil crusts, reduction of water infiltration, as well as removal of vegetative cover has led to increased soil erosion. A lower infiltration rate means less water will be available for plants and more surface erosion may occur.

For instance, an experiment in Arizona looked at how vegetation changes have led to increases in interrill areas, decreases in runoff infiltration and possibility of greater susceptibility to frost action (Abrahams et al., 1995).

Soil compaction reduces water absorption for plants including making it more difficult for them to spread their roots (Boarman, 2002). A review of grazing impacts on hydrological impacts concluded that grazing at any intensity reduced water infiltration (Gifford and Hawkins, 1978).

Water run-off experiments tests showed that compared to lightly grazed areas, moderate grazing areas had seven times the runoff and heavily grazed areas had 10 times the runoff as lightly grazed areas (Boarman, 2002).

Another effect of soil compaction and erosion are changes in soil temperatures. In fact, grazing by livestock can increase soil temperatures; hence water evaporation as well as amplifying the already hot conditions found close to the ground in desert areas. For instance, a significant increase in soil temperature at depths of 2.5, 7.5, and 15 cm was observed in clipped versus unclipped plots (Steiger, 1930).

Trampling by hooves also can affect seeds biomass. A study in the Mojave Desert (U.S.) found native seeds were higher in an area protected from livestock grazing and off road vehicles (examples of vehicle types) compared to areas outside of the enclosure, even though there were more seed-eating rodents inside the enclosure as well (Brooks, 1995).



Fig. 2 Biocrust cover soil surface reducing erosion, and water losses.

Riparian Areas

Riparian areas are those lines of water influenced green vegetation found along waterways. Estimates suggest that riparian areas occupy about 1–2% of the land area in many arid landscapes. Despite their relative scarcity, their combination of water, and lush vegetation growth, these thin, green lines are very productive sites, and ecologically critical to 60–70% of wildlife in the western United States. Riparian areas support about a third of all plant species found in the arid West, and one study of Arizona arid lands concluded that 70% of all threatened and endangered species are riparian obligates (Johnson, 1989) (Fig. 3).

The highest densities of breeding birds in all of North America are reported from southwestern riparian woodlands. More than 75% (127 of 166) of southwestern bird species nest primarily in riparian woodlands and neotropical migrants comprise 60% of the 98 landbirds (Bock et al., 1993).

Due to the abundance of green vegetation, shade, and water, riparian areas are particularly attractive to domestic livestock. Their foraging in these areas has multiple impacts (Behnke and Raleigh, 1978; Kauffman and Krueger, 1984; Armour et al., 1991; Poff et al., 2012). These include trampling and break down of banks and channel entrenchment. Livestock alters the stream channel leading to more extensive and shallow profiles. These channel modifications in turn lead to higher stream temperatures and velocities which can be detrimental to fish including a three to four times decline in trout (*Salmo*) in grazed versus ungrazed stream sections (Fig. 4).

Another review study documented that livestock grazing was found to affect water quality and seasonal quantity negatively, stream channel morphology, hydrology, riparian zone soils, instream, and streambank vegetation, and aquatic and riparian wildlife (Belsky et al., 1999).



Fig. 3 Riparian areas are critical to 60–70% of wildlife. Here cattle have eliminated streamside vegetation, broken banks, and compacted soils.



Fig. 4 Cattle grazing riparian area on the Tonto National Forest, Arizona.

Browsing on streamside shrubs and trees like willow reduce shading of the creek as well as habitat for nesting songbirds. More than 75% (127 of 166) of southwestern bird species nest primarily in riparian woodlands and neotropical migrants comprise 60% of the 98 landbirds (Johnson et al., 1977).

Soil compaction from livestock (as discussed above) reduces water infiltration and the “sponge” effect of riparian areas. The loss of sponge effects can lead to a reduction in late season flows.

Removal of grass and other streamside vegetation by livestock reduces hiding cover for many species. For instance, sage grouse chicks rely on tall streamside vegetation for feeding as well as hiding cover (Thompson et al., 2006).

When grass is cropped to golf course height (1 cm), many species from amphibians to reptiles to birds and mammals in riparian areas are exposed to predators.

Forage Competition

As previously stated, productivity in arid climates is generally low; thus, any forage removal by domestic animals can have a disproportionate impact on native species (Willers, 2002). For instance, desert tortoise (*Gopherus agassizii*) remain in their burrows for extended periods and only emerge to feed when their favorite foods are green and nutritious. Tortoises selectively feed on herbaceous vegetation that is also the same plants favored by domestic livestock. In fact, Avery (1998) in the Mojave Desert demonstrated that tortoise foraging behavior was altered where cattle and tortoises overlapped. In the absence of livestock, tortoises primarily ate herbaceous perennials (91% of diet), whereas, in the grazed areas, tortoises mainly ate annual grasses (59%) followed by herbaceous perennials (21%). Enough forage removal by livestock affected tortoise reproduction with fewer eggs laid in drought years where livestock competed with tortoises for food (Tracy, 1996).

Another example can be found in sage grouse. Although the sage grouse as its name implies relies on sagebrush (*Artemisia* spp.) much of the year, the chicks rely on forbs during the first 4–6 weeks of their lives. Grazing by domestic livestock can remove many of these favored plants.

A third example can be found with desert bighorn sheep (*Ovis canadensis nelsoni*; Fig 5). Domestic sheep and bighorn sheep consume substantially the same foods, and if a herd of domestic sheep moves through wild sheep habitat, they can leave little forage for the bighorns.



Fig. 5 Desert Bighorn sheep

Social displacement also influences forage use. Many native species avoid areas that are actively being grazed by domestic animals. Studies have documented that mule deer, pronghorn, and elk (*Cervus canadensis*) will avoid grazing in the same pastures as domestic animals and are displaced—presumably to less suitable habitat. For instance, in one study in a mountain uplands (so not desert), 94% of the observations of elk *Cervus canadensis* occurred in pastures which were unoccupied by livestock (Frisina, 1992).

Another impact of “forage competition” is the loss of hiding cover for small mammals, reptiles, and ground-nesting birds. For instance, sage grouse are dependent on having tall vegetation to hide their nests from predators (DeLong et al., 1995).

Invasives and Weeds

Invasive plants and animals are species that are either exotics from other countries, or native to the region but found in a new location. Among the most problematic invasives in the western US deserts are cheatgrass (*Bromus tectorum*), and Russian thistle (*Salsola tragus*) that are favored by disturbance caused by livestock. Other exotics are purposely planted to improve forage for livestock like crested wheatgrass (*Agropyron cristatum*). As a result of these factors, the spread of exotics is facilitated indirectly or directly by livestock.

Water Competition

Water is typically scarce in desert ecosystems. There are three primary ways that livestock production impacts water: (1) direct water consumption and pollution; (2) dewatering of natural water sources like rivers and springs for irrigation to provide hay for supplemental forage; and (3) construction of dams and reservoirs primarily to store water for irrigation.

In many deserts, natural springs and seeps are tapped to provide water for domestic animals that can reduce the availability for native species. Not only do domestic animals often trample the areas around such water sources, often leading to soil compaction and a reduction of flows, but ranchers usually pipe flows into water troughs, making it more difficult for native species to access. Loss of springs and seeps via dewatering has been shown to reduce native snails (Frest Terrance, 2002) and amphibians (Engle, 2002).

The mere presence of domestic animals may socially displace native species. Some native species will wait until domestic animals are absent before they access waterholes. For instance, a study of pronghorn (found that nearly one-half of pronghorn—feral horse interactions resulted in the exclusion of pronghorn from the water).

The production of hay as supplemental forage for livestock is common in desert areas. Nearly every natural meadow along streams has been converted from natural vegetation of sedges, water birch (*Betula nigra*), alder (*Alnus* spp.), and willows (*Salix* spp.) to nonnative grasses. The losses of the native vegetation shrubs have a huge impact on native species. Many songbirds nest and feed in this streamside vegetation (Fig. 6).

Many dams and reservoirs built in the western U.S. and other arid regions are constructed primarily for water storage for irrigation. In many instances, that irrigation water is used to grow forage crops for livestock. These dams have many negative impacts on native species—for example, one study documented that riparian forests dominated by cottonwoods (*Populus* spp.) are declining due to disruptions in natural flood cycles and groundwater levels by dams, groundwater pumping and water diversions (Beauchamp et al., 2005). Changes in water temperatures and flows as a result of dam releases also negatively impacted desert dwelling native fish like humpback chub (*Gila cypha*) (USFWS, 2017).

The water stored in most western reservoirs is used primarily for irrigation of livestock forage crops.

A review by McAllister et al. (2014) of dams and their associated reservoirs impact freshwater biodiversity by blocking movement of migratory species up and down rivers, causing extirpation or extinction of genetically distinct stocks or species; changing turbidity/sediment levels to which species/ecosystems in the rivers affects species adapted to natural levels. Trapping silt in reservoirs deprives downstream deltas and estuaries of maintenance materials and nutrients that help make them productive ecosystems; filtering out of woody debris which provides habitat and sustains a food chain.

Dam management that diminishes or stops normal river flooding of these plains will impact diversity and fisheries. Changing the normal seasonal estuarine discharge which can reduce the supply of entrained nutrients, affecting the food chains that sustain fisheries in inland and estuarine deltas. Modifying water quality and flow patterns downstream.

Disease Transmission to Wild Animals

Many wildlife species, especially those closely related to domestic animals, often suffer from disease transmitted from domestic animals. Chronic Wasting Disease, Bovine Tuberculosis, and brucellosis found in wildlife all have origins with domestic animals. A well-documented relationship exists between population decline in wild bighorn sheep and the spread of pneumonia transmitted from domestic sheep (Schoenecker, 2004).



Fig. 6 Irrigated hay production for livestock is a major factor in the dewatering of rivers and streams, compromising aquatic ecosystems.

Predator Control

Another consequence of livestock production is the tendency to kill predators to protect domestic animals. Predators like wolves (*Canis lupus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), and bears (*Ursus* spp.) are known as “top-down” species that shape ecosystems. Loss or reduction of these species can have significant ecosystem consequences. For instance, the presence of wolves in Yellowstone National Park is credited with reducing elk browsing on willows, and the rejuvenation of riparian areas (Ripple and Beschta, 2011).

Loss of large apex predators creates a release whereby mesopredators like coyote numbers increase. Bobcats (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), and Virginia opossums (*Didelphis virginiana*) were detected more often at sites occupied by pumas, whereas coyotes and raccoons (*Procyon lotor*) were detected less often. The detection probabilities of smaller mesopredators were related to coyotes, a dominant mesopredator (Wang et al., 2015).

Pest Control

Many native species are considered “pests” by livestock operators who seek to reduce or eliminate them from grazing lands. Prairie dogs (*Cynomys ludovicianus*), gophers (*Thomomys* spp.), ground squirrels (*Spermophilus* spp.), and other rodents are often the target of control efforts, sometimes to the point where native species may be endangered (Wuerthner, 1997).

Grasshoppers and other insects are controlled by poison (Shewchuk and Kerr, 1993). The loss of mammals or insects has impacts to desert ecosystems since these animals all are prey for other species from fish to birds to mammals.

Carbon Storage

Deserts have a low capacity for carbon storage; however, since arid regions cover about 47% of the earth’s land mass, they are thought to make up the world’s third-largest carbon sink on land. Nevertheless, new research suggests that some endorheic desert basins represent a vital carbon sink on the global scale, with a magnitude similar to deep ocean carbon burial (Li et al., 2017).

Vegetation Loss

Greater grazing pressure on the Mexican side of the International border provided a good comparison on how different livestock management policies can affect the land. For example, there was far less green vegetation on the heavily grazed Mexican side of the line (Berelev and Madsen, 2011).

A study of the Mexican-U.S. (Arizona) border found that the more heavily grazed Mexican desert was consistently warmer than the Arizona stations. The stations in Sonora (Mexico) warm at a statistically significantly faster pace than the stations in Arizona and the stations in Sonora reveal a significant increase in the diurnal temperature range during the summer season (Balling et al., 1998).

Higher temperatures near the surface of the soil can negatively affect insects like native bees and ants, reptiles like snakes, tortoises, and small mammals who move around close to the soil surface.

Climate Change

Although the overall number of domestic animals supported by desert ecosystems is low due to the limited productivity of these sites, domestic livestock has been identified as one the major contributors to global greenhouse gas emissions (GHG). While there are no numbers that break out just the domestic animals produced in desert regions, worldwide estimates suggest that domestic livestock may be contributing as much as 14% of all GHG emissions (Steinfeld, and Food and Agriculture Organization of the United Nations, and Livestock, Environment and Development (Firm), 2006). A more recent estimate put total global livestock contribution to GHG emissions at 23% (Reisinger and Clark, 2017).

Conclusions

Livestock production is one of the most significant influences on desert areas where it occurs, often leading to greater desertification and loss of biodiversity. When you consider the overall large landscape footprint and the cumulative effects of livestock production including the damage to riparian areas, forage competition with native wildlife, disease transfer, soil compaction, alteration of plant communities, predator control and dewatering of streams for irrigated forage production, it is easy to understand why some assert it is the greatest threat to our desert ecosystems.

Due to the natural aridity of desert landscapes, the ability to support livestock is limited. If a full accounting of both the economic and ecological costs impacts were done, it is difficult to justify continued livestock production in desert ecosystems.

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Mechanical Recreation Impacts on Desert Ecosystems

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Abstract

Mechanical recreation is a growing threat to our arid lands. Motorized and on-motorized Thrillcraft (machines used for entertainment and excitement) fragment wildlife habitat, disrupt and disturb native wildlife, spread weeds, compact soils, reduce water infiltration, trample or break vegetation, and displace other desert recreational users.

Thrillcraft is a term that collectively covers all means of mechanical recreational machines, including dirt bikes, four-wheelers, mountain bikes, electric mountain bikes, dune buggies, four-wheel-drive jeeps, and pickup trucks. In short, any mechanical device used to travel off highways and roads. Other collective names including ORV (Off-Road Vehicle), OHV (Off-Highway Vehicle) and ATVs (All Terrain Vehicles). All of these terms can and will be used interchangeably (Fig. 1).

No matter their name, the primary purpose of these machines is for traversing off highway trails, roads, or even where there are no designated trails. Although all of these machines have practical applications as necessary work-related transportation—you might have a four-wheel-drive pick up to traverse a snowy or muddy road or a four-wheeler to check on hay irrigation operations—all of these machines are used primarily for non-work recreation. The main goal of users is speed and the ability to overcome natural obstacles, i.e., thrills.

The research on the environmental impacts of Thrillcraft is limited. In many cases, research on the ecological effects of roads is used as a proxy since it is assumed that a trail has a similar impact on wildlife, soils, vegetation, and environmental processes (Trombulack and Frissell, 2000). Nevertheless, there are some well documented ecological and social impacts (Stokowski and LaPointe, 2000).

Their influence and effects have increased dramatically due to technological innovation. For instance, mountain bikers now use 29-in. tires which are quicker and allow riders to cover more distance, while the adaptation of electric motors to mountain bikes creating e-bikes also contributes to greater range and speed (<https://www.redbull.com/gb-en/polarising-mtb-tech>). The advent of electric Thrillcraft will only increase the use of these machines. For instance, Volkswagen is introducing an electric dune buggy (<https://www.foxnews.com/auto/volkswagen-is-bringing-back-the-dune-buggy>).



Fig. 1 Dune buggy in California desert. Photo by George Wuerthner.

The sales of these machines have increased significantly. In 1972 there were 5 million Thrillcraft registered in the United States that by 2004 had grown to 36 million (Patterson, 2007).

The use of these machines often results in significant environmental damage, including soil erosion, noise pollution, air pollution, fragmentation of wildlife habitat, loss of wilderness values, destruction of vegetation, social displacement of wildlife and social displacement of other recreationists.

In desert biomes where aridity and its limits challenge plant and animal species, the presence of Thrillcraft can have severe ecological impacts.

Weed Distribution

Weed seeds carried and spread by machines can “invade” new areas miles from other “infection” sites (Fig. 2). For instance, one study found that a single ATV might have as many as 2000 spotted knapweed seeds that were spread over a 10-mile area (Proescholdt, 2007).

Soil Impacts

Soil changes induced by Thrillcraft can change vegetation, facilitating invasion by exotic species (Greenberg et al., 1997). The primary effects of Thrillcraft use on soils and overall watershed function include altered soil structure (soil compaction in particular), destruction of soil crusts that stabilize soils, and soil erosion. By compacting soil, permeability (the rate at which water or air infiltrate soil) is decreased. The soil compact not only increases runoff effectively drying soils, exacerbating the already arid conditions in the desert, but it can also reduce root penetration, and affect vegetation (Ouren et al., 2007).

Under controlled conditions Adams et al. (1982) measured soil crust properties to determine how rapidly they were altered by passing vehicles. They determined that routes impacted by a single vehicle pass had soil strengths 5.3–28.4 kg/cm² greater than undisturbed soil, indicating that just a single pass can begin to affect soil strength. Mean soil strength on routes exposed to 10 and 20 passes was too high to measure.

In a rainfall simulation test, vehicle-use plots had about five times more runoff and 10–20 times greater sediment yield than adjacent unused plots (Iverson et al., 1981). Webb (1982) described the impact of motorcycles on desert soils and has measured compacted as deep as 1 m (Webb, 1982). Soil compaction limits water infiltration exacerbating the already arid conditions, and often increasing soil erosion.

Thrillcraft destruction of soil crusts which protect desert soils from erosion is a serious concern (Belnap, 2002).

Vegetation Impacts

Thrillcraft can also trample and break vegetation. The creation of dust also inhibits photosynthesis that can lead to a reduction in plant growth (Ouren et al., 2007; Fig. 3).



Fig. 2 The yellow vegetation in this photo are exotic weed species spread by the disturbance created by the ORV use. Photo by George Wuerthner.



Fig. 3 Dust from ORVs can inhibit photosynthesis in plants Photo by George Wuerthner.

One study of the time required for the full recovery of ecosystems degraded by Thrillcraft as well as other disturbances like live-stock grazing may be 3000 years (Lovich and Bainbridge, 1999).

Wildlife Impacts

ORV threatens many desert species. For instance, in the American Southwest destruction of habitat is a threat to the Sand Mountain blue butterfly (genus species) because its host plant the Kearny buckwheat (*Eriogonum nummularae*) is damaged by vehicle traffic.

A study of two plots in the Mojave Desert with desert tortoise (*Gopherus agassizii*) found the plot without Thrillcraft had 1.7 times more live plants, 3.9 times more plant cover, 3.9 times more desert tortoises and 4 times more active tortoise burrows than a nearby area used heavily by OHVs (Bury and Luckenbach, 2002).

Loud Thrillcraft noise caused hearing losses in sand lizards (*Uma scoparia*) and kangaroo rats (*Dipodomys deserti*) lasting for weeks after being exposed to less than 10 min of playback recordings of dune buggy sounds. The loud noise associated with some ORVs which can mimic thunder that causes the desert spadefoot toad (*Scaphiopus couchii*) to emerge prematurely from its hibernation to breed (Brattstrom and Bondello, 1983).

In a review of Thrillcraft impacts on biodiversity in the Algodones Dunes, a popular ORV recreation area in the California desert, found heavy Thrillcraft use virtually eliminated all native plants and animals (Luckenbach and Bury, 1983).

Other endangered species equally threatened by Thrillcraft include the Peninsula Ranges Bighorn sheep desert (*Ovis canadensis nelsoni*), desert tortoise, flat-tailed horned lizard (*Phrynosoma mcallii*), and Sonoran pronghorn (*Antilocapra americana sonoriensis*).

Zone of Influence

No matter what two factors magnify environmental impacts that Thrillcraft have on plants and wildlife. First, the linear distance that a machine can travel in a day is far greater than someone walking or riding a horse. The speed of mechanical Thrillcraft is also easier for wildlife to perceive, and this may account for the fact that elk (*Cervus canadensis*) detected both mountain bikes and ATVs at distances three times greater than detection of a hiker.

Roadless and trailless areas are critical to the survival of many desert species, especially those persecuted or those that are sensitive to human disturbance. Recent research has shown even the voice of hikers can influence the behavior of large predators like mountain lions (*Puma concolor*). In the Santa Cruz Mountains, researchers played tapes of humans talking and found that it reduced the feeding time of mountain lions and often led to the abandonment of kills. This disturbance also resulted in an increased kill rate of 36% (Smith et al., 2017). However, Thrillcraft are so pervasive that in southern Utah, some 99% of all public lands are within a mile of a motorized zone.

Mechanical access dramatically expands the potential impact of humans on wildlife. For instance, only 3% of the United States is more than 3 miles from a road. The US Forest Service alone has more than 643,737 km of road, which is enough to circle the globe more than 16 times. There are another 131,966 km of roads and "trails" for Bureau of Land Management lands where the bulk of all US desert ecosystems are located (https://www.fhwa.dot.gov/policy/2015cpr/chap12.cfm#_Toc463603405). This amount of existing access is then expanded further as Thrillcraft use the road and trail system—to create new routes and trails—often without any authority from the managing agencies.

Thrillcraft can influence and negatively impact the behavior of many wildlife species beyond the route traveled by a machine. Because human intrusions can effectively shrink the habitat used by wildlife, it's essential to consider the total influence, not just the narrow route that might be used by recreationalists.

Thrillcraft can influence wildlife in three ways: stress and disturbance, alteration of habitat, and collision/mortality (Quinn and Chernoff, 2010).

In a study of desert bighorn sheep researchers using ATVs deliberately harassed bighorns in a heavily used area and a lightly used area. The bighorns from the highly disturbed area responded with running flight 83% of the time, while the bighorns from the lightly used area only ran 46% of the time (King, 1985; Fig. 4).

In a controlled experiment, female elk were monitored in response to four types of recreational disturbance: all-terrain vehicle riding, mountain biking, hiking, and horseback riding. In one of the few comparative studies, the scientists recorded movement, flight responses, habitat selection, and security cover choices under disturbed and control conditions. Compared to control periods when elk spent most of their time feeding and resting, travel time increased in response to all recreational disturbance. Thrillcraft use eliciting the greatest increase in travel time, horseback riding resulting in the least (Wisdom et al., 2004; Naylor et al., 2009). Preisler et al. (2006) studied the response of elk to all-terrain vehicle use in a controlled-access area and found that once displaced from an area by human activity, and they habitually avoided those areas regardless of the attractiveness of the habitat within the zone of social influence.

Riparian areas are critical to many desert species. These thin green lines of vegetation supported by the presence of water are vital habitat to 70%–80% of all wildlife. Unfortunately, these riparian habitats, particularly dry streambeds, are often the choice route for Thrillcraft. For example, the Jeep Jamboree held in Moab Utah every year traverses a number of dry creek beds and wetlands. <https://jeepjamboreeusa.com/trip/southern-utah-adventure/>.

Social Factors

One of the problems with Thrillcraft is the outlaw culture that appears to dominate some members group. Compared to hikers, bird watchers, and other outdoor enthusiasts, Thrillcraft operators are willing to violate numerous restrictions and rule about where and when one can tear up the land.

This outlaw mentality idea applies to mountain bikers. ATVs, and other Thrillcraft. Trails and illegal use is common. For instance, in 2003 Forest Service Chief noted that “unmanaged” motorized recreation was responsible for more than 1600 km of unplanned roads and trails on Montana’s Lewis and Clark National Forest (Bosworth, 2003).

A study done on the Lewis and Clark National Forest found that there were at a minimum of 1348 unauthorized roads and trails extending for 1039 km (Meadows et al., 2008).

Demographics

One of the taunts thrown at those who advocate environmental restraint and protection for fragile lands is that they are “elitists.” However, demographic studies find that the majority of all Thrillcraft enthusiasts, including mountain bikers, are overwhelmingly male and between the ages of 20 and 40 (Fig. 5). They tend to be college educated and have above average incomes (Havlick, 2007). A 2004 New Hampshire study found that the average state ATV license holder owned two ATVs, one off road motorcycle, and spent more than \$3100 a year on clothing and related gear (Okrant and Goss, 2004).



Fig. 4 Desert bighorn sheep expend scarce energy running from ORVS in heavily used areas. Photo by George Wuerthner.



Fig. 5 The average Thrillcraft owner has average to above average income. The gear and equipment is expensive to buy and maintain. Photo by George Wuerthner.

Organizations that advocate for more Thrillcraft use and access like the Blue Ribbon Coalition tend to be supported in part by equipment manufacturers—ORV companies, mountain bike companies and the like (see history of Blue Ribbon Coalition here <https://sharetrails.org/aboutus/>).

As a consequence, they have a disproportional influence on public lands. For instance, the International Mountain Biking Association (IMBA) mission is to advocate for more trails and access (<https://www.imba.com/>). By contrast, I am not aware of even one full-time person working for any environmental group in the entire United States whose primary responsibility is to monitor and counter any ill-advised access. Indeed, IMBA brags that it has created more than 5000 new trails across the country.

Beyond just the ecological impacts, Thrillcraft use negatively impacts other recreational users of public lands. For instance, one Montana study found that 89% of hikers and 84% of horse riders found the presence of motorcycles was incompatible with their activities and impacted their experiences (Wuerthner, 2007).

Conclusions

Thrillcraft is a significant environmental impact on public and private lands in the United States, but their ecological impacts are greater in desert regions. The wide-open terrain and limited vegetation tend to favor cross country travel creating new trails. In addition, the growing population of cities near desert areas like Las Vegas, Phoenix, Tucson, and Salt Lake City has exacerbated this trend. These impacts negatively affect watersheds, vegetation, soils, wildlife, plant communities, and ecological processes. Restricting Thrillcraft to specially designated and concentrated areas could go a long way towards reducing these negative impacts.

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Desert Conservation and Management: Development Impacts, Thar Desert, India

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Abstract

The Thar Desert lies in the westernmost part of India. It is characterized by low and erratic rainfall, low humidity, high solar radiations, strong winds and sparse vegetation. Livestock forms an integral part of the livelihoods of the people living in the Thar. Some of the districts in this region are characterized by a livestock density that is even higher than the human population density. The population in this region is also increasing at a rate faster than the national average. This has led to increased pressure on land for food security of the increasing population and fodder security for livestock. The forest land and the area under other land uses are being converted into arable lands. This can have serious implications on sustainability of the livelihoods and extent of poverty of the people in these districts. In this paper, we used Markov Chain analysis to see the direction of change in the land use pattern in the districts covered under the Western Dry Region. Among the various land use patterns, there was a high probability of the land under forest being diverted to cultivation. This could have serious implications in terms of desertification as all the nine districts covered under the Western Dry Region of Rajasthan are already very low in terms of forest area. We also examined the linkages between various human development indicators of these districts in light of the changing land use pattern in the districts. Using various development and desertification indicators, we worked out respective indices for the nine districts. We identified the districts which had high development indicators and drivers of desertification indicators.

Introduction

Salient Features of the Thar Desert Region

Rajasthan is the largest state in India in terms of area and 8th most populous state in the country, occupying around 5.7% of the country's population. According to 2011 Census, the population of Rajasthan is 68 million. Around 75% of the population lives in rural areas and only 66% of the total population of the state is literate. Being situated at the North Western part of the country, one of the main features of the state is the Aravali Ranges running across the state from South-west to North-east, dividing the state into two, with 60% of the area of the state lying in the northwest of Aravali and 40% in the southeast. The area in the North-west of the Aravali Ranges also inhabits the "The Great Indian Desert" or the Thar Desert (Fig. 1).

The moisture laden South-west monsoon winds are intercepted by the Aravali Ranges, placing the northwestern part of the state at the leeward side. This side receives very little rainfall and is mostly covered by desert. For efficient natural resource management, the Planning Commission of India has divided the country into 15 Agro-climatic Zones. Nine out of the 33 districts of Rajasthan come under the Western Dry Region. This zone covers most part of Thar Desert in Rajasthan. The nine districts of this Zone are Bikaner, Jaisalmer, Barmer, Jodhpur, Jhunjhunu, Churu, Jalore, Nagaur and Sikar which constitute the Thar Desert region of the state. Thar Desert is characterized by extreme summer and winter temperatures and very low rainfall.

The average temperature of this region varies from 45°C in May–June to 2°C in December–January. The annual rainfall in this region is around 400 mm with very high year to year variation. The cropping intensity or the percentage of area sown more than once in a given agricultural year is more in districts with high annual rainfall or high percentage of irrigated area. In six of the districts of the region, wells are accessed as the main source of irrigation. More than 90% of the irrigation in these districts is through wells. The forest cover in all the districts is much less than the optimum requirement of 33%. In three out of nine districts, the forest cover is <1% (Table 1). The region is at high risk of land degradation. Wind erosion is the major contributor of land degradation in this

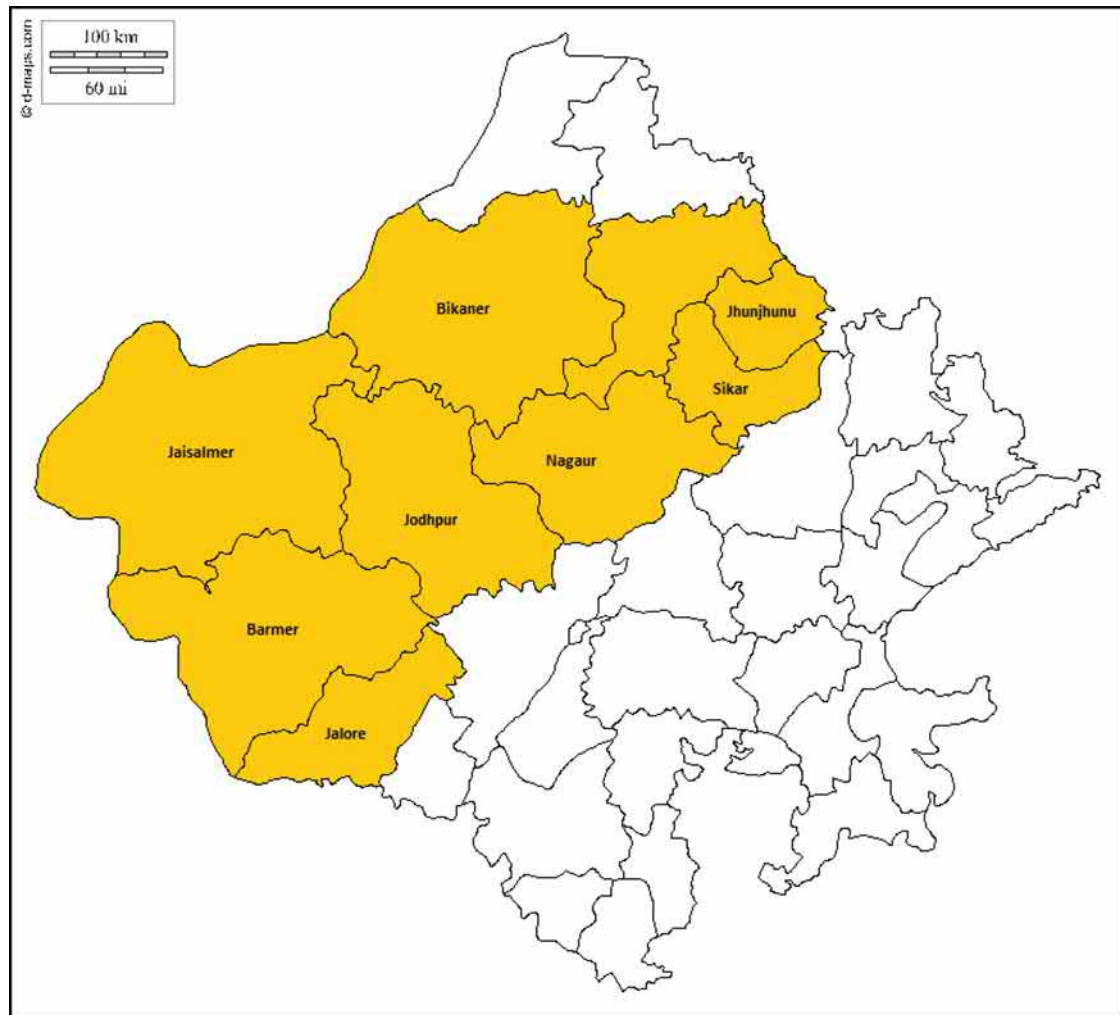


Fig. 1 Map of the study area.

Table 1 Features of Thar Desert region.

Districts	Percent forest area	Annual rainfall (2015–16) in mm	Percent irrigated area	Cropping intensity	Sources of irrigation (%)		
					Canals	Wells	Other sources
Barmer	1.18	429.2	18.74	112	7.61	92.35	0.03
Bikaner	3.11	353.8	37.90	124	47.45	52.55	0
Churu	0.48	433.1	15.31	119	5.6	94.4	0
Jaisalmer	0.71	310.1	31.34	128	61.61	38.38	0.01
Jalore	2.24	674.4	42.72	138	24.32	75.68	0
Jhunjhunu	6.77	378.5	39.48	158	0	100	0
Jodhpur	0.37	359.9	41.29	124	0.21	99.62	0.17
Nagaur	1.05	434.5	22.78	119	0	99.98	0.02
Sikar	7.89	539.1	40.72	142	0	100	0

Source: Rajasthan Agricultural Statistics at a Glance, 2015–16 and 2016–17.

region. It affects 11,419,000 ha. Highly affected districts are Jaisalmer (2,753,000 ha), Bikaner (2,119,000 ha), Barmer (1,908,000 ha), Churu (1,346,000 ha) and Jodhpur (1,235,000 ha) (Maji et al., 2010). Considering the eco-fragile desert region, some of these characteristics are a cause of concern. For example, the forest area in these districts is very low, and, most of the irrigation is through wells, a cause of concern because ground water levels are already very low.

Importance of Livestock in Rajasthan

Land and livestock are the two basic means of livelihood for majority of the farmers in Rajasthan. Livestock rearing is a major economic activity in Rajasthan and makes significant contributions towards improving rural livelihood and reducing poverty, especially in the arid and semi-arid regions of the state (Das et al., 2014). Rajasthan possesses 11% of the total livestock of the country. The quantity and quality of livestock possessed is considered as an indicator for prosperity and social status of a family in the state. Livestock is particularly important in the state and more particularly in the drought prone Thar Desert region for several reasons. The agriculture in the state is marred by insufficient and erratic rainfall with frequent drought spells. Hence livestock has been very closely interwoven with agriculture as an integral part of the rural economy since ages. It is a source of nutrition to the households in terms of providing milk and meat, it provides added income to the households by selling of milk, the cow dung is dried and used as fuel in rural Rajasthan, selling of livestock during the events of crop failure or any other adverse financial conditions also helps the farmers to get immediate cash in times of need.

The composition of livestock population in Rajasthan has seen a major shift over the years (Table 2). The share of cattle in total livestock population has declined over the years while that of buffalo population has increased. While the percent of sheep has declined over the years in Rajasthan, the percent goat population has increased (Fig. 2).

The reasons for the increase in the goat population might be linked with increase in demand for chevon by consumers, easy management practices for goat over other livestock species, high remunerative price for chevon over other products, etc. (Soju and Meena, 2017). The camel population as well as its share in total livestock population has declined over the years. In an effort to save the camel population, it was named as the official state animal in 2014.

Table 2 Shift in composition of livestock population in Rajasthan. Department of Animal Husbandry Dairying and Fisheries, 19th livestock census 2012, 2012, Ministry of Agriculture, New Delhi.

Species	1961	1966	1972	1977	1983	1988	1992	1997	2003	2007	2012
Cattle	39.2	35.01	32.07	31.18	27.2	26.69	24.08	22.37	22.08	21.38	23.08
Buffalo	11.99	11.27	11.81	12.26	12.17	15.5	15.98	17.95	21.28	19.58	22.48
Sheep	21.97	23.49	22.01	24.03	27.05	24.24	25.78	26.33	20.41	19.75	15.73
Goats	24.03	27.54	31.28	29.76	31.18	30.79	31.55	31.16	34.17	37.95	37.53
Camel	1.7	1.74	1.92	1.82	1.52	1.76	1.53	1.22	1.01	0.75	0.56
Pigs	0	0.22	0	0	0	0	0.52	0.55	0.68	0.37	0.41
Others	1.11	0.7	0.9	0.95	0.88	1.02	0.47	0.39	0.39	0.22	0.21

Source: Department of Animal Husbandry Dairying and Fisheries. (2012). *19th Livestock Census Rajasthan, 2012*. New Delhi: Ministry of Agriculture (<http://cazienvs.nic.in/Content/livestock19th.html>).



Fig. 2 Livestock production in the Thar Desert.

Thar Desert Region: The Human, Crop and Animal Dynamics

The Thar Desert is typically characterized by a low human population density which is lower than the livestock population density in most of the districts. Despite limitations of an arid environment, there is an increasing trend in the human and livestock population in the region. Between 1961 and 2011 census, human population has increased by >250% while between 1956 and 2012 census, the animal population has increased by about 125.2% (Moharana et al., 2016). The rise in human population has been higher in the drier districts of Bikaner, Barmer, and Jaisalmer (Table 3). Over the last ten years, the growth in the area under cultivation has also been very high in the districts of Bikaner, Jaisalmer and Jodhpur. So far, Jaisalmer had negligible area under irrigation but now, with the Indira Gandhi Canal Project covering some parts of the district, the scenario is changing at a greater pace (Pathak, 2015).

Materials and Methods

Direction of Land Use Change

The first order Markov chain approach was used to analyze the change in direction of land use. Central to Markov chain analysis is the estimation of the transitional probability matrix P . P_{ij} is the probability of transition from a land use i at time t to land use j at time $t + 1$. Elements of P are non-negative and each row sums to 1. In the matrix P , elements P_{ij} indicate the probability of switching of land use from i th use to j th use with the passage of time. The diagonal elements of the matrix measure the probability that the share of land use will be retained.

In the context of the current application, seven major land uses were considered. The average share of land to a particular use was considered to be a random variable which depends only on the past shares to that land use, which can be denoted algebraically as

$$E_{it} = \sum_{i=1}^r E_{it-1} * P_{ij} + e_{it} \quad (1)$$

where, E_{it} = share of land use from i th to j th use during the year t , E_{it-1} = share of land use from i th to j th use during the period $t - 1$, P_{ij} = Probability that the shares will shift from i th use to j th use, e_{it} = The error term which is statistically independent of E_{it-1} , t = Number of years considered for the analysis, r = Number of land uses considered.

The transitional probabilities P_{ij} which can be arranged in a $(c \times r)$ matrix, have the following properties:

$$0 \leq P_{ij} \leq 1 = 1 \quad \text{for all } i$$

There are several approaches to estimate the transitional probabilities of the Markov chain model such as unweighted restricted least squares, weighted restricted least squares, Bayesian maximum likelihood, unrestricted least squares. In the present study, minimum absolute deviations (MAD) estimation procedure was employed to estimate the transitional probabilities which minimize the sum of absolute deviations. For this purpose district wise land use data from 2007–08 to 2015–16 was taken. The conventional linear programming technique was used, as this satisfies the properties of transitional probabilities of non-negativity restrictions and row sum constraints in estimation (Varghese, 2011). Linear programming formulation is stated as

$$\text{Min } OP^* + Ie$$

Subject to,

$$XP^* + V = Y$$

Table 3 Human, crop and livestock dynamics in the Thar Desert region.

	Human population	Human population density	Increase in human population in the last decade (%)	Livestock population	Livestock population density	Area under cultivation	Growth in Area under cultivation in last 10 years
Barmer	2,603,751	92	32.52	5,366,732	189	1,893,964	0.22
Bikaner	2,363,937	78	41.19	2,773,315	102	2,048,099	4.30
Churu	2,039,547	147	6.01	1,849,833	110	1,472,996	0.33
Jaisalmer	669,919	17	31.81	3,195,213	83	1,092,113	5.79
Jalore	1,828,730	172	26.21	1,631,175	153	934,026	1.36
Jhunjhunu	2,137,045	361	11.67	1,284,657	217	629,296	−0.04
Jodhpur	3,687,165	161	27.74	3,590,264	157	1,765,593	3.03
Nagaur	3,307,743	187	19.20	3,150,011	178	1,641,646	1.08
Sikar	2,677,333	346	17.03	2,118,046	274	724,169	0.16

Source: <https://www.census2011.co.in/census/state/districtlist/rajasthan.html>; 19th Livestock Census Rajasthan, 2012; Rajasthan Agricultural Statistics at a Glance, 2015–16, Commissionerate of Agriculture, Jaipur, Rajasthan.

$$GP^* = 1$$

$$P^* \geq 0$$

where, O = is the vector of zeroes, P^* = is the vector in which probability P_{ij} are arranged, I = is an apparently dimensioned vector of area, e = is a vector of absolute error (1 U 1), Y = is the vector of area under each land use, X = is the block diagonal matrix of lagged values of Y , V = is the vector of errors, G = is the grouping matrix to add the row elements of P arranged in P^* to unity.

Development Indicators

Development is a multidimensional concept and cannot be represented by a single indicator. In this paper, a combination of demographic, health and economic indicators was used to analyze development. A composite index was developed based on a combination of all these indicators. Similarly some indicators which act as drivers to desertification were identified. Composite indices for development and drivers to desertification were worked out using these indicators for all the nine districts. The indicators considered for development include decadal growth rate of population, percent female population, percent rural population, percent literacy, percent female literacy, percent households with access to electricity, percent households with access to clean drinking water, percent households with access to toilet facilities, infant mortality rate, under five mortality rate, sex ratio, work participation rate, per capita net district domestic product. Similarly, the indicators taken as drivers to desertification include cropping intensity, percent forest area, share of primary sector in employment, percent irrigation by well, livestock density and human population density.

The composite index developed by (Narain et al., 2009) was used. As the values of the variables have different measures, they are not suitable for combined analysis. Hence, the variables were transformed into z scores for the combined analysis. Then the indices were calculated using the formula

$$D_i = \bar{C} + 3S_i$$

where $\bar{C}$ = Mean of C_i , S_i = Standard deviation of C_i

Where

$$C_i = \left[\sum_{j=1}^k \left(\frac{R_{ij}}{(CV)_i} \right) \right]^{1/2}$$

where $R_{ij} = (Z_{ij} - Z_{oj})^2$, Z_{ij} = Z scores of each indicator, Z_{oj} = best value of each indicator, CV = Coefficient of variation.

The best value (Z_{oj}) was taken as the minimum standardized value or Z score for unfavorable indicators (e.g., infant mortality) which have a negative direction of impact and maximum standardized value or Z score for favorable indicators (e.g., Literacy) which have a positive direction of impact.

In order to find out the correlation between development and drivers of desertification, spearman's rank correlation coefficient was used.

$$r = 1 - \frac{6 \sum d^2}{n(n^2 - 1)}$$

where, r = spearman's rank correlation coefficient, d = difference between ranks, n = number of observations.

Results and Discussion

Changing Land Use Pattern

Changing direction of land use in all the nine districts of Thar Desert region of Rajasthan was worked out using Markov chain analysis. The transition probability matrices were obtained for each of the districts. From these matrices, the probability of shift in each of the land use were separated and are presented in the following tables. Table 4 shows the change in land under forest cover in the nine districts. The probability of retention of forest land by each of the district is given in bold. While Churu, Jaisalmer, Jhunjhunu and Sikar have 100% probability of retaining the forest land, Barmer, Bikaner and Jalore showed 0% probability of retention of land under forest cover. In Bikaner and Jalore, all the land under forest has the probability of being diverted to agricultural cultivation. The area under forest in Barmer, Bikaner and Jalore is 1%, 3% and 2% respectively which is very low as compared to the optimum level of 33%. When the forest land is diverted to agriculture and the land is tilled during windy summer season, the soil is left exposed to erosion by wind. Deforestation, especially in the deserts has adverse consequences. Lodh (2017) suggested that the expansion of the Thar Desert at the expense of cultivated and irrigated land (Indus basin) significantly impacts the summer monsoon precipitation over the entire Indian subcontinent, both locally and at regional scale.

All grazing land including permanent pastures and meadows come under the category of permanent pastures and other grazing land. The common grazing lands of villages are also included under this land use category. Community grazing lands are a common feature in the crop and livestock based livelihood systems of the Thar Desert. There has been drastic shrinkage and deterioration of

Table 4 Changing land under forest cover in Thar Desert.

	<i>Forest</i>	<i>Area not available for cultivation</i>	<i>Permanent pastures and other grazing lands</i>	<i>Land under misc. tree crops and groves</i>	<i>Culturable waste land</i>	<i>Fallow land</i>	<i>Net area sown</i>
Barmer	0.0000	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Bikaner	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Churu	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Jaisalmer	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Jalore	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Jhunjhunu	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Jodhpur	0.8288	0.0000	0.0000	0.0000	0.0000	0.0000	0.1712
Nagaur	0.6027	0.3813	0.0160	0.0000	0.0000	0.0000	0.0000
Sikar	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

such grazing lands due to encroachment and increasing human and livestock population leading to overgrazing and also putting them to other land use. The probability of retention of land under permanent pastures and other grazing lands by each of the districts is shown in bold. Bikaner, Jhunjhunu and Nagaur show 0% probability of retention of land under this land use (Table 5). In Nagaur and Jhunjhunu the land under permanent pastures has the probability of being put to crop cultivation. Jhunjhunu has high livestock and human population density. With increasing demand for food, more and more land under other uses is being diverted to agriculture. However, diverting land under pastures, could lead to increase in fodder insecurity among animals specially in districts with high livestock density. It is paradoxical that despite the livestock strength, the rangelands in the region are degraded and permanent pastures mostly devoid of grasses and shrubs (Kar, 2014).

Area under miscellaneous tree crops includes all cultivable land which is not included in net sown area. Land under trees, thatching grasses, bamboo bushes and other groves for fuel, etc. which are not included under "Orchards" are classified under this category. The probability of retention of land under miscellaneous tree crops and groves by each of the districts is shown in bold. The districts of Churu, Jalore, Nagaur and Sikar have zero probability of retention of land under this category (Table 6). In Churu, Jalore and Nagaur, the probability is of this land being diverted to cultivation.

Culturable waste land includes land once cultivated but which has not been cultivated for five years in succession. Fallow land on the other hand includes lands which were taken up for cultivation but has not been under cultivation for not <1 year and not

Table 5 Changing land use under permanent pastures and other grazing land in Thar Desert.

	<i>Forest</i>	<i>Area not available for cultivation</i>	<i>Permanent pastures and other grazing lands</i>	<i>Land under misc. tree crops and groves</i>	<i>Culturable waste land</i>	<i>Fallow land</i>	<i>Net area sown</i>
Barmer	0.0425	0.1518	0.8014	0.0000	0.0000	0.0042	0.0000
Bikaner	0.0000	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Churu	0.0000	0.0000	0.4357	0.0000	0.0000	0.0000	0.5643
Jaisalmer	0.0000	0.0000	0.9310	0.0000	0.0690	0.0000	0.0000
Jalore	0.0000	0.0000	0.4735	0.0000	0.0000	0.0000	0.5265
Jhunjhunu	0.0000	0.0822	0.0000	0.0000	0.0000	0.0000	0.9178
Jodhpur	0.0000	0.0571	0.8365	0.0000	0.0000	0.0000	0.1064
Nagaur	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Sikar	0.0000	0.0000	0.7190	0.0000	0.0000	0.0000	0.2810

Table 6 Changing land use under tree crops and groves in Thar Desert.

	<i>Forest</i>	<i>Area not available for cultivation</i>	<i>Permanent pastures and other grazing lands</i>	<i>Land under misc. tree crops and groves</i>	<i>Culturable waste land</i>	<i>Fallow land</i>	<i>Net area sown</i>
Barmer	0.0000	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000
Bikaner	0.0000	0.2249	0.1721	0.6031	0.0000	0.0000	0.0000
Churu	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Jaisalmer	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000
Jalore	0.1272	0.0000	0.0952	0.0000	0.0000	0.0000	0.7776
Jhunjhunu	0.0000	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000
Jodhpur	0.0000	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000
Nagaur	0.3970	0.0000	0.6030	0.0000	0.0000	0.0000	0.0000
Sikar	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000

>5 years. Studies have shown that land fallowing is beneficial to soil quality, crop production and overall long term sustainability (Cusimano et al., 2014). Wastelands can result from inherent/imposed disabilities such as by location, environment, chemical and physical properties of the soil or financial or management constraints. Thus, land under this category is vulnerable to severe degradation (Iyengar, 2003). The probability of retention of land under culturable waste land by each of the districts is shown in bold. Barmer and Jodhpur have zero probability of retention of land under culturable waste land (Table 7). In Barmer the probability of shift is in favor of net sown area. The culturable wastelands that are brought under cultivation are not very productive, have lower crop yield and may not be cultivated every year due to lack of appropriate technologies, crops, and irrigation facilities (Sharma, 2015). Community grazing land comprises mostly of culturable waste land and fallow land. The probability of retention of land under fallow land by each of the districts is shown in bold. Churu, Jaisalmer, Jhunjhunu, Jodhpur and Nagaur have zero probability of retention of fallow land and in all these districts the maximum probability is of the shift away from fallow land in favor of net sown area (Table 8). Any deviation away from culturable waste lands in favor of cultivation is a positive indication as land devoid of any vegetation, especially in the eco-fragile Thar Desert region makes it prone to land degradation due to wind erosion (Fig. 3).

Most of the districts in the Thar Desert region show a good probability of retention of land under net sown area. Barmer, Churu, Jhunjhunu and Sikar show >70% retention of area under cultivation (Table 9). The numbers in bold show the probability of retention of land under net sown area. Also noteworthy is the fact that >90% of irrigation in these districts is through wells. Increasing demand for food and fodder has led to intensification of agriculture in the Thar Desert region (Fig. 4).

Development and Desertification

“Desertification” is land degradation in arid, semi-arid, and dry sub-humid areas resulting from various factors, including climatic variations and human activities (Fig. 5).

It remains potentially the most threatening ecosystem change impacting the socio-economic conditions of millions of people living in the drylands, which account for a significant proportion of the Earth's land (Ambalam, 2014). In contrast to popular perceptions, desertification is not the natural expansion of existing deserts, but the degradation of land in arid, semi-arid, and dry sub-humid areas (Grainger et al., 2000). The chief drivers of desertification include deforestation, over cultivation, increasing population both human and livestock, excess grazing on the rangelands, industrialization and poor land use practices. Desertification is a major challenge in the drylands. Besides, people living in arid areas lag behind in terms of various welfare indicators like literacy, health, availability of basic facilities needed for a decent living etc. In this section, an attempt has been made to find out how the districts in the Thar Desert region fair in terms of various desertification and development drivers. Twelve indicators of

Table 7 Changing land under culturable waste land in Thar Desert.

	Forest	Area not available for cultivation	Permanent pastures and other grazing lands	Land under misc. tree crops and groves	Culturable waste land	Fallow land	Net area sown
Barmer	0.0000	0.0046	0.0020	0.0000	0.0000	0.0000	0.9934
Bikaner	0.0000	0.1029	0.0244	0.0000	0.4429	0.0000	0.4298
Churu	0.0000	0.0583	0.0000	0.0000	0.9417	0.0000	0.0000
Jaisalmer	0.0000	0.0195	0.0029	0.0001	0.9775	0.0000	0.0000
Jalore	0.0000	0.0000	0.0059	0.0000	0.7872	0.0000	0.2069
Jhunjhunu	0.0000	0.0000	0.2216	0.0000	0.1807	0.0000	0.5976
Jodhpur	0.0000	0.0000	0.0000	0.0000	0.0000	1.0000	0.0000
Nagaur	0.0000	0.0000	0.0000	0.0000	0.2848	0.0000	0.7152
Sikar	0.0000	0.0000	0.0000	0.0000	0.0369	0.0000	0.9631

Table 8 Changing land under fallow land in Thar Desert.

	Forest	Area not available for cultivation	Permanent pastures and other grazing lands	Land under misc. tree crops and groves	Culturable waste land	Fallow land	Net area sown
Barmer	0.0154	0.0020	0.0209	0.0000	0.0841	0.3347	0.5427
Bikaner	0.0087	0.0838	0.0164	0.0000	0.0000	0.1012	0.7899
Churu	0.0000	0.0000	0.0133	0.0000	0.0000	0.0000	0.9867
Jaisalmer	0.0000	0.1155	0.0000	0.0001	0.0000	0.0000	0.8844
Jalore	0.0290	0.0245	0.0061	0.0000	0.0000	0.0866	0.8538
Jhunjhunu	0.0000	0.0056	0.0641	0.0000	0.0020	0.0000	0.9284
Jodhpur	0.0000	0.0000	0.0134	0.0000	0.0000	0.0000	0.9866
Nagaur	0.0057	0.0796	0.0361	0.0000	0.0000	0.0000	0.8787
Sikar	0.0000	0.0031	0.0199	0.0001	0.0158	0.5940	0.3670



Fig. 3 Wind erosion in absence of vegetation.

Table 9 Changing land under net sown area in Thar Desert.

	<i>Forest</i>	<i>Area not available for cultivation</i>	<i>Permanent pastures and other grazing lands</i>	<i>Land under misc. tree crops and groves</i>	<i>Culturable waste land</i>	<i>Fallow land</i>	<i>Net area sown</i>
Barmer	0.0094	0.0000	0.0175	0.0000	0.0915	0.1582	0.7234
Bikaner	0.0067	0.0955	0.0179	0.0000	0.2192	0.2009	0.4599
Churu	0.0000	0.0071	0.0171	0.0000	0.0015	0.0899	0.8844
Jaisalmer	0.0000	0.0818	0.0000	0.0002	0.0120	0.2775	0.6285
Jalore	0.0279	0.0315	0.0061	0.0000	0.0068	0.2331	0.6946
Jhunjhunu	0.0000	0.0110	0.0645	0.0000	0.0120	0.1444	0.7681
Jodhpur	0.0010	0.0049	0.0095	0.0000	0.0012	0.4010	0.5824
Nagaur	0.0047	0.0745	0.0337	0.0000	0.0077	0.2181	0.6612
Sikar	0.0000	0.0108	0.0182	0.0001	0.0137	0.0637	0.8935



Fig. 4 Agriculture in the Thar Desert region.



Fig. 5 Sand dunes formed by the desert winds.

Table 10 Indicators for development and desertification indices.

<i>S. No.</i>	<i>District</i>	<i>Indicators for desertification index</i>	<i>Rank</i>	<i>Development indicators index</i>	<i>Rank</i>
1	Bikaner	0.47	1	0.28	1
2	Jhunjhunu	0.53	2	0.35	4
3	Sikar	0.57	3	0.38	5
4	Jalore	0.64	4	0.44	9
5	Jaisalmer	0.71	5	0.48	7
6	Nagaur	0.72	6	0.50	6
7	Churu	0.73	7	0.66	2
8	Jodhpur	0.78	8	0.71	3
9	Barmer	0.79	9	0.74	8

development and six indicators which are drivers to desertification were taken. Indices were worked out for both and the districts were ranked in terms of both the indices. This analysis has helped in identifying the most vulnerable districts in terms of both desertification and development drivers. For example, Bikaner, Churu and Jodhpur are the most developed districts, whereas Jalore, Barmer and Jaisalmer lag behind in terms of development indicators (Table 10). The districts which lag behind in development in the Thar Desert region are also those which have maximum area of desert. Similarly, the most vulnerable districts in terms of the drivers of desertification are Bikaner, Jhunjhunu and Sikar. Jhunjhunu and Sikar have the highest human population and livestock density. Food and fodder security becomes a major cause of concern in these districts. The cropping intensity is also highest in these two districts. Besides, 100% irrigation in these two districts is through wells. This results in depletion of ground water. According to (Narain and Kar, 2006), Jhunjhunu and Sikar are one of the most affected areas in terms of groundwater depletion where withdrawal exceeds annual replenishment through rainfall.

Key Findings for Policy Makers

Some of the results of this study from which policy suggestions can be drawn include

- The forest cover in the Thar Desert region is very low. Any shift away from forests in favor of agriculture would lead to further decline in the forest area.
- The land under permanent pastures and grazing land in some districts has the probability of being shifted to agriculture. This leads to increasing pressure on remaining pastures to meet the fodder security of the growing livestock population.

- iii. People practice mixed farming of crop and livestock in this area. There has been an increase in both human and livestock population in this area. This has increased pressure on the region's marginal land.
- iv. Considering the drivers of desertification, Bikaner, Jhunjhunu and Sikar are most vulnerable.
- v. Jalore, Barmer and Jaisalmer are the districts that lag the most in terms of development indicators.

Conclusions

Desertification and land degradation is a problem that needs urgent action in the Thar Desert region. The populations of humans and livestock are the major drivers of desertification in this region. Excess cultivation, over grazing, over use of ground water resources, and shifting land under various uses in favor of cultivation are the major pressure variables. There is an urgent need for policy interventions to ease the pressure on land in this fragile eco-region.

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Desert Conservation and Management: Energy

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Abstract

As the effects of climate change advance, the development of renewable energy is a critical component in efforts to reduce greenhouse gas emissions to avoid the worst consequences of global warming. Deserts plants and animals are particularly vulnerable to increases temperatures and potentially decreasing rainfall. Adaptation strategies often rely on natural migration to latitudes and elevations that can support the life processes of these tough but fragile flora and fauna, otherwise they will become part of the current extinction crisis. In some cases, assisted migration may be necessary to help prevent extinction. Deserts are also desirable locations for utility scale solar and wind projects because of reliable and copious sun and wind. However, renewable energy must be carefully sited to avoid impacts to sensitive flora and fauna in order to be truly sustainable and conservative of the unique desert ecosystem processes.

Development of renewable energy is a critical component of efforts to reduce greenhouse gas emissions to avoid the worst consequences of global warming. Ambitious efforts are being adopted by regional governments to support rapid renewable energy development needed to meet emission reductions goals. Deserts plants and animals are particularly vulnerable to increasing temperatures and potentially decreasing rainfall. Adaptations strategies often rely on both natural and assisted migration to latitudes and elevations that can support the life processes of these tough but fragile flora and fauna, otherwise they will become part of the current extinction crisis.

With the need to transition to a fossil fuel free world, the southwestern deserts of North America are a magnet for solar energy development because they provide some of the best solar radiation in the world ([National Renewable Energy Lab, 2018](#)). California's deserts also have modest but important areas with consistently strong winds that have already been tapped to create significant wind energy areas ([National Renewable Energy Lab, 2013](#)). In addition, because of the unique geodynamics of the area, significant geothermal resources have been developed in several areas of the California deserts ([California Energy Commission, 2019](#)). With the need to quickly transition off of fossil fuels to avoid the worst impacts to the climate, these renewable energy resources have the added benefit of being close to one of the most significant electrical load centers in North America—coastal southern California with an estimated population in 2019 of almost 24 million people ([World Population Review, 2019](#)).

In the pursuit of incorporating renewable energy into national energy supplies, solar, wind and geothermal developers have focused great attention on the California deserts and floated many proposals to build vast industrial solar and wind facilities of various types. By May 2008, the Bureau of Land Management, a federal agency that manages over 100 million ha (248 million acres) of public lands primarily in the arid western part of the United States, had received 67 applications for large-scale solar developments, covering over 210,150 ha (519,293 acres) in the state of California alone. Thirty-eight percent of these applications were for photovoltaic systems. An additional 27% were solar parabolic trough projects, using mirrors to focus solar radiation on tubes to superheat liquids, which are then used to superheat water; resulting in steam to drive turbines that generate electricity (very much like typical power plants). The remaining 35% were a mixture of other types of solar technologies including power towers, solar hydrogen, solar thermal quad dishes, Sterling engines, and others. To date, over 15 large-scale solar projects have been approved in the California desert and of those over 10 have been constructed. Many of the early applications were speculative and ultimately withdrawn, while eight applications were rejected by the BLM because of conflicts with existing land-management plans and

conservation mandates. The active applications were initially checkerboarded throughout the California deserts, with some adjacent to existing transmission facilities while others would require significant new transmission lines to be built.

The focus on the desert southwest region was dubbed a “green rush” because of the rush to build industrial scale renewable energy projects to meet new renewable energy targets and obtain federal grant funding. However, because industrial development in these deserts which are one of the least ecologically fragmented and fragile areas left in the United States (Randall et al., 2010), development in this area raised significant concerns as well. To reduce CO₂ emissions, alternative renewable energy sources are essential to replace coal- and gas-burning power plants. But the rush for renewable energy development also must ensure that renewable energy is developed in a way that protects the unique and precious ecosystems of fragile desert ecosystems. It must also be properly sited to prevent blocking of wildlife connectivity corridors at the local, regional and landscape scales in order to keep the desert landscape connected. Preserving wildlife connectivity must also incorporate a variety of local species ranging from plants which primary move through seed and propagule dispersal, to less vagile terrestrial animals including ground dwelling insects, small mammals and reptiles to charismatic megafauna including bighorn sheep and coyotes.

How to balance these issues is complex, and critical to maintaining ecologically functional desert landscapes. Certainly, placing industrial solar as close to the load centers as possible is most efficient because it cuts down on transmission losses and provides energy where it is needed. Using existing disturbed lands in the deserts is another important factor to be seriously considered and perhaps mandated. Of course, renewable energy production on the already built environment (e.g., distributed solar on rooftops, parking lots, and urban brownfields), as well as increasing energy efficiencies is the least damaging and most efficient way to implement renewable energy and reduce our carbon footprint.

Deserts are Biologically Unique

From the biological perspective, there are many unique plants, animals, and habitats that are found on the lands that may also have prime solar resources. Some of these species are naturally rare and others have become threatened or endangered due to habitat loss, increased predation, and other factors. Agassiz’s desert tortoise (*Gopherus agassizii*), which is protected under federal and California Endangered Species Act laws due to their steeply declining populations are found throughout the Mojave Desert and inhabit areas with high solar insolation that have sandy soils and are generally flat to gently rolling hills. This type of habitat is often desirable for renewable energy projects as well as other types desert development including housing, industrial and military development. Habitat development results in desert tortoises being moved from project sites to adjacent areas that are home-ranges of other desert tortoises. Increasing local tortoise densities can exceed the carrying capacity of the landscape to support all the animals and tragically results in mortalities of both translocated and resident tortoises (Field et al., 2007). Both rare and endangered species increasingly rely on their remaining habitats to sustain them in an inhospitably arid landscape. Many resources are unique and rare in the desert landscape, like riparian areas and water sources that are essential for migrating birds and resident species alike. Fully inventorying and avoiding impacts to the rare and unique resources is key to any long-term sustainable development of industrial scale solar in the desert landscape.

In an effort to help steer solar development away from the most sensitive desert sites, data sets on areas that contain rare and unique biological resources were collected and assembled in order to inform decision-makers on the ecological and cultural values of the desert landscapes in California’s deserts. As those familiar with the desert already knew (Keeler-Wolf, 2003), these data sets confirmed that many of the areas of the California deserts already have significant existing unique resources, including landscape-scale wildlife connectivity corridors that are critical to allow for movement as climate change continues, where any type of development should be avoided. Many of these important areas also tend to be located in remote areas far from where energy is consumed. In contrast, rare and unique resources are far less common on previously disturbed lands and therefore efforts were made through planning processes to focus development options for large-scale renewable energy projects to lands that were already disturbed from prior land uses (farming, mining and other surface disturbing activities), near existing transmission and outside of crucial wildlife habitat and connectivity areas (including migration corridors).

However, as with any data-driven mapping exercise, the data are biased to what is known and where rare resources surveys have been conducted. Many areas of the deserts have not been well studied. Surveys are labor intensive and expensive, and few private or public land managers have the luxury of initiating much less completing comprehensive surveys. These data are often only collected when a change in land management (i.e. development of some sort) is proposed. Therefore, the paucity of data creates uncertainty about the status of the on-the-ground resources across large swaths of the desert landscapes.

Thoughtful consideration of how we will most efficiently and effectively achieve our carbon-reduction goals is clearly the path on which we must now embark. Combining distributed solar production and energy efficiency with careful placement of renewable energy projects can ensure our commitment to reducing CO₂ pollution while still respecting and preserving our deserts’ unique and world-class biodiversity.

Solar Energy

Desert landscapes seem like the perfect place for solar energy based on the abundant sunshine for which the deserts are renowned. Indeed, desert lands have been targeted for solar development particularly when the deserts are close to large cities (electrical loads) or existing transmission facilities that carry the power to loads centers.

Solar projects that are remotely located in undisturbed deserts all share common impacts on the terrestrial landscape: habitat fragmentation due to road and facility construction including fencing of the facility; conversion of intact landscapes into industrial facilities including in some cases complete removal of all vegetation and loss of stabilized soils. In addition, in order to get energy to the grid, off-site transmission infrastructure which requires numerous substations and hundreds of miles of roads, electrical towers and lines often need to be constructed. Poorly sited solar projects impact crucial wildlife connectivity corridors that are especially important as climate change pressures plants and animals to seek viable habitat elsewhere. Poorly sited solar projects have been constructed on lands critical to endangered or rare species.

The current technologies being used in desert landscapes are generally of three types, each of which successfully produces energy, and each impacting unique desert resources differently.

Photovoltaic (PV) Panels

Photovoltaic (PV) panels are a popular technology that have been implemented on large and small scales. The panels can be either stationary or on “trackers” that allow the panels to rotate on an east-west axis to maximize sun exposure. Popular panels are mostly manufactured as non-toxic crystalline silicon panels, but some are manufactured as cadmium-telluride panels, which is a potentially toxic material if not handled carefully. Crystalline silicon panels are the same type of panels deployed on roof-top and small-scale installations as well as large-scale utility installations indicating their flexibility of installation.

For large industrial scale PV installations in the desert, an unanticipated environmental issue arose in the deserts in California. Surveys for avian species were required as part of the environmental review for these projects, and those surveys detected typical desert avifauna, which would likely be displaced by the solar project. However, once solar PV projects were built, injuries and mortalities of ducks, grebes, pelicans and other waterbirds were documented during post-construction monitoring ([KCET-PBS So Cal, 2013](#)). From a distance, panels covering thousands of hectares appear lake-like from a human visual perspective, giving rise to the new category of research involving the hypothesis of a “lake effect.” The lake effect hypothesizes that utility-scale installations of PV panels may reflect and polarize light, even at night, making the PV field appear to be a water body. Migratory waterbirds in particular, when transiting across the desert, may be attracted to such installations, because the birds perceive them as a water body. The mortalities and injuries occur either from direct impact from crashing into the panels or, for certain waterbirds that require water in order to become airborne, the birds become stranded on the panels or on the adjacent ground after falling off the panels. Either way, this impact to the avifauna reliant on waterbodies was unanticipated and a point of current research.

Scientific research documents that polarized light attracts water-loving insects to oviposit on surfaces that polarize light but are not water, resulting in an ecological trap that causes complete reproductive failure for individuals ([Horváth et al., 2009](#)). PV panels produce polarized light which may be attracting birds as well as insects. Nonpolarizing white borders and white grates on the PV panels also reduces their attraction to water-loving insects ([Horváth et al., 2010](#)). However, this solution increases the actual footprint of the utility-scale PV project, causing a greater terrestrial footprint of disturbance.

Depending on the project, some desert utility-scale PV installations remove all above ground vegetation and smooth the landscape surface—by traditional grading or “cut and roll” treatment—prior to construction in order to facilitate installation of the PV panels. These treatments not only remove habitat, at minimum temporarily, but destabilizes desert soils by removing the crucial cryptobiotic soil crusts. Cryptobiotic soil crusts which are living symbiotic associations between cyanobacteria, lichens, algae and fungi, play a critical role in the ecology of arid regions in many deserts including in the southwestern United States. These cryptobiotic soil crusts create a protective surface layer that keeps underlying soil from wind and water erosion, retain water when precious precipitation occurs, provide safe sites for seed germination, increases soil fertility and are generally slow to regenerate once disturbed ([US Geological Survey, 2016](#)). Because these fragile soil crusts are often undetectable to the human eye, they are overlooked for the important ecological functions that they provide. Disturbances to these soil crusts from grading, “cut and roll,” and other soil disturbing activities at large-scale solar sites creates a cascade effect that destabilizes surface soils, causing increased erosion, loss of plant biomass, reduced soil fertility, reduced water retention and an increase in emissive particulates in the air, contributing to increased air pollution (PM₁₀ and _{2.5}).

At some industrial PV projects, vegetation has been allowed to regrow under the panels and is trimmed regularly to prevent coming in contact with the PV arrays themselves in order to reduce fire risk. Other PV projects prevent vegetation growth under the arrays.

Solar Thermal

Solar thermal projects superheat fluids that are typically run through a heat exchange facility to generate steam that runs turbines that generate electricity. Two main types of solar thermal projects have been implemented at an industrial scale include solar power towers and solar trough projects.

Power Towers

Solar power towers use reflective mirrors to focus the sun's radiation onto a collector at the top of a tower. The collector superheats fluids that ultimately drive turbines typically located at the base of the tower to generate electricity. The mirror field requires road construction along with the installation of the infrastructure. This type of construction creates the same fragmentation of the landscape as PV projects, and the same impacts to cryptobiotic soil crusts and resident animals.

Once in place, this technology poses a unique ecological impact to avian species—burning from the concentrated solar radiation flux. The sun's radiation is concentrated as it converges near the collector, and birds that fly into that concentrated solar flux can be impacted. Impacts range from feather singeing to direct mortality (Kagan et al., 2014). The concentrated solar flux also attracts insects into harm's way. Insects attracted to the intense light of the solar flux in turn attract insectivorous birds into harm's way as well, creating a “mega-trap” (Kagan et al., 2014).

During operation, the solar flux regularly needs to be refocused from the collector to another area for necessary collector repairs or to reduce the amount of radiation flowing into the system. The flux is typically redirected to standby points or arranged as a standby halo nearby the tower, which still threatens avifauna and insects that fly through or are attracted to the concentrated solar flux.

Numerous treatments have been proposed or implemented to try to divert avifauna from entering the solar flux area, but the diversion methods incur their own sets of impacts. From volatilizing a non-toxic grape extract (methyl anthranilate) distasteful to avifauna across the solar site, to the proposed use of acoustic devices that broadcast loud noises to scare away birds, to releasing trained predatory raptors to “patrol” the fence line of the power tower site and chase off birds, each of these treatments to reduce avian mortality at power tower installations are still experimental at this time but will require a full analysis of potential impacts to other species when implemented.

Solar Trough

Solar trough technology is one of the oldest solar thermal technologies. It utilizes a parabolic mirror that focuses the sun's radiation on a tube that contains a heat transfer fluid that is superheated from the focused radiation and circulates through the system to a heat exchanger. The heat exchanger engine then creates steam that drives turbines to produce electricity.

Solar trough technology requires laser-precise ground elevations in order for the heat transfer fluid in the tube to circulate freely through the parabolic mirror arrays and into the heat exchange system. These precise elevations require complete elimination of all vegetation and cryptobiotic soils in order to contour the ground to the technology's exacting specifications. No vegetation is allowed to regrow under the arrays. This technology can employ “wet cooling” that condenses the turbine-driving steam into water for reuse. But in the arid desert, the use of water to cool the steam is not prudent, so most all of the solar trough projects are required by local permitting agencies to only use “air cooling,” where the ambient outside temperature allows the turbine-driving steam to change state back to water.

Typically, the solar trough technology requires a series of ponds, where the fluid in the tube can be released for maintenance or other purposes. These ponds have been found to be impactful to avifauna, and particularly to water birds who try to land on them. While project permitting often requires netting of the ponds to prevent birds from landing on them, entanglements have been documented leading to bird mortalities (Kagan et al., 2014). Terrestrial animals have also been known to be trapped in ponds, despite fencing and netting.

Wind Energy

Wind energy has typically capitalized on the strong steady winds at specific locations, some of which are often located along the deserts' edges in passes and with consistent wind patterns. Traditionally large wind turbine arrays have been constructed to capture the wind energy by rotating turbine blades that drive the generation of electricity. Some experimental designs do not use turbine blades, but the vast majority of wind energy projects still employ varying blade configurations. The produced electricity, like solar-generated electricity, is collected at local substations and put onto the electrical grid via transmission lines.

Birds, bats and insects are vulnerable to being hit or affected by the turbine blades, causing injury and mortality. Impacts can occur all along the blade length, with rotational speed increasing along the length of the blade. Depending on the rotor size, wind speed and blade length, tips of the blades can reach 80 m per second (180 miles per hour). Wind turbines affect avian species differently. For example, large raptors that hunt by day are more vulnerable to impacts from wind turbines based on their flight behaviors. Coupled with raptors' relatively long lives, slow maturation and low reproductive rates, their populations are more affected by wind turbines than other types of birds (US Fish and Wildlife Service, 2018).

Bat injuries and mortalities have also been documented to occur from wind turbines. Direct strikes from turbines can cause injury and mortalities, as well as from barotrauma. Barotrauma is caused when bats encounter extreme changes in atmospheric pressure that occur near the blades of turbines. These air pressure changes can rupture air-containing structures such as lungs in mammals which causes internal bleeding and, potentially, death (Baerwald et al., 2008).

Insect mortalities are an emerging concern associated with wind turbines. Modeling of insect mortalities identifies vast numbers of insects are impacted by turbines (DLR, 2019); however, the implications of these vast numbers of mortalities remain unclear. Insect mortalities, as they collect on turbines blades, are known to significantly decrease the efficiency of the wind turbines by up to 50% (Corten and Veldkamp, 2001).

There are a number of actions that can be implemented in order to reduce the impacts to wildlife from wind farms. Newly designed or repowered wind farms can use careful “micro-siting” of each turbine on the landscape, which has been documented to greatly reduce the impacts to some raptors, other birds and bats. Wind turbine operation can also reduce impacts to birds and bats, by modifying the “cut-in” wind speed (the speed at which the turbine blades are allowed to start rotating and producing energy) above the wind speed at which birds or bats are able or likely to fly. Other experimental systems are currently being tried which detect and track large birds as they approach a wind farm and trigger a turbine shut down if the bird is projected to come into a turbine rotor-swept area.

Geothermal

Geothermal energy is a very location specific issue, and the terrestrial footprint is generally quite small in comparison to solar and wind energy projects. However, in the arid deserts, geothermal energy can impact the local water resources that plants and animals rely on for survival.

Energy Storage

Renewable energy production is an intermittent energy source. With solar energy relying on sunshine and not operating efficiently on cloudy days and not at night, and wind energy only operating when adequate wind is blowing, the need for energy storage has become of significant interest as we transition off of fossil fuels. Pumped storage projects, which rely on water flowing downgradient to generate electricity during times when renewable energy is not available and pumping the water upgradient when renewable energy is available, have become of interest even in arid parts of the desert. However, pumped storage projects use more energy than they generate (US Energy Information Administration, 2013), are not limited to using renewable energy to pump upgradient, and most often rely on open reservoirs to create their gradient differential. Open reservoirs are subject to significant evaporation in the deserts, coupled with the fact that initial water in the reservoirs is often procured from ground water, which can easily overdraft the local ancient aquifers. In addition to the documented net-energy-loss of pumped storage projects, the lack of binding requirements to use only renewable energy to pump upgradient and the significant use of groundwater makes pumped storage projects unsustainable in arid regions.

Threats From Industrialization

Habitat fragmentation remains a significant concern when industrial projects, including renewable energy, are implemented. Each facility requires fencing that inhibits terrestrial wildlife movement, although some projects try to minimize that impact by providing wildlife permeable fencing into project areas that will not harm wildlife. Careful siting of projects is requisite in order to avoid siting project in important wildlife movement corridors.

Energy produced at large-scale industrial renewable energy projects must also reach the electrical grid which requires new transmission lines and substations. Every transmission line requires a new road for construction and on-going maintenance. Often times these transmission lines are hundreds of miles (kilometers) long, further fragmenting habitat for biological organisms and losing an average of 5% of the energy they are carrying due to “line loss” (US Energy Information Administration, 2019). Transmission lines have also long been known to be a significant threat to avian species, particularly during nocturnal migration (US Geological Survey, 1978).

Typically, when projects are built on undisturbed desert lands, numerous new roads are required to be constructed to aid the actual project construction and ongoing operations. The new roads often remain for project maintenance purposes at solar sites, and at wind sites a roads are maintained to access each turbine. The new roads also provide vehicular access into new undisturbed desert lands. This additional habitat fragmentation creates new impacts including the introduction of new invasive species, edge effects and illegal trespass into formerly undisturbed lands.

Land Use Planning

Focused land use planning for renewable energy in deserts can benefit our transition to renewable energy and greatly limit the impacts to ecologically functional landscapes. For example, in 2016, a key planning process in California’s deserts—the Desert Renewable Energy and Conservation Plan (Desert Renewable Energy Conservation Plan, 2019)—crafted a plan across 10 million acres (over 4 million ha) of desert on federal public lands. The public lands planning allows for potential development of carefully

sited solar and wind energy on 388,000 acres (over 150,000 ha) in specific areas or zones close to existing transmission corridors, while providing greater conservation protections for over 4.2 million acres (over 1.7 million ha). The local jurisdictions including counties in this area have also undertaken planning to steer private lands development of large scale solar and wind projects to appropriate sites. This type of land use planning allows for streamlined transition to renewable energy near one of North America's largest energy loads while protecting one of the most intact ecosystems remaining in the continental United States.

Smart Renewable Energy Solutions

While industrial-scale renewable energy projects play a part in our transition to fossil fuel-free energy production, siting renewable energy projects in the already-built environment, close or in existing energy load centers has many benefits. These benefits include constructing projects on existing infrastructure near or on the site of energy consumption which eliminates most of the transmission line losses. It creates jobs in existing communities instead of remote areas in the desert that lack basic services. It also conserves the integrity of our ecologically intact and functional desert lands for future generations to enjoy.

Conclusion

While wide-open deserts near load centers will continue to appear attractive for renewable energy development, these fragile and easily damaged landscapes provide essential habitat and resources for rare and unique plants and animals that are adapted to live under ecological conditions that challenge most living things. Careful planning, based on the best available science, can identify appropriate areas for development of renewable energy in places with the least conflicts. Considerations for maintaining ecosystems need to include principles of conservation biology regarding maintaining large blocks of habitat that contain focal populations, maintaining well distributed populations across species ranges, minimizing habitat fragmentation, providing connectivity between habitat blocks and preserving peripheral population which are reservoirs of unique genetics. This conservation approach is critically important as climate change proceeds.

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Protected Areas and Connectivity

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Abstract

More than 2800 species inhabit desert biome, of which many are threatened. Despite high biological diversity, deserts have largely been neglected in conservation plans. Species declines in deserts are mainly due to habitat loss and widespread hunting. We provide information on the protection coverage of deserts by global network of protected areas. We then broaden our discussion by including the subject of landscape connectivity. In this part, the necessity of incorporating connectivity in desert conservation plans is deliberated. In addition, relevant examples of desert species for which increasing connectivity is imperative for their persistence are provided. Finally, we introduce different modes of landscape connectivity in deserts including hydrological connectivity, landscape heterogeneity, and desert oases facilitating movement of a range of species from small invertebrates to large vertebrates. Hydrological connectivity is the result of water flow among water pools and is an important factor in persistence of aquatic species in deserts. Heterogeneous habitats both facilitate species movements and provide escape terrain from predators or human disturbances. Stopovers such as oases have great importance for migrating species crossing deserts.

Why We Need to Protect Deserts?

Until before the middle of 20th century, deserts were only valued as places for tourism and human explorations. However, developments of environmental concepts such as ecology, biodiversity conservation and human geography revealed other unknown values of deserts and resulted in introduction of eremology, the systematic study of deserts, their features and formation by Theodore Monod (founder in 1938 of IFAN, l'Institut Français d'Afrique Noire, Dakar, Sénégal). Today, deserts are recognized as areas with high biological and ecological values that may counterbalance with those of other biomes around the world. Despite low global coverage of around 17%, deserts are home to surprisingly high numbers of plant and animal species (Safriel et al., 2005). Along with xeric shrublands, desert areas are one of the top three richest biomes for terrestrial vertebrates harboring nearly 25% of the terrestrial vertebrates of the world (Mace et al., 2005).

Many desert-dwelling species have high conservation concern globally. Currently, more than 2800 species of plants and animals inhabit desert areas, of which many are threatened. With more than 1500 species, plants are the dominant group of organisms in deserts. Compared with animal groups, plants have the highest number of threatened species in each IUCN conservation category (Table 1). Among animal groups, reptiles and mammals account for the majority of species in deserts habitats (about 40% and 33.7%, respectively). Mammals make up the most threatened group of desert animals with the highest number of critically endangered, endangered and vulnerable species.

Large mammals constitute considerable proportions of threatened desert species. Many of desert herbivore species such as white antelope (*Addax nasomaculatus*), Saiga antelope (*Saiga tatarica*), Dama gazelle (*Nanger dama*), Slender-horned gazelle (*Gazella leptoceros*), Goitered gazelle (*Gazella subgutturosa*) and African wild ass (*Equus africanus*) are among the threatened species. In addition, the vulnerable cheetah (*Acinonyx jubatus*) and its critically endangered subspecies, the Asiatic cheetah (*A. j. venaticus*; Griffith, 1821) and also the critically endangered subpopulation of western African lion (*Panthera leo*) are the most prominent carnivores of desert biome. The Asiatic cheetah has disappeared across much of its historical range across central and southeast Asia. Only very small numbers of this large cat persist across deserts of central Iran as its last stronghold (Ahmadi et al., 2017). Birds, amphibians and insects are lesser common groups of threatened animals in desert habitats; however, they also include several species of high conservation concern such as hooded vulture (*Necrosyrtes monachus*, CR), Chilean woodstar hummingbird (*Eulidia yarrellii*, CR), Asian houbara bustard (*Chlamydotis macqueeni*, VU), *Telmatobius vilamensis* (the only CR species of amphibians

Table 1 Number of desert-inhabiting animal and plant species within the IUCN conservation categories

Kingdom	Group	CR ^a	EN ^b	VU ^c	NT ^d	LC ^e	Total
Animals	Reptiles	12	16	21	14	439	502
	Mammals	14	19	28	23	350	434
	Birds	5	5	8	9	221	248
	Insects	5	3	3	1	40	52
	Amphibians	1	1	2	3	42	49
Plants	—	64	76	86	60	1252	1538
Total		101	120	148	110	2344	2823

Data on species richness was extracted from iucnredlist.org

^aCritically Endangered.

^bEndangered.

^cVulnerable.

^dNear Threatened.

^eLeast Concern.

Data on species richness was extracted from IUCN Red List of Threatened Species (www.iucnredlist.org).

occurring in deserts), Sinai Baton Blue butterfly (*Pseudophilotes sinaicus*, CR) and Rugose Sand Grasshopper (*Sphingonotus rugosus*, EN). There are still many desert animal and plant species that have not been categorized into IUCN Red list due to lack of data (data deficient, DD) or have not been evaluated yet (NE). Therefore, if the required data are available for detailed evaluations, the number of threatened animal and plant species in desert biome may increase.

Deserts with significantly high numbers of endemic threatened species have the potential to be qualified as biodiversity hotspots. However, these habitats have largely been neglected as biodiversity hotspots (Durant et al., 2012) and or priority conservation areas due to their low biological productivity (Durant et al., 2014). Species declines in deserts are mainly due to habitat loss and widespread hunting (Safriel et al., 2005). An example is the Horn of Africa with more than 2500 endemic species of birds, mammals and plants. Nearly 95% of species' habitats in this region have been degraded by human activities and without proper protection, ongoing human threats will increasingly result in loss of many species not found elsewhere in the world. To avert biodiversity loss in this region, and for deserts in general, it is necessary to expand conservation actions across this biome.

Protection Coverage of Deserts

Protected areas (Hereafter PAs) coverage for desert biome is provided by the World Database on Protected Areas (WDPA). The database includes six IUCN management categories and three categories of Not reported, Not assigned, and Not applicable (Fig. 1) (UNEP-WCMC, 2016) (Ia: Strict nature reserve, Ib: wilderness areas, II: National park, III: Natural monument and Natural feature, Habitat management area and Species management area, VI: Protected landscape and Protected seascape). Assessments that considered all these categories, provided close estimations for desert protection level ranging from 9% to 11% (Brooks et al., 2004; UNEP-WCMC, 2008; Chape et al., 2008; Jenkins and Joppa, 2009). However, when only strictly PAs are considered (IUCN categories I-IV), protection coverage for desert biome drops to 4.2% (Jenkins and Joppa, 2009). Unlike warm deserts, the protection coverage of cold deserts has rarely been considered. Chape et al. (2008) estimated a protection coverage of 8% for cold deserts using all the data in WDPA. Based on this assessment, cold and warm deserts together are among the habitats with relatively high percentage of area protected (18% coverage). In terms of biogeographic realms, highest protection for desert biome is provided by the network of PAs in Nearctic region (mostly in North America) followed by Afrotropic realm (mostly in Africa) (Brooks et al., 2004; Jenkins and Joppa, 2009).

Importance of Connectivity for Desert Species

Distribution of Desert Species

Species living in desert regions usually display patchy and isolated distribution due to scarcity of required resources (Murphy et al., 2012). This pattern of distribution has resulted in many desert species distributed across large areas, but with low population densities (Kahal, 2015). Although the comparably large size of desert PAs (Chape et al., 2008) may support proportions of suitable habitats and resources, they may not be large enough to cover the full range of widely distributed habitats for species throughout the year. This is particularly true for migratory and wide-ranging species of herbivores and carnivores inhabiting desert habitats. Habitat ranges of these species usually span large areas with an order of magnitude larger than the size of individual PAs. A notable example is the migratory wild ass (*Equus hemionus*) that has been documented to travel across areas of more than 80,000 km² in search of resources in Gobi Desert.

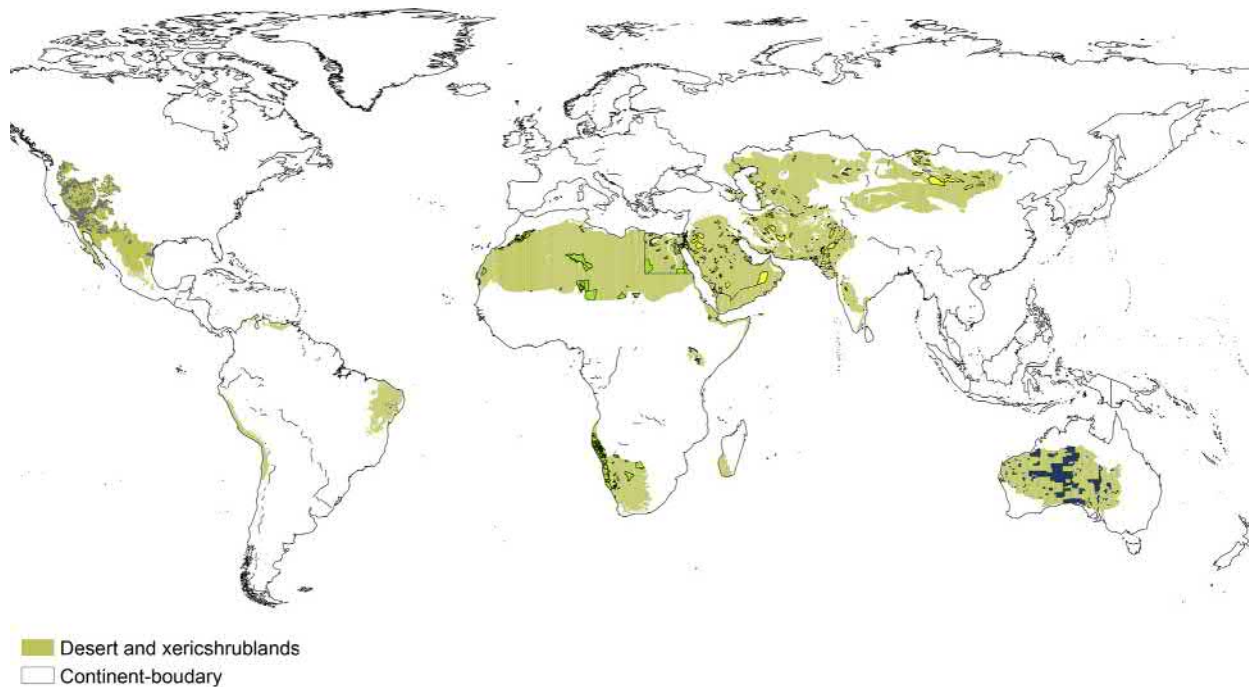


Fig. 1 Global distribution of desert and xeric shrublands across continents and within the network of PAs. Colored polygons indicate proportion of desert biome and PAs overlap in continents of America (gray polygons), Africa (green polygons), Asia (yellow polygons) and Australia (dark blue). The PAs include all six categories of IUCN and three categories of Not Reported, Not Assigned and Not Applicable. Spatial data on desert biome and PAs in each continent were respectively obtained from the Nature Conservancy (<http://maps.tnc.org>) and WDPA.org.

Anthropogenic Impacts on Desert Species

Human developments such as roads, agricultural lands and urbanization have largely altered desert landscapes across the world. Habitat loss and fragmentation as adverse impacts of human activities increasingly isolate already disconnected desert habitats and populations. Transportation developments increase risk of species road collisions (Lovari et al., 2007) and may act as movement barriers reducing species ability to move among populations and habitats (Frair et al., 2008).

Human activities may pose a great conservation challenge in desert areas as some of the most threatened migratory (Berger, 2004) and wide-ranging species in the world live in these habitats. High movement ability and wide habitat requirements make large mammal species particularly vulnerable to anthropogenic interventions in deserts. As an example, monitoring movements of Mongolian gazelles (*Procapra gutturosa*) and Asiatic wild ass (*Equus hemionus*) in Gobi Desert revealed avoidance of both ungulates from crossing railroads and fences in the border of China and Mongolia (Ito et al., 2013). Large carnivores are other group of wide-ranging desert species impacted by human interventions in these habitats (see Dickson et al., 2013; Ahmadi et al., 2017; McClure et al., 2017). An important example of these species is the critically endangered Asiatic Cheetah (*Acinonyx jubatus venaticus*) inhabiting central Iran. Reduction in density of prey within Iranian PAs (Ziaie, 1996) has forced populations of this large cat to move across large desert areas outside the PAs (Farhadinia et al., 2013). Nearly all core habitats for the species are surrounded by roads (Ahmadi et al., 2017) and the individuals have to cross these constructions to reach other habitats. Currently, road collision is a major cause of decline of Asiatic Cheetah population and a serious threat to survival of this carnivore (Farhadinia et al., 2017). In addition to large species, impacts of human developments on habitat availability and connectivity have also been documented for smaller desert species. For example, Kadaba et al. (2013) showed the impact of wind and solar energy facilities on 13 of the 16 critical corridors identified for movements of the desert kit fox (*Vulpes macrotis arsipus*) in California.

Concerns over the adverse impacts of human developments on desert species also exist for species with metapopulation structure. Metapopulation is a set of locally distributed populations connected by dispersal (Hanski and Simberloff, 1997). These movements play a critical role in maintaining the viability of metapopulations. By providing recolonization opportunity, dispersal helps the recovery of locally extinct subpopulations. Movement of individuals also helps in increasing genetic diversity and prevents adverse impacts of inbreeding. In deserts, metapopulation structure is common for species in mountains that are surrounded by the desert matrix such as Black bear (*Ursus americanus*) populations restricted to highland forested woodlands in the Chihuahuan desert (Pelton, 2003) and bighorn sheep in the desert mountains of southern California (Epps, 2004). Unsuitable environmental conditions in the desert matrix may limit movements of these species; however, they are not complete barriers as have been crossed by individuals (Epps, 2004; Onorato et al., 2004). Creation of barriers and an inhospitable matrix may result in complete isolation

of local populations of black bear and bighorn sheep. For these species, conserving the least impacted movement pathways within the matrix could contribute to maintain movements among metapopulations.

Climate Change and Desert Habitat Connectivity

Since climate is the main environmental factor in shaping deserts, these habitats represent high vulnerability to climate change (Yang et al., 2009). Climate change is expected to put already warm and dry deserts in more extreme conditions either directly through the effects on thermal and water stress or indirectly through impacts on quantity and distribution of habitat resources (Iknayan and Beissinger, 2018). Desert species may respond to direct impact of climate change by shifting their range to areas where suitable habitat conditions are available. Physiological adaptations may enable desert species to withstand unsuitable environmental conditions. However, if changes in climatic factors exceed species physiological tolerance and reduce survival, range shifts are expected (Moses et al., 2012).

A major concern is climate change impacts to PAs. With respect to the high velocity of climate change projected for desert biome (Loarie et al., 2009), it is expected that change in climatic conditions occur across large areas greater than the size of individual PAs. Hence, current desert PAs may change to unsuitable habitats that are no longer efficient for species within them. For instance, future projections estimated a 75% reduction in efficiency of central Iranian desert PAs to conserve goitered gazelle (*Gazella subgutturosa*) by 2070 (Malakoutikhah et al., in press; under review manuscript). In addition, high velocity of climate change in deserts means that the nearest suitable habitats in future may be considerable distances away from the current habitats. Under such circumstances, survival of desert species largely depends on their ability to move and find suitable habitats elsewhere. This highlights the importance of connecting current PAs to suitable habitat areas in future as the most effective strategy for species persistence under future climate change (Heller and Zavaleta, 2009). For some desert species, however, the distance to the nearest future suitable areas may be beyond species dispersal ability. For example, future projections for the scimitar-horned-oryx (*Oryx dammah*) showed that the species needs to travel thousands of kilometers from Sahel to nearest suitable habitat in Kalahari Desert, which is not possible considering the species movement ability (Thuiller et al., 2006). In these cases, assisted migration could be an effective approach to conserve this species (Hunter, 2007).

Increasing habitat connectivity also helps in reducing the synergic impacts of land use and climate change on species. In many cases, species tracking suitable habitats have to cross inhospitable landscapes dominated by human land uses (Lawler et al., 2009). In the absence of connectivity among landscape patches, many species may not be able to escape from unsuitable habitats and will be seriously threatened by climate change (Baranyi et al., 2011). For instance, climate change has caused desert bighorn sheep to lose proportions of their original range during the past few years (Epps et al., 2004). Human land uses on the other hand, increasingly contribute to fragmentation of the species habitats and isolation of the populations (Kahal, 2015). To survive negative impacts of climate change, populations of bighorn sheep must move to access habitats at higher elevations. However, they are most likely encountering human barriers in the matrix. Thus, conserving the most permeable part of the Californian desert that facilitate movements of big-horn individuals is critical for persistence of this ungulate in a changing climate.

Currently, only 6.7% of the desert biome is covered by protected connected habitats (Saura et al., 2017). It is expected that habitat connectivity will be degraded in desert areas as a result of climate change. Therefore, as an adaptive conservation approach; it is a priority to prevent loss of habitat connectivity in desert areas under climate change.

Landscape Connectivity in Deserts

Landscape connectivity is defined as the ability of a landscape in facilitating or impeding species movements (Taylor et al., 1993). Structural and functional connectivity are two components of landscape connectivity (Tischendorf and Fahrig, 2000). Structural connectivity describes physical features in a landscape such as vegetation, topography and hydrology that facilitate species movements (Rudnick et al., 2012). Functional connectivity on the other hand, describes movement of species or gene flow across a landscape (Rudnick et al., 2012).

Structural and functional connectivity are important for movement of desert species among habitat patches. In general, natural patchiness and isolation of habitats limit the structural connectivity in desert habitats. However, this component plays a key role in survival of species with low dispersal ability such as those inhabiting mountains and isolated freshwater pools in deserts. Functional connectivity on the other hand, is usually observed for large desert species with high mobility. Although for these species patches of suitable habitat may be located within large distances; high dispersal ability enables them to access distant isolated habitats.

Hydrological Connectivity

The most common type of structural connectivity in deserts is hydrological connectivity. Water resources harbors high levels of biodiversity in deserts and acts as micro-hotspots for desert biodiversity (Vale et al., 2015). In deserts, due to variability in climate, water pools remain isolated most of the year, which could have adverse impacts on species survival. Hydrological connectivity is the result of water flow among water pools and is an important factor in persistence of aquatic species in deserts (Vale et al., 2015). This type of structural connectivity in deserts is provided for limited periods of time; when freshwater pools are connected through floods resulting from precipitation. In addition to climate change (Woodward et al., 2010), anthropogenic factors such as overexploitation of desert water resources, and intentional alternation of water flow are other major contributors reducing fresh water connectivity in

these ecosystems (Vorosmarty et al., 2010). Another type of hydrological connectivity in deserts is the connections provided by permanent source of flowing water such as rivers. An example of such connection is the Nile River corridor. In addition to facilitating dispersal of aquatic species, by providing vegetation and riparian habitats, this corridor also allows migration of a range of terrestrial species along its path (Brito et al., 2014).

Deserts Landscape Heterogeneity and Connectivity

Habitat heterogeneity refers to the diversity of physical features such as topography in a landscape. Landscape heterogeneity constitutes the structural component of landscape connectivity as it determines the amount and continuity of available habitats to species (Taylor et al., 2006). Because of dominance of low-relief areas, deserts have very low habitat heterogeneity. However, high topographic complexity and hence heterogeneity exist in mountainous parts of deserts. One important function of heterogeneous landscapes in desert ecosystems is to assist movements of species particularly those living in desert mountains. Similar to many desert species, mountain species in deserts display spatially fragmented distribution. Adaptation to especial climatic or environmental conditions has narrowed the climatic niche of these species. Thus, environmental conditions in the desert matrix could act as major barrier to movement of mountain species. For these species, mountainous habitats function as key connectivity habitats in providing structural connectivity and decreasing negative impacts of isolation on populations. Furthermore, heterogeneous habitats allow species to access to larger climatically suitable areas in response to climate change.

Apart from facilitating movements, heterogeneous habitats may also provide the opportunity to escape from predators or human disturbances. For example, bighorn sheep select a variety of connectivity habitats such as plains, canyon bottoms, and washes to move between mountains (Penrod et al., 2012). However, the species main preference is to move along ridgetops of mountain hills or open habitats in proximity to escape terrains where higher safety is provided (Penrod et al., 2012). Likewise, topographically complex habitats in deserts play an important role in maintaining movements of large desert carnivores. Wide home range size along with vast areas of open space in deserts make large carnivores rather conspicuous. In addition, availability of prey species has been documented to be high across rugged habitats (Dickson et al., 2013; McClure et al., 2017; Ahmadi et al., 2017). For these species, rugged terrains provide enough security and stalking cover helping individuals to maintain movements across topographically complex landscapes (Beier et al., 1995; Stoner et al., 2008).

Role of Desert Oases in Maintaining Connectivity

Long-distance migrations of species cannot usually be fulfilled if stopover sites are not available along their migration routes. This is particularly challenging for migration pathways crossing desert areas as harsh habitat conditions in deserts can be seriously threatening. Long-distance migratory species crossing desert areas require habitat patches within their migration routes to rest and recover their energy stores. In desert areas, small isolated oases formed along water resources are critical stopover sites providing resting and foraging opportunities (Williams et al., 2006). Stopovers are of particular importance for birds that travel long distances, crossing unsuitable areas. For instance, for neotropical birds traveling thousands of kilometers yearly between breeding and wintering habitats in North America and tropics, xeroriparian habitats in Sonoran deserts, southwest Arizona, are important stopovers during spring migration (Hardy et al., 2004). Likewise, many migratory passerines use riparian habitats in Sahara Desert of Africa as their stopover while traveling to other places (Bairlein, 1988).

Although oases occupy small proportion of desert areas, they are critical in maintaining the integrity of migration movements. These habitats could function as stepping stones (Hendricks, 2011) and help in maintaining connectivity among desert areas or deserts and other habitats at larger spatial scales. With respect to the role of these small and isolated habitats, their degradation (by hydrological manipulation, over-harvesting and conversion of habitats, etc.; National Research Council, 2002) could lead to disruption of long-distance species migrations. Therefore, protection of oases should be a priority for conservation of migratory species crossing desert habitats.

Conclusion

Deserts are known as one of the most biodiverse biomes with many species of high conservation value. Some deserts harbor considerably large numbers of unique species that are not found elsewhere and have the potential to function as biodiversity hotspots. However, little conservation efforts have been dedicated to properly conserve desert habitats and species. Currently, about 9%–11% and 6.7% of desert habitats are respectively covered by PAs and connected habitats. This low level of habitat protection could be challenging with respect to ongoing anthropogenic threats such as habitat loss and fragmentation, overhunting, and climate change. As a result of climate change, many desert species need to shift their current ranges resulting in reduction of PAs' efficiency in future. In addition, expansion of anthropogenic developments may be a serious threat to desert species as they can destroy and interrupt potentially suitable habitats and connectivity areas. Under this condition, inclusion of new conservation sites, expansion of current PAs based on species future distribution and maintaining connectivity among them are effective conservation efforts for future protection of this fragile ecosystem in a changing climate.

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Desert Conservation and Management: Ecotourism

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Abstract

Deserts harbor unique natural and cultural heritage that is found nowhere else in the world. However, threats to these heritage resources are rising due to increasing levels of accessibility, human population and exploitation of natural resources. Thus, new alternative tools are needed to safeguard these fragile environments. In this respect, ecotourism has the potential to preserve the desert biome while supporting local cultures, traditional livelihoods and sustainable development. Deserts display many opportunities to promote ecotourism, such as unique biodiversity protected by large national parks and reserves, geological features, archeological and historical sites evidencing past cultures, and a great variety of ethnic groups and costumes. Still, protection of desert heritage is challenged in many countries due to low levels of security, development and political stability. Ecotourism generates a plethora of environmental, economic and socialcultural impacts that need to be considered when developing tourist activities in desert environments. However, ecotourism should not be envisaged as a panacea for all the challenging impacts that deserts are facing, but it can offer a sustainable tool to contribute positively to the wellbeing of people and communities living within deserts. Ultimately, desert ecotourism can contribute to the 2030 agenda of the United Nations for the Sustainable Development Goals and the conservation and management of desert heritage.

Introduction

Ecotourism has been suggested as a tool for the conservation and management of deserts' natural and cultural heritage. As one of the fastest growing sectors of global tourism industry, ecotourism has a potential to serve as an environmentally, socioculturally and economically viable option for promoting sustainable development in the desert biome. Many factors provide opportunities to develop ecotourism in deserts, which need to be carefully considered for both nature conservation goals and local socioeconomic wellbeing. For this article, we start by contextualizing ecotourism and its research in deserts, and then describe possible attractions and constraints exhibited by deserts to develop ecotourism. We conclude with a discussion of the potential positive and negative impacts that ecotourism may derive on different desert facets.

Brief History of Ecotourism and Its Research on Deserts

The relationship between the environment and tourism has interested conservation researchers and managers for a long-time (Wagar, 1964; Budowski, 1976). The term ecotourism became popular in the 1990s, when scholars started raising interest in the conflicts and potential solutions and symbiotic relations between tourism and the natural environment (see Ceballos-Lascurain, 1996). Multiple definitions of the term have been proposed and revised since then. In general, ecotourism refers to tourism in natural environments involving a conservation element, environmental education components, and benefit sharing with local communities (Fennell, 2001). Some scholars (Weaver, 2001a; Fennell, 2015) consider that ecotourism needs to address the following factors:

- (1) be developed at small scales, for example, in typically low-density groups of travelers;
- (2) foster behaviors that help preserve local biodiversity and habitats, particularly by potentiating environmental awareness and learning experiences among tourists, and with local communities, the importance of biodiversity preservation through environmental education;
- (3) contribute economically to the preservation, maintenance, and enhancement of biodiversity and habitats;
- (4) respect the integrity of host communities (local beliefs and livelihoods) while committing to promote local culture and ensuring folklore maintenance (i.e., orientated to locals);
- (5) generate net positive incentives to the local economies and the well-being of communities (i.e., improving the welfare of local people) sufficient to make them value and protect the surrounding wildlife heritage as an income source;
- (6) balance the biocentric and anthropocentric views to ensure long-term sustainability of projects;
- (7) be moderately commercialized.

Therefore, developing ecotourism is not a simple task, and planners, managers, and policy makers need to understand and contextualize these dimensions if they want to achieve sustainable development in tourism.

Being the fastest growing segment of the tourism industry, ecotourism is estimated to generate annual revenues of more than \$28.8 billion for developing countries (Kirkby et al., 2011). This is 34% more than what is spent annually by governments, private donors and official aid agencies in global conservation projects (Waldron et al., 2013), and, for example, 44% of the value needed to cover the global annual costs of protecting and managing Important Bird Areas (McCarthy et al., 2012). Yet, there are no reliable financial figures on ecotourism for specific biomes, such as deserts (UNEP, 2006a). Different types of ecotourists contribute to these expenditures and market segmentation divides them into “hard” and “soft” ecotourists according to their motivations, attitudes, and behaviors. Hard ecotourists are considered as having strong biocentric attitudes and commitments to environmental issues, they desire deep and meaningful interactions with the environment, travel in small groups, and search for physically challenging experiences requiring few or no tourism supporting infrastructures, while soft ecotourists exhibit the opposite traits in the ecotourism continuum. As such, the hard ecotourist may spend more time with local communities to understand their relationships with nature, whereas the soft ecotourist opts for experiences of shorter duration (Weaver, 2001a). Market segmentation is, therefore, important also for ecotourism developers as it helps to manage the natural resources and their utilization. These strategies help maximize the economic and environmental contributions of ecotourism to achieve the United Nations Sustainable Development Goals (UN-SDGs; UNWTO and UNDP, 2017), particularly in alleviating poverty, providing decent work and economic growth for all, promoting gender equality (reducing inequalities), protecting desert life, and establishing strong partnerships between the business, local communities, governments, academia, and NGOs.

The desert biome is still underrepresented in the general literature of ecotourism research (Santarém and Paiva, 2015). Deserts are home to 6% of the world’s human population, mostly poor and marginalized (UNDP, 2011). They have been mostly neglected for conservation and development funding schemes (Waldron et al., 2013). Furthermore, they contain some of the most threatened biodiversity, fragile environments, and vulnerable cultures in the world (UNEP, 2006b; Brito et al., 2014, 2016, 2018). As such, ecotourism constitutes a complementary step to preserve the natural and cultural heritage of deserts while potentially improving local livelihoods. Additional efforts are needed to design desert ecotourism products that translate into sustainable development in tourism.

Potentials and Constraints of Deserts to Develop Ecotourism

Deserts exhibit a plethora of potential attraction elements motivating tourists to visit these areas but also involve several constraints for ecotourism development (Table 1). Both aspects are crucial to consider, and they should take into account the pressures that ecotourism can create on the environment and the existing economic and sociocultural uses of the desert biome (UNEP, 2006b).

Desert Attraction Elements for Ecotourism Development

Most deserts and arid regions classify as being among the last wild biomes on Earth (Watson et al., 2018), which offers excellent opportunities for ecotourists seeking “last-chance-to-see” places (Lemelin et al., 2012) that are considered as wilderness areas (Saarinen, 2018). Deserts are also characterized by the high “visibility factor” that increases the likelihood of successful wildlife

Table 1 Potential attraction and constraining elements of the desert biome to develop ecotourism

<i>Attraction elements</i>	<i>Constraining elements</i>
Natural features	
<i>Landscape</i>	Security conditions
<i>Biodiversity</i>	Developing conditions
<i>Conservation</i>	Political conditions
Human features	
<i>Historical</i>	Increased accessibility
<i>Sociocultural</i>	Natural resource exploitation

Courtesy of Frederico Santarém, Jarkko Saarinen and José Carlos Brito.

encounters (Weaver, 2001b), including unparalleled natural sceneries and geological features, especially by ecotourists focusing on nonliving natural phenomena (Weaver, 2001a).

Natural features

Deserts display remarkable landscape features highly attractive for ecotourism (Fig. 1). They are considered natural laboratories for investigating the history of Earth, as extreme aridity and sparse vegetation provide large areas of exposed bedrock materials showing the record of geological processes operating for millions of years. Deserts provide a large number of paleontological findings (UNEP, 2006b), with the most noteworthy examples including:

- Badland terrains of the Gobi Desert, where 65 million years-old dinosaurs and mammal fossils were unraveled;
- Ténéré Desert in Niger, where excavations revealed 25 tons of dinosaur fossils;
- Pisco Basin in Peru, where stratigraphic sequences of Miocene to Pliocene rocks show assemblages of fossil marine mammals;
- Colorado Desert in California (United States), where one of the most complete records of late Cenozoic land mammals for North America can be found.

One of the most iconic landscape features of deserts is sand dunes. Among them, the Skeleton Coast in Namibia, the 168,350 km² of parallel dunes of the Simpson Desert in Australia, and the world highest sand dune in Atacama Desert, Chile (Cerro Medanos at 2100 m) are the most remarkable. Sand dunes provide scenic settings that provoke strong emotional connections to nature, offer relief from high-stress daily life of urbanized people, and provide exceptional opportunities for experiencing solitude and tranquility. Other prominent landscape features of deserts are high-altitude mountains. For example, the Tibesti mountains in Chad, the Al Hajar Mountain in Oman, or the Kerman mountains in Iran all rise above 3000 m (UNEP, 2006b). Isolated rock formations that rise abruptly from a surrounding plain, known as island-mountain or inselberg, are also highly attractive, and an iconic example is the Uluru in the Northern Territory (Australia).

Indeed, deserts contain spectacular geological features of potential interest for ecotourists. A few examples from around the globe are as follows:

- Volcanic cones, such as the Trou au Natron and Emi Koussi (2450 and 3445 m elevation) in the Saharan Chad;
- Meteorite impact craters, such as the Wabar Craters in Saudi Arabia;
- Rock canyons (deep cleft between escarpments or cliffs resulting from weathering and the erosive activity of a river over geologic timescales), such as the majestic 450-km long and 1.5-km deep Grand Canyon (United States) or the Iherir-Imirhou valley in the Tassili n'Ajjer (Algeria);
- Rock arches formed by wind and water erosion processes, such as the Aloha Arch in the Saharan Chad, the Jabal Umm Fruth Bridge in the Wadi Rum of Jordan, or the Arches National Park (United States);
- Desert potholes (shallow puddles or deep pools that collect precipitation from small catchments), such as in the Colorado Plateau (United States);
- Eolian *yardang* landforms (massive corrugated ridges), such as in the Lut Desert in Iran;
- Saltpans (natural flat expanses of ground covered with salt and other minerals), such as the Chott El Djerid in the Tunisian Sahara.

Finally, wetlands are abundant in some desert areas and, given the generalized arid character of the desert landscapes, they are highly attractive to ecotourism.

Deserts contain biodiversity features that can be highly attractive for ecotourism. These include endemic species exhibiting unique adaptations to aridity that are found in no other biomes (Fig. 2; Weaver, 2001b). Examples of extreme adaptations and uniqueness's found in deserts include:

- Namib Welwitschia (*Welwitschia mirabilis*), among the most ancient organisms in the Plant kingdom and considered a living fossil;



Fig. 1 Examples of landscape features typical of the desert biome with potential for ecotourism. (A and B) Sossusvlei in Namib-Naukluft National Park (Namibia); (C) Es Sba (Mauritania); (D) Guelb el Makhsar (Mauritania); (E) Tassili n'Ajjer (Algeria); (F, G and H) Tadrart (Algeria). Courtesy of José Carlos Brito and Jarkko Saarinen.



Fig. 2 Examples of biodiversity features in the desert biome with potential for ecotourism: (A) African golden wolf (*Canis anthus*); (B) Felou gundi (*Felovia vae*) and Rock agama (*Agama boulengeri*); (C) Desert elephant (*Loxodonta africana*); (D) Namibian giraffe (*Giraffa camelopardalis angolensis*); (E) Greater hoopoe-lark (*Alaemon alaudipes*); (F) Brown-necked Raven (*Corvus ruficollis*); (G) Lanner falcon (*Falco biarmicus*); and (H) Desert monitor (*Varanus griseus*). Courtesy of Frederico Santarém and Jarkko Saarinen.

- Southwestern USA Joshua tree (*Yucca brevifolia*), the symbol of the local National Park that displays a very specialized mutualistic pollination system with the yucca moth (*Megathymus* sp.), which spreads pollen while laying eggs inside the flower in a communal way;
- Fringe-fingered lizards (*Acanthodactylus* spp.) that perform sand-swimming to escape predators in the Sahara Desert;
- Australian thorny devil (*Moloch horridus*) that displays a unique water transportation system through its ridged thorny scales that enable the animal to collect water from simply touching it.

These remarkable adaptations to arid conditions have been used to market them as flagship species, that is, species that due to their morphological, behavioral, and cultural traits can be used as the focus of broader conservation campaigns and can be distinctly promoted according to specific market segment traits. For example, soft ecotourists may prefer large and easily visible species, while hard ecotourists may opt for “last-chance-to-see” endemic endangered species (Lemelin et al., 2012; Santarém et al., 2019). Deserts contain also some of the most endangered species in the world, which may prompt ecotourists to pay high fees to see them in the wild and, thus, contribute financially to their preservation. In addition, wetlands in deserts constitute local biodiversity hotspots supporting particular fauna suitable for ecotourism purposes. For example, the rock-pools of Mauritanian Sahara gather relict populations of West African crocodiles (*Crocodylus suchus*; Brito et al., 2014) and the wetlands near the archeological city of Palmyra (Syria) support a relict colony of the critically endangered Northern Bald Ibis (*Geronticus eremita*; Serra, 2007), thus offering a great opportunity for desert wildlife viewing.

Deserts contain conservation features that improve the chances of wildlife encounters, which enrich the recreational experience for ecotourists. Unique biodiversity is generally safeguarded by a network of protected areas. For instance, the Aïr and Ténéré Addax Sanctuary and the Termit-Tintoumma Natural and Cultural Reserve in Niger were designated to protect the critically endangered and flagship species Addax (*Addax nasomaculatus*), and the Joshua Tree National Park (United States) was established for protecting the native Joshua trees (UNEP, 2006b). Protection of biodiversity and ecological processes is strongest in North American and Australian deserts, where the Grand Canyon (1919) and Simpson Desert (1967) National Parks were established a relatively long time ago. On the contrary, the desert areas of developing countries are still under protected (Brító et al., 2016; Weaver, 2001b). Multiple protected natural sites displaying outstanding evolutionary and landscape features have been recognized even in the most remote parts of deserts, which appeal to a specialized segment of ecotourists that are able to travel long distances to observe unique desert features (hard-desert ecotourists; Santarém et al., 2018).

Human features

Numerous features associated with the historical human occupation of deserts make them attractive to ecotourism (Fig. 3). These include rock art found in caves, mostly depicted as paintings and engravings, illustrating past livelihoods and even past climatic shifts. The World Heritage site of Tassili n'Ajjer in Algeria and the Messak Settafet in Libya are considered open books of History, with thousands of rock paintings and engravings catalogued. Rock art is highly recognizable among international ecotourists because in deserts it is easy to find it in large concentrations, offering abundant possibilities to interpret how humans interacted with the environment and how they developed associated spiritual and community values, making rock art in the desert biome among the best sources of human history.

The low disturbance of desert soils preserved remarkable archeological remains and help to understand how past societies lived in arid environments. Ruins, tombs and other sites of historical land occupation highlight how successive human societies shaped the desert environment (UNEP, 2006a; Serra, 2007). For example:

- The earliest run-off irrigation system supporting large cultivated fields in the world was discovered in the Negev Desert (Israel);
- The ancient city of Palmyra in Syria—where for centuries nomadic Bedouins traded livestock and relative products—has been revealing artifacts of world recognized value;
- Tombs in Egypt show how people worshiped iconic desert species such as the crocodile, represented in art linked to Sobek, god of Nile.

The historical crossing of deserts along trading routes allowed the establishment of trading villages, acting as commercial warehouses and resting places. For instance, the old salt caravans in the Sahara or the Silk Road in Central Asia crossed desert areas through established routes with stopovers in caravan villages. Some of these villages are now classified as World Heritage Sites and offer extensive opportunities to explore desert history (UNESCO, 2018), such as Tombouctou (Mali) and Chinguetti (Mauritania) where extensive trading network enabled the establishment of ancient libraries of notable historical importance.

Deserts display several cultural features associated with human presence that add value to the general recreational experience of the ecotourist and enhance strong connections between dissimilar societies (Fig. 4). Firstly, desert people domesticated camels and dromedaries due to their adapted physiology to withstand hyper-arid conditions and to transport goods along extensive trade routes. Also, humans have long adapted to the harsh environment by using desert elements to counter the high temperatures, strong winds and lack of water (Saarinen, 2016). For instance:

- Tuareg tribes in the Central Sahara use dried bulrush (*Typha elephantina*) to build the roofs of their houses (locally called *Zeribas*) and transport water and milk in reservoirs made of goat skin (called *Guerba*) that keep the water fresh;
- Moors in the West Sahara use dromedary fur and local trees to build their tents (called *khaimas*);

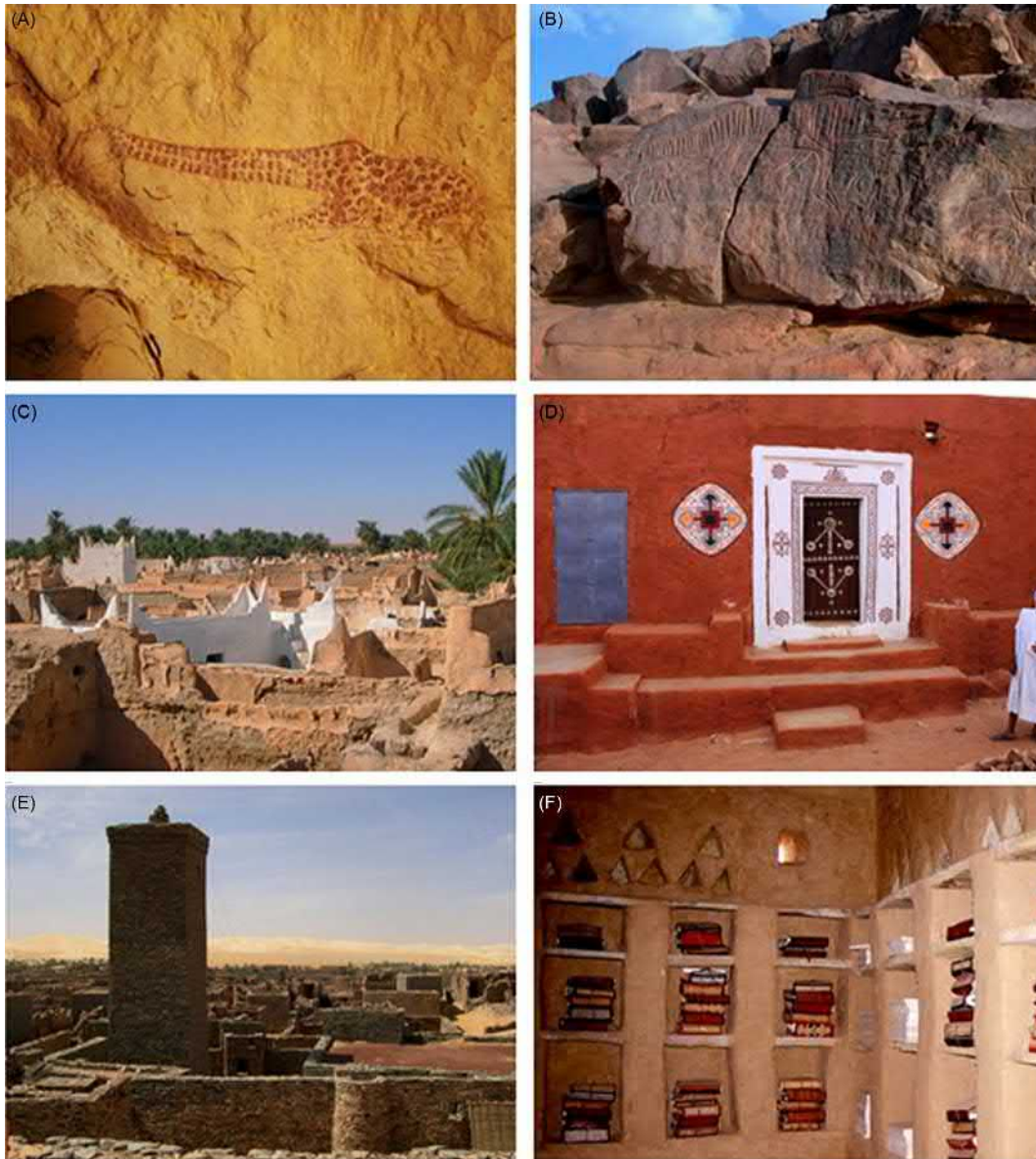


Fig. 3 Examples of historical features associated with human occupation of the desert biome with potential for ecotourism: (A) rock-art representation of giraffe (Tadrart; Algeria); (B) rock-art representation of crocodile (Messak Settafet; Libya); (C) World Heritage Site of Ghadames oasis (Libya), (D) Oualata and (E) Tichit (Mauritania), ancient stop-points for caravans crossing the Sahara; (F) historical library in Chinguetti (Mauritania). Courtesy of José Carlos Brito.

- OvaHimba people (considered the last nomadic people of Namibia) cover their bodies with a self-prepared cosmetic mixture containing an ochre pigment that protects them from the extreme dryness and gives their skin a red characteristic;
- Wool hand-made crafts are manufactured in Egypt for millennia and are now highly appreciated by foreigners looking for desert handicrafts.

Secondly, due to the unpredictability of rain in deserts, humans shaped the environment to benefit their livelihoods and prosper in less favorable climatic times. The best examples of these modifications in the arid environment are the oasis, fertile green areas created for agriculture (mostly date palms, *Phoenix dactylifera*) and whose location has been of critical importance for trading and transportation routes because of the provided shade in the hyper-arid landscape. Oases become fertile when freshwater is extracted on the land surface or underground using man-made structures. Examples include:

- The extensive rock-walled terraces built by the Trincheras people of northern Sonora desert (United States) (surface extraction);
- The *qanats*, networks of subterranean channels developed by the Persian in Iran and now used throughout the North African and Asian deserts (underground extraction).



Fig. 4 Examples of cultural features associated with human occupation of the desert biome with potential for ecotourism: (A) settlement and food-storage systems of OvaHimba people in Opuwo (Namibia); (B) settlement in Ounianga Serir (Chad); (C) oasis (Ziz valley, Morocco); (D) riverbank village (Tassili n'Ajjer, Algeria); (E) desert village (Agadez, Niger); (F) trading route (Air mountains, Niger); (G) Watering livestock from rock-pool; and (H) excavated well from dry riverbed (Tagant, Mauritania). Courtesy of José Carlos Brito and Jarkko Saarinen.

In the region of Gourara and Touat in the Algerian Sahara, about 500 of these systems are still working. Where water-bodies are far from the oases, as in much of the Sahara, the water is lifted to the surface by cantilevered bucket systems (called *shadufs*). Oases vary in extension, but one of the largest and most spectacular is in Uzbekistan, which supports 230,000 ha of irrigated land.

Thirdly, early hunter-gatherers developed uses for local plants and animals to enrich their medicine and diets. For instance, the Topnaar people of the Namib Desert have known uses for 81 plant species and the San people of the Kalahari Desert list more than 100 species of food plants and 55 animal species, some of them with medical uses.

There are unique ethnic costumes and ceremonies that can only be appreciated in deserts. For example:

- Religious ceremonies are pursued by the Shoshone people around the Yucca Mountain (United States) and by the aboriginal people around Uluru (Australia);
- Assyrians, indigenous to Western Asia, are well known by the *khigga*, a folk dance that is traditionally performed during wedding ceremonies.

All modern people living in deserts represent a great repository of knowledge concerning the life in harsh environments, which must be protected and acknowledged by specialized ecotourists seeking to deep their knowledge on local desert cultures (UNEP, 2006a,b; Weaver, 2001a).

Constraints to Ecotourism Development

Desert environments involve certain features that may constraint the development potential of ecotourism. Some may affect particular deserts, such as armed conflicts or poor development conditions limiting accessibility. Others limiting issues may refer to common trends across world deserts, such as increased accessibility and exploitation of natural resources. In all cases, these constraints diminish some of the most valuable desert assets to ecotourists (Santarém and Paiva, 2015; Brito et al., 2016). However, hard and soft ecotourists may perceive these constraints differently and may be prompting to travel or not, respectively, to desert regions where these constraints critically shape desert ecotourism attractiveness (Santarém et al., 2018). For instance, hard ecotourists may support the idea of traveling to remote desert regions of poor accessibility, lacking the comforts provided by regular infrastructures, while soft ecotourism may benefit from the same transportation system created by mining or other extractive industry development purposes (Weaver, 2001a).

Security conditions

Poor security conditions diminish the attractiveness of some deserts to ecotourists, who may feel insecure to travel to regions facing on-going, and, in some cases, long-term conflicts. For example, warfare in North Africa, the Middle East, and in Southwestern Asia has caused environmental destruction (e.g., first Gulf War) and the massacre of local people, migrants and travelers (e.g., Darfur conflict). Conflicts in the Sahara-Sahel are contributing to the extirpation of threatened populations of flagship desert species at the fastest rate ever (Brito et al., 2018). Additionally, conflicts threaten cultural sites of global recognizable importance, such as the historical libraries in Tombouctou (Mali) or the archeological city of Palmyra (Syria). The depletion of natural and cultural values threatens the long-term sustainability of local ecosystems to support any form of tourism (Serra, 2007). Furthermore, the attacks against civilians and, specifically, the kidnapping for hostage taking counteracts against the countries where attacks are perpetrated. For instance, the Ministries of Foreign Affairs of developed countries generally issue advises against traveling to such countries (or define “no-go areas” within countries) as response to protect their national travelers. Another negative aspect of hostage taking for future ecotourism development is the long-lasting reputation of danger associated to the region and the psychological burden imposed by traveling in those regions (even after conditions ameliorate).

Under-developed conditions

Large portions of the world deserts span countries with poorly developed conditions (UNEP, 2006b). In general, desert regions in North and South America, in Australia, and in Southern African countries are perceived as socioeconomically developed and have relatively good infrastructure, whereas deserts in North Africa, the Middle East, and Southwestern Asia display poorer social conditions and infrastructures. Underdeveloped airports, hazardous roads, lack of regular transportation networks, alongside the lack of supporting infrastructures (e.g., hospitals, accommodation, restaurants) may affect the attractiveness of deserts for ecotourists. For example, central Saharan countries, such as Niger and Chad, are considered among the least infrastructure-developed countries in the world, whereas Namibia is recognized to be among the top countries in developed tourism infrastructures, specifically in the desert biome. Although deserts experience less disease outbreaks in comparison to other world biomes, ecotourists may get severely ill from local epidemics, such as the Arizona (United States) endemics Hantavirus Infection, the Rocky Mountain Spotted Fever, and the Coccidioidomycosis Valley Fever (AZDO, 2019).

Political conditions

Ecotourists may express prejudice against visiting deserts located in countries with poor levels of democratic functioning or under sanctions by the international community. The political agendas of several countries in the Sahara-Sahel, Arabian Peninsula and Southwestern Asian deserts are not always aligned with the interests of both local and international communities. In countries ruled by dictatorial regimes, where freedom of thought and speech are often suppressed, animosity between locals and ecotourists may

generate, which negatively affects the promotion of desert ecotourism and the attractiveness of particular regions (Brito et al., 2014, 2016). Furthermore, the high levels of bureaucracy and corruption that usually characterizes dictatorial regimes hamper the establishment of successful ecotourism businesses.

Increasing accessibility

Accessibility plays a critical role in attracting soft and hard ecotourists to deserts but the assessment of its suitability to attract both groups remains poorly studied. On the one hand, increasing accessibility promotes the visit of soft ecotourists, but on the other hand it will tend to deter the hard ecotourists (Santarém et al., 2018). In addition, human population is growing worldwide, and desert areas are no exception; urbanization is increasing, and nomads are becoming sedentary in many world deserts (UNEP, 2006b). These developments cause generalized landscape degradation, with cascading negative effects upon large-sized animals needing vast wild areas during seasonal migratory movements. For example, migratory populations of the flagship African savannah elephant (*Loxodonta africana*) in Mali have been particularly affected by increasing human sedentary in elephant's migratory pathways (Brito et al., 2018). Land degradation and biodiversity loss lessen ecotourists expenditures as desert natural features disappear.

Exploitation of natural resources

The exploitation of natural resources in world deserts, including oil and gas pumping and minerals extraction is expanding. Besides deteriorating habitats in which ecotourism operations are based, they also affect the ecotourists' experience (Weaver, 2001a). For example, oil exploration activities have increasingly affected populations of the critically endangered Addax in Niger. This flagship species has been experiencing dramatic declines since oil exploitation activities started (Brito et al., 2018), which prevent ecotourists from traveling there, as the most important ecotourism asset may be completely depleted from the ecosystem.

Impacts of Ecotourism on Different Desert Facets

Resolutions adopted by the General Assembly of the United Nations highlighted the positive impacts of ecotourism to eradicate poverty and to protect the environment (UNWTO, 2018). Ecotourism has a potential to contribute to these aims in desert environments (Table 2) but it is important to realize that this "potential" can be positive or negative and direct or indirect. Positive impacts tend to occur at broad scales, whereas negative impacts are more localized. Developing desert ecotourism should also consider these aspects to maximize return-on-investment scenarios at multiple scales (from the business owner to local communities passing through state governments) and to diminish economic inefficiencies in peripheral regions, while preserving local environments at the same time. Despite these potential negative impacts, ecotourism has been suggested to be among the best tools to address economic and social imbalances in deserts (Santarém and Paiva, 2015).

Table 2 Potentially positive and negative impacts from ecotourism in the desert biome

Positive	Negative
● Protects species and habitats ● Repairs degraded habitats ● Funds protected areas ● Maintains ecosystem services ● Subsidizes scientific research ● Raises conservation awareness and fosters environmental-friendly behaviors ● Generates direct/indirect employment and revenues ● Multiplies systems of generating revenues ● Funds community-based projects ● Stimulates other forms of tourism ● Supports pharmaceutical investigation ● Improves education ● Diminishes gender inequalities ● Sustains ancient practices ● Provides spiritual benefits ● Fosters social inclusiveness	<i>Environmental impacts</i> ● Disturbs or destroys wildlife ● Potentiates species invasiveness ● Restructures habitats permanently ● Generates local pollution and waste ● Boosts water abstraction ● Diverts funds from less to more charismatic species <i>Economic impacts</i> ● Needs substantial initial investments and operational costs linked to remoteness and climate ● Sensitivity to long-term uncertainties in generating revenues ● Increases medical assistance costs ● Disrupts local subsistence ● Creates income inequalities and increases economic pressures <i>Sociocultural impacts</i> ● Increases cultural shocks ● Erodes local power ● Generates animosity/resentment

Modified from Weaver, D. B. (2001). Ecotourism. Queensland, Australia: John Wiley & Sons Australia, Ltd.

Ecological Impacts

Positive

Ecotourism may protect desert biodiversity through financial mechanisms that support breeding, feeding, translocation, antipoaching, and other conservation programs with direct positive effects on species population growth and viability (Buckley et al., 2016). For instance, the populations of cheetah (*Acinonyx jubatus*) in the Kgalagadi Transfrontier Park (South Africa) and of the Western Barred Bandicoot (*Perameles bougainville*) in the Arid Recovery Reserve (Australia) rely on tourism revenues for their conservation. Ecotourism may also benefit biodiversity and human populations when it contributes to the restoration of degraded habitats and environments that help to maintain and safeguard ecosystem services (Buckley et al., 2016; Weaver, 2001a). These include provision of clean water, which in deserts is a scarce and highly valuable asset, and raw materials, such as palm trees for timber production, and medical resources, such as venoms from desert vipers for antivenom development (Weaver, 2001a). Ecotourism may fund the establishment of new protected areas in desert countries and maintain and increase old ones. For instance, 12% of the Namibian protected areas' budgets are assured by tourism expenditures (Buckley et al., 2012).

Ecotourism may also subsidize scientific research on species and protected areas (Wearing, 2001), by making people donating more funds to environmental causes and creating "environmental watchdogs" (nature activists that will intervene in favor of the environment; Weaver, 2001a). For example, the conservation of the northernmost population of the African savannah elephant in the Gourma region (Mali) is enforced by a community-based vigilance network composed by 520 "eco-guardians" living throughout the elephant range, which continually patrol and alert about elephant locations, numbers and behavior, elephant deaths, and poaching incidents (Brito et al., 2018). By raising conservation awareness and fostering environmental-friendly attitudes among local communities, policy makers and the likes, ecotourism may influence communities' nature-pro behaviors, improving the sustainable harvesting of food and natural resources (Lindberg, 2001; Wearing, 2001; Weaver, 2001a).

Negative

Recreational activities in deserts are usually based in all-terrain vehicles, which may degrade the landscape and increase local pollution. The exhaust gases released to the atmosphere may also affect sensitive desert vegetation. For example, many plants of the Mojave Desert (United States) died when exposed to various vehicles' pollutants in a laboratory experiment. The impacts of chemical fuel leakage to the ground and of soil compacting and erosion may take decades to disappear. For instance, the soils of the Joshua Tree National Park (United States) were found to be compacted from 2 to 5 cm because of constant vehicles traffic (Ouren et al., 2007). Motorized driving may also run-over desert fauna or destroy vertebrate ground nests. For example, the populations of desert tortoise (*Gopherus agassizii*) and Couch's spadefoot toad (*Scaphiopus couchii*) have decreased in areas with high off-road vehicles passage in Mojave and Colorado deserts (United States) because vehicles collapsed burrows. In addition, they may produce noise that disturbs local fauna, which ultimately alters animal behavior, reduces preys' capabilities of detecting predators, and stimulates aestivating animals to emerge from their burrows at inappropriate times. For instance, kangaroo rats (*Dipodomys deserti*) in California deserts (United States) experienced hearing loss when exposed to continuous sound produced by dune buggies, which made them unresponsive to predator sounds for weeks (Ouren et al., 2007). Additionally, desert vegetation is under increased risk of vehicles passage, being reported that lichen communities of the coastal Namib desert are eliminated by a single vehicle passage (UNEP, 2006b).

Transportation can contribute to the proliferation of invasive species in deserts, particularly when humans assist plant seeds or invertebrates to travel long distances, for instance attached to vehicles. Proliferation of invasive species may also be facilitated by vehicles' exhausting gases. For example, annual grasses prone to wildfires proliferated after a CO₂ increase in the atmosphere of the Mojave Desert (United States), accelerating local fire frequency in regions where they did not exist before (UNEP, 2006b). Keeping vehicle speeds down and, more importantly, using other forms of transportation, such as camel trekking or air ballooning, can reduce air and soil pollution, preserve the quality of the surrounding environment, and minimize wildlife direct damages (UNEP, 2006a).

Permanent environmental restructuring may occur when setting and operating tourism-supporting infrastructures. Locally, the surrounding landscapes may become less natural, sound and light pollution may become more frequent, and the soils sustaining those infrastructures may become permanently altered. In the long-term, ecotourism may also generate waste and contaminate soils and the scarce water resources available, if wastes and sewage waters are not properly treated (Serra, 2007; UNEP, 2006a). As ecotourism potentiates the development of other economic activities, additional infrastructures may be constructed, which can magnify impacts on soil and water, particularly when less-benign energy sources are used (Weaver, 2001a).

Several measures should be taken to minimize the ecological impacts of ecotourism. For example, construction of infrastructures should opt for local materials to minimize landscape impacts. Alternative energies should be preferred when building/recovering infrastructures, such as wind and solar energy that provide feasible energy production in deserts. Ecotourists should be encouraged to take toxic wastes (like batteries and aerosols) back home and arrangements should be enforced to deal with waste removal. For example, companies from Mauritania and France set-up a joint waste collection protocol in Chinguetti, a highly visited UNESCO World Heritage Site (UNEP, 2006a).

Water abstraction for serving ecotourism activities and accommodation may cause water shortages. This problem is amplified by the natural dryness of deserts. For example, the small dune fields throughout the Taffilat region of Morocco are threatened by the massive and unsustainable construction of tourism facilities, which are progressively surrounding them. Making use of systems that reduce water-levels consumption and recycle sewage waters should be preferred whenever possible. Raising awareness among

ecotourists about the consequences of their actions should stress the scarcity of water resources and the unsustainable nature of its excessive use in desert environments (UNEP, 2006a).

To a lesser extent, the promotion of the most charismatic desert species by ecotourism operators may counteract against other species less appealing to the general public, diverting funds from the latter to the former. This may have a negative impact on less charismatic desert species when international ecotourists restrain from conserving them (Weaver, 2001a). In alternative, the promotion of flagship fleets, that is, groups of species displaying similar appealing traits that raise the profile of more than one species to attract different segments of the society, may maximize conservation marketing and return-on-investment scenarios for ecotourism in deserts (Santarém et al., 2019).

Economic Impacts

Positive

Ecotourism can provide direct and indirect economic benefits to desert communities, offering local employment as tour guides, receptionists, cooks, planners etc. Some jobs are desert-specific and benefit from local people's in-depth knowledge of the environment, such as camel drivers, who become indispensable to convey desert cultural knowledge to ecotourists. Ecotourism may also provide alternative ways of empowering local communities, for instance by creating opportunities for selling desert crafts to travelers (UNEP, 2006a), further benefiting the whole community. Ecotourism may stimulate other forms of tourism, such as cultural tourism or adventure tourism, and act also as a catalyzing agent to generate other jobs that feed it directly or indirectly. By creating employment, ecotourism displays an underlying multiplier effect that benefit local communities and regional and national governments (Wearing, 2001; Weaver, 2001a). For instance, it may help creating jobs in provisioning (such as food production or bed linen) and services sectors (such as water cleaning, infrastructure maintenance or banking and accounting). These indirect effects occur, for instance, when local restaurants use ecotourists' expenditures to purchase local goods and services from other businesses, and to pay employees that will spend their wages in buying external goods and services. This generates a circular economy where all parts benefit. Additionally, all these sectors must pay taxes, fees, and licenses that generate increased stimulus to fiscal policies (Lindberg, 2001). Peripheral and marginalized regions of some world deserts should be the ones to benefit the most, which labels ecotourism as a sustainable tool to eradicate extreme poverty (Lindberg, 2001; UNWTO, 2018; Weaver, 2001a). For instance, local people generated multiple jobs (directly and indirectly related to the tourism sector) after successive Communal Conservancies were created in Namibia.

Residents of ecotourism destinations may benefit from revenue-sharing programs that fund community-based projects, such as sustainable agriculture or clinic and school construction and upgrade. For example, ecotourism helped the Torra Conservancy of Wilderness Safaris' Damaraland Camp in Namibia to release c.\$120,000 of the profits to upgrade local schools in 2002 (Butler et al., 2009). Ecotourism may also increase the investigation and procurement of desert natural assets for food production, such as palm dates, or pharmaceutical developments, such as desert snake venoms, which benefit both local and global communities (Weaver, 2001a).

Negative

Initial investments on land acquisition, materials' purchases (including vehicles), initial staff training, and promotion have substantial costs, but on-going operational costs, such as wages, infrastructures and vehicles maintenance (meaningful in deserts due to the remoteness and harsh climate of the biome—temperature, sand and salt winds), and continuous marketing bail out most of the operational costs when developing desert ecotourism (Serra, 2007). Ironically, these costs translate into benefits when considered from the perspective of the people that benefit from them (Weaver, 2001a). Building infrastructures nearer established cities, villages and oases, and opting for vehicles with anticorrosive materials may diminish the depreciation speed of these goods.

Ecotourism development in the desert biome may be sensitive to long-term uncertainties in generating revenues. These may arrive from the general supply-and-demand risks but also from specific traits of some deserts, such as regional insecurity, or diseases outbreaks. These aspects may make initial investments unreliable, resulting in no-profit situations or, even worse, in substantial economic losses (Brito et al., 2014, 2016; Weaver, 2001a). Ceasing regional conflicts and developing control measures to prevent disease outbreaks helps to reestablish operations. For instance, after a 10-year break period following the growing in regional insecurity, only recently international tourist agencies are again offering services to visit some Sahara-Sahel countries. That is the case of Mauritania, where French carriers reestablished flights to well-known touristic places in the Adrar and Ouadane areas.

Ecotourism may incur in indirect economic costs when wildlife encounter accidents occur, particularly when flagship species protected for ecotourism become cause of human injuries. For example, the venomous desert snakes American horned rattlesnake (*Crotalus cerastes*) and the North African horned viper (*Cerastes cerastes*) are among the world's most toxic and they may bite visiting ecotourists, generating additional costs related to medical assistance, notwithstanding the animosity that injured people create towards typical desert flagship species (Weaver, 2001a). Developing clinics and hospitals in strategic places would allow injurers to be healed faster and properly, reducing the costs of transportation of diseased people. Multinational pharmaceuticals can also target efforts to develop strong antidotes specific to each of the several desert venom species, which entail substantial costs in research and development but translate into profits for the world society at many scales in the long term.

Especially in the Global South, ecotourism operations are often owned and monopolized by international business and foreign actors controlling all processes from the land acquisition to the establishment of an ecotourism company, including the provision of related services. Considerable negative impacts might arise if foreign control and importation of external products leak all the

revenues away from the local community and the regional states where ecotourism takes place (Lindberg, 2001; Weaver, 2001a). Including local communities in early strategic ecotourism development plans and developing strong policies against monopolies and expropriation of local deserts from foreigners enforces local people rights and grants that most of the revenues stay with who need them the most. Corporate social responsibility is a recent type of business self-regulation that can help on this issue, as it includes men, women and the youth in strategic plans to increase long-term companies' profits.

Ecotourism, as any other form of tourism, may sometimes exacerbate income inequalities within community members (Lindberg, 2001). Ecotourism may counteract against local interests and preferences by increasing demand-to-supply and the prices of house rents, local goods and services, which create economic pressures that may disrupt people financial stability and obliges them to leave the region, and may extirpate local ancient cultures (Lindberg, 2001; Wearing, 2001; Weaver, 2001a). In Mmatshumo village of the Makgadikgadi pans landscape (Botswana), for example, some communities have become involved in ecotourism, which has resulted in a decline or even termination in traditional livelihood activities like subsistence hunting and gathering. However, not all community members have been able or willing to work with ecotourism and related employment, which has caused increasing inequalities in communities (Lenao et al., 2014). To avoid ecotourism related local inequalities, strong national policies promoting equitable access to resources and considering the needs of local people may boost the development of desert communities. Additionally, alternative jobs should be considered in remote regions where few desert attractions for ecotourism exist, thus allowing people to sustain the same lifestyle as those living in ecotourism-rich regions. Regional agreements and international conventions must develop strong legal frameworks for the protection of desert natural assets and the interests of indigenous people.

Sociocultural Impacts

Positive

Successful ecotourism development can diminish gender inequalities and give power to women and youth embracing qualified jobs. It has the potential to improve education in peripheral and marginalized desert regions and to generate resources for community-based development projects, improving people's acceptance of alternative ways to generate income while preserving desert resources (UNWTO, 2018). For instance, nomadic Bedouins that once hunted birds in Palmyra (Syria) adopted more sustainable activities by becoming ecoguides (Serra, 2007). Ecotourism creates markets for local products, thereby sustaining and promoting ancient practices, and making local people proud of their traditions. By turning local knowledge, cultural skills and traditional craft skills into attractions to travelers, ecotourism may help to preserve the desert cultural heritage. For example, the Ksour Route is a project developed to show ecotourists the old trade routes across the Southern Algerian Sahara and that aims to rehabilitate traditional architectural heritage. A spectacular example comes from the La Ruta de Sonora Ecotourism Association, which is a transboundary commitment between United States and Mexico to protect the natural and cultural heritage of the Sonora desert through desert trans-frontier ecotourism (UNEP, 2006a). Ecotourists that spend more time understanding host communities' habits and patterns will likely respect local knowledge and traditions and promote them in their own countries, creating a society ruled by respectful understanding of social differences (Wearing, 2001).

Ecotourism may provide many spiritual benefits to the individual, maximizing nature enjoyment for locals and ecotourists alike (Weaver, 2001a). Deserts are particularly prone to this spiritual relief sensation, given their extensive landscapes that offer a perception of solitude and deepens root-connections with nature. Ecotourism may also potentiate social inclusiveness by accommodating a wide spectrum of the society, particularly individuals with substantial physical and mental limitations that could find barriers to their enjoyment in other types of activities (UNWTO, 2018; Weaver, 2001a). Deserts are especially suitable to accommodate disabled people, as their extensive plains and sparse vegetation may facilitate locomotion.

Negative

While having a great potential to benefit communities, ecotourism operations can generate cultural conflicts and shocks between ecotourists and indigenous communities when certain aspects of local lifestyle are in opposition with principles defended by ecotourists (e.g., brutal killing of a charismatic animal for ecotourists that is at the same time a valuable food for local people; Weaver, 2001a). To prevent conflicts and cultural shocks, thematic travel arrangements should respect desert traditions and be made only after consulting desert local communities (UNEP, 2006a). Marketing ecotourism should make aware the local traditions and potential conflicts of interest to visitors when visiting particular desert regions.

Ecotourism may transform and erode local power systems and structures when new business-oriented local or nonlocal elites take control over local assets. Businesses that impose control over local desert assets, like food and water, may create resentment among local people. Also, disruption of established social relationships may potentiate local resentment upon nature that is protected for ecotourism, particularly when local access to natural assets is blocked due to stringent nature protection laws but allowed to ecotourists visiting the region. Deliberate acts against nature (e.g., intentional wild killing and habitat destruction) may occur to intentionally shock the visitors (Lindberg, 2001; Serra, 2007; Wearing, 2001). Fortunately, there are few or no reported records of these behaviors in deserts to date. Ecotourism may be seen as a complementary tool to other local practiced land-uses, and not a mean to the obstruction of ancient practices. Therefore, access to local resources should not be exclusively granted to foreigners or passively prohibited to locals.

Ecotourism may generate resentment among people from the same community, when some or all of them are not involved in the ecotourism planning process, or when locals feel their visions and traditions are being neglected. Even worse, foreign-owners of



Fig. 5 An example of successful cooperation between local communities, research institutions, national park staff and governmental institutions in the promotion of environmental responsible acts in deserts and in early adoption of ecotourism as a means to preserve the West-African crocodile (*Crocodylus suchus*) in Diawling National Park, Mauritania. Courtesy of José Carlos Brito.

ecotourism businesses may impose alien values (e.g., globalism and Western modernization) that can erode local ones and may lead to sociocultural tensions. The involvement of local communities is one of the most critical components in determining the success of local support for nature conservation and desert ecotourism development (Fig. 5; Serra, 2007; Wearing, 2001). Inclusive local participation in ecotourism development through corporate social responsibility initiatives can help to establish scenarios that benefit all ecotourism stakeholders without jeopardizing local values (UNWTO, 2018). To achieve the best standards of social fairness and equity it is required to consider the inherent specificities of each desert community when developing ecotourism. An example of good practice in action came from Uluru Kata Tjuta National Park (Australia), where desert Aboriginal people operated a tour company and managed all the activities, including the interpretation of Aboriginal rock-art, medical plants, and bush cookery (UNEP, 2006a).

Conclusions

The desert biome contains a wide spectrum of potentials and constrains for ecotourism planning, development and management. On the other hand, ecotourism may deliver different levels and extents of environmental, economic and sociocultural impacts across global deserts. To have successful ecotourism operations, the diversity of potential impacts needs to be understood and proactively considered. Particularly because they may contribute to the increase or the depletion of desert natural and cultural features appreciated by ecotourists. We suggest that the various impacts of ecotourism are managed in respects with the specificities of each desert context, considering its people, wildlife and ecosystems. In the desert biome, ecotourism should be developed in ways that are based on effective management tools and responsible practices leading to sustainable governance and use of the natural and cultural heritage resources of deserts. Additional research efforts are highly needed in this regard, particularly in what refers the studying of alternative and sustainable development methods. Although ecotourism is not a panacea for widespread biodiversity losses, if properly managed, it can relief some of the threats to desert biomes. Ultimately, desert ecotourism can act as a sustainable tool to achieve the Sustainable Development Goals of the United Nations, contributing positively to the wellbeing of people living within deserts and to threatened desert heritage.

Acknowledgments

This study was developed under AGRIGEN-NORTE-01-0145-FEDER-000007, supported by Norte Portugal Regional Operational Programme (NORTE2020), under the PORTUGAL 2020 Partnership Agreement, through the European Regional Development Fund (ERDF). FS and JCB are supported by Fundação para a Ciência e a Tecnologia through grants PD/BD/132407/2017 and contract IF/00459/2013, respectively. JS is supported by Academy of Finland, grant number 272168.

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Overview: Ice Sheets and Polar Deserts—Ice of Life

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Abstract

Life near the poles is tough but vulnerable. The very adaptations that allow both marine and terrestrial life to survive the bitterly cold winters and short, cool summers can become liabilities in a rapidly warming world. Ecological patterns and long-term species associations are already starting to break down in some Arctic regions. Thus far, the marine biota of Antarctic waters has not experienced such high rates of environmental change, but incursions of warm water caused by changes in wind patterns and ocean circulation will wreak havoc if they melt the sea ice and cause changes in krill distribution patterns.

Introduction

The two polar regions of planet Earth are very different except for two common denominators: bitter cold and division of the year into a long season of darkness (winter), followed by a long season of constant sunlight (summer). The extreme cold of polar winters is quite remarkable, given the more-or-less temperate climate of much of the planet. The average yearly temperature of the planet is 15 °C. The average winter temperature at the North Pole is –40 °C, and at the South Pole it is –60 °C. The South Pole is so much colder than the North Pole because the South Pole sits near the middle of an ice-bound continent, Antarctica. The South Pole sits atop a featureless, barren, windswept ice sheet at an elevation of 2835 m above sea level (Fig. 1). This pole is located about 1300 km inland from the nearest sea, so there is no moderating effect of oceanic climate here. In contrast, the North Pole sits atop the Arctic Ocean. Although this location is covered year-round by sea ice, it sits at sea level and regional temperatures are moderated somewhat by the proximity to ocean waters. This difference between the poles is brought out by their average summer temperatures. The North Pole averages 0 °C in summer, while the South Pole averages –28 °C. Antarctic climates are reviewed by Gonzalez and Vasallo. Climates of High Arctic regions are reviewed by Davy. Climates of Arctic tundra regions are reviewed by Serreze. Greenland climates are reviewed by Westergaard-Nielsen et al.

Life in Antarctica

Antarctic terrestrial biomes are reviewed by Parnikoza and Kozeretska. Not surprisingly, there is essentially no life on the Antarctic ice sheets and only small patches of life along the ice-free margins of the Antarctic ice sheets. In fact, less than 1% of the surface of Antarctica is free of ice. The diversity of life in these small patches of the continent is extremely small. Only two species of flowering plants are found here: Antarctic hair grass (*Deschampsia antarctica*) (Fig. 2, upper right) and Antarctic pearlwort (*Colobanthus quitensis*) (Fig. 2, upper left) (British Antarctic Survey, 2019a). These occur on the South Orkney Islands, the South Shetland Islands and along the western Antarctic Peninsula. The dominant plants of Antarctica are the cryptogams, including 100 species of mosses (Fig. 2, center left), 25 species of liverworts, 300–400 species of lichens (Fig. 2, center right) and more than 20 species of macro-fungi. The greatest abundance and diversity of these primitive plants occur on the western side of the Antarctic Peninsula where the climate is generally warmer and wetter than elsewhere in the Antarctic continent. But there is also plant life in the very dry, cold, ice-free regions known as the dry valleys of Victoria Land. Here there are algae, fungi, and lichens that live in cracks and pore spaces inside the sandstone and granite rocks. These endolithic organisms live just inside the surface of rocks—sheltered from the desiccating, freezing winds, but close enough to the surface to collect enough sunlight to carry out photosynthesis.

Terrestrial animals of the maritime regions of Antarctica include arthropods (primarily springtails and mites), earthworms and mollusks (British Antarctic Survey, 2019b). Higher insects include spiders, beetles, and flies, but there are only found in the areas with the least severe climate, such as the sub-Antarctic islands. A small number of micro-invertebrate species are also present. These

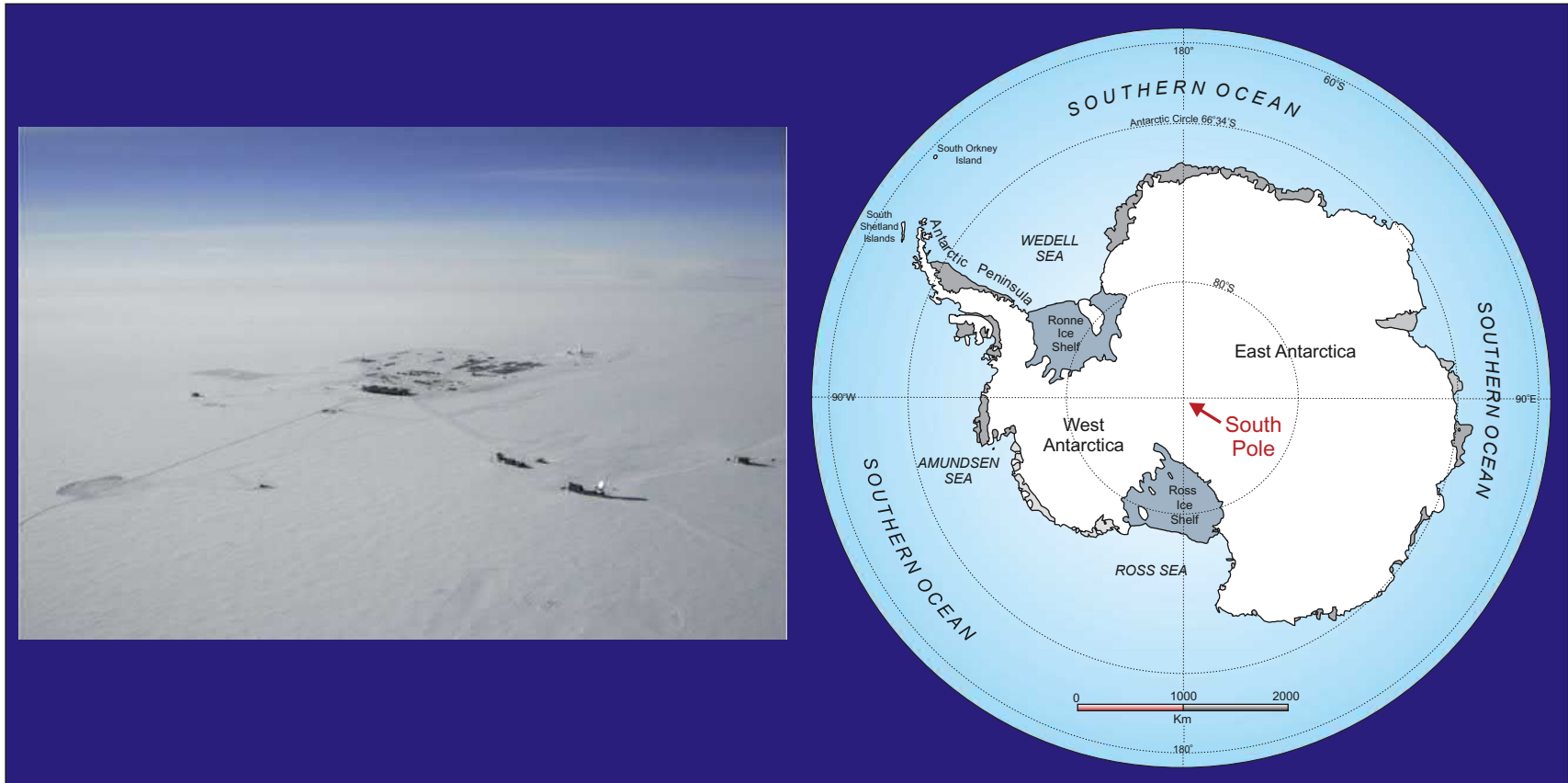


Fig. 1 Left: Photo of the South Pole, site of Amundsen-Scott South Pole Station (photo of South Pole Station by NSF, in public domain); Right: Map of Antarctica, showing the location of the South Pole (by author).



Antarctic pearl wort



Antarctic hair grass



Antarctic moss (*Schistidium antarctici*)



Yellow lichen (*Xanthoria parietina*) and black moss (*Muelleriella crassifolia*)



Red algae growing on glacier, Pleneau Island

Fig. 2 Upper left: Antarctic pearlwort (*Colobanthes quitensis*); upper right: Antarctic hair grass (*Deschampsia antarctica*); middle left: Antarctic moss (*Schistidium antarctici*); middle right: Yellow lichen (*Xanthoria parietina*) and black moss (*Muelleriella crassifolia*); bottom: Red algae on glacial ice, Pleneau Island, Antarctic Peninsula. All photos courtesy of the Australian Antarctic Division, in public domain.

include nematodes, tardigrades, and rotifers. The population densities of these tiny organisms are often high. The interior regions of the continent are almost devoid of invertebrates. No higher insects are present, and micro-arthropods are restricted to the limited patches of vegetation. Nematodes are the dominant group here. From one to three different nematode species are known to inhabit the cold deserts, one of which is a predator on the others. These cold desert soils represent the least diverse habitats on Earth.

Plankton

The greatest abundance and diversity of life in the South Polar region is found in the Southern Ocean. Because the seawater here is very cold, it holds high concentrations of oxygen, facilitating the biological productivity of these waters. Like all ecosystems, the Antarctic marine system begins at the bottom of the food chain, with plankton. The plankton of open Antarctic seas is reviewed by Smith and Meyer. The phytoplankton of Antarctic waters are dominated by diatoms, with nanophytoplankton, haptophytes, and dinoflagellates important locally. Antarctic krill (*Euphausia superba*) are an important macrozooplankton. Krill are small crustaceans that grow up to about 6 cm in length. These are among the largest species of the Antarctic plankton. Krill are the most important organisms in the diet of many predators, including fish, squid, penguins, whales, and seals. Hunting for krill is facilitated by their habit of living in dense swarms of 10,000 or more individuals per cubic meter of water. Copepods are also an important component of the Antarctic zooplankton. They feed on phytoplankton and in turn, are eaten by krill and fish.

Marine Mammals

The ecology, behavior, and distribution of Antarctic marine mammals are reviewed by Bester. Whales were almost wiped out in the Southern Ocean by whalers in the 19th and 20th centuries, but their numbers have rebounded in recent years ([British Antarctic Survey, 2019c](#)). The whales of the Southern Ocean head to warmer waters during the Antarctic winter. Calves are born in these warmer seas, as the Southern Ocean is simply too cold for them during the first few months of life. The whales return to the Southern Ocean in austral spring, following the receding margins of sea ice. These boundary waters between sea ice and open ocean are areas of high biological productivity that provide rich feeding grounds.

Two groups of whales are found in the Southern Ocean near Antarctica: the toothed whales and the baleen whales. The toothed whales prey on fish, squid, penguins, sea-birds, seals and sea lions, using echolocation to find their prey. Toothed whales include the sperm whale (*Physeter macrocephalus*) ([Fig. 3](#), upper left), more than 20 species of beaked whales, and the killer whale (*Orcinus orca*) ([Fig. 3](#), upper right), which is actually not a whale, but is the largest of the dolphin species. The killer whale population of the Southern Ocean now numbers over 160,000 individuals. The other dolphin species found in the Southern Ocean is the hourglass dolphin (*Lagenorhynchus cruciger*) ([Fig. 3](#), center left).

Baleen whales have fibrous plates of baleen instead of teeth, which they use to strain plankton and small fish from seawater ([Fig. 3](#)). The baleen whales of the Southern Ocean include the blue whale (*Balaenoptera musculus*), the fin whale ([Fig. 3](#), center-right) and the humpback (*Megaptera novaeangliae*). The most numerous baleen whale is the Minke whale (*Balaenoptera acutorostrata*), a species that spends much of its time in the Antarctic near the edge of the sea ice.

Seals are divided into two groups: true seals and eared seals, the latter comprising fur seals and sea-lions. The numbers of individuals can be quite high. For instance, there are 65,000 breeding fur seals on Bird Island. Seals feed on fish, squid, and krill. Thick layers of blubber beneath their skin provide a food reserve as well as insulation. All Antarctic seals also have a layer of fur, giving additional insulation when they are hauled out on land or ice. Seals leave the water to breed, rest and molt. There are six Antarctic seal species. Four of these are ice-habitat specialists. They breed on sea ice in spring. These include the leopard seal (*Hydrurga leptonyx*) ([Fig. 3](#), lower left), the Ross seal (*Ommatophoca rossii*), the Weddell seal (*Leptonychotes weddellii*) and the crab-eater seal (*Lobodon carcinophagus*) ([Fig. 3](#), lower right). The Antarctic eared seals comprise just two species, the Antarctic fur seal (*Arctocephalus gazella*) and the elephant seal (*Mirounga leonina*) ([Fig. 3](#), bottom). Both species swim north of the pack-ice zone and breed in dense colonies on beaches.

Probably the greatest immediate threat to Antarctic krill-feeders (baleen whales, seals, penguins) is the constriction of seasonal pack ice, combined with a decline in krill biomass in the Southern Ocean. Antarctic krill (*Euphausia superba*) populations have declined by 40–80% in the last three decades around the South Shetland Islands near the tip of the Antarctic Peninsula ([Trivelpiece et al., 2011](#)). Historically, krill have been one of the most abundant macro-zooplankton on Earth, with a combined biomass equal to that of all fishes in the ocean. Their decline in recent decades is due to multiple factors, including reduction of sea ice from regional climate warming and the development of commercial krill fishing to supply omega-3 oil capsules to the health food industry ([Fig. 4](#)). The western Antarctic Peninsula is warming faster than most of the rest of the planet. Winter temperatures have risen about 6 °C over the past 60 years, reducing sea ice cover. Krill use the sea ice both for shelter from predators and to harvest algae growing below the ice.

Krill are a vital food resource for eight species of baleen whales in Antarctica; 17 species of penguins rely on krill for food. The six seal species of Antarctic waters rely either directly or indirectly on krill. The loss of sea ice has a negative effect on krill numbers as well as negative effects on seals, because sea ice loss reduces the availability of suitable breeding and resting habitats for seals, as well as providing protection from predators, such as killer whales. A major issue in Antarctic marine mammal conservation is our lack of knowledge concerning the population sizes of the various species and the infrequency of censuses. As things stand today, only large-scale changes can be detected, so gauging marine mammal responses to gradually developing threats is almost impossible.



Sperm whale



Killer whales



Hourglass dolphins



Fin whale



Leopard seal



Crabeater seals



Elephant seals

Fig. 3 Cetaceans and pinnipeds of Antarctic waters. Upper left: sperm whale (*Physeter macrocephalus*); upper right: killer whales (*Orcinus orca*); middle left: hourglass dolphins (*Lagenorhynchus cruciger*); middle right: fin whale (*Balaenoptera physalus*); lower left: leopard seal (*Hydrurga leptonyx*); lower right: crabeater seals (*Lobodon carcinophagus*); bottom: elephant seals (*Mirounga leonina*). All photos courtesy of NOAA, in public domain.

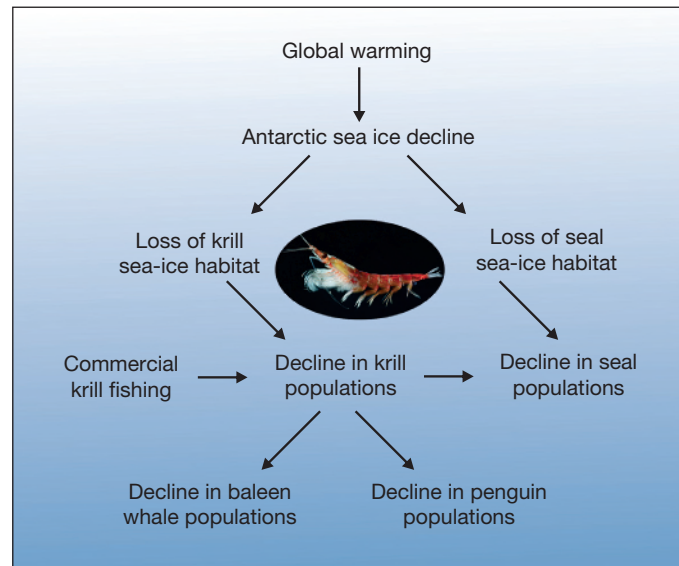


Fig. 4 Flow chart illustrating the causes of recent Antarctic krill (*Euphausia superba*) declines (by author) and impacts on penguins and marine mammals that feed on krill. Krill photo courtesy of the Australian Antarctic Division.

One topic in Antarctic ecosystems that was not covered in this section concerns declines in penguin populations. Some dramatic declines have taken place in recent decades. For instance, [Weimerskirch et al. \(2018\)](#) report that the largest king penguin colony in the world, on Ile aux Cochons in sub-Antarctic waters, has declined by 88% over the past 35 years, from more than 500,000 breeding pairs to just 60,000 pairs. The reason for this decline remains unknown, although possible causes include climate change, disease, competition for resources, and an El Niño event in 1997.

Sea-surface temperature (SST) has been found to play a key role in penguin distribution and abundance. [Evans et al. \(2019\)](#) studied population changes in the little penguin (*Eudyptula minor*) during a marine heatwave in 2016 off the coast of Tasmania. During this high SST event, the probability of penguin presence decreased rapidly as the temperature rose above the long-term average SST. Regional SSTs were markedly cooler in 2018, but again the authors found that the probability of penguin presence decreased almost linearly in locations with temperatures above the mean. In fact, these penguins selected a mean SST of 17.8 ± 0.4 and 17.4 ± 0.2 °C in 2016 and 2018 respectively. Similarly, penguins opted for a narrow summer thermal range in other colonies studied. But it is not the water temperature per se that is attracting the penguins. The penguins feed on krill, and the krill live in cooler waters. Hence, there is a link in this region between the cold-adapted krill species and the preference shown by little penguins for cooler water regions. Penguins target krill and perhaps small fish that also feed on krill in cooler water. Thus, the penguins follow the krill. This demonstrates that penguins need water of a certain temperature to feed on their preferred prey. If sea-surface temperatures rise in the Southern Ocean because of global warming, then penguins, krill-feeding marine mammals, and other top-end predators may face food shortages.

Life in the High Arctic

Unlike the Antarctic, where a large continent is situated over the pole, the Arctic region is almost equally divided between land and sea. The land areas include the northern regions of North America and Eurasia, Greenland, and groups of islands that extend north to about 83°N. Both animal and plant life decline in abundance and diversity in the High Arctic, which is essentially polar desert.

Marine Life

As discussed by Lovejoy, the plankton of the Arctic Ocean are taxonomically and functionally diverse, and most species have pan-arctic distributions. The Arctic Ocean and adjacent seas are a combination of highly productive shelf regions and polynyas, and extremely oligotrophic basins north of 70° latitude. The plankton form complex trophic webs that support substantial populations of marine mammals and birds. As with the Antarctic phytoplankton, the lack of light for much of the year in the northern high latitudes, combined with ice cover, constrains annual photosynthetic productivity by the phytoplankton. Both Arctic and Antarctic seas have polynyas: areas of open water surrounded by sea ice that persist throughout the year. Polynyas provide year-round access to light which, combined with the resuspension of nutrients, extends the normally short arctic phytoplankton bloom. This boost in primary productivity helps maintain diverse zooplankton communities.

The cold, nutrient-rich waters of the Arctic, especially the seas on the margins of the Arctic Ocean, support a rich and diverse marine mammal fauna ([Fig. 5](#)). The shelf regions of the Arctic Ocean are the most extensive of all oceans, covering about 50% of its total area.



Humpback whale



Narwhals



Beluga whales



Harp seal



Bearded seal

Fig. 5 Marine mammals of the Arctic. Top left: humpback whale (*Megaptera novaeangliae*); top right: narwhals (*Monodon monoceros*); center: beluga whales (*Delphinapterus leucas*); lower left: harp seal (*Pagophilus groenlandicus*); lower right: bearded seal (*Erignathus barbatus*). Narwhal photo by Paul Nicklen; humpback whale photo by Whit Welles, courtesy of Wikimedia Commons; all other photos courtesy of Corel Corporation.

These shallow waters contribute to the abundance and diversity of Arctic marine life. Arctic marine ecosystems are home to more than 2000 species of algae, and over 5000 animal species, ranging from zooplankton, fish, and seabirds to apex predators such as the polar bear (*Ursus maritimus*) and narwhal (*Monodon monoceros*). The marine mammals of this region are discussed in Elias.

Current threats to Arctic ecosystems are discussed by Gamburg. One widespread problem is the pollution of land and sea by mercury from anthropogenic sources. Mercury levels in the Arctic are now three times higher in freshwater and 10 times higher in marine ecosystems than they were in pre-Industrial times. Over the past 150 years, there has been a 10-fold increase in mercury levels in the upper trophic level marine animals, including beluga, ringed seal, polar bear, and birds of prey. Mercury, like persistent organic pollutants (POPs), accumulates in animal tissues and concentrations increase up the food chain. Populations of some species at the top of the marine food chain, such as the polar bear, pilot whale, narwhal, beluga, and hooded seal are at high or severe risk of mercury poisoning.

Both the lands and seas of the Arctic are rapidly warming in response to steady increases in global Greenhouse Gas (GHG) emissions. Summer sea surface temperatures (SST) in the Arctic Ocean are driven mainly by the amount of incoming solar radiation

absorbed by the sea surface. Greater warming occurs in ice-free regions because the open water reflects little light back into space, whereas sea ice reflects a great deal of solar energy. The open ocean reflects only 6% of the incoming solar radiation and absorbs the rest, while sea ice reflects 50–70% of the incoming energy. August SSTs have warmed significantly since 1982 for most regions of the Arctic Ocean that are ice-free in August. One of the biggest biological impacts of this warming is the loss of sea-ice cover. Sea ice loss represents a huge habitat reduction for sea-ice algae and phytoplankton. This habitat loss has severe consequences for the Arctic marine food chain because these phytoplankton represent 57% of the primary productivity of the Arctic Ocean. Sea-ice also serves as a stable platform from which various marine mammals operate in the winter months, including walrus, seals, and polar bears.

One of the greatest obstacles to our understanding of the ongoing changes in the biodiversity of Arctic marine ecosystems is the fragmented nature of our knowledge and the paucity of consistent and regular long-term monitoring programs (Michel et al., 2013). Anthropogenic changes are happening at unprecedented rates. These range from GHG warming to the opening up of new shipping routes, the increasingly northward development of fishing grounds, and the drilling of oil and gas wells on the continental shelves. The effects of these stressors on Arctic marine ecosystems remain poorly understood, and the impact of cumulative effects make predictions of biotic responses extremely difficult. Shifts in ecosystem structure, species interactions, and trophic pathways need to be understood in the context of both short- and long-term trends, to develop management strategies to maintain the diversity and sustainability of Arctic marine ecosystems.

Terrestrial Vegetation

The vegetation zones of the Arctic are divided into three groups: the sub-arctic, the low arctic, and the high arctic (Fig. 6). The sub-arctic regions extend to regions south of 60°N in both Eurasia and North America. This vegetation is dominated by coniferous trees.

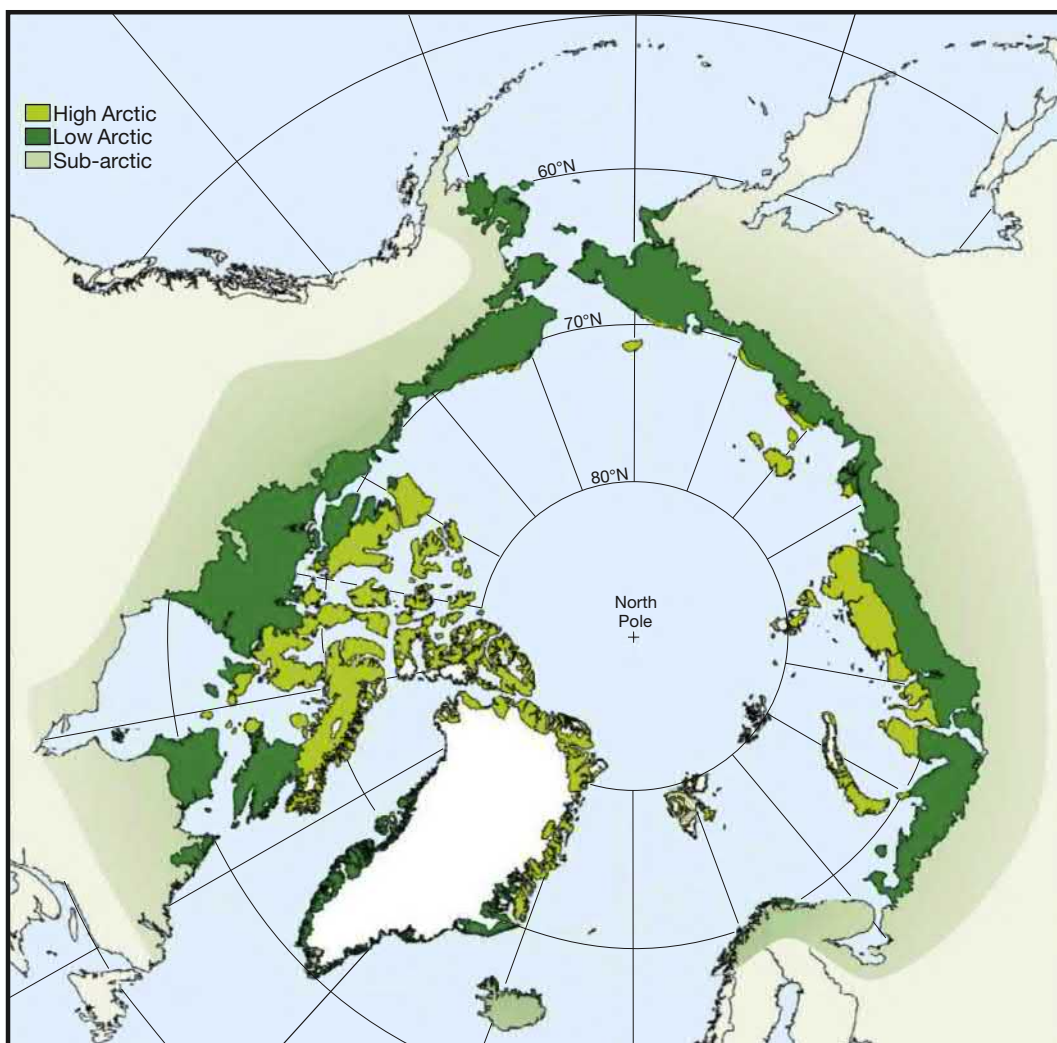


Fig. 6 Map of the Arctic, showing the principal vegetation zones (High Arctic, Low Arctic, Sub-Arctic) (by author).



Fig. 7 Dwarf shrub tundra near Kotzebue, Alaska (photo by author).

Few broadleaved trees can survive the very low winter temperatures. This type of forest is known as boreal forest in North America and is also known as taiga in Eurasia. Plant diversity is low in the sub-arctic, but the boreal forest is the largest forest biome on Earth. Most boreal forests are in northern Russia and Canada.

The low arctic zone occupies the northern edges of the two continents, the southern half of the coastal regions of Greenland, Baffin Island, and Victoria Island in Canada. The general term for the vegetation of this region is tundra. The word tundra originates from the Finnish word *Tunturi*, which means “completely treeless heights.” The number of vascular plants in low arctic tundra ranges from fewer than 50 species near the northern boundary of the biome to as many as 500 species at the southern boundary, near treeline. Altogether, the low arctic regions of the world are home to about 1700 plant species. The vegetation in most low arctic landscapes is dominated by dwarf shrubs, heaths, mosses and lichens (Fig. 7). In North America, the dwarf shrubs include dwarf birch (*Betula nana*) (Fig. 8, upper left), Arctic willow (*Salix arctica*) (Fig. 8, upper right), Labrador tea (*Rhododendron tomentosum*) (Fig. 8, middle right), crowberry (*Empetrum* sp.) (Fig. 8, lower left), Lingonberry (*Vaccinium vitis-idaea*) (Fig. 8, bottom right), and white dryas (*Dryas octopetala*) (Fig. 8, lower right). Herb and lichen species are also very common, in mixture with other vegetation. One important lichen species is reindeer lichen (*Cladonia rangiferina*) (Fig. 8, lower left), which forms an important part of the diet of caribou, moose and muskox in North America and for reindeer in Eurasia. Wetlands are very common in lowlands throughout the North American tundra. The height of woody plants in the North American arctic depends mainly on the summer temperature regime. At the northern end of the low arctic tundra, where average July temperatures range from 3 to 5 °C, there are only prostrate dwarf shrubs. Further south, where average July temperatures range from 5 to 7 °C, the shrubby vegetation increases in height up to 15 cm. Close to the southern boundary of low arctic tundra, erect dwarf shrubs grow up to 40 cm tall. Here the average July temperatures are 7–9 °C. At the treeline, mean July temperatures are between 10 and 12 °C, and woody shrubs grow up to 2 m tall.

The Arctic tundra of the Eurasian mainland is similar in appearance to that of North America, but some different plant species are dominant. These include cotton grass (*Eriophorum* sp.) (Fig. 8, middle left), sedges (*Carex* sp.), a different species of dryad (*Dryas punctata*), in addition to dwarf shrub willows, crowberry (*Empetrum* sp.) (Fig. 8, bottom left), lingonberry (*Vaccinium vitis-idaea*), and mosses.

The amplified warming of the Arctic has brought changes to the vegetation in all three tundra zones. In the low arctic zone, shrubs have been increasing at the expense of herbs and forbs. For instance, a study of vegetation changes in north-central Canada from 1984 to 2016 showed that the most significant trends were increased productivity in shrub-dominated environments.

High Arctic vegetation is found on the rest of the islands of the Canadian Arctic Archipelago, the northern half of the coastal regions of Greenland, Svalbard, and the northern edge of and Arctic islands of Eurasia. The High Arctic flora is reviewed by Zwolicki et al. These plant communities are the least diverse in the Northern Hemisphere and are dominated by cryptogams (mosses and lichens). Nevertheless, the High Arctic supports a greater variety of flowering plants than are found in Antarctica. There are almost 50 species of angiosperms in the High Arctic, which is polar desert. These plants grow low to the ground and occur as single, scattered individuals within mats of cryptogams less than 2 cm above the ground. Although the High Arctic regions are warming rapidly, the lack of soil moisture in most regions is a major factor limiting plant growth there.



Dwarf birch

Wikimedia commons



Dwarf willow

Wikimedia commons



Cottongrass

Wikimedia commons



Labrador tea

Wikimedia commons



Reindeer lichen

Wikimedia commons



White dryas

Wikimedia commons



Crowberry



Lingonberry

Fig. 8 Top left: dwarf birch (*Betula nana*); top right: Arctic willow (*Salix arctica*); middle left: cotton grass (*Eriophorum* sp.); middle right: Labrador tea (*Rhododendron tomentosum*); lower left: reindeer lichen (*Cladonia rangiferina*); lower right: White dryas (*Dryas octopetala*); bottom left: crowberry (*Empetrum nigrum*); bottom right: lingonberry (*Vaccinium vitis-idaea*). All photos courtesy of Wikimedia Commons, in public domain.

Terrestrial Mammals

The Arctic regions are too cold to support reptiles and amphibians—only warm-blooded mammals and birds are found on these landscapes. Arctic tundra mammals are reviewed by Hope and High Arctic mammals are discussed by Elias. There are about 80 species of Arctic mammals, all adapted to life in extreme cold. Many species may be found in tundra across the Holarctic region, although only about a third of these are found exclusively on Arctic tundra. Most are either habitat generalists that are widespread throughout the northern latitudes, or they are predominantly boreal forest dwellers whose ranges extend north onto the tundra. The endemic Arctic tundra mammals are year-round residents, although many species are less than fully active in winter. They undergo either hibernation or torpor in the coldest months of the year. Hibernation is a voluntary state into which an animal enters to conserve energy, survive when food is scarce, and minimize the need to face the elements in the cold winter months. It is a truly deep sleep. Torpor is also a survival tactic used by animals to survive the winter months. Like hibernation, it also involves a lowering of body temperature, breathing rate, heart rate, and metabolic rate. But unlike hibernation, torpor is an involuntary state that an animal enters as the conditions dictate. Hibernation generally lasts many weeks or months. Torpor lasts only short periods. Arctic mammals have evolved in response to multiple glacial/interglacial cycles through the last 2.6 million years (the Quaternary period). They have developed life histories that reflect changing associations with other species and other biomes through time. However, the current warming of the Arctic is at a rate and magnitude that is approaching the limits of what tundra mammals have experienced at any time through the history of this biome. The continued persistence of Arctic tundra mammals will depend on the resilience and plasticity of adaptations among the species. One option that will no longer be available to them will be to migrate North in response to warming. Since even the High Arctic is warming, there is no cooler region for them to go. There are already indications there are changes afoot in the distribution of northern mammals. For instance, there is good evidence that indicates that the range of the arctic fox (*Vulpes lagopus*) has been retracting in the circumpolar tundra zone, while the red fox (*Vulpes vulpes*) is expanding its range northwards into the Arctic. Red foxes are one-third larger than arctic foxes, and the former has been observed interfering with arctic fox breeding dens in the Siberian tundra. The red fox is not as well adapted to cold as the arctic fox, but as the Arctic regions become warmer, the adaptation to extreme cold becomes less important.

Another example of a mammalian response to Arctic warming concerns the polar and grizzly bears of Canada. Since 2006, eight bears have been found in the Canadian Arctic Archipelago that are hybrids between grizzly bears (*Ursus arctos*) and polar bears (*Ursus maritimus*). DNA tests of tissues taken from these bears confirm their hybrid status. Until recently, grizzly bears have rarely been seen far north of the coast of mainland Canada, but since the 1990s there have been multiple sightings of grizzlies on arctic islands as much as 500 km north of the mainland.

Conclusions

The current environmental changes in the polar regions are happening at a pace and an amplitude hitherto unknown in these regions. Scientists are trying to keep track of the changes, and their effects on polar biota. Global warming from anthropogenic GHG emissions is probably having the greatest impacts on Arctic and Antarctic environments. In the Arctic, the interactions between land, sea, and ice are serving to amplify the warming, and all but the most stringent scenarios to reduce GHG emissions will very likely lead to a complete transformation of Arctic environments. It is already clear to see that the sea ice of the Arctic Ocean and adjacent seas will be gone in a few decades at most. No one knows just how the Arctic biota will respond to these environmental changes, but modeling efforts point to a breakdown of existing ecosystems.

Antarctica has not yet experienced the dramatic warming trend seen in the Arctic. However, Antarctic ice sheets are melting, albeit slowly, thus far. The total weight of ice loss averaged 43 gigatons per year from 1992 to 2002. Since then the melting has accelerated five-fold, to an average of 220 gigatons per year from 2012 to 2017. Ice loss from the West Antarctic Ice Sheet (WAIS) is known to be driven by changes in ocean melting of ice shelves in the Amundsen Sea. A study by [Holland et al. \(2019\)](#) has revealed that the most likely cause of this ocean melting is enhanced import of warm Circumpolar Deep Water onto these ice shelves, driven by a change in wind patterns. These patterns have been changing on a decadal scale, but in recent decades the conditions that cause warm water anomalies have become much more frequent. Current climate model projections show that if atmospheric GHG concentrations continue to increase as they are now, the warm ocean anomalies will become the norm by 2100, accelerating the loss of ice from the WAIS.

But the climate of Antarctica is not warming across the continent. Studies have shown that the climate is actually cooling toward the center of the continent, with the area of strongest cooling at the South Pole. Other regions are undergoing warming, with the greatest amelioration along the Antarctic Peninsula. A study by [Bromwich et al. \(2013\)](#) found that from 1958 to 2010, the average temperature at Byrd Station (80°S latitude) rose by 2.4 °C. Thus, a locality which is in the heart of the West Antarctic Ice Sheet is one of the fastest-warming places on Earth. However, as we have seen, most of the biota associated with Antarctica are residents of sub-Antarctic islands or live in the Southern Ocean. Unlike the Arctic, so far there is no evidence of a decline in Antarctic sea ice cover. This bodes well for the organisms in the marine food web.

Life near the poles is tough but vulnerable. The very adaptations that allow both marine and terrestrial life to survive the bitterly cold winters and short, cool summers can become liabilities in a rapidly warming world. Ecological patterns and long-term species associations are already starting to break down in some Arctic regions. Thus far, the marine biota of Antarctic waters has not

experienced such high rates of environmental change, but incursions of warm water caused by changes in wind patterns and ocean circulation will wreak havoc if they melt the sea ice and cause changes in krill distribution patterns.

One aspect of polar science that has cropped up repeatedly in data reports and review papers is a plea for additional observations on regional climates, oceanographic conditions, and the state of the polar biota. The polar regions remain remote, difficult to reach, expensive to study, and technically challenging to research. Nevertheless, we must make the effort to collect more data on these topics if we are going to come to grips with the changes now occurring in the Arctic and the Antarctic.

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Climates of Tundra and Alpine Biomes

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Abstract

Tundra exists in unglaciated parts of polar regions where it is too cold for the establishment and survival of trees. The primary climate control is summer temperature, but other factors can be important. Tundra is widespread in high latitudes of the Arctic, and is also found in some areas of Antarctica, notably the Antarctic Peninsula and islands surrounding the continent. Treeless alpine vegetation similar to tundra exists even in tropical latitudes provided that mountains are high enough and conditions hence sufficiently cold. The altitude and latitude of polar and alpine treelines is highly variable across the planet, reflecting controls on summer temperature by latitude and continentality, as well as regional and local factors including snow cover, slope and aspect. There is evidence that treelines, tundra and alpine vegetation environments are responding to the warming climate; shrub invasion into Arctic tundra and thawing of Arctic permafrost are notable examples.

Introduction

The term “tundra” is generally accepted as originating from the Finnish word “tunturia”, meaning barren land devoid of trees. Tundra vegetation is primarily comprised of grasses, sedges, dwarf shrubs, wildflowers, mosses, and lichens. The existence of tundra is primarily the result of temperatures during the growing season being too low for trees to become established and survive. Reflecting the fundamental control on temperature by latitude, tundra is a characteristic of polar environments. The boundary between tundra and forest is termed the polar treeline. The latitudinal limits of tundra broadly align with a mean July surface air temperature of around 10 °C (50 °F) and growing-season soil temperatures between 5 °C and 8 °C (41–46 °F) (Körner and Paulsen, 2004), just above the minimum temperature (5 °C) required for tissue formation in plants (Körner, 2008).

Tundra can be divided into Arctic and Antarctic tundra. Arctic tundra covers large areas of northern Canada and Russia, parts of Alaska, Greenland, Iceland and northern Scandinavia (Walker and Raynolds, 2018) (Fig. 1). It also covers the unglaciated parts of the Antarctic continent and surrounding islands. Because of the low moisture-holding capacity of the atmosphere in cold, polar latitudes, regions of tundra are also regions of generally low precipitation; some areas are characterized as polar desert and support only sparse vegetation. Tundra is also associated with permafrost—perennially frozen ground with an active layer that thaws and re-freezes on an annual basis and has strong impacts on vegetation. Despite low precipitation, tundra environments may be rather wet at the surface with thaw lakes. This reflects poor drainage (due to permafrost) as well as limited evapotranspiration (due to small energy inputs to the surface and sparse vegetation).

Treeless landscapes are also found in alpine regions in all latitudes of the planet where the elevation is sufficiently high and conditions hence sufficiently cold. This includes the Tibetan Plateau, sometimes referred to as the planet’s Third Pole as well as the highest altitudes of Mauna Loa and Mauna Kea in Hawaii. This is also true of the higher reaches of Mount Kilimanjaro, lying just north of the equator and also home to one of the world’s few remaining tropical glaciers. While similar to tundra vegetation in some respects, the vegetation above alpine treelines is viewed as sufficiently different that the term “alpine vegetation” is more appropriate than tundra, and that nomenclature is adopted here. Permafrost need not underlie regions of alpine vegetation, but parts of the Tibetan Plateau are underlain by permafrost. Precipitation on some alpine vegetation zones can be quite high, while it is meager in others.

Thermal conditions associated with treelines, whether they be polar or alpine, are not just a function of latitude and elevation, but are determined by proximity to marine influences, termed continentality, how much area surrounding individual peaks lies at high elevation (mass elevation effects), as well as local influences such as slope and aspect. Factors such as precipitation, winds, tree

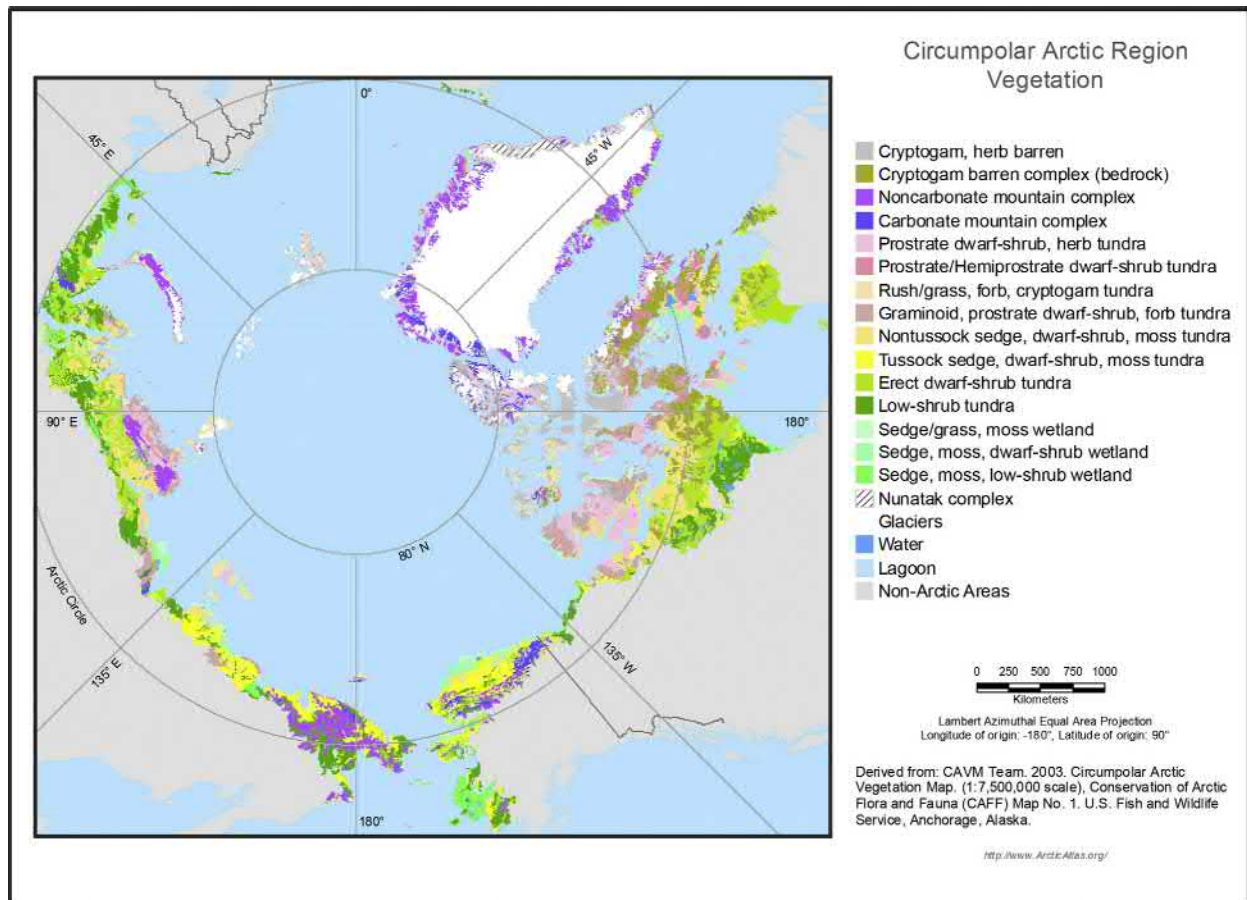


Fig. 1 Distribution of Arctic tundra types. From Walker, D.A., Raynolds, M.K. (2018). *Pre-ABOVE: Circumpolar arctic vegetation, geobotanical, physiographic data, 1982–2003*. Oak Ridge, TN, USA: ORNL DAAC. 10.3334/ORNLDAAC/1323.

species and disturbance can also play a role, as can harsh winter conditions that can damage trees (Peregrine and Payette, 1998). While soil physical conditions, nutrient availability, carbon and nitrogen uptake and other biotic and abiotic factors can also influence treelines, there is ongoing debate as to their importance in comparison to the dominant control by summer warmth (Muller et al., 2016).

There is growing evidence that in response to recent climate warming, treelines are beginning to advance poleward and climb in altitude. Shrubification—an encroachment of woody plants into tundra regions, has been especially noticeable in the Arctic. However, both observed and anticipated treeline responses to climate change are complex and cannot be simply viewed as responses to rising summer temperatures.

Tundra and Treelines

General Features

Tundra is commonly viewed as synonymous with the Arctic environment. However, as is evident in Fig. 1, in many areas boreal forest extends well north of the Arctic Circle, such as over much of Siberia, northwestern Canada, and Alaska. By contrast, in other regions, notably over north central Canada, southern Baffin Island and northern Labrador, tundra extends well south of the Arctic Circle. There is a general correspondence between the southern limit of Arctic tundra depicted in Fig. 1 and the location of the 10 °C (50 °F) July isotherm at the surface in July (Fig. 2). The location of the 10 °C July isotherm is itself a function of large-scale controls by features of the atmospheric circulation and continentality, along with regional to local influences such as elevation and proximity of the land to cold or warm ocean currents.

The large-scale atmospheric control is the tropospheric circumpolar vortex. The circumpolar vortex can be broadly thought of as comprising the region of cold polar air north of the polar front jet stream; the jet stream is the dividing line between cold polar air and warmer air to the south. The vortex generally dips to the south over the Canadian Arctic Archipelago and into Labrador and as such, summer temperatures are especially low in this part of northern North America (in meteorological parlance, the region typically sits within a longwave trough). The interiors of Alaska, Canada, and Eurasia, by contrast, are isolated from ocean moisture



Fig. 2 The north polar region showing the location of the average 10 °C July isotherm at the surface. CIA World Factbook (free use under Public Domain).

sources and moderating marine influences on temperature, and hence have continental climates characterized by a large seasonal range in air temperatures. Winter temperatures can be bitterly cold. However, continentality means that summers are warm enough to maintain the treeline north of where it would be expected simply considering latitude.

The Brooks Range, which runs broadly west to east across northern Alaska, is an interesting example of topography controlling the treeline. Trees can exist on the southern (and south facing) side of the Brooks Range (at lower elevations) but cannot exist on the northern (and north facing) side. The Brooks Range also acts as a topographic barrier, preventing cold Arctic air from spilling southward. Hence, there is a very sharp difference in summer temperature at similar elevations just north and south of the Brooks Range (Serreze et al., 2001).

In Norway, the existence of trees well north of the Arctic Circle is explained by ocean circulation—the North Atlantic Drift Current, which brings warm water from the south into the Arctic, maintains much milder climate conditions than would be expected on the basis of latitude alone. Ocean influences also help to explain the existence of tundra on the Labrador Peninsula of Canada. While as noted, there is a large-scale control here by the tropospheric circumpolar vortex, the cold Labrador Current also keeps summer temperatures considerably lower than would be expected for this latitude. Because the Labrador Peninsula has a much more marine climate than central Canada and also lies at fairly high elevations (much of the area is a plateau), tundra extends south to 53°N. Similarly, proximity to cold ocean waters helps to explain why the Aleutian Islands of Alaska (not shown in Fig. 1) are almost completely treeless.

Forest-Tundra Ecotone (Treeline)

The transition between the Arctic tundra, where summer temperatures are too cold for trees to exist, and the boreal forest that lies to the south, is seldom abrupt. Rather, there is a transition zone, or ecotone, of varying width between the two biomes. In this sense, the term “treeline” is perhaps misleading. In northwestern Canada, for example, the transition zone, or ecotone, averages 145 km in width, widening markedly from west to east (Timoney et al., 1992). Fig. 3 captures the character of the ecotone on the south side of the Brooks Range in Alaska during April, photographed by the author while traveling north along the Dalton Highway, which largely parallels the Alaskan oil pipeline. In this case, the latitudinal control on the limit of trees is conflated with the altitudinal control; while there are still trees (black spruce) in the foreground, the mountains in the background, where temperatures are lower, are covered by tundra vegetation. As noted, trees cannot exist on the north side of the Brooks Range under the present climate.

Polar Desert

Arctic tundra is far from uniform; Fig. 1 clearly shows that there are many different categories that are reflective of the variety of climate conditions, soils, nutrient availability drainage and other factors. While it is not the objective of the present review to dwell upon the different tundra types, it is important to acknowledge that tundra generally becomes more “severe” the further north one goes, which makes sense given the fundamental control on tundra by summer temperature. The most extreme Arctic tundra landscape is known as polar desert, found in the Canadian Arctic Archipelago, parts of coastal Greenland (such as Peary Land on the north coast), and the Russian island of Novaya Zemlya. In an analysis of different polar desert sites in the Canadian Arctic Archipelago, L.C. Bliss (1997) recorded only a 2–3% plant cover, rising to 25–35% in favored areas where snowbanks provide meltwater.

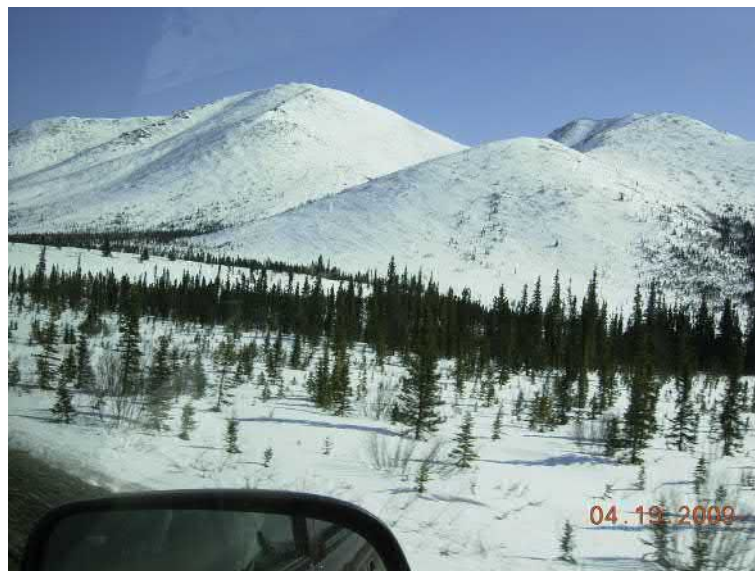


Fig. 3 The forest-tundra ecotone on the south side of the Brooks Range of Alaska, as photographed by the author during April.

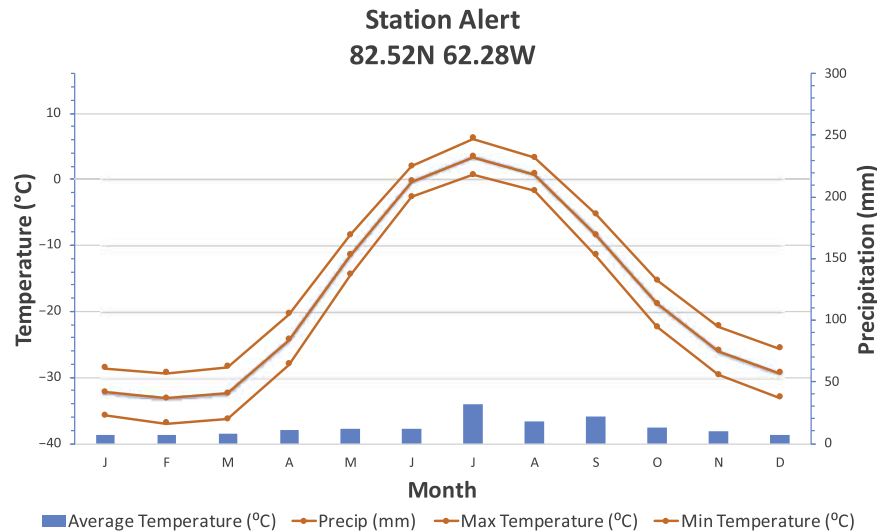


Fig. 4 Average daily surface air temperature, average daily maximum and minimum surface air temperature, and average monthly precipitation at station Alert, northern Ellesmere Island, Nunavut, Canada. Government of Canada.

Stones and fine sediments are often organized as patterned ground such as rings and stripes. Polar desert tundra environments are characterized by very cold winters, very cool summers and—as the name polar desert implies—scant precipitation.

The station Alert, located on the northern end of Ellesmere Island at 82.5°N in Nunavut, Canada, is a good example of a polar desert environment. **Fig. 4** shows monthly mean temperature, average daily temperature maxima and minima, and average monthly precipitation at the site. The daily average temperature during the warmest month of July is only 3.4 °C (38 °F) while daily highs are typically around 6 °C (43 °F). Average daily lows in July are just above freezing, while those in the neighboring months of June and August are below the freezing point. Thus, the growing season is quite short. The tundra is underlain by permafrost and snow covers the ground for >40 weeks per year. Because of low precipitation, the winter snowpack is quite shallow; values of 300–500 mm are typical of the area ([Serreze and Barry, 2014](#)). Annual precipitation at Alert averages only about 160 mm. While essentially all precipitation during the cold season is in the form of snow, snow can fall even during summer. As is typical of polar desert regions, precipitation is least during winter and peaks during summer; the peak at Alert, in July, is about 30 mm. The seasonal cycle in precipitation closely follows the seasonal cycle in column integrated atmospheric water vapor, which in turn reflects the control on saturation vapor pressure by temperature. With more water vapor in the atmosphere in summer, there is simply a greater likelihood for precipitation to fall, provided that the mechanisms are in place to cause uplift and condensation of air parcels ([Serreze and Etringer, 2003](#)).

Antarctic Tundra

Most of Antarctica is covered by glacial ice and the climate is extremely cold and arid, indeed, more arid than polar desert sites in the Arctic. However, tundra does exist on unglaciated coastlines and on Antarctic and sub-Antarctic islands. The Antarctic is home to two flowering plant species, Antarctic hair grass and Antarctic pearlwort, and areas of exposed rock may support lichens. More vegetation is supported on the unglaciated parts of the Antarctic Peninsula. The famed Dry Valleys of Antarctica have been studied as a possible analog to the environmental processes on the surface of Mars. The Dry Valleys represent one of the world's most extreme deserts and to call this inhospitable area tundra, which implies vegetation such as grasses and sedges, would seem to be a stretch. Endolithic (living inside rock) photosynthesis bacteria as well as anaerobic bacteria have been found in the Dry Valleys ([Barnett et al., 2007](#)).

Alpine Biome

General Features

The alpine treeline, representing the boundary between alpine vegetation at higher elevations and forest at lower elevations, varies greatly with respect to latitude and with regional to local factors that control temperature, modulated by influences such as the duration of the seasonal snowpack, winds, precipitation and soils. As noted, the regions of treeless alpine vegetation are not necessarily underlain by permafrost. Recall that the Arctic treeline is not abrupt - rather it is a transition zone, or ecotone, from boreal forest to tundra. In the same sense but on a smaller scale, the alpine treeline is usually a transition zone, but can be fairly abrupt in some cases. Within the transition zone, trees are commonly stunted and deformed by cold and windy conditions. This zone of stunted



Fig. 5 The alpine treeline at Craigieburn, New Zealand. Courtesy of Ellen Cieraad, Institute for Environmental Science at Leiden University.

trees is referred to as “krummholz”, a German word for “crooked wood”. **Fig. 5** provides a good example of an alpine treeline in New Zealand.

Variations in Alpine Treelines

It has long been observed that alpine treelines in the Southern Hemisphere tend to be at lower elevation than those in the Northern Hemisphere. Countering the idea that the difference relates to the types of trees found in the Southern Hemisphere, a more probable explanation is that at similar latitudes, summers in the Southern Hemisphere are generally cooler than those in the northern half of the planet. This reflects the landmass distribution—much more of the Southern Hemisphere is covered by ocean, meaning a stronger ocean influence in general, leading to cooler conditions (Cieraad et al., 2014). While alpine treelines in both hemispheres are associated with about the same summer air temperature, the critical air temperature in the Southern Hemisphere below which trees cannot exist is found at lower elevations.

As an example of regional variability in the Northern Hemisphere, the alpine treeline lies at about 4600 m (15,000 ft) in southeastern Tibet, while only 650 km to the east, it drops to 3600 m (11,800 ft) in the Balang Mountains. On a more local scale, in the Northern Hemisphere, treelines on north-facing slopes tend to be lower in elevation than those on south-facing slopes. This is because solar radiation receipts are lower on north-facing slopes and the snowpack takes longer to melt, which means a shorter growing season for trees (Peet, 2000).

The climate at the summit of Mount Washington (6288 ft or about 1900 m), the highest peak in the White Mountains of New Hampshire, near the northeast coast of the United States, provides an interesting example of an alpine vegetation environment. **Fig. 6** shows the annual cycles of temperature and precipitation at the Mount Washington Observatory, at the summit of the mountain. For ease of comparison with station Alert, **Fig. 6** uses the same vertical scales as **Fig. 4**. The treeline in the White Mountains, while ragged, lies at around 1400 m (4,500 ft). Mount Washington is part of the Presidential Range, and all the peaks in this range lie in the alpine zone. Reflecting latitude, air temperatures for all months are considerably higher than for the polar desert site Alert. The average temperature in July at the Mount Washington Observatory is close to 10 °C (50°F), with a typical daily highs of 12 °C (54 °F) and typical daily lows of about 8 °C (46 °F). Nevertheless, the growing season is short, and the use of monthly averages hides the fact that even in July, temperatures can fall below the freezing point. The record lows for June, July and August at the Observatory are -13 °C, -4 °C, and -7 °C (8 °F, 24 °F and 20 °F) respectively.

An interesting aspect of the Mount Washington alpine climate is that precipitation is quite high in all months; precipitation at the summit for the driest month (~160 mm in January) is almost as great as precipitation at the Alert polar desert site for the entire year. The annual total at the Mount Washington Observatory is just shy of 2500 mm (97 in.). The ample precipitation reflects the combination of the much higher atmospheric water vapor content compared to Alert (related to both temperature and proximity to the Atlantic Ocean), the frequent passage of storms (Mount Washington is located at the convergence of several storm tracks) as well as orographic uplift—forced uplift, cooling and condensation of moist air parcels.

At the landscape and local level, winds can have a significant effect on alpine treelines (Holtmeier and Broll, 2010). Winds generally increase with elevation in the middle and higher latitudes and as such, the treeline tends to be a windy place. While winds can greatly deform and stunt trees, they can also disperse seeds, bury trees under snow drifts, and scour slopes bare of snow. Winds also increase transpiration and evaporation, leading to the drying of soils. Strong winds can hence lead to conditions unfavorable for

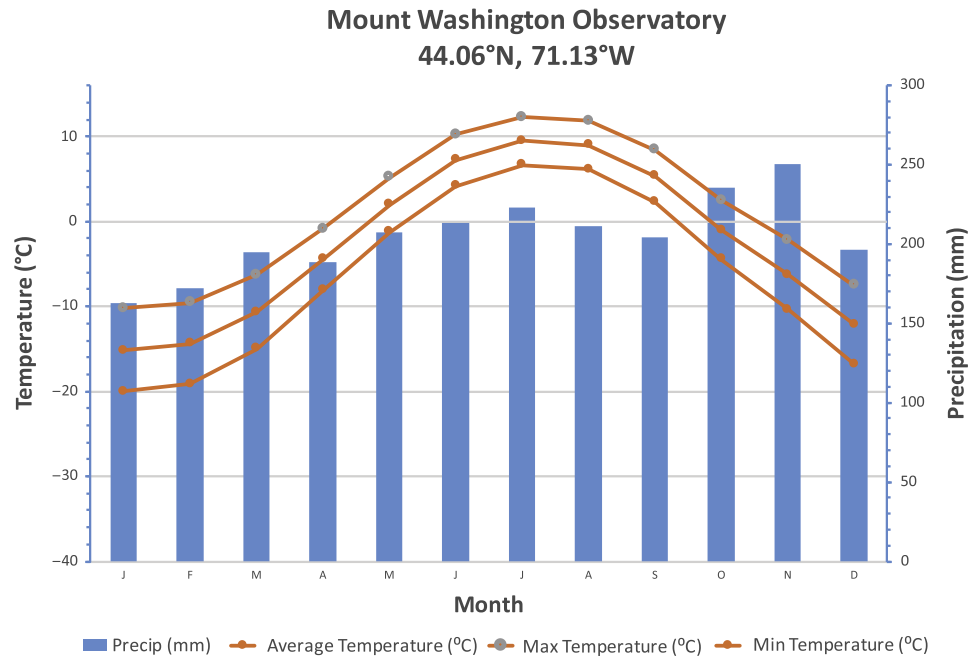


Fig. 6 Average daily surface air temperature, average daily maximum and minimum surface air temperature, and average monthly precipitation at the Mount Washington Observatory, New Hampshire, United States. Mount Washington Observatory.

trees and can delay or even preclude the establishment of seedlings. In this context, another notable aspect of Mount Washington is its extremely high wind speeds. Average winds are high in all months and most notably, peak winds in all months are at least those of a Category 4 hurricane. The fastest wind speed ever recorded on Mount Washington was 103 m per second (231 mph).

It is instructive to compare conditions at the summit of Mount Washington to the conditions in the Tetons, about 3000 km to the west, at the southern gateway to Yellowstone National Park. Despite being at similar latitude, the treeline in the Tetons lies at roughly 3050 m (10,000 ft), more than twice as high as Mount Washington. This difference is due to the effects of continentality discussed earlier. While winters are cold, and winds are certainly fairly high in the alpine zone, continentality means that summers are warmer than one would find in a marine-influenced environment at the same latitude.

Another effect that relates to the higher treelines in the western interior of the United States, compared to the east, is that large areas surrounding individual peaks also lie at fairly high altitudes. Viewed most simply, the elevated land surrounding the peaks acts as an elevated heating source, resulting in what is termed a mass-elevation or Massenerhebung effect. The “mass” in this context refers to of the size of the area surrounding a given mountain that lies at a significant elevation above the surrounding plain. The greater the area, the greater the mass elevation effect. The mass elevation effect can be defined as the temperature difference at given elevation between inside and outside of a mountain mass. A completely isolated peak would hence not experience a mass elevation effect. This concept was first introduced by [De Quervain \(1904\)](#) to explain the observation that treeline and snowline occur at higher elevations in the central European Alps than on their outer margins. The Massenerhebung effect is now recognized to exist in many parts of the world ([Barry, 2008](#)), the Rocky Mountains being a notable example. The mass elevation effect in the Rocky Mountains averages about 1.8 °C, with the largest values in Colorado and in the basins of southern Wyoming ([Wang et al., 2017](#)). On continental or regional scales, the alpine treeline altitude can be viewed as related both to geographical location (latitude and longitude) and to the Massenerhebung effect, with the relative influence of these factors being strongly scale- and region-dependent ([Han et al., 2012](#)).

The Massenerhebung effect is, however, more complex than a simple elevated heat source. [Flohner \(1953\)](#) proposed that the summer warmth of elevated plateau surfaces results from the altitudinal increase in solar radiation and the relative constancy of net longwave radiation (incoming minus outgoing) with height, a hypothesis supported in subsequent studies. One argument here is that condensation, precipitation and cloud cover will tend to be greatest along the flanks of the mountain mass, leaving the interior with less cloud cover and hence stronger receipts of solar radiation. [Barry \(2008\)](#) argued that vegetation boundaries extending to higher elevations in the central Alps are related primarily to a shorter seasonal snow cover duration. With less snow cover, more solar radiation is absorbed at the surface, translating into a longer and warmer growing season. [Flenley \(2007\)](#) suggested that the Massenerhebung effect could partly be the result of a high dose of ultraviolet radiation due to reflection from clouds.

Along the west coast of the United States, in the Olympic Mountains of Washington State where the climate is strongly influenced by proximity to the Pacific Ocean, the treeline is again quite low in elevation (around 1500 m, or 4900 ft). The reason for the low elevation of the treeline here is similar to that of Mount Washington, which is also strongly marine influenced. However, an important driver in the Cascades is very heavy winter snow that buries trees until late summer.

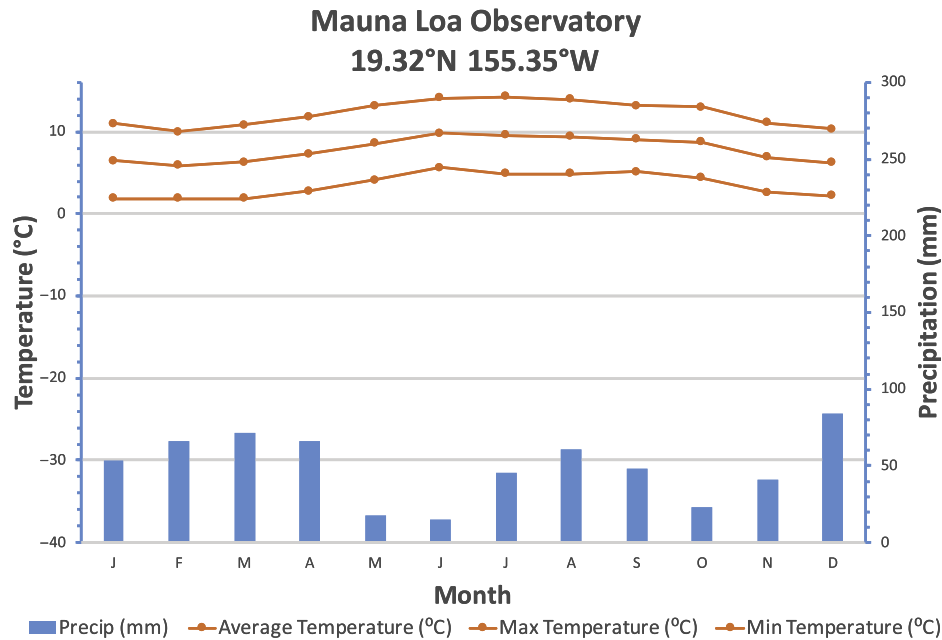


Fig. 7 Average daily surface air temperature, average daily maximum and minimum surface air temperature, and average monthly precipitation at the Mauna Loa Observatory, Hawaii, USA. Mauna Loa Observatory.

Finally, consider the climate at the summit of Mauna Loa Hawaii (4169 m, or 13,678 ft), as recorded at the Mauna Loa Observatory (Fig. 7). As is the case for the neighboring and slightly taller shield volcano Mauna Kea, the summit of Mauna Loa lies in the alpine zone. In contrast to climates of both station Alert and Mount Washington, Mauna Loa experiences only a small range in average temperatures over the year. This is characteristic of low latitude mountains, where the annual ranges of incoming solar radiation and day length are small. Snowfall is not uncommon in winter, and there is occasionally enough to ski. However, precipitation for all months is fairly small. The contrasts between the situations at Alert (Fig. 4), Mount Washington (Fig. 6) and Mauna Loa (Fig. 7) serve to illustrate the remarkable variety of climates in which arctic tundra and alpine vegetation can be found. The common thread between these sites is the lack of summer warmth.

Tibetan Plateau

The Tibetan Plateau spans approximately 1000 km north to south and 2500 km east to west and has an elevation exceeding 4500 m (14,800 ft). It is surrounded by high mountain ranges, including the Hindu Kush to the west, the Himalayas to the south, the Kunlun Mountains to the north, and the Qilian Mountains to the northeast. As noted, The Tibetan Plateau is sometimes referred to as the earth's Third Pole. The plateau becomes progressively higher and drier to the north and northwest, where altitudes exceed 5000 m (16,000 ft). On the north and northwest side, annual precipitation is only 100–300 mm, similar to that of polar desert. Much of the plateau is characterized as montane grassland. However, permafrost is extensive, and parts of the plateau, such as the Qinghai-Tibet Plateau (Wang et al., 2011), are characterized by an alpine-like environment.

Effects of Climate Change

Recent warming is leading to expansion of woody plants in many areas of the Arctic and alpine, a process termed shrubification (Mod and Luoto, 2016). Arctic permafrost temperatures are rising, and permafrost is thawing, but with large variability from region to region (Romanovsky et al., 2010). Areas of thawing ice-rich permafrost are undergoing thermokarst, characterized by a highly irregular surface of marshy hollows and small hummocks. To the south, woody vegetation has advanced into alpine meadows in the southeastern Qinghai-Tibet plateau, the headwater regions of the Yangtze and Yellow rivers (Baker and Moseley, 2007; Wang et al., 2011). Warming in the Qinghai-Tibet plateau has largely paralleled the warming pattern of the whole country (Wang et al., 2007).

While tundra and alpine ecosystems are arguably among the most sensitive to climate change (Christensen et al., 2004), it is increasingly recognized that both observed and anticipated responses of tundra, alpine environments and treelines to climate change will be far from uniform across the globe and will involve much more than increases in summer temperature (Holtmeier and Broll, 2005). For example, a number of studies link observed treeline advances to winter warming (Harsch and Bader, 2011), acting to reduce winter stress on trees and improve recruitment. As an example of regional influences, in a study of northern

Quebec-Labrador treelines, Payette (2007) found contrasting responses to recent climate change depending on geographic position relative to the Labrador Sea. Along the coast, the northernmost latitudinal and altitudinal treelines responded positively to warming over the previous 50 years with spruce invading several tens of meters above the current treeline into the tundra. By contrast, white spruce treelines across the wind-exposed Labrador plateau, located much higher in altitude, receded a few tens of meters beginning around AD 1740–1750 and have not yet recovered. Adding to this complexity, while it is expected that the warming climate will affect species diversity and composition, the increase in the abundance of woody plants will further alter vegetation by modifying biotic interactions (Mod and Luoto, 2016). Non-climatic factors can also be important, such as topographic conditions. In Northern Europe, treeline positions are often controlled not so much by climate, but by herbivores (Cairns and Moen, 2004).

In short, while continued global warming is certainly expected to facilitate the advance of trees into higher altitudes and higher latitudes, sensitivities will vary by region and responses will likely involve a range of time scales. As to what tundra and alpine environments will look like 100 years from now, there are no simple answers.

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The Nature of Arctic Soils

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Abstract

Soils of the Arctic region occur in one of the coldest parts of the Earth. Therefore, their development is dominated by cryogenic processes, resulting in unique soil properties. In soil classification the permafrost-affected soils are called Gelisols in the USA and Cryosols in Canada. The term Cryosol is also used in the international World Reference Base of soil (WRB) whereas in the Russian soil classification scheme these soils are not recognized as a separate order. Cryoturbation in the active layer is the most important process in turbic permafrost-affected soils. The soils in the Arctic sequestered large amounts of organic carbon and stored this carbon in the subsoil for thousands of years. Most of this carbon is still in a frozen state but has started to be released into the atmosphere as greenhouse gases due to climate warming. These released greenhouse gases in the Arctic then further accelerate the global warming in other parts of the world.

Introduction

The Polar Regions surrounding the North and South poles include most of the global permafrost regions (Nuttal, 2005). These regions are known as the Arctic in the Northern Hemisphere and as Antarctica in the Southern Hemisphere. Small permafrost areas can be found globally in high mountain terrains. Since the regions around the poles have the Earth's coldest climates, most of their soil materials are perennially frozen and their development is dependent on the amount of moisture in the soil and the stability of the landscape (French, 2007). In this article the focus is on the nature of soils in the Arctic.

Since about the last two decades Arctic soils are investigated because of climate change (Kimble, 2004) and because huge amounts of soil carbon are stored in these soils (e.g., Ping et al., 2008; Tarnocai et al., 2003a, 2009; Hugelius et al., 2013). To raise awareness on polar soils the Soil Atlas of the Northern Circumpolar Region was published and made available (Jones et al., 2010).

Northern Circumpolar Region

The northern circumpolar region is characterized by permafrost in most parts. Permafrost is defined as soil or rock that remains at or below 0 °C for at least two consecutive years (French, 2007). Permafrost is continuous in large areas of the Arctic and usually the terrain is associated with patterned ground (Fig. 1). The northern circumpolar soils cover approximately 19×10^6 km² and about half of this area is associated with permafrost and thus perennially frozen soils (Fig. 2) (Tarnocai et al., 2003b). South of this area the landscapes are characterized by seasonally frozen soils. Russia and Canada are the countries in the Northern Hemisphere with the largest areas covered with perennially and also seasonally frozen soils (Goryachkin and Karavaeva, 2004; Tarnocai, 2004a; Mikhailov, 2016).

Short, cold summers and long, extremely cold winters characterize the climates of the polar region. Mean daily temperatures above 0 °C occur only during the warmest part of the summer. Total annual precipitation is generally low and occurs mostly as snow (Nuttal, 2005). The common vegetation associated with the northern circumpolar soils is a conifer forest in the southern part of this region and, moving northward, north of the treeline, a shrub-tundra grading into a sparse vegetation cover. The ecosystems of the Arctic are very vulnerable. They are most influenced by climate change but during the last years also by tourism (e.g., Broll et al., 2003).

^aRetired.



Fig. 1 Patterned ground, Pangnirtung Pass, Baffin Island, Canada. The ice wedges are located in the polygonal trenches. Photo: Broll.

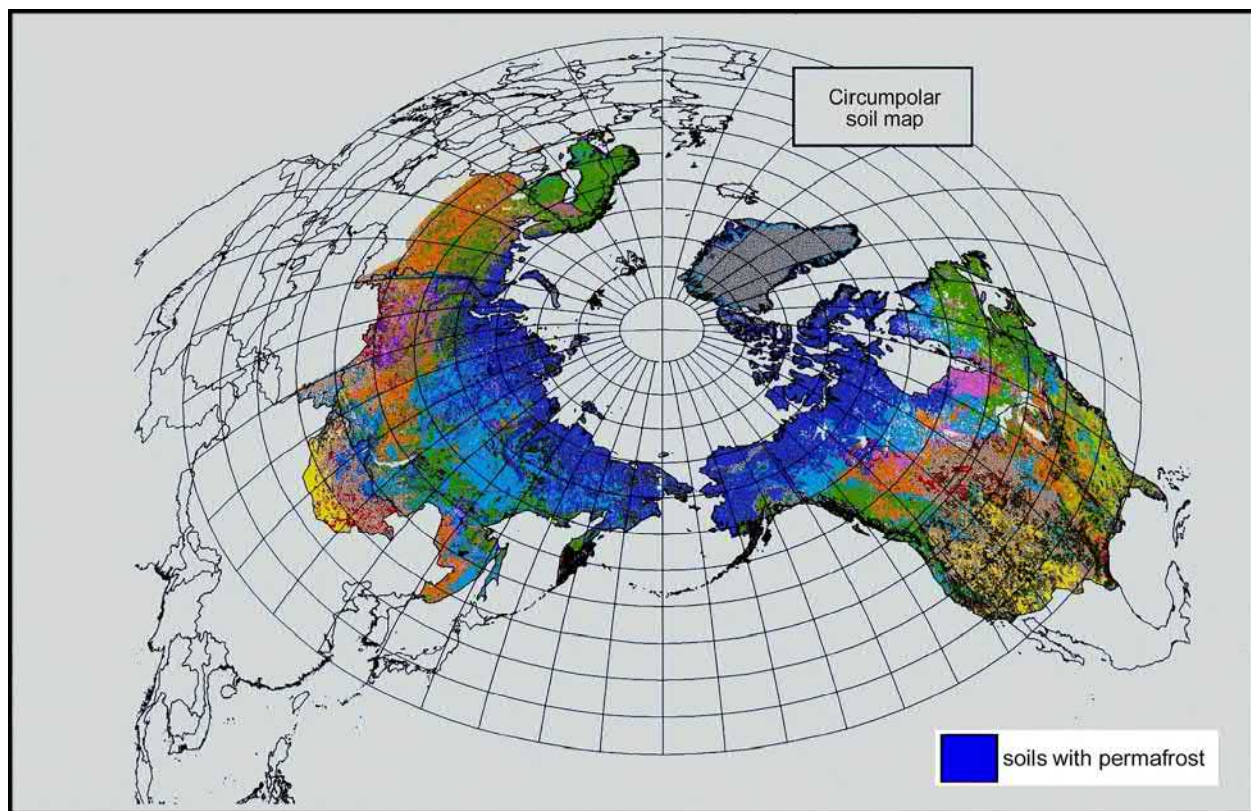


Fig. 2 The map shows the distribution of permafrost-affected soils (blue color) in the northern circumpolar area (Tarnocai et al., 2003b).

Soil-Forming Processes and Soil Characteristics

Soil genesis starts with weathering of the solid or loose parent material. Weathering processes are slow in the Arctic. Physical weathering including frost weathering takes place mostly at the surface. The dominant chemical weathering process in these soils is oxidation. Clay mineral formation is limited (Van Vliet-Lanoe et al., 2004; French, 2007).

The active layer is the layer of the ground in areas underlain by permafrost which thaws during summer (French, 2007). The active layer protects the underlying permafrost. The thickness of the active layer is controlled by soil texture and moisture, thickness of the surface organic layer, vegetation cover, aspect, and latitude. In perennially frozen soils, the active layer normally extends from 25 to 120 cm below the soil surface (Tarnocai, 2008).

Soil formation in the northern circumpolar region is dominated by cryogenic processes, which are driven by the presence and mobility of unfrozen soil water as it migrates towards the frozen front, along the thermal gradient in the frozen system. These processes, which produce a dynamic landscape, include freeze-thaw, cryoturbation or frost churning, frost heave, cryogenic sorting, thermal cracking, patterned ground and ice segregation (Van Vliet-Lanoe et al., 2004; Bockheim, 2015). Cryoturbation, which is very common in this region, results in irregular or broken soil horizons, involutions, organic intrusions (Fig. 3), organic matter build-up in the subsoil (often with concentration of this material along the top of the permafrost table), oriented rock fragments, silt-enriched layers, and silt caps (Bockheim and Tarnocai, 1998). Cementation very often results in characteristic soil structures, for example platy structure (Smith et al., 1991). Permafrost-affected soils contain various amounts of ice in the form of ice crystals, vein ice, ice wedges, and massive ground ice several meters thick (Fig. 4).

Particle size distribution in perennially frozen soils ranges from silty clay to coarse, gravelly sand. The composition of the fine-earth fraction is commonly dependent on the mode of deposition of the parent material (Tarnocai, 2008). The acidity in these soils varies greatly and also depends on the chemistry of the parent materials. The similarity of pH to that of the parent material is caused, in part, by cryoturbation, which not only mixes parent material with soil materials, but also mixes soil material among the horizons (Tarnocai, 2008). The nutrient content of perennially frozen soils is generally low since most of these nutrients are locked into compounds contained in the surface organic layer (e.g., Broll et al., 1999). Salt crusts, which form by translocation of salts from the subsurface horizons, develop during dry periods in the summer because of increased evaporation from the soil surface. Such salt crusts are common on the surfaces of High Arctic soils. Calcareous crusts on the underside of rocks are also a common phenomenon, especially in coarse-textured soils. Soils developed on fine-textured marine sediments usually have both high conductivity and high salt content (Tarnocai, 2008).

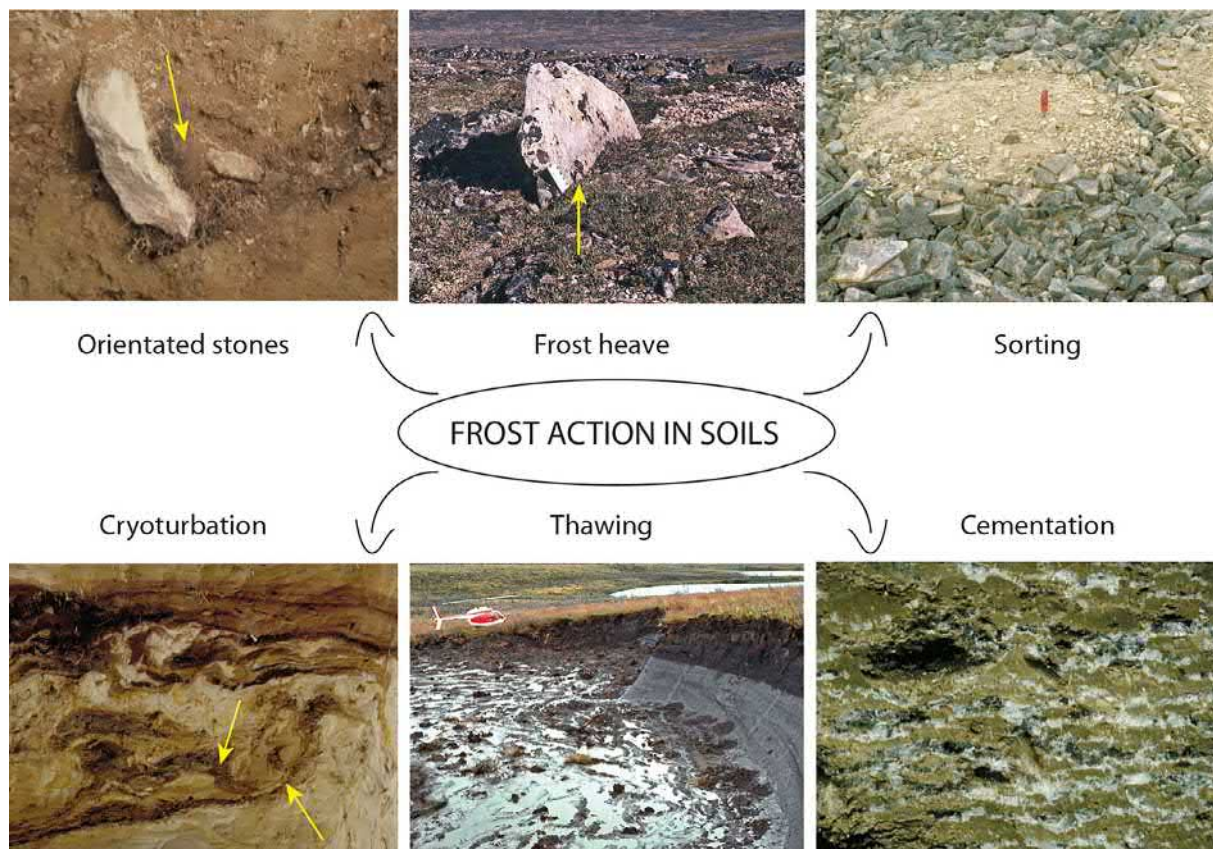


Fig. 3 Overview of frost action in soils. Cryoturbation is displayed by the strongly contorted mineral and organic horizons.



Fig. 4 Ice-wedge polygon area associated with Cryosols. The ice wedge is approximately 3 m wide. Mackenzie River Delta area, Canada. Photo: Tarnocai.

Soil Genesis and Soil Classification

The northern circumpolar soils generally have high moisture content, especially near the permafrost table, so beside cryoturbation gleying, associated grayish colors and redoximorphic features develop on most landforms, including those on better-drained positions. These soils are very often saturated because the active layer (the upper layer of the soil that freezes and thaws annually) is shallow. Thin, eluvial or leached horizons and brunification associated with coarse-textured soils are common in soils in the southern part of the discontinuous permafrost zone, but very seldom occur in the northern regions (Tarnocai, 2008).

Northern circumpolar soils are called Cryosols in Canada (Tarnocai, 2004b) and Gelisols in the USA (Ahrens et al., 2004). The World Reference Base of Soils (WRB) adapted the term Cryosol as well (Tarnocai et al., 2004). Russia developed an individual system for classifying the permafrost-affected soils (Mazhitova, 2004). Following the U.S. soil taxonomy Turbels are the dominant soils covering approximately $6.5 \times 10^6 \text{ km}^2$. The second most common soils are the Histels ($2.7 \times 10^6 \text{ km}^2$) and followed by the Orthels ($1.1 \times 10^6 \text{ km}^2$). In the Canadian classification the Cryosols are distinguished in Turbic, Static and Organic Cryosols. Seasonally frozen soils occur commonly in the southern part of the northern circumpolar region and these are dominantly Inceptisols, Spodosols, and Histosols (Ahrens et al., 2004; Tarnocai et al., 2003b).

Earth hummocks and hummocky terrain are characteristic for those sites in the landscape where there is enough fine soil material and enough moisture during summer. Earth hummocks are related to cryoturbation in most cases (Fig. 5) (Tarnocai and Zoltai, 1978) but can also develop due to eolian processes as so-called turf hummocks (Fig. 6) (Broll and Tarnocai, 2002). The hummocky terrain shows different physical and biological characteristics (Müller et al., 1998, 1999).

Soil Organic Carbon and Climate Change

Soils in the northern circumpolar region contain the single largest component of the terrestrial carbon pool. An estimate made by Tarnocai et al. (2009) shows that organic soils (Histosols and Histels) and perennially frozen cryoturbated mineral soils (Turbels) have the highest organic carbon contents ($32.2\text{--}69.6 \text{ kg m}^{-3}$) (Fig. 7).

Organic carbon pools estimated by the same authors also shows that the perennially frozen soils in the northern circumpolar region contain approximately 191.3 Pg for the 0–30 cm depth, 495.80 Pg for the 0–100 cm depth, and 1024.00 Pg for the 0–300 cm depth. Carbon pools in depths deeper than 300 cm were estimated to be 407 Pg for yedoma deposits and 241 Pg for deltaic deposits. Therefore, based on these estimates, the soils in the northern circumpolar region contain 1672 Pg of organic carbon with approximately 88% occurring in permafrost-affected soils and deposits. This 1672 Pg of the northern circumpolar region carbon accounts for approximately 50% of the total below-ground global organic soil carbon. This total is greater than the amount of carbon stored in the atmosphere or in the biosphere (Tarnocai et al.,

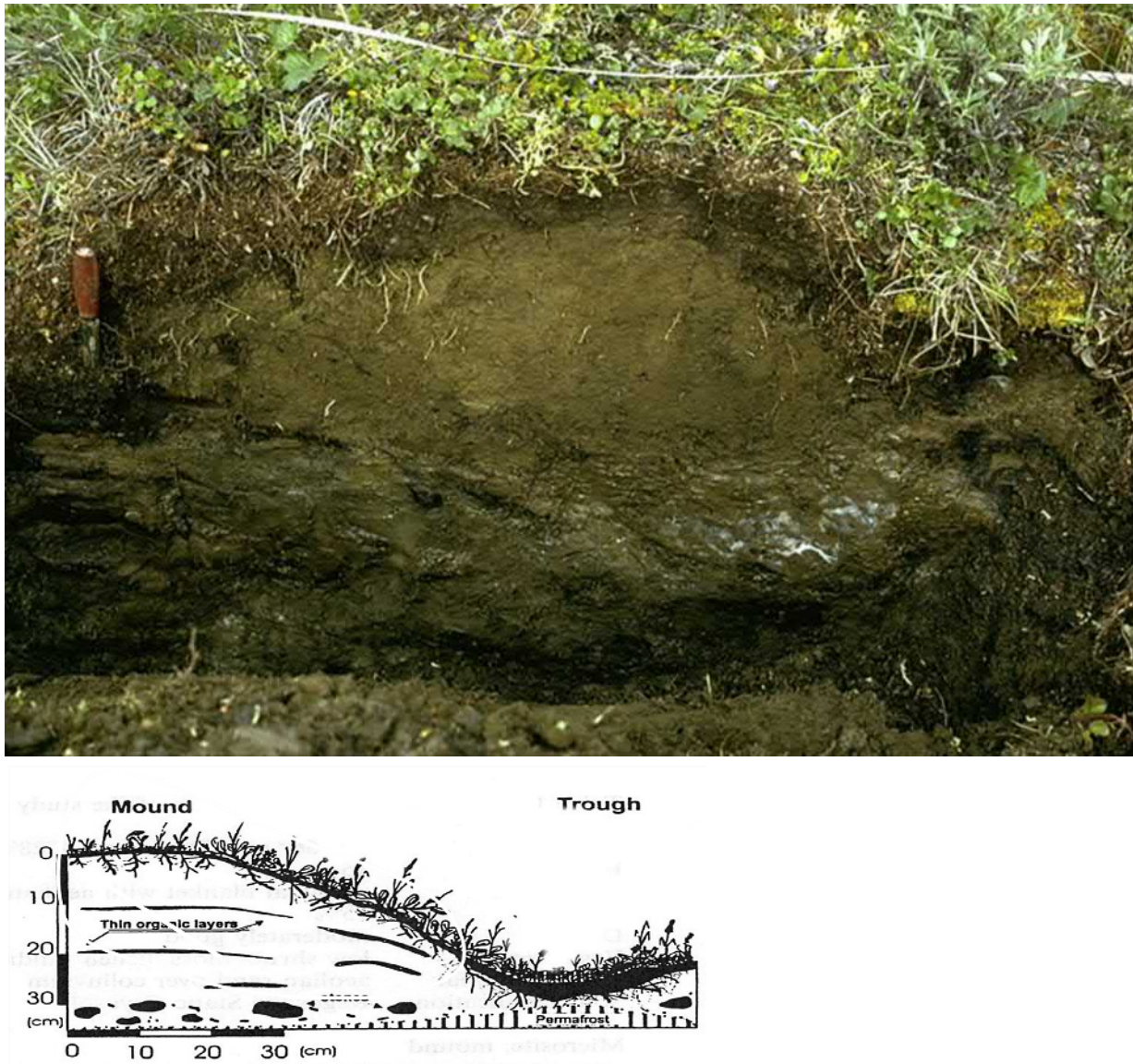


Fig. 5 Hummock in the Canadian Low Arctic, Turbic Cryosol. Photo Tarnocai, Sketch: From Müller G, Broll G, and Tarnocai C (1998) Soil temperature regimes in Baffin Island soils and their relationship to soil properties and microrelief. In: Lewkowicz AG and Allard M. (eds.) *Proceedings 7th International Conference on Permafrost*, pp. 771–776. Quebec: IPA.

2009). Because of the global significance of this soil carbon, research was carried out by soil scientists and ecologists especially on the decomposability of this soil carbon producing carbon dioxide and methane due to temperature increase (e.g., Knoblauch et al., 2013; Schuur et al., 2015; IPCC, 2019).

The global importance of soils in the polar regions was only recently recognized, when the role they play in global climate change was discovered. It is now widely accepted that climate warming has been, and will continue to be, much greater in both the northern and the southern circumpolar regions than in other parts of the globe with great effects on carbon cycling (e.g., Tarnocai and Broll, 2008; Tarnocai et al., 2009; Ping et al., 2015; IPCC, 2019). Changes in carbon cycling and carbon leaching have long been known, due to agriculture and fire in cold regions. In both cases the vegetation cover is destroyed, and the permafrost table moves downward (Fig. 8). Nowadays climate warming is the main reason for thawing of the permafrost as can be recognized throughout the Arctic (Fig. 9).



Fig. 6 Turf hummocks in the Canadian High Arctic, Ellesmere Island. Brunisolic Static Cryosols and Regosolic Static Cryosols developed from eolian sandy loam. Photos Broll.

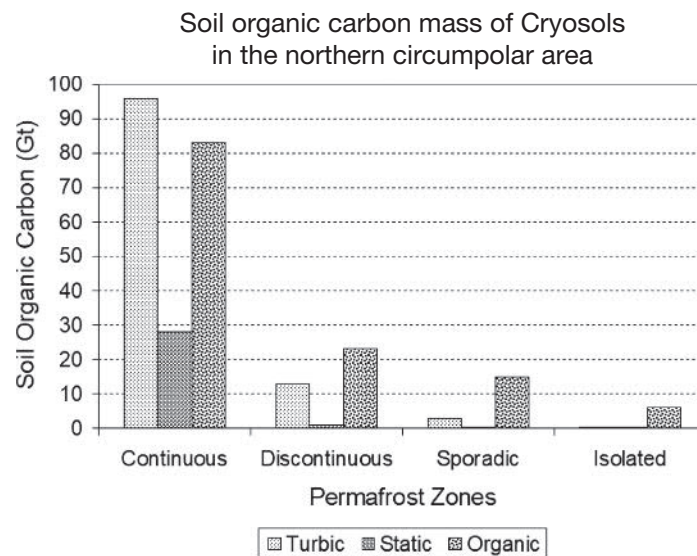


Fig. 7 Soil organic carbon mass of Cryosols in the northern circumpolar area (Tarnocai et al., 2003a).

Conclusion

Soils of the circumpolar regions are the coldest soils on Earth. These soils have been studied since the mid-1900s, but these studies greatly accelerated during the last two decades. There is now considerable knowledge of the processes that led to the formation of these soils, and of their role in relation to the unique ecosystems of the Arctic. However, their global significance was only recently recognized when the role they play in global climate, due to the huge amounts of organic carbon they stored for thousands of years due to their unique processes and properties.

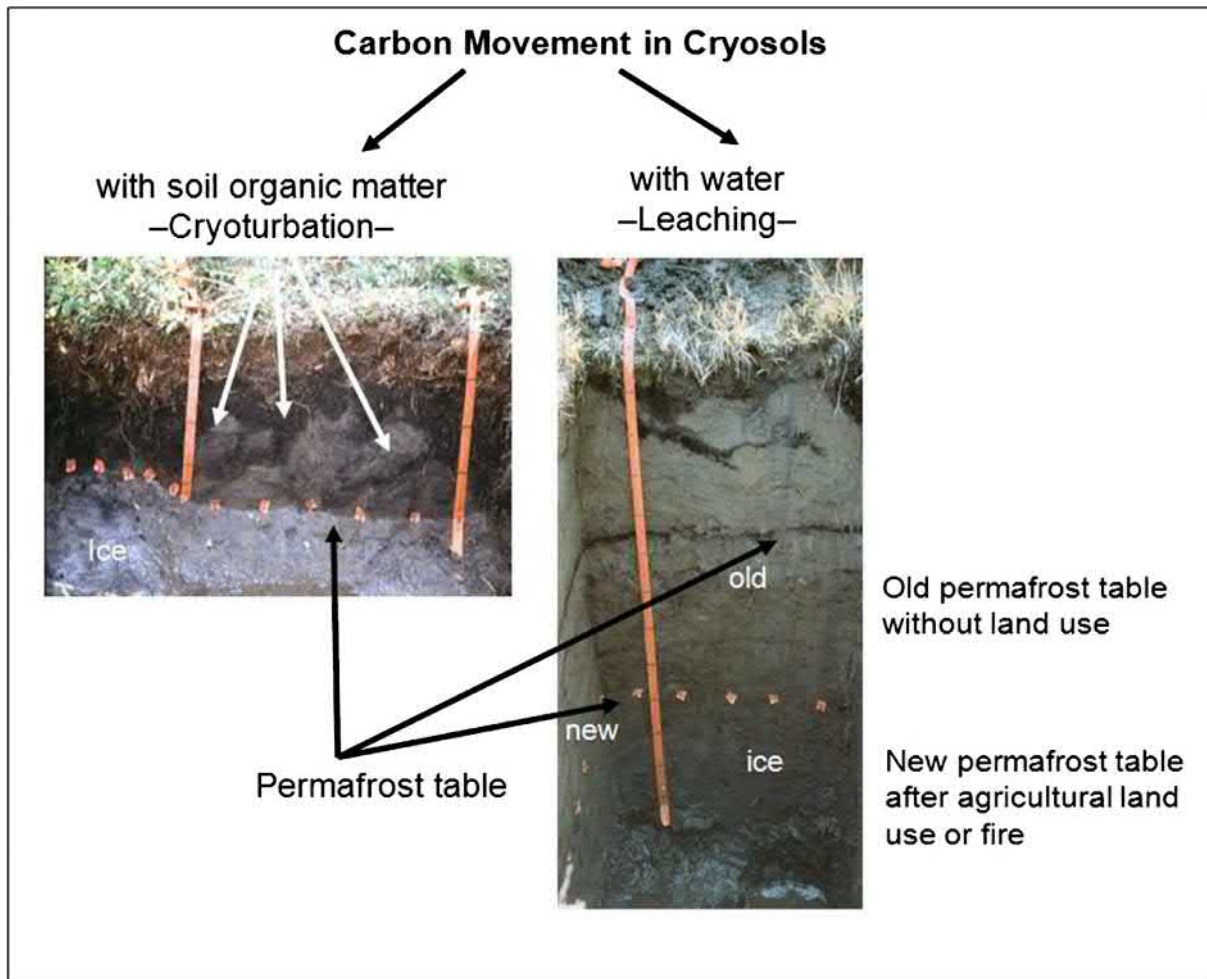


Fig. 8 Left: In case of a natural vegetation cover organic carbon stays within the active layer. It is affected by cryoturbation and partly it is accumulated at the permafrost table. Right: Due to agriculture or fire leaching and decomposition of organic carbon is going on.



Fig. 9 Ice wedges are thawing because of climate warming. Erosion processes are induced, Ellesmere Island, Canadian High Arctic. Photos: Broll.

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Permafrost Landscape Features

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Abstract

Permafrost underlies the tundra of the circumpolar North. The landforms of permafrost regions are formed from the development or thawing of ground ice. The most ubiquitous features in tundra lowlands are ice-wedge polygons, the irregular nets of three- to seven-sided units at the surface of the landscape. The boundaries of the polygons are ice wedges, developed in cracks that open at temperatures below -10°C as the ground contracts in winter. The little, conical, ice-cored hills that occur in some tundra landscapes, pingos, are the iconic landforms of permafrost terrain. They develop as growing ice deforms the overlying permafrost, either in drained lake basins, as the unfrozen ground in the former lake bottom freezes back, or at the base of hillslopes where hydraulic pressure may supply water to maintain ice growth. Landforms associated with thawing permafrost are also prevalent in the tundra because permafrost degradation may be initiated by local disturbance as well as climate warming. Thermokarst (thaw) lakes are common features of ice-rich terrain. They commonly expand laterally at a relatively steady rate, but the rate of deepening reduces over time. Retrogressive thaw slumps form where ice-rich permafrost is exposed by erosion of lake shores, riverbanks, and at the coast. These slumps develop rapidly and have become especially prominent in landscapes that contain buried glacier ice remnant from the last glaciation. Development of all these features has been affected by climate change enhancing the probability of near-surface permafrost thaw.

Introduction

The principal landforms of the tundra biome are closely associated with the presence of permafrost. They represent deformation of the terrain due to growth or melting of ground ice. Permafrost, ground that remains at or below 0°C for 2 years or more (ACGR, 1988), is a product of climate. At the continental scale its two most important drivers are air temperature and winter snow cover. Permafrost underlies almost all the terrain in the tundra biome because of the low air temperatures, low snow-holding capacity of the vegetation, and absence of trees to prevent drifting of snow. Ice-wedge polygons, perhaps the most ubiquitous landform in tundra lowlands (Fig. 1), are generated by low winter ground temperatures due to these factors (Mackay, 2000). Pingos, the iconic little hills of some tundra regions, are most abundant in sandy sediments of drained-lake basins after permafrost has aggraded into them (Fig. 2) (Mackay, 1979).

The top of permafrost in unconsolidated sediments is characteristically ice rich, so that if the ground ice melts, the ground surface will subside or, on hill slopes, may fail. Such thawing leads to development of thermokarst terrain, the pitted relief that results from melting of ground ice (Burn, 1992). Thermokarst lakes are common in much ice-rich ground and are now of interest for their association with climate change (Fig. 3). Permafrost degradation beneath them occurs in an anaerobic environment, leading to production of methane when organic matter previously entombed in frozen ground is thawed and decomposed (Walter et al., 2006). Retrogressive thaw slumps, landslides that are common after exposure of ice-rich permafrost, develop the most rapidly of all landforms in the permafrost landscape (Fig. 4) (Burn and Lewkowicz, 1990). They have become increasingly common in the last 20 years as air temperatures and rainfall totals have risen in the Arctic (Kokelj et al., 2015; Lewkowicz and Way, 2019).



Fig. 1 Ice-wedge polygons in Old Crow Flats, Yukon, Canada. The rectangular polygons are outlined by shrubs growing on ridges beside the ice wedges. Photograph by C.R. Burn.



Fig. 2 Ibyuk Pingo within its drained lake basin near Tuktoyaktuk, NWT, Canada. Photograph by C.R. Burn.

Above permafrost is a surficial layer of ground that thaws each summer called the active layer. A hummocky micro-relief commonly develops in active-layer soils which contain enough silt and clay to be frost susceptible (Fig. 5) (Tarnocai and Zoltai, 1978). Hummocks are associated with a buried ice-rich organic layer at the top of permafrost that is also a potential source of greenhouse gases when permafrost thaws (Mackay, 1958).

Hummocks

Hummocks are circular mounds about 1 m in diameter with a relief of up to 20 cm (Fig. 6). Mud hummocks (Fig. 5) are features for which the intensity of frost action and, perhaps, climatic conditions prevent establishment of vegetation on the ground surface. Earth hummocks, in contrast, have a continuous vegetation cover (Fig. 6). Hummock centers are composed of mineral soil, but



Fig. 3 Thermokarst lakes on Richards Island, western Arctic Canada (see [Burn, 2002](#)). Photograph by C.R. Burn.



Fig. 4 Retrogressive thaw slumps developed above Canoe Lake, Richardson Mountains, Canada. The slumps have developed in ice-rich deposits remnant from the last glaciation. The limit of glaciation is visible on the hillside, at the lowermost extent of visible bedrock. Photograph by C.R. Burn.

the small troughs between adjacent features are filled with organic material ([Fig. 7A](#)). Consequently, the active layer beneath the center of the features is deeper than in the troughs and the frost table is bowl shaped ([Figs. 6 and 7B](#)).

The hummock form is maintained by soil circulation, with upwelling in the middle of each feature, movement to the periphery, and the soil flux continuing downward toward the frost table and toward the lower parts of the bowl ([Mackay, 1980](#)). The circulation is perpetuated by ice segregation at the top and bottom of the hummock in autumn and early winter, with ice lenses growing parallel to the ground surface with downward freezing or to the top of permafrost by up freezing causing a small lateral displacement of soil. As these lenses thaw in spring and summer, soil settlement results in a net outwards movement near the surface and inwards movement at depth ([Mackay, 1980](#)). Upward movement in the center of the hummock is necessary for continuity of



Fig. 5 Mud hummocks, western Arctic coast, Canada. Photograph by the late J.R. Mackay.



Fig. 6 An earth hummock in tundra on Richards Island, western Arctic coast, Canada. The dowel rods have been inserted to the frost table. The exposure of the rods indicates the surface relief of the hummock, while the tops of the rods indicate the relief of the frost table. Photograph by C.R. Burn.

circulation. This may be facilitated by high moisture content at the base of the hummock's active layer in summer lowering soil density and promoting diapiric movement. In some environments, similar features are known as *frost boils* due to soil near its liquid limit emerging at the surface. Sorted circles of coarse clasts also develop in a similar manner (Fig. 8).

The circulation moves surface organic material to the peripheral edges of the hummocks and then carries some downwards into the base of the feature (Fig. 7A). Since the porosity (percentage of total volume that is pore space) of organic material is greater than mineral soil, less saturated organic material may thaw over the summer than proximal mineral soil. The downward movement of organic material by soil circulation is a prime cause of substantial buried organic materials beneath hummocks (Fig. 7A), and the high porosity of organic material is one of the reasons for the high near-surface ice content of hummocky terrain (Fig. 7B). The ice content is enhanced by ice segregation during up freezing, with gradual addition of organic-rich sediment at depth leading to an ice-rich zone beneath the hummocks that may be over 1 m deep.

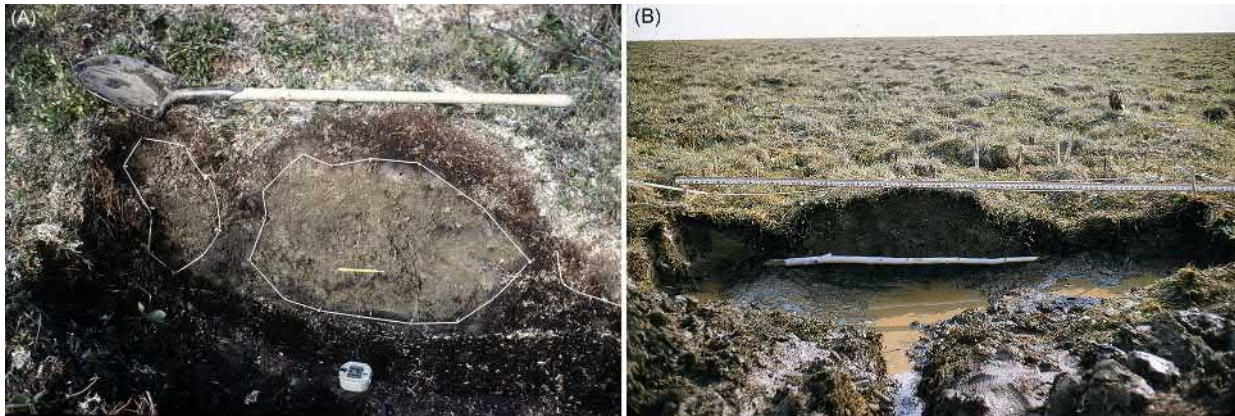


Fig. 7 (A) Cross-section of an earth hummock, showing the central mineral soil surrounded by brown (thawed) or black (frozen) organic material; (B) earth hummocks showing the ice-rich top of permafrost beneath them and the bowl-shaped frost table (see Mackay, 1980). Photographs by the late J.R. Mackay.



Fig. 8 Sorted circles of frost-shattered bedrock, Bunker Hill, Yukon, Canada. The centers of the circles have a soil matrix, but the peripheries are composed of stones and rocks. Photograph by C.R. Burn.

Destruction of surface vegetation by forest fire or other disturbance leads to a deepening of the active layer, thawing of ice-rich permafrost, and flattening of the hummock micro-relief (Mackay, 1995). As vegetation subsequently re-establishes, aggradation of permafrost and growth of ice lenses in the basal bowl shape squeezes the hummock from below and re-establishes its micro-relief (Kokelj et al., 2007).

Ice-Wedge Polygons

Polygonal ground is a ubiquitous feature of terrain underlain by unconsolidated sediments in the tundra biome (Figs. 1 and 9) (Mackay, 2000). Tundra polygons have long been widely recognized in lowlands and other flat terrain, but they also occur on hill slopes (Mackay, 1990a). They are characteristically 15–20 m wide in lowlands and may possess 3–7 sides (Fig. 9A). On hill-slopes and uplands they may be considerably larger, with widths up to 40 m (Fig. 9B). LeCompte (2004) digitized aerial photographs of more than 3400 polygons near the Canadian western Arctic coast and found the average area of lowland polygons was 309 m² ($n = 1998$) and of upland polygons was 796 m² ($n = 1480$). The polygons are bounded by a network of shallow troughs that in lowlands commonly lie between two ridges, one in each adjacent polygon. Some polygons are subdivided by troughs so that the primary features may be composed of smaller secondary or even tertiary units (Fig. 10) (Mackay, 2000). The troughs are underlain by V-shaped wedges of massive ice, whose development establishes the polygonal network (Fig. 11).

Our understanding of ice-wedge formation and growth was established by E. de K. Leffingwell after almost a decade of field studies in the early 20th century on the northern coastlands of Alaska and has been well developed theoretically by Lachenbruch (1962). However, the most comprehensive field investigations that have led to our current understanding of both the polygons and



Fig. 9 Ice-wedge polygons in (A) lowland and (B) upland settings Richards Island, western Arctic coast, Canada. The polygons in drier upland settings are larger than the polygons in the wet lowlands (see [Mackay, 1990a](#)). (A) Photograph by Sam Cornish and (B) photograph by C.R. Burn.



Fig. 10 Primary, secondary and tertiary ice-wedge troughs, Old Crow Flats, northern Yukon. Photograph by C.R. Burn.



Fig. 11 Ice wedge exposed in a coastal bluff near Tuktoyaktuk, NWT. The image shows a thermal contraction crack in the ice wedge and upturned bedding in the adjacent sediments that have deformed during long-term growth of the wedge. Photograph by C.R. Burn.

their bounding ice wedges were published by J.R. Mackay from field studies near the western Arctic coast of Canada, especially on Garry Island and at the experimentally drained lake basin, Illisarvik, on Richards Island (Mackay, 2000). At Illisarvik, Mackay examined the development of these features from their inception (Mackay, 1986), while at Garry Island he was able to assess their long-term behavior based on nearly 40 years of measurements (e.g., Mackay, 2000).

Ice-Wedge Development

The ice wedges that bound the polygons are among the few diagnostic indicators of permafrost (Fig. 11). Their origin was interpreted by Leffingwell after living for several winters on the tundra, where he heard sudden loud noises accompanied by a shock sufficient to rattle dishes in a field cabin. Subsequently, he found open cracks in hard-packed snow that penetrated the ground (Fig. 12). He pointed out that in spring, meltwater may infiltrate the cracks and freeze to form a vein of ice or, alternatively, hoar frost crystals may grow in the crack from saturated vapor. The cracks originate in response to thermal stress (tension) that develops as the ground cools after freezing of the active layer (Lachenbruch, 1962). Cracking is repeated at the same location because the ice vein is a locus of weakness in the ground, with the fracture commonly originating at the top of permafrost. Repeated cracking, infilling with meltwater, and freezing leads to the growth of the ice wedges. Over time, growing ice wedges incrementally push the bounding permafrost apart, creating troughs at the ground surface.

Several observations of the temperature of frost cracking indicate that the ground is below -10°C when it yields by brittle failure (Fortier and Allard, 2005). Lachenbruch (1962) indicated that cracking occurs during relatively rapid decreases in ground temperature, normally provoked by a cold snap at the surface. Mackay's (1993) observations generally confirm this, but he noticed variation in cracking temperatures between new wedges at Illisarvik and established forms at Garry Island. Following the initial rupture, the ice-wedge crack may widen to release further stress if the ground cools and it may propagate along the trough. Presumably, widening of the crack will be accompanied by deepening but this has not yet been reported from the field. In spring, the cracks may close as the ground warms before snow melt, so the long-term rate of ice-wedge growth (mm a^{-1}) is normally less



Fig. 12 Thermal contraction crack in the floor of Illisarvik experimentally drained lake from the first winter after drainage, 1978–79. The crack is about 4 cm wide (see Mackay, 1986). Photograph by the late J.R. Mackay.

than the annual crack width (cm). Cracking may not occur during winters in which the ground cools insufficiently or if thermal stress is relieved by cracking of other wedges.

Polygon Rims

While a trough develops over a growing ice wedge, the ground on either side may be raised to create a rim around each polygon (Fig. 13). Development of these bounding ridges is to accommodate the volume of the growing ice wedge, the growth of peat, the formation of ice in the rims from water sourced in the trough during freezing, and lateral compression during expansion of permafrost and the active layer in summer. The latter process transports soil from the polygon center to the rims, at a rate measured on Garry Island in 1966–79 of $0.4\text{--}0.6\text{ cm a}^{-1}$ (Mackay, 2000). Net outward movement is possible because contraction is confined



Fig. 13 Ridges on sides of ice-wedge troughs and depressed polygon centers, Tuktoyaktuk Peninsula, western Arctic coast, Canada (see Mackay, 2000). Photograph by C.R. Burn.

in winter, but in summer expansion may occur into the trough. When ice wedges crack frequently and ground deformation is in progress, the polygon centers are lower than the ridges, but not the troughs. These polygons are known as low-centered. Low-centered polygons may evolve into high-centered polygons if the wedges cease cracking and peat growth raises the center. If ice wedges thaw, the troughs become deep, the ground becomes well drained, the ridges collapse, and the polygons become distinctly high-centered (Mackay, 2000).

Polygon Development

Mackay (1974), studying the western Arctic coastlands of Canada, noted the development of a polygon network in a well-drained former lake basin within 10 years of drainage, but he did not find any networks at poorly drained sites in 100 years since drainage. No networks of polygons have evolved at Illisarvik since drainage in 1978 (Mackay, 2000). Growth of vegetation in the lake basin at Illisarvik has led to increased snow depths, increases in ground temperature and cessation of initial thermal contraction cracking (Mackay, 1986). Where networks have developed in drained lake basins, the polygons have commonly been irregularly organized. However, in the flood plain of a migrating river or if a lake shrinks in its basin the polygons are commonly quadrilaterals and have cracks parallel and perpendicular to the moving water body (Lachenbruch, 1962).

The primary hypothesis for evolution of the polygon network from a lattice of primary troughs to subdivision of polygons with secondary and tertiary troughs attributes the smaller troughs to infrequent cracking during severe winters. The hypothesis is weak because it does not consider changes in the thermal regime of ice-wedge troughs as a result of ridge development, which in turn reduces the probability of cracking by increasing local snow depths and ground temperatures. The hypothesis may also be criticized as the expansion of cracks over winter releases further incremental thermal stress, and therefore a primary network may respond by itself to a range of thermal conditions. It appears that historical factors associated with trough and ridge/rim development may weigh considerably in network evolution. On hillslopes, where down slope movement of the active layer hinders ridge development, and other settings where ridges do not develop well, the networks have few secondary troughs.

Pingos

Pingos are the iconic little hills of tundra environments that have a core of ice and, like ice wedges, are diagnostic of permafrost (Fig. 14). The name of these features comes from an Inuktitut word for conical hill. They are rarely more than 50 m high and are characteristically circular in plan form, with dilation cracks running along their crest lines from separation of the ground on either side of the feature as it rises upwards and steepens. The basal circumference of pingos may vary over orders of magnitude from tens to hundreds of meters. They are found in two principal settings, (1) where the ice core is fed by ground water under hydraulic pressure to raise the open-system type, or (2) where the uplift is from expansion due to freezing of water in confined ground, such as a drained lake basin, to create closed-system pingos. The former type is found in Greenland and Svalbard where hydraulic pressure is generated in proximal ice caps (Liestøl, 1996), while the latter are most well-known from the western Arctic coastlands of Canada (Figs. 2 and 14) (Mackay, 1979, 1998).



Fig. 14 Split Hill Pingo, near Tuktoyaktuk, NWT, Canada. Photograph by the late J.R. Mackay.

Closed-System Pingos

The closed-system forms are found in drained lake basins of Arctic plains, where permafrost has grown into formerly unfrozen sediments (Fig. 2). They are primarily restricted to sandy ground (Mackay, 1973). Lakes are found in Arctic plains, even in coarse grained sediments because seepage is impeded by the surrounding permafrost, so water may collect in depressions. Unfrozen ground is normally found beneath water bodies of sufficient depth to remain unfrozen at the bottom for most of the year, because over the year the temperature there is on average $> 0^{\circ}\text{C}$. The unfrozen ground surrounded by permafrost is known as talik. If a lake drains, as has been reported from many locations (Jones and Arp, 2011), the sediments will be exposed to the atmosphere and permafrost will aggrade into the talik.

Permafrost aggradation into sandy sediments is characterized by expulsion of water from freezing ground in order to accommodate the volume expansion as water turns to ice. For sands of porosity 0.3, there is almost a 3% increase in total volume as a result of freezing, and this is entirely in the pore water. Since permafrost aggradation occurs downwards from the ground surface and laterally from the permafrost surrounding the talik, the water expelled during freezing is confined in the remaining unfrozen ground and its pressure will increase (Mackay, 1973). Commonly, the expelled water will have a freezing-point depression associated with solutes in the groundwater that have been excluded from the ice and expelled ahead of the freezing front. Hence the talik may remain unfrozen at temperatures $\leq 0^{\circ}\text{C}$.

The pressure within the talik continues to increase until water is released to the surface through a fracture or the talik freezes through (Mackay, 1977). However, pressure development may lead to deformation of the surface, especially in an area of relative weakness. Such sites are likely to be associated with residual ponds in the lake basin, which reduce permafrost aggradation directly beneath them. Where deformation occurs, the uplift of the ground has a volume equivalent to the supporting pore water, which forms a lens of water in the talik just below the frozen ground. The water lens gradually freezes, creating a core of ice for the deformed ground (Fig. 15). The volume of deformation is equivalent to the volume of excess pore water. The initial deformation establishes the footprint of the pingo, but growth continues as further permafrost aggradation supplies more water to the water lens. The uplift rate of a pingo varies along the side of the feature with distance from the pivot point at the base of the pingo (Mackay, 1979, Fig. 19). The highest rates of growth, over 20 cm a^{-1} , have been measured at the tops of pingos (Mackay, 1979).

Pressures measured in the water lens have been equivalent to the weight of the overlying frozen ground and ice lens (Mackay, 1977). Artesian flow occurs when water lenses are punctured. If the drill hole is on the side of the pingo, geysers have gushed upwards (Fig. 16), but when the drill hole is on top of the pingo the water flows out over the ground surface, confirming the equivalence of water and overburden pressures. The pressures that develop by freezing are sufficient to support features that are as large as Ibyuk Pingo near Tuktoyaktuk, the largest pingo in Canada, almost 50 m high. Given the 15 m overburden of Ibyuk Pingo and the 35 m of ice above the water lens, and that Ibyuk Pingo has been growing recently (Mackay, 1979), the pressure in its water lens is about 6 atm.

The growth rate of a pingo depends on the expulsion of water during freezing and its rate of addition to the water lens. Permafrost aggradation occurs at a rate that declines over time as the distance between the cold ground surface and the point of freezing increases. The rate follows the Stefan relation, discussed below, where z (m) the depth of freezing is related to time, t (a):

$$z = b \sqrt{t} \quad (1)$$

the constant, b , depends on the thermal conductivity of frozen soil, the mean annual surface temperature, and the latent heat of fusion for pore water in the sands (Mackay, 1979). The nature of the relation was validated by Mackay (1990b, Fig. 9) who



Fig. 15 Pingo ice exposed on the coast of Tuktoyaktuk Peninsula, western Arctic Canada. Photograph by the late J.R. Mackay.



Fig. 16 Geyser on a pingo from a punctured water lens, Tuktoyaktuk Peninsula, western Arctic Canada (see Mackay, 1977). Photograph by the late J.R. Mackay.

examined the successive thickness of annual growth bands in pingo ice and showed a very close fit between band width and Eq. (1) where t is the time after ground freezing reaches the water lens.

The uplift of a pingo characteristically splits the feature so that the summit resembles a crater (Fig. 2). Multiple dilation cracks are common (Fig. 17). Dilation cracks may be filled with ice, similarly to ice wedges, although the crack is formed by upward movement of the frozen strata as well as thermal contraction. Some dilation cracks are continuous with thermal contraction cracks in the drained lake flats. At the base of the slopes, uplift may create a fracture in permafrost open to the water lens and groundwater may emerge at the surface. Alternatively, a subsidiary pingo may grow at such locations if the water ejected up the fracture is confined (Fig. 18).

Pingos may cease growth if the talik freezes, or they may collapse because of oversteepening of the sides or exposure of ice in the summit crater (Mackay, 1998) (Fig. 19). The collapse may take several years and may be arrested if exposed ice is covered by material slumping as the permafrost thaws. If the sides of the pingo become steep during its growth, soil may creep downhill to transfer ground materials within the footprint of the feature. When the feature subsequently collapses a circular rampart may survive (Fig. 20). The centers of collapsed pingos do not form deep depressions because the height of the pingo is due to the ice and water lenses. Once these lenses melt, the surface elevation is close to that of the original lakebed.

Open-System Pingos

In comparison with the research by J.R. Mackay on the closed-system pingos of the Tuktoyaktuk Peninsula area, there is relatively little documentation of open-system pingos and no survey of growth rate. There are several examples of these features known from Greenland and Svalbard (Liestøl, 1996), where they are thought to be fed by water originating from three sources: geologic faults, taliks beneath ice sheets and glaciers, and permafrost aggradation following emergence from the ocean due to isostatic rebound. In Svalbard, several pingos have water draining from the pingo throughout the year, creating substantial icings on the flanks of the features. High pressures are required to lift these pingos, as with the closed-system type. One example on Svalbard rises to 42 m above the valley floor.



Fig. 17 Dilation cracks on a pingo, Tuktoyaktuk Peninsula, western Arctic coast, Canada. Photograph by C.R. Burn.



Fig. 18 Collapsing pingo with subsidiary pingo that has grown beside it, Richards Island, western Arctic Canada. Photograph by C.R. Burn.

The ice core of an open-system pingo on Svalbard was a series of massive ice lenses rather than simply one massive icy body, as has been most commonly observed with the closed-system type (Yoshikawa, 1993). This indicates that growth of these features may be episodic and depend on the pressure emanating from the water source. Yoshikawa (1993) also suggests that conduits for water from sub-permafrost aquifers may become frozen, and new routes may open, leading to mounds of different ages growing inside each other (Liestøl, 1996). While closed-system pingos are characteristically circular or oval in plan view, the open-system type may be elongated and irregular in shape.

Thermokarst Lakes

Thaw lakes are water bodies that fill “a closed depression formed by settlement of the ground following melting of ground ice” (ACGR, 1988, p. 89). The lakes are common in ice-rich terrain throughout the permafrost zones, developing after disturbances



Fig. 19 Massive ice exposed in summit crater of a collapsing pingo on Richards Island, western Arctic Canada. Photograph by C.R. Burn.



Fig. 20 Remnant pingo rampart, Richards Island, western Arctic Canada. Photograph by Sam Cornish.

such as forest fires or climate change (Burn and Smith, 1990). The shape and depth of the lakes depend on the time since thawing began and the local distribution of ground ice. In ice-rich sediments, the lakes keep growing until the ground ice body is exhausted (Fig. 21).

The key thermal relations that maintain thermokarst development depend on lake water depth (Roy-Leveillee and Burn, 2017). If the water body is too deep to freeze to the bottom in winter, then the lake-bottom temperature will be above freezing year-round and thawing will proceed beneath the lake. Where surface ice reaches the lake bottom in winter, permafrost may be stable below the lake bottom even if annual mean lake-bottom temperature (T_{lb}) is above freezing, depending on the ratio of freezing to thawing degree days. This is due to higher thermal conductivity (λ , $\text{W m}^{-1} \text{ } ^\circ\text{C}^{-1}$) of frozen than thawed sediments, which affects the net heat balance of the lake substrate. If $T_{lb} < 0 \text{ } ^\circ\text{C}$, permafrost is expected beneath a lake-bottom active layer. In Canada's western Arctic coastlands, permafrost is preserved beneath water depths less than two-thirds of the winter ice thickness (Burn, 2002). In the lakes of Old Crow Flats, northern Yukon, permafrost degradation may occur beneath shallow water where snow accumulation on the ice surface affects the temperature, and hence the freezing degree days at the lake bottom (Roy-Leveillee and Burn, 2017). In warmer conditions of central Yukon, lake ice is thinner, and thawing appears to proceed at the edge of lakes (Burn and Smith, 1990). In lakes where the bottom remains unfrozen year-round, T_{lb} is characteristically $2\text{--}4 \text{ } ^\circ\text{C}$. As a result, thaw lakes provide the greatest local adjustment of ground temperatures in the permafrost regions from patterns determined by climate (Burn, 2002).



Fig. 21 Thermokarst lakes of Richards Island, western Arctic Canada. Photograph by C.R. Burn.

Lake Growth

Thaw lakes develop from an initial disturbance where the active layer deepens into ice-rich ground. Melting of excess ice leads to subsidence of the ground and creation of a depression where water may collect. The elevated water content increases the time required for freeze back and raises the mean annual ground temperature. The depression then becomes a locus for soil water that promotes further thawing. Additional subsidence will continue so long as the thawing permafrost is ice rich. The pond acts as an area of higher temperature on the ground surface, and while the surface is depressed, heat flows both downward and laterally into the surrounding permafrost. Consequently, horizontal and vertical expansion of the water body occurs.

Thaw of permafrost occurs at a rate that depends on the ice content of the ground, the temperature gradient between the lake bottom and the surface of permafrost, and the thermal conductivity of thawed lake sediments. Where a thaw lake is growing, the depth to permafrost and the depth of the lake increase over time, at a rate that diminishes as the temperature gradient declines. The depth of thaw (z) is governed by the Stefan equation (Burn and Smith, 1990):

$$z = \sqrt{\frac{2\lambda T_{lb} t}{\rho L}} \quad (2)$$

where the t is time since thawing began, ρ is the volume fraction of ice in permafrost, L is the latent heat of fusion (J m^{-3}), and other terms are as defined above, using the absolute value for T_{lb} . The annual rate of expansion of lake radius may be obtained from Eq. (2) by setting $t = 1$ a. Near Mayo, Yukon, field observations of both lateral expansion (0.5 m/year) and lake deepening have validated this relation in ice-rich ground (Burn and Smith, 1990). In some cases, lake growth leads to coalescence of lakes (Fig. 22), but in others it may lead to drainage (Mackay, 1988).

Lakes will continue to expand in ice-rich sediments until the local ground ice is exhausted. However, in sandy deposits the ice content may be close to the porosity of the sand and there is little subsidence as the ground thaws. Furthermore, sand-sized particles are less easily transported away from the lake edge, unlike silts and clays that may become suspended in the water during storms, and hence sand characteristically accumulates and stabilizes the shoreline. Many thaw lakes developed in sands have wide subsurface terraces that may support permafrost beneath shallow water around the lake edge (Fig. 3) (Burn, 2002).

Talik Configuration

The talik beneath a thaw lake represents a thermal disturbance that may be confined by perennially frozen ground or may penetrate through permafrost. The configuration of the talik may develop as described by Eq. (2), but in time it will reach an equilibrium state. In the simplest case, of a circular lake at equilibrium, the temperature T_z in the center of the talik at depth z beneath the lake is given by (Burn, 2002, Eq. 3):

$$T_z = T_g + \frac{z}{I} + (T_{lb} - T_g) \left(1 - \frac{z}{\sqrt{z^2 + R^2}} \right) \quad (3)$$



Fig. 22 One thermokarst lake formed from three, with lake ice floating above the central pool of each lake, Richards Island, western Arctic Canada. Photograph by C.R. Burn.

where T_g is the mean annual temperature of permafrost at the surface, I is the geothermal gradient in permafrost ($\text{m } ^\circ\text{C}^{-1}$), and R is the radius of the lake (m). Eq. (3) shows that while temperatures in the talik are sensitive to the lake-bottom temperature and conditions in the surrounding permafrost, they also depend on the size of the lake. Where R is large, temperature in the talik increases with depth following the geothermal gradient, and there may be no permafrost beneath the lake. For smaller values of R , the talik will be closed at depth, but the base of permafrost will rise beneath the body of unfrozen ground. Since regional temperatures in the ground and in lakes vary little, the width of thaw lakes is the principal local control on whether taliks are closed or penetrate permafrost. For given values of T_g and T_{lb} a critical radius can be calculated for which the temperature at any depth beneath the center of a lake $\geq 0^\circ\text{C}$. In Canada's western Arctic, critical R is approximately 200 m (Burn, 2002). Where there are littoral terraces, critical R is for the central pool of the lake, and diminishes as terrace width increases, because permafrost beneath the terraces has a higher temperature than in the surrounding terrain.

Lake Orientation

Many thaw lakes in the Arctic coastal plains of Canada, Alaska, and Siberia are elongated and aligned in a common direction. Some of the lakes are oriented in depressions eroded by ice sheets (Figs. 3 and 21), but many appear to be caused by wind-activated circulation of the lake water (Mackay, 1963). In the sandy plains of the western Arctic coastlands, the lakes are oriented perpendicular to the prevailing wind direction. This has been attributed to the movement of water in two cells from the windward shore to each end of the lake, then to the lee shore, and back across the lake. The current should be fastest at the ends of the lake because of the integrated flow along the windward shore. In contrast, in the silts and clays of Old Crow Flats, the elongation is parallel to the prevailing winds. The difference is due to the minimal erosion effected by cross lake currents in sediments that are generally not suspended in the lake water but accumulate at the site of wave action, and the substantial erosion that occurs when finer sediments may be suspended and removed from the lake shore (Roy-Léveillé and Burn, 2016).

Drainage

Disappearance or shrinkage of thaw lakes is generally by catastrophic drainage. This is caused by the following factors: (1) there is little sediment in surface water to fill lakes; (2) growth of vegetation is relatively slow in the tundra environment; and (3) there is only a short period for evaporation each year (Burn, 1992). On average, several lakes drain each year along the western Arctic coast of North America, perhaps in a period of hours (Jones and Arp, 2011). The rapid drainage is commonly initiated by spring melt-water impounded in the basin. The water overtops a snow dam and then erodes ice wedges or other ice-rich ground as flow is initiated. The rapid drainage means that the lake bottom is turned quickly from a lacustrine to a terrestrial surface beneath which permafrost aggradation begins the following winter.

Thaw Lake Cycle

Drainage of thaw lakes leaves a basin, perhaps containing residual ponds. Permafrost aggradation is initially rapid because of the absence of vegetation to trap snow, but the rate of aggradation slows with time as sedges and shrubs colonize the basin. With time, networks of ice wedges develop in these basins and some aggradational ground ice forms in the sediments. However, the extent of ground ice formation during the Holocene has been insufficient to raise the ground surface to its original elevation, and therefore restore the terrain to the conditions prior to initial thaw lake development. This means that while ice-wedge polygons, pingos, hummocks, and other features that depend on ground ice may form in these basins, renewed thaw lake development encompassing the whole basin does not occur, unless the drainage outlets become obstructed (Fig. 23). In sandy deposits, the margins of drained lake basins tend to be higher than the centers, but in finer-grained sediments, such as in Old Crow Flats, the centers are domed (Jorgenson and Shur, 2007; Roy-Léveillé and Burn, 2016). These relations are likely a product of the extent of intra-basin sediment transport that occurs due to variation in suspension of each particle-size type during storms. Finer-grained sediments are transported into the basin center, unlike sands that remain near the location of erosion (Roy-Léveillé and Burn, 2016).

Retrogressive Thaw Slumps

Thaw slumps have characteristically been the most rapidly developing landforms in the permafrost environment. They comprise a steep headwall of 20–90° angle, commonly with exposed massive ice, and a low-gradient foot slope. The foot slope is covered by debris that has fallen from the headwall and a slurry from ablation of the exposed permafrost (Burn and Lewkowicz, 1990). Thaw slumps are initiated by erosion that exposes ice-rich permafrost in riverbanks, lake shores, at the coast, or in a few cases by sliding of the active layer (Fig. 24). The headwall ablation of the features is commonly over 10 m a^{-1} . Supersaturated slurry may flow away from the headwall, even on slopes as low as 3 degrees. The features continue to develop until the headwall reaches ice-poor ground, fallen debris covers it, or the foot slope rises sufficiently to meet the terrain surface, thereby covering the headwall. Apparently stable materials in the foot slope may be remobilized by rainstorms that reactivate sediment transport out of the feature and prolong development of the slump. Stable features, especially along the Arctic coast, may also be reactivated by erosion at the water body removing surficial materials and providing a new base level for the feature.

Thaw slumping has been a focus of significant interest with the recent development of very large features, mega-slumps, that have headwalls over 25 m high and are over 1 km across, cover areas of up to over 52 ha, and have retreat rates up to over 25 m a^{-1} (Fig. 25) (e.g., Lacelle et al., 2015). Sediment from these features alters the chemistry of water courses, may dam the receiving creeks, and affects the sustainability of the streams as viable fish habitat (e.g., Kokelj et al., 2013). Mega slumps may be clearly visible on satellite images and have been mapped at subcontinental scale in close association with the limits of glaciation (e.g., see Fig. 4) (Kokelj et al., 2017). Many of the features are in relict glacial ice that has only recently yielded their development in association with climate change, particularly through increases in the number and intensity of rainstorms (Kokelj et al., 2015). Thaw-related factors, also enhanced by climate change, are well correlated with the widespread development of thaw slumps on Banks Island, Arctic Canada, where over 4000 features were initiated between 1984 and 2015 (Lewkowicz and Way, 2019).



Fig. 23 The Illisarvik drained-lake basin, western Arctic coast, Canada. The basin was drained in 1978 (see Mackay, 1986). Photograph by Sam Cornish.



Fig. 24 Retrogressive thaw slump on Pelly Island, western Arctic coast, Canada. Photograph by C.R. Burn.



Fig. 25 Mega-slump on Peel Plateau, NWT, Canada. The feature is over 1 km wide. Photograph by C.R. Burn.

Mega slumps are huge individual features in the permafrost landscape, a terrain that characteristically has had little sediment movement. Yet there are few depressions in the regions where the slumps are currently found to indicate a prior period of comparable thaw slump development. The early Holocene (~ 8000 years ago in the Arctic) was a period of exceptional warmth in the western Arctic, and unconformities representing greater active-layer thicknesses are visible in many mega-slump headwalls. It is possible that initiation of the slumps has required incision of the landscape by streams through the Holocene to develop slopes that have only recently been destabilized by climate change effects.

Conclusion

Many of the landforms of permafrost regions are directly associated with the growth or melting of ground ice. In the 20th century, most features were considered as part of an environment in equilibrium with its climate, and so growth or degradation of features was commonly associated with disturbances, i.e., the appearance of fresh substrates for permafrost aggradation or damage to

vegetation cover leading to permafrost degradation. In the 21st century, effects of climate change on the permafrost landscape have become widespread in regions with sufficient ground ice. Degradation of ice-rich ground is now widely reported. The surficial effects have been best observed in relatively cold environments, because the active layer there is thin and so a small-scale change requires little additional energy. In contrast, in regions where the active layer is thick, even though the permafrost may be considerably warmer, the permafrost landscape appears to be more resilient to climate change. As the climate shifts, it is difficult to foresee how any component of the geomorphological systems in the tundra biome will remain unaffected.

Acknowledgment

This article was written while the author was a Visiting Scientist at the Geological Survey of Canada, in Ottawa, ON.

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Cold Adaptations of Tundra Insects

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Abstract

Even though insects cannot regulate their internal temperature through metabolism, they manage to live in some of the coldest regions of the planet. They achieve this through a wide variety of adaptations. The active part of their life cycle is compressed into the few short weeks of Arctic summer. In order to build up the necessary nutrients and metabolic energy to fulfill their life cycle, most Arctic insects live several years, either in the larval or adult stage. Arctic insects avoid lethal polar winter air temperatures by seeking shelter beneath snow, inside plant tissues, beneath leaves or in mud. As summer turns to winter, polar insects prepare physiologically for freezing temperatures. Some species are freeze-tolerant, and others avoid freezing. Most Arctic insects are freeze-tolerant, meaning they allow ice to form inside their body cavities, but carefully control the location of ice crystals to avoid tissue damage. Freeze avoiding insects build up antifreeze chemicals in their hemolymph that allow their bodies to super-cool to temperatures well below the normal freezing point of water. Some small and soft-bodied insects that live in soil allow most of the water in their bodies to be drawn out into the soil as it freezes, and so avoid frozen tissues through desiccation.

Introduction

Insects, like other invertebrate animals, are poikilothermic. This means that they cannot regulate their own body temperatures except by behavioral means such as basking in the sun or burrowing in the soil. As [Everatt et al. \(2015\)](#) so succinctly put it, "Invertebrates, more so than any other animal group, are at the whim of their environment." Of course in regions such as the tropics, where temperatures are generally both warm and stable throughout the year, this aspect of insect physiology puts little or no environmental stress on insects. This is certainly one factor that contributes to the incredible diversity of tropical insects. However, seasonality and cold temperatures increase in the higher latitudes, and winter air temperatures become lethal to insects in the Polar Regions. There are very few insects living in Antarctica because of its ice cover. This article therefore deals primarily with insect adaptations for life in the Arctic.

Insects have many ways of dealing with cold climates. Surprisingly, the one adaptation that is not utilized by arctic insects is migration to lower latitudes during winter. Nearly all arctic insects and other invertebrates remain there throughout the year. Their behavioral adaptations are mainly focused on seeking shelter from winter air temperatures. Their physical adaptations include small body size and dark-colored exoskeleton. Their physiological adaptations include freeze resistance, freeze tolerance, and cryoprotective dehydration. Their life history adaptations include multiyear life spans, especially of larvae and adults, as well as adaptations in their phenology: the timing of periodic events in their life cycle. Each of these topics are discussed in some detail, below, after a brief discourse on the natural history of arctic insects.

Insect Life in the Polar Regions

The Arctic regions are generally inhospitable to insects and other invertebrates. The winters are very long and incredibly cold, with air temperatures that are lethal to insects persisting for several months of the year. Summers are short, and the length of the growing

season decreases with latitude. The growing season in arctic tundra regions averages 50–60 days. Regions far north of the Arctic Circle ($66^{\circ}33'N$), the High Arctic, have only sparse, intermittent plant cover (Fig. 1). Thus, the diversity of plant feeding insects, predators and scavengers is extremely low here.

An example of the physical environment of the High Arctic can be found in the Zackenberg valley, situated at $74^{\circ}28'N$ in northeast Greenland, as described in a study by Westergaard-Nielsen et al. (2017). Here, the mean annual mean temperature is about $-9.0^{\circ}C$. Mean July temperature is $6.3^{\circ}C$ and mean February temperature is $-19.8^{\circ}C$. As in most High Arctic regions, mean annual precipitation is less than 250 mm, of which approximately 85% falls as snow. Maximum snow depth is remarkably shallow, ranging from 0.13 to 1.44 m over recent years. In this valley, the growing season is 51 days. This represents the time of year when the ground surface is not frozen, so plants may grow. The High Arctic is a cold desert. A survey of the insect life of all the High Arctic regions by Hodkinson et al. (2013) found only 296 species. A survey of ground beetles of northern Canada (Ernst and Buddle, 2015) found that just four species: *Pterostichus haematopus*, *P. brevicornis*, *P. caribou*, and *Amara alpina* accounted for 44% of all beetles captured by pitfall trapping in the High Arctic. By comparison, the boreal forest regions of Canada have more than 32,000 insect species.

One useful measure of the biological productivity of an ecosystem is its Net Primary Productivity, or NPP. NPP is the rate at which all the plants in an ecosystem produce useful chemical energy; it is equal to the difference between the rate at which the plants in an ecosystem produce useful chemical energy (GPP) and the rate at which they use some of that energy during respiration. In the arctic tundra ecosystems, 87% of the estimated NPP is produced in the Low Arctic. For polar desert regions of the High Arctic, above-ground NPP ranges from 0 to 50 g per m^2 of surface area per year (Gould et al., 2003). Not surprisingly, the species diversity of insect orders is far greater in the Low Arctic than in the High Arctic (Danks, 1981) (Table 1). As shown in Fig. 2, the productivity of the High Arctic regions is less than a tenth of the productivity of the boreal and temperate regions. The productivity of mainland arctic tundra is about one-quarter of the productivity of the boreal forest and temperate grasslands.

Antarctica is even more inhospitable to insect life than the Arctic. In fact, there are very few insects living on the Antarctic continent. Ice-free areas cover only one-third of 1% of Antarctica. These rare ice-free areas include nunataks, which are mountain peaks and other rock formations exposed above a glacier or ice sheet. In recent years, these bleak, windswept exposures have been found to harbor invertebrate life, including springtails (Fig. 3). Springtails (Collembola) are primitive, minute, six-legged arthropods. Most of the invertebrates that live in Antarctica, including Protozoa, mites, nematodes, springtails and midges live in the moss beds and melt water lakes. The Antarctic fauna includes 20 species of springtails (Collembola), two species of midges (Diptera), and a number of parasitic insects that are associated with coastal birds and marine mammals, including 37 species of biting lice



Fig. 1 Polar desert vegetation at Isachsen, Ellef Ringnes Island, Nunavut, Canada ($78^{\circ}46'N$). Photo by F.J.A. Daniëls, University of Münster, used with permission.

Table 1 Number of families and species of insects in the North American Arctic

Order	Number of Arctic families	High Arctic species	Low Arctic Species
Ephemeroptera (Mayflies)	5	0	11
Odonata (Dragonflies)	3	0	6
Plecoptera (Stoneflies)	6	0	22
Orthoptera (Grasshoppers)	1	0	4
Phthiraptera (Lice)	9	33	58
Hemiptera (True bugs)	12	5	65
Thysanoptera (Thrips)	Not recorded	1	2
Neuroptera (Alderflies, dobsonflies)	2	0	3
Coleoptera (Beetles)	17	10	200
Diptera (Flies)	17	135	345
Hymenoptera (wasps and bees)	22	54	197

Data from Danks, H.V. (1981). *Arctic arthropods: A review of the systematics and ecology with particular reference to the North American fauna*. Entomological Society of Canada: Ottawa.

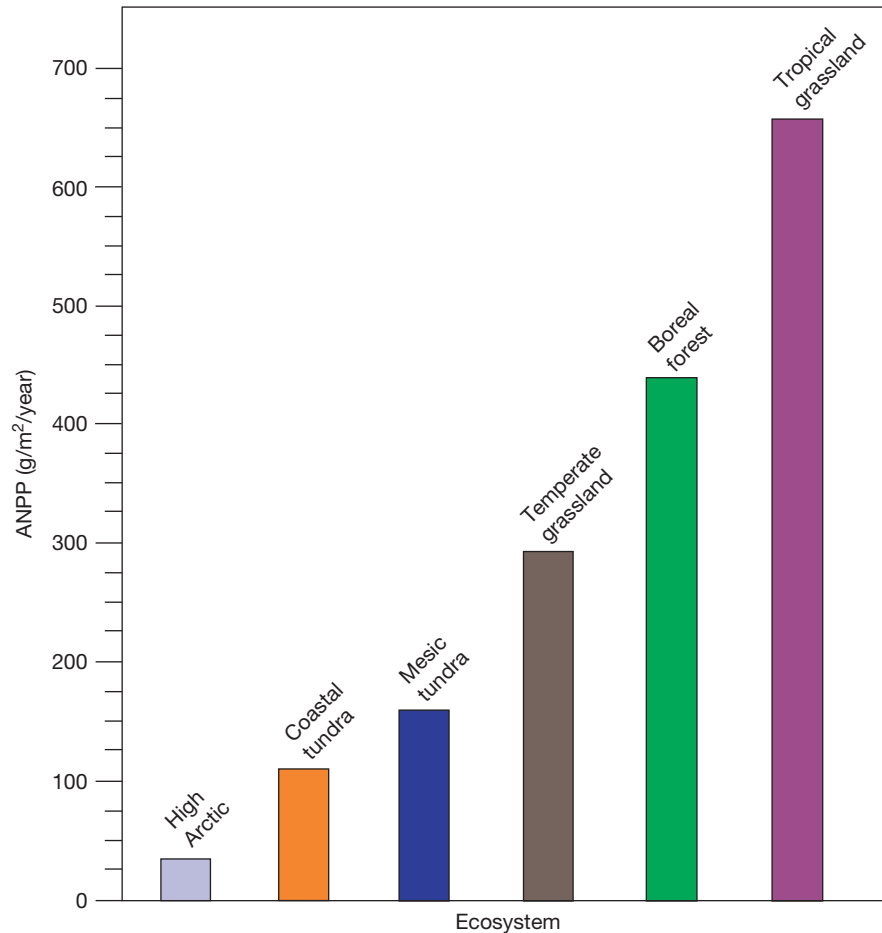


Fig. 2 Above-ground net primary productivity measurements for various ecosystems in North America, shown in grams per square meter per year. High Arctic datum from Gould, W.A., Reynolds, M., Walker, D.A. (2003). Vegetation, plant biomass, and net primary productivity patterns in the Canadian Arctic. *Journal of Geophysical Research-Atmospheres* **108**(D2), 8167. Coastal tundra, boreal forest, temperate grassland and tropical grassland data from NASA (2018). *NPP multi-biome: Grassland, Boreal Forest, and Tropical Forest Sites, 1939–1996*. https://daac.ornl.gov/NPP/guides/NPP_MULTIBIOME.html (Visited August 1, 2018).



Fig. 3 Photograph of springtails (*Cryptopygus sverdrupii*) living on a nunatak in the Sør Rondane Mountains, Dronning Maud Land, Antarctica. Photo by Mark Stevens, South Australian Museum, used with permission.

(Mallophaga), 5 species of sucking lice (Anoplura), and 1 species of flea (Siphonaptera) (Gantait and Chandra, 2017). The flightless midge *Belgica antarctica* is the largest purely terrestrial animal in Antarctica, measuring up to 6 mm in length.

Arctic Insect Life Cycles

Because of the brevity of summer warmth in the Arctic, many insects are unable to complete their entire life cycle from egg to larva to pupa to adult in a single summer. They are forced to overwinter in one or more stages of their life cycle. Different groups of insects have different life cycle patterns. The life cycle of 23 ground beetle species (Carabidae) of dry and mesic, open tundra habitats in the Tromsø region of northern Norway was studied by Andersen (2013), who examined the reproductive period and the seasonal occurrence of larvae, teneral, and fully hardened adults. Teneral are the earliest stage of adult insects, immediately after molting. For a brief interval, their exoskeleton is soft and immature in coloring. He found that nine species breed in spring to early summer, have summer larvae and hibernate exclusively as adults. Nine species mainly breed from June to September, and in this group the larvae as well as adults hibernate. Insect hibernation is known as diapause. This is a period of suspended development in insects, during unfavorable environmental conditions. The beetles that undergo diapause as both adults and larvae frequently seem to need more than 1 year to complete their development. The species with winter larvae start to reproduce much earlier in the year in Northern Norway than do populations living farther south. Eggs and/or pupae as well as larvae and adults of three further species hibernate. Andersen estimated that the tiger beetle *Cicindela campestris* needs at least 3 years to fulfill its development in Tromsø. Arctic ground beetles are much more likely to have overwintering larvae than temperate zone species.

Fielding and Defoliart (2010) studied embryonic developmental rates in northern populations of grasshoppers (Table 2). In cold climates, these insects spend two winters in the egg stage. Prediapause and postdiapause embryonic developmental rates were measured in the laboratory over a wide range of temperatures for two species of cold-adapted grasshoppers: *Melanoplus borealis* and *Melanoplus sanguinipes* (Fig. 4). The authors fit a model to the data and used it to predict dates of egg hatch in the spring and prediapause development in the fall under different temperature regimes. Actual soil temperatures were recorded at several locations over 5 years. Laboratory environmental chambers were used to simulate climate warming, so that 2°C, 3°C, or 4°C were added to each hourly recorded temperature in the insects' natural habitat. The results suggest that a 2°C, 3°C, or 4°C increase in soil temperatures will result in eggs hatching 3, 5, or 7 days earlier than predicted, respectively (Table 2). An increase of 3°C would be required to advance prediapause development enough to allow for a portion of the population to complete its life cycle in 1 year. This 1-year life cycle in insects is called univoltine. In another experiment, 2°C and 4°C were subtracted from observed temperatures. The authors determined that a 4°C decrease in winter soil temperatures could delay hatching by 8 days.

Table 2 Observed median hatch dates and predicted hatch dates of *Melanoplus borealis* based on soil temperatures and developmental rates from laboratory

Years	Observed median hatch date	Predicted median hatch date	Differences in predicted hatch date (days) with altered temperature regime			
			−4° C	−2° C	+2° C	+4° C
2000	4 June	31 May	+8	+4	−4	−6
2002	28 May	30 May	+7	+3	−3	−5
2004	29 May	23 May	+8	+4	−3	−5
2006	1 June	3 June	+8	+4	−3	−6
2008	5 June	10 June	+8	+4	−3	−6

After Fielding, D.J. and Defoliart, L.S. (2010). Embryonic developmental rates of northern grasshoppers (Orthoptera: Acrididae): Implications for climate change and habitat management. *Environmental Entomology* **39**, 1643–1651.

*Melanopus borealis**Melanopus sanguinipes*

Fig. 4 Two species of grasshoppers found in northern North America: *Melanopus borealis* and *M. sanguineus*. Photo of *M. borealis* by Robert A. Pfadt (2009). Photo of *M. sanguineus* by Kerry Matz, used with permission.

Danks (1981) presented an excellent review of this topic. Northern arthropods normally take one or more years for a generation. The proportion of species taking longer than 1 year to complete their life cycle increases with latitude. Relatively few high arctic species complete their life cycles in a single year. The duration of the life cycle also depends on habitat, since relatively rapid development is possible in warm microhabitats, such as inside plants or in warm shallow ponds. Slow life cycles can be attributed to reduced resources of heat and food. The fecundity of arctic insects tends to be low, with species from many insect groups producing only one or a few eggs per year. This low egg production is apparently due to a combination of factors, including short, cold summers, and poor food supply. In northern regions where food supply is abundant, either more eggs are laid per clutch, or eggs are laid two or three times during the summer.

Research in Iceland showed that there were two generations per year in the midge *Tanytarsus gracilentus*, a species that in the low arctic is univoltine, but in the high arctic takes several years to develop. The springtail *Hypogastrura tullbergi*, which took 3–5 years to develop in the High Arctic, completes a generation in only 2 months to a year in temperate regions. Some remarkably long life cycles have been demonstrated for various insect groups in the Arctic. Typical estimates are as follows. For arctic midges (Chironomidae), 2–7 years; for arctic crane flies (Tipulidae), 4 years or more; in northern horseflies (Tabanidae), at least 3 years; for high arctic tussock moths of the genus *Gynaephora*, 3–5 years; for high arctic scale insects (Coccidae), up to 5 years; for high arctic blow flies (Calliphoridae), 1–2 years; for high arctic spiders, up to 7 years. Life cycles typically are longest in larger insects.

Hågvar et al. (2017) studied the life cycles of nine species of cold-adapted ground beetles during a 2-year period in Norway. A 2-year (biennial) life cycle was documented for three of these species, based on the simultaneous hibernation of larvae and adults. In at least one species (*Patrobis septentrionis*), both larvae and adults showed considerable activity in winter, beneath the snow. The most cold-adapted ground beetle of the Northern Hemisphere, *A. alpina* and a near-relative species, *Amara quenseli* had larval hibernation.

The data indicated that some individuals might hibernate a second time and thus experience two egg-laying seasons.

Berman and Leirikha (2018) published a study of cold-hardiness in ants (Formicidae) that live in the coldest region of the Northern Hemisphere, in northeastern Siberia. Whereas nearly all ants in the temperate zone produce at least one brood of offspring per year, in northeastern Siberia the ant larvae develop very slowly, taking 2–3 years to complete this part of their life cycle. However, the limited super-cooling ability in the ants of the genus *Formica* prevents them from living in regions where winter air temperatures are colder than about -25°C , including the upper reaches of the Kolyma River and even more so in the upper reaches of the Yana and Indigirka rivers, where winter temperatures drop below -50°C .

A comparison of trapped adults of *A. alpina* and *Cymindis vaporariorum* in 2007 and 2008 showed that summer temperature regime plays a significant role in the timing of adult emergence and entering into diapause (Fig. 5). In 2007, both species had active adults on the landscape as early as May 30. Average monthly temperature rose from 4°C to 9.8°C between May and June that year. In 2008 the earliest appearance of adults for both species was during the interval of June 28–July 10. Average June temperatures that year were 7.8°C (Fig. 6). However, summer warmth in 2007 apparently ended by the end of August. Average August temperatures

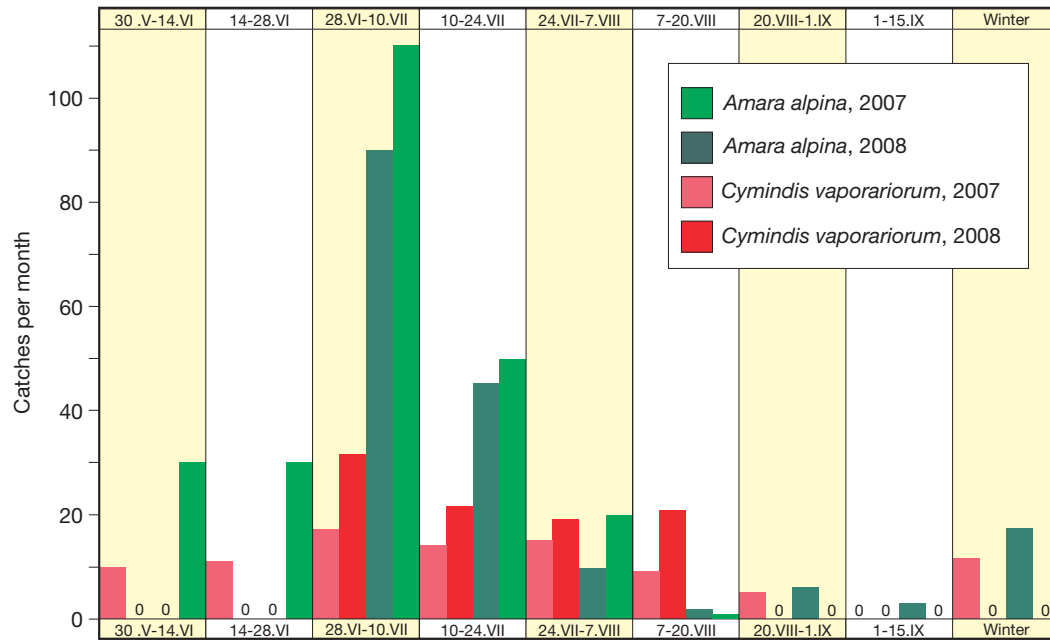


Fig. 5 Record of captured specimens of *Amara alpina* and *Cymindis vaporariorum* in the Finse region of Norway during the summers of 2007 and 2008. Data from Hågvar, S., Steen, R., Flø, D. (2017). Ecology of alpine carabid beetles (Coleoptera, Carabidae) in a Norwegian glacier foreland, with a special focus on claw wearing to indicate relative age. *Norwegian Journal of Entomology* **64**, 82–111.

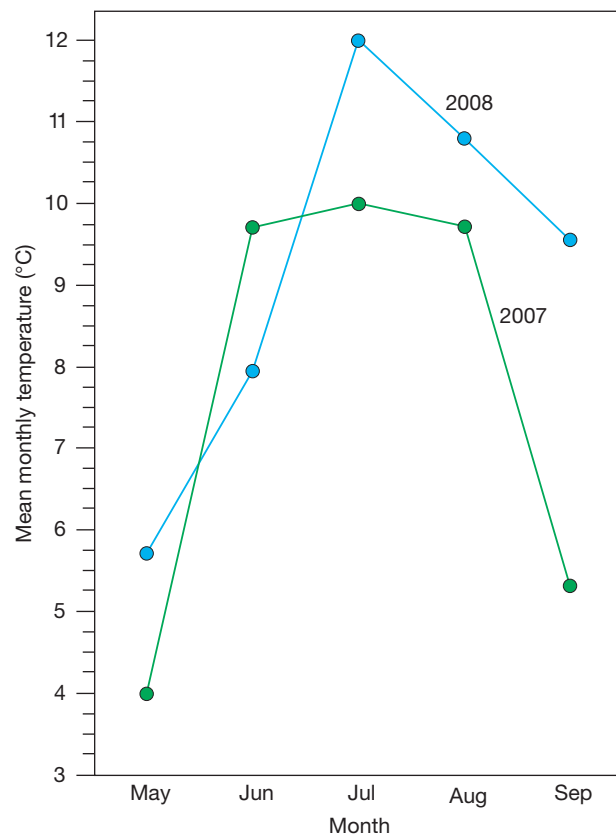


Fig. 6 Mean summer monthly temperatures for the Finse, Ulvik region of Norway for 2007 and 2008. Data from the Norwegian Meteorological Institute (2018). *Climate statistics, Finse, Ulvik (Hordaland)*. <https://www.yr.no/place/Norway/Hordaland/Ulvik/Finse/climate.month09.html> (Visited August 1, 2018).

that year were 9.8°C, but fell precipitously to 5.3°C by September (Norwegian Meteorological Institute, 2018). In 2008 *A. alpina* remained active through the first 2 weeks of September, when the average temperature was above 9.5°C. Both species had a few individuals captured during winter months, most likely emerging from the snow during brief warm intervals.

The timing of events in an organism's life cycle is known as its phenology. The phenology of arctic insect life cycles tends to be pushed ahead in spring. For instance, arctic midges emerge as adults even before the lakes where they over-winter as larvae are ice-free. Soil-dwelling insects are able to remain active after the beginning of freezing temperatures because of the latent heat in the soil.

Melanism and Body Size

Most northern insects are darker in color and smaller in size than southern species. In species that have ranges that include both temperate and arctic regions, there are population differences. Northern specimens of these species are both smaller and darker than southern specimens. Melanism is an adaptive response that makes the most of limited solar warming in cold regions. Absorption of solar energy by the exoskeleton warms the insect's internal organs, facilitating activity at lower temperatures. The effectiveness of melanism is demonstrated by the fact that it is present in all genera of arctic butterflies, in addition to a reduction in size and basking behavior. Another example of melanism concerns arctic ground beetles. All of the species of arctic ground beetles in the *Cryobius* group of the genus *Pterostichus* have a black integument.

In larger insects, melanism is often combined with hairiness of the integument. Shiny hairs permit the entry of short-wave radiation but prevent the loss of heat accumulated by the dark surface of the insect. This heat would otherwise escape through the emission of long-wave radiation. This is essentially a biological example of the greenhouse effect. Most arctic insects are small by comparison with insects that live in warmer regions. For instance, the average body length of the 27 species in the northern *Cryobius* group of *Pterostichus* is 6.8 mm, compared to the overall average length of 12.4 mm for the 55 *Pterostichus* species from the temperate and boreal regions of North America (data from Lindroth, 1966). The exceptions to this are some large-sized arctic caterpillars, adult butterflies and bumble bees. All of these spend their time in or near protected microhabitats such as flowers and plant cushions. They are also dark colored and hairy, enabling them to trap solar energy.

Brachyptery

Brachypterous insects have very reduced wings, so that they are unable to fly. This is a common feature of some arctic insect groups. For instance, all of the *Cryobius* species of the genus *Pterostichus* are brachypterous (Lindroth, 1966). This structural modification has also been observed in arctic stoneflies, chironomid flies (midges), other beetle families, and ichneumon wasps (Danks, 1981). There are several theories concerning the reason for arctic insect brachyptery. In regions dominated by low summer temperatures, insect flight may be quite restricted. This is because flight muscles need to reach a certain temperature before they can function. If the necessary air temperatures are rarely or never reached in a given region, then winged flight becomes impossible, and wings become useless. The development of wings requires metabolic energy. If wings do not confer any advantage, then natural selection would favor flightless forms, because the latter may have more energy available for other life processes, including reproduction. Beetles have elytra, or wing covers, that must be raised before the flight wings beneath can be used. In flightless beetles, the elytra are often fused together, forming a more-or-less solid cover over the abdomen that allows heat to accumulate inside the abdominal cavity.

Behavioral Adaptations

Those arctic insects that do fly generally fly very close to the ground, where heat reflected from the soil creates a warm microhabitat. Resting adult insects often select particularly warm sites, such as locations with dark surfaces, as well as inside the heads of flowers that have a parabolic shape to trap solar energy. Basking in the sunshine is an important behavior for flying insects, as they need to warm their flight muscles before they can fly. Basking has been observed in the Antarctic midge, *B. antarctica*.

Temperature thresholds for development and activity are commonly very low in Arctic species. Development of many species of midges and mosquitoes has been observed taking place throughout the winter, even when the lakes remain ice-covered and the lake water temperature is close to freezing. Tundra species of shore bugs (Saldidae) and crane flies (Tipulidae) are active at 0.5°C (Danks, 1981).

Dietary Adaptations

Because of the short growing season and paucity of insect food resources, especially in the High Arctic some insect groups that are carnivorous in the lower latitudes have species that are either omnivorous or even herbivorous in the Arctic. As shown in Table 3, increasing latitudes in Canada are correlated with increasing omnivory and herbivory of ground beetle species (Ernst and Buddle, 2015). At Banks Island in the Canadian High Arctic, 69% of ground beetle species are omnivorous, while less than 1/3rd are strict predators. The most commonly found omnivore in the High Arctic is the opportunistically predacious granivore, *A. alpina*.

Table 3 Dietary composition of ground beetles and rove beetles in latitudinal transect of northern Canada

Locality	Latitude	Ecological zone	% Carnivores	% Omnivores	% Herbivores
Moosonee, ON	51.28°N	North Boreal	95	5	0
Schefferville, PQ	54.76°N	Subarctic	80	16	4
Churchill, MB	58.74°N	Subarctic	88	7	5
Yellowknife, NWT	62.52°N	North Boreal	81	6	12
Tombstone Mountains, YT	64.61°N	North Boreal	94	4	2
Norman Wells, NWT	65.29°N	Subarctic	84	2	14
Kugluktuk, NU	67.78°N	Subarctic	76	22	2
Cambridge Bay, NU	69.12°N	High Arctic	36	61	3
Banks Island, NWT	73.22°N	High Arctic	31	69	0

Data from Ernst, C.M. and Buddle, C.M. (2015). Drivers and patterns of ground-dwelling beetle biodiversity across Northern Canada. *PLoS One* **10**(4), e0122163.

In contrast to this, in boreal forest localities, such as Moosonee, Ontario, 95% of ground beetle species are carnivorous. In the High Arctic, the dietary flexibility of this otherwise predaceous beetle family gives them a better chance to survive in an environment that has only meager animal food resources.

Selection of Overwintering Sites

All arctic arthropods on land or in shallow waters are exposed to freezing temperatures for much of the year. Nevertheless, even in permafrost areas, overlying snow insulates against air temperatures that are lower still. Good protection beneath snow is available at tree line, and adults of the mosquito *Culiseta alaskaensis*, hibernating for example in snow-covered clumps of grass, experience temperatures no lower than -7°C to -9°C , and appear to lack cryoprotectants. Bottom sediments in shallow arctic ponds likewise are warmer than the air.

Pond temperatures of about -20°C occur in the coldest month at Barrow, Alaska (71°N) when mean air temperatures were about -33°C . Such temperatures probably persist for several months, and can be compared with temperatures not below -15°C in shallow ponds at Churchill (59°N) and, by analogy with soil measurements with temperatures of about -30°C at Lake Hazen in the Canadian High Arctic (82°N). Chironomid larvae in ponds at Barrow were killed by temperatures below -18°C . Larvae of the Antarctic midge *B. antarctica* did not survive temperatures much lower than -15°C (Baust and Edwards, 1979).

Oviposition (egg laying) of overwintering eggs on withered rather than green leaves by female butterflies, provide for a more sheltered winter site. Ovipositing high arctic mosquitoes select sites that have clear advantages for early spring egg hatch, and selection does not necessarily relate to winter conditions.

Some arctic species hibernate fully exposed on ridges swept free of snow by wind. The ground beetle *Amara glacialis* has been observed hibernating in small grooves excavated in the sand (and mainly prepared by the end of August), rather than penetrating to deeper layers. Such habits seem to correspond with the earlier amelioration of exposed sites in spring. Some other features of overwintering sites are not related to temperature. For example, the tremendous spate in spring in northern streams may carry away organisms that have overwintered in the substrate. However, this potential instability might be mitigated in arctic streams, except in the most superficial sites, by the fact that most of the run off would take place while organisms were still safely frozen into the stream bed. As a general rule, the overwintering stage is inactive (e.g., eggs) only in species of fairly stable habitats; then the overwintering site is selected by an earlier life stage. In many other species an active overwintering insect itself selects the overwintering site.

Only freeze-resistant and desiccation-resistant mosquito eggs can overwinter in the Arctic. These insects must complete their life cycle each year. Bumblebee colonies must develop sufficiently each summer to produce sexual forms, as only queens overwinter. Apparently most arctic insects overwinter in their larval stage. Very few insects overwinter as pupae in the High Arctic. On the contrary, the pupal phase is usually very short in arctic insects, especially species that pupate with the onset of spring.

It is well known that air temperature records in the Arctic fail to accurately describe the thermal conditions of sheltered microhabitats. This is particularly the case during winter, when snow cover insulates terrestrial habitats from extreme air temperature fluctuations. Surprisingly few studies have been done on the cold hardiness of High Arctic insects. One exception is a study carried out in Svalbard by Convey et al. (2015). They assessed the survival of High Arctic soil invertebrate communities contained in soil and vegetation cores when exposed to winter temperature variations. The overwintering temperatures the invertebrates experienced were manipulated by deploying cores in locations with varying snow accumulation: No Snow, Shallow Snow (30 cm) and Deep Snow (120 cm) (Fig. 7). Winter air temperatures at the study site fluctuated between -3°C and -24°C , and the No Snow soil temperatures matched air temperatures closely. Soil temperatures varied less under 30 cm of snow, and did not decrease below -12°C . Temperatures beneath deep snow were even more stable and did not decline below -2°C . Surprisingly, there were no clear differences in survival of the invertebrate fauna between the three sets of environments. The survivors included several groups of soil mites, spiders, springtails (Collembola), mosquito larvae, and beetles. The study demonstrated previously

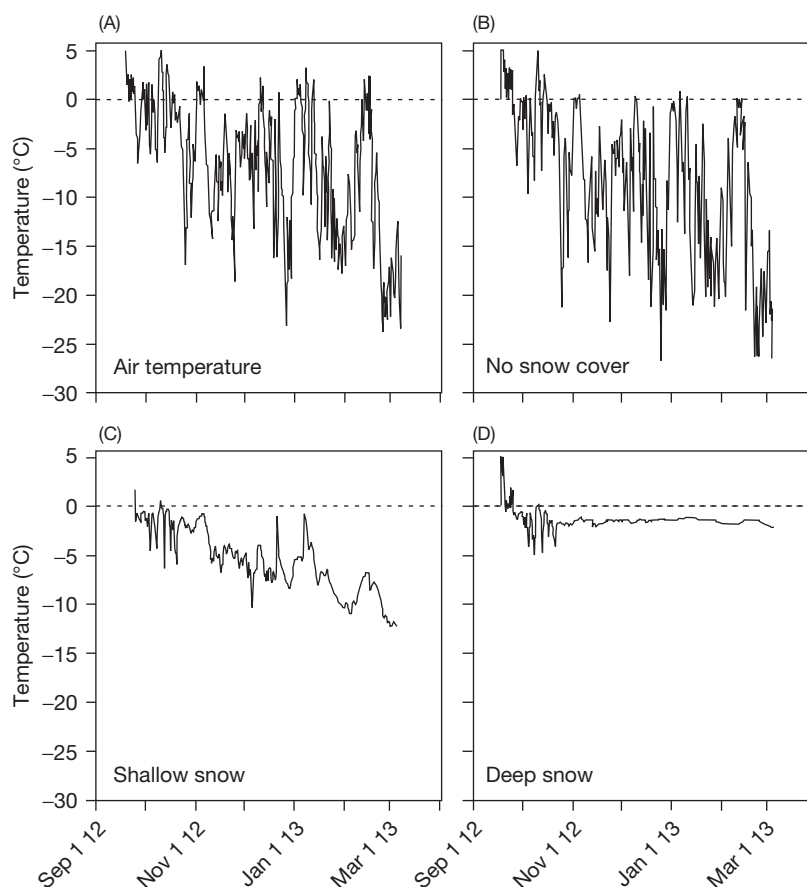


Fig. 7 Soil (2 cm) and air temperatures at Endalen study site, Svalbard, from September 2012 to March 2013. (A) Air temperatures recorded at Svalbard Airport; (B) Soil temperature with no snow cover; (C) Soil temperature beneath shallow snow; (D) Soil temperature beneath deep snow. Svalbard airport temperature data from Norwegian Meteorological Institute. Figure after Convey, P., Abbandonato, H., Bergman, F., et al. (2015). Survival of rapidly fluctuating natural low winter temperatures by high Arctic soil invertebrates. *Journal of Thermal Biology* **54**, 111–117.

undocumented tolerance of extreme cold temperatures for the spiders, mosquitoes, and beetles. These invertebrates were able to withstand temperatures as low as -24°C , as well as the series of the rapid, large scale changes of temperature. The research suggests that most of these taxa are highly cold tolerant.

Cold-Temperature Physiology

Cold-adapted insects are able to function at temperatures near freezing because of their unique physiological adaptations. Their body chemistry is geared to function at temperatures near or below freezing. For instance, coordinated neuromuscular activities have been observed in the cold-adapted ground beetle, *Pterostichus brevicornis*, at temperatures as low as -12°C . In cold-acclimated beetles, motor nerve fibers showed six different activity types, compared with only two types in warm-acclimated beetles. Indeed, feeding and ovarian development have been reported in these beetles during February, when temperatures were still well below freezing. The metabolism of cold-adapted insects has been observed to function at rates similar to those of temperate-zone insects living in moderate temperatures. Cold-adapted insects have evolved “cold-adapted” enzymes that facilitate chemical reactions at low temperatures (Georlette et al., 2004). Enzymes are organic catalysts, and the package of enzymes in cold-adapted insects have a high catalytic efficiency. However, this efficiency comes at a price: their effectiveness breaks down at higher temperatures. One might be tempted to think that cold-adapted insects would thrive in the kind of warm temperatures experienced in the temperate zone, but this is not the case. Because cold-adapted metabolism is facilitated by enzymes that work *only* at low temperatures, arctic insects exposed to temperatures above about $15\text{--}20^{\circ}\text{C}$ often die because of metabolic failure. Specifically, the weak stability of these enzymes at even moderate temperatures causes them to become ineffective and even break down (Georlette et al., 2004). Cold-adapted insects produce enzymes that have a specific activity at low temperatures that is up to tenfold higher than the enzymes in warm-adapted insects. This is the principal physiological adaptation to cold at the enzyme level. It compensates for the otherwise inhibitory effect of low temperatures on chemical reaction rates, providing the insect with sufficient metabolic activity to carry out its life cycle in frigid temperatures.

Recent studies have examined the unique aspects of metabolic regulation and cell preservation that facilitate natural cold hardiness. Because cold-hardy insects seek shelter beneath the surface (i.e., underneath snow cover, in frozen mud, under piles of plant debris), their access to atmospheric oxygen becomes limited. Furthermore, insects living in Polar Regions survive the winter either in their egg stage, or as overwintering larvae or adults that undergo diapause. Insect metabolism requires oxygen, but because environmental oxygen is limited or unavailable to overwintering insects in cold regions, they must be able to cope with anoxia. Oxygen requirements fall as insect metabolic rates slow during diapause. Winter survival of cold-adapted insects is enhanced by active suppression of energy-expensive cell functions, including mitochondrial activity. However, survival in oxygen-poor or oxygen-starved environments does not include the suppression of all biochemical functions. There is up-regulation of the hypoxia inducible factor, HIF-1, to coordinate responses that provide hypoxia protection and prevent loss of hemolymph flow to vital organs. This involves increased cellular response to molecular stimulus due to an increase in the number of receptors on the cell surface. Overall, the studies summarized by Storey and Storey (2010) show that cold hardy insect species use a suite of dynamic responses to modulate cellular metabolism in response to seasonal, low temperature, and freeze/thaw cues.

Acclimation and Cooling Rates

The difference between summer and winter temperatures is quite large in many parts of the Arctic and Antarctic. On exposed surfaces, temperatures can vary by as much as 100°C between seasons. A few invertebrates, such as the nunatak-inhabiting springtail, *Cryptopygus sverdrupi*, remain in a cold hardy state all year round. However, most polar insects acclimatize to the cold in the weeks just before winter (Everatt et al., 2015). They prepare themselves physiologically and improve their low temperature tolerance. As autumn progresses, insects use environmental signals such as shortening day lengths and gradually decreasing temperatures to trigger seasonal cold-hardening adaptations. These mechanisms include dramatic changes in biochemistry, cell function and gene expression that permit improved cell function and viability at low temperature (Teets and Denlinger, 2013). Rapid cold hardening mechanisms include dramatic changes in biochemistry, cell function and gene expression that provide improved cell function and viability at low temperature.

Rapid transitions from summer to winter can leave polar insects unprepared. If they fail to achieve cold-hardiness in time, the survival of freeze-tolerant species is threatened. Such quick seasonal transitions also raise the supercooling point of freeze-avoiding species, and reduce the capacity of these animals to survive chilling injuries. However, many Arctic insects have developed a survival mechanism that allows them to cope with rapid temperature drops. This is called rapid cold hardening. This response allows insects to adjust quickly to falling temperatures within a few days or less. However, relatively little is known about the physiological mechanisms that lie behind rapid cold hardening.

DeJong and Saastamoinen (2018) studied the development of cold tolerance in a population of the Glanville fritillary butterfly (*Melitaea cinxia*) (Fig. 8) in the Åland Islands of Finland. These islands lie at the northern limit of the species' range. They measured



Fig. 8 Photo of the Glanville fritillary butterfly (*Melitaea cinxia*), used by permission of Peter Hunt.

chill coma recovery (CCR) following two temperature treatments during late larval and pupal development. When insects are cooled sufficiently, they suffer an initial loss of neuromuscular function. This is called chill coma. It is caused by decreased exchange of molecules into and out of cells. This depresses the electrochemical signals to muscle cells, causing them to lose function. The adaptation and acclimation responses that allow some insects to tolerate low temperatures involve multiple factors, several physiological systems, and biochemical adjustments (Overgaard and MacMillan, 2017). The ability to recover from chill coma is a well-established proxy for cold tolerance at the beginning of the adult stage. Then they tested the effects of both thermal treatments during the adult stage on late adult CCR. Their results demonstrate that cooler temperatures during the insect's development into an adult lead to reduced cold tolerance in the early adult stage, whereas cooler conditions during the adult stage lead to increased cold tolerance. This suggests that adult acclimation is key to this butterfly's survival in cold regions.

Freeze Tolerance and Freeze Avoidance

Insects have evolved various adaptations to cold, from avoidance of freezing temperatures to tolerance to freezing. These topics are covered in-depth in Denlinger and Lee (2010). The ability to acclimatize to cold conditions is determined by natural selection for cold adaptation. There are two physiological mechanisms by which cold-adapted insects survive freezing temperatures. The first of these is freeze-avoidance; the other is freeze tolerance. Freeze-avoiding insects range across both the Arctic and Antarctic regions, where they outnumber freeze-tolerant species in most cases. These insects can be separated into four different groups (Everatt et al., 2015). These include true freeze-avoiding taxa, for which their lower lethal temperature equals the supercooling point. There are also a group of chill-tolerant taxa that show minimal pre-freeze mortality, as well as chill-susceptible taxa that die well above their supercooling points. Finally, there are opportunistic survival taxa that are unable to survive below their developmental threshold.

For insects inhabiting cold environments, resistance to freezing temperatures allows them to occupy extremely cold regions. Most cold hardy insects develop freeze avoidance mechanisms because the indiscriminate formation of ice inside the body is lethal. The development of ice nucleators and antifreeze proteins are of critical importance for cold-hardy insect survival in winter. They survive at low temperatures by removing ice nucleating agents from their body fluids that could potentially cause spontaneous internal freezing. They also accumulate low molecular weight compounds (glycerol or other polyols) in such high concentrations that their bodies remain unfrozen, even at temperatures as low as -40°C to -60°C . Thus, they overwinter in a super-cooled state, stabilized by the production of internal antifreeze compounds. Supercooling is principally achieved via three processes, and is biochemically simpler than freeze tolerance. The first is the removal of ice nucleating agents. Another method of prohibiting ice formation inside freeze-avoiding insects is the accumulation of antifreeze proteins, as well as the production of polyols (organic compounds with multiple hydroxyl groups), sugars and amino acids. Together, these chemical compounds serve both to protect insects from freezing and to enhance their metabolic functions at lower temperatures.

Supercooling points (SCP, nucleation temperature, or crystallization temperature) of insects and other terrestrial arthropods vary greatly, from -2°C to -100°C or lower (Duman et al., 2010). Supercooling is affected by a number of factors, including the volume and water content of the organism, and the ability of the body surface to prevent inoculative freezing by external ice. Freeze-tolerant species often exhibit high SCPs (above -10°C) and have selected for extracellular ice nucleators, while freeze-avoiding insects generally have selected against ice nucleators and for antifreezes, allowing them to supercool below ambient temperatures to which they are exposed over the winter. Protein ice nucleators limit supercooling by organizing water into an ice-like structure, the embryo crystal that promotes freezing at a temperature higher than that where ice would otherwise form. Experiments have shown that this strategy lowers the supercooling point of bodily fluids by up to 20°C in some insects (Everatt et al., 2015).

Freeze-tolerance is another vital survival mechanism for insects subject to long-term exposure to subfreezing temperatures. This tolerance allows insects to survive through the use of selective internal ice formation. This induced freezing takes place at temperatures just below the freezing point of water (-3°C to -10°C) (Everatt et al., 2015), in a controlled manner that minimizes cell damage. Experiments have shown that this strategy lowers the supercooling point of bodily fluids by up to 20°C in some insects. The vast majority of freeze-tolerant insects restrict ice formation to internal body compartments outside their vital organs. This is chiefly done through the accumulation of ice-nucleating agents, including specialized proteins, food particles, crystalloid compounds, and even microorganisms. All of these act as locations of water molecule aggregation. By accumulating these agents in the hemolymph (insect blood) and gut, as well as in other tissues, ice formation is encouraged to take place outside of cells. At near-freezing temperatures, ice crystal growth is relatively slow, allowing time for water to be released from cells and join the newly formed ice crystals. Cellular fluids (cytoplasm) therefore become more concentrated and cell walls are less susceptible to splitting open because of water freezing inside them. The strategy is most often found in regions that experience extremely low winter temperatures, such as the Arctic and continental boreal regions.

Freeze-tolerant insects also produce antifreeze proteins and/or antifreeze glycolipids. These compounds stop the expansion of large ice crystals and instead promote the growth of many small crystals that do less damage to tissues. However, these compounds cannot prevent all cellular damage from ice, so freeze-tolerant insects also accumulate additional antifreeze compounds, such as polyhydric alcohols, glycerol, sorbitol, and trehalose. Within the cell, these compounds stabilize proteins and membranes, and prevent tissue freezing.

Nevertheless, freeze tolerance poses many challenges to the insect. Freezing can cause cellular dehydration and mechanical damage. As discussed above, Existence at temperatures below 0°C greatly inhibits metabolic processes. While freeze-tolerant insects accumulate many potentially protective molecules, the mechanisms underlying freeze tolerance have not yet been fully explored (Toxopeus and Sinclair, 2018). It is thought that freeze-tolerant insects survive the winter by controlling the quality and quantity of

ice that forms in their bodies, by preventing or repairing cell damage, by managing biochemical processes while frozen and while thawing, and by restoring their physiological processes after their bodies have thawed (Toxopeus and Sinclair, 2018).

Several species of insects combine both strategies. Insects of this kind are able to super-cool and at the same time be tolerant to freezing. Such insects have been found in Alaska, Canada, and Siberia. The molecular basis of this combination of properties remains unknown.

Desiccation Tolerance

An ability to tolerate water loss is crucial for the survival of polar insects that are less resistant to desiccation. Antidesiccation adaptations have a good deal in common with freeze-avoidance, including the production of polyols and sugars. Soil-dwelling insects and many immature stages of above-ground species spend most of their time in the soil. These must cope with soil ice during winter. Most of these insects have only two options for survival: either tolerate internal freezing or dehydrate. In frozen soil, there is a strong tendency for ice outside the insects' bodies to draw the liquid water out of their bodies, causing desiccation of tissues (Holmstrup, 2015). A cold tolerance mechanism that retards this process is called cryoprotective dehydration (CPD). Utilization of this protective mechanism requires an insect to withstand substantial dehydration of its bodily fluids. However, CPD is essentially a freeze-avoidance strategy, and the associated physiological traits are essentially the same as those found in freeze tolerance. Dehydration virtually eliminates the risk of tissue ice formation, ensuring survival in frozen soils. Thus, winter survival of soil-dwelling invertebrates depends more on dehydration than on supercooling. However, cryoprotective dehydration can be slow, so some supercooling capacity is needed in its initial phases (Sørensen and Holmstrup, 2011).

Case Studies of Insect Cold-Hardiness

In a study done in the Yakutia region of northeast Russia (Li, 2016), the vast majority of studied beetle species were found to be freeze tolerant (Fig. 9). The Yakutian climate is extremely harsh, even by Siberian standards. The coldest regional temperatures are below -64°C , and the long winters have sustained temperatures between -47°C and -55°C . A total of 30 insect species were investigated (Table 4), and 93% were found to be freeze tolerant. Among 22 studied species from 8 beetle families, only one, the boreal longhorn beetle *Rhagium inquisitor*, was found to exhibit freeze avoidance. In addition to beetles, all studied species flies (Diptera) were found to be freeze tolerant. Only one species of Lepidoptera, a noctuid moth, *Apatele psi*, was identified as freeze avoiding. The goat moth, *Cossus cossus*, was the only species in the study that could switch strategies between freeze avoidance in northern

Europe to freeze tolerance in Yakutia. Nearly all the insect species in Li's study were found to take shelter in thermally buffered habitats during winter.

In the coldest region of the Northern Hemisphere, the region of northeast Siberia known as the "Pole of Cold," the resident insect fauna is regularly subjected to extremely low temperatures and very long winters. Here, average January temperatures run as low as -50°C , and absolute minimum temperatures have been recorded at -70°C . Freezing temperatures may persist from October to

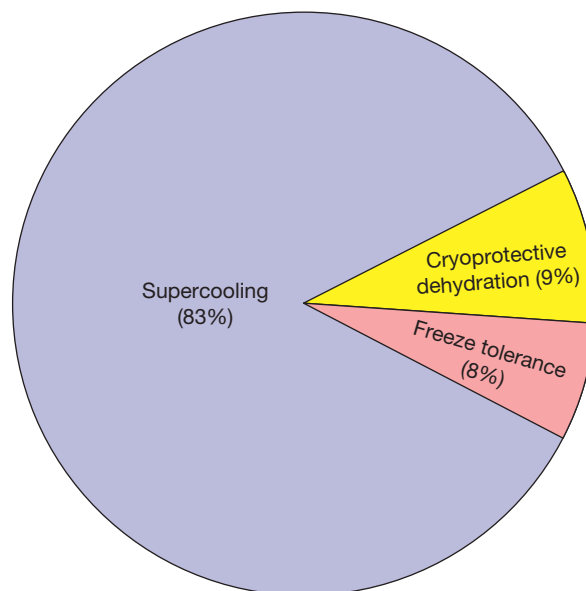


Fig. 9 Percentage composition of cold adaptations of beetles living in the Yakutia region, northeastern Siberia. Data from Li, N.G. (2016). Strong tolerance to freezing is a major survival strategy in insects inhabiting central Yakutia (Sakha Republic, Russia), the coldest region on earth. *Cryobiology* **73**, 221–225.

Table 4 Super cooling point, ice nucleating temperature, and overwintering habits of beetle species found in central Yakutia

Species	Super cooling point (°C)	Ice nucleating temperature (°C)	Overwintering habit
Carabidae			
<i>Curtonotus torridus</i> (Panz.)	-6.0 ± 1.2	-5.9 ± 0.1	Soil litter, under snow cover
<i>Amara similata</i> (Gyll.)	-7.0 ± 0.52	-6.9 ± 0.61	Soil litter, under snow cover
<i>Pterostichus eximius</i> (Moraw.)	-9.6 ± 0.24	-9.5 ± 0.91	Soil litter, under snow cover
<i>Pterostichus magus</i> (Mannh.)	-7.5 ± 1.4	-7.2 ± 0.85	Soil litter, under snow cover
<i>Cicindela nitida</i> (Wiede.)	-7.5 ± 0.8	-7.3 ± 0.23	Soil litter, under snow cover
<i>Cicindela campestris</i> L.	-10.0 ± 0.36	-9.5 ± 1.1	Soil litter, under snow cover
Elateridae			
<i>Adelocera fasciata</i> L.	-6.5 ± 1.12	-6.1 ± 0.7	Unknown
<i>Stenogostus undulatus</i> DeG.	-8.8 ± 0.65	-8.0 ± 0.67	Under pine bark, above snow line
Cerambycidae			
<i>Monochamus sutor</i> L.	-3.0 ± 0.92	-3.0 ± 1.2	Under pine and larch bark, above snow line
<i>Monochamus urusovi</i> (Fisch.)	-6.8 ± 1.54	-6.1 ± 0.45	Under pine and larch bark, above snow line
<i>Rhagium inquisitor</i> (L.)	-33.0 ± 2.15	–	Under dead conifer bark, under snow cover
<i>Acanthocinus aedilis</i> (L.)	-18.0 ± 7.58	–	Under dead pine bark, under snow cover
Tenebrionidae			
<i>Upis ceramboides</i> (L.)	-7.5 ± 2.6	-7.0 ± 0.28	Under birch bark, some above snow line
Silphidae			
<i>Silpha carinata</i> Herbst	-8.0 ± 1.3	-7.8 ± 0.89	Inside plant debris, below snow line
Chrysomelidae			
<i>Chrysolina graminis</i>	-6.9 ± 0.33	-6.5 ± 0.25	Unknown
<i>Galerucella nymphaea</i>	-7.3 ± 0.14	-7.7 ± 0.31	In soil, under snow
Curculionidae			
<i>Hylobius albosparsus</i>	-8.5 ± 1.25	-8.35 ± 1.5	Soil litter, under snow cover
<i>Ips subelongatus</i>	-9.9 ± 0.75	-9.2 ± 0.45	Sometimes under larch bark

Data from Li, N.G. (2016). Strong tolerance to freezing is a major survival strategy in insects inhabiting central Yakutia (Sakha Republic, Russia), the coldest region on earth. *Cryobiology* **73**, 221–225.

April. A study by Berman and Leirikha (2018) focused on cold-hardiness of insects and other invertebrates in this region. They found that 30 of the 37 species of insects they studied employed super cooling to survive subfreezing temperatures. Freeze tolerance and cryoprotective dehydration were more-or-less equally employed among the remaining seven species.

Part of this study focused on the cold-hardiness of Siberian ants (Fig. 10). The lowest average super cooling point (about -40°C) is characteristic of three species of ants: *Leptothorax acervorum*, *L. muscorum*, and *Camponotus herculeanus* (Fig. 11); their capacity for significant supercooling is associated with the accumulation of 16%–20% of polyols in their hemolymph. The population of the

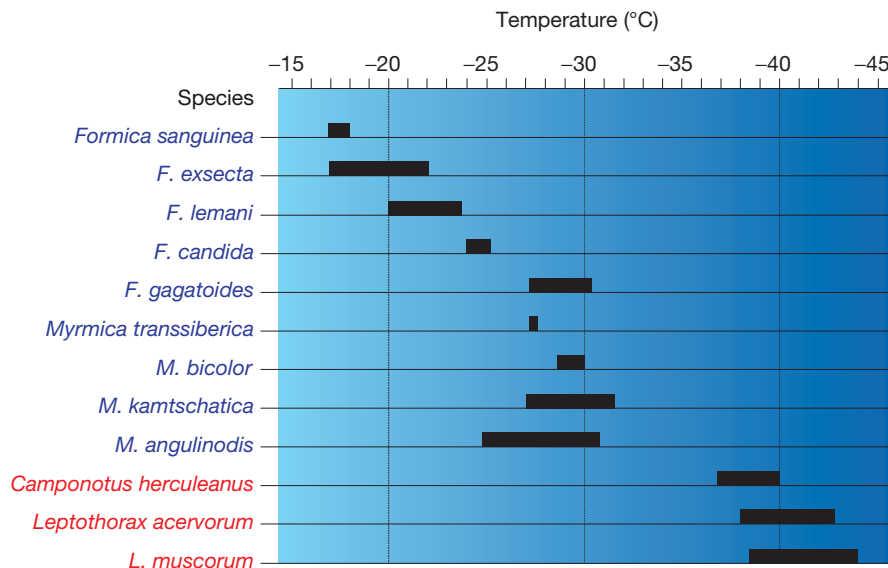


Fig. 10 Measured super cooling points (°C) of ant species from northeast Siberia. Species names shown in blue have a Palearctic distribution. Species names shown in red are Holarctic in distribution. Data from Berman, D.I. and Leirikha, A.N. (2018). The cold hardiness of mass soil invertebrates of northeastern Asia 2. The cold hardiness of soil invertebrates as adaptation to climate. *Entomological Review* **97**, 1008–1019.

*Camponotus herculeanus**Leptothorax acervorum**Leptothorax muscorum*

Fig. 11 Ant species discussed in text. Top: *Camponotus herculeanus*; Middle: *Leptothorax acervorum*; Bottom: *Leptothorax muscorum*. Photo of *C. herculeanus* by Tom Murray, used with permission; photo of *L. acervorum* by Martin Pfeiffer, used with permission; photo of *L. muscorum* by Alex Wild, used with permission.

carpenter ant, *C. herculeanus* from the upper Kolyma River basin is more cold-resistant than North American populations from the more southern and warmer boreal regions of Canada, such as Pincher Creek, Alberta, (50°N, 114°W), where the mean SCP was -28.7°C and the glycerin content was 5.8%.

In the animals with moderate cold resistance, the winter survival mechanisms are equally diverse. For the most part, they overwinter in a super cooled state with an SCP of about -30°C . The decrease in SCP in winter can also be accompanied by the accumulation of polyols and sugars, but in a smaller amount than in the first group, for instance, up to 10% in the ant *Myrmica kamtschatica*. The species that are the least resistant to cold are characterized by SCP values in the range of -17°C to -22°C . These species also have lower quantities of low-molecular antifreezes. In the ants of the genus *Formica*, cold hardiness is ensured by a highly stable super cooled state in winter.

Conclusions

The ability of insects to live in extremely cold environments is truly remarkable, and involves every aspect of their lives, from timing of events in their annual life cycles to their behavior patterns and their internal physiology. Most of these adaptations are encoded in

their DNA, and geneticists are only now starting to unravel the location and function of genes that control the processes described in this article. In the vernacular, we would say that polar insects are *hard wired* to live where they do. However, these very adaptations to cold make polar insects and other invertebrates extremely vulnerable to global warming, which is amplified at the poles. As temperatures rise, especially in the Arctic, the native fauna of the tundra will suffer and decline. As they are already living so far north, there are no more northerly places available for immigration. The rising temperatures will cause decreased fitness in cold-hardy insects, and they will also be forced to compete with more warm-adapted insects, invading from the south. Likewise, changes in the composition of high latitude plant communities, a phenomenon already documented in many Arctic regions, will disturb the balance of tundra ecosystems, including long-established plant-insect interactions. The cold-hardiness of Arctic insects, their greatest asset for survival in previous millennia, may very well become their greatest liability in the coming decades.

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Arctic Insect Distribution Patterns

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Abstract

Arctic insects are a small but noteworthy group. Out of the millions of insect species in the world, only a few thousand are adapted to withstand the rigors of Arctic climate and its short growing season. There are about 3000 insect species living in the Arctic today. There is a general trend in Arctic insect faunas: decline in diversity with increasing latitude. This trend corresponds closely with the northward decline in summer temperatures, as reflected in the mean July temperature. Diptera (flies) dominate the insect fauna of all Arctic regions.

Cold intervals saw the distributions of Arctic insects shift either southwards, or into the Beringian refuge. Warm intervals saw their expansion into recently deglaciated landscapes. This natural process has repeated itself dozens of times since Quaternary glaciations began. The fossil record demonstrates that each major climatic change brings about a new reshuffling of species into specific regions. However, Arctic insects are extremely vulnerable to the current global warming, which is amplified at the poles.

Introduction

Arctic insects are a small but noteworthy group. Out of the millions of insect species in the world, only a few thousand are adapted to withstand the rigors of Arctic climate and its short growing season. Chernov (1995) estimated that there are about 3000 insect species living in the Arctic today. But it is not possible to say exactly how many insect species live there. There are several reasons for this. First, there is a lack of knowledge of the taxonomy of poorly studied insect groups, especially the families in the orders Diptera, Hymenoptera, and Lepidoptera—that is, which species are which? Second, because the Arctic is a costly region to visit, regional collections and data on regional faunas are woefully incomplete—that is, who lives there? Third, the knowledge we do have on Arctic insect systematics is confused by the large number of incompatible synonyms used by taxonomists in Russia, North America, and Western Europe—that is, what do we call them? Russian entomology during most of the 20th century developed in isolation from that of the rest of the world, leading to multiple names being given to the same Holarctic species. There is even a difference in the terminology used to describe the biological zones of the Arctic between the Russian literature and the literature from Europe and North America (Fig. 1). The High Arctic zone of Western literature is divided into the Polar Desert Zone and the Arctic Tundra Zone in the Russian literature. The Low Arctic Zone of Western literature is divided into the Typical Tundra, Southern Tundra, and Forest Tundra Zones in the Russian literature.

The dominant distribution patterns of Arctic insects fall into three categories: Nearctic, Palearctic, and Holarctic. Nearctic species are found in Arctic North America. Palearctic species are found in Arctic Eurasia. Holarctic species are found in both the Palearctic and Nearctic regions.

Trends in Arctic Diversity

There is a general trend in Arctic insect faunas: decline in diversity with increasing latitude. This trend corresponds closely with the northward decline in summer temperatures, as reflected in the mean July temperature (Fig. 2). As demonstrated by Chernov (1995), there is a very clear decline in the number of insect species between the summer temperatures associated with the Boreal zone ($>12^{\circ}\text{C}$) and those of the High Arctic zone ($<4^{\circ}\text{C}$).

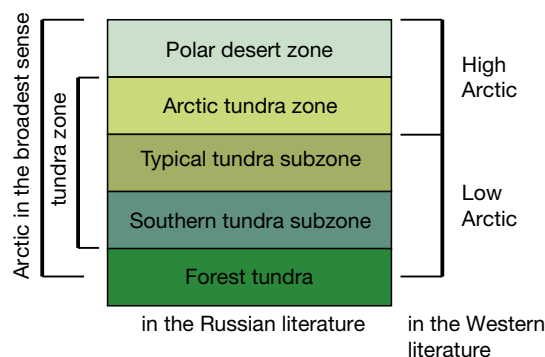


Fig. 1 Differences in the terminology used to describe the biological zones of the Arctic between the Russian literature and the literature from Europe and North America. After Chernov, Y.I., Makarova, O.L., Penev, L.D., and Khruleva, O.A. (2014). Beetles (Insecta, Coleoptera) in the Arctic fauna: Communication 1, faunal composition. *Entomological Review* **94**, 438–478.

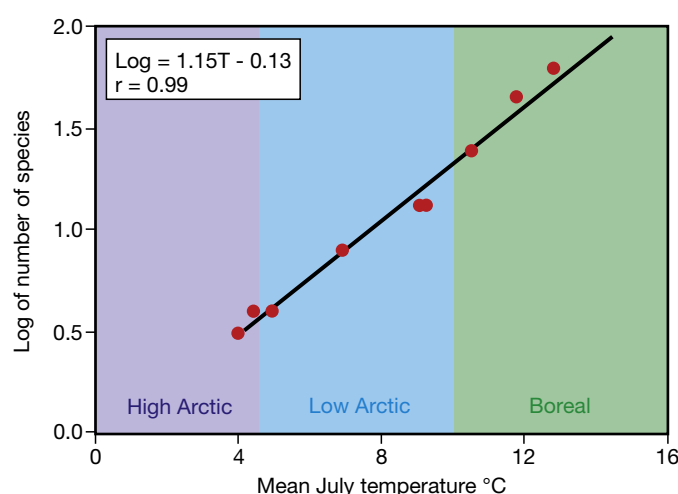


Fig. 2 Northward decline in summer temperatures, as reflected in the mean July temperature. Data from Chernov, Y.I. (1995). Diversity of the Arctic terrestrial fauna. In Chapin, F.S. III., and Körner, C. (eds.), *Arctic and alpine biodiversity: Patterns, causes and ecosystem consequences*, pp. 81–95. New York: Springer.

There are four orders of insects that dominate arctic faunas: Coleoptera (beetles), Lepidoptera (butterflies and moths), Hymenoptera (wasps and bees), and Diptera (flies). As shown in Fig. 3, the proportion of the world's insect faunas contributed by these four orders is quite different from their relative proportions in Arctic faunas. While beetles (Coleoptera) are the largest order of insects by far (more than 350,000 described species, making up almost 40% of all known insects), they comprise only 13% of the Arctic fauna, and only 2% of the High Arctic fauna (Chernov et al., 2014). The number of known species of moths and butterflies (Lepidoptera) is about 300,000. That represents about 17% of the world's insect diversity. Their numbers throughout the Arctic comprise 11% of the insect species, and their species numbers drop to 6% of the High Arctic insect fauna. The Hymenoptera are more evenly distributed in faunal diversity. The number of species worldwide accounts for 17% of insect species, including many species of ants, which are altogether lacking in the Arctic. The diversity of wasps and bees in the Arctic accounts for about 14% of insect species, and the percent composition of Hymenoptera in the High Arctic jumps to 20% of the insect fauna. The species of lice (Phthiraptera) are relatively few in most of the Arctic, except on Svalbard (Fig. 4). Finally, flies (Diptera) account for about 18% of worldwide insect species diversity, but they make up almost half of all Arctic species, and 57% of the High Arctic insect species (Chernov et al., 2014).

The general trend among Arctic insect orders is one of decline in both diversity and abundance of species from the Low to High Arctic. However, this trend does not work the same way in all insect groups. Some orders decrease in importance or even disappear at very high latitudes (e.g., Coleoptera). In other orders, species richness changes in proportion to the overall decrease in animal diversity (e.g., Lepidoptera and Hymenoptera). A third group of taxa, such as the Diptera, maintains a relatively high level of biodiversity, and their relative contribution to the whole insect fauna increases greatly at high latitudes. This peculiar feature of the arctic fauna reflects the presence of some very-well adapted groups of arctic species. This trend is expressed to differing degrees at different taxonomic levels: classes, orders, and families.

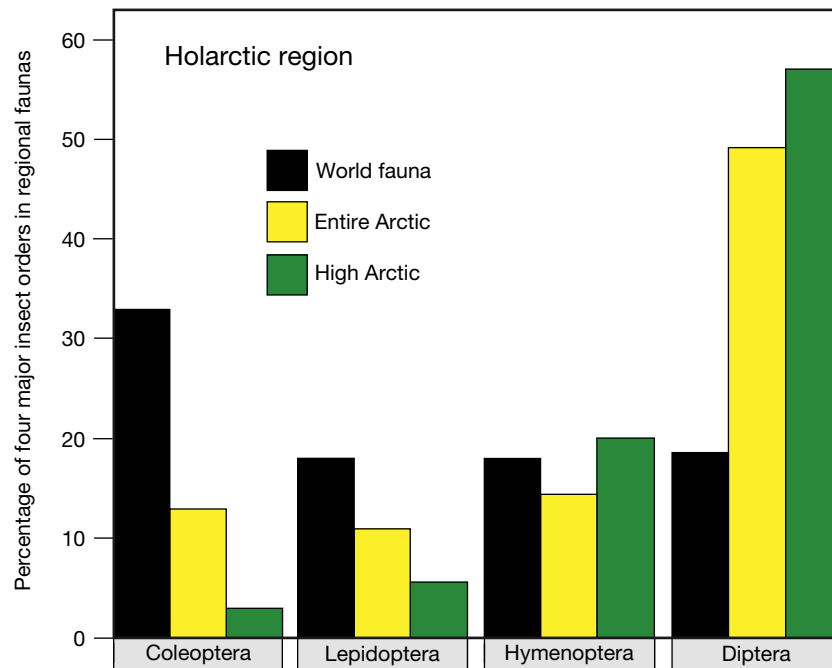


Fig. 3 Holarctic percentage composition of insect faunas from all regions, the Low Arctic and the High Arctic. Data from Chernov, Y.I., Makarova, O.L., Penev, L.D., and Khruleva, O.A. (2014). Beetles (Insecta, Coleoptera) in the Arctic fauna: Communication 1, faunal composition. *Entomological Review* **94**, 438–478.

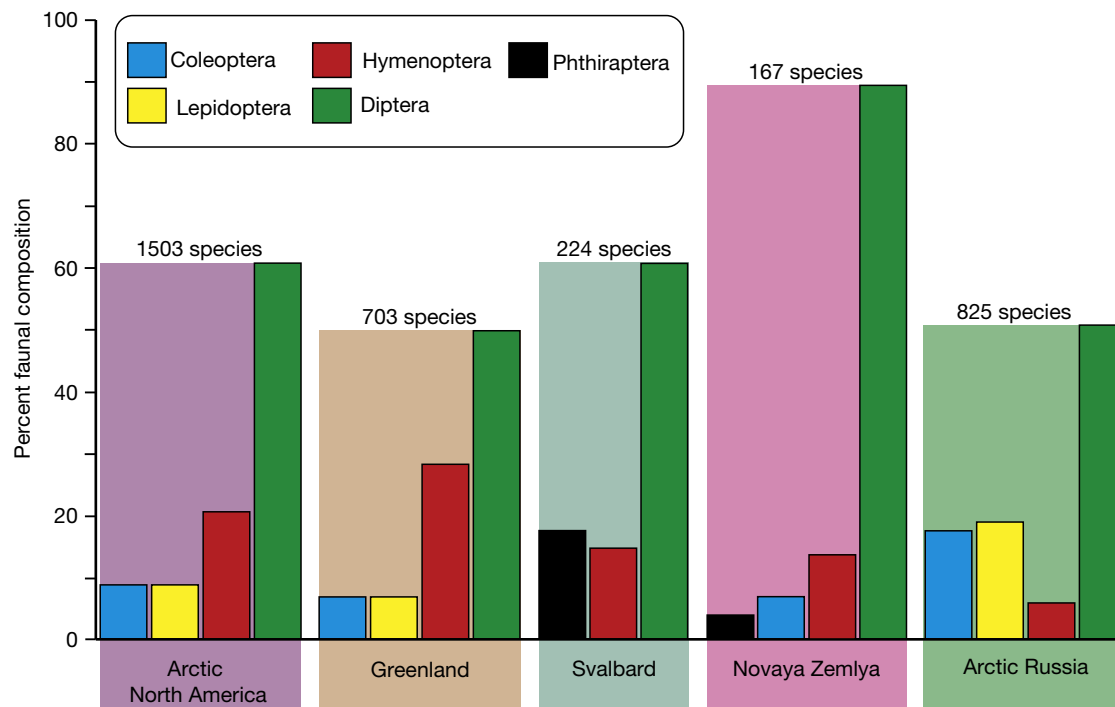


Fig. 4 Percent composition of dominant insect families in the Arctic regions discussed in text.

Russian Arctic

In the Russian High Arctic region, dominated by polar desert, many insect groups are either absent altogether, or are represented by very few species, or even by one species. For instance, in the southern shrub Siberian tundras of Taimyr and Yamal, the ground beetle (Carabidae) fauna includes about 60 species. Throughout the Russian Arctic, there are ~139 species of beetles in 18 families

(Table 1). In the Typical Tundra zone there are 15–20 species, and in the High Arctic Tundra there are 2–6 species, with only one species found in the Siberian polar desert. One interesting trend in the Arctic beetle fauna is the increasing importance of the subfamily Omaliinae in the family Staphylinidae (rove beetles) with increasing latitude. Chernov et al. (2014) commented on this trend and noted that many omaliine staphylinids are cold adapted, and are active beneath the snow on the Siberian tundra. The only rove beetle that is found today in the polar desert zone of Siberia is the omaliine, *Micralymma brevilingue* (Fig. 5).

The southernmost of the Siberian tundra zones is the Forest-Tundra, where fingers of boreal forest (taiga) extend north into the tundra. In this region, upwards of 15 insect orders are significantly represented, especially the Plecoptera (Stoneflies), Hemiptera, Coleoptera, Trichoptera (caddisflies), Lepidoptera, Hymenoptera, and Diptera. The Russian Arctic Hemiptera fauna includes more than 75 species of aphids (Stekolshchikov and Buga, 2009). One of these is *Cavariella archangelicae*, the willow—angelica aphid (Fig. 5). Its host plants alternate between willows (*Salix* spp.) and angelica (*Angelica*).

The Russian Arctic Lepidoptera fauna includes upwards of 200 species in 18 families of moths and butterflies. The most diverse of these families are the Tortricidae (38 species), Geometridae (26 species), Noctuidae (47 species), Nymphalidae (21 species), and Satyridae (22 species) (Table 2).

Much the same pattern of insect order diversity holds true in the Southern Tundra and Typical Tundra zones of Siberia (Fig. 6). The Russian Arctic Hemiptera includes the families Miridae (2 species), Pentatomidae (5 species), Acanthosomatidae (2 species), and Aphididae (2 species). Of these, only the aphids persist into the High Arctic regions. The Russian Arctic Diptera fauna includes more than 260 species in 11 families. The most important of these are the Culicidae (12 species), Syrphidae (116 species), Tabanidae (11 species), and Chironomidae (96 species) (Table 1). The Russian Arctic is the only Arctic region where Chironomidae are not the most diverse group of insects.

However, in the Arctic Tundra zone, equivalent to the High Arctic zone in the Western literature, many insect orders are only poorly represented, and the only important orders are the Plecoptera, Coleoptera, Lepidoptera, Hymenoptera, and Diptera. It is worth noting that stoneflies are part of this group, as they are not found in the High Arctic faunas of North America, Greenland or Svalbard. Fochetti and de Figueroa (2007) note that Asian stonefly diversity is much greater than that of Europe or North America. The stonefly fauna of the Russian Far East is rich and unique, including 139 species from 45 genera and 8 families, with endemism at the generic level (Teslenko, 2009). Siberian stonefly distribution patterns fall into three groups: Beringian, East Siberian, and East Asian. The nonrelict stonefly fauna apparently originated from three primary sources: a southern source on the Asian mainland by way of the Amur River Basin, a northwestern North American source from across the Bering Land Bridge, and a western source in Siberia, including a few European taxa. Three stonefly families are found in the Arctic zones of Siberia, including three species.

The Polar Desert Zone of Siberia only has species of Coleoptera, Lepidoptera, Hymenoptera, and Diptera. These same four orders are the dominant insects throughout the High Arctic regions of the world.

North America

The North American Arctic insect fauna has been reviewed by Danks (1981). The dominant orders of North American Arctic insects are the Coleoptera, Lepidoptera, Hymenoptera, and Diptera (Fig. 7), with a smaller contribution from the Hemiptera. There are just 66 species of true bugs in the North American Arctic, including 18 species in the Canadian Arctic Islands and 6 species in the Canadian High Arctic. One prominent family of Hemiptera in the Canadian Arctic is the Saldidae, or shore bugs. These are active predators. As the name implies, they are usually found near water, in damp habitats. The moths and butterflies (Lepidoptera) are more diverse here, but there are only 162 species throughout the North American Arctic, 39 species in the Canadian Arctic Islands and 23 species in the Canadian High Arctic. Although beetles (Coleoptera) are the most diverse order of insects throughout the world, in the North American Arctic there are just 203 species, including 30 species in the Canadian Arctic Islands and 13 species in the Canadian High Arctic. The two most diverse orders in the North American Arctic are the Hymenoptera and Diptera. The Hymenoptera comprise 272 species in the North American Arctic, including 106 species in the Canadian Arctic Islands and 80 species in the Canadian High Arctic. As in the rest of the Arctic, there are no ants (Formicidae) in the North American Arctic fauna. The Arctic Hymenoptera are comprised of bees and wasps. It is worth noting that Hymenopteran diversity in the American High Arctic is six times greater than that of Coleoptera, and more than three times greater than that of the Lepidoptera. However, here, as elsewhere in the Arctic, the most diverse order is the Diptera, or true flies. There are 787 fly species in the North American Arctic, including 307 species in the Canadian Arctic Islands and 200 species in the Canadian High Arctic.

A survey of the insect fauna of Ellef Ringes Island (78°N) illustrates the paucity of most orders at such high latitudes in the Canadian Arctic. McAlpine (1965) found one species of Anoplura (sucking louse—*Hoplopleura acanthopus*—Fig. 5) that is an external parasite on *Dicrostonyx groenlandicus*, the northern collared lemming, one species of geometrid moth (*Psychophora sabini*—Fig. 5), one species of ichneumon wasp, and 26 species from 6 families of Diptera.

Most of the beetle species found in the North American Arctic are predators in the families Dytiscidae (predaceous diving beetles), Carabidae (ground beetles), and Staphylinidae (rove beetles) (Table 3). However, in the High Arctic some ground beetles are omnivorous, taking both plant and animal food. These include the highly cold-adapted species *Amara (Curtonotus) alpina* (Fig. 5). Plant-feeding families, such as the Chrysomelidae (leaf beetles) and Curculionidae (weevils) are found in the Low Arctic tundra of North America (12 and 10 species, respectively), but are not known from the High Arctic regions. Table 4 shows the distributions and known host plants of Arctic leaf beetles.

Table 1 Summary of the composition of genera and 823 species of the dominant orders of insects in Arctic Siberia

Taxon	Arctic		High Arctic	
	Genera	Minimum Spp.	Genera	Minimum Spp.
Plecoptera (10+ species)				
Capniidae	3	5	2	2
Nemouridae	?	?	1	1
Perlodidae	1	1	0	0
Chloroperlidae	1	1	0	0
Hemiptera (15 species)				
Miridae	2	2	0	0
Pentatomidae	4	5	0	0
Acanthosomatidae	2	2	0	0
Aphididae	2	2	1	1
Coleoptera (150)				
Carabidae	4	4	2	2
Dytiscidae	2	2	2	3
Gyrinidae	1	1	0	0
Hydrophilidae	1	1	4	5
Staphylinidae	8	12	4	6
Byrrhidae	5	15	1	3
Cryptophagidae	1	1	0	0
Coccinellidae	7–8	20	0	0
Latridiidae	2	2	0	0
Curculionidae	30	40	20	33
Trichoptera (8 species)				
Limnephilidae	1	6	0	0
Phryganeidae	1	1	0	0
Apatanidae	1	1	0	0
Lepidoptera (158 species)				
Eriocraniidae	1	2	0	0
Hepialidae	1	1	0	0
Incurvariidae	1	1	0	0
Prodoxidae	1	1	0	0
Tineidae	1	1	0	0
Plutellidae	1	2	1	1
Oecophoridae	1	1	0	0
Coleophoridae	1	2	0	0
Momphidae	1	2	0	0
Scythrididae	1	1	0	0
Gelechiidae	3	4	0	0
Tortricidae	15	23	1	1
Pterophoridae	4	7	0	0
Pyalidae	6	9	2	2
Sphingidae	1	1	0	0
Geometridae	8	15	3	3
Noctuidae	11	29	2	3
Lymantriidae	1	1	2	2
Arctiidae	4	5	0	0
Hesperiidae	2	3	0	0
Papilionidae	2	2	0	0
Pieridae	5	9	0	0
Lycaenidae	4	5	0	0
Nymphalidae	5	19	0	0
Satyridae	3	13	0	0
Hymenoptera (50+ species)				
Pamphiliidae	1	1	0	0
Agridae	1	2	0	0
Cimbicidae	1	1	0	0
Tenthredinidae	1	8	1	2
Cephidae	1	1	0	0
Ichneumonidae	?	?	12	20
Braconidae	1	1	2	4

Table 1 Summary of the composition of genera and 823 species of the dominant orders of insects in Arctic Siberia—cont'd

Taxon	Arctic		High Arctic	
	Genera	Minimum Spp.	Genera	Minimum Spp.
Sphecidae	2	2	0	0
Vespidae	3	4	0	0
Apidae	1	1	1	3
Siphonaptera (12 species)				
Vermipsyllidae	1	1	0	0
Ceratophyllidae	7	8	1	1
Ctenophthalmidae	2	2	0	0
Diptera (420 +)				
Calliphoridae	4	5	?	?
Culcidae	2	12	?	?
Dolichopodidae	7	37	4	5
Empididae	5	21	1	4
Syrphidae	38	125	?	?
Tabanidae	2	9	?	?
Tachinidae	7	8	?	?
Chironomidae	?	> 100	44	104

?, unknown number of genera or minimum spp.

Data from Siberian Zoological Museum, Chernov, Y.I., Makarova, O.L., Penev, L.D., and Khruleva, O.A. (2014). Beetles (Insecta, Coleoptera) in the Arctic fauna: communication 1, faunal composition. *Entomological Review* **94**, 438–478; Kozlov, M. V., Kullberg, J., and Dubatolov, V. V. (2006). Lepidoptera of the Taymyr peninsula, northwestern Siberia.

Entomologica Fennica **17**, 136–152; Krashenninnikov, A.B. (2013). Preliminary data on fauna and distribution of chironomids (Diptera, Chironomidae) from Russian Arctic islands. Bulletin of Perm University. *Biology* **1**, 32–36; Makarova, O.L., Sviridov, A.V., and Klepikov, M. (2013). Lepidoptera (Insecta) of polar deserts. *Entomological Review* **93**, 225–239; Nazarova, L.B., Self, A.E., Brooks, S.J., Solovieva, N., Syrkh, L.S., and Dauvalter, V.A. (2017). Chironomid fauna of the lakes of the Pechora Basin (East of European part of Russian Arctic): Ecology and reconstruction of recent ecological changes in the region. *Contemporary Problems of Ecology* **10**, 350–362; Teslenko, V.A. (2009). Stoneflies (Plecoptera) of the Russian Far East: Diversity and zoogeography. *Aquatic Insects* **31**, 693–706.

The Diptera of the North American Arctic includes 21 families, dominated by the 155 species of midges (Chironomidae) (Table 3). In the High Arctic, midges comprise more than half the insect fauna. The larvae are aquatic and thrive in shallow tundra ponds that warm in the 24-h daylight of Arctic summers. In dry arctic sites, a group of terrestrial midges complete the larval portion of their life cycle in musk-ox dung (Chernov et al., 1977). Arctic mosquitoes (Culcidae) include only 16 species, but numbers of individuals are extremely high. Individual swarms can be so numerous (thousands to millions of individuals) as to kill young caribou through dehydration (Culler et al., 2015). Fungus gnats (Mycetophilidae) and dark-winged fungus gnats (Sciaridae) are also successful fly families in the North American Arctic. Flies in both these families feed on fungi and live in damp, decaying vegetation. Some Sciaridae have atrophied wings (brachypterous). Another diverse group of flies in the North American Arctic is the Muscidae, or house/stable flies. In the High Arctic, the genus *Spilogona* is particularly abundant. The larvae of this genus prey on midge larvae in High Arctic ponds (Danks, 1981).

The moths and butterflies are not as diverse or abundant on the landscapes of the North American Arctic as the Diptera. The caterpillars of Tortricidae are leaf-rollers. In the High Arctic these attack lousewort (*Pedicularis*) and Mountain avens (*Dryas*) leaves (MacKay and Downes, 1969). Members of the butterfly family Lycaenidae (blues, coppers, and hairstreaks) include five Holarctic species found in the North American Arctic. They feed on *Oxyria* (sorrel), such as *O. digyna*, a common plant of the Arctic tundra that extends north to Ellesmere Island in the Canadian High Arctic (Danks, 1981). There are 14 known species of butterflies in the family Nymphalidae in North America. Three live in the High Arctic, where the larvae feed on *Dryas*, and the dwarf shrubs in the genera *Salix* (willow), and *Vaccinium* (blueberry). Nine species live in both the Arctic and boreal regions. The snout moths (Pyralidae) have 13 species in the North American Arctic, including eight species found only east of Hudson Bay. This huge bay has formed a very important barrier to biotic dispersal since the end of the last glaciation in Canada. The larvae of geometrid moths are known as “inchworms” because of their habit of repeatedly looping a given distance along a plant surface. More than 21 species have been found in Arctic North America, but many of these are essentially boreal species that have ranged slightly north onto the tundra. However, one species, *Psychophora sabini* ranges into the polar desert regions of the High Arctic. This is a Holarctic species, also found in northern Greenland and northern Siberia (Fig. 5). The other moth family that is reasonably well-represented in the North American Arctic is the family Noctuidae, or owlet moths. There are 25 species so far known from this region, including five species in the High Canadian Arctic. The caterpillars of some species feed on conifers in the boreal region, but then the adults fly north onto the tundra (Danks, 1981).

Greenland

The insect fauna of the largest island in the world, Greenland, includes over 700 species (Table 5). This island is nearly 10 times the size of Great Britain, but the vast majority of Greenland—80%—is covered by an ice sheet that has waxed and waned over the last

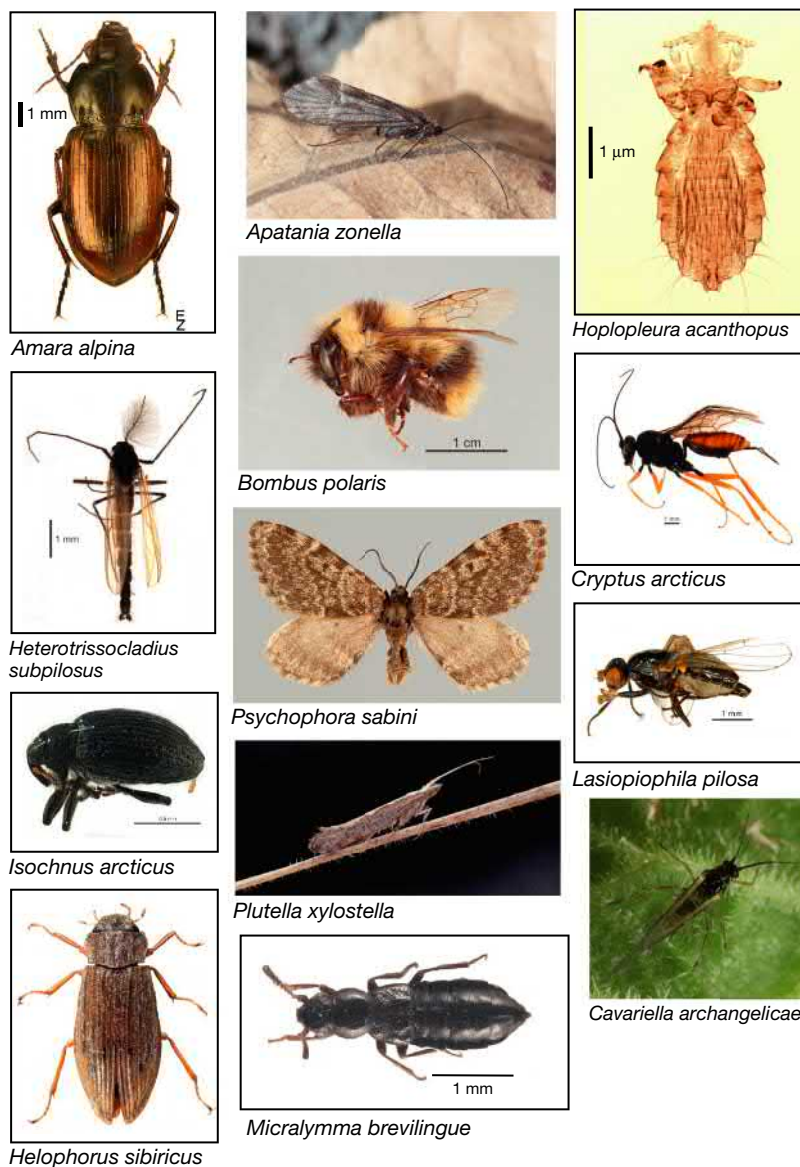


Fig. 5 Arctic insect species discussed in the text. Photo of *Psychophora sabini* by Jürgen Rodeland; photo of *Plutella xylostella* by Valerie Bugh; photo of *Arcynopteryx compata* by Derek Sykes; photo of *Caraviella archangelicae* by David Fenwick; photo of *Amara alpina* by Evgenij Zinovyev; photo of *Apatania zonella* by Erling Ólafsson; photo of *Aelia sibirica* by Boris Loboda; photo of *Hoplopleura acanthopus* by Crystal Sobel and Maria Arroyo. All photos used with the author's permission. Photos of *Isochnus arcticus*, *Lasiopiophila pilosa*, and *Micralymma brevilingue* are in the public domain.

Table 2 Lepidoptera fauna of the Russian High Arctic

Species	Severny Island, Novaya Zemlya (74–77° N; 60° E)	Northwest Taimyr Peninsula (73.6° N; 83° E)	Bolshevik Island Severnaya Zemlya (77.9–79.4° N; 102.5° E)	Northern Wrangel Island (71.5° N; 179° W)	Herald Island, Chukchi Sea (71.4° N; 175.6° W)
<i>Psychophora</i> cf. <i>cinderella</i> (Viidalepp)	+	–	+	–	–
<i>Psychophora</i> cf. <i>sabini</i> (Kby)	–	–	–	–	+
<i>Xestia lyngei</i> (Rebel)	+	–	–	–	–
<i>Xestia aequaeva</i> (Benjamin)	–	+	+	+	–
<i>Xestia liquidaria</i> (Eversmann)	–	+	–	+	–

Data from Makarova, O.L., Sviridov, A.V., and Klepikov, M. (2013). Lepidoptera (Insecta) of polar deserts. *Entomological Review* **93**, 225–239.

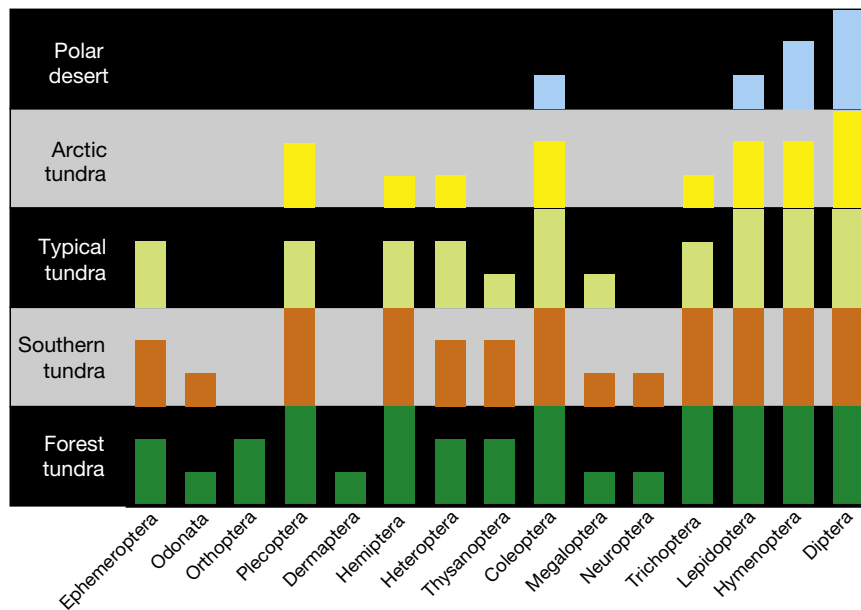


Fig. 6 Pattern of insect order diversity for the various tundra zones of Siberia. Data from Chernov, Y.I. (1995). Diversity of the Arctic terrestrial fauna. In Chapin, F.S. III., and Körner, C. (eds.), *Arctic and alpine biodiversity: Patterns, causes and ecosystem consequences*, pp. 81–95. New York: Springer.

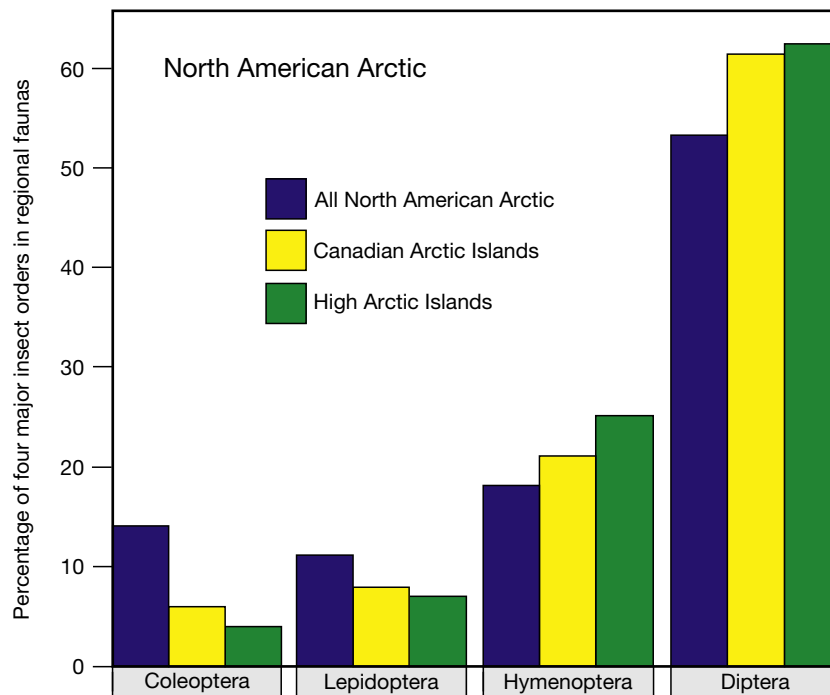


Fig. 7 Percent composition of the four most important insect orders in the North American Arctic. Data from Danks, H.V. (1981). *Arctic arthropods*. Ottawa: Entomological Society of Canada.

125,000 years (Fig. 8). This ice sheet varies in thickness from 2000 to 3000 m. Nevertheless, the east-central, northern, and south-western coastal regions are ice-free, along with narrower strips of land around the rest of the island. The ecological zones of Greenland are divided into three categories: Sub-Arctic, Arctic, and High Arctic. The Sub-Arctic regions of the island include southern Greenland where birch (*Betula*), willow (*Salix*), and rowan (*Sorbus*) form small woodlands. Southwest and Southeast Greenland also form part of the Sub-Arctic zone because of their relatively mild climates. The Arctic Zone includes the coasts of the northeast and northwest portions of the island. Here the climate is more severe: colder and drier. The far northern regions represent the High Arctic Zone, which is essentially polar desert.

Table 3 Summary of the composition of genera and 1503 species of the dominant orders of insects in the North American Arctic

Taxon	Arctic		High Arctic	
	Genera	Minimum Spp.	Genera	Minimum Spp.
Coleoptera (142 species)				
Carabidae	18	78	1	1
Dytiscidae	5	20	1	2
Staphylinidae	17	22	4	4
Curculionidae	10	14	1	1
Diptera (910 species)				
Family Trichoceridae (winter crane flies)	1	5	1	2
Family Tipulidae (crane flies)	13	42	5	6
Family Culcidae (mosquitoes)	2	16	1	3
Family Ceratopogonidae (biting midges)	4	7	3	7
Family Chironomidae (midges)	60	155	38	94
Family Mycetophilidae (fungus gnats)	8	15	6	9
Family Sciaridae (dark-winged fungus gnats)	8	14	3	11
Family Cecidomyiidae (gall midges)	2	2	1	1
Family Empididae (dance flies)	4	19	2	6
Family Dolichopodidae (long-legged flies)	5	28	1	2
Family Phoridae (scuttle flies)	1	3	1	1
Family Syrphidae (hover flies)	14	23	5	6
Family Piophilidae (skipper flies)	5	6	3	4
Family Agromyzidae (leaf miners)	7	18	3	4
Family Heleomyzidae (sun flies)	5	9	2	2
Family Ephydriidae (shore flies)	5	9	1	1
Family Scathophagidae (dung flies)	9	24	3	5
Family Anthomyiidae (root-maggot flies)	19	132	3	6
Family Muscidae (house flies; stable flies)	25	162	3	21
Family Calliphoridae (blow flies)	10	12	3	3
Family Tachinidae (parasitic flies)	8	9	6	6
Lepidoptera (142 species)				
Family Tortricidae (leaf roller moths)	10	16	2	3
Family Pieridae (whites, sulphurs, yellows)	4	13	1	2
Family Lycaenidae (blues, coppers, hairstreaks)	5	5	2	2
Family Nymphalidae (brush-footed butterflies)	7	14	2	3
Family Pterophoridae (plume moths)	3	3	1	1
Family Pyralidae (snout moths)	8	14	1	1
Family Geometridae (geometrid moths)	15	22	2	2
Family Lymantriidae (tussock moths)	1	2	1	2
Family Arctiidae (tiger moths)	4	5	1	1
Family Noctuidae (owlet moths)	15	26	5	5
Hymenoptera (309 species)				
Family Tenthredinidae (common sawflies)	8	34	4	14
Family Braconidae (braconid wasps) ^a	10	15	4	6
Family Ichneumonidae (ichneumon wasps) ^a	68	162	30	49
Family Eulophidae (eulophid wasps) ^a	1	1	1	1
Family Encyrtidae (encyrtid wasps) ^a	3	3	2	2
Family Pteromalidae (pteromalid wasps) ^a	3	3	2	2
Family Chalcidae (chalcid wasps) ^a	1	1	1	1
Family Apidae (bees)	1	12	1	3

^aParasitic groups.Data from Danks, H.V. (1981). *Arctic arthropods*. Ottawa: Entomological Society of Canada.

The Greenland insect fauna has some unique characteristics, as discussed in Böcher et al. (2015). Some orders that are of little importance elsewhere in the Arctic are better-represented here, while others that are typically important in much of the Arctic are of lesser importance here. For instance, the Hemiptera are represented by 34 species in Greenland, while there are only 46 species of Coleoptera, a little less than 7% of the insect fauna. The Lepidoptera are represented by 51 species in 15 families. Hymenoptera are one of two dominant orders, with 203 species in 16 families, comprising 29% of the Greenland insect fauna. It is interesting to note that more than half of the Hymenoptera species are ichneumon wasps: 118 species. These include 15 species thought to be endemic to Greenland. A typical ichneumon wasp of Greenland is *Cryptus arcticus* (Fig. 5). This species and other members of the subfamily Cryptinae are idiobiont parasitoids. This means that the wasps prevent further development of their hosts after initial parasitization.

Table 4 Leaf beetles (Chrysomelidae) of the Arctic regions

Species	Paleartic	Nearctic	Distribution pattern	Host plants
<i>Chrysolina subsulcata</i> (Mannh.)	+	+	Amphiberingian	<i>Parrya</i> , <i>Senecio</i> , <i>Nordosmia</i> , <i>Oxytropis</i>
<i>Chrysolina septentrionalis</i> (Mén.)	+	+	Amphiberingian	<i>Ranunculus</i> , <i>Delphinium</i> , <i>Pedicularis</i>
<i>Chrysolina bungei</i> (Jacobs.)	+		Arctic Siberia	?
<i>Chrysolina cavigera</i> (Sahlb.)	+	+	Amphiberingian	?
<i>Chrysolina arctica</i> Medv.	+		Wrangel Island	<i>Artemisia</i>
<i>Chrysolina hudsonica</i> Brown		+	Arctic Canada	<i>Achillea</i> , <i>Tanacetum</i>
<i>Chrysolina finitima</i> Brown		+	Arctic Alaska	?
<i>Chrysomela taimyrensis</i> Medv.	+		Arctic Siberia	<i>Rubus chamaemorus</i>
<i>Chrysomela wrangelina</i> Medv.	+		Wrangel Island	?
<i>Galerucella stephanssoni</i> Brown		+	Arctic North America	?

Data from Silfverberg, H. (1989). The problem of arctic Chrysomelidae (Coleoptera). *Fauna Norvegica Series B* **36**, 53–55; Silfverberg, H. (1994). Chrysomelidae in the Arctic. In: Jolivet, P. H., Cox, M. L., Petitpierre, E. (eds.), *Novel aspects of the biology of Chrysomelidae*, pp. 503–510. Dordrecht: Springer; Bieřkowski, A.O. (2007). *A monograph of the genus Chrysolina Motschulsky, 1860 (Coleoptera: Chrysomelidae) of the world, Part 1*. Moscow: Techpolygraphcentre Publishers.

Table 5 Summary of the composition of genera and 703 species of the dominant orders of insects in Greenland

Taxon	Subarctic		Arctic		High Arctic	
	Genera	Species	Genera	Species	Genera	Species
Thysanoptera (7 species)						
Thripidae (7)	3	3	5	7	2	2
Ephemeroptera (1 species)						
Baetidae (1)	1	1	1	1	0	0
Hemiptera (34 species)						
Psyllidae (3)	2	2	1	2	0	0
Aphididae (17, incl. 5 endemic species)	10	11	13	17	5	5
Coccidae (1 endemic species)	1	1	1	1	0	0
Pseudococcidae (7, incl. 4 endemic species)	3	5	5	5	2	2
Eriococcidae (2)	2	2	0	0	0	0
Cicadellidae (2)	2	2	0	0	0	0
Lygaeidae (1)	1	1	1	1	1	1
Miridae (1)	1	1	0	0	0	0
Coleoptera (46 species)						
Carabidae (4)	4	4	1	1	0	0
Dytiscidae (2)	2	2	2	2	2	2
Gyrinidae (1)	1	1	1	1	0	0
Hydrophilidae (1)	1	1	0	0	0	0
Staphylinidae (13, incl. 1 endemic species)	7	11	2	4	3	3
Byrrhidae (4)	2	2	2	2	0	0
Cryptophagidae (1)	1	1	0	0	0	0
Coccinellidae (2)	2	2	1	1	1	1
Latridiidae (2)	2	2	1	1	0	0
Chrysomelidae (1)	1	1	0	0	0	0
Curculionidae (5)	5	5	0	0	0	0
Trichoptera (8 species)						
Limnephilidae (6)	2	6	0	0	0	0
Phryganeidae (1)	1	1	0	0	0	0
Apatanidae (1)	0	0	1	1	0	0
Lepidoptera (51 species)						
Gracillariidae (1)	1	1	0	0	0	0
Plutellidae (2)	2	2	1	1	0	0
Elachistidae (1)	1	1	1	1	0	0
Coleophoridae (2)	1	2	0	0	0	0
Scythrididae (1)	1	1	1	1	0	0
Gelichiidae (2)	1	2	0	0	0	0
Tortricidae (5)	2	3	3	3	2	2
Pterophoridae (1)	0	0	0	0	1	1
Pyralidae (7)	5	5	2	2	0	0
Pieridae (1)	0	0	1	1	1	1
Lycaenidae (1)	0	0	1	1	1	1

(Continued)

Table 5 Summary of the composition of genera and 703 species of the dominant orders of insects in Greenland—cont'd

Taxon	Subarctic		Arctic		High Arctic	
	Genera	Species	Genera	Species	Genera	Species
Nymphalidae (4)	3	3	3	3	3	3
Geometridae (5)	3	4	3	3	2	2
Erebidae (1)	1	1	1	1	1	1
Noctuidae (17)	11	14	6	10	4	4
Hymenoptera (203 species)						
Tenthredinidae (8)	3	5	2	4	2	4
Megaspilidae (2)	1	2	0	0	0	0
Aphelinidae (1)	1	1	0	0	0	0
Encyrtidae (8, incl. 1 endemic species)	6	6	1	1	4	4
Eulophidae (6)	4	4	0	0	2	2
Mymaridae (3)	3	3	0	0	0	0
Pteromalidae (9)	8	8	1	1	2	2
Trichogrammatidae (1)	1	1	0	0	0	0
Figitidae (5)	5	5	2	2	2	2
Platygastridae (6)	5	5	1	1	0	0
Diapriidae (4)	4	4	1	1	0	0
Braconidae (28, incl. 4 endemic species)	18	18	6	6	9	9
Ichneumonidae (118, incl. 15 endemic species)	72	95	15	16	38	45
Dryinidae (1)	1	1	0	0	0	0
Vespidae (1)	1	1	1	1	0	0
Apidae (2)	1	2	1	2	1	2
Neuroptera (2 species)						
Hemerobiidae	2	2	0	0	0	0
Siphonaptera						
Pulsidae (2, Includes 1 endemic species)	2	2	1	1	1	1
Ceratophyllidae (6)	2	2	2	2	4	4
Diptera (349 species)						
Tipulidae (5)	3	4	1	2	2	3
Limoniidae (9)	4	8	1	1	3	3
Trichoceridae (4)	1	1	1	1	1	2
Culcidae (2)	1	2	1	2	1	2
Simuliidae (3)	2	3	0	0	0	0
Ceratopogonidae (9)	6	8	0	0	2	2
Chironomidae (125, Incl. 4 endemic species)	30	65	6	7	18	50
Bibionidae (1)	1	1	0	0	0	0
Scatopsidae (1)	1	1	0	0	0	0
Keroplattidae (1)	1	1	0	0	0	0
Bolitophiliidae (1)	1	1	0	0	1	1
Mycetophilidae (30)	10	20	1	1	8	9
Psychodidae (1)	1	1	0	0	0	0
Cecidomyiidae (1)	1	1	1	1	0	0
Empididae (5, Incl. 2 endemic species)	3	3	2	2	1	3
Dolichopodidae (4)	2	2	1	1	1	4
Phoridae (5, Incl. 1 endemic species)	1	2	0	0	2	3
Syrphidae (15)	6	12	4	7	5	9
Sciomyzidae (1)	1	1	0	0	0	0
Sepsidae (2)	2	2	0	0	0	0
Piophilidae (5)	3	3	2	2	3	3
Agromyzidae (9)	4	8	2	2	5	6
Heleomyzidae (5)	3	4	2	2	3	3
Sphaeroceridae (6)	5	6	0	0	0	0
Chamaemyiidae (1)	1	1	0	0	0	0
Canacidae (1)	1	1	0	0	0	0
Ephydriidae (10)	8	9	1	2	2	3
Anthomyiidae (33)	9	27	11	14	12	18
Fanniidae (3)	1	3	0	0	1	1
Muscidae (36)	10	30	5	10	6	24
Scathophagidae (6)	2	3	1	2	2	4
Calliphoridae (5)	4	5	2	3	3	4
Oestridae (2)	2	2	1	1	1	1
Tachinidae (5)	2	2	2	2	2	2

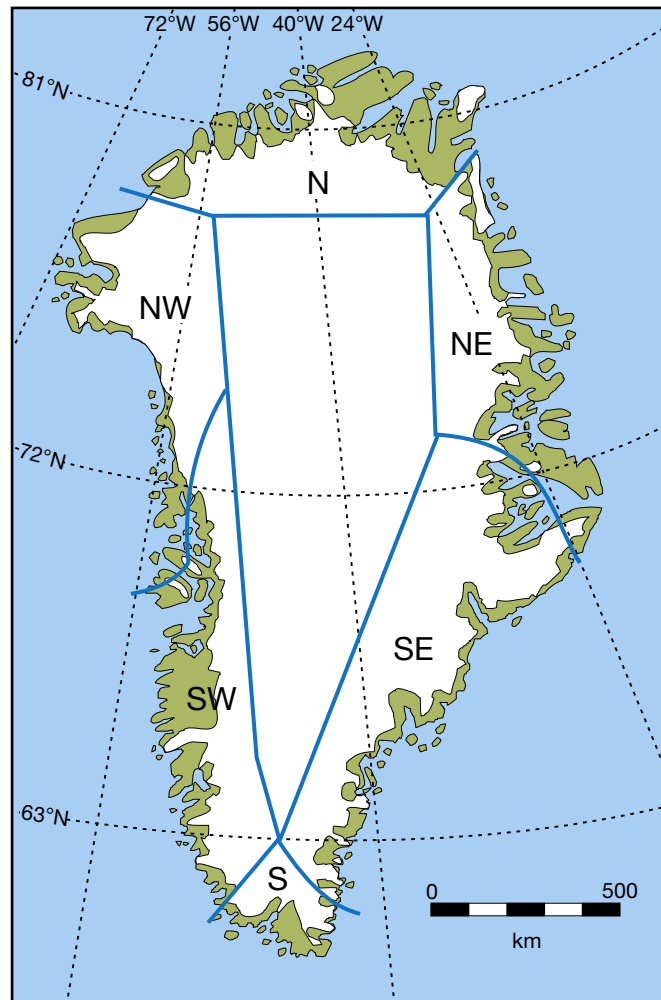


Fig. 8 Map of Greenland, showing the ecological zones along the coasts. After Böcher, J., Kristensen, N.P., Pape, T., Vilhelmsen, L. (eds.) (2015). *The Greenland Entomofauna. Fauna Entomologica Scandinavica*, vol. 44, p. 881. Leiden: Brill.

The host insects are attacked during their pupal life stage, and chemicals released by the parasitic wasp larva prevent the maturation of the host while the parasite feeds on it.

There are two species of Apidae in Greenland: *Bombus polaris* (Fig. 5) and *B. hyperboreus*. *B. polaris* is a social bee that survives near freezing temperatures. This species is an important pollinator of arctic vegetation, including arctic poppies, roses, and willows. It is found in Arctic North America, Greenland and Russia. *Bombus hyperboreus* is a parasite of *B. polaris* throughout the latter species' range. Queens of *B. hyperboreus* attack the nests of *B. polaris*, killing the queen and taking over the nest. The offspring of the parasite are then raised by the *B. polaris* workers (Böcher et al., 2015).

But here, as elsewhere in the Arctic, Diptera are dominant. The Greenland fauna contains at least 349 species in 34 families. Arctic flies are important pollinators of flowering plants on the tundra. For instance, the cheese fly (Piophilidae) *Lasiopiophila pilosa* (Fig. 5) pollinates *Cerastium arcticum* (Arctic mouse-ear) in Greenland. The Greenland fly fauna includes 125 species of midges (Chironomidae), including 4 species thought to be endemic.

Chironomid Abundance and Diversity

As we have seen, nonbiting midges (Chironomidae) are typically the most diverse and often also the most numerically abundant insect group on Arctic landscapes. In one count, researchers estimated 50,000 midge larvae per m² in a Greenland lake. In addition to the 125 midge species in Greenland, there are 155 species in Arctic North America, 96 species in Arctic Russia, more than 66 species in Svalbard, and more than 73 species on Novaya Zemlya. There are several factors in chironomid anatomy, physiology, and behavior that make them so successful in the Arctic, as discussed by Lindegaard (2015). Following the progression of four larval stages (instars), midge larvae pupate. In Arctic lakes, the pupal stage survives the winter beneath the surface of frozen lakes and

ponds. All preadult stages grow rapidly under favorable conditions (warm water and abundant food) but grow much slower under adverse conditions (cold water and meager food supply). The former conditions are more prevalent in southern Greenland, while the latter exemplify northern Greenland. The pupae emerge from the ice in spring as adults. In the north, midges may persist in their immature stages for several years, slowly building the chemical energy reserves to emerge as adults. In central and northern Greenland, midges must employ strategies to survive freezing temperatures for many months of the year. The principal survival method is for midge larvae to undergo dehydration of their bodies. With water content kept to an absolute minimum, these larvae are virtually immune to the effects of cold environments. Other midges burrow deeply in the mud at the bottom of ponds and lakes, and so insulate themselves from winter air temperatures.

Arctic midges live in a wide variety of freshwater and terrestrial habitats. These range from shallow ponds to deep lakes and damp riparian habitats. The shallow littoral zone of lakes is much more productive of midge larvae than colder deep waters. In addition to their variety of habitats, Arctic midges also display a wide diversity of food preferences. Some larvae, such as the Tanypodinae, are predaceous, but the first two instars also feed on algae. Other subfamilies have mouthparts adapted for scraping algae and plant detritus off of surfaces. Midges play a key role in aquatic (freshwater) food chains in the Arctic. They contribute an average of 60% of benthic production in Arctic lakes. The lack of competition by other aquatic insect groups, especially in the High Arctic, results in the dominance of chironomids here. They are particularly important in nutrient-poor (oligotrophic) lakes, where they can make up 96% of benthic secondary productivity. Finally, colonization of new regions by midges is facilitated by their small, light-weight, winged adults. These are able to be carried great distances by winds.

Distribution Patterns of Greenland Insect Fauna

The west coast of Greenland is separated from Ellesmere Island by Nares Strait, a body of water ranging from 20 to 140 km across. So it is not surprising that many Greenland insect species are also found in Arctic Canada. All five species of butterflies exhibit this Nearctic distribution pattern, as do 6 out of 8 caddisfly species. The Greenlandic spider fauna contains 20 Nearctic species, about 10 Palearctic species, and 45 species that are Holarctic. Flies in the family Muscidae represent a mixture of Nearctic (10 species) and Holarctic distribution patterns (27 species). The beetle fauna is divided almost equally between Palearctic and Holarctic species (Böcher et al., 2015). The underlying trend here is that the insects that are strong fliers, or disperse easily, are dominated by species with Nearctic distributions, while the more earthbound taxa are predominantly Palearctic in distribution.

The postglacial colonization of Greenland by insects is somewhat easier to explain for the Nearctic taxa than for the Palearctic. For instance, the butterfly fauna of Ellesmere, once established there, could easily have colonized the deglaciated northwest coast of Greenland. But for species that have Palearctic distributions, the method(s) and timing of the immigration, presumably from northern Europe, remain obscure at best. The shortest distance between Greenland and Norway is more than 2500 km, across some of the most hostile stretches of ocean in the stormy North Atlantic. As pointed out by Böcher et al. (2015), there has not been a land bridge between Europe and Greenland during the Quaternary. Transportation by migratory birds has been mooted, but seems more likely for plant seeds than for most insect groups. Survival in situ in unglaciated refugia or mountaintops (nunataks) has also been put forward, but the glaciological evidence does not support the existence of ice-free areas on Greenland during the last glaciation. *Trans*-Atlantic crossings on drifting ice-rafted debris coming off the waning Fennoscandian Ice Sheet have also been proposed, but this seems a more likely scenario for the colonization of Iceland, which is 1000 km closer to northern Europe than is Greenland. Sadler (1999) supported the ice-rafted debris mechanism of colonization for the North Atlantic islands, and emphasized a youthful biota (hence, the lack of endemic species) and the operation of severe filters and sweepstakes during postglacial colonization. If, indeed, Greenland was colonized by European insects that managed to float for weeks or months on the open ocean before accidentally landing on the east coast of Greenland, then such a trip would represent a true sweepstakes colonization.

A good example of how cold-adapted species come and go in regional Arctic faunas is the weevil, *Isochnus arcticus* (Fig. 5). Böcher (2012) found fossil specimens of this species in sediments dating from the last interglacial period (c. 125,000 years ago). There is no obvious reason why *I. arcticus* should not have returned to Greenland after the end of the last glaciation, but it has not been found there in any modern collections. The host plant for this weevil, *Salix arctica*, is certainly widespread in Greenland today. This weevil is found today across the North American and Russian Arctic, but failed to colonize Greenland in the current interglacial.

The evidence from the Greenland fauna itself is difficult to interpret. Sadler's (1999) argument about the lack of endemic species has since been at least partially refuted by the discovery of nine endemic species of bugs, one endemic beetle species, 20 endemic species of wasps, 1 endemic flea species, and 7 species of endemic flies (see Table 5).

Svalbard

The insect fauna of Svalbard has been well-described by Coulson et al. (2014). The group of islands that make up the Svalbard archipelago are all situated in the Arctic and High Arctic zones. Svalbard is a group of five main islands that fall between 10° and 35°E and 74° and 81°N (Fig. 9). These islands include Spitsbergen, Nordaustlandet, Edgeøya (Edge Island), Barentsøya (Barents Island), and the southern outlier, Bjørnøya (Bear Island). The archipelago has a land area of about 63,000 km² of which 60% is covered by permanent ice and snow. Mean July temperature at Longyearbyen on Spitsbergen is 5.2°C. Mean January temperature is –15.3°C.

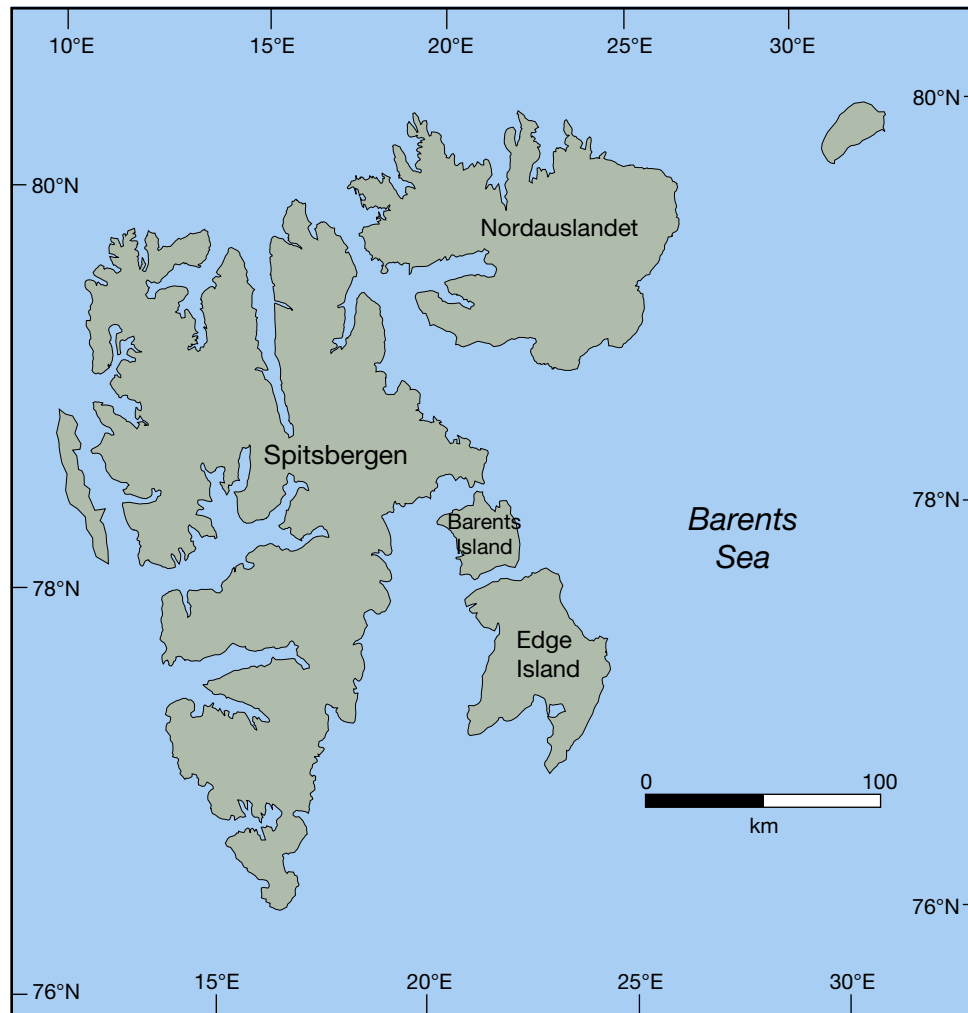


Fig. 9 Map of Svalbard.

Mean annual precipitation is only 191 mm. Air temperature is heavily influenced by the surrounding ocean currents. The northernmost extension of the North Atlantic Drift carries relatively warm water along the west side of Svalbard, while the east coast is chilled by the polar waters of the East Spitsbergen Current.

The unglaciated landscapes of Svalbard are frozen and snow-covered for 9 months of the year. Biological and geological field research has been carried out on Svalbard since the foundation of the Norwegian Polar Institute there in 1928. The scope of research activities expanded in the 1970s, with the establishment of an airport on Spitsbergen. Therefore, unlike many other Arctic regions, the insect fauna of Svalbard has been relatively well-studied. In fact Svalbard has perhaps the most complete inventory of the invertebrate fauna of any Arctic region (Hodkinson, 2013).

The dominant insect orders of the Svalbard fauna are the Phthiraptera (lice), Diptera, and Hymenoptera (Table 6). There are 41 known species of lice on Svalbard. These are all external parasites on birds and mammals. The majority of these lice attack shore birds. Some shore birds lose so many feathers to louse attack that they cannot keep themselves warm, and die of pneumonia.

There are two resident species of aphids on Svalbard, *Acyrtosiphon svalbardicum* and *Sitobion calvulum*. These aphids exhibit a number of unusual life history traits associated with life in the High Arctic, as explained by Coulson et al. (2014). Most aphids living in temperate regions have 12–20 generations per year, whereas the two Svalbard aphid species have only 2–3 generations per year. Most temperate aphids exhibit winged forms on a regular basis, whenever they experience crowding, whereas the Svalbard aphids are apterous. The development of sexual forms is stimulated by shortening day length in temperate regions, whereas the cue for development of sexual forms on Svalbard is 24-h daylight.

A mere 17 species of beetles are known from Svalbard. Of these, only three are common: the rove beetles *Atheta subplana* and *Atheta graminicola*, and the weevil *Isochnus flagellum*. These three species are widespread in the Arctic. Several beetle species identified from Svalbard are synanthropic—brought there by humans and only found living indoors. The Svalbard beetle fauna must be considered depauperate in comparison with other arctic faunas, such as that of Greenland (46 native species) or Novaya Zemlya (28 native species).

Table 6 Summary of the composition of genera and species of the dominant orders of insects of Svalbard, Franz Joseph Land, and Novaya Zemlya

Taxon	Svalbard (224 species)			Franz Joseph Land (13 species)			Novaya Zemlya (> 167 species)		
	Families	Genera	Species	Families	Genera	Species	Families	Genera	Species
Order phthiraptera (lice)									
Suborder Ischnocera (Chewing lice)	1	10	27	0	0	0	1	1	6
Suborder Amblycera (Chewing lice)	1	4	8	0	0	0	1	1	1
Suborder Anoplura (Sucking lice)	1	1	2	0	0	0	0	0	0
Order hemiptera (true bugs)									
Family Aphididae (Aphids)	1	2	3	0	0	0	1	1	1
Order coleoptera (beetles)									
Family Dytiscidae (Predaceous diving beetles)	0	0	0	0	0	0	1	2	2
Family Staphylinidae (Rove beetles)	1	1	2	0	0	0	1	5	6
Family Chrysomelidae (Leaf beetles)	1	1	1	0	0	0	1	2	2
Family Curculionidae (Weevils)	1	1	1	0	0	0	1	1	1
Order diptera (flies)									
Family Chironomidae (Nonbiting midges)	1	25	> 66	1	4	5	1	?	> 73
Family Simuliidae (Black flies)	1	1	1	0	0	0	?	?	?
Other Diptera families	19	39	69	1	1	1	9	?	> 75
Order hymenoptera (ants, wasps, bees)									
Family Ichneumonidae (Ichneumon wasps)	1	20	22	0	0	0	1	?	20
Family Braconidae (Braconid wasps)	1	2	5	0	0	0	1	?	4
Family Tenthredinidae (Common sawflies)	1	2	7	0	0	0	0	0	0
Family Bombidae (Bumblebees)	0	0	0	0	0	0	1	1	3
Lepidoptera (butterflies and moths)									
Family Plutellidae (Diamondback moths)	1	1	1	1	1	1	0	1	2
Family Pyralidae (Snout moths)	1	1	1	1	1	1	0	0	0
Family Noctuidae (Owlet moths)	1	1	1	1	1	1	0	1	2
Family Tortricidae (Leafroller moths)	0	0	0	1	2	2	0	1	2
Family Geometridae (Geometrid moths)	0	0	0	1	2	2	0	2	2
Siphonaptera (fleas)									
Family Ceratophyllidae (Ceratophyllid fleas)	1	2	2	0	0	0	1	1	1
Order trichoptera (caddisflies)									
Family Apataniidae (Apataniid caddisflies)	1	1	1	0	0	0	1	1	1

Data from Hodkinson, I.D. (2013). Terrestrial and freshwater invertebrates. In: Mølltofte, H. (ed.), *Arctic Biodiversity Assessment. Status and Trends in Arctic biodiversity*, pp. 194–223. Akureyri: Conservation of Arctic Flora and Fauna; Makarova, O. L., Sviridov, A. V., and Klepikov, M. (2013). Lepidoptera (Insecta) of polar deserts. *Entomological Review* **93**, 225–239; Chernov, Y. I., Makarova, O. L., Penev, L. D., and Khruleva, O. A. (2014). Beetles (Insecta, Coleoptera) in the Arctic fauna: Communication 1, faunal composition. *Entomological Review* **94**, 438–478.

As elsewhere in the Arctic, Diptera comprise the most important insect order on Svalbard. As discussed above, Diptera are better adapted to the cold, harsh Arctic climate than any other order of insects. They form the dominant order in all regional Arctic insect faunas, in terms of both abundance and diversity. A total of 136 species are known from this archipelago, dominated by more than 66 species of midges (Chironomidae).

As with the Coleoptera, Svalbard has surprisingly few wasps (Hymenoptera). Coulson et al. (2014) list 39 species of Hymenoptera from this archipelago. The majority of these are parasitic wasps in the families Ichneumonidae (22 species) and Braconidae (5 species). There are also seven species of sawflies (Tenthredinidae). The braconid wasps from Svalbard parasitize the two endemic aphid species. The Hymenoptera fauna of Greenland includes 203 known species, more than 5 times the number of species on Svalbard. The disparity in the diversity of Coleoptera and Hymenoptera between Svalbard and Greenland must be due, in part, to the differences in the area of ice-free land between the two Arctic island groups, but it would seem that the serendipity of post-glacial colonization must have also played a role in these differences.

The Lepidoptera fauna of Svalbard is extremely depauperate. The resident species total just three, the diamondback moth *Plutella polaris*, the snout moth *Pyla fusca*, and the owlet moth, *Apamea exilis*. *P. polaris* is apparently endemic to Svalbard. Another *Plutella*, *P. xylostella* (Fig. 5), is occasionally collected on Svalbard, but is too warm-adapted to overwinter there. Again for comparison, Greenland has 51 known resident species of Lepidoptera, representing 15 families of moths and butterflies. Svalbard has one species of caddisfly: *Apatania zonella* (Fig. 5). The larvae are active throughout the summer, using their mouthparts to scrape food (detritus or algae) from rocks in streams.

The Svalbard insect fauna is made up of Holarctic and Palearctic species. It would appear that the archipelago was colonized almost exclusively from northwestern Eurasia after the last ice age. The distances from North America are too great, and the ocean currents and winds flow in the wrong directions to facilitate North American insect dispersal to Svalbard.

Coulson (2007) noted that more than 80% of insect faunal surveys on Svalbard come from just three locations along the west coast. This introduces a bias in our knowledge of the invertebrate fauna, because the west coast has a relatively mild climate due to the influence of the North Atlantic Drift. There has been little study of the ice-free regions of the east coast of Svalbard, but these regions likely have a different insect fauna, for two reasons. First, the predominant winds and oceans currents originating from the north east create considerably colder conditions here. Second, because of the influences of different winds and currents, this coast will have experienced a different colonization history.

Franz Josef Land and Novaya Zemlya

Franz Josef Land lies north-east of Svalbard between $79^{\circ}73'$ and $81^{\circ}93'N$ and 37° and $65^{\circ}50'E$. It comprises ~ 191 uninhabited islands with a total land area of $12,334 \text{ km}^2$ (Fig. 10). Cape Fligely, on the north coast of Prince Rudolf Island ($81^{\circ}50' N$), is the northernmost point in Eurasia and the Eastern Hemisphere. About 85% of the island landscapes are covered with glacial ice, leaving only about 1850 km^2 of ice-free land. This area is about 14% of the ice-free area of Svalbard. The mean July temperature is 2.1°C . The mean January temperature is -22.7°C . Mean annual precipitation is 259 mm. The islands are surrounded by sea ice from about September to June. Skies are cloudy about 90% of the time, reducing solar heating at ground level.

Franz Josef Land was a closed military area for much of the 20th century and even today access requires permission from the Russian government, including the Federal Service of National Security and the Administration of Reserves and Protected Areas. Little work has been done on the insect fauna of these High Arctic islands.

Novaya Zemlya consists of two main islands and some smaller adjacent islands. The islands lie north of the Nenetsia Russian coast. The two principle islands, Severny to the north and Yuzhny to the south, are separated by the Matochkin Shar strait. The island group is situated between 70° to $77^{\circ}N$ and 51° to $69^{\circ}E$ (Fig. 11). The main islands stretch almost 900 km along a north-east to southwest trending arc that is up to 145 km wide. Novaya Zemlya has an area of $81,280 \text{ km}^2$ of which 27% is currently glaciated, leaving over $59,000 \text{ km}^2$ of ice-free landscapes, more than twice the ice-free area of Svalbard. Mean July temperature at the Malye Karmakuly meteorological station ($72^{\circ}22'N$, $52^{\circ}42'E$) on southwest Yuzhny Island is 7.3°C . Mean January temperature is -14.1°C . Mean annual precipitation is 336 mm. As with Svalbard, the climate of Novaya Zemlya is heavily influenced by the surrounding ocean waters. The west coast is warmed by warm North Atlantic waters, while east coast is chilled by the cold waters of the Kara Sea. This coast is ice-bound during winter.

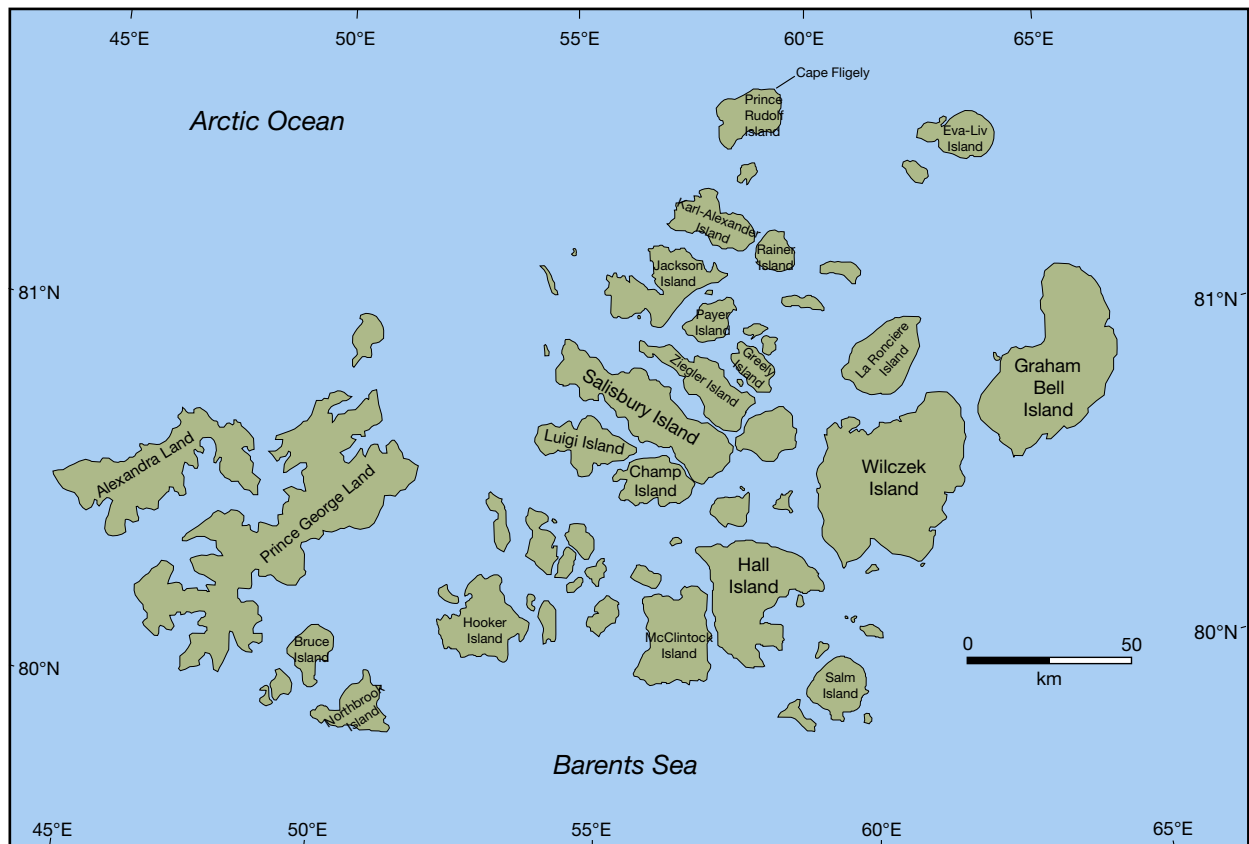


Fig. 10 Map of Franz Josef Land.

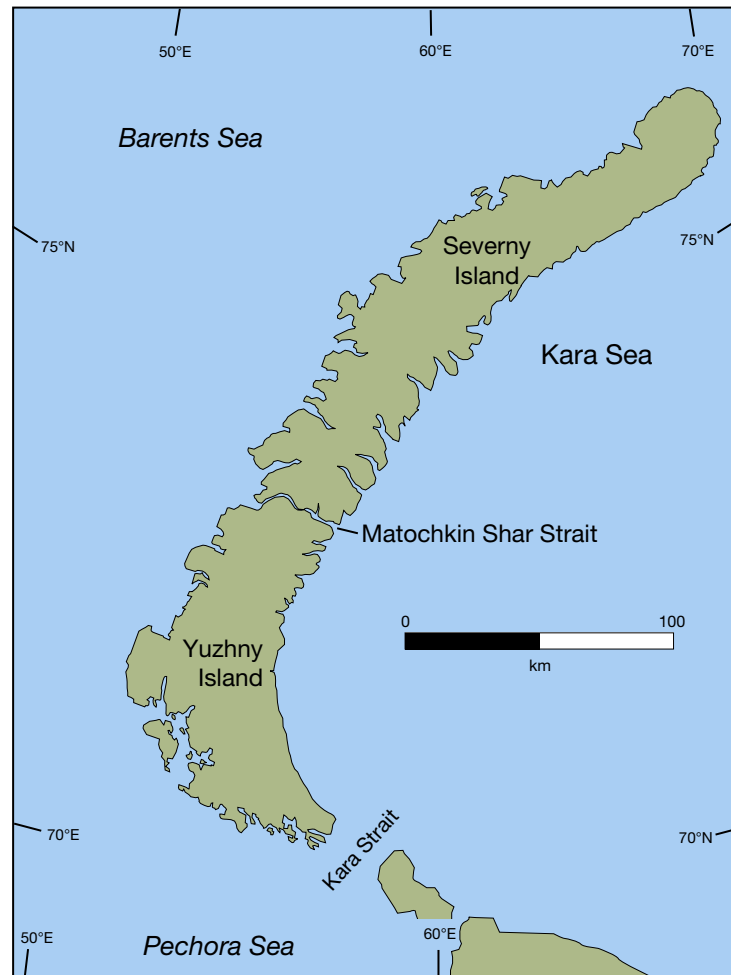


Fig. 11 Map of Novaya Zemlya.

During the Cold War, parts of both main islands of Novaya Zemlya were used as nuclear test sites. Since 1954, 224 nuclear detonations have been carried out on Novaya Zemlya. The islands remain a closed military region and thus difficult for biologists to visit.

Because of its extreme northern position and predominance of ice-covered landscapes, the islands that make up Franz Josef Land have only 13 recorded species of insects ([Table 6](#)). It could well be that many more species would be found if more extensive entomological field investigations were carried out there, but the extremely cold temperatures and lack of biological productivity of these Polar Desert islands precludes great diversity of insect species there. Vascular plant cover here is restricted to less than 15% of the landscape.

The Franz Josef Land fauna includes five species of chironomids, one dark-winged fungus gnat (Sciaridae) and seven species of moths. No wasps or beetles have been found there. No lice or fleas have been found. The Novaya Zemlya insect fauna is far more abundant and diverse, as might be expected. More than 167 insect species have been identified from these islands ([Table 6](#)). These include 7 species of lice, one aphid, 11 species of beetles, more than 73 species of chironomids and more than 75 species from other Diptera families, 20 species of ichneumon wasps, 4 species of braconids, and 3 species of bumblebees. There are 14 resident species of Lepidoptera known from Novaya Zemlya. The fauna contains mainly species with circumpolar Arctic distributions.

Given that the three archipelagos are in relatively close proximity to each other ([Fig. 12](#)), it is somewhat surprising that they share very few insect species in common. As shown in [Table 7](#), the greatest number of species in common (35) are shared between Svalbard and Novaya Zemlya. Franz Josef Land has only one species of moth in common with Svalbard, and no species in common with Novaya Zemlya. Apparently there has been very limited connectivity between these island groups. We clearly need a better understanding of the relative importance of eastern and western sources of colonization over time in order to unravel this anomaly.

[Coulson et al. \(2014\)](#) commented on the small number of endemic species, both on the individual archipelagos and for the region as a whole. There are several possible explanations for this phenomenon. One may be the lack of extensive insect collecting, especially on Novaya Zemlya and Franz Josef Land. Or the paucity of endemism may reflect the young age of the communities, having become established only during the Holocene. On the other hand, the insect fauna of Greenland includes 34 endemic

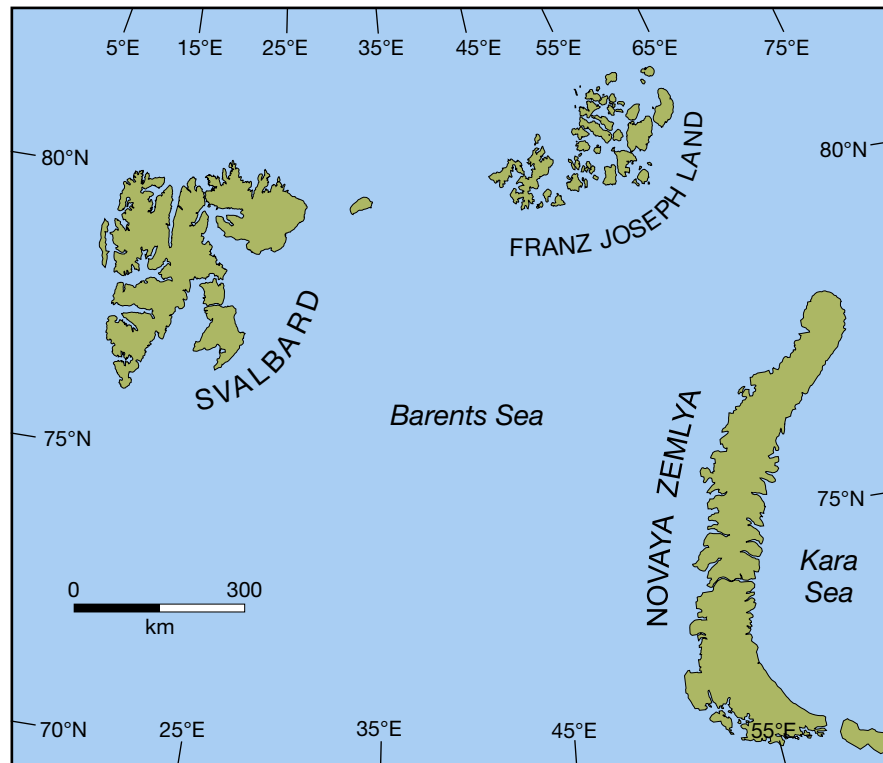


Fig. 12 Map of the Barents Sea and adjoining seas, showing the proximity of Svalbard, Franz Josef Land and Novaya Zemlya.

Table 7 Insect species in common between the three archipelagos

Order	Novaya Zemlya to Svalbard	Franz Josef Land to Svalbard	Franz Josef Land to Novaya Zemlya
Phthiraptera	4	0	0
Coleoptera	1	0	0
Diptera: Chironomidae	19	1	0
Other Diptera families	10	0	0
Siphonaptera	1	0	0

Data from Coulson, S.J., Convey, P., Aakra, K., Aarvik, L., Ávila-Jiménez, M.L., et al. (2014). The terrestrial and freshwater invertebrate biodiversity of the archipelagoes of the Barents Sea: Svalbard, Franz Josef Land and Novaya Zemlya. *Soil Biology & Biochemistry* **68**, 440–470.

species representing 10 families scattered in 5 orders of insects. Greenland was likewise fully glaciated during the Late Pleistocene, so its fauna had no more time to evolve new species than the Barents Sea archipelagos.

The Beringian Refuge

Beringia is an ancient arctic landscape that no longer exists as an intact body of land. During Late Pleistocene glaciations when global sea level was lowered by 60 m or more, the shallow continental shelf regions between northeastern Siberia and western Alaska became dry land, forming a land bridge between the two continents. The Bering Land Bridge was not a narrow isthmus between Siberia and Alaska. Rather, it was a more-or-less hourglass-shaped landscape that was twice the size of the state of Texas. This land bridge not only allowed the passage of many species of plants and animals between the two continents, it was essentially the *only* land connection between the Old World (the Palearctic region) and the New World (the Nearctic). That this land bridge remained unglaciated throughout the Pleistocene is quite remarkable, since the vast majority of Arctic landscapes were covered with glacial ice during each glacial interval, and the glaciations span as much as 90% of the last 2.5 million years.

Beringia has long been the focus of biogeographic research. There are two principal reasons for this. First is the connection between Asia and North America provided by the Bering Land Bridge. Second, it has been established that Beringia played a key role as a refuge for Arctic biota during repeated episodes of Pleistocene glaciation. Not only the Bering Land Bridge, but also the vast lowland regions of northeastern Siberia, interior Alaska, and the Yukon Territory of Canada remained essentially ice-free,

even during times of maximum glaciation. As discussed above, such an Arctic refuge was not available to the flora and fauna of Greenland or the Barents Sea archipelagos.

Thus the region we call Beringia provided critical habitats for the cold-adapted biota of the Arctic, and it also provided a terrestrial pathway linking the two major continents of the Northern Hemisphere. The Holarctic modern distributions of many mammalian species led biogeographers as far back as Wallace (1876) to speculate on an ancient connection between Siberia and Alaska. More substantial evidence for the Bering Land Bridge was provided by botanist Erik Hultén in 1937, based largely on his studies of the modern floras of Alaska and Siberia. Beginning with Hopkins (1967) and continuing with Hopkins (1982) and Hoffecker and Elias (2007), research on Beringian paleoenvironments has been well summarized.

Arctic Insects and Climate Change

Arctic insects have survived the waxing and waning of polar ice sheets and glaciers since time immemorial. The fossil record indicates that many species have persisted throughout the Pleistocene, the last 2.6 million years. The record holder for longevity of an arctic species is the water scavenger beetle, *Helophorus arcticus* (Fig. 4). Fossils of this species have been found in Siberian deposits dating back ~20 million years (Fikáček et al., 2011). Arctic insects have survived not by evolving new adaptations, but by shifting their distributions in response to climate change. Cold intervals saw the distributions of Arctic insects shift either southwards, or into the Beringian refuge. Warm intervals saw their expansion into recently deglaciated landscapes. This natural process has repeated itself dozens of times since Quaternary glaciations began. The fossil record demonstrates that each major climatic change brings about a new reshuffling of species into specific regions. However, Arctic insects are extremely vulnerable to the current global warming, which is amplified at the poles. This is because the pace and amplitude of the current and predicted future changes greatly exceed those of previous warming intervals. As temperatures rise, especially in the Arctic, the native fauna will suffer and decline. Insects living in the High Arctic can find no more northerly places available for immigration. The rising temperatures will decrease the fitness of cold-hardy insects, and they will also be forced to compete with more warm-adapted insects, invading from the south. Likewise, changes in the composition of high latitude plant communities, a phenomenon already documented in many Arctic regions, will disturb the balance of Arctic ecosystems, including long-established plant-insect interactions. The cold-hardiness of Arctic insects, their greatest asset for survival in previous millennia, may very well become their greatest liability in the coming decades.

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Arctic Tundra Mammals

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Abstract

The Arctic tundra biome has had a brief but highly variable history of formation compared with other world biomes, culminating in the modern northern flora and fauna that collectively maintain biodiversity connections on a global scale. Terrestrial Arctic tundra mammals constitute a fauna of approximately 80 species, to varying degrees adapted for life north of treeline. In addition to specializations for cold environments, Arctic mammals have evolved in response to dramatic climate cycling through the last 3 million years of the Quaternary period, developing life histories that reflect changing associations with other species and other biomes through time. This article focuses on evolutionary development of the modern Arctic tundra mammal assemblage, the environmental processes that have influenced their diversity and distribution across the northern hemisphere through time, and their collective ecology that drives continued community changes. In modern times, the Arctic is experiencing climate warming and associated anthropogenic environmental disturbances that are approaching the limits of what tundra mammals have experienced at any time through the history of this biome. Continued persistence of mammals within the Arctic tundra will depend on resilience and plasticity among species, and on concerted efforts by us to understand the processes that impact Arctic biodiversity in general. By doing so, scientists may anticipate focal species, local communities, or geographic regions at highest risk of population declines, investigate the consequences of changing species associations for competition, future evolutionary potential, and spread of disease, and ultimately manage and conserve these ecosystems and tundra wildlife more effectively.

Introduction

Mention of Arctic tundra will generally conjure images of a cold, stark, open landscape intermittently dotted with shaggy beasts fending off inclement weather, biting flies, or other shaggy beasts. These vistas (e.g., Fig. 1) often include pre-historic components of megafaunal assemblages that are now extinct and no longer interact within high latitude communities. Although large mammals continue to epitomize Arctic tundra landscapes, this classic view of mammalian tundra communities in the North is somewhat inaccurate, being under-representative of the diversity of mammals that contribute to a functional Arctic tundra biome today. This review focuses on all living (and some extinct) Arctic tundra mammal species and their environments through time from the perspective of both foundational and emerging research. These studies are refining our view of the environmental, ecological and evolutionary processes of change that have influenced Arctic species through the last 3 million years (Myr), and are providing informed predictions for future trends that may guide more effective management and conservation of tundra mammals and their associated communities (ACIA, 2005; Meltofte et al., 2013).

It is worth introducing this system through some definitions. The “Arctic” is variably defined as all land north of (a) the Arctic Circle, (b) the 10°C isotherm for average summer temperature, or (c) northern treeline. All are related, as global orbital processes govern seasonality, insolation, and the environmental conditions necessary for establishment or exclusion of boreal forests across latitude. However, a “north of treeline” view possibly captures best the current biotic associations of Arctic mammals, although this has certainly not been consistent through geologic time.

The term “tundra” is here defined in the context of most terrestrial (and non-riparian) habitats currently occurring north of treeline. Tundra communities as they exist today are characterized by flora and fauna that are adapted to cold environments, shallow wet-humic or dry-rocky soils built on surficial permafrost, with often prolonged winter snow cover, overcast and wet summers, and correspondingly short growing seasons. Despite an abundance of surface water, frozen conditions for much of the



Fig. 1 Artistic reconstruction of a Quaternary landscape within Beringia, illustrating a hypothetical mammalian community including steppe, tundra, and boreal associated species, having no modern analog. Original Artist: Mauricio Antón.

year combined with low annual rainfall translates to an arid biome relative to most others (Callaghan et al., 2004). This view of Arctic tundra is often confusingly interchanged with terms such as steppe-tundra, steppe, or tundra-steppe, particularly when considering pre-historical conditions at northern high latitudes. However, as discussed below, the abiotic criteria of shallow permafrost and often waterlogged soils in defining Arctic tundra is essential for interpreting changes in associated biotic communities through time (Guthrie, 2001).

Arctic tundra mammals are endothermic vertebrate species sharing ancestral mammalian features (i.e., hair, mammary glands) but often with uniquely derived adaptations for living through cold winters, wet summers and highly seasonal environments (Callaghan et al., 2004). This fauna is comprised of relatively few species (~80; Table 1) that may be found in tundra across the Holarctic, although only roughly a third of these are endemic to Arctic tundra. Most are either habitat generalists, widespread through northern latitudes, or are predominantly associated with boreal forest habitats, being found within tundra only near the northern forest edge. Two of the most iconic Arctic mammals, the polar bear (*Ursus maritimus*) and Arctic fox (*Vulpes lagopus*) only inhabit the coastal fringe of tundra, and are primarily maritime species spending much of the year on sea ice. The consequent mixing of species from distinct biomes has been a pervasive process through the history of the modern tundra mammal assemblage.

Despite a relatively depauperate fauna, the scientific literature on Arctic mammals is extensive, reflecting a broad spatial and temporal focus that has drawn evidence from across the earth and life sciences. Ecological associations among living species (such as trophic webs, species interactions, and requirements of climate, habitat and microhabitat) increase our understanding of how current communities function (Meltøfte et al., 2013). Paleontological studies have revealed much of the life histories of now-extinct mammals or extirpated populations of species that highlight changing distributions and faunal assemblages through time (Guthrie, 2001). Geographic origins and evolutionary relationships among mammal species can be interpreted from genetic or morphological signatures of modern species. A combination of current species distributions, ancestral fossil localities and paleo-environmental reconstructions reflect multiple prolonged episodes of isolation, reconnection, and interactions within northern biomes (Markova et al., 2009). Increasingly, comparative investigations of co-distributed species and particularly of co-evolved species, such as combined evidence from mammalian hosts and their parasites, are revealing exciting biodiversity perspectives of faunal assemblages through time that cannot be learned from individual species assessments (Hoberg et al., 2017). These collective studies include evidence of relatively rapid formation of new species through time, past extinctions, and the corresponding complexity of shifting interactions between mammals and other groups of species across the Arctic, and globally. Under the lens of multiple integrated scientific disciplines, the study of tundra mammals can help us to define the drivers of biogeographic and natural history of species from multiple biomes through time (Hoberg et al., 2003).

History, Biogeography, and Ecology—Development of the Arctic Tundra Mammal Assemblage Through Time

Ice-Age Climate

The Arctic tundra biome dates to the Late Pliocene, roughly 3 million years ago (Ma; Abbott and Brochmann, 2003). At that time, coniferous forests were distributed northward to the Arctic Ocean and global temperatures were higher than today, although climates were changing. Following development of a permanent Arctic polar ice-cap around 2.6 Ma (Knies et al., 2014), global climate transitioned into the Quaternary period, accompanied by cooling, and onset of a cyclic climate regime that has typified long

Table 1 Extant mammal species that occur in Arctic tundra, indicating distributions, ecological associations, and associated phylogeographic assessments. Introduced species are not considered

Order	Family	Genus	Species	Common name ^a	Geography	Habitat ^b	Biome ^c	Citations ^d
Primates	Hominidae	<i>Homo</i>	<i>sapiens</i>	Human	Holarctic	boreal/ tundra	ubiquitous	N/A
Rodentia	Castoridae	<i>Castor</i>	<i>canadensis</i>	American beaver	Nearctic	boreal/ tundra	boreal	108
Rodentia	Castoridae	<i>Castor</i>	<i>fiber</i>	Eurasian beaver	Palearctic	boreal/ tundra	boreal	28, 30, 107
Rodentia	Cricetidae	<i>Alticola</i>	<i>lemminus</i>	Lemming vole	Palearctic	tundra/ boreal	tundra	68
Rodentia	Cricetidae	<i>Arvicola</i>	<i>terrestris</i>	Eurasian water vole	Palearctic	boreal/ tundra	boreal	120
Rodentia	Cricetidae	<i>Dicrostonyx</i>	<i>groenlandicus</i>	Northern collared lemming	Holarctic	tundra	steppe	33, 35, 37, 131
Rodentia	Cricetidae	<i>Dicrostonyx</i>	<i>hudsonius</i>	Ungava collared lemming	Nearctic	tundra	tundra	35, 43
Rodentia	Cricetidae	<i>Dicrostonyx</i>	<i>richardsoni</i>	Richardson's collared lemming	Nearctic	tundra	tundra	43
Rodentia	Cricetidae	<i>Dicrostonyx</i>	<i>torquatus</i>	Palearctic collared lemming	Palearctic	tundra	tundra	34, 38, 99
Rodentia	Cricetidae	<i>Lasiopodomys</i>	<i>gregalis</i>	Narrow-headed vole	Palearctic	tundra/ boreal	steppe	96, 97
Rodentia	Cricetidae	<i>Lemmus</i>	<i>amurensis</i>	Amur lemming	Palearctic	tundra/ boreal	tundra	1
Rodentia	Cricetidae	<i>Lemmus</i>	<i>lemmus</i>	Norway lemming	Palearctic	tundra/ boreal	tundra	34, 36, 38, 39
Rodentia	Cricetidae	<i>Lemmus</i>	<i>sibiricus</i>	Siberian brown lemming	Palearctic	tundra	tundra	38, 39, 51
Rodentia	Cricetidae	<i>Lemmus</i>	<i>trimucronatus</i>	Nearctic brown lemming	Nearctic	tundra	tundra	39, 51
Rodentia	Cricetidae	<i>Microtus</i>	<i>abbreviatus</i>	Insular vole	Insular	graminoid tundra	tundra	130
Rodentia	Cricetidae	<i>Microtus</i>	<i>agrestis</i>	Field vole	Palearctic	boreal/ tundra	boreal	52, 62
Rodentia	Cricetidae	<i>Microtus</i>	<i>hyperboreus</i>	Siberian vole	Palearctic	tundra/alpine tundra	steppe	None
Rodentia	Cricetidae	<i>Microtus</i>	<i>middendorffii</i>	Middendorf's vole	Palearctic	tundra	tundra	None
Rodentia	Cricetidae	<i>Microtus</i>	<i>miurus</i>	Singing vole	Nearctic	tundra/ boreal	tundra	77, 130
Rodentia	Cricetidae	<i>Microtus</i>	<i>oeconomus</i>	Tundra/root vole	Holarctic	boreal/ tundra	tundra	8, 9, 44, 61, 74
Rodentia	Cricetidae	<i>Microtus</i>	<i>pennsylvanicus</i>	Meadow vole	Nearctic	boreal/ tundra	boreal	63
Rodentia	Cricetidae	<i>Microtus</i>	<i>xanthognathus</i>	Taiga vole	Nearctic	boreal/ tundra	tundra	None
Rodentia	Cricetidae	<i>Myodes</i>	<i>glareolus</i>	Bank vole	Palearctic	boreal/ tundra	boreal	2, 25, 83, 133
Rodentia	Cricetidae	<i>Myodes</i>	<i>rufocanus</i>	Gray-sided vole	Palearctic	boreal/ tundra	boreal	17, 68
Rodentia	Cricetidae	<i>Myodes</i>	<i>rutilus</i>	Northern red-backed vole	Holarctic	boreal/ tundra	boreal	69
Rodentia	Cricetidae	<i>Myopus</i>	<i>schisticolor</i>	Wood lemming	Palearctic	boreal/ tundra	boreal	40
Rodentia	Cricetidae	<i>Ondatra</i>	<i>zibethicus</i>	Muskrat	Nearctic	boreal/ tundra	boreal	78
Rodentia	Cricetidae	<i>Sicista</i>	<i>betulina</i>	Northern birch mouse	Palearctic	boreal/ tundra	boreal	None
Rodentia	Cricetidae	<i>Synaptomys</i>	<i>borealis</i>	Northern bog-lemming	Nearctic	boreal/ tundra	boreal	None
Rodentia	Erethizontidae	<i>Erethizon</i>	<i>dorsatum</i>	North American porcupine	Nearctic	boreal/ tundra	boreal	None
Rodentia	Sciuridae	<i>Marmota</i>	<i>broweri</i>	Alaska marmot	Nearctic	tundra	steppe	48
Rodentia	Sciuridae	<i>Marmota</i>	<i>caligata</i>	Hoary marmot	Nearctic	boreal/alpine tundra	boreal	64

(Continued)

Table 1 (Continued)

<i>Order</i>	<i>Family</i>	<i>Genus</i>	<i>Species</i>	<i>Common name</i>	<i>Geography</i>	<i>Habitat</i>	<i>Biome</i>	<i>Citations</i>
Rodentia	Sciuridae	<i>Urocitellus</i>	<i>parryi</i>	Arctic ground-squirrel	Holarctic	tundra/ boreal	steppe	31, 46, 77
Rodentia	Sciuridae	<i>Urocitellus</i>	<i>undulatus</i>	Long-tailed ground squirrel	Palearctic	boreal/ tundra	boreal	88, 110
Lagomorpha	Leporidae	<i>Lepus</i>	<i>americanus</i>	Snowshoe hare	Nearctic	boreal/ tundra	boreal	15, 90
Lagomorpha	Leporidae	<i>Lepus</i>	<i>arcticus</i>	Arctic hare	Nearctic	tundra	steppe	127
Lagomorpha	Leporidae	<i>Lepus</i>	<i>othus</i>	Alaskan hare	Nearctic	tundra	tundra	13, 127
Lagomorpha	Leporidae	<i>Lepus</i>	<i>timidus</i>	Mountain hare	Palearctic	tundra/ boreal	tundra	50, 89, 111, 127
Lagomorpha	Ochotonidae	<i>Ochotona</i>	<i>collaris</i>	Collared pika	Nearctic	alpine tundra	steppe	45, 75, 76, 77
Lagomorpha	Ochotonidae	<i>Ochotona</i>	<i>hyperborea</i>	Northern pika	Palearctic	boreal/ tundra	boreal	None
Lagomorpha	Ochotonidae	<i>Ochotona</i>	<i>turuchanensis</i>	Turuchan pika	Palearctic	boreal/ tundra	boreal	None
Soricomorpha	Soricidae	<i>Neomys</i>	<i>fodiens</i>	Eurasian water shrew	Palearctic	boreal/ tundra	boreal	14
Soricomorpha	Soricidae	<i>Sorex</i>	<i>araneus</i>	Common shrew	Palearctic	boreal/ tundra	boreal	81, 109, 124, 133
Soricomorpha	Soricidae	<i>Sorex</i>	<i>arcticus</i>	Arctic shrew	Nearctic	boreal/ tundra	boreal	81, 114
Soricomorpha	Soricidae	<i>Sorex</i>	<i>caecutiens</i>	Laxmann's shrew	Palearctic	boreal/ tundra	boreal	93
Soricomorpha	Soricidae	<i>Sorex</i>	<i>cinereus</i>	Masked shrew	Nearctic	boreal/ tundra	boreal	27, 56
Soricomorpha	Soricidae	<i>Sorex</i>	<i>hoyi</i>	American pygmy shrew	Nearctic	boreal/ tundra	boreal	57, 115
Soricomorpha	Soricidae	<i>Sorex</i>	<i>jacksoni</i>	St. Lawrence Island shrew	Insular	tundra	tundra	27, 56
Soricomorpha	Soricidae	<i>Sorex</i>	<i>leucogaster</i>	Paramushir shrew	Insular	graminoid tundra	tundra	27, 56
Soricomorpha	Soricidae	<i>Sorex</i>	<i>minutissimus</i>	Holarctic least shrew	Holarctic	boreal/ tundra	boreal	54, 94
Soricomorpha	Soricidae	<i>Sorex</i>	<i>minutus</i>	Eurasian pygmy shrew	Palearctic	boreal/ tundra	boreal	124, 125
Soricomorpha	Soricidae	<i>Sorex</i>	<i>monticola</i>	Montane shrew	Nearctic	boreal/ tundra	boreal	26
Soricomorpha	Soricidae	<i>Sorex</i>	<i>portenkoi</i>	Portenko's shrew	Palearctic	tundra	tundra	27, 56
Soricomorpha	Soricidae	<i>Sorex</i>	<i>pribilofensis</i>	Pribilof Islands shrew	Insular	graminoid tundra	tundra	27, 56
Soricomorpha	Soricidae	<i>Sorex</i>	<i>roboratus</i>	Flat-skulled shrew	Palearctic	boreal/ tundra	boreal	None
Soricomorpha	Soricidae	<i>Sorex</i>	<i>tundrensis</i>	Tundra shrew	Holarctic	boreal/ tundra	tundra	6, 55
Soricomorpha	Soricidae	<i>Sorex</i>	<i>ugyunak</i>	Barrenground shrew	Nearctic	tundra	tundra	27, 56
Carnivora	Canidae	<i>Canis</i>	<i>latrans</i>	Coyote	Nearctic	boreal/ tundra	boreal	67
Carnivora	Canidae	<i>Canis</i>	<i>lupus</i>	Grey wolf	Holarctic	boreal/ tundra	tundra	29, 66, 98, 101, 126, 128
Carnivora	Canidae	<i>Vulpes</i>	<i>fulva</i>	North American red fox	Nearctic	boreal/ tundra	boreal	113
Carnivora	Canidae	<i>Vulpes</i>	<i>lagopus</i>	Arctic fox	Holarctic	tundra/ maritime	maritime	18, 19, 20
Carnivora	Canidae	<i>Vulpes</i>	<i>vulpes</i>	Eurasian red fox	Holarctic	boreal/ tundra	boreal	4, 72, 113, 122
Carnivora	Felidae	<i>Lynx</i>	<i>canadensis</i>	Canada lynx	Nearctic	boreal/ tundra	boreal	103
Carnivora	Felidae	<i>Lynx</i>	<i>lynx</i>	Eurasian lynx	Palearctic	boreal/ tundra	boreal	104
Carnivora	Mustelidae	<i>Gulo</i>	<i>gulo</i>	Wolverine	Holarctic	boreal/ alpine/ tundra	boreal	70, 123, 136

Table 1 (Continued)

<i>Order</i>	<i>Family</i>	<i>Genus</i>	<i>Species</i>	<i>Common name</i>	<i>Geography</i>	<i>Habitat</i>	<i>Biome</i>	<i>Citations</i>
Carnivora	Mustelidae	<i>Lontra</i>	<i>canadensis</i>	North American river otter	Nearctic	boreal/ tundra	boreal	None
Carnivora	Mustelidae	<i>Lutra</i>	<i>lutra</i>	Eurasian otter	Palearctic	boreal/ tundra	boreal	None
Carnivora	Mustelidae	<i>Martes</i>	<i>americana</i>	American marten	Nearctic	boreal/ tundra	boreal	24, 73, 117, 118
Carnivora	Mustelidae	<i>Martes</i>	<i>martes</i>	Eurasian pine marten	Palearctic	boreal/ tundra	boreal	21, 73b, 105, 117
Carnivora	Mustelidae	<i>Mustela</i>	<i>erminea</i>	Ermine/stoat	Holarctic	boreal/ tundra	tundra	16, 23, 42, 71, 85
Carnivora	Mustelidae	<i>Mustela</i>	<i>lutreola</i>	Eurasian mink	Palearctic	boreal/ tundra	boreal	112
Carnivora	Mustelidae	<i>Mustela</i>	<i>nivalis</i>	Least weasel	Holarctic	boreal/ tundra	steppe	71, 79, 87, 102
Carnivora	Mustelidae	<i>Mustela</i>	<i>vison</i>	North American mink	Nearctic	boreal/ tundra	boreal	None
Carnivora	Ursidae	<i>Ursus</i>	<i>americanus</i>	American black bear	Nearctic	boreal/ tundra	boreal	10, 100, 116, 134
Carnivora	Ursidae	<i>Ursus</i>	<i>arctos</i>	Brown bear	Holarctic	boreal/ tundra	tundra	3, 7, 22, 53, 91, 119, 121
Carnivora	Ursidae	<i>Ursus</i>	<i>maritimus</i>	Polar bear	Holarctic	maritime/ tundra	maritime	11, 32, 49, 84, 95
Artiodactyla	Bovidae	<i>Ovibos</i>	<i>moschatus</i>	Muskox	Holarctic	tundra	tundra	12, 47, 82
Artiodactyla	Bovidae	<i>Ovis</i>	<i>dalli</i>	Dall's sheep	Nearctic	alpine tundra/ tundra	tundra	80, 106
Artiodactyla	Bovidae	<i>Ovis</i>	<i>nivicola</i>	Snow sheep	Palearctic	alpine tundra/ boreal	boreal	None
Artiodactyla	Cervidae	<i>Alces</i>	<i>alces</i>	Moose	Holarctic	boreal/ tundra	boreal	58, 59, 60, 92
Artiodactyla	Cervidae	<i>Rangifer</i>	<i>tarandus</i>	Caribou	Holarctic	tundra/ boreal	tundra	5, 41, 65, 86, 129, 135

^aDue to continental differences in biogeographic history, most Eurasian species with steppic associations at the last glacial maximum currently occur south of the boreal belt in central Asia and are therefore excluded.

^bHabitat is designated in order of predominance within current distributional range.

^cBiome associations are designated as a best approximation of both glacial and interglacial phase associations through the late-Quaternary, as reflected by phylogeographic evidence of refugial persistence in the Arctic, peri-glacial fossil evidence, or from the most current literature that may reflect diet (e.g., grass or moss) or substrate (e.g., mesic or xeric) preferences.

^dFull phylogeographic study citations are provided in the *Reference* section. Regional phylogeographic assessments considering only lineages south of Arctic tundra are not included.

¹Abramson et al. (2008), ²Abramson et al. (2009), ³Anijalg et al. (2018), ⁴Aubry et al. (2009), ⁵Banks et al. (2008), ⁶Bannikova et al. (2010), ⁷Barnes et al. (2002), ⁸Brunhoff et al. (2003), ⁹Brunhoff et al. (2006), ¹⁰Byun et al. (1997), ¹¹Cahill et al. (2018), ¹²Campos et al. (2010), ¹³Cason et al. (2016), ¹⁴Castiglia et al. (2007), ¹⁵Cheng et al. (2014), ¹⁶Colella et al. (2018), ¹⁷Cook et al. (2004), ¹⁸Dalén et al. (2002), ¹⁹Dalén et al. (2004), ²⁰Dalén et al. (2007), ²¹Davison et al. (2000), ²²Davison et al. (2001), ²³Davison et al. (2011), ²⁴Dawson et al. (2014), ²⁵Deffontaine et al. (2005), ²⁶Demboski and Cook (2001), ²⁷Demboski and Cook (2003), ²⁸Ducroz et al. (2005), ²⁹Dufresne et al. (2018), ³⁰Durka et al. (2005), ³¹Eddingsaas et al. (2004), ³²Edwards et al. (2012), ³³Ehrlich et al. (2000), ³⁴Fedorov (1999), ³⁵Fedorov and Goropashnaya (1999), ³⁶Fedorov and Stenseth (2001), ³⁷Fedorov and Stenseth (2002), ³⁸Fedorov et al. (1999), ³⁹Fedorov et al. (2003), ⁴⁰Fedorov et al. (2008), ⁴¹Flagstad and Røed (2003), ⁴²Fleming and Cook (2002), ⁴³Fulton et al. (2013), ⁴⁴Galbreath and Cook (2004), ⁴⁵Galbreath and Hoberg (2011), ⁴⁶Galbreath et al. (2011), ⁴⁷Groves (1997), ⁴⁸Gunderson et al. (2012), ⁴⁹Hailer et al. (2012), ⁵⁰Hamill et al. (2006), ⁵¹Haukismäki et al. (2016a, b), ⁵²Herman et al. (2014), ⁵³Hirata et al. (2013), ⁵⁴Hope et al. (2010), ⁵⁵Hope et al. (2011), ⁵⁶Hope et al. (2012), ⁵⁷Hope et al. (n.d.), ⁵⁸Hundertmark and Bowyer (2004), ⁵⁹Hundertmark et al. (2002), ⁶⁰Hundertmark et al. (2003), ⁶¹Iwasa et al. (2009), ⁶²Jaarola and Searle (2002), ⁶³Jackson (2016), ⁶⁴Kerhoulas et al. (2015), ⁶⁵Klüttsch et al. (2012), ⁶⁶Kobl Müller et al. (2016), ⁶⁷Kobl Müller et al. (2012), ⁶⁸Kohli et al. (2014), ⁶⁹Kohli et al. (2015), ⁷⁰Krejsa (2017), ⁷¹Kurose et al. (2005), ⁷²Kutschera et al. (2013), ⁷³Kyle and Strobeck (2003), ⁷⁴Kyle et al. (2003), ⁷⁵Lance and Cook (1998), ⁷⁶Lanier and Olson (2013), ⁷⁷Lanier et al. (2015a), ⁷⁸Lanier et al. (2015b), ⁷⁹Laurence et al. (2011), ⁸⁰Lebarbenchon et al. (2010), ⁸¹Loehr et al. (2006), ⁸²Mackiewicz et al. (2017), ⁸³MacPhee et al. (2005), ⁸⁴Male et al. (2012), ⁸⁵Malenfant et al. (2016), ⁸⁶Martinková et al. (2007), ⁸⁷McDevitt et al. (2009), ⁸⁸McLean et al. (2012), ⁸⁹Melo-Ferreira et al. (2007), ⁹⁰Melo-Ferreira et al. (2014), ⁹¹Miller et al. (2006), ⁹²Niedziałkowska et al. (2014), ⁹³Ohdachi et al. (2001), ⁹⁴Ohdachi et al. (2012), ⁹⁵Peacock et al. (2015), ⁹⁶Petrova et al. (2015), ⁹⁷Petrova et al. (2016), ⁹⁸Pilot et al. (2010), ⁹⁹Prost et al. (2010), ¹⁰⁰Puckett et al. (2015), ¹⁰¹Randi (2011), ¹⁰²Reig (1997), ¹⁰³Rueness et al. (2003), ¹⁰⁴Rueness et al. (2014), ¹⁰⁵Ruiz-González et al. (2013), ¹⁰⁶Sage and Wolff (1986), ¹⁰⁷Senn et al. (2014), ¹⁰⁸Serrano (2012), ¹⁰⁹Shchipanov and Pavlova (2013), ¹¹⁰Simonov et al. (2017), ¹¹¹Smith et al. (2017), ¹¹²Statham et al. (2014), ¹¹³Stewart et al. (2002), ¹¹⁴Stewart et al. (2003), ¹¹⁵Stone and Cook (2000), ¹¹⁶Stone and Cook (2002), ¹¹⁷Stone et al. (2002), ¹¹⁸Taberlet and Bouvet (1994), ¹¹⁹Taberlet et al. (1998), ¹²⁰Taberlet et al. (1998), ¹²¹Talbot and Shields (1996), ¹²²Teacher et al. (2011), ¹²³Tomasik and Cook (2005), ¹²⁴Vega et al. (2010), ¹²⁵Vega et al. (2016), ¹²⁶Vilà et al. (1999), ¹²⁷Waltari and Cook (2005), ¹²⁸Weckworth et al. (2010), ¹²⁹Weckworth et al. (2012), ¹³⁰Weksler et al. (2010), ¹³¹Wickström et al. (2003), ¹³²Wójcik et al. (2002), ¹³³Wójcik et al. (2010), ¹³⁴Wooding and Ward (1997), ¹³⁵Yannic et al. (2014), ¹³⁶Zigouris et al. (2013).

term environmental change up to the present. Cycles consisted of relatively short warmer (interglacial) climate phases transitioning abruptly to more prolonged cold (glacial) phases. In the mid-Quaternary (~800 thousand years ago [ka]) climate cycles changed in their regular periodicity from every 41 thousand years (kyr) to 100 kyr, and cycle amplitude also increased. These most recent and extreme climate cycles, particularly since the transition to longer and more intense phases, had profound consequences for the distributions, processes of diversification, and interactions among biodiversity (Hewitt, 1996).

Although global in scope, the impact of this Quaternary “Ice Age” was most pronounced in the Arctic. Not only did species need to endure colder conditions, but during glacial phases, build-up of regional glaciers and continental ice-sheets as well as changing local conditions forced species to shift their ranges repeatedly, and dramatically (Pielou, 1991). In response to each climatic oscillation between glacial and interglacial, local species populations could either move, adapt to local changes, or experience significant population declines, often culminating in regional extirpation or range-wide extinction (Gilg et al., 2012). Any of these outcomes would have resulted in changing evolutionary trajectories, essentially both promoting diversification in some areas while eliminating local diversity from others through time (Lister, 2004). Over 20 major climate cycles were recorded through the Quaternary, with many additional and influential stadials/interstadials (more minor intra-cycle climate fluctuations; Wooler et al., 2018), affecting significant evolutionary change among tundra mammals.

Quaternary Biogeography

The cyclic nature of Quaternary climate and associated habitat fluctuations might be visualized as a see-saw that within the Arctic has oscillated between cool, wet conditions during interglacial phases, and cold, dry conditions during glacial phases. It is important to note that our current global warming trend through the present interglacial (=Holocene) is still markedly cooler ($\geq 3^{\circ}\text{C}$) on average than pre-Quaternary climate (Brigham-Grette et al., 2013).

Each climatic transition to a glacial phase was characterized by a net annual accumulation of terrestrial snow and ice, developing over thousands of years into continental ice-sheets, corresponding lowered sea-levels, and exposed land-mass, causing a rearrangement of the distributions of terrestrial mammals and their associated habitats. In this way, greater than 3 vertical kilometers of ice was deposited over much of Canada during the last glacial maximum (LGM; 21 ka), displacing the resident mammals into ice-free glacial refugia around the periphery of ice-sheets. In North America, populations of many Arctic mammals were repeatedly displaced south during glacial phases into peri-glacial refugia all across what are now the northern contiguous United States, including both brown (*Lemmus trimucronatus*) and collared (*Dicrostonyx groenlandicus*) lemmings (Burns, 2004). Other populations were shunted to coastal areas where they persisted in sometimes cryptic refugial areas of exposed continental shelf that became submerged again during interglacial phases. In Europe, mammal populations similarly shifted to more southern or coastal refugia as ice-sheets repeatedly developed over northwestern Eurasia (Fløjgaard et al., 2009). At the same time that large portions of the Arctic were fragmented and unavailable to mammals during glacial phases, much of central and eastern Asia remained ice-free, and lowered sea-levels resulted in connections between previously isolated land masses, opening corridors for species movement. The prime example in the Arctic is the region known as Beringia (Hultén, 1937), an ice-free terrestrial region extending from northeastern Siberia eastward across the Bering Land Bridge to unglaciated regions of Alaska and the Yukon Territory. Beringia promoted the intercontinental spread and diversification of Arctic mammals repeatedly through the Quaternary (Rausch, 1963; Waltari et al., 2007).

Each transition from glacial to interglacial phase resulted in a change to net annual loss of snow and ice, gradually melting glaciers and ice-sheets. The Beringian land-connection between Eurasia and North America was repeatedly lost as sea levels rose by as much as 130 m worldwide. Although many exposed coastal-shelf refugia were re-submerged at these times, populations from around the periphery of ice-sheets could again expand to fill newly exposed mainland areas (Pielou, 1991).

These dynamic environmental changes through the Quaternary were a strong driver of diversification among all extant Arctic tundra mammals, as well as those that are now extinct (Graham, 1986). What has been much less clear until recently is what environmental conditions were optimal for the proliferation of the Arctic tundra biome and what processes were most influential in promoting diversification among tundra mammals.

Split Origins of Arctic Mammals

The earliest Arctic tundra habitats at the onset of the Quaternary are thought to have originated from arid and cold adapted alpine floras that occupied mountaintop meadows, or from plants associated with mesic grasslands and forests that persisted and spread above treeline following the retreat of tree species (Abbott and Brochmann, 2003; Hoffmann et al., 2010). Provided mammal species were not constrained by a reliance on trees, or tree resources, early Arctic mammals may have stemmed from forest, grassland, or alpine taxa, adapting to cooling climates and habitats as floral communities experienced turnover (Lister, 2004). Many tundra mammal species today may be found broadly through both forest and tundra habitats. Other mammals such as the tree squirrels *Sciurus vulgaris* in Eurasia or *Tamiasciurus hudsonicus* in North America, or their associated predators the pine marten (*Martes martes*) or American marten (*Martes americana*), respectively, remained specialized within forests and became part of modern boreal communities.

But as species became adapted to colder environments across the north, there was a key dichotomy, with two unique biomes developing as a consequence of Ice Age conditions, including both Arctic tundra and what is now known as “mammoth steppe” (Guthrie, 2001). The distinction between these two biomes is of requisite importance as they define not only the associated floras

and faunas, but also the time frames during which they repeatedly rose and fell from prominence through the Arctic (Sher et al., 2005; Kahlke, 2014). Arctic tundra spread broadly across the north during interglacial phases when conditions were cool and wet, supporting dominant plants and fungi such as mosses, lichens, forbs, tussock grasses and dwarf shrubs growing on waterlogged acidic soils. In contrast, the mammoth steppe was associated with colder, and very dry conditions during glacial phases, and was dominated by grasses and sedges growing in deep, well-drained and alkaline soils (Guthrie, 2001). It is difficult to imagine an expanse of wind-swept arid grasslands across the unglaciated regions of the Arctic through a glacial maximum, displacing forests as far south as Mongolia and China in Central Asia; this is likely because virtually all of the steppe biome is now gone, and with it, many of the mammal species that relied on these environments.

A fundamental concept based on most recent evidence of Arctic ecology is that tundra, despite being a “cold associated” biome, was likely most patchy and limited in extent during the coldest glacial phases, when instead the mammoth steppe biome predominated across the north (Guthrie, 2001; Rabanus-Wallace et al., 2017). At these times, tundra communities were seemingly restricted to mesic refugia associated with major river drainages and other low-lying areas. One such region in central Beringia has helped to solidify this view. Evidence from terrestrial core samples taken from different locations through central Beringia have unearthed fossil beetle remains (Elias and Crocker, 2008), pollen samples, and isotopic values that together allow us to recreate the boundaries of a “mesic buckle” through the last glacial phase (Guthrie, 2001). Glacial phase samples through this region indicated ground water and wet conditions that supported tundra beetles and plants, whereas other sites of the same age, particularly through western and easternmost Beringia instead supported species associated with steppe and with radiocarbon dates, floral and faunal evidence indicating extreme aridity (Sher et al., 2005; Elias et al., 2006). Over the entire unglaciated regions of the Holarctic, despite some isolated mesic areas, the vast majority of sites sampled from this time period reflect a predominance of mammoth steppe (Zazula et al., 2007).

Conversely, during interglacial periods, Arctic tundra was more widespread, allowing tundra mammals and their communities to expand ranges. As tundra spread, mammoth steppe retreated, and in its place, warmer and wetter climates promoted northward establishment of boreal forests and their associated mammals. These major floral changes were likely a strong driver of changing faunal distribution and diversity (Rabanus-Wallace et al., 2017).

Ecology of Arctic Mammals Past and Present

Wet Arctic tundra supports most of the mammal species north of treeline that we see today, including rodents such as the brown and Norwegian lemmings (*Lemmus sibiricus* and *L. lemmus*, respectively) that feed largely on mosses and wet grasses. Collared lemmings (*Dicrostonyx* sp.) forage for berries, and bark from dwarf shrubs growing on higher ground among freeze-thaw polygons, and Arctic ground squirrels (*Urocitellus parryi*) cache grasses, wet sedges, and forbs for winter hibernation in well-drained upland soils where permafrost is sufficiently deep for burrow construction. Soricine insectivores such as the barren-ground shrew (*Sorex ugyunak*) and tundra shrew (*S. tundrensis*) thrive in interstitial and subnivean spaces, eating abundant arthropods within tussock and shrub-tundra. The few extant megafaunal species include caribou (*Rangifer tarandus*), often ranging in dense herds, and muskox (*Ovibos moschatus*), both of which eat a variety of tundra foods including lichens and dwarf shrub browse. The combined foraging of both small and large herbivores can heavily impact the shallow-rooted and relatively fragile tundra flora (Ravolainen et al., 2011). Scars of caribou trails across the tundra are a legacy of their extensive migrations both in response to seasonal weather changes, and to track available food resources. Norwegian lemmings, as well as some vole species (*Microtus* sp. and *Myodes* sp.) can exhibit dramatic multi-year population cycles (Krebs et al., 2002). Population explosions may deplete food resources or increase predator densities, causing population crashes, and lagged recovery of both habitats and mammal numbers (Korpimäki et al., 2004; Ims and Fuglei, 2005). These herbivore populations are intimately associated with mammalian predator species that thrive through the northern tundra (Gilg et al., 2003). The grey wolf (*Canis lupus*) effectively hunts both large ungulates through cooperative pack behavior, and small rodents, depending on local supply through a given year. This versatility is perhaps reflective of the cosmopolitan historic distribution of wolves through the Northern Hemisphere. Equally versatile is the brown bear (*Ursus arctos*) that will graze, browse for berries, scavenge carcasses or actively hunt fish and other mammals, passing these learned skills through generations of young. Smaller predators include the ermine (or stoat; *Mustela erminea*) that can easily navigate the rugged structure of developed tundra in search of voles, their primary food source.

In contrast to Arctic tundra, the arid mammoth steppe largely supported grazing mammals. The hard, dry ground that provided substrate for growth of deep-rooted grasses also supported loading from hooves of heavy megafaunal species (Mann et al., 2013). As the name suggests, this steppe was home to the iconic woolly mammoth (*Mammuthus* sp.), and many other large grazers including steppe bison (*Bison priscus*), Yukon horse (*Equus lambei*), woolly rhino (*Coelodonta antiquitatis*), camels (*Camelops* sp.), saiga antelope (*Saiga tatarica*) and yak (*Bos grunniens*). Of these, only the saiga still persist in isolated populations, and the yak as a semi-domesticated animal, both occurring in central Asian arid grasslands south of the boreal zone. Predators also abounded through the steppe, including the wolf, scimitar cat (*Homotherium* sp.), Eurasian cave lion (*Panthera spelaea*) and short-faced bear (*Arctodus simus*). Again, only the wolf has survived to the present, with determinant extinctions of other hunting species accompanying loss of large mammal prey as the mammoth steppe gave way to Arctic tundra since the last glacial phase. Steppe-associated survivors of the Holocene transition are mostly smaller mammals. Predators such as least weasels (*Mustela nivalis*) hunted steppe rodents including narrow-headed voles (*Lasiopodomys gregalis*), Siberian voles (*Microtus hyperboreus*) and species belonging to many genera of arid-adapted small mammals. Examples include steppe lemmings (*Lagurus* sp., *Eolagurus* sp.), steppe voles (*Alticola* sp.), marmots (*Marmota* sp.) and jerboas (*Alactaga* sp.). Rabbit kin (lagomorphs), including hares (*Lepus* sp.) and pikas (*Ochotona* sp.) are also still

represented in steppe-like environments. All of these mammals persist through central Asia across remnant habitats. This region surrounding the mountains and plains of Kazakhstan, Mongolia, and northern China may constitute both a refugial area for steppe species, and also have served as a major geographic and evolutionary source of the mammoth steppe fauna through the Quaternary (Kahlke, 2014).

Much of what we know of the relationship of mammoth steppe and Arctic tundra in the context of their mammals is from paleontological investigations of fossil-rich sites such as caves and pits that are stratified through time as they collect dead specimens, providing sometimes well-defined layers of mammal remains along with other fauna and flora (Hopkins et al., 1982). Results of fossil surveys, dated using a combination of calibrating layer depth with radiocarbon isotopes, provide evidence of mammalian communities that have no modern analog, containing species associated with both Arctic tundra, boreal forests, and mammoth steppe that seemingly co-existed during glacial phases (Zazula et al., 2007). Whether tundra and steppe mammals did interact within diverse mixed assemblages is a matter of debate (Guthrie, 1982). Many mammal species are highly mobile, and may have been transient through an area rather than being a permanent resident. Some mammal species tend to be over- or under-represented in fossil deposits in relation to their densities across the landscape, giving an inaccurate impression of community composition (Graham, 1986). Additionally, many thousands of years of accumulation can often be compressed and partially mixed without the ability to resolve more fine-scale community changes across local landscapes over even multiple centuries of climatic variability.

More likely, these fossil deposits support the concept of an Arctic that has been highly variable and heterogeneous through time, where the three major high-latitude biomes of tundra, mammoth steppe, and forest formed a complex and shifting mosaic (Fig. 1; Graham, 1986; Lanoë et al., 2017). Relatively distinct mammal communities would have ebbed and flowed in their prevalence according to climatic variability, with the extremes of wet or dry conditions supporting more purely tundra- or steppe-associated faunas, respectively (Kahlke, 2014). An additional dynamic through multiple climate cycles is that species have progressively adapted to new habitats, eventually forming new lineages or species associated with different biomes (Hope et al., 2013a). The proximity of tundra and steppe habitats through glacial phases, or tundra and forest habitats through interglacials, would have provided abundant opportunity for ecological and evolutionary diversification (Zazula et al., 2007). It is also evident from modern day Arctic mammal assemblages that many species are habitat generalists, equally likely to be found in either Arctic tundra, or boreal forest regions. These species may be intermediates on the adaptive scale between specialized extremes, or simply less constrained by habitat affiliations than by climatic conditions (McCain et al., 2018).

Contemporary field surveys and studies of Arctic biodiversity spanning the major ecotone (environmental transition zone) between Arctic tundra and boreal forest biomes clearly indicate that (1) overall mammal diversity is higher in these areas of contact between biomes than purely boreal forest or Arctic tundra (Barrio et al., 2016), (2) habitat generalists are a major component of mammalian richness through the Arctic tundra, particularly across transition zones, and are predicted to contribute significantly to the dynamics of future Arctic biodiversity (Hof et al., 2012; Elmhagen et al., 2015), and 3) forest mammals are generally shifting northward as climate continues to warm, often faster than the establishment of tree species (Hope et al., 2015).

Research Priorities and Outlook

Mammals within Arctic tundra are not only a vital resource for local peoples and economies (e.g., Klein, 1970), but they are intimately connected with the broader Arctic biodiversity that collectively maintains functional Arctic ecosystems through time. In turn, intact tundra supports global linkages, through movement of avian, marine, and other taxa, and through source/sink dynamics of energy/nutrient transfer and long-term storage between and within atmosphere, land and oceans (Metcalf and Olofsson, 2015). Arctic biodiversity is low compared with most other biomes, and a broken connection through species decline or extinction, disruption of habitat and food resources through disturbance, or community turnover through invasion or introduction of nonnative species may have disproportionately negative and cascading impacts on one of the largest but most vulnerable of the world's biomes (Meltotte et al., 2013).

A principal value of studying tundra mammals is their usefulness as indicators of Arctic change (Hope et al., 2016). Most tundra mammals are resident year-round, highly adapted to northern environments, and sensitive to change through time. We can therefore use knowledge of how mammals have evolved in response to past environmental changes, assess current distributions through field sampling, monitor trends in population size and species traits such as genetic or phenotypic diversity, and consequently make more informed predictions for continued trends (Hope et al., 2013b). In association with understanding mammalian responses, it will be increasingly important to resolve the fundamental connections between mammals and other species both within the tundra biome, among other northern biomes, and globally.

Lineage Diversification, Warm and Cold Refugia, and Geographic Discontinuities

In the past three decades, the discipline of phylogeography has matured to effectively bridge the gap between the traditions of population genetics (analysis of intra- and inter-population diversity) and phylogenetics (higher-level evolutionary relationships) by resolving the evolutionary history of species across their geographic range on an intermediate timescale, roughly coincident with formation of species through the Quaternary (Avice, 2000). As such, phylogeographic studies have provided powerful insights on how Arctic tundra mammals evolve in response to their environments across space and through time. Since its inception, the field

has expanded to address more nuanced questions related to the processes of speciation, community assembly, risk of extinction and associated co-evolutionary consequences of change (Cook et al., 2017). Given that most Arctic tundra mammals have already been the focus of a phylogeographic investigation (Table 1), there is now great potential for synthesizing our knowledge of mammalian community dynamics of the Arctic tundra, and making informed predictions for continued population and species trajectories into the Anthropocene (Hope et al., 2015; Lanier et al., 2015).

A key advantage of phylogeographic inference is that studies establish regional centers of diversity both within and among species, and through time. Evidence based on DNA sequence data indicates that most species vary genetically across their range, often punctuated according to geographic discontinuities which may be congruent across multiple species. Classic examples of these dynamics from Arctic mammals include comparative assessments through both Europe (Hewitt, 2000, 2004) and North America (Rand, 1954; MacPherson, 1965; Shafer et al., 2010). Through time, dynamic climate change led to population fluctuations, and generated new lineages, which eventually became new Arctic species. But, as some lineages or species formed, others just as readily disappeared, such as evidenced from divergence and periodic disappearance of distinct lineages of collared lemmings (*Dicrostonyx torquatus*; Brace et al., 2012), resulting in local community turnover through time.

The refugia, geographic breaks, transition zones between biomes, and periodic corridors for movement of Arctic mammals varied strongly by climate phase (Figs. 2 and 3). A preponderance of evidence indicates that tundra mammal distributions (in contrast to arid steppe mammals) were most fragmented during coldest peaks of glacial phases. Within Europe and North America at these times isolated populations occupied refugia south of continental ice-sheets in peri-glacial mesic tundra, where permafrost (Vandenberghe et al., 2014) had developed. These southern pockets of tundra were in proximity to forest communities also shunted southward, forming mixed ecotonal species assemblages (Stewart and Lister, 2001; Markova et al., 2009). In largely ice-free Asia, glacial refugia were instead likely associated with lowland pockets of mesic tundra in major river drainages (Hope et al., 2011), and surrounded by mammoth steppe. Similarly, the mesic buckle of tundra in central Beringia was bounded by steppe habitats to both west and east (Fig. 2; Guthrie, 2001), allowing for generation of endemic tundra diversity (Cook et al., 2005). Such extensive occurrence of allopatry (isolation) of tundra mammal populations during glacial phases would have often resulted in relatively

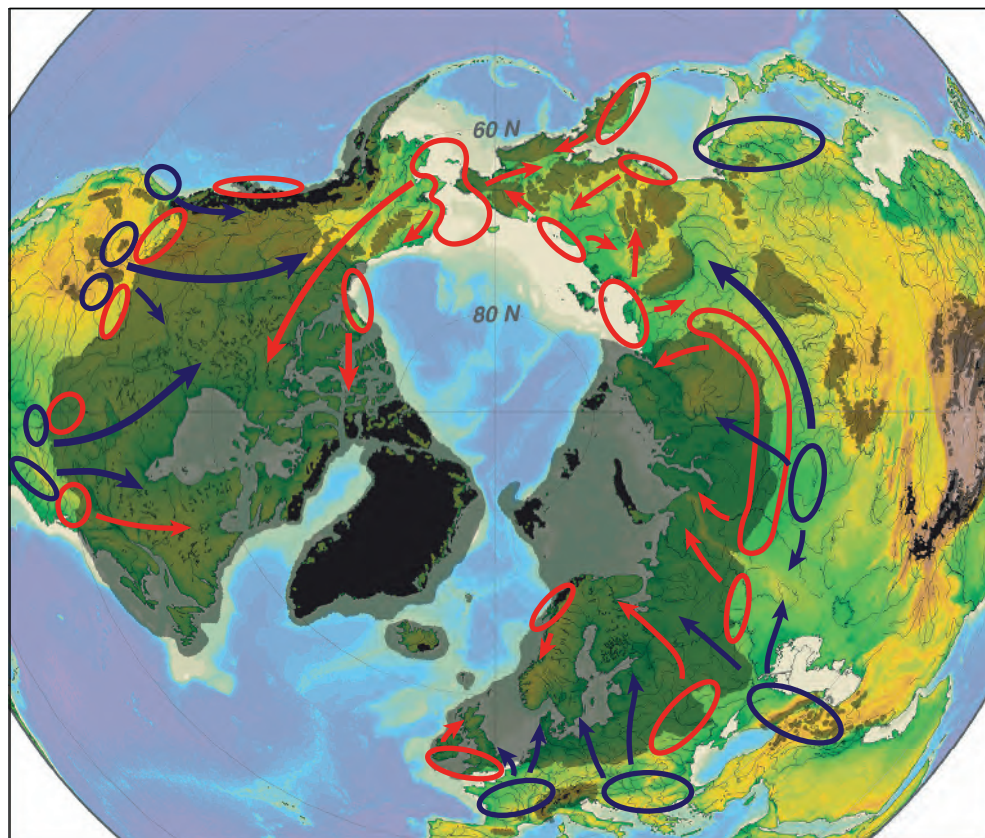


Fig. 2 Hypothetical glacial phase refugia and source areas for Arctic tundra mammals (red ellipses). In addition are shown hypothetical southern refugia for boreal mammals (blue ellipses). Post-glacial expansion routes (arrows) indicate likely sources for recolonization. Other refugia (without arrows) were more likely either sink populations, not contributing to Holocene gene pools or long-term endemics. Evidence for potential refugia have been built from regional clustering of genetically distinct lineages across many species, and based on phylogeographic literature as listed in Table 1. Shading indicates recent (black) and maximum (grey) glaciation during Quaternary climatic cycles. Much of the ice-free land area during glacial phases would have supported steppe habitats. Adapted from figure under license by Creative Commons Attribution 3.0; File: Iceage north-glacial hg. png.

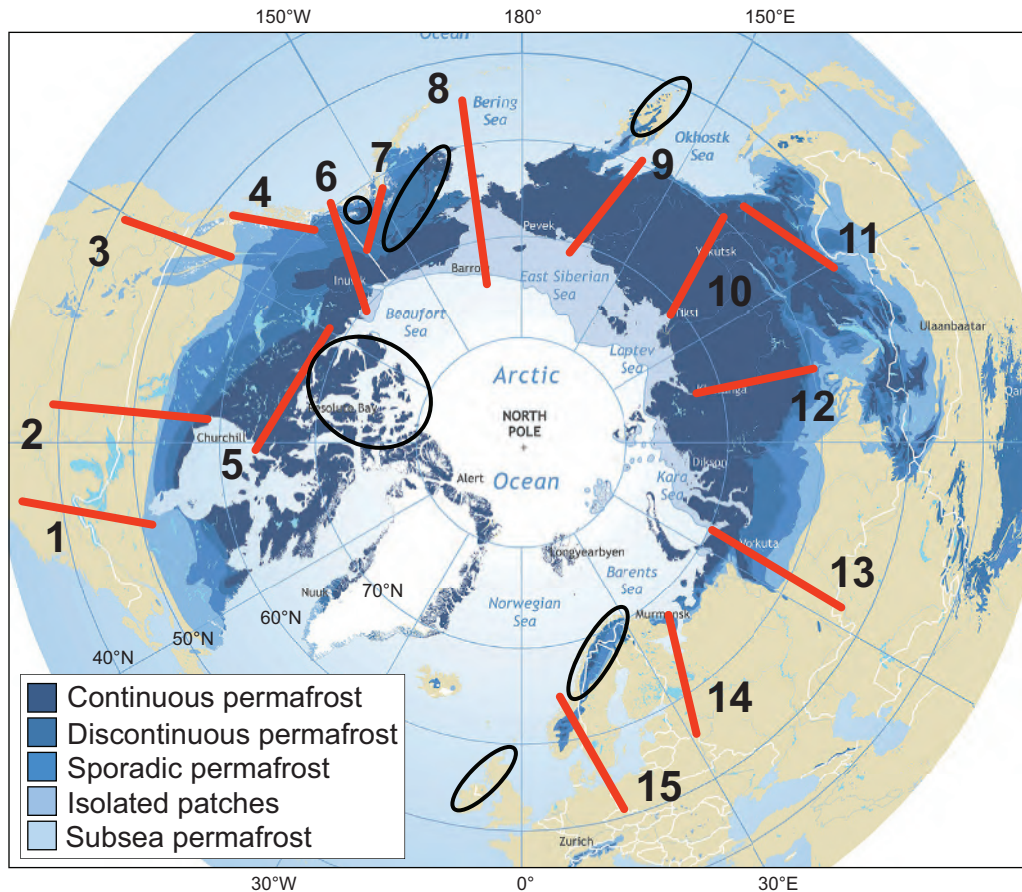


Fig. 3 Holocene (current) interglacial contact zones (discontinuities between distinct genetic lineages) coincident with geographic regions compiled from phylogeographic studies of Arctic tundra mammals (see Table 1). Additional phylogeographic structure for some wide-ranging boreal mammal species is omitted. Also indicated are select warm phase refugia for fragmented populations of tundra mammals occurring on islands, or insular patches of Arctic or sub-Arctic tundra surrounded by boreal forest habitat. Descriptive names for contact zones may also coincide with geographic barriers to dispersal during glacial phases: 1 = Eastern North America; 2 = Mid-continent; 3 = Columbia Plateau; 4 = North Pacific Coast; 5 = High Arctic; 6 = Eastern Beringia; 7 = Alaska Range; 8 = Bering Strait; 9 = Kolyma Uplands; 10 = Verkhoyansk Range; 11 = Stanovoi Range; 12 = Central Siberian Plateau; 13 = Ural Mountains; 14 = Scandinavia; 15 = Northwestern Europe. Shading indicates modern extent of permafrost. Adapted from Brown, J., Ferrians, Jr., O. J., Heginbottom, J. A. and Melnikov, E. S. (eds.). (1997). *Circum-Arctic Map of Permafrost and Ground-ice Conditions*. Washington, DC: U.S. Geological Survey in Cooperation with the Circum-Pacific Council for Energy and Mineral Resources.

small populations, and evolutionary divergence dominated by genetic drift (Provan and Bennett, 2008). During each transition to an interglacial phase, widespread population expansion and much larger populations among tundra mammals would have promoted continued diversification, including increased opportunities for adaptive selection.

Current Arctic mammal distributions offer the best evidence that at the onset of interglacial periods, previously isolated mammal populations expanded from refugia along with their tundra habitats, to near-continuous ranges across the Holarctic. However, as forested habitats shifted northward, some northern tundra regions became fragmented into modern tundra refugia, particularly along continental edges (Fig. 3; e.g., Stewart et al., 2010). In addition, not all glacial refugia were sources for post-glacial expansion, and phylogeographic studies can often also identify which refugial populations were sources (more often northern; e.g., Fedorov et al., 2003), versus sinks where populations were possibly repeatedly shunted, then extirpated through multiple cycles (Fig. 2; more often southern peri-glacial; Stewart and Dalén, 2008; Fulton et al., 2013). Additional complexity is often revealed from populations occupying coastal refugia during glacial phases. The best examples of these include once-exposed continental shelf in Ireland (Martínková et al., 2007), northern Scandinavia (Fedorov and Stenseth, 2001; Brunhoff et al., 2006), the High Arctic of North America (Fedorov and Stenseth, 2002; Waltari and Cook, 2005), or Southeast Alaska (Cook et al., 2001, 2006), all isolated between ocean and continental ice. Not only were these refugia generally small, leading to rapid genetic drift and bottlenecked populations, but as ice-sheets receded, isolation was maintained by rising sea levels, promoting long-term (multi-cycle) regional endemism among these insular mammal populations.

Holocene Environments and Anthropogenic Impacts

Holocene climate has been relatively stable by Quaternary standards, but global environments through the last century have been rapidly changing, with projected global temperature increases for the next century that may rival or exceed Pliocene (pre-Arctic tundra biome) temperatures (Hinzman et al., 2005). In particular, anthropogenic contributions to atmospheric carbon dioxide, methane, and other greenhouse gas emissions have enhanced a warming trend with disproportionately high rates through the Arctic, that have no analog within the last 3 Myr (Gilg et al., 2012). Humans (also a mammal associated with tundra) have been present through the Arctic since the last glacial phase, impacting other tundra mammal populations through to the present time (Kahlke et al., 2011; Wooler et al., 2018). Abundant archaeological evidence indicates that humans hunted tundra and steppe megafaunal species coincident with their declines since before the onset of the Holocene climatic transition (Lanoë et al., 2017). Now, a combination of rising human populations, increasing development through the Arctic, and global-scale industrial activities will likely have more far-reaching consequences for tundra biodiversity (Barnosky et al., 2012). Despite the anomalously high warming rate, we know that the previous Eemian (Sangamonian in North America) interglacial (130–115 ka) attained slightly warmer peak temperatures than at present, and forests had advanced northward to the Arctic coast in many places, fragmenting Arctic tundra populations, particularly for tundra specialist mammals. Present day climate models and projected species distribution models provide increasingly rigorous predictions that the circumpolar Arctic tundra will experience continued fragmentation in the coming century (Hope et al., 2013b). Mammals will be forced to respond to this modern warming. Shrinking Arctic tundra will in effect lead to modern refugia for tundra mammals and their communities (Stewart et al., 2010). A priority for scientists, land- and wildlife managers will be to locate refugial centers for the tundra biome, and focus efforts on regional conservation coupled with maintaining connectivity more broadly across the Arctic. A related threat is that predicted refugial areas for tundra wildlife may be coincident with regions of active or planned human development, particularly for access to abundant reserves of fossil fuels across the northern permafrost zone and the Arctic Ocean. Balancing the competing demands of human growth and economy with maintenance of intact wild systems will be a continuing challenge (Hope et al., 2013b).

Contact Zone Community Dynamics and Co-evolution

A productive setting for investigating interactive change among Arctic mammals is across contact zones. Contact zones are geographic regions where distinct populations, species, or communities meet (Fig. 3). Often these areas reflect secondary contact between previously isolated and reconnected flora and fauna (Swenson and Howard, 2005). Across the Arctic there are numerous longitudinal contact zones both within and among mammal species that help to delimit regional diversity (Fig. 3). In addition, latitudinal zones of contact occur between major biomes such as the ecotone between tundra and boreal forest that spans the Holarctic, or between northern tundra and the Arctic Ocean, connecting terrestrial and marine ecosystems. All of these dynamic regions may be considered natural ecological and evolutionary “experiments,” providing insight into the unique interactions between communities (Hewitt, 2011). Such interactions include competition for resources or space, interbreeding (hybridization) among lineages or closely related species, and transfer of parasites, pathogens and other materials.

Competition across contact zones is difficult to study directly, given that interactions among species of mammals, particularly small species, are seldom possible to rigorously assess in a field setting (Ale et al., 2011). However, through the Arctic, northward shifts of boreal plants and animals accompanied by displacement of tundra populations is being well-documented. Studies have also assessed the dynamics surrounding leading or trailing edges of species ranges and the associated diversity, adaptive potential, and competitive pressure (Hampe and Petit, 2005). Although boreal mammals at the leading (northern) edge of forest and shrubby expansion may have relatively low genetic diversity (Hewitt, 2000), these taxa also tend to be generalists, able to quickly fill available niche space. Resident tundra species with adaptations for tundra habitats could in theory have a competitive advantage (Svenning et al., 2014), but this may be balanced by continued climate warming, making local conditions progressively sub-optimal for more specialized cold-adapted tundra populations (Killengreen et al., 2007; Clavel et al., 2011).

Community mixing across contact zones is often accompanied by interbreeding between related taxa, resulting in gene flow between regions. The cyclic nature of Quaternary climate change caused progressively divergent lineages and species to reconnect and repeatedly hybridize through their history and this gene flow has been a pervasive evolutionary process, often detrimental, but also offering evolutionary potential (Bridle and Vines, 2007). Hybridization may lead to the homogenization of previously distinct genetic pools, or may reinforce divergence across contact zones if hybrid offspring are less fit for survival or only locally fit within the contact zone. Increasing evidence suggests that hybridization plays a pivotal role on the speciation continuum (Abbott et al., 2013).

Among Arctic mammals, gene flow has occurred across a number of longitudinal contact zones including the vicinity of the Kolyma and Omolon Rivers in Siberia between lineages of tundra voles (*Microtus oeconomus*; Galbreath and Cook, 2004), and the eastern edge of Beringia between divergent lineages of ermine (Colella et al., 2018). Perhaps more intriguing are instances of hybridization between tundra and boreal forest species during interglacial phases. Mountain hares (*Lepus timidus*) have interbred with multiple other hare species across the Northern Hemisphere (Melo-Ferreira et al., 2014). Red-backed voles (*Myodes rutilus*) have hybridized with congeneric forest species in both Eurasia (*M. glareolus*; Deffontaine et al., 2005) and North America (*M. gapperi*; Runck et al., 2009). Likewise Arctic ground squirrels (*Urocitellus parryi*) have interbred with their temperate relatives (McLean et al., 2016), and shrews (*Sorex cinereus* and *S. ugyunak*) are actively interbreeding across the boreal-tundra ecotone in northern Alaska (Hope, unpublished data).

Study of the dynamics of genomic mixing among species, and the impacts that this has on either or both of the parent species is only now being developed with the modern utility of genomic sequencing, but should greatly enhance studies of speciation, and of adaptive changes in response to changing environments (Colella et al., 2018). For instance, although boreal mammals were periodically extirpated from Arctic regions through Quaternary glacial phases as forest habitats shifted southward, it is likely that a legacy of hybridization from the previous interglacial was retained at high latitudes within tundra populations, with the potential to reconnect with successive boreal populations as they returned north during the following interglacial (Runck et al., 2009). Tracing the history of genomic signatures through time to recreate past community associations is an exciting future prospect. An insightful example of gene flow, speciation, and adaptive advantage of hybrids has been demonstrated through sequencing of both fossil and modern DNA from polar bears and brown bears. These studies suggest that hybridization may enhance survival in transition (contact zone) habitats, but with continued directional gene flow (introgression) eventually eroding genomic legacies from one species (here polar bears) in favor of the prevailing biome (Edwards et al., 2011; Miller et al., 2012; Cahill et al., 2018).

An emerging area of study across northern contact zones is the co-evolutionary dynamics between Arctic mammals and their parasites and pathogens (Cook et al., 2005, 2017). We can use knowledge of the relationships between mammal hosts and their parasites as proxies for understanding environmental change within Arctic tundra. In particular, parasites generally exhibit complex lifecycles that are governed at least partially by external environments. As host and parasite species are intimately associated through these life-cycles, they can be particularly valuable for interpreting generalizable biodiversity responses to accelerating change (Hoberg et al., 2012; Kutz et al., 2014). Parasites may be specialized for a given host mammal, or may more generally infect a broad diversity of mammals. But regardless of specificity, these diverse yet understudied organisms are highly sensitive to climatic variability, and may respond dramatically to threshold environmental changes, particularly via climate warming that both stresses mammalian hosts and facilitates parasite proliferation (Bradley et al., 2005). For instance, lung nematodes that infect muskox as the definitive hosts also require intermediate hosts such as slugs with parasite life stages occurring at ambient environmental temperatures. Until recently cold climates have limited parasite developmental stages to a 2-year life-cycle. But, as climate warms in the Arctic, these parasites can develop faster, resulting in annual life-cycles, amplified parasite loads in muskox and resulting increased morbidity and mortality (Kutz et al., 2004).

The evolutionary history of mammalian parasites through the Arctic has also been used as multiple lines of corroborative evidence for mammal phylogeographic histories, often paralleling patterns of host geographic colonization and diversification (e.g., Wickström et al., 2003; Haukioja et al., 2016a, b). Interactions between hosts and parasites may change as a result of host-switching (Koehler et al., 2009), mammal hybridization or simply population mixing that influences relative susceptibility of mammals to infection, or through changes in the relative pathogenicity of infections with changing environments (Kutz et al., 2014). Parasite histories also reflect previous host associations with mammal species that were locally extirpated or are now extinct, carrying forth a legacy of past Arctic mammal communities in the absence of host specimens (Rausch, 1994). An example, again with muskox, considers reinfection by another nematode species as a result of muskox being re-introduced to their historic range following overhunting in the 19th century. This nematode was transferred back to the muskox from Dall sheep, the latter an alternate mammalian host which successfully maintained nematode populations in this region until muskox established secondary contact and were re-infected (Kutz et al., 2004).

The vast Holarctic extent of Arctic tundra, interconnected mammal distributions, and a circumpolar transition into the boreal biome presents broad opportunity for global spread of mammalian parasites and pathogens. Future persistence of Arctic tundra mammals will depend both on species resilience and plasticity, and an increased understanding of the intimate biotic connections linking these “communities *within* communities” (Hope et al., 2016).

Future Prospects

A major hurdle to Arctic mammal research is incomplete knowledge of species distributions, both past and present. Much of this review highlights research that relies on samples from physical specimens collected across Arctic landscapes and archived in natural history repositories that vouch for the existence of species at a given locality and time. But the tundra biome is extremely remote, and field expeditions are generally both expensive and logistically challenging (Cook et al., 2017). Informed and effective conservation and management of Arctic mammal diversity will rely on continued expeditionary fieldwork through all Arctic nations, to strive for comprehensive geographic coverage, long-term sampling at a given locality, and rigorous sample sizes per site of existing mammal and associated parasite biodiversity (McLean et al., 2015). The potential for emerging mammalian disease is increasing globally as climate warms, non-native species introductions increase, native biodiversity decreases, long-separated communities progressively mix, and environmental thresholds for Arctic taxa are exceeded (Keesing et al., 2010). Integrating an increasingly advanced toolset across multiple disciplines with improved knowledge of species histories, current distributions, and biotic associations will improve potential for maintaining functional Arctic systems within a non-analog modern world (Hinzman et al., 2005).

A positive outlook given the scientific evidence is that most tundra mammal species have survived through multiple warm and cold climate phases as well as rapid transitions between the two. The current extent of Arctic tundra is close to its maximum, and although currently contracting, a future with intact Arctic tundra communities should be possible with limited future global temperature rise. Besides the cascading effects of continued global change and a warming Arctic, the biggest threat to mammals and their communities is an increasing human footprint through the Arctic (Hinzman et al., 2005). Predicting the location of future hotspots or modern refugia for Arctic diversity, developing a better understanding of the ecology of community interactions, and reducing local anthropogenic impacts through these regions may be our best chance for conserving mammalian diversity through

the Arctic tundra biome. The charisma of Arctic mammals and the affection that humans share for shaggy beasts of all sizes, and for yet-wild places epitomized by the tundra will continue to motivate efforts for enhancing conservation of Arctic biodiversity.

Acknowledgements

Thanks to B. S. McLean, and L. H. Zeglin for insightful comments on an earlier draft.

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Colonization of the Eurasian Arctic

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Abstract

The oldest evidence of human settlement in the western Arctic regions of Eurasia has been found at a site at 66°N in the Northern Urals, where people lived about 40,000 years ago. A site at the mouth of the Yenisei River was apparently occupied 45,000 years ago. Further east, in Western Beringia, there are two sites dating to about 40,000 years ago. The well-established age of these human occupations suggests that the Arctic region of Northern Eurasia was inhabited by humans during the interstadial warm period of MIS 3, about 50,000 years ago. All the evidence, including ancient DNA, indicates that the human occupation of the Eurasian Arctic was by anatomically modern people who had important advantages over Neanderthals. These early residents of the Arctic developed four critical innovations: obtaining food by hunting, the manufacture of clothing, housebuilding and transportation vehicles in the form of frame boats and dog sleds. Microblade technology developed only at the beginning of the Holocene, coinciding with the demise of the mammoth population.

Introduction

The continental regions of the Arctic are occupied by various kinds of tundra ecosystems, from polar desert, common in Eurasia along the coasts of the Arctic Ocean and some islands, to the relatively richer vegetation of shrub tundra and forest-tundra in the southern regions of the Arctic. Since the beginning of Arctic scientific research, about 400 years ago, European and Russian travelers and researchers have observed that all the Arctic regions have long been inhabited by humans, despite the harsh climate and the paucity of the natural resources.

It has been established that the cultures of Arctic peoples are excellent examples of human adaptation to the challenging conditions of the natural environment, and that these cultures have been quite stable throughout the region. Ethnographically, maritime adaptations developed in coastal areas, while the culture of continental hunters evolved from ancient hunting and gathering to reindeer herding, which became widespread across Northern Eurasia, but never reached Arctic North America. Harness dog breeding for use in sledge transportation has been a common adaptation among all Arctic aboriginal peoples. The physical evidence indicates that the indigenous people of the Arctic have lived there for a very long time.

Earliest Human Occupation of the Arctic

Archeologists have been trying to discover when people first came to the Arctic. The search for an answer to this question, despite more than a century of archeological research in the region, remains one of the most important areas of archeological research.

The first archeological excavations in the Arctic were carried out in 1787 by the Russian researcher Gavriil Sarychev. He searched for signs of prehistoric human occupation in a region east of the mouth of Kolyma River near Cape Baranov. However, systematic archeological study of the Arctic and subarctic territories started a century later, at the end of the 19th century. These studies were quite active between WWI and WWII. By the 1930s, the concept of a land bridge connecting northeast Siberia to Alaska was taking shape, based on botanical data collected by Swedish botanist Eric Hultén (1937). Since the end of WWII, the volume of archeological research in the Arctic has increased significantly. New archeological studies are being implemented in the 21st century, making use of an entire arsenal of recently developed methods.

The chronicle of human settlement in the Arctic begins about 50,000 years ago (Fig. 1). The human occupation of the Arctic represents the opening act of the last phase of the global settlement by anatomically modern humans. This resulted in the human mastery of the Arctic regions of Northern Eurasia, followed by human migration to the New World, the last part of the world to become inhabited. Humans spread across the Arctic territories of North America and Greenland, completing the process of human migration and settlement in the far north.

Thus, the Arctic territories were the scene of some of the most important events in the history of mankind. On the geological time scale, this process covers a significant portion of MIS 3 (57,000–29,000 years ago) and MIS 2 (29,000–14,000 years ago), culminating in the Holocene (MIS 1: 14,000 years ago, to the present day). The Holocene was mainly a time of redistribution of human populations in previously populated areas of the Arctic, often associated with the influx of new human groups.

These processes were driven by various abiotic and biotic factors, such as changes in plant and faunal associations, changing landscapes, changes in the forest boundary, and changes in the population dynamics of large herbivores, driven by climate. Changes in any of these components, which were in complex interaction, were significant for ancient peoples. Opportunities for the settlement of humans in different regions of the Arctic varied significantly in different areas. These opportunities were determined by the course of development of landscapes, flora and fauna, following the deglaciation of regions such as the Canadian Arctic and the coastal margins of Greenland.

The Arctic regions of the Eastern Hemisphere, apart from the area occupied by the Scandinavian Ice Sheet, were mostly available for human settlement during the late Pleistocene.

The cycles of glaciation are associated with global changes in sea level, which fell during glacial intervals and rose during interglacial warm periods. These sea level changes affected different regions of the world to a greater or lesser extent. They were most dramatic in the Arctic, where large areas of regional seas have broad, shallow shelves. When sea level fell, a large land bridge formed between Siberia and Alaska: the Bering Land Bridge (BLB). Also, the northern shores Arctic waters of northeast Siberia shifted considerable distances northward, exposing large regions of continental shelf. These changes in regional geography were extremely important for human populations, as they influenced, directly and indirectly, the spatial distribution and composition of plant and animal groups, and served as a factor in climate change, contributing to the strengthening of climatic aridity in the continental regions.

The oldest evidence of human settlement in the western Arctic regions of Eurasia has been found at the Mamontovaya Kurya site at 66°N in the Northern Urals, where people lived about 40,000 years ago (Pavlov et al., 2001). A site on the Sopochynaya Karga Cape, on the border of western and eastern Siberia at the mouth of the Yenisei River (Fig. 1), was apparently occupied 45,000 years ago (Pitulko et al., 2016). Further east, in the Siberian side of Beringia, known as Western Beringia, there are two sites dating to about 40,000 years ago: the Yana Upstream Point locality and the Bunge-Toll-1885 site (Pitulko et al., 2017). The well-established age of these human occupations suggests that the Arctic region of Northern Eurasia was inhabited by humans during the interstadial warm period of MIS 3 (Seierstad et al., 2014), about 50,000 years ago.

The MIS 3 Interstadial

In Arctic West Beringia this time interval was apparently warmer and wetter than conditions a few thousand years earlier, i.e., at the end of MIS 4. The region supported an ecosystem of open spaces that became dominated by grasses and forbs (Andreev et al., 2011), which in turn supported herds of megafaunal grazers, including woolly mammoth. The regional population of mammoths grew rapidly and reached an all-time peak at about 45,000 years ago (Andreev et al., 2011). The biome that formed is termed the Mammoth Steppe. Because it supported abundant populations of large game animals, it played a crucial role in the settlement of humans in Northern Eurasia (Fig. 3).

Identity of Earliest Arctic Peoples

The demonstrated antiquity of human presence in the Arctic zone of Northern Eurasia immediately raises the question of the identity of these people. They were living a relatively short time before the extinction of Neanderthals. There would have been sufficient time for Neanderthals to have moved into the Arctic before their extinction, perhaps responding to the pressure of being pushed out of more southerly regions of Asia by migration waves of the modern man. It should be noted that, with regard to Byzovaya site in Northern Urals, archaeologists did indeed suspect that this site was occupied by Neanderthals, based on the age of the finds and the morphology of a few artifacts (Slimak et al., 2010). However, this hypothesis has come under criticism (e.g., Zwyns et al., 2012). In fact, there is no reliable evidence for the settlement of Neanderthals or other archaic forms of *Homo* north of 55° latitude, either from any anatomical remains or any characteristic stone tools.

On the contrary, there is reliable physical evidence of the presence of anatomically modern people in the sub-Arctic region of Siberia during the Late Pleistocene (Fig. 2). One example is human bone, from the Ust-Ishim site situated at 57°N, which dates to 45,000 years ago (Fu et al., 2014). Physical remains of anatomically modern humans also come from the Yana site (Sikora et al., 2019).

However, lithic tools made by humans during the late Pleistocene across Northern Eurasia are characterized by a certain primitive, archaic quality (Pitulko et al., 2004; Svendsen et al., 2010). More precisely, the tools exhibit some roughness in their finish, and have simplified shapes (Pitulko et al., 2013). However, this says little about the highly developed culture of these people, which

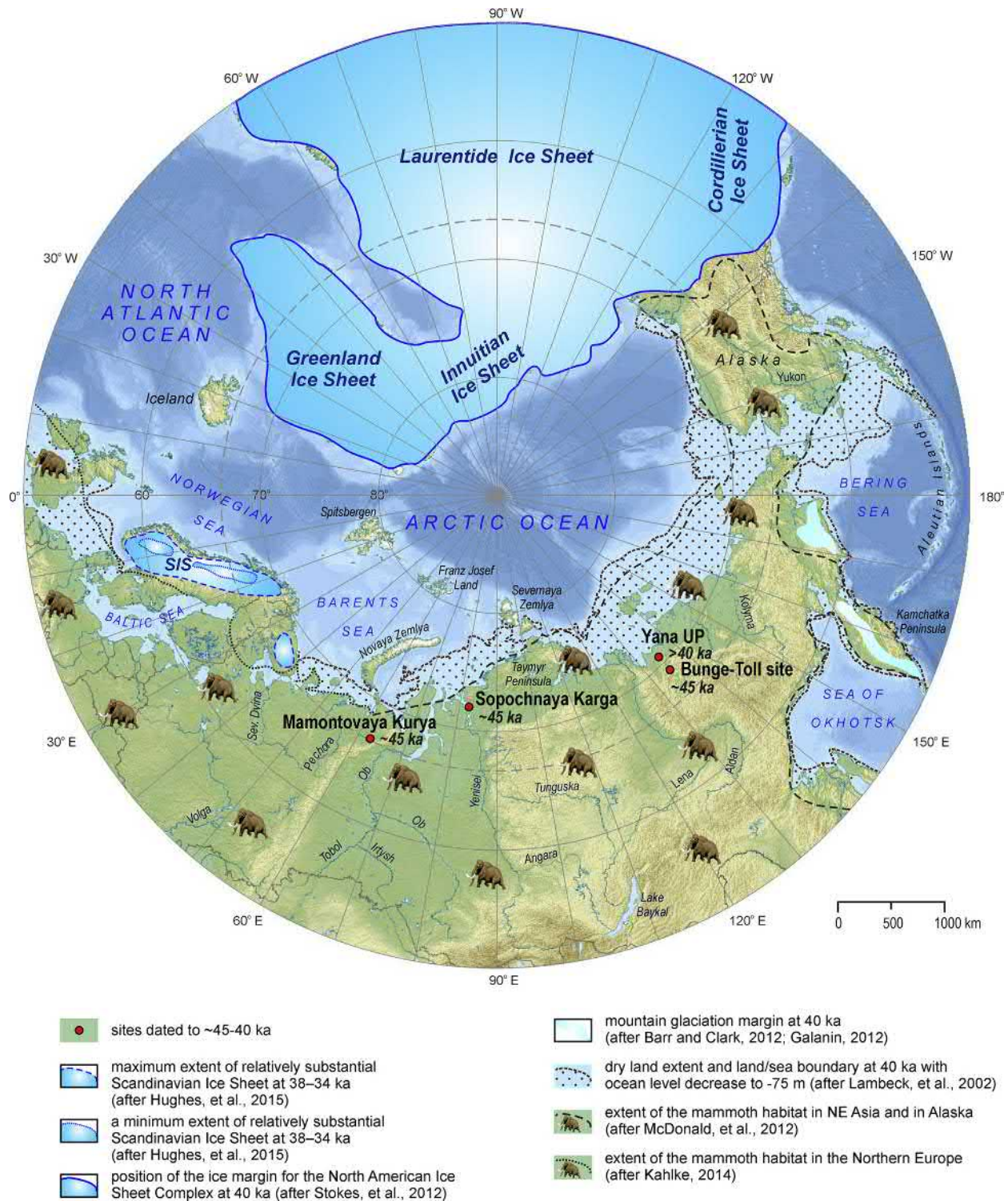


Fig. 1 Arctic and sub-Arctic archeological sites dated to 45,000–40,000 years ago (45–40 ka), middle MIS 3, and major environmental settings for this time slice based on data published in: Barr I. D. and Clark C. D. (2012). Late Quaternary glaciations in Far NE Russia; combining moraines, topography and chronology to assess regional and global glaciation synchrony. *Quaternary Science Reviews*, **53**, 72–87; Galanin A. A. (2012). Age of the Last Glacial Maximum on Asian North-East. *Kriosfera Zemli* **XVI**(3), 39–52; Hughes, A. L. C., Gyllencreutz, R., Lohne, Ø. S., Mangerud, J., and Svendsen, J. I. (2015). The last Eurasian ice sheets—A chronological database and time-slice reconstruction, DATED-1. *Boreas* **45**(1), 1–45; Kahlke, R.-D. (2014). The origin of Eurasian Mammoth Faunas (Mammuthus—Coelodonta Faunal Complex). *Quaternary Science Reviews* **96**, 32–49; Lambeck, K., Esat, T. M. and Potter, E.-K. (2002). Links between climate and sea levels for the past three million years. *Nature* **419**(6903), 199–206; McDonald, G. M., Beilman, D. W., Kuzmin, Y. V., Orlova, L. A., Kremenetski, K. V., et al. (2012). Pattern of extinction of the woolly mammoth in Beringia. *Nature Communications* **3** 893; Stokes, C. R., Tarasov, L., and Dyke, A. S. (2012). Dynamics of the North American Ice Sheet Complex during its inception and build-up to the Last Glacial Maximum. *Quaternary Science Reviews* **50**, 86–104.

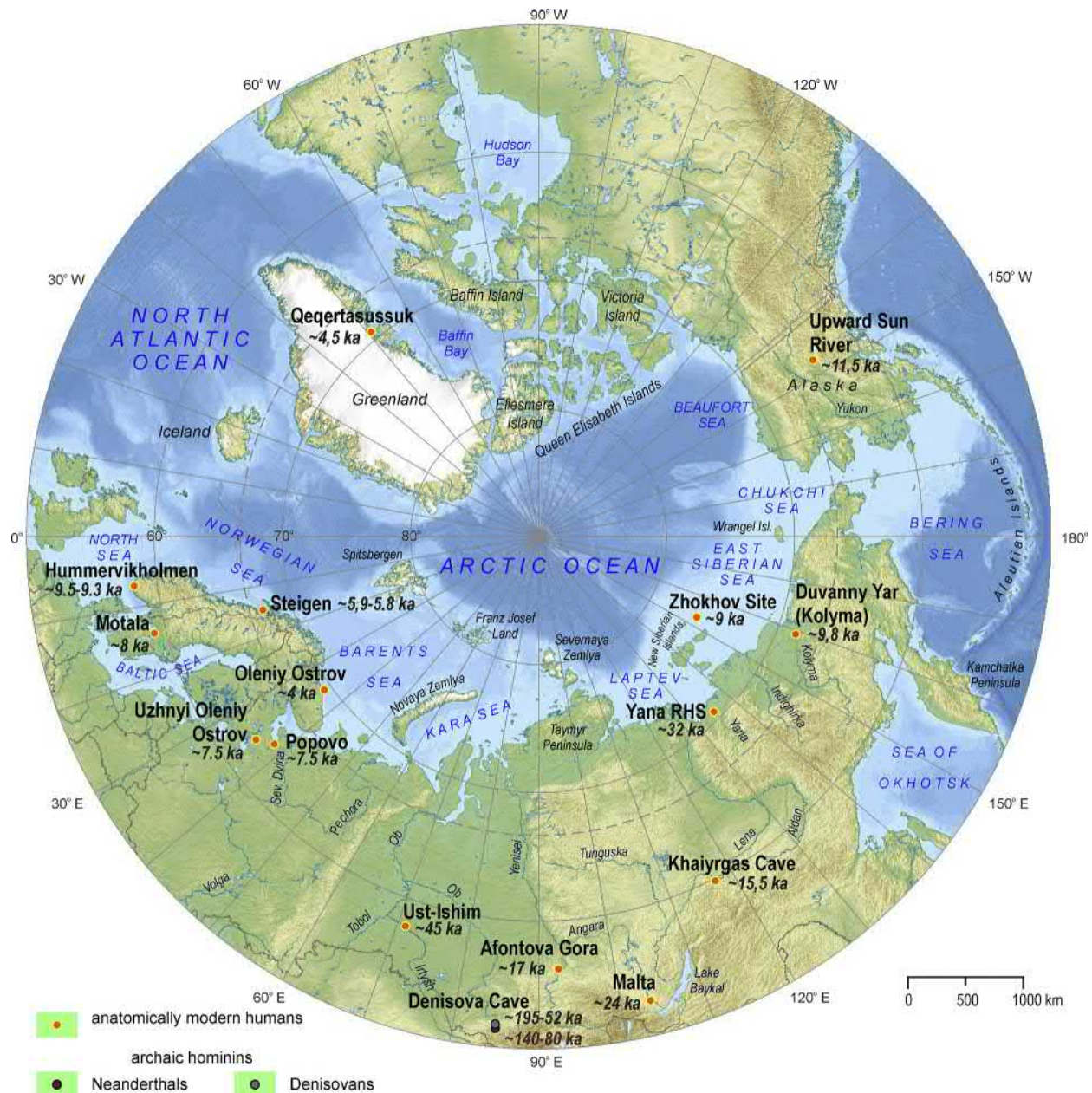


Fig. 2 Dated anthropological remains discovered in the Arctic and surrounding area, largely used in paleo DNA studies to model human settlement of the Arctic regions in the past.

represents a bone tool industry of the highest level and quality (Pitulko et al., 2012; Pitulko et al., 2015a), with developed sets of ornaments and ornamental systems, known from the materials of the Yana River site (Fig. 3). The people who occupied the Yana site led a mobile lifestyle, traveling hundreds of kilometers, presumably to exchange trade goods with other groups of people. For instance, the Yana site has yielded specimens of amber that most likely came from the New Siberia Island, 800 km north. As discussed below, in the treeless regions of the Arctic, mammoth bones and tusks were highly prized materials for the making of tools.

Important Technological Innovations

Thus, it is fair to conclude that human occupation of the Arctic regions is associated solely with anatomically modern people (Fig. 2) who had important advantages over Neanderthals. These benefits are repeatedly described as top-paleolithic innovations, listed by Mellars (2005). His list shows the 15 most important innovations. First, they are found in their material culture, reflecting the direct interaction of humans and the environment.

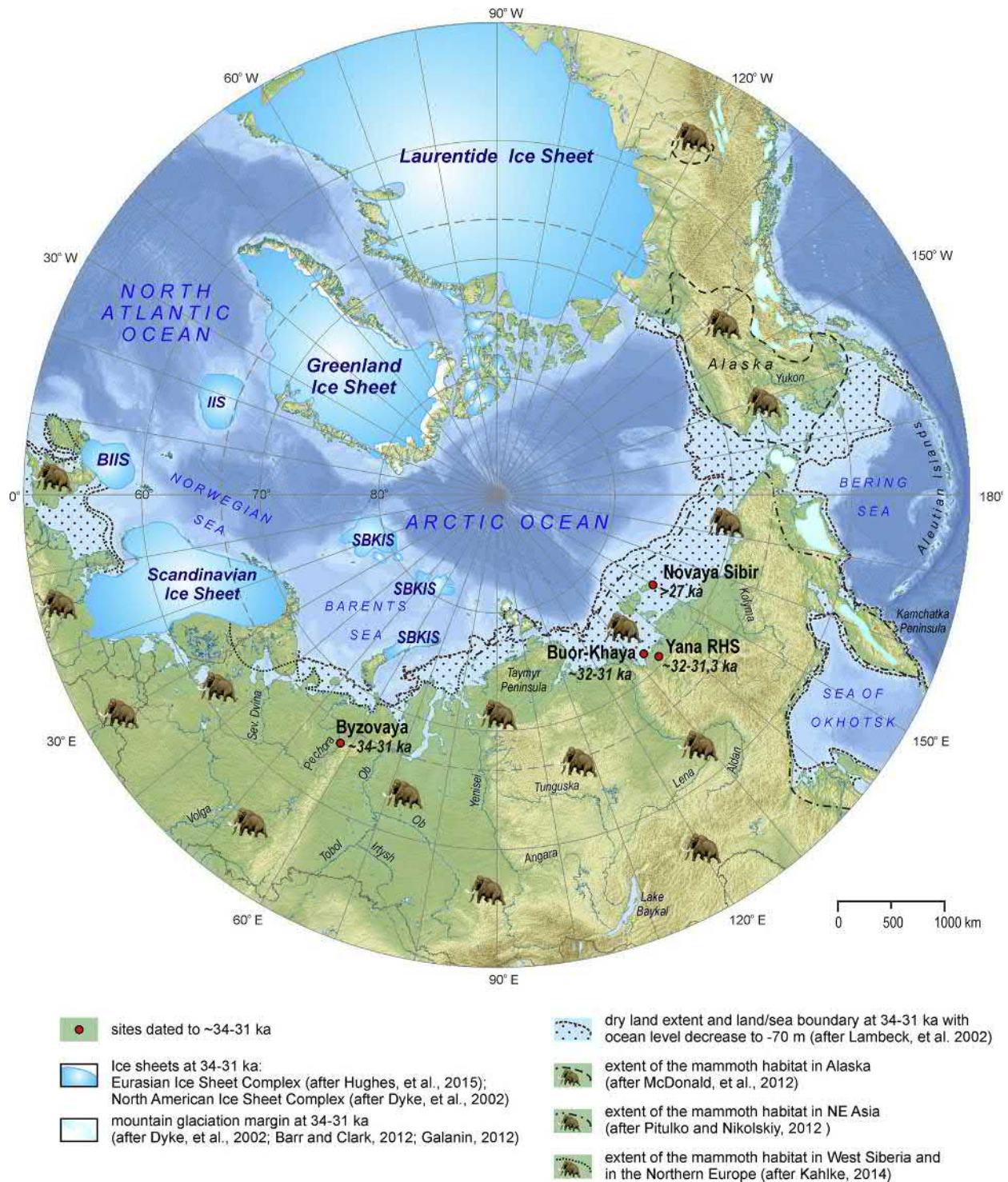


Fig. 3 Arctic and sub-Arctic archeological sites dated to 34,000–31,000 years ago (34–31 ka), and major environmental settings reconstructed for late MIS 3 based on data published in: Barr I. D. and Clark C. D. (2012). Late Quaternary glaciations in Far NE Russia; combining moraines, topography and chronology to assess regional and global glaciation synchrony. *Quaternary Science Reviews* **53**, 72–87; Dyke, A. S., Andrews, J. T., Clark, P. U., England, J. H., Miller, G. H., et al. (2002). The Laurentide and Innuitian ice sheets during the Last Glacial Maximum. *Quaternary Science Reviews* **21**(1–3), 9–31; Galanin A. A. (2012). Age of the Last Glacial Maximum on Asian North-East. *Kriosfera Zemli* **XVI**(3), 39–52; Kahlke, R.-D. (2014). The origin of Eurasian Mammoth Faunas (Mammuthus—Coelodonta Faunal Complex). *Quaternary Science Reviews* **96**, 32–49; Lambeck, K., Esat, T. M. and Potter, E.-K. (2002). Links between climate and sea levels for the past three million years. *Nature* **419**(6903), 199–206; McDonald, G. M., Beilman, D. W., Kuzmin, Y. V., Orlova, L. A., Kremenetski, K. V., et al. (2012). Pattern of extinction of the woolly mammoth in Beringia. *Nature Communications* **3**, 893; Pitulko, V. V. and Nikolskiy, P. A. (2012). Extinction of woolly mammoth in Northeastern Asia and the archaeological record. *World Archaeology* **44**(1), 21–42.

These important innovations include noticeable advances in stone tool processing technologies, such as the widespread use of blades, the emergence of new forms of scrapers and burins (an engraving tool with a diamond-shaped point), the appearance of improved projectile points for hunting, and the high level of production of bone and horn products. The latter include items of hunting equipment and needles. In addition to improvements to their material culture, these people also developed changes in behavior, such as improved hunting strategies and tactics, the emergence of a well-defined hunting specializations, and the production of materials that indicate complicated social behavior. Introduction of these technological innovations allowed anatomically modern people to master subarctic and then Arctic territories.

The innovations represented in Arctic archeological sites from the Late Pleistocene reflect the technological complexity of the culture of ancient people (Hoffecker and Hoffecker, 2017). One of the most important of these is the making of tailored clothes and other products from animal skins (Pitulko and Pavlova, 2019). The main technologies recognized by Mellars (2005) do not have a hierarchy, but in an Arctic context, the most important of these were actions directly related to the technology that allowed humans to survive the bitterly cold winters on the open tundra-steppe regions of northern Eurasia.

Primarily, three of the innovations are the most significant: obtaining food by hunting, the manufacture of clothing, and house-building. However, over time (probably in the later Pleistocene), they added a fourth important component: transportation vehicles in the form of frame boats and dog sleds. The hunting of large mammals supplied the raw materials (animal hides, sinews, etc.) to produce leather products. Hunting also supplied the animal bones needed to produce bone tools, of which the most important were hunting weapons and sewing needles.

In fact, sewing technology was obviously one of the two critical technologies needed for human occupation of the frigid Arctic. Key to the development of the sewing needle is the ability to create an eye, through which sinews may be threaded. The oldest of these (eyed needles) have been found in Siberia, where they have been found in numbers indicating mass production and use in MIS 3 (Pitulko and Pavlova, 2019). The presence of needles with an eye allowed the production of multi-layered clothing, sewn to fit the wearer, as well as the whole range of sewing products, including shoes, sleeping bags, soft containers and bags, and dwelling covers. Based on the evidence from the Yana site excavations, the dwelling structures were light ground constructions with inside hearths used to burn various fuels including animal bones. In Arctic regions that lack wood for fuel, people burned the bones of large animals, including mammoths. These bones contained greasy marrow that would burn.

The development of sewing technology is a prerequisite for successful human life in the subarctic and Arctic zones, where modern average annual temperatures vary from 0 to -16°C , and where any slight decrease global average temperatures will significantly worsen environmental conditions. Such changes have occurred repeatedly, of which the LGM and Younger Dryas Cooling are best known of the Late Pleistocene. But smaller-scale climatic changes were much more numerous (Rasmussen et al., 2014) and undoubtedly forced changes in the spatial distribution of humans, as well as driving certain changes in the material culture in response to environmental changes.

Life in a Treeless Landscape

Throughout MIS 3 and 2, the territories of Northern Eurasia were occupied by tundra-steppe vegetation, which had considerable variability in space and time (Figs. 1, 3–6). One of the dominant features was the complete absence of woody vegetation. This circumstance was extremely significant for the ancient people of the Arctic. Trees serve not only as fuel, but also as a building material used for the construction of the frames of dwellings, in addition to their use in the manufacture of hunting weapons, namely, the shafts of spears and darts.

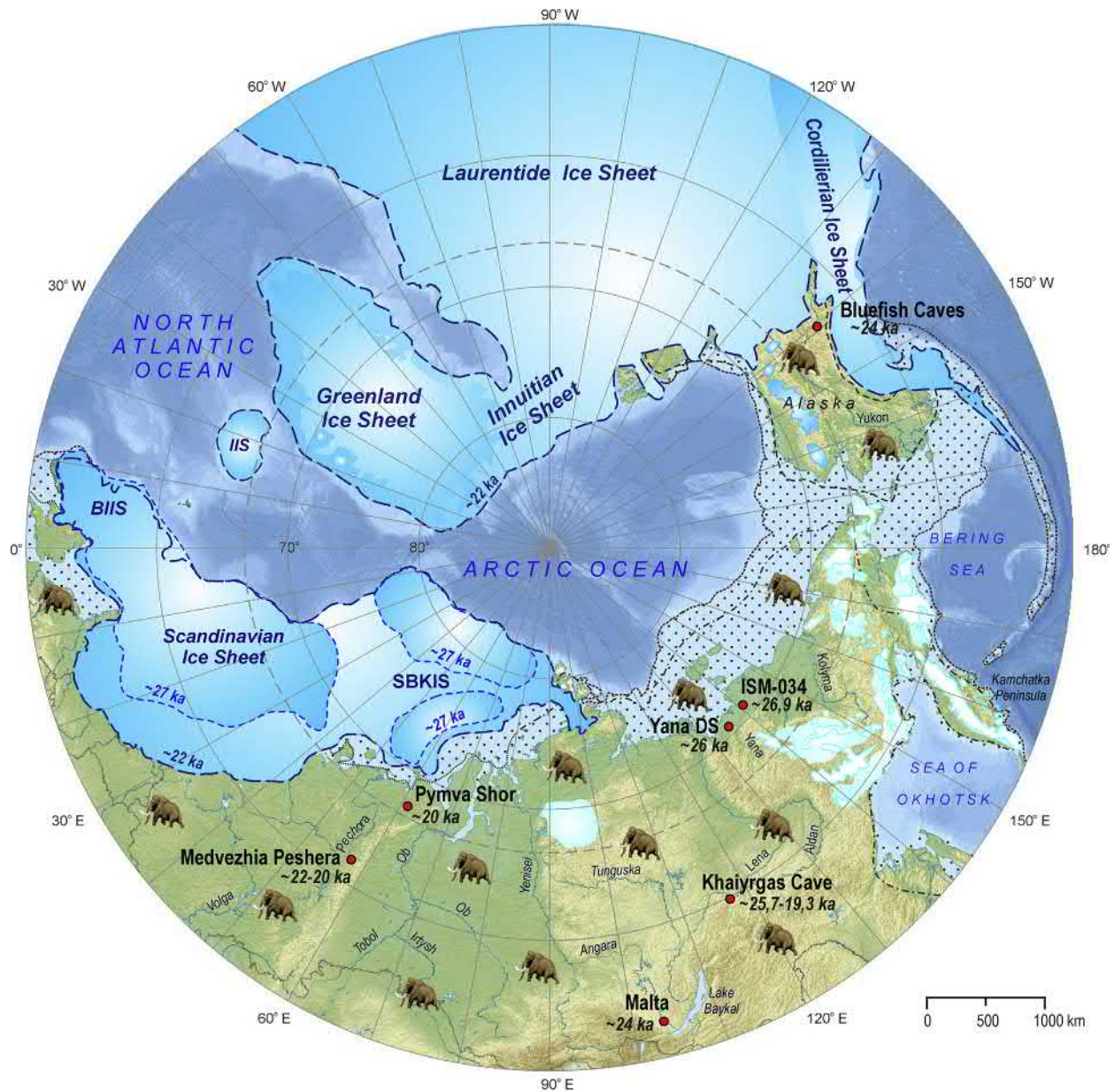
In the case of fuel for burning, alternatives can be found in the Arctic, for instance, the use of branches of shrubs, peat, bones and fat animals for fuel. Alternative building materials for the frames of dwellings may be found in the large shoots of shrubs, which can easily reach 3–4 m lengths in warm microhabitats. However, much higher quality material is needed to make the shaft of a spear. Thus, the importance of wood as a cultural resource can only be fully assessed if it is not available at all. This is the situation that faced the first people who entered the Arctic tundra during the Late Pleistocene in the Eurasian Subarctic and Arctic.

To overcome the lack of wood, the Upper Paleolithic people, including inhabitants of the Yana River site, developed a special technology to longitudinally split the tusks of woolly mammoths. In this way they obtained strong shafts of ivory up to 2 m long - the length needed for the shaft of a full-size spear. Traces of this technology are documented in several localities across arctic Western Beringia including the Yana and Berelekh sites (Pitulko et al., 2015a). The ivory-shafted spears were needed to hunt large Pleistocene herbivores, including the mammoths from which the ivory was obtained.

Mammoth Hunting

Mammoth hunting was an important activity, but was carried out on a limited basis, primarily to obtain important raw materials, the tusks, bones and possibly fat, which, along with bones, could be used as fuel in winter. Mammoth meat was used for food but did not play a significant role in the diet of ancient hunters of the Siberian Arctic. Instead they hunted large numbers of Pleistocene bison, horse, and reindeer. There is no evidence of mass single-use mammoth hunting. Based on the fossil evidence, mammoth hunting was most likely carried out at a very low rate (1–2 animals per year) and was undoubtedly associated with the extraction of important bone raw materials (Nikolskiy and Pitulko, 2013; Pitulko et al., 2015a).

The mammoth population of Eastern Siberia experienced a notable decline in numbers toward the end of the MIS 3 interstadial, and during the LGM their numbers decreased even more. Pitulko and Nikolskiy (2012) suggest that mammoth populations



- sites dated to ~27–20 ka
- Eurasian Ice Sheet Complex at 27 ka (after Hughes, et al., 2015)
- Ice sheets at 22 ka: Eurasian Ice Sheet Complex (after Hughes, et al., 2015); North American Ice Sheet Complex (after Stokes, 2017)
- mountain glaciation margin at 27–20 ka (after Svendsen, et al., 1996; Glushkova, 2001; Barr and Clark, 2012; Galanin, 2012)
- dry land extent and land/sea boundary at 27–20 ka with ocean level decrease to -120 m (after Lambeck, et al., 2002)
- extent of the mammoth habitat in Alaska (after McDonald, et al., 2012)
- extent of the mammoth habitat in NE Asia (after Pitulko and Nikolskiy, 2012)
- extent of the mammoth habitat in West Siberia and in the Northern Europe (after Kahlke, 2014)

Fig. 4 Arctic and sub-Arctic archeological sites dated to 27,000–20,000 years ago (27–20 ka), with LGM environmental settings based on data published in: Barr I. D. and Clark C. D. (2012). Late Quaternary glaciations in Far NE Russia; combining moraines, topography and chronology to assess regional and global glaciation synchrony. *Quaternary Science Reviews* **53**, 72–87; Galanin, A. A. (2012). Age of the Last Glacial Maximum on Asian North-East. *Kriosfera Zemli* **XVI**(3), 39–52; Glushkova, O. Y. (2001). Geomorphological correlation of Late Pleistocene glacial complexes of Western and Eastern Beringia. *Quaternary Science Reviews* **20**, 405–417; Hughes, A. L. C., Gyllencreutz, R., Lohne, Ø. S., Mangerud, J., and Svendsen, J. I. (2015). The last Eurasian ice sheets—A chronological database and time-slice reconstruction, DATED-1. *Boreas* **45**(1), 1–45; Kahlke, R.-D. (2014). The origin of Eurasian Mammoth Faunas (Mammuthus—Coelodonta Faunal Complex). *Quaternary Science Reviews* **96**, 32–49; Lambeck, K., Esat, T. M., and Potter, E.-K. (2002). Links between climate and sea levels for the past three million years. *Nature* **419**(6903), 199–206; McDonald, G. M., Beilman, D. W., Kuzmin, Y. V., Orlova, L. A., Kremenetski, K. V., et al. (2012). Pattern of extinction of the woolly mammoth in Beringia. *Nature Communications* **3**, 893; Stokes, C. R. (2017). Deglaciation of the Laurentide Ice Sheet from the Last Glacial Maximum. *Cuadernos de Investigación Geográfica* **43**, 377–428.

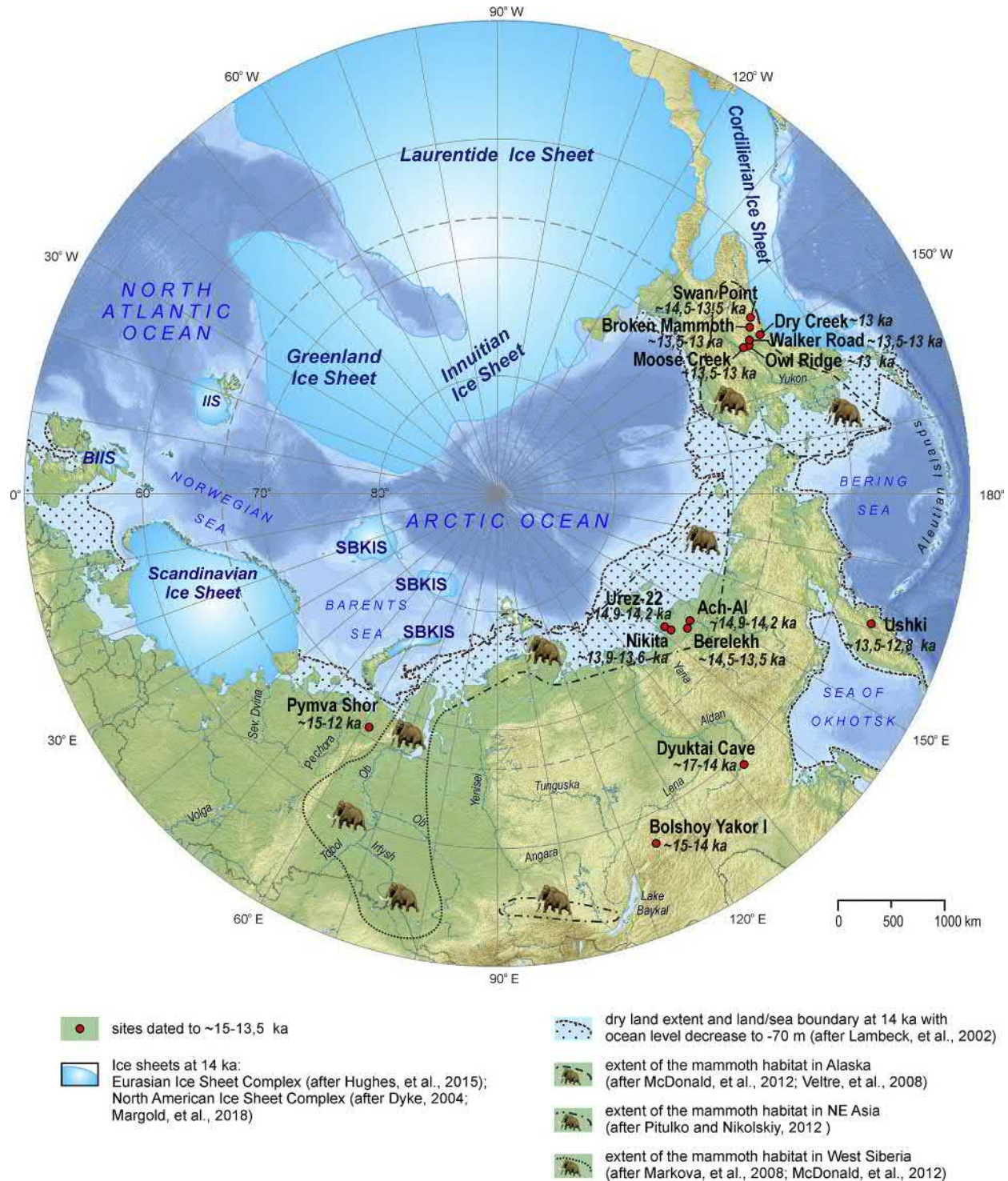


Fig. 5 Selected Arctic and sub-Arctic archeological sites dated to 15,000–13,500 years ago (15–13.5 ka); environment settings are shown for 14,000 years ago time slice based on data published in: Dyke, A. S. (2004). An outline of North American deglaciation with emphasis on central and northern Canada. *Developments in Quaternary Sciences* **2B**, 373–424; Hughes, A. L. C., Gyllencreutz, R., Lohne, Ø. S., Mangerud, J., and Svendsen, J. I. (2015). The last Eurasian ice sheets—A chronological database and time-slice reconstruction, DATED-1. *Boreas*, **45**(1), 1–45; Lambeck, K., Esat, T. M., and Potter, E.-K. (2002). Links between climate and sea levels for the past three million years. *Nature* **419**(6903), 199–206; McDonald, G. M., Beilman, D. W., Kuzmin, Y. V., Orlova, L. A., Kremenetski, K. V., et al. (2012) Pattern of extinction of the woolly mammoth in Beringia. *Nature Communications* **3**, 893; Margold, M., Stokes, C. R. and Clark, C. D. (2018). Reconciling records of ice streaming and ice margin retreat to produce a palaeogeographic reconstruction of the deglaciation of the Laurentide Ice Sheet. *Quaternary Science Reviews* **180**, 1–30; Markova A. K., van Kolfschoten T., Bohncke S., Kosintsev P. A., Mol J., et al. (2008). *Evolution of European ecosystems during Pleistocene–Holocene transition (24–8 kyr BP)*. Moscow: KMK Scientific Press; Pitulko, V. V. and Nikolskiy, P. A. (2012). Extinction of woolly mammoth in Northeastern Asia and the archaeological record. *World Archaeology* **44**(1), 21–42; Veltre, D. W., Yesner, D. R., Crossen, K. J., Graham, R. W., and Coltrain, J. B. (2008). Patterns of faunal extinction and paleoclimatic change from mid-Holocene mammoth and polar bear remains, Pribilof Islands, Alaska. *Quaternary Research* **70**, 40–50.

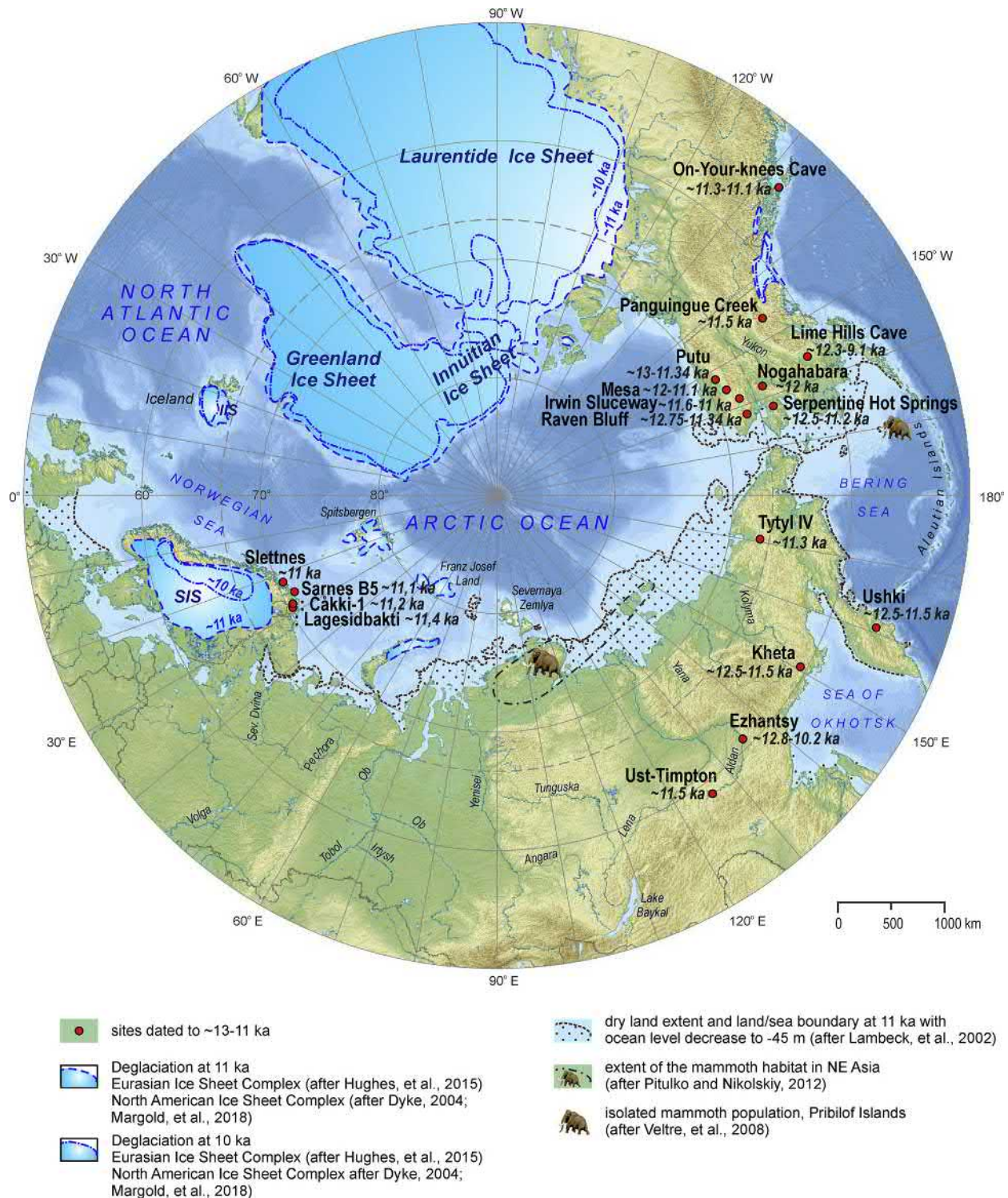


Fig. 6 Selected Arctic and sub-Arctic archeological sites dated to 13,000–11,000 years ago (13–11 ka); environment settings are shown for 11 ka time slice based on data published in: Dyke, A. S. (2004). An outline of North American deglaciation with emphasis on central and northern Canada. *Developments in Quaternary Sciences* **2B**, 373–424; Hughes, A. L. C., Gyllencreutz, R., Lohne, Ø. S., Mangerud, J., and Svendsen, J. I. (2015). The last Eurasian ice sheets—A chronological database and time-slice reconstruction, DATED-1. *Boreas* **45**(1), 1–45; Lambeck, K., Esat, T. M., and Potter, E.-K. (2002). Links between climate and sea levels for the past three million years. *Nature* **419**(6903), 199–206; Margold, M., Stokes, C. R., and Clark, C. D. (2018). Reconciling records of ice streaming and ice margin retreat to produce a palaeogeographic reconstruction of the deglaciation of the Laurentide Ice Sheet. *Quaternary Science Reviews*, **180**, 1–30; Pitulko, V. V. and Nikolskiy, P. A. (2012). Extinction of woolly mammoth in Northeastern Asia and the archaeological record. *World Archaeology* **44**(1), 21–42; Veltre, D. W., Yesner, D. R., Crossen, K. J., Graham, R. W., and Coltrain, J. B. (2008). Patterns of faunal extinction and paleoclimatic change from mid-Holocene mammoth and polar bear remains, Pribilof Islands, Alaska. *Quaternary Research* **70**, 40–50.

decreased from south to north in northeastern Siberia. It is noteworthy that this decline in mammoth numbers took place just as a new hunting technology was spreading northwards from Northern China and Mongolia. This new technology involved a newly invented lithic toolkit based on wedge-shaped core knapping. The northward spread of this technology was most likely due to human migration in eastern Asia, in response to the sharp cooling and increased aridity of the climate associated with the LGM. The growth of continental ice sheets and glaciers during the LGM also brought a lowering of sea level, exposing more of the continental shelf regions surrounding Northern Eurasia (Fig. 4).

Events of the Last Glacial Maximum

The quantity of archeological data used to evaluate the timing and processes of human settlement in the Arctic is quite large, but unevenly distributed (Hollesen et al., 2018). Thus, there are large chronological and spatial gaps in sites providing evidence of initial colonization (Figs. 4–6). As of this writing, there are no Arctic sites that provide a continuous, unbroken archeological record that documents the full history of human occupation of any Arctic. In some cases, such gaps span tens of thousands of years. For instance, in the Arctic zone of Northeast Europe, there is clear evidence for the presence of humans in the late Pleistocene prior to the Last Glacial Maximum (LGM), as evidenced by data from the Mamontovaya Kurya site, dated to ca. 40,000 years ago. There is also good evidence for human occupation of this region near the end of the last glaciation, based on data from the Pymva-Shor site, dated from 16,000 to 12,500 years ago (Svendsen et al., 2010), as well as evidence from the early Holocene, documented by a continuous archeological record that extends from northwestern Siberia to the Taimyr Peninsula. The dates of human occupation of these sites range from 8100 years ago in the west to 6800 years ago in the east (Fig. 7).

The best studied areas with a relatively short history of human occupation are northern Fennoscandia in the East (starting at 10,000–9000 years ago) and the American Arctic (starting at 13,000–12,000 years ago) in the Western Hemisphere. The vast Arctic territories of Northern Eurasia from the Barents Sea coast in the west to the Bering Strait in the east have been studied far less, but the existing data nevertheless allow us to assess the processes associated with human settlement of these regions in their essential details (Fig. 7).

Thus, LGM coastlines shifted north of their current position. Also, the desertification of the continental interior caused changes in vegetation cover, with northerly shifts of vegetation zones that would have caused redistribution of faunal populations. Of course, the hunter-gatherers of Arctic Siberia relied chiefly on these large herbivores for their food, so these animals served as a resource base for the human population of these areas. The LGM therefore caused environmental stress on the regional human population, forcing them out of their traditional hunting grounds. This, in turn, was the apparent driver for new weapon technology. The emergence of microblade technology, based on the splitting of wedge-shaped cores, is most likely a consequence of environmental changes associated with the disappearance of mammoth from the southern tundra belt of Northern Eurasia. As discussed above, mammoth tusks served as an important raw material for the production of hunting equipment, such as spear shafts (Pitulko and Nikolskiy, 2012).

It is important to note that despite the serious climatic deterioration during the LGM, the Arctic and subarctic territories of Beringia remained suitable for human life (Fig. 4), although the size of human populations, which had never been high, apparently became even lower. The human occupation of Eastern Beringia (i.e., unglaciated regions of Alaska and the Yukon) during the LGM is indicated by archeological evidence from Bluefish Caves, northern Yukon Territory (Bourgeon et al., 2017). However, it is difficult to interpret the culture of the Bluefish Cave population because of the lack of data.

In Western Beringia, reliable but rare traces of human activity during the LGM are known from the middle stretches of the Lena River at Khaiyrgas Cave site (Kuzmin et al., 2017) to the Yana-Indighirka lowlands in Arctic Siberia (Pitulko et al., 2017). Evidence of human occupation comes from radiocarbon ages of artifacts and sediments. In addition, ancient DNA evidence has recently revealed that the carriers of this culture were associated with a powerful influx of people from East Asia that completely replaced and/or assimilated the former populations of the ancient North Siberian population (“the Yana” people) (Sikora et al., 2019). This is in line with archeological evidence.

The main archeological features of their material culture are wedge-shaped cores, used to make microblades and bifacial spearheads. Beringian microblade technology first appeared regionally in the Amur Basin, approximately 24,000 to 23,000 years ago. In the interval of 18,000–12,000 years ago, this technology spread in the subarctic areas (e.g., the lower occupation component of Dyuktai Cave and the complex of layer 6 from the Ushki Lake), and rapidly spread to the Pacific coast. Thus, its earliest traces were found in Alaska, in the site occupation of Swan Point (cultural component 4), where it has an age of 14,500 years ago, as well as in several other sites, whose age is not less than 11,000 years ago. These latter sites belong to the Denali complex, dated to 13,500 years ago (Graf and Buvit, 2017).

Holocene History

It is noteworthy that in the Siberian Arctic region of Northern Eurasia, as far as can be judged by the evidence from dated archeological sites (Urez-22 and Tytylvaam IV), microblade technology developed only at the beginning of the Holocene, coinciding with the timing of the demise of the regional mammoth population (Pitulko and Nikolskiy, 2012; Pitulko et al., 2017). Artifact collections from the Tytylvaam site include both wedge-core and micro-prismatic technologies for microblade production. The stone tool industry from the Urez-22 site cannot be explicitly interpreted as wedge-shaped core technology. However, the morphology of the

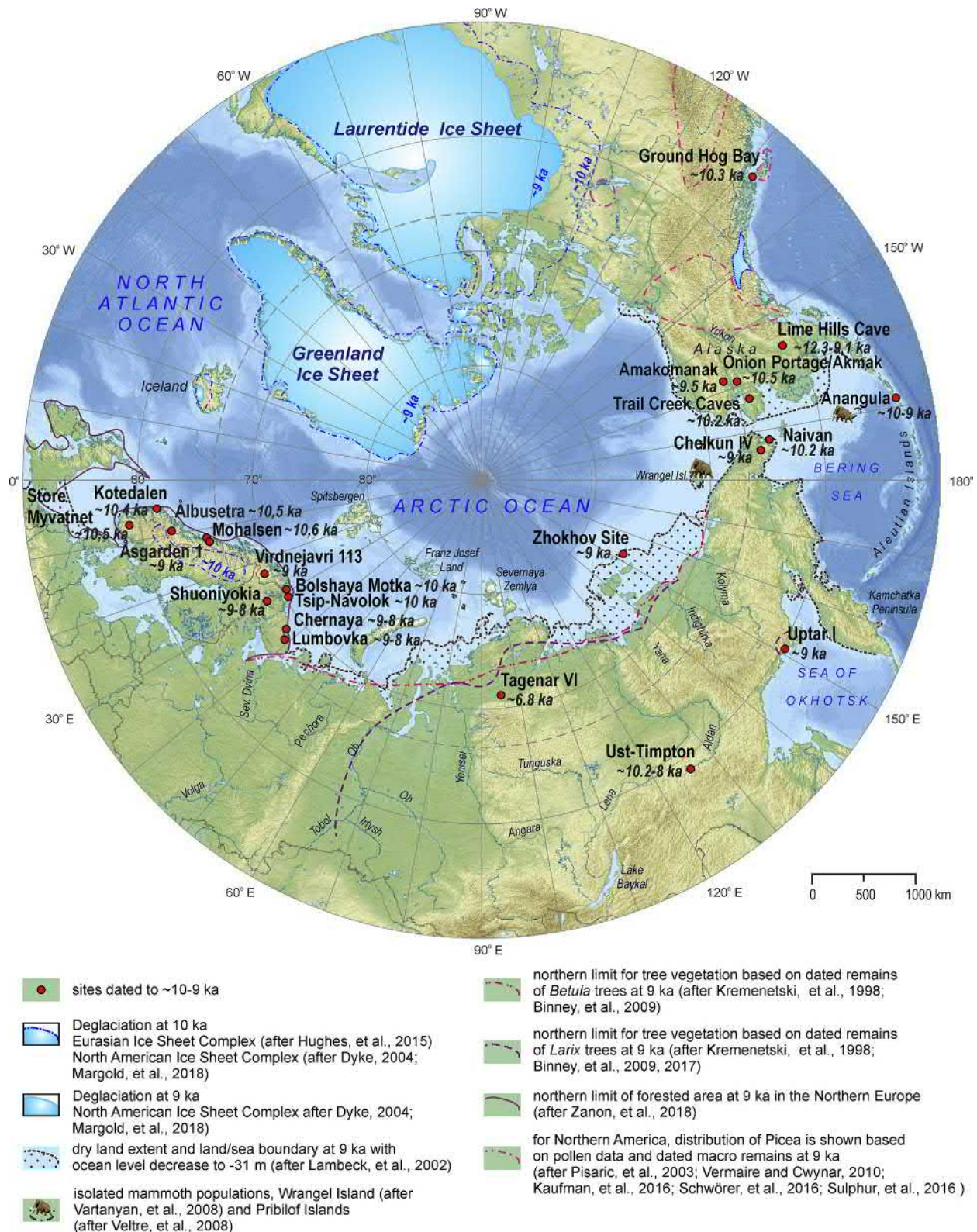


Fig. 7 Selected Arctic and sub-Arctic archeological sites dated to 12,000–9,000 thousand years ago (12–9 ka); environment settings are shown for 9 ka time slice based on data published in: Binney, H. A., Willis, K. J., Edwards, M. E., Bhagwat, S. A., Anderson, P. M., et al. (2009). The distribution of late-Quaternary woody taxa in northern Eurasia: evidence from a new macrofossil database. *Quaternary Science Reviews* **28**, 2445–2464; Binney, H., Edwards, M., Macias-Fauria, M., Lozhkin, A., Anderson, P., et al. (2017). Vegetation of Eurasia from the last glacial maximum to present: Key biogeographic patterns. *Quaternary Science Reviews* **157**, 80–97; Dyke, A. S. (2004). An outline of North American

microblades suggests wedge-shaped technology was being used instead of prismatic knapping. Simplified wedge-core technology that post-dates the Pleistocene/Holocene boundary has also been found in other sites from various regions of Beringia, such as the Lake Baikal region, the Upper Kolyma region, and the Chukchi Peninsula, as well as in Alaska, where it is part of the Paleo-arctic tradition, and where it persisted until 5000 years ago.

The microblade tradition in Western Beringia was rapidly replaced in the beginning of the Holocene by microprismatic blade technology. Its earliest evidence is found in the Aldan river valley about ~12,500/12,000 years ago at Ust-Timpton site. However, at ~10,000–9000 the same technology was adopted in the eastern Chukotka (e.g., Ul'hum, Chelkun IV, Nivan sites). At ~9000 years ago, it reached the northernmost limits of the continent, as revealed by the microprismatic industry together with inset tools from the Zhokhov site (76°N, New Siberian islands). This is the oldest known archeological site in high-latitude Arctic (Pitulko and Makeyev, 1991). The regions in which this tradition was adopted extend from the Taimyr Peninsula in the West and to Bering Strait in the East, with an extension into NW North America. This stone tool tradition persisted through the first half of the Holocene (Fig. 7). According to the human genetics of the area, this phenomenon marks population changes due to migration from the southern areas to the Arctic (Sikora et al., 2019), driven by the sharp environmental deterioration of the Younger Dryas cold event in the deep continental regions.

The rapid northward advance of these populations was apparently due to progressive landscape change driven by several waves of the thaw-lake thermokarst development. The evidence indicates that it occurred after 15,000, ~10,500, 5000, and 2000 years ago, respectively. The first wave of immigration was the most powerful, followed by the northern shift of tree line. Thus, in Northern Eurasia, the herb-dominated tundra-steppe belt with open landscapes was largely replaced by forest. In the Arctic, steppe-tundra was transformed into dwarf-shrub tundra.

The cumulative impacts of environmental change at the end of the Pleistocene caused the steppe-tundra habitat to retreat northwards. The large Pleistocene herbivores, including mammoths, followed the steppe-tundra to the North, and the humans who exploited them followed after the megafauna (Pitulko and Nikolskiy, 2012). The last mammoths of continental Northern Eurasia persisted in the northern Taimyr and on the modern New Siberian islands until about 10,500 years ago (Nikolskiy et al., 2011). The Pleistocene horse and bison persisted in northern Eurasia somewhat longer (Lorenzen et al., 2011). It is likely that humans reached the northernmost limits of Eurasia following the animal migrations.

Reindeer is one of the species that survived the Pleistocene to Holocene transition. However, it likely suffered a serious reduction in population size at the onset of the Holocene. Because of the lack of large game animals, early Holocene Arctic hunters had either to develop a complex economy with elements of coastal adaptation where possible or seek unusual food resources.

Thus, the Zhokhov site provides evidence for year-round habitation based mostly on reindeer exploitation except in winter. In winter these hunters apparently killed polar bears in their dens (Pitulko et al., 2015b). Similar hunting tactics are widely known but the hunting of the world's largest terrestrial predator for use as a main food source has not been documented anywhere else in the world. The Zhokhov hunters must have had compelling reasons to hunt polar bears, e.g., limited availability of regular, or less dangerous, food sources.

Additionally, the Zhokhov site yielded the earliest reliably documented evidence for the use of a land transportation system based on dogsleds (Pitulko and Kasparov, 1996). Zhokhov dogs were physically identical to modern sled dogs by body weight and size. Apparently these dogs had been bred for sled hauling over a long period of time (Pitulko and Kasparov, 2017). The ancient sleds had well-developed construction with socketed uprights supporting the platform in a style similar to recent (ethnographically known) patterns. Indirectly, presence of such complex constructions also suggests the possible use of frame boats.

Introduction of the dogsled transport system is the most important innovation in Arctic human culture at the Holocene boundary. This element of adaptation allowed the early Holocene hunters of the Siberian Arctic and northwestern North America to move quickly over vast areas, adapting to changes in resource availability. They would also have obtained the ability to develop long-distance exchange systems. Geochemical signatures of obsidian artifacts from the Zhokhov site (Pitulko et al., 2019)

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Fig. 8 Obsidian exchange systems in sub-Arctic and Arctic regions of East Siberia (after Kuzmin, 2019; Pitulko et al., 2019) and Alaska (after Potter, et al. 2017) revealed by geochemical signatures found for specific source areas based on data published in: Kuzmin, Y. V. (2019). Obsidian acquisition and exchange in prehistoric cultures of the Russian Far East and Northeast Russia: a review of the 25 years of research. *Prehistoric Archaeology. Journal of Interdisciplinary Studies* 1, 92–107; Pitulko, V. V., Kuzmin, Y. V., Glascok, M. D., Pavlova, E. Y., and Grebennikov, A. V. (2019). 'They come from the ends of the earth': Long-distance exchange of obsidian in the early Holocene of the High Arctic (Zhokhov site, eastern Siberia). *Antiquity* 93(367), 28–44; Potter, B. A., Reuther, J. D., Holliday, V. T., Holmes, C. E., Miller, D. S., and Schmuck, N. (2017). Early colonization of Beringia and Northern North America: Chronology, routes, and adaptive strategies. *Quaternary International* 444B, 36–55.

demonstrate that the source stone came from ~1500 km east of the archeological site, on Krasnoye Lake in the lower reaches of Anadyr river (Fig. 8).

The amount of obsidian found at the Zhokhov site is negligible compared with the quantity of the local chert. Since there is no evidence for any particular use of the obsidian, the real purpose of the developing contacts with people in remote areas may not have simply to facilitate exchange of goods. The driving force may well have been intellectual interest, rather than material gain. These findings indicate not only the existence of long-range exchange systems ~9000 years ago but speak of complex socio-cultural interactions that existed over vast areas.

The deposit on Krasnoye Lake is major obsidian source on the Siberian side of the Bering Strait (Kuzmin, 2019). Rocks imported from this obsidian source indicate that stable regional exchange networks existed throughout the Holocene. In addition to the Zhokhov site, this obsidian has been found at archeological sites on the lower reaches of Kolyma, in Chukotka and Kamchatka. Trans-Beringian imports of this obsidian into Alaska are also noted, but in low numbers.

The earliest evidence of human occupation of northern Scandinavia (Finmark) is dated about 10,000–9000 years ago (Olsen, 1994). By this time the first settlers were mastering shoreline resources (Fig. 8). The diet of the early Holocene population of the North Atlantic coast of Scandinavia shows a well-developed marine adaptation, as opposed to the population of the southern and eastern regions of Scandinavia, where the economy combined terrestrial and freshwater resources with a notable contribution of terrestrial foods. The diet of the inhabitants of the coasts of Scandinavia and the Kola Peninsula became more diverse with time, but with well-expressed elements of marine adaptation, as reflected in fossil remains (e.g., shell middens) and rock art. However, this adaptation never became as specialized as the maritime adaptations of the ancient cultures of the Bering Strait, the Canadian Arctic and Greenland.

Even after the early postglacial inundation of the continental shelves in the Eastern Siberian Arctic, the evidence for marine adaptation by regional populations begins only about 3500 years ago, and even this evidence is based on a single site: the Devil's Gorge site on Wrangel Island (Dikov, 1988). It is noteworthy that around the same time of the establishment of a maritime economy on Wrangel Island, the isolated population of dwarf mammoths (Vartanyan et al., 2008) died out. However, the human contribution to this event remains unclear.

Nevertheless, the Neolithic culture of North-East Asia may have certain connections with the Arctic Small Tool tradition. Genetic data indicate that back migration from Alaska and the Aleutians to northeast Asia took place about 5000 years ago (Sikora et al., 2019). Similar reverse migrations took place more recently, likely due to population growth in the Bering Strait area during warm intervals (Fig. 9), e.g. at ~2000 years ago (Roman Warm Period) and ~1000 years ago (Medieval Warming). Both intervals are clearly marked in the archeological record, by the emergence of the Old Bering Sea culture, and by the less known spread of the

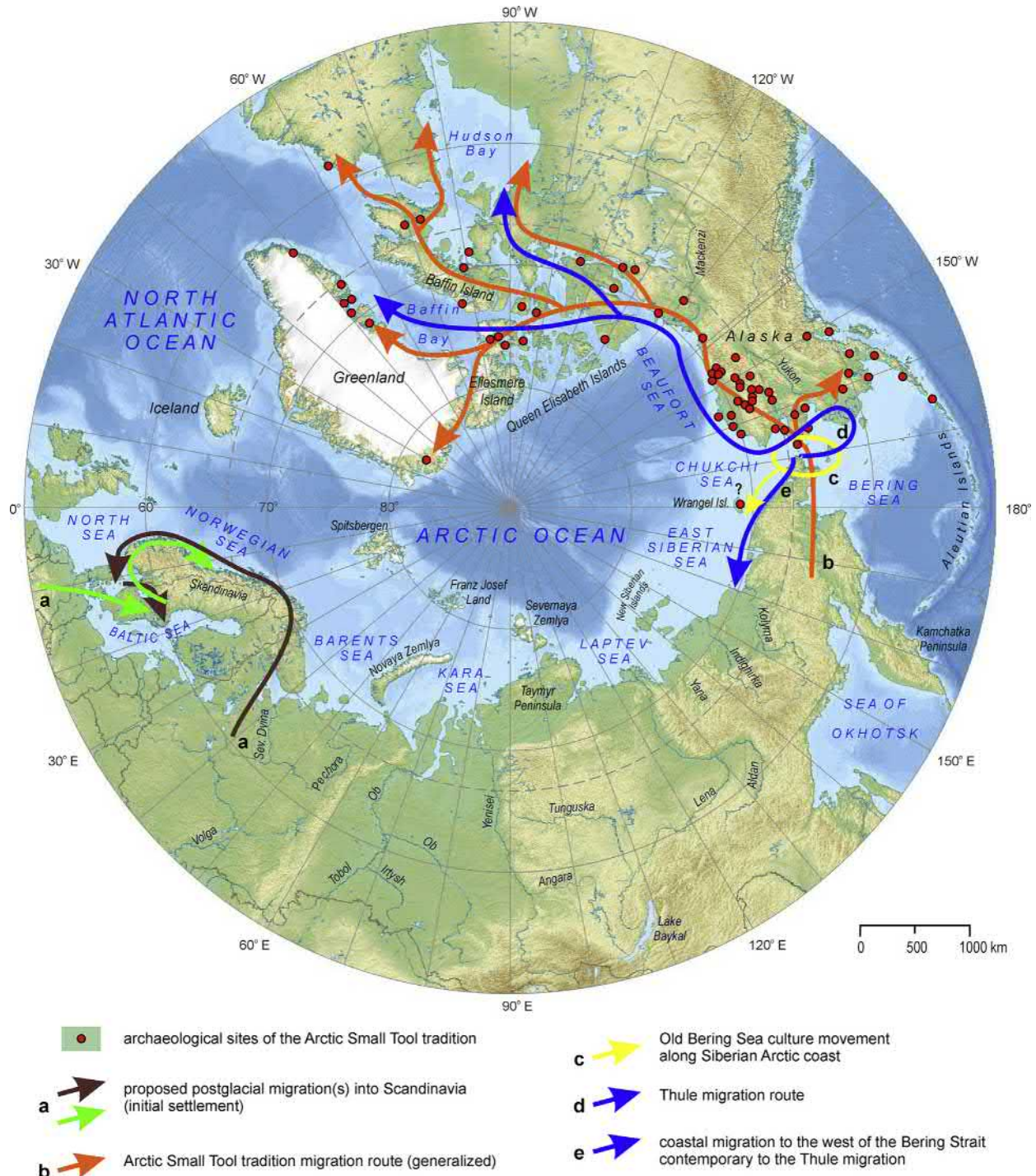


Fig. 9 Selected Arctic and sub-Arctic archeological sites dated younger than 9000 years ago, and major coastal migrations in the Arctic: (a) postglacial migration(s) into Scandinavia; (b) Arctic Small Tool tradition spread into Alaska, Canadian Arctic and Greenland at around 5000 years ago; (c) Old Bering Sea culture spread to the west of the Bering Strait about 2000 years ago; (d) Thule migration ~1000 years ago; (e) migration to the west of the Bering Strait contemporary to the Thule migration.

Eskimo culture to the Kolyma river mouth (Pitulko and Pavlova, 2016), which was contemporary with the Thule migration into the Canadian High Arctic. Thus, possible cultural connection between northeast Asia and Thule advance into northern Canada may provide evidence for the earliest phase of that cultural pulse, but not its ancestry.

Bronze Age

Although Bronze Age metal artifacts are rarely found in Arctic and sub-Arctic archeological sites (Fig. 10), there is indirect evidence for introduction of metal tools before they appeared in the archeological record. It may be seen in the degradation of lithic



Fig. 10 Introduction of metals into the Arctic regions: possible directions of exchange systems with metallurgical centers of the Eurasian metallurgical province, Siberian metal trade route, Bronze Age metalworking sites in the Arctic (Sandvika, Ust-Polovinka, Abylaakh), and the earliest finds of iron working in the Arctic at Ust-Polui, West Siberia.

microblade industries starting ~4000 years ago, even though technologies had been thriving for millennia elsewhere in the Arctic. Since that time, the degradation in regional lithic industries developed rapidly.

Indirectly, this also indicates a stable long-range exchange between the people of the Arctic and the people who developed Bronze Age metallurgy centers in the Eurasian Steppe Belt. This trade allowed arctic peoples to acquire the most desirable sort of tools, i.e., products with a long sharp cutting edge. This acquisition of bronze cutting tools eliminated the need for mass production of blade inserts for composite tools. Thus, in the Northern Urals the blade industry was replaced by flake-based technology about 4000 years ago. This highly developed bifacial technique still survives in this region today. Not far from this region, about 1000 km away, there were metal working centers in the Kama river region and in the Middle Urals. In East Siberia, Ymyyakhtakh Late Neolithic culture has been identified, with highly developed lithic technology, including blade production. But ~3000 years ago, prismatic knapping technology was replaced by flakes. The Baikal Lake region may have been a source for metal imports into northeast Siberia. The two regions are connected by an ideal transportation system along the Yenisei and Lena rivers.

Metal working technology is extremely rare in the Arctic (Fig. 10). In the early metal era, bronze casting is recognized in Scandinavia by the discovery of molds made of soap stone. The earliest traces of this technology are probably at least 3800 years old. The northernmost find comes from the Sandvika settlement at 70°N, dating to ~3000–2500 years ago (Arntzen, 2015). However, the earliest bronze casting in the Arctic was recorded at sites on the Taimyr Peninsula, north of 70°N. These are Abylaakh and Ust-Polovinka sites whose ages are ~3200 years ago (Khlobystin, 2005).

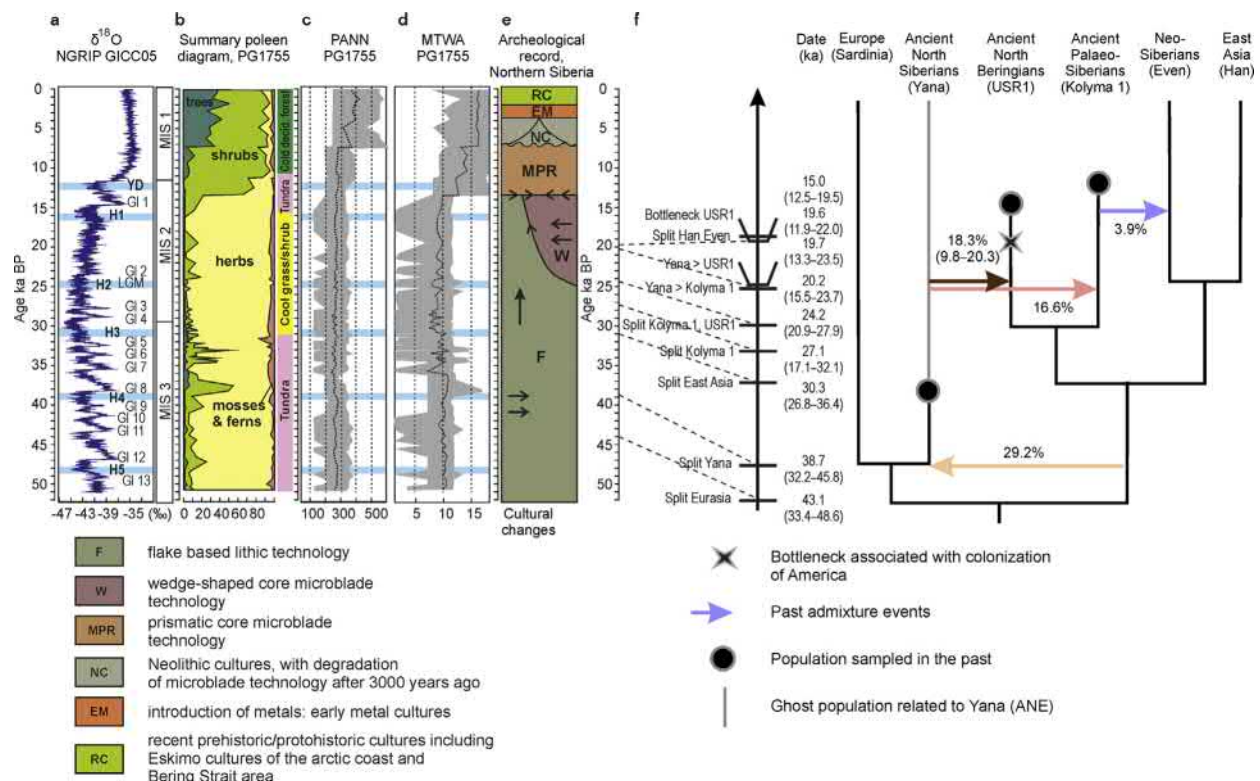


Fig. 11 Climatic, environmental, and archeological record of the East Siberia versus paleogenetics of Beringia: (a) the NorthGRIP $\delta^{18}\text{O}$ profile and the Greenland Interstadials (GI) 1 to 13 (after Svensson, et al., 2008), blue bars indicate approximate positions of the Younger Dryas (YD) and Heinrich events H1 to H5 (after Tierney, et al., 2008); (b) summary pollen diagram (percentages are based on total sum of pollen and spores identified at each level) and biome zones derived from the PG1755 core record (based on Müller, et al., 2010); (c) annual precipitation and (d) mean temperature of the warmest month (based on Tarasov, et al., 2013, dashed lines indicate most probable values and gray bands show range of the best modern analogues for each reconstructed variable, along with the NorthGRIP $\delta^{18}\text{O}$ profile); (e) archeological record, East Siberia; (f) demographic modeling of Siberian and Native American populations: inferred parameters for model with Siberian and Ancient Beringian populations, dates of events are given as (ka), and admixture estimates are shown as percentages along the arrows (modified from Sikora et al., 2019). Data collected from: Müller, S., Tarasov, P. E., Andreev, A. A., Tütken, T., Gartz, S., et al. (2010). Late Quaternary vegetation and environments in the Verkhoyansk Mountains region (NE Asia) reconstructed from a 50-kyr fossil pollen record from Lake Billyakh. *Quaternary Science Reviews* 29, 2071–2086; Sikora, M., Pitulko, V. V., Sousa, V. C., Allentoft, M. E., Vinner, L., et al. (2019). The population history of northeastern Siberia since the Pleistocene. *Nature* 570, 182–188; Svensson, A., Andersen, K. K., Bigler, M., Clausen, H. B., Dahl-Jensen, D., et al. (2008). A 60,000 year Greenland stratigraphic ice core chronology. *Climate of the Past* 4, 47–57; Tarasov, P. E., Müller, S., Zech, M., Andreeva, D., Diekmann, B., et al. (2013). Last glacial vegetation reconstructions in the extreme-continental eastern Asia: Potentials of pollen and n-alkane biomarker analyses. *Quaternary International* 290–291, 253–263; Tierney, J. E., Russell, J. M., Huang, Y., Sinningh, Damsté, J. S., et al. (2008). Northern Hemisphere Controls on Tropical Southeast African Climate During the Past 60,000 Years. *Science* 322(5899), 252–255.

Iron Age

Early examples of iron working in the Arctic are even rarer than that of copper and bronze (Fig. 10). The only object whose age corresponds to the early spread of iron working technology is known from the Ust-Polui complex in the lower reaches of the Ob river, West Siberia dated to ~2500 years ago (Vodyasov et al., 2017).

The penetration of metals into Arctic Siberia is associated with another wave of human migration into the region, stimulated by the progressive cooling of the early Neoglacial, about 4200 years ago (Wanner et al., 2011). The arrival of peoples who knew the secrets of metalworking came somewhat later. This took place about 3500 years ago and coincides with a southern shift of treeline (Binney et al., 2017) that culminated with the establishment of its current position in Northern Eurasia (Payette and Lavoie, 1994). As this new forest-tundra boundary became established, so did new regional cultures: the classic deer hunter cultures of Northern Eurasia.

Conclusions

The main events and processes related to the settlement and life of modern humans in the Arctic are discussed above. It is easy to see that the human history of Arctic Eurasia is closely associated with both the largest paleogeographic and geological events in the history of the region, as well as less visible climatic changes. An example of the longest occupied site in the archeological record of Eastern Siberia shows that changes in the material culture were closely tied with climate change (Pitulko and Pavlova, 2016; Pitulko et al., 2017). These climatic variations drove changes in vegetation and landscapes, which in turn brought about changes in the composition and abundance of the regional fauna (food resources). The series of environmental changes were a driving force in the replacement of the original population of inhabited areas with new groups, mostly coming from the southern regions (Fig. 11). This process was repeated across the Eurasian Arctic.

In the Stone Age, the population of the Siberian Arctic hardly exceeded modern numbers. Perhaps only 50,000 people inhabited this region in antiquity. Even if this figure is greatly underestimated, it can be doubled, but 100,000 people also represent an extremely low population density, which appears to have been the case. In comparison, the Upper Paleolithic population in Europe is estimated to have been higher. Modeling of human population trends based on the spatial distribution of archeological sites during several time slices from 30,000 to 13,000 years ago suggests dramatic population declines during the LGM and consistently low population density in the northern areas. Human population density in more temperate regions, such as the Mediterranean, are estimated to have been one person per 100 km² at best (Tallavaara et al., 2015). But even this meager population level was much higher than it was in the Arctic.

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Colonization of the Arctic in the New World

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Abstract

The first entry of people into northwestern North America in the Late Pleistocene was a highly significant event in the history of the spread of humans across the planet. Many questions remain to be answered concerning the timing of people entering North America, their origins, what caused them to leave Siberia and cross the Bering Land Bridge, and where did they manage to survive the extreme environmental conditions of the Last Glacial Maximum? Part of the problem in addressing these questions is that some key elements of the story very likely took place on the Bering Land Bridge (BLB), the exposed continental shelf regions that linked northeastern Siberia with Alaska during the last glaciation. Since the land bridge flooded near the end of the last glaciation, any evidence of human occupation there is now deeply submerged in the Bering and Chukchi Seas. We discuss these topics in turn and devote the remainder of this review to examining the peopling of Arctic North America during the middle to late Holocene.

Introduction

The first entry of people into northwestern North America in the Late Pleistocene was a highly significant event in the history of the spread of humans across the planet. The Americas were the last continents to be entered by our species, and apparently the gap between the human occupation of Eurasia and the eventual entry into the Americas was tens of thousands of years. The only region where Eurasia and North America are close together happens to be in the Arctic, probably the least hospitable region for human beings that evolved in the tropics. Yet we now know that at least two sites (and probably many more) in northeastern Siberia were occupied by anatomically modern humans, at least 50,000 years ago (Figs. 1 and 2). They hunted megafaunal mammals, such as mammoth, horse, bison and reindeer. They developed a rich material culture including many specialized tools and weapons made of mammoth tusk ivory. These Paleolithic residents of the Siberian Arctic apparently remained in that region until the climatic deterioration associated with the onset of the Last Glacial Maximum (LGM) drove them to seek new hunting grounds further east. These are the demonstrable archeological facts that secure our understanding of the colonization of the Siberian Arctic, but the subsequent sequence of events concerning one or more groups of people leaving their homeland and traveling east to the Bering Land Bridge and eventually onto the North American continent remain obscured.

Many questions remain unanswered. When exactly did these people enter the New World? Who were they? What drove them to leave northeastern Siberia? Which migration route did they use? Where did they reside during the Last Glacial Maximum (LGM)? What route did they take to leave Alaska and migrate south to the temperate latitudes? These all remain open questions, but one starting point may be found in the Beringian Standstill Hypothesis.

The Beringian Standstill Hypothesis

According to the Beringian Standstill Hypothesis, a population of anatomically modern humans migrated east from Western Beringia, onto the Bering Land Bridge (BLB). Based on the level of genetic differentiation between modern natives of northeast Siberia and Native Americans, this population was genetically isolated from its source population in Northeast Asia at the beginning of the Last Glacial Maximum (LGM), about 30,000 years ago. The Beringian LGM population carried distinctive DNA. After the LGM,

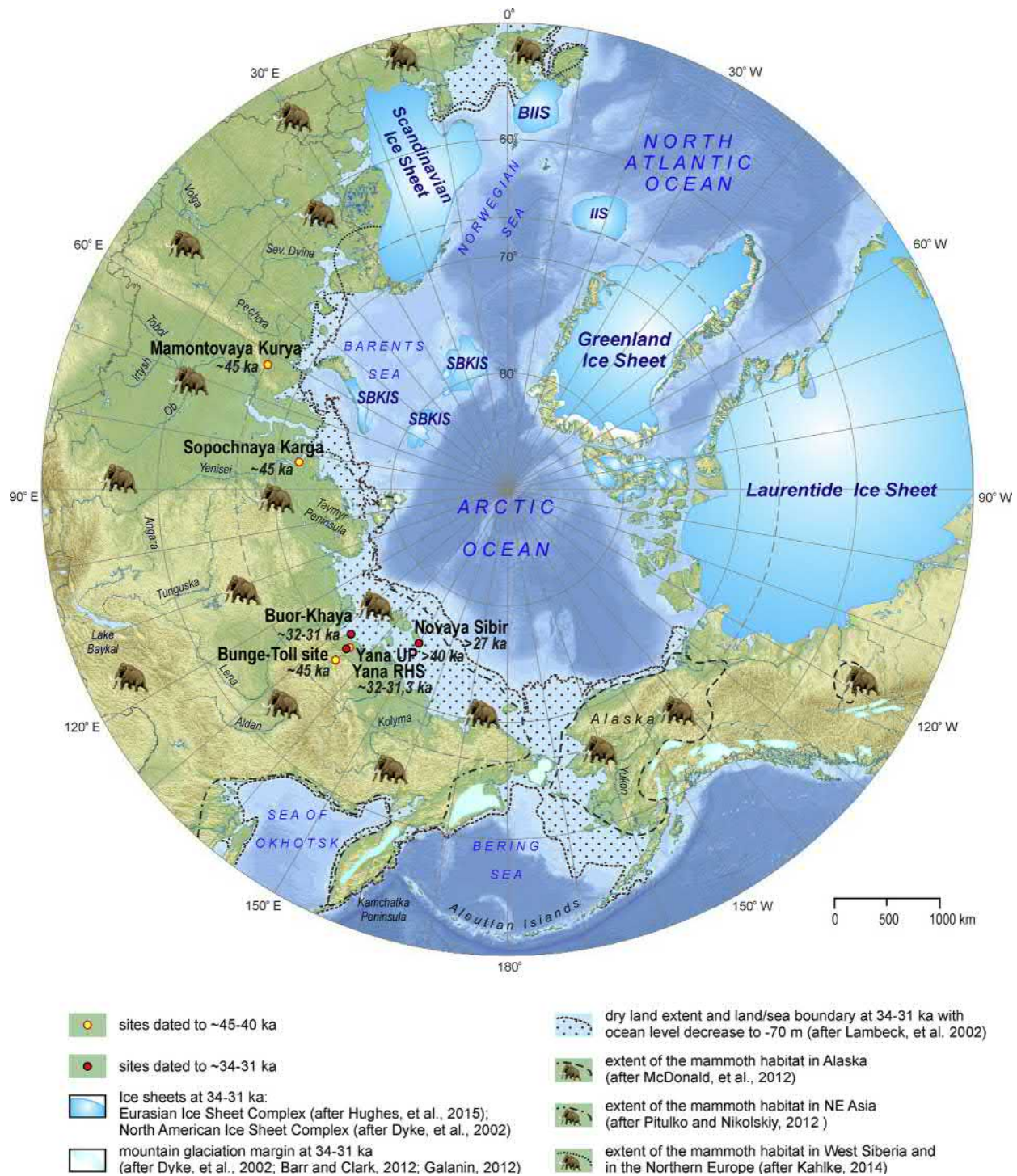


Fig. 1 Evidence for pre-LGM human habitation in the arctic Siberia dated from 45,000 to 31,000 years ago, with major environmental settings reconstructed for late MIS 3 based on data published in: Barr ID and Clark CD (2012). Late Quaternary glaciations in Far NE Russia; combining moraines, topography and chronology to assess regional and global glaciation synchrony. *Quaternary Science Reviews* 53, 72–87; Dyke AS, Andrews JT, Clark PU, England JH, Miller GH, et al. (2002). The Laurentide and Innuitian ice sheets during the Last Glacial Maximum. *Quaternary Science Reviews* 21(1–3), 9–31; Galanin AA (2012). Age of the Last Glacial Maximum on Asian North-East. *Kriosfera Zemli* XVI(3), 39–52; Kahlke R-D, (2014). The origin of Eurasian Mammoth Faunas (Mammuthus—Coelodonta Faunal Complex). *Quaternary Science Reviews* 96, 32–49; Lambeck K, Esat TM, and Potter E-K (2002). Links between climate and sea levels for the past three million years. *Nature* 419(6903), 199–206; McDonald GM, Beilman DW, Kuzmin YV, Orlova LA, Kremenetski KV, Shapiro B, Wayne RK, and van Valkenburgh B (2012). Pattern of extinction of the woolly mammoth in Beringia. *Nature Communications* 3, 893; Pitulko VV and Nikolskiy PA (2012). Extinction of woolly mammoth in Northeastern Asia and the archaeological record. *World Archaeology* 44(1), 21–42.

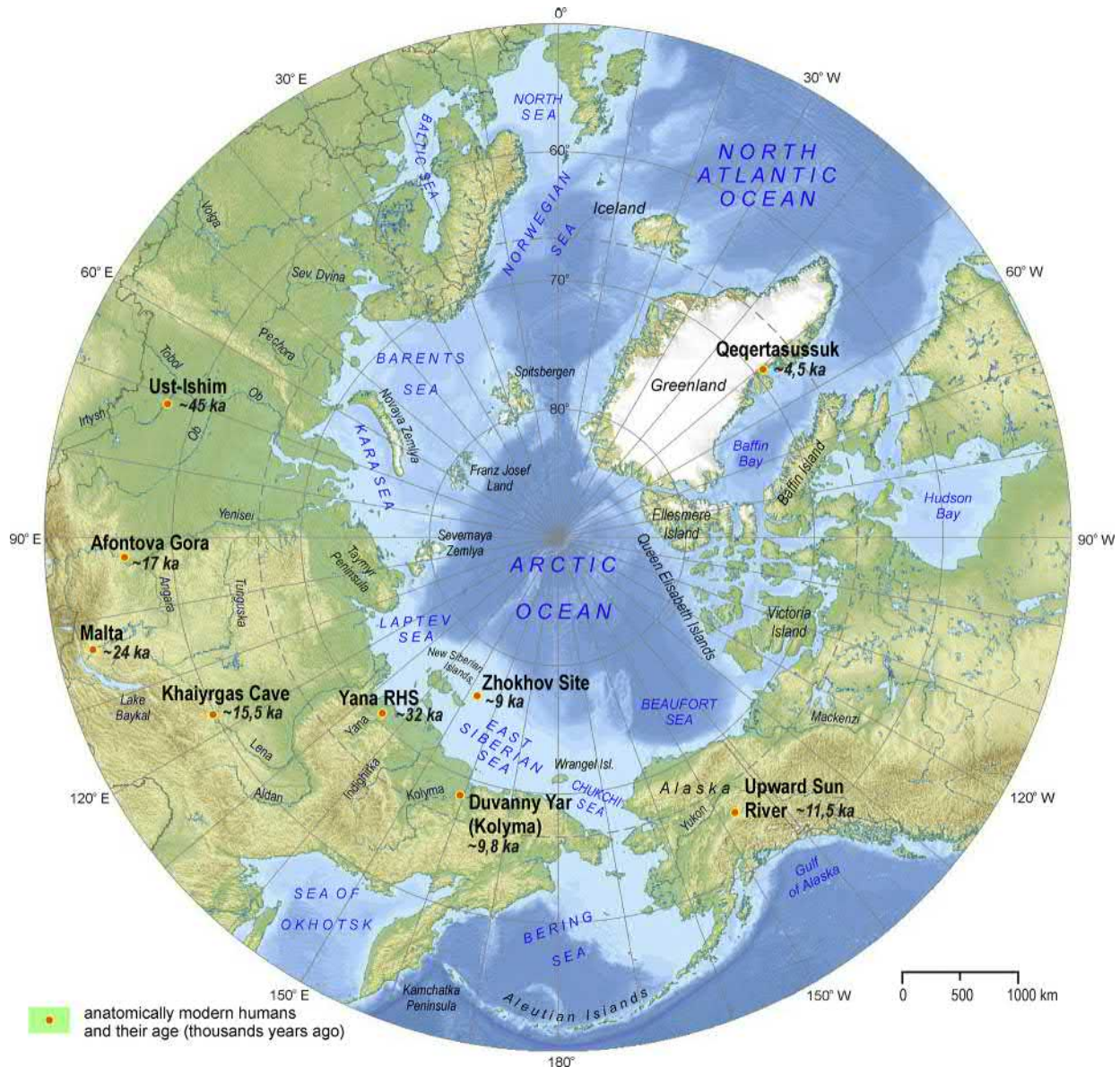


Fig. 2 Dated finds of anatomically modern humans discovered in the arctic Siberia, in the New World Arctic and in adjacent regions, largely used in paleo DNA studies to model human settlement of the New World Arctic regions in the past.

about 14,000 years ago, the descendants of this isolated population spread into mid-latitude North America and South America, although the DNA evidence indicates that some of the “standstill” population moved back into Northeast Asia (Hoffecker et al., 2016). There is also DNA evidence for another migration of people from Northeast Asia into North America, following the LGM.

The genetic evidence of the Siberian ancestors of the “standstill” population (Fig. 3), based on a study of ancient DNA from human remains at the Mal’ta site (24,000 years ago) and from the Afontova Gora site (17,000 years ago). The genetic evidence demonstrates the contribution of the Western Eurasian Lineage (Raghavan et al., 2014). The ancient DNA extracted from human remains at these two sites provides evidence in agreement with the aDNA evidence recently obtained from human remains at the Yana River site in Arctic Siberia (Sikora et al., 2019). All three sets of human genomes show great genetic diversity.

The people of the Yana River site, or Ancient Northern Siberians, made a significant contribution to the genome of the ancient Beringian population that colonized the Americas (Sikora et al., 2019). The population of Beringia was formed as a result of a mixture of the genetic lines of the ancient local population and the East Asian population (Fig. 3). This is indicated from genetic evidence from either side of the Bering Strait. In Siberia, a large fragment of human skull from the Duvanny Yar site (Sikora et al., 2019) yielded aDNA whose closest match comes from human remains at the Upward Sun River site in central Alaska (Moreno-Mayar et al., 2018), as well as the genome of modern Native Americans. In turn, in the first half of the Holocene the ancient Paleo-Siberian population (the Kolyma1 genome), was replaced by a new wave of East Asian origin - the ancestors of the modern

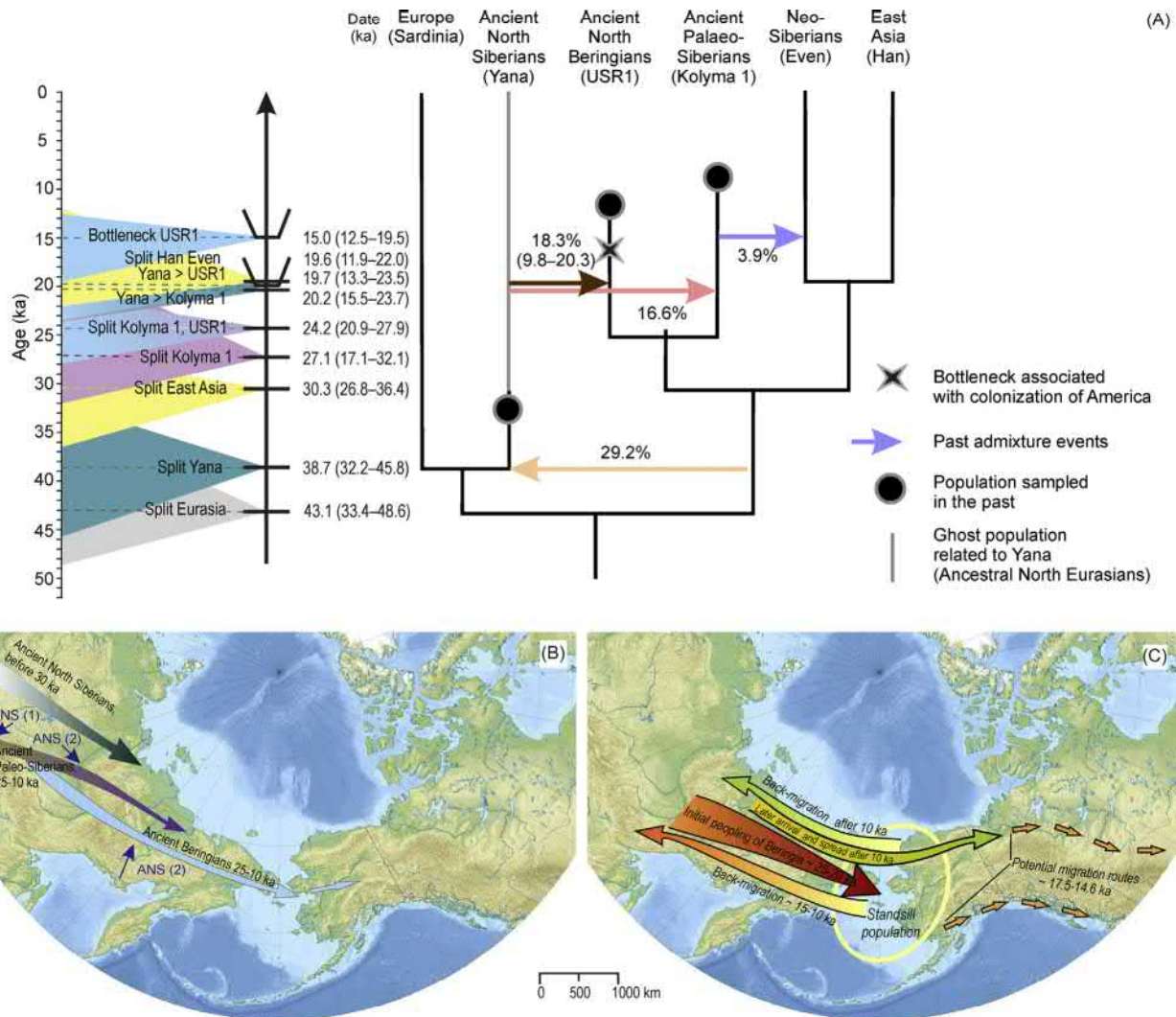


Fig. 3 Human interactions in the late Pleistocene Beringia: (A) Demographic modeling of Siberian and Native American populations and (B) Major hypothesized migrations into northeast Siberia before 30–10 ka based on data published in: Sikora M, Pitulko VV, Sousa VC, Allentoft ME, Vinner L, et al. (2019) The population history of northeastern Siberia since the Pleistocene. *Nature* 570: 182–188. (C) Migrations in Beringia at 25–10 ka based on genetics data published in: Tamm E, Kivisild T, Reidla M, Metspalu M, Smith DG, et al. (2007) Beringian standstill and spread of Native American founders. *PLoS One* 2(9): e829. Potential migration routes into the Americas based on data published in: Moreno-Mayar JV, Potter BA, Vinner L, Steinrücken M, Rasmussen S, et al. (2018) Terminal Pleistocene Alaskan genome reveals first founding population of Native Americans. *Nature* 553(7687): 203–207; Waters MR (2019). Late Pleistocene exploration and settlement of the Americas by modern humans. *Science* 365, eaat5447.

Tunguso-Manchu peoples, who are most closely related to Evenks, the most widespread ethnic group among the present-day Siberian natives (Sikora et al., 2019).

As discussed above, the Beringian Stand-Still model (Fig. 3) is built mainly on genetic evidence. The DNA of the ancient “stand-still” population contains a significant number of genetic mutations that took place after these people left their Asian parent groups, but before the Beringian population spread throughout North and South America. These mutated genes are widespread among living Native Americans in mid-latitude North America and South America. Based on human genetic mutation rates, Tamm et al. (2007) calculated that the people who became isolated from their Asiatic ancestors remained in isolation for about 10,000 years before they began to disperse throughout the Western Hemisphere.

Dispersal Routes Out of Alaska

Additional, independent information that may have a bearing on the Beringian Standstill Hypothesis comes from recent computer modeling of the Cordilleran and Laurentide ice sheets, which coalesced in western Canada, sealing Beringia off from a land route to the lower latitudes of North America. The glacial model suggests that these massive ice sheets completely blocked any possible

interior route from Alaska and the Yukon to more southerly regions during MIS 3 and MIS 2, i.e., from about 55,000 to 15,000 years ago (Stokes et al., 2012). In other words, it appears unlikely that there was a human population in either mid-latitude North America or South America before 15,000 years ago. It also appears extremely unlikely that humans entered these regions prior to 50,000 years ago, because there is no evidence for humans in Northern Asia at that time (Fig. 1), so there would have been no founding populations from which to draw any north Asian migrants into the New World. Thus, the archeological, glacial and genetic evidence, taken together, suggest that a population of modern humans, descended from Asian peoples, became geographically and therefore genetically isolated for 10,000 years or more, before they had the opportunity to migrate south to the ice-free regions of the Americas. Also, most of the time estimates for the genetic divergence from this isolated population to their Native American descendants suggests that this dispersal happened after 15,000 years ago, which is consistent with the glacial chronology (Hoffecker et al., 2016).

However, in contrast to the interior ice-free corridor route, Lesnek et al. (2018) proposed that the initial departure of people Beringia took place as early as 16,000 years ago via a deglaciated corridor along the North Pacific coast (Fig. 3). Of course, such a route was only feasible if the western edge of the Cordilleran Ice Sheet (CIS) had retreated by that time, and if a coastal route was habitable, in terms of biological resources (marine and/or terrestrial) along the coast. The authors used ^{10}Be exposure dating and ^{14}C dating of bones from a cave in order to date the culmination of maximum CIS conditions in southeastern Alaska, a potential bottleneck region for human migration. These dates fell within the window of ~20,000 to 17,000 years ago. They also found fossil evidence that productive marine and coastal ecosystems were established almost immediately following deglaciation, after 17,000 years ago. They concluded that the retreat of the CIS provided an open and ecologically viable pathway for humans to travel through southeastern Alaska, which may have been traversed by early humans as they colonized the Americas.

Changing Arctic Environments

What drove the Late Pleistocene people of northeastern Siberia (Fig. 1) to abandon their territory during the LGM, 30,000–16,000 years ago? Even if they could have withstood the extreme cold and/or aridity that descended on Siberia during the LGM, it appears likely these climatic changes caused serious declines in the game animals hunted by these Western Beringians. The environmental changes caused shifts in regional vegetation cover, which in turn affected the large grazers. The cold, dry climate would have lowered the Net Primary Productivity (NPP) of the ecosystem. NPP is the rate of carbon uptake by plants from atmospheric CO_2 , minus the carbon used by the plants in respiration.

Pollen data indicate that NPP was greatly reduced in the continental regions of both Western and Eastern Beringia during the LGM. This sharp decline in NPP probably pushed the human population of Western Beringia over the edge of sustainability, as their prey animals dwindled on the landscape.

One of the effects of the build-up of continental ice sheets during the LGM was to draw down global sea level. Because of the very shallow seas between Siberia and Alaska, when the LGM sea level dropped about 120 m, it exposed a significantly larger area on the BLB (roughly 1.4 million km^2) than existed in MIS 3. Much of the newly exposed land was in the southeastern margin of the land bridge, the Bristol Bay region. This region is well south of the Arctic, falling between about 56–58°N. Modeling of LGM NPP showed a relatively high level of plant productivity in this southern region of the land bridge. It would have been not only warmer than Arctic Beringia, but it also received far more moisture, because it was adjacent to the North Pacific. Furthermore, ocean temperature reconstructions suggest that sea surface temperatures were only slightly cooler than today in the Bering Sea and the Gulf of Alaska. The continental shelf regions, newly exposed during the LGM, formed a relatively low relief plain where rivers meandered across a poorly drained landscape. This would have increased the available moisture on the landscape. Hoffecker et al. (2016) contend that the LGM actually created new habitat for hunter-gatherer peoples on the southern portions of the BLB.

A Possible Human Refuge on the Land Bridge

In recent decades, a substantial body of proxy data on Beringian LGM environments has been collected (Fig. 4), including information from sediment cores drilled into the former surface of the land bridge. These data, including pollen, plant macrofossils, and insect fauna, confirm the presence of a mesic tundra environment, not only on the exposed Bering Platform, but also extending into adjoining lowlands of Chukotka and Alaska. Even the more arid, steppic areas outside central Beringia supported a higher tundra component than was previously thought. Based on paleobotanical data, there were no trees growing anywhere else in Beringia during the LGM, but there is pollen evidence that the southern parts of the BLB supported the growth of spruce, birch, and alder (Westbrook et al., 2012). The insect fauna from central Beringia indicates a smaller decline in temperature (3–5 °C) than that estimated for many other parts of the Northern Hemisphere (Elias, 2001). The combination of warmer temperatures and greater precipitation in the southern areas of the BLB would have facilitated the growth of these boreal tree taxa.

The modeling of NPP for LGM Beringia described above, complemented by the other paleoenvironmental data, allows us to address the question of whether the LGM environments of the southern BLB could have supported a sizable human population. The paleoclimate model output suggests that there was a relatively productive NPP zone in the southeastern margins of the land bridge.

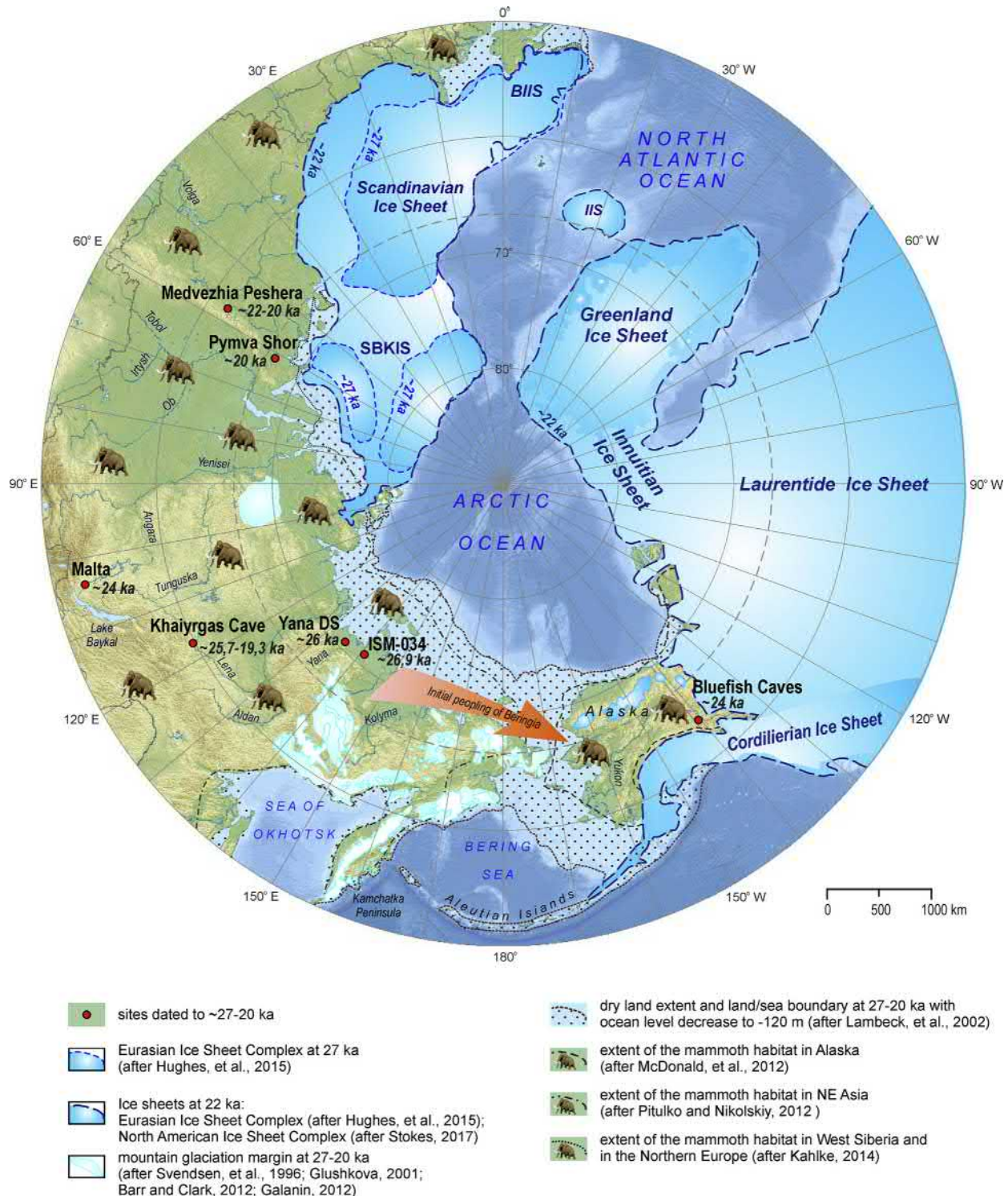


Fig. 4 LGM environments in the Arctic and near-Arctic regions in Siberia and NW North America, and archeological sites dated to 27,000–20,000 years ago (27–20 ka) based on data published in: Barr ID and Clark CD (2012). Late quaternary glaciations in Far NE Russia; combining moraines, topography and chronology to assess regional and global glaciation synchrony. *Quaternary Science Reviews* 53, 72–87; Galanin AA (2012). Age of the Last Glacial Maximum on Asian North-East. *Kriosfera Zemli* XVI(3), 39–52; Glushkova OY (2001). Geomorphological correlation of Late Pleistocene glacial complexes of Western and Eastern Beringia. *Quaternary Science Reviews* 20, 405–417; Hughes ALC, Gyllencreutz R, Lohne ØS, Mangerud J, and Svendsen JI (2015). The last Eurasian ice sheets—A chronological database and time-slice reconstruction, DATED-1. *Boreas* 45(1), 1–45; Kahle R-D (2014). The origin of Eurasian Mammoth Faunas (Mammuthus - Coelodonta Faunal Complex). *Quaternary Science Reviews* 96, 32–49; Lambeck K, Esat TM, and Potter E-K (2002). Links between climate and sea levels for the past three million years. *Nature* 419(6903), 199–206; McDonald GM, Beilman DW, Kuzmin YV, Orlova LA, Kremenetski KV, Shapiro B, Wayne RK, and van Valkenburgh B (2012). Pattern of extinction of the woolly mammoth in Beringia. *Nature Communications* 3, 893; Stokes CR (2017). Deglaciation of the Laurentide Ice Sheet from the Last Glacial Maximum. *Cuadernos de Investigación Geográfica* 43, 377–428.

Potential Size of the Isolated Population

How many people were in this isolated group that had little or no contact with other peoples? A recent estimate of standstill population size, based on genetic diversity and substitution rates, concluded that at least 1000 people lived on the BLB (Mulligan and Kitchen, 2013). However, a total population of 8000–10,000 is considered possible. The NPP of the southern BLB would have supported a population of hunter-gatherers at a density of at least 2.5 individuals per 100 km². At this level, a standstill population of 5000–10,000 individuals would have required a territory of about 125,000 to 250,000 km², but this would have represented, at most, 20% of the area of the BLB (Hoffecker et al., 2016; Hlusko et al., 2018).

How did the “standstill” population survive the LGM? If they were concentrated in settlements at or near the southern coast of the BLB, then they had access to the coastal and marine resources offered by the North Pacific, which would have included shellfish along the shore, and fish and marine mammals out to sea. But these people had a deep cultural heritage of megafaunal mammal hunting, and it seems unlikely that they would have abandoned big game hunting completely. However, if the paleoecological reconstructions are correct, then the southern sector of the BLB was mostly covered in mesic tundra, a habitat unsuitable for large grazers because of the lack of grasses and forbs. It would thus appear that the hunters would have been forced to travel to the upland regions adjacent to the BLB to find their megafaunal prey. We are now getting a glimmer of evidence that megafaunal mammal hunting parties did travel to the interior of Eastern Beringia. Interestingly, the only clear-cut evidence of this comes from a site in the northeast corner of Eastern Beringia, at Bluefish Caves.

Hunting Excursions in Eastern Beringia

Bourgeon et al. (2017) re-evaluated the artifacts and faunal remains from Bluefish Caves, a site in the northwestern part of the Yukon Territory. It appears that the Bluefish Caves (Fig. 4) were used only occasionally as a short-term hunting site. The lithic assemblages recovered from the site include about one hundred artifacts, including microblades, microblade cores, burins and burin spalls. While the artifacts cannot be dated with precision, they are similar to the tools of the Dyuktai culture of Western Beringia. In Siberia, Dyuktai sites range in age from about 15,000 to as old as 22,000 years ago.

The most important finds made by Bourgeon et al. (2017) were 15 bone samples with clear indications of cut marks made by humans. These cut marks, indicating locations on an animal carcass where meat or sinews were cut away from bone, were observed on specimens representing Pleistocene horse (*Equus lambei*), caribou (*Rangifer tarandus*), elk (*Cervus elaphus*), and possibly Dall sheep (*Ovis dalli*) and Pleistocene bison (*Bison priscus*). These were apparently the most common game animals hunted by the people who came to Bluefish Caves. Six of the cut-marked bones were selected for AMS radiocarbon dating. The results range between 12,000 and 24,000 cal BP. Thus, the Bluefish Caves site clearly shows that people were in Eastern Beringia during the LGM, by at least 24,000 cal BP. This site provides long-awaited archeological support for the “Beringian standstill hypothesis” (Tamm et al., 2007).

Late Glacial and Early Holocene Sites in Alaska

The findings from Bluefish Cave indicate the presence of humans in the North American Arctic during the LGM. The artifacts from Swan Point (component 4), while somewhat younger, reflect the earliest cultural manifestation in Alaska with an archeologically distinct appearance, representing a continuation of the microblade tradition of Western Beringia (Fig. 5). This line is further developed in artifacts from sites of the Denali complex, which are spread over a wide area and have an age of 12,500–10,000 years ago.

In addition to the Denali complex, two other groups of lithic assemblages are known from sites in northwestern North America (Fig. 5). These should probably be seen as evidence of the existence of other human populations that settled in Eastern Beringia between 14,500 and 10,000 years ago. During this interval the dominant plant communities shifted from mammoth-steppe to mesic shrub tundra, starting in central and southwestern Alaska (14,000–12,900 years ago), and then spreading northwards by about 11,000 years ago.

The occurrence of archeological sites from the beginning of this interval is probably due to the arrival of a new wave of people into Eastern Beringia. The artifact assemblages from the first half of this interval are classified as the Nenana Complex (13,500–13,000 years ago). These sites are quite numerous (e.g., the Dry Creek, Owl Ridge, Moose Creek, and Walker Road sites). The Broken Mammoth and Little John sites should also be included in this list. The main feature of the stone tool industry of the Nenana Complex is the absence of microblades and the presence of teardrop-shaped and triangular spear points (incomplete bifaces) known as Chindadn points.

The duration of the existence of archeological sites from the end of the last glaciation is only about 1000 years, despite the fact that they range from the northeastern Siberia to the Yukon River basin in northwestern North America. Interestingly, such distinctive, short-lived cultural manifestations are not unique. The North American sites associated with the Clovis culture have an even shorter history, falling between 13,000 and 12,700 years ago (Waters and Stafford Jr., 2007). Nevertheless, Clovis artifacts have a very wide spatial distribution across the continent (Waters and Stafford Jr., 2007; Waters et al., 2015).

In both the Nenana and Clovis cases, it appears that the emergence of diagnostic artifacts is more related to changes in adaptations than to the emergence of new population groups, as both Nenana complex and Clovis sites are spread across areas where there

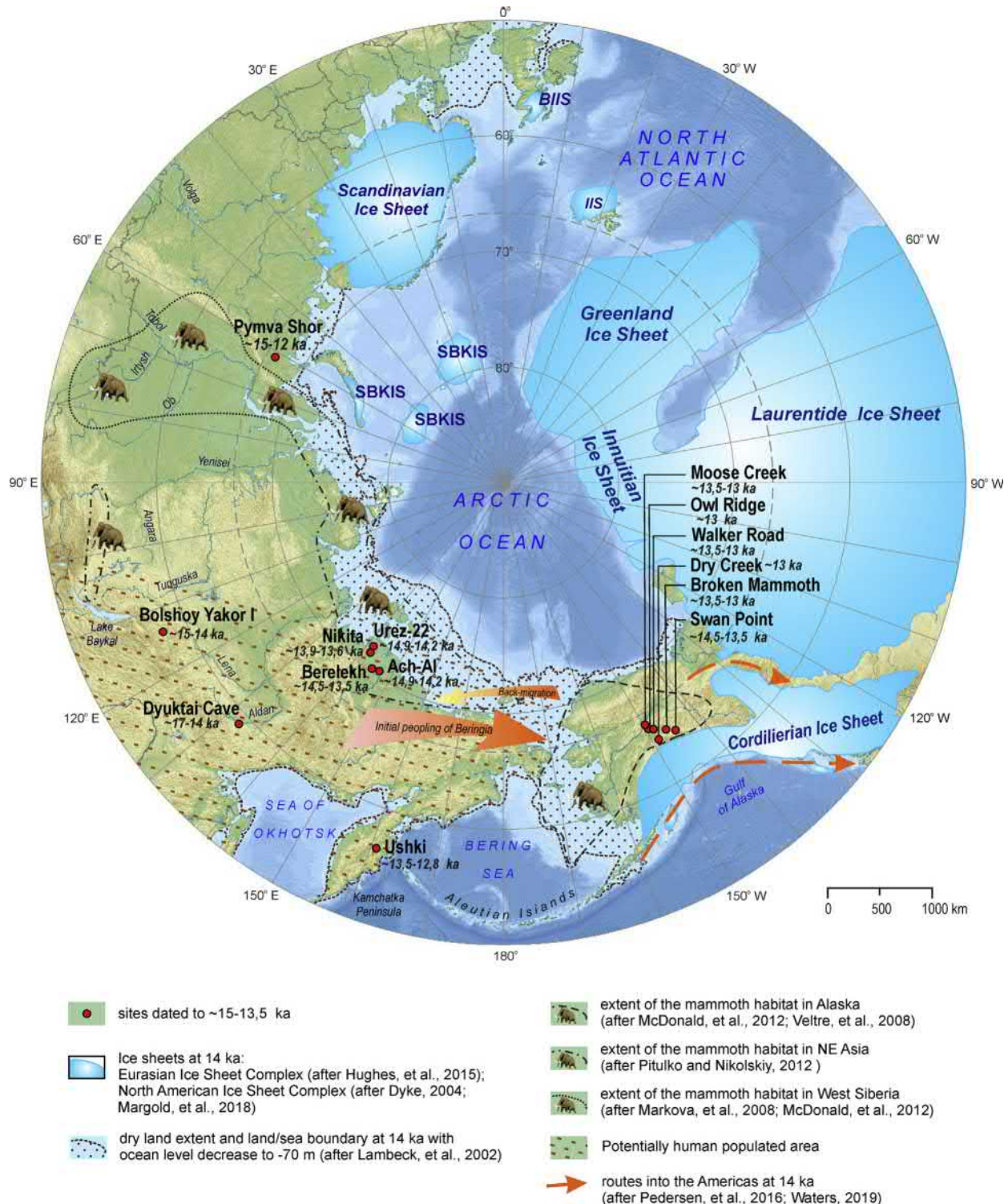


Fig. 5 Human settlement of the Arctic 15,000–13,500 years ago (15–13.5 ka); environment settings are shown for 14 ka time slice based on data published in: Dyke AS (2004). An outline of North American deglaciation with emphasis on central and northern Canada. *Developments in Quaternary Sciences* 2B, 373–424; Hughes ALC, Gyllencreutz R, Lohne ØS, Mangerud J, and Svendsen JI (2015). The last Eurasian ice sheets—A chronological database and time-slice reconstruction, DATED-1. *Boreas* 45(1), 1–45; Lambeck K, Esat TM, and Potter E-K (2002). Links between climate and sea levels for the past three million years. *Nature* 419(6903), 199–206; McDonald GM, Beilman DW, Kuzmin YV, Orlova LA, Kremenetski KV, Shapiro B, Wayne RK, and van Valkenburgh B (2012). Pattern of extinction of the woolly mammoth in Beringia. *Nature Communications* 3, 893; Margold M, Stokes CR, and Clark CD (2018). Reconciling records of ice streaming and ice margin retreat to produce a palaeogeographic reconstruction of the deglaciation of the Laurentide Ice Sheet. *Quaternary Science Reviews* 180, 1–30; Markova, A. K., van Kolfschoten, T., Bohncke, S., Kosintsev, P. A.,

is or there was a population that did not use Chindadn points, respectively. With regard to sites containing Chindadn points, many of them are characterized by the presence of mammoth remains, and in Western Beringia sites with Chindadn points (Pitulko et al., 2016) appear in the Arctic region just before the demise of the local mammoth population (Pitulko and Nikolskiy, 2012).

The disappearance of Chindadn points was undoubtedly due to environmental factors, including the replacement of the Pleistocene mammoth steppe with tundra landscapes. Mesic shrub tundra would not have been able to sustain populations of megafaunal grazers. At the same time, boreal forests were advancing north and west in Eastern Siberia, reaching their modern limits in some regions by about 9000 years ago. Stands of birch and larch apparently spread beyond their modern limits at the end of the Pleistocene (McDonald et al., 2012; Zimmermann et al., 2017). It is noteworthy that ancient DNA evidence indicates that mammoths and horses persisted in the interior of Alaska until about 10,500 years ago (Haile et al., 2009). This generally confirms the dating of bone residues from these megafauna (Mann et al., 2015).

The people of the Denali and Nenana complexes apparently took part in the settlement of the New World. Presumably they entered no later than 16,000 years ago. Thus far, no archeological sites of this age have been found in southeastern Alaska. In fact, all the Paleolithic archeological sites from Eastern Beringia are in the interior and belong to a clearly expressed adaptation to megafaunal mammal hunting, including mammoths. In this regard, the formation of a maritime economy during the process of settlement of the Americas remains archeologically invisible.

People who settled in Eastern Beringia, in turn, divided (Fig. 3). Nevertheless, the ancient Beringian population maintained genetic integrity for quite a long time in the interior of Alaska (Moreno-Mayar et al., 2018) and did not participate in the further splitting and recombination of the indigenous populations of the Americas. These non-Alaskan native groups eventually divided into northern and southern branches. Human settlement in Arctic North America in the middle Holocene is also associated with a powerful genetic flow of Siberian origin (Gilbert et al., 2008).

When the LGM was over, there is also the possibility of reverse (Alaska to Siberia) human migration from the BLB to Western Beringia. A possible result of such a migration may have been the influx of a wave of population during the end of the Pleistocene. In this scenario, people from both Eastern and Western Beringia shared the toolkit of the Chindadn complex. It has been noted that all sites that yielded Chindadn points in Western Beringia (e.g., Berelekh, Nikita Lake, Achchaghyi-Allaikha) are associated with concentrations of mammoth bone remains (Pitulko et al., 2016). Interestingly, there is genetic evidence that this east-to-west migration pattern was followed by woolly mammoth, as the presence of a strong genetic signal originating from North America has been identified in the genome of mammoths of that lived in Northern Eurasia (Palkopoulou et al., 2013).

In any case, the question of the timing of human entrance into the New World is far from decided. In the non-glaciated regions of the North American continent there are no archeological sites dated beyond 16,000 years ago. This conclusion is the consensus of the archeological community.

An important element of the cultural diversity of the Arctic zone of northwestern North America, but not related to the problem of its settlement, is the presence of sites associated with the Northern Paleo-Indian tradition (Fig. 5), known from the Seward Peninsula in Alaska to the Yukon (e.g., Raven Bluff, Serpentine Hot Springs, Mesa, Irving Sluiceway, etc.). Their distinctive characteristic consists of spear heads with bilaterally processed edges, sometimes with a refined or fluted base similar to the Clovis and Folsom projectile points from unglaciated regions of North America, related to the interval of 12,500 to 11,500 years ago (Fig. 6). However, in Alaska these artifacts are clearly younger than those of the Clovis culture.

It has been shown (Smith and Goebel, 2018) that these diagnostic artifacts appear in northwestern North America as the result of a reverse migration (from south to north) through the ice-free corridor, after the beginning of deglaciation. Their appearance in northwestern North America, among other data on the existence of the Clovis people in the unglaciated regions of the continent (e.g., Waters et al., 2015, 2018) in the period leading up to the opening of the ice-free corridor route, suggests that the infiltration of human groups into glacial North America occurred earlier than 15,000 years ago. However, the specific model of this process remains undeveloped (Potter et al., 2018).

Bison also migrated south to north along the ice-free corridor, after it opened. This is indicated by aDNA evidence from the remains of these animals (Heintzman et al., 2016). This hypothesis is backed by the radiocarbon evidence. There are no dated remains of bison in Alaska during the Late Glacial, but then relatively high numbers are recorded afterward (Mann et al., 2015). Perhaps the same migration corridor served as an avenue of exchange between the Beringian and more southern North American populations of horses and mammoths toward the end of the Pleistocene. This northerly migration might have been driven by environmental changes under the same scenario as in Northern Eurasia (Nikolskiy et al., 2011; McDonald et al., 2012), where the distinctive northward shift of populations of Pleistocene megafauna is associated with the collapse of the steppe-tundra biome at the end of the Pleistocene, and the subsequent transformation into the modern tundra.

Mol, J., et al. (2008). Evolution of European ecosystems during Pleistocene–Holocene transition (24–8 kyr BP). Moscow: KMK Scientific Press; Pitulko, V. V. and Nikolskiy, P. A. (2012). Extinction of woolly mammoth in Northeastern Asia and the archaeological record. *World Archaeology* 44(1), 21–42; Tamm, E., Kivisild, T., Reidla, M., Metspalu, M., Smith, D. G., et al. (2007). Beringian standstill and spread of Native American founders. *PLoS One* 2(9), e829. Migration routes into the Americas are shown based on data published in: Pedersen, M. W., Ruter, A., Schweger, C., Friebe, H., Staff, R. A., Kjeldsen, K. K., Mendoza, M. L. Z., Beaudoin, A. B., Zutter, C., Larsen N. K., Potter, B. A., Nielsen, R., Rainville, R. A., Orlando, L., Meltzer, D. J., Kjær, K. H., and Willerslev, E. (2016). Postglacial viability and colonization in North America's ice-free corridor. *Nature* 537(7618), 45–49; Waters, M. R. (2019). Late Pleistocene exploration and settlement of the Americas by modern humans. *Science* 365(2019), eaat5447.

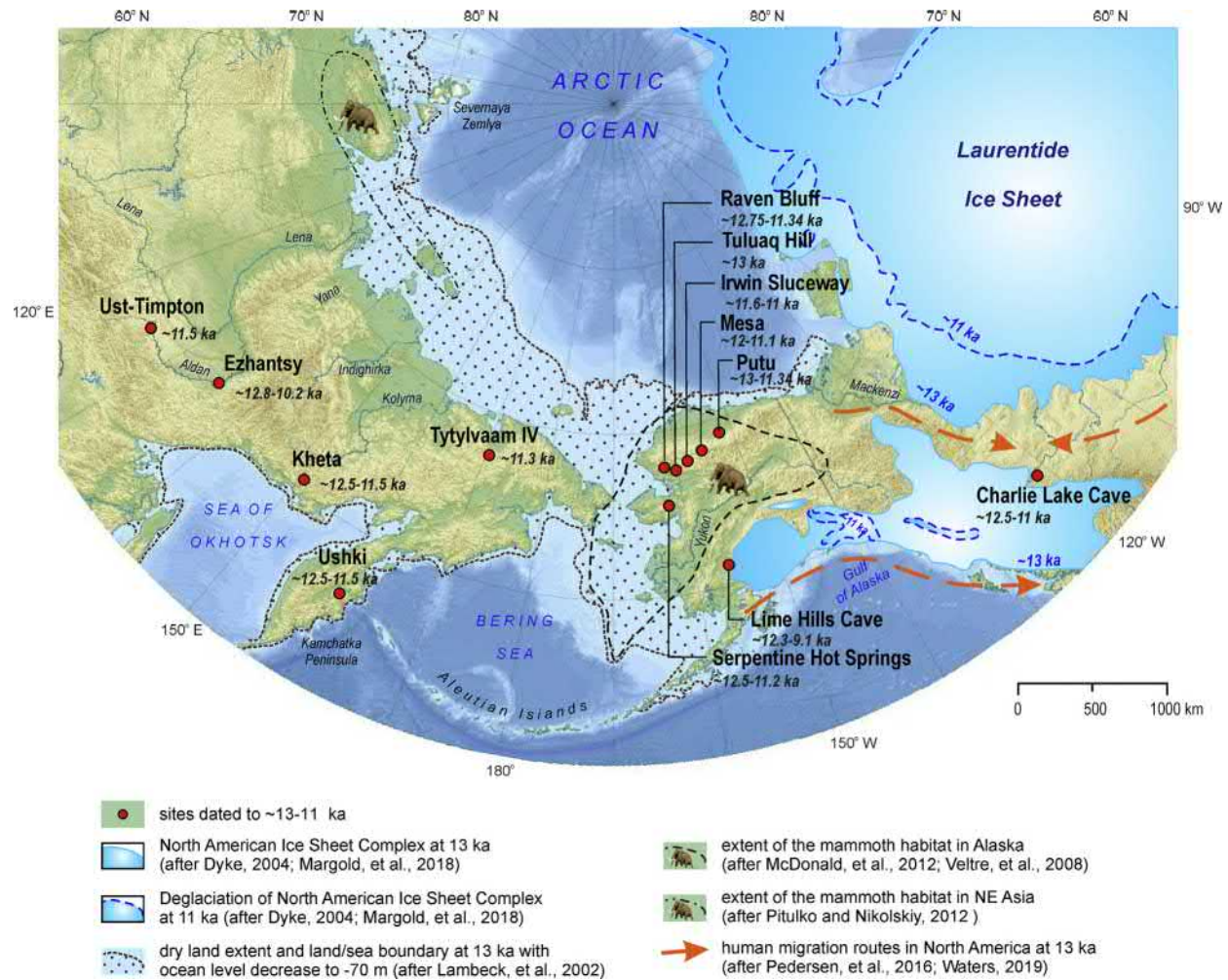


Fig. 6 Arctic and sub-Arctic archeological sites dated to 13,000–11,000 years ago (13–11 ka) in Siberia and Alaska; environment settings are shown for 13 ka time slice based on data published in: Dyke, A. S. (2004). An outline of North American deglaciation with emphasis on central and northern Canada. *Developments in Quaternary Sciences* **2B**, 373–424; Hughes, A. L. C., Gyllencreutz, R., Lohne, Ø. S., Mangerud, J., and Svendsen, J. I. (2015). The last Eurasian ice sheets—A chronological database and time-slice reconstruction, DATED-1. *Boreas* **45**(1), 1–45; Lambeck, K., Esat, T. M., and Potter, E.-K. (2002). Links between climate and sea levels for the past three million years. *Nature* **419**(6903), 199–206; Margold, M., Stokes, C. R., and Clark, C. D. (2018). Reconciling records of ice streaming and ice margin retreat to produce a palaeogeographic reconstruction of the deglaciation of the Laurentide Ice Sheet. *Quaternary Science Reviews* **180**, 1–30; Pitulko, V. V. and Nikolskiy, P. A. (2012). Extinction of woolly mammoth in Northeastern Asia and the archaeological record. *World Archaeology* **44**(1), 21–42; Veltre, D. W., Yesner, D. R., Crossen, K. J., Graham, R. W., and Coltrain, J. B. (2008). Patterns of faunal extinction and paleoclimatic change from mid-Holocene mammoth and polar bear remains, Pribilof Islands, Alaska. *Quaternary Research* **70**, 40–50. Migration routes into the Americas are shown based on data published in: Pedersen, M. W., Ruter, A., Schweger, C., Friebe, H., Staff, R. A., Kjeldsen, K. K., Mendoza, M. L. Z., Beaudoin, A. B., Zutter, C., Larsen N. K., Potter, B. A., Nielsen, R., Rainville, R. A., Orlando, L., Meltzer, D. J., Kjær, K. H., and Willerslev, E. (2016). Postglacial viability and colonization in North America's ice-free corridor. *Nature* **537**(7618), 45–49; Waters, M. R. (2019). Late Pleistocene exploration and settlement of the Americas by modern humans. *Science* **365**(2019), eaat5447.

On the eve of the end of the land connection between Northern Eurasia and North America (Jakobsson et al., 2017), archeological sites of a different technological tradition spread via the BLB into northwestern North America (Fig. 7). The most important feature of this culture was the microprismatic technique of stone splitting, associated with the use of linear tools, found in caves at Trail Creek (Larsen, 1968) and the Lime Hills (Ackerman, 1996). In some cases, e.g., on Anangula Island in the Aleutians (Coutouly, 2015) it is supplemented by the production of large blades. This technology has also commonly been found in younger sites in Alaska, such as Amakomanak and Panguingue Creek, as well as in younger assemblages from the Anangula site, and in sites along the Pacific Northwest coast, such as Richardson Island, Lille Bay, and Echo Bay (Magne and Fedje, 2007). Despite the lack of direct material evidence, the localization of these technologies along coasts and islands indicates a developed maritime adaptation using boats.

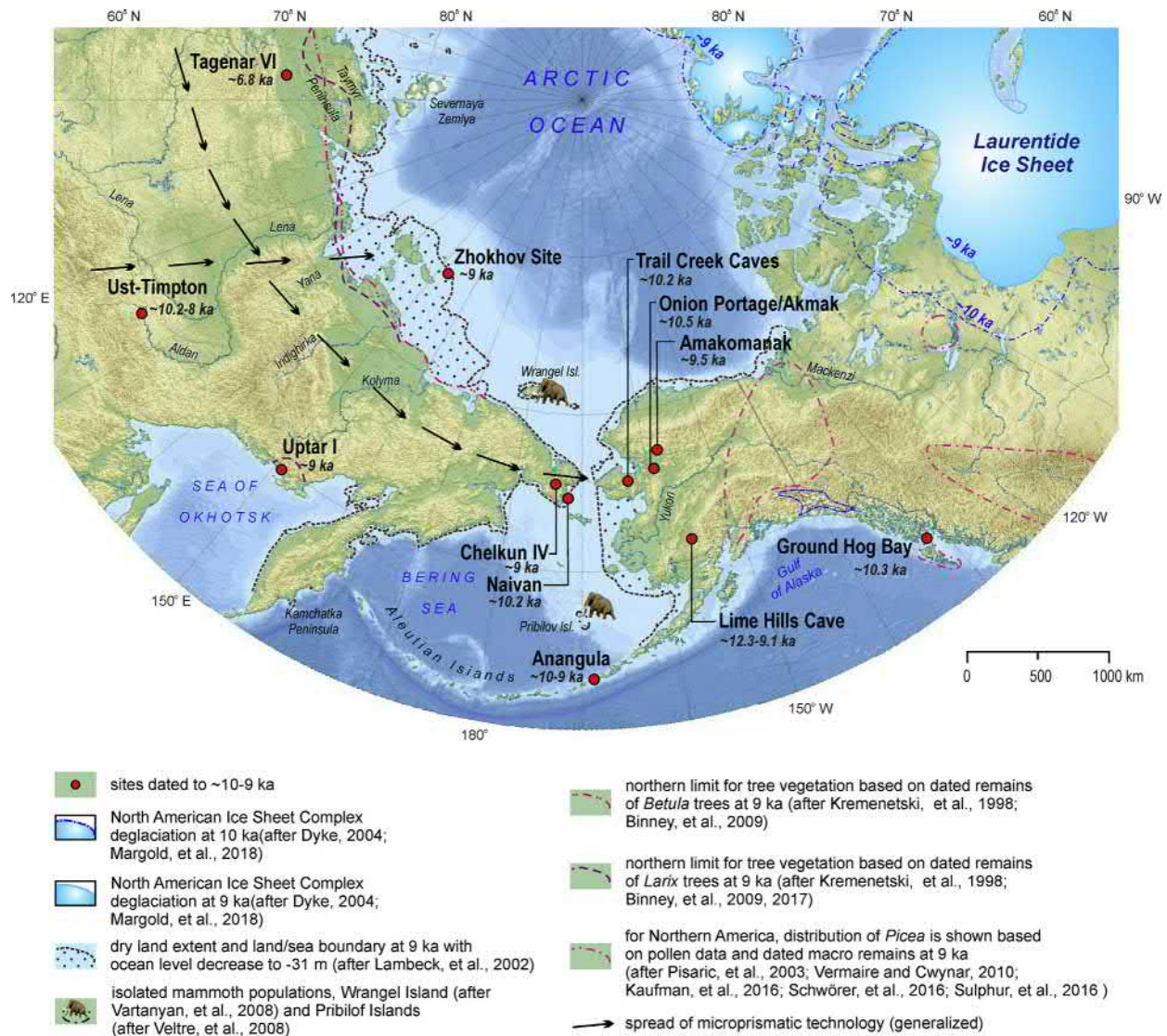


Fig. 7 Appearance and spread of microprismatic blade tradition across arctic East Siberia and NW North America indicated by archeological sites that date to ~10,000–9000 thousand years ago (~10–9 ka). Environment settings are shown for 9000 years ago time slice based on data published in: Binney, H. A., Willis, K. J., Edwards, M. E., Bhagwat, S. A., Anderson, P. M., et al. (2009). The distribution of late-Quaternary woody taxa in northern Eurasia: Evidence from a new macrofossil database. *Quaternary Science Reviews* **28**, 2445–2464; Binney, H., Edwards, M., Macias-Fauria, M., Lozhkin, A., Anderson, P., et al. (2017). Vegetation of Eurasia from the last glacial maximum to present: Key biogeographic patterns. *Quaternary Science Reviews* **157**, 80–97; Dyke, A. S. (2004). An outline of North American deglaciation with emphasis on central and northern Canada. *Developments in Quaternary Sciences* **2B**, 373–424; Kaufman, D. S., Axford, Y. L., Henderson, A. C. G., McKay, N. P., Oswald, W. W., et al. (2016). Holocene climate changes in eastern Beringia (NW North America)—A systematic review of multi-proxy evidence. *Quaternary Science Reviews* **147**, 312–339; Kremenetski, C. V., Sulerzhitsky, L. D., and Hantemirov, R. (1998). Holocene history of the northern range limits of some trees and shrubs in Russia. *Arctic and Alpine Research* **30**, 317–333; Lambeck, K., Esat, T. M., and Potter, E.-K. (2002). Links between climate and sea levels for the past three million years. *Nature* **419**(6903), 199–206; Margold, M., Stokes, C. R., and Clark, C. D. (2018). Reconciling records of ice streaming and ice margin retreat to produce a palaeogeographic reconstruction of the deglaciation of the Laurentide Ice Sheet. *Quaternary Science Reviews* **180**, 1–30; Pisaric, M. F. J., Holt, C., Szeicz, J. M., Karst, T., and Smol, J. P. (2003). Holocene treeline dynamics in the mountains of northeastern British Columbia, Canada, inferred from fossil pollen and stomata. *The Holocene* **13**, 161–173; Schwörer, C., Gavin, D. G., Walker, I. R., and Hu, F. S. (2016). Holocene tree line changes in the Canadian Cordillera are controlled by climate and topography. *Journal of Biogeography* **44**(5), 1148–1159; Sulphur, K. C., Goldsmith, S. A., Galloway, J. M., Macumber, A., Griffith, F., et al. (2016). Holocene fire regimes and treeline migration rates in sub-arctic Canada. *Global and Planetary Change* **145**, 42–56; Vartanyan, S. L., Arslanov, K. A., Karhu, J., Possnert, G., and Sulerzhitsky, L. D. (2008). Collection of radiocarbon dates on the mammoths (*Mammuthus primigenius*) and other genera of Wrangel Island, northeast Siberia, Russia. *Quaternary Research* **70**, 51–59; Veltre, D. W., Yesner, D. R., Crossen, K. J., Graham, R. W., and Coltrain, J. B. (2008). Patterns of faunal extinction and paleoclimatic change from mid-Holocene mammoth and polar bear remains, Pribilof Islands, Alaska. *Quaternary Research* **70**, 40–50; Vermaire, J. C. and Cwynar, L. C. (2010). A revised late-Quaternary vegetation history of the unglaciated southwestern Yukon Territory, Canada, from Antifreeze and Eikland ponds. *Canadian Journal of Earth Sciences* **47**, 75–88.

Importance of Dog Sledding

The apparent ability of prehistoric humans to selectively breed dogs for specific traits, combined with the complexity of the sled design known from the Zhokhov site in arctic Siberia (Pitulko and Kasparov, 2017), suggest that these skills have evolved over a period of several thousand years. The development of this mode of transportation was an enormous breakthrough for Arctic peoples. Assuming they traveled in winter, dog-sled transport would have greatly aided the Beringian “stand-still” population in their hunting forays into the adjacent continental regions of either Siberia or Alaska and the Yukon. Even today, the peoples of the North American Arctic find it much easier to travel long distances over the snow in winter than to attempt long journeys over the vegetated, often boggy terrain of summer. Dog sleds may already have been known to people in the American Northwest on the eve of the discovery of the ice-free corridor. Perhaps North American sled dogs descended from animals pulling sleds across the BLB, before its inundation at the end of the Last glaciation (Leathlobhair et al., 2018).

Sled dog breeding is the most important innovation of the Holocene Arctic frontier. This element of adaptation allowed early Holocene hunters in the Siberian Arctic and northwest North America to quickly traverse vast areas, so they could take advantage of shifting resources on the landscape, such as migrating herds of grazers. The distances traveled are indicated by the presence of obsidian tools at the Zhokhov site in northeastern Siberia (Fig. 8) that originated from a source of the obsidian 1500 km away, in the lower Anadyr River (Pitulko et al., 2019).

In northwestern North America, several sources of obsidian have been identified, and these have likewise been distributed widely (Fig. 8). They are localized both in the interior of Eastern Beringia and in the coastal areas of the northwest coast (Potter et al., 2017). It has been shown (Potter et al., 2017) that obsidian from interior Eastern Beringia occurs in archeological sites with ages greater than 13,000 years ago, while the movement of obsidian in the coastal zone is characteristic for younger sites. Indirectly, this fact suggests the absence of migration of human groups along the “coastal route” (Fig. 3) prior to 13,000 years ago.

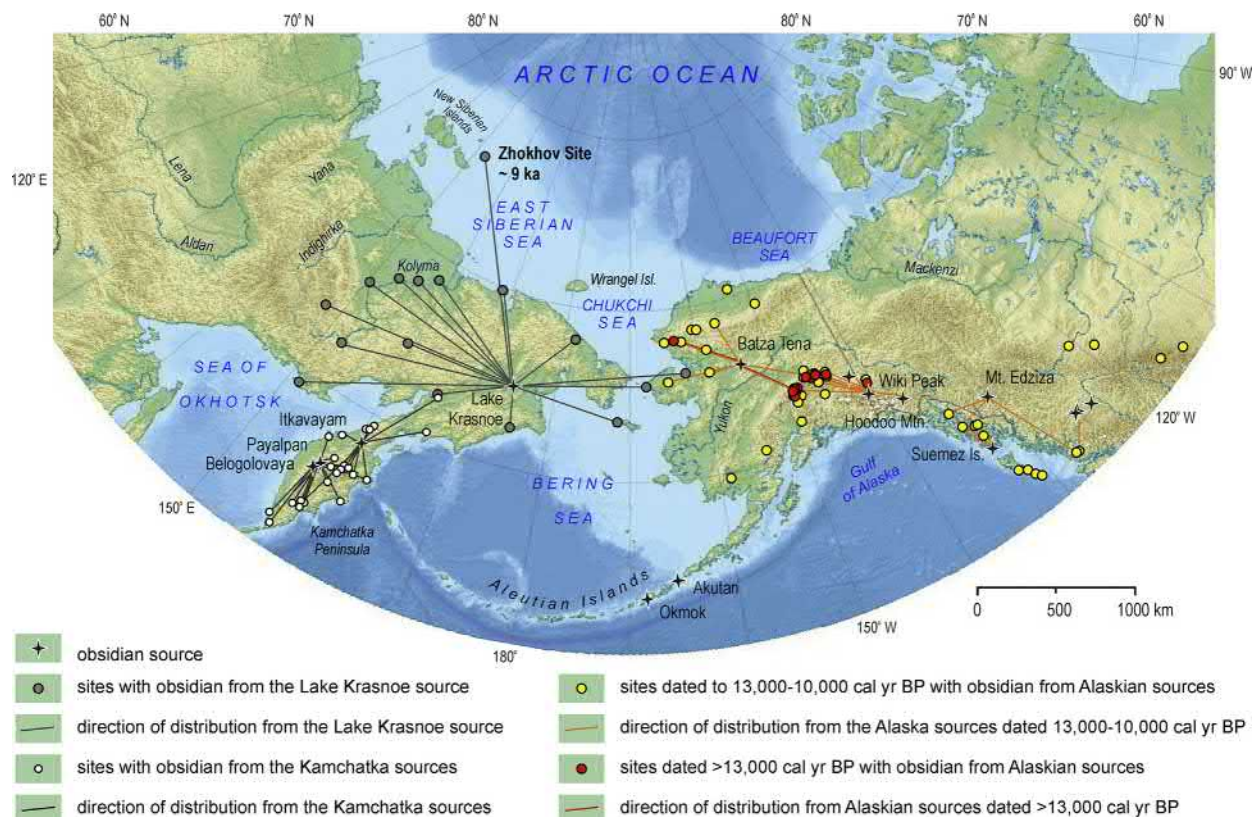


Fig. 8 Obsidian exchange systems in sub-Arctic and Arctic regions of East Siberia (after Kuzmin, 2019; Pitulko et al., 2019) and Alaska (after Potter et al., 2017) revealed by geochemical signatures found for specific source areas based on data published in: Kuzmin, Y. V. (2019). Obsidian acquisition and exchange in prehistoric cultures of the Russian Far East and Northeast Russia: a review of the 25 years of research. *Prehistoric Archaeology. Journal of Interdisciplinary Studies* 1, 92–107; Pitulko, V. V., Kuzmin, Y. V., Glascock, M. D., Pavlova, E. Y., and Grebennikov, A. V. (2019). ‘They come from the ends of the earth’: long-distance exchange of obsidian in the early Holocene of the High Arctic (Zhokhov site, eastern Siberia). *Antiquity* 93(367), 28–44; Potter, B. A., Reuther, J. D., Holliday, V. T., Holmes, C. E., Miller, D. S., and Schmuck, N. (2017). Early colonization of Beringia and Northern North America: Chronology, routes, and adaptive strategies. *Quaternary International* 444B, 36–55.

Spread of Arctic Peoples in the Late Holocene

By the start of the Holocene, three vast areas of the Arctic remained unpopulated (Fig. 5). These were Scandinavia and the Kola Peninsula in the Old World, the Canadian Arctic in the New World, and Greenland. While the Canadian Arctic and Greenland remained inaccessible to humans for a long time, the settlement of Scandinavia became possible soon after deglaciation (Fig. 9). It is believed that late-Paleolithic peoples whose origins are associated with both Eastern and South-Western Europe were the first post-glacial inhabitants of Scandinavia (Dolukhanov et al., 2002; Zvelebil, 2008).



Fig. 9 Selected Arctic and sub-Arctic archeological sites dated younger than 9000 years ago, and major coastal migrations in the Arctic: (a) postglacial migrations into Scandinavia; (b) Arctic Small Tool tradition spread into Alaska, Canadian Arctic and Greenland at around 5000 years ago; (c) Old Bering Sea culture spread to the west of the Bering Strait about 2000 years ago; (d) Thule migration ~1000 years ago; (e) migration to the west of the Bering Strait contemporary to the Thule migration.

By the middle Holocene, only the Canadian Arctic and Greenland remained unoccupied. Human settlement was hindered by the late deglaciation of the Canadian Arctic islands, around 4000 years ago. At about that time the Paleo-Eskimo culture spread across the Canadian Arctic and Greenland (Fig. 9). It is characterized by the Arctic Small Tool tradition, which is a combination of pre-Dorset local variants in significant parts of the Canadian Arctic and Labrador, the Independence I culture in northern Greenland and High Arctic islands, and Saqqaq culture in Greenland (Friesen and Mason, 2016). Sites of the Denbigh complex in Alaska represent the earliest expression of this cultural tradition. The rate of migration and settlement of these people across the Arctic remains unknown, but it is clear that by 4500 years ago they had occupied all the regions discussed above.

The Palaeo-Eskimo group were the first inhabitants of Greenland, arriving in several waves of migration from about 2500 BC–1400 AD, originating in Alaska or Siberia and crossing the Canadian High Arctic, finishing in Greenland (Sørensen, 2019). The Palaeo-Eskimo people organized themselves in small mobile groups that were able to carry all their goods from place to place using dog sleds. They apparently built no permanent structures but lived in tents. Their great mobility allowed them to exploit food resources at wide-ranging localities through the year. They hunted both marine mammals such as whales, seals and walrus, and terrestrial herbivores, such as caribou and muskox. Their hunting weapons reveal a high level of specialization. For instance, a Paleo-Eskimo site on an island in Disco Bay yielded a suite of hafted artifacts dating back to the Saqqaq Culture (2500–1000 BC) representing one of the most sophisticated prehistoric tool technologies found anywhere in the world. Their hunting tool-kit included nine types of hafted compound tool types, each designed for a specialized use. There were various lances with fore shafts, harpoons with toggling harpoon heads, atlats, three-pronged bird darts, and bows and arrows. In addition to their use of dog sleds over ground, they went to sea in kayaks.

The economy of at least two groups includes a significant marine element, and for pre-Dorset it is assumed that the caribou population was also exploited. It is clear, however, that in order to pursue local caribou populations on the Arctic islands, humans had to have the appropriate technology to provide coastal travel, as well as the skills to exploit marine resources as a back-up option. This allowed the subsequent transition to the maritime adaptation when it became necessary, as evidenced by the Independence and Saqqaq cultures (Grønnow, 2017).

Genetically, these early people of the high arctic were considerably different from both the Native American population who migrated to the Americas at the end of the Pleistocene, and from the bearers of the Thule culture (Inuit people) who spread in the Canadian Arctic and Greenland around 700 years ago. Their closest modern relatives are the inhabitants of Arctic East Siberia—Nganasans, Koryaks and Chukchi (Rasmussen et al., 2010) and the modern inhabitants of the Aleutian Islands (Raghavan et al., 2014). Given the age estimate for the oldest materials in Alaska attributed to Denbigh complex (Giddings, 1964; Harritt, 1998), and the estimated age for the genetic split between Saqqaq and Chukchi (6400–4400 years ago). (Rasmussen et al., 2010), the beginning of the migration across Arctic North America is believed to be ~5500 years ago. The roots of this migration are seen in the material culture of the East Siberian middle Neolithic (Powers and Jordan, 1990; Raghavan et al., 2014), while it remains unclear to what extent it is related to the formation of ASTs.

The latest large-scale migration of Thule culture started from the Bering Strait area about 1000 years ago during the Medieval Warming (Fig. 9). In Canadian Arctic and Greenland, this population replaced the Paleo-Inuit, who lived there for about 4000 years. Contemporary westward migration is less known, but an Eskimo population moved west of the Bering Strait and reached the Kolyma river area (Pitulko and Pavlova, 2016). During the Medieval Warming, the East Siberian arctic coast, which is generally quite barren, became habitable because of the availability of marine resources. In the Canadian Arctic and Greenland, despite the subsequent worsening of conditions, descendants of this population still live today, but the arctic coast of East Siberia soon became abandoned due to the onset of the Little Ice Age, when ice conditions worsened, and the biodiversity of the marine ecosystem decreased.

Abundance of Arctic Marine Resources

An archeological site in the eastern Canadian Arctic (Howse, 2013) reveals a great deal about the abundance of marine food resources and how these were exploited by Arctic Stone Age people in the Canadian High Arctic and adjacent coasts of Greenland. This particular site was occupied by Early Thule Inuit people. They first migrated into the Eastern Arctic from an ancestral homeland somewhere in western Alaska. Their arrival at Skraeling Island, located on the eastern edge of the Canadian High Arctic, near the southeast coast of Ellesmere Island, is one of the earliest known Inuit occupations in this region. A total of 23 Thule Inuit house ruins, numerous tent rings, kayak and umiak supports, and food caches were found on the island. The site was apparently a year-round encampment. Radiocarbon dating of organic artifacts indicates that the island was occupied by these pioneers during the 13th century AD. Their material culture was very similar to that of Alaskan Thule sites, including harpoon head types and a house layout where a separate kitchen was accessed by a tunnel that ran parallel to the main entrance tunnel.

The island was very likely chosen by the Thule people because of its proximity to the North Water Polynya. Polynyas are areas of persistent open water in regions otherwise covered in sea ice for much of the year. For the most part, they tend to be roughly oval or circular in shape, and may be 100 km long, or longer. The water remains open because of oceanic processes that prevent sea ice from forming. Marine mammals, fish, and sea birds congregate at polynyas throughout the winter. Year-round access to these ice-free waters would have made Skraeling Island an attractive location to Arctic peoples, because important marine resources were readily available year-round. Large populations of beluga, narwhal, bowhead whale, and walrus are found there today during the summer

months, and smaller numbers of these animals spend the winter there. Polar bears are present year-round and abundant along the edge of the polynya throughout the winter, since they hunt seals from the edge of the ice. The seal fauna found in the polynya include ringed seal and bearded seal, which are also year-round residents. Harp seals pass through the region during their summer migration. So even though the island itself experiences extremely cold climate and is essentially polar desert, the paucity of terrestrial game animals was of little concern to these highly adapted maritime people. In fact, it appears that they harvested both abundant and diverse foods from the sea.

The bones of the following species of birds, marine mammals and terrestrial mammals have been identified from the Early Thule sites on Skraeling Island: goose, eider, common raven, arctic hare, narwhal, beluga whale, bowhead whale, arctic fox, polar bear, walrus, bearded seal, gray seal, ringed seal, harbor seal, harp seal, caribou and muskox. Seal bones dominated the faunal samples, contributing more than two-thirds of the identified mammal remains. Dog bones were also frequently encountered in the excavations, testimony to the use of dog sleds.

The Early Thule people not only relied on marine mammals for their food, they also made use of some of their bones as building materials. The inhabitants of the site on Skraeling Island used the skulls and other bones of whales and walrus to form most of their house structures. One house had seven walrus skulls built into a wall. The gaps between bones were likely filled in with blocks of turf. Thus, it appears that the Early Thule Inuit lived in robust, well-insulated houses during the winter, and that they slept in tents during warm weather, based on the presence of several tent rings on the island.

Metallurgy in the Arctic

The cultures of the Arctic Stone Age, long before the advent of metallurgy, remained stable for millennia. This does not imply that Arctic cultures stagnated. On the contrary, they were very dynamic, but they achieved the right balance between technology and habitat. Metal working in the New World began with cold hammering of native copper at about 6000 years ago, in the Great Lakes region of the North America well south of the Arctic and with no indication for smelting of raw materials and casting technology (Bebber and Eren, 2018). No evidence for bronze casting exists in the New World Arctic, contrary to the arctic Eurasia. The earliest and only known evidence for iron working discovered in this region comes from Canadian Arctic and dates about 1000 years ago (Sutherland et al., 2015).

The use of metal products in the Arctic Stone Age cultures was not critically important. Thus, in Thule culture, a significant amount of iron products (including meteoritic iron) is known, but such products are mainly a result of long-distance exchange with Siberian territories (Cooper et al., 2016). There is no single element in Thule material culture which could have not been made simply by using stone tools. In similar fashion, bone tools apparently fulfilled all the needs of the people of the Old Bering Sea culture, even though iron in small quantities was available to them.

It is clear from this that metal working technology was not a significant aspect of ancient Arctic peoples. Metal tools were not critically important to these people. Their production is very labor-intensive, and it did not lend itself to production by the small groups of people that made up hunter-gatherer bands. In addition, such technological knowledge is more-or-less useless in regions that lack the raw materials for metallurgy. So, while metal tools were desirable, they never became a critical element of culture and survival technology. Arctic exchange systems, including ultra-long-distance, existed at least 5000 to 6000 years before the advent of metals. These transactions were much more effective in terms of the use of time, which in the Arctic is limited to the short summer-spring season.

Concluding Comments

The human occupation of the Arctic during and after the Last glaciation staggers the imagination. As mentioned above, *Homo sapiens* evolved in tropical Africa, and our physiological and morphological adaptations have changed little through the Late Quaternary. But the undeniable fact is that humans did not just survive in the Arctic with just their Stone Age technology, they actually thrived there. Certain technological innovations were critical to this success. The human body, exposed to the elements, starts to shiver at 35.5 °C, and we enter hypothermia when our core body temperature falls to 35 °C. So, the first vital piece of technology was the invention of tailored clothing to insulate their tropically adapted bodies from the bitter Arctic cold. Since they were living in a treeless landscape, these first Arctic inhabitants managed to survive winter nights by burning the fatty marrow inside large mammal bones. Their stone tool kit was sufficiently lightweight and compact to allow them to take it with them on long trips, yet it included highly sophisticated weapons that brought down large animals. In short, these Stone-Age peoples of the Arctic are a testimonial to human ingenuity.

We are only now beginning to understand the prehistoric occupation of Arctic regions. The extraction and identification of Ancient DNA from fossil human bones and teeth represents a vital breakthrough in our understanding of the genetic relationships of the First Americans. However, the Arctic is one of the most remote regions on Earth. Access to potential archeological sites is costly, difficult, and restricted to a few weeks of the summer. For these reasons, many of the Arctic territories remain archeologically unexplored, and a significant number of research questions remain largely open.

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Human Impacts on Arctic Ecosystems

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Abstract

Although much of the Arctic remains pristine, the developed countries of the world have used the Arctic tundra as a dumping ground, for nuclear testing, and an industrial site. Since the 20th century, Arctic regions have been exploited for mineral and petroleum resources with a mixed level of concern for environment (some in USA and Canada, very little in Russia). The remoteness of the Arctic has made it a target for extensive Russian nuclear testing (Novaya Zemlya), and proposed nuclear engineering (NW Alaska). The warming of the Arctic climate, though not originating from Arctic sources, is melting the sea ice cover, melting the permafrost, and changing tundra ecosystems. Ironically, anthropogenic warming is even now facilitating further human exploitation of the High Arctic for its fossil fuel resources, navigational short-cuts, and previously unobtainable fish stocks. These new incursions into the Arctic may well drive a number of marine mammals and other vertebrate species to extinction, unless strong conservation initiatives are put in place immediately.

Introduction

The arctic tundra is not a frozen wasteland of monotonous mosses and lichens, barely clinging to life. In fact, the tundra is as diverse in vegetation communities as the boreal forest or temperate grassland biomes to the south. Tundra covers about 360,000 km² in Alaska, 2,480,000 km² in Canada, 2,167,000 km² in Greenland and Iceland, and 2,560,000 km² in Russia (Bliss and Matveyeva, 1992). The simplest definition of arctic tundra is the land beyond the northern limit of trees, but there are extensive regions where patches of tundra extend south into the boreal forest. This forest-tundra ecosystem is much more extensive in northern Siberia than in North America.

For the purposes of this review it is convenient to divide the biome into high and low arctic ecosystems (Fig. 1). The High Arctic, also known as polar desert, occurs in the far north, such as the Canadian Arctic Archipelago, northern Greenland, and the islands north of Siberia. Here the vegetation cover is generally sparse, and the plant diversity is quite low. The climate is extremely cold, with mean July temperatures from 1 °C to 4 °C and mean January temperatures in the –20 °C to –40 °C range. Mean annual temperatures are well below freezing, from about –6 °C to –15 °C. Mean annual precipitation is very low, ranging from about 60–400 mm, with most of this falling as snow. The High Arctic is a frigid desert. The low arctic tundra is much more floristically diverse and extensive in area. Depending on latitude, slope, aspect, and available moisture, the vegetation ranges from tall shrubs to prostrate herbs, lichens, and mosses. Mean July temperatures in the Low Arctic range from 4 °C to 12 °C; mean January temperatures range from about –15 °C in arctic Scandinavia to –50 °C in the coldest parts of north-eastern Siberia. Mean annual temperatures range from about –1 °C to –15 °C. Mean annual precipitation ranges from about 120–550 mm. Because the mean annual air temperatures of all these tundra regions are below freezing, the entire region, both low- and high-arctic, have permanently frozen soils, or permafrost. The upper layers of these soils, the top 0.4–4 m, generally thaw in summer, forming an active layer in which plants can take root, and draw moisture and nutrients. The soil remains frozen below this active layer, often to depths of hundreds of meters. The coldest parts of north-eastern Siberia have soils frozen to depths exceeding 1500 m.

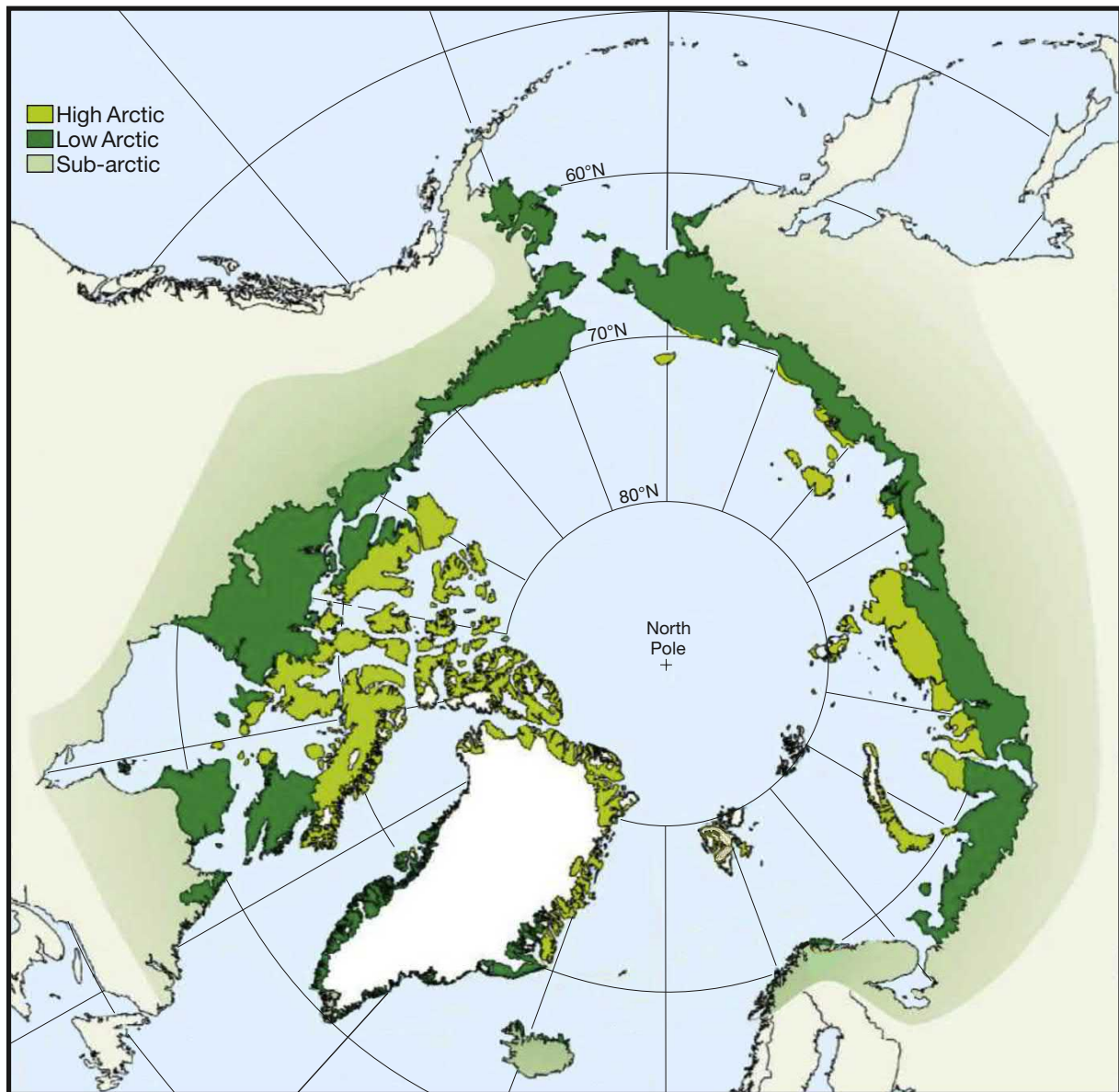


Fig. 1 Map of the northern high latitudes, showing the High Arctic and Low Arctic regions.

Tundra plants are highly adapted to survive the very short growing season, low summer temperatures, extremely cold winters, and lack of moisture. Many tundra plants are perennials. This life strategy allows them time to slowly accumulate the metabolic energy needed to set seeds, a process that may take several summers. Likewise many tundra insects live multiple years in order to accumulate enough energy to reproduce. There are very few year-round resident vertebrates in the Arctic. Most birds are only summer visitors, taking advantage of the rapid growth of plants in the continuous daylight, and the lack of predators they face in lower latitudes, to quickly raise a brood of chicks in the short, intense Arctic summer. The few resident birds, such as ptarmigan, burrow under the snow in winter, thus avoiding the deathly cold air temperatures at the surface. These birds build up as much fat as possible in the summer, and survive the winter by a combination of burning fat reserves and foraging on dwarf willow and birch shrubs beneath the snow. There are 39 resident terrestrial mammals in the Arctic, including 21 species found in both the Low and High Arctic, 17 species found only in the Low Arctic, and only one species found only in the High Arctic (Table 1).

Threats to the High Arctic

Declining Sea Ice (Global Warming)

Sea ice forms in the Arctic Ocean and adjacent seas from autumn to early summer. Prior to the 1980s–90s, annual layers of sea ice would build up for several years, thickening the ice pack considerably. This pack ice provides a stable platform from which polar

Table 1 Terrestrial mammals of the Arctic, showing their IUCN conservation status.

Common name	Scientific name	Range	IUCN status
Muskox	<i>Ovibos moschatus</i>	Low and High Arctic	Least concern
Caribou	<i>Rangifer tarandus</i>	Low and High Arctic	Vulnerable
Moose	<i>Alces alces</i>	Low Arctic	Least concern
Gray wolf	<i>Canis lupus</i>	Low and High Arctic	Least concern
Arctic fox	<i>Vulpes lagopus</i>	Low and High Arctic	Least concern
Red fox	<i>Vulpes vulpes</i>	Low and High Arctic	Least concern
Canada lynx	<i>Lynx canadensis</i>	Low Arctic	Least concern
Brown bear	<i>Ursus arctos</i>	Low and High Arctic	Least concern
Black bear	<i>Ursus americanus</i>	Low Arctic	Least concern
Polar bear	<i>Ursus maritimus</i>	Low and High Arctic	Vulnerable
Wolverine	<i>Gulo gulo</i>	Low and High Arctic	Least concern
Short-tailed weasel	<i>Mustela erminea</i>	Low and High Arctic	Least concern
Least weasel	<i>Mustela nivalis</i>	Low and High Arctic	Least concern
American mink	<i>Neovison vison</i>	Low Arctic	Least concern
American marten	<i>Martes americana</i>	Low Arctic	Least concern
River otter	<i>Lontra canadensis</i>	Low and High Arctic	Least concern
Sable	<i>Martes zibellina</i>	Low Arctic	Least concern
Mountain hare	<i>Lepus timidus</i>	Low and High Arctic	Least concern
Arctic hare	<i>Lepus arcticus</i>	Low and High Arctic	Least concern
Snowshoe hare	<i>Lepus americanus</i>	Low Arctic	Least concern
Collared pika	<i>Ochotona collaris</i>	Low Arctic	Least concern
Northern pika	<i>Ochotona hyperborea</i>	Low Arctic	Least concern
American beaver	<i>Castor canadensis</i>	Low Arctic	Least concern
Muskrat	<i>Ondatra zibethicus</i>	Low Arctic	Least concern
Arctic lemming	<i>Dicrostonyx torquatus</i>	Low and High Arctic	Least concern
North American brown lemming	<i>Lemmus trimucronatus</i>	Low and High Arctic	Least concern
Brown lemming	<i>Lemmus sibiricus</i>	Low and High Arctic	Least concern
Northern collared lemming	<i>Dicrostonyx groenlandicus</i>	Low and High Arctic	Least concern
Wrangel Island collared lemming	<i>Dicrostonyx vinogradovi</i>	High arctic	Data deficient
Meadow vole	<i>Microtus pennsylvanicus</i>	Low Arctic	Least concern
Tundra vole	<i>Microtus oeconomus</i>	Low and High Arctic	Least concern
Singing vole	<i>Microtus miurus</i>	Low Arctic	Least concern
Northern red-backed vole	<i>Myodes rutilus</i>	Low Arctic	Least concern
Alaska marmot	<i>Marmota broweri</i>	Low Arctic	Least concern
Arctic ground squirrel	<i>Urocitellus parryi</i>	Low and High Arctic	Least concern
Red squirrel	<i>Tamiasciurus hudsonicus</i>	Low Arctic	Least concern
Porcupine	<i>Erethizon dorsatum</i>	Low Arctic	Least concern
Hoary bat	<i>Lasiurus cinereus</i>	Low Arctic	Least concern
Tundra shrew	<i>Sorex tundrensis</i>	Low and High Arctic	Least concern

bears, arctic foxes and walruses hunt. However, the extent and thickness of sea ice has been decreasing rapidly in recent years, because multiyear ice has almost disappeared from Arctic waters. In recent decades, rapid warming of Arctic climates has seen a major sea ice loss along the coasts of arctic Russia, Canada, and Alaska. Sea ice cover reached a record low in 2012, and more than 2 million km² has been lost since 2000. This represents a loss of 49% of the extent of sea ice cover observed from 1979 to 2000 (Fig. 2). Recent forecasts by NOAA (2018) suggest that Arctic sea ice cover is shrinking by 12.8% per decade. This indicates the very likely disappearance of Arctic sea ice cover during the first half of the 21st century (Fig. 3). So it appears to be a question of *when* Arctic sea ice cover is lost, not *whether* it will be lost. The loss of sea ice cover creates a positive feedback loop for general atmospheric warming of the Arctic region. The white surface of sea ice reflects a large proportion of solar radiation back out to space. That white surface turns to a very dark surface when sea ice gives way to open water. The open ocean absorbs a great deal of solar energy, which in turn warms the entire Arctic region. In 2017, Arctic sea surface temperature was 4 °C warmer than the 1982–2010 average.

Biological Impacts

Since 1981, the loss of summer sea ice cover has been 1.6 million km², an area roughly 40% of the size of the European Union countries. Thus this sea ice cover has become unavailable to arctic marine mammals by the end of summer. The loss of sea ice and associated regional warming are exerting environmental pressure on the regional biota, both in the Arctic Ocean, and in the near-shore environments on land. Post et al. (2013) reviewed the biological impacts of sea ice reduction, showing that sea ice loss represents a huge habitat reduction for sea-ice algae and phytoplankton. These organisms represent 57% of the primary

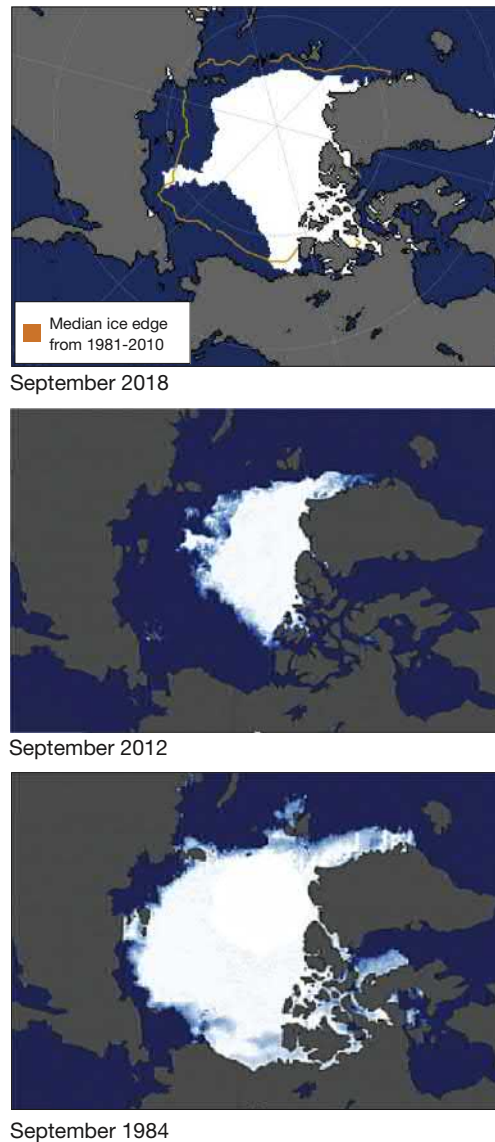


Fig. 2 Map of the northern high latitudes, showing the extent of September sea ice in 2018, 2012, and 1984. Data from National Snow and Ice Data Center.

productivity in the Arctic Ocean. Organic detritus frozen into the pack ice is released into the water column as the ice melts in spring. This pulse of organic material is used by phytoplankton and zooplankton to facilitate their growth and reproduction as summer comes on. This burst of biological productivity makes its way up the food chain. The phytoplankton feed the zooplankton, which in turn feed crustaceans and small fish. Cod and capelin feed on smaller fish. Beluga whales feed on a wide variety of bottom-dwelling fish, squid, crabs, and other invertebrates. Walrus feed almost exclusively on mollusks, but also take other marine invertebrates. They use the pack ice as a platform for pupping and sea-floor foraging, as do Arctic seals. Walrus use sea ice for molting, mating, resting between hunts for food, and walrus mothers nurse their young on pack ice. Pacific walrus females and their young spend the summer on sea ice in the Chukchi Sea between Alaska and Siberia. This region could be free of summer sea ice cover by 2060 or sooner, according to the U.S. Fish and Wildlife Service.

The Arctic supports a particularly rich diversity of seal species, including ribbon seals, bearded seals, ringed seals, spotted seals, harp seals, and hooded seals. Because of the disappearing sea ice, several of these species are under consideration by the United States government for listing under the Endangered Species Act. The most threatened species is the ribbon seal, which lives on the outermost edges of sea ice, near deep water. These are most likely to be affected by loss of habitat as sea ice continues to shrink. Polar bears spend the winter on the pack ice, hunting seals as they come up for air in small openings in the ice. Arctic foxes often follow behind the bears, scavenging seal carcasses after the bears have abandoned them.

Without sea ice cover, the whole process described above will cease to exist. The volume of organic detritus will be severely decreased, greatly curtailing the annual phytoplankton productivity bloom. Phytoplankton are primary producers of this marine

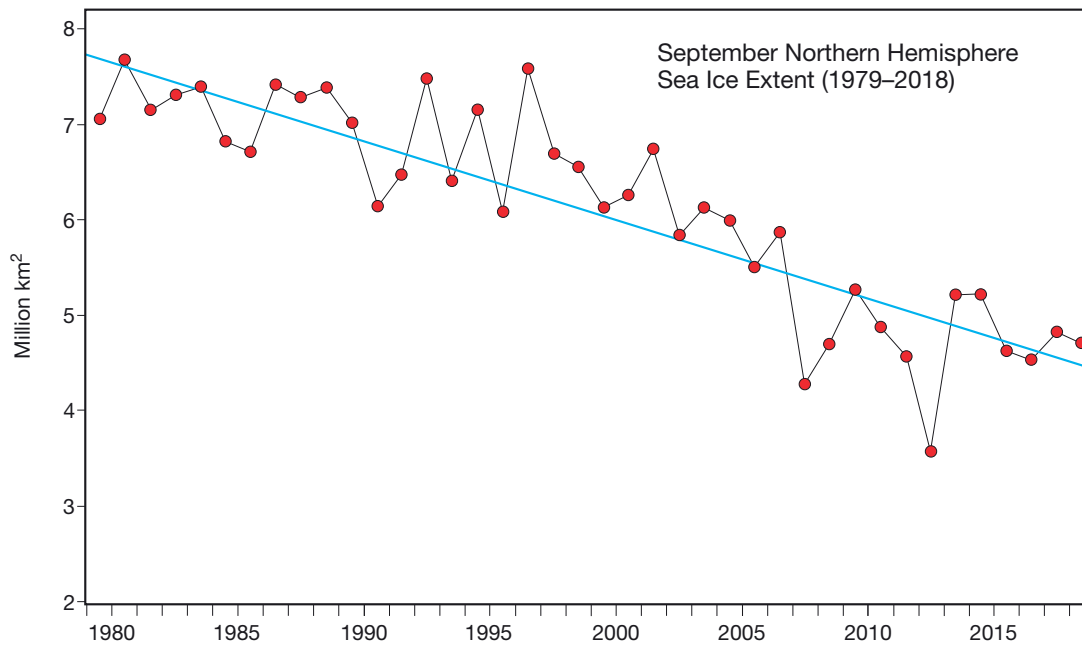


Fig. 3 Graph showing the decline in September Arctic sea ice from 1979 to 2018. Data from National Snow and Ice Data Center.

ecosystem. Without sufficient primary productivity, all the consumers, from the zooplankton to the marine mammals, suffer from a lack of food. The lack of sea ice cover is already shortening the polar bears' hunting season, as the bears must now wait several extra weeks for the sea ice to form in the autumn. If the sea ice cover disappears, the polar bear is likely headed for extinction. Walrus are also being forced to haul out onto land to bear their pups and rest, increasing over-crowding of walrus on beaches, facilitating disease transmission within populations.

Oil and Gas Development

As the extent and thickness of sea ice declines in the Arctic Ocean, both Russia and the United States have been exploring the possibilities of oil and gas well development in the High Arctic, including drilling in the Arctic Ocean. Only about one-third of the Arctic is covered by land; another third consists of the offshore continental shelf, with waters generally less than 500 m deep. The remaining third comprises deep ocean waters. Most of the Arctic waters are currently ice-covered for most of the year. But as we have seen, Arctic sea ice cover has been receding in recent years. The Arctic region contains portions of six countries that have Arctic shorelines: Canada, Greenland, Iceland, Norway, Russia, and the United States. Finland and Sweden do not border on the Arctic Ocean and are the only Arctic countries without jurisdictional claims in the Arctic Ocean and adjacent seas. An assessment of oil and gas potential in the Arctic by the US Geological Survey concluded that 770–2990 trillion cubic feet of natural gas reserves lie north of the Arctic Circle, mostly in Russia (Gautier, 2011). Overall, the Arctic is estimated to contain between 44 and 157 billion barrels of recoverable oil. Approximately 84% of these fossil fuel resources are expected to be found offshore, so governments, government-owned oil and gas companies, and private companies are now considering Arctic Ocean drilling. The burning of the fossil fuels extracted in these enterprises will exacerbate global warming, which in turn will melt more Arctic sea ice.

In fact, oil drilling in the Arctic Ocean is just about to begin. In October 2018, U.S. Interior Department officials announced their approval of a plan to drill for oil 6 miles off the northern Alaskan coast in the shallow waters of the Beaufort Sea. Hilcorp, based in Houston, plans to build a nine-acre gravel island about 20 miles east of Prudhoe Bay, not far from the Arctic National Wildlife Refuge. Such activities will alter habitats and disturb marine life. Of particular note is the disturbance of the region's rich marine mammal fauna, as discussed by Huntington (2009). He reckons that offshore oil and gas facilities will disturb marine mammals through noise from seismic surveys, shipping, and drilling. Chronic pollution, in addition to potential oil spills, will contaminate Arctic waters, producing cumulative impacts that will extend beyond the continental shelf regions where these activities will take place. Bowhead whales have already shifted migratory routes in the Beaufort Sea to avoid noise from oil and gas development activities, such as drilling. If preferred habitats for breeding, calving, feeding and migration are disturbed over large areas, the overall fitness of marine mammal populations in the Arctic Ocean will decline.

Navigation of High Arctic Waters

One of the greatest ecological threats of declining sea ice is the increased access to the Arctic Ocean this will give to non-native peoples. European explorers started looking for a Northwest Passage through Arctic waters as far back as the late 15th century

with the voyages of John and Sebastian Cabot. The waters of the Canadian Arctic Archipelago were clogged with drifting sea ice during the summers of the next several centuries, and only in the 20th century was a route successfully navigated. In 2013, a large freighter navigated the Northwest Passage. In November 2013, the Russian company Gazprom made the first ever delivery of liquefied natural gas through the Arctic north-east route, sailing from Norway east to Japan. Large volumes of commercial shipping via the Arctic are probably 10 years away, but this appears to be another inevitable outcome of warming in the Arctic.

Black carbon (BC) is a particulate matter produced by ships through incomplete burning of diesel fuel. International shipping emits between 71,000 and 160,000 metric tons of BC annually. In the Arctic region in 2004, approx. 609 tons of black carbon was released. These black particles fall on the snow and ice surfaces of arctic sea ice and lands, where they absorb solar radiation and cause melting (Fig. 4). Although the amount of BC is currently low, as shipping traffic increases in the Arctic, the effects of BC described above means that even small amounts could have a potentially disproportionate impact on ice melt and warming of the region. A recent study found that the heaviest CO₂ and BC emissions were found in the Bering Sea region, around Iceland, along the Norwegian coast and in the Barents Sea.

The Arctic marine environment is highly sensitive to impacts from increased shipping, as discussed by Eger (2018). A large number of marine species travel throughout the Arctic to feed, mate, give birth, take care of their young and molt. These aspects of their life cycles will be exposed to various kinds of disturbances from shipping. Toxic substances are released as emissions to the air or as discharges to the water, including the accidental releases of oil or hazardous cargo. Disruption of marine life is caused by ship noise and by collisions. In the long term, ships are likely to accidentally introduce invasive marine species into Arctic waters as they have elsewhere. There are 280 species of birds, marine mammals and fish known to migrate through Arctic waters, and around 450 species are known to breed in Arctic waters or along Arctic shores. Many species that undertake annual migrations appear to use seasonal changes in oceanic environmental conditions as cues. Unfortunately, the migration routes used by mammals and birds correspond closely with the main shipping routes into and out of the Arctic. Presently, there is limited overlap between marine fauna and ships during the spring, as all shipping activity typically occurs later in the spring than the animal migrations. This situation may change if the date of ice break up moves earlier in the year. In the autumn there is a greater probability of interaction between ships and migrating marine species, as both are leaving the Arctic in advance of the formation of pack ice. The spring migration routes of marine mammals and birds are especially sensitive to disturbance. The brief feeding seasons of these animals mean that if feeding is disrupted, the animal may not survive the next winter. These unique characteristics make Arctic species vulnerable to disturbances caused by shipping activities. If large ships rely on ice-breakers to open shipping lanes, then the ice-breaking ships also add to wildlife disturbances. For instance, they are known to disrupt birthing of seal pups on the ice. The regulation of tanker traffic, such as that in the Barents Sea, will require intergovernmental cooperation between Norway and Russia.

Pollution

Creeping in from the south, air pollution has been acidifying arctic lakes in recent decades, even though the source of pollution is thousands of km to the south. More than 20 years ago, Douglas et al. (1994) found that the characteristic diatom floras of lakes and ponds in the Canadian High Arctic had changed dramatically in the previous two centuries. Such changes are probably linked to multiple factors, including air pollution, warming temperatures, and increased levels of ultra-violet radiation. Persistent organic



Fig. 4 Black particles coat the surface of snow and ice at an Arctic remote weather station. Photo by Jason Box, Geological Survey of Denmark and Greenland used with permission.

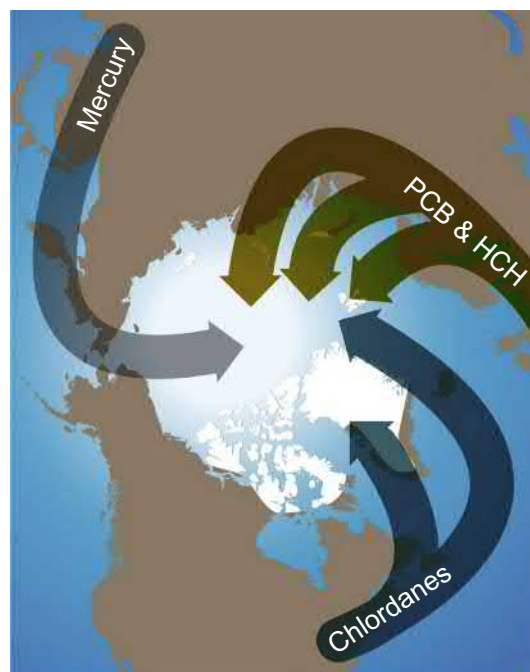


Fig. 5 Sources of persistent organic pollutants and mercury that make their way to the Arctic Ocean. After figure by the Norwegian Polar Institute.

pollutants (POPs) are being transported into the High Arctic from sources well to the south (Fig. 5). The Norwegian Polar Institute (2018) reports that traces of these and other pollutants are found throughout the arctic environment, including pollutants in the air, soil, snow, sea ice and glaciers, seawater and fresh water, birds, mammals and people. Unfortunately, the Arctic acts as an indicator region for known and new pollutants. If a pollutant is found in the Arctic, it is an indication that the substance has been transported a long distance, is poorly degradable and is taken up in organisms.

A number of POP compounds have made their way from the mid-latitudes to Arctic waters (Fig. 5). PCB is polychlorinated biphenyl, a group of organochloride compounds that were widely used as dielectric and coolant fluids in electrical equipment until they were banned by many governments in the late 1970s and 1980s. This group of toxic compounds persists today in the Arctic. PCB values from air measurements at a research station in Svalbard show higher levels than at corresponding stations in Canada, suggesting that the European Arctic receives more PCB than the North American Arctic. The PCB levels in polar bears in Svalbard are two to six times higher than in polar bears from North America. Polar bear tissues have also been found to contain high levels of certain kinds of brominated flame retardants. Scientists have also found a number of newly developed chemical compounds that are polluting the Arctic, such as various kinds of brominated and fluorinated substances. Another POP is Hexachlorocyclohexane, or HCH. This is another organochloride compound that was used as a pesticide in the 1960s and 1970s, but persists in the environment throughout the world's oceans. Chlordane is an agricultural insecticide that is highly toxic to aquatic organisms, both freshwater and marine. It washes from farmer's fields into waterways and eventually makes its way to the world's oceans. Once there, it takes a very long time to break down. It binds strongly to ocean sediments and accumulates rapidly in the tissues of many aquatic species, working its way up the food chain. Even though the import and export of Chlordane has been banned by international conventions, it has become widely dispersed and has been found in arctic air, and water, where it threatens the health of fish, marine mammals and humans.

In addition to these exotic pollutants, sources of pollution closer to the target areas are also being produced in the European Arctic and subarctic. These include dioxins from smelters in Norway, heavy metals from industrial activities in the Kola Peninsula and the Norilsk industrial complex in northwest Russia. Mining takes place in several parts of the Arctic, such as the Pechenga-Nikkeli district of Svalbard, and in parts of Siberia, and it represents a local source for contaminants such as PAH, heavy metals and PCBs. The contaminants are transported to the Arctic by rivers, winds and ocean currents, and new substances are constantly appearing.

Unfortunately, dioxins, polychlorinated biphenyl (PCB), other organic compounds, and heavy metals such as mercury tend to accumulate in the tissues of vertebrates. Because the polar seas are the recipients of these pollutants, the marine animal life of the region has been poisoned by them. These pollutants tend to accumulate in the fatty tissues of marine mammals, so their concentrations become far higher than those found in organisms lower down the food chain. A summary of the accumulation of organic pollutants and mercury in Canadian arctic vertebrates by Braune et al. (2005) showed that the concentrations of PCBs in zooplankton range from about 15–55 ng per gram of dry weight. Beluga whales eat fish that have eaten other fish and zooplankton. The concentrations of PCBs in beluga blubber in the Canadian arctic range from about 3000 to 5000 ng per gram of blubber, a concentration about 150 times that found in zooplankton. Polar bears eat mainly ringed seals in these waters. The seals eat fish that have eaten other fish and zooplankton. The concentration of PCBs in polar bear fat is about 1000–2500 ng per gram.

Following the mercury trail

According to a recent study (Lamborg et al., 2014), the total anthropogenic mercury released into the ocean is estimated to be as much as 80,000 metric tons. Two-thirds of this mercury is found in shallow marine waters (less than 1000 m) where many fish live. Mercury becomes bio-accumulated in marine food chains in the form of highly toxic methyl mercury which can cause health risks to marine mammals and humans. Obrist et al. (2017) studied the sources of mercury in Arctic Ocean waters. They found that most of the mercury (about 70%) in the interior Arctic tundra is derived from gaseous elemental mercury deposition, with only minor contributions from the deposition of mercury coming from rain or snow. They found that deposition of elemental mercury, the form present throughout the global atmosphere, occurs throughout the year in the Arctic, and that its concentration on arctic tundra is enhanced in summer through the uptake of mercury by vegetation. Plant uptake of gaseous mercury leads to soil concentrations greatly exceeding the levels found in temperate soils. The authors suggest that high tundra soil mercury concentrations might also explain why Arctic rivers annually transport large amounts of mercury to the Arctic Ocean.

Wang et al. (2018) attempted to track mercury once it enters the Arctic Ocean. Mercury is a contaminant of major concern in Arctic marine ecosystems. Decades of observations in marine biota from across the Canadian Arctic show generally higher mercury concentrations in the west than in the east. Methyl-mercury (MeHg) is the compound that accumulates and biomagnifies in marine biota. Wang et al. (2018) performed a series of high-resolution vertical profiles of total mercury and methyl-mercury in seawater along a transect from the Canada Basin, across the Canadian Arctic Archipelago and Baffin Bay, and into the Labrador Sea. They found that total mercury concentrations are lower in the western Arctic, in contrast to the pattern of the mercury concentrations in marine organisms, which are higher in the western Arctic and decrease eastward (Fig. 6). However, they also found that methyl-mercury shows distinctive maximum concentrations at depths of 100–300 m in the Arctic Ocean, with its peak concentration in the west, and decreasing eastwards. In these water depths, the maximum concentration of methyl-mercury lies within the habitat of zooplankton and other lower trophic-level biota. These small organisms take up methyl-mercury in their tissues, and are then eaten by fish, which are eaten by seals, that are eaten by polar bears. Thus the biological uptake of subsurface methyl-mercury at the bottom of the food chain leads to subsequent biomagnification in fish, marine mammals, and humans. This explains the east-west biotic mercury concentration gradient.

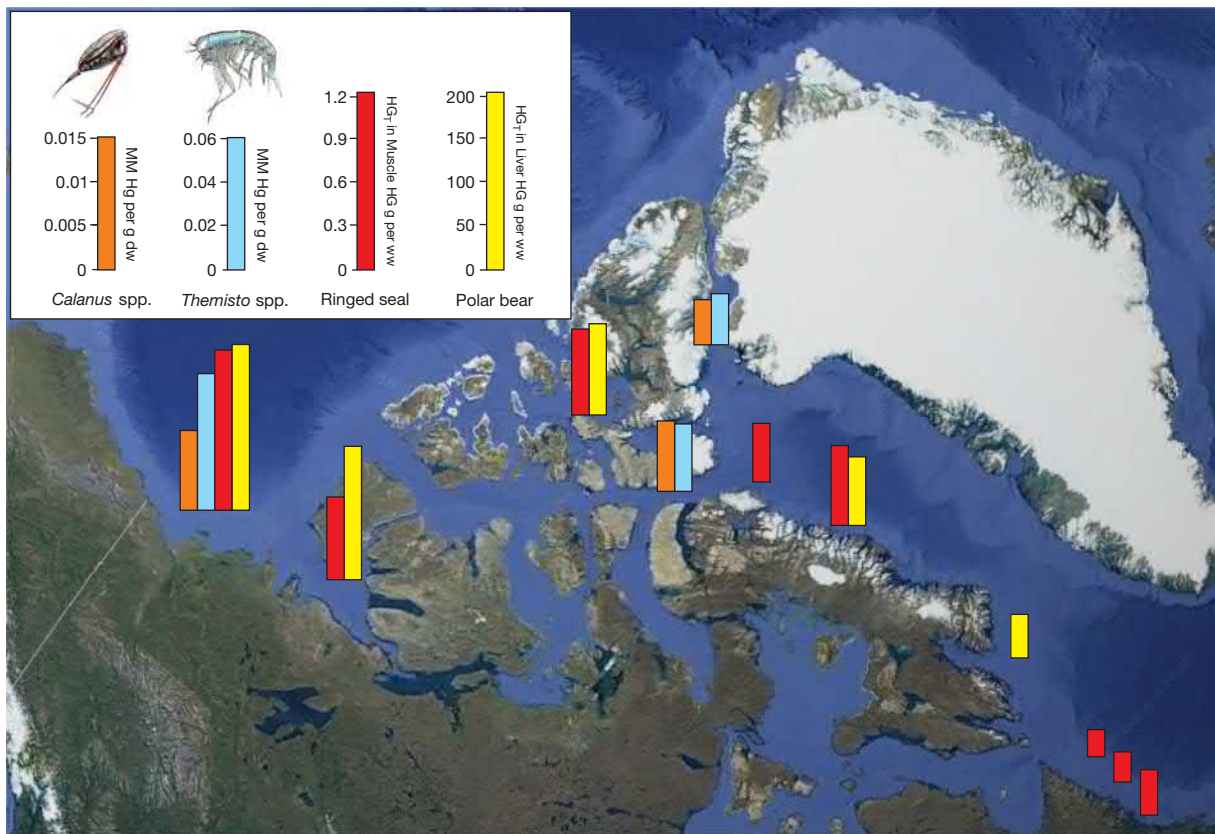


Fig. 6 Mercury concentration levels in two zooplankton taxa (*Calanus* and *Themisto*), ringed seals, and polar bears, across the Canadian High Arctic region. Data from Wang, K., Munson, K. M., Beupr -Laperri re, A., Mucci, A., Macdonald, R.W. et al. (2018). Subsurface seawater methylmercury maximum explains biotic mercury concentrations in the Canadian Arctic. *Nature Scientific Reports* 8, 14465. Photo of *Calanus glacialis* courtesy of Arctic Ocean Diversity web site (http://www.arcodiv.org/watercolumn/copepod/Calanus_glacialis.html). Photo of *Themisto libellula* by Maria Włodarska-Kowalczyk, used with permission.

Threats to the Low Arctic

Population Pressure

About 4 million people live in the Arctic. Only a few thousand live in the High Arctic. The rest live in the Low Arctic, almost half living in Arctic Russia (Fig. 7). Because Arctic Russia, Alaska, Canada and Greenland are such large regions, the population density remains very low (less than 50 people per 100 km²) in these regions. Arctic Scandinavia has higher population densities. Farming is virtually impossible in the Arctic and the traditional hunter-gatherer lifestyle of the native Arctic peoples has diminished greatly since the second half of the 20th century, so most Arctic residents live in towns and villages. For the most part, these communities do not generate potent environmental impacts on surrounding landscapes, although home heating oil and diesel-powered vehicles contribute to the black carbon problem. Most of the serious environmental impacts come from regional industrial sources, such as oil wells and pipelines, gold mines and other mineral extraction facilities, and ore smelting plants in Arctic Russia.

Chemical Pollution and Vehicular Damage

The most polluted arctic region is the Kola Peninsula of northwest Russia, where mining operations and emissions from nickel smelters in and around the city of Norilsk emit up to 2460 tons of nickel, 1600 tons of copper and 500,000 metric tons of sulfur-dioxide per year (Moiseenko and Kudryavtseva, 2001). Copper and nickel concentrations in soil and water are at toxic levels within a 30 km radius of the city. These toxic heavy metals, and especially sulfates, have been found in air samples in the atmosphere surrounding Norilsk. Simonenkov et al. (2016) found that at a distance of 92 km from the source, air samples contained pollution dominated by sulfates, followed by chlorine, bromine, lead, nickel, calcium, iron, potassium, sodium, and ammonium.

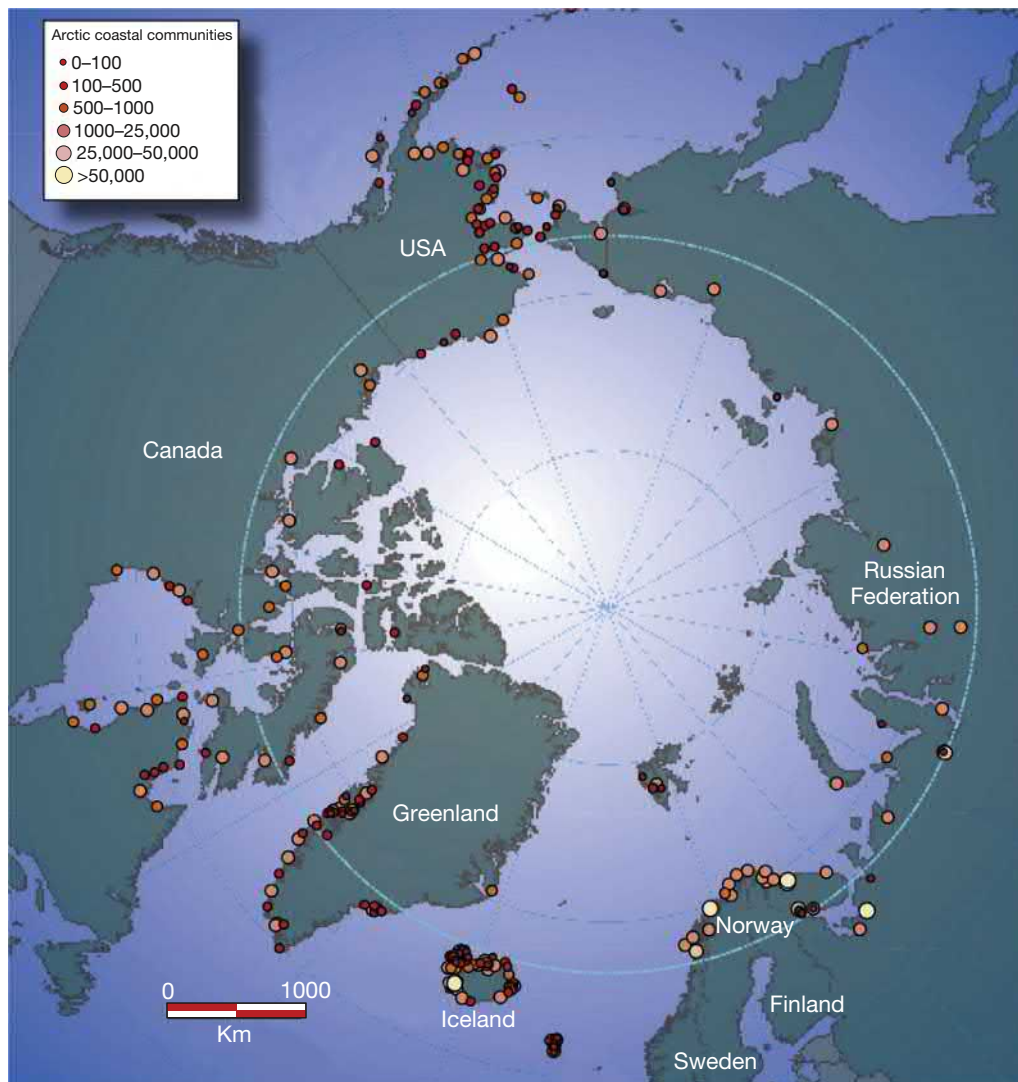


Fig. 7 Population centers along Arctic coastlines. NOAA Arctic Program (public domain).

Tundra vegetation and soils are particularly vulnerable to chemical pollution. Toxic chemicals stay in the shallow active layer of soils. The permafrost boundary prevents chemicals from moving down to deeper layers. Near-freezing soil temperatures in the active layer slow the breakdown of pollutants, keeping soils toxic for decades or centuries after the initial contamination. As discussed above, atmospheric circulation brings air pollution from lower latitudes, and the pollutants tend to concentrate in polar regions. Tundra vegetation is also particularly vulnerable to physical disturbances. Arctic plants recover with difficulty after disturbances, because they grow very slowly, and may only set seed every few years. Heavy vehicles driven over the tundra degrade the permafrost, leading to the melting of frozen ground (thermokarst). Deep scars from this melting persist for many decades. Roads, buildings and other structures must be insulated from the permafrost, or the heat they generate causes the ground beneath to melt.

Climate Change and Permafrost Melt

As arctic temperatures climb with global warming, the southern edge of the permafrost zone is retreating northward. The permafrost is rapidly receding, especially in the European part of the Russian Arctic. Between 1995 and 2005, the southern boundary of the regions with continuous permafrost (areas where at least 90% of the landscape is underlain by permafrost) migrated north by up to 50 km (Alfred Wegener Institute for Polar and Marine Research, 2018). In areas with discontinuous permafrost (areas where 10–90% of the land is underlain by permafrost), the boundary receded by as much as 80 km. This retreat of the permafrost zone has impacts on natural systems, because tundra vegetation evolved to grow in the shallow active zone above permafrost. As permafrost disappears, other plants, adapted to unfrozen soil regimes, can out-compete the native tundra vegetation.

Niittynen et al. (2018) performed a modeling assessment of the effects of both increased mean annual temperatures and decreased snow cover on the diversity of tundra plants for a region of northern Scandinavia (Fig. 8). They ran their model on 273 vascular plant, moss and lichen species in 1200 study sites spanning a wide range of environmental conditions. One of their model runs was based on a climate change impact model in which temperature increases are likely not to exceed 2 °C above the long-term average. They found that higher temperatures increased overall species richness and caused only one species to lose a suitable habitat. In contrast, a shorter winter snow cover duration (SCD) led to accelerated rates of species' local extinctions after a tipping point of 20–30% SCD decrease (Fig. 8). When a decrease in SCD reached 40%, plant and moss species extinctions exceeded 15%. Lichen species were more resistant to snow cover loss.

Fossil Fuels Development

Oil and gas extraction began in the Arctic during the 20th century. Major oil and gas deposits were found in arctic Alaska in the 1950s and 1960s. The Alaskan Prudhoe Bay oil field came online in 1977; peak production was 2 million barrels of oil per day in 1988. By 2017, the Prudhoe oil field produced only 280,000 barrels per day, a drop of 86% from 1977 levels. However, increases at other North Slope oil fields boosted the flow of oil through the Trans-Alaska Pipeline to an average of 526,000 barrels per day in 2017. The crude oil is transported 1290 km south to the port of Valdez via the trans-Alaska pipeline. The pipeline is above ground

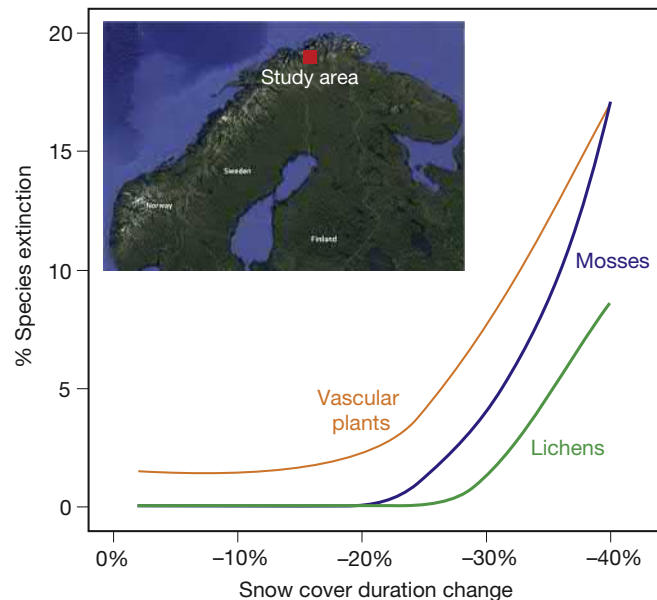


Fig. 8 Predicted extinction rates of vascular plant, moss and lichen species for a suite of test sites in northernmost Scandinavia, versus changing snow cover duration, given greenhouse gas emission scenario RCP 4.5 (increase of mean temperatures ≤ 2 °C). Data from Niittynen, P., Heikkinen, R.K., Luoto, M. (2018). Snow cover is a neglected driver of Arctic biodiversity loss. *Nature Climate Change* 8, 997–1001.

over the tundra, on insulated stilts that keep the permafrost from melting. So far, 17 billion barrels of oil have gone down the pipeline since 1977. These have been transported by more than 12,000 oil tankers for transport by sea around the world. One of these tankers, the *Exxon Valdez* ran aground in 1989, spilling 53 million gallons in Prince William Sound. The ecological devastation of that oil spill has not fully dissipated.

The US Congress established the Arctic National Wildlife Refuge (ANWR) in 1980. Congress deferred a decision regarding future management of the 1.5-million-acre coastal plain in recognition of area's potentially enormous oil and gas resources and its importance as wildlife habitat. Numerous test wells have been drilled and oil fields discovered near ANWR. In 2017 the Trump Administration announced its intention to open ANWR to oil and gas development. This led to a new assessment of oil and gas reserves in Arctic Alaska by the federal government. In 2018 the US Department of the Interior announced that Alaska's combined onshore and offshore fossil fuel reserves collectively hold about 739 billion gallons (2.8 trillion liters) of oil and more than 50 trillion cubic feet (1.4 trillion cubic meters) of natural gas. In August 2018, a Department of Interior official said the agency is moving forward to open a portion of the Alaska National Wildlife Refuge (ANWR) to oil and natural gas leasing in 2019, and predicted that a lease sale scheduled for the region will attract significant interest from producers. The Bureau of Ocean Energy Management revised the estimated recoverable petroleum resources in the Beaufort Sea Outer Continental Shelf Planning Area to 374 billion gallons of oil and 27.7 trillion cubic feet (780 billion cubic meters) of natural gas.

ANWR provides habitat for millions of migratory birds, caribou, polar bear, grizzly and black bears, wolves, Dall sheep, musk-oxen, arctic and red foxes, wolverines. The proposed oil and gas development would occur on the 607,000 ha coastal plain. This area is the most sensitive for wildlife in the entire refuge and any habitat loss that occurs here will impact the entire Arctic Refuge.

There is a particular concern about the effects of oil and gas production on polar bears. Disturbance of female polar bears while denning could cause them to abandon cubs. Damage or destruction of essential polar bear habitat (e.g., feeding, breeding, and especially denning areas) may be caused by dumping, dredging, drilling and construction of platforms, pipelines, roads, and support facilities. Attraction of the bears to industrial areas may lead to habituation to humans, forcing the need for increased control actions, including the trapping or shooting of habituated bears. Harassment (disturbance) by aircraft, ships and other vehicles will cause the bears stress, both when they are on land, and when they are at sea in the winter. Finally, the offshore oil and gas facilities will have detrimental effects on the polar bear's main source of food, ringed seals, due to impacts of oil, noise and chemical contaminants. Marine mammals (whales, seals, and walrus) will very likely be affected by offshore drilling in the Beaufort Sea.

Oil production in Arctic Eurasia focuses on western Siberia, where 68% of Russian gas and oil extraction take place. The biggest of these are in the Ob River basin, where 300 oil fields have pumped 65 billion barrels of oil since 1965, four times the quantity of oil pumped through Trans-Alaska pipeline. The Russian government estimates that at least 5% of the oil recovered from western Siberian wells has been spilled on the tundra surface since the 1960s. This amounts to 3 billion barrels of oil spilled in the Ob River and adjacent basins. A report by [Salmina \(2010\)](#), a regional ecologist, states that there is no fish life in the Ob, Nadym, Pur, and Sob rivers because of pollution from oil production. The pollution is not limited just to the oil itself. Salts and heavy metals are in the brine that comes to the surface with oil from wells. These by-products are dumped on the land. The Russian oil industry tacitly acknowledged the level of water pollution in oil field regions when it installed water purification plants on-site, as the local water is unsafe to drink.

Russian oil drilling on the continental shelf regions of the Arctic Ocean has also accelerated recently. In April 2017, the Russian state-controlled oil giant Rosneft started drilling the northernmost well on the Russian Arctic shelf in the Laptev Sea ([Paraskova, 2017](#)). The oil firm said that recoverable reserves at the field exceed 24.6 billion gallons. Geological data point to reserves at the field at 92 billion gallons. The Prirazlomnoye oil field in the Pechora Sea started pumping oil in late 2013. The field is estimated to hold 21.5 billion gallons of oil, with annual production averaging 1.7 billion gallons at full capacity.

Fisheries

Until now, commercial fishing has been quite limited in the Arctic Ocean. Baffin Bay and the Barents Sea have had the most commercial fishing thus far, along with the sub-arctic waters of the Bering and Norwegian seas. Sea-ice declines will allow commercial fisheries to expand into the Arctic in the coming decades. This will diminish fish stocks in the Arctic Ocean. As has been seen in the North Atlantic and other over-fished regions, diminished stocks of predatory fish such as cod alter food-web dynamics. Such changes in food supply will also add extra stress to fish-feeding marine mammals in Arctic waters, such as some whales, seals and sea lions.

Nuclear Testing

From 1954 to 1990, the Russian islands of Novaya Zemlya were used extensively for both above- and below-ground nuclear weapons testing. The indigenous Nenets population was forcibly resettled and the islands were divided into different testing zones. Novaya Zemlya was the site of 130 nuclear detonations, including the "Tsar Bomba," the biggest nuclear device ever detonated (50 megatons) ([Nuclear Risks, 2018](#)). In addition to bomb testing, the Russian government used these islands to dump nuclear waste. The cores of 13 broken-down nuclear reactors, along with spent fuel from nuclear submarines, were dumped along the coast of Novaya Zemlya and into the Barents and Kara seas. Two of the most contaminated sites on Novaya Zemlya are the Abrosimov and Stepovogo Fjords in the southern part of the island.

The Russians were not the only ones who considered their Arctic regions suitable places for nuclear weapons testing. In 1957 the US Atomic Energy Commission set up a project to use hydrogen bombs to create an ocean harbor in arctic Alaska, as a peacetime use of nuclear weapons. They chose a site in northwestern Alaska, at Cape Thompson. The story of this project is told in "The Firecrackers Boys" by O'Neil (1995). The region was considered uninhabited by the AEC, and it was well away from population centers, so the resulting radiation would not poison the population. As it turned out, quite a number of Inupiat Eskimo families did live and hunt at Cape Thompson. They had no need of a new harbor in this region, as the waters along the cape were blocked by sea ice for 8–9 months of the year. However, the project got the support of the newly formed state government in Alaska. As soon as the plans were made public, opposition came from the tiny Inupiat Eskimo village of Point Hope, from the scientists engaged in environmental studies under AEC contract, and a from handful of conservationists.

Environmental studies commissioned by the AEC suggested that radioactive particles from the blast would land on lichens, be eaten by caribou, and end up in people (for whom caribou was a primary food source). The people of Point Hope wrote to President Kennedy, petitioning him to end the project. The project was finally canceled in 1962, as the AEC faced increased public uneasiness over the environmental risk and potential danger to the Inupiat people.

Concluding Remarks

The developed countries of the world have used the Arctic tundra as a dumping ground, a nuclear playground, and an industrial site. Since the 20th century, Arctic regions have been exploited for mineral and petroleum resources with a mixed level of concern for environment (some in United States and Canada, very little in Russia). The remoteness of the Arctic has made it a target for extensive Russian nuclear testing (Novaya Zemlya), and proposed nuclear engineering (NW Alaska). The warming of the Arctic climate, though not originating from Arctic sources, is melting the sea ice cover, melting the permafrost, and changing tundra ecosystems. Ironically, anthropogenic warming is even now facilitating further human exploitation of the High Arctic for its fossil fuel resources, navigational short-cuts, and previously unobtainable fish stocks. These new incursions into the Arctic may well drive a number of marine mammals and other vertebrate species to extinction, unless strong conservation initiatives are put in place immediately.

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Current Ecosystem Changes in the Arctic

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Abstract

This article untangles the story of environmental change in the Arctic in the 21st century, and explores some of the interactions between the arctic biosphere, cryosphere, and marine environments. The Arctic region comprises about 30 million km² of land and sea north of the Arctic Circle (66° 33' 44"). The northern polar latitudes comprise an almost equal mix of land and sea. The land regions of the Arctic are divided into the northern sectors of the Eurasian and North American continents, the island of Greenland, and numerous high arctic island groups. The current environmental changes in the Arctic are happening at a pace and an amplitude hitherto unknown. Global warming from anthropogenic GHG emissions is probably having the greatest impacts on Arctic environments. Because of the intricate interactions between land, sea, and ice, the global warming signal is greatly amplified in the Arctic, and all but the most stringent scenarios to reduce GHG emissions will very likely lead to a complete transformation of Arctic environments. No one knows just how the Arctic biota will respond to these environmental changes, but modeling efforts point to a breakdown of existing ecosystems.

Introduction

The Arctic: a remote region that most people will never visit and is often perceived as a frozen, uninhabitable wasteland (Fig. 1). In recent months and years, the Arctic has been in the news on a regular basis. We hear that the sea ice is disappearing, that the



Fig. 1 The High Arctic often appears bleak and forbidding, as in this aerial photo of Ellesmere Island. Courtesy of NASA.

Greenland Ice Sheet is melting, that the Arctic is being subjected to a much higher level of global warming than the rest of the planet. The above statements are a mixture of fact and fiction. As is usual with scientific topics, the facts that are being uncovered are far more complex than were previously thought. This article aims to untangle the story of environmental change in the Arctic in the 21st century, and to explore some of the interactions between the arctic biosphere, cryosphere, and marine environments.

The Physical Environment

As generations of explorers have learned, and the ancestors of the native peoples grasped long ago, the Arctic is a harsh, unforgiving region. The long, dark winters with their bitter cold temperatures, the frozen sea surfaces, the permanently frozen ground, and the great distances between human settlements, make the Arctic a treacherous place. Seemingly small mistakes can be deadly (Fig. 2). The employment of caution in decision making is not just preferable, it is often the only way to survive the circumstances. Yet this physically demanding environment is in many ways incredibly fragile. The plant and animal life of Arctic lands and seas are highly specialized—adapted to survival in some of the harshest environments on Earth. Let us begin with brief descriptions of the physical environments of the Arctic, as a necessary step in setting the stage for later discussion of the ecosystems of the region.



Fig. 2 The logistic errors of 19th century Arctic explorers often ended in death. This photo shows an archaeologist uncovering the remains of a sailor who perished on King William Island as part of the Franklin Expedition of 1845. Photo by Robert W. Park, University of Waterloo, used by permission.

Land vs sea areas

The Arctic region comprises about 30 million km² of land and sea north of the Arctic Circle (66° 33' 44"). The northern polar latitudes are quite different from the southern polar latitudes, where the continent of Antarctica dominates the polar region. The Arctic regions, on the other hand, are almost an equal mix of land and sea. The Arctic Ocean covers 15.6 million km² or 52% of the Arctic. The combined lands of the Arctic cover approximately 14.5 million km², or 48% of the Arctic. The land regions of the Arctic are divided into the northern sectors of the Eurasian and North American continents, the island of Greenland, and numerous high arctic island groups (Fig. 3).

The greatest number of Arctic islands are found in the Canadian Arctic Archipelago, which consists of 36,563 islands above the Arctic Circle in Canada. These islands encompass 1.4 million km² of land. Almost two-thirds of this land is found on the six largest of these islands, including Baffin Island (507,451 km²), Ellesmere Island (196,236 km²), Devon Island (55,247 km²), Axel Heiberg Island (43,178 km²), Melville Island (42,149 km²) and Prince of Wales Island (33,339 km²).

Greenland is the world's largest island, at 2.166 million km². The island spans bioclimatic zones from subarctic in the south to High Arctic in the north (59°–83°N latitude). The Greenland Ice Sheet covers 81% of the land, containing about 2.8 million km³ of ice. The thickness of the ice sheet ranges from about 2–3 km, with most of the ice flowing from the center towards the coasts.

The islands of the Russian Arctic are all situated within the Arctic Circle, scattered through the Barents, Kara, Laptev, East Siberian, Chukchi, and Bering Seas. There are 56 major islands and hundreds of small ones. They cover about 215,500 km² in total.

Svalbard is the northernmost archipelago of Europe, an unincorporated area of Norway. It consists of 61,022 km² of land spread over nine major islands.

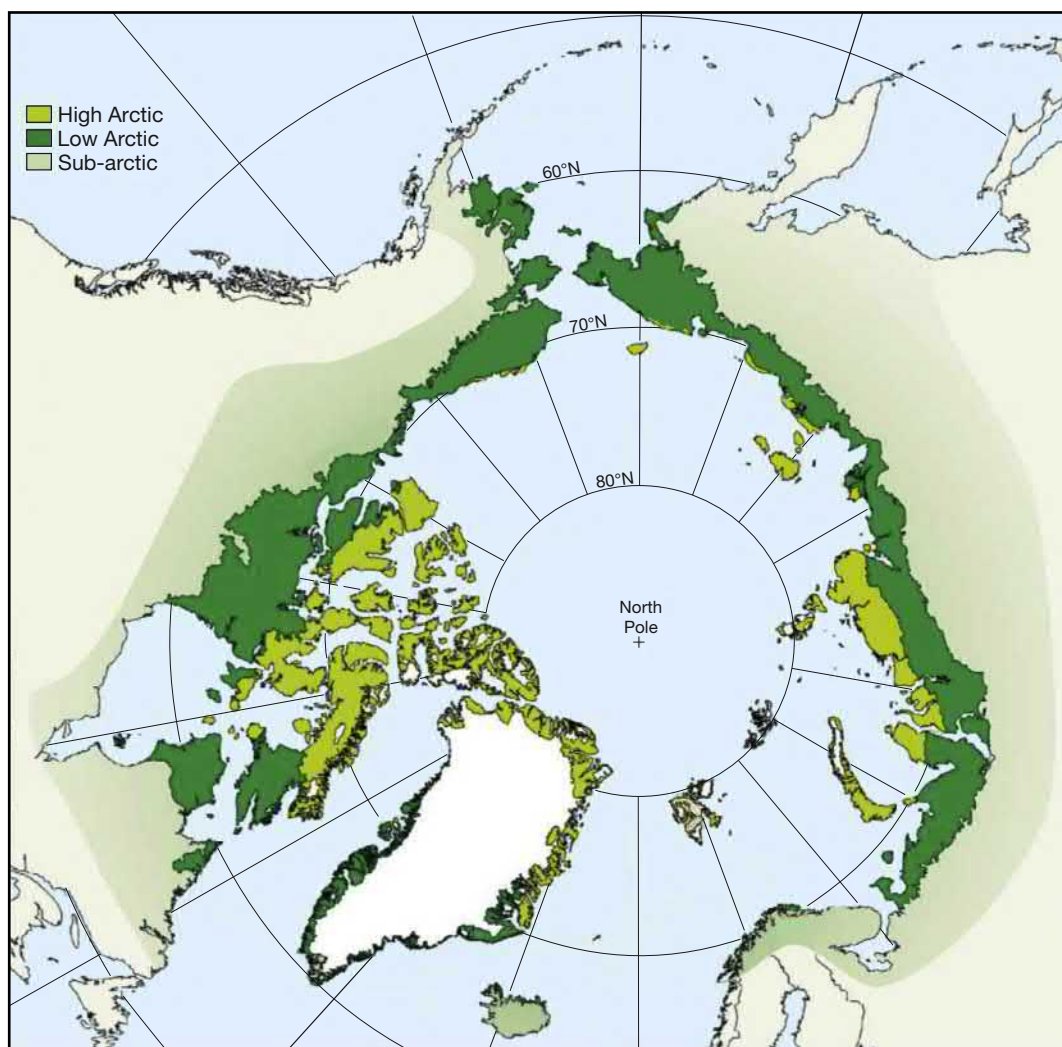


Fig. 3 Map of the Arctic, showing the principal vegetation zones (high Arctic, low Arctic, sub-Arctic).

Arctic Ocean circulation

As summarized by Woodgate (2013), the Arctic Ocean is the smallest of the world's oceans. Situated entirely within the Arctic Circle, it contains deep basins, and extensive shelf areas. For centuries, the hallmark of the Arctic Ocean has been its perennial (multiyear) sea-ice. Sea ice forms in the Arctic Ocean and adjacent seas from autumn to early summer. Prior to the 21st century, sea ice-covered half of the Arctic Ocean. Since 2007, minimum sea-ice cover has decreased by around 40%. Average sea ice thickness has thinned by 50%. Prior to the 1980–90s, annual layers of sea ice would build up for several years, thickening the ice pack considerably. However, the extent and thickness of sea ice has been decreasing rapidly in recent years, and multi-year ice has almost disappeared from Arctic waters.

The presence of Arctic sea-ice greatly affects the stratification of the water column, creating a fresher surface layer when it melts, and causing the mixing of surface waters as brine is excluded from ice formation during the freezing process. Arctic Ocean waters are more-or-less uniformly cold ($< 2^{\circ}\text{C}$), so the density of Arctic Ocean waters is primarily determined by salinity.

The Arctic Ocean plays two roles in global ocean circulation. It provides an oceanic pathway between the Pacific and the Atlantic, and it also takes the relatively warm, salty Atlantic surface waters, cools and freshens them, and returns them as deep water to the Atlantic. The continual influx of warm water into the North Atlantic polar ocean keeps the regions around Iceland and southern Greenland mostly free of sea ice year-round. The entrance of Pacific waters into the Arctic is through Bering Strait (Fig. 4). These waters are the dominant source of nutrient inputs into the Arctic Ocean. The entrance of Atlantic currents into the Arctic brings warmer, saltier waters through Fram Strait and the Barents Sea. These routes are both wider and deeper than Bering Strait, and they transport about ten times more water than the inflow from the Pacific. Eurasian rivers contribute roughly two-thirds of the freshwater entering the Arctic. Arctic Ocean waters flow out only into the Atlantic, via the western side of Fram Strait, or through the channels of the Canadian Arctic Archipelago.

Cryosphere

Ice covers many mountain regions, parts of the high Arctic islands, and 80% of Greenland. In addition to the Greenland ice sheet, isolated glaciers and small ice caps cover between 76,000 and 100,000 km² around the periphery of the island. The ice caps on the

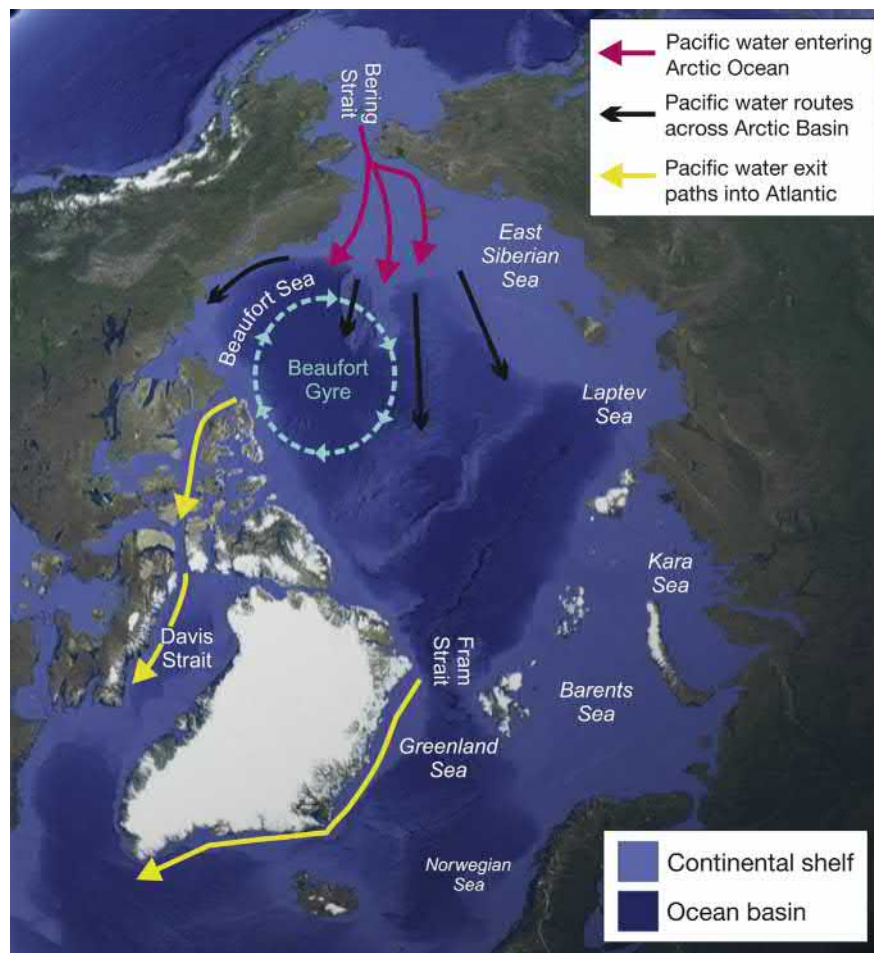


Fig. 4 Map of the Arctic region, showing routes of entry and passage of Pacific waters. Drawing after Woodgate, R. (2013). Arctic Ocean circulation: Going around at the top of the world. *Nature Education Knowledge* 4(8), 8.

islands of the Canadian Arctic Archipelago cover more than 100,000 km² of the region. The Svalbard archipelago has eight ice sheets and 180 glaciers. North and east of Svalbard lies Franz Josef Land, a group of 192 islands covering a combined area just over 16,000 km². These Russian islands fall roughly between 80° and 82°N in the Arctic Ocean. Because of their extreme northern location, 85% of the land is glaciated.

Arctic soils

Most arctic soils are in permafrost. This is ground that remains frozen for at least two consecutive years. Permafrost occurs both on land and beneath offshore Arctic continental shelves. Its thickness ranges from < 1 m to > 1000 m. During the summer, the uppermost layer of the ground thaws, forming an “active layer.” Thus, for a few weeks of summer, there is a shallow layer of thawed soil on many Arctic land surfaces. The thickness of the active layer on Arctic landscapes varies from about 0.3 to 4 m. Permafrost regions occupy approximately 22.8 million km² mostly between latitudes of 60°N and 68°N. Permafrost declines sharply in regions north of 67°N, because most of the exposed land surface gives way to the Arctic Ocean.

Because the active layer thaws and re-freezes both on an annual basis and even within the summer season, the instability of the surface and the growth of ice crystals have strong impacts on Arctic vegetation. Nearly all of the Arctic receives so little precipitation that it is properly considered a desert. Yet despite this low precipitation, tundra environments may be rather wet at the surface, and have many thaw lakes. Permafrost blocks the drainage of moisture below the active layer, so almost all of it remains at the surface. Also, very low temperatures keep surface moisture from evaporating back to the atmosphere.

Climates

The most defining feature of Arctic climate is the strong seasonality in sunlight that reaches the surface. It is this strong seasonality in insolation (incoming solar radiation) that drives the large seasonal cycle in surface temperatures in the Arctic. In the winter the surface receives very little or no insolation and the surface loses energy in the form of infrared radiation that is released back out into space.

Meteorological data are scarce in the High Arctic, because of the lack of weather stations. The Canadian Arctic Archipelago has two high latitude stations: Alert and Resolute. The Alert station is on the northern end of Ellesmere Island—the furthest north location in Canada at 82.5°N latitude. The Resolute station is on Cornwallis Island at 74.7°N. The two localities have very similar climates (Fig. 5). Above-freezing temperatures occur only in June to August, and mean daily temperatures do not exceed 5 °C. The average annual temperature is –17.6 °C at Alert and –16.2 °C at Resolute. Precipitation is incredibly low at both sites, as it is throughout much of the Canadian Arctic Archipelago.

The northernmost weather station in Greenland is called Station Nord, situated near the north coast of the island at 81.7°N. The climate profile of Station Nord is quite similar to that of the Alert station, across the Nares Strait on Ellesmere. Average summer temperatures do not exceed 4 °C, the summer season is short, and the average annual temperature is –16.2 °C. The average daily temperature in March is about –28 °C. Station Nord receives 135 mm of precipitation per year—another polar desert region (Fig. 6).

Svalbard, although situated in the High Arctic, receives some warmth from the West Spitsbergen Current (WSC), a branch of the Gulf Stream. The North Atlantic Current flows along the coast of Norway and continues north, where it is called the WSC. Almost 60% of the water entering the Arctic Ocean comes by way of the WSC. By the time the WSC reaches Svalbard, its surface temperature is about 2.75 °C. Even this moderate level of warmth is sufficient to alter the climate of this archipelago. For instance, at the Barentsburg weather station on Spitsbergen (78°N), above-freezing temperatures extend a few weeks into September (Fig. 6). The mean annual temperature is –5.9 °C, and the station receives 424 mm of precipitation per year—more than triple the amount that falls on the northern stations in Canada and Greenland.

Further east, at the Golomyanniy Meteorological Station in the Severnaya Zemlya archipelago of Russia (79.5°N, 90.6°E), the temperature regime is quite similar to those in High Arctic Canada and Greenland: a mean annual temperature of –15 °C, mean July temperature just above freezing, and an average February temperature of –27 °C (Fig. 7). However, this archipelago receives a similar amount of precipitation to Svalbard: 420 mm/year. This moisture comes from storms that drift northeast from the North Atlantic.

Continuing east across the International Dateline, the village of Utqiagvik (formerly Barrow) Alaska lies at the northernmost point of the United States (71.3°N). Because of its relatively lower latitude, this locality has above-freezing average temperatures from June through mid-September. The temperature and precipitation profiles are quite similar to those of the Alert and Resolute stations in Canada (Fig. 7).

Summary of Existing Ecosystems

Birds

The Arctic is seasonally populated by roughly 190 species of birds (Table 1). In contrast to more southerly latitudes, the dominant ecological and taxonomic groups among Arctic birds are waterfowl, shorebirds and seabirds, which constitute 75% of the avifauna. A particularly high species richness is found on both sides of the Bering Strait. Overall, species diversity is more than twice as high in the low Arctic than in the high Arctic. Arctic and subarctic ocean waters are home to huge numbers of sea birds, many of which feed on the abundant shoals of fish that thrive in the cold waters (Fig. 8).

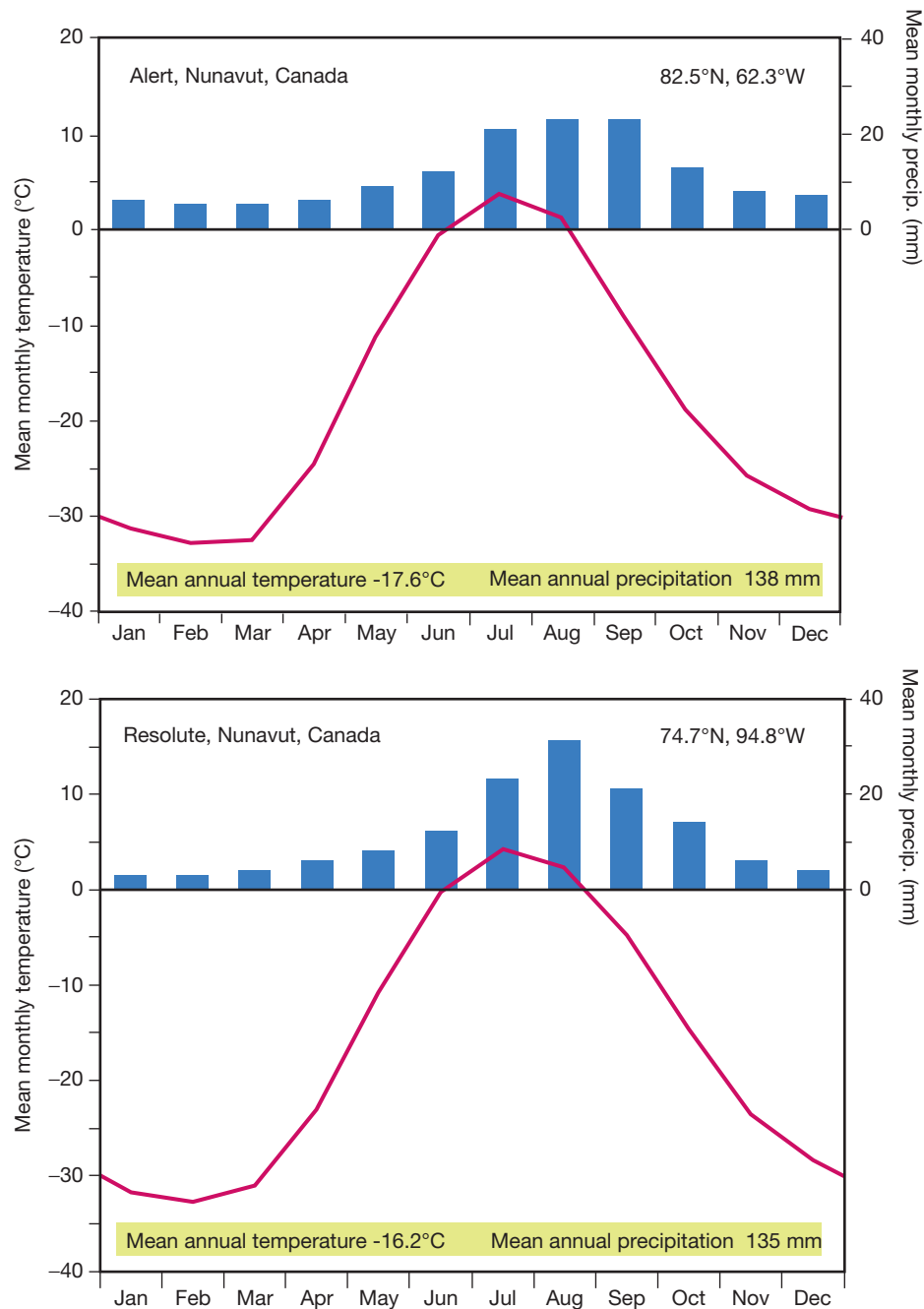


Fig. 5 Climate summary (monthly mean temperature and precipitation) for the Resolute and Alert weather stations in the Canadian High Arctic. Data from Environment Canada.

Fish

At least 127 species of freshwater and diadromous fishes (species that start life in freshwater and then spend most of their lives at sea) occur in Arctic freshwaters. These fish species fall mainly within five families, including more than 50 species of char, whitefishes, and salmon, 25 species of minnows, nine species of sculpins, eight species of perch and six species of lampreys. Freshwater fish diversity decreases with latitude. For instance, there are 40 species living at 60°N, 31 species living at 70°N, three species at 74°N, and only one farther north than this. The greatest freshwater fish diversity is found in areas that were unglaciated during the last ice age, particularly the former landmass known as Beringia. Diversity declines to low levels in regions that were the last to be deglaciated after the last ice age, such as the eastern Canadian Arctic and the coastal fringes of Greenland. Recent evidence suggests that the distributions of freshwater fishes are shifting northwards along river corridors and that diadromous species are becoming established in more northerly marine environments where waters are warming.

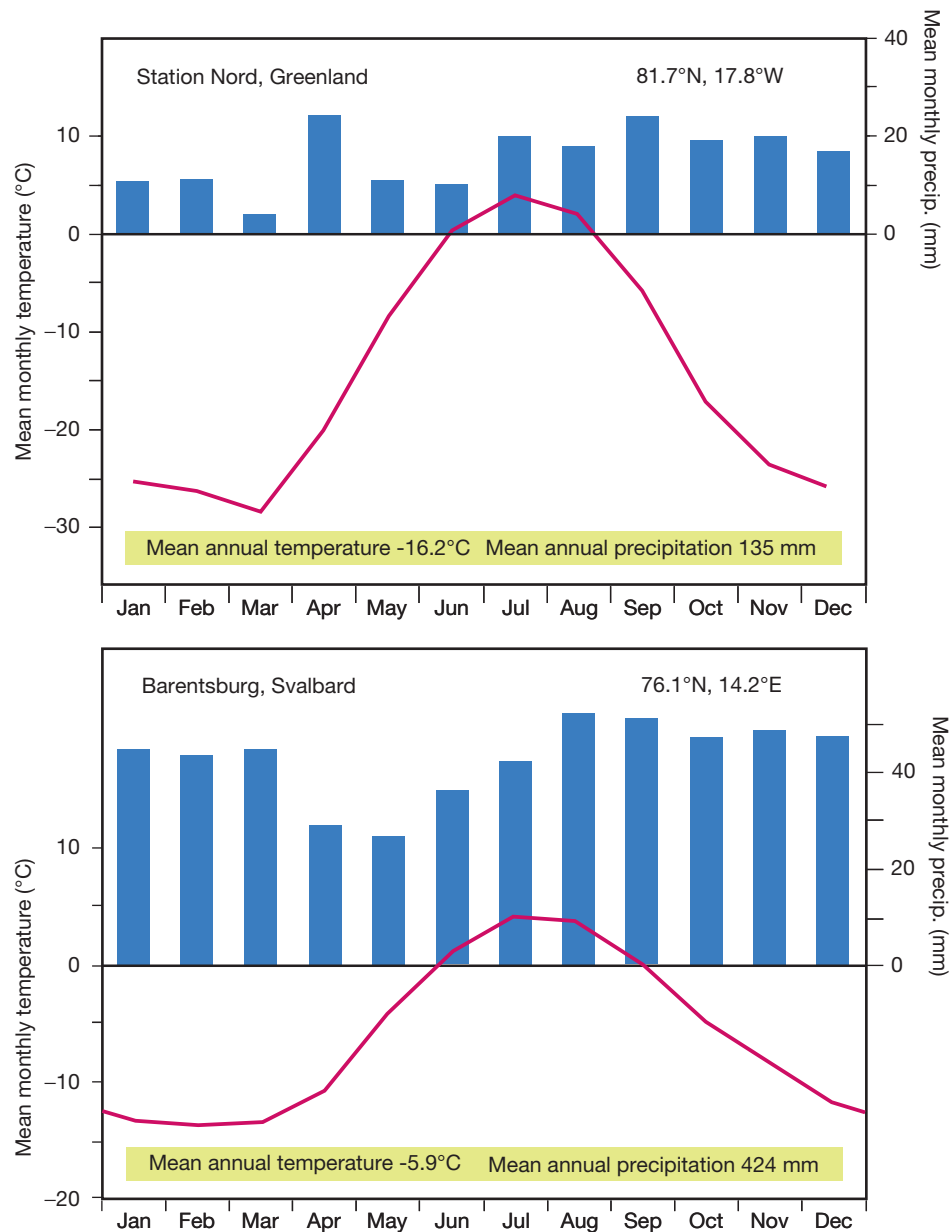


Fig. 6 Top: Climate summary (monthly mean temperature and precipitation) for the Station Nord weather station in the northeast Greenland. Data from Danish Meteorological Institute; Bottom: Climate summary (monthly mean temperature and precipitation) for the Barentsburg weather station, Svalbard. Data from the Sveagruva Climate Guide.

According to [Mecklenburg et al. \(2013\)](#), about 633 marine fish species are known from the Arctic Ocean and the adjacent seas, collectively known as the Arctic Gateways ([Table 2](#)). The fish faunas of the Arctic Gateways support some of the largest commercial fisheries in the world. These include 385 fish species in the Bering Sea, 204 species in the Norwegian Sea and 153 species in the Barents Sea. The fish fauna of Arctic Ocean contains less than 90 known species.

Marine mammals

A total of 35 species of marine mammals are found in Arctic waters ([Wilson and Reader, 2005; Table 3](#)). These include two species of sea lions, the walrus, eight species of seals, three species of right whales, five species of rorquals, the gray whale, the beluga and narwhal, the sperm whale, and four species of beaked whale. Three species of dolphins and two species of porpoises swim in Arctic waters. Polar bears are rightly considered marine mammals because they spend much of the year at sea, hunting from pack ice. More than half of the species of the Arctic marine mammal fauna swim in High Arctic waters, though none are restricted to these polar latitudes.

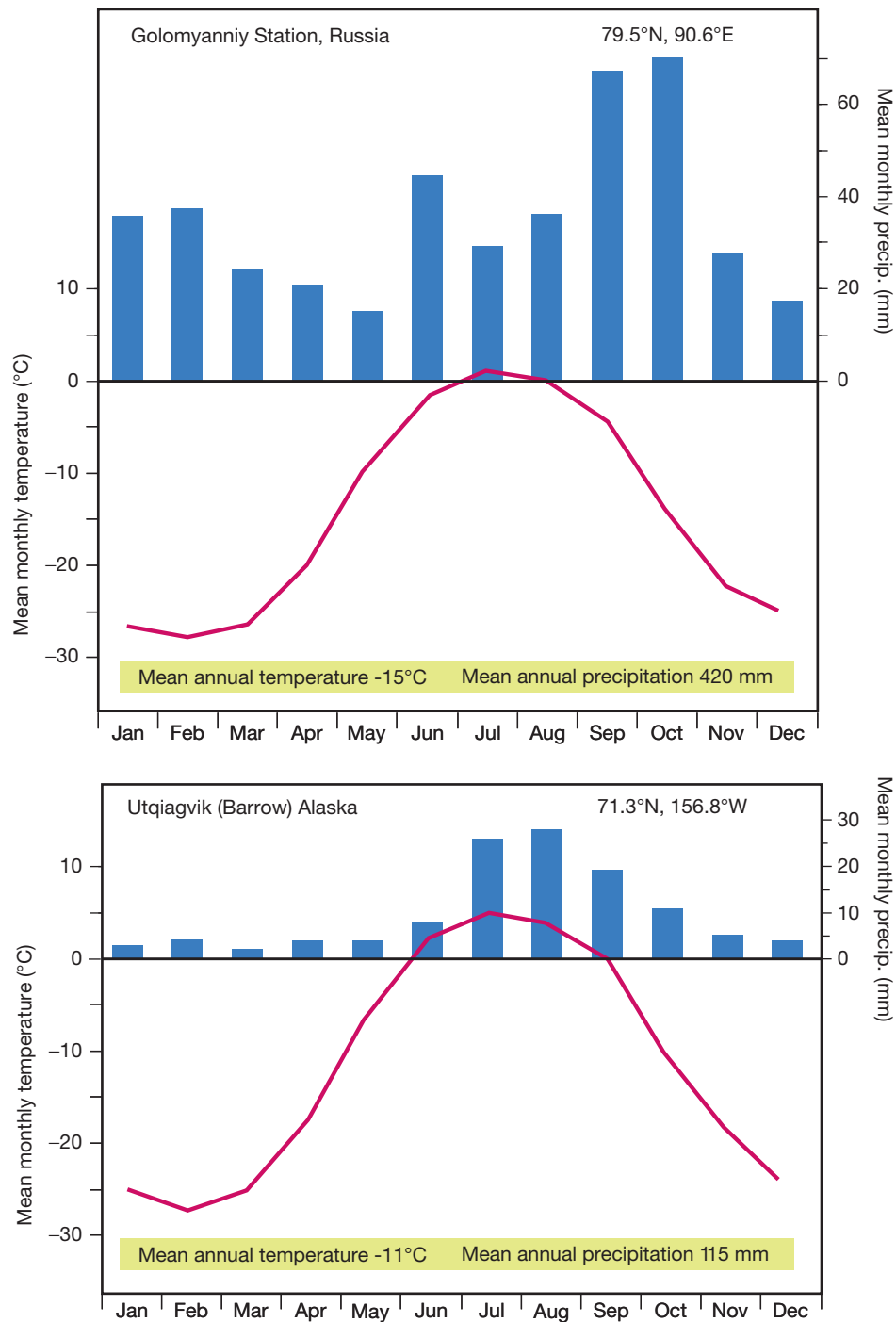


Fig. 7 Climate summary (monthly mean temperature and precipitation) for the Golomyanniy Meteorological Station in the Severnaya Zemlya and for Utqiagvik, Alaska. Top: Weather Data for Golomyanniy Meteorological Station; Bottom: data from US National Weather Service.

Terrestrial mammals

According to Wilson and Reader (2005) there are 63 species of terrestrial mammals on Arctic landscapes (Table 4). These include a surprising diversity of shrews (13 species). There are four species of Arctic hares, three species of pikas, three squirrels, the beaver, and 18 species of voles and lemmings. The large grazers include the Eurasian elk, the moose and the reindeer (caribou), as well as two species of sheep and the muskox. Predators include the gray wolf, coyote, and two species of fox. There are two species of bears and two species of lynx. Rounding out the list of predators are five species of mustelids, ranging from the least weasel, weighing in at 25 g, to the wolverine, weighing an average of 136 kg.

Table 1 Arctic bird species.

<i>Group</i>	<i>No. of species</i>	<i>Low Arctic species</i>	<i>High Arctic species</i>
<i>Waterfowl</i>			
Anatidae			
Geese	13	13	8
Swans	2	2	1
Wigeons	2	2	1
Ducks (Teals, Mallards, Eiders, Goldeneyes)	17	15	7
Scoters	5	5	1
Haematopodidae			
Oyster catcher	1	1	0
Charadriidae			
Plovers	8	8	7
Scolopacidae			
Sandpipers, Snipes, Curlews, Phalaropes, Stints	50	50	22
Total numbers of ducks, geese and shorebirds	98	96	47
<i>Seabirds</i>			
Gaviidae			
Loons	5	5	4
Procellariidae			
Fulmar	1	1	1
Sulidae			
Gannet	1	1	0
Phalacrocoracidae			
Cormorants, Shags	3	3	1
Stercoriidae			
Skuas, Jaegers	4	4	4
Laridae			
Gulls, Terns, Kittiwakes	16	15	8
Alcidae			
Auks, Murres, Guillemots, Auklets, Puffins	13	12	5
Total numbers for seabirds	43	42	24
<i>Landbirds</i>			
Phasianidae			
Ptarmigan	2	2	2
Accipitridae			
Hawks, Eagles	4	4	1
Falconidae			
Falcons	3	3	2
Gruidae			
Cranes	2	2	0
Strigidae			
Owls	2	1	1
Corvidae			
Ravens, Crows	2	2	1
Alaudidae			
Larks	1	1	1
Phylloscopidae			
Warblers	2	2	0
Turdidae			
Thrushes, Robin, Ouzel	4	4	0
Muscicapidae			
Chats, Old World Flycatchers	2	2	1
Cinclidae			
Dippers	1	1	0
Motacillidae			
Pipits and Wagtails	8	8	3
Fringillidae			
Finches	3	3	1
Parulidae			
New World Warblers	2	2	0
Emberizidae			

(Continued)

Table 1 Arctic bird species.—cont'd

Group	No. of species	Low Arctic species	High Arctic species
New World Sparrows, Buntings	6	6	0
Calciariidae			
Larkspurs, Snow Bunting	4	4	2
Total numbers for landbirds	48	47	15
Overall total	189	186	85

Data from Ganter, B., Gaston, A. J., Anker-Nilssen, T., Blancher, P., Boertman, P., et al. (2013). Birds (Chapter 4). In: Møller, H., Josefson, A. B., Payer, D. (eds.) *Arctic biodiversity assessment, 2013. Status and trends in Arctic biodiversity*. Tromsø, Norway: Arctic Council.

Only about one-quarter of the Arctic terrestrial mammals are found in the High Arctic. Of these only the Wrangel Island collared lemming is restricted to the High Arctic, as it is endemic to this High Arctic island off the northeast coast of Siberia. All the other High Arctic species also inhabit the Low Arctic regions.

Terrestrial vegetation

Because of the harsh climates and brief growing season for terrestrial vegetation, the biological productivity of Arctic landscapes is quite low. The best measure of this is Net Primary Productivity (NPP), the rate of carbon flux from the atmosphere into plants, minus the carbon they use in respiration. In low arctic tundra environments, NPP averages about 600–1000 g/m². In the high arctic polar desert, most regions have less than 50% plant cover, with NPP values of 100 g/m² or less (Gould et al., 2003). For comparison, the average NPP of boreal forest regions is 3500 g/m² and it is 2000 g/m² for temperate grasslands.

As one regional example, let us consider the high- and low-arctic vegetation of Canada, as discussed in Gould et al., 2003. The high arctic vegetation of Canada is dominated by four plant associations, called “Plant functional types.” These include (1) Crustose lichens and mosses; (2) Cushion plants and forbs (an herbaceous flowering plant other than a grass); (3) Dry grasses, mosses and cushion plants; (4) Prostrate dwarf shrubs and cryptogams (ferns, mosses, liverworts, lichens, algae, and fungi). All of these plants grow very close to the ground, thus avoiding the desiccation and tissue damage caused by wind-blown snow crystals. In contrast to the sparsity of vegetation types in the High Arctic, the tundra vegetation of the Canadian Low Arctic comprises seven different plant functional types, ranging from wet grasses and mosses in wetlands to low and tall shrubs (willow, alder, and others) and tussock tundra grasses.

Ecosystem Changes Caused by Climate Forcing

Warming of the Land

Global warming is amplified in the Arctic. Climate data show that air temperatures have risen two to three times faster than elsewhere on Earth since the 1990s (Lindsey, 2017). As shown in Fig. 9, the greatest degree of warming in 2016–17 was centered over the Arctic Ocean, where air surface temperatures were as much as 6 °C warmer than the long-term average (NOAA, 2017).



Fig. 8 Alkefjellet, Svalbard: breeding locality for more than 200,000 guillemots. Photo by Daniel Kordan, used with permission.

Table 2 List of families with five or more species of marine fishes from the Arctic Ocean and adjacent seas.

Family	Common name	No. of Arctic species
Rajidae	Skates	28
Clupeidae	Herrings	7
Microstomatidae	Pencilsmelts	8
Platyroctidae	Tubeshoulders	6
Gonostomatidae	Bristlemouths	7
Sternoptychidae	Marine hatchettfishes	5
Stomiidae	Barbeled dragonfishes	5
Paralepididae	Barracudinas	5
Myctophidae	Lanternfishes	16
Macrouridae	Grenadiers	10
Moridae	Deepsea cod	6
Phycidae	Phycid hakes	9
Gadidae	Cods	24
Syngnathidae	Pipefishes and seahorses	5
Scorpaenidae	Scorpionfishes	22
Hexagrammidae	Greenlings	5
Cottidae	Sculpins	69
Hemitriptidae	Sailfin sculpins	6
Agonidae	Poachers	17
Psychrolutidae	Fathead sculpins	11
Cyclopteridae	Lumpfishes	17
Liparidae	Snailfishes	77
Labridae	Wrasses	6
Zoarcidae	Eelpouts	73
Stichaeidae	Pricklebacks	23
Anarhichadidae	Wolffishes	6
Ammodytidae	Sand lances	7
Gobiidae	Gobies	10
Scophthalmidae	Turbots	6
Pleuronectidae	Righteye flounders	31
Total from these families: 527		

Data summarized from Mecklenburg, C. W., Karamushko, O. V., Møller, P. D. R., Lynghammar, A., Christiansen, J. S. (2013). Chapter 6, Fishes. In: Mølltofte, H., Josefson, A. B., Payer, D. (eds.) *Arctic biodiversity assessment, 2013. Status and trends in Arctic biodiversity*. Tromsø: Arctic Council.

The future warming of the Arctic is a certainty. However, the pace and degree of that warming depend to a great extent on the level of greenhouse gas emissions in the coming decades. The Intergovernmental Panel on Climate Change (IPCC, 2013) Fifth Assessment Report (AR5) developed a series of possible future warming scenarios from Coupled Model Intercomparison Project Phase 5 (CMIP5) of the World Climate Research Program. These scenarios are referred to as Representative Concentration Pathways (RCPs). The Fifth Assessment by the IPCC (2013) states that the Arctic will continue to warm more rapidly than the global mean, and that the mean warming over land will be larger than over the ocean and larger than global average warming. In a recent study, Overland et al. (2019) used three sets of RCPs to predict potential future warming trends in the Arctic in the coming decades. Their primary interest was in RCP 4.5, a “middle of the road” scenario in which aggressive but not implausible mitigation leads to temperature rises somewhat above the global mitigation aim of $+2^{\circ}\text{C}$ by the end of the 21st century. This level of warming above the historic long-term average (1900–50) corresponds to GHG concentrations stabilizing near 540 ppm in the second half of the century and globally averaged air temperatures in 2100 of $+2.4 \pm 0.5^{\circ}\text{C}$. A more rigorous mitigation of atmospheric GHG levels, a low emission scenario, is termed RCP 2.6. This ambitious scenario requires both a cessation of anthropogenic GHG emissions over the next few decades and assumes negative emissions in the second half of the 21st century. RCP 2.6 produces a global warming of $\sim 1.6^{\circ}\text{C}$ for 2046–65 and stabilizes more of the Arctic cryosphere than the RCP 4.5 scenario. At the other end of the spectrum of future scenarios is a high end, “business as usual” emission scenario, RCP 8.5. This scenario assumes no measures will be taken to lower GHG emissions.

The best-case scenario (RCP 2.6) prediction for mean annual air temperatures in the Arctic is a warming of $+3.3 \pm 0.9^{\circ}\text{C}$ for the years 2050 and 2100 (Table 5). The RCP 4.5 prediction for mean annual Arctic temperatures is $+4.0 \pm 0.9^{\circ}\text{C}$ for 2050, and $+5.2 \pm 1.5^{\circ}\text{C}$ for 2100. The worst-case scenario (RCP 8.5) for mean annual Arctic temperatures is $+4.8 \pm 1.1^{\circ}\text{C}$ for 2050, and $+9.5 \pm 1.9^{\circ}\text{C}$ for 2100. Both RCP 4.5 and RCP 8.5 temperature predictions would mean extreme transformations of Arctic landscapes and biota by the end of the 21st century. The most severe warming under all three RCPs is predicted to occur during Arctic winters (Table 5). Under RCP 2.6, winter temperatures will warm $+4.7 \pm 1.1^{\circ}\text{C}$ by 2100. Under RCP 4.5, winter temperatures will warm $+7.1 \pm 2.1^{\circ}\text{C}$ by 2100, and under RCP 8.5, winters will warm by a remarkable $+13.3 \pm 2.2^{\circ}\text{C}$ by 2100.

Table 3 Marine mammals of the Arctic region.

Species	Common name	High Arctic	Low Arctic	IUCN status
Bears (Ursidae)				
<i>Ursus maritimus</i>	Polar bear	Yes	Yes	Vulnerable
Sea lions (Otariidae)				
<i>Callorhinus ursinus</i>	Northern fur seal	No	Yes	Vulnerable
<i>Eumetopias jubatus</i>	Steller's sea lion	No	Yes	Endangered
Walrus (Odobenidae)				
<i>Odobenus rosmarus</i>	Walrus	Yes	Yes	Data deficient
Seals (Phocidae)				
<i>Cystophora cristata</i>	Hooded seal	Yes	Yes	Vulnerable
<i>Erignathus barbatus</i>	Bearded seal	Yes	Yes	Least concern
<i>Halichoerus grypus</i>	Gray seal	No	Yes	Least concern
<i>Phoca largha</i>	Spotted seal	Yes	Yes	Data deficient
<i>Phoca vitulina</i>	Harbor seal	No	Yes	Least concern
<i>Phoca groenlandica</i>	Harp seal	Yes	Yes	Least concern
<i>Phoca fasciata</i>	Ribbon seal	Yes	Yes	Data deficient
<i>Pusa hispida</i>	Ringed seal	Yes	Yes	Least concern
Right Whales (Balaenidae)				
<i>Balaena mysticetus</i>	Bowhead whale	Yes	Yes	Least concern
<i>Eubalaena japonica</i>	Pacific Northern right whale			
<i>Eubalaena glacialis</i>	Atlantic Northern right whale	No	Yes	Endangered
Rorquals (Balaenopteridae)				
<i>Balaenoptera musculus</i>	Blue whales	Yes	Yes	Endangered
<i>Balaenoptera physalus</i>	Fin whales	Yes	Yes	Endangered
<i>Balaenoptera borealis</i>	Sei whales	No	Yes	Endangered
<i>Balaenoptera acutorostrata</i>	Minke whale	Yes	Yes	Least concern
<i>Megaptera novaeangliae</i>	Humpback whale	Yes	Yes	Least concern
Gray Whale (Eschrichtiidae)				
<i>Eschrichtius robustus</i>	Gray whale	Yes	Yes	Least concern
Dolphins (Delphinidae)				
<i>Orcinus orca</i>	Killer whale	Yes	Yes	Data deficient
<i>Lagenorhynchus albirostris</i>	White-beaked dolphin	Yes	Yes	Least concern
<i>Globicephala melas</i>	Long-finned pilot whale	No	Yes	Data deficient
Beluga and Narwhal (Monodontidae)				
<i>Delphinapterus leucas</i>	Beluga	Yes	Yes	Near threatened
<i>Monodon monoceros</i>	Narwhal	Yes	Yes	Near threatened
Porpoises (Phocoenidae)				
<i>Phocoena phocoena</i>	Harbor porpoise	Yes	Yes	Least concern
<i>Phocoenoides dalli</i>	Dall's porpoise	No	Yes	Least concern
Sperm Whales (Physeteridae)				
<i>Physeter catodon</i>	Sperm whale	No	Yes	Vulnerable
Beaked Whales (Ziphiidae)				
<i>Berardius bairdii</i>	Baird's beaked whale	No	Yes	Data deficient
<i>Mesoplodon stejnegeri</i>	Stejneger's beaked whale	No	Yes	Data deficient
<i>Ziphius cavirostris</i>	Cuvier's beaked whale	No	Yes	Least concern
<i>Hyperoodon ampullatus</i>	Northern bottlenose whale	Yes	Yes	Data deficient
Otters (Mustelidae)				
<i>Enhydra lutris</i>	Sea otter	No	Yes	Endangered

Data from Wilson and Reader (2005).

Aschwanden et al. (2019) used the same three RCP projections to model the response of the Greenland Ice Sheet (GIS) to future warming scenarios. Each of the RCPs yielded different patterns of ice retreat in Greenland. The least severe scenario (RCP 2.6) showed the ice retreating in the west and north, while the moderate scenario (RCP 4.5) showed ice retreat around the island, except for in the highest elevation areas. The most severe scenario (RCP 8.5), in which emissions continue to increase at their present rate, predicted the loss of more than 99% of the ice sheet by 3000. But well before the ice sheet disappears, the progressive melting of the GIS could contribute 5–33 cm to sea level by 2100. Furthermore, Aschwanden et al. (2019) report that in the next 200 years, melting at the present rate could contribute up to 160 cm to global sea level rise. This new estimate is 80 % higher than previous estimates, which forecasted up to 89 cm of sea level rise by 2100 from the melting of the GIS.

Table 4 Terrestrial mammals of the Arctic region.

Species	Common name	High Arctic	Low Arctic	Dominant biome	IUCN status
Shrews (Soricidae)					
<i>Sorex cinereus</i>	Cinereus shrew	No	Yes	Boreal	Least concern
<i>Sorex monticolus</i>	Dusky shrew	No	Yes	Boreal	Least concern
<i>Sorex hoyi</i>	Pygmy shrew	No	Yes	Boreal	Least concern
<i>Sorex tundrensis</i>	Tundra shrew	No	Yes	Boreo-Arctic	Least concern
<i>Sorex ugyunak</i>	Barren-ground shrew	No	Yes	Arctic	Least concern
<i>Sorex yukonicus</i>	Alaska tiny shrew	No	Yes	Boreal	Least concern
<i>Sorex pribilofensis</i>	Pribilof Island shrew	No	Yes	Arctic	Endangered
<i>Sorex jacksoni</i>	Saint Lawrence Island shrew	No	Yes	Arctic	Least concern
<i>Sorex araneus</i>	Common shrew	No	Yes	Boreal	Least concern
<i>Sorex caecutiens</i>	Eurasian Masked shrew	No	Yes	Boreal	Least concern
<i>Sorex portenkoi</i>	Portenkoi's shrew	No	Yes	Arctic	Data deficient
<i>Sorex minutissimus</i>	Eurasian Tiny shrew	No	Yes	Boreal	Least concern
<i>Sorex roboratus</i>	Flat-skulled shrew	No	Yes	Boreal	Least concern
Hares (Leporidae)					
<i>Lepus americanus</i>	Snowshoe hare	No	Yes	Boreal	Least concern
<i>Lepus othus</i>	Alaska hare	No	Yes	Arctic	Least concern
<i>Lepus arcticus</i>	Arctic hare	Yes	Yes	Arctic	Least concern
<i>Lepus timidus</i>	Mountain hare	Yes	Yes	Boreal	Least concern
Pikas (Ochotonidae)					
<i>Ochotona turuchanensis</i>	Turuchan pika	No	Yes	Boreal	Least concern
<i>Ochotona hyperborea</i>	Northern pika	No	Yes	Boreal	Least concern
<i>Ochotona collaris</i>	Collared pika	No	Yes	Boreal	Least concern
Squirrels (Sciuridae)					
<i>Marmota broweri</i>	Alaska marmot	No	Yes	Arctic	Least concern
<i>Marmota camtschatica</i>	Black-capped marmot	Yes	Yes	Boreal	Least concern
<i>Spermophilus parryi</i>	Arctic ground squirrel	Yes	Yes	Boreo-arctic	Least concern
Beaver (Castoridae)					
<i>Castor canadensis</i>	American beaver	No	Yes	Boreal	Least concern
Voles and lemmings (Cricetidae)					
<i>Arvicola amphibius</i>	Eurasian water Vole	No	Yes	Boreal	Least concern
<i>Alticola lemmings</i>	Lemming mountain Vole	No	Yes	Boreal	Least concern
<i>Dicrostonyx hudsonius</i>	Ungava collared Lemming	No	Yes	Arctic	Least concern
<i>Dicrostonyx nelson</i>	Nelson's collared Lemming	No	Yes	Arctic	Least concern
<i>Dicrostonyx richardsoni</i>	Richardson's collared lemming	No	Yes	Arctic	Least concern
<i>Dicrostonyx torquatus</i>	Paleartic collared lemming	Yes	Yes	Arctic	Least concern
<i>Dicrostonyx vinogradovi</i>	Wrangel Island collared lemming	Yes	No	Arctic	Data deficient
<i>Lemmus lemmus</i>	Norway lemming	No	Yes	Boreo-arctic	Least concern
<i>Lemmus trimucronatus</i>	Nearctic brown lemming	Yes	Yes	Boreo-arctic	Least concern
<i>Lemmus sibiricus</i>	Siberian brown lemming	Yes	Yes	Arctic	Least concern
<i>Microtus abbreviatus</i>	Insular vole	No	Yes	Arctic	Least concern
<i>Microtus miurus</i>	Singing vole	No	Yes	Boreo-arctic	Least concern
<i>Microtus oeconomus</i>	Tundra vole	No	Yes	Boreo-arctic	Least concern
<i>Microtus middendorffii</i>	Middendorff's vole	No	Yes	Boreal	Least concern
<i>Microtus gregalis</i>	Narrow-headed vole	No	Yes	Boreal	Least concern
<i>Microtus levis</i>	East European vole	No	Yes	Boreal	Least concern
<i>Myodes rufocanus</i>	Gray red-backed vole	No	Yes	Boreal	Least concern
<i>Myodes rutilus</i>	Northern red-backed vole	No	Yes	Boreal	Least concern
<i>Ondatra zibethicus</i>	Muskrat	No	Yes	Boreal	Least concern
Field mice (Muridae)					
<i>Apodemus sylvaticus</i>	Long-tailed field mouse	No	Yes	Boreal	Least concern
Birch Mice (Dipodidae)					
<i>Sicista betulina</i>	Northern birch mouse	No	Yes	Boreal	Least concern
Antlered ungulates (Cervidae)					
<i>Alces alces</i>	Eurasian elk	No	Yes	Boreal	Least concern
<i>Alces americanus</i>	Moose	No	Yes	Boreal	Least concern
<i>Rangifer tarandus</i>	Reindeer or Caribou	Yes	Yes	Boreo-Arctic	Least concern
Horned ungulates (Bovidae)					
<i>Ovis nivicola</i>	Snow sheep	No	Yes	Boreal	Least concern
<i>Ovis dalli</i>	Dall's sheep	No	Yes	Boreal	Least concern

(Continued)

Table 4 Terrestrial mammals of the Arctic region.—cont'd

Species	Common name	High Arctic	Low Arctic	Dominant biome	IUCN status
<i>Ovibos moschatus</i>	Muskox	Yes	Yes	Arctic	Least concern
Dogs (Canidae)					
<i>Canis lupus</i>	Gray wolf	Yes	Yes	Boreo-Arctic	Least concern
<i>Canis latrans</i>	Coyote	No	Yes	Boreal	Least concern
<i>Vulpes lagopus</i>	Arctic fox	Yes	Yes	Arctic	Least concern
<i>Vulpes vulpes</i>	Red fox	Yes	Yes	Boreal	Least concern
Bears (Ursidae)					
<i>Ursus arctos</i>	Brown bear or Grizzly bear	No	Yes	Boreo-Arctic	Least concern
<i>Ursus americanus</i>	American black bear	No	Yes	Boreal	Least concern
Cats (Felidae)					
<i>Lynx canadensis</i>	Canadian lynx	No	Yes	Boreal	Least concern
<i>Lynx lynx</i>	Eurasian lynx	No	Yes	Boreal	Least concern
Weasels (Mustelidae)					
<i>Mustela nivalis</i>	Weasel or least weasel	Yes	Yes	Boreo-Arctic	Least concern
<i>Mustela erminea</i>	Stoat, ermine, short-tailed weasel	Yes	Yes	Boreo-Arctic	Least concern
<i>Gulo gulo</i>	Wolverine	Yes	Yes	Boreo-Arctic	Least concern
<i>Neovison vison</i>	American mink	No	Yes	Boreal	Least concern
<i>Lontra canadensis</i>	North American river otter	No	Yes	Boreal	Least concern

Data from Wilson and Reader (2005).

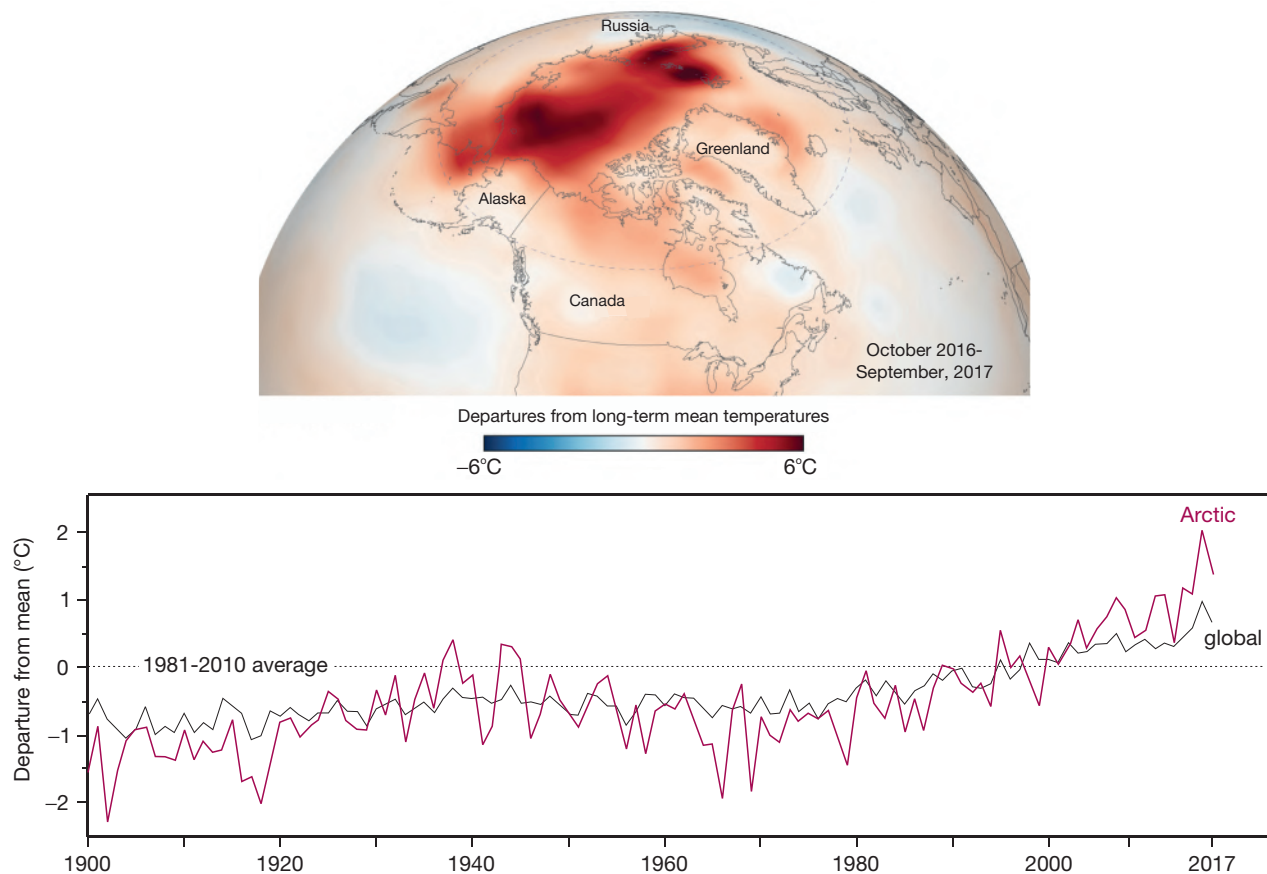


Fig. 9 Top: Heating of the Arctic region during the interval from October, 2016 to September, 2017; bottom: long term average air temperatures for the world and for the Arctic. Data and images from NOAA (2017). Arctic report card, 2017. https://arctic.noaa.gov/Portals/7/ArcticReportCard/Documents/ArcticReportCard_full_report2017.pdf.

Table 5 Predicted air temperature changes (°C) under different greenhouse gas scenarios.

	Scenario	Change
Mean annual change—global		
Year 2050	RCP 2.6	+1.4 ± 0.5
	RCP 4.5	+1.8 ± 0.3
	RCP 8.5	+2.2 ± 0.3
Year 2100	RCP 2.6	+1.5 ± 0.5
	RCP 4.5	+2.5 ± 0.5
	RCP 8.5	+4.6 ± 0.75
Mean annual change—Arctic		
Year 2050	RCP 2.6	+3.3 ± 0.9
	RCP 4.5	+4.0 ± 0.9
	RCP 8.5	+4.8 ± 1.1
Year 2100	RCP 2.6	+3.3 ± 0.9
	RCP 4.5	+5.2 ± 1.5
	RCP 8.5	+9.5 ± 1.9
Winter mean change—Arctic		
Year 2050	RCP 2.6	+4.5 ± 0.7
	RCP 4.5	+5.6 ± 1.2
	RCP 8.5	+6.6 ± 1.3
Year 2100	RCP 2.6	+4.7 ± 1.1
	RCP 4.5	+7.1 ± 2.1
	RCP 8.5	+13.3 ± 2.2

Data from Overland, J., Dunlea, E., Box, J. E., Corell, R., Forsius, M., et al. (2019). The urgency of Arctic change. *Polar Science* 21, 6–13. <https://doi.org/10.1016/j.polar.2018.11.008>.

Changes in Arctic climate will entail more than temperature rises. Eythorsson et al. (2019) used global circulation models and remote sensing observations to model future changes in Arctic climate and snow cover. Their results show that across the Arctic warmer climate classes have and will continue to replace polar tundra and cold summer regions, and that by the end of the 21st century the coverage of the most common historic Arctic climate class, cold climate with cold summers and no dry season, will decrease by about 40% (Table 6). The second most common class, Polar tundra, is expected to decrease by 34% during the same period. The authors predict that as these colder climate classes recede further north, climate classes associated with warm and hot summers will expand in coverage by 185% and 733% respectively.

Table 6 Coverage of polar and cold climate classes within the Arctic AMAP boundary and changes between 1951–60 and 2090–99.

		1951–60	2090–99	Net change
	<i>Polar climate</i>	26.4%	17.3%	–35%
	Polar ice	0.4%	0.1%	–86%
	Polar tundra	26.0%	17.2%	–34%
Cold climate	<i>Very cold winters</i>	15.9%	3.1%	–80%
	Dry winters	4.3%	0.1%	–97%
	Dry summers	11.5%	3.0%	–74%
	<i>Cold summers</i>	49.1%	43.8%	–11%
	No dry season	30.4%	18.0%	–41%
	Dry winters	2.9%	1.8%	–41%
	Dry summers	15.8	23.9%	51%
	<i>Warm summers</i>	6.6%	18.7%	185%
	No dry season	4.3%	12.9%	197%
	Dry winters	0.2%	1.2%	518%
	Dry summers	2.1%	4.6%	126%
	<i>Hot summers</i>	2.0%	16.9%	733%
	No dry season	0.9%	7.6%	770%
	Dry winters	0.5%	1.1%	125%
	Dry summers	0.7%	8.3%	1099%

Data from Eythorsson, D., Gardarsson, S. M., Ahmad, S. K., Hossain, F., Nijssen, B. (2019). Arctic climate and snow cover trends—Comparing global circulation models with remote sensing observations. *International Journal of Applied Earth Observations and Geoinformation* 80, 71–81.

Permafrost Degradation

One essential aspect of the Arctic is the interconnectedness of the land, ice and sea. Because of the almost equal balance of land and sea in the northern high latitudes, changing environmental conditions on land also affect conditions in the Arctic Ocean and adjacent seas, and vice versa. Likewise, changes in snow and ice cover affect Arctic soils and vegetation. The rise in atmospheric temperatures over Arctic landscapes has led to an unprecedented rate of melting of permanently frozen soils. These interacting responses to external forcing (i.e., global warming) cause Arctic warming to be amplified in intensity and pace (Fig. 10). Model projections by Overland et al. (2019) show a 20% decrease in Northern Hemisphere permafrost area. Permafrost currently covers an area of



Sparse vegetation of saxifrage, mosses and lichens on Elles Ringes Island, Canada



River beauty growing on bank of meltwater stream, Ellesmere Island



Arctic willow on Ellesmere Island



Tundra vegetation, Herschel Island, Yukon, 1987



Tundra vegetation, Herschel Island, Yukon, 2017

Fig. 10 Photos of Arctic vegetation. Upper left: Sparse vegetation cover on Ellef Ringnes Island, Canadian High Arctic (photo by F.J.A. Daniels); upper right: streamside vegetation on Ellesmere Island, Canadian High Arctic (photo by Paul Gierszewski); middle right: luxuriant growth of arctic willow on Ellesmere Island, Canadian High Arctic (photo by Anne Bjorkman); lower left: photo of tundra vegetation on Herschel Island, Yukon, taken in 1987; lower right: repeat photo of the same location on Herschel Island, Yukon, taken in 2017 (photos by Isla Myers-Smith). All photos used with the author's permission.

15 million km². Regardless of the RCP scenario invoked, this area will decrease to 12 million km² by 2040. Under RCP 4.5, there will be a 50% loss of permafrost area by 2080. Under RCP 2.6 and 4.5, the extent of permafrost will stabilize by the end of the century. By the year 2100, permafrost losses will range somewhere between 33% and 85% of their current area, depending on the GHG scenario.

Land Ice Losses

Glacial ice cover will also decline in the coming decades. As summarized in [Table 7](#), [Overland et al. \(2019\)](#) estimate that with a minimum of additional warming of the land and sea, even with a successful limitation of mean global warming near 2 °C, the loss of land ice will not stabilize before the end of the century. Because large bodies of ice have a great deal of thermal inertia, just to be in equilibrium with current temperatures, Arctic glaciers should lose an additional ~35% of their volume.

Changing Plant Communities

Although climate change will affect all the world's ecosystems, those of the Arctic are especially vulnerable because they are limited to the northern fringes of the continents, so they have no way to find refuge as distributions shift northwards. In keeping with the interconnectedness of Arctic environmental changes, changing vegetation patterns will in turn affect regional climates through vegetation-controlled changes in albedo, surface roughness, evapotranspiration rates, energy flux, and snow redeposition ([Gould et al., 2003](#)). With climate warming, ecosystem interactions in the Arctic are generally accelerating due to a large extent to increases in soil processes and associated increased nutrient availability for plant growth ([Klein et al., 2008](#)). Availability of soil moisture has been and will continue to be a major factor limiting plant growth in land areas of the High Arctic. [Klein et al. \(2008\)](#) studied the effects of climate warming on the vegetation of ice-free regions of northeast Greenland. Here, many species of tundra plants rely on insects for pollination. The long-established relationships between specific insect pollinators and their host plants are beginning to break down, as the seasonal timing of plant life cycles changes in response to warming are not necessarily matched by the seasonal cycles of their pollinators. The effects of climate warming that enhance conditions for plant growth in Northeast Greenland and accelerate invasion of new species are necessarily tied to the relationships between specific plant species and their insect pollinators. Accordingly, those plants that are self-pollinated may have an initial advantage in an environment where insects and their plant relationships are being altered by the changing climate.

A recent study by [Bjorkman et al. \(2018\)](#) states that rapid climate warming in the Arctic is driving changes in the structure and composition of tundra ecosystems with potentially global consequences. They point out that as much as 50% of the world's below-ground carbon stocks are held in permafrost soils, and the melting of permafrost in Arctic tundra regions is expected to contribute the majority of warming-induced soil carbon loss over the next century. Plant traits strongly affect carbon cycling and the energy balance of the ecosystem, which can in turn influence regional climates. Strong temperature- and moisture-related spatial gradients in plant species traits related to competitive ability (for example, height) and resource capture and retention (for example, leaf nitrogen and specific leaf area) reflect trade-offs in plant ecological strategy in response to either benign (warm, wet) or extreme (cold, dry) conditions. Their models predict that Arctic warming may lead to a community-level shift towards more acquisitive plant strategies in wet tundra sites, but towards more conservative strategies in drier sites as moisture becomes more limiting.

[Bonney et al. \(2018\)](#) used remote sensing to analyze trends in vegetation changes in north-central Canada from 1984 to 2016. They found that the largest positive and more significant trends in vegetation changes were associated with increased productivity in shrub-dominated environments, especially at, and north of the treeline in localities with favorable growing conditions ([Fig. 10](#)). Smaller and less significant trends in boreal forest environments south of the treeline were likely associated with long-term successional change following disturbance rather than large-scale climatic changes.

Another study of Arctic North American vegetation change in recent years was done on the North Slope of Alaska by [Duchesne et al. \(2018\)](#). Their research concluded that the abundance of tall shrubs had increased in the study region, signaling that these shrubs expanded during the period 2000–2010. They found that of the study locations that exhibited a robust change during that decade, 94% of showed a positive trend toward an increase in shrub cover.

Table 7 Predicted losses of land ice under different greenhouse gas scenarios.

	Scenario	% Ice volume loss
Year 2050	RCP 2.6	–30% ± 11%
	RCP 4.5	–30% ± 10%
	RCP 8.5	–38% ± 10%
Year 2100	RCP 2.6	–33% ± 11%
	RCP 4.5	–50% ± 8%
	RCP 8.5	–85% ± 12%

Data from Overland, J., Dunlea, E., Box, J. E., Corell, R., Forsius, M., et al. (2019). The urgency of Arctic change. *Polar Science* 21, 6–13. <https://doi.org/10.1016/j.polar.2018.11.008>.

Changes in Vertebrate Faunas

Warming Arctic climates are facilitating the northward expansion of boreal mammals into the Arctic. One example of this is reported by Rodnikova et al. (2011), who directly observed a red fox (*Vulpes vulpes*) intruding into an arctic fox (*Vulpes lagopus*) breeding den from the southern Arctic tundra of Yamal Peninsula, Russia. The range of the arctic fox has been retracting in the circumpolar tundra zone, while the red fox is expanding its range northwards into the Arctic. The ecologist's observations support the view that direct interference from red foxes on arctic fox breeding dens may be contributing to the range retraction of arctic foxes from the southern limits of the Arctic tundra in Russia. The red fox is not as well-adapted to the extremes of Arctic winters, but as Arctic winter temperatures rise, the red fox has been able to exploit higher latitudes. It is about 1/3 larger and more powerful than the arctic fox, and so out-competes it when the two species come in contact.

Another example of a possible mammalian response to Arctic climate warming concerns the polar and grizzly bears of Canada. Since 2006, eight bears have been found in the Canadian Arctic Archipelago that represent hybrids between grizzly bears (*Ursus arctos*) and polar bears (*Ursus maritimus*). All of these bears were descended from the same female polar bear (Richardson et al., 2017). DNA tests of tissues taken from these bears confirm their hybrid status. Until recently, grizzly bears have rarely been seen been far north of the coast of mainland Canada. In 1991 one or more grizzly bears were documented hunting seals along with polar bears on the sea ice near Melville Island, over 500 km from the mainland coast. Since the start of the 21st century, however, sightings of grizzlies in the Canadian Arctic Archipelago have been on the increase. Grizzly bears have apparently also been extending their range east across northern Canada in the Barren Ground tundra towards Hudson Bay.

Warming of the Seas

Summer sea surface temperatures (SST) in the Arctic Ocean are driven mainly by the amount of incoming solar radiation absorbed by the sea surface. Greater warming occurs in ice-free regions because the open water reflects little light back into space, whereas sea ice reflects a great deal of solar energy. The open ocean reflects only 6% of the incoming solar radiation and absorbs the rest, while sea ice reflects 50%–70% of the incoming energy (Timmermans and Ladd, 2018). This reflectivity is termed “albedo.” Other factors that affect Arctic Ocean SSTs include cloud cover and upper-ocean stratification. In the Barents and Chukchi seas, there is an additional source of ocean heat that comes from the advection of warm water from the North Atlantic and North Pacific oceans, respectively. Arctic SSTs are an essential indicator of the role of the ice-albedo feedback mechanism in any given melt season. As the extent of sea ice cover decreases, more incoming solar radiation is absorbed by the ocean. This forms a positive feedback loop, as the warmer ocean melts more sea ice (Fig. 11). Arctic Ocean ecosystems are greatly influenced by SST. The surface water temperature affects the timing and developmental cycles of plankton.

A report on Arctic SSTs was prepared for NOAA by Timmermans and Ladd (2018). They found that August mean SSTs have warmed significantly, beginning in 1982, for most regions of the Arctic Ocean that are ice-free in August (Fig. 11). However, this warming of SSTs has not been uniform across the Arctic Ocean and adjacent seas. The authors found that spatial patterns of August 2018 SST anomalies relative to the 1982–2010 August mean are due to regional variability in sea-ice retreat, regional air temperatures, and advection of waters from the Pacific and Atlantic oceans. For instance, they note that Northern Barents Sea August mean SSTs show significant cooling trends for 1982–2018 (Fig. 12). This SST cooling trend is attributed to sea ice conditions and ocean heat transport that are unique to this region.

Loss of sea-ice plankton communities

Post et al. (2013) reviewed the biological impacts of sea ice reduction and documented that sea ice loss represents a huge habitat reduction for sea-ice algae and phytoplankton. This habitat loss has severe consequences for the Arctic marine food chain, as these

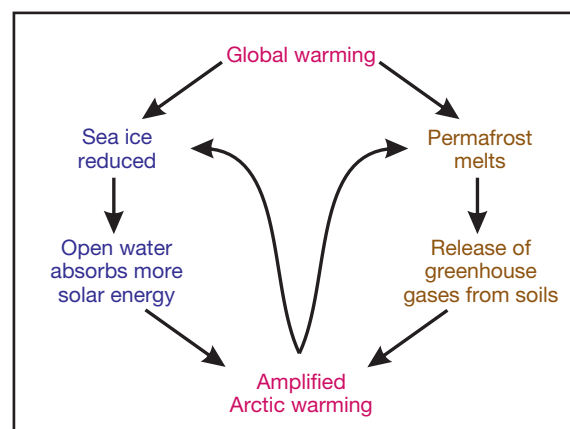


Fig. 11 Flow chart illustrating the means by which global warming is amplified in the Arctic.

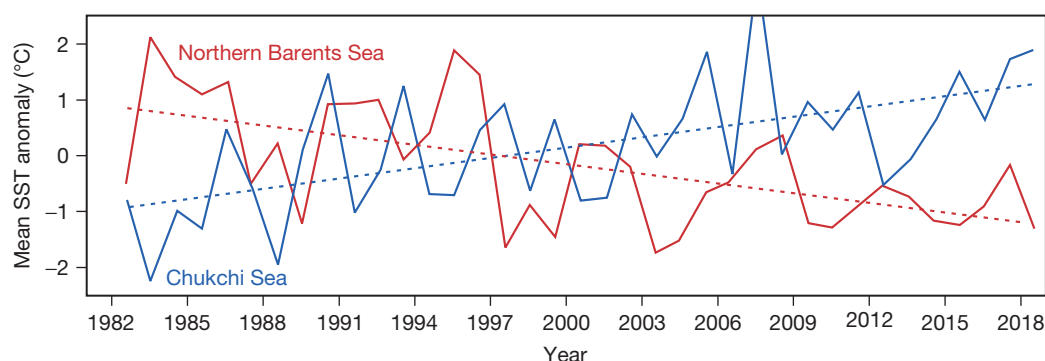


Fig. 12 Diagram illustrating mean annual and long-term trends in sea-surface temperatures in the Northern Barents Sea and the Chukchi Sea. Data from Timmermans, M. L. and Ladd, C. (2018). Arctic report card: Update for 2018. <https://arctic.noaa.gov/Report-Card/Report-Card-2018>.

phytoplankton represent 57% of the primary productivity of the Arctic Ocean. Changes in the timing of sea ice melt disrupt the seasonality of the life cycles of phytoplankton and create mismatches with the timing of zooplankton production. In the past, organic detritus frozen in sea ice was released into the water column as the ice melted in spring. This pulse of organic material was taken up by phytoplankton and zooplankton, facilitating their growth and reproduction as the days grew longer. The burst of biological productivity made its way up the food chain. The phytoplankton fed the zooplankton, which in turn fed crustaceans and small fish. Disruptions of this long-standing pattern are bound to cause breakdowns in the Arctic marine ecosystem.

Loss of sea-ice platform for marine mammals

Sea-ice forms a stable platform from which various marine mammals operate in the winter months. Walrus use the pack ice as a platform for pupping and sea-floor foraging, as do Arctic seals. The Arctic supports a particularly rich diversity of seal species. Probably the most threatened species is the ribbon seal, which lives on the outermost edges of sea ice, near deep water. These are most likely to be affected by loss of habitat as sea ice continues to shrink. Polar bears spend the winter on the pack ice, hunting seals as they come up for air in small openings in the ice. Arctic foxes often follow behind the bears, scavenging seal carcasses after the bears have abandoned them.

Shifting patterns of ocean fish stocks

The presence of sea ice has always limited commercial fishing in the Arctic Ocean. However, as sea-ice declines, commercial fisheries will undoubtedly expand in the Arctic, diminishing fish stocks in the Arctic Ocean. As has been seen in the North Atlantic and other over-fished regions, diminished stocks of predatory fish such as cod alter food-web dynamics. Such changes in food supply will also add extra stress to fish-feeding marine mammals in Arctic waters, such as seals and sea lions.

Impacts of warming seas on marine mammals

There are a number of negative impacts on marine wildlife, due to interacting effects of temperature changes near the shore (Post et al., 2013). In recent years, walrus have been forced to haul out onto the shore for greater periods of time, because activities such as calving that used to take place on sea ice have now shifted to the land. Available hauling-out localities become crowded (Fig. 13), increasing the spread of disease, causing battles between bulls, and contributing to infant mortality. The loss of sea ice also limits the number of days per year that polar bears can hunt seals, and makes their migration between land and sea more difficult. The bears are forced to wait many weeks for the sea ice to form in the autumn, during which time they eat very little. All of these obstacles to hunting reduce their overall fitness. A recent study has shown that the polar bears of the Hudson Bay region of Canada now spend an average of nearly 30 days longer on land than they did 30 years ago. Stirling and Derocher (2012) found that these bears lose nearly 1 kg of body weight each day they're on land, so by the time they return to the sea ice, they will have lost an average of 27 kg, compared with the bears of 30 years ago.

Ecosystem Changes Caused by Regional and Exotic Sources of Pollution

Pollution From Arctic Sources

Since the latter half of the 20th century, Russian companies developed mineral mining, ore smelting and petroleum extraction in their Arctic regions. Since the 1970s, American companies developed the Prudhoe Bay oil field on the Beaufort Sea coast of Alaska.

Local sources (Russian industry in Kola Peninsula and W Siberia)

Mining is the basis of the Kola Peninsula's economy. The Severonikel copper–nickel industrial complex on the Kola Peninsula is one of the largest active sources of SO₂ and heavy metals in northern Europe. A study of soil contamination by heavy metals done by



Fig. 13 Walrus fighting for space on Svalbard. Photo by Daniel Kordan, used with permission.

Kashulina (2017) showed that the current concentrations of Ni and Cu in the upper organic soil horizons in the impact zone reach extreme levels of 9000 and 6000 mg/kg, respectively. The level of copper and cobalt contamination in the soils near the industry exceeds safe background levels by several times. The level of nickel contamination is more than a thousand times the safe background level.

Oil production in Arctic Russia focuses on western Siberia, where 68% of Russian gas and oil extraction take place. The biggest of these fossil fuel production sites are in the Ob River basin, where 300 oil fields have pumped 65 billion barrels of oil since 1965. The Russian government estimates that at least 5% of the oil recovered from western Siberian wells has been spilled onto the tundra since the 1960s. This amounts to 3 billion barrels of oil spilled in the Ob River and adjacent basins. A report by Salmina (2010), a regional ecologist, states that there is no fish life in the Ob, Nadym, Pur, and Sob rivers because of pollution from oil production. The ground water in the oil field regions is so polluted that the petroleum companies must import all drinking water from elsewhere.

Drilling on the Alaskan North Slope has not resulted in any significant oil spills on the tundra. However, a major oil spill did occur near the terminus of the pipeline built to transport the North Slope oil to the southern Alaskan port of Valdez. In March, 1989, a catastrophic oil spill occurred in Prince William Sound, Alaska. The *Exxon Valdez*, an oil tanker bound for Long Beach, California, struck a reef close to shore in Prince William Sound and spilled 37,000 metric tons of crude oil over the next few days. The oil eventually contaminated 2100 km Alaskan of coastline, of which 320 km were heavily or moderately affected. Despite the extensive cleanup attempts, less than 10% of the oil was ever recovered. The immediate effects of the spill included the deaths of as many as 250,000 seabirds, at least 2800 sea otters, approximately 12 river otters, 300 harbor seals, 247 bald eagles, and 22 orcas, and an unknown number of salmon and herring.

Long-distance transport of aerial pollutants

For the past half-century, air pollution from exotic sources has been acidifying arctic lakes, even though the source of pollution is thousands of km to the south. Such changes are probably linked to multiple factors, including air pollution, warming temperatures, and increased levels of ultra-violet radiation. Within the Arctic there has been minimal direct production and use of industrial contaminants like persistent organic pollutants (POPs) and mercury (Hg). However, POPs are carried into the Arctic from more southerly latitudes via long-range atmospheric transport as well as via ocean currents and rivers.

Effects of global warming on Arctic pollutants

A warming Arctic will likely release previously sequestered mercury from permafrost, glaciers, ice and snowpack. Warmer temperatures will also alter what happens to this newly-released mercury, such as its transfer between air, ocean and terrestrial compartments, as well as altering mercury atmospheric chemistry and geochemistry (Foster et al., 2019). Increased shipping through the Northwest Passage will introduce local sources of anthropogenic mercury. Foster et al. (2019) did a meta-analysis of 83 time series datasets, and found no consistent temporal trend in mercury pollution levels over the past 30 years. However, they did find

a longitudinal gradient in the data, with mercury decreasing from west to east (i.e., Canadian/Greenland to North Atlantic/European Arctic). Mercury is a potent neurotoxin that causes physiological, neurological, behavioral, and reproductive harm to wildlife, including seabirds. Mercury readily biomagnifies, resulting in increasing concentrations as it moves up the food chain. Because these birds are relatively high up on the food chain, they are subject to higher levels of contamination.

While the levels of POPs have been declining in the Arctic in recent years, global warming may at least temporarily reverse that trend. This is because increasing temperatures provide the necessary thermodynamic forcing to drive POPs out of reservoirs, such as soil, vegetation, water and ice, and into the atmosphere where they can be transported by winds, eventually reaching locations where lower temperatures prevail, such as the Polar Regions (Ma et al., 2016). The major environmental concern with POPs is their toxicity. At high enough levels of exposure, POPs have been shown to cause endocrine disruption, reproductive and immune dysfunction, neurobehavioral and developmental disorders, and cancer.

Effects of air pollution on terrestrial ecosystems

Dietz et al. (2019) reviewed the toxic effects of environmental contaminants that accumulate in fatty tissues of Arctic animals. These lipophilic contaminants, such as POPs and methylmercury (MeHg) bioaccumulate in Arctic organisms and biomagnify through Arctic food webs, generating concern for the health of exposed wildlife and for indigenous populations that consume the meat of these animals as part of their traditional diet. The harmful effects of many POPs, largely comprised of chlorinated, brominated and/or fluorinated organo-halogenated compounds (OHCs), on human and environmental health have long been recognized.

Chemicals and heavy metals are not the only aerial pollutants affecting Arctic flora and fauna. Burger and Lichtscheidl (2019) examined the impacts of radioactive strontium contamination in Arctic ecosystems. Much of the strontium emissions in the Arctic stem from nuclear reactor waste and from above-ground nuclear testing done in the latter half of the 20th century. Strontium particles are dispersed throughout the global atmosphere, along with other radionuclide species. Analysis of radionuclides that are deposited on Arctic tundra vegetation has shown that 65% of these radioactive particles, including Sr-90, accumulate in the top three cm of vegetation cover (especially noted on tundra lichen cover). It also accumulates in the uppermost layers of soils, from whence it migrates into plant tissues. Once deposited, Sr-90 is consumed by herbivores, including caribou and muskox. From there it passes up the food chain to human hunters of these animals. Exposure to Sr-90 increases the risk for several diseases including bone cancer, cancer of the soft tissue near the bone, and leukemia.

Pollution in the Arctic Ocean and Adjacent Seas

Pollution of Arctic Ocean waters used to be caused almost exclusively by long-distance transport of pollutants via ocean currents or from rivers draining into the Arctic Basin. As Arctic sea ice is becoming less of a threat to shipping and offshore petroleum drilling, local pollution is in the process of becoming a serious problem in Arctic waters.

Local sources

Increased human access to the Arctic Ocean will enable the development of new oil and gas fields on the continental shelves surrounding the Arctic Ocean. Drilling of new offshore oil and gas wells is already being planned in these waters, as sea ice retreats. Such activities will alter habitats, pollute the water, and disturb marine life. Of particular note is the disturbance of the region's rich marine mammal fauna. Offshore oil and gas facilities will disturb marine mammals through noise from seismic surveys, shipping, and drilling. Vergeynst et al. (2018) have reviewed the process of biodegradation of spilled oil in Arctic waters near Greenland. They point out that the new economic developments such as shipping and oil exploitation bring with them increased risks of marine oil spills. In warmer ocean waters, microorganisms play a key role in degrading and reducing the impact of oil spills. However, in the Arctic, and in particular in pristine waters, the self-cleaning capacity and biodegradation potential of the natural microbial communities remain unknown. Some of the characteristic features of Arctic waters are low temperature, the seasonal presence of sea ice, oligotrophic (nutrient-limited) environments, poor microbial adaptation to hydrocarbon degradation, mixing of stratified water masses, and massive phytoplankton blooms and suspended sediment plumes. All of these characteristics of Arctic seawater tend to work against the biodegradation of spilled oil, whether the source of the spills is oil drilling or fuel oil accidentally released from large ships passing through the Arctic.

Chronic noise pollution is increasing in Arctic waters, producing cumulative impacts that extend beyond the continental shelf regions where these activities will take place. Already, bowhead whales have been observed to shift migratory routes in the Beaufort Sea to avoid noise from oil and gas development activities, such as drilling. If preferred habitats for breeding, calving, feeding and migration are disturbed over large areas, the overall fitness of marine mammal populations in the Arctic Ocean will decline.

Ocean transport ships are a major source of noise pollution in the ocean. The emerging tanker traffic predicted to take place in the Arctic Ocean in the coming decades will increase the impacts on marine mammals from noise pollution, but also from other disturbances, such as the release of pollutants into the water. If large ships have to rely on ice-breakers to open shipping lanes, then the ice-breaking ships also add to these disturbances, as they are known to disrupt birthing of seal pups on the ice.

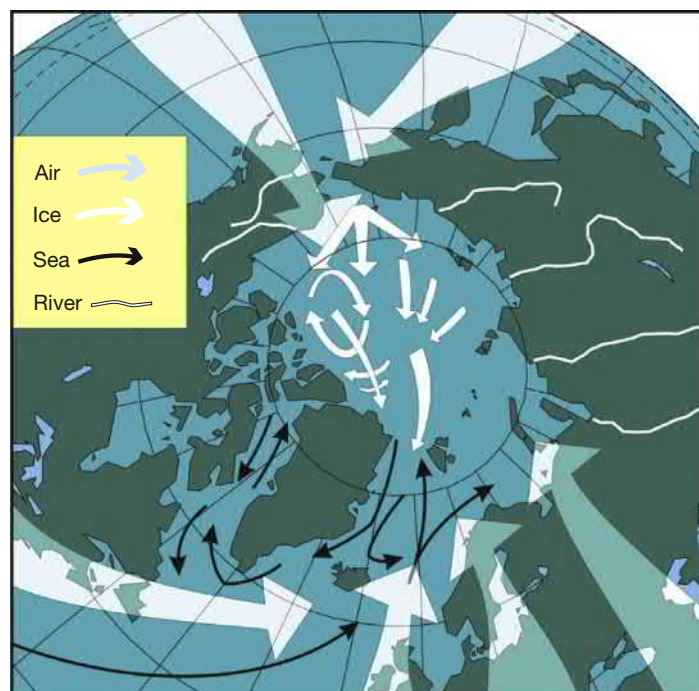


Fig. 14 Map of the Northern Hemisphere showing multiple sources of pollution entering the Arctic. After Burkow, I. C. and Kallenborn, R. (2000). Sources and transport of persistent pollutants to the Arctic. *Toxicology Letters* **112–113**, 87–92.

Long-distance transport of chemical pollutants

Burkow and Kallenborn (2000) have mapped multiple sources of pollution entering the Arctic. These pollutants arrive in the North via air currents, ocean currents, on drifting sea ice, and from rivers emptying into the Arctic basin (Fig. 14). Some toxic chemicals and heavy metals are produced either in or near to the Arctic, in Scandinavia and northern Russia. Other pollutants travel thousands of kilometers before arriving in the Arctic.

Effects of ocean pollution on Arctic ecosystems

Just as on land, POPs and methylmercury (MeHg) bioaccumulate in Arctic marine organisms and biomagnify through marine food webs. Unfortunately, POPs such as dioxins and polychlorinated biphenyl (PCB) and heavy metals such as mercury tend to accumulate in the tissues of many marine organisms, from zooplankton to fish and marine mammals. These pollutants tend to accumulate in the fatty tissues of marine mammals, so their concentrations become far higher than those found in organisms lower down the food chain. Tracing the pathways of this biomagnification up the marine food chain, Braune et al. (2005) showed that the concentrations of PCBs in zooplankton range from about 15 to 55 ng/gram of dry weight (Fig. 15, top). Beluga whales eat fish that have eaten other fish and zooplankton. The concentrations of PCBs in beluga blubber in the Canadian arctic range from about 3000 to 5000 ng/gram of blubber, a concentration about 150 times that found in zooplankton (Fig. 15, middle). Polar bears eat mainly ringed seals in these waters. The seals eat fish that have eaten other fish and zooplankton. The concentration of PCBs in polar bear fat is about 1000–2500 ng/gram of fat (Fig. 15, bottom). Dietz et al. (2019) identified quantifiable effects of POPs and mercury on the health of various Arctic marine mammals. They found that these pollutants interfere with many aspects of vertebrate physiology. In marine mammals (the best studied group), the pollutants disrupted or damaged vitamin metabolism, immune function, thyroid and steroid hormone balances, oxidative stress, tissue pathology, and reproduction capacity.

Conclusions

Environmental change in the Arctic in the 21st century is happening at a pace and an amplitude hitherto unknown in this region. Scientists are trying to keep track of the changes, and their effects on Arctic biota. Global warming from anthropogenic GHG emissions is probably having the greatest impacts on Arctic environments. Because of the intricate interactions between land, sea and ice, the global warming signal is greatly amplified in the Arctic, and all but the most stringent scenarios to reduce GHG emissions will

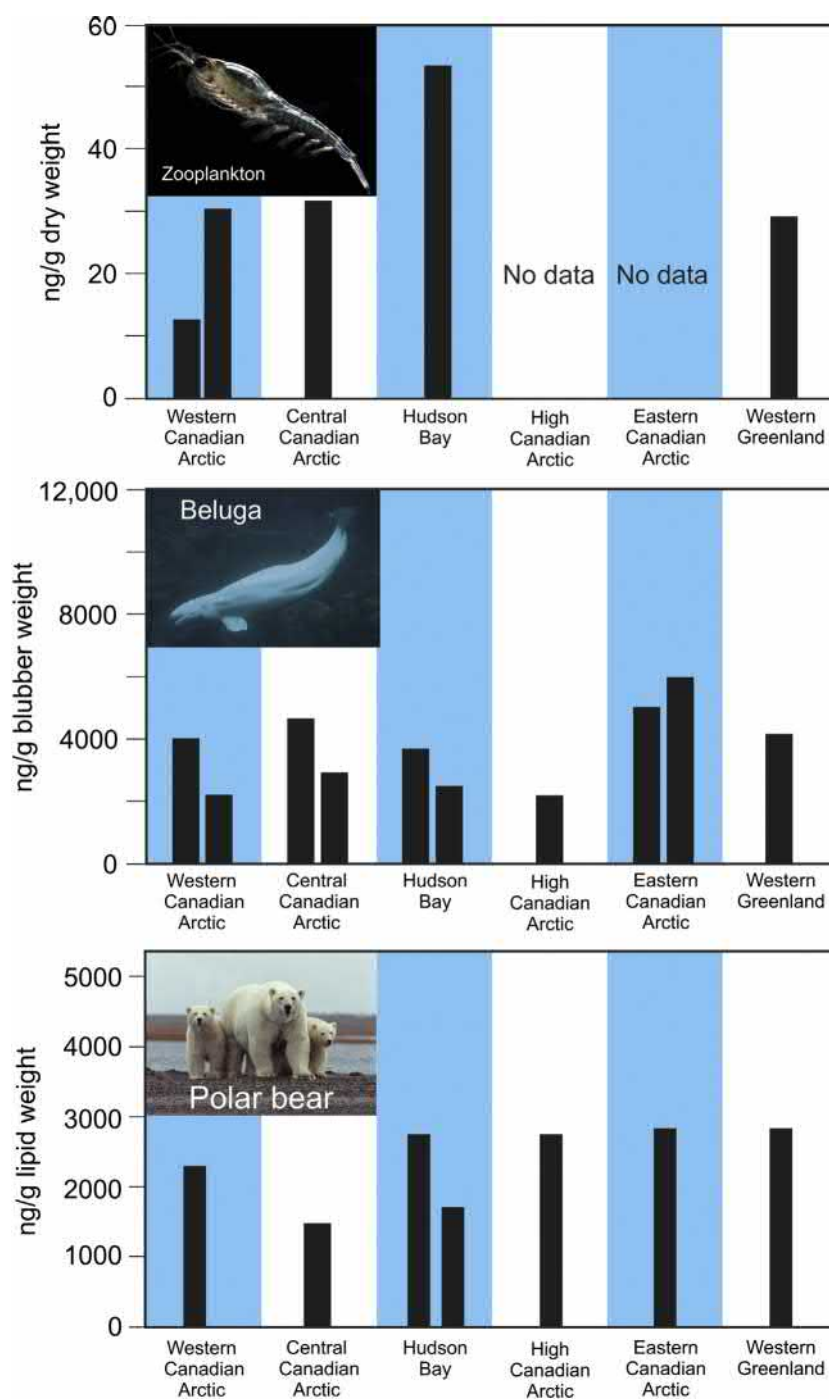


Fig. 15 Concentrations of PCBs in Arctic marine zooplankton (top), beluga blubber (middle), and polar bear fat. Data from Braune, B. M., Outridge, P. M., Fisk, A. T., Muir, D. C. G., Helm, P. A., et al. (2005). Persistent organic pollutants and mercury in marine biota of the Canadian Arctic: An overview of spatial and temporal trends. *Science of the Total Environment* **351–352**, 4–56. and Dietz, R., Letcher, R. J., Desforages, J. P., Eulaers, I., Sonne, C., et al. (2019). Current state of knowledge on biological effects from contaminants on arctic wildlife and fish. *Science of the Total Environment* **696**, <https://doi.org/10.1016/j.scitotenv.2019.133792>.

very likely lead to a complete transformation of Arctic environments. It is already clear to see that the sea ice of the Arctic Ocean and adjacent seas will be gone in a few decades at most. The 2019 sea ice minimum (Fig. 16) was the second lowest on record. No one knows just how the Arctic biota will respond to these environmental changes, but modeling efforts point to a breakdown of existing ecosystems.

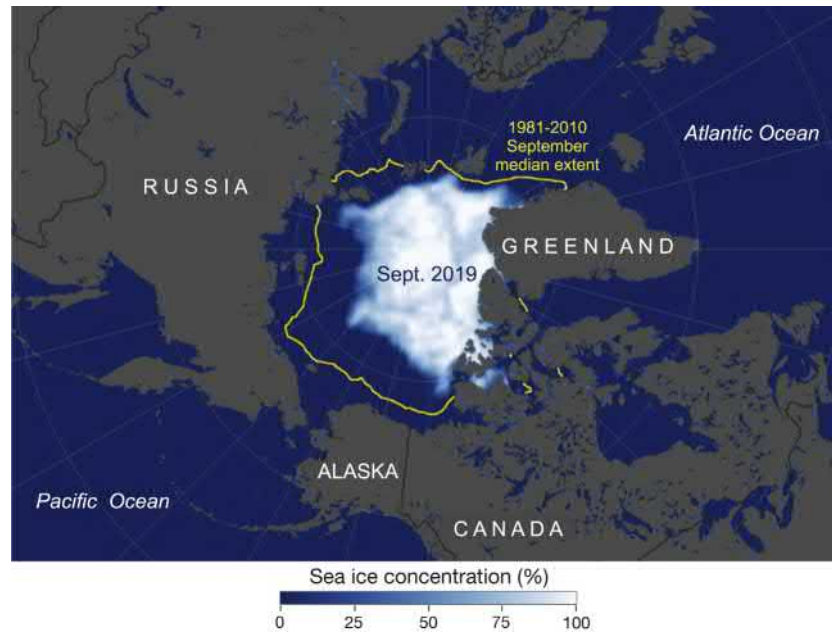


Fig. 16 Minimum (September) sea ice for 2019, compared with the long-term average (yellow line). Satellite image by NASA.

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Herbivory in Arctic Ecosystems

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Abstract

Plant-herbivore interactions are a key driver of ecosystem dynamics in arctic regions. Herbivores can influence plants, plant communities and ecosystem processes, but to which extent they do so and in which direction depends on a complex set of environmental factors. Plant-herbivore interactions in arctic environments occur under particular environmental conditions, characterized by marked seasonality, short growing seasons, low temperatures and low primary productivity. These conditions limit the ability of tundra plants to respond to herbivory and imply that herbivores require specific adaptations to cope with the highly heterogeneous plant production. Here, we provide an overview of arctic herbivores and their influences on plants, vegetation, and ecosystem processes in arctic environments, and how these interactions are likely to be altered by the rapid environmental changes happening in this region. We review current efforts and methods used to study plant-herbivore interactions in the Arctic, including recent developments related to invertebrate herbivory and managed grazing systems. Herbivory is an active topic of research in arctic environments given the potential of herbivores to counteract some of the changes associated with recent environmental changes. The field is moving forward, and the increased coordination of research efforts will allow generating more robust predictions of the consequences of the rapid ongoing environmental changes in this region.

Introduction

General ecological theory predicts that the strength of biotic interactions, including herbivory, will be weaker at higher latitudes. According to the latitudinal herbivory hypothesis (LHH), the intensity of herbivory decreases toward the poles (Coley and Barone, 1996; Pennings et al., 2009), so herbivory in arctic ecosystems is expected to be low compared to ecosystems farther south. While this might be generally true (Kozlov et al., 2015) and plant biomass consumption might be relatively low in tundra (Mosbacher et al., 2016; Barrio et al., 2017), many studies have acknowledged the importance of herbivory in these high-latitude systems (Mulder, 1999; Olofsson et al., 2012; Oksanen and Oksanen, 2000).

Herbivory is the interaction between plants and the animals that eat them. It is, in essence, a local process where an animal interacts with a plant. However, the impacts of herbivory go beyond the direct effects of consumption and can have consequences at larger spatial and temporal scales (Yu et al., 2017; Olofsson et al., 2012). Herbivores can affect plants through nonconsumptive activities that change the physical environment, like trampling, or that alter nutrient availability, for example through waste deposition (Barthelemy et al., 2018). Further, through their influence on vegetation structure and composition, herbivores can alter ecosystem processes and initiate feedbacks to the climate system (Te Beest et al., 2016). However, the impacts of herbivory are highly variable and depend on where and when the interaction takes place. The causes of this variation are not well resolved but presumably the role of herbivory is modified by ecosystem-specific conditions, including human management (Normand et al., 2017; Biuw et al., 2014), the coevolutionary history between plants and herbivores (Bryant et al., 2014), grazing history (Väisänen et al., 2014), nutrient availability (Gough et al., 2012) or variations in geological substrate (Bråthen et al., 2007). Understanding what drives this variability is critical to forecast the responses of tundra ecosystems to ongoing environmental changes.

One of the particularities of herbivory in arctic ecosystems is the environmental conditions under which this interaction takes place. Arctic ecosystems are markedly seasonal, with short growing seasons, low temperatures and low plant productivity (Jefferies

et al., 1994). Nutrient and water availability limit plant growth and the ability of tundra plants to respond to herbivory (Chapin, 1980). In turn, herbivores need specific adaptations to cope with the limited plant production and the strong seasonality. We provide an overview of arctic herbivores and their influences on plants, vegetation, and ecosystem processes in arctic environments, and how these interactions are likely to change under rapid environmental changes in this region. Most research has focused on vertebrate herbivory (mammals and birds), and these results have shaped our current understanding. The effects of invertebrate herbivory are still poorly known, and for this reason are discussed in a separate section. Finally, we review current efforts and methods used to study herbivory in the Arctic and suggest further directions for research. Overall, our intention is to expand upon two core references in arctic herbivory which focused mainly on tundra ecosystems of North America (Mulder, 1999; Jefferies et al., 1994). Specifically, we include some recent developments related to invertebrate herbivory and managed grazing systems in ecosystems around the circumpolar Arctic.

Arctic Herbivores

Herbivores in the Arctic encompass a variety of organisms, from large and small mammals and birds to invertebrates (Barrio et al., 2016a; Fig. 1). There are 73 species of vertebrate herbivores in the Arctic, with the greatest species richness associated with areas of higher primary productivity (Barrio et al., 2016a). We know less about the diversity of invertebrate herbivores, but in general, the proportion of herbivorous taxa declines toward higher latitudes (Danks, 1986). The composition of herbivore communities is an important factor determining the impacts of herbivores on vegetation, because different herbivores can have complementary effects on vegetation (Metcalfe and Olofsson, 2015; Ravolainen et al., 2014). For example, in the forest-tundra ecotone, intense summer browsing by reindeer in birch forests affected by severe moth outbreaks can slow down forest recovery by preventing the establishment of new trees (Biuw et al., 2014). Similarly, small mammals (voles and lemmings) can contribute to maintaining the distinct vegetation of historical reindeer milking grounds even decades after their use has been discontinued (Egelkraut et al., 2018a).

Herbivores in the Arctic have evolved different strategies to cope with the harsh environmental conditions and the low primary productivity, and the strategy they adopt will have important consequences to their interactions with plants (Schmidt et al., 2018). The seasonal availability of resources and the timing of life events is critical to the survival of arctic herbivores. To avoid winters, some vertebrate herbivores migrate within or outside the Arctic, others hibernate, and some others, like voles and lemmings, remain active in winter in the subnivean space (Soininen et al., 2015). Invertebrate herbivores have a number of adaptations to arctic environments, including slow growth and cold-resistant overwintering stages (Bale et al., 2002).

Productivity of arctic ecosystems is low, typically characterized by aboveground growth of less than 300 g DWT m⁻² y⁻¹ but varies greatly among habitats (Shaver and Chapin, 1991) or at even smaller spatial scales (Henry, 1998). Differences in soil moisture and snow accumulation driven by topography can create a highly heterogeneous landscape and influence plant-herbivore



Fig. 1 Arctic herbivores encompass a variety of organisms, from large (A; Svalbard reindeer *Rangifer tarandus platyrhynchus*), small mammals (B; Norwegian lemming *Lemmus lemmus*) and birds (C; rock ptarmigan *Lagopus muta*), to invertebrates (D; caterpillar of the moth *Gynaephora groenlandica*). Differences in their feeding strategies have important consequences to their interactions with plants. Photo credits: Eeva Soininen (A–C), Isabel C Barrio (D).

interactions (Kankaanpää et al., 2018). For example, the timing and distribution of snow mediate the impact of ptarmigan browsing on shrubs, with heavier browsing on branches that protrude the snowpack (Tape et al., 2010). Local topography can also influence patterns of foliar concentrations of nitrogen and phenolic compounds through its effects on snow accumulation and plant phenology, which ultimately affects the intensity of herbivory (Torp et al., 2010).

Arctic herbivores tend to be generalist in their food selection, in the sense that they can eat plants from a range of taxonomic groups (Jefferies et al., 1994), but they feed selectively and show preferences for certain species or plant groups, and between plant parts within an individual (Schmidt et al., 2018). Many invertebrate herbivores show narrower host selection at higher latitudes, probably due to a tighter phenological bond between the herbivore and its host (Hodkinson, 1997). Both forage quantity and quality are important determinants of habitat and food selection of vertebrate arctic herbivores (Iversen et al., 2014; van Der Wal et al., 2000). Selectivity in food preferences can change along the growing season following phenological changes in food quality. Herbivores tend to be more selective in their food and habitat choices early in the season when more palatable phenological stages are available (Iversen et al., 2014).

Populations of some arctic herbivores fluctuate over time, which results in temporal variation of grazing impacts on vegetation. For instance, the population cycles of voles and lemmings drive synchronous fluctuations in plant biomass (Olofsson et al., 2012), and periodic outbreaks of geometrid moths can cause vegetation shifts in the tundra-forest ecotone (Jepsen et al., 2008). Population cycles of vertebrate herbivores have been extensively studied in boreal and arctic ecosystems because of their influence on ecosystem functioning (Ims et al., 2008; Ims and Fuglei, 2005). The expected dampening of population cycles under climate warming will likely have important consequences to the functioning of arctic ecosystems (Box 1).

Responses of Tundra Plants to Herbivory

Herbivores influence plant performance by removing plant biomass, altering resource availability and changing the physical environment (Mulder, 1999). It has been hypothesized that herbivore effects in arctic environments, where abiotic factors are the main drivers of plant community structure, occur through the influence of herbivores on abiotic factors (Mulder, 1999), as changed abiotic conditions can affect the competitive ability of different plant species (van der Wal and Brooker, 2004). The influence of herbivores on plants depends on many factors, including resource availability, levels of competition and timing of biomass removal. For example, deciduous shrubs invest in leaf production earlier in the season so they are more sensitive to spring herbivory (Chapin, 1980). Moderate grazing by geese early in the season increased net aboveground primary production of the grass *Puccinellia phryganodes*, but the ability of swards to recover from the effects of grazing decreased over the course of the summer (Hik and Jefferies, 1990). However, throughout the season, the deposition of goose droppings on grazed swards (and associated nutrient recycling) contributed to the rapid regrowth of grazed plants (see below).

Responses to Biomass Removal

Tundra plants can be divided into functional groups depending on the traits that control their response to environmental change and herbivory (Chapin et al., 1996). These functional groups correspond broadly with growth forms, and are defined by their growth rates and woodiness (Chapin et al., 1996). Graminoids, and to a lesser extent deciduous shrubs, recover more easily from herbivory because they usually have large belowground reserves, and higher rates of photosynthesis, leaf turnover and nutrient absorption (Chapin, 1980). Tundra sedges and rushes, like most graminoids, are well adapted to herbivory and respond to defoliation by rapid regrowth of leaves (Henry, 1998; Bråthen and Odsasz-Albrigtson, 2000; Jónsdóttir, 1991). Woody species are generally less able to respond positively to herbivory than graminoids, but some deciduous shrubs like willows can compensate moderate levels of browsing by producing longer shoots and more buds (Christie et al., 2014). Evergreen shrubs are generally less preferred by vertebrate herbivores (Christie et al., 2015) but can be vulnerable to trampling and browsing where animals are at high densities.

Herbivores can influence plant population dynamics by altering flower or seed production (Cooper and Wookey, 2003; Kuijper et al., 2006), by consuming seedlings (Egelkraut et al., 2018a; Ravolainen et al., 2014) or by altering the availability of microsites for seed germination. For example, browsing by ptarmigan and moose on distal axillary buds that would become catkins interferes with

Box 1 Dampening of small rodent cycles

Climate forcing seems to be the general underlying cause of the collapse of population cycles of many species over the last decades (Ims et al., 2008). Winter weather and snow conditions affect the dynamics of small rodents through changes in the quality and availability of subnivean space (Kausrud et al., 2008) that provides small rodents with shelter from predators, thermal insulation, and access to food. Some species of rodents, like lemmings, are more sensitive than others to climate variation (Ims et al., 2011), but cycles are determined by complex interactions. The collapse of population cycles will have severe consequences to the functioning of arctic ecosystems through the disruption of pulses in the flow of resources (Ims et al., 2008). Dampening of the population cycles of small rodents are reflected in dramatic declines in northern predators (Schmidt et al., 2012; Gilg et al., 2009) and changes in vegetation (Rydgren et al., 2007; Olofsson et al., 2012). The magnitude of these trophic cascades however, is context specific and will depend for example on the food web structure at a given site (Schmidt et al., 2012).

sexual reproduction of felleaf willow (*Salix alaxensis*) (Christie et al., 2014), and continuous grazing by reindeer (Cooper, 2006; González et al., 2010) and geese (Kuijper et al., 2006) can deplete seed and propagule banks in many tundra sites.

Responses to Altered Nutrient Availability

Given the limited availability of nutrients in arctic ecosystems, plant-herbivore interactions in northern latitudes are driven by nutritional pulses (Jefferies et al., 1994). Under some circumstances, plants can respond to defoliation with rapid regrowth (Jefferies et al., 1994), resulting in an increase in quality, quantity or accessibility of food, which in turn influence the population dynamics of both plants and herbivores (Person et al., 2003). These areas are called grazing lawns (McNaughton, 1984; Fig. 2), or their equivalent in browsing systems, browsing hedges (Christie et al., 2014). The mechanisms that allow these responses include fertilization via feces and urine (van der Wal et al., 2004; Hik and Jefferies, 1990), and changes to plant physiology and development that facilitate compensatory growth (McNaughton, 1983). These high-quality foraging areas are maintained by repeated grazing and have a greater carrying capacity than nongrazed areas (Jefferies et al., 1994; van der Wal, 2006). Some examples of the creation of these grazing lawns in northern ecosystems are *Carex* swards grazed heavily by Black Brant geese (*Branta bernicla*) in Alaska (Person et al., 2003), tundra vegetation grazed by brown lemmings (*Lemmus trimucronatus*) in northern Alaska (Johnson et al., 2011), graminoid-dominated mires used by muskoxen (*Ovibos moschatus*) in Greenland (Falk et al., 2015) and graminoid dominated vegetation grazed by high densities of reindeer in Fennoscandia (Olofsson et al., 2004) (Fig. 2).

Herbivores can thus cause profound changes in the structure and functioning of plant communities (Johnson et al., 2011). For example, reindeer can drive vegetation shifts from moss- or shrub-dominated tundra to graminoid-dominated vegetation (van der Wal, 2006). These shifts in vegetation are dramatic and relatively sudden, and have been linked to the large-scale transition from grass-dominated steppe to moss dominated tundra in Beringian ecosystems at the end of the Pleistocene following the extinction of megaherbivores (Zimov et al., 1995). A contemporary example of these vegetation shifts are the historical reindeer milking grounds, where semi-domesticated reindeer were gathered. These swards can persist long after discontinuation of their use, effectively functioning as alternative stable states (Egelkraut et al., 2018a) and can be maintained by plant-soil feedbacks (Egelkraut et al., 2018b). In these systems, plant-herbivore interactions are strongly dependent on high rates of nutrient turnover via positive feedback processes, that can result in intense foraging by the herbivores (Jefferies et al., 1994).

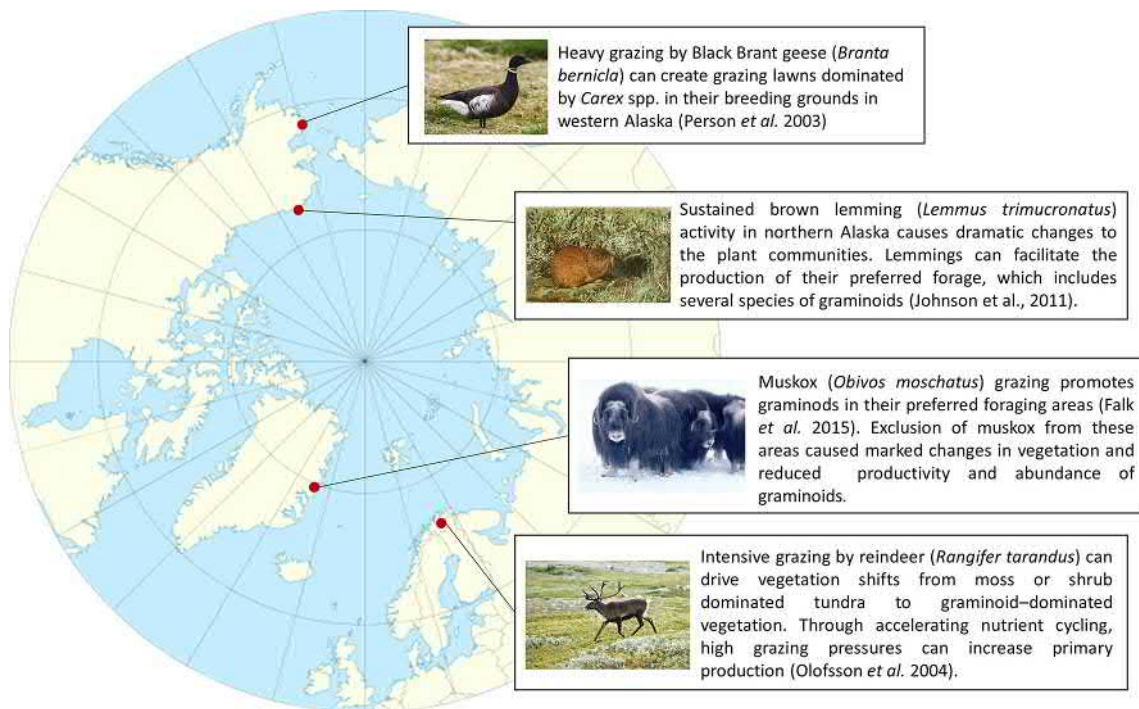


Fig. 2 Arctic herbivores induce changes in vegetation. Under some circumstances, fertilization through feces and urine together with repeated grazing that stimulates plant re-growth can maintain high-quality foraging areas. These grazing lawns are dominated by grazing-tolerant species with high nutrient concentrations and can support a higher density of herbivores than nongrazed vegetation. Four examples are illustrated, but grazing lawns are very common across the arctic region. Photo credits: Black Brant geese—Ómar Runólfsson; Brown lemming—National Geographic Society; Muskox—US Fish and Wildlife Service; Reindeer—Alexander Buisse.

Responses to Altered Physical Environment

As well, herbivores can cause changes in community and ecosystem functioning as a result of altering physical conditions. Trampling by reindeer and geese compacts the moss layer, resulting in increased summer soil temperatures that, together with grazing and fecal deposition promote the productivity and expansion of graminoids (van der Wal et al., 2004). Trampling can also affect the competitive abilities of plants, favoring plants that are less sensitive to trampling (Jónsdóttir, 1991). Other physical disturbances, such as belowground feeding by geese (grubbing) affect plant communities differently depending on their intensity and extent; the recovery after disturbance depends on initial biotic and abiotic properties of the community (Speed et al., 2010a,b). Indeed, some heavily grazed communities may undergo a complete change in their equilibrium state and never recover (Jefferies et al., 2006).

Effects of Herbivory on Ecosystem Processes in the Arctic

The effects of herbivory in arctic ecosystems extend beyond changes in the structure and composition of vegetation. For example, herbivores can alter nitrogen and carbon cycling and net ecosystem productivity. Further, through changes in the structure of vegetation, herbivores can influence the energy balance of tundra ecosystems, with consequences to global climate feedbacks (Cohen et al., 2013; Te Beest et al., 2016).

Effects of Herbivores on Nutrient Cycling

Herbivores can influence nutrient cycling of arctic ecosystems directly through waste and urine deposition (Barthelemy et al., 2018; Hik and Jefferies, 1990; van der Wal et al., 2004), or indirectly through changes in plant litter quality and degradability (Olofsson and Oksanen, 2002), or through changes in soil microbial activity. For example, increased soil temperatures in trampled areas can enhance microbial decomposition processes (Olofsson et al., 2004). Herbivores can either accelerate or decelerate nutrient cycling. It is generally assumed that herbivores increase N availability and enhance primary production in nutrient-rich environments, while they have negative effects on nutrient cycling in nutrient-poor environments. However, these patterns do not always hold (Sitters et al., 2017; Stark et al., 2015a,b) and might be masked through the transport of nutrients across the landscape by herbivores from more to less fertile sites (Stark et al., 2015a,b). For example, muskoxen in Greenland forage mainly in graminoid dominated areas and use snowbed habitats for resting, which results in a net nutrient transfer from nitrogen-rich to nitrogen-poor habitats (Mosbacher et al., 2016).

Herbivores can also influence carbon (C) balance in arctic ecosystems (Falk et al., 2015; Sjögersten et al., 2008). Atmospheric CO₂ is fixed by plants through photosynthesis, so consumption of photosynthetic tissue by herbivores can suppress C uptake. As well, other changes brought about by herbivores, like altered plant C allocation, soil processes and changes in the structure and composition of plant communities, can influence C balance in tundra ecosystems (Cahoon et al., 2012; Väisänen et al., 2014; Metcalfe and Olofsson, 2015; Falk et al., 2015; Yläne et al., 2015). For example, early season belowground foraging by pink-footed geese strongly influenced net ecosystem exchange, reducing C sink strength (van der Wal et al., 2007). Similarly, long-term heavy grazing by reindeer in northern Norway caused vegetation shifts toward communities dominated by graminoids, which are a weaker C sink than lightly-grazed communities dominated by dwarf shrubs (Väisänen et al., 2014). In this sense, the net C sequestration associated with the shrubification of the Arctic predicted under warming scenarios could be counteracted by herbivores (Cahoon et al., 2012).

Effects of Herbivores on Climate Feedbacks and Energy Budgets of Tundra

Large herbivores can influence the energy balance of tundra ecosystems (Te Beest et al., 2016; Cohen et al., 2013). By reducing plant height and vegetation cover, grazing can create surfaces that reflect more solar radiation into the atmosphere, that is, with higher albedo, during the growing season (Shao et al., 2017; Te Beest et al., 2016). For example, high reindeer densities in some parts of Fennoscandia have reduced shrub height and abundance (Olofsson et al., 2004). These structural shifts in vegetation increase summer albedo, resulting in lower energy absorption and an overall cooling effect (Te Beest et al., 2016), which has feedback implications onto the local climate (Shao et al., 2017).

In addition, changes in vegetation structure brought about by herbivores can also affect albedo during snowmelt (Cohen et al., 2013; Biuw et al., 2014), a period that is critical to the energy budget of tundra ecosystems. Snow is a highly reflective surface that helps keep air temperatures low by reducing the absorption of solar radiation. Taller vegetation protrudes above the snowpack, reducing its albedo and accelerating snowmelt (Cohen et al., 2013). Tall and more abundant vegetation in seasonal pastures may result in earlier snow melt and increased ground heating during the snowmelt season, relative to pastures grazed year-round (Cohen et al., 2013).

Invertebrate Herbivory in Tundra

The role of invertebrate herbivores in tundra ecosystems has received less attention than that of vertebrate herbivores, in part because their impacts are less noticeable and invertebrate herbivores are not harvested by arctic residents. The proportion of

herbivore taxa among invertebrates declines toward higher latitudes (Danks, 1986), and invertebrate herbivores are generally less abundant in tundra (Haukioja, 1981). Therefore, it has been generally assumed that the effects of invertebrate herbivores in high-latitude ecosystems are negligible (Haukioja, 1981; MacLean, 1981). However, outbreaks of invertebrate herbivores can cause dramatic losses of plant biomass in the forest-tundra ecotone (Jepsen et al., 2008; Kaukonen et al., 2013; Bjerke et al., 2014) and in some tundra ecosystems (Post and Pedersen, 2008; Lund et al., 2017). Massive defoliation during outbreaks can have large impacts on nutrient cycling of subarctic birch forests (Kaukonen et al., 2013; Parker et al., 2017) and can cause shifts from forests to open vegetation (Jepsen et al., 2013; Olofsson et al., 2013).

In contrast, background herbivory is the chronic consumption of plant biomass when invertebrates occur at low densities (Kozlov and Zvereva, 2017), and it is ubiquitous in tundra (Barrio et al., 2017). Recent estimates of the amount of plant biomass removed by invertebrate herbivores at background levels in tundra are around 1% (Kozlov et al., 2015; Barrio et al., 2017). Similarly, the contribution of invertebrate herbivores to N and C cycling in tundra is small relative to that of invertebrates involved in detritus-based food webs (Koltz et al., 2018). However, background invertebrate herbivory may still play an important ecological role. Studies from boreal forests suggest that background invertebrate herbivory can have strong effects on plant growth (Zvereva et al., 2012) and seed germination (Lundbye et al., 2012), and can influence nutrient cycling at the ecosystem level (Metcalfe et al., 2016). Background herbivory in tundra can also affect community processes, by affecting foraging choices of other herbivores (Barrio et al., 2013).

Changes associated with climate warming in arctic ecosystems will also influence invertebrate herbivores and their effects on tundra plants. The intensity of herbivory is expected to increase with warmer temperatures (Barrio et al., 2017), and this increase is predicted to be stronger at higher latitudes (Kozlov, 2008; Wolf et al., 2008). Warmer temperatures increase the intensity of invertebrate herbivory (Barrio et al., 2016; Birkemoe et al., 2016), as well as the prevalence and intensity of insect outbreaks in high latitude ecosystems (Jepsen et al., 2013). What such increases in the intensity of background invertebrate herbivory will mean for tundra plants remains to be investigated. The strong recovery of tundra plant communities following insect outbreaks in West Greenland suggests that tundra ecosystems may be well adapted and resilient to insect outbreaks (Dahl et al., 2017; Post and Pedersen, 2008). However, environmental changes can reduce the ability of plant communities to recover after outbreaks (Dahl et al., 2017).

Trends and the Future

Arctic ecosystems are changing rapidly as a result of changes in climate and in human management, and the outcomes of plant-herbivore interactions will be modulated by (or can mediate the responses to) these major external drivers of tundra ecosystems. The influence of these drivers will depend both on how their effects on plants determine resource availability and quality for herbivores, and on how their effects on herbivores affect net primary production and community composition. For example, increased primary production in response to warmer temperatures can support larger herbivore populations, which in turn can intensify herbivore pressure leading to habitat degradation and subsequent reduction of the carrying capacity (Madsen et al., 2011).

Climate Change

Arctic regions have experienced the fastest rates of warming over the past 30 years (IPCC, 2013). Arctic ecosystems are sensitive to variability in temperature (Seddon et al., 2016), and warming has been identified as one of the major causes of biodiversity loss in the Arctic (Post et al., 2009).

Changes in plant community composition and structure have been documented throughout the Arctic as a response to warming (Elmendorf et al., 2012), for example through a rapid expansion of woody shrubs (Myers-Smith et al., 2015). Interestingly, it seems that the same traits that allow fast responses of plants to warming also make them more susceptible to herbivory (Olofsson and Post, 2018). Vertebrate herbivores can reduce the encroachment of woody species onto tundra (Christie et al., 2015; Speed et al., 2012; Olofsson et al., 2009). Grazing by caribou and muskoxen can reduce the biomass of deciduous shrubs *Betula nana* and *Salix glauca* (Post and Pedersen, 2008), and similar effects have been described for small mammals in warming experiments (Kaarlejärvi et al., 2015). Models incorporating both herbivory and climate change predict that in a warmer climate, where herbivores are abundant, evergreen shrubs will have an advantage over more palatable and widely consumed deciduous shrubs (Yu et al., 2017). However, herbivores may not be able to control shrub expansion everywhere (Morrissette-Boileau et al., 2018) and regional differences are controlled by a complex set of mechanisms that depend on the identity of the shrub and herbivore species, and herbivore density (Christie et al., 2015; Bråthen et al., 2017).

Large herbivores can also buffer the destabilizing effects of warming on tundra plant communities (Post, 2013; Kaarlejärvi et al., 2017) and increase the resilience of tundra ecosystems to warming (Olsen and Klanderud, 2014; Kaarlejärvi et al., 2015). For instance, by selectively consuming certain species, herbivores can mitigate the declines in plant species richness associated with warming, and help maintain plant diversity (Kaarlejärvi et al., 2017). Similarly, other warming-related changes in tundra ecosystems, including carbon dynamics (Väisänen et al., 2014; Cahoon et al., 2012) and climate feedbacks (Cohen et al., 2013) can also be counteracted by herbivory. Thus, grazing management has been proposed as a strategy to moderate some of the effects of warming on tundra ecosystems (Biuw et al., 2014; Bråthen et al., 2017), at least locally. Intense reindeer grazing during summer can reduce ground heating during the snowmelt period (Cohen et al., 2013) and decrease latent and sensible heat fluxes during the growing

season (Te Beest et al., 2016). Similarly, a more diverse herbivore assemblage could be more effective in buffering the effects of climate change on tundra ecosystems, so there is some potential in increasing the diversity of large herbivores in arctic systems through rewilding to preserve arctic vegetation in the future (Olofsson and Post, 2018).

Increased temperatures will also affect the timing of life history events, phenology, which is a critical aspect of trophic interactions in highly seasonal environments like the Arctic. Summers in the tundra are short, so animals have a narrow time window to reproduce and rear their young. A lack of synchrony between the periods when herbivores have high demands for resources and the periods when high-quality food is available can reduce the reproductive success and recruitment of herbivores (Post and Forchhammer, 2008; Doiron et al., 2015) (Box 2). Phenological mismatches are frequent in migratory species, such as geese (Lameris et al., 2017) or caribou (Post and Forchhammer, 2008), because the timing of migration from wintering areas may not be cured by the same drivers or change to the same extent.

Human Management

Climate change alone provides an incomplete explanation for the observed changes in arctic vegetation. For instance, the changes in abundance and distribution of woody plants in the Arctic do not always coincide with recent warming trends (Myers-Smith et al., 2015). The legacies of human activities also contribute to vegetation change in the Arctic (Normand et al., 2017). In parts of Northern Fennoscandia, forest range expansion that had been attributed to climate change is now considered to be the product of regrowth after the gradual abandonment of transhumance activities (Speed et al., 2010a).

Human activities, through hunting and herding can influence herbivore pressure in the Arctic. For example, prehistoric human hunting together with changes in climate likely drove many large herbivores to extinction in the Arctic (Nogués-Bravo et al., 2013), resulting in the species-poor assemblages of large herbivores we see today (Olofsson and Post, 2018). The extinction of these megaherbivores likely contributed to vegetation changes from a graminoid dominated steppe to a higher abundance of woody species (Zimov et al., 1995; Willerslev et al., 2014). Current management policies for large-bodied herbivore populations vary across the Arctic, and this is likely to have large impacts on tundra ecosystems. For example, in Northern Fennoscandia differences in reindeer herding practices between countries, from seasonal migration to sedentary regimes, have led to distinctive differences in vegetation and ecosystem function (Box 3).

Changes in land use beyond the Arctic region can also affect plant-herbivore interactions in the Arctic. For example, the extensive use of fertilizers and other crop management activities in agricultural areas on the southern wintering grounds has contributed to a rapid increase in populations of many Arctic breeding geese (Abraham et al., 2005). These increases in herbivore populations can result in large scale destruction of vegetation (Jefferies et al., 1994). For example, pink footed geese (*Anas brachyrhynchos*) in Svalbard cause extensive soil disturbance through belowground feeding early in the season, causing a reduction of C stocks in arctic tundra (van der Wal et al., 2007). Lesser snow geese have had a similar impact on coastal salt-marshes in Hudson Bay (Jefferies et al., 2006).

Box 2 Migratory geese and trophic mismatch in the Arctic

Warming has been associated with a rapid advancement of the onset of spring in terrestrial Arctic ecosystems (Høye et al., 2007; Post et al., 2009) and earlier plant phenology (Prevéy et al., 2017), but herbivores may not be able to adjust their breeding phenology to compensate these changes in the timing of high-quality food plants (Doiron et al., 2015). Increasing temperatures in the Arctic, with warmer springs and earlier snowmelt, will advance and shorten the peak of nitrogen-rich forage at the breeding grounds (Doiron et al., 2015; Lameris et al., 2017). However, phenology will not advance simultaneously in the Arctic and in the temperate regions along their migratory flyway. Led by environmental cues at their wintering areas, migrating geese will arrive to their Arctic breeding grounds too late (Lameris et al., 2017). Geese are only partially able to adjust their breeding phenology to compensate for annual changes in the timing of high-quality food plants, leading to mismatches of up to 20 days between the two (Doiron et al., 2015). This combination will likely decrease goose reproductive success under climate warming by reducing growth and survival of goslings after hatching (Doiron et al., 2015).

Box 3 Herding can substantially increase grazing pressure

The effects of human management on arctic vegetation through herding of reindeer are evident in the Fennoscandian tundra. A fence was built between Finland and Norway in the 1950s to prevent reindeer crossing the state border. On the Finnish side grazing occurs year-round, while in the Norwegian side grazing is limited to some periods outside the summer, during winter or in the spring/autumn migration. Differences in management across the fence have caused large differences in vegetation: summer grazing by reindeer significantly reduces woody vegetation cover (Olofsson et al., 2009; Bråthen et al., 2017), so vegetation in summer pastures is shorter and less abundant than in winter pastures (Cohen et al., 2013). The higher herbivore pressure due to summer grazing in the Finnish side has reduced the height and abundance of willows in favor of graminoids (Kitti et al., 2009). A remote-sensing study the two sides of the fence showed that grazing-induced vegetation changes resulted in differences in albedo dynamics (Cohen et al., 2013). The shorter and sparser vegetation on the Finnish year-round pastures results in delayed snow melt, increased surface albedo and decreased ground heating during the snowmelt season (May–June), compared to Norwegian pastures.

Future Directions

Herbivory is an active field of research in arctic ecosystems, but there are still many gaps. For example, we still know relatively little about background invertebrate herbivory in tundra. Recent estimates indicate that background herbivory is ubiquitous across the tundra biome and occurs at low intensity, but is likely to increase significantly with arctic warming (Barrio et al., 2017). Similarly, changes in plant chemistry and how they will affect plant-herbivore interactions in a warmer future deserve further investigation. For example, phenolic compounds are expected to decrease with increased temperature (Stark et al., 2015a,b), but the response to warming might differ depending on what type and combination of secondary metabolites plants have (Graglia et al., 2001).

One of the main limitations in our current knowledge of arctic herbivory is the large context-dependency of the results of single-site studies (Bernes et al., 2015). Many factors can modulate how plants respond to herbivores, and how herbivores respond to altered food availability. Being able to generalize the results of herbivory studies in the North will let us generate more robust predictions of the consequences of the rapid ongoing environmental changes in this region (Soininen et al., 2018). This is particularly true for vast and remote areas like the Arctic, where difficult access usually implies unequal sampling efforts (Metcalfe et al., 2018). Coordinated research efforts and the development of theoretical frameworks can help move forward. For example, the concept of functional traits and functional groups is broadly used in arctic plant ecology (Chapin et al., 1996) and has been used for invertebrate herbivores elsewhere (Deraison et al., 2015), and could be a promising approach to generalize the effects and responses of arctic herbivores. Identifying key functional traits of herbivores that mediate their impacts on arctic ecosystem structure and function, such as body size (Legagneux et al., 2014), is thus a first step forward.

One of the challenges when studying plant-herbivore interactions is the design of studies that match sampling of two organisms that occur potentially at different scales, and the need of long term observations to detect trajectories of change in slowly responding tundra plant communities (Olofsson et al., 2013). In some sites, herbivore exclusion triggers rapid changes in vegetation (Falk et al., 2015), whereas in others a time scale of 10 years is not enough to observe a major shift in vegetation (Gough et al., 2008). However, long and short term responses can be qualitatively and quantitatively different because they can be driven by different mechanisms and processes (Väisänen et al., 2014). Similarly, increasing or decreasing herbivore densities may not lead to the same effects on vegetation (Olofsson, 2006) and aspects like the history of grazing need to be taken into account (Väisänen et al., 2014).

Different types of studies and methodologies have been used to study plant-herbivore interactions in the Arctic, ranging from observational studies quantifying signs of herbivory or herbivore activity, to experimental manipulations of herbivore densities or simulated herbivory (Soininen et al., 2018). As well, various remote-sensing techniques using satellite observations have been used to detect large-scale changes in vegetation in areas with different management (Cohen et al., 2013) or following a peak in small mammal abundance (Olofsson et al., 2012). Harmonizing research efforts will help make more robust generalizations across sites and plant-herbivore systems (Barrio et al., 2016b). International research networks, like the Herbivory Network (<http://www.herbivory.lbhi.is>) are promoting such coordinated research efforts that will ultimately improve our understanding of the role of herbivory in these systems.

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Relevant Website

<http://www.herbivory.lbi.hi.is>—Herbivory Network.

Climate of the High Arctic

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Glossary

Atmospheric boundary layer This is the lowermost level of the atmosphere where interactions with the surface strongly affect the properties of the air. In the Arctic it can range from just ten meters to several kilometers deep. It is characterized by the presence of turbulence which acts to mix the air and facilitate the exchange of particles, water and heat between the surface and atmosphere.

Surface inversion Defined as when the air close to the surface, in the lowest tens of meters, is thermally stably-stratified i.e., the air above is warmer than the air below. They typically extend from the surface up to a few tens or a couple of hundred meters.

Arctic amplification This is the phenomenon that the Arctic warms more rapidly than the global-average in response to a change in radiative forcing e.g., from the increase in concentration of greenhouse gases.

Abstract

The climate of the high Arctic is unique, and one of the most sensitive to ongoing global change. It is shaped by a strong seasonal cycle which ensures much of the land surface remains snow covered for a large part of the year. Large areas of the land are also covered in permafrost where the ground is either permanently or seasonally frozen. This defines many of the key features of the climate in the high Arctic from the seasonal cycle in air temperature to the hydrology and surface water availability. The sensitivity of the Arctic climate is not just important locally, but also to the global climate system. Many of the largest climate tipping-points that have been identified are located in the high Arctic. Two of the most important tipping points are associated with the irreversible release of carbon dioxide and methane from melting permafrost. The Paris agreement set the target of limiting global warming to less than 2°C in part because this was identified as the level of warming at which we expect these permafrost tipping points to be reached.

Essential Features of the Arctic climate

The Arctic is generally defined as the region of the globe north of the Arctic circle, which lies at approximately 66 °N. This marks the boundary at which in mid-winter the sun does not rise above the horizon, and at mid-summer the sun does not set below the horizon. The most defining feature of the Arctic climate is the strong seasonality in sunlight that reaches the surface. It is this strong seasonality in insolation (incoming solar radiation) that drives the large seasonal cycle in surface temperatures in the Arctic. In the winter the surface receives very little or no insolation and cools radiatively to space. The only source of heat is the intermittent advection of warm and moist air from the lower latitudes and from open water in the Arctic ocean. However, it is worth noting that many features that are often associated with an Arctic climate, such as the presence of permafrost, can be found far south of the Arctic circle.

Fig. 1 shows the climatologies of the annual mean, January (coldest month) and July (warmest month) surface air temperature in the Arctic. The visual separation between temperatures above and below the freezing point of water is deliberately emphasized because in the annual-mean this line indicates where there is some amount of permafrost cover. These figures clearly illustrate how Scandinavia and western Russia have much milder winters compared to the same latitude in the interior of Russia. This is due to the Gulf Stream which brings warm water to northern Europe, triggering the advection of warm, moist air across these regions. In contrast, in North-East Russia there is relatively little advection of warm air from lower latitudes and the winter air temperatures can average below −30°C. A similar pattern of a relatively warm West coast can be seen in the winter over the North American continent.

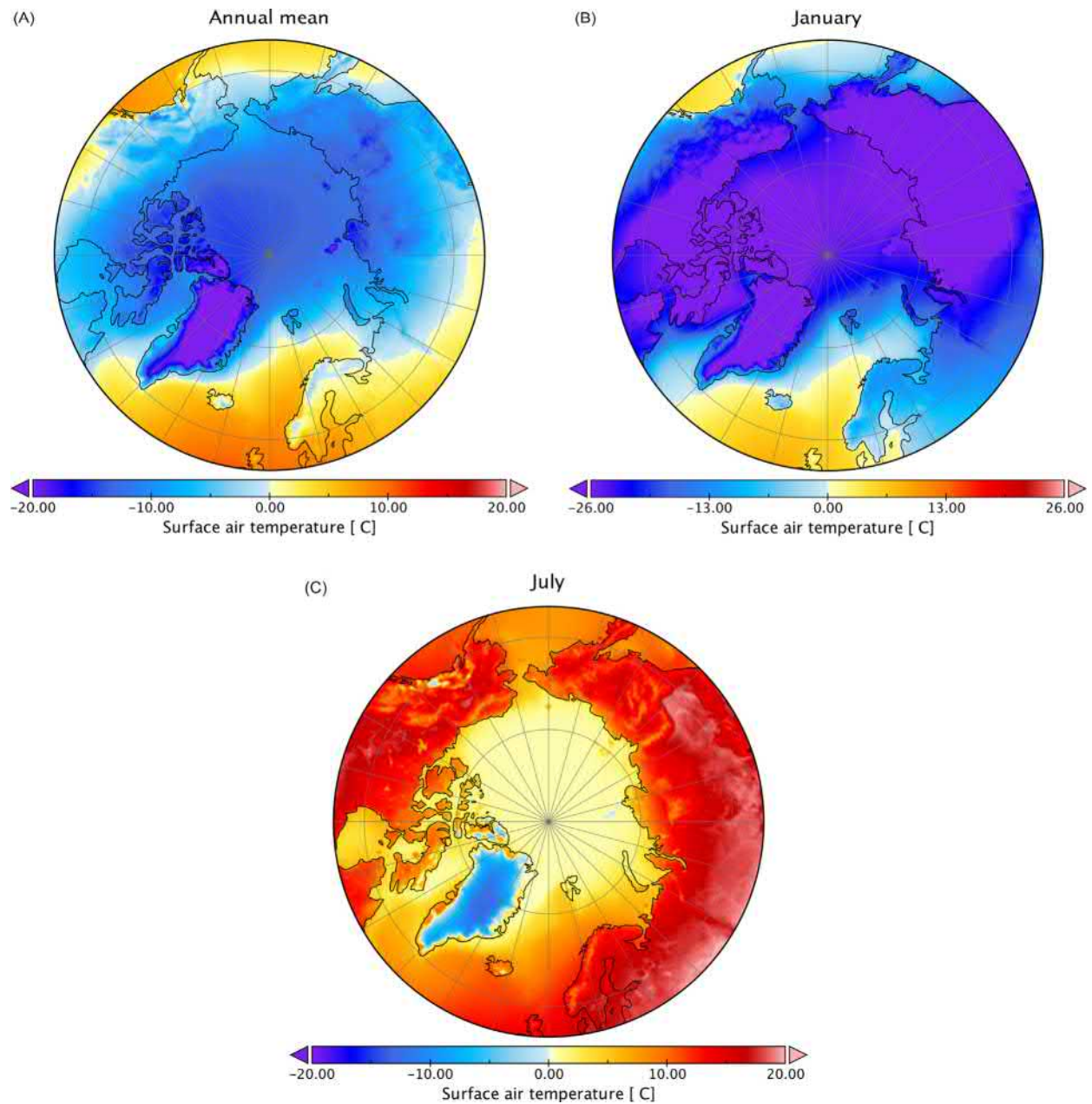


Fig. 1 The climatology of the (A) annual mean, (B) January, and (C) July surface air temperature over the period 1979–2018. Data are from the ERA5 reanalysis.

In contrast to the winter pattern, the peak summer surface air temperatures are much more homogenous across continents and are determined more by latitude (and hence the amount of solar radiation reaching the surface) and local topography than by large-scale circulation patterns.

We can see from Fig. 1 that a large part of the Arctic land surface is underlain by permafrost. Permafrost forms when the annual average temperature is below the freezing point of water (0°C) for an extended period. The characteristics of permafrost therefore define the surface climate across much of the Arctic. Permafrost is defined as ground that is frozen year-round but typically has a shallow active layer which is seasonally thawed. Below the active layer is the permafrost layer where the ground is perennially frozen. The depth of this perennially-frozen layer is limited by the geothermal gradient in the ground, whereby the temperature increases with depth, and so at some critical depth the ground becomes perennially thawed. The seasonal freezing at the surface is what allows the surface air temperature to drop to such cold temperatures in January in these regions (Fig. 1). In the very dry air of the permafrost regions the surface and air can rapidly cool.

Accompanying this seasonal cycle in surface air temperature is a large seasonal cycle in snow cover. In the winter months much of the Arctic region is covered in snow, although the depth of snow cover is highly heterogenous due to the frequency and intensity of

precipitation, local topography, and the redistribution by wind. The heterogeneity of snow cover can now be reliably obtained from satellite remote sensing products (Rittger et al., 2013). The presence of snow creates a strong intra-seasonal feedback loop on the surface air temperature (Hall, 2004). Snow has a much higher albedo than exposed ground and so a snow-covered region is slower to warm in spring than is a region of bare ground. This means that in those winters with more extensive snow cover, there tends to be a cooler spring as it takes longer for the air to warm, given the same amount of solar radiation. This is because a larger fraction of the available energy from the solar radiation goes to melting snow, rather than warming the air. This feedback can persist even once the snow has melted: as the snow melts more water is added to the soil, and a higher moisture content in the soil also reduces the amount of solar radiation that goes to warming the air.

The climate of the high Arctic is strongly affected by the presence of the Arctic Ocean and the presence of sea ice. The ocean has a much higher heat capacity than the air and the temperature of sea water never drops below -2°C . Therefore, the land surrounding the Arctic ocean is strongly constrained towards this temperature when the water is exposed, i.e., when there is no sea ice. The strong seasonal cycle in surface air temperature drives the seasonality of sea ice cover in the Arctic. But there are also strong feedbacks between the amount of sea ice cover and the surface air temperature, both within the seasonal cycle and interannually (Robock, 1980). When sea ice forms it cuts off the supply of heat from the relatively warm ocean to the colder atmosphere. This allows the atmosphere to cool even further, enhancing the growth of sea ice. These thermal feedbacks are slower in the ocean due to the much higher heat capacity of water than air, and so there is a lag between the peak surface air temperature (July) and the minimum in sea ice extent (September), and correspondingly between the minimum surface air temperature (January) and the maximum in sea ice extent (March). The climatology of the sea ice cover in the annual mean, and at the seasonal maximum and minimum are shown in Fig. 2.

An important feature of the Arctic climate is the presence of atmospheric thermal inversions close to the ground (Bradley et al., 1992; Zhang et al., 2011). These form when the surface cools radiatively to space and the near-surface air becomes cooler than the air above. This creates a stable stratification that suppresses turbulent mixing in the air as buoyancy forces act to stop the air from mixing. This stable stratification can be very strong with temperature differences of up to 5°C in the lowest ten meters of the atmosphere. Such stable stratification is referred to as a surface inversion, and these inversions are an important characteristic of the Arctic atmosphere. They are also a common feature in the Arctic. Fig. 3 shows the frequency of occurrence of these inversions and we can see they occur more than half the time inside much of the Arctic circle (Esau et al., 2012). These surface inversions lead to a high degree of spatial heterogeneity in surface temperatures with even small differences in elevation having a large effect on the surface air temperature. This makes the Arctic surface climate highly heterogeneous. The presence of surface inversions is the principle reason why the Arctic has been warming at around twice the rate of the global average; a feature referred to as Arctic amplification.

Arctic Amplification

The Arctic is a region particularly sensitive to changes in thermal or radiative forcing, for example from an increase in atmospheric greenhouse gas concentrations. In recent decades we have seen the Arctic warm at more than twice the rate of the global-average temperature (Johannessen et al., 2004; Serreze et al., 2009; Serreze and Barry, 2011). This enhanced warming in the Arctic is referred to as Arctic amplification and it is not a new phenomenon. Arctic amplification has been observed as far back as the early part of the 20th century, during the so-called “early warming period,” but the signature of Arctic amplification has also been seen in proxy records going back 1000s of years (Miller et al., 2010).

Fig. 4 shows the amplitude of Arctic amplification over the last century, as defined by the difference in the temperature anomaly in the Arctic ($>66^{\circ}\text{N}$) and in the Northern Hemisphere as a whole (Davy et al., 2018). The data are taken from two records of gridded observations, i.e. station data which has been homogenized and interpolated onto a regular grid. There were relatively few observations from inside the Arctic circle during the early 20th century, and so there is some uncertainty regarding the strength and spatial extent of this early Arctic amplification. While the early warming period was primarily driven by low frequency natural variability in the climate system (the approximately 70-year period cycle of the North Atlantic Oscillation), the current Arctic amplification is likely driven by a combination of this and other sources of natural variability and further enhanced by the buildup of greenhouse gases in the atmosphere (Bengtsson et al., 2004; Wood and Overland, 2010).

The magnitude of Arctic amplification has a strong seasonal cycle. While there is some signature of Arctic amplification in the spring and autumn seasons, it is strongest in winter (Davy et al., 2018). In comparison, during the summer the melting of sea ice keeps the surface air temperature over the ice at constant temperatures near 0°C . So even if heat is added to the system, the surface air temperature does not increase much above this value. Instead, the extra heat enhances the melting of ice. However, increases in the melting of ice have consequences for the rest of the seasonal cycle, leading to a delay in the re-freezing, or simply a reduction in the amount of ice formed in the following winter (Serreze and Francis, 2006).

There are many explanations in the literature for Arctic amplification. These include the sea ice-albedo feedback (Curry et al., 1995; Screen and Simmonds, 2010), snow-albedo feedback (Hall, 2004), atmospheric and oceanic advection, lapse-rate feedback and the presence of persistent surface temperature inversions (Pithan and Mauritsen, 2014). The sea ice-albedo feedback is caused by the much lower albedo of open water compared to that of sea ice. As the Arctic warms, the extent of sea ice is reduced, exposing more of the open water underneath to incoming solar radiation. Since the open water has a lower albedo, more solar radiation is absorbed, enhancing surface warming. While the heat stored by the absorption of solar radiation is built-up in the summer, its effects are principally seen in winter when there is the largest difference between the temperature in the ocean and in the air,

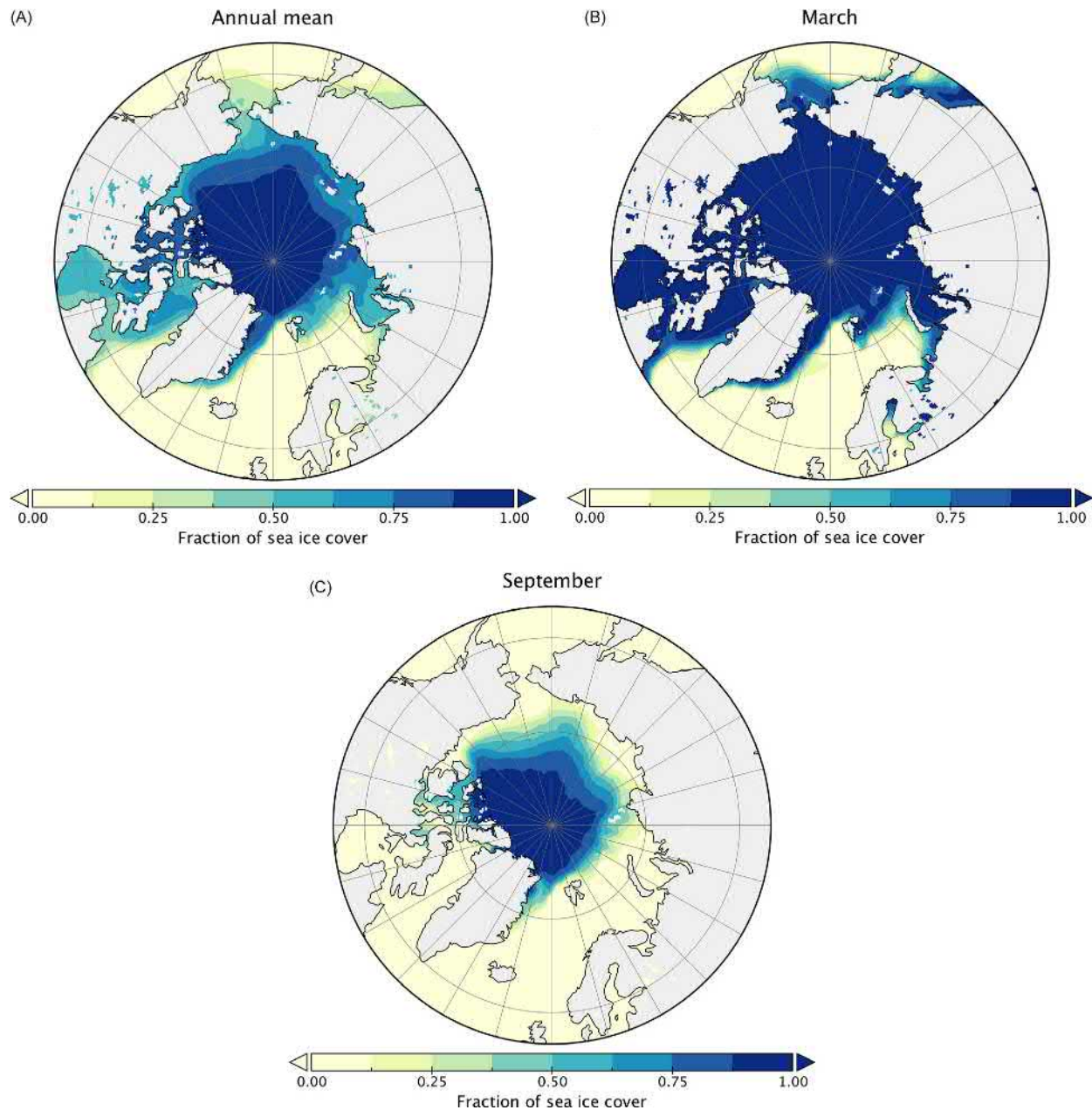


Fig. 2 The climatological mean of the fraction of sea ice cover for the (A) annual mean (B) seasonal maximum in March and (C) the seasonal minimum in September over the period 1979–2018. Data are from the ERA5 reanalysis.

and so a large amount of heat can be transferred from the ocean to the atmosphere. The snow-albedo feedback is caused by changes in the surface area of the Arctic covered in snow in winter. If the amount of snow cover in a given month slowly decreases over the years due to a general warming trend, then the lower albedo of the surface due to the reduced snow-cover results in more radiation being absorbed at the surface and hence more surface warming.

While these feedback processes play an important role in amplifying climate change in the Arctic, surface inversions in the atmosphere are the primary reason for Arctic amplification. Extra heat that gets added to the climate system at the surface, either through changes to the radiation balance or directly through thermal forcing, gets trapped in a thin layer of air close to the ground by the surface inversion. This means that heat added to the Arctic system causes a disproportionately larger change in air temperature here than in the tropics, because the extra heat is spread through a smaller volume of air (Davy and Esau, 2016).

The overall global warming trend is not just asymmetrical in space as exemplified by Arctic amplification, but also in time. Despite the overall global warming trend, there are some regions and times which have seen local cooling in recent decades due to changes in large scale atmospheric circulation patterns or other sources of natural variability. One of the most prominent examples of this is the winter time cooling trend that was observed over continental Asia from the mid-1980s through to the early

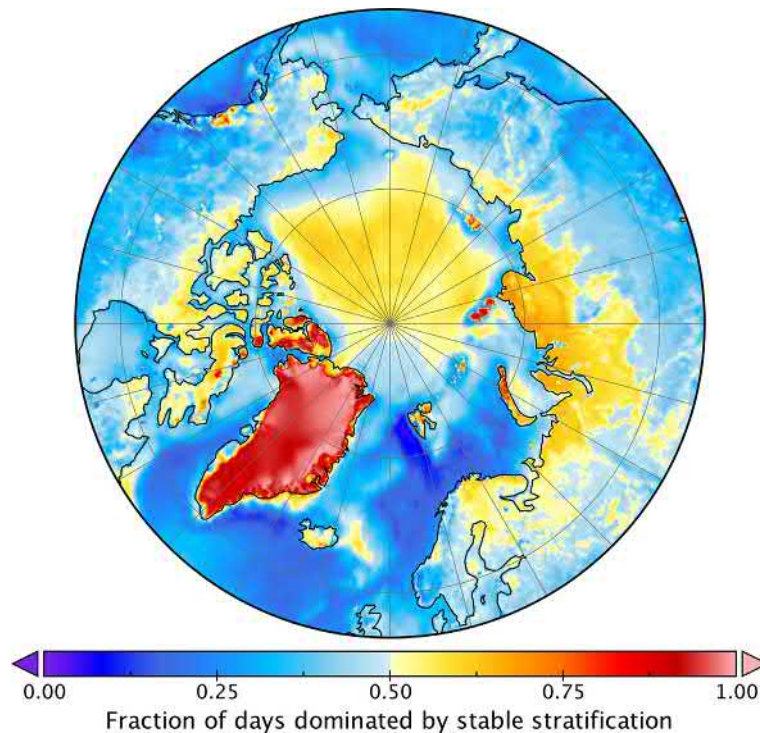


Fig. 3 The fraction of days with a surface-based inversion, defined as days with a negative average surface sensible heat flux over the period 1979–2018. Figure reproduced from Esau, I., Davy, R. and Outten, S., (2012). Complementary explanation of temperature response in the lower atmosphere. *Environmental Research Letters*, **7**(4), p.044026.

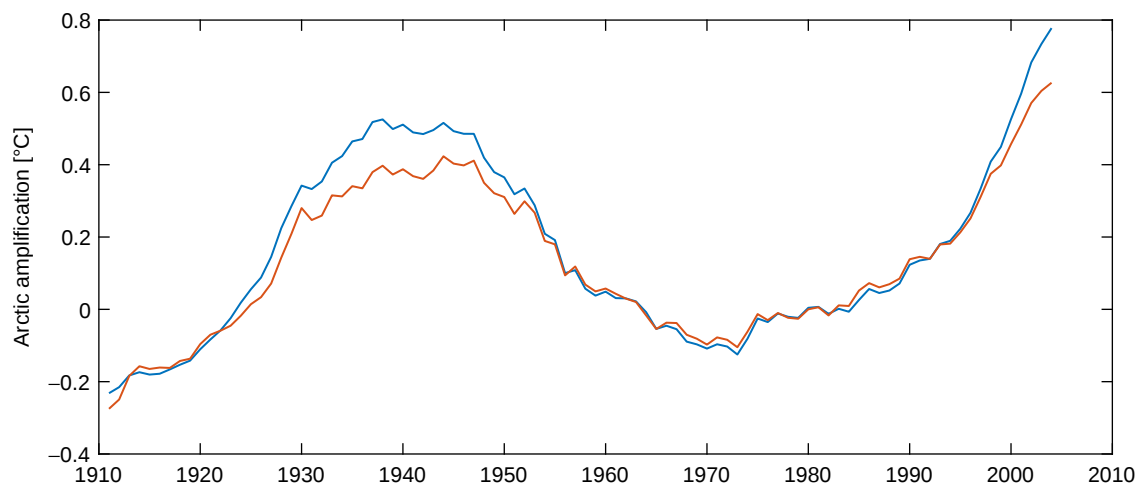


Fig. 4 Observed Arctic amplification over the period 1910 to 2005 as defined by the difference between the annual-mean temperature anomaly in the Arctic and the northern hemisphere. Data are from the Hadley center (*blue*) and the NASA GISS (*orange*) gridded observations, smoothed using a 21-year running mean.

2000s (Cohen et al., 2012). This has been shown to be related to the loss of sea ice in the Barents and Kara seas, although causal relationships have yet to be demonstrated. Nevertheless, there is a large amount of inter-annual variability in the Arctic climate compared to other regions, and this is partly due to the strong influence of large-scale circulation patterns which also exhibit inter-annual variability. This high level of variability can mask some of the long-term changes in the Arctic climate system.

Consequences of Arctic Amplification

The strong Arctic amplification means that air temperatures in the Arctic have increased by more than 2°C over the last 40 years. This has wide ranging consequences for the Arctic climate. One of the most important implications is the effect of this rapid warming on

permafrost. Observations from the last few decades show that there has been a retreat in the surface area covered by permafrost and a deepening of the active layer in permafrost regions (Kane et al., 1991; Åkerman and Johansson, 2008). While historically the Arctic has acted as a net sink of atmospheric carbon dioxide, studies of carbon fluxes from regions with marginal permafrost indicate that this could switch as permafrost melts and soil that was previously frozen year-round becomes biologically active (Zimov et al., 2006; Schaphoff et al., 2013; Schaefer et al., 2014). In addition to being a source of carbon dioxide, there are also large quantities of methane frozen in permafrost. Methane is a much more potent greenhouse gas than carbon dioxide, although it has a much shorter lifetime in the atmosphere. Therefore, the release of methane into the atmosphere may accelerate climate change in the short term, further supported by these positive feedbacks (Walter et al., 2007). Together, the release of methane and carbon dioxide make up two potentially very large positive feedbacks for climate change. Estimating the magnitude of these feedbacks is an important and ongoing topic of research.

Another important tipping point in the high Arctic is the melting of the ice on land, especially Greenland (Lenton, 2011). In the early 2000s a tipping point was identified in the rate of melting of the Greenland ice sheet, mostly due to increased discharge from glaciers in the southeast and northwest of Greenland (Velicogna and Wahr, 2006). This has fueled a great deal of research into determining the effects this has on the climate system, both locally and for the region as a whole. However, a recent increase in the melt-rate of the ice sheet has been observed, leading to increased river discharge and to flooding (Bevis et al., 2019).

Additionally, the rapid warming in the Arctic has meant that wildfires are now more common and are expected to increase in the future (Hu et al., 2015). These fires affect the climate system in various ways. There are the direct impacts: they release a large amount of carbon dioxide into the atmosphere (Mack et al., 2011) which further contributes to global warming (estimated to be 5%–10% of annual emissions); the aerosols emitted from fires can have a cooling or warming effect, depending on their radiative properties, lifetime in the atmosphere, and interaction with other components of the climate system (Kim et al., 2005). Fires also damage or destroy the vegetation that would otherwise absorb atmospheric carbon dioxide, reducing the natural sink of atmospheric carbon. But there are also numerous indirect effects of fires on the climate: the emission of greenhouse gases from decomposing wood in the wake of fires can often exceed the direct emissions from the fires; new-growth of plants after fires can absorb large quantities of carbon dioxide; these new-growth plants tend to have a higher albedo, and so reflect more sunlight and have a cooling effect, compared to old-growth plants. Therefore the net effect of wildfires on the climate system is therefore very difficult to quantify and remains a topic of ongoing research. It requires a thorough understanding of the physical and chemical processes in the atmosphere, biosphere and land-surface (Randerson et al., 2006).

Future of the Arctic Climate

All climate model projections predict that in the coming century the Arctic climate will change more than any other region on Earth. The amount of warming principally depends upon the concentration of carbon dioxide in the atmosphere—the estimates of emissions of carbon dioxide from human activity over the next century are the largest source of uncertainty in modeling how Arctic climate will change over the next 100 years (Overland et al., 2014). However, there is also a lot of uncertainty in these projections related to the strength of feedback processes present in the Arctic, and in our understanding and ability to model the physics, chemistry and biology of the Arctic climate system (Hodson et al., 2013).

However, even if we manage to keep global mean warming to under 2°C, in keeping with the Paris agreement, this will likely mean more than 3°C of warming in the Arctic, due to Arctic amplification. Even this ‘limited’ warming scenario will therefore lead to major changes to the Arctic climate. At this level of warming we can expect the Arctic ocean to be completely free of sea ice in one out of every ten years. This will have a profound impact on the surrounding land, leading to an increase in cloud cover and precipitation, including rain. This warming will also lead to a further reduction in the extent of permafrost with all the associated effects described earlier (IPCC Special report on 1.5°C warming, 2018).

Despite the projected warming for the Arctic, there are some key features of Arctic climate that will remain constant or change little in the future. These are primarily related to the seasonal cycle in solar radiation. The amount of cloud cover can substantially alter the amount of solar radiation reaching the surface, and we can expect significant changes to the cloud cover, driven by the loss of sea ice and to changes in large-scale circulation patterns (Abe et al., 2016; Screen et al., 2018). However, these changes are only relatively small compared to the magnitude of the seasonal cycle which will continue to dominate the features of the climate in the high Arctic.

Micro-Climates

An important feature of Arctic climate is that in cold climates it is easier to form small-scale micro-climates due to the limited amount of atmospheric mixing that acts to homogenize the air. The physical climate and biological systems are fundamentally inter-linked through numerous feedback processes and this is especially apparent in the Arctic in the formation of micro-climates (Carleton, 2017).

Local topography has a large impact on the formation of micro-climates through topographic influences on surface air temperature, including the effects of katabatic and anabatic winds; slope angle and direction can substantially affect the amount of solar radiation absorbed at the surface and so create strong heterogeneities in the surface climate. Also, in discontinuous permafrost regions the variations in the depth of the active layer due to differences in soil properties can help form small-scale micro-climates.

In addition to these horizontal heterogeneities creating important micro-climates for biological activity, there are also microclimates formed in the strong vertical gradients in climate properties. There can be large temperature differences within the first few centimeters below the surface and small-scale features in the topography (down to the scale of a few centimeters) can lead to large differences in the amount of solar radiation, exposure to wind, temperature and humidity. The differences in these micro-climates can be especially pronounced in winter and spring and so have a large effect on the length of the growing season.

The Urban Arctic

While the Arctic is often perceived as a pristine environment, human activity is leaving an ever-increasing footprint in the Arctic climate system. There are numerous cities within the Arctic circle, and they have a profound impact on the local and regional climate. It has been known for more than a 100 years that the air in cities tends to be warmer than in the surrounding country, an effect referred to as the urban heat island. However, combined data from numerical models, in-situ and satellite observations have recently demonstrated the existence of urban heat islands in the Arctic. The urban heat island effect in mid-latitude climates is principally due to the reduced water availability at the surface which means that more of the incoming energy gets converted into heat rather than being used to evaporate water. However, in the high latitudes a more important effect is the presence of surface inversions. These act to trap the heat from anthropogenic warming close to the surface, leading to temperatures inside cities which can be more than 10°C warmer than in surrounding regions (Varentsov et al., 2018). This effect is exacerbated by the inefficiency in heating and low-quality insulation of many buildings in the Arctic. Most of the cities in the Arctic have been constructed using standards and methods adopted from the more hospitable southern climates. They are constructed quickly to satisfy the immediate needs of an economy focused on mineral and petroleum extraction, without due consideration for the extreme cold. Consequentially, there can be a large amount of residual heat emitted from these buildings. Furthermore, many power stations in Arctic cities use local water bodies for cooling. When emitted from power stations, this water can be tens of degrees warmer than the temperature of water at the intake.

These large temperature anomalies can extend for hundreds of square kilometers around cities and strongly affect the surrounding biosphere. Ironically, these urban heat islands can offer a window into the future for the Arctic climate system.

Ice roads are an important means of connectivity in the Arctic. There is a widespread network of roads servicing the numerous small and large communities in all Arctic nations. The sustained usage of these roads can have important effects on the local climate in the Arctic (Raynolds et al., 2014). The continued use of ice roads across permafrost leads to an artificial compression of the ground underneath the road, while simultaneously raising of height of the surrounding ground. This significantly changes the thermal properties of the soil and can lead to local thawing of the permafrost with many knock-on effects, including the growth of trees. These roads can also act as pathways for invasive species to enter the Arctic as the surrounding environment can offer favorable micro-climates.

The Arctic climate is changing faster than in any other region of the world due to the numerous feedbacks and other processes which amplify the global warming observed over the last century. This is an indirect effect of anthropogenic emission of greenhouse gases and it has already led to an increase of annual-average temperatures in the region of more than 1.5°C. However, the warming caused by the direct effects of human activity in the Arctic can be just as large, with some cities having net annual-average temperature anomalies of 3°C. The implications of these large temperature anomalies on society, infrastructure, and ecology are just now beginning to be understood (Hjort et al., 2018).

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Relevant Webpages

- ACIA, n.d., <http://www.acia.uaf.edu/>—Arctic climate impact assessment.
- ESRL, n.d., <https://www.esrl.noaa.gov/gmd/ccgg/>—Global network for monitoring greenhouse gases.
- IPCC, n.d., <https://www.ipcc.ch/sr15/>—“IPCC special report on global warming of 1.5°C.
- UNFCCC, n.d., <https://unfccc.int/process-and-meetings/the-paris-agreement/the-paris-agreement>—Summary of the Paris agreement to limit climate change.

High Arctic Vegetation

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Abstract

Vegetation is the basic element of all terrestrial ecosystems, therefore vegetation types are fundamental in the classification of terrestrial biota across all scales, from communities through ecosystems and finally, biomes. The Arctic tundra biome is geographically restricted to a relatively narrow strip around the margins, including the archipelagos, of the Arctic Ocean (Halliday, 2002). The High Arctic Vegetation (HAV) is characterized by low-growing vegetation of low complexity, mostly comprising bryophytes (mosses and liverworts), lichens, small stature vascular plants and algae (micro- and macroalgae) that together constitute the least diverse terrestrial ecosystems in the Northern Hemisphere.

The HAV represents a component of the High Arctic bioclimatic zone and the northern part of the Arctic tundra biome (Thomas et al., 2008; Barry et al., 2013). The main driving factor influencing the complexity and productivity of tundra vegetation is a latitudinal/environmental gradient, based on which the zonal structure of the Arctic biome can be differentiated (Elvebakk, 1999; Walker et al., 2005). According to the Circumpolar Arctic Vegetation Maps, the definition of the High Arctic followed here includes the three northern-most subzones (A—Arctic polar desert; B—northern Arctic tundra; C—middle Arctic tundra), which are distinguished based on botanical and climatic criteria (Elvebakk, 1999; CAVM Team, 2003; Walker et al., 2005) (Fig. 1 and Table 1).

Distribution and Borders

The High Arctic Vegetation has a circumpolar distribution around the highest latitudes of the North American, Greenland and Euroasian coastlines and associated island groups. The spatial diversity of HAV is strongly shaped by island, biogeographic features, as large parts of the High Arctic are comprised of islands and archipelagos. The largest archipelagos, such as the Canadian Arctic Archipelago, Svalbard, Franz Joseph Land, Novaya Zemlya, North Land, and the New Siberian Islands are exclusively occupied by HAV. The total area of the subzones (A–C) comprising HAV is about 2 billion km², of which terrestrial vegetated and non-glaciated land contributes 1.7 billion km² (Walker et al., 2005).

Climatic Distinctiveness

The climate of the Arctic is largely determined by the low solar angles experienced at high latitudes. Differences in photoperiod between summer and winter become more extreme with increasing latitude and result in the 24-h polar day in summer and a polar night in winter. Annually there are only 2–4 months with positive mean air temperatures, with mean temperatures in the warmest month, July, typically being below 5°C and varying between 1°C in subzone A and 7°C in subzone C (Matveyeva, 1998; CAVM Team, 2003; Convey et al., 2018), and an integrated total of 50–350 day degrees above 0°C over the summer. There is, however, a

spatial variation around the High Arctic, in particular with the warming influence of the North Atlantic Current extending as far north as northwest Svalbard.

Precipitation in the High Arctic is generally low, and mostly falls as snow in winter, but amounts increase dramatically from north to south. A good illustration of this gradient is observed for the Baffin Island (the largest island of the Canadian Arctic), over which the total annual precipitation varies from over 200 mm (north) to about 500 mm (south) (Serreze and Hurst, 2000). Spitsbergen and the Taymyr Peninsula receive up to about 400 mm per year, but some northern areas of the High Arctic receive as little precipitation as the Sahara desert, around 40 mm annually (Jonasson et al., 2000). Lack of precipitation can be particularly severe for vegetation during summer, for example in the Kaffiøyra region of north-west Spitsbergen, which receives only 24.5 mm (Kejna et al., 2010). Despite this, the Arctic cannot simply be considered as dry, as low rates of evaporation, high air humidity and snow melt help soils to remain moist during the short summer growth period (Bovis and Barry, 1974).

Plant Biodiversity

The Arctic flora comprises 2218 species of vascular plants (including spore-producing plants (clubmosses—*Lycopodiophyta*, ferns—*Pteridophyta*, and seed-producing plants (*Gymnospermae*, *Angiospermae*)). However, the High Arctic plant diversity is lower and includes about 478 species (102 species in subzone A, 220 species in subzone B, 477 species in subzone C) (Elven, 2011; Barry et al., 2013). There are seven plant species endemic to the High Arctic: *Puccinellia svalbardensis*, *P. gorodkovii* x *Puccinellia vacillans* (sterile hybrid between *Phippsia algida* and *Puccinellia vahliana*), *Saxifraga nathorstii*, *S. svalbardensis*, *Braya humilis* ssp. *ellesmerensis*, *B. glabella* ssp. *prostrata* and *Draba arctica* ssp. *ostenfeldii*. Cryptogamic spore-bearing organisms (lichens, bryophytes, algae) dominate the plant cover of Arctic tundra vegetation (Pointing et al., 2015; Wietrzyk et al., 2016). Their contribution to Arctic vegetation, documented in the most up-to-date flora checklists, includes ca. 900 species of bryophytes, 1860 species of lichens (1610 true lichens, and 250 lichenicolous fungi), and ca. 4000 species of algae (Elven et al., 2011; Meltofte, 2013). Bryophytes and lichens have largest contribution to Arctic tundra plant diversity, (6% and 10% respectively), although their precise numbers of species are not fully known (Lewis et al., 2017). In contrast, vascular plants contribute only 1% of overall Arctic tundra plant diversity.

Vegetation Typology

Arctic vegetation is divided into five bioclimatic subzones (from A—the coldest and most barren, to E—the warmest and most lush and diverse). As noted, only three of these subzones characterize HAV, which is typified by sparse and very low stature vegetation, usually developing on bare mineral soils: A—Arctic polar desert; B—northern Arctic tundra; C—middle Arctic tundra, within which several types of vegetation have been distinguished (Elvebak, 1999; Walker et al., 2005). The most characteristic features of these subzones, along with vegetation types representing them, are presented in Table 1.

Barrens

B1—Cryptogam, herb barren: dominance of cushion forbs and graminoid vascular plants, pronounced occurrence of mosses, liverworts as well as lichens and cyanobacteria.

Dominant vascular plants: cushion forbs e.g., *Papaver dahlianum* ssp. *polare*, *Draba* sp., *Potentilla hyparctica*, *Saxifraga oppositifolia*; graminoids for example, *Alopecurus alpinus*, *Deschampsia* sp., *Poa abbreviata*, *Puccinellia angustata*, *Phippsia algida*, *Luzula nivalis*, *L. confusaa*.

Dominant lichens: species of the genera *Caloplaca*, *Lecanora*, *Ochrolechia*, *Pertusaria*, *Mycobilimbia*, *Collema*, *Thamnolia*, *Cetraria*, *Flavocetraria*, *Cetrariella*, *Stereocaulon*.

Dominant bryophytes: species of the genera *Racomitrium*, *Schistidium*, *Orthothecium*, *Ditrichum*, *Distichium*, *Encalypta*, *Pohlia*, *Bryum*, *Polytrichum*, *Gymnomitrium*, *Cephaloziella*.

Representative syntaxa: *Thlaspietea rotundifolii* (e.g., *Papaveretum dahliani* Hofm. 1968) and *Salicetea herbaceae* (e.g., *Phippsietum algidae-concinnae* Nordh. 1943).

B2—Cryptogam barren complex (bedrock): dominance of saxicolous lichens on bedrock and dwarf shrubs, and fruticose lichens commonly present in areas between bedrock (Fig. 2).

Dominant vascular plants: dwarf shrubs e.g., *Arctous alpina*, *Cassiope tetragona*, *Vaccinium* sp., *Hierochloë alpina*.

Dominant lichens: saxicolous lichens of the genera *Lecidia*, *Lecanora*, *Buellia*, *Porpidia*, *Rhizocarpon*, *Umbilicaria*, *Parmelia*, *Xanthoria*, *Caloplaca*, *Aspicilia*; terricolous lichens of the genera *Cladonia*, *Cladina*, *Flavocetraria*, *Stereocaulon*, as well as the species *Masonhalea richardsonii*, *Bryocaulon divergens*, *Alectoria ochroleuca*.

Representative syntaxa: *Rhizocarpetea geographici*.

B3—Noncarbonate mountain complex: dry acidic tundra complexes occurring on mountains and plateaus with non-carbonate bedrock. Examples include nunatak areas, with many non-carbonate mountain peaks surrounded by glaciers, and plant communities growing on wind-swept, rocky ridges, scree, and dry fellfields, alternating with snowbed plant communities.

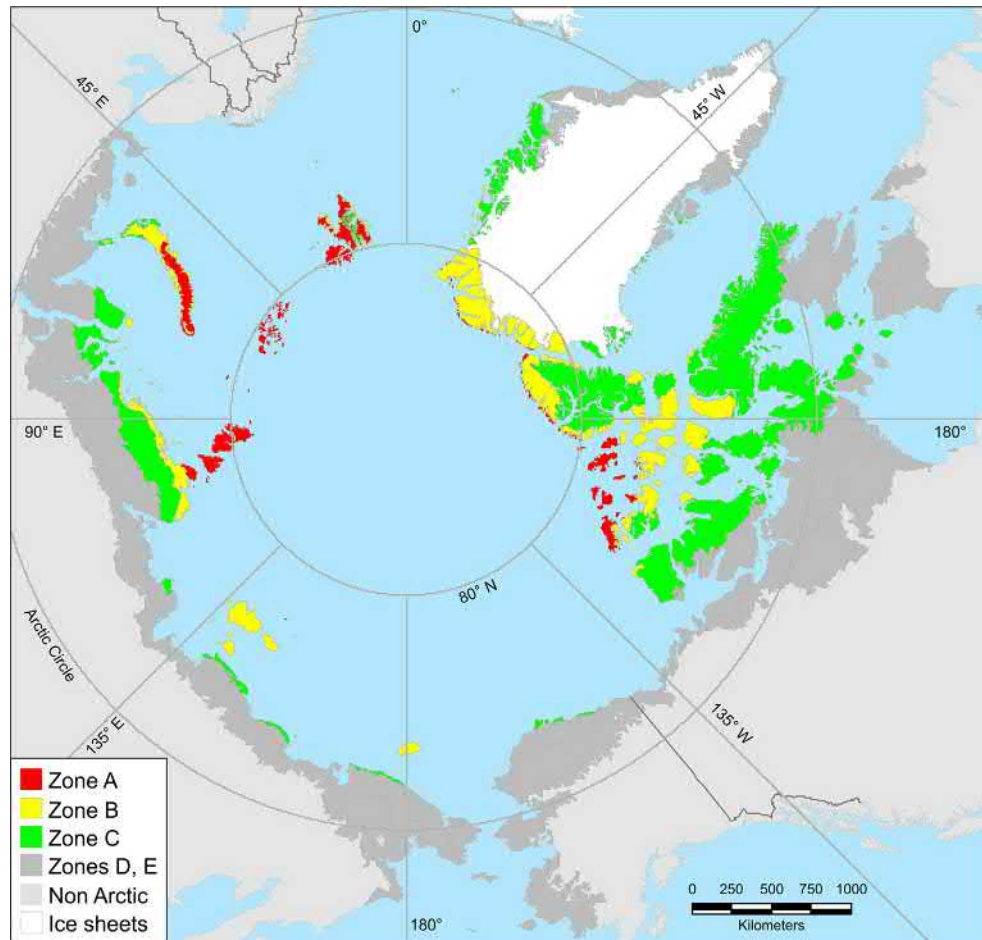


Fig. 1 The circumpolar distribution of the High Arctic Vegetation bioclimatic subzones. Subzone A—red, Subzone B—yellow and, Subzone C—green. Modified based on Walker, D. A., Reynolds, M. K., Daniëls, F. J., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., Yurtsev, B. A. and CAVM Team. (2005). The circumpolar Arctic vegetation map. *Journal of Vegetation Science* **16**, 267–282.

Vegetation changes with elevation in the mountains, forming elevation belts where vegetation is physiognomically similar to that of bioclimate subzones with a comparable summer climate.

Representative syntaxa: *Thlaspietea rotundifolii* (e.g., *Papaveretum dahliani* Hofm. 1968, *Papaveretum radicatae* Dierrss. 1992), *Carici-Kobresietea* (e.g., *Carici-Dryadetum integrifoliae* Dan. 1982 (Ohba 1974)), and *Loiseleurio-Vaccinietea* (e.g., *Cassiopeetum tetragonae* (Bösch. 1933) Dan. 1982).

B4—Carbonate mountain complex: dry calcareous tundra complexes occurring on mountains and plateaus with limestone or dolomite bedrock. Examples again include nunatak areas, with many carbonate mountain peaks surrounded by glaciers, and plant communities growing on wind-swept, rocky ridges, scree, and dry fell-fields, alternating with snowbed plant communities. Vegetation changes with elevation in the mountains, forming elevation belts where vegetation is physiognomically similar to that of bioclimate subzones with a comparable summer climate.

Representative syntaxa: *Thlaspietea rotundifolii* (e.g., *Papaveretum dahliani* Hofm. 1968, *Carici-Dryadetum integrifoliae* Dan. 1982, *Carici-Dryadetum integrifoliae* Dan. 1982).

Graminoid Tundras

G1—Rush/grass, forb, cryptogam tundra: dominance of grasses and rushes occurring in moist tundra on fine-grained, often hummocky soils, also in more protected areas with moderate snow cover. Common presence of cryptogamic crusts composed of cyanobacteria and crustose lichens.

Dominant vascular plants: grasses e.g., *Alopecurus alpinus*, *Dupontia fisheri*, *Deschampsia borealis/brevifolia*, *Poa abbreviata*, *P. arctica*; and rushes e.g., *Luzula nivalis*, *L. confusa*; forbs e.g., *Cardamine bellidifolia*, *Cerastium regelii*, *Minuartia rossii*, *Papaver dahlianum* ssp. *polare*, *Potentilla hyperarctica*, *Saxifraga oppositifolia*, *Ranunculus hyperboreus*, *Draba*, *Stellaria*, *Oxyria digyna*.

Table 1 Characteristics of the High Arctic Vegetation bioclimatic subzones

<i>Bioclimatic subzone (according to Elvebakk, 1999)</i>	<i>Vegetation types (Walker et al., 2005)</i>	<i>Mean July temperature in °C (Matveyeva, 1998)</i>	<i>Sum of mean monthly temperatures > 0° C (Young, 1971, modified by Walker et al., 2005)</i>	<i>Plant cover (Walker et al., 2005)</i>	<i>Plant community structure (Walker et al., 2005)</i>	<i>Number of vascular plant species (Walker et al., 2005)</i>
A—Arctic polar desert	B1—Cryptogam, herb barren (24%) B3—Noncarbonate mountain complex (7%) G1—Rush/grass, forb, cryptogam tundra (19%) P1—Prostrate dwarf-shrub, herb tundra (0.2%) W1—Sedge/grass, moss wetland (1%) Other: glacier areas with nunataks (7%); glaciers (41%)	1–3	<6	<5% of vascular plants ≤40% of cryptogams	Cryptogam layer: < 2 cm tall; single, scattered low vascular plants	<50
B—Northern Arctic tundra	B1—Cryptogam, herb barren (24%) B2—Cryptogam barren complex (bedrock) (0.2%) B3—Noncarbonate mountain complex (13%) B4—Carbonate mountain complex (10%) G1—Rush/grass, forb, cryptogam tundra (17%) G2—Graminoid, prostrate dwarf-shrub, forb tundra (9%) P1—Prostrate dwarf-shrub, herb tundra (11%) W1—Sedge/grass, moss wetland (3%) Other: glacier areas with nunataks (0.3%); glaciers (12%); lakes (0.2%)	4–5	6–9	5%–25% of vascular plants ≤60% of cryptogams	Cryptogam layer: 1–3 cm; herbaceous layer: 5–10 cm; prostrate dwarf-shrub layer: <5 cm	50–100
C—Middle Arctic tundra	B1—Cryptogam, herb barren (4%) B2—Cryptogam barren complex (bedrock) (14%) B3—Noncarbonate mountain complex (11%) B4—Carbonate mountain complex (1%) G1—Rush/grass, forb, cryptogam tundra (1%) G2—Graminoid, prostrate dwarf-shrub, forb tundra (23%) G3—Nontussock sedge, dwarf-shrub, moss tundra (3%) P1—Prostrate dwarf-shrub, herb tundra (16%) P2—Prostrate/hemiprostrate dwarf-shrub tundra (8%) W1—Sedge/grass, moss wetland (6%) Other: glacier areas with nunataks (1%); glaciers (9%); lakes (1%)	6–7	9–12	5%–50% of vascular plants	Cryptogam layer: 3–5 cm; herbaceous layer: 5–10 cm; prostrate and hemi- prostrate dwarf-shrub layer: <15 cm	75–150

Summary characteristics for particular vegetation types (from B1 to W1) are given below, following Walker et al. (2005).



Fig. 2 Example of Cryptogam barren complex. © P. Wietrzyk-Pelka.

Dominant bryophytes: *Aulacomnium turgidum*, *Tomentypnum nitens*, *Ditrichum*, *Oncophorus wahlenbergii*, *Polytrichum*, *Racomitrium*, *Schistidium*.

Dominant lichens: species of the genera *Lecanora*, *Biatora*, *Pertusaria*, *Ochrolechia*, *Thamnolia*, *Cetrariella*, *Flavocetraria*, *Stereocaulon*.

Representative syntaxa: *Thlaspietea rotundifolii* (e.g., *Saxifraga stellaris*-*Oxyrion digynae* Gjaerev. 1950), and *Salicetea herbaceae* (e.g., *Luzulion nivalis* Gjaerev. 1950).

G2—Graminoid, prostrate dwarf-shrub, forb tundra: dominance of prostrate dwarf-shrubs and graminoids in plant communities (e.g., *Cassiope tetragona* snowbeds, well-developed mires, and streamside plant communities) occurring in moist to dry tundra on fine-grained, often hummocky near-neutral soils with moderate snow.

Dominant vascular plants: sedges e.g., *Carex misandra*, *C. lugens/arctisibirica/bigelowii*, *C. rupestris*, *Eriophorum triste*, *Kobresia myosuroides*, *C. aquatilis* ssp. *stans*; rushes e.g., *Luzula nivalis*, *L. confusa*; prostrate dwarf-shrubs e.g., *Salix polaris*, *S. rotundifolia*, *S. arctica*, *S. reticulata*, *Dryas* sp.; grasses e.g., *Alopecurus alpinus*, *Puccinellia vahliana*, *P. wrightii*, *Poa arctica*; forbs for example, *Potentilla hyparctica*, *Cardamine bellidifolia*, *Draba nivalis*, *Saxifraga cernua*, *S. hirculus*, *Stellaria* sp., *Pedicularis capitata*, *Papaver* sp.

Dominant bryophytes: *Racomitrium lanuginosum*, *Oncophorus wahlenbergii*, *Campylium stellatum*, *Aulacomnium turgidum*, *Warnstorfia sarmentosa*, *Hylocomium splendens*, *Polytrichum* sp., *Tetralophozia setiformis*, *Anastrophyllum minutum*.

Dominant lichens: *Sphaerophorus globosus*, *Cladina rangiferina*, *Cladonia pyxidata*, *Thamnolia* sp., *Dactylina arctica*, *Flavocetraria* sp., *Masonhalea richardsonii*.

Representative syntaxa: *Carici-Kobresietea* (e.g., *Carici-Dryadetum integrifoliae* Dan. 1982).

G3—Nontussock sedge, dwarf-shrub, moss tundra: dominance of sedges, prostrate and hemiprostrate shrubs, and bryophytes occurring in moist tundra.

Dominant vascular plants: sedges e.g., *Carex arctisibirica/bigelowii/consimilis/lugens*, *C. misandra*, *C. scirpoidea*, *C. membranacea*, *Eriophorum triste*; prostrate and hemiprostrate dwarf shrubs e.g., *Dryas* sp., *Salix arctica*, *S. reticulata*, *S. polaris*, *Arctous rubra*, *Cassiope tetragona*; grasses for example, *Arctagrostis latifolia*, *Deschampsia borealis*, *Poa arctica*; basiphilous forbs e.g., *Bistorta vivipara*, *Silene* sp., *Pyrola grandiflora*, *Senecio frigidus*, *Pedicularis lanata*, *P. capitata*, *Chrysanthemum integrifolium*, *Tofieldia coccinea*, *Lagotis*, *Eutrema edwardsii*, *Astragalus umbellatus*, *Sagina nivalis*, *Saxifraga oppositifolia*.

Dominant bryophytes: *Tomentypnum nitens*, *Hylocomium splendens*, *Aulacomnium turgidum*, *Rhytidium rugosum*, *Ditrichum flexicaule*, *Distichium capillaceum*, *Ptilidium ciliare*.

Dominant lichens: *Thamnolia* sp., *Flavocetraria* sp., *Peltigera* sp., *Dactylina arctica*, *Mycobilimbia lobulata*, *Cladonia pocillum*, *Psoroma hypnorum*.

Representative syntaxa: *Scheuchzerio-Caricetea nigrae* (e.g., *Carici arctisibiricae-Hylocomietum alaskani* Matv. 1994).

Prostrate-Shrub Tundras

P1—Prostrate dwarf-shrub, herb tundra: dominance of prostrate dwarf-shrub communities with presence of lichen and bryophytes occurring in dry tundra (on non-acidic bedrock the dominant vegetation is *Dryas-Salix arctica* communities (Fig. 3), while on acidic substrates it is *Luzula-Salix arctica*).



Fig. 3 Mountain avens (*Dryas octopetala*). © P. Wietrzyk-Pelka.

Dominant vascular plants: prostrate dwarf-shrubs e.g., *Dryas* sp., *Salix arctica*, *S. polaris*, *S. rotundifolia*, *S. phlebophylla*); sedges e.g., *Eriophorum triste*, *Carex rupestris*; rushes for example, *Luzula confusa*, *L. nivalis*, *Juncus biglumis*; grasses e.g., *Alopecurus alpinus*, *Deschampsia* sp.; forbs e.g., *Saxifraga hirculus*, *S. caespitosa*, *S. oppositifolia*, *Novosieversia glacialis*, *Oxytropis* sp.

Dominant bryophytes: *Ditrichum flexicaule*, *Distichium* sp., *Sanionia uncinata*, *Encalypta* sp., *Pohlia* sp., *Polytrichum* sp., *Hylocomium splendens*, *Aulacomnium turgidum*, *Tomentypnum nitens*.

Dominant lichens: *Thamnolia* sp., *Flavocetraria* sp.

Representative syntaxa: *Carici-Kobresietea* (e.g., *Carici-Dryadetum integrifoliae* Dan. 1982) and *Loiseleurio-Vaccinietea* (e.g., *Gymnomitrio-Loiseleurietum* Dan. 1982).

P2—Prostrate/hemiprostrate dwarf-shrub tundra: dominance of hemiprostrate dwarf-shrub communities with presence of lichen and bryophytes (especially communities dominated by *Cassiope tetragona*) occurring in moist to dry tundra on acidic bedrock.

Dominant vascular plants: Prostrate and hemiprostrate dwarf shrubs e.g., *Cassiope tetragona*, *Dryas* sp., *Rhododendron lapponicum*, *Salix arctica*, *S. polaris*; rushes e.g., *Luzula confusa*, *L. nivalis*; forbs e.g., *Oxyria digyna*, *Bistorta vivipara* (Fig. 4), *Silene acaulis*.

Dominant bryophytes: *Aulacomnium turgidum*, *Tomentypnum nitens*, *Hylocomium splendens*, *Sanionia uncinata*, *Polytrichum juniperinum*.

Dominant lichens: e.g., *Peltigera aphthosa*, *Cetrariella delisei*, *Stereocaulon rivulorum*, *Solorina* sp., *Thamnolia* sp.

Representative syntaxa: *Loiseleurio-Vaccinietea* (e.g., *Cassiopetum tetragonae* (Bösch. 1933) Dan. 1982) and *Carici-Kobresietea* (e.g., *Dryado-Cassiopetum tetragonae* (Fries 1913) Hadač 1946).

Wetlands

W1—Sedge/grass, moss wetland: dominance of sedges, forbs, grasses and bryophytes occurring in wet areas and moist elevated microsites.



Fig. 4 Alpine Bistort (*Bistorta vivipara*). © P. Wietrzyk-Pelka.

Dominant vascular plants: sedges e.g., *Carex aquatilis*, *Carex misandra*, *C. membranacea*, *C. atrofusca*, *Eriophorum triste*, *E. scheuchzeri*, *Kobresia simpliciuscula*; forbs for example, *Cardamine pratensis*, *Cerastium regelii*, *Caltha arctica*, *Bistorta vivipara*, *Saxifraga cernua*, *S. foliolosa*, *Pedicularis sudetica*; grasses e.g., *Arctophila fulva*, *Alopecurus alpinus*, *Pleuropogon sabinei*, *Dupontia fisheri*, *Poa pratensis*; shrubs e.g., *Salix arctica*, *S. reticulata*.

Dominant bryophytes: *Calliergon giganteum*, *Warnstorfia sarmentosa*, *Cinclidium arcticum*, *Hamatocaulis vernicosus*, *Campylium stellatum*, *Plagiomnium ellipticum*, *Bryum pseudotriquetrum*, *Tomentypnum nitens*.

Representative syntaxa: *Scheuchzerio-Caricetea* (e.g., *Poo arcticae-Dupontiae fisheri* Matv. 1994, *Meesio triquetrae-Caricetum stantis* Matv. 1994, *Eriophoretum scheuchzeri* Fries 1913 (Fig. 5), *Caricetum rariflorae* Fries 1913, *Arctophiletum fulvae* Thannh. 1976, *Caricetum stantis* Barrett and Krajina 1972).

Zoo-Anthropogenic Disturbed Vegetation

Bird-cliff vegetation: vegetation of open grassy tundra of bird-manured and disturbed cliff vegetation (Fig. 6).

Dominant vascular plants: *Alopecurus magellanicus*, *Cerastium arcticum*, *Poa alpigena*, *Saxifraga cernua*, *S. caespitosa*, *S. hyperborea*.

Representative syntaxa: *Saxifrago cernuae-Cochlearietea groenlandicae* (e.g., *Cerastio arctici-Saxifragion cernuae* H. Hartmann ex Mucina et Daniëls all. nov. hoc loco 2016).

Anthropogenic vegetation: vegetation of open grassy tundra disturbed due to anthropogenic activities and cryoturbation.

Dominant vascular plants: *Cochlearia officinalis*, *Phippsia algida*, *Phippsia concinna*, *Puccinellia angustata*, *Poa alpina*.

Dominant bryophytes: *Leptobryum pyriforme*, *Encalypta mutica*.

Representative syntaxa: *Saxifrago cernuae-Cochlearietea groenlandicae* (e.g., *Cochleariopsion groenlandicae* Hadač 1989).



Fig. 5 *Eriophoretum scheuchzeri* plant community with its dominant vascular plant Polar White Cottongrass (*Eriophorum scheuchzeri*). © P. Wietrzyk-Pelka.



Fig. 6 Bird-cliff vegetation. © K. Zmudczyńska-Skarbek.

Initial Vegetation

Vegetation developing in deglaciated areas of glacier forelands dominated by lichens, bryophytes, liverworts, and algae.

Progressive retreat of glaciers in the Arctic has been observed since the end of the Little Ice Age, in approximately the mid-19th century (Mann, 2002), and accelerating since the start of the industrial era, and in particular since the mid-20th Century. This on-going process results in the rapid enlargement of ice-free areas in marginal zones of Arctic glaciers, providing new habitat area accessible for colonization by different organisms. These first arrivals are often pioneer cryptogamic species, such as cyanobacteria, lichens, mosses and liverworts. The colonization is typically led by bryophytes, followed by vascular plants and lichens (Wietrzyk et al., 2018). The number of cryptogamic species capable of colonizing freshly deglaciated forelands considerably exceeds that of vascular plants (Wietrzyk et al., 2016, 2017).

Environmental Factors Controlling Vegetation Differentiation

Multiple factors underlie the division of HAV into three large zones (Walker et al., 2005; Jónsdóttir, 2005). These include large-scale geographic patterns in climatic conditions, primarily mean summer temperatures and length of the growing season, as well as the strong influence of warm ocean currents on terrestrial ecosystems, snow cover depth and duration, active layer depth and soil moisture content in summer. Environmental severity gradually increases from zone C to zone A, while the amount of soil organic matter and vegetation cover decrease. Heterogeneity in regional plant communities also results from past glaciation, influenced by time since deglaciation, erosion, and vegetation succession (Walker, 1995).

There are several additional factors that differentiate vegetation within these larger zones, creating a mosaic of unique (micro-) habitats and communities. Among the most important forces, structuring HAV on a landscape scale, are topography associated with temperature and substrate moisture, along with water movement downslope over time, active-layer dynamics, sun, wind and snow exposure (often depending on slope and aspect), and snow depth (Thomas et al., 2008; Convey et al., 2018). Vegetation developing along typical hill-slope toposesquences has been divided into four types (starting from the hill top): open-ridge, zonal, snow-bed, and wet site vegetation (Elvebakk, 1999, Fig. 7). Exposed mountain ridges are usually free from snow and thus subject to strong desiccating winds and extremely low temperatures in winter as well as relatively high temperatures and radiation exposure in summer. Small rosette- and cushion-forming plants and cryptogams, associated with well-drained soil that is poor in organic matter, further suffer from water deficits in summer. In contrast, more amenable sites, such as those associated with late-melting snow beds, are well protected from unfavorable winter weather and buffered from the extreme low air temperatures and exposed ground (Convey et al., 2014, 2018), and have higher water and organic matter content in soil, as well as vegetation cover. However, the growing season in such sites starts later (up to one month) there than in neighboring open areas, which can be a significant limitation to plant growth and development in the short High Arctic summer (Semenchuk et al., 2015, 2016). Moss and graminoid wetlands with 100% ground cover develop in places with the highest continuous water availability (Elvebakk, 1999).

Vegetation growing on slopes may be also disturbed by the mass movement of soil, sediment, and rock triggered by rapid snowmelt, rapid thaw of the active layer or episodic heavy rainfall (Cannone et al., 2010). Vegetation community development and composition depend on rates of colonization and succession. In Ellesmere Island, Canada, this process starts with grasses (*Poa* sp.), then efficient seed producers (such as *Polygonum viviparum*, *Draba* sp.) sporadically became established 2–3 years after landslides occur, and finally woody and semi-woody plants (*Salix arctica*, *Dryas integrifolia*) appear in the community after a minimum of about 10 years. Average total plant cover and species richness generally increase with time after the landslides.

Small-scale differentiation of HAV resulting from microtopography and the action of permafrost is exemplified by patterned ground (Fig. 8). The elevated centres of frost-heave features such as non-sorted circles and polygons are much less vegetated, and sometimes even barren, as compared with their margins and the ground between them (Cannone et al., 2004; Walker et al., 2008). The latter have more protected and stable soils and enhanced water and nutrient availability, which promote plant growth and diversity.

The crucial role of substrate pH cannot be overlooked, as it governs the availability of essential plant nutrients such as calcium and phosphorus, as well as it has wider influence on soil temperature, active layer thickness, photosynthesis, respiration, decomposition rates, and fluxes of trace gases, energy, and water (Elvebakk, 1999; Walker et al., 2005). Local pH variation and gradients are linked with different bedrock types, cryoturbation and glacial history. On a scale of metres or even centimeters, substrate chemistry, including pH, is strongly modified by allochthonous supplies of organic and inorganic compounds originating from the sea, such as those contained in sea spray close to the coast, or deposited in the large amounts of guano in the vicinity of seabird colonies and solitary nests, making these areas outstandingly green and lush oases of life (Euroala and Hakala, 1977; Zwolicki et al., 2013, 2016b; Zmudczyńska-Skarbek et al., 2017; see also Seabird influence subchapter).

Vertebrate herbivores are another biotic agent with the ability to shape specific plant communities in the High Arctic, for example, through the burrowing of rodents, grubbing for roots and rhizomes by geese, trampling, grazing and manuring by reindeer (caribou) and other mammals (Jefferies et al., 1994; Pedersen et al., 2013; Johnson et al., 2011, Fig. 9). The availability of increased nitrogen drives the transition from dwarf shrub, moss and/or lichen-dominated ecosystems to graminoid domination (Johnson et al., 2011).

Additional natural or anthropogenic disturbances can alter HAV at small physical scales, such as detachment of rocks or boulders from cliffs, which destroys parts of the plant communities growing below and promotes damage-resistant and/or fast-growing

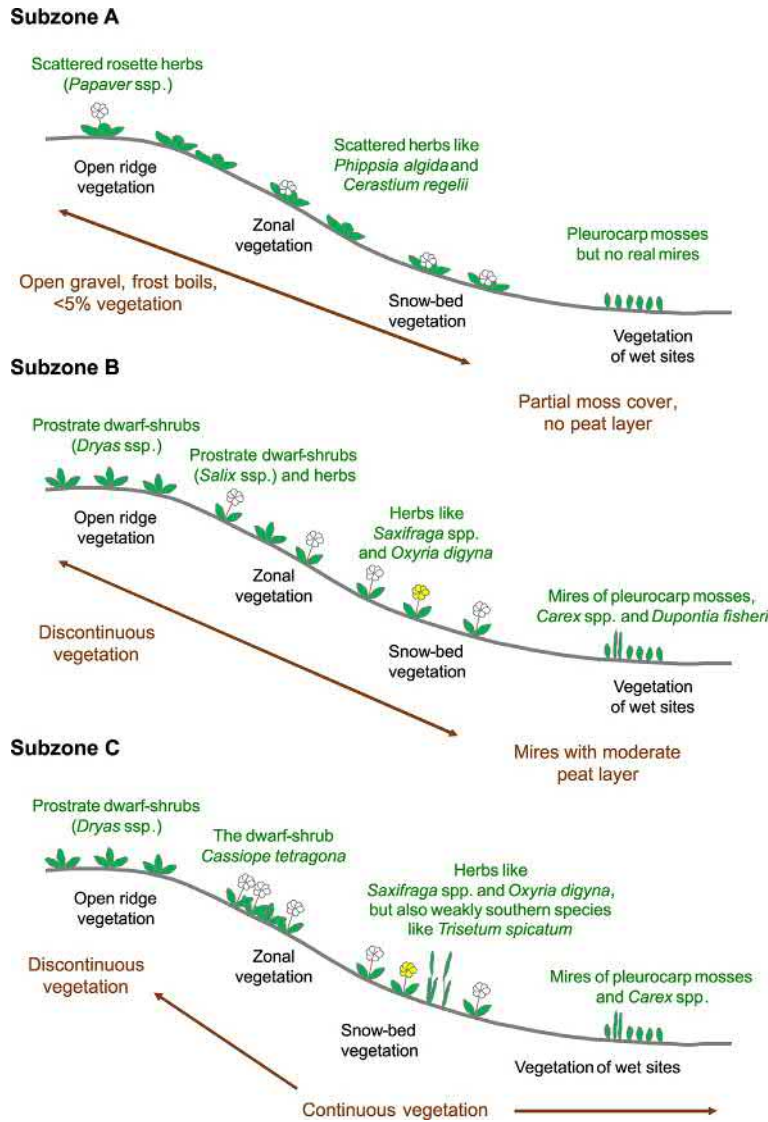


Fig. 7 Generalized toposequences for High Arctic Vegetation in A, B, and C bioclimate subzones. Adapted from Elvebakk, A. (1999). Bioclimatic delimitation and subdivision of the Arctic, In: *The Species Concept in the High North: A Panarctic Flora Initiative*, pp. 81–112. Oslo: The Norwegian Academy of Science and Letters.



Fig. 8 Non-sorted circles in Revdalen, SW Spitsbergen, as an example of patterned ground. © K. Zmudczyńska-Skarbek.



Fig. 9 Barnacle geese (*Branta leucopsis*) with non-flying chicks, grazing on HAV. © P. Wietrzyk-Pełka.

species (Zmudczyńska-Skarbek et al., 2013). Vegetation patches often develop close to locations of vertebrate dung or the bones of dead animals (Fig. 10), which locally provide an extra source of nutrients. Anthropogenic introduction of alien species is increasingly prominent, especially around human settlements, and because of tourism development (Liška and Soldán, 2004; Ware et al., 2012).

Seabird Influence

In the harsh conditions of the High Arctic terrestrial environment, which generally suffers from chronically low levels of nutrients, seabirds act as bio-vectors transferring nutrients from marine to terrestrial ecosystems, and locally play a crucial role in the development of HAV (Euroala and Hakala, 1977; Elvebakk, 1994; Wojciechowska et al., 2015; Zwolicki et al., 2016a,b). Marine birds feed in the sea and breed on land, often in sizeable colonies where they deposit large amounts of guano (rich in nitrogen, phosphorus and other elements) as well as carcasses and egg shells, which enter the terrestrial ecosystem. As a consequence, the vicinities of seabird nesting sites are characterized by much higher nutrient concentrations, compared to areas beyond the influence of birds (Zwolicki et al., 2013; Fig. 6). This local soil fertilization promotes graminoids and forbs with high growth rates, rapid tissue turnover and low nutrient use efficiencies (e.g., *Poa alpina* and *Cochlearia groenlandica*; Fig. 11). They form lush communities with relatively low diversity, outcompeting slower-growing dwarf shrubs with long-lived leaves and high nutrient use efficiency (e.g., *Saxifraga oppositifolia* and *Salix* sp.) (Wojciechowska et al., 2015; Zwolicki et al., 2016a). The importance of seabird impact is most spectacular in the vicinity of large colonies, but even a single bird carcass could have long lasting influence on vegetation (Street et al., 2018). On a smaller and more scattered scale this phenomenon is also observed in the vicinity of solitary nesting seabirds such as skuas or gulls (Zmudczyńska-Skarbek et al., 2017).

These “bird-cliff” vegetation communities may differ geographically, and are also influenced by differences in bird species diets (plankton-feeders or fish-feeders) and excreta (Elvebakk, 1994; Zwolicki et al., 2013). As a result, bird-cliff vegetation can be



Fig. 10 Vegetation patch developing on and around old whale bones. © P. Convey.



Fig. 11 *Poa alpina* and *Cochlearia groenlandica*, typical representatives of Bird-cliff vegetation. © K. Zmudczyńska-Skarbek, P. Wietrzyk-Pelka.

subdivided into subtypes based on the diet of the respective influencing bird colonies, which promote different plant communities (Zwolicki et al., 2016b). Recently observed oceanographic changes in the Arctic, caused by climate warming, are leading to changes in the structure of marine zooplankton communities and may influence the balance between plankton-feeding and fish-feeding seabird populations, and consequently modify the proportion of the bird-cliff vegetation supported by each population (Stempniewicz et al., 2007; Weydmann et al., 2014; Zwolicki et al., 2016b).

Plant Adaptations and Growth Forms

Since the High Arctic flora is young in the context of global evolution, relatively few plant species have adapted sufficiently to survive and propagate in the severe environmental conditions. The “winners” have had to adjust their structure (e.g., plant height and biomass, leaf and root dimensions), water relations (including leaf and root resistance), photosynthesis rates, temperature sensitivity, growth rates, and allocation patterns. Population characteristics, such as density, dispersal, and age structure have also changed in response to selection pressures (Webber et al., 1980; Callaghan, 2001).

Biotic factors that have driven the adaptations of High Arctic flora include interactions between plants, which may provide benefits such as sheltering from wind and abrasion. Decreased water loss is accomplished by possession of tightly-packed shoots, that can also lead to slope stabilization through extensive root systems (Brooker and Callaghan, 1998). Frequent symbiotic associations with mycorrhizae (fungi), and also cyanobacteria, in some species (e.g., *Cassiope tetragona*, *Salix* sp., *Dryas* sp. for mycorrhizae, and mosses; e.g., *Sanionia uncinata* for cyanobacteria) enhance the plants’ nutrient-uptake abilities (Kohn and Stasovski, 1990; Väre et al., 1992; Solheim et al., 1996). Plant-nutrient dynamics are controlled by edaphic limiting factors and, even though locally most higher plants invest a majority of their biomass in roots and rhizomes to increase the surface area for nutrient acquisition, some species also respond to soil nutrient deficiencies by the direct acquisition of soil amino acids (some non-mycorrhizal sedges), or nutrient adsorption through the leaf surface (e.g., some mosses; Skrzypek et al., 2015). Internal nutrient management can be very efficient, for instance keeping low nutrient concentrations in the tissues, producing evergreen and long-lasting structures, and recycling nutrients from senescing to young tissues almost completely. Many plants have to survive periodic anaerobic conditions, for instance when above- and/or below-ground parts become water-logged and frozen during spring and autumn (Crawford et al., 1994). Substrate movement resulting from freeze-thaw cycles further disturbs vegetation development, restricting root development (Jonasson and Callaghan, 1992). In response to physical environmental selective forces, primarily low temperatures (including freezing and freeze-thaw cycles) and solar radiation during the short growing season, plants must develop appropriate physiological and biochemical responses, and many also extend their life cycle from one to 2–5 years. Plant morphology can be an effective means by which plants influence and increase the microhabitat temperatures within which their tissues exist. Compact cushion and mat growth forms are common in HAV. General features of HAV plants include relatively low stature, well-protected buds, long-lived or evergreen leaves, densely aggregated shoots, and limited woody tissues. Different species have evolved different growth forms as strategic adaptations to the demands of varied Arctic habitats. Webber et al. (1980) distinguished ten growth form categories (some of which are also broad taxonomic groups) commonly occurring within the tundra zone, and the classification is valid also for HAV. These are: lichens, mosses, cushion, mat, erect, and rosette forbs (broad leaved herbs), caespitose and single graminoids, and deciduous and evergreen shrubs (see the examples on Fig. 12).



Fig. 12 Examples of High Arctic Vegetation growth forms (based on Webber et al., 1980): *Rhodiola rosea*, cushion forb (A), *Cerastium arcticum*, mat forb (B), *Draba* sp., rosette forb (C), *Luzula* sp., caespitose graminoid (D), *Salix polaris*, deciduous shrub (E), *Cassiope tetragona*, evergreen shrub (F). © D. Kidawa, K. Zmudczyńska-Skarbek, A. Zwolicki.

Anthropogenic Impact

Arctic ecosystems are among the least anthropogenically impacted on Earth, with almost pristine marine and tundra habitats. However, High Arctic ecosystems host a relatively low number of species, connected through simple food webs. Such simplicity makes these ecosystems particularly vulnerable to any environmental change.

Effects of Climate Change

“Latitudinal gradients suggest that arctic plant diversity is sensitive to climate” (Callaghan et al., 2005). The most threatened is probably the High Arctic Vegetation, which occupies the coldest areas and has no possibility of northward dispersal because of the lack of land at higher northern latitudes (Callaghan et al., 2005). Climate is the key ecological factor influencing Arctic terrestrial ecosystems on different time scales, historically and recently.

Recently observed global climate warming, caused predominantly by increasing atmospheric greenhouse gas concentrations, is well documented (IPCC, 2014, 2018). Moreover, instrumental records over the past 50 years show that the Arctic warms faster than areas at lower latitudes. The average Arctic surface temperature has increased by nearly 0.1°C per decade over the past century, causing snow and ice melting, while at the same time, darker land and ocean surfaces absorb more of the sun’s energy, in turn further accelerating the warming of the Arctic. Additionally, relatively warm Atlantic waters, transported northwards with the West Spitsbergen Current, increasingly penetrate more northern parts of the European Arctic which, coupled with the sea temperature rise (Walczowski et al., 2012), intensifies observed changes in the environment. The lower atmospheric layers over the Arctic are shallower than in lower latitudes and thus warm faster, supplied by the increased heat transfer from the ice-free seas to the atmosphere. The amount of energy trapped in the atmosphere, of which only a small part is used in increased evaporation, leads directly to warming, causing a particular threat to Arctic ecosystems (ACIA, 2004; McBean et al., 2005).

The response of Arctic vegetation to contemporary climate warming, similarly as historical responses, is characterized mainly by species relocation rather than adaptation. Changes in populations are influenced by climatic trends and also extreme events, sea-ice decrease and glacier retreat, as well as permafrost and snow cover changes. The soil active layer and coastal permafrost are particularly sensitive to climate warming, which can lead to drastic changes in geomorphology, including major impacts on human infrastructure (Callaghan et al., 2005; Bokhorst et al., 2008, 2011).

High Arctic Vegetation is sensitive to oceanographic and climatic changes, especially to increasing air temperatures in summer. Impacts are apparent in the northern-most Arctic polar desert subzone (A), where mean July temperatures hover near freezing, resulting in changes in plant productivity and species diversity, as well as in shifts in altitudinal and zonal vegetation boundaries. In this case even a small summer warming may lead to a shift towards plant communities that are compositionally and functionally characteristic of more southern subzones (Walker et al., 2008).

Recent remote-sensing records indicate a “greening of the Arctic,” suggesting increased photosynthetic activity and net primary productivity, mostly through shrub expansion (Sturm et al., 2001), although this process is somewhat slower in the High Arctic (Jia et al., 2003). Strong positive relationships between growth and temperature are observed not only in dwarf shrubs such as willows (*Salix* sp.) or Arctic bell-heather *Cassiope tetragona* but also in mosses such as the glittering wood-moss *Hylocomium splendens* (Havström et al., 1995; Callaghan et al., 1997). Additionally, the increasing number of extreme events such as winter warming spikes, tundra fires or surface icing through rain on snow events can also lead to “Arctic browning,” a direct reverse of Arctic greening, which causes drastic declines in vegetation biomass and productivity (Phoenix and Bjerke, 2016).

The main feedback mechanisms between the impacts of climate change on Arctic terrestrial ecosystems and the global climatic system occur through decreasing albedo and increasing release of greenhouse gases, especially methane. Changes in vegetation biomass and structure will have important feedbacks to the permafrost, hydrological cycles, wildlife, and human life. An important aspect of functional changes in tundra soils, driven by warming and drying, is that of their carbon status, which has already changed from a sink to a source, through changes in decomposition and microbial respiration. Moreover, increased carbon dioxide and ultraviolet-B radiation levels affect plant tissue chemistry and are predicted to have long-term impacts on the ecosystem processes that reduce nutrient cycling and have a potential to decrease productivity (Callaghan et al., 2005). Finally, it should be noted that most of the current knowledge on the Arctic floristic evolution and diversity is based on studies of vascular plants. However, it is the relatively poorly studied bryophytes that dominate the High Arctic Vegetation and play a crucial role in global carbon storage and biogeochemical cycles (Lewis et al., 2017).

Other Threats

The impact of direct human activities, such as infrastructure development and exploration for sources of hydrocarbons and minerals, increasingly threaten significant damage to tundra ecosystems. Pollution associated with these activities is a serious threat to the local marine and coastal ecosystems. Construction of pipelines and roads can also physically disturb and fragment habitats and obstruct migration routes. Additionally, as noted above, increased melting of the permafrost can lead to major damage to infrastructure. In parts of the Siberian, Alaskan and Canadian Arctic, erosion following loss of coastal permafrost and fringing sea ice can lead to the loss of up to 100 ft of the coast per year (IPCC, 2014). The vulnerable tundra surface can take years or decades to recover from vehicular tracks.

Air pollution from remote sources at lower latitudes, transported in the upper atmosphere, is being deposited in the Arctic, causing soil contamination and directly affecting organisms. The United Nations Environment Programme has identified the 12 most common persistent global organic pollutants, which are also affecting the Arctic (DDT, heptachlor, texaphene, mirex, aldrin, endrin, dieldrin, chlordane, hexachlorobenzene, PCB, dioxins and furans). Lichens and mosses are particularly vulnerable to air pollution, what is especially important because they serve as significant food sources for many animals, such as reindeer and geese (Arctic Monitoring and Assessment Programme, 1997).

Shipping, resource development corridors, and also tourism are rapidly growing commercial activities in the Arctic. The Arctic cruise industry has rapidly expanded in the past 15 years, and with it the risk of environmental accidents and the introduction of alien species, which may displace native vegetation and impact biodiversity (Stewart et al., 2007; Meltofte, 2013). The well documented reductions in Arctic sea ice, with predictions of an ice-free Arctic Ocean in summer within the next few decades, have led to increasing commercial interest in Arctic shipping, with attendant risks of pollution, accidents, and species movements.

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Mammals of the High Arctic

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Abstract

This article deals with the mammal fauna of the High Arctic region—the region with the least number of mammal species, outside of Antarctica. The lands of the High Arctic fall between about 70° and 80°N latitude. The vegetation cover is quite sparse and biological productivity at the bottom of the food chain is low, so the terrestrial regions of the High Arctic cannot support large numbers of plant consumers and their predators. These mammals employ a wide variety of strategies and adaptations for cold winter survival, as they are all year-round residents. Unfortunately, the very adaptations that fit mammals for life in the High Arctic may prove to be their downfall as global warming threatens to make their homelands essentially uninhabitable.

Introduction

According to the most recent estimate (Burgin et al., 2018), there are 6400 species of mammals in the world today. Most of these live in the tropical regions, with Brazil ranking first among the nations for greatest number of mammal species (600). The number of mammal species (and most other groups of organisms) decreases toward the poles. This chapter deals with the mammalian fauna of the High Arctic region—the region with the least number of mammal species, outside of Antarctica. As shown in Table 1, the High Arctic region is home to just 45 species of mammals. Of these, 21 (47%) are terrestrial, and 24 (53%) are marine mammals. This proportion of terrestrial to marine mammals is unique to the Arctic. For instance, in North America as a whole, 374 (85%) of the mammal species are terrestrial and 65 (15%) are marine mammals. Why is the High Arctic fauna so different?

The lands of the High Arctic fall between about 70° and 80°N latitude (Fig. 1). The High Arctic is essentially a bitterly cold desert (Fig. 2). If it were not for its polar latitude, this biome could be included in the “Deserts” section of this encyclopedia. An example of the physical environment of the High Arctic can be found in the Zackenberg valley, situated at 74°28′N in northeast Greenland, as described in a study by Westergaard-Nielsen et al. (2017). Here, the mean annual temperature is about −9.0°C. The mean July temperature is 6.3°C and mean February temperature is −19.8°C. As in most High Arctic regions, mean annual precipitation is <250 mm, of which approximately 85% falls as snow. Maximum snow depth is remarkably shallow, ranging from 0.13 to 1.44 m over recent years. In this valley, the growing season is 51 days. This represents the time of year when the ground surface is not frozen, so plants may grow. The vegetation cover is quite sparse in many regions. It grows very slowly and almost all plant species grow very close to the ground, thus avoiding exposure to chilling winds and wind-blown snow and ice crystals. Because biological productivity at the bottom of the food chain is so low, the terrestrial regions of the High Arctic cannot support large numbers of plant consumers and their predators.

One of the best ways of assessing the biological productivity of any ecosystem is its Net Primary Productivity (NPP). NPP is the rate at which atmospheric or aqueous carbon dioxide is converted by primary producers into organic material. Primary production via photosynthesis is a key process within all ecosystems, as the producers form the base of the food web, both on land and in the seas. On land, primary production is mostly carried out by macroscopic plants. In the ocean, primary production is mostly carried out by microscopic phytoplankton.

Gould et al. (2003) studied the vegetation, plant biomass, and net primary productivity patterns of the High Canadian Arctic regions. Their results showed that about 40% of the region has vegetation cover of <5%. About 60% has vegetation cover of 5–50%. Furthermore, about 25% of the Canadian High Arctic has net primary productivity (NPP) of 0–20 g of carbon per square meter per year. The rest of the Canadian High Arctic has NPP of 20–50 g C/m²/year.

Table 1 Mammal species presence/absence in the four High Arctic regions and their IUCN status.

Common name	Scientific name	Canada	Greenland	Svalbard	Russia	IUCN status
Northern pika	<i>Ochotona hyperborea</i>	—	—	—	•	Least concern
Mountain hare	<i>Lepus timidus</i>	—	—	—	•	Least concern
Arctic hare	<i>Lepus arcticus</i>	•	•	—	—	Least concern
Arctic ground squirrel	<i>Urocitellus parryi</i>	•	—	—	—	Least concern
North American brown lemming	<i>Lemmus trimucronatus</i>	•	—	—	—	Least concern
Northern collared lemming	<i>Dicrostonyx groenlandicus</i>	•	•	—	•	Least concern
Arctic lemming	<i>Dicrostonyx torquatus</i>	—	—	—	•	Least concern
Wrangel Island collared lemming	<i>Dicrostonyx vinogradovi</i>	—	—	—	•	Data deficient
Brown lemming	<i>Lemmus sibiricus</i>	—	—	—	•	Least concern
Tundra vole	<i>Microtus oeconomus</i>	—	—	—	•	Least concern
Tundra shrew	<i>Sorex tundrensis</i>	—	—	—	•	Least concern
Gray wolf	<i>Canis lupus</i>	•	•	—	•	Least concern
Arctic fox	<i>Vulpes lagopus</i>	•	•	•	•	Least concern
Red fox	<i>Vulpes vulpes</i>	•	•	—	•	Least concern
Grizzly or brown bear	<i>Ursus arctos</i>	•	—	—	—	Least concern
Polar bear	<i>Ursus maritimus</i>	•	•	•	•	Vulnerable
Short-tailed weasel (Stoat)	<i>Mustela erminea</i>	•	—	—	•	Least concern
Least weasel	<i>Mustela nivalis</i>	•	—	—	—	Least concern
Wolverine	<i>Gulo gulo</i>	•	—	—	•	Least concern
Walrus	<i>Odobenus rosmarus</i>	•	•	•	•	Vulnerable
Hooded seal	<i>Cystophora cristata</i>	•	•	•	—	Vulnerable
Harp seal	<i>Pagophilus groenlandicus</i>	•	•	•	•	Least concern
Harbor seal	<i>Phoca vitulina</i>	•	•	•	—	Least concern
Spotted seal	<i>Phoca largha</i>	—	—	—	•	Least concern
Common seal	<i>Phoca vitulina</i>	—	—	—	•	Least concern
Ringed seal	<i>Pusa hispida</i>	•	•	•	•	Least concern
Bearded seal	<i>Erignathus barbatus</i>	•	•	•	•	Least concern
Ribbon seal	<i>Histiophoca fasciata</i>	—	—	—	•	Least concern
Minke whale	<i>Balaenoptera acutorostrata</i>	•	•	•	•	Least concern
Blue whale	<i>Balaenoptera musculus</i>	•	•	•	•	Endangered
Fin whale	<i>Balaenoptera physalus</i>	•	•	•	•	Endangered
Humpback whale	<i>Megaptera novaeangliae</i>	—	—	—	•	Least concern
Bowhead whale	<i>Balaena mysticetus</i>	•	•	•	•	Least concern
North Atlantic right whale	<i>Eubalaena glacialis</i>	•	•	—	—	Endangered
Beluga whale	<i>Delphinapterus leucas</i>	•	•	—	•	Least concern
Narwhal	<i>Monodon monoceros</i>	•	•	—	•	Least concern
Sperm whale	<i>Physeter macrocephalus</i>	—	•	—	•	Vulnerable
White-beaked dolphin	<i>Lagenorhynchus albirostris</i>	•	•	—	•	Least concern
Atlantic white-sided dolphin	<i>Lagenorhynchus acutus</i>	•	•	—	—	Least concern
Killer whale, Orca	<i>Orcinus orca</i>	•	•	—	•	Data deficient
Long-finned pilot whale	<i>Globicephala melas</i>	—	•	—	—	Data deficient
Harbor porpoise	<i>Phocoena phocoena</i>	•	•	—	•	Least concern
Northern bottlenose whale	<i>Hyperoodon ampullatus</i>	—	•	—	—	Data deficient
Caribou	<i>Rangifer tarandus</i>	•	•	•	•	Vulnerable
Muskox	<i>Ovibos moschatus</i>	•	•	•	—	Least concern

In contrast to the unproductive landscapes of the High Arctic, this region's oceans are significantly more productive. The cold waters of the high latitudes hold more dissolved gases than the warmer waters of the middle and low latitudes. NPP of the High Arctic seas ranges from 35 g C/m²/year in the Western Arctic to 83 g C/m²/year in the Barents Sea (Frey et al., 2016). Of course one of the most limiting factors in Arctic biological productivity, on both land and sea, is the greatly limited seasonality of sunlight. Primary productivity is strongly dependent upon light availability and the availability of nutrients, and thus is highly seasonal in the Arctic region. On land, nutrient availability is essentially limited to the summer season when there is an active layer of thawed soil from which plants may obtain nutrients. In Arctic seas, the melting and retreat of sea ice in spring are strong drivers of primary production. Productivity is particularly high along the continental shelves because the shallow water enhances light availability. Thus, the relatively high NPP of the Arctic Ocean and adjacent seas supports a greater abundance and diversity of mammals than the relatively unproductive High Arctic landscapes.

It is beyond the scope of this review to discuss every High Arctic mammal in detail. Table 2 shows the basic life history information for all species, from the tundra shrew, weighing just 11 g, to the blue whale, tipping the scales at just under 190 million grams. Some of these mammals are remarkably prolific, such as lemmings that produce litters of multiple offspring in as little as

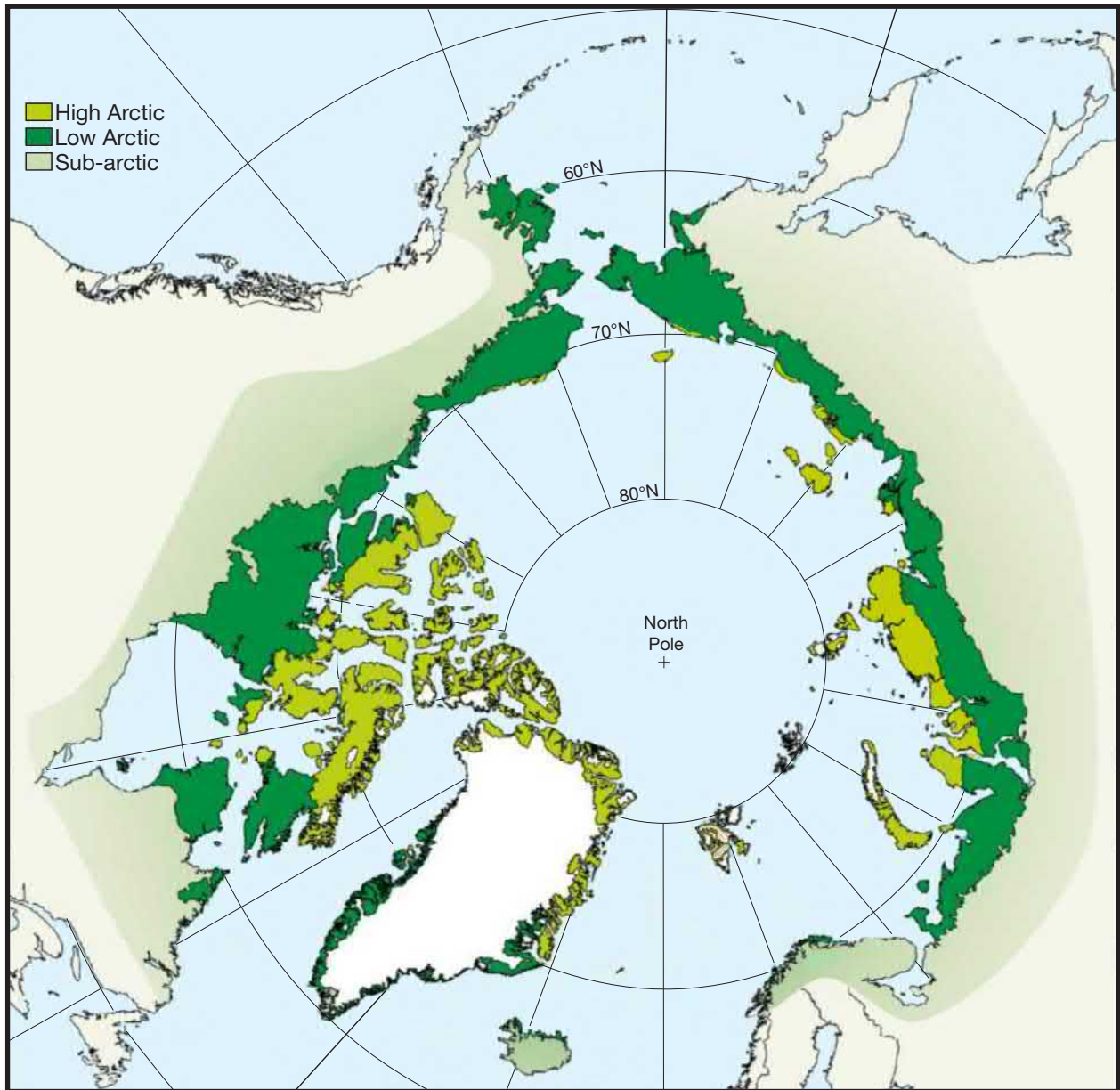


Fig. 1 Map of the northern high latitudes, showing the High Arctic, Low Arctic, and Sub-Arctic vegetation zones (after map by University of Tromsø, Arctic Council).

17 days. Others, such as the whales, reproduce very slowly. This review focuses on a handful of species that show the diversity of strategies and adaptations of the terrestrial mammals that manage to survive in the frozen lands of the High Arctic.

Terrestrial Mammals

All High Arctic terrestrial mammals have one thing in common: they all have to survive the rigors of winter. None of them migrates south during the winter months. Many share common strategies and adaptations. These are grouped into categories, below. Strategies and adaptations used only by carnivores and scavengers are marked with a *star*. Strategies and adaptations used only by herbivores are marked with a *square*. Strategies and adaptations used by both carnivores and herbivores are marked with a *circle*.

- Conserve energy by sleeping most of the time.
- Conserve energy by hibernating (lowered body temperature and metabolic rate).
- Conserve energy by growing a very warm winter coat.



Fig. 2 Photograph of muskox in polar desert on Ellesmere Island. Photo by Christopher Gatto, used with permission.

- Avoid competition with other species for limited winter food resources.
- Optimize ability to extract energy from food.
- Make a hay pile under the snow (herbivores) and defend it from all competitors.
- Eat plants or lichens that are not hidden by the snow.
- Eat plants or lichens buried by snow, but in locations unknown to other herbivores.
- Curl up together in a group nest for shared body warmth.
- Stay beneath the snow most or all of the time (temperatures are much warmer there than in the air).
- Build up a thick layer of fat to get through times of fasting or food scarcity.
- ★ Scavenge the carcasses of other animals that do not make it through the winter.

Small Terrestrial Mammals

Small mammals, such as voles, shrews, pikas and lemmings, have a very large surface-to-volume ratio. This causes them to lose a great deal of heat to the environment during the winter. Not surprisingly, then, the small mammals of the High Arctic avoid exposure to winter air temperatures to the best of their ability. Most of them gain protection from winter air temperatures by tunneling beneath the snow. Snow provides excellent insulation from cold air temperatures. In a study done during a Svalbard winter, [Convey et al. \(2015\)](#) measured ambient temperatures where there was no snow cover, shallow snow cover (30 cm) and deep snow cover (120 cm). Local air temperatures at the study site fluctuated between -3 and -24°C through the study. Where the ground was bare of snow, soil temperatures matched air temperatures closely. Soil temperatures varied less under 30 cm of snow, and did not decrease below -12°C . Temperatures beneath 120 cm of snow were even more stable and did not decline below -2°C . Another key aspect of snow cover is moisture. Tunnels made by small mammals beneath the snow are not only substantially warmer than the air above, they also hold considerable moisture. This relatively warm, moist air helps small mammals avoid both the freezing and desiccation they would face on the surface.

Lemmings

Lemmings are vital to the functioning of many High Arctic ecosystems. They occur in large numbers, reproduce rapidly, and consume large quantities of vegetation. In turn, they are the principal prey of many arctic predators. [Gilg et al. \(2009\)](#) note that the northern collared lemming ([Fig. 3](#)) is the single most important prey of four predators in the High Arctic: the snowy owl (*Bubo scandiacus*), the Arctic fox ([Fig. 4](#)), the long-tailed skua (*Stercorarius longicaudus*), and the short-tailed weasel ([Fig. 5](#)). There are five species of lemmings listed in [Table 1](#). These include the northern collared lemming and the brown lemming, discussed below.

Arctic lemmings all excavate runways at the snow-ground interface. During the short summer months, the northern collared lemming is found on dry, sandy or gravelly habitats on the tundra. Unlike other lemmings, it turns white in winter, and grows elongated claws that help it dig through snow. This species builds extensive runways and nesting areas beneath the snow. Like other lemmings, the northern collared lemming is probably a pure herbivore, eating a variety of plants. Willows and sedges are the dominant plants used as forage by northern collared lemmings in arctic Greenland. Willow leaves provide high quality forage in

Table 2 Life history information for High Arctic mammals. Data from [Animal Diversity Web \(2018\)](https://www.iucnredlist.org/) and the IUCN Redlist (<https://www.iucnredlist.org/>)

<i>Species</i>	<i>Mass</i>	<i>Life span (years)</i>	<i>Gestation (days)</i>	<i>Litter size</i>	<i>Habitat in High Arctic</i>	<i>Diet in High Arctic</i>
Northern pika	120 g	≤ 9	28	3–4	Found on talus and other rocky slopes	Grasses and other herbs; makes hay piles for winter food
Mountain hare	3 kg	9	47–54	1–4	On open arctic tundra	Tundra herbs and forbs
Arctic hare	≤ 68 kg	3–5	50	2–8	Mountainous tundra, rocky plateaus and treeless coasts	Willow, mosses, lichens, buds, berries, leaves, roots
Arctic ground squirrel	≤ 15 kg	8–10	25–30	4	Open tundra (lives in burrows)	Plants, small vertebrates, eggs, carrion
North American brown lemming	58–68 g	≤ 1	23	4–9	Open tundra (lives in burrows)	Feeds on herbs, cotton grass, mosses, lichens, roots
Northern collared lemming	30–112 g	3	19–21	4–8	Open tundra (lives in burrows)	Willow buds, fruits, flowers, grasses and twigs
Arctic lemming	20–30 g	≤ 4	17	5–6	Open tundra (lives in burrows)	Willows, birches, grasses, flowers
Wrangel Island collared lemming	30 g	?	?	3–6	Dry rocky slopes	Willow and birch shrubs, grasses
Brown lemming	45–130 g	≤ 1	21	2–13	Tundra meadows	Grasses, sedges, mosses
Tundra vole	25–80 g	≤ 2	20–21	3–9	Damp, densely vegetated riparian areas	Grasses, sedges, seeds
Tundra shrew	7–11 g	1	13–28?	8–12	River meadows with dense vegetation	Insects, worms, grasses
Gray wolf	23–80 kg	5–13	63	6–7	Wide ranging on all tundra habitats	Eggs, small mammals, caribou, muskox, carrion
Arctic fox	3–8 kg	12–15	46–58	3–8	Often in coastal regions; scavenge on pack ice in winter	Birds, small mammals, fish, eggs, insects, carrion
Red fox	3–14 kg	3–7	49–55	1–9	Open tundra	Birds, small mammals, fish, eggs, insects, fruit, carrion
Grizzly or brown bear	80–250 kg	20–30	180–266	2	Open tundra, coasts	Mammals, fish, carrion, insects, leaves, roots, fruit
Polar bear	150–800 kg	25–30	195–265	1–4	Arctic Ocean pack ice	Ringed seals, bearded seals, hooded seals, harp seals, walrus, sea birds, fish
Short-tailed weasel (Stoat)	25–116 g	1–2	280	4–9	Open tundra	Small mammals, birds, fish, eggs, insects
Least weasel	30–50 g	2–4	35	1–13	Open tundra	Birds, small mammals, fish, eggs, carrion, insects
Wolverine	9–30 kg	5–7	120–272	1–5	Open tundra	Birds, mammals, eggs, carrion
Walrus	600–1500 kg	30–40	331	1	Coastal marine waters; pack ice; beaches	Mollusks, crustaceans, other marine invertebrates
Hooded seal	160–300 kg	30–35	240–250	1	Coastal marine waters; pack ice, beaches	Fish, cephalopods, crustaceans
Harp seal	120–135 kg	20–35	228	1	Coastal marine waters; pack ice; beaches	Fish, crustaceans
Harbor seal	80–170 kg	26–34	253	2	Coastal marine waters; pack ice; estuaries; beaches	Fish, cephalopods, crustaceans
Spotted seal	65–115 kg	29–35	213–365	1	Sea ice in shallow waters	Fish, mollusks, crustaceans
Common seal	80–170 kg	32–40	253	1–2	Shallow marine waters and estuaries	Fish, cephalopods, marine crustaceans
Ringed seal	32–124 kg	15–28	330	1	Marine waters with ice floes and pack ice	Fish, aquatic crustaceans, other marine invertebrates
Bearded seal	200–430 kg	20–25	259	1	Shallow marine waters with ice floes and pack ice	Mollusks, crustaceans, fish
Ribbon seal	72–90 kg	20–30	300–330	1	Deep marine waters with small pack ice	Cephalopods, crustaceans, fish
Minke whale	6000–9000 kg	45–50	300–330	1	< 170 km from shore, well into pack ice	Krill, small fish
Blue whale	≤ 190,000 kg	80–90	330–365	1	Open ocean	Krill, other marine invertebrates
Fin whale	≤ 70,000 kg	75–95	330–365	1	Ocean waters > 200 m deep	Crustaceans, small fish, squid
Humpback whale	30,000 kg	77–95	342	1	Open and coastal waters, well into pack ice	95% fish, krill
Bowhead whale	75,000–100,000 kg	≤ 200	365–488	1	Shallow waters, following receding ice drifts	Crustaceans, zooplankton
North Atlantic right whale	55,000–95,000 kg	50–67	365	1	Often in coastal waters	Copepods, krill, zooplankton

Table 2 Life history information for High Arctic mammals. Data from *Animal Diversity Web* (2018) and the IUCN Redlist (<https://www.iucnredlist.org/>)—cont'd

<i>Species</i>	<i>Mass</i>	<i>Life span (years)</i>	<i>Gestation (days)</i>	<i>Litter size</i>	<i>Habitat in High Arctic</i>	<i>Diet in High Arctic</i>
Beluga whale	1350–1500 kg	25–30	425	1	Inlets, bays, shallow arctic seas, river mouths	Fish, mollusks, marine worms, crustaceans
Narwhal	900–1600 kg	30–55	396	1	In deep water around loose pack ice	Squid, fish, crustaceans
Sperm whale	35,000–50,000 kg	60–70	427–488	1	Deep waters > 1000 m	Squid (esp. giant squid), fish, sharks, skates
White-beaked dolphin	200 kg	?	?	1	Cold, open waters	Fish, cephalopods, crustaceans
Atlantic white-sided dolphin	180–250 kg	22–27	316	1	Cold, open waters > 40 m depth	Fish, mollusks, crustaceans
Killer whale, Orca	4000–7200 kg	36–63	365–547	1	In all marine waters, generally prefer depths of 20–60 m	Seals, sea lions, smaller whales and dolphins, fish, sharks, cephalopods
Long-finned pilot whale	1800–3800 kg	46–60	488	1	In deep and coastal waters	Mollusks (especially squid) and fish
Harbor porpoise	45–60 kg	12–13	335	1	Shallow coastal waters	Fish, cephalopods
Northern bottlenose whale	5800–7500 kg	35–40	365	1	In waters > 1000 m, at or near North Atlantic ice shelf	Squid, fish, benthic invertebrates
Caribou	55–318 kg	5–15	232	1	Open tundra	Leaves, roots, tubers, wood, bark, mosses, lichens in winter
Muskox	180–400 kg	14–20	228–259	1–2	Open tundra	Leaves, roots, tubers, stems, seeds, fruit, flowers, mosses, lichens

the early stages of their annual growth, but protein content and digestibility decline markedly by late summer, whereas sedges remain high in forage quality throughout the growing season. This species prefers to overwinter in willow-dominated communities, and relies heavily on willows for winter food.

Northern collared lemmings average about 12 cm in length and weigh about 40 g. Mating takes place as early as January, but extends through September. Females may have up to three litters per year, averaging 4–5 offspring per litter. Most northern collared lemmings live only 1 year, so there is a rapid turnover of individuals.

Northern collared lemming populations go through boom-and-bust cycles. Ten periods of high abundance and nine periods of low abundance of northern collared lemming took place from 1932 to 1990 in arctic North America. [Pitelka and Batzli \(1993\)](#) documented these lemming population cycles, noting that variations in lemming populations in the Northwest Territories of Canada appear to be related to a variety of factors, including the intensity of cold periods in autumn, the phenology of change from summer to winter morphology, and snow depth. Mild autumn weather and deep winter snow work together to favor high populations of lemmings, whereas cold autumn weather and shallow winter snows cause severe hardships, leading to much lower populations. These lemmings seek out the deepest snow to excavate tunnels leading to nests.

It is clear that global change is altering arctic ecosystems, starting with vegetation cover. There is also some evidence that the boom-bust cycles of arctic lemmings are changing in response to environmental disturbances ([Gill et al., 2009](#)). Because the northern collared lemming is such an important prey species in the High Arctic, any changes in its boom-bust population cycle will have serious impacts on its predators, as well. However, it is extremely difficult to predict the ecological impacts of climate change, because individual species' responses depend on various aspects of their life histories, and the different species in a food web are also affected by interactions between species. The lemming–predator community is one example of these complicated interactions. However, [Gill et al. \(2009\)](#) concluded that predicted climate change will increase the length of the lemming population cycle and decrease their maximum population densities. The smaller booms in lemming population will hurt predator populations because they are adapted to exploit the years of lemming population booms. Climate change may eventually lead to the decline and local extinction of some of these predators. Recent anomalous observations about lack of cyclic lemming dynamics in eastern Greenland may well be the first signs of a severe impact of climate change on the lemming–predator communities in Greenland and elsewhere in the High Arctic.

The brown lemming ([Fig. 5](#)) ranges across most of the Arctic. Brown lemmings also undergo population cycles that run every 4–6 years, though there is no clear pattern to these cycles. Every local population appears to have its own population cycle. Many theories have been put forward to explain lemming population cycles, in fact this topic has seen a lively debate in the ecological literature since Elton began publishing his studies in 1924. So far, theories have linked lemming boom-bust cycles with sun spots, changing weather, social stress, dispersal patterns, depletion of food resources, decline in nutritional content of food, grazing-induced chemical defenses in plants, predation by resident or nomadic predators, parasites, disease, and the structural quality of habitat. No clear answers have emerged, but it seems most likely that a combination of many of the above factors is responsible for the timing and intensity of these puzzling cycles.



Muskoxen



Red fox



Mountain hare



Northern pika



Northern collared lemming



Tundra shrew

Fig. 3 Mammals of the High Arctic region I. Photos of muskoxen and red fox courtesy of Corel Corporation. Photo of mountain hare by Alistair Kemp; photo of northern pika by Ivan Shapvalov; photo of northern collared lemming by Jeremy Gatten; photo of tundra shrew by Andrew Hope, US Geological Survey. All photos used by permission.

Fauteux et al. (2015) recently carried out a study of brown lemming population cycles on Bylot Island (73°N) in the Canadian High Arctic. They recorded population booms during the summers of 2004, 2008, 2011. Their results show that high lemming mortality causes population declines during summer and fall, which suggests that predation is sufficient to cause population crashes, whereas high winter fecundity is the primary factor leading to population booms. They noted a connection between deep winter snow and early summer survival, and suggested that deeper snow cover deters predators. It is still unclear why reproduction remains low during the low phase. Duchesne et al. (2011) also studied lemming predation on Bylot Island. They concluded that predation by short-tailed weasels was more successful where lemmings were concentrated beneath the snow, and that weasel predation was greater on collared lemmings than on brown lemmings. Snow cover did not affect the probability of predation of lemming nests by weasels, but deep snow cover limited predation attempts by arctic foxes. They also concluded that snow cover plays a key role in the spatial structure of wintering lemming populations and potentially in their population dynamics.



Caribou (Reindeer)



Grizzly bear



Arctic ground squirrel



Gray wolf



Arctic fox



Wolverine

Fig. 4 Mammals of the High Arctic region II. Photos of caribou, brown bear, gray wolf, arctic ground squirrel and wolverine courtesy of Corel Corporation.

Erlinge et al. (2011) studied interactions between brown lemmings and their food plants in northern Siberia in a transect of study sites from the Kola Peninsula to Wrangel Island. Sedges (*Carex*) form an important part of lemming diet in the Arctic. It is known that arctic sedges produce defensive chemical compounds in response to grazing pressure, and that these chemicals affect the foraging of lemmings. In particular, proteinase inhibitors (PI) are produced in response to grazing and reduce the action of the herbivore's proteolytic enzymes. This inhibits the lemmings' ability to absorb proteins from their food. Proteins are essential for animal growth and reproduction. The authors found that when levels of PI were high in the lemmings' food plants, the number of embryos per pregnant female declined significantly. This chemical defense phenomenon is not the only cause of lemming boom and bust cycles, however (Fig. 6). Predator numbers also increase in response to lemming population rises, and then decline as lemming numbers decline. In addition, there is competition within the lemming population for vital resources, such as the best foraging locations. Apparently the more mature females out-compete the younger females for the best feeding locations, and are therefore able to produce more offspring. Of course the criteria for best places for lemmings to feed must include safety from predation. The risk of being caught by predators shapes the foraging habits of lemmings, as is seen from their concentrated grazing close to runways and shelters.



Fig. 5 Mammals of the High Arctic region III. Photo of short-tailed weasel by Alberto Olivero; photo of least weasel courtesy of Free Nature Images; photo of brown lemming by Dave Krueper; photo of tundra vole by Paul van Hoof; photo of North American brown lemming by Jeremy Gatten; photo of Wrangel Island collared lemming courtesy of National Travel-RU. All photos used by permission.

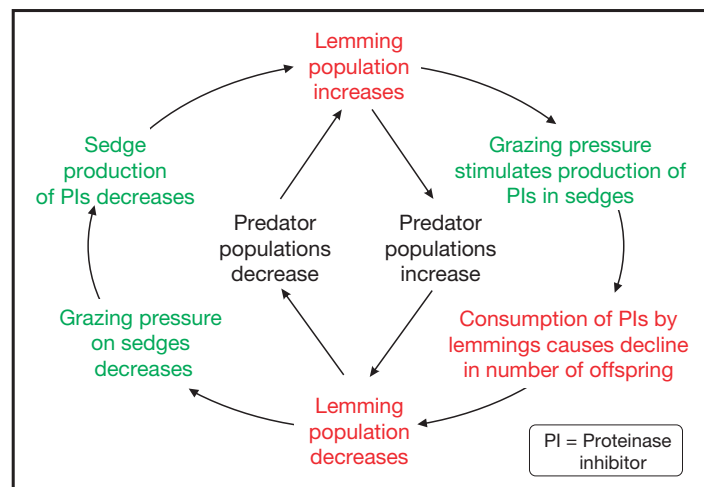


Fig. 6 Lemming-food plant-predator interactions. Concepts from Erlinge et al. (2011).

There are major differences between the diets of the brown and collared lemming (Batzli and Pitelka, 1983). Brown lemmings eat mostly grasses, sedges, and mosses, whereas collared lemmings prefer willow leaves and forbs. Brown lemming diets change with season and habitat. Monocotyledons such as grasses are always the most important food items in winter and in drier habitats mosses became a more important part of the diet. This species of lemming reaches much higher densities than collared lemmings in some regions. They prefer lower, wetter habitats than do collared lemmings. Brown lemmings appear to concentrate in higher habitats during early summer when melt water floods lower habitats, then shift to lower habitats where preferred food is more available as the waters recede. Nearly all patterns of lemming habitat use seemed to be linked to food availability.

Tundra shrew

One of the least-understood small mammals of the High Arctic is the tundra shrew (Fig. 3). This is the smallest mammal of the region, and very little is known of its habits. We do know that shrews are generally insectivores and that their very high metabolic rate dictates that they must hunt for prey almost continuously, night and day. As a group, shrews must consume 80–90% of their body weight daily, in order to survive. We also know that shrews are not able to store significant quantities of fat, so they are not able to hibernate in winter. Thus the great mystery concerning the tundra shrew: how does it survive the Arctic winter, when its prey (insects and other invertebrates) are virtually impossible to find, and cold temperatures place even higher energy demands on its metabolism? Some shrews are able to enter a condition called torpor—a state of decreased physiological activity. But without significant stored body fats, can torpor sustain them through 8–10 months of subfreezing temperatures? Until a scientific study of the life history of the tundra shrew is performed, these questions will remain unanswered.

Arctic ground squirrel

This species (Fig. 4) lives in colonies with an elaborate burrow system. A resident burrow system is used through most of the year. A 30-ha study region on the North Slope of Alaska had 66 resident burrow systems, and each system had between 20 and 50 openings at the surface. The other type of burrow system is used only for breeding. All burrows are dug in well-drained sites with low vegetation (good visibility at burrow openings is essential for predator awareness). Such localities as stream banks, glacial moraines, the flanks of pingos, and beach ridges are used.

Unlike some other arctic rodents, arctic ground squirrel populations do not go through boom and bust cycles. Arctic ground squirrels have an annual activity pattern that varies little from year to year. Hibernation begins in September or early October, followed by emergence between mid-March and mid-April. Real activity does not begin in earnest until snow cover is diminished. Summer foraging includes nightly rest periods, in spite of the round-the-clock daylight of the arctic summer. The squirrels build a substantial layer of fat in preparation for their winter hibernation. Adult squirrels build up about 350 g of fat over a period of 60–70 days prior to hibernation.

Arctic ground squirrel diet includes a wide variety of herbs (over 40 species of plants) and shrubs. Mosses, shrub leaves, meat, and eggs make up about half the squirrels' diet in early summer, while herbs, seeds, and horsetails constitute >80% of their diet in mid- and late summer. These squirrels take eggs from willow ptarmigan nests. They also prey on collared lemmings.

Arctic ground squirrels have come under intense study by biologists in recent years because of their remarkable hibernation physiology. Arctic ground squirrels are perhaps the most extreme rodent hibernator, hibernating up to 8 months of the year at body temperatures below freezing. However, they arouse every 1–3 weeks to elevate body temperature to normal levels for <24 h before re-entering torpor. Unlike some other arctic mammals, arctic ground squirrels do not hibernate communally. Individuals within colonies enter each torpor separately, and remain solitary throughout the winter (Lee et al., 2016). The minimum body temperature (T_b) recorded in ground squirrels was –2.0°C. These squirrels decrease their T_b below freezing to minimize the difference between body and ambient temperatures. They allow T_b to decrease below the ice nucleation point of their tissues and thereby minimize the thermal gradient and rate of heat loss. Richter et al. (2015) found that arctic ground squirrels maintain steady state torpor at ambient temperatures as low as –26°C. They accomplish this through a 36-fold increase in their torpor metabolic rate (TMR), compared to their minimum TMR when ambient air temperatures are at or near freezing.

Large Terrestrial Mammals

In contrast to the small mammals, the large mammals have a far smaller surface-to-volume ratio, so they lose much less internal metabolic heat to the environment. Many of these larger mammals remain active in the arctic winter, such as the polar bear, arctic fox, muskox and caribou. Their exposure to low winter temperatures is not without cost, however. All of these animals lose weight through the cold months. Grazers, including caribou and muskox, must continue to forage for food throughout the year, in order to maintain the gut micro-organisms that are essential to their digestion. Snow conditions are critical to the health and survival of grazing mammals in the Arctic. When snow cover is too deep, many grazers may starve before the end of the winter season.

Caribou

The two grazing mammals of the High Arctic are the muskox (*Ovibos moschatus*) (Fig. 3) and caribou, or reindeer (*Rangifer tarandus*) (Fig. 4). Research on the dietary patterns and overall fitness of these two species in High Arctic populations shows the striking effects of snow cover depth. A study of female barren-ground caribou on Coats Island in the Canadian High Arctic was done by Adamczewski et al. (1988). The population density of caribou on the island was 0.38 animals per km². The population density of this species in subarctic Norway is six times higher: 2.45 animals per km². Of course the carrying capacity of a given region is

closely tied to its NPP. In this study, NPP for Coats Island averaged 50–60 g per m² in mesic and wet meadows, the most productive habitats. Caribou fed almost exclusively in these meadows in summer, and their diet was dominated by willow leaves. During the year of this study, the winter snowpack consisted of hard-packed snow in depths of 50–80 cm on all low-lying vegetation. The caribou were not able to scrape away the snow with their antlers and hooves in the heavily covered lowlands. They were limited to seeking dried vegetation in places where the snow was < 20 cm deep. These shallow snow conditions were found only the slopes of wind-blown ridges and the tops of high-centered polygons. The available forage in these localities was drastically reduced in quantity and quality compared with forage available in summer. During that winter, prolonged deep snow cover killed many calves.

The stomach contents of these animals dropped from a weight of 13 kg per day in August to 8 kg per day in October, and the content changed dramatically, from willow leaves to dried grasses. The weight of stomach contents doubled by March, but the March stomach contents were dominated by highly fibrous foods with low nutritional content. The caribou burned large amounts of body fat and protein from their skeletal muscles to sustain themselves through winter.

The IUCN (2018) currently lists *Rangifer tarandus* as “Vulnerable.” This classification is due to a 40% decline in numbers over three generations (about 21–27 years) across the Arctic. Caribou numbers have declined from about 4,800,000 to about 2,900,000 individuals. There is considerable uncertainty about the under-lying causes of this decline, but one of the chief causes has been habitat changes. In particular, habitat fragmentation has been critical in parts of northern Eurasia, including the establishment of barriers (related to human activities and infrastructure development), which can disrupt migration routes and destroy seasonal habitat. Predicted future warming of climate will certainly bring habitat alterations, and will have exacerbating effects on disease transmission and parasitism including the possibility of epidemics.

While the caribou herds of the High Arctic are not likely to suffer the effects of human-caused habitat fragmentation in the near future, the effects of global warming will be amplified in the High Arctic, potentially causing large-scale changes in vegetation patterns that will affect entire ecosystems, including the grazers.

Muskox

Muskoxen face the same threats of malnutrition in the High Arctic winter. As most northern ungulates, they rely heavily on fat reserves built up over summer and autumn to get them through the snow-covered period. Mosbacher et al. (2016) performed an isotopic study of muskox hair samples to determine the quality of their forage through the different seasons. It is known that nutritional stress is particularly great on adult females that must use body stores of fat to get through pregnancy and lactation, which happen in late winter through spring. The health of muskox herds is thus strongly influenced by the nutritional state of the females. By the end of the rutting season, adult females must replenish their fat reserves to about 20% fat of their body weight in order to mate and bear young. In the summer, muskoxen forage mainly on the energy-rich grasses found in the more productive, wetter habitats. In winter their diet shifts to willows found exposed on barren, wind-swept ridges. Interestingly, this shift from summer diet of grasses to winter diet of willows is the exact opposite of the seasonal grazing pattern of caribou, discussed above. Pregnancy rates can exceed 90% in wild muskox populations, but under less favorable conditions, such as winters with deep snowpack, pregnancy rates decline, and occasionally no calves are born at all.

Gray wolf

For many people, the gray wolf (Fig. 4) is the symbol of Arctic wilderness. Driven to near extinction in most of its former range in the temperate latitudes, the wolf hangs on in the north. Males may reach 65 kg in weight, and full size is attained in the first year of life. This is a highly social animal that lives in packs that include a mated pair, the young of the year, and some yearlings. Pack size ranges from two to as many as 30, although most packs consist of less than 12 wolves. Wolves range widely in search of food. Their home ranges average about 1550 km² in northern Alaska. In the temperate zone where prey is plentiful, wolf home ranges average only about 150 km².

The arctic wolf is a subspecies or race of the gray wolf (*Canis lupus*). Year-around white coats and slightly shorter noses and ears distinguish these wolves from other races of the gray wolf, and the life of the arctic wolf is basically the same as the lives of wolves everywhere. The arctic wolf lives in the area along the northern edge of the North American continent and northward to the North Pole, as well as along the eastern and northern shores of Greenland. Several large islands occupy the region between the north edge of the continent and the Pole. Although ice and snow permanently cover much of the area, parts of these islands become snow free between mid-June and mid-August and support enough low-growing plants to feed musk-oxen, caribou, and arctic hares. These creatures constitute most of the food supply for the arctic wolves. Arctic wolf packs must hunt over vast territories to meet their needs. Many pack territories cover 2600 km² or more. Observations on wolves reveal some common patterns in their hunting habits. Wolves almost always prey on young, very old, and sick animals. Their predation of the latter two groups helps keep herds of grazing mammals healthy. Their predation on the young helps keep prey animal numbers in check.

Little is known arctic wolf movements near the northern extreme of their range in the High Arctic. There, wolves prey primarily on muskoxen and must survive 4 months of winter darkness and temperatures down to –53°C. Mech and Cluff (2011) studied the movements of a pack of > 20 wolves on Ellesmere Island (80°N latitude) using a GPS collaring system on a lead wolf in the pack. They found that the pack traveled 6640 km² from July 2009 to April 2010. This represents the largest wolf range ever reported (Fig. 7). The wolf and presumably his pack once made a 263-km foray in a nine-day winter trek. Ulf (2008) reported that an arctic wolf pack in northeast Greenland once trekked 76 km in 12 h. Interestingly, wolf pack movements during the dark winter months on Ellesmere Island did not differ from those of the rest of the year.

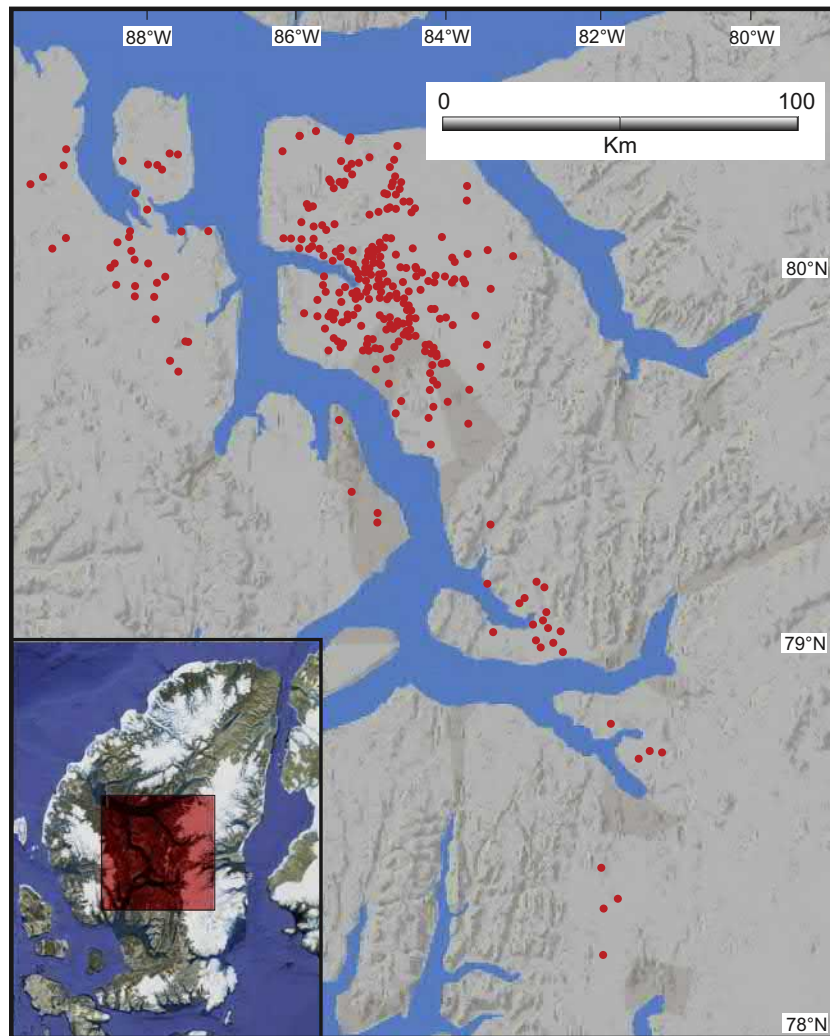


Fig. 7 Map of south-central Ellesmere Island, Canada, showing locations (*red* dots) of a wolf pack tracked by [Mech and Cluff \(2011\)](#) through the winter of 2009–2010. Inset: Map of Ellesmere Island, showing study area (highlighted in *red*).

The limited food resources of the High Arctic affect arctic wolf fitness and reproduction. A study by [Ulf \(2008\)](#) on a wolf pack in northeast Greenland from 1978 to 1998 showed a mean litter size of only two pups per litter. This represents the lowest mean litter size recorded for wolves in North America, where the overall average is 4–6 pups per litter. The most likely cause of these small arctic wolf pup litters is low availability of ungulate prey. However, the larger the wolf pack, the greater the number of pups per litter. Large packs (4–7 adults) produced significantly more pups than smaller packs. Ulf's study indicates that maximum productivity of wolves in Greenland was 58% below that of wolves elsewhere.

A detailed study of arctic wolf diet was carried out by [Dalerum et al. \(2018\)](#). They determined prey items by examining wolf scats collected at three sites in the High Arctic region of Canada and northwestern Greenland. The scats contained 55% arctic hare remains, followed by 39% muskox remains. Study of the available literature on arctic wolf diet suggests that they preferentially feed on caribou and muskoxen, but can sustain themselves on arctic hares and northern collared lemmings in areas with limited or no ungulate populations.

Brown bear and Polar bear

Until recently, the range of the brown bear, or grizzly ([Fig. 4](#)), extended north to the Arctic Sea coasts of North America and Eurasia. As their populations approach their northern limits, the home ranges of brown bears increase in size. A study by [Edwards et al. \(2009\)](#) found that male bear home ranges in the Mackenzie Delta region of northwest Canada averaged just over 1200 km² while female home ranges were about 680 km². By way of comparison, the home ranges of brown bears on the Japanese island of Hokkaido are about 28–50 km². Since about 2000, brown bears have begun appearing on the High Arctic Islands of northwest Canada. The first documented sighting of brown bears in this region came during geological fieldwork Melville Island in 2003–2004. DNA from a hair sample collected here matches brown bear populations along the northern mainland coast.

Because of their low population density in the Arctic, brown bears must also roam great distances to find mates. However, a study of mating behavior by [Edwards and Derocher \(2015\)](#) found that brown bears near the northern edge of the species' range in the Canadian Arctic devote more time and energy seeking out food, than seeking mates. Finding quality habitat with better food resources appears to take precedence over finding a mate. The recent northward advance of brown bears onto the Canadian Arctic Archipelago has brought this species into more regular contact with polar bears, with some interesting consequences. Over the last decade, brown bears have been mating with polar bears in this region. Using genetic evidence, [Pongracz et al. \(2017\)](#) were able to trace eight hybrid individuals to a single female polar bear who mated with two grizzly bears in recent years.

The polar bear's scientific name is *Ursus maritimus*—the marine bear ([Fig. 8](#)). This is a very good name for a bear that spends the majority of the year at sea, hunting from the pack ice. Their coats are pure white, year-round. This provides good camouflage when hunting on the ice, as the only parts of the bear that are not white are the eyes and the nose (they have been seen covering their black noses with their paws when stalking seals). This bear ranges across the whole High Arctic region, coming ashore in northern Canada, Greenland, Svalbard, northern Scandinavia, northern Siberia, and northern Alaska. These bears are solitary for most of the year, seeking each other out only during the mating season (March through May). Pregnant females find dens in late October through November; their dens may be on land near the coast, or on the pack ice. Pregnant polar bears that enter maternity dens in late summer/autumn may fast for up to 8 months in addition to meeting the nutritional demands of gestation and lactation. Prior to entering dens, pregnant females are obese, containing as much as one pound of fat per pound of lean body mass. While fasting, bears lose about 43% of their body mass. Of the total energy expended on maintenance and reproduction, >90% is drawn from fat stores. Fatter bears produce heavier cubs that are more likely to survive. The young are born in December, and the mother and cubs emerge from their den in late March or early April. The cubs remain with their mother for about 2 years, and females generally breed every 3 years.

Polar bears are the only truly carnivorous bears in the Arctic. Their diet consists almost entirely of meat. They are also very large, with adult males averaging 273–545 kg and females averaging 182–318 kg. The largest recorded male weighed 726 kg. The life span of the polar bear is about 25 years, but only a small proportion of polar bears live past 15–18 years.

These bears are highly mobile, as revealed by research using satellite telemetry. The movements of an adult female polar bear were monitored as she traveled from the Alaskan Beaufort Sea coast to northern Greenland. Polar bears are very proficient at hunting seals from pack ice. They are the most important predator of ringed seal. A study from the Canadian High Arctic showed that 10–24% of hunting attempts were successful, with seal pups making up 75–100% of the seals killed. Polar bears are also known attack beluga whales. Bear predation may occur when whales are entrapped by ice or while whales are passing through leads or surfacing at holes in melting ice sheets. While this predation has little effect on beluga populations, belugas are large in comparison to other polar bear prey, and may be of some local importance in polar bear diets.

Polar bears have some remarkable adaptations for life in arctic seas. Their fur appears white, but individual hairs have almost no pigment, and are hollow. These clear, hollow hairs act as tiny greenhouses to trap light and hold its warmth next to the bear's skin. Since they spend much of their time in sea water that is very near the freezing point, these bears must be well-insulated to protect against hypothermia. Their layer of blubber is up to 11 cm thick beneath the skin, and forms excellent insulation from cold water. These bears need lots of high-energy food to sustain themselves, and they consume an average of 2 kg of fat per day. A ringed seal weighing 55 kg provides enough fat to sustain a bear for up to 8 days. Polar bears digest fat more efficiently than protein.

Polar bears are currently listed as "Vulnerable" by the International Union for the Conservation of Nature (IUCN), principally because of the current and predicted future loss of critical sea-ice habitat. The IUCN predicts a decline of >30% of the polar bear population size in the coming decades. However, that projection was based on the IPCC report of 2013, which was more conservative in its sea-ice loss estimates. [Hoegh-Guldberg et al. \(2018\)](#), in the most recent IPCC report, now estimate that just a 1.5–2°C



Fig. 8 A polar bear tests the strength of thin sea ice. Photo by Mario Hoppmann, NASA.

warming above historical temperature levels will increase the risk of an ice free Arctic Ocean to 50% or higher. This loss of sea ice would mean a critical loss of habitat for polar bears. They would no longer have any effective means of hunting for seals, their primary prey.

As if habitat loss were not sufficiently threatening to polar bear survival, these top-end marine predators are also being systematically poisoned by industrial chemicals that pass up the food chain from marine plankton to fish, from fish to seals, and from seals to polar bears.

The suite of toxic chemical substances found in arctic waters includes persistent organic pollutants (POPs) such as polychlorinated biphenyls (PCBs) as well as the more recently developed POPs such as brominated flame retardants and other toxic compounds. These chemicals, and heavy metals such as mercury, tend to accumulate in the tissues of vertebrates. Because the polar seas are now contaminated by these pollutants, arctic marine life has been poisoned by them. These pollutants accumulate in the fatty tissues of marine mammals, so their concentrations become far higher than those found in organisms lower down the food chain. A summary of the accumulation of organic pollutants and mercury in Canadian arctic vertebrates by Braune et al. (2005) showed that the concentrations of PCBs in zooplankton range from about 15–55 nanograms per gram of dry weight. By the time these pollutants have passed up the food chain to polar bears, their concentration in polar bear fat is about 1000–2500 nanograms per gram of fat, or up to 166 times higher than it is at the bottom of the marine food chain.

A detailed, long-term assessment of the impacts of POPs on Greenland polar bear health was published by Dietz et al. (2018). They found that the risk quotients from exposure to POPs have been above the toxic threshold for the reproductive and immune systems of polar bears throughout all 30 years of testing (1983–2013). The risks of various cancers were also above the toxic threshold for this period.

Conclusions

The terrestrial vertebrate fauna of the High Arctic consists of just a few species of mammals that are highly adapted to the rigors of life in this highly inhospitable region. The active season is very short and food resources are extremely limited, yet these animals have adapted to these conditions, and also manage to survive the incredibly long, cold winter season. Year-to-year survival in the High Arctic is often precarious. Seemingly small changes in the environment may tip the balance for these animals. That is why the current anthropogenic changes to arctic environments are so potentially hazardous to regional ecosystems. A simplistic view might be that global warming will be of great benefit to High Arctic ecosystems, reducing the harshness of the climate and thereby making survival of the flora and fauna easier. Unfortunately this is not the case. The high arctic biota has evolved adaptations for cold climate—not warm. The muskoxen and caribou graze on the kind of herbaceous tundra vegetation that grows in a cold, dry Arctic climate. As the climate warms, this vegetation gives way to shrubby vegetation that is far less suitable for grazers. The polar bear needs pack ice cover from which to hunt seals in the Arctic Ocean. The disappearance of pack ice may open up Arctic shipping lanes for boats, but it also would eliminate critical habitat for polar bears. Persistent organic pollutants (POPs) may not have been manufactured in the Arctic, but they now reach all oceans waters of the world, even at the highest latitudes.

As the world warms, the Arctic regions warm with greater amplitude, so that a 1.5°C average global warming will likely bring warming of up to 8°C to the Arctic. During the Middle Pliocene Warm Period, the most recent time period when CO₂ concentrations were similar to present, the global temperature was > 1°C and Arctic temperatures about 8°C warmer than preindustrial levels (Brigham-Grette et al., 2013). Unfortunately, the very adaptations that fit mammals for life in the High Arctic may prove to be their downfall as their homelands become essentially uninhabitable to them.

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Plankton of the Open Arctic Ocean

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Abstract

This article deals with the marine plankton of the High Arctic region, which includes both highly productive shelf regions and polynyas, and extremely oligotrophic basins above 70° latitude. Living phytoplankton and associated heterotrophic single celled microbial eukaryotes, Bacteria, Archaea and viruses are suspended in the water column. Zooplankton are also displaced by currents, but are often vertically mobile and migrate up and down the water column. The plankton form complex trophic webs that support substantial populations of marine mammals and birds. Phytoplankton and other microbial eukaryotes are the primary food for crustacean copepods that account for much of the plankton biomass in the Arctic Ocean. Microbial plankton are also food for gelatinous zooplankton, which can occasionally form blooms in the high Arctic. The upper waters of the Arctic are relatively less saline than deeper waters, creating a stratified water column separating the photic zone from the nutrient rich deep waters. The lack of light for much of the year combined with ice cover, constrains annual photosynthetic productivity by the phytoplankton. Under a warming climate, early ice melt and increasing open waters could increase net production, however ice-melt also adds fresher less dense water to the surface leading to greater stratification, preventing nutrients from entering the photic zone. This means that although some marginal seas of the Arctic may see increased production, the high Arctic could actually become more oligotrophic and unable support displaced populations of marine mammals that rely on ice during much of their life cycles.

Introduction

The Arctic Ocean is surrounded by land with inputs of Atlantic-origin water through Fram Strait and the Barents Sea, Pacific-origin water through Bering Strait to the Chukchi Sea shelf and large freshwater inputs from the surrounding continents of Eurasia and North America. Upon entering the Arctic, the Pacific and Atlantic water masses move below the surface mixed layer and flow across relatively shallow (200 m) shelves before entering the two main Arctic basins, which are separated by undersea ridges. Water is constrained and circulates within the basins, and the timing and extent of waters flowing out of the central Arctic is strongly linked to the Atmospheric Oscillations in the Arctic and North Atlantic (Proshutinsky et al., 2015). Within the Arctic Ocean, waters are

substantially modified by physical and biogeochemical processes prior to flowing into the North Atlantic via several routes: Fram Strait east of Greenland, the complex straits and channels of the Canadian Arctic Archipelago and Nares Strait, which is between Greenland and Ellesmere Island Canada (Williams and Carmack, 2015).

Light and nutrient availability generally limit production in the Arctic Ocean, with multiyear ice persisting in higher latitudes, while other regions are covered with seasonal ice well into June or July. The complex currents and circulation in the Arctic Ocean result in major differences in overall productivity among Arctic regions. The most productive areas in the High Arctic are across the inflow shelves and in polynyas, which are open waters surrounded by ice. Most Arctic polynyas occur where wind and latent heat maintain ice free conditions, or by tidal forcing within smaller inlets. For these polynyas, the early access to light and resuspension of nutrients prolongs the normally short arctic phytoplankton bloom (Booth et al., 2002), which helps maintain diverse zooplankton communities (Dvoretzky and Dvoretzky, 2015).

Until recently, the productivity of the deep basins has been primarily limited by light, which is blocked by thick multiyear ice preventing photosynthesis in summer. This is changing because the Arctic is warming more rapidly than global averages and much of the multi-year ice is becoming seasonal (Bluhm et al., 2015). However, higher productivity may not necessarily follow, as nutrients can remain trapped below the upper mixed layer and out of the euphotic zone (Hunt et al., 2016). Given the few connections between the Arctic and the World Ocean, it is not surprising that, just as many marine mammals are endemic and confined to the Arctic, so too are many of the planktonic species that support them.

Plankton refers to taxonomically and functionally diverse aquatic organisms that passively move with ocean currents. Plankton range in size from submicron ($<0.1\ \mu\text{m}$) to decimeters or even meters in the case of jellyfish and other colonial zooplankton (Purcell et al., 2010). Plankton historically were classified into the functionally defined categories of phytoplankton and zooplankton, a bifurcation that followed an Aristotelian view of the natural world consisting of plants and animals. The analogy with plants was logical since phytoplankton have chloroplasts and carry out photosynthesis and zooplankton are animals visible to the naked eye and at the base of a food chain leading to the larger animals that are harvested from the sea for food and material goods.

As tools for examining biodiversity have expanded, first by way of high-resolution microscopy, and more recently using molecular techniques, it is clear that plankton in the Arctic and elsewhere are much more diverse than previously imagined. This holds true for both the visible zooplankton, where species and populations are more easily distinguished using DNA markers (Choquet et al., 2017) and more profoundly among the microscopic, mostly single celled plankton that include three domains of life: Eukaryota, Bacteria and Archaea (Pedros-Alio et al., 2015), and the viruses that infect them (Gregory et al., 2019). The plummeting cost of DNA sequencing has resulted in a proliferation of environmental gene surveys that are able to distinguish the staggering range of evolutionarily distinct lineages within microscopic plankton. The small subunit ribosomal RNA gene (SS rRNA) is particularly useful since it is universal and has both conserved regions amiable to primer design and variable regions that can be used as genetic markers. The 16S rRNA gene for Bacteria and Archaea and the 18S rRNA gene for Eukaryota are suitable for reconstructing evolutionary relatedness (phylogeny) and identifying organisms, often to the level of species. One result of the now widespread use of SS rRNA gene surveys is the realization that microscopic plankton form complex ecological systems, rather than linear food chains. The interactions among microbial plankton maintain global ecosystem services, such as carrying out key steps in carbon, nitrogen and sulfur cycles and producing about half of the oxygen in the atmosphere. Of relevance here is that microscopic plankton maintain the biodiversity of animals in both pelagic and benthic habitats in the Arctic, and more generally in the Global Ocean. Here I provide a brief introduction to the planktonic zooplankton in the Arctic, followed by more detailed descriptions of the newly appreciated diversity of the microbial eukaryotic plankton, with a brief summary the co-occurring Bacteria and Archaea.

Metazoan Zooplankton

Metazoan zooplankton are true animals and, in the Arctic Ocean, as elsewhere, include an array of invertebrates, including some invertebrate larval stages as well as larval stages of fish (ichthyoplankton). However, here we focus on zooplankton that are planktonic for their entire life cycle. The majority of zooplankton actively swim and have some control over their vertical position in the water column. Copepods in particular carry out daily and seasonal vertical migrations (Darnis et al., 2017). Newly hatched invertebrate zooplankton live for months to years and most have well defined life cycles, with feeding and egg production closely tied to ice algal and phytoplankton productivity (Leu et al., 2011; Dvoretzky and Dvoretzky, 2015), with predictable seasonal cycles. Most deep water species are also found within specific depth ranges across the Arctic's central basins (Kosobokova and Hopcroft, 2010).

Arctic zooplankton are taxonomically and trophically diverse, ranging from species that consume bacteria and single celled microbial eukaryotes to those that prey on other zooplankton. Around one-quarter of the zooplankton species found in the Arctic are restricted to the Arctic, with most other species shared with the plankton fauna of the North Atlantic or North Pacific (Lovejoy et al., 2017). By far the best-studied zooplankton in the Arctic are copepods. These are estimated to account for 80–90% of the zooplankton biomass in the Arctic, with over 150 copepod species among the c. 350 zooplankton species reported for Arctic (Bluhm et al., 2011).

Copepods are directly consumed by many fish, some seabirds, and baleen whales (Darnis et al., 2012). Three species of *Calanus*, with somewhat similar life cycles, dominate Arctic zooplankton; *C. glacialis*, *C. hyperboreus*, *C. finmarchicus*. All three species feed in surface waters during spring and summer with daily migrations in and out of the photic zone. They migrate to deeper waters over winter, triggered by day-length or in response to “adequate” lipid stores (Hafker et al., 2018; Schmid et al., 2018). Once in the deep

waters they maintain low metabolic rates referred to as diapause until spring, when they return to the surface in response to physiological or environmental signals.

Larger crustaceans such as hyperiid amphipods and euphausiids (krill) feed on smaller zooplankton and in turn serve as prey for marine vertebrates. Arctic euphausiids are mostly reported at the inflows to the Arctic and in more productive regions, but are almost absent from the central basins (Lovejoy et al., 2017). The most widespread free-living hyperiid amphipods are species of *Themisto*.

Another ubiquitous zooplankton group in the Arctic Ocean and surrounding seas are the appendicularian tunicates *Oikopleura vanhoeffeni* and *Fritillaria borealis*, which are widespread in productive open water regions of the Arctic (Deibel et al., 2017). Appendicularia are suspension feeders, making a mucilaginous “house” that collects bacteria and small phytoplankton. The “house” and trapped prey are subsequently consumed by the animals, creating a key linkage between the smallest microbial plankton and higher trophic levels.

Microbial Plankton

Phytoplankton are colored and as in higher plants, the primary pigment used for photosynthesis is Chlorophyll *a* (Chl *a*). Other pigments such as beta carotenoids and mycosporine-like amino acids are photoprotective and absorb harmful UV radiation. Phytoplankton species range in size from 1 µm to over 200 µm and while many are single celled others are colonial, and can occur as ribbons of cells, spheres or beautifully arranged branching colonies. While by definition all phytoplankton are photosynthetic, many species can also capture bacteria and other small cells for energy and nutrients, making them mixotrophic. Other microbial eukaryotes are heterotrophic and include bacterial grazers that adhere to particles and consume attached bacteria, and predators that capture bacteria or other eukaryotes using a variety of techniques. With few exceptions the microbial eukaryotes are food for macroscopic zooplankton.

Under natural light, the Chl *a* molecule is green, but other cellular pigments and cell structures often mask the presence of chlorophyll in both live and preserved samples. A useful characteristic of Chl *a* is that it fluoresces red when excited by blue wavelengths of light, which makes it simple to visualize even tiny chloroplast-containing cells using epifluorescence microscopy (Fig. 1). With rare exceptions, arctic phytoplankton are microbial eukaryotes with membrane-bound chloroplasts. These microbial eukaryotes are evolutionarily diverse with lineage-specific ancillary pigments that can be used to characterize bulk communities in the Arctic (Vidussi et al., 2004). Aside from Chl *a*, the major pigments used to capture photons include chlorophylls *b* and *c*₁, *c*₂ and *c*₃ and several other specific pigments including fucoxanthin (Fuco) and prasinoxanthin (Pras).

Established classification systems following botanical and zoological nomenclature rules do not accurately reflect our current understanding of the evolutionary histories of microbial eukaryotes. Higher order taxonomic relationships are in flux, and as more genomes become available, emerging phylogenies are only partially reconciled with established taxonomies. More detail on recent higher order classifications can be found in (Adl et al., 2019). Adl et al. (2019) also attempted to standardize functional terminology and I follow their suggestions here, with the exception that I use the more common term flagella, rather cilium, for cellular structures that are primarily involved in physical displacement of free living cells. The approach here is to discuss the more common groups of phytoplankton and single celled heterotrophs, and to mention ecological interactions with viruses, bacteria and zooplankton, where known.

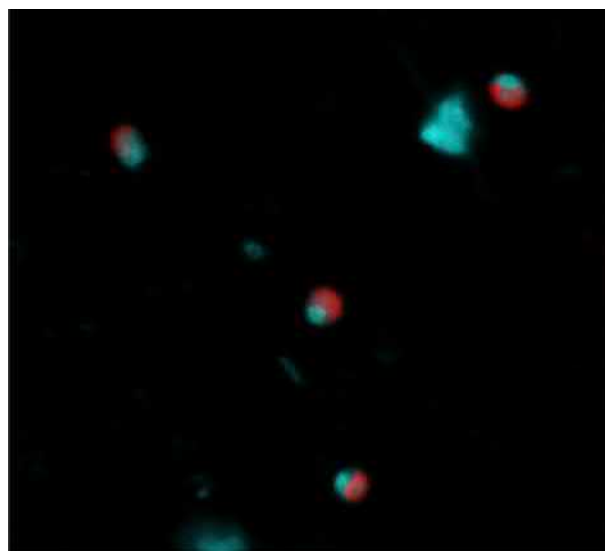


Fig. 1 Epifluorescence image of 4 *Micromonas polaris* cells and an unidentified heterotrophic flagellate with DAPI stained nucleus (blue). Chloroplasts in red. The *M. polaris* cells are c. 1.5 µm. Sample from the North Water Polynya, Credit: C. Lovejoy.

Chlorophyta

Chlorophyta or “green algae” are green due to the presence of an additional chlorophyll pigment, chlorophyll *b*, which is also found in land plants. They are taxonomically diverse with a dozen or so major evolutionary lines, many of which are found only in freshwaters. The chlorophytes in Arctic phytoplankton are mostly confined to three major lineages; Chlorophyceae, Mamiellophyceae (Mamiellales) and Pyramimonadales. The Chlorophyceae in the Arctic mostly occur in sea ice and melt ponds (Poulin et al., 2011) and are rare in the plankton, but several *Chlamydomonas* species may occur in the plankton associated with sea ice melt. The Mamiellales are mostly smaller than 5 µm with three picoplankton (<2 µm) size genera; *Micromonas* (Fig. 1), *Bathycoccus*, and *Ostreococcus*, with *Ostreococcus* restricted to warmer regions and not found in the Arctic. Molecular analysis has recently revealed that the genus *Micromonas* contains multiple species including one likely Arctic endemic species *M. polaris* (Simon et al., 2017), which dominates the pico-sized phytoplankton in most Arctic marine waters (Lovejoy et al., 2007). Other *Micromonas* spp. and *Bathycoccus prasinos* are also recovered in molecular gene surveys, usually at lower proportions compared to *M. polaris*. These may reflect seasonal differences or complex host-viral interactions (Joli et al., 2017). The two genera differ, despite their similarly tiny size, in both morphology and behavior, with the *Micromonas* being motile with one short flagellum and *Bathycoccus* having scales that may serve a defensive role. One other genus in the Mamiellales, *Mantoniella*, is slightly larger and occasionally reported. The third green algal group, Pyramimonadales are often reported from microscopy, in marker gene surveys and from culturing studies, with *Pyramimonas* the most common genus. *Pyramimonas* species tend to be bright green and with 4 flagella but can have up to 8. A number of species are likely to be restricted to the Arctic (Daugbjerg and Moestrup, 1993; Balzano et al., 2012; Haroardottir et al., 2014). This genus has also been associated with ice and ice to open water transitions (Haroardottir et al., 2014).

Cryptophyceae

Cryptophytes have two unequal flagella that move independently in the forward and reverse directions, enabling them to swim short distances. Many cryptophytes are easily recognized by general morphology with droplet-shaped cells, the two flagella and furrow-gullet complex referred to as an oral groove. Cryptophytes are also mixotrophic and capture small prey items, such as bacteria. This provides considerable metabolic flexibility, enabling the cells to function in both photosynthetic autotrophic and heterotrophic modes. The photosynthetic cryptophytes contain chlorophylls *a* and *c*₂, xanthophylls and blue-green or red phyco-biliproteins that fluoresce bright red or orange under epifluorescence microscopy. At least one endemic species *Baffinella frigidus* has been isolated from the Arctic, and tolerates a range of light and salinity conditions but not temperatures above 9 or 10 °C (Daugbjerg et al., 2018). Other genera such as *Teleaulax* and *Rhodomonas* have been reported from microscopy but molecular gene surveys suggest that these may also be divergent and represent new species (Lovejoy et al., 2006). One cryptophyte genus reported in the Arctic is *Goniomonas* (Poulin et al., 2011). This genus lacks functional chloroplasts and requires bacterial prey. In addition, distantly related to the cryptophytes, are the kathablepharids, which are also colorless predators targeting bacteria, and are occasionally reported both from microscopy and 18S rRNA gene surveys in the Arctic.

Stramenopiles—Heterokonts

Stramenopiles include lineages that have, or ancestrally had, two structurally different flagella at some stage in their life cycle. The term heterokont refers to the flagella, one smooth and the other called a flimmer flagellum because it is covered in the small hair-like structures called tripartite mastigonemes. The higher-level botanical classification Heterokonta was applied to brown and golden algae and has been largely replaced by the more inclusive term Stramenopiles. This major branch of eukaryotes includes single cells ranging from 1 µm diameter to giant kelp. While many are photosynthetic, there are also parasitic and heterotrophic representatives that do not have functional chloroplasts. The planktonic lineages detailed below are ubiquitous with pan-arctic distributions.

Chrysophyceae

Chrysophytes contain chlorophyll *a*, chlorophyll *c*, and are often called golden algae because of the presence of fucoxanthin, a yellowish-brown carotenoid pigment. Currently five Order level lineages are recognized with four of these being found mostly in freshwaters. Most marine chrysophytes are in the order Ochromonadales, with several species common in the arctic phytoplankton. Many chrysophytes are unicellular and free swimming, but others such as *Dinobryon* live in vase-shaped loricae, made of chitin fibrils and polysaccharides. Several species of solitary *Dinobryon* have been reported from the Arctic, but the most common and sometimes very abundant species is *D. balticum* which forms large colonies, with the lorica arranged in a way that resemble branching trees, and a with a single cell within each lorica (Fig. 2). *Dinobryon*, as well as single celled ochromonads, are mixotrophic. Several single celled Arctic ochromonads have been isolated and maintained in culture, including one undescribed species (CCMP2298) that requires bacteria or high concentrations of organic matter for growth, since it cannot take up inorganic nitrogen (Terrado et al., 2015). Another common ochromonad genus in the Arctic, *Spumella* is colorless (Balzano et al., 2012) and requires bacteria or organic matter for both carbon and nitrogen.

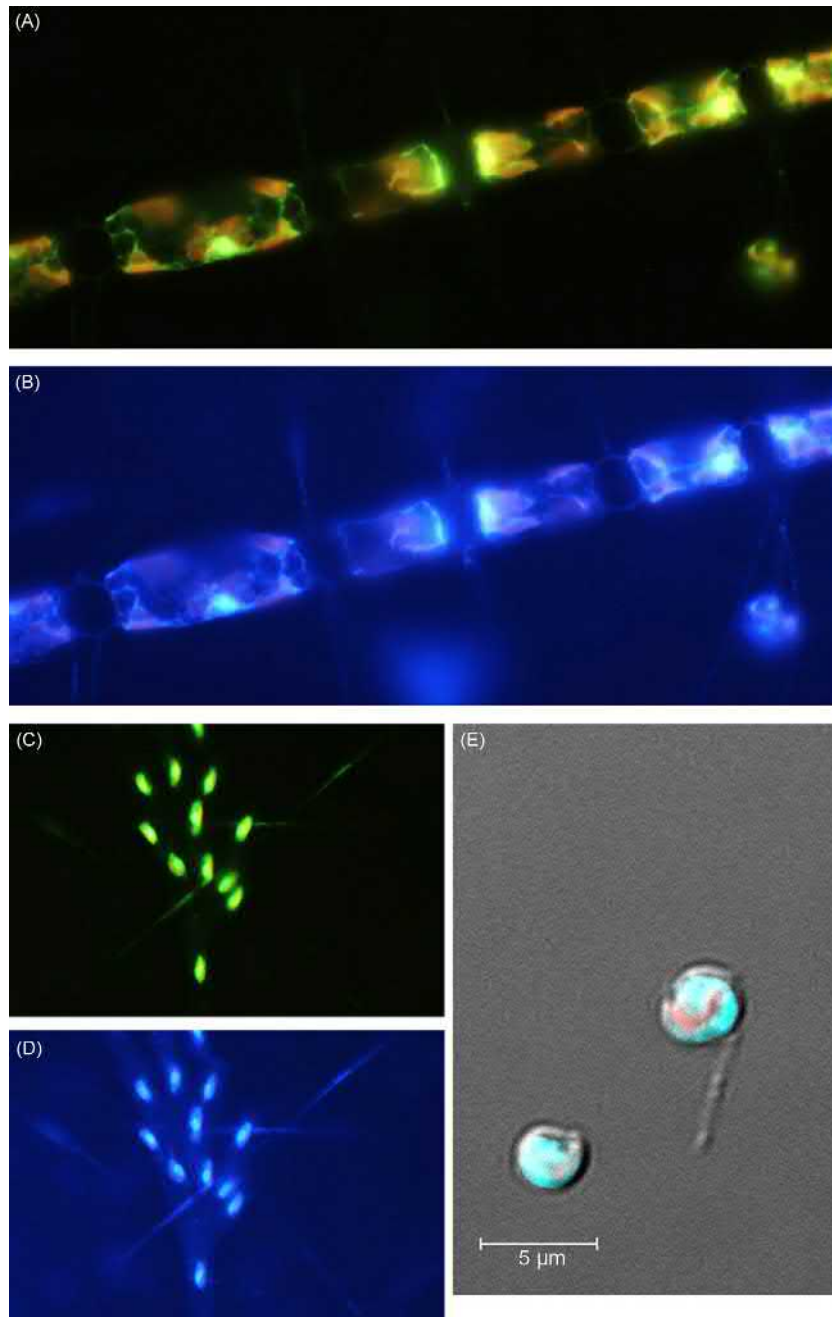


Fig. 2 Stramenopiles: (A and B) chain of *Chaetoceros gelidus*, (A) under blue excitation showing chloroplasts in red, (B) blue nucleus seen under UV excitation after staining with the DAPI fluorochrome; (C and D) *Dinobryon* colony, (C) under blue excitation, showing chloroplast (red) and nonspecific autofluorescence (green) and (D) under UV excitation with DAPI; (E) free living *Ochromonas*, false color composite of a confocal laser microscopy image, chloroplast appears red and large nucleus is blue. Credit: (A–D) Nathalie Joli and C. Lovejoy. (E) Marianne Potvin and C. Lovejoy.

Pelagophyceae

Pelagophytes are small usually coccoid cells, with one or two flagella usually present (Fig. 2). They are distantly related to the chrysophytes with ancillary chlorophylls c1 and c2. They first came to the attention of phycologists when they were identified as sources of harmful algal blooms forming “brown tides”. To date, brown-tide forming species of pelagophytes have not been conclusively found in the Arctic, but several diverse undescribed pelagophytes have been recovered in molecular surveys (Lovejoy et al., 2006; Marquardt et al., 2016) and have cultured representatives (Terrado et al., 2015; Balzano et al., 2012). Pelagophyte blooms appear to be linked to coastal hydrological changes and nutrient enrichment, and should be monitored in the Arctic.

Dictyochophyceae

There are two recognized orders of Dictyochophyceae found in the Arctic Ocean: Dictyochaetales with silica skeletons present for at least part of their life cycle and Pedinellales. The Dictyochaetales have been reported from the Arctic for over 100 years and are easily recognized by their distinct skeletons, using light microscopy (Lovejoy et al., 2002a,b). The second order consists of both chloroplast-containing and aplastidic genera, that tend to attach to particles and capture passing bacteria. The chloroplast-containing Dictyochophyceae are mixotrophic and also prey on bacteria. At least one Pedinellales is recorded from gene surveys, has cultured representatives and is likely endemic (Terrado et al., 2015).

Bolidophyceae–Parmales

These small cells are phylogenetically related to diatoms. They occur as either rapidly swimming cells (bolidophytes) or non-motile cells covered in silica plates (parmales). The ridges of the plates can be quite decorative. The morphologically distinct parmales were first identified using scanning electron microscopy on samples from cold waters, whereas the bolidophytes were isolated and then characterized genetically. It was only later that it was realized that they were related and it has been suggested that they represent different life stages (Ichinomiya et al., 2011). Bolidophytes and Parmales are ubiquitous in Arctic plankton but are rarely found at high relative concentrations.

Diatoms

In the Arctic diatoms occur as either solitary or joined, often resembling chains and ribbons (Fig. 2), and are both planktonic, and a major component of the ice algae. Diatom cells range from 2 µm to over 200 µm in diameter. Because they rely on silicon for cell wall formation, growth and reproduction of diatoms is often limited by silicon supply. Diatoms have complex life cycles, where cells typically become smaller with multiple divisions due to the constraints of their silica cell wall, and after an extended pelagic growth phase form larger cells usually following sexual recombination (D'Alelio et al., 2010).

Diatoms are among the most abundant, widespread and productive phytoplankton in Arctic waters, and serve a central role in planktonic food webs. Recently re-examination of the morphological details and the availability of molecular phylogenies have upended the traditional Centric versus Pennate diatom dogma. Today, generally three major lineages are recognized, however with more molecular data becoming available from more taxa this may change. What were previously called centric diatoms are now divided into two major lineages corresponding to the Classes Mediophyceae and Coscinodiscophyceae, with the pennate Bacillariophyceae remaining as a third Class. The Coscinodiscophyceae encompasses radially centric groups that look like round pill boxes. In the Arctic these round diatoms include large *Coscinodiscus* species that occur early in the spring bloom (Lovejoy et al., 2002a,b) and are an important source of nutrition for the largest arctic copepod *Calanus glacialis*. The second lineage, Mediophyceae can appear to be quite round, for example *Thalassiosira* spp., but have two or more poles of centricity. Mediophyceae includes many of the iconic late spring and summer diatoms including two arctic species of *Chaetoceros*, *C. gelidus* (Chamnansinp et al., 2013), and *C. neogracilis* (Balzano et al., 2017), and *Thalassiosira* species that form necklace like strings of cells in late spring. *Thalassiosira antarctica* var. *borealis* and several other species may be restricted to the Arctic and often co-occur with more boreal species (Luddington et al., 2016).

The pennate Bacillariophyceae are much more common in the ice where they live in brine channels and are released to the water column when sea ice melts in spring. These ice algae sink rapidly out of the photic zone but are occasionally recovered in plankton nets. During the spring bloom ribbon chains of several species of diatoms can also dominate biomass (Fig. 5) Later in the season the planktonic pennate genus, *Pseudo-nitzschia*, can release a toxin that causes amnesia in vertebrates (D'Agostino et al., 2017). For instance, marine mammals become disoriented and forget to feed their young. *Pseudo-nitzschia* species are consistently reported from the Arctic but usually at low concentrations and at least one species *P. arctica* may be endemic (Percopo et al., 2016). The causes of toxin producing *Pseudo-nitzschia* blooms are unclear, but may be related to overall nutrient ratios, and the availability micronutrients such as iron. In the Baffin Bay region, *Pseudo-nitzschia* could be favored by the input of micronutrients from the melting of the Greenland Ice Sheet (Joli et al., 2018). In essence there is a real danger of blooms becoming more common and releasing toxins (Harardottir et al., 2015) and potential harm to marine mammals should not be ignored.

Marine Stramenopiles (MASTs)

The MASTs consist of clades of Stramenopiles that are mostly uncultivated and known from 18S rRNA gene surveys. Seven MAST clades are reported from the Arctic (MASTs 1a, 1b, 1c, 2, 3, 7 and 8) and tend to occur in upper waters (Monier et al., 2013), where the higher productivity by the photosynthetic groups supports bacterial prey for these small heterotrophs.

Haptophyta

The most conspicuous, well-known haptophytes, are coccolithophorids that are covered in calcium carbonate “coccoliths,” which are the source of ancient deposits of calcareous earth. Arguably the most successful haptophyte on Earth is *Emiliania huxleyi*, which forms vast blooms in the North Atlantic and elsewhere. However, to date, no blooms have been reported from the Arctic, and coccolithophorids tend to be absent from High Arctic molecular gene surveys. Non-coccolithoid haptophytes fall into two major clades: the Prymnesiophyceae and the Pavlovaales. Both lineages are primarily unicellular, with chlorophylls a and c, and are often a golden-brown color because of the presence of the carotenoid accessory pigments diadinoxanthin and fucoxanthin. The motile

Prymnesiophyceae usually have two equal flagella and a haptonema, which is a filamentous appendage that is used for capturing bacteria and small phytoplankton prey.

Two genera of Prymnesiophyceae are frequently reported from the Arctic: *Chrysochromulina* and *Phaeocystis*. Several *Chrysochromulina* species are able to produce ichthyotoxins, which can harm or kill fish, but to date no such events have been documented in the Arctic. Both genera produce dimethyl sulfide (DMS), which can form cloud nuclei when released to the atmosphere, but is usually rapidly scavenged by marine bacteria as a source of organic carbon and sulfur (Motard-Cote et al., 2012). At low concentrations DMS is associated with the “smell of the sea” but at high concentrations is noxious-smelling and can alter fish migration routes. *Phaeocystis pouchetii* can occur as either small motile single cells or form larger gelatinous colonies composed of non-motile cells. In less oligotrophic Arctic regions *Phaeocystis pouchetii* proliferates toward the end of the spring diatom bloom, when silicon concentrations tend to limit diatom growth. This species seems to be quite flexible and persists over the polar night (Vader et al., 2015) and has also been implicated in under-ice blooms (Kauko et al., 2019). In contrast to the Prymnesiophyceae, Pavlovales are rare. The small solitary cells have one or two visible flagella and a rudimentary haptonema. A cultured representative referred to as CCMP2436 in Terrado et al. (2015) although not yet described, is likely endemic (Fig. 3).

Alveolates

Dinoflagellates and ciliates form a monophyletic super group referred to as Alveolates. Ciliates and dinoflagellates tend to have larger cells and contain large genomes and multiple copies of rRNA genes, which means that they tend to be over-represented in gene marker surveys. Apart from spring diatom blooms, these large cells also dominate net plankton (>50 µm). Because they tend to capture and eat phytoplankton, they are often referred to as microzooplankton. The efficacy of microzooplankton grazing in the Arctic varies (Sherr et al., 2009).

Dinoflagellata

Dinophyceae, referred to as core dinoflagellates, range from less than 10 µm to over 1000 µm and although often occurring as single cells, many species can also form long swimming chains. The core dinoflagellates usually have two flagella, with one transverse and the other longitudinal. In combination, this results in rapid forward and lateral movement (Video 1 in the online version at <https://doi.org/10.1016/B978-0-12-409548-9.11979-7>). Dinoflagellates are surrounded by a complex covering called the amphiesma, which consists of outer and inner continuous membranes, and between which lie a series of flattened vesicles. In armored forms, these vesicles contain cellulose plates called thecae. The surface plate patterns of theca are used to classify dinoflagellates. If this armor is lacking or shed under certain environmental conditions, the cells are called athecate. Even for athecate species, patterns similar to plate patterns can be discerned using transmission electron microscopy, these are used in their taxonomic classification. Under epifluorescence microscopy dinoflagellates tend to be easy to recognize when stained using a nucleic acid fluorochromes as the nucleus appears to be granular since their chromosomes lack histones and are not condensed (Fig. 4A).

Around half of described dinoflagellates are photosynthetic, possessing chlorophyll *a*, other chlorophylls and often the carotenoid peridinin. Non-peridinin dinoflagellates seem to be particularly common in the Arctic (Onda et al., 2017). Among these are dinoflagellates, which have acquired chloroplasts from other algae, including prasinophytes, haptophytes, cryptophytes

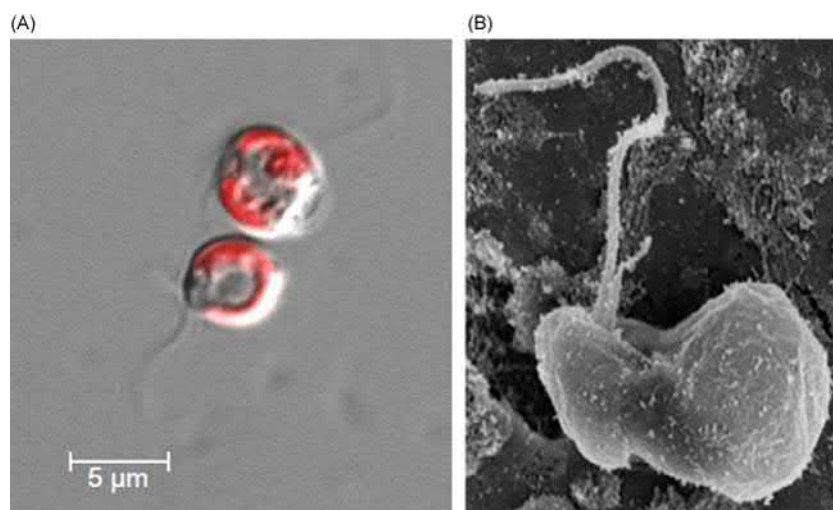


Fig. 3 (A) Two cells from a culture (CCMP2436) of a Pavlova (Haptophyta) from Northern Baffin Bay. False color composite of a confocal laser microscopy image, showing the position of the chloroplasts in the cell. Note the unequal flagella in this species, the vestigial haptonema is not visible in the light micrograph. (B) Scanning Electron Microscope image of a cell from the same culture after critical point drying to see surface features, kindly provided by Dr. Wenche Eikrem at the Department of Biosciences, University of Oslo.

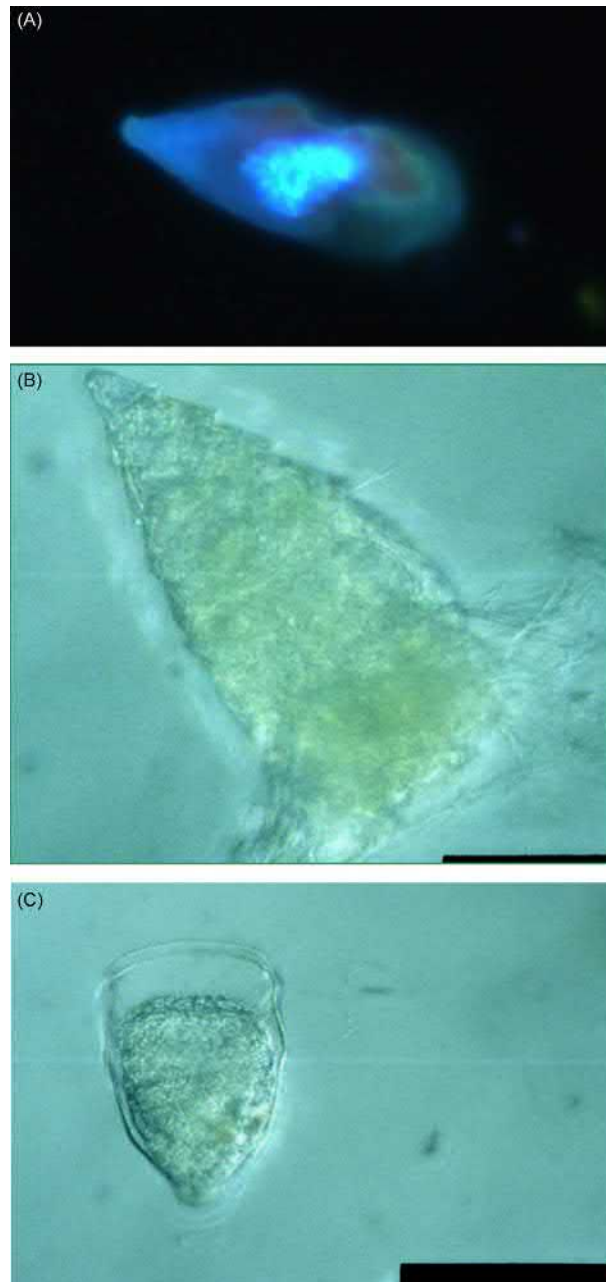


Fig. 4 Alveolates: (A) Dinoflagellate, *Gyrodinium* sp. under UV excitation showing large nuclei in blue. This cell is c. 20 μm long; (B) Oligotrichous ciliate, *Laboea strobila*, green color is from chloroplasts captured from prey; (C) Tintinnid ciliate *Ptychocylis obtusa*. The black scale bar (B and C) is 25 μm .

and even diatoms (Janouskovec et al., 2017). Most photosynthetic dinoflagellates are facultative heterotrophs, engulfing and ingesting bacteria and phytoplankton as prey. Dinoflagellates can form large, and in some cases harmful, blooms but to date none have been reported in the Arctic. However, microscopy and 18S rRNA gene surveys have revealed the presence of potentially harmful genera including *Gyrodinium*, *Dinophysis* and *Prorocentrum* (Poulin et al., 2011; Onda et al., 2017).

Approximately 50% of dinoflagellates lack functional chloroplasts and need to feed on other microscopic plankton. The larger thecate forms tend to prey on other phytoplankton and ciliates using an incredible array of attack and ingestion methods, for example some single celled dinoflagellates can consume entire chains of diatoms (Jacobson and Anderson, 1986). Several dinoflagellates produce light through bioluminescence, which can be seen during the Polar night (Cronin et al., 2016). Dinoflagellates also have complex life cycles with both asexual and sexual stages forming cysts (Video 1 in the online version at <https://doi.org/10.1016/B978-0-12-409548-9.11979-7>) that are able to survive in the sediment over long periods of time. For many of these cysts the vegetative form of the cell is unknown and paleo-oceanographers have devised a separate cyst-based taxonomy based on cyst morphology to reconstruct past climates (de Vernal et al., 2013). However, many of these dinoflagellates are not ancient extinct

forms and accurate interpretation of climate proxies would benefit by matching living dinoflagellates with their cysts (Potvin et al., 2013). This also highlights the more general problem that a high proportion of dinoflagellates from Arctic samples cannot be identified to species from their 18S rRNA. An additional marker gene, such as the Large Subunit of the rRNA gene, seems to be needed to separate dinoflagellate species. Most smaller athecate species, which are particularly common in the Arctic (Onda et al., 2017), (Fig. 4A) have not been morphologically described, and there are few reports matching morphological and genetic data. In parallel, there are many morphological species of dinoflagellates that have been validly described, but have only been reported once (Thessen et al., 2012), increasing the difficulty of reconciling gene markers with morpho-species.

Distinct from the core dinoflagellates are Syndinales. Known species are parasites on zooplankton, fish and other protists. The Euduboscquellidae, which target ciliates and Radiolaria and the poorly known Ellobiopsidae that parasitize copepods, are almost always recovered in Arctic gene surveys along with Amoeboophryidae that target core dinoflagellates (Onda et al., 2017). The majority of the Syndinales are known only from gene surveys and are referred to as different clades of Marine Alveolates or MALVs. These seem to be particularly common in the Arctic and can dominate 18S rRNA gene surveys.

Ciliates

Ciliates, like dinoflagellates, tend to be larger and the literature on morphological species for the most part has not been paired with molecular surveys. In particular, tintinnid ciliates are characterized by their loricas (Fig. 4C) and some species appear to be widespread in the Arctic (Dolan et al., 2017). This is in contrast to molecular marker studies in which many ciliates can only be identified to the order level of order or higher, because of a lack of reference sequences. As with dinoflagellates, there is a need to closely examine the validity of species that are only known from their original morphological descriptions. One advantage of gene surveys is that it is evident that certain ribotypes are widespread in the Arctic, with pan-arctic distributions (Onda et al., 2017; Lovejoy et al., 2006; Marquardt et al., 2016). Many ciliates in the Arctic also appear to be kleptoplastidic, meaning that they acquire and maintain the chloroplasts of specific co-occurring algae over long periods of time. These include the common coastal species complex *Mesodinium rubrum* and *Laboea strobila* (Fig. 4B).

Other Heterotrophic Groups

Heterotrophic groups with diverse prey preferences and feeding strategies need to be considered in the wider context of how the planktonic biome of the Arctic Ocean functions. A brief summary of the most frequently encountered groups follows.

Rhizaria

Rhizaria are a supergroup of diverse lineages of microbial eukaryotes that have pseudopodia used for feeding and movement. They range from small (5–15 µm) flagellates to >500 µm cells with mineral skeletons or spines. Among the smaller Rhizaria are the Cryomonadida, represented by the pan-arctic genus *Cryothecomonas*, (Fig. 5B), which is associated with ice edge blooms and likely parasitizes diatoms (Thaler and Lovejoy, 2012). Other Rhizaria were first collected in the 19th century and described by Haeckel (Caron, 2016). Most of the major lineages have been reported from the Arctic. These include Phaeodrea, Acantharea, Taxopodida, and Polycystinea (Lovejoy et al., 2006; Monier et al., 2013; Dolan et al., 2014; Ikenoue et al., 2019). Many of these species evidently form complex symbiotic relationships with other organisms and further ecological work in the Arctic is needed.

Choanoflagellata

Choanoflagellates are small cells (5–20 µm) with a single flagellum that is surrounded by a distinct “collar,” used to capture and ingest bacterial prey (Fig. 5A). The choanoflagellates are distantly related to animals and fungi. The majority of choanoflagellates

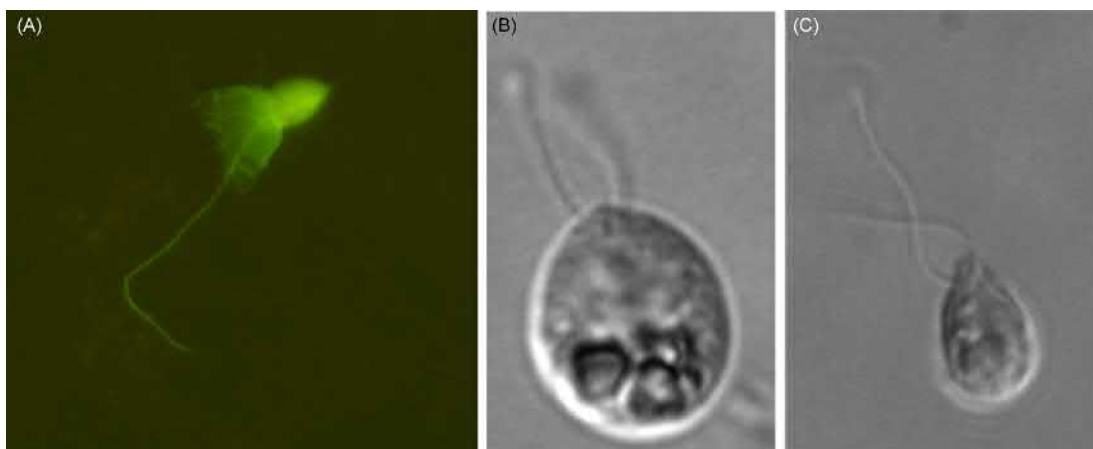


Fig. 5 Other heterotrophic flagellates. (A) collared choanoflagellate under blue excitation. The bright green autofluorescence is common among heterotrophic groups; (B) *Cryothecomonas* sp.; (C) *Telonema* sp. All cells are c. 10 µm.

reported from the Arctic are in the Acanthoecida, with taxonomically characteristic lorica made up of silica containing costal strips. Many morphologically undifferentiated Acanthoecida are persistently reported from 18S rRNA gene surveys, but the most complete study to date relied mostly on microscopy, with 50 or so taxa reported, including likely endemic species (Thomsen and Ostergaard, 2017).

Microbial fungi

Although Fungi were once classified with plants, they are a sister clade to multicellular animals. Marine fungi tend to be microscopic and do not form the large reproductive structures typical of many terrestrial fungi. Recently, marine microscopic fungi have been reported from molecular surveys (Hassett et al., 2019), and are widespread in the Arctic. Among these are chytrids that likely parasitize diatoms. These appear near the end of the spring diatom bloom, suggesting a major role in carbon and energy cycles in the Arctic.

Incertae sedis

Other small heterotrophic flagellates are ubiquitous in the ocean and often account for non-negligible contributions to gene surveys in the Arctic. These include unrelated taxa that currently cannot be placed into larger universal phylogenies and are referred to as *Incertae sedis*. Among these is the bacterial predator *Telonemia* (Fig. 5C) and a tiny (1–2 µm) flagellate in the *Picozoa* (Thaler and Lovejoy, 2015), which likely subsists on viral particles and organic matter polymers.

Bacteria and Archaea

Bacteria and Archaea are responsible for remineralization of nutrients and play essential roles in the global Nitrogen, Sulfur and Carbon biogeochemical cycles. The biodiversity of Bacteria and Archaea has only been appreciated since the advent of the molecular era. To date, at least one bacterial clade seems to be specifically adapted to Arctic organic substrates (Colatritano et al., 2018) and, as with other plankton in the Arctic, it is reasonable to assume that more arctic ecotypes and species of Bacteria and Archaea will eventually be discovered.

Cyanobacteria

Cyanobacteria are true bacteria, lacking a well-defined nucleus and membrane-bound organelles. With some exceptions in warm tropical seas, planktonic cyanobacteria are >2 µm picoplankton. The two most common planktonic genera have well-defined latitudinal limits. The smallest *Prochlorococcus* is rare above 40° latitude. *Synechococcus* is distributed further north, but is extremely rare in Arctic Ocean where the green alga *Micromonas* occupies the picophytoplankton niche (Li et al., 2009). *Synechococcus* and most other cyanobacteria can be counted using epifluorescence microscopy or flow cytometry because of the presence of bright fluorescing biliproteins. The disappearance of these cells detected using flow cytometry crossing the polar front in both the Arctic and Antarctic is striking (Dubreuil et al., 2003). Occasionally freshwater forms of *Synechococcus* are reported offshore in the Arctic, but they are unable to grow in marine waters and are likely washed in from large rivers surrounding the Arctic Ocean (Vincent and Quesada, 2012). The lack of *Synechococcus* in Arctic marine waters is possibly due to temperature limitations with growth rates lower than losses from grazing.

Heterotrophic bacteria

Bacterioplankton are essential for degrading organic carbon in the open ocean, including the Arctic. The distributions of major Bacteria clades were recently reviewed in Pedrós-Alió et al. (2015), who found that at the level of Class, Arctic bacterioplankton were similar to other open oceans. Some evidence suggests that higher proportions of *Betaproteobacteria* and *Gammaproteobacteria*, compared to *Alphaproteobacteria*, are indicative of recent ice cover. However, as with other Arctic organisms, at the species level (inferred from 97% to 99% similarity of 16S rRNA genes). Arctic bacterioplankton are distinct from Global Ocean populations outside of Polar Seas (Ghiglione et al., 2012), and arctic-specific clades of major lineages are known.

Archaea

Archaea superficially resemble bacteria in that they have no membrane-bound organelles. Early work investigating 16S rRNA genes first established them as a separate domain of life and later they were found to be omnipresent in world oceans, including two major lineages (Crenarchaeota MGI, now Thaumarchaeota and Euryarchaeota) in the central Arctic (Bano et al., 2004). Marine Archaea are involved in several key biogeochemical cycles, for example, in the Arctic Thaumarchaeota can take up urea and oxidize ammonium to nitrite, which is then converted to nitrate (Alonso-Saez et al., 2012). Metagenomic studies, where entire microbial communities are sequenced and then reconstructed using bioinformatics tools, have begun to elucidate some of the functions of what are referred to as Marine Group (MG) II and MG III Euryarchaeota, which tend to occur at low abundance and evade cultivation. MG II, which has been proposed as a candidate Order level lineage (*Canidatus* Poseidoniales), are considered photoheterotrophs, harvesting light using proteorhodopsin (Rinke et al., 2019). MG III Euryarchaeota are thought to specialize in the degradation of high molecular weight organic compounds. An early study using high throughput sequencing found that MG I (Thaumarchaeota) was overall the most abundant group in the Arctic Ocean (Galand et al., 2009). MG III Euryarchaeota were more abundant in deep-water masses and represented the largest archaeal group in the deep Atlantic layer of the central Arctic Ocean. Coastal surface waters, in turn,

harbored more MG II Euryarchaeota. The MG II sequences that dominated surface waters differed from the MG II sequences detected in deep waters, suggesting functional differences in closely related groups.

Summary Statement

Overall Arctic plankton tend to have pan-arctic distributions and a high proportion of endemic species, and Arctic Biome should be considered as a major contributor to global biodiversity.

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Life in Arctic Sea Ice

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Glossary

Brine Salty solution between ice crystals.

Primary production Amount of organic carbon produced through photosynthesis.

Sea ice meiofauna Small metazoan fauna living inside brine channel system.

Sea ice algae Microalgae (mainly diatoms) living inside brine channel system.

Abstract

Arctic sea ice provides habitat for unique, highly specialized communities ranging from viruses, bacteria, and microalgae to seals and polar bears. Life inside the sea ice occurs in the salty brine channel system, and its environmental settings (mainly temperature, salinity, and light) control the biodiversity and the seasonal cycle of the associated flora and fauna to a very large extent. An overview of the associated diversity is provided, followed by a discussion of the seasonal succession contrasting activity and controls for fall/winter, spring and summer. The biological relevance of ice formation and ice melt are discussed. Sea ice habitat is not isolated from water column and sea floor habitats. In contrast strong biological coupling occurs through the migratory life cycles of benthic invertebrates and the vertical flux of organic matter in the form of living algal aggregates or fecal pellets even down to water depths exceeding 1000 m. Implications of observed climate change effects and associated changes in the physical properties of sea ice are discussed and the need for further research is highlighted.

Introduction and Outline

While polar oceans appear to humans as rather hostile environments, they are the habitats for thousands of species living at the sea floor (benthos), within the water column (plankton and nekton) and sea ice (sympagic communities). Sea ice (Fig. 1) itself is a unique feature in polar seas and, although they look similar, Arctic and Antarctic sea ice are distinctly different in their physical and chemical characteristics (Eicken, 2003). This article will thus only focus on Arctic sea ice, as conditions and biological properties in Antarctic sea ice are different. Habitat properties vary with the age of the sea ice and the types of ice formation, all of which causes differences in sea ice biota in different parts of the Arctic. This article will start with an introduction to the macro- and microscale properties of Arctic sea ice, its seasonal and regional occurrence as well as its main physical properties. We will explore the challenging living conditions experienced by sea ice biota, followed by an overview of the known biological diversity of Arctic sea ice biota. A discussion of the adaptations of ice biota is followed by discussion of the seasonal development of the ice biota and their role in the Arctic marine food web. Finally, the implications of climate change effects on sea ice biota are reviewed.



Fig. 1 Sea ice landscapes of the Arctic Ocean. (A) Newly forming pancake ice (diameter of the individual pancakes ca. 30 cm), (B) newly formed nilas ice (thickness less than 10 cm), (C) ice floes with thicknesses of around 1.5 m and snow cover behind nilas, (D) scientists working on fast ice close to the Alaskan shore.

Macro- and Microscale Habitat Properties of Sea Ice

Seasonal Changes in Sea Ice Extend Across the Arctic Ocean

The extent and concentration of Arctic sea ice may be assessed these days for any day of the year based on high quality remote sensing data (**Fig. 2**) (Stroeve et al., 2011). This information is freely available from various websites (see Relevant Websites). Time series observations of sea ice extent typically go back to 1979, when the first observations were made public. The long term mean conditions (climatology) demonstrate a large seasonal variation along a reduction due to climate change (Polyakov et al., 2017). Typically, Arctic sea ice reaches its maximum in March. Until recently, this maximum ice extent covered to 14–15 million km². Summer ice melt greatly reduces the ice extent, reaching a minimum in September. Until about 10 years ago typical summer values averaged around 7 million km². However, over the last 10 years summer ice extent has been greatly reduced due to accelerated melting rates and later formation dates. Today Arctic sea ice covers only 3.5–5 million km² in summer (**Fig. 2**). The seasonality of sea ice cover is driven by the balance between formation and thickness growth of sea ice during the dark, cold winter months and melting during the midnight sun summer period. Sea ice surviving the summer months and starting a new freezing cycle is called second- or multi-year ice. The thickness of the multi-year ice varied historically between 2.5 (summer) to ca. 3.5 m (winter) in undeformed areas. Pressure ridges built by colliding ice floes can greatly exceed these values and ice drafts of over 30 m have been reported. The drastic loss of summer sea ice has caused a large reduction in multi-year sea ice. This has been replaced by newly forming first-year sea ice over vast areas of the Arctic (**Fig. 2**). First year ice (both land-fast and pack ice, see below) is slightly more salty than multi-year sea ice (providing more inhabitable brine space) and also thinner than multi-year ice (typical winter thicknesses < 2 m).

The sea ice cover of the central Arctic Ocean consists of individual free drifting units (see below). Two major drift patterns exist: the Transpolar drift transports sea ice across the Arctic Ocean from the Russian shelves to the North Atlantic in ca. 3–5 years, while the Beaufort Gyre is a clockwise wind-driven circulation pattern, in which one rotation of the ice pack requires about 10 years. In

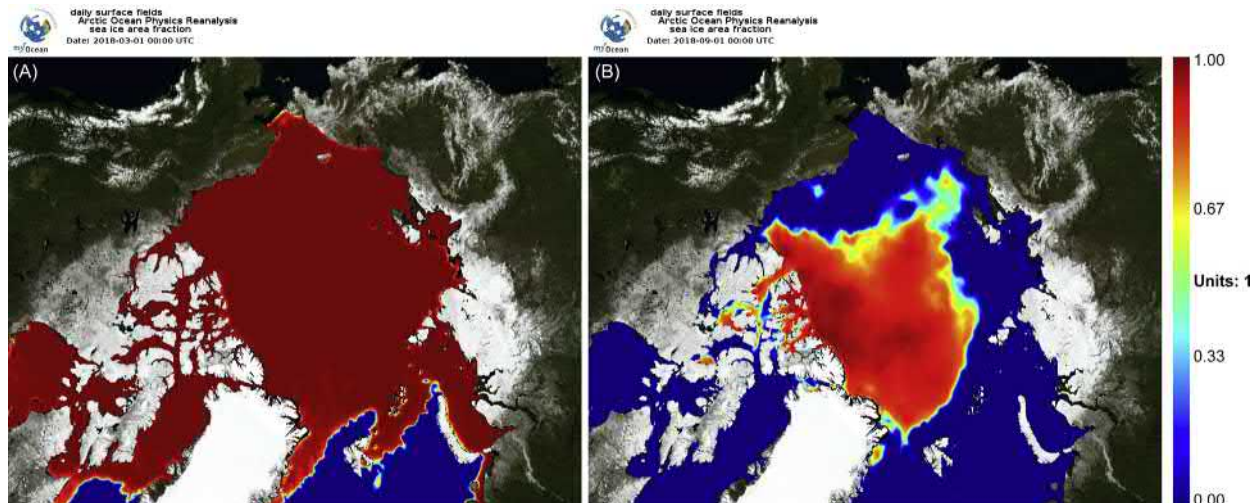


Fig. 2 Remote sensing of the seasonally changing sea ice extent in 2018. (A) Winter sea ice extent in March 2018. (B) Summer sea ice extent in September 2018. Source: <http://marine.copernicus.eu/services-portfolio/access-to-products/>.

contrast to pack ice, land-fast ice is attached to the coast and does not drift with the wind and/or the ocean currents. It is formed close to land and can extend for a few to dozens of kilometers from the shore line onto deeper parts of the shelf. Most of the fast ice forms annually and melts completely in spring/summer. Along the boundary areas between fast and pack ice, open water areas exist even in winter. These are termed “coastal flaw lead polynyas.”

During ice formation, several distinct growth stages can be distinguished, all of which are relevant to our understanding of the development of sea ice biota. As air temperatures decrease, sea water cools to its freezing temperature which, depending on salinity, is between -1.4 and -1.8 °C. Further cooling initiates ice formation in the form of freely floating ice crystals which accumulate at the surface due to their density being lower than that of sea water. However, these are resuspended in the water column through vertical mixing by wave action. Under calm conditions however, a thin skin of ice (nilas ice, Fig. 1) can cover dozens of km² of the ocean surface, while under wavy conditions, these sheets are broken up into small pieces which become rounded through constant collisions, giving them the distinctive shape of pancake ice. In the initial stages, ice crystals grow individually in different orientations and can collect particles while moving through the water column. These particles include sediment and biota, and they become incorporated into the growing ice sheet. Further cooling consolidates the pancakes into large ice cakes or ice floes and ice growth no longer occurs through mixing of individual ice crystals at the surface but rather through new ice growth at the bottom of the existing ice floes. Under such conditions, ice growth leads to differently shaped ice crystals at the bottom of the ice.

As mentioned above, ice crystals suspended in the water column are mixed through wind and wave action through the uppermost meters of the water column before becoming consolidated into nilas or pancake ice. During the suspension process sticky particles such as sediment grains, bacteria, and microscopic algae become attached to the ice crystals and float with the ice into the ice sheet. This process explains how developing sea ice becomes loaded with microscopic life forms. Specifically, bacteria and algal abundances can be enriched by several orders of magnitude within the growing sea ice, compared to their concentrations in the underlying sea water (Gradinger and Ikävalko, 1998). However, not all these organisms survive within the sea ice, so local selection leads to distinct communities that differ in relative composition compared to what is found in the water column below. Part of the seeding of ice might also come from other ice floes surrounding the growing ice—explaining the existence of endemic (only in one habitat/region) occurring species of algae and small crustaceans and nematodes in Arctic multi-year ice regions.

The Microscale Brine Channel System Within Arctic Sea Ice

The small remaining fraction of salty water (brine) that is trapped between the ice crystals is critically important to our understanding of the relevance of sea ice as a habitat. This salty water forms the so-called brine channel system (Fig. 3) (Krembs et al., 2000). The size of the saltwater filled brine pockets and channels are mainly in the μm to mm size range, limiting the ability of larger organisms to live there. The volume and salinity in the brine channels is largely determined by sea ice temperature and the total amount of salt remaining in the system (Eicken, 2003). Under typical summer conditions, the brine volume in sea ice may reach values approaching 25% of the entire ice volume at the bottom of the ice (where it is relatively warmest and most salts are contained), while in the ice interior and at the top in winter sea ice (very cold, low remaining salt content) values are generally below 5%. Ice temperatures are often close to atmospheric temperatures at the top of the ice, while they are close to the freezing point of water (see above) at the bottom. Very cold temperatures cause very high brine salinities and values over 150 have been observed, and these hypersaline waters cause enormous osmotic stress on sea ice organisms, specifically in the coldest uppermost parts of the ice. In contrast, near constant temperatures close to the freezing point foster near sea water salinities at the bottom of the



Fig. 3 Visualization of the Arctic brine channel network accomplished by pouring red dye onto the bottom block of sea ice—Please note that the red dye penetrates deeply into the interconnected brine channels for several dm. Picture taken in Svalbard, fast ice system.

ice, making the ice bottom layers the most favorable habitat for organisms. These favorable conditions include (a) relative warmth, (b) salinities close to ocean water levels, (c) provision of large brine volumes and (d) easy access to nutrients or seeding populations from the water below. It therefore should not come as a surprise that the highest abundances of any organisms in Arctic sea ice are found at the bottom of the ice, often exceeding values in the ice interior by several orders of magnitude (**Fig. 4**) (e.g., [Gradinger, 1999](#)).

The above short introduction into the macro- and microscale characteristics of Arctic sea ice demonstrates that sea ice is not a homogeneous biological habitat. Rather, sea ice is quite variable on scales from mm to km, fostering considerable biological



Fig. 4 Ice floe turned around by icebreaker action, showing the dark brown bottom layer of sea ice thickness. Diameter of the ice floe ca. 3 m.

variability. Consequently, study of the biota associated with coastal fast ice does little to aid our understanding of deep Arctic Ocean systems with very different ice characteristics.

Diversity of the Arctic Sea Ice Biota

Although great progress has been made in our understanding of the diversity and activity of Arctic sea ice biota, it is clear that inventory of known species remains incomplete and is likely to increase dramatically during the coming decades. By now we know that the sea ice brine channel system is the habitat for several thousand species of viruses and bacteria, between 1300 and 1500 species of microalgae and small protozoans, and about 40 different species of small metazoans (sea ice meiofauna) (Bluhm et al., 2011). Factors constraining the presence and abundance of sea ice biota are linked to the physical environment (see above) as well as the strong seasonality in biological processes (see below).

Brine channel system dimensions provide an upper limit for the size of organisms living within the ice. No limitations exist for the tiny bacteria and viruses, and for most of the microalgae. However, metazoans are often excluded from the brine channel network due their larger size, specifically the large (several mm to over 1 cm long) herbivorous crustaceans (copepods of the genus *Calanus*) that dominate the water column below. To a large extent, this grazer exclusion explains why the growth of primary producers (algae) within the ice is not controlled by grazing but by physical variables such as light, temperature, brine salinity, brine volume fraction, and by availability of plant nutrients (mainly nitrate), coming from the water column below.

Microalgae (Poulin et al., 2011) are likely the best studied component of the sea ice biota (Fig. 5) in terms of biomass, diversity and regional differences. The highest number of species and highest biomass are likely contributed by diatoms. All diatoms are characterized by a silicate frustule, their ability to photosynthesize, their complex life cycles and the large variation in their shapes and forms. Within Arctic sea ice, algal communities are often dominated by relatively large colonial diatoms, with taxa such as *Nitzschia frigida* and various species of *Fragellariopsis* occurring in the brine channels in all parts of the Arctic. Some of the diatom species can form morphological resting stages (called spores), but many species do not. Unique to the Arctic are curtain-like diatom colonies hanging down from the ice-water interface to the water column below. These brownish colonies make exceed lengths of several meters and are formed by a single species called *Melosira arctica*. Long chains of cells of this species are intertwined and embedded in a slimy matrix, ensuring the stability of the curtains. It is believed that the ends of the chains extend into brine channels at the ice bottom, using slime as a glue to ensure attachment to the bottom of the ice.

Diatoms are not the only phototrophic inhabitants inside the sea ice. There are perhaps hundreds of species of flagellated taxa including haptophytes, prasinophytes, dinophytes, and euglenophytes that also inhabit the ice interior. Many of these taxa are not obligatory phototrophs. A whole range of different nutritional modes has been observed, ranging from photo- to mixo- to obligatory heterotrophic species. Some of the heterotrophic flagellates (large euglenophytes such as *Anisonema* sp.) feed directly on ice diatoms, while others form part of the microbial food web, recycling organic matter inside the ice by feeding on bacteria.

Fungi have also very recently been discovered in Arctic sea ice (Hassett et al., 2019). One group called thraustochytrids are parasites, attacking specific diatom species. However, research on these fungi is still in an early exploratory phase.

Sea ice heterotrophs inside the brine channels include small flagellates (size range of ca. 5–100 μm), ciliates (size range of 20–200 μm) and small metazoans (typically above 70 μm in size). For metazoans inside the ice, different water depths beneath the ice translate to large differences in species composition (Bluhm et al., 2018). In nearshore areas where water depth is < 100 m (often in fast ice areas), juvenile stages of benthic (bottom living) invertebrates such as polychaetes, mollusks and gastropods are released



Fig. 5 Example of a sea ice brine community dominated by diatoms (picture taken in the Bering Sea, pack ice, March 2010). Size of the diatom cells ca. 40–80 μm .

into the water column and swim towards the ice system to feed on the high abundance of diatoms in the ice bottom layer. Other taxa such as nematodes, acoel turbellarians, rotifera and copepods are found in all parts of the Arctic. Most of these taxa are herbivores, feeding on ice algae. However, there is an ice-inhabiting jellyfish (*Sympagohydra tuuli*) that appears to be the top predator in this food web, ingesting a wide range of other sea ice meiofauna.

Similar to *Melosira arctica*, no size limitation exists for animals using the bottom of Arctic sea ice as a substrate. Here Arctic ice endemic species of amphipods (*Apherusa glacialis*, *Onisimus* sp., *Gammarus wilkitzkii*) are found from the nearshore to the deep Arctic basins, living in permanent association with sea ice (Hop and Pavlova, 2008). Although closely related genetically, these amphipods inhabit different ecological niches. *A. glacialis* is mainly herbivorous; *Onisimus* spp. are omnivores and *Gammarus wilkitzkii* is a carnivore. *G. wilkitzkii* not only preys on other ice associated amphipods, but it also harvests pelagic crustaceans such as *Calanus* spp. if they stray too close to the bottom of the ice where *C. wilkitzkii* lives.

Fish inhabit the ice water interface as well, mainly *Boreogadus saida* (Arctic cod). This species uses the sea ice as a hideout from potential predators such as birds or seals, while feeding on ice-associated or pelagic crustaceans. Not all *B. saida* populations are ice associated. This fish also occurs in high abundances in open Arctic areas.

Sea ice is not only a habitat for marine organisms. Arctic birds, seals and the polar bear use sea ice for resting, travel, reproduction and (in the case of polar bears) as a hunting platform. Not all ice related seals feed directly on the ice-associated fauna as does the ringed seal, for example. Walrus and bearded seals use sea ice as a platform for reproduction and to dive down to the sea floor to feed on benthic communities. Polar bears are likely the most charismatic megafauna associated with sea ice. In conclusion the Arctic ice habitat plays an essential role for a variety of marine mammals.

Seasonal Development of the Arctic Sea Ice Biota

Fall/Winter

From the human perspective fall/winter are the most hostile months in the Arctic. Air temperatures drop below -30°C , causing fast ice growth, high brine salinities and adding snow on top of the ice. Periods without sun light vary dependent on the latitude, but time spans of complete darkness in Arctic Seas range from 3 to 5 months with the only light coming from the moon or from bioluminescence. Light levels are so low that no photosynthesis by algae occurs.

During winter, the abundance of organisms in the ice and in the water column are at a minimum. Some species of diatoms overwinter by reducing their metabolism to an absolute minimum, which allows them to rest for months, relying on their nutritional reserves in the form of e.g., lipid droplets. Other organisms switch to heterotrophy by ingesting bacteria or detritus (dead organic matter). However, it should be noted that winter is the least studied period of the annual cycle due to the difficulties of winter-season research in Arctic waters. Therefore, it must be said that the winter biological adaptations of the ice flora and fauna are poorly investigated.

Within the ice, very cold temperatures lead to high brine salinities that induce osmotic stress in sea ice biota (e.g., Kiko et al., 2008). Different metabolic pathways have evolved to acclimate these organisms to varying salinities. These adaptations range from ion pumps to the production of organic chemicals called osmolytes, both of which have been studied in sea ice algae and ice inhabiting metazoans. However, these protective measures come at a metabolic cost, so growth rates of these organisms decline sharply as they are exposed to higher salinities. The highest salinities that sea ice biota are able to survive range from 80 (for metazoans) to 150 (for sea ice microalgae).

Spring

After months of darkness, the return of sun light marks the beginning of early spring. Arctic sea ice algae are among the best adapted species on Earth to photosynthesize under very low light intensities. Even 0.1% of the surface light intensity (e.g., at surface above $1000\ \mu\text{mol photons m}^{-2}\text{ day}^{-1}$) on a sunny day is sufficient to start ice algal growth. Low grazing pressure, adequate supply of inorganic nutrients and increasing light intensities cause massive bursts of development of ice algae at the bottom of the Arctic sea ice during the few weeks in early spring. The timing of the bloom varies with latitude. For instance the onset occurs in March in the Bering Sea and in April/May in the Beaufort Gyre. In addition to the latitudinal gradient, local conditions such as nutrient load in the water column or light reducing thick snow layers on top of the ice cause small to large scale variations in the ice algal biomass accumulation.

In the field, maximum ice algal concentrations in the lowermost 1 cm of the sea ice can exceed concentrations found in the water column by 1–3 orders of magnitude. It thus is no surprise that in nearshore waters, juvenile stages of benthic invertebrates can dominate the meiofauna community for several weeks (until the juveniles go back to the sea floor or the ice melts). Feeding on dense masses of sea ice diatoms allows for much faster growth than feeding on the less concentrated phytoplankton biomass. Reproductive events of the sea ice meiofauna are also linked to the ice algal bloom. Small copepod nauplii or egg cases or small juveniles of ice nematodes can be found in the ice in spring. At the bottom of the ice, ice amphipods such as *A. glacialis* and *Onisimus* spp. graze on the ice algal bloom. Amphipod fecal material (fecal pellets) is very dense and sinks quickly to the sea floor, providing the first fresh pulse of organic matter to the benthic fauna since the previous summer.

Summer

Continued solar heating transforms the sea ice habitat from spring to the summer melting stage. Increased surface heating opens up the brine channel network causing flushing of melt water through the sea ice and also melting of the bottom layer. With the flushing and/or the melting, a sudden release of accumulated organic biomass in the form of the ice algae occurs. Algae, including the under-ice species *M. arctica*, clump together and form larger aggregates that sink to the sea floor at rates of hundreds of meters per day. This input provides high quality undigested food to the benthic fauna, and benthic holothurians, for example, have been observed feeding on *M. arctica* aggregates at water depths exceeding 1000 m (Rybakova et al., 2019).

Melting not only reduces the abundance of all ice related organisms, but low salinity accumulations can also cause osmotic stress. Here ice flora and fauna respond by moving to deeper water. Here they settle on ice pressure ridge keels with depths exceeding 10 m, or some enter a pelagic life stage (as typical for Antarctic sea ice flora and fauna) (Gradinger et al., 2010).

Consequently, summer is not necessarily the peak time of ice related biological productivity. Rather, it is the early spring months right after the return of sun light, during which most biological activity occurs at the bottom of the ice, not visible from the surface. This is in striking contrast to processes in the water column. Here the melting of the sea ice in the marginal ice zone actually stimulates phytoplankton growth in the water column by increasing light availability as the ice melts. There is also less mixing of waters with different densities. Such strong blooms of phytoplankton in the marginal ice zone can be detected from space by changes in ocean color and often occur earlier than mass developments of phytoplankton in seas south of the ice covered regions.

In conclusion, sea ice harbors a diverse community and a very active dense layer of primary producers (often dominated by diatoms) in the bottom few cm of the sea ice, close to the ice-water interface. Annual estimates reveal that the ratio between sea ice algal production and total Annual Arctic Ocean production varies with region. In seasonally ice-covered coastal seas with shorter ice cover and longer open water periods, ice algae may contribute ca. 5–25% of biological productivity. In the central Arctic Ocean, permanently covered by sea ice, this value increases to ca. 50% (e.g., Gradinger, 2009). Through the ice-based food web including amphipods and fish, part of the organic matter produced by ice algae contributes substantially to the nutrition of seals, birds and polar bears (e.g., Cusset et al., 2019).

Climate Change and the Arctic Sea Ice Habitat

The physical properties of Arctic sea ice have received considerable scientific and public attention over the last few decades, using those as one of the canaries in the coal mine to reveal climate change. Substantial loss of summer and multi-year sea ice, increased dominance of thinner first year ice, later ice formation and earlier ice melt have been documented around the Arctic. All of those factors have biological consequences, some of them obvious, some of them cryptic, thus far.

Obviously, loss of sea ice habitat causes severe stress on sea-ice organisms, from diatoms to seals and walrus. The future existence of this sea-ice biota will depend on whether they will be able to follow the receding ice edges and stay with the ice (e.g., ringed seals). This is not the case for all species. Walrus, which are bottom feeders, cannot dive to the vast depths of the central Arctic Ocean to get to their benthic food sources and ice loss on the shallower seas will leave them without their feeding platform. Alternatively, pelagic or benthic life stages might be able to survive without sea ice. This is a currently anticipated outcome for at least one amphipod species formerly considered to be ice endemic (*Apherusa glacialis*).

The loss of the contribution of sea ice algae to total algal productivity will likely be compensated by increased water column (phytoplankton) productivity. Indeed, expeditions in the Beaufort Sea and in the Nansen Basin revealed substantial under-ice algal phytoplankton blooms, supported by high light intensities allowed by melting snow and large leads of open water. Of greater biological concern is the timing of ice melt associated with ice algal bloom development. As specialists, ice algae can grow under very low light intensities, thereby forming the foundation of the sea-ice based food web. The biology of these algae is also closely coupled to water column and sea floor biological processes through export in the form of fecal pellets or living algal aggregates. Very early ice melt might reduce this input by reducing the spring ice algal blooms. A delay in the commencement of phytoplankton growth could lead to extended periods of low food supply to the sea floor fauna beyond the already long Arctic winter. Only future observations will provide answers concerning the responses of Arctic sea ice habitat and its associated biota to future environmental changes. It appears certain that changes in biological diversity, production and connectivity could lead to unanticipated cascading ecological effects.

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- <http://marine.copernicus.eu/services-portfolio/access-to-products/>—Arctic physical, chemical and biological properties: Copernicus service.

Life In and Around Arctic Ice Sheets and Glaciers

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Abstract

Plant life around ice sheets and glaciers develops in the process of primary succession by means of a gradual colonization of the barren substrate by cyanobacteria, lichens, bryophytes and vascular plants. These plants create initial plant communities in the forelands of Arctic glaciers; under such harsh conditions, particularly cryptogamic species, create biological soil crusts. The number of cryptogamic species colonizing freshly deglaciated forelands exceeds the number of vascular plant species. Cryptogams that initiate the colonization process in the forelands modify the edaphic and microclimatic conditions and favor the growth of other taxa that create the next successional community and may replace previous species by competition. Currently, due to the fast rate of retreat of glaciers, this process is easy to observe. The gradual deglaciation of Arctic landscapes over more than one century, which started since the end of the Little Ice Age at the end of 19th century, gives a unique opportunity to investigate this process in detail. At the beginning of 20th century the primary succession process was described as linear and directional, ending in a final climax community. However, this view is questioned today. Primary succession is no longer necessarily considered to be a linear and directional process due to species turnover, and species equilibrium is rarely reached. Plant communities that develop in glacier forelands exhibit the properties of near-climax communities.

Introduction—What Is the Primary Succession Process?

The succession process is defined as species change over time and it is divided into two types: primary succession occurring on substrates with no previous biological life; and secondary succession happening on substrates with a biological legacy that has been disturbed. The processes of primary succession on a barren substrate by living organisms are rarely observed in nature. There are only a few places where the conditions for the existence of these phenomena are possible: areas submerged with lava after volcanic eruptions, volcanic islands emerging from the sea, and areas recently exposed from beneath the ice. These provide a natural laboratory where we can trace ecosystem formation from the earliest stages. Primary succession begins when microorganisms, plants and animals start to colonize a new substrate. Here we will focus on plant succession and vegetation development in glacier forelands in the Arctic.

At the beginning of 20th century, Clements (1916) proposed an approach in which succession has a linear and directional character and ends in a final climax community. This view has been questioned by Gleason (1917, 1926) and further elaborated by Eglar (1954), Drury and Nisbet (1973) and Whittaker (1974). Currently, primary succession is not always considered as a linear process due to the turnover of the component species. Therefore the process rarely reaches species equilibrium (Walker and del Moral 2003).

Climate change is currently driving the expansion of ice-free areas in glacier forelands, indicating the need for research on the primary succession. Consequently, Arctic regions offer perfect opportunities for studying this processes on the freshly deglaciated areas gradually inhabited by different groups of organisms: microorganisms, lichens, bryophytes and vascular plants (Frenot et al.,

1998). The process of colonization depends not only on availability of diaspores of surrounding vegetation (Bullock et al., 2002; Jones and del Moral, 2009; Del Moral and Erin, 2004; Řehounková and Prach, 2006), but also on the various abiotic factors that characterize the habitat (Matthews, 2008), and geomorphological processes shaping the surface after the disappearance of ice. As a result, interdisciplinary research combining botany, geomorphology, meteorology and soil science is needed to provide a detailed knowledge of primary succession. Currently, research on the succession on glacier forelands is still needed because of the rapid growth of ice-free areas and the increasing rate of melting glaciers due to climate change (Laspoumaderes et al., 2013). There are still mechanisms and environmental factors influencing these processes that have not yet been investigated (Walker and del Moral, 2003; Prach and Rachlewicz, 2012).

Climate Change and Glacier Recession

The Arctic is one of the regions most threatened by climate change. Global system changes have happened regularly throughout the history of Earth and are not a new phenomenon (Huntley, 1991), but in polar regions the main problem is the current rate of climate change, which is so fast that these ecosystems may not be able to adapt to all shifts in a natural way (Duarte et al., 2012).

In recent decades global climate changes, including a gradual temperature increase, have been widely documented and monitored (e.g., Hansen et al., 2012; Pachauri et al., 2014). Currently, the Arctic temperature rise is the greatest (Menne and Kennedy, 2010): from 1995 to 2005, the average annual temperature has increased by more than 1°C compared to the average for the period 1951–90 (Przybylak, 2007). During the years 1961–2004, the Arctic regions (without the contribution of ice sheets in Greenland) were the second main water sources responsible for increasing global sea level (Kaser et al., 2006; Lang et al., 2015). Moreover, the ice loss in the Arctic has reached c. 50% of all ice caps and glaciers (Gardner et al., 2013). Many reports based on climate models (Holland et al., 2010; Vavrus et al., 2012; Stocker et al., 2013) predict a further rise of temperature, humidity and cloud cover, and a decrease of ice cover, with an enormous influence on terrestrial and marine habitats and their ecological dynamics (Grémillet et al., 2015). These will result in, for example, a further expansion of shrubs and forest into the north, permafrost degradation, and glacier regression (Stocker et al., 2013; Pachauri et al., 2014; Jorgenson et al., 2015).

Since the beginning of the 20th century, documentation of glacier ranges and thickness changes is wide ranging and includes both polar regions and mountains. Data collected within the international monitoring of glaciers (World Glacier Monitoring Service) clearly shows a loss of glaciers on all continents, progressing especially in the second half of the 20th century (Fig. 1; Zemp et al., 2008; Nuth et al., 2013).

History of Primary Succession Studies in the Glacier Forelands

The history of research on primary succession of vegetation in the glacier forelands started in the early 20th century. However, the majority of these studies came from the last few decades because of the accelerated rate of glacier recession worldwide, which strongly effects recruitment of glacier foreland species (Mondoni et al., 2015).



Fig. 1 View of retreating glacier in Ringhornsdaalen. © P. Wietrzyk-Pelka.

The first published observations from Glacier Bay, Alaska referred to the characteristics of ecological conditions on the forelands of retreating glaciers (Cooper, 1923a), as well as a description of the plant communities in different substrate ages and the adaptation strategies of pioneer species (Cooper, 1923b). During these studies permanent sample plots were established to follow the succession process in subsequent years (Cooper, 1931, 1939). Research in Glacier Bay also included the effect of vegetation on soil development within the glacier marginal zones (Crocker and Major, 1955). The study of plant succession on European mountain glaciers forelands began in the middle of the 20th century (Palmer and Miller, 1961; Worsley and Ward, 1974; Sommerville et al., 1982). Even today, mountain glacier forelands are of great significance for research on various aspects of primary plant succession (Erschbamer et al., 2008; Robbins and Matthews, 2009; D'Amico et al., 2014; Mizuno and Fujita, 2014). Intensive studies have also been carried out in the polar regions. Most data from the Southern Hemisphere comes from the Maritime Antarctic, West Antarctica (Olech, 1996; Olech and Massalski, 2001; Casanova-Katny et al., 2014) and the Subantarctic Kerguelen Islands (Frenot et al., 1998), as well as from the Northern Hemisphere, especially from the Canadian Arctic (Chapin et al., 1994; Jones and Henry, 2003; Fastie, 2009; Mori et al., 2017), and Svalbard, where research on primary succession of vegetation has been initiated by Kuc (1964). A significant portion of the world's latest research on primary succession on glacier forelands comes from Ny-Ålesund region (NW coast of Svalbard) where the following topics have been covered: plant community evolution (Hodkinson et al., 2003; Moreau et al., 2005, 2008), pioneering species (Nakatsubo et al., 2010), and species ecology (Nakatsubo et al., 2005; Uchida et al., 2006; Yoshitake et al., 2007), as well as the role of soil microorganisms (Bekku, 2004), including mycorrhizal fungi (Cázares et al., 2005; Fujiyoshi et al., 2010). Research has been conducted in other parts of Svalbard by Tishkov (1986), Ziaja and Dubiel (1996), Fabiszewski (1975) and Wojtuń et al. (2008). However, most research on primary succession in Svalbard has concentrated on the transformation of vascular plant communities (e.g., Pirożnikow and Górniak, 1992; Nakatsubo et al., 2010; Prach and Rachlewicz, 2012; Yoshitake et al., 2011), or their interactions with mycorrhizal fungi (Těšitel et al., 2014; Davey et al., 2015). Other components of the vegetation of glacier marginal zones (in particular bryophytes and lichens), were often overlooked or treated in a general way, without detailed species identifications. Spore-bearing organisms, bryophytes and lichens, are the main tundra component and also often the dominant species in initial communities developing in glacier forelands. This indicates their great importance in the primary succession process (Wietrzyk et al., 2016).

Main Colonizers

Cyanobacteria

Cyanobacteria are dominant in the cold polar ecosystems of the Arctic, occurring in extremely cold habitats, such as glacier foreheads, glacier forelands, glacial rivers, and lakes (Fig. 2). They are one of the first colonizers of glacier forelands from which ice cover has retreated, where they play an important role in carbon and nitrogen supplies. The ecophysiological features of cyanobacteria that contribute to their success and domination include an ability to grow in a wide range of temperatures, tolerance to the stresses of drying, freezing and salinity, different adaptation strategies against high levels of solar radiation (including ultraviolet radiation) in vulnerable habitats, and acclimation to shaded environments (Vincent, 2000). During the 19th century it was discovered that cyanobacteria occur in small melt cavities filled with water (cryoconite) on the foreheads of glaciers. Previous research has shown that this specific micro-habitat is inhabited by filamentous cyanobacteria of the genera *Phormidium*, *Lyngbya*,



Fig. 2 Cyanobacteria of the genus *Nostoc* in microscopic section. © P. Wietrzyk-Pelka.

Microcoleus, and *Nodularia*. Furthermore, kettles, ponds, rivers and smaller glacial streams formed by geomorphologic processes are very rich in cyanobacteria from the orders *Oscillatoriales* and *Nostocales* (Vincent, 2007). Their presence is connected with the early stages of primary succession, when the substrate exposed by retreating ice is devoid of nutrients. Presumably, cyanobacteria species originally transported by glacial waters are deposited on various types of foreland substrate, being one of the first organisms on the barren surface and also having the ability to assimilate atmospheric nitrogen. Thus, they play an important role in the nitrogen availability for plants in these habitats (Bliss and Gold, 1994) and their presence triggers soil-forming processes; this increase in biogenic elements facilitates the subsequent colonization of bryophytes, lichens, and vascular plants on glacier foreland.

Lichens

Lichens as cryptogamic organisms are one of the main components of tundra communities in Arctic regions. Early stages of lichen succession can be observed in the foreland of glaciers, where thanks to the early presence of prokaryotic and eukaryotic algae, the lichenization of both components, fungus and algae, occurs. The species of lichens colonizing glacier forelands can be divided into two groups: epilithic lichens, which overgrow gravel and rocks, and epigeic lichens, which, together with algae, bacteria and fungi, form biological soil crusts (Fig. 3; Belnap et al., 2001). Of all lichens, a special role is played by species with a cyanobacteria component; their ability to utilize atmospheric nitrogen enhances the substrate with nitrogen. The lichen thalli, supported by algal mats, also bind large amounts of organic carbon as a result of photosynthesis, and after their decomposition, contribute to the enrichment of the initial soil. The dominant species are from the *Collema* genus, which occur both close-in and distant from glacier foreheads. Species of this genus are cyanolichens (the hosts for cyanobacterial symbionts) and this feature influences their colonization potential (Sancho et al., 2011). Recent research shows that one of the main factors limiting the occurrence of epigeic lichens on glacier forelands is the stability of the substrate. In the case of epilithic lichens, colonization may start earlier due to their more stable substrate (especially regarding large block of rocks), but colonization of the soil by epigeic lichens is not as long as that of epilithic species, however, in relation to bryophytes or algae it requires a longer period than one season of the Arctic summer (Longton, 1988). Glacier forelands do not represent a homogeneous substrate; along the whole of their length the geomorphologic processes cause various disturbances making substrates very unstable, especially in areas with a steep slope or river activity. Surface erosion impedes epigeic lichen colonization. Even the presence of epilithic lichens may be limited by rock movement or surface washing by glacial rivers; in such disturbed and wet areas, bryophytes are usually more apparent.

Bryophytes

Unlike lichens, bryophytes (mosses and liverworts) show a much faster growth rate, and produce a greater biomass (Longton, 1988). In glacier forelands subjected to strong erosion, for instance the activity of glacial rivers, bryophytes are able to colonize the substrate in a short time, tolerating increased soil moisture levels (Fig. 4; Walker et al., 2001; Wietrzyk et al., 2016). In addition to cyanobacteria, bryophytes are the organisms that are able to occupy habitats closest to glacial ice margins. Unlike epigeic lichens, they have developed a system of rhizoids that function as a root, thereby surviving in periods of high surface water and being better



Fig. 3 Cryptogamic species creating biological soil crust dominated by *Protopannaria pezizoides*. © P. Wietrzyk-Pelka.



Fig. 4 The moss, *Polytrichum piliferum* colonizing the foreland of Rieperbreen. © P. Wietrzyk-Pelka.

adapted to a less stable ground. Recent research has identified bryophyte species growing close to glacial margins (Wietrzyk et al., 2018) that are also usually commonly found in mature tundra communities, such as *Bryum pseudotriquetrum*, *B. caespiticium*, *Calliergon sarmentosum*, *Ditrichum flexicaule*, *Encalypta alpina*, *Pohlia cruda*, *Polytrichum piliferum*, and *Sanionia uncinata*. Their presence in the coldest and most unstable regions of the foreland indicates their particular adaptation to extreme conditions.

Vascular Plants

Vascular plants appear to be the final organisms to colonize glacial forelands, after the barren substrate has already been significantly transformed by cryptogam colonization and soil-forming processes. However, studies have shown that vascular plants are usually not the last group of colonizers, and some species may even appear as first colonizers (Fig. 5; Wietrzyk et al., 2016). The plants' life forms and their spreading methods also influence the colonization potential of individual species. All monocotyledon plants recorded in the early and later stages of glacial foreland succession form loose clumps or grow individually. Individual and young plants are most likely to be found in early successional stages. Seed production plays an important role in the succession process since most of the species observed on the studied foreland have a high germination capacity (Cooper et al., 2004). The seed bank in the soil on glacier forelands is many times smaller than in mature tundra communities of Svalbard (Cooper et al., 2004). However, the effective colonization of glacier forelands by seedlings germinating from the seed bank is possible. A cascade effect is also possible, when germination takes place faster in places overgrown with vegetation than in areas lacking plant cover, as observed in the glacier forelands in the central Alps (Erschbamer et al., 2008). Production of runners is another strategy that allows colonization. The species which are dominant in forelands mostly reproduce vegetatively, as observed in the Arctic and the Alps



Fig. 5 *Saxifraga cespitosa* growing between rocks in the Rieperbreen foreland. © P. Wietrzyk-Pelka.

(Stöcklin and Bäumler, 1996; Wietrzyk et al., 2016). Additional strategies that facilitate succession include pseudoviviparous reproduction, a condition in which vegetative propagules replace some or all of the normal sexual flowers in the flower heads. Vascular plant colonization is also related to the availability of propagules of fungi that form mycorrhizal associations which may be vital for successful vascular plant establishment in glacier forelands (Trappe and Luoma, 1992; Cázares et al., 2005).

A Case Study—Primary Succession in Glacier Forelands of the Svalbard Archipelago

Study Area

In Svalbard, where almost 60% of the area is glaciated (Jónsdóttir, 2005), a progressive recession of glaciers has been observed since the termination of the Little Ice Age at the end of 19th century (Błaszczuk et al., 2009). Glaciers have been reduced both in their thickness and areal extent. Measurements from north-western Spitsbergen (Moreau et al., 2005) and south of the island (Ziaja et al., 2011), indicate the intensification of glacial recession from the 1980s onwards. Glacial volume has decreased, especially in western Svalbard (James et al., 2012; Nuth et al., 2013), as exemplified by the following results from primary succession process studies conducted in the forelands of four glaciers (Fig. 6).

Longyearbreen

Longyearbreen, located in Nordenskiöld Land in central Spitsbergen, is a rather small valley glacier, which flows northeast from the accumulation zone located at c. 1000 m a.s.l. and ends at c. 250 m a.s.l. (Hagen et al., 1993). The glacier covers an area of 2.52 km², and is 3.6 km in length with a mean width of c. 500 m and an average ice depth of 53 m (Etzelmüller et al., 2000; Langford et al., 2014). Due to its location near Longyearbyen, the main settlement in Svalbard, the glacier and its foreland are frequently visited by tourists. In recent decades, when a coal mine operated on the eastern slope of the glacier valley, the intensity of human and vehicular traffic was high. Currently, there is a popular hiking route running through the glacier and its moraine (Fig. 7).

Rieperbreen

Rieperbreen, also located in Nordenskiöld Land, is a valley-confined glacier connected to the Foxfonna glacier complex; it is c. 2 km in length and less than 400 m wide, the elevation of its outlet varying from 200 to 500 m a.s.l. (Lyså and Lønne, 2001).

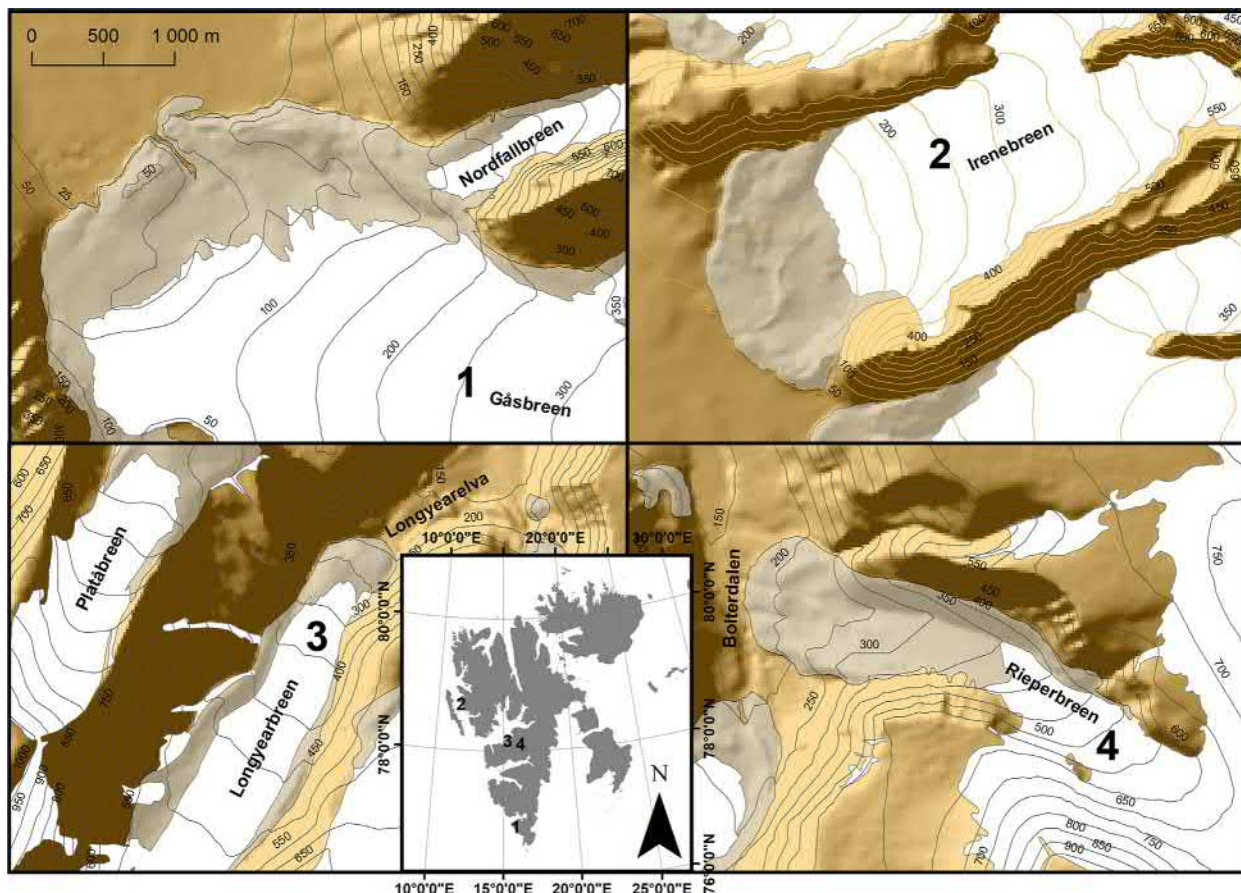


Fig. 6 Map of the locations of glacier forelands in Svalbard. © Norwegian Polar Institute 2018.



Fig. 7 Longyearbreen glacier and its foreland in 2018. © M.H. Węgrzyn.

In comparison with Longyearbreen, the glacier is much less often visited by tourists because of its location at the end of Bolterdalen valley (c. 14 km from Longyearbreen) (Fig. 8).

Irenebreen

Irenebreen, located in Oscar II Land, NW Spitsbergen, is one of seven glaciers surrounding the Kaffiøyra Plain. It is a valley glacier c. 4 km in length and between 1 and 1.5 km in width, bordered by Gråfjellet in the north, and by Prinsesserygen in the south, Prins Heinrichfjella in the east (Sobota, 2011). This glacier covers a total area of c. 4.1 km², the elevation of its outlet varying from c. 150 to 600 m a.s.l. (Fig. 9; Sobota, 2011).

Gåsbreen

Gåsbreen is located in the north-western part of the Sørkapp Land, on the southern shore of Hornsund (south Spitsbergen). It is a medium-sized valley glacier (c. 7.3 km in length, 14.3 km² and with a volume of 1.6 km³ in the 1990s) (Figs. 10 and 11; Hagen et al., 1993).

Methodological Approach

Fieldwork was carried out in the summers of 2008, 2011, 2012, and 2015 in the moraines of Gåsbreen, Longyearbreen, Irenebreen and Rieperbreen, respectively. One linear transect, consisting of 1 m² plots, was designated across each of the studied



Fig. 8 Rieperbreen foreland in 2017. © P. Wietrzyk-Pełka.



Fig. 9 Irenebreen and its foreland in 2012. © M.H. Węgrzyn.



Fig. 10 The forehead of Gåsbreen in 2008. © M.H. Węgrzyn.



Fig. 11 Gåsbreen foreland in 2008. © M.H. Węgrzyn.



Fig. 12 The 1 m² frame used for the determination of species percentage cover. © P. Wietrzyk-Pelka.

forelands from the front of the glacier to the end of the foreland. Percentage cover of each vascular plant, bryophyte and lichen species was recorded from every plot with the aid of a frame measuring 1×1 m divided into 100 squares (each of 10×10 cm) (Fig. 12).

Vegetation Development and Order of Species Colonization

Similar habitat conditions prevailing on glacier forelands appear to contribute to a similar composition of species communities, as well as similar trends in the development of plant cover. However, based on studied glacier forelands, differences in the colonization process are noticeable. Within the recorded species, a group of early, intermediate and late colonizers can also be identified, among which the differences between the forelands are also visible (Table 1; Figs. 13 and 14). The four studied forelands

Table 1 Types of plant colonizers

	Type of colonizer	Gåsbreen	Longyearbreen
1. Early colonizers—species appeared first on the exposed substrate in the first stage of primary succession	1.a. Vascular plants appearing in the first succession stage and disappearing in the later stages	<i>Carex lachenalii</i> , <i>Cochlearia groenlandica</i>	–
	1.b. Vascular plants appearing in the first stage of succession, which, although not disappeared in subsequent stages, reached the maximum occurrence early on the transect	<i>Saxifraga cespitosa</i> , <i>Saxifraga cernua</i> , <i>Sagina nivalis</i> , <i>Poa alpina</i> var. <i>vivipara</i> , <i>Cerastium regelli</i>	<i>Cerastium arcticum</i> , <i>Papaver dahlianum</i> , <i>Saxifraga cernua</i> , <i>Oxyria dygina</i>
	1.c. Bryophytes appearing in the first succession stage and decreasing their number in the later stages	<i>Bryum pseudotriquetrum</i> , <i>Brachythecium turgidum</i>	<i>Bryum pseudotriquetrum</i> , <i>Brachythecium turgidum</i>
	1.d. Species present in the most of the transect, appeared in the first stage of succession, but reached the maximum occurrence in the final stage of succession	<i>Saxifraga oppositifolia</i> , <i>Cerastium arcticum</i>	<i>Saxifraga oppositifolia</i> , <i>Cerastium arcticum</i>
2. “Intermediate” group—plants that appeared for the first time in the second stage of primary succession		<i>Draba</i> sp., <i>Salix polaris</i>	<i>Draba</i> sp. <i>Salix polaris</i> , <i>Saxifraga cespitosa</i> , <i>Bryum calophyllum</i> , <i>Pohlia drummondii</i> , epilithic lichens
3. Late colonizers—species which appeared for the first time at a considerable distance from the beginning of the transect in the third or fourth stage of succession		<i>Puccinellia vahliana</i> , <i>Micranthes nivalis</i> , <i>Silene acaulis</i> , all lichens	<i>Porpidia tuberculosa</i> , <i>Pseudephebe pubescens</i> , <i>Rhizocarpon grande</i> , <i>Umbilicaria</i> sp., <i>Cetraria</i> sp., <i>Collema</i> sp., <i>Cladonia</i> sp., <i>Flavocetraria</i> sp., <i>Ochrolechia</i> sp., <i>Stereocaulon</i> sp.

Examples of species were identified along the forelands of Gåsbreen (Wietrzyk et al. 2016) and Longyearbreen.



Fig. 13 *Papaver dahlianum*, an example of an early colonizer. © P. Wietrzyk-Pelka.



Fig. 14 *Salix polaris* growing in the foreland of Rieperbreen. © P. Wietrzyk-Pelka.

showed differences in the number of species of particular plant groups and in the order of species appearance, as well as in the composition of the initial communities.

Within the Gåsbreen marginal zone, 17 vascular plant, 13 bryophyte and 18 lichen species were recorded. Vascular plants that appeared as the first on the designated transect were dominant. In the Longyearbreen foreland, 21 vascular plant, 13 bryophyte and 45 lichen species were recorded (Wietrzyk et al., 2016). The general schemes of appearance order of particular groups of organisms on Gåsbreen and Longyearbreen forelands were similar. The vascular plants were the earliest colonizers on both transects, and concurrently or shortly thereafter, the first bryophytes appeared, followed by the epilithic lichens. *Saxifraga oppositifolia* (Fig. 17) proved to be dominant on both forelands, and *Cerastium arcticum* was frequently recorded. Vascular plants were mostly found in areas with a moderate slope, avoiding both the most exposed slopes and wetlands in lower areas. They also occupied surfaces between large blocks of rock, but the majority of bryophytes occurred in wet places, and on the fine grained substrate between stones. Epilithic lichens were observed on large stone blocks and smaller stones, even in steeply sloping areas. The Longyearbreen foreland was dominated by lichens, mostly epilithic. The low number of epigeic lichens and vascular plants seems to be caused mainly by human trampling on the foreland as a result of a significant increase in tourism, which has expanded along Longyearbyen (Kaltenborn, 2000). Such trampling greatly inhibits or even prevents the development of terrestrial lichens (Wietrzyk et al., 2017). Regarding Irenebreen and Rieperbreen forelands, cryptogams were the most numerous group: 113 lichen species and 49 bryophyte species, while vascular plants comprised only 29 species. In both moraines, bryophytes were the first to colonize the freshly deglaciated areas. For all recorded taxa, lichens were the dominant group, with 88 species recorded for the Rieperbreen moraines and 60 species for the Irenebreen foreland. For bryophytes, 37 and 19 species were noted in Rieperbreen moraines and Irenebreen foreland, respectively. Vascular plants were the least numerous, with 21 species recorded in the Rieperbreen foreland and 20 species recorded in the Irenebreen foreland. Figs. 15 and 16 show the development of lichen, bryophyte and vascular plant cover and first appearance of each species along the forelands of Irenebreen and Rieperbreen.

The order of entry of particular groups in the studied foreland and other glacier moraines of Svalbard seem to be similar. Bryophytes or vascular plants appear first, while epigeic lichens enter later, when the substrate is more stable (Moreau et al., 2005, 2008). The most abundant species of vascular plants are *Saxifraga oppositifolia* and *Cerastium arcticum*, but *Sagina nivalis* and *Saxifraga cespitosa* are also often recorded in glacier forelands. *S. oppositifolia* was the dominant species in deglaciated areas in both the north (Hodkinson et al., 2003; Moreau et al., 2005) and the south of Svalbard (Pirożnikow and Górniak, 1992; Wojtuś et al., 2008). *Cerastium arcticum*, together with *Cochlearia groenlandica*, *Sagina nivalis*, and *Saxifraga cespitosa* were usually recorded in the younger parts of the Midtre Lovénbreen and Werenskiöldbreen marginal zone (Moreau et al., 2008). The same trend was observed in the Longyearbreen and Gåsbreen forelands, but *Sagina nivalis* was recorded rather in the older fragments of the Irenebreen, Rieperbreen and Werenskiöldbreen forelands (Wojtuś et al., 2008; Wietrzyk et al., 2018).

Among all taxa forming Arctic vegetation, cryptogamic species seem to be the principal components. Their participation in the formation of plant communities as a result of the primary succession process in freshly deglaciated areas of glacier forelands is significant. The rapid enlargement of ice-free areas within marginal zones of Arctic glaciers provides new habitats for possible

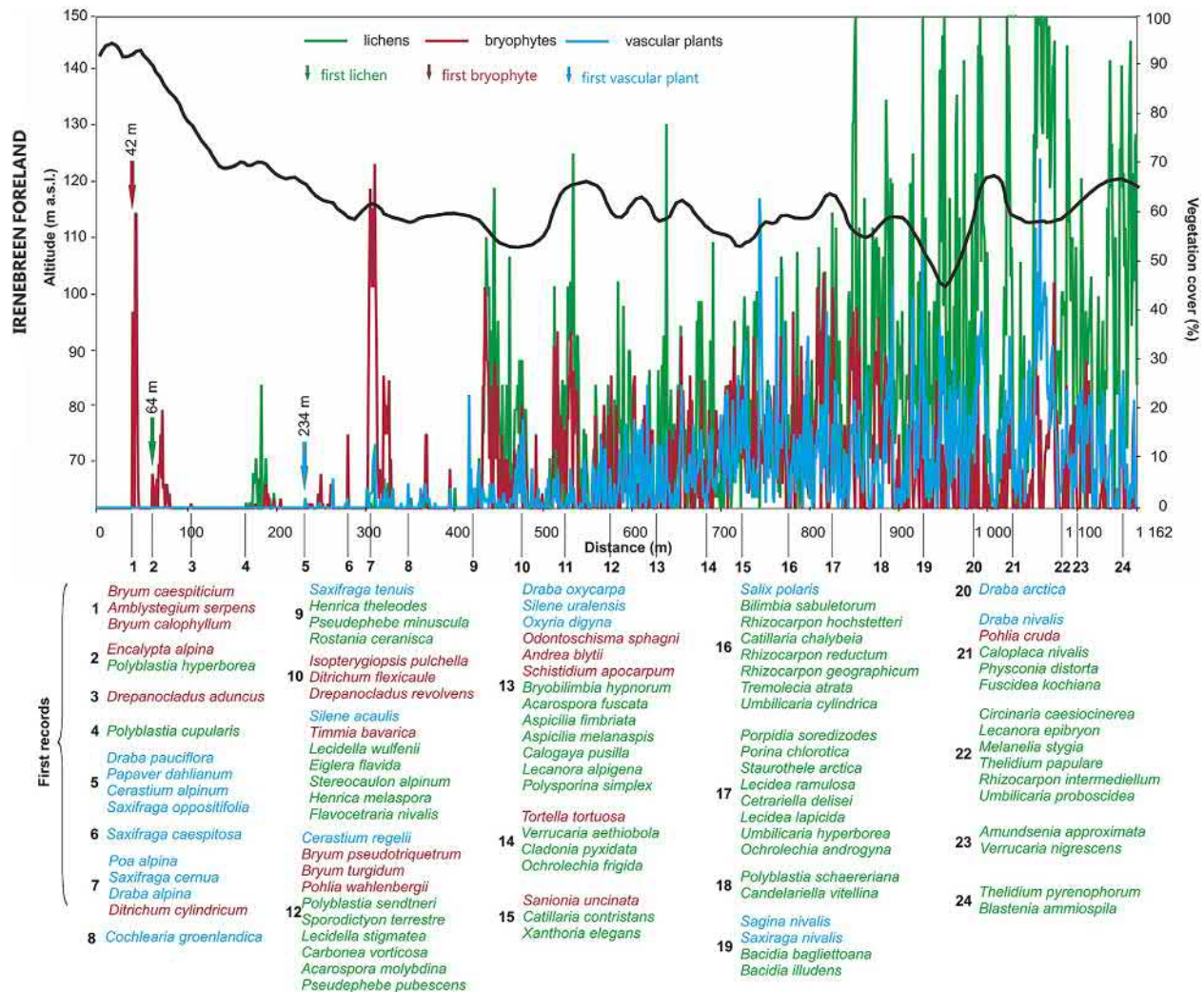


Fig. 15 Development of vegetation cover and species appearance during primary succession in the Irenebreen foreland.

colonization by organisms. These areas are firstly inhabited by cryptogams, such as cyanobacteria, mosses, liverworts and lichens, due to their strong pioneering abilities which allow them to survive in the extremely harsh environments of glacier forelands. In the case of lichens, epilithic taxa may also occur close to the glacier forehead since they colonize stable rocks uncovered by the retreating ice (Fig. 18). Epigeic lichens usually inhabit more mature parts of the foreland, where ice had disappeared earlier, and species have had sufficient time to colonize the substrate, and where the influence of dead-ice thawing and glacier-affected microclimate is reduced (Wietrzyk et al., 2018). For all glacier forelands in Svalbard, epigeic lichens appeared in the older parts of the moraine (Moreau et al., 2009; Wietrzyk et al., 2016, 2018). Apart from common *Collema* species, such as *C. ceraniscum*, species from the genus *Stereocaulon* (Fig. 19) were frequently recorded (Moreau et al., 2009; Wojtuń et al., 2008; Wietrzyk et al., 2016, 2018). These species, apart from *Chlorophyta* photobiont, also contain cyanobacterial symbionts which bind atmospheric nitrogen, influencing the colonization potential of these lichens. These probably play an important role in the soil-forming processes (Sancho et al., 2011). In the studies conducted in Werenskioldbreen, Tishkov (1986) emphasized the importance of so-called micro-depressions, which allow a faster process of primary succession, because of an optimal condition regarding the snow accumulation and moisture contents. Compared to lichens, bryophytes, especially minerotrophic species, inhabit moist areas that dominate the younger parts of the foreland and seem to tolerate the erosional activity of proglacial rivers that form periodically near the glacier forehead (Walker et al., 2001; Atherton et al., 2010; Wietrzyk et al., 2018). It should be noted that the number of cryptogamic species colonizing freshly deglaciated forelands exceeds the number of vascular plants species (Wietrzyk et al., 2016, 2017). Consequently, the glacier forelands seem to offer habitat conditions where cryptogams are less vulnerable and less exposed to competition from vascular plants, compared to tundra communities with better-developed vascular plant cover (Alatalo et al., 2017). As regards climate warming, glacier melting and the phenomenon of Arctic greening, glacier forelands may serve as cryptogam refugia in future, where such species will be able to withstand competition from vascular plants.

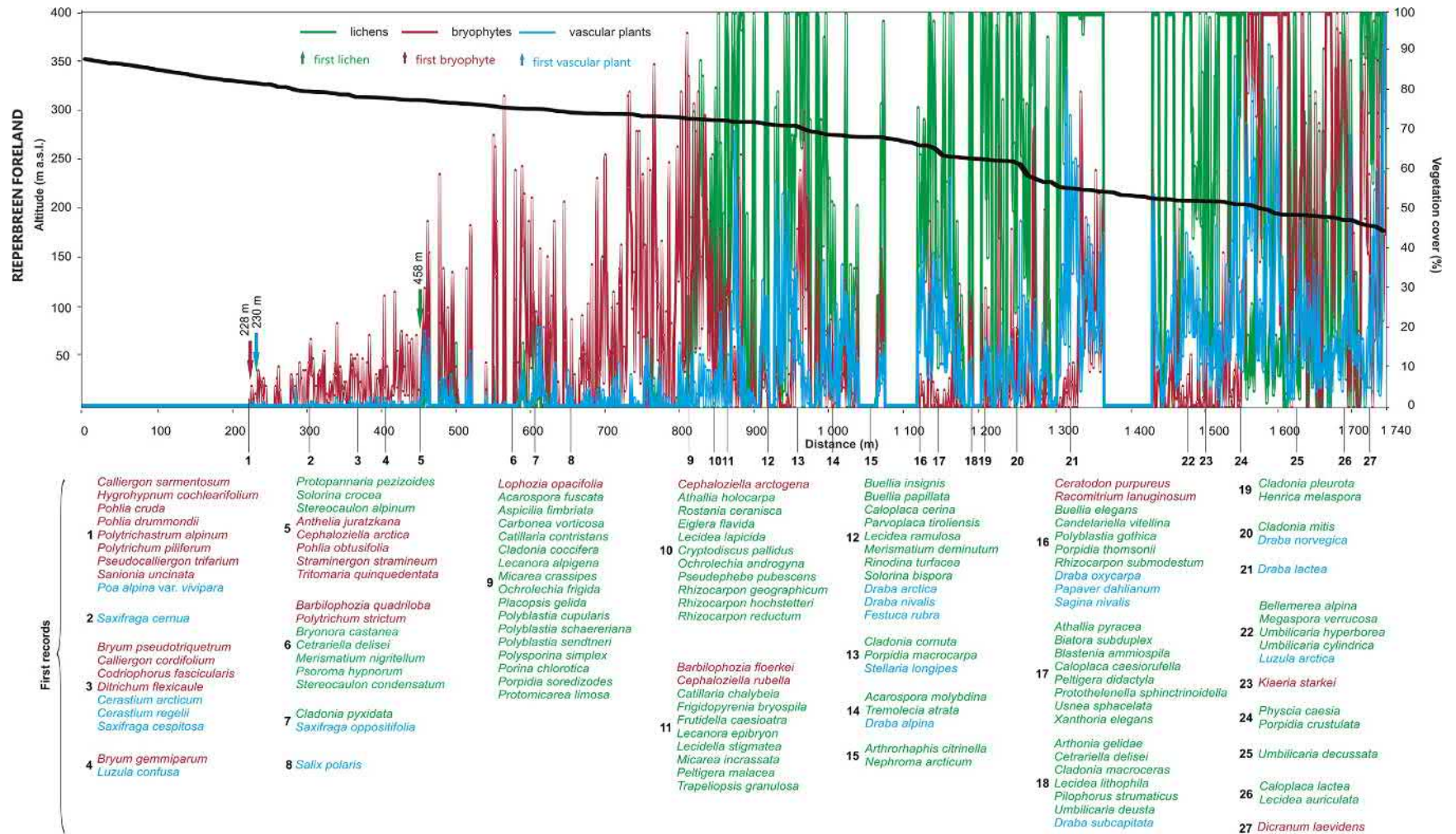


Fig. 16 Development of vegetation cover and species appearance during primary succession in the Rieperbreen foreland.



Fig. 17 *Saxifraga oppositifolia* growing in the foreland of Rieperbreen. © P. Wietrzyk-Pelka.



Fig. 18 Epilithic lichens overgrowing a large rock. © P. Wietrzyk-Pelka.

Environmental Factors Influencing Life Around Arctic Glaciers

Clements (1916, 1928) indicated that the following processes drive succession: denudation, migration, establishment, competition, reaction, and stabilization. Within these, denudation plays a vital role, since this process of disturbance creates a barren substrate largely devoid of biota (Walker and del Moral, 2003). Due to the relationship between primary succession and geomorphological processes, the moraine's vegetation does not develop in the climax communities but only reaches the near-climax communities. Initial communities developing in the forelands are often disturbed by environmental factors. It is believed that river runoff is one of



Fig. 19 *Stereocaulon alpinum* growing in the foreland of Rieperbreen. © P. Wietrzyk-Pelka.



Fig. 20 *Salix polaris* and *Saxifraga cespitosa* in flower. © P. Wietrzyk-Pelka.

the most influential process in the formation of lowlands and slopes in the glacier moraines and therefore has an important impact on vegetation development. Within strongly eroded regions, younger succession stages were observed than in the same aged parts of the foreland without flooding (Moreau et al., 2008). Wojtuń et al. (2008) also drew attention to the relationship between the type of substrate and the occurrence of particular groups of plants, while Kuc (1996) emphasized lichen preference for a stable substrate. Research conducted in Gåsbreen foreland (Wietrzyk et al., 2016) showed that the distance from the front of the glacier was the main factor influencing the distribution and abundance of vegetation; also, the fine grain material and slope steepness had a great importance. Studies by Wietrzyk et al. (2018) in the Irenebreen foreland demonstrated that apart from soil pH, distance from the glacier forehead and total nitrogen content also affects species occurrence and vegetation development. The greater percentage cover of vascular plants and terrestrial lichens in the older part of a moraine was associated with a lesser impact of glacier microclimate due to greater distance to the glacier forehead, as well as more stable substrate unaffected by glacial rivers and ice-cores (Fig. 20). The stable substrate allows more time for plant colonization; in contrast, poorer vegetation, mainly composed of bryophytes and algae, occur in wet and unstable places, periodically eroded by glacial rivers.

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Threats to Arctic Ecosystems

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Abstract

Pollution, ocean acidification and global warming are all major threats to Arctic ecosystems and are all inextricably linked. Major global air and ocean currents bring pollutants north to the “Arctic sink” where they accumulate over time, affecting ecosystems and wildlife. Meanwhile, carbon pollution from fossil fuels is causing widespread ocean acidification and global warming, which is happening two to three times faster in the Arctic than other regions. While climate change is having direct effects on Arctic ecosystems, the dynamics of pollutants within Arctic ecosystems are also being affected, enhancing pollutant mobility and effects in some cases.

Contaminants

Contaminants travel to the Arctic from more industrialized southern areas through the atmosphere (days/weeks), rivers (weeks/years) or the ocean (years). Because of the cold climate in the Arctic, and the nature of the contaminants, they tend to persist in this environment, cycling among abiotic matrices (air, water, snow, sediment) and making their way into the food web (Fig. 1). Many of these compounds bioaccumulate (build up in an animal over its lifetime) and/or biomagnify (concentrate up the food chain so that top predators have the highest levels). Long-term and/or high-level exposure to contaminants can lead to serious health effects in wildlife and people. Contaminants of concern in the Arctic include mercury, radioactivity, plastics and a broad range of persistent organic pollutants, which, for the most part, are man-made carbon-based compounds. All these contaminants are of concern because they are persistent in the environment and toxic.

Mercury

Mercury is a naturally occurring element that, since industrialization, has been emitted to the atmosphere through coal combustion; more recently, artisanal and small-scale gold mining has become an additional major source. The total amount of mercury released to the air each year from anthropogenic sources is estimated to be about 2000 tonnes each year. A further 3000–4000 tonnes are released to the air either from natural sources, or as a result of re-emission of mercury that has previously been deposited onto surfaces, back into the air. It has been estimated that Arctic Ocean seawater currently accumulates about 25 tonnes of mercury each year (AMAP, 2011). Mercury tends to accumulate in muscle and liver tissue of vertebrates and can have toxic effects on the nervous, digestive and immune systems, particularly in the unborn fetus. Mercury is considered by the World Health Organization as one of the top 10 chemicals of major public health concern (WHO, 2017).

Mercury is mostly deposited from the air in inorganic forms which are not very bioavailable. However, bacteria can methylate these forms, creating methylmercury, a toxic organic form that is readily bioavailable, bioaccumulates within animals (and people) and biomagnifies up the food chain. Methylation can occur in aquatic environments, sediments and wetlands. Virtually all the mercury present in fish is in the toxic methylmercury form, allowing biomagnification through the Arctic marine food chain to seals and fish-eating seabirds, and on to polar bears (*Ursus maritimus*) and people. As a result, mercury levels tend to be higher in marine as compared with terrestrial ecosystems. In contrast, in the terrestrial system, mercury (mostly the less toxic inorganic forms) accumulates in caribou and reindeer (*Rangifer tarandus*) liver and kidneys from lichens, the primary winter forage. Lichens have no roots, just anchors, and effectively absorb their nutrients (and contaminants) from the atmosphere. Other terrestrial ungulates, such as moose (*Alces alces*) and muskox (*Ovibos moschatus*), have much lower levels of mercury since they do not normally consume lichens and their diet of browse and grasses contains little mercury.

Mercury levels in the Arctic are now three times higher in freshwater and 10 times higher in marine ecosystems than they were in the early 1800s. Over the past 150 years, there has been a 10-fold increase in mercury levels in upper trophic level marine animals (beluga, ringed seal, polar bear, birds of prey); over 90% of that increase is believed to be anthropogenic in origin (AMAP, 2011). Accumulation of mercury varies geographically within the Arctic, with levels being higher in beluga (*Delphinapterus leucas*), ringed

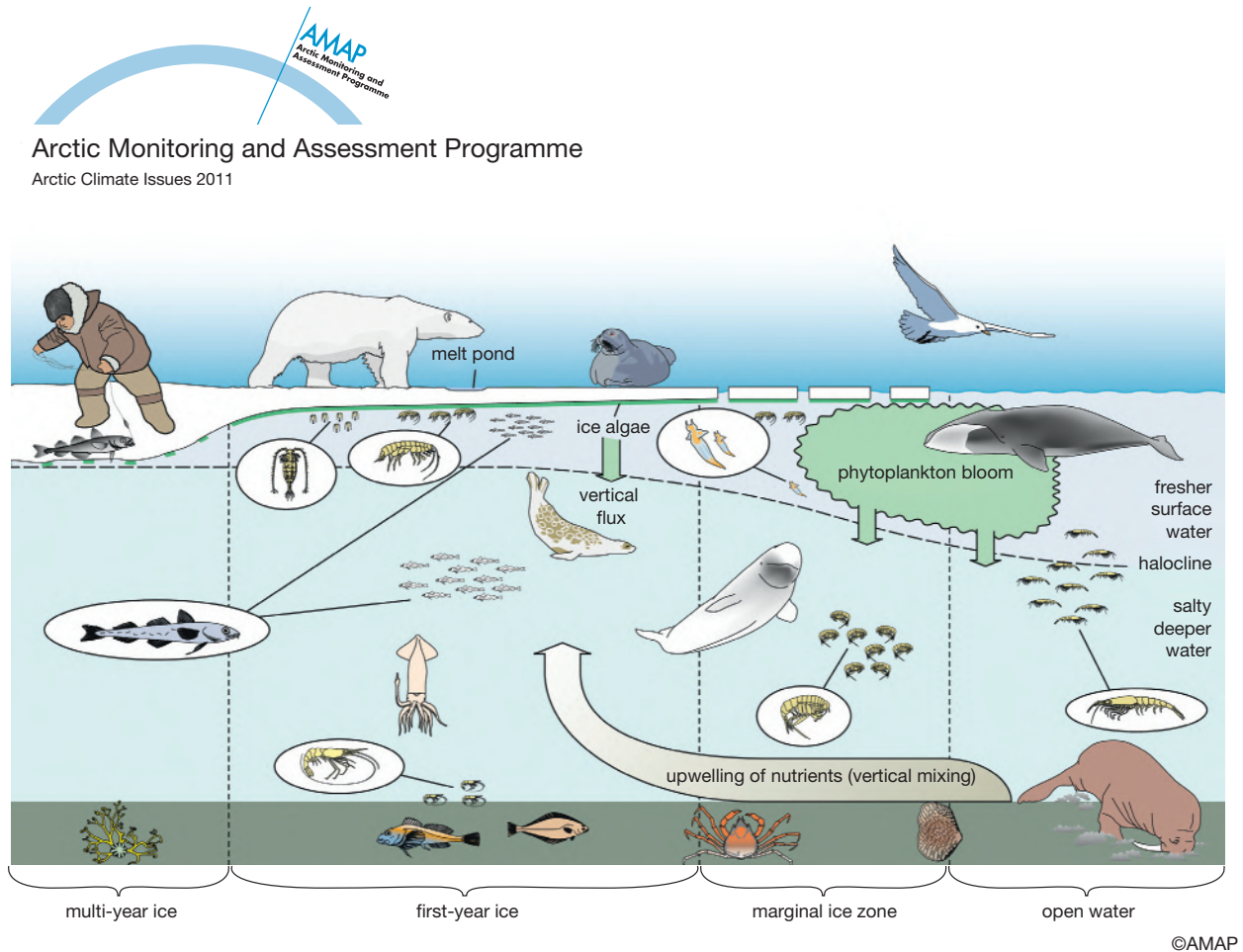


Fig. 1 The Arctic marine food web (AMAP, 2012).

seals (*Pusa hispida*) and polar bears from the Beaufort Sea as compared with other Arctic regions. This is likely due to habitat use and food web structure. Latitudinal trends have also been observed for ringed seals and seabirds, with greater concentrations in the High Arctic than at sub-Arctic sites (AMAP, 2011). Research is continuing to try to identify underlying processes leading to temporal and geographic variability in mercury levels in Arctic wildlife.

Although most terrestrial and marine mammals are at low risk of toxicological effects from mercury exposure, for some species at high marine trophic levels, such as polar bear, pilot whale (*Globicephala melas*), narwhal (*Monodon Monoceros*), beluga and hooded seal (*Cystophora cristata*), a proportion of the population is at high or severe risk (AMAP, 2018a). Measured biological effects in these species include inhibition of brain neurochemical receptors and immune suppression. Mercury concentrations in Arctic birds were above toxicity benchmarks in many areas of the marine environment, particularly for seabirds. Some bird species have mercury levels in their eggs sufficiently high to raise concern about negative effects on reproductive success. New research focusing on the effects of mercury exposure on gene expression holds promise for increasing our understanding of subtle toxicological effects (AMAP, 2011).

Toxicological effects of mercury in the Arctic are not limited to wildlife. Although blood mercury levels in residents of Nunavik have declined since the early 1990s, in 2013, 44% of Inuit women from Nunavut still had levels that exceeded health guidelines and nearly 60% of preschool children in Nunavut exceeded the provisional tolerable weekly intake level for methylmercury set by the World Health Organization (Tian et al., 2011). Although it is promising that levels are declining, we know from wildlife research that this is not due to declining mercury concentrations in traditional food (Arctic wildlife), but more likely from a decline in traditional food consumption. In addition, a long-term study on the effects of mercury from prenatal exposure in Nunavik found developmental effects including lower estimated IQ, poorer comprehension, perceptual reasoning, memory and early processing of visual information, and increased risk of attention problems and ADHD behavior (CACAR, 2017). This is still clearly a health issue for Arctic people, particularly those relying on the marine environment for subsistence food.

Concern over high mercury levels in the environment led the United Nations Environmental Program to create the Minamata Convention on Mercury, a global treaty to protect human health and the environment from the adverse effects of mercury. The Convention came into force in 2017 and bans or limits mercury mining, uses, emissions to air and releases to land and water

(UNEP, 2018a). Although it is too early to see the effects of the Convention in environmental mercury concentrations, it is an encouraging step.

Radioactivity

Radionuclides occur naturally in the environment as radioactive minerals and cosmic radiation from outer space. They are also produced by medicine and industry, and may result from accidents in nuclear facilities and nuclear bomb explosions. Radon is a naturally occurring radioactive gas and the second leading cause of lung cancer after tobacco smoking. It can be increased by industrial activities such as mining and fracking, often due to dumped waste products. Nuclear testing in the Pacific, Russia and elsewhere (1945–95) resulted in global fallout of radionuclides throughout the Northern Hemisphere, including the Arctic (UNSCEAR, 2000). Meanwhile, regular dumping of liquid and solid radioactive waste in the Arctic was practiced by the former Soviet Union and later by Russia from the early 1960s until the early 1990s. Dumping of radioactive waste was also carried out by other countries in the Atlantic and Pacific oceans despite strict international guidelines to the contrary (Sivintsev et al., 2005). The Arctic Ocean has received additional inputs of radioactivity from the 1989 sinking of a Russian nuclear submarine containing a nuclear reactor and two nuclear-warhead torpedoes (Gladkov et al., 1994), discharges from nuclear fuel reprocessing plants at Sellafield, United Kingdom and Cap de la Hague (AMAP, 2010) and the nuclear power plant accidents at Chernobyl in 1986 and Fukushima Daiichi in 2011. Radionuclides accumulate in the muscle tissue of animals and people. Exposure to low-levels of radiation does not cause immediate health effects, but can increase the risk of cancer over a lifetime.

In the terrestrial ecosystem, cesium-137 can readily accumulate in lichens, a major food source for Arctic caribou and reindeer. This radionuclide can be released into the environment from nuclear facility accidents and nuclear bomb explosions. In Arctic Canada, cesium-137 continues to decline in caribou from the original input from nuclear testing in the 1960s and did not increase as a result of the Chernobyl or Fukushima accidents (Macdonald et al., 2007; Stocki et al., 2016). However, cesium-137 did increase in reindeer in Scandinavia as a result of atmospheric fallout from the Chernobyl accident. Levels have been decreasing since that time, but since the early 2000s there has been a slower decline, indicating that radioactive contamination is being maintained in the system, bound in the soil. This was confirmed by a sudden rise in cesium-137 in reindeer from southern Norway in 2014, caused by an unusually large number of mushrooms on their feeding grounds, some of which are known to be efficient accumulators of radioactive cesium (Skuterud and Thørring, 2012). Current levels of anthropogenic radioactivity measured in Arctic marine and freshwater environments are very low and generally declining.

Persistent Organic Pollutants (see Table 1 for Acronyms)

Persistent organic pollutants (POPs) have been used industrially (e.g., PCBs) and agriculturally (e.g., DDT) since the early 20th century and enter the environment during their production, use or disposal. New POPs, being created as household products such as stain guards, nonstick coatings and flame retardants, are finding their way from local drains and landfills into the ecosystem, and new compounds are being created constantly. Most POPs tend to accumulate in the fatty tissue of vertebrates, including the liver, and can affect immune, endocrine and reproductive function. POPs may also cause increased susceptibility to disease and damage to the nervous system.

Most POPs that have been banned for an extended period of time (>20–30 years) in developed countries are now showing slower rates of decline in Arctic air and biota, indicating that they are approaching steady state with other environmental media and secondary sources now dominate. However, some POPs are showing no declines in some areas (e.g., PBDEs in air at Alert, Canada, possibly related to influence from a nearby military site and generally much higher PBDE use in North America), while some are still increasing (e.g., HCB and PCBs in air in Svalbard and Iceland; HCB, PBDEs, PFOS, β -HCH in some wildlife populations). This may be related to revolatilization from the open ocean due to significant ice retreat or melting glaciers in recent years as a result of global warming (AMAP, 2014).

Biological effects of POPs in wildlife are challenging to quantify. Laboratory studies are the usual benchmark for ascertaining a cause-and-effect relationship between a contaminant and an effect. However, due to the sheer number of POPs in the Arctic environment, these studies are virtually incapable of duplicating an accurate field scenario. Scientists have opted to investigate biomarkers (e.g., hormones, vitamins, immune system activation, liver enzyme activity) in wildlife, as indicators of biological effects and specific effects associated with POPs have been reported in several Arctic species. Based on PCBs being the dominant effect contributor, killer whales (*Orcinus orca*) were the species most at risk, while long-finned pilot whales from the Faro Islands and several populations of birds of prey (white-tailed eagles [*Haliaeetus albicilla*], peregrine falcons [*Falco peregrinus*]) are also at risk. Genotoxicity has also been shown for polar bears and some birds and fish, mainly driven by PCB exposure (AMAP, 2018a).

Levels of certain POPs (e.g., oxychlordane, DDT) are 2- to 10-fold higher among Inuit from the eastern Canadian Arctic and Greenland as compared to other populations in the Arctic (Norway, Sweden, Iceland, western Canada). However, concentrations of many of these compounds have decreased over the last two decades, particularly in the Inuit from the eastern Canadian Arctic (AMAP, 2014). For example, levels of POPs have declined by about 80% from 1992 to 2013 in pregnant Inuit women and by about 40% in Inuit children from Nuavik, likely due to the lowering of environmental levels of these compounds (CACAR, 2017). Studies of contaminant levels in the blood of residents in northern Norway and parts of Arctic Russia show that levels of POPs and PFASs subject to international regulations or bans have been decreasing over the past three decades in local residents, while concentrations

Table 1 Chemicals of concern to the Arctic as designated under the Stockholm Convention (UNEP, 2018a), the Minamata Convention (UNEP, 2018b) and Chemicals of Emerging Arctic Concern (AMAP, 2017)

		Acronym	Chemical
Minimata Convention	Initial “Dirty Dozen” (2004)	Hg	Mercury
Stockholm Convention			Aldrin
			Chlordane
		DDT	Dichloro-diphenyl-trichloroethane
			Dieldrin
			Endrin
			Heptachlor
			Mirex
			Toxaphene
			HCB
	Added (2009)	PCBs	Polychlorinated biphenyls
		PCDD/PCDF	Polychlorinated dibenzo- <i>p</i> -dioxins/furans
		HCH	Hexachlorocyclohexane (α , β , γ)
			Chlordecone
		HBCDD	Hexabromocyclododecane
		PBDEs	Polybromodiphenyl ethers
		HBCD	Hexachlorobutadiene
		PeCB	Pentachlorobenzene
		PCP	Pentachlorophenol
		PFOS	Perfluorooctane sulfonic acid
	Proposed for listing (2018)	PCNs	Polychlorinated naphthalenes
		SCCPs	Short-chain chlorinated paraffins
			Endosulfan
			Dicofol
		PFOA	Perfluorooctanoic acid
		PFHxS	Perfluorohexane sulfonic acid
Chemicals of emerging Arctic concern		PFASs	Per- and polyfluoroalkyl substances (including PFOS, PFOA, PFHxS)
		BFRs	Brominated flame retardants (including PBDEs)
		CFRs	Chlorinated flame retardants
			Organophosphate-based flame retardants and plasticizers
		Phthalates	
	SCCPs	Short-chain chlorinated paraffins	
		Siloxanes	
	PPCPs	Pharmaceuticals and personal care products	
	PCNs	Polychlorinated naphthalenes	
	HCBd	Hexachlorobutadiene	
CUPs	Current-use pesticides		
PCP	Pentachlorophenol		
PCA	Pentachloroanisole		
		Organotins	
	PAHs	Polycyclic aromatic hydrocarbons	
		New’ unintentionally generated PCBs	
		Halogenated natural products	
		Marine plastics and microplastics	

of unregulated PFASs are still increasing (AMAP, 2017). This is an indication of the success of international regulation of the specified contaminants.

The Stockholm Convention on POPs is a global treaty created to protect human health and the environment through the reduction, restriction or elimination of the production and use of specified POPs. The Convention came into force in 2004 with a list of 12 POPs, the “Dirty Dozen” and the addition of another 16 POPs since that time (UNEP, 2018b). As a result of this initiative, concentrations of many POPs have decreased in the Arctic environment. Although new emissions of these chemicals have been virtually eliminated, large quantities remain in environmental reservoirs (oceans and forests). These POPs will eventually break down, but the some compounds (e.g., PCBs) will persist for a long time. Meanwhile, scientists continue to discover previously unknown contaminants in the Arctic; many of these newer POPs will continue to increase in the environment until they are regulated on a global basis. Table 1 provides a list of chemicals currently being regulated (or being considered for regulation) and those considered by the Arctic Monitoring and Assessment Program to be of emerging Arctic concern (AMAP, 2017).

Plastics

Plastic debris has emerged as a major environmental concern worldwide. Plastics are made from a wide range of organic polymers that are semipersistent, breaking down from larger to smaller plastic particles through exposure to ultraviolet light and physical abrasion, but this is a slow process (Gewert et al., 2015). Most marine plastics are currently in the form of microplastics (<5 mm) (Cózar et al., 2014). Plastics are released into the environment during industrial activities such as commercial fishing, use of plastic abrasives and spillage of plastic pellets, but also from domestic applications such as washing of plastic microfiber clothes, use of personal care products containing microplastics (e.g., toothpaste and exfoliators) and municipal wastewater. Another major source of plastics in the oceans is landfills in coastal cities.

Plastics affect marine organisms through entanglement and blockage of intestines (Laist, 1987), but also through toxicological effects of plastic-related chemicals (Koelmans et al., 2014). Research on microplastics and their effects in Arctic ecosystems is just beginning, but they have been discovered in Arctic sea ice (Obbard et al., 2014), sea water (Lusher et al., 2015), sediments (Bergmann et al., 2017), fish (Kühn et al., 2018) and marine birds (Travail et al., 2015). Microplastics exhibit many of the same characteristics of POPs that make them a risk to Arctic ecosystems and people.

Ocean Acidification

Arctic marine waters are experiencing widespread and rapid ocean acidification, with important physiological and geochemical thresholds already surpassed. The primary driver of this change is uptake of carbon dioxide emitted to the atmosphere by human activities, but other biogeochemical processes are also contributing. This phenomenon is intensified in the Arctic relative to other regions due to low ocean temperatures that increase gas solubility and the inflow of naturally acidic water from the Pacific Ocean, river runoff and ice melt. The degree and distribution of acidification is not uniform across the Arctic Ocean, resulting in high temporal and spatial variability. This is driven by sea-ice extent, freshwater inputs, ocean currents, water temperature and the effects of biochemical processes.

Projections indicate that acidification in the Arctic Ocean will continue, although with considerable regional variability. It is anticipated that parts of the Arctic Ocean will experience significant ecological shifts over the coming decades, with direct and indirect effects on marine life, including changes in calcification, growth, reproduction, metabolic rates and food availability and quality. Calcification of the shells of marine invertebrates is key to their survival. As Arctic waters acidify, the potential failure of marine invertebrate shell formation threatens a major component at the bottom of the marine food chain. These effects are likely to be variable, depending on the ability of each species to adapt to the changing environment. Changes in fish and marine mammal populations may ultimately pose risks to commercial, subsistence and recreational fisheries and hunting (AMAP, 2018b).

Global Warming

Warming is occurring faster and with greater magnitude (two to three times higher) in the Arctic as compared with other regions mainly because of feedback mechanisms associated with less snow and ice now in this region. As a result, the Arctic is one of the regions at disproportionately higher risk from global warming (IPCC, 2018). Higher average temperatures in the Arctic will cause a reduction in glaciers, sea ice and permafrost, and will result in some shifts in habitat as more southern species gradually move north (this includes plant as well as animal species). Increasing temperatures will also affect the movement of contaminants around the globe, including movement into the Arctic. More intense, frequent and unpredictable extreme weather events are predicted for the all regions, including the Arctic.

Sea ice is expected to diminish, both in terms of cover and thickness. This will affect wildlife that use sea ice for feeding and habitat (Arctic cod [*Boreogadus saida*], seals, walrus (*Odobenus rosmarus*) and polar bears) and may cause shifts in feeding ecology and habitat use. The melting of the sea ice itself (along with melting glaciers) will increase sea level, changing ecosystems as some rivers disappear. Melting ice may in turn release contaminants stored in the ice, including mercury, POPs and microplastics (Obbard et al., 2014). It will also provide increased access and resulting opportunities for shipping and resource extraction in the Arctic, inherently increasing risks associated with habitat loss and fragmentation, wildlife disturbance, increased fishing harvest and pollution. A bigger risk is related to potential accidents, both in the Arctic Ocean and on the land, which could introduce significant sources of pollution to the environment but are particularly difficult to predict.

Melting permafrost in the Arctic will increase erosion and create instability for infrastructure (housing, municipal services, coastal structures), with implications for health, safety and well-being as well as economic considerations. Permafrost soils store nearly twice as much mercury as all other soils, the ocean and the atmosphere combined, and it is estimated that 793 Gg (793 million kg) of mercury could be released to the environment from permafrost thawing over the next century (Schuster et al., 2018). This could have major health implications for the freshwater and marine environments as well as humans using wildlife as subsistence food sources.

Increasing temperatures will affect how contaminants move around the planet. Atmospheric models show that higher temperatures due to global warming will enhance volatilization and re-emission of POPs and mercury from soils, water bodies and ice to air, increasing their atmospheric transport to the Arctic. However, this impact may be offset for some POPs by increased degradation

due to increased temperatures and by decreasing emissions. Overall, model studies of POPs do not show clear agreement on whether climate changes will reduce or increase concentrations of POPs in the Arctic; chemical responses will depend on the properties of each group of POPs (AMAP, 2014). In addition to enhanced volatilization, the biogeochemical cycling of mercury is likely to be affected by increased methylation of inorganic mercury due to increased algal growth in lakes. The most significant increase in radiation exposure to Arctic residents may arise from enhanced release of radon-222 from soil due to thawing of permafrost and decreased snow cover (with a resulting increase in environmental levels of lead-210 and polonium-210) (AMAP, 2010). New potential sources of radioactivity to the Arctic include the planned decommissioning of nuclear power plants which may lead to temporary increases in radioactive discharges that could eventually reach the Arctic. New power plants are also planned in areas distant from the Arctic and many older plants have been granted extensions to their operating licenses; accidents such as those at the Chernobyl and Fukushima Daiichi nuclear facilities have demonstrated that even accidents far from the Arctic have the potential to affect the Arctic region. The waste streams produced in the extraction of hydrocarbons and minerals—including uranium mining—contain naturally-occurring radioactive substances found in bedrock and will likely lead to enhanced releases and mobilization of naturally-occurring and technologically-enhanced naturally occurring radioactive material to the environment (AMAP, 2010). There may also be redistribution of mercury and radionuclides from natural events such as forest fires, that are expected to increase in frequency and intensity with global warming.

Encroachment of southern species into the home ranges of Arctic populations may result in changes in wildlife health from a number of perspectives: potential habitat loss and/or fragmentation, changes in migration routes, food web structures, feeding habits and diet, parasite loads, incidence of disease, and potential new introduced parasites and diseases. Increased human exploitation of Arctic resources will also likely result in loss of habitat, increased disturbance and an increase in local pollution, including plastics. These factors, along with the increase in extreme weather events, will cause increased cumulative stress in many Arctic wildlife populations, which can in turn, enhance the sensitivity of some species to certain pollutants.

On a human level, fishing, hunting and gathering activities are key parts of the northern economy and an important way of life for Arctic indigenous people. These activities will be strongly affected by unpredictable extreme weather events and the availability and health of wildlife species being directly affected by global warming and pollutants.

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Greenland Climates

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Abstract

This chapter describes the general climates of Greenland, and summarizes the main driving factors.

Introduction

Greenland is the largest island in the world, covering approximately 2.17 million square kilometers. The majority of the island is covered with ice bodies of which the Greenland Ice Sheet (GrIS) is by far the largest, covering about 80% of the island. A minor part, around 420,000 km², is ice-free land, and home for the terrestrial ecosystem. The island is surrounded by the North Atlantic Ocean to the southeast, the Greenland Sea and the Arctic Ocean to the northeast and north, respectively, and separated from Canada by Baffin Bay to the north and the Labrador Sea further south. The interplay between these waters, the GrIS, incoming radiation, and lastly the wind systems that pass or form over Greenland, determines the general climate on the island.

Ocean Currents and Sea Ice Around Greenland

From a global perspective, the most critical ocean current in the waters around Greenland is the North Atlantic Current, which maintains heat transport through the ocean around southeast Greenland ([Fig. 1](#)). The thermal difference in sea temperatures, occurring from differences in solar heating between low and high latitudes, combined with a haline forcing in the North Atlantic, drives a northward flow of warm surface water, and a southward flow of cold deep water. This thermohaline circulation is part of the Atlantic meridional overturning circulation (AMOC), which is a system of ocean currents in the North Atlantic, including the aforementioned North Atlantic Current. In its current state, the northward flow of relatively warmer surface water and the linked evaporation bring warmth and precipitation to southern Greenland. Climatic warming may trigger a weakening of the AMOC, resulting from less formation of cold and haline sinking water. From modeling studies, it has been suggested that a marked weakening of the thermohaline process within AMOC could decrease temperatures in southern Greenland by 6–10°C ([Stouffer et al., 2006](#)) and decrease precipitation by 0–0.3 m year^{−1} within 20–30 years after a shutdown ([Vellinga and Wood, 2002](#)). Such model results have an inherent uncertainty. However, current observations of sea surface temperatures show a local cooling anomaly southeast of Greenland over the past century, and a recent study attributes this to a 15% weakening of the AMOC since the mid-20th century ([Caesar et al., 2018](#)).

At a smaller scale than the AMOC and North Atlantic Current, two ocean currents of importance for the Greenlandic climates are the east and west Greenland Currents. The East Greenland Current originates in the Arctic Ocean, and begins with a southward flow through Fram Strait, along the continental shelf on the east coast of Greenland ([Fig. 1](#)). The temperature of the surface water is generally below 0°C, but it can reach 3–5°C in the summer ([Buch, 2001](#)). The current flows to the southern

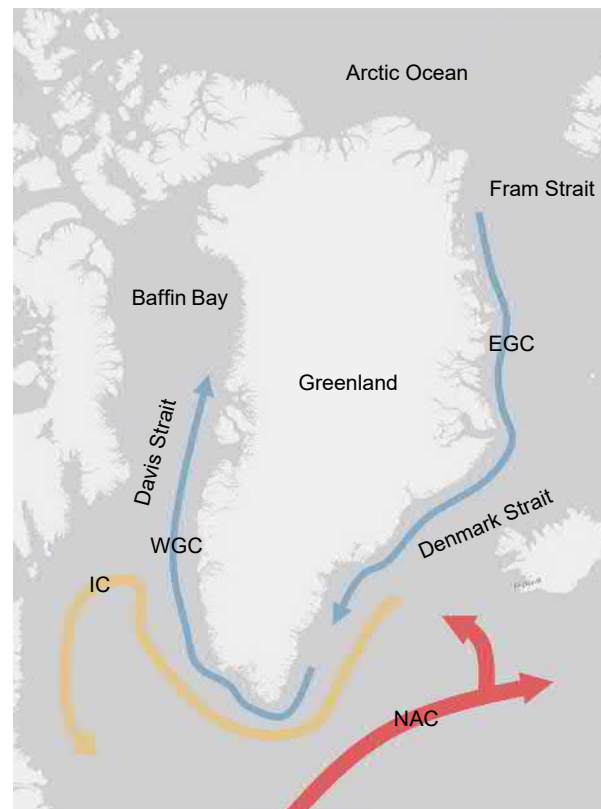


Fig. 1 Four prominent ocean currents with relevance for Greenland's Climates. NAC = North Atlantic Current; WGC = West Greenland Current; EGC = East Greenland Current; IC = Irminger Current.

tip of Greenland, Nunap Isua/Cape Farewell, and then curves back northward along the west coast of Greenland, eventually becoming the West Greenland Current. The West Greenland Current transports this now cold (below -1°C ; Cuny et al., 2002) water northward, parallel to the coastline of western Greenland. Icebergs are carried by the current towards $60\text{--}70^{\circ}\text{N}$, after which the current turns west and transports larger icebergs away from the coast and into Baffin Bay at $70\text{--}75^{\circ}\text{N}$. At these northern latitudes, the West Greenland Current meets with waters from the Canadian Arctic, forming the southward Baffin Current (Melling et al., 2001). Another current, the Irminger Current, originates from convection in the Irminger Sea southeast of Greenland, where a mixture of Atlantic and local low-salinity water moves from east to west Greenland (Fig. 1). It meets the warmer Subatlantic waters (can be above 5°C during the winter), which originate from a branch of the thermohaline North Atlantic Circulation. Together, they result in warmer winter conditions as well as high precipitation levels year-round in the coastal areas of south Greenland.

The East Greenland Current transports sea ice from the Arctic Ocean and southward along the Greenlandic east coast. This sea ice, named "Storis," is formed at high northern latitudes. It is consequently perennial in origin and in most cases about 3 m thick during winter, resulting in an estimated average annual ice flux of approx. $2200\text{ km}^3\text{ year}^{-1}$ (Kwok et al., 2004). The Storis covers the ocean near the east coast of Greenland most of the year, and has its greatest extent in February and March. The minimum extent occurs in August and September with a southern boundary of the sea ice around 75°N . The other type of sea ice with importance for Greenland climates is the West ice, which forms in Baffin Bay and Davis Strait during winter. It reaches its maximum extent around March, with a thickness of approx. One meter (Buch, 2001). It builds up from the north, and reaches Northwest Greenland in October, where after it expands southward. The southernmost border has moved northward during recent decades. During particularly warm winters this boundary can be found around Disko Bay (Fig. 2). This sea-ice decline has been reported to influence the general climate on the west coast, including plant growth in the region (Hollesen et al., 2015). The West ice never reaches southernmost Greenland due to the inflow of relatively warmer Irminger water and Subatlantic water during winter. Rapid disintegration of the West ice does not start before May, and the West ice is fully melted by late summer (Fig. 2).

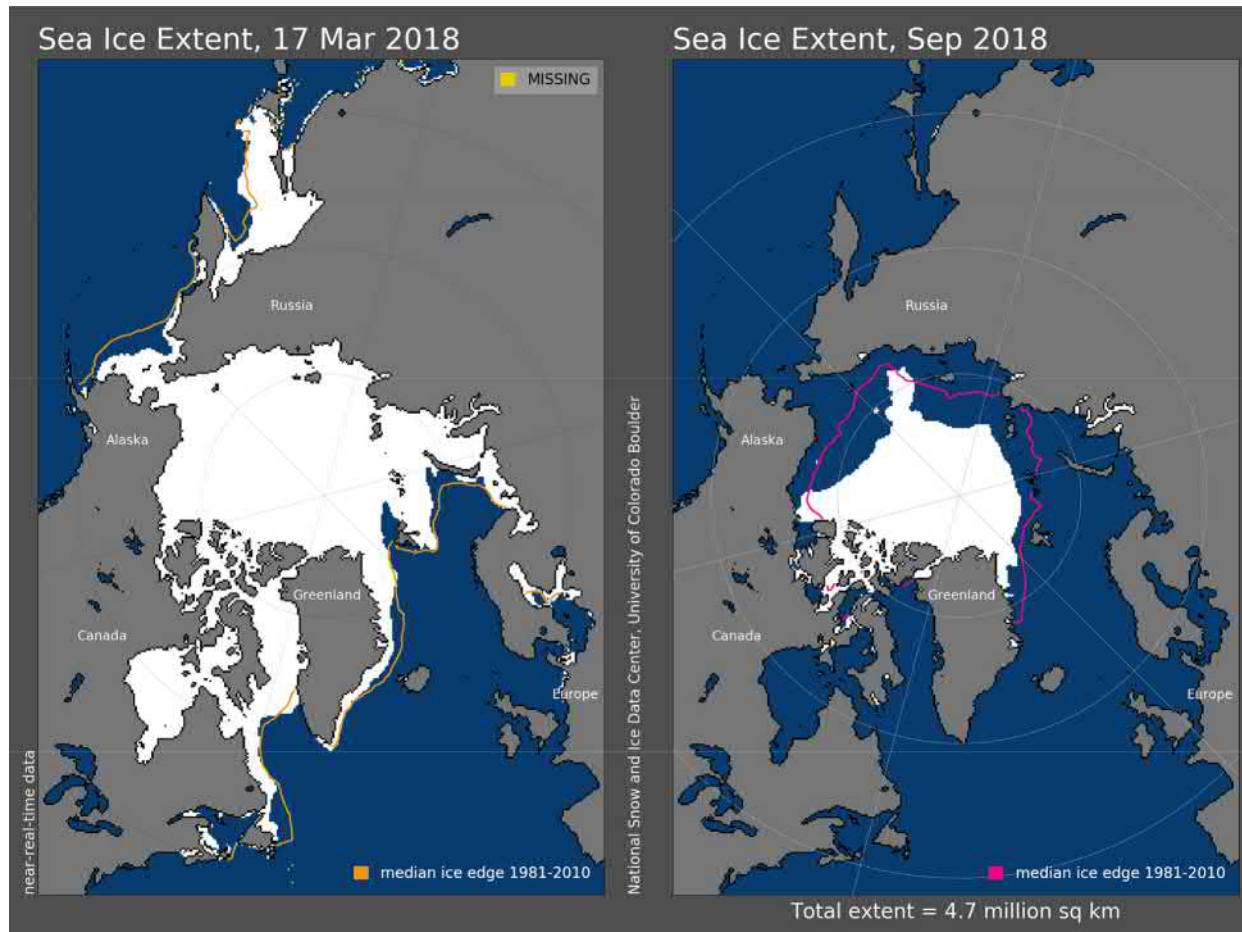


Fig. 2 Sea ice distribution in 2018 at its maximum (mid-March) and minimum (September) extent, as observed by satellite. This year can be compared to the median ice edge (1981–2010) to illustrate the low extent of sea ice, particularly in September. National Snow and Ice Data Center, University of Colorado, Boulder, United States.

Atmospheric Circulation and Wind Patterns

Regional Circulation and Wind Patterns

There are three air masses that are essential to the climate of Greenland: the Tropical-, the Polar-, and the Arctic air masses (Hansen, 2001). The Tropical air masses originate from high-pressure systems in the subtropics. Part of these air masses are formed over the Atlantic Ocean in the region between Bermuda and the Azores. Consequently, these are marine, meaning warm and moist, particularly in their lower layers. The Polar air masses influencing the Greenland climates originate from continental northern Siberia and Canada, whereas the colder Arctic air masses form over the Polar Sea and Arctic basin. Both the continental Polar and Arctic air masses are primarily formed over snow- and ice-covered surfaces, and are consequently dry and cold.

The boundary where the Tropical air masses meet the Polar and Arctic air is known as the Polar front, whereas the Polar and Arctic air masses meet at the Arctic front. When irregularities arise along the Polar front, a wave of unstable air is formed which leads to cyclogenesis, that is, they turn into low pressure systems (see a cyclone example in southeast Greenland on Fig. 3A). Eventually, the low pressure systems take on a cyclonic motion, often traveling from west to east. If formed west of Greenland, these traveling cyclones will be deflected by Greenland, in particular the GrIS, and will then continue to travel parallel to the coast. Their embedded frontal systems cause unstable weather in the areas over which they pass. The location of the Polar front is most variable during summer, but is generally positioned over Greenland's latitudes (Hansen, 2001). The cyclones formed west of Greenland rarely travel across the high GrIS. Rather they travel northward along the west coast, until they dissolve over the sea between Canada and Greenland. During winter, the colder northern air masses usually drive the Polar front south of Greenland, and the low-pressure areas pass over the southern parts of the island, or travel northward in the Denmark strait between Greenland and Iceland. In periods unaffected by low pressure systems, it is common for Greenland to experience inversions of the thermal lapse rate (see section **Temperature and Precipitation and Terrestrial Ecosystems**). This causes stable and very calm conditions, which prevail 20%–30% of the time, particularly on the east coast (Hansen, 2001) which is less affected by the low-pressure systems from the West, according to meteorological observations from the Danish Meteorological Institute (DMI).

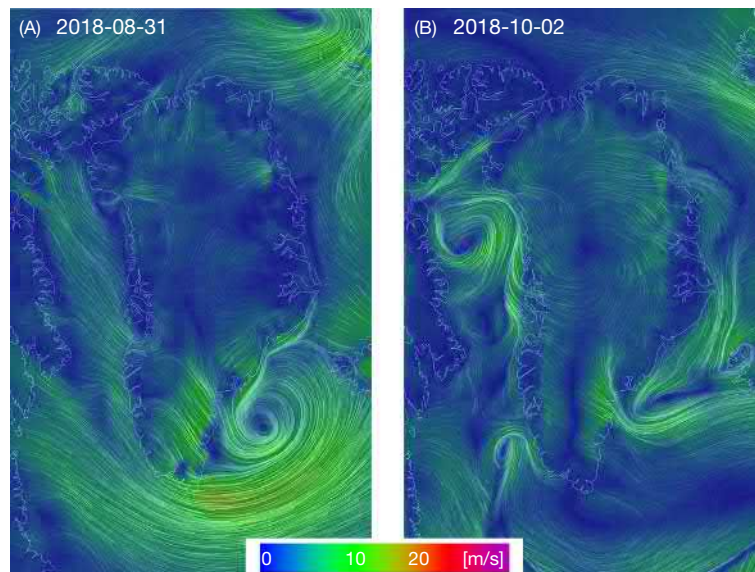


Fig. 3 Wind at the surface pressure level. (A) Shows a low pressure system in southwest Greenland in the Tasiilaq area. This low pressure system has wind speeds up to 25 m s^{-1} , and is strong enough to blow across the southern part of the Greenland Ice Sheet (GrIS). In typical situations, the winds are deflected by the high elevations of the GrIS. The low pressure system also breaks up the katabatic winds in the southern part of Greenland. (B) Depicts a typical calm day with katabatic winds around $6\text{--}8 \text{ m s}^{-1}$, and with the distinct canalizing wind stream from the GrIS and southeast-ward across Tasiilaq. Source: earth.nullschool.net and NCEP.

Circulation and Wind Patterns Related to the Greenland Ice Sheet

The GrIS has a negative net radiation balance due to the high albedo snow- and ice-covered surface reflecting the majority of the incoming radiation away from the surface of the Earth. This causes a cooling of the air masses above the GrIS and forms a relatively stable thermal high-pressure system year-round. At the surface, the wind direction across the GrIS is generally affected by the pressure gradient between this high pressure and a lower pressure over the coastal zone and beyond. The higher density of the cold air masses formed over the GrIS causes air to sink towards the coasts under gravitational influence in all directions away from the GrIS. These descending winds are known as katabatic winds, and their speed varies on a local scale depending on slope and pressure gradient, although they are often around $6\text{--}8 \text{ m s}^{-1}$. The katabatic winds are more prevalent during winter and better developed on clear days with low temperatures over the GrIS (Przybylak et al., 2003). This advecting dry air generally affects the adjacent ice-free landmasses along the margin of the ice-sheet. It shields the ice-free land from precipitation systems originating from the ocean. An example is shown on Fig. 3A and B where katabatic winds descend from the GrIS and out towards the coasts.

Local Wind Patterns

Locally, the wind patterns are controlled by the topography, ice caps, and proximity to larger water bodies. One example of this topographic control occurs around the Kangerlussuaq fjord on the east coast, where the topography shelters the land from strong katabatic winds (Sechrist et al., 1989) (not to be confused with the more commonly known settlement Kangerlussuaq on the west coast). Other areas are exposed to very strong katabatic winds through a canalizing effect (Cappelen et al., 2001). The latter situation is depicted on Fig. 3B, showing the canalizing effect of katabatic winds around Tasiilaq in east Greenland. A peculiar phenomenon related to the katabatic winds is the so-called Piteraqa, which is a combination of ambient katabatic winds combined with a sudden and fast drainage of cold air otherwise stored at a topographic plateau at higher elevations. Wind speeds of more than $70\text{--}80 \text{ m s}^{-1}$ (up to 288 km per hour) have been recorded during a Piteraqa, thus living up to its name “that which attacks you.”

Also other local wind patterns are directly related to the topography, oftentimes with a diurnal or seasonal cycle. Valley wind systems develop in many areas: Surface heating early in the day results in upward moving air masses along the mountain slopes, and subsequently the wind direction turns to ascend up the valley. The opposite air movement occurs at night when cold air blows towards the valley bottom. Another diurnal pattern occurs in coastal areas and land areas near great lakes, where the differential heating of land- and water-masses causes a movement of air from the water towards land during the day and the other way around during night. However, this breeze phenomenon also has an annual cycle with onshore winds during summer and offshore winds during winter, as observed, for instance, in wind direction data from Nuuk with winds from the northeast during winter and from the southwest during summer (Hansen, 2001). However, it must be noted that such systematic wind patterns are dissipated when frontal systems associated with cyclones pass through.

Similar to other mountainous areas, Foehn winds are common across Greenland. The dynamically induced Foehn winds are drier and warmer than the lower lying air masses in the fjord areas, as a result of an adiabatic descent from higher elevations. Foehn

winds are common along the west coast of Greenland, whereas the colder Katabatic winds are more widespread on the east coast (Cappelen et al., 2001). The Föhn situations can bring rapid, marked changes in air temperature, for instance resulting in episodic snow melt events with subsequent consequences for the ecosystem (Pedersen et al., 2015).

Temperature and Precipitation

The Greenland Inland Ice Sheet

The surface air temperature over the GrIS varies with latitude, elevation, and albedo, and can fluctuate quite markedly between seasons. For instance, at the summit (72.6°N, 38.4°W and ca. 3200 m a.s.l.), the mean annual air temperature is -31°C , with an annual range of approx. 30°C (Fig. 4). In this central part of the GrIS, temperatures as low as approx. -70°C have been recorded (Cappelen, 2017). Moving west or east from the summit, the temperature changes with approx. 0.8°C per degree latitude (Steffen and Box, 2001).

The temperature profile over the GrIS is also strongly affected by surface inversion layers. These thermal inversions in the tropospheric thermal lapse rate are particularly formed in periods with negative surface energy balance, such as periods with low solar

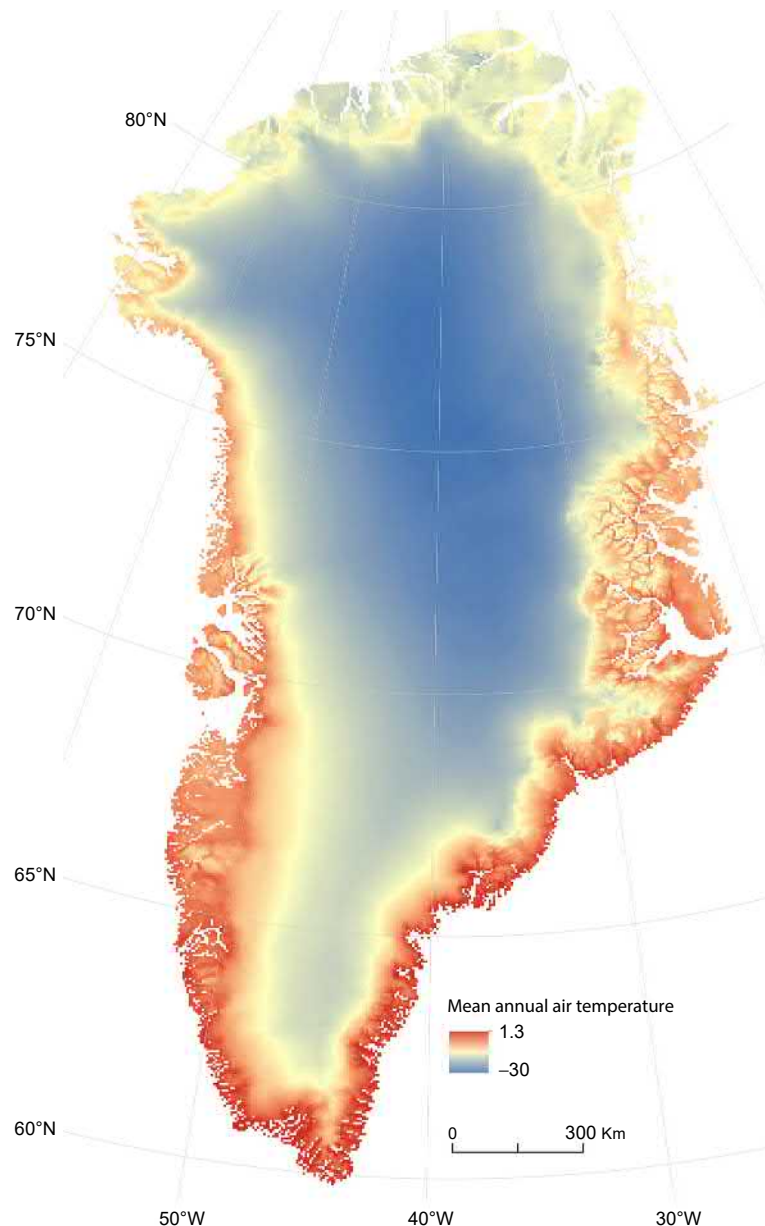


Fig. 4 Mean air temperature for the whole Greenland, derived from MARv3.5.2 RCM data from 1986 to 2015 (Fettweis et al., 2017).

radiation (and thus minimal heating of the Earth's surface), and over snow- and ice-covered surfaces with high albedo. These inversions are strongest during winter (Cappelen, 2017), but also occur in the summer. Cyclones passing over the GrIS create enough atmospheric mixing to disturb the inversions. Stable conditions reappear when the cyclones have passed.

The mid- and northern parts of the GrIS are highly arid resulting from the low humidity of cold air masses, while large precipitation amounts fall especially in the southeastern part. While the inner part of the GrIS gains mass through precipitation and rarely experiences melt conditions, the main ablation occurs in the lower lying margin of the ice sheet. Ice motion transports this surplus of mass from the interior to the margins.

Ice-Free Greenland

Although the ice-free part of Greenland only constitutes approx. 20% of the island's area, it covers a great variety of climatic regimes following its extent that covers several latitudinal and longitudinal degrees. In general, the ice-free part of Greenland represents a narrow band of land strongly influenced by the above-mentioned climate at sea and over the GrIS. The northern parts are subject to continuous permafrost, while discontinuous and sporadic permafrost is found south of 70°N. In southern Greenland, most of the ice-free regions only have permafrost at high elevations (Westergaard-Nielsen et al., 2018, Fig. 5). The complexity of local gradients such as the coast-inland-GrIS transects, makes Greenland a challenging place to study climate and related processes.

Latitudinal gradients

Greenland spans more than 23° of latitude, from 59.8 to 83.6°N. This results in quite varied climates, from high arctic polar desert in the north to humid low arctic tundra in the south. The latitudinal gradient in surface air temperature is mainly controlled by incoming radiation, and temperatures have consequently been described as almost linearly decreasing with latitude (Hansen et al., 2008; Rysgaard et al., 2003). However, the aforementioned ocean currents, and particularly sea ice conditions, are also important factors in controlling surface air temperatures across Greenland (Cappelen et al., 2001). In addition, cyclonic activity plays an important role, bringing unstable weather but also slightly warmer temperatures to the areas they cross (Przybylak et al., 2003).

The largest latitudinal temperature differences exist during winter and shoulder seasons during which the greatest differences in radiation balance and sea ice conditions are found. This temperature gradient is on the other hand small during summer, when the north/south variation in incoming radiation is less pronounced due to the midnight sun north of the Arctic Circle. In July, the average air temperature in Peary Land (Northernmost Greenland) is 2–3°C and it is 4–5°C around Nunap Isuata (Southernmost Greenland; Westergaard-Nielsen et al., 2018), despite a latitudinal difference of 23°. In January, the difference is much more pronounced, with –29 to –28 in Peary Land and –12 to –11 at Nunap Isuata (1986–2015 climate normal period, Fig. 6). This winter difference is higher when storm tracks with warmer temperatures reach the southern parts of Greenland. The variation in annual temperatures are also exemplified by the number of consecutive days with temperatures above freezing, as shown on Fig. 7. This figure illustrates the marked differences between north/south as well as east/west across Greenland over the course of the year.

Generally, the amount of annual precipitation decreases with latitude due to a combination of the warmer southern air masses being capable of carrying more moisture, longer periods with open waters, and higher evaporation from the sea surface. In addition, the percent of annual precipitation falling as snow is 80%–90% in the northernmost region (Hansen et al., 2008). Reliable precipitation measurements are scarce in Greenland, but data from the Danish Meteorological Institute (DMI) suggest 100–150 mm year^{–1} in the driest parts of North Greenland, and more than 2400 mm year^{–1} in the wettest areas of southeast Greenland (data from 1961 to 1999, Fig. 7). The spatial distribution of precipitation is illustrated in Fig. 8A and B. From a hydrological perspective, the latitudinal difference also results in an interesting shift in water balance. South Greenland has a positive net water balance (i.e., there is a higher input of water from precipitation than is lost from evapotranspiration); there is a negative net water balance in North Greenland. The shift is a continuum, but goes from positive to negative north of Disko Island, at around 70°N. This variation in water balance is crucial for ecosystem functioning, including soils. The negative water balance results in upward moving water, higher salinity and even salt precipitation on the soil surface in the north in contrast to soils in the south, which are more deeply weathered and nutrient poor, due to the leaching of nutrients. Both conditions influence plant growth and the response of vegetation in the Arctic to a generally warmer climate.

Longitudinal differences

The differences in air temperature and precipitation between the west- and east coasts result from the aforementioned sea ice dynamics etc., but also from a difference in topography and the area of ice-free land. The ice-free part of east Greenland south of 68°N is limited to a narrow strip of a few kilometers between the Denmark Strait and the GrIS. The topography is mountainous with elevation differences of more than 1000 m over 2–3 km. Consequently, this coastline is a significant orographic barrier for wind masses moving west from the Denmark Strait, and it receives a factor of two to three times more precipitation than the west coast at the same latitude, according to recent modeling (Fettweis et al., 2017), see Fig. 8. Besides the sea-ice conditions, the topography also plays a role in the lower average air temperatures than on the West coast, due to the higher elevations on average (Karami et al., 2017, Fig. 9).

The west coast south of 70°N has relatively mild winters, because of the absence of widespread sea ice, while north of 70°N, both the west- and east coast have quite stable and almost continental winter climates due to a persistent sea ice cover in Baffin Bay and the Storö, respectively. Winds from northerly directions are frequent during winter at both the west- and east coast

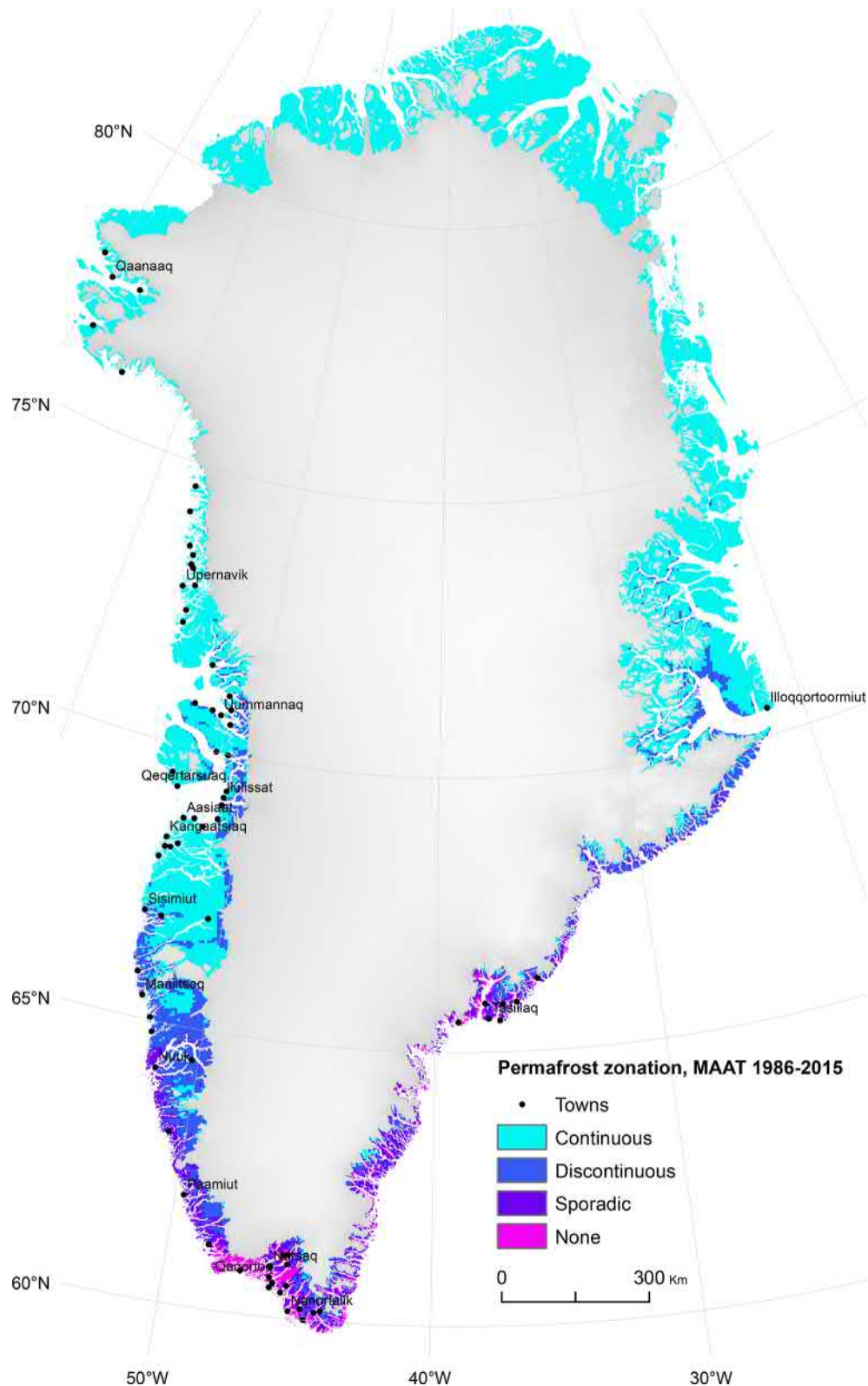


Fig. 5 Permafrost zonation in the ice-free part of Greenland. North of 70°N, the vast majority of ice-free land is subjected to permafrost, while permafrost is only found in high elevations south of 63°N. Westergaard-Nielsen, A., Karami, M., Hansen, B.U., Westermann, S., Elberling, B. 2018. Contrasting temperature trends across the ice-free part of Greenland. *Scientific Reports* 8(1), p. 1586.

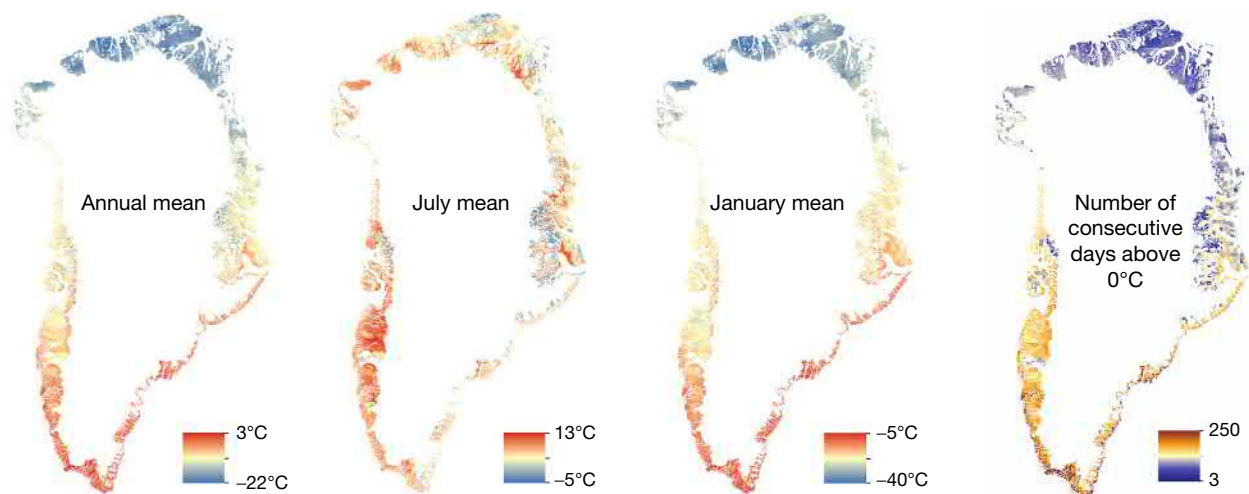


Fig. 6 Annual air temperature averages for the ice-free part of Greenland derived from MARv3.5.2 RCM data from 1986 to 2015 (Fettweis et al., 2017). Few differences in temperature can be observed in peak summer (July), while a strong north/south gradient exists during January. Westergaard-Nielsen, A., Karami, M., Hansen, B.U., Westermann, S., Elberling, B. 2018. Contrasting temperature trends across the ice-free part of Greenland. *Scientific Reports* 8(1), p. 1586.

north of 68°N, and are oftentimes associated with clear high-pressure weather at the coast (Cappelen, 2017). During winter, the low-pressure systems formed at the Polar front will occasionally pass along the Westcoast and disturb the clear weather with high wind speeds from south/southeast, precipitation, and higher temperatures, however not as frequently as during summer. A similar pattern occurs at the East coast north of 68°N, due to cyclonic activity over the Greenland Sea.

Coast-inland gradients

There are substantial differences between the climates at the outer coast and the inner fjords. Temperature differences along this gradient can be associated with the thermal properties of the ocean and land. However, Greenland is characteristic in the sense that the coast-inland gradients are usually east/west oriented, and therefore fall along the same latitude. Besides this, the coastal-inland gradients are also a continuum between the coastal zone and the GrIS.

In general, the winters are milder towards the coast with more precipitation. During summer, the coastal areas are colder than the protected inner fjord areas. This is the result of the proximity to cold waters, but it is also due to less incoming shortwave radiation during cloudy conditions, which are more frequent towards the coast. Again, the summer precipitation decreases when moving inland from the coast. For instance, Sisimiut has an annual precipitation of approx. 380 mm year⁻¹, an average summer temperature (June, July August) of 5.3°C, and –12.3 during winter (December, January, February) (data from 1961 to 1990, DMI). Kangerlussuaq, which is located on a similar latitude but 130 km further inland, receives only 150 mm year⁻¹, has an average summer temperature of 9.2°C, and an average winter temperature around –19.2°C (data from 1973 to 1999, DMI). Another example is the difference between Nuuk near the coast and Kangerlussuaq (Fig. 7).

Terrestrial Ecosystems

The primary productivity of Greenlandic terrestrial ecosystems mainly reflects summer temperatures, growing season length and precipitation. Greenland lies within the high-, low-, and sub-arctic vegetation zones. The high- and low arctic zones are separated roughly by the 5°C July isotherm, and the sub-arctic zone by the 10°C July isotherm and a growing season of 3–5 months. The sub-arctic zone is only found in the inner fjords in south Greenland. Here, low birch forests grow at protected sites, alongside shrub willows reaching 2 m in height. These areas also serve as grazing areas for sheep (Westergaard-Nielsen et al., 2015). The sub- and low arctic zones are characterized by a high biological diversity for a region experiencing arctic climate, with around 600 different species including mosses and lichens (Bay et al., 2001). The high diversity is especially found at moist and wind protected sites, but the majority of the low-lying areas in the low arctic zone are covered with a combination of vascular plants (especially dwarf shrubs), mosses, and lichens. Moving to the high arctic, the diversity decreases to approx. 100–300 species, and the vegetation is more open. Dwarf shrubs are less dominant, while lichens are more prominent. The coverage of vegetation in the high arctic areas is around 5%. Some species are found throughout coastal Greenland, such as willow and some sedges growing in moist wetlands, although the abundance of both is minimal in the north.

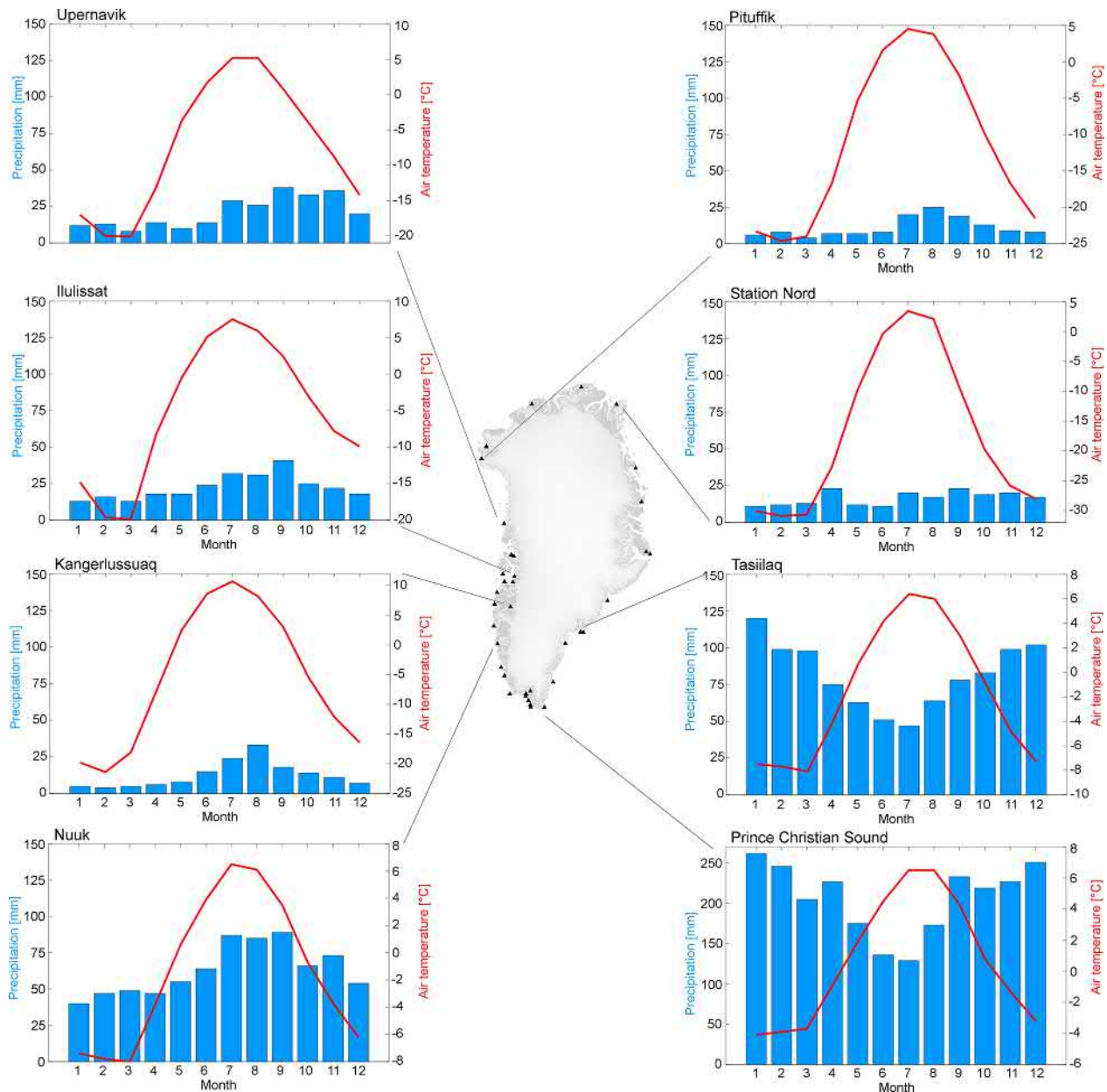


Fig. 7 Measured temperature and precipitation across Greenland, illustrating the differences in temperature amplitude and precipitation amounts from a coastal area (e.g., Nuuk) and inner fiord area (e.g., Kangerlussuaq). Likewise there is a distinct decrease in precipitation towards the north, resulting from the lower absolute moisture levels in the atmosphere.

The North Atlantic Oscillation and Its Effect on Greenland Climates

The North Atlantic Oscillation (NAO) is considered the most prominent and recurrent system of atmospheric variability over the mid- and high northern latitudes (Hurrell et al., 2003), which is also true for Greenland, especially during winter. It is driven by a surface pressure difference between the region around the Azores, and around Iceland. NAO is considered in a positive phase during large pressure differences and a negative phase when the difference is low. A significant positive state during winter results in stronger westerly winds over the North Atlantic and northerly winds which carry cold air from northernmost Canada and Greenland southward. This generally results in colder than average land and sea surface temperatures over northeast America and most of Greenland. The same general pattern occurs during summer, although it is less pronounced. The increase in northerly winds traveling southward over Greenland during a strong positive NAO transports low amounts of atmospheric moisture, which again results in a higher likelihood of below average precipitation over Greenland. Gridded climate data suggests that NAO-driven changes in winter precipitation are less predictable than changes in summer precipitation (Harris et al., 2014). Consequently, a strong positive NAO-phase during summer can generally increase the precipitation in southwest Greenland.

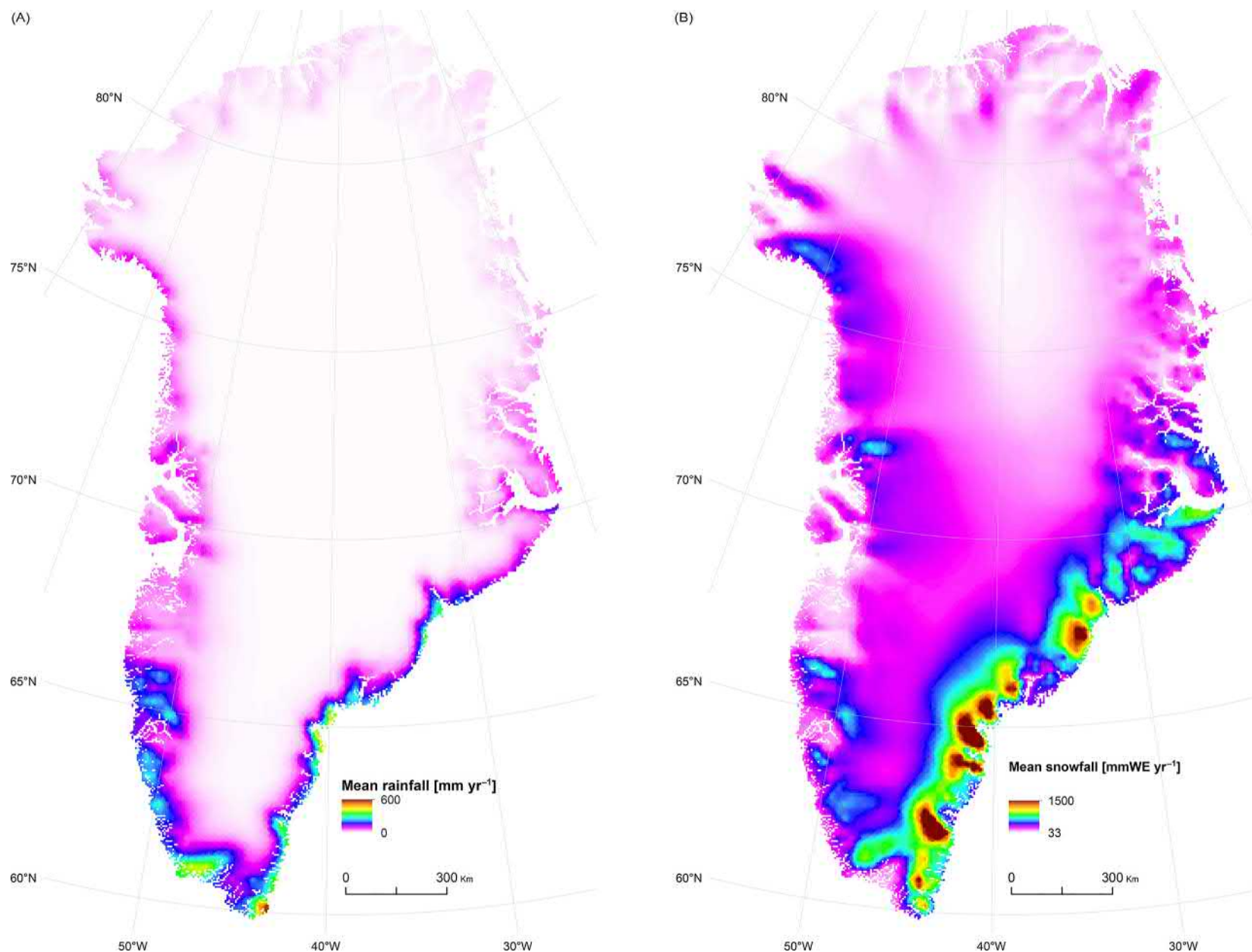


Fig. 8 Precipitation across Greenland averaged from 1986 to 2015 using MARv3.5.2 RCM data from 1986 to 2015 (Fettweis et al., 2017). (A) Illustrates rainfall, (B) Illustrates snowfall. Particularly the south- and southeast coast receives large amounts of precipitation coming with the warmer ocean currents from sub-Atlantic waters.

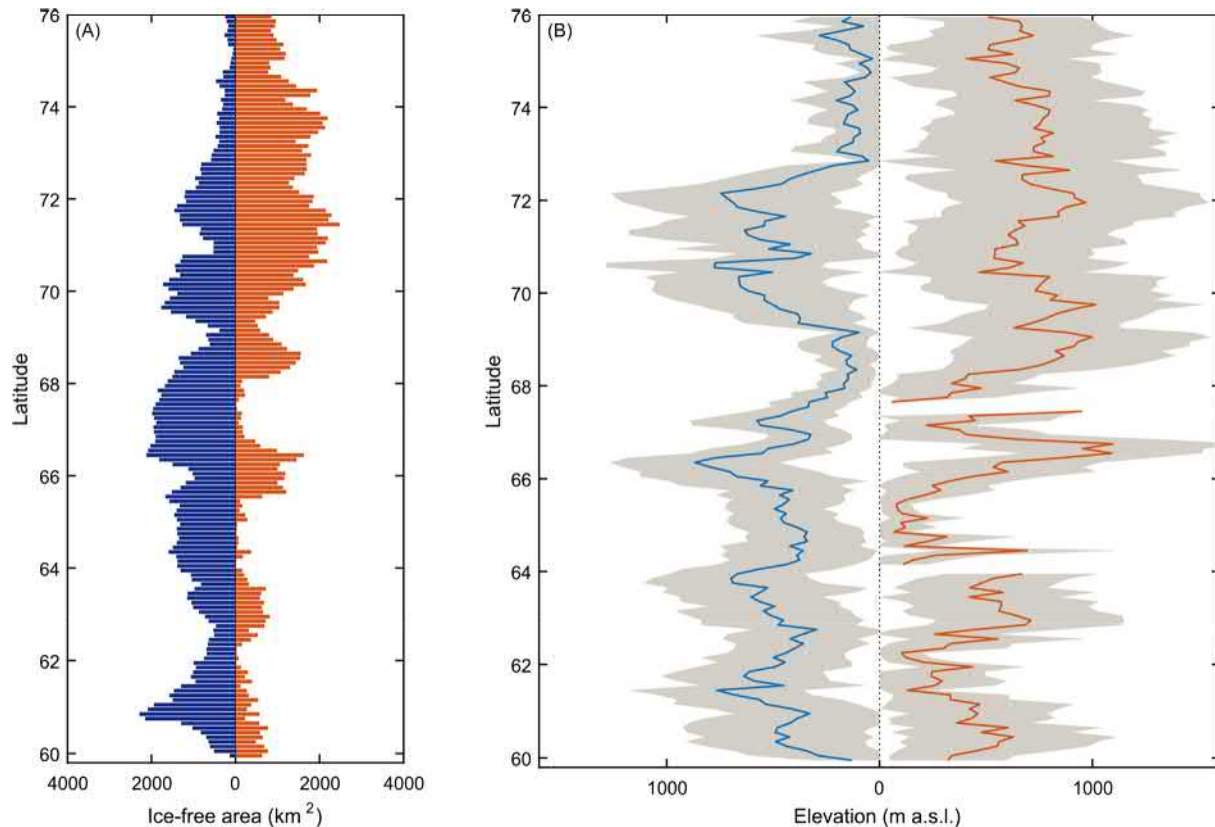


Fig. 9 Latitudinal differences in ice-free area and elevation. *Blue* bars and lines represent the west coast, *red* bars and lines represent the east coast. *Gray* areas represent the total elevation dataset, while the *blue* and *red* lines show the average elevation in m a.s.l. Karami, M., Hansen, B.U., Westergaard-Nielsen, A., Abermann, J., Lund, M., Schmidt, N.M. and Elberling, B., 2017. Vegetation phenology gradients along the west and east coasts of Greenland from 2001 to 2015. *Ambio* **46**(1), pp. 94–105.

A negative NAO increases the likelihood for drier than average conditions in the southern third of Greenland, and warmer temperatures across west Greenland.

NAO is known to have downstream effects reaching far into Europe and North America.

Acknowledgments

The work was supported by the Danish National Research Foundation (CENPERM DNRF100), and University of Copenhagen. This work was also supported by Greenland Ecosystem Monitoring (GEM), The Ministry of Energy, Utilities and Climate, and participating institutions.

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Terrestrial Ecosystems of West Greenland

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Abstract

The contemporary terrestrial ecosystems of West Greenland from ~64 to 70 °N and their environmental context are described. Regional geology is predominantly Archean basement volcanic rocks and climate ranges from maritime low arctic to continental low arctic in the dry interior with a corresponding switch from intermittent to continuous permafrost. There is a pronounced gradient in effective precipitation which is clearly reflected in surface water chemistry and vegetation. Vegetation is characterized by dwarf shrub tundra, and plant community structure reflects the overarching regional climate gradient but also local topographic controls and processes (relief, aspect, altitude). The moist outer coastal areas are characterized by *Empetrum nigrum* and cryptogams with fellfield communities at higher altitudes, while the dry, continental interior has a more relatively luxuriant assemblage of woody plants, notably *Betula nana* and *Salix glauca* where water availability permits. Closer to the ice sheet margin and at higher altitudes, landscapes are steppe-like with plant community structure reflecting the more extreme and inhospitable (cold and windy) conditions. Soil types and distribution broadly reflect these climate and vegetation gradients. The role of climate and immigration changes since deglaciation in molding the modern ecosystems are described, notably the effect of the Holocene climatic optimum and Neoglacial cooling. The effect of grazing by the two large herbivores (*Rangifer tarandus* and *Ovibos moschatus*) on vegetation and carbon dynamics are considered as well as the synergistic interactions of herbivores and vegetation with rapid climate changes (moisture stress, warming and increased late-winter precipitation) that have occurred since 1996. Recent phenological change and altered winter precipitation have driven trophic mismatches in *Rangifer tarandus* and the Greenland White-fronted goose (*Anser albifrons flavirostris*) possibly related to climate teleconnections across the North Atlantic, such as the Greenland Blocking Index.

Because 80% of Greenland is ice-covered, the diverse terrestrial ecosystems of West Greenland are contained in a relatively small area, which coupled with the strong regional environmental gradients in temperature and precipitation make it a natural experimental area. Rapid recent warming (mean June temperatures have increased by 2.2 °C since 1994) has occurred while extensive ecological research is being undertaken which is allowing critical insights into processes and linkages between temperature, moisture and external disturbances (grazing, insect outbreaks and atmospheric nutrient inputs: dust deposition and reactive nitrogen). The results of this research are providing a deeper understanding of terrestrial and aquatic ecosystem development, resilience and change, both in terms of how past processes and landscape history, natural environmental gradients shaped their formation and how they are responding to recent rapid climate change.

Introduction

Greenland is home to the second largest ice mass on Earth today. Ice covers some 80% of the island and while the ice sheet is a major focus of research, the ice-free areas include a diverse range of terrestrial and aquatic habitats. The strong environmental gradients that are created by the close juxtaposition of ice, land and ocean provide a range of natural experimental environmental scenarios that are increasingly being utilized by scientists. These longitudinal and latitudinal gradients also offer glimpses of what the ice marginal environments of the Fennoscandian and Laurentide ice sheets would have been like during the last glaciation. Moreover, the Greenland ice sheet is now changing rapidly with major implications for functioning of the earth system, through sea-level rise and climate dynamics. While the recent changes in the Greenland ice sheet are themselves representative of global warming, the changes in terrestrial communities are also indicative of wider set of problems affecting high altitude ecosystems,

namely the interaction of warming, changing precipitation with altered biogeochemistry (e.g. long-range nutrient deposition) and atmospheric pollutants. The continued decay of the ice sheet will create new terrestrial environments as previously glaciated areas are exposed but also impact those habitats that were established following its contraction from its maximal extent due to changing physico-chemical gradients at the land-ice interface (Anderson et al., 2017). Today, terrestrial environments range from the extremely unproductive polar deserts of the north and north-east to the sub-arctic birch (*Betula pubescens*) copses of the southern tip ($\sim 60^\circ\text{N}$), an area where agriculture is practiced today and human impact on vegetation is also most pronounced (Fredskild, 1992).

This contribution focusses on the terrestrial ecosystems (and associated inland waters) of west Greenland from the area around Ilulissat and Disko Island (ca. 70°N) to that around Nuuk, the provincial capital (64°N) (Fig. 1). This stretch includes the widest ice-free margin on the island, along Kangerlussuaq (Søndre Strømfjord in Danish). The region encompasses strong climatic and environmental gradients that exert considerable control on vegetation and soil processes and hence regional biogeochemistry. The interior around the head of Kangerlussuaq fjord was one of the first areas to be explored scientifically (Böcher, 1949) and the establishment of the airport has facilitated a range of research on the outlet glaciers from the Greenland ice sheet, glacial geomorphology and hydrology, as well as vegetation and lakes (Anderson et al., 2017). The contemporary vegetation distribution and

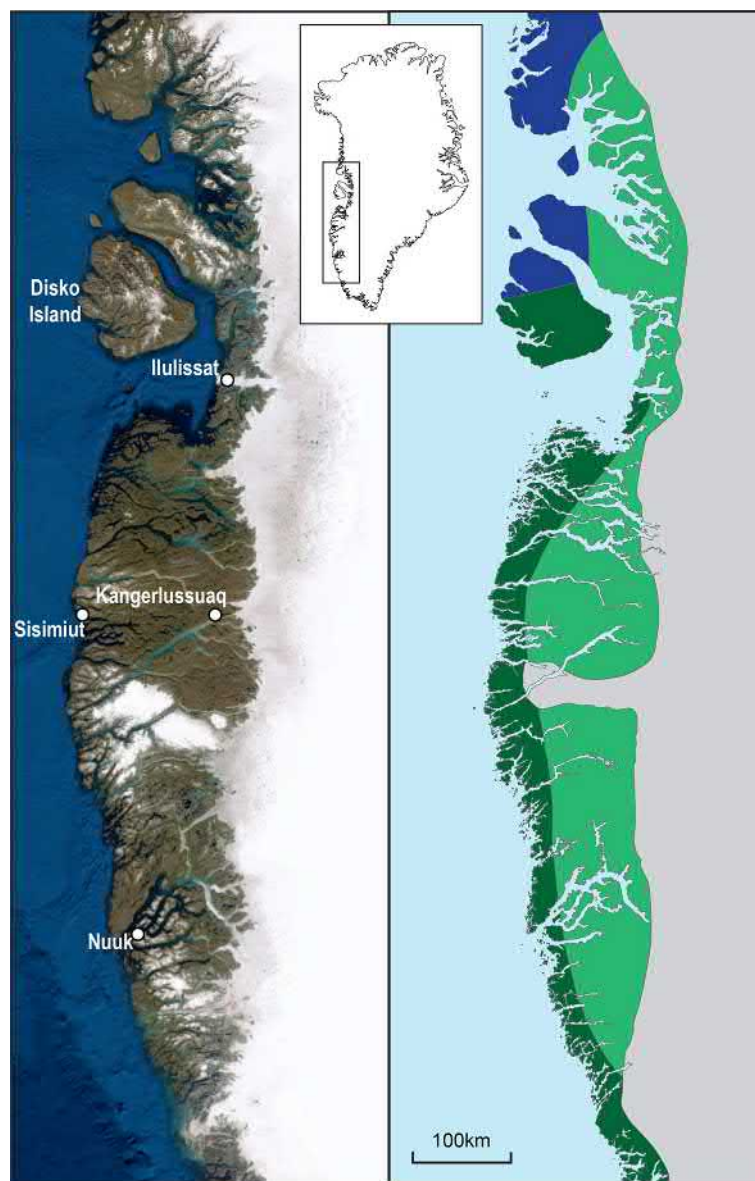


Fig. 1 Location map showing the broad physiographic nature of the study area (left) and the change in vegetation community structure between coastal and inland areas.

fauna of the area is well described (albeit in Danish mainly; see Further Reading). This synthesis briefly reviews the ecological research and attempts to integrate them in the context of recent climate change. There is also a longer-term perspective of ecosystem changes derived from paleoecological methods (Bennike, 2000). These contemporary and palaeoecological investigations coupled with some of the longest temperature records in the Arctic (Hanna et al., 2012) provide a critical context/perspective for an area that is now changing rapidly (Anderson et al., 2017).

The range of contemporary ecological research allows the effect of these recent climate changes to be viewed in an integrated fashion. Given the rapidity of recent environmental change in the Arctic and in Greenland in particular, here emphasis is placed on the effects of environmental and climatic change on integrated cross-system interactions, both biological and physical, as much as a process-based narrative of the main terrestrial habitats.

Physical Setting: Geology and Climate

Geology

The geology of Greenland is dominated by ancient crustal crystalline rocks. The central part of the western ice-free margin described here (Fig. 1) is mainly Precambrian granodioritic gneisses with localized ultra-basic intrusions which weather to create geologic and water chemical anomalies. Around Disko Island to the north of the study region there are Tertiary basalts and to the south are very old rocks from the Caledonian orogeny. The combination of hard local geology with scouring by the ice sheet has created a predominantly glacially-smoothed landscape that is dissected by the fjords cut by outlet glaciers. Because of this, and in contrast to much of northern North American and Siberia, thermokarst landscape processes are less prevalent. Locally, this rounded, relatively low relief is broken by structurally-controlled features (i.e. dykes/intrusions) while at the coast there is more vertical relief and local valley and cirque glaciers are present.

Climate

The climate of the coastal zone is predominantly low-arctic maritime with mean annual temperatures of -4.5°C , -3.6°C and -1.2°C at Ilulissat, Sisimiut and Nuuk respectively (Fig. 1). There are long-term temperature records for some of these locations which has provided an important temporal perspective on regional warming in Greenland (Hanna et al., 2012). Inland areas ($>80\text{ km}$ from the coast) experience a more continental climate (mean annual temperature at Kangerlussuaq is -5.6°C ; the annual temperature range is $>30^{\circ}\text{C}$) with warm, dry summers. There is a reduced annual temperature range ($\sim 20^{\circ}\text{C}$) at the coast where summers are cool and wet while winters are a little milder. The area is underlain by continuous and semi-continuous permafrost, the latter mainly found towards the coast. There is, however, considerable local variability: talik zones occur under larger lakes, while local relief, which influences snow cover, as well as the distribution of organic rich soils and fens can affect permafrost depth and active layer thickness. Active layer thickness varies between 0.5 and 1.5 m, with depth of the annual thaw determined largely by vegetation cover, organic matter and water content. At Qeqertarsuaq on Disko Island the thaw generally started in early June (in the sampling period 1991–1996) but with some inter-annual variability. The onset of freezing was more consistent, beginning in late-September/early-October (Humlum, 1998). Recent warming means these patterns will be changing but contemporary data are limited. Recent surveys at a lake catchment close to the ice margin observed the active layer to be $\sim 1\text{ m}$ thick at the end of August (Johansson et al., 2015).

There is a strong gradient in effective precipitation across the Kangerlussuaq area of west Greenland in part due to the rain shadow effect caused by the Sukkertoppen ice cap. Throughout the coastal zone annual precipitation can exceed 500 mm yr^{-1} . Where the terrestrial, ice-free zone exceeds $\sim 100\text{ km}$ in width, the climate of the interior becomes more continental and drier: for example, the area around Kangerlussuaq has low precipitation ($<200\text{ mm yr}^{-1}$) and evaporation exceeds precipitation during the summers. The intrusion of marine fjords into the landmass alters this general pattern as some of the longer fjords freeze in the winter, whereas the open sea south of 68°N does not. The regional climate gradient continues towards the ice sheet margin with more extreme conditions adjacent to the ice sheet: colder and windier. Winds in this area are variable but are dominated by cold, mainly easterly katabatics flowing off the ice sheet; during the winter wind speeds can reach $>30\text{ m s}^{-1}$. Warm, foehn winds also occur and, in the winter, can cause melt events and the subsequent refreeze can create ice crusts which may cause mass mortality of reindeer due to starvation.

Beyond the low mean annual temperature, two aspects of the regional climate of west Greenland are pertinent to terrestrial ecosystem development and functioning: the amount of snow accumulation at the coast and the high evaporation rates of the arid interior during the summer. Snow cover can exceed 2 m at the coast (Curtis et al., 2018), which has a pronounced impact on local hydrology in Spring, whereas inland the initial snow amounts are much lower but are also reduced by sublimation and winter thaw events by mid- to late-April (Fig. 2). Adjacent to the ice sheet, wind scouring and redeposition of snow in more sheltered parts of catchments is important.

Surface hydrology reflects the regional gradient in effective precipitation. Overland flow events during summer and streams are most obvious at the coast while in inland areas, streams only occur as outflows from lakes. Summer precipitation in the dry, continental interior, only very rarely reaches the intensity to support overland flow. Lakes are abundant across the region reaching up to 14% of the land area (Anderson et al., 2009) and their water chemistry and dissolved organic matter characteristics reflect the regional gradient in effective precipitation: lakes at the coast are dilute ($<100\text{ }\mu\text{S cm}^{-1}$) and oligotrophic while inland conductivity



Fig. 2 Photographs illustrating hydrological differences across West Greenland. A, moat at ice-out; B, fossil shorelines reflecting past high lake-levels; C, ice-dammed lake and pond in foreground; D, late-winter view near the head of the fjord showing the thin to absent snow cover. All photographs: N J Anderson.

is greater ($> 200 \mu\text{S cm}^{-1}$) with substantial major ion and dissolved organic matter concentrations (Anderson and Stedmon, 2007). Ice marginal lakes that are not fed by glacial meltwater are intermediate between these two end members in terms of their limnology and water chemistry (Whiteford et al., 2016). Close to the ice sheet there are numerous ice-dammed lakes some of which drain periodically (Fig. 2C).

At the coast, the spring thaw can be rapid (flashy) and lake hydrological retention times during the summer ice-free period are short, certainly in comparison to those inland. In terms of the water balance of lakes in the interior, the seasonal thawing of the active layer and/or the melting of any remaining snow is the main hydrological input: summer precipitation is essentially offset by evaporation. Oligosaline lakes occur between 51.5 and 50.5°W ; their occurrence reflects landscape morphology (catchment:lake ratio, absence of an outflow) as well as the low precipitation and high rates of evaporation. Reconstruction of lake water conductivity (a proxy for salinity and hence effective evaporation), coupled with $\delta^{18}\text{O}$ stable isotope records and analysis of fossil shorelines (that reflect higher lake-levels) indicate that precipitation has varied considerably throughout the Holocene in the arid interior (Aebly and Fritz, 2009). Today, lakes are responding heterogeneously to increased regional evaporation (Law et al., 2018). While some are shrinking due to evaporation, others are increasing, possibly due to the role of permafrost melting. Recent work on the effect of moisture stress dwarf shrub tundra (see below), suggests that these past changes in effective precipitation will have impacted terrestrial vegetation and carbon cycling.

Climate History

Coastal west Greenland became ice free from approximately 11.4–10 kyr BP with regional variability caused by local conditions, e.g. topography. The contraction of the ice sheet to its most easterly minimum from its maximum extent took some 2900 years. Briner et al. (2016) provide a synthesis of long-term climate reconstructions for Greenland. In the context of this synthesis, apart from the obvious constraint of the timing of ice withdrawal which permits terrestrial and aquatic community development, three aspects of Holocene climate history are pertinent for terrestrial communities and regional biogeochemistry, namely the Holocene climatic optimum, the onset of Neoglacial cooling and the Little Ice Age (see below). Although cooling for much of the late 20th century, west Greenland is now undergoing rapid warming (Saros et al., 2019).

Vegetation and Soils

Modern Vegetation Distribution

The vegetation of Greenland south of 70 °N is mainly low arctic tundra but with a clear demarcation between the coastal and inland, continental areas reflecting the regional climate gradient described above (Fig. 1). Vegetation at the coast is classified as moist [maritime] shrub tundra, with *Empetrum nigrum* as the dominant woody plant. In more sheltered areas at lower altitude there are occasional abundant expanses of *Salix glauca*. However, even at lower altitudes vegetation cover can be relatively thin and lichens and mosses are abundant. Vegetation cover decreases with altitude and snow bed and fell-field communities become more common (Fig. 3). Further north, *Cassiope tetragona* is a more typical representative of the woody tundra plants found in the southern High Arctic vegetation zone.

As one moves inland, *Empetrum nigrum* becomes less frequent and *Betula nana* increasingly common. In the dry interior, on north facing slopes the dry dwarf shrub tundra can become quite luxuriant (a mix of *B. nana*, *Salix glauca*, and *Ledum palustre* ssp. *decumbens*, *Vaccinium uliginosum* and occasional beds of *Rhododendron lapponicum*) (Fig. 4) while on south facing slopes moisture stress reduces vegetation cover to a mix of bare ground, steppe-like grasslands and fell-field communities on the hill tops (Fig. 4). At higher altitudes (> 300 m asl) closer to the ice sheet margin steppe-like communities become dominant but again with extensive bare patches due to moisture stress and wind scouring (Heindel et al., 2017) (Fig. 5).

Soils

There has been relatively little work on soils in Greenland since Böcher's initial surveys (Böcher, 1949), but recent studies have highlighted the considerable local scale variability in soil thickness and type. Given the strong regional gradients in climate, relief and vegetation from coast to ice sheet margin, the soil types and their distribution largely reflect these changing macro controls. Most soils in Greenland tend to be varieties of rego- and cryosols and given the underlying geology, acidic. Soils are often thin; cryonival and soliflucted soils are typical at the coast, occasionally thixotropic soils occur. Inland, organic rich soils accumulate (mean thickness ~50 cm but locally deeper) on the north facing slopes with little to none on the south facing ones. In valley bottoms and at slope breaks, thicker (> 1 m) fen-like, organic rich deposits accumulate. Despite recent studies there is relatively little information



Fig. 3 Photographs illustrating coastal environments and landscape. A and B, note the high relief, limited vegetation cover and emergent coastal platform due to isostatic rebound. C and D, catchments to the north of Sisimiut showing thin vegetation cover and fell-field. All photographs: N J Anderson.

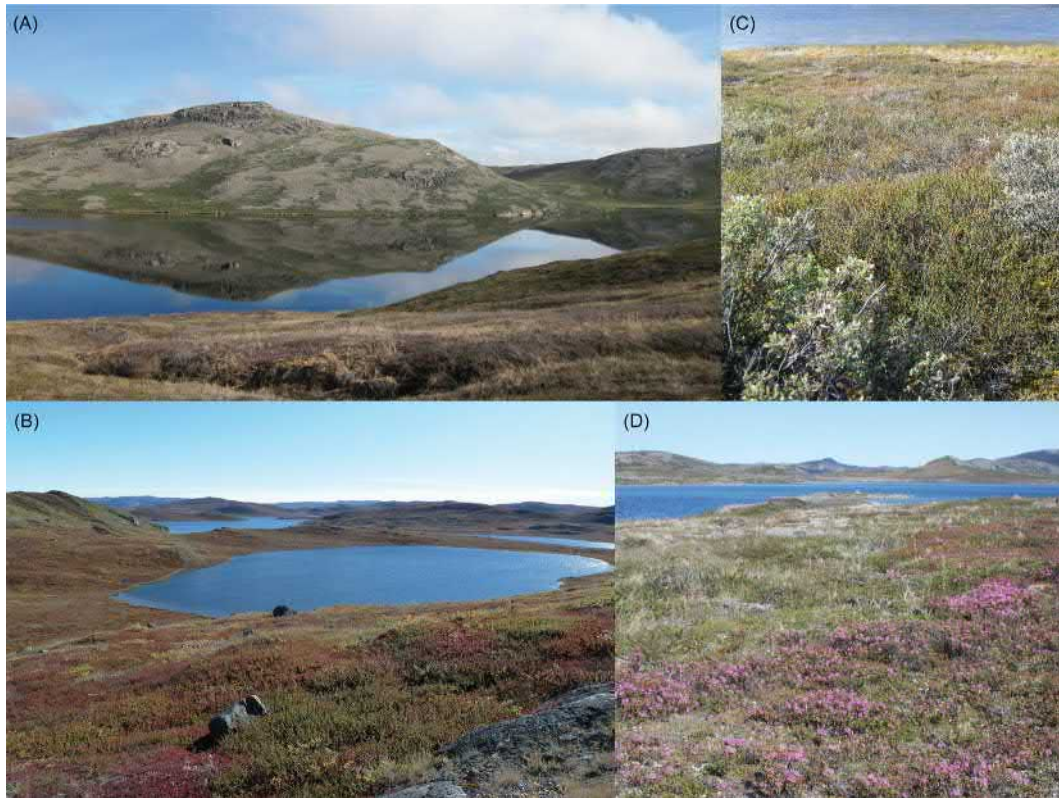


Fig. 4 Photographs illustrating the vegetation of the dry interior around the head of the fjord. A, a south facing slope showing the absence of vegetation due to moisture stress; B–D, dwarf shrub tundra dominated by *Betula nana* and *Salix* (C) and *Rhododendron* (D). All photographs: N J Anderson.

on the soils associated with the *B. nana*/*Salix glauca* dominated dwarf shrub tundra that characterizes much of the area between the coastal zone and the steppe-landscape close to the ice sheet margin (Fig. 5).

At the local scale, heterogeneity is a key landscape characteristic (Figs. 4 and 5) with soil type and thickness reflecting landscape age, vegetation, aspect and topography and local geomorphic processes. As a result of deflation of the fluvio-glacial deposits on the sandurs, the ice marginal zone is influenced by aeolian dust deposition and the development of loess deposits which form biological crusts. Proximity to the ice sheet is important both in terms of providing a steady supply of dust sources and exposure to strong winds that can scour and erode thin soils, with subsequent redeposition of the minerogenic fraction and loss of organics (Bradley-Cook and Virginia, 2018; Henkner et al., 2016).

The intensity of dust deposition varies both seasonally and over longer timescales (Fig. 6). Silt deposition declines with distance from the ice sheet margin/sandurs) and as wash out by precipitation increases. In the inland areas in the late-winter/early-spring in dust cover is particularly noticeable on snow patches and vegetation, reflecting peak deflation at the end of the winter following snow sublimation (Fig. 7A,B). However, the increase in the amount of late-winter snow over the last 30 years (Saros et al., 2019) is having an impact on this process. While deflation from sandurs is a regular and visible phenomenon (Fig. 7), local erosion and reworking of older aeolian deposits and its movement across catchments and between soils and lakes is more difficult to quantify (Saros et al., 2019). Given the process and timescale of the development of loess deposits and associated microbial communities this may be locally important. The implications of these processes for regional biogeochemistry are only now being addressed (Anderson et al., 2017).

Jensen et al. (2006) determined C stocks and accumulation rates on a coastal platform on Disko Island. The soils investigated developed on *Cassiope* heath and were acidic (pH range 5.6–6.4) but the oldest terraces had a pH of 4.5 indicating long-term acidification associated with landscape ageing and weathering. Soil C stocks (to a depth of 60 cm) were 2.6 ± 0.7 and 8.4 ± 2.4 kg C m⁻² on *Cassiope* heath and *Salix* vegetation cover respectively, increasing to ~ 28 kg C m⁻² in water-logged grass-dominated fens (study average: 6.7 kg C m⁻²).

Ozols and Broll (2005), in a detailed survey of 3 sampling plots ($< 40 \times 20$ m) within a small area (2×2 km) south of the large lake Sanningasoq (some 10-km east of the airport at Kangerlussuaq), showed considerable variability of soil type and geochemistry, depending on the dominant vegetation (*B. nana*, *Kobresia myosuroides* and *Salix glauca*). Carbon was enriched under *Kobresia* meadows while there was a clear acidification trend under *B. nana* heath due to organic acids associated with the accumulation of *Betula* litter.



Fig. 5 Photographs of ice marginal environments and landscape including ice sheet margin and moraines. A–B, end moraine complexes showing the close juxtaposition of ice, morainic debris and tundra/steppe at present; C, a view of the steppe-like landscape close to the present day ice margin; D and E, wind scour, blow-outs and fell-field adjacent to the ice sheet margin. All photographs: N J Anderson.

Bradley-Cook and Virginia (2018) reported an area weighted average soil C content of 16.4 kg C m^{-2} (to a depth of 50 cm) for the steppe-dominated landscape close to the ice sheet margin near Kangerlussuaq. There was considerable variation in C content, however, from minimal on the wind-eroded slopes to $> 22 \text{ kg C m}^{-2}$, again in moist, organic-rich fens. Average nitrogen content ranged from 0.06 to 4.85 kg N m^{-2} and the C/N ranged from ~ 13 to 20 across all vegetation types. Henkner et al. (2016) reported 14 kg C m^{-2} (30-cm depth) for an area south-east of Kangerlussuaq airport but considerable local variability related to landscape units, with aspect and vegetation type being the most important factors contributing to their classification.

As soils can be quite thin across Greenland, for a variety of reasons, carbon standing stocks are quite low compared with organic rich permafrost soils elsewhere in the Arctic. Anderson et al. (2009) suggested that given the relatively high lake density in parts of the Kangerlussuaq area lake sediments may sequester as much organic C as do soils regionally; lake sediment C burdens can approach 40 kg C m^{-2} , but there is considerable uncertainty in this estimate. However, the standing stock of soils is likely to reduce with regional warming as permafrost thaws and active layer depths increase, resulting in higher rates of organic matter mineralization. In this scenario, lakes will become important sites of carbon sequestration.

Vegetation History: Immigration and Climate

Holocene vegetation dynamics are a function of climate change, the timing of deglaciation (i.e., the creation of new habitats to be colonized), ontogenetic soil processes plant and immigration. The Holocene vegetation history of Greenland was reconstructed by Fredskild in the 1970s using pollen analysis primarily (Fredskild, 1983). Despite the limitations of this approach in arctic environments with low pollen production and limited taxonomic resolution (Pennington, 1980), subsequent plant macrofossil analyses have largely confirmed the spatial and temporal successional patterns determined by Fredskild. Bennike (2000), Wagner and Bennike (2012), and Heggen et al. (2010) provide detailed reconstructions of local vegetation change as recorded by plant macrofossils in lake sediment cores from a number of sites in west Greenland.

Recently deglaciated terrain is characterized by unstable substrates with low nitrogen availability. Lake sediment core records from W. Greenland indicate abundant cations and initial rapid weathering of the freshly communitied glacial morainic material is suggested by high $\delta^{13}\text{C}$ of the inorganic C fraction (Anderson et al., 2018). These inferences of early deglacial biogeochemistry are supported by geochemical and isotopic surveys of the present-day ice margin (Henkemans et al., 2018). Scribner et al. (2015) found that there was a greater than expected (based on the 2 to 3,000 yr difference in deglaciation exposure history) weathering gradient from the coast to the inland area, mainly due to the higher precipitation at the coast.

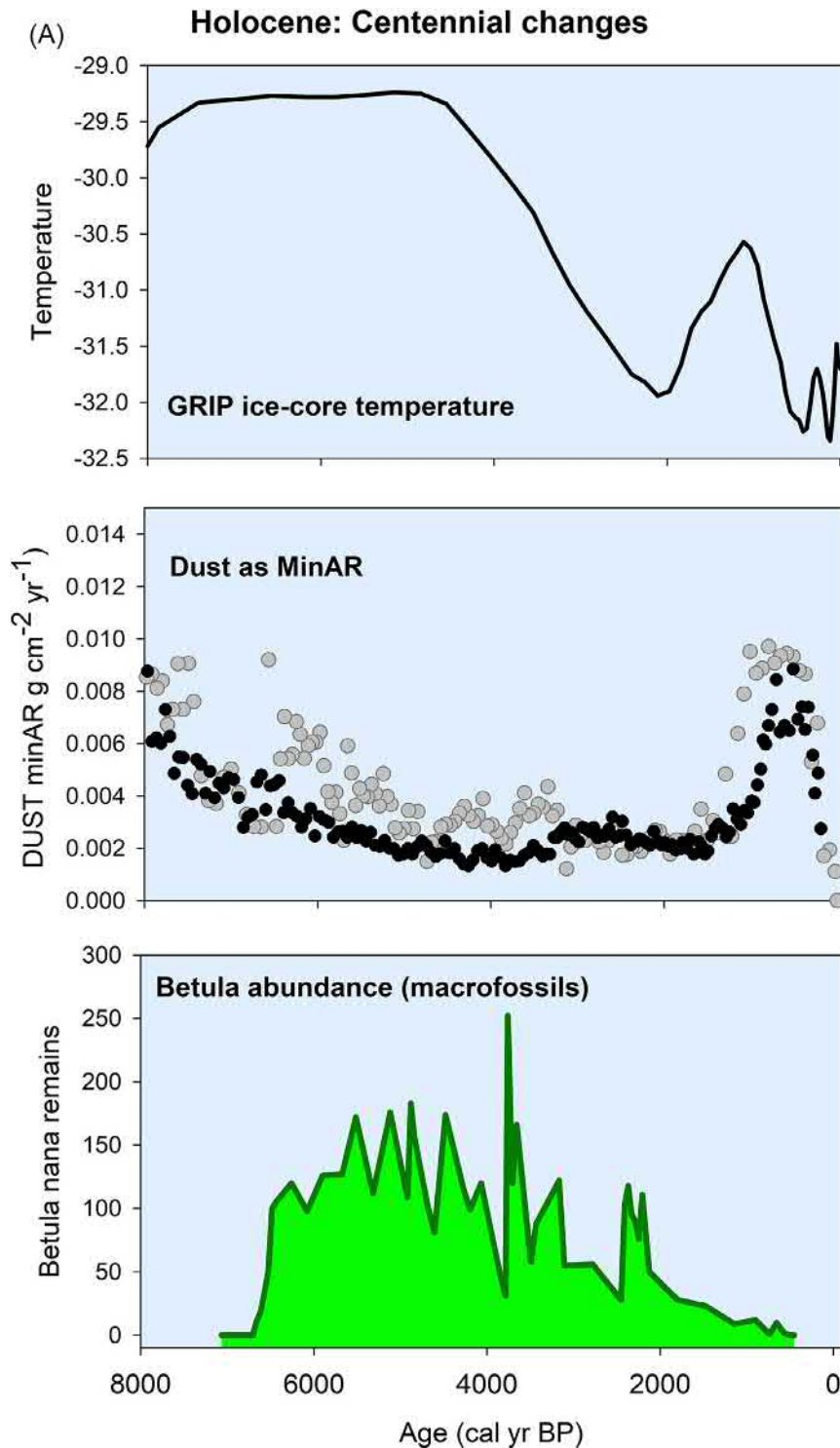


Fig. 6 Data plots showing changes in environmental drivers and biological response at two timescales (millennial during the A, Holocene and B, decadal changes during the 20th–21st centuries). Data taken from (Anderson et al., 2012; Boyd and Fox, 2008; Dahl-Jensen et al., 1998; Fox and Glahder, 2010; Gamm et al., 2018; Heggen et al., 2010; Saros et al., 2019).

Newly deglaciated landscapes are inhospitable and are not conducive for plant colonization and as a result are characterized by pioneer herb species, the absence of woody plants and the presence of large areas of bare ground (Fig. 5). Together with terrestrial cyanobacteria, *Dryas integrifolia* is an important early colonizer because of its ability to fix N (Heggen et al., 2010). Sediment lacustrine pigment records along Kangerlussuaq indicate abundant cyanobacterial abundance in the earliest period after lake formation,

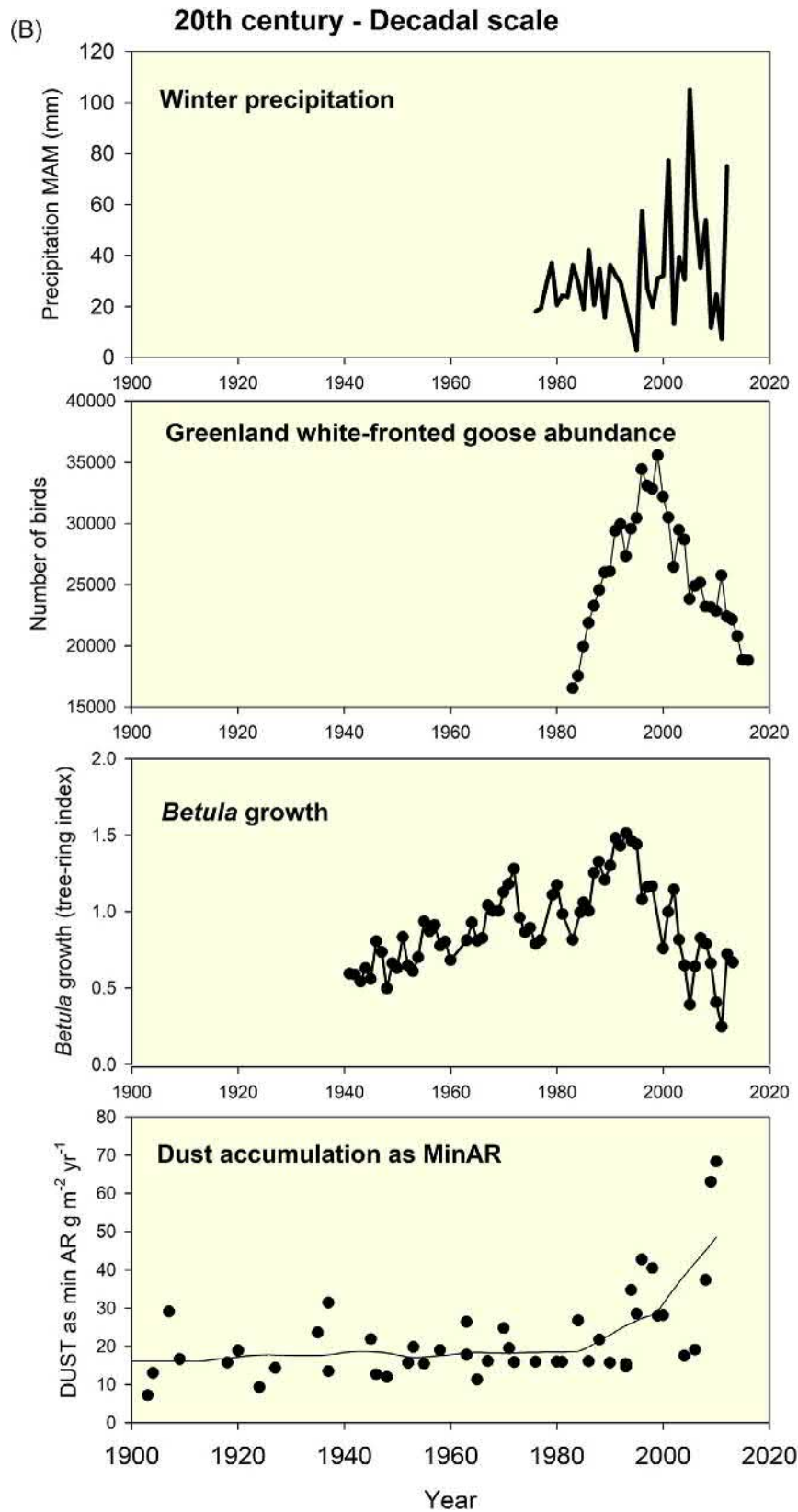


Fig. 6 (continued).



Fig. 7 Photographs illustrating drivers of ecological change. A, dust deposits and caterpillars of the noctuid moth on rocks in the littoral zone of an ice margin lake; B, dirty snow due to dust deposition in late-April in the inland area; C, goose droppings at the margin of a lake; D, a dust storm in April adjacent to a sandur (outwash plain). All photographs: N J Anderson.

suggesting that N-limitation occurred across both terrestrial and aquatic ecosystems (McGowan et al., 2008). Wagner and Bennike (2012) inferred that this pioneer stage persisted for several thousand years at the coast due to immigration delays as much as the limited soil development. It is unlikely that temperature was a limiting factor given the rapid warming in the early Holocene and into the Holocene climatic optimum. Some support for this lack of a temperature constraint on the development of dwarf shrub tundra is provided by the occurrence of warmth-demanding herb species and thermophilous aquatic species (Bennike, 2000). In contrast, by the time the inland areas were deglaciated, the main dwarf tundra species had immigrated to Greenland and the pioneer phase was much shorter.

The development of the present-day vegetation gradient from coast to inland is reflected in the fossil record; *Betula nana* is rare in coastal lake sediment records while *Salix glauca* is more common in the late-Holocene (Wagner and Bennike, 2012). In the coastal area near Sisimiut, *Empetrum nigrum* was the first woody plant to colonize, 10.3 kyr BP and *B. nana* arrived around 4700 cal. yr BP (Wagner and Bennike, 2012). In the inland region, the period from 6500 cal. yr BP, when *B. nana* immigrated, to the start of the Neoglacial around 3800 cal. yr BP, saw the maximum extent of dwarf shrub tundra, as indicated by both pollen and macrofossil records (see Heggen et al., 2010) (Fig. 6A).

The onset of Neoglacial cooling from 3800 cal. yr BP resulted in enhanced instability and vegetation dieback across the region but responses of the terrestrial ecosystems varied between the coast and inland areas, largely reflecting the differences in precipitation and catchment hydrology. Inland, cooling was exacerbated by decreasing precipitation (increasing moisture stress) and *B. nana* abundance decreased (Fig. 6A), while at the coast vegetation dieback was coupled with increasing soil instability due to greater precipitation, relief and cryonival processes. In coastal lake-catchments, soil instability and increased erosion are indicated by lake sediment records of $\delta^{13}\text{C}$ in organic matter and the inwash of *Cenococcum* hyphae and *S. herbacea* remains (Anderson et al., 2018). In a paleolimnological study of a small lake at the head of Kangerlussuaq, Anderson et al. (2008) suggested that the dieback of *B. nana* with Neoglacial cooling had a significant effect on lake ecosystem functioning.

Biotic Interactions

Rangifer tarandus (reindeer or caribou) and muskox (*Ovibos moschatus*) are the only ungulates found on Greenland today. Greenlandic reindeer are characterized by a number of populations which have interacted to varying degrees. Two extant populations

in west Greenland are recognized (referred to as the Nuuk and Sisimiut populations) and their numbers have varied considerably over historic time. They migrate seasonally from their over-wintering grounds to a summer range where they give birth although there is some suggestion that more recently this migration has been more constricted. Historically only found in north and north-east Greenland, muskox were introduced to west Greenland in 1962 and their numbers have increased substantially since then, peaking at ~4000 in 1990, in the main due to resource availability and the absence of natural predators. Using long-term historical population estimates, both reindeer and muskox were shown to have synchronous spatial relationships across Greenland that correlated to the NAO (Post and Forchhammer, 2002).

Cahoon et al. (2012) in a field experiment near the large lake Asjuitsup Tasia (some 15-km east of the airport at Kangerlussuaq) showed that exclusion of herbivores resulted in increased shrub cover, leaf area and ecosystem photosynthesis as well as increased net C uptake by a factor of three. Simulated warming enhanced these responses but only when the herbivores were excluded. These results, although based on short-term experiments highlight the possible impact of historic variability in reindeer populations in this area on regional C dynamics.

The role of extreme events, i.e. winter warming and snowmelt, and their effect on ecosystem functioning in the Arctic is receiving increased attention. As well as abrupt, extreme weather events, fires and insect outbreaks can also have dramatic impacts on terrestrial ecosystems. On Greenland, the larvae of the noctuid moth (*Eurois occulata*) (Fig. 7) have been shown to cause widespread defoliation of dwarf shrub tundra during major outbreaks. In the Kangerlussuaq area, two outbreaks have been observed recently, in 2005 and 2011. Lund et al. (2017) estimated that defoliation reduced the C sink in their study area (Kobbefjord near Nuuk) by 118–143 g C m⁻² in 2011 but notably, the years following the outbreak there was increased primary production, possibly due to enhanced nutrient turnover rates. Lund et al. (2017) suggested that there is a role for climate in triggering outbreaks due to reduced egg mortality during warmer winters. There is the possibility of more frequent outbreaks associated with regional winter warming but their implications for vegetation dynamics and soil chemistry are difficult to predict.

Aquatic-terrestrial nutrient transfers and cross-system subsidies in West Greenland are largely unquantified but include passerines (e.g. the northern Wheatear; *Oenanthe oenanthe*) feeding on emergent (adult) diptera, for example chironomids and mosquitoes. Geese have been shown to play an important role in nutrient transfer between terrestrial and aquatic habitats elsewhere in the Arctic but there has been little work on this in Greenland, although the population dynamics of the native, Greenland white-fronted goose (*Anser albifrons flavirostris*) have been well studied (Boyd and Fox, 2008; Fox and Glahder, 2010). When molting, geese remain within a few meters of lake shores as the open water provides a refuge from predators (such as the Arctic fox); during this phase of their life cycle they defecate extensively along lake shores (Fig. 7C).

The population of *Anser albifrons flavirostris* has been declining since ~2000 (Fig. 6). The reasons for this decline are unclear but may relate to conditions in their over-wintering grounds in NW Europe and Iceland and/or climate change processes in West Greenland (Boyd and Fox, 2008) (see below). A possible contributory factor may be the rapid increases in the populations of the Canada goose (*Branta canadensis*) which have approached 40,000 over the last 30 years (Boyd and Fox, 2008; Fox and Glahder, 2010). While the two species are not in direct competition, it has been shown that the Greenland white fronted goose has a poorer dietary intake during its molting period due to pressure on its preferred resources from Canada geese (Boyd and Fox, 2008). Regarding nutrient transfer between land and water, the increase in numbers of *Branta canadensis* may be more relevant as they nest and graze on lake shores more consistently than does the Greenland white-fronted goose.

Cultural-Vegetation-Landscape Interactions

Greenland has a long history of human colonization, but two factors suggest that the historical cultural footprint is very light over much of the island: low population densities and the nature of human subsistence. As hunter gatherers with a primary use of marine resources supplemented by reindeer hunting during the summer, early Greenland settlers had limited impact on terrestrial and aquatic ecosystems functioning and hence regional biogeochemistry, despite pronounced ecosystem nutrient limitation. Given the demonstrable impact of herbivores on tundra vegetation shown by exclusion experiments, the large documented fluctuations in reindeer populations (Post and Forchhammer, 2002) may have had some impact on local vegetation and soil nutrients. Seasonal reindeer butchering sites, some of which have been used for long periods (Aasivissuit, for example, was used intermittently for ~2000 years (Grønnow et al., 1983)), where large numbers of carcasses have been processed must have had an impact on soil chemistry and perhaps the water chemistry of the littoral zones of nearby lakes. The butchering site at Aasivissuit (some 20 km west of the airport at Kangerlussuaq) is adjacent to a large oligotrophic lake (Grønnow et al., 1983). However, despite the extremely low nutrient concentrations in such large lake, any effect of the butchering process will have been confined to the littoral zone if only because of the large water volumes relative to nutrient inputs and the short, seasonal nature of the summer hunt (Grønnow et al., 1983). Some support for the localized impact of early human settlement on local biogeochemistry is, however, provided by soil and vegetation analyses of archaeological sites near Nuuk (Fenger-Nielsen et al., 2019). At all sites the soil nutrient (Olsen-P and NO₃) content around the house remains was increased relative to control sites by 2 to 6x, and vegetation structure changed as well (Fenger-Nielsen et al., 2019). They also suggested that the culturally-impacted vegetation was less affected by local climate variability. These observations, when considered in light of the results of contemporary warming and grazing exclusion experiments (see above), suggest that soil biogeochemistry may change rapidly in future decades.

Agriculture is restricted to southern Greenland today and apart from the relatively short-lived Norse occupations at the Eastern and Western Settlements (ca. 986 to 1450 AD) was not developed elsewhere. The issues surrounding the collapse of the Norse settlements are beyond the scope of this review (Dugmore et al., 2012) but there have been several recent studies using lake sediment

records to look at climate and environmental changes in relation to human settlement history on Greenland. D'Andrea et al. (2011) used alkenone-inferred temperatures to assess climate as a driver of human occupation. Over-grazing by sheep today is a problem in southern Greenland and has resulted in increased soil erosion (Fredskild, 1992).

Recent Warming and Environmental Change

West Greenland has seen dramatic increases in temperature and precipitation starting in 1994, climate changes that are having a cascading effect on regional ecosystem functioning and hence C dynamics. Since 1994 mean June air temperatures are 2.2 °C higher than the preceding 40 years and since 2006, mean July temperatures have increased by 1.1 °C. Winter precipitation has doubled from 21 to 40 mm in this time period and these changes were related to the Greenland Blocking Index (GBI) by Saros et al. (2019). There is growing evidence for phenological shifts in West Greenland driven by winter warming events and milder, earlier Springs; for example, May 2019 was 7 °C warmer than the long-term average with the growing season starting nearly 3 weeks earlier than usual.

Cahoon et al. (2016) showed that communities dominated by *Betula nana* have been stronger C sinks since 2002 in part due to the earlier start of the growing season. However, this enhanced C sink may be offset by moisture stress in the late summer. It is possible that *B. nana* may have a competitive advantage in warmer and drier conditions. However, Gamm et al. (2018) showed a major recent decline in the growth of *B. nana* in SW Greenland from (Fig. 6B) using dendrochronological and stable isotope methods. Their results indicated an air temperature of ~7 °C together with moisture limitation may be a critical in explaining the decline. *Salix glauca* also showed a decline in growth but this started later and highlights the inter-specific responses of dominant tundra species to changing environmental conditions. The decline in *B. nana* was exacerbated by moth outbreaks (see above) in 2005 and 2011 (see Fig. 6B) further highlighting the role of multiple stressors (herbivory, temperature, moisture) in determining response of terrestrial ecosystems to environmental changes in the Arctic in the 21st century.

In a study of *Betula nana* dynamics over a 100 year period on Disko Island using a tree ring record of radial growth patterns, Hollesen et al. (2015) highlighted the importance of winter climate conditions, in particular the effect of snow depth on soil temperatures as well as the timing and rate of spring thaw. Warmer spring temperatures resulted in earlier snowmelt and soil drainage and consequently soils warm quicker. They postulate that these processes may accelerate regional greening, but this conclusion has to be compared with the growing evidence for negative effects of summer moisture stress discussed above. The contrasting inferences about future trends in vegetation dynamics between the Hollesen and Gamm studies reflect to some extent the fundamental differences between maritime, coastal environments and the more arid interior in West Greenland. Despite this, changing species abundance and community composition have implications for C and N cycling in west Greenland in the immediate future.

With recent phenological changes in vegetation, Kerby and Post (2013) highlighted the cascading effect of early summer vegetation development on reindeer reproduction. This trophic mismatch is in part due to the reproductive strategy of *Rangifer*, which is an income breeder. In the latter, calving is synchronized with resource phenology—the females aim to arrive at the summer calving areas as vegetation growth is initiated; earlier springs are disrupting this relationship. Muskox in the same area have not been similarly affected as they considered to be capital breeders (see Kerby and Post (2013) for a full discussion).

Another recent climate change driven trophic mismatch may also be responsible for the decline of the Greenland White fronted goose (Fig. 6B). As discussed above, competition with *Branta canadensis* may be a factor in the decline of *Anser albifrons flavirostris* (Fox and Glahder, 2010), but the population decrease is also correlated with the recent increase in late-winter snow cover. The latter is associated with the broader weather patterns in the North Atlantic: Boyd and Fox (2008) show a link to the Atlantic Multidecadal Oscillation (cf. the GBI, Saros et al., 2019). During heavy snow years the females have reduced access to resources and as a result poorer reproductive capacity. Boyd and Fox (2008), however, consider this to be only a contributory factor in their decline as poor recruitment has also been observed during light snow years.

Synthesis: Climate-Landscape Synergies in West Greenland

The Arctic plays a key role in the terrestrial C cycle through storage of organic C in permafrost affected soils. In the future, feedbacks to the climate system will increase with enhanced organic matter mineralization and CO₂ release to the atmosphere. But these processes also release nutrients which can confound warming effects on vegetation processes. The combination of strong environmental gradients, unusual but informative abiotic and biotic events, coupled with very recent, rapid regional warming means that West Greenland offers the opportunity to understand the complex interaction between multiple stressors and ecological responses. Looking beyond the effect of temperature increases, the interaction of multiple nutrient sources (locally derived atmospheric phosphorus-rich dust and long-range transport of reactive nitrogen coupled with altered soil nutrient stoichiometry) with changing herbivore populations in West Greenland underscores the need to see arctic ecosystem response in an integrated fashion (Anderson et al., 2017). As well as this, the inland area around the head of Kangerlussuaq also offers a glimpse into a future, warmer and drier Arctic. The results of palaeoecological approaches, the availability of long-term climate data coupled with field experiments means that research on West Greenland terrestrial ecosystems offers an integrated view of past and future environmental change, with relevance both regionally and across the wider Arctic. In the early Holocene, the disjunct interactions between climate change and vegetation development brought about by delays in the immigration and colonization offer insights to possible effects of future change.

Past vegetation dynamics indicate that future changes associated with continued warming and retreat of the ice sheet may be unpredictable and reflect delays in species' immigration response, biogeochemical constraints as much as temperature forcing. Likewise, the implications for soil nutrient stoichiometry and carbon sequestration are unclear.

Further Reading

The results of many early studies on the ecology of Greenland are available in the monograph series *Meddelelser om Grønland*, much of it an invaluable historical resource. The flora of Greenland is described by Flemming Rune's (2011) *Wild Flowers of Greenland* (Gyldenlund Publishing, both English and Danish text) and a more general description of the Greenland nature is provided by Benny Génsbøl's (1999) *Naturguide til Grønland* (2nd Edition, Gads Forlag), republished in English as *A Nature and Wildlife Guide to Greenland* (2004).

This chapter focuses on west Greenland and the diversity of the research in this area, much only touched upon in this review, is highlighted by a recent special issue of *Arctic, Antarctic and Alpine Research* (volume 50, DOI: 10.1080/15230430.2018.1433786). The initial results of the long-term Danish research programme at Zackenberg (NE Greenland) are available in a special issue of *Advances in Ecological Research* (volume 40, 2008) entitled *High-Arctic Ecosystem Dynamics in a Changing Climate*. Details of ongoing long-term monitoring around Nuuk are available as report cards from the Greenland Ecosystem Monitoring (G-E-M) network (<https://g-e-m.dk/gem-localities/nuuk-basic/>).

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Birds of Greenland

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Abstract

Greenland is the largest island of the world and is situated in the Arctic climate zone. The climate varies from humid oceanic to polar desert, and an ice sheet covers roughly 80% of the island. Sea ice is a significant factor, blocking most coasts in winter and many coasts in summer.

The bird fauna is depleted compared to other Arctic areas, due to the relatively isolated position of the island and the short history of being ice free, and most species have immigrated from their origins in Europe.

Many bird species leave Greenland for the winter to warmer regions in Western Europe, West Africa, the southern Atlantic and North and South America. However, the southwestern part of Greenland is an important winter quarter for seabirds from the northern Atlantic region.

Numerous seabirds including local breeders, non-breeders from all over the Atlantic and molting postbreeders from Canada utilize the productive seas off West Greenland in summer.

In recent decades, modern tracking methods that use electronic devices have confirmed results from previous decades of banding programs and revealed much new and exiting insights in the migratory patterns of Arctic birds.

Seabirds have been an important resource to the native Greenlanders, and some seabird populations became over-harvested due to the increased efficiency of the hunters. This is especially true for the thick-billed murre population, which do not show signs of recovery, despite improved management, while the over-harvested common eider showed a strong recovery response following a reduction in the spring hunt.

Introduction

Greenland is the biggest island in World. It is c. 2500 km long from north to south, with the northernmost point only 770 km from the geographic North Pole. It covers 2.19 million km², of which 1.8 million km² are covered by an up to 3000 m thick ice sheet, leaving a narrow fringe of land—up to 200 km wide—between the ice and the ocean on both sides. Except for a small inland sub-Arctic area in the utmost south, Greenland is within the Arctic climate zone, which means that the mean July temperature is below 10 °C. The Arctic Circle crosses the southern part of the island. Therefore, above the Arctic Circle there is continuous daylight in summer and continuous darkness in winter. Moreover, the summer season is restricted to a few months, depending on the latitude. This limits the breeding season for birds and most other life. The largest bird in Greenland, the white-tailed eagle, has a five-month breeding cycle, and must begin egg-laying by about 1 April when it is still winter, in order to fledge the young well ahead of the onset of the subsequent winter in October.

The topography of the ice-free land is generally mountainous with lowlands along coasts and in wide valleys—more extensive lowlands are only found in a few places. The widespread wet tundra seen on the North Slope of Alaska or in Arctic Siberia does not occur in Greenland. The vegetation in the lowlands is dominated by dwarf scrub heath in the dry localities, and by grasslands, fens and marshes along rivers and in other moist habitats. Extensive willow scrubs are found in the low Arctic, and a few low birch woods occur in the sub-Arctic. The vegetation cover decreases with the latitude and is, for example, extremely low in the high Arctic desert of North Greenland.

The marine environment is characterized by wide shelf waters, which in West Greenland are very productive and subject to two surface current patterns with very different properties. A cold current transporting drift ice south from the Polar Basin runs along the entire east coast, while a relatively warm current flows northwards along the west coast all the way to 76°N. This warm water usually keeps the coastal waters of West Greenland free of ice, even in winter, as far north as 68°N, and this open water area is an important winter habitat for seabirds (Fig. 1).



Fig. 1 Map of Greenland with bio-climatic zones, sea ice regime and polynyas.

The climate varies much between sites, first because of the size of the island, but also governed by the ocean currents described above. There is a strong contrast between the relatively mild and wet climate of the low Arctic southwest and the extremely dry and cold high Arctic polar desert of the far north. There are marked local variations between relatively mild and wet 'oceanic' coastlands and the more 'continental' inland areas at the same latitude. A dominant characteristic of the climate is that precipitation decreases by a factor of one hundred from south to north. This not only has a marked impact on the timing of snowmelt, but also, in combination with temperature, brings about marked differences in the regional vegetation. Trees that grow to several meters height are found only in the sub-Arctic south, while knee-high shrubs grow in much of the low Arctic, and only ankle-high vegetation is found in the high Arctic.

Seen from a bird perspective, the most significant habitat features are the duration of snow cover in spring, and the presence of sea ice and biological production in the sea.

Bird Diversity

Regularly breeding birds in Greenland include 61 species, of which 37 are associated with inland and freshwater habitats (in the breeding season) and 24 are marine birds. At least 10 other species have occasionally bred in Greenland (Boertmann, 1994). Only 11 of the breeding species are true Arctic taxa, i.e. their breeding range is restricted to this zone. Among these are brant goose, sanderling, red knot and ivory gull (Meltofte, 2013). The remaining species also breed in the temperate zone and in some cases have their main distribution there, such as the white-tailed eagle.

Inland Birds

A few inland species breed all along the ice-free areas of Greenland, such as red-throated diver, long-tailed duck, rock ptarmigan, gyrfalcon, common ringed plover and northern raven, although some of them avoid the northernmost parts. Many species are confined either to the high Arctic zone or to the low Arctic zone. High Arctic species include most of the shorebirds, the geese (snow, barnacle,

pink-footed and brant) and Arctic redpoll. Low Arctic species include the greater white-fronted goose, mallard, red-breasted merganser, white-tailed eagle, peregrine falcon, Lapland longspur and common redpoll. All of these species also occur at lower latitudes in Europe and/or North America. One species is only found in the sub-Arctic: the recently immigrated redwing.

The snowy owl and long-tailed skua are both dependent on collared lemmings as prey in the breeding season, and their ranges are similar to the range of the lemming in the high Arctic North and Northeast Greenland. However, the long-tailed skua has a very small breeding population in central West Greenland, where they live from resources in the marine environment, like Arctic skuas (Kampp, 1982). Two shorebirds, whimbrel and European golden plover, have very restricted breeding ranges in East Greenland, which must be considered as extensions of the nearby large Icelandic populations.

Even though there are more species in the inland habitats compared to the sea, the density of land birds is astonishingly low. Bird densities are especially low in the low Arctic, where only four species of shorebirds and two species of geese breed. In particularly rich habitats—such as willow copses and lush mountain slopes—densities of passerines may reach 98 pairs per km² (Frimer, 1991), but generally densities of breeding birds are much lower. The highest density of shorebirds recorded in the low Arctic is six pairs of purple sandpipers per km² (Joensen and Preuss, 1972). In the high Arctic, where 10 species of waders and four species of geese breed, densities are generally higher, and up to 17 pairs of waders per km² have been recorded (Meltøfte, 1985).

A likely explanation for the higher shorebird diversity and population densities in the high Arctic, compared to the low Arctic, is the low vegetation height in the high Arctic, combined with the availability of more snow free ground during the egg-laying season in June. This allows shorebirds to lay eggs relatively early and disperse their nests, so that it is difficult for their main predator, the Arctic fox, to find the nests (Meltøfte, 1985). The shrubbier habitats of the low Arctic are more favorable for passerines, as demonstrated by their higher diversity and density there.

In addition to breeding activities, some regions are also important molting areas for non-breeding segments of populations. Especially in the lowlands of Northeast Greenland, more than 80,000 pink-footed geese arrive from Iceland in mid-summer and spend their flightless period molting in undisturbed habitats (Boertmann et al., 2015). During the second half of the 20th century, their range has expanded considerably northward, in parallel with an extreme population increase (Mitchell, 2016), so that they now occur by their thousands, even on the barren north coast of Greenland (Boertmann et al., 2015).

Seabirds

Seabirds are generally numerous in Greenland waters, although there is high spatial variation in their population densities. The highest densities of breeding seabirds are found in the productive waters of West Greenland and in the polynyas (ice-free areas in otherwise ice-covered waters) near North and East Greenland. Widespread breeding species include the glaucous gull, black-legged kittiwake, Arctic tern and black guillemot. Species such as the great cormorant, Iceland gull, great black-backed gull and razorbill are confined to the low Arctic. Species found only in the high Arctic include the ivory gull and Sabine's gull. A number of species are more localized in their breeding range. These are restricted to specific parts of the coast, such as polynyas or areas with early break-up of the winter ice. These include the thick-billed murre, dovekie and northern fulmar, which all are extremely concentrated at these sites (Laidre et al., 2008; Møller et al., 2018). The dovekies breed at the margins of two large polynyas—the North Water in northwest Greenland and the Scoresby Sound Polynya in East Greenland. Both areas hold millions of pairs, comprising over 80% of the world population of the species (Nettleship and Evans, 1985; Kampp et al., 1987; Egevang et al., 2003). Thick-billed murres are found in large colonies at early ice-free coasts or at polynyas, with the highest concentrations in the Thule-area of North Greenland (362,000 attending individuals in five colonies in 2016) (Laidre et al., 2008; Merkel et al., 2014).

Several populations of seabirds utilize Greenland waters in summer, but do not breed there. The great shearwater breeds in the South Atlantic, but spends the southern winter in the northern Atlantic, including Greenland waters. High numbers of non-breeding northern fulmars, pomarine skuas and kittiwakes from breeding populations in Canada, Northwest Europe, Svalbard and Greenland also utilize the food-rich waters of West Greenland in summer.

The rocky coasts of Greenland provide excellent breeding localities for most of the colonial seabirds, and colonies of black guillemot and gulls are widespread and numerous. Kittiwakes and murres place their colonies on steep cliffs facing the sea. Other colonial species breed on small, low and fox-free islands. The most extreme colony sites are those of the ivory gull, as some are placed on remote nunataks up to 200 km from their feeding grounds along the coast. However, many are also found on cliffs and lowlands near the coast and even on gravel-covered ice floes or icebergs (Boertmann et al., 2010; Nachtsheim et al., 2016).

Endemics

There are no endemic bird species in Greenland, but some of the populations are considered separate subspecies that do not breed elsewhere. These include the Greenland white-fronted goose, mallard, dunlin and a number of rock ptarmigan subspecies (Boertmann, 1994).

Migration

Most of the land birds leave Greenland for the winter. However, a few can survive the winter conditions by moving south within Greenland, including the gyrfalcon, rock ptarmigan, and northern raven. Others move to the ice-free coastal environment in

Southwest Greenland, such as the purple sandpiper, mallard, red-breasted merganser, and white-tailed eagle. Gyr falcons and snowy owls even exploit seabirds in the partly ice-covered seas, far from the coast in winter (Burnham and Newton, 2011; Therrien et al., 2011).

The results of extensive bird-banding programs between the 1950s and the 1970s show that most of the land birds move southeast to winter in Western Europe and West Africa (Lyngs, 2003). The barnacle, white-fronted and pink-footed geese move to the British Isles, while one population of brant geese fly to Denmark and another to Ireland. The shorebirds move primarily to the British Isles, the Dutch-German-Danish Wadden Sea, and to West Africa. Some sanderlings migrate as far as southwest Africa in winter. Northern wheatears perform a remarkable flight from Greenland across the Atlantic to the British Isles, the Iberian Peninsula and northwest Africa in autumn (Thorup et al., 2006). Only a few Greenlandic species move to the southwest to winter in the Americas. These include the peregrine falcon that migrates to Central and South America (Lyngs, 2003), Baird's sandpiper that migrates more than 12,000 km to southern South America, and red-necked phalarope that winters on the Pacific off tropical Central and South America (Bemmelen et al. 2019). The snow buntings of Greenland disperse on two different flyways: the west Greenland birds migrate to central North America, and northeast Greenland birds to central Russia. Both populations winter in cold prairie/steppe habitats.

Among the seabirds, the migration patterns are even more diverse. This is demonstrated by data gathered from traditional bird banding, supplemented in recent decades by various electronic tracking methods. These modern tracking methods have confirmed previous knowledge about the migration patterns of Greenland birds, but they have also revealed interesting new insights into the movements, winter habitats and molting grounds of these birds. Not only does this newly acquired knowledge have important scientific value, but it has also become a very important tool for dealing with conservation issues of the species.

One of the first studies using light sensitive data-loggers (geolocators) for tracking migrating birds was on Arctic terns in Greenland and Iceland. This study confirmed the extreme long-range migration undertaken by this species as it migrates to Antarctic winter grounds. The new tracking data has also revealed how the autumn and spring movements follow different routes across the ocean (Egevang et al., 2010) (Fig. 2).

The new tracking information also identified an oceanic autumn stop-over site between the Grand Banks and the Charlie-Gibbs fracture zone (along the Mid-Atlantic Ridge between the Azores and Iceland), which later was also shown to be used by long-tailed skuas from Greenland, and by other seabird species at different seasons (Sittler et al., 2010; Boertmann, 2011).

Modern tracking methods have also contributed to a better understanding of the winter population of thick-billed murres in the important winter area off Southwest Greenland, where birds from Canada, Svalbard and Iceland mix with birds of local Greenlandic origin (Frederiksen et al., 2016).

In 2003, satellite transmitters were implanted into king eiders at a breeding site in Arctic Canada and at a molting locality in West Greenland. The birds were tracked for up to 2 years and the tracking data revealed a very important offshore winter habitat on Store Hellefiskebanke in Davis Strait. Subsequent surveys have revealed that up to half a million birds spend the winter here (Mosbech et al., 2007). A single bird circumnavigated Baffin Island (loop migration) for 2 years in a row (Mosbech et al., 2013). Satellite transmitters also tracked the movements of breeding king eiders in East Greenland to their late autumn staging grounds along the west coast of Svalbard, and to a hitherto completely unknown winter ground on the offshore Spitsbergen Bank, as well as Bjørnøya (Bear Island) (Mosbech et al., 2012b) (Fig. 3).

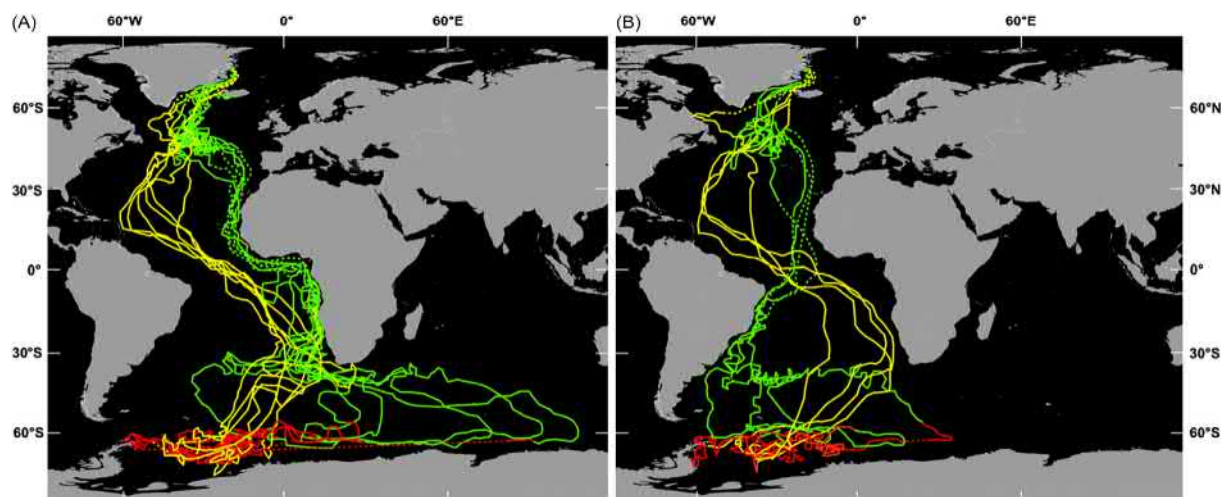


Fig. 2 Tracking of 10 Greenland and one Icelandic Arctic tern from the breeding sites to the winter quarter and back to the breeding site (Egevang et al., 2010), *Green* = autumn, *red* = winter, *yellow* = spring. (A) Shows birds moving along Africa in autumn and (B) birds that move along South America.

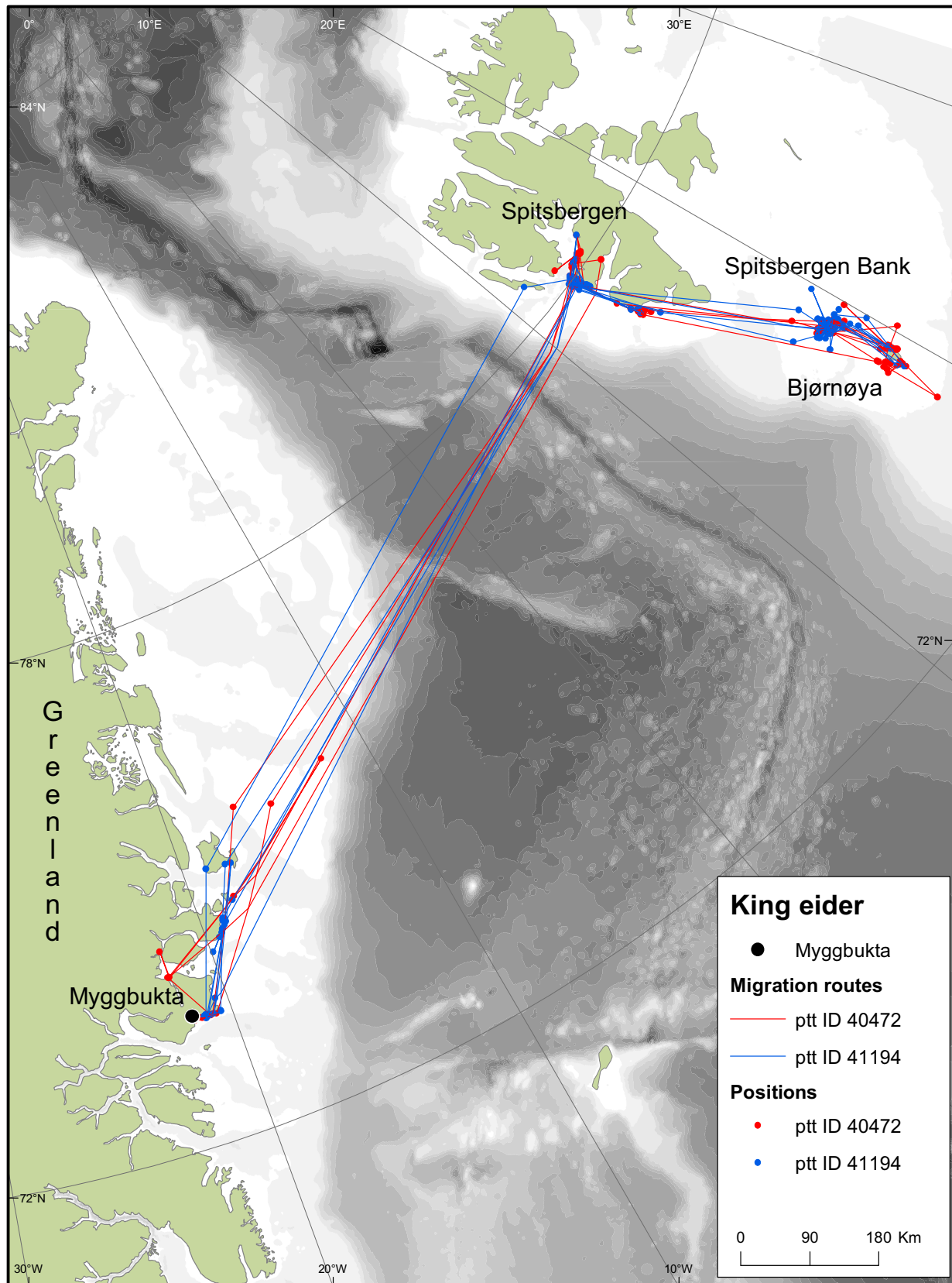


Fig. 3 Tracking of king eiders from breeding sites in Northeast Greenland to staging areas along the west coast of Spitsbergen and further on to a hitherto unknown winter quarters near Bjørnøya in Norway (Mosbech et al., 2012b).

Geolocators were deployed on little auks in East Greenland in 2007 and 2008. These revealed that after the breeding season the birds moved quickly northwards to a restricted molting ground in the Greenland Sea, where they stayed for several weeks before moving to their winter quarters on the Grand Banks (Mosbech et al., 2012a).

Greenland as Winter Quarter

It may be surprising that an Arctic area like Greenland can serve as a winter quarter for birds that breed elsewhere. Nevertheless, several seabird populations and a few inland birds from the Northern Hemisphere move annually to the very productive and more-or-less ice-free waters (and adjacent coasts) of Southwest Greenland (Boertmann et al., 2004). Most of these birds do not travel the traditional bird migration route between a northern breeding ground and southern winter quarters, but rather they migrate in an east-west direction each season. The most numerous of these birds is the thick-billed murre. More than 1.5 million individuals winter off Southwest Greenland. They arrive primarily from breeding grounds in Arctic Canada, Iceland, Svalbard and from breeding sites further north in Greenland (Frederiksen et al., 2016) and to a lesser degree from Russia (Lyngs, 2003). Common eiders are also very numerous, and the winter population is a mixture of Greenland and Arctic Canadian birds. In 2004, their numbers were estimated at 500,000, but the breeding population has grown since then, so that the winter numbers are probably much higher today. Several other seabird populations winter in southwest Greenland, including great cormorants (from Greenland), gulls, and probably large numbers of dovekies. As mentioned above, several inland birds from freshwater habitats also move to the coasts for the winter. These include local mallards, red-breasted mergansers and up to half a million king eiders from distant regions, ranging from Arctic Canada to eastern Alaska. These eiders spend the winter on shallow offshore banks (Mosbech et al., 2007). Harlequin ducks winter along southern Greenland's exposed rocky coasts, where the population is a mixture of local Greenland birds and Canadian birds.

Besides wintering in this area, Canadian king eiders and harlequin ducks perform a molt migration to West Greenland waters in summer (Salomonsen, 1968; Frimer, 1994; Mosbech and Boertmann, 1999).

Biogeography

Compared to the land bird fauna of Arctic North America and Siberia, the Greenland fauna is species-poor. This phenomenon is most pronounced among the shorebirds of which Greenland holds 11 breeding species compared to 16 species on adjacent Baffin and Ellesmere Islands, and even more diverse shorebird faunas farther west in the Canadian Arctic and in Arctic Siberia. This relatively poor bird fauna can be explained by the rather isolated position of Greenland, an island that was almost completely covered by ice during the most recent glacial period of the Pleistocene. Because of this glacial dominance, land birds have 'only' had 10,000 years to immigrate. Most likely several more species could breed there, but have not yet found their way to Greenland. Immigration is still taking place, however. For instance, two species have immigrated and established widespread and numerous populations since 1990. These are the Canada goose and lesser black-backed gull, arriving from either side of the Atlantic (Boertmann, 2008; Fox et al., 2012; Boertmann and Frederiksen, 2016). The first breeding records of these species in Greenland were recorded during a period of regional cooling (Boertmann, 2008), so recent climate changes cannot explain their arrival in Greenland, but at least their expansion there is favored by the current warming. Some of the occasional breeders may be taking their first steps towards permanent immigration, such as the tundra swan, gray plover, buff-bellied pipit, and others. Immigration of new breeding species is expected to be boosted by current climate changes; an example is that the bohemian waxwing has bred in Greenland during the past 3 years in a tree plantation in South Greenland. Another species likely to be favored by the climate changes is the redwing, which recently has established small populations in the plantations in South Greenland.

The migration routes of the different land birds and some seabird populations to some degree reflect their places of origin during the Holocene (Nørrevang, 1963). Most have apparently arrived from Northwest Europe, many using Iceland as a stepping stone. These include the white-tailed eagle and the northern wheatear. This immigration pattern has also been demonstrated by a recent immigrant, the lesser black-backed gull. Bird species of North American origin include the Canada goose, peregrine falcon, Baird's sandpiper, the great northern diver and the harlequin duck. These Nearctic migrant birds are also constrained by the long distance between the northernmost spring staging grounds and the Greenland breeding grounds (Alerstam et al., 1986), a barrier that also likely contributes to the low numbers of breeding bird species in Greenland.

Humans and Birds

Greenland has been inhabited by humans in several discrete periods since 2500 BCE, and the different populations have until recently lived primarily from hunting of mammals and birds. The Inuit ancestors of the modern Greenlanders immigrated from Arctic Canada in about 1200 CE and had a culture based primarily on seal hunting. They first established a population around the North Water Polynya, which acted as a gateway for their dispersal to most ice-free regions of Greenland. Seabirds were an important resource during some periods. One such example is the little auks that breed along the coasts of the North Water. These birds were an important food resource during summer. Until WWII, hunting was the most important occupation in Greenland, but since then a modern fishery has developed, and today only a small proportion of the population has hunting as a primary

occupation. On the other hand, hunting has become a sport and spare-time occupation, especially for the people in the larger towns. Although the Greenland population only numbers 56,000 people distributed along several thousand kilometers of coast, the hunt has had a significant negative impact on both seabird and marine mammal populations (Hansen, 2002). This is caused by a combination of human population growth, introduction of highly efficient modern weaponry, and fast motor boats. These boats put all of the coastal areas of West Greenland within easy reach of people sailing from towns and settlements. Before 1977, a largely unregulated bird hunting also contributed to the depletion of the bird populations (Mølte, 2013).

Several seabird populations in West Greenland have suffered strong decreases due to human harvesting, primarily the thick-billed murres (Fig. 4) and the common eiders, which are the most popular quarry. In the mid-1990s an estimated 200,000–250,000 murres were bagged annually, but nowadays the official bag record (Piniarneq) reports 60,000–80,000 annually, illustrating that the hunting pressure on this species has decreased. At least six thick-billed murre colonies, of which two held tens of thousands of breeding pairs, have been extirpated since the 1970s, mainly due to spring and summer harvesting of adult birds. This has also been exacerbated by the bycatch of murres in salmon drift nets, which until the mid-1970s took an estimated 250,000–750,000 murres annually, although many of the birds came from breeding sites in Canada and Svalbard (Merkel et al., 2014). Eider colonies were previously raided for eggs, and adult birds were shot in spring, resulting in the disappearance of numerous colonies, especially in Northwest Greenland (Merkel, 2010) (Figs. 4 and 5).

In 2001, hunting regulations of the common eider hunt were tightened, making the spring hunt illegal. This immediately initiated a population recovery, which still goes on today (Fig. 5) (Merkel, 2010). The regulation of the thick-billed murre hunt has also underwent changes, but due to strong pressure from hunting organizations, the regulation changes have not been sufficient, and the decrease in thick-billed murres continues. In recent years, changes in oceanographic conditions have probably also contributed to this decline (Merkel et al., 2014).

Climate Change

Climate change is particularly evident in the Arctic (ACIA, 2005), and the bird fauna is responding or is expected to respond accordingly.

Some of the most obvious signs concern range expansions, especially of low Arctic species shifting northward into the present high Arctic. Common eiders were found breeding on the north coast of Greenland in 2009, which represented a 200 km northwards extension since the 1980s, facilitated by reduced ice cover along the northern coast of Greenland (Boertmann et al., n.d.). Peregrine falcons are now observed much further north than previously, for instance in high Arctic Northeast Greenland and in 2017, Lapland longspurs have been found breeding six degrees farther north than their hitherto known range (Lee, 2018).

In the high Arctic itself, the balance between snowfall and spring temperatures is a critical habitat feature for breeding birds. Precipitation is expected to increase in high Arctic Northeast Greenland, mainly as winter snow. If this is not counterbalanced by higher spring temperatures, it may result in later snow-melt. Shorebirds are dependent on snow-free lowland areas when they arrive in late May and early June. Too much snow reduces their breeding success (Mølte et al., 2008). On the other hand, if higher spring temperatures result in earlier snow-melt, it may benefit the shorebirds in the short term, that is until low Arctic vegetation spreads across the high Arctic tundra. Most likely, we will see both phenomena: but also much higher variability and thereby a higher frequency of extreme events that may include years with high adult mortality (Mølte et al., n.d.) As these birds

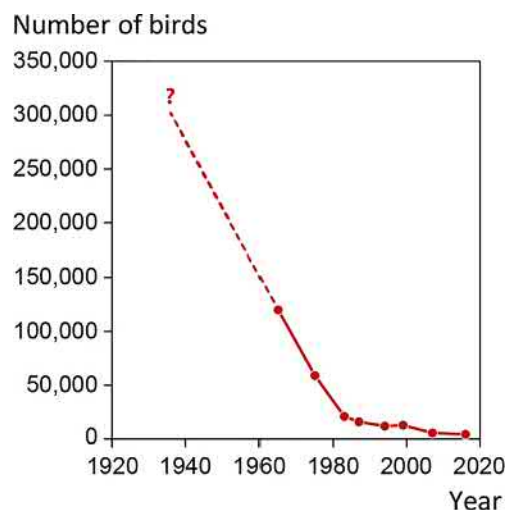


Fig. 4 Development in the central West Greenland colonies of thick-billed murres since the first estimates were made in the 1930s.

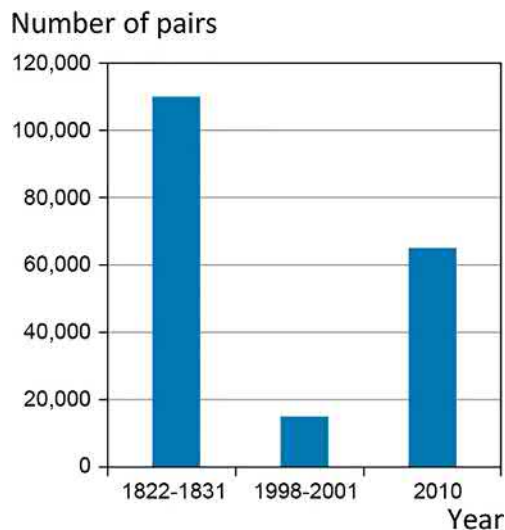


Fig. 5 Development in the west Greenland colonies of common eider since the first estimates were made in the early 1800 hundred based on down trade. From Meltofte, H. (2013).

also suffer from habitat deterioration on their winter quarters, there is serious concern for the populations on the long term (Meltofte et al., 2007).

Another species expected to be affected by climate change is the ivory gull, a species associated with ice-covered seas, both when breeding and in the winter quarters (Gilg et al., 2009, 2016). The adjacent population of this species in Arctic Canada has shown a serious decline since the early 1980s (Gilchrist and Mallory, 2005), while trends in the Greenland population remain unknown, although there are signs of a decrease in the southernmost colonies (Boertmann et al., in press).

There are also signs of disrupted lemming population cycles in the high Arctic, and if they become manifest, predatory bird species dependent on this resource may suffer decreases, especially snowy owl and long-tailed skua (Schmidt et al., 2012).

On the other hand, many of the coastal species wintering in low Arctic Greenland are expected to be favored by milder winters with reduced ice cover, since winter mortality most likely is the main factor regulating the populations of these species. For example, reduced ice means increased access to seabed feeding grounds for diving ducks. Species, which could be expected to increase, both in their population size and in the size of their ranges, include the great cormorant, common eider, mallard, long-tailed duck, harlequin duck, red-breasted merganser, white-tailed eagle and purple sandpiper.

Finally, a range of species from lower latitudes may immigrate to Greenland, especially from expanding populations in neighboring countries. Seabirds like great skua and northern gannet are likely candidates (Boertmann et al., n.d.).

Bird Conservation in Greenland

Bird protection in Greenland is done through official hunting regulations, which indicate open season for the species available to the hunters. Besides closed seasons, some species also have quotas in order to limit the harvest. All other species are, in principle, protected, although the regulations are often not observed.

No areas in the populated parts of Greenland are protected from hunting and related human disturbances (except for the towns) outside the breeding season. This means there are no areas where staging coastal birds can find refuge from the threat of shooting and disturbance. Safe staging areas outside the breeding season, and particularly for coastal birds in migration periods and winter, are in high demand in West Greenland.

Only a few Greenland bird species are globally red listed according to the IUCN list of threatened species (Table 1) (BirdLife International, 2018). More species are included in the national red list (Table 1) (Boertmann and Bay, 2018).

Besides defining the open seasons, the hunting regulations also designate about 40 'bird protection areas,' which are seabird breeding colonies, where traffic and admission is regulated in the breeding season, in order to protect the breeding birds from disturbance.

Several areas are nature protection areas, but bird hunting is usually possible in these. Only in the large and remote National Park of North and East Greenland hunting is forbidden (no people live there).

The bird populations of highest conservation concern in Greenland today are white-fronted goose, thick-billed murre and ivory gull which are threatened by hunting and/or climate changes. Several other species with small populations and restricted breeding ranges, such as white-tailed eagle and whimbrel are also of concern, but their threats are less serious and can in many ways be managed.

Table 1 Red listed bird species in Greenland

<i>Red listed bird species in Greenland</i>			
<i>Species</i>		<i>Global</i>	<i>National</i>
Common loon	<i>Gavia immer</i>	LC	NT
Pale breasted brant	<i>Branta bernicla hrota</i>	LC ^a	NT
Greenland white-fronted goose	<i>Anser albifrons flavirostris</i>	LC ^a	EN
Common eider	<i>Somateria mollissima</i>	NT	LC
Long-tailed duck	<i>Clangula hyemalis</i>	VU	LC
White-tailed eagle	<i>Haliaeetus albicilla</i>	LC	VU
Gyr falcon	<i>Falco rusticolus</i>	LC	NT
European golden plover	<i>Pluvialis apricaria</i>	LC	NT
Red knot	<i>Calidris canutus</i>	NT	LC
Whimbrel	<i>Numenius phaeopus</i>	LC	NT
Sabines gull	<i>Xema sabini</i>	NT	LC
Black-headed gull	<i>Larus ridibundus</i>	LC	VU
Ross's gull	<i>Rhodostethia rosea</i>	LC	VU
Black-legged kittiwake	<i>Rissa tridactyla</i>	VU	VU
Ivory gull	<i>Pagophila eburnea</i>	NT	VU
Arctic tern	<i>Sterna paradisaea</i>	LC	NT
Common murre	<i>Uria aalge</i>	LC	EN
Razorbill	<i>Alca torda</i>	NT	LC
Atlantic puffin	<i>Fratercula arctica</i>	VU	VU
Snowy owl	<i>Bubo scandiaca</i>	VU	NT
Meadow pipit	<i>Anthus pratensis</i>	NT	LC
Redwing	<i>Turdus iliacus</i>	NT	DD

LC = Least concern, NT = near threatened, VU = vulnerable, EN = endangered, DD = data deficient.

^aApply to the entire population on species level.

From BirdLife International (2018) and Boertmann, D. and Bay, C. (2018).

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Marine Mammals of the Greenland Seas

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Abstract

This article describes the relationship between sea ice and marine mammals around Greenland, the possible effects of climate change and the importance of subsistence hunting in modern Greenland. We also summarize the biology, conservation status and utilization of the polar bear, walrus, seal and whale species of Greenland.

Sea Ice, Climate Change and Marine Mammals in Greenland

Sea ice has a major influence on the movements of marine mammals in Greenland. Nine of the marine mammals in Greenland waters are endemic to the Arctic and associated with sea ice (**Table 1**): bowhead whale (*Balaena mysticetus*), narwhal (*Monodon monoceros*), beluga (*Delphinapterus leucas*), walrus (*Odobenus rosmarus*), polar bear (*Ursus maritimus*), bearded seal (*Erignathus barbatus*), ringed seal (*Pusa hispida*), hooded seal (*Cystophora cristata*) and harp seal (*Pagophilus groenlandicus*). The last four are also known as ice seals, as they use sea ice for whelping. In addition, cetaceans with more boreal distributions, such as rorquals (minke whale, *Balaenoptera acutorostrata*; fin whale, *B. physalus*; blue whale, *B. musculus*; humpback whale, *Megaptera novaeangliae*, and to a lesser extent, sei whale, *B. borealis*), harbor porpoise (*Phocoena phocoena*), white beaked dolphins (*Lagenorhynchus albirostris*), white sided dolphins (*L. acutus*), long finned pilot whales (*Globicephala melas*), killer whales (*Orcinus orca*), sperm whales (*Physeter microcephalus*) and bottlenose whales (*Hyperoodon ampullatus*) spend the summer feeding in ice-free Greenland waters. Also present is the harbor seal (*Phoca vitulina*), which does not necessarily associate with ice but lives in some parts of Greenland year round. The gray seal was documented in Greenland for the first time in 2009 (and observed again in 2010), but has not been reported since then. **Table 1** shows the different populations of marine mammal that are common in Greenland, together with their most recent abundance estimates, status in relation to historical levels and population trends (i.e. increasing, decreasing or stable), when known.

The Arctic is warming twice as fast as the rest of the planet (see refs in [Laidre et al., 2015a,b](#)). In Greenland, the open water season has increased by about 10 days per decade since the 1970s ([Stern and Laidre, 2016](#)). One expected consequence is that the range of the nine Arctic species will shift northwards following their preferred temperature ranges and available sea ice habitat, while the boreal species will extend the period of time they are in Greenland, and move into habitat not previously available. For ice-dependent species like the ice seals and polar bear, we expect that the reduction of sea ice will cause declines in body condition, reproduction, survival and abundance.

Regions Around Greenland and Seasonal Marine Mammal Occurrence

Based on the seasonal changes in sea ice and movement patterns of marine mammals, the seas around Greenland can broadly be divided in four general regions (**Fig. 1**).

Northwest Greenland: In Baffin Bay, sea ice forms during fall and winter in the west and north, advancing from Canada to Northwest Greenland. Polar bears range over the sea ice, while walrus, bowhead whales, narwhals and belugas follow the ice formation from Canada to Greenland. During spring and summer, the sea ice melts from the southeast to the northwest, and many of the animals return to their summer grounds in the Canadian Arctic and the boreal cetaceans and harp seals move in.

North and Northeast Greenland: In North and Northeast Greenland, there is year round multi-year sea ice, with nearly total to partial coverage during winter, except for the polynyas. Polynyas are areas of open water surrounded by ice during winter, kept open by strong currents and winds. The North Water Polynya (NOW) is located between Northwest Greenland, and Ellesmere

Table 1 Populations or management stocks of marine mammals in Greenland, with known abundances, status and trends.

Species	Population/stock	Area of Greenland	Abundance (with 95% confidence interval (CI) or coefficient of variation (CV) if available)	Year of census	Status: unknown, reduced or not reduced	Trend: unknown, increasing, decreasing or stable	References
Polar bear	Arctic Basin	North	Unknown	–	Unknown	Unknown	IUCN/PBSG (2019)
	Baffin Bay	Northwest	2826 (95% CI 2059–3593)	2013	Not Reduced	Unknown	IUCN/PBSG (2019)
	Davis Strait	Southwest	2158 (95% CI 1833–2542)	2007	Not Reduced	Stable	IUCN/PBSG (2019)
	E Greenland	Northeast, Southeast, Southwest	Unknown	–	Unknown	Unknown	IUCN/PBSG (2019)
	Kane Basin	North	357 (95% CI 221–493)	2014	Not reduced	Increasing	IUCN/PBSG (2019)
Walrus	N Hudson Bay-Hudson Strait-SE Baffin Island-N Labrador						
	“West Greenland winter aggregation”	Northwest	1408 (95% CI 922–2150)	2012	Reduced	Increasing	Heide-Jørgensen et al. (2013a)
	Baffin Bay “Winter component in Greenland”	North	2544 (95% CI 1513–4279)	2014	Reduced	Increasing	Heide-Jørgensen et al. (2016b)
Ringed seal	East Greenland	Northeast	559 (95% CI: 357–875)	2009	Unknown	Stable	NAMMCO (2018)
	Baffin Bay	North, Northwest	1,200,000	1990s	Unknown	Unknown	Kingsley (1998)
	Greenland Sea & Southeast Greenland	Northeast, Southeast	Unknown		Unknown	Unknown	
	Labrador	Southwest	Unknown		Unknown	Unknown	
Bearded seal	Arctic Basin	North	Unknown		Unknown	Unknown	
	<i>E. barbatus</i> subspecies						
	Eastern Canada and West Greenland	North, Northwest, Southwest	Unknown		Unknown	Unknown	
Harp seal	East Greenland	Northeast, Southeast	Unknown	–	Unknown	Unknown	
	Northwest Atlantic	North, Northwest, Southwest, Southeast	7,420,000 (95% CI 6,360,000–8,360,000)	2012	Not Reduced	Stable	Hammill et al. (2015)
	Greenland Sea	Northeast, Southeast	627,410 (95% CI 470,540–784,280)	2012	Not Reduced	Increasing	ICES (2013)
Hooded seal	Northwest Atlantic	North, Northwest, Southwest, Southeast	593,500 (95% CI 404,400–728,300)	2005	Reduced	Increasing	Hammill and Stenson (2006)
	Greenland Sea	Northeast, Southeast	84,020 (95% CI 68,060–99,980)	2013	Reduced	Stable	Øigård et al. (2014)
Harbor seal	South Greenland	Southeast, Southwest	Unknown		Reduced	Increasing	NAMMCO (2019)
	West Greenland	Southwest, Northwest?	Unknown		Reduced	Stable	NAMMCO (2019)
Gray Seal	East Greenland	Southeast	Unknown		Reduced	Unknown	NAMMCO (2019)
	South Greenland	Southeast?	Unknown		Unknown	Unknown	NAMMCO (2019)

Table 1 Populations or management stocks of marine mammals in Greenland, with known abundances, status and trends.—cont'd

<i>Species</i>	<i>Population/stock</i>	<i>Area of Greenland</i>	<i>Abundance (with 95% confidence interval (CI) or coefficient of variation (CV) if available)</i>	<i>Year of census</i>	<i>Status: unknown, reduced or not reduced</i>	<i>Trend: unknown, increasing, decreasing or stable</i>	<i>References</i>
Bowhead	E Canada-W Greenland (BBDS and FBHB)						
	“West Greenland winter component”	Northwest	1538 (95% CI 827–2249)	2012	Reduced	Stable	Rekdal et al. (2014)
	Svalbard-Barents Sea						
	“NE Greenland summer component”	Northeast	318 (95% CI 110–956)	2017	Reduced	Unknown	Hansen et al. (2018)
	“NEW polynia winter component”	Northeast	301 (95% CI 127–769)	2017	Reduced	Unknown	Hansen et al. (2018)
Narwhal	“W Greenland winter aggregation”	Northwest	18,583 (95% CI 7308–47,254)	2012	Reduced	Stable	NAMMCO/JCNCB (2015)
	Smith Sound	North	16,360 (CV 0.65)	2013	Not Reduced	Unknown	NAMMCO/JCNCB (2015)
	Inglefield Bredning, W Greenland	North	8368 (95% CI 5209–13,442)	2007	Reduced	Stable	NAMMCO/JCNCB (2015)
	Melville Bay, W Greenland	Northwest	3091 (95% CI 1228–7783)	2014	Reduced	Decreasing	NAMMCO/JCNCB (2015), GINR unpublished data
	E Greenland “Scoresby Sund management stock”	Southeast	433 (95% CI 186–1099)	2016	Reduced	Decreasing	Hansen and Heide-Jørgensen (2019)
	“Kangerlussuaq management stock”	Southeast	269 (95% CI 137–550)	2016	Reduced	Decreasing	Hansen and Heide-Jørgensen (2019)
	“Tasiilaq management stock”	Southeast	206 (95% CI 76–562)	2008	Reduced	Decreasing	Hansen and Heide-Jørgensen (2019)
	NE Greenland “Dove bugt summer component”	Northeast	1395 (95% CI 744–2641)	2018	Not reduced	unknown	Hansen et al. (2019)
	E high Arctic-Baffin Bay						
Beluga	“West Greenland winter”	Northwest	9072 (95% CI 4895–16,450)	2012	Reduced	Stable	NAMMCO/JCNCB (2015)
	“NOW Polynya winter”	Northwest	2324 (95% CI 1786–2820)	2014	Reduced	Unknown	NAMMCO/JCNCB (2015)
	Southwest Greenland winter	Southwest	0	ca. 1930	Extirpated	Extirpated	Heide-Jørgensen and Laidre (2006)
Blue whale	Western North Atlantic	Southwest, Northwest	Unknown		Reduced	Unknown	
	Central and Eastern North Atlantic	Southeast, Northeast (offshore)	3000 (95% CI 1377–6534)	2015	Reduced	Increasing	Pike et al. (2019)

(Continued)

Table 1 Populations or management stocks of marine mammals in Greenland, with known abundances, status and trends.—cont'd

<i>Species</i>	<i>Population/stock</i>	<i>Area of Greenland</i>	<i>Abundance (with 95% confidence interval (CI) or coefficient of variation (CV) if available)</i>	<i>Year of census</i>	<i>Status: unknown, reduced or not reduced</i>	<i>Trend: unknown, increasing, decreasing or stable</i>	<i>References</i>
Fin whale	West North Atlantic						
	“West Greenland coastal”	Southwest	2215 (95% CI 1107–4823)	2015		Fluctuating	Hansen et al. (2019)
	Central North Atlantic						
	“Iceland/Faroe Islands”	Southeast (offshore), Northeast (offshore)	36,773 (95% CI 25,811–52,392)	2015			Pike et al. (2019)
	“East Greenland coastal”	Southeast (nearshore)	6440 (95% CI 3901–10,632)	2015		Increasing	Hansen et al. (2019)
Minke whale	West Greenland						
	“West Greenland coastal”	Southwest, Northwest	5095 (95% CI 2171–11,961)	2015		Fluctuating	Hansen et al. (2019)
	Central Atlantic						
	“East Greenland coastal”		2762 (95% CI 1160–5574)	2015	Not reduced	Fluctuating	Hansen et al. (2019)
Sei whale	North Atlantic						
	“West Greenland coastal”	Southwest	1599 (95% CI 690–3705)	2005	Unknown	Fluctuating	Heide-Jørgensen et al. (2007)
Humpback whale	North Atlantic						
	“West Greenland Coastal”	Northwest, Southwest	933 (95% CI 434–2272)	2015	Not reduced	Fluctuating	Hansen et al. (2019)
	“East Greenland Coastal”	Southeast	4223 (95% CI 1845–9666)	2015	Unknown	Increasing	Hansen et al. (2019)
Harbor porpoise	“West Greenland”	Southwest Greenland	83,321 (95% CI 4377–160,047)	2015	Unknown	Unknown	Hansen et al. (2019)
	“West Greenland”	Southeast Greenland	1642 (95% CI 318–8464)	2015	Unknown	Unknown	Hansen et al. (2019)
Killer whale	Unknown populations	Northwest, Southwest, Southeast	Unknown		Unknown	Unknown	
Pilot whale	“West Greenland”	Southwest, Northwest	9190 (95% CI 3635–23,234)	2015	Unknown	Unknown	Hansen et al. (2019)
	“East Greenland”	Southeast	258 (95% CI 50–1354)	2015	Unknown	Unknown	Hansen et al. (2019)
White beaked dolphin	“West Greenland”	Southwest, Northwest	15,261 (95% CI 7084–33,046)	2015	Unknown	Unknown	Hansen et al. (2019)
	“East Greenland”	Southeast	11,889 (95% CI 4710–30,008)	2015	Unknown	Unknown	Hansen et al. (2019)
Atlantic white sided dolphin	Unknown populations	Southwest	Unknown		Unknown	Unknown	
Sperm whale	North Atlantic	Northwest, Southwest, Southeast	Unknown		Unknown	Unknown	
Bottlenose whale	Unknown populations	Northwest, Southwest, Southeast	Unknown		Unknown	Unknown	

Island, while the North East Water Polynya (NEW) is at the northernmost part of East Greenland. Polynyas are important for marine mammals, especially walrus and beluga in the NOW and walrus and bowhead whale in the NEW. Narwhals, bearded seals, ringed seals and polar bears use the polynyas, as well as other areas with higher concentrations of sea ice. Kane Basin lies to the north of the NOW and is important habitat for polar bears.



Fig. 1 Marine mammals areas of Greenland.

Southeast Greenland: During winter or early spring, the fjords of Southeast Greenland freeze, while the offshore areas are dominated by drift ice transported from the north by the southern flow of the East Greenland current. Polar bears, ringed seals and bearded seals thrive in the frozen fjords. In summer, the sea ice in the fjords melts and the amount of drift ice offshore gradually decreases. Several fjords are dominated in summer by freshwater ice coming from calving glaciers. Polar bears, narwhals, ringed seals and bearded seals retreat mainly into glacier dominated fjord systems, while harp seals, rorquals, pilot whales and killer whales move into the open coastal waters. Sperm whales and bottlenose whales stay in the deeper waters.

Southwest Greenland: The East Greenland Current (ECG) mixes with a branch of the north Atlantic current, along the southeast Greenland coast. The current transports sea ice, bearded seals, ringed seals and polar bears from the east to the west around the southern tip of Greenland. The current transports sea ice north along the west coast for about 200 km, with a peak around July. Polar bears are regularly seen in the southernmost part of Southwest Greenland, while walrus, narwhal, and beluga are occasional stragglers. The beluga population that migrated to the fjords of Southwest Greenland from autumn to June was extirpated by hunting last century. The southern tip of West Greenland is the only place in Greenland where all 6 species of seals from the North Atlantic have been seen (ringed seal, bearded seal, harp seal, hooded seal, harbor seal and gray seal). The boreal cetaceans, especially rorquals and harbor porpoise are abundant in Southwest Greenland.

Marine Mammals and People in Greenland

Hunting: The ancestors of Greenlanders were Inuit that came from Arctic Canada, traveling over the sea ice with dog sledges and by sea with kayaks and umiaqs ("women boats"). Marine mammals were a fundamental part of their diet. Even though human's diet in Greenland is nowadays supplemented with imported products and agriculture is developing in Southern Greenland, marine mammals are still hunted for subsistence and their products are an important part of the local economy. Hunting provides food for subsistence hunters and their families, as well as food for sledge dogs. Hunting also provides a source of revenue, through the sale of animal products, including meat, mattak (whale skin and blubber, spelled "muktuk" in the Western Arctic), fur from seals and polar bear and narwhal or walrus tusks. The challenges imposed by climate change on subsistence hunters in Greenland include a shortening of the season when it is safe to travel over sea ice with dog sledges and snow scooters. Some winter routes have become unsafe. As a consequence of the reduction of sea ice, the population of sledge dogs is dwindling. Skiffs are used more than

before for fishing and hunting and in some areas, especially in Southeast Greenland, hunting during summer has shifted from narwhals to dolphins, pilot whales and killer whales.

Management: Greenland is a country under the kingdom of Denmark, with a high degree of autonomy in several areas, including, since 1979, the management of wildlife. The Greenland Institute of Natural Resources (GINR), established in 1993, conducts research and monitoring to provide the Government with management advice to secure that fishing and hunting are sustainable. Much of the marine mammal research and monitoring work is done in coordination with organizations regulated by international government agreements. Thus, GINR presents research and monitoring results to the scientific working groups of the relevant organizations and, after a review of results and an assessment process, the organizations provide advice to the management authorities of the government of Greenland. The government then takes this advice, together with input from hunters, to decide upon regulations such as hunting seasons or quotas.

The international organizations that advise Greenland include the International Whaling Commission (IWC) for large whales; the North Atlantic Marine Mammal Commission (NAMMCO) for pinnipeds and cetaceans; the Canada/Greenland Joint Commission for the Conservation of Narwhal and Beluga (JCNB) for narwhals and belugas in West Greenland; a working group under the International Council for the Exploration of the Seas (ICES), the North Atlantic Fisheries Organization (NAFO) and NAMMCO for harp and hooded seals and the Canada-Greenland Joint Commission on Polar Bear for polar bears in Baffin Bay and Kane Basin. Management of Polar bears in all of Greenland is done following the 1972 Agreement on the Conservation of Polar Bears under the Polar Bear Range States Agreement, whose scientific advisor is the Polar Bear Specialist Group of the International Union for the Conservation of Nature (IUCN). Effects of trade in endangered species are overseen under the Council for International Trade of Endangered Species (CITES).

Biology, Status and Utilization of Marine Mammals in Greenland

Polar Bear

Polar bears are dependent on sea ice for all aspects of their life, including travel, breeding and foraging for ice seals. In the areas where the sea ice melts annually during summer, polar bears either fast on land, spend the summer on multi-year sea-ice, or spend the summer near glaciers where limited opportunities for feeding on seals resting on glacial ice may arise.

There are 19 subpopulations of polar bears around the Arctic, five of which live in Greenland: Baffin Bay, Kane Basin, Arctic Basin, East Greenland and Davis Strait (Table 1).

As of the 2010s, polar bears from the Baffin Bay subpopulation are showing effects of reduced sea ice and a longer open water season. These include smaller home range, northwards shift of the subpopulation range, more time fasting on land during the open water season, reduced body condition, maternity dens built on higher ground and shorter maternity denning periods (SWG, 2016).

In contrast, the Kane Basin population, that occupies the small area with multi-year ice in the far north, between North Greenland and Ellesmere Island, appears to be stable or increasing. This is likely because the multi-year ice is transitioning to annual ice which is more productive, and the hunting pressure by humans is lower than before (SWG, 2016).

There are fewer polar bears in the Arctic Basin than in other parts of the Arctic (IUCN/PBSG, 2019). The area, especially the parts close to North Greenland and the Canadian Archipelago, will likely be important for polar bears in the future, as the thick multiyear ice will melt and transition to seasonal ice, which is good habitat for seals and polar bears. This is expected to be the last refuge for polar bears across the Arctic when the southern parts of their current habitat disappear because of climate change.

In East Greenland polar bears occupy areas with reduced sea ice habitat and their habitat use has changed (Laidre et al., 2018). The abundance of polar bears in East Greenland is unknown, as is the connectivity of bears along the coast. An assessment of East Greenland polar bears is ongoing and our knowledge will increase considerably during the 2020s.

The Davis Strait population of polar bears was assessed as stable, with basis on an inventory terminated in 2007. Fieldwork for a new census based on genetic mark recapture was carried out in 2017 and 2018. Davis Strait polar bears spend the summers in Canada and only a small part of their range is in Greenland, when the sea ice forms during winter. As the extent of sea ice recedes due to climate change, the proportion of polar bears from this subpopulation wintering in Greenland is becoming smaller.

Polar bears are classified as Vulnerable under both the global Red List (<https://www.iucnredlist.org/>) and Greenland's national Red List (<https://natur.gl/leksikon/roedliste/>) because it is probable that the world population will be reduced by 30% between 2015 and 2050 due to reductions in sea ice.

Polar bears are important for human subsistence in Greenland, however loss of sea ice and the introduction of hunting quotas in 2005 have also increased human-bear conflicts where polar bears that approach towns and settlements are being killed to protect human lives and property. During 2017–19, an average of 143 polar bears were taken annually in Greenland, including an average of 7 taken in defense of life and property (Anon, 2019; Wilken, 2019).

Atlantic Walrus

Walrus are social animals. They haul-out for resting over land or over sea ice and feed on shellfish at the seabed in waters shallower than 50 m. Feeding bouts can last 3–4 days, followed by 1–2 days resting. There is some degree of sexual segregation, where females and calves tend to spend summer months further north than the adult males. Mating occurs during winter, in waters with high concentrations of sea ice. Seasonal movements follow the formation of sea ice, with walrus spending summers close to land

and winters close to the ice edge (Born, 2011, 2017). There are three populations of walrus in Greenland: Baffin Bay, West Greenland Winter Aggregation and East Greenland.

Walrus in northern Baffin Bay spend summers along the northeastern coast of Arctic Canada, mainly off Ellesmere Island, and winter on the Greenland side of the North Water Polynya (Heide-Jørgensen et al., 2017).

Similarly, some of the walrus that summer in Southern Baffin Island spend winters feeding on the shallow banks off West Greenland.

In East Greenland, walrus are abundant only in the National Park. An interesting feature of the walrus in East Greenland is that many males migrate hundreds of kilometers north to spend winter with the females in the North East Water Polynya (Born, 2011).

Atlantic walrus are listed as Near Threatened in the global red list. The populations in Baffin Bay and West Greenland are increasing, recovering from previous hunts, and listed as Vulnerable in the Greenland Red List. Walrus in East Greenland are listed as Near Threatened in the Greenland Red List, which is a more favorable status.

Greenlandic hunters reported taking an average of 157 walrus per year in 2016–18 (<https://nammco.no>). Nowadays, the Greenlandic subsistence hunt is sustainable. However, in the period 2013–15, catches in Baffin Bay were higher than the scientific advice from NAMMCO, which led to a self-imposed ban on export of walrus products in July 2016. This ban had not been lifted at the time of writing this text.

Past hunting has resulted in walrus being rare in some of their original range in Greenland. This includes East Greenland, south of the national park, where they no longer use terrestrial haul-outs, and current catches consist of stragglers from the north (Born, 2011). Today, walrus in West Greenland haul out almost exclusively on sea ice and their former haul-out sites on land have been abandoned for at least 50 years (Born, 2017).

Seals

There are five or maybe six species of seals inhabiting the seas around Greenland. Four of them are strongly associated with sea ice, and depend on ice for whelping, molting and resting. The remaining two species, the harbor seal and the gray seal, are coastal seals that haul-out on land. The majority of the seals of these two species live in temperate waters. Some small harbor seal populations however, live permanently in the Arctic (including Greenland) and a few gray seals may sometimes stray into Greenland waters.

Ringed seal: Some ringed seals (especially adult seals) maintain breathing holes in the ice throughout the winter and others (especially juvenile seals) winter in areas with light ice conditions, where they do not need to maintain breathing holes. They are generally solitary, although a few seals may share one breathing hole and rest beside it during molt in spring and early summer. Ringed seals make birth lairs in compact snowdrifts that are associated with a breathing hole. They feed on fish, such as polar cod and Arctic cod and are, themselves the favored prey of polar bears in most areas. Ringed seals are widely spread throughout the Arctic and are listed as Least Concern in both the global and the Greenland red list.

Ringed seals are important for the subsistence economy of Greenlanders in some regions. The average annual reported catches during 2012–17 were 56,000 seals (<https://nammco.no>). The meat is food for humans and sledge dogs. The national tannery purchases many of the skins.

Bearded seal: Bearded seals eat fish and invertebrates found on the seabed. They live alone or in small groups, in close association with sea ice, which they use for whelping and resting, especially during molting. They have a circumpolar distribution in the Arctic. East and West Greenland probably have separated stocks, but their population status and trends are unknown. Both the IUCN and Greenland Redlists have bearded seals as Least Concern.

The average annual reported catches during 2012–17 were 1200 seals (<https://nammco.no>). This hunt is likely sustainable, as bearded seals only are hunted in a small part of their wide distribution area. The skin from bearded seals is tough compared to that from other seals and often used to make soles for kamiks (Inuit footwear) and the whips used to guide the sledge dogs.

Hooded seal: Hooded seals have an impressively wide home range. They feed along the continental shelves in the North Atlantic and dives to depths of 1652 m have been recorded (Andersen et al., 2013). They mainly feed on large fish and squid. Females give birth on sea ice in March to April and they only nurse their pups for 4 days, after which they mate again and leave the whelping area. Pups remain alone on the ice for a few days, before taking to sea, spreading and learning to feed by themselves. There are two stocks in the North Atlantic, one in the Northwest Atlantic (whelping in the Gulf of St Lawrence, off Newfoundland and in the Davis Strait) and one that whelps in the Greenland Sea. Hooded seals from both stocks swim in and out of Greenland's waters. Based on surveys conducted in 2005, the West Atlantic population was estimated to be around 600,000 seals (Hammill and Stenson, 2006). No full surveys have been conducted since then and the present population trends and status remain unknown. The Greenland Sea stock decreased during a period with very high catches following the Second World War. The stock has now stabilized at a low level and Hooded seals are therefore listed as "Vulnerable" in both the global and the Greenland Red List.

There is no longer commercial sealing on hooded seals. The average annual reported subsistence catches in Greenland during 2012–17 were 1700 seals almost exclusively from the West Atlantic population (<http://nammco.no>). This catch level should not have any noticeable effect on the populations.

Harp seal: Adult harp seals often swim in large groups when foraging during summer and fall. They forage in most of the Greenland waters that are not ice covered, from offshore open water to deep inside fjords and close to glaciers. They feed on a variety of fish and invertebrates, but small schooling fish, especially capelin, but also polar cod and sand lance seem to be the most important. The West Atlantic harp seals give birth off Newfoundland around the start of March, whereas the population in the Greenland Sea

whelp about a month later. At the beginning of this century a small group of harp seals (around 1000) started to give birth on the drift sea ice off Southwest Greenland (Rosing-Asvid, 2008).

Overharvest greatly reduced the North Atlantic harp seal stocks as long ago as the 19th century, but regulations of the catches since the 1970s have allowed a strong recovery (Hammill et al., 2015). Harp Seals are listed as “Least Concern” in the global and the Greenland Red Lists.

The subsistence catch of harp seals is important in most parts of Greenland. The average annual reported catches in Greenland during 2012–17 were around 59,000 seals (<http://nammco.no>). The main purpose of the catch is to obtain meat for human consumption and for dog food, but hunters also sell skins to the national tannery.

Harbor seal: During molting and breeding, harbor seals concentrate in colonies that in Greenland typically are on small off shore rocks or sandy beaches inside fjords. Their diet includes arctic char, and some groups summer near estuaries and river mouths where this fish is abundant. Harbor seals are the only seal in Greenland that frequently swim up rivers. Although probably never numerous, harbor seals were once spread over much of the West Greenland coast. Due to excessive hunting and perhaps interactions with fisheries, harbor seals disappeared or became extremely rare throughout most of their former range. Harbor seals are now only regularly observed at three breeding/molting localities, but observations of individual seals and small groups of seals far from these localities, indicate that other small remnant populations still exist. Harbor seals are listed as of Least Concern in the global Red List, but are Critically Endangered in the Greenland Red List.

The skin from harbor seals are traditionally used in the women’s national costume and therefore specially coveted but hunting of this species has been banned in Greenland since 2010.

Gray seal: Gray seals were not conclusively documented in Greenland before 2009, when two seals were photographed during an inventory in a colony of harbor seals, near the southernmost tip of Greenland (Rosing-Asvid et al., 2010). The following summer, a gray seal pup was live-captured by scientists in a net in the same area, and it had a satellite-linked transmitter glued to its back. Unfortunately, the tag only lasted for 29 days during which the seal swam 224 km up along the Greenland east coast. This capture is the last documented contact with a gray seal in Greenland.

Arctic Cetaceans

There are three arctic whales that live year-round in Greenland: Bowhead whale, narwhal and Beluga. These are cold water species endemic of the Arctic, often associated with sea ice.

Bowhead whale: The bowhead whale is, together with blue and fin whales, one of the largest animals of Greenland. They feed on copepods, small zooplankton found in productive areas. In West Greenland, bowhead whales are especially abundant in Disko Bay, where they arrive during winter. Bowhead whales prefer water colder than 2 °C, so they leave Disko Bay in June, when water temperatures begin to increase, even though this means they miss the peak on abundance of *Calanus* prey at the surface (Chambault et al., 2018). The bowhead whales coming to Disko Bay are primarily mature females in resting year without calves (Heide-Jørgensen et al., 2010). They belong to the larger East Canada–West Greenland (ECWG) population.

Bowhead whales may reach ages of more than 200 years, were hunted to near extinction in East Greenland during the 18th and 19th century, and severely depleted in West Greenland during the 19th and 20th century (Cooke and Reeves, 2018 and references therein). They were protected worldwide by the League of Nations in 1932. By then, they were thought extinct in East Greenland and rare in West Greenland. After the 1990s, bowhead whales in West Greenland showed a steep recovery, to the point that, in 2009 the IWC agreed to give Greenland a quota of 2 whales per year for subsistence whaling. However, no bowhead whales were caught in Greenland between 2016 and 2019.

Bowhead whales in East Greenland belong to the East Greenland–Svalbard–Barents Sea population, also called the “Spitsbergen stock,” which shows small signs of recovery. The population nowadays is in the hundreds. This is a difficult population to study because the whales keep themselves inside areas with high density of sea ice.

The EGSBS population is listed as endangered in the IUCN Red List, while globally, bowhead whales are listed as Least Concern. The Greenland red List lists bowhead whales in West Greenland as Nearly Threatened and in East Greenland as Vulnerable.

Narwhal: Narwhals swim in groups, often spread over a large area in clusters made by a few animals of the same gender, such as only males or only females with calves, swimming very close to each other. Narwhals can live to be 100 years old and, together with humans, are one of the few species in which females live a considerable part of their life after menopause. The male’s left tusk is a very long tooth which pierces the skin of the upper lip and grows in a spiral form in front of the head. In medieval times these tusks were believed to be unicorn horns. It is a sexual trait that males use to establish dominance and hierarchy. Narwhals can dive to more than 1700 m to feed on Greenland halibut, although can also find their prey, including squid, shrimp and fish at depths of 200–600 m (Watt et al., 2015). Narwhals spend summers in fjords with glacier fronts. They have a high degree of site fidelity and return to the same areas every summer (Heide-Jørgensen et al., 2015). During winter, when the fjords freeze, narwhals migrate to offshore areas with high concentrations of sea ice. Narwhals from several summer stocks in Arctic Canada and Northwest Greenland mix during winter in areas with high concentration of sea ice of Baffin Bay, Davis Strait and West Greenland (Heide-Jørgensen et al., 2013b).

The global Red List lists narwhals as Least Concern, while the Greenland red list considers them Nearly Threatened in West Greenland and Endangered in East Greenland. Greenlanders are highly motivated to hunt narwhals because their mattak (skin

and blubber) is a delicacy and sells for high prices. A yearly average of 445 narwhals were reported hunted in Greenland in 2016–18 (<http://nammco.no>). The smallest populations are at the edge of their summer range in Melville Bay in Northwest Greenland and south of the National Park in East Greenland (i.e. south of 72°N), where they are decreasing in numbers due to unsustainable hunting, warming temperatures caused by climate change and disturbance from increased boat traffic (NAMMCO, 2019).

Beluga: Belugas and narwhals belong to the same family, Monodontidae, and can produce hybrids (Skovrind et al., 2019). Belugas swim in groups and feed on pelagic fish, such as arctic cod (*Boreogadus saida*). A large population of belugas spends summers in Arctic Canada, then migrates every winter, when the sea freezes, to West Greenland. Some of them overwinter at the North Water Polynya, while others continue following the ice edge to Midwest Greenland. Until the early 1920s, there was another aggregation of belugas that lived most of the fall, winter and early summer in the fjords of Southwest Greenland. The belugas of Southwest Greenland were driven to extinction by unsustainable hunting (Heide-Jørgensen, 1994).

Belugas are listed as least concern both in the global and the Greenland Red List.

The Arctic Canada—West Greenland population is hunted and was in decline during the second half of the 20th century. Because of the reduction of sea ice due to climate change, the preferred habitat for the belugas, which is by the ice edge, is getting further away from the coast of West Greenland, and they have become less accessible to Greenlandic hunters. This, together with the introduction of quotas in 2005, resulted in a reduction of catches and the population is therefore increasing (Heide-Jørgensen et al., 2016a). During 2016–18, a yearly average of 204 belugas were landed in West Greenland (<http://nammco.no>). In East Greenland, belugas are only occasional vagrant visitors and protected by law.

Boreal Cetaceans

Boreal cetaceans visit the ice-free waters of the Arctic and other northern seas during summer and migrate to warmer waters during winter. In Greenland, these include four rorquals and six toothed whales.

Rorquals: Rorquals are baleen whales with grooves on their throat. The grooves allow the mouth cavity to expand, gulping large quantities of water to trap prey such as schooling fish or krill. The five species of rorquals in the North Atlantic are the minke whale, fin whale, humpback whale, blue whale and sei whale. They all migrate from southern breeding grounds in the winter to northern feeding grounds in the summer, including the ice free waters of Greenland. Rorquals produce low frequency sounds, and the increasing levels of sound pollution in the ocean probably have an effect on the ability of rorquals to communicate with each other over long distances. Unsustainable whaling by industrialized countries depleted most stocks of baleen whales during the 20th century. However, numbers are recovering because of whaling regulations. In the global Red List, minke whales and humpback whales are listed as Least Concern, while fin whales are listed as Vulnerable and blue whales and sei whales are still listed as endangered. In the Greenland red list, minke whale, fin whale and humpback whale are listed as Least Concern, Blue whale as Vulnerable and sei whale as Endangered.

During 2016–18, Greenlanders caught a yearly average of 141 minke whales, 4 humpback whales and 8 fin whales for subsistence (<http://nammco.no>). Blue whales and sei whales are protected in Greenland.

Harbor porpoise: Harbor porpoise is the smallest cetacean in the seas around Greenland. They usually swim alone or in small groups and feed on several species of fish and squid. Harbor porpoise tagged in the summer in Southwest Greenland traveled long distances during winter, into deep oceanic waters close to the Azores and offshore waters of East Greenland, and returned to the coastal waters of Southwest Greenland the following summer (Nielsen et al., 2018). Thus, Greenland harbor porpoises travel over longer distances than porpoises tagged in the North Sea. They also dive deeper, with average depths of 248 m and a maximum depth of 410 m.

Harbor porpoise are listed as “Least Concern” in the IUCN Red List and in the Greenland Red List.

The average yearly subsistence catch in the years 2015–17 was 2275, according to hunter’s reports (<http://nammco.no>). This number is higher than the 1869 recommended by NAMMCO (NAMMCO, 2019).

Delphinids: Four species of the dolphin family use the seas of East and West Greenland during the open water season: killer whale, long finned pilot whale, white beaked dolphins and white sided dolphins. White sided dolphins are rare so far north, and their distribution may be limited to the southern parts of Greenland. They are all social animals that swim in groups.

Before 2009, killer whales were seen (and hunted) without clearly regular patterns; every year they would show up at different places of Greenland and during different months. That is still the case in most of Greenland, except from Southeast Greenland, where they are hunted every year since 2009 (Jourdain et al., 2019). A similar situation applies for pilot whales and white sided dolphins, except that these two species are more abundant in Greenland. The increased occurrence of boreal cetaceans in Southeast Greenland is probably a result of climate change, with the sea being warmer, less sea ice coming from the north with the East Greenland Current and boreal fish species moving in.

Killer whales from East Greenland are genetically related to killer whales from Iceland and Norway (Foote et al., 2013). The majority of killer whales in Iceland and Norway feed on herring, while the killer whales in East Greenland feed on seals, whales and fish. This is interesting because killer whales in other parts of the world have cultural traditions regarding food and hunting techniques, specializing in either fish or marine mammals (review in Jourdain et al., 2019).

Dolphins and pilot whales feed on fish and squid. However, dolphins feed relatively close to the surface, while pilot whales are deep divers. Pilot whales occasionally feed on other marine mammals.

Killer whales are listed as Data Deficient in the global and Greenlandic Red Lists. Pilot whales and white beaked dolphins are Least Concern in both lists, while white sided dolphins are Least Concern in the global Red List and Data Deficient in the Greenland Red List.

Average reported yearly catches in Greenland in 2015–17 were 12 killer whales, 289 pilot whales and 108 dolphins (<http://nammco.no>). The North Atlantic Marine Mammal Commission has not assessed whether these catches are sustainable, but advises Greenland to regulate the catches of killer whales, as it is not known if the killer whales caught in Greenland belong to a small population or not (NAMMCO, 2019).

As top predators, killer whales accumulate chemical pollutants consumed by their prey and by the prey's prey. This pollution is magnified through the food chain from phytoplankton to zooplankton to fish to marine mammals to killer whales. This process of magnification occurs in all marine mammals, but because killer whales are the absolute top predator, and have long live spans, they are also much contaminated by chemical pollutants, to the point that the pollution may affect their survival and fertility (Desforges et al., 2018). Killer whales, pilot whales and dolphins are used as food for humans and sledge dogs in Greenland. In 2018, the health authorities in Greenland issued a press release recommending people to abstain from eating killer whale products, as it may be unhealthy due to its contaminant load. An ongoing study indicates that contaminant levels on pilot whales and dolphins in Greenland may also be high (Roos et al., 2019).

Sperm whale and bottlenose whale: The two largest toothed whales are the sperm whale and the bottlenose whale. They are both inhabitants of deep, offshore waters, although sperm whales venture into the deep fjords of Greenland. Bottlenose whales swim in groups that include males, females and calves. Sperm whales have a strong sexual segregation, with females and calves living in groups in tropical and subtropical waters, while males move to feed at high latitudes. Thus, there are only male sperm whales in Greenland. Sperm whales and bottlenose whales are both deep divers that hunt squid and deep-water fish such as halibut.

Both species were hunted by European and North American whalers for their oil in the 20th century, while sperm whales were caught in the 18th and 19th century as well. Sperm whales were depleted in the North Atlantic but have been protected globally since the 1980s and their numbers have increased. The conservation status of bottlenose whales is not known, but they seem to be abundant. Sperm whales are listed as Vulnerable in the global and Greenland Red Lists, while in both lists bottlenose whales are listed as Data Deficient.

Sperm whales are protected in Greenland. It is legal to hunt bottlenose whales, but their meat is believed to have a strong laxative effect and therefore Greenlanders do not consider them edible. Both species are known for "stealing" halibut from fishing lines and have been unpopular among fishermen. Nowadays, however, offshore fisheries in Greenland waters are carried out by trawlers and there are no conflicts with these species.

Conservation Status of Marine Mammals in Greenland

Of the 55 stocks of marine mammals from Greenland listed in **Tables 1**, 26 have an unknown status, 23 are stable or increasing, four are in decline and one was extirpated in the 1920s. Most of those with unknown status appear to be numerous and are either protected or harvested in a sustainable way. Thus, we can conclude that the majority of marine mammals in Greenland are managed on a sustainable way, and many of the populations that have declined because of overhunting in the past have recovered or are now recovering. There are a few exemptions, though.

NAMMCO has voiced concern for the unregulated catches of killer whales in East Greenland, as the size of the population has not been assessed and they may already be compromised by high levels of contaminants (NAMMCO, 2019). It remains to be seen if the recommendations by the health authorities to limit the consumption of killer whale meat will have an effect on the number of killer whales taken by subsistence hunters.

Reported catches of harbor porpoises are higher than recommended by NAMMCO (2019), and there is a risk for population decline. However, there are still tens of thousands of porpoises in Greenland, so their population is not facing imminent risk of extinction.

Harbor seals were almost wiped out from most of their range in West Greenland. Since their protection in 2010, the colony of Cape Farewell, at the southern tip of Greenland has become larger. In other locations however, harbor seals are still rare. It seems like their recovery is hampered by poaching, entanglement in fishing gear or accidental hunting as they are mistaken for other seals and shot in open water.

As a species, narwhals are not in the risk of extinction yet, since they are protected in the national park of Northeast Greenland, and relatively abundant in north Greenland north of the North Water Polynya and in arctic Canada. However, the small populations at the southern edge of the narwhal's summer distribution, in Melville Bay (Northwest Greenland) and East Greenland south of the national park, are the ones most affected by warming climate. Those small populations are also under increasing stress from boat traffic and, most importantly, they are under pressure from unsustainable subsistence hunt and their future is uncertain (NAMMCO, 2019).

Narwhal, beluga, bowhead whale, walrus, polar bear and ice seals are endemic of the arctic and their survival depends on sea ice and cold temperatures. They are or will be negatively affected by climate change, their ranges are expected to shrink northwards and their long term future depends on the global actions taken by people and governments during the next few decades to reduce the emission of greenhouse gases.

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History of Human Occupation of Greenland

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Abstract

Greenland represents the most northern human habitation in the world. The climate is high arctic, arctic and in most southern region subarctic. The first human migrations happened c. 4,500 years ago into the Thule region from Ellesmere Island, Canada. This group of people is archeologically defined as Palaeo-Eskimos and has a cultural origin in Alaska and Siberia. During the following 3 millennia, different Palaeo-Eskimo cultures inhabited different regions of Greenland. These are defined as: Independence I, Saqqaq, Pre-Dorset, Greenlandic Dorset and Late Dorset cultures. The Palaeo-Eskimo cultures were small scale hunter-gatherers with an extreme specialization in the Arctic world. Within the first half of the 1st millennium AD, two other cultural and ethnic groups arrived in Greenland. These are the Inuit of the Thule Culture, coming into the Thule region, having an origin in Alaska and Siberia, and the Norse people coming into South and Southwest Greenland from Iceland, having a Scandinavian origin. Around c. 1500 AD the only group of people sustaining and thriving in Greenland were the Thule Culture Inuit, while Late Dorset and Norse people had disappeared. The Thule Culture was a hunter-gatherer society that was extremely well adapted to arctic conditions. They had a thriving culture throughout Greenland during the 13th–19th century. During the 16th–18th centuries, increasing contact between Thule Culture Inuit and European whalers/explores were made in West Greenland. This resulted in Inuit migrations towards Disco Bay where much trade was made. With the cooling of the Little Ice Age during the 18th–19th century, the most northern regions of Greenland (Northeast Greenland) are abandoned, while the Thule region was repeatedly re-colonized by Inuit from Canada. In 1721 the European colonization of West Greenland began with the arrival of the priest Hans Egede, and during the following decades Danish colonial trade stations with churches and Danish inhabitants emerged along the West coast of Greenland, attracting permanent Inuit settlements and forming a market and service economy. Today Greenland is a modern self-ruled nation state with a population of Thule Culture origin, as well as of European origin. The prehistory of Greenland is described in this chapter separately for the Thule region, Northeast Greenland and for West, South and East Greenland, because these different regions of Greenland are naturally, topographically and culturally different, and because they have different histories of human occupation.

Introduction to Greenland and Its Human History

The history of human occupation in Greenland has been discontinuous and complex. Greenland is geographically placed as the most eastern island of the Arctic, the nearest land being Ellesmere Island, Canada. The Nares Strait that separates Ellesmere Island and Inglefield Land in the High Arctic Thule region is only 40 km wide, making this most northwestern part of Greenland the “gateway to Greenland” (Gulløv et al.), that is, the natural entrance into the world’s largest island. It is through this area that all indigenous migrations of people to Greenland have arrived, and from here they have occasionally continued into high Arctic Northeast Greenland or down into Western, Southern and Eastern Greenland, populating the low and subarctic regions of Greenland. Greenland is c. 2500 km from south to north comprising three climatic zones (subarctic, low arctic and high arctic) and is characterized by the “inland ice.” The Greenland ice sheet is the second largest glacier in the world covering c. 80% of the island, making only coastal zones and inner fjord inlands inhabitable (see Fig. 1). Greenland can be divided into at least three different biomes with different emigrational history and occupation: The Thule region, Northeast Greenland, and West, South and East Greenland. Each of these areas are separated by specific topographies that are not easily transversed by humans and terrestrial fauna, making them regions with different human settlement histories. Moreover, each of these areas has specific climates, landscapes, icescapes and resources, giving rise to different cultures and economies.

Generally, three different groups of populations have migrated into and occupied Greenland through time: The Palaeo-Eskimo group, the Inuit group and the European group (see Fig. 2). The first was the Palaeo-Eskimo group, from c. 2500 BC–1400 AD, arriving in several migrations through time from Canada, but originating out of the western Arctic, that is, Alaska/Siberia. Archeologically, the Palaeo-Eskimo group in Greenland is defined as five different Palaeo-Eskimo groups depending on their material culture. Through time, these Palaeo-Eskimo cultures populated all parts of coastal Greenland. The Norse group arrived from Iceland and Scandinavia into southwest Greenland c. 900 AD and disappeared c. 1400 AD, occupying only fjords in

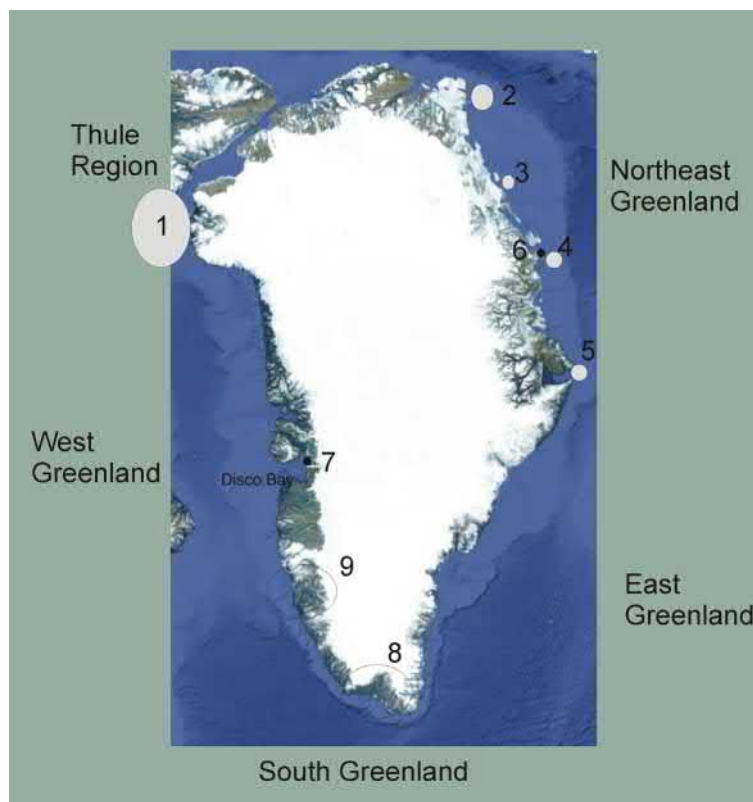


Fig. 1 The regions of Greenland. (1) the North Water polynia, (2) The Northeast Water polynia, (3) The Ile-de-France polynia, (4) The Sirius Water polynia, (5) The Scoresbysund polynia, (6) Walrus Island, (7) Sermermiut, (8) Norse colonization in South Greenland, (9) Norse colonization in West Greenland. Graphics by M. Sørensen.

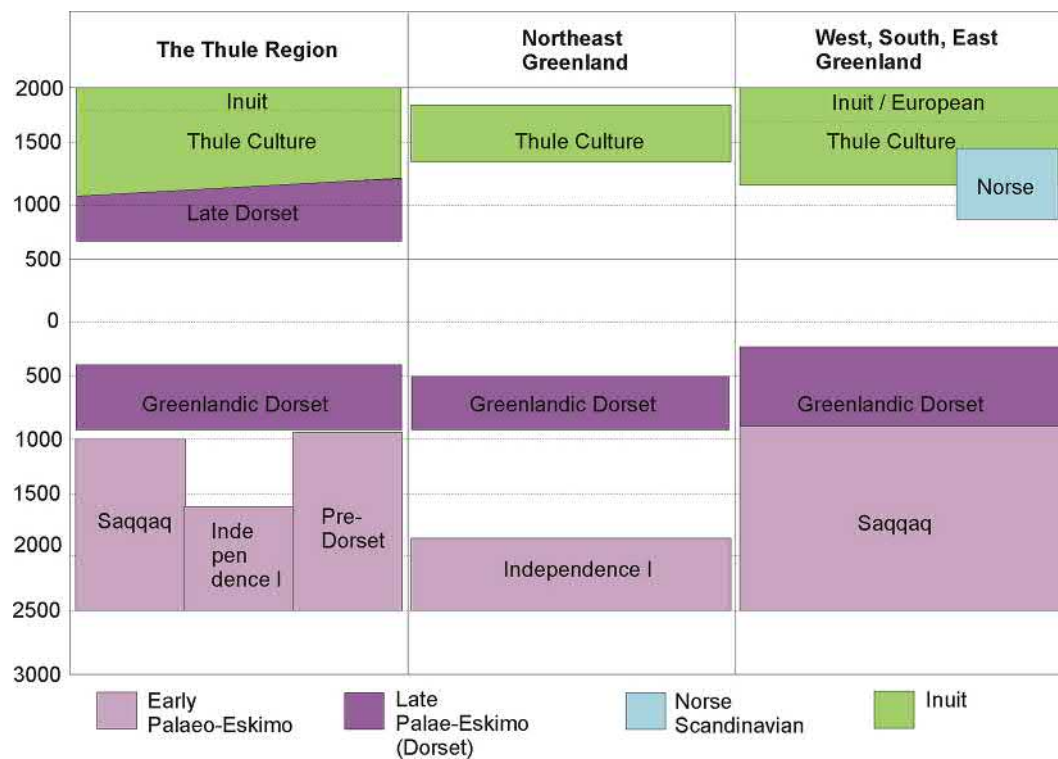


Fig. 2 Chronology of human habitation of the different regions of Greenland. Graphics by M. Sørensen.

South- and Southwest Greenland (see [Figs. 1 and 2](#)). The Inuit group arrived c. 1200 AD into Greenland via the Thule region, and is the only of these three occupations that has endured to the present day. This group is archeologically defined as the Thule Culture and dated from the 12th century AD until the 18th century AD when the European colonization of Greenland took place (see [Fig. 2](#)). From the 16th century AD and onwards, European explorers and whalers regularly had contact with the Thule culture Inuit of western Greenland, while the Inuit populations of East and most northern Greenland was first encountered by Europeans as late as the 19th and early 20th century. Danish colonization of West Greenland began in 1721 and ended officially in 1953, and has strongly influenced Greenland's society and culture. Today Greenland is an autonomous constituent country of the [Kingdom of Denmark](#). The modern culture of Greenland can be understood as a unique globally influenced hybrid between traditional European and Arctic cultures.

Cultural Preconditions to Live in the Arctic and Arctic Hunter-Gatherer Societies

There are several technological and social inventions that are crucial to sustain life in the most northern biome ever inhabited by humans. High Arctic Greenland is characterized by c. 4 months of winter darkness and 4 months of constant light during summer. The Arctic landscapes and the fauna change radically through the seasons, from a landscape with open sea and modest vegetation to a complete icescape, where sea ice cover ties land and water together, facilitating long distance travel for humans. Clothing, heating, hunting equipment, architecture, logistics, social organization and ideology are among the factors that need sophisticated development in order to survive in these regions. Remarkably, humans developed a life style in which specific knowledge and sophisticated technologies made it possible to live in the high Arctic for the past 4500 years.

The Palaeo-Eskimo People

The Palaeo-Eskimo people were organized in small mobile groups that were able to carry all their goods including tents with a size of 3×4 m in ground plan ([Andreasen, 2003](#); [Odgaard, 2003](#)). This mobile organization enabled this society to exploit resources at particular favorable places, often far apart, during the seasons. The hunting of marine and terrestrial resources is well documented from food remains found in frozen middens and from excavated tent ruins in many areas of Greenland ([Grønnow and Jensen, 2003](#); [Grønnow, 2017](#); [Jensen, 2006](#)) and from excavated tools and weapons that reveal great specialization. At the Qeqertasussuk site at the island of Qeqertasussuk in Disco Bay, well preserved hafted artifacts dating back to the Saqqaq Culture have revealed one of the most sophisticated prehistoric hunter-gatherer tool technologies, consisting of no less than nine hafted compound tool types with specialized use, for example, different lances with foreshafts, harpoons with toggling harpoon heads, atlatl, three-pronged bird darts, bow and arrow ([Grønnow, 2017](#)). Remnants of what is interpreted as boat frames from kayak-like vessels have also been found at the Qeqertasussuk site. The presence of summer camp sites on islands further suggest that the Palaeo-Eskimo people went to sea in simple vessels ([Grønnow, 2017](#)). Saqqaq sites in west Greenland also have evidence of the earliest blubber lamps in the eastern Arctic, made from sandstone and steatite, thus documenting that marine mammal blubber was used as fuel for heat and light as early as 2000 BC ([Grønnow et al., 2014](#)).

The Thule Culture

The Thule culture has been documented archeologically and historically to have been extremely well adapted to the Arctic world, employing much the same toolkit as the Palaeo-Eskimo cultures ([Whitridge, 2016](#)). However, in addition, the Thule culture brought many inventions with them from Beringia, making them the most advanced hunter-gatherer society to have occupied Greenland ([Holtved, 1954](#); [Morrison, 1999](#)). Among these inventions are the umiak, a skin boat up to 10 m long that can carry a large crew. This boat was used for transportation and for large whale hunting. Other advanced equipment included a dry suit made from animal skins. The hunting of large whales and other marine mammals allowed the High Arctic Thule culture to produce food, not only for themselves, but also for sled dogs. The large dog-driven sledge is thus another technology not seen earlier in the Arctic. It provided the Thule culture with superior logistic capabilities. The high seasonal mobility of the Thule culture also affected their architecture ([Whitridge, 2016](#)). In the winter, turf and stone built semisedentary houses were constructed. Supplies could be transported to these lodgings from hunting expeditions or meat caches. During winter journeys, snow houses (igloos) were employed as temporary shelters. During summer, tents of light portable construction were used.

The Thule Region—A Magnet for Prehistoric Migrations

To understand the human history of Greenland it is necessary to address their motivations for making long distance migrations into new lands. More than any other region in Greenland, the Thule region of the northwest holds the key to our understanding of the first migrations. Biologically, the Thule region is characterized by the "North Water polynia" (see [Fig. 1](#)), an open water area between Ellesmere and Ingfield land, formed where sea currents of the polar basin meet upwelling waters from the Atlantic, a process that creates open nutritious waters almost year round, despite extremely low air temperatures ([Schledermann, 1980](#)). The "North Water" is accessible both from the Thule region and from Ellesmere, linking these areas together both biologically and culturally. The North

Water polynia supports a vast marine fauna, including large mammal species such as narwhal, belugas, walrus and bowhead whales. Further, the polynia supports millions of sea birds such as little auks and thick-billed murre. These nest in seaside colonies, fertilizing the land by their guano and thereby creating improved conditions for grasses and a mammal fauna, such as hares, foxes, reindeer and muskoxen (Hastrup et al., 2018). Thus the Thule region is a High Arctic larder of resources that has attracted humans throughout prehistory. Because of this, the Thule region has by far the most complicated human history of Greenland. Prehistoric Arctic hunter-gatherers have frequently passed through this area. Archeological investigations have revealed no less than seven culturally different occupations by Arctic hunter-gatherer societies in the Thule region (Sørensen, 2010, 2012b; Grønnow and Sørensen, 2006; Hastrup et al., 2018). On the other hand, there have also been times when the Thule region appears to have been devoid of human occupation, for example, from around year 200 BC to c. 700 AD (Grønnow and Sørensen, 2006).

The first human occupation of the Thule region, and therefore of Greenland, took place during the middle of the 3rd millennium BC with the arrival of the Saqqaq, the Independence I and the Pre-Dorset cultures (Grønnow and Sørensen, 2006; Sørensen, 2010) (see Fig. 2). Since the 1950s, ancestors to these Early Palaeo-Eskimo groups have been considered the Denbigh Culture in the Bering Strait region, due to resemblances in lithic technology and artifact morphology. This idea has recently been supported with ancient human DNA (aDNA) data, suggesting a Palaeo-Eskimo origin in the Bering Strait region and Siberia (Tackney et al., 2016). The absolute dating of early Palaeo-Eskimo archeological contexts in the Thule region indicates occupations from 2500 to 200 BCE, and again from c. 700–1200 AD. However, a continuous population history cannot be reconstructed for these intervals, because it appears that there were many migrations between Canada and Greenland by different groups with slightly different material culture during this interval. Around c. 800 BCE, a Palaeo-Eskimo group of Late Pre Dorset origin arrived in the region, developing into what is today termed the Greenlandic Dorset. Around c. 200 BCE, this group disappeared, not only from the Thule region but from the whole of Greenland. Thus the island appears to have been devoid of humans for at least 800 years (Jensen, 2016). Around 700 CE, a Late Dorset Palaeo-Eskimo group migrated into the Thule region from low arctic Canada (Appelt et al., 2016) and in the 12th century the Thule culture arrived, subsequently defined as the Ruin Island phase and the Classic Thule culture (Lemoine and Darwent, 2016). It is convincingly argued from excavations in Inglefield Land that the Late Dorset and the Thule Culture people encountered each other, and that they lived in the region concurrently for more than a century (Appelt and Gulløv, 1999, 2009). Moreover, it has been argued from European artifacts found in Late Dorset and Thule culture contexts that Norse people also made their way to the Thule region (Appelt and Gulløv, 2009). The Thule culture people in the Thule region were encountered by Europeans for the first time by John Ross in 1818 at Cape York.

Northeast Greenland—A Vulnerable Place to Live

The region of Northeast Greenland topographically comprises the areas of northern Greenland south to Scoresby Sund Fjord, where the steep 500 km long Blossville coast forms a natural barrier from East Greenland. Northeast Greenland is climatically defined as High Arctic desert, having little precipitation and average summer temperatures below 5°C. Similarly to the Thule region, a number of polynias appear along this coast, driven by sea currents and winds. From a cultural standpoint, the most important of these are the “Northeast water,” the “île-de-France polynia,” the “Sirius water” and the “Scoresby Sund Polynia” (see Fig. 1) (Sørensen and Gulløv, 2012; Sørensen, 2013). The region also is characterized by large inner fjord areas where relatively fertile vegetation and terrestrial mammals can be found (Bennike et al., 2008). The resources of Northeast Greenland are similar to those described for the Thule region. However, the coastal waters are not as nutrient-rich as those along the coasts of West and Northwest Greenland, and the sea mammal populations are therefore generally smaller in Northeast Greenland. Conversely, the terrestrial fauna (reindeer and musk oxen) enjoy better living conditions, but the biological productivity of the region is argued to have been fluctuating through time. This historical phenomenon is also known from other Arctic regions, occasionally making terrestrial resources scarce and prehistoric habitation vulnerable. Substantial archeological and interdisciplinary field work in the region has demonstrated three prehistoric occupations: the Independence I culture, the Greenlandic Dorset culture and the Thule culture (see Fig. 2) (Grønnow and Jensen, 2003; Sørensen and Gulløv, 2012). Further, it has been demonstrated that the archeological remains of these occupations are very often discovered at the very same locations in the vast landscapes of the region, pointing to similar hunting and resource strategies. In other words, a good hunting campsite is a good hunting campsite, regardless of the cultural period.

The history of human occupation of Northeast Greenland is closely linked to the Thule region but it is less complex and far more discontinuous than that of the Thule region. The first migration into the region appeared c. 2500 BCE by Palaeo-Eskimo people, defined as the Independence I culture. The archeologist E. Knuth, who was the first person to uncover Palaeo-Eskimo habitations in the region, defined their migration as the “musk ox way,” due to evidence of musk ox bones in excavated ruins at Peary Land (Knuth, 1967). However, later research has demonstrated that many of the Independence I habitations were actually placed at locations near polynias where there were reliable marine mammal resources. This suggests that the majority of their diet actually was marine. The Independence I occupation of Northeast Greenland lasted not longer than c. 300 years from c. 2400–2100 BCE (Grønnow and Jensen, 2003), based on radiocarbon dating. Thereafter northeast Greenland was devoid of people for around 1300 years, before the second Palaeo-Eskimo migration, the Greenlandic Dorset culture, appeared in the region (Jensen, 2016). Ruins excavated in Pearyland suggest that the Greenlandic Dorset people could have arrived from the Thule region, but as they have a circum-Greenlandic settlement pattern, they may have migrated from East Greenland, instead (Jensen, 2016). The Greenlandic Dorset settlements in Northeast Greenland are mostly found at coastal locations along the northeast coast. At the island Il-de-France, a Greenlandic Dorset site, not less than several hundred settlement structures have been identified, making this site the

largest known Palaeo-Eskimo site ever recorded (Grønnow and Jensen, 2003). Even though these habitations were not all occupied at the same time, they suggest seasonal aggregations of a hitherto unknown size, suggesting a specialized social and economic strategy in Northeast Greenland. It is thought that large marine mammals, for example, walrus or belugas, were hunted corporately here. Similar but smaller Greenlandic Dorset aggregation sites have been found at all the polynias along the coast of Northeast Greenland (Sørensen, 2013). Radiocarbon dating suggests that the Greenlandic Dorset occupation in Northeast Greenland lasted not more than a few hundred years, at most c. 500 years. Afterwards, Northeast Greenland was devoid of human occupation, this time for at least 1600 years. Most of the Greenlandic Dorset settlement structures are identified by their tent rings, often with mid-passage features. However, two other types of habitation structures are also recognized. The first evidence of snow house construction in Greenland is provided by the presence of triangular pavements and “cleaned” circular compressed ground areas with artifacts scatters. Neither of these features have tent rings, hence their interpretation as snow house structures (Sørensen, 2013).

The Thule Culture Inuit arrived in Northeast Greenland c. 1400 AD. That their migration came from the Thule region is well documented by similar artifact morphologies and the diagnostic umiak (an 11 m. long skin boat) with artifact inventory dated to the 15th century, found at Herlufsholm Strand. This site is situated on the most northeastern coast of Peary Land (Knuth, 1980). The Thule culture in Northeast Greenland developed particular cultural characteristics, for example, a harpoon shaft with proximal wings, flat harpoon heads and house architecture with recesses in the front wall (Sørensen and Gulløv, 2012). It is argued that these characteristic material traits were borrowed or inspired not only from the Thule culture in Thule but also from the Punuk culture of Alaska and from the late Dorset culture (Gulløv, 2004:311). The Thule culture winter habitation clusters in the southern area of the region have often been found on southern coastal slopes. Large habitation sites were particularly placed near where large marine mammals are known to gather for example, the Sirius polynia and the Scoresby sund polynia. However, many smaller settlements have also been found in the inner fjords where ringed seals can be caught on the fast ice and terrestrial mammals are known to appear (Gotfredsen, 2010). Similar to what was seen in the Palaeo-Eskimo culture, the importance of the polynias is paramount to the Thule Culture. At the 2 km long Walrus Island in the Greenlandic Sea, 118 temporary Thule culture tent foundations, 70 stone build shelter constructions, 479 small stone build caches (size of a seal), 459 large caches (size of walrus or larger), and several large aggregation structures from communal hunting have been recorded at the hostile boulder field terraces (Grønnow et al., 2011) (see Fig. 1). A similar site with numerous caches is located at Scoresby Land near the Scoresby Sund polynia (Sandell and Sandell, 1991). The Walrus site and other polynia sites show that a key strategy for the people of the regional Thule Culture was to hunt and create a surplus of food and fuel from large marine mammals, that is, walrus, large seals and whales, at particular favorable hunting sites close to the recurrent polynias. The Thule Culture diet in prehistoric Greenland has been investigated by faunal analysis and isotopic studies of human bones. The results show that the diet in Northeast Greenland was more terrestrial-based than in any other region of Greenland (Gulløv, 2012).

During the 19th century the Inuit population of the region gradually decreased and it contracted in the southern Scoresby Sund area before it finally disappeared (Sørensen and Gulløv, 2012). It is unknown why the population disappeared, but small scale migrations have been documented south into East Greenland, suggesting that at least some people left the area. Other arguments focus on the cooling of the little ice age (LIA), that made living conditions unfavorable in the region. Another suggestion is that European large whale hunting in the Greenland sea during the 17th century diminished the whale population to such degree that this food resource disappeared from Northeast Greenland. The cause of the regional abandonment remains unknown, yet these peoples' living for almost 500 years as an isolated population in a High Arctic environment, considering the vulnerability of such a population, is a remarkable achievement.

West, South and East Greenland—The Land of Plenty and of Cultural Encounters

West and South Greenland comprises the most fertile regions of Greenland and has the most continuous human habitation history. From north to south the climate zones are arctic and subarctic. The regions are characterized by coasts, fjords, large islands and archipelagos with diverse and abundant marine resources and a rich avian fauna. However, Central West Greenland also holds Greenland's largest unglaciated inland areas, where herds of reindeer are numerous, even today.

Probably the most important regional archeological site is the Sermermiut site in Disco Bay, where stratigraphy reveals occupations of Saqqaq, Greenlandic Dorset and Thule Cultures up to historical times (see Fig. 1) (Larsen and Meldgaard, 1958). Saqqaq sites with permafrozen middens have been excavated (see above) at Disco Bay, and these middens have also yielded the first human remains from Greenland: a lump of hair from a human male. The hair was DNA-sequenced, revealing genetic similarities to modern populations from the Bering Strait region (Rasmussen et al., 2010). This strengthens the archeological interpretation that human migrants from the Bering region were the first pioneers in Greenland. The Saqqaq people populated and traveled along all parts of the coasts in West and South Greenland. From an archeological perspective, they employed a very conservative and static lithic technology during their entire habitation, in which a large number of carefully manufactured, primarily bifacial lithic tool types, were produced. These were manufactured by means of direct soft techniques, pressure tool technique and grinding. The conservative nature of the technology also included the choice of lithic raw materials chosen for lithic tools. Burins, adzes and bifacial tools were generally made from dark, tough, silicified slates and schist, while scrapers and pressure blades were generally made from fine grained microcrystalline quartz such as agates, chalcedony and rock crystal (Sørensen, 2012b). In West Greenland, a particular lithic raw material source, located at the “Nuussuaq” peninsula north of Disco Bay, was systematically employed, at least up to 800 km from its outcrop. This raw material is a metamorphosed slate termed “killiaq.” The primary use

of this raw material suggests that Saqqaq society, at least in some periods, had a social network through which they regularly traded over very long distances (Jensen, 2006; Sørensen, 2012b).

The main prey taken by people of the Saqqaq Culture was the same as all the other of hunter-gatherer societies of the Eastern Arctic: marine fauna and especially seals. This has been documented from preserved faunal materials at sites with organic preservation (Meldgaard, 2004), and also inferred from the fact that their settlement locations most often are found in landscapes with good access to seals. However, inner fjord and inland sites with remains of preserved reindeer bone demonstrate that inland hunting, probably conducted by bow and arrow, was part of their economy (Grønnow et al., 1983). The dating of the Saqqaq culture reveals that they existed in the regions from c. 2400–800 BCE, that is, about 1600 years. From radiocarbon dating and regional analysis there is evidence that the Saqqaq Culture left the rich Disco Bay area, and possibly also areas in south and east Greenland, to relocate in central West Greenland (Jensen, 2006), where the youngest occupation dates occur at the Nipisat site in the Sisimiut area (Gotfredsen and Møbjerg, 2004). Around c 800 BCE, evidence for the Saqqaq culture disappeared completely. Yet, at the same time a group of Early Dorset, deriving from the Predorset Culture in Canada, arrived in the Thule region and down into West Greenland. This Dorset group, formerly termed the Independence II or the Dorset 1 culture, is now termed the Greenlandic Dorset. It represents the second cultural habitation of West Greenland, and it is possible that this Dorset culture encountered the very last people of the Saqqaq culture in central West Greenland (Jensen, 2016). The Greenlandic Dorset Culture employed many of the same coastal settlement sites that were used by the Saqqaq people, while evidence for inland occupation is scarce (Jensen, 2006). Their lithic technology comprises many of the same methods and techniques seen in the early Palaeo-Eskimo cultures. However, there are also significant differences in their technology. Their raw material choice was more flexible and generally without long distance import; they did not produce arrow heads and drills, they produced many micro blades of high quality, and the shape of their bifacial tools is different (Sørensen, 2012b). Radiocarbon dating shows that the Greenlandic Dorset people lived in West Greenland for around 800 years. Around the year 1 AD, they disappeared completely and the region seemingly became unoccupied for around c. 1000 years.

The Norse people of Scandinavian and European origin next settled West Greenland, and more particularly in the fjords of South Greenland and in the Inner Nuuk fjord in West Greenland (Arneborg, 2008). From radiocarbon dating and Saqa literature it can be deduced that they must have arrived c. 985 AD, and that they initially migrated from Iceland. Unlike any earlier people in Greenland, the Norse people were farmers, employing land for agriculture, primarily pasture for cows and sheep. The Norse were part of a North Atlantic European society, and they maintained regularly contact with Europe throughout their Greenland occupation. A key technology that enabled the Norse people to sail to Greenland was their clinker-built sea going long ships with square sails. With these vessels they were able to maintain contact with Europe and make expeditions to other parts of Greenland as well as to North America. An important trade ware was walrus tusk that the Norse exported to Europe, replacing elephant tusk which was not available in Europe during the early middle ages (Dugmore et al., 2007). The Norse disappeared from Greenland in the 15th century. It is not known why they abandoned Greenland, but the cooling of “the little ice age” made their pastoral lifestyle untenable. There was also a general contraction of the North Atlantic societies due to the Black Death. These two explanations are considered the most likely.

Around 200 years after the Norse arrived in Southwest Greenland the Inuit of the Thule Culture arrived in West Greenland from the Thule region (see Fig. 2) (c. 1200 AD). There are no signs of Inuit settlements in the fjords and regions where the Norse lived during their stay in Greenland (Gulløv, 2007, 2008). Thus, the archeological material as well as the saqa literature provide no evidence that Inuit and Norse people had strong relations in Southwest Greenland. On the contrary, their possible few encounters seems to have been hostile. The Inuit traveled all around Greenland and inhabited most coastal fjords and areas with their mobile lifestyle, except those of the Norse, until after the 15th century.

During the 16th and 17th century European explorers and whalers had regular contact with Inuit people. During the 17th and the first part of the 18th century, whalers, especially Dutch whalers, traded regularly and annually with the Inuit at Disco Bay (Gulløv, 2016). Based on historical sources and archeological material, this trade with Europeans was very attractive to the Inuit. The Dutch trade initiated Inuit seasonal journeys from South and East Greenland to Disco Bay. This activity lasted several years. One of the major changes in Inuit life and society, the communal long house, was introduced in this period. It is argued that this architectural innovation was a consequence of the trade journeys, reflecting the large size of the journeying groups (Gulløv, 1997). Thus, while the cooling of the little ice age probably was a great disadvantage to Norse farmers, it seems not to have had negative impacts on Inuit hunting societies living in the same environments that the Norse abandoned (Sørensen, 2012a). This paradox cannot be explained simply by the difference in economies, as the Norse were able to catch many marine species, and they did so increasingly during their occupation of Greenland (Arneborg et al., 2012). Culture and identity are important parameters to any people and society, and the fact that the Norse people lost trading and contact to Europe, and probably could not proceed as successfully with pasturing livestock, must have seriously endangered their identity and existence as Norse people.

With the Danish colonization of Greenland the history of Greenland, and particularly West Greenland, completely changed. The colonization started in 1721 and was led by the priest Hans Egede. A network of colonial trade stations and churches was established along the coasts of West Greenland where seagoing vessels could enter. As a consequence, the Inuit increasingly made permanent settlements at the trade stations during the 18th century, and thereby lost their traditional mobility and their economic independence. Christianization increasingly changed their traditional societal structure and religion. With the colonization of Greenland, people became dependent on imported food and most other materials as they adopted the European lifestyle. Thus, even though the biomes of Greenland have endured almost intact through the history of human habitation, the delicate interplay and human dependency on the sea and land and its resources have become increasingly altered since Danish

colonization. Today traditional hunting is foremost a hobby to most Greenlanders and only in the Thule region and few other places in West and East Greenland are some people still living from full time hunting. Greenland is today a modern nation and state with c. 56,000 inhabitants and a strong national identity.

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Antarctic Climates

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Abstract

Antarctica is the coldest, driest, windiest, and highest continent in the world. The harsh conditions of this remote continent are a major challenge for all species which inhabit these areas. Inland elevated areas of the Antarctic Plateau present extreme cold and dry conditions. Coastal areas of the continent are milder; however, they are subjected to strong katabatic winds flowing from the plateau. Climate conditions over the Antarctic Peninsula are less severe and wet which support well-developed plant communities including vascular plants. West Antarctica is now undergoing great changes, the large warming occurred in the second half of the 20th century and the basal melting produced by the intrusion of relatively warm ocean water are driving an unprecedented ice retreat and new ice-free areas are emerging, providing new opportunities and challenges for Antarctic biota. This will ultimately result in changes of coastal Antarctic ecosystems.

Physical Geography

Antarctica is the southernmost continent in the world and it is centered asymmetrically around the geographic South Pole and surrounded by the Southern Ocean (Fig. 1). Its entire territory covers an area of 14 million km² that lies south of 60°S of which only a 0.3% is deglaciated. Almost the whole continent is covered by an enormous ice sheet that contains more than 26×10^6 km³ of ice, an amount equivalent to about 58 m of sea-level rise (Fretwell et al., 2013). The ice sheet has an average thickness of about 2.1 km, making Antarctica the highest continent in the world. The continent is geographically divided into two by the Transantarctic Mountains: East Antarctica and West Antarctica. East Antarctica is a wide and high territory with semicircular shape that is almost totally within the Eastern Hemisphere. West Antarctica is smaller than East Antarctica in height and extension and is irregularly shaped. Its northernmost tip ends with a large peninsula called the Antarctic Peninsula. Hereafter West Antarctica and Antarctic Peninsula will be discussed separately.

On both sides of West Antarctica lie two massive floating platforms of ice called the Ross Ice Shelf and the Filchner-Rone Ice Shelf. These extend from grounded glaciers on land and flow down onto the ocean. Ice shelves range from 100 to 1000 m thick and there are many more smaller ones surrounding most of the Antarctic coasts. Unlike ice shelves, sea ice is thinner, only few meters thick. When the sea surface freezes in winter, the continent doubles its extension (Fig. 2). On its maximum extension in September, sea ice extent covers almost all of the sea area south of 60°S. Sea ice cover has a seasonal regime. Antarctic sea ice is almost totally melted in summer, reaching its minimum extent in February. Consequently, unlike Arctic sea ice, the Southern Ocean is mostly covered in winter by only first-year ice that is less than 1 m thick.

Large-Scale Circulation

Radiative balance in Antarctica is negative. This is produced because outgoing longwave radiation is uncompensated by incoming shortwave radiation. In Antarctica, annually averaged shortwave radiation incomes are low, owing to the large solar zenith angles and the high albedo of the snow cover. Despite the cold surface, outgoing longwave radiation at the top of atmosphere is relatively large due to the dry polar atmosphere. The resulting negative radiation budget should be restored by a poleward energy flux. The ultimate consequence of the large-scale circulation of the oceans and the atmosphere is the poleward transfer of heat that restores the energy budget.

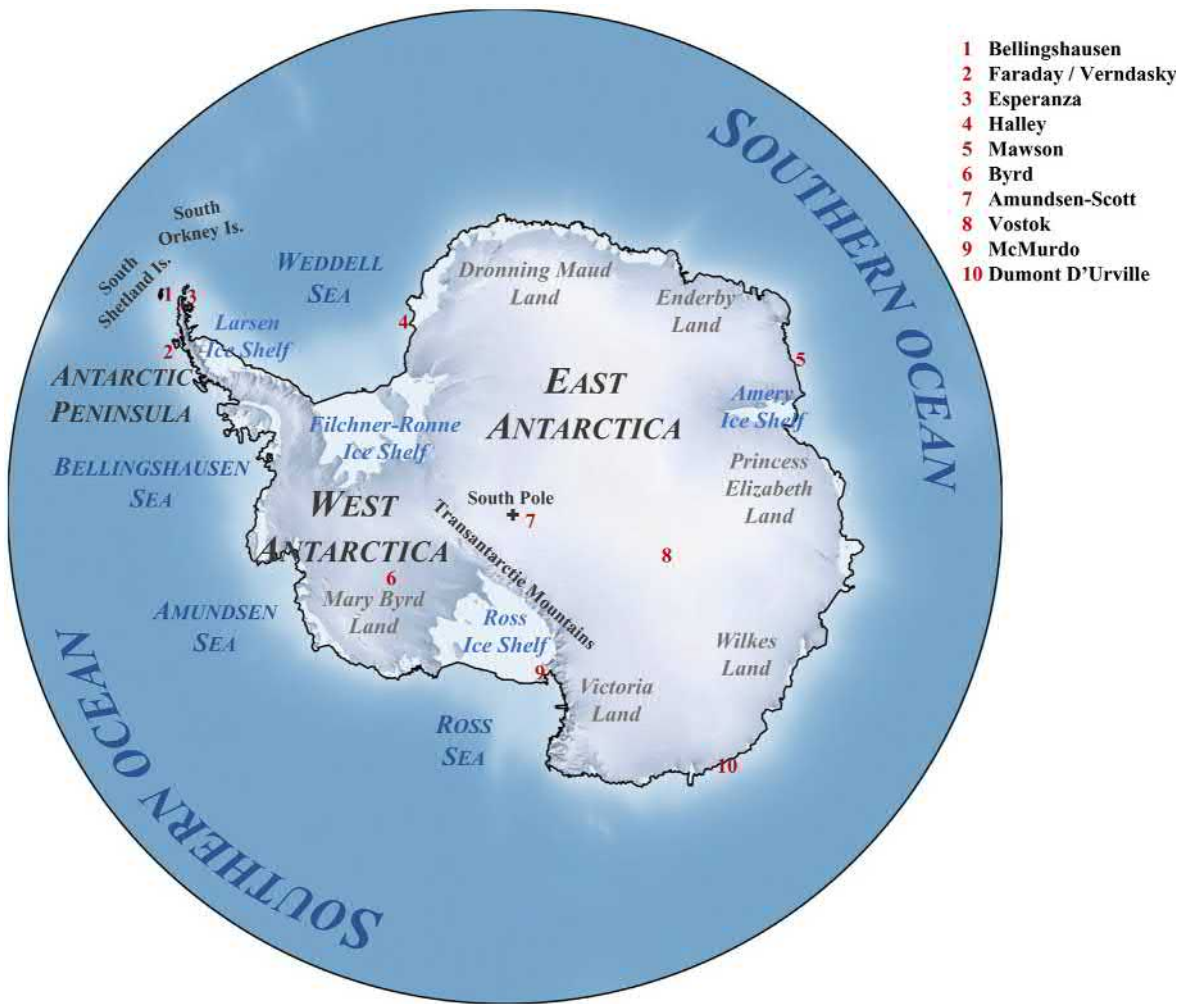


Fig. 1 Map of Antarctica with the locations referenced in the text.

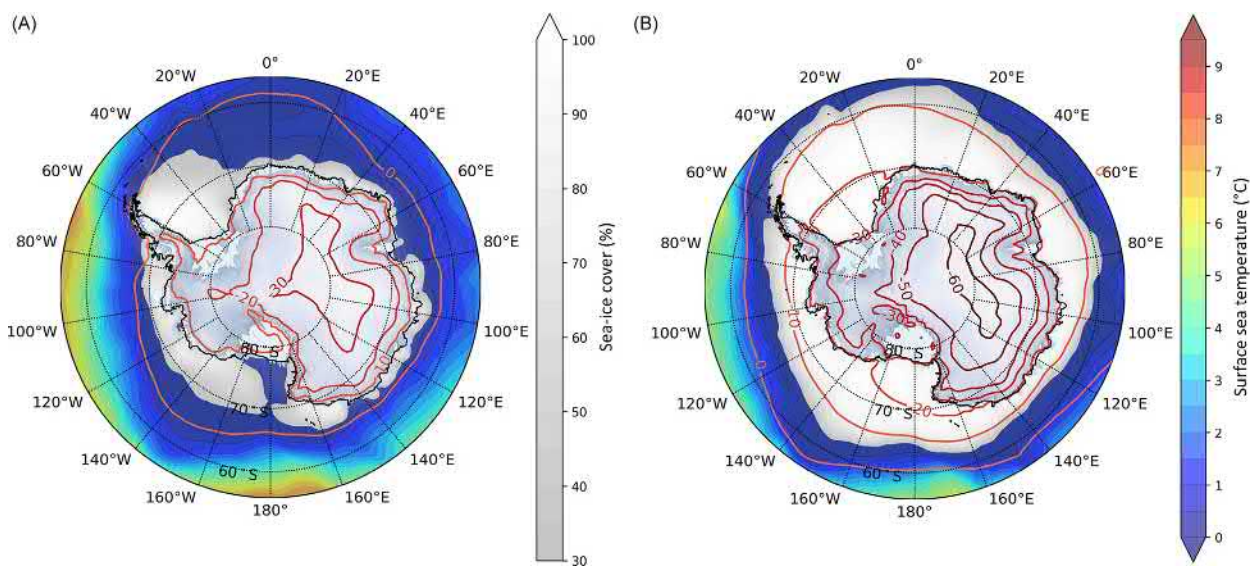


Fig. 2 Mean surface air temperature (2 m over surface) and sea ice extent in (A) summer (December–January–February) and (B) winter (June–July–August).

The Southern Ocean is connected with the major oceans of the planet and plays an important role in Earth's climate system. The most dominant feature of the Southern Ocean is the Antarctic Circumpolar Current that flows eastward around Antarctica due to the momentum applied by the strong westerly winds. Westerlies also induce a northward Ekman transport near the surface of the Southern Ocean. Following this movement, cold Antarctic water in the south meets and sinks under the relatively warmer Subantarctic water at the Antarctic Convergence. Annually averaged, meridional heat transport contribution by overturning circulation is directed northward while horizontal gyres and transient eddies of the Southern Ocean contribute to the southward meridional heat transport (Spence et al., 2012). The total contribution of the Southern Ocean to the meridional heat transport is directed southward; nonetheless, most of the poleward heat transfer in the southern high latitudes is led by the atmosphere (Trenberth and Caron, 2001).

The Antarctic continent is centered approximately inside the thermally direct atmospheric polar cell of the tricellular large-scale atmospheric circulation system. Therefore, cold air subsides over the continent by gravity and flows near the surface to lower latitudes while turning to the west due to the Coriolis force caused by Earth's rotation. Around the continent, cold continental air converges with the temperate marine air, creating a strong horizontal thermal gradient that develops several low-pressure areas around the continent where the air is able to uplift to the high troposphere. In order to restore the air drained to the north on the surface, the air risen at the polar front flows back aloft to the pole, closing the loop of polar circulation. Through this process, the atmosphere effectively transports heat to the pole and balances the net radiative loss of heat of the continent.

The ring of low-pressure systems that encircle the Antarctic continent from 60°S to 70°S is known as the Antarctic circumpolar trough (Jones and Simmonds, 1993). It is one of the most active cyclonic areas of the world. On any day, the Antarctic continent is surrounded by several cyclones (Fig. 3). As the low-pressure systems turn clockwise in the Southern Hemisphere, there is a climatological belt of westerlies north of the circumpolar trough and easterlies south of it. Cyclones generally track eastward with a small southward component over the Southern Ocean off the Antarctic coast. Often, cyclones turn to the south where they provide relatively warm and moist air and precipitation, but they can barely penetrate onto the plateau, except on very rare occasions. The Antarctic circumpolar trough is not zonally symmetric, but it has a climatological wave number 3 pattern. That is, the circulation makes three waves around the South Pole, with the cyclonic centers close to 30°E, 100°E, and 150°W (Fig. 4A). The latter is known as the Amundsen-Bellinghousen Seas low, and is the most pronounced. The meridional temperature gradient has two maxima around the equinoxes. Because of this, the Antarctic circumpolar trough contracts and deepens southward in spring and autumn and weakens and displaces northward in summer and winter in a movement known as Semi-Annual Oscillation that affects the whole atmospheric circulation of the continent (van Loon, 1967).

In addition to the synoptic-scale cyclones, mesoscale cyclones are frequent over the Southern Ocean. Mesoscale cyclones, also called polar lows, are defined as cyclones with less than 1000 km diameter and a lifetime shorter than 24 h (Rasmussen and Turner, 2003), but satellite imagery has shown that most of them have a horizontal diameter less than 500 km and may exist in a wide range

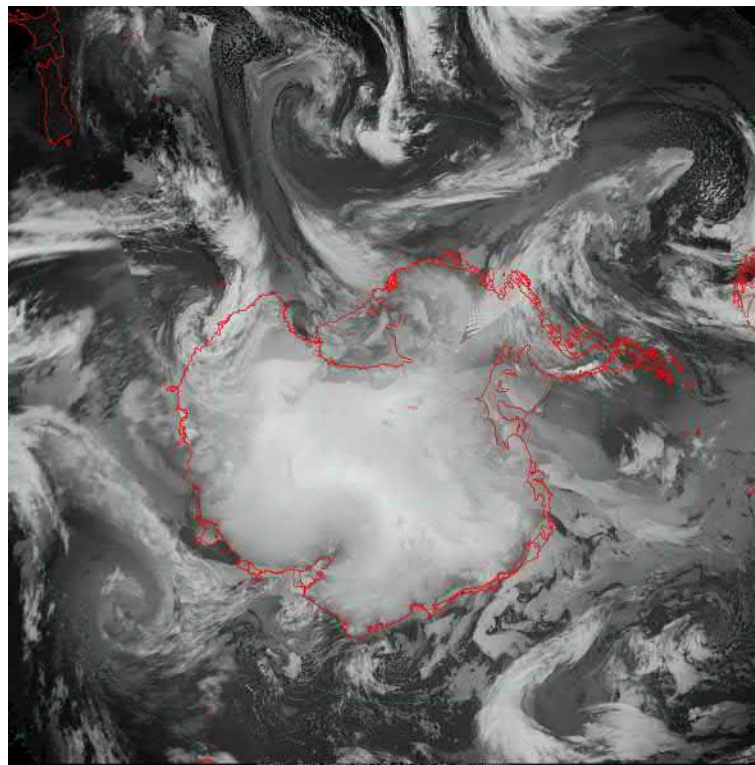


Fig. 3 Satellite Antarctic Infrared composite on 2 Mar 2019 at 19:00 UTC. Provided courtesy of UW-Madison SSEC AMRC.

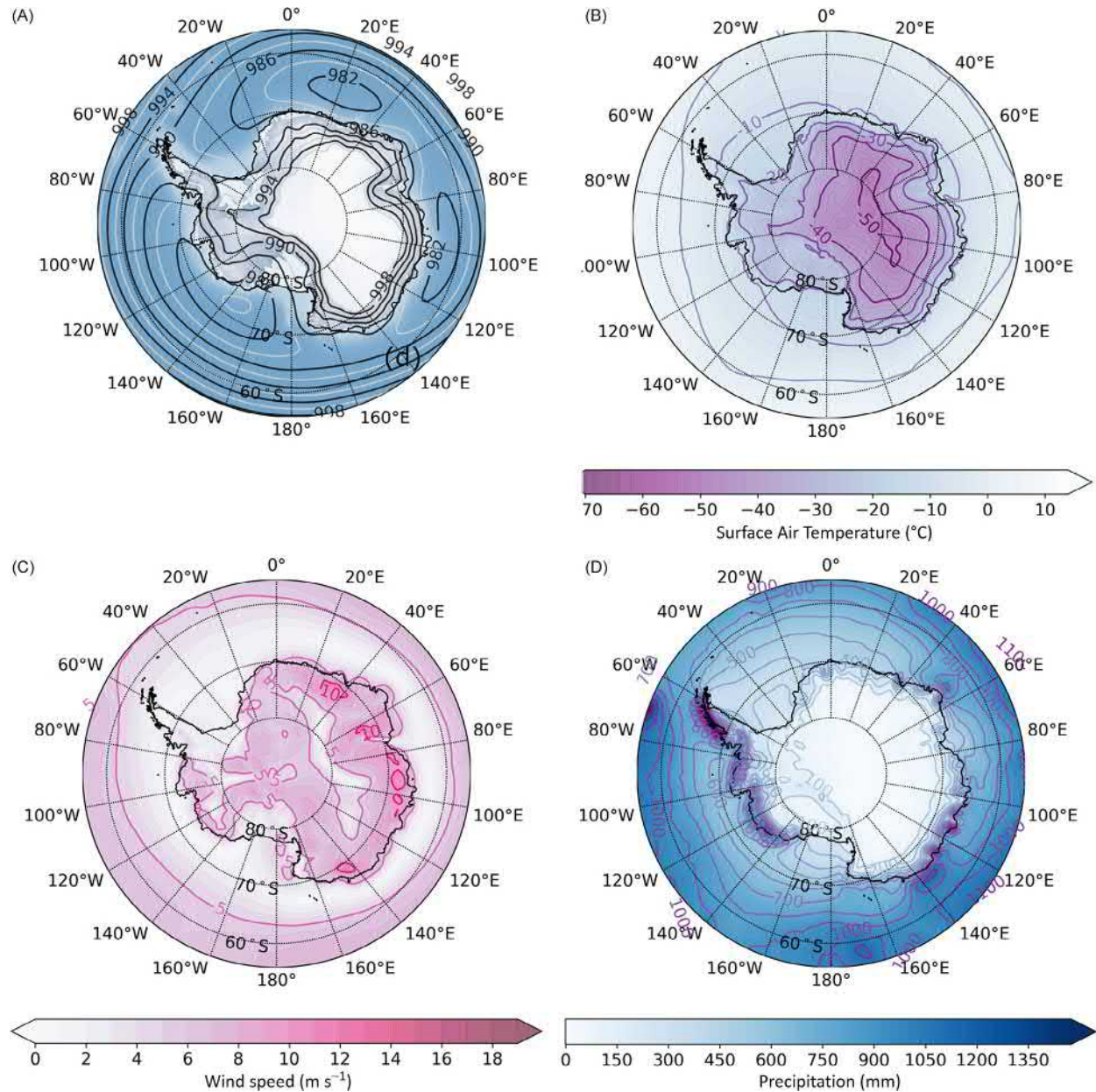


Fig. 4 Annually averaged values of (A) mean sea-level pressure [not plotted above 3000 m], (B) temperature, (C) wind speed, and (D) precipitation from the ERA-Interim.

of time scales, from few hours to several days. Despite their small size and short life, mesoscale cyclones have an appreciable influence over the Antarctic coasts, due to their high wind speeds and associated increased precipitation. Climatologically, in the Southern Hemisphere their maximum density is located at 5–10° north of the Antarctic sea ice, with maxima over the Amundsen and Bellingshausen Seas and off the coast of Wilkes Land (Irving et al., 2010). Their maximum activity is in autumn while the lowest activity has been observed in spring (Irving et al., 2010).

Climatic Regions in Antarctica

Overview of the Climate of Antarctica

Antarctica is the coldest, windiest, and driest place on Earth. Those conditions are the result of the continent's location and height. Most of Antarctica is characterized by a polar climate (category ET) in the Köppen climate classification, except for some coastal areas of the Peninsula that have a tundra climate (category EF) that is, at least a month with an average temperature above 0°C.

Mean annual temperature in Antarctica decreases with latitude, due to the angle of incidence of the solar radiation on the Earth's surface. Of course, the temperature also decreases with altitude. This means that the coastal regions of the Antarctic Peninsula are the warmest areas and the high ice domes of East Antarctica are the coldest places of the continent (Fig. 4B). The high surface albedo of the ice and the radiative cooling of the continent also contribute to the low temperatures of the inner lands.

Indeed, winds over the continent are highly influenced by the radiative cooling of the ice cover. The air, very cold and dense, drains downslope by gravity, enclosed in a layer <1000 m thick with the maxima between 100 and 200 m (Parish and Bromwich, 2007). These winds are known as katabatic winds and they overlap and dominate over the polar cell described in "Large-Scale Circulation" section (Fig. 5). Katabatic winds are weak over the domes and flow perpendicular to the height levels and increase with slope angle, blowing hard and rather constantly over the coastal areas, especially in winter (Fig. 4C). By contrast, winds over the Antarctic Peninsula and Southern Ocean are dominated by the mobile cyclones as they pass over the area, and when wind directions are averaged, they tend to come from the west and northwest.

Often it is hard to identify clouds in Antarctica, either because of blowing snow, very thin cirrus cloud cover, or the absence of daylight in winter. Satellite imagery provides no better solution, due to the similarity of the bright temperatures of the snow and clouds. However, the combination of observational, satellite studies and computer simulations has been able to discern the cloud structure of the continent. The western side of the Antarctic Peninsula and the continental coast are extremely cloudy areas throughout the year with dominant low stratiform clouds and fog. Conversely, cloudiness is scant in the inner plateau and dominated by thin cirrus clouds that do not obscure the sky.

Precipitation is also difficult to measure in Antarctica because it falls mainly in form of snow that is prone to be deflected by the wind as it falls into precipitation gauges. Measurements of snow on the ground are also unreliable because the snow is often redistributed by wind after falling. Nonetheless, recent precipitation measurements indicate that mean annual precipitation derived from reanalysis is a reliable estimate (Palerm et al., 2017). The corrected estimates indicate that precipitation is abundant in the coastal areas but is scarce over the plateau, which is essentially a frozen desert (Fig. 4D).

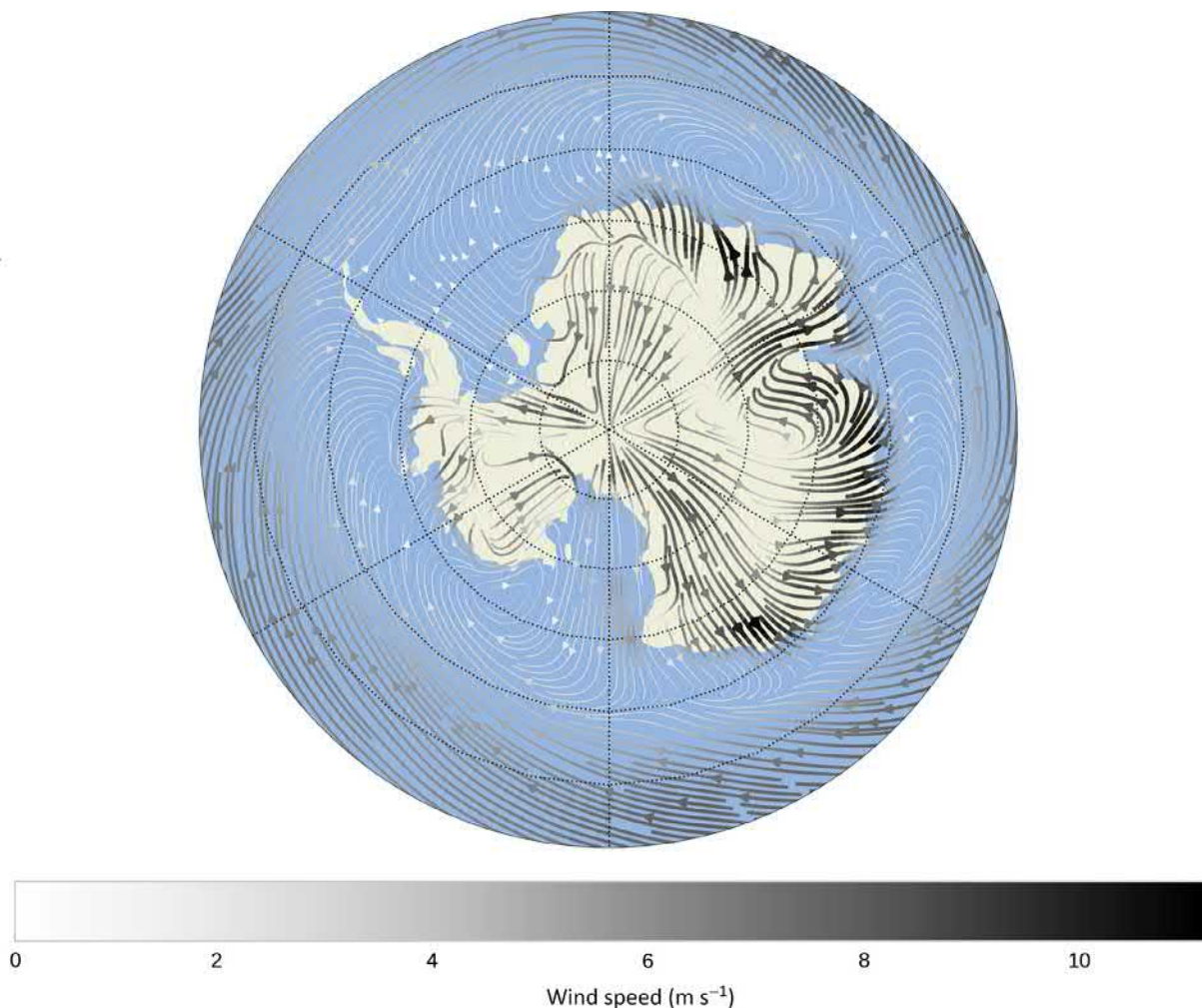


Fig. 5 Annually averaged surface wind streamlines over Antarctica from ERA Interim. Width and color represent the mean wind speed.

Due the homogeneity of the continent, the climate of Antarctica is very uniform. Nonetheless it is worth to classify the climate of Antarctica into three different regions: peninsula, continental coast, and continental plateau, each of which exhibits special features.

Antarctic Peninsula

The Antarctic Peninsula (AP) is the wettest and the mildest area of Antarctica and it is broadly located outside the Antarctic polar circle. Its climate is known as maritime Antarctic and it is able to support well-developed moss and lichen communities, liverworts, and the only two Antarctic species of vascular plants. The vegetation grows in the relatively abundant deglaciated areas (Longton, 1967). Different kinds of marine mammals and sea birds and few insect species live on the coasts. Unlike the rest of the continent, it has a very complex orography and many small islands. Almost all the territory is located near to the sea. The sea provides a moisture source to the area, and when it is not covered by ice, the difference between day and night temperatures becomes reduced. However, the mountain range orientated in the north–south direction, perpendicular to the prevailing westerlies, causes a sharp variation in weather conditions between the western and eastern side (WAP and EAP) of the AP. A third region subjected to little different conditions is the South Shetland and South Orkney Islands, located in the Southern Ocean at the northern tip of the AP.

AP localities near the sea are characterized by having several months with mean temperature above 0°C in summer. In particular, summer temperatures exceed 0°C on the Southern Ocean islands for 3–4 months of the year (see Bellingshausen in Fig. 6A), at WAP for 2–3 months (see Faraday/Vernadsky in Fig. 6B) and at EAP for 1–2 months (see Esperanza in Fig. 6C).

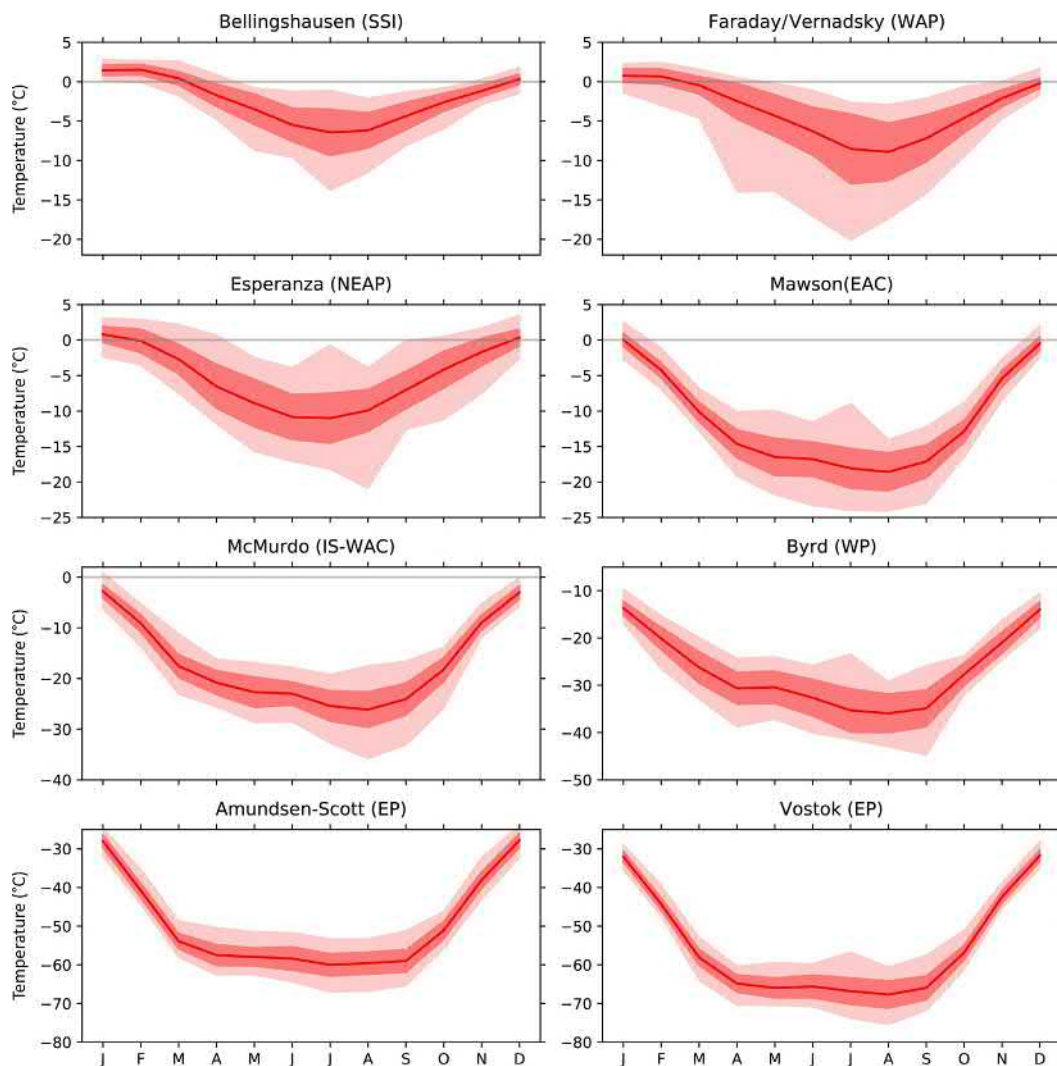


Fig. 6 Monthly Surface Air Temperature at different stations with their location in parentheses. SSI: South Shetland Islands, WAP: West Antarctic Peninsula, NEAP: North-East Antarctic Peninsula, EAC: East Antarctic Coast, IS-WAC: Ice Sheet—West Antarctic Coast, WP: Western Plateau, EP: Eastern Plateau. Source for the data used in creating the figure: RADER station surface data Turner, J., Colwell, S.R., Marshall, G.J., Lachlan-Cope, T.A., Carleton, A.M., Jones, P.D., Lagun, V., Reid, P.A., Iagovkina, S., 2004. The SCAR RADER project: Toward a high-quality database of mean Antarctic meteorological observations. *Journal of Climate* 17, 2890–2898. doi:10.1175/1520-0442(2004)017<2890:TSRPTA>2.0.CO;2.

variation is less than 10°C on the Southern Ocean Islands with winter mean temperatures between −5 and −10°C. Farther south at the WAP, annual thermal variation increases because of the region's isolation from moisture sources, caused by sea ice cover in winter. But it is on the EAP where winter temperatures are colder, due to the even further isolation from moisture sources, caused by the mountain range, the Larsen Ice Shelf, and the often-iced Weddell Sea. In this area, mean annual temperature variation exceeds 15°C. Throughout the AP, temperatures may present sharp variations due to the cyclonic conditions, as polar front waves progress, and warm or cold air is advected. On any given day, even in winter, temperatures may reach 0°C.

Wind speeds at the AP vary widely as they are associated with the frequent cyclones that cross the area. However, when their direction is averaged, the AP is subject to climatological westerly winds associated with the circumpolar trough. Westerlies have a seasonal behavior due to the Semi-Annual Oscillation, being stronger at the equinoxes and weaker at the solstices, when the circumpolar trough contracts (equinoxes) or extends (solstices) (van den Broeke, 1998; van Loon, 1967). Westerlies are often blocked by the AP mountain range, but when they have sufficient velocity to overtake the barrier they lose their moisture on the windward side of the range and flow dry and warm downslope on the leeward side (Parish, 1983). These winds are known as foehn winds, and play a crucial role on the surface melting of the EAP ice shelf (Elvidge et al., 2015). When winds flow from the east, the damming up of cold stable air against the mountain ranges creates strong northward winds that run parallel to the mountains on the EAP (Parish, 1983).

The AP is a very cloudy area, especially over the islands and on the western side, where mean cloud cover is over 80% in any month. As moisture coming from the west is released on the windward side of the mountain range, cloudiness decreases sharply in the EAP. At the moment, reliable precipitation measurements are not yet available for the Antarctic Peninsula. However, model reanalysis and satellite data suggest that precipitation may exceed 800 mm year^{−1} in many places on the WAP (Palerm et al., 2014). Precipitation is also greater on the Southern Ocean islands, especially those with high mountains. Conversely, precipitation decreases sharply on the EAP, due to the moisture blocking of the AP mountains. Autumn is the wettest season because of the contraction of the circumpolar trough, and therefore the increase of the cyclonic conditions coincides with moisture sources of the still-open seas. In summer, much precipitation over the AP falls as rain.

Continental Coast and Ice Shelves

The low lands and ice shelves of the rest of the continent are influenced both by inland dry and cold air and by the more temperate and moist air from the Southern Ocean. At East Antarctica and some parts of West Antarctica, the ice sheet rises in elevation relatively quickly, roughly at 200 km inland of the coast. In contrast to this, the large flat and low Ross and Filchner-Ronne ice shelves extend hundreds of kilometers inland. Except for small ice-free areas called the Antarctic oasis, most of the coast is covered by glacier ice or ice shelves. On some of these ice-free areas moss and lichen communities may be found. The major ice-free area of the continent is the McMurdo dry valleys, on the west side of the Ross ice shelf. These valleys constitute a cold dry desert of about 4500 km² (Fountain et al., 2010).

Mean temperatures at the East Antarctic coast are higher than those of the West Antarctic coast located further south. Temperatures at all the research stations situated on the eastern coast share similar temperature records (here Mawson is plotted in Fig. 6D). At these stations, mean monthly temperatures may exceed 0°C in December or January when open waters are close to the coast. In winter, mean temperature remains above −20°C. At the southern coasts of West Antarctica and the Ross and Filchner-Ronne ice shelves (see McMurdo in Fig. 6E), summer mean temperatures are about −5°C and winter temperatures fall between −25°C and −45°C. During winter, the temperature over the inland ice sheets may fall below −60°C (Costanza et al., 2016). Research stations at the continental coast, as well as those over the plateau, experience a coreless winter (van Loon, 1967), that is, temperature decreases quickly in autumn and remains almost constant throughout the winter. This is produced by different causes, among which is constant radiational forcing during the dark season enhanced by the low heat conductivity of the snow and circulation changes.

All the Antarctic coast experiences katabatic winds descending from the plateau (Fig. 5). Those winds are very constant in direction and very strong (Parish and Bromwich, 2007). They usually reach the maximum velocity at 200 km inland and then slowly decelerate by friction along most of the coast. Katabatic winds are persistent, stronger in winter than in summer, and can blow over 10 ms^{−1} for weeks. The katabatic regime at the coast is modulated by the surrounding cyclones, being suppressed by southward cyclonic winds, and enhanced by northward cyclonic winds, as lows approach, or move away, respectively (Parish and Bromwich, 1998). Cape Denison, near Dumont d'Urville, is believed to be the windiest place in the world with mean annual winds around 20 ms^{−1} (72 km/h) (Wendler et al., 1997). Once the wind reaches the coast it suffers a hydraulic jump, sharply decreasing its velocity offshore. Katabatic discharge also helps in creating conditions to generate mesocyclones on the Antarctic coasts. Katabatic flow also produces barrier winds at the Transantarctic Mountains side of the Ross ice shelf when statically stable air interacts with the mountain range (Costanza et al., 2016; Parish et al., 2006).

Clouds are frequent over coastal areas and are often associated with synoptic-scale weather systems. Cloudiness varies little with the seasons. Moisture sources for cloud or fog formation and precipitation in summer come from the near-to-the-coast open sea. However, in winter the ice edge is far away from the coast. Nonetheless, the action of katabatic winds on the sea ice generate unfrozen areas next to the coast, called polynyas (Bromwich and Kurtz, 1984); these open water areas may provide moisture to sustain winter clouds and precipitation. Snowfall measurements indicate that precipitation on the East Antarctic coast averages between 300 and 900 mm year^{−1} (Souverein et al., 2018). Precipitation aloft is higher but most of it is sublimated by the strong katabatic winds (Grazioli et al., 2017). Precipitation levels are not evenly distributed along all the coastal areas; there are preferential

areas. Coastal zones located east of the climatological lows in such locations as Enderby and Wilkes land, where northern winds are more common, receive more precipitation than those coasts located further west, such as Dronning Maud and Princess Elizabeth lands, which are more prone to have southerlies due the position of the cyclonic centers of the circumpolar Antarctic trough (Bromwich, 1988). Most of the precipitation falling on the East Antarctic coast occurs in a few large events. These storms account for more than 70% of annual precipitation and are associated with atmospheric rivers (Gorodetskaya et al., 2014).

Antarctic Plateau

Antarctic plateau is the coldest place on Earth. It consists of an elevated, ice-covered desert located in the inner continent. The terrain is flat and homogeneous, with slight negative slopes that increase from the high interior to the coast. Two differentiated regions can be distinguished: the relatively small and low West Antarctic plateau and the higher and wider East Antarctic plateau. These two regions are divided by the Transantarctic Mountains. The East Antarctic plateau has three high altitude domes with elevations of 3810 m (Dome F), 3233 m (Dome C), and 4093 m (Dome A), from north to south respectively. The geographic South Pole is located on the East Antarctic ice sheet, but near the boundary with the West.

Mean annual temperatures on the Antarctic ice sheet vary with altitude. Thus, the West Antarctic Plateau (see Byrd in Fig. 6F) experiences warmer temperatures than the East Antarctic Plateau (see Amundsen-Scott in Fig. 6G and Vostok in Fig. 6H). Because the West Antarctic plateau is lower in elevation than the East Antarctic plateau, the former is more prone to intrusions of marine warm and moist air than the latter. Coreless winter conditions are more pronounced here than in coastal areas, where even a winter temperature reverse may occur in May or June (Thompson, 1969). Summer mean monthly temperatures reach -10 to -15°C at Byrd Station; they average -25 to -30°C at Amundsen-Scott Station, and -30 to -35°C at Vostok. From March to September, mean temperatures fall to -25 to -40°C , -50 to -65°C , and -60 to -70°C , at Byrd, Amundsen-Scott and Vostok stations, respectively. The lowest near-surface air temperature on Earth was recorded in Vostok, with -89.2°C (Turner et al., 2009).

The Antarctic Plateau wind field is dominated by katabatic winds constrained in direction and speed by topography (Fig. 5). They are generally calm over the Antarctic Domes and flow downward perpendicular to the height level and accelerating with slope. Wind fields have a seasonal variability, being slower from December to February than in winter months (Parish and Bromwich, 2007). The net northward air mass flux is restored by a broad scale subsidence owing to the polar cell.

Over the Antarctic Plateau there is a fine veil of ice crystal clouds (cirrus). These clouds are semitransparent, and almost perpetually cover the sky. This makes it difficult to determine whether the sky is cloudy or clear (Turner and Pendlebury, 2004). The Antarctic Ice Sheet is one of the driest areas of the world. Absolute humidity is low because the maximum moisture content of the air decreases with temperature. Precipitation here is scarce and often falls as diamond dust, that is, small ice crystals falling from clear or nearly clear cirrus skies (Turner and Pendlebury, 2004). Snow is quickly redistributed by the wind after falling to the ground.

Climate Change, Ozone Depletion, and Modes of Variability in the Southern Hemisphere

Since the 1970s, climate change over the Southern Hemisphere has been characterized by the radiative cooling of the stratosphere, owing to ozone depletion caused by anthropogenic emissions of chlorofluorocarbons (Solomon, 1999). The ozone reduction over Antarctica is much larger in the southern spring, when approximately half of the total stratospheric ozone over Antarctica declines sharply, producing the well-known ozone hole. As a result, circulation patterns in the lower stratosphere and troposphere have experienced several changes such as a reinforcement of the westerly winds and the poleward movement of the southern polar jet, modifying the climate modes of variability of the Southern Hemisphere (Bandoro et al., 2014).

Climate modes of variability are spatial patterns in which most climate variance can be explained by temporal variations. There are several modes of regional variability around the world but there are two that specially affect the Antarctic climate: the Southern Annular Mode (SAM) and El Niño Southern Oscillation (ENSO):

- SAM is the principal mode of atmospheric variability in the nontropical Southern Hemisphere and it causes large impacts on Antarctic climate (Marshall, 2003). Broadly speaking, SAM represents the zonally averaged latitudinal gradient of pressure, and it controls the latitudinal position of the midlatitude jet. When SAM is positive, pressure is anomalously high over Antarctica and low at the mid-latitudes. When SAM is negative, pressure is anomalously low over Antarctica and high at the mid-latitudes. Positive SAM is associated with the contraction and intensification of the circumpolar westerly wind belt and the poleward shift of the cyclone track. This is linked to warming in the Antarctic Peninsula and cooling in the rest of the continent. The disturbance in the ocean circulation linked to the SAM-related wind patterns may affect regional sea-ice extent (Lefebvre et al., 2004).
- ENSO explains the interannual variability of the equatorial Walker circulation. During the warm phase of ENSO (El Niño Southern Oscillation), the Walker cell weakens or reverses, resulting in a very little upwelling of cold water in the eastern equatorial Pacific and warmer than average ocean temperatures. In the cold phase (La Niña), the Walker cell strengthens and the ocean cools. Tropical convection related to ENSO, together with other factors, such as the zonally asymmetric structure of the SAM, produces a tropospheric wave train that strengthens the Amundsen-Bellingshausen Seas Low during the ENSO cold phase and weakens it during the ENSO warm phase. This strongly affects the climate of the Antarctic Peninsula and the Ross sector of the continent (Fogt and Bromwich, 2006).

Temperatures over different research stations throughout Antarctica show large annual variability as they are very sensitive to the different climate modes of SAM and ENSO, and the position of the Amundsen-Bellinghousen Seas Low (Hosking et al., 2013). In summer, temperatures in coastal areas show weak variability due to the damping effect of the open water (Monaghan et al., 2008). This contrasts with the high variability of the temperatures recorded during the cold season in coastal areas. These temperatures are highly dependent on the extent of sea ice cover and the proximity of open water (including the formation of polynyas). Regional ocean circulation and air-sea-ice feedbacks also play key roles and contribute to increasing temperature variability of the continent.

Temperatures over the Antarctic Peninsula also show long-term natural variability, that is large persistent cooling or warming trends consistent with natural variability. Still, this area has undergone a large warming since mid-20th century, with a linear trend over $+0.3^{\circ}\text{C}/\text{decade}$ followed by a slight cooling during the first years of the 21st century (Gonzalez and Fortunyn, 2018). 20th century warming is linked to regional changes in troposphere circulation, due to the increase of northerly winds and cyclonic conditions. These changes are caused by the shift in position and strength of Amundsen-Bellinghousen Seas Low and the positive trend of the Southern Annular Mode in response to greenhouse gases increasing and stratospheric ozone depletion (Marshall, 2007; Raphael et al., 2016). Those changes also yield to an unprecedented warming over the West Antarctic region during the second half of the 20th century. This region is one of the most rapidly warming places of the world (Vaughan et al., 2003). Conversely, East Antarctica has not shown any warming during this period. Actually, this region exhibited a slight cooling trend since 1958 that may be attributed to internal climate variability (Smith and Polvani, 2017), atmospheric circulation changes related to ENSO (Clem et al., 2017) or to the recently discovered negative greenhouse effect (Schmithüsen et al., 2015).

Antarctic Future

Recent satellite measurements showed that the Antarctic ice sheet is losing ice and that the rate of ice loss is increasing (Shepherd et al., 2018). Ice loss is uneven over the continent; while East Antarctica may slightly gain some ice, the Antarctic Peninsula and especially West Antarctica ice sheets are thinning quickly. Most of the ice sheets are confined by ice shelves near the sea. If these shelves collapse, ice sheet thinning would rapidly increase the rate of ice loss. The southern progression of the summer 0°C isotherm is contributing to ice sheet retreat in the Antarctic Peninsula, occasionally leading to catastrophic breakup due to hydrofracturing driven by surface melting such as Larsen B collapse in 2002 (van den Broeke, 2005). However, surface temperature is not the main driver of West Antarctic ice sheet thinning. Here, most of the thinning is in the bottom of the ice shelves due to the basal melting produced by the intrusion of relatively warm ocean water into subshelf cavities (Shepherd et al., 2018). This results in the retreat of ice sheet grounding lines and in reduced basal traction, both of which speed up the thinning process. The rate of deep-water intrusion is controlled by wind stress and direction on the surface.

Climate projections predict a rapid retreat of the Antarctic Peninsula and West Antarctic ice sheets in the near future (DeConto and Pollard, 2016). Certainly, over the next century, large extensions of new Antarctic ice-free areas will emerge, most of them on the Antarctic Peninsula. Many islands may also become totally ice-free. This will result in new habitats and opportunities for both native or invasive biota, and an increase of connectivity (Lee et al., 2017). The most catastrophic scenario would be the collapse of the West Antarctic Ice Sheet. This may occur in the next centuries (DeConto and Pollard, 2016). This scenario would also produce regional changes in atmospheric circulation, along with a 4.8 m rise in global sea level.

Appendix: Supplementary material

Supplementary material related to this chapter can be found on the accompanying CD or online at <https://doi.org/10.1016/B978-0-12-409548-9.11876-7>.

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Further Readings

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Antarctic Terrestrial Biome—Most Poor, Extreme and Sensitive on the Planet

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Abstract

The Antarctic terrestrial biome includes terrestrial vegetation communities and inland aquatic ecosystems of lakes and streams. Its formation relates to the history of the southern supercontinent Gondwana. Before the split of Gondwana and the separation of continents, the Antarctica played an important role as a bridge facilitating the spread of terrestrial ecosystems from South America to Australia and New Zealand. Upon the formation of the Drake Passage, ca. 30–50 million years ago, Antarctica started to cool down and its terrestrial ecosystems mostly perished. Its modern ecosystems are quite simple and harbor limited biodiversity. The ecosystems feature a significant role of prokaryotes, cryptogams and invertebrates. The species composition and biodiversity of the terrestrial biome depend on the biogeographic region. The Antarctic is divided into the richer maritime Antarctic and the much poorer continental Antarctic. Prokaryotes, algae (biodiversity only now being examined) and lichens (totaling ca. 380 known taxa) are the most diverse groups in the Antarctic. There is a substantial degree of endemism among the Antarctic lichens and invertebrates, which could indicate that they are remnants of a pre-glacial flora and fauna. Alongside lichens, community-forming taxa include multiple bryophytes: 27 species of liverworts (*Marchantiophyta*) and 111 species of mosses (*Bryophyta*). The reasons for the extreme poverty of Antarctic vascular plants flora (only two native species) remain unclear. Antarctic terrestrial communities are classified according to the types of vegetation. The environmental role of the Antarctic terrestrial biome lies in the accumulation of organic matter and creation of conditions for terrestrial life in one of the most extreme environments on the planet. Its terrestrial communities are susceptible to climate change and anthropogenic pressure and require constant monitoring and protection in particular by Antarctic Specially Protected Area (ASPA) creation.

Introduction

Antarctic is extremely remote and experiences the coldest temperatures on the planet. Its biome exist in the most extreme environment on Earth, characterized by very low temperatures and lack of accessible water. In this article, we describe the distinctive features of the Antarctic terrestrial biome, which in this work will include terrestrial ecosystems as vegetated areas, as well as lakes and streams. Bacteria, algae, cryptogams and invertebrates dominate here, therefore these ecosystems are rather simple. Because of the harsh environments, Antarctic ecosystems have very low productivity. Their biodiversity is also limited by the remoteness of the region. The diversity of community types is also low due to the narrow range of environmental conditions variations. These traits contrast the terrestrial biome with the high biodiversity of the surrounding Antarctic marine biome. The Antarctic terrestrial biome is among the most susceptible to climate change. Meanwhile, Antarctica is the only one of the Earth's continents not to have a long-term history of human habitation. In view of this, its terrestrial biome requires a delicate approach and protection.

Origin

Since the first appearance of angiosperms on Antarctica in the Cretaceous, more than 100 million years ago (Ma), the Antarctic terrestrial biome has undergone a significant dramatic change (Rees-Owen et al., 2018). The initial stages of vegetation development in Antarctica are unclear due to the absence of a fossil record (Cantrill and Poole, 2012). During the Ordovician glaciation (443–458 Ma), current Antarctica was likely free of ice. During the following Permo-Carboniferous glaciation, exact time of which is debated (ca. 300 Ma), an ice sheet covered most of Antarctica (Smith, 1997). The end of the Permo-Carboniferous glaciation was accompanied by the restoration of mild humid climate and, as a consequence, all of Gondwana was covered by the seed fern *Glossopteris* forests (McLoughlin, 2011). Until 55 Ma, the history of life on Antarctica was very similar to that on other southern continents,

especially Australia. Their respective fossil records are very close, with abundant terrestrial plants and animals. There are abundant plant fossils from this period in many parts of Antarctica. In the late Triassic greenhouse world, the warm climatic conditions promoted a spread of forest vegetation far into the polar regions of southern subcontinental Gondwana (Bomfleur et al., 2014).

In the late Cretaceous a podocarp-southern beech temperate forest spread here (Fig. 1). A low diversity Antarctic tundra flora was dominated by angiosperms in the Neogene (Rees-Owen et al., 2018). Antarctica, including its offshore archipelagos, was covered by continental ice sheets from the Oligocene (ca. 60 Ma) until the Pleistocene (1 Ma). There is paleobotanical evidence that forest existed in Antarctica during the Oligocene and probably until the Miocene (12–23 Ma), relatively complex alpine communities must have persisted around the moister coastal fringes of the continent (Ochyra et al., 2008). The Last Glacial Maximum (LGM) was perhaps the most challenging for biotic survival and most of the biota went extinct. The modern flora and fauna were likely formed in two ways. The endemism of the Antarctic lichens, bryophytes and invertebrates suggests that they survived Pleistocene glaciations in refugia. Studies demonstrate the presence of refugia in continental Antarctica, at least in the Pleistocene (0.01–2.6 Ma), and possibly in the Miocene. In the maritime Antarctic, all low-altitude coastal regions are believed to have been covered by much-expanded glaciers and ice sheets during the LGM, and only reexposed as the ice retreated during the last 10,000 years. However, recent biogeographical studies indicate that this view may be overly simplistic and inaccurate at smaller scales (Peat et al., 2006). Alongside survival in refugia, it is believed that other organisms such as most bryophytes are post-Pleistocene migrants from South America or other regions. Prolonged winds are considered to have been the most important factor of transfer. Occasionally, birds could have served the same purpose. Antarctic soils contain large numbers of bryophyte diaspores that do not germinate (Ochyra et al., 2008). It remains unclear whether vascular plant refugia existed in Antarctica during glacial periods, or whether or vascular plants recolonized the continent from elsewhere, and in the latter case—when it occurred (Parnikoza et al. 2007).

Habitat and Biogeographic Zonation

Only about 2% of Antarctica is free of ice and snow. The Antarctic terrestrial biome occupies only part of this territory and consists of terrestrial ecosystems that are classified according to vegetation type, as well as biotopes of streams and lakes. Local habitat and biodiversity depend on the region of the continent or offshore islands. In terms of biogeographic zonation, Antarctic basically is divided into continental and maritime (Riffenburgh, 2007) (Fig. 2).

The continental Antarctic zone includes both the continent and its offshore islands south of Alexander Island, excluding the western side of the Antarctic Peninsula north of 70 degrees. Continental Antarctica can be divided into Ice Plateau, Slope and Coastal provinces. The Ice Plateau province has extreme continental climate with temperatures averaging less than -15°C in the summer and less than -50°C in the winter. This region receives little precipitation, no rain, and 1–3 months of continuous daylight in summer. The region is practically devoid of vegetation, even lichens, algae's and cyanobacteria. The Slope province has extremely cold and arid climate, with temperatures averaging less than -5°C in the summer and less than -30°C in the winter. Precipitation



Fig. 1 Fragments of fossil tree *Nothofagoxylon antarcticus* Torres (54 Ma) from King George Island. Photo by Ivan Parnikoza.

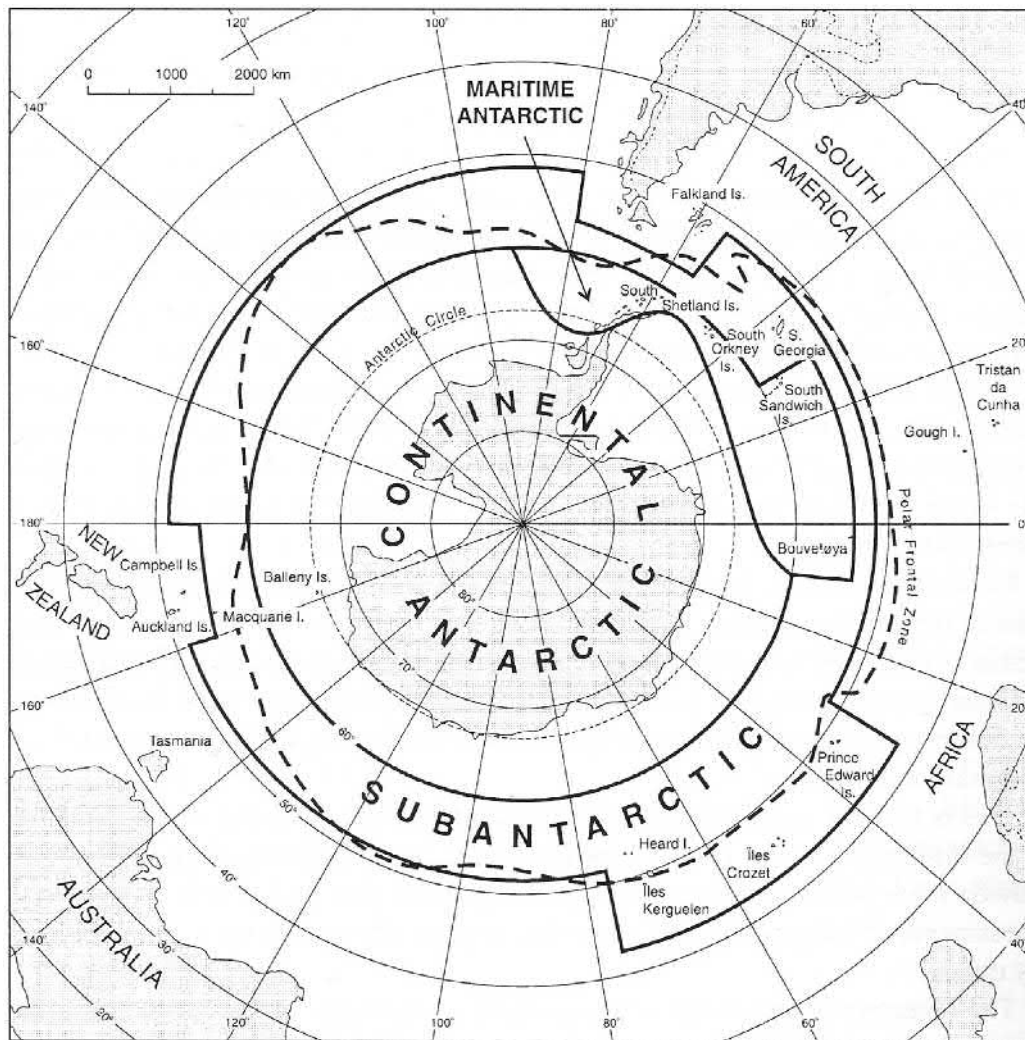


Fig. 2 Biogeographic zonation of Antarctic: Antarctic Southern Ocean, sub-Antarctic Islands, showing the Polar Frontal zone (also known as the Antarctic convergence) showing as a broken line as well as Antarctic biographic zones are indicated. Data from Bednarek-Ochyra, H., Vána, J., Ochyra, R., and Lewis Smith, R. I. (2000). *The liverwort flora of Antarctica*. Cracow: Polish Academy of Sciences, Institute of Botany.

here is less than 100 mm water equivalent, all falling as snow, no rain. There are 1–3 months of continuous daylight in summer. The Coastal province has a cold, arid climate, with monthly temperatures averaging above 0°C for 0–2 months in the summer. Winter monthly means temperatures average from -5 to -25°C with some maritime influence that narrows the temperature range. Precipitation is ca. 100–150 mm water equivalent and rain is very rare. The snow-free period at sea level is ca. 10–15 weeks. The Coastal province is the richest biotically in continental Antarctic, with relatively diverse biota in some regions, such as Joinville Island, Dundee Island, Vega Island, James Ross Island, Seal Nunataks, Cabinet Inlet, parts of the eastern and north-eastern coast of Alexander Island and Charcot Island. Parts of the coastal region of Eights Coast (Thurston Island) have probably the most diverse biota in continental Antarctic (Øvstedal and Lewis Smith, 2001; Ochyra et al., 2008).

The maritime Antarctic divided to northern part, that includes Bouvetøya, South Sandwich, South Orkney and South Shetland Islands as well as western coast of the Antarctic Peninsula to ca. 68° (66 degrees in other source) and southern part, that includes west coast of Antarctic Peninsula from ca. 68° (66 degrees in other source) to 70°S and offshore islands as well as the northeast coast to ca. 64° . The northern part of the region is characterized by a cold moist maritime climate, with mean monthly temperatures averaging above 0°C for 3–4 months in the summer, but rarely less than -10 to -12°C in the winter. The precipitation averages 350–500 mm per year, which mostly falls as rain in the summer. The snow-free period lasts ca. 15–20 weeks. The southern part has a cold dry maritime climate, with mean monthly temperatures averaging above 0°C for 1–3 months in the summer but rarely below less than -15°C in the winter. The precipitation averages less than 350 mm per year with occasional rains. The snow-free period at sea level lasts 12–18 weeks (Øvstedal and Lewis Smith, 2001; Ochyra et al., 2008).

Main Components

The uniqueness of the Antarctic terrestrial biota is that it primarily consists of microorganisms, fungi, algae, lichens, bryophytes, and invertebrates. The biology of Antarctica, more than any other continents, is dominated by microorganisms. Studies reveal a greater diversity of microbes here than had been estimated previously (Tytgat et al., 2014). Species symbiotic with plants occur among the bacteria (Cid et al., 2016). A significant role in ecosystems is also played by cyanobacteria, particularly in continental Antarctica (Pandey et al., 2004).

A substantial portion of the terrestrial and freshwater biodiversity consists of algae. Their biodiversity is only well studied for some regions, in particular for the Argentine Islands, where 78 species and intraspecific taxa of algae are known (Polishuk et al., 2009). Snow algae that use mineral elements from snow and ice are the only inhabitants of continental regions (Davey, et al., 2019). Entire microcommunities of endolithic algae are scattered in continental Antarctica (Broady, 1981).

The Antarctic terrestrial biome also includes fungi, including some specific groups, such as the fungi of cryptoendolithic communities and rock-inhabiting fungi. In the maritime Antarctic, in particular the Argentine Islands region, mushrooms of the genus *Omphalina* occur, as well as parasitic fungi, such as *Nectria antarctica* (Speg.) Rossman (Smith and Corner, 1973; Longton, 1979). Mycorrhizal fungi occur in Antarctica as well (Upson et al., 2008) (Figs. 3 and 4).

Most of the unglaciated regions of Antarctica are dominated by lichens, totaling ca. 380 known taxa. Lichens are dominate the Antarctic biome in a broad range of conditions. Only the wettest patches of cyanobacteria communities lack lichens. The epicenter of lichen biodiversity in Antarctica is the Antarctic Peninsula, harboring 264 taxa. The continental Antarctic, on the other hand, has at least 88 taxa. The small and isolated volcanic South Sandwich Islands have 46, South Orkney Islands has 221, and the South Shetland Islands has 211 taxa. The biogeography of the species is difficult to describe, as the species' distribution is poorly understood. The most species-rich genera include *Buellia* (32 species), *Caloplaca* (29), *Cladonia* (27), *Lecanora* (25) and *Verrucaria* (16). Among the Antarctic lichens, the share of cosmopolitan and bipolar species decreases southwards (Øvstedal and Lewis Smith, 2001).

Bryophytes are another group that characterizes the Antarctic biome, particularly its green part created by vegetation. The bryophytes include the liverworts and mosses. Antarctic flora of liverworts counts 27 species. There are no liverwort species endemic to Antarctica. Biogeographically this group includes 9 sub-Antarctic and 11 south temperate species, together comprising 75% of the Antarctic liverwort flora. 6 bipolar and 1 pan-continental phytogeographical elements are also present (Bednarek-Ochyra et al., 2000).

Antarctic mosses have a total of 111 species and two varieties, which is more than on some sub-Antarctic Islands, regardless of the more favorable climate on islands. The South Shetland Islands are the richest in moss species diversity and in the development of moss communities, harboring 87 species, 12 of which have not been collected from other parts to Antarctica. Some species are only known in Antarctic from the volcanic Deception Island. The moss flora of the eastern shore of the Antarctic Peninsula is rather distinctive. In continental Antarctica 24 species and 2 varieties of mosses occur. 4 species are found only in Antarctic continent. The biogeographic distribution is as follows: Antarctic endemics—11 species, sub-Antarctic species—18, south temperate—26, bipolar—50, cosmopolitan—5, tropical—1. Therefore, bipolar taxa dominate. Only five species of bryophytes collected beyond 80°S, all in the trans-Antarctic mountains, southern Victoria Land. Some species grow above the 1000 m elevation (Ochyra et al., 2008).

Vascular plants that define the face of biomes on other continents are only represented with two species in Antarctica, *Deschampsia antarctica* É. Desv. and *Colobanthus quitensis* (Kunth) Bartl. For comparison, the sub-Antarctic flora includes near 70 native species

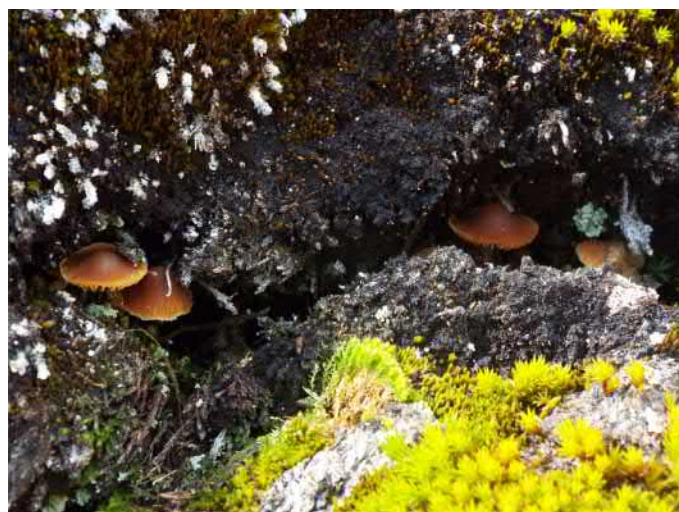


Fig. 3 Mushroom *Omphalina* sp., Oasis Rasmussen, Graham Land, 2019. Photo by Ivan Parnikoza.



Fig. 4 Parasitic fungus *Nectria antarctica* on moss *Sanionia georgicouncinata* (Müll. Hal.) Ochyra & Hedenäs, Western Corner Island, the Argentine Islands, 2016. Photo by Ivan Parnikoza.

of vascular plants, Falklands/Malvinas—about 170 species. In the Northern Hemisphere, Svalbard had 173 species of vascular plants. Overall, the Arctic flora incorporates 900 native species. The reason for the extreme paucity of vascular plants flora in Antarctica remains unclear (Ochyra et al., 2008). In fact, alien vascular plant species outnumber the flora of Antarctica. These include *Poa annua* L., *P. pratensis* L. and *Nassauvia magellanica* J. F. Gmel., probably transferred to the continent by humans. Diasporas of other species have been reported from soils in places of high human activity (Fuentes-Lillo et al., 2017).

Invertebrates dominate the fauna of the terrestrial biome, both terrestrial and freshwater types. According to a generalizing study by Russell et al. (2014), the soils of the Antarctic Peninsula harbor 11 species of collembolan, 23 species of actinedid mites, 5 species of oribatid mites, 4 species of gamasin mites, and 39 species of nematodes (Fig. 5). The Antarctic midge (*Belgica antarctica*) is a native endemic species of Chironomidae associated with vegetation (Convey and Block, 1996) (Fig. 6). Invertebrate diversity is the result of local abundance of organic matter in the soil and the development of vegetation. Overall, ca. 30 bdelloid rotifers, ca. 70



Fig. 5 Collembolan *Cryptopygus antarcticus*, Fanfary Island, the Argentine Islands, 2016. Photo by Ivan Parnikoza.



Fig. 6 Antarctic midge *Belgica antarctica*, Grotto Island, the Argentine Islands, 2016. Photo by Ivan Parnikoza.

monogonont rotifers, ca. 70 nematodes and 62 tardigrade species are known from the entire Antarctic region (Velasco-Castrillón et al., 2014; Vecchi et al., 2016). These small numbers of identified species lead us to suspect that most of the microinvertebrates in this region are still unknown. Close to 90% of the known continental Antarctic species and almost 50% of the maritime Antarctic mesofauna are endemic (Russell et al., 2014).

Communities

Terrestrial communities of Antarctica are classified on the basis of their plant communities. Plant communities, in turn, significantly change along the north-south gradient. In the north of the region, in particular on the Southern Shetland Islands, they form continuous areas which may be described as Antarctic tundra. Here, vegetation covers wet depressions which are free of snow as early as November and through late March. In Antarctica, the ecological optimum for Antarctic hairgrass is likely located in the vicinities of Point Thomas Oasis (King George Island), where the most developed communities occur (Komárková et al., 1985). Some 400 km south from King George Island on the Argentine Islands, vegetation already exists only on elevated above the snow level patches, thus vegetation period in some seasons goes on from January to half of March. In the meantime, local habitat variations, such as microclimate and local impact by animals greatly influence vegetation. As a result of these factors, communities of different degrees of resilience may be found within single regions.

Vegetation classification for the Antarctic terrestrial communities was developed on the basis of the composition of bryophytes and lichens species (Smith and Corner, 1973; Øvstedal and Lewis Smith, 2001; Ochyra et al., 2008). The *Short moss turf and cushion subformation* is prominent. According to a different approach, this community that includes rock fruticose lichens defined as *Fruticose lichen and moss cushion subformation* (Smith and Corner, 1973). In the maritime Antarctic, it is the variant with *Usnea antarctica* Du Rietz—*Umbilicaria antarctica* Frey & I. M. Lamb. as well as *Andreaea* mosses that forms compact cushions (Fig. 7).

The *Tall moss turf subformation* is represented by assemblages of mosses with turf growth-form, some communities of which accumulate peat up to more than 1.5 m deep with permafrost about 20–30 cm below the surface, usually colonized by crustose and fruticose lichens (Ochyra et al., 2008). These communities of *Polytrichum strictum* Brid. and *Chorisodontium aciphyllum* (Hook. f. & Wilson) Broth. form moss banks that occupy large areas (which allows mapping them) (Fig. 8). The oldest moss banks are known from Elephant Island of the Southern Shetland Islands Archipelago and are believed to be ca. 5500 years old (Björck, 1991). A variant of this community, the *Campylopus association*, in Antarctic occurs exclusively on thermal patches of South Sandwich Island (Longton, 1979).

Communities formed predominately by pleurocarpous mosses of shallow turf-like carpet and prostrate mat growth-forms and similar forms of foliose and thallose liverworts are wide spread on moist soils named the *Bryophyte carpet and mat subformation* (Figs. 9 and 10). The more sporadically represented community of high hummock mosses *Bryum pseudotriquetrum* (Hedw.) P. Gaertn., B. Mey. & Scherb. and *Brachythecium austrosalebrosum* (Müll. Hal.) Kindb. is designated as the *Tall moss cushion (hummock) subformation* (Smith and Corner, 1973; Ochyra et al., 2008).

The crustose lichen community—*Crustose lichen subformation* is also wide spread in Antarctic (Fig. 11).

Among the communities dominated by algae, two types are defined: the *Alga subformation* (a community of terrestrial algae) and the *Snow alga subformation* (Figs. 12 and 13).



Fig. 7 Fruticose lichen and moss cushion subformation, *Usnea aurantiacoatra* (Jacq.) Bory association on the Fildes Peninsula, King George Island, 2019. Photo by Ivan Parnikoza.



Fig. 8 Tall moss turf subformation—*Polytrichum strictum* and *Chorisodontium aciphyllum* moss bank, Berthelot Island, Graham Land, 2019. Photo by Ivan Parnikoza.

Vascular plant communities are classified as the *Antarctic herb tundra formation*, in particular the *Grass and cushion chamaephyte subformation* (Smith and Corner, 1973) (Figs. 14–16).

In Antarctica, the ecological processes of vegetation succession are practically absent; although a gradual development of some community from colonization by the most enduring species up until others settle the prepared substrate does take place (Longton, 1979). Probably only radical habitat changes can trigger whole community exchange.



Fig. 9 Bryophyte carpet and mat subformation, a drier variant with *Sanionia georgicouncinata*. Skua Island, the Argentine Islands, 2016. Photo by Ivan Parnikoza.



Fig. 10 A wetter variant of the Bryophyte carpet and mat subformation with *Warnstorfia fontinaliopsis* (Müll. Hal.) Ochyra, Southern part of Uruguay Island, the Argentine Islands, 2016. Photo by Ivan Parnikoza.

Freshwater streams, subglacial and subaerial lakes (wherever they are brackish) form a separate component of the terrestrial biome in Antarctica. Some lakes in high latitudes have a permanent ice cover. Most of the biomass of Antarctic non-marine ecosystems accumulates in lakes. The main phototrophs in Antarctic inland waters are cyanobacteria (*Phormidium*, *Oscillatoria*, *Lyngbya*, etc.), flagellates such as *Cryptomonas* and *Chroomonas* (*Cryptophyceae*), *Ochromonas* (*Chrysophyceae*), *Clamidomonas* (*Chlorophyceae*), *Pyramimonas* (*Prasinophyceae*) as well as *Chlorococcaleans* such as *Ankistrodesmus* and *Schroederia*. In particular, cyanobacteria are the most abundant component of the freshwater ecosystems in Antarctica (Bargagli, 2005) (Fig. 16).



Fig. 11 Crustose lichen subformation at Brown Bluff, the Tabarin Peninsula, 2016. Photo by Ivan Parnikoza.



Fig. 12 Alga subformation, Brown Bluff, the Tabarin Peninsula, 2016. Photo by Ivan Parnikoza.

They occur as part of the plankton or form mats covering bottom sediments. Some mosses, such as *Bryum pseudotriquetrum*, may grow as benthic phototrophs in lakes of maritime and continental Antarctic (Bargagli, 2005; Ochyra et al., 2008).

In maritime Antarctica, lakes are enriched with animal organic matter (e.g., penguin feces) and become zones of intensive growth of aquatic mosses and algae. They can overgrow and convert to peatlands.

Phototrophs support a wide range of heterotrophic bacteria, fungi, protozoans and microinvertebrates (rotifers, nematodes and tardigrades) (Bargagli, 2005). Freshwater crustaceans occur in both maritime and continental Antarctic lakes (Bayly et al., 2003; Polishuk, 2009) (Figs. 17 and 18). Lakes also harbor a species of chironomid midge *Parochlus steinenii*. Outside Tierra del Fuego (South America), it inhabits fresh waters and probably brackish waters from South Georgia to the South Shetland Islands (Hahn and Reinhardt, 2006). The trophic structure and inhabitants of many freshwater bodies in Antarctica differ.



Fig. 13 *Snow alga subformation*, Galindez Island, the Argentine Islands, 2016. Photo by Ivan Parnikoza.



Fig. 14 A community of the *Antarctic herb tundra formation*, Point Thomas Oasis, King George Island, 2006. Photo by Iryna Kozeretka.

The Ecological Role

The main ecological role of the Antarctic terrestrial biome could be defined as the accumulation of organic matter in the extreme terrestrial habitats of Antarctic. The terrestrial biome receives organic deposits from seabirds and mammals which contributes to the development of terrestrial vegetation and soil formation. Numerous decomposers transform organic matter into accessible soil elements. The type and characteristics of Antarctic soils are strictly dependent on the available ecological condition and the local



Fig. 15 A community with participants of *Deschampsia antarctica*, Irizar Island, the Argentine Islands, 2016. Photo by Ivan Parnikoza.



Fig. 16 A community with participants of *Deschampsia antarctica*, Lagotellerie Island, the Marguerite Bay, 2019. Photo by Barbora Chattová.

degree of development of the terrestrial biome (see [Bockheim, 2015](#)). The communities formed by *Deschampsia antarctica* are particularly conducive to soil formation. Additionally the Antarctic terrestrial biome plays a significant role in the life of sea birds. In particular, kelp gulls (*Larus dominicanus*), skuas (*Catharacta*) and some other birds use vegetation for nest building ([Parnikoza et al., 2018a](#)), thus Wilson's storm petrel (*Oceanites oceanicus*) creates burrows in eroded moss banks ([Smith and Corner, 1973](#)).



Fig. 17 A freshwater lake, the habitat of the freshwater copepod *Boeckella poppei*, Cruls Island, the Argentine Islands region, 2019. Photo by Ivan Parnikoza.



Fig. 18 Crustaceans *Branchinecta granulosa* in freshwater lake Eight Island, the Argentine Islands, 2019. Photo by Ivan Parnikoza.

Modern Impacts

For the last 50 years, the Antarctic terrestrial biome along the west seashore of the Antarctic Peninsula has experienced the effects of climate change (Turner et al., 2005). Evidence for changes in the terrestrial ecosystem comes from microarthropods communities study (Convey, 2003), from range extensions of plants (Fowbert and Smith 1994; Parnikoza et al., 2009) and from the successful establishment of alien species (Frenot et al., 2005).

Among the natural factors beyond climate change, the influence of bird colonies is notable, the largest impact being by penguin colonies. In maritime Antarctica, number and size of Gentoo penguins (*Pygoscelis papua*) colonies have increased, which is likely a result of climate change (Peña et al., 2014) (Fig. 19). Flying sea birds and pinnipeds also impact the local composition of the terrestrial biome. Flying sea birds, by using plants for nest building, also promote the spread of the terrestrial biome into new



Fig. 19 Moss banks that died due to Gentoo penguin influence, Galindez Island, the Argentine Islands, 2016. Photo by Ivan Parnikoza.



Fig. 20 Gulls rocks—rocks colonized by plants used for nest building by the kelp gulls, Primavera Cape, Cierva Cove, San Martín Land, 2016, Photo by Ivan Parnikoza.

territories. Kelp gulls create some specific biotopes as well, the so-called Gulls rocks—habitats enriched in limpet shells that are inhabited, in particular, by Antarctic hairgrass ([Parnikoza et al., 2018a](#)) (**Fig. 20**).

The Antarctic terrestrial biome has also experienced human impact during the last 100 years, chiefly due to the activity of local research stations and tourism. The former leads to transformation of the natural terrain and vegetation for station construction and



Fig. 21 Large scale transformation of a terrestrial biotopes of Fildes Peninsula, King George Island, 2019. Photo by Ivan Parnikoza.

maintenance (Fig. 21). Station operation lead to contamination of the biome with trace elements and other pollutants (Bargagli, 2005, Parnikoza et al., 2017). Meanwhile, construction also leads to the formation of habitats artificially shielded from winds, which makes them favorable for vegetation. Dispersal of aboriginal plants into human-changed environments has been reported from Point Thomas Oasis, King George Island, as well as near the Ukrainian Academic Vernadsky and US Palmer stations. At the Academic Vernadsky station, colonization of buildings and constructions of the British period (built in the 1950–70s) by crustose and foliose lichens has also been reported (Parnikoza et al., 2018b) (Fig. 22).

The second factor, tourism, has been increasing dramatically in the 21st century. According to the last IAATO reports (2019, <https://iaato.org/documents>), the total number of Antarctic visitors in 2017–18 was estimated at 51,707, an increase of 17% compared to the previous season, where the majority (41,996) of visitors traveled by sea to Antarctica on vessels offering excursions ashore. This number includes both tourists arriving to Antarctica onboard of a cruise ship accompanied by trained guides, as well as people who travel to the continent on small yachts, catamarans, etc. Independent tourists are able to get to almost anywhere because of very lax controls. These unguided intrusions pose a potentially serious threat (Fig. 23), increased tourism, among other impacts, also increases the threat of biological invasions (Fuentes-Lillo et al., 2017).

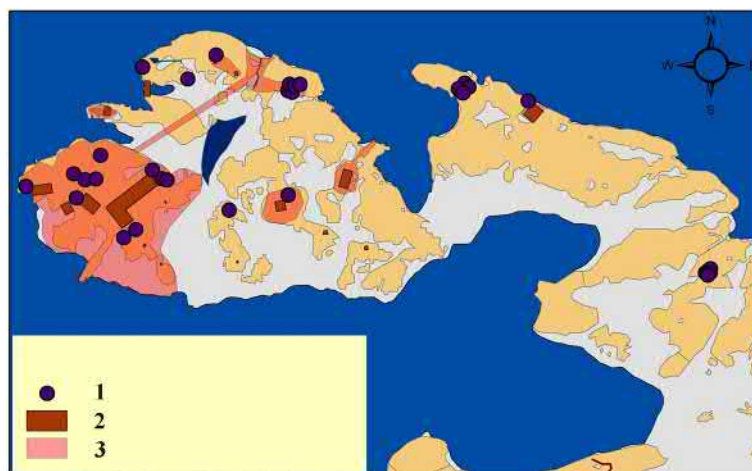


Fig. 22 Elements and constructions of the Ukrainian Academic Vernadsky station (2) colonized by lichens (1), zones of technogenic pressure (3), according to Parnikoza et al. (2018b).



Fig. 23 Communities of fruticose and foliose lichens are incredibly susceptible to the carelessness by tourists, Eight Island, the Argentine Islands, 2019. Photo by Ivan Parnikoza.

Conservation Measures

In view of the above-mentioned, the terrestrial biome needs to be studied in detail by revision all of its most valuable components and patches, that need to be protected (Fig. 24). Initially it should be protected as part of station management plans in case of station vicinity or in frame of visiting rules in case of touristic sites. The next step might be the creation of a representative network of natural reserve areas with a protected status (strict protection, Ia IUCN)—the Antarctic special protection areas (ASPA) (Fig. 25). Existed ASPA network is not sufficient and need to be expanded. It is also necessary to expand monitoring of climate changes and human impact on terrestrial ecosystems with the involvement of a broader circle of the Antarctic Treaty countries.



Fig. 24 The most valuable objects near Antarctic research stations should be protected by station management plans. Smith moss bank, Galindez Island, in the vicinities of the Ukrainian Academic Vernadsky station, 2016. Photo by Ivan Parnikoza.



Fig. 25 A small ASPA Green Island is not sufficient to protect terrestrial ecosystems on the Argentine Islands region, 2019. Photo by Ivan Parnikoza.

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Marine Plankton of Open Antarctic Seas

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Abstract

The Southern Ocean biological system is dominated by physical processes such as strong winds, ice retreat and formation, and seasonal disruption and generation of vertical stratification in the water column, although these physical features are not uniform over the entire region. Antarctic plankton respond quickly to these physical variations in stratification and nutrient inputs, resulting in a heterogeneous distribution of phytoplankton and zooplankton. Phytoplankton of the Antarctic are dominated by diatoms, but nanophytoplankton, haptophytes, and dinoflagellates are locally important. A major feature of Antarctic phytoplankton is that they are large relative to those in warmer waters, and this allows for the establishment of a shorter food web and a more direct transfer of organic matter to higher trophic levels. Antarctic krill are important macrozooplankton, but their abundance is extremely variable in waters around the continent. Copepods are also important grazers of phytoplankton and transfer energy to krill and other higher trophic levels. Microzooplankton have a relatively reduced role in the Southern Ocean, especially when compared to more tropical, oligotrophic systems. Because the physical features of the Southern Ocean are expected to change substantially in the coming century, plankton will also change, although the impacts of predicted climate change on the quantity and composition of the plankton of the Southern Ocean remain unclear. Understanding the present state of Antarctic waters is essential to forecasting the changes that will occur in the near future and to predict the impacts on Antarctic food webs and biogeochemical cycles.

Introduction

Waters surrounding the Antarctic continent are among the most physically controlled of all marine systems. Not only are the temperatures extremely low (from -2°C to 4°C), but the surface is covered by ice for a large portion of the year. The retreat and advance of ice generates substantial changes within the water column with regard to its stratification, nutrient content, and availability of light, and these in turn drive large changes in marine plankton. Furthermore, the entire Southern Ocean is dominated by the world's largest (by volume) current—the Antarctic circumpolar current (ACC). This current not only restricts exchanges with more temperate waters but facilitates exchanges of biota throughout the entire region (Hunt et al., 2016). It occurs in deep waters (ca. 3000 m), is driven by large-scale wind patterns, and its characteristics (temperature, salinity, frontal structure) have been known for decades (Sverdrup et al., 1942). It drives a circumpolar divergence which results in exceptionally high macronutrient (nitrate, phosphate) levels at the surface year round. While the definition of the Southern Ocean varies among oceanographers, this review will consider Antarctic waters to be those influenced by ice. That effectively puts the boundary at the core of the ACC (ca. 60°S), which is generally the maximum extent of ice.

Despite the importance of the ACC and other extensive currents, waters of the Antarctic are far from homogeneous. A number of marginal seas exist that have restricted exchanges with the ACC, and these areas have substantially different plankton from the waters of the ACC. These marginal seas are also shallower and encompass large portions of the continental shelf; being close to the continent, they are influenced by continental processes such as glacial inputs, winds, and exchanges with the benthos. The major

marginal seas include the Ross, Weddell, Amundsen and Bellingshausen Seas; other marginal seas exist, but they are less isolated and influenced more by exchanges with the ACC.

The global heat budget is the primary feature structuring the Southern Ocean. That is, solar energy is greatly reduced during the austral winter, and the net heat flux is negative, driving ice formation. In summer, the heat flux is positive, and forces ice melting and retreat. The annual cycle of the Southern Ocean is dominated by this process (Fig. 1). During ice formation in winter, seawater begins to freeze, forming small crystals called frazil ice, which rise to the surface. Frazil ice accumulates and is compressed into larger ice forms (pancake ice), which in turn is solidified into broad sheets of ice from 1 to 2 m thick. This ice breaks frequently under the pressure of winds and currents, creating gaps in the ice (leads), but these areas freeze quickly and generate more ice. Thus, even during winter the ice and ocean surface is a dynamic and constantly changing feature that provides a unique and variable environment for plankton. In summer, ice begins to melt. The melting seawater can generate a surface layer with reduced salinity in close proximity to the ice edge, and hence the vertical density stratification of the upper water column is increased. The strength of the stratification is a function of the rate of meltwater input and the strength and direction of regional winds, which act to mix the surface waters and disrupt the stratification.

One significant role of ice that is often overlooked is the presence of biota within the sea ice. The sea ice biota consist of autotrophs, heterotrophs and mixotrophs, and can originate from seawater during freeze-up, and be released into the surface layer during melting. This interaction introduces an unusual feature to Southern Ocean plankton, and the characteristics of this biota are treated in Thomas and Dieckmann (2002).

Plankton of the Southern Ocean

As in the rest of the ocean, there are different energetic strategies employed by Southern Ocean plankton. The first is autotrophy, or the generation of reduced carbon compounds from carbon dioxide using radiant energy produced by photosynthesis. The second is

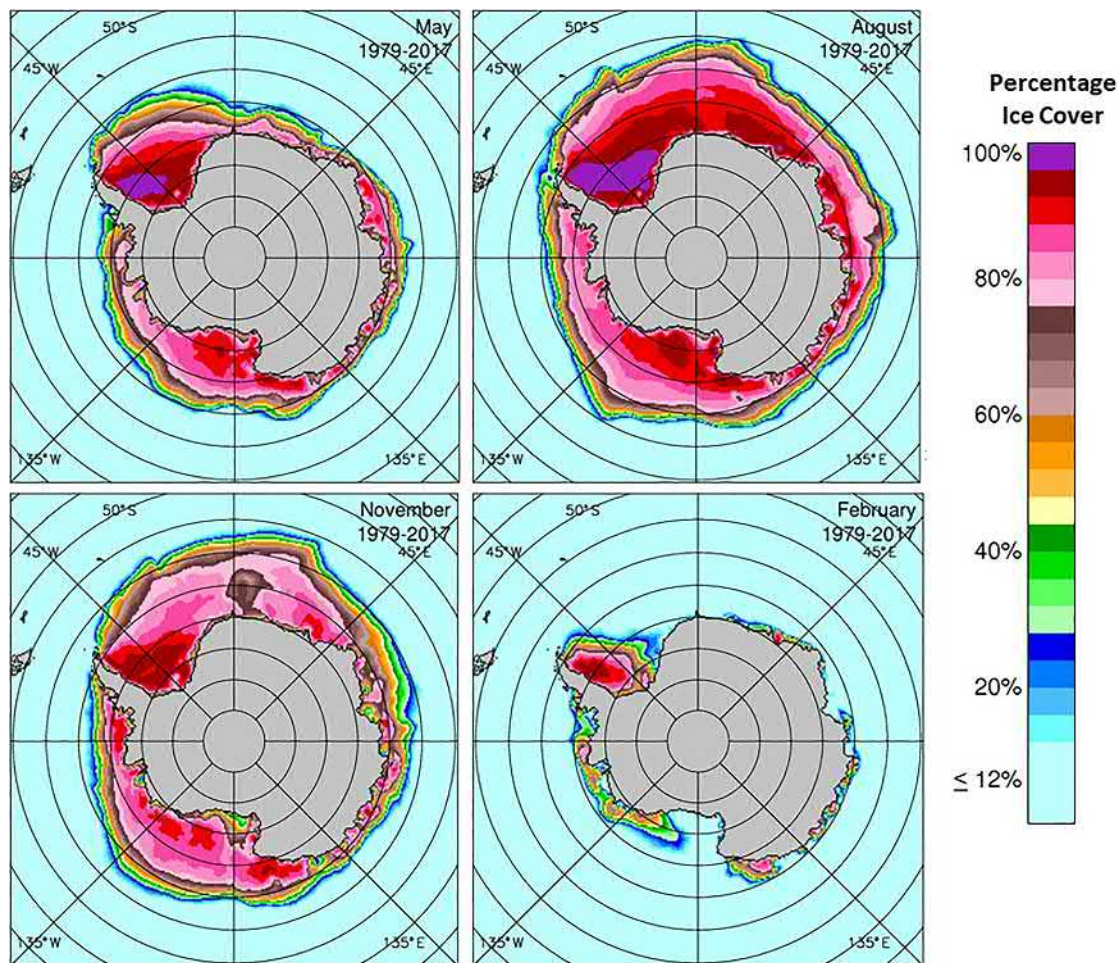


Fig. 1 Mean distribution and percentage ice cover of sea ice in the Southern Ocean. Figure courtesy of C. Parkinson's and Nick DiGirolamo, NASA Goddard Space Flight Center.

heterotrophy, or the oxidation of organic compounds to provide energy to synthesize needed compounds within the organism. The organic compounds can be obtained by a number of “feeding” mechanisms, including the ingestion of particles, the absorption of dissolved organic matter, or a combination of both. Some organisms combine photosynthetic processes with direct use of organics (mixotrophy), but in large part plankton can be divided between auto- and heterotrophs. Microbial organisms (the so-called bacteria) have a broad diversity and ability to use organic matter, and will not be discussed here.

Phytoplankton

General features and composition

Phytoplankton in Antarctic waters have numerous characteristics that make them different from those in tropical and temperate waters. Most oceanic waters consist of cyanobacteria, diatoms, haptophytes, prasinophytes, dinoflagellates, and chlorophytes. However, in the Southern Ocean cyanobacteria are largely absent and inactive, and dinoflagellates play a relatively minor role. Coccolithophorids (a type of haptophyte) are also relatively unimportant. The reduced abundance of these forms, which can be dominant in other waters, increases the importance of the other groups. For decades, diatoms have been considered the dominant planktonic form (Fig. 2A–C), although more detailed examinations in a variety of regions demonstrate the importance of other forms as well. Haptophytes, and specifically the genus *Phaeocystis*, occur in numerous regions (Fig. 2D), and cryptomonads can also be important in some regions. The types of habitats vary not only spatially, but temporally as well. Despite the similarities in some features, such as ice cover and low temperatures, it has been recognized in recent decades that the Southern Ocean is far from homogenous. Because phytoplankton respond relatively quickly to changing environmental conditions (such as altered irradiance fields and nutrient concentrations), it is challenging to characterize the importance of various groups of phytoplankton throughout the Southern Ocean, since phytoplankton composition varies with spatial and temporal patterns in the environment.

One feature that is more easily described is the total standing stock of phytoplankton. The major pigment of autotrophs is chlorophyll, which can be quantified by the analysis of satellite imagery. While this is possible only during cloud-free periods, over longer periods of time (e.g., days, weeks to months) a composite record of phytoplankton chlorophyll can be generated (Fig. 3). Chlorophyll can be used as a measure of total phytoplankton abundance, which drops to extremely low levels from April through September (austral winter), but begins to increase as solar energy increases (and ice begins to recede). Rapid increases and accumulation of phytoplankton can occur, forming “blooms” of enhanced standing stocks. Once blooms are formed, they can be

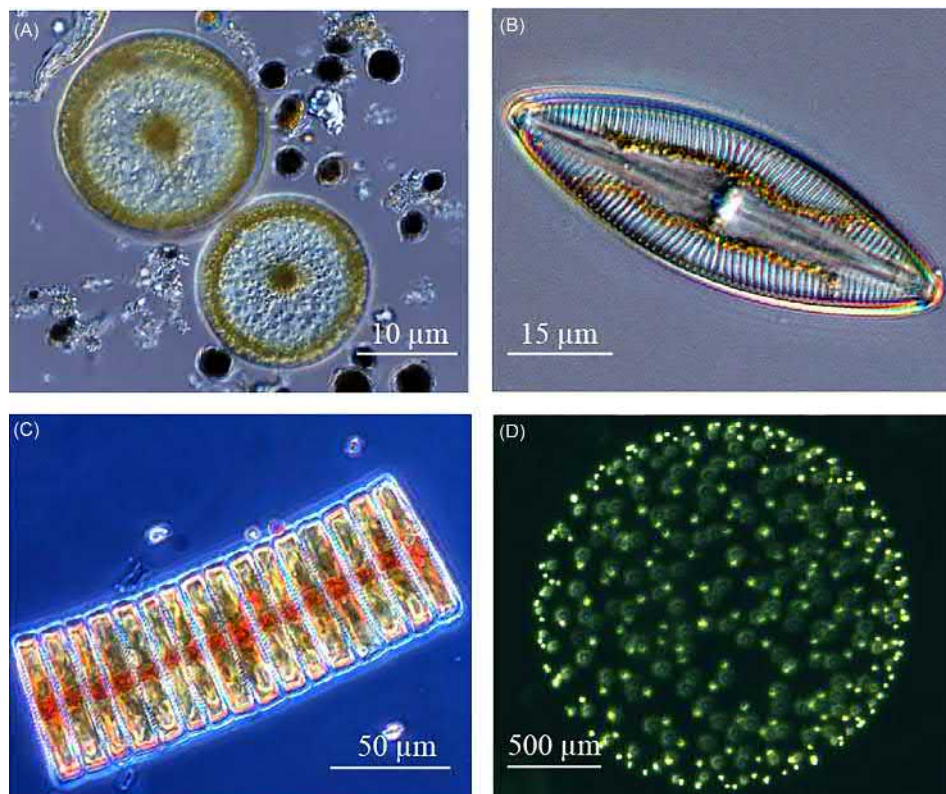


Fig. 2 *Coscinodiscus centralis* (A), *Navicula trivialis* (B), *Fragilariopsis* sp. chain (C), and the abundant *Phaeocystis antarctica* (D). Images courtesy of The Phytoplankton encyclopedia (Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Unported License; (A and B), the Virginia Institute of Marine Science (C), and Pete Countway, Bigelow Laboratory (D).

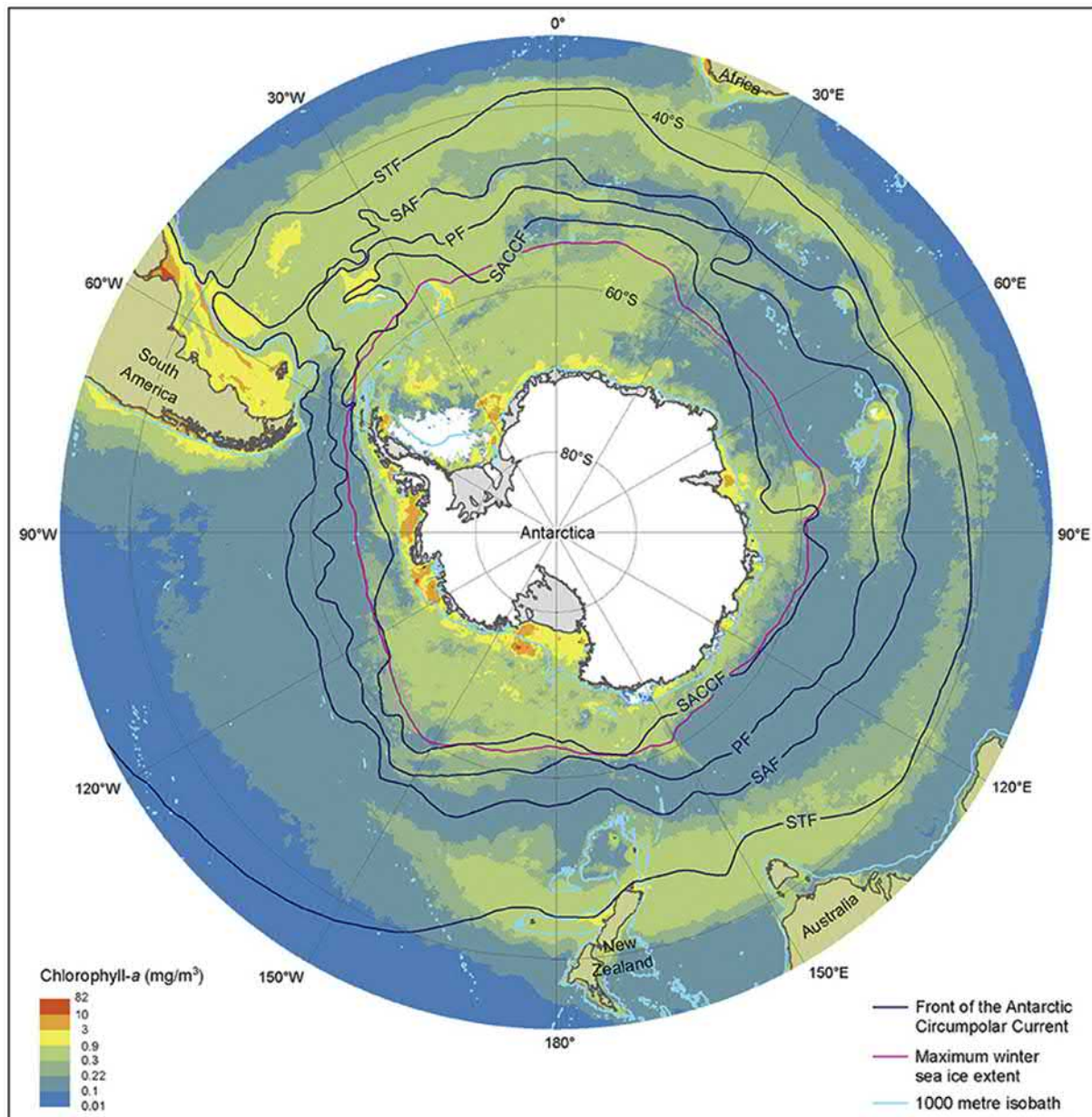


Fig. 3 Mean annual surface chlorophyll concentrations in the Southern Ocean. The greatest concentrations occur on the continental shelves. Also indicated are the fronts that occur in the Antarctic Circumpolar Current, the winter ice extent, and the 1000 m isobath. From Deppeler, S. L. and Davidson, A. T. (2017). Southern ocean phytoplankton in a changing climate. *Frontiers in Marine Science*. <https://doi.org/10.3389/fmars.2017.00040>.

disrupted by physical (vertical mixing with deeper waters) or biological (grazing, sinking) processes (Fig. 4). Some regions have sustained blooms (e.g., Ross Sea) with elevated biomass that persists for months, whereas others have shorter blooms that often are not observed from space due to their short existence. Blooms are generally dominated by only a few species that respond to the in situ environmental conditions by growing and accumulating faster than other forms. For example, *Phaeocystis* appears to grow in some iron-rich, low light environments (Smith et al., 2014; Alderkamp et al., 2012), while cryptomonads seem to be favored in waters influenced by glacial run-off (Moline et al., 1996). Diatoms also bloom within the marginal ice zone in numerous locations (Smith and Nelson, 1985; Moore et al., 1999; Vernet et al., 2008). Given the ephemeral nature of blooms and the restricted access to waters of the Southern Ocean, our knowledge of bloom composition throughout the waters surrounding Antarctica is incomplete.

An additional significant characteristic feature of phytoplankton in the Southern Ocean is their size. Many dominant phytoplankton, especially diatoms, are large (that is, greater than 50 μm in the longest dimension), and the mean size of phytoplankton in Antarctic waters is much greater than in warmer seas. This has an important ecological impact, in that larger phytoplankton can be

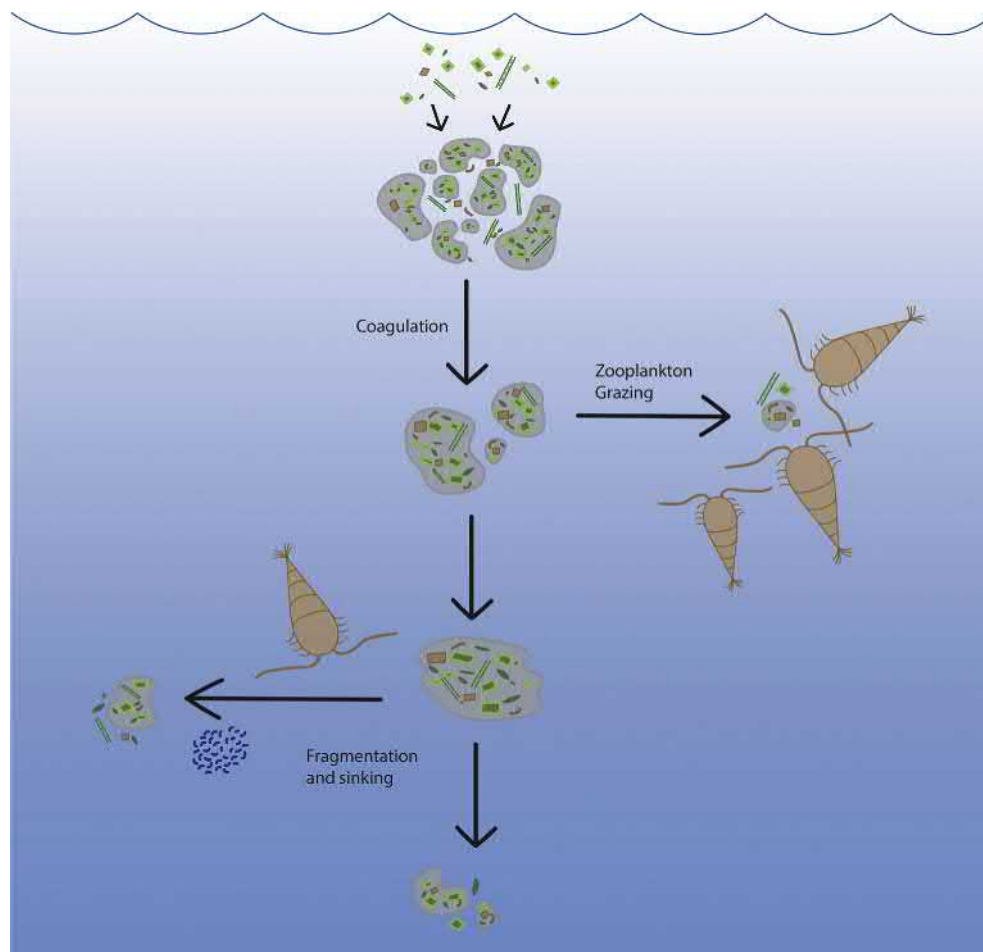


Fig. 4 Illustration of biological disruptors (i.e., zooplankton grazing or sinking) or processes that reduce surface phytoplankton standing stocks. Adapted from Burd, A. B. and Jackson, G. A. (2009). Particle aggregation. *Annual Review of Marine Science* 1, 65–90. <https://doi.org/10.1146/annurev.marine.010908.163904>.

grazed by larger herbivores, which in turn can be eaten by larger carnivores. This results in a more compressed food web and perhaps a more efficient transfer of carbon and energy to higher trophic levels. This is at least one factor that contributes to the large biomass of higher trophic levels (whales, seals, penguins, pelagic birds) found in the Southern Ocean (Ryther, 1969).

General distribution

The overall standing stocks of phytoplankton are well known from satellite data (Fig. 3), but the composition of those stocks is far less known. Selected regions and marginal seas have characteristic compositions that are relatively predictable (e.g., Ross Sea, where haptophytes bloom in spring and are replaced by diatoms after iron limitation occurs; Smith et al., 2014), but data for the entire Southern Ocean are lacking. Nanoflagellates can be commonly found in deeper waters and appear to represent a relatively stable assemblage, even upon manipulation of micronutrients (Schulz et al., 2018).

Controls on growth and accumulation

Phytoplankton in the Southern Ocean are considered to be limited by available resources, and more specifically, by the resource that is in the smallest supply relative to requirements. The highly seasonal nature of the environment creates a situation where one environmental resource limits phytoplankton growth for part of the year, and another for the rest of the year. The major factor controlling phytoplankton growth over much of the year is light. Light availability varies with latitude, date (solar angle), ice distribution, clouds, mixing within the water column, and ocean wave height. For much of the Southern Ocean within the Antarctic Circle, light limits phytoplankton for large periods simply because the sun falls below the horizon for much or all of the day. Even when the solar angle increases, ice (and especially the associated snow cover) absorbs and reflects much of the incoming radiation (generally more than 97% of incident radiation). Hence, one measure of light limitation is simply ice distribution.

Vertical mixing in the water column also can contribute to light limitation. This is more common in deeper, less stratified waters of the ACC, but is also important anywhere that physical processes induce deep mixing in the water column (Fischer et al., 2014). If

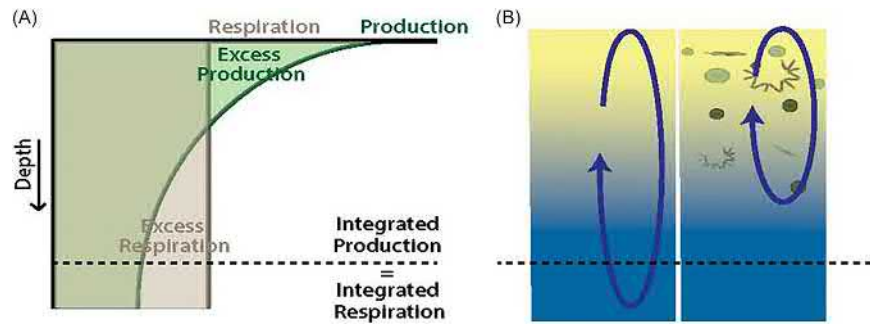


Fig. 5 Conceptual diagram of the “Sverdrup Hypothesis” explaining the regulation of the onset of a phytoplankton bloom by vertical mixing and irradiance. From Fischer, A.D., Moberg, E.A., Alexander, H., Brownlee, E.F., Hunter-Cevera, K.R., Pitz, K.J., Rosengard, S.Z. and Sosik, H.M. 2014. Sixty years of Sverdrup: A retrospective of progress in the study of phytoplankton blooms. *Oceanography* **27**, 222–235.

the water column is mixed to a critical depth, net photosynthesis (integrated over depth and time) cannot be positive, and no net growth can occur (Fig. 5). Only when mixing is less than this critical depth can net growth proceed. As mixed layers in the Southern Ocean can exceed 200 m (Constable et al., 2014), light limitation via mixing is a common feature controlling phytoplankton growth.

During spring and summer, when ice is melting and receding (creating stratification within the water column), mixing and light penetration into the water are no longer limiting factors. Phytoplankton then grow at their maximum rates as determined by temperature (Eppley, 1972), until another factor limits their growth—such as nutrients. Nutrients, such as N, P, Si, Fe, Ca, and a host of metals, are required for cellular synthesis and growth. Due to substantial upwelling associated with the ACC and large-scale currents, macronutrients (nitrate, phosphate), rarely drop to levels that limit phytoplankton growth. However, micronutrients, and especially iron, fall to extremely low concentrations and can limit phytoplankton growth. Bio-available iron levels are low throughout much of the ocean, and it was not until oceanographers developed trace-metal clean sampling techniques that the role of iron in regulating phytoplankton growth was elucidated. There are two sources of iron: from the atmosphere as eolian inputs, and from upwelling or mixing of deeper water. Atmospheric inputs are low throughout the Southern Ocean, as the continent is largely covered by ice and exchanges occur with air masses farther north are limited. Iron fluxes via upwelling set an upper limit to surface concentrations, but these are quite small as well, because iron is removed rapidly by biological and chemical processes (uptake, scavenging by particles). After phytoplankton growth in increased light conditions occurs, iron concentrations drop to vanishingly low levels (less than 0.1 nM; macronutrient concentrations are at least three orders of magnitude higher). Such low concentrations have been shown repeatedly to limit phytoplankton growth. While the locations where iron has been shown to be limiting are small (due to the difficulty of sampling using trace metal clean techniques), and only a few locations have physical mechanisms to provide adequate iron continuously (e.g., from glacial melt), iron is a significant factor in regulating phytoplankton growth throughout the Southern Ocean.

Phytoplankton standing stocks are regulated not only by growth and accumulation, but by losses. Losses can result from grazing by zooplankton, sinking, or lysis (the rupturing of cell membranes, either by attack from viruses or by autolysis, the destruction of cell walls by the cell's own enzymes). Grazing—the ingestion of phytoplankton by heterotrophic organisms—by micro- or meso-zooplankton can be an important process in any ocean system. In waters of the Southern Ocean, grazing is highly dependent on the stage of the phytoplankton bloom and predation on the grazers by organisms in higher trophic levels. For example, Atkinson et al. (1999) suggested that copepods (often the major grazer on phytoplankton) had their biomass and grazing impact limited by krill predation. Other studies have suggested that these grazing impacts tend to be restricted in time (e.g., Smith et al., 2011). In less productive waters, grazing can consume a significant fraction of phytoplankton productivity (Calbet, 2001; Saba et al., 2014). In contrast to tropical waters, microzooplankton grazing is generally minimal (Caron et al., 2000; Garzio et al., 2013; Mosby and Smith, 2015). Passive sinking of phytoplankton is generally slow, but more rapid sinking can occur when blooms become nutrient limited (Jones and Smith, 2017). Viral lysis of plankton cells in the Antarctic has not been studied, and autolysis is unknown.

Zooplankton

General features and composition

Like phytoplankton, zooplankton in the Southern Ocean are diverse, and have a number of characteristics that make Antarctic zooplankton different from those in temperate and tropical waters. One feature is the occurrence and importance of different types of krill (euphausiids) that are often considered to be keystone species of the Antarctic (Fig. 6A). It has been estimated that the biomass of krill is approximately 379 million tons, equal to that of all fishes in the ocean (as well as being equal to that of humans; Atkinson et al., 2009). Distribution of krill is far from spatially uniform, with the largest concentrations being found near the Antarctic Peninsula and the islands downstream from this area (Atkinson et al., 2004). The life cycle of krill is complex, with eggs sinking to depth to hatch, and the larvae migrating to the surface layer to feed within the marginal ice zone. Krill are omnivorous; they ingest a variety of particles, including diatoms, protists, and ice algae. Larval krill are often associated with ice, and total

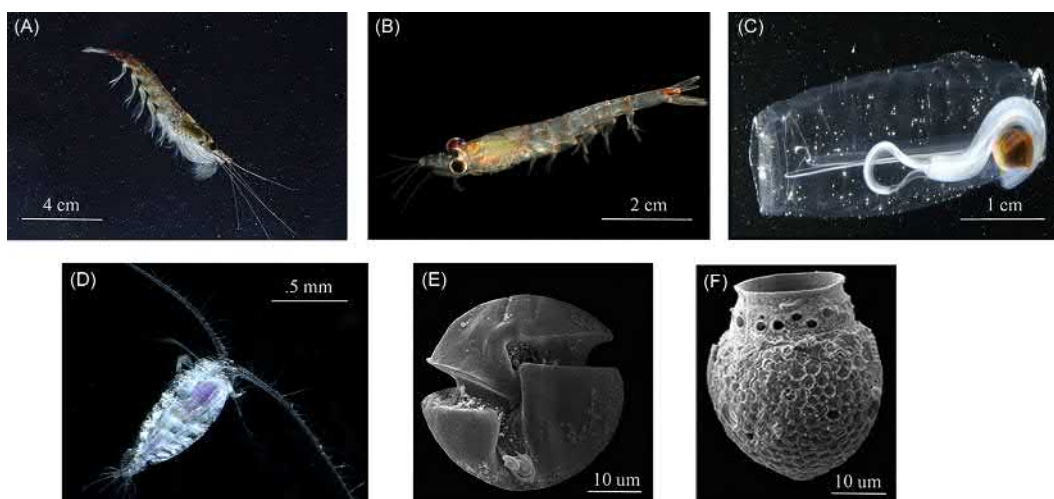


Fig. 6 *Euphausia superba* (A), *E. crystallarophius* (B), *Salpa cylindrica* (C), *Euaugaptilus ractus* (D), dinoflagellate (E), and ciliate (F). Images courtesy of Russ Hopcroft (A, C, and D), Volker Siegel (B), and the Australian Antarctic Division (E and F). All scales are approximate.

krill biomass appears strongly correlated with ice concentrations (Loeb et al., 1997). Given the large size of adults, they can migrate vertically to great depths, and have been observed feeding on benthic phytodetritus during winter (Clarke and Tyler, 2008).

Two major types of krill occur in the Southern Ocean. The best known species is Antarctic krill (*Euphausia superba*), which is ca. 8 cm in length as an adult, and individuals can live up to 7 years (Fig. 6A). Krill are harvested commercially in certain locations of the Antarctic and form the major prey for many baleen whales, crabeater seals, large fishes, pelagic birds, and penguins. The second species is crystal krill (*E. crystallarophius*), which is smaller (adult length ca. 5 cm) and commonly found on continental shelves (Fig. 6B). It is the food of many higher trophic levels as well, but much less is known about its distributions and ecological role.

During years of low ice concentrations and distributions, krill appear to be ecologically replaced by salps (Loeb et al., 1997). Salps are urochordates that filter substantial volumes of water and can multiply rapidly, even in the cold waters of the Southern Ocean (Fig. 6C). They are capable of utilizing smaller sizes of particles than krill, and as phytoplankton tend to be smaller during years of reduced ice, salps can effectively utilize the available food during these periods. Salps and krill have a greatly different ecological role; krill are an excellent protein source for higher trophic levels, whereas salps have a large amount of water and reduced amounts of organic matter relative to their size, making them a less useful food source. Hence, the presence or absence of krill and salps has considerable ecological impact and has been shown to structure food webs of the Southern Ocean.

Another group of zooplankton which are important in Antarctic waters (and the entire ocean) are copepods (Fig. 6D). Copepods occur throughout the ocean and are a major consumer of phytoplankton, as well as the major conduit for organic matter to higher trophic levels. In the Southern Ocean they occur frequently, although their importance is often overshadowed by the presence of krill. They have been shown to be major grazing organisms in many regions of the Antarctic, and often are responsible for the majority of the metabolism by zooplankton in the surface layer (Ashjian et al., 2004). As in temperate and tropic waters, copepods are an important grazer of phytoplankton and protists, and contribute significantly to energy transfer within food webs. They also are food for krill and small fishes.

The smallest size of grazers is occupied by a variety of protists (Fig. 6E and F). These are largely single-celled organisms that can feed on smaller phytoplankton as well as larger forms. Given their small size (from 40 to 200 µm), then can grow as rapidly as phytoplankton, and thus potentially are an important means to reduce phytoplankton biomass. Examples of protists include heterotrophic dinoflagellates, ciliates, tintinnids, radiolarians, and foraminifera. While they provide some food to larger organisms such as copepods and krill, their major role is to recycle nutrients for use by phytoplankton and thus contribute to the “microbial loop” (Sherr and Sherr, 1994). In the Antarctic the role of the microbial loop is reduced relative to warmer waters, but still is important to the functioning of energy and nutrient fluxes of pelagic systems.

General distribution

Standing stocks of zooplankton can only be assessed using discrete net sampling, and as a result are far less known than that of phytoplankton. Most studies are restricted to selected regions (e.g., Atkinson et al. 1999; Steinberg et al., 2008; Smith et al., 2017). However, some estimates of distributions of some forms have been constructed. (Figs. 7 and 8). Antarctic krill have their greatest abundance downstream of the Antarctic Peninsula, an area that serves as a “seed bed” where sub-adults grow and are advected in the ACC downstream (Hofmann and Murphy, 2004). Conversely, salps have their greatest densities in areas where krill do not reach high abundances, such as the Indian and Pacific sectors off the continental shelves. Copepods have some distributional features that are similar to those of Antarctic krill (e.g., elevated abundances near the islands in the northern portions of the ACC, low abundances in the ice-covered Weddell Sea) but also shown regional maxima that are not associated with krill (e.g., high concentrations at the

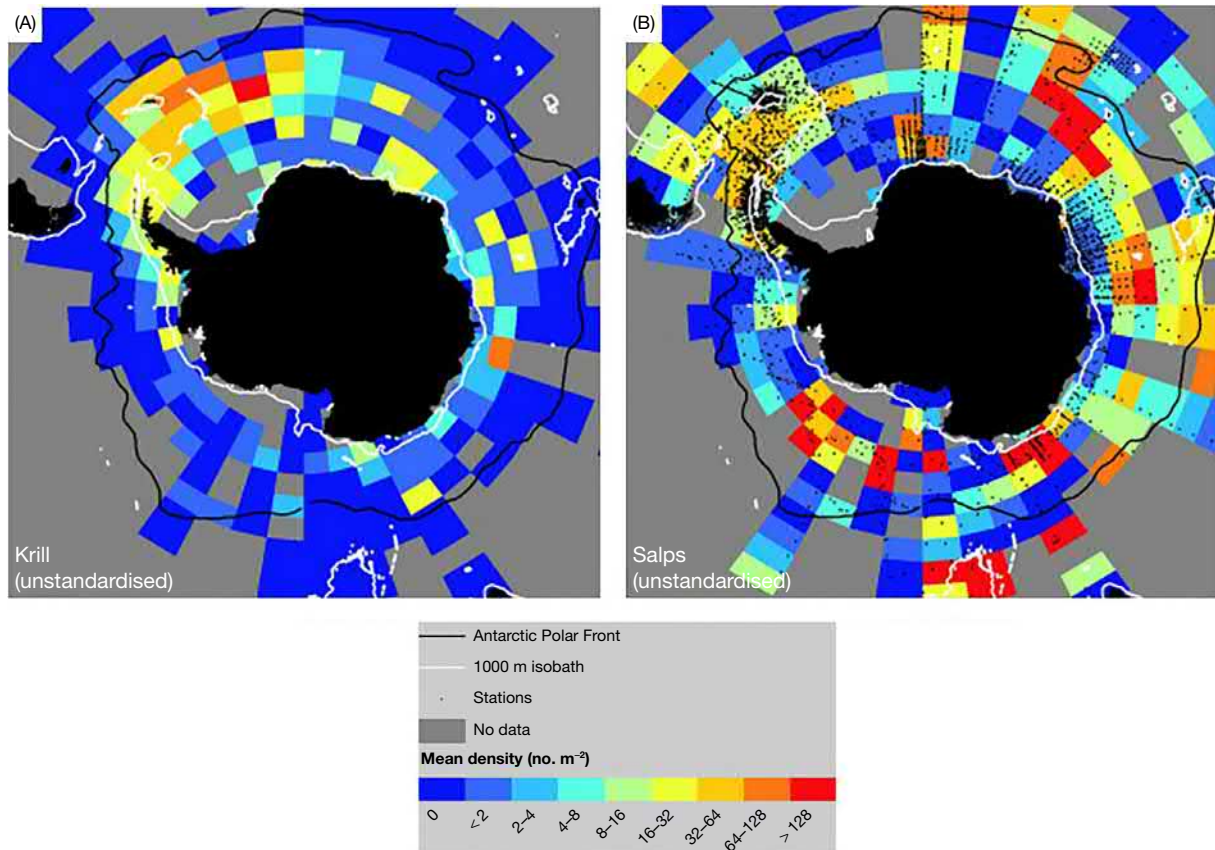


Fig. 7 Distribution of unstandardized krill and salp densities in the Southern Ocean. Salp densities appears to be more variable than those of krill. Unstandardized density values are not corrected for biases relating to differing sample depths, time of day and year, and net types. From Atkinson, A., Hill, S. L., Pakhomov, E. A., Siegel, V., Anadon, R., Chiba, S., Daly, K. L., Downie, R., Fretwell, P., Gerrish, L., Hosie, G. W., Jessopp, M. J., Kawaguchi, S., Krafft, B. A., Loeb, V., Nishikawa, J., Peat, H. J., Reiss, C. S., Ross, R. M., Quetin, L. B., Schmidt, K., Steinberg, D. K., Subramaniam, R. C., Tarling, G. A. and Ward, P. (2016). *Earth System Science Data*. <https://doi.org/10.5194/essd-2016-52>.

edge of the continent near 23°E). More research is needed to extend these distributional maps to the entire Southern Ocean and to verify these patterns.

Controls on zooplankton growth and accumulation

The regulation of zooplankton biomass is far less known than that of phytoplankton, largely because it is more difficult to experimentally determine their growth, rates of ingestion, and population losses. Indeed, it is likely that different sizes and types of zooplankton experience different controls. Some groups may be food limited, given the strong seasonality of phytoplankton growth and production, whereas others can be limited by strong predation. For example, krill can accumulate to incredibly high concentrations (called superswarms; which can reach mean concentrations of 100 krill m⁻³ and stretch for multiple kilometers at 30 m; Tarling et al., 2009). At those concentrations it is likely that all food would be removed in localized patches. Similarly, food for zooplankton in the water column is extremely low in winter, and most zooplankton have evolved means to survive long periods of no food availability (e.g., storing lipids, feeding on ice and phytodetritus). In contrast, predation by penguins and whales has been suggested to be important factor in controlling krill vertical distribution (Ainley et al., 2015) and potentially biomass. Food webs in the Southern Ocean are complex, but in general have fewer trophic transformations due to the large sizes of phytoplankton and zooplankton (Fig. 9). Zooplankton standing stocks likely represent a balance between food limitation and losses due to predation by upper trophic levels.

Future Plankton

The future of Antarctic plankton is uncertain. Climate change is drastically altering environmental conditions, and associated organism climate envelopes, globally. While scientific models can predict the degree and severity of some ecological changes, the oceanic lag effect means current atmospheric greenhouse gas concentrations will have impacts for hundreds to a thousand years to come (Keeling et al., 2010). Given their latitude, polar regions and the organisms that exist there are particularly susceptible to the

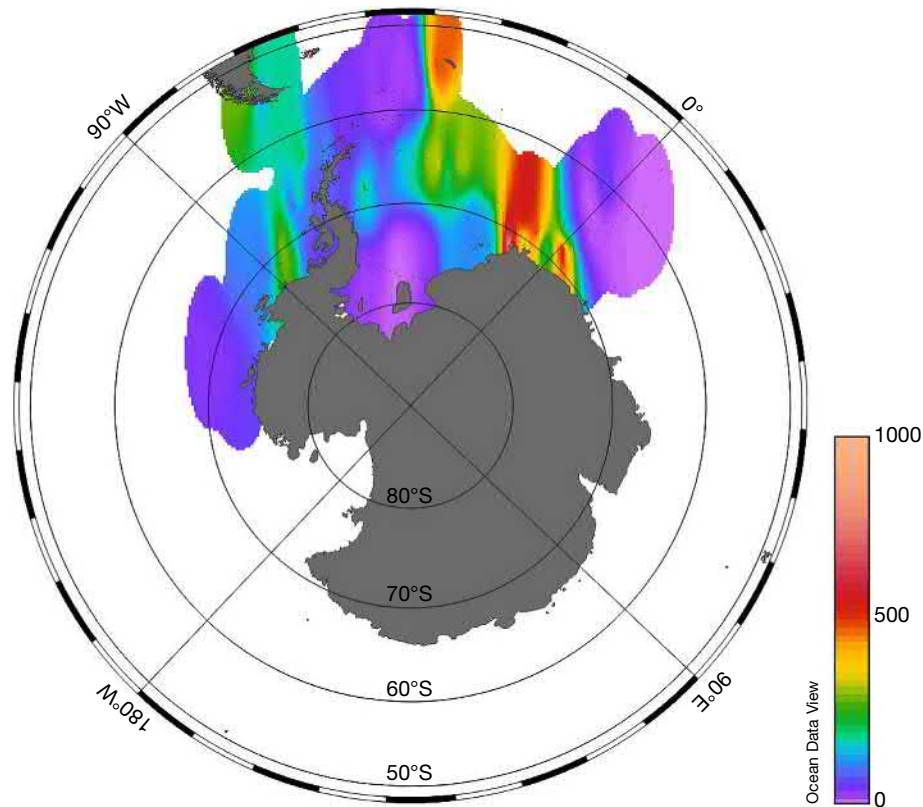
Total Southern Ocean Copepod Distribution ($\#/m^3$)

Fig. 8 Copepod distribution (individuals m^{-3}) in regions of the Southern Ocean that have been sampled from 1980 to 2005 as part of the National Oceanic Atmospheric Administration COPEPOD: The Global Plankton Database project.

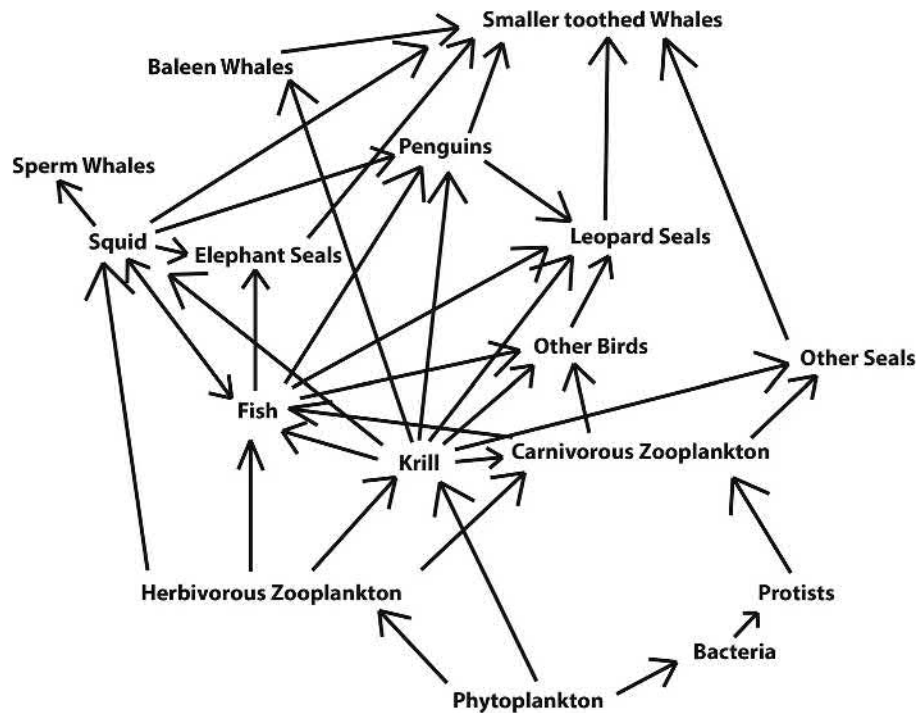


Fig. 9 Food web of the Southern Ocean ecosystem. Adapted from McBride, M. M., Dalpadado, P., Drinkwater, K. F., Godo, O. R., Hobday, A. J., Hollowed, A. B., Kristiansen, T., Murphy, E. J., Ressler, P. H., Subbey, S., Hofmann, E. E. and Loeng, H. (2014). Krill, climate, and contrasting future scenarios for Arctic and Antarctic fisheries. *ICES Journal of Marine Science* **71**, 1934–1955. <https://doi.org/10.1093/icesjms/fsu002>.

physical and chemical changes induced by climate change. The importance of sea ice to light and nutrient availability and the subsequent importance of light and nutrients to plankton growth was illustrated earlier; the mass, extent, and seasonal onset of changes in sea ice is changing as a result of climate change.

Phytoplankton

Because they form the base of food webs, the impacts of climate change on phytoplankton abundance, distribution, and type will determine larger changes to Antarctic ecosystems. Changes in phytoplankton dynamics will be dependent on all factors that impact their growth in any climate (i.e., nutrient availability, light availability, temperature, etc.). In the Antarctic Peninsula region, there is evidence of a transition from a diatom-dominated to cryptophyte-dominated community, likely resulting from changes in ice cover, mixing depths, and glacial meltwater input (Montes-Hugo et al., 2009; Flores et al., 2012). Like all aspects of climate change, ecological responses vary; microflagellate populations may increase as a result of increased temperatures (Flores et al., 2012), but in the Ross Sea diatoms are associated with water temperatures above 0° (Liu and Smith, 2012). Future changes in the Ross Sea have also been modeled. These results suggest that the overall importance of haptophytes will increase because future open ice periods will increase with earlier ice retreat (generating longer times for growth in a low irradiance environment; Kaufman et al., 2018). Similar modeling efforts have not been applied to the entire Southern Ocean, however.

Zooplankton

The impacts of climate change on zooplankton are non-uniform but, in general, are likely to be negative. Because of their dependence on phytoplankton for food and on adequate ice concentrations for spawning, krill populations have been curtailed with decreased ice extent and the reduction of phytoplankton blooms (Atkinson et al., 2004; Meredith and King, 2005). This decrease in krill abundance has been significant in the southwest Atlantic sector, where standing stocks, which usually account for nearly 50% of total Southern Ocean krill, have been decreasing since 1970 (Atkinson et al., 2004). Contrastingly, salps tolerate warmer water conditions and have expanded their range due to climate shifts (Atkinson et al., 2004). Because krill are a more important link in the Antarctic food web than salps, higher trophic levels in the future will likely experience population declines due to reduced krill biomass and range (Atkinson et al., 2004).

Smith et al. (2014) modeled the impacts of future changes in ice concentrations and distributions in the Ross Sea, the effects on phytoplankton, and the impacts on the food web. While they concluded that primary productivity will increase slightly in the coming century, they also suggested that the greatest impacts will be on crystal krill, as those populations are generally associated with ice and ice will decrease substantially in the next 100 years. They also predicted an increased importance of copepods and small fish (such as Antarctic silverfish, *Pleuragramma antarcticum*) that feed on copepods and serve as food for penguins, seals and other top predators. While the food web will respond to multiple changes in the future, it was concluded that the Ross Sea food web may be strongly disturbed and damaged relative to its present (and largely pristine) state.

Constable et al. (2014) reviewed the expected future changes in biota in the entire Southern Ocean. They emphasized that many habitat parameters will change regionally, although some will impact the entire Antarctic (e.g., warming, reduced salinity, strengthening of winds). They also suggested that lower trophic levels would be impacted more than higher trophic levels, but that all changes would involve numerous interactions among the habitats, physical forcing, food web ecology, and biological diversity (Fig. 10). They also made predictions on specific biological groups with respect to eight physical parameters that are expected to change. The impacts on diatoms were generally positive in waters less than 3°C and those on flagellates were negative; impacts

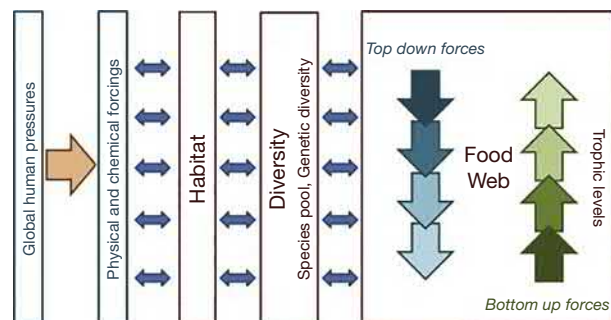


Fig. 10 Schematic description of the impacts of climate change factors on the resultant food webs of the Southern Ocean. From Constable, A. J., Melbourne-Thomas, J., Corney, S. P., Arrigo, K. R., Barbraud, C., Barnes, D. K. A., Bindoff, N. L., Boyd, P. W., Brandt, A., Costa, D. P., Davidson, A. T., Ducklow, H. W., Emmerson, L., Fukuchi, M., Gutt, J., Hindell, M. A., Hofmann, E. E., Hosie, G. W., Iido, T., Jacob, S., Johnston, N. M., Kawaguchi, S., Kokubun, N., Koubbi, P., Lea, M., Makhado, A., Massom, R. A., Meiners, K., Meredith, M. P., Murphy, E. J., Nicol, S., Reid, K., Richerson, K., Riddle, M. J., Rintoul, S. R., Smith Jr. W. O., Southwell, C., Stark, J. S., Sumner, M., Swadling, K. M., Takahashi, K. T., Trathan, P. N., Welsford, D. C., Weimerskirch, H., Westwood, K. J., Wienecke, B. C., Wolf-Gladrow, D., Wright, S. W., Xavier, J. C. and Ziegler, P. (2014). Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. *Global Change Biology* 20, 3004–3025, <https://doi.org/10.1111/gcb.12623>.

on copepods were uniformly positive, while those on Antarctic krill were positive in the Antarctic and negative in the sub-Antarctic. Clearly the impacts of climate change and other future changes in Southern Ocean oceanography are uncertain, and a great deal more remains to be learned about how this unique system will respond in the future.

Summary

The Southern Ocean is changing as a result of natural and anthropogenic changes. Such changes have occurred in the past, but the region is now changing faster than ever before. Given the dependence of Southern Ocean plankton on the physical environment, Antarctic plankton are expected to change dramatically as well. Despite our understanding of this change, it is challenging to document, given the difficulty of sampling at appropriate spatial and temporal scales in such a harsh environment. However, substantial progress has been made in recent years, and further advances will come with the development of new technologies to sample the remote areas of the ocean. Understanding the changes and their ecological impacts is difficult, but essential to protect and conserve this pristine environment.

Acknowledgments

Preparation of this manuscript was supported in part by NSF grant OCE-1657855 (WOS). We thank our colleagues who made photomicrographs available to us for use in this manuscript.

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Antarctic Marine Mammals

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Abstract

Sixteen species of cetaceans and pinnipeds frequent the Antarctic biome to various extents, from its northern limit in the Southern Ocean at the Antarctic Polar Front down to the Antarctic Continent that is fringed by numerous Antarctic islands and the seasonally contracting and expanding pack ice and fast ice. Each species is considered within Antarctic biome context, emphasizing their distribution, abundance, biomass, life history, seasonality and foraging ecology. In the face of likely direct and indirect anthropogenic impacts on Antarctic marine mammals, threats to, and the conservation status of these animals are also considered.

Introduction

This article considers only those marine mammal species found regularly south of the Antarctic Polar Front (APF), the oceanic region that marks the northern limit of the Antarctic Zone. For the 16 species dealt with here, the taxonomy, origin of species names, physical appearance and identification appear exhaustively in various publications such as [Watson \(1981\)](#), [Laws \(1993\)](#), [Reeves](#)

et al. (2002), Perrin et al. (2009), Hund (2014), Bester et al. (2017), and Würsig et al. (2018). I therefore concentrate on the distribution, abundance, body size and foraging ecology (diving characteristics and diet) of the selected species, i.e., those characteristics that make sense in a biome context and are likely to respond to the shifting of the state of the world's oceans that is magnified in polar regions. Such shifts may include increased acidity, warmer seas, higher sea levels, reduced sea ice, and regionally variable shifts in productivity and marine biodiversity (Moore, 2018). I also consider the threats to these Antarctic marine mammals in the face of perceived human impacts. These include climate change (Nicol et al., 2008; Evans et al., 2010; Massom and Stammerjohn, 2010; Turner et al., 2014; Moore, 2018), sealing/whaling, ship strikes, underwater noise, tourism, marine litter, chemical pollution, disease, and entanglement in fishing gear (Bester, 2014a; Risch et al., 2019).

Details of cetaceans and pinnipeds were gleaned primarily from Watson (1981), Laws (1993), Stewardson (1997), Rice (1998), Reeves et al. (2002), Berta et al. (2006), Best (2007), Bester and Hofmeyr (2007a); Fontaine (2007), Simmonds and Isaac (2007), Siniff et al. (2008), Perrin et al. (2009), Kovacs et al. (2012), Southwell et al. (2012), Parsons (2013), Ropert-Coudert et al. (2013), McIntyre et al., 2014; Hund (2014), Bester et al. (2017), Würsig et al. (2018), and Risch et al. (2019).

Cetacea

Based on their ecological requirements, Antarctic cetaceans can be divided into three groups: those associated with fast ice, those associated with pack ice, and those that live in the open ocean (Boyd, 2009). The Antarctic minke whale (*Balaenoptera bonaerensis*), southern bottlenose whale (*Hyperoodon planifrons*), and killer whale (*Orcinus orca*) regularly associate with the Antarctic sea ice zone throughout the year. Sperm whales (*Physeter macrocephalus*), blue whales (*Balaenoptera musculus*), and Arnoux's beaked whales (*Berardius arnuxii*) are often found at or within the ice edge during summer. Humpback whales (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*), both cosmopolitan cetaceans, regularly occur south of the APF and their vocalizations were detected by hydrophone in the Antarctic coastal area off the Ekström Ice Shelf in both winter and summer (vide Bester et al., 2017). The hourglass dolphin (*Lagenorhynchus cruciger*) and southern right whale (*Eubalaena australis*) also penetrate the APF. Although listed as true Antarctic species (Lowther, 2018), I disregard sei whales (*B. borealis*), long-finned pilot whales (*Globicephala melas*) and strap-toothed whales (*Mesoplodon layardii*), as they are rarely found south of the APF in the Antarctic.

Antarctic Minke Whale

The Antarctic minke whale *B. bonaerensis* (Fig. 1A) has a circumpolar distribution and is abundant from 60°S to the ice edge during summer. They also occur in the loose pack ice and polynyas, and in more consolidated ice. Some overwinter in the Antarctic, but most retreat to breeding grounds in the mid-latitudes off Australia, South Africa and Brazil. The most recent estimate of overall abundance of Antarctic minke whales is around 500,000 individuals, down from an estimated 720,000 in earlier assessments (Risch et al., 2019). Perhaps these estimates represent a real decline in minke whale numbers, although this is unclear.

This whale grows to 8.9–9.0 m and 8.5–8.6 m at maturity in females and males respectively, and they weigh an estimated 9000–10,000 kg. Estimated longevity is >40 years and the age of sexual maturity is 5–9 years in both sexes. It is thought that peak calving takes place in July and August in warmer waters at low latitudes after a pregnancy of ~10 months. The nursing period appears to last 5–6 months, with a peak in conceptions between August and November. Conception probably takes place in winter in warmer waters, and a calving interval of 14 months (equivalent to a calving rate of about four calves every 5 years) suggests that females eventually get out of phase with the breeding season, and then must pass into a resting stage once lactation has ended.

Minkes feed predominantly on euphausiids (krill), with no substantial fish component to their diet, both on their summer feeding grounds and winter migrations. At the ice edge and offshore of the ice-edge zone, krill (*Euphausia superba*) dominates their diet. They feed close to the surface. Their diving behavior is unknown, but the intervals between visible blows suggest that dives are usually rather short (most less than 2 min) and shallow (perhaps <60 m). Within the Antarctic biome they may range as far south as 65°S, but generally are more common on the feeding grounds north of 60°S during the austral summer.

Threats and Conservation Status

Minkes are fully protected in their range since a moratorium on commercial whaling began in 1986/87. Japan continues to take Antarctic minke whales annually, purportedly for purposes of scientific research. Their nonaggregating nature and remote foraging habitat shelter them from other direct interactions with human activities while in Antarctica. Perhaps the most important threat is the loss of foraging habitat accompanying ocean climate warming and constriction of seasonal pack ice. Whales that use sea ice and ice-edge habitats are at risk as they prey on species linked with the pack ice ecosystem. Antarctic minke whales are listed as "Near Threatened" under the IUCN Red List. They are included on Appendix I of CITES, as well as Appendix II of the Convention on Migratory Species (CMS).

Arnoux's Beaked Whale

Arnoux's beaked whales *B. arnuxii* (Fig. 1B) have a circumpolar distribution, ranging from the Antarctic continent and ice edge to temperate waters. Frequently found in summer in the Antarctic, and in the pack ice in August, individuals sometimes become trapped by ice and are forced to overwinter in the Antarctic. Their simultaneous presence off the coasts of southern continents and in the Antarctic in summer suggests different populations, but their wintering and breeding grounds, and their population size are unknown.

The largest known Arnoux's beaked whale is 10.06 m long. Body mass of adults, maximum life expectancy, the ages of sexual maturity and the reproductive cycle are unknown. These whales are accomplished divers, with dive durations within leads in the Antarctic pack ice averaging 35–65 min, and a maximum of at least 70 min. They are presumably cephalopod feeders, based on unidentified beaks found in the stomach of only one individual. They may also take deep-sea fish.

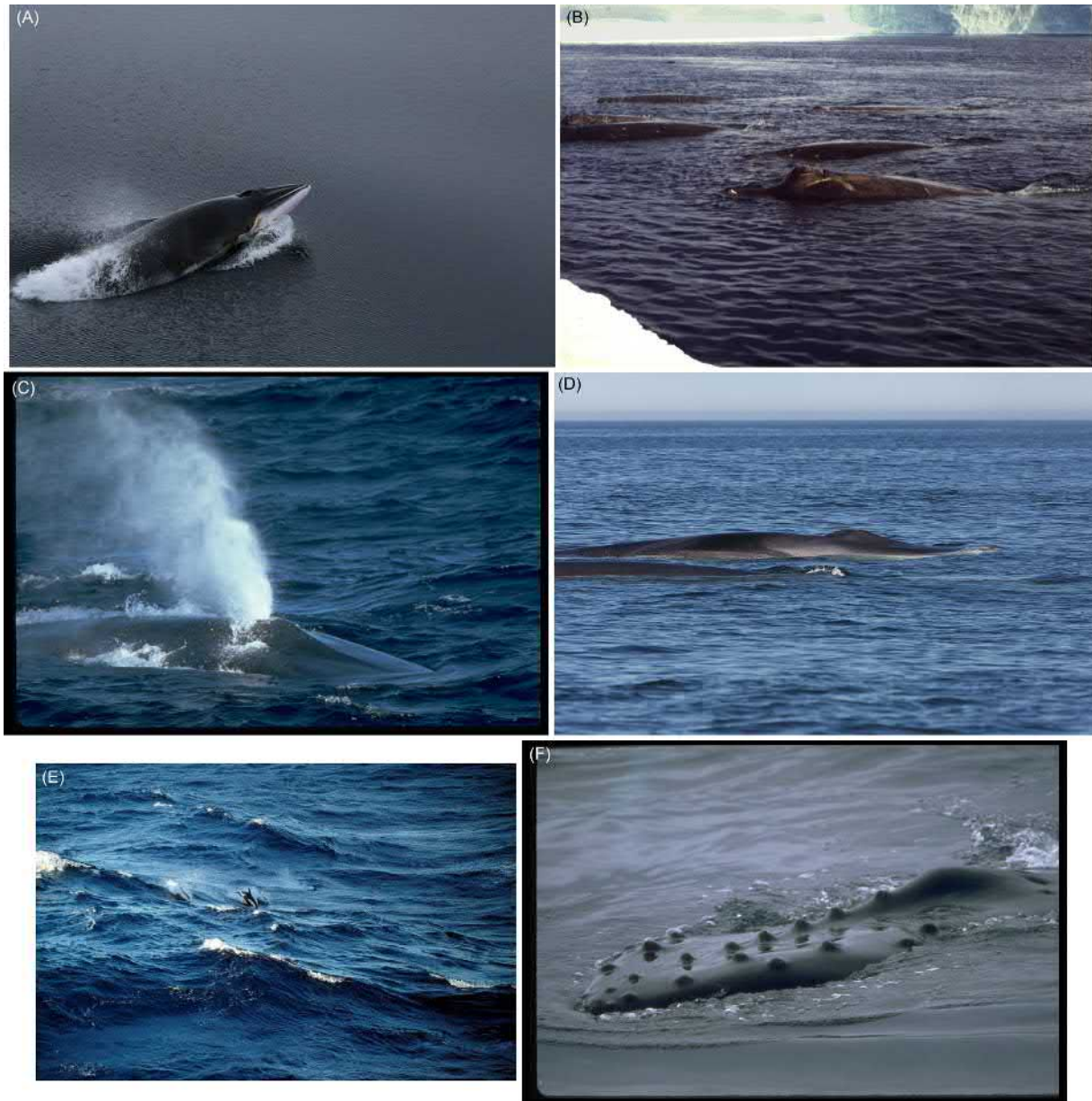


Fig. 1 Antarctic cetaceans. (A) Antarctic minke whale, (B) Arnoux's beaked whales, (C) blue whale, (D) fin whales, (E) hourglass dolphins, (F) humpback whale, (G) killer whales, (H) southern right whale, and (I) sperm whale. (A) Photograph by H. Huang, GEOMAR. (B) Photograph by Horst Bornemann, AWI. (C) Photograph by S. Elias, UC. (D) Photograph by S. Golaski, Simon Elwen: Sea Search. (E) Photograph by B. Dyer, DEA. (F) Photograph by S. Elias, UC. (G) Photograph by H. Huang, GEOMAR. (H) Photograph by D. du Plessis, Simon Elwen: Sea Search. (I) Photograph by S. Elias, UC.



Fig. 1 (continued).

Threats and Conservation Status

The greatest threat to this species is the loss of foraging habitat accompanying ocean climate warming and constriction of seasonal pack ice, especially for those that use ice-edge and pack ice habitats for foraging. Arnoux's beaked whale is listed as "Data Deficient" by the IUCN, and included in Appendix I of CITES, but not listed by CMS.

Blue Whale

Antarctic blue whales *B. musculus* (Fig. 1C) have a circumpolar distribution, and are abundant south of 60°S, especially close to the edge and within the pack ice in summer. Most of these whales may not move more than 90 degrees of longitude while in high latitudes. Much of the population migrates to low latitudes in winter, although some overwinter in the Antarctic. No specific winter breeding ground is known for blue whales. After their virtual extinction by whaling, blue whale populations are increasing in the higher latitudes of the Antarctic, with perhaps a still-small population of about 1700 present in 1996.

Blue whales are the largest animals ever to have lived on Earth. Females grow to a length of 25.9 m and males grow to 24.1 m. Body weights of adults generally range from 50,000 kg to 150,000 kg, although one female specimen taken in 1947 weighed 190,000 kg. The maximum life expectancy of blue whales ranges from 65 to 70 years to greater than 80–90 years. Their age of sexual maturity is probably about 8–10 years in both sexes. The reproductive cycle is perhaps 2 or possibly 3 years, including a resting period. Calving takes place between late March and early July at low latitudes, after a pregnancy of approximately 12 months. The nursing period appears to last 7 months, followed by a resting stage, resulting in females being pregnant sometimes at intervals of more than 2 years.

Krill (*E. superba*) dominates the blue whale diet at the ice edge and in high latitudes, with copepods and amphipods also taken. Short shallow dives are most common, lasting generally 8–15 min, although 20 min dives occur frequently. Shallow dives (10–20 consecutive dives) are often followed by a deep dive of 10–30 min.

Threats and Conservation Status

This species has been fully protected from commercial whaling since 1986/87. The loss of foraging habitat accompanying ocean climate warming and constriction of seasonal pack ice may be a threat, especially for those that use ice-edge habitats. The blue whale is listed as "Endangered" by the IUCN, and included in Appendix I of both CITES and CMS.

Fin Whale

The fin whale *B. physalus* (Fig. 1D) occurs worldwide in all oceans. They migrate from summer feeding grounds in high latitudes, where they avoid the ice edges, to winter breeding grounds in lower latitudes, however, the actual locality of their breeding grounds remain unknown. South of 37°S an estimated 38,200 individuals frequent temperate and cold waters, with perhaps 2100–5500 living in the Antarctic south of 60°S.

Fin whales grow to 21 m in males and 22 m in females; sexual maturity is attained at ages of about 6–7 years in males and 7–8 years in females. Adult fin whales weigh 60,000–80,000 kg. Their life span is most likely around 100 years. Gestation is 11 months, and the calving interval is usually 2 years. The nursing period lasts 6–7 months, followed by a 6-month resting period. The nursing period rarely extends to 12–13 months.

Fin whales feed almost exclusively on krill in the Antarctic region, while during their winter migration they also take copepods, amphipods and occasionally fish (unidentified). They normally lunge-feed and their dives are limited to 100–200 m, lasting 3–10 min. Their deeper dives coincide with the upward vertical migration of krill.

Threats and Conservation Status

Fin whales have been fully protected from commercial whaling since 1986/87, although a small number is taken for scientific purposes. Collisions with vessels, incidental catches in fishing gear and anthropogenic noise are of little consequence in the remote Antarctic zone, and insignificant at the population level. This species is listed as “Vulnerable” by the IUCN, and included in Appendix I of CITES and on Appendices I and II of CMS.

Hourglass Dolphin

Only found in the southern ocean, the hourglass dolphin *L. cruciger* (Fig. 1E) occurs in areas on and south of the APF in the South Atlantic and South Pacific, and all the way to the edge of the pack ice in summer. They may migrate south in summer to higher latitudes. They are relatively common in cold southern waters, and an estimated 144,300 individuals occur south of the APF in summer.

Adult hourglass dolphin males grow to 1.78 m and adult females to 1.83 m. Body weights of adults are unknown but may reach 100 kg or more. Maximum life expectancy, the ages of sexual maturity and the reproductive cycle are insufficiently known. They seem to prey primarily on midwater species at night, including a wide range of cephalopods and both myctophid and hake fish.

Threats and Conservation Status

The remote and harsh environment associated with this species has thus far prevented large-scale human impact. Changes in foraging habitat adjacent to the constricting seasonal pack ice accompanying ocean climate warming may change this. This species is listed as “Least Concern” by the IUCN and included in Appendix II of CITES, but they are not listed by CMS.

Humpback Whale

The humpback whale *M. novaeangliae* (Fig. 1F) a cosmopolitan species of baleen whale, moves between summer feeding grounds in high latitudes within the APF and winter breeding grounds in lower latitudes. It does not enter the pack ice zone, but forages up to the ice edge during summer. Some humpbacks remain in the Antarctic during winter. Heavily exploited in the past, there are possibly about 80,000 in the Southern Hemisphere as of 2015.

Mature humpbacks typically grow to 11–17 m and weight 20,000–35,000 kg, although in the past some grew to 19 m and weighed as much as 40,000 kg. The heaviest specimen on record was a male that weighed in at 59,400 kg and was 14.2 m long. This whale stranded in July 1995 (Best, 2007). The estimated longevity of humpback whales is 45–100 years with the age of sexual maturity about 4–5 years in both sexes. Females have their first calf at around 11–12 years. Gestation is 11–12 months, with the females producing calves usually every 2 years. The nursing period lasts 10.5–11 months.

Humpbacks have a diet that varies with season and foraging area. They feed on krill *sensu lato*, amphipods, stomatopods (mantis shrimp) and pelagic schooling fish. They forage near the surface, extending down to 15 m, and are known to dive to 150 m. Deep dives last < 10 min in summer and about 15–20 min in winter. These dives can extend to 45 min. Hunting for food is a communal effort on the higher latitude feeding grounds in summer.

Threats and Conservation Status

Humpbacks are resilient to depletions, and it appears that stocks are recently recovering. Entanglement in fishing gear or collisions with ships take a toll, but these hazards appear insignificant at the population level. Being a very vocal species during migration and

breeding, anthropogenic noise may impact the species, although less so in the Antarctic biome. Humpbacks are now listed as “Least Concern” by the IUCN, and included on Appendix I of both CITES and CMS.

Killer Whale

The killer whale *O. orca* (Fig. 1G) is a cosmopolitan dolphin species with the highest densities in high latitudes and largest numbers occurring in Antarctica. An overall pattern of migration is suggested, with most killer whales found in warm waters in winter and in high latitudes in summer. Killer whales recorded south of 60°S in mid-winter within the pack ice might be restricted to an “ecotype(s)” that might forego migration. Killer whales present a range of behavioral, social and morphological characteristics that are interpreted as evidence to categorize individuals or groups. Although morphologically distinct forms (Type A, B, C, and D) seem to occur in the Southern Ocean, ecotypic status classification for Southern Ocean killer whale morphotypes lacks sufficient evidence-based ecological and taxonomic data (de Bruyn et al., 2012). The Antarctic summer population was estimated at about 80,400 in the period 1976–1988.

Killer whales grow up to 9.0 m, though the females rarely exceed 7.9 m. Adults weigh from 3079 to 7903 kg. The maximum lifespan of males is 50–60 years, and females live about 80–90 years. The age of sexual maturity is about 12–16 years in females and 10.5–17.5 years in males, with physical maturity attained at a mean age of 21 years. Calving may take place year-round, with peaks in autumn and spring depending upon locality, after gestation periods of 15–18 months. The nursing period lasts about 18 months. Estimated average calving intervals in the Antarctic are between 3.5 and 5.2 years. Females give birth for the first time at 12–16 years.

Killer whales feed on just about anything at sea, especially marine mammals, fish, birds, and turtles. Diet specialization amongst different communities of killer whales in the Northern Hemisphere, broadly classified as fish-eating (residents) and mammal-eating (transients), may also have developed amongst killer whales within the Antarctic. They hunt singly or cooperate to hunt large prey such as cetaceans and to maintain balls of baitfish. They also steal fish from long-lines and scavenge on discarded fishery bycatch.

They generally dive to depths below 150 m, reaching a maximum of 330+ m, but remain mostly in the top 20 m of the water column. Group diving and surfacing can become synchronized and regular with a series of short, shallow dives (e.g., 5–12 dives of 10–30 s), followed by a dive, perhaps deeper, that can last 3–5 min. Dives of up to 30 min are common, but killer whales do not have well-defined and characteristic blowing and surfacing behavior.

Threats and Conservation Status

This species frequently scavenges fish from long-line and other hook-and-line fisheries in the Southern Ocean, resulting in large losses of catch. Fishermen purportedly retaliate by shooting offending killer whales. Ocean climate warming and the resultant constriction of seasonal pack ice may have an influence on killer whales that perhaps preferentially frequent pack ice habitats. Killer whales are listed as “Data Deficient” by the IUCN, and are included in Appendix II of CITES, and CMS.

Southern Bottlenose Whale

Southern bottlenose whales (*H. planifrons*) have a circumpolar distribution, ranging from the Antarctic ice edge to temperate waters, generally south of about 30°S. Frequently sighted in summer from October to March in the Antarctic, they can occur at the ice edge, their highest densities being within 111 km of the ice edge. Sightings suggest a migratory pattern with a northwards movement from higher latitudes in late summer, and a movement back south again in spring, but their wintering grounds are unknown. They are abundant, with an estimated 600,000 beaked whales south of the APF, mostly southern bottlenose whales.

Adult males reach a length of 7.0 m and adult females 7.45 m. Body weights of adults are unknown but may reach at least 3400 kg. Maximum life expectancy, the ages of sexual maturity and the reproductive cycle are not known, apart from a female of 5.7 m lactating. They are cephalopod feeders and squid of both Antarctic and Subantarctic origin were isolated from only two stomachs (collected in mid-latitude South African waters), while a stomach from south of the APF at Heard Island (15 species of nine families of squid) also had remains of Patagonian tooth fish. Likely to be accomplished divers, dive durations of an hour or more are punctuated by blows every 30–40 s. Dive cycles recorded for 12 groups of beaked whales (presumably mostly bottlenose whales) in the Antarctic had mean submergences of 25.3 min, interspersed with surfacing bouts of on average 3.7 s.

Threats and Conservation Status

This species has little direct involvement with fisheries. Loss of foraging habitat accompanying ocean climate warming and constriction of seasonal pack ice might play a role. The southern bottlenose whale is listed as “Least Concern” by the IUCN and included in Appendix I of CITES, but not listed by CMS.

Southern Right Whale

The southern right whale *E. australis* (Fig. 1H) occurs throughout the middle latitudes of the Southern Ocean, between approximately 20 and 60 degrees latitude. They migrate from southern middle latitudes as winter begins and stay more-or-less near continents where they breed near coastlines. The total number of southern right whales may exceed 25,000–30,000 animals.

These whales grow to 12–18 m as adults, and weigh up to 60,000 kg, with the females being slightly larger. The largest known specimens weigh in excess of 100,000 kg. They become sexually mature at 8–10 years, and the females produce calves every 3–5 years. Their life span ranges from 50 to more than 70 years. They are skimmer and lunge-feeder specialists, taking krill, primarily *E. superba* in the Antarctic. However, in the lower latitudes they also feed on other euphausiids, amphipods, copepods and fish (unidentified). Feeding occurs at or near the surface, although sometimes much deeper. Their dives last for 10–20 min.

Threats and Conservation Status

Indications are that global climate change and warming sea-surface temperatures drive this species' population dynamics (Leaper et al., 2006). Inadvertent entrapment in fishing gear and collision with ships, although unlikely in the Antarctic, may have a negative effect. The southern right whale is protected throughout its range. This species is listed as "Least Concern" by the IUCN and included on Appendix I of both CITES and CMS.

Sperm Whale

Widely distributed in both Northern and Southern Hemispheres, the sperm whale *P. macrocephalus* (Fig. 1I) is the largest of the toothed whales. They occur from the tropics to the Antarctic ice edge. Only adult males move from tropical and temperate waters to the ice edge in summer, with females and immatures seldom found beyond 40°S. Movements and migrations are associated with food availability. Sperm whales were heavily exploited from the early 18th century to the late 20th century, and their worldwide population is estimated at 360,000, down from a prewhaling population of about 1,110,000.

Sperm whales grow to 17.3 m, although males of 20 m or more are known from historic records. Females rarely exceed 11.7 m. Adult sperm whales weigh from 10,800 kg to in excess of 32,700 kg. Their maximum life expectancy (both sexes) is at least 60–70 years, and age of sexual maturity is about 9 years, although males only reach social maturity at an age of 25–27 years. The reproductive cycle perhaps lasts 4–6 years, with calving between January and April, after a pregnancy of 15–16 months. The nursing period apparently lasts on average 2 years, the next calf being born after an interval of about 5 years. Large, mature males in their late 20s and older return to tropical breeding grounds to mate, and usually roam independently between groups of females.

Sperm whales principally eat medium-sized squid, and they also take demersal and mesopelagic fish, amongst others. Giant squid (*Architeuthis* spp.) and jumbo squid (*Dosidicus* spp.) are also taken. Males eat species that are largely restricted to higher latitudes such as the colossal squid, *Mesonychoteuthis hamiltoni*, of Antarctic waters. While foraging, sperm whales make repeated deep dives with a modal depth of 600 m. These dives last about 45 min. Recovery periods between dives at or near the surface are about 9 min. Dives can be deeper (to over 1000 m), shallower (depending on the bathymetry) and longer (over an hour). The longest recorded dive lasted at least 2 h 18 min, while the deepest was to 2035 m.

Threats and Conservation Status

The most abundant of the large whales, and fully protected from commercial whaling by the IWC moratorium on commercial whaling since 1986/87, interactions between sperm whales and longline fishing for Patagonian toothfish, may have an effect. Inadvertent entrapment in fishing gear and collision with ships, although unlikely in the Antarctic, may have a negative effect. Sperm whales are listed as "Vulnerable" by the IUCN and included in Appendix I of CITES, and on both Appendices I and II (presumably different populations) of CMS.

Pinnipedia

Four phocid species, the crabeater seal (*Lobodon carcinophaga*), leopard seal (*Hydrurga leptonyx*), Ross seal (*Ommatophoca rossii*), and Weddell seal (*Leptonychotes weddellii*), are intimately tied to the circumpolar Antarctic sea ice. Another phocid, the southern elephant seal (*Mirounga leonina*), and one otariid species, the Antarctic fur seal (*Arctocephalus gazella*), breed almost exclusively on both Antarctic and Subantarctic islands and some age/sex classes migrate seasonally to the sea ice to forage. Occasional visitors to the Antarctic biome such as the Subantarctic fur seal *A. tropicalis*, are not considered here.

Antarctic Fur Seal

The Antarctic fur seal *A. gazella* (Fig. 2A) breeds on Southern Ocean islands, mostly south of the APF (Hofmeyr et al., 2016) primarily at South Georgia. Numerous smaller populations within the Antarctic biome breed on Bouvet, Heard, McDonald, Kerguelen, South Shetland, South Sandwich, and the South Orkney islands. There are an estimated 2–3 million Antarctic fur seals (Hofmeyr et al., 2016).

Adult females may grow to ~1.45 m and weigh 50 kg. Adult males grow to 2 m and weigh 230 kg. Females may live to about 23 years and become mature sexually at ~2–5 years, pupping after a gestation period of about a year. Males may survive to 14 years and become mature sexually at ~3–4 years and socially at ~7 years when they may control harems on breeding colony beaches. The age of first pupping is 3 years, and all females pup by age 6 years, usually producing one pup at a time. The breeding season extends from late November to late December, with the peak pupping date in the range 4–8 December, and births are highly synchronized, 90% occurring within ~21 days. Males are fiercely territorial during the breeding season when they mate with females within about 7 days after these females have given birth to a pup. Subsequently, females undertake foraging trips of about 1 week long, punctuated by periods of ~3 days ashore to attend to their pups, although overnight trips also take place. Weaned at 4 months old, pups finally depart to sea after molting their black pelage. Molting of older animals is gradual and completed by the time they become pelagic. Females remain at sea continually between breeding seasons, although some return



Fig. 2 Antarctic pinnipeds. (A) Antarctic fur seals, (B) crabeater seals, (C) leopard seal, (D) Ross seal, (E) southern elephant seals, and (F) Weddell seals. (A) Photograph by C. Oosthuizen, MRI. (B) Photograph by N. Lübcker, MRI. (C) Photograph by C. Oosthuizen, MRI. (D) Photograph by M. Wege, MRI. (E) Photograph by H. Bornemann, AWI. (F) Photograph by H. Bornemann, AWI.

to their breeding localities for short periods during winter. Male Antarctic fur seals migrate southward during the postbreeding period.

Males dive deeper (~354 m) and longer (~9 min) than females (~208 m and ~4 min). These seals are nocturnal foragers, employing short, shallow dives throughout the night (~1 min to ~15 m depth, rarely >126 m). Deeper, longer dives occur towards dawn and dusk as they presumably follow vertically migrating prey. They usually take myctophid fish, cephalopods, krill, pelagic icefish, and nototheniids, but their prey varies geographically and within areas and seasons. Males may also kill and eat gentoo, king and macaroni penguins.

Threats and Conservation Status

Killer whales *O. orca* and leopard seals *H. leptonyx* prey on fur seals. Their foraging range overlaps with fishery activities, especially long-lining and trawling. Individuals frequently become entangled in lines, hooks and strapping which may result in death. Probable sensitivity to climate-change related alterations in habitat and predator responses are potential threats (e.g., [Forcada et al., 2005](#)). This seal's population size and distribution are likely influenced by changes in their food resources due to significant sea ice loss, leading to open water and the possible resultant expansion of the krill fishery in the future.

The Antarctic fur seal is listed as "Least Concern" on the IUCN Red List and is protected under legislation of the various states that have sovereignty of island sites; within the Antarctic Treaty Area it is protected under the Protocol on Environmental Protection to the Antarctic Treaty, but it is no longer designated a specially protected species. However, it is fully protected under the Convention for the Conservation of Antarctic Seals (CCAS) and the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR).

Crabeater Seal

Breeding populations of crabeater seals *L. carcinophaga* ([Fig. 2B](#)) are confined to the circumpolar pack ice of Antarctica ([Hund, 2014](#)). Most abundant in pack ice habitats and rarely frequenting open waters, they tend to stay over the continental shelf during the breeding season, but are more widespread in the pack ice during summer and autumn. An Antarctic-wide estimate of crabeater seals ranges between 7,000,000 and 15,000,000.

Crabeater seals grow to 2.65 m long, rarely 277 cm, and adults weigh around 210 kg, rarely attaining 410 kg. Females are usually larger than males. Their maximum longevity is 40 years, but a typical life span is 20–25 years. They mature sexually at approximately 4–5 years of age. Pups are born from October to early November, perhaps into December, the exact timing varying by region. Mating presumably takes place in the water in pack ice habitats from December to early January, within approximately 4 days after females wean their single pups following about 2–3 weeks of nursing, the exact timing of which may vary regionally. Pupping season probably varies with location. Crabeater seals molt through January to March.

The mean dive depth ranges of these seals is from 40 to 140 m, rarely to 713 m, and usually lasts less than 5 min. Diving patterns vary seasonally, preferentially during darkness. They haul out during daylight in summer and autumn. Overall, these seals dive deeper in winter (average 92 m, range 6–713 m) and longer (on average 5.26 min, range 0.2–23.6 min). During winter they also haul out during the night rather than the day ([Burns et al., 2004](#)). Diurnal or diel patterns in the diving behavior of the seals are likely in response to diel vertical migrations of prey. Seasonal shifts in foraging patterns, consistent with foraging on vertically migrating prey, also occur. Contrary to what their name suggests, crabeater seals feed primarily on Antarctic krill, but also eat fish and cephalopods when krill is not available.

Threats and Conservation Status

Climate-change related alterations in habitat and constriction of seasonal pack ice will likely affect them most. A major krill consumer, recent rapid environmental change has led to sea ice loss and a less predictable, declining krill biomass is likely to have detrimental effects. Sea ice loss will reduce suitable breeding and resting habitat, as well as protection from predators. It will also increase the distance these seals must travel to reach feeding grounds. These factors may combine to potentially reduce food for pack ice seals in general, and for crabeater seals in particular ([Forcada et al., 2012](#)).

Crabeater seals are listed as "Least Concern" on the IUCN Red List. They are protected under the Protocol on Environmental Protection to the Antarctic Treaty. Crabeaters are also protected under the CCAS, Annex I of which provides for commercial harvests of limited numbers, as do the CCAMLR, Article II.

Leopard Seal

The breeding populations of leopard seals *H. leptonyx* ([Fig. 2C](#)) are confined to the circumpolar pack ice of Antarctica ([Hund, 2014](#)). They occur all around the Antarctic continent and are most abundant in pack ice and fast-ice habitats especially along the Antarctic Peninsula. An Antarctic-wide estimate of leopard seals is somewhere between 220,000 and 440,000.

Leopard seals grow to about 4.5 m long and weigh up to 600 kg, with females being larger than males. Maximum longevity is possibly up to 25 years, and sexual maturity may be attained at 4–5 years of age. Pups are likely born from October to mid-November. Mating occurs from December to early January, evidently in the water, at about the same time as females wean their pups. Females likely nurse their pups for a month, or perhaps less. The exact timing may be dependent on the region of the Antarctic and the pupping season probably varies with location. Leopard seals molt through January to February.

Leopard seals are primarily short (~2 min) shallow divers, mostly to depths of 10–50 m and only occasionally ≥ 200 m. They feed on a variety of prey including fish, cephalopods, crustaceans, penguins, and other seals. The composition of their diet varies between seasons and regions.

Threats and Conservation Status

The nonaggregating nature and remote breeding habitat of leopard seals shelter them from direct interactions with commercial fishing activities. The most important threat may be the loss of breeding habitat accompanying ocean climate warming and constriction of seasonal pack ice. The effects of changes in sea ice on leopard seal foraging seem unlikely to be detrimental since they often forage at considerable distances from the continent, beyond the sea ice. Population size and distribution may be altered through changes in food web dynamics. Their nonbreeding season foraging north of pack ice zones may overlap with southern elephant seals, Antarctic fur seals and other migratory Subantarctic marine vertebrates.

Leopard seals are listed as “Least Concern” on the IUCN Red List, it is protected in its range under the Protocol on Environmental Protection to the Antarctic Treaty and under the CCAS, Annex I of which provides for commercial harvests of limited numbers, as does the CCAMLR, Article II.

Ross Seal

Ross seal *O. rossii* (Fig. 2D) breeding populations are confined to the circumpolar pack ice of Antarctica (Bester and Hofmeyr, 2007b; Hund, 2014). Areas of higher density appear to be in the Ross Sea, the King Haakon VII Sea and perhaps parts of the western Weddell Sea. An Antarctic-wide population estimate is 130,000–220,000 individuals.

Ross seals reach 2–2.5 m and weigh up to 216 kg. Their estimated longevity is 21 years with age of sexual maturity at 3–4 years for males and 2–7 years for females. Pups may be born from mid-October through November, mating probably occurring in December and early January. The nursing period seems to be 13 days in mid-November, and perhaps up to a month overall, with mating occurring at the end or shortly after the nursing period, likely from the last week of November. Exact timing depends on the region of the Antarctic and the pupping season probably varies with location. Ross seals molt from late December, but especially through late January to early February. Just after the molt in February, adults head north and stay pelagic in the area south of the APF, until October when they go south into the pack ice.

Throughout the year they make about 100 dives a day, mostly to a depth of 100–300 m, the deepest being 792 m. Most dives, outside the breeding and molting period, last for 5–15 min. They feed on mid-water Antarctic silverfish, squid, and to some extent krill (*E. superba*), when in the pack ice, and myctophid fish and several species of squid, when in the open ocean.

Threats and Conservation Status

The apparent solitary behavior and broad distribution of nonbreeding seals may reduce direct interactions with commercial fishing activities. The loss of breeding habitat accompanying ocean climate warming and constriction of seasonal pack ice may be a threat. However, the latter might not be detrimental since Ross seals often forage at considerable distances from the continent, beyond the sea ice. Population size and distribution may be altered through changes in food web dynamics and their foraging habitats north of pack ice zones outside of the breeding and molting seasons may overlap with southern elephant seals and other migratory Subantarctic marine vertebrates.

Ross seals are listed as “Least Concern” on the IUCN Red List, it is protected in its range as Specially Protected Species under Annex II to the Protocol on Environmental Protection of the Antarctic Treaty, and under the CCAS.

Southern Elephant Seal

South of the APF, southern elephant seals *M. leonina* (Fig. 2E) breed almost exclusively on islands and occasionally on seasonal pack ice near Signy Island, South Orkney Islands (Laws, 1956; Le Boeuf and Laws, 1994). Large populations breed on South Georgia, Iles Kerguelen and on Heard Island with numerous smaller populations primarily on the South Shetland, South Sandwich and the South Orkney islands (Hund, 2014). Elephant seals primarily use beaches for breeding, and vegetated areas inland from breeding beaches during the month long molt haul-out. A Southern Ocean wide estimate of their numbers is around 650,000 (de Bruyn et al., 2016).

Females may grow to about 2.8 m and weigh up to 900 kg. Adult males are considerably larger, growing up to 5 m in length and weighing up to 5000 kg. They live to 23+ years; females become sexually mature at about 2–6 years, while males are able to breed at

about 4–5 years but mature socially at 6–8 years. The majority of breeding bulls are 9–12 years old. Females aged 3–23+ years give birth to single pups from late September to early November, usually within aggregations of two or more females. The largest known aggregation was 1600 females, observed on Heard Island in October 1985 (Bester, 2014b). Pups nurse for a period of 3 weeks, to late November, with the timing of events usually delayed at higher latitudes. Just before the pups wean, females mate on land with dominant beachmasters, including with assistant beachmasters in harems greater than 60 females. After the breeding season, adults depart to sea, then return for a drastic molt on land from December to March, with younger age classes commencing the molt as early as November.

Elephant seals dive deeply, feeding primarily in the mid-water regions of the water column at depths of around 200–600 m. Their dives last about 20–30 min, and go as deep as 2133 m. These very deep dives may last 2 h. They spend up to 90% of their time at sea, diving with surface intervals of ~2–3 min. They show diel diving patterns, diving to shallower depths at night, and to greater depths during the day. These diving patterns are likely a response to vertically migrating prey. Myctophid fish and cephalopods are the usual prey, although their diet may vary substantially with latitude as well as within areas and seasons.

Elephant seals move predictably: there is a postbreeding pelagic period of about 2–3 months in females (approximately late October to mid-January) and of about 6 months in males, where they may remain in reasonably well circumscribed areas during their 8 month postmolting period. Their feeding grounds are 2000–3100 km distant from shore. These numbers vary in different populations and with the bathymetry of their foraging areas, as well as whether the animals use a pelagic or benthic diving strategy (McIntyre et al., 2011, 2012). Elephant seals from a number of breeding populations in particular exploit the marginal sea ice zone and areas of increased productivity associated with the ice edge, whilst avoiding areas of persistent ice cover. They also exploit areas of high sea-ice concentrations (e.g., Tosh et al., 2009), usually seals tracked from high latitude breeding colonies, such as those located around the Antarctic Peninsula and some of the southern-most islands.

Threats and Conservation Status

Depleted populations of elephant seals have recovered under protection after commercial exploitation, but then their numbers declined from the 1950s. A subsequent stabilization followed, and their numbers are currently increasing. Their foraging ranges overlap with fisheries activities, especially long-lining for Patagonian toothfish, and individual seals frequently become entangled in lines and hooks. The distribution and abundance of the ice-tolerant southern elephant seal will be the least negatively influenced by changes in pack ice characteristics due to climate change. Population size and distribution may also be influenced by changes in their food resources due to factors other than climate.

Southern elephant seals are listed as “Least Concern” on the IUCN Red List. It is also protected under legislation of the various states that have sovereignty of island sites. Within the Antarctic Treaty Area they are protected under the Protocol on Environmental Protection to the Antarctic Treaty, the CCAS and the CCAMLR.

Weddell Seal

The breeding populations of the Weddell seal *L. weddellii* (Fig. 2F) are largely confined to the circumpolar fast ice and some pack ice habitats of Antarctica (Hund, 2014). They primarily use fast-ice and nearby pack ice habitats close to the coast. Small populations also breed on South Georgia, the South Sandwich Islands, the South Shetland Islands and the South Orkney Islands. A continent-wide estimate of Weddell seals is approximately 800,000, although it may exceed 1,000,000 individuals.

Weddell seals may grow to about 3.3 m long and weigh up to 550 kg. Females may be slightly larger than males. They live to at least 25 years and females mature sexually at about 3–6 years; males mature at about 7–8 years. Weddell seals give birth to single pups, mostly within colonies of up to 50 females, from late September to early November, depending on location. Pups nurse for periods of 7–8 weeks, to December. After the pups wean, females mate in the water with dominant males that defend underwater territories (maritories) in fast-ice habitats. Adults molt from December to March.

Weddell seals dive deeply, feeding primarily in the mid-water regions of the water column at depths of around 100–300 m, and to about 600 m for up to 82 min. They may also exhibit diurnal feeding patterns within two depth layers (0–160 m and 340–450 m) as a response to vertically migrating prey. Fish (mainly Antarctic silverfish, Antarctic toothfish, several species of nototheniids and myctophids), followed by cephalopods and crustaceans, are the usual prey. There appears to be substantial geographic variability in prey taken, as well as considerable variability within areas and seasons.

Adult Weddell seals are reluctant to leave the fast-ice where they bred until March or April. They then mostly remain within 50–100 km of their summer breeding colonies, although some seals move longer distances and spend long periods in heavy winter pack ice. Year round occupancy of maritories might give an advantage for resident males over nonterritorial males or males that move away in winter, because the resident males are already there when the females begin to arrive at the breeding sites. In East Antarctica they forage off-shore within pack ice in winter for periods of up to 30 days, but return to the stable fast-ice to haul out. There is no predictable migration in Weddell seals.

Threats and Conservation Status

Changes in the extent, persistence and type of annual sea ice through climate change may negatively affect the distribution and abundance of Weddell seals. Population size and distribution may be altered through changes in food web dynamics. Changes in sea ice may negatively affect Weddell seal foraging because they forage on species that are linked with the pack ice ecosystem.

The Weddell seal is listed as “Least Concern” on the IUCN Red List and it is protected in its range under the Protocol on Environmental Protection to the Antarctic Treaty, the CCAS, Annex I of which provides for commercial harvests of limited numbers, as does the CCAMLR, Article II.

Conclusion

Overall, Antarctic seals are currently adequately protected directly by CCAS (1978) and indirectly by protection of the ecosystem upon which they rely through CCAMLR (1982), the latter also providing indirect protection for cetaceans through ecosystem management (Lowther, 2018; this study). In addition, Annex II to the Protocol on Environmental Protection to the Antarctic Treaty (1998), Conservation of Antarctic Fauna and Flora (see Lukin, 2014), provides further protection. Overall, a major issue for Antarctic marine mammal conservation is the uncertainty surrounding their population sizes and the infrequency of censuses. It is therefore impossible to detect anything but very large changes, making any response to developing threats difficult. The influences of shifts in the world’s oceans such as increased acidity, warmer seas, higher sea levels, reduced sea ice, and regionally variable shifts in productivity and marine biodiversity (Moore, 2018) would be difficult to detect. Human impacts such as sealing/whaling, ship strikes, underwater noise, tourism, marine litter, chemical pollution, disease and entanglement in fishing gear currently have little impact in the Antarctic marine biome. Current fishing levels are not an issue, but increases in catch levels or changes in the spatial distribution of fishing effort have the potential to cause negative impacts. However, the biggest threat to Antarctic marine mammals, in particular those species dependent upon sea ice for breeding, resting and refuge from predators, is climate change and any subsequent changes in sea ice. Access to feeding grounds, whether within the pack ice and/or along its outer edge, has implications for all species, as sea-ice reduction is expected to negatively impact on their food availability.

Acknowledgments

I am indebted to Scott Elias (University of Colorado) who generously allowed use of his blue, humpback and sperm whale images. Simon Elwen from Sea Search provided me with images taken by Darren du Plessis (southern right whale) and Sarah Golaski (fin whale). Horst Bornemann (Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research) provided the images of Arnoux’s beaked whales, southern elephant seals and Weddell seals. Huang Huang (GEOMAR, University of Kiel) allowed use of his minke whale and killer whales images. Bruce Dyer (Department of Environmental Affairs, South Africa) contributed the hourglass dolphins image. Nico Lübcker (crabeater seal), Chris Oosthuizen (Antarctic fur seals and leopard seal) and Mia Wege (Ross seal) from the MRI contributed their images.

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Development of Antarctic Science

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Abstract

The investigation of Antarctica, the last continent to be discovered, began in earnest with European expeditions in the early 20th century. Their aim was to reach the South Pole before the competition. Major scientific expeditions began in the 1950s, especially during the International Geophysical Year of 1957–58, when 12 nations built research stations and carried out scientific projects. Geophysical survey transects across the continent, combined with aerial photography, began the extremely labor-intensive task of mapping the continent and estimating the thickness of ice cover. Ice thickness measurements and the identification of bedrock features beneath the ice were greatly aided by aerial radar surveys and satellite remote sensing in recent decades. The radar studies revealed the presence of hundreds of subglacial lakes, and ice-core drilling down to the ice-water interface allowed the sampling of lake waters, which were found to harbor micro-organismic life. Isotopic and trace gas studies from the thousands of layers in Antarctic ice cores have provided crucial evidence of global climate change through the last 800,000 years, encompassing 10 glacial-interglacial cycles. Life in the small ice-free regions consists almost exclusively of microbes and fungi: primitive organisms that have demonstrated remarkable adaptations to life in the most extreme environments of the planet.

Introduction

The human history of Antarctica has unfolded over the past three centuries. It began with European ships entering Antarctic waters in the late 18th century, followed by some brief landings in the 19th century. The early 20th century was an age of heroic exploration, with several parties of Europeans going incredible lengths to be the first to reach the South Pole, where they could plant their country's flag. Since the 1950s, international cooperation, guided by the provisions of the 1959 Antarctic Treaty, has led to many remarkable discoveries about this frigid, desolate continent that has been called "The Last Place on Earth" (Huntford and Theroux, 1999).

History of Antarctic Exploration

Let us begin with the written history of Antarctic exploration, keeping in mind the possibility that prehistoric visits to Antarctic waters by the Maoris of New Zealand may have taken place, according to their legends. Sailing in Antarctic waters has always been dangerous. The wooden ships of the 18th and early 19th centuries were quite vulnerable to the enormous waves, hurricane-force winds, and crushing pack ice of the Southern Ocean. The first explorer to circumnavigate Antarctica was Captain James Cook. Cook set sail from England in July 1772, and by December his ship, *Discovery* entered Antarctic waters, encountering icebergs. They crossed the Antarctic circle in January 1773, and then were forced to head north again because of pack ice. In December 1773 and again in January 1774 *Discovery* sailed across the Antarctic Circle, entering the Amundsen Sea at latitude 71° 10'S. Finally, in February 1775, Cook's ship completed the circumnavigation of Antarctica.

Captain Thaddeus von Bellingshausen commanded Russia's first Antarctic voyage of exploration. On January 15, 1820, Bellingshausen's flagship, the *Vostok*, crossed the Antarctic Circle. Travel further south was blocked by the Finibul Ice Shelf. He and his crew were the first to see the Antarctic continent. The following year this expedition became the second to circumnavigate Antarctica, 44 years after James Cook.

The first people to actually set foot on Antarctica may have been sailors from the American sealer *Cecilia*, commanded by Captain John Davis. They landed at Hughes Bay (64°01'S) on February 7, 1821 and remained on land less than an hour, having found no seals. The first well-documented landing on the continent was on 24 January 1895, when the Norwegian whaling ship *Antarctic*, under the command of Captain Leonard Kristensen, landed a party at Cape Adare in the northern Ross Sea.

Another important 19th century voyage to Antarctic seas was led by Captain James Weddell of the British brig *Jane*. In February 1823 Weddell entered what is now called the Weddell Sea. Later that month his ship reached 74°15'S – the furthest south anyone had ever gone, and a record that would stand for more than 80 years.

In the 1830s, the French, British and American governments funded marine expeditions to find the South Magnetic Pole. The first of these voyages was led French captain Jules-Sebastien-Csar Dumont d'Urville in the ship *Astrolabe*. In February and March of 1838, d'Urville surveyed parts of the Antarctic Peninsula. During a second southern excursion d'Urville's ships reached within 4 miles of the continent. In January 1839, some of d'Urville's sailors landed on a small island close to the shore, and claimed the land they had seen for France. D'Urville named it Adélie Land, after his wife.

In August 1838, an American expedition set sail with 6 ships and 433 crew—the largest expedition ever sent to the Southern Ocean. This fleet was commanded by Lt. Charles Wilkes. Their first penetration of southern waters was along the coast of the Antarctic Peninsula, and yielded no new discoveries. The second excursion was more successful, and Wilkes charted several hundred miles of new coastline, starting with Cape Hudson in Adélie Land on January 16, 1840 and ending with what is now called the Shackleton Ice Shelf on February 21. There were several inaccuracies in Wilkes' charted positions, however, such that James Clark Ross later sailed over some areas where Wilkes had drawn land on his charts. As with d'Urville, ice prevented Wilkes from more southerly penetrations, but much of the area he charted is now known as Wilkes Land.

First Landing on the Continent

James Clark Ross, a British explorer, set out to find the South Pole in 1839. Ross had already found the north magnetic pole in 1831, so he was experienced in navigating polar waters. Ross' flagship was the *Erebus*. The men spent the austral winter of 1840 in Australia. On January 9, 1841, Ross's ships entered what is now called the Ross Sea. Two days later they sighted a range of mountains that Ross named the Admiralty Range. On January 12 he landed on Possession Island and claimed the land for England. Further southerly exploration was eventually blocked by an ice shelf, now called the Ross Ice Shelf. Having sailed so far south, Ross determined that the south magnetic pole lay inland on the continent. After Ross' voyages there was, with a few notable exceptions, a 50 year hiatus in Antarctic exploration. The attentions of governments had turned to the Arctic and the search for the Northwest Passage.

By the end of the 19th century, the world at large was becoming more fully aware of this unexplored continent. Accordingly, the 6th International Geographical Congress passed a resolution in 1895:

The exploration of the Antarctic Regions is the greatest piece of geographical exploration still to be undertaken. In view of the additions to knowledge in almost every branch of science which would result from such a scientific exploration, the Congress recommends that the scientific societies throughout the world should urge, in whatever way seems to them most effective, that this work should be undertaken before the close of the (19th) century.

Before the start of World War I, scientific expeditions to Antarctica had been carried out by teams from Australia, Belgium, England, France, Germany, Japan, Norway, Scotland, and Sweden. The most widely publicized Antarctic expeditions at the start of the 20th century were the groups from Britain and Norway that vied for the honor of being the first to reach the South Pole.

Roald Amundsen, a 39-year-old Norwegian explorer, spent most of his adult life venturing in the Polar Regions. He had been to Antarctica in 1897–99, when he served as first mate on the *Belgica*, the ship of the Belgian Antarctic Expedition. The *Belgica* was trapped in pack ice off an island west of the Antarctic Peninsula. The crew endured an Antarctic winter in the ice. From 1903 to 1906 Amundsen led a naval expedition that successfully traversed the Northwest Passage. In 1909, Amundsen had planned to reach the North Pole, but he was beaten to this by American explorers Frederick Cook and Robert Peary, who claimed to have reached the pole that year. Without telling his financial backers or even his crew at first, Amundsen sailed the *Fram* to Antarctica to make a try at reaching the South Pole. He sent a telegram to Scott, who was still in Australia. It read simply: "Beg leave to inform you *Fram* proceeding Antarctic. Amundsen." Amundsen's plan to reach the South Pole was simpler than Scott's. Amundsen would use only sled dogs, sledges, and men on skis to reach the pole (Fig. 1).

Captain Robert Falcon Scott was a British Royal Navy officer who led two expeditions to the Antarctic. The first of these, called the Discovery Expedition (1901–04), did not reach the South Pole, but Scott's team set a new southern record by reaching latitude 82°S. They also discovered the Antarctic Plateau, on which the South Pole is located. The relative success of this mission spurred the Royal Navy to send Scott on a second trip to Antarctica, known as the Terra Nova Expedition (1910–13).

Amundsen set up camp on the Ross Ice Shelf in the Bay of Whales, a location about 100 km closer to the Pole than Scott's base at McMurdo Sound. And unlike Scott, whose expedition was burdened by its scientific obligations, Amundsen was focused only on reaching the Pole and returning safely. "Science," he later admitted, "would have to look after itself."

After spending the early part of 1911 laying down advance caches of food and supplies for their polar journeys, Amundsen and Scott's expeditions took shelter and spent several months waiting out the dark and frigid Antarctic winter. On October 20, 1911,



Fig. 1 Amundsen and his men at the South Pole, 14 December 1911. Photo courtesy of the National Library of Australia.

weather conditions improved enough for Amundsen's five-man team to begin their dash to the Pole. Scott got underway just a few days later on November 1 (**Fig. 2**).

Amundsen and Scott had very different plans for their polar excursions. Scott brought along sled dogs, Manchurian ponies and some newly invented motorized tractors. One of the tractors sank while being off-loaded from the ship, and the others quickly broke down. The ponies struggled to walk on snow and ice, grew weak, and had to be shot. Scott decided to send the sled dogs back to base camp, so he and his team were forced man-haul their heavy supply sledges on foot (**Fig. 3**). This was a critical error,

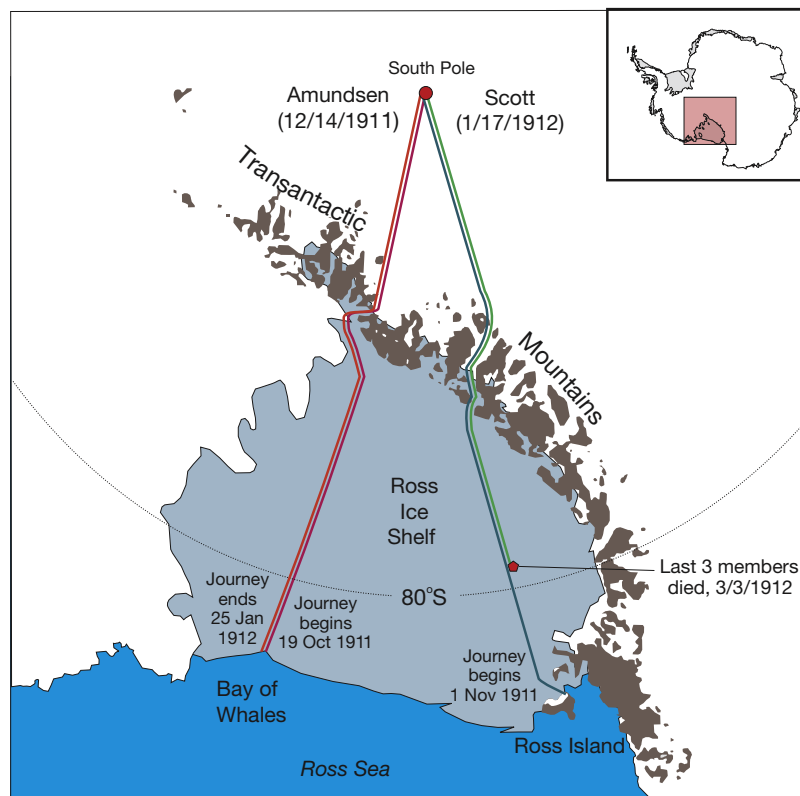


Fig. 2 Map of West Antarctica, showing the routes to the South Pole taken by Amundsen and Scott in 1911.



Fig. 3 The Scott expedition team on their way to the South Pole. Photo courtesy of the Scott Polar Institute, Cambridge, United Kingdom.

because the men hauling the sledges burned far more calories per day than they were taking in through their rations. A later analysis of the expedition estimated that even under optimistic assumptions their rations contained little more than half the calories actually required for the man-hauling of sledges. Amundsen, meanwhile, relied solely on skis and sled dogs to cross the ice. The Norwegian team took 4 sledges and 52 dogs. Amundsen's plan was to kill most of the dogs along the way, to provide fresh meat for his men. The dog sleds, accompanied by men on skis, allowed Amundsen's party to achieve a pace of over 20 miles per day, and they accomplished this in just eight-hours of travel. Their team rested 16 h a day. After crossing the Ross Ice Shelf, the team spent 4 days reaching the top of the uncharted Axel Heiberg Glacier. Having arrived at the edge of the Polar Plateau on 21 November, they took just 23 days to cross the plateau, arriving at the South Pole on 14 December 1911. Five men and 16 dogs reached their destination. Amundsen planted the Norwegian flag and posed for pictures, but they only remained at the South Pole for a few days before beginning their return to base camp. On return to base camp, the men on Amundsen's team actually gained weight. This is in sharp contrast to Scott's party, who were slowly starving throughout their journey. Six weeks after reaching the pole, the Norwegian team returned to their base camp (25 January 1912). The five men returned with 11 surviving dogs. On January 17, 1912, Scott's team reached the Pole. Much to their dismay, they spotted the tent left by Amundsen, with a letter for Scott left inside (Fig. 4). "Great God!" Scott wrote in his diary. "This is an awful place and terrible enough for us to have labored to it without the reward of priority."

The return to base for Scott's team quickly became a disaster. The weather was turning much colder and Scott's men were surviving on meager rations. When reached food and fuel caches, they discovered that much of their fuel had evaporated, so they were forced to eat frozen food. The first of Scott's party to die, Edgar Evans, succumbed on February 17. Scott had ordered that dog teams be sent from base camp to meet the polar expedition party on their way back, but through a series of disobeyed orders, mishaps, and bad weather, the dog teams never reached Scott's party. On March 16, Lawrence Oates sacrificed himself



Fig. 4 Scott's team at the South Pole, standing by the tent erected by Amundsen, 34 days earlier. Photo courtesy of the Scott Polar Institute, Cambridge, United Kingdom.

by leaving his tent and wandering off in the snow. Finally, the last three members of the team: Scott, Edward Wilson and Henry Bowers died of starvation and exposure during a blizzard, on or about March 29. By the time the three bodies were found in November 1912, Amundsen had already returned to a hero's welcome in Norway.

The next high profile exploration of Antarctica came in 1928–30. Richard Byrd, an American naval aviator, had begun flying airplanes to remote regions in 1926. He was the first to fly over the North Pole in a trimotor monoplane. This flight brought Byrd great fame in America. He was promoted to the rank of Commander and awarded the Congressional Medal of Honor. Byrd's next mission was to fly over the South Pole and to explore previously uncharted regions of Antarctica. This expedition was the first major American exploration in Antarctica since 1840, and it launched new American interest in Antarctica. The expedition landed on the Ross Ice Shelf and established a base called "Little America." Photographic expeditions and geological surveys were launched that Antarctic summer, and then the expedition's three airplanes were buried in the snow for the upcoming winter. As the Antarctic summer was beginning on November 28, 1929, a crew of four flew south in a Ford trimotor airplane, the *Floyd Bennett*, in an attempt to reach the pole. Byrd acted as navigator, accompanied by pilot Bernt Balchen, co-pilot/radioman Harold Gurnee, and photographer Ashley McKinley. Shortly after midnight on November 29, 1929, they flew over the South Pole. They refueled at a fuel dump part way to the pole, and then returned to Little America, completing a trip of 18 h, 41 min.

Post-War Research

After the Second World War, the U.S. Navy Antarctic Developments Project, Operation Highjump, was launched in 1946–47. This project was organized by Byrd, who by this time was a Rear Admiral in the United States Navy. This was the largest ever Antarctic expedition, with more than 4700 military personnel on 13 ships, and 33 aircraft. The expedition was organized into five task forces. During 1946–47 they flew over more than 1.5-million square miles of the continent, scouting for possible locations for permanent bases of operation, and gathering electromagnetic, geological, geographic, hydrographic, and meteorological data. Another U.S. Navy expedition, Operation Windmill followed in 1947–48. This effort included the use of ship-based helicopters to obtain geodetic ground control points to help locate the exact locations of aerial photos taken the year before.

Human habitation of Antarctica is extremely difficult and costly, as everything except freshwater must be brought in from other parts of the world. The first permanent camps built in Antarctica were research bases funded by the governments of several countries. One of the overriding themes of the Antarctic story is that the development of all kinds of new technologies made possible every advancement in Antarctic research. The establishment of remote bases in Antarctica would have been impossible without the development of large, powerful cargo planes, reliable tracked vehicles for over-the-snow transportation, and ships with reinforced hulls that could successfully navigate pack ice in order to reach Antarctic shores. These transportation technologies became available in the 1940s and 1950s. The scientific exploration of Antarctica only became possible as new technologies were developed for mapping the depth and movement of the ice cover, for drilling long ice cores, and for the analyses of small ice samples for trace elements, isotopes, and other constituents of ancient ice.

The Cold War environment of the 1950s spurred both the USSR and the United States to launch various forms of arms races. Doel (2003), a political scientist, pointed out that "Cold War tensions helped make Earth's polar regions valuable new targets of research." The polar regions (especially the Arctic) were considered strategic geographic regions by both sides. Scientific research, especially the field of Geophysics, played a critical role in assessing the physical environment of the Polar Regions. This is one reason that the two super powers were keen to participate in the International Geophysical Year research in the polar regions.

IGY and the Antarctic Treaty

Antarctic research received a large boost from studies performed under the auspices of the International Geophysical Year (IGY), which took place in 1957–58. Before the IGY, the legal status of the Antarctic was unfixed and largely undefined (Collis and Dodds, 2008). IGY was proposed by the international scientific community as a comprehensive global study of geophysical phenomena and their relationships with solar activity. IGY included studies of an array of areas of scientific interest including meteorology, geophysics, glaciology, oceanography, and seismology. Antarctica was considered an area of major importance, and 12 nations participated in IGY Antarctic programs. The complicated geopolitics of competing land claims and scientific research programs in Antarctica are discussed in Collis and Dodds (2008) and by Doel (2003).

The idea for an international scientific year came in 1950, when it was proposed that scientists take advantage of increasing technological developments to study the Polar Regions. Preparations for the IGY began in Antarctica in 1955. First, coastal research bases were established in the summer of 1955–56. Inland stations were established just before the official opening of IGY on July 1, 1957. A total of 18 months of intensive research was accomplished. Fig. 5 shows the locations of 25 research bases built during IGY, and their nationalities. In addition to bases established on the Antarctic mainland, 25 bases were also established on the Antarctic Peninsula and nearby islands.

IGY proved to be a hugely successful scientific experiment, demonstrating that many nations could work cooperatively in the Antarctic. Perhaps the greatest contribution was the political moratorium by the governments and the cooperative interchange between scientists of participating nations. The spirit of cooperation that evolved during IGY prompted proposals that this unique scheme should be continued, leading to formation of the Antarctic Treaty in 1959. The Scientific Committee on Antarctic Research (SCAR) was established in February 1958 to continue the international coordination of scientific work in Antarctica. It was

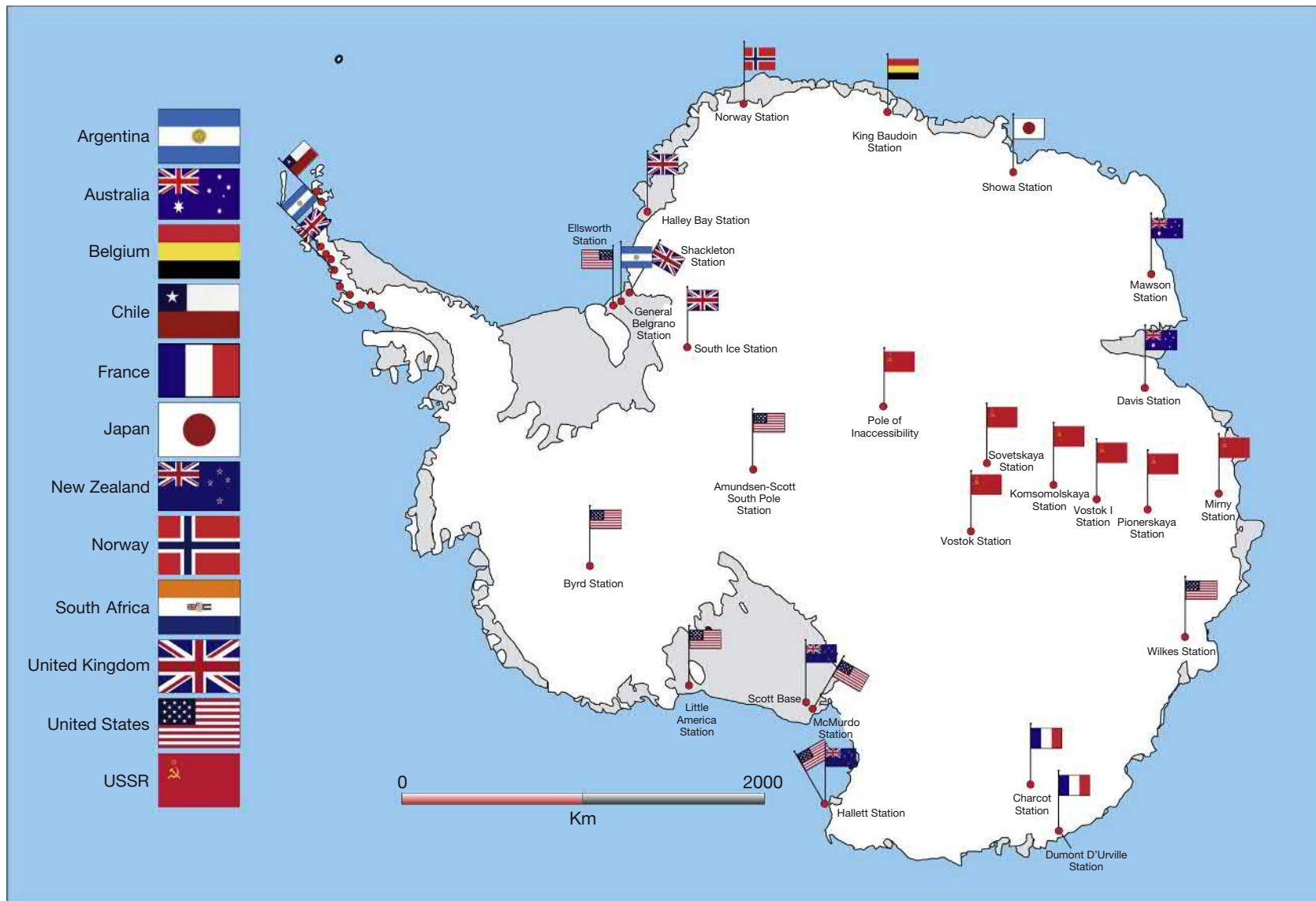


Fig. 5 Map of Antarctica, showing the location of research stations built for IGY projects in 1957–58, and the nationalities represented.

acknowledged that continued international scientific cooperation in Antarctica needed to be codified and to be agreed by all concerned nations. SCAR members worked closely with diplomats from the various countries to develop a treaty.

Twelve countries signed the Antarctic Treaty in December 1959, including Argentina, Australia, Belgium, Chile, France, Japan, New Zealand, Norway, Poland, Russia (USSR), South Africa, the United Kingdom, and the United States of America. The treaty paved the way for peaceful scientific research on the continent without the political ambitions of countries claiming parts of the continent for themselves. The main points of the treaty were as follows:

1. No military use shall be made of Antarctica, though military personnel and equipment may be used for peaceful purposes.
2. There will be complete freedom of scientific investigation.
3. Antarctic Treaty Nations will exchange plans for their scientific programs, scientific data will be freely available and scientists will be exchanged between expeditions where practical.
4. All territorial claims are put aside for the duration of the Treaty. No activities under the Treaty will affect claims to sovereignty of any part of Antarctica made by any nation.
5. Nuclear explosions and nuclear waste disposal are banned from Antarctica.
6. The Treaty applies to all land and ice shelves south of 60° South, but not to the seas.
7. All Antarctic stations and all ships and aircraft supplying Antarctica shall be open to inspectors from any Treaty nation.
8. Observers and exchange scientists shall be under the jurisdiction of their own country regardless of which national station they may visit. National laws do not apply to stations or areas, but only to the citizens of those countries.
9. Treaty nations will meet to consider ways of furthering the principles and objectives of the Treaty. Attendance at these meetings shall be limited to those countries that are engaged in substantial scientific research activity in Antarctica. Unanimous approval will be necessary for any new measures to become effective (i.e., everyone has to agree).
10. All Treaty Nations will try to ensure that no one carries out any activity in Antarctica that is against the Treaty.
11. Any dispute by Treaty Nations, if not settled by agreement, shall be determined by the International Court of Justice.
12. The Treaty may be modified at any time by unanimous agreement. After 30 years any consultative Party may call for a conference to review the operation of the Treaty. The Treaty may be modified at this conference by a majority decision.
13. The Treaty must be legally ratified (agreed to) by any nation wishing to join. Any member of the United Nations may join as well as any other country invited to do so by the Treaty Nations. All notices and records are deposited with the Archives of the United States of America.

The Treaty entered into force on 23rd of June 1961, and as of 2019 there are 53 signatory nations.

The Protocol on Environmental Protection was added to the Antarctic Treaty and signed in Madrid on October 4, 1991. It entered into force in 1998. Article 2 designates Antarctica as a “natural reserve, devoted to peace and science.” Article 3 sets forth basic principles applicable to human activities in Antarctica and Article 7 prohibits all activities relating to Antarctic mineral resources, except for scientific research. Until 2048 the Protocol can only be modified by unanimous agreement of all Consultative Parties to the Antarctic Treaty. The Environment Protocol established a Committee for Environmental Protection (CEP) as an expert advisory body to provide advice and formulate recommendations to the Antarctic Treaty Consultative Meeting (ATCM) in connection with the implementation of the Environment Protocol. The CEP meets every year in conjunction with the ATCM.

Studies of Antarctic Ice Properties

As late as the early 1950s, little was known of the properties of the Antarctic continent, including the volume of ice stored there, and how this had changed through time. As discussed above, Antarctic expeditions up to this point had mainly been adventurous, rather than scientific. Also, the technology required to perform widespread surveying of the ice sheet and the land beneath had not yet been developed (Siegert et al., 2018). The invention of geophysical techniques such as seismic sounding, coupled with the development of glaciology as a scientific discipline, allowed the first serious attempts to measure ice thickness, starting with a Norwegian–British–Swedish expedition to East Antarctica in 1952. Much greater progress was made during the IGY in 1957–58. A review of IGY research in Antarctica is presented by Naylor et al. (2008). These studies showed that Antarctica was one landmass—a fact unknown prior to this time. The IGY studies also demonstrated that the West Antarctic Ice Sheet (WAIS) rests on a bed as much as 2 km below sea level, while much of the East Antarctic ice sheet covers bedrock that is largely above sea level (Fig. 6).

U.S. research in Antarctic during the IGY focused mainly on measuring ice thickness, accumulation rates, and temperatures. The research questions of the project were as follows: What is the present area and volume of the Antarctic ice and of the land beneath? What is the present status of the ice sheet in terms of mass and energy? What is the history of the Antarctic continent? What is the future of Antarctica? What are the main characteristics of the floating ice shelves? Many of these questions were barely addressed during the IGY, but would help direct the course of much of the Antarctic research agenda in subsequent decades.

Three methods were used to study the thickness of the Antarctic ice sheets. First, seismograph units were placed at Byrd, Wilkes, South Pole and Hallett stations. Seismograph data can be used to study the dispersion characteristics of shock waves from earthquakes, providing data used to determine ice thickness over bedrock. Second, seismic reflection and refraction studies were used along a series of traverses. These traverses radiated out from Little America, Byrd, and Ellsworth Stations (Fig. 7), using large tracked vehicles called Snowcats (Fig. 8). They covered almost 10,000 km across the continental interior and some ice shelves. In seismic reflection studies, a hole is drilled in the ice, an explosive charge is detonated in the hole, and the characteristics of the resulting shock waves are used to estimate the thickness of the ice cover. The actual methodology was described by John Behrendt (1998).

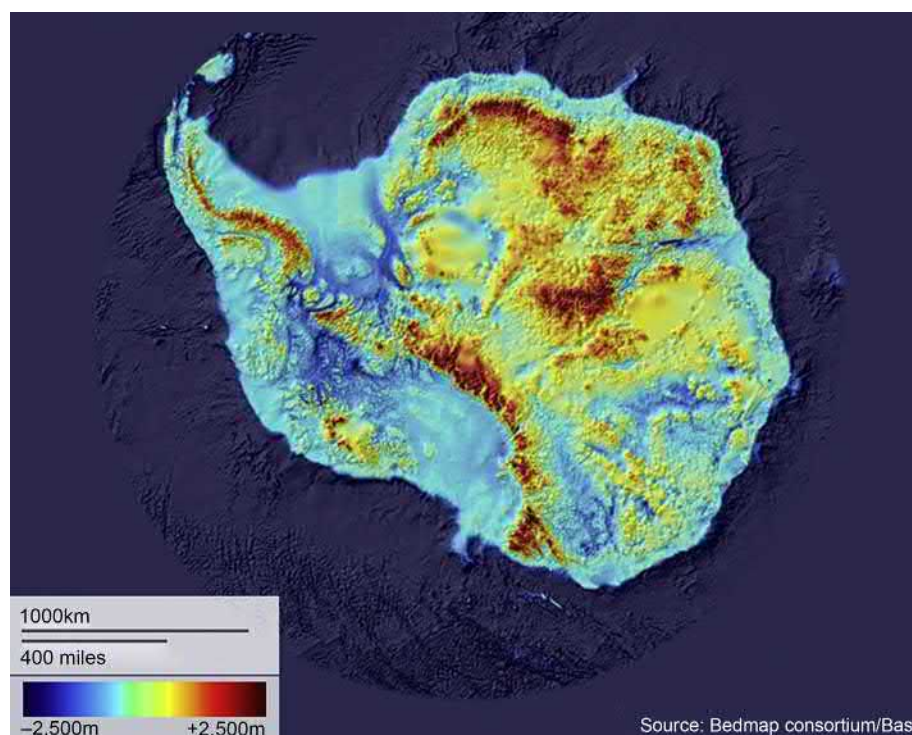


Fig. 6 Map of bedrock in Antarctica. Note the *deep blue* regions that are below modern sea level. Image courtesy of the Bedmap Consortium, British Antarctic Survey.

We lay out our 1200-ft seismic cables in an L shape, which we unrolled from chest reels. We would hand-drill a four-inch diameter hole from 6 to perhaps 25 ft. (2–8 m) deep, usually at the apex of the L. We fired a small explosive charge of one to five pounds of ammonium nitrate detonated with an electric blasting cap and a one-pound high-explosive primer charge. The sound waves penetrated to the ice-water contact (in the case of the floating ice shelf) and to the water-rock (or ice-rock) contact and reflected back to the surface where they were picked up by the geophones. Each of the 24 geophones was attached to one of the channels in the cables.

When completed in 1959, these traverses provided a broad coverage of the WAIS and the land beneath. Third, gravimeter observations were taken in order to supplement the seismic data, allowing some interpolations of ice depths between seismic depth points, and in “no-reflection” areas. The elevation of various parts of the ice sheet was also measured during the traverses, using altimeters on land and in over-flights by airplanes. Extensive aerial photography was used to map the topography of the ice sheet, and to map exposed ranges and nunataks (exposed mountain peaks). More detailed and extensive surveys of ice thickness have been undertaken since the end of the IGY project, using increasingly more sophisticated technologies. Technology drove ice-sheet research forward again in the late 1980s and early 1990s, with the invention of satellite remote sensing, especially the European Remote Sensing satellite (ERS-1), which yielded highly accurate measurements of the ice surface elevation, and Radarsat, which produced detailed images of ice surface morphology (Siegert et al., 2018).

The Bedmap2 project, an international collaborative effort, has obtained the most recent estimates of Antarctic ice volume. Their project (Fretwell, 2013) estimated that Antarctica holds about 26.5 million cubic km of ice. It is difficult to imagine such large numbers, but if all the Antarctic ice melted, global sea level would rise by 58 m. The Bedmap2 project included 60 scientists from 35 institutions in 14 countries. The Bedmap2 ice thickness grid is made from 25 million measurements. The methods used by the Bedmap2 project to measure ice thickness included radio-echo sounding data from airborne and ground based sources, seismic surveys, swath and gridded bathymetric data, satellite elevation data, pre-gridded elevation datasets, contour data from rock outcrops, glacier profiles, grounding lines and visual interpretation of the ice sheet-ice shelf interface. The project benefited greatly from the many airborne radar surveys flown during the previous 20 years. Radar surveying is particularly useful for measuring ice thickness over bedrock. Unlike rock, ice is transparent to radar. Radio pulses are fired through the overlying ice sheet and return echoes are recorded. Using the radar reflection data, it is possible to measure the distance to bedrock. By subtracting the surface elevation of the ice sheet at that point, the depth of ice cover can be calculated. Fig. 9 is a surface elevation map Antarctica. Ice cover on the continent ranges from no ice cover in the Dry Valleys of Antarctica to a maximum ice thickness of 4776 m at a region known as the Astrolabe Subglacial Basin. The Bedmap2 project scientists estimate that the mean thickness of the Antarctic ice sheet is 2160 m. This project has also revealed a serious threat to the stability of the WAIS. Ice loss in West Antarctica is being driven by marine ice sheet instability. Changing ocean currents are bringing warmer water into contact with the floating ice shelves, causing

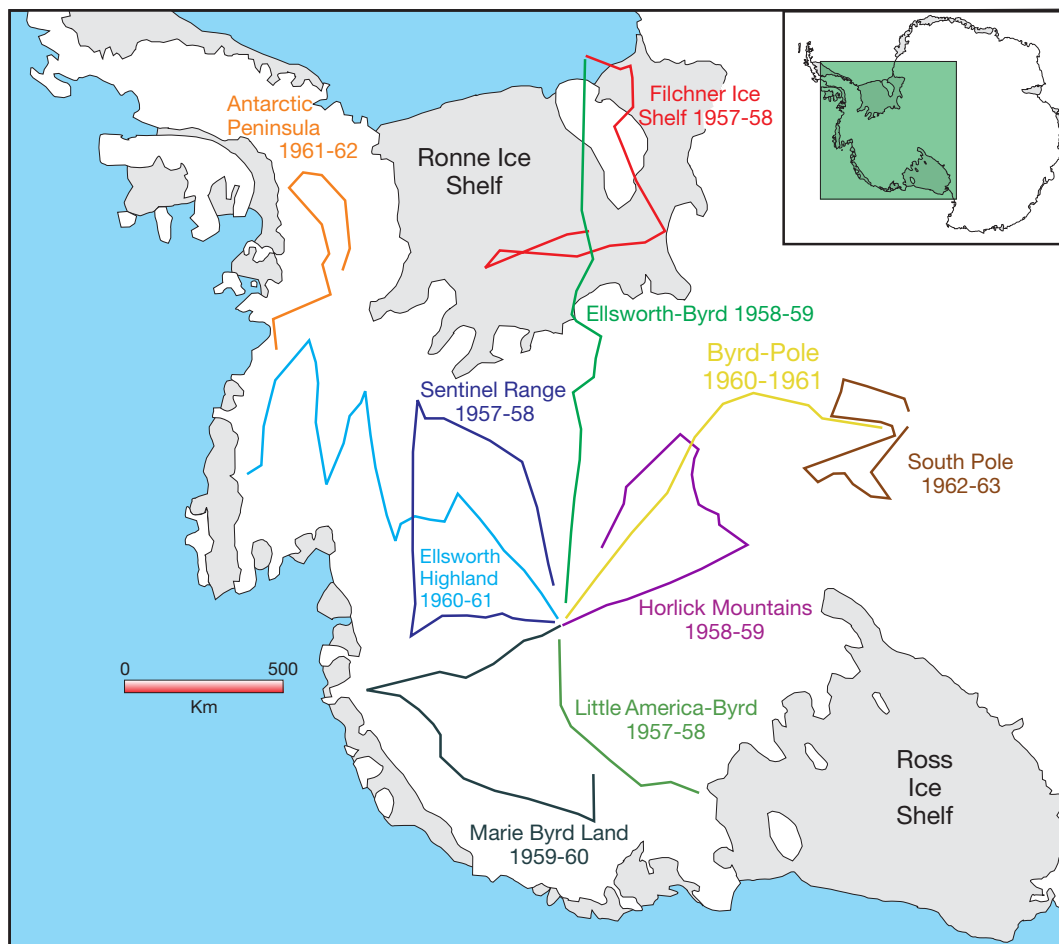


Fig. 7 Map of Antarctica, showing the seismic traverses undertaken during the IGY project in 1957-58.



Fig. 8 Snowcats ready to go on a traverse, November 1957. The boxy structure on the first sled is the wannigan, a small hut mounted on a tractor-pulled sled. A P2V reconnaissance aircraft flies overhead. Photo courtesy of Byrd Polar Research Center, Ohio State University.

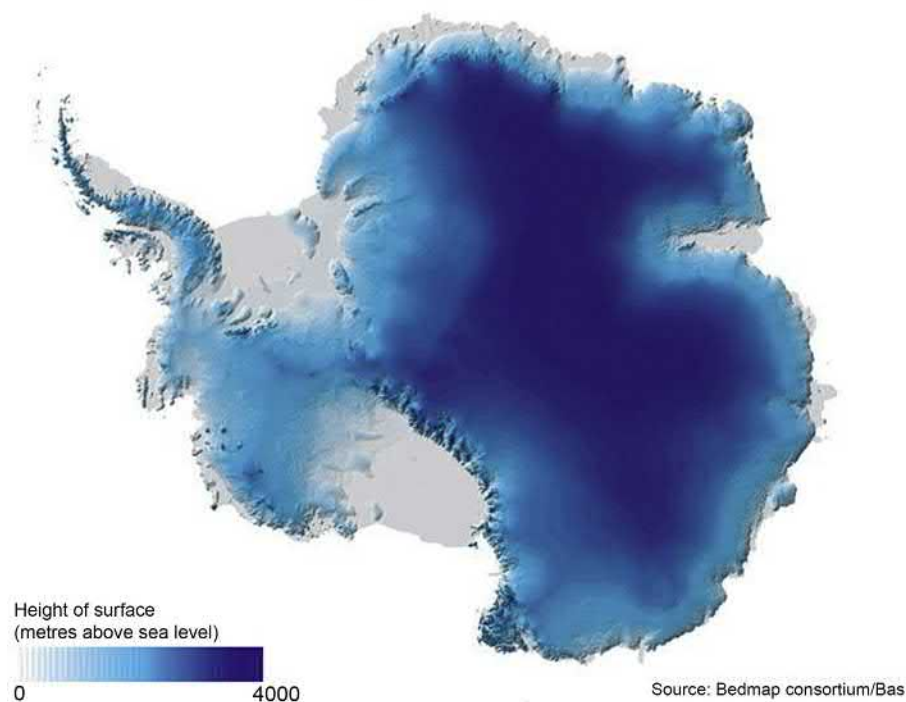


Fig. 9 Map of the elevation of the ice covering Antarctica. Courtesy of Bedmap Consortium, British Antarctic Survey.

the melting of ice at the grounding line (i.e., the point at which the marine shelf ice meets bedrock). Grounding line recession is a real concern. If it continues unabated, there will be significant ice loss to the WAIS.

Ice Core Research

Ice cores are typically drilled by means of either a mechanical or thermal drill. Both types of drills cut a circle, around a central, vertical core. Ice drilling technology has improved more-or-less continuously since the first attempts in the 1950s. A mechanical drill is a rotating pipe (drill barrel) with cutters at the head. When the drill barrel is rotated, the cutters incise a circle around the ice to be cored until the barrel is filled with ice. In deep ice drilling, the drill barrel is driven downwards by an electromechanical motor (**Fig. 10**). The length of the drill barrel determines the maximum length of a core section that can be retrieved in a single drill run. Ice cores are typically retrieved in sections that are 1–6 m in length, and typically 50–132 mm in diameter ([National Science Foundation Ice Core Facility, 2018](#)). The collection of a long ice core thus requires many repetitive cycles of lowering the drill, cutting a core section, raising the drill back to the surface, removing the ice core section from the barrel, and readying the drill to go back down the hole to retrieve more ice. In Antarctic drilling, the retrieved sections of ice cores are typically stored in a snow cave below the surface, where extremely cold temperatures are relatively constant. At depths of about 300 m or more, the borehole may start to close up during the drilling process, because the plastic nature of ice causes it to flow under pressure. To keep the borehole open, a drilling fluid is pumped into the borehole. This fluid ensures that the pressure in the borehole is approximately the same as that of the surrounding ice, which prevents closure of the borehole. One of the great logistical difficulties to be overcome in ice sheet drilling is simply the difficulty of working at extremely low temperatures (**Fig. 11**). At -50°C and colder (not atypical temperatures for most of the interior of Antarctica), metal becomes brittle and tends to break. Fluids freeze. Motor bearings seize up when their lubricating oil solidifies. It is noteworthy that the Russian crew drilling the Vostok ice core worked through the Antarctic winter, when temperatures dropped below -70°C . The long-term storage of ice cores is done at special facilities, where the temperatures are maintained at -36°C . It was discovered that at temperatures between -20°C and -30°C , the oxygen trapped in the air bubbles in the ice eventually diffuses out of the ice.

Cores from polar ice sheets were first taken in Greenland in the 1950s. A history of the first 50 years of Antarctic ice core research is presented by [Jouzel \(2013\)](#). The first Antarctic ice core was drilled by the Russians near their Mirny station in 1957. This core recovered ice to a depth of 377 m. The first attempt at deep-hole ice drilling was done by the Russians at their Vostok station. This coring operation started in April 1970, reaching a depth of 506.9 m after 5 months of drilling. An international consortium of Russian, French and American scientists has worked at the Vostok site from the 1980s onward, and their drilling at the Vostok site culminated in the recovery of the deepest ice core thus far obtained: 3623 m. In 2012 they were able to extend the Vostok ice core drilling down to the bottom of the ice at a depth of 3769 m, where they encountered water from subglacial Lake Vostok. These extremely long ice cores represent great lengths of time. A core of 2755 m, taken in 1994, contained ice that accumulated over two

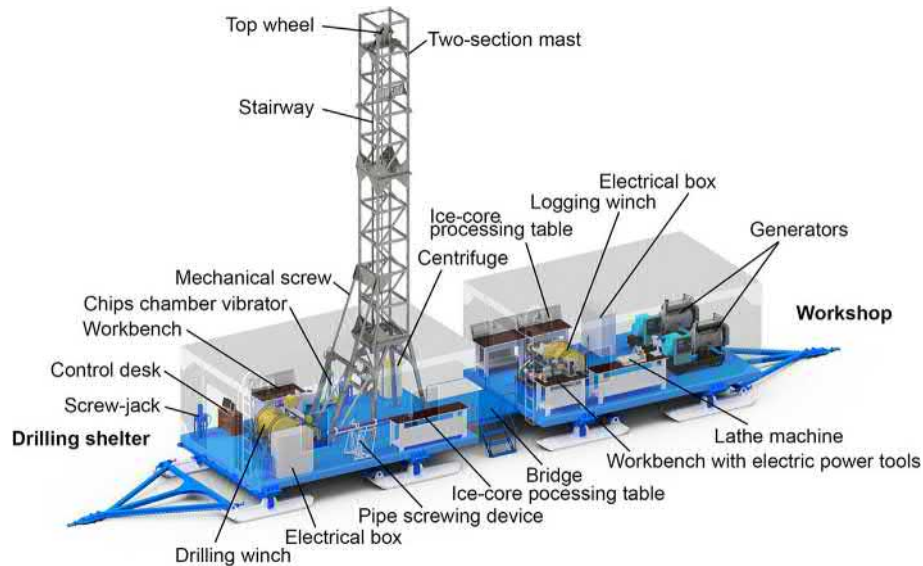


Fig. 10 Drawing of the ice coring rig used in the drilling project at Gamburtsev Subglacial Mountains, East Antarctica. Illustration courtesy of the Geological Society of London.



Fig. 11 Ice coring camp at Law Dome, 2008. Photo courtesy of Australia Antarctic Division.

glacial-interglacial cycles (Jouzel et al., 1996). A core of 3350 m in length at Vostok was taken in 1996. The base of this core has an estimated age of 420,000 years before present (yr BP) (Petit et al., 1999). The greatest time interval yet achieved in an ice core comes from the Dome C ice core. As discussed below, the ice from this core spans the last 800,000 years. Fig. 12 shows the locations of important ice coring localities in Antarctica.

Once an ice core has been drilled, it is vital to establish a chronology as precisely as possible.

On cold-based ice sheets, such as those in the Antarctic interior, no ice mass is lost by internal melting. However, because ice is plastic in nature, it deforms under its own weight, and therefore the layers become progressively thinner with depth (and age). The upper 50–150 m of an ice sheet consists of consolidated snow, known as “firn.” Air is continuously trapped in the lower 10% of the firn, at the firn–ice transition, where the interstitial spaces around the firn grains are progressively closed off until the air, trapped in minute bubbles within the ice matrix, is permanently isolated from the overlying atmosphere (Schwander, 2013). Because the firn

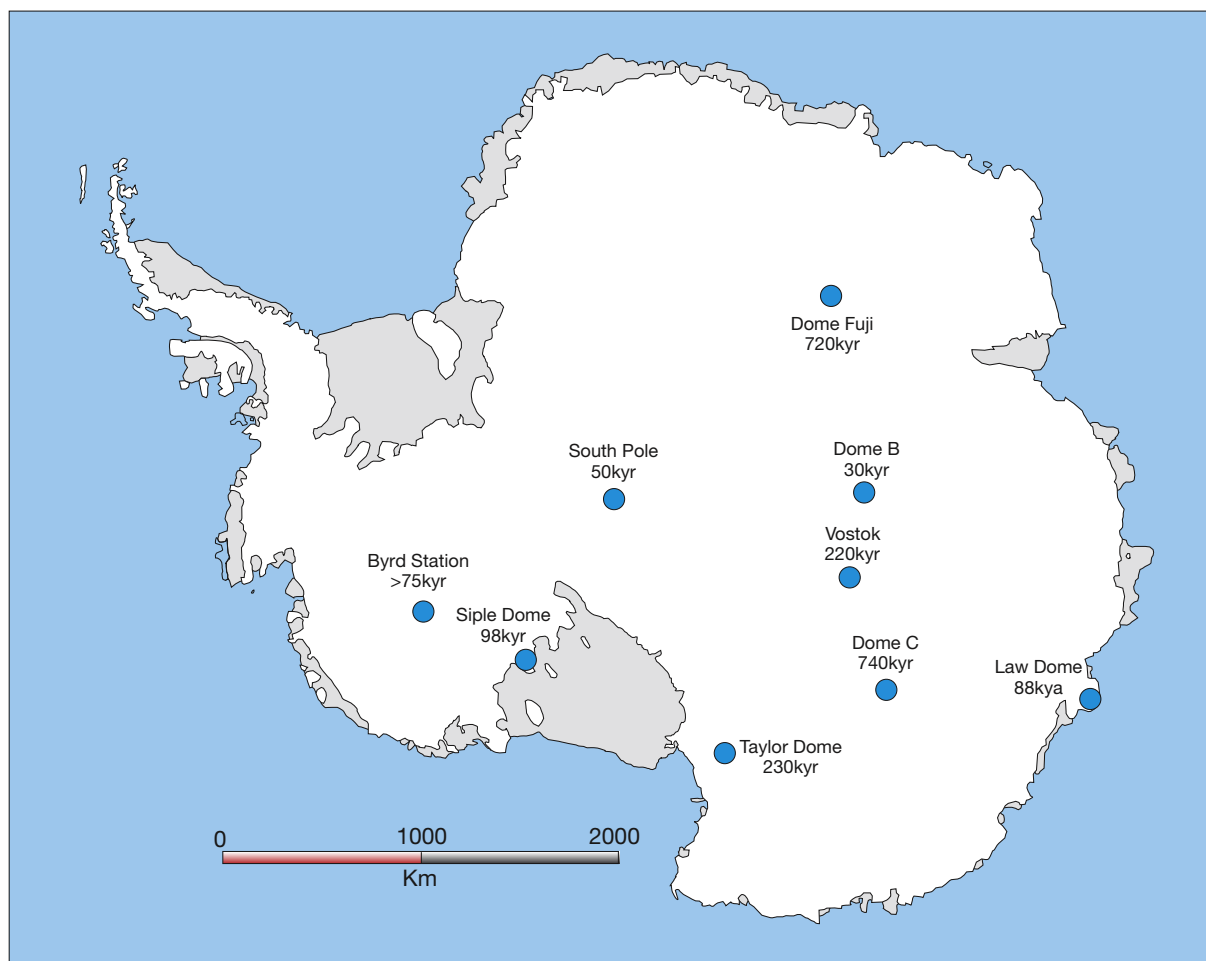


Fig. 12 Map showing the locations of important ice coring sites in Antarctica.

layer remains permeable to gases, the air above the firn–ice transition region is able to exchange with the atmosphere via diffusion and convection. As a consequence, the age of the air in a sample of an ice core differs from the absolute age of the ice.

Seasonal variations in temperature and atmospheric circulation are reflected by variations in trace substances and stable isotopes in ice core layers. The classic method for tracing seasonal variations in ice cores is the analysis of the ratios of the stable water isotopes $^{18}\text{O}/^{16}\text{O}$ and $^2\text{H}/^1\text{H}$. As these isotopic ratios are strongly affected by the condensation temperature of precipitation, they reflect seasonal temperature variations. In the consolidated ice (i.e., below the firn layer), the self-diffusion of the water molecules is much smaller than diffusive transport in the firn, and seasonal variations in the oxygen and hydrogen isotopes are preserved for many thousands of years. Trace substances are generally less affected by diffusion, especially particulate matter. However, there is always a lower limit of the annual accumulation rate, below which the annual variations are lost. The dating of ice older than can be counted by annual accumulation is done through a combination of techniques, including ice-flow modeling and orbital tuning. Antarctic ice cores are often drilled on ice divides or local domes because of the relatively simple pattern of ice flow. At such sites, all ice retrieved in a core originates from snow deposited in the vicinity of the drill site. The orbital tuning method is based comparisons of observations of long-term changes in the concentrations of CO_2 , methane, and other gases with the known timing of glacial-interglacial cycles based on long-term changes in Earth's orbit around the Sun, which are thought to be the main drivers of glacial cycles. Trace markers of known age, such as volcanic tephra layers, are used to correlate same-age surfaces across different cores.

The reconstruction of paleotemperatures based on ice core data is based on a number of proxies trapped in the ice. Chief among these are the deuterium-hydrogen ratios (δD), $^{18}\text{O}/^{16}\text{O}$ ratios ($\delta^{18}\text{O}$), and CO_2 and methane levels found in minute air bubbles trapped in the layers of ice. **Fig. 13** shows a reconstruction of departures from modern temperatures based on δD measurements from the Dome C ice core. The ice from this deep core spans the last 800,000 years, encompassing 10 glacial-interglacial cycles (Lüthi et al., 2008). These very long time series allow paleoclimatologists to study the duration and intensity of past climatic events.

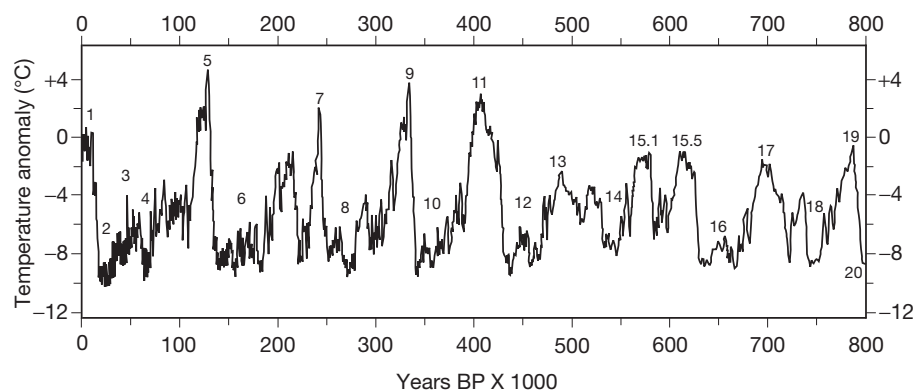


Fig. 13 The Dome C temperature anomaly record with respect to the mean temperature of the last millennium (based on original deuterium data interpolated to a 500-year resolution). The numbers above the curve are marine isotope stage numbers, signifying glacial intervals (even numbers), and interglacial intervals (odd numbers). After Lüthi, D., LeFloch, M., Bereiter, B. et al. (2008). High-resolution carbon dioxide concentration record 650,000–800,000 years before present. *Nature* **453**, 379–382.

In addition to the stable isotope data, the network of ice cores from Antarctic sites have yielded concentration data on CO₂, methane, and aerosols that show strong linkages with global climate on many timescales (Brook and Buizert, 2018). These records demonstrate long-distance connections between Antarctic climatic events and those of distant locations. Antarctic ice research has shown that the Earth's atmospheric composition has changed dramatically over the last 800,000 years. Further coring is now being planned, but in extremely difficult locations of the continent. The goal of the new research initiatives is to find even older ice, if it exists. Older records, perhaps pushing beyond 1 million years old, will help climate scientists unravel the mechanisms underlying the shift of glacial events from 40,000-year to 100,000-year cycles that took place about a million years ago.

Subglacial Lakes

One example of multinational collaborative research in Antarctica is the exploration of subglacial lakes. These are bodies of fresh water sitting on the bed of the ice sheet. Their existence was scarcely even considered before radar mapping of the continent was carried out. The history of subglacial lake research has been summarized by Siegert (2018). The first of these lakes beneath the ice sheet was discovered from data collected on one of the first long-range survey flights in 1969. An unusually flat subglacial radio-echo surface beneath the Russian Sovetskaya Station in East Antarctica was attributed to a thick layer of water beneath the ice. Shortly thereafter, an inventory of subglacial lakes documented the presence of 17 bodies of water beneath the ice in East Antarctica. In the 1990s, satellite observations of ice-surface altimetry, such as the data generated by the European Remote Sensing satellite (ERS-1), combined with radio echo sounding data, confirmed in 1996 that Lake Vostok is over 240 km long and more than 50 km wide. Between 1997 and 1999, additional remote sensing data indicated that at least some of the subglacial lakes are not isolated, but rather are connected by streams, for instance in bedrock trenches. The flow of water between subglacial lakes demonstrated that there is an active hydrological system beneath the ice. An inventory of subglacial lakes in 1996 identified the location of 77 lakes. This number rose to 145 subglacial lakes in an inventory taken in 2005 (Fig. 14), then it rose again in 2012 and 2016, and now stands at 402 lakes (Siegert, 2018). A study by Seroussi et al. (2017) showed that a source of geothermal heat called a mantle plume was most likely responsible for the creation of lakes and streams of water beneath Marie Byrd Land in West Antarctica (Fig. 15). Mantle plumes are localized columns of hot magma rising by convection in the mantle.

Since the end of the 20th century, SCAR has facilitated this line of research, culminating in a field program to measure and sample three individual lakes in 2012/13. These were Lake Vostok, led by a Russian team; Lake Ellsworth, led by a British team; and Lake Whillans, led by an American team (Siegert, 2018).

Life Beneath the Ice Sheet

Lake Whillans was the first subglacial lake to be accessed and sampled in 2013, following the development of protocols to prevent contamination of lake water during the sampling process.

Water and sediment samples were taken, examined at the surface, and then sent to laboratories in the United States. They showed that water within Lake Whillans contained living micro-organisms, and that the lake water was mostly glacial ice melt water, with a small amounts of seawater. Glaciological study of the region showed that it had been subjected to seawater inundation during

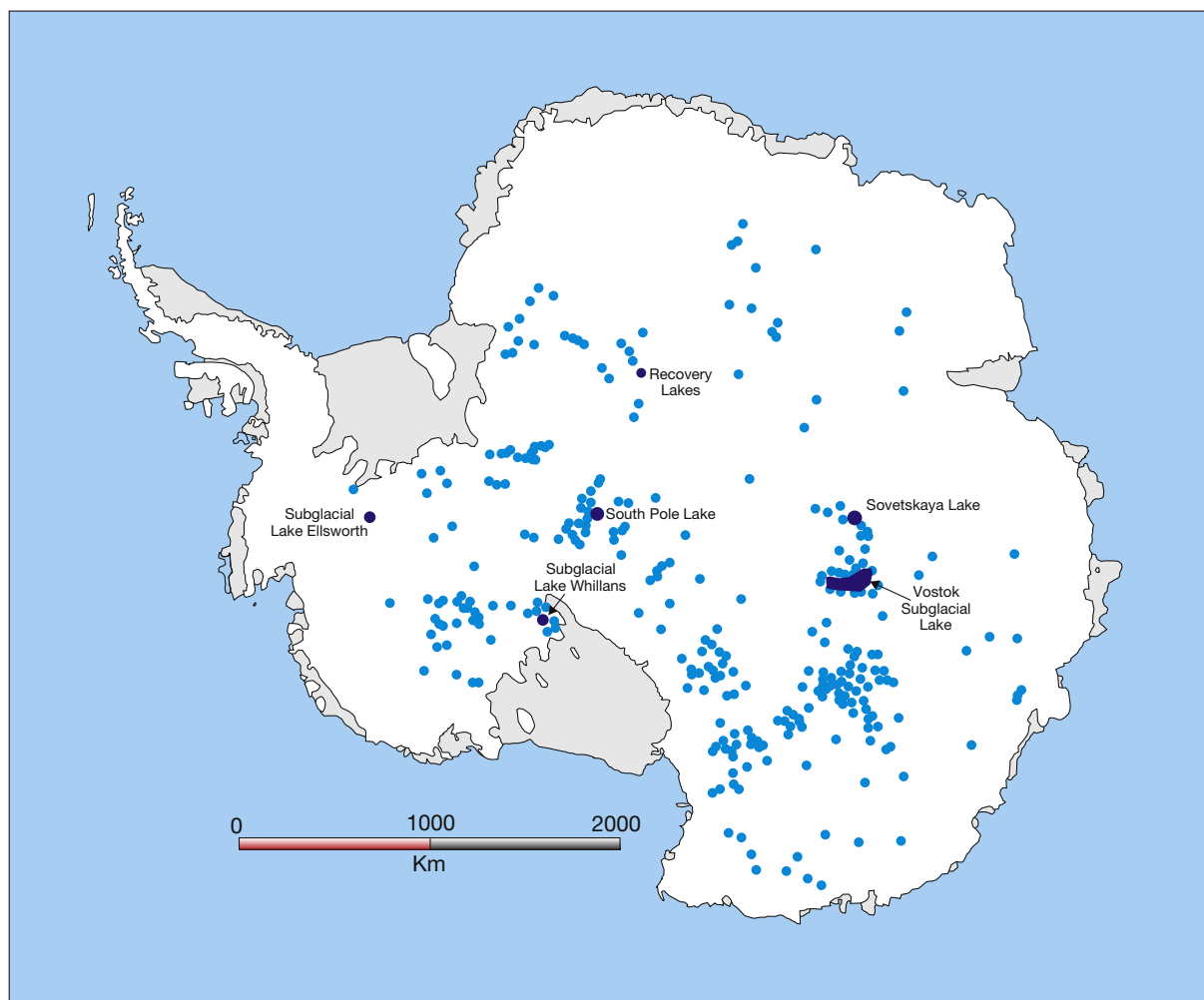


Fig. 14 Map showing the location of 145 Antarctic subglacial lakes inventoried as of 2005. After Siegert, M.J., Dowdeswell, J.A., Gorman, M.R. and McIntyre, N.F. (1996). An inventory of Antarctic sub-glacial lakes. *Antarctic Science* 8, 281–286.

previous interglacial periods. The sub-glacial environment has been isolated from the atmosphere and from sunlight for at least 100,000 years. In the total darkness, thousands of meters from sunlight, these micro-organisms rely on energy gained from the oxidation of chemicals or detrital organic matter. A study by Christner et al. (2014) concluded that the microorganisms are a diverse mixture of bacteria and archaea. The latter are one of the most primitive single-cell life forms on Earth. Together, the aquatic microbes in Antarctic subglacial lakes form an ecosystem of producers and consumers. The producers gather chemical energy, and are, in turn, consumed by some of the bacteria.

Current Changes in the Antarctic Ice Sheets

The ice sheets of Antarctica are far from static. Movements of glaciers and ice streams channel flowing ice from the interior to the oceans (Davies, 2018). These ice streams are fed by substantial inland catchment areas (Fig. 15) (Rignot et al., 2011). Fluctuations in the mass of ice sheets over bedrock are caused by differences between net snow accumulation at the surface and melt-water runoff and ice discharge into the ocean. In recent decades, reductions in the thickness and extent of floating ice shelves have disturbed inland ice flow, triggering retreat, acceleration, and drawdown of many ice streams that terminate in the Southern Ocean. The progressive thinning of ice shelves and the retreat of ice shelf margins has led to a progressive draw-down of inland ice, by way of ice streams. It is thought that increased temperatures in the Southern Ocean are the major cause of ice shelf degradation. The most significant losses of ice shelves have been on the Antarctic Peninsula, where there are no ice streams. This is where we can most clearly see the response in the glaciers behind them. They are only just starting to stabilize about 30 years after initial ice-shelf loss. A recent analysis of satellite observations of the changing volume of Antarctic ice cover, combined

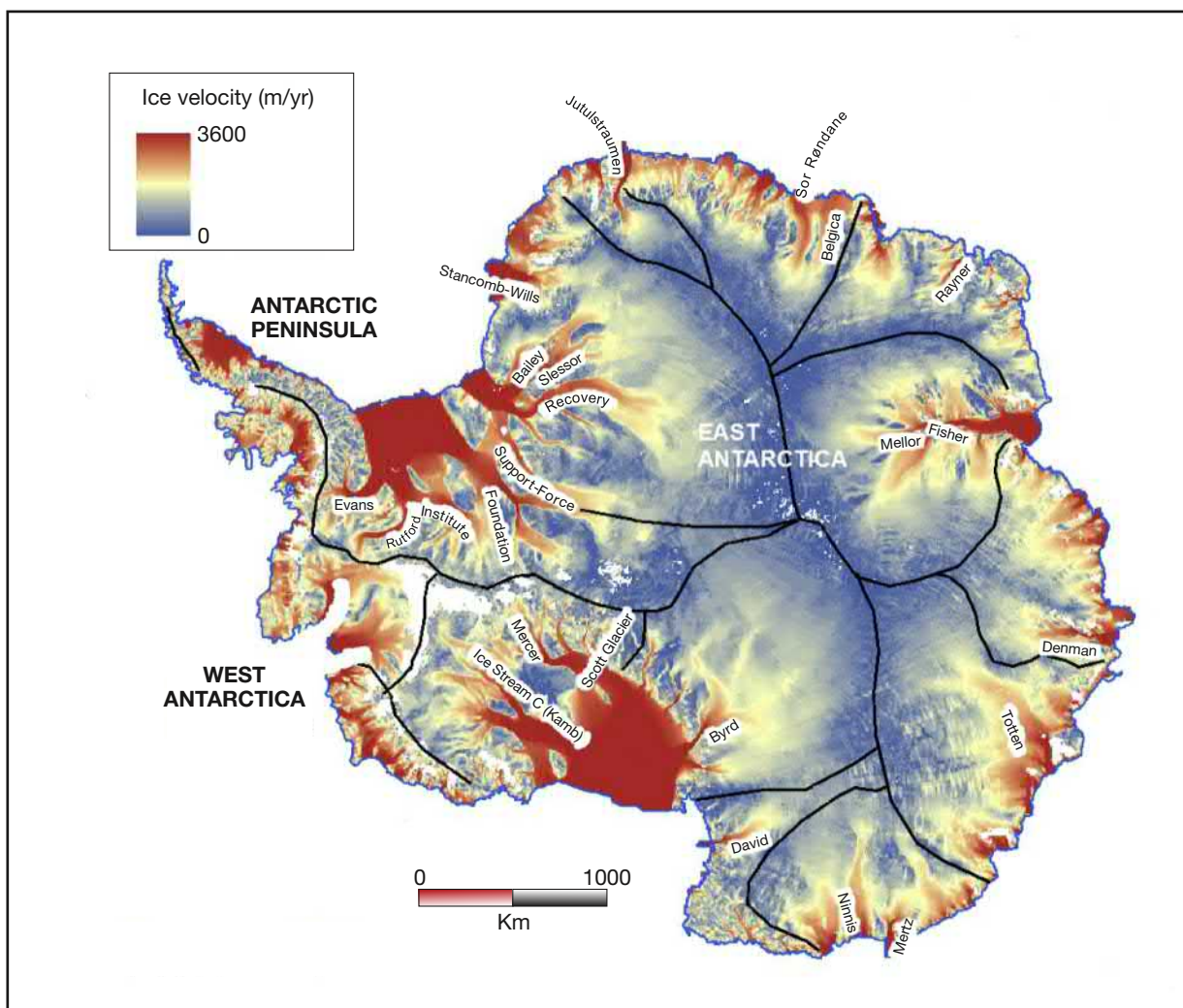


Fig. 15 Map showing the ice streams of Antarctica and the velocity of ice movement. Velocity data from Rignot, E., Mouginot, J., Scheuchl, B. (2011). Ice flow of the Antarctic Ice Sheet. *Science* **333**, 1427–1430, Map after Davies, B. (2018). Ice streams. <http://www.antarcticglaciers.org/modern-glaciers/types-of-glacier-2/ice-streams/> (visited July 15, 2018).

with modeling of its surface mass balance, show that the continent lost 2720 ± 1390 billion tonnes of ice between 1992 and 2017 (Shepherd et al., 2018). This corresponds to an increase in mean sea level of 7.6 ± 3.9 mm (errors are one standard deviation). Over this 24 year interval, ocean-driven melting has caused rates of ice loss from West Antarctica to triple, from 53 ± 29 billion to 159 ± 26 billion tonnes per year. The rate of ice-shelf collapse has increased four-fold during this interval. Ice shelves collapse largely in response to long-term thinning from below, with collapse triggered by hydrofracture from ponded meltwater during warm summers. Under pressure, the ponded water forces new fractures (crevasses) in the glacial ice, creating points of weakness (Fig. 16).

Life in Ice-Free Regions

Ice-free areas cover only one-third of 1% of Antarctica. These rare ice-free areas include nunataks, mountain peaks and other rock formations exposed above a glacier or ice sheet. One of the best known ice-free regions is the Dry Valleys region near McMurdo Station (Fig. 17). Even the few ice-free regions of Antarctica have extremely harsh environments dominated by bitterly cold temperatures and permanently frozen soils (permafrost). However, a very shallow layer of soil thaws during the Antarctic summer (the so-called “active layer”). The growing season in Antarctica, when the soil surface temperature is above freezing and liquid water is available, lasts 25–75 days (Pushkareva et al., 2018). Biological soil crusts (BSCs) are common in this type of environment. These are composed of soil aggregates held together by communities of living bacteria on the surface (Fig. 17). Cyanobacteria are the dominant components of most soil communities in Antarctic BSCs and they are the primary colonizers of poor Antarctic soils. They are able to produce simple sugars through photosynthesis. Cyanobacteria are particularly well adapted to survive in harsh

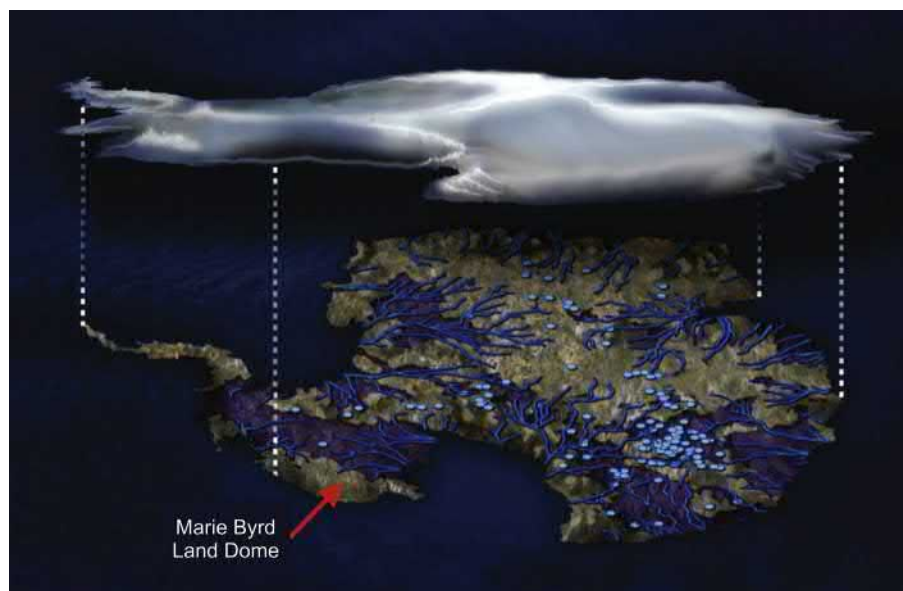


Fig. 16 Map of major under-ice lakes and streams in Antarctica, highlighting the location of the proposed mantle plume under a dome in Marie Byrd Land, West Antarctica. Image courtesy of NASA-JPL.

and variable conditions. They have developed a wide range of strategies that help them minimize or avoid the harmful effects of harsh environments. One of the secrets of their success in Antarctica is that they exude polymers onto the surface of the cell that protect them from desiccation. They also have pigments that protect them from ultraviolet radiation. They become dormant through the long Antarctic winters. A soil survey in the Sør Rondane Mountains of East Antarctica found 18 different species of cyanobacteria (Pushkareva et al., 2018).

A group of microbial biologists recently discovered a reasonably diverse assemblage of bacteria surviving in this kind of environment. Papale et al. (2018) found more than 50 species of bacteria living in the shallow active layer in an unglaciated region at Edmonson Point, Northern Victoria Land. The bacteria had very small cell sizes ($<0.1 \mu\text{m}^3$), indicating the occurrence of stressed, dormant and/or starved cells. The soil bacteria appeared to be metabolically active, acting as decomposers of organic matter, some of which was transported from coastal or oceanic sources (i.e., bird droppings). These bacteria withstand freezing for perhaps 10–11 months of each year, then become biologically active during the few short weeks of summer when the top layer of soil thaws.

The hyper-arid deserts of the McMurdo Dry Valleys present some of the most extreme dry, cold environments on the planet. In fact the conditions are so extreme that even microbial life struggles to exist on rock surfaces. In these environments, microbes find shelter from desiccating winds by living just below the surface of porous rocks, where they form endolithic microbial communities. These, in fact, are the most widespread life-form in the ice-free areas of Continental Antarctica. Recently, biologists interested in the kind of life forms that could potentially be found on other planets have tested the ability of colonies of the Antarctic black fungus *Cryomyces antarcticus* to survive the extreme low temperatures, hyper-arid, cold, nutrient-poor conditions, and strong UV irradiation found on Mars. The fungal colonies survived more than a year of tests of exposure to space radiation on the International Space Station (Fig. 18) (Selbmann et al., 2018; Onofri et al., 2015).

On the whole, Antarctica is the least biological of all the continents, with more than 99% of the land covered in permanent ice. Thus, the history of scientific research in Antarctica is chiefly a history of geological, geophysical, and glaciological studies. As discussed in this section, the coasts of the continent host a variety of bird and mammal life, but these are essentially marine organisms that visit Antarctic shores to mate, lay eggs, or give birth to live young. They rely exclusively on the biological resources of the sea to feed themselves, for as we have seen, Antarctica itself has none to offer. The human visitors to Antarctica live much as they would have to do on a lunar or Martian colony, except that they can breathe the Antarctic air. They must live in heated shelters, they venture outside in highly protective clothing, and must have all the resources required to sustain life brought in from other countries, except fresh water. The technological advances of the 20th and 21st century have allowed humans a foothold on this continent, and they have performed some prodigious feats of scientific research in spite of working in more-or-less life threatening conditions whenever they were outdoors. In fact, the exploration and scientific investigation of Antarctica has taken hundreds of lives since the beginning of the 20th century, mostly through transportation accidents. The greatest single cause of accidental death has been airplane crashes, which have taken 336 lives. Shipwrecks in Antarctic waters have caused 32 fatalities since 1900, and fires inside research station buildings have taken another five lives.

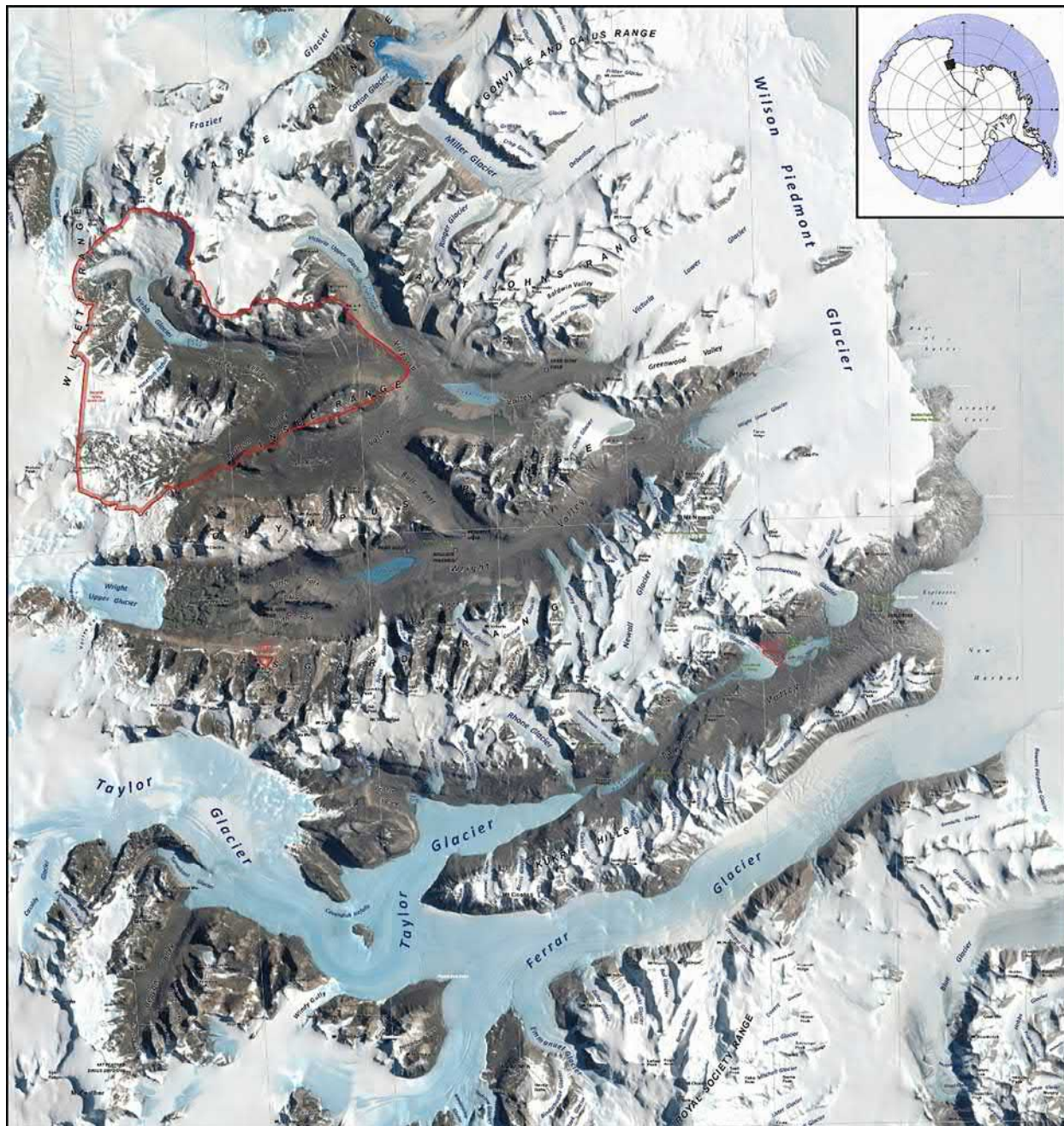


Fig. 17 Image of the Dry Valleys region of Antarctica, courtesy of the Antarctic Geospatial Information Center.

Looking Toward the Future

Antarctic science has turned out to be much more important than just finding out how much ice covers the bedrock. Antarctic ice cores have yielded the longest unbroken records of terrestrial climate change. Some of the most exciting research has concerned the existence of micro-organismic life in subglacial lakes: archaea and bacteria living in total darkness, deriving chemical energy from minerals and sediments. The discovery of bacteria and fungi living *inside* the surface of rocks has been another startling discovery. Not only do these discoveries enlighten us as to the tenacity and ingenuity of life in this planet's most extreme environments, they also point towards the very real possibility of this kind of life on Mars, or in water beneath the icy surface of moons in this Solar System, such as Saturn's moon Enceladus and Jupiter's moon Europa. Thus Antarctica has become a kind of laboratory to help space scientists understand how extra-terrestrial ice-covered bodies work (Carroll and Lopes, 2018). Hopefully the spirit of international cooperation that was launched in Antarctic will persist in future scientific endeavors in space.



Fig. 18 Cyanobacterial mats—desiccated cyanobacteria entwined with algae. Photo courtesy of the U.S. National Science Foundation.

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Current Changes in Antarctic Ecosystems

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Abstract

Antarctica's contemporary terrestrial biota have adapted to the continent's environmental challenges over many millions of years. It now faces the twin challenges of the multiple aspects of global and regional environmental change and the direct impacts of human presence and activity. Most native terrestrial biota possess wide physiological and ecological flexibility, well beyond the expected scale of environmental change over the next century and, when considered in isolation, are likely to show positive responses to environmental ameliorations, particularly the combination of increased thermal energy and liquid water availability, through increased production, populations, local distribution extent, and community complexity. However, over this timescale other, direct, human impacts on Antarctic terrestrial ecosystems and biodiversity are likely to have greater and negative consequences. Major sources of such impacts are likely to come through physical damage to the limited available area of terrestrial habitats, and the anthropogenic introduction of non-native species, a proportion of which are likely to become invasive and act as ecosystem engineers.

Introduction to Antarctic Biogeography and Biota

Antarctica is a continent of extremes and has long been a source of fascination. In contrast with the Arctic north, which is a relatively small ocean surrounded by large continental landmasses, Antarctica is itself a large continent, roughly twice the area of Australia, lying over the geographical South Pole. It is isolated from the other Southern Hemisphere continents by the vastness of the Southern Ocean (Fig. 1). Antarctica was part of the supercontinent Gondwana and remained at high southern latitudes while the other southern continents moved northwards away from it. Its final links were with Australia and South America, which were broken around 30–35 million years ago. Many tens and hundreds of million years ago, global climates were considerably warmer than now, and Antarctica was not glaciated. Even with its southern position, it hosted temperate and even subtropical vegetation and animals (see Convey et al., 2018 for an overview of Antarctic biological and glacial history).

As the southern continents separated, the formation of a major circumpolar ocean current took place, the Antarctic Circumpolar Current. This, combined with the strong and unobstructed atmospheric circulation that could then develop surrounding the continent and a global trend of decreasing atmospheric carbon dioxide concentration at the time, isolated Antarctica from lower latitudes, leading to cooling and eventually the formation of continental ice sheets in the Miocene. The extent of glaciation has fluctuated widely since the first formation of these ice sheets. In Victoria Land there is fossil evidence for the persistence of tundra-like ecosystems until around 12–13 Ma, and possibly even later in the northern Antarctic Peninsula.

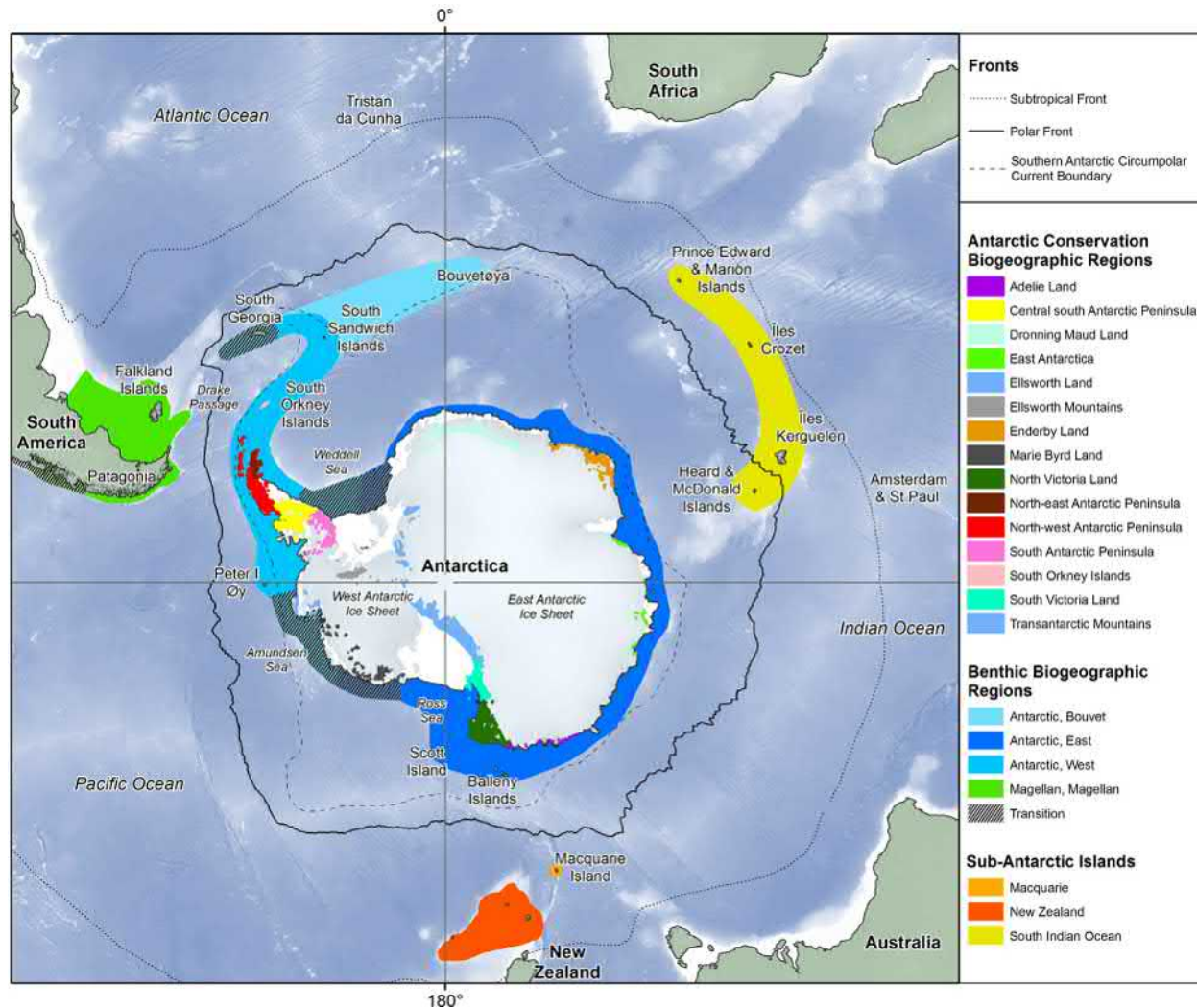


Fig. 1 Map of Antarctica and the Southern Ocean, indicating the complexity of biogeographic regionalisation now appreciated. Continental Antarctic Conservation Biogeographic regions (ACBRs) are indicated as described by Terauds and Lee (2016), along with sub- and peri-Antarctic regions. Reproduced from Chown SL and Convey P (2016) Antarctic entomology. *Annual Review of Entomology* 61: 119–137.

Today, Antarctica is a continent buried in ice, with less than 0.4% of its area ice- or snow-free. Terrestrial ecosystems are mostly limited to ice-free areas, typically including exposed nunataks, cliffs, slopes, boulder and scree fields, and valleys, along with exceptional and unusual geothermal areas (Convey, 2017) (Fig. 2). Conventionally, Antarctic terrestrial habitats and biodiversity include freshwater (lakes, ponds, streams) and snow and ice ecosystems (snow algae, cryoconite). Most Antarctic terrestrial biodiversity develops in coastal regions of the continent, where air temperatures hover close to or just above zero in the summer months and liquid water—the major driver of the continent’s diversity (Convey et al., 2014)—is more predictably available. However, life is present in all ice-free areas of the continent, even on the southern-most nunatak high on the continental ice plateau.

Antarctic Terrestrial Biogeography

In common with most scientific effort on the continent, terrestrial biological research commenced in earnest in the 1960s, although scientific collections had been an important element of most of the exploring expeditions from the early 20th century. Over most of the subsequent 50–60 years, three Antarctic biogeographic zones were generally recognized, the sub-, maritime, and continental Antarctic (e.g., Smith, 1984). Respectively, these zones include (a) a ring of chronically cool, remote and isolated islands at mid to high latitude in the Southern Ocean (ca. 45–54°S), (b) the western Antarctic Peninsula to ca. 73°S along with the Scotia Arc archipelagos of the South Shetland, South Orkney and South Sandwich Islands plus the isolated Bouvetøya and Peter I Øya, and (c) the



Fig. 2 Pictures illustrating typical features of the main Antarctic biogeographical regions. (A) Much of continental Antarctica experiences frigid desert conditions, as here in the Davis Valley, Pensacola Mountains, a “dry valley” at the eastern-most exposure of the Transantarctic Mountains and one of the least biodiverse ecosystems known. (B) Forlidas Pond, also in the Pensacola Mountains, an example of a lake that is almost completely permanently frozen other than a thin layer of hypersaline brine beneath the ice and a seasonal small “moat” of summer meltwater; the pond is surrounded by evidence of ancient lake shorelines and multimillion year-old patterned ground. (C) Inland ice-free ground in the continental Antarctic is typified by remote nunataks and mountain ranges, such as the Behrendt Mountains in Ellsworth Land, surrounded by ice sheets of 1–2 km thickness. (D) Extremely nutrient-enriched ground near vertebrate aggregations may be so polluted by guano that the only visible vegetation is the alga *Prasiola crispa*, as here on Saunders Island, South Sandwich Islands, northern maritime Antarctic. (E and F) Cryptogamic vegetation (mosses, liverworts, lichens, algae) typifies the maritime Antarctic, as here on Robert Island, South Shetland Islands, where some of the most extensive continuous vegetation in the region is found. (G) Most ice-free ground in the maritime Antarctic consists of steep cliffs, with even shallower ground being predominantly ice-scoured rock and periglacial in nature, as here at Evensen Point, Antarctic Peninsula. (H) Lake ecosystems are well-represented on sub-Antarctic South Georgia, as here at Maiviken; lake faunas consist only of invertebrates, although there are two native species of duck. (I and J) With an alpine mountain backbone rising to almost 3000 m, South Georgia is a rugged sub-Antarctic island; milder coastal areas and sheltered northern valleys are densely vegetated, predominantly by tussock and other grasses. (K) Campbell Island, one of the “New Zealand sub-Antarctic islands” illustrates the inclusion of woody bushes in the native vegetation of this milder region. (L) Above the treeline on Isla Navarino, in the Magellanic Sub-Antarctic Ecoregion of Tierra del Fuego, vegetation is dominated by cushion plants, grasses and mosses, many in common with the sub-Antarctic islands. (M) Cool temperate Gough Island, just south of the oceanic Sub-Antarctic Front, hosts forests of the tree *Phylica pubescens*. (N) Just north of the Sub-Antarctic Front and technically humid subtropical, the aptly named Inaccessible Island in the Tristan da Cunha archipelago is ringed by almost impenetrable tussock grass at the base of its cliffs, in common with the islands further south, wherein sub-Antarctic fur seals breed. Photo credits: (A–J, L–N) Peter Convey, (K) Krystyna Saunders.

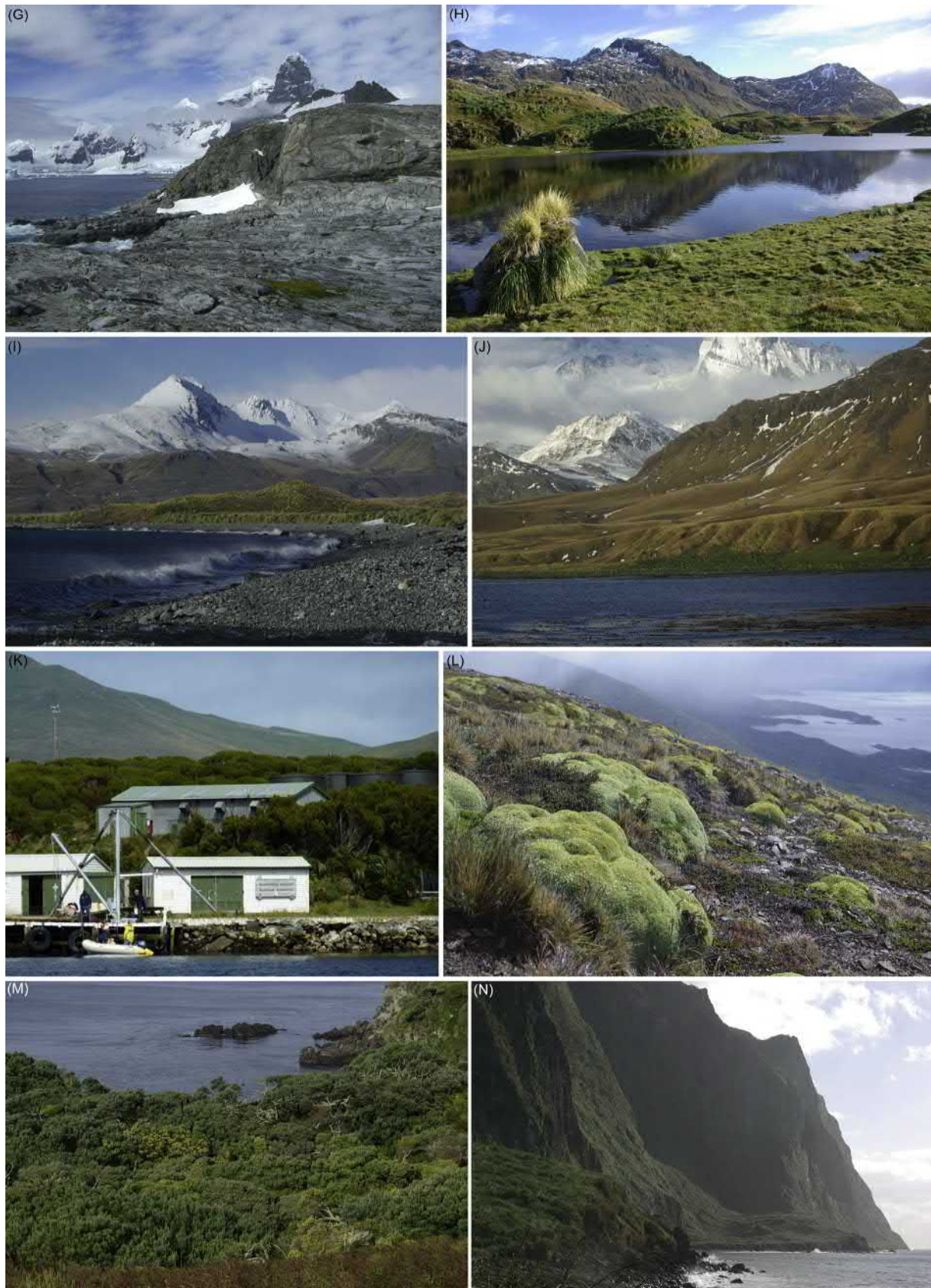


Fig. 2 (continued).

main body of the Antarctic continent plus the eastern part of the Antarctic Peninsula. Terauds et al. (2012), updated by Terauds and Lee (2016), using multi-layer spatial analyses based on quality-controlled and spatially explicit terrestrial biodiversity data available in the SCAR Antarctic Terrestrial Biodiversity database (www.scar.org/data-products/bio-database/), recognized far greater biogeographic structure in Antarctica than previously thought. As a result, 16 distinct “Antarctic Biogeographic Conservation Regions” (ACBRs) are now recognized within the Antarctic continent and Peninsula (Fig. 1). This analysis did not extend to the sub- or other peri-Antarctic islands, which clearly add further analogous regions. However, the original tripartite formulation still has utility, with ecosystems in each zone sharing important features of environmental conditions, ecosystem structure and overall representation of different biological groups.

Sub-Antarctic

Various broader or narrower definitions of the sub-Antarctic region exist in the literature (see Selkirk, 2007). A “core” sub-Antarctic region can be recognized, defined by the general lack of woody plants (trees and shrubs) and true terrestrial vertebrates. This includes South Georgia, Marion and Prince Edward Islands, the Crozet and Kerguelen archipelagos, Heard and McDonald Islands, and Macquarie Island, with most other than South Georgia and Heard Island being close to or north of the boundary of the Antarctic Circumpolar Current (Fig. 1). These islands have chronically cool climates, with annual temperature variation strongly buffered by the vast expanse of surrounding cold ocean, and much reduced environmental seasonality compared with the Antarctic zones further south.

Further islands and island groups are often described as “sub-Antarctic,” in particular the New Zealand associated Snares, Campbell, Bounty and Chatham Islands, and also the Magellanic sub-Antarctic region of Tierra del Fuego. Some of these (e.g., Diego Ramirez, south of Tierra del Fuego) are colder than some of the core sub-Antarctic islands year-round. Finally, there is biological connectivity, particularly in terms of marine diversity, with the lower latitude cool temperate Falkland Islands and Gough Island, Îles Amsterdam and St. Paul, and even the technically sub-tropical Tristan da Cunha archipelago. The terrestrial diversity of all these latter islands includes groups absent from the core sub-Antarctic.

Maritime Antarctic

This zone experiences strong marine influence at least during the summer months, with the stable Southern Ocean sea temperatures close to the coast, always within a degree or two of freezing, driving the overlying air temperature. About 3% of the area of the Antarctic Peninsula and Scotia Arc archipelagos is ice-free, a somewhat greater proportion than the continent as a whole. Ice-free land is most extensive at low altitude near the coast. While mean air temperatures are just above zero for the short Antarctic summer, those of terrestrial microhabitats can show considerably more variation and higher averages, with dark rock, soil and vegetation habitats, as well as shallow freshwater habitats, absorbing solar energy (Peck et al., 2006). In contrast with a general perception of Antarctica being a frigid desert, precipitation is high in this region, and increasingly falls as rain in the summer months. The South Sandwich Islands, Deception Island in the South Shetland Islands, and Bouvetøya are unusual Antarctic examples of active volcanic islands, and host exceptional and distinctive biological communities on areas of heated ground (Convey et al., 2000) (Fig. 3).

Continental Antarctic

By far the largest of the three conventional biogeographic zones, the continental Antarctic includes all of East Antarctica, the Balleny Islands, all remaining parts of West Antarctica south of the maritime Antarctic, and the eastern side of the Antarctic Peninsula. Ice-free land extent is much more limited—only 0.2 to 0.4% overall—and, excepting the Dry Valley region of Victoria Land, typically consists of nunataks and other small island-like areas of ground that can be extremely isolated. Similar to the maritime Antarctic, there are a number of ice-free coastal oases spread along the East Antarctic coastline. Mean air temperatures are positive for as little as 1 month in coastal oases and never inland, where they rarely if ever become positive even briefly in summer in the latter. Beyond the Antarctic Circle there is extreme seasonality in day length.

Habitats

Across the Antarctic continent and Peninsula most low lying terrestrial habitats experience at least some snow cover for part of the year, buffering them to varying extents from extreme low temperatures. This is not the case for many of the sub-Antarctic and lower latitude islands, which typically have only intermittent snow cover, and then often only at higher altitudes. The extent and depth of vegetation cover, even on colder islands such as South Georgia and Heard Island, means that microhabitat temperatures often remain close to and even above zero, allowing year-round biological activity.

Antarctic soils are poorly developed, lacking the multiple distinct horizons of more familiar lower latitude soils, and generally have low organic content (Thomas et al., 2008). Permafrost and periglacial processes and features are a ubiquitous feature of soils of the maritime and continental Antarctic. However, permafrost is not present on most sub-Antarctic islands, certainly at lower altitudes. True “brown” soils are widespread in the sub-Antarctic, but are only found under larger stands of the two native species



Fig. 3 There are few active geothermal areas within the limited ice-free ground of the Antarctic, but those that exist host exceptional plant and invertebrate communities, with some species only able to survive in the Antarctic because of the permanent source of heat and water, although there are also extremes of chemical stress. (A–C) Lush moss and liverwort communities develop around fumaroles and areas of intensely heated ground within the crater on Bellingshausen Island, South Sandwich Islands; the concentric pattern of vegetation is a function of the different thermal tolerances of the species present. (D) Patches of moss develop along the rim of a small active crater on Candlemas Island, subject to temperature and chemical stresses. (E) Lush vegetation around the mouth of a fumarole on Candlemas Island. (F) Vegetation patches develop around areas of gentler heating on Deception Island, South Shetland Islands, in otherwise largely barren scoria slopes. Photo credits: All photos Peter Convey.

of flowering plants in the maritime Antarctic. The development of deep and extensive peat deposits in wet valleys is a feature of the sub-Antarctic islands. Peat is much more restricted in the maritime Antarctic and differs in comprising mesic moss species whose growth is absorbed into permafrost without decaying, even remaining viable for up to ca. 2000 years (Roads et al., 2014) (Fig. 4).

Terrestrial Biota

Native terrestrial vertebrates are virtually absent from all Antarctic regions, meaning that the fauna is almost entirely invertebrate (Fig. 5). Exceptions are an endemic passerine bird (the South Georgia pipit) and two otherwise South American freshwater ducks on sub-Antarctic South Georgia and/or Kerguelen, and two scavenging sheathbills, one occurring in the maritime Antarctic and



Fig. 4 Moss bank vegetation in the maritime Antarctic. (A) Relatively young *Polytrichum strictum* bank formed on Candlemas Island, South Sandwich Islands, known not to have been present when the islands were surveyed after eruptions in the early 1960s. (B and C) Development of extensive and deep moss banks comprising *P. strictum* and *Chorisodontium aciphyllum* is a feature of the western Antarctic Peninsula and Scotia Arc archipelagos, as here on Signy Island, South Orkney Islands; these banks can be 2 m or more deep, entering permafrost at 20–30 cm depth, and their bases have been dated to be up 5–6000 years old. (D) Ice thinning in recent decades in the maritime Antarctic is re-exposing buried mosses and moss banks: the band of black moss here on Signy Island is recently re-exposed, continuous with the green living moss bank above; in some instances, mosses re-exposed after several hundred years' burial have been viable and shown regrowth. (E) The most southern known *P. strictum* peat bank formation, in Lazarev Bay, northern Alexander Island (69°S); the presence of these banks of around 50 cm depth illustrates the importance of local microclimate, they do not contain permafrost, but have provided records of climate and biological activity over more than the last hundred years. (F) Peat cores and monoliths provide important climate and biological proxies enabling environmental reconstruction, this example is a monolith collected near Volunteer Point in the oceanic cool temperate Falkland Islands. Photo credits: (A, E, F) Peter Convey, (B–D) James Fenton.

South Georgia, and the other endemic to Marion and Prince Edward Islands, both scavenging species largely reliant on marine vertebrate colonies and aggregations. Native terrestrial mammals, reptiles, amphibians and freshwater fish are absent, although anthropogenically introduced mammals and, on some islands, fish have had considerable negative impacts on terrestrial and freshwater ecosystems. Antarctic marine vertebrates (penguins, seabirds, seals) are responsible for considerable transfer of marine-derived nutrients into terrestrial ecosystems, thereby being important drivers of terrestrial diversity and biomass in coastal regions of the sub-, maritime and continental Antarctic (Bokhorst et al., 2019), with this influence extending several hundred kilometers inland in parts of the latter.



Fig. 5 Examples of the terrestrial invertebrate diversity of the Antarctic; arthropods are the largest and most visible members of the terrestrial and freshwater invertebrate community. (A) Aggregation of multiple instars of the oribatid mite *Alaskozetes antarcticus*, with a single individual of the maritime Antarctic endemic midge *Belgica antarctica*, the largest terrestrial invertebrates in the Antarctic continent. (B) An individual of the predatory mesostigmatid mite *Gamasellus racovitzai*, the largest terrestrial predator on the Antarctic continent. (C) The springtail *Cryptopygus antarcticus*, one of

Freshwater ecosystems in the maritime and continental Antarctic zones, and on the colder sub-Antarctic islands like South Georgia, are seasonally or permanently ice-covered. Shallower ponds and streams on the continent freeze to the bottom or cease flowing entirely in the winter months. Only a single river is formally recognized on the Antarctic continent—the Onyx River in the Victoria Land Dry Valleys. Lake ice cover leads to high stability and stratification in the water column, and some continental Antarctic lakes are meromictic. Others become hypersaline through evaporation, at the extreme consisting of a lens of ice overlying a few centimeters of hypersaline brine, such as seen at Forlidas Pond in the Pensacola Mountains. A number of coastal epishelf lakes exist around Antarctica, such as Ablation Lake on Alexander Island, where permanent surface ice covers permits a stable freshwater layer to overlie tidal marine water, with a steep halocline at the boundary between the water masses. Such lakes host entirely independent communities typical of fresh or marine water. Some continental lakes may be hundreds of thousands of years old. Finally, it is now realized that several hundred subglacial lakes exist at the base of the continental ice sheets, some of them forming part of active drainage systems. The largest of these is Lake Vostok, at ca. 200 km long and 500 m deep. The possibility of these lakes containing microbial and even metazoan ecosystems has been a subject of some controversy and is attracting considerable research attention (Pearce, 2009). Sampling these lakes without contamination is challenging.

As with the terrestrial invertebrate fauna, the representation of higher taxonomic groups in the Antarctic flora emphasizes that many groups familiar from lower latitudes are absent (Fig. 6). Restricting consideration to the “core” sub-Antarctic islands, these absentees include trees and other woody plants, other than dwarf-shrub-like rhizomatous herbs (*Acaena*), and the dwarf shrub *Coprosina* on Macquarie Island. There are also no insect-pollinated plant species (with a similar lack of insect pollinators). Smith (1984) provides an accessible and thorough overview of Antarctic floras, although there have been subsequent advances in taxonomy. Monographs of the Antarctic lichen (Øvstedal and Smith, 2001) and bryophyte (Ochyra et al., 2008) floras are available. Trees and shrubs are clearly important elements of communities in the less extreme New Zealand sub-Antarctic islands, the Magellanic sub-Antarctic and the remote cool temperate oceanic islands.

Sub-Antarctic

Other than the few exceptions mentioned above, Antarctic terrestrial faunas are entirely invertebrate (see Convey, 2017 for an overview). Faunas of the sub-Antarctic islands include true insects, with the greatest diversity in the flies (Diptera) and beetles (Coleoptera) and only a few species in other groups (e.g., Lepidoptera, Hymenoptera, Hemiptera) (Chown and Convey, 2016). Other arthropod groups are also present (Aranaea, Isopoda), along with some molluscs and annelid worms. Relatively high diversities are present in groups of micro-arthropods (Acari, Collembola), micro-invertebrates (Nematoda, Tardigrada, Rotifera) and microscopic and polyphyletic Protozoa, although many of these non-charismatic and cryptic groups have received very limited critical attention, particularly in recent years following the advent and rapid expansion of molecular phylogenetic techniques.

Freshwater ecosystems in the sub-Antarctic have very simple structure in comparison with those of lower latitudes, and also in comparison with the Arctic. Freshwater ducks are native on South Georgia and Îles Kerguelen, and their diets include freshwater and terrestrial invertebrates, and even carrion. Native fish are entirely absent, although some have been introduced on Îles Kerguelen. Top predators within the freshwater communities are typically crustaceans, although a single predatory diving beetle plays this role on South Georgia. Faunas otherwise include various Crustacea (cladocerans, copepods, ostracods, anostracans), micro-arthropods, nematodes, tardigrades, rotifers and protozoans.

Flowering plant floras of the different sub-Antarctic islands have affinities with either southern South America, South Africa or New Zealand. In the absence of grazing mammals or birds, there has been exceptional development of large “megaherbs” and tussock grasses, with a suggestion that at least some of these may represent lineages driven from Antarctica itself by the glaciation of the continent (Winkworth et al., 2015). While there is almost complete cover and high vegetation biomass in low altitude coastal regions, at higher altitudes this community is replaced by a cryptogamic flora dominated by mosses and lichens, with many species in common with the flora of the maritime Antarctic.

Maritime Antarctic

In the maritime Antarctic only two native higher insects are present, both chironomid midges (Diptera). As with the sub-Antarctic, communities of mites (Acari) and springtails (Collembola) are present, and micro-invertebrates are also well represented. These again have not been well-studied, although classic, molecular and integrated taxonomic approaches are now starting to demonstrate considerable cryptic speciation in the groups examined. Particular attention has been paid recently

the most common terrestrial arthropods in the maritime Antarctic and parts of the sub-Antarctic. (D) Ground aggregation of the swarming midge *Parochlus steinenii* on the South Shetland Islands, a species that also occurs in the sub-Antarctic and southern South America, and the only flying insect occurring naturally within the Antarctic continent. (E) Adult diving beetle, *Lancetes angusticollis*, the top invertebrate predator within lake ecosystems on sub-Antarctic South Georgia. (F) The tardigrade *Acutuncus antarcticus*, a widespread continental species. (G) A gravid female of the copepod *Boeckella poppei*, a species that unusually occurs across all three of the major Antarctic biogeographic regions as well as in southern South America. Photo credits: (A–C) Elisabeth Biersma, (D) Felipe Simoes, (E) Gonzalo Arriagada Kritzer, (F) Megumu Tsujimoto, (G) Claudia Maturana.



Fig. 6 Illustration of the variety of different Antarctic vegetation. (A) A diverse range of soil fungi are known from Antarctica, but basidiomycete “toadstools” are relatively unusual and limited to warmer microhabitats in the maritime Antarctic (including geothermal habitats), although more widespread in the sub-Antarctic; this example is on Léonie Island, ca. 67°S, almost the furthest south location known. (B and C) Across the continental Antarctic, moss and lichen vegetation development is limited, with small clumps in isolated microhabitats being the typical form found; these examples from Arrival Heights, McMurdo Sound, and Ross Island, Victoria Land. (D) In the maritime Antarctic, as here on Lagoon Island, close to Adelaide Island, visible vegetation is dominated by clump, carpet and turf forming mosses, and distribution strongly influenced by water availability. (E) Only two species of flowering plant, the hairgrass *Deschampsia antarctica* and the pearlwort *Colobanthus quitensis*, occur on the Antarctic continent, both also found on sub-Antarctic South Georgia and in southern and Andean South America; they often grow together as here in Lazarev Bay, Alexander Island. (F) Diverse lichen communities develop on rock faces, boulder and scree slopes and fellfields in the maritime Antarctic; this example from Lagoon Island. (G) Extensive and dense coastal tussock grass is a feature of the natural environment of many sub- and peri-Antarctic islands, as here in East Cumberland Bay, South Georgia. (H) The sub-Antarctic has much greater native flowering plant diversity than the regions further south, with the species *Acaena magellanica* seen here at Husvik, South Georgia, being distributed across most core sub-Antarctic islands as well as in southern South America. (I and J) With more severe conditions rapidly taking over at higher altitude, diverse cryptogamic fellfields rapidly become dominant, as at Bird Island, South Georgia. (K) Dense vegetation, dominated by *Acaena magellanica*, the cushion plant *Azorella selago* and the Kerguelen cabbage *Pringlea antiscorbutica*, on Île Australia, sub-Antarctic Îles Kerguelen. (L) A shallow pond on Île Australia, with aquatic *Ranunculus pseudotrullifolius* surrounded by flowering *Acaena magellanica*. (M) An example from Campbell Island of the “megaherb” vegetation that has evolved on the sub- and milder peri-Antarctic islands in the absence of native vertebrate grazers. Photo credits: (A–J), Peter Convey, (K and L), Francoise Hennion, IPEV PlantEvol, (M) Krystyna Saunders.



Fig. 6 (continued).

to Collembola, identifying considerable intra-specific differentiation and cryptic speciation and providing rapidly strengthening support for the biogeographic regionalisation integral to the recognition of Antarctic Conservation Biogeographic Regions (ACBRs; Terauds et al., 2012). It is likely that application of similar approaches to Acari, Nematoda, Tardigrada and Rotifera will lead to similar outcomes. While invertebrate distributions are strongly limited by the minute extent of ice-free ground, and within that of suitable habitat, population densities are often high, tens of thousands to millions of individuals per square meter; counter to common expectation, such values are comparable with many temperate and tropical ecosystems for these groups. While Antarctic terrestrial food webs have simple structure, the typical trophic functions are represented (producers, consumers, predators, parasites, detritivores), while the overall low diversity makes these systems attractive models within which to study the ecosystem consequences of environmental change. However, there remains a lack of detailed and species-specific autecological studies.

Freshwater communities are similarly of low diversity and complexity. Planktonic herbivores include single copepod (*Boeckella poppei*) and anostracan (*Branchinecta gaini*) species, with predators represented by the copepod *Parabroteas sarsi*. Benthic cladocerans and ostracods are also present, as well as abundant tardigrades, rotifers and nematodes, and microscopic protists. The microbial loop, which consists of phytoplankton, bacteria and protozoans, is functionally very important in maritime and continental Antarctic lakes (Laybourn-Parry, 1997). *Boeckella poppei* poses intriguing biogeographic questions, as it is the only crustacean and indeed only arthropod species of any sort that is thought to occur across all three of the main Antarctic biogeographic zones, as well as extending into southern South America (Maturana et al., 2019).

Maritime Antarctic floras are dominated by cryptogams (bryophytes, lichens, algae) (Smith, 1984). Extensive areas of vegetation, consisting of communities of carpet- and turf-forming mosses, are exclusively coastal and low altitude. At more exposed or extreme sites, fellfield communities develop, consisting of cushion and turf-forming mosses, liverworts and diverse lichens. Only two native flowering plants occur, the hairgrass (*Deschampsia antarctica*) and the pearlwort (*Colobanthus quitensis*). While both only rarely occur at high densities, they are present throughout the maritime Antarctic to southern Marguerite Bay (ca. 69°S), and also occur in parts of the sub-Antarctic, southern South America and at higher altitude in the South American Andes. One feature of the typical cryptogamic vegetation is that it is fragile and easily physically damaged. Therefore, areas close to vertebrate concentrations where there is a lot of trampling are often dominated by the foliose alga, *Prasiola crispa*. Similarly, careless human activity on foot or using vehicles can lead to long-term damage to this fragile vegetation.

Continental Antarctic

There are no insects in the continental Antarctic. Similar overall diversities of Acari, Collembola and Nematoda are present to the maritime Antarctic (Convey, 2017), often with congeneric species and again noting the caveat that modern molecular approaches are likely to reveal considerable increases in these diversities. The continental Antarctic includes multiple ACBRs, with species endemism within particular regions being a common feature (e.g., Adams et al., 2006). Even with current levels of diversity knowledge, a particularly striking feature in comparing maritime and continental Antarctic diversity is that, at species level, no or almost no species are shared between the two zones in the Acari, Collembola and Nematoda. This is an important and ancient biogeographic feature and led Chown and Convey (2007) to erect the Gressitt Line across the base of the Antarctic Peninsula, analogous to the widely known Wallace Line in south-east Asia. The continental Antarctic includes some of the simplest faunal communities known on Earth.

As with the maritime Antarctic, continental Antarctic vegetation is cryptogamic, although lichens dominate. Around 25 bryophytes occur in this zone, compared with ca. 110 in the maritime Antarctic, with greatest community development in the coastal oases. No flowering plants are present.

Microbial Systems

Perhaps more than any other continent, microbial groups dominate Antarctic terrestrial (including snow and ice) ecosystems and the functions and services they provide (Cavicchioli, 2015; Chown et al., 2015), as primary producers, decomposers, and vital in primary colonization and soil stabilization. Modern molecular techniques now confirm that Antarctic microbial and viral communities contain far higher diversity than previously suspected, in contrast with the trend for multicellular organisms (Cary et al., 2010; Aguirre de Cárcer et al., 2015). In some of the most extreme environments, microbial life retreats to endolithic habitats, existing within tiny fissures open to the rock surface, or between crystals within the rock matrix. Such habitats are considered as one limit to life on Earth and are used as model systems in exobiological research (Fig. 7).

Antiquity of the Antarctic Terrestrial Biota

Overall similarity is clear between the invertebrate and plant communities of both polar regions (the dominance of Acari, Collembola, other micro-invertebrates and cryptogamic flora). Indeed, amongst microbial groups and mosses in particular, there are significant proportions of truly bipolar or amphitropical species (Biersma et al., 2017), reflecting the ability of these groups to disperse widely using microscopic spores or other propagules. However, even in these groups, as well as in the various invertebrate groups

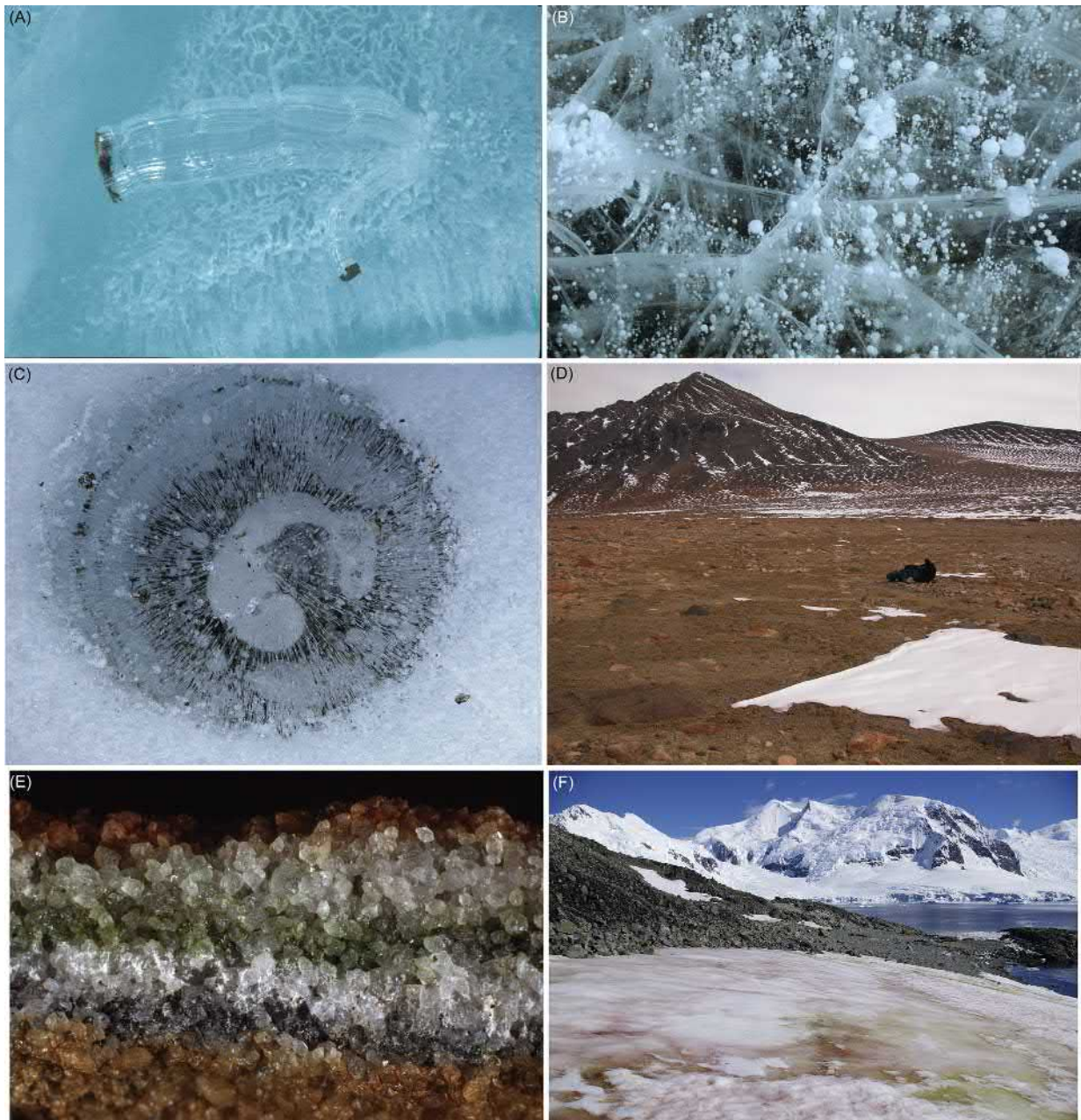


Fig. 7 Microbial ecosystems are dominant across much of Antarctica. (A) Pieces of cyanobacterial mat detached from a continental Antarctic lake benthos become entrapped in permanent lake ice, moving slowly towards the surface in their own private melt pool over a few weeks each summer. (B) Trapped gas bubbles in the ice of permanently frozen lakes and over seasonal moats along the edge of glaciers, indicate active microbial life beneath. (C) Cryoconite “holes” develop where dark mineral debris initially accumulates in small depressions on glacier surfaces, absorbing solar energy and melting to form a small pool within which microbial and micro-invertebrate communities live. (D) An unusual example of extensive dried cryptobiotic cyanobacterial mats formed in an area very occasionally flooded by meltwater. (E) Endolithic microbial life within the crystal matrix of a sandstone rock, showing a black pigmented fungal layer, a white non-pigmented layer of fungal hyphae, and a green layer of photosynthetic algae. (F) Rich snow algal communities develop in coastal regions especially in the maritime Antarctic, where water is present in the snowpack during the summer, and nutrient input is received from surrounding marine vertebrate aggregations. (G) The foliose alga *Prasiola crispa* forms seasonally extensive carpets in areas receiving nutrient enrichment from neighboring vertebrate colonies, being able to thrive in higher concentrations than most Antarctic vegetation. (H) Extensive cyanobacterial mats can form in freshwaters, even at close to freezing temperatures. (I) Intense biological activity is apparent in flooded mixed communities of moss, cyanobacteria and algae. Locations of photographs: (A–D) Davis Valley, Dufek Massif, (E) Battleship Promontory, Victoria Land, (F) Léonie Island, off Adelaide Island, (G) Anchorage Island, off Adelaide Island, (H and I) Coppermine Peninsula, Robert Island, South Shetland Islands. Photo credits (A–D, F–I) Peter Convey, (E) British Antarctic Survey.



Fig. 7 (continued).

typical of the Antarctic, considerable species-level endemism is documented (Pugh and Convey, 2008). These levels approach 100% in groups such as Nematoda, Acari and Collembola.

Over the last two decades, rapid advances in classical biogeographic and molecular phylogeographic research have led to a paradigm change in our understanding of the origin and antiquity of the Antarctic terrestrial biota (Convey et al., 2008). Studies carried out across all ice-free regions of the continent, and all the major terrestrial taxonomic groups, have confirmed that long-term presence in these regions is the norm, requiring persistence of both the organisms and terrestrial habitats through the multiple cycles of glaciation Antarctica has experienced (see Convey et al., 2020, for comprehensive review). Some phylogeographic studies have identified signals of persistence since the final breakup of Gondwana and separation of Antarctica. Others have identified a range of dates between the late Pleistocene and early Miocene, with this remaining a rapidly moving field of research. The overall antiquity of the terrestrial biota, combined with high levels of endemism and strong regionalisation, provide an important foundation element of the recognition of the ACBRs as described above, as well as emphasizing the high conservation value of the Antarctic terrestrial biota, and the governance challenges this presents to the signatory nations of the Antarctic Treaty (Chown et al., 2015, 2017).

Antarctic Environmental Change

The world's polar regions are facing some of the most rapid rates of warming and other environmental changes seen globally, through a process known as "polar amplification." In Antarctica this applies particularly to the Antarctic Peninsula and Scotia

Arc, which have been one of the three most rapidly warming regions globally, although most of the Antarctic continent has to date been protected from the effects of global warming (Convey and Peck, 2019). Over the last two decades the Antarctic Peninsula warming trend has paused, thought to be a result of natural variation, although it is expected to resume and, by 2100, the entire continent is expected to be similarly affected. Even so, temperatures away from the continental coastline will remain well below zero, and this is not likely to lead to biological impacts. However, near the coast, and particularly in the maritime Antarctic, mean air temperatures are already slightly positive. Here, warming is of greater biological significance, providing extra energy, longer seasons, and increased melt and ice-free area (Convey and Peck, 2019). Environmental change involves multiple variables, with precipitation and liquid water availability and, conversely, desiccation, being of great significance to biology (Convey et al., 2014). Several sub-Antarctic islands show increasingly strong signs of biological impacts from reduced precipitation and desiccation. In the maritime Antarctic, conversely, precipitation is both increasing and, during the summer months, falling as rain rather than snow. Antarctica was also where the stratospheric ozone hole was discovered, a further consequence of atmospheric pollution, generating concern about the harmful effects of ultraviolet-B radiation to biological systems.

Antarctic lakes are particularly sensitive to warming, even magnifying the already rapid rates recorded in air temperature (Quayle et al., 2002). Warming and changes in precipitation in the maritime Antarctic, in combination with changing marine vertebrate distributions and influences, lead to changes in biological production, including eutrophication, and water column mixing. Continental Antarctic limnological studies have identified changes in other indicators, such as drier conditions and evaporation leading to increased salinity associated with changes in prevailing winds. Similarly, drier conditions in parts of the continental Antarctic coastline are also implicated by changing patterns of moss distribution and health (Robinson et al., 2018).

Biological Responses to Change in Antarctica

Natural Ecosystems

The sensitivity of Antarctic terrestrial ecosystems to change has long been recognized (Convey and Peck, 2019). However, responses of these ecosystems to warming may not be negative, as is often generally assumed to be the case elsewhere. Noting that the currently biodiverse parts of the maritime Antarctic in particular, but also coastal regions of the continental Antarctic, already experience positive temperatures especially at microhabitat scale, warming will lead to more energy being available to support activity of biota. Increased snow and ice melt, as well as precipitation as rain, increases the availability of liquid water—the major driver of Antarctic diversity—as well as expanding the area of ice-free ground available. Reduction in the limits imposed by low temperature and desiccation will generally result in greater productivity, population growth and expanded distributions at local scale. However, specific outcomes will be influenced by local features. Should water supply from snowmelt or other sources be exhausted then local biological communities will face greater stress. Changes in nutrient supply can also be important. Nitrogen provided by marine vertebrates is another important driver of terrestrial diversity (Bokhorst et al., 2019) and, thus, changes in vertebrate distributions driven by environmental change should lead to consequential changes in the distribution of this diversity. Similarly, large changes in key ecosystem services such as decomposition can be caused by the colonization of new community members, with the known examples to date being associated with human introduction of non-native species. In maritime Antarctic vegetation communities, increased nutrient availability is predicted to be advantageous for stronger competitors for nitrogen.

Much of terrestrial Antarctica is characterized by physical isolation and strong barriers to dispersal between individual “islands” of terrestrial habitat across hostile sea or ice. If warming continues unabated, current trends of ice and snow recession are predicted to lead to a 300% increase in ice-free area in the Antarctic Peninsula region (although this reduces to 25% across the entire continent) (Lee et al., 2017). In the former in particular, this increase will result in the coalescing of currently isolated areas of ground, bringing the potential for genetic homogenization and irreversible loss of genetic diversity (Chown and Convey, 2007) and providing a major conservation challenge. An analogous diversity challenge is posed by human-assisted transfer between different isolated populations of native biota.

A predicted consequence of environmental change globally is that species distributions will change, and that currently non-native species will arrive in previously isolated areas. Throughout the Antarctic, one important isolating factor or barrier is that of the environmental stresses that must be faced both during transfer and on arrival at a potentially colonisable location. Where environmental change reduces these barriers, even in the absence of human assistance it is likely to increase the chance of transfer and establishment.

In concert with this, the balance between abiotic and biotic drivers of diversity is likely to change, with the latter becoming more important, such as competition, herbivory and predation. Native maritime and continental Antarctic biota are generally described as “adversity selected,” investing considerable resources in strategies permitting survival of abiotic stress at the expense of poor competitive ability (Convey, 1996). Further, while biotic interactions are clearly greater on the sub-Antarctic islands, predation is a weak force in the absence of most familiar groups of invertebrate predators (e.g., spiders other than linyphiid “money spiders,” carabid beetles, hymenopterans). Thus, native invertebrate communities across all three Antarctic biogeographic zones are vulnerable to the arrival of stronger competitors, as already demonstrated by the anthropogenic introduction of aggressively predatory carabid beetles to sub-Antarctic South Georgia and Îles Kerguelen (Convey and Peck, 2019) (Fig. 8).

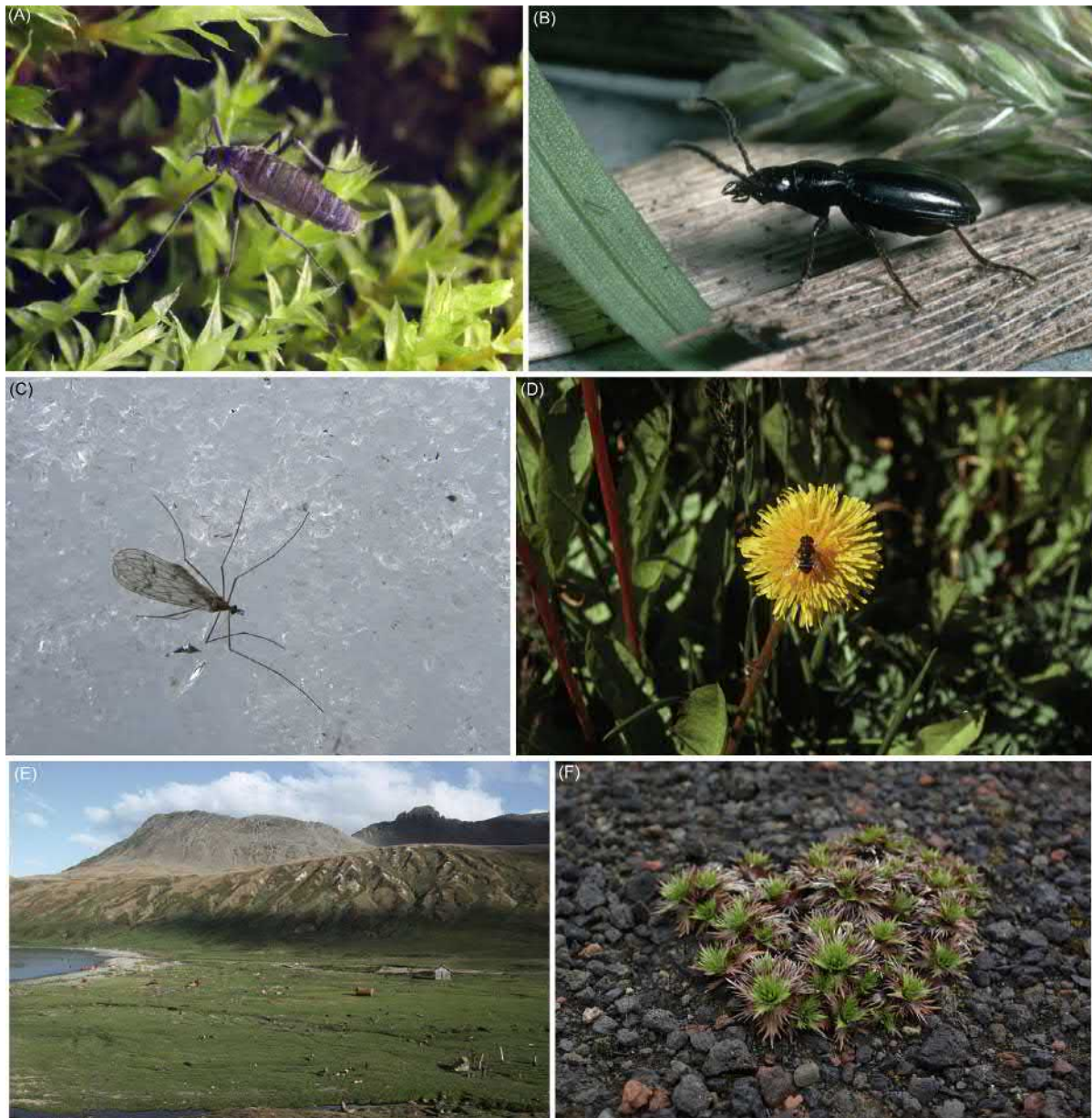


Fig. 8 Direct human impacts on Antarctic terrestrial ecosystems come in a number of forms, the most significant of which include the introduction of non-native species and use change through the construction of stations and facilities, and long-lasting damage to fragile ecosystems. (A) The chironomid midge *Eretmoptera murphyi* is endemic to sub-Antarctic South Georgia but was introduced to maritime Antarctic Signy Island in the 1960s, where it is now spreading rapidly and can lead to an order of magnitude increase in peat decomposition. (B) Predatory carabid beetles have been introduced to sub-Antarctic South Georgia (two species) and Îles Kerguelen; as an entirely new guild of aggressive predators for these islands, the native terrestrial invertebrate community has no defense against them. (C) The trichocerid fly *Trichocera maculipennis* was introduced to King George Island, South Shetland Islands in the late 2000s; in terms of physiology and diet this northern boreal detritivore is well pre-adapted to the maritime Antarctic, and appears to be spreading rapidly on the island, including crossing glacial barriers. (D) The hoverfly *Eristalis croceimaculata* was first noted on South Georgia in the mid-2000s, along with the blowfly *Calliphora vicina*; adults of both species are plant pollinators, a function not represented in the native invertebrate community. While the native flora is wind- or self-pollinated, a number of non-native species, such as the dandelion *Taraxacum officinale*, can be insect pollinated, which for some will lead to a step-change in their potential reproduction and dispersal. (E) The non-native grass *Poa annua* occurs on many sub-Antarctic islands; on South Georgia it has spread to completely carpet valley floors around sites of previous whaling activity. (F) *Nassauvia magellanica* is a native montane species occurring in Tierra del Fuego that was temporarily established before eradication close to the historic Whalers Bay site on Deception Island, South Shetland Islands. (G) Large decaying industrial sites, such as the Husvik whaling station on South Georgia abandoned in the 1960s, continue to be a largely uncontrolled source of debris and pollution into the local environment. (H) Grytviken whaling station on South Georgia has been partially remediated and conserved, although its overall footprint remains large, and it is now a very popular tourist visitor site. (I) Whalers Bay on Deception Island includes both the remains of a 1930s whaling station, and of a United Kingdom research station abandoned after the island erupted in the late 1960s; although now a historic site, the remaining buildings and facilities are in poor condition and much dispersed debris is present. (J) Abandoned amphibious vehicles around stations on the Fildes Peninsula,

Surprisingly few studies of biological responses to change have been published from natural Antarctic terrestrial ecosystems. There has been a focus on studies of population increases in the two native flowering plants of the maritime Antarctic (Cannone et al., 2016), although this often results in an inaccurate statement that these species have expanded their distributions southwards, which is not the case. There is increasing evidence that terrestrial invertebrates are sensitive to the magnitude of environmental changes being seen, including extreme events. While there is considerable media reference to the “greening of Antarctica” through expansion of the native vegetation communities and rapid colonization of new ice-free areas, only two robust studies are currently available, both from the maritime Antarctic, for mosses (Cannone et al., 2017) and lichens (Sancho et al., 2017).

The combination of increased spatial resolution in future climate models for parts of Antarctica and detailed knowledge of ecophysiological and microclimatic requirements of individual species has facilitated the application of distribution modeling approaches to both native and non-native species in Antarctica. For example, the native dipteran *Parochlus steinenii* is currently restricted to the maritime Antarctic South Shetland Islands. However under both the IPCC RCP4.5 and 8.5 (the latter being “business as usual”) scenarios the species could occupy habitats much further south along both east and west coasts of the Antarctic Peninsula, and even parts of the East Antarctic coastline given transfer opportunity (Contador et al., 2020). Similarly, the non-native midge, *Eretmoptera murphyi*, a native endemic of sub-Antarctic South Georgia that was accidentally introduced to Signy Island in the maritime Antarctic in the 1960s, is now rapidly expanding its local distribution on the island. Future distribution modeling confirms the likelihood of further considerable distribution expansion on Signy, and that the species is capable of establishing throughout the western Antarctic Peninsula (Perterra et al., 2019). A similar outcome has been reported for the invasive grass *Poa annua*, which has been established on King George Island (South Shetland Islands) for around 40 years and has the potential to spread much further south.

Environmental Manipulation as a Proxy for Climate Change

Long-term field manipulation studies attempting to mimic some of the predictions of climate change models have been an important experimental approach to testing the predicted consequences of changes in environmental conditions for individual species and communities in the Antarctic (reviewed by Bokhorst et al., 2013). Early studies provided very unrealistic manipulations, and problems have not been entirely resolved even with advances in techniques, as inevitably all methodologies affect multiple environmental variables, and rarely provide a good representation of predicted changes over the annual cycle, in some cases even being opposite to the expected changes. Newsham and Robinson (2009), in a meta-analysis of field studies mimicking predicted ozone hole impacts on ultra-violet radiation exposure, found little consistency in the effects obtained. Despite the methodological limitations, even the early warming manipulation studies found that typical maritime Antarctic terrestrial communities responded rapidly with increased biomass, population densities and ground cover. More recent studies with greater replication, more realistic manipulations and multivariate approaches, and accurate micro-environmental monitoring have given these findings greater strength.

Other Direct Human Impacts

Historical and contemporary human activity in Antarctica have posed threats to terrestrial ecosystems and diversity distinct from those directly associated with climate change (Fig. 8). Historically, the main onshore industrial activities in the sub- and maritime Antarctic were associated with the exploitation of, first, fur seals and, later, the great whales. The ongoing impacts on land are mostly focused around the remains of whaling stations, including some major industrial sites such as Leith Harbor on South Georgia. Although ecological impacts during the times of site occupation went undocumented, the physical extent of some of these stations inevitably means that very large areas of native habitat were destroyed, as well as being subjected to extensive pollution. Two such stations, Grytviken (South Georgia) and Whaler’s Bay (Deception Island), have been stabilized or restored, with some effort at pollution remediation. These are now historical monuments, and popular visitor sites for the increasing Antarctic tourism industry. However, other sites have neither been maintained nor cleaned up, and continue to suffer from increasingly dispersed debris and pollution. Another incidental consequence of these historic marine industries for the sub-Antarctic islands, along with accidental shipwrecks, was the introduction (both inadvertent and deliberate) of around half of the non-native species now known from these islands (Convey and Lebouvier, 2009). This is also the case for the lower latitude peri-Antarctic islands with, for instance, an estimate from South Atlantic Gough Island that, on average, every second ship visit over the history of human contact with the island has resulted in one new non-native species establishment.

King George Island, the densest concentration of international research stations in Antarctica as well as a tourist visitor site and entry point, shed debris into the natural environment. (K) Direct human impacts, such as these vehicle tracks on the Fildes Peninsula, easily damage the delicate vegetation and soil surface and take many years to recover; pollution from unsuitably stored fuel and waste is similarly hard if not impossible to remediate. (L) The American McMurdo Station on Ross Island is the largest operational station in Antarctica, accommodating over 1000 personnel in the summer; the station footprint occupies much of the available ice-free area on southern Ross Island, destroying the original sparse terrestrial habitats. Photo credits: All photos Peter Convey.



Fig. 8 (continued).

For practical reasons of accessibility and logistic simplicity, most contemporary human activity is concentrated on the small proportion of the continent that is ice-free. Most research stations and visitor sites are therefore located at or near the coast, in areas where terrestrial ecosystems are most developed and biodiversity greatest, as well as where marine vertebrate colonies are found. In reality, there is already considerable competition for the very limited ice-free land, a large proportion of which is already impacted by human activity ([Chown and Brooks, 2019](#)).

All types of transport and infrastructure used in Antarctica create detectable chemical pollution. They can also lead to local dispersal of dust and can damage soil surfaces, vegetation and freshwater ecosystems ([Bargagli, 2005](#)). The potential is not limited to heavier vehicles and major constructions—even a single person's footfall can compress soil, damage vegetation and measurably alter invertebrate community structure, with recovery taking many decades at least.

Non-native Species

A specific and fundamentally important direct human impact affecting biodiversity in parts of Antarctica already and, without effective regulation, into the future, is that of the human-assisted movement of non-native species, followed by their establishment. This applies both to movement of species from other regions beyond the Antarctic itself ([Frenot et al., 2005](#)) and to movement of species

native to one region of Antarctica to other regions where they are not native (Hughes et al., 2019). Human assistance enables organisms to overcome the environmental and transfer time barriers that otherwise protect Antarctica from colonizing organisms. While dispersal is a natural process, and few studies have documented the frequencies of natural and anthropogenic colonization events, data from some sub-Antarctic Marion Island and cool temperate Gough Island suggest that the human-assisted route has resulted in at least two orders of magnitude more establishment events since these islands' discovery. Furthermore, there are no known examples of species becoming established in the maritime or continental Antarctic since the initiation of human contact with them, while human-assisted establishment in the maritime Antarctic is increasing.

The majority of non-native species that have become established in the Antarctic to date are found on the various sub-Antarctic islands, with well over 200 species known to date virtually all of which are most likely linked with either national Antarctic operations or the preceding whaling and sealing industries (Frenot et al., 2005). Some aggressively invasive non-native species can be particularly significant, even acting as ecosystem engineers, through introducing new ecological guilds and functions that can lead to step changes in ecosystem services. Historical introductions of grazing and predatory vertebrates to most sub-Antarctic islands clearly had major destructive impacts on both their terrestrial ecosystems and on breeding marine birds. Whilst some have been eradicated in expensive and logistically demanding operations, sometimes with unpredicted consequences, many remain. However, of particular and urgent contemporary concern as noted above, the introduction of new guilds of invertebrate predators to some sub-Antarctic islands raises the very real threat of extinction of some native endemic invertebrate species, with "strict" terrestrial diversity to date receiving insufficient attention in sub-Antarctic conservation decision making.

It is clear from the existing record of establishment that many species that are not native to Antarctica are capable of surviving and establishing in Antarctic terrestrial habitats if presented with the opportunity to make the transfer into the region. This is particularly the case for the sub-Antarctic (and lower latitude peri-Antarctic) region, but also applies to the maritime Antarctic and in a few instances the continental Antarctic. The risk of microbial introductions has also been recognized, although few specific studies are available. Risk assessments have identified a number of species or groups as being of particularly high risk of establishment in the coming decades (Hughes et al., 2020), and some have already been confirmed as new arrivals on Deception Island in the South Shetland Islands, a geothermally active and highly visited location thought to be one of the most vulnerable to invasions in the Antarctic. As noted earlier, future distribution modeling studies emphasize that, under current regional climate change scenarios, both native and existing non-native species can be expected to considerably expand their distributions within Antarctica. There is also the realization that synergy between climate similarity and human connectivity (through logistic or tourism operations) further compounds the risk of human-assisted transfer (Hughes et al., 2019).

Concluding Thoughts

Antarctic terrestrial ecosystems and biodiversity today face two distinct but interwoven challenges. First, from the multifaceted elements of global and regional environmental change and, second from the direct impacts of human activity at more local scale within the different regions of Antarctica. Indeed, while climate change is one of the greatest overall challenges facing human society today, on a 21st century timescale it may not lead to widespread negative consequences for Antarctic terrestrial ecosystems that are generally observed or expected elsewhere. Rather, direct consequences of human activity, particularly, development and human activity on land and biological invasions, stand to have far greater impacts on this timescale on Antarctic ecosystems terrestrial ecosystems than climate change itself.

Addressing global climate change is beyond the Antarctic community alone, although it is appropriate to note that the majority of signatory nations to the Antarctic Treaty are also signatories to or engaged in the major global conservation or climate change conventions. In principle, the governance mechanisms are already in place within the Antarctic Treaty System to facilitate appropriate action being taken to control and mitigate the direct impacts of human activity, and to take appropriate action to properly protect Antarctic ecosystems and biodiversity (Chown et al., 2017; Convey and Peck, 2019), and the same is the case for the nationally-administered sub-Antarctic islands. Clear and actioned commitment to continent-wide biodiversity and ecosystem monitoring programmes is required from national operators and funding agencies. These must be appropriately funded and resourced in terms of expertise. Wide education programmes are also required within national operator programmes and tourist operations to ensure clear awareness of the dangers of direct human impacts, and engagement with robust biosecurity measures to minimize the risk of further biological introductions.

Acknowledgment

Peter Convey is supported by NERC core funding to the BAS 'Biodiversity, Evolution and Adaptation' Team.

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Forest Biome: Trees of Life

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Abstract

Nearly one third of the Earth's terrestrial surface are covered by forests of some type, the world's largest terrestrial biome. Forests collectively cleanse the air we breathe; purify our drinking water; play a vital role in regulating regional and global climatic processes; support at least half of all terrestrial species on Earth, especially in the tropics; and provide economic, spiritual, and cultural benefits for millions of people worldwide. Global rates of deforestation and forest degradation have slowed recently based on country-specific reporting overseen by the Food and Agriculture Organization. However, the alarming loss of primary (unlogged) forests remains a global concern (e.g., Global Forest Watch). Gains in forest cover from tree planting do not offset losses. Thus, international initiatives (e.g., UN Sustainability Goals and REDD+ Programme, Convention on Biological Diversity, Paris Climate Agreement) along with national/regional conservation need to protect remaining primary forests and intact forest landscapes while restoring primary forests through "proforestation."

What is a Forest (Definitions and Perspectives Matter)?

A forest is one of those places that you just know you are in when you see it, hike in it, experience all its magnificence, and interact with the constituent parts. But we each see the forest the way we want. Some see it only for the trees, others as an intricate-web- and way-of life.

A forester sees a crop of trees to be "harvested" when the rate of return on investment is optimized. Trees planted in neatly spaced rows (like corn fields), grow money for the owner over time, but lack the structural complexity and biodiversity of "natural forests" (Fig. 1). An ecologist sees a dynamic "self-willed" ecosystem where the sum-of-the ecosystem parts (native species, processes, functions—also known as integrity) is greater than the whole. Indigenous peoples derive sustenance, medicines, food and shelter, and deep-rooted, long-established cultural and spiritual connections to the forest. Their survival depends on the forest.

All told some 800 (<http://www.terisas.ac.in/mct/pdf/assignment/VENKATESWARLU.pdf>) to 1500 (Lund, 2018) forest definitions are used throughout the world, encompassing a range of utilitarian, indigenous, biodiversity, ecosystem and climate change perspectives (Chazdon et al., 2016).

Wikipedia defines a forest as a large area generally dominated by trees consisting of such distinguishing factors as tree density, tree height, land use, legal standing and ecological function (https://en.wikipedia.org/wiki/Forest#cite_note-1).

The Food and Agriculture Organization (FAO) of the United Nations, which oversees the tracking of forest cover by some 163 countries and territories through its Forest Resource Assessments (FRA), has its own definitions. FAO (2015) groups forests into categories that can then be compared with more ecologically based ones (Table 1). Also see Keenan et al. (2015) for limitations of the FAO definitions and related FRA forest loss/gain inventories by reporting countries.

Forests are distinguishable from each other based on classification schemes of various resolution, stepping down from global to local. For instance, using a life zone classification (i.e., Holdridge), forests can be arranged along a three-dimensional axis according to differences in climate, latitude, and altitude (see forest hexagons on the right side of Fig. 2). This classification uses five global forest biomes: boreal (northern most latitudes), cool temperate (high latitudes), warm temperate (mid latitudes), subtropical (lower latitudes), and tropical (equatorial). Within biomes, forests can be arranged by ecoregions—large land masses having similar vegetation, climate, and species assemblages (for an excellent mapped based resource of ecoregions of the world see, <https://ecoregions2017.appspot.com/>).

At finer resolution, potential natural vegetation within a forested region is diagnostic (e.g., Olympic Peninsula, Washington; <https://www.sciencebase.gov/catalog/item/4ffaff70e4b0c15d5ce9fae2>).



Fig. 1 (A) *Radiata* pine plantation, and (B) wet sclerophyll (hard leaved) forest dominated by Mountain ash (*Eucalyptus regnans*) as seen from a canopy tower, New South Wales, Australia. Photo: D. DellaSala.

At the individual stand or site level, forests are defined by species composition, structure (canopy height, dead trees, logs, shrubs), and function (the inner workings of a forest) (Fig. 3).

Land-use features also are diagnostic of the differences in forest quality. For instance, contrast primary (i.e., no evidence of industrial activities) vs. logged (Figs. 4 and 5), and intact forest landscape (e.g., see www.intactforests.org) vs. fragmented (broken apart by human activities) (Figs. 6 and 7).

Where Do Forests Occur?

We live on a green planet; forests, the dominant terrestrial biome, represent ~30% of the terrestrial surface. Currently, about ~3.7 billion ha are considered “natural forests” by FAO (2016), although see Keenan et al. (2015) for data limitations along with a lower bound on global forest estimates in Hansen et al. (2010, 2013) using stricter definitions and satellite tracking. Forests are found on every continent except for Antarctica (Fig. 8). Most of the global forest area (using FAO definitions) is tropical (44%), followed by temperate (26%), boreal (22%), and subtropical (8%) (Keenan et al., 2015).

Table 1 FAO (2015) definition of forests compared to ecologically based approaches

FAO (2015) category	FAO (2015) definition	Limitations/ecological suggestions
Forest	Land spanning >0.5 ha, trees >5 m tall, canopy cover >10%, or trees able to reach these thresholds in situ. Areas temporarily unstocked due to clear-cutting but expected to regenerate within 5 years to reach the criteria. Forest roads, firebreaks and other small open areas; national parks, nature reserves, other protected areas such as environmental, scientific, historical, cultural or spiritual interest. Windbreaks, shelterbelts and corridors of trees with an area > 0.5 ha and > 20 m wide. Abandoned shifting cultivation with regeneration of trees that have, or are expected to reach the forest criteria. Mangroves in tidal zones, rubberwood, cork oak and Christmas tree plantations, bamboo and palms.	Includes forests with varied human activities based on minimum tree cover (e.g., Christmas tree plantations, forests in national parks). Needs to address ecological integrity (native species, processes, functions) and forest quality indicators (e.g., using higher levels of forest cover, e.g., >25%)
Primary forest	Naturally regenerated forest of native species, with no clearly visible indications of human activities and ecological processes are not significantly disturbed. Natural forest dynamics, natural tree species composition, dead wood, natural age structure and natural regeneration processes; large enough to maintain natural characteristics; no known significant human intervention or the last significant human intervention was long enough ago to have allowed the natural species composition and processes to have become re-established.	Can be improved (see Fig. 3). Many nations lack the resources to report this category to the FAO and thus there are data quality problems (see Keenan et al., 2015). Importantly, the Convention on Biological Diversity COP 14 recently adopted a resolution stating the importance of primary forests and ecological integrity. Primary forests should be the reference or baseline for comparisons to all other forest types because of superior ecological integrity (see Mackey et al., 2014; Kormos et al., 2017).
Other naturally regenerated forest	Clear visible signs of human activities: selectively logged; regenerating following agricultural land use; recovering from human-induced fires; mix of naturally regenerated trees and planted/seeded trees; naturally regenerated trees >50% of growing stock at stand maturity.	Could be improved by attention to native species composition, age class distributions, forest structures (especially large live and dead trees/down wood), and ecosystem processes. In the tropics, selective logging results in loss of native species, especially endemics (see Zimmerman and Kormos, 2012). Lower integrity compared to primary forest.
Other naturally regenerated forest of naturalized introduced species	Predominantly naturalized introduced species: trees spread and multiply by natural regeneration and are well established, acclimatized for several years and are an integral part of a region's flora. Specifically excludes invasive species.	Could be improved by attention to native species composition, age class distributions, forest structures (especially large live and dead trees/down wood), and ecosystem processes. Lower integrity compared to primary forests.
Planted forest	Trees established through planting and/or deliberate seeding expected to constitute >50% of the growing stock at maturity. Coppice from trees originally planted or seeded; rubberwood; cork oak and Christmas tree plantations. Excludes self-sown trees of introduced species.	By some definitions, this is not even a forest (see DellaSala in this volume). Lower integrity compared to primary forest.
Planted forest of introduced species	Planted/seeded trees predominantly introduced species expected to constitute >50% of the growing stock at maturity.	By some definitions, this is not even a forest (see DellaSala in this volume). Lowest integrity compared to primary forest.
Mangroves	Area of forest and other wooded land with mangrove vegetation	Could also include all wetland forest types—e.g., bogs, swamps, bottomland hardwoods, riparian areas

What Do We Get From Forests (Biodiversity and Ecosystem Services)?

Ecosystem Services

Forests are the most biodiverse terrestrial ecosystems on the planet with half of the known terrestrial species in tropical rainforests alone that cover just under 2% of the Earth's land mass (<https://rainforests.mongabay.com/0301.htm>). Forest biodiversity is essential for maintaining myriad ecosystem services upon which humanity depends (Brockerhoff et al., 2017). In general, forests:

- Cleanse the air we breathe;
- Regulate the global and regional climate;
- Purify drinking water;
- Perform pollination services;

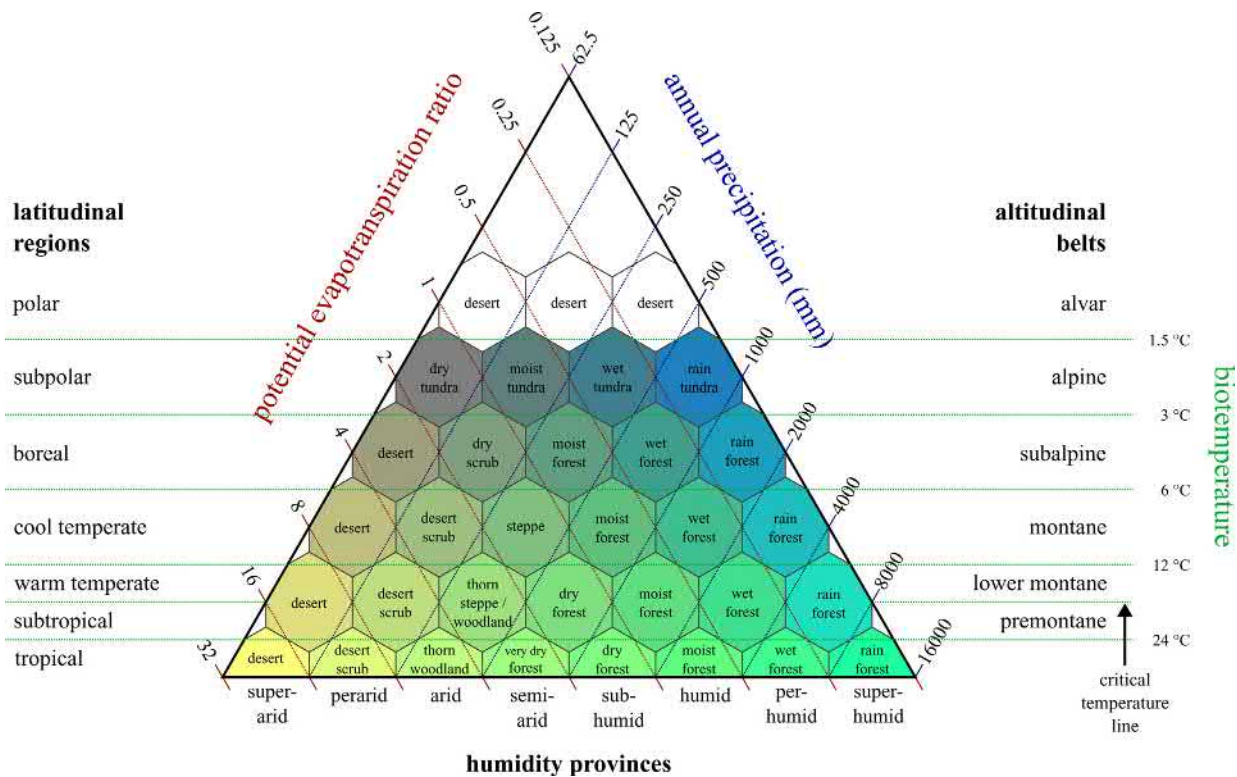


Fig. 2 Holdridge life zones https://en.wikipedia.org/wiki/Holdridge_life_zones. file:///C:/Users/Greens%20Bushwackers/Downloads/Lifezones_Pengo.svg.

- Provide migratory and overwinter sites for countless wildlife (Fig. 9); and
- A source of income, sustenance (food and spirituality), phytochemical medicinals, recreation, and a way of life for millions of people (among myriad other services).

World-wide forests currently absorb some 9 billion tons of CO₂ per year, equivalent to ~one-third the total fossil fuel emissions annually (Pan et al., 2011). However, the global forest sink is limited and can switch to a source of emissions due to drought stress and increases in tree mortality from uncharacteristic wildfires (e.g., tropics) and logging-related losses (see below).

Notably, tropical rainforests play a critical role in regulating climatic processes via evapotranspiration and the hydrological cycle (<https://rainforests.mongabay.com/0906.htm>). In the Amazon, rainforests generate over 50% of annual rainfall through forest-climate feedbacks (dubbed “rivers of the air”). When these forests are cut down, rainfall patterns can change (e.g., droughts related to intensively logged Amazonia).

In boreal forests, with significant snow cover, increases in surface reflectivity (albedo) due to natural disturbances (wildfires, insect outbreaks) can have regional cooling effects (<https://today.oregonstate.edu/archives/2011/oct/%E2%80%99Calbedo-effect%E2%80%99D-forest-disturbances-can-cause-added-warming-bonus-cooling>). By contrast, in large clearcuts, where the surface is exposed and ground unusually darkened, albedo decreases and this can magnify warming. On a global scale; however, warming due to the buildup of greenhouse gases is a much larger climate forcing than changes in regional albedo effects.

Canada’s boreal forests contain ~one-fourth of the world’s total wetlands and freshwater systems critically important to migratory birds and the flow of water into polar regions for ice formation (<https://www.borealbirds.org/boreal-forest>). The region’s wetlands and peat bogs store the equivalent of some 25 years of global emissions (<http://www.borealscience.org/wp-content/uploads/2012/06/report-forestofblue.pdf>).

Wood Fiber and Fuel

Nearly one-third of the world’s forests are designated primarily for production, more than half of this is distributed in high- vs. 8% low-income countries (FAO, 2016). According to FAO (2016), ~3 billion m³ of wood was removed globally in 2011, ~0.6% of the total “growing stock.” About half of the total wood removals are for fuel with low-income countries removing most of this share. During this time, the forest sector contributed ~\$600 billion to the global Gross Domestic Product (GDP) with forestry and logging representing nearly 20% of the total distributed, in part, among high- (41%) vs. low (5%) income-countries (FAO, 2016). Some 12.7 million people were employed in forestry and logging with nearly 80% of these jobs in Asia alone (mainly Bangladesh, China, India; FAO, 2016).

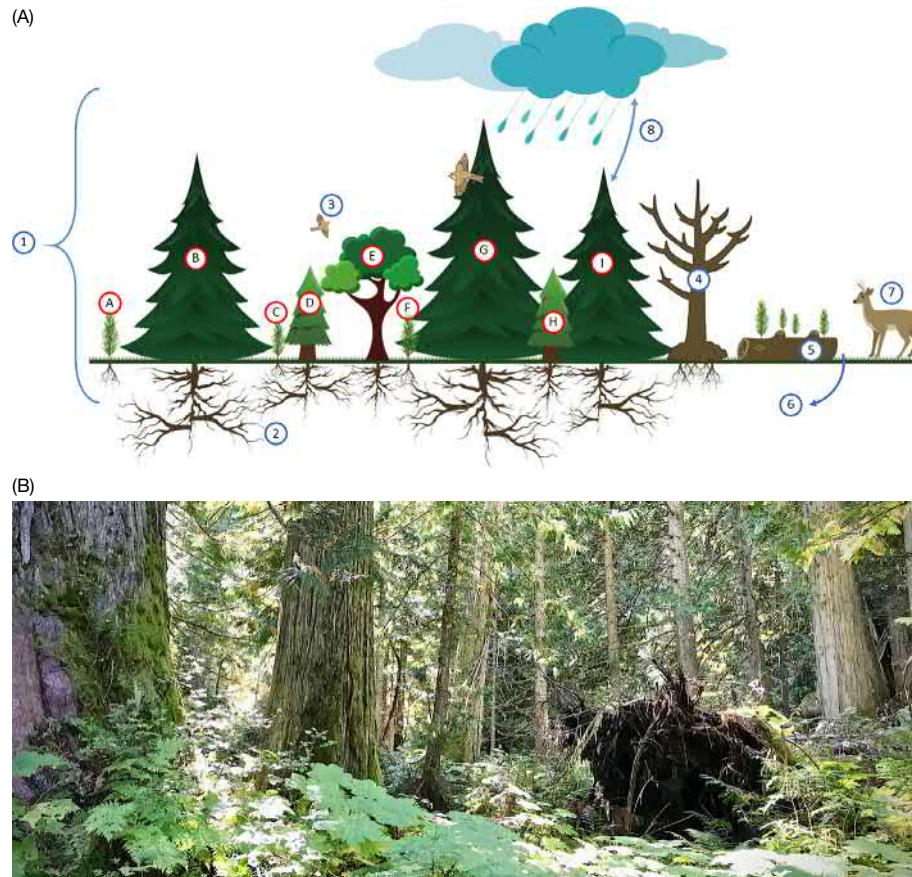


Fig. 3 (A) Cartoon illustration of forest composition, structure, and ecosystem processes. Composition: A-I represent different native species; structure: represented by the contribution of vegetation layering #1, #4 snags, #5 down logs; processes represented by below-ground connections such as mycorrhizae #2, avian predation, pollination, seed dispersal #3; nutrient cycling #6; herbivory #7, and evapotranspiration/hydrological cycle #8. (B) Stand level features of primary, inland rainforest, British Columbia (photo: D. DellaSala). This forest is dominated by western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) that can live for centuries. Note complex structures and layering from the ground-up.

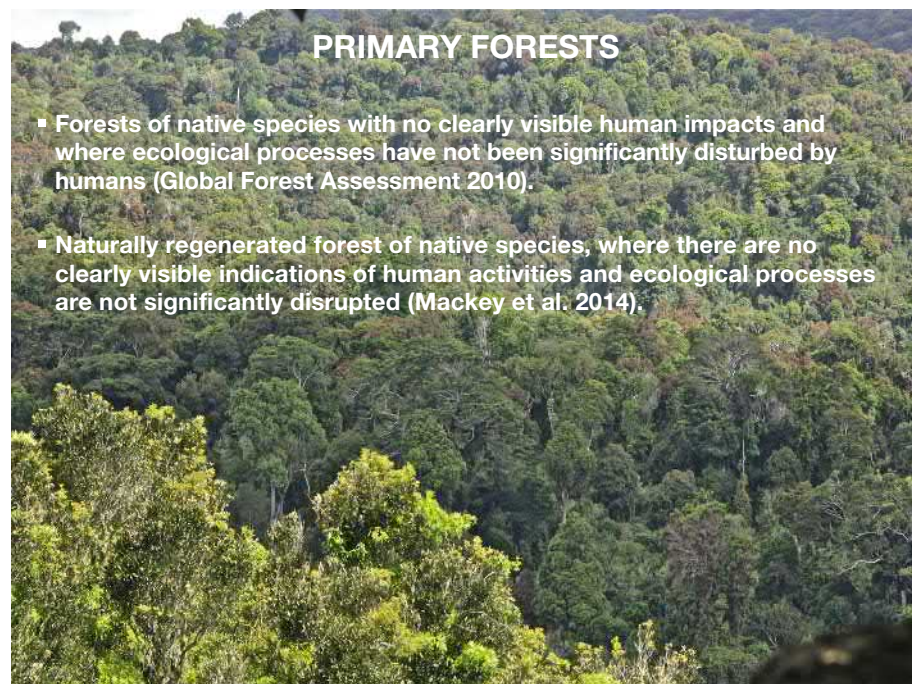


Fig. 4 Primary forest Lamington National Park, Australia Photo: D. DellaSala.

Attribute	Primary Forest	Logged Forest
Patch size and distribution	Large, intact connected at water shed scale – low extirpations	Small and fragmented (roads) – insular with high high turn over/extirpation
Biodiversity	Generally high across taxa and levels	Uniformly low with losses across levels
Keystone processes	Intact trophic levels, carbon uptake/storage, hydrology, soils, nutrient cycling, pollination, fire	Highly altered dominated by edge effects (predation, severe fires)
Successional stages	All seral stages present	Type conversions – use of herbicides/pesticides
Biological legacies	Abundant	Rare
Invasive species	Low	High
Climate change adaptation potential	Resistance/resilience; may act as refugia	Vulnerable, cumulative impacts

Fig. 5 Unique attributes of primary forests compared to logged forests. Photo: J. Schoen, Tongass National Forest, Alaska, permission granted.

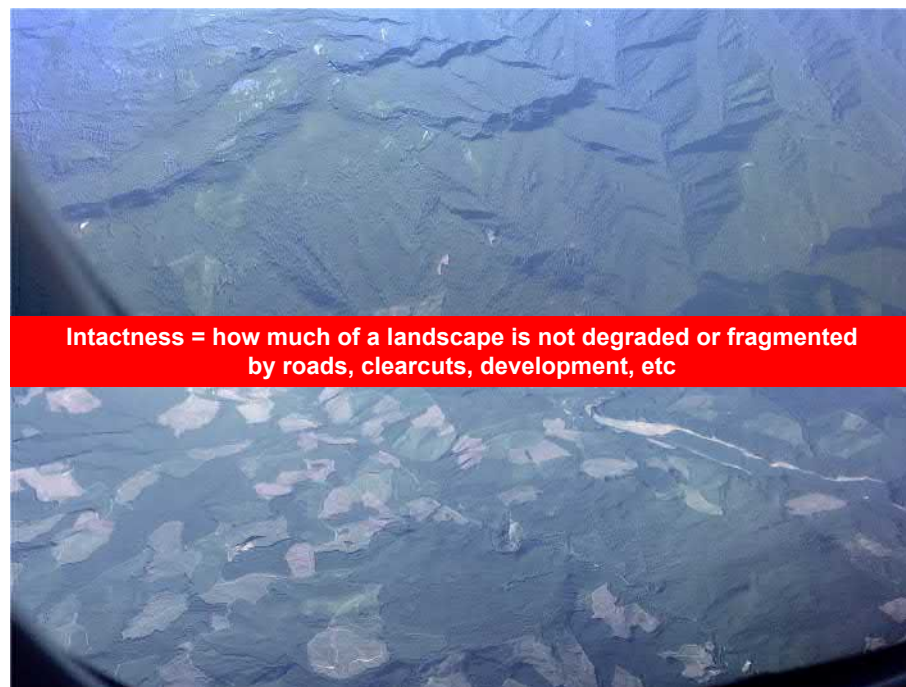


Fig. 6 Relatively intact (upper panel, right side) vs. fragmented forest (lower panel) in the western Oregon Cascade Range as seen from commercial airline flight. Photo: D. DellaSala.

If a Tree Falls Does Anybody Care (Status of the World's Forests)?

The deforestation footprint of humanity goes back thousands of years to at least the time when Vikings were sailing ships across the Atlantic and the Roman empire was prospering. Throughout this long history, entire countries were deforested for agricultural expansion; wood for heating, smelting, leather manufacturing; masts for ships; and other needs (Williams, 2006). Notably, deforestation has been linked to the collapse of early civilizations and is an indicator of imminent collapse of current ones (see Diamond, 2005). Over time, ~45% of the world's original forests were destroyed, mostly within the last 100 years, as industrial societies, population pressures, and consumption levels rose dramatically (<https://www.cbd.int/forest/about.shtml>).

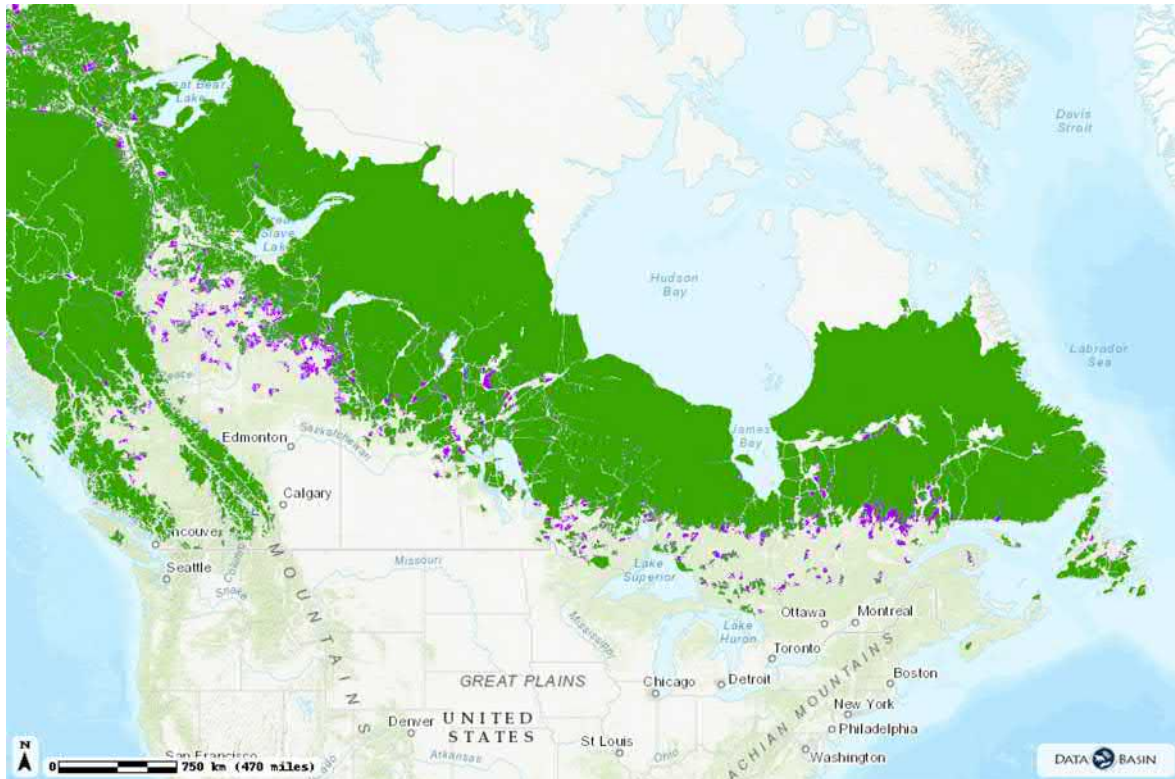


Fig. 7 Remaining intact areas (green) boreal forest, Canada, based on 2013 imagery (with permission from Databasin.org). An intact forest landscape (IFL) is defined by Global Forest Watch Canada as >50,000 ha (see databasin.org for details) with no visible human disturbances. At this coarse scale, some IFLs may actually have undetectable logging and forest roads within them and thus this is likely an overestimate.

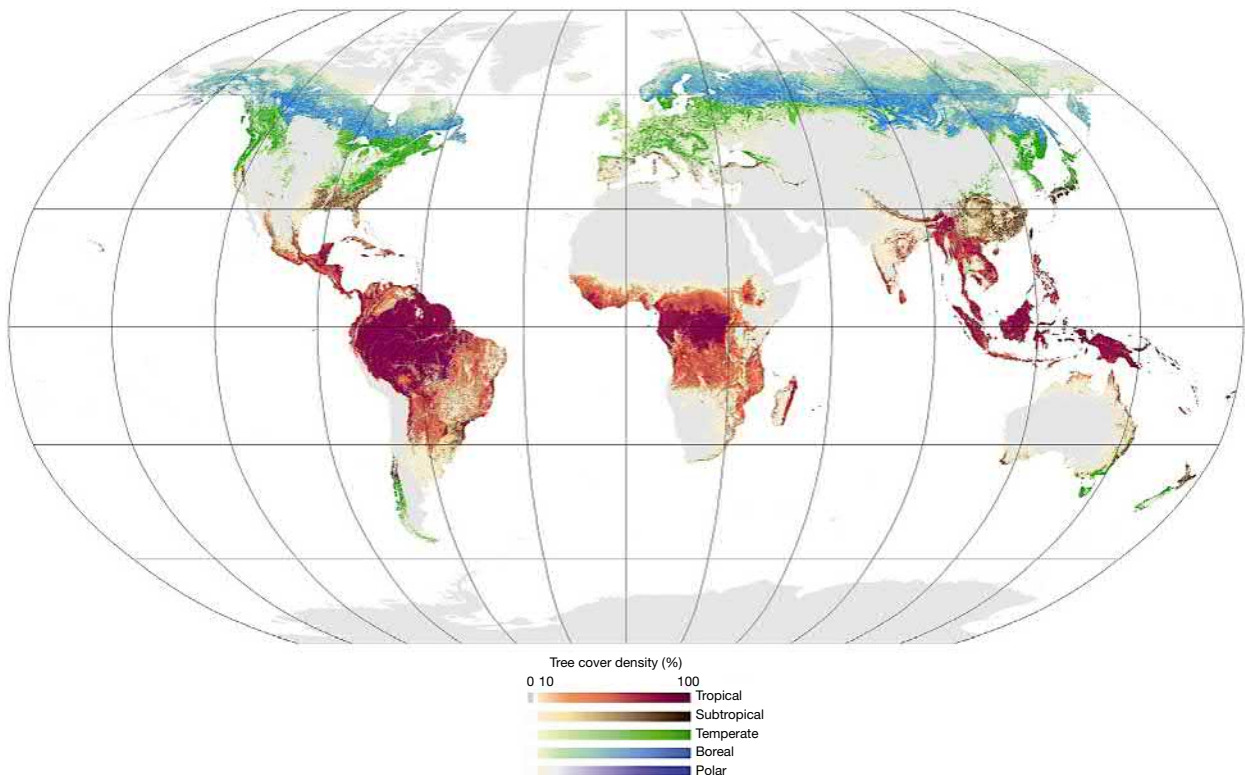


Fig. 8 The world's forests by climatic domain. Compliments of FAO (2010), Rome (<http://www.fao.org/forestry/fra/80298/en/>).



Fig. 9 Monarch butterfly overwintering grounds at El Rosario Monarch Butterfly Preserve, central Mexico. Photo: B. Hartl with permission.

Contemporary forest losses can be tracked using a number of estimators of forest gains/losses to illustrate some of the problems with deforestation and forest degradation metrics and to showcase particular “hot spots” where forest losses are serious regional and global problems.

Total Forest Area

Using [FAO \(2016\)](#) reporting, total forest area (all categories, natural and otherwise) declined by 3% from 1990 to 2015, 4.128 billion ha to 3.999 billion. It should be noted that FAO considers forest losses to include natural disturbance events (insects, disease, forest fires). While forest cover is reduced, this is not equivalent to losses from logging given that forests are resilient to natural disturbances that reset successional processes (an exception being unnatural fires in the tropics). The change rate (gains/losses) in forests reported by FAO also is not comprehensive and there are differences in data quality among reporting countries ([Keenan et al., 2015](#)). Aside from general categories (primary, natural, planted), FAO statistics do not include forest quality, ecological integrity, intactness, and other factors important to forest functions on local, regional, and global scales. By contrast, when more ecologically based definitions are used (e.g., forest defined as > 25% cover), a lower bound (relative to FAO) of total forest cover is 3.269 billion ha in 2000, declining to 3.168 billion ha by 2005 ([Hansen et al., 2010](#)). Although even these estimators have limitations given the coarse resolution of MODIS imagery, FAO estimates need to be calibrated with finer resolution mapping at the country and regional level to improve forest reporting metrics using more ecologically based definitions (see [Table 1](#)).

Natural Forest Area

Further breaking down the FAO totals for 1990–2015, natural forest area declined by 6% (twice the percentage of all forest cover) from 3.961 billion ha to 3.721 billion ha, while planted forest (including rubber plantations) expanded from 168 million to 278 million ha ([Keenan et al., 2015](#)). Alarming, tropical forests declined (2010–15) at an annual rate of 5.5 million ha; however, this was 58% of the rate in the 1990s ([Keenan et al., 2015](#)). Tropical forest losses (2010–15) were greatest in Brazil (984 K ha per year; K = thousand), followed by Paraguay (325 K), Argentina (297 K), Bolivia (289 K), and Peru (187 K) ([Keenan et al., 2015](#)). In Asia, net annual losses were greatest in Indonesia (684 K) and Myanmar (546 K). Africa, Nigeria (401 K), Tanzania (372 K), Zimbabwe (312K), and Democratic Republic of Congo (311K) each lost forests ([Keenan et al., 2015](#)).

In contrast, temperate forest expanded at an annual rate of 2.2 million and boreal and sub-tropical remained relatively constant ([Keenan et al., 2015](#)). Forest area expanded in Europe, North America, the Caribbean, East Asia, and Western-Central Asia, while it declined in Central and South America, South and Southeast Asia, and Africa ([Keenan et al., 2015](#)). China reported greatest forest expansion during this period (2010–15). These estimates do not distinguish loss of primary forests from gains in planted forests.

Importantly, primary forest account for only 36% of the global forest cover ([Mackey et al., 2014](#)), declining by 40 million ha from 2010 estimates ([Fig. 10](#)); although [FAO, 2016](#) reports recent increases in primary forests due to more countries reporting. Nevertheless, there is uncertainty in this estimator given not all countries report, difficulty in detecting certain logging activities (e.g., selective logging) and hard to detect (from satellites) roads under dense forest canopies.

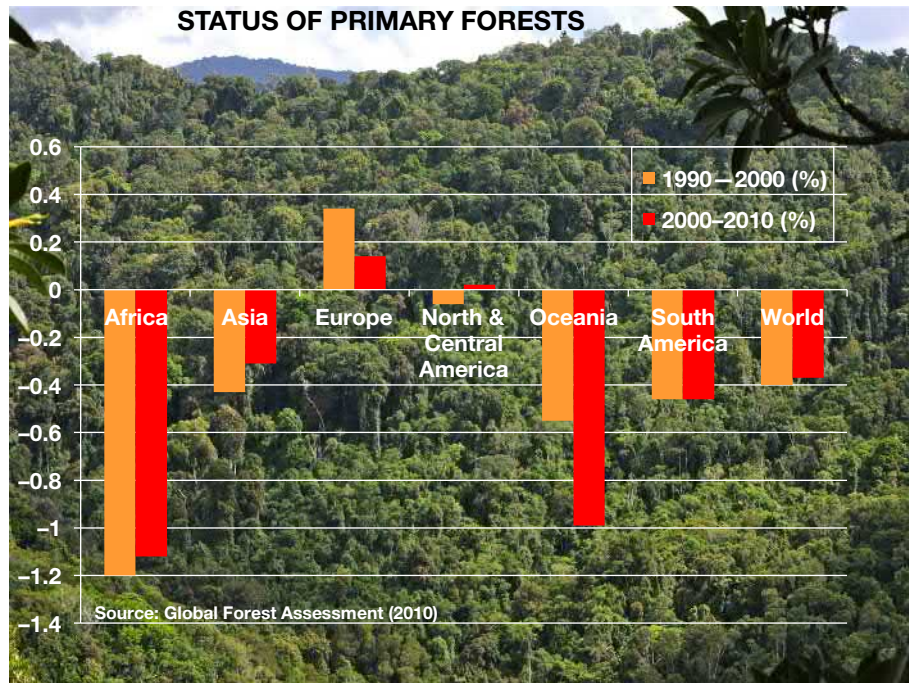


Fig. 10 Primary forest losses and gains based on FAO 2010 (photo: D. DellaSala). Note: recent increases are due to more countries reporting.

New spatially explicit (“big data”) forest monitoring systems are becoming increasingly available for real-time global and regional projections. Examples include.

- Global Forest Watch time lapse deforestation operated by the World Resources Institute (<https://www.globalforestwatch.org/>; Fig. 11),
- Google Earth platforms of time lapse deforestation rates (<https://earthengine.google.com/timelapse/#v=44.85742,-123.70911,9.608,latLng&t=0.00>),
- Deforestation tracking of the Amazon by Mongabay.com (<https://data.mongabay.com/brazil.html#land>);
- Satellite tracking and deforestation visuals provided by National Geographic (<https://www.nationalgeographic.com/environment/global-warming/deforestation/>).

In sum, we are getting better at tracking deforestation but not at stopping it. Nevertheless, FAO deforestation/degradation estimates should be calibrated using these platforms wherever possible (although it is difficult to track degradation from selective logging using remote systems).

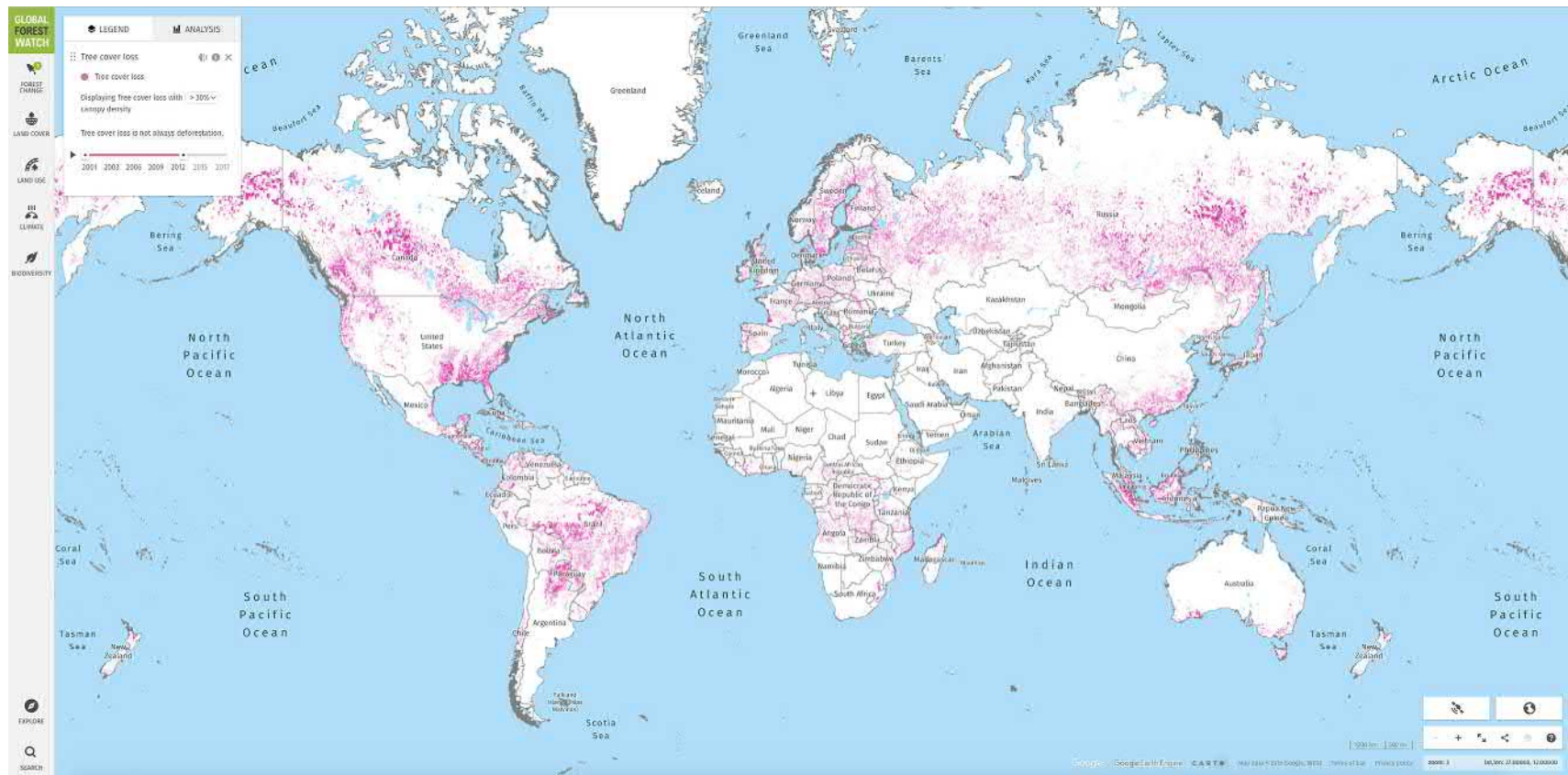
Notably, according to WWF (Taylor et al., 2015), 230 million ha are projected to be deforested by 2030 within 11 “deforestation fronts,” if no actions are taken (Fig. 12). All of these major losses are in tropical regions; however, losses to primary forest and intact forest landscapes are a serious global problem as noted.

What are the Drivers of Forest Loss?

The United Nations Programme REDD+ (Reducing Emissions for Forest Degradation and Deforestation: <http://www.un-redd.org/>), encourages countries to develop action plans that reduce forest losses via conservation incentives. The program was developed by the Parties to the United Nations Framework Convention on Climate Change (UNFCCC) to reduce forest losses, which account for 17% of the global carbon emissions, more than the entire transportation network and second only to energy (<https://www.unredd.net/about/what-is-redd-plus.html>).

Importantly, the main drivers of deforestation in tropical countries are commercial and subsistence agriculture, while drivers of forest degradation are timber extraction, fuelwood collection, charcoal production, unnatural fire (as in tropical rainforests) and livestock grazing (Hosonuma et al., 2012). Keenan et al. (2015) report that as countries develop overtime there is a switch (transition) from net forest loss to net forest gain. However, before the inflection point to forest gain is reached, primary forest losses are substantial. Thus, recent gains in forest cover (mainly from planting) come largely at the expense of primary and intact forest landscapes during transitional shifts.

Deforestation rates also have been coupled to high rates of poverty (Zwane, 2007), loss of traditional languages (<https://www.language-magazine.com/deforestation-linked-to-language-loss/>), subjugation of aboriginal cultures (<https://wikispaces.psu.edu/display/AnthSpace/How+Tropical+Deforestation+Affects+Cultural+Environment>) (Figs. 13 and 14), and degraded ecosystem



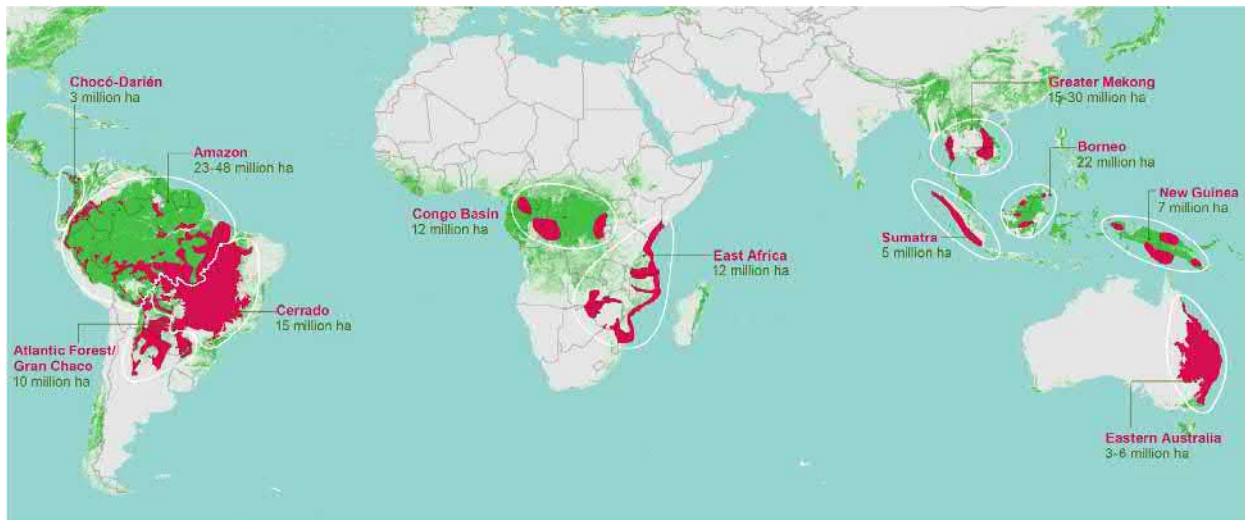


Fig. 12 Deforestation fronts based on projections to 2030 from Taylor et al. (2015). With permission of WWF—World Wide Fund for Nature (Formerly World Wildlife Fund), Gland, Switzerland (© Text and graphics: 2015 WWF All rights reserved, H. Miller).

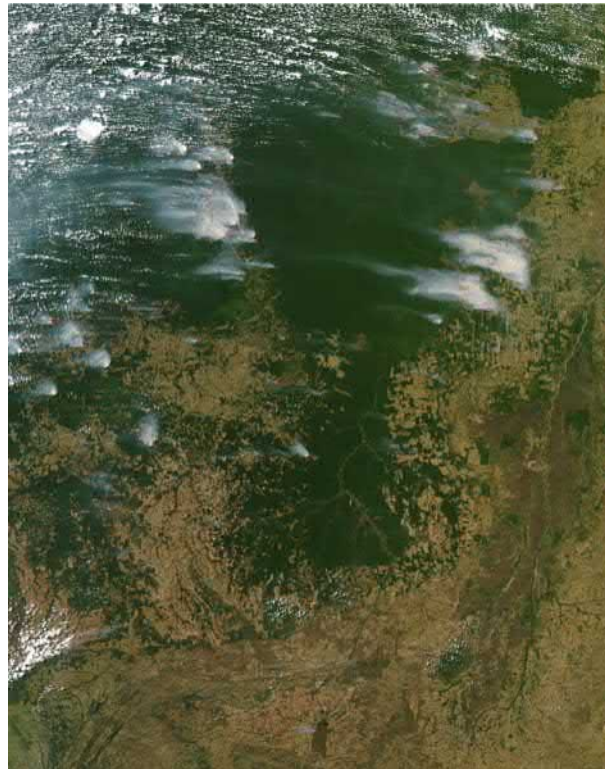


Fig. 13 Satellite image (2004) showing plumes of smoke from ranchers burning primary forest remnants near the border of Kayapo indigenous land in Brazil. Brown is deforestation except for two light patches with Kayapo land that are naturally occurring savanna (cerrado) on the rocky plain of the Brazilian shield. Photo with permission from B. Zimmerman.

services like clean water and climate regulation (<https://news.mongabay.com/2007/02/amazon-deforestation-damaging-critical-ecosystem-services/>).

Can We Save the Forest in Time?

The hopeful answer is yes, if the political will, disincentives to log primary forests are in place (e.g., regulations, policy reforms), stepped up conservation measures are being employed (e.g., investments in rapid transitions, non-logging income to local



Fig. 14 Kayapo meeting in 2014 uniting to protect traditional lands from incursions by miners. Photo with permission from B. Zimmerman.

communities), and land-tenure issues are resolved (e.g., aboriginal rights). Here, are some conclusions and recommendations from chapter authors of *Forest Biomes*:

- Dudley (this volume) estimates that 13% to 20% of the world's forests are in some form of protection and this needs to increase dramatically to achieve representation (e.g., half of Earth's forests in some form of protection) and sustainability goals.
- Javar-Salas (this volume) evaluates different conservation management and protection scenarios for dry Hawai'i forests showing that the status quo scenario will not achieve representation or resilience objectives without stepped up conservation.
- Gomez-Diaz (this volume) discusses the urgent need for protecting large fragments of pine-oak and humid montane forest belts in biologically diverse regions of Central Veracruz, Mexico where < 3% is protected and the remaining natural areas are essential for maintaining plant diversity and ecosystem services.
- Frelich (this volume) provides three major recommendations for boreal forests: (1) follow all of the articles of the Paris Climate Agreement to reduce greenhouse gas emissions and limit the magnitude of global warming; (2) establish large nature reserves to keep tracts of boreal forests in a primeval state (e.g. as proposed by the boreal songbird initiative) and; (3) manage remaining areas outside reserves under enforced forest certification standards.
- Maser (this volume) recommends protecting intact forests so carbon can be captured from the atmosphere and cycled through forests in sufficient quantities.
- Houghton (this volume) indicates that without a massive, global program of forest expansion, the potential for negative emissions from ending deforestation and forest degradation is modest and small relative to fossil fuel reserves.
- Ibisch (this volume) calls on policy-makers to give roadless areas conservation priority in sustainable development.
- Abrams (this volume) argues that nations need to conserve biodiverse old world tropical rainforests to avoid collapse of well-known charismatic megafauna.
- Krasilnikov (this volume) discusses the importance of montane cloud forests, a unique and highly fragmented system endangered by climate change, agricultural expansion and intensive logging that should be protected in natural heritage sites.
- Kulakowski et al. (this volume) discuss how logging following insect outbreaks, windstorms, and fires amounts to a secondary disturbance that can inhibit ecosystem resilience.
- Curry and Cornelisse (this volume) review the ecological and social setting of overwintering forests used by iconic migratory monarch butterflies, an endangered migratory phenomenon.
- Kerr (this volume) proposes shifting most fiber production from forests to farmlands by 2040 to relieve pressure on forests.
- Hall (this volume) discusses how forestry practices can be improved through independent third-party certification that balances social, economic, and ecological factors.
- Zimmerman (this volume) discusses the importance of protecting aboriginal land tenure and cultural lifestyles in Amazonia, a region under enormous threats from illegal logging, ranching, and gold mining incursions on aboriginal territory.
- Roth (this volume) argues that the Klamath-Siskiyou bioregion of southwest Oregon/northern California will continue to act as refugia for native species provided substantial reversal of habitat loss, particularly old-growth forests.
- Niemi (this volume) explains the contributions forests make to human well-being by providing ecosystem services that generate benefits for individuals, families, businesses, communities, and the global society.
- Urquhart (this volume) discusses the amazing biodiversity of the largest expanse of rainforest on the planet in the Neotropics, and how deforestation primarily from agriculture is affecting regional climatic processes.

- Graham (this volume) highlights opportunities and challenges in reducing emissions from forests, and offers a regional perspective from Southeast Asia; a region in the spotlight for the mass expansion of oil palm plantations and frequently occurring wildfires.
- Furnish, in two articles (this volume), provides his personal accounts of how >23 million ha of national forest roadless area protections in the US was among the great conservation achievements in public land history, and how emergent forest restoration on Oregon's Siuslaw National Forest charted a path forward from old growth logging.
- Coxson et al. (this volume) describe the globally unique inland temperate rainforest and interior wetbelt of northwest North America, especially the extraordinary epiphytic lichen diversity and imperiled mountain caribou.
- DellaSala (this volume) discusses how plantations are "fake" forests in terms of greatly altered species composition, structure, and processes but that existing plantations may offset the need to log old-growth forests on the Tongass rainforest in southeast Alaska.

All told, there are unprecedented impacts to forests globally, accumulating in space and time as fewer intact landscapes and primary forests remain, more species are pushed to the brink of extinction, and natural forests are displaced by planted ones lacking biodiversity and ecosystem services. Many policies have been proposed to end deforestation and forest degradation globally as summarized.

The Paris Climate Agreement (Article 5) emphasizes the critical importance of forests in helping to stabilize climate change (Box 1).

The Convention on Biodiversity (<https://www.cbd.int/sp/targets/rationale/target-5/>) Target 5 states: "by 2020, the rate of loss of all natural habitats, including forests, is at least halved and where feasible brought close to zero, and degradation and fragmentation is significantly reduced (Box 2).

Box 1 Paris Climate Agreement with respect to forest carbon "sinks and reservoirs"

<https://climatefocus.com/sites/default/files/20151223%20Land%20Use%20and%20the%20Paris%20Agreement%20FIN.pdf>

Article 5 (1) Parties should take action to conserve and enhance, as appropriate, sinks and reservoirs of greenhouse gases as referred to in Article 4, paragraph 1(d), of the Convention, including forests. (2) Parties are encouraged to take action to implement and support, including through results based payments, the existing framework as set out in related guidance and decisions already agreed under the Convention for: policy approaches and positive incentives for activities relating to reducing emissions from deforestation and forest degradation, and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries; and alternative policy approaches, such as joint mitigation and adaptation approaches for the integral and sustainable management of forests, while reaffirming the importance of incentivizing, as appropriate, non-carbon benefits associated with such approaches.

Box 2 Convention on Biological Diversity (Conference of the Parties, United Nations).

Nearly all Parties report that habitat loss is the most important factor driving biodiversity loss. Largely undisturbed or *primary habitat* is a particular priority for reducing this loss (emphasis added). Degradation, which reduces the capacity of ecosystems to provide goods and services, is similarly important. Habitat fragmentation, though more difficult to quantify at a global level, is a related pressure driving biodiversity loss. While economic, demographic and social pressures are likely to mean continued habitat loss, degradation and fragmentation, particularly due to land use change beyond 2020, the rate of change needs to be substantially reduced. While for some ecosystems it may be possible to bring the rate of habitat loss close to zero by 2020, for others a more realistic goal is to halve the rate of loss. Significantly reducing habitat degradation and fragmentation will also be required in order to ensure that those habitats which remain are capable of supporting biodiversity. Ultimately, there must be limits to the conversion or degradation of natural habitats. This is particularly the case for some ecosystems, where continued loss risks passing "tipping points" that could lead to large scale negative effects on human well being. The target refers to rate of loss, and should be regarded as a step toward halting the loss of natural habitats. Further it should be noted that the use of net rather than gross rates of loss could obscure the loss of mature ecosystems as a result of restoration. Whilst restoration activities can restore many of the attributes of primary ecosystems, they cannot be restored completely in the short to medium term. The emphasis of this target should be on preventing the loss of high-biodiversity value habitats, such as primary forests and many wetlands. Recent evidence suggests that the global rate of deforestation is already decreasing.

Implementation: Reduction in the loss and degradation of natural habitats through land use change could be achieved through improvements in production efficiency and land use planning, and enhanced mechanisms for natural resource governance combined with recognition of the economic and social value of ecosystem services provided by natural habitats. In particular, catchment value (water provision), erosion control, the value of carbon sequestration by forests and wetlands, and other ecosystem services (such as denitrification by wetlands) provide contemporary incentives for reducing the net loss of these habitats, and reversing their decline. Taking a landscape-wide perspective to land use planning offers a useful way to integrate global level ecosystem services (e.g., climate change mitigation) with local level ones (e.g., biodiversity conservation, water supply and quality, timber and non-timber forest products). The programmes of work on forest, marine and coastal, inland water and dry and sub-humid lands biodiversity and the Convention's work on sustainable use are particularly relevant to this target. An initiative that could be further built upon in working toward this goal relates to the signing, by Ministers of 68 Parties to the Convention on Biological Diversity during the ninth meeting of the Conference of the Parties, of WWF's call to stop net deforestation by 2020.

Box 3 Example goals NY Forest Declaration.

Goal 1: At least halve the rate of loss of natural forests globally by 2020 and strive to end natural forest loss by 2030. Based on estimates provided by the signatory parties, relative to 2001–13, the average gross annual rate of global tree cover loss was 42% higher in 2014–17, the years following adoption of the resolution.

Goal 6: Include ambitions, forest conservation and restoration targets for 2030 in the post-2015 global development framework as part of new international sustainable development goals, providing a means for countries to integrate forest conservation into sustainability platforms.

The 2014 New York Forest Declaration (**Box 3**), endorsed by > 190 governments, corporations, nongovernmental and indigenous peoples' organizations, included ten ambitious goals aimed at halting natural forest loss by 2030 (<http://forestdeclaration.org>).

The Secretariat of the Convention on Biological Diversity (CBD Secretariat) in 2014 adopted 20 global targets under the strategic plan for biodiversity 2011–20. The targets were grouped by five strategic goals:

1. Address the underlying causes of biodiversity loss by mainstreaming biodiversity across government and society.
2. Reduce the direct pressures on biodiversity and promote sustainable use.
3. Improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity.
4. Enhance the benefits to all from biodiversity and ecosystem services.
5. Enhance implementation through participatory planning, knowledge management and capacity building.

A vision for forests in a sustainable world—global conservation initiatives need to be advanced alongside sustainable development if we are going to save the world's forests in time (e.g., see <https://sustainabledevelopment.un.org/?menu=1300>). Sustainability strategies need to stop and then reverse the loss of natural forests through restoration and protection of primary forests and intact forest landscapes because they are irreplaceable in human lifetimes. Ecologically meaningful increases in forest protections (at least half of a given region in some form of protection, see Noss et al., 2012; <https://www.half-earthproject.org/>), responsible forest management (e.g., FSC), and reduced/shifted consumption of wood fiber (e.g., alternative fibers, fallowed agricultural lands) are critical to a sustainable relationship with forests and any hope for a wild planet where forest creatures of all shapes and sizes prosper, the climate is safe, clean drinking water is available (**Fig. 15**), especially to the economically disadvantaged, and the cultural connections and survival of aboriginal peoples are passed on from generation to generation. Importantly, proforestation—growing and restoring existing forests to become intact overtime—needs to be implemented to maximize carbon sequestration, biodiversity, water and air quality, flood and erosion control, public health, recreation, and scenic beauty (Moomaw et al., 2019). The alternative, widespread deforestation and forest degradation, will forever compromise the irreplaceable services we receive from the world's forests.



Fig. 15 Boreal spruce (*Picea* spp.) forest in Sweden illustrating some of the ecosystem services (clean water) we get from forests. Photo: L. Frelich with permission.

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How Carbon Cycles Through a Forest

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Abstract

Beginning with the investment of solar energy and the reinvestment of carbon dioxide, water, and minerals from the soil, every forest is a source of sequestered carbon through photosynthesis, which is then stored and recycled worldwide. Within each forest, various mammals and birds eat mycorrhizal fungi that help connect the flow of energy from trees' crowns to their roots, and from their roots to their crowns. As trees grow, they sequester and store carbon. As they die and fall to the forest floor, they not only created a micro-topography that conserves water and helps prevents soil from creeping downslope but also reinvest their stored carbon and other elements in the soil, thereby nurturing the next forest. And, some of the fallen trees make their way, as driftwood, into the oceans, where they help balance the marine-carbon requirements that sustain oceanic life worldwide.

All things in Nature's forest are neutral. Nature assigns no values. Each piece of a forest, whether a bacterium or a 1000-year-old tree, is allowed to offer its evolved structure, carry out its evolved function, and interact with other components through their evolved, interrelated processes. None is more valuable than another; each is only different from the countless others. However, assigning a value to something in the forest—like a tree as a commercial product—begins to adjust that object in our focus, where bringing one thing into focus simultaneously forces almost everything else out of focus. For example, rodents were poisoned for decades in the name of forestry, because they were perceived as having only a negative value. They ate the seeds that industry wanted to grow into merchantable trees. Today, forest rodents are viewed differently. Some still eat tree seeds, but at the same time they disperse viable spores of mycorrhizal fungi, nitrogen-fixing bacteria, and yeast, which, working in unison, stimulate tree growth and thus the acquisition and storage of carbon in a forest.

How Carbon Gets Into and Moves Around in a Forest

The following vignette of the northern flying squirrel in the coniferous forests of the Pacific Northwestern United States illustrates but one example of the myriad dynamic, interdependent relationships in forests the world over, beginning with solar energy.

The Only True Investment in a Forest

The *only true investment* in a forest is energy from solar radiation (materialized sunlight), which takes an average of 8 min and 20 s to reach the Earth and affects all life worldwide in one way or another (Cain, 2018). Everything else is merely the recycling—reinvestment—of already-existing energy.

In a business sense, for example, one makes money ("economic capital") and then takes a percentage of those earnings and *recycles* them by putting them back into the infrastructure of the enterprise for maintenance of buildings and equipment to facilitate making a profit by protecting the integrity of the initial outlay of capital over time. In a business, one recycles economic capital *after* the profits have been earned.

However, the “biophysical capital,” of a forest must be “recycled” *before* the profits are earned, if the forest is to remain biophysically sustainable. This means forgoing some potential monetary gain by leaving enough of a forest ecosystem intact for it to function in a productively sustainable manner. For instance, one must leave some proportion of the merchantable live trees to gather enough solar radiation and produce living tissue, wherein carbon is sequestered, that will subsequently die—and together with the already-dead trees—rot, recycle into the soil, and thereby replenish the fabric of the living system. With this in mind, and because I am writing about a forest (a highly complex, biophysical system), I will focus my discussion primarily on the trees, wherein the sequestered carbon is temporarily stored.

It has long been understood that green plants use chlorophyll molecules to absorb sunlight and use its energy to synthesize carbohydrates from carbon dioxide and water. These carbohydrates, in turn, are partly stored energy from the sun (an original input) combined with carbon dioxide and water, as well as nutrients from the soil in which the trees grow (all existing—recycled—chemicals), to create a renewable source of energy (Cheng and Fleming, 2009; May, 2018). This process is known as “photosynthesis,” from the Greek *photo* (“light”), *syn* (“with, together”), and *thesis* (“putting, placing”). In other words, photosynthesis is the fusion of energy embodied in sunlight with the recycled energy stored in earthly materials.

The Fungal Connection

The combination is the basis for sustaining the life processes of plants in every forest because a tree’s leaves or needles capture sunlight, transform it into carbohydrates, which travel from a tree’s crown, through the trunk into the roots, where an obligatory, symbiotic relationship is formed with certain fungi central to the processes of the tree’s capturing nutrients from the soil. In fact, fossil evidence of the earliest terrestrial plants, as well as current molecular studies, show that plant roots and certain fungi coevolved as symbiotic partners to form structures known as *mycorrhizae*, a word that comes from the Greek *mykes* (a fungus) and *rhiza* (a root). Mycorrhizae are generally distributed throughout forests worldwide (Maser et al., 2008; Calvo et al., 1989).

The hyphae, or individual fungal strands, each one to two cells thick, form the main structural elements of the mycorrhizal fungi. (“Hypha,” singular, comes from the Greek *hyphe*, a web.) The hyphae either penetrate the cells of a plant’s roots to form an “endomycorrhiza” (*endo* = mycorrhiza *inside* the root) or ensheath the root of form an “ectomycorrhizae” (*ecto* = mycorrhiza *outside* the root).

In the nutrient-deficient conditions of most forests, at least 90% of a tree’s “feeding” roots are colonized by ectomycorrhizal fungi and results in a layer of fungal tissue or “mantle” that forms around the tree’s roots (Photo 1), thereby creating an active, reciprocity of life, with the tree as the conduit, between the investment of solar energy and the inorganic, soil elements. From this mantle, individual hypha aggregate and organize into root-like structures called “rhizomorphs” (*rhizo* = root + the Greek *morphe* = shape) that grow out from the feeding roots into the soil, where they act as an extension of the tree’s root system. The aggregate of hyphae is also referred to as “mycelia” (singular = mycelium), which in New Latin means “made of mushrooms.” A mycelium is a given mass of hyphae that forms the nonreproductive part of a fungus.

Some mycorrhizal fungi are host-specific, meaning that a given mycorrhizal fungus colonizes a single species of plant, whereas others are generalists and colonize a number of host plants. Douglas-fir (*Pseudotsuga menziesii*) or birch (*Betula* spp.), for example, can be colonized by many species of mycorrhizal fungi. In turn, these fungi extend from tree to tree and so form linkages among trees. The generalized nature of host compatibility ensures that almost all trees, and many other plants, in an undisturbed forest ecosystem, regardless of species, are interconnected by billions of miles (kilometers) of hyphae, organized into mycelial systems, that stem from a diverse population of mycorrhizal fungi. If, therefore, you could pull up a whole forest and gently wash the soil from the roots of the plants, you would find a mycelial net connecting the entire forest—one of the reasons an old-growth forest is so retentive of its soil-nutrient capital (Read, 1997, 1998; van der Heijden et al., 1998).

Ectomycorrhizal fungi profoundly affect the forest ecosystem. Through the obligatory, symbiotic mycorrhizal association, a plant, such as Douglas-fir, provides carbohydrates to its mycorrhizal symbiont, while the fungal symbiont mediates the plant’s uptake of nitrogen, phosphorus, other minerals, and water. In addition, the mycorrhizal association promotes the development of fine roots; produces antibiotics, hormones, and vitamins useful to the host plant; protects the plant’s roots from pathogens and environmental extremes; moderates the effects of heavy metal toxins; and promotes and maintains soil structure and the forest food web. This mycorrhizal association is expensive, however, with an estimated 50%–70% of the host plant’s net annual productivity being translocated through the roots of the plant to their associated mycorrhizal fungi (Amaranthus et al., 1966; Luoma, 2001; Smith et al., 2002).

When access to nutrients is increasingly restricted in a forest ecosystem that is already nutrient-impovertished, mycorrhizal fungi can influence both the interactions among plants and the species composition of the plant community itself. It appears there is an additive, beneficial effect that comes with each species of mycorrhizal fungus that colonizes a given plant, which, in turn, could mean that both biodiversity and ecosystem productivity, as well as the acquisition and storage of carbon, will increase with an increasing number of fungal symbionts. This scenario seems likely because experimentation has shown that, as the number of fungal symbionts is increased, so too is the collective biomass of roots and shoots, as well as the species diversity of the plant community. Conversely, as a forest is disturbed through exploitive forestry practices and the use of artificial fertilizers, the function of the mycorrhizal system can be impaired.

In addition to gleaning nutrients from the soil and translocating them into the host plant, mycorrhizal fungi, along with roots of the host plant and the free-living microbial decomposers in the soil, are significant components of the global balance of carbon. Much of the carbon balance is mediated by photosynthesis and drives the respiration or “breathing” of the soil. Both photosynthesis



Photo 1 Note the light-colored tissue of an ectomycorrhizal fungus forming a “mantle” around the lodgepole pine’s (*Pinus contorta*) root tips. USDA Forest Service Photograph by C.P.P. Reid.

and mycorrhizal symbionts are critical in maintaining the soil’s respiration, through which carbon is extracted from the soil. Although the carbon made available to the soil through photosynthesis helps to balance the loss of carbon from the soil through respiration, the production of photosynthates is mediated more by annual seasonality than by the temperature of the soil (Högberg et al., 2001).

The Truffle Connection

Truffles—the belowground, fungal fruiting-bodies—are the initial link between, mycorrhizal fungi, and the northern flying squirrel (*Glaucomys sabrinus*). Flying squirrels nest and reproduce in the tree canopy and come to the ground at night where they dig and eat truffles. As a truffle matures, it produces an aroma that attracts the foraging squirrel. Evidence of a squirrel’s foraging remains as shallow pits in the forest soil and, occasional, partially eaten fruiting-bodies (Pyare and Longland, 2001).

Truffles contain the nutrients required by the small animals that eat them. In addition to nutritional value, truffles also contain water, fungal spores, nitrogen-fixing bacteria, and yeast, all of which become important in the forest network.

The Squirrel Connection

Keeping the above in mind, let’s consider the coniferous forests of the Pacific Northwest in which Douglas-fir and western hemlock (*Tsuga heterophylla*) predominate in the old-growth canopy. Herein live the Northern Spotted Owl (*Strix occidentalis*), which preys on the flying squirrel as a staple of its diet (Forsman et al., 1984; Thomas et al., 1990; Carey, et al., 1990; Maser, 1998). The flying squirrel, in turn, depends on truffles, which it digs out of the forest soil.

When flying squirrels eat the truffles, they consume fungal tissue that contains nutrients, water, viable fungal spores, nitrogen-fixing bacteria, and yeast (Photo 2). Pieces of truffle move to the stomach, where the tissue is digested; then on through the small intestine, where absorption takes place, and then to the cecum. The cecum is like an eddy along a swift stream; it concentrates, mixes, and retains fungal spores, nitrogen-fixing bacteria, and yeast. Undigested material, including cecal contents, is formed into excretory



Photo 2 A truffle. USDA Forest Service Photograph by James M. Trappe.

pellets in the lower colon; these pellets, which are expelled through the rectum, contain the viable spores and accompanying microorganisms necessary to inoculate the root tips of trees.

The Pellet Connection

Flying squirrels dine heavily on truffles. The fate of their fecal pellets varies, however, depending on where they fall. In the forest canopy, the pellets might remain and disintegrate in the tops of the trees. Or a pellet could drop to a fallen, rotting tree and inoculate the wood. On the ground, a squirrel might defecate on a disturbed area of the forest floor, where a pellet could land near a feeder rootlet of a Douglas-fir that may become inoculated with the mycorrhizal fungus when the spores, having been washed into the soil by rain, germinate. If environmental conditions are suitable and root tips are available for colonization, a new fungal colony may be established. Otherwise, hyphae of germinated spores may fuse with an existing fungal thallus (the nonreproductive part of the fungus) and thereby contribute and share new genetic material (Maser et al., 1978a,b, 1985, 1986; Luoma, et al., 2002).

A fecal pellet is more than a package of waste products; it is a “pill of symbiosis” dispensed throughout the forest. Flying-squirrel pellets usually contain four components important to the forest: (1) viable spores of mycorrhizal fungi, (2) yeasts, (3) nitrogen-fixing bacteria, and (4) the complement of nutrients necessary for the survival and function of the nitrogen-fixing bacteria—like the yolk that feeds the chicken forming in the white of an egg.

The yeast, as a part of the nutrient base, has the ability to stimulate both growth and nitrogen fixation in the bacterium *Azospirillum* spp. Nitrogen thus made available can be used both by the fungus and the host tree. Yeast cells may also aid spore germination because spores of some mycorrhizal-forming fungi are stimulated in germination by extractives from other fungi, such as yeasts (Li and Castellano, 1995; Li et al., 1986a,b; Li and Maser, 1986).

The northern flying squirrel thus exerts a dynamic, functionally diverse influence within the forest. The complexity of effects ranges from the crown of the tree inhabited by the squirrel, from which it can rain fecal pellets to the soil, where the fungi depend on large, rotting trees lying on and buried in the forest floor for water and the formation of humus. *Humus*, which lends soil its dark color, is the Latin word for “the ground, soil” or alternatively the New Latin word *humos*, meaning “full of earth.” Further, nitrogen-fixing bacteria occur on and in the ectomycorrhizae, where they convert atmospheric nitrogen into a form that is usable by both fungus and tree (Li et al., 1986a,b).

The pellets contain spores, microorganisms, and nutrients, which work into the soil’s root zone, where the fungi form mycorrhizae that absorb nutrients, which are conducted into the roots, up the trunk, and into to the crown of the tree, perhaps into the squirrel’s own nest tree. The trees, in turn, help to create the forest, which may be part of a catchment basin that collects and stores water required for human consumption—drinking, irrigation, or electricity, which says nothing of wood products, foods, and medicines used as products to sustain the material comfort of society—all thanks to the help of forest-dwelling rodents and fungi, which touch the quality of our lives in so many ways. The consequence of the foregoing is that trees sequester carbon as they grow, carbon that is not only stored but also helps to shape the forest.

The Rotting Wood Connection

To add to the overall complexity of a late-successional, indigenous forest, a live old tree eventually becomes injured and/or sickened with disease and begins to die. How a tree dies determines how it decomposes and reinvests its biophysical capital (organic material, carbon, and other chemical elements) into the soil and eventually into the next forest.

A tree may die standing as a snag to crumble and fall piecemeal to the forest floor over decades, or it may fall directly to the forest floor as a whole tree. How a tree dies, is important to the productive sustainability of the forest because its manner of death determines the structural dynamics of its body, as habitat. Structural dynamics, in turn, determine the biological-chemical diversity hidden within the tree's decomposing body, as ecological processes incorporate the old tree into the soil from which the next forest must grow. What goes on inside the decomposing body of a dying or dead tree is one example of the hidden biological and functional diversity that is totally ignored in a typical economic valuation of a forest. Consequently, that trees continue to become injured, diseased, and die is critical to the long-term biophysical sustainability of a forest that itself is an interactive, organic whole defined not by the pieces of its body, but rather by the interdependent functional relationships of those pieces creating the whole—the intrinsic value of each piece and its complementary function.

Regardless of how it dies, the snag or fallen tree is only an altered state of the live tree; so, the large, live tree must exist before there can be a large snag or large fallen tree. A basic problem inherent in understanding this scenario lies in the fact that, if asked, few of the world's leading scientists, legislators, policy-makers, or business executives could name the five classical Kingdoms of Nature (bacteria, fungi, algae, plants, and animals) or explain how they complement one another. This dearth of ecological literacy shows a basic lack of understanding how ecosystems—and their self-reinforcing, biophysical, feedback loops—work, as well as a basic lack of understanding the long-term, systematic consequences of short-term, symptomatic, political/economic decisions.

Finally, the various functions of individual species, when melded in the collective, form a self-reinforcing feedback loop of mutually dependent interrelationships in which the spotted owl preys on the flying squirrel; the flying squirrel eats the truffle; the fungus is closely associated with large wood on and in the forest floor for water and the formation of humus (the fungus, spotted owl, and flying squirrel are all dependent, either directly or indirectly, on the same large, decomposing wood on the forest floor). The fungus feeds the tree; the tree feeds the fungus; the squirrel inoculates the trees roots with fungal spores that help keep the tree alive and growing. The tree houses the flying squirrel and the spotted owl, and so on (Maser and Trappe, 1984; Maser et al., 1979, 1984a,b).

How Carbon Stored in Trees Shapes a Forest

How a tree dies is important to the health of the forest because its manner of death determines the structural dynamics of its "body" as habitat. A tree may die standing as a snag to crumble and fall piecemeal to the forest floor over decades. Or, it may fall directly to the forest floor as a whole tree. To reiterate, regardless of how it dies, the snag and the fallen tree are only altered states of the live tree. Consequently, the live old-growth tree must exist before there can be a large snag or a large fallen tree.

There are three major sources of coarse woody debris in an old-growth Douglas-fir forest: (1) uprooting of live trees, with or without complete crowns; (2) breakage of crown and stem of live trees; and (3) breakup and fall of snags. Because size of trees and the manner in which woody material comes to be on the ground varies widely, the resulting pieces of woody debris are heterogeneous in size and shape. Regardless of its original size, wood passes through the various stages of decay; the smaller it is, the faster it breaks down and disappears.

Structural dynamics of a dying or dead tree, in turn, determine the biological/chemical diversity hidden within the tree's decomposing body, greatly affecting the ecological processes that incorporate the old tree, and its stored carbon, into the soil from which the next forest must grow. What goes on inside the decomposing body of a dying or dead tree is the hidden biological and functional diversity that is totally ignored by economic valuation. Consequently, the fact that trees become injured and diseased, die, and remain in place is critical to the long-term structural and functional sustainability of a forest. The forest is an interactive, organic whole defined, not by the pieces of its body, but rather by the interdependent, functional relationships of those pieces—the intrinsic value of each piece and its complementary function as they interact to create the whole.

Placement of Fallen Trees

Fallen trees that are oriented horizontally along the contours of a slope seem to be used more by vertebrates than are trees vertically oriented across contours, especially on steep slopes. Large, stable trees lying along contours help reduce erosion by forming a barrier to creeping and raveling soils. Soil and nutrients deposited along the upslope side of fallen trees reduce loss of nutrients from the site. Such spots are excellent for the establishment and growth of vegetation, including tree seedlings.

Vegetation becomes established on and helps stabilize this new soil, and, as invertebrates and small vertebrates begin to burrow into the new soil, they not only nutritionally enrich it with their feces and urine but also constantly mix it by their burrowing activities.

The interactions of fallen trees with soil are directly affected by steepness of slope and ruggedness of terrain; a fallen tree on flat ground, for example, is much more likely to contact the soil over its entire length than is one oriented either across or along contours on steep or rough terrain (Photo 3). The proportion of a tree in contact with the soil affects the water-holding capacity of the wood. The moisture retention in fallen trees in old-growth Douglas-fir forests through the summer drought is best in the side of trees in contact with the soil. The moisture-holding capacity of the wood, in turn, affects its internal processes and therefore the succession of plants and animals. In addition, the orientation of a fallen tree to aspect and compass direction and the amount and duration of sunlight it receives, drastically affect its internal processes and biotic community.



Photo 3 A fallen tree lying across another. Note that the one underneath is in direct contact with the forest floor. Photograph by Chris Maser.

How Fallen Trees Are Reinvested in the Forest Soil

A newly fallen tree interacts only passively with the surrounding forest because its interior is not accessible to plants and most animals. But once fungi and bacteria, which are smaller than the wood fibers, gain entrance, they slowly dissolve and enter the wood cells, and wood-boring beetles (Coleoptera), carpenter ants (*Camponotus* spp.), and termites (Isoptera) chew their way through the wood fibers. Meanwhile, many other organisms, such as plant roots, mites (Acari), springtails (Collembola), amphibians, and small mammals, must await the creation of internal spaces before they can enter. The flow of plant and animal populations and communities, air, water, and nutrients between a fallen tree and its surroundings increases as the tree's decomposition process continues. For example, the water-holding capacity of a large, fallen tree varies by day, season, year, decade, and century, adding yet another dimension of diversity to the forest.

Surface area develops within a fallen tree through physical and biological processes. A tree cracks and splits when it falls and then dries. Microbial decomposition breaks down the cell walls and further weakens the wood. Wood-boring beetle larvae and termites tunnel through the bark and wood, not only inoculating the wood with microbes but also opening the tree to colonization by other microbes and small invertebrates. Wood-rotting fungi produce zones of weakness, especially between the tree's annual growth rings, by causing the woody tissue laid down in spring to decay faster than that laid down in summer. Plant roots that penetrate the decayed wood split and compress it as the roots elongate and thicken in diameter. Because of all this internal activity, the longer a fallen tree rests on the forest floor, the greater the development of its internal surface area. Most internal surface area results from biological activity, the cumulative effects of which not only increase through time but also act synergistically—insect activity promotes decomposition through microbial activity that encourages the establishment of rooting plants.

Thus, fallen trees offer myriad organisms multitudes of external and internal habitats that change yet persist through the decades. Of the organisms, only the casual observer might notice a few of the fungi, such as mushrooms or bracket fungi. These structures, however, are merely the fruiting bodies produced by mold colonies that run for miles (kilometers) within the tree. Many fungi fruit within the fallen tree; so, they are seen only when the tree is torn apart. Even then, only a fraction of the fungi present might be noticed because the fruiting bodies of most appear for only a short time. The smaller organisms, not visible to the unaided eye, are also important components of the forest. We humans do not begin to grasp the notion that microbes and fungi change a forest just as surely as a raging fire, only inconspicuously and more slowly. There is an unseen function that is just as critical, and just as great as any in the forest. We are awed by a towering fir but not by a lowly fungus, and yet it is the fungi that convert the tree to soil and eventually to a new forest with its sequestration and storage of carbon (Maser and Trappe, 1984; Maser, 1989).

Therefore, it is not only species of plants and animals that become extinct with the liquidation of a late-successional forest but also the old "grandparent trees." As crop after crop of young trees replace liquidated old trees, the ecological functions performed by the old trees, such as creation of the "pit-and-mound" topography on the floor of the forest with its mixing of mineral soil and organic topsoil, become extinct processes. Why? Because there are no more grandparent trees to blow over; yet, "windthrow," which creates "blowdown," is an extremely important event in forests, especially in such forests as those in southeast Alaska, where fire plays a minimal role in the disturbance regime, but windthrow is critical (Bormann et al., 1995; McClellan et al., 1990; Deal et al., 1991).

Pit-and-Mound Topography

“Pit” refers to the hole left in the forest floor, as a tree’s roots are pulled from the soil, and “mound” refers to the soil-laden mass of roots, called a “rootwad” suddenly thrust into the air above the forest floor as the old tree topples. The young trees that replace the grandparent trees are much smaller and different in structure; so, they cannot perform the same functions in the same ways. Of all the factors that affect the soil of the forest, the roughness of the surface caused by falling grandparent trees, particularly the pit-and-mound topography, is the most striking.

Uprooted trees enrich the forest’s micro-topography by creating new habitats for vegetation. They also provide opportunities for new plants to become established in the bare mineral soil of the pit and the mound. In addition, fallen trees open the canopy, allowing additional light to reach the floor of the forest, that, in combination with the pits and mounds, creates and maintains a richness in the species of plants forming the understory and the herbaceous ground cover. As large trees fall, they bring with them nitrogen-rich lichens from the canopy to the forest floor, where the lichens decompose and add their nitrogen to the soil layer. With time, the fallen tree itself presents habitats that can be readily colonized by tree seedlings and other plants.

Extinction of the grandparent trees changes the entire complexion of the forest through time, just as the function of a chair is changed when the seat is removed (Photo 4). The “roughness” of the forest floor that, over the centuries, resulted from the



Photo 4 A “grandparent” Sitka spruce along the Oregon coast surrounded by young trees. Photograph by Chris Maser.

cumulative addition of pits, mounds, and fallen grandparent trees will become unprecedentedly “smooth”—without pits and mounds; without large, fallen trees.

Water moves differently over and through the soil of a smooth forest floor, one that is devoid of large, fallen, rotting trees acting as reservoirs, storing water throughout the heat of summer, and holding soil in place on steep slopes. Gone are the huge snags and fallen trees that acted as habitats for creatures wild and free. Gone are the stumps of the grandparent trees with their belowground “plumbing systems” of roots hollowed out by rot that guided rain and melting snow deep into the soil (Photo 5).

This plumbing system of decomposing tree stumps and their large, deep, hollow roots frequently form interconnected, surface-to-bedrock channels that rapidly drain water from heavy rains and melting snow. As roots slowly rot away, the collapse and plugging of these channels forces more water to drain through the soil matrix, reducing its cohesion and increasing the hydraulic pressure, thereby increasing the probability of mass soil movements.

These plumbing systems cannot be replaced by the young trees of modern forests because their roots are too small and shallow to form the conduits necessary to rapidly move large quantities of water deep into the soil. Local extinctions of the ecological functions performed by grandparent trees, alive and dead, seems to pass unnoticed into the shadow-realm of bygone forests because their passing takes place unnoticed in the “invisible present.”

And, finally, the world’s forests send a percentage of their stored carbon, in for form of driftwood, to the oceans of the world, where its structure and function is critical to the biophysical integrity and productive sustainability oceans worldwide.

How Carbon Leaves a Forest and Feeds the Ocean

Leaving the rivers of the world, driftwood enters the oceans, where the currents transport it throughout the worldwide seascape. For example, driftwood along the shores of Iceland takes 4–5 years, traveling between 250 and 620 miles (402 and 998 km) each year, to reach Iceland from the North coast of Siberia ([An International Team of Scientists Studying Driftwood Along Icelandic Shores, 2016](#)).

Driftwood in the Open Ocean

Trees drifting at sea are usually heavily populated with plants and animals, including both pelagic and nearshore species, acquired during the tree’s transit to the open ocean. Once in the open ocean, other organisms use them.

In addition to the organisms actually attached to or secreted within the driftwood itself, communities or other organisms form around it. More than a 100 species of invertebrates and some 130 species of fishes are known to congregate on and around floating objects. With respect to these open-ocean communities, wind-induced water movements in the ocean’s upper layer are among the most important factors leading to the aggregation and survival of organisms near driftwood.

The formation of communities associated with driftwood, particularly fishes, may depend on shade, refuge from predaceous fishes, an abundance of food, or protection from waves. On the other hand, shadows cast by floating trees may make zooplankton more visible to predators or pelagic fishes simply seek shade. Then again, drifting trees may serve as sites for egg attachment, or where pelagic fishes can secure algal and invertebrate food, or where they can clean external parasites off themselves.

In addition, it’s thought that small fishes are initially attracted to a floating tree as a point of reference, swimming with it while feeding on the small planktonic organisms in its vicinity. Along with the planktivores come juveniles of carnivorous species and



Photo 5 The root of a mountain hemlock (*Tsuga mertensiana*) that has been hollowed out by rot and acts as a conduit for water to penetrate from the surface of the soil deep within the soil. Photograph by Chris Maser.

then, larger obligate predators arrive and eat the accumulated prey. Thus, within 3–5 weeks after a tree initially arrives in the open ocean, the combined weight of its associated tunas (*Thunnus* spp.) alone may reach as much as hundred tons.

The prey responds by using the floating tree as protection. The predators rapidly deplete the available prey, albeit only temporarily. In their search for food, the predators move away from the tree only to return and use it as a point of reference.

Large driftwood in general plays an important role in the life cycles of many eastern Pacific species by aggregating them, which would otherwise be dispersed throughout the pelagic environment, aggregations similar to those around islands and seamounts.

In fact, massive accumulations of large driftwood behaves essentially as free-floating islands or reefs. The ecological role played by these “free-floating islands” is probably different for different species because the assemblage is dynamic, changing in space and time, albeit with some degree of organization. The faunal aggregation may show different developmental stages, say changes in species composition, as the driftwood, entrained in the current, covers hundreds of miles (kilometers) through the weeks and months at sea.

It thus seems that driftwood is adaptive for most species in that some may seek shelter or food, but for most, driftwood is a vehicle bringing them into rich feeding grounds because driftwood, originating at river mouths, travels through biologically rich coastal areas and tends to accumulate in rich parts of the ocean. In this way driftwood can be used as “stepping stones” in the movements of large fishes, as it links major features in the circulation of ocean currents and the fishes’ migration paths with the location of a region’s islands and seamounts.

In the biogeographic sense, driftwood acts as free-floating islands, carrying subsets of epipelagic fauna from one biologically-rich area to another, an idea that can provide a unified approach to the ecological study of pelagic faunal assemblages associated with large driftwood in the open oceans of the world (Maser et al., 1988; Maser and Sedell, 1994; Maser, 2014).

Driftwood as Habitat and Food on the Ocean Floor

Although the sources, forms, and routes that supply organic material to the energy-poor deep sea are little known, it is known that drifting trees in nearshore currents become water-logged and sink over the continental shelves or in the deep sea, where they represent terrestrially-fixed carbon. In the Pacific Northwest and other areas, deep-sea, wood-boring bivalves (Mollusca) live in waters ranging from about 6000–11,500 ft (19,685–37,739 m) deep, where they rely on sunken driftwood for food.

There are at least three species of deep-sea wood-borers that quickly invade wood and grow rapidly, which, at a depth of about 6000 ft (19,685 m) in the North Atlantic, means wood can become infested with a dense population within 104 days. There, they convert wood into fecal pellets, which settle to the sediment surface and attract other bottom-dwelling animals. The conversion of wood into a readily available source of detritus supports the development of a complex, local community of bottom-dwelling organisms.

Deep-sea wood-borers have a high reproductive rate, grow rapidly, mature early, and have high-density populations, all of which are characteristics suitable for effectively using wood, the supply of which is erratic, unpredictable, and transient in the deep ocean. Their piles of fecal pellets, which are finely ground wood fragments, may attract more than 40 species of other deep-sea invertebrates. Enrichment of the bottom, a result of disintegrating wood and the accumulating fecal pellets, thus contributes to the development of a diverse fauna.

Wood in the deep-sea supplies energy in an energy-scarce environment and is a source of habitat diversity. It is not surprising, therefore, that a single, water-logged tree on the deep-ocean floor is the focus of intense and abundant life. Although wood is frequently found in dredges from fishing the deep-sea floor and deep-sea trenches, it is most common off mouths of rivers and wooded coastlines.

The complete role of intact driftwood in the open-ocean food web, whether it’s floating on the surface or resting on the bottom, remains unknown, as does the potential role of offshore, marine wood-borers in the initial reduction of wood. Nevertheless, 95% of the organic carbon from plant materials in the sediments off the mouth of the Columbia River, along the Northwest Coast of the United States, is terrestrial in origin. Organic carbon in the nearshore sand is about 20%, and that of midshelf silts, about 25 miles (40 km) offshore, is between 40% and 60%.

Although it takes years for large driftwood from the forest to finally reach the sea, the story cannot be told in the concept of time because it’s too limiting for an understanding of the myriad cycling pathways to which driftwood is subjected on its seaward journey (Maser et al., 1988; Maser and Sedell, 1994; Maser, 2014).

How and Why People Overexploit the Carbon in a Forest

When unconscious of something’s material value, we are free of its psychological grip. Yet, the instant we perceive its material value (“conversion potential” of trees into products), we also perceive the psychological pain of its potential loss, a fear that fosters the over-exploitation of our inherited natural resources, such as forests, because not to exploit them is perceived as losing the opportunity, as well as the coveted material value, to someone else. And it is this feeling of loss that we humans fight so hard to avoid. In this sense, it is more appropriate to think of resources “managing” us as opposed to us managing resources, which answers why the timber industry is so dogmatically insistent on cutting every old-growth tree. The industry has nothing invested in the growing of the old trees, and so ever old tree represents a “windfall profit.” The industry’s only investment is associated with getting the old trees—and thus the forest’s stored carbon—to the mill. In this sense, the timber industry knows exactly what it wants—old-

growth trees. How many it wants—all of them. When it wants them—now. Why it wants them—because they're essentially free for the taking. Where it wants them—at the mill. The profit margin is all that matters; so, the future is discounted. Karl F. Wenger, President of the Society of American Foresters, makes this point clear:

The fact is, Nature knows nothing. Nature is deaf, dumb, blind, and unconscious. . . . It reacts blindly and unconsciously according to the properties and characteristics of its components. These have no intrinsic values, since only the human race can assign values. Nature doesn't care what we do to it. . . . Clearly, the people's needs are satisfied much more abundantly by managed than by unmanaged forests.

(Wenger, 1998)

This said, the level of consciousness that created a problem in the first place is not the level of consciousness that can fix it. We must, therefore, raise our level of consciousness with respect to how we opt to caretake forests worldwide. We can do this because we, as a people, as a society, are *not* "locked" into our way of thinking. Because we, as a people, as a society, can always choose to choose again, there is hope for the generations of the future (Maser, 2004).

How Caretaking Allows Carbon to Maintain a Sustainable Forest

If we honor Nature, we can find the place where culture and Nature meet and both are more nearly sustainable, but that requires a reassessment of "waste." The economic concept of "waste" says in effect that anything not used directly by humans is wasted. But, in a biophysical sense, there is no such thing as waste in a forest or any other ecosystem—managed or unmanaged. Consider that a tree rotting in a forest, composting as it were, is a reinvestment of Nature's biophysical capital in the long-term maintenance of soil productivity, and hence of the forest itself. Biophysical capital includes such things as inorganic components, organic material, and biological and genetic diversity. And to reinvest means to invest again, to put back. How might this work? First, we must ask ourselves what we want from an acre of land, such as a forest, and then we must ask ourselves how we need to treat that acre to *allow* Nature to provide our desired outcome on a sustainable basis.

For example, an indigenous, old-growth forest has three prominent characteristics: large live trees, large standing dead trees or snags, and large fallen trees—none of which would exist without the biophysical system cycling carbon throughout the forest over the decades and millennia. As noted earlier, the large snags and the large fallen trees, which are only altered states of the live old tree, become part of the forest floor and are eventually incorporated into the forest soil, where myriad organisms and processes make the nutrients stored in the decomposing wood available to the living trees. Further, the changing habitats of the decomposing wood encourage nitrogen fixation to take place by free-living bacteria (Nitrogen fixation is the conversion of atmospheric nitrogen to a form usable by living organisms, such as a tree.) These processes are all part of Nature's rollover accounting system that includes such assets as large dead trees, biological diversity, genetic diversity, and functional diversity, all of which count as reinvestments of biological capital—not economic capital—in the growing forest.

With the foregoing in mind, it is clear that a forest does not—and cannot—function sustainably on economic capital. It requires biophysical capital—leaves, twigs, branches, and the decomposing wood of large fallen trees, including biological diversity, genetic diversity, functional diversity. The reinvestment of such biophysical capital is necessary to maintain the productive capacity of the soil that, in large measure, equates to the long-term productive capacity of the forest. In turn, the productive, sustainable capacity of a forest equates to the long-term economic stability of the timber industry and so human communities.

Be not deceived, however; without balancing withdrawals of products, such as timber, with investments of solar radiation through photosynthesis and biophysical reinvestments of soil elements and decomposing wood, both biophysical interest *and* principal are spent, which inevitably means that economic productivity must eventually decline.

If those who caretake a forest are concerned with the productive capacity of the topsoil, as they must of necessity be, they need to accept the lessons of history. One of the most distinctive historical lessons might be that the birth of agriculture caused civilizations to rise, whereas abusive agricultural practices—based on overexploitation due to flawed, linear, economic thinking—destroyed the topsoil and fostered the collapse and extinction of some of those same civilizations.

History is replete with lessons pointing out that once the sustainable, productive capacity of soil is destroyed, it takes many human lifetimes to replace it. And yet, with all the glaring lessons of history spread before us around the world, we insist on walking the historical path of abusing the soil.

Consequently, the resilience of forested sites following a human-caused disturbance (such as clear-cutting or salvage logging) is at least partly related to the ability of the soil to retain nutrients and water and to maintain its structural and functional integrity during the period in which plants—and trees—are becoming reestablished. Beyond that, the sustainable fertility of the soil is reflected in the productive growth of a forest and the quality of the timber available to harvested on a sustainable basis—sort of a carbon economy.

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Large Scale Forest Conservation With an Indigenous People in the Highly Threatened Southeastern Amazon of Brazil: The Kayapo

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Abstract

We examine the struggle of the Kayapo indigenous people to protect their constitutional rights over the 40 years since the frontier of settlement and resource extraction exploded around their territories in the highly threatened southeastern Amazon of Brazil. We explore conditions that enable and threaten the Kayapo's continued success in thwarting deforestation and we identify strategies for continued protection. We show that 21st century alliances of the Kayapo with conservation NGOs have enabled protection of over 9 million ha of their contiguous ratified territories. Satellite analysis of Kayapo territory between 2001 and 2019 reveals significant correlation between the location of deforestation hotspots and the presence/absence of NGO investment with Kayapo communities. Key to success has been the development of scalable resource management and income generation activities with Kayapo communities, and strengthening of Kayapo territorial surveillance and control that is essential in the absence of government enforcement of indigenous land rights. Conservation NGOs enabled Kayapo communities to set up their own indigenous NGOs that are critical to build capacity for managing territories sustainably. It is philanthropic investment into the Kayapo over the past two decades that has made the difference between protection and rampant invasion and degradation of Kayapo territories.

Introduction and Background

The Xingu River arises in the woodland-savanna and transitional semi-deciduous forest of northern Mato Grosso and flows north through high moist forest of Pará for 2700 km to empty in the Amazon. A clear water river, it drains a landscape of ancient crystalline Precambrian shield. The Xingu basin covers 51 million ha, of which ~20 million ha is officially recognized indigenous land, while another 8 million ha is protected areas (Campanili, 2012).

The 280,000 km² of indigenous lands and protected areas of the Xingu river basin form a continuous forest corridor larger than the United Kingdom, inhabited by 25 indigenous peoples and traditional riverine families. Immersed in the one of the world's most intense deforestation zones in Pará and Mato Grosso states, the Xingu indigenous lands and protected areas network demonstrate how Brazilian government policy had been working to reduce Amazon deforestation. This progress is regressing due to infrastructure projects, mines, intensifying illegal logging and gold mining, worsening lack of governance, emerging climate change impacts and government proposals to weaken indigenous land rights. This despite the global significance of these natural ecosystems for climate change mitigation, biodiversity conservation and the preservation of traditional cultures.

The Xingu basin has been continuously occupied over at least the last 1200–1500 years (Balée, 1989; Heckenberger et al., 2008). Kayapo fleeing colonists, gold miners, rubber tappers and missionaries occupied the still relatively isolated middle Xingu in the first half of the 19th century. Intensive occupation of the basin only began in the 1970s, with the construction of highways through the basin and the arrival of colonists from southern Brazil. The middle and upper Xingu region has undergone the typical "boom and bust" cycle of frontier occupation and has become a major cattle and soy-producing region such that today, some 1 million people live in 35 counties throughout the basin (Campanili, 2012; Rodrigues et al., 2009).

The official recognition of the Xingu Indigenous Lands and Protected Areas from the late 1940s to 2008, is a product of regional conflicts over land and natural resources and the strategies of indigenous and local communities to both resist and accommodate successive frontiers. The 1988 Constitution recognized indigenous groups' right to maintain traditional cultures permanently, granting them permanent and exclusive usufruct rights over their traditional lands (República Federatva do

Brasil, 1988; Santilli, 1991) and became the basis for large-scale demarcation of indigenous territories. In numerous local struggles and in the forum of national law and policy, indigenous peoples successfully gained recognition of their rights to their traditional lands and now control over 20% of the Amazon.

From the late 1980s the relations between Xingu indigenous groups and the national society changed radically. Mato Grosso and southern Para rapidly became major timber, soy and cattle producing regions, surrounding indigenous territories with agriculture, ranches, roads and towns (Mertens et al., 2004). Regional cities became accessible. Up until this time, FUNAI, the federal government Indian Agency mandated to uphold indigenous rights, had mediated and largely controlled all interactions with the outside world. But with shrinking budgets and diminished capacity, FUNAI decentralized services and some indigenous groups developed independent relations with outsiders. Pressure from outsiders on the natural resources of indigenous territories increased dramatically, as did internal demand for industrialized goods and technology. With increased dependence on manufactured goods and health care, semi-nomadic groups like the Kayapo became sedentary.

The reality faced by indigenous peoples of the Xingu is that enforcement of protected areas and indigenous territories by government authorities went from inadequate (Ferreira et al., 2014) to nonexistent in 2019. Although at a much lower rate than in surrounding lands, deforestation, forest degradation and invasion of Xingu protected areas and indigenous lands by loggers, gold miners and land grabbers has been on the upswing over the past decade (Azevedo-Ramos and Moutinho, 2018; Venâncio et al., 2018).

Conservation Significance of Kayapo Territories

Much of the 20 million ha of the Xingu basin indigenous territories is covered in near intact Amazon primary forest: part of the world's most biodiverse terrestrial ecosystem that is large enough to maintain a full complement of floral and faunal species diversity and rainfall regimes (Benchimol and Peres, 2015; Ewers et al., 2017; Gibson et al., 2011; Jones et al., 2019; Laurance et al., 2006; Michalski et al., 2007).

The 10,600,000 ha block of ratified indigenous territory of the Kayapo is of particular conservation value because of its vast size and interdigitation of both closed-canopy Amazonian forest and central Brazilian savanna or *cerrado*. Of critical conservation significance, Kayapo territory is likely large enough to protect regeneration processes of primary forest tree species (ter Steege et al., 2015). Most primary forest tree species occur locally at very low densities but maintain large absolute populations sizes over large areas (Pitman et al., 1999) and most tree species depend on co-evolved animal vectors for pollination and seed dispersal across large inter-individual distances. Small areas do not contain animal vector populations sufficient for regeneration of many forest tree species over the long term (Ewers et al., 2017; Laurance et al., 2006; ter Steege et al., 2015). The dauntingly intricate web of interdependence among Amazonian species requires large areas to function and persist.

Surveys have shown that much of Kayapo territory remains largely undisturbed as evidenced by population densities of some of the more vulnerable vertebrate species found in Amazonian forests. Large-bodied game species, which are preferred by local peoples throughout the Amazon, are abundant within the hunting range of Kayapo communities. The relatively high densities of game animals (that also include large cracid birds, several monkey species, lowland tapir, giant armadillo and white-lipped peccary) indicate an ecosystem that is little impacted by hunting because non-hunted areas predominate. Indeed, no other large forest reserve in southeastern Amazonia safeguards a full complement of disturbance-sensitive wildlife and the entire vegetation transition from open savanna (*cerrado*) to close-canopy forests (Zimmerman et al., 2001).

Kayapo lands and the contiguous 2.8 million-ha Xingu Indigenous Park to the south protect more than 400 km of the Xingu river from degradation by deforestation, pollution and over-fishing. Preliminary surveys indicate that as many as 1500 fish species inhabit the Xingu River. Fish are the most important source of protein for local people of the Xingu. Sixteen species of fish are considered endemic to the Xingu as they have only been collected from this watershed (Perez, 2015).

Consolidation of the Xingu Corridor is the only remaining possibility for conserving the last large, intact forest of the southeastern Amazon, and maintaining the connectivity of this ecoregion with the western Amazon. Kayapo lands play a particularly important role in the Xingu corridor because of their multilandscape size under the control of a single ethnic group that is on its way to acquiring the skills needed for protected areas management. In addition to biodiversity conservation, the Xingu corridor contributes substantially to maintaining rainfall regimes and carbon stocks of global importance (Gibson et al., 2011; Sakschewski et al., 2016; Soares-Filho et al., 2010; Walker et al., 2014; Leite-Filho et al., 2019).

Warrior Tradition and Land Gain: The Kayapo

Most Kayapo groups were first contacted in the 1950s and 1960s and inhabited widely dispersed settlements. Sub-groups following different chiefs were subject to ongoing internal feuds and regularly raided regional Brazilian settlements for trade goods, particularly firearms, and captives (Verswijver, 1992). While many sub-groups were decimated by epidemics, "contact" with the surrounding society was shaped by Kayapo strategies to access outsiders' goods for their own ends (Gordon, 2003; Verswijver, 1992). Their pro-active warrior attitude combined with well-developed political and social organization served the Kayapo well to secure legal recognition of their territory and defend it from invasions during the 1980s and 1990s.

Through the 1980s and 1990s the Kayapo repeatedly staged highly visible demonstrations, blocked roads, took hostages and expelled gold miners and ranchers from their territory in the process of winning official recognition of their land rights (Turner, 2000). The result of this aggression was official ratification and demarcation of a block of five contiguous indigenous territories (TI) of the Kayapo that span 10,598,616 ha (~106,000 km²): TI Kayapo, TI Bau, TI Mekranoti, TI Badjonkore and TI Capoto/Jarina. At the same time, nearly all Kayapo chiefs negotiated deals with illegal mahogany loggers and in a few cases in the east, with gold miners. In the early 2000s, with mahogany stocks in decline and ramped up NGO investment in conservation and development programs, most, but not all, Kayapo ceased selling logging concessions in their territory. Today some 10,000 Kayapo live in more than 80 communities and small family settlements.

Alliance with Conservation NGOs

In the struggle to protect their lands, the objectives of Amazonian indigenous peoples coincide with a conservation mission of preserving biodiversity and natural ecosystems. Indigenous Amazonians repeatedly assert a fundamental interdependence between cultural identity and territory. Indigenous “traditional knowledge” of forest ecology and the grounding of culture and identity in territory represent a distinctly different world view from that of Western culture and science. While Western science concerns itself with the natural world ruled by material forces and not the cultural realm of values, conventions and concepts, Amazonian indigenous societies include animals, plants, and other natural phenomena in the domain of culture and society (Viveiros de Castro, 1998; Descola, 1994; West, 2005). Indigenous resource knowledge arises from mutual recognition, active communication and exchanges among people, animals, plants, geographic features, spirits, and the dead conceived as actors in the same socio-cosmological networks. Indeed, sustainability of indigenous territories cannot be conceived or measured in purely ecological or economic terms; rather there is also a question of the viability and vitality of cultures (Schwartzman et al., 2013). The Kayapo fight to protect their culture, their livelihoods and very existence. Their goal overlaps with the conservation community in the need to protect what remains of the world’s richest terrestrial ecosystem.

In 1992, at the request of leaders of the Kayapo village of A’Ukre, the international conservation NGO Conservation International (CI) enabled the founding of a biological research station as an income alternative to mahogany logging. The community declared 10,000 ha off-limits to hunting and logging in exchange for fees from researchers and training of Kayapo assistants, with benefits distributed equitably in the community—unlike mahogany payments which were controlled by chiefs. The research station was the Kayapo’s first exposure to a subculture of outside society that places high value on traditional indigenous knowledge, culture and ecosystem protection services and was not seeking exploitation for financial gain. Researchers and NGO personnel offered an alternative development vision to the community of A’Ukre that was based on sustainable resource management and forest conservation (Zimmerman et al., 2001).

The success of the research station to benefit the community equitably while conserving a highly valuable undisturbed population of mahogany trees (*Swietenia macrophylla*) that were under intense pressure to log led Conservation International (CI) to convene a series of meetings over a 6-year period with Kayapo leaders from the entire block of Kayapo territory. The purpose was to: (i) present and discuss the idea of a Kayapo-conservation NGO alliance with the objective of strengthening Kayapo capacity for sustainable resource management, economic autonomy and territorial control, and; (ii) provide opportunity for Kayapo leaders to reinforce traditional bonds and unite under a single vision for the future. By 2006, the majority of Kayapo leaders chose to ally with the NGOs and reject illegal activity and predatory resource exploitation on their land.

With consensus reached on the goal of a Kayapo-NGO alliance, CI helped the Kayapo to establish their own local NGOs: Instituto Raoni (IR) formed in 2001 and based in Peixoto de Azevedo, Mato Grosso to represent the south-western Kayapo; the Associação Floresta Protegida (Protected Forest Association) (AFP) formed in 2002 and based in Tucuma, Para, to represent the north-eastern Kayapo, and Instituto Kabu (IK) formed in 2008 and based in Novo Progresso, Para, to represent the northwestern Kayapo. No local NGO was set up to represent the southeastern Kayapo because by the time CI arrived on the scene, the mid- to south-eastern Kayapo centered at their main community of Gorotire had fallen firmly into the clutches of the illegal sector. The Gorotire Kayapo were the first to face the main onslaught of the frontier during the 1980s. After valiant and successful land battles but facing hordes of gold miners, the Gorotire Kayapo were drawn into illegal resource extraction on their land in collusion with local frontier society.

Kayapo NGOs have fought hard to resist frontier pressure on their land and resources. As the frontier of roads, ranching and towns consolidated around them over the past three decades, the Kayapo gained much greater access to towns and manufactured goods. The young generation of Kayapo especially seeks technology and education. Today, Kayapo face a choice between unsustainable, illegal but in the short term high-value activities, and lower-value conservation-based enterprises that take longer to develop but are sustainable and legal. Kayapo NGOs have been developing a successful portfolio of nontimber forest product and service enterprises with their communities that fit with Kayapo culture and that generate equitably distributed benefits:

- **Brazil nut:** In 2019 32 communities participated in the harvest and sale of Brazil nut to the domestic food industry for a favorable price brokered by their NGOs. Kayapo NGOs subsidize harvest and transportation costs. Brazil nut sales now generate over US \$350,000 per year for community members.
- **Cumaru nut (tonka bean).** As with Brazil nut, cumaru is a fruit produced by a primary forest tree that is harvested by the Kayapo in natural forest after falling to the ground. The United Kingdom cosmetics company Lush buys 100% of the Kayapo cumaru harvest. Cumaru sales now generate over US\$45,000 per year for Kayapo harvesters of 24 communities.

- *International field course*: the Pinkaiti field station of the community of A'Ukre hosts two international university field courses every summer in partnership with Brazilian universities. This generates about US\$25,000 per year for this community.
- *Catch-and-release sportfishing*: the northeastern Kayapo NGO AFP partners with sport fishing company "Untamed Angling" to host a catch-and-release sport fishing enterprise based out of Kendjam village on the Iriri river. This enterprise generated US \$50,000 in 2019 for the two communities on the Iriri river. The AFP and Untamed Angling are opening a second sport fishing and ecotourism enterprise on the Xingu river that will serve six communities located there.
- *Handicrafts*: the sale of handicrafts including bead jewelry and paintings generated over US\$40,000 for Kayapo communities in 2019.

Sustainable income alternatives are now generating close to half a million dollars per year for Kayapo communities of the NGO alliance. Although reliable markets for these nontimber products and services exist, these enterprises are not yet 100% financially sustainable and require business management and administration subsidy.

The local Kayapo NGOs organize border surveillance. Guard posts established at key entry points have proven effective at blocking invasions by loggers, gold miners and ranchers. Government enforcement of Kayapo indigenous land rights ended in 2019 making the Kayapo surveillance program even more crucial for territorial protection.

The criterion for a Kayapo community to receive philanthropic investment is no involvement in illegal activity. The monetary value of payments from loggers and gold miners to Kayapo individuals is higher in the short term than from conservation enterprises and requires no Kayapo labor. However, in addition to being unsustainable and leading inevitably to severe cultural and environmental degradation as well as territorial loss, illicit activities do not fulfill egalitarian values of Kayapo society. Loggers and gold miners negotiate concessions on Kayapo land with chiefs and generally do not distribute payments among community members; whereas NGO supported non-timber forest product enterprises and border guard posts generate equal opportunity work and equitably distributed benefits, as is compatible with Kayapo culture. Communities will not support individuals proposing to take them down an illicit unsustainable path when sustainable options that materially benefit all are available.

Hotspot Analysis Demonstrates Success of Kayapo NGO Alliance

The overarching goal of the Kayapo-conservation NGO alliance is to empower the Kayapo to defend their constitutional rights, protect their ecologically intact territories and develop sustainable economic autonomy within the lawless frontier zone of the southeastern Amazon. Kayapo NGOs and their partners have worked over almost two decades to grow and diversify a portfolio of sustainable conservation-based enterprise, generate equitably distributed benefits, and strengthen territorial monitoring and surveillance over a vast roadless area demarcated by some 2000 km of border.

Other factors besides money figure in Kayapo development decisions. Perhaps most highly of all, the Kayapo value protecting their constitutional right to exclusive occupation and control over their territory; their concern is the survival of their culture and descendants. Once they gain a foothold, loggers and gold miners quickly overwhelm Kayapo traditional governance systems and take control of an area. The eastern Kayapo were drawn into the illicit frontier economy in the 1980s and 1990s having had no experience with these activities and no support to develop economic alternatives or to foresee the inevitable and irreversibly destructive consequences of predatory logging and gold mining. Immersed in a region where lawlessness and corruption prevail, they have lost control over roughly 1.2 million ha of their territory in the east (Fig. 1) which is now a no-man's land dominated by gold miners, loggers and other illegal actors. The Kayapo living in these eastern communities depend on these actors to provide the manufactured goods they have come to need. Most rivers in this area are choked with mud and polluted by mercury used in gold mining. Forest is degraded by logging which removes most of the big, old growth primary forest trees so pivotal to the overall ecology of this biome. This opens these once resilient forests to fire. Traditional culture breaks down in lockstep with environmental degradation and the introduction by loggers and miners of alcohol, drugs and prostitution.

The intact environmental and social conditions of NGO-allied Kayapo territory contrast starkly with the breakdown in the east. As of 2019, the total Kayapo population numbers almost 10,000 people living in 82 communities and small family settlements located throughout their 10.6 million-ha block of territory (Fig. 1). Of this land, 89%, or 9,400,000 ha, is controlled by 61% of the Kayapo population who live in 48 communities and small settlements that have allied with the NGOs to pursue sustainable economic autonomy and territorial control (Fig. 1). Ninety percent of the approximately 4000 Kayapo living in 34 communities and small family settlements involved with the illicit frontier economy reside in the 1,200,000-ha band of eastern territory that fell to the frontier of predatory resource extraction before the arrival of NGOs (Fig. 1) or before NGO programs were developed enough to help the Kayapo bar the intense wave of illegal activity resurgent in the region after 2010.

Deforestation Hot Spots Analysis

We analyzed the Kayapo territory for loss events using Hansen et al.'s (2013) global forest change 2000–18 imagery from the Google Earth Engine data catalog and GLAD alert imagery (Hansen et al., 2013) for 2019. Loss events were extracted and tallied for each year within the time series for the Kayapo territory and the respective east and west boundaries. Loss events found within 5 km of a village or in naturally occurring non-forest landscapes (i.e., cerrado/savanna, rock outcrops) were omitted.

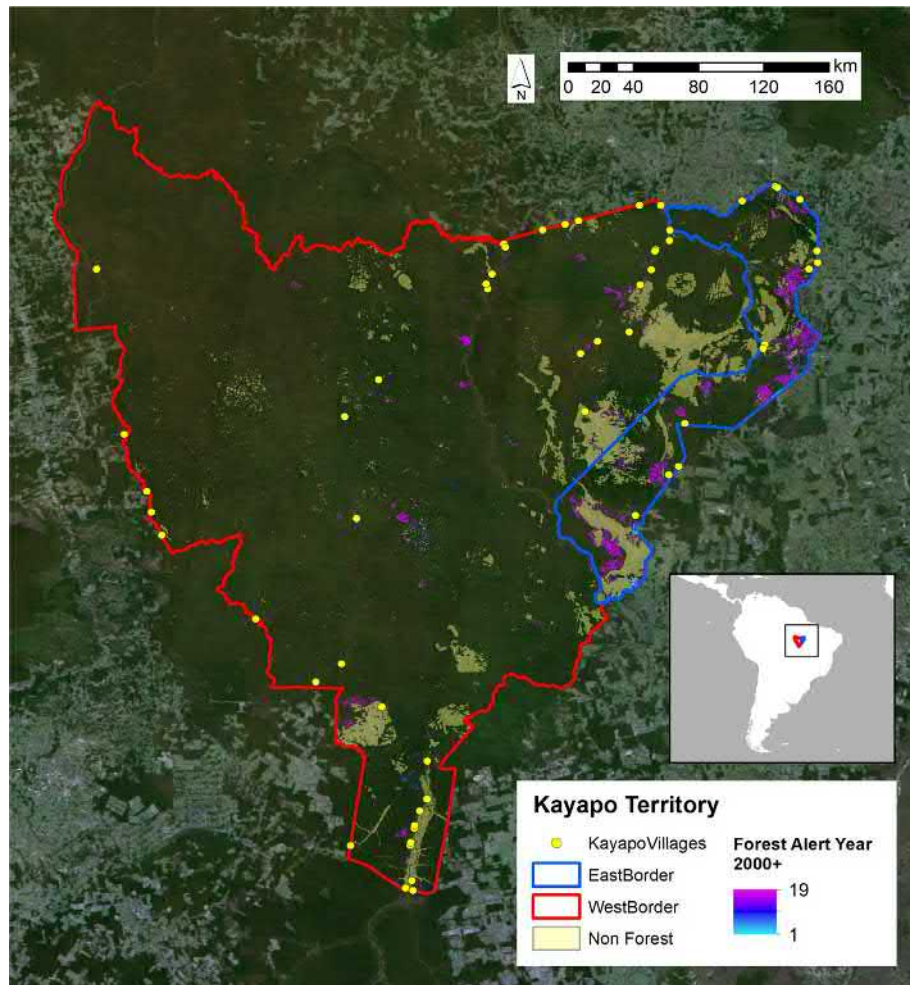


Fig. 1 The block of five contiguous Kayapo indigenous territories (TI) from space (TI Kayapo, TI Bau, TI Mekragnoti, TI Capoto/Jarina, TI Badjonkore). The light colored non-forest in Kayapo territory denotes naturally occurring savanna-woodland on plateaus and outcrops of Brazilian shield rock. The locations of villages with more than 50 people are shown. Red outlines 9.4 million ha of Kayapo territory that is represented by a local Kayapo NGO and receives outside conservation and development investment. Blue outlines 1.2 million ha of Kayapo territory that receives no NGO investment. Alerts indicate forest cover loss.

An optimized hot spot analysis was performed using ArcGIS® Desktop (ESRI, 2018). The optimized hot spot tool uses the Getis-Ord Gi statistic (Getis and Ord, 1992; Ord and Getis, 1995) to create a map of statistically significant hot (areas of higher incidence) and cold (areas of low incidence) spots given the event points. The focus is on presence or absence rather than measured attributes associated with each point. The hot spot analysis was performed for all of the loss events within the Kayapo territory from 2001 to 2019.

Hot Spot Analysis Results

From space we observe significant correlation between the location of deforestation hotspots and the presence/absence of NGO investment with Kayapo communities (Figs. 1–3). The absolute number of loss events are greater for the western zone for most years. However, the western zone is 9,423,000 ha, approximately eight times the area of the eastern zone (1,200,000 ha). When this is taken into account looking at the loss events per hectare, we see that the eastern zone has much greater densities of loss events per hectare (Fig. 3).

Discussion

Indigenous territories are known to have formed effective barriers to frontier expansion and deforestation (Nelson and Chomitz, 2009; Nepstad et al., 2006; Nolte et al., 2013; Pffaf and Robalino, 2013). Deforestation in the Xingu Basin is heavily concentrated outside of the indigenous lands and protected areas. Of the ~10 million ha deforested in the basin through 2010, 91% was outside of protected areas, 3% was in indigenous lands, 1.4% in Federal protected areas and 4% in state protected areas (Campanili, 2012).

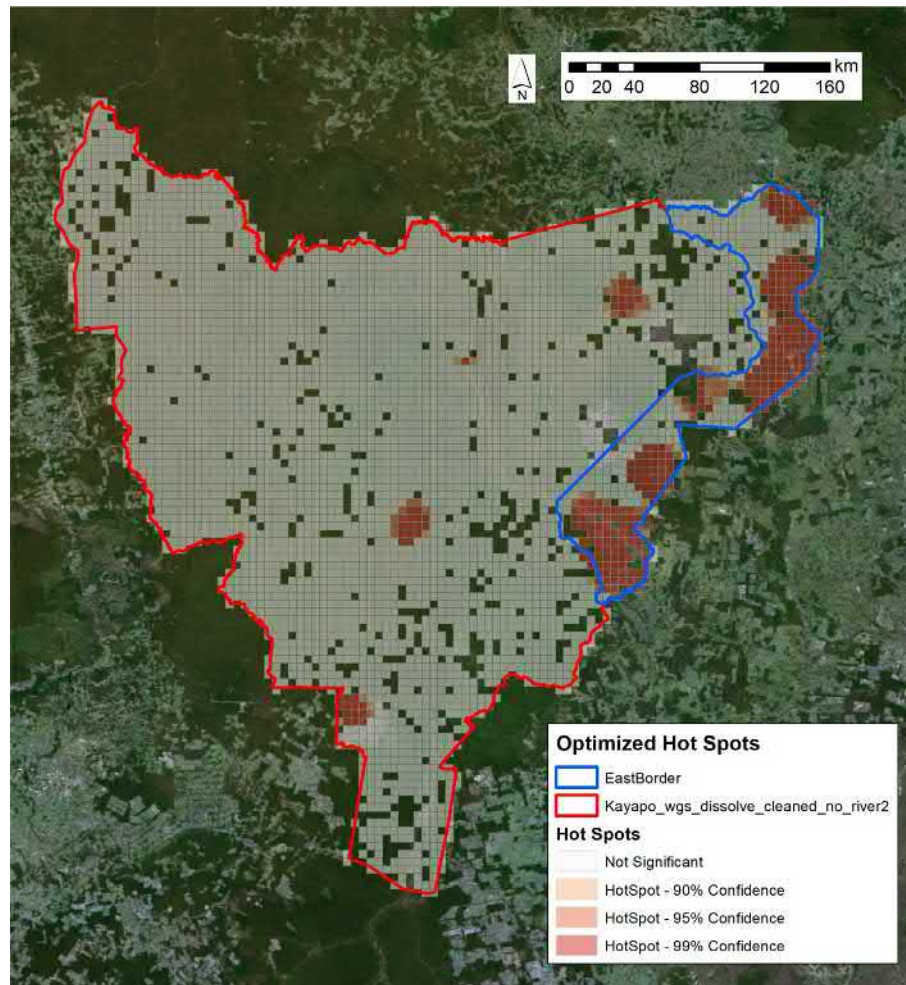


Fig. 2 Hot spot analysis of all forest cover loss events across Kayapo territory from 2001 to 2019. The map shows statistically significant areas of higher hot spot incidence (in red) given the event points. Hot spots indicate deforestation events.

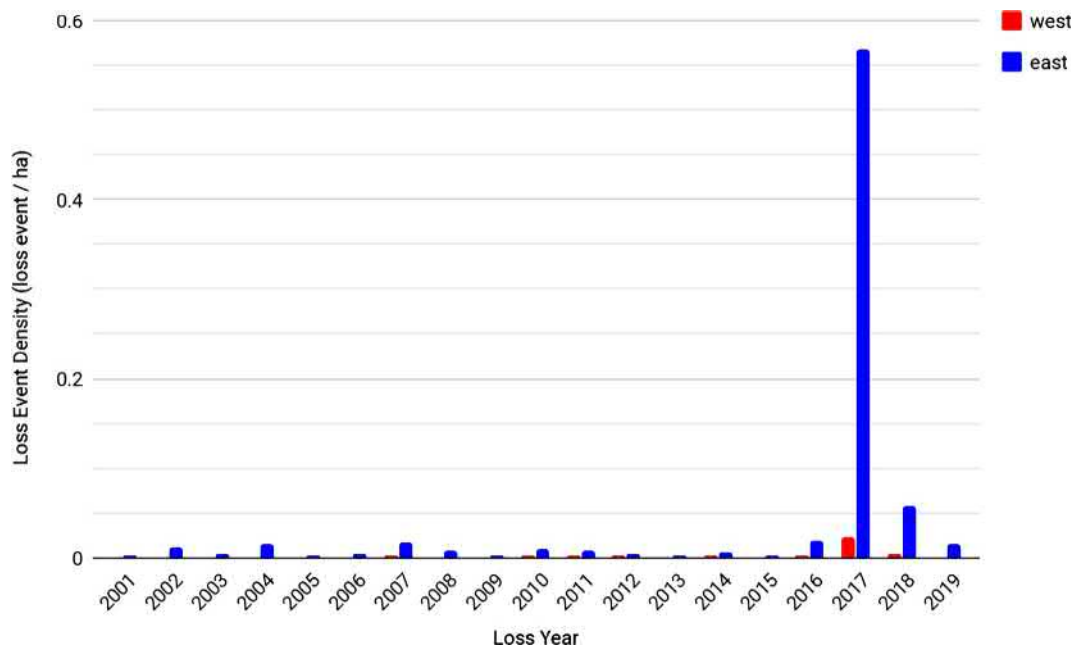


Fig. 3 Forest loss event densities for the east and west sectors of Kayapo territory. The blue bars are the eastern (no NGO investment) Kayapo territory loss events per hectare per year. The red bars are the western (NGO investment) Kayapo territory loss events per hectare per year.

However, the Xingu basin spans the most high-deforestation region of the Amazon frontier and pressure on indigenous territories and protected areas has ramped up dramatically over the past decade. There was a 54% increase in overall deforestation in the Xingu basin during the first 2 months of 2019 compared with the same period in 2018 (Siradx, 2019a). The number of fire hotspots in the Xingu basin detected between July and August 2019 increased 271% from the same period in 2018 with deforestation in indigenous territories increasing 158% during the summer of 2019 compared to 2018 (Siradx, 2019b). Intense activity by illegal loggers and gold miners combined with lack of law enforcement by government authorities has led to significant losses along the eastern band of Kayapo territory (Fig. 1). Gold mining and logging continue to expand in the non-NGO represented areas of eastern Kayapo territory (Figs. 1–3). Beginning in about 2015, over 1500 ha were being lost annually to gold miners in eastern Kayapo territory.

The relative lack of deforestation and degradation throughout more than 9 million ha of Kayapo territory to the west compared to the heavily degraded 1.2 million-ha eastern band of Kayapo territory can be explained by philanthropic investment into Kayapo empowerment for territorial control. Where Kayapo communities receive help to monitor and control their territory, develop equitable and sustainable sources of income and gain insight into threats, their borders largely hold and forest remains largely intact. Kayapo territory that receives no conservation and development investment is being heavily invaded by gold mining and fire in forest degraded by logging (Figs. 1–3). A low density of hot spot alerts overlaps almost exactly with Kayapo territory that is represented by and receives program support from Kayapo indigenous NGOs that in turn are supported by international conservation NGOs (Figs. 1–3). This pattern cannot be explained by cultural differences as the eastern and western Kayapo belong to the same ethnic group whom share the same history (Verswijver, 2018); nor can it be explained by distribution of gold and timber which is found throughout Kayapo territory. Also, access and exposure to the frontier is similar across all Kayapo territory: there is nowhere in Kayapo territory that loggers and gold miners cannot reach.

Governance in the southeastern Amazon region has always been weak. After gold mining resurged in the eastern region of Kayapo territory in about 2013, the federal Ministry of Environment (IBAMA) performed helicopter supported enforcement operations designed to deter goldmining and logging. Between 2015 and 2018 IBAMA executed 12 raids on illegal goldmining and logging afflicting Kayapo territory. Although several millions of dollars of illegal heavy equipment was destroyed and dozens were arrested, an under resourced IBAMA was unable to apply operations with enough frequency to shut down illegal activity completely. Nevertheless, there was a deterrence effect and goldminers and loggers were hesitant to enter new areas.

In 2019, with government enforcement operations halted, loggers and goldminers became emboldened to enter Kayapo land. The three Kayapo NGOs which together are responsible for protecting over 9 million ha of Kayapo territory have responded with a ramped up territorial surveillance and more border guard posts. This territorial surveillance program depends in large part on international philanthropy.

Conclusion

Kayapo territories are a critical source of ecosystem services—biodiversity conservation, carbon storage, watershed protection and maintenance of rainfall regimes. As with other indigenous peoples of the Xingu region, the Kayapo clearly and consistently affirm that their territory, cultural identity and traditional knowledge are mutually interdependent. Self-reflexive understanding and valuing of traditional culture and knowledge as distinct from Western values and science, including dialogue between Western science and traditional knowledge, are key conditions for the sustainability of these territories.

Creation of protected natural reserves and legal recognition of indigenous territories has largely formed a barrier to deforestation until now; but illegal logging and gold mining remain pervasive threats and deforestation rates are intensifying. NGO investment has been effective in enabling the Kayapo to maintain control over almost 90% of their vast territory, mostly by supporting their local indigenous institutions (NGOs) to develop sustainable enterprises and manage and control their territories. Economic alternatives to logging and goldmining have clearly had an impact but need to develop further in order to fully meet community demand for income and market access. Kayapo NGOs have responded to intensifying threats by ramping up their territorial surveillance programs and establishing border guard posts that have proven effective for controlling access to their territory. These projects are scalable but will require continued philanthropic investment to grow as well as continued capacity building for community members to effectively manage local enterprises. In essence, outside support for Kayapo NGOs and their programs can be viewed as payment for ecosystem services. The Kayapo have demonstrated that partnerships between indigenous people of the Amazon and conservation organizations can achieve protection of primary forest and concomitant empowerment of indigenous rights.

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The Ecology of Forest Disturbances

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Abstract

Forest disturbances are among the most spectacular manifestations of ecological change. They are the subjects of countless scientific studies, newspaper headlines, local and national legislation, and international initiatives. Despite the ubiquity of disturbances in forests globally, many central questions remain unresolved and many policy strategies are at odds with contemporary ecological understanding. Here we consider the causes and consequences of forest disturbances and discuss related ecosystem management. While throughout much of the history of the science of ecology, disturbances were considered aberrations or disruptions to functioning ecosystems, there is now clear recognition that disturbances are integral components of functioning ecosystems, representing a necessary part of the ecological whole. Although disturbances, especially large and severe ones, can be challenging from a management perspective, it is often possible to incorporate disturbances into management plans that provide multiple ecosystem services. Eliminating disturbances is neither possible, nor always desirable. Although passive management of all disturbed forests is not necessarily feasible, allowing disturbances, even large ones, to shape some forest ecosystems may promote ecological resilience in the face of climatic and environmental change.

Introduction—What are Disturbances?

Forest disturbances are among the most spectacular manifestations of ecological change. They are the subjects of countless scientific studies, newspaper headlines, local and national legislation, and international initiatives. Despite the ubiquity of disturbances in forests globally, many central questions remain unresolved and many policy strategies are at odds with contemporary ecological understanding of disturbance behavior, likelihood, effects, and roles in long-term, basic ecosystem functioning. Here we consider the causes and consequences of forest disturbances and discuss related ecosystem management.

Various definitions of forest disturbances have been proposed, but one of the most enduring and simple definitions is still one of the most useful. In 1985, White and Pickett defined a disturbance as “any *relatively discrete* event in time that disrupts ecosystem, community or population structure and *changes* resources, substrate availability, or the physical environment” (italics added). The fact that disturbances are limited to *relatively discrete* events implies that climate and climate change usually are not considered disturbances in and of themselves. However, the indirect effects of climate and climate change, such as wildfires and insect outbreaks, are considered disturbances. The scientific literature is inconsistent in categorizing drought as a disturbance, in part because droughts vary in their temporal discreteness and their ecological effects. For the purpose of this chapter, we consider drought as a climatic effect rather than a disturbance. The second part of White and Pickett’s definition emphasizes a *change* in resource availability or the physical environment. All disturbances change affected ecosystems, by the initial disturbance (e.g., a wildfire) as well as by any subsequent related disturbances (e.g., insect population increases due to downed wood or post-disturbance logging). Such linked and compounded disturbances are discussed later in the chapter. Both criteria for a disturbance—temporal discreteness and resource change—depend on the scale of investigation. Increases in resources via

fine-scale tree mortality may be significant for processes operating at fine scales, but insignificant at broader (e.g., regional) scales where patterns may be shaped primarily by topography and climate. Conversely, the effects of large disturbances can be contingent on fine-scale pre-disturbance heterogeneity (e.g., Mietkiewicz et al., 2018). Importantly, we underscore that conceptualizing disturbances as changing stand structure and resource availability emphasizes the fact that disturbances normally do not destroy ecosystems. Instead, disturbances abruptly change ecosystems in ways that are often significant and not always predictable.

Disturbances are complex and each event is seemingly unique due to the nuanced interplay of factors involved. Despite this, there are commonalities among disturbances that have led to classification systems based upon various attributes. The most common categories are based on the agent (fire, insect, wind, avalanche, etc.), source (natural vs. anthropogenic), origin (endogenous vs. exogenous), affected strata (canopy vs. understory), and status (abiotic vs. biotic). Grouping disturbance events by commonalities allows for cross-system comparisons, even if it glosses over complexities in each event as well as the interplay between apparent opposites. For example, natural (e.g., insect outbreaks) and anthropogenic (e.g., logging) disturbances differ in their ecological effects and in the degree to which forest species are adapted to them. However, during the Anthropocene, most so-called natural disturbances are influenced by anthropogenic climate change, which can affect the disturbance agent as well as the resistance of trees to that agent. Similarly, the classic dichotomy of endogenous versus exogenous disturbances is limited by the recognition that the effect of so-called exogenous disturbances is determined by ecosystem structure and composition (e.g., tree species vary in their susceptibility to wind damage), while so-called endogenous processes are shaped by past disturbances (e.g., fine-scale regeneration patterns can be affected by the spatial distribution of coarse woody debris, which reflects the history of past disturbance). Although some disturbances do affect only the canopy or the understory of a forest, most affect both to varying degrees. For example, emphasizing that a windstorm kills canopy trees may be correct, but it also may overlook the damage or mortality to understory trees. Similarly, although it is useful to contrast fires and other disturbances as being either low or high severity, the recognition that many wildfires have mixed severity components underscores the ecological importance of even few survivors in otherwise high-severity events.

The cumulative disturbance types and their characteristics that affect a particular area are referred to as a disturbance regime, which can be described by the frequency, return interval, rotation period, size, intensity, and severity of disturbances (Pickett and White, 1985). Thus, disturbance regimes vary with the temporal and spatial scales in question (Clark, 1989). Although it is clear that climate change is affecting forest disturbances in general, considering specific attributes of disturbance regimes allows us to more precisely identify and understand the aspects of disturbances that are changing. For example, although recent outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) in the western US are clearly influenced by climatic conditions (Hart et al., 2014), very extensive and synchronous outbreaks are not necessarily unprecedented over the past centuries (Jarvis and Kulakowski, 2015). This recognition and specificity allows us to focus on the effects of climate on the *intensity* of outbreaks rather than their *size*. In contrast, although wildfires have shaped forests of the western United States for millennia, recent climate change has increased the *intensity* and *size* of fires in some forests (Running, 2006; Westerling, 2016). In other cases, wholly new disturbance phenomena are emerging, such as root freezing as a result of snow loss in high latitudes, that cause mass mortality over extensive areas (Buma et al., 2017b). Thus, considering the specific attributes of disturbance regimes facilitates more nuanced comparisons and analyses—including of possible thresholds, tipping points, and alternate stable states.

Why, When, and Where Do Disturbances Happen?

Disturbances, in some sense, can be seen as entropy reasserting itself. Ecosystems are comprised of organisms in highly ordered and energetic states; disturbances disrupt that state. Forests are an excellent example of such a state—long lived organisms, with considerable chemical energy contained in their structures, in complex stratified arrangement (Lowman and Rinker, 2004). Fires are an example of the chemical energy stored in those bonds being re-released as heat; windstorms are an example of the orderly structure being reconfigured.

What is the Limiting Factor?

While each disturbance process (e.g., fire, wind, landslides) and each disturbance itself has its own characteristics and mechanisms, generally speaking, the occurrence of a forest disturbance depends on the confluence of three factors: sufficient biomass to be disturbed, some instigating factor to initiate a disturbance event, and external conditions that can sustain the disturbance beyond the initial mortality event.

Sufficient biomass—The amount of live and dead material in a forest is key for the propagation and effects of a disturbance to be recognized as such. This biomass must also be structured in a way as to be exposed to a given disturbance type. While conditions capable of causing tree mortality may be present, if a tree or forest are not developed to a susceptible structural stage, that disturbance will not occur or will not propagate. For example, very young trees do not typically have the structure (rigid stems, substantial height) to be disturbed by windstorms. Similarly, the suitability of a given tree to bark beetle infestation is restricted by the size of the tree (e.g., Kärvelo et al., 2016). At broader scales, a very sparsely forested area may not have the tree density necessary to carry a fire (Song and Lee, 2017). An important caveat is that extreme climate or weather can relax the structural requirements for disturbances of trees (e.g., warm temperatures can make small diameter trees susceptible to bark beetle infestation) or landscapes (e.g., strong winds can render a landscape functionally connected for fire spread).

Instigating factor—Instigating factors are required for a disturbance. For fires, an ignition source; for landslides, the initial slope failure. While for each disturbance type this instigating factor is different, each has the characteristic of starting a process that is, in many cases, at least partially self-sustaining. In fires, the initial ignition (perhaps caused by lightning) causes further ignition of individuals, spreading the fire. In windstorms, the first initial tree failure (blowdown or snapping) allows for more intense wind to enter a stand, leading to increased stress on neighboring trees and an expanding blowdown patch.

External conditions—Given sufficient biomass and structure and the instigating event, the proper conditions must be present to drive a disturbance event beyond initial mortality. As before, negative examples are illustrative. In southeast Alaska, sufficient biomass is present for extremely large wildfires. At >500 Mg/ha density, extremely complex crowns with substantial ladder fuels, and very homogenous spatial arrangement, the forests could carry very large and intense fires. Lighting is infrequent, but not nonexistent, and anthropogenic ignitions are present, as evidenced by occasional small events. Yet there is no evidence of large, severe fires in the northern part of this region since the last Glacial maximum (~12,000 years). The lack of a summer dry period is the likely reason—the region receives around 20% of its rainfall in the driest quarter, meaning fuels have no opportunity to reach a condition suitable to sustain large fires. As a result, while sufficient biomass and structure exist, conditions suitable for fires are rare. The situation for windstorms is quite different, however – high winds are relatively common and correspond with wet autumn storms that soften soil, increasing tree susceptibility. As a result, wind mortality is the most common disturbance event in the region.

Frequency of disturbances

The frequency of disturbances varies spatially and temporally and depends on the limiting factors discussed above. A recent fire-scale (30 m) quantification across the entire North American continent found that some forested ecoregions were disturbed at rates <0.1% per year, while other disturbance rates in other ecoregions were >10% per year (Buma et al., 2017a). At the global scale, forest disturbance patterns are variable but high disturbance activity is most correlated with climate (Sommerfeld et al., 2018), though the climate-fire relationship is weaker in areas of high anthropogenic pressures, potentially a signal of human impacts on ignitions (e.g., suppression or intentional burning) or biomass (Abatzoglou et al., 2018; Syphard et al., 2017).

Understanding past and current drivers of the frequency of disturbances enables predictions of climate change or anthropogenically driven effects. For example, in Yellowstone National Park, weather and climate conditions conducive to fires are generally assumed to be the primary driver of large fires. This leads to expectations of much more frequent fires in the future as conditions more frequently approximate those that have been associated with historically severe fire years (Westerling et al., 2011)—or at least until biomass limitation reduces fire extents. In contrast, landslides remain a challenging disturbance to anticipate (especially in terms of frequency) because they are generally limited by initiation—in other words, conditions that are associated with landslides are not uncommon (Caine, 1980), and sufficient biomass (and soil mass) is similarly common, yet actual initiation and subsequent disturbance are infrequent and remains difficult to predict (Zhu et al., 2018) due to the fine spatial scales and uncertainties involved. As always in disturbance ecology, the limiting factor depends on the scale of investigation. Very large, infrequent fires are often limited by broad scale weather and climate, whereas smaller fires in the same area may be more limited by ignition frequency.

Interacting Disturbances

As climate is increasing the frequency and extent of disturbances such as wildfire, bark beetle outbreaks, and windstorms, forests and other ecosystems are increasingly being affected by multiple disturbances over relatively short periods. Potential interactions among disturbances can affect ecosystem patterns and processes, including susceptibility to subsequent disturbances. Disturbances exert a strong control on subsequent disturbance probabilities (Buma, 2015; Kulakowski and Veblen, 2015), often by limiting biomass or influencing its structure in such a way as to increase or decrease the likelihood, extent, or severity of a second disturbance event (Seidl et al., 2016). In fact, research over the past decades has highlighted the fact that disturbances do not act in isolation, but rather interact with other disturbances to shape ecological structure and function. For example, fires have been shown to reduce subsequent susceptibility of forest to outbreaks of some bark beetles by reducing tree size following fire (Kulakowski et al., 2003, 2006; Veblen et al., 1994). However, such resistance to disturbances conferred by preceding disturbances may be reduced as climate change increases the intensity of disturbances (Kulakowski et al., 2012). This resistance is dampened because pre-disturbance stand conditions generally become less important in determining the susceptibility of a forest to disturbance as disturbance intensity increases (Turner, 2010).

While in some cases, climate change can dampen the interactions between linked disturbances, in other cases climate can serve as an underlying driver of multiple disturbances in the same landscape. For example, over the past decades, occurrence of large wildfires across the western United States has been driven primarily by warm and dry climate conditions. At the same time, extensive outbreaks of mountain pine beetle across the same region have also primarily been driven by climatic conditions that promote the growth of beetle populations and reduce host resistance. Despite the co-occurrence of these two disturbances in the same landscape (and common assumptions), the current state of knowledge indicates that co-occurrence of wildfires and outbreaks are due to a common climatic driver, rather than interactions between these disturbances (Buma, 2015; Kulakowski and Veblen, 2015; Mietkiewicz and Kulakowski, 2016).

The Disturbance Regime

Disturbance regimes (as introduced above) are the cumulative total of all disturbance types including their severity and frequency, over some period. Disturbance regimes can also be considered for individual disturbance types (e.g., the wind regime). In all cases, it is important to recognize that regimes vary across spatial and temporal scales. For example, protected (leeward slopes) within a region may only experience blowdowns every ~1000 years, or may have never experienced a blowdown. Thus, defining spatial and temporal scales is extremely important when describing a disturbance regime.

Historical range of variability

Many disturbance regimes have characteristic variabilities over discrete periods. Some forested ecosystems have had relatively regular disturbance regimes, at least prior to human intervention (Fulé et al., 1997). Other systems, especially those where disturbance occurrence depends on the confluence of rare initiation events and weather/climatic conditions, have highly variable disturbance return intervals (Schulte and Mladenoff, 2005; Turner et al., 1993). Variability and non-equilibrium processes, even in systems generally considered predictable, is common (Mori, 2011).

Characterizing a disturbance regime is commonly done by defining a historical range of variability (HRV), or the anticipated range of possible disturbance attributes (extent, severity, etc.), return intervals, and types as defined by historical events. The HRV is typically reconstructed via historical records or paleoecological techniques such as tree cores or pollen/sediment cores. While the validity of the HRV is often questionable over long time periods or broad spatial extents (Baker and Williams, 2018), it is still utilized as a useful concept for ecosystem description. Most notably, HRV can be used to assess deviance of an ecosystem from its characteristic behavior as a result of climate change or other human influence.

Deviations from HRV

Rapid changes in disturbance regimes can be caused by alterations to any of the primary limitations on the regime—biomass, ignition, or drivers (e.g., climate). For fires, for example, extensive documentation exists for rapid disturbance regime shifts associated with changing initiation sources (increases or decreases, Fulé et al., 1997; McWethy et al., 2010; Nevle and Bird, 2008), biomass (increasing or decreasing, Coffman et al., 2010; Hiremath and Sundaram, 2005; Keeley and Brennan, 2012), interactions between disturbance legacies (Buma, 2015), and climate conditions becoming more conducive to disturbance propagation (e.g., fire spread, Westerling, 2006). While the latter have received much of the attention of modelers and scientists due to the obvious tie to climate change, the “climate-independent” factors (Pausas and Keeley, 2014) also must be considered alongside rapid climate change as triggers for disturbance regime change in the future.

Disturbances as Integral Components of an Ecosystem

While throughout much of the history of the science of ecology, disturbances were considered aberrations or disruptions to functioning ecosystems (Clements, 1936), there is now clear recognition that disturbances are integral components of normally functioning ecosystems, representing a necessary part of the “ecological whole.” Disturbances have exerted an evolutionary force on species, and species are typically well adapted to the historical disturbance regimes of the ecosystems in which they occur (Pausas and Keeley, 2014). Though there is still debate as to the exact role of disturbances, especially fire, in driving species-level genetic adaptation (Bradshaw et al., 2011; He and Lamont, 2018; Pausas et al., 2017; Poulos et al., 2018), there is little doubt that at the ecosystem scale, disturbances are integral to normal structure and functioning.

Relatively complex structure, both vertically and spatially, is characteristic of forested landscapes. Complex physical and compositional structure is generally positively correlated with biodiversity (Camargo et al., 2018; McElhinny et al., 2005), carbon storage, and long-term resource use efficiency (Curtis and Gough, 2018). Disturbance processes maintain the structure and function of ecosystems, both in terms of habitat heterogeneity and successional stage of those habitats, by creating and responding to landscape heterogeneity and favoring species with disturbance-associated resistance or resilience strategies (Bond and Keeley, 2005). The spatial mosaic of biomes (e.g., forest vs. savannah ecosystems) can be driven by disturbance processes themselves, in addition to factors like climate, soil, and topography (Bond and Keeley, 2005; Dantas et al., 2016).

Within forests, a major function of disturbances is the creation and maintenance of spatial heterogeneity (Fig. 1). Multi-aged landscapes have a variety of characteristic species, structure, and biogeochemical properties (Swanson et al., 2011). This heterogeneity provides an added dimension to the underlying spatial heterogeneity imposed by differences in species composition and physical setting (Donato et al., 2011; Mori et al., 2018). Further complexity is introduced by intermediate or mixed severity disturbances and multiple disturbance types, both of which can vary across space and time (Meigs and Keeton, 2018; Peterson, 2019).

Nutrient Cycling

Nutrient cycling is strongly influenced by forest disturbances shaping nutrient availability and stoichiometry (i.e., ratios of available nutrients) immediately after disturbance and the species composition of the post-disturbance landscape. While considerable work has focused on the effects of disturbances on nutrient cycling immediately post-disturbance, less attention has been paid to the



Fig. 1 Natural disturbances can create spatial heterogeneity (e.g., variation in the amount and arrangement of surviving forest patches or trees) that often promotes biodiversity, primary production, wildlife habitat, hydrogeologic protection, and ecosystem resilience. Routt National Forest, Colorado. Photo: D. Kulakowski.

fundamental role of disturbances in nutrient cycling in the long-term, as a component of the entire ecosystem (Kranabetter et al., 2016).

Nutrient availability and stoichiometric ratios of forests change rapidly post-disturbance on multiple timescales and are strongly mediated by the forest microbiome. While the shifts partially depend on the characteristics of the disturbance event itself (e.g., fire vs. wind), all disturbances have the effect of moving nutrients and carbon from living pools into dead pools, thus making them available for mineralization and ultimately re-uptake, long-term sequestration, or export (Certini, 2005; Santos et al., 2016). Generally, the coupling between nutrient cycles in mature forests is relatively tight; disturbances have the effect of decoupling pathways temporarily (Keiser et al., 2016). For example, nitrogen availability increases either due to mineralization in the event itself (e.g., fire) or decreased uptake, with the magnitude of the effect related to the severity of the disturbance (Nave et al., 2011). At a fundamental level, this provides heterogeneity in the biogeochemical landscape that various species can exploit (Swanson et al., 2011; Townsend et al., 2008).

Species composition shifts associated with disturbances can significantly impact nutrient cycling over longer timespans, perhaps most obviously via favoring species with nitrogen-fixing symbioses. These plant species are typically light demanding, corresponding to a need for higher carbon fixation to offset the cost of their nitrogen-fixing partnerships, and thus often post-disturbance colonizers. For example, in many northern hemisphere forests, *Alnus* species are prevalent in disturbed environments. These species can deliver substantial amounts of nitrogen to ecosystems, and with episodic, disturbance-driven events can drive extraordinarily high levels of nitrogen in forest soils ($23,000 \text{ kg N ha}^{-1}$, Perakis et al., 2011). In forests where N-limitation decreases post-disturbance, the emergence of other biogeochemical limitations (Perakis et al., 2013) are emerging fields of research.

Absence of Disturbance

The fact that disturbances are fundamental components of forest ecosystems is perhaps best exemplified by forests without major disturbance processes. Many forests without occasional disturbances eventually undergo ecosystem retrogression processes—long-term (multi-generational) declines in productivity (Buma and Thompson, 2019) associated with gradual water saturation or nutrient limitation. In cooler forests, paludification (i.e., conversion of forest to peatlands) of forests is common in the absence of disturbance, characterized by the gradual conversion to peatlands with no intermediate aquatic phase. For example, in boreal forests, fires release organically fixed nutrients, decrease thickness of the soil organic matter layer, and results in more rapid decomposition in early successional stands. In old, undisturbed stands, nutrient availability, productivity, and decomposition rates decline, ultimately leading to soil moisture increases, and Sphagnum bogs that can replace the forest (Simard et al., 2007). Disturbance severity is also an important factor, with higher severity fires forestalling paludification and lower severity fires accelerating it. This same relationship of lowered productivity (estimated as lower baseline carbon stocks) exists at broad spatial scales in temperate forests exposed to only wind and landslides (Buma and Thompson, 2019). Soil disruption appears key in the process of maintaining productivity by directly impacting the nutrient cycling patterns discussed above and limiting soil moisture

increases; forest harvest that does not disrupt the soil, much like low-severity fires, can accelerate paludification by decreasing transpiration without also disrupting the thick, organic layer (Renard et al., 2016).

A second driver of lowered productivity is gradually increasing nutrient limitations due to long-term leaching losses or restricted availability, most commonly phosphorus but also nitrogen (Peltzer et al., 2010). Without disruptive disturbance processes to free up parent material for phosphorus and nitrogen (Houlton et al., 2018) or create habitat for strong nitrogen-fixation, inputs of those nutrients (and others) frequently cannot keep pace with losses. Access to nutrients can also be restricted by impermeable soil pan formation or thick, water-rich organic layers. Overall, productivity declines due to nutrient limitations (Peltzer et al., 2010) contribute to declines in tree biodiversity (Wardle et al., 2008) and mycorrhizal diversity (Krüger et al., 2015), though vascular plant diversity overall can increase and some species may specialize in these “retrogressive” forests (Wardle et al., 2008). This highlights the fundamental role that disturbances, especially those that cause soil disruption, have in maintaining productivity. Even high biomass, mature, “climax” forests, in which structure, composition, and biodiversity are shaped by gap-phase dynamics, are generally temporary (though possibly long-lasting) stages in much the same way as are early successional stages—without the occasional disturbance, the landscape will continue to change.

What Happens After Disturbance?

The concept of resilience has become central in discussions of global environmental change. Most generally, resilience refers to the ability of a system to be disturbed without shifting to a different state controlled by different processes (Gunderson, 2000; Holling, 1973). However, the “state” of the system may be defined any number of ways, including by tree size, forest structure (e.g., multiple-aged stands), forest type (e.g., spruce forests), vegetation type (e.g., forests), or even broader categories (Buongiorno et al., 1994; Vogt et al., 1995). Given this breadth of possible criteria, it logically follows that our working definition of resilience affects our assessment of ecological change. The broader the range of conditions that we consider normal, natural, or acceptable, the more resilient we will understand a system to be (Kulakowski et al., 2017). Questions of whether disturbances threaten or promote resilience; whether recent disturbances are unprecedented, or simply infrequent; and what characterizes natural ecosystems require a fundamental and often long-term understanding of ecological dynamics (Johnstone et al., 2016; Peterson, 2000; Shugart, 1984; Turner, 2010). Thus, our understanding of what happens after recent disturbances can be understood not only by observing recent phenomena, but also by contextualizing those processes in terms of long-term ecosystem variability (Buma et al., 2019; Landres et al., 1999). With this broad-scale and long-term view in mind, we turn to the question of what happens after disturbances.

Post-disturbance forest development depends on disturbance severity, pre-disturbance forest structure, and biophysical setting (e.g., Kulakowski et al., 2013; Vacchiano et al., 2014). In many systems, mixed severity events may maximize heterogeneity across the landscape. Stand-replacing disturbances (that leave no or few surviving trees) can create relatively homogenous regenerating forest structure in the decades that follow, unless underlying environmental heterogeneity is substantial (Palmer, 1994; Wohlge-muth et al., 2002) or unless surviving biological legacies drive structural and compositional diversity (DellaSala and Hanson, 2015). Regeneration following such higher severity disturbances typically depends more on seed or rhizome sources, whereas surviving vegetation is more important in shaping forest development following lower severity disturbances. While stand development is normally slow, natural disturbances, such as insect outbreaks and windstorms, can greatly accelerate the creation of structural and compositional complexity at stand and landscape scales, especially in stands that are in early stages of development (*sensu* Oliver, 1980).

An accurate estimate of disturbance severity and of pre-disturbance structure is essential for projecting post-disturbance dynamics. For example, even high severity windstorms and beetle outbreaks normally preferentially kill canopy trees rather than understory individuals. Therefore, all other things being equal, post-wind or post-beetle regeneration is more rapid in stands with a higher density of advanced regeneration (also referred to as advance regeneration) and understory trees (i.e., stands in latter stages of development) at the time of the disturbance. Because disturbance history strongly affects stand structure, this example illustrates why disturbance history not only determines susceptibility to subsequent disturbances, but also post-disturbance regeneration. Importantly, although beetle outbreaks historically have primarily affected stands in latter stages of structural development, climate change has intensified outbreaks of bark beetles and weakened tree defenses, together resulting in younger stands in early stages of succession being severely affected by outbreaks (Kulakowski et al., 2012). One critical consequence of this novel phenomenon is that post-outbreak regeneration may become substantially slower than it has been over the past centuries because outbreaks are now occurring in stands without abundant advanced regeneration.

As disturbance severity increases, the role of pre-disturbance vegetation decreases, but does not disappear. Regeneration following even high-severity fires normally depends on seeds or rhizomes because such fires typically kill both canopy and sub-canopy individuals. In such cases, the effects of pre-fire vegetation on post-fire regeneration include variation in the dominance of trees that regenerate via resprouting or serotiny. However, it is important to note that even very high severity fires typically leave some survivors, which can then play a disproportionately large role in post-disturbance regeneration. Pre-fire structure also can shape post-fire substrate and heterogeneity of regeneration niches, with critical implications for post-disturbance forest development.

Post-disturbance regeneration following multiple disturbances in short succession is often quantitatively and qualitatively different from that following single disturbance events (Fig. 2). Understanding regeneration following such compounded disturbances is particularly important as disturbances become larger and more frequent under climate change, thus increasing the likelihood that a given forest is affected by multiple disturbances in short succession. Furthermore, compounded disturbances



Fig. 2 Regeneration following two or more disturbance is often slower than following a single disturbance. In some cases, such compounded disturbances can tip the ecosystem away from forest dominance toward an alternate stable state. Mount Zirkel Wilderness, Colorado. Photo: D. Kulakowski.

can exceed the resilience of some forests and lead to fundamentally different conditions, which may range from a shift in species composition (Gill et al., 2017; Johnstone et al., 2010; Kulakowski et al., 2013) to clear state change of non-forest vegetation (e.g., Buma and Wessman, 2011; Odion et al., 2010; Savage and Mast, 2005). The risk of such tipping points is especially high when post-disturbance climatic conditions are not favorable to the regeneration of native tree species.

Shifts in species composition following compounded disturbances in the Rocky Mountains have involved a change from dominance of conifers (that regenerate exclusively from seed) to dominance of angiosperms (specifically aspen (*Populus tremuloides*) that regenerate vegetatively). Interestingly, because aspen are less susceptible to most types of disturbance in the region, such a change in species composition may represent disturbance-mediated adaptation to climate change involving negative feedbacks that may reduce fire and other disturbances (Kulakowski et al., 2013). From the perspective of post-disturbance management, an additional difficulty stems from the fact that regeneration following compounded disturbances is more variable and less predictable than following individual disturbance. Thus, observed regeneration in the initial years following compounded disturbance can be a poor predictor of disturbance one or two decades later (Gill et al., 2017).

Compounded disturbances can occur for several distinct reasons—(1) similar underlying drivers of two or more disturbances increasing the frequency or extent of both disturbances, as with bark beetle outbreaks and fires (e.g., Mietkiewicz and Kulakowski, 2016); (2) an initial disturbance increasing the likelihood of a secondary disturbance, as with windstorms and insect outbreaks; or (3) a natural disturbance being followed by post-disturbance logging. Although tree cutting following disturbances is a common management response, from an ecological perspective, this practice can be considered a compounded disturbance that often magnifies the severity of the initial disturbance (Fig. 3). The increase in total disturbance severity is largely associated with intentional or accidental (e.g., caused by heavy machinery) mortality of individuals that survive the initial disturbance.

Managing Forest Disturbances

Appropriate forest management depends on ecological and social spatiotemporal context. The former refers to the particular requirements of species and ecosystems and the latter refers to social desires for the ecosystem in question (e.g., wilderness, timber production, etc.). Forests provide multiple ecosystem services, including those related to biodiversity, carbon, water, timber, protection from natural hazards, recreation, and spiritual values. Many of these services are mutually compatible and management can often promote multiple ecosystem services in the same forest. Although disturbances, especially large and severe ones, can be challenging from a management perspective, it is often possible to incorporate disturbances into management plans.

The ecological benefits of disturbances are well known (e.g., Stephens et al., 2013). Ecological disturbances can create spatial heterogeneity (e.g., variation in the amount and arrangement of surviving forest patches or trees) that can promote biodiversity, primary production, wildlife habitat, hydrogeologic protection, and ecosystem resilience (Johnstone et al., 2016; Seidl et al., 2014). Furthermore, variability of tree, stand, and landscape patch conditions can modulate disturbance size and severity and increase the likelihood of survival of individual or groups of trees (Buma and Wessman, 2011; Kulakowski et al., 2003; Kulakowski and Veblen, 2002) that subsequently can be important in post-disturbance regeneration. By contributing to forest resilience, spatial heterogeneity also facilitates ecological adaptation to future environmental change and helps sustain important ecosystem services (Turner, 2010). Consequently, a common goal of recent management is to increase structural diversity and other attributes of heterogeneity,



Fig. 3 Logging and associated road building following natural disturbances compounds and often intensifies the severity of the initial disturbance. Zakopane, Poland. Photo: D. Kulakowski.

in part as a safeguard for future conditions (Schütz, 2002). Post-disturbance logging often limits potential disturbance-created heterogeneity (Thorn et al., 2017) and reduces natural post-disturbance regeneration (Beghin et al., 2010).

Windthrow and insect outbreaks increase dead wood and light availability and, as a consequence, the abundance and diversity of many insect, plant, bird, and mammal species (Thorn et al., 2017). Disturbances can also introduce structural complexity in regions where long and intensive land use has homogenized landscapes and reduced the extent of structurally complex old-growth and structurally complex early-seral forests (DellaSala et al., 2017). Consequently, the role of natural disturbances in restoration has long been recognized in many different ecosystems (Noss et al., 2006; Turner et al., 2003). Restoration activities to create late seral conditions frequently involve felling and girdling trees to create snags—mimicking some of the effects of natural disturbances (Halme et al., 2013; Seibold et al., 2015). Selective post-disturbance logging (Priewasser et al., 2013) can maintain some ecologically important structural characteristics. However, soil compaction, soil nutrients, coarse woody debris, structural diversity, biological legacies, amount of surviving post-disturbance regeneration, and establishment of new post-disturbance regeneration are substantially different in most forests that have been clear-cut or logged following natural disturbance compared with forests that have been affected only by natural disturbance (Lindenmayer, 2009; Lindenmayer and Noss, 2006).

While disturbances often promote heterogeneity, if disturbances are too large, severe, or frequent, legacies of the pre-disturbance system may be lost and the ability of affected ecosystems to regenerate may be compromised (Kuuluvainen et al., 2017). This loss can shift ecosystems to alternate stable states, sometimes over extensive areas (Johnstone et al., 2016). Consequently, for management it is essential to understand the range of variability of disturbances that promote resilience, as well as identify the threshold beyond which disturbances may compromise it. Similarly, it is important to understand how resilience may be changing as a result of climate change (Seidl et al., 2017). Increased warming may intensify disturbance events, alter post-disturbance regeneration, and result in novel ecosystems including even non-forest alternate stable states. Tipping points are most likely to be crossed as a result of extreme climate events that increase the size, frequency, and intensity of disturbances (Allen et al., 2010), compounding events (Buma and Wessman, 2011), and post-disturbance climatic conditions that hinder post-disturbance regeneration (e.g., Harvey et al., 2016; Rigling et al., 2013).

Although disturbances have become larger, more frequent, or more severe because of recent changes in land use and climate (Seidl et al., 2011), in most cases, they do not, in and of themselves, threaten forest persistence (Kulakowski et al., 2017). Disturbances can, however, pose a risk to human populations and challenge forest management. For example, some ecosystem services such as timber production and natural hazard mitigation can be affected negatively by natural disturbances (Thorn et al., 2017; Vacchiano et al., 2014). Furthermore, potential risk to human populations associated with natural disturbances are intensified by urban expansion into forested areas as well as by forest expansion into urban areas. Consequently, in spite of advances in the fields of ecology and forestry, there is strong legal and social pressure to continue to suppress disturbances and control the natural dynamics of disturbed forests (Fares et al., 2015). This command-and-control approach to forest management

will become increasingly difficult to implement in the future as disturbances increase in size, frequency, and severity, which highlights the need for intensified conversations about how societies can coexist with disturbances.

Conclusions

Working with, rather than against, natural processes in managing forests is of paramount importance, especially in light of projected changes in climate (Moritz et al., 2014). Given the inevitability of disturbances in forest ecosystems and the ecological benefits of many disturbances, a key question is whether it is feasible to allow disturbances in some forests to operate as natural ecological processes and if so, how to optimize their ecological benefit while protecting human safety and well-being and maintaining other desired ecosystem services.

Approaches to forest management vary in intensity from passive management to intensive agro-forestry timber production (Duncker et al., 2012). Forest management needs to balance promoting natural processes while meeting societal needs for timber, fiber, and other raw materials (Kuuluvainen and Grenfell, 2012). Promoting natural processes requires an understanding of ecosystem variability in order to define acceptable limits of change. It is important to identify areas where letting natural processes shape forest ecosystems is compatible with other desired ecosystem services.

Disturbances are critical components of forest ecosystems. They cannot be considered in isolation, but rather as distinct and important stages in long-term forest health. By maintaining spatial heterogeneity in cover types, a range of successional stages, and a variety of biogeochemical states (stoichiometric ratios of nutrients and overall stocks) they foster biodiversity and resilience. Eliminating disturbances is neither possible, nor necessarily always desirable. Allowing disturbances, even large ones, to shape some forest ecosystems may promote ecological resilience in the face of climatic and environmental change. In some areas, containment of natural hazards may be of paramount social or economic importance (e.g., closest to homes and towns). However, disturbances can also provide important ecosystem services and can be compatible with multiple goals of forest use, even in densely settled and developed regions. Acceptance and appreciation of natural disturbances by the general public, especially in tightly couple human-natural systems, would facilitate (and may be necessary for) land managers and policy makers maintaining forests in more natural states.

Acknowledgment

We thank A. Hoffman for helpful comments.

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“Real” vs. “Fake” Forests: Why Tree Plantations Are Not Forests

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Abstract

Tree plantations make up some 4% of the world's forests and are increasing as native forests are cut down to meet rising wood product demands. An additional 30% of the world's forests are in “production,” as defined by the Food and Agriculture Organization (FAO) of the United Nations. Compared to native (“real”) forests, plantations (“fake”) are often characterized by genetically modified tree genomes, over simplified forest structures (deficient in snags, down wood, large trees, and understory vegetation), single species monocultures, and greatly altered ecosystem processes (e.g., natural disturbances, hydrology, nutrient cycling, pollination, and food-web dynamics). Existing plantations can be managed to improve ecological integrity by enhancing structures otherwise absent in intensively managed systems. Conversion of native forests to plantations, however, needs to cease along with reducing wasteful consumption, increasing reliance on alternative wood fibers (e.g., hemp), recycling, and the use of engineered wood products that do not come from native forests.

What Exactly is a Forest?

Is a forest merely a collection of trees forming a canopy overstory (i.e., tree cover)? If we plant trees, does that make it a forest? How much of the Earth's forests is planted (more correctly termed “tree farms”)? How do planted forests differ from native forests? Can we meet wood demands while minimizing our ecological footprint?

To begin, when it comes to a forest, we each see what we want.

A forester sees a crop of trees to be extracted for timber-profit as soon as possible—the economic bottom line. An ecologist sees an ecosystem where the parts are interwoven and uniquely sculpted by natural processes; deforestation is antithetical to the sum-of-the parts.

When I take a hike into a native (unlogged) forest, I see a rich tapestry of life. This intimate dance of plant and animal, form and function, process and outcome is lacking in a plantation, especially plantations embedded in a sea of industrialized forestry. A walk in an industrial landscape has a different feel, smell, and much fewer dance partners. Wally Menne, a member of the Timberwatch coalition (<http://www.timberwatch.org.za>), aptly calls timber plantations “fake” forests (<http://wrm.org.uy/oldsite/countries/SouthAfrica/difference.html>). I adopt his terminology to distinguish real from fake, native from plantation, natural from engineered. In science, terminology matters—in this case, do we see forests as living, self-willed ecosystems or a crop to be manipulated for the bottom line?

How Are Forests and Plantations Defined and Counted?

To get at the root of the issue (literally), let's first explore some basic definitions.

Early Forest Definitions

The term “forest” has many origins (<https://en.wiktionary.org/wiki/forest>). From Latin—“foris” means outside and “forestis silva,” wood outside. Old French and Middle English terminology refer to forests as a wooded area kept for hunting. The Proto-Germanic

word is “furho” for fir-pine, and Proto-Indo European “perkus” means oak, to name a few. Ancient European cultures managed forests and woodlands as hunting grounds for royalty while also clearing woodlands for pasture and wood for building materials, heating, smelting, and leather production. Aboriginal peoples applied spiritual connection to forests (e.g., see <http://www.native-languages.org/legends-forest.htm>). In sum, forests and woodlands have been in cultivation for thousands of years, ultimately leading to widespread deforestation (Williams, 2003) and contributing to the collapse of early civilizations (Diamond, 2005). Deforestation and forest degradation is rapidly consuming the world’s native forests (Williams, 2003; Mackey et al., 2014).

Common Forest Definitions

According to Merriam, a forest is “a usually large group of plants and especially trees under cultivation.” The Food and Agricultural Organization (FAO, 2010) of the United Nations defines forest as “a land area of greater than 0.5 ha, with a tree canopy cover of greater than 10%, which is not primarily under agricultural or other specific nonforest land use. In the case of young forests or regions where tree growth is climatically suppressed, the trees should be capable of reaching a height of 5 m in situ, and of meeting the canopy cover requirement” (<https://www.cbd.int/forest/definitions.shtml>). However, FAO’s definition is based on minimum forest cover only (quantity) and lacks attention to forest quality.

Ecological Forest Definitions

Most standard text books of forest ecology (e.g., Perry et al., 2009) define forests as a community of interacting species organized by structural elements and species composition that perform specific functions. Structure refers to the physical aspects of a forest, such as the overstory canopy. Notably, from a structural standpoint, trees can be alive or dead and standing or down. Some forests, such as mature (>80 years) Douglas-fir (*Pseudotsuga menziesii*)/western hemlock (*Tsuga heterophylla*) in the Pacific Northwest are comprised of a continuous, multilayered canopy from the ground up—shrubs, lower, mid, and overstory strata. Composition refers to the actors, the characteristic species and genomes. Functions are the inner workings of a forest that orchestrate processes like photosynthesis, nutrient cycling, carbon sequestration (photosynthesis), disturbance dynamics, and food-web interactions. A native forest has all the parts working together—structure (all age classes especially older), composition (the natives), and function (e.g., natural disturbances, food-web dynamics). It should be noted that a forest is not just a collection of plants. The animals codesign the fundamental elements. For instance, the waste pellets of flying squirrels (*Glaucomys sabrinus*) are packed with fungal spores that inoculate top soil with mycorrhizae fungi that then form underground networks that aid plants in uptake of water, minerals, and vital nutrients (a sort of *Avatar* communication subhighway). Invertebrates aid in decomposition and nutrient cycling. Bats, birds, and insects disperse seeds and pollinate flowers. In turn, these codependent relations determine the structural elements of the forest community (Maser, 1994). When we tinker (or engineer) with the parts in forestry operations, we lose most of the key structural elements, which in turn affects forest relations and functions.

Common Plantation Definitions

Wikipedia defines a plantation as a large-scale farm that specializes in cash crops. In particular, tree plantations (tree farms) have an explicit purpose—high-yield production of wood fiber in the shortest time. This often includes one or two commercially valuable or crop species (e.g., Douglas-fir, *Pinus*, *Eucalyptus*, *Poplar*, *Picea* spp.) (Fig. 1A and B). Tree seedlings are grown in tree “nurseries,”



Fig. 1 (A) Douglas-fir timber plantation (foreground) on US Department of Interior Bureau of Land Management lands in western Oregon showing extensive clear-cuts and plantations (background) within an industrial landscape matrix. (B) Old-growth Douglas-fir/hemlock stand showing vertical (tree-size class variability, snags) and horizontal (shrubs, forbs) complexity. Canopy gaps created by tree fall from natural causes provide diverse successional stages within the forest stand that are not present in plantations. Photo: D. DellaSala.

sometimes genetically manipulated for certain growth features (straight stem, rapid wood accumulation) and resistance to disease. Seedlings are planted in tight rows to maximize yield. In some places (e.g., southeast Alaska), tree planting is not necessary because a natural seed source is available and ideal growing conditions are sufficient without propagation. In other regions (e.g., Indonesia), tree regeneration is not even attempted leading to deforestation and widespread conversion (e.g., palm oil or slash and burn agriculture of the tropics).

The Forest Stewardship Council (FSC) (n.d.) defines plantations as:

forest areas lacking most of the principal characteristics and key elements of native ecosystems as defined by FSC-approved national and regional standards of forest stewardship, which result from the human activities of either planting, sowing or intensive silvicultural treatments (source: FSC-STD-01-001).

FSC Explicitly States That Plantations Include

the use of establishment or subsequent management practices in planted forest stands that perpetuate the stand-level absence of most principle characteristics and key elements of native forest ecosystems will result in a stand being classified as a plantation. ... Except for highly extenuating circumstances the following are classified as plantations: cultivation of exotic species or recognized exotic sub-species; block plantings of cloned trees resulting in a major reduction of within-stand genetic diversity compared to what would be found in a natural stand of the same species; cultivation of any tree species in areas that were naturally non-forested ecosystems.

Site Preparation

Preparing a site for a plantation often involves the use of herbicides to reduce tree competition with shrubs and other noncommercially valuable species. Plantation management can include fertilizers and pesticides to enhance tree growth and reduce tree mortality. After the dense tree canopy closes (1–2 decades depending on site factors—i.e., “pole” stage), this is often followed by precommercial thinning (although some commercial value is possible as pulp or woody biomass) to reduce competition among tree stems. Decades later a commercial thin can be performed to further reduce competition and extract economic value. Once past the point of maximum growth (referred to as cumulative mean annual increment), trees are then logged again to maximize profit and jumpstart the commercial process (note: some landowners may skip the culmination phase and harvest trees even sooner). Fast growing trees on short logging rotations replace the diversity of natural successional stages with fake forests kept in a perpetual stage of young growth, clearcut harvest, and regrowth.

Planted Forest

According to FAO (2010), forest plantations are a subset of planted forests consisting primarily of introduced species that make up nearly 4% of total forest area, or 140 million hectares globally. Productive forest plantations, primarily established for wood and fiber, account for 78% of forest plantations, and “protective” forest plantations, primarily established for conservation of soil and water, 22%. The area of forest plantations increased by about 2.8 million hectares annually from 2000 to 2005, 87% of which is productive forest plantation. Additionally, while not plantations per se, FAO (2015) reports 1.2 billion (30%) of ~4 billion hectares of forests world-wide are in “production” (Fig. 2). As noted, FAO defines a forest as having tree cover >10%.

Carle and Holmgren (2008) define “planted forests” as: (1) forests of native species established through planting, seeding, or coppice of planted trees; (2) forests of introduced species, and in some cases native species, established through planting or seeding mainly for production of wood or nonwood goals; and (3) forest of native or introduced species established through planting or seeding mainly for provision of services. They provide an overall estimate of planted forests summed for all three categories and projected forward under different management scenarios (Fig. 3). For instance, planted forest projections show the current global

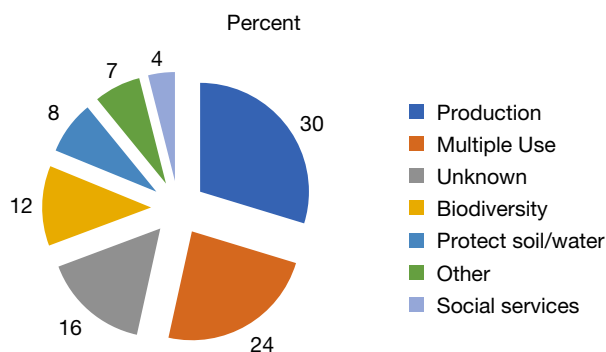


Fig. 2 The world's forests by management category (FAO, 2010).

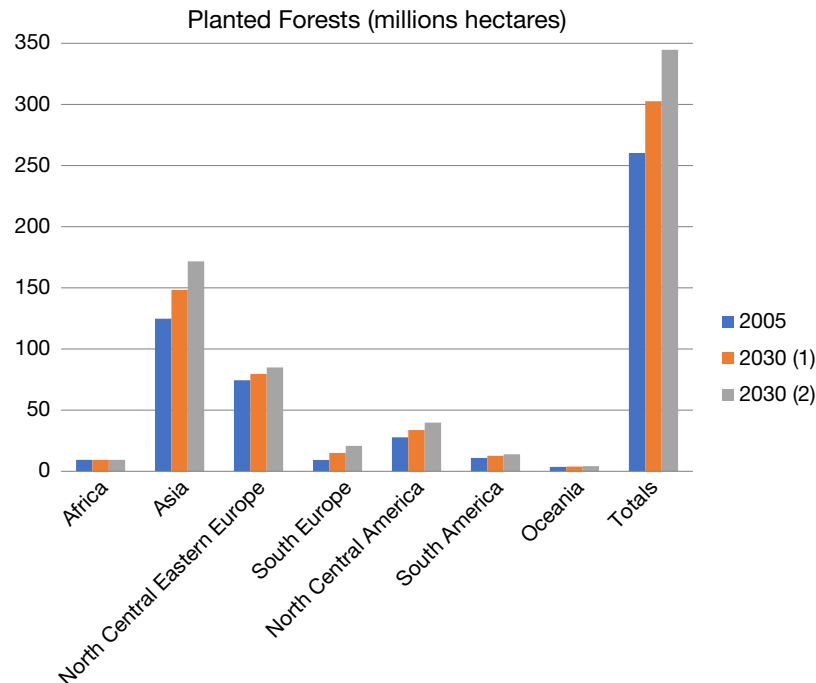


Fig. 3 Area of planted forests ($\times 10^6$ ha) in 2005 (blue) vs. two projected scenarios for 2030 (from Carle and Holmgren, 2008). Scenario 1 (orange) assumes no increase in productivity and the current expansion of planted forests slows down. Scenario 2 (gray, combined scenarios 2 and 3 of Carle and Holmgren, 2008) assumes planted area continues at the current rate and/or increases as a result of genetic modifications and technological improvements.

increase may continue at least until 2030, particularly in Asia (e.g., palm oil production). It can be assumed that, as planted forests increase, so too will deforestation of native forests.

How Do Real vs. Fake Forests Differ Ecologically?

While this article focuses on comparing plantations to native forests, other forest manipulations, such as “seminatural” and “modified natural,” deserve recognition given their global prominence. For instance, Carle and Holmgren (2008) define modified natural as forest naturally regenerated with native species where there are visible signs of human activity. Additionally, seminatural is considered a forest where silvicultural practices are in place for intensive management (e.g., selective or high-grade logging). Thus, the level of human intervention can be illustrated along an ecological integrity gradient from highest (native) to lowest (plantation; Fig. 4). Integrity refers to native species, functions, and processes expected for a specific ecosystem type based on historic or reference conditions.

Regional and site-specific factors need to be considered in any comparison of fake vs. real forests; however, some general patterns emerge (Table 1). Real forests are much more complex at all levels of biological organization: genetic (genomes are highly variable compared to nursery “stock”), native species richness, and ecosystem processes—the latter both above and below ground. In this case, the sum-of-the-ecosystem parts is greater than the whole while plantations sum to much less than the whole.

Can Plantations Be Managed (Restored/Enhanced) for Ecological Integrity?

The first principle of restoration is to stop the loss (hemorrhaging) of integrity before it even happens—that is—conversion of real to fake. However, for plantations already in production and lacking key elements, restorative actions can make plantations as “seminatural” as possible by planting with diverse native seeds and enhancing structures present on site. For instance, forest thinning (e.g., precommercial) in a dense stand of young trees (thicket or “dog-hair” stands) can enhance structural diversity by opening forest canopies to increased sunlight that stimulates understory development (Fig. 5A and B). Girdling (killing) trees for snag creation provides nesting, foraging, and dens sites for wildlife, while felling trees and leaving them on site provides downed logs (along with moist microclimates and nutrient cycling) for amphibians, invertebrates, and aquatic species when logs fall into streams. Horizontal diversity also can be enhanced via stops and gaps in thinning (i.e., unthinned trees alternating with created openings). While restoration can improve integrity at the site level, the net effect at the landscape scale is small especially given chronic impacts (e.g., to aquatics) from an extensive road network needed to access plantations (Fig. 6).

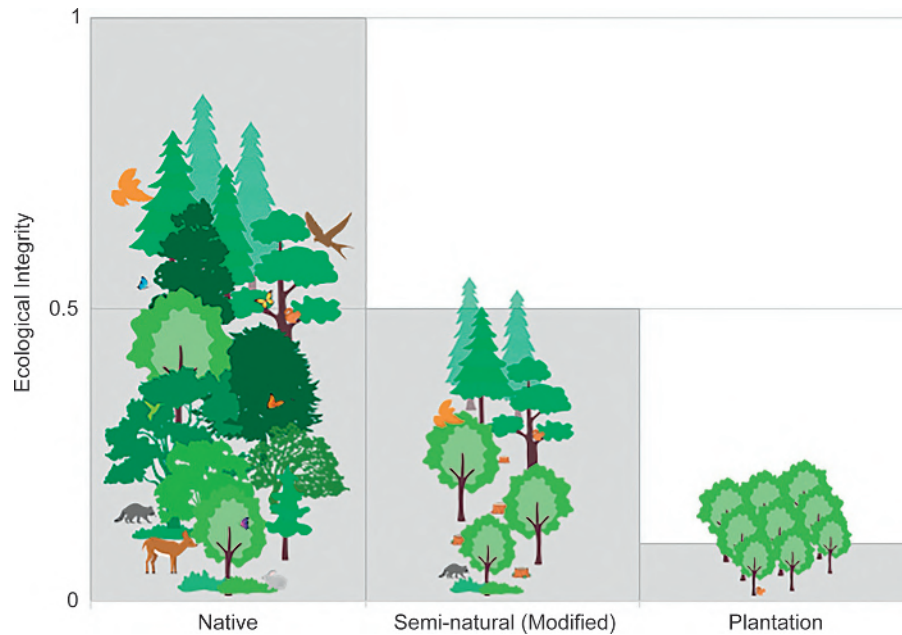


Fig. 4 Hypothetical integrity (native species, structure, function/processes) gradient based on degree of alteration of composition, structure, and function. Graphics created by Freepik, modified by Christina Mills.

Table 1 Generalized characteristics and differences between “real” vs. “fake” forests

Characteristic	Real Forest	Fake Forest
Genetic diversity	Highly varied and adaptive/ resilient to climate change	Greatly simplified and low resilience to climate change
Tree and other plant species richness	Medium-exceptional depending on site factors and forest type (tropical, temperate, boreal)	Low, monoculture
Animal richness	Medium-high-extraordinary (e.g., tropics)	Low
Apex predators	Important habitat	Highly degraded and typically absent
Imperiled species	Important/critical habitat	Highly degraded and typically absent
Soils and below-ground processes	Productive, well-developed soil horizons, soil biota (e.g., decomposers, mycorrhizae, native seed sources), abiotic processes (nutrient cycling, decomposition) (although soil nutrients deficient in tropical rainforests and forests on ultramafic substrates)	Often damaged, depleted and requiring fertilization
Snags and down wood	Abundant with diverse size and decay classes	Scarce/rare
Structural diversity (vertical, horizontal complexity)	Generally abundant depending on site factors, forest types, age classes	Little to none
Forest age classes	Full successional gradient often present at site or landscape scale, especially rare types such as structurally complex young and old growth stages	Even aged
Climatic refugia (e.g., relatively cool, moist microclimates)	Present and functional	Highly altered or absent
Hydrological cycle	Intact	Dysfunctional especially in areas of high road densities
Carbon sequestration and storage	Medium-high-extraordinary depending on site and forest type (carbon sink)	Sequestration but very low carbon stores and limited carbon retention (carbon source initially)
Natural disturbances	Functional (e.g., fires, floods, insects) with many resistant and resilient forest properties	Highly altered with low levels of resilience/resistance often amplifying or compounding natural disturbances (e.g., more intense forest fires due to dense planting of small trees that act as tinder)
Societal benefits	Myriad ecosystem services (multi-functional) but often de-valued (clean air, clean water, recreation)	Economics predominate decision making (one dimensional)
Invasive species, diseases, insect outbreaks	Absent or in low numbers with high levels of resistance	Present or in high numbers with little resistance
Intactness/connectivity (landscape scale)	Corridors, elevation and latitudinal gradients	Highly fragmented especially when combined with roads and industrial-scale logging
Deforestation/degradation pressure	High-extreme pressures across all forest biomes	Highly degraded and likely not being used to relieve pressure to native forests
Integrity (sum of native species composition, function, process)	High to exceptional	very low (see Figs. 2, 3)

Relative differences depend on regional and local site factors, forest types, and management intensity.



Fig. 5 (A) Dense “dog-hair” stand of Douglas-fir that was planted on an industrial landscape after clearcutting coast redwood (*Sequoia sempervirens*) in northern California. (B) Redwood National Park thinning of young Douglas-fir to increase growing space for restoring previously logged redwood stands, the native forest type in this region. Note light penetrance in thinned area. Photo: D. DellaSala.



Fig. 6 Deforestation and roads in Borneo. No amount of restoration can recover this landscape destroyed from cumulative (chronic) effects of industrial logging rampant in Malaysia. Photo: D. DellaSala.

Notably, the FSC has developed 10 principles and related criteria and indicators for forest certification to address ecological, social, and economic interests in forest management. Principle 10, in particular, is specific to plantations ([Appendix 1](#)). FSC assumes plantations managed this way provide necessary wood fiber while reducing pressures to native forests that otherwise would not need to be logged. While this is important in principle and should be encouraged, it is not occurring at a scale sufficient to reduce deforestation globally.

Conclusions

Plantations are fake forests because they lack the integrity of real forests. Fake forests are expanding globally, at the expense of real forests. Notably, it is often claimed that tree plantations have an indirect conservation benefit in reducing pressures to native forests as in the case of New Zealand, where native forest logging has ceased and logging is restricted to existing plantations. However, this is the exception rather than the rule. Nonetheless, *Sedjo and Botkin (1997)* estimated that, in order to meet global demand for wood products, some 5% of the world forests would need to be maintained in plantations. We are nearly at the 5% level, as plantations continue to increase globally along with rising population and consumption levels. Plantation and planted forests are projected to increase or slow down through 2030, resulting in even more deforestation, unless remaining native forests are conserved. Reduction in wasteful consumption, use of alternative wood fibers (e.g., hemp), recycling, and engineered wood products can all play an increasing role in reducing pressures to the world’s native forests. In the meantime, existing plantations can be managed to limit their ecological footprint by enhancing structures, planting with native seed sources, and FSC certification or equivalent management. Moreover, real forests are grossly under-valued for myriad ecosystem benefits and biodiversity values that they provide to society, as pressures to log them continue to mount.

Appendix 1 FSC Principle 10 for Plantation Management (Note: more specific regional guidance, intent, and application is provided by FSC but not included here for simplicity)

Plantations shall be planned and managed in accordance with Principles and Criteria 1–9, and Principle 10 and its Criteria. While plantations can provide an array of social and economic benefits, and can contribute to satisfying the world’s needs for forest products, they should complement the management of, reduce pressures on, and promote the restoration and conservation of natural forests.

C10.1 The management objectives of the plantation, including natural forest conservation and restoration objectives, shall be explicitly stated in the management plan, and clearly demonstrated in the implementation of the plan.

- Indicator 10.1.a Consistent with all the indicators within Principle 10 and requirements of Principle 7, the management plan contains clear descriptions of the management goals and prescriptions for plantations on the FMU (forest management unit), of the rationale for plantation management within the FMU, and the relationship between the plantations and natural forest conservation and restoration objectives within the unit.
- Indicator 10.1.b The forest owner or manager demonstrates clear progress in implementation of the components of the management plan addressing natural forest conservation and restoration objectives as they pertain to plantation management.

C10.2 The design and layout of plantations should promote the protection, restoration and conservation of natural forests, and not increase pressures on natural forests. Wildlife corridors, streamside zones and a mosaic of stands of different ages and rotation periods shall be used in the layout of the plantation, consistent with the scale of the operation. The scale and layout of plantation blocks shall be consistent with the patterns of forest stands found within the natural landscape.

- Indicator 10.2.a For plantations established on soils capable of supporting natural forests, harvest units shall be arranged to provide or maintain areas of vegetative cover that allows populations of mid to late successional and sedentary native plant and animal species to survive or be reestablished within the plantation.
- Indicator 10.2.b New plantation establishment does not replace, endanger, or otherwise diminish the ecological integrity of any existing natural ecosystems on the FMU, including primary, natural, or seminatural forests on the FMU. Note that restoration plantations may be established on degraded forests.
- Indicator 10.2.c In all regions except the Pacific Coast, openings lacking within-stand retention are limited to a 40-acre average and an 80 acre maximum. Harvest openings larger than 80 acres must have retention as required in Indicator 10.2.d and be justified by credible scientific analysis. The average for all openings (with and without retention) does not exceed 100 acres. Departures from these limits for restoration purposes are permissible but also must be justified by credible scientific analysis.
- Indicator 10.2.d On openings larger than 80 acres that are justified by credible scientific analysis, live trees and native vegetation are retained in a proportion and configuration that are consistent with the characteristic natural disturbance regime in each community type, unless retention at a lower level is necessary for restoration purposes.
- Indicator 10.2.e In all regions except the Southeast, before an area is harvested, regeneration in adjacent forested areas (either natural forest or plantation) on the FMU must be of the subsequent advanced successional habitat stage, or exceed 10 ft in height, or achieve canopy closure along at least 50% of its perimeter.

C10.3 Diversity in the composition of plantations is preferred, so as to enhance economic, ecological and social stability. Such diversity may include the size and spatial distribution of management units within the landscape, number and genetic composition of species, age classes and structures.

- Indicator 10.3.a Plantation management alone or in combination with natural forest management contributes to the economic stability of the local community, or helps the owner maintain the property as a working forest.

- Indicator 10.3.b On plantations established on soils capable of supporting natural forests, the forest owner or manager maintains, conserves, and/or restores forest health and diversity, including wildlife habitat and soil productivity, by maintaining appropriate diversity of size, structures, age classes, species and genetics across the plantation FMU.

C10.4 The selection of species for planting shall be based on their overall suitability for the site and their appropriateness to the management objectives. In order to enhance the conservation of biological diversity, native species are preferred over exotic species in the establishment of plantations and the restoration of degraded ecosystems. Exotic species, which shall be used only when their performance is greater than that of native species, shall be carefully monitored to detect unusual mortality, disease, or insect outbreaks and adverse ecological impacts

- Indicator 10.4.a Species shall be used for planting that are suitable and appropriate to the site and are consistent with maintaining FMU health and productivity. Species native to the region are preferred to other species (not native to the region).
- Indicator 10.4.b For the Northeast, Ouachita/Ozark, Rocky Mountain, Southwest, Pacific Coast and Lake States regions, the use of exotic species (i.e., species not native to the region) is contingent on credible scientific analysis confirming that the species in question is non-invasive, will not create significant risk to forest health, and performs better than species native to the region. If exotic plants are used, their provenance and the location of their use are documented and their ecological effects are monitored.

C10.5 A proportion of the overall forest management area, appropriate to the scale of the plantation and to be determined in regional standards, shall be managed so as to restore the site to a natural forest cover.

- Indicator 10.5.a Areas of forest and/or plantation to be restored to natural conditions are chosen through a landscape analysis that focuses on enhancing principle characteristics of the native ecosystem or providing important ecological benefits at the stand or landscape level.
- Indicator 10.5.b Areas to be restored to natural conditions are prioritized where the analysis indicates the greatest conservation gain and are designed for long-term restoration.
- Indicator 10.5.c Management plans should clearly state the extent and location of areas selected for such restoration, as well as the rationale for their selection.
- Indicator 10.5.d Areas of forest and/or plantation to be restored or maintained as natural forests are managed to provide a diversity of community types, wildlife habitats, and ecological functions native to the site.
- Indicator 10.5.e The ratio and spatial distribution of plantations, with respect to natural and seminatural forests, maintains and/or restores the landscape diversity of community types, wildlife habitats, and ecological functions similar to a mosaic of natural forests.
- Indicator 10.5.f Where natural ecosystems were previously converted to plantations, a percentage of the total area of the FMU must be maintained and/or restored to natural or seminatural cover. The minimum percentage area that is maintained and/or restored in natural or seminatural state is:
 - For 100 acres or less, at least 10%.
 - For 101–1000 acres, at least 15%.
 - For 1001–10,000 acres, at least 20%.
 - For >10,000 acres, at least 25%
- Indicator 10.5.g All plantations on forest soils on public lands are managed to restore and maintain natural forest vegetation, structure, function, and habitats, and fully meet, at the earliest possible time, all aspects of Principles and Criteria 1–9 that are relevant to natural forests for the area.

C10.6 Measures shall be taken to maintain or improve soil structure, fertility, and biological activity. The techniques and rate of harvesting, road and trail construction and maintenance, and the choice of species shall not result in long term soil degradation or adverse impacts on water quality, quantity or substantial deviation from stream course drainage patterns.

- Indicator 10.6.a Forest operations do not result in long-term adverse impacts to soil productivity, water resources, and hydrology. Soil disturbance is minimized during road/trail work and site preparation, and site preparation is done in accordance with BMPs.
- Indicator 10.6.b Tree seedlings are planted in a way that minimizes damage to the soil, while facilitating seedling survival. Tree seedling species are selected appropriate for maintaining long-term site productivity.
- Indicator 10.6.c Thinning is implemented in a manner that minimizes site disturbance and damage to the residual stand of crop trees and other desired vegetation (See Criterion 6.5).
- Indicator 10.6.d Fertilizer is applied only when all the following conditions are met:
 - Soil classification or foliar analysis indicates one or more nutrients are a limiting factor for forest productivity. Data and/or scientific literature suggest that the response to fertilization is economically justified. Where necessary due to topography, soils, or other conditions, measures are taken to prevent damage from fertilizer runoff or leaching. This includes preventing influences on native low-nutrient ecological systems, such as pitcher plant bogs, or on ground and surface water quality. Fertilizer application maintains or enhances soil condition and site productivity.
- Indicator 10.6.e Sufficient woody debris and other organic matter is retained within plantation stands to ensure adequate soil structure and nutrient recycling.

C10.7 Measures shall be taken to prevent and minimize outbreaks of pests, diseases, fire and invasive plant introductions. Integrated pest management shall form an essential part of the management plan, with primary reliance on prevention and biological control methods rather than chemical pesticides and fertilizers. Plantation management should make every effort to move away from chemical pesticides and fertilizers, including their use in nurseries. The use of chemicals is also covered in Criteria 6.6 and 6.7.

- Indicator 10.7.b A strategy is in place to control fire damage. Where applicable, prescribed burns are conducted according to BMPs and with adequate planning, equipment, training and weather conditions to maintain control of the burn within the burn plan area.
- Indicator 10.7.c The forest owner implements a strategy to prevent or control invasive species, as noted in Indicator 6.3.h

C10.8 Appropriate to the scale and diversity of the operation, monitoring of plantations shall include regular assessment of potential on-site and off-site ecological and social impacts, (e.g. natural regeneration, effects on water resources and soil fertility, and impacts on local welfare and social well-being), in addition to those elements addressed in Principles 8, 6 and 4. No species should be planted on a large scale until local trials and/or experience have shown that they are ecologically well-adapted to the site, are not invasive, and do not have significant negative ecological impacts on other ecosystems. Special attention will be paid to social issues of land acquisition for plantations, especially the protection of local rights of ownership, use or access.

- Indicator 10.8.a Monitoring of the impacts of plantations, both on and off-site, is conducted in the same manner as the monitoring of natural forests, in accordance with Principles 4, 6, and 8.

C10.9 Plantations established in areas converted from natural forests after November 1994 normally shall not qualify for certification. Certification may be allowed in circumstances where sufficient evidence is submitted to the certification body that the manager/owner is not responsible directly or indirectly of such conversion.

- Indicator 10.9.a For plantations established in areas converted after 1994, the forest owner or manager demonstrates to the CB that the manager/owner was not directly or indirectly responsible for the conversion of the natural forest to the plantation.
- Indicator 10.9.b For plantations established in areas converted after 1994, the forest owner or manager develops and implements a plan to restore the plantation stands to conditions characteristic of natural forests and to manage those stands in compliance with all Indicators of Principles 1–9 as quickly as feasible.

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The Neotropical Rainforests

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Abstract

The Neotropical rainforests combine to form the largest expanses of rainforest on the planet. Holding the highest levels of biodiversity on earth, the Neotropical rainforests range from southern Mexico and the Caribbean to Brazil and Bolivia. Found below 500 m elevation, lowland rainforests are characterized by a tall canopy with emergent trees extending above it and multiple layers of vegetation below. The isolated evolution of floras and faunas in North and South America and the eventual connection of the two continents led to the great “American Interchange” of species, contributing to the high diversity of both. Although they can be broken down into four regions (Amazon, Atlantic/Paraná, Chocóan, and Mesoamerican/Caribbean), when combined the rainforests of the Neotropics are greater in extent than any other rainforest ecosystems. Serious threats to the Neotropical rainforest come from agricultural frontiers driven by both cattle ranching and crop agriculture and resulting in clearing of large expanses of forest. Forest loss is exacerbated by and contributes to climate change, with increases in drought, forest fire, and hurricane severity all further imperiling the forests. However, there are positive advances in conservation of the Neotropical rainforests, with some countries leading the way and increased grassroots and indigenous engagement leading to a promise of better protection of the monumentally important rainforests of the Neotropics.

Introduction

Hyperdiverse, expansive, and increasingly threatened, the Neotropical rainforests are both the terrifying jungles that struck fear into early European explorers and the biological wonders that amaze scientists today. Since long before European intervention, they have been both the irreplaceable context to local cultural traditions and crucial to global climate function. Neotropical rainforests are found in the Americas, ranging from southern Mexico and the Caribbean Islands south to Bolivia (Fig. 1). Their geography in the “New World” (Neo, from Greek *neos* means new) is not the only aspect that distinguishes them from the other rainforests of the world. They contain a large proportion of the earth’s biodiversity, including holding the most species-rich locations on the planet, on the eastern slope of the Andes mountains. Although the Amazon basin rainforests are the best known of the Neotropical rainforests, there are several other distinct regions, including the Mesoamerican and Caribbean rainforest, the Chocóan rainforest of Colombia, Panama and Ecuador, and the Atlantic and Paraná rainforest of coastal Brazil (Fig. 1).

Tropical rainforests are defined biogeoclimatically by receiving at least 2000 mm of rainfall each year and occurring between 23° 27' N latitude and 23° 27' S latitude. Lowland rainforests, below 500 m elevation comprise the largest extent of Neotropical rainforests. Between 500 and 1700 m, premontane rainforests are found, and montane cloud forests occur from around 1200 and 1700 m. Species do not recognize these divisions but have their own habitat limitations, thus lowland, premontane, and montane forests share some species as well as having their own unique assemblages. The focus of this entry will be on Neotropical *lowland* rainforests.

Rainforests are characterized by different layers of vegetation: understory, mid-level, canopy, and emergent. In the Neotropics, canopy height is typically 30–50 m, but giant trees called “emergents” rise above the canopy and reach well over 50 m tall (Fig. 2). Like other tropical rainforests, herbaceous vines and woody vines called “lianas” are ubiquitous, with larger lianas indicating a relatively undisturbed forest. The understory is filled with tree saplings along with a diverse community of woody and herbaceous monocots, with high species richness in the families Arecaceae (palms) and Heliconiaceae (heliconias). The lowest layers receive relatively little light and growth of tree seedlings and saplings in closed canopy conditions is very slow. Treefall gaps and the pioneer species that take advantage of them play an important role in maintaining diversity of Neotropical rainforests. The complex, layered structure of the forest plant communities allows for a multitude of niches for animals to occupy, one of the key reasons that rainforest faunas are the most diverse on the planet.



Fig. 1 Lowland rainforest regions of the Neotropics, indicating the extent of where rainforests occurred historically. Figure prepared by Joel T. Betts using Ecoregions 2017 shapefiles for forest delimitation (Dinerstein et al., 2017) and ESRI, USGS, and NOAA basemaps.



Fig. 2 Rainforest canopy in southeastern Nicaragua still undergoing regeneration 20 years after hurricane impact. Photo by G. R. Urquhart.

Rainforests of the Americas have the most tree species at low densities (<2 stems >10 cm dbh per hectare) of any ecosystem in the world. There is high plant diversity at the local scale (alpha diversity) and high diversity between sites (beta diversity). Overall there are an estimated 50,000 plant species in the Amazon Basin alone (Hubbell et al., 2008). A single hectare of Amazonian rainforest may contain over 300 tree species and 900 vascular plant species (Balslev et al., 1998). A 50-ha plot on Panama's Barro

Colorado Island has over 650 woody species, with over 500 species of trees over 10 cm diameter at breast height (Condit et al., 2005). Even though high diversity and low species density are the norms for lowland Neotropical rainforests, some forests are noted for having a single species overrepresented. The Sarapiquí region of Costa Rica, where La Selva Biological Station is located, is known for its high densities of *Pentaclethra macroloba*, yet still maintains high overall beta diversity.

Biogeographical Distribution

Lowland rainforests are distributed across the Neotropics where sufficient rainfall occurs. Larger Caribbean islands with consistent rainfall have rainforest, with large expanses found on Puerto Rico, Hispaniola, Cuba, Jamaica, and Trinidad and Tobago. The Caribbean Coasts of Mexico, Central America, and northern South America have extensive rainforests, and the Atlantic coast of Brazil is home to unique Atlantic rainforest. Along the Pacific Coast of Central America some rainforest occurs, but due to prevailing winds and orographic lifting, much of the Pacific side of Central America is tropical dry forest. The Darién of Panama and the Pacific lowlands of Colombia and Ecuador are home to the distinct Chocó rainforest ecoregion. Finally, the Amazon watershed from the foothills of the Andes to the mouth of the mighty river is extensively covered in rainforest, with several unique ecoregions making up the largest tropical rainforest on earth.

Prevailing “easterly” winds in the Neotropics blow primarily from east to west, with slight variation as northeasterly or southeasterly based on the position relative to the Intertropical Convergence Zone (ICTZ). To the north of the seasonally-shifting ICTZ, winds blow from northeast to southwest, and to the south they blow from southeast to northwest. The typically northeasterly winds of Central America thus make landfall on the Caribbean Coast carrying moisture absorbed over the sea, depositing rain as they move inward. Mountain ranges that cause uplift of moist air are further responsible for rainfall patterns, leading to heavy rainfall on the eastern side of Central American mountain ranges.

The lowland rainforests of North and South America have many distinct forms. In areas where flooding is not a regular occurrence, “terra firme” forests grow. While there is no typical terra firme forest that characterizes the Neotropics, there are shared characteristics. Terra firme forests are dominated by broad-leaved evergreen trees that often reach incredible size. Trees typically have smooth trunks and buttressed roots. Tree limbs are in the upper third of the tree where they can access sunlight that reaches the canopy. Terra firme forests often have very poor soil quality, with heavy clays and little topsoil. Leaf litter decays almost as soon as it reaches the forest floor, creating a rapid nutrient cycle with little accumulation of nutrients in the soil. The overall root system is shallow because both nutrients and water are most available near the surface. Terra firme forests have very high alpha (local) and beta (regional) diversity.

Seasonal flooding produces different types of rainforests. Along the Amazon, two types of “flooded forest” exist: Igapó and Varzea. Floodplain forests like these comprise about 4% of the Amazon basin. The Igapó forest is found along blackwater rivers and flooding extends high into the Igapó during parts of the year. The Varzea is associated with “whitewater” rivers, those in the Amazon that carry high sediment load. In both types, fish enter the forest itself during flooding, and many fish species are involved in fruit consumption and seed dispersal. The large Pacu, a type of tetra and best known of the seed-eating fish, has the ability to crush large seeds with strong teeth and throat plates. The other major drainage of tropical South America, the Orinoco River system, has similar types of flooded forests.

In Central America, the Colombian Chocó, and the Amazon Delta, seasonally inundated forests are often dominated by the large palm, *Raphia taedigera*. This sole native representative of a largely African genus has leaves reaching 18 m in length, and was once thought introduced by European trade. Neotropical palm swamps are not only formed by *Raphia*, but *Mauritia flexuosa* also forms large monodominant stands along tributaries of the Amazon and Orinoco rivers.

Historical Biogeography: Creation and Isolation of the Neotropics

Africa and South America were once merged as a massive land form called West Gondwana, a subsection that broke off of the larger Gondwanaland supercontinent. Before West Gondwana split, a large contiguous rainforest spread over much of the megacontinent. The split of Africa and South America occurred around 110 million years ago (mya), before many of the modern families of plants and animals emerged. Thus, groups like the “New World Monkeys” evolved after the split of West Gondwana, in isolation from their counterparts in the Old World.

South America was an isolated continent for approximately the next 100 million years. North America and South America existed in isolation from each other until around 2.8 mya when the Central American isthmus closed the gap in western Panama (O’Dea et al., 2016). Thus, distinct floras and faunas evolved in the two regions and the great “American Interchange” occurred when the isthmus formed a land bridge. Locations in southern Central America, like Costa Rica and Panama, show a high proportion of species from both continents.

Groups that evolved in South America include the cavimorph rodents (pacas, guinea pigs, capybaras), the New World monkeys with their prehensile tails, smaller cats in the genus *Leopardus*, and the *Heliconia* herbs. North America produced the even-toed ungulates like peccaries and deer and the large cat species. Once the land bridge was completed, these spread into the new continent. Although 2.8 million years have passed since they spread northward, cavimorph rodents have not extended outside of the Mesoamerican tropical forests into North America’s other ecosystems. Conversely, an amazingly adaptable large cat, the puma

(*Puma concolor*), colonized the rainforests of South America and eventually extended as far south as the temperate biomes of Tierra del Fuego.

Biodiversity

Species richness in the Neotropical rainforest can be higher than any other location on earth, with eastern Ecuador, Peru, and Colombia having the highest local biodiversity. Colombia is home to ~18% (>1800 species) of the earth's bird species with only 0.02% of the earth's land surface. Ecuador is home to ~15% of the bird species in an even smaller land area. Although Colombia and Ecuador are home to a wide variety of ecosystems, which explains some of the diversity, the lowland rainforest bird diversity is particularly high, in part because both Colombia and Ecuador are home to lowland rainforests in the Amazon and the Chocó regions, each of which has unique taxa and many related but distinct species.

Insect diversity is extremely high in the Neotropical rainforests. Erwin (1982) found 955 beetle species on a single tree species (*Luehea seemanni*) in Panama. From this extreme diversity, he recalculated the upper bound for how many species of arthropod may exist on earth, and other scientists extended his estimates to claim that there may be 50 million species on the planet. The key to Erwin's and other arguments lies in the extreme diversity of trees in the tropical rainforest and the host-specificity of many insects.

Many hypotheses exist for the high species richness in the tropics (Chazdon and Whitmore, 2002), but none singularly can explain the immense biodiversity of the Neotropical rainforest. Three major factors contribute to high species richness in the Neotropics: (1) the immense geographical extent of the Neotropical rainforest, especially the contiguous Amazon basin; (2) the floral and faunal exchange between the North American and South American biotas; and (3) the Andes and other mountains and elevational gradients.

Neotropical rainforests extend over a greater geographical area than any other tropical rainforest region. The Amazon basin holds over 60% of the world's remaining tropical forests (Laurance et al., 2005) and an estimated 50,000 plant species (Hubbell et al., 2008). The 5.3 million square kilometers of closed canopy forest in the Amazon is equivalent to the size of western Europe, constituting the single largest rainforest on earth. The small geographic ranges of many species in the Neotropics mean that over the great extent of the Amazon, several similar but unique species are encountered.

The floral and faunal interchange that took place after the completion of the isthmian land bridge in Panama strongly contributes to the biodiversity of Neotropical rainforests. South American species migrated northward and North American species spread into the southern continent. This mixing of already diverse floras and faunas contributes to the incredibly high diversity found in northern South America.

Elevational gradients are well known to increase diversity because species specialized for certain elevations will overlap at transitional elevations. The mountain ranges that form the sierras of Central America and the Andes of western South America create elevational gradients that lead to specialization. It is no surprise that the most diverse regions on earth are the foothills of the Andes in eastern Ecuador and Peru.

Important Species and Biological Groups

Neotropical rainforests are home to thousands of notable and unique species. Stunning flowers, colorful butterflies, charismatic mammals, and countless other organisms all contribute to the splendor of the rainforest (Fig. 3). To highlight some of the more notable groups and species, examples from different taxa are described below. Those selected below serve only to highlight some of the unique groups and are in no way intended to say that those chosen are more important than other organisms.

Fungus: *Vesicular arbuscular mycorrhizae* (VAM): Mycorrhizal fungi live in association with plant roots and provide a vast underground network of hyphae allowing the movement of nutrients necessary to support the tree growth of the forest. Although ectomycorrhizae that ensheath the tree roots are most prevalent in the Dipterocarp rainforests of southeast Asia, the rainforests of the Neotropics are more dependent on endomycorrhizae. Vesicular arbuscular mycorrhizae are a form of endomycorrhizae that are typified by an extensive branching network and penetration of hyphae into the roots of plants. Through the penetration of the roots, VAM distribute vital nutrients (especially phosphorus) absorbed from decomposition to the tree roots and withdraw sugars from the tree roots, providing energy for their growth. This mutualistic association is arguably the most important biological interaction in the Neotropical rainforest.

Plants: *Palms*. The vast majority of biomass in the Neotropical rainforest is plant matter, with trees comprising the bulk of this. From tiny epiphytic orchids to massive emergent trees, plants of all shapes and sizes fill the forest. It is difficult to choose one group that represents the standout among Neotropical plants, but palms (Arecaceae) are one of the most diverse groups and contribute unique ecological roles in the rainforest. Ranging from understory genera like the diminutive *Chamaedorea* to the massive *Mauritia flexuosa* (up to 35 m tall), palms are found in every type of Neotropical rainforest. *Mauritia* and *Raphia taedigera* form monodominant stands in their preferred habitats, with *Raphia*-dominated swamps in Caribbean Nicaragua and the mouth of the Amazon covering thousands of contiguous hectares. Inside the forest, small palms combine with other monocots to dominate the understory. Multiple species of birds depend on their fruits the palms depend on the birds for seed dispersal.

Insects: *Leafcutter Ants* (*Atta* spp.) (Fig. 3A). There may be as many as 10 million species of arthropods in the Neotropical rainforest, with countless species playing important roles. However, none match the magnitude and scale of impact that leafcutter



Fig. 3 Representative species of the Neotropical Rainforest. (A) Leafcutter ants (*Atta cephalotes*) are a very important insect species in the ecology of the rainforest (photo by J. P. Lawrence). (B) Three-toed sloths (*Bradypus variegatus*) represent a unique evolutionary line in the Neotropics as seen here in an important pioneer tree genus, *Cecropia* (photo by G. R. Urquhart). (C) Poison dart frogs like this *Oophaga pumilio* from Escudo de Veraguas, Panama are highly visible members of the herpetofauna in the Neotropics (photo by J. P. Lawrence). (D) The White-necked Jacobin (*Florisuga mellivora*) is a hummingbird in the family Trochilidae, a New World family of birds Photo by B. G. Urquhart.

ants have on the Neotropical rainforest. Leafcutter ants clip leaf fragments (around 1 cm round) from plants throughout the layers of the tropical forest, including the high canopy. The ants transport leaf fragments to a massive underground nest along cleared “highways” constructed by the ants. In the underground nest chambers, another caste of ants scrapes the waxy cuticle from the leaves and spreads spores on the fragment to raise a fungus that serves food for the colony. Ants harvest the fungus as food and feed it to developing larvae. The importance of leafcutter ants comes not from this unique fungus farming relationship, but from the massive relocation of nutrients that the ants perform, moving leaf material from aboveground to their belowground chambers. The leafcutters harvest a sizeable amount of the biomass production, with estimates of as high as 17% of total leaf production harvested by the ants (Cherrett, 1986).

Amphibians: Poison Dart Frogs (Fig. 3C). Amphibians play a minor role in the overall ecology of a forest, but some species stand out as unique for their remarkable survival strategies. The poison dart frogs of the family Dendrobatidae are an example of extreme aposematic coloration combined with other selective forces leading to a rainbow of colors both between and within species (e.g., *Oophaga pumilio*). The poisonous frogs of the Dendrobatidae (not all members of the family are poisonous) collect poisons from the arthropod species they consume and physiologically move the plant-derived, arthropod-vectored alkaloid toxins to the surface of their skin. Some species are highly toxic, with the Batrachotoxin found in the genus *Phyllobates* considered one of the most toxic substances known.

Reptiles: Green Iguana. Reptiles of the Neotropical rainforest are highly varied, with venomous snakes and giant anacondas receiving the most public attention and small *Norops* lizards being the most numerous. The Green Iguana (*Iguana iguana*) is a very large lizard, reaching lengths of 2 m including the tail. Remarkable about the Green Iguana is that it is completely herbivorous. It spends a great deal of time in the forest canopy, where it is one of the most important herbivores. Iguanas come to the ground to burrow a nest into riverbanks and other suitable soil. The bright green hatchlings are heavily preyed upon by many species.

Fish: The Characiphysi Fish. The Characiphysi clade of fish includes the orders Siluriformes (catfish), Characiformes (piranhas and tetras, over 1200 species in the Americas), and Gymnotiformes (knifefish). These fish possess the specialized Weberian Apparatus that connects vertebrae and auditory systems allowing for extreme sensitivity to sound, essential for living in the turbid waters found in major systems like the Amazon and Orinoco. Catfish comprise the largest percentage of fish biomass in the Amazon and range from small herbivores to the predatory Giant Amazon Catfish (up to 200 kg). Tetras include tiny “aquarium fish” as well as the large herbivore and frugivore species like the Pacu (important in flooded forest ecology described above). The knifefish not only have the Weberian Apparatus produce electrical discharges for navigating and locating prey. Together, the three orders of the Characiphysi group demonstrate the diversity and evolutionary uniqueness of Neotropical fishes.

Birds: Tanagers. The Neotropical rainforest holds both high diversity of birds (roughly 25% of all bird species) and evolutionarily unique lineages like the Oilbird (*Steatornis caripensis*) and the Hoatzin (*Opisthocomus hoatzin*). New-World-only families include the hummingbirds (Trochilidae, Fig. 3D), toucans (Ramphastidae), tyrant flycatchers (Tyrannidae), cotingas (Cotingidae), and the highly diverse tanagers (Thraupidae). The many tanager species occupy a diverse range of niches from canopy to understory, nectarivore to insectivore, with many playing important roles as seed dispersers for small-seeded plants. Often found in mixed species flocks, the tanagers are also some of the most brilliantly colored birds of the rainforest.

Mammals: Bats. Although sloths (Fig. 3B) may be the most unique mammals of the Neotropics, bats are by far the most diverse and arguably the most ecologically important group of mammals. In some countries, almost 50% of the mammal species are bats, and bats fill niches including pollinator, seed disperser, insectivore. There are even species specialized to feed on fish (bulldog fishing bat) and mammal blood (vampire bats).

Major Threats and Losses

Deforestation throughout the Neotropics has emerged as one of the greatest conservation crises of the late 20th and 21st centuries. Roughly 20% of the Amazon basin and an even higher proportion of Mesoamerican, Chocóan, and Atlantic rainforests have been deforested in the past century. Throughout the Neotropics, a variety of causes contribute but the major drivers in most regions are cattle ranching and large-scale crop production. However, the process of deforestation is often more nuanced.

Until the 1960s, large plantations and commercial logging accounted for most of the net deforestation. Small-farm agriculture in the Neotropics historically occurred on a rotational, “slash-and-burn” model, resulting in little net forest loss. After forest clearing, a small plot would be cultivated for 3–7 years until nutrient levels diminished and then left fallow to regenerate into forest. However, this changed as agricultural frontiers began to form along major access routes (rivers and highways) and were motivated by changes in the culture and politics of land ownership.

Agricultural frontiers in South and Central America are consuming tropical rainforest at an alarming rate. Different processes of frontier advancement affect the rate, but the underlying causes are often similar. Smallholder agriculture on the leading edge of the frontier is followed by larger scale replacement as the frontier advances. That is, it is often poor family farms leading the deforestation with the cleared lands eventually occupied by more permanent farms. As a result, small farms are no longer modeled on a rotational farm-fallow-forest cycle and the advancing frontier leads to great forest loss.

The Amazon basin lost 20,000 square km per year from 1980 to 2005, and has lost an estimated 20% of its total extent since 1970 (Foley et al., 2007). Cattle ranching is responsible for approximately two-thirds of the deforestation, with crop agriculture responsible for most of the rest. Logging is estimated at only 2%–3% of total forest cover loss but selective logging (which does not lead to complete deforestation) is much more extensive (Foley et al., 2007). Unlike other regions of tropical rainforest, clearcut logging is rarely practiced in the Neotropics because of a low density of high quality timber species. An alarming trend of increased forest fires in rainforests, especially in the Amazon, is likely a combined effect of logging and climate change (Nepstad et al., 1999).

Cattle ranching has long been the biggest threat to the Amazon (Fig. 4). Campaigns to address demand for rainforest beef slowed cattle-driven deforestation temporarily in the 1990s, but the increase in soy production minimized the overall improvement in deforestation rates. Soy production has emerged as a rapidly-growing threat to the Amazon rainforest. Unlike other agricultural practices that are heavily tied to labor inputs from humans, mechanized soy production can occur on a large scale with machinery doing most of the work.

Mineral mining is widespread in the Neotropical rainforest regions and contributes partially to deforestation rates. The greater risk of mineral extraction is the runoff created and the toxic chemicals used in the process. Sediment loads in rivers greatly increase as entire hillsides are blasted away with water cannons. Gold mining uses mercury to aid in the extraction process, resulting in increased mercury levels in the tributaries of the Amazon and Orinoco, where gold mining is practiced. In the Madre de Dios region in Peru, illegal mining has destroyed over 600 km² of forest (USAID, 2018). The Casseterita Mine in Rondônia (inset B in Fig. 4) covers over 9 km² and has resulted in loss of surrounding forest in ponds where mine tailings are deposited. Originally a tin mine, the discovery of gold in the mine has renewed investment.

Climate Change

Climate change impacts Neotropical rainforests in obvious and obscure ways. The most optimistic hope is that increased temperature may result in higher potential evapotranspiration if accompanied by stable or increased precipitation, allowing for greater carbon sequestration by forests. In models this holds true, but climate change’s impact on precipitation is often to reduce or change patterns of precipitation. A less obvious impact is climate change is that it has driven an upturn in the strength of hurricanes that make landfall, causing great concern for their impacts on rainforests of the Caribbean Islands and coastal Central America.

The Amazon forest is a particularly interesting case study for climate change. Because of its sheer size, the Amazon self-generates a lot of local and regional climatic conditions. Because of the prevailing easterly winds (east to west movement), evaporation in the east directly impacts precipitation in the west. When forests are cleared in the east, precipitation flows across the land surface into rivers instead of being absorbed by plants and evaporating through transpiration. Water that should enter the atmosphere and create



Fig. 4 Western Brazil and northeastern Bolivia, illustrating the pattern of deforestation that has occurred as roads and colonization policies in Brazil led to large forest clearing in the Brazilian state of Rondônia. Inset A shows a closeup of the deforestation pattern along main and side roads. Inset B is the Casseterita Gold Mine in Rondônia. Imagery sources: Google Earth. Main image and inset A are Landsat 2017 images, inset B is Digital Globe 2018.

clouds flows out to the sea, thus decreasing cloud cover and precipitation downwind from the deforested areas. The result of deforestation is thus not only loss of local forest but climate impacts to other regions of the Amazon.

Droughts are also increasing in the Amazon, from one approximately every 50 years to multiple droughts in a single decade. Major droughts in 2005 and 2010 had strong impacts on the rainfall throughout the basin and long-term impacts on the canopy of the forest. Predictions are that longer and more severe droughts are in the future for the Amazon severely threaten the forest.

Not surprisingly, forest fires are on the rise in the Amazon even though they are extremely rare in the paleoecological record for the region. Recent alarming trends of increased forest fires, and cryptic fires burning below the canopy, represent a new threat to the Amazon. Post-fire impacts have been demonstrated for canopy dieback, fruit production, large mammal distribution, understory bird abundance, and other forest health indicators.

Elsewhere in the Neotropics, climate change impacts are affecting forests in different ways. Changes in seasonality and increased severity of hurricanes are two climate change phenomena that heavily impact the Mesoamerican and Caribbean rainforests. In rainforests of Central America with a significant dry season (Belize to Costa Rica), recent years have had variation in the onset and length of the wet season. This can create an extended burning season for agricultural fires and delay the rains needed to stop these fires from spreading.

In the Caribbean and Central America, hurricane damage has increased and spread. Hurricane Otto's impact in southeastern Nicaragua and northeastern Costa Rica marks the farthest south a Caribbean hurricane has heavily impacted rainforest in recorded history. Hurricane damage is a two-pronged disaster for the forests. The minor impact is actually the wind and flood damage; the economic response to hurricane damage is often the more problematic. In Nicaragua, hurricane-damaged forests are considered degraded even though research shows they will regenerate relatively quickly and maintain their biodiversity. However, the government's response is to allow salvage logging in the damaged forests, an operation that impedes the natural regeneration and causes further physical damage to the forest. After 1988s Hurricane Joan, salvage logging operations created new roads and degraded the forest, allowing peasant farmers to enter the area and establish a new agricultural frontier that has advanced rapidly in the ensuing 30 years.

Conservation Needs

Halting deforestation is the single most important step necessary for conserving the immense biodiversity of the Neotropical rainforests. This holds true for all four major forest regions, but is especially true in the smaller Atlantic and Chocó rainforests. The Amazon has different needs as deforestation is combined with climate change impacts, damming of major tributaries, and changing economic drivers of forest loss. The Mesoamerican rainforest is primarily threatened by agricultural expansion, with highly unsustainable levels of deforestation occurring in Nicaragua and Honduras.

Of all the Neotropical rainforest regions, the Atlantic and the Chocó should be of highest urgency because of their limited extent and vulnerability to deforestation. The Atlantic forest of Brazil have already experienced significant deforestation and it continues at an unsustainable rate. Unique species like endangered Golden Lion Tamarin (*Leontopithecus rosalia*) and critically endangered Black-faced Lion Tamarin (*Leontopithecus caissara*), as well as several other endemic primates, all face the possibility of extinction if the deforestation continues in the Atlantic forest. Because a large percentage of Brazil's human population is concentrated in the regions that historically held Atlantic rainforest, the deforestation is driven by a combination of population pressures like urban expansion. The Chocóan rainforest, extending along the Pacific side of the Andes and into Panama, has experienced high levels of fragmentation, isolating its endemic species into small patches.

The overall biodiversity of the Amazon dictates that its protection should also be of high priority. Recent trends of increased crop agriculture (soy), road expansion, dam construction, and increased population need to be slowed or reversed to protect the basin's forests and species. Brazil made advances in slowing deforestation from 2005 to 2015, but the trend has reversed and the new surge of anti-environment politicians do not bode well for controlling deforestation.

The largest Central American lowland rainforests, found in Honduras and Nicaragua, are being cleared at an increasing rate as governments fail to enforce protected areas. Instead, the governments knowingly ignore the proliferation of both cattle ranches and oil palm plantations within designated nature reserves. Nicaragua's Indio-Maíz Biological Reserve and Bosawas Biosphere Reserve along with Honduras' Río Plátano Biosphere Reserve have agricultural frontiers that have penetrated far past the borders of the reserves. Active deforestation in Bosawas has reached a critical level but unwilling leaders in Nicaragua do nothing to prevent it.

Even countries like Costa Rica, with a high percentage of land in protected areas, have nonetheless experienced high levels of past deforestation outside the protected areas. Costa Rica is making advances in forest cover, but much of the "reforested" area is in the form of monocultural tree plantations with little biodiversity benefit. The future of Costa Rica's forests lies in continued protection of reserves and improved techniques for reforestation in the degraded areas between the reserves.

Examples of Positive Outcomes

Conservation initiatives in the Neotropical rainforest take on many forms, from "fortress conservation" to locally-driven participatory projects. The 1980s and 1990s saw many countries setting aside large percentages of their national territory at various levels of protected status. While some countries like Costa Rica and Belize invested in the protection of natural areas, poorer countries like Nicaragua and Honduras did not provide sufficient resources to protect their reserves.

Costa Rica. Costa Rica is often heralded as a "green paradise" where conservation has succeeded in reversing trends of forest loss. Many positive outcomes have resulted from the country's very aggressive conservation programs. The government established an extensive network of protected areas, setting aside over 27% of national territory in national parks, wildlife refuges, forest reserves, and other statuses. However, there are some shortcomings of the model adopted by Costa Rica. Although Costa Rica created an excellent network of reserves, lands in between the reserves experienced high levels of degradation as they were transformed into plantations for pineapple and bananas. In recent decades, Costa Rica has reversed this trend and experienced a net increase in forest cover, roughly 1% per year since 2005. This too is more problematic than it initially appears, because much of the forest cover increase is due to plantation forests. Overall Costa Rica serves as a positive example of Neotropical rainforest conservation, but like any solution there are also some shortcomings.

Panama. Some argue that forest conservation in Panama is a positive model for other countries (Condit, 2015). However, the historical constructs that led to the bountiful forests are unique and unlikely to be chosen by other countries. Panama's rainforests benefitted from an unusual relationship—the occupation of the central zone by the United States military from 1903 to 1999. The central area was protected to ensure the viability of the Panama Canal, with protection of the large Chagres River watershed and a buffer strip around the Canal. Reforestation occurred in treeless areas, and a healthy and diverse rainforest now occupies the buffer around the canal and the Chagres watershed (Condit, 2015).

Reducing Emissions From Deforestation and Forest Degradation (REDD+): Climate change is driven by carbon emissions, and the loss of forests globally is responsible for 11%–17% of annual global carbon emissions. Keeping the carbon stored in trees and soil represent a way to curb increasing emissions. In 2005, the United Nations Framework Convention in Climate Change developed the REDD concept as a way for wealthy, carbon-releasing countries to help protect carbon resources held in forests, particularly tropical rainforests which have high capacity for carbon storage. The REDD+ program provides incentives to developing countries to reduce emissions through protecting their forest resources. Using the general concept of payment for ecosystem services, REDD+ provides a model for results-based payments for actions that reduce forest carbon emissions. REDD+ projects are certified at three levels: Readiness, demonstration, and implementation. Projects can be developed at a national or local level. REDD+ has great potential



Fig. 5 Squirrel monkey in the Neotropical rainforest. New World monkeys have prehensile tails. Photo by Benjamin Urquhart.

to slow deforestation and provide economic value to protected forests. As with other conservation efforts, concerns do arise about who benefits from REDD+ and who controls forests in the program. It is often the desperate and poor who live in close contact with Neotropical rainforests, and REDD+ must benefit these people to be a truly sustainable mechanism for forest conservation and carbon management.

Indigenous movements: Humans and the Neotropical rainforest have not always had an adversarial relationship. For 10,000 years the Native American cultures that called Central and South America home found ways to live in the forests without large-scale environmental destruction. In the last 500 years, the indigenous peoples of the Neotropics have witnessed a blitzkrieg assault on their lands. Because imported diseases depleted their populations and they faced technological superiority of European invaders, indigenous cultures were decimated and unable to stop the destruction of both ecosystem and culture. Not until late in the 20th century did politics catch up and begin to protect indigeneity, but some countries have resisted allowing the rights that global bodies like the United Nations recognize. The result has been continued marginalization of indigenous peoples, removal from and seizure of their lands, and destruction of the territories they and their ancestors called home.

However, in some areas this trend is reversing. Indigenous groups have found a voice through international law and a willingness of philanthropic foundations to help support their efforts to reclaim their lands. In southeastern Nicaragua, the Rama people have taken protecting the Indio-Maíz Biological Reserve into their own hands after watching the national and regional governments do little to protect it. They have established forest patrols to monitor illegal colonization and are appealing to the government for help removing illegal settlers. In northern Nicaragua and Honduras, the Miskito are trying similar tactics. In Ecuador, it is the Huaroaní trying to balance oil extraction with protecting their native lands. In Brazil, several indigenous groups are fighting back against plans to dam the major tributaries of the Amazon. Throughout the Neotropics, indigenous led conservation efforts represent the uprising against unsustainable agricultural frontiers, gold mines, dams, and logging. With great hope, the indigenous people and conservationists hope that the 21st century can be a change from the way cultures originated in Europe have treated our most precious biome, the Neotropical rainforest.

Conclusion

The Neotropical Rainforest is the most biodiverse—and arguably most important—biome on the planet. High levels of both plant and animal biodiversity occur on a local and regional scale, creating areas where in a single 100×100 km cell, more plant and animal species are found than in the entire temperate portion of North America. Each of the four major regions (Fig. 1) of Neotropical Rainforest has unique species and conservation priorities (Fig. 5). The greatest threat to all regions remains deforestation, but in each region different drivers of deforestation come into play. Climate change increases the likelihood of fire and the severity of hurricanes, exacerbating the losses due to deforestation. Conservation efforts must recognize the nuances of biodiversity and the coupling of human activity with the natural systems to generate long-term solutions to one of the greatest crises facing humankind—the loss of the Neotropical rainforest.

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Why Should We Care So Much About Old World Tropical Rainforests?

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Abstract

The challenges of conserving Old World Tropical Rain Forests range from direct human impacts to the unanticipated consequences of conservation policies, not to mention that the rate of global warming is outpacing the capacity for the region's plants and animals to adapt in a balanced manner. The biodiversity is irreplaceable of the rain forests found across the African and Asian basins. Even if we completely preserved the rest of the planet's tropical ecology, the Old World spreads over so many physiographic domains that it is unmatched in its endemic species throughout the Earth's biomes. The brief description herein of the Old World tropical rainforests is only a glimpse of those values, but the threats to them are readily detailed. What is happening, where it is occurring, why forest impacts exist and spread, and when did it start all inform attitudes of how we should react. Clearly, humanity needs to stop the loss of forest habitat, but we must also take action to restore forests in a technically sound fashion. Who should do this work? Everybody has a stake: the adverse impacts to our atmosphere mean that no nation or people can escape these losses, and each decade sees us closer to the time when we would be forced to live without these resources. Due to the broad physical range and biological network of the forests of tropical Africa and Asia, their preservation could offer refuge to survivors of the future, including plants and research opportunities that give us life-saving medicines. Oh, and our most precious animals live in these regions: Elephant, Rhino, Orangutans, Lions, Snow Leopards, and more birds than we can count!

It is not coincidence that the richest forest ecosystems are in the tropics, where so much legend arose during the 1700–1800s. Tropical forests are a global resource where the sun and water combine to drive much of the globe's hydrology. These irreplaceable habitats are threatened by climate change, human population growth and resource extraction. Here we discuss the richness of Old World Tropical Rainforests (Fig. 1), but unfortunately, must spend too much effort discussing the threat of forest loss. The silver lining is that by addressing the facts of, and possible actions against, forest loss, we educate and motivate society to prevent the losses by properly protecting and managing the forests we have.

The questions surrounding forest cover change are not simple, especially in rainforests where even the smallest break in canopy is met with a rush of volunteers to take it back over. When there is regrowth of forest, is it likely to return an area to its original ecology? Should we resist such changes, even though they may result in more forest cover? Must conservation policy accept only preservation of existing forest, or do we attempt restoration in answer to inevitable anthropogenic losses? AND, what must we know to determine how to direct the preservation or recovery?

Ecological theory guides conservationists as they prioritize investment in habitat protection and restoration because funding for the environment is limited. Theorists create tools to decide how to select locations, areas and species that are to be restored or preserved. While a review of the many efforts to create such guidelines is beyond the scope of this article, the questions addressed herein underpin forest conservation. Clear examples of how such protection efforts succeed include regulation of wetlands in the United States, global programs of Marine Protected Areas, various national parks programs, and of course, the many laws concerning endangered species, both national and international. In a review of global biomes, Watson et al. (2016) show that tropical and subtropical moist forests comprise 15% of the world's biomes, and of that only 12% is still considered wilderness, but there are a remarkable 11 World Heritage Sites within this biome.

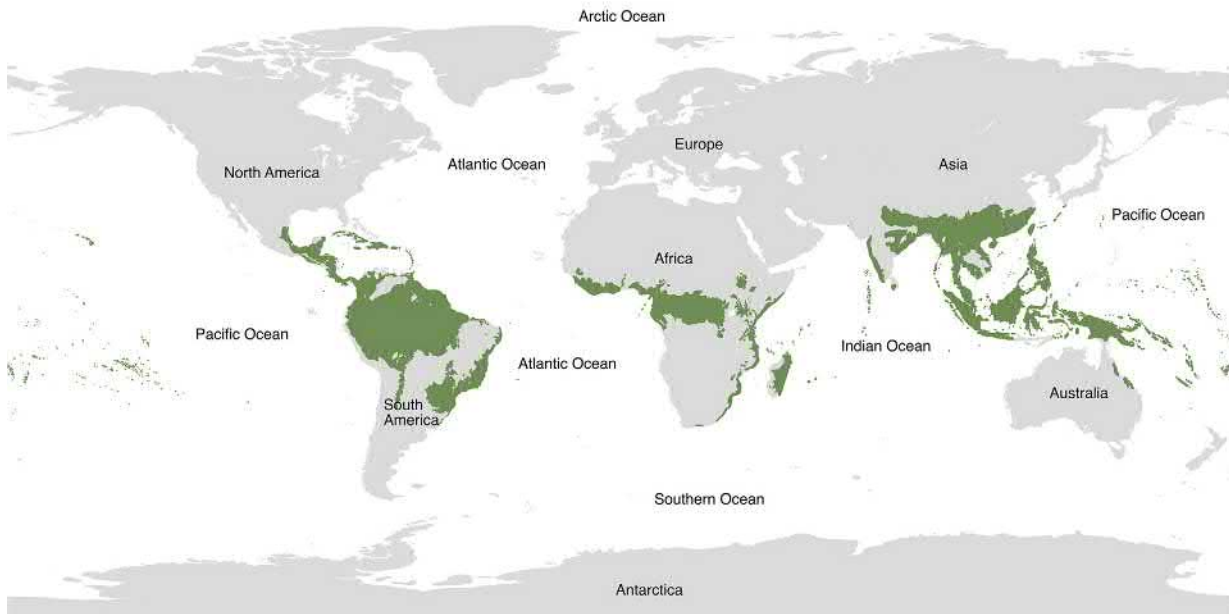


Fig. 1 Global view of tropical forest regions.

Scientific Significance of Old World Tropics

Legends reflect the historic fascination of Europe with the African and Asian ocean basins, opening those regions to commerce and eventually challenging humanity to understand how to manage their natural wealth. A child's imagination about "far-away" places often reaches to the savannah of Serengeti, where lions roam, or the jungles of the Congo where Stanley tried to meet Livingstone the historic missionary, or the jungles of India where Rudyard Kipling teased our minds about colonial escapades of tigers and panthers. Now, our experts must teach us how to conserve those resources.

Roughly half of the global forest loss is in the Old World areas (Curtis et al., 2018), much of it tropical (Fig. 2) (Hansen et al., 2013). It is ironic that at the outset of creating this article, a major study was published that challenges the biogeographical basis for labeling the Old World versus the New World regions (Slik et al., 2018). So, aside from the sheer bulk of habitat, ecosystems and wildlife housed and threatened within Old World Tropics, these regions continue to be at the heart of the theoretical basis of ecology. This "taxonomic/biogeographic challenge" is so new that we have decided to use the existing definition of these regions in this article. Suffice it to say, this debate will be critical to future literature, so the reader is warned to pay attention to that debate. For now, however, we consider Africa to southeast Asia as "Old World," and the American continents as "New World," since the literature to date takes that perspective.



Fig. 2 Map of forest loss between 2000 and 2018. Data source: Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., and Townshend, J. R. G. (2013). High-resolution global maps of 21st-century Forest cover change, *Science* 342, 850–53. Data available online from: <http://earthenginepartners.appspot.com/science-2013-global-forest/UMD/> Google/USGS/NASA.

The high species richness and diversity of tropical forests, especially rain forests, provides ecological theorists challenges in explaining global patterns of nature. Through these studies, we are actually learning how life developed and protects itself, lessons from which humans can learn about protecting the resources we depend on. Are life patterns predictable? Or are the patterns we observe in life all random (as posited by the “Neural theory” of evolution). Tropical forests are fertile ground for testing theories of biodiversity and ecological resilience: [Molino and Sabatier \(2001\)](#) showed us that tropical forests adhere to the “intermediate disturbance hypothesis,” which states that the highest numbers and diversity of species occurs at stages of intermediate recovery from disturbance. Such studies in tropical rainforests produce results faster than elsewhere because life cycles turn over so quickly in wet and warm habitats. Accordingly, [Ricklefs and Renner \(2012\)](#) were able to address neutral theory and showed that communities are formed in response to such dynamic factors as animal behavior and habitat structure using comparisons of similar tropical forests in South America, Africa, and Asia.

In addition to the academic value of tropical forest studies, the reason we care about Old World Forests is that the ground they sit on provides irreplaceable ecosystem services, functions that are maintained by the mosaic of original forest types. The soils, water and air that support Earth’s life are present in a special mixture, and as with any recipe, if the proportions of ingredients are changed, the product is changed. [Kooyman et al. \(2013\)](#) showed us that forest loss and recovery does not follow an intuitive pathway, and that the more opportunistic species (vines and other pioneers) do not need intervention to protect them, while the mature canopy trees are easily threatened. Failure to understand such dynamics in conservation planning can translate to losing some species forever. This process is already documented because the pace of climate change is outstripping the original natives by advancing competitors not originally dominant in a given area ([Curtis et al., 2018](#); [Pradhan et al., 2018](#)). The shifting of wildlife geography is a threat to natural migration, because migration evolved in concert with the rain cycles, for example, on grasslands. Climate change is occurring so fast that it forces changes in plant and animal assemblages that are no longer in concert with the behavior patterns that took eons to evolve at a much slower pace.

Tropical Forest Types and Locations

There is no one “tropical forest,” or a single type of “rainforest,” so we begin here by reviewing the wide range of forest types within the biogeographic region termed “tropical.” When most people think of “tropical forests” the stereotypical overgrown tropical rainforest from tales such as “The Jungle Book” most likely comes to mind ([Photo 1](#)). However, even within the tropics, ecosystem subdivisions can be made mainly based on the length of the rainy and dry seasons, but are not so clear cut because these habitats change so quickly when disturbed. Across the tropics there is a gradual transition from wet (rainforest) to dry (savanna) as one moves away from the equator, or into areas that lack the rain to sustain rainforests. Within each tropical ecosystem there is a great deal of diversity, and it is impossible to describe their intricacies in one short article. However, what we provide here serves as an introduction to the three main tropical biomes ([Table 1](#)) ([Brown and Lugo, 1984](#)) and the diversity of tropical, woody ecosystems, showing the context for rainforests themselves.

Tropical rainforests are the most biologically diverse and complex forests on earth. They grow around the equator in South America, Africa, and Southeast Asia, within the area bounded by latitudes 23.5°N and 23.5°S. Tropical forests are characterized by their stable, warm temperatures, high rainfall, and distinct seasonality. There are only two seasons, rainy and dry, and the length of daylight is around 12 h with little variation. Tropical forests are known for their wide range of flora and fauna, including many endemic species, having the highest species diversity per area in the world. Furthermore, tropical forests also play a critical role in mitigating climate change because they act as a carbon sink. Despite the beauty and importance of tropical forests, they are rapidly disappearing around the globe, mostly due to anthropogenic pressures. More than half of tropical forests have already been



Photo 1 A typical broad view of rainforest canopy.

Table 1 Area and biomass of world's tropical forests.

	Closed Forest						Total	Open Forest		
	Broadleaf			Conifer						
	Undisturbed-productive	Logged	Unproductive	Undisturbed-productive	Logged	Unproductive		Unproductive-productive	Unproductive	Total
Tropical America										
Area (10 ⁶ ha)	452.98	53.5	147.45	1.53	13.64	9.56	678.66	142.89	74.11	217
Total biomass (10 ⁹ tons)	70.28	6.31	13.10	0.21	0.69	0.47	91.06	11.02	2.47	13.49
Tropical Africa										
Area (10 ⁶ ha)	118.18	43.57	52.66	0.27	0.31	0.54	215.53	169.22	317.23	486.45
Total biomass (10 ⁹ tons)	28.09	7.79	6.82	0.03	0.02	0.05	42.8	7.83	6.54	14.57
Tropical Asia										
Ares (10 ⁶ ha)	97.26	94.62	100.08	1.77	3.83	2.8	300.36	8.53	22.42	30.95
Total biomass (10 ⁹ tons)	19.09	8.82	13.18	0.26	0.43	0.29	42.07	0.67	0.59	1.26
Total Tropics										
Area (10 ⁶ ha)	668.42	119.6	300.19	3.57	17.78	12.9	1194.55	320.64	413.76	734.4
Total biomass (10 ⁹ tons)	117.46	22.92	33.1	0.5	1.14	0.81	175.93	19.52	9.6	29.12

Data source: Brown, S. and Lugo, A. E. (1984). Biomass of tropical forests: A new estimate based on forest volumes. *Science* **223** (4642), 1290–1293.

destroyed. For example, approximately 48 million hectares (ha) of these varied tropical forests, an area larger than the state of California, were cut down between 2000 and 2005 (Hansen et al., 2010). The drivers of deforestation differs amongst forest types as well as amongst geographical regions. Here we will discuss the types of tropical forests and where they are found, and the threats to these unique and important habitats.

The complexity of ecological responses to different rain and temperature regimes (along with variations in elevation and soil conditions) is nearly infinite. This extreme capacity for variations is precisely the reason that rainforests are so threatened: the plants available to “invade” or take over from the original species in a given patch of forest make it very difficult for the original assemblages to persist once disturbed (Kueffer, 2017). Unfortunately, when changes occur to the plant assemblages, the wildlife are not generally as adaptable, so disturbance favors opportunists, and disfavors endemic species which are adapted to an original and narrow range of physiographic conditions.

Tropical Rainforest

Tropical rainforests grow close to the equator, between 10° north and south. Tropical Moist Forests are characterized by low variability in annual temperature and high levels of rainfall (>200 cm annually), with either no or a short dry season. The temperature is stable year-round, around 27 °C. The high temperatures, abundant rainfall, together with 12 h of light a day promotes the growth of many different plants and results in large trees that are green year-round. The trees grow very densely together and the branches and leaves block most of the light from penetrating to the understory (Photo 2). The soil can be several

**Photo 2** Typical view of rainforest understory.

meters deep, but due to nutrient leaching, it lacks most of the essential nutrients for plant growth. The thin topsoil layer contains all the nutrients from decaying plants and animals, and this thin layer sustains the many plant species in the forest. Forest composition is dominated by semi-evergreen and evergreen deciduous tree species. The tropical rainforest biome covers about 17 million km² in three regions: Southeast Asia, Central Africa, and Amazonia. Human use has affected >20% of this area, with approximately 20% used as pasture or cropland in 2000 (Ramankutty et al., 2008). Tropical rainforests have the highest species diversity per area in the world, containing millions of different species. Even though they cover only a small part of the earth, they house at least one half of all species. As you can tell from the name, it rains a lot in these forests.

Tropical rainforests are fragile habitats that are sensitive to plowing, overgrazing, and excessive burning due to their high moisture and thin nutrient-poor soils (Mann, 2002). The plant species inhabiting tropical rainforests have a somewhat unique ability to take advantage of nutrient poor soils with characteristics that somewhat echo the traits of invasive species, and result in their high biodiversity. However, due to the rapidity with which changes can occur in the rainforest species assemblages, these habitats are also in delicate balance, and it is too easy for them to lose their natural species combinations when the soil, water or canopy are disturbed.

The transition zones from wet to dry habitats are crucial regions across the globe, partly because climate change is shifting these lines (Pech et al., 2017), but also because there are significant “edge-effects” between biomes (Pfeifer et al., 2017). Habitat edges provide unique habitat and refugia that allow species to transition between habitat types. Habitat changes are occurring at rates that exceed the capacity of ecosystems to “evolve” naturally (Siepielski et al., 2017), thereby elevating the threat to their survival. Hence we cannot predict the results of climate-driven adaptation in such dynamics systems, so we are limited in our ability to aid plants and animals by proactive management.

Tropical Savanna

As one moves further from the equator the forests gradually transition to savannas, which have a few trees but are mostly vast landscapes of grasses and shrubs. Large expanses of land in the tropics do not receive enough rainfall to support extensive tree cover. Here, the wet season is short and the longer dry season leads to more frequent fires. These factors combine to suppress the growth of trees and allow grasses to dominate, although scattered trees may be common. Savannas are prevalent just south of the dry forest in northern Australia, and in parts of Southeast Asia. However, African savannas are the most well known and are famous for their diverse and abundant wildlife. In Africa there are large areas of savanna that cover the landscape south of the Sahara Desert. The savanna biome covers 20 million km², or about 15% of Earth’s ice-free surface. Of this area approximately 50% was used as pasture or cropland in 2000 (Ramankutty et al., 2008). There is a diverse assemblage of large mammals that have evolved to take advantage of these habitats. These ecosystems are mainly threatened by climate change, which is causing the spread of wet areas, resulting in more tree growth as moist forests expand.

Tropical Dry Forest

Discussions on vegetation in the tropics often focus on shifts between forests and savannas, but ignore dry forests. However, tropical dry forests are distinct from moist forests in their seasonal drought and consequent deciduousness and differ from savannas in that they rarely experience fire. Although the tropical dry forest biome may be less well known than tropical rainforest or savanna, it is the most threatened of the major tropical forest types (Jansen, 1988). Identifying dry forests is a complex issue, as dry forests grade into other vegetation types such as wet forests, savannas and woodlands. However, in simplest terms dry forests may be defined as forests occurring in tropical regions characterized by pronounced seasonality in rainfall distribution, resulting in a dry season that spans several months. Most tropical dry forests are between 10 and 25° north and south of the equator. Dry tropical forests, with their longer dry seasons, are dominated by deciduous trees which have a leafless period during the dry season. This loss of leaves opens the canopy layer, enabling sunlight to reach ground level and facilitate the growth of thick underbrush. It is estimated that only 1,048,700 km² of tropical dry forest remains, distributed throughout the three tropical regions, with over 50% found in South America, and the remaining half in Africa and Asia (Miles et al., 2006). In Africa, tropical dry forests are extensive across many parts of the continent, extending to the north, east, and south of the Congo Basin rainforest. Tropical dry forests also cover much of India, extend into parts of China, and are a major type of land cover in Australia. Though less biologically diverse than rainforests, tropical dry forests are still home to a wide variety of species, many of which display extraordinary adaptations to the difficult climate. Virtually all of the tropical dry forests (about 97%) that remain are currently exposed to a variety of different threats, largely resulting from human activity.

Unique Ecological Characteristics = Endemism

If we accept the definition of Old World as being the Africa-Asia basins, it is a region with a large proportion of the planet’s endemic biodiversity, some of it still very remote. The preservation of endemic species (i.e., those found only in a given region or site) is perhaps the most critical of conservation objectives because many of these species cannot find new homes as the planet changes, so they would be lost forever. Why is that important? The particular characteristics that contribute to isolating species from other regions allows them to evolve unique, endemic genetic profiles, but these same traits “trap” them in their home region, confirming

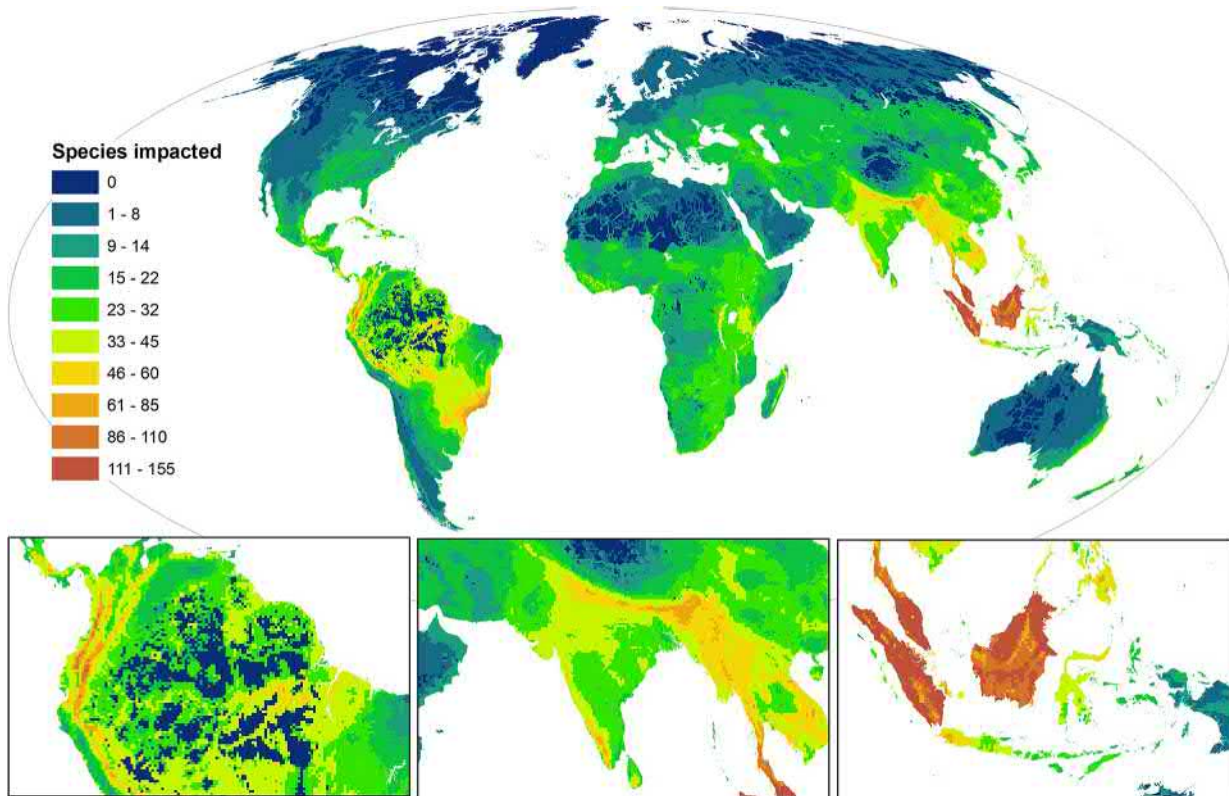


Fig. 3 Estimates of the number of species impacted by human activity. Reproduced with permission from Allan, J.R., Watson, J.E.M., DiMarco, M., O'Bryan C.J., Possingham, H.P., Atkinson, S. C., & Venter, O. (2019). Hotspots of human impact on terrestrial vertebrates. *PLoS Biology*. <https://doi.org/10.1371/journal.pbio.3000158>.

theories of natural selection. The extent of the threat to wildlife in the rainforests of Indonesia and Malaysia are more severe than elsewhere (Fig. 3), and the level of endemism is so high that these are potentially catastrophic.

The habitat which comprises rainforests is multi-dimensional and dense, which is often difficult for a casual observer to see (Photo 3). Can you see the “trail” that our leader followed? But the wildlife using such habitat is adapted to patterns and “layers.” The layers can be characterized by physical parameters: the understory (ground level) is hot and wet, with no wind, and only minimal, reflected sunlight under a closed canopy. At the top of the forest, within the canopy, sunlight is absorbed, and rain and wind have distinct effects. The mid-layer is inhabited by epiphytes. Often found in pockets created between tree limbs, these plants are not rooted in the ground, because they thrive using moisture, carbon dioxide, etc. from the atmosphere. Within and just below canopy are an array of micro-habitats that are important for food production. Nutrient recycling beneath the canopy occurs amongst the mosses and lichens, creating organic habitat for exotic plants (e.g., orchids and bromeliads).

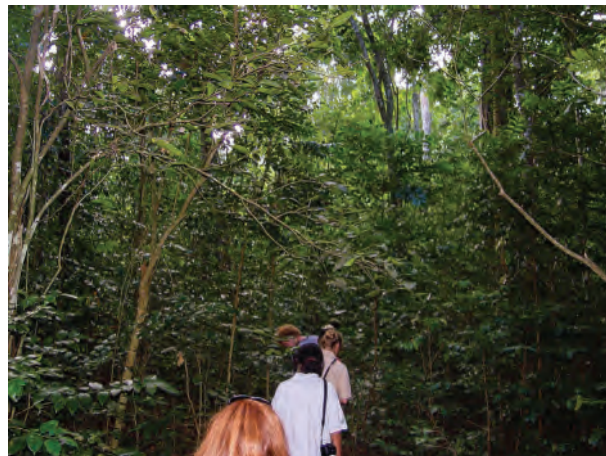


Photo 3 People walking along a rainforest trail.

The widely varying micro-habitats created by the mosaic of plant and animal species in rainforests result in too many assemblages to review in this article, but some examples of remarkable species are briefly described.

Kapoc (*Ceiba pentandra*) is one of the largest tree species in the world, reaching two hundred feet tall with a trunk diameter of nine feet; these trees came from the New World in their global spread. Shorea trees (*Shorea gratissima*), members of the dipterocarp family, are the most common tree in the rainforests of Southeast Asia (the species is often >10% of the trees in a typical canopy layer). Custard Apple Trees (*Annonaceae*) are common in the Philippines and Africa. Other common tree families are Rubiaceae, Lauraceae, Leguminosae, Rutaceae, Apocynaceae, and Solanaceae. "Strangler fig" (*Ficus* spp.) represents several species of fig tree, a plant that winds its way up any vertical object, such as rocks, other trees and even buildings. The vine is actually strong enough to strangle its host. Figs are important food for bats and its various forms ensures some fruit being in season all year. People eat figs and use the plant material in varied ways. There are a variety of plants in the tropics that have symbiotic relationships, such as Cecropia trees who rely on fierce ants to defend them against depredation by wildlife and insects. These ants can even attack other plants when they overgrow their host (Fig. 4) (Lawton, 2018).

As a popular illustration of the unique character of rainforests, conservationists point to the many wildlife species that are indigenous to specific geographic areas. On Mount Kenya is a stand of Bamboo (*Yushania alpina*) in the rainforest belt where Elephants roam with Leopard. In Uganda live Mountain Gorillas amongst the Ruwenzori Mountains, and an endless array of primates living in the Congo's rainforest. In Borneo there are Clouded Leopards and Orangutans dependent on rainforest habitat which is fast being fragmented (Laurance and Watson, 2016). And in India, the Bengal Tiger is running out of habitats in which to seek refuge (Ranganathan et al., 2008).

It is important to note that the global problem of "invasive species" has long been the bane of rainforests. These "pioneer species" grow in the rainforest understory as soon as the canopy is broken by fire or other causes of clearing (natural and anthropogenic). Pioneers are the fastest growing species in any habitat because they are adapted only to rapid growth, and do not have the long term biological defenses against molds, bacteria and viruses, or retardants to wildlife depredation. But they quickly cover the ground needed by slow growing Kapoc and the *Dipterocarpaceae*, species which can dominate given time and suitable hydrological conditions. Once established, the larger species gain the advantage of blocking light to the pioneers. A natural

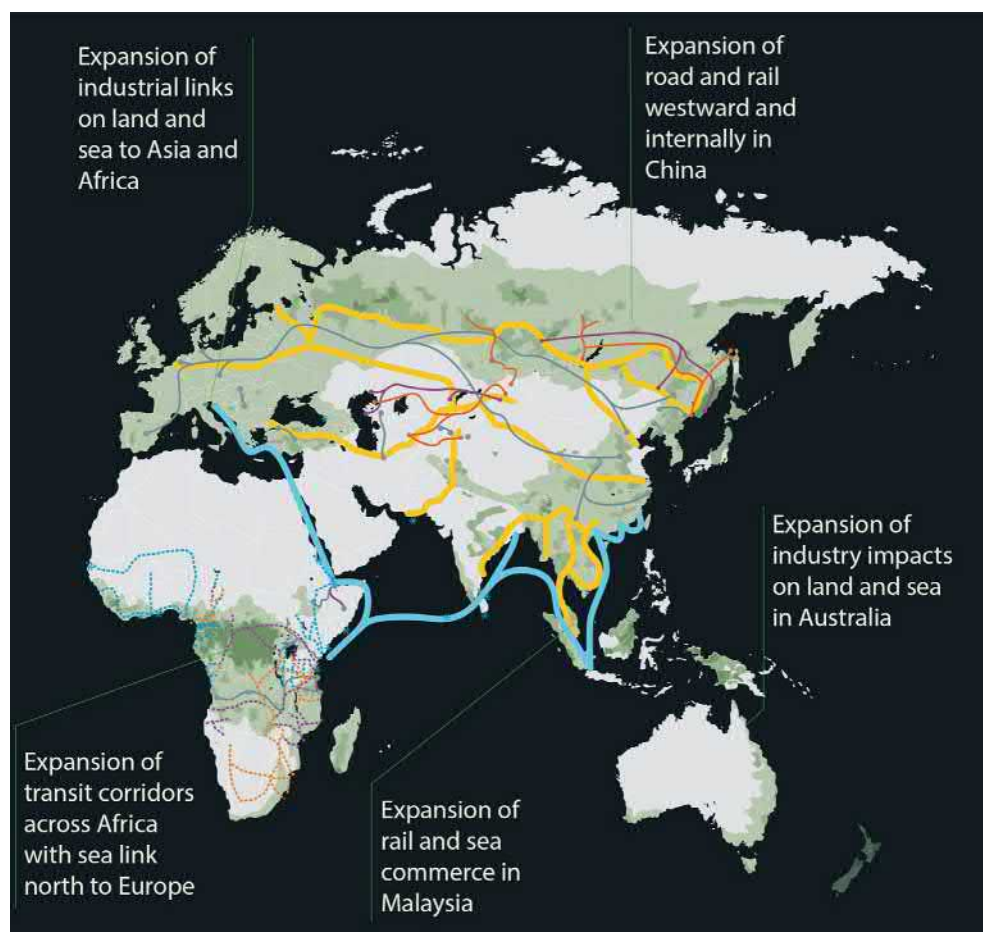


Fig. 4 Map of impacts of road development. Modified from Lawton G. (2018). Road kill. *New Scientist* 36–41.

understory provides food for wildlife and people: bananas, mango, papaya and oil palm. Spices and medicines are abundant in rainforests.

Here is where the story of rainforests becomes troublesome: palm trees grow so well and provide palm oil. Palm oil trees are native to West Africa, favoring riverine and wetland habitats. The disbursement of this plant across the globe is associated with a rush to generate income from the oil as a substitute for many uses, including cooking and cosmetics. Although palm oil represents substantial wealth for farmers in the tropics, the clearing of native woodlands for its production has created a crisis in all tropical habitats, especially rainforests. In Malaysia and Indonesia the loss of such habitat has impacted many animals, like orangutans, with extinction as a direct threat from palm oil plantations. The conservation threats to tropical forests are discussed below at length.

What is Happening to Old World Tropical Forests?

The impacts to forest cover across our planet are as diverse as the many cultures living amongst these habitats. These impacts include clearing of forests, sale of wood and wood products and ancillary impacts such as global warming that threatens entire ecosystems, changing rainfall patterns, wildlife migration and even soil microbiology (Abrams et al., 2017; Morris et al., 2016). The growth of the human population on Earth has caused the loss of all habitats, and this is especially true in Africa and Asia as such forests have long been harvested for their natural resources, such as unique hardwoods. The abundant sun and water in the tropics encourage local populations to grow crops wherever open ground can be found or created by woodland clearing, to support local, developing economies. The loss of forest cover since humans advanced agriculture is estimated at 35%, and people have impacted >80% of the remaining 40 million km² (Watson et al., 2018). Logging and clearing have had ecosystem level consequences throughout the tropics, such as the cascade of impacts to wildlife from the loss of habitat (Bello et al., 2015; Erb et al., 2018).

The cascade of wildlife impacts has already begun, for example in the southeast Asian rainforests, where an obscure species, the moonrat (*Echinosorex gymmura*), is clearly losing its population continuity in the pathway of oil palm plantation development (Brozovic et al., 2018). In general, such small mammals attract little attention, but they are usually survivors, so their fate is a strong signal of trouble for the region's rain forests. In the Gorongosa National Park of Mozambique, the loss to human pressure of leopard and African wild dog has led to a cascade affecting first vegetation, and eventually the whole park. Atkins et al. (2019) explain how the loss of these top predators spurred the spread of bushbuck (*Tragelaphus sylvaticus*), which expanded their foraging into floodplains, and consumed a novel diet including waterwort (*Bergia mossambicensis*). This change in foraging behavior and diet creates multiple impacts: the bushbuck is exposed to new dangers in open range, and the other species that forage on the waterwort (including humans who use it also for medicinal purposes) have new competition.

There are two major ways in which habitat is destroyed, some by people knowing they are cutting forest, and some as indirect consequences of other practices, such as road and infrastructure development. In a historic sense, it took many centuries before humans recognized they were harming their world, and still certain harmful practices are not fully recognized and regulated.

The incursion into forests in Africa, for example, when it was done simply by manual labor or unsophisticated machinery (e.g., 19th or early 20th century rudimentary agricultural equipment) was a starting point for habitat loss, albeit a modest impact. Accordingly, these traditional and historic practices were slow, and the forest was able to recover to a certain extent because of the immense effort required to clear truly large tracts. But with "modernization" of land development since World War II, and in the current age of globalization, the pace and scope of the threat is far more severe.

The road and corridor development process in emerging nations has reached epidemic proportions, and in 33 planned or developing transportation corridors across sub-Saharan Africa, there are direct impacts to 69 key Protected Areas (PAs) (Sloan et al., 2016). Amongst these PAs are sites designated as RAMSAR, World Heritage, National Parks, UNESCO Reserves, all deemed significant on a global scale and to which substantial social, economic and political commitments have been made. The challenge now is to understand the importance to local communities of the commercial value of the transportation and who actually benefits from the initiative to "modernize" remote regions, and is amongst the most important policy issues of this age.

It is not always simply forest loss by logging or burning that is a concern, but rather management (or lack thereof) can also be a problem. In southeast India, in the Odisha region, the Andhari Sacred Forest is a dry forest which offers a window into understanding the ecological history of such woodlands because it, and a number of other forest patches in the region, have benefited from cultural protection (Pradhan et al., 2018). The species richness and composition of these protected areas are higher than control sites, but they also demand special management since natural turnover is suppressed, so species that regenerate more robustly are taking over.

The similarity in biological traits between native and invasive species results in tropical rainforests being susceptible to take-over by foreign species. While invasive species have the potential to permanently eliminate a natural species assemblage, some of them are desired by local people. In Madagascar, the Guava tree (*Psidium cattleianum*) can provide food and even income if grown in abundance for export. In Asia, Wild Ginger (*A. angustifolia*) is both a medicine and food resource. The bead tree (*Adenanthera pavonina*) and Bamboo (*Bambusa vulgaris*) are widely introduced as landscape species, but once in the vicinity of natural habitats, these spread and take over with their aggressive style of forming thickets with deeply rooted systems so hard to exterminate. Some species, like the shrub Siam weed (*Chromolaena odorata*) observed in Tanzania possess powers of allelopathy, whereby their biochemistry produces compounds that retard competitors. Some species, such as a Mahogany (*Swietenia macrophylla*) in Asia, offer a potential for forestry production with high monetary values.

The relationship between biodiversity and endemic species is complex: when endemic species disappear from a habitat, invasive species take over. Invasive species have the advantage in general of being able to live in conditions that are marginal to them, that is how they invade, and after establishing in a new area, they begin to convert it to conditions that prevent the original species from living there. There are limited programs to control invasive species, which are mostly aimed at isolated patches along roadways, adjacent to or on farms, in suburban areas, etc. However, the control of invasive species in rainforests, where clearings occur due to people's activities, is a pursuit not widely addressed.

In a case study of the Bamburi Cement plant in Mombasa Kenya, a regrown forest was justified because it replaced ancient coastal reef structures, where no other forest would ever exist anyway. The selection of suitable tree species was aimed merely at rapidly covering a mining operation, and the ecosystem services were simple: erosion control, soils recovery, water quality protection and wildlife habitat. If there had been an objective for a specific type of wildlife assemblage (e.g., game farming), more attention would have been paid to the species of trees and resultant forest type.

For example, one strain of the common reed (*Phragmites australis*) spread around the world during the 16th to 19th century as ships went between the south Pacific and the Atlantic, and now the species is excluding the endemic strain in North America. *P. australis* converts a coastal wetland from a tidal cycle marsh to a marginal, raised substrate, which eliminates the habitat that served as a nursery to so many finfish. And of course, there is a cascade of adverse effects: the high level of filtering provided by the marshlands is lost and the birds that relied on these finfish nurseries for food are reduced as their habitat degrades. This process occurs in the tropics and temperate zones, and rainforests as oil palm, for example, replaces native species assemblages. While oil palm 'invades' by intentional planting, species of the families *Myrica* and *Mimosa* are spread to forest openings by wind and wildlife, and lead to long-lasting changes in habitat quality.

When is Old World Forest Loss happening?

Common sense tells us that forest loss is a continuing process related to a variety of factors. The history of forest loss is glimpsed in two recent studies: [Curtis et al. \(2018\)](#) report forest loss in Africa and Asia (not necessarily all tropical, but mostly) of 150 million hectares between 2001 and 2015, or a rate of 1 million hectares per year! The study by [Aleman et al. \(2018\)](#), looking at data from 1900 to 2000, reports forest loss for all tropical African areas studied as 21.7%, or 754,000 ha year⁻¹. The recent advances in satellite telemetry allow the resolution of forest loss at finer spatial and temporal scales than ever before (e.g., 3m², daily images, [Finer et al., 2018](#)), and it is critical that globally coordinated monitoring be maintained. By 2007, desperation calls from Borneo warned that this ecological refuge may be the last hold-out for Asian tropical rainforest ([Stone, 2007](#)).

"This is the only place [in Southeast Asia] where tropical rainforest can still be conserved on a large-enough scale to remain permanently viable," says Rahimatsah Amat, chief technical officer for Borneo with the World Wide Fund for Nature (WWF) in Malaysia.

An understanding of the problem of "When" is highlighted by [Alamgir et al. \(2019\)](#) from their analysis that shows how road and rail planning underway now threatens contiguous forest in Indonesian Borneo (Kalamantin) as soon as the funding can be put in place. The historic condition of Borneo's forests will be divided by transit corridors to a greater or lesser extent as the roads and rails develop. Central Africa, Indonesia, Malaysia, Borneo, Solomon Island region all provide some refuge to rainforest habitat and wildlife, and face the growing threat of sea and land links to meet the economic demands of these nations ([Fig. 5](#)). And the creation of transportation corridors is breaking up habitat for seriously endangered animals, such as the Tapanuli orangutan (inset, [Fig. 5](#)).

Where is Old World Forest Loss Happening: Regional Considerations?

Forest loss or disturbance is global, and accelerating as emerging nations seek the wealth and "modern" advances they observe in Europe, China and North America. Over the years 1982 to 2016, the planet experienced a net gain in forest, but the tropics actually lost about 4% of its cover. In a comparison of tropical forest loss, the Old World tropical forests in the Congo and Miombo woodlands of central and west Africa, as well as Asian areas in Vietnam, Myanmar, Cambodia and Indonesia, along with parts of Queensland, Australia, were all impacted by smallholding agriculture and more recently, crop-based commercial farming ([Song et al., 2018](#)). Following the classic definition of "Old World," a comparison by [Saatchi et al. \(2011\)](#) shows us that half of the carbon stocks of tropical forests are in South America (49%) and half in the forests of sub-Saharan Africa (25%) and Southeast Asia (26%). Hence the "Old World" holds half the bio-carbon of the forests, and also much of the untapped mineral and fossil fuel resources. These resources, combined with a desire by local people to achieve "modern wealth," means there is no sector of the planet that is not under threat from forest loss. The summary of threatened species hotspots across the globe makes this abundantly clear ([Fig. 3](#)).

Why is Old World Forest Loss happening?

There are two broad answers: economics and climate change. A simple answer is that local economies want to garner the wealth promised by the resources at hand, cutting trees for firewood, clearing land for smallholding agriculture and more recently, a move to create incomes from global demand for such crops as palm oil. The "why" of forest loss also has some arcane elements which are

Dammed to extinction

The entire population of Tapanuli orangutans lives in three patches of forest in northern Sumatra. A planned hydroelectric dam will cut off connections between them and probably doom the species

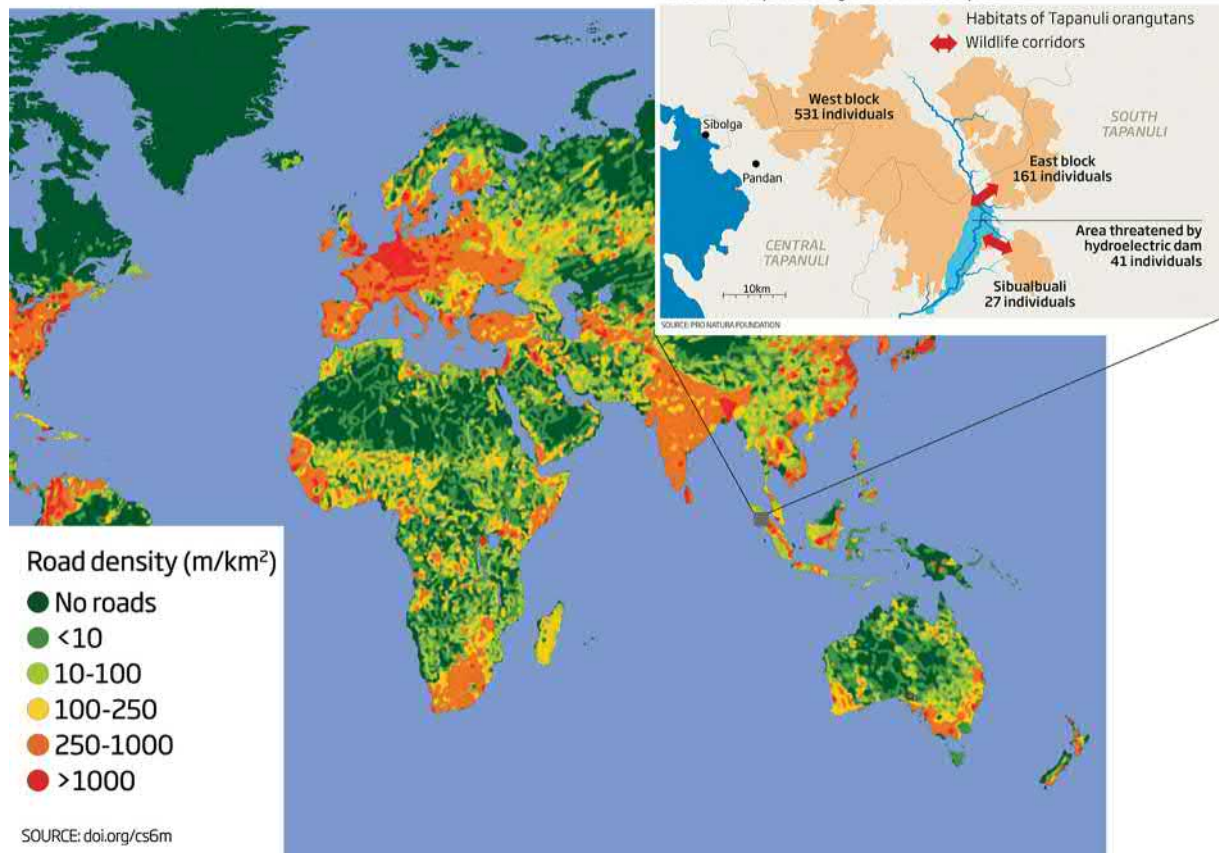


Fig. 5 Road density in the Old World and its consequences. Modified from Lawton G. (2018). Road kill. *New Scientist* 36–41.

just now becoming clear: global warming changes terrestrial ecosystems, and no part of the world is left out of this pattern (Nolan et al., 2018). This warming causes crop loss to insects which benefit from higher temperatures, quite notable for wheat, rice and maize crops in central Africa and throughout India and Southeast Asia (Deutsch et al., 2018). Loss of crop productivity encourages people to clear more woodlands to expand their income. And it is a short step from clearing for local agriculture to clearing for industrial scale resource extraction (e.g., oil, gold, uranium, rare earths, etc., Abrams et al., 2009).

What Do We Do About Forest Loss: Conservation Considerations?

The human response to any environmental disaster is generally twofold: prevent it and/or replace the lost resource. While many lessons have been learned about habitat restoration and replacement, a first question is: Are we too late? Then we need to prioritize our actions as we consider the alternatives. If we choose to restore habitats, how do we know what should be the model forest in a given location, which habitats are most valuable?

Ironically, one of the signs of degradation is the spread of woodlands where grasslands once dominated. Philosophically, the reaction of conservationists and policy-makers alike is to wonder if we should just live with and justify the changes. Will conservation policy resist forest losses, or adapt to life without the remarkable tropical forests? Simply put, will humanity make the necessary effort to preserve our atmosphere and hence our terrestrial habitats. It is imperative that the losses of woodlands be defined and their ecological processes understood. A comprehensive look at forest changes between 1900 and 2000 shows that global forest losses have been poorly studied, and that in fact, in certain areas there are actually numerical gains in tropical forest as savannah grows into woodlands (Aleman et al., 2018). Yet, we do not know if such 'gains' should be conserved or resisted.

The changes in global forest cover have many causes and consequences, ranging from shifts in wildlife populations (Allan et al., 2019; Woolley et al., 2008; Fullman et al., 2017) to suppression of fire (Abrams, 2015). The most disastrous cause-affect cycles are global warming and changes in rainfall which change habitat so fast that neither plants nor animals can adapt (Watson et al., 2018; Lézine et al., 2019).

Forest Protection/Preservation

The global effort to preserve open spaces, whether these be forests, grasslands, wetlands or marine protected area, began a mini-boom at the dawn of the 21st century. The IPCC had reached global acceptance with the Paris Agreement, within which was the proof that tropical forests provide not only enormous biodiversity benefits, but also sequestered the carbon dioxide that was shading Earth, making it warmer and warmer. The United Nations promoted the Interfaith Rainforest Initiative with their expressed mission: *The Interfaith Rainforest Initiative is an international, multi-faith alliance that works to bring moral urgency and faith-based leadership to global efforts to end tropical deforestation* (www.interfaithrainforest.org). The IRI works in Congo and Indonesia in the Old World region.

Rainforest preservation involves the complex issues of land ownership, local economic dependence on wood and demand for agricultural production. During the 1990s, as an awakening began about forest loss, a hope was expressed by Bawa and Seidler (1998) that parkland management might be an answer, but they acknowledged a lack of data to study the effectiveness of parks and preserves. Now, 20 years later, Bowker et al. (2017) have assembled data showing how parks in sub-Saharan Africa have reduced forest loss especially where human access is controlled. Burivalova et al. (2017) have shown this effect in Papua New Guinea using innovative technology that reads “soundscapes” to assess human presence. Clearly, the conservation of tropical forest is enhanced when land-use activity is controlled, be it through remoteness or local commitment (Fig. 6).

Replacement (Natural Recovery, Restoration)

For decades there have been examples of forward-thinking corporations, academics or individuals who have recognized and taken action against forest loss by planting trees or preventing mowing/burning. However, these disparate forces were only unified on a global scale for the sake of forest conservation during the late 20th century when the specter of climate change was called out at the 1992 Rio Conference. In the rush to respond to the early REDD initiatives which arose in the 1990s, particularly in southeast Asia, good concepts fell victim to abuse. Eventually the practice of cutting a woodland and then asking to replace it with REDD funding was halted in REDD+ as rules for the program were tightened.

So, how does one rebuild or restore forest habitat, and where and why is it happening? Early efforts began long ago, tied to commercial wood production, and focused on native or introduced species that grew quickly and produced large quantities of saleable wood. On a parallel track, conservationists began asking... How do we know what to plant? Can we combine commercial wood production with conservation of natural ecological communities? These remain the leading questions in the 21st century, and Cernansky (2018) reminds us at the ecosystem level to ask ourselves “...about matching trees to their locations, about the effects on nearby insects and other animals and about relationships with soil and the changing climate.”

Some progress on forest recovery has been reported, for example, in East Africa, but the challenges in just ecology alone are substantial. Chapman and Chapman (1995) and Cordeiro and Howe (2001) found particularly slow tree recruitment, and also slow growth in trees that were planted from cuttings, because savanna grasses and shrubs are so much more effective in capturing nutrients and moisture. In Kenya, a unique project used the Asian tree, *Casuarina* to restore lands scarred by mining (Abrams, 2018).

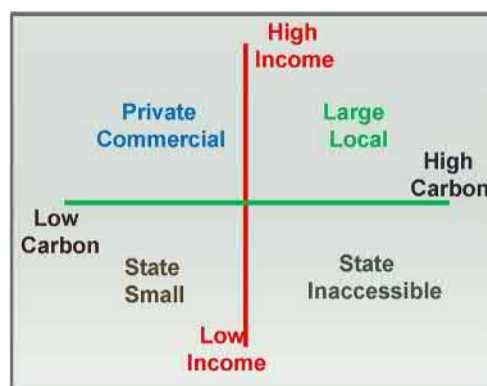


Fig. 6 Empirical comparison of types of preserve areas that conserve high carbon (i.e., biomass) under different ownerships (Abrams, 2011 from concept in Chhatre and Agrawal, 2009).

Conclusions

It is particularly difficult to measure climate induced changes in a place so diverse and ever changing as a rainforest, making this irreplaceable habitat an easy target for our abuse of the environment. There is ample proof, though, that if we manage native habitat by blending ecological theory with local knowledge, we can generate substantial gains in saving habitats that will sustain themselves to a greater or lesser extent. If intervention is necessary, it must be entirely for the benefit of the habitat, not simply for economic profit. Conservationists are accustomed to limitations, and are fully aware of economic pressures on land owners and government. But if scientific planning is given the license to direct land use and it is focused on resource protection by local jurisdictions, both people and nature can persist. The prevailing fear amongst conservationists now for the regions holding tropical rainforests is that the global push to spread “modernity” will not honor the ecological resources in those areas. There is a bona fide threat here because so many of the people of emerging nations seek the advantages garnered by the developed nations, and we can only hope to help them recognize the values they already have in their forests as conserved habitats.

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From the Sea to the Mountains

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Abstract

The elevational gradient at the Cofre de Perote in the central region of Veracruz State (eastern Mexico) is considered as one hotspot of plant diversity in the Neotropics. This is mainly due to the landscape heterogeneity and transition between biogeographical areas. In this study, we assessed the distribution patterns of vascular plant diversity, the underlying abiotic factors, and the impact of anthropogenic disturbance on floristic diversity. We treated the most relevant aspects of the composition and diversity of the vascular flora present within the different forest biomes along the elevational gradient, as well as the environmental problems of the region in which it is immersed. For this, we took ferns (terrestrial and epiphytic), terrestrial herbaceous angiosperms and shrubs as representative examples. We established a method of studying local plant diversity through sampling plots of 400 m². These plots were distributed in eight different elevational belts (six vegetation types) from the sea level to 3500 m, approximately every 500 m in elevation. Furthermore, we sampled in plots at different habitats (i.e., old-growth forest, degraded forest and secondary forest) in order to study the impact of the anthropogenic disturbance on plant diversity within each elevational belt. Our results showed a total of 551 vascular plant species (6.4% of the State's and 2.3% of the country's flora). The highest diversity of each study group was found at different elevations, mainly in areas with presence of humid montane forest. The highest diversity of terrestrial and epiphytic ferns, as well as terrestrial herbs, was found in mid-elevations between 2000 and 2500 m. The richness peak of shrubs was found generally in areas below 1000 m. Both extremes of the elevational gradient present contrasting climatic conditions in different periods of the year which limit the presence of a high diversity of the studied plant groups. A large portion of the flora is affected by anthropogenic disturbance. Thus, it is necessary to establish conservation plans for the area that include interconnected fragments to allow the dispersal of species.

Introduction

"Nowhere else it is possible to see better the admirable order of the different plant associations occurring, one above the other, then when one goes up from Veracruz to the plateau of Perote mountain in the space of a few hours, the man of science travels the whole scale of vegetation" (von Humboldt, 1827; Zamudio and Butanda, 1999). During his journey through Mexico, the naturalist Alexander von Humboldt left a record of the diversity of environments that he observed passing through the elevational gradient on the eastern slope of the state of Veracruz in 1803. This gradient begins at the port of Veracruz, on the coast of the Atlantic Ocean (Gulf of Mexico), and extends to the upper parts of the inactive Cofre de Perote volcano (4282 m.a.s.l.). Along a straight line of approximately 81 km, it is possible to travel through four climatic zones (*tierra caliente*, *templada*, *fría*, *helada*), six forest biomes (tropical semideciduous, tropical oak, humid montane, pine-oak, pine, fir forest) and alpine vegetation above timberline (Fig. 1). The presence of these different vegetation types and a high diversity of plant species along the elevational gradient is caused by an environmental heterogeneity defined by the combination of climatic, topographic and edaphic (soil) factors (Stein et al., 2014).

The upper zone of the elevational gradient (above 1500 m) forms part of the Trans-Mexican Volcanic Belt (TMVB). The lower part is formed by small hills extending to the coastal plain of the Gulf and the Sierra de Manuel Díaz. This is a mountain formation located across from the sea originating from pyroclastic flows of the Tertiary (Geissert and Enríquez, 2011). Finally, at sea level, there are the coastal lagoons of "La Mancha-El Llano," which are part of the area designated as "Ramsar" site.

Due to geomorphological conditions, the study area presents a wide variation of climates, (i.e., warm environments in the lower part, temperate in the mid-montane areas and cold in the upper part) (Soto Esparza and Giddings, 2011). Both the temperature and precipitation vary according to elevation (Fig. 1). The temperature shows a linear decrease with increasing elevation, while the average precipitation is higher in the middle parts and decreases at the extremes of the gradient (Carvajal-Hernández et al., 2017).

Numerous studies have been carried out that describe the elevational patterns of various taxonomic groups in different tropical zones of the world (e.g., Rahbek, 1995; Blackburn and Gaston, 1996; Kessler, 2001; Krömer et al., 2005; Grau et al., 2007). These studies have shown that biodiversity can depend either directly or indirectly on elevation. However, little is known about how species richness varies in the transitional zone between the Nearctic and Neotropical regions, as is the case in Mexico, particularly in

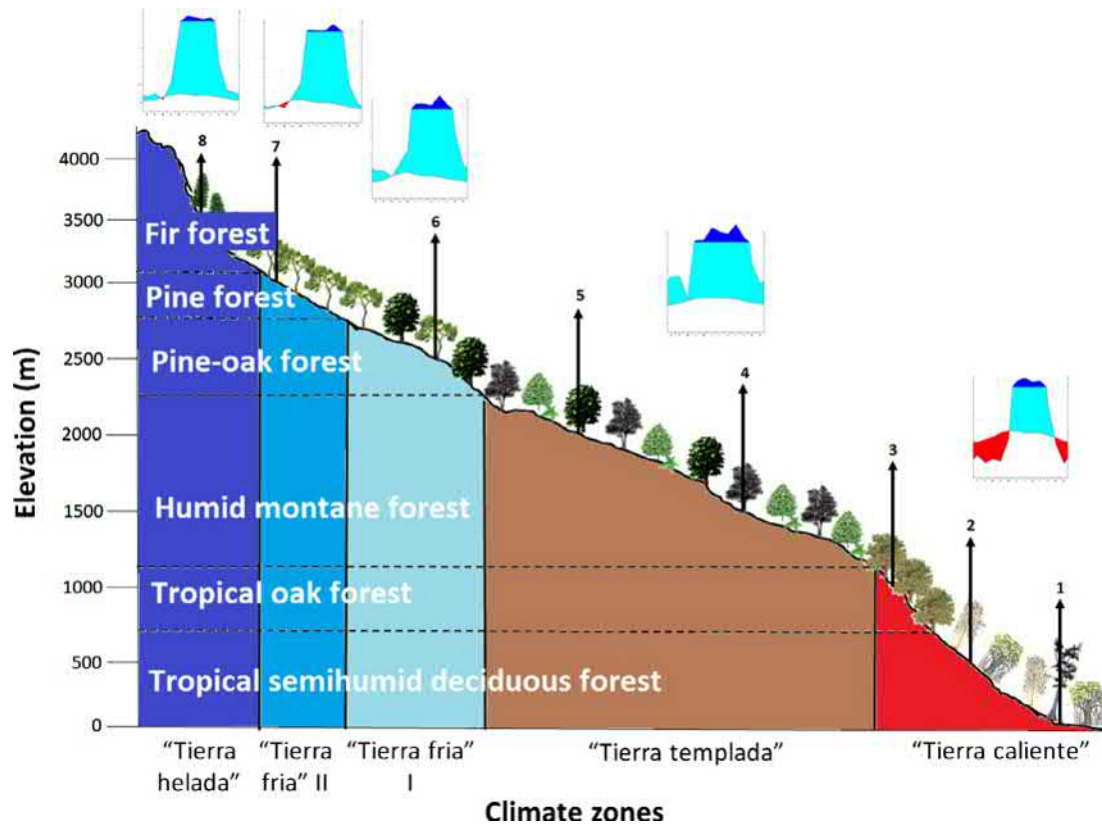


Fig. 1 Schematic representation of the types of vegetation and climatic zones present along the elevational gradient of the Cofre de Perote, Veracruz, Mexico (Gómez-Díaz et al., 2018).

the state of Veracruz. Furthermore, very few studies have analyzed the anthropogenic influence in different elevational belts and its impact on biodiversity (Kessler et al., 2001). This last issue is of great importance because currently, anthropic landscapes dominate the surface in Mexico (Sánchez Colón et al., 2009). The state of Veracruz is no exception with a loss of over 90% of its pristine vegetation (Castillo-Campos et al., 2011).

Over the course of 8 years, we have studied the distributional patterns of vascular plant diversity and the underlying abiotic factors in this region. Additionally, we studied the impact of anthropogenic disturbance on floristic diversity. All this has been realized within the framework of the interdisciplinary project entitled “BIOVERA: Exploration and explanation of biodiversity patterns along gradients of altitude, climate and anthropogenic influence in central Veracruz, Mexico.” This article deals with the most relevant aspects of the composition and diversity of the vascular flora present within the vegetation types along the elevational gradient, as well as the environmental problems of the region in which it is immersed. For this, we took ferns, terrestrial herbaceous angiosperms and shrubs as representative examples.

The first plant group includes many taxa associated with conserved environments, and thus ferns are considered as bioindicators of ecosystem quality (Krömer et al., 2013, 2014; Carvajal-Hernández et al., 2014; Armenta-Montero et al., 2015). In contrast, herbaceous plants have been associated with secondary ecosystems (Barlow and Gardner, 2007; Gómez-Díaz et al., 2017a, 2017b). Although no in-depth studies have classified shrubs as bioindicators, Bautista-Bello et al. (2019) have observed an increase in their richness and changes on the floristic composition with human disturbance. But this only happens in warm environments (at elevations lower than 1000). Thus, it is likely that some taxonomic groups could be used as an indicator of human disturbance.

Vegetation Types

The orographic and climatic differences that occur along the transect allow the presence of different types of forest vegetation. These climates range from dry and warm environments in the lower part (tropical semi-humid deciduous forest and tropical oak forest) to humid-temperate zones at mid-elevations (humid montane forest and pine-oak forest), and cold conditions in the upper part (pine forest and fir forest) (Figs. 1 and 2).

Hereinafter, the different vegetation types are described according to our field observations and considering information published by Castillo-Campos et al. (2011), Carvajal-Hernández and Krömer (2015), Gómez-Díaz et al. (2017a, b), and Bautista-Bello (2018).

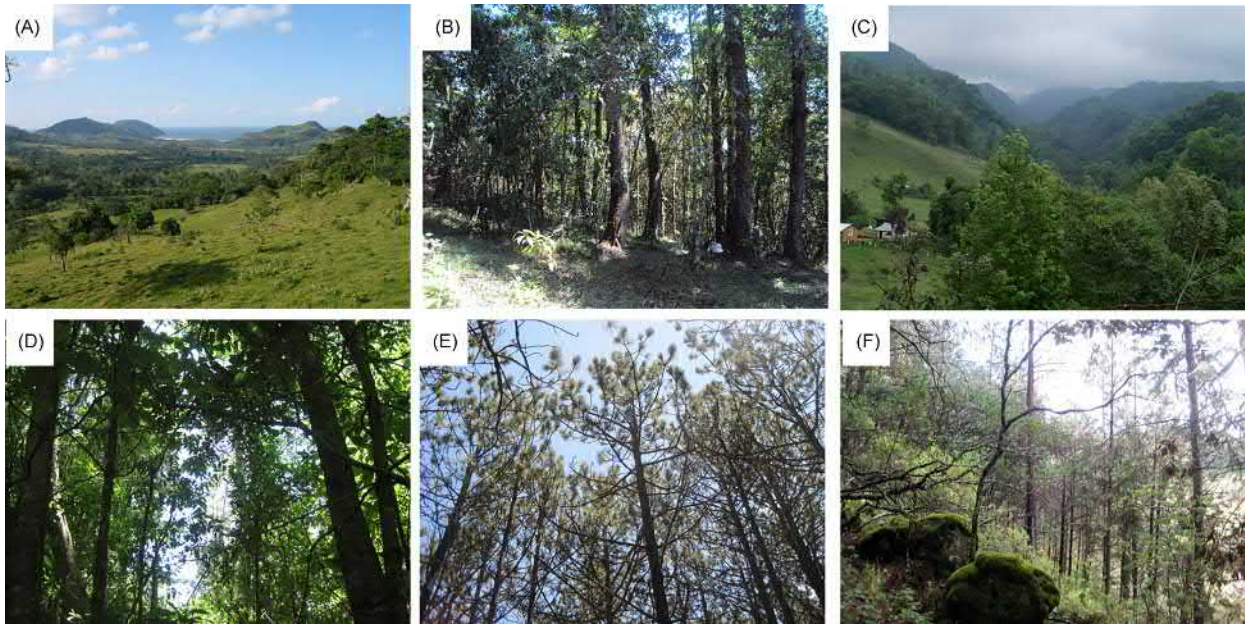


Fig. 2 Views of vegetation types along the elevational gradient of the Cofre de Perote, Veracruz, Mexico. (A) Tropical semihumid deciduous forest; (B) Tropical oak forest; (C) Humid montane forest; (D) Pine-oak forest; (E) Pine forest; (F) Fir forest.

Tropical semihumid deciduous forest is found from sea level to 800 m in the elevational gradient studied and is represented in fragments isolated by anthropogenic activity. *Bursera simaruba* (L.) Sarg., *Comocladia engleriana* Loes., and *Plumeria rubra* L. stand out in the arboreal stratum (Fig. 2A). Due to the proximity with the transition zone of the tropical oak forest, it is also possible to find individuals of the genus *Quercus*. The shrub layer is dominated by *Dioon edule* Lindl., *Chusquea* Kunth., and some species of *Chamaedorea* Liebm. ex Mart. The herbaceous stratum is dominated by fern species of the genera *Adiantum* L. and *Tectaria* Cav. The hemiepiphytes are also represented by aroids of the genera *Monstera* Adans. and *Philodendron* Schott.

Tropical oak forest is found in the elevational gradient between 900 and 1100 m (Fig. 2B). The most representative species are *Quercus oleoides* Schltdl. and Cham., *Q. peduncularis* Nee and *Q. sapotifolia* Liebm. in combination with some lowland species, such as *Byrsonima crassifolia* (L.) Kunth and *Pouteria campechiana* (Kunth) Baehni. Epiphytic orchids, such as *Brassavola nodosa* (L.) Lindl., *Epidendrum ciliare* L. and *Prosthechea radiata* (Lindl.) W.E. Higgins, also occur together with abundant bromeliads (e.g., *Tillandsia ionantha* Planch., *T. paucifolia* Baker, and *T. filifolia* Schltdl. and Cham.) and lianas (*Smilax regelii* Killip and C.V. Morton). *Acacia cornigera* (L.) Willd., *A. pennatula* (Schltdl. and Cham.) Benth., *Malvaviscus arboreus* Cav., *Erythrina herbacea* L., *Lysiloma acapulcense* (Kunth) Benth., and *Bambusa amplexifolia* (J. Presl) Schult. grow in the shrub layer. In the herbaceous stratum, *Bromelia pinguin* L. and *Blechnum occidentale* L. stand out. This vegetation type is represented in isolated fragments, which are remnants of the Pleistocene of boreal origin that replaced the tropical vegetation during the last glaciations (Arriaga et al., 2000).

Humid montane forest can be found in the study gradient between 1300 and 2200 m of elevation (Fig. 2C). It is characterized by the presence of *Carpinus caroliniana* Walter, *Liquidambar styraciflua* L., *Clethra mexicana* DC., *Meliosma alba* (Schltdl.) Walp., *Styrax glabrescens* Benth., and several species of *Quercus* L., which dominate the arboreal stratum. The most common shrubs are *Psychotria* L. and tree ferns of the genera *Cyathea* Kaulf. and *Alsophila* R.Br. Epiphytic herbs are abundant in this environment with ferns represented by several genera. The families Bromeliaceae and Orchidaceae stand out for their species diversity.

Pine-oak forest occurs between 2300 and 2600 m of elevation (Fig. 2D). *Quercus crassifolia* Bonpl. and *Q. laurina* Bonpl., *Pinus patula* Schltdl. and Cham., and *Taxus globosa* Schltdl. are the species that stand out in the arboreal stratum. The shrub layer is represented mainly by species of the genus *Senecio* L. Species of the Asteraceae and Poaceae dominate the herbaceous stratum along with ferns of the genera *Dryopteris* Adans., *Plagiogyria* Bower, and *Polystichum* Roth.

Pine forest is located at elevations between 2700 and 3000 m and exhibits reduced plant richness (Fig. 2E). The most representative tree species are *Pinus pseudostrobus* Lindl., *P. montezumae* Lamb., and *Arbutus xalapensis* Kunth. In the shrub layer, *Baccharis conferta* Kunth stands out. The herbaceous stratum is mostly represented by species of the Poaceae, Asteraceae, and Crassulaceae, the latter mainly of the genus *Echeveria* DC., as well as ferns of the genus *Dryopteris* Adans. Epiphytism is scarce, represented mostly by two fern species (*Pleopeltis polylepis* (Roem ex Kunze) T. Moore and *Polypodium plebeium* Schltdl. and Cham.)

Fir forest is confined to high mountain sites, between 3100 and 3600 m (Fig. 2F). This plant community is composed of arboreal elements whose height varies between 20 and 40 m. The characteristic feature of its dominant elements is the typical triangular shape of its cups. *Abies religiosa* (Kunth) Schltdl. and Cham. is well represented in the upper part of the Cofre de Perote, where the shrub and herbaceous strata are scarce.

Alpine vegetation occurs in areas above timberline (± 3900 m). It is composed mainly by species of the Poaceae family, which dominate the landscape of this vegetation type. Additionally, some shrub elements such as *Juniperus monticola* Martínez, as well as species of the Berberidaceae and Grossulariaceae can be found. Below that elevation, the arboreal vegetation starts with *Pinus hartwegii* Lindl. trees of low stature.

Distributional Patterns of Vascular Plant Richness Along the Elevational Gradient

The vegetation types present along the elevational gradient are found in isolated fragments immersed in a landscape that is strongly transformed by human activities (e.g., livestock, coffee, mango, and sugarcane plantations). Thus, the area is not exempt from the factors that have led to the sharp decline in the original vegetation of the state of Veracruz (i.e., represented by less than 10% of its original surface across the state) (Castillo-Campos et al., 2011; Ellis et al., 2011). For the study area, it has been shown that the surface of the remaining forests has decreased by 57% with an increase of the deforestation rate from 2000 to 2014 (Gómez-Díaz et al., 2018). This environmental degradation is particularly striking because Veracruz is recognized for its high floristic diversity and for showing a high degree of plant endemism (Gómez-Pompa et al., 2010). The state ranks as having the third highest number of vascular plant species in the country, following Chiapas and Oaxaca (Villaseñor, 2016).

Given the high diversity of environments and species in the study area and considering the evident loss of forest cover, we considered the following research questions:

- Which are the distribution patterns of vascular plants?
- What impact does the anthropogenic disturbance have on plant diversity?

To answer the above questions, we established a method of studying local plant diversity through sampling plots of 400 m^2 (Kessler and Bach, 1999). These plots were distributed in eight different elevational belts from the sea level up to 3500 m, approximately every 500 m in elevation (Fig. 3).

It is important to clarify that, for this study, no plant sampling was realized in the alpine vegetation (above 3900 m) because no forest cover is found here. Thus, comparisons with the rest of the data are not possible. Along this elevational gradient, we sampled ferns, terrestrial herbaceous angiosperms and shrubs in all forest vegetation types, from the tropical forests at the lower part to the coniferous forests at the upper zone of the transect. Furthermore, to study the impact of the anthropogenic disturbance on plant diversity within each elevational belt, we sampled in plots at different habitats: old-growth forest (without evident disturbance), degraded forest (with evident anthropogenic disturbance, for example, selective logging, livestock grazing, firewood collection, roads, etc.) and secondary forest (of about 15 years of regeneration) (Table 1).

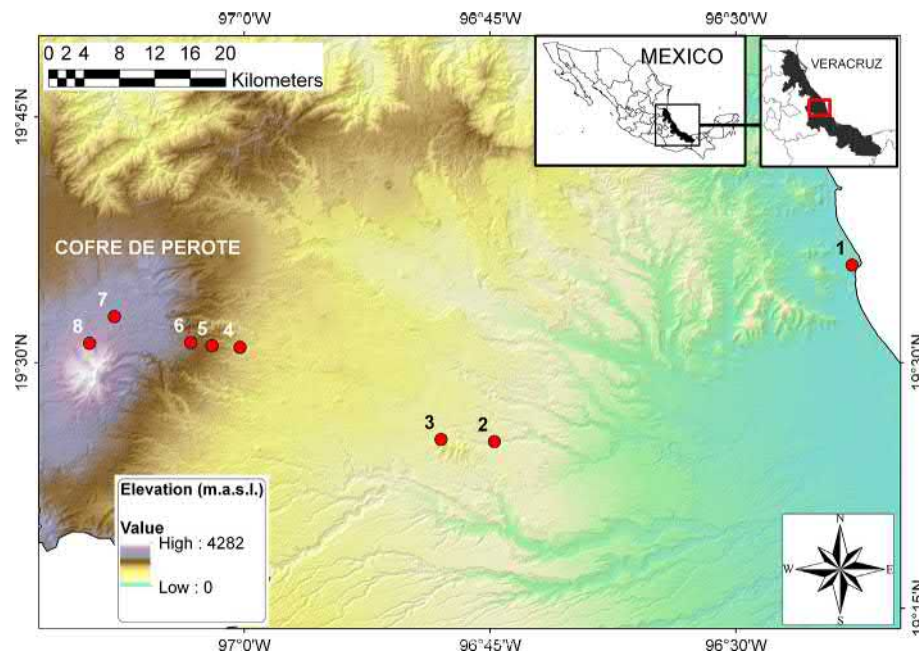


Fig. 3 Location of the elevational transect on the eastern slope of the Cofre de Perote, Veracruz, Mexico. (1) La Mancha (20 m); (2) Palmarejo (500 m); (3) Chavarrillo (1000 m); (4) Los Capulines (1500 m); (5) El Zapotal (2000 m); (6) El Encinal (2500 m); (7) Los Pescados (3000 m); (8) El Conejo (3500 m) (Gómez-Díaz et al., 2017a).

Table 1 Classification of habitats with different forest-use intensities according to the main physiognomic characteristic, the gap fraction in the canopy, dominance of canopy trees, percentage of shrubs and the presence of lianas, along the elevational gradient of Cofre de Perote, Veracruz, Mexico

Habitat	Characteristic	Gaps (%)	Forest-use intensity	Canopy trees	Shrub (%)	Lianas
Old-growth	No obvious forest use, dominance of mature trees	<10	Low	High	<30	Very low
Degraded	Selective logging, grazing and understory removal	11–25	Medium	Low	30–50	Low
Secondary	regrown after clear-cut	>25	High	Very low	>50	High

In total, we recorded the presence of all species of ferns (terrestrial and epiphytic), herbaceous angiosperms and shrubs in 120 plots (4800 m²). Additionally, we placed data loggers in each of the six vegetation types present in the region. These loggers recorded the microclimate (temperature, relative humidity, and light incidence) during a full year between 2014 and 2015.

Our results showed a total of 551 vascular plant species (Bautista-Bello et al., 2019; Carvajal-Hernández and Krömer, 2015; Gómez-Díaz et al., 2017a). In Veracruz, there are 8497 vascular plants and in Mexico 23,314 (Villaseñor, 2016), thus the study area represented 6.4% of the State's and 2.3% of the country's flora (Table 2).

The species distribution patterns along the gradient varied according to each group. For example, the highest richness was found at 2000 m for ferns (Carvajal-Hernández and Krömer, 2015) and at 2500 m for terrestrial herbs (Gómez-Díaz et al., 2017a), which both showed a hump-shaped diversity pattern. In contrast, for shrubs, we observed a peak at 1000 m followed by a decrease of species with increasing elevation (Bautista-Bello et al., 2019).

Nevertheless, the highest diversity of ferns and herbs was generally located between 1500 and 2500 m. This area coincides with the presence of humid montane forests, which have been shown to be the habitats with the highest plant diversity per surface area in Mexico (Rzedowski, 1996; Gual-Díaz and Rendón-Correa, 2014). On the other hand, the humid montane forest represents less than 1% of the surface in Mexico, with a decreasing tendency due to its continuous deforestation and fragmentation (CONABIO, 2010; Gual-Díaz and Rendón-Correa, 2014). Taking the ferns as an indicator group of the quality of the ecosystems (Carvajal-Hernández et al., 2014; Krömer et al., 2014), this study corroborated previous findings that the humid montane forest suffers the greatest loss of species richness due to anthropogenic influence. Furthermore, it is necessary to consider that the decrease in fern richness also leads to a loss of ecosystem functions (Carvajal-Hernández et al., 2017, 2018a). This combination of factors makes the humid montane forest the most-affected vegetation type along the studied elevational gradient.

In the elevational range where humid montane forests are found, mean annual temperature ranges between 16°C and 12°C, mean annual precipitation ranges between 1700 and 1800 mm, and relative humidity between 85% and 90% (Carvajal-Hernández et al., 2017). The data loggers placed in the study area showed that temperature and relative humidity values decreased uniformly with increasing elevation. However, anthropogenic disturbance led to an increase in temperature and incidence of light in the microclimate, which caused a decrease in relative humidity. Although it is true that this phenomenon occurs in all the elevational belts studied, these changes were more accentuated in the humid montane forest (Carvajal-Hernández et al., 2017).

Another factor that must be highlighted is that both elevations of 1000 m and 2500 m (where shrubs and terrestrial herbs, respectively, are most diverse) correspond to transitional sites between different vegetation types (Fig. 1). This suggests that these are areas where the confluence of mainly climatic factors allows a mixture of species coming from areas around the transition sites and increases the diversity of these groups (Heaney, 2001; De León-Mata et al., 2013; Llambi, 2015).

The temperate pine and fir forests of the upper zone of the elevational gradient, as well as the vegetation types of the lower zones, presented the lowest diversity of all study groups (Fig. 1 and Table 2). We attributed this to several factors. For example, ferns have less beta and functional diversity related to the changes in species composition when a disturbance occurs. Therefore, the species

Table 2 Species richness of the groups studied along the elevational gradient of Cofre de Perote, Veracruz, Mexico (Bautista-Bello et al., 2019; Carvajal-Hernández and Krömer, 2015; Gómez-Díaz et al., 2017a)

Elevation (m)	Vegetation type	OG			DE			SE			Total species richness		
		F	H	S	F	H	S	F	H	S	F	H	S
20	TSDF	3	4	20	3	6	16	3	8	12	4	13	26
500	TSDF/TOF	11	12	11	7	35	13	7	11	24	28	45	38
1000	TOF	7	11	24	7	13	21	8	19	32	14	27	49
1500	HMF	44	24	9	23	21	13	22	20	8	66	48	20
2000	HMF	46	16	15	35	18	20	29	20	16	62	38	32
2500	POF	39	47	17	35	41	14	32	38	8	46	72	25
3000	PF	7	22	7	6	26	11	6	37	9	9	50	14
3500	FF	4	9	8	3	13	3	7	10	6	7	18	10

Type of vegetation: TSDF: tropical semideciduous forest, TOF: tropical oak forest, HMF: humid montane forest, POF: pine-oak forest, PF: pine forest, and FF: fir forest. OG: old-growth; DE: degraded forest; SE: secondary forest. F: Ferns; H: Herbs; S: Shrubs.

that occur at the extremes of the gradient are specifically adapted to the stressful conditions of that extreme (i.e., high temperatures and prolonged droughts in the lower zones and low temperatures, winter snowfall, and summer droughts in the upper zones).

The above indicates that conditions of relative climatic stability prevail in the middle part of the elevational gradient. This is an important factor in establishing a higher number of species due to the existence of favorable circumstances for the diversification of niches, following the arguments that explain the higher diversity observed in the tropics (Hildebrand, 2004). In contrast, this situation does not occur at the extremes of the gradient, where climatic heterogeneity exerts a strong pressure on diversity, limiting the presence of species to those with the capacity to adapt to these mostly unfavorable conditions.

Anthropogenic Impact on Species Richness

We observed that the anthropogenic disturbance had different impacts on species richness depending on the plant group. For example, in the case of ferns, disturbance generated a loss of species, while a higher richness of herbs was observed in the zones with moderate forest-use intensity (Table 3).

Ferns have been used as a study group to understand the patterns of species richness worldwide for two main reasons. First, they are widely distributed on the planet with approximately 11,000 species (PPG, 2016). Second, due to their reproduction by spores, the dispersion of the species is highly dependent on environmental conditions such as temperature, humidity, and the substrate. This minimizes their dependence on biotic factors. These features have also resulted in their use as bioindicators of ecosystem quality (Carvajal-Hernández et al., 2017).

In contrast, little is known about the influence of human disturbance on herbaceous angiosperms, despite their importance for tropical diversity and ecosystem function (Willinghöfer et al., 2012; Cicuzza et al., 2013). Studies published thus far indicate that many primary and endemic forest herbaceous species were also recorded in areas with secondary vegetation (Barlow et al., 2007). Therefore, such anthropic habitats could help to conserve endemic species (Marin-Spiotta et al., 2007).

Furthermore, particularly little is known about the human impact on the diversity and distribution of shrubs. The few studies that consider shrub species suggest that disturbance and fragmentation affect the seeds and seedlings of the understory in lowland forests by modifying microclimatic conditions in a fragmented landscape. Apparently, this group is adapted to moderate conditions of humidity and temperature that, respectively, decrease and increase with the intensity of forest-use (e.g., Dale et al., 2001; Leicht-Young and Pavlovic, 2015; Schnitzer, 2015).

Our sampling method (described in the previous section) revealed that ferns were sensitive to changes in the microclimate caused by disturbance, whereas herbaceous plants exhibited no influence from disturbance. For shrubs, we observed that changes in forest structure caused by human action can increase the total richness within the forest fragments. However, their floristic composition was modified due to a loss of species of 7%–26% when changing from an old-growth forest to a secondary one (Tables 2 and 3).

Modifications in the structure of the humid montane forests caused by human action considerably affected fern communities, as evidenced by a 40% to 70% reduction in species richness in disturbed vegetation (Carvajal-Hernández et al., 2017) (Table 3). This reduction was largely due to changes in the microclimate and forest physiognomy (Köster et al., 2009). In the elevational belts of 1000 and 3500 m, the secondary forests harbored the same richness as the old-growth forests due to the presence of species adapted to extreme conditions of drought and temperature, which are not affected by the disturbance (Hietz, 2010). The richness of 155 ferns found in this study represent 27% of the 574-species recorded for Veracruz (Krömer et al., 2015; Carvajal-Hernández et al., 2018b) and 15% of the 1030 Mexican pteridophytes (Tejero-Díez et al., 2014). However, only three of these 155 are endemic to Mexico and nine are protected by Mexican law (NOM-059-SEMARNAT-2010) for presenting some status of extinction risk. Considering that this richness was registered in a small sample area (4800 m²), the elevational gradient studied protects an important proportion of the country's pteridophyte flora. The epiphytic component of the ferns represented almost 50% of the total richness, however, its proportion changed according to elevation (Carvajal-Hernández and Krömer, 2015).

The influence of disturbance on ferns was not only observed in terms of richness but also in terms of species turnover. We observed a strong exchange of species between an old-growth forest and disturbed sites, as well as a loss in functional diversity (mainly in the humid montane forest). However, at 500 m richness decreased, but functional diversity remained constant, indicating functional redundancy in that environment (Carvajal-Hernández et al., 2017, 2018a).

Regarding herbaceous angiosperms, we recorded 264 species of which 31 are endemic to Mexico (Gómez-Díaz et al., 2017a). Both alpha and gamma diversity showed a hump-shaped pattern with a peak of richness between 2500 and 3000 m, respectively.

Table 3 Species richness by plant group and by environment/habitat (OG: old-growth; DE: degraded; SE: secondary forest) reported along the elevational gradient of Cofre de Perote, Veracruz, Mexico

Group	Total	OG	DE	SE	Elevation (m) with a peak of species richness
Shrubs	132	111	111	115	1000
Ferns (terrestrial and epiphytes)	155	161	119	114	2000
Terrestrial angiosperm herbs	250	145	173	163	2500
Total	551	417	403	392	

We inferred that the belt of 2500 m is particularly sensitive to anthropogenic disturbance and intensification of forest-use. At 3100 m, a high total diversity (50 species) was driven by a high beta diversity within the habitats (Table 2). Here, a loss of a specific forest area could be compensated if similar assemblages are produced in nearby areas. High beta diversity and endemism suggested that mixtures of different habitats are needed to maintain a high gamma diversity of terrestrial herbs along the elevational gradient. In general terms, the disturbance does not affect the species richness, as indicated by the fact that the values of alpha diversity remained constant with disturbance. However, the beta diversity was observed to be higher when comparing mature forest with secondary forest.

Regarding shrubs, we recorded a total of 118 species and 14 morphospecies (a taxonomic species based wholly on morphological differences from related species and that its identity has not been possible due to the lack of any element of taxonomic importance) (Bautista-Bello et al., 2019). Forest fragments in the elevational belts of 500 and 1000 m are the most species-rich but are at the same time the most susceptible to human disturbances. The anthropogenic influence on these forests can increase the diversity of species locally, but also modify the floristic composition of an old-growth habitat when transformed to a secondary one. Furthermore, there were six endemic species to Mexico and one under protection (*Oreopanax echinops* (Schltdl. and Cham.) Decne. and Planch.) according to the IUCN Red List of threatened species. The conservation of these species represents an important topic considering the scarce floristic and ecological information on this and other plant groups.

It is important to mention that no shrub species registered in this study appears in the NOM-059-SEMARNAT-2010 (SEMARNAT, 2010), which protects native species of flora and fauna in Mexico. Nevertheless, the list of plants included in the NOM is incomplete or outdated, and thus the number of endangered shrub species in the area is uncertain. There are new, rare or endemic species like *Hoffmannia arqueonervosa* Cast.-Campos and *Psychotria perotensis* Cast.-Campos (Castillo-Campos et al., 2009, 2013), which have recently been discovered in fragments near the study gradient which should be considered as threatened. Likewise, there are species from other groups of plants that are endemic to the central region of Veracruz, such as *Monstera florescanoana* Croat, T. Krömer and Acebey, *Peperomia chazaroi* G. Mathieu and T. Krömer and *Resinanthus aromaticus* (Cast.-Campos and Lorence) Borhidi (Croat et al., 2010; Gómez-Pompa et al., 2010; Mathieu et al., 2015), and which are endangered due to the reduction of their populations and anthropic pressure exerted on the plant communities where they occur. Therefore, it is important to study the ecological patterns of all plant groups as these are not distributed following a general pattern but respond differently to biotic and abiotic factors (Tables 2 and 3).

General Conclusions

The elevational gradient studied traverses six different forest biomes between sea level and the upper slopes of the Cofre de Perote mountain, which represent a considerable part of the species richness of the vascular flora of the state of Veracruz and Mexico. This high diversity of vegetation types and plant species is a result of varying climatic and topographic conditions that occur along the mountain range (Figs. 1 and 3). In general terms, although it depends on the plant group, the diversity of species is concentrated in the middle part of the gradient, in the humid montane forest, or in the adjacent transition zones. In the cases of terrestrial and epiphytic ferns and terrestrial herbs, the highest diversity was found in mid-elevations between 2000 and 2500 m. In the case of shrubs, the richness peak was found generally in areas between 500 and 1000 m. Both extremes of the elevational gradient present contrasting climatic conditions in different periods of the year (prolonged droughts and extreme temperatures) that limit the presence of a high diversity of species of the studied plant groups (Table 3).

The forest cover in the study area has been constantly reduced for the implementation of livestock and agricultural land. Based on several recent studies, it is known that the region harbors an important part of the state's plant diversity. However, a large portion of the flora is affected by anthropogenic disturbance, and thus it is necessary to establish conservation plans for the area that include interconnected fragments to allow the dispersal of species. This will ensure the conservation of the high plant diversity, as well as of other organisms that depend on the vegetation, still found in the montane region of eastern Mexico.

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The Inland Temperate Rainforest and Interior Wetbelt Biomes of Western North America

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Glossary

Biogeoclimatic ecosystem classification system (BEC) An ecosystem-based classification system that groups ecologically similar sites based on climate, vegetation, soils, and topography. BEC is widely used throughout British Columbia as a framework for resource management and scientific research.

Canopy veteran A tree of advanced age which dominates the upper canopy of a forest. Veteran trees often provide important microhabitats such as cavities, bare wood and dead branches that support birds and mammals and tree-dwelling lichens, mosses and liverworts.

Climate envelope The specific temperatures and rainfall patterns associated with the locations where a particular species currently exists. Climate envelope models are used to predict the hypothetical distribution of species under various future climate change scenarios.

Climatic moisture deficit An index of moisture availability, reflecting the degree to which monthly evapotranspiration demand of local vegetation is exceeded (or met) by monthly precipitation. A deficit represents the amount of moisture plants must capture from other sources (fog, ground water, etc.).

Coarse woody debris (CWD) Fallen dead trees and the remains of large branches on the ground in forests. Standing and dead fallen trees are a critical component of forested ecosystems and contribute to nutrient cycling, long-term carbon storage, tree regeneration, wildlife habitat, and biological diversity. CWD is defined as having a cross-sectional diameter of ≥ 10 cm.

Cumulative environmental impact Changes to the environment (both physical and ecological) caused by multiple past and present human actions. Cumulative impacts are often difficult to predict.

Decadent forest A term applied by the logging industry to forests containing dead, broken, deformed, or very old trees. Such forests are ecologically among the most valuable because they sustain a disproportionately high number of biological processes and living species (biodiversity).

Edge effects Changes in population or community structure (the number and type of organisms that are present) caused by an abrupt transition between two quite different adjoining habitats. Edge effects commonly result in the loss of forest dependent species after forests have been fragmented by roads and logging.

Gap dynamics A common process of tree growth in mature and old-growth forests whereby the death of one or a few large dominant trees permits smaller trees within the forest understory to grow and fill their place.

Old-growth Management Area (OGMA) In British Columbia, a spatially defined area of (ostensibly) old-growth forest where logging and other forestry development is discouraged or constrained in order to achieve biodiversity targets; but see Fig. 12.

Orographic rain Precipitation produced when moist air is lifted, cools, and forms clouds as it moves over a mountain range.

Rain shadow An area with relatively little precipitation due to the effect of a topographic barrier, usually a mountain range, which causes the prevailing winds to release their moisture on the windward side, causing the leeward side to be dry.

Silvicultural system Techniques used to control the establishment, growth, composition, and quality of forest vegetation for a specific suite of forest resource objectives. Activities may include planting, brushing, spacing, thinning, fertilizing, and application of herbicides.

Subboreal A biogeographic zone that approaches the boreal in climatic condition but is neither as cold nor as dry.

Toe-slope A topographic position where the lower slopes of a U-shaped valley meet the flat valley bottom.

Abstract

The Inland Temperate Rainforests (ITR) of Northwest North America represent a globally significant biome characterized by a unique assemblage of oceanic and boreal taxa. Here we recognize two major ITR ecosystems in British Columbia, both of which were historically dominated by old-growth forests: (1) the Kispiox ITR in the rain shadow of the North Coast Mountains; and (2) the Caribou ITR on the windward side of the North Columbia Mountains. A third major biome, the Interior Wetbelt, stretches southward from the Caribou ITR into Montana, Idaho, and Washington State. The Interior Wetbelt contains topographically induced pockets of rainforest, but is characterized by a more open mosaic of forests and grassland. The loss of old-growth forests in ITR ecosystems, primarily due to logging, has now reached critical thresholds. Only 31.7% and 23.1% respectively of Kispiox and Caribou ITR landscapes remain as old-growth forests, with the Interior Wetbelt down to 4.6% old-growth forest. This poses major threats to old-growth-dependent taxa such as the critically endangered deep-snow mountain caribou. We recommend an immediate moratorium on clear-cut logging in forest stands older than 250 years within the Kispiox and Caribou ITR. Given the extreme rarity of old-growth forests in the Interior Wetbelt, remaining stands exceeding 150 years in age should be designated as protected areas. Management plans in all three regions should include measures to ensure that remnant old-growth forest stands are buffered from the adverse impacts of adjacent cut-blocks. This should be accompanied by the development of landscape-level conservation designs, recognizing the needs for connectivity and continuity of old-growth forest cover.

What is the Inland Temperate Rainforest?

The Coastal Temperate Rainforest (CTR) biome is characteristic of mid-latitude maritime regions, where coastal mountain ranges causes onshore winds to release much of their moisture as rain or snow before heading inland (DellaSala et al., 2011a). In the northern hemisphere, CTRs are restricted primarily to the western and eastern margins of North America and Eurasia, where they are defined by their mild maritime climate, moderate seasonal temperatures, and significant precipitation spread more or less evenly over the year (Alaback, 1996; DellaSala et al., 2011a). The most extensive such forests occur along the Pacific coast of North America, stretching >2500 km from southeast Alaska in the north, through British Columbia (B.C.), and southward into northern California (Fig. 1).

Also present in western North America, Europe and Asia are inland variants of the temperate rainforest biome. Such ecosystems, variously termed Inland Temperate Rainforests and Inland Per-humid Rainforests (Goward and Arsenault, 2000; Stevenson et al., 2011; DellaSala et al., 2011b,c), occur exclusively in the Northern Hemisphere and are much more circumscribed than their coastal counterparts (DellaSala et al., 2011a). In this article we characterize three Inland Temperate Rainforest (ITR) ecosystems that have been recognized in western North America, here referred to as the Kispiox ITR, the Caribou ITR and the Interior Wetbelt (Fig. 1).

Unlike the Pacific CTR, which forms a broad continuous band along the west coast of the continent (Fig. 1), ITR ecosystems in western North America are generally constrained within mountain valleys, making them more linear and essentially discontinuous. This is especially the case with the Interior Wetbelt, where forest stands with ITR characteristics are generally confined to small areas such as mesic canyons and the spray zones of waterfalls (McCune and Allen, 1984; Goward and Spribille, 2005).

The Kispiox Inland Temperate Rainforest

The Kispiox ITR occurs between ca. 55° N and 56° N in the immediate rain shadow of the Coast Mountains in the Skeena and Nass River watersheds (Fig. 1). Transitional to the Pacific CTR, its forests are classified within the Interior Cedar-Hemlock (ICH) biogeoclimatic (BEC) zone of Meidinger and Pojar (1991). Included here are both the wetter and cooler “Wet Cold” and “Very-Wet Cold” ICH BEC subzones of the Iskut and Nass River watersheds, and the somewhat drier and warmer “Moist Cold” ICH BEC subzone of the upper Skeena watershed (Fig. 1).

Reflecting its transitional status, the Kispiox ITR supports a mix of both coastal temperate rainforest trees, such as amabilis fir (*Abies amabilis*), and Roche spruce (*Picea glauca* × *sitchensis*), and subcontinental trees, such as hybrid spruce (*Picea engelmannii* × *glauca*) and subalpine fir (*Abies lasiocarpa*). The climate of the Kispiox ITR is strongly influenced by colder and drier continental air masses that periodically occupy B.C.’s central-interior plateau, with proportionately more winter precipitation occurring as snow than in coastal locations (Fig. 2). Predicted mean annual precipitation at Date Creek in the Kispiox River watershed (Fig. 1) is 801 mm (Fig. 2), well below the predicted annual total (2694 mm) at Butze Rapids (Fig. 1) in the Pacific CTR (Fig. 2). Importantly, this difference in absolute precipitation is partly compensated for by the relatively low climatic moisture deficit (mm) during the growing season (64 mm total; from Wang et al., 2012), a function of relatively wet, cool summers (Fig. 2) and shelter from wind.

The Caribou Inland Temperate Rainforests

The Caribou ITR occurs between ca. 50° 30' and 54° N along the windward slopes of the Columbia and Rocky Mountains, where the upper Fraser River and upper Columbia River watersheds overlap with the “Wet” and “Very Wet” subzones of ICH BEC zone (Fig. 1). Climatically, these landscapes are characterized by long snowy winters and cool wet summers. At the Ancient Forest Trail

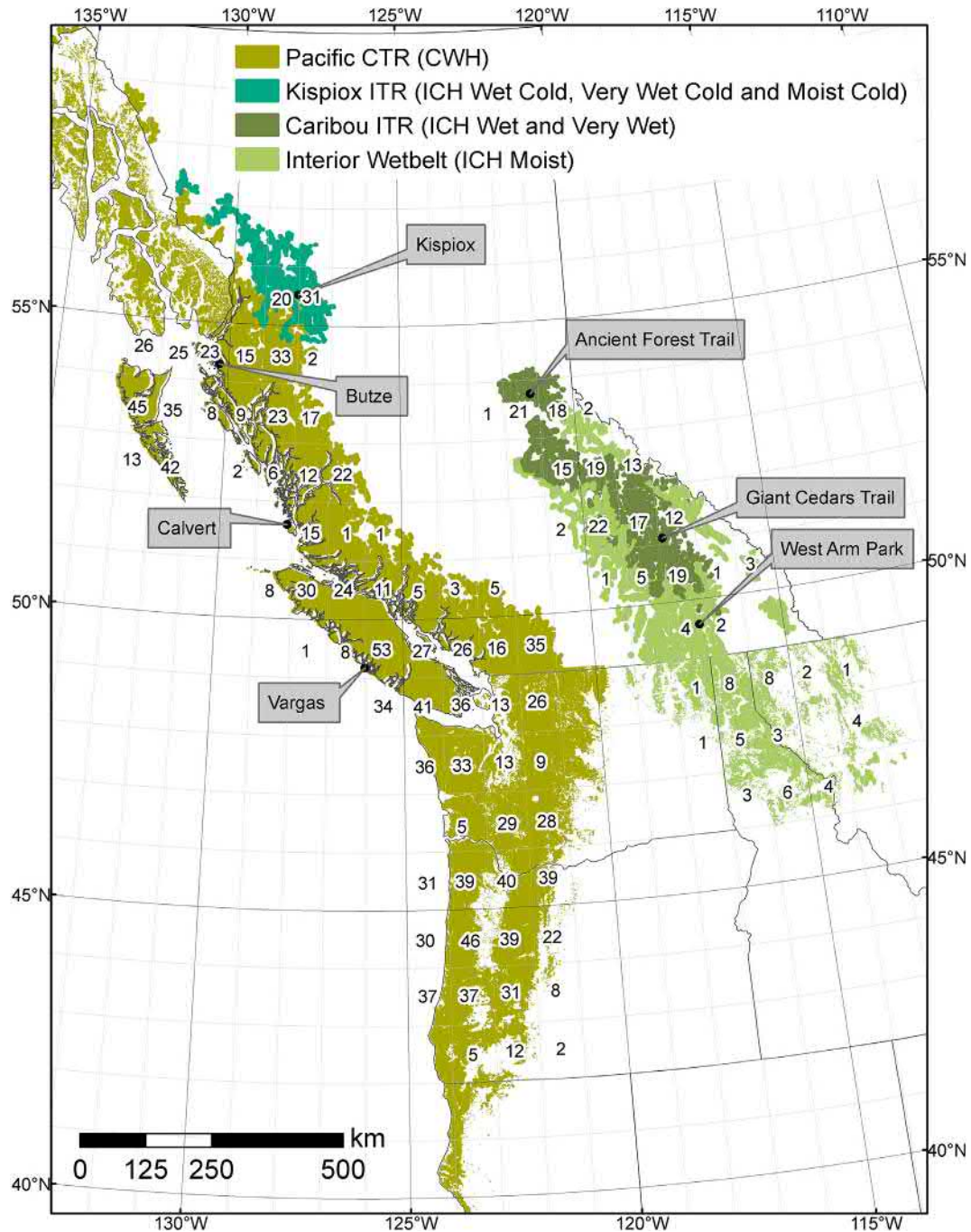


Fig. 1 Distribution of the Pacific Coastal and Inland Temperate Rainforest (CTR and ITR respectively) and Interior Wetbelt ecosystems in western North America. CTR distribution is indicated in British Columbia by the distribution of the Coastal Western Hemlock (CWH) biogeoclimatic (BEC) zone (after Meidinger, D and J Pojar. (1991). *Ecosystems of British Columbia*. British Columbia Ministry of Forests, Special Report Series 6: 1–330, British Columbia Victoria. <https://www.for.gov.bc.ca/hfd/pubs/docs/srs/srs06.htm>), and in the United States (Alaska, Washington, and Oregon) by the occurrence of western hemlock (*Tsuga heterophylla*) (from Data Basin, Wilberforce Foundation). The Kispiox ITR is indicated by the combined “Very Wet Cold,” “Wet Cold,” and “Moist Cold” Interior Cedar Hemlock (ICH) BEC subzones in the upper Skeena and Nass River watersheds. The Caribou ITR is indicated by the combined “Wet” and “Very Wet” ICH BEC subzones in the headwaters of the Fraser and Columbia River watersheds. Interior Wetbelt is indicated by the “Moist” ICH BEC zone in the B.C. interior, and by the occurrence of western hemlock in comparable ecosystems southward into Washington State, Idaho, and Montana. The number of “rainforest” lichen indicator species (oceanic lichens) is shown for coastal and inland locations within a $1 \times 1^\circ$ longitude-latitude grid (adapted from Goward, T, and T. Spribille. (2005). Lichenological evidence for the recognition of inland rain forests in western North America. *Journal of Biogeography* 32: 1209–1219. 10.1111/j.1365-2699.2005.01282.x). The location of reference climate data sites (see Fig. 2) is indicated by place name labels.

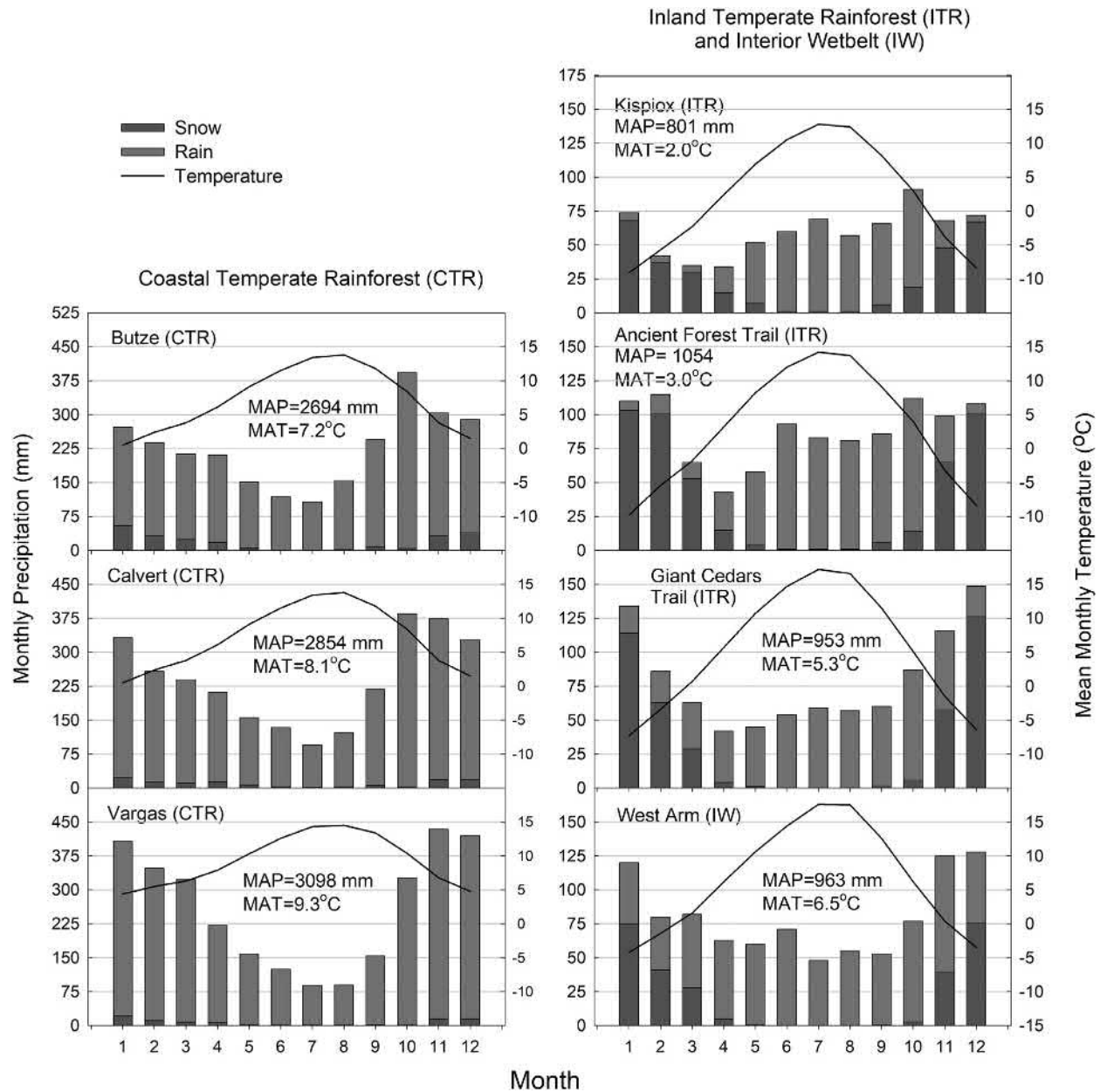


Fig. 2 Predicted climate variables (mean annual precipitation—MAP, mean annual temperature—MAT, mean monthly temperature, mean monthly precipitation as snow, and mean monthly precipitation as rain) for Coastal Temperate Rainforest (CTR) sites at Butze Rapids near Prince Rupert (Butze), Calvert Island (Calvert) on the British Columbia central-coast, and Vargas Island (Vargas) off southern Vancouver Island; for the Kispiox Inland Temperate Rainforest (ITR) at Date Creek (Kispiox); for the Caribou ITR sites at the Ancient Forest Trail (ITR), and Giant Cedar's Trail (ITR); and for the Interior Wetbelt (IW) at West Arm Park. See Fig. 1 for location of sites. Climate data estimated for the historical period (1961–90) using Climate BC—ClimateWNA version 6.00 (Wang et al., 2012). Note that the range for plotted precipitation estimates is greater for CTR (up to 525 mm) than for the ITR and IW sites on the right (up to 175 mm).

site in the headwaters of the Fraser River watershed (Fig. 1), for example, about 40% of total annual precipitation (1054 mm) falls as snow, while the average mean temperature for June–July–August is only 13.3 °C (Fig. 2). Our choice of the name “Caribou ITR” reflects the findings of Apps and McLellan (2006), who emphasize a high degree of correspondence between the areal extent of these ICH BEC subzones and the probability of long-term persistence by the deep-snow mountain caribou (*Rangifer tarandus caribou*) (see also Moskowitz, 2018).

Historically, the Caribou ITR was dominated by old-growth forest cover, with western redcedar and western hemlock present over a wide range of site series (Radies et al., 2009). DeLong (1998) estimated that the natural range of variability for old-growth forest (> 140 years) cover in “wet-trench” forests of the upper Fraser River valley was between 76% and 84%. Stand structure in the Caribou ITR has correspondingly been shaped mainly by processes of gap dynamics, where new trees establish in openings

created by the death of canopy veterans (Lertzman et al., 1996). Foresters have often characterized old-growth forest in the Caribou ITR as “decadent,” on the assumption that such stands are near the end of their life, unable to sustain themselves over time (see quotes in Chapter 5, Stevenson et al., 2011). In work on Vancouver Island, however, Daniels (2003) notes that old and very-old CWR stands need relatively few regenerating trees to maintain stand structure under processes of gap dynamics, a finding that would apply equally to old Caribou ITR forests.

Although processes of stand regeneration and stand structure share many similarities between the Pacific CTR and Caribou ITR (Goward and Arsenault, 2000), the climate of these two regions differs significantly. Predicted mean annual precipitation (MAP) at the Giant Cedars Trail site in the upper Columbia River watershed (Fig. 1), for instance, is 953 mm (Fig. 2), well below Alaback's (1996) estimated threshold of 1400 mm MAP required for designation of coastal forests as temperate rainforest ecosystems. As noted by DellaSala et al. (2011a,b), however, more recent modeling suggests that MAP thresholds for temperate and boreal rainforest designations are highly influenced by site specific and regional factors. These models suggested that ITR development is possible at MAP values as low as 846 mm (DellaSala et al., 2011a), especially at the northern limit of the ITR, where melt from winter snowpack coupled with elevated early-summer precipitation mitigates evapotranspiration demands on rainforest trees (Gavin and Hu, 2006; DellaSala et al., 2011b). This is particularly relevant to the Caribou ITR, where discharge from deep winter snows (see Figs. 2 and 3) sustains numerous springs and seepage areas on middle and lower hillslopes (Déry et al., 2014). The resultant wet soils create conditions of high ambient humidity and at the same time buffer trees from summer drought (Fig. 4). Konchalski (2014), for instance, found that growth rings of western redcedar do not show a dry-season signal associated with summer precipitation patterns.

The higher canopy humidity in wet “toe-slope” positions also limits the spread of fire after lightning strikes. Individual trees hit by lightning typically burn without spreading into the surrounding stand. Evidence from Sanborn et al. (2006) suggests that fire return intervals in wet “toe-slope” positions may reach 1600 years, while Gavin et al. (2009) reported sites that showed no evidence of wildfire in the two to three millennia since the arrival of redcedar into this portion of its range. The exceptional age and stature attained by such stands (Fig. 4) led Goward (1994) to argue for recognition for “antique” or multigenerational stands, in which the age of the forest exceeds the age of the oldest trees within it. Importantly, protection from stand-level wildfires does not extend to adjacent mid-slope stands growing on steeper terrain and typically dominated by western hemlock (Fig. 5); though even here stands can exceed 250 years in age, with many reaching 400–600 years (Coxson pers. obs.).



Fig. 3 Deep winter snow plays important roles in Inland Temperate Rainforests, preventing frost from penetrating into the ground and protecting shrubs, herbs and soil biota from extreme winter cold. Melt of the winter snowpack is vital for groundwater recharge, sustaining springs and seepage areas that support ancient cedar stands. Image shows late winter snowpack in an “antique” western redcedar (*Thuja plicata*) stand in the Ancient Forest/Chun T’oh Whudujut Provincial Park in the Caribou ITR. Such forests can greatly predate the age of the oldest trees within them.



Fig. 4 Stands of ancient western redcedar (*Thuja plicata*) trees are well developed in the lower “toe-slope” topographic position of the upper Fraser River watershed, shown here at the “Radies” tree along the Ancient Forest Trail in the Ancient Forest/Chun T’oh Whudujut Provincial Park in the Caribou ITR (see Fig. 1 for location). Well developed “buttress” roots are a notable feature of the ancient cedar trees at this location, likely indicating that the water table is close to the surface. Photograph courtesy of UNBC.



Fig. 5 Old western hemlock (*Tsuga heterophylla*) stands dominate rocky mid-slope positions in the upper Fraser River watershed (Caribou ITR), in sites where stand-destroying events such as fire typically occur every 200–500 years. This stands in marked contrast to the very-old “Antique” or “Ancient” cedar stands found in the wet “toe-slope” topographic positions (see Figs. 3 and 4).

The Interior Wetbelt

The third stronghold of inland rainforests is the Interior Wetbelt (Fig. 1). Whereas this term is generally applied to the ICH as a whole, here we adopt it in a more restricted sense. Extending southward from about 50° N in British Columbia to 46° N in northern Montana, Idaho, and Washington, the Interior Wetbelt corresponds mostly to the “Moist-Warm” subzone of the ICH, a region much drier and warmer than the Kispiox and Caribou ITRs. By way of comparison, the predicted summer moisture deficit (mm) for the Ancient Forest Trail site (Caribou ITR; see Figs. 1 and 2) is 53 mm, compared to 186 mm at West Arm Park (Interior Wetbelt) (Fig. 2) (Wang et al., 2012). Reflecting these drier conditions, forest cover in the Interior Wetbelt is typically not continuous over a full range of site series, with drier sites often supporting shrub-dominated or even grassland communities.

Western redcedar and western hemlock, although widely present in the Interior Wetbelt (Fig. 1), are typically restricted to wetter sites, especially where sheltered from frequent wildfire. Arno and Davis (1980) describe fire return intervals of < 150 years for these trees in Northern Idaho, while McCune and Allen (1984) note that stands with western redcedar trees occur only where protected from fire by deep canyons in the Bitterroot Range of western Montana. Gavin and Hu (2006) note that the range of western hemlock in the region covered by the Caribou ITR and Interior Wetbelt is far smaller than would be predicted by examination of the climate envelope for western hemlock in Coastal Temperate Rainforests, a disparity they attribute to the limited time for dispersal since the ITR biome emerged.

Related Ecosystems

We do not include in our treatment of Inland Temperate Rainforests the perhumid forests of the “Very Wet” Sub-Boreal Spruce BEC subzone, which extend northward from the Caribou ITR into the Peace River watershed (Meidinger and Pojar, 1991). These forests have previously been treated as a northern extension of the interior wetbelt (Stevenson et al., 2011), and support many of the same large faunal elements, such as grizzly bear (*Ursus arctos*), wolves (*Canis lupus*) and, in part, deep-snow mountain caribou. However, because they contain few of the oceanic biota which characterize ITR and Interior Wetbelt ecosystems to the south (Goward and Spribille, 2005), we prefer to regard them as boreal rather than temperate (see also Cannings and Cannings, 2015); further work is needed.

Biota of the Inland Rainforest

ITR and Interior Wetbelt forests support 376 wildlife species, including 8 amphibians, 7 reptiles, 293 birds, and 68 mammals (BC CDC, 2019). Among this last group is a full complement of large and small forest carnivores, including grizzly bear, black bear (*U. americanus*), wolf, wolverine (*Gulo gulo*), fisher (*Pekania pennanti*), marten (*Martes americana*), lynx (*Lynx canadensis*), and cougar (*Felis concolor*). Long-term viability for all these species requires large tracts of suitable habitat. Also found throughout the Caribou ITR are at-risk stocks of coho (*Oncorhynchus kisutch*), sockeye (*O. nerka*), and chinook salmon (*O. tshawytscha*) as well as bull trout (*Salvelinus confluentus*) (BC CDC, 2019).

Among the many animals that depend on old-growth ITR forests, the endangered “deep-snow mountain caribou” is certainly the most iconic (Seip and McLellan, 2008). Behaviorally adapted for survival in mountainous regions of deep snow, these caribou walk atop the winter snowpack in search of canopy hair lichens (mostly *Bryoria*), their primary winter forage. Not only are deep-snow caribou endemic to B.C. (see below), they also depend on extensive tracts of old-growth forests both for sufficient winter forage (Goward, 1998) and as a buffer against predation (Wittmer et al., 2005). Past conservation strategies for mountain caribou have focused mainly on protection of high-elevation winter ranges, leaving animals highly vulnerable to predation, as well as to loss of habitat when they venture into adjacent valley-bottom old-growth ITR forests (Kinley et al., 2007) (Fig. 6). This has resulted in steep population declines for most of the Caribou ITR and Interior Wetbelt herds (Fig. 7), with the latter now under imminent threat of extirpation (SARA, 2018). In early 2019, the remaining animals in the Purcell South and South Selkirk herds were captured and relocated to penning areas, bringing about the functional extirpation of free-ranging mountain caribou herds across the U.S.-Canada border (Cox, 2019).

A major indicator group for sites with high conservation value in the CTR and ITR alike is canopy macrolichens. Goward and Spribille (2005) used tree-dwelling macrolichens to assess the degree of environmental congruence between the Inland and Coastal Temperate Rainforest biomes. They showed that about 70% of oceanic species disjunct from the Pacific CTR are restricted within the ITR to regions north of 51° N, with relatively few extending southward into the Interior Wetbelt (Fig. 1). Correlated with this southward decrease in “oceanic” lichens, they noted a parallel decrease in summer precipitation (compare the 81 mm July precipitation at the Ancient Forest Trail site with 48 mm at West Arm Park in the southern B.C. interior; Fig. 2), albeit not with mean annual precipitation. Goward and Spribille (2005) concluded that the ITR is optimally developed between 54° N and 50° N; however, they noted that ITR features occur in a subset of locations further south, for instance, in waterfall spray zones. The importance of spray zones can be seen in preliminary studies conducted at Dawson Falls in Wells Gray Provincial Park, where > 470 lichen species have been recorded, including a high representation of oceanic species (Bjork pers. comm.) (Fig. 8). The total lichen flora of the Wells Gray Park and vicinity is expected to exceed 1000 species (Goward and Björk, 2013), a globally significant lichen assemblage, consistent with habitat values of the Caribou ITR.



Fig. 6 “Deep-Snow” mountain caribou are particularly vulnerable to loss of old-growth forest habitat and increased predation when they descend in the spring (shown here) and fall to forage in valley-bottom ITR stands and to migrate between different local mountain ranges.

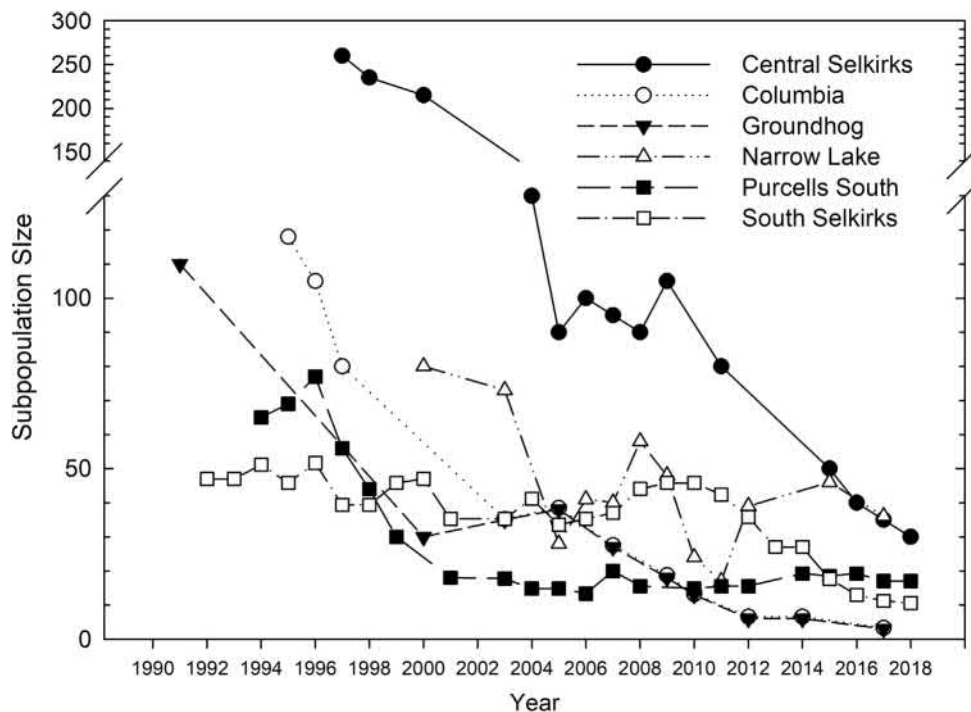


Fig. 7 Trends in mountain caribou abundance for selected herds in the Caribou ITR (Central Selkirk, Columbia, Groundhog, Narrow Lake, South Selkirk) and Interior Wetbelt (Purcells South). Adapted from British Columbia provincial government status reports (<https://www2.gov.bc.ca/gov/content/environment/plants-animals-ecosystems/wildlife/wildlife-conservation/caribou>).

Inland Rainforests and Carbon Sequestration

An important ecological and biophysical attribute of ITR stands is their role in carbon sequestration. This is particularly true for the Kispiox and Caribou ITR, where extended intervals between stand-level fires favors accumulation of significant biomass in standing stems (Fig. 4), coarse woody debris (Fig. 9), and forest soils. Matsuzaki et al. (2013) found that total forest carbon stocks in old-growth ITR stands averaged $455 \pm 156 \text{ Mg C ha}^{-1}$, close to that of Pacific CTR (Fig. 10). After clear-cutting, carbon stocks in the ITR stands measured by Matsuzaki et al. were reduced by > 70%—a not insignificant contributor to greenhouse gas emissions. Plantation stands will take many centuries to re-sequester this carbon lost at harvest, especially in wet ITR and CTR stands. Partial-cutting silvicultural systems seemed to provide the best alternative among the logging treatments examined by Matsuzaki et al. (2013), with group-selection logging retaining a high-proportion of the previously sequestered carbon (Fig. 10).



Fig. 8 Waterfall spray zones like this one at Dawson Falls in Wells Gray Provincial Park (Caribou ITR), can provide enhanced ITR characteristics for oceanic lichen and vascular communities in adjacent forests. Photograph courtesy of J. Hollinger.



Fig. 9 Large coarse woody debris, including fallen trees and snags, contributes to high rates of carbon sequestration in old and very-old (“antique”) stands of the Caribou Inland Temperate Rainforest, estimated at over 500 t/ha in the upper Fraser River watershed. Image from the Ancient Forest Trail in Ancient Forest/Chun T’oh Whudujut Provincial Park.

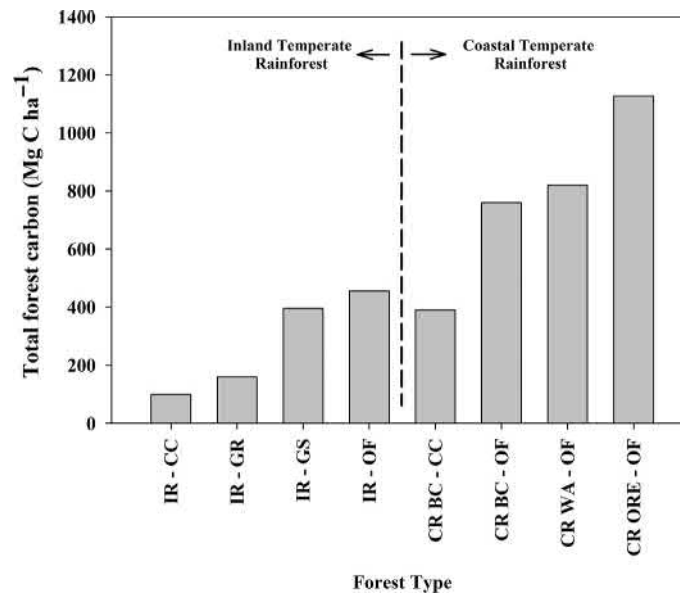


Fig. 10 Total carbon sequestration in Caribou Inland Temperate Rainforest stands after clear-cut logging (IR-CC), group-retention logging (IR-GR), and uncut old-growth forest (IR-OF), compared to logged Coastal Temperate Rainforest stands on Vancouver Island (CR BC—CC), and old-growth Coastal Temperate Rainforests from Vancouver Island (CR BC—OF), Washington State (CR WA—OF), and Oregon (CR ORE—OF). Source data Matsuzaki et al. (2013) for Inland Temperate Rainforest, Trofymow et al. (2008) for Coastal Temperate Rainforest stands on Vancouver Island, and Smithwick et al. (2002) for Coastal Temperate Rainforest stands in Washington State and Oregon.

History and Use of the Inland Rainforest and Interior Wetbelt

After thousands of years of habitation by indigenous peoples—the Lheidli T'enneh, Simpcw, Sinixt, Gitxsan, Nisga'a, Tahltan, and Wet'suwet'en,—colonial settlement in the 19th century and railway construction in the early 20th century brought about major changes in the utilization of the ITR for resource extraction, with logging of redcedar for shakes and poles, and conversion of valley-bottom lands for agriculture (Stevenson et al., 2011) (Fig. 11). Such activities, though widespread, occurred at relatively low intensity until the introduction of clear-cut logging in the 1960s.



Fig. 11 The Rocky Mountain Trench is a major physiographic feature of the Inland Temperate Rainforest and Interior Wetbelt, separating the older Columbia Mountains (seen in distance) from the younger Rocky Mountains. View is south from McBride Peak, showing past development of agricultural lands within the Caribou ITR.

Table 1 Conservation status of the Kispiox and Caribou Inland Temperate Rainforests (ITR) and the British Columbia (B.C.) portion of the Interior Wetbelt.

Region	BEC zone type	Total area (ha)	Road density (km/km ²)	% Cut-blocks ^a	% Young to mid-seral ^b	% Old ^a	% Old in OGMAs ^c	% Old in Parks ^c
Kispiox ITR	Wet	795,544	0.36	20.2	49.2	30.6	4.6	< 0.1
	Moist	277,095	0.84	12.3	52.8	34.9	10.3	9.6
	All	1,072,639	0.72	18.1	50.2	31.7	8.7	6.9
Caribou ITR	Wet	1,312,164.4	0.99	23.0	53.9	23.1	21.3	25.3
Interior Wetbelt	Moist	1,857,832.5	1.37	29.5	65.9	4.6	29.2	22.4
	All	3,169,996.9	1.09	26.8	61.0	12.2	23.0	24.6

Biogeoclimatic (BEC) zones used within each region are the: Kispiox ITR (Wet = combined “Very Wet Cold” and “Wet Cold” ICH; Moist = the “Moist Cold” ICH); Caribou ITR (Wet = “Wet” and “Very Wet” ICH); Interior Wetbelt (Moist = combined “Moist Cool,” “Moist Mild,” and “Moist Warm” ICH BEC zones). Parks includes both provincial and national parks, while OGMAs refer to spatially defined Old Growth Management Areas. Cut blocks includes all past clear-cuts identified within the BC Government database. Old-growth forests are stands >250 years. Young to mid-seral stands denotes the remaining forested land base (not a cut block or old-growth forest), including areas previously burned by wildfires. Data source: British Columbia Data Catalogue^d (<https://data.gov.bc.ca/>), accessed September 2, 2018.

^aExpressed as percentage of landscape (ha) in this BEC subzone.

^bGIS Spatial Layers used: Forest cover inventory (WHSE_FOREST_VEGETATION.VEG_COMP_LYR_L1_POLY); BEC classification

(WHSE_FOREST_VEGETATION.BEC_BIOGEOCLIMATIC_POLY); OGMA (WHSE_LAND_USE_PLANNING.RMP_OGMA_LEGAL_ALL_SVW); Roads (WHSE_BASEMAPPING.DRA_DGTL_ROAD_ATLAS_MPAR_SP); Forest harvest (WHSE_FOREST_VEGETATION.VEG_CONSOLIDATED_CUT_BLOCKS_SP, WHSE_FOREST_TENURE.FTEN_CUT_BLOCK_POLY_SVW, WHSE_FOREST_VEGETATION.RSLT_OPENING_VW in directory RSLT_OP_VW); Protected areas (WHSE_TANTALIS.TA_PARK_ECORES_PA_SVW, WHSE_ADMIN_BOUNDARIES.CLAB_NATIONAL_PARKS).

^cExpressed as percentage of old-growth forests (ha) in this BEC subzone.

In the Kispiox ITR, logging has reduced old-growth forest cover to 31.7% (Table 1), a major decline for a region that would have historically been dominated by old-growth forests. Significantly, only 6.9% of old-growth forests in the Kispiox ITR occur in parks and protected areas, with another 8.7% in old-growth management areas (OGMAs) (Table 1)—a level of protection unlikely to ensure the long-term persistence of at-risk lichens like tarpaulin tarpaper (*Collema coniophilum*), smoker’s lung (*Lobaria retigera*) and cryptic paw (*Nephroma occultum*), all recently designated as threatened under Canada’s endangered species legislation (COSEWIC, 2019). Crucially, these figures are based on a 250-year threshold for recognition of old-growth forests, consistent with recruitment schedules of old-growth forest dependent lichens (Campbell and Fredeen, 2004; Goward and Arsenaault, 2018).

Compounding the relatively low level of habitat protection for old-growth forest in the Kispiox ITR is the highly irregular and elongate shape of many of the Kispiox ITR protected areas, especially OGMA reserves. With edge effects for old-growth forest-dependent lichens known to extend 100 m from the margins of clear-cuts (Gauslaa et al., 2018), many of the current protected areas in the Kispiox ITR will not provide the “interior” habitats required by such lichens once adjacent stands are logged.

The figures for the Caribou ITR are even lower, with old-growth forest cover (>250 years old) currently at 23% (Table 1). About a quarter of this old-growth is located in protected areas, notably Wells Gray Provincial Park, while a further 30% has received provisional protection as OGMAs; but see also Fig. 12. Ancient forest stands, where individual trees can reach 1000 years or more (Lewington and Parker, 1999), have been particularly vulnerable to logging in the Caribou ITR (Fig. 13). In the upper Fraser River watershed, for example, ancient western redcedar stands now occupy between 3% and 7% of the landscape, down from >30% historically (Radies et al., 2009) (Fig. 14).

Old-growth representation within the B.C. portion of the Interior Wetbelt is lower still, at only 4.6% (Table 1). Less than a quarter of these forests occur in parks and protected areas, with another 29% in OGMAs. The proportion of past cut blocks in this landscape is also the highest of any of the three regions examined, just below 30% in total (Table 1).

A major related concern is relatively high road density, mostly in the form of haul roads for logging operations (Fig. 12). Road density in excess of 0.6 km/km² is commonly used as a threshold in habitat degradation beyond which populations of large vertebrates begin to decline (Foreman et al., 1997). By comparison, road density currently stands at 0.84 km/km² in the Kispiox ITR (“Moist” ICH BEC subzone only), 0.99 km/km² in the Caribou ITR, and 1.37 km/km² in the Interior Wetbelt (B.C. only) (Table 1). Such densities are likely unsustainable for large-bodied species like moose (*Alces alces*) (Beazley et al., 2004) and grizzly bear (Nielson et al., 2009).

Compounding the effects of the loss of old-growth forests to logging in the ITR are the ongoing and predicted impacts of climate change. The climate envelope for the “Wet” and “Very Wet” ICH BEC subzones is predicted to shift dramatically by 2050, shrinking and moving upslope in the central and southern part of the Caribou ITR, while expanding outward to the central-interior plateau farther north, where more precipitation is forecast in the summer period (Stevenson et al., 2011). The potential loss of old-growth forests from valley-bottom habitats would have a major impact on the ITR, eliminating the very subset of stands with the greatest site continuity (time between major stand-level fires).

Recent research suggests that these impacts will be exacerbated by many of our current forest management practices. Lindenmayer et al. (2009) noted that logging of old-growth forests in humid regions like the ITR can significantly shorten fire-return intervals due to changes in canopy microclimate and fuel-loading. Bradley et al. (2016) similarly found that where forests in the western United States had higher levels of protected area designation, they had overall lower fire severity values, notwithstanding their



Fig. 12 The construction of forest access roads for logging has significant cumulative impacts on Inland Temperate Rainforest and Interior Wetbelt ecosystems, changing patterns of surface run-off and creating deleterious “edge effects” that can extend far into the adjacent canopy. The Fraser Flats Forest Access Road, shown here, was built through the middle of an Old Growth Management Area specifically set aside to conserve regionally rare ancient cedar stands in the Caribou ITR.



Fig. 13 The distribution of logging cut blocks (*light green*) within mountain valleys of the Caribou Inland Temperate Rainforest is heavily biased towards the lower slope position, often described as the “toe-slope” position, shown here in a Google Earth image (from 2007 Landsat image) for the McGregor River valley in the upper Fraser River headwaters (see location in **Fig. 14**). Historically, conditions in these lower slope topographic positions favored widespread development of ancient cedar stands.

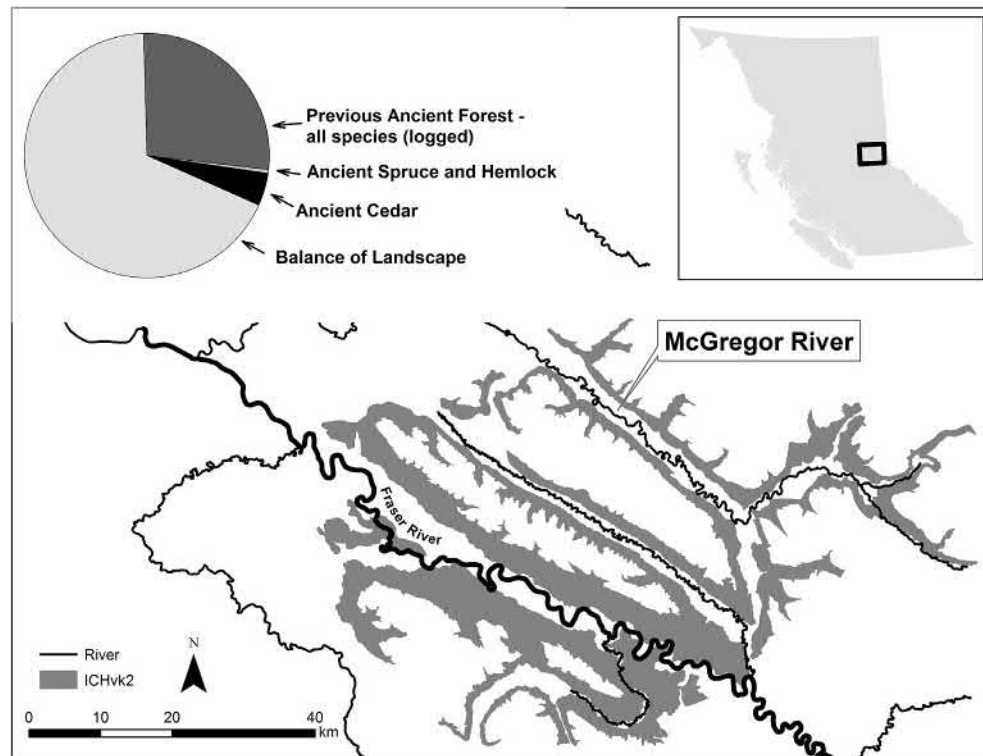


Fig. 14 The proportion of sites currently occupied by ancient forest stands versus those that have been logged is shown by leading tree species (inset pie chart) for the Very Wet Cool Interior Cedar—Hemlock biogeoclimatic (BEC) subzone (ICHvk2) in the upper Fraser River watershed (Caribou ITR). Ancient forest stands were mapped by aerial photo interpretation (ILMB, 2004). Listed tree species are Cedar (western redcedar—*Thuja plicata*), Spruce (hybrid Engelmann-white spruce—*Picea engelmannii* x *glauca*), and Hemlock (western hemlock—*Tsuga heterophylla*). “Balance of Landscape” refers to areas in the ICHvk2 that would not have historically supported ancient forest stands due to topographic position, i.e., irrespective of their present-day status as “logged” or “ancient.” Data adapted from Radies et al. (2009). The reference area (forested ICHvk2 BEC zone) is 110,000 ha.

greater biomass and fuel loading levels. These findings highlight the need to protect existing old-growth forest ITR and interior Wetbelt stands to maintain ecological resiliency in the face of climate change.

Conclusions

The cumulative environmental impacts of resource extraction and climate change on the Inland Temperate Rainforest and Interior Wetbelt can only be managed effectively when they are anticipated and addressed proactively through effective conservation policy and land-use regulations. With the ongoing loss of old-growth forest ecosystems comes the inevitable loss of resiliency for many species that depend on them (Baldwin and Bradfield, 2010). Given the collapse and pending extirpation of most deep-snow mountain caribou herds, it is clear that critical disturbance thresholds, beyond which the decline and extirpation of old-growth forest dependent taxa begins, have been reached across the ITR and Interior Wetbelt.

We recommend an immediate moratorium on clear-cut logging in forest stands older than 250 years in age within the Kispiox and Caribou ITR. Given the extreme rarity of old-growth forests stands in the Interior Wetbelt, remaining old-growth forest stands exceeding about 150 years in age should be designated as protected areas. Management plans in all three regions should include measures to ensure that remnant old-growth forest stands are buffered from the adverse impacts of adjacent cut-blocks (see discussion in Chapter 11, Stevenson et al., 2011) and are incorporated into a network of conservation areas, providing connectivity and safeguarding critical habitat.

Finally, comprehensive steps towards broader landscape-level restoration of old-growth forest ecosystems should be put in place immediately within the Kispiox, Caribou, and Interior Wetbelt ecosystems. This will require measures that allow existing younger to mature forest stands to remain undisturbed for long periods of time, particularly where they provide conservation corridors between remnant old-growth forest stands. This will be especially important in topographic sites such as wet “toe-slope” positions, locations which historically would have been occupied by old-growth forest stands. Restoration ecology efforts should be guided by our knowledge of the natural range of variability in temperate rainforest ecosystems (Agee, 2003; DeLong, 1998; Pearson, 2010; Wong et al., 2003).

Crucial to achieving these goals are key changes in forest management practices across the timber-harvesting land base. Included here are longer logging rotations, adoption of partial-cutting silvicultural systems, and efforts to reduce cut block dispersal (DeLong, 1998; Stevenson et al., 2011). An important example of how such conservation planning can be integrated across a mosaic of protected areas, conservation corridors, and designated harvest-intensity zones is the Great Bear Rainforest (GBR) Conservation Accord which recently came into effect in coastal B.C. (MFLNRO, 2016; Price et al., 2017). Significantly, this initiative was achieved, in part, through greater recognition of Aboriginal rights and title (Curran, 2017), a significant issue in many parts of the Inland Temperate Rainforest and Interior Wetbelt regions (see CBC, 2019).

Acknowledgments

We thank Aita Bezzola for preparation of maps and graphics, Jason Hollinger for permission to use the photo of Dawson Falls, and Curtis Björk for permission to cite his unpublished study on the lichens and bryophytes of Dawson Falls, in southern Wells Gray Provincial Park.

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Boreal and Taiga Biome

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Abstract

Boreal forests, or taiga, are the Earth's northernmost forests, covering vast tracts of land across Alaska, Canada, northern Europe, Russia and northeastern China, between the arctic tundra to the north and cold-temperate forests and grasslands to the south. The most characteristic climatic features are long duration of snow cover and short cool summers. They are among the world's leading purveyors of ecosystem services, including carbon storage and clean water, and they have a large impact on climate at local, regional and global scales. Boreal forests harbor globally significant wildlife populations, including songbirds, migratory waterfowl, bears, wolves, moose, lynx and Siberian tigers. Spruce, fir, pine and larch dominate these forests along with birch and aspen. Boreal forests are flammable, and large fires which renew forest ecosystems and regulate their value as wildlife habitat are common. Trees and other plants in the boreal biome have many adaptations to fire, such as abilities to store seeds in serotinous cones or in the soil for release after a fire, sprouting from the stump or roots, or thick bark that insulates trees from fire. Although large tracts of unlogged, primeval forest are still present, unsupervised logging, mining, oil extraction and climate change pose threats.

Introduction

Boreal forests (also known as taiga) are one of the world's leading purveyors of ecosystem services including carbon storage and clean water (Schindler and Lee, 2010). Boreal forests have a large impact on climate at local, regional and global scales (Snyder et al., 2004). They also harbor globally significant wildlife populations (Schmiegelow et al., 1997), and large tracts of unlogged primeval forest are still present which show how natural disturbances, landforms, and ecosystem processes work to maintain biodiversity (Bengtsson et al., 2000; Wardle et al., 2012; Frelich, 2017).

With 12.1 million km², boreal forests comprise 33% of all forests on the Earth (Kuusela, 1992). They cover vast areas in the northern hemisphere, across North America (central Alaska to Labrador, Canada), northern Europe and Asia (Norway, Sweden, Finland, and Russia), with a few excursions of small extent into the northern conterminous United States, China and Mongolia (Fig. 1). The term "circumboreal" has been coined to describe the belt of boreal forests that circles the globe (i.e., it occurs at all longitudes with suitable land) at high latitudes. Russia and Canada have the largest proportions of boreal forests (65% and 27%, respectively), while Scandinavia and the U.S. have much smaller portions with about 4% each.

Physiognomy, Climate and Relationship With Adjacent Biomes

Boreal forests are closed-canopy conifer forests with a significant admixture of deciduous trees (Fig. 2A and B). They are also the world's coldest forests; dominated by the most cold-tolerant tree species, conifers—spruce (*Picea* spp.), fir (*Abies* spp.), pines (*Pinus* spp.) and larch (*Larix* spp.), with variable admixtures of cold-tolerant deciduous tree species; birch (*Betula* sp.), alder (*Alnus* spp.) and aspen (*Populus* spp.). Boreal species within these genera can withstand extreme winter temperatures as low as -80°C (Brandt, 2009) by moving water outside of cell walls, or outside of sensitive organs such as buds. These mechanisms of cold tolerance are superior to the deep supercooling mechanism that occurs in trees of the temperate zone, which are limited to -40°C to -45°C (George et al., 1974). Regardless of winter survival, boreal tree species are also capable of growing in areas with very short summers compared to trees of the temperate biome.

Boreal climates are characterized by long, cold, snowy winters, and short, cool summers (Peel et al., 2007). With some exceptions discussed below, they lie in the region between the summer position of the arctic front on the north and the winter position of the

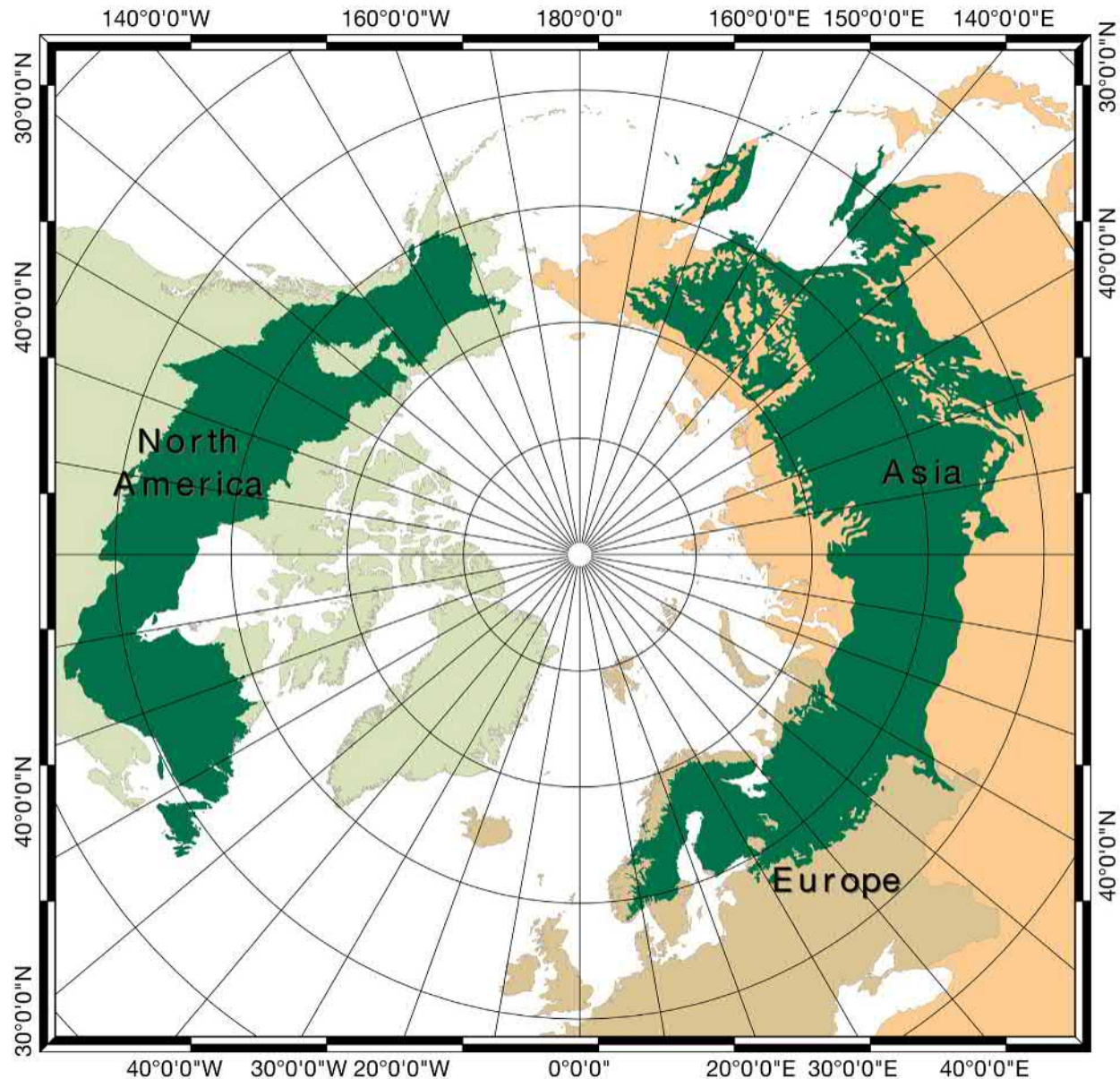


Fig. 1 Polar-view map of the boreal biome. Courtesy of David Wilson, University of Minnesota.

arctic front on the south. Within this region, summers are long and warm enough for boreal tree species to complete their life cycle—3 months with mean temperatures in the range of 10–17°C. Towards the south, in regions with continental climates, winters may be cold enough to exclude temperate tree species by directly killing them in cases where their limit for winter minimum temperature is regularly exceeded. These regions have “winter boreal” climates, and in mid-continental southern boreal areas with relatively warm summers, boreal forests are maintained against invasion by temperate forests by winter cold. However, some southern boreal forests in areas of maritime climates have relatively mild winters compared to interior continental boreal forests, although summers may still be too short and/or too cool for temperate tree species to complete their life cycle or to effectively compete with boreal tree species—so called “summer boreal” climates. These occur near large, cold water bodies, and occur in areas close to the ocean, such as Newfoundland, Canada, parts of Scandinavia, and the Great Lakes of North America.

The circumboreal belt at northern latitudes occupied by boreal forests extends from the edge of arctic tundra on the north, to cold-temperate climates on the south, where they mingle either with grasslands in dry interiors of North America and Eurasia or temperate forests dominated by oak (*Quercus* spp.), maple (*Acer* spp.) and basswood or linden (*Tilia* spp.) in eastern Canada and the United States and northern Europe, eastern China, Korea, and Japan. Boreal forests also intergrade with high elevation montane forests, many of which have very similar physiognomy and species composition at the generic level, with spruce, fir, birch and aspen. These montane forests extend south of the boreal zone in high-elevation places such as the Rocky Mountains in North America and Ural Mountains in Russia. Boreal forests are usually divided into northern, with low productivity and often low density



Fig. 2 Two views of boreal forest in northern Scandinavia. (A) Landscape view with Norway spruce (*Picea abies*) forest. Photo by Jacek Oleksyn. (B) Interior of Scots pine (*Pinus sylvestris*) stand. Photo by Kajar Köster.

of trees on permafrost, and southern boreal with relatively productive forests on suitable sites (although still lower in productivity than temperate or tropical forests).

The region with mixed forests of boreal and temperate species to the south of purely boreal forests is referred to as hemi-boreal or near-boreal forest (Fig. 3, Jögiste et al., 2017). In eastern North America, northern Europe and eastern China, these hemi-boreal forests gradually change along a climate gradient from nearly pure boreal with small inclusions of temperate forest, to nearly equal mixtures, to nearly pure temperate forest with small inclusions of boreal vegetation (Fisichelli et al., 2014). Mean summer temperatures generally range from 17–19°C in this transition zone, and there are generally 4 months with mean temperatures above 10°C. At the northern edge of hemi-boreal forest, temperate forest inclusions occur on south-facing slopes. At the southern edge of hemi-boreal forest, small areas of boreal vegetation occur in basins with cold air pooling at night, north-facing slopes with cold water seepage, and upwelling of cold water on the shores of large lakes that cause summer climates cool enough for boreal species. These isolated boreal forests are often advanced colonies responding to the generally cooling climate of the late Holocene (ca. last 4000 years), although some have persisted through the mid-Holocene warm period, prior to which their surrounding landscape was all boreal, and are true relicts. Both types of boreal inclusions occur as much as 200–300 km south of the main range of the boreal forest.

In addition, stands of boreal species occur naturally on sites with rocky or sandy, nutrient-poor soils within the temperate biome, such as Jack pine (*Pinus banksiana*) in North America, or were planted on such sites, e.g., Scots pine (*P. sylvestris*) in Europe. However,



Fig. 3 Hemiboreal forest in Estonia, regenerating after a windstorm, with trembling aspen (*Populus tremula*), mountain ash (*Sorbus aucuparia*), Norway spruce and Norway maple (*Acer platanoides*). Photo by Kalev Jõgiste.

these forests are commonly mixed with temperate tree species that are clearly capable of growing on rocky and sandy soils. Therefore, climate is the main factor leading to the development of temperate or boreal forests, rather than poor site conditions. Also in the temperate zone, human activity has led to artificial “borealization” of landscapes in parts of Europe, where the boreal species Norway spruce (*Picea abies*) has been widely planted.

In some interior continental regions (central North America and Eurasia), southern boreal forests form an ecotone with grasslands. Drought stress is a limiting factor for trees in these regions. A positive balance between annual potential evapotranspiration and precipitation is needed for development of forests, and determines the location of the boreal forest-grassland ecotone (Hogg, 1994). Mosaics of boreal woodlands and grasslands (referred to as aspen parkland in North America) can occur due to differential water-holding capacity of soil bodies, and north/south slopes with different moisture balances in this forest-grassland ecotone. In addition, high fire frequencies in grasslands can prevent tree growth for variable distances into the zones with climates potentially favorable for boreal forest.

Soils and Ecosystem Development

Much of the boreal forest lies on young glaciated, rocky landscapes with numerous lakes, or on glacial drift—for example the Canadian Shield of exposed rocks that underlies the boreal forest of central North America (Fig. 4). Cold temperatures with low decomposition and evaporation rates lead to sphagnum peatlands on wet sites and thick organic horizons (duff layer or forest floor) on well-drained sites. Some of the boreal forest also lies on older soils that escaped glaciation in northern Alaska and Siberia. Upland soils are generally classified as spodosols (United States) or podzols (Europe and Asia). These distinctive soils have thick organic horizons with distinct litter, fragmentation (or fermentation) and humus layers, underlain by an eluvial horizon which is light in color and an illuvial horizon where iron leached from the upper A horizon is deposited. There has been extensive formation of peatlands in the boreal biome over the last few thousand years, with deep organic (histosol) soils.

Surprisingly, ecosystem retrogression—ecosystem aging, a progression from the maximal biomass phase to the retrogressed phase with lower productivity and biomass (Peltzer et al., 2010)—occurs relatively fast in boreal ecosystems compared to temperate and tropical forests. This can be caused by chemical processes that occur in cold environments. Ecosystem acidification, a process by which production of organic acids, by sphagnum mosses, coniferous needles, and slow decomposition of organic matter on the forest floor, can eventually overwhelm chemical buffer systems in soils and lakes (Ford, 1990). In uplands, accumulation of organic forest floor material and mosses retain water and insulate the soil, leading to shorter growing seasons for roots, or even permafrost in northern boreal regions, in turn leading to waterlogging, low availability of nutrients (especially nitrogen) and stunted tree growth—a process very common in boreal forests and known as paludification. If most of a watershed has paludified soils, then lakes can also be acidified, leading to loss of fish species diversity, and some lakes can convert to bogs with floating mats, very low pH and no fish.

Fires can be a renewal process that retards acidification and paludification by removing the organic horizon and liberating cations (Ca, K, Mg) which neutralize acids—therefore fires are an integral renewal process important to maintain forest productivity over long periods of time (millennia, Payette et al., 2012). Retrogression from a maximal state of biomass production allowed by



Fig. 4 Black spruce (*Picea mariana*) forest on Canadian Shield exposed bedrock in central North America. Photo by Elias Anoszko.

the soils and climate of a given boreal forest, to a retrogressed state with stunted vegetation can occur within several centuries to a few millennia in the absence of fires. This could occur in small areas—refugia sheltered from fire by landform on landscapes with frequent fire—or over entire landscapes in boreal regions where fires are rare. An example of the former is southern boreal forests with high-severity crown fires every 50–100 years in central North America (Saskatchewan, Manitoba, and western Ontario, Canada) while the latter occurs more frequently in places with wet climates like eastern Quebec, Canada, or northern Sweden.

Aquatic and Wetland Features

The boreal biome comprises enormous fresh water resources. The two countries that comprise the vast majority of boreal forest, Canada and Russia, have the first and second largest areas of fresh water in the world, respectively. Millions of lakes, large river systems, and extensive wetland complexes with sedge meadows, marshes, bogs and forested swamps are common within the boreal biome. Glacial lakes carved in bedrock, or in kettle holes of glacial outwash plains are numerous in boreal forest regions such as central North America and Finland. Superior, Great Bear, Great Slave, and Athabasca in North America, and Baikal in Russia are among the world's largest lakes with >30% (by volume) of the world's surface fresh water. Vast river systems occur on relatively flat lands between mountain ranges, or on plains that have arisen from the ocean after the departure of glaciers via isostatic rebound (the latter includes the clay belt along Hudson's Bay in northern Ontario and land adjacent to the northern Baltic Sea in Sweden). Most of Russia and Canada are in the Arctic Ocean drainage basin with huge rivers such as the Ob, Yenisey, Lena and Amur Rivers in Russia, and the Mackenzie, Nelson and Yukon Rivers in North America. All of these are among the world's largest rivers and drain water from vast swathes of boreal forest and tundra.

Although acidic peatlands occupy vast acreages, high pH wetlands and lakes also occur where nutrient input from weathering of rocks such as basalt or limestone occurs. Surprisingly, the pH of many lakes can be in the range of 6–6.5, and the lakes are buffered by cations that are replenished by intense fires in the watershed, even on landscapes with nutrient-poor granitic bedrock (Leys et al., 2016). These lakes are able to support diverse food webs with many species of fish.

Peat bogs and lakes with sediments that date to the last glaciation, or much older, occur throughout the boreal forest, so that paleoecological reconstructions of ecosystem development since the last glaciation are possible, based on fossil pollen and macrofossils such as buds, seeds and needles or wood. Thus, it is possible to paint a picture of change with climate during the Holocene Epoch (the last 11,700 years); especially the mid-Holocene warm spell (centered around 5000–7000 years before present) can be used as an analog for a future moderate climate warming scenario, since summers were generally about 2°C warmer.

Flora and Fauna

With a few exceptions plant species are hard to pin down as strictly boreal. Among tree species, for example, black ash (*Fraxinus nigra*) and northern white cedar (*Thuja occidentalis*) in North America and Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) in Europe occur at high abundances in both temperate and boreal forests—their ranges are split basically 50:50 between the two biomes—although further east in Russia Scots pine is almost totally located in the boreal biome. Gray alder (*Alnus incana*, with

various varieties in North America, Europe and Asia), Quaking aspen (*Populus tremula*) in Eurasia and *P. tremuloides* in North America, Jezo spruce (*Picea jezoensis*), Silver birch (*Betula pendula*), Paper birch (*Betula papyrifera*), and Siberian silver birch (*Betula platyphylla*), are among the species that are important across huge expanses of boreal forests, but which also occur extensively in temperate forests.

White spruce (*Picea glauca*), black spruce (*P. mariana*), tamarack (*Larix laricina*) and balsam poplar (*Populus balsamifera*) occur at the edge of arctic tree line and throughout the boreal forest, while balsam fir (*Abies balsamea*) occurs mostly in the boreal biome of North America. In Eurasia, Dahurian larch (*Larix gmelinii*), Siberian larch (*Larix sibirica*), Siberian spruce (*Picea obovata*), Siberian pine (*Pinus sibirica*), and Siberian fir (*Abies sibirica*) occur mostly in the boreal biome. These species are more properly classified as boreal, although they also occur to some extent in colder parts of the temperate biome.

One of the unique features of biodiversity in boreal forests is the large number of circumboreal plant and wildlife species—namely the same species occur at all forested longitudes at the latitude of boreal forest. There are also cases where species are different, but the genera are in common between the two land masses in North America and Eurasia. For example there are few, if any, circumboreal tree species—the genera are circumboreal, with similar species in Eurasia and North America. This similarity at the species and generic taxonomic levels has come about because Alaska has been periodically joined to Russia during glacial periods, allowing migration of species and genetic exchange from Eurasia to North America.

Circumboreal herbaceous plants include twinflower (*Linnaea borealis*), bearberry (*Arctostaphylos uva-ursi*), and Lingonberry (*Vaccinium vitis-idaea*). Forest floors in boreal forests have complex microhabitats, with decaying coarse woody debris, snags, tip-up mounds, rocks, and arboreal surfaces, with large variability in light availability, allowing for a diverse assemblage of mosses, clubmosses, ferns and small herbaceous plants that make up the plant community (Fig. 5A and B).

Very large species richness of mosses and lichens occurs in boreal forests (Fig. 5C and D), because the climate favors species with those growth forms, and because of the microhabitat variability. The three feather moss species red stemmed feathermoss (*Pleurozium schreberi*), splendid feather moss (*Hylocomium splendens*) and ostrich plume feathermoss (*Ptilium crista-castrensis*), as



Fig. 5 Diversity of the forest floor in boreal forests. (A) Moss covered forest floor with rocks and coarse woody debris. (B) Bark surfaces on old-growth pine and needle-covered forest floor. (C) Feathermoss (*Pleurozium schreberi*) covered forest floor with wintergreen (*Gaultheria procumbens*). (D) The lichen *Lobaria pulmonaria* growing on decaying wood. Photos by Lee Frelich.

well as a number of *Sphagnum* species, are very abundant on the forest floors of moist boreal forests across vast extents. Well-drained sites feature species of reindeer moss (lichens in the genus *Cladonia*) and a set of moss species adapted to dry microhabitats.

Boreal forests are habitats for iconic, large wildlife species. Circumboreal species with ranges mostly in the boreal forest include moose (*Alces alces*, also called Elk in Europe), Woodland caribou (*Rangifer tarandus*, also called reindeer in Eurasia), Gray wolf (*Canis lupus*), Wolverine (*Gulo gulo*), Brown bears (*Ursus arctos*, also called grizzly bears in North America). Additional wildlife species include the Lynx—a circumpolar genus with two species (Eurasian lynx, *Lynx lynx* and Canadian lynx, *Lynx canadensis*), the endangered Siberian tiger (*Panthera tigris tigris*) with a small range in far eastern Russia and northeastern China, and the wood bison (*Bison bison athabasca*) in western Canada, and Black bear (*Ursus americanus*) in North America.

Long-term studies, over several decades, of trophic relationships among boreal wildlife species are quite famous. One example is the 8–11 year cyclic relationship between Lynx and Snowshoe hare in Canada, due to interactions of predation and food supplies. The hares overgraze plants in their habitat, undergo a population crash, stabilize for several years and then increase when the plants recover; lynx populations rise and fall with the hares, but with a few years delay due to their longer life cycle (Krebs et al., 2001). Another case is the 50+ year study of moose and wolves on Isle Royale National Park, a large island in Lake Superior, United States. Here, the moose population is sometimes regulated by wolves, and sometimes not, due to fluctuations in wolf population caused by a variety of fluctuating factors, including winter snowfall and population revitalization by new individuals migrating from the mainland over an ice bridge that forms at irregular intervals in recent years, due to the warming climate (Adams et al., 2011).

The boreal forest provides habitats for massive numbers of migratory and non-migratory birds. The neotropical migrant birds in North America include many species of warblers and thrushes that spend the winter in the Caribbean, Mexico or South America. Massive flocks of waterfowl—geese, ducks and pelicans—inhabit boreal forests during the summer. Resident circumboreal bird species include the raptors Golden eagle (*Aquila chrysaetos*) and Great gray owl (*Strix nebulosa*). Separate but related species of boreal grouse occur in North America and Eurasia, Spruce grouse, and Siberian spruce grouse (*Falcapennis canadensis*, and *Falcapennis falcapennis*, respectively), while the Blackbilled capercaillie, (*Tetrao urogalloides*) is a large grouse that occurs only in Eurasian forests.

Fire and Adaptation to Fire

Many vast tracts of boreal forest are still intact ecosystems, allowing opportunities to characterize ecological processes little influenced by human activities. This includes disturbance regimes and their relationships to landscape patterns. Coniferous boreal forests are among the world's most flammable fuel types and regularly support some of the largest fires on Earth. These fires regulate the nature of the landscape mosaic of vegetation and the process of succession—replacement of early successional species that appear right after fire by late-successional species. The vegetation mosaic in turn determines which wildlife species can live on the landscape, since wildlife species depend on proportions and spatial distributions of successional stages.

One of the fascinating aspects of boreal ecology is how plants are adapted to the high occurrence of fire. Two tree species that are mainstays of the North American boreal forest—jack pine and black spruce—have serotinous cones. Their cones remain closed in the canopy until the heat of a fire opens the scales, allowing seeds to be shed. This is an adaptation to infrequent, high-severity fire (return times of 50–150 years), that assures that a post-fire cohort of newly germinated seedlings will replace mature trees killed by a fire (Fig. 6A and B). Several years of cone/seed production is available to be distributed whenever a fire occurs, and whether or not a fire occurs during a mast year with high seed production is not important. These species typically grow in dense stands with high canopy bulk density, which facilitates spread of high-intensity fire. In a sense, the adult trees sacrifice themselves by promoting fire, although such fires also kill competing late-successional species such as balsam fir, that would otherwise replace jack pine. These

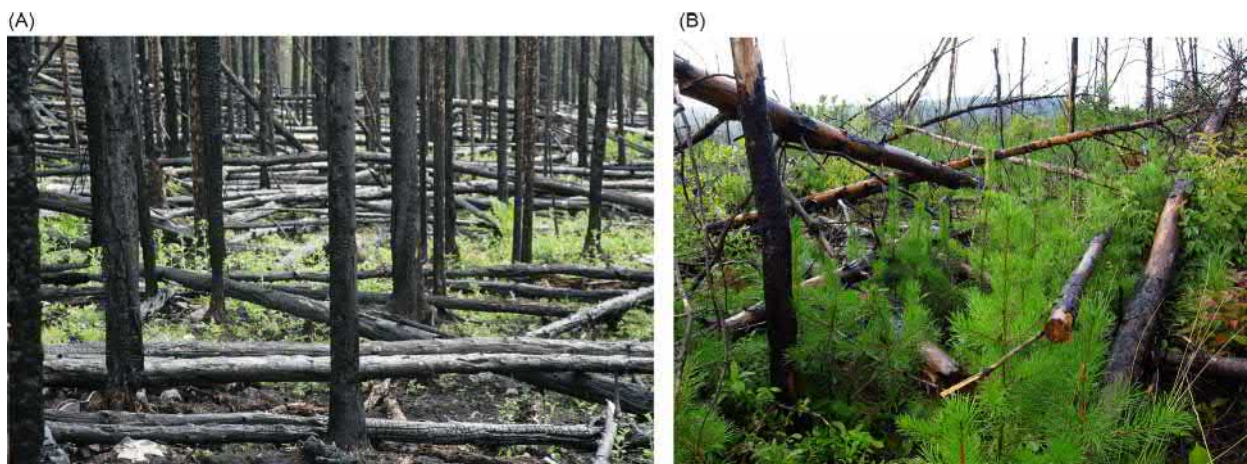


Fig. 6 Regeneration by serotinous seed after high-severity fire. (A) Post-fire jack pine (*Pinus banksiana*) forest. Photo by Dave Hansen. (B) Regeneration 6 years post fire. Photo by Elias Ansozko.



Fig. 7 Regeneration by sprouts and buried seeds after high-severity fire. (A) Stump sprout of a top-killed paper birch. (B) Jack pine and black spruce forest 1-year post fire—seedlings are pin cherry germinated from buried seeds. Photos by Dave Hansen.

forest types may have little succession for centuries; regeneration mirrors the pre-fire canopy composition and only a small proportion of stands across the landscape are missed by fire and become old enough to undergo succession (Johnson, 1992).

Post-fire sprouting is another important strategy. The circumboreal birch and aspen species, as well as shrubs such as hazel (*Corylus cornuta*), mountain maple (*Acer spicatum*) and willows (*Salix* spp.) sprout after fire (Fig. 7A). Depth of burn into the forest floor tends to be low in spring fires, and deeper in summer or fall fires. Therefore, spring fires favor regeneration of aspen (with root sprouts throughout the spatial extent of the root system and spring seed dispersal), while summer/fall fires favor birch (with stump sprouts and fall seed dispersal).

Seeds of both the birch and aspen genera are small, with good long-distance dispersal, so that these species can also return post fire via a long-distance seed dispersal strategy if sprouting should fail. The circumboreal species with bright magenta flowers, known as fireweed (*Chamaenerion angustifolium*), also has plumed seeds and a long-distance seed dispersal strategy to colonize post-fire environments.

A final seed-related adaptation to fire, is the buried seed strategy. Pin cherry (*Prunus pensylvanica*), a small boreal tree species, and Bicknell's geranium (*Geranium bicknellii*) are two species that require sunny post-fire environments that help to quickly revegetate soils right after fires, preventing erosion. These species produce large seed crops during early succession after fire, which fall on burned soil and become buried in the forest floor. These seeds survive for decades or even centuries, and germinate when they detect light after a subsequent fire (Fig. 7B).

Pine and larch species (e.g., red pine in North America and Scots pine in Eurasia) can resist the effects of fire, and grow in climates or on landforms that promote more frequent fires than species that employ a serotinous seed strategy. These trees species are tall with thick bark, have good self-pruning of lower branches, and bear their foliage high above the forest floor when mature. These traits help to avoid scorch of the cambium underneath the bark or the foliage during surface fires. Individual trees can be scarred at the base by fires, but can survive for centuries afterwards. Most years for seed production are common in these species, and it may take several mast years to gradually reseed the forest over a few decades, in addition to having several cohorts of trees that germinated after fires, resulting in mixed age stands (Fig. 8).

Finally, some species employ a fire avoidance strategy. White spruce and balsam fir are explosively flammable, with pitch in their sap, high foliar density, and thin bark that allows girdling of the cambium at the base of the tree very easily during fires. Why would such species exist and grow on a landscape where fire is a major force? There are many places—fire refugia—on the landscape, especially in recently glaciated terrain, where fires do not occur. During periods of time when fires are not as frequent (return time for fires varies over the centuries with fluctuations in climate), these species advance from their refugial locations and cover significant proportions of the landscape, however, during times of frequent fire, they persist, restricted to the refugia. Many landscapes, such as the Canadian shield, have numerous fire refugia caused by rock outcrops, forested swamps, open wetlands and lakeshores. These species also dominate in regions with wet climates.

Successional Dynamics in the Boreal Forest

When the fire regime and adaptations of the dominant tree species are in synch with each other, fires can maintain the same composition of tree species for centuries; alternatively, fires can lead to replacement by different sets of tree species and initiate a succession sequence (Frelich, 2002) as follows.

- Frequent low-severity regimes. These can occur in southern-boreal larch and pine forests—species with the resistance strategy—on dry interior continental sites near grassland-boreal ecotones. Stands have open understories with fires every ca. 5–40 years.



Fig. 8 Uneven-aged Scots pine forest with young and old post-fire regeneration cohorts, and fire-scars at the base of the larger pines. Photo by Kajar Köster.

Regular ignitions are caused by lightning or indigenous peoples maintain such forests. Purposeful burning to maintain wildlife habitat or to regenerate food plants (e.g., blueberries in North America) was, and still is in some regions, a common practice.

- Mixed-severity fire regimes can have frequent low-severity fires, with occasional high-severity fires, and are also dominated by tree species with the resistance strategy. Such regimes have a lot of spatial and temporal variability in fire size and severity; sprouting and serotinous species are often mixed with the fire-resistant species (Figs. 7A and 8).
- Infrequent high-severity fire regimes occur on landscapes dominated by species with the serotinous cone or sprouting strategies. On conifer-dominated sites, little succession occurs as long as fire intervals are longer than the time needed for the conifers to build up canopy-stored seeds (10–20 years) but not longer than it takes for fire-sensitive, shade tolerant species to invade (>150 or 200 years). This is especially common on rocky terrain with low-quality soils, such as the Canadian Shield. On better quality sites in the southern boreal, alternation of deciduous (birch and aspen species) and fire-intolerant coniferous species (persisting in nearby refugial locations) can occur. This represents genuine succession from birch and aspen to shade tolerant conifers, which is reset to deciduous species every time a severe fire occurs. Note that succession to conifers is needed to facilitate severe fires.
- Infrequent fire regimes exist on islands, in forested wetlands, and in regions with constantly wet climates. Disturbance regimes are dominated by gap dynamics due to treefall and insects. Derechos (severe thunderstorms with straightline winds) occur in continental interiors, and heavy wet snow events in autumn and spring also take down trees. Insects such as spruce budworm (*Choristoneura fumiferana*) in eastern North America, which infest balsam fir in the southern boreal forest, and bark beetles on spruce and larch species, are common causes of individual tree death in areas without severe fires. Late-successional dominance can be perpetuated for many generations of trees, until interrupted by fire.

Threats

Boreal forests are susceptible to climate change and vast areas are now being logged, flooded for hydro power, stripped to access tar sands, or subjected to mining deposits of metals such as iron, nickel and copper (Saucier et al., 2015).

Boreal forests play an important role in the Earth's atmospheric cycles, including its huge carbon pool. Not only the trees that cover vast acreages sequester carbon; boreal soils have slow decomposition rates, and large buildups of forest floor organic material, and moss blankets in many places. Boreal forests have been sinks for carbon, or close to equilibrium with fires and decay processes at the continental and global scales. However, boreal forests are expected to become net sources of CO₂ to the atmosphere, as fire frequencies increase in a warming climate (Flannigan et al., 2009). More fires combined with logging lowers the average age of stands across the landscape. Finally, invasive earthworms from the south or other continents are consuming the forest floor (Cameron et al., 2015). These factors can decrease carbon storage on boreal landscapes.

Boreal forests have long histories of migration over large ranges of latitude with numerous glacial cycles during the Quaternary Period of the last 2.6 million years. The forests that we are familiar with today disappear during glacial maximums, when the boreal forest is slowly pushed south into temperate latitudes. In Europe and central North America, the broad range of the boreal forest is pushed into a relatively small area and mixed with temperate tree species during peak glacial cycles, and the vast, far northern extent of boreal forest we are familiar with today develops anew during each interglacial.

The problem with human-driven climate change during the 21st century is that we are starting from a warm interglacial climate and will proceed into super-interglacial conditions that probably have not existed since the Neogene Period (23 million–2.6 million ybp). Boreal forests may run out of room; as temperate tree species or grasslands infiltrate the southern boreal, the northern edge of the boreal is pushing northwards as well, onto lands currently occupied by arctic tundra. At some longitudes—e.g., northern Scandinavia and north central Canada—there is not much room for northwards movement of the boreal forest before it runs into the Arctic Ocean, or Hudson Bay, respectively. At the same time, the Arctic Ocean will move southwards due to sea level rise associated with warmer climate, leaving the boreal forest with much less room. In any case, the boreal forest is headed for a unique future that will require novel management solutions.

There are several mechanisms by which a warming climate can kill the southern boreal forest:

- Gradual infiltration of temperate tree species through gap dynamics as boreal tree species die. This can occur whenever the temperature regime becomes suitable for temperate species (i.e., release from very cold winter minimum temperatures or short/cool summers) and the seed sources are available (Fisichelli et al., 2012, 2014, Fig. 9A).
- Rapid conversion from boreal to temperate tree species when wind storms remove large swaths of boreal forest and suddenly release temperate understory trees. There are many forests in the southern boreal region with boreal (e.g., *picea*, *Abies*, *Betula*) overstories and temperate (*Acer*, *Quercus*) understories (Fig. 9B).
- Compound disturbance such as wind storms followed by high-intensity fires, leading to conversion from conifer-dominated boreal forests to deciduous-dominated forests of birch and aspen (Fig. 9C), or temperate forest dominated by disturbance adapted temperate species, for example red maple (*Acer rubrum*) or bur oak (*Quercus macrocarpa*).
- Heat and drought stress killing large swaths of boreal forest along the prairie-forest border with replacement by grasslands or savannas. This scenario could occur if rising temperatures cause a negative precipitation-evaporation balance. Massive mortality of aspen (*Populus tremuloides*) forests has already occurred via this mechanism along the southern edge of the boreal forest in Alberta and Saskatchewan, Canada (Michaelian et al., 2011).
- Insect infestation (native and exotic insect species) due to lack of extreme cold that formerly kept insect populations at bay, could kill large areas of boreal forest (Logan et al., 2003). For example, mountain pine beetle (*Dendroctonus ponderosae*), although



Fig. 9 Climate-related changes in forest regeneration. (A) A sugar maple (temperate species) sapling next to balsam fir in the understory of a boreal forest in 2016, that had no invasion of temperate species 30 years earlier. Photo by Lee Frelich. (B) Boreal paper birch, spruce and fir forest in northern Minnesota with temperate species (*red maple*) in the understory. Photo by Dave Hansen. (C) Paper birch regeneration replacing jack pine and black spruce forests 5 years following a compound disturbance event with windthrow followed by fire. Photo by Dave Hansen.

native in western North America, has exploded in recent years after a run of several warm winters, and has killed millions of hectares of lodgepole pine (*Pinus contorta*). This insect pest may be able to reach boreal forests in eastern North America dominated by jack pine, which has been shown to be a suitable host (Rosenberger et al., 2017).

Although most models project gradual change from boreal forest to temperate forest or savanna, most of these mechanisms have the capability to quickly transform large swaths (tens to millions of km²) of boreal forest to other vegetation types. Therefore, many large surprises are likely to occur in the southern boreal forest over the next century, with major impacts on forest productivity, ecosystem services, and wildlife habitat.

Conservation Initiatives

If the future super-interglacial world materializes, a number of important questions arise: Where will boreal forest be replaced by other biomes? On such landscapes where will the remnants or climate refugia occur? Where will new boreal forest appear in former tundra? Scientists are working on answers to these questions.

Climate refugia are defined as “areas relatively buffered from contemporary climate change over time that enable persistence of valued physical, ecological, and socio-cultural resources” (Morelli et al., 2016). For refugia, the past is the key to the future; refugia of boreal forests in a warmer world can be studied by examining past refugia that formed as the glaciers retreated 18,000–6000 ybp. For example, early Holocene (ca. 11,700 ybp) boreal forests in the Midwestern USA—Minnesota, Wisconsin and Michigan—were replaced by temperate forests of oak, maple, elm and basswood between 11,000 and 6000 ybp. However, small-to-medium sized landscape features, 10s–1000s of hectares in size, retained boreal forests for millennia, some even until today. These included numerous lowlands that regularly experience cold air pooling at night, which became peatlands where black spruce or tamarack forests persisted to the present day. Some boreal forests also persisted in areas near large lakes with cold-water upwelling. Perhaps the most famous example is on the Door Peninsula of Wisconsin in Lake Michigan, where boreal forests persist due to cool summer temperatures brought in by lake effect breezes that pass over cold upwelling water just before coming ashore, creating a narrow belt (1–3 km wide) of boreal forest along the shore. Studies are underway to find future climate refugia like these within the current extent of the boreal forest. Boreal forest may persist locally in these refugia, even as the surrounding landscape becomes temperate forest or even grassland.

Major initiatives in boreal forest conservation include the Boreal Songbird Initiative of the Pew Charitable Trust, The World Wildlife Fund (WWF) Forests Program, the Boreal Conservation Framework, and The Nature Conservancy Boreal Conservation Program. These programs seek to reserve large areas of land from development and timber harvesting, and to develop best management practices (BMPs) to make harvesting more compatible with natural disturbance regimes (e.g., close to nature forestry) in other areas. Due to the remoteness of the boreal forest, setting aside very large acreages from development is feasible, and has happened in parts of Canada, United States, and Russia.

BMPs are partly government regulated and partly accomplished through certification of forest management and chain of custody (following certified wood from harvest through products to the consumer). The Forest Stewardship Council (FSC) and Programme for the Endorsement of Forest Certification (PEFC) are non-government, non-profit certification organizations with guidelines for proportion of acreage harvested annually within a given ownership, as well as considerations for maintaining biodiversity, wildlife, water quality, and indigenous rights. About 10% of forest land worldwide, and in the boreal forest, is registered in one or both of these certification programs. Proportions of certified land are much higher in the temperate forest biome, suggesting room for improvement in boreal forests. However, large acreages of boreal forest are registered with one or both certifying agencies in Canada, Sweden, Finland and Russia (FSC, 2018; PEFC, 2018).

Conclusions

Boreal forests comprise one third of all forests on the planet; due to their remoteness and cold climate, many large intact boreal ecosystems still exist. Due to their importance to ecosystem services, wildlife and water resources, at regional and global scales, many efforts are underway to preserve and improve management of boreal forests. However, because of warming climate, large changes are likely to occur in the southern half of the boreal forest over the next several decades, including death of boreal trees caused by several mechanisms, and replacement by temperate forests or grasslands. This transition will be messy, but could be minimized by mitigating CO₂ emissions, by, for example, strictly following the COP21 Paris Climate Accords. Using history as a key to the future, scientists are working to develop solutions for managing change in the boreal forest.

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Coniferous Forests of the Klamath-Siskiyou Region, Northwest California and Southwest Oregon

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Abstract

One of the world's densest geo-climatic, evolutionary, and ecogeographic diversities alongside low density human populations gives the Klamath bioregion a huge advantage in maintaining most of its biodiversity into the next century. With sufficient protection from and mitigation of major anthropogenic drivers of genetic loss at most scales, Klamath species will continue to accumulate species largely as a result of a high habitat density. This spurs speciation and migration and slows extinction rates due to nearby refuges quickly accessed even during rapid climate change. Unless temperatures reach mid-Pliocene levels in a geologic instant, speciations, and migrations will remain high and are likely to increase. However, one labels the enchanting intricacy of this bioregion, conserving its biodiversity in all its major forms and processes highlights the need to know and to care for that which is rare.

Introduction

The near perfect geographic match of the Klamath Mountains province with its bioregion underlines one of the world's great synergies of rock, water, and life.

Dozens of mountain uplifts and gravity or erosional deflations dominate Klamath geo-history. Some of these events and processes are so geologically recent or uneven in intensity that jagged peaks seem somewhat evenly interspersed with older flatter surfaces and newer river terraces, a topographic pattern that tends to maximize biodiversity. Meeting moist winter air from the Pacific Ocean with this topography creates one of the world's densest and most diverse set of rain shadows, soils, slope types, and drainage networks. How much water the Klamath's five ranges catch and hold drops dramatically in moving downhill or from west to east, with over 3.5 m annually near the coast and down to less than half a meter in deep valleys just tens of kilometers inland.

More specifically, the collusion of geology and biology together defines biodiversity centers and biologically porous borders much more than just geography. The diffuse, gradual bio-boundaries of the Klamaths speak of the many habitats that the bioregion shares with adjacent bioregions. This overlap has aided migrations, especially those from adjacent biodiverse mountain ranges, four of which together uniquely link up with the Klamaths.

Like most anything that builds Klamath biodiversity, what makes the bioregion so special is neither straightforward nor singular. It's more likely to be the sum of all the relicts, endemics, hybrids, migrants, range limited taxa, their main subdivisions, and processes known and unknown that may be as high per hectare in the Klamaths as most anywhere else.

Far <1% of visible Klamath taxa has been studied beyond scientific descriptions that briefly describes how their locality, anatomy, and/or genetics compares to near relatives. That suggests that the number of taxa that highlight many of the bioregion's diversity processes are at least an order of magnitude more than what hundreds of studies have shown. Yet perhaps the most telling argument for the Klamath's exceptionalism is that most other regions with similar geo- and biodiversity would cover much more area than the 25,595 km² or so of the Klamaths.

Climatic complexity in such a limited space but mind numbing timespans fostered a greater sum, density, range, and/or accumulation of soils, topographies of erosion and uplift than most other bioregions. All this promotes a higher density of taxa than that which occurs in most other extra-tropical regions and in many places closer to the equator. Some 70,000 nonmicrobial species embody a broad range and density of taxonomic scales and trophic levels of generalists, specialists, opportunists, parasites, mutualists, and commensals that includes:

- (1) Documented speciation includes >33 taxa that are cryptic, taxa that are hard to separate out based on physical characteristics. In parentheses are the numbers of other taxa thought to have originated from physical separation of populations (>119), ecologically separated in the same place (>140), and limited gene flow in caves (>25), on mountains (>104), and in soils (>195). There are other ecogeographic speciations that range from the postulated originations of several superfamilies to dozens of underground fungi to thousands of varieties of plants and animals spurred by an increasingly intense Mediterranean climate of dry summers and wet winters that has produced >28 taxa. Toxic soils and increased drought from this climate change decreased woody diversity. However, in a process known as ecologic release, the reduced competition for sunlight so increased herb species richness that it has more than made up for this loss. Speciation has also been enhanced by dozens of hybrid zones, hundreds of bootstrapping co-speciations, and thousands of ecotones.
- Over 3800 disjunctions larger than the Klamaths occur. Disjuncts occur where taxa are geographically separated even though there are habitable areas for a particular taxa that lie between populations. There are over 100 intracontinental disjunct taxa in Klamath wetlands just from presumed relict distributions or from bird assistance in intracontinental plant migrations. Breaks in the gene flow of >84 taxa and over 4000 taxa at range limits also attest to how a dense array of intersecting habitats has enhanced speciation and/or finely divided niche hyperspace.
- (2) Moderate, seasonal, and soil disturbances that vary the duration and proportion of successional and non-successional ecologic states sufficient for successful colonization. Many migrants come from the region, several oceans and other ranges and valleys, most continents, now vanished land bridges, close to a dozen mini-continents, and at least two supercontinents.
- (3) Havens for three monospecific endemic families, four more widespread monogeneric families, and refuges for at least 106 other relict taxa restricted in geography or taxonomy. This is due in part to low extinction rates afforded by a lack of relatively major and geologically rapid disturbances such as continental scale glaciations, ashfall from supervolcanoes, continental flood basalts, large interior seaways, and/or widespread desertification. A higher habitat density than most anywhere helps to mitigate the negative biodiversity effects of lesser calamities and/or enhance their positive effects.



Charina bottae (rubber boa) belongs to a relict group.

A low extinction, and high migration and speciation sum make the region's cumulative effects of time as prominent if not more so than the effects of the region's dense collection of colliding, overlapping, and intergrading ecosystems that make up its biomes. Thus time added to vertical, east-west, and north-south dimensions of the Klamaths more properly creates a geo-bio region or bioregion rather than just an ecoregion. That the region's processes surpasses many either/or dualities or other conceptual constraints in many sciences form one of region's most distinctive and ongoing traits.

Klamath exceptionalism stands out the most in a global context. The Klamath's sum of different kinds of biodiversity largely depends on the geodiversity of one of the world's oldest and highest densities of ~eight climates and ~17 land masses and seafloors arriving from elsewhere. Within these areas are > 50 types of rock, including hundreds of caves and huge granitoid masses of once molten rock (plutons), and thousands of square kilometers of rarely exposed rock whose soil increases speciation of plants that can adapt to conditions too dry or toxic to most plants. Drainages are in the thousands, and there are uncounted large to tiny springs and faults, where rock may have slid many kilometers or just meters, thus increasing side-by-side sharp contrasts in soils and the effects this has on vegetation.

The province may have had up to 17 cycles of stretchings and fusion from collisions that lead to ever larger land and seafloor amalgamations. Pressure-release melting, dropping heavy minerals, and drawing up less dense melts differentiated the liquids and residues into varied rock types. Water added to rocks left behind morphed peridotite into water-rich serpentine, both rock types with great effects on biodiversity. Melts later crystallized as diorite-like rock typical of land volcanoes but whose big crystals made poor sandy soils on which endemics also developed with little competition. That includes the endemic *Lupinus aridus* var. *ashlandensis*, and members of relict Tetrigidae grasshoppers and Gryllotalpidae crickets that can dig their tunnels in sandy soils.

Seafloors were thrust so deep underground that water squeezed out of them flux-melted basalts like salt on ice. The pressure-release of pull-apart basins and mountains undergoing gravitation collapse also melted rock. Heavier minerals dropped out, leaving melts that solidified as relatively less dense diorite in huge masses known as granitoids.

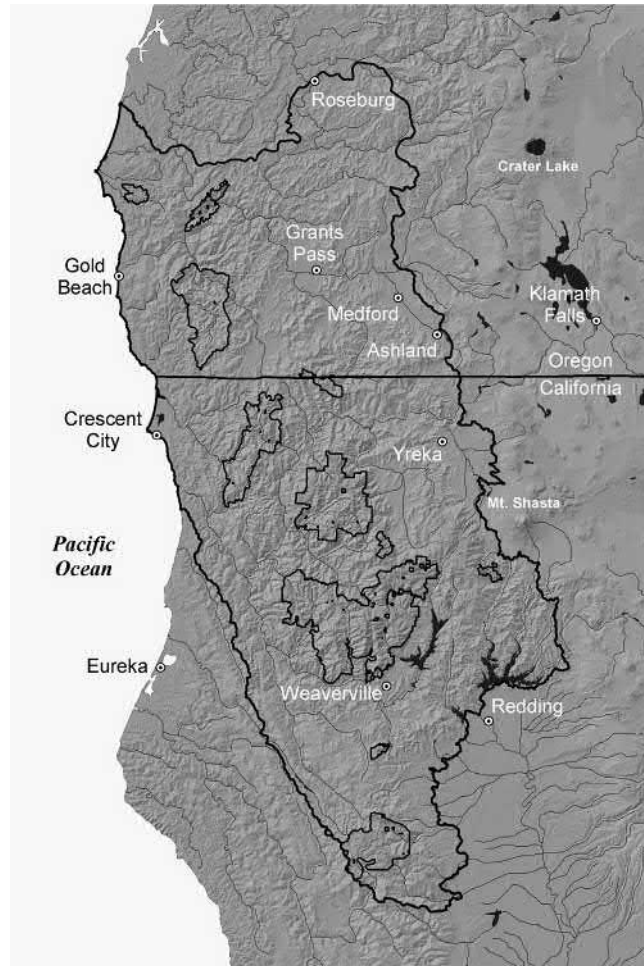
Like a now taller ice cube pushed deep down and squeezed by collisions, the amount of these less dense rocks added to nearly half a billion years of crustal buoyancy that lies at the heart of Klamath species richness. Despite at least a dozen uplifts and tens of miles of vertical erosion, the Klamaths are rising once again to continue its great diversity of slopes, climates, and soils that are the basis of its biodiversity.



Pull-apart geology can increase caves and buoyant granitoid plutons.

Geography

The Klamath Mountains bioregion makes up a major part of southwestern Oregon and northwestern California, with two prongs bounded in the south by the most expansively defined San Francisco Bay region with the Klamath bioregion extending northward to the city of Roseburg in southwestern Oregon. The Siskiyou are north of the Klamath River and so comprise the smaller part of the region. Therefore most people call the whole complex the Klamath-Siskiyou Mountains or just the Klamaths. Of the Klamath ranges, the Trinities link to the Scott, Salmon, and Marble Mountains. But rivers, climates, rock types, and valleys slice through the mountains. They typify the topography of the region as much as any set of ranges.



Outlined Wilderness Areas with Klamath-Siskiyou. From Dominic DellaSala.

Geology

Buoyant Rocks

The lightweight granitic “roots” of many old mountains have been largely lost to erosion, like a boat no longer rising because so little is left to remove and lighten its load. Most old mountains also have been crowded out by incoming seafloors and land masses and so are now too far away from a coast or are too thin perpendicular to prevailing winds to have much climate variation not determined by elevation. Coastal mountains often lack collisional shortening to have risen high or aren’t broad enough from amalgamated land masses to diversity their climates. Ranges in the Americas are mostly aligned north to south, thus receiving similar precipitation and evaporation rates on mostly east and west facing slopes.



Cryptocercus: Appalachian and Pacific Northwest relict.

Based on fossils of some of the world's earliest animals, the Klamaths contains what may be America's sediment. Many parts of the Klamaths traveled across a universal ocean larger by far than half the planet's surface, one that had many more seafloor plates to build and shape a superterrane than is the case for any ocean today. Sideways collisions between lands and seafloors split open basins. Fast sinking seafloors also stretched the crust, moving rocks and their melts up from tens of miles deep far more often than most any other province. Collisions from massive mini-continents, oceanic plateaus, and mid-ocean ridges shoved these heavy rocks on top of Earth's crust and greatly shortened it, uplifting the Klamaths like a squeezed ice cube now floating higher in liquid.

Multiple sunken seafloors, collisions, uplift after dense parts fell off, and subsequent gravitational collapses also have made the Klamaths unusually broad for a province still close to a coast. Many of these crustal movements have changed in speed or intensity in the last 150 million years compared to perhaps thinner crusts and hot and slipperier mantle rock beneath them in older times. The Klamath's great age thus may be a clue as to why in part the bioregion appears exempt from the patterns of most American mountains. In essence, the mold is broken and such terranes aren't made anymore.



Collisions tilt seafloors and shorten buoyant crust, causing uplift.

Coastward Continuance

A province so old is more likely to have a multitude of geologic forces acting on it that makes it differ from the location, height, and orientation of younger mountain systems. While the Sierra and Blue Mountains were pushed inland by thick rock plates, a hot, thin, and bendable ocean floor may have slid under the Klamaths, leaving it near the climate diversity of coastal areas during dinosaurian times (Ernst, 2013). The Klamaths and Sierra Mountains then moved in opposite directions wedged open by an expanding inland sea that eventually drained, creating the Great Valley of California. Like a door opening, greater movement in the south caused the Klamaths to twist.

The Sierras moving northward and a sideways collision with an oceanic plateau (Siletzia) added to this rotation by tilting the Klamaths. Caught between the Pacific Ocean and continental plates, the Klamaths were rolled between sideways sliding faults that were cousins to the San Andreas. Most or all of these motions would have rotated the Klamaths clockwise, causing the ranges to lie aslant of the normal pattern of most American mountains running north and south (Alt and Hyndman, 2016).

Climates

As with serpentine, the Klamaths have a broad Goldilocks' "just right" climatic diversity. Coastal mountains to the north ("mostly wetter") or south ("mostly drier") don't add nearly as much to their own climatic diversities as does the west to east and southwest to northeast directions of the Klamaths that may funnel precipitation into some areas but not into others.

Climatic diversity allows species to escape regional or global extinction by rapidly accessing refugia during climate change. For example, some 40 Klamath near-endemic vascular plants have dozens of sites in the bioregion but only one to five sites in the Sierras and a few sites in other nearby ranges, all areas without the high density of varied refuges that the Klamaths offers.



Little Kerby Peak overlooking Illinois Valley.

Biology

Overview

The Klamaths are the wetter part of the California Floristic Province (CFP) which stretches from southwestern Oregon to northern Baja California and from the coast east to the Sierras. It is defined by a winter-wet, summer-dry climate like that in the Mediterranean Basin. It boasts a species richness of > 5500 native vascular plant species with about 1800 endemics. Just the Klamaths alone have a total of about 192 vascular plant endemics with ~ 28 near endemic taxa having the most sites in the bioregion but which are also found in fewer sites in the northern North Coast Ranges (NCR) down to Clear Lake. The number of strict endemics is more than one would expect as the Klamaths is only about 8% of the CFP.

The CFP is one of the richest floras on the planet, a place where low extinction rates have been more important than either migrations or speciations in determining biodiversity. This is especially true in the Klamath section where old floras and faunas survive due to more abundant precipitation and more equable and stable climates than in the rest of the CFP ([Lancaster and Kay, 2013](#)). Of all parts of the CFP, only an area east of Los Angeles in the rain shadow of the San Bernardino Mountains and with a great variety of elevations is there a higher density of endemics.

Based on known sites and suitable habitat, about 40,000 insects, arachnids, and other arthropod species live in the region. That compares to the 50,000–70,000 species thought to be in the mountains of the Pacific Northwest ([US Geological Survey, 2015](#)). There are hundreds of hybrid plants and at least 23 endemic species apparently created by hybridization.

Biodiversity Behemoth

Aside from a Mediterranean or other temperate peak in diversity in vascular plants and stoneflies, water and carabid beetles, and other groups far from the equator, one can point to other taxa with high diversity. Of the ten mollusk provinces in the United States, three intersect in the Klamaths, the most of any US bioregion ([Burke, 2013](#)). Sciomyzidae and tipulid fly diversity is highest in northwestern California. More reptiles and amphibians inhabit the Klamaths than any other Far West range. Fish species in the Klamaths and Modoc Plateau is only exceeded in the United States in the Southeast ([Allister et al., 1986](#)). Crane fly diversity is higher than in any other Western state ([Alexander, 1967](#)). Compared to other areas of the Nearctic, the ancient Blephariceridae (net-winged) and Deuterophlebiidae (mountain) midges and several ancient spider families each appear to have an endemic peak in the Klamaths.

Of all conifers west of the Rockies, over half are in the Klamaths. With some 3500 vascular plant species in the Klamaths, there is expected to be over 6300 species of macrofungi. Presumably due to a slowly drying climate, hypogean fungi are especially diverse with 44 species in just one genus, 24 in another, and up to five endemics. One small Klamath watershed has more than a third of all known Pacific Northwest lichens in an area comprising $< 1\%$ of Oregon. Just the Oregon part of the Klamaths holds nearly a quarter of all bryophytes north of Mexico ([Villegla et al., 2013](#)).

Relicts

Due to ancient and extensive serpentine soils toxic to most plants, and an abundance of north-facing slopes at mid-elevations, serpentine obligate, boreotrophic, and other relicts total up to one of the three greatest concentrations of paleoendemics Far West

bioregions. Limnanthaceae (meadowfoam), Ascaphidae (tailed frog), and Trilliaceae (trillium) families may have originated here even though some of their descendants are now more widespread.

Taxa starting in the Klamaths also may include two superfamilies of millipedes and spiders, three families of spiders and millipedes, one of fairy shrimp and water mites, and genera of flowering plants (*Phacelia*, *Perideridia*, *Downingia*, *Vancouveria*), heathers (*Pyrola*, *Kalmiopsis*, *Darlingtonia*), true lilies (*Hastingsia*, *Calochortus*, *Camass*), asters (*Tracyina*, *Psilocarphus*, *Wyethia*), and saxifrages (*Bensoniella*, *Romanzoffia*, *Fragariopsis*). Perhaps the world's first spruce, Brewer spruce once lived in much of the West but that range has shrunk to a small part of the Klamaths ([Ledig et al., 2005](#)).



Picea breweriana: endemic relict.

Centers of Diversity

Animal genera with centers of diversity include seven spiders (*Aptostichus*, *Calymmaria*, *Hesperocranum*, *Antrodiaetus*, *Liocranoides*, *Tenggella*, *Titiotus*), three water mites (*Scutolebertia*, *Cyclothyas* and *Siskiyouthyas*), a beetle (*Pinodytes*), katydid (*Idionotus*), hypogean fungi (*Balsamia*), and shrub (*Amelanchier*).

Certain Klamath endemics may be clades of Ericaceae, Taxaceae, *Arabis*, and Saxifragaceae), complexes (*Smilax*), lineages (*Manzanita*, fire-adapted *Pinus*), sections (*Prunus*, *Allium*, *Sedum*, *Quercus* white oaks), series (*Iris*), subgenera (*Fritillaria*, *Penstemon*, *Arnica*), subsections (*Rhododendron*), subspecies (*Pinus balfouriana*), tribes (Cleomaceae) and subfamilies of Scrophulariaceae, Alliaceae, and Agavaceae.



Sadler oak, 1st white oak?

Refugia

Even small areas can provide both refugia and speciations. With northern taxa protected from drought and southern taxa from freezing, certain beetles in caves (*Pterostichus*, *Pinodytes*, *Catoptrichus*), diplurans (*Occasjapyx*), grylloblattids (*Grylloblatta*), harvestmen (*Taracus*, *Sabacon*), crickets (*Pristoceuthophilus*), pseudoscorpions (*Pseudogarypus*), and spiders (*Calymmaria*, *Cybaeus*, *Pityohyphantes*) may have had a long time to speciate at the edge of their ranges as they often belong to relict or other ancient groups. Serpentine patches extend northern range limits in which budding speciation may have produced new *Salix* (willows), *Silene* (catch-flies), *Erigeron* (fleabanes), *Sedum*, *Kalmiopsis*, *Boechera* (rockcresses), and *Calochortus* and *Hastingsia* (rush) lilies.



Kalmiopsis.

Like caves, coastal areas, and north facing slopes at mid-elevations, the refugia-within-refugia of running water (fens, hyporheic, springs, rivers, streams), and bogs, deep groundwater, and vernal pools tend to have low extinction rates by virtue of species being largely protected from hard freezes or severe drought. These habitats contain some of the oldest families, including those of frogs (Ascaphidae), fishes (*Petromyzon*, *Acipenser*), flies (*Deuterophlebia*) and beetles (Amphizoidae), and three Klamath near-endemic mite genera.

Other ancient aquatic or partly aquatic animals include certain bryozoans, crane flies (*Pediciidae*), crustaceans (Notostraca, Anostraca, Mysida, and Conchostraca), syncarids (*Pacificabathynella*), dragonflies (Petaluridae, Gomphidae), hydrozoans (*Hydra*, Hydrozoa), mayflies (Ephemerellidae, Siphonuridae), fishflies (Corydalidae), and sponges (*Spongilla*). Water-loving archaic groups include certain ferns (Blechnaceae, Osmundaceae), herbs (*Aristolochia*, *Anemopsis*, *Aralia*), waterlilies (*Nuphar*, *Menyanthes*), skunk cabbage (*Lysichiton*), hornworts (*Ceratophyllum*), horsetails (*Equisetum*), quillworts (*Isoetes*), and pitcher plants (*Darlingtonia*).



Darlingtonia.

Some old groups are not strictly aquatic even in their juvenile stages but they do rely on abundant water. Due to primitive kidneys that poorly conserve water, the relict monogeneric Aplodontidae (mountain beavers) feed mainly on succulent vegetation and burrow in moist soils. Single cell cercozoans who live in damp cave soils are related to the much larger foraminiferans that form much of the limestone of the pyramids. Shasta Springs has even less acreage than riparian or coastal areas. This thermal refuge within an aquatic refuge probably dates to about a hundred million years ago though the centipedes (*Kiberbius remex* and *Nadabius oreinus*), springtails (*Microcreagris magna*) and diplurans (*Haplocampa wheeleri*) only found there may be relatively new.

Other ancient groups not aquatic include lizards (Anguidae), diplurans (Japygidae), spiders (Mygalomorphae, Pimoidae, Lep-tonetidae, Anapidae, Hypochilidae), pseudocentipedes (Scutigereidae), harvestmen (Sironidae, Triaenonychidae), proturans (Acerentomidae), roaches (Cryptocercidae), and springtails (Neelidae). Ancient plant groups include certain families of club mosses (Lycopodiaceae) and conifers (Pinaceae, Cupressaceae), and genera or lineages of flowering trees (*Quercus* white oaks, *Platanus*, *Salix*, *Rhamnus*, *Staphylea*, *Betula*, and *Juglans*).

Endemism

Prior to over 34 million years ago, at least several hundred genera of plants and animals had come to the Klamaths. As climates cooled and dried they became more restricted in their geographic range or they became extinct. Many still inhabit north-facing slopes at moderate elevations, places neither too cold nor too dry and thus similar to the semitropical habitats of the boreotropics that once stretched across the northern hemisphere. Not only did such slopes offer refugia but they may have been centers of isolation-speciation as well, with about 81% of Klamath endemics found inland versus endemics or near-endemics from more coastal sites. Part of the reason for this likely is because near-coastal areas are closer to the Klamath boreotropic climates than mid-elevation slopes further inland.

However, the reduced area and increased competition in coastal areas compared to other refugia lessened biodiversity. Trees and shrubs likely have suppressed herbaceous plant speciation and/or increased extirpations while the ease of low elevation migrations along the coast has reduced the number of narrow endemics. Consequently, compared to inland areas, only about 6% of Klamath plant taxa are shared with the adjacent coast as near-endemics (~13 vs. 188 taxa). About half of ~633 Klamath animal endemics or near-endemic species are shared with the coast, indicating that more animal endemics have originated from near-coastal montane genetic isolation and/or more taxa have been preserved by coastal climate buffering than is the case with plants shaded out by competitors.

The numbers and distribution of taxa suggests that the Klamath's mid-domain location enhanced biodiversity before and after its terranes had been sutured together with granitoid stitching plutons. Generally from the most to the least, prehistoric emigrants above the level of species include those from Asia (>230 taxa + >15 Himalayan taxa), South America (>120), three supercontinents (>21), and Europe (>11 + >9 Mediterranean and 7 Caucasus regions). Most of these Klamath taxa are now disjunct from relatives living in postulated origination areas.

Compared to genera native to North America, fewer of these genera and those emigrating to other continents gave rise to two or more Klamath endemic species (~22 vs. ~48). Apparently the high mobility advantage of most migrators moving in from various intercontinental directions increased gene flow. Thus reducing the likelihood of speciation. Instead, many endemics may have come from Klamath or nearby areas, places where genetic divergence may have been initiated by disturbances, geographic barriers, or ecologic release. Klamath/Sierran and mid-continent seaways may have helped diverge more than ten species while a meteorite impact may have fragmented the populations of >38 species. Even hitchhiking on birds may have separated >144 species on opposite sides of the continent. Post-uplift drought and increased climate seasonality may have helped to fragment populations, with the resulting genetic separations perhaps leading to >408 species.

More migrations from other regions and a moderate climate lessened extinctions and extirpations near the coast. There Klamath near-endemic plants derived from genera thought to have emigrated from other continents rises to about half of those thought to be derived from native genera (68 vs. 133) (Harris et al., 2013). Due to the even greater intercontinental mobility of animals, including many if not most Klamath endemics, there is an evening of the emigrant/native taxa ratio at ~322 vs. ~322.

Serpentine

Of all rock groups, serpentinite and peridotite have the greatest effect on biodiversity and speciation. Klamath serpentinite beds have been less tilted and more duplicated and stretched by faulting than serpentinite in the California Sierras or Oregon Blue Mountains. This produces wider and greater numbers of serpentine belts in the Klamaths. Unlike the Sierras and Blue Mountains, Klamath serpentine soils derived from a more even mix of peridotite and serpentinite. This adds to microhabitat diversity due in part to peridotite shading and runoff from its boulders. In other words, a more diverse microtopography shelters a greater diversity of plants in this rock type compared to the number of species in more topographically uniform, barren-looking soils derived from serpentinite.



Serpentine: rare rock elsewhere but common in Klamaths.

The percentage of serpentine endemics is way out of proportion to the area of serpentine. Endemics make up about 10% of the CFP vascular plant endemics yet serpentine soils in California comprise <1% of the state's surface. The ratios in the Klamaths are even more lopsided as serpentine covers about 14% of its land area, perhaps the most of any bioregion in the world. As a result, of all Klamath near-endemics shared with the NCR, ~191 taxa or 87% have serpentine affinities.

California plants on serpentine in relatively moist sites common in the Klamaths are more diverse in function and genetically more different from each other than those on drier sites (Anacker, 2011). This also indicates a low Klamath extinction rate and thus a long enough residence for plants to become neoendemics or even paleoendemics or relicts or both. The high evenness of microhabitats and the sheer areal cover of serpentine areas of the Klamaths also reduces the likelihood of developing a biologic sink in which species become extinct. As a result of differential extinction, speciation, and migration rates, there are about three times more plant taxa entirely or largely confined to serpentine in the Klamaths compared to that of any other region in North America (Coleman and Kruckeberg, 1999).

Peripheral speciation at the southern end of the Klamaths may have also played a role in boosting biodiversity. If so, then a greater net migration from a Klamath source to the northern NCR may have helped result in producing ~28 shared near-endemic species. In contrast, the southern North Coast Range (sNCR) has fewer shared near-endemics (~15 taxa) and less areal exposure of serpentine soils and is further away from most potential near-endemic migrants.

There's not only a north-south difference in serpentine obligates. There are fewer serpentine-dependent taxa in coastal areas compared to more inland areas, a pattern that may be due to higher species competition. Fewer serpentine species in the Sierras compared to most of the Klamaths may be due in part to more drought extirpations. There also are fewer endemics in both areas compared to the Klamaths, in part because of fewer and geologically more recent serpentine outcrops.

Being close to the birth of seafloors allowed the still heat expanded and so light enough oceanic slabs to be pushed on top of the Klamaths. These collisions were so strong that seafloor sequences were fault duplicated and preserved rather than sinking back down below Earth's crust. The Klamaths thus are in a not-too-wet/not-too-dry, just right Goldilocks zone of many ancient and isolated serpentine areas conducive to speciation and much larger areas of continuous serpentine that reduces extinction rates (Harrison et al., 2004).

Serpentine soils also impact fungal diversity. Out of 14 endemic or near-endemic peas, only four can tolerate serpentine, most likely because of its toxicity to many of their symbiotic root fungi. This intolerance to certain heavy metals and/or a high magnesium to calcium ratio may extend to other fungi as there are no mushrooms with fruiting bodies that are known only from Klamath serpentine. However, 32 of 74 ectomycorrhizal fungi associated with Garry's oak (scientific name) were unique to serpentine soil (Moser et al., 2005). Such underground fungi mostly fruit in the spring and so are not as dependent on a moist fall to ensure spore dispersal, as are most above-ground fungi.

Calcite

Though rare, calcite rocks and their soils host about half a dozen flowering endemics, several hypogean fungi, a possibly new species of moss, dozens of snails, and at least ten lichens largely or wholly restricted to marble or calcium rich springs. The Hosselkus and McCloud rock formations alone have four endemics among *Erythronium*, *Adiantum*, *Ageratina*, and *Neviusia*, as well as a snail and

three salamander endemics, and, according to one botanist, an “outrageous shrub diversity.” Leaf-wise, the calcite endemic *Neviusia* has a virtually identical species that dates back to the boreotropical era. The closest relatives of the *Batrachoseps* salamanders may be in Korea (Vieites et al., 2011), suggesting that the genus also is relict.

In contrast, the Scott Bar’s salamander’s (*Plethodon asupak*) geographic location and genetic closeness to the endemic Del Norte salamander (*P. elongatus*) suggests it’s a neoendemic that separated from the older species at the edge of its range. This evolution, known as budding speciation, may be very common in the Klamaths, given the large number of range limited species. It is less dependent on soil types than is the speciation of serpentine plants, although caves and sandy soils can also increase the range limit and hence geographic separation of animals and plants, rendering them more likely to become isolated from larger populations and develop into new species.

Soils

Not only are Klamath rocks exceptionally varied with unusual percentages of normally rare rocks, their debris is even more so as its soils track the most varied of climates in time and space with some of the world’s shortest geographic distances between climates. Due to multiple uneven uplifts and thick layers of tilted and varied bedrock rare elsewhere, a great range of soils have been relict from past climates, including extensive areas of iron-rich lateritic soils formed in tropical times near sea level. Based on woody plant diversity, a high density of soils/climate interactions sustained cradles of creation and museums of Klamath biodiversity for at least 16 million years (Barnett, 2008). Fossils indicate that in an area known as the Far West (Alaska to California), at least 107 genera (> 90% woody spp.) from these times became extinct or extirpated largely due to increasingly drier summers and/or colder winters. However, reduced shading competition likely sped up speciation of thousands of herbaceous plants.

Fire Influences on Plant Diversity

Frequent fires of varying intensity, the unusually diverse mix of hardwoods and conifers, and a moderate variation in climates may prevent single vertical plant levels from dominating as they do in more extreme conditions in tundra, coastal savannas, and grasslands respectively to the north, west, and east of the Klamaths.

Multi-level canopies or other structural complexity can increase the species richness of certain mammal, bird, lichen, and arthropods. The diversity of galls made by nematodes, flies, mites, moths, and gall wasps may exceed that of most other mountains. Klamath gall-making houses thousands of species including three Cynipidae wasps, one Cecidomyiidae midge, and one Cosmopterigidae moth, all regional endemics or near endemics because they live as larvae on trees or shrubs endemic or near-endemic to the bioregion.

A dense set of habitats greatly varying in moisture and slope steepness builds biodiversity via bootstrapping in part by allowing or enhancing a variety of fires in their intensity, frequency, and coverage. That is in part because fires that reach a habitat different from where it started will often change in intensity, rate of spread, or even die out altogether due to sharp geographical contrasts in fuel loads, soils, and slope gradients. This fine-grained variation in habitat and the resulting patchy nature of fire and its severity favors the ecology of fast-reproducing migrants in some cases and genetic diversification of those not so mobile in others.

In particular, mixed-severity fire regimes common in the Klamaths likely increases resilience, an ecological “bounce back” so that even local extirpations are few, thus promoting diversity on regional and local scales especially in disturbance-adapted riparian zones, savannas, and oak woodlands. Similar to how evenness of species populations tends to maintain biodiversity, more or less equal proportions of different habitats shaped by fire frequency, intensity, and duration or its absence is a pattern most likely to prevent regional or even local extirpation due to close by areas that have suitable habitat for migrants looking for a new home. Fire may most benefit specialized hemiparasites and predators among plants in serpentine fens, such as *Castilleja* (paintbrushes), *Pinguicula* (bladderworts), and *Darlingtonia* (pitcher plants).

Conservation

Tools to restore or maintain biodiversity and the ecosystem services they provide include managed and let-burn fires, including wildfires across a range of size and fire severity, prescribed burning, and variable density thinning. All are ways that can help match prehistoric-like climate variation in sites, snowpack, and disturbances and their effects on ecological resilience, and distribution and richness of species, including birds and mammals. Removal of invasives and/or increasing resistance to homogenizing monocultures can also help restore native biodiversity in certain amphibians, bats, microbes, and birds.



The nearest relative to the tailed frog depicted here is in New Zealand.

Judicious use of hands-off management, manual fuels reduction, and prescribed fire that best matches the effects of prehistoric fires can prevent encroachment of conifers into oak woodlands and fens, preserve ponderosa forests, and prevent shading out of shorter trees such as madrones. Thinning of <8 in. diameter trees can improve drought and fire resistance although competition by exotic species, fire suppression, and limited funding confounds attempts to accelerate old-growth traits in second-growth forests. However, even small scale efforts can heighten biodiversity in arthropods, butterflies in particular, and strengthen vegetative resilience in oak woodlands.

Provided there's substantial mitigation of the decline in biodiversity from the effects of non-natives, old-growth reduction, and extremes beyond the intensity, frequency, and/or range of climates in the last 11 millennium, the Klamath bioregion will continue to be a refugia for genetic diversity at all levels by continuing ecosystem services for natives and for arguably its most key non-native. Given these protections, the bioregion will retain its outstanding density of microrefugia at certain elevations for many species (Olson et al., 2012; Harrison and Noss, 2017). North-facing slopes at mid-elevations may offer refugia to some species during rapid warming and are likely to be less affected by anthropogenic change than is the case for other elevations. This contrasts with subalpine plants that may be subject to the competitive exclusions of taller growing plants benefiting from longer growing seasons. Taxa at lowland areas may be lost from extreme multi-year droughts or a higher rate of other human disturbances.

In support of the latter effects, relatively low elevations are where endemic Klamath taxa once lived but likely are now extinct. These may include a *Fluminicola* undescribed snail species, two popcorn flowers (*Plagiobothrys lithocaryus* and *P. lamprocarpus*), two caddisflies (*Rhyacophila amabilis* and *Agapetus denningi*), and two mariposa lilies (*Calochortus monanthus* and *C. indecorus*).

Increased regeneration of aspens, bird diversity, early seral mixed hardwoods, flowering species migrating from the south, and butterfly diversity will increase under most climate change scenarios. This would require that forest openings and the vertical structural diversity of tree canopies be maintained through mixed severity fire regimes, subalpine areas be protected from tree encroachment, and human impacts like overgrazing and off road traffic be contained and/or minimized. Based on numerous studies on climate change, many aquatic taxa will increase with the anticipated greater increase in broadleaf forests and their arthropod associates, provided that water and air quality and quantity can be maintained or improved.

Education of decision makers, general public, and politicians can heighten commitment to preserve intertwined biodiversity and ecosystem services, especially in biodiverse but still poorly understood areas like the Klamaths. However, such education must convince most human stakeholders that species richness contributes to services on a much broader and in depth scale than what has been understood so far. We have barely begun but we now know from many sciences what most cultures knew for millennium, that contact with the wild keeps us healthy on immune, cognitive, empathic, communal, evolutionary, and spiritual levels. Learning or remembering to appreciate the reciprocity of this mutual flourishing is a necessary step in attaining sustainability at all levels as we only protect well that which we love.



Wood eating fungi.

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Evergreen Oak Woodlands—Southern Europe and Northern Africa

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Abstract

From the Bronze Age the increase of human pressure such the livestock farming, crops harvesting, forests exploitation and the coming of the widespread urbanization, after the Roman Empire, have intensely transformed the woodlands in the Mediterranean basin. Mediterranean landscapes are profoundly different from the original ones prior to large-scale human degradation. The vast impenetrable forests have mostly been replaced by fragmented patches and by a sparse vegetation. Nevertheless, it remains a biodiverse landscape where waves of colonization left remnants of original forests that can provide clues for restoration of Mediterranean evergreen oak forests.

Mediterranean Forest Types

Broadleaved evergreen forests dominated by sclerophyllous oaks (*Quercus ilex*—holm or round-leaved oak, *Quercus coccifera*/*calliprinos*—kermes/palestine oak, *Quercus suber*—cork oak) are essential elements in the assessment of the Mediterranean forest ecosystems. These oaks aggregate form a zonal forest belt around the coastal districts of the Mediterranean Sea with only one large gap in N Africa, from Libya to Southern Levant, and with the sole exception of a small isolate in Cyrenaica (see Fig. 1).

Stands of broadleaved evergreen forest are also spread inland in the Atlas mountains, throughout the nearly whole Iberian peninsula (except for its N Westernmost coastal districts), south France (from Provence to the west side of the Central Massif and the Aquitanian coast), peninsular Italy (up to middle altitudes), southern and Aegean Greece and islands and from western and southern Anatolia to the mountains of Lebanon. They remain confined close to the coasts in northern Italy, Dalmatia and southern Palestina.

Together with the dominant oaks, an array of evergreen woody, mostly sub-arboreal species can be found: *Laurus nobilis*—bay laurel, *Myrtus communis*—common myrtle and *Viburnum tinus*—laurestine are the most common. Although numerous studies have investigated the structure and function of this ecosystem, the definition of the typical plant assemblage of Mediterranean forest has been quite ambiguous or unclear throughout the history of European plant ecology.

The classic Mediterranean landscape has been perceived and celebrated as the realm of a snuggled twisted scrub, with few scattered low trees, at least from the time of the “Grand Tour” onwards (Black, 2003), be it rich of suggestions and hints to the pastoral, fragrant landscape of an idealized classicism or biblical world (see Figs. 2 and 3). This interpretation was accepted in the scientific debate, focusing on a very widespread, changing, species-rich vegetation mosaic of treelets, low, woody shrubs, and open patches with dwarf shrubs with species from genus *Arbutus*, *Phillyrea*, *Rhamnus* *Erica*, *Pistacia*, *Myrtus* etc. as standard and ultimate elements in the structure of this vegetation.

Its original structure of almost closed and high, non-fragmented forest, dominated by evergreen oaks, has been widely ignored. The heavy impact of human disturbance, since the onset of the agro-pastoral colonization of the Mediterranean coastal regions (8–6 Millennium BP), through the degradation inducted by tillage, anthropogenic fires, charcoal processing, forest grazing, turned this forest vegetation into that celebrated, iconic shrubland called “Macchia” (in Italian for “coppiced stools”, copses) or “Maquis” (in French). For a long time, these woodlands have been erroneously considered a kind of zonal, structurally stable, representative plant cover of the Mediterranean landscape. The famous botanist and phytosociologist Braun-Blanquet in his pivotal works on phytosociological nomenclature in 1933 and 1936 stressed the structure of the Mediterranean evergreen forests as zonal, late successional association of evergreen sclerophyllous woody species (*Quercetum ilicis galloprovinciale*). From this moment on, its status as a forest biome began to be acknowledged by researchers. Up to the middle of the 20th century, *Q. ilex* and even more *Q. coccifera* were considered shrubby oaks, small to medium-sized, long-living trees and only exceptionally large trees (Giacomini and Fenaroli, 1958; Pignatti, 1979). Most of the known location throughout the Mediterranean region were degraded to pastured woodlands or were coppiced at short time intervals due to their nearly unailing capacity of resprouting.

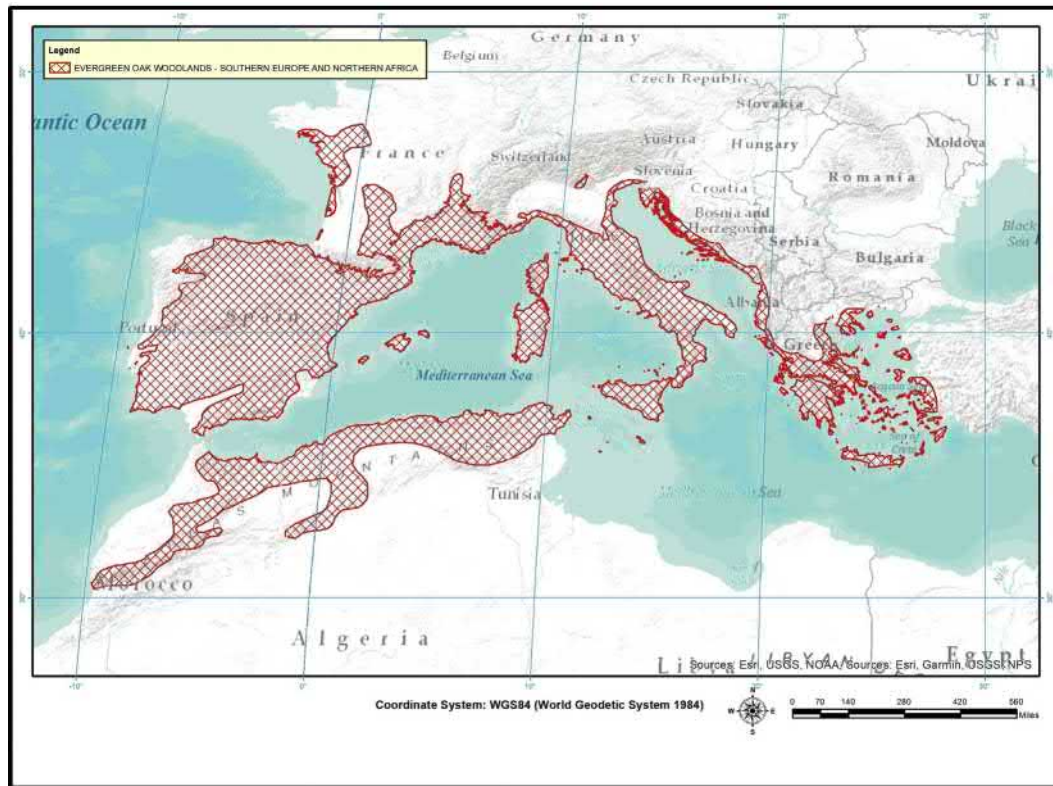


Fig. 1 Distribution map of evergreen oak woodlands in southern Europe and northern Africa, according EUFORGEN maps (see <http://www.euforgen.org/species/>), European Vegetation Archive (<http://euroveg.org/eva-database>; Chytrý et al., 2016) and references (e.g., Caudullo et al., 2017).



Fig. 2 The coastal landscape of Tuscany (Italy), the evergreen oak forest. Photo by Emiliano Agrillo.

The general reduction of coppicing in the Mediterranean countries during the last hundred years, or the much longer clearing intervals (in terms of cycle length), induced an overall transition from scrub to forests. This process is now active on vast areas and is ensured by conservation measures and directives, at least in Europe (e.g., the “Habitats” Directive 92/43/EC). *Quercus ilex*, reveals in mature present day stands (e.g., Tyrrhenian Italy) the crown habit and architecture of a tall, late-successional tree adapted to closed, dense canopies more than any other deciduous or evergreen Eurasian oaks. This species is also capable of active seed regeneration in the nearly dark light conditions of the forest floor. *Q. coccifera/calliprinos*, also long considered a shrub or a lower



Fig. 3 Holm oak and cork oak forest (Central Italy). Photo by Emiliano Agrillo.

treelet, in Crete and Anatolia (Jalas and Suominen, 1988; Vogiatzakis and Rackham, 2008) is often a real tree, attaining 20 m tall as relic of former now disrupted forest stands. The ultimate rehabilitation of its status as representative of the Eurasian evergreen broadleaved forest biome, is due to the works of Specht and Moll (1983) and Mai (1989).

Sclerophyllous Forest Distributions and Patterns

The distribution pattern of the three main taxa of the sclerophyllous forest is highly explanatory. A major distinctive character in the structure is the dominance and spread of *Q. ilex* in the W part of the Mediterranean region (N Africa, Italy, Iberia and France where it reaches the Atlantic coasts). East of the longitude of Rhodos and Northern Caria in W Anatolia, *Q. coccifera* becomes the only arbo-real representative of this evergreen broadleaved sclerophyllous forest, as well as in the Cyrenaican isolated enclave. Quite rare and scattered in the Central Mediterranean region (SE Italy, S Sicily and SW Sardinia), this oak conversely becomes very common again throughout the Atlas, S and E Iberia and Provence, thus displaying a nearly bipolar Mediterranean range (Fig. 1). *Q. suber* has the bulk of its range centered in the westernmost Atlantic districts of the Iberian Peninsula (see Agrillo et al., 2018), as well as in the Atlantic districts of Morocco, reaching the Tyrrhenian islands (Balearic Islands, Corse, Sardinia and Sicily) and the coastal fringe of Western Italy. It becomes extremely rare already in the Adriatic districts, with a few scattered stands in SE Italy (Apulia) and N Dalmatia where it occurs in a few locations, more often as hybrid populations (*Quercus crenata*—false cork oak) with its deciduous, temperate, subcontinental relative, *Q. cerris*—Turkey oak. Outside the SW Iberian core area, *Q. suber*, among the mentioned oaks, exhibits the most fragmented and discontinuous range.

All three taxa converge, coexist and cover their largest expanses in the Western Mediterranean region with Iberia and Morocco as core areas. Particularly intriguing is the occurrence of *Q. suber* disjunct stands along the Atlantic coast of Central France, where *Q. ilex* even reaches the Bretagne region (i.e., N Aquitania, Ile de Noirmoutier). The species exhibits scattered and rare populations along the coasts of the Black Sea of N Anatolia, long outside its zonal range.

This complex pattern, better than any other parametrization, synthetically outlines the different individual ecological demands among the species of oaks of the Mediterranean evergreen oak woodlands and sheds light on their developmental history.

Considering a global gradient of increasing xericity from W to E from the Atlantic coast to the Levant and the subordinate superimposed effect of more mesic macroclimatic conditions at the Western sides of any of the Mediterranean peninsulas. A rough outline of their basic requirements puts *Q. suber* at a warmer and moister side of a macroclimatic gradient. *Q. coccifera* is at the warmest and driest end (districts in the Ebro valley experience dry, nearly semidesert conditions), while *Q. ilex* apparently occupies an intermediate, alternatively more eurieious, position shifting towards the cooler end of the gradient in the oaks.

An amount of lower taxonomical rank has been suggested throughout the ranges of these oaks. Hybrids, introgressions, different interpretations of the same species by different authors, with an often-emphasized endemic character, have been asserted and proposed during time, neglecting the effect of phenotypic plasticity in species scattered along gradients of high environmental heterogeneity.

Major differentiations within *Q. ilex* might occur in the Iberian Peninsula and throughout NW Africa to Algeria (up to 2200 m a.s.l.). Here a very closely related taxon (*Q. ballota*) is reported as vicariant, coexisting with *Q. ilex* only within a narrow fringe of the Cantabrian coasts of N Spain and all along the E coasts of Spain. Within the *Q. coccifera* circum-Mediterranean species

complex, differences are even more indistinctive and clinal. The latter might merely be a more xerotolerant and eastern morphotype of the former, with denser hairiness on the younger shoots, reported from N Algeria, the SE coasts of the Italian Peninsula, to Turkey, Cyprus and further East to Palestina.

A closely related *taxon* to *Q. coccifera*, *Q. alnifolia* is known for its densely golden or brownish tomentose leaves below, and is endemic to Cyprus (Barbero and Quézel, 1979). *Quercus aucheri* (*Q. coccifera* sub-species *aucheri*) strongly pubescent, a dubitative distinct species (Toumi and Lumaret, 2010), is reported from the Aegean island of Cos and in the district of Istanbul.

In fact, *Q. coccifera*, *Q. calliprinos*, *Q. aucheri* and *Q. alnifolia* are apparently part of a very variable but genetically indistinguishable complex (Denk and Grimm, 2010) with its highest morphological diversity in the East. Additionally, all the western Eurasian *Ilex* oaks (*Quercus* subg *Sclerophyllodrys* sensu Schwarz 1959; *pro parte* subgenus *Cerris* sensu Denk; *Quercus alnifolia*, *Q. aucheri*, *Q. coccifera* and *Q. ilex*) are resolved as a monophyletic group (Denk and Grimm, 2010). These representatives of intriguing episodes of the evolutionary history within the *Cerris* group (sensu Denk and Grimm, 2010), suggests persistence of a higher degree of relictuality in the East, in the peri-Anatolian area for the xeric representatives.

In the W, more common are interspecific hybrids both among the evergreen and submediterranean deciduous or semi-deciduous oaks. The following taxa are reported: *Q. x airensis* (*Q. ilex* x *Q. coccifera*) in France, Spain, Portugal, Morocco, Algeria, Sicily, Greece); *Q. x autumnalis* (*Q. ilex* x *Q. rotundifolia*) in Spain; *Q. x mixta* (*Q. ilex* x *Q. suber* = *Q. morisii*) in France, Spain, Portugal, Italy, Sardinia, Sicily, Algeria; *Q. diosdadoi* (*Q. pyrenaica* X *Q. rotundifolia*) in SW Spain (Extremadura); *Q. x senneniana* (*Q. faginea* x *Q. rotundifolia*) in N Spain; *Q. afares* (*Q. canariensis* X *suber*) in North Africa (see Barbero et al., 1992), suggesting at least higher evolutionary dynamism for the more mesophilous representatives in the W.

Climatic Effects on Evergreen Forests

Traditionally, evergreenness in the Mediterranean oaks and their associates are assigned to a fundamental adaptation to the ruling Mediterranean-type climate of the region. They are characterized by summer drought, winter rain of cyclonic origin and mean annual temperature of $15 \pm 5^\circ\text{C}$. This trend recurs in other parts of the world at around 35 degrees latitude, where ruling actualism in geobotany strongly emphasizes the occurrence of physiognomically and adaptive similar, convergent forms of vegetation (American chaparral, S African fynbos, Australian mallee, Chilean matorrales). This pattern attracted most studies in modern plant ecology (Terradas, 1999).

Evergreen oaks are therefore drought tolerant when compared to the winter deciduous trees of the temperate forests. Summer dry, evergreen forest ecosystems apparently thrive under these constraints. Their species develop thick, leathery, hard-surfaced drought resistant, long living sclerophyllous leaves with waxy coatings, enabling them to withstand water loss during severe summer drought while their evergreen habit enables them to benefit from winter moisture (see Fig. 4 modified diagram; Pavari, 1959).

The rationale of the evolutionary success of the sclerophyllous model characterizing the plant cover in the Mediterranean region is centered around the observed links between the adaptive traits of these oaks, those of their associates and the ruling climate. Nevertheless, their evergreenness is primary in the history of the *taxon* and in the history of most of their woody associates, achieved long before the onset of a Mediterranean type climate in the Old World.

Nevertheless, shifting degrees in Mediterranean evergreen oaks of sclerophylly facing laurophyllly, suggest close phylogenetic relationships with an array of evergreen subtropical oaks of Himalayan or SE Asian range, like *Quercus baloot*—holly oak and *Q. floribunda*—moru oak, a tall tree very closely related to *Q. ilex* (and for some Authors, its Asian form). Also molecular data suggest that *Q. aucheri*, *Q. alnifolia*, *Q. coccifera* and *Q. ilex* share a common origin with the Himalayan *Q. floribunda* and *Q. baloot* (Denk and Grimm, 2010; Simeone et al., 2016; Hubert et al., 2014).

These species, all reaching higher altitudes in W Himalaya (1700–3000 m) and other “ilicoid” oaks (*Q. semecarpifolia*—Brown oak, *Q. leucotrichophora*—woolly oak, *Q. glauca*—blue Japanese oak) belong to the subgenus *Cerris* sensu Denk evolved from an originary, late Neogenic Indo-Malesian stock (Zohary, 1973), close to fossil western Eurasian evergreen macrothermic oak species of late Neogene (*Q. drymeja* and *Q. mediterranea*: Denk et al., 2017).

A geographical continuity in the evolutionary processes of species and ecosystems between the present-day Mediterranean region and the laurel forests of E Asia must, therefore, be postulated. The analogy among the five enclaves of Mediterranean-type ecosystems in the world is probably at least partly misleading when the coenological (i.e., ecological community) history of these formations is taken into account. Indeed, all of them are rather comparable only to the disrupted assessment of the present-day Mediterranean evergreen broadleaved forest biome dominated by sclerophyllous oaks. Late successional recovery of these evergreen oak woodlands should shift the analogies to climatically different regions of the Old World, where the dominant Mediterranean evergreen oaks find their most outstanding aspects of their evolutionary history shared by laurel forest species. The laurel forest of the Canary Islands can provide useful insights in the development of the Mediterranean broadleaved forest biome in the framework of its phylogenetic connections to the E Asian analogues.

Lauroid termo-hygrophilous relic species such as pontic rhododendron (*Rhododendron ponticum*), laurel (*Laurus nobilis*, *Laurus azorica*), Portugal laurel (*Prunus lusitanica*/P. *laurocerasus*), English holly (*Ilex aquifolium*), box (*Buxus sempervirens*/B. *balearica*), mediterranean palm (*Chamaerops humilis*) or myrtle candleberry (*Myrica faya*), are considered a footprint of the disappeared Madrean-Thetyan paleotropical vegetation (Axelrod, 1975; Mai, 1989). Their ancestors were widespread in Paleo-Europe during the warm and humid late Tertiary (Palamarev, 1989). However, several waves of cooling and aridization started at the end of the Paleogene led to the extinction of the majority of the laurophyllous lineages (Barrón et al., 2010; Palamarev, 1989). When

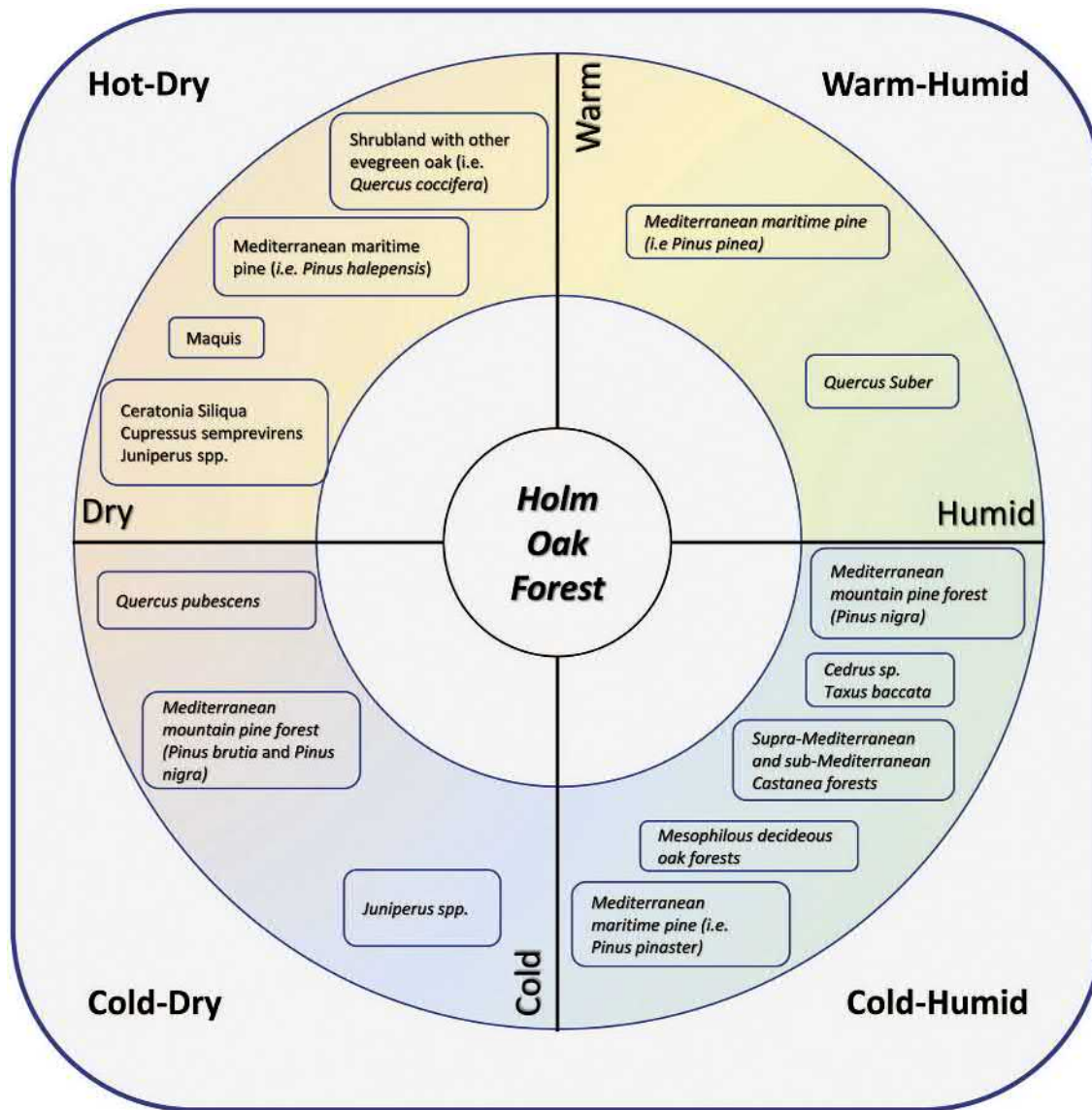


Fig. 4 Environmental and climate gradient belts of Evergreen Oaks forest in the Mediterranean region dominated by Holm Oak.

the present-day Mediterranean climate established (about 4.5 ka B.P.), only a few relic laurophylls persisted within refuges of southern Europe (Axelrod, 1975; Barrón et al., 2010; Suc, 1984). Indeed, many of these relic laurophylls are nowadays restricted to Macaronesia and in the Western Caucasus where the climate is still humid. On the other hand, only a few of them occur in the Mediterranean region, since they are limited by low winter temperature and scarcity in precipitation (Alessi et al., 2019; Rodríguez-Sánchez and Arroyo, 2008). Here, relic laurophylls occur in extrazonal groves, where micro-topography provides sufficient moisture for their termo-hygrophilous demands (Alessi et al., 2018; Costa et al., 2015). These extrazonal sites act as modern refugia for laurophylls following the latest climatic deterioration (Alessi et al., 2019; Rodríguez-Sánchez and Arroyo, 2008).

The biogeographical history of laurophylls is hence strongly related to that of the Mediterranean oaks and their associated species. The extant evergreen oaks of Europe may have been arisen from the laurophyllous vegetation and its elements (Barrón et al., 2010; Denk et al., 2017; Jiang et al., 2019). Indeed, Mediterranean oaks derive from East Asian ancestors occurring within the Eocene subtropical-tropical forest (Denk et al., 2017; Jiang et al., 2019; Simeone et al., 2018). However, while all of the extant Asian oak species grow today in regions influenced by proximity to monsoon climatic conditions, providing seasonal high amount of precipitations, their closest relatives of the Mediterranean region occur within the drier Mediterranean macroclimate (Box, 2015). Thus, the evolutionary history of the Mediterranean oaks and their ecosystem has been extended far beyond the present-day environmental assessment of Eurasia, in the framework of a completely different paleoecological and paleogeographical scenario (Denk et al., 2017; Jiang et al., 2019).

Habitat Directives for Sclerophyllous Forests

The importance of maintaining this landscape has been recognized by a legal and regulatory framework. The conservation of Mediterranean sclerophyllous forests is ensured in Europe under the application of the Habitats Directive (92/43/EC). Six different habitat types with evergreen oaks (Table 1) are targeted for conservation as listed in Annex I of the Directive (http://ec.europa.eu/environment/nature/legislation/habitatsdirective/docs/Int_Manual_EU28.pdf).

Another important initiative at European level is the Red List of European Habitats http://ec.europa.eu/environment/nature/knowledge/redlist_en.htm. It reviews the current status of all natural and semi-natural terrestrial, freshwater and marine habitats and highlights the pressures they face. Using a modified version of the IUCN Red List of Ecosystems categories and criteria, it covers the EU28, plus Iceland, Norway, Switzerland and the Balkan countries and their neighboring seas. In this List evergreen forests (Table 2) are considered an outstanding example of typical characteristic of the Mediterranean biogeographical region, in terms of area, species composition, structure and functioning. They are recorded under the G2.1 Mediterranean evergreen *Quercus* woodland, with a category of Low Concern assessment <https://forum.eionet.europa.eu/european-red-list-habitats/library/terrestrial-habitats/g.-forests/g2.1-mediterranean-evergreen-quercus-woodland>.

Conservation Challenges and Threats

Whereas in the past there still lasting natural spaces to hosting the iconic species of these forests in a proper viable condition, throughout the natural spread in the Mediterranean ecosystem, massive changes in abiotic and biotic condition put this outstanding representative of the Mediterranean Biome under a major threat.

Mediterranean forests are still exposed to serious threats that put biodiversity at risk. Severe fires, degrading land use practices (such as monoculture, plantations of introduced species, excessive grazing) and extensive human pressure (urbanization) exacerbate the already heavy impacts of climate change with scenarios that foresee an increase in temperatures and aridity in the Mediterranean basin.

In fact, the Mediterranean Basin is affected by numerous aspects of environmental change, a combination of changes in land use with overexploitation, increasing pollution of air and water and declining biodiversity. It is one of the most vulnerable regions to the impacts of global warming with an increase of flooding events, heat waves and biodiversity loss anticipated. With increasing aridity, fire risk becomes more frequent. The Intergovernmental Panel on Climate Change (IPCC, 2013) identifies the Mediterranean as one of the region's most vulnerable to the impacts of global warming, nevertheless the effects on Mediterranean evergreen forest are not widely agreed. Since no single climate change scenario for a site/area is likely to be definitive, no human intervention can provide any realistic global counterweight. As long as world vegetation will respond to climatic patterns, changes to plant communities will be, and have always been, implicit in the system.

This appealing phenomenological category and concept cannot be applied to conservation since it implies management actions of far-reaching unrealistic silviculture that will only artificialize habitats by converting them into gardens. In fact, silviculture and afforestation are basically threatening the biogeographical assessment of Mediterranean forests, mainly through active afforestation. Conifer plantations are the best example. Plantations of Mesogean pines all over the coasts and inland warmer sites have deleted natural biogeographical gaps. Moreover, they are likely to have induced dilution or even extinction of local genotypes selected by long term isolation (*Pinus pinea*—Italian stone pine, *Pinus halepensis*—Aleppo pine, *Pinus pinaster*—maritime pine, *Pinus nigra*—black pine). *Abies alba*—a common fir forest—has undergone the same destiny. Silvicultural practices may also be responsible for the annihilation of the value of forest habitats, in case of management actions aiming to “ameliorate” the viability or competitive ability of a representative or charismatic species in the formation.

Today the Mediterranean landscapes are profoundly different from the original ones. The vast impenetrable forests have mostly been replaced by fragmented patches, in turn more or less degraded, and more often by a sparse vegetation that fails to mask the outcropping rocks. Agro-silvo-pastoral system processes (i.e., the practice of combining forestry, grazing and farming) caused a progressive canopy opening and a simplification of the original closed forest (Correia, 1993). Dried up lands, picturesque but stripped cliffs, and beaches of Umbrella Pine or Stone Pine (*Pinus pinea*), are what Mediterranean Italy looks like today to those

Table 1 List of Mediterranean sclerophyllous forests from Annex I Habitat Directive.

Habitat Directive code	Description
9310	Aegean <i>Quercus brachyphylla</i> —Aegean oak woods
9330	<i>Quercus suber</i> —cork oak forests
9340	<i>Quercus ilex</i> and <i>Quercus rotundifolia</i> —holm oak forests
9350	<i>Quercus macrolepis</i> —valonia oak forests
9390	Scrub and low forest vegetation with <i>Quercus alnifolia</i> —Cyprus golden oak
93A0	Woodlands with <i>Quercus infectoria</i> —Lusitanian oak

Table 2 Area of Occupancy and trends in conservation status of Mediterranean evergreen *Quercus* woodland in Europe.

Country	Current area of habitat (km ²)	Recent trend in quantity (last 50 y)	Recent trend in quality (last 50 y)
Croatia	361	Stable	Stable
Cyprus	94	Increasing	Increasing
France	4000	Increasing	Stable
Greece	1837	Stable	Increasing
Italy	8050	Stable	Decreasing
Portugal	2930	Increasing	Unknown
Slovenia	0.5	Stable	Stable
Spain	31,855	Increasing	Stable

who access it along the most popular tourist routes. But those who like to search in more wild recesses, in the hills, in the coastal valleys, in the solitary lands, the vestiges of a more spontaneous vegetation, can give some idea of the ancient original forms of the forest cover that covered these shores, these first coastal heights. Relics of these evergreen forest can be found scattered only in small patches, especially in Tuscany and Roman Campagna (see Figs. 2 and 5), mainly on riverine slopes where the forest exploitation is naturally avoided. Structure and function of these relic woodlands must be taken into account for any restoration program in order to respect coherently the original pattern.

Conclusions and Conservation Recommendations

The evergreen forests of the Mediterranean do not seem to need further efforts in terms of the establishment of protected areas, as shown by the assessments conducted in various protectionist areas (see Red List and Article 17 of the Habitats Directive).

However, some management aspects can be addressed in order to improve the ecological function of Mediterranean evergreen forests. For example, it is necessary to ensure the maintenance of the tree cover and diversity (in structure and species composition) in order to protect the ecological niches of insects (e.g., several species of beetle for example the great capricorn beetle), nesting birds (i.e., woodpeckers, Eurasian wryneck and hoopoe) and bats. In general, the maintenance of the evergreen cover limits the effects of climate change, reducing the effect of drying up the soil while maintaining a good humidity level of its and consequently the ability to efficiently maintain active biogeochemical soil cycles (e.g., nitrogen cycle and of carbon). Specifically, in order to keep the aforementioned functions active, it is considered necessary to recommend management activities that limit the cutting of trees (see Fig. 6), grazing of domestic animals in the forest (see Fig. 7), and extraction activities especially for cork-oak woods (i.e., bark harvesting). Excessive cuts or poor silvicultural management can decrease forest diversity, density and biomass, destroying the necessary tree cover of the land and triggering species extinction and land erosive phenomena especially in years of poor atmospheric precipitation.

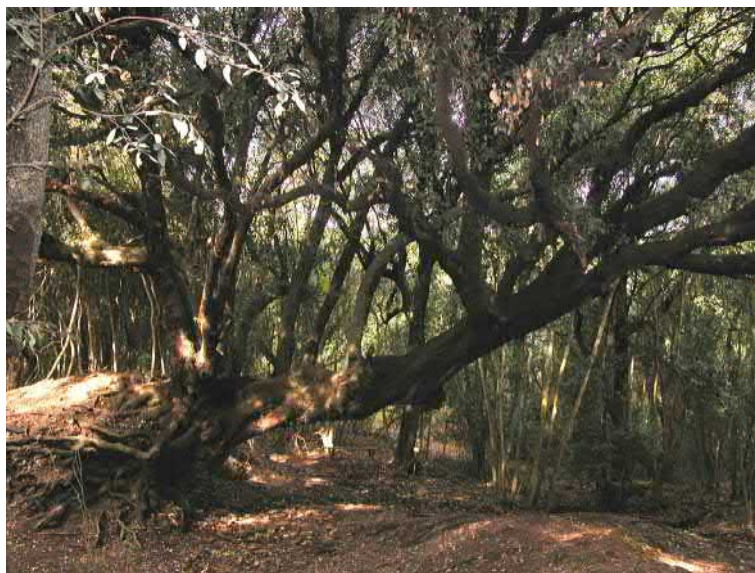


Fig. 5 An example of relict holm oak forest in the Roman Campagna, in the picture the all growth forest of Castelporziano Presidential Natural Reserve (Central Italy). Photo by Emiliano Agrillo.



Fig. 6 Tree harvesting in evergreen oak forests (Central Italy). Photo by Nicola Alessi.



Fig. 7 Pasture in the evergreen oak forests (Central Italy). Photo by Laura Casella.

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Montane Cloud Forests

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Abstract

Montane cloud forests (MCF) are a tropical mountainous biome that forms on the mountainous slopes oriented towards the sea under extremely wet climate in the temperate zone covered with clouds for the most part of the year. MCF receive water not only with rainfalls but also as mist. Most MCF are found mainly at the altitude between 500 and 2500 m above sea level (asl), but in places they extend to lower and higher elevations. Commonly these forests are divided into lower MCF belt, upland MCF belt and subalpine elfin forest. This biome is characterized by low stature and productivity compared with lowland rain forests due to excessive moisture, colder climate, acid nutrient-depleted soils and insufficient solar radiation. The physiognomy of MCF is characterized by numerous epiphytes that play an important role in moisture accumulation. Species diversity of MCF is lower than that of lowland tropical rain forests in absolute figures, but the biodiversity per area unit may be higher. Due to fragmentized distribution, the speciation in MCF is exceptionally high with increased levels of plant and animal endemism. The C stock of MCF is less than that of lowland tropical rainforests, but higher than of other mountainous forest types. The C stock in MCF is distributed evenly between the aboveground biomass and belowground stock (roots plus soil organic carbon). High biodiversity and endemism make MCF a priority area for conservation; currently this biome is endangered due to agriculture, settlements expansion and logging. Climatic change also may have a critical effect on MCF functioning and require special attention.

Introduction

The first studies of montane cloud forests (MCF) were in the 19th century, but a significant growth of interest in these ecosystems was observed in 1990s (Williams-Linera, 2015). Since then, several comprehensive reviews have appeared that provide an overview of this interesting and extremely vulnerable biome (Webster, 1995; Bubb et al., 2004; Bruijnzeel et al., 2010). MCF are tropical arboreal ecosystems with low plant stature, increased stem density and reduced nutrient cycling rates (Bruijnzeel and Veneklaas, 1998). MCF are affected by clouds continuously covering the mountains: the moisture comes to MCF both as rainfalls and mist. Since MCF represent a broad group of forest ecosystems varying with continent, altitude, and particular environment, it is difficult to give a brief definition of this biome. Hamilton et al. (1995) provided an extensive description of the physiognomic characteristics of MCF. The most characteristic features of the MCF are gnarled trunks, dense compact crowns, small, thick and hard leaves, and abundant epiphytes of various groups. Another interesting morphological feature is extra pigmentation due to the presence of anthocyanins and flavonoids (Flenley, 1995). Ohsawa (1995) indicated that in Asia in places it was difficult to distinguish MCF among other tropical rain forests, which were morphologically similar, and recommended using indicator species for forest classification.

Bruijnzeel et al. (2011) distinguish three MCF types commonly differing in hydrology and stature: tall lower montane cloud forest (LMCF); upper montane cloud forest (UMCF) of intermediate stature; and a group that combines stunted subalpine cloud forest (SACF) and “elfin” cloud forest (ECF). Though the absolute biodiversity of MCF is lower than of tropical rain forests, they have the highest species diversity per unit area. For example, in Mexico MCF includes 10%–12% of flora (2500–3000 vascular plant species) and 12% of terrestrial vertebrates found in the country (Toledo-Aceves et al., 2011; Sosa et al., 2016). The phenomenon may be ascribed to a high level of local endemism in MCF reaching 10%–24% of vascular plants, which can occur in ecologically isolated forests as small as 5–10 km² (Gentry, 1992). In Mexico the endemism of plants in MCF is estimated as high as 30% (Toledo-Aceves et al., 2011). The striking feature of MCF is abnormally quick speciation of plants that was estimated as taking 40 years (Webster, 1995), while for orchids speciation takes just 15 years (Gentry, 1992). The phenomenon can be mediated by genetic drift in small founder populations and thus the diversity in MCF does not come to any equilibrium and practically has no limits (Gentry, 1989).

MCF is one of the most endangered biomes in the worlds (Aldrich et al., 1997) due to the limited area, dependence on unique environmental conditions and extreme anthropogenic pressure.

Biogeography

Specific environments of cloudy mountains determine the physiognomy of MCF. Bruijnzeel and Veneklaas (1998) ascribe low stature of the MCF to a complex of environmental conditions such as low temperature, insufficient insolation due to the presence of permanent or continuous clouds, and excessive moisture. In general, the unique morphology and ecology of MCF is formed by the combination of permanent or prolonged inflow of moisture with cool but constant temperature and low insolation. These specific environments of MCF separate them from other forest biomes: MCF are colder than lowland tropical rainforests, wetter than mountainous deciduous or semideciduous forests, and do not have temperature fluctuations as temperate forests.

The most important environmental factor for MCF is rainfall together with humidity influenced by stable cloud condensation belts and the occurrence of frost that might limit the distribution of many tropical species (Hemp, 2006). The annual rainfall in MCF varies from 500 to 6000 mm (Bubb et al., 2004). Compared with other tropical forests, MCF receive 184 mm per year more rainfall on average and are 4.2°C cooler (Bruijnzeel et al., 2010). Also most researchers agree that cloud and mist occurrence is the most important microclimatic feature affecting the distribution and function of the plants in MCF, particularly for epiphytes (Oliveira et al., 2014). Bruijnzeel et al. (2011) studied the hydrology of MCF and showed that a significant part of water was received by this ecosystem as “cloud-water” interception. The amount of this source varied in a broad range from 22 to 1990 mm per year.

Low insolation is another feature related to prolonged cloud coverage of MCF: clouds reduce total insolation by about 30% (Bruijnzeel et al., 1993). Flenley (1995) noted a paradox of MCF: according to the general view trees grown in humid area with low insolation should be tall and have large, thin, and pale leaves. In contrast, most trees in MCF are stunted and have hard thick leaves. These features and elevated content of polyphenols in leaves of many plant species should be ascribed to extra UV-B light received by tropical high-altitude forests (Rozema et al., 1997). In this respect, the living forms of MCF plants reflect adaptation to negative effect of UV-B light; clouds protect MCF from harmful radiation but also reduce the income of energy required for photosynthesis.

Paleoecological reconstruction in northern Mesoamerica indicates that the present disjunct distributions of temperate and MCF woody genera in Mexico and Central America have resulted from climate change during the Neogene and Pleistocene, and that the colonization of tropical tree species and dynamics of cloud forests attributed solely to Pliocene processes has been obscured by Pleistocene climate changes (Sosa et al., 2016). During the Last Glacial Maximum, increased aridity strongly affected MCF causing their fragmentation, because some places remained fairly moist and served for MCF refugia (Ramírez-Barahona and Eguiarte, 2013). Repeated cycles of cloud forest contraction and expansion due to Pleistocene climatic cycling shaped genetic divergence in the MCF (Bruijnzeel et al., 2011).

The distribution of MCF biome has a good correspondence with the cloud circulation, and thus may be identified using remote sensing data (Nair et al., 2008). Also, Landsat allows direct identification of MCF and assessment of their area in particular sites (Cayuela et al., 2006). The majority of MCF is found at the altitudes between 500 and 2500 m, but strong fluctuations exist both for the lower and upper limit of this ecosystem. Small isolated mountains and especially islands are strongly affected by the Massenerhebung effect (“telescopic effect,” when altitudinal bioclimatic belts are found at lower elevations in small isolated mountains than in high mountainous systems) (Bruijnzeel et al., 1993; Flenley, 1995). Pouteau et al. (2018) reported the lower limit of MCF at 300 m asl on the small islands in Micronesia and Vanuatu, while on the big islands like Cuba and Hispaniola it was as high as 1600 m asl. In some specific cases, the occurrence of MCF at low elevation, like at 300–500 m asl in Angola, might be ascribed to paleoenvironments (Gioda et al., 1995).

The areal extent of MCF biome is estimated at 215,000 km² that is 6.6% of all montane tropical forests (Bruijnzeel et al., 2011) or 2.5% of the entire area of tropical forests. Bubb et al. (2004) report 381,166 km² of potential MCF worldwide with 25.3% located in the Americas, 15.0% in Africa and 59.7% in Asia. According to Scatena and Bruijnzeel (2010), about 43% of MCF is in Asia, 41% in North and South America, and 16% in Africa. Minor areas of MCF are found on many mountainous islands in Oceania (Meyer, 2010). The area of MCF may be also estimated on the basis of remotely sensed frequencies of cloud occurrence: fog-affected forest may occupy as much as 2,210,000 km² (Bruijnzeel et al., 2011) or 23% of the area of tropical forests (Toledo-Aceves et al., 2011), but it is not clear, if such forests would fit the central image of the MCF biome. MCF differ among continents: in Africa, they are generally drier than in Asia (Gioda et al., 1995; Bruijnzeel et al., 2010), while in the Americas these forests vary in humidity in a broad range.

It is important to note that most of the detailed studies on the diversity, ecology, and biomass in MCF have been from several well-studied localities. One of the most studied MCF sites is located in the Monteverde Cloud Forest Reserve, Costa Rica (Nadkarni and Longino, 1990; Nadkarni et al., 1995; Pounds et al., 1999; Köhler et al., 2007; Anchukaitis and Evans, 2010; Bruijnzeel et al., 2010; Tanner et al., 2016). In Mexico, multiple studies were conducted in Sierra Norte de Oaxaca (Bautista-Cruz and del Castillo, 2005; Álvarez-Arteaga et al., 2008, 2012, 2013, 2014; Meave et al., 2017) and the central part of Veracruz state (Pineda et al., 2005; Martínez et al., 2009; Williams-Linera and Vizcaíno-Bravo, 2016; Hernández-Pérez et al., 2018). Also, it is necessary to mention Luquillo Experimental Forest, Puerto Rico, where Brown et al. (1983) made their seminal detailed study.

Vegetative Community

General taxa—The biodiversity of tropical forests, including MCF, is still poorly known: Gentry (1992) estimated that each ecologically isolated patch of MCF in Andes had at least 20% of undescribed vegetative species. Meave et al. (2017) made an inventory of vascular plant species in Chinantla, Southern Mexico, and discovered 1021 species, 471 genera and 162 families; the authors estimate that the total number of species must be around 1650. Bruijnzeel et al. (2010) mention that in some sites the assessment of the diversity of vegetation is an almost impossible task. The number of plant species may go up to more than 1200 in Africa, 4000 in Asia and 5000 in Central America. It is notable that woody plants are also studied insufficiently in MCF, especially the trees of the diverse and poorly ordered families *Sapotaceae* and *Lauraceae* (Gentry, 1992).

Tree species—Brown et al. (1983) reported *Calycogonium squamulosum* as the dominant species in an elfin forest in Luquillo Experimental Forest, Puerto Rico among 23 arboreal plants found there; however, the major part of the canopy was constituted by other species, *Tabebuia rigida* and *Ocotea spathulata*. Nadkarni et al. (1995) studied a 4-ha plot in the Monteverde Cloud Forest Reserve, Costa Rica at the altitude 1480 m asl and with annual precipitation 2000–2500 mm. *Lauraceae* was the most abundant family of arboreal species and this was unusual for MCF. The authors ascribed the phenomena to the specific composition of bird population that could distribute the seeds of these trees. One hundred and eleven tree species were discovered; all but six constituted less than 2.5% of basal area, and one species *Ocotea tonduzii* constituted 23% of the total basal area of the trees. In other studies, the number of arboreal species varied in a broad range from 19 (Gunang Silam, Sabah) to 119 (Papua New Guinea) (Nadkarni et al., 1995). However, in some MCF, especially in small fragments and/or in relatively dry conditions, the diversity of arboreal species may be low. García-De La Cruz et al. (2013) found only 14 species of trees in the fragmented MCF of Veracruz, Mexico: *Quercus salicifolia*, *Liquidambar styraciflua*, *Quercus leiophylla* and *Alchornea latifolia* were the most abundant species. In dryer conditions in Sierra Gorda, Mexico, the number of tree species was even less and decreased with decreasing humidity of the habitats (Krasilnikov et al., 2016). Dominant tree species were *Liquidambar styraciflua*, *Dalbergia velutina*, *Trema micrantha*, *Carpinus caroliniana*, *Sambucus mexicana* and *Clethra mexicana*. A general observation on the composition of arboreal vegetation in MCF is that most of the sites have several dominant species, while other species are much less frequent, though the overall diversity may be high.

The diversity of plants generally decreases with elevation; also, it is broadly recognized that diversity is higher at mid-elevations between 500 and 2000 m than in subalpine forests (Bruijnzeel et al., 2010). Mean canopy and understory height also decreases with increasing elevation within the MCF belt (Gerold et al., 2008). In the Peruvian Andes, the dominant families of arboreal species at the elevation more than 3000 m asl were *Weinmannia*, *Clusiaceae*, *Canoniceae* and *Hesperomeles* (Girardin et al., 2010). *Canoniceae* and *Lauraceae* were abundant at 2720 m asl, *Clusiaceae*, *Clethraceae*, *Myrtaceae* and *Alzateaceae* dominated at 1855 and 2020 m asl. *Euphorbiaceae*, *Fabaceae* and *Lauraceae* were the dominant families at 1500 m asl, and *Moraceae*, *Fabaceae* and *Rubiceae* at 1000 m asl (Girardin et al., 2010). Though the abovementioned study did not establish clear boundaries between the lower and upper MCF, this example indicates that for the upper zone *Clusiaceae* is the family present in all the sites, while the lower MCF have *Fabaceae* family as a typical dominant.

Herbaceous and shrub species—Nontree species are often overlooked in the faunistic studies in tropical forests (Gentry, 1992). However, they may be indicative and even endemic for MCF. Ohsawa (1995) mentions that two fern genera, *Dicranopteris* and *Gleichenia*, are indicators of MCF in South-East Asia.

Epiphytes—also are characteristic of MCF and their presence is an indispensable attribute of this biome. In lower MCF, the majority of epiphytic vegetation is represented by flowering plants, and with increasing elevation the contribution of pteridophytic plant groups (vascular plants that disperse spores) increase (Bruijnzeel et al., 2010). The proportion of mosses and liverworts also increases with elevation, and they completely dominate in high-altitude elfin forests.

A small (300 ha) area of MCF within Brazilian Atlantic Forests hosted 224 species of vascular epiphytes (Furtado and Neto, 2018). These plants were distributed into 23 families of which *Orchidaceae* was the richest with 87 species. In Western Panama, 155 species of vascular epiphytes were discovered (Gómez-González et al., 2017). Hu et al. (2015) studied orchids at the Hainan Island, China and recorded 317 species and 102 genera of *Orchidaceae* for all the biomes of the island, however, without specifying how many of them were detected in MCF. They also mention that 158 species were epiphytic and associated with forests of high humidity. A recent study in Mexico showed that orchids in MCF prefer bigger trees with fissured bark (Hernández-Pérez et al., 2018).

Nonvascular epiphytes are also of importance in MCF: about 50% of mosses and 80% of liverworts reported for tropical Americas are restricted to MCF (Bruijnzeel et al., 2010). Brown et al. (1983) reported 18 species of mosses found on the trees in elfin forest in Luquillo Experimental Forest, Puerto Rico. The hydrological function of epiphytes is the capture of water directly from the mist and provision of a variety of microhabitats for fungi, invertebrates and amphibians; the decaying epiphytes form so-called “canopy humus” on the stems and branches of the trees. Both vascular and nonvascular epiphytes abundance depends on the canopy openness (Toivonen et al., 2017).

Fauna

Mammals—MCF are known for the high diversity of animals and especially for a high level of endemism. In Monteverde, Costa Rica the mammal list includes opossums, shrews, bats, monkeys, sloths, armadillos, anteaters, rabbits, porcupines, squirrels, rats, mice,

pacas, agoutis, large cats, coyote, gray fox, skunks, raccoons, tapir, peccaries and deer (Bruijnzeel et al., 2010). Perhaps the most well-known inhabitant of MCF in Africa is the mountain gorilla (*Gorilla beringei beringei*) (Doumenge et al., 1995). Bruijnzeel et al. (2010) estimated mean species richness for mammals in MCF to be 107.75 that was significantly higher than species richness in noncloud forests (74.65), while mean endemism in MCF was more than three times higher than in noncloud forests. These authors noted that the highest species diversity of mammals in MCF was observed in South-East Asia and in north-eastern Andes. The percentage of endemic mammals in the MCF of Andean region is estimated between 32% and 63% (Bubb et al., 2004).

Bats were studied intensively in MCF; over 40% of the animal species in the Monteverde cloud forest, Costa Rica mammals are bats (Bruijnzeel et al., 2010). In three sites in Veracruz, Mexico 10 species of bats were collected (Pineda et al., 2005). In Manu Biosphere Reserve, Peru the number of species of bats decreased with altitude within MCF from 30 to 10 (Willig and Presley, 2016). Similar pattern was detected for rodents: the number of species decreased from 18 to 10 with altitude (Willig and Presley, 2016).

Birds—Bird richness is also diverse in MCF with over 2500 species confined specifically to MCF, 1000 of them living in the South and North American MCF (Bruijnzeel et al., 2010). The same authors report highest diversity of birds in MCF within Atlantic forests in Brazil, the Guyana shield and the eastern Andes. Avian endemism is high: around 260 species of birds are endemic for MCF and other 315 species are typical for MCF plus similar habitats (Bubb et al., 2004). Together this makes almost a quarter of all bird species in the MCF having a restricted geographic range.

The distribution of birds depends on the altitude, for example, in Tilaran Mountains, Costa Rica the number of bird species decreased with altitude from 60 to 42 from the lower to the upper limit of MCF belt (Willig and Presley, 2016); in the mountainous rain forest below MCF the diversity of birds was higher. In Manu Biosphere Reserve, Peru the number of passerine species decreased with altitude within MCF from 220 to 120 (Willig and Presley, 2016). The diversity of birds also depends on the orientation of the slope. In Monteverde, Costa Rica on the drier Pacific slope there were 165 species of birds, while on the wetter Caribbean slope there were 315 species (Bruijnzeel et al., 2010).

Lloyd et al. (2012) studied avian richness in Kcosñipata Valley, Department of Cusco, southern Peru and detected about 50 species within the MCF. Compared with the tree-line and puna grassland vegetative communities, MCF had the highest bird diversity during both the dry and wet seasons; during the dry season the species richness of birds was slightly higher. Patterson et al. (1998) studied spatial patterns of distribution both of mammals and birds (901 bird species, 129 bat species, and 28 species of mice). The bat and bird faunas had a distinct limit at 1400 m asl between tropical low mountain and MCF ecosystems. For mice, the faunal transition took place nearer to 2000 m asl.

Herpetofauna—Bruijnzeel et al. (2010) showed that the mean species richness did not differ for amphibians in MCF and noncloud forests (24.69 vs. 23.50), but mean endemism was an order of magnitude higher for the MCF. They report the highest diversity of amphibians in the most humid part of Atlantic forests in Brazil, on the Guyana shield, in eastern escarpment of Andes, eastern Madagascar, Guinea and northern Kalimantan. In Mexico, endemism of amphibians and reptiles in MCF is estimates as 33% and 39%, respectively (Toledo-Aceves et al., 2011).

Invertebrates—this taxa has been insufficiently studied until now. More than a half of the species of beetles are site-specific in MCF (Bubb et al., 2004). The French Polynesia MCF host many rare species, for example aquatic insects such as endemic damselflies belonging to the genus *Bedfordia* and terrestrial arthropods such as spiders and weevils belonging to the genus *Rhyncogonus* (Meyer, 2010). Termites are common in lower MCF, while at higher elevations earthworms and beetles are more abundant (Bruijnzeel et al., 2010).

Nadkarni and Longino (1990) studied the invertebrates in the canopy and in soil litter and humus in the Monteverde Cloud Forest Reserve, Costa Rica and found the following taxa there: *Acarina* (mites), adult *Coleoptera* (beetles), insect larvae, *Formicidae* (ants), *Collembola* (springtails) and *Crustacea* (amphipods and isopods). The density of invertebrates was higher in the topsoil than in the canopy, the relative abundance of ants and mites was almost the same in these two strata, but the beetles and larvae were more abundant in the canopy, and the crustaceans dominated in soil. The number of species was not recorded in this study.

Soils

There is no specific soil group typical for all the MCF around the world: in each locality soil formation depends on the particular parent material, hydrology and composition of vegetation (Roman et al., 2010). The common features of the majority of soils under MCF are strong acidity, low content of nutrients and exchangeable bases and thick organic layer on the surface. Bruijnzeel and Veneklaas (1998) indicated that poor soil conditions result in a relatively strong development of root systems of the trees in MCF that probably leads to underdevelopment of aboveground parts of the arboreal plants.

Within the biome, soils commonly differ between the lower and upper MCF. Álvarez-Arteaga et al. (2008) showed that in the lower MCF in Sierra Norte de Oaxaca, Mexico the soils were *Folic Cambisols* (*Humic, Hyperdystric*) (IUSS Working Group WRB, 2014), brown acid soils rich in organic matter, while in the upper MCF belt the soils were *Folic Podzols* and *Folic Stagnosols*, soils with a bleached eluvial and/or saturated with perched water horizon under forest litter. In the Bolivian Andes, the main soil forming processes were podzolization and processes related to hydromorphism, such as gleying and peat accumulation (Schawe et al., 2007), and hydromorphism increases with increasing elevation. Álvarez-Arteaga et al. (2008) showed that the majority of the soils in the upper MCF belt and elfin forest had evidence of podzolization and gleying, in places a combination of these two processes, and accumulation of peat, including the formation of *Histosols* (organic soils) in the least drained localities. In lower MCF, the typical soils were *Cambisols* and *Ferralsols* (strongly weathered soils). In some relatively dry MCF, soils have evidences of clay

movement and have high base saturation in subsoil (Krasilnikov et al., 2016). The presence of specific substrates such as volcanic ash or limestone leads to the formation of peculiar soils that still reflect the MCF environments. Indicator tree species might differ depending on soil properties (Williams-Linera and Vizcaíno-Bravo, 2016): in Veracruz state, Mexico the composition of arboreal species was different on soils derived from volcanic material and from limestone. The indicators for shallow limestone-derived soils were *Cercis canadensis*, *Clusia guatemalensis*, *Garrya laurifolia*, *Ostrya virginiana* and *Quercus pinnatifida*, whereas for soils developed in volcanic material indicator species were *Carpinus tropicalis*, *Clethra macrophylla*, *Liquidambar styraciflua* and *Quercus xalapensis*.

Soil microbiology and mycology has not been studied much in MCF. Arias and Abarca (2014) detected 131 species of soil fungi mostly of the genera *Penicillium*, *Humicola*, *Fusarium*, *Trichoderma*, *Chaetomium* and *Paecilomyces* in central Veracruz state, Mexico that evidences the potential prospect of studying the fungi and microbial population of MCF soils.

Soils are commonly transformed if the forest is cut down and the land is used for agriculture. After reforestation, the soils are expected to return back to their initial state. Bautista-Cruz and del Castillo (2005) studied changes in soil properties in a chronosequence of recovering MCF in Sierra Norte de Oaxaca, Mexico after agricultural use. The soils under recovering forest vegetation during the first 100 years showed progressing growth of forest litter layer, loss of exchangeable bases and increase in exchangeable acidity returning back to the properties typical for MCF natural soils.

Biomass and C Stock Distribution

The biomass of MCF is less than that of lowland tropical rainforests, but higher than of other mountainous forests types (Keith et al., 2009). The biomass and total carbon stock of the ecosystem varies depending on the environmental conditions and elevation. However, a number of studies allow estimating the range of values; Álvarez-Arteaga et al. (2014) provided a review of the studies on the biomass and soil carbon stock in tropical mountainous forests. The biomass in MCF varied from 70 to 528 t ha⁻¹, soil carbon stock from 90 to 599 t ha⁻¹, and total C stock of the ecosystem from 162 to 946 t ha⁻¹. The data should be considered with caution, because the studies differed in methodologies.

Nadkarni et al. (2004) calculated the biomass in Monteverde Cloud Forest Reserve, Costa Rica to be 523.1 t ha⁻¹, with 33.1 t ha⁻¹ incorporated in “canopy organic matter,” that is, epiphytes and associated humus on the trunks. Dead organic matter or so-called “canopy humus” constitutes approximately half of the canopy organic matter (Nadkarni and Longino, 1990). The weight of epiphytic matter that includes living plants, canopy humus, litter and associated invertebrates and fungi varies from approximately 1000 to 44,000 kg ha⁻¹ (Gómez-González et al., 2017). Total biomass in two other MCF sites in the same reserve varied from 318.4 to 522.0 t ha⁻¹, where aboveground biomass was 159 to 457 t ha⁻¹ (Tanner et al., 2016). Köhler et al. (2007) also worked in the Monteverde Cloud Forest Reserve, Costa Rica and estimated the weight of bryophytes mat as 16,215 kg ha⁻¹ in an old-growth forest. The epiphytic vegetation on the trees was dominated by bryophytes with the weight 11,505 kg ha⁻¹ (71% of the entire canopy biomass). Canopy humus was 2095 kg ha⁻¹ (13%), whereas contributions by vascular plants were 2615 kg ha⁻¹ (16%), including 1228 kg ha⁻¹ of ferns and 131 kg ha⁻¹ of *Bromeliads*. It should be noted that the abovementioned study has been done in an extremely humid area with annual precipitation around 6000 mm; in drier conditions the bryophytes have lower relative abundance. On the forest floor in Luquillo Experimental Forest, the biomass of living plants was 3140 kg ha⁻¹, leaf litter and twigs 780 kg ha⁻¹ and roots 5770 kg ha⁻¹ (Brown et al., 1983). The mass of epiphytes and soil-like material on the stems consisted of living plants—2650 kg ha⁻¹, roots 1250 kg ha⁻¹ and “soil” 1120 g m⁻².

Girardin et al. (2010) studied an altitudinal sequence in the Kosñipata Valley, Peruvian Andes. The stem biomass carbon varied from 38.6 to 102.8 t ha⁻¹, belowground biomass from 14.8 to 19.3 t ha⁻¹, mineral soil C stock from 1.42 to 15.7 t ha⁻¹, and organic soil C stock from 8.45 to 68.8 t ha⁻¹. Stem and belowground biomass had a tendency to some decrease with elevation, but strongly varied, while soil carbon showed a regular decrease in mineral soil and increase in organic soil carbon with increasing altitude. Gerold et al. (2008) showed that soil C stock in a Bolivian MCF was the highest at the altitude 2000–2500 m asl (350–550 t ha⁻¹) and reduced to 200–300 t ha⁻¹ at higher elevations. Tanner et al. (2016) found that soil organic matter stock varied from 242.1 to 302.6 t ha⁻¹ in Monteverde Cloud Forest Reserve, Costa Rica. Álvarez-Arteaga et al. (2013) studied an altitudinal sequence in lower and higher MCF in Sierra Norte de Oaxaca, Mexico and found the total C stock to vary from 330.23 to 439.76 t ha⁻¹, with the highest values on the uppermost site (2500 m asl) and the lower limit (1500 m asl) and lower values between these points. Soil C stock decreased with elevation from 222.5 to 158.2 t ha⁻¹, and constituted 38%–59% of the total C stock of the ecosystem. In all the sites except of the most elevated the major part of soil C was stores in organic layers (Álvarez-Arteaga et al., 2012).

The biomass of MCF is inferior to the lowland rainforests due to lower intensity of physiological processes under unfavorable environments in the cloud belt. The mean photosynthesis rate of MCF trees is 7.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ that is lower than that in lowland tropical forests (10 $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Gotsch et al., 2016). As a result net primary productivity (NPP) assessment in the Kosñipata Valley, Peruvian Andes resulted in a range from 4.11 to 7.07 t C ha⁻¹ year⁻¹ (Girardin et al., 2010) that was slightly lower than the range reported for MCF by Gotsch et al. (2016) from 7 to 12 t C ha⁻¹ year⁻¹. NPP decreases with elevation and is especially low in elfin and subalpine cloud forests. In “dwarf forest” after clearcutting the biomass increased slowly: in the first 2 years the accumulation was 95 g m⁻² per year and then increased to 212 g m⁻² per year (Brown et al., 1983).

MCF Under Anthropogenic Pressure

Anthropogenic pressure to MCF is extreme worldwide. In Africa, agricultural fields are found at altitudes up to 2400 m asl, and pastures up to 3000 m asl, and in South America, fields go up to 3700 m asl and pastures to 4000 m asl (Doumenge et al., 1995). Conversion of MCF to coffee or tea plantations or to pastures is widespread all over the world (Martínez et al., 2009). Toledo-Aceves et al. (2011) name cattle grazing, illegal logging, land tenure conflicts, agriculture, roads construction, inappropriate use of fire, and extraction of stone materials among the main threats to MCF in Mexico. In Veracruz, Mexico the area of MCF decreased to almost half their original surface during the period between 1973 and 2003 (Martínez et al., 2009). Sarmiento and Frolich (2002) argue that the distribution of MCF in Andes is geographically limited by human activities such as grazing and potato cultivation. Bubb et al. (2004) report that the area of mountainous forests, some of which are cloud forests, in the eastern part of Madagascar declined from 8 million ha in 1900 to 7 million ha in 1950, and to less than 1 million ha by 1995. Urban sprawl is becoming a growing challenge for MCF, especially informal settlements represent a menace for this fragile ecosystem in the developing countries (Benítez et al., 2012).

Land use change results in the loss of biodiversity. The MCF in Veracruz, Mexico had 260 plant species, while coffee plantations under natural vegetation had 237 and grassland only 183 species (Martínez et al., 2009). Shannon's diversity index decreased in the sequence MCF-coffee plantation-grassland in the sequence 5.576-5.464-5.193 for all plant species and 4.654-3.850-3.258 for woody species (Martínez et al., 2009). The species richness of frogs was one-fifth less in coffee plantations than in forest fragments, and only one-third of the frog species occurred in both forest fragments and coffee plantations. The number of beetle species and their abundance was significantly greater in coffee plantations than in the forest fragments, whereas species richness and species composition of bats were virtually the same in both habitats (Pineda et al., 2005). Though recent studies (Brüning et al., 2018) show that small-scale agriculture can even promote biodiversity of amphibian in MCF, the reduction of the area of MCF results in fragmentation of the forest that may lead to the negative effect on the animals inhabiting the remnants of the forest (Cayuela et al., 2006). It should be also stressed that besides biodiversity the loss of MCF also affects other ecosystem services, especially water quality (Martínez et al., 2009).

MCF Under Climatic Change

Modeling climatic change scenario of doubled CO₂ concentration showed that the relative humidity surface in the mountains might be shifted upwards several hundreds of meters (Still et al., 1999). Warming also can lead to the reduction in the number of days with mist (Pounds et al., 1999); in combination with increased evapotranspiration with escalated temperature the climatic change would lead to the reduction and in places even extinction of MCFs (Foster, 2001). Modeling of climatic change using general circulation model (GCM) until 2050 suggests a strong effect on the hydrology and ecology of MCF, although different models provide contradictory results (Bruijnzeel et al., 2011). Poor quality of prediction might be explained by coarse resolution of GSMs (1°) that is insufficient to reflect complex topography typical for MCF habitats (Hu and Riveros-Iregui, 2016). Loope and Giambelluca (1998) shared concern of possible climatic change effect on the extremely fragile MCF ecosystems on Hawaii Islands. However, on small islands the effect of the increased temperature may be minor: recent estimation for tropical islands was 4.4 m shift of relative humidity surface per 1°C increase in mean annual temperature (Pouteau et al., 2018). Hu and Riveros-Iregui (2016) mention that most of the studies focus on the change in the environments and not the reaction of MCF trees on reduced moisture availability. The authors propose a new approach based on coupled $\delta^{18}\text{O}_{\text{cellulose}}$ and $\delta^{13}\text{C}_{\text{cellulose}}$ that has the potential for understanding physiological effect of reduced cloud water interception due to climate drying. Benzing (1998) showed that epiphytes are the most sensitive species, which might be used as early indicators of the response of MCF to the climatic change. The reaction of epiphytes in MCF to the El Niño caused droughts was stronger and the recovery slower than in other drier habitats that shows their high vulnerability to drought stress (Gotsch et al., 2018). Rapp and Silman (2014) experimentally showed that epiphytes strongly differed in their response to drying, the species from the upper limit of MCF distribution being more sensitive than the species from the lower MCF.

Twenty of 50 species of frogs and toads disappeared from 1976 to 1999 in Monteverde Cloud Forest Reserve, Costa Rica due to the decreased frequency of mists that was ascribed to the increase in air temperatures that followed a step-like warming of tropical oceans (Pounds et al., 1999). Anchukaitis and Evans (2010) used stable oxygen isotope measurements from trees without annual rings to reconstruct a century of hydroclimatology in the same reserve and found no evident trend related to global warming. However, they found significant oscillations related to El Niño events, and ascribed the extinction of the Monteverde golden toad to a dry period associated with El Niño. It should be mentioned that the climatic change effect may vary in the MCF in different parts of the world, and further research is required for understanding the threats of climatic change for MCF biodiversity.

The MCF ecosystems are vulnerable and difficult to restore, but their reforestation is still possible (Bruijnzeel et al., 2010). After abandonment of the agricultural fields in the MCF zone natural vegetation recovers, but the process is long, and after 30 years of secondary forest development the epiphytes did not reach the abundance and biomass typical for old-growth MCF (Köhler et al., 2007). The restoration of MCF is a complex task that should include best available science, native species production in nurseries, monitoring, training for local stakeholders, knowledge dissemination and land protection (Ramírez-Soto et al., 2018). The pressure on MCF should be minimized, and systematic policies should be developed to conserve the unique MCF biome (Peh et al., 2011).

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Forest Protected Areas

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Abstract

Motivations for establishing forest protected areas have expanded over the years from a focus on landscape and species towards social needs, biodiversity conservation, and maintenance of ecosystem services. Protected areas are defined and their range of management approaches and governance types described. Other similar area-based approaches that are not full protected areas are also described. Estimates of forest protected areas range from 13.5% to 20.1% of remaining forest cover globally. Some of the social issues surrounding forest protection are discussed and management effectiveness described in terms of both forest cover and the survival of biodiversity in the face of land clearance, poaching of wildlife and timber, and pervasive threats such as climate change. The future of forest conservation is discussed briefly, including new threats from anti-environmental populist politicians and the potential for steps to control climate change providing a unifying factor for forest protected areas.

Introduction

Areas of forest have been set aside from exploitation for thousands of years. Motivations have varied: many societies protected particular sacred groves for religious reasons (Porteus, 1928). In Europe, forests were maintained and guarded as hunting grounds for the aristocracy (Schama, 1995). In countries such as Japan (Kumazaki et al., 1991) and Switzerland (Dapples et al., 2002) conserved forests on steep slopes have reduced erosion and avalanches for hundreds of years. And in the Middle East the *hima* system protected dryland forests for their ecosystem services (Bagader et al., 1994).

The contemporary model of a protected area came much later. The first handful of national parks were established in the United States, Australia, and India at the end of the 19th century and numbers increased gradually in the first half of the 20th century, before expanding rapidly after 1980 (Gissibli et al., 2012). Most modern protected areas have been set up in the last 30 years; it is hard to think of another conscious, large-scale change of land use that occurred so fast.

The reasons for establishing protected areas have changed over time; or rather additional reasons have been added to older motives (Watson et al., 2014). The earliest national parks were identified largely for their landscape values, as in the Blue Mountains National Park outside Sydney, Australia, or to protect a single species as in Kaziranga National Park, Assam, India, conserving the Asian rhinoceros (*Rhinoceros unicornis*) (Mathur et al., 2007). Next, recreation became a driving force as in the Peak District, the first British national park, created largely to provide city dwellers with access to the countryside (MacEwan and MacEwan, 1982).

Rapid rate of forest loss, particularly in the tropics, created a wave of concern from the 1970s onwards. Between 1980 and 1990, the Food and Agriculture Organization of the United Nations (FAO) estimated annual losses in the developing world of over 150,000 km² (FAO, 1997); figures that other analysts felt were too low (Matthews et al., 2000). Countries like the Philippines and Cote d'Ivoire lost virtually all natural forests in a generation. While forest area in the temperate and boreal regions was generally increasing after a historical low, natural forests were frequently replaced by severely degraded forests and pulpwood plantations, with forests untouched for 200 years averaging less than 1% of total forest area in most European countries (UNECE and FAO, 2000) and rapid loss of old-growth forests in North America causing an intense debate (DellaSala, 2011). These changes, coupled with a rapid rate of species loss (Myers, 1979) and new understanding about biodiversity, created an impetus for setting aside native forest throughout the world. Protected areas were designated explicitly to protect forest ecosystems and the global network grew rapidly (Schmidt et al., 2009). More recently, forest protection has paid increasing attention to maintaining ecosystem services, including the storage and sequestration of carbon in response to climate change.

What is a Forest Protected Area? Definitions and Varieties

"Protected area" is a problematical concept, and people's understanding of the term differs around the world and between stakeholder groups. National parks, nature reserves, wilderness areas and a wide variety of community or indigenous conservation

approaches all fall under the general term. The UN Convention on Biological Diversity (CBD) defines a protected area as: “a geographically defined area which is designated or regulated and managed to achieve specific conservation objectives.” The International Union for Conservation of Nature (IUCN) has a different definition, which the CBD recognizes as being equivalent: “A clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values” (Dudley, 2008).

Some of the words are particularly important. “Conservation” refers to the in situ maintenance of ecosystems and natural and semi-natural habitats and of viable populations of species in their natural surroundings. “Dedicated” implies binding commitment to long term conservation through international conventions, national and local law, customary law, NGO covenants, private trusts and company policies. “Managed” assumes conscious steps to conserve the protected area’s values. “Legal or other effective means” implies that protected areas must be gazetted (established legally) under statutory civil law, recognized through an international convention or agreement, or managed through means such as traditional community rules or the policies of established nongovernmental organizations. “To achieve” assumes effectiveness (Dudley, 2008).

These definitions are guidelines: the details of what “counts” as a protected area, and is listed in the United Nation’s World Database on Protected Areas (WDPA), is determined by national policy and legislation. Protected areas are not all managed in the same way, and can vary between areas entirely without human presence to cultural landscapes that include settled human communities. Both IUCN and the CBD recognize six management categories, as summarized in Table 1, as long as the area also meets the definition of a protected area.

Not all protected areas are under the control of the state and other stakeholders sometimes make the management decisions. IUCN recognizes a range of governance types (Borrini-Feyerabend et al., 2013), as in Table 2.

Forest protected areas are therefore variable in both management aims and management authority, albeit under a single definition. Deciding what falls inside or outside the definition has created long debates, particularly in Europe (Dudley and Phillips, 2006). The situation is further complicated by the existence of several other management approaches that, whilst not strictly protected areas according to the IUCN definition, play a similar role in area-based conservation. Many countries, particularly in Africa and Asia, have a system of “forest reserves,” initially established to maintain timber stocks (Burgess et al., 2007). While some have disappeared or become timber plantations, others have high conservation value and can be regarded as part of the conservation estate. Indeed, a proportion has been converted into protected areas, for example, in Uganda (Howard et al., 2000).

A potentially much larger, but more complicated category, agreed by signatory states of the CBD in November 2018, is Other Effective Area-Based Conservation Measures (OECMs), commonly known as Conservation Areas. When the CBD agreed a target for global protected areas in Sendai, Japan in 2010, the text referred to “protected areas and other effective area based conservation measures” without defining the latter (Woodley et al., 2012). It took eight years of deliberation and a task force from IUCN to agree a definition: “a geographically defined area other than a protected area, which is governed and managed in ways that achieve positive and sustained long-term outcomes for the in situ conservation of biodiversity, with associated ecosystem functions and services and where applicable, cultural, spiritual, socio-economic, and other locally relevant values” (CBD, 2018). Forests recognized as OECMs will likely be increasingly important in area-based conservation in the future, although they are by definition not protected areas.

Table 1 IUCN and the CBD recognize several different management categories

Management category	Details
Ia	Strictly protected areas to protect biodiversity and also possibly geological/geomorphological features, where human visitation and use are strictly controlled and limited. Such areas can serve as reference areas for scientific research. Example: Maltion luonnonpuisto, Finland
Ib	Usually large unmodified or slightly modified areas, retaining their natural character and influence, without permanent or significant human habitation, which are protected and managed to preserve natural condition. Example: Misty Fjords National Monument in Alaska, United States, part of the Tongass National Forest
II	Large natural or near-natural areas protecting large-scale ecological processes, along with characteristic species and ecosystems, while providing environmentally and culturally compatible spiritual, scientific, educational and recreational opportunities. Example: Volcanoes National Park, Rwanda
III	Generally quite small areas to protect a specific natural monument, which can be a landform, sea mount, submarine cavern, geological feature or even a living feature like an ancient grove. Example: Coal River Springs in Canada
IV	Areas protecting particular species or habitats, where management reflects this priority. Many category IV protected areas will need regular, active interventions to meet the needs of particular species or habitats, but this is not a requirement of the category. Example: Otun Quimbaya Fauna and Flora Sanctuary, Colombia
V	Areas where the interaction of people and nature over time has produced a distinct character with significant ecological, biological, cultural and scenic value: and where safeguarding the integrity of this interaction is vital to sustaining the area and its values. Example: native woodland in Snowdonia National Park, Wales United Kingdom
VI	Areas conserving ecosystems and habitats, with associated cultural values and traditional natural resource management. They are generally large, mostly in natural condition, with a proportion under low-level nonindustrial natural resources use compatible with conservation. Example: Peru Mountain Forest Reserve in Jamaica

Table 2 Governance types: IUCN and the CBD recognize four governance types of protected areas

A	Governance by governments: a government body (a Ministry, Park Agency or sometimes an NGO contracted by government) manages the protected area and determines its management aims and objectives. Example: Bwindi Impenetrable Forest National Park in Uganda
B	Shared governance: complex institutional mechanisms and processes share management authority and responsibility amongst a plurality of (formally and informally) entitled governmental and nongovernmental actors. Example: 13 national parks in Canada are jointly managed by the government and First Nation groups
C	Private governance: protected areas under individual, cooperative, NGO or corporate control and/or ownership set up and managed under not-for-profit or for-profit schemes. Example: the forest reserves owned and managed by the Woodland Trust in the United Kingdom
D	Indigenous or community governance: Includes two subsets: (1) indigenous peoples' areas and territories established and run by indigenous peoples. Example: Indigenous Protected Areas in Australia; (2) community conserved areas established and run by local communities. Example: some community conservancies in Namibia

Borrini-Feyerabend, G., Dudley, N., Jaeger, T., Lassen, B., Pathak Broome, N., et al. (2013). *Governance of protected areas: From understanding to action*. Best Practice Protected Area Guidelines number 20. Gland: IUCN.

Governments sometimes prioritize other forests for soil protection, erosion and landslide control, as water sources and for carbon storage. Some may be managed in ways that are indistinguishable from forest protected areas and will likely eventually be recognized as OECMs or as protected areas.

How Much Forest Protected Area Exists?

The global coverage of protected areas has expanded rapidly, with rates of designation moving much more quickly than anyone expected. When IUCN first suggested that 10% of the world's land surface should be in protected areas the target was viewed as little more than a fantasy (IUCN, 1992). But by 2010, signatory countries of the CBD agreed to a target of 17% of land surface and 10% of the oceans (CBD, 2010) and there is a growing movement amongst ecologists that this remains way too low (e.g., Half-Earth: Noss et al., 2012; Wilson, 2016).

As of June 2018, there were 238,563 designated protected areas on the World Database on Protected Areas (WDPA). Those on land cover over 20 million km², 14.9% of the earth's land surface (UNEP WCMC, IUCN and NGS, 2018). Precise figures change; new areas are designated, existing areas are finally reported, and some areas lose their protection status, a phenomenon known as Protected Area Downgrading, Downsizing and Degazettement (PADDD) (Mascia and Pailler, 2010).

Working out the proportion of terrestrial protected areas that are also forest protected areas is more complicated. Governments do not report ecosystem types to the WDPA and even if they did many protected areas contain a mixture of ecosystems. There is a continuing debate about the definition of forest (e.g., Putz and Redford, 2009), particularly in sparsely wooded areas like tundra and drylands. Nonetheless, estimates exist. In 2014, the UNEP World Conservation Monitoring Centre estimated that 7,848,782 km² of forest was in protected areas, 20.1% of the global forest area, meaning that roughly a fifth of the world's forest is now under some kind of protection (Juffe-Bignoli et al., 2014), see Table 3.

This is larger than an estimate in the 2015 *Global Forest Resources Assessment* from FAO, which proposed a global figure of 6,510,000 km² forests in protected areas, although confusingly in the same publication FAO reported forest managed primarily for biodiversity conservation at only 5,240,000 km² (Food and Agriculture Organization of the United Nations (FAO), 2015), or 13% of total forests. This smaller figure accorded with a 2009 study by Schmidt et al., who estimated protected forest area cover at 13.5%; however, many more forest protected areas have been established since.

FAO also distinguishes forests managed primarily for their ecosystem services, principally coastal stabilization, clean water, erosion control, and desertification. Statistics reported from some countries go well beyond protected areas: 71% of forests in North and Central America managed for soil and water protection; 80% of forests in Uzbekistan managed for erosion control (Food and Agriculture Organization of the United Nations (FAO), 2018); and so on. These general designations are not all protected areas and not considered here.

What Do Forest Protected Areas Provide?

Protected areas are designated primarily for nature conservation, which includes all aspects of biodiversity (ecosystems, species and intra-specific genetic variation) and also geodiversity, geology, and landforms. Over time, the sophistication of protected areas selection has increased, from an initial focus on rare species, such as pandas in Sichuan, to consideration of ecosystems, gap analysis (Dudley and Parrish, 2006), biodiversity richness, irreplaceability (Ferrier et al., 2000), connectivity (Beier et al., 2008), and extinction risk (Ricketts et al., 2005). The key biodiversity area (KBA) concept emerged as a unifying measure, defined as "sites contributing significantly to the global persistence of biodiversity" (IUCN, 2016). It is not always necessary to designate all or any part of a KBA as a protected area to maintain its biodiversity values, but the existence of a KBA is an important factor in protected

Table 3 Estimates for area and proportion of forests within protected areas listed by the UN

<i>Realm</i>	<i>Natural forest area (km²)</i>	<i>Forests in protected areas (km²)</i>	<i>Forests in protected areas (%)</i>
Australasia	1,787,015	395,644	22.1
Afrotropic	6,818,852	1,198,400	17.6
Indo-Malayan	2,568,626	457,534	17.8
Nearctic	7,314,463	748,839	10.2
Neotropical	8,754,932	3,466,784	39.6
Oceanian	5836	781	13.4
Palaearctic	11,827,242	1,580,800	13.4
World	39,076,966	7,848,782	20.1

Juffe-Bignoli, D., Burgess, N. D., Bingham, H., Belle, E. M. S., de Lima, M. G. et al. (2014). *Protected planet report 2014*. Cambridge: UNEP World Conservation Monitoring Centre.

area planning (Smith et al., 2018). The proportion of KBAs in protected areas is increasing, although no separate analysis has been carried out for forested KBAs (Food and Agriculture Organization of the United Nations (FAO), 2018).

The existence of better planning tools does not necessarily mean that protected areas are always designated according to conservation criteria. Social, commercial and political influences remain important. But there is increasing interest in choosing forests that are the most significant for biodiversity. The concept of representativeness, ensuring that all ecosystems and species are represented in protected areas, has also assumed higher importance.

Although protected areas prioritize nature conservation, the IUCN definition refers to “associated ecosystem services and cultural values” (Dudley, 2008). These values have a growing role in determining the designation and management of forest protected areas.

The Millennium Ecosystem Assessment grouped ecosystem services into four categories of supporting, provisioning, regulating and cultural services (Millennium Ecosystem Assessment, 2005). Supporting services are ecosystem processes and functions that keep life on the planet running: soil formation and nutrient cycling; lifecycle maintenance by for instance providing fish nursery habitats; seed dispersal and other species interactions; and biodiversity conservation. Provisioning services are the tangible resources that ecosystems provide directly or help to support and include contributions to food and water security, and access to raw materials, medicines and other genetic resources. Regulating services refer mainly to the role of natural ecosystems in helping control extreme weather events, the water cycle, earth movements, and natural processes that impact on agriculture such as pollination. They include the role of ecosystems in storing and sequestering carbon, thus reducing the rate of climate change. Finally, cultural services refer to the many cultural, psychological, and spiritual links that humans have with the natural world and range from aesthetic appreciation to religious associations.

Forest protected areas supply multiple ecosystem services (Stolton and Dudley, 2010). They are critical to supporting services, as sources of soil and water, maintenance of pollinators and other biodiversity for food and agriculture and through driving key aspects of the global weather cycle. For example, circulation of billions of tonnes of water vapor from the Amazon forest has been termed the “flying rivers” of the Amazon, providing water for agricultural areas further south (Nobre, 2014). Globally, almost 9.5% of forests are managed primarily for soil and water conservation (Food and Agriculture Organization of the United Nations (FAO), 2018), although it is not clear how much of this is in protected areas.

Forest protected areas play a critical role in many provisioning services, particularly related to water and food security. Natural forest ecosystems generally produce purer water from their catchments than most other land uses, partly because less polluting activities take place within forests and partly due to ecological processes that remove some pollutants (Dudley and Stolton, 2003). A smaller proportion of forests, principally tropical mountain cloud forests, also increase the net water flow from the catchment (Hamilton and King, 1983). The role of forest protected areas in supplying drinking water is recognized; a third of the world’s top 100 cities draw a significant proportion of their water from forest protected areas (Dudley and Stolton, 2003).

Forest protected areas also supply a certain amount of food, through managed collection by local people and sometimes because game species spill over from protected forests into the wider landscape. However, illegal hunting of bushmeat in protected areas, whilst understandable as a source of protein and money for poor communities currently undermines the effectiveness of many protected areas as discussed below.

The role of forest protected areas in regulating services is more varied, and includes stabilizing soils, rocks and snow and thus reducing landslide and avalanche, coastal protection from mangroves, and riparian forests to mitigate flood events and store water to release more gradually during periods without rain (Kumagai et al., 2013). FAO estimates that 1% of global forests are managed for coastal protection, while countries like Tajikistan consciously manage forests on steep slopes to reduce avalanches (Food and Agriculture Organization of the United Nations (FAO), 2018). Increasingly important is the role of forests and forest soils in storing and sequestering carbon (Keith et al., 2009). Research shows that forests continue to store carbon even in old-growth phase by building up soil stocks (e.g., Keith et al., 2009; Lewis et al., 2009), while removing or burning forests results in an abrupt spike of carbon loss. Protected areas have an important and increasingly recognized role in maintaining carbon stocks (Dudley et al., 2009), particularly those centered on primary forests (Mackey et al. 2014).

Cultural ecosystem services cover benefits ranging from tourism to spiritual fulfillment. The tourism values of forests include local amenity, walking and outdoor sports, landscape values and nature tourism. Tourism is replacing agriculture and forestry as a rural source of income in many areas and for countries like Rwanda can be the largest earner of foreign exchange (Sabuhoro

et al., 2017). Some forest protected areas contain important buildings, such as temples or prehistoric sites, in other cases forest management systems can themselves be of historical significance. Forests in many countries contain spiritual and aesthetic values to faith groups, including the existence of sacred trees and groves (e.g., Salick et al., 2007). Given that most protected area managers come from a scientific background, managing cultural, historical and sacred sites often means learning new skills and working with new partners. Guidelines tailored to protected areas are becoming more readily available (e.g., Wild and McLeod, 2008).

Social Dimensions of Forest Protected Areas

Protected areas also have a human dimension in terms of people who visit them, rely on their ecosystem services and most importantly who live in and around protected areas. Human interactions with protected areas have not always been straightforward. When establishing protected areas, many countries introduced legislation stating that they should be empty of human habitation, with all resource uses banned. This caused immediate problems in those ecosystems where people were living. Over 20 years ago, estimates in Latin America found that 86% of national parks contained human habitation (Amend and Amend, 1995). Where they occurred, forced relocations, sometimes without adequate (or any) compensation, created a social crisis and people with nowhere else to go frequently continued to occupy protected areas illegally, poaching species they had traditionally hunted. Critics accuse some protected areas of serious human rights abuses (Brockington et al., 2008). Conversely, and adding further complication, in successful protected areas where wildlife numbers remain high, new settlers are sometimes drawn by the possibility of a large bushmeat harvest.

In the last 20 years, and particularly following the 2003 World Parks Congress (IUCN, 2005), many countries have worked hard to address social inequalities in protected areas through changing legislation, working with local communities, developing realistic compensation packages and negotiating access and user rights. While problems remain, global experience in reconciling protected areas and people is far more advanced. Many protected areas have forged new and positive relationships with indigenous peoples, working in partnership rather than in opposition (Stevens, 2014). Processes such as Free, Prior and Informed Consent (Ward, 2011) and the *United Nations Declaration on the Rights of Indigenous People* (UN, 2007) raise expectations for a strong human rights approach in conservation and provide tools to help achieve this.

When they work well, forest protected areas provide many social benefits; in terms of the range of ecosystem services and in many cases also safe places to live for vulnerable human communities. But poorly planned, top-down protected areas can result in significant displacement and loss of livelihoods, creating tensions, and usually a backlash in the form of illegal occupation and use and sometimes direct vandalism and threats to managers and rangers. These problems are not confined to protected areas and occur even more acutely under other management regimes; responsibly managed protected areas can indeed provide a model suitable for application in the wider landscape.

Management Effectiveness—Do Forest Protected Areas Work?

Rapid expansion of protected area has meant an equally rapid development in terms of management, and a growing number of protected areas are assessing management effectiveness as a standard part of annual planning. Effectiveness in forest protected areas needs to consider two distinct issues: whether a forest protected area is an effective way of keeping the forest intact; and whether it is effective in conserving the constituent biodiversity.

Protected areas are not perfect mechanisms and continued degradation often takes place, particularly at the boundaries as people chip away at forests for fuelwood, building materials or to create farmland. Pressures include land conversion, infrastructure development (particularly roads), poaching and over-collection but also sometimes factors such as visitor pressure, air and water pollution and, increasingly important, climate change.

Nonetheless, research shows that protected areas are amongst the most effective ways of maintaining native forests. A study in 22 tropical countries concluded that most protected areas are successful in protecting ecosystems (Bruner et al., 2001) while research in the Amazon (Asner et al., 2005) and in a variety of tropical countries (Joppa et al., 2008) found forest protected areas are generally effective in maintaining forest cover. A global review by the World Bank found that tropical protected areas, especially those conserved by indigenous peoples lose less forest than other management systems (Nelson and Chomitz, 2009).

Whether or not forest protected areas maintain their constituent biodiversity is less clear. Serious problems of species loss in protected areas is well known (Grumbine, 1990) and the phenomenon of “empty forests,” where most wildlife has been removed through over-collection and poaching, has long been recognized (Redford, 1992). Bushmeat hunting remains a critical threat in large forest areas of Asia, Africa and Latin America. Recent research identified poaching as a significant factor in the decline of 301 terrestrial mammal species threatened with extinction (Ripple et al., 2016). Retention of the constituent ecosystem makes it much easier to recover species numbers or to reintroduce species if pressures are reduced; this is occurring in many parts of Europe for example where populations of large mammals are recovering slowly from historical lows. However, the current pressures within some forest protected areas, for example in Vietnam (Drury, 2011) and parts of West Africa (McNamara et al., 2015), remain extremely severe.

The Future of Forest Protected Areas

Depending on the estimates taken, the world already has up to a fifth of its native forests in protected areas. These global figures mask regional disparities. For instance, the Neotropical zone has double the global average while Oceania, the Nearctic and Palearctic have significantly less (see [Table 3](#)). At a finer level of analysis many particular forest types, and ecoregions, remain poorly protected. Wilderness areas and the most intact forests continue to decline ([Watson et al., 2016](#)) despite the high biodiversity values maintained within intact forests ([Watson et al., 2018](#)). Deforestation continues apace and the conservation organization WWF has identified 10 deforestation fronts, where the majority of deforestation will likely occur until 2030 ([Taylor et al., 2015](#)). Furthermore, the long-term security of many forest protected areas remains uncertain. A rise in populist politicians, often proclaiming an explicitly anti-environmental message, could see many of the conservation gains of the last two decades rolled back again unless conservation advocates can find new arguments to persuade skeptical and powerful people of the value of natural forests.

Conversely, the importance of protected areas is generally recognized around the world ([Watson et al., 2014](#)). Despite the rhetoric from a handful of influential governments, the global consensus on the reality and seriousness of climate change continues to grow. The value of maintaining native ecosystems as a bulwark against rapid environmental change is gaining increasing recognition ([Olson et al., 2012](#); [Watson et al., 2013](#)), both from the perspective of carbon storage ([Grassi et al., 2017](#)) and the wider issues of ecosystem services ([Stolton and Dudley, 2010](#)). Forest protected areas will hopefully continue to play a pivotal role in helping to maintain global biodiversity and other ecosystem services into the future.

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An Introduction and Perspectives on Forest Certification

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Abstract

Leadership forest certification systems can provide valuable independent measures of more ecologically, socially, and economically sustainable forest management, thereby empowering businesses and other consumers wishing to make informed purchasing decisions for forest products, supporting resource managers who use and adopt leadership forest and ecosystem management practices, and contributing to broader discussions over resource management and conservation. However, questions remain over which forest certification systems merit recognition as leadership systems, the limits of any certification systems' abilities to (by themselves) halt global deforestation and achieve other outcomes, and how certification systems will respond to climate change and other priority and emerging challenges. This article introduces the concepts and basic components of forest certification, outlines considerations for researchers wishing to compare certification systems, and highlights other topics of interest for the evolution of certification and its role in responsible forest management, forest conservation, and sustainable business practices.

Basic Concept, Goals, and Approaches

While the function and significance of forest certification can depend on one's perspective, a good starting point is to think of it as a market-based mechanism for distinguishing wood, paper, rubber, tree nuts, and other forest products associated with more environmentally, socially, and economically desirable and exemplary forest management. Certification systems like the Forest Stewardship Council (FSC) are meant to enable consumers and businesses to identify and purchase products from timber companies, community forests, Indigenous Peoples, and other forest managers who follow the system's forestry standards, thus also enabling them to avoid products from deforestation and other harmful practices.

Long the pre-eminent forest certification system, the FSC has also been a leader within the broader eco-labeling movement and, to varying degrees, a model for other systems. Indeed, systems like the Marine Stewardship Council and Sustainable Agriculture Network were largely inspired by the FSC. The FSC was established in 1993 by environmental and social non-governmental organizations (NGOs), forest sector businesses, and other nascent eco-forestry initiatives. Their interests included concerns with tropical deforestation, loss of old growth and other primary forests, degradation of forest ecosystems, injustices in the forestry sector against Indigenous Peoples and other at-risk social groups, and/or insufficient market recognition for more sustainable forestry practices.

From an economics and public policy perspective, leadership certification systems embody the potential for helping to correct existing markets' and regulatory systems' failure to account for important environmental and social impacts, and long-term economic sustainability (i.e., environmental and social externalities). Such leadership systems also embody an implicit goal of empowering consumers to make informed and responsible purchasing decisions. Whether individuals will choose to exercise their economic "votes" is another question, and in some markets (e.g., the United States), the evolution of corporate sustainability and procurement programs has done far more to create market demand for certified forest products. As discussed in [Conroy \(2007\)](#) and elsewhere, the NGO advocacy campaigns that helped motivate these corporate programs have also advanced leading certification systems, including as an alternative to sourcing products from endangered ecosystems.

Unlike some other certification systems, transparency, balanced stakeholder input and governance, and democratic decision-making have been core values in the FSC's design. This is evidenced most dramatically at the triennial General Assemblies (GAs) of the FSC's governing membership. As such, the FSC is an imperfect and cumbersome, but surprisingly successful experiment. Indeed, the system's credibility and role as a leading international voice on forestry topics is probably due largely to its efforts at governance by a membership that balances environmental, social, and economic voices, including from both developed and developing nations.

Today, the following are among the FSC's basic components. Some of these elements are also found in competing forestry schemes, while others are not, or are not employed as effectively.

- An independent, non-governmental institution that officially comprises and manages the system on a day-to-day basis.
- High-order governance of the system by a balance of environmental, social, and economic stakeholders and experts. In the FSC's case, by international and national memberships, and by international and national boards of directors elected by the membership bodies.
- Forest management standards developed by a balance of environmental, social, and economic stakeholders and experts, and approved by the system's governing bodies, to provide independent objectives and thresholds for environmentally, socially, and economically well-managed forests. The FSC's standards include internationally-applicable Principles and Criteria (P&C), and more granular national/regional Indicators that address variations in forest ecosystems and other contexts, and that are used to assess forest managers' compliance with the P&C.
- On-product certification labels, including: "FSC 100%," for products wholly from FSC certified forests; "FSC Mix," for product lines partially from certified forests; and "FSC Recycled," for products wholly from recycled or reclaimed sources.
- A process for auditing and certifying the forest management practices of participating forestry companies and other forest managers. Third-party certification bodies (CBs) are hired to evaluate participants' management systems and on-the-ground operations. Products from forest units that meet the FSC's forest standards may be marketed with a corresponding label.
- "Chain of custody" (CoC) certification and related quality control mechanisms, to ensure that labeled products originate from certified forests, and to prevent and correct any fraudulent claims. All entities in the supply chain for FSC products must be CoC certified.
- A quality control mechanism for CBs and their audits. Accreditation Services International (ASI) accredits and audits CBs on behalf of FSC.
- Additional consultation, transparency, and dispute resolution provisions. Public consultation is required during development of FSC standards and during FSC certification audits, for example. The FSC also publishes summaries of audit reports, and uses channels such as its GAs and board meeting reports for open communication with its multi-stakeholder membership. Certificate holders, national FSC offices, and FSC and ASI must also respond to appeals of certification decisions or other complaints.

In a sense, certification systems can themselves be certified. The International Standards Organization (ISO) establishes basic best practices and technical procedures for certification systems in all sectors (see the standards of the ISO Committee on Conformity Assessment (CASCO)). The ISEAL Alliance also maintains Codes of Good Practice for certification systems. This topic and others are covered in more detailed introductions to forest certification, for example, [Nussbaum and Simula \(2013\)](#).

Evaluating and Comparing Forest Certification Systems

The extent to which different certification systems require significant improvements in forest conservation and management, protect social and cultural values, and embody leadership approaches in their governance, auditing procedures, and other components is an important topic with much room for further study. In many regions, stiff competition has emerged in the forest certification sector, including from systems initiated by industry trade associations and governments in support of forest practices much closer to business-as-usual norms. (For more on the origins of such systems, see [Nussbaum and Simula \(2013\)](#) and [Ozinga \(2004\)](#).) As a result, consumers and businesses wishing to make responsible and informed purchasing decisions can no longer simply look for a forestry eco-label, but must also distinguish between certification systems and labels. Ironically, the systems with the lowest standards may also have the most readily available and widely labeled products.

Some existing comparisons of different forest certification systems are of note, both for their findings and their analytical approaches. For example, [Ozinga \(2004\)](#) and [Ford and Jenkins \(2011\)](#) provide a look at various systems from the perspective of leading conservation and social NGOs, are informative on considerations for evaluating different systems, and illustrate the importance of considering sources outside of academia. [Smith and Perreault \(2017\)](#) compare the FSC and Sustainable Forestry Initiative (SFI) from the perspective of Indigenous Peoples, and touch on the question of whether competition between systems has been productive. [Judge-Lord et al. \(2018\)](#) provide an academically robust comparison, and discuss the role of certification relative to other governance mechanisms. Meanwhile, [Clark and Kozar \(2011\)](#) is an example of a comparison based on a meta-analysis of other studies.

When comparing and evaluating forest certification systems, one may wish to give particular attention to research questions that focus on priority forest management and conservation topics, and on elements of certification systems that are especially important to their credibility and effectiveness. Opportunities to utilize more readily available data may also be of interest. With this in mind, [Appendix IA](#) highlights some research considerations regarding certification systems' institutions and governance. Examples of topics covered in the Appendix include how the systems were established and whether they are governed by open, multi-stakeholder memberships, are transparent and accountable, and meet the ISO and ISEAL best practices for certification systems.

Similarly, [Appendix IB](#) summarizes questions and approaches to consider regarding certification systems' forest management standards. For example, are the standards performance and outcome-oriented, and do they require significant improvements in forest management beyond regulatory norms? How thoroughly do the standards protect and restore priority natural resources

and cultural values? Examples of such priorities include: managing for a full range of native tree species, vegetation, and habitats; prohibiting the conversion of natural forests to tree plantations and non-forest land uses; protecting Indigenous Peoples' traditional rights over lands and resources by securing their Free, Prior, Informed Consent (FPIC); and protecting rare and endangered ecosystems, including Intact Forest Landscapes (IFLs). Likewise, what is the system's "bottom line" for certification, as evidenced by certified forest management in indicative situations?

Finally, [Appendix IC](#) highlights questions and considerations regarding certification systems' audits and label claims. Examples include: whether audits are conducted by third-parties with a full range of environmental, social, and forestry expertise; mechanisms for transparency and accountability; the system's track record in addressing non-compliant certificates; and mechanisms to ensure that label claims are accurate and backed-up by CoC verification.

These topics and others covered in [Appendix I](#) are by no means complete lists of necessary elements for forest certification systems' institutions, procedures, and standards. For additional considerations, see the Credibility Principles and Codes of Best Practice of the ISEAL Alliance, [WWF \(2015\)](#), and the ISO CASCO standards. The FSC can also be considered a benchmark against which to evaluate other systems.

Other Current and Emerging Points of Interest

An important ongoing area of study is whether certification systems adequately protect forest ecosystems and biodiversity, or otherwise leverage significant improvements in forest management from environmental, social, and long-term sustainability perspectives. The subject of certification outcomes has received some attention in the context of FSC certification in the tropics. However, the topic has not received much attention in other regions, for example, North America and Europe—or with regard to other major forest certification systems.

An illustrative cross-section of the existing work on certification outcomes might include: [Newsom et al. \(2006\)](#), which used corrective action requests (CARs) as an indicator of management improvements stemming from certification. [Zimmerman and Kormos \(2012\)](#), which raised questions about the sustainability of reduced impact logging (RIL) practices. [Ebeling and Yasué \(2009\)](#), which looked at how contextual factors affect the ability of certification to improve forest management. [Romero et al. \(2017\)](#), which references and discusses many existing evaluations of FSC certification outcomes, and provides recommendations for evaluating certification outcomes in the tropics. And finally, [Sheil et al. \(2010\)](#), whose articles, case studies, and survey of experts provide perspectives on a number of topics, including biodiversity and certification in the tropics.

Deforestation continues to be a serious problem globally, leading some observers to question whether certification is effective at curbing outright forest loss. With some certification systems, the problem may lie partly with insufficient prohibitions on deforestation in their standards. However, with FSC certification, the issue is not the system's standards, which forbid significant conversion of natural forests to tree plantations, agriculture, and other non-forest conditions.

Rather, as [Sheil et al. \(2010\)](#) suggest, the challenge rests more with how only a portion of tropical forests (and others) are FSC certified, and with inherent limits in certification systems' ability to affect management in non-certified forests. This raises the question of whether the economic value of certification to forest owners and managers can be improved, to offset the opportunities they see in conversion and deforestation—and how often deforestation is driven by market trends that can be affected by certification systems, sustainable purchasing decisions, and increasing certification-related revenues for forest managers. Some parties that convert forests to agriculture, residential development, and other land uses in both developed and developing countries may simply not be interested in managing for forest products.

Of course, definitions and data can also factor into the deforestation picture. Conversion of natural forests to plantations and some non-forest uses can be missed by data based on definitions of "forest" that rely too simplistically on minimum canopy cover. Public and private sector initiatives might then be compromised, should they rely on such data and definitions. Short-term loss of forest cover due to timber harvest followed by tree planting or natural regeneration should also not be confused with deforestation (though it might still involve the conversion of natural forests to plantations).

Similar dynamics and questions are emerging in the debate over certification and Intact Forest Landscapes (IFLs) (i.e., mostly forested landscapes of at least 50,000 ha that have been minimally influenced by human activity, per [IF and GFW, 2006](#)). Unlike other systems, the FSC has implicitly, and now explicitly, prohibited degrading the majority of IFLs to non-IFL conditions. As with deforestation more generally, IFL loss continues to be a problem globally (see [Potapov et al., 2017](#)). Here too, forest managers' incentive to become certified may be outweighed by lucrative opportunities to remove timber from largely untouched "wilderness" forests, given that maintaining forests as IFLs inherently sets sharp limits on road construction, logging, and other industrial forestry operations. Thus some observers argue that it would be better to allow IFLs to be converted to managed but certified forests, than to see them impacted by even more intensive non-certified operations. Researchers looking at forest canopy closure in the tropics have also argued that careful road construction, timber harvest, and road closure practices can enable IFLs to return to IFL condition over time; see [Kleinschroth et al. \(2018\)](#), for example.

Meanwhile, many environmental NGOs point-out that IFLs represent some of the planet's last remaining intact wild ecosystems, and that their biodiversity, carbon storage, and other environmental and cultural values argue for more strict protection from industrial activities. Some research also suggests even the lightest-touch industrial forestry can result in significant harm to IFL values, regardless of canopy closure. [Morgan et al. \(2018\)](#), for example, found chimpanzees among the imperiled species impacted by selective logging of primary forests, including in certified forests. Perhaps not surprisingly, even [Kleinschroth et al. \(2018\)](#) suggest

that saving the world's last frontier forests may require enhanced protected area networks and other approaches beyond certification alone.

There is a difference, of course, between finding that certification alone is unlikely to solve all of the world's forestry related challenges, and suggesting that certification is unimportant or lacking in value. As long as deforestation, degradation of managed forest ecosystems, and social injustices continue to be of concern in the forest sector, consumers and businesses may continue to find value in avoiding products associated with those practices. Instead, they may wish to associate their brands with more environmentally and socially progressive forest management.

Questions regarding the circumstances for certification to be successful are also relevant beyond the tropics and other regions where IFLs and deforestation have received more attention. In the United States at least, it has been a challenge to establish price premiums for certified products, and to ensure that any premiums "trickle down" to the forest owners and managers who ultimately decide whether to certify their forests. Indeed, it remains to be seen whether consumers in the United States can be encouraged to focus on purchasing certified products, even at price parity. With market access being a principle factor in demand for certified forestry in such regions, the bigger question may be whether sustainable corporate purchasing programs will continue to give preference to leadership systems like the FSC, as public attention shifts to climate and other topics—and whether NGOs will continue to play a role in influencing those purchasing priorities.

While threats remain to some IFLs, old-growth forests, imperiled species' habitats, and other conservation priorities in regions like the United States and Europe, occurrences of these values are now rarer, making their protection less challenging, at least for leadership-oriented certification systems. In such regions, the greater challenge may lie with finding the ideal balance between ecological restoration and continued commercial forest management. It is not always easy to sustain and repair biodiversity in ecosystems impacted by generations of intensive management, while enabling forest managers to make reasonably competitive financial returns. With the FSC in the midst of updating its national/regional forest management standards, these are pertinent and timely questions.

The proper balance among environmental, social, and economic objectives can also depend on other contexts, such as land tenure. While the FSC's international standards (i.e., the FSC P&C and more recently adopted International Generic Indicators (FSC, 2018)) are intended to provide some global consistency across all forests, the system's use of regional/national Indicators to flesh-out and implement the P&C has long recognized that ecological, silvicultural, social, legal, and other contexts vary greatly among and within regions. To varying degrees, the SFI and some FSC regional/national standards also recognize that publicly owned forests may need to be managed for a different balance of objectives than private commercial timberlands. Many systems also recognize that less demanding and costly certification procedures are warranted for the smallest and least intensively managed forests. For example, those managed by some local communities, families, and other "smallholders" or non-industrial private forest owners. The FSC continues to explore new approaches, and might benefit from research on the approaches best suited for different regions and types of smallholders. The capacity and needs of smallholders in regions like the US and Europe will be quite different than in developing countries.

The condition of the surrounding forest landscape can also be an important contextual variable. The FSC's international standards recognize that when operating in landscapes with lower levels of ecosystem protection, for example, forest managers should do more to conserve and restore "representative sample areas" of fully functioning ecosystems in their management units. This includes management units that may be currently managed as plantations.

Another topic to watch is whether the FSC's new Ecosystem Services Procedure can enable greater levels of ecosystem protection and restoration to be economically feasible for forest managers. (The Procedure builds on lessons from the Forest Certification for Ecosystem Services Project.) An obvious and important opportunity is for governments, local communities, Indigenous Peoples, and other forest owners to secure financing to help expand protected areas networks and high carbon forests, water quality, and other ecosystem services. If successful, this could enable the FSC to help support forests where commercial management is not the primary goal. However, might the approach also potentially support more conservation oriented management of commercial forests?

Some systems are also exploring risk-based approaches to certification. Thus far, the quality and effectiveness of these approaches appears to vary widely. The FSC's long-standing recognition of the precautionary principle may represent the high-quality end of the spectrum, though it is unclear how consistently the principle is applied in practice. At the other end perhaps, lie approaches taken by forest-related systems like the Sustainable Biomass Partnership, where cursory regional data on forest trends is used in lieu of assessments of actual conditions in source forests (see NRDC and DA, 2017). The FSC's "Controlled Wood" system for minimizing the risk of controversial forest sources being included as non-certified content in product lines bearing the "Mix" label has also been of questionable efficacy, but is evolving and is more ambitious than competing systems' approaches.

The FSC's ongoing round of standards development also merits attention, as it is serving as an ad hoc testing ground for new approaches to risk. Updates to the FSC P&C in 2012 more explicitly provide for some certification requirements to be proportionate to differing contexts of "scale, intensity, and risk" (SIR). In turn, FSC (2016) outlines approaches for FSC national/regional indicators to codify those requirements. Put most simply, FSC (2016) encourages more thorough approaches to forest management (e.g., assessments, planning, monitoring) in higher risk contexts (e.g., larger-scale or more intensive forest management operations, or more vulnerable natural resources or cultural values). Conversely, more streamlined approaches are encouraged in lower risk contexts.

Certification systems are also being challenged to more effectively adopt and implement social justice promises. While the road has been bumpy at times (such as evidenced during debates at the 2017 GA), the FSC continues to lead with renewed commitments

to fully respecting the rights of Indigenous Peoples and communities to exercise FPIC over management affecting lands and resources to which they hold traditional rights. It remains to be seen whether other certification systems will follow suit—and how all systems will approach the topic in regions where FPIC implementation has received less emphasis to date. The same might be said for the FSC and other systems, with regard to commitments to respecting workers' rights and gender equity.

Some of these topics are likely to play out in new High Conservation Value (HCV) Frameworks. The 2012 updates to the FSC P&C (and further amendments in 2014) also clarified the system's definition of HCVs, including for IFLs and for the role of engagement with Indigenous Peoples and local communities during HCV identification. In 2015, the FSC called for national/regional standards to begin including HCV Frameworks, to provide nationally/regionally specific interpretations of, and management approaches for, the P&C's six HCV definitions. A template and guidance for Frameworks are now being finalized. These Frameworks are likely to build on existing HCV guidance, toolkits, and interpretations documents, including those already found in some national/regional standards, and those developed for some countries by the High Conservation Value Resource Network. However, this is also new territory in some regards, and input from environmental and social scientists and other experts may be timely.

Looking Down the Forest Road

Certification systems with more rigorous standards and higher expectations can face challenges not felt by systems that focus more on endorsing status quo forestry practices. Meeting leadership certification systems' higher standards for forest management and conservation can involve significant opportunity costs for forest managers, in addition to the transaction costs of the certification process. Meanwhile, as noted above, leadership systems like the FSC have found it difficult to provide participating forest managers with price premiums, and also face being undercut in the market by competing systems that demand far less change in forest management. Other pertinent challenges include fully addressing the rights of Indigenous Peoples, and finding the right balance in addressing environmental and social risks associated with the non-certified content of mixed-source products. Likewise, while growth in the FSC's membership and roles has been an indicator of success, it has also posed challenges for a system that values democratic, member-driven governance, which is not always the most efficient process.

Maintaining and enhancing carbon stores and sequestration in certified forests should arguably be a top priority for all certification systems, both as part of more comprehensive strategies to minimize catastrophic climate change, and because of synergies with goals for protecting remaining intact forests and other ecological and social values. However, this remains a topic where certification systems' forest industry members have largely stymied progress.

Emerging dialogues over "sustainable intensification" also raise interesting and difficult questions. Is it possible there are "cake and eat it too" solutions to the conflict between continued growth in demand for wood, paper, and other forest products, and the finite (and in fact, often shrinking) nature of the resource base of forest ecosystems (i.e., supply)? This conflict is all the more acute, given that many forest ecosystems may already be over-tapped from the perspectives of imperiled species, water resources, carbon budgets, climate change adaptation, and other values. If not, is there realistic hope for alternate solutions, such as improved utilization efficiency and reducing, or at least stabilizing, global demand for consumption of forest products?

Likewise, how should certification systems and other market and governmental institutions decide which forests should be managed for commercial forest products, and which should remain mostly wild and dedicated primarily to ecosystem conservation and traditional use by Indigenous Peoples and local communities? Unlike some other systems, the FSC at least attempts to answer these questions, in part by requiring conservation of IFLs, HCVs, and other priority environmental values, and by requiring consultation with Indigenous Peoples, local communities, conservation NGOs, and experts. Yet even the FSC is still, quite understandably, largely oriented to operating in managed forests. This was recently evidenced in the United States, when the FSC US' new standard for certification of National Forests fell dramatically short of environmental NGOs' expectations for a standard that would focus on the conservation and restoration of these public forests, given their role in the broader forest landscape.

At the end of the day, it seems likely that certification will continue to be an important part of the forest conservation and sustainable business landscape, and global trade in forest products. Likewise, greater attention to topics such as those mentioned above can surely help improve the scope and effectiveness of certification systems, and also help purchasers and others make informed choices between leadership systems and their competitors. At the same time, questions will surely remain about what even the best certification systems can reasonably be expected to achieve, and where additional initiatives will remain imperative, including stronger public policies and regulatory frameworks for the protection and restoration of forest ecosystems and forest carbon stocks.

Appendix I: Additional Considerations for Comparing and Evaluating Forest Certification Systems

A Factors and Questions Regarding the Systems' Institutions and Governance

- How the system was established. While certification systems evolve, they tend to do so incrementally, and understanding their origins can be informative, including with regard to their underlying mission and sense of identity. For example, was the system originally established more to recognize the best forestry practices, or status quo practices?
- How the system is governed. Is there a multi-stakeholder governing membership, inclusive of forest producers, retail forest products companies, smallholders, Indigenous Peoples, other traditional forest communities, labor advocacy NGOs,

environmental advocacy NGOs, independent scientists, etc.? How open is the membership? Who elects or appoints governing board members? How do these bodies balance input and decision-making among stakeholder groups? What are the system's main sources of funding?

- How the system's forest management standards and policies are developed. Are the standards written and approved by multi-stakeholder bodies, and if so, how representative are those bodies of a true diversity of interests? How responsive are the standards developers to input from public and stakeholder consultations?
- How transparent and accountable are the system's decision-making bodies and institutions, including to the system's members and to a broad diversity of stakeholders?
- The extent to which the system meets the requirements and best practices established for certification systems by ISO and ISEAL.
- The organizations that endorse and support the system, including NGOs and retail companies. Do they include leading advocacy organizations, expert institutions, other civil society groups, and brands with strong commitments to environmental and social values?

B Questions and Approaches Regarding Certification Systems' Forest Management Standards

- The extent to which the standards are performance and outcome-oriented. Do they merely require forest managers to have systems and plans in-place, or do they also require managers' plans and on-the-ground practices to achieve explicit and clear outcomes? Are the standards written in a manner that requires independent verification of compliance, including in areas such as legal compliance, and compliance with social standards?
- The management practices and in-the-forest outcomes required by the standards, for priority topics such as:
 - Prohibiting the replacement of natural forests by tree plantations that lack most natural forest structure and biological diversity, or by agriculture or other non-forest conditions and land uses.
 - Requiring that successive harvest of timber and other forest products not deplete resource stocking levels, and that management is also financially sustainable.
 - Prohibiting the use of genetically modified organisms within certified forests.
 - Protecting all rare, threatened, and endangered species and their habitats, including those designated at national and subnational levels.
 - Protecting rare and endangered ecosystems, including old growth forests in regions where they are now rare, and Intact Forest Landscapes (IFLs) (i.e., mostly forested landscapes of at least 50,000 ha that have been minimally influenced by human activity, per [IF and GFW \(2006\)](#)).
 - Setting-aside reserve areas, especially within larger forest management units.
 - Protecting and restoring (where needed) unstable slopes, streamside zones, stream structure, water quality, and other watershed functions.
 - Effectively limiting the use of the most toxic herbicides and pesticides, including by encouraging silvicultural practices that can reduce dependence on such chemicals.
 - Managing for a full range of native tree species, vegetation, and habitats, and other forest structure and composition.
 - Fully recognizing and protecting the rights and cultural and natural resources of Indigenous Peoples and traditional local communities (e.g., people who do not identify as Indigenous but have similar long-standing cultures and use claims), including by securing their Free, Prior, Informed Consent (FPIC) over management affecting lands and resources to which they hold traditional rights.
 - Ensuring that forest tenures and harvest licenses were legally issued, without corruption.
 - Fully respecting the rights of forest workers, including those established by the International Labor Organization (ILO).
 - Adequately surveying the forest and consulting stakeholders and experts, to identify resources and values needing protection or restoration.
- The extent to which the standards require performance beyond compliance with existing forestry, environmental, and social regulations.
- Non-conformances (NCs) (formerly known as corrective action requests (CARs)) flagged by CBs in certification assessments and reports, to address situations where forest management does not yet fully meet the certification system's forest management standards. Do the NCs—and the corrective actions adopted by forest managers—indicate that the standards leverage significant improvements in forest management? Does a lack of NCs suggest the system tends to certify status-quo forestry, or forest operations that are already exemplary? (Note that NCs is the terminology used by FSC; other systems may use different terminology.)
- The condition of certified forests and how they are managed in regard to priority topics. What is the system's "bottom line" for certification, as evidenced by the most intensive forestry practices that are certified, and/or by certified management in regions where past management has severely impacted ecosystems, where native biodiversity and other values remain relatively intact and thus vulnerable, and/or where higher levels of social controversy exist? Are more degraded forests being restored to improved conditions? Are past violations of land tenure rights or other social injustices being redressed?

C Questions and Considerations Regarding the Systems' Certification Audits and Label Claims

- Whether certification audits must be conducted by independent, third-party CBs and auditors with a full range of environmental, social, and forestry science expertise. Do CB accreditation and audit procedures meet the best practices established by ISEAL?
- The extent to which the certification auditing process requires comprehensive stakeholder notification and consultation.
- The extent to which audit reports are made public and contain information sufficient to enable stakeholders to understand how the certified forests are managed, and what NCs have been issued to improve their management.
- The system's track record in addressing complaints filed against certificates for forests alleged to not be in compliance with the system's standards. What proportion of complaints result in corrections to the certificate, or the complainants otherwise feeling their concerns were addressed? Is the complaints system reasonably open and accessible to begin with, including per the best practices of ISEAL?
- The system's procedures for minimizing the risk of environmentally and socially controversial sources being included in the non-certified content of mixed-source products, that is, products not entirely from certified forests. How comprehensive and performance-oriented are these requirements?
- The extent to which label claims for mixed-content products must be proportionate to the products' inputs from certified forests, for example, via explicit indications of the percentage of certified inputs, or by limiting the application of labels to that percentage of product.
- Whether CoC verification is required for all products bearing the system's labels.

Acknowledgments

My sincere thanks for the insights and time of the many colleagues and experts who suggested topics or reviewed drafts of this paper, in particular Dr. Robert Hrubec and Dr. Marion Karmann, who both provided significant contributions.

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Forests and Ecosystem Services

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Abstract

Ecosystem services (ESs) is the concept and term used to represent the benefits that people obtain from an ecosystem. No ideal system for identifying and classifying ESs has emerged, but the scheme developed by the Millennium Ecosystem Assessment (MEA, 2005) is used extensively. Investigations of ESs help provide the basis for measuring the benefits individuals, families, businesses, communities, and the global society receive from forests; for weighing the increases and decreases in benefits from actions that alter the forest; and for describing the disparate effects on different groups affected by the actions. Most forests are managed to emphasize the production of logs, fuel wood, and other goods readily exchanged for cash through market transactions. This emphasis diminishes forests' ability to provide nonmarket benefits, such as mitigating climate change by sequestering atmospheric carbon dioxide and sustaining indigenous cultures and lifestyles. The value of the forgone benefits can exceed the value of the commercial products derived from forests. Detailed studies in the Pacific Northwest of the U.S. demonstrate that the loss can exceed the value of commercial log production by, perhaps, more than 80-to-1. Proposals for reducing the harm from the production of commercial products include paying forest managers to produce nonmarket benefits and punishing them for not doing so.

Ecosystem Services From Forest Biomes

By recognizing that ecosystems provide specific benefits to people, MEA (2005) provides a useful framework for understanding the many ways in which ecosystems are important, both positively and negatively, to individuals, families, businesses, communities, and the global society. It also provides a foundation for measuring the socioeconomic value of ecosystems in terms similar to those used to measure the value of goods and services produced by human activities. This information can provide the basis for quantitatively determining if actions, such as logging or habitat restoration, that alter an ecosystem, will yield net benefits or net costs for different groups and for society as a whole.

MEA (2005) aggregated ESs into four categories:

1. Provisioning services, which involve the production of materials or energy useful to humans in the form of food, water, building materials, and fuel wood.
2. Regulating services, which benefit humans by regulating the characteristics of the environment that affect human wellbeing. These services influence the quality of air, soil, water; remove carbon dioxide from the atmosphere; moderate floods; filter waste products from streams; control pests and vector-borne diseases.
3. Cultural services, which provide humans with opportunities for ecosystem-based spiritual experiences and sense of place; inspiration for culture, art, and design; attractions for recreation and tourism; enhancement of mental and physical health.
4. Supporting services, which lay a foundation for the three other categories of services through habitats for plants and animals, and genetic diversity.

The MEA's chapter on "Forest and Woodland Systems" (Shvidenko et al., 2005) aggregated the ESs provided by forest biomes into 14 categories (Fig. 1).

The MEA's four-category classification system is widely accepted and used, but it has weaknesses as well as strengths. The strengths include recognition that some ESs influence the quantity and quality of *goods* derived from forests, while others influence the quantity and quality of *experiences* people have when they interact with forests. Forest ecosystems, for example, can influence the amount, timing, location, and temperature of water in streams. They also can provide opportunities for participating in outdoor recreational activities, reinforcing spiritual beliefs, sustaining a culture, and enjoying aesthetically pleasing scenery. Applications

Category	Category
Biodiversity	Sports fishing/hunting
Climate regulation	Recreation
Spiritual	Ecotourism Health
Cultural	protection
Historical	Soil protection
Industrial wood	Water protection
Fuel wood	Nonwood forest products

Fig. 1 Major categories of forest ecosystem services identified by the Millennium Ecosystem Assessment. Shvidenko, A., Barber, C. V., Persson, R. et al. (2005). *Forest and woodland systems*. Millennium Ecosystem Assessment; From Figure 21.6 Major Classes of Forest Services, p. 601.

of the MEA's framework have facilitated the compilation of information about the individual ESs themselves, i.e., the actual benefits the specific groups of humans derive from ecosystems, as well as the structures, processes, and functions that produce them. This work has clarified both the ability of existing research methods to identify, quantify, and socioeconomic importance of some ESs, and the limitations in their ability to describe others. Investigations into ESs, based on the MEA's framework, also have provided insights into the human activities that enhance or diminish the quantity, quality, and value of different ESs.

Experience using the MEA's framework has revealed two major weaknesses (Binder et al., 2017). One stems from unevenness in the data regarding the four categories of ESs. Provisioning services often involve the production and consumption of goods, e.g., logs and fuel wood, that are traded in market transactions. These transactions can provide voluminous data on the good's location and quantity, quality and value, and sellers and buyers. Market data also are available to describe many regulating services. For example, prices for houses in a floodplain might decline, relative to prices of comparable housing elsewhere, following an announcement to log an upstream forest and thereby diminish the forest's ability to regulate runoff and reduce downstream peak streamflows. In contrast, an ecosystem's cultural and supporting services typically are more removed from market transactions. Moreover, some of them, such as those associated with the role a forest plays in sustaining the culture of an indigenous group, are generally incompatible with market concepts.

The disparity in descriptive information and valuation data often has resulted in studies that focus primarily on the socioeconomic importance of market-oriented provisioning and regulating services (Zhang and Stenger, 2014). Such efforts can induce decision-makers and the public to conclude that the greater volume of data for market-oriented services means that these services are the only ones that exist or that they are more important than those that are not traded in markets and for which the data are limited. These beliefs then can lead to biased forest-management decisions that favor the production of market goods and disfavor the forest's ability to provide cultural benefits to indigenous and other groups, even when these, in truth, have greater value.

Another weakness in the MEA's framework stems from its lack of clarity about what is and is not an ES. Some have used it to focus on the immediate circumstances where people realize a benefit, e.g., when they log a tree, remove water from a stream, or hike a forested trail. Others have looked away from those events to focus on the ecosystem structures and processes that underlie them. This ambiguity is confusing and it can lead to a double-counting of ESs that shows a forest producing benefits for people once, when circumstances enable people to realize them and again when ecosystem processes create those circumstances.

In one significant effort to overcome the ambiguity (Boyd and Banzhaf, 2006), many economists have sought to refine the definition of an ES so that it includes only the components of nature that people directly enjoy, consume, or use to enhance their wellbeing. This approach has several key features. It focuses on the direct interaction with a component of an ecosystem that produces a benefit for people, not on the underlying ecosystem processes. Thus, it parallels the accounting economists use to measure the benefits consumers realize when they enjoy, consume, or use goods and services produced by human systems. It recognizes that, in most cases, people derive benefit not from an ecosystem in isolation but through interactions between the ecosystem and human-produced goods and services. For example, people don't realize a benefit from a forest's production of timber and fuel wood until workers, using tools, cut trees down. When such an interactive process is necessary to realize benefits from an ecosystem, then the ecosystem service is responsible for just a component of the benefit, not all of it.

This refined definition of ESs also recognizes that the direct enjoyment, consumption, or use of a component of nature can occur through vastly different activities at various scales, involving individuals, families, business and other organizations, communities, and society as a whole. People realize benefits from a forest's timber-production ESs embodied in trees having the size, location, and quality characteristics that can be converted into merchantable logs. The benefit from these ESs accrue to a single entity: the commercial enterprise that employs labor and machines to convert the trees into logs and then uses the logs as an input to its production processes. Recreational ESs lie latent until people enter the forest for hiking, biking, etc. Multiple people can realize the recreational benefits without extracting goods from the forest. The benefits from climate-related ESs materialize outside the forest, when forest growth sequesters and stores atmospheric carbon dioxide, thereby enabling individuals, businesses, and communities around the world to enjoy a reduction in climate-related risks. The benefits from ecosystem-existence ESs similarly manifest themselves without direct interactions with the forest, as individuals derive enjoyment from knowing that forest structures, processes, and species currently exist, with the prospect of passing these features to future generations.

A forest can produce many distinct streamflow-related ESs that accrue to different groups, within and downstream from the forest. For example, the forest might convey benefits to:

- Downstream farmers, as they use water the forest delivered to the stream in amounts and at times useful for irrigating crops.
- Downstream municipal/industrial consumers, as they use water the forest delivered to the stream in suitable amounts and with appropriate quality characteristics (e.g., favorable turbidity and unharmed compounds).
- Downstream communities, as they enjoy reduced flooding because the forest regulated water runoff and diminished peak flood flows.
- Subsistence, commercial, and recreational fishers, as they seek to catch fish that are in the stream because the forest provides suitable habitat.
- Educators and students, as they observe and study fish that migrate between forest and downstream habitats.
- Water-sports enthusiasts, as they enjoy in-forest and downstream streamflows in amounts and with quality characteristics suitable for kayaking, rafting, etc.

These examples suggest the broad diversity of ESs that can directly provide benefits to people living nearby and to those living far away. Some of the ESs, such as those associated with reducing climate-related risks, manifest themselves as people enjoy benefits directly from components of the forest ecosystem, but without direct physical interaction with the forest. Others, such as those associated with timber production and recreational hiking, do not exist without direct activity of people in the forest. Many ESs embodied in a forest's influence on streamflow become manifest through a direct interaction with a component of the natural environment but outside the forest's borders.

The focus on the direct enjoyment, consumption, or use of a component of the ecosystem is useful for economic analyses that seek to quantify the value of ESs in monetary terms. It is less useful for those concerned with ESs that don't fit with monetization, either conceptually or empirically or both. To fill this gap, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) has developed a different approach for defining and weighing ESs (Diaz et al., 2018). Although it does not overcome limitations in the data available for measuring some ESs, it places greater emphasis on nonmarket services. It also emphasizes using perspectives, such as those of indigenous peoples, that can complement market data regarding the definition of the services themselves, the interactions between natural and social systems that govern the delivery of these services, and the multiple ways in which the services contribute to human wellbeing. The IPBES has identified 18 distinct ESs (Fig. 2). This approach is new and it remains to be seen how well it boosts future understanding on ESs, monetary as well as nonmonetary.

Other categorization systems focus more narrowly, recognizing the tension between market-oriented and nonmarket ESs. These often look first at ESs associated with extractive activities, distinguishing between those that produce timber and those that produce bushmeat, fruits, nuts, livestock fodder, and other products. They then consider nonextractive ESs. Some of these are associated with specific benefits to people, e.g., removal and storage of atmospheric carbon dioxide to mitigate climate-related risks, and streamflows suitable for irrigation or municipal/industrial uses and without peak flows that threaten high flood damage. Others are associated with sustaining forest structures, processes, and species perceived to have existence or bequest value, or to be necessary for preserving a forest's ability to produce extractive products in the future.

Economic Values

Willingness to Pay and Willingness to Accept

Any effort to measure the socioeconomic importance of forest ESs should make clear the perspective from which the measurement is taking place. Economists typically employ one or both of two perspectives. One considers value from the perspective of a buyer's

Category	Category
1. Habitat creation and maintenance	10. Regulation of detrimental organisms and biological processes
2. Pollination and dispersal of seeds and other propagules	11. Energy
3. Regulation of air quality	12. Food and feed
4. Regulation of climate	13. Materials, companionship, and labor
5. Regulation of ocean acidification	14. Medicinal, biochemical, and genetic resources
6. Regulation of freshwater quantity, location, and timing	15. Learning and inspiration
7. Regulation of freshwater and coastal water quality	16. Physical and psychological experiences
8. Formation, protection, and decontamination of soils and sediments	17. Supporting identities
9. Regulation of hazards and extreme events	18. Maintenance of options

Fig. 2 Categories of nature's contributions to people (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services). Diaz, S., Pascual, U., Senseke, M. et al. (2018). Assessing nature's contributions to people. *Science* 359, 270–272; Source: Supplementary Material. Figure 1, Table 1.

willingness to pay (WTP) for something she does not already possess. The other looks at what a seller is willing to accept (WTA) as compensation to relinquish something she already possesses. In some market settings, with many fully-informed buyers and sellers making small transactions, the two perspectives likely yield identical estimates of the value of the good or service being traded. These conditions, however, are unlikely to exist when estimating the value of most ESs. As a result, the two perspectives can yield very different values.

Differences most often arise because the WTP values depend on the potential buyer's ability to pay, i.e., his accumulated amount of money. This perspective, thus, is biased against those who are poor. For example, if two communities, one rich and one poor, compete for a forest component, the WTP perspective would favor the richer community because it has a greater ability to pay, even if, in truth, the poorer community would realize a greater benefit if it won the competition.

Additional differences arise because, in general, people require more compensation to relinquish something than they are willing to pay to acquire the same thing. The difference may be small for a market-traded good or service that exists in substantial quantity and for which there exist substitute goods or services. With a nonmarket good or service closely associated with a community's spiritual or cultural identity, or with its beliefs in what is right or wrong, then the WTA perspective of value may far exceed the WTP perspective of value. In some circumstances, a community may conclude that no amount would adequately compensate them for relinquishing a good or service. These circumstances can readily arise when a commercial entity seeks to displace an indigenous community from lands or waters it has long occupied. Using the WTP perspective to estimate the value of the community's loss could starkly under state the true harm members of the community would experience.

Despite the significance of the distinctions between WTP and WTA perspectives of the value of ESs, most available data on value represent the former. Those who use these data should remain aware of the potential for bias in situations where WTA would more appropriately represent the value people place on ESs when faced with losing them.

Estimates of Value

Numerous efforts have sought to quantify and estimate the value of particular ESs from a particular forest biome (Costanza et al., 2017). These efforts contributed to Costanza et al. (2014), which summarized the relevant literature to estimate the global average value (US\$, 2007) of ESs provided in 2011 by different biomes. The estimates for tropical and temperate/boreal forests were \$5382 and \$3137 per hectare per year, respectively. These estimates build on an earlier attempt, Costanza et al. (1997) to quantify the global economic value of ESs throughout the world. The results from that earlier effort show the distribution of value generated by different types of ESs (Fig. 3), with nutrient cycling and climate regulation accounting for more than half of the total. The percentages shown should be considered extremely rough estimates, but they nonetheless provide a general sense of perceptions at that time about the relative importance of different forest ESs.

Siikamäki et al. (2015) estimated, for each country, the value of nonwood ESs from forest biomes. The estimates update values used by the World Bank to describe the total value of each country's forest resources and to evaluate the benefits and costs associated with actions that alter the area or productivity of forest resources. The researchers found (Fig. 4) that, across the globe, ESs associated with recreation, habitat and species protection, nonwood forest products, and water produce benefits worth US\$95 per hectare per year (2013 U.S. dollars). Regional values range from US\$13 (Sub-Saharan Africa) to US\$156 (East Asia & Pacific). The researchers also estimated the present value, a single amount today that is the sum of annual benefits expected over the next 25 years, and each annual value discounted 4% per year in the future. The present value can be useful for comparing the value of nonwood forest ESs against the present value of the wood products that would be produced by managing the forest with that emphasis over the same period.

Tradeoffs

Many, perhaps most, economic assessments in recent years of forest ESs have focused on the tradeoffs associated with the production of wood products. Many assessments look beyond the nonwood forest products included in Fig. 4 to focus on the ability of living trees to mitigate the effects of human-caused changes in climate [including other changes, such as in ocean acidification] by removing carbon dioxide from the atmosphere, through photosynthesis. Unlogged forests also can store carbon in living and dead matter on the forest floor and in forest soils. Logging accelerates the release back into the atmosphere of some of the carbon stored in the forest. It also stops the trees from continuing to remove more carbon dioxide from the atmosphere in the future and, although the growth of smaller replacement trees can offset some of the forgone sequestration, it can take years, decades, even centuries, for total offset to occur if at all given most logging is on short rotation intervals. In the meantime, the additional forest carbon in the atmosphere will contribute to intensification of climate change.

Few studies have directly compared the value of the benefits humans realize from the fiber/fuel ESs that manifest themselves when trees are killed against the value of the climate-mitigation ESs realized when trees are left in the forest. Measuring the value of the fiber/fuel ESs involves using market data on "stumpage value," i.e., the value of trees just before they are logged, which isolates the value of the ESs associated with the forest's production of wood fiber from the value of human-provided services that kill the trees, process them, and convey logs and fuel wood to market.

Ecosystem Service	Percent of Total Global Value per Hectare per Year
Nutrient cycling	37
Climate regulation	15
Raw materials	14
Erosion control	10
Waste treatment	9
Recreation	7
Food production	4
Genetic resources	2
Soil formation	1
Water supply	<1
Disturbance regulation	<1
Water regulation	<1
Biological control	<1
Cultural	<1
Total	100

Fig. 3 Relative value of different ecosystem services from forest biomes. Costanza, R., d'Arge, R., de Groot, R. (1997). The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–260.

	Value of nonwood forest ecosystem services (2013 U.S. dollars per hectare)	
World Bank region	Average annual value ^a	Present value of expected services over the next 25 years ^a
Global	95	1,312
East Asia & Pacific	156	2,309
Europe & Central Asia	70	733
Latin America and Caribbean	105	1,610
Middle East & North America	43	654
North America	147	2,001
South Asia	27	410
Sub-Saharan Africa	13	202

^aAnnual value includes recreation, habitat/species protection, nonwood forest products, and water. Present value does not include habitat/species protection.

Fig. 4 Estimated value of nonwood forest ecosystem services, by region. ^aAnnual value includes recreation, habitat/species protection, nonwood forest products, and water. Present value does not include habitat/species protection. Siikamäki, J., Santiago-Ávila, F.J., and Vail, P. (2015). *Global assessment of nonwood forest ecosystem services*. Washington, DC: Program on Forests, World Bank; Table 14 and Table 15.

Social Cost of Carbon

Measuring the value of the climate-mitigation ESs of forests left unlogged involves estimating the social cost of carbon dioxide (SC-CO₂). This variable represents the net global economic damage expected to result from a 1-ton increase in atmospheric carbon dioxide or, alternatively, the damage that would be avoided by removing the same amount from the atmosphere.

One of the most thorough comparisons of fiber/fuel ESs and climate-mitigation ESs comes from calculations by the U.S. Bureau of Land Management (BLM) for forestlands it manages in western Oregon, in America's Pacific Northwest. These forests are among the best in the world for their ability to sequester carbon and produce wood fiber, and market data suggest that, if dedicated to timber production, these lands would command prices exceeding US\$12,000 per hectare. Recognizing the high productivity, the

BLM's analysis provided calculations for several alternatives that show the stumpage value of trees that would be logged annually and the SC-CO₂ of trees that would be left standing. Comparing alternatives with more logging against others with less reveals the tradeoffs between timber-production ESs and climate-mitigation ESs. The comparisons show that, for alternatives that increase logging, the value of the global damage resulting from the associated carbon dioxide emissions would exceed the stumpage-value of the logs by >4-to-1.

This ratio reflects 2013 research that estimated the SC-CO₂ to be about US\$40–50 per metric ton of carbon dioxide emitted over the next few years. Subsequent research (Ricke et al., 2018) revised the estimate upward, to more than \$400 per ton carbon dioxide, with \$800 per ton as the upper bound of potential outcomes. Hence, the new research suggests that the climate-mitigation ESs provided by these forests exceed the fiber ESs by at least 30-to-1 and, perhaps, by >80-to-1. The actual ratio likely would be even higher, insofar as these estimates of the SC-CO₂ represent only a subset of damages resulting from carbon dioxide emissions and exclude others, such as those associated with all the potential economic harm from ocean acidification.

These numbers strongly suggest that logging less, rather than more, of these forests would result in a higher level of wellbeing for global society. They do not, however, definitively show that halting all logging across all of the forestlands managed by BLM is warranted. The values for climate-mitigation ESs and fiber ESs reflect the averages for the entire area. Spatially specific data likely would show a lower ratio for some hectares and a higher ratio for others. It is possible that a reverse ratio, i.e., showing log value exceeding climate-mitigation value, might obtain for lands with trees capable of producing high-value lumber and proximate to a lumber mill with the productive capacity to do just that.

Other Ecosystem Benefits

Other research in the Pacific Northwest illustrates the range of values for ESs other than those associated with timber production and mitigation of climate risks. Most of these are tradeoffs for timber production and cobenefits for climate-risk mitigation. Unlogged forests, for example, can increase streamflows during arid summer months, because mature forests typically consume less water than do younger trees that are planted after logging. In addition, mature trees have greater ability to condense fog, which drips to the ground, soaks into the soil, eventually leaks into streams, and becomes available to irrigators and municipal/industrial users during dry months. In some locations, these processes can increase the amount of water reaching the soil by about 0.5 m. Limited information from transactions involving streamflows suggest that the increased annual streamflow produced by the ESs of unlogged forests can exceed US\$125 per hectare.

Federal forests of the Pacific Northwest are notable in part because of decisions in the 1990s to reduce logging markedly in response to research showing that continued logging would seriously jeopardize the continued existence of species dependent on unlogged forests. Attention focused on one species, the Northern Spotted Owl (*Strix occidentalis caurina*), and the change in forest management afforded economists with an opportunity to measure the public's preference for protecting this species and its habitat relative to the market value of the timber that would be produced if the lands were logged. Economists (Hagen et al., 1992) carefully surveyed U.S. households to ascertain their average willingness to pay for the continued protection of owls and the old-growth forests that provide them habitat. This amount, multiplied times the total number of U.S. households, provides an estimate of the overall benefits of protecting old-growth forests and owls.

The economists recognized that these results required further validation because most people have little experience with expressing their willingness to pay to protect a species and its habitat. Hence, they might not fully comprehend that protecting the owls and their habitat would come at considerable cost, through the reductions in the supply of and higher prices for lumber and other wood products that would accompany the constraints on logging necessary to provide the protections. To verify that survey respondents understood the consequences of expressing what they would be willing to pay, they researchers asked them to compare this amount against the value of the forgone timber. Under varying analytical assumptions, they found that survey respondents perceived that the ratio of benefits to costs for sustaining the forests' old-growth habitat ESs for owls ranged from 3.5 to 42.6. This finding is consistent with similar analyses of the benefits and costs of protecting other rare, threatened, or endangered species. A 1996 review of 20 studies of the economic value Americans place on such species found that the costs per household of protecting endangered and threatened species fall "well below" the benefits. A 2009 update of the review (Richardson and Loomis, 2009) found that Americans' valuation of threatened and endangered species has increased over time.

Synthesis of the economic studies of the value of diverse ESs produced by federal forests in the Pacific Northwest provides insights into the overall importance of benefits derived from forest products relative to other benefits. Economists from the U.S. Forest Service (Haynes and Horne, 1997) found that, for forests managed by that agency in the state of Washington, the value of timber production represented <8% of the total value of ESs in 1995, and they predicted this value would fall to <2% by 2045. The value of camping, fishing, and other recreational benefits, in contrast comprised >30% of the total value in 1997, with expectations that this would grow to >60% by 2045. Values associated with the ability of unroaded areas to sustain the existence of structures, processes, and species associated with native forests accounted for almost 60% of the total value in 1997 and almost 35% of the expected total value in 2045.

Payments for Ecosystem Services

Emphasis on Extractive Products

Management of the world's forests generally emphasizes ESs associated with the extractive products. [Marta-Pedroso et al. \(2014\)](#) reports that more than one-half of the world's forestlands are managed to capture value from a specific, narrow set of ESs: 30% focus on provisioning ESs associated with the production of wood, fiber, biomass, and nonwood forest products, 11.5% on conserving biodiversity, 8.2% on conservation of regulating services, and 3.7% on recreation, education, cultural heritage and other social services. Another 22.6% of forestlands are managed with a different specific focus, lack a focus, or have a focus that could not be classified. The remaining 24% are managed for multiple uses to capture value from a broader set of ESs.

The emphasis on managing forests to produce extractive products rather than nonmarket ESs reflects market realities. Many forest managers want to generate cash income from the sale of market-oriented goods and services, such as logs and fuel wood. Over time, these actions have diminished the productivity of ESs associated with nonmarket goods and services. This shift favoring market goods and services can occur even when their value is less than the value of the lost nonmarket goods and services, so that the total value of all ESs diminishes. Historically, a common approach for arresting or avoiding such outcomes has entailed placing prohibitions on logging and other activities in protected areas. This approach often proves ineffective, however, because enforcing the prohibitions can become expensive and subject to corruption.

Payments for Nonmarket ESs

Over the past several decades, another approach has evolved ([United Nations Development Programme, 2018](#)). It involves providing forest managers with cash or other incentives to sustain a forest's ability to produce nonmarket ESs. These incentives, commonly called payments for ecosystem services (PES) can take several different forms. For example, a national government might provide tax subsidies to forest landowners that help conserve water quality in streams by not logging trees in riparian zones. A downstream community vulnerable to flooding might seek to reduce peak flood flows by paying an upstream community to not log trees that intercept and slow the runoff from storms. A corporation seeking to develop expensive homes on a parcel of land might pay the owner of adjacent forestland to forgo logging of trees that will increase home prices by providing an aesthetically pleasing view. A conservation group might provide cash income, health services, and other assistance to induce an indigenous to help prevent outsiders from logging trees illegally.

The PES approach generally seeks to reshape powerful market forces so that they encourage the production of diverse ESs. When successful, it creates a new market. In this market, landowners and forest managers sell services that produce clean water, reduce peak floods, attractive views, etc., and entities that see the value of these things become buyers. In concept, these new markets should work as effectively and efficiently as the markets that govern selling and buying of countless goods and services every day. In practice, though, efforts to establish these markets often fall short. They often have difficulty defining what is being bought and sold. Many ESs are hard to define and measure precisely, making it difficult to develop a sound seller-buyer contract and, once executed, to determine that all parties are living up to its terms. Evolving science likely will diminish these difficulties over time, but it will not address another problem. PES proposals often encounter broad resistance because they seek to replace the polluter-pays-principle, a socio-political structure in which a polluter must pay society for degrading ESs, with the beneficiary-pays-principle, in which society pays a landowner not to degrade the ESs. Those who resist PES proposals might see opportunities to use the evolving science in litigation aimed at broadening the application of the polluter-pays-principle to punish landowners that harm society by degrading nonmarket ESs.

Conclusion

Forests provide many benefits to people throughout the world, but they cannot produce all types of benefits to all the people all of the time. Activities that emphasize the production of some benefits for some groups can diminish a forest's ability to produce other benefits for other groups. Many forests now produce a narrower set of benefits than in the past, with an emphasis on the production of logs, fuel wood, and other market-oriented goods. This emphasis yields direct socioeconomic benefits for commercial entities that use these products, but harms those who no longer can realize benefits from the enjoyment, consumption, or use of components of the forest that are displaced by the commercial production. Careful research, especially in the Pacific Northwest of the U.S., demonstrates that the overall harm to society can outweigh the value of the logs produced by industrial timber operations.

The widespread emphasis on extracting commercial products from forests occurs because these products can readily be converted into cash through market transactions. Efforts are underway to develop similar opportunities for forest managers to receive cash for producing benefits that currently are not traded in markets, through processes that generally receive the label, payments for ecosystem services. The establishment of such payments has been slowed, though, by technical difficulties in ensuring that forest managers satisfy contractual obligations to deliver the specific services and by philosophical opposition to paying managers when they produce these services rather than punishing them when they don't. Anticipated improvements in the ability to measure the impacts of management activities on a forest's ability to produce various services, and to measure the harm resulting from the diminution of noncommercial benefits, may promote both efforts to pay managers to produce these benefits and efforts to punish those who don't.

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Threats to Mekong Forest Ecosystems: Last Chance for the Indo-Burma Biodiversity Hotspot

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Abbreviations

CEPF Critical Ecosystem Partnership Fund
LULUCF Land Use, Land-Use Change and Forestry
VFA Voluntary Forestry Agreements
WTO World Trade Organization
WWF Worldwide Fund for Nature

Abstract

The Mekong region (Cambodia, Laos, Myanmar, Thailand, Vietnam) forms the majority of the Indo-Burma Biodiversity Hotspot, one of Earth's richest, most diverse terrestrial biomes. Its forests and wildlife survived various modern conflicts and for centuries enabled traditional peoples to live from their bounty. Since 2000, more than 12 Mha has been lost, and some 1.3 Mha of the most valuable forest ecosystems are now being destroyed each year. (In 2018 an additional ~1 Mha was destroyed.) As Earth faces mounting pressure from global warming, forest habitats, wildlife and biodiversity in the Mekong are being rapidly destroyed by industrial-scale illegal logging that precedes agricultural expansion for export commodities, made possible by uncontrolled timber trafficking and exports. Current prospects for improvements in forest governance and biodiversity conservation are dim, given authoritarian governments, institutionalized corruption at all levels and lack of space and safety for genuine civil society participation.

Introduction—Historical and Cultural Context

Scenes from Stanley Kubrick's 'Apocalypse Now' brought to the world, a visceral impression of the dense tropical forests in which lived many upland tribal peoples. Until then sporadic TV coverage depicted forests engulfed in flames as incendiary bombs blasted the landscapes, marking perhaps the beginning of serious destruction of old-growth forest ecosystems that occupied over half the Mekong region's land area only half a century ago.

Forests are deeply woven into everyday regional cultural and spiritual beliefs—from upland animists to lowland Buddhists, even for those now living in large urban areas—and play a special, often sacred role in their lives. Almost all rural villages in the region have sacred forest groves and temples. Widening forest destruction, including logging sacred forests, results in enduring cultural, spiritual and economic suffering, especially for traditional communities. It is not possible here to explore the manifold effects of forest destruction and biodiversity loss on the millions of people who once lived in the region's forests. These include widespread loss of lineages, cultures and languages, effects on gender roles, loss of livelihood resources and dispossession.

Post-WWII newly independent national governments claimed responsibility for enacting and enforcing laws governing allocation of land and how it is used. They asserted ownership and control of almost all forested land, classifying it for production, protection or conservation; the latter including national parks and biodiversity protected areas.

Over the last two decades over 12 million hectares (Mha) of forests, the majority dense or primary forests, in the region has been destroyed, a historic and continuing failure of governments to protect what is considered to be national heritage and a public good. Ever expanding forest destruction has resulted in impoverishment of thousands of forest-dwelling ethnic groups, theft of their lands, livelihoods and heritage, including their skills as forest managers.

Until about two decades ago forest destruction was, arguably, mainly driven by agricultural expansion to feed growing populations. But in the last two decades the scale and rate of forest destruction has far outstripped meeting regional needs, partly due to slowing population growth, even after taking into account rising affluence. In brief, governments have presided over the destruction of their nations' natural heritage, all too often for personal gain.

This study commences with an assertion that the main threat to regional forest ecosystems is illegal logging, to which must be added massive illegal trafficking in unprocessed wood. Approximately half of the wood exported from the region is unprocessed logs and sawnwood, which according to existing regional export bans is illegal. Approximately 90% of this is imported by Chinese businesses, and officially documented by Chinese customs authorities.

This conclusion parallels Eyster's (2019) in 'Last Days of the Mighty Mekong'—published just after this chapter was drafted. Conserving the Mekong's riparian ecosystems and cultures, as with Mekong's forest ecosystems, depends on China ceasing its practice of increasingly exploiting its neighbor's natural heritage for its own economic benefit.

If Chinese companies were prevented from importing massive amounts of wood from old-growth forests, the reduction in demand would about halve the area being logged annually in the Mekong region. This would reduce regional forest destruction to about the level it was in 2008, before China became dominant importer of unprocessed wood from the Mekong's ancient forests.

The Mekong Region

The Mekong region (1.9 M km²) covers the majority and core of the Indo-Burma Biodiversity Hotspot (Mittermeier et al., 2004), with four forest biomes: tropical and subtropical coniferous, dry broadleaf forests, and moist broadleaf forests, and mangrove forests. The quality of Mekong forest ecosystems and species diversity were key criteria in nominating the region as a globally important Biodiversity Hotspot.

The Indo-Burma Hotspot (Fig. 1) includes all of Cambodia, Laos and Myanmar (Burma), and nearly all Thailand and Vietnam, plus parts of eastern Bangladesh, northeast India and southeastern China. Cambodia, Laos, Myanmar, Thailand and Vietnam form the majority of the hotspot. For several reasons these are grouped as the 'Mekong region.' The Mekong River watershed (0.9 M km²) encompasses over a third of the overall area.

The forests, rivers, wetlands, and limestone karsts are habitat for some 7000 endemic plant and 1048 animal species. As of 2019 there were approximately 2000 threatened species in the Mekong region: 250 mammals, 230 birds, 186 reptiles, 70 amphibians, 349 fishes and 554 plant species (IUCN, 2019).

The Mekong River connects all five countries; forests are logged, forest products traded (wood, wildlife, plants), poached and smuggled by people from all five countries (and others). Forest destruction in one affects biodiversity downstream and in neighboring countries. The region's national borders remain 'porous' for people and goods and even more porous and interconnected with regard to natural stocks and flows.

Mekong Forest History

This study focuses on forest cover changes in the Mekong Region in the 21st Century. At the beginning of the 20th century a range of estimates suggests that dense moist and dry tropical, dry upland, flooded and mangrove forests—covered about 90% of the ~2M km² regional landscape—about 66 Mha of lowland and 102 Mha of upland forests. In the uplands above 300 m (55% of the region) forest cover may have been as high as 95% until the early 1900s (Robichaud et al., 2009).

It is relevant to note environmental and social impacts of the French (1946–54), and American (1954–75) wars in Indochina—widespread bombing, defoliation and forced resettlement severely disrupted forest ecologies, traditional swidden and forest management practices in Vietnam, Cambodia and Laos. After the wars, governments in the region embarked on implementing 'forest conversion' with the purpose of converting forest resources and land into capital (Peluso et al., 1995), to be exploited for profit, often by outsiders.

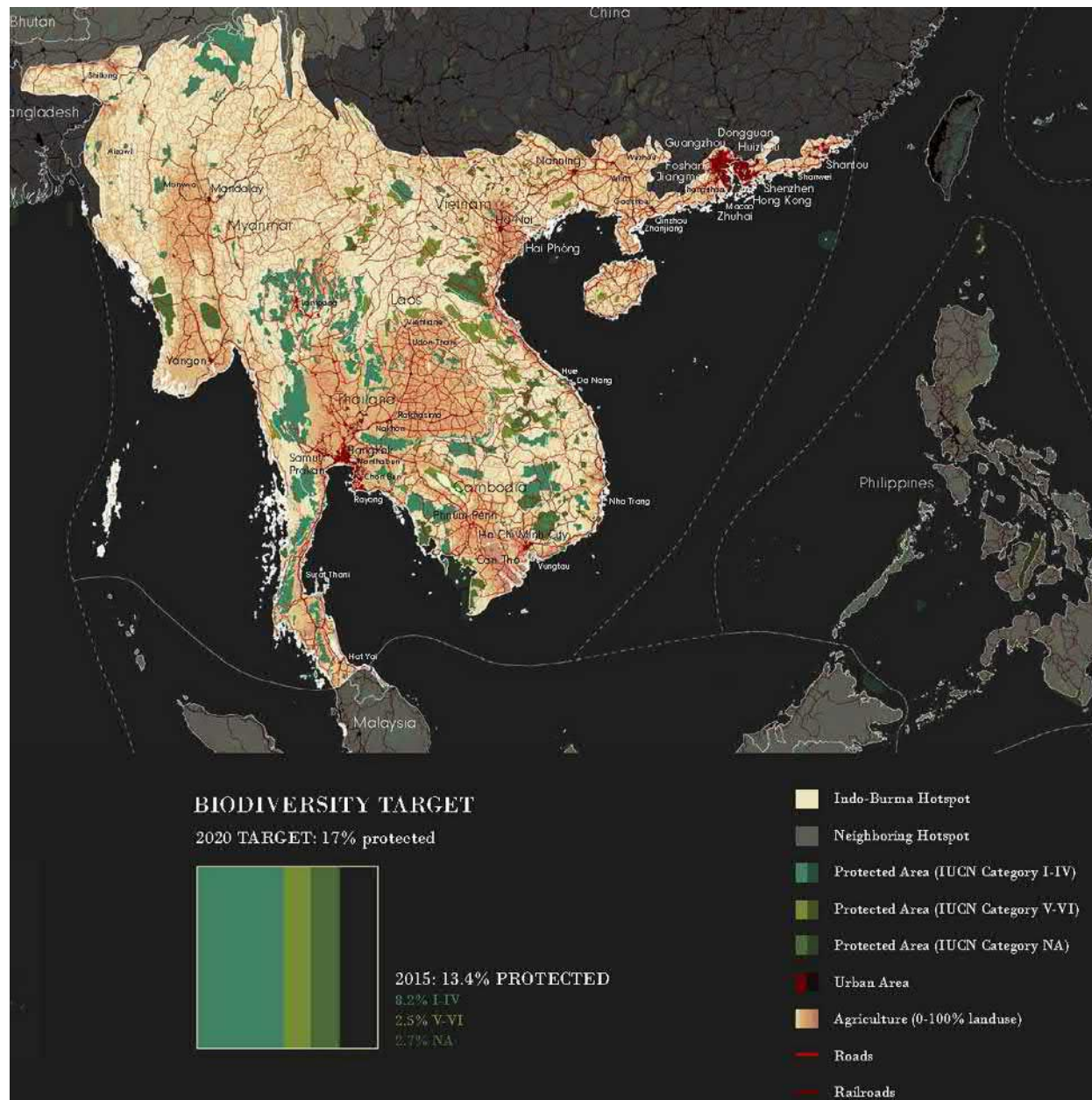


Fig. 1 The Indo-Burma Hotspot. Notes: Green = protected areas (IUCN I-VI & NA), red areas = urban, yellow-brown areas = agriculture (0–100%), red lines = road network. From Weller, J.W., Hoch, C. and Huang, C. (2017) Atlas for the end of the world, <http://atlas-for-the-end-of-the-world.com>.

Using Thailand as an example, tropical wet and dry forests (38 and 51 Mha respectively) covered approximately 75% of the landscape in 1913. This declined to about 30 Mha by the late 1950s, and only 20 Mha remained by 1974 (Delang, 2006). By the 1970s almost all of dipterocarp and dry evergreen forests on Thailand's vast Korat plateau had been replaced by a mosaic of irrigated and rainfed rice fields, plus maize, soy and sugar (Rambo, 2017). The Khorat Plateau, the large 'white' area in central Thailand in Figs. 1 and 3 was historically mixed seasonal forest ecosystems (White, 1995) with significant populations of elephants and tigers.

Since the 1970s the Mekong region has lost one-third of its forests and, based on current trends, it is likely to lose another third by around 2030 (Carroll, 2018). Since 2001, destruction of 8 Mha of dense forests (> 75% canopy) and the flora and fauna within them, has substantially increased overall biodiversity threat levels.

Forest destruction since then, primarily for commercial agriculture expansion, but also uncontrolled industrial and illegal logging, hydropower dam construction and mining, has greatly reduced old-growth forests that covered most of the land for about 10,000 years. The last 20 years have seen the rate of forest destruction in all five countries accelerate. Over 2014–18, destruction of forests with > 30% canopy cover amounted to 5.9 Mha. Current indicators point to the likelihood this will continue or increase in years ahead.

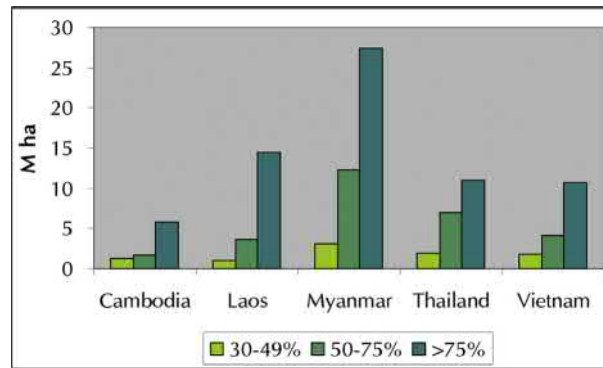


Fig. 2 Mekong region forest quality by percentage of canopy cover (2000). From GFW 2018: <http://earthenginepartners.appspot.com/science-2013-global-forest>. Accessed through GFW on 09Nov18. www.globalforestwatch.org.

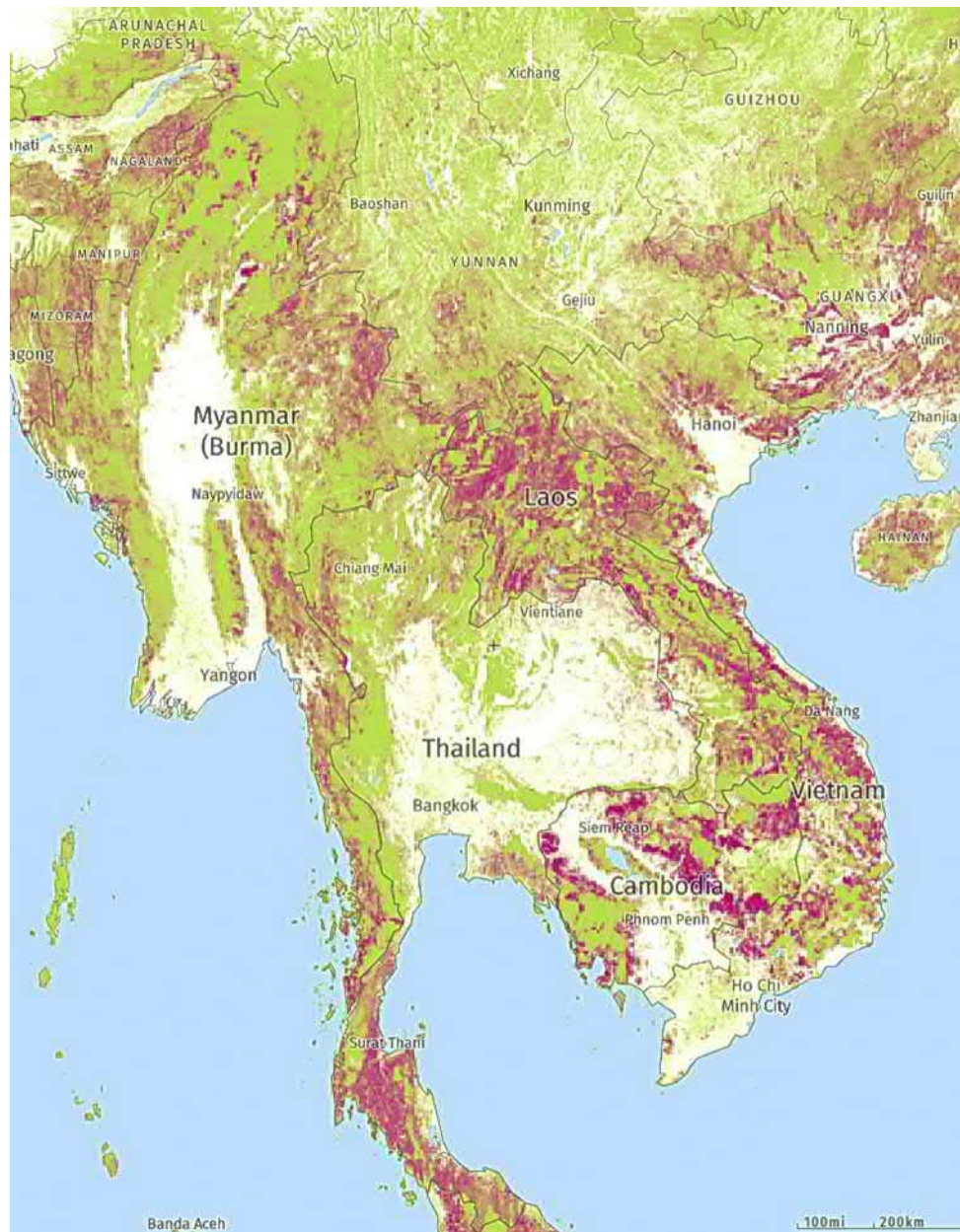


Fig. 3 Mekong region—forest destroyed 2000–17. Based on GFW 09Nov18. Notes: Areas with red stipple indicate forest cover (>30% canopy) lost over 2000–17; color intensity indicates greater total quantity of forest cover loss.

All five nations of the Mekong region are currently ruled by authoritarian/quasi-military governments, descendants of anti-colonial struggles. After 1975, new roads and technology enabled governments to extend their control to forested uplands populated by traditional ethnic communities. Closer state control and centrally dictated forest land zoning provided the means by which forests could be claimed as ‘state land’ and then logged.

Nominally logging requires permission, official or unofficial, from government agencies, traditional forest dwelling communities have no role or authority in this process. Authoritarian/military governments severely limit the rights and opportunities for citizens to oppose public and private ‘development’ projects likely to affect them ([Global Witness, 2013](#); [Transparency International, 2018](#)).

As a result, hundreds of thousands of people have been and continue to be forced from their ancestral homes, and alienated from their traditions, livelihoods and landscapes. Large-scale quasi-legal and illegal logging and timber trafficking have become the regional norm. Pervasive and deep seated corruption by political and economic elites appears to be the ultimate cause of unrestrained, illegal exploitation of the region’s natural heritage (see e.g., [EIA, 2019](#)).

More recently, rapid expansion of export agriculture continues to perpetuate the process of forest destruction for the benefit of elite national groups and foreign investors. As a consequence, hunger, protein and micronutrient malnutrition among formerly robust forest dwelling people, previously rare because of access to abundant and diverse forest foods, have become more widespread.

Satellite imagery shows other proximate threats include linear infrastructure: roads, railways and power lines, as well as hydro-power development, mining and urbanization. While these are important, in terms of area logged, these are relatively minor compared to agricultural expansion preceded by illegal logging.

In 2011 it was estimated only 5% of Indo-Burma Hotspot habitats remained in “pristine” condition, another 10–25% were considered damaged to varying degrees, but still “ecologically functional” ([CEPF, 2012](#)). Since 2011, the situation has worsened, but full follow-up studies have yet to be undertaken.

By 2014, lowland forests covered only 18 Mha (21%) and upland forests 59 Mha (55%), or 40% of the Mekong region. In brief, some 100 Mha of forest were destroyed in just over 100 years. These historical changes provide background for the discussion on forest cover changes since the beginning of the 21st century to the present.

[Hoare \(2015\)](#) estimated that some 80% of wood products exported from Laos in 2013, came from illegal logging. [Forest Trends \(2018\)](#) documents huge volumes of wood imported by China (and other countries) over 2006–16 from the region, despite export bans being in place. A third source ([Smirnov, 2015](#)) gives detailed evidence of fraudulent documentation and other means used to smuggle some four times the annual national quota of logs and sawnwood from Laos into Vietnam in 2013 and before. A series of reports by the [EIA \(2010-19\)](#) provides additional detail on smuggling from Cambodia and Laos into Vietnam.

In short, there can be little doubt widespread corruption facilitates massive illegal logging and smuggling, and may be the ultimate and greatest current and near-term future threat to the region’s forests. Corruption reduces government revenues from royalties and taxes available for funding basic needs such as health and education services. Without pervasive corruption by government officials—civilian and military—at all levels, large-scale illegal logging and smuggling could not occur.

Key Question

The key question regarding threats to Mekong forest ecosystems and biodiversity is: *What has caused the escalation of forest degradation and destruction during the last 20 years?*

Assessing Forest Destruction in the Mekong Region

The initial global dataset ([Hansen et al., 2013](#)) used by GFW (and others) covered the period 2001–12, it now extends to 2018. It was one of the first satellite-based analyses to systematically document global forest destruction (deforestation), based on 30-m resolution Landsat imagery. This dataset includes all forest canopy cover classes (from < 25% to > 75%). This and two sources noted below have estimated classification accuracies of about 95%.

GFW’s work provides a near current, ecologically valid perspective on changes in land and forest cover, at global, national and provincial levels. Their forest definition differs from FAO’s and relies on: ‘biophysical criteria (height, canopy cover and extent of trees) ... monitors all forms of tree cover including natural forests and tree plantations.’ ([GFW, 2016](#)), it defines a ‘forest’ as an area with > 30% canopy cover and at least 5 m in height. It includes all types of forest cover, official and unofficial, based on pixel-by-pixel and grouped classification and analysis of Landsat imagery; it is preferred by environmental scientists and ecologists.

The following analyses are based on GFW’s data and analysis, supplemented by deeper analysis of the main causes (drivers) of forest loss by [Curtis et al. \(2018\)](#) and [Zeng et al., 2018a](#).

The Mekong region lost over 12 Mha (11.3%) of forest with over 30% canopy cover between 2000 and 2017, roughly equal to two-thirds of the total land area of Cambodia. The area of loss was greatest in Myanmar and least in Thailand; Cambodia lost a quarter of its remaining forests during this period.

Almost all level or undulating land along the Mekong mainstream and tributary valleys and on plateaus has long been cleared for agriculture. Old-growth forests survive only in remote and upland areas. The region's push for hydropower has flooded many river valleys allowing access to illegal loggers and poachers.

Forest destruction has expanded into formerly intact remote upland forests during the last decades, accelerated by the region's integration into global markets for land-based export commodities which now cause significantly more forest destruction than industrial logging. New mines, hydropower dams and reservoirs, and increasing forest fragmentation by new and upgraded roads worsen the situation.

As in over 100 other countries, forest clearance for commodity production is generally preceded by (illegal) logging operations, though it may not be classified as such; Lebloisy et al. (2016) show agricultural commodity expansion for export is closely related to deforestation. In all five Mekong countries government policies plus donor support, have been promoting logging as an approach to rural and regional economic development, despite mounting evidence that human health and biodiversity are being adversely affected.

Regional Forest Destruction

Fig. 4 illustrates the area of forest canopy cover classes for the five countries in 2000, the baseline for analyses of changes over 2001–17. Of total regional forest area (107 Mha), one quarter was 'medium' forest (canopy cover 50–75%) and two-thirds of the area 'dense' forest (canopy cover > 75%)—Laos had the highest and Thailand the lowest percentage of dense forest.

GFW's analysis (Fig. 2) has recently been complemented by analyses of 'dominant drivers' of forest loss conducted by Curtis et al. (2018).

Intense forest destruction, while common throughout the region, has clearly been concentrated in specific, usually upland, areas in each country, a pattern confirmed by Zeng et al. (2018b). The largest portion of forest losses (77%, > 6 Mha over 2000–14) were in the uplands (> 300 m asl), compared to lowland losses of ~4 Mha—from a total over 9 Mha. The greatest losses were in:

- Cambodia—across a broad central swathe and close to the Thai and Vietnamese borders;
- Laos—all across the north and close to the Chinese and Thai borders;
- Myanmar—northeast uplands close to China and the southern region;
- Thailand—northwest uplands and most intensively in the southern peninsular; and
- Vietnam—northeast, close to China and throughout the central uplands from north to south.

Destruction of forest with over 30% canopy cover amounted to 12.1 Mha over 2000–17. Proportionately, losses in Cambodia were the greatest—almost a quarter of its 2000 forest area—Laos and Vietnam each lost about one seventh of their forests. In terms of area, Myanmar lost the greatest amount, a quarter of total regional losses (Table 1). High quality old growth forest (> 75% canopy cover) comprised the great majority of regional losses.

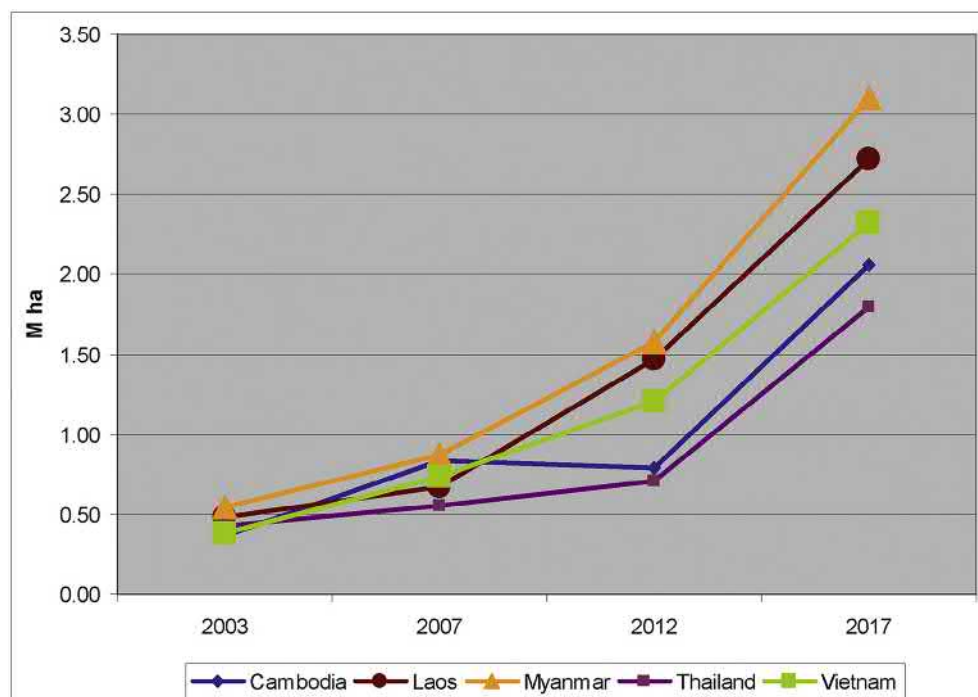


Fig. 4 Mekong region—area of forest ecosystems with over 30% canopy cover destroyed 2003–17. Source: Based on data from Global Forest Watch. 'Tree cover loss in Cambodia, Laos, Myanmar, Thailand, and Vietnam'. Accessed on 09Nov18 from www.globalforestwatch.org.

Table 1 Mekong region—forest cover losses 2000–17.

Country	2000	2017	Loss 2000–17	
	Tree cover (> 30%) Mha	Mha	Mha	%
Cambodia	8.81	6.75	2.06	23.4
Laos	19.13	16.42	2.71	14.2
Myanmar	42.86	39.76	3.10	7.2
Thailand	19.96	18.17	1.79	9.0
Vietnam	16.55	14.14	2.42	14.6
Mekong	107.32	95.24	12.08	11.3

Notes: Calculations based on data from Global Forest Watch. 'Tree cover loss in Cambodia, Laos, Myanmar, Thailand, and Vietnam'. Accessed 09 Nov 18 from www.globallforestwatch.org.

By 2008 the Mekong region was losing almost 0.5 Mha of forests annually. After 2014 this jumped to 1.0 Mha year⁻¹ and in 2017 to 1.3 Mha year⁻¹. Since 2001, and in each subsequent 5-year period, the area of forest destroyed and rate of loss have doubled every 5 years—it is now equal to total regional forest destruction during the first 5 years of the 21st century—Figs. 4 and 5.

Stop Press: In 2018 an additional 1.1 Mha of forest was destroyed, nearly two-thirds being medium forest and one third dense (possibly primary) forest.

Country-Level Forest Destruction

Prior to 2003 the area of annual forest destruction in each country was less than 50,000 ha year⁻¹, and total regional losses about 0.2 Mha year⁻¹ (GFW data). By 2004 it had risen to 60–100,000 ha year⁻¹ and total regional losses to over 400,000 ha year⁻¹. In only 5 years (2013–17) Myanmar lost over 3% of its remaining forests, Laos and Vietnam only slightly less.

In 2003 the rate of loss (Fig. 5) in all five countries was about the same, over 2012–17 losses in Cambodia increased rapidly to about 30% of its remaining forest area, with Laos and Vietnam following a slightly slower trajectory.

Roughly half the Mekong region is above 300 m in altitude. In 2000, in four countries 58%–94% of forests (64 Mha) were in the uplands; Cambodia was the exception with only 20%. By 2014 upland forest area had declined to 59 Mha. Upland forest losses in these four countries ranged from 61% in Thailand to 94% in Laos (Zeng et al., 2018a).

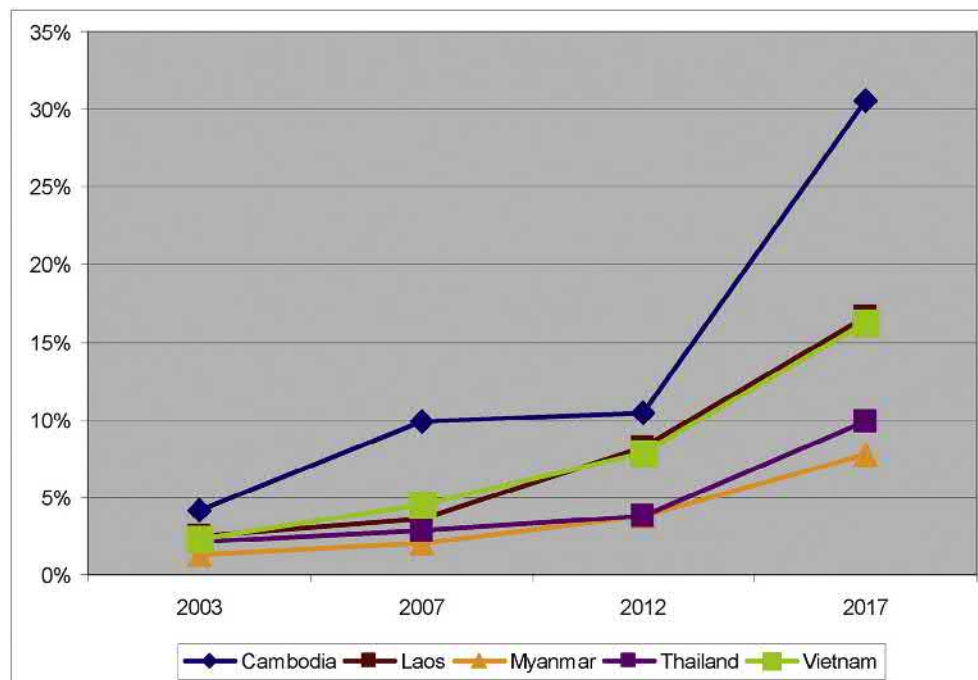


Fig. 5 Mekong region—rate of forest ecosystems destroyed—2001–17. Based on data from Global Forest Watch. 'Tree cover loss in Cambodia, Laos, Myanmar, Thailand, and Vietnam.' Accessed on 09Nov18 from www.globallforestwatch.org.

Analyses of satellite data identified agricultural expansion, preceded by illegal logging, in regional uplands as the cause of about 90% of forest destruction (ibid). This included primary and protected forests, recovering secondary forests, and former swidden lands.

Primary Tropical Forest Ecosystems Destroyed

Percentage canopy cover was used as a proxy for forest quality, species richness and resilience. Forest ecosystems with over 50% cover are considered to be old growth forests; those with over 75% cover are often intact primary forests.

Analysis for 2000 and 2017 compared the relative quality of forests destroyed (total ~12 Mha) based on density of canopy cover. At a regional level, losses were greatest in dense, high quality forests which suffered two-thirds or more of total losses, and in medium density forests which lost about one-quarter of their total area. This broad, long-term pattern of accelerating destruction of high quality forests is illustrated in Fig. 6.

Mangrove Ecosystem Destruction

Coastal mangrove ecosystems are vital for sustaining aquatic production and a critical element in subsistence food supply. Additionally, mangrove coastal barrier forests have become increasingly important as sea levels rise and the frequency and intensity of extreme weather events increase due to global warming.

All Mekong countries except Laos have mangrove forests, these covered some 1 Mha in 2000. By 2014 about 100,000 ha had been lost to different forms of land use change. Since 2014 the trend of habitat loss has likely continued and the rate of loss increased (Richards and Friess, 2016).

In Myanmar mangroves ecosystems were destroyed by conversion to rice fields and aquaculture, to a lesser though significant extent, by wood, pole and fuel harvesting and charcoal production (42,000 ha). In Cambodia aquaculture (11,000 ha) and oil palm in Thailand (43,000 ha) were the main causes, Vietnam lost the least area (3000 ha). Urbanization was not a significant factor (ibid).

Erosion of the Mekong Delta in Vietnam, due to upstream dam construction is leading to changes in Mekong hydrology causing reductions in sediment transport and deposition and nutrient flows, endangering mangroves and other forests in the delta (MRC, 2017) and is exacerbated by rising sea levels.

Loss of Flooded Forests—Tonle Sap, Siphandon and Mekong River

The Great Lake Tonle Sap in Cambodia covering some 3500 km² is long and shallow in the dry season. At the peak of the monsoon it expands to around 14,500 km² and its volume increases by ~40 times to 1.5 km³. Probably the most productive freshwater fishery in the world, some 500,000 tons of fish are harvested during and after the monsoons.

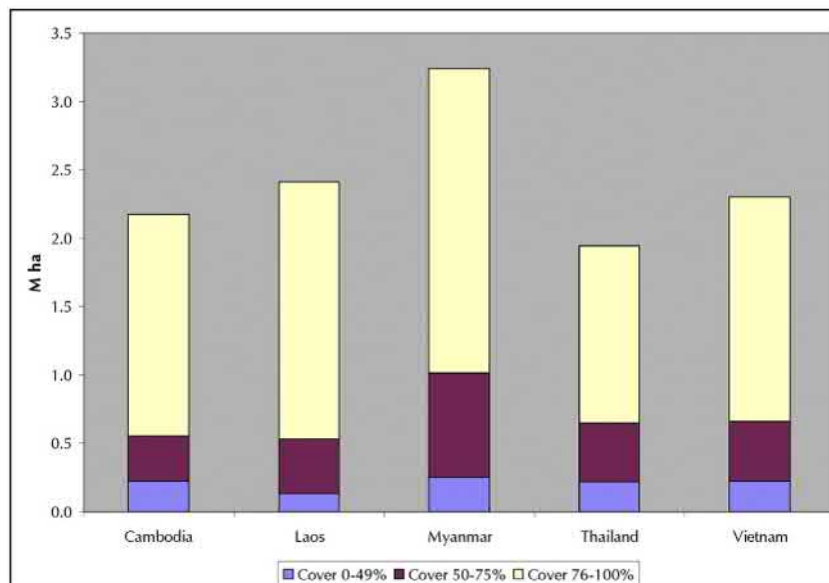


Fig. 6 Mekong region—quality of forest ecosystems destroyed—2001–17. Based on data from Global Forest Watch. 'Tree cover loss in Cambodia, Laos, Myanmar, Thailand, and Vietnam'. Accessed on 09Nov18 from www.globalforestwatch.org. Note: Forest destruction has been greatest in the highest quality regional forests—equating with the most significant cause of rapidly intensifying habitat and biodiversity losses.

The permanent lake is surrounded by ‘flooded forests’ of freshwater mangroves and water-tolerant trees and shrubs. These are breeding grounds and nurseries for hundreds of species of fish and habitats for a broad range of birds and other wildlife. Nutrients washed into the lake and detritus from the forest make the water nutrient-rich. Historically this flooded forest covered some 7000 km², but due to clearing for agriculture and logging it is badly degraded and only about half of its former size.

Further upstream, seasonally flooded forests are situated just above the 20 m high Mekong falls (Khone Phapheng) on the geological fault at the Lao-Cambodian border, and downstream on the braided section of the Mekong mainstream near Stung Treng in Cambodia. All these are under mounting pressure. No data is available on the extent of degradation or destruction.

Dominant Causes of Forest Destruction

Among the more insidious and corrupt practices is the granting of large agriculture concessions on forested lands. This results in destruction (logging) of forest ecosystems prior to land preparation for plantation crops or trees. The area logged, commonly illegally, and volume of wood removed for sale prior to clearing is usually not considered in concession contracts or is vastly under-represented.

Forest losses due to the main causal factors increased variably at 12–18% per year. Fig. 7 illustrates forest destruction by the dominant causes between 2001 and 2015, with sharp increases in the rates of loss in 2009–10 and again in 2013–14, and Fig. 8 forest destruction by country and cause at the beginning and end of this period.

The trend of increasing forest destruction appears nearly certain to continue, facilitated, albeit indirectly, by government policies, strategic donors, (e.g. Asian Development Bank [ADB]), and private investors. All encourage agricultural commodity and forestry exports and greater global market integration (ADB, 2014). Rising forest losses parallels continuing implementation of ADB’s so-called Greater Mekong Sub-Region (GMS) strategy and the major infrastructure projects it supports and/or funds.

Figure 9 illustrates regional distribution of forest destruction by three dominant causes for the period 2001–15; color intensity indicates severity. Rotational swidden agriculture is widespread throughout the region and concentrated in highland areas (>300 m). These regenerate naturally as secondary forest after being left fallow for at least 5–7 years (Fox 2000). Forest losses to urbanisation are minor (<1%) and barely visible (regional total ~24,000 ha over 2001–15).

Infrastructure Development as an Ecosystem Destroyer

Authors stress different but significant threats to regional forests (e.g. Kissinger et al., 2012a,b, Costenbader et al., 2015). Those commonly cited are rarely quantified or prioritized. The key question is the relative scale of these threats, singly or in combination. One threat infrequently mentioned is habitat fragmentation by infrastructure. Some contend it is as great a threat as forest destruction (Fraser, A. pers. comm.; Saravia et al., 2018). It is anticipated increasing destruction and fragmentation of forest habitats and connectivity will result from planned infrastructure projects, leading to cascading and widening negative effects on ecosystems and biodiversity (Balmford et al., 2015).

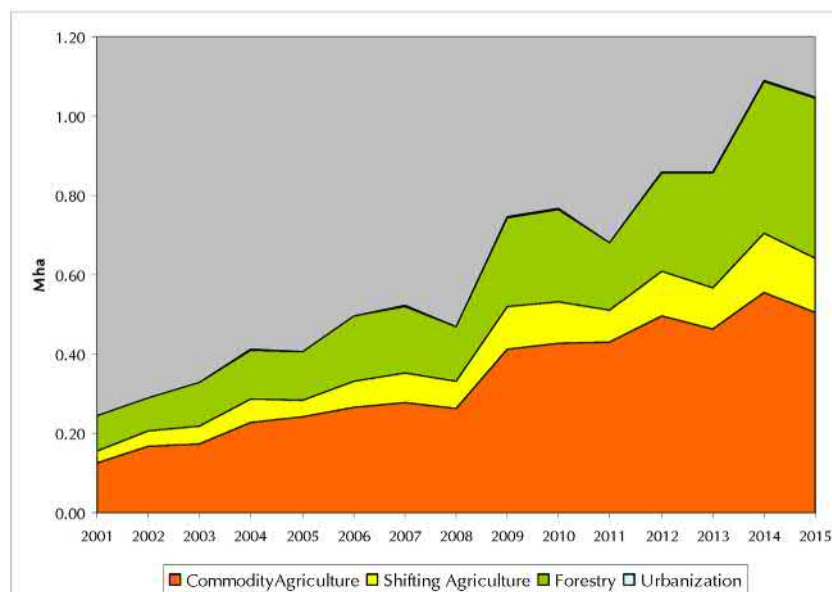


Fig. 7 Mekong region—dominant causes of forest destruction 2001–15. Based on data from Global Forest Watch. ‘Tree cover loss in Cambodia, Laos, Myanmar, Thailand, and Vietnam’. Accessed 09Nov18 from www.globalforestwatch.org.

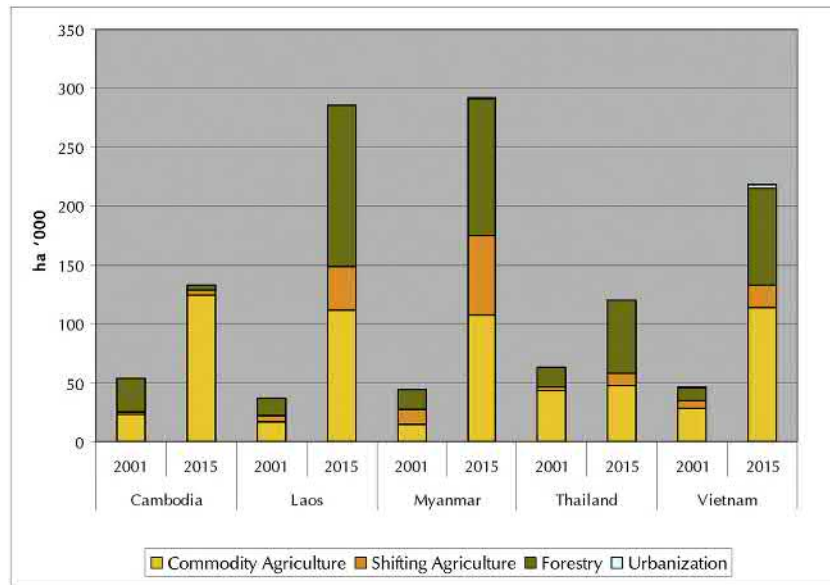


Fig. 8 Mekong region—forest destruction by dominant causes—2001 and 2015. Based on data from Global Forest Watch. ‘Tree cover loss in Cambodia, Laos, Myanmar, Thailand, and Vietnam’. Accessed on 09Nov18 from www.globalforestwatch.org.

While, in theory at least, logged primary forests can recover as secondary forests, along with remnants of biodiversity, major physical barriers like roads, railways and energy corridors permanently fragment landscapes, endangering, inhibiting or preventing wildlife movement essential for accessing (seasonal) food sources, water and salt, and species dispersal or migration for reproduction. Moreover, roads and reservoirs provide easy access deep into forest landscapes for hunters and poachers, well known as major threats to wildlife in remaining old-growth forest ecosystems (e.g. Hill et al., 2011; Kleinschroth et al., 2019). ‘When a new road penetrates intact forest, it can facilitate illegal deforestation, poaching, fires and land investors ...’ (Laurance, 2018).

ADB (2012) is an important funder of infrastructure development via its GMS development strategy. For two decades improving transport networks to facilitate domestic and international trade has been high on the agenda of ADB and other donors, and lies at the core of ADB’s GMS strategy of improved ‘connectivity’ (Stone and Strutt, 2009). The negative effects of new roads facilitating illegal logging, poaching and trafficking was recognized over a decade ago (ADB, 2008). Negative impacts on forest integrity and connectivity have significantly increased since then (recall the Thai road network depicted in Fig. 1).

Central to China’s new Belt and Road Initiative (BRI) in the region is a north-south high speed railway running through Laos and Thailand, and possibly onward through Malaysia to Singapore, cutting a swath through some of the remaining primary forests in Laos and displacing thousands of farming families. Rail traffic is a major danger to both humans as well as domestic animals, elephants and other wildlife. Broadly, BRI infrastructure investments present a series of serious environmental assessment and management problems, including directly destroying, further fragmenting and increasing access for logging in the remaining forest landscapes (Ascensão et al., 2018). These risks have not yet been properly assessed.

Rapid Rise of a New Threat

The rapid rise and increasing scale of regional forest destruction suggests a new threat emerged in the last decade. Commercial wood from large areas of forest, nominally being cleared for agriculture, is being exported from the Mekong in massive quantities. To explore this, wood export-import data for 2000–17 were analyzed using UN trade data (<https://comtrade.un.org>).

The two largest categories of wood exports from the Mekong region are unprocessed logs and sawnwood, from about 2010 onwards accounting for over half the total. Various bans on export of ‘unprocessed timber’ from the region have been in place since the late 1980s, though enforcement has usually been absent or minimal. Cambodia banned export of ‘timber larger than 25 cm’, i.e. logs and sawnwood in 1996; Laos banned exporting any wood not ‘finished and fully processed’ in 1989, reactivated in 2015; Myanmar banned export of ‘raw logs’ in 2014, Thailand did so in 1989, and Vietnam banned export of logs and ‘sawn timber’ from natural forests in 1992 (WRI/Forest Legality, 2018). In essence these bans cover all wood from natural forests categorized under the UN Commodity Trade Harmonized System as HS4403 (logs) and HS4407 (sawnwood)—making export illegal.

Under WTO rules whether goods are ‘legal’ or ‘illegal’ is not an issue for countries which do not have voluntary bilateral agreements on wood ‘legality’, for example, a Voluntary Partnership Agreement banning log and sawnwood exports or imports. However, wood imports (legal and illegal) are recorded by customs officials, as governments need this data to calculate import duties and

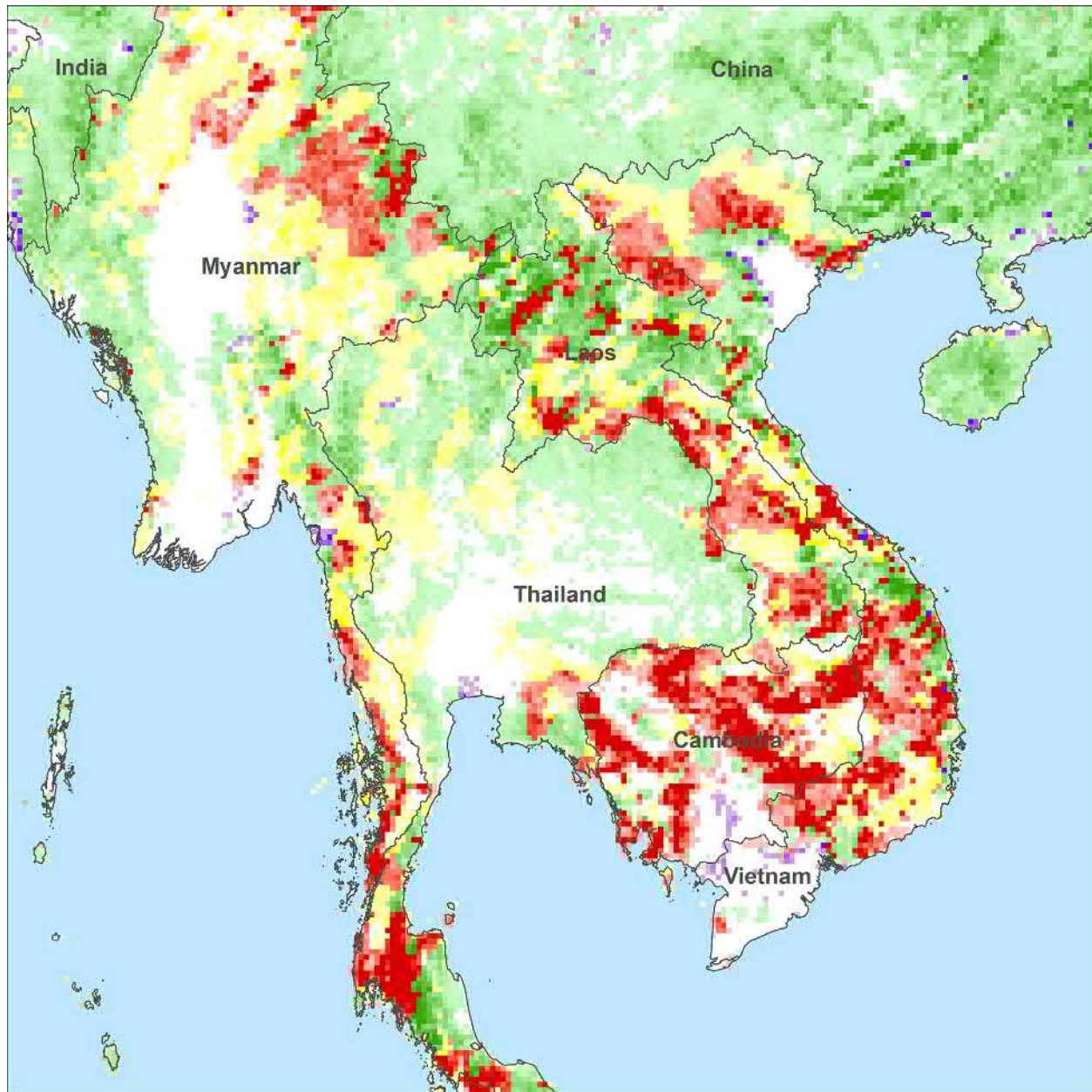


Fig. 9 Mekong region—forest destruction by dominant cause—2000–15. Notes: Each colored square 10 km × 10 km = 100 km². Dominant deforestation drivers: red = commodity production, green = industrial logging, yellow = shifting agriculture (swidden). Based on Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A. and Hansen, M.C. (2018) Classifying drivers of global forest loss. *Science* 361, 1108–1111, 14Sep18, Supplementary Materials: www.sciencemag.org/content/361/6407/1108/suppl/DC1.

taxation. No Mekong country had implemented such an agreement by 2017. As national government forestry and wood trade export statistics for the Mekong are known to be unreliable (Fraser, 2012) UN Commodity Trade statistics were used in preference.

The China Factor

The rapid rise in wood exports (recorded as imports) during 2000–17 (Fig. 10), shows a step-change beginning in about 2010. This was the result of radical increases in imports by Chinese companies of unprocessed wood (logs, sawnwood) and, commencing a few years later, particle and fiber board. By 2017 their combined volume accounted for 80%–90% of all Mekong wood exports—two-thirds of which were logs and sawnwood.

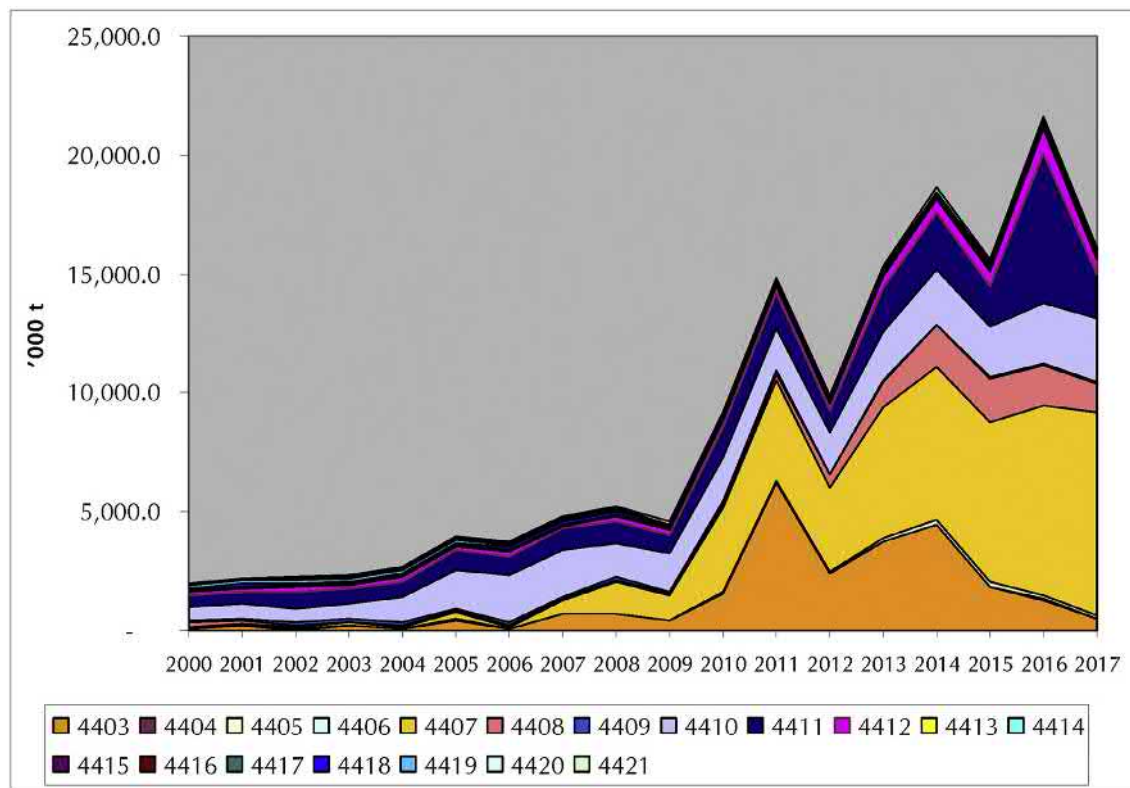


Fig. 10 Mekong region—exports of wood, all categories (2000–17). Notes: Y-axis '000 Tm. The two lower yellow and orange bands are those for logs and sawnwood (HS4403 and HS4407). Note: No adjustment has been made for approximately one-third loss of mass in rough sawing logs to sawnwood, this adjustment would increase the mass of HS4407 exports by this amount. From UN Comtrade Database (www.uncomtrade.un.org).

The apparent decline in exports of logs in 2017—lowest band in Fig. 10—may be due to incomplete data for 2017, but more likely due to logs (HS4403) being misclassified as sawnwood while still in the forest. Hence the significant increase in sawnwood (HS4407) trucked across land borders to evade log export bans (c.f. Smirnov, 2015).

The pattern of forest destruction, volume and value of exports for 2001–17 is illustrated in Fig. 11. There is a high, statistically significant correlation ($r = 0.912$, $f = 0.023$) between the annual area of regional forest destruction, volume and value of annual wood exports during this period. That is, forest destruction provided the wood for (illegal) exports, almost wholly going to China. These are the only two categories of wood in the Mekong region subject to export bans.

Total annual exports of all categories of wood grew from 2 Mt. (USD 2.81 bn) in 2000 to 16.13 Mt. (USD 8.52 bn) in 2017—a radical increase in exports of logs and sawnwood largely drove this change. Fig. 12 shows logs and sawnwood dominated exports over 2010–17, accounting for half or more (45%–73%) of total exports. The great majority of logs and sawnwood were destined for China.

Time series analysis directly links increases in area and rate of forest destruction to (illegal) exports from the region. The strong correlation ($r = \sim 0.70$ to > 0.90) between the volume and value of total timber imports by China, allows discussion to focus on the physical quantities involved.

It is widely accepted significant quantities of wood come from widespread illegal logging in national parks and protected areas, and from clearing for new hydropower reservoirs, mine sites and road upgrading; there are also many credible reports of regional military involvement (e.g. EIA, 2015).

Step-Change in Forest Destruction

Some 80% by volume and 60% by value of total wood exports from the Mekong region during 2000–17 occurred between 2010 and 2017. Rough logs and sawnwood have repeatedly been identified as the main products trafficked from Cambodia, Laos and Myanmar to Vietnam and China (e.g. EIA, 2015, 2017a,b, Forest Trends, 2010, Smirnov, 2015; Schape and Canby, 2018); Smirnov emphasized logs being consistently ($\sim 90\%$) miscategorised as sawnwood, i.e. 'processed wood,' to evade export bans.

Logs and sawnwood are eminently suited to trafficking, requiring no or minimal processing these can be transported directly across land borders as logs or rough sawn slabs. On-the-ground covert investigation over the last decade revealed the actual scale of illegal logging and trafficking (EIA, 2011, 2012, 2015, 2017a, 2018) even at local border crossings away from main roads.

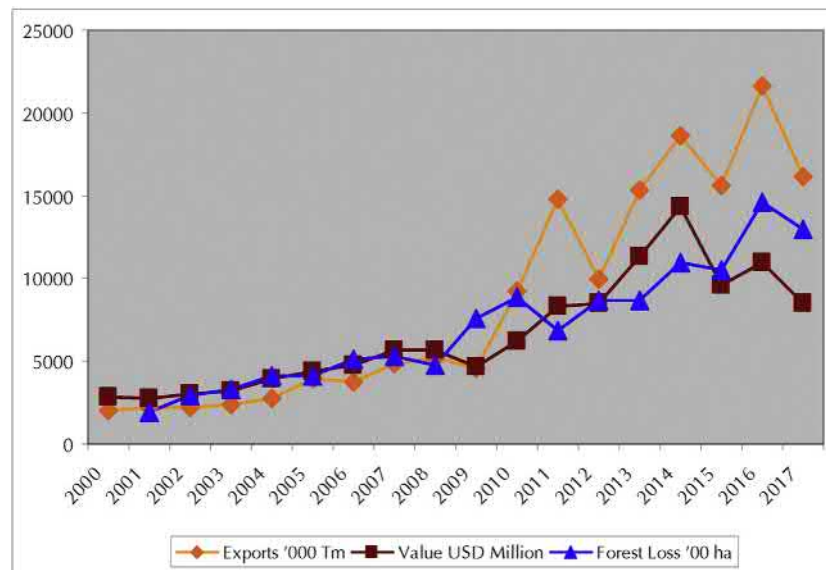


Fig. 11 Mekong region—forest losses, volume and value of wood exports 2001–17. Notes: Timber export data are based on reported global imports from the Mekong region. From GFW accessed 09Nov18. (www.globalforestwatch.org) and UN Commodity Trade Statistical Database (<https://comtrade.un.org>).

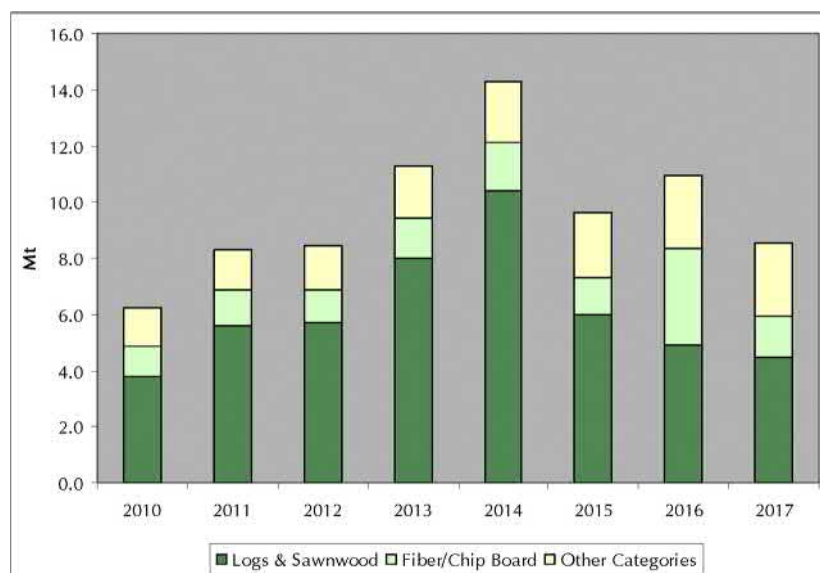


Fig. 12 Mekong region—wood exports by category 2010–17. Notes: Units: Millions of tons (Mt) or 10^6 . Logs and sawnwood (HS4403 & HS4407), particle and fiber board (HS4410 & HS4411), all 17 other timber categories (HS44**). From Calculated from UN Comtrade Database (<https://comtrade.un.org>).

In 2000, China imported about 26% of total exports of logs and sawnwood from the Mekong, in 2017 alone it imported 54% (8.7 Mt) of total wood exports from the region. During 8 years (2010–17) China imported over three-quarters of the region's total wood exports of 69 Mt. (Fig. 13), of this 54 Mt. (69%) were logs and sawnwood.

Wood Exports and Destruction of Primary Forests

For a large Biodiversity Hotspot like Indo-Burma a region-wide perspective is appropriate. From this perspective, it matters not whether forest destruction is legal or illegal—forest ecosystems and biodiversity are destroyed by both.

It is clear the majority of wood exports come from the Mekong's old-growth, often primary forests. The step-changes (2010 and 2014) in forest loss were almost completely the result of significantly increased and continuing destruction of the region's richest forest ecosystems, those with the most complex, complete ecosystems and, arguably, the best wildlife and biodiversity habitats.

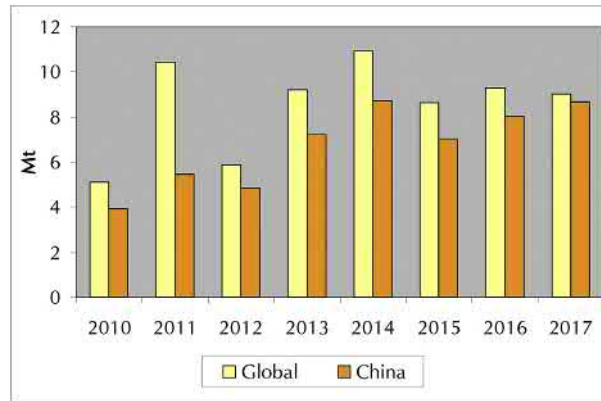


Fig. 13 Mekong region—global and Chinese imports, logs and sawnwood (2010–17). Notes: Units Mt. ($\times 10^6$); unprocessed logs and sawnwood. From Calculated from UN Comtrade Statistical Database (<https://comtrade.un.org>).

The combined annual wood exports by the five Mekong countries for 2001–17 illustrates this pattern (Fig. 14). The upper line traces the volume of wood logged and exported from dense (old growth) forest ecosystems.

Over 2001–17 there is a close correlation between volume of wood exports and area of dense old growth forests destroyed ($r = 0.879$, $f = 0.159$). While logging more valuable old growth forests makes financial sense for loggers and importers (who buy high quality wood cheaply), the result is ever more rapid destruction of the region's most ecologically important forests and biodiversity.

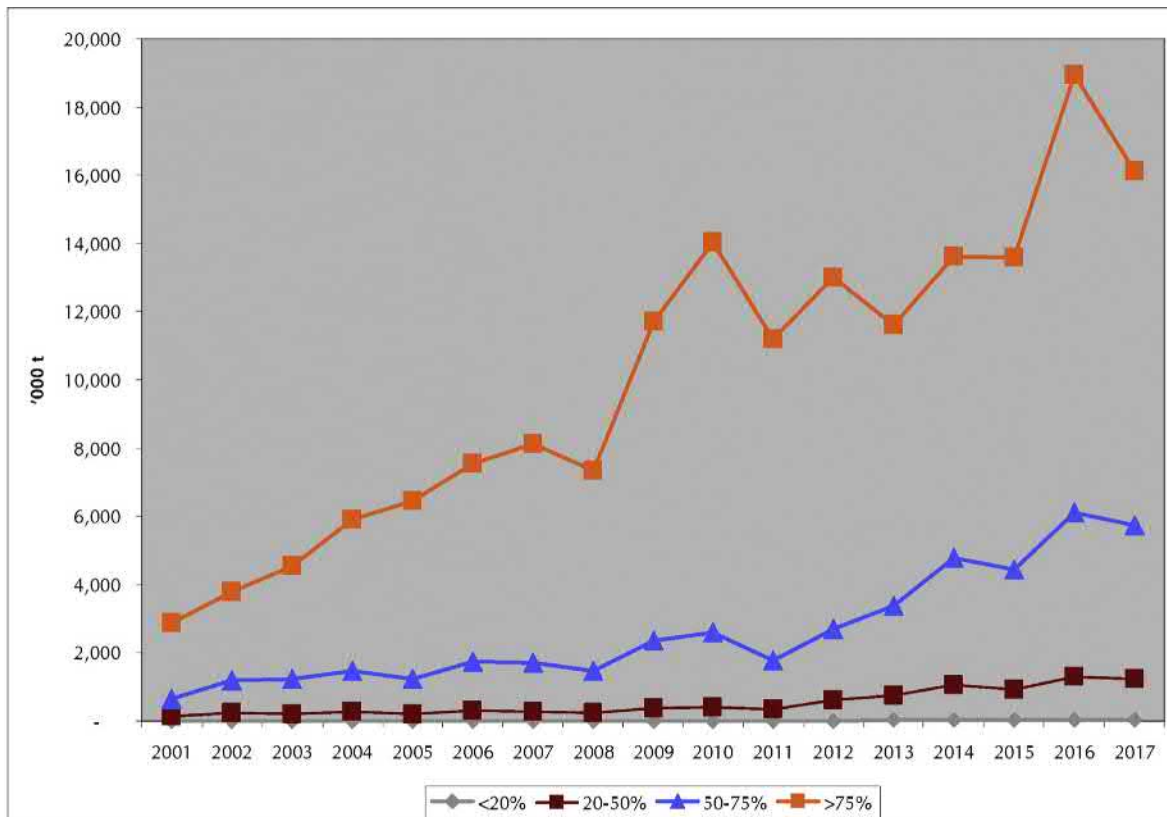


Fig. 14 Mekong region—wood exports vs forest losses by canopy class (2001–17). Notes: Exports '000 tons/year by canopy class. Commercial yield based on canopy cover class and average yield per ha (22%); yield per canopy class: <20% $11 \text{ m}^3/\text{ha}^{-1}$, 20–25% $61 \text{ m}^3/\text{ha}^{-1}$, 50–75% $88 \text{ m}^3/\text{ha}^{-1}$, and >75% $137 \text{ m}^3/\text{ha}^{-1}$ (Fraser, Pers. comm.). Calculation based on GFW forest loss data and UN Comtrade export/import data.

Financial Snapshot of Forest Destruction

The financial aspects of logging and wood exports are critical to understanding the process, as massive, unaccounted cash flows facilitate corruption essential for illegal logging and trafficking. Since 2010 the nominal value of wood exports has always been greater than USD 0.5 bn per month and reached USD 1 bn per month in 2014. Fig. 15 is based on the value of imports reported by UN Comtrade.

The regional summary distinguishes between amounts reported for all categories of significantly processed timber and for unprocessed logs and sawnwood. In 2017 the total value of wood exported from the Mekong region was USD 8.52 bn (Fig. 15), well over half this was for logs and sawnwood—China imported almost all (96%) of this wood (cf Fig. 12).

Summary of Findings

Regional governments are complicit partners in allowing forest ecosystems to be ever more rapidly destroyed for private profit. Traditional forest-dwelling communities continue to be victims of this process. The wildlife, much of it endogenous, in these forest habitats has been largely extirpated. There are growing indications the Mekong region's forest ecosystems and unique biodiversity may be nearing a point of collapse (Saravia et al., 2018).

Private financial incentives for illegal logging and timber trafficking are immense. In the absence of bilateral agreements (e.g. VFAs) WTO's international trade rules allow illegally logged and traded wood to be freely imported without penalties. In the absence of such agreements, including effective enforcement, it is regarded as very unlikely that governments in the region will prevent intra-regional and international trafficking. Given this, external action may be the best or only alternative. Chinese companies are clearly the dominant importer of what is plausibly identified as a massive trade in illegal wood, and action by the Chinese government to halt this may offer the best hope for conserving Mekong forests and the global heritage of the Indo-Burma Biodiversity Hotspot.

Since 2000, many of the large areas of intact and primary forests that evolved during the last ~10,000 years (Holocene Era) have been radically disrupted, degraded or destroyed. An unprecedented amount of this has occurred during the past decade. This has been caused by industrial logging, plus agricultural expansion covertly combined with illegal logging, and massive trafficking and illegal exports, mainly to China. With no sign these trends are slowing, threats to critical regional ecosystems of all types and biodiversity in the Mekong appear set to increase in coming decades (Corlett, 2013).

Concluding Remarks—Politics of Conservation

A recent assessment of conservation priorities and capabilities in the Mekong region was prepared by CEPF (2017). It builds on earlier assessments in 2008 and updated in 2011. It notes a major decline in donor funding for biodiversity conservation amid increasing threats; significant funding being switched to addressing threats from global warming.

It identified >400 Key Biodiversity Areas (KBA) and 66 'conservation corridors', from which a region-wide priority investment list was prepared. Most terrestrial KBA are located in or are forests, of which in 2015 only a minor proportion (13%) were 'protected' by national laws and regulations (Weller et al., 2017).

The assessment explicitly recognizes the vital role civil society has to play in conserving biodiversity, as without being able to freely (and safely) contribute it is very unlikely conservation goals can be achieved. The report identified three criteria needed to achieve and maintain national capabilities for ecosystem conservation to achieve a 'transition' away from relying on investments and technical support from donors. These were:

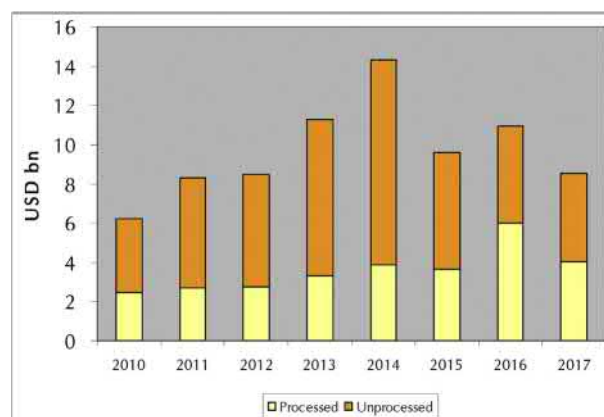


Fig. 15 Mekong region—value of wood exports 2010–17. Calculations based on UN Commodity Trade Statistics Database.

- *Political stability*—the absence of war or civil strife—considered likely for all five countries;
- *Economic stability* (and resilience)—considered likely, except for Myanmar and Laos; and
- *Open political environment*, considered ‘most open’ in Vietnam and Thailand, ‘intermediate’ in Cambodia and Myanmar, but ‘unfavorable’ in Laos. (However, the situation for civil society in Cambodia, Myanmar and Thailand has deteriorated since the CEPF report was prepared.)

According to CEPF’s assessment long-term biodiversity conservation and protection success requires that:

- Conservation priorities guide biodiversity conservation investments.
 - Local civil society groups have the capacity, rights, and ability to influence decisions on sustainable societies and economies.
 - Adequate and continual financing for conservation efforts is available.
 - Public policies and private sector operations support conservation.
 - Mechanisms exist to identify and respond to emerging challenges.
- (CEPF, 2017:40).

Given the report’s critical assumptions, especially the need for an ‘open political environment’, the chances of being able to conserve forests ecosystems and their biodiversity in the Indo-Burma Biodiversity Hotspot, Earth’s largest and possibly most threatened, appear to be growing dimmer.

Acknowledgments

Many thanks to my old friend Andrew Mittelman, who’s regional knowledge and critical editing made the text more readable. Percy Allen’s sharp eye identified and corrected errors in language and logic. Not least, many thanks to my wife and partner, Melody Kemp, for editorial support and encouragement.

Heartfelt thanks to Mikaela Weisse and Liz Bourgault of Global Forest Watch/WRI for providing additional access to GFW’s data and analysis on forest cover changes. Special thanks to Philip Curtis who undertook analysis of the dominant drivers of forest destruction with GFW and was generous in further clarifying his results. Thanks also to Zhenzhong Zeng, now of Princeton University, for further analysis of his research findings. Alistair Fraser, friend and colleague, provided insights and data from his archives, based on his extensive forestry work in the region.

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Migrating Most US Fiber Production From Forests to Farms

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Glossary

CO₂e The global warming potential of a molecule of carbon dioxide or other molecules (e.g. methane, nitrous oxide, etc. weighted as if they acted the same as CO₂.

Discount rate Defined in per cent to reflect the time value of money.

Ecosystem services For temperate forests, ecosystem services include gas regulation, climate regulation, water supply, soil formation, nutrient cycling, waste treatment, biological control, habitat/refugia, food production, raw materials, recreation, and cultural services, but are limited to them.

Fair market value (FMV) An estimate of value of real property where both the buyer and seller are comparably knowledgeable of the property, have equal bargaining power and the transaction is voluntary for both parties.

Net present value (NPV) The current value of an investment with future cash flows, appropriately discounted to reflect money today is worth more than money in the future.

Nonraw material ecosystem services (NRMES) All ecosystems services specified for ecosystem services, save for raw materials (fiber, fuel or fodder).

Time value of money Money to be received at a point in the future is worth less than money received today.

Tonne 1000 kg, also called a “metric ton” that can be confused with a “US ton,” “short ton,” “British ton,” “imperial ton,” or “long ton.” As any difference is well within $\pm 2\%$, and as a tonne is a ton of something, do not sweat it.

Abstract

The highest and best uses of US public and private forestlands (e.g. carbon sequestration and storage, biological diversity, ecosystem function, watershed integrity, and aesthetic enjoyment) are severely diminished by the most common uses of forests: logging for the production of fiber for construction and paper products. This irreconcilable conflict between the value of private forestlands for private profit and their societal value by the provision of nonraw material ecosystem services can be ameliorated by large-scale fiber switching from trees (multidecadal, centennial and even millennial fibers) to fiber grown on farms (annual, biennial and at most decadal fibers). Such a transition is technically feasible and can be economically feasible if markets demand it and/or government requires it. Many species can be farmed for fiber that can make comparable or superior construction and paper products. No conflict with food production is projected. As private forestlands are retired from fiber production they can be dedicated to their highest and best uses by conversion to public ownership by sale from willing sellers. Workers that lose jobs in the transition would be compensated, as would local governments for lost tax revenues. Funding for a migration of most US fiber production from forests to farms can be met by either a modest increase motor fuel taxes or a very modest tax on carbon emissions.

Introduction

The inherent and irreconcilable conflict between the logging of forests for fiber or fuel and conserving and restoring forests for ecosystem services—including, but not limited to, carbon storage and sequestration, biological diversity, ecosystem function, watershed integrity, and aesthetic enjoyment—has caused many a forest aficionado to cry out for alternative fibers with which to make construction and paper products that today are mostly manufactured from tree flesh (commonly known as wood).

The good news is that it is technically feasible to migrate most US fiber production from forests to farms. There are tree-free fiber alternatives—both fibers from agricultural waste products from existing crops and from intentionally grown fiber—that can meet most US demand for fiber. This demand can be met from annual, biennial, and—at the most—decadal fiber crops, all grown on farmlands. The multidecadal, centennial, and millennial fibers (commonly known as trees) that grow on forestlands can be dedicated to their highest and best uses: the provision of nonraw material ecosystem services (NRMES).

The bad news is that presently, the widespread replacement of forest fiber with farm fiber is not economically feasible. However, a combination of market demand, government purchasing policies, government regulation, and reallocation of government subsidies can result in a massive changeover of fiber feedstocks. The results would be more sustainably managed forestlands and more sustainable and profitable farmlands.

The great news is that industries change in response to market demand and/or government policy. Political and market demands—for forest conservation, cleaner and more water, sustainable products, and a climate somewhat near what we have known and loved—can converge to make the transition of fiber feedstock from forests to farms a reality.

This article relies on “Migrating Most US Fiber Production from Forests to Farms: A Model,” an Excel workbook (here after “fiber migration model” [FMM]) developed by the author (Kerr, 2018).

Irreconcilable Conflict in Forest Management: Fiber or Nonraw Material Ecosystem Services

US professional forestry has two major camps: production forestry and ecological forestry (Table 1). Production forestry (Bettinger et al., 2016) is dominant, but as public and private forestland owner preferences continue to evolve, ecological forestry (Franklin et al., 2018) is gaining landowner and social acceptance.

Table 1 Fundamental contrasts between ecological forestry and production forestry

<i>Ecological forestry</i>	<i>Production forestry</i>
Maintains an array of ecosystem structures, function (processes), and biota at larger spatial scales	Maintains a limited set of ecosystem structures, function and biota consistent with economic goals
Emphasizes ecosystem diversity and resilience to reduce risks from major ecosystem disruptions	Emphasizes fast-growing species on short rotations to reduce financial risks
Tends to increase management and social options	Tends to reduce management and social options
Values complexity and heterogeneity	Values simplicity and homogeneity
Accommodates landowner and social goals by adjusting the ecological model	Accommodates landowner and social goals by adjusting the economic/agronomic model

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For the provision of NRMES, ecological forestry is far superior to production forestry—but still inadequate compared to the full conservation and restoration of forestland. (DellaSala et al., 2013) For the provision of fiber, production forestry is superior to ecological forestry—but is unsustainable.

There is an irreconcilable conflict between conservation and fiber production on forestlands. Both production forestry and ecological forestry assume that since fiber for US paper and construction products have historically come from wood that such fiber can only come from wood. However, this conflict can be mostly resolved by increased use of farm fibers.

Private Value Versus Societal Value of US Forestlands

There is a huge disparity between the worth of US private forestland to a private landowner and what that same land is worth to society. Private value accrues from the sale of raw materials, while societal value comes from the enjoyment of NRMES. Private profit has a social cost.

Fair Market Value to Private Landowners of Private Forestlands

The fair market value (FMV) of an average acre of US private forestland is \$1823 (\$4505/ha) (Mendell, 2017). Though the average value, the range of land values is wide and dependent upon site productivity, species composition, distance to markets and other factors. Assuming a 5.5% rate of return (or discount rate), the average income on the average acre is ~\$80/acre/year (\$198/ha/year).

Fair market value (FMV) is an estimate of value of real property where both the buyer and seller are comparably knowledgeable of the property, have equal bargaining power and the transaction is voluntary for both parties (Macaraeg, 2018).

FMV is mostly based on the ability of the forestland to produce fiber and/or land appreciation. Private forestlands with development potential have higher value than those valued for just timber. For the private forestland owner to fully realize profit, forestland must be intensively managed for fiber production, which usually involves clearcutting and short-rotation timber harvesting. Alternatively, if the market exists, the forestland can be sold for development for at a higher value than for timber production.

Net Present Value to Society of Private Forestlands

“Ecosystems provide a range of services that are of fundamental importance to human well-being, health, livelihoods, and survival.” (Costanza et al., 2014).

For temperate forests, ecosystem services include a variety of values of benefit not only to the private landowner, but to society as a whole (Costanza et al., 1997). The value of NRMES to society from an average acre of temperate forest is \$1364 each year (\$3371/ha/year) (Table 2). The value of raw material (fiber, fuel, or fodder) ecosystem services is \$84 per acre per year (\$206/ha/year), or 6% of total temperate forest ecosystem services annual value (Costanza et al., 2014).

Net present value (NPV) is a way to quantitatively value an investment, in this case private timberland. NPV is current value of an investment factoring anticipated future cash flows using an appropriate discount rate to reflect the time value of money—money today is worth more than money in the future (Gallo, 2014). The higher the discount rate, the less the value of the investment. In determining the societal NPV of NRMES, the FMM considered three discount rates (Table 3):

- 5.5%, the average rate used by of over 80% of industrial timberland owners (Lyster et al., 2017);
- 2.6%, the present rate of the U.S. government (Office of Management and Budget, 2017); and
- 0%, the rate at which future generations are valued the same as the present generation.

Table 2 Quantified ecosystem services for temperate forests (\$2018)

<i>Ecosystem service</i>	<i>\$/Acre/year</i>	<i>\$/Hectare/year</i>
Climate regulation	\$70	\$173
Water supply	\$88	\$218
Soil formation	\$6	\$16
Nutrient cycling	\$43	\$106
Waste treatment	\$55	\$137
Biological control	\$108	\$268
Habitat/refugia	\$398	\$983
Food production	\$138	\$341
Raw materials	\$84	\$206
Recreation	\$456	\$989
Cultural	\$0.5	\$1
Total (all)	\$1447	\$3576
Total (w/o raw materials)	\$1364	\$3371

Costanza R, de Groot R, Sutton P, van der Ploeg S, Anderson SJ, Kubiszewski I, Farber S, Turner RK (2014) Changes in the global value of ecosystem services. *Global Environmental Change* **26**:152–158.

Table 3 Societal net present value an average acre (hectare) of temperate forestland

<i>Discount rate</i>		<i>Analysis horizon</i>					
		<i>20-Year</i>		<i>100-Year</i>		<i>1000-Year</i>	
<i>%</i>	<i>Used by/for</i>	<i>Acre</i>	<i>Hectare</i>	<i>Acre</i>	<i>Hectare</i>	<i>Acre</i>	<i>Hectare</i>
5.5%	US Timberland Owners	$\$21 \times 10^3$	$\$52 \times 10^3$	$\$50 \times 10^3$	$\$124 \times 10^3$	$\$55 \times 10^3$	$\$136 \times 10^3$
2.6%	US Government	$\$28 \times 10^3$	$\$69 \times 10^3$	$\$162 \times 10^3$	$\$400 \times 10^3$	$\$16 \times 10^6$	$\$40 \times 10^6$
0%	Intergenerational equity	$\$37 \times 10^3$	$\$91 \times 10^3$	$\$828 \times 10^3$	$\$2.0 \times 10^6$	$\$312 \times 10^{15}$	$\$771 \times 10^{15}$

Kerr A (2018) Migrating most US fiber production from forests to farms: A model. Ashland, OR: The Larch Company.

It is usual for an NPV analysis for private forestland to have a discount rate higher than that of the government. It is unusual to use 0%. An NPV analysis also requires defining an investment horizon. Private timberland investments are often 5 to 25 years with an average of 10 years (Bullard et al., 2002). It is also highly unusual to use an NPV time horizon of greater than 20 years. Choosing a longer investment horizon results in less intergenerational inequity. To reflect the premise that this generation should make decisions with future generations in mind, the FMM considered 20, 100, and 1000 years.

Even using the highest discount rate (5.5%) with the shortest analysis period associated with NPV to private landowners (20 years), the societal NPV of NRMES provided on an average parcel of US private timberland is \$20,000 per acre (\$49,000 per hectare) If one considers longer time horizons (after all, NRMES are not a depreciating societal asset) and assumes that members of a society in the future are just as valuable as members today, then the NPVs attain astronomical values (Table 3).

Contrasting Private Fair Market Value and Societal Net Present Value of Private Forestlands

In theory, and with a rational market, NPV equals FMV. The only way that a US private timberland owner can monetize their investment is to log (or develop), at the expense of NRMES values to society. If society fully compensated private landowners for ecosystem services received from US private forestlands, an average acre of private forestland would have an FMV of, at a minimum, ~\$20,000 (\$49,000/ha)—the private FMV would be equal to the societal NPV. But society does not pay private landowners for the NRMES it receives from private forestlands. The average FMV is \$1823 per average acre (\$4505/ha). The societal NPV for that same average acre is at least \$20,000 (\$49,000/ha), a mismatch of over 11 times. When rational outcomes for private landowners do not lead to a rational outcome for society, economists call it a market failure (Investopedia, 2018).

The Most Common Use of US Forestland Is Fiber Production

The US has 766 million acres (310 million hectares) of forestland, of which 521 million acres (211 million hectares (68%) is timberland (Table 4). About 10%, 74 million acres (30 million hectares), is reserved for conservation and other purposes. Some of the reserved lands are logged, albeit to a lesser degree than timberland. Some logging also occurs on “other” forestlands, including woodlands and scrub forests. The most intense logging is on industrial timberlands and nonindustrial owners who manage their forestlands with an industrial mindset. The US also has 53 million acres (22 million hectares) of woodlands (< 10% covered with

Table 4 US forest by ownership class and region.

	Region							
	US		North		South		West	
	Million							
	Ac	Ha	Ac	Ha	Ac	Ha	Ac	Ha
All owners	766	310	176	71	241	98	346	140
Timber land	521	211	167	68	210	85	144	58
Reserved forest	74	30	7	3	4	2	63	25
Other forest	172	70	2	1	31	13	139	56
National forest	145	59	12	5	13	5	120	49
Timber land	98	40	10	4	12	5	75	30
Reserved forest	27	11	1	0	1	0	24	10
Other forest	20	8	0	0	0	0	20	8
Other public	176	71	35	14	20	8	122	49
Timber land	63	25	29	12	15	6	19	8
Reserved forest	47	19	5	2	3	1	39	16
Other forest	67	27	0	0	2	1	65	26
Private corporate	147	59	29	12	65	26	53	21
Timber land	111	45	29	12	61	50	21	8
Reserved forest	0	0	—	—	0	0	0	0
Other forest	36	15	0	0	4	2	32	13
Private noncorporate	298	121	100	40	147	59	51	21
Timber land	249	101	99	40	121	49	28	11
Reserved forest	0	0	0	0	0	0	0	0
Other forest	48	19	1	0	25	10	22	9

Totals may not add correctly due to rounding of original data.

Italics denotes hectares and Roman denotes acres.

Oswalt SJ and Smith WB (2014) U.S. Forest resource facts and historical trends. Washington, DC: USDA Forest Service.

trees). Most timber volume comes from private forestlands, which account for 56% of all forestland. Forty two percent of all forestland is owned by individuals and families who often own their forestlands for the enjoyment of their aesthetic value and wildlife activity. Almost half of these lands are owned by people over 65 (Oswalt and Smith, 2014).

Current US Forest Fiber Use

With 5% of the world's population and 7% of the world's land area, the United States has 8% and 10% of the world's forest land and timber inventory respectively, and uses 28% of the world's timber for industrial products (Oswalt and Smith, 2014).

In 2017, the US produced 335 million tonnes of finished wood products, of which 61 million tonnes were exported and an additional 39 million tonnes were imported. Production plus imports, totaling 375 million tonnes, equals US consumption (UN Food and Agriculture Organization, 2018). Sawnwood—lumber and other products made of solid wood—were ~15% of the total forest fiber produced and imported (Table 5).

Table 5 US major forest fiber product groups finished products (2017).

Finished products	2017 Production (million tonnes)	2017 Import (million tonnes)	2017 Export (million tonnes)*
Wood charcoal	0.9	0.1	0.0
Wood chips, particles and residues	19.6	0.3	2.3
Wood pellets and other agglomerates	6.9	0.4	5.3
Sawnwood	42.1	13.2	4.3
Wood-based panels	82.9	7.3	1.1
Wood pulp	49.2	5.4	16.3
Other pulp	0.5	0.0	0.2
Recovered paper	47.6	0.9	18.3
Paper and paperboard	85.6	11.8	13.3
Total	335.4	39.3	61.0
Grand total (production + imports)	375		

*US exports are a subset of US production.

Source: UN Food and Agriculture Organization: <http://www.fao.org/faostat/en/#data/F0>.

Highest and Best Use of US Forests Is Nonraw Material Ecosystem Services

NRMES are degraded by logging (Norse, 1990). The more forestland area that is logged and/or the more intensely the logging on each parcel, the less NRMES are available from that forestland parcel.

All ecosystem services provided by forestland are eliminated by development, which results in complete deforestation. Development is causing not only the direct loss of forestland cover, but also of interior forest, which intactness is more beneficial to wildlife and other forest values. From 2001 to 2006, the US had a net loss of forests of 1.2%, while the loss of interior (intact) forest was 4.3%. (Oswalt and Smith, 2014) Such fragmentation leads to losses of species, habitat, gene pools, biological diversity, biomass, and natural processes, and altered nutrient cycles (Haddad et al., 2015).

While the most common use of public and private forests in the United States is logging for fiber, such is not the highest and best use—and especially so if there are alternative sources of fiber.

Securing the Value of Ecosystem Services on US Forestlands for This and Future Generations

The market for US forestland incentivizes logging or developing forests for profit. Since society cannot rely on the market to continue to provide NRMES over time, other methods must be sought to achieve forest conservation.

This could mean better regulation of logging on forestlands, but the level of regulation adequate to secure the continuation—if not expansion—of nonraw material forest ecosystem services would be politically unacceptable. Governments could pay a forestland owner not to log or develop by acquiring the timber and development rights. As the cost of the rights to log and develop a parcel is often a very high fraction (especially in the case of development) of the entire market value of the private forestland and there is also an ongoing monitoring and enforcement cost which can be expensive (Schuster and Arcese, 2015), it would often be more cost-effective to convert the private timberland to public forestland by acquiring the land outright so it could be fully managed for NRMES values.

Alternative Agricultural Fibers

A 1994 comprehensive literature review found 53 alternative fibers had been considered for the production of building materials. These included plants intentionally grown for fiber, but mostly materials left over after processing a plant for its intended purpose (sugar, nuts, grain, fruit, etc.) (Youngquist et al., 1994, 1996). Much research on and utilization of agricultural waste fibers occurs outside the United States in nations that have abundant agricultural waste fiber and little to no forest fiber availability (Dungani et al., 2016).

Technically, there are several annual, biennial or, at most, decadal farm fibers that could replace (Table 6) the multidecadal, centennial, and even sometimes still millennial forest fibers. There are three categories of farmland fiber that could displace forest fiber consumption at meaningful scales:

- (1) waste fibers (fibrous waste products left over after harvest or primary processing);
- (2) intentional fibers (grown for the purpose of harvesting fiber); and
- (3) trees grown on farmland (not on forestland, and with extremely short rotations).

Technically Feasible

From a technical standpoint, fiber is generally fungible. Paper and construction products can be made out of almost any fiber (Brand, 1911; Youngquist et al., 1993; Miller, 1975; Rowell et al., 1997; Bowyer et al., 2004; Ashori, 2006; Enayati et al., 2009; Langholtz et al., 2016; Favero et al., 2017; Fahmy et al., 2017; Heller, 2017; Economist, 2018). Farm fiber can also be used to produce paper board, hardboard particle board and other construction products (Youngquist et al., 1993; Li et al., 2014; Sam-Brew and Smith, 2015; Fahmy et al., 2017; Lühr et al., 2018; Mirski et al., 2017; Sam-Brew and Smith, 2017; Mirski et al., 2018).

Table 6 US farm fibers to replace forest fibers.

<i>Waste fibers</i>	<i>Intentional fibers</i>	<i>Trees grown on farmland</i>
Bagasse, wheat straw, oat straw, corn stocks, corn cobs, cotton stalks, rice husks, straw, sunflower hulls, sunflower stocks, alfalfa straw, flax, sisal, barley straw, canola stalks, rye straw, grass seed straw, sorghum stalks	Bamboo, kenaf, rice, jute, hemp, <i>Arundo donax</i>	Southern pine, poplar hybrids, <i>Eucalyptus</i>

Ashori (2006), Bowyer et al. (2004), Enayati et al. (2009), Fahmy et al. (2017), Heller (2017), Langholtz et al. (2016), Miller (1975), Rowell et al. (1997), Thomas and Liu (2013), and Youngquist et al. (1993).

Availability

There can be nearly 700 million tonnes of US farm fiber that is available to replace forest fiber in a sustainable manner (**Table 7**). Nearly 200 million tonnes is byproducts from existing agricultural crops, either as crop residue on the field or waste from primary processing (e.g. hulls, peels, etc.) (**Fig. 1**). Utilization scenarios modeled by the US Department of Energy (USDOE), do not consider all crop residues as available—enough is reserved to maintain soil organic carbon and soil nutrient recycling (Langholtz et al., 2016). These residues and wastes are available today but are usually burned off, contributing to climate change and air pollution.

Nearly 500 million tonnes annually of intentional fibers is what the USDOE analysis says could be sustainably grown on farmland without competing with demand for food, livestock feed, fiber, and timber (including export products) (Langholtz et al., 2016). USDOE's interest in biomass energy dictated its choice of which herbaceous and woody crops it modeled. Biomass is mostly fiber, so the acreage is available to grow intentional farm fiber crops destined for paper and construction products.

Substitution Potential

Wood has been the nation's go-to source for construction and paper products because of its abundance and physical qualities. However, there are other fibers with comparable or superior physical qualities than could be obtained and utilized in abundance, so that forestlands could be conserved and restored without a diminution in available fiber for products.

To reverse the loss of both the quantity and quality of forests, US farm fiber must replace a very significant amount of US forest fiber. The more fiber production is migrated from forests to farms, the more NRMES than be obtained from forestlands.

While 100% replacement would be perfect from a forest perspective, absolutes are rarely good public policy or economically attainable. The marginal additional costs of attaining the last increments often requires extremely high costs.

US forest fiber products can be grouped into three major categories:

- pulp and paper (54%);
- wood-based engineered composites (smaller pieces of wood that is not reduced to pulp before use) (32%); and
- sawnwood (solid wood products) (15%).

Table 7 Technically available agricultural substitute fibers (million tonnes) per year.

Existing byproducts	188
• Agricultural residues	171
• Agricultural wastes (from primary processing, not animal manure)	18
Intentional agricultural crops grown on farmland	496
• Herbaceous crops (switchgrass, Miscanthus, energy cane and biomass sorghum)	445
• Woody crops (willow, eucalyptus, poplar, pine)	51
Total	684

Langholtz MH, Stokes BJ and Eaton LM (leads) (2016) *2016 Billion-ton report: advancing domestic resources for a thriving bioeconomy, Volume 1: Economic availability of feedstocks*. Oak Ridge, TN: US Department of Energy Oak Ridge National Laboratory.



Fig. 1 Bagasse is the dry pulpy residue left after the extraction of the juice from sugar cane. Courtesy of TreeZero.

Technologically, the substitution of farm fiber for forest fiber is substitutable to varying degrees:

- Highly substitutable (95%): Pulp and paper (Figs. 2 and 3).
- Very substitutable (75%): Wood-based engineered composites (Figs. 4 and 5).
- Substitutable (50%): Sawnwood (Fig. 6).

The substitution estimate for sawnwood is very conservative as processing and engineering could result in a higher rate of substitution.

Engineering and Innovation

Though fiber is generally fungible, the farm-fiber feedstocks will be different enough from forest-fiber feedstocks to require additional, or at least different, engineering and innovation to profitably manufacture paper and construction products. The largest volume of farm fiber could come from waste fiber from existing crops. The remainder could come from crops intentionally grown for fiber, such as hemp (Fig. 7).

A particular challenge with hemp is the efficient separation (decortication) high- and low- value fibers found respectively on the outside and inside of the stalk (Cherney and Small, 2016; Tahir et al., 2011). Another challenge is the storage and timing of shipping agricultural fibers to processing facilities. Wood, because of its high lignin content, can be stored exposed to the weather and can be harvested much, if not all, of the year. Farm fibers cannot be stored outdoors, are often far bulkier than farm fiber, and the harvest (Fig. 8) is mostly a short window in the fall (Fike, 2016).

Irreplaceable Wood Products

Most, but certainly not all, products could be made from farm fiber rather than forest fiber. For some products, because of technical or quality reasons, farm fiber is just not substitutable—though most of these products have their nonwood substitutes. Wine casks, whiskey barrels, musical instruments, firewood, popsicle sticks and baseball bats made from wood are often preferred by the market for their quality and/or tradition. Budweiser® beers are aged with beechwood chips (Goldman, 2016) and need not change. In certain cases, the highest and best use of forest fiber is wood products.

Economics of Nonwood Plant Fiber and Changing Consumer Demand

Today, in almost all cases, forest fibers out-compete farm fibers in terms of delivered price to processing facilities. For example, hemp pulp in Europe costs five times that of wood pulp (Cherney and Small, 2016). Not that one needs to use 100% hemp



Fig. 2 Made of bagasse, this tree-free office paper is indistinguishable from that made from wood. Courtesy of TreeZero.



Fig. 3 A tree-free paper towel made of bamboo and bagasse. Courtesy of Who Gives a Crap.



Fig. 4 Sorghum board. Courtesy of Kirie.



Fig. 5 Bamboo veneer. Courtesy of Kirie.



Fig. 6 3-ply bamboo. Courtesy of Kirie.

pulp to substitute for 100% wood pulp, but rather one could use a blend of the more-expensive hemp fiber with the less-expensive agricultural waste fiber. Still, the price differential is large.

The current infrastructure of the manufacture of building products is based on forest fiber and facilities were built near forests and not farms. Agricultural waste fiber is bulky and therefore expensive to transport long distances.

However, markets respond to consumer demand as well government policies, be they the stick of regulation or the carrot of subsidy. The projected 20-year migration period allows time for an orderly and efficient transition.

Successful firms respond to market demand. As consumers demand, suppliers will meet that demand. However, there is very little demand for nonwood paper and construction products primarily because there is very little supply of nonwood paper and construction products. Determined consumers can identify such products, but they are hard to find and are of limited variety.

Intentional Fiber

There are several fibers that could serve as intentionally grown farm fibers *Arundo donax* (known as giant cane, giant reed or other names), bamboo, hemp, jute, kenaf, and rice (Table 6). While the market will ultimately decide, the most favorable intentional fiber(s), hemp was chosen for the fiber migration model because of superior technical qualities. However, because of the effective illegality of cultivating hemp in the US since 1937, hemp is a current disadvantage. As the Congressional Research Service notes: "Most researchers acknowledge the potential profitability of industrial hemp, but also the potential obstacles to its development. Current



Fig. 7 A field of hemp. Wikipedia Commons Creative Commons Attribution-Share Alike 3.0 Unported.



Fig. 8 The harvest of hemp in France. Courtesy of Ralf Pecenka/Leibniz Institute for Agricultural Engineering and Bioeconomy (ATB). Permission granted.

challenges facing the industry include the need to reestablish agricultural supply chains, breed varieties with modern attributes, upgrade harvesting equipment, modernize processing and manufacturing, and identify new market opportunities" (Johnson, 2018).

Hemp

The term "hemp" is used to describe certain varieties of the species *Cannabis sativa* L.). Other certain varieties of the same species are called "marijuana." "Industrial hemp" is often used to distinguish hemp from marijuana. Marijuana is bred to have a high amount of Δ^9 -tetrahydrocannabinol (THC), the intoxicating cannabinoid in *C. sativa*. Hemp strains have insignificant amounts of THC and far high amounts of another cannabinoid, cannabidiol (CBD), which though also psychoactive, is not intoxicating (Cherney and Small, 2016).

In 2018, hemp was fully legalized by Congress. Hemp is no longer legally considered to be marijuana. While previous US law nominally allowed for the hemp cultivation, as a practical matter it did not happen because the Drug Enforcement Administration treated hemp and marijuana as one in the same (Kerr and Moran, 2016).

Hemp is an agricultural commodity cultivated for a wide variety of products including foods, beverages, cosmetics, personal care products, nutritional supplements, fabrics, textiles, yarns, spun fibers, paper, construction materials, insulation materials, auto parts, animal bedding, oil absorbents and other manufactured goods. Hemp is cultivated to maximize seed or fiber or both (Johnson, 2018).

Hemp fiber comes in two kinds (Fig. 9). The outer ring of the plant is composed of long phloem (“bast” or “bark”) fibers. The inner core of the plant is composed of short xylem (“wood”) fibers. With the remnants of stem pith, the nonbast fibers are collectively known as “hurd.” The long bast fibers amalgamate into bundles that are very long (Cherney and Small, 2016).

While there are several potential intentionally grown farm fibers, hemp was chosen for the FMM because of several important characteristics:

- Fiber length. Hemp bast fiber length averages 25 mm and ranges from 5 to 55 mm. The bast fibers are positioned along the outside of the stalk. The inner core, or hurd, fibers have an average length of 0.5–0.8 mm (Han, 1998). In comparison, the average softwood and hardwood fiber lengths are 3.67 and 1.3 mm respectively (Forest Products Laboratory, 1953).
- Low lignin content. Hemp’s low lignin content (3%) makes it valuable for papermaking (Han, 1998).
- Wide geographic range. In 2018, hemp was being grown in 19 states totaling 25,541 acres (10,336 ha) that are for the purposes of the sale of fiber, grain and seed, mostly in a research context. The largest market for hemp products is for cannabidiol (CBD) extracts which are being sold for medical purposes (Johnson, 2018).
- Yields. A survey of reported per acre yields in North America and Europe found an average of 3.7 tonnes/acre (9.1 tonnes/ha) of plant material (Kerr, 2018).
- Potential in building products. Cherney and Small (2016) note: “From a building materials standpoint, hemp and other natural fibers have light weight, high strength to weight ratio, high insulating potential, and are more recyclable than conventional materials.”

The Fiber Migration Model

The fiber migration model (FFM) was developed to simulate the migration of US fiber production from forests to farms (Kerr, 2018). FMM is in two parts:

- substituting forest fiber with farm fiber (Part 1); and
- converting private timberland to public forestland (Part 2).

Both are necessary to fully achieve full conservation and restoration of forestlands to optimally provide for NRMES.

Part 1: Substituting Forest Fiber With Farm Fiber

Major modeling steps

- The dry weights of US wood products by major categories were determined (UN Food and Agriculture Organization, 2018).
- Potentially available farm fiber (existing byproducts and potential intentional fiber crops) were analyzed (Langholtz et al., 2016).
- Estimates were made as to the achievable substitution of forest fiber with farm fiber: pulp and paper (95%), wood-based engineered products (75%), sawnwood (50%).
- Estimates were made as to how much of the substituted farm fiber would come from existing agricultural byproducts (60%) and from intentionally grown fiber crops (40%). Intentionally grown crops have longer fibers than existing agricultural waste fibers, necessary for adding strength to construction and some paper products.



Fig. 9 The outer bast fiber on a stalk of hemp. Wikipedia Commons. Released into the public domain.

Key findings

- 78% of US fiber from forests could effectively be substituted with farm fiber.
- 32.2 million acres (13 million ha), or 9.5% of US cropland (340 million acres [138 million ha]) would have to be dedicated to hemp cultivation.

Part 2: Converting Private Timberland to Public Forestland

Private forestlands should be converted to public forestlands for two major reasons. First, to secure the provision for this and future generations of the multiple NRMES of forestlands, the lands should be in public ownership. Second, as most US fiber production migrates from forest to farm, the market value of private timberland will decrease significantly. This will result in stranded investments for industrial timberland owners and a reduction of net worth for private timberland owners. As the fiber migration would be a result of directed government policy it is appropriate to compensate affected private forestland owners, as well as affected local and state governments, and displaced forest and mill workers.

Major migration steps

- Determine the average fair market value of US forestland (\$1823/acre [\$4505/ha]) and the amount of private timber to be converted to public forestland (78%; the result from Part 1), and determine a timeframe for the migration (20 years). Though a relatively rapid transition time, two decades was chosen because of the vital need for rapid and dramatic action to avoid the worst of climate change, during which the world must limit the increase in global temperature to no $> 1.5^{\circ}\text{C}$ (Allen et al., 2018).
- Determine a source of revenue to fund the transition. The FMM analyzed two options to raise the revenues necessary to carry out the migration of most US fiber production from forests to farms over a 20-year migration period:
 - increasing the motor fuel tax on gasoline and diesel by \$0.42/gal; or
 - tax carbon emissions at a rate of \$13.13/t CO₂e

(For comparison, the average combined local, state and federal motor fuel tax in the US per gallon of gasoline and diesel is \$0.5249 and \$0.6051 respectively (American Petroleum Institute, 2018). Three Republican members of the US House of Representatives have introduced a bill that would tax emissions at \$24/tonne CO₂e (Curbelo, 2018) and a group of distinguished Republican conservatives have proposed a \$40/t CO₂e tax (Baker et al., 2017). Of course, to adequately address climate change, any tax on carbon needs to be significantly higher than \$13.13/tonne CO₂e (Carr, 2018).)

- Provide for not only fair market value compensation to affected landowners, but also:
 - (1) assist affected state and local governments;
 - (2) assist forest workers displaced by the transition;
 - (3) provide an endowment fund for the ongoing operational costs of managing the again public forestland; and
 - (4) and cover overhead costs of acquisition.

Key findings

- 8 million acres per year of private timberland could be converted to public forestland over a 20-year period (280 million acres, 112 million hectares) at an average cost of \$1823/acre (\$4504/ha), or \$510 billion total.
- An additional 25% of the average per-acre cost (\$456 [\$1127/ha]) would be provided to cover overhead costs of acquisition.
- An additional 100% of the average per-acre cost (\$1823/acre [\$902/ha]) would endow a fund to pay for annual operations, which if invested at 5% would yield \$91/acre/year (\$225/ha/year). The cost of managing federal public forestlands in western Oregon ranges between \$24/ and \$86/acre (\$59/ and \$213/ha) in 2018 dollars (Kerr, 2012a).
- An additional 100% of the average per-acre cost (\$1823/acre [\$902/ha]) would be given to state and local government to offset lost tax revenues, which if invested at 5% would yield \$91/acre/year (\$225/ha/year). Since such governments barely tax private timberland (Greaves, 2009; Kerr, 2012b, c), this will result in more revenues to affected governments than by continuing to tax them.
- An additional 10% of the average per-acre cost (\$182/acre [\$450/ha]) would be placed in a fund to compensate displaced forest and mill workers, which would result in them receiving 10 years of their average median wage.

The 20-year migration timeframe was chosen to allow for an efficient economic and less stressful social transition resulting from moving most US fiber production from forest to farm.

Who Would Manage the Forests?

Private timberlands converted to public forestlands will need to be managed by an appropriate public agency. There are multiple agencies, at the federal, state and local level that are suited for the task.

The four major federal land management agencies are the Bureau of Land Management (BLM), Fish and Wildlife Service, Forest Service, and National Park Service. There are large amounts of generally forested private forestlands that are inholdings within the boundaries of the units of the National Forest System, National Park System, National Wildlife Refuge System, and BLM's National Landscape Conservation System and other BLM holdings. For example, only 54% of the lands within the official boundaries of eastern national forests are federal public lands. Nationally, only 83% of the lands within the boundaries of the National Forest System is Forest Service-owned (Kerr, 2017). Besides rounding out existing conservation system units, entire new conservation units could be established with the converted forestlands.

At the state level, there could be many more and expanded state parks, forests, wildlife areas, and recreation areas. At the local level there could be many more and expanded county and city forests and parks, as well as surface drinking watershed protection areas.

Surface Water Protection

Americans use 198 billion gallons per day of freshwater drawn from surface sources. 70% of all fresh water use is from surface sources. 61% of public water supplies (residential, commercial and industrial) come from surface-water sources (Dieter et al., 2018). 53% of surface water watersheds are forestland (Oswalt and Smith, 2014). 68% of Americans use public water systems that are supplied by surface water. As the Centers for Disease Control (2018) notes, "Even though most community drinking water (especially from surface water sources) is treated before entering the home, the cost of this treatment and the risks to public health can be reduced by protecting source water from contamination."

Most surface water sources are not managed to protect water quality and quantity values. Private forestlands in municipal watersheds could be acquired to protect surface drinking water quality and quantity.

Deed Stipulations

As the purposes of the newly acquired public lands is the secured and continuous provision of NRMES, (e.g. the conservation and restoration of biological diversity, the protection of water quality and quantity, the sequestration and storage of carbon, and the provision of compatible recreation), it is important the lands are managed as such.

All transfers of deed to the receiving public agency should have a provision that restricts incompatible uses. The deed should also include reversionary or diversionary clause so that if the managing agency violates the terms, the forestland is transferred to another public agency. Finally, the managing agency would have to agree to be citizen-suit judicial enforcement of the agreement.

Some surface drinking water sources are protected by law. New York City's water supply in the Adirondack Mountains of upstate New York is constitutionally protected. Article XIV of the New York Constitution requires that "The lands of the state, now owned or hereafter acquired, constituting the forest preserve as now fixed by law, shall be forever kept as wild forest lands. They shall not be leased, sold or exchanged, or be taken by any corporation, public or private, nor shall the timber thereon be sold, removed or destroyed" (New York Department of Environmental Conservation, 2018).

Policy Changes Necessary to Migrate US Fiber Production to Farm From Forest

Expressions of consumer demand can also be channeled through the political process by voters (all of which are consumers) to demand action by their elected officials. Thus, the federal government could encourage the migration of US fiber production from forests to farms by:

- Redirecting a portion of farm subsidy programs away from the major commodity crops (corn, wheat and soybeans, etc.) toward intentional fiber crops and the utilization of agricultural waste fibers.
- Eliminating subsidies to timber production in the federal tax code (Landy, 2012; Kerr, 2012d)—if not also redirecting them toward farm fiber.
- Ending subsidies to the timber industry from the sale of timber on federal public forestlands (Taxpayers for Common Sense, 2016)—if not also redirecting them toward farm fiber.
- Impose a price on the emission of carbon into the atmosphere (World Bank, 2016) not only by fossil fuel extraction from underground, but also by fiber extraction from forests. Carbon dioxide emitted from either the burning of fossil fuels or harvest of forest fiber are indistinguishable to the atmosphere.

State and local governments could similarly impose a price on atmospheric carbon emissions and end their general practices of taxing forestland at below market values (Greaves, 2009; Kerr, 2012b, c).

Aspects and Impacts of a US Fiber Transition From Forests to Farms

Moving US fiber production from forest to farm will have environmental, economic and social impacts, both positive and negative. The FMM mitigates most of the major negative impacts.

Climate

Adding value to waste fibers mean less field burning of agricultural crop wastes with resultant CO₂ emissions to the atmosphere. Intentional fiber as an additional rotation crop will also tend to decrease CO₂ emissions, as well as nitrous oxide (N₂O) emissions from farming (Behnke et al., 2018; King and Blesh, 2018). N₂O is a greenhouse gas with a global warming potential 298 times that of CO₂ (Environmental Protection Agency, 2018).

The most significant effect would be the reduction of carbon emissions and the additional sequestration and storage that would result from ending logging on approximately fourth-fifths of US private timberlands. The FMM (based on Harris et al., 2016; Le Quéré et al., 2018) estimates that during the 20-year fiber migration period and the following 30 years of, that ~11.3 gigatonnes of US CO₂e emissions to the atmosphere due to logging would be avoided, equivalent to is ~2 times US 2016 emissions (Environmental Protection Agency, 2018). These avoided emissions mean that global CO₂ levels would not increase ~6.5 ppm. To avoid the worst of climate change, the world must limit the increase in global temperature to no more than 1.5 °C (Allen et al., 2018). As the forestlands grows—and are no longer logged—the greater the probability of meeting the <1.5 °C necessity.

Forests

NRMES—including but not limited to carbon storage and sequestration, biological diversity, ecosystem function, watershed integrity, and aesthetic values—would increase as logging ended on lands and are converted from private timberlands to public forestlands.

It is a well-established principle of the science of conservation biology that to have a functioning ecosystem, both across the landscape and over time, between one-quarter and three-quarters of that ecosystem must be conserved (Wilson, 2016). If the migration of US fiber from forest to farm does occur as modeled, 92% of US forestlands would be in public ownership, with most of it managed primarily for the provision of NRMES. Given the imperatives of also removing excess carbon from the atmosphere, and providing for clean and plentiful drinking water and other NRMES, the large percentage is ecologically, economically and socially justified.

Private Forestland Owners

There are two major categories of private timberland owners: industrial and nonindustrial. As the FMM would provide for fair market value compensation to willing sellers, industrial timberland owners would have their land and standing timber assets liquidated and would invest the funds in other investments, perhaps more lucrative ones. Much nonindustrial timberlands are held by owners who also have the goal of profit maximization, so they are similar to industrial timberland owners. Other nonindustrial private forestland owners may sell their lands for public ownership, perhaps reserving small amounts for a home. They may decide to keep their forestland, even though its market value has decreased as there would no longer be a market for fiber extraction. In other cases, current nonindustrial private timberland owners will decide to keep their forestland, but their heirs may decide to sell.

Forest Workers

The fiber migration model predicts that ~156,000 jobs (78% of 2017 workers) would be lost as US fiber production migrates from forest to farm over the course of 20 years. The FMM would compensate displaced workers with 10 years of wages. Some workers will choose to retire, others might improve their education to help find employment in other occupations, immediately find a new job, pay off debt, invest for retirement, etc.

Forest Fiber Processing Facilities

US fiber production, now centered on forests, especially in the Pacific Northwest and the South, will migrate to the Midwest, where there are plentiful agricultural waste fibers and opportunities to insert intentional fiber crops into farmland rotations. The transition of US fiber production from forests to farms will have dramatic effects on industries that manufacture paper and construction products. There will be winners and losers. However, the FMM's projected US fiber migration from forests to farms of 20 years is long enough for the owners of existing forest fiber processing facilities to fully amortize their investments. Some forest-fiber processing facilities could convert to farm fibers because they are located near farm sources of fiber. This includes much of the South where farms and forests are more interspersed than elsewhere in the US and where most US pulp and paper manufacturing facilities are located (Stritholt, 2008). This also includes some pulp and paper facilities in Oregon's Willamette Valley located near ryegrass fields.

Food

In modeling the utilization of a ~1 billion tonnes of US farm fiber for bioenergy production annually, the USDOE report says the change to farmland allocation will not affect the food supply, either for fruits and vegetables directly consumed by humans, or for feed consumed by livestock (Langholtz et al., 2016).

Farms

In general, rotation of crops improves productivity (Behnke et al., 2018). Integrating profitable intentional fiber crops into rotation can improve soil organic carbon, which means increased farm productivity and sustainability.

Farmers

As value is added to waste fiber from existing crops that is now burned or otherwise disposed of and new profitable intentional fiber crops are introduced in rotation, farming will tend to become more profitable and sustainable.

State and Local Governments

The FMM provides for compensation to governments for loss of tax revenues equal to the market value of affected private forestland. If state and local government would invest those funds, an endowment would be created with annual revenues in excess of what the governments now receive in taxes.

Bioenergy Versus Fiber Production

In 2017, 38.1 million acres (15 million ha), or one-tenth of US farmland was dedicated to ethanol (from the sugar in corn kernels) and biodiesel (from the oil in soybeans) (Merrill and Leatherby, 2018). Current biofuel production does not conflict with fiber and in fact produces a lot of waste fiber. The US Department of Energy has a different vision for most farm fiber biomass: cellulosic ethanol (US Department of Energy, 2018). The FMM has a vision for farm fiber: paper and construction products in lieu of wood. These visions are generally incompatible. Both visions have challenges. Challenges for cellulosic ethanol, which uses extremely fibrous feedstock, are primarily that it is not presently, in the absence of a large subsidy, profitable with current technologies (Hirtzer and Renshaw, 2017). Yet efforts to commercialize cellulosic ethanol continue (Environmental and Energy Study Institute, 2017). Cellulosic ethanol may turn out not be able to compete as a liquid transportation fuel, especially if the US transportation fleet (automobiles, delivery trucks and tractor trailers) continues toward electrification (Bloomberg New Energy Finance, 2017; Heid et al., 2017).

If not rolled back, achievable US fuel efficiency standards for passenger cars, light trucks (Plumer and Popovich, 2018), and heavy trucks (Vlasic, 2016) can dramatically reduce demand of both fossil fuels and farm fuels. As farm fiber production increases, the prices, supplies and demands for farm fuel can adjust, often though efficiency gains that need not materially affect prices.

Food Versus Fuel Versus Fiber Fight?

The United States land area is 1.9 billion acres (0.8 billion ha), 392.7 million acres (158.9 million ha) of which is cropland (Table 8). The FMM finds that ~10% of US farmland currently in production (neither idle nor fallow) would have to be dedicated to intentional fiber production to migrate most US fiber production from forests to farms.

As demand for farmed fiber increases, will it be met at the expense of farmed food? USDOE say food production will not be affected by utilizing agricultural wastes and growing intentional fibers for fuels (Langholtz et al., 2016). Such would also be the case if the fiber were used for paper and construction products. But what if food and fiber from farms does conflict?

Increasing farm fiber production need not come at the expense of the nation's fuel or food supplies, as current food and fuel consumption practices are quite wasteful and inefficient. Great gains could be made in response to competing demands for farmland that would tend to increase food prices. For example, 133 billion pounds (59.4 billion kg) or 31% of the nation's 430 billion pounds (195 billion kg) of food produced in 2010, with a retail value of \$162 billion, was thrown away uneaten at the retail and

Table 8 Cropland use in the United States.

<i>Cropland use</i>	<i>Million acres</i>	<i>Million hectares</i>	<i>Percentage</i>
Livestock feed	127.4	51.6	32%
Food we eat	77.3	31.3	20%
Other grain and feed exports	62.8	25.4	16%
Idle/fallow	52.0	21.0	13%
Ethanol, biodiesel	38.1	15.4	10%
Wheat exports	21.5	8.7	5%
Cotton	13.6	5.5	3%
Total	392.7	158.9	100%
Total not idle/fallow	340.7	137.9	—

Merrill, D and Leatherby, L (2018) Here's how America uses its land. New York, NY: Bloomberg.

consumer levels (Buzby et al., 2014). This does not include losses at the point of production on farms (e.g. fruits and vegetables with imperfect-color and/or -shapes).

If the price of red meat (produced from the one-third of cropland dedicated to livestock feed) increases due to competition of land for forage or fiber, consumption will likely decrease as would greenhouse gas (GHG) emissions. Reducing red meat consumption lowers the risk of dying from eight major diseases by 26% (Etemadi et al., 2017). Animal agriculture contributes between 10% and 25% of total global GHG (higher figure includes deforestation and other land use changes). GHG emissions from beef are orders of magnitude more than other meats. The consumption of 2.2 pounds (1 kg) of beef is equivalent to driving an automobile 99 miles (160 km) (Schwarzer, 2012).

Conclusion

The vast and irreplaceable array of NRMES provided by US forestlands demand that most of such lands no longer be managed for fiber production, but for conservation. It is technically feasible to meet US fiber demand from mostly nonwood plant fibers. With changes in government policy and in consumer demand, US fiber industries can be profitably transformed for the benefit of forestlands, farmlands, the climate, and society.

“All models are wrong, but some are useful” (Box and Draper, 1987). This article outlines a method and presents a very simple model of how to migrate US fiber production from forests to farms. This fiber migration model (FMM) does not consider many variables including, but not limited to, increases or decreases in (1) fiber consumption, (2) fiber recycling, (3) forestland prices, (4) farming costs, (5) population, and many other factors that should be included in further analyses.

Criticism of and suggestions for the model are very welcome. However, it may more the intent and direction of the model—moving most US fiber production from forests to farms—rather than the specifics that is most bothersome to the critic.

The fiber migration model assumes a direct path without diversions, dead-ends and setbacks, or political opposition from vested interests. All will undoubtedly occur, but all can be overcome.

“If you have built castles in the air, your work need not be lost;
that is where they should be. Now put the foundations under them.” Henry David Thoreau, *Walden* (1854).

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Forests Are Not Fuel

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Abstract

As the world seeks solutions to climate change, and in light of the 2015 Paris Climate Agreement, attempts to decarbonize the electric power sector by 2050, a primitive form of energy generation has reemerged as a possible environmentally-friendly solution to fossil fuels. Bioenergy, defined here as the process of turning woody plant based matter into a combustible fuel used in the electric power generation sector, is perhaps the oldest source of energy that humans have known. While bioenergy has been branded as an environmentally-sound solution to the problems of electric power sector decarbonization and climate change, there are a number of issues with an increased global dependence on bioenergy as a replacement for fossil fuels.

This article details the current trends in bioenergy in the United States and globally, with a focus on the European Union. We detail why there has been an increased interest and demand for bioenergy as a substitute for fossil fuels in the electricity sector. Then, we examine the climate impacts of burning forests as fuel. Finally, we document the troubling ecological impacts of increased bioenergy production, alongside some of the troubling human community impacts that arise as a result of bioenergy harvesting, logging, processing, and shipping.

Introduction

As the world seeks solutions to climate change, and in light of the 2015 Paris Climate Agreement, attempts to decarbonize the electric power sector by 2050, a primitive form of energy generation has reemerged as a possible environmentally-friendly solution to fossil fuels. Bioenergy, defined here as the process of turning woody plant based matter into a combustible fuel used in the electric power generation sector, is perhaps the oldest source of energy that humans have known. Bioenergy is an energy-lite resource (8262 Btu/lbs), compared to fossil fuels such as coal (9507 Btu/lbs) and natural gas (19,000 Btu/lbs), meaning that it requires more mass to generate an equivalent amount of electricity ([U.S. Energy Information Administration \(EIA\), 2019b](#)).

Humans have been turning trees and other woody material into burnable fuels to heat our homes and cook our food for thousands of years. Like all combustion-based technologies, wood-based bioenergy (referred to alternatively as bioenergy, biomass, or wood pellets herein) has direct and potentially significant impacts to surrounding air quality through the release of local air

pollutants, as well as carbon dioxide as a result of the combustion process. In addition, there are a number of local hydrological, ecological, and biodiversity impacts to ecosystems from which bioenergy is harvested. While bioenergy has been branded as an environmentally-sound solution to the problems of electric power sector decarbonization and climate change, there are a number of issues with an increased global dependence on bioenergy as a replacement for fossil fuels (Drax Group PLC, 2019).

We detail the current trends in bioenergy development in the United States and globally, with a focus on the European Union (EU), and why there has been an increased interest and demand for bioenergy as a substitute for fossil fuels in the electricity sector. Then, we examine the climate impacts of burning forests as fuel and why this will not help us turn back the rising threat of climate change nor avoid the need to invest in truly renewable energy solutions. We further discuss the troubling ecological impacts of increased bioenergy production, alongside some of the troubling human community impacts that arise as a result of bioenergy harvesting, logging, processing, and shipping. Finally, we highlight a number of environmental justice impacts, primarily within the southeastern United States, as a result of an increasing reliance of bioenergy.

Current Trends in Bioenergy Production and Demand: US and Globally

In the developed world, prior to the emergence of bioenergy as a possible substitute for fossil fuels in the electric power generation sector, bioenergy was and is still widely used in the residential home heating sector. According to the US Energy Information Administration's (EIA) 2015 residential energy survey, wood burning stoves are the primary source of heating for 3.5 million US households (roughly 3% of all households) and the secondary source of heating for 9.2 million households (U.S. Energy Information Administration (EIA), 2019a). In the European Union, an estimated 40% of all wood consumed in 2015 was in the residential heating sector, representing the largest portion of bioenergy consumption (Birdlife, FERN, and Transport and Environment, 2017). However, over the last 15 years, there has been a marked increase in the use of bioenergy in the non-residential sector, in order to produce electricity and thermal energy for commercial and industrial processes. According to the EIA, biomass electricity generation increased 18% between 2005 and 2015, with biomass accounting for almost 1% of all US electricity generation. In 2018, it accounted for around 0.5% of all US electricity generation (U.S. Energy Information Administration (EIA), 2019b) (Fig. 1).

While in the United States, the role of bioenergy in the electric power sector remains small, it has ballooned in the European Union (EU). Over 44% of renewable energy in the EU comes from bioenergy or waste wood, with bioenergy accounting for 7.5% of EU-wide gross final energy consumption in 2016 (Brack et al., 2018). EU demand for bioenergy is substantial and growing, and while European nations are able to produce a significant amount of bioenergy, it is not enough to meet regional demand.

Much of this growth in European demand for bioenergy is being met by increasing global imports. In 2016, it is estimated that 40% of overall wood pellet consumption in the EU was from imports. (Brack et al., 2018) In the United States, bioenergy export production and capacity has increased rapidly over the last few years. In 2012, the United States exported 1.9 million metric tonnes of densified biomass fuel. By 2018, that number had jumped to 6.1 million metric tonnes, more than a 300% increase in just 6 years (U.S. Census Bureau, 2019) (Fig. 2).

The southeastern United States has been the largest source of this expanded global demand for biomass fuels, and each pellet-producing mill has a 120 km sourcing radius (Fig. 3). Since 2012, the US Southeast has been responsible for over 98% of wood pellet exports. This demand eclipses pre-existing demand for other forest products, primarily pulpwood, from the region. From 2012 to 2015, pulpwood generation in the US Southeast decreased by 6.8 million metric tonnes, about 4.5%; in the same time period, the equivalent amount of wood pellet production increased by 5.6 million metric tonnes, or 249% (Table 1). Although

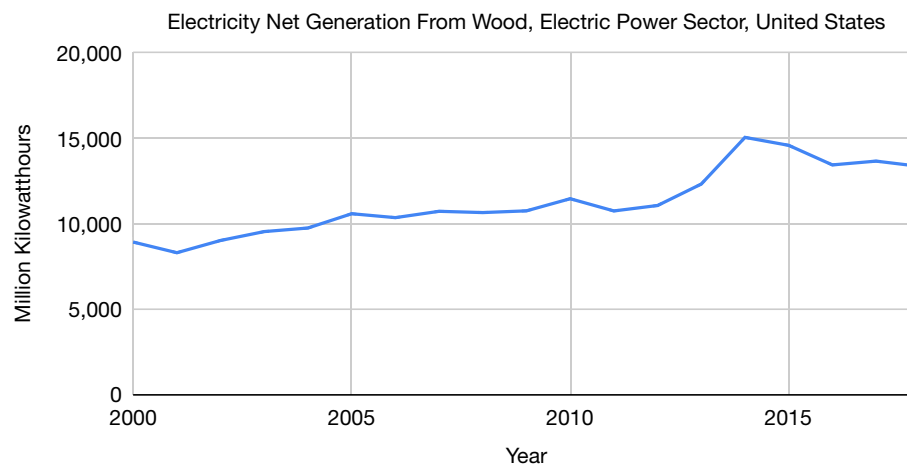


Fig. 1 Electricity (million kilowatt hours) generated from wood, 2000–2018, in the United States.

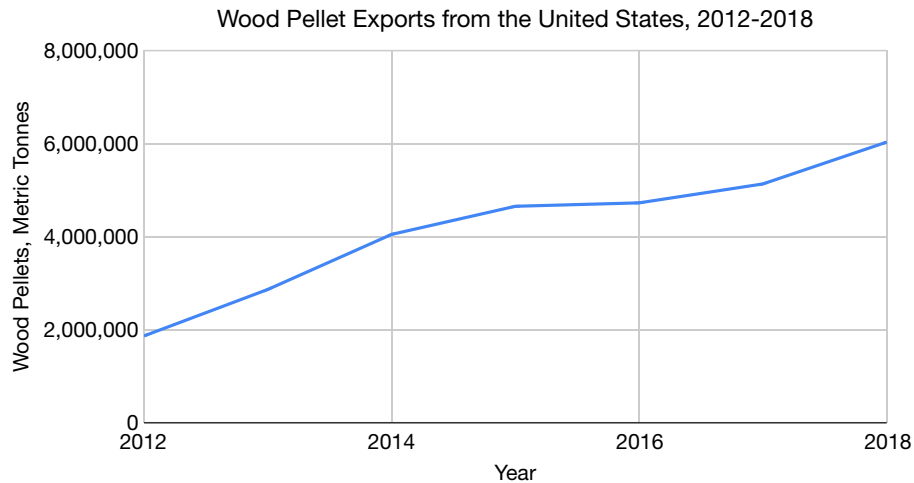


Fig. 2 Wood pellet exports from the United States, 2012–2018. Exports tripled in just 6 years, with nearly all wood pellets (>98%) coming from the US Southeast.

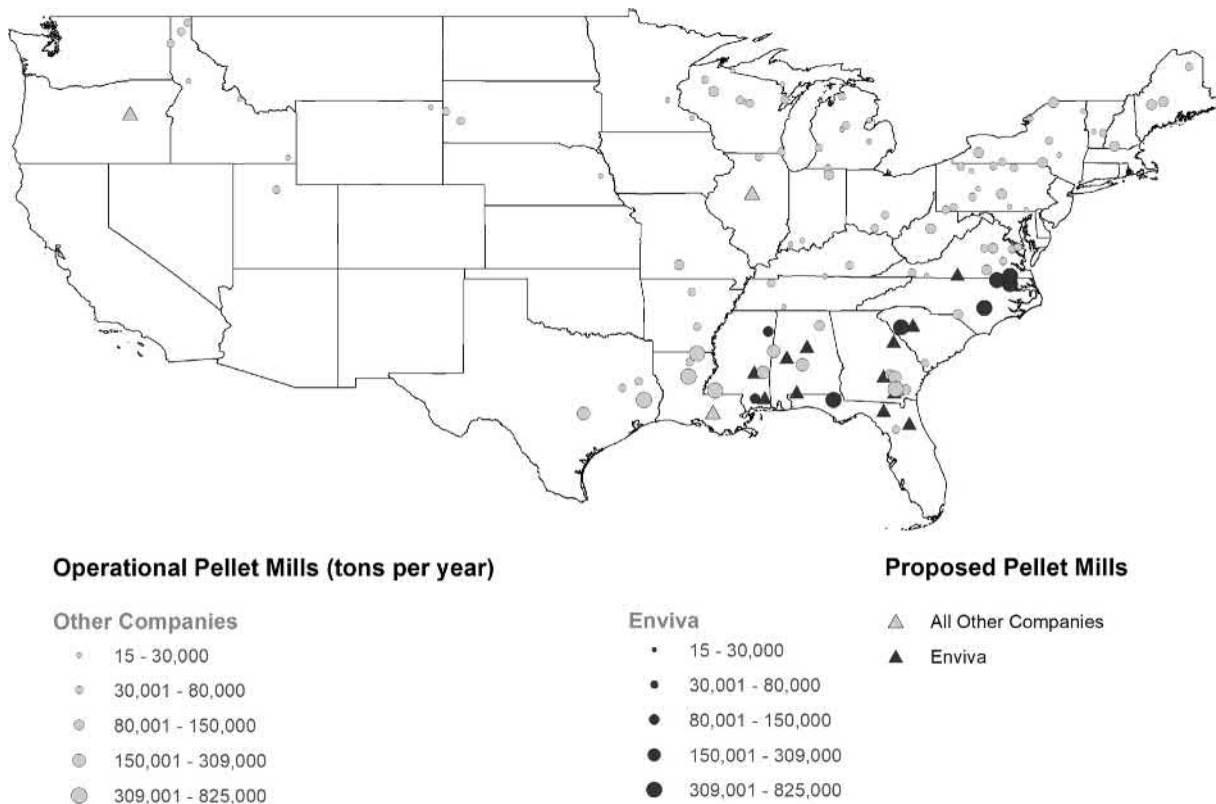


Fig. 3 The locations and operating capacities of current pellet production facilities in the United States.

the demand for bioenergy still represents a relatively small portion of the pulpwood market in the United States, it is growing steadily and may present supply problems in the near future for non-wood pellet US forest products companies. (See [Table 1](#)).

Policy Drivers of Bioenergy Demand

Much of the increased demand for densified bioenergy fuel results from recent changes in international and national policies. We identify two potential reasons for the increased reliance on bioenergy in the electric power sector around the world. First, the rise in global demand for bioenergy has been spurred by a number of national and international climate and energy policies aimed at

Table 1 Pulpwood and Wood Pellet production, 2012–15, US Southeast.

<i>Year</i>	<i>Pulpwood, Green Tonnes</i>	<i>Wood Pellets, Green Tonnes</i>
2012	153,591,595	3,730,472
2013	151,816,980	5,711,590
2014	149,411,769	7,981,178
2015	146,740,931	9,289,367
% Change	4.46%	249.01%
Total change	–6,850,664	5,558,896

Pulpwood green tons retrieved from (Gray et al., 2016) and previous years of reports, converted to metric tonnes. Wood pellet dry tons retrieved from (U.S. Census Bureau, 2019) and converted to green metric tonnes, assuming a standard 50% water content.

encouraging a low-carbon transition and tackling climate change. Second, some countries, such as the United Kingdom subsidize bioenergy use as an alternative to fossil fuels. And finally, subsidizing existing coal-fired powered plants to burn bioenergy is a political win because transforming coal-fired power plants to co-firing plants is a fairly easy process that extends the useful life of an otherwise stranded generation asset.

National and International Climate and Energy Drivers

First, worldwide climate treaties have created perverse incentives to rely on bioenergy to meet climate goals. International climate treaties like the 1997 Kyoto Protocol establish that carbon emissions from direct combustion (excluding harvest, production and transportation of woody material) are counted under the country of origin's Land Use/Land Use Change (LULUC) emissions category (Grubb et al., 1997). However, the United States never ratified the Kyoto Protocol, meaning that bioenergy exported from the US to other countries is not subject to the accounting procedures demanded by the Kyoto Protocol (Hovi et al., 2003). In practice, this means that imports from North America to countries that are parties to the Kyoto Protocol, treaty countries, such as the European Union, are considered “carbon neutral” by the Kyoto Protocol without accounting for the carbon emissions from the combustion process anywhere within the accounting system. This accounting loophole has created a perverse incentive for treaty countries to import bioenergy from non-treaty countries and only account for a fraction of the associated carbon emissions. In addition, the European Union, which established a renewable energy target of 20% by 2020 in 2009 and increased it to 32% by 2030, classifies most woody bioenergy as carbon neutral (Klessmann et al., 2011).

Fuel Switching and Existing Infrastructure

With large and increasing renewable energy targets, countries subject to those targets must consider the cost and extent of switching from coal and other fossil fuels to renewable energies. With many operational coal power plants being potentially phased out in favor of renewable and low carbon energy production options, there has been continued interest in repurposing coal power plants through either co-firing biomass with coal, or conversion to complete biomass combustion (Demirbaş, 2003; Hughes, 2000). In contrast to other renewable energies, biomass presents an opportunity to reuse or improve existing infrastructure instead of needing to build new plants, windmills, or solar panel fields. As a result, many countries party to renewable energy goals, like the Kyoto Protocol, have promoted the use of bioenergy through subsidies and credits.

National Subsidies and Support for Bioenergy

In planning for climate change mitigation, many countries created pathways that rely heavily on the adoption of bioenergy as a pathway to transition away from fossil fuels. As a result, several countries have created substantial subsidy programs to encourage the adoption of co-firing biomass with coal, or transitioning coal-powered plants entirely to wood pellet fuel. In 2012, 12 EU member countries contributed 8.3 billion Euros (9.4 billion USD) in subsidies to biomass usage (Alberici et al., 2014) (Fig. 4).

In the United Kingdom (UK), the largest importer of US wood pellets, renewable energy from biomass and other sources is subsidized through the Renewable Obligation Certificates system, where the government rewards companies with credits for producing renewable energy, which can then be sold to energy delivery companies. The UK's largest power producer, Drax, reported 468 million pounds in profits from Renewable Obligation Certificates, equivalent to just over 593 million USD in 2018 (Drax Group PLC, 2019).

As the use and subsidization of bioenergy rises rapidly in the international economy, many scientists have expressed worry about the longevity and feasibility of bioenergy as a widely adopted renewable technology (Duffy et al., 2016; Editorial Board, 2016; Söderberg and Eckerberg, 2013). There are potentially major impacts to forest biodiversity, resilience, ecosystem services, and carbon balance, as well as impacts to air and water quality, equity, and quality of life in nearby human communities.

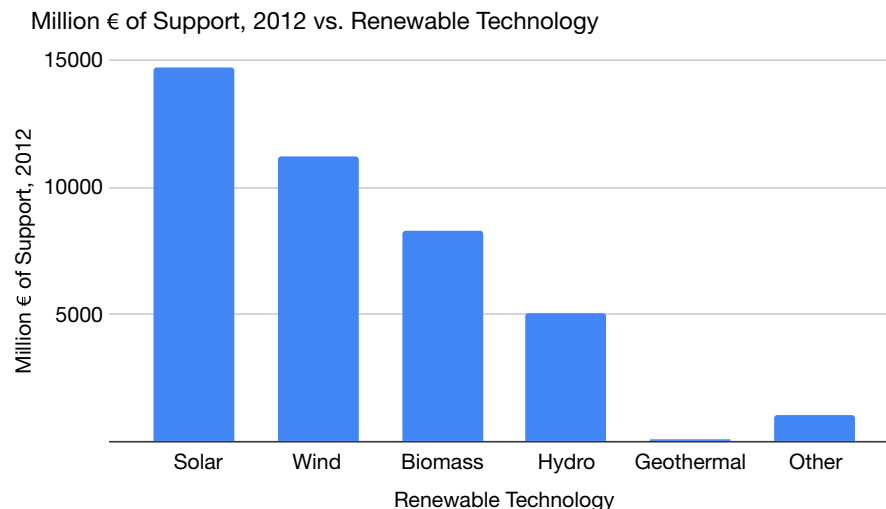


Fig. 4 Financial support from EU member countries to renewable technologies, 2012. Data from Alberici, S., Boeve, S., van Breevoort, P., Deng, Y., Förster, S., Gardiner, A., van Gastel, V., Grave, K., Groenenberg, H., de Jager, D., Klaassen, E., Pouwels, W., Smith, M., de Visser, E., Winkel, T., Wouters, K., 2014. Subsidies and costs of EU energy. European Commission.

Climate Impacts of Forests as Fuel

The extraction of timber for wood pellet production creates direct and indirect greenhouse gas (GHG) emissions into the atmosphere. GHG emissions come not only from pellet burning, but also from the production and transportation processes as well. Furthermore, forest operations can impact soils, altering physical, biological, and chemical properties due to the use of agrochemicals, heavy machinery, and the correlated requirements of lubricants and fuels (Cambi et al., 2015). A suitable way to evaluate the environmental performance and climate impact of the wood pellet industry in terms of pollutant emissions and energy consumptions is through a life cycle assessment (LCA) (see Fig. 5). LCAs assess the extraction and consumption of resources including GHG emissions throughout the entire lifecycle of production extraction and creation (Campbell et al., 2011).

Comparing GWP From Bioenergy to Other Renewable Energies

With many possible GHG emissions from different chemical compounds, it is often necessary to standardize the impact of those chemicals on the global carbon cycle. The Global Warming Potential (GWP), defined by the U.S. Environmental Protection Agency (EPA) as a measure of how much energy the emissions of 1 t of a greenhouse gas will absorb over a given period of time (commonly 100 years), relative to the emissions of 1 t of carbon dioxide (CO₂), is one such measure (Environmental Protection Agency, 2017). This potential depends on the radiative efficiency of the gaseous species and its atmospheric lifetime.

A study conducted in British Columbia, Canada found that the GWP for the production of wood pellets and overseas transportation is 723 kg CO₂ e/t or 0.15 kg CO₂ e/KWh of wood pellets when using natural gas as fuel, and 532 kg CO₂ e/t or 0.11 kg CO₂ e/KWh when using sawdust as fuel in the production process, with an additional 916 kg CO₂ e/t, or 0.19 CO₂ e/KWh stored in the wood and combusted during electricity generation (Magelli et al., 2009) (Because this paper produced numbers by tonne instead of kilowatts, there is some conversion that needs to take place in order to compare between technologies. We estimate that there are 4800 KWh per tonne of wood pellets, and divided accordingly.). Together, this means a GWP range of 0.30–0.34 kg CO₂ e/KWh for wood pellet electricity generation, assuming combustion at 100% efficiency. However, electricity generation from biomass fuel combustion is still only 20–25% efficient (Biomass Energy Resource Center, 2009), and so a final, more realistic calculation would be 1.35–1.53 kg CO₂ e/KWh for wood pellet electricity generation.

On the other hand, similar LCA studies for wind turbines reported GWP values of approximately 0.06 kg of CO₂ e/KWh (Bayindir et al., 2018) and 0.029 kg of CO₂ e/KWh (Tazi et al., 2018). A study made on photovoltaic power systems used in the production of solar energy assets GWP values of 1 kg of CO₂ e/KWh (Frischknecht et al., 2015). In terms of GWP, both photovoltaic power systems (solar) and wind turbines have lower GWP than wood pellets used to generate electricity.

In 2018, the United States exported 6 million metric tonnes of wood pellets which likely released approximately 9 million tonnes of CO₂ e into the atmosphere. If industries continue to invest aggressively in bioenergy and the demand increases by 20% (conservative, based on previous years' expansion rates), in the next 5 years, carbon released into the atmosphere from wood pellet consumption could rise to 22 million metric tonnes of CO₂ e per annum, equivalent to an addition 4.7 million vehicles on the road each year.

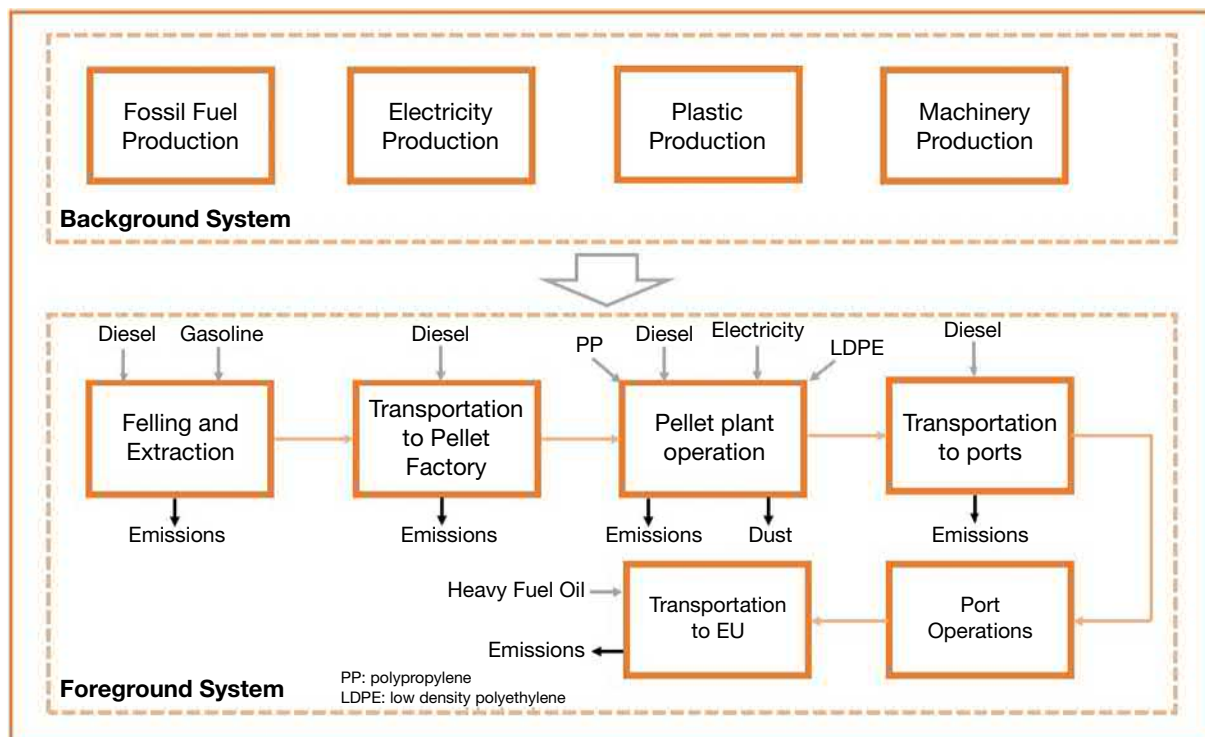


Fig. 5 A model Life Cycle Analysis for wood pellet production. It displays the system boundaries, identifying the different processing stages involved in the LCA for wood pellet production. Additionally, it includes the types of energy used and the emissions associated with the production and transportation.

The Inaccuracies and Assumptions of Carbon Neutrality

Many analyses of wood pellet GHG emissions automatically exclude the carbon stored in the fuel (former trees) itself (Brack et al., 2018; Hoefnagels et al., 2014; Magelli et al., 2009). This is based on the net-growth theory—in short, that because forests are continuing to grow in a given region (predominantly the US Southeast), one can assume that the landscape is automatically absorbing new carbon to replace the carbon in wood pellets that will be burned internationally. Although this is both simple and convenient, this net-growth theory fails to account for the lost growth potential of acres harvested for bioenergy. That is, regional acres will continue to grow whether or not bioenergy harvests occur. There is no additionality to replace the carbon lost during bioenergy harvest.

Instead, consider the acres on which the bioenergy harvest occurs. After harvest there will be a “carbon debt” (C Debt) on those acres until they regrow enough to restore the carbon lost during harvest, and exceed the carbon benefits from previous fossil-fuel based power generation (Mitchell et al., 2012; Walker et al., 2010). Estimates of carbon debt vary widely and are based on variables that primarily include the type of harvest (tops and limbs, large residues, or whole trees) and pre-existing land cover (natural or artificial stands). One study indicates that even just removing harvest residues (tops, limbs) from a harvested site can reduce the mitigation potential by 10–40% (Zanchi et al., 2010). Modeling a coal plant conversion to wood pellets in Ontario, Canada revealed that the carbon debt repayment for their source would not occur until a full 91 years after operation if harvesting specifically for bioenergy (Ter-Mikaelian et al., 2015). The oft-termed “Manomet study” reveals a carbon debt repayment period between 20 and 90 years (Walker et al., 2010). Finally, if a natural forest is replaced with a plantation for bioenergy, carbon debt repayment may take 150–200 years (Zanchi et al., 2010).

The Reality of Bioenergy Production in the US

Carbon debt repayment and GHG emission estimates often make assumptions about the source of wood for pellets that may be inaccurate in the lived reality of the wood pellet market. For example, when studies consider only small residues harvested additionally from sites where other forest products are being sourced from, their relative impact is small (Walker et al., 2010; Zanchi et al., 2010). However, in practice, a large portion of harvested materials in the United States for bioenergy production comes from whole trees and large residues. The standard harvest method in the United States, and especially the US Southeast, is clearcutting. The best wood may go to lumber production, but the bulk of it will go to pulpwood production: paper products and wood pellets.

Enviva, the largest US-based wood pellet export company, reports that < 18% of their input material is from “Sawdust, shavings, residuals from wood manufacturing, or arboricultural sources” (Enviva, 2017). The remaining 82% of input material comes from pine plantations (38%), mixed pine and hardwood forests (40%), and other hardwood forests (5%). Under current conditions, carbon debt repayment is on a timescale much longer than the time currently available to address carbon emissions and prevent the worst impacts of climate change from occurring. Finally, these practices contribute to wide scale impacts on the carbon balance of forests in the US Southeast and nationally.

Ecological Impacts of Forests as Fuel

There are many similarities between traditional forest harvest and forest harvest for bioenergy. As a result, it is necessary to discuss the general impacts of anthropogenic forest disturbance through forest harvest, as well as the additional impacts that demand for bioenergy has brought into natural ecosystems.

Impacts of Harvest on Forest Ecosystems

The United States leads in forest harvest rates

The US, and predominantly the US Southeast, is the second largest producer of pulp and paper products in the world (Food and Agriculture Organization, 2018). As a result, the US Southeast has one of the highest forest turnover rates in the world, four times higher than the rate of South American rainforests (Hansen et al., 2013). Less than half of the forest stands in the US Southeast are older than 40 years (Oswalt et al., 2014).

Impacts on carbon balance of US forests

Although forests in the United States are considered a net sink, not a net source of carbon, this was not always the case. Widespread logging from the 1700 to 1935 released 42,000 Tg (4.2 billion metric tonnes) of carbon into the atmosphere. From 1935 to 2010, just 15,000 Tg (1.5 billion metric tonnes) had been recovered by US forests (McKinley et al., 2011).

Despite current successes in net growth of US forests, modern forest harvests still significantly reduce the growth rate of the terrestrial carbon sink. A joint study between scientists at nonprofit institutions and the US Forest Service revealed that forest harvest activities account for 85% of the carbon emissions from US forests, more than insects, drought, disease, wind, and conversion combined (Harris et al., 2016).

Impacts on rare species

Forest harvest also reduces the frequency of valuable habitat for rare species. The Fish & Wildlife Service found that 56% of all wetland losses in the United States from 2004 to 2009 were attributable to silvicultural activities (Dahl, 2011). Wetlands and wetland forests in particular are reserves of remarkable biodiversity (Junk et al., 2006; Thiere et al., 2009).

Logging activities can impact biodiversity for decades after a forest harvest occurs. In the Mississippi Alluvial Valley, two species of concern, prothonotary warbler (*Protonotaria citrea*) and Acadian flycatcher (*Empidonax virens*), were impacted by the opening of gaps in the forest canopy from harvest activities, and differences in species composition between stands were found for up to 35 years after a forest harvest (Heltzel and Leberg, 2006). Historically, logging has been implicated in the decline of several species, including *Pieris virginienensis*, a rare butterfly native to the eastern US (Davis and Cipollini, 2016). Additional logging impacts are documented in the Pacific Northwest region of the United States (DellaSala et al., 2015), nationally (Heilman et al. 2002), and across the world (Benkman, 1993; Czech et al., 2000; Mackey et al., 2015).

Impacts on water quality in riparian forest systems

During forest harvest, it is often necessary to install temporary or permanent roads, which include temporary or permanent stream crossings for the transport of equipment and logs. Even temporary stream crossings have impacts on temperature, sediment load, and pH (Aust et al., 2011). Even abandoned roads contribute to sediment loads in forest streams (Reid and Dunne, 1984). Although there are voluntary standards (“Best Management Practices”) to prevent the worst impacts to water quality during forest harvest operations, compliance is not always 100%, and compliance rates during biomass harvest has been documented as significantly less than compliance during traditional forest harvest (Barrett et al., 2016). In addition to sediment, high nitrate runoff has been documented from clearcut and patchcut forests for three to 5 years after the harvesting event (Mupepele and Dormann, 2016).

Logging and salvage activities reduce resilience to extreme events

As climate change increases the frequency of extreme events and natural disasters, the desire to engage in “salvage logging” of disturbed ecosystems increases. Often a highly political or economic move, salvage logging could be a significant source of fuel for bioenergy production in the near future (Lindenmayer et al., 2008). However, evidence tends to show that post-disturbance clearcut logging compacts soils, kills seedlings and shrubs associated with forest renewal, increases fine fuels that aid the spread of fire in wildfire prone habitat, and degrades fish and wildlife habitat (Lindenmayer et al., 2008).

Intensive harvest practices harm soil structure and carbon

Nearly 70% of the biosphere's carbon is stored below the ground, in forest soils, around the world (Karsenty et al., 2003). Global soils hold 2400 Petagrams of carbon, about three times the amount of atmospheric carbon currently warming the planet (Paustian et al., 2016). However, forest harvest and especially intensive forest harvest for biomass damages the soil carbon in forests. One study found that over half of the extractable soil carbon was lost in a temperate forest after clear cutting (Lacroix et al., 2016). A meta-analysis showed that biomass harvests reduce soil carbon 15% more than traditional logging, and soils could lose up to 60% of their carbon sink potential after intensive biomass harvest (Achat et al., 2015).

Additional Impacts of Bioenergy Demand on Forest Ecosystems***Bioenergy impacts more acres than solar photovoltaic fields***

Converting wood energy in to usable electric or thermal energy is also less efficient than solar photovoltaic generation. A 50 MW biomass-only electricity generating station with 55.4% efficiency (5 year average from (U.S. Energy Information Administration (EIA), 2019b)) would produce 242,650 MWh per year in usable electric energy under normal operating circumstances in the United States, and use approximately 6300 acres per year of harvested wood and residues (Phillips, 2016). In contrast, a solar photovoltaic field of equivalent MWh would take up roughly 124 acres. In addition, whereas the solar photovoltaic field has a productive life of 25 years, to produce a comparable amount of energy from forest bioenergy would require annual harvest of thousands of acres each year.

Demand for unmerchantable wood

Wood product processing facilities often have strict specifications for accepting incoming wood products. Trunks that are too large, curved, or hollowed can be rejected in favor of better quality of wood. This unmerchantable wood, e.g., curved or hollowed trunks, is accepted and processed by wood pellet plants, and represent a substantial resource for the forest products industry (Hoefnagels et al., 2014). However, these mostly untapped resources also serve as reserves for both carbon and biodiversity (Davis and Cipollini, 2014; Heltzel and Leberg, 2006; Pacific Northwest Research Station, 2003; Rudolphi et al., 2014). Dead-wood legacies, in particular—the type of unmerchantable wood used for bioenergy—accounts for 20–25% of carbon stores in a forest even 62 years after the initial harvest (Schaedel et al., 2017). Expansion of the forest products industry into previously unharvestable areas means that, across the landscape, forest stand age, and therefore, carbon sequestered, will decrease.

Large increases in bioenergy production could impact food security

The pending impacts of climate change include the potential for food insecurity in light of growing populations, increasing frequency and scale of natural disasters, and changes in water availability (Bohle et al., 1994; Brown and Funk, 2008). In addition to these stressors on arable land, the increasing use of wood pellets for electricity and heat generation represents another market pressure on the availability of land for food. Models demonstrating the possibility of major increases in the use of biomass for electricity generation assume massive increases in efficiency of food production coinciding with subsequent decreases in meat consumption (Strapasson et al., 2017). In the United States, if domestic combustion for electricity begins to increase, the U.S. Energy Information Agency estimates an additional 18% increase in US forest harvest is required for every 1% added to current energy production (Duffy et al., 2016).

Community Impacts of Forests as Fuel

The environmental and health impacts to the communities in which bioenergy wood pellets are logged, harvested, processed, and shipped is significant. In the US Southeast, where the bioenergy economy has grown substantially over the last decade, there are 35 wood pellet facilities with a total annual capacity of 9 million dry tons per year (U.S. Energy Information Administration (EIA), 2019b). Due to the economics of harvesting and transporting whole logs to wood pellet processing facilities, most of the timber harvested to produce wood pellets is sourced within a 120 km radius of a facility, which creates a new and substantial burden on roads within the sourcing radius of the pellet facility (Magelli et al., 2009; NRDC, 2015).

Woody biomass and fossil fuels are often burned on-site at wood pellet processing facilities in order to generate thermal energy to dry and process the pellets, which causes an increase in noise and ambient air pollutants such as volatile organic compounds (VOCs) in the immediate vicinity of the wood pellet plant (Anderson and Powell, 2018). The 21 US wood pellet mills exporting to Europe emit a total of 14,500 t of air pollutants per year, including particulate matter, nitrogen oxides, carbon monoxide, and organic compounds. These plants also release 2.8 million tonnes of GHG emissions annually (Anderson and Powell, 2018).

Wood pellet processing tends to have disproportionate impacts on the communities in which pellet facilities and ports are located. According to the National Association for the Advancement of Colored People (NAACP), African-Americans who live within close proximity to a biomass power plant are more likely than any other racial group in the United States to suffer from increased exposure to smog, asbestos, sulfur dioxide, and other air pollutants (Wilson et al., 2011). Finally, there may be other sources of air and water pollution located in communities that have wood pellet facilities, such as meat and poultry farms, industrial and chemical manufacturing, and rail yards and other transportation infrastructure. For example, one county in North Carolina with

a large wood pellet processing plant is also home to a freight train station, natural gas pipeline, chicken processing facility, and natural-gas fired power plant, all sources of local and global air pollutants (Koester and Davis, 2018).

“Environmental justice” was a term that originated in the 1980s and has its roots in the social-environmental justice struggles in the southeastern US. The famous 1982 PCB contamination case of Warren County, North Carolina, a community that was 84% black with per capita incomes 25% below the state median, represents a quintessential example of environmental justice. This case led many poor people of color to demand that their communities not become dumping grounds for toxic waste and harmful industrial and chemical manufacturing (McGurty, 2007). The communities in which wood pellet production facilities are located also tend to be designated environmental justice communities. One study found that poor (above the state median poverty level) communities of color (over 25% percent nonwhite population) in the US Southeast are 50% more likely to have a wood pellet facility sited in their county than wealthier, majority white counties (Koester and Davis, 2018). This trend illustrates the potential environmental justice concerns at play with the expansion of the bioenergy economy in the United States and the increasing global demand for wood pellets.

One recent example illustrates the community and environmental justice concerns of the growing bioenergy industry in the US Southeast. In Hamlet, North Carolina, Enviva, the world’s largest producer of bioenergy wood pellets, opened a 480,000 t-per-year capacity bioenergy processing facility. Hamlet, NC is in the 70th to 90th percentile for Superfund-site proximity, traffic, ozone, PM 2.5, air toxics and cancer risk (US Environmental Protection Agency, 2014). The median poverty level in Hamlet, NC is 27.3%, 7 percentage-points higher than the state overall (Census of Housing, 2013). The nonwhite population of the Richmond County is 37.5%, roughly 16 percentage points higher than the state average (Census of Housing, 2013). In 2019, Enviva was granted an air quality permit from the state’s Division of Air Quality to increase annual production by 16 percent to 570,000 t of dry pellets annually, and then was subsequently challenged in court by three environmental groups, and agreed to install additional air pollution controls to prevent further harm to the overburdened community (Stone, 2019).

Conclusions

Although bioenergy is a “renewable” energy source, it comes with significant costs and impacts to the global climate situations, as well as regional and local ecological and human community impacts. Bioenergy may have a place in the world’s current energy portfolio, however, it should be limited and phased out as quickly as possible. The lifespan, footprint, and climate impacts of other energies are much more attractive than bioenergy as a renewable fuel source.

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Going beyond Forestry: FAO's State of the World's Forests Report 2018

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Abstract

The State of the World's Forests 2018 advocates forests and its linkage to Sustainable Development Goals (SDGs) as a pathway to sustainable development and provides detailed analysis aimed at capturing the contribution of forests and trees to 28 targets relating to 10 SDGs. The report summarizes key policy implications, highlighting the need to: raise awareness and market the benefits of forests and trees to policy-makers and beyond; engage the private sector; integrate forests with the broader sustainable development agenda; invest in transforming the informal sector to unlock missed development opportunities and improve employment conditions.

State of the World's Forests

The State of the World's Forests (SOFO) report was released by Food and Agriculture Organization (FAO) during the World Forestry Week in July 2018. As the full title of the report suggests the data and information analysis provided in the report are focused toward forests being seen as a pathway to sustainable development and linked to the Sustainable Development Goals (SDGs).

In his foreword, Jose Graziano Da Silva, the FAO Director General says, "*The State of the World's Forests 2018* provides detailed analysis aimed at capturing the contribution of forests and trees to 28 targets relating to 10 SDGs."

Table 1 indicates the full range of impacts that forests and trees have on other crucial areas of sustainable development ranging from poverty eradication, gender equality, access to water and energy to conservation of forests, halting biodiversity loss and reversing land degradation. **Box 1** indicates key messages from the State of the World's Forests report.

This publication frequently uses the phrase "forests and trees." A "forest" is defined as land spanning more than 0.5 ha with trees higher than 5 m and a canopy cover of more than 10%, or trees able to reach these thresholds in situ; it does not include land that is predominantly under agricultural or urban use (FAO, 2015). Although trees outside forests are not technically considered as "forests," according to this standard definition they provide multiple economic, social and environmental benefits (UN, 2008) and so have been included within the scope of SOFO 2018.

Using trees along with forests and referring to planted forests on occasions, SOFO 2018 has consciously left out the term plantations thereby avoiding the controversy of re-defining a forest as distinct from plantations and hiding plantations behind trees.

Table 1 Ten Sustainable Development Goals (SDGs).

Sustainable Development Goals (SDGs)	Related to
SDG 2	Ending poverty in all its forms everywhere
SDG 5	Achieving gender equality and empower all women and girls
SDG 6	Ensuring availability and sustainable management of water and sanitation for all
SDG 7	Ensuring access to affordable, reliable, sustainable and modern energy for all
SDG 8	Promoting sustained, inclusive and sustainable economic growth, full and productive employment and decent work for all
SDG 11	Making cities and human settlements inclusive, safe, resilient and sustainable
SDG 11	Ensuring sustainable consumption and production patterns
SDG 13	Take urgent action to combat climate change and its impacts
SDG 15	Protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests
SDG 15	Combat desertification, and halt and reverse land degradation and halt biodiversity loss

Box 1 Key messages from the State of the World's Forests Report

- a. Governments need to foster an all-inclusive approach that promotes the benefits of forests and trees, engaging all stakeholders.
- b. Strategies to achieve the SDGs should consider interlinkages with forests and trees.
- c. Actions on forests, agriculture, food, land use, rural and national development must be integrated in the future if the 2030 Agenda is to be realized.
- d. Investing in the agents of change will spur entrepreneurship and the sustainable management of forests.
- e. Integrating landscape approaches into national strategies and development priorities is part of building the forests of the future.
- f. Policies must be geared toward incentivizing companies and small producers to engage in sustainable forest management, addressing potential barriers to investment and removing motives for clearing forests.
- g. Corporate responsibility for zero deforestation is key.
- h. Trees, parks and forests are a must for planners designing the sustainable cities and peri-urban landscapes of the future.
- i. Clearer picture of the social, economic and environmental impacts of forests and trees across the SDGs will be critical in calculating incentives and managing sector trade-offs, fashioning forest and food security.
- j. Initiatives, measuring out social safety nets, investing in technology and innovation, and determining the level of support needed for different sectors of the economy.

Pathways to Sustainable Development

SOFO 2018 markets the benefits of forests and trees to policy-makers, the donors and the private sector by advocating integration of forests with the broader sustainable development agenda. The report indicates that it “seeks to examine evidence about the contribution that forests and trees – and the people who use and manage them – can make to sustainable development.” “The objective is to strengthen forest pathways to sustainable development as part of the transformational change needed to implement the 2030 Agenda” (p. 2).

In short, “Pathways to sustainable development summarizes key policy implications, highlighting the need to: raise awareness and market the benefits of forests and trees to policy-makers and beyond; engage the private sector; integrate forests with the broader sustainable development agenda; invest in transforming the informal sector to unlock missed development opportunities and improve employment conditions; undertake national and subnational analytical studies; and improve data availability” (p. xiii).

The existence of quantifiable information is the criterion influencing the choice of targets. SDG indicators are used for most of the targets under SDG15, while for the other nine selected SDGs (whose formulation does not refer to forests) “thematic metrics were developed to show evidence of a relationship between forests and trees and the selected SDG target.”

Considering the relationship between forests and trees to nine SDGs, the respective targets can only be achieved if priority and emphasis are given on achieving SDG 15, especially SDG 15.2 which refers to “By 2020, promote the implementation of sustainable management of all types of forests, halt deforestation, restore degraded forests and substantially increase afforestation and reforestation globally.”

In this context when the report states that “the impacts of forests and trees go well beyond SDG15 to contribute to achieving multiple goals and targets across the 2030 Agenda,” (p. xvi) it is not clear where the priority and the emphasis lie since SDG 15 is at the core to stop immediate deforestation. Without achieving SDG 15 by 2020 none of the other SDGs can be achieved.

In Chapter 2 of the report, while quantifying the contributions of forests to the sustainable development goals, “SDG indicators were used for most of the targets under SDG15, while for the other nine selected SDGs (whose formulation does not refer to forests) thematic metrics were developed to show evidence of a relationship between forests and trees and the selected SDG target” (p. 8).

SOFO 2018 admits that “Quantification of forest contributions to the SDGs involves methodological challenges due to a lack of agreed definitions as well as disaggregated statistics and data sets. In several cases, the methodology for this analysis had to rely on literature, case studies, and assumptions, which can provide an overview of trends in contributions but not exact figures” (p. 65).

Assumptions and Trade Offs

While quantifying contributions of forests and trees to SDGs, the report has constantly used presence of markets and access to markets as significant indicators. So, “landscapes made up of farmland and trees or near the forest edges – ecosystems that can support much larger populations than dense forests” contribute more to poverty eradication and “an association between high forest cover and high poverty rates has been confirmed.” Commenting on relationship between poverty levels and remoteness, SOFO 2018 assumes that “governance and rights in remote areas can also be weak” (p. 10).

This is a clear indication of FAO disincentivizing conservation and protection of natural and primary and intact forests.

Similarly confusing and controversial is how FAO, in this report, deals with the complex issue of extraction and harvesting of wood failing to have a robust analysis of impacts for traditional use and practices, and industrial use for energy and consumption. The tenor of its argument is set on a wrong premise where the report states:

"Modernizing the traditional wood energy sector has the power to improve livelihoods, create sustainable value chains and unlock resources for investments in sustainable forest management. The potential of forests is perhaps no better illustrated than by the fact that wood grows back" (p. xi).

The following inferences from the report explain well the problematic:

- Clear and secure forest tenure rights are key for sustainable woodfuel production, as they foster management practices that ensure regrowth or regeneration at least equal to the level of extraction.
- Woodfuel production and harvesting can lead to sustainable green energy. The widespread availability of woodfuel and its ubiquitous market are opportunities for employment and sustainable development.
- Forests and trees contribute to achieving SDG7 by providing woodfuel for cooking, heating and industrial needs (including power generation and cogeneration of heat and power).
- One widespread practice for improving the fuel properties of wood is to convert it into charcoal (which has a greater energy content by weight than fuelwood) so that it burns more slowly and releases less smoke during combustion.
- Woodfuel is also a major component of the global renewable energy supply.
- FAO has estimated that energy from woodfuel is equivalent to roughly 40% of the world's renewable energy supply, which is as much as solar, hydroelectric, and wind power combined. This figure provides an indication of the major contribution that wood-fuel from sustainable sources can make to the global renewable energy mix.

In SOFO 2018, FAO uses available data and statistical analyses to point out a series of trade offs between forest conservation, production forestry and consumption of forest products to attain sustainable development and SDGs. Eradicating poverty, employment and livelihood generation and food security are being shown as reasons for these trade-offs. FAO also proposes unlocking agricultural economy by linking small holder agriculture in forest areas to global value chain. "Harnessing value chains and taking advantage of private sector capacity can increase productivity and local incomes."

The report further uses data for area under long term management plans to show that such area increased by 2.1 billion ha by 2010, equally distributed between production and conservation purposes. Supporting sustainable logging, and independently verified forest management certification schemes, SOFO 2018 indicates that "certified forest area increased from 285 million hectares to 440 million hectares between 2010 and 2014."

These suggested trade-offs and resulting contradictions emerge from the simplistic notion that "Renewability, resource efficiency and responsible sourcing of forest products are at the heart of the concept of sustainable production and consumption" (p. 45).

Though the report identifies agriculture as one of the causes for deforestation, the strategy involves dovetailing forestry with agriculture with focus on agriculture in the periphery and linked to forests. The dovetailing of forestry and agriculture, where small scale agriculture is advocated to be intensified will have its impact on forestry in terms of transforming subsistence agriculture into catering for the market and cash economy, scaling up and using external inputs for increased production and invasion of alien varieties of seeds which can be damaging for the forest lands in terms of biodiversity and soil fertility loss changing the face of forest based agriculture.

Eliminating emissions from land-use change is critical to achieving the Paris Agreement's goal of limiting warming to 1.5 °C. We are barely 11 years away from a critical juncture (2030) by when we need to act to limit global warming to 1.5°. The SDGs also indicate a time limit of 2030 mostly while it is 2020 for forests and natural ecosystems. At the same time, addressing food sovereignty while minimizing ecological losses is one of the major challenges the world faces, and key to many of the Sustainable Development Goals (SDGs). These aims do not represent choices or trade-offs, but challenges that must be approached in an integrated and holistic manner that respects human rights and ensures ecosystem integrity (Dooley et al., 2018).

The sustainable pathway lies in avoiding conversion of natural sinks and enhancing and protecting terrestrial ecosystems, prioritizing transformative agricultural practices to help eliminate over-production and consumption, including shifting diets and reducing demand for land for agricultural expansion. Where natural forests cannot be further logged, advocating even responsible production and consumption in the forest sector cannot be a policy direction to stem global warming and limiting temperatures to 1.5 or 2° and aiming for sustainable development. The first call is to stop deforestation followed by reforestation and restoration.

Agents of Change: Rights of Local Communities and Smallholders

FAO report advocates policies that secure tenure rights for the poor and vulnerable, including indigenous people, landless farmers, rural women and youth, will go a long way to ending poverty and food insecurity. "Investing in these agents of change will spur entrepreneurship and the sustainable management of forests." SOFO 2018 elaborates on the above when it states:

"Integrating forests into sustainable development strategies requires effective partnerships and private sector engagement. Clear legal frameworks, community engagement and coherent policy measures that balance stakeholder interests are part of the enabling environment needed. Policies must be geared toward incentivizing companies and small producers to engage in sustainable forest management, addressing potential barriers to investment and removing motives for clearing forests" (p. xvii).

According to the FAO report, clear and secure tenure rights are recognized as an important prerequisite for the sustainable management of natural resources. The tenure rights cover at a minimum the right to access, make management decisions and withdraw resources from a particular area.

Ensuring only these sets of rights and avoiding rights over forest land, community rights over forest resources, ownership rights over NTFPs and most importantly, the right to community governance (and not simply community-based management) leading to decentralized forest governance, will not be transformative in action. What is also missing is a clear acknowledgement of the role of indigenous peoples and local communities and FPIC. Most of the time, the report has used terms like small scale holders and stakeholders. Not even right holders.

FAO reports from official country statistics show that in 2010, 3% of global forest area was under community ownership (FAO, 2015). The Rights and Resources Initiative (RRI), found that in 2013 in 52 countries (representing nearly 90% of the global forest area) over 15% of forests—or 512 million ha—were either under community ownership or designated for community control. In addition, substantial areas of forest are *traditionally* managed without legal recognition by local communities and indigenous peoples, especially in Africa and elsewhere where customary land rights prevail (RRI, 2015). Estimating that around 100 million ha of forest are partially under community control, SOFO 2018 concludes that “the proportion of forests under community and smallholder management may be as high as 28 percent of the world’s forest area” (p. 12).

In the context of global efforts to protect the world’s remaining forests, securing collective tenure rights represents one of the most cost effective, sustainable and equitable strategies to protect and restore vital ecosystem functions, conserve biodiversity, and reduce rates of forest loss and degradation caused by agribusiness and other industrial land uses (Dooley et al., 2018).

Whereas FAO, through its SOFO 2018, literally uses the policy of secured tenure rights to open up forests to private sector, investment companies, facilitating forestry enterprises, as source of bioenergy and logging, and linking forests and small holder agriculture to global value chains thus advocating increased commercialization and commodification of forests for sustainable development.

It seems that this overt support to security of tenure and rights for forest communities and small-scale holders where secured tenurial rights define the relationship between the land and forests, and the individual or communities, rather than the state controlled and appropriated forest land, is therefore, geared to attract investors.

To attract both public and private investments, with emphasis on more private sector involvement, the report is filled up with lots of data, information and analysis to open up forests as an attractive destination for investment having multiple values and with synergy across multiple sectors.

Ode to sustainable wood

Across the world, the forest sector has provided numerous examples of sustainable wood production and consumption. These include developing policies that encourage the use of wood products for construction, which has been found to have lower embodied energy than comparable building systems using concrete, steel, or bricks. Wood could be used much more in the construction not only of houses but also other structures (such as bridges), although this could be hampered by regulations that do not specifically cover wood, as well as by certain insurance conditions. Although there are positive signs in some countries, the use of wood in construction is still not increasing on a global scale (p. 45).

Norwegian biorefinery Borregaard produces a wide range of biochemicals, biomaterial and biofuel from wood residues that can substitute oil-based products. Speciality cellulose is consumed by the construction, pharmaceutical and food industries, and is used in the production of cosmetics, filters, hygiene products, textiles and paints. One of its key components, lignin, is used in the production of concrete, textile dyes and food ingredients. Its binding properties allow for a significant reduction in the water and cement content of concrete, thus decreasing energy and water use as well as CO₂ emissions in the production process. Borregaard is the world’s largest manufacturer of second-generation bioethanol, with a production of around 20 million litres per year. At present, the refinery delivers bioethanol from its Sarpsborg facility for heavy goods vehicles and buses in the Oslo region (p. 46).

Using wood (including wood waste and residues) more efficiently to meet this demand – doing “more with less” – is crucial to achieving a more resource-efficient, circular and bio-based economy (p. 47).

Conclusions

It is not surprising and unexpected, therefore, that SOFO 2018 dovetails the sustainable forest management with SDGs in trying to establish “forests and trees” as pathways to sustainable development.

Therefore, one of the key findings of the report indicates that forests are being managed more sustainably, and that forests and trees contribute to achieving SDGs related to: livelihoods and food security for many rural poor; access to affordable energy; sustainable consumption and production; climate change mitigation; sustainable forest management.

From the point of view of achieving SDGs, poverty eradication, food security, sustainable forestry, with the slogan of “forest beyond forestry,” the report basically points to the need for integration of forests to the capitalist economy through sustainable (read certification and such other schemes) supply and value chains in exploiting timber, NTFPs and other ecosystem services like tourism.

Wood as fuel and that it provides more than half of national energy supplies in 29 countries including sub-Saharan Africa, is then extrapolated as “Access to affordable energy,” further adding that “forests supply about 40 percent of global renewable energy in the form of woodfuel – as much as solar, hydroelectric and wind power combined” (p. 88).

Forests are, therefore, seen as the source for next generation renewables through utilization of wood as fuel and ushering in of bio-economy. In that sense, even after the phasing out of the extractive industry, forests will be the next source of extraction as “it is a renewable resource,” which is a flawed argument as natural forests cannot be regained; unless in the garb of increasing forest cover and carbon sequestration there is an increase of trees (read plantations).

In Chapter 4 of SOFO 2018, the key findings seem to pose more challenges than suggesting concrete policies to move forward. From providing informal sector jobs, to agroforestry, tourism, sustainable cities, empowerment of women, climate change adaptation to tackling land degradation and biodiversity loss, sustainable forest management (without any clear definition or conceptual clarity) is conclusively demonstrated as a clear winner. A one stop solution to all, being sold as a win-win situation.

In the process of marketing the benefits of forests and its “true value,” FAO loses the plot when it says, “there is a need for the forest sector to become less forest-centric and to focus more on using the 2030 Agenda as an opportunity for a fresh look at what sustainable forest management means in practice” (p. 92). That practice, as advocated in SOFO 2018, essentially highlights certification schemes, sustainable logging, afforestation and REDD+, increasing biomass stock, sustainable tourism, green infrastructure and green economy, harnessing value chain and taking advantage of private sector capacities, zero-deforestation supply chains, multi-stakeholder partnerships to invest in forests and responsible governance.

This linkage of forests and forest communities to the global capitalist market economy will render the forest communities as mere producers and not owners/stewards of forest resources who protect and conserve forest and biodiversity. Customary rights and laws which protects the rights and property rights of the communities are intrinsically linked to resources and traditional practices and not to the market while tenurial rights define the relationship with land and resource use in terms of market where both the market and investment can clearly identify the relationship and, therefore, is seen as an unlocking potential. The customary rights and laws do not clearly identify that and therefore, in the context of the market, locks up the land and resources. The emphasis on tenurial rights and local governance is a ploy to mitigate potential conflict with a notion of protecting the producers, otherwise the production and profits will both collapse.

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Can Young-Growth Forests Save the Tongass Rainforest in Southeast Alaska?

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Abstract

The Tongass National Forest in southeast Alaska is one of the last relatively intact temperate rainforests in the world. Due to public controversy over old-growth logging, the USDA Forest Service finalized a plan in 2016 to transition out of old-growth logging but not until 2032 as the agency claims it needs to log ~17,000 ha of old growth as “bridge timber” until some 114,000 ha of young growth regenerating from prior clearcut logging is readily available. Transitioning out of old growth logging faster than proposed by the Forest Service would maintain fish, wildlife, and climate benefits along with timber industry needs more aligned with the limits of what the Tongass rainforest can sustain. Recent young growth (mainly 55-year old precommercially thinned stands) inventories on the Tongass suggest that the Forest Service can begin a transition out of old-growth logging within 5 years and on a much smaller (~50,000 ha) and predominately young growth land base than the agency proposes in its transition plan, if certain conditions are met.

“The Tongass National Forest is a national treasure. Today, I am outlining a series of actions by USDA and the Forest Service that will protect the old-growth forests of the Tongass while preserving forest jobs in southeast Alaska. I am asking the Forest Service to immediately begin planning for the transition to harvesting second growth timber while reducing old-growth harvesting over time.”

July 3, 2013 Press Release, USDA Secretary Tom Vilsack

Tongass as a World Class Temperate Rainforest

At 6.8 million hectares, the Tongass National Forest in southeast Alaska is the largest national forest in the United States and one of the world’s last relatively intact temperate rainforests (DellaSala, 2011). This national forest is hemmed in by glaciated Coast Mountains to the east and numerous near-shore islands to the west ranging from the Yakutat Forelands in the north to Prince of Wales Island south (one of the largest islands in North America) (Fig. 1).

Some 90% (>2 million ha) of forests on the Tongass is considered “productive” old growth, consisting of structurally complex, multilayered forests with trees >150 years (Schoen and Orians, 2013, also see Fig. 1). Old-growth Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) forests on the Tongass are global carbon sinks (Leighty et al., 2006) that store atmospheric carbon for centuries primarily because the maritime climate limits fire occurrence. The region’s relatively intact watersheds provide ideal conditions (compared to the lower 48 states) for five species of salmonids (*Oncorhynchus* spp.), a principal food source for grizzly bears (*Ursus arctos*), wolves (*Canis lupus ligoni*, unique subspecies), and bald eagles (*Haliaeetus leucocephalus*).

In spite of its global significance, the Tongass is the only national forest in the nation that still clearcuts (clear-fells) old growth on an industrial scale. Old-growth logging began in earnest in the 1950s with peak logging levels achieved in the 1960s–80s (Fig. 2). At the time, “high-grading” of the largest trees was a common practice that concentrated logging in low-elevation systems and on productive karst (limestone base) topography (Schoen and Orians, 2013).

The Tongass is now at a critical juncture regarding its status as a global carbon sink and relatively intact rainforest. Compared to the Pacific Northwest, which overcut old growth decades ago resulting in a shutdown of federal lands logging due to litigation over the imperiled Northern Spotted Owl (*Strix occidentalis caurina*), the Tongass currently has no endangered species. Therefore, there is a unique opportunity to transition out of old-growth logging to avoid future controversial listings.

In 2016, the USDA Forest Service finalized an amendment to the Tongass land use plan to transition out of old-growth logging if certain conditions were met. The transition would provide a potential means to end decades of controversy where the choices were limited to either protect some or clearcut much of the old growth (Fig. 3). A transition would present a third option that would eventually rely mostly on limiting logging to young forests regenerating from prior clearcut logging.



Data sources: NACP Aboveground Biomass and Carbon Baseline Data (NBCD 2000), Aboveground forest biomass for Alaska, USDA-FS FIA & RSAC (from Data Basin by the Conservation Biology Institute)

Fig. 1 Tongass National Forest, southeast Alaska. Map provided by J. Leonard, Geos Institute. Dark green shows forests exceptionally high carbon-biomass important in climate regulation and climate refugia (DellaSala, 2011).

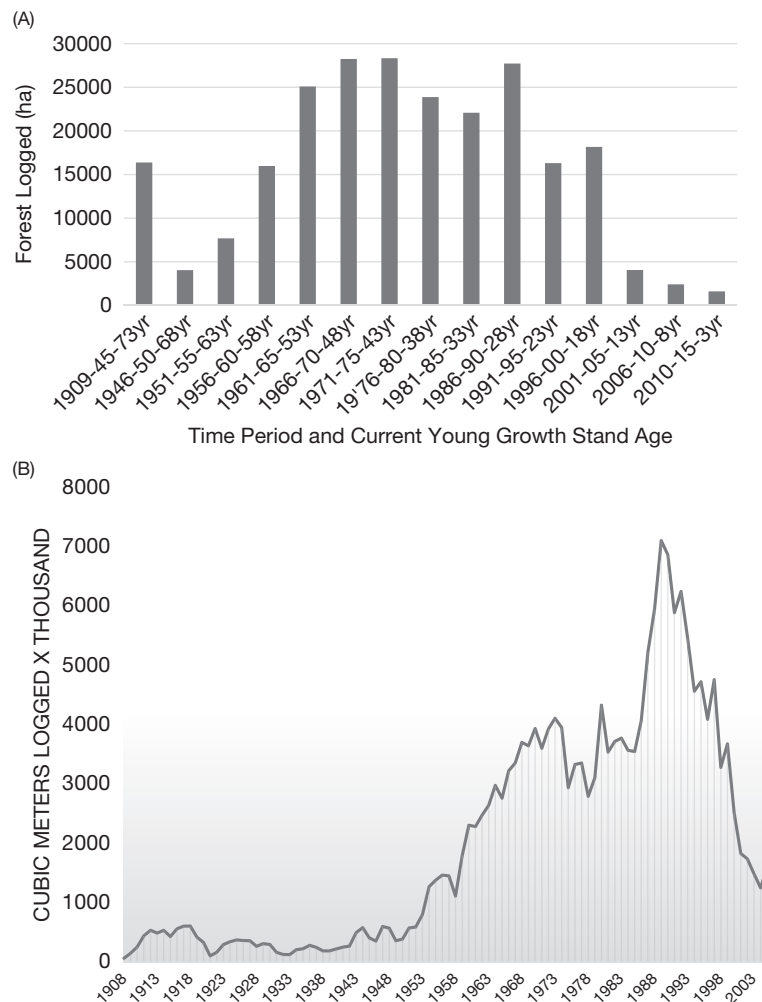


Fig. 2 (A) Tongass National Forest old-growth forest logged from 1909 to 2015 and current (2018) age of logged young stands. (B) Timber volume logged from 1908 to 2006 on the Tongass National Forest. Volume calculations (cubic meters) are based on green and rough sawn at 1 full inch containing ~ 2.4 cubic meters of usable material. Actual recovery of lumber is greater than estimated long log scale and therefore a conversion factor of 6.25 was used to express the data in cubic meters. Data for both figures were extracted from available timber harvest records courtesy of A. Brackley, USDA Forest Service, Pacific Northwest Research Station, Sitka, AK, United States.

To achieve its transition, the Forest Service specified that it would need to log another $\sim 17,000$ ha of old growth during the next 16 years (presumably to 2032) before getting to $\sim 114,000$ ha of young growth needed to sustain industry over a 100-year period at a projected volume of 287.5 million cubic meters annually.

Setting a Transition Timeline: Young Growth Volume

Determining when to transition out of old growth centers on how much young growth is available now and into the future and the commercial viability of young trees (i.e., can industry make a profit?). Only the volume necessary to meet a transition timeline is estimated herein. More detailed timber volume estimates and a study of economic value of young growth trees are currently in progress.

Adjusting Cumulative Mean Annual Increment (CMAI)—young growth stands on the Tongass must reach 95% of CMAI, generally the time at which annual growth of trees begins to level off before a regeneration (clearcut) harvest is attempted (~ 80 – 90 years, pers. commun. A. Brackley). However, the Forest Service can relax this requirement if logging is deemed consistent with other plan components of its land management plan, which, in this case, is a transition out of old-growth logging. Shorter rotation ages allow capture of timber volume in younger age stands. We argue that a rotation age of 55-years can be used to achieve transition quickly, as this age class corresponds to the oldest young growth stands currently available on the Tongass (Fig. 2) and the average quartile mean diameter-at-breast-height of 28 cm, which is currently being exported on private lands in the region.



Fig. 3 Three choices on the Tongass rainforest: (A) protect some of the old growth for ecological, cultural, and climate benefits; (B) log most of the accessible old growth and convert it to commercially producing plantations; and (C) transition into previously logged and now regenerated young growth (D. DellaSala). Note on the Tongass, regeneration following clearcut logging is via natural seed source. No planting is necessary.

Ecological and Operability Constraints on Young Growth Logging—Based on Forest Service inventories, the Tongass has over 173,000 ha of young growth of varying ages (mostly < 50 years; Fig. 2); 71% of this is within roaded and development land-use designations and technically within the timber base (USDA Forest Service 2014). Notably, the Forest Service uses the most current and complete data available on young growth, which provided a foundation for a faster transition (<http://databasin.org/maps/d4ee7a0d9662463289b17bf429f6a0ff/active>).

For this estimate, we included young stands (55 years) within 240 m of operable roads that were either precommercially thinned (PCT) or commercially thinned (CT), on slopes < 72% (based on prior Forest Service analysis), and not within ecologically sensitive areas (Table 1). Precommercial thinning on the Tongass is designed to reduce competition among densely packed young trees (speeding up growth rates) and usually occurs 15–30 years after stand initiation. A second entry via commercial thinning typically occurs at ~60 years with extraction of commercial product.

Young Growth Timber Volume Projections—Based on the logging constraints proposed, sufficient young growth timber volume would be readily available on the Tongass to meet transition requirements (~287 million cubic meters annually) beginning as soon as 2020 (Table 2). Obtaining young growth volume from these stands would reduce the timber land base by > 60% of the Forest Service’s transition footprint. In sum, ~50,000 ha of predominately young growth PCT and CT stands within five Ranger Districts closest to milling operations could support a more rapid transition with reduced insert “environmental” conflicts.

Young Growth Economics: The Bottom Line

Determining the market potential of young growth on the Tongass is in early stages but initial results are promising (Fig. 4). For instance, a commercial thinning project (“Dragon Point commercial thin”) in 70-year old young growth offered by the Forest Service yielded 28.1 million cubic meters with an appraised value of \$440,035. All four timber sale bids received by the agency were above appraised value and one was 81% above appraisal (<http://sitkawild.org/2014/06/dargon-point-timber-sale-local-wood-local-benefits/>). The private sector (mainly Sealaska Native Corporation) also exports Sitka spruce round logs from 50 to 70-year-old young growth in the region.

Table 1 Ecological and operability constraints for a 55-year old young growth timber base within five Tongass Ranger Districts (Thorne Bay, Craig, Petersburg, Wrangell, Ketchikan) closet to timber mills

	<i>Importance</i>
<i>Ecological constraint</i>	
Karst topography	Known to be highly productive and likely to become future old growth via restoration (also the terrain tends to be unstable due to physical and chemical weathering of the bedrock geology)
Wilderness, land-use II designations, national monuments, inventoried roadless areas	High ecological values, mostly old growth, mostly off-limits to logging (out of the timber base)
Beach fringe, riparian buffers	Highly productive ecotones for salmon, bears, eagles, and other wildlife and where logging is restricted via forest plan standards and guidelines
Slopes > 72%	Unstable and erosive
Natural disturbances	To allow for development of complex early seral forests and succession to old growth
Not in the suitable harvest base	Already restricted due to environmental concerns
<i>Operability constraint</i>	
5 Ranger districts with prior log sourcing	Hauling distance
Precommercially thinned within 240 m of operable roads (as determined by the Forest Service)	Already productive with road access
Precommercially thinned with at least partial overlap with a 240-m road access buffer	May have access problems given part of the stand lies outside the 240-m buffer
Commercially thinned stands within 240 m of road access	Additional young growth sites for volume estimates

Table 2 Timber volume scenarios within five Tongass ranger districts (Craig, Wrangell, Ketchikan, Thorne Bay, Petersburg) projected over a six-decade period using precommercially thinned (PCT) stands within ~240 m of operable roads. Carryover volumes are based on harvest levels remaining consistent for each of the scenarios with the carryover from prior periods being used to supplement the harvest base such that there are no rolling green outs

<i>Time period</i>	<i>Annual cubic meters × thousand</i>	<i>Annual carryover/deficit cubic meters × thousand</i>	<i>Additive annual carryover/deficit cubic meters × thousand</i>
2015–19	142,512	– 4362	
2020–24	524,968	290,594	290,593
2025–29	520,119	285,744	576,338
2030–34	475,569	241,194	817,531
2035–39	394,338	159,962	977,494
2040–44	299,850	65,475	1,042,969
2045–49	205,206	– 29,169	1,013,800
2050–54	42,881	– 191,494	822,306
2055–59	194	– 234,181	588,125
2060–64	0	– 234,375	353,750
2065–69	0	– 234,375	119,375
2070–74 ^a	142,512	– 91,862	27,521
2075–79	524,969	290,594	318,106

^aRe-harvest of 2015–19 units begins.

As an important next step to securing a rapid transition, an economic study is needed to determine lumber grade of 55-year old logs, in consultation with experts from the timber industry and Forest Service. Recently proposed on the Tongass, a wood products study would allow mills to sort young growth by “value-added” lumber and determine market response, securing the best possible information on young growth log and lumber recovery, young growth value-added grade recovery, and market response to young-growth wood products.

Climate Benefits of a Rapid Transition

Tongass rainforests not only store more carbon than any national forest in the United States, but also may function as a critically important climate refuge (i.e., first line of defense) given maritime influences that moderate more extreme climate events anticipated for interior Alaska and temperate regions further south (DellaSala et al., 2017). Relatively intact watersheds also provide refuge for old-growth dependent species (including many that are important to subsistence needs), while buffering salmon from cumulative effects of climate change and more extensive logging in the surroundings (especially on private lands) (Watson et al., 2013).

Notably, prior estimates of carbon flux from logging scenarios on the Tongass indicate that *only a no-logging scenario* maintains carbon stores over time. Carbon also has future economic value in terms of avoided costs from global warming pollution and development of carbon-offset markets. For instance, if carbon were stored long-term in old-growth forests instead of being released to the atmosphere by logging, estimated annual economic value of stored carbon would be comparable to revenue generated from Tongass timber sales should carbon markets mature (Leighty et al., 2006). Importantly, an Interagency Working Group on Social Cost of Carbon estimated that the costs of carbon from global warming effects would be \$27–221 per ton by 2050. Recent evidence suggests the costs may be much higher, including large demographic displacements of human settlements along coastlines (Pizer et al., 2014).

Soon after logging old growth, carbon is emitted to the atmosphere via decomposition of logging slash, fossil-fuel emissions from transport and wood processing (e.g., up to 50% of Tongass logs can be shipped overseas), and decay or combustion (within 40–50 years) of forest products in landfills. Planting or growing young trees or storing carbon in wood products does not make up for emissions released from a logged forest, especially one on short timber rotations (< 100 years compared to old-growth forests that store carbon for centuries). Indeed, after an old forest is clearcut, the young forest remains a net CO₂ emitter for 5–50 years, depending on site productivity (see Harmon et al., 1990; Law and Harmon, 2011) (Fig. 5).

Globally, deforestation (8%–15%) and forest degradation (6%–13%) contribute more greenhouse gas pollution than the world's entire transportation network (Estimates are conservative as they were mainly derived from the tropics where the majority



Fig. 4 (A) Young trees on a log deck awaiting processing. (B) Milled beams processed by local Alaskan mill (D. DellaSala).



Fig. 5 Logging on the Tongass National Forest contributes greenhouse gas emissions while depleting fish and wildlife habitat (D. DellaSala).

of forest losses occur—boreal and temperate losses are not available at this time (Intergovernmental Panel on Climate Change, 2007; Houghton et al., 2012). Recognizing the importance of unlogged forests as carbon sinks, scientists have repeatedly called for protecting carbon stored in primary forests as integral to stabilizing global climate change (Mackey et al., 2014), which is why countries have committed to reducing emissions and protecting forest sinks (COP 21 climate agreements).

Tongass Climate Change Refuge: Uncertainties and Risks

Follow Up Research and Monitoring—reliably estimating carbon flux under different transition scenarios requires comprehensive carbon assessment tools. Without the benefit of such analysis, however, the Forest Service claims that logging old-growth forests “could result in *either a net loss or gain of carbon*” (emphasis added) depending on logging practices used even though clearcut logging (a substantial emissions source) is the method of choice on the Tongass (some young tree retentions and small (<4 ha) clearcuts are proposed in young forests within Old Growth Reserves and Beach buffers by the agency). Follow up work, ideally conducted by the Forest Service, in consultation with carbon scientists, is needed to determine logging emissions; however, in prior simulations (as noted), only a no-logging alternative results in continued long-term carbon storage (Leighty et al., 2006).

Climate Shift Happens—effects of climate change on forest productivity represent significant and costly risks to the Tongass’ global status. As the climate warms, other vegetation types may replace carbon-dense conifer forests on the Tongass that evolved during a cooler climate (DellaSala et al., 2017). For instance, during the Miocene millions of years ago, Alaska was a much warmer place dominated by hardwood forests. As current climate change accelerates, it could lower carbon storage potential of conifer forests as hardwoods gradually replaces conifers and some conifers die off (thereby emitting CO₂ as is currently happening with an extensive die-off of Alaska yellow cedar *Cupressus nootkatensis*; Hennon et al., 2012). However, the maritime climate of the Tongass also might ameliorate some of climate-mediated impacts compared to more extreme changes for interior Alaska and temperate rainforests to the south, but only if old-growth forests are intact (DellaSala et al., 2017) (Fig. 6).

In sum, the Tongass is a global carbon sink; however, this sink may increasingly become an emissions source due to old-growth logging (DellaSala, 2011). Choosing a climate responsible and rapid transition for the Tongass would better safeguard Alaska’s climate, comply with the COP 21 Paris climate change agreements and the global pledge by governments and entities to end global deforestation.

“We share the vision of slowing, halting, and reversing global forest loss while simultaneously enhancing food security for all. Reducing emissions from deforestation and increasing forest restoration will be extremely important in limiting global warming to 2°C.” United Nations Climate Summit New York Declaration on Forests (agreed to by 157 governments, including the United States, indigenous groups, corporations, NGOs, and others).



Fig. 6 Relatively intact forest landscape (potential climate refuge) within Mendenhall Glacier National Park near Juneau, Alaska (A. DellaSala).

Conclusions

The Tongass is one of the last places on Earth where primary forests (unlogged) are still relatively abundant but declining. This critically important rainforest provides Alaskans with unparalleled economic (e.g., recreation and tourism economies greatly exceed logging related jobs and revenue), ecological, and climate benefits (Schoen and Orians, 2013). Using Forest Service inventories, a rapid transition could (1) begin in 2020 as 55-year stands become increasingly available compared to the agency's 2032 transition that relies mostly on old growth logging to get to a transition stage; (2) achieved on a much smaller land base (~50,000 ha of young growth vs. a mix of 114,000 ha of young growth and 17,000 ha of old growth); and (3) result in substantially less carbon emissions along with ecological and cultural benefits sustained over time. Under a rapid transition, logging would occur within areas of relatively low controversy, reducing litigation costs and uncertainty of timber supply to local mills. An economic assessment of young growth is needed to fully assess viability of young trees.

The Tongass is the only national forest still clear cutting old growth on an industrial scale. Other national forests such as the Siuslaw in Oregon are generating young growth timber volume as part of a 1990s-transition due to policy reforms enacted. The time for the Tongass to make a transition is rapidly approaching if the Forest Service will act while there is still significant old growth remaining to conserve and without the controversy of future endangered species listings and ongoing timber wars.

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Negative Emissions From Stopping Deforestation and Forest Degradation

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Abstract

The magnitude of gross sources and sinks of carbon from current land management practices suggests that, if deforestation and forest degradation from human activities were stopped, and forests were allowed to recover (e.g., harvested forests and the fallows of shifting cultivation), an estimated 4.4 PgC might be removed from the atmosphere each year for the next century or more. Although the cumulative removal by 2100 would amount to ~360 PgC, this long-term estimate represents a gross removal. The net removal would be considerably less because carbon held presently in wood products and in cultivated and disturbed soils would be emitted to the atmosphere even if further deforestation and harvests were stopped. Accounting for these committed emissions, a more likely estimate is that 100–130 PgC might be removed from the atmosphere by 2100 in recovering forests. The quantity is not enough to counter emissions under a business-as-usual future, but it is large (30–60%) relative to the carbon emissions *allowable* for staying under a warming of 2°C. Thus, land management, and forest management in particular, could help stabilize concentrations of CO₂ in the atmosphere and provide a bridge for the transition from fossil fuels to renewable forms of energy.

Introduction

Forests play a large role in the global carbon cycle and thus in the world's climate. Carbon dioxide is the principal greenhouse gas responsible for the warming of the earth, and forests hold nearly as much carbon in their vegetation (about 450 PgC) (1 petagram = 1000 metric tons) and soils (380 PgC) as is contained in the atmosphere (currently about 850 PgC). Furthermore, the carbon held in forests is dynamic. It is released to the atmosphere almost instantaneously when a forest burns, and is withdrawn from the atmosphere and re-accumulated again on land as forests grow. Thus, the potential for forests to change the concentration of carbon dioxide in the atmosphere is large.

The total amount of carbon held in the vegetation of forests at present is about half the amount they would hold in the absence of human activity (Erb et al., 2017), for example, the expansion of agricultural lands and the harvest of wood for fuel and building material. The losses of carbon occurred over centuries as a result of population growth and economic development, and continue today as forests are cleared for new agricultural lands, especially in the tropics. Current net emissions of carbon from land management account for about 10% of total anthropogenic emissions of carbon, which were 11.2 PgC year⁻¹ in 2016.

If society is serious about limiting warming to an increase of no >2°C, emissions of carbon dioxide and other greenhouse gases must be reduced sharply. The *allowable emissions* (the amount of carbon that can be released to the atmosphere with a reasonable chance (66%) of staying below a warming of 2°C) are 160–338 PgC, equivalent to between 14 and 30 years at current emissions rates. Because transitioning from fossil fuels to renewable fuels (largely solar and wind) will not be easy or fast, society will have to find ways to remove carbon dioxide from the atmosphere. Stopping deforestation is not enough. The good news is that terrestrial carbon reservoirs are only half full as a result of past management. Although most agricultural lands are unlikely to be returned to forests, there are large areas of land that could be reforested and large increases in carbon stocks that could be achieved simply through growth of trees within forests.

One approach to removing carbon dioxide from the atmosphere (negative emissions or Carbon Dioxide Removal (CDR)) is through forest growth, increasing both forest area (through reforestation) and carbon storage per unit area (through improved forest management) (Griscom et al., 2017). Other, more high-tech approaches are advanced, but they are largely experimental or being

developed. They suffer from the energy required to remove carbon dioxide from the atmosphere. Trees do it for free, although there is an opportunity cost for dedicating land for forest growth. The other advantage of using forests to remove carbon dioxide from the atmosphere is that the consequences are known and generally benign. The same cannot be said for technological solutions for CDR. Forests provide reservoirs of biodiversity as well as food, fiber, fuel, recreation, and spiritual gratification for millions of people.

Stopping deforestation is not enough. Lands, and forest management in particular, offer the potential to take carbon dioxide out of the atmosphere. How much carbon might be withdrawn from the atmosphere through management, and how rapidly, are the subjects of this article.

The Global Carbon Budget

Before reviewing estimates of the potential for forest management to remove carbon dioxide from the atmosphere, it is useful to explore how forest management has affected carbon storage until now. That background will provide a perspective and some guidance for the future. Annual emissions of carbon to the atmosphere and the distribution of those emissions in the atmosphere, land, and oceans are summarized in the global carbon budget (from [Le Quéré et al., 2018](#)). The units are PgC year⁻¹ averaged over the 10-year period 2007–16.

Emissions		Distribution		
Fossil fuel and cement production	Land management	Accumulation in the atmosphere	Oceanic uptake	Residual terrestrial sink
9.4 ± 0.5	1.3 ± 0.7	4.7 ± 0.1	2.4 ± 0.5	3.6 ± 0.8

An important observation for this article is that the land appears twice in this budget, first as the net emissions from land management (e.g., deforestation and reforestation, harvest of wood products), and second as the net uptake of carbon by land ecosystems (the residual terrestrial sink). As the name implies, this residual terrestrial sink is calculated by difference. It exists because the global carbon budget is balanced, and the four other terms are obtained independently. A terrestrial sink of nearly the same magnitude as the residual is calculated by terrestrial carbon models (DGVMs = Dynamic Global Vegetation Models), strongly suggesting that its causes are reasonably well known. The sink represents the response of terrestrial ecosystems to indirect and natural effects (i.e., CO₂, climate change, nitrogen deposition). More simply, the first terrestrial term refers to the effects of management, and the second to indirect or natural environmental effects on terrestrial ecosystems.

Both terrestrial terms are net values (positive indicates emissions to the atmosphere; negative indicates removals from the atmosphere). The net emissions from land management include the gross emissions from burning and the decay of wood products and cultivated soils, and the gross removals from the re-growth of forests following harvest and the re-accumulation of carbon in soils following agricultural abandonment. Similarly, the residual terrestrial sink is composed of both gross emissions, for example from droughts, forest fires and thawing permafrost, and larger gross sinks from CO₂ fertilization, longer growing seasons, and warming of cold regions.

Separating the management effects from environmental effects is nearly impossible for any unit of land smaller than the globe. Thus, while managed and unmanaged lands can be distinguished, and the emissions from managed lands can be assigned to particular areas, the same is not true for the residual net sink. The residual term applies to both managed and unmanaged lands because they both respond to changes in the environment. As a consequence, assigning the residual sink to particular locations or types of land use is difficult.

Emissions of Carbon From Land Management: The Past

Land management is also referred to as Land Use and Land-Cover Change (LULCC), where land use (LU) includes management within an ecosystem (e.g., wood harvest) and where land-cover change (LCC) includes the conversion of one type of ecosystem to another (e.g., deforestation for croplands). A recent study by [Houghton and Nassikas \(2017\)](#) reconstructed annual changes in five types of LULCC over the period 1850 to 2015: croplands, pastures, tree plantations, industrial wood harvest, and fuelwood harvest. Rates of wood harvest and agricultural expansion were obtained primarily from the FAO after 1960 and from other sources of data before that date. A carbon-tracking (bookkeeping) model was used to simulate conversions and harvests of 20 types of native ecosystems based on the distribution of managed lands relative to native ecosystems. Carbon densities of forests (MgC/ha) in 1700 were adjusted to yield ending (2015) national densities reported by [FAO \(2015\)](#), the assumption being that 300+ years of land and forest management changed the average carbon density of a country's forests. Carbon densities decreased as primary forests were converted to secondary forests as a consequence of wood harvest. The turnover times of wood products depended on end uses, which included fuelwood (1 year⁻¹), pulp and paper products (0.1 year⁻¹), and lumber products (0.01 year⁻¹) ([FAOSTAT, 2015](#)).

[Houghton and Nassikas \(2017\)](#) used a bookkeeping model with prescribed changes in the carbon density of vegetation and soils in response to management. The model accounted for all pools of carbon on managed lands, including living vegetation, dead vegetation (or slash), wood products, and soil carbon. The emissions of carbon from anthropogenic burning and draining of peatlands in Southeast Asia were included. Rates of decay and regrowth varied geographically but were assumed constant from 1700

to 2015. That is, the effects of elevated CO_2 , climate change, and nitrogen deposition on rates of carbon accumulation or loss were not included in the calculations. Only the direct effects of land management were considered. Thus the analysis quantified the first terrestrial term in the global carbon budget.

The calculated annual emissions of carbon from land management in the tropics and northern and southern mid-latitudes are shown in Fig. 1. Annual net emissions, globally, varied for most of the last 165 years between 0.5 and 1.0 PgC year^{-1} , grew to a peak of about 2.0 PgC year^{-1} in the 1990s, and declined since then. Although the net emissions from northern temperate zone and boreal forests dominated global emissions until about 1910, those lands have become a growing net sink for carbon since about 1960. Currently that net sink is about $-0.3 \text{ PgC year}^{-1}$ (Table 1). In contrast, the emissions from tropical forest management generally increased over the last 165 years to a current value of 1.4 PgC year^{-1} .

Total carbon emissions from land management amounted to 145 PgC over the period 1850 to 2015 (Table 2). By far the greatest emissions resulted from the expansion of croplands, in part because cultivation results in a loss of 25–30% of the carbon in the top meter of soil, whereas other types of management have lesser effects on soils. Estimated emissions from the expansion of pastures were probably underestimated by Houghton and Nassikas (2017) because the study did not include the losses of soil carbon from overgrazing. Note that carbon accumulated in forests (negative emissions) as a result of fire management in the U.S. and as a result of the expansion of tree plantations, globally.

The analysis by Houghton and Nassikas (2017) provides a starting point for asking how past management might be changed to maximize the removal of carbon dioxide from the atmosphere. More specifically, how much carbon might be removed from the atmosphere if deforestation and wood harvest were stopped, and if shifting cultivation were to be replaced by permanent agriculture, allowing fallow lands to return to forests?

Potential Negative Emissions

The critical information for estimating the potential for forests to remove carbon dioxide (negative emissions) is the *gross* rate at which carbon is removed from the atmosphere as a result of land management. So far this article has discussed net emissions of carbon. It is now appropriate to discuss the gross emissions and removals that comprise net emissions. Gross emissions result from burning and decay of wood and from oxidation of soil organic carbon, and the gross removals result from forest growth (following harvest) and recovery of soil carbon when cultivated lands are abandoned.

Not all land management practices yield gross emissions. For example, there are no sinks with deforestation; gross emissions are the same as net emissions. In contrast, the harvest of wood includes both positive emissions from decay of debris and oxidation of wood products and negative emissions in recovering forests. Rotational uses of land generally have large gross emissions, often removals offsetting emissions, with lower net emissions than uni-directional land conversions (e.g., deforestation).

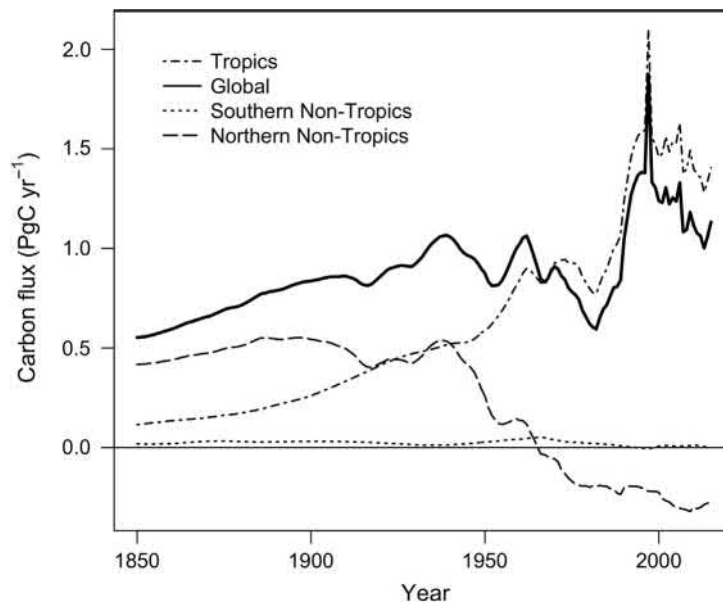


Fig. 1 Annual net emissions of carbon from changes in land management 1850–2015. From Houghton, R.A. and Nassikas, A.A. (2017). Global and regional fluxes of carbon from land use and land-cover change 1850–2015. *Global Biogeochemical Cycles* **31**, 457–472.

Table 1 Net and gross sources (+) and sinks (–) of carbon from land management (PgC year^{–1} averaged over the 10-year period 2006–2015)

	<i>Net emissions^a</i>	<i>Gross emissions^b</i>	<i>Gross sinks^b</i>
Temperate and boreal regions	–0.3	0.8	–1.1
Tropical regions	1.4	4.7	–3.3
Global	1.1	5.5	–4.4

^aFrom Houghton, R.A. and Nassikas, A.A. (2017). Global and regional fluxes of carbon from land use and land-cover change 1850–2015. *Global Biogeochemical Cycles* **31**, 457–472.

^bFrom Houghton, R.A. and Nassikas, A.A. (2018). Negative emissions from stopping deforestation and forest degradation, globally. *Global Change Biology* **24**, 350–359.

Table 2 Total net emissions over the period 1850–2015 attributable to individual land uses

<i>Land use</i>	<i>1850–2015 Cumulative emissions (PgC)</i>
Crop	98.4
Pasture	16.3
Deforestation for other lands	16.1
Fuel wood	13.5
Industrial wood	11.8
U.S. fire management	–10
Peat	6
Planted forest	–7
Total net emissions	145.5

From Houghton, R.A. and Nassikas, A.A. (2017). Global and regional fluxes of carbon from land use and land-cover change 1850–2015. *Global Biogeochemical Cycles* **31**, 457–472.

Forest Biomes in Temperate and Boreal Zones

Most countries in the temperate zone and boreal regions carry out systematic and repeated forest inventories that provide estimates of forest growth, harvest, and mortality. With some exceptions, forest dynamics and, more broadly, land use and management are generally better documented in these countries than they are in tropical regions.

According to the analysis by Houghton and Nassikas (2017) annual net emissions of carbon from the world's temperate and boreal forests were ~0.5 PgC year^{–1} for most of the 19th century but declined after ~1940 and became negative after ~1970 (Fig. 1). Gross removals of carbon from the atmosphere (negative emissions) were twice as large, averaging a little more than –1.1 PgC year^{–1} in recent years (Table 1), and provide one estimate of the role that non-tropical lands could play in slowing global warming if the (positive) emissions from deforestation and forest degradation were eliminated.

The term “degradation” is perhaps unfortunate here. It refers to a reduction in carbon storage: a harvested forest holds less carbon in its trees than it did before harvest (Kurz et al., 2018). Unfortunately, even sustainably managed forests are “degraded” in terms of carbon stocks, although they are far from degraded in a forester's view.

Not all emissions will be eliminated if harvests are stopped. Some of this year's emissions result from pools of wood products and debris that have built up over decades and from continued losses of soil carbon associated with recent changes in management or land use that have not yet come to equilibrium. The legacy or committed emissions will continue even if the clearing and harvesting of forests are discontinued, as illustrated in Fig. 2A, in which all land use and harvests were stopped after 2015. Gross (positive) emissions did not fall to zero in 2016 when land harvests were stopped but did decline exponentially, as expected from rates of decay, and were about 0.1 PgC year^{–1} by 2100.

Gross negative emissions will also decrease if deforestation and harvests are stopped because young forests will no longer be created, and aging forests remove carbon from the atmosphere at a lower rate. The net effect of stopping any further management results in an initial surge in negative emissions but then a decline as gross removals fall faster than gross emissions. Over the period 2016 to 2100, 19 PgC would be removed from the atmosphere if deforestation and degradation were discontinued in the temperate zone and boreal regions (Table 3); i.e., if no wood harvest were to occur after 2015.

Stopping all further LULCC after 2015 sets a biophysical upper bound on negative emissions without consideration of land ownership, costs, or other social factors. To provide alternatives to such an extreme change in management, Houghton and Nassikas (2018) considered two additional simulations. In one, they stopped only deforestation after 2015 but allowed wood harvest to continue into the future at today's rates. In the second simulation, they enhanced the carbon sequestration potential of harvested wood products by increasing their lifetimes by a factor of 10 and by harvesting more efficiently (halving the amount of slash or woody debris left on the harvested site). Again, these simulations represent what is possible, biophysically; they are not projections of future land management.

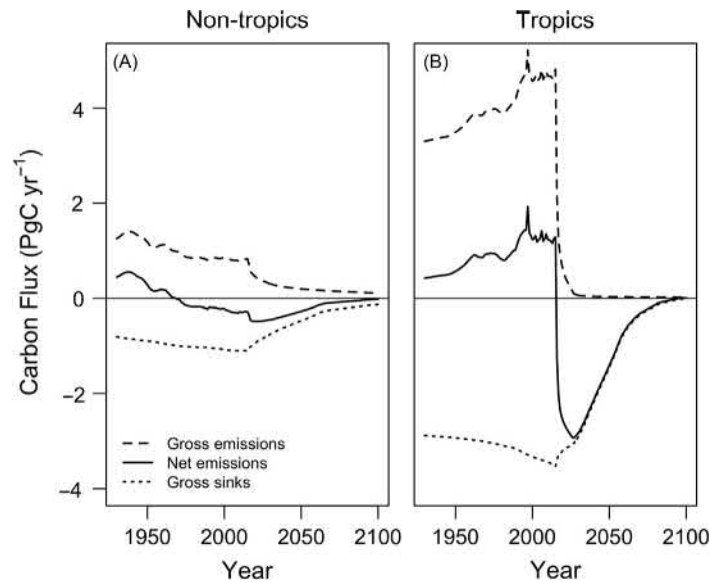


Fig. 2 Annual net and gross emissions of carbon from land management in northern mid-latitudes (A) and tropical forests (B). After 2015, clearing and harvesting of forests was stopped in the simulations and lands in shifting cultivation (forest fallows) were allowed to return to forests. From Houghton, R.A. and Nassikas, A.A. (2018). Negative emissions from stopping deforestation and forest degradation, globally. *Global Change Biology* **24**, 350–359.

Table 3 Cumulative amount of carbon (PgC) added to (+) or removed from (–) the atmosphere between 2016 and 2100 according to simulations described in the text

Simulation	Temperate and boreal regions	Tropical regions	Global
Business-as-usual (includes shifting cultivation in the tropics)	–10	56	46
Stop all LULCC after 2015	–19	–15	–34
Stop all LULCC after 2015 and abandon shifting cultivation	–19	–98	–117
Stop deforestation only	–8	–2	–10
Extend lifetimes of wood products	–28	–8	–36

From Houghton, R.A. and Nassikas, A.A. (2018). Negative emissions from stopping deforestation and forest degradation, globally. *Global Change Biology* **24**, 350–359.

Increasing harvest efficiency and lengthening the lifetimes of wood products increased cumulative negative emissions in temperate and boreal forests to –28 PgC (Table 3). This simulation resulted in the largest cumulative negative emissions for temperate and boreal zones.

Surprisingly, the negative emissions from stopping deforestation (–8) were less than in the business-as-usual simulation (–10), where rates of deforestation and harvest continued at 2015 rates. The explanation for lower negative emissions is partly that wood harvest resulted in a net gain of carbon in wood products and forests, and partly that some deforestation was for tree plantations. When deforestation was stopped, more harvests were in primary forests (higher biomass) instead of plantations, and the associated emissions were higher.

In general, both negative and positive emissions declined in the simulations. Negative emissions declined because the area of secondary forests declined; and that area declined because harvesting was stopped. Once recovered from harvest, forests were assumed not to accumulate additional carbon in the bookkeeping model. Positive emissions declined as well, in part because of reduced deforestation and reduced harvests, but in part because the large pools of wood products present in 2015 also declined. Future net emissions can be thought of as the balance between starting (2015) pools of wood products (future sources), on the one hand, and starting areas of secondary forests (future sinks), on the other. Rates of release and uptake by these respective pools are not necessarily symmetric, and annual net emissions will vary over time. Fig. 2A shows the two declining gross emissions (positive and negative) after 2015, when all LULCC was discontinued.

Tropical Forest Biomes

In the tropics the *gross* rate at which carbon is removed from the atmosphere as a result of land management is uncertain. Because systematic forest inventories are rare, the area of tropical forests growing as a result of current and past land use is not known. At one extreme, it is possible that most tropical forests are recovering from previous harvests, clearing, and abandonment (i.e., they are

dynamic). At the other extreme, it is possible that most forests in the tropics are fully grown (i.e., static). Management is so rare in the latter case, that most forests are “recovered” and not “recovering”—or at least not accumulating carbon as a result of management. Large areas of secondary forests suggest large gross sinks (negative emissions), that could become *net* sinks if the activities generating positive emissions (harvests and degradation) were stopped.

A Conservative Estimate

One estimate of gross removals (negative emissions) in the tropics was given by Houghton and Nassikas (2017) ($-0.5 \text{ PgC year}^{-1}$ over the decade 2006–2015). That estimate is conservative because the only rotational land use the analysis included was harvest of wood, while a major form of rotational land use in the tropics is shifting cultivation. Although data on the practice of shifting cultivation are lacking at a tropics-wide scale (the study by van Vliet et al. (2012) is an exception), there are at least two indications that shifting cultivation, or something very much like it, has increased the area of secondary, or growing, forests.

The term shifting cultivation is used broadly here to include any rotational land use. It includes the traditional practice: clearing forest, cropping the land for a few years, allowing forest recovery during a period of fallow (5–20 years), and then re-clearing. But it also includes any form of temporary slash and burn agriculture that clears land every few years. The practice refers to the temporary use of forest for short-term crops or pasture, subsistence agriculture, agroforestry, illegal logging, and other uses. It represents the area of forest that was recently or is repeatedly used.

An Excess Loss of Forest Area

One indication that rotational land use in the tropics is more common than assumed by Houghton and Nassikas (2017) is the observation that rates of tropical deforestation reported by the FAO often exceed the increase in permanent agricultural lands (croplands and pastures) (Fig. 3). The most recent Forest Resource Assessment (FRA) (FAO, 2015) reports changes in forest area only since 1990, but as much as 40% of deforestation since then has been for “other land”. Other lands are defined by FAOSTAT (FAOSTAT, 2015) as all lands that are not permanent croplands, pastures, or forests: the area is simply calculated as a residual. The reported changes raise two questions. If forests were not converted to croplands or pastures, what were they converted to? And, what were the rates of deforestation for these other lands before 1990, when the data were first reported?

Since 1990, the annual conversion of tropical forest to other land has averaged about 3 million ha/year and was sometimes as high as 6 million ha/year. The annual increase seems too large to be accounted for by increases in urban or settled lands or by an expansion of mining or other non-agricultural activities. It also seems unlikely that all of the “excess loss” is an error. Some forest loss may have been overestimated by the FAO (precision varies among countries reporting), and the sum of the reported increases in croplands and pastures may have been underestimated, but the discrepancy is too large to be entirely the result of error.

The rates of tropical deforestation reported by the FAO (2015) (an average of 9.0 million ha/year between 2000 and 2012) are not larger than the rate of forest loss observed with satellites (Hansen et al., 2013) (average of 9.4 million ha/year).

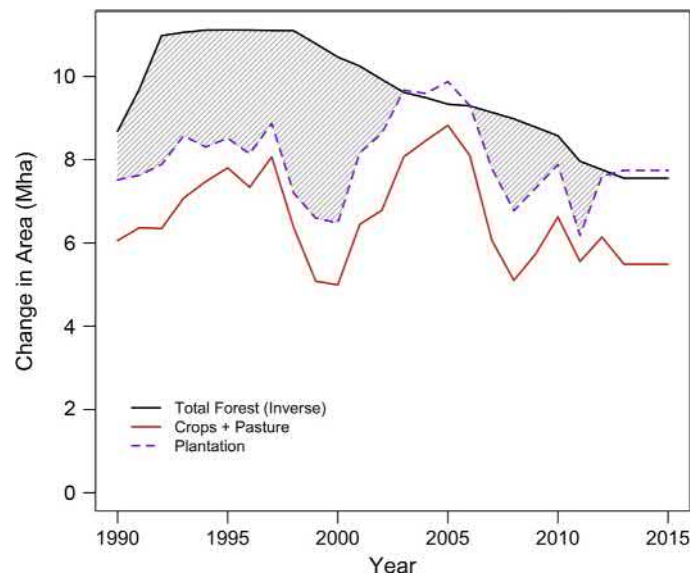


Fig. 3 Annual rates of tropical forest loss and annual rates of gain in crops and pastures and forest plantations for those tropical countries losing forests. Only in the years around 2005 and after 2012 was the loss of forest area “explained” by increases in plantations and agricultural areas. For all other years, the loss of forest area (shaded) exceeded the increase in agricultural area. From Houghton, R.A. and Nassikas, A.A. (2018). Negative emissions from stopping deforestation and forest degradation, globally. *Global Change Biology* **24**, 350–359.

Because the FAO defines deforestation as the loss of forest to other cover types, while Hansen et al. (2013) include temporary losses of forest area from logging and burning, one might expect the FAO estimates of deforestation to be lower than the rates of forest loss reported by Hansen et al. (2013). And that turns out to be the case when gross rates of forest loss are adjusted for bias (Tyukavina et al., 2015). The adjustment yields an average gross forest loss of 11.7 million ha/year for the period 2000–2012. Thus, rates of deforestation as reported by the FAO (9.0 million ha/year) appear not to be overestimated when compared with independent estimates.

Differences in methods and definitions may explain other discrepancies in reported rates of forest loss. For example, the FAO (2015) reports declining rates of deforestation, while some satellite data suggest an increasing rate (Hansen et al., 2013; Kim et al., 2014). The FAO defines deforestation as the conversion of forest to another land cover (FAO, UNFCCC), while the measurements of forest loss by satellite include disturbances (e.g., storms, droughts, or fires) and harvests, neither of which are considered deforestation by the FAO. If satellite data could identify the fate of deforested lands, the two estimates of deforestation might converge and reveal an unambiguous trend.

It is possible, of course, that anthropogenic rates of deforestation are declining in the tropics, while non-anthropogenic disturbances are increasing. In that circumstance satellite and ground inventory data would be different but not necessarily inconsistent. For example, recent drought-induced fires in the Amazon have increased the emissions from fires at the same time that emissions from deforestation have declined (Aragão et al., 2018).

According to analyses of Landsat data (De Sy et al., 2015; Tyukavina et al., 2015), shifting cultivation does not seem to account for a large fraction of deforestation, but pixel by pixel analyses of Landsat data (spatial resolution 30 m) do not necessarily detect changes within the mosaics of land covers that include shifting cultivation (Molinario et al., 2015). Similarly, selective logging may be undetected if it does not reduce forest cover to <25%, the cut-off used by Hansen et al. (2013). Quantification of forest degradation with satellite data may be possible with LiDAR data (Baccini et al., 2017).

Area of Primary Forest

A second indication that tropical forests are lost at a higher rate than inferred from changes in agricultural area comes from FAO estimates of the percent of forests considered primary, or unmanaged. FAO (2015) reports that only 36% of tropical forests were primary forests in 2015. In contrast, the reconstructions of LULCC by Houghton and Nassikas (2017) yielded percentages that were 81% primary. Those reconstructions overestimated the area of primary forests because they used *net* annual changes in agricultural area to drive deforestation, when, in reality, gross rates of forest clearing may be higher than net losses, and balanced by rates of agricultural abandonment (i.e., reforestation). That is, some amount of forest clearing may be simultaneous with agricultural abandonment, and net changes in area probably underestimate the rate of secondary forest formation.

A potentially more important explanation, however, is that land-use statistics from FAOSTAT fail to account for shifting cultivation. The agricultural division of FAO does not count shifting cultivation as agricultural land, but the forestry division does count the conversion of forest to shifting cultivation as deforestation.

The repeated use of forests is important because rotational land uses, such as shifting cultivation and wood harvest, lead to large gross losses and gains of carbon. Disturbances result in carbon emissions, while subsequent recovery, even partial recovery, results in carbon sinks (negative emissions). If the areas are large, the gross sources and sinks of carbon are also large, although the net flux may be nearly zero if the same lands are used repeatedly. On the other hand, if the temporary use of land is a minor activity, most tropical forests may be considered grown. One would expect rates of carbon accumulation in mature forests to be lower than in growing forests. The observation that grown forests may be sinks for carbon (Phillips et al., 1998; Luyssaert et al., 2008) suggests that those sinks may be attributable to environmental changes (e.g., CO₂ fertilization) rather than to recovery.

Some have argued that the small proportion of primary forests reported by the FAO is a result, not of recent management, but from the use of tropical forests long ago. There is a growing recognition that disturbances, both natural and anthropogenic, have long-lasting effects on forest composition, structure and dynamics (Vlam et al., 2016). Thus, many of the “old-growth” forests in the Amazon may still be recovering from ancient (pre-European) human impacts. This possibility seems unlikely because forests cannot accumulate carbon at high rates for a long time (500 years) without having biomass densities much higher than observed.

A Simulation With Shifting Cultivation

In a more recent analysis, Houghton and Nassikas (2018) assumed that the discrepancy between forest loss and agricultural gain represented an expansion of shifting cultivation. They constructed a simulation in which the “excess loss” of forests (Fig. 3) was interpreted as the conversion of forests to shifting cultivation, swidden, or some other temporary use of the land. Furthermore, once lands were in this temporary category, they were repeatedly cleared, used, abandoned, and then used again in the model. The first time a forest was cleared for this temporary use, the conversion was called “deforestation.” Thereafter, the clearing of fallow was within the shifting cultivation cycle; re-clearing did not include conversion or deforestation.

In the conservative estimate Houghton and Nassikas (2017) assumed the “excess forest loss” replaced worn out croplands, which, in turn, were re-classified as “other lands.” That is, forests were cleared for new croplands, while old croplands were abandoned. Forests were lost, but cropland area was unchanged. That assumption resulted in 81% of forest area being primary forest, not the percentage estimated by the FRA (FAO, 2015) (36%). To account for a larger area of secondary forest in their more recent analysis, Houghton and Nassikas (2018) started the analysis (in 1700) with 33% of tropical forest area already in temporary

use. These areas in use continued to be used through the simulations, changing only in response to reported increases in “other lands.” “In use” means that young forests (fallow) were repeatedly used, never recovering to primary, or grown, forests. Under this assumption, the fraction of forest area in primary forests at the end of the simulation (2015) was similar to the FAO’s estimate of 36%. The assumption is simplistic, but historical inaccuracies in the area of shifting cultivation will have little effect on the net and gross fluxes between 1990 and 2015, the period important for predicting current gross removals and future negative emissions.

Over the 10-year period 2006–2015, gross negative emissions in the tropics averaged $-0.5 \text{ PgC year}^{-1}$ under the (conservative) simulation from Houghton and Nassikas (2017) and $-3.3 \text{ PgC year}^{-1}$ under the (generous) simulation from Houghton and Nassikas (2018).

The generous simulation was used to calculate the gross negative emissions that would result if rotational land uses were stopped in 2016. Gross emissions fell immediately, and the gross negative emissions became net emissions because forest growth continued even after deforestation was stopped. These gross negative emissions were large in this simulation (Fig. 2B) because the fallow forests in shifting cultivation were allowed to recover. The simulation assumed that shifting cultivation would be replaced by permanent agriculture, enabling fallow lands to return to forest. Stopping harvest of wood in the conservative simulation resulted in negative emissions of 15 PgC between 2016 and 2100 (Table 3). Including the abandonment of shifting cultivation (83 PgC) led to cumulative negative emissions of 98 PgC by 2100.

The decline in tropical negative emissions that accompanies what amounts to a moratorium on deforestation and the abandonment of rotational forest use seems steep, but it is consistent with rates of growth of tropical forests ($2.6 \text{ MgC ha}^{-1} \text{ year}^{-1}$ in the analysis versus $3.05 \text{ MgC ha}^{-1} \text{ year}^{-1}$ for secondary tropical forests in Latin America (Poorter et al., 2016)). With this rate of growth, forests reach 75% of their initial carbon density in about 50 years and were assumed to recover to their initial biomass density in another 50 years. Lower rates of growth would extend the period of negative emissions but would also lower the amount removed per year. Thus, the total removal over the long term (~ 100 years) is little changed by assuming different rates of growth.

Harvesting more efficiently and lengthening the lifetimes of wood products had a modest effect on projected tropical emissions (-8 PgC) (Table 3) because harvests of industrial wood (as opposed to fuelwood) are low in the tropics. Stopping only deforestation generated cumulative negative emissions (-2 PgC), much smaller than those created by abandonment of shifting cultivation (-83 PgC).

Global Synthesis

The greatest potential for negative emissions in the tropics results from stopping deforestation and allowing the fallows of shifting cultivation to return to forests. Outside the tropics the greatest potential comes from lengthening the lifetime of wood products. Adding together the results from the simulations with the highest negative emissions yields a maximum of 126 PgC ($98 + 28$) (Table 3). The potential is somewhat less than the total loss of carbon from changes in LULCC since 1850 (145 PgC) (Houghton and Nassikas, 2017), but a full recovery is unlikely as much of that loss resulted from the expansion of permanent agricultural lands, which are unlikely to be reforested. In fact, new agricultural lands needed for a growing world population will probably reduce the potential further unless increased production is accomplished through increased yields rather than expanded areas.

Putting the tropical, temperate, and boreal forests together, yields a global gross sink (2006–2015) of $4.4 \text{ PgC year}^{-1}$. Although this sink is large (47% of global emissions from fossil fuels for the same decade), it will be offset to some extent by emissions from wood products and slash and from changes in soil carbon that were initiated before 2016. Accounting for these delayed emissions, the net sink for carbon will be greatest immediately after harvests cease and will decline as regrowing forests age. The net global carbon sink obtainable if deforestation and harvests were stopped would be -34 PgC by 2100 ($15 + 19$). If, in addition, lands in rotational agriculture were allowed to return to forest, the cumulative sink would be -117 PgC (Table 3). Extending the lifetimes of wood products would add another 9 PgC ($28 - 19$) for a global maximum of 126 PgC.

The management options considered here suggest potential negative emissions as large as $4.4 \text{ PgC year}^{-1}$ if the gross annual emissions of $5.5 \text{ PgC year}^{-1}$ from deforestation and degradation were stopped. On the other hand, the gross negative emissions of $4.4 \text{ PgC year}^{-1}$ are largely offset by the emissions that are likely to continue even without further deforestation and harvests. Emissions will continue from native soils recently brought into cultivation and from the pools of carbon in wood products accumulated over past decades. One can manage emissions by stopping deforestation or harvest; it is more difficult to eliminate emissions from existing paper products, landfills, wooden buildings and infrastructure. The *net* negative emissions of 117 PgC by 2100 would amount to only 31% ($117 \text{ PgC} / (4.4 \text{ PgC/year} \times 85 \text{ year})$) of the amount that would be sequestered if the gross sinks in 2016 were to continue to 2100 (i.e., without counting the committed emissions).

Three Broad Categories of Forest Management for Reducing Emissions or Increasing Sinks

One can imagine three types of carbon management using land. First, stopping tropical deforestation would reduce current emissions by $1.3 \text{ PgC year}^{-1}$ (including the emissions from draining and burning of peatland soils in Southeast Asia) (Houghton and Nassikas, 2017). To the extent the residual terrestrial sink is in forests, stopping deforestation has the additional benefit of reducing the loss of this sink.

Second, stopping degradation, in this case the harvest of wood, may not be the most effective strategy for managing carbon. On the one hand, a gross source of $1.0 \text{ PgC year}^{-1}$ could be avoided if harvests were stopped globally and previously harvested forests were allowed to recover. On the other hand, the harvest of wood for long-lasting products could result in a greater storage of carbon on land (the sum of carbon in forests and in harvested products) if the harvests were sustainable. The analysis by Houghton and Nassikas (2017) found, however, as others have for Europe, that industrial wood harvests led to a *reduction* in carbon storage in countries outside the tropics, 18% less than in a simulation without industrial wood harvest. The reduction in forest biomass (30.9 PgC) was larger than the increased storage in products and slash (14.6 PgC). Harvests did not result in greater carbon storage because harvested forests were sometimes cleared for agriculture, thus eliminating the sinks that would otherwise have been attributed to harvest. The net effect varied through time and among regions. As shown in one simulation, increasing the lifetimes of wood products resulted in a larger effect, increasing cumulative negative emissions to -28 and -8 PgC in the extra-tropics and tropics, respectively (Table 3).

Strictly speaking, stopping deforestation does not lead to negative emissions. Neither does stopping wood harvest, although sustainable harvests could result in an accumulation of carbon in long-lasting wood products. Nevertheless, reducing emissions of carbon is equivalent to increasing sinks, in this case allowing existing gross sinks to be manifest as net sinks.

The third type of carbon management, and one that does increase negative missions, is the expansion of forest area. In these analyses forest expansion was simulated by allowing the lands in shifting cultivation to return to forests (for a sink of 83 PgC by 2100) (Table 3). No other lands were assumed to be available for forest expansion, and in this respect, the estimate is conservative. However, the expansion of forests in boreal and temperate zone regions, though good for taking carbon out of the atmosphere (biogeochemistry), may have a net warming effect because of changes in biophysics (albedo, evapotranspiration, turbulence), depending on the emissions of volatile organics and resulting aerosols (Spracklen et al., 2008).

Net Versus Gross Fluxes

This discussion has focused on the gross sources and sinks of carbon resulting from deforestation and wood harvest. From the perspective of managing carbon, gross emissions and gross removals are the more appropriate metric because these fluxes identify the potential for reducing emissions or enhancing sinks. In contrast, *net* emissions from land use is a poor indicator of potential. Net emissions today are about 10% of total anthropogenic carbon emissions, implying that land management is likely to have only marginal effects on reducing emissions. On the contrary, when rotational land uses in the tropics are considered, the gross emissions ($5.5 \text{ PgC year}^{-1}$, globally) (Table 1) represent 37% of total carbon emissions (fossil fuel emissions are currently about 10 PgC year^{-1}). From the perspective of carbon management, gross emissions are the fluxes with management potential.

In addition to the losses and gains of carbon on land as a result of management, there is also a large net uptake of carbon ($3.6 \text{ PgC year}^{-1}$) thought to be caused by environmental changes (e.g., elevated CO_2 , nitrogen deposition, or changes in climate). That residual terrestrial sink is consistent with the accumulation of carbon in forests, both managed and unmanaged, as measured by forest inventories (Pan et al., 2011). Together with the gross sources and sinks from forest management, these two pathways demonstrate the importance of land, and particularly forests, in the global carbon budget (Fig. 4). When gross emissions are considered, land management accounts for 37% of total emissions (not 10%), and land, including both management and the residual sink, accounts for 43% of the global sink (not 30%). Represented this way, terrestrial ecosystems and land management appear large in the global carbon balance. The challenge is to preserve and enhance negative emissions while eliminating or limiting their associated positive emissions.

Conclusions

Two conclusions emerge from this investigation. First, without a massive, global program of forest expansion, the potential for negative emissions from ending deforestation and degradation is modest (on the order of 100 PgC). Even under the unrealistic projections simulated here, the potential for land management to withdraw carbon from the atmosphere is small relative to the potential for fossil fuel use to add carbon. But this is the wrong comparison. The appropriate comparison is between potential for negative emissions and the total carbon emissions *allowable* for staying within a warming of 2°C ($160\text{--}338 \text{ PgC}$ from 2015 onwards (Rogelj et al., 2016)). In that comparison, the potential for negative emissions from forest management represents 30–60% of the allowable emissions. This finding is fundamental. Land management is vital if 2°C , or less, is indeed the goal.

Because the estimate of 100 PgC is based on biophysical potential, and not on economic or ownership conditions, it is likely *generous*. On the other hand, there are at least three reasons why it is *conservative*. First, it assumes that existing supplies of wood products, as well as pools of slash and soil carbon, will all be lost to the atmosphere. It is possible that some of these pools could be managed in such a way as to “seal” them from oxidation (i.e., keep them from the atmosphere). Second, stopping harvest of wood, thereby allowing forests to grow to maturity (or over maturity), misses the opportunity to remove carbon from the atmosphere through sustainable harvests of long-lasting wood products, where the total carbon in products plus forests is potentially greater than it would have been in unharvested forests. Sustainable forestry with a goal of long-term storage would increase the potential of negative emissions. And third, the analysis does not consider the full possibility for expanding forest area. There may be large areas

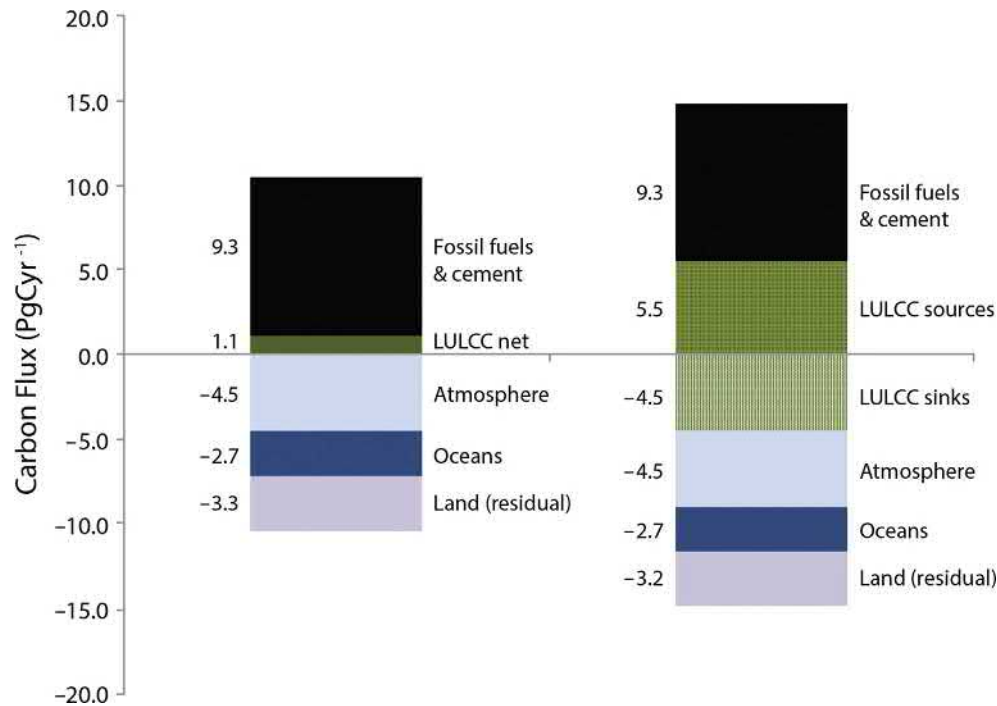


Fig. 4 Average annual sources and sinks of carbon for the period 2006–2015. (Left) Net emissions from land use. (Right) Gross emissions from land use. From Houghton, R.A. and Nassikas, A.A. (2018). Negative emissions from stopping deforestation and forest degradation, globally. *Global Change Biology* **24**, 350–359.

of degraded or unused lands that could be reforested if carbon removal were profitable. Such reforestation would have to be done carefully, taking into account other values besides carbon, such as biodiversity and human rights.

The second conclusion is that negative emissions are possible because ecosystems are below their natural carbon densities as a result of land use. That is, potential negative emissions are directly coupled to past positive emissions. There is nothing magic about these negative emissions. They simply restore carbon lost previously. The corollaries of this conclusion are (1) that negative emissions will diminish as forests recover to their undisturbed state (negative emissions will only work for a few decades) and (2) that much of that recovery will have occurred before 2100, according to these simulations.

The residual terrestrial sink, on the other hand, the accumulation of terrestrial carbon believed to be caused by changes in the global environment, is entirely different (see “The Global Carbon Budget” section). This terrestrial sink is not the result of land management. If the processes responsible for that residual sink (e.g., CO₂ fertilization, climate change) continue, the sink may also continue. However, one of the reasons for keeping the warming to <2°C is that these natural sinks may be reduced as a consequence of warming. Ecosystem respiration, for example, is temperature dependent. Furthermore, thawing of permafrost and forest die-back from droughts seem to be increasing, potentially lowering the current and future sink. Satellites have recorded the greening of the planet (increased productivity) for decades, but a recent analysis reports an increase in browning (reduced productivity) (Pan et al., 2018). The observations are worrisome for the persistence of the residual terrestrial sink, and without it, management of the global carbon budget will be much more difficult.

Old-growth, or primary, forests have an important role in storing carbon. First, per hectare they hold more carbon in their vegetation and soils than secondary forests, and their deforestation would result in large positive emissions of carbon. It is not clear how much of the residual carbon sink, currently 3.2 PgC year⁻¹, is in old-growth forests. The world’s forests account for much of this sink (Pan et al., 2011), and there is evidence that old-growth forests continue to accumulate carbon in biomass and soil for centuries. From the perspective of negative emissions, it seems prudent to maintain existing areas of old-growth forest as well as to allow large areas of secondary forests to age/grow.

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Roadless Areas as Key Approach to Conservation of Functional Forest Ecosystems

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Abstract

Roadless areas are free from any kind of road(-like) infrastructure and their direct or indirect impacts on the ecosystems. The largest tracts of ecologically most valuable roadless areas refer to large unfragmented forests regions, both in the tropics and the boreal zone (Amazon, Congo basin, East and Southeast Asia). Among all terrestrial ecosystems, roadless forests are the single most important strongholds of regulating ecosystem services: among others, soil protection, water retention, buffering of the local and regional climate and mitigation of global climate change via capturing of atmospheric carbon. But roadless areas also comprise much demanded natural resource assets, such as timber, often also minerals and space for agricultural development. There is a substantial conflict between diverse short-term economic interests and the long-term conservation of roadless areas. Large roadless areas can serve as a measurable surrogate for the most pristine and functional ecosystems. Roadlessness is a property of areas, which are not impacted by roads; it can be used as a proxy for assessing ecosystem integrity and the absence of many anthropogenic disturbances. We recommend that policy-makers give roadless areas conservation priority over areas that have already been fragmented. It is essential to establish roadlessness as a criterion for the planning of ecosystem-based, cost-effective sustainable development. In parallel with measures to protect roadlessness, we recommend alternative approaches to mobility that can work under roadless conditions, e.g., related to railroads, blimps and other low-energy technologies with low infrastructure requirements. Even if “climate-friendly” renewable energy was available for road transport on a large scale, the construction, existence and operation of roads would continue to severely impair ecosystem functionality.

How Do Roads Impact Ecosystems?

The manifold impacts of roads on ecosystems start with local and direct effects caused by construction, continue when the road is used and maintained, and then radiate into the wider landscape (Font et al., 2014; Forman and Alexander, 1998; Riley, 1984). Environmental degradation, changes in ecological processes, and decline of biodiversity on all hierarchical levels are the consequence (Chaplin-Kramer et al., 2015; Fahrig and Rytwinski, 2009; Forman, 2000; Forman et al., 2003; Kleinschroth and Healey, 2017; Martin et al., 2000; Riitters and Wickham, 2003; Young, 1994) (Figs. 1 and 2).

Direct impacts of road construction include the physical conversion of sites, soil compaction, dust, salt, and heavy metal pollution, changes to the microclimate by creating extended surfaces that heat up and do not retain water as well as the creation of edges that are vulnerable to windthrow of trees. Noise and light pollution degrade the quality of faunal habitats, and vehicle collisions cause increased wildlife mortality (Benítez-López et al., 2010; Ferreras et al., 2001; Gibbs and Shriver, 2005; Jaarsma et al., 2007; Kaphegyi et al., 2013; van Langevelde et al., 2009; Seiler, 2001; Wadey et al., 2018). Furthermore, roads cause the fragmentation of continuous ecosystems and the isolation of remnant landscape patches, create barriers, cutting off populations and restricting gene flow, which can eventually lead to local extinction (Ceia-Hasse et al., 2017; Epps et al., 2005; Rytwinski and Fahrig, 2015). The barrier effect of roads is species-specific and depends on body size, mobility and speed of fauna. In addition to the road itself, fragmentation of populations of certain species can become much more severe by building fences along roads to prevent wildlife crossings and accidents (Epps et al., 2005; Linnell et al., 2016). Roads reduce landscape connectivity, alter species behavior, and can lead to changes in species composition (Forman et al., 2003; Hansen and Cleverger, 2005; Freudenberger et al., 2012).

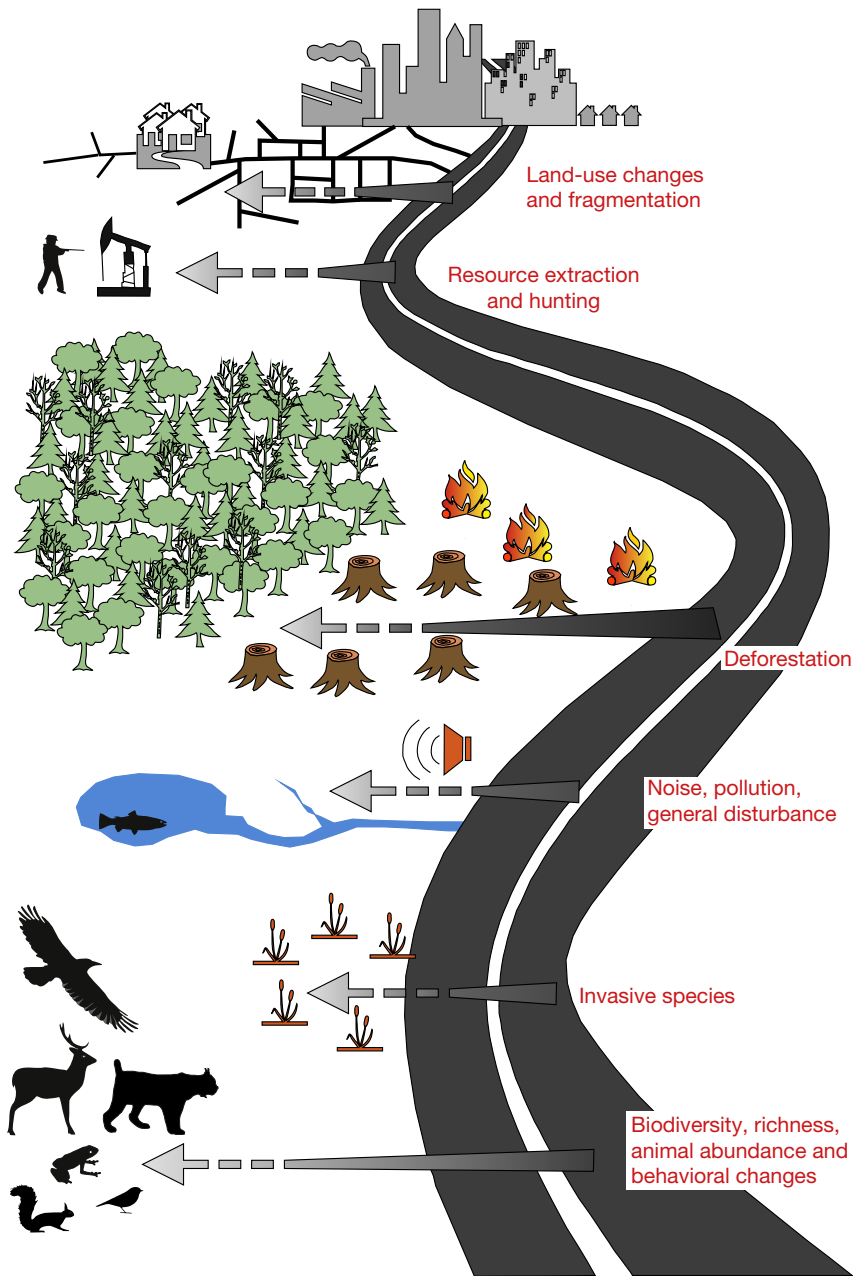


Fig. 1 Schematic representation of different categories of road impacts on biodiversity. Road impacts diminish with the distance from the road. From Ibisch, P. L., Hoffmann, M. T., Kreft, S., et al. (2016). A global map of roadless areas and their conservation status. *Science* **354**(6318), 1423-1427, supplementary material.

The “contagious effect” of roads (Selva et al., 2015) describes how newly constructed roads in previously inaccessible areas trigger a cascade of disturbances and impairments of ecosystems. Indirect impacts of roads are caused by promoting socioeconomic activities such as resource extraction, agriculture or tourism, which previously were rather restricted or even absent. They provide access to remote and scarcely inhabited areas and often lead to deforestation, urbanization, mining, human-caused wildfires, hunting, poaching, and fishing, all together resulting in further degradation of habitats and ecosystem functionality (Laurance, 2009; Laurance and Arrea, 2017; Liu et al., 2008; Selva et al., 2011; Trombulak and Frissell, 2000). Especially in forest ecosystems the microclimatic and biotic changes along the road edges can increase the risk of wildfires and trigger further destabilizing consequences for ecosystem functionality (e.g., Chaplin-Kramer et al., 2015; Lembrechts et al., 2017; Foley et al., 2003; Norris et al., 2012; Eigenbrod et al., 2015).

Direct impacts of roads can be quantified in various ways by counting wildlife road kills or measuring habitat loss and fragmentation, whereas indirect impacts can be very complex, time-lagged and go far beyond main roads that often trigger the development of smaller trails and paths, which makes it more difficult to understand and assess them (Forman et al., 2002; Freitas



Fig. 2 Impressions of diverse road impacts on forests. Logging roads and trails often start the cascade of degradation. Among the most prominent impacts are soil compaction and opening up forest canopies (A: Skidding trail in temperate Carpathian beech forest, Ukraine; B: Harvester providing access to planned clearcut area in boreal forest, Arkhangelsk region, Russian Federation). In mountain areas downstream road impacts multiply first direct effects; they commonly lead to erosion, destabilization of slopes and disturbance of rivers (C: Recently improved road in Andean montane rain forest, Ecuador). Roads provide access to highly vulnerable areas such as peatlands, drive land use change and cause changes in the landscape hydrology (D: Oil palm plantation on peatlands replacing a former tropical peat swamp forest at the edge of the Klias reserve in Sabah, Borneo, Malaysia). Roads become veins of colonization in remote regions introducing contagious effects into the wider landscape (E: Main road with a belt of increasing settling and land use activities such as cattle ranching in northern Kalahari, Kavango region, Namibia). Roads are often built even in the centre of protected areas leading to loss of habitat, change of microclimate and increasing the risk of wildfires or neobiota (F: Road with tourists within Ku-Ring-Gai National Park, Australia). All photographs by Pierre Ibisch.

et al., 2015; Jędrzejewski et al., 2018; Selva et al., 2011; Shilling et al., 2015; Wilkie et al., 2000). Direct and indirect effects of roads on ecosystems are scale-dependent and have to be analyzed with regard to their spatial scopes. Forman and Alexander (1998) termed the area influenced by roads “road-effect zone” (REZ). A REZ comprises the areas which extend beyond an actual road but are still affected by road construction, usage or maintenance. Type and degree of impact changes, depending on the zone that is affected. The REZ is determined by various factors such as the distance from the road surface, environmental conditions, season, landscape structure, topography, or traffic intensity (Forman and Deblinger, 2000).

Species and ecosystems react specifically to the diverse combinations of road effects and landscape conditions; impacts can be asymmetrical along roads and vary temporally or seasonally (Ibisch and Selva, 2017; Kleinschroth et al., 2016; Morán-López et al., 2017). Hence, it is not possible to identify a single road-effect zone combining all direct and indirect road effects on biodiversity and

species. For instance, a highly altered and structurally impoverished grassland impacted by a new concrete road with heavy traffic cannot be compared to a complex, intact and functional forest ecosystem crisscrossed by narrow dirt roads used by poachers and illegal loggers. In mountains, there are also downstream effects of roads that can extend over large distances. These would be related to run-off, soil erosion, and river water quality, among others (Ibisch and Selva, 2017; Seutloali and Beckedahl, 2015). In the Southwest Amazon rainforest region, indirect effects have been recorded up to 45 km around main roads (Southworth et al., 2011). In contrast, the road-effect zone for desert turtles in California is over 400 m from the road (Boarman and Sazaki, 2006). Bat activity increases more than threefold between 0 and 1600 m from the road (Altringham and Kerth, 2016). For anurans in Canada, Eigenbrod et al. (2009) estimated a REZ of 250–1000 m. Dutch birds were affected by roads within a distance of 40–2800 m from the road, depending on the species and traffic volume (Reijnen et al., 1995). A population decline extends over distances up to 5 km for mammal species and up to 1 km for bird species (Benítez-López et al., 2010). Most of the direct negative impacts caused by roads are at a distance of one kilometer to the nearest road (Ibisch et al., 2016).

Roads and Roadless Areas in Forests

Often, forests are mapped as roadless within heavily roaded landscapes such as in Germany. However, upon closer inspection these areas are by no means truly road-free ecosystems; rather, there are countless forest trails and forest roads that have not yet been mapped (Hoffmann and Ibisch, 2017). Even if these are not public roads and characterized by very low traffic intensity, they can contribute to ecosystem vulnerability:

- As forests are the most biomass-rich and structurally most complex terrestrial ecosystems, they are especially vulnerable to physical, chemical and biological degradation mechanisms that can be referred to the presence of roads. The complex, three-dimensional structure established by trees—often organized in various strata—together with high biomass facilitate a pronounced physical moderation and regulation of environmental conditions. For instance, forests produce their own cooler, more buffered and moister microclimate, which is a key property to their resistance and resilience against disturbance (e.g., Norris et al., 2012). By opening up the canopy and creating linear breaches, roads affect the self-regulating capacity of forest ecosystems, reducing the microclimatic buffering capacity.
- The combination of higher temperatures and lower humidity along roads, the presence of combustible fuel such as remnants of cut or dying trees, often amplified by secondary vegetation with combustible plants, and the presence of people, who tend to inconsiderately light fires, multiplies the risk of forest fires.

What Are Roadless Areas and Where Are They?

Roadless areas are free from any kind of road(-like) infrastructure and their direct or indirect impacts on the ecosystems. In the research for the first global map of roadless areas (Ibisch et al., 2016), a 1 km buffer was chosen as a relatively conservative measure, acknowledging that there are impacts that can be recorded beyond this distance from the road. Due to the absence of the road impacts described above, roadless areas play a special role in the conservation of biodiversity and ecosystem functionality (Martin et al., 2000; Stritholt and DellaSala, 2001; Crist et al., 2005; Selva et al., 2011). They increase landscape connectivity between habitat patches and protected areas (Stritholt and DellaSala, 2001; Goetz et al., 2009) and can contribute to the conservation of native, vulnerable, and endangered species (Campaign, 2001; Gelbard and Harrison, 2003). They are particularly essential for species that require and move across large territories (Crooks, 2002; Blake et al., 2008; Kaphegyi et al., 2013; Kuemmerle et al., 2018). Roadless functioning ecosystems have a higher buffer capacity and are more resilient than roaded areas, making them less vulnerable to the effects of climate change (McGarigal et al., 2001; Crist et al., 2005). Even small roadless areas can be of importance, as they serve as habitat, stepping-stones, and climate refugia for certain species, as well as reference areas for restoration. Clearly, biological diversity is positively related to the size of a conservation area (Develice and Martin, 2001), and larger roadless areas are especially valuable.

The very first OpenStreetMap (OSM)-based global analysis of roadless areas distribution across Earth's biomes showed substantial geographical differences (Ibisch et al., 2016). The Tundra and Rock and ice-covered biomes were nearly roadless. A high share of roadless areas was also found in Tropical and Subtropical Grasslands, Savannas, Shrublands, and Moist Broadleaf Forests in Montane Grasslands and Shrublands, Deserts and Xeric Shrublands, as well as in Boreal Forests/Taiga. Half of the Mediterranean Forests, Woodlands, and Scrublands appeared to be roadless, whilst in Temperate Broadleaf and Mixed Forests the roadless share was <50%. In the Tropical Forests large roadless areas exist in South America, Africa, and Southeast Asia. The largest tracts of roadless areas exist in the Sahara, but also in forest regions such as the northern and western Amazon and the boreal forests in northern and northeastern Russia and Canada (Figs. 3 and 4).

Highest road density can be observed in the Temperate Broadleaf and Mixed forests biome, especially in industrialized countries with high population density and economic outputs, such as the (eastern and central) USA, most European countries, South Korea or Japan. This reflects both the completeness of the road data sets and actual economic development. In Asia, South America and Africa road infrastructure is rapidly developing. In Africa and Southeast Asia, in many countries, the national share of (1 km OSM) roadless areas between 2013 and 2018 has substantially decreased by >30% (e.g., Sri Lanka from 66% to 26%; own unpublished



Fig. 3 Roadless area in eastern Noel Kempff Mercado National Park in Bolivia. Vast tracts of tropical moist forests in contact to Cerrado woodlands and savannas represent huge complexes of free-willed, functional ecosystems Photograph: Pierre Ibisch.

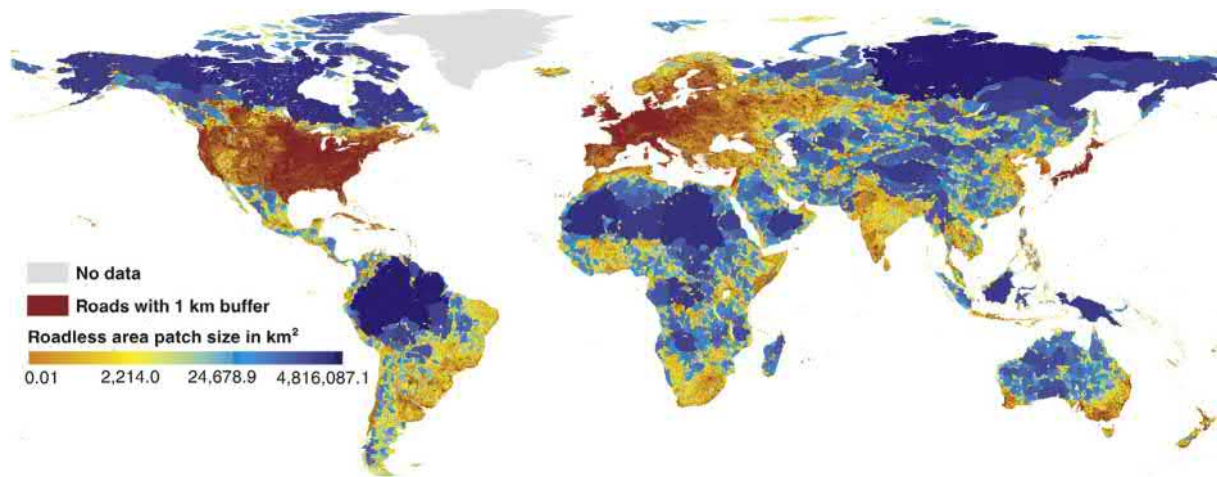


Fig. 4 Map of global roadless area patch sizes in km². From Ibisch, P. L., Hoffmann, M. T., Kreft, S., et al. (2016). A global map of roadless areas and their conservation status. *Science* **354**(6318), 1423-1427.

data). This would mainly be due to intensified OSM mapping efforts, but should also reflect progressing road infrastructure (see below, following section).

To understand the relative importance and ecological value of roadless areas it is important to assess their ecologically relevant features and the presence of non-road related threats. An example for roadless, but used landscapes are rangelands. Often large, intensively managed agricultural areas, mining or military sites appear as roadless areas if the distance to the road is >1 km. Still, they are not necessarily free from traffic, and land use can have severe degradation effects on ecosystems (Hoffmann and Ibisch, 2017). As in the context of assessing the quality of wilderness areas, certain criteria can be applied for further understanding the relative ecological value and conservation priority of roadless areas. In the context of the first global map, Ibisch et al. (2016) proposed the Ecological Value Index of Roadless Areas (EVIRA). This index encompasses three indicators. The first indicator consists of the Ecological Functionality Index (EFI) (Freudenberger et al., 2012), the second is patch size and the third is connectivity of the patches using Thiessen polygons. Ecological Functionality was weighted by 50% the last two by 25% each. The largest tracts of ecologically most valuable roadless areas refer to large unfragmented forests regions, both in the tropics and the boreal zone (Amazon, Congo basin, East and Southeast Asia; Fig. 5). There are also very important roadless areas in some temperate and subtropical regions (e.g., Himalaya, eastern Russia, Caucasus, eastern Mediterranean).

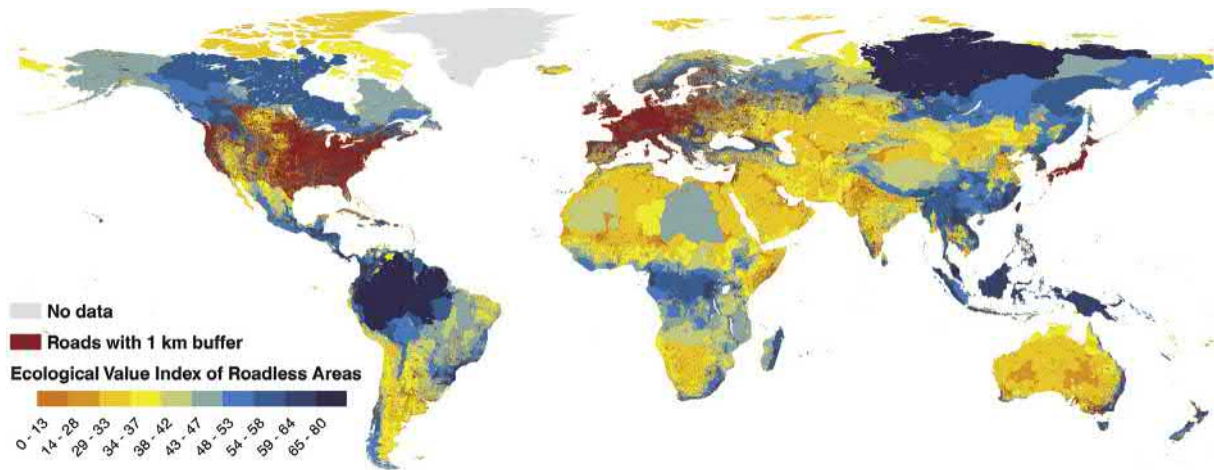


Fig. 5 Map of Ecological Value Index of Roadless Areas (EVIRA). From Ibisch, P. L., Hoffmann, M. T., Kreft, S., et al. (2016). A global map of roadless areas and their conservation status. *Science* **354**(6318), 1423-1427.

What Are the Data Needs and Prospects Regarding Roadless Big Data Management and Research?

Cartographically, roadless areas are identified as areas that remain once roads and buffers (on each side of the road) are removed from the country data set. The buffer can be adapted to the road category or condition of the ecosystem (e.g., 1 or 5 km, see Ibisch et al., 2016). For the first global map of roadless areas open-source data was used, created by OpenStreetMap (OSM). OpenStreetMap works with volunteered geographic information (VGI), where citizens collect confirmable geodata (Goodchild, 2009; Mooney and Corcoran, 2013). The 1 km buffer was applied on each side of all roads across all road categories that are included in the OSM road data set (Ibisch et al., 2016) (Fig. 4).

The road network from 2013 was used in the roadless area study. It showed gaps in some regions, especially in Southeast Asia (Ibisch et al., 2016; Hoffmann and Ibisch, 2017). Because OSM is a crowd-sourcing project, data collection is an ongoing process (Mocnik et al., 2017). The OSM dataset of 2013 comprised almost 37 million km of roads. By 2018, the worldwide OSM data on roads has doubled. The OSM data set is updated constantly, missing roads but also newly constructed roads are added. Several quality assessments were conducted to evaluate the quality of OSM data (Koukoletsos et al., 2011; Barron et al., 2014; Zhao et al., 2015). In a study published in 2017, the authors found that OSM is 83% complete in >40 countries (Barrington-Leigh and Millard-Ball, 2017). The popularity of OSM is increasing and with it the number of mapped roads. Citizens shall be encouraged to actively participate in creating geodata for open access purposes. A new road data set was published by GLOBIO in 2018 with 21 million kilometers of roads that also incorporated OSM road data for the European Union (Meijer et al., 2018). An automated road mapping algorithm that would use artificial intelligence identifying different road types on satellite images would be highly useful for a reliable global monitoring (Laurance, 2018).

One of the downsides of global data sets is the size of the data and the consequent processing time and required computer capacities. Big data has become an issue in many scientific fields. The amount of data is increasing exponentially, but systems that can process this large amount of information are more likely to exist in commercial enterprises than in conservation-oriented research entities. Big data processing is challenging (Demchenko et al., 2012). This is related both to the amount of data and to the existing infrastructure and architecture, which, due to the volume, diversity, speed, truthfulness, volatility and quality of the data, cannot process the information the way it was previously processed (Nasser and Tariq, 2015). Big data with high resolution need storage space and proper running systems to handle and maintain them (Marx, 2013; Bargellini et al., 2013). This field is developing fast, and hopefully, in the future, it will be affordable for a broader public. Although the roads are well mapped in OSM according to their location in most of the regions the meta data or attributes accompanying the data are often insufficient. Information on the road category, lane and or width would be helpful in assessing the impact of roads more precisely. Traffic intensity is not yet included in the OSM data, but can be used together with population density information to assess roadless areas at risk of conversion due to demographic pressure. Even though there is an increasing amount of freely available data, geodata are not always accessible and not consistent enough to be used on a large scale. Download times for large datasets can easily exceed 24 h (unless they are integrated into systems like Google Earth Engine) and companies offering cloud computing services for data processing are initially very expensive.

Roadless Areas and Society

The societal view on roadless areas shifts with changes in socioeconomic lifestyles. Indigenous, forest-dwelling people often recognize disadvantages and risks related to roads such as diseases, poachers or invading settlers (e.g., Finer et al., 2008; Clements

et al., 2018). Abrupt contact with modern life-styles via new roads has been observed to socially disrupt local communities in remote forest regions. Worldwide attention was paid to the case of a road project through the Isiboró-Securé National Park and Indigenous Territory in Bolivia, where indigenous peoples effectively protested against the government's development plans (El Deber, 2018).

In remote rural areas with predominantly agriculture-based livelihoods, local people by tendency would strive for improved road access. Case studies have indicated that roads reduce poverty and increase consumption growth, and the incidence of hunger seems to increase with distance to roads (compare Ibisch et al., 2016, Table S10, supplementary material), but there are also socioeconomic risks (Alamgir et al., 2017). Today, most relevant actors would consider road infrastructure an essential condition for economic development (Fan and Chan-Kang, 2005; Turner, 2006; Calderón and Servén, 2014). Especially in the case of forests, roadless areas comprise much demanded natural resource assets, such as timber, but often also minerals and open space for agricultural development. The substantial conflict between short-term economic interests and the long-term conservation of roadless areas must not be denied.

The general awareness for the impacts of the global road network on ecosystems is relatively underdeveloped. When the first global map of roadless areas was published in 2016 there was a substantial global media echo reflecting that journalists recognized the importance of the topic, several of them acknowledging that the fragmentation of Earth took place largely unnoticed, although virtually everyone uses roads. Theoretically, the current challenges to conventional mobility that led to overcrowded and polluted cities and faces the need to move away from fossil energy sources, could trigger innovation towards more ecosystem-friendly solutions. Unfortunately, the recent hypes around electro-mobility and autonomous smart driving perpetuate visions related to individual automobiles that require roads. Currently, roadless mobility options, including railroads or low-energy flying devices with limited requirements for permanent infrastructure (e.g., zeppelins, blimps), do not seem to be sufficiently developed for representing an attractive alternative.

Roadless Areas Policy: What Are the Messages for Policy Makers?

With the global population expected to reach over 11 billion by 2100 (United Nations, 2017) and the global ecological deficit gradually increasing up to 8380 million global hectares (Gha) (Global Footprint Network, 2018), a bold policy statement of setting aside half of Earth as permanently protected areas for biodiversity conservation has been suggested for humanity to stave off a cataclysmic extinction event (Wilson, 2016). Large roadless areas can serve as a measurable surrogate for the most pristine and functional ecosystems. Given the importance of roadless areas for sustaining essential services to society, and their rapid diminishment globally, the key message to policy-makers is clear: Give roadless areas conservation priority over areas that have already been fragmented. *Roadlessness* is a more or less easily measurable condition of an ecosystem serving as a meaningful proxy for its integrity and the absence of many anthropogenic disturbances. It is essential to establish roadlessness as a criterion for the planning of ecosystem-based, cost-effective sustainable development (Ibisch et al., 2016).

Roadlessness is tightly linked to the concepts of wilderness or intactness. Such global templates focus mainly on forests and include the "High-biodiversity wilderness areas" (developed by Conservation International), "Last of the Wild" (The Wildlife Conservation Society and Center for International Earth Science Information Network, Columbia University) and "Intact Forest Landscapes" (Greenpeace and partners). Another global prioritization scheme was suggested focussing on ecologically functional regions under climate change (EcoSocioClimateWise priority setting model; Freudenberg et al., 2012). Global priorities according to all these templates turn out to focus heavily on roadless forests. To ascertain that development is sustainable on the long-term, it is important to secure regulating and maintaining ecosystem services. Among all terrestrial ecosystems, roadless forests are the single most important stronghold of regulating services: among others, soil protection, water retention, buffering of the local and regional climate and mitigation of global climate change via capturing of atmospheric carbon (Fig. 6). As a possible solution, some have proposed balancing the value of an area for species conservation, as a proxy indicator for maintaining ecosystem services, with its value for food production, as an essential provisioning ecosystem service (Laurance et al., 2014).

The added value and novelty of roadlessness is that it is based on one of the most important direct and indirect key drivers of biodiversity loss. The extent of roadless areas or even simply road density can be easily used as a measurable entity assessing the extent of anthropogenic pressures at multiple scales. The conservation of roadless areas represents a proactive approach, in contrast to reactive approaches that are directed at mitigating or reversing biodiversity losses ex post (see Brooks et al., 2006, for a comparison of proactive and reactive priority-setting in global conservation). A proactive approach favoring policies for ecosystem-based sustainable development bears several advantages. Most importantly, the long-term opportunity costs for protection of roadless areas will often turn out to be lower than the ones resulting from dissection by roads and subsequent exploitation of an area. Proactive policies may also come with a lower political cost. Sparing regions from road development will help forego both immediate protests by informed stakeholders and posterior opposition by people negatively affected by unsustainable development unfolding in the region.

There is an urgent need for a global strategy and relevant legal frame development for the effective conservation, restoration and monitoring of roadless areas and the ecosystems they encompass. The USA initiated this process by protecting over 20 million ha of roadless area >2000 ha each, amounting to approximately 1/3 of its national forest system (see Stritholt and DellaSala, 2001). Starting with the US Wilderness Act (1964), indirectly promoting conservation of roadless areas, the US Forest Service adopted the Roadless Area Conservation Rule (2001) hampering road construction, road reconstruction, and timber harvesting in inventoried



Fig. 6 Tropical moist forest in a protected roadless area with the Maya Biosphere Reserve, Guatemala, providing important regulating ecosystem services such as water retention and mesoclimatic cooling and buffering Photograph: Pierre Ibisch.

roadless areas on National Forest System lands, clearly enhancing species conservation (Loucks et al., 2003), but not without severe political conflicts (Bies, 2006). No such legal frame exists in other more densely populated parts of the world such as Europe, where the importance of roadless areas has only been underlined in some reports on fragmentation (Jaeger et al., 2011), besides scientific calls for roadless areas conservation (Selva et al., 2011; Psaralexi et al., 2017).

As an important first step, policy-makers should commission a fine-scale inventory of roadless areas and their value for sustainable development (see above: Roadless areas and society). In the official national report of Greece towards the European Environmental Agency (Kati, 2018) the number and extent of roadless areas have been introduced for the first time as a fragmentation index and as an indicator for monitoring the fragmentation rate of natural and semi-natural areas (SEBI 13). Such national reports adopt the system of Streamlining European Biodiversity Indicators 2020 (EEA, 2012) under the scope of monitoring the progress of each Member State towards achieving Aichi targets (UNEP/CBD/COP, 2010) and the European Unions' 2020 Biodiversity Strategy targets (EC, 2011).

The most direct proactive measure for roadlessness is a regional moratorium for road construction in roadless areas with an identified high priority. A complementary policy may consist in proactively reducing the future demand for roads. This may be achieved by efforts to promote provisioning ecosystem services elsewhere, e.g., by ecologically intensifying agricultural production in already cultivated and disturbed areas. There is the urgent need to discuss sufficiency in the context of road infrastructure: Although options for further shortening travel routes may exist, certain densities of road infrastructure should be acceptable without the need for ever reducing travel times (Hoffmann and Ibisch, 2017). A maximum threshold of an ecologically tolerable road density should be lower in regions that have yet experienced only moderate disturbance from road development. Additionally, any approach should take into account ecosystem-specific vulnerability.

A moratorium for road construction can be accomplished through establishment of protected areas that are managed according to legal prescriptions that exclude road construction and thus conserve the state of roadlessness. So far, the global system of protected areas has performed poorly in effectively conserving roadless areas, as these are not recognized by governments as *sui generis* (unique) conservation targets (Ibisch et al., 2016). Many roadless areas enjoy *de facto* protection due to natural factors that hamper physical access, such as steep or swampy terrain (Fig. 7). However, with technological progress, enhancing economical resources and increasing pressures from population growth and more or less justified economical interest, this *de facto* protection is precarious. In addition, the economic value of resources harbored in a roadless area may increase. For example, forest in a roadless area may become more attractive to extraction in an otherwise exploited landscape, and with it for road construction. For these reasons, a wise policy will proactively impose a moratorium for road building in key roadless areas, for instance, by establishment of strict protected areas.

Cases may occur where a road construction moratorium is considered impossible, or not opportune under given sociopolitical circumstances. If avoidance is no option, decision-making on roadless areas should explore all options for maximum reduction of road impacts. These options (in order of decreasing preference) include: re-routing a planned road, bundling it together with existing linear infrastructure, and maximizing size of roadless fragments left over from dissection (Laurance et al., 2014).



Fig. 7 Intact Southwest Amazon rain forest in Peru. Large remote roadless areas allow for conserving vast tracts of valuable ecosystems with their functions and services, even without formal protection. But with progressing development they are at risk if protected area policies do not recognize roadlessness as key criterion for nomination and prioritization. Photograph: Pierre Ibisch.

Proactive policies and measures, despite their above described advantages, may still be overturned by road development interests. In these cases, policy-makers should recur to reactive approaches. In the course of compensatory measures that would target minimizing net loss of biodiversity, environmentalists should vehemently insist for an appropriate *quid pro quo*: Any loss of a roadless area through the construction of a new road should at least be compensated with the dismantling of another road that recreates a roadless area of the same ecological value (Hoffmann and Ibisch, 2017). As long as roads are continued to be built, however, the single most important policy is strict regulation of subsequent human activities in the region. First and foremost, areas to the side of a new road must be kept safe from “contagious development,” a cascade of exploitative land use leading to the short-sighted desire for new roads (Ibisch et al., 2016). This then generates new economic interests, thus perpetuating the process until a former roadless area and its functional ecosystems are “used up” (Laurance et al., 2014; Selva et al., 2015).

In parallel with measures to protect roadlessness, work on alternative approaches to roadless mobility needs to be intensified. Even if environmentally friendly renewable energy might turn out to supply road transport on a large scale, roads will continue to severely impair ecosystem functionality. The currently observable megatrends such as electromobility and autonomous driving illustrate the path dependency, which masters the current (and future) mobility discourse.

Conclusions and Outlook

- There is strong evidence for the ecological importance of roadless areas. It is related to the absence of complexly interacting, direct and indirect anthropogenic drivers of ecosystemic stresses.
- Roadlessness, in many ecosystems, is becoming a rare attribute. It is a proxy for ecosystem integrity that can be assessed more or less easily, and shall serve as criterion for conservation and land use planning. Extent and ecological quality of roadless areas (such as Ecological Value Index of Roadless Areas—EVIRA) are recommended for the global reporting on the accomplishment of the Sustainable Development Goals, especially those targeting sustainable infrastructure and the conservation of terrestrial ecosystems.
- First existing models that show the way to develop monitoring systems and policies for conserving roadless areas deserve special attention.
- Published maps and datasets of roadless areas substantially underestimate the extent of roads, but data quality is rapidly improving.
- The enhanced and dynamic mapping and monitoring of both extent and ecological quality of roadless areas is urgently needed for building up a global observation system and informing regional, national, and local policy makers.

- As dozens of millions of road kilometers crisscross the global terrestrial ecosystems and the negative impacts of roads on biodiversity have been extensively studied, there is the need to establish a *roadless ecology* that further proves and quantifies the multiple environmental and socioeconomic benefits of roadlessness.
- A discourse on “road sufficiency” is needed (“How many roads should be enough under given conditions?”). Slight improvements in access and reduction of travel time cannot be justified at the cost of degrading the last ecologically valuable roadless areas.
- The evolution of mobility technologies seems to be trapped in a path-dependency carefully maintained by the stakeholders involved in road-dependent mobility. It is therefore equally important that research highlights the benefits and avoided damage of alternative approaches to mobility and transport, which are likely to include more conventional technologies such as railways or modern, environmentally friendly, low-energy flying vehicles.

Acknowledgments

PLI and MTH co-conceived the first draft of the manuscript and edited the final version. SK and VK contributed to the writing, especially of the section on roadless policy. PLI acknowledges the research professorships “Biodiversity and natural resource management under global change” (2009–15) and “Ecosystem-based sustainable development” (2015 onward) that were awarded by Eberswalde University for Sustainable Development. MTH is supported by a grant from the Institute of Botany of the Polish Academy of Sciences Krakow (fellowship to students of interdisciplinary doctoral studies at the IB PAS).

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The Importance of Forests for Monarch Butterflies

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Abstract

Most monarchs (*Danaus plexippus plexippus*) overwinter in the volcanic mountains of central Mexico clustering in oyamel fir (*Abies religiosa*) forests described as a hot-water bottle, blanket, and umbrella that maintain a microclimate warm enough for the butterflies not to freeze, but cool enough to save lipids for northward migration. In the mid-1990s butterflies covered 21 ha of forest, but by 2017–18 the population had dropped more than 80% and the butterflies covered only 2.5 ha, less than half the minimum population size to be out of the danger of migratory collapse. As monarchs spread throughout North America over multiple summer generations, they lay eggs exclusively on milkweed (*Asclepias* spp.). Monarchs are threatened by milkweed loss, pesticides, logging, and climate change. The monarch is a symbol of conservation and cooperation and people are working across sectors and national boundaries to protect this familiar and beloved butterfly for future generations.

Biodiversity Importance

Social and Cultural Importance of Monarchs

The monarch, *Danaus plexippus plexippus* (Linnaeus, 1758), with its dramatic orange-and-black stained-glass like wings, is one of the most well-known butterflies (Fig. 1).

Monarchs play an important role in science and in the popular imagination. For generations students in North America have reared monarchs in classrooms during lessons on metamorphosis, mimicry and coevolution. As a result, adults and children alike have learned to recognize and revere monarchs as they lay eggs on milkweed and nectar on flowers in gardens and urban parks. This familiarity and knowledge has positioned the monarch as a critical wildlife ambassador and flagship species for conservation.

The monarch is unique among insects in that its iconic status unites people across national boundaries and across the political spectrum who admire the butterfly and its wondrous migration (Gustafsson et al., 2015), a fact visualized in its many uses as symbol of conservation and cooperation. The monarch is an emblem of transnational conservation initiatives and is on the logo of the Commission for Environmental Cooperation of the North American Free Trade Agreement. A monarch icon is used as the verification symbol for nongenetically modified food products. Celebrated for their annual migrations across international borders, monarch images are commonly used as symbols of migration (Fig. 2).

Monarch icons are commonly used to mark buildings offering sanctuary to migrating peoples. In Mexican folklore, monarchs represent the souls of departed love ones and Day of the Dead celebrations coincide with the arrival of the first fall migrants.



Fig. 1 Photograph of a newly metamorphosed monarch adult by Tierra Curry.



Fig. 2 Photograph by Tierra Curry of a monarch butterfly migration mural painted by artist Roger Peet in Minneapolis, Minnesota.

Across sectors of society, passion for monarch butterflies has led to numerous protection efforts, including volunteer habitat creation and monitoring efforts as well as visits to overwintering colonies. In an attempt to quantify this passion, one survey of U.S. households estimated that people would be willing to grow monarch-friendly plants and make donations to monarch conservation organizations up to a value of \$6.6 billion U.S. (Diffendorfer et al., 2014). Other studies have estimated the time spent volunteering to help monarchs at nearly 34,000 h per year valued at \$750,000 U.S. (Ries and Oberhauser, 2015; Semmens et al., 2018). Thousands of people in Mexico volunteer to protect the monarch's winter habitat from illegal logging, and tourism at monarch winter sanctuaries in Mexico generates approximately \$2.8 million U.S. in direct annual income (Semmens et al., 2018). While people are clearly willing to pay to protect this iconic butterfly, the long-term wellbeing of the monarch is invaluable.

Ecological Importance of Monarchs

Monarchs play a valuable role in the web of life because they provide food for a number of species. Monarch caterpillars and eggs provide food for many invertebrate predators including ants, flies, spiders, lacewings, and wasps, and migrating and breeding adults are food for numerous predators including birds, wasps, spiders, mantids, and dragonflies (Oberhauser et al., 2015). Black-backed orioles (*Icterus abeillei*) and black-headed grosbeaks (*Pheucticus melanocephalus*) consume millions of monarchs at their overwintering sites in Mexico (Brower and Calvert, 1985). Small forest mammals such as the black-eared mouse (*Peromyscus melanotis*) also consume large numbers of overwintering monarchs (Glendinning, 1993).

Despite its prominence as a representative of the pollinator community, the monarch's value as a pollinator has not been extensively studied. Monarchs nectar on a wide variety of flowering plants at a continental scale and could serve as incidental pollinators for many species. This contribution may be significant due to the butterfly's abundance and long-distance migrations.

Natural History of Monarchs

Description and life cycle

The monarch butterfly (Lepidoptera: Nymphalidae) is mostly orange and black with a 4-in. wing span. The orange wings have striking black-lined veins and a black margin with two rows of white spots on the black margin; the spots are never on the orange background. They are native to North America but have spread globally and now occur in 91 countries; populations in North, Central, and South America are genetically distinct from other populations (Pierce et al., 2014; Zhan et al., 2014).

Monarchs lay their pearly eggs singularly on milkweed plants (genus *Asclepias* and related genera), which serve as the sole host food for caterpillars. Eggs hatch in 3–8 days and larvae take 9–14 days to pass through five instars, or stages between molts. Larvae emerge as small whitish larvae with black heads and molt into tubular caterpillars with bands of black, white, and yellow and two pairs of protruding black antennae-like filaments (Fig. 3).

Larvae form a green chrysalis with gold dots and pupate into an adult within a few weeks (Fig. 4).

Migration

North American monarchs are renowned for their migration of more than 4000 km, one of the longest of any insect. At the end of summer, most monarchs east of the Rocky Mountains, by far the largest monarch population in the world, fly from the northern United States and southern Canada to the mountains of central Mexico to overwinter in high-elevation coniferous forests. In spring this “super generation” of monarchs flies north again to lay eggs in the southern United States. Successive generations then live for only a few weeks, continuing to fly north and spread throughout the eastern United States and southern Canada. The final summer generation will live for seven or more months and return to the forests of Mexico where their ancestors overwintered (Fig. 5).

A second smaller population migrates from states west of the Rockies to California coastal zone forests to overwinter. While overwintering monarchs form clusters, dense concentrations of adults huddled together on tree limbs and trunks.

Ecology of Forests Used for Overwintering

Eastern migratory population overwintering forests

Early attempts to track monarch migration began in the late 1930s, but not until 1975 did guides Ken Brugger and Cathy Aguado first record the location of overwintering grounds in the Trans-Mexican Volcanic Belt west of Mexico City (Urquhart and Urquhart, 1976; Malcolm, 2018).

The butterflies overwinter on five isolated mountain massifs within an 800 km² area in the states of Michoacán and México where the combination of high altitude (2400–3600 m) and tropical latitude (19–20°N) provides suitable microclimate conditions for monarch overwintering. By migrating south before the winter in the northern hemisphere, monarchs avoid freezing. The cool conditions in the mountains of Mexico prevent them from becoming too active and depleting lipid stores needed to survive the winter and return north the following year. Ambient temperatures that are too warm could cause the butterflies to break reproductive diapause or migrate too soon and nectar sources are sparse during winter months.

Monarchs cluster tightly on tree boughs and trunks (Fig. 6).

The forests where they gather are dominated by oyamel fir (*A. religiosa*) and in the absence of disturbance the canopy closure is > 70% (Navarrette et al., 2011). The dense canopy has been described as an umbrella and a blanket that protects the butterflies



Fig. 3 Photograph of a monarch caterpillar by Tierra Curry.



Fig. 4 Photograph of a monarch chrysalis by Tierra Curry.

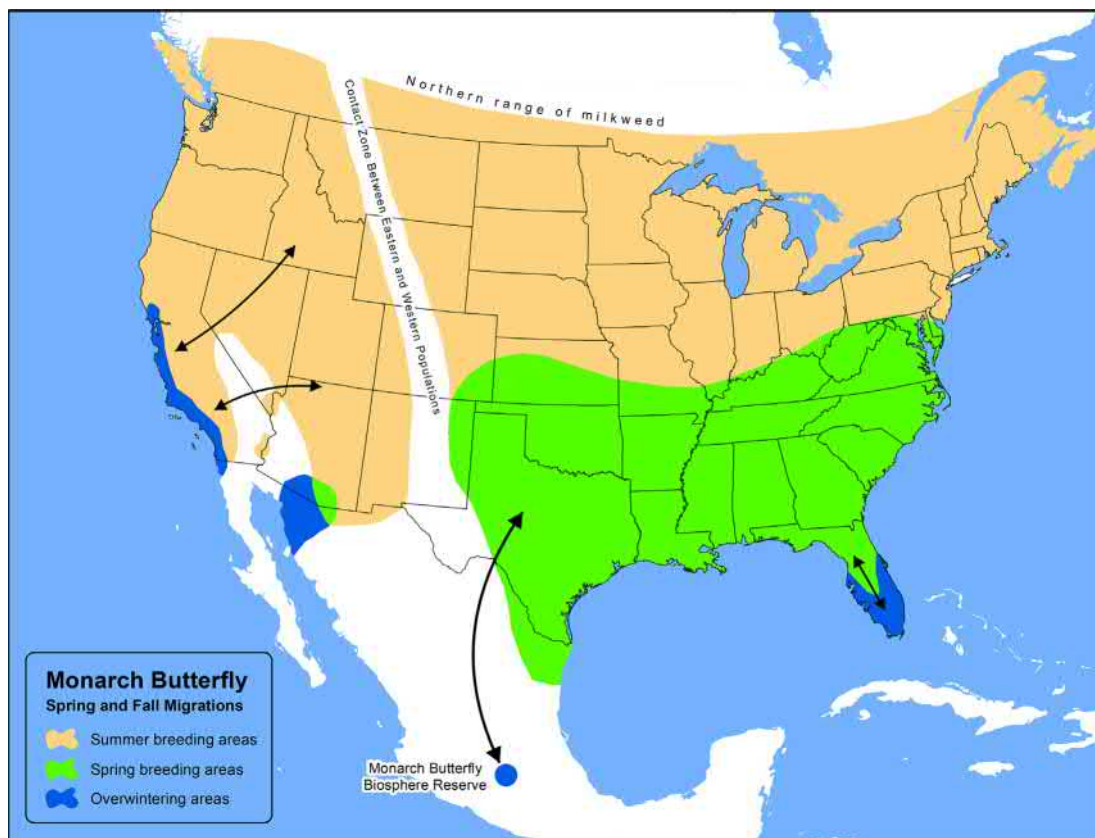


Fig. 5 Map of monarch migration by Curtis Bradley.

from excessive wetting and freezing during winter storms (Anderson and Brower, 1996) with surrounding forests acting as a screen to block severe wind (Brower et al., 2017). Because large diameter trunks have high heat capacity, mature trees have been compared to hot-water bottles that protect clustered butterflies (Fig. 7) from freezing temperatures (Brower et al., 2009).

Within the forests, butterflies are often located in arroyos near stream headwaters on moderately steep southwest-facing slopes (Slayback et al., 2007).

The oyamel forests are relicts from the Pleistocene that now have an island-like distribution. Additional species of trees in the overwintering grounds include primarily pines *Pinus* (Pinaceae) and oaks *Quercus* (Fagaceae). With the advancement of spring the butterflies move down arroyos into lower-elevation forests dominated by smooth-bark Mexican pine (*Pinus pseudostrobus*). Understory vegetation includes herbaceous and bushy species primarily in the aster (Asteraceae) and mint (Lamiaceae) families. Scientists have documented a total of 97 families, 337 genera and 694 species of plants in the overwintering forest area, 38% of which are endemic to Mexico (Cornejo-Tenorio and Ibarra-Manriquez, 2017). Local communities gather plants from the forest for food, medicine, fodder, fuel and to sell for income, making use of 213 plant species and 31 species of edible mushrooms (Farfán et al., 2007).



Fig. 6 Photograph of monarchs clustering on an oyamel fir tree bough by Brett Hartl.



Fig. 7 Photograph of monarchs clustering on an oyamel fir trunk by Brett Hartl.

Western Migratory Population Overwintering Forests

Though some eastern and western monarchs overlap and interbreed, the vast majority of migratory monarchs west of the Rocky Mountains overwinter along the Pacific coast in a 1000-km stretch from Baja California in northwestern Mexico to Mendocino County in northern California. Historically monarchs have been recorded clustering at more than 450 coastal locations, but only about 30 sites still host more than 1000 monarchs annually ([Xerces Society for Invertebrate Conservation Western Monarch Count Resource Center, 2017](#)). Western monarchs can be found overwintering in forests within a few kilometers of the coast at <90 m elevation and in locations protected from severe wind and full sun such as shallow canyons or the sheltered side of hills ([Lane, 1993](#)).

Most of the western monarch's overwintering sites are now dominated by blue gum eucalyptus (*Eucalyptus globulus*) and red gum eucalyptus (*E. camaldulensis*) introduced from Australia in the 1850s. Despite the prominence of eucalyptus at overwintering sites, monarchs cluster disproportionately on native trees when present, which may provide more protection for the butterflies ([Griffiths and Villablanca, 2015](#)). Native tree species used for clustering include Monterey pine (*Pinus radiata*), Monterey cypress (*Hesperocyparis macrocarpa*), coast redwood (*Sequoia sempervirens*), western sycamore (*Platanus racemosa*), and coast live oak (*Quercus agrifolia*).

Principal Anthropogenic Stressors and Trends

Population Status and Trends

Scientists began estimating the size of overwintering monarch populations in the 1990s. In the mid-1990s the eastern migratory population numbered nearly 1 billion adults covering 21 ha of forest, but the population has since declined by more than 80%.

The overwintering population size is projected by multiplying the hectares of forest by the number of estimated butterflies clustered per hectare. Scientists have continuously calculated more approximate estimates of butterflies supported per hectare from 50 million butterflies ha^{-1} (Slayback et al., 2007) to 37.5 butterflies ha^{-1} (Vilsack and McCarthy, 2015) to 21.1 butterflies ha^{-1} (Thogmartin et al., 2017). In the winter of 2017–18, the overwintering monarchs covered only 2.5 ha, an estimated population of 52–93 million butterflies (Fig. 8).

The western migratory population has declined from 1.2 million overwintering adult monarchs in 1997 to fewer than 200,000 in 2017–18, and the 2018–19 count is expected to decline dramatically, numbering as few 30,000 total monarchs (Xerces Society for Invertebrate Conservation Western Monarch Count Resource Center, 2017).

Decades ago scientists warned that due to numerous threats the monarch migration could be at risk of collapsing, deeming it an “endangered phenomenon” (Brower and Malcolm, 1991). “Quasiextinction” is the likelihood that a population will decline below a threshold at which population recovery becomes impossible. The eastern migratory population is estimated to have a quasiextinction risk of up to 57% by 2036 (Semmens et al., 2016). Western monarchs have a quasiextinction risk of 72% by 2037 (Schultz et al., 2017).

Loss of Breeding and Migratory Habitats

Monarchs are threatened in their summer breeding grounds by a number of factors including loss of milkweed host plants to urban and suburban development, industrial agriculture, herbicides, and persistent drought (Center for Biological Diversity et al., 2014). They are vulnerable to widely-used insecticides including neonicotinoids which are toxic to young monarch larvae (Pecinka and Lundgren, 2015). Fragmentation and degradation of fall migratory habitat due to lack of high-quality nectar plants and insecticide-residues may also be contributing to monarch decline (Inamine et al., 2016).

Loss of Winter Habitat

Eastern migratory population forest loss

Because of their critical importance in sustaining the monarch migration, the Mexican government protected portions of the ever-green forests that provide the monarch’s over-wintering grounds as the Monarch Butterfly Biosphere Reserve (MBBR) in 2000, modifying earlier designations from 1980 and 1986 that were less comprehensive. After a small expansion in 2009, the MBBR now includes 13,555 ha in designated “core” zones where only activities that do not significantly alter the forest, such as scientific research, are permitted, and 42,704 ha in designated “buffer” zones, where logging, agriculture, and tourism are permitted (Manzo-Delgado et al., 2014).

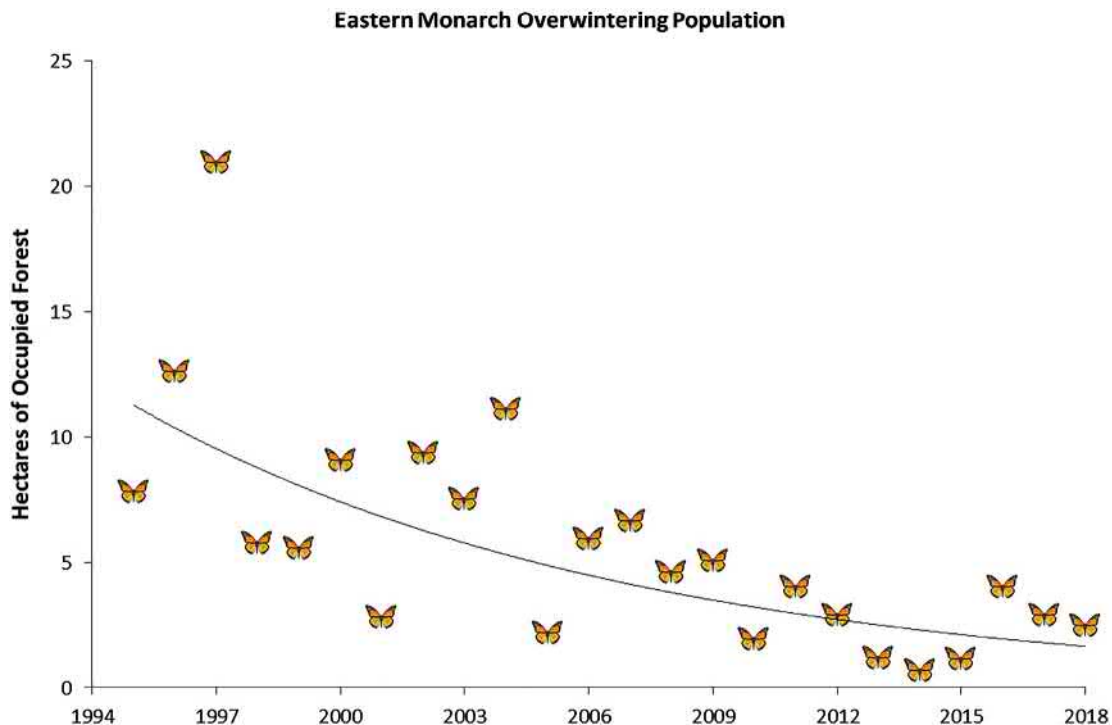


Fig. 8 Graph of eastern migratory monarch winter population size by Tierra Curry, adapted data from World Wildlife Fund Mexico. Scientists have estimated that the minimum size of eastern overwintering monarchs for the population to maintain viability is 6 ha (Semmens et al., 2016).

While logging is prohibited in core zones, the land is owned and managed by various groups, including communal agricultural groups known as *ejidos* (6509 ha), indigenous communities (4953 ha), small private owners (1018 ha), and the state (708 ha) (Brenner and Job, 2006). Not all monarchs overwinter inside the reserve. From 2004 to 2014 the MBBR housed 14 overwintering sites, or colonies, on average (Vidal and Rendón-Salinas, 2014a), with nine colonies present in the winter of 2017–18; there were five colonies outside the MBBR boundaries during both time periods (Rendón-Salinas et al., 2018).

Deforestation and fragmentation threaten the butterflies both within and outside of the reserve. Even within the MBBR legal boundaries and core zones, habitat is being lost to illegal logging, authorized extraction, domestic harvesting, agricultural clearing, forest fires, storms, and disease and senescence of trees (Honey-Rosés, 2009).

Illegal logging within the MBBR is a persistent problem. The designation of protected zones in 1986 restricted traditional livelihoods of property owners without compensation; as a result, deforestation increased and more than 2000 ha of forest were degraded between 1984 and 1999 (Brower et al., 2002). The process of delineating new MBBR boundaries in 2000 was more inclusive of property owners, but deforestation has continued. From 2001 to 2012 in the core zones, more than 1500 ha fell to large-scale logging and 554 ha fell to small-scale logging (Vidal and Rendón-Salinas, 2014b).

Nearly 30,000 people live within the reserve's buffers, and more than 1 million people live around the reserve (Vidal and Rendón-Salinas, 2014b). Poverty levels are high and many people lack basic services and extract trees to meet needs for housing and fuel. Subsistence logging represents approximately one-fourth of the forest area that was lost and degraded from 2001 to 2012 (Vidal and Rendón-Salinas, 2014b).

While the problem is slowing, illegal logging remains a threat to the monarch's overwintering habitat (Honey-Rosés, 2009). In 2015 approximately 10 ha were illegally cleared, mostly on state land (Brower et al., 2016). From 2016 to 2018 two additional ha were illegally clear-cut (World Wildlife Fund Mexico, 2018).

The causes of illegal logging fall into several categories ranging from mafia-style gangs who steal timber to supply illicit trade, to authorized cuts that exceed allotments, and poverty-driven subsistence logging (Brenner and Job, 2006; Honey-Rosés, 2009; Navarrete et al., 2011). The sophistication of illicit logging operations has made it exceedingly difficult for communities and government officials to curtail, even with military assistance (Honey-Rosés, 2009).

Salvage logging, both legal and illegal, also threatens the monarch's overwintering habitat. Following a particularly severe winter storm in March 2016 that impacted 54 ha, the federal government authorized salvage logging in core zones. Salvage logging raises concerns from scientists that such activities will exacerbate damage and inhibit forest recovery (Brower et al., 2017; Leverkus et al., 2017).

Because overwintering butterflies have specific microhabitat requirements to avoid freezing, desiccating, or depleting their lipid stores, dense forest provides more protection, particularly during episodes of severe weather (Brower et al., 2011), making them exceedingly vulnerable to canopy reduction and forest thinning (Anderson and Brower, 1996). The extensive dense forest structure also captures moisture that in turn sustains the high-elevation cloud forests, making thinning a threat to the hydrological integrity of the ecosystem (Slayback et al., 2007).

Western migratory population forest loss

Loss of overwintering forests for the western migratory monarch population is also ongoing. Urban and housing development has destroyed dozens of monarch overwintering sites on the California coast. Overwintering groves are also threatened by tree senescence, restoration to remove exotic and aging trees, drought and winter storms (Xerces Society for Invertebrate Conservation, 2017). In 2017 a grove managed by California State Parks that had supported 9000 butterflies in 2013 was removed due to hazard concerns and in the following census only six butterflies were counted (Xerces Society for Invertebrate Conservation Western Monarch Count Resource Center, 2017). While long-term habitat restoration is planned and initiated, immediate mitigation strategies are needed for overwintering monarchs along the Pacific coast.

Changing Climatic Conditions

Monarch population dynamics and migratory success are intricately linked to weather events and to climate (Zipkin et al., 2012; Flockhart et al., 2017). Global climate change threatens the butterflies in their breeding, migrating, and overwintering ranges. The distribution and quality of milkweeds, their sole host plants, are strongly influenced by climatic conditions (Batalden et al., 2007; Stevens and Frey, 2010). In addition, monarch adult activity and larval development are dependent on temperature (York and Oberhauser, 2002; Saunders et al., 2018). Monarchs may lose part of their breeding range in the southern and western United States due to increasing summer temperatures and severe drought conditions that could be harmful to both the butterflies and their host plants (Zalucki and Rochester, 2004; Stevens and Frey, 2010). Environmental factors experienced during migration also affect the butterflies' ability to successfully overwinter and migrate north again in spring (Agrawal and Inamine, 2018).

Some monarch populations in Florida and other warm areas do not migrate and remain reproductively active year round, often in relation to the availability of tropical milkweed (*Asclepias curassavica*). Both widespread milkweed planting efforts and global warming could expand the range of tropical milkweed outside of its native range, thus preventing some monarchs from entering reproductive diapause and migrating. Nonmigrating populations of monarchs harbor more parasites than migrating populations (Satterfield et al., 2015). In addition, higher temperatures could change the chemistry of tropical milkweed and reduce its nutritional value for monarch larvae (Faldyn et al., 2018).

Multiple models predict that the monarch's current overwintering ranges will no longer maintain the narrow microclimatic window needed by the butterflies to remain in diapause and conserve lipid stores. Sáenz-Romero et al. (2012) examined the future distribution of oyamel fir trees and forecasted that by 2090 no suitable monarch habitat would remain within the current boundaries of the MBBR. One potential yet highly uncertain solution, assisted colonization of oyamel fir trees, would require the trees be transplanted to higher mountain ranges outside the MBBR where it is unknown if they would survive or if the butterflies would follow considering it is unknown which cues they use to choose suitable overwintering sites (Sáenz-Romero et al., 2012). The effects on forest community dynamics of assisted migration are also unknown and potentially detrimental to currently established species.

Climate-related factors are already driving loss of trees in the MBBR. The region has been in drought since 2008 which stresses trees, making them more vulnerable to diseases (Vidal and Rendón-Salinas, 2014b). Drought damaged nearly 4 ha of trees from 2017 to 2018 (World Wildlife Fund Mexico, 2018). Climate change could also increase the frequency of other threat factors including floods, strong winds, and forest fires (Vidal and Rendón-Salinas, 2014b; Brower et al., 2017).

Oberhauser and Peterson (2003) used ecological niche modeling to project monarch distribution onto future climate scenarios and found that winter conditions were likely to become increasingly unsuitable in the MBBR within 50 years due to an increase in the frequency of large-scale mortality events, such as winter storms. Large-scale mortality events killed millions of overwintering monarchs in the winters of 1980–81, 1995–96, 1999–2000, 2001–02, 2003–04, 2009–10, and 2015–16 (Brower et al., 2017). The threat of increasingly frequent and intense lethal winter storms to monarchs is exacerbated by decreasing population size driven by habitat loss in the summer breeding range.

The western migratory population's overwintering habitat in California is also threatened by global climate change due to warming temperatures, drought, storm events, fires, and tree diseases (Xerces Society for Invertebrate Conservation, 2017; Fisher et al., 2018).

Conservation Strategies and Challenges

Safeguarding the Monarch Butterfly Biosphere Reserve

Supporting local communities

To protect the monarch's overwintering forests in Mexico, perpetual enforcement is necessary along with support for local residents. The forests not only harbor monarchs, they are also the source of livelihood for people whose primary economic activities are agriculture, ranching, and harvesting of forest products. As such, efforts that support monarch conservation must also support and empower local communities through mechanisms that promote a sustainable economy and curtail illegal forest uses. Ongoing programs are required to alleviate poverty and unemployment, engage property owners in management decisions and provide adequate security against armed illegal loggers.

Successful community-based conservation often requires coordination and cooperation between local institutions and people, governmental agencies, and nonprofit organizations (Romero-Brito et al., 2016). The necessary cooperation can fall short in and around the MBBR, as governmental and local monitors have been underequipped. Community patrols may lack basic supplies such as warm clothing and communication devices, and community guards have been injured by gunfire from illegal loggers (Tucker, 2004; Mexico News Daily, 2016). Community enforcers may also not receive adequate support from the state or federal government as there are instances of apprehended poachers being released without consequence (Tucker, 2004; Mexico News Daily, 2015).

Though the challenges are daunting, much progress has been made in reducing large-scale illegal logging in the MBBR via law enforcement, payments to *ejidos*, and efforts to empower local communities and provide incentives for forest protection (Vidal and Rendón-Salinas, 2014b). Payment for Environmental Services (PES) programs have helped reduce deforestation in the MBBR by strengthening community participation and supporting sustainable alternatives to timber extraction (Manzo-Delgado et al., 2014; Ramírez-Reyes et al., 2018). When the reserve boundaries were reformulated in 2000 to include input from affected residents, the Monarch Butterfly Conservation Fund, a PES-like program, was established to compensate communal land owners in the core zones for forfeited timber rights and for areas of conserved forests (Honey-Rosés, 2009; Honey-Rosés et al., 2009). The fund has also provided compensation to communities harmed by illegal logging via support for community-based enforcement efforts (Honey-Rosés et al., 2009).

Because the monarch spans North America and people in the United States and Canada benefit from overwintering habitat protected in Mexico, international investment by governments could help support impoverished communities who have yielded their land-use rights (Semmens et al., 2018). Pesticide corporations that degrade monarch breeding habitat in the United States and Canada could also contribute funding to protect overwintering grounds to compensate for drastic reductions in common milkweed (*Asclepias syriaca*) in croplands (Brower et al., 2012). Ultimately, a sustainable local economy must be established that creates more opportunities for residents without reliance on timber extraction.

Tourism

From November to March thousands of tourists visit the forests to observe the overwintering phenomenon; the Mexican government reported 230,000 visitors during 2017–18. Community groups collect fees for entrance, parking, tour guides and horse rides, and sell food and souvenirs. Travel agencies in Mexico City and Morelia arrange day tours to the sanctuaries, though some visitors stay overnight in towns including Angangueo, Ocampo, Valle de Bravo, and Zitácuaro. Because nearly half of visitors arrive on bus tours, the economic benefit to local communities is reduced, hindering sustainable regional development (Brenner and Job, 2006). The direct annual income from tourism is estimated to be \$2.2–\$2.8 million U.S. (Brenner and Job, 2006; Semmens et al., 2018).

Tourism provides important benefits but can also threaten the forest and butterflies it supports. For example, tourists can disturb butterflies, causing them to fly and deplete lipid stores, decreasing their ability to survive the winter and the northward migration (Vidal and Rendón-Salinas, 2014a, b). Researchers have issued an urgent call to improve tourism management so that it ultimately contributes to long-term monarch conservation while improving local social and economic conditions (Vidal and Rendón-Salinas, 2014a, b). Tourism to the MBBR has great potential for supporting forest protection if it provides direct benefit to the local economy (Brandt and Buckley, 2018).

Restoration

Degraded areas in forests in and around the MBBR are recovering due to active restoration efforts, reduced logging and grazing pressures, postfire recovery, and abandonment of agricultural areas (Manzo-Delgado et al., 2014; Honey-Rosés et al., 2018). The reserve receives funding from numerous sources for reforestation efforts, and many areas are demonstrating resiliency and natural recovery (Honey-Rosés et al., 2018). Like tourism, restoration and management initiatives could be used to bolster financial and livelihood opportunities for local residents.

Safeguarding the Monarch's Future

Following decades of concern about mounting threats to the monarch from pesticides and habitat loss, in the winter of 2013–14 the eastern monarch's overwintering population dropped to only 35 million butterflies covering only 0.67 ha of forest, down from an estimated 1 billion covering 21 ha 20 years prior. This precipitous decline raised grave concerns about the butterfly's future and catalyzed further conservation efforts.

The presidents of Mexico, the United States, and Canada committed to saving the monarch's migration at summits held in 2014 and again in 2016. At the 2016 summit then-president of Mexico Enrique Peña Nieto said that the monarch's pilgrimage shows how the three countries are intertwined. Then-U.S. president Barack Obama called the monarch "spectacular" and pledged to make sure that future generations get to see them.

In August 2014 the Center for Biological Diversity, Center for Food Safety, Xerces Society for Invertebrate Conservation and Dr. Lincoln Brower petitioned the U.S. Fish and Wildlife Service to protect the butterfly as a threatened species under the Endangered Species Act. The service issued a positive finding on the petition and launched a status review that will lead to a decision on the butterfly's protection in 2019.

The Committee on the Status of Endangered Wildlife in Canada in 2016 recommended that the monarch be protected as an endangered species. The Minister of the Environment and the Canadian Endangered Species Conservation Council are now deciding whether to add the butterfly to the country's endangered species list. In Mexico monarchs are classified as a species subject to special protection.

The MBBR was designated by the United Nations Educational, Scientific and Cultural Organization (UNESCO) as a World Heritage Site in 2008 due to its outstanding biological value. In 2015 a coalition of conservation groups petitioned UNESCO to designate the reserve as a "World Heritage Site in Danger" due to the population decline of monarch butterflies. The World Heritage committee is evaluating the designation and has asked the United States and Canada to provide information on monarch conservation status in the breeding range.

At least five international conferences have now been held on monarch conservation and biology to share knowledge, advance conservation and sustainability goals, and to establish research priorities. Scientists are currently working to further evaluate threats to the butterfly in its breeding, migratory and winter habitats as well as working with citizen scientists to map the entire flyway, including currently unknown paths between Texas and the overwintering grounds. Studies are also underway to better understand how monarchs navigate to overwintering grounds. This knowledge would help develop strategies to mitigate loss of forest habitat due to climate change.

Globally, monitored invertebrate populations have shown a 45% decline in mean abundance since 1970 (Dirzo et al., 2014). Populations of many pollinators are in decline in North America and Europe including many species of butterflies. The monarch is uniquely positioned as a flagship species for invertebrate losses due to its familiar and cherished status and allies across the social and political spectrum.

Migrating monarchs have been described as "the personification of happiness" (Lane, 1993, p. 341) and as a "river of orange sunshine" (Shapiro, 2013, p. 3). The widespread attention this charismatic insect has harnessed from the media and policy makers is certainly cause for hope for the beloved butterfly's future. If this passion translates into pesticide reform, action to combat global climate change, and ongoing protection for the monarch's overwintering forests, then future generations will have the opportunity to marvel at the winged-wonder's spectacular migration.

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Reducing Emissions From Tropical Deforestation and Forest Degradation

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Abstract

Forests are an integral element of life on earth. Providing oxygen to breathe, watershed protection, erosion control, carbon storage, and opportunities for people to connect with nature. Science warns us that at the rate forests are being destroyed, humans will alter the planet so significantly, that many lives (human and other species) will be extirpated. Recognition of the true value of forests, for their carbon storage function, is driving global agreements and policies to promote emissions reductions from land use across all biomes, but particularly in the tropics. Sizable levels of financial support have been directed at reducing emissions from deforestation and forest degradation, in the scope of USD 1.1–2.7 billion per year. But is this enough? This level of investment is still dwarfed by income from timber, agriculture, mining and palm oil cultivation—key drivers of tropical forest loss. We describe opportunities for reducing emissions from deforestation and forest degradation, discuss risks in measuring emissions reductions and draw attention to key political, social and environmental challenges from a regional perspective of Southeast Asia; a region in the spotlight for the mass expansion of oil palm plantations and polluting wildfires.

Introduction

Unprecedented and rising concentrations of carbon dioxide (CO₂), methane and nitrous oxide in the atmosphere that are resulting from energy production, agricultural output and industrial activity, are trapping heat in the lower atmosphere; causing the phenomenon of climate change. In 2015, parties to the United Nations Framework Convention on Climate Change held in Paris (COP 21) agreed that limiting global warming in this century to well below 2 °C and as close to 1.5 °C as possible to pre-industrial levels (UNFCCC, 2015) would be the most optimistic climate scenario to target. Moving to alternative energy sources could be slow, and fossil fuel burning accounts for the majority of emissions (Houghton et al., 2015). Four years post-Paris, the world collectively remains a long way from meeting these emissions targets. Short-term emissions reductions can be achieved from protecting, restoring and better managing tropical forests, which could reduce half the carbon emissions required to limit atmospheric warming to 2 °C and the carbon benefits would be relatively fast (Houghton et al., 2015). Consequently, it is widely understood that global agreements to mitigate climate change must include policies to reduce emissions from land use in the tropics. Forests are estimated to cover approximately 4 billion hectares of Global land area, according to the Forestry and Agriculture Organization of the United Nations (FAO). Of this, tropical forests represent approximately half of all forests, more than any other forest type. Around 9 million hectares of tropical forest cover were lost every year since 1990, representing the largest loss in any forest type for the period (FAO, 2015).

Strategies for Reducing Forest Carbon Emissions in the Tropics

Net emissions from land use change currently account for approximately 10% of anthropogenic carbon emissions. Reducing deforestation and degradation is one critically important way to lower global carbon emissions. Tropical forests are located mainly in Latin America, Southeast Asia and Africa. In Latin America, the highest rates of deforestation occur in Brazil, where 60% of the Amazon forest is situated. In Southeast Asia, the majority of deforestation occurs in Indonesia, followed by Malaysia. The majority of deforestation in Africa occurs in the Democratic Republic of Congo. Fig. 1 shows the total area of tropical primary forest cover loss for the top 10 countries in 2018 and the per cent increase from 2017. Brazil lost the most forest cover, followed by the Democratic Republic of the Congo and Indonesia.

Despite significant international efforts to reduce deforestation in the tropics, the success of these initiatives lies at the national and local level. National and local-level strategies and action plans to reduce deforestation include: reducing deforestation of natural forests and peatlands, sustainably managing oil palm and timber plantations, reduced-impact logging, restoration and improving the management effectiveness of existing protected forests.

Reducing Deforestation of Natural Forests

Global efforts to reduce emissions from deforestation in the tropics are largely driven by climate change policies. A study from 2008, reported that forest-based emissions could be cut by 75% by 2030 with international initiatives supported under the United Nations Framework Convention on Climate Change, such as REDD+ (Reducing Emissions from Deforestation and forest Degradation plus conserving, sustainably managing forests and enhancing forest carbon stocks; Eliasch, 2008). However, tropical forest cover loss has continued to escalate. In 2016, global tropical primary forest cover loss was the highest year on record since 2002. Declines occurred in 2017 and 2018, yet they are still among the largest forest loss years experienced this century (Fig. 2).

Southeast Asian forests are among the most ancient, diverse, carbon-dense and critically threatened of all forests in the world. Consequently, the region is a major focus of policies for reducing emissions. Regional initiatives to reduce deforestation include the Singapore Declaration on Climate Change Energy and Environment, which has mandated the Association of Southeast Asian Nations (ASEAN) members to:

promote cooperation on afforestation and reforestation, and to reduce deforestation, forest degradation, forest fires, including by promoting sustainable forest management, combating illegal logging, protecting biodiversity, and addressing the underlying economic and social drivers.

Agricultural production drives 73% of tropical forest loss worldwide, followed by urban expansion (10%), infrastructure (10%) and mining (7%; Hosonuma et al., 2012). A movement toward renewable energy has seen an increase in the production of biofuels, which unintentionally has had major consequences for emissions by contributing to an increase in tropical deforestation to grow

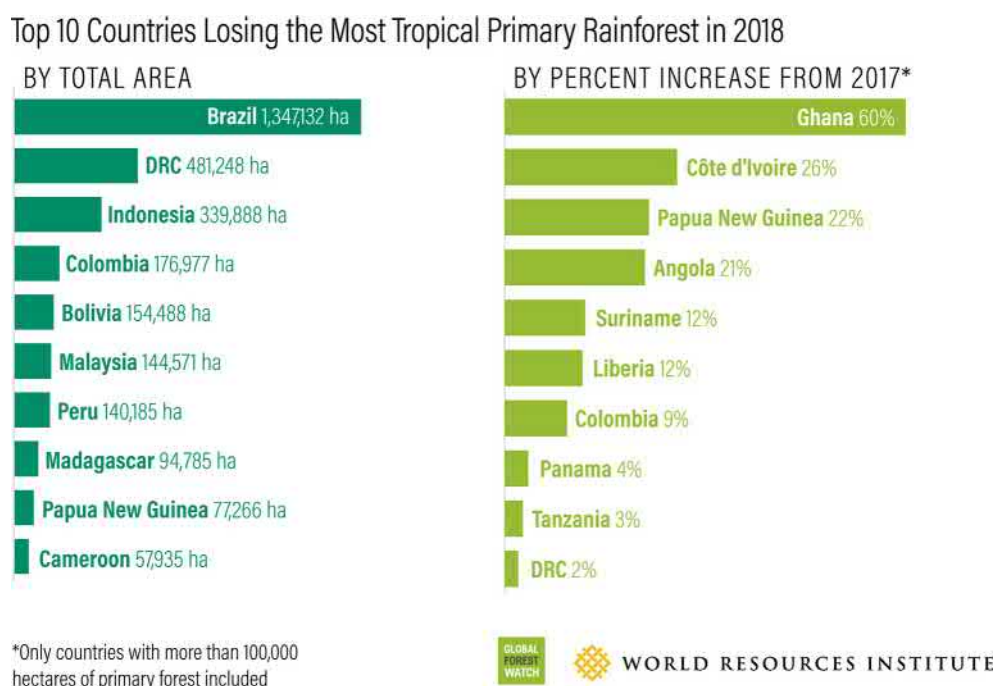


Fig. 1 Total tropical primary forest cover loss (in hectares) in 2018 for the top 10 countries. Source: Global Forest Watch, World Resources Institute, www.wri.org.

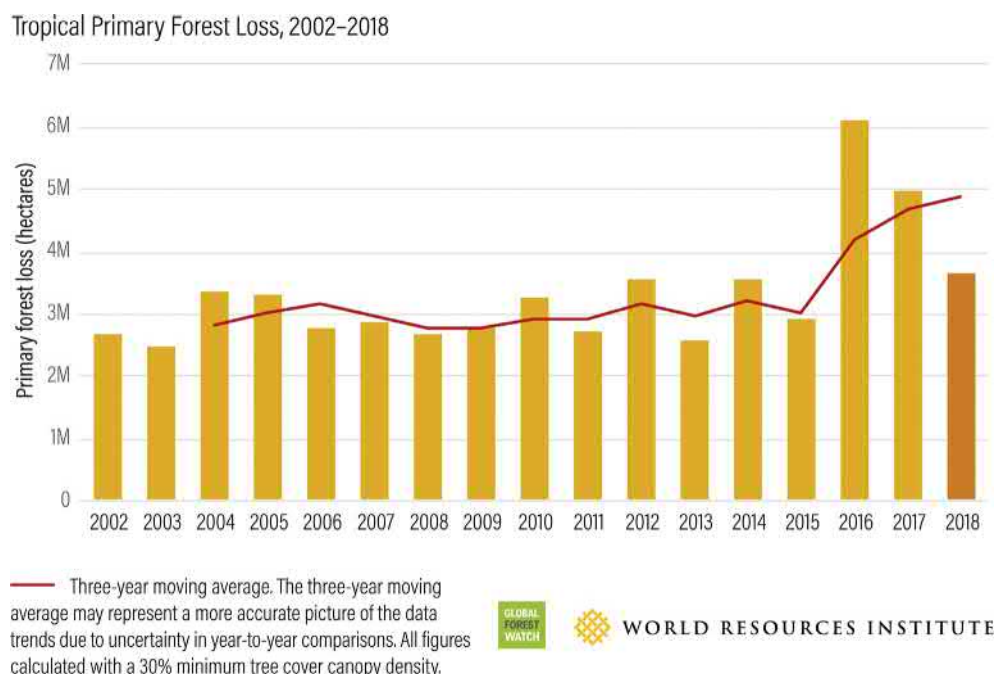


Fig. 2 Trends in tropical primary forest cover loss (in millions of hectares) from 2002 to 2018. Source: Global Forest Watch, World Resources Institute, www.wri.org.

biofuel products. According to the European Commission, greenhouse emissions from biofuels are three times higher than biodiesel. Palm oil is a commonly used product to produce biofuels. While palm oil has been linked to catastrophic deforestation, it is difficult to detect a direct link between first and second generation of biofuels and deforestation at a global level due to limited availability of time series data.

Forest moratorium

In 2011, the Indonesian government issued a moratorium on the conversion of primary forests and peatland forests under Presidential Instruction (No. 10/2011), which aims to suspend the granting of new concession licenses for logging and forest conversion in primary forest and peatlands. Since its initiation, it was extended three times in 2013, 2015, and 2017—yet deforestation remained alarmingly high. One of the issues limiting the success of the moratorium in the first 6 years, was that local governments continued issuing licenses despite the central government prohibiting further issuance. In addition, the Presidential Instruction did not entail legal consequences for perpetrators. With a decentralized political system in Indonesia, sub-national leaders were able to issue local policies that undermined the moratorium. In 2017, the annual deforestation rate dropped by 60% in Indonesia, followed by another small decline in 2018; two of the lowest deforestation years in this century (Fig. 3). The 2017 annual deforestation rate of protected peat areas also dropped by 88% in Indonesia. Over a quarter of protected peatlands have pulpwood and oil palm concession areas within their boundaries, or licenses to establish them. The Indonesian Government implemented a land swap program to prevent further conversion in protected peatlands (see “Land Swaps” section).

Sustainably Managing Oil Palm and Timber Concessions

Oil palm and timber concessions are two major drivers of tropical forest loss in Southeast Asia. The majority of global palm oil consumed comes from tree plantations in Indonesia and Malaysia. In 2016, Indonesia produced 34,520,000 tonnes of palm oil, and Malaysia produced 17,320,000 tonnes. To meet the high global demand for palm oil and timber, primary forests across the Indo-Malayan islands of Sumatra and Borneo have undergone rapid transformation into expanses of oil palm and timber plantations. Borneo became a hotspot of deforestation in the late 20th century, with land clearing for oil palm and pulpwood plantations contributing to a 34% loss in primary forest cover between 1973 and 2015 (Gaveau et al., 2016). Of the 18.7 million hectares cleared during this period, 14.4 million hectares were in Indonesian Borneo (Kalimantan) and 4.2 million hectares were in Malaysian Borneo (Sabah and Sarawak), respectively.

Efforts to reduce deforestation from oil palm and timber production encompass a range of standards, certification schemes and policies driven by government, industry and non-government organizations (NGOs). For example, palm oil industry representatives and NGOs benchmark the performance of palm oil producers against a set of Certified Sustainable Palm Oil (CSPO) standards under the Roundtable on Sustainable Palm Oil (RSPO). Companies who comply with the CSPO standards around environmental and social sustainability, receive certification and can charge a premium on their products. The European Union, the third largest importer of Malaysian palm oil, have called for banning the use of palm oil as a biofuel by 2030. In 2018, European

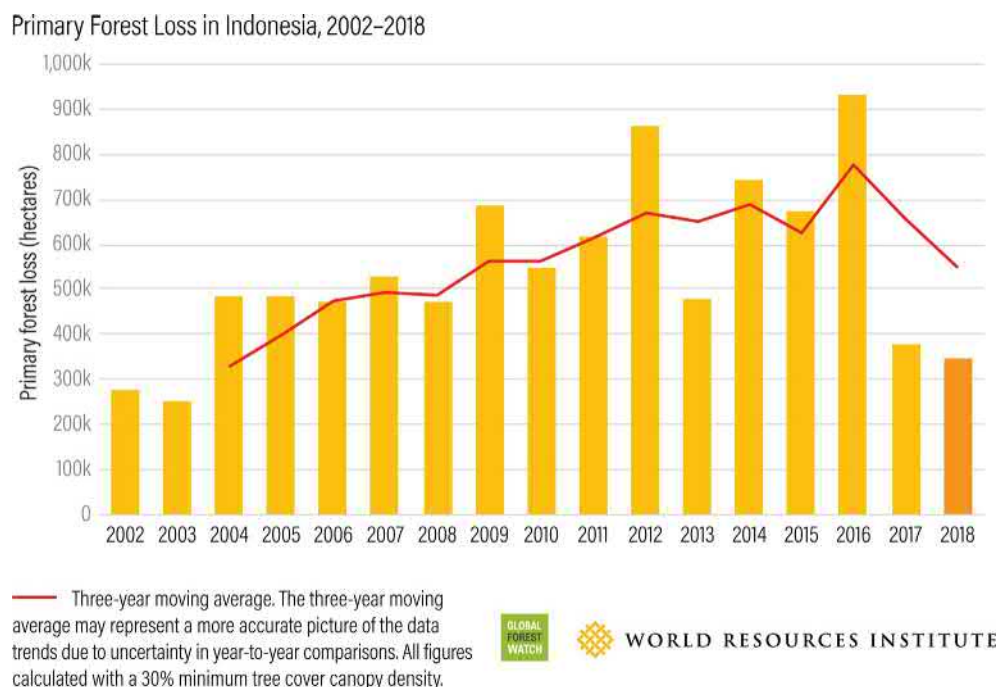


Fig. 3 Total area of primary forest cover loss (in hectares) in Indonesia from 2002 to 2018. Source: Global Forest Watch, World Resources Institute, www.wri.org.

parliamentarians proposed to restrict imports of Malaysian palm oil-based biofuel within the union, with Norway the first to commit to banning palm oil biofuels from 2020. Government led initiatives include the palm oil moratorium issued in 2018 by the Indonesian President Joko Widodo. Under Presidential Instruction (No 8/2018) on the Delay and Evaluation of Permits and Elevated Productivity of Oil Palm Plantations, new permits for oil palm plantations were suspended for 3 years. During this time, the government is also seeking to review the current allocation of permits, of which some are located on land classified as “forest area.” Stemming from the Government’s commitment to reducing deforestation, the three-year palm oil moratorium is intended to address issues around overlapping tenures and licenses, and the rights of smallholders to equal partnership with large-scale plantations. Similar industry led initiatives are focused on sustainable forestry and tree plantations.

Reduced-Impact Logging

The extraction of timber from forests is one of the most widespread forms of tropical land use, with over 20% of humid tropical forests subject to log-harvesting. Reduced-impact logging (RIL) is a practice of timber extraction that adheres to guidelines aimed to reduce wastage and collateral damage during logging activities. Forests logged according to RIL methods have less initial carbon loss than conventionally logged-forests, and fewer years of carbon declines before they start recovering carbon. Guidelines include reducing road and landing pad construction impacts, and reducing collateral damage to remaining trees during extraction by directional felling and protection of water courses. Field studies across Southeast Asian sites found forests logged according to RIL methods saved 20% more carbon over 30 years than those logged using conventional log-harvesting techniques (Pinard and Cropper, 2000; Healey et al., 2000; Putz et al., 2008). Further emissions benefits can be generated from selective logging of forests where minimal disturbance occurs to peat hydrology. Despite the environmental potential of RIL, the practice is not widely implemented and furthermore, concerns remain about how environmentally sustainable it really is. For example, Zimmerman and Kormos (2012) contend that sustainable forestry management cannot be truly sustainable under current practices, due to increased management and training costs, and decreased harvestable timber volumes, associated with achieving sustainable high-value tropical timber yields. A key concern is the length of the cutting cycle, with some studies contending that 60 years is necessary for forest structure to recover to baseline conditions. Another concern is whether highly specialized biological interactions will recover post-logging (e.g., endemic tree species and pollinator interactions). However, an opportunity exists in locally-managed timber harvesting, which can successfully protect relatively intact tropical forest systems and promote sustainable livelihoods—if locally-managed forests are backed by national legislation (e.g., ratification of community land tenure). Selectively logged-forests are one of the less degrading of land use scenarios for carbon stocks and biodiversity observed in Southeast Asia, and can be equally as effective at reducing deforestation as protected areas (Gaveau et al., 2013).

Restoration

Carbon loss that has already occurred due to deforestation and forest degradation can be somewhat recovered by reforestation, where forests and their carbon stores, are assisted or allowed to recover. The restoration of tropical forests reduces net anthropogenic carbon emissions by accruing carbon above and below ground. Forest restoration can include replacing trees that have been cleared with new plantings or allowing the natural regrowth from seed banks, often on degraded land that was set aside for agriculture but is no longer under active management. Degraded or secondary forests can be restored for the purpose of fire prevention and biodiversity conservation (often with the aim of conserving key seed dispersers to aid seed dispersal). Successful restoration also benefits communities in terms of enhanced food security, improved air and water quality, climate change resilience, job creation, and more. Restoration can be on mineral or peat soils, below we discuss key differences.

Peat restoration

Tropical peatlands cover a global area of 44.1 million hectares, with 56% of these occurring in Southeast Asia, storing 69 billion tonnes of carbon (Miettinen et al., 2012; Page and Rieley, 2016). Tropical peatlands represent 11% of land in Indonesia and store up to 20 times more carbon than non-peat mineral soils. Their drainage and degradation is responsible for 5% of anthropogenic CO₂ emissions. Once drained, peatlands are highly susceptible to prolonged episodes of burning. The worst peat fire years in Indonesia occurred in 1997, 2006, 2009, 2012, 2013 and 2015. Emissions from the 1997 El Niño fires were equivalent of 13%–40% of annual global emissions from fossil fuels (Page et al., 2002). Although this was a particularly bad year for peat fires, it illustrates the magnitude of such an event. Again in 2015, the traditional burning practice widely used in Sumatra and Borneo for land clearing was exacerbated by a long drought period, causing wildfires to burn for 2 months and releasing 97% of the annual carbon emissions from Indonesia in those 2 months alone (Huijnen et al., 2016).

As a response to the forest fire crisis in 2015, the Indonesian government launched the Peatland Restoration Agency in 2016, which ambitiously aims to restore 2 million hectares of peatland in seven provinces (Riau, Jambi, South Sumatra, West Kalimantan, Central Kalimantan, South Kalimantan and Papua). Peatland restoration is expensive and requires substantial investment from private companies, where many concessions are located, as well as support from local communities. Peatlands are naturally wet areas, and to remove timber in these areas the wetland is firstly drained before the timber is accessible. Peatland restoration, therefore, can involve blocking canals to encourage flooding, rewetting these areas and then replanting. It is consequently much more expensive than restoration on dry mineral soils.

Land swaps

Also in response to the 2015 mega fires, the Government of Indonesia initiated a nation-wide peatland governance reform. As part of this reform, peatland was rezoned based on its ecological characteristics, into conservation or cultivation function. On peatland with conservation function, a permanent moratorium is applied in which only research, ecosystem protection and education are allowed. Over 200 forest plantation concessions overlap with the new “peat with conservation function” designation, prohibiting the concessionaires from cultivating the land. As a form of compensation, a land swap policy was prepared by the Ministry of Environment and Forestry (MOEF) for timber concessionaires whose plantations overlap with protected peat systems by more than 40%, offering them less fire-prone land in exchange. A map was released showing the location of the new land swap sites in Kalimantan, Sulawesi and Papua that are asserted as having low-quality forest cover. A civil society coalition found that 40% of the land proposed as suitable for swaps contains primary or secondary forest. Other potential risks of the policy include the potential for concessionaires to dodge their obligations to restore degraded peatlands under the guise of taking the land swap avenue, and stirring further sociopolitical conflict if the lands proposed for swaps are inhabited or managed by local people.

Improving the Management Effectiveness of Protected Areas

Protected areas aim to safeguard natural assets and conserve biodiversity, yet they are not spared from global patterns of forest loss and degradation. Though the proportion of total area under protection is increasing, rising from 8% in 1990 to 15% in 2019, the land inside protected areas remains exposed to threats and in some places the biodiversity inside protected areas is declining. Curtailing illegal deforestation in protected areas represents a significant opportunity for reducing emissions from land use change. Adequate law enforcement and staff, infrastructure and equipment is dependent of funding, which has historically been poor in tropical nations. Increased investment in protected area management resourcing, education and training programs could substantially lower the illegal deforestation, logging, burning and agricultural encroachment that are common in parts of Southeast Asian protected areas. A significant opportunity for climate mitigation and biodiversity conservation lies in abating the high level of illegal forest loss and the carbon emissions predicted to occur in the future if the current pace of tropical forest loss continues. Between 2000 and 2010, approximately 2% of forest cover was lost every year illegally, inside boundaries declared by the International Union for the Conservation of Nature (IUCN) as protected. Projections for the next 30 years, are that an additional 414 million tonnes of carbon would be emitted from Indonesian protected areas if the 2000/10 pace of illegal deforestation continues (Graham et al., 2017).

Small-scale encroachment for agriculture and plantations, as well as illegal timber harvesting, are some of the drivers of forest loss inside park boundaries. A range of socioeconomic and political conditions underlie these activities, such as local migrants moving into protected areas, local governments recognizing villages and communities within National Park boundaries, inadequate resourcing, National Park agencies lacking the capacity and authority to enforce their mandates and a lack of support from local government for national policies. An example of encroachment can be seen in Kutai National Park in the province of East Kalimantan, Indonesian Borneo, which has areas that are occupied as villages and oil palm plantations (Fig. 4).

History of Development: From RED to REDD to REDD +

Payments for Ecosystem Services (PES) are a type of market-based instrument that provide economic incentives to stakeholders for retaining and improving the size or quality of natural assets resulting in improvements to ecosystem services (e.g., providing carbon credits to landowners for conserving forests). REDD + is the most prominent international financial mechanism currently being practiced for conserving tropical forests and reducing carbon emissions from forestry and land use in the tropics. REDD + facilitates monetary incentives to developing nations that preserve or enhance the carbon storage function of natural forests. For example, Norway has significantly contributed to REDD + programs in Indonesia, as well as Bolivia, the Democratic Republic of the Congo, Panama, Papua New Guinea, Paraguay, Tanzania, and Vietnam. The scheme aims to offer both environmental and economic benefits to host countries; including improvements in the long-term natural resource pool and financial benefits to local forest-dependent communities.

REDD + was first officially proposed in 2005 by a group of 15 developing countries led by Papua New Guinea and Costa Rica known as the Coalition for Rainforest Nations (www.rainforestcoalition.org). When REDD + was more formally discussed in 2007 at the COP13 in Bali, it was solely concerned with providing a cost-effective solution to reducing emissions from deforestation (RED) and only later grew to include forest degradation (becoming REDD). In 2008, the idea of including the conservation, sustainable management and enhancement of forest carbon stocks was discussed and REDD “+” was introduced. This was an important developmental milestone as it opened up two activities: (1) channeling more funds to improve the management effectiveness of protected areas; and (2) promoting the restoration of degraded forests. By 2010, it was recognized that REDD + needed some sort of protection against perverse outcomes for local forest-dependent communities and biodiversity, resulting in the inclusion of “safeguards” in the Cancun agreements and later refined in Paris in 2015. These are sometimes referred to as “non-carbon outcomes.”

One of the key objectives of REDD + is to enhance the wellbeing of local communities that are hosting projects. Community Forest Management is defined as the use, management and conservation of forests by communities, whether ownership is held by the community or by a state agency with involvement from the community. Community-managed forests are a common and growing governance arrangement in developing countries. Globally, approximately 15% of forests are owned or assigned to indigenous peoples and local communities. Some scholars argue that community forest management is a win-win scenario for reducing deforestation, conserving biodiversity and contributing positively to local community livelihoods. Indonesia has at least



Fig. 4 Oil palm plantation inside enclave village in Kutai National Park, Indonesian Borneo. Credit: Laely Nurhidayah.

four different types of community forests, including: village forests (*Hutan Desa*), community forests (*Hutan Kemasyarakatan; HKM*), *Adat Forest*, *Community Based Plantation Forest*, and *Private forest (Hutan Rakyat)*.

Results-Based Finance via REDD+

To qualify for results-based finance via REDD+, countries must have demonstrated they have a national strategy or action plan for reducing forest-based emissions, a system for monitoring and reporting on emissions, a baseline (reference level) against which emissions reductions are measured, and a safeguard system to protect against confounding environmental or social issues stemming from REDD+ projects (Seymour and Busch, 2016). As the outcomes of REDD+ are measured against reference levels, it is necessary to adopt a transparent and fair methodology in calculating these benchmarks. Countries can access REDD+ “readiness” funding to support the development of these requirements. A key difference between REDD+ and other financial mechanisms such as the Clean Development Mechanism (cdm.unfccc.int), is that REDD+ relies on results-based finance and can be funded through bilateral or multi-lateral agreements or the carbon market. Previous schemes have had less flexibility in their mode of financial operation. The Paris Agreement allows for the “international transfer of mitigation outcomes” meaning developed countries can purchase carbon credits through REDD+ to offset their emissions.

REDD+ finance in the first 10 years of implementation has almost solely been from voluntary commitments from donor countries. However, in 2019 Norway announced its first results-based payment to Indonesia as part of their REDD+ agreement, in recognition of a 60% drop in forest loss from 2016 to 2017. Global estimates of finance being pledged or already committed to REDD+ are USD 1.1–2.7 billion per year, compared to the estimated USD 15 billion per year required (Centre for Global Development; Olesen et al., 2018). The Forest Carbon Partnership Facility (forestcarbonpartnership.org), with the World Bank as trustee, has also committed US\$399 million in readiness activities to fund training and monitoring activities.

Challenges of Measuring Emissions Reductions

A large amount of criticism has been directed toward the process of measuring, reporting and verifying (MRV) carbon reductions to ensure that only “real” carbon reductions are being incentivized. These challenges include: additionality (paying to reduce emissions that would not have occurred under the business-as-usual scenario), permanence (emissions reduced now that are offset by increased emissions in the future) and leakage (emissions reduced in one location that are shifted to another location without the same controls). There are two methods commonly applied to carbon accounting, both have risks. A historical approach, that assumes past rates of deforestation will continue, favors countries shifting from high to low deforestation and therefore has the risk of encouraging intensified deforestation prior to REDD+ implementation. Simulated models have also encountered distortions in measuring emissions reductions, as modeled predictions of future land cover change have been shown to have very high error rates, particularly when regional trend data are applied to small local sites (Pontius et al., 2008). The definition of a forest is also very different, depending on who is providing the definition. Today, there are known to be >800 official definitions of forest. For example, the Forestry and Agriculture Organisation (FAO) apply a definition of tree cover of >10% to measure forests. It is important that REDD+ hosts and donors agree on the type of land use and land cover change that qualifies for incentives.

Where Are We Now?

A review led by the Centre for International Forestry Research (CIFOR) has synthesized the learnings from more than 350 REDD+ projects for the 10-year period till 2018 and reviewed progress in lowering deforestation and forest degradation, reducing emissions, improving livelihoods and strengthening forest governance in developing countries (Angelsen et al., 2018). There are three key messages:

- i. REDD+’s distinguishing design feature of results-based payments remains yet to be tested at scale. Funding has been less than anticipated and is mostly from voluntary commitments rather than via the carbon market.
- ii. REDD+ has helped forests gain a prominent narrative across the world stage at both political and community level. This attention has contributed to significant advancements in forest and carbon monitoring capacities, stakeholder involvement and programs to address indigenous and community land rights for many nations across the tropics.
- iii. Further work needs to be done to better integrate forestry and other land use opportunities into national development and climate mitigation policies.

Concluding Remarks

The significant climate mitigation potential of REDD+ is yet to be utilized at a cost-effective global scale that can influence future emissions and climate trajectories; yet momentum is building in some regions. Despite the negative press attracted by the growing

palm oil industry and polluting forest fires, Southeast Asia has made substantial progress in identifying and addressing key challenges of reducing emissions from deforestation and forest degradation. Recent initiatives in Indonesia include the government led primary forest and oil palm moratoriums, the land swap policy, the peatland restoration program, support for community managed forestry and the high volume of REDD+ readiness activities underway. Our case studies below highlight a couple of these recent initiatives. The first case study compares the range of costs and benefits that can be achieved through REDD+ activities when spatial context is considered, and the second case study emphasizes the importance of aligning activities with local initiatives to address land access inequality issues. Looking forward, the decreasing rate of deforestation seen in 2017 and 2018 in Indonesia provides some reason for cautious optimism that these initiatives are starting to work.

Case study: Comparison of costs and benefits of REDD+ strategies

The range of opportunities financed through REDD+ is diverse and not all activities deliver equal carbon incentives (Graham et al., 2016). Restoration of tropical Southeast Asian forests has high carbon incentives, which makes it a cost-effective strategy to implement (per tonne of carbon reduced) and has large scope, due to the vast areas of degraded land that are candidate sites for reforestation. Based on past deforestation rates, reducing illegal deforestation could generate large carbon gains, if projects are targeted to deforestation hotspots and carbon rich forests (e.g., peatforests). The costs of this strategy include better resourcing of protected areas, such as employing more law enforcement officers and erecting clear boundary markers and fences, while the incentives include the carbon benefits alongside biodiversity, tourism and, if well managed, local livelihoods through non-timber forest economies.

Environmental threats, as well as the carbon benefits and costs of implementing conservation strategies are influenced by the spatial context in which they occur. Site-specific factors, including terrain, carbon density, distance to markets and soil type influence the costs and benefits of conservation strategies. A study by Graham et al. (2017) estimating the costs, benefits and scope of REDD+ in Indonesia found the range of costs varies significantly for all strategies. For example, reducing deforestation from oil palm and timber plantations had high potential carbon gains, and some cost-effective locations in areas where oil palm plantation licenses have been granted on unproductive land or peatlands.

Aside from financial costs and carbon benefits, important ecological considerations include the carbon-biodiversity trade-offs of REDD+ activities. For example, biodiversity benefits from restoration can be large where regrowth is promoted on degraded forests, but one of the most serious risks to biodiversity is afforestation, which could lead to carbon-rich plantation forests being valued over biodiverse, low-carbon grasslands. Social concerns of REDD+ include the risk of “fortress conservation” in which the priorities of international investors are privileged over those of local forest users. Community opposition and poor knowledge and communication have been seen to stall project development. In the forest frontier district of Kapuas Hulu, Indonesian Borneo, communities resisted to engage with proponents due to uncertainty about the terms of inclusion and future rights to resources under proposed governance models. Such resistance could significantly delay projects and incur large additional costs.

Case study: Social Forestry in Indonesia

In Southeast Asia, a key strategy to reduce deforestation and improve tenure security for forest communities is through national social forestry programs. Social forestry (or community forestry) is a strategy to restore community access to forested land. According to the Association of Southeast Asian Nations (ASEAN) Social Forestry Network, social forestry has three objectives: (1) environmental conservation in the form of sustainable forest management; (2) indigenous people’s land rights and local knowledge; and (3) community benefits. These traits align with REDD+, which has played an important role in financially supporting the advancement of social forestry in the region. Cambodia, Indonesia, Myanmar, the Philippines, Thailand and Viet Nam have established national targets for the area of land to be allocated to local people under their social forestry programs. If achieved, this would result in over 30 million hectares of forest land being managed under social forestry programs in the ASEAN region by 2030.

The ASEAN members established a Social Forestry Network in 2005 to facilitate knowledge exchange and promote community involvement in social forestry. Each ASEAN member state has developed its own definitions and modalities to implement social forestry, therefore, social forestry takes different forms, depending on national laws and policies, the forest type, and the aims and objectives for engaging them in forest management. The definition of forest adopted in Indonesia was created as a mechanism of state capture of land and natural resources (Astuti and McGregor, 2017). The issuance of the Basic Forestry Law in 1967 was followed in the 1970s with a map that divides land in Indonesia into two categories: forest land and non-forest land. Forest land falls under the authority of the Ministry of Forestry and non-forest land under the National Land Agency.

The issue of land grabbing is a national priority that the Indonesian Government is aiming to address through their social forestry program. According to the Central Bureau of Statistics, 60–70 million people live in or around forests. Yet the control or ownership of the majority of forests is with a small group of stakeholders: pulp and paper operators, and oil palm and logging concessionaires. The national Social Forestry Program, launched in 2014, aimed to distribute 12.7 million hectares of forested land under President Joko Widodo’s regime from 2014 to 2019. However, tenure conflicts resulting from the issuance of forestry plantation concessions has resulted in only a fraction of this area currently planted, with the remaining lands being contested with local and indigenous communities. Land tenure conflicts typically arise when local people have a customary belief in ownership of the land, without a written deed. Communities that are required to apply to lease land that they have managed for a long time, can feel disempowered. Despite significant challenges, there are some examples of social forestry schemes working well. Lampung Province on the Indonesian island of Sumatra has been hailed a model of social forestry. For nearly two decades, a government scheme has granted the community rights to use and manage forest resources, and the social and environmental benefits include: reduced rates of land clearing, improved overall community welfare and reduced inequality within the community. Similar reduced deforestation evidence has been documented from social forestry schemes in Indonesian Borneo.

Acknowledgments

Victoria Graham would like to acknowledge James Cook University and the Skyrail Rainforest Foundation for financially supporting this work. Laely Nurhidayah would like to acknowledge the Indonesian Institute of Sciences, the National University of Singapore, the Australian National University and the SMERU Research Institute for financially supporting this work. Rini Astuti would like to

acknowledge the financial support of the Singapore Ministry of Education Social Science Research Council (SSRC) for a grant entitled “Sustainable Governance of the Transboundary Environmental Commons in Southeast Asia” (MOE2016-SSRTG-068).

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- <https://www.wri.org/>—World Resources Institute.

Solving the Spotted Owl Crisis: Including People in the Solution

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Published by Elsevier Inc.

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Abstract

Aggressive logging of public old-growth forests in the Pacific Northwest came to an abrupt halt in 1992 due to litigation involving the federally threatened northern spotted owl (*Strix occidentalis*). Much has been written about the ensuing crisis, but not about how Forest Service officials resolved it in ensuing years. The effort to create a new forestry model relied on applying important holistic concepts to restore biological function to Douglas-fir (*Pseudotsuga menziesii*) forests. The crisis also necessitated reengineering inclusive social processes to restore hope to disenfranchised parties. A successful new social contract emerged for managing public lands stuck in gridlock that has proven effective, durable, hopeful, and resilient.

It had the feeling of a meat locker door clunking shut behind you... and then hearing a bolt lock into place. Judge Dwyer had spoken. The good old days of unmitigated clearcut logging were gone forever.

In 1991, a ruling from federal district judge William Dwyer stopped the Forest Service from cutting timber from forests inhabited by the northern spotted owl. The injunction clamped the jugular of federal timber that reliably fed timber mills in the Pacific Northwest, sending a deep shudder through the industry that depended on these forestlands for raw material. The end had finally come to the decades-long liquidation of old-growth forests.

Prior to Judge Dwyer's ruling, the Forest Service had inexorably, incrementally sought to tame the vast and valuable forests of the Pacific Northwest. Aggressive logging of public land rested on a foundation of a growing nation's demand for wood. And the nation trusted the Forest Service as long as its policies seemed consistent with public values. But public values can change. Distrust can grow.

Dwyer's judgment concluded a hard-fought legal and public relations campaign by a determined environmental community that viewed government management of their public lands with skepticism, cynicism, and outrage. Few people accepted sweeping vistas dominated by clear-cuts and new roads. Instead, they valued naturalness, clean water, abundant fish and wildlife, and a deep sense of connection with the land. They anguished at what the Forest Service was taking from the forest at the expense of current and future generations.

You can plant all the trees you want, but you can't make a forest. That's God's business. Environmental groups used the northern spotted owl as the arrow to successfully pierce bureaucracy's armor. The agency's own planning regulations required it to protect the viability of wildlife, including owls. Judge Dwyer based his ruling on convincing evidence from the plaintiffs that the Forest Service was cutting down the very same old-growth forest habitat that was essential for owl viability. Using Forest Service scientific research that demonstrated population declines, environmental groups proved that federal laws did not allow the agencies to threaten the owl's viability. In this, they scored one of the most significant legal victories in the battle between commerce and the environment.

Siuslaw National Forest, where I served as supervisor from 1992 to 1999, sat in the crosshairs of the spotted owl controversy. In response to the ensuing chaos and crisis, the Siuslaw forged a new vision and strategy for managing federal forestlands. This new Siuslaw model uses management approaches that nurture, rather than eliminate, mature and old-growth forests and their associated fish and wildlife habitats. It also reflects the values and aspirations that most people in the region have for their national forests. I say most, because some traditionalists within the Forest Service, and certainly the timber industry, remain opposed.

The Siuslaw, located in Oregon's highly productive Coast Range, became the antithesis of the kind of industrial forestry practiced on national forests for decades. What if all national forests undertook a thorough and fundamental rethinking of how to achieve the basic mission of stewarding public lands in the face of changing values and circumstances, such as climate change?

I confronted the wrenching challenge of reframing the mission subsequent to the owl crisis. We made profound changes to forest management that produced real triumphs. Yet relatively little has been written about the social strategies and consequences associated with the intense biological and political fallout.

In winter, dense fog often cloaks Oregon's Willamette Valley. After several days of oppressive grayness, people yearn for a glimpse of sunshine. Similarly, the loss of hope—and onset of despair—enveloped the Pacific Northwest region, and this remains one of the

great, yet subtle, casualties of the spotted owl crisis. Restoring ecological function to the great Douglas-fir forest region, but also meaningful hope to the people who lived, worked, and managed these majestic forests became essential. Success ultimately turned on achieving strong and enduring consensus among various factions and interests that had formerly feuded over national forest logging policies. Though the Forest Service had lost its luster as a “trusted broker” (if it had ever enjoyed such prestige), Siuslaw National Forest staff needed to engage interested parties, invite them to link arms and strive jointly to address our bleak future head on.

Which Comes First—Chicken or Egg?

An important consideration confronted agency leaders: Should we first declare a vision and use public engagement processes to gain consensus, or should we convene people around a blank slate and collectively create a vision from scratch?

This has profound implications for agencies managing public lands. Decades-long controversy over clear-cutting old-growth forests had plagued the Forest Service in particular, with precious little nuance left to be cussed and discussed. In response to Dwyer’s judgment, President Bill Clinton, accompanied by Vice President Al Gore and most of his cabinet, convened a 1-day forest conference in Portland OR in April 1993 to review the “state of knowledge” and then determine how best to proceed in the face of a virtual shutdown of a major regional economic driver. Clinton closed the conference by tasking forest land agencies to develop a solution within 90 days. A hastily convened cluster of scientists completed this Herculean task on time. This draft “Clinton Plan” was published and subjected to public review and comment, and ultimately became the “Northwest Forest Plan” (NWFP) to govern future management of public forests on over 10 million hectares of federal agency lands. The NWFP embodied a complex set of rigorous standards and guidelines, but I did not view it as a recipe to be followed, lock-step. I saw the NWFP as a fairly detailed black-and-white sketch, with requisite color and local detail to be filled in based on our unique conditions.

The NWFP, in my view, adhered to the “vision, then consensus” model cited above. Scientists had distilled research findings and management principles to create architecture—a vision—to move forward. The hope was that the NWFP would be viewed as a robust and trustworthy “solution”; therefor combatants would lay down their weapons, and consensus would engender lasting peace. Hope may spring eternal, but in this case reality prevailed.

Context

Siuslaw National Forest, established in 1907, has a history of aggressive timber harvest, mostly in the post-World War II era. Siuslaw timber management mirrored industrial forestry—clear-cut the standing timber, burn logging slash to prepare for planting a dense monoculture of Douglas-fir, spray herbicides to eliminate competition, and (often) plant genetically superior seedlings, then fertilize to give it all a boost. The Siuslaw spent more money per hectare than any other national forest because it generated the most wood and revenue per hectare.

About 1990, Siuslaw timber production began to decline precipitously in the aftermath of lawsuits and legislation. Three pivotal factors affected the Siuslaw: spotted-owl population declines; then conflicts over the marbled murrelet (*Brachyramphus marmoratus*) (a small oceanic bird that nests in big coastal conifers); and finally plummeting Pacific salmon (*Oncorhynchus* spp.) stocks.

An essential first element of problem resolution is problem recognition. The real message from Judge Dwyer was that institutional denial and resistance to changing traditional forest management prevailed at the highest levels of the Forest Service and permeated all levels of leadership. Judge Dwyer’s 1991 opinion stated: “The problem here has not been any shortcoming in the laws, but simply a refusal of administrative agencies to comply with them. This invokes a public interest of the highest order, the interest in having government officials act in accordance with the law. More is involved here than a simple failure by an agency to comply with its governing statute.... The most recent violations of the NFMA (National Forest Management Act) exemplifies [sic] a deliberate and systematic refusal by the Forest Service and the Fish and Wildlife Service to comply with the laws protecting wildlife. This is not the doing of the foresters, rangers, and others at the working levels of these agencies. It reflects decisions made by higher authorities in the Executive branch of government.”

Former Forest Service chief Dale Robertson was among those found by Dwyer to have deliberately and systematically refused to comply with laws protecting wildlife. Robertson had been forest supervisor of both Siuslaw and Mt. Hood National Forests early in his career. Remarkably, Robertson assumed leadership of the Siuslaw at the very young age of 31, indicating that superiors recognized his great potential. Robertson, highly respected throughout the Forest Service, continued to rocket up through the agency and became chief at 47. He and other leaders knew the Pacific Northwest forests well. I think they consistently maintained timber harvest at high levels in the well-intended belief that this policy best served the interests of the public and the agency.

I could see that the policies and actions of these leaders laid bare a deep schism between the past and the future—forest management as it had been done and what it needed to become. The goal for decades had been to maintain the annual timber harvest total for all national forests at a level of about 11 billion board feet (~26 million cubic meters). Thus, Forest Service leaders managed owl issues to minimize disruption of timber production. Timber harvest transcended even legally required protection of the owl and other wildlife. The lawsuit successfully demonstrated that this policy was both illegitimate and illegal. A different approach was needed.

The same schism evidenced itself throughout the nation at the field level. Siuslaw managers issued their forest plan in 1990, just before I arrived in late 1991, having taken almost 10 years to complete the effort. The scientific basis for protecting the owl had started with researcher Eric Forsman's 1976 master's thesis, completed while he was a graduate student at Oregon State University. Forsman had become interested in the owl after observing them in the Corvallis watershed (a source of drinking water for the town), which lies along the eastern fringe of Siuslaw National Forest. He described the critical link between late-successional (mature) forests and the owl's habitat needs. Eliminate these forests, his research suggested, and you eliminate owls. In 1987, the Forest Service hired Forsman as a research wildlife biologist at the Corvallis Forest Sciences Lab.

If Forsman's research had an embedded message for the Forest Service and its timber management practices, one would think it would have been heard most clearly in Corvallis. Yet dedicated adherence to timber production marked the 15-year period between 1976 and Dwyer's judgment in 1991, both on Siuslaw National Forest and throughout the Pacific Northwest region.

The owl controversy had become white-hot by the time Siuslaw managers released their forest plan just prior to Dwyer's injunction. The plan established an allowable timber sale quantity of about 0.5 million cubic meters per year, a reduction from the 0.75 annual sale level throughout the 1980s. Many thousands of jobs and billions of timber dollars hung in the balance. Although the owl issue had already begun to threaten traditional timber policy and harvest levels, the Siuslaw plan made a very clear statement that timber occupied the seat of highest priority, and that clear-cutting of mature timber would continue. Minimal measures—the least possible—would be taken to protect the owl.

Numerous other plans for national forests in owl habitat followed the same thinking as the Siuslaw's. The Forest Service was doubling down on its bet against owls.

But Dwyer's injunction dramatically changed all this. As the new Siuslaw forest supervisor in the immediate aftermath of the injunction, I observed widespread anger and avowed defiance. Yet a small number of employees expressed philosophical agreement with Dwyer, pleased that the obsession with timber harvest might possibly be coming to an end.

Indeed, when Wendy Herrett became forest supervisor in 1990, she tried to refocus the Siuslaw's mission away from timber and toward other forest values, but she encountered intransigence from many employees who regarded her with deep suspicion, even hostility. Herrett seemed almost relieved that Judge Dwyer had imposed his decision on the Forest Service. Herrett sought to carefully navigate through this unstable environment, recognizing, inevitably, that a very different future lay in store.

The spotted-owl controversy emerged as a key environmental issue in the 1992 presidential election. I cannot recall another Forest Service or environmental issue that figured so prominently in a presidential race. Candidate Clinton visited Oregon, then a swing state, saying that he would fix the owl problem. Now President, making good on this campaign promise, Clinton convened a one-day forest conference in Portland, Oregon (as noted earlier), on April 2, 1993 with heavy regional news coverage. Almost all the President's cabinet along with Vice President Al Gore attended, listening all day long to sincere and desperate pleading from all sides that had a stake in the outcome.

The President noted in his opening remarks, "The worst thing we can do is nothing. As we begin this process, the most important thing we can do is to admit, all of us to each other, that there are no simple or easy answers. Let's confront problems, not people."

In the months following Clinton's Portland appearance, the leadership group of Siuslaw National Forest had engaged in a discussion of our resource management purposes for this landscape. I have never been involved in a more rancorous and passionate clash over resource ideology. Our capacity for unified leadership was clearly fractured; achieving consensus seemed impossible. Yet, I think this exercise helped the Siuslaw's leadership team prepare for the sweeping changes that resulted from the forest conference because we had already contemplated a dramatically different future.

In the "owl region" (western portions of WA, OR and northern CA), the planning effort to develop the owl solution yielded a draft NWFP in July 1993, an astoundingly swift, 90-day effort. The final NWFP, a sweeping new vision for federal forest management, was issued in April 1994.

Briefly, the NWFP accomplished two aims: it satisfied Dwyer's demand that vertebrate species populations remain viable (a legal requirement of the National Forest Management Act), and it also struck a new balance point between owl habitat protection and timber production by sharply reducing logging on federal lands inhabited by owls. The reductions took the harvest level down from about 9.4 million cubic meters per year to less than 2.5 million.

The NWFP was very complex, and radically different from the management plans it replaced. With my first reading, I was aghast. Many of the plan's foundational concepts were theoretical and untested. As a transformational forest management model, it placed an enormous burden on our field organization to make profound and swift changes to how we did business.

The Journey Begins: Implementation

I vividly recall announcing the NWFP decision to a large group of Forest Service and Bureau of Land Management employees at Corvallis's Majestic Theater. I began my remarks with a simple rhetorical question: "Do you believe this plan can work?"

I thought this was the central issue because it focused on personal will. The NWFP had been crafted by research scientists, unlike all the individual forest plans that had been developed by local forest managers. Most managers resented the idea that researchers had usurped their prerogatives to dictate how their forest should be managed. Managers also assumed the new plan would be an unwieldy, impractical, unworkable guide. These factors fomented skepticism. There seemed to be remarkably little commitment to make the NWFP work, or even to give it a chance.

However brilliant the NWFP might be, field personnel had to believe in it or it would not work. I suspected many, perhaps most, employees thought the NWFP flawed, deficient, and unworkable. I assumed the work of implementing the NWFP would be difficult, yes, but it merited my best effort. So I answered my own question: "Yes. I believe the plan can work."

In addition, just after the release of the NWFP, I delivered a speech to the public and agency employees, titled "Uncle, Thank You, Please." The speech sent a message to the public and agency employees that the NWFP openly admitted a need for change ("Uncle"), that we owed a debt to environmentalists for their passionate insistence on principles of sustainable stewardship ("Thank You"), and that we needed time and patience to perform up to new expectations ("Please").

How deep the hole we found ourselves in? The NWFP reduced Siuslaw annual timber harvest by 97%, far exceeding even my most severe prediction. This dramatic change held dire implications for the timber industry and our workforce, since timber harvest had been the lifeblood for the Siuslaw. This level of reduction would mean thousands of loggers, truckers, and millworkers would lose their jobs, as well as hundreds of our staff.

Moreover, few agency leaders outside the planning team itself had an opportunity to methodically consider the natural resource implications of the NWFP because of the secrecy surrounding the plan before its release. In general terms, Siuslaw staff could, given enough time, put the pieces together for how to comply with the NWFP. Bringing a distrustful, cynical public along with us was an entirely different matter.

Clearly, it seemed a losing proposition to continue to invest effort and large sums of money in traditional clear-cut harvests of mature timber, even at a vastly reduced pace. Some critics thought the Siuslaw targeted owl habitat for destruction, but it was more the case that the birds used virtually all the available mature forest habitat. If we cut big timber, we necessarily bumped into birds.

On top of that, we had to think about the dramatic reduction in wild fisheries over the past decades. Urgency demanded that we try to restore fish habitat on the Siuslaw's abundant streams.

The Forest Service has navigated its way through numerous controversies in the past century, but few have been as complex, layered, and consequential as the northern spotted owl issue. The NWFP rationale for drastic reductions in timber harvest was based on the fact that large-scale clear-cutting of old-growth forest profoundly affects fish and wildlife habitats. The convergence of owl, murrelet, and salmon habitats in the Oregon Coast's temperate rainforest coalesced to bring Siuslaw timber production to a virtual standstill.

I regarded the NWFP as an explicit admission that this incredibly productive landscape could not simultaneously maximize both wood products and wildlife. The forest was the womb that sustained this natural abundance. Thus, the NWFP made the hard choice for federal land. The remaining mature forest in the Coast Range would stay standing.

Building a New Boat

Economics was really the only motive for cutting mature timber. Most stands in the Coast Range originated in the mid- to late-1800s and could be characterized as being in the prime of life, since they often lived to be 500 years old. Biologically speaking, no need or urgency existed for logging mature timber.

Our tree plantations, however, were another matter. We knew that nearly 50,000 ha of young stands had grown up on sites that had been clear-cut starting back in the 1950s, emulating industry practices of clear-cut, remove snags, burn the site, plant seedlings, and spray herbicides. Many of these young stands were, or soon would be, of sufficient size to support commercial thinning.

These plantations were not natural in the same sense that coastal forests naturally regenerated themselves following the large, infrequent, severe fires that have swept through the Coast Range over centuries. I thought about it this way: when you cut and remove all the standing trees, then plant only one species (Douglas-fir) to densities that exceed 1000 trees per hectare, the dense packing of these trees ultimately exclude almost all other plant life. And that was the point—to grow Douglas-fir (because of its economic value) and eliminate the competition. The plantations had a destiny: clear-cut again at age 70 and start the process all over again.

So there was a legitimate concern that these tree plantations would not attain our desired mature-forest character evident in natural stands without further management. Having been created and managed solely for timber production, plantations had far too many trees, and they also lacked diversity. We decided to focus our available budget and resources on management of these young stands, but not for wood production. We thinned plantations, rather than clear-cut at age 70, to reorient them toward a new destiny as old-growth forest.

Our simplified strategy would allow the mature forests in the Coast Range to age and become old growth in time, without our intervention. Our management strategy would focus on the many young stands peppered throughout the landscape to improve the likelihood that they too would someday provide high-quality old growth (Fig. 1).

We knew our thinning strategy would also have significant financial consequences. The stumpage value (value of standing trees on the stump) of logging mature forests often approached 20,000 dollars per hectare in 1994 when the NWFP was issued. Thus, the value of standing timber on this relatively small forest easily exceeded \$10 billion. In contrast, thinning a young stand might yield only a few hundred dollars per hectare.

Politically speaking, many environmentalists familiar with the management and history of the Siuslaw remained skeptical and distrustful. They were pleased that the NWFP dramatically reduced logging and promised to save fish and wildlife, but reserved judgment on future steps to restore forest ecosystems. We desperately needed to create a credible scientific premise for our strategy, and decided to work closely with both Oregon State University and the agency's Pacific Northwest Research Station.



Fig. 1 Levi Beelart; thinning in young plantation to reorient to become eventual old-growth forest. Photo: Alan Honick.

Good Intentions and Good Fortune Meet

A research project, Coastal Oregon Productivity Enhancement (COPE), helped our progress significantly. COPE, a 10-year research partnership supported by money from government, industry, and interest groups, was housed at Oregon State University. As a COPE board member, I sensed we had a unique opportunity to do thinning research. Stu Johnston, a forester at Mapleton Ranger District, designed a study to evaluate three different levels of thinning on plantation sites that had more than 500 trees per hectare. The thinning study called for taking out most of the young trees, but leaving stands with 250, 150, and 75 trees per hectare, as well as establishing a control site where no thinning would occur.

We used a traditional commercial timber-sale process to achieve the treatments, awarding the contract to a high bidder. We conducted this study and several replicates to see which thinning treatments work best in encouraging a young stand of trees to grow into the old-growth forest characteristics that certain wildlife need for their habitat.

The COPE partnership conducted several field seminars in hopes of establishing that this unique management approach really could work in young forest stands. I vividly recall the tension when we first met with a pretty sizeable group on a wet day in early morning at the Mapleton Ranger Station before proceeding to the woods. For environmentalists, the rage of feeling ignored and abused for decades haunted the tours. For loggers whose bubble had burst, they begrudged their diminished role and being asked to come back to work as “partners” with the Forest Service under radically different rules. Slowly, incrementally, we gained credibility, building on the scientific rigor of our harvest trials and the evident sincerity of our “good intentions”. This was no ruse designed to just log our way out of the impasse. Within a period of about 2 years we had swayed doubters to at least give us a fair chance to continue our efforts at forest restoration. More specifically, forest thinning achieved one of three principal goals. The other two: significantly reduce the environmental footprint of the vast road network, and undertake targeted stream restorations. In combination, these three comprised our best assessment of what it would take to make measurable progress on the NWFP’s wildlife and fish goals.

As a result, we gained credibility with a variety of interest groups—federal regulatory agencies such as the US Fish and Wildlife Service and the National Marine Fisheries Service, state and federal forest managers, industry foresters, and environmental organizations. These stakeholders now united to assent to our 3-pronged restoration management framework, which could be seen as largely consistent with the NWFP.

The above describes what I consider an ad hoc, seat of the pants, informal approach to gaining traction, perhaps permission, on a new social contract with our “forest owners”—the amorphous public. The NWFP mandated several formal structures as well, such as interagency working groups, and a large 24-person resource council (a mix of agency officials and selected citizen representatives of notable interests; timber industry, environment, and such). I viewed these formal settings as essential, but not ultimately decisive in moving the needle related to the broad field of public sentiment and values. The informal approaches seemed more authentic and transactional, giving private citizens of all stripes a voice, and an opportunity for face-to-face dialogue and accountability.

Getting our story out through media contacts also helped immensely. For example, High Country News, a biweekly newspaper “for people who care about the West” requested permission to reprint the “Uncle, Thank You, Please” speech, and I gladly consented. HCN, well respected and widely read, offered a huge media footprint for people who cared about national forest issues. Scott Stouder, a logger turned environmental writer (featured on 60 Minutes with correspondent Ed Bradley), penned several investigatory articles in the Corvallis Gazette that helped local people keep up with changes afoot on the Siuslaw. Jeff Barnard, an AP reporter, repeatedly reported on key stories, particularly about salmon restoration. And the late Kathy Durbin, reporter for the Portland Oregonian and author of *Tree Huggers*, enthusiastically carried word of the “timber evolution” on the Siuslaw.

Revisiting the chicken and egg analogy, I am convinced that changing public sentiment from avowed opposition to positive support hinged on first creating a credible plan, and to then coalesce a variety of interests around the new vision and approach. If we had tried to ask citizen help to build from an empty tableau, I doubt we could have succeeded.

Why? Despair and confusion reigned thick and suffocating in the aftermath of the Dwyer decision. I could not conceive of appearing in public settings with no semblance of a road map and destination. The untested NWFP provided a general framework, but we needed to add layers of local specificity to lay out a credible way forward. It needn't be perfect, but it must signal a significantly different approach that addressed the crisis at hand.

Slowly, over a transition period that lasted about 3–4 years, we moved public perceptions of Siuslaw management from suspicion to curiosity, curiosity to acceptance, and acceptance to enthusiastic support. An important metric related to project appeals and litigation. When I arrived in 1991, every timber sale was aggressively opposed by numerous parties. Opposition fell to nearly zero, of course, as our logging approached a near dead stop. As we retooled our timber program to feature thinning young plantations and then accelerated, we held our breath to see if the old combat terms would return.

Remarkably, there has not been a single timber sale appeal or lawsuit since 1995. Siuslaw National Forest enjoys this singular distinction among all 154 national forests. I describe this phenomenon as literally unheard of in agency history. This outcome testifies to the salubrious benefits of restoring good will and trust, and the occasional triumph of human endeavors in overcoming past acrimony.

Thus, I'd say our good intentions met with good fortune, and we seized opportunities where found. Lest I leave the impression that the Forest Service alone achieved such successes, I note the numerous amazing citizens who stepped forward to make contributions large and small. It was as if the sight of an open field afforded them the opportunity to unleash their collective love of their public lands to help create a viable way forward.

Looking back over those tumultuous times, I can identify one pivotal event in 1994 that crystallized the moment our forest organization made the leap from the old to the new. Our leadership team was in a rather heated discussion about where to go with our timber program. Some were trying to persuade us to retain as much of our traditional clearcutting activity in mature forests as possible ("We're the Siuslaw! It's what we do!"), while others thought we should acknowledge that was a dead end, that it was time to pursue thinning. We needed a decision.

I had heard enough, and my guts told me to take a stand. I said, "We will no longer clear-cut mature timber on the Siuslaw." It seemed a bit like stepping into the abyss, but from that moment forward we would devote all our energy to thinning plantations. This was our future for as far as I could see; we had decades of this work before us. Today the Siuslaw is still at it, but with a wary eye toward that future year, estimated to be about 2030, when the work of thinning old plantations is done.

Pressing the Priority of Fish

Restoring streams to assist the recovery of depleted salmon formed an important bookend to our forest work. Merging more holistic terrestrial and aquatic environments yielded a more comprehensive product, and fit well with the Siuslaw because it is, more than any other national forest, a "timber and fish place." To have done one without the other would have been a significant injustice. And, as with our timber work, the social dimension of our aquatic work significantly improved the process and product.

During my first summer on the Siuslaw in 1992, I took a trip to Mapleton to visit an innovative fish-habitat project. I left my parked car and headed for the sound of workmen in Knowles Creek, which meets the highway from Eugene to the Coast a few miles east of Mapleton, where it joins the Siuslaw River. Mapleton's district ranger invited me out to look at the Knowles Creek Project, promising a look at some cutting-edge salmon restoration.

Knowles Creek runs only about 15 miles from beginning to end. The creek's drainage basin includes land owned by the Forest Service, the Bureau of Land Management, and Hancock Timber Resource Group, a spinoff of the insurance giant, whose timber holdings lay nearby. Like most coastal streams, Knowles Creek had a once-abundant fishery that had been damaged by serial assaults over the years.

Huge cedar stumps dotted the floodplain, evidence of the mighty trees that had once grown there. Numerous clear-cuts blanketed the hillsides above us. Sadly, Knowles Creek seemed typical of most coastal streams—pounded by logging, its fish largely gone, with little trace of naturalness.

It was late summer, with just a trickle of water moving. Huge logs, some as big as 3 m in diameter, lay strewn about ready to fabricate a logjam. Long, stinger-like drill bits pierced holes through the logs and also into sandstone bedrock. Then wire cables were inserted through the trees and epoxied into the sandstone to anchor the logs in place.

I met forest technician Lynn Hood, who enthusiastically explained how this logjam, and others like it, would slow the water and trap gravel to improve salmon habitat. I didn't see much water, and I sure didn't see any gravel.

I confess, it seemed a bit comical. Such big logs, so little water - a bit like the folly of Noah's Ark, unless you knew there was a flood coming.

Perhaps sensing my skepticism, Hood said I needed to come back during a winter storm, when Knowles Creek was galloping with about two meters of water. He was confident the logjam would hold tight and do its job.

I said, "What about the gravel? Where's the gravel?"

He pointed upstream. "Oh, it's up there. Trust me. It'll come." Hood smiled, but his conviction conveyed serious belief. I'm sorry, but I wanted to laugh.

The three-way collaboration involved the Forest Service (labor and money), Hancock (logs), and Pacific Rivers Council (the design and know-how of Charlie Dewberry, the Council's staff fisheries biologist). I was standing at one of about 15 artificial logjam

sites, each constructed in an effort to replicate natural conditions. Such logjams commonly occurred as a natural component of stream function when towering trees fell into the water.

Government foresters once required that timber companies remove these logs because they thought the logs obstructed salmon migration. Later, research showed that in situ wood in streams greatly improved salmon habitat. Now we were putting logs back.

Fast-forward a few years to an epic 1996 flood that dumped about 65 cm of rain into the Knowles Creek basin, hammering the vicinity. Dewberry revisited the area, his hopes high. If his design proved sound, the flood would use the logjams and further the work that human hands had started, dramatically improving salmon habitat.

Dewberry was pleased to see that almost all his structures had held. Huge, deep gravel bars lay neatly deposited upstream from where the logjams had slowed the floodwaters. I too have been back to Knowles Creek many times. I can scarcely believe it is the same place I first saw. On my first visit, Knowles Creek resembled a sandstone bowling alley, slicked to bedrock, devoid of gravel and wood. Today it looks natural, utterly transformed.

What's more, rigorous sampling of fish numbers reveals dramatic increases. Chinook (*Oncorhynchus tshawytscha*) and Coho salmon are now prospering where they once hung by a thread. Even Chum (*Oncorhynchus keta*) salmon, which had completely disappeared, now return.

This is a remarkable success story. Unfortunately, salmon populations have faded in literally thousands of other Knowles Creeks needing similar work. Given the saturation level of the problem, how does progress happen? One step at a time.

Another big step in our fisheries restoration effort occurred at Enchanted Valley. Located a few kilometers northeast of Florence, the aptly named valley is traversed by Bailey Creek, which empties into Mercer Lake and thence into Sutton Lake before threading its way a couple more kilometers under a new name (Sutton Creek) through low, open sand dunes into the Pacific Ocean. Enchanted Valley is much like, but smaller than, many of Oregon's mid-coastal valleys due to the area's geology. Mountain streams emerge into broad, flat valleys, then into freshwater lakes, before making a brief run to the ocean.

Dairy farmers found these valleys ideal for their herds. Farmers improved their pastures by literally moving these slow, meandering streams to the edge of the valley with dikes and ditches. Farmers filled in old creek channels and removed bankside trees. This agricultural "improvement"—usually subsidized by the US Department of Agriculture—ruined habitat for the resident salmon. Beautiful though it was, Enchanted Valley looked nothing like the way it did in 1900. As elsewhere, Bailey Creek's salmon suffered.

Coho salmon once thrived in these systems. Adults wildly spawned in the upper forested reaches of Bailey Creek, their eggs yielding new hatchlings that would grow to become smolts in the creek's lazy meanders and the lakes' depths before making the short run to the ocean. Salmon have a strong fidelity to particular streams. Adults almost unerringly return to the same stream where they were born. Consequently, once a fishery is lost, restoration can prove difficult since native fish do not often wander to repopulate neighboring streams. Numerous Coho populations, including the population in the Bailey Creek area, are now endangered.

Unlike Chinook salmon that hatch and return to saltwater in just a few months, Coho spend over a year in freshwater. Young smolts need to survive both the low water flows and high temperatures of summer and the heavy, roiling floods of winter. Life in a ditch spells trouble, but a natural creek is ideal.

Crack fisheries biologists on my staff spoke to me passionately about the opportunity to restore Enchanted Valley, describing Bailey Creek as almost perfect for restoration. The idea was to dig an artificially meandering channel in the middle of Enchanted Valley where Bailey Creek had once flowed, and then plug the ditch and return water to our "manufactured" creek. Reducing the gradient in this way would double the length of the creek and slow the water before it enters Mercer Lake. Importantly, such channel engineering allows the stream to leave its banks during high flows to reconnect with the flood plain. The last step is to plant shrubs and trees such as cedar and spruce to improve shading and help keep waters cold.

I grasped that this relatively cheap concept had a high probability of success. The State of Oregon volunteered to help finance the project. If it worked, the strategy could be replicated on numerous other coastal streams to create pockets of high-value Coho salmon habitat.

But once again, competing resource uses complicated what seemed at first to be a simple bonus for fish. The Rocky Mountain Elk Foundation had purchased Enchanted Valley in about 1985 and then brokered a deal transferring ownership to the Forest Service in return for assurances that the valley would be managed for elk (*Cervus elaphus*) winter range. The Siuslaw Rod and Gun Club played a prominent role in hyping this deal. The former cattle pasture became tremendous elk habitat, abetted by the Forest Service, which mowed the meadows every fall to keep the grass in a "juvenile" condition to enhance its palatability for elk. I can attest to the fact that elk loved it because I saw them on almost every visit. Hunters enjoyed having a big local elk herd that afforded high-quality hunting.

When we aired the idea of a fisheries restoration project in Enchanted Valley, controversy gathered like iron filings to a magnet.

Officers of the Siuslaw Rod and Gun Club let me know they viewed my ideas as a threat. How could the Forest Service—and more particularly I, myself—ever consider "ruining" perfectly good elk range for the benefit of fish? Hadn't the Forest Service acquired title to the valley by virtue of the Rocky Mountain Elk Foundation's generosity? Elk advocates strongly felt I violated the spirit of that deal. I also heard rumblings from local Forest Service staff that even they thought the proposal did not keep faith.

I saw things differently. Elk were not hurting in the Coast Range, but salmon were in deep trouble. Our actions would slightly diminish both the quantity and quality of elk habitat once the streamside trees grew to large size, but would not eliminate it. Changes would occur slowly, giving the elk herd time to adapt. If the fisheries project worked—and we thought it could, though we could not guarantee it—the benefits to salmon would be huge, and we would have a tested, viable technique that could be applied in many other places.

At the public meeting we held in Florence, citizens had plenty to say, mostly opposing the project. They had heard that even Forest Service opinions split between elk and salmon since many Forest Service employees were avid elk hunters. Not surprisingly, no consensus emerged.

I ultimately decided to do the Enchanted Valley project after careful consideration of dissenting views. The Rod and Gun Club appealed my decision, but, on review, the regional forester in Portland supported my decision. We pulled money together, issued contracts, and the dirt started to fly.

The transformation of Bailey Creek was rapid and dramatic. The new streambed emerged from the construction phase, and vegetation quickly healed the raw spots. The day came to cut the water loose into the new channel, an event welcomed with nervous anticipation. Bailey Creek performed like a perfect gentleman, the water easing into the channel and slowly sauntering toward Mercer Lake. The creek embraced its new course as if returning to the haunts of its youth.

Then the fish did their job. Salmon returned to spawn, and the new channel proved a happy home (Fig. 2).

It takes 3–4 years to complete the salmon cycle—smolts head for the ocean, mature, and return as adults to spawn. The first year those spawning adults returned to Bailey Creek, their numbers had increased by about 10-fold. And succeeding years have continued to strengthen the population. Bailey Creek is now a high-quality salmon stream—and the elk continue to graze in the valley.

After I left the Siuslaw in 1999, much bigger salmon restoration projects followed in several places, including Karnowski Creek and the Salmon River estuary, applying techniques from Knowles Creek and Enchanted Valley. Great things are happening. I occasionally think back to Knowles Creek and my opinion that little could be accomplished. I was so wrong.

Levering Salmon, Our Beloved Icon

Unlike the old-growth forest debate—with opponents lined up on both sides over whether big trees needed to stand or fall—salmon were much loved by all. Salmon represented the best of Oregon: wild, beautiful, romantic, hardy, and adventurous. And also in rapid decline. Siuslaw National Forest, with its dense network of salmon waters, estimated at 1.6 lineal kms per square km of forest, enjoyed a reputation as a “fish forest”; more so than any other outside of Alaska and British Columbia. If salmon were to enjoy meaningful recovery, the Siuslaw represented a potent opportunity. Public sentiment ran strong for recovery efforts, but did lack a crucial ingredient—funding. If a way could be found to finance stream restoration, we knew we had strong public support to build an aggressive program.

We benefitted from strong synergies that tied our successes in forest restoration to strengthen stream and fisheries funding. “Stewardship contracting” authorities made their way through Congress, built in part on Siuslaw achievements, enabling us to retain profits from our forest thinning program for discretionary local spending. In addition, Senator Ron Wyden (D, OR) authored a bill that authorized expenditure of federal monies on private land to benefit fisheries. These outcomes created a virtuous circle—non-controversial timber thinning achieved forest restoration while generating jobs and money, the money created



Fig. 2 Creating a new streambed, Fivemile-Bell Project near Florence OR. Photo: Justin Anderson USDA Forest Service.

opportunities for badly needed stream restoration projects, forest ecosystems and salmon fisheries both improved, and these outcomes deepened and strengthened public support and commitment to the Siuslaw's new business model.

The chicken and egg syndrome animated our approach to stream and salmon restoration, much as it did in navigating our approach to forest restoration. Our nascent approach to stream restoration achieved demonstrable results that informed discussions about how best to restore endangered salmon stocks. With sound techniques available to answer the "how," we still had to answer the question of "where" and "when."

The NWFP required that we develop watershed restoration plans, and these provided an anvil for us to hammer out consensus on best practices to achieve both forest and stream restoration. We chose to create watershed "councils" as the fora to process our deliberations. We also chose to keep our several councils very informal, intending to avoid onerous provisions of the Federal Advisory Committee Act. Importantly, formal committee structures tend to yield less effective and timely business transactions. Our *modus operandi* featured ad hoc structures and consensus decision-making. Forest Service staff experts would provide details on project proposals to interested parties in attendance—often nearby landowners, environmental group representatives, timber industry personnel, and private citizens. Project descriptions included location, cost and revenues, techniques, resource objectives, known issues, potential cooperators, and so on. Facilitated discussion allowed participants to speak their views, then worked through "red flags," desired modifications, and positives, to ultimately yield consensus on sequencing selected projects, and an understanding of anticipated benefits and consequences.

Improving the plight of salmon served as a strong unifying force to allow foes (remember that long-term, bitter controversy had heretofore dominated dialogue) to take the first tentative steps to respectfully talk to one another and negotiate in good faith. The Forest Service took on the role of honest broker, being unfailingly honest, transparent, well-behaved, and resolute that something would get done. We could not afford to waste people's time and effort. Applicable laws and regulations bounded decision space, but, beyond that, we made every effort to accommodate consensus decisions.

Slowly but perceptibly, progress emerged. People found they could work together and bridge disagreements. It is trite, but true nonetheless, that opponents actually agreed on more things than they once thought possible. Trust and hope began to grow. It took years to achieve strong, cohesive working groups. But these groups developed a deep pride of accomplishment at working through what had once been insurmountable hurdles to agree on broadly supported priorities and projects to restore their public lands. I thought it quite remarkable that a national forest that had been in total disarray could so quickly be "resurrected" through the effective teamwork of government officials and private citizens, working in concert to address persistent resource issues while overcoming deep enmity among participants.

I describe the approach as "letting the owners back in the room," and the Forest Service commonly uses such collaborative approaches now. Yet, while collaboration brings many positive forces to decision-making, I offer a few words of caution.

First, government staff, operating as meeting facilitators and brokers, plays a key role in setting the tone and gently refereeing disputes. The virtues of respect, trust, honesty, balance, and lack of guile are crucial. If other participants sense that cards are withheld or not revealed, dialogue is poisoned, usually irreparably. Favoritism is also toxic, as is any hint that outcomes are foreordained. But exemplary behavior is rewarded with optimal outcomes.

The agency must also be clear on how applicable laws and regulations bound the decision space so that participants don't waste time on creating solutions that cannot be implemented. If people have a clear understanding where the walls are and how big the room is, reasonable decisions will follow.

A subtle danger of collaboration is settling for the least offensive solution, in the misguided belief that this constitutes success. When dealing with a landscape in need of restoration, people should be encouraged to develop optimal, not minimal, solutions. Groups need to grapple with the question "what's *really* going on?" and craft solutions that answer the question effectively.

Lastly, government officials need to trust in outcomes that represent the group's best effort. Substituting individual judgment for a group's hard won consensus surely destroys trust.

A Last Word

In hindsight, I am still astonished that the Forest Service sold more timber in 1989 than ever in its history. Environmental groups escalated their opposition throughout the 1970s and 1980s, and the Forest Service response was to increase timber harvest. It is true that powerful political interests influenced the Forest Service timber agenda. Long-tenured western senators favored a robust timber program, and a lengthy series of Republican presidents who were traditionally pro-commerce—Nixon, Ford, Reagan, and Bush—combined to weight the scales in favor of industry, but I did not see much evidence of principled push-back from a compliant Forest Service.

The crisis visited on the Pacific Northwest via the northern spotted owl seems almost inevitable in hindsight. Remarkably, Siuslaw National Forest - a landscape caught in a powerful vortex of opposing forces—was transformed by bureaucrats and citizens working in concert to create a hopeful future. The Siuslaw pushes forward with strong public support and little controversy. The environmental community now endorses the Siuslaw's embrace of forest restoration principles and pleads, "Why can't all national forests be managed this way?"

Managers of Siuslaw National Forest chose to approach the future by focusing on managing for properly functioning ecosystems, rather than timber production, spurred on by a new forest plan that envisioned a radically different policy for public forests. Now 25 years old, the Northwest Forest Plan's track record has been marked by the tug and pull of successive administration's

political priorities. The federal agencies in charge of public lands, notably Forest Service and Bureau of Land Management, have been less than heroic, wobbly even, in their willingness to adhere to the tenets of the Plan in the face of political pressures. Significant threats remain to be addressed as climate change worsens and barred owls (*Strix varia*) have overwhelmed spotted owls throughout much of their range. Politicians renew the push for more logging on federal lands with seemingly little care for or attention given to the circumstances that, painfully neglected, created one of the great environmental crises of our time. Policy makers may forget, but these magnificent forests bear scars. This is no time to ignore history.

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Overlap Between Carbon Stores and Intact Boreal Woodland Caribou Ranges in Canada's Boreal Forest

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Abstract

Canada, like many nations around the world, is struggling to find solutions to both climate change impacts and biodiversity loss. Given the enormity of these problems, opportunities to align government policy responses are highly appealing. In Canada's Boreal Forest biome there is a compelling case that conservation designations of large landscapes can help slow biodiversity losses, including of iconic threatened species like boreal woodland caribou (*Rangifer tarandus caribou*), while increasing the likelihood that massive stores of carbon in those landscapes will remain there. The Boreal Forest biome of Canada is estimated to hold a minimum of 208 billion tons of carbon. Only 11% of the total carbon stored in soils and vegetation in Canada is now within existing protected areas. At least 69 billion tons of carbon are stored in unprotected intact landscapes that support woodland caribou.

Introduction to Boreal Forest and Its Carbon Stocks

North America's Boreal Forest biome ([Fig. 1](#)) is one of the most ecologically intact on the planet with the footprint of human industrial activity ([Fig. 2](#)) estimated at between 17% and 26% while the area protected is between 8% and 13% ([Lee and Cheng, 2010](#); [Andrew et al., 2014](#); [Carlson et al., 2015](#)). The largest proportion (88%) of the North American Boreal Forest biome lies within the national boundaries of Canada ([Brandt, 2009](#)).

The biome is known to hold an immense amount of carbon in storage ([Fig. 3](#)), the result of thousands of years of accumulation of sequestered carbon in plant materials that was then prevented from decomposing by cold temperatures and acidic ground conditions. The total amount of carbon within the biome held in storage, mostly in soils and peat and under permafrost has been estimated to be a minimum of 206 Gt ([Carlson et al., 2009, 2010](#)).

Even this amount is considered likely a gross underestimate as only a relatively small proportion of the 6.27 million km² biome have been adequately sampled and the extent of deep peat deposits, especially those under permafrost, is poorly understood ([Schindler and Lee, 2010](#)). To put this in global perspective, the total amount of carbon in Canada's Boreal Forest region is equivalent to a minimum of 71 years of current annual emissions from China, the world's largest polluting nation and 111 years of current annual emissions from the United States, the world's second largest polluter and over 1000 years of current annual emissions from Canada.

The density of carbon across the Boreal Forest biome is estimated to be approximately twice that of the density of carbon in tropical forests because of the exceptionally long residence time of biological carbon within Boreal Forest ecosystems ([Carlson et al., 2009](#)). This is in contrast with the rapid decomposition of carbon sequestered in warm, tropical forest ecosystems. Tropical forest ecosystems sequester more carbon annually than do Boreal Forest ecosystems but much of that carbon is returned to the atmosphere quite quickly and does not build up in the soils. Boreal forest ecosystems sequester less carbon annually than do tropical forest ecosystems but the carbon has remained in the soils, peat, and under permafrost for thousands of years, building up a much larger storage bank of carbon overall.

Peatland systems including bogs, fens, and forested wetlands within the biome are particularly carbon rich ([Wells et al., 2010](#)). One of the largest wetland and peatland systems in the world is the Hudson Bay-James Bay Lowlands, an immense 373,700 km² area extending from Manitoba, across northern Ontario to western Quebec ([Abraham and Keddy, 2005](#); [Warner and Asada, 2006](#)). These wetlands are estimated to hold 30–35 billion tonnes of carbon ([Riley, 2011](#); [Humphreys et al., 2014](#); [Packalen et al., 2016](#)), making up nearly 20% of all the carbon stored in Canada's Boreal Forest biome.



Fig. 1 The extent of the North American Boreal Forest biome as delineated by Brandt (2009).

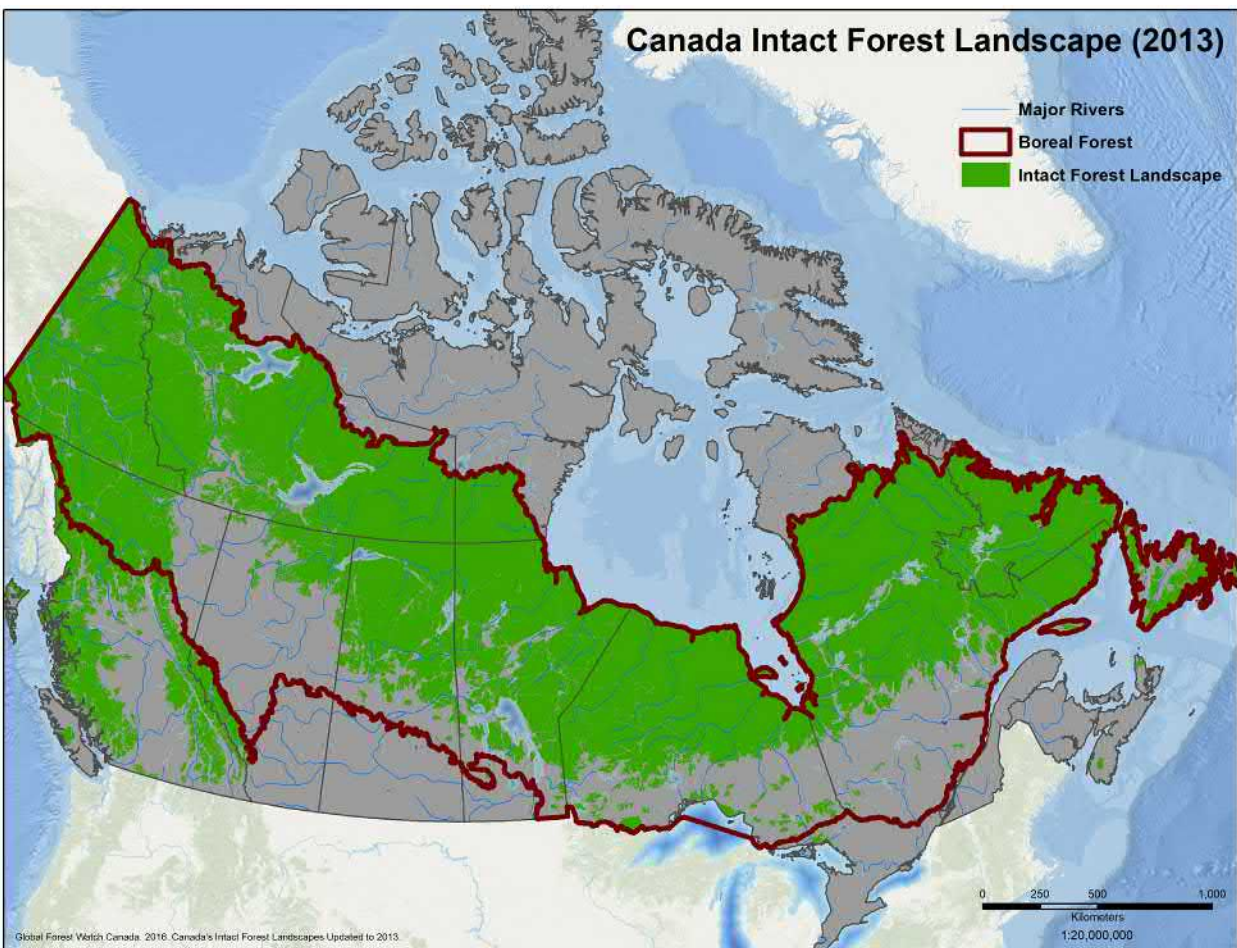


Fig. 2 The Canadian portion of the Boreal Forest biome with intact areas that have very little human industrial footprint shown in *green*. More than 70% is still considered intact, making it one of the last, very large ecological areas on the planet.

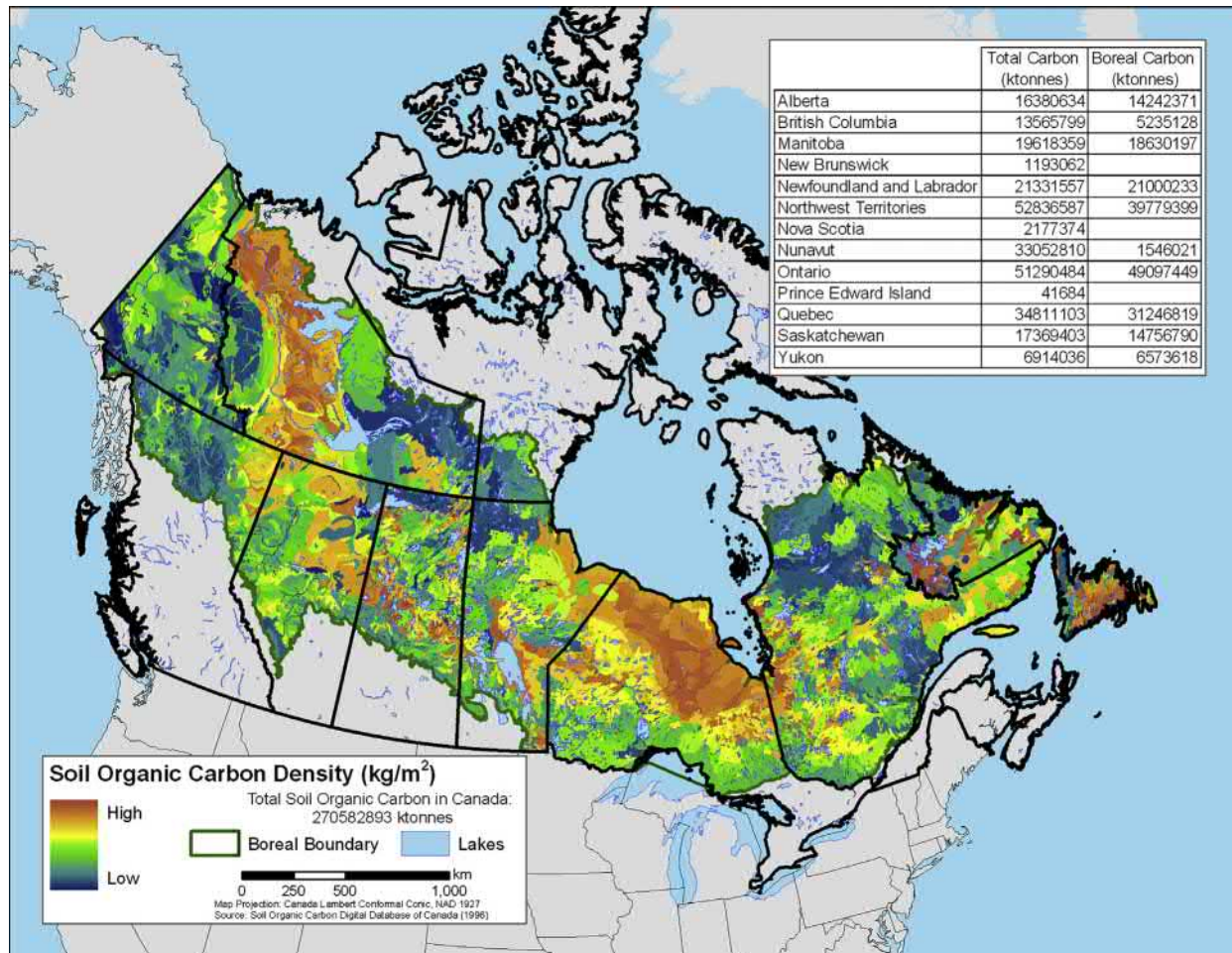


Fig. 3 Soil organic carbon density across Canada's Boreal Forest biome. Particularly carbon rich areas occur in the Hudson Bay-James Bay Lowlands of Ontario, Manitoba, and Quebec, and in the Mackenzie Valley of the Northwest Territories.

Potential Impacts to Stored Boreal Carbon Stocks

Industrial development and the resulting supporting infrastructure can impose major changes to the landscapes of the Boreal Forest region (Far North Science Advisory Panel, 2010). These changes can include disruptions of hydrological levels, flows, and cycles any of which can have profound implications for releasing organic carbon stored in peat and soils, and releasing highly impactful greenhouse gases, especially methane. Industrial development can also cause changes that increase permafrost thaw in some areas, again allowing the release of carbon stores that have been in place for thousands of years.

Just as in the field of medicine, the approach to taking care of the carbon stores of the Boreal Forest biome should be to "do no harm." Such a precautionary approach would lead to the conclusion that along with advancing global policies to decrease atmospheric carbon levels, decision makers should advocate for maintaining as much of the Boreal Forest as possible free from human industrial activities that increase the chances that its carbon stores will be lost to the atmosphere (Carlson et al., 2009).

Today only about 10% of the carbon stores of Canada's Boreal Forest lie within the boundaries of protected areas (Fig. 4). However, at least two-thirds of the carbon within Canada's Boreal Forest is within still intact forest blocks (Fig. 4). That means that it is still possible to establish very large protected areas that contain within their boundaries much of these vast stores of carbon so that carbon will be protected from loss caused or exacerbated by resource extraction activities.

Boreal Biome Landscapes Are also Biodiversity Rich

The same boreal forest ecosystems that sequester carbon and hold it in storage below ground, support globally significant biodiversity, largely above ground (Bradshaw et al., 2009). Those globally significant features include:

- Some of the highest densities and largest individual numbers of northern tree species anywhere in the world (Crowther et al., 2015);

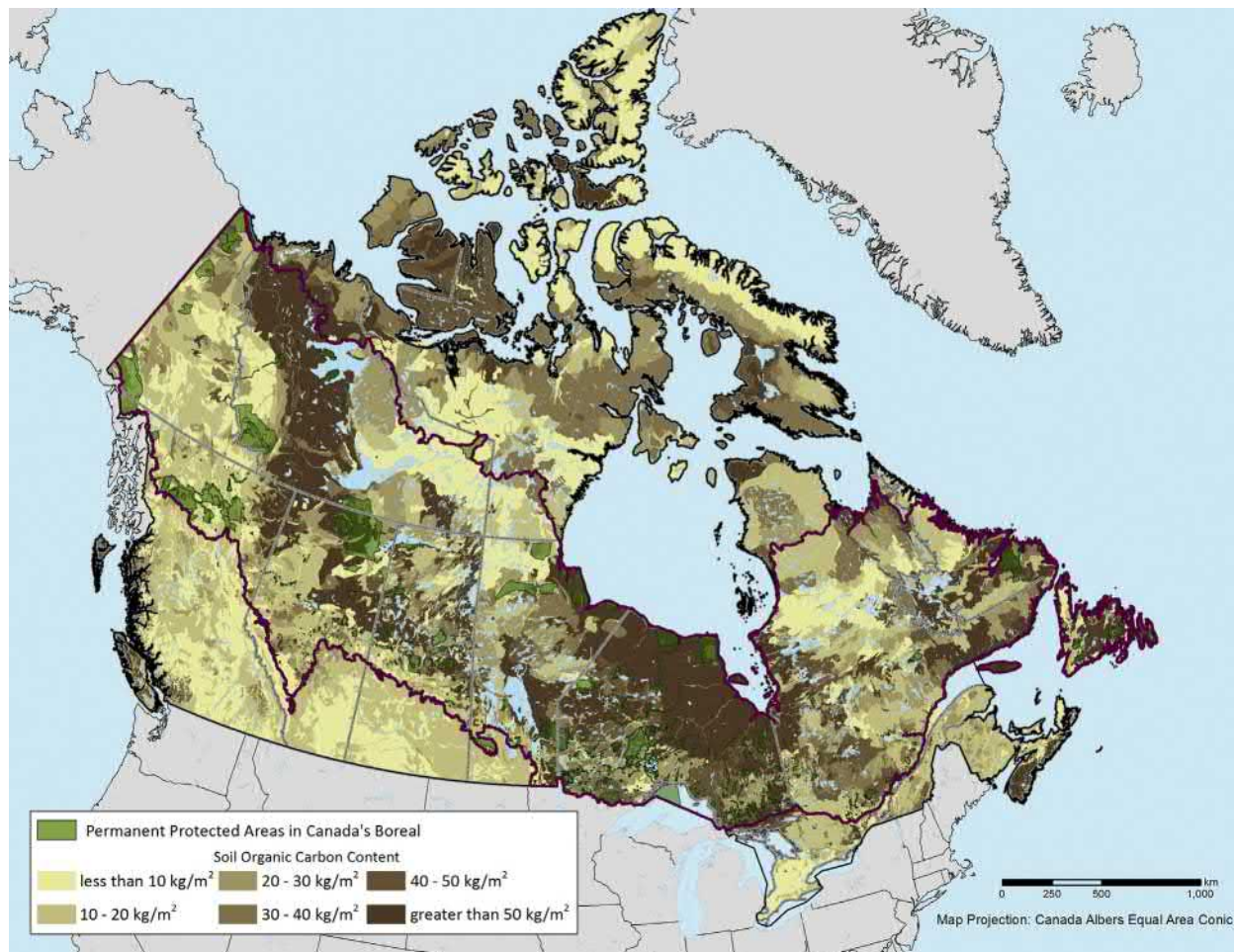


Fig. 4 Overlap between soil organic carbon stores and protected areas across Canada's Boreal Forest region.

- Billions of nesting birds, most of which migrate south to populate temperate and tropical biomes across the Western Hemisphere during the northern winter season (Blancher and Wells, 2005; Wells, 2007; Wells and Blancher, 2011);
- Large and wide-ranging populations of large mammal species including herbivores like caribou (*Rangifer tarandus*)—including boreal woodland, mountain, Newfoundland, and tundra forms—wood bison (*Bison bison athabasca*), and moose (*Alces alces*), and large predators like gray wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and polar bears (*Ursus maritimus*), and wolverines (*Gulo gulo*) (Laliberte and Ripple, 2004; Hummel and Ray, 2008; Wells et al., 2013);
- East-west ice-sheet species divergences and ice age refugia lineages across a broad array of taxa, yielding surprising and little-known levels of biodiversity (Wells et al., 2013).

History of Boreal Woodland Caribou in Canada

The boreal woodland caribou was once a widespread species occurring as far south as the northern U.S. (Fig. 5). An advancing frontier of development in New England, the Maritimes, and Quebec led to a steady disappearance of boreal woodland caribou from its southern extent. The species disappeared from Vermont by 1840, Wisconsin by 1850, the St. Lawrence Valley of Quebec by the mid-1800s, Prince Edward Island by 1873, New Hampshire by 1881, Maine by 1910, Nova Scotia by 1912, Cape Breton by 1925, Michigan by 1931, and Minnesota by 1942 (Ray, 2010). The decline and northward range retraction have continued so that woodland caribou are gone from 60% of their original range in Alberta, 50% of their original range in Ontario, and 40% of their original range in British Columbia (Hummel and Ray, 2008). In Ontario the species range has retracted north at a rate of 34 km per decade from 1880 to 1990 (Vors et al., 2007; Schaefer, 2003). The boreal woodland caribou was listed as Threatened under Canada's Species at Risk Act in 2000 (International Boreal Conservation Science Panel, 2011).

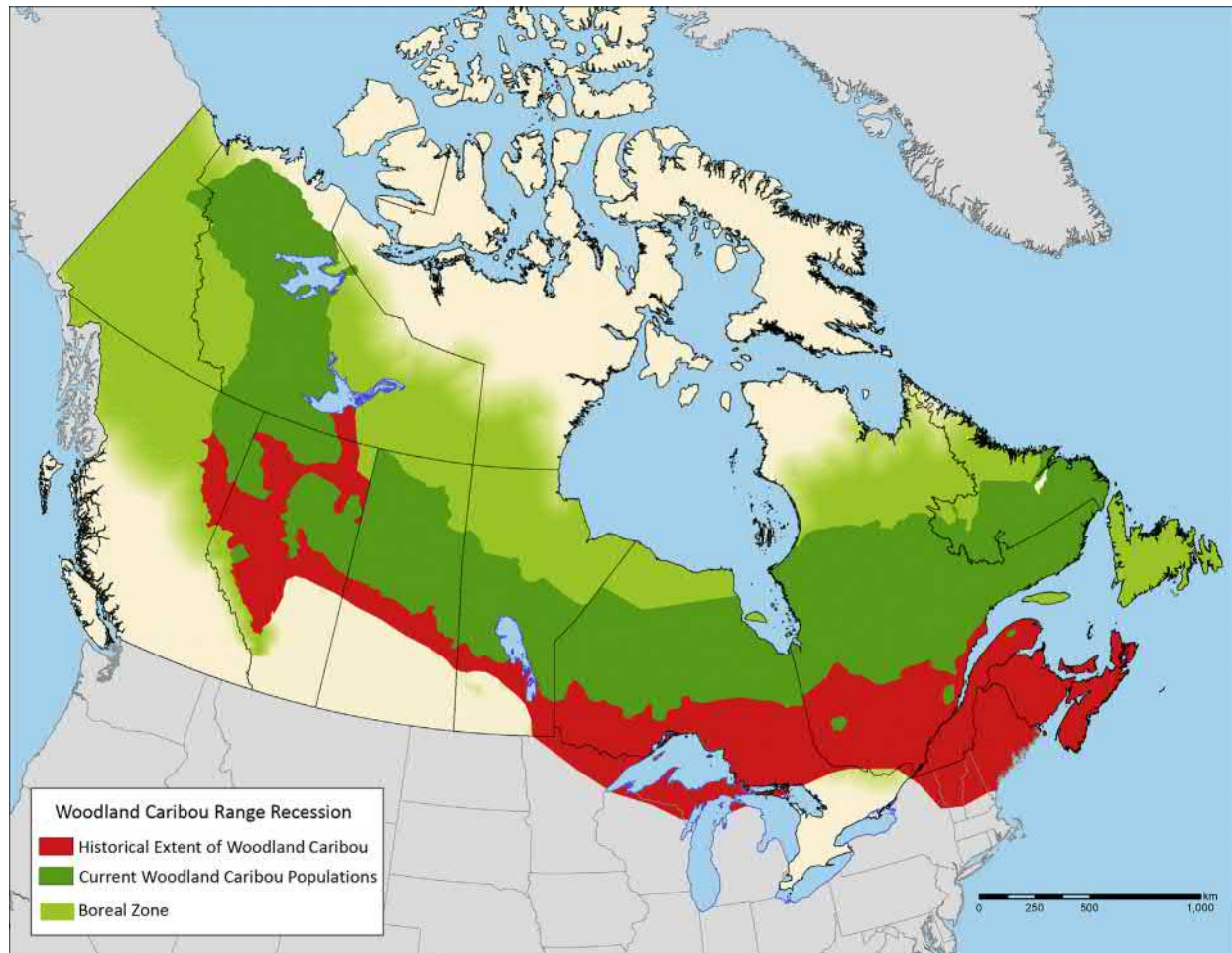


Fig. 5 Current (dark green) and former (red) range of the Boreal Woodland Caribou.

Boreal woodland caribou have survived and adapted under the often-harsh conditions of the northern latitudes through a strategy of using vast landscapes to maintain distance from key predators and obtain food (Hummel and Ray, 2008; Schaefer, 2008). For example, in perhaps the most critical time of the year for caribou populations—the spring/summer calving period—females become solitary and move to islands, peatlands, and lake shore areas where they and their newborn calf will have the least likelihood of being found and preyed upon by wolves, bears, or other predators (Schaefer, 2008). This strategy of being able to shift around the landscape as conditions change and to space themselves out from predators, each other, and other ungulates requires large areas of the species preferred habitat mosaic of 50–100 year old mature spruce or pine forest, large peatlands, lakes, and rivers (International Boreal Conservation Science Panel, 2011).

Boreal woodland caribou avoid broadleaf and mixed-wood forests, as well as cut-over forest, roads, powerlines, and other forms of industrial human impacts while wolves and their targeted prey of moose, deer, and smaller mammals occur in higher numbers in such habitat. As a boreal woodland caribou herd's range becomes converted to non-caribou habitat, not only is there less habitat for them to use and more predators to try to avoid, but there is less ability for the species to avoid predators and find preferred habitat (Schaefer, 2008; International Boreal Conservation Science Panel, 2011). In fact, the number of calves that are born and survive shows a constant decrease as the proportion of the landscape impacted by human industrial activities increases (Environment Canada, 2008, 2011). A general rule of thumb indicated by this research is that a herd has a high probability of local extinction once more than about 38% of their range has been converted either through human-caused changes to the landscape or fires or a combination of the two. In fact, maintaining a low density boreal woodland caribou herd (not necessarily a density that would allow the herd to withstand hunting pressure or climate change impacts) is thought to require single unfragmented habitat blocks at least 10,000–20,000 km² though only six protected areas of this size have been established within the species range (International Boreal Conservation Science Panel, 2011).

Boreal woodland caribou have now been lost from half of their original range and this loss is likely permanent as there are no known cases of woodland caribou reoccupying portions of their range where they have been extirpated despite a number of sophisticated and expensive attempts at reintroductions (Schaefer, 2008; Festa-Blanchet et al., 2011). This loss is clearly the result of human-caused changes to the landscape working in combination with resulting changes in associated predator-prey communities that negatively

impact woodland caribou. If this rate of range loss were to continue, the species would be lost from Ontario within 100 years. If the same rate were applied to other provinces, the species would be lost from Alberta and Manitoba within 100 years, and Saskatchewan and Quebec within 200 years. Unfortunately, the expectation is that the rate of loss will likely increase because of climate change and the degradation of the species' ability to rebound and recolonize. In fact, [Environment Canada \(2008\)](#) estimated that only 17 of the total of 57 surviving boreal woodland caribou herds or population units had a greater than 50% probability of being self-sustaining ([Fig. 6](#)). These 17 units encompassed approximately 25% of the entire boreal woodland caribou's remaining range. Environment Canada's 2008 assessment also estimated that in 46 (80%) of the 57 boreal woodland caribou herds or population units, maintaining or developing the potential for that population to be self-sustaining would require a halt in further industrial disturbance.

Preventing further losses and ensuring long-term viable and abundant populations of boreal woodland caribou in Canada will require setting aside very large proportions of boreal forest habitat from large-scale industrial disturbance ([International Boreal Conservation Campaign, 2011](#)). Populations should be maintained and increased to levels that also allow for harvest for use by Indigenous peoples for sustenance and maintenance of cultural values ([UPCART, 2017](#)).

Protecting the Boreal Landscape to Mitigate the Effects of Climate Change on Boreal Biodiversity

The effects of climate change to the world's biota are, sadly, already well underway. The northward movement of thousands of organisms retreating from hotter and harsher condition as a result of the increase in global temperature is now very well documented from numerous studies ([Root et al., 2003](#); [Parmesan and Yohe, 2003](#); [La Sorte and Thompson, 2007](#); [Zuckerberg et al., 2009](#); [Langham et al., 2015](#)). One of the most important global strategies for allowing species to adapt and survive climate change impacts is through the maintenance of the last remaining blocks of intact, primary forest worldwide ([Carlson et al., 2009](#); [International Boreal Conservation Campaign, 2013](#)). Boreal forest regions are particularly important because they are the last reservoirs of habitat for species forced northward by intensely warm and hostile ecological conditions in temperate regions of the globe ([Wells et al., 2018](#)).

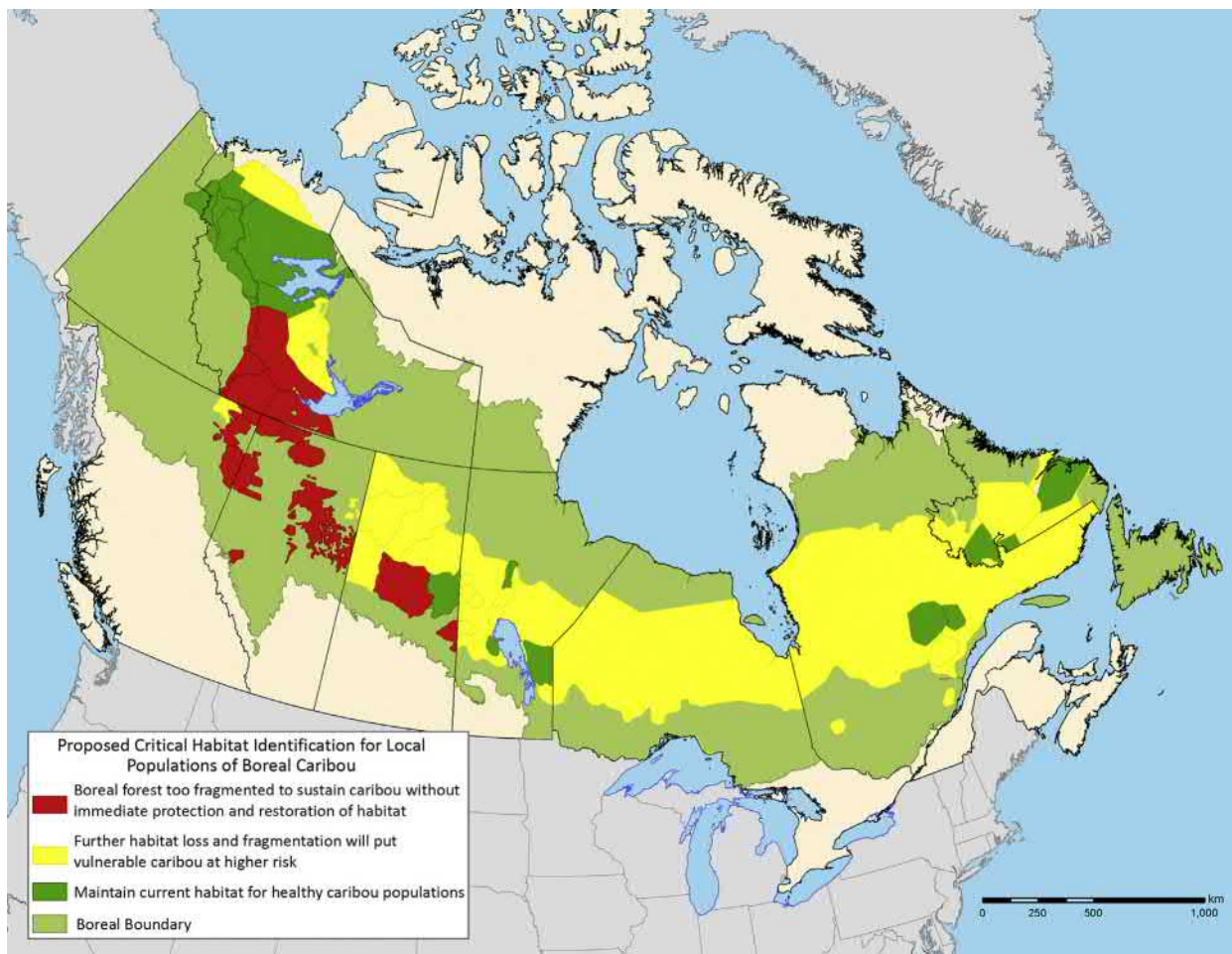


Fig. 6 Survival probability of each of 57 Boreal Woodland Caribou herds or population units as described by Environment Canada (2008). Only those herds shown in *green* are thought to have a high chance of persistence through maintenance of the current habitat conditions.

Other species are in need of immediate conservation action to prevent their current rapid declines and stabilize their populations enough to ensure that they have a chance of maintaining resiliency in the face of climate change. Species like boreal woodland caribou that have already lost nearly half of their historic range and are listed under Canada's Species at Risk Act as Threatened, are likely to disappear from vast portions of Canada without rapid protection of their remaining intact habitats.

Boreal Woodland Caribou Ranges and Carbon Stores Show Wide Overlap

Mapping the overlap of boreal woodland caribou range in Canada with best available soil organic carbon data (Tarnocai et al., 2009) shows broad overlap with the largest area of high-density carbon stocks within the still-intact portions of woodland caribou ranges at the national scale (Fig. 7). The total estimated stock of soil organic carbon summed across the entire ranges of all herds of woodland caribou including the already impacted portions of their ranges is 129 Gt, amounting to more than half of all the carbon stocks estimated for the entire Canadian Boreal Forest biome.

Portions of boreal woodland caribou ranges that are free from any industrial disturbance (including logging and major roads) hold 69 billion tons of carbon in storage within the soils, peat and permafrost beneath the habitat with 7.7% (10Gt) estimated to be encompassed within the boundaries of protected areas. This is more than a third of the total stock of carbon estimated to be held within the soils, peat, permafrost and forest vegetation of Canada's Boreal Forest biome.

Clearly, protecting boreal woodland caribou habitat would also have great benefits for protecting carbon stores and vice versa. There are countless other examples of the potential co-benefits of establishment of very large protected areas for protecting carbon stores as well as for the maintenance of biodiversity today and under the future challenges imposed by climate change. Incentives should be developed to support stewardship of terrestrial carbon stores that conserve large intact landscapes that support woodland caribou populations. Such incentives could include financial support to support Indigenous protected and conserved area development (ICE, 2018) and management tied to voluntary or government-mandated carbon-reducing policy mechanisms and markets.

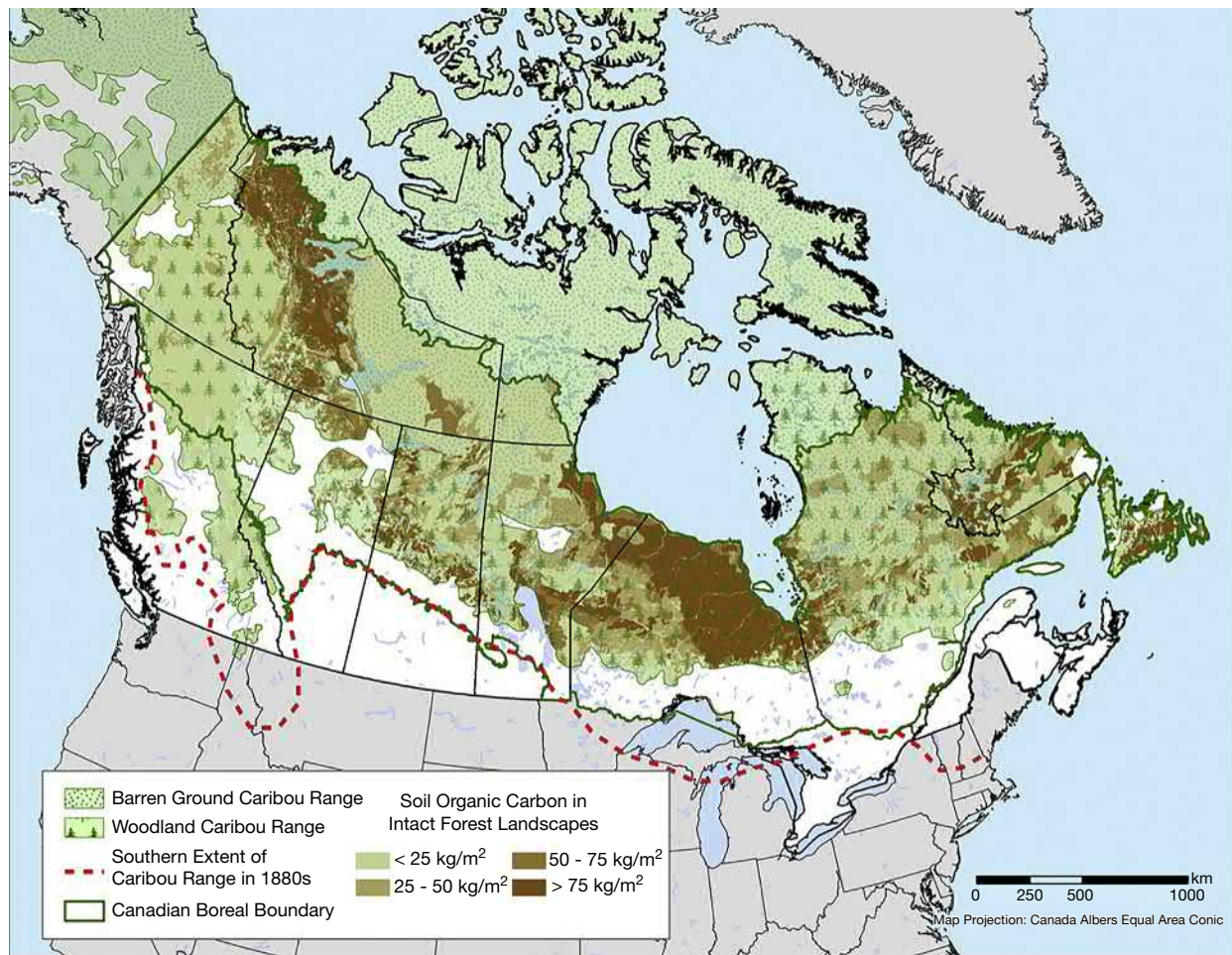


Fig. 7 Overlap of soil organic carbon stores and caribou ranges in Canada.

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Roadless in the Pacific Northwest: Ecology and History

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Published by Elsevier Inc.

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Abstract

A great values clash unfolded in the late 1990's as the US Forest Service sought to resolve a long-festering environmental conflict over the fate of roadless public lands, comprised of 25 million hectares largely in the American West and Alaska; fully 2% of the entire land area of the United States. Conservationists had bitterly opposed the continued logging of these natural areas while the Forest Service relied on unlogged roadless lands to supply a beleaguered timber industry. The clash was particularly noteworthy in the Pacific Northwest, home of most of the remaining intact forests, following immediately on the heels of the spotted owl crisis that was resolved in favor of conservation interests to severely limit further clearcutting of old-growth forests. The Roadless Area Conservation Rule (2001) again resolved a consequential issue in favor of conservation interests by limiting commercial logging and roadbuilding in roadless areas. Lengthy litigation followed, culminating in 2013 when the Tenth Circuit Court of Appeals supported the Rule. A notable but unexpected outcome of this dramatic policy shift is a significant increase in stored forest carbon following logging reductions. Such carbon gains team with other "free" environmental services like clean water and air, and high quality wildlife and fish habitat to illustrate important non-commercial forest values.

The Untold Story of Roadless Area Protection

The legitimacy and relevancy of the US Forest Service stood at a crossroad: one road led down a familiar, increasingly arduous and costly path—that of pursuing logging and roadbuilding into untouched reaches of public forest; the other road led in a new direction—turning away from a utilitarian mindset to protection of 23 million hectares of natural lands (2% of all US lands), as yet untouched by commercial logging.

The answer emerged in due time; the Roadless Area Conservation Rule took effect on January 6, 2001 in one of President Clinton's last official acts.

What follows is a glimpse into the unseen bureaucratic battle to craft this regulation, as seen from my perspective as Deputy Chief of the Forest Service when I played a key role in bringing the regulation to fruition.

The Context

I assumed my duties as deputy chief in May 1999, and I had come prepared with my short list of priorities representing what I hoped would engage my best efforts to move the agency's national forests in a new direction.

I soon learned that the Forest Service Chief, Mike Dombeck, also had a short list that subsumed mine. I knew of his focus on watershed restoration, such as salmon recovery and protecting forest headwaters that supplied much of America's domestic waters. In fact, my interest and accomplishments in this area had everything to do with my being selected as deputy chief.

A major surprise lay in my path. Within days of my arrival, Dombeck informed me that the Forest Service would undertake promulgation of a regulation to protect roadless areas. Although I had a hint of this proposal from an earlier moratorium on road construction within inventoried roadless areas, the audacity and sweep of this proposal stunned me.

For decades, roadless areas had been the source, or pool of lands, from which Congress designated wilderness. Roadless lands also served as the best source of new timber because they generally had little or no prior logging. Roadless areas enjoyed no official status until the Forest Service undertook a national Roadless Area Review and Evaluation, begun in 1967 and completed in 1972. The RARE review, as it was called, recommended that 5 million hectares be set aside for wilderness. However, the accompanying environmental impact statement was challenged in court and judged to be deficient.

USDA's assistant secretary Rupert Cutler, a former executive with The Wilderness Society, initiated a subsequent Roadless Area Review and Evaluation (RARE II) during the Carter presidency in 1977, seeking to improve on the original study. RARE II recommended 6 million hectares for wilderness and another 10.8 million for further study.

Given this heightened interest, subsequent Forest Service logging and road-construction activities in roadless areas were often stopped by environmental lawsuits. The environmental community attached great importance to protecting the wildness of roadless areas, and they regarded the Forest Service as a threat to protecting roadless-area values.

This values conflict echoed the lengthy battles over cutting old-growth forests. Forest Service dogma called for logging to convert old forest to “healthy” stands of young, vibrant trees. Yet the agency’s own research increasingly revealed that old-growth forests contained incredible diversity and complexity and served vital ecosystem functions. Far from being worthless, old growth held astounding value if one looked beyond mere timber products. The notorious spotted owl (*Strix occidentalis caurina*) controversy that dominated environmental politics in the Pacific Northwest in the late 1980’s had been the point of the spear in halting the systematic elimination of old-growth forests.

Similarly, roadless areas had long been regarded by the Forest Service as merely the next place one goes to log more trees. Even so, in 2000, after nearly 100 years of Forest Service management, there still remained about 23 million hectares of inventoried roadless areas—equivalent to an area the size of Wyoming. Congress had already created about 14.5 million hectares of wilderness. Thus, in aggregate, about half of the 78 million total hectares of national forest remained undeveloped.

Wilderness areas were predominantly high-elevation lands. Roadless areas, in contrast, occupied much more of the niche of mid-elevation lands that tended to be more heavily forested. The timber industry, as well as many people in Forest Service leadership, continued to view roadless-area protection as antithetical to multiple-use mandates. The Forest Service seldom championed the wilderness cause, and could even be said to resist it.

For example, in 1984, after a crippling recession had hurt companies with Forest Service timber contracts, Oregon’s Democrat Senator Mark Hatfield steered a bill through Congress that traded wilderness protection for a “release” of some roadless areas for immediate timber harvest. I recall, fresh upon arriving on the Siuslaw National Forest in 1992, looking at a road leading right into the bulls-eye of what had been one of the Siuslaw’s few remaining large roadless areas near Hebo, Oregon. When built, the road (which accessed several 1985-era clear-cuts) permanently nullified the area’s unmanaged, untrammelled character.

These roads were legal, thanks to Hatfield’s legislation. However, the “release” language did not require that roadless lands be compromised by logging and road construction. The swift action taken by the Forest Service eloquently symbolized the agency’s operational values. Protect roadless areas? Not if there were logs to be had. Furthermore, acting swiftly to compromise the area’s roadless character eliminated the nuisance factor, making future management less complex.

Roadless-area protection and timber production had been engaged in a slow-motion collision for at least 20 years. You’ve seen bighorn rams size each other up in slow-motion? There will be a crash! Yet, it seemed clear to me that the Forest Service controlled both variables (protection and production) and could have engineered a durable solution. However, the Forest Service made itself—quite intentionally—the greatest threat to roadless areas. When Chief Dombeck proposed that the Forest Service develop a regulation for permanent protection of roadless areas, agency traditionalists felt downright insulted.

But Chris Wood, Dombeck’s policy advisor, said that, in opting to protect roadless areas, “The Forest Service is becoming relevant again.” I won’t forget that remark. The sharp contrast between insulting and relevant made me ponder. I took Wood to mean that roadless areas were a huge issue to a vast constituency of environmentalists who viewed the Forest Service as an abuser rather than a protector of roadless areas and public lands in general. I thought this perception should have greatly alarmed agency leaders, but it didn’t seem to.

Agency Dinosaurs?

The fissures that appeared after Dombeck’s proposal revealed the agency as something less than one big happy family. Gloria Flora, Humboldt-Toiyabe National Forest supervisor in Nevada, made a rather public offhand remark about “dinosaurs” in Forest Service leadership who needed to retire. This outraged many forest supervisors who demanded that Chief Dombeck disavow her remarks.

Dombeck called me on the phone. “Could you come see me right away?” I took the back stairs to his office, which was just above mine. He asked me to read a letter he’d just received from Mike Lunn, Oregon’s Siskiyou National Forest supervisor. Dombeck told me the letter had been electronically copied to “almost everybody” in the Forest Service. He asked what I thought he should do.

The letter was a direct, personal appeal to the chief outside the normal chain of command—except that it spoke to agency culture, not land management. Mike Lunn took umbrage at Flora’s statement, and he gave the chief a hard-edged testimonial as to how the “dinosaurs,” including himself, had built and sustained a great organization. The letter was a forceful defense of the old guard, tinged with defiance, contempt, and disrespect. The letter was also honest. Lunn was clearly calling Dombeck out as to how the chief felt about dinosaurs—like Lunn himself. The chief had an upcoming interview with *Time* magazine and now expected questions on this brouhaha.

Lunn’s letter demanded an immediate response, and I suggested that Dombeck first call Lunn to thank him for his letter, for having the guts to tell him what he was thinking. I told him, don’t argue; just be open, and listen if he’s got more to say. Then reassure him that you value agency leaders and all they do and have done for the Forest Service. I said that Lunn needs to hear that the chief of the Forest Service doesn’t consider him and his colleagues to be dinosaurs. Then, I said, write him a brief response, reiterating these few points. Address the reply to Lunn only. If Lunn wants to mail it around, let him. Don’t escalate, but don’t be dismissive.

Dombeck did this. In a few days, many thousands of agency employees had seen Lunn's letter as it spread via email. In these days before blogging, hundreds of commentators piled on via email using a "reply all" command, so that the effect multiplied geometrically. Folks generally piled on adulation for Lunn's "telling it like it is!" I recall almost no recognition of Dombeck's response.

Emboldened, Lunn wrote yet another letter, basically doubling down and getting in more licks. Dombeck took the high road—no response this time. But the Lunn letters boldly revealed in our field leadership a lack of trust in Dombeck and feelings of betrayal. Hard stuff.

Ticking Clock

Hermann Gucinski, a Forest Service research scientist in Corvallis OR, was lead author of *Forest Roads: A Synthesis of Scientific Information*. This comprehensive report described both the benefits and the adverse consequences of roads and road use. Other research demonstrated that roadless lands are the best landscapes in terms of water quality, fish and wildlife populations, endangered species, and healthy forests. These lands are also bulwarks against invasive species because they have an essentially robust natural character that road construction tends to degrade.

The Forest Service now found itself caught in a powerful vortex, a result of failing at the critical task of solving prominent problems. Until now, I had been at the field level striving to facilitate logging to meet agency targets (as noted, much of the timber supply came from roadless areas) while being generally aware that the agency flailed in court defending such actions. This had been going on for some two decades, and attested that the former approach failed to resolve the issue—figuratively kicking the can down the road year after year, time and money both wasted. Effectively serving the public demanded that the Forest Service craft a progressive policy to deal decisively with roadless areas and resolve the issue.

I found it remarkable that politicians in the Clinton administration, notably Chief of Staff John Podesta and Council on Environmental Quality Chair George Frampton, trusted the Forest Service for the undertaking. One overwhelming, simple reason accounted for that: Chief Mike Dombeck. The chief often lamented that the Forest Service had become extremely defensive and apprehensive trying to defend its logging legacy. "It's going to be a lot more fun playing offense," he'd say, grinning broadly. He believed roadless-area protection would be very popular and likely to win the admiration and restore the trust of a cynical environmental community. News media often editorialized about how Forest Service leadership drifted weakly in the face of public antipathy, seeming to have run off the rails. Dombeck relished the idea of sitting down in front of editorial boards from the *New York Times*, *Washington Post*, and *Los Angeles Times* to discuss the opportunity to contend for roadless-area protection.

Several difficult realities confronted the Forest Service in resolving one of the most sweeping and controversial issues of the past several decades. Completing a regulation governing 23 million hectares would affect virtually every national forest from coast to coast. Opposition would quickly mount, particularly from the conservative western states that held the vast majority of roadless lands. As anticipated, but sadly, some of the most intense opposition would come from within the Forest Service.

And there was the clock. This was summer 1999. A presidential election loomed in November 2000. Political reality required that a regulation be completed before President Clinton left office. There were two reasons: first, the Democrat Clinton wanted credit for a key environmental accomplishment; second, we needed to sustain momentum, because we knew the election of a Republican would stop the effort dead. We submitted a project calendar with all the requisite time periods—60 days for this, 90 days for that—indicating we could complete the project by mid-December 2000, after the election and before the January inauguration of a new president. An achievable assignment, but one with no margin for error or delay.

But we had no task team organized for the roadless issue. We were figuratively entering unknown territory without a map. Dombeck approached me with the challenge to find someone to lead the roadless effort—one of the most significant Forest Service challenges in its history. The job needed to be done well, it had to be done on time, and failure was not an option. I thought to myself, "I've got just the person in mind."

Bill Sexton, my old boss on the San Juan National Forest, was now laboring in a staff position in DC. He had openly voiced his hopes for a promotion to become a prestigious regional forester. I mentally connected the dots—take on the roadless issue, get it done, and the Forest Service will owe Bill Sexton a favor. Name your dream job. It's yours! It didn't hurt that Sexton was capable of doing just about anything he put his mind to.

I spoke with Sexton and made the pitch. His response was matter-of-fact: "Not interested. There will be a Republican president in 2000. Anyone who touches this roadless thing will be dead meat."

I bristled. I had not expected such a blunt assessment; so much for nuance. In that moment, any thought I had of cajoling or persuading Sexton into leading the roadless team vaporized because we needed a leader who believed in the work without reservations. I then called Sharon Heywood, Shasta-Trinity forest supervisor in California. Not interested. I put out an SOS call to all regional foresters. I needed help, urgently. Regional foresters acted stumped. Perhaps they agreed with Bill Sexton's sentiments and didn't wish to sacrifice anyone to political suicide?

Finally, Brad Powell, regional forester for California, called to say he had someone in mind: "Scott Conroy on the Modoc."

I felt a deep anxiety. I had met and knew most of the 120-plus forest supervisors, but I'd never even heard of Scott Conroy. And few considered the Modoc National Forest (office in Alturas, in the far northeast corner of California) to be an impressive locale. It seemed we were nearing the dregs of our candidate pool, when I was seeking the crème de la crème. I reminded Powell that this was the most important thing the agency had done in decades. Can we trust this issue to Conroy? A lot hangs on the outcome.

Powell told me that he thought Conroy might be just what we needed. He was competent, very disciplined, and could be relied on to get things done.

I reported to Dombeck on my efforts to find a person to lead the roadless effort. I noted my disappointment that the regional foresters couldn't help us identify any top-flight candidates. I also mentioned the Bill Sexton episode. Dombeck noted that at least Sexton was honest and agreed that we didn't want him: "We need a believer."

I got the nod to vet Conroy. Frankly, I had few options left. Maybe I needed to trust in Conroy's competence simply because the Forest Service always tried to pick capable people for forest supervisor jobs. That, coupled with Powell's endorsement, encouraged me. Then everyone I spoke to enthusiastically supported Conroy. Now it was time to speak to him myself.

Conroy immediately impressed me with his deep desire to help the Forest Service accomplish this historic task. He knew it would be tough sledding, but he liked a challenge. My concerns that he might be unequal to the task, or worse, oblivious to the difficulties, waned. Importantly, he believed roadless areas needed protection and wanted to be a part of it.

I said there were no guarantees, but if we could pull this off, he'd likely get a good promotion. Was he interested in greater responsibilities? Yes!

We had our team leader. I called Brad Powell to thank him for his help, though I still harbored doubts that we could succeed.

Making Hay

In the next few months, bureaucratic wheels turned quickly. We published a Notice of Intent in the Federal Register to prepare an Environmental Impact Statement and regulations to achieve roadless-area protection. Scott Conroy recruited eager, enthusiastic specialists of all kinds for his task team. We swung into our public involvement effort, the most ambitious in agency history. We conducted roadless-issue meetings for all 125 national forests, as well as many formal public hearings. We cooperated with other agencies such as BLM, Park Service, and Department of Justice. It was an incredibly hectic full-on press.

Since most roadless areas were in the West, timber industry groups and western Republican governors whipped up strong headwinds to blow the effort off course or, better yet, onto the rocks (Fig. 1). Chris Wood and I traveled to Salt Lake City to meet with several governors' representatives, all suspicious of the political overtones of the effort. The meeting was hostile and tense.

"Why now?" was the trenchant question. Everybody recognized roadless protection as a potent issue. We all knew the implications of the coming election as the political clock ticked on. Wood gamely explained that roadless issues had grown and festered for

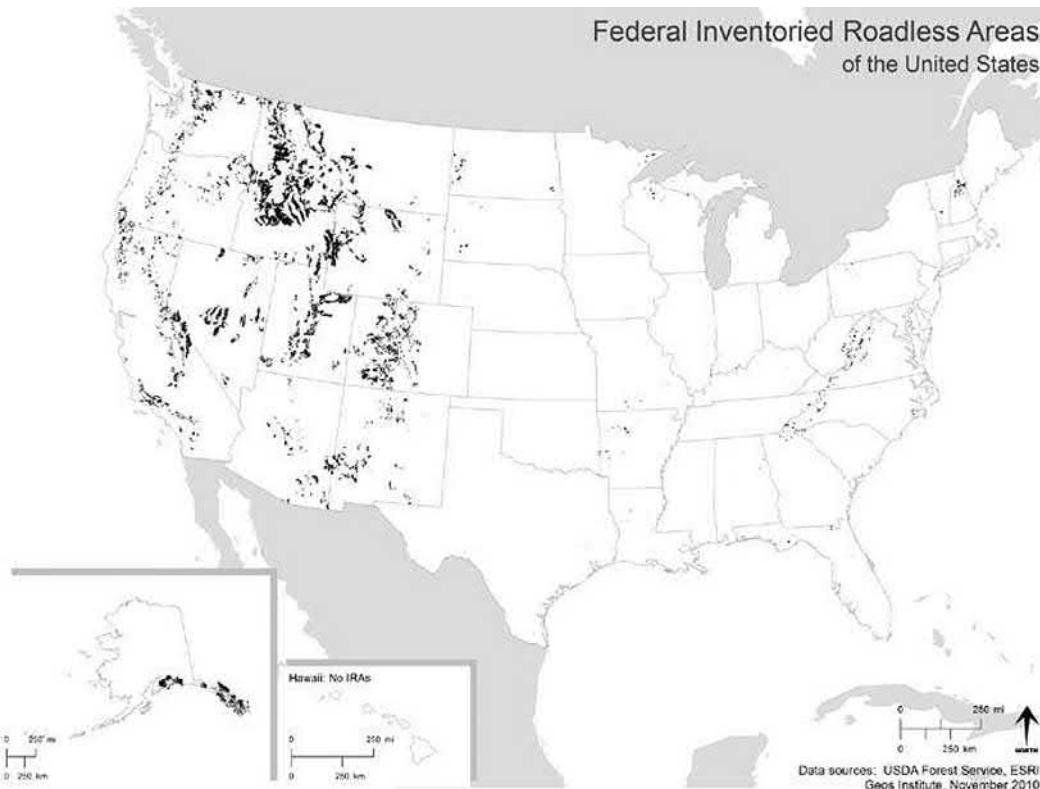


Fig. 1 Distribution of roadless areas throughout the United States, with heaviest concentrations in western states and Alaska. Source: USDA Forest Service.

decades, fostering doubt, legal uncertainty, and needless expense. It served no one's interest to leave this important issue undressed. While Wood spoke, I got the feeling the gang mentally searched for the best way to stop us.

Wood and I had anticipated that some of them would ask for cooperating agency status, which would essentially make them partners in our effort, a figurative bone thrown their way. But this would effectively give these prospective partners power to sabotage the project. And they did ask, but we fended them off, saying that it would be impractical and unworkable, since so many states were involved. If we made one state a cooperating agency, we'd have to do the same for all. We vowed to keep the states' governors informed throughout, but we were firm that only federal agencies would be cooperating agencies.

Pandemonium ensued. When Montana's representative pressed us hard on this issue, we asked why he counted this privilege as essential. He said, "We want to delay the process so that you can't finish the job before Clinton leaves office." They would take their chances from there on a hoped-for Republican White House pulling the plug on roadless-area protection.

Silently, I gave him high marks for honesty. After overcoming my shock at his brazen position, I stated that this was not a valid rationale for a cooperator. We left with a firm "No. You'll be hearing from us. Thanks for coming."

Other aspects of developing the rule flowed well. As the Forest Service held hundreds of public meetings, the volume of comment on the rule was massive, unprecedented. With Pew Environment Group funding a big advocacy campaign, the Forest Service received well over 1 million comments on our draft proposal. We had no precedent for processing and analyzing this volume of feedback, yet a task team heroically accomplished this as well. The trajectory of our effort held pretty tightly to the project calendar. We were still optimistic about concluding our work in December 2000.

Alaska, as usual, required special handling. Among the 23 ha of roadless areas, Alaska's two national forests, the Tongass and Chugach, contained about 5 million hectares—fully 20%. Of the two, the Tongass National Forest in southeast Alaska (remarkably, a bit larger than West Virginia) has long been a political hotbed. With 11,000 miles of coast and 57,000 miles of streams, the spectacular Tongass is regarded by the environmental community as the crown jewel of all national forests. For its part, Alaska's congressional delegation historically regarded the Tongass as its parochial domain, passing out logging and mining favors to local residents and businesses. The Forest Service is caught in a pincer-like grip between environmental constituents and powerful politicians.

With nearly 4 million hectares of Tongass roadless area distributed throughout this vast 7-million-acre archipelago of coastal rainforest (along with 3 million hectares of designated wilderness and National Monument lands), the destiny of these roadless areas loomed as a huge unresolved issue. Rather than propose any particular preference in the draft Environmental Impact Statement, we chose to defer the ultimate fate of Alaska's roadless lands to the final decision phase and simply invited public comments about the issue.

Mike Dombeck asked my opinion about the best future for Alaska's roadless lands. Having never visited Alaska, I told Dombeck I lacked a good enough feel for Alaska to provide a sensible answer. Thus, in August 2000, I made an unforgettable trip to Alaska with the chief's question in mind.

I immersed myself in the splendors of Alaska, accompanied throughout by Forest Service officials, primarily Rick Cables, the regional forester. Alaska's enormous spaces, raw exuberance, and uniqueness left me deeply touched, almost speechless. All Americans should visit Alaska to let it speak to their souls.

Over a period of several days, Cables conveyed that Alaska's roadless lands needed to remain available to local citizens for subsistence, commerce, and the basics of community sustainability. Uniquely, almost all of southeast Alaska is national forest land, meaning Forest Service management and decisions govern every aspect of life for Alaskans. In brief, Cables believed the lands' greatest value lay in utility, not protection.

Upon my return to Washington, I met with Dombeck to discuss my view on protecting Alaska's roadless lands. I described as best I could the nature and complexity of Alaska's roadless issue, ultimately siding with Cables's view that comprehensive, extensive roadless protection was unnecessary. Dombeck's face remained deadpan and he said little beyond thanking me. The few questions he did ask seemed rhetorical. I left with a sense that he disagreed with and was disappointed in my position.

Ultimately, the Forest Service decided to apply restrictions on further logging and road building to all of Alaska's roadless lands. Dombeck explained the key decision criteria to me like this: "Alaska's roadless lands are the best we have. We need to protect the best."

His logic had a simple, profound elegance that perhaps I failed to appreciate at the time. There exists much nuance between the poles of protection and wise use of lands. The choice is almost never clear, and claims are often mutually exclusive. I found the arguments of both sides compelling. Alaskans do rely heavily on the Tongass for the basics of life. Ecologically, the Tongass is of global significance. That makes the Tongass roadless area situation a wicked dilemma and why I found it difficult to see this clearly at a crucial moment.

In early December, we published the final Environmental Impact Statement and the proposed Roadless Area Conservation Rule, with a 30-day waiting period before it became effective. George Frampton, chairman of the Council on Environmental Quality (CEQ) and the president's leading spokesman on environmental matters, chaired a briefing for all federal agencies interested in the roadless proposal.

The Department of Energy was one very interested agency. The Roadless Rule proposed to ban any more road building in connection with oil and gas leases, beyond roads that existed or those needed for current leases only. North Dakota's Little Missouri National Grassland held a potentially huge but relatively undeveloped gas field for which restrictions on road building would make development, if not impossible, much more costly and difficult.

A contingent of several Department of Energy officials made an impressive (and late) entrance. The one woman among them wore a bright red dress, exuding power.

The leasing issue quickly arose. Frampton laid out the premise of the regulation on leasing. The Department of Energy quickly weighed in using strong, unequivocal terms: this must change. Frampton countered that the prohibition on new roads was a well-considered element of the rule. Acknowledging an explicit trade-off, Frampton said it was needed to protect roadless lands from the probability of more “dry holes” that would achieve little except to ruin more precious roadless lands.

The DOE contingent ratcheted up the argument, saying it would not accept any outcome other than making a last-minute change to the regulation.

It seemed clear to me that this conflict would have to come before White House Chief of Staff John Podesta and maybe President Clinton himself. And sure enough, in the next few days the regulation was rewritten to exempt any renewed lease from road-building restrictions. DOE won the argument, while CEQ gained some solace by retaining restrictions for all future leases. Prophetically, the lands in question later became a centerpiece of resurgent oil and gas industry in North Dakota as federal energy policy fostered a friendly environment for fracking.

The final rule was published in the Federal Register on January 6, 2001. Two weeks before George W. Bush assumed the presidency, William Jefferson Clinton, clad in a black overcoat, proudly made a presidential announcement at the National Arboretum, with gently falling snow dappling his shoulders. It seemed a perfect ending to a strenuous but deeply satisfying effort.

I reflected on all that happened in the past 18 months. I’d been given the opportunity to help resolve a festering conflict by fashioning regulatory protection for roadless areas. Nearing the end of my career, I had helped fashion a sweeping, bold policy for the environment. The same Forest Service that had been aggressively logging and building a vast network of roads into natural landscapes wheeled about-face to strive for durable protection—but protection from what? From the Forest Service itself.

Upon Reflection

It may prove useful to consider changes set in motion by roadless area protection that I consider to be profound: (1) a major victory for the environmental community alongside cessation of old-growth forest logging; (2) a new perspective forced on the Forest Service to consider more protective management options for roadless lands; and (3) forest carbon sequestration getting its due as vitally important to managing climate change factors.

Let’s look at these changes through the lens of public land forestry in the vast Douglas fir (*Pseudotsuga menziesii*) forests of the Pacific Northwest where sharp contrasts exist between activity pre- and post-roadless protection since 2002.

The Pacific Northwest is home to much America’s most intact forests, and these forests are also the most economically valuable. But any consideration of values must also include biological and even spiritual factors. The northern spotted owl controversy epitomized the clash of monetary and other at-odds values in a highly visible and protracted fight ultimately decided in the courts in 1991. Winners and losers became evident, but the courts offered no path forward. The Clinton administration resolved the legal morass by crafting a political pathway in 1994, in which commercial timber interests decisively lost ground following a decisive swing toward more ecologically conscientious policies. The environmental community declared victory but remained wary of backsliding (which did occur during the succeeding Bush administration).

Logging in the Pacific Northwest relied heavily on roadless lands for further old-growth harvests, even after the Clinton Plan reduced quotas from 9.6 million m³ to 2.4 million per year. Thus, roadless area protection increased the bind by restricting commercial logging and road building. Whereas the spotted owl victory achieved a notable regional win for the environmental community, roadless protection achieved a monumental national victory. Remarkably, every legal challenge to the Roadless Conservation Rule failed in spite of the Bush administration electing to provide no defense. Environmental organizations intervened as friends of the court to mount a successful multi-pronged 12-year defense that ultimately vindicated the legitimacy of roadless protection.

These two remarkable environmental victories grew out of the Clinton administration’s sensitivity to values other than commercial timber, and have largely endured due to changing public values and legal requirements. Yet insistent voices for the primacy of commerce on public lands remain effective, if wounded. As I write, the Trump administration prods the Forest Service via executive order to increase logging by 30% in hopes of reducing risk of catastrophic fire, such as Paradise CA experienced in late 2018. Personally, I doubt that logging one’s way out of the current climate-driven fire conundrum will work.

The second point reflects, until now at least, the durability of roadless protection. Rather than logging and roadbuilding being the defining characteristics of Forest Service roadless policy, rules now legally require the agency to restrict commercial logging and new road construction in favor of protecting roadless area attributes and values like clean water and naturalness. This change clashes with a residue of traditionalist culture in the Forest Service, and has proven difficult to embrace.

The Bush administration fashioned a “work-around” whereby any state could petition to create unique roadless policies, though at considerable time and expense. Idaho and Colorado did so shortly after the original 2001 rule took effect, and Alaska and Utah began additional petition efforts in 2018–19. Forest Service officials quite eagerly made requisite cooperative gestures. In each case, the respective Governor chose to surgically loosen certain protections in the 2001 rule (such as for the ski industry in CO, and phosphate mining in ID), but the bulk of protections remain in effect currently. Thus, in spite of a few erosions, significant protections remain in effect to guide Forest Service actions in 23 million hectares of roadless areas, about 30% of the entire national forest land base.

The regressive move back to localized solutions unique to individual states reflects a long-standing reluctance to deal with national issues at a national, agency-wide level (e.g., clearcut logging, old-growth forest protection). The 2001 Roadless

Conservation Rule sought to resolve a decades-old national scale issue at a national level, after repeated local efforts had failed to pass legal muster, nor provide consistency. The environmental community exhibited enthusiastic support for a comprehensive policy that restricted commercial logging and roadbuilding—one governing all national forests—while critics (including many Forest Service officials) groused at loss of local control.

Furthermore, some Western states, notably Utah, remain fixed on converting federal lands to state ownership—a solution that would moot federal roadless area protection. The notion that federal lands should be given to states is deeply rooted in the premise that the federal government's ownership of public lands in western states is illegitimate. This notion is in direct contravention of the Property Clause of the US Constitution (Article 4), whereby the federal government reserved ownership of public lands unto itself when granting statehood to western states, and has been settled law based on Supreme Court rulings for over 100 years. The notorious 2016 occupation of the Malheur National Wildlife Refuge by “The Bundy Brothers” symbolized this fanciful movement.

Thus, although protection of roadless lands has strong and tested legal underpinnings, the political arena remains somewhat fraught.

Thirdly, the importance of forests in mitigating climate change dynamics has emerged relatively recently, both globally as well as in the Pacific Northwest region where Douglas-fir forests are among Earth's most prodigious carbon stores. Yet the relationship between climate change and forest carbon went largely ignored as recently as 2000 by those of us formulating the Roadless Area Conservation Rule. Remarkable new data from Forest Service inventories of forest carbon tells an interesting tale.

Using Oregon as an example, we see that the capacity of forest lands to store carbon increases when timber harvest declines (Fig. 2). Recall that the Northwest Forest Plan (1994) reduced federal timber harvest from 9.6 million m³ per year to 2.4 million. That plan, in combination with restrictions on commercial timber sales in roadless areas, resulted in significant increases in storage of forest carbon between 1996 and 2012 (see Figs. 2 and 3). The annual rate of acquired carbon on national forests increased from 13 million to 34 million metric tons of CO₂ between 1996 and 2012. In fact, in the short time period 1990 to present, Oregon's federal forest lands have shifted from being a net source of carbon to being a very large sink today. This contrasts with private industrial forest lands that have reduced carbon stores in the same period, largely due to continued heavy logging.

Total national forest timber harvests have plunged from a high of about 26 million m³ per year to the current level of about 10 - million. Extrapolating from the example of Oregon, carbon stores on national forests increased as logging decreased. If carbon were

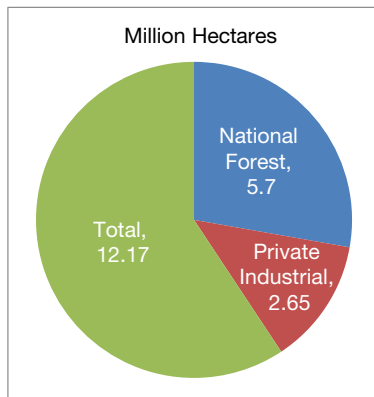


Fig. 2 Amount of forest lands in Oregon. Source: USDA Forest Service.

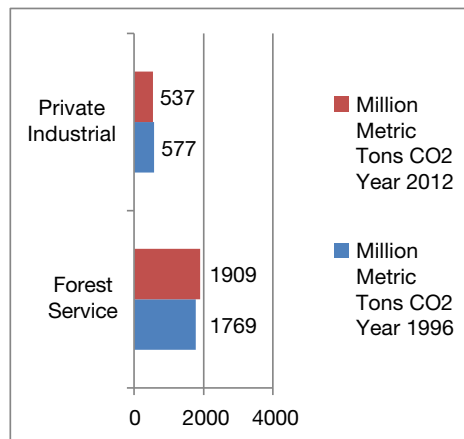


Fig. 3 Changes in forest carbon 1996–2012. Source: USDA Forest Service.

to be monetized at rates considered by the Office of Management and Budget, its value would greatly exceed that of wood products. This is not to say that logging on public lands should be eliminated. But the legacy of important conservation measures like the Roadless Area Conservation Rule has been to increase forest-based carbon significantly, even though this may have been an unintended consequence. In light of the urgency of climate change, forest carbon should be an important decision criterion in weighing the relative merits of carbon sequestration versus logging in federal forest policy discussions.

In conclusion, I believe my long Forest Service career gives me legitimacy to suggest that many agency officials remain unenthusiastic about the obligation to protect, rather than log, roadless lands. Time, research, and insight have demonstrated the long-term benefits associated with conserving roadless area character and values. The Roadless Area Conservation Rule remains among the most controversial policy initiatives in Forest Service history, and also among the most environmentally consequential. The federal government chose not to defend the Rule in court, yet it prevailed against numerous challenges due to dedicated defense by environmental groups. The Bush administration tried to scuttle the Rule but failed. Once again, the Trump administration seeks to water it down in Alaska and Utah. My hope has been that as time rolls on, the wisdom of protecting roadless values would become more apparent, obvious even. In sum, the roadless rule stands as a landmark national legacy and an important example of global opportunities available for other nations if we are going to slow down climate change.

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Hawaiian Islands Dry Forest

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Published by Elsevier Inc.

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Abstract

We present a status assessment of the Hawaiian islands dry forests, including the current status, stressors, and future viability. Dry forests generally have relatively low rainfall and are found on the leeward sides of the islands in lowland or in montane-subalpine zones. Historically, dry forests were located on all of the main Hawaiian islands and currently they are still found there. However, the quality of these forests is largely composed of a mix of native/nonnative vegetation. In addition to the native lowland and montane-subalpine dry forests that characterized dry forests historically, introduced dry forests and tree plantations are now classified as dry forests. Our assessment of dry forest viability, defined as the likelihood of persistence over the long term, is based on the conservation biology concepts of representation, redundancy, and resiliency. The main stressors to dry forests are invasive ungulates, plants, other herbivores, wildfires; drought; and agriculture and human development. Ongoing conservation efforts help to protect remnant patches of dry forests but this depends largely on combined efforts of various stakeholders. We developed four plausible future scenarios, each differing in levels of natural resource management, to evaluate the status of dry forests into the foreseeable future. Two of the scenarios, which are based on no change in conservation actions (Scenario One; status quo) and a slight increase in conservation actions (Scenario Two) have the highest likelihood of occurring in the foreseeable future while the other two, which are based on a slight to moderate

decrease in conservation actions (Scenario Three) and a moderate to large increase in conservation actions (Scenario Four) do not. Scenario Three would severely degrade and fragment native dry forest and result in reduced resiliency, redundancy, and representation. In Scenario Four, the substantial improvements in restoration of native dry forests would result in increased resiliency, redundancy, and representation.

Introduction

The Hawaiian archipelago is the most isolated landmass in the world separated by >3700 km from California. The archipelago consists of an expansive chain of islands located almost in the center of the Pacific Ocean, formed by the northwest movement of the Pacific tectonic plate over a volcanic hotspot where magma rises through the earth's mantle until it erupts through the seafloor. These islands range from small atolls in the northwest of the archipelago, to high volcanic islands in the southeast. As the islands increase in age they are carried northwest on the continental plate away from the hotspot. Currently located above the most active area of the hotspot, the island of Hawai'i is the youngest island in the chain and is still experiencing frequent, geologically-recent volcanic activity.

Climate in the Hawaiian archipelago is characterized by mild and equable temperatures year-round, low to moderate humidity, persistence of northeasterly trade winds, remarkable differences in rainfall within short distances, and infrequent hurricanes and severe storms (Wagner et al., 1999). Most areas in the Hawaiian archipelago experience only two seasons. Warmer and drier "summer" weather occurs between about May and September and slightly cooler and wetter "winter" weather occurs between about October and April (Wagner et al., 1999). The steep and rugged mountains of Hawai'i significantly influence its weather and climate.

The Hawaiian archipelago has an abundant range of biomes due to extreme variations in elevation, wind, rain, topography, substrate, and hydrology. The archipelago's remote location in the vast Pacific Ocean contributes to its physical geography. Each island and atoll has unique physical and biological features. We provide an overview of the dry forest in the Hawaiian archipelago and describe the ecological factors that have influenced the dry forest biome over time and into the future. A thorough introduction of the Hawaiian Islands can be found in the chapter by Harrington in this work.

Description

Defining Dry Forest Characteristics

Here we use the definition of a forest as a plant community characterized by vegetation with >25% tree cover (a woody perennial that usually has a single trunk) (Gagne and Cuddihy, 1999). Dry forests in Hawai'i typically have this woody overstory, and an understory which can be shrubby and/or herbaceous.

Dry forests in Hawai'i generally are located on the leeward sides of the islands in lowland or in montane-subalpine zones (Gagne and Cuddihy, 1999). These zones are differentiated by elevation and climate that primarily dictate which species can exist in them (Gagne and Cuddihy, 1999), and are described further in their respective subtype descriptions in the **Pre-human Condition** and **Current Condition** sections.

There are many ways to classify plant communities such as using elevation, moisture, and physiognomy. For example, Gagne and Cuddihy (1999) defined dry plant communities based on a moisture regime of 1200 mm of annual rainfall. Thus, we defined and characterized the dry forests of Hawai'i using two existing geospatial datasets (Amidon, 2018a,b). The 2014 LANDFIRE data was used to represent the current vegetation types of the main eight Hawaiian islands (LANDFIRE, 2011, 2014; Rollins, 2009). LANDFIRE data layer identified 40 land cover/vegetation types on the main Hawaiian islands. For the dry forest this included four categories: lowland dry forest, montane-subalpine dry forest and woodland, introduced dry forest, and tree plantation (introduced); which are described as subforest type in the **Current Condition** section. The moisture zone maps (Price and Jacobi, 2012), created by Price et al. (2012) of the main Hawaiian islands were used to define the dry regions on each island for the introduced dry forest and tree plantations only. Dry regions are a combination of the arid (areas that have a moisture availability index (MAI) value less than -689 mm), very dry (areas that have an MAI value between -389 and -689 mm), and moderately dry zones (areas that have an MAI value between 0 and -389 mm) as identified by Price et al. (2012). Estimated MAI values statewide were calculated using maps of estimated median annual precipitation and potential evapotranspiration values (Price et al., 2012). Therefore, the introduced dry forest and tree plantations are identified as having an estimated annual rainfall ranging between 10 to <160 cm, and rainfall is highly variable by elevation (Price et al., 2012).

Dry Forests occur on all of the main Hawaiian islands from 0 to 2900 m (sea level to 9500 ft) in elevation. Annual rainfall ranges between 30 and 200 cm (12 and 79 in) in lowland dry forest and montane-subalpine dry forest and woodland (LANDFIRE, 2016).

Geology

Substrates are highly variable but are generally well-drained, sandy loam soils derived from volcanic ash or cinder and weathered 'a'a or pāhoehoe basaltic lava for the lowland dry forest (LANDFIRE, 2016). The substrate conditions found within the montane-subalpine dry forest range from cinder, well-drained, loam soils derived from volcanic ash, and weathered 'a'a or pāhoehoe basaltic lava with little soil development (Gagne and Cuddihy, 1999).

Physical/life history components

Natural recruitment in the dry forest is driven by numerous factors including disturbance from fires, drought, hurricanes, volcanism, storms, pathogens, diseases, and invertebrate pests. It can also be influenced by rainfall, light, and nutrient availability.

Water availability in the dry forests is dependent on rainfall and elevation. In the lowland dry forests, rainfall occurs mainly in the winter (Gagne and Cuddihy, 1999). Whereas, in the montane-subalpine dry forest, drought conditions occur during the summer (Gagne and Cuddihy, 1999). Rainfall in the dry, leeward sides of the Hawaiian islands most commonly occur as a result of frontal storm systems that are distributed over a large area and are broad; and convective storm cells, which are localized to a particular area and are small (Cordell and Sandquist, 2008). The sporadic appearance of rainfall during drought periods from convective storms, although small and for the most part do not account substantially to annual primary productivity in dry grasslands and shrublands, are important in the maintenance and existence of woody plants (Cordell and Sandquist, 2008).

Fire can act as a primary driver for change in dry forests. Most native species in Hawai'i are not specifically fire adapted (Smith and Tunison, 1992), however, may respond favorably after disturbance if environmental conditions are optimal. Fire can reset the successional clock in this ecotype by removing a substantial amount of plants. Some seeds will survive and be able to germinate following the fire, however, others rely on dispersal from other sources such as the wind or animals.

Vegetation composition and vegetation structure

Vegetation composition and structure is defined by an open to dense tree layer ranging from 3 to 18 m (10 to 59 ft. tall (LANDFIRE, 2016). The dominant species of dry forests in Hawai'i are found in these species-rich families: Malvaceae (14 sp.), Rubiaceae (12 sp.), Rutaceae (9 sp.), Euphorbiaceae (8 sp.), and Fabaceae (7 sp.) (Pau et al., 2009). The most species-rich genera are *Melicope*, *Chrysodracon* (formerly known as *Pleomele*), *Psychotria*, and *Wikstroemia*, each containing six species (Pau et al., 2009).

Endemism in the tree species of the dry forests of Hawai'i are unusually high with 90% of all species endemic, 10% indigenous (native nonendemic), and 37% are single-island endemics (Pau et al., 2009). Most trees in the dry forests are evergreen (97%) and only four species are deciduous (tree shedding its leaves annually) (Pau et al., 2009).

Biodiversity

The biodiversity in native dry forests is high when compared to other native ecotypes in the Hawaiian islands (Gagne and Cuddihy, 1999; Cabin et al., 2000). The diverse native dry forests support many native bird and invertebrate species. Historically, native birds included large flightless geese and ducks (family Anatidae) and frugivores such as crows (family Corvidae) and thrushes (family Turdidae) (Chimera and Drake, 2011). Native frugivores aided in the processing of fruit or pulp removal of native plants and contributed to seed dispersal and germination (Chimera and Drake, 2011). Native birds and invertebrates also assisted in pollination within the dry forests resulting in increased reproduction and genetic diversity. Seabirds provided important nutrients from the marine environment such as nitrogen and phosphorus to the dry forests which are essential to vegetation recovery and health (Young and VanderWerf, 2016; Fukami et al., 2006; VanderWerf et al., 2014).

Pre-Human Condition

Dry Forest Subtypes

Before the arrival of humans, dry forest was represented by two forest subtypes: lowland dry forest and montane-subalpine dry forest (see Table 1 for a description).

Vegetation composition and vegetation structure of dry forest

In general, the pre-human dry forests in Hawai'i were comprised of 109 tree species in 29 families, with 90% of all species endemic, 10% indigenous, and 37% being single island endemics—with the greatest number of single island endemics located on Kaua'i and the island of Hawai'i (Pau et al., 2009). It is important to clarify, that this high diversity of species only takes into account the species composition found in the canopy layer of dry forests. The understory may have contained plants that commonly describe the dry grassland and shrubland ecotype such as *Heteropogon contortus* (pili) or *Dodonaea viscosa* ('a'ali'i). Additional information on the diversity of the species located in the chapter on Hawai'i dry grasslands and shrublands in this work.

Physical/life history components of dry forest

The historical fire regime in Hawai'i was characterized by infrequent, low severity fires, as few natural ignition sources existed (Cuddihy and Stone, 1990; Smith and Tunison, 1992). Prior to human colonization, fuel was sparse in dry plant communities and native vegetation had a low flammability (Smith and Tunison, 1992) and could not carry fire effectively before the introduction of nonnative grasses. Although fires were infrequent, Vogl (1969), in Cuddihy and Stone, 1990) proposed that naturally occurring fires may have been important in the development of some of the original Hawaiian flora, adding to the species richness of ecotypes, including the dry forests. The primary ignition sources were volcanism and lightning (Baker et al., 2009). In addition, lava flows as a result of volcanism can cover areas of forest and reduce their size.

Table 1 Prehuman conditions and current conditions of the dry forest subtypes of the Hawaiian islands.

Dry forest subtypes	Precipitation ^a (cm)	Elevation ^a (m)	Pre-human condition		Current condition	
			Characteristic plants ^b	Extent/range	Characteristic plants ^{a,b}	Extent/range ^{b,c,d,e}
Lowland Native Dry Forest	50–200	> 1000	<i>Alphitonia ponderosa</i> (kauila), <i>Bobea sandwicensis</i> ('ahakea), <i>Chrysodracon hawaiiensis</i> (hala pepe), <i>Colubrina oppositifolia</i> (kauila), <i>Diospyros sandwicensis</i> (lama), <i>Erythrina sandwicensis</i> (wiliwili), <i>Metrosideros polymorpha</i> ('ōhi'a), <i>Mezoneuron kavaense</i> (uhiuhi), <i>Myoporum sandwicense</i> (naio), <i>Myrsine lanaiensis</i> (kōlea), <i>Nestegis sandwicensis</i> (olopua), <i>Nothocestrum breviflorum</i> ('aiea), <i>Planchonella sandwicensis</i> ('āla'a), <i>Polyscias sandwicensis</i> ('ohe makai), <i>Psydrax odorata</i> (alahe'e), <i>Rauvolfia sandwicensis</i> (hao), <i>Santalum</i> spp. ('ilihi), <i>Sapindus oahuensis</i> (āulu, lonomea), <i>Sideroxylon polynesianum</i> (keahi), <i>Sophora chrysophylla</i> (māmane), and <i>Xylosma hawaiiense</i> (maua)	All of the main Hawaiian islands; across southwest and northeast Kaua'i, the entire island of Ni'ihau, the southern Ko'olau and Wai'anae mountains and a portion of the northern Ko'olau and Wai'anae mountains of O'ahu, parts of north, southeast, and western Moloka'i, the lowlands of the entire islands of Lāna'i and Kaho'olawe, the leeward slopes and central area of Maui, and the leeward slopes, parts of the southeast and northern portion of the island of Hawai'i (see Figs. 1–4)	'ōhi'a, lama, kauila, wiliwili, <i>Acacia koa</i> (koaia), <i>Gardenia brighamii</i> (nānū), <i>Hibiscadelphus</i> spp. (hau kuahiwi), <i>Kokia</i> spp., keahi, <i>Polyscias sandwicensis</i> ('ohe), <i>Achyranthes</i> spp., <i>Nototrichium</i> spp., 'a'ali'i, <i>Leptecophylla tameiameia</i> (pūkiawe), <i>Doryopteris decipiens</i> ('iwa'iwa), <i>Pellaea ternifolia</i> (laukahi)	All the main Hawaiian islands. However, areas consisting of predominantly native species are now rare and are best represented on the leeward sides of the islands
Montane-Subalpine Native Dry Forest	Between 30 and 120	Between 1000 and 2900	<i>Acacia koa</i> (koa), <i>Euphorbia celastroides</i> var. <i>lorifolia</i> ('akoko), <i>Euphorbia olowaluana</i> ('akoko), <i>Melicope hawaiiensis</i> (alani), 'ōhi'a, naio, kōlea, olopua, 'aiea, and māmane	Maui and the island of Hawai'i (see Figs. 1–4)	'ōhi'a, māmane, naio, koa, <i>Euphorbia celastroides</i> ('akoko), <i>Euphorbia olowaluana</i> ('akoko)	Maui and the island of Hawai'i. Best developed in the saddle region between mountains on the island of Hawai'i, with rich native plant communities. The range has decreased since pre-human conditions (see Figs. 1–4) primarily due to the expanding range of introduced dry forest and dry shrublands and grasslands

Table 1 Prehuman conditions and current conditions of the dry forest subtypes of the Hawaiian islands.—cont'd

Dry forest subtypes	Precipitation ^a (cm)	Elevation ^a (m)	Pre-human condition		Current condition	
			Characteristic plants ^b	Extent/range	Characteristic plants ^{a,b}	Extent/range ^{b,c,d,e}
Introduced Dry Forest	Generally between 50 and 200	Generally below 1000 m, but occasionally higher elevations	N/A	N/A	<i>Prosopis pallida</i> (kiawe), <i>Lantana camara</i> (lantana), <i>Schinus terebinthifolius</i> (Christmas berry), <i>Leucaena leucocephala</i> (koa haole), <i>Pennisetum setaceum</i> (fountain grass), <i>Andropogon virginicus</i> (broomsedge), <i>Schizachyrium condensatum</i> (beardgrass), <i>Cenchrus ciliaris</i> (buffelgrass), <i>Megathyrsus maximus</i> (guinea grass)	On the leeward sides of all the main Hawaiian Islands
Managed Tree Plantations	Various	Various	N/A	N/A	<i>Corymbia</i> spp. (gum tree), <i>Pinus</i> spp. (pine), horticultural or agricultural trees (coffee, fruit, nut orchards), <i>Casuarina</i> spp. (ironwood), <i>Paraserianthes</i> spp. (albizia), <i>Fraxinus</i> spp. (tropical ash), <i>Grevillea</i> spp. (spider flower)	Managed tree plantations are found on Kaua'i, O'ahu, Moloka'i, Maui, and the island of Hawai'i

^aLANDFIRE. (2016). LANDFIRE/GAP land cover map unit descriptions. U.S. Department of Interior, Geological Survey. Accessed 9 April 2018 at <https://www.landfire.gov/documents/LF-GAPMapUnitDescriptions.pdf>.

^bGagne, W. C., and Cuddihy, L.W. (1999). Vegetation. In Wagner, W.L., Herbst, D.R., and Sohmer, S.H. (eds.), *Manual of the flowering plants of Hawai'i* (pp. 45–114). Honolulu: University of Hawai'i Press, Bishop Museum Press.

^cLANDFIRE. (2014). Existing vegetation type layer, LANDFIRE 1.4.0, U.S. Department of the Interior, Geological Survey. Accessed 16 February 2018 at <http://landfire.cr.usgs.gov/viewer/>.

^dThe Nature Conservancy (TNC). (2006). Ecosystem vegetation descriptions (lowland dry, montane dry, and subalpine). In Hawaiian high islands ecoregion. Available at <http://www.hawaiiecoregionplan.info/targets.html>.

^eThe Nature Conservancy of Hawai'i (TNCH). (2007). Geographic information system (GIS) map layers showing ecosystem regions for the main Hawaiian islands, as developed by The Nature Conservancy Hawai'i's ecoregional planning team. Unpublished data.

Dry Forests Viability of Prehuman Conditions

The Hawaiian dry forest viability depends on maintaining multiple and distributed populations (redundancy) of sufficient quality and size (resiliency) with species richness and genetic range (representation) to survive across their ecological environment over time.

Historically, dry forests in Hawai'i covered large areas (Figs. 1–4) and were comprised of a wide range of species and diversity (see above). This high quality and large size would have helped dry forests tolerate natural, annual variations in the environment and recover from periodic disturbances (i.e., floods, minor fires, etc.). Should a period disturbance have occurred, the seed source had a large enough range and diversity of species to allow the dry forest to recover, thus making it resilient.

Both lowland and montane-subalpine dry forests were historically distributed and had wide ranges across all of the main Hawaiian islands (Figs. 1–4). This redundancy made dry forests less susceptible to catastrophic events such as an occasional hurricane or volcanic eruption. In the case of lava flows, these were localized events affecting only some populations of dry forests across the landscape. The distribution of dry forest in multiple units across the landscape and across the islands provided redundancy, which provided the ability to withstand events only affecting smaller areas of dry forests on individual or a few islands (e.g., single volcanic eruptions or hurricanes affecting multiple islands).

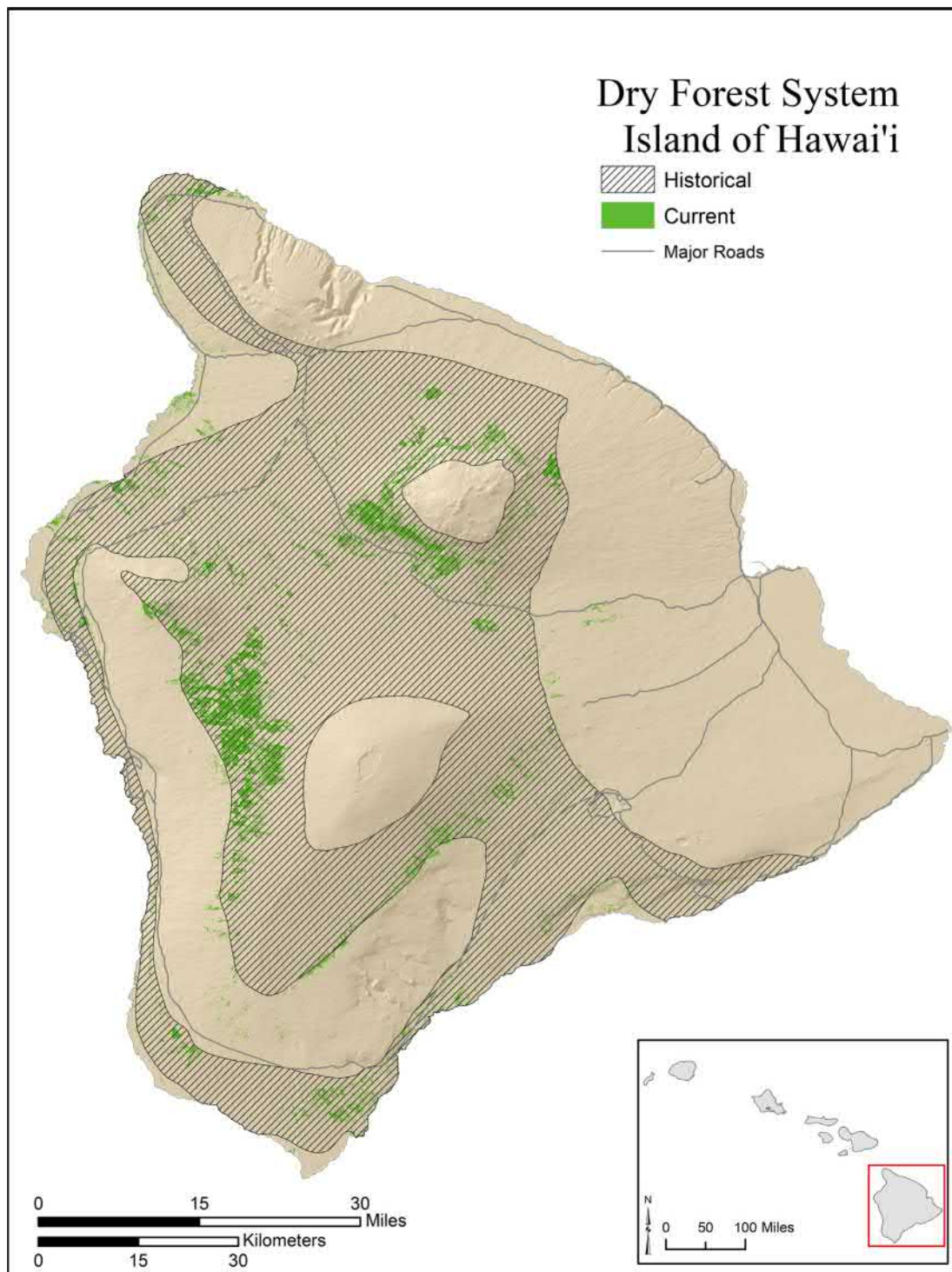


Fig. 1 Map of historical and current extent of dry forest in the island of Hawai'i. Word from Reeves, M. K., and Amidon, F. (2018). Habitat status assessment methods—Hawai'i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439.

The high diversity of tree species within dry forests (see above) is part of the high representation (the ability to adapt to changing environmental conditions and is measured by the variation across the landscape) found in this ecotype (Rock, 1913). Prior to human arrival, all plants, animals, and invertebrates arrived in Hawai'i by accident or by drift. Because of this isolation, species

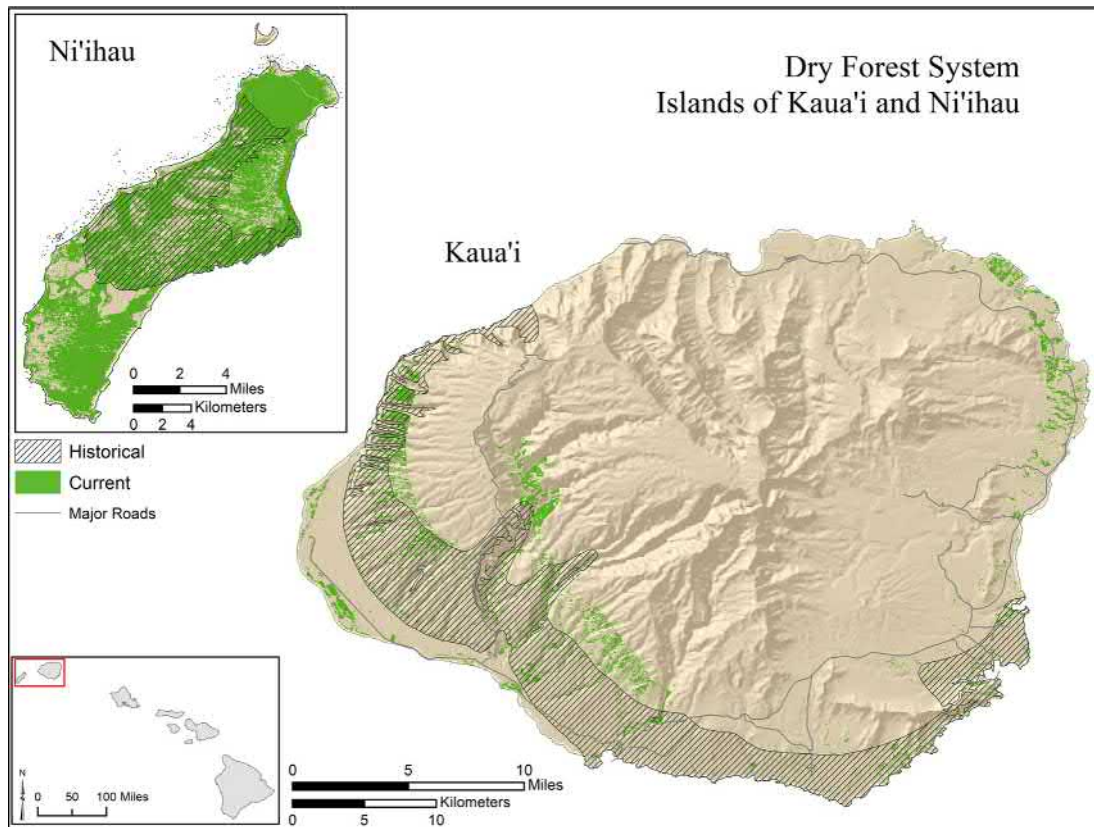


Fig. 2 Map of historical and current extent of dry forest in Islands of Kaua'i and Nii'hau. Word from Reeves, M. K., and Amidon, F. (2018). Habitat status assessment methods—Hawai'i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439.

were able to fill empty niches not already occupied by other species that lead to speciation (adaptive radiation) and a high rate of endemism; 90% for dry forests (Pau et al., 2009). As described, this endemism and diversity existed across the pre-human dry forest subtypes, thus leading to high representation.

Current Condition

Dry Forest Subtypes

While dry forests were represented by two subtypes before the arrival of humans, it can now be further subdivided to include not only the lowland and montane-subalpine native dry forest, but also introduced dry forests and tree plantations. Introduced dry forests are characterized by being dominated by introduced vegetation, but does not refer to tree plantations. Tree plantations are a forest type that was created by humans. A short description of each prehuman and current dry forest subtypes follows in Table 1.

Current Dry Forest Extent/Range

Tropical dry forests of the Hawaiian islands are ranked as the most threatened tropical forest ecosystem worldwide (Miles et al., 2006). Charles N. Forbes of the Bernice P. Bishop Museum, and the distinguished Joseph Rock of the then College of Hawai'i (now the University of Hawai'i at Mānoa) were the first botanists to characterize the flora of the Hawaiian islands in 1908–20 (Wester, 1992) and 1910, respectively (Rock, 1913). Rock (1913) noted the dry forests of Kahikinui District on Haleakalā, Maui, and Pu'uwa'awa'a in the district of north Kona on the island of Hawai'i, as the richest botanical regions in the islands. These lowland dry and mesic forests once were considered to have more native tree species than any other region and any rainforest in the Hawaiian islands (Rock, 1913).

For decades, biologists have cited that over 90% of native Hawaiian dry forests have been destroyed (Bruegmann, 1996; Cordell et al., 2008); however, the actual current extent of native dry forest cover may be as low as 1% of the original (Pau, 2018). Thus, reducing the resiliency and redundancy of dry forests. Forty-five percent of the dry forest plant species in Hawai'i are at risk of

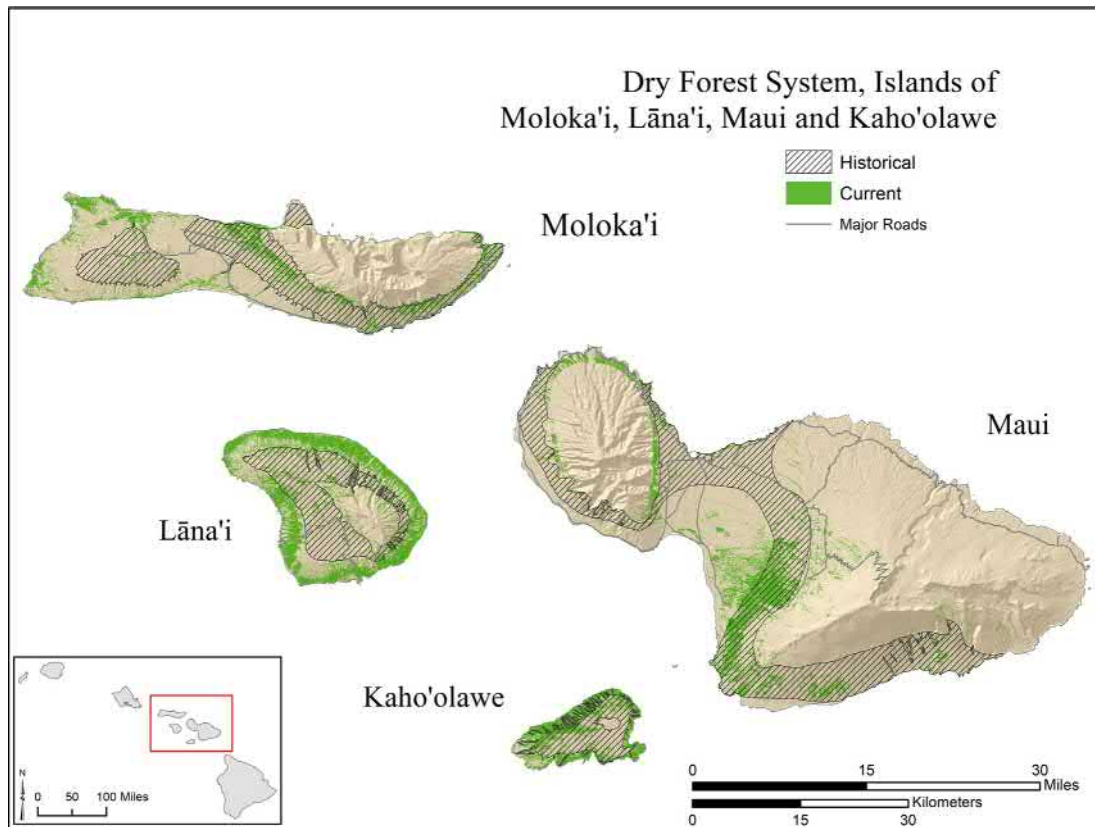


Fig. 3 Map of historical and current extent of dry forest in Islands of Moloka'i, Lāna'i, Maui and Kaho'olawe. Word from Reeves, M. K., and Amidon, F. (2018). Habitat status assessment methods—Hawai'i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439.

endangerment (Pau et al., 2009). Twenty-five percent of the endangered plant taxa in the Hawaiian islands are from the dry forests, and approximately 20% of dry land plant taxa in the Hawaiian Islands are known to be extinct (Cabin et al., 2000; Sakai et al., 2002), which has reduced the representation of this forest.

Most of the remaining and relatively intact native dry forests are currently found in areas that contained rough lava substrates that were unsuitable for ungulates (one of the stressors on dry forests, see below) to walk on thereby reducing the levels of browsing (Medeiros et al., 1993). Additionally, these areas were able to withstand fires because the young undeveloped substrates contained fewer invasive species, more particularly invasive grasses that serve as high fuel loads which are able to carry fires further into the forest (Medeiros et al., 1993).

The current extent of dry forests occurs on all of the main Hawaiian islands, but these forests are largely composed of a mixture of native /nonnative vegetation (Figs. 5 and 6). The island of Hawai'i contains the largest amount of dry forest in the main Hawaiian islands with >37,231 ha (92,000 ac), roughly 4% of the island and 2% of the area of all the main Hawaiian islands. Following the island of Hawai'i, Maui contains approximately 14,199 ha (35,087 ac) of dry forest. Ni'ihau contains the highest percent of dry forest related to island size at 71%, while Kaua'i has the least amount of dry forest at 3% compared to island size (Fig. 5, Table 2).

Roughly 29,127 ha (71,974 ac) of dry forests in Hawai'i are native species dominated (containing >50% native vegetation), with the majority (28,742 ha (71,023 ac)) located on the island of Hawai'i (Fig. 6). In comparison, approximately 68,188 ha (168,497 ac) of dry forests in Hawai'i are native/nonnative mixed and 6435 ha (15,902 ac) are classified as heavily disturbed (Fig. 6). Although, introduced dry forests are widespread, native dry forests are still found in both the lowland and montane-subalpine zones. Tree plantations are found on Kaua'i, O'ahu, Moloka'i, and the island of Hawai'i (Fig. 7).

Stressors

There are a number of stressors currently impacting dry forest. These stressors are listed here, and the most significant in this habitat are further explained in the below subsections:

- Invasive Ungulates
- Invasive Plants
- Plant Disease

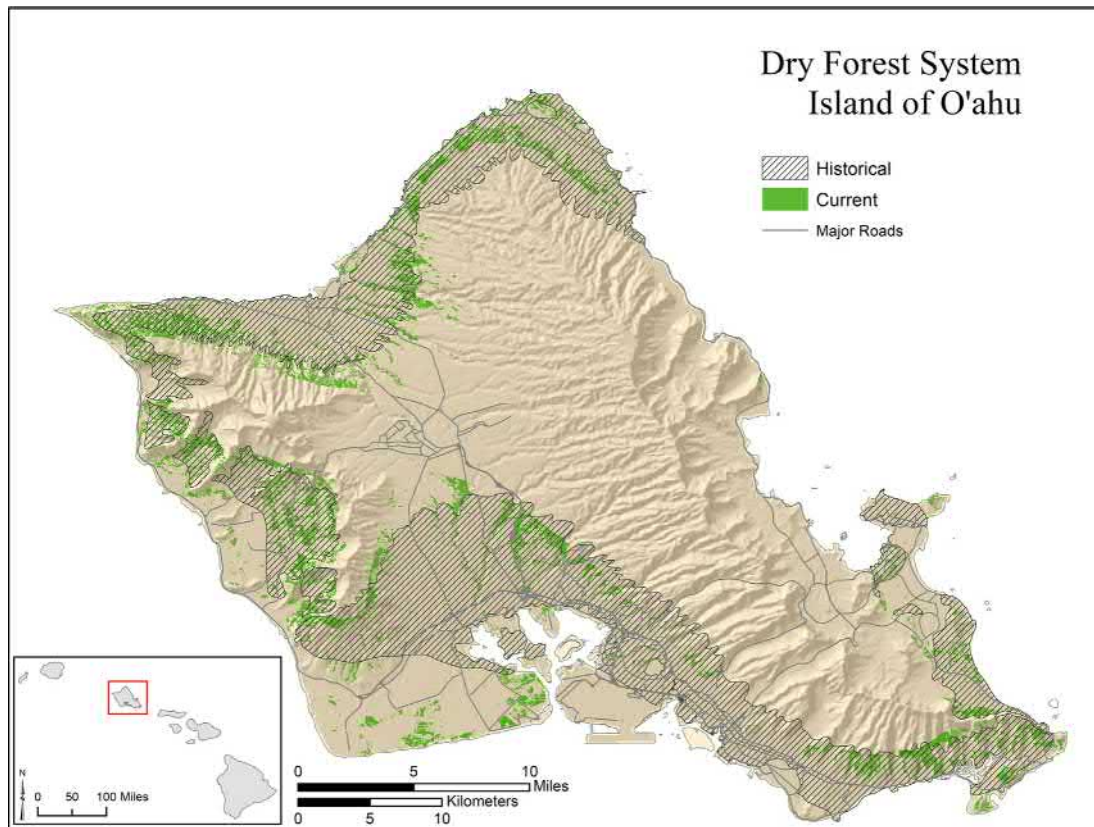


Fig. 4 Map of historical and current extent of dry forest in the Island of O'ahu. Word from Reeves, M. K., and Amidon, F. (2018). Habitat status assessment methods—Hawai'i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439.

- Invasive Herbivores
- Fire
- Drought
- Natural Disasters
- Climate Change
- Agriculture and Urban Development

Invasive ungulates

Impacts to the native species and ecosystems of Hawai'i accelerated following first human contact with the arrival of Captain James Cook in 1778. The Cook expedition and subsequent explorers intentionally introduced a European race of pigs or boars and other livestock, such as goats, to serve as food sources for seagoing explorers (Tomich, 1986; Loope, 1998). The mild climate of the islands, combined with the lack of competitors or predators, led to the successful establishment of large populations of these invasive mammals, to the detriment of native Hawaiian species and ecosystems. The presence of these mammals is considered to be an extremely important cause in the decline of native plant communities and ecotypes in the Hawaiian islands (Cuddihy and Stone, 1990). Dry forests are currently threatened by the destruction or degradation due to invasive ungulates, including pigs, goats, axis deer, mouflon, and cattle.

The effects of ungulates include the destruction of vegetative cover; trampling of plants and seedlings; direct consumption of native vegetation; soil disturbance; dispersal of invasive plant seeds on hooves and coats, and through the spread of seeds in feces; and creation of open disturbed areas conducive to further invasion by invasive plant species. All of these impacts can lead to the subsequent conversion of a native plant community to one dominated by invasive species (Nogueira-Filho et al., 2009). Because ungulates inhabit terrain that is often steep and remote (Cuddihy and Stone, 1990), foraging and trampling contributes to severe erosion of watersheds and degradation of streams. As early as 1900, there was increasing concern expressed about the integrity of island watersheds due to effects of ungulates and other factors, leading to the establishment of a professional forestry program emphasizing soil and water conservation (Nelson, 1989).

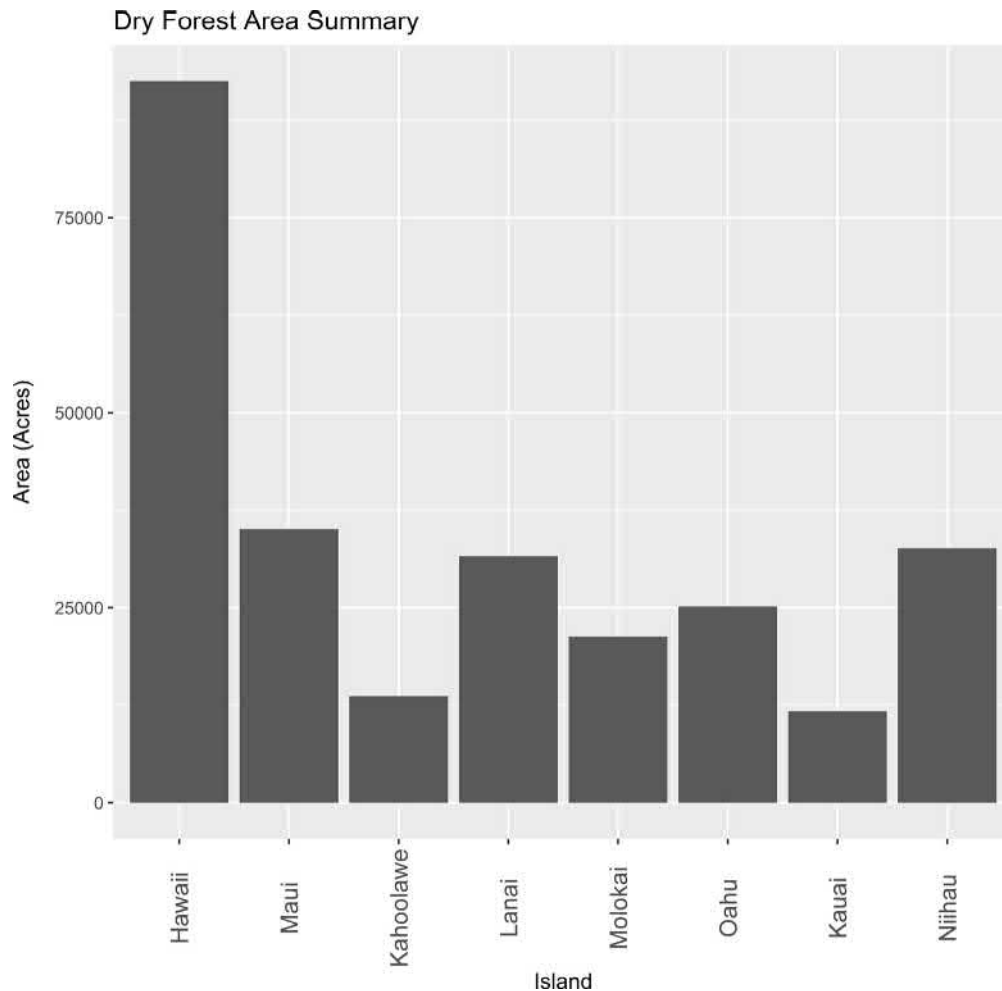


Fig. 5 Distribution of dry forests in the main Hawaiian islands. Word from Reeves, M. K., and Amidon, F. (2018). Habitat status assessment methods—Hawai'i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439.

Invasive plants

Native vegetation on all of the main Hawaiian islands has undergone extreme alteration because of past and present land management practices, including ranching, the deliberate introduction of nonnative plants and animals, and agricultural development (Cuddihy and Stone, 1990). Over 800 plant taxa have been introduced from elsewhere, and nearly 100 of these have become pests (e.g., injurious plants) in Hawai'i (Smith, 1985; Cuddihy and Stone, 1990). Some of the nonnative plants were brought to Hawai'i by various groups of people, including the Polynesians, for food or cultural reasons. Plantation owners (and the territorial government of Hawai'i), alarmed at the reduction of water resources for their crops caused by the destruction of native forest cover by grazing feral and domestic animals, introduced nonnative trees for reforestation. Ranchers intentionally introduced pasture grasses and other nonnative plants for agriculture, and sometimes inadvertently introduced weeds as well. Other plants were brought to Hawai'i for their potential horticultural value (Scott et al., 1986; Cuddihy and Stone, 1990).

Invasive plants adversely affect microhabitat in the dry forest by modifying availability of light and nutrient cycling processes, and by altering soil-water regimes (Smith, 1985). Some invasive plants may release chemicals that inhibit growth of other plants. They also alter fire regimes leading to incursions of fire-tolerant, nonnative plant species in native ecotypes (Cuddihy and Stone, 1990; Smith, 1985). These competitive advantages allow invasive plants to convert native-dominated plant communities to nonnative plant communities (Cuddihy and Stone, 1990; Vitousek, 1992).

Plant disease

The primary plant disease that impacts dry forests are two species of the fungal genus *Ceratocystis* that cause mortality in 'ōhi'a, which is commonly referred to as rapid 'ōhi'a death (ROD). 'Ōhi'a is Hawai'i's most common and widespread native tree, occurring from sea level to 2500 m (8200 ft) elevation (Keith et al., 2015) and is often a dominant species in lowland and montane-subalpine dry

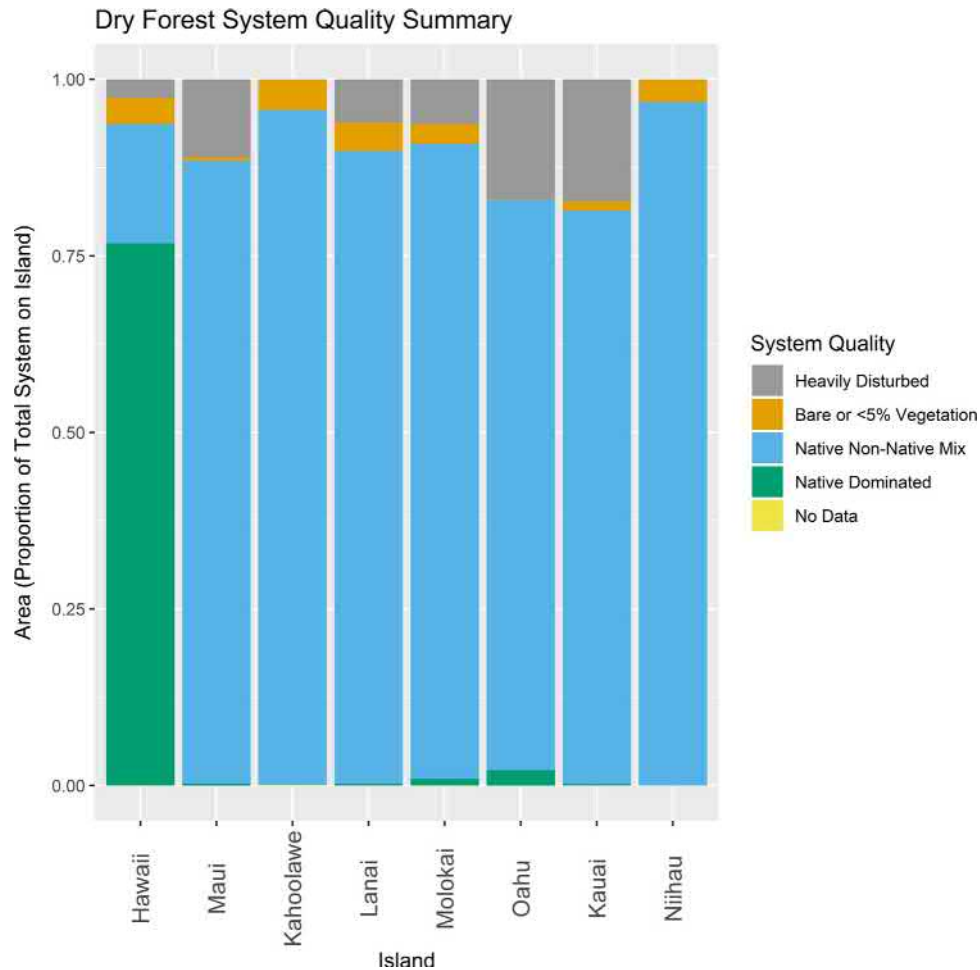


Fig. 6 Quality of dry forests in the main Hawaiian islands. Word from Reeves, M. K., and Amidon, F. (2018). Habitat status assessment methods—Hawai‘i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439.

Table 2 Current distribution of dry forests in the main Hawaiian islands

Island	Area (acres)	Percent of island	Percent of main Hawaiian islands
Kaho’olawe	13,657	48	< 1
Ni’ihau	32,624	71	1
Lāna’i	31,610	35	1
Moloka’i	21,281	13	1
Kaua’i	11,734	3	< 1
O’ahu	25,161	7	1
Maui	35,087	8	1
Hawai’i	92,516	4	2

Word from Reeves, M.K., and Amidon, F. (2018). Habitat status assessment methods—Hawai‘i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439.

forest. It is an ecologically important species that defines native forest succession and ecosystem function, provides habitat to many native species, and is culturally significant (Keith et al., 2015).

Rapid ‘ōhi’a death is a significant and poorly understood disease that was identified in 2012, and is only known to occur on the island of Hawai‘i. The disease causes browning in the crowns of ‘ōhi’a trees and ultimately leads to mortality. By the end of 2014, it was reported that approximately 2428 ha (6000 ac) of forest stands from Kalapana to Hilo showed > 50% mortality (Friday et al., 2015). And by 2017 approximately 30,351 ha (75,000 ac) showed symptoms of Rapid ‘ōhi’a death, including areas in Kona where dry forest occurs (CTAHR, 2018). Once a stand is infected, nearly 100% of the trees can succumb to the disease within 2–3 years

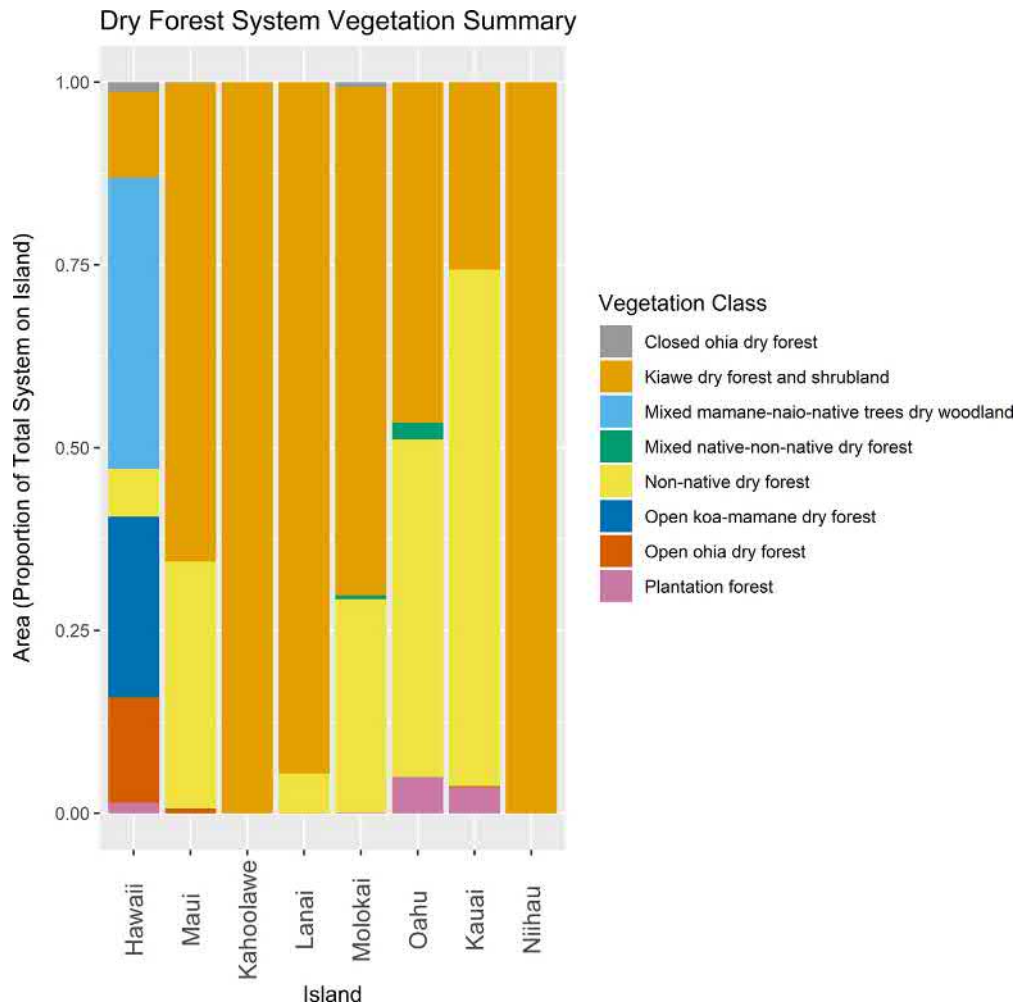


Fig. 7 Vegetation summary of dry forests in the main Hawaiian islands. Word from Reeves, M. K., and Amidon, F. (2018). Habitat status assessment methods—Hawai'i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439.

(CTAHR, 2018; Friday et al., 2015). Humans are thought to be a primary vector of transmission by moving infected wood, or contaminated tools, gear, and vehicles from one location to another (CTAHR, 2018). In addition, research has identified a nonnative ambrosia beetle as another likely vector. The beetles bore into trees and create a fine dust, referred to as frass, that can be carried by the wind and enter 'ōhi'a through wounds (CTAHR, 2018).

Invasive herbivores

One of the primary invasive herbivores that impact the dry forests are rats. There are three species of rats, all of which are introduced, in the Hawaiian islands: Polynesian rat (*Rattus exulans*), black rat (*Rattus rattus*), and Norway rat (*Rattus norvegicus*). The Polynesian and black rat are the most abundant rat species found in the wild, in dry to wet forests (Lindsey et al., 1999; Cole et al., 2000) and are the rodent species that have the most prominent impact in the dry forest. Rats are omnivorous and eat almost any type of food (Nelson, 2012). They impact native plants by eating fleshy fruits, seeds, flowers, stems, leaves, roots, and other plant parts (Atkinson and Atkinson, 2000), and by stripping bark and cutting small branches (twig cutting) in search of moisture and nutrients, seriously affecting vigor and regeneration (Abe and Umeno, 2011; Nelson, 2012). In the Hawaiian islands, rats may consume as much as 90% of the seeds produced by some native plants, and in some cases prevent regeneration of forest species completely (Cuddihy and Stone, 1990). Hawaiian plants as well as other plants from island ecosystems, are particularly susceptible to rat predation because they lacked native rodents, which can prevent successful reproduction (Cuddihy and Stone, 1990; Chimera and Drake, 2011). For the most part, rodents tend to target large seeds and since numerous dry forest plants contain fruits with one to few large seeds, rodents could be limiting seedling germination by the direct effect of seed mortality (Chimera and Drake, 2011). Given their impacts on native vegetation, rats have the potential to significantly alter dry forests and evidence of this is common in the dry forests of Hawai'i (Chimera and Drake, 2011).

The erythrina gall wasp (*Quadrastichus erythrinae*) is an invasive invertebrate that impacts dry forests, particularly the tree species *Erythrina variegata* (tall erythrina), *E. crista-galli*, and perhaps most importantly the native wiliwili. The erythrina gall wasp was first discovered on O'ahu in 2005 and subsequently spread to the other main Hawaiian islands (Heu et al., 2008). Like other gall-forming wasps, they insert their eggs into young leaf and stem tissue. The larvae develop and eventually cut exit holes to emerge as adults. Heavily galled plants result in a loss of growth and vigor, while severe infestations lead to defoliation and death (Heu et al., 2008; Yang et al., 2004). This species has been described as a destructive pest on native wiliwili trees, thus impacting dry forests.

The black twig borer (*Xylosandrus compactus*) also impact dry forests. This invasive pest was first discovered on O'ahu in 1961 and has become widespread throughout the main Hawaiian islands (Nelson and Davis, 1972). Black twig borers tunnel into woody twigs or branches to lay their eggs. This excavation and the introduction of pathogens damages the host, leading to die-back. Severe infestation can kill the host plants, including large trees (Tenbrink and Hara, 2007; Nelson and Davis, 1972). The black twig borer has been identified as a major threat to the native species *Mezoseuron kawaiense* (uhiuhi), *Alectryon macrococcus* (māhoe), *Nothocestrum latifolium* ('aiea), and *Flueggea neowawraea* (mēhamehame) (USFWS, 2013a,b, 2015, 2016a). Black twig borers have also infested invasive understory shrub species like koa haole, *Psidium guajava* (guava), and Christmas berry; as well as stands of nonnative tree species like *Lophostemon confertus* (brushbox), *Syncarpia glomulifera* (turpentine tree), *Melaleuca quinquenervia* (paperbark), *Eucalyptus sideroxylon* (red-ironbark eucalyptus), and *E. pilularis* (blackbutt eucalyptus) (Nelson and Davis, 1972).

Myoporum thrips or naio thrips (*Klambothrips myopori*) are a more recent invasive invertebrate to Hawai'i. It was first detected on the island of Hawai'i in 2008 attacking the native naio (HDLNR et al., 2013). The naio thrips feed on the host plant's foliage, resulting in leaf distortion and galls. Heavy infestations lead to leaf curling, dieback, defoliation, and mortality (HDLNR et al., 2013). Naio is a dominant species found in dry forests, and naio thrips have caused high levels of infestation and mortality on the species. In addition, naio mortality also impacts native fauna that rely on naio for food and/or habitat, such as insect herbivores and pollinators (HDLNR et al., 2013). Unfortunately in November 2018, naio thrips were detected on O'ahu by the Hawaii Department of Agriculture (HDLNR, 2019). A response team was implemented and infected trees were cut down, sprayed with insect killing soap, and then disposed of from the property. Efforts are underway to prevent naio thrips from further spreading across O'ahu and onto other islands.

Fire and drought

Fire is an increasing, human exacerbated threat to native species and ecosystems in Hawai'i. Fires inadvertently or intentionally set by the Polynesian settlers probably contributed to the initial decline of native vegetation in drier areas. These early settlers practiced slash-and-burn agriculture that created open lowland areas suitable for the opportunistic invasion and colonization of nonnative, fire-adapted grasses throughout the archipelago (Kirch, 1982; Cuddihy and Stone, 1990). Beginning in the late 18th century, Europeans and Americans introduced plants and animals that further degraded native Hawaiian ecosystems. Ranching and the creation of ranch lands in particular created highly fire-prone areas of nonnative grasses and shrubs (D'Antonio and Vitousek, 1992). Although fires were infrequent in mountainous regions, extensive fires occurred in lowland dry areas, leading to grass-fire cycles that converted native dry forest to nonnative grassland (D'Antonio and Vitousek, 1992).

Because of the greater frequency, intensity, and duration of fires that have resulted from the human alteration of landscapes and the introduction of nonnative plants, especially grasses, fires are now more destructive to native Hawaiian ecosystems (Brown and Smith, 2000), and a single grass-fueled fire often kills most native trees and shrubs in the area (D'Antonio and Vitousek, 1992). Fire destroys dormant seeds of these native species, as well as the individual plants themselves, even in steep, inaccessible areas or near streams and ponds. Successive fires remove habitat for native species by altering microclimate conditions, creating conditions more favorable to nonnative plants. Nonnative grasses (e.g., fountain grass), many of which may be fire-adapted, produce a high fuel load that allows fire to burn areas that would not otherwise burn easily, regenerate quickly after fire, and establish rapidly in burned areas (D'Antonio and Vitousek, 1992; Tunison et al., 2002). Native woody plants may recover to some degree, but fire tips the competitive balance toward nonnative species (National Park Service 1989 in Cuddihy and Stone, 1990; Takeuchi, 1991). Due to the seasonal drought conditions in the dry forest, the risk of fire and its associated impact is exacerbated and considered a significant stressor usually resulting in loss of forest land in favor of grassland.

Drought is also a stressor to the dry forests and is not uncommon in the Hawaiian islands. Drought is a cyclical weather phenomenon that is beyond human control. Between 1860 and 2016, there have been 38 periods of Statewide drought (Giambelluca et al., 1991; One World One Water, LLC, 2017). The most severe drought events over the past 15 years were associated with the El Niño phenomenon (Hawai'i State Civil Defense, 2011). Drought also leads to an increase in the number of forest and brush fires (Giambelluca et al., 1991), causing a reduction of native plant cover (D'Antonio and Vitousek, 1992) and a reduction in availability of host plants for invertebrates and other fauna. In addition, the increased risk for wildfires associated with drought brings the increased potential for all of its aforementioned impacts.

Natural disasters

In addition to their direct effects on plants, hurricanes exacerbate the impacts from other threats such as habitat modification and destruction by ungulates and competition with nonnative plants. By destroying vegetation, hurricanes open the forest canopy, thus modifying the availability of light, and create disturbed areas conducive to invasion by nonnative pest species (Asner and Goldstein, 1997; Harrington et al., 1997).

Climate change

Changes in environmental conditions that may result from global climate change include increasing temperatures, changing precipitation, and increasing storm intensities and frequencies. These changes may lead to the loss of native species due to direct physiological stress, the loss or alteration of habitat, or changes in disturbance regimes (e.g., droughts, fire, storms, and hurricanes). In a recent assessment of vulnerability to climate change, native Hawaiian plant species found primarily in dry forests were found to have higher vulnerability scores than species from any other habitat type (Fortini et al., 2013).

Agriculture and urban development

The consequences of past land use practices such as agricultural or urban development have resulted in little or no native vegetation below 600 m (2,000 ft) throughout the Hawaiian islands (TNCH, 2007), largely impacting the coastal and lowland dry ecosystems, including lowland dry forests. Although agriculture has been declining in importance, large tracts of former agricultural lands are being converted into residential areas or left fallow (TNCH, 2007). In addition, the population in Hawai'i has increased almost 10% in the past 10 years, further increasing demands on limited land and water resources on the islands (HDBEDT, 2013).

Conservation Efforts

Impacts from stressors are addressed through various management approaches such as active (on-the-ground) management (i.e., predator and invasive species control, fencing, reintroduction, etc.), land protections, laws and regulations, and education and outreach. These approaches are implemented by numerous government agencies (federal and state), private organizations, and nongovernmental organizations (NGOs). Given that land ownership of dry forest is spread among these parties (Fig. 8),

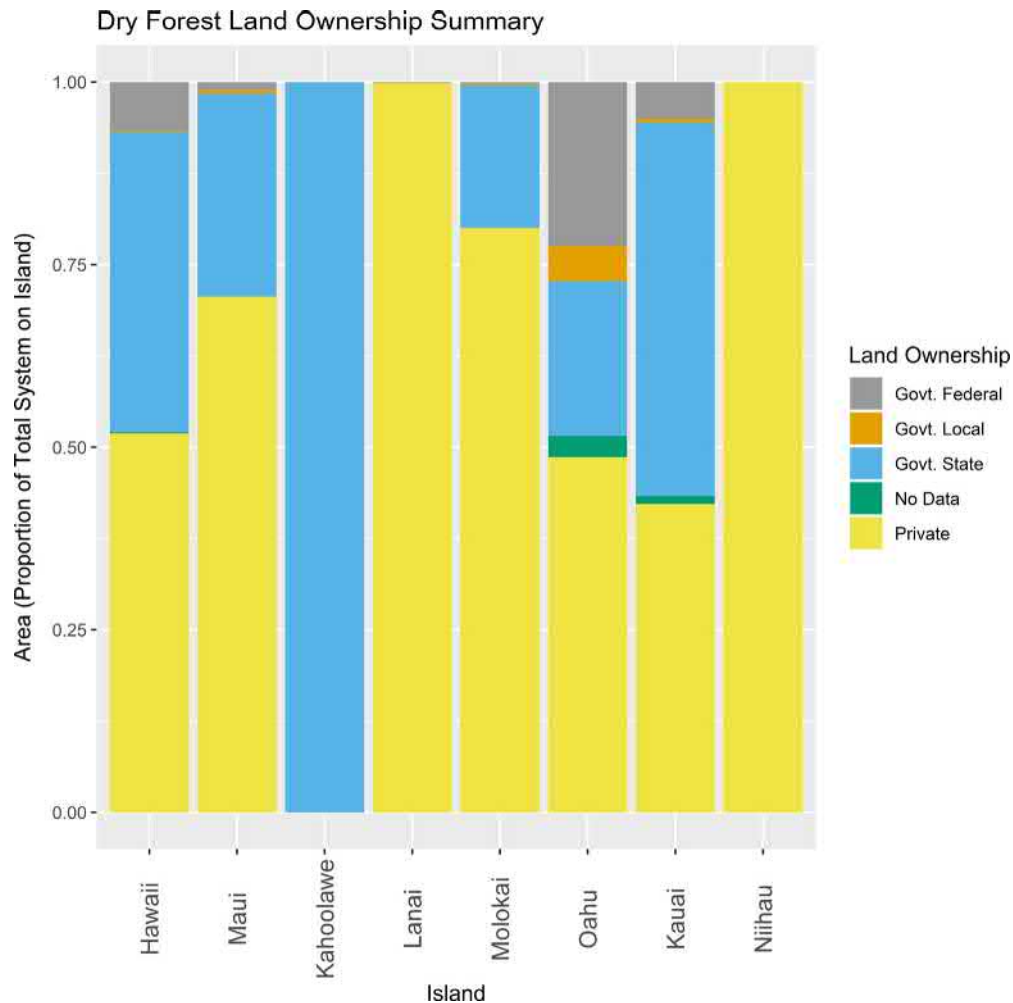


Fig. 8 Land ownership of dry forests in the main Hawaiian islands. Word from Reeves, M. K., and Amidon, F. (2018). Habitat status assessment methods—Hawai'i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439.

partnerships are also formed to manage the forest collectively. The following subsections detail many of the conservation efforts related to dry forests, however they do not encompass all that exist.

Federal

Endangered Species Act

The Endangered Species Act of 1973 (ESA) aims to provide a framework to conserve and protect endangered and threatened species and their habitats. As habitat loss is the primary threat to most imperiled species, the ESA allowed the US Fish and Wildlife Service (USFWS) and National Marine Fisheries Service (NMFS) to designate specific areas as critical habitat zones. In 1978, Congress amended the law to make critical habitat designation a mandatory requirement for all threatened and endangered species.

Approximately 13,098 ha (32,365 ac) of dry forests have been designated as federal critical habitat for 237 threatened and endangered species in the main Hawaiian islands (Fig. 9; Table 3). The majority of designated critical habitat that is also classified as dry forest is located on the island of Hawai'i at 8378 ha (20,702 ac) (Fig. 9). Species listed under the ESA are automatically added to the State of Hawai'i list of endangered species, and are thus also protected by State regulations.

Approximately 3821 ha (9442 ac) or 38% of dry forests are protected in reserve areas across the main Hawaiian islands (Fig. 10). Reserve areas are defined as those designated as parks and reserves. These may include areas designated as a national park, national wildlife refuge, NAR, or Nature Conservancy preserve (Reeves and Amidon, 2018). The amount of dry forest protected in reserve areas varies by island, with 2967 ha (7366 ac) or <5% on the island of Hawai'i to 31 ha (76 ac) or <5% on Kaua'i (Fig. 10). Of those 2967 ha (7366 ac) protected in reserves areas on the island of Hawai'i roughly 2716 ha (6711 ac) or <1% are classified as native dominated ecotype (Fig. 10). Ni'ihau and Kaho'olawe contain the least amount of dry forest protected in reserve areas in the State with <2 ha (4 ac) each or <4% (Fig. 10). Knowing that <3821 ha (9442 ac) of dry forests are protected in reserve areas in

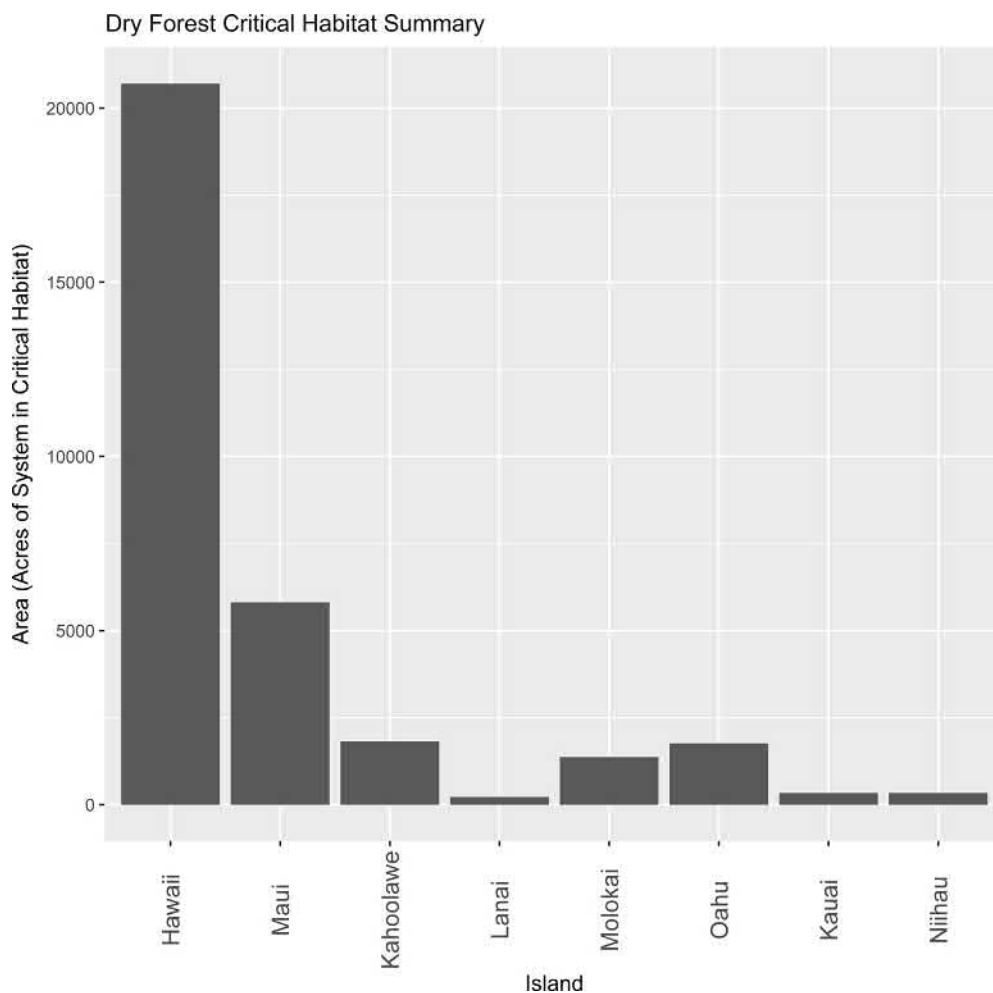


Fig. 9 Federally designated critical habitat in dry forests across the main Hawaiian islands. Word from Reeves, M. K., and Amidon, F. (2018). Habitat status assessment methods—Hawai'i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439.

Table 3 Record of federally listed threatened and endangered species with designated critical habitat in the dry forests of the main Hawaiian islands (USFWS, 1977, 1983, 1984, 2001, 2003a,b,c, 2012, 2016b, 2018).

Island(s) designation	Scientific name	Current federal register name	Endangered species act status	Species group
O'ahu	<i>Abutilon sandwicense</i>	<i>Abutilon sandwicense</i>	Endangered	Plant
Maui	<i>Acaena exigua</i>	<i>Acaena exigua</i>	Endangered	Plant
Hawai'i	<i>Achyranthes mutica</i>	<i>Achyranthes mutica</i>	Endangered	Plant
O'ahu	<i>Achyranthes splendens</i> var. <i>rotundata</i>	<i>Achyranthes splendens</i> var. <i>rotundata</i>	Endangered	Plant
Kaua'i	<i>Adelocosa anops</i>	<i>Adelocosa anops</i>	Endangered	Invertebrate
Hawai'i, Maui, Moloka'i	<i>Adenophorus periens</i>	<i>Adenophorus periens</i>	Endangered	Plant
Maui, Moloka'i, O'ahu	<i>Alectryon macrococcus</i> var. <i>macrococcus</i>	<i>Alectryon macrococcus</i>	Threatened	Plant
Hawai'i	<i>Argyroxiphium kauense</i>	<i>Argyroxiphium kauense</i>	Endangered	Plant
Maui	<i>Argyroxiphium sandwicense</i> ssp. <i>macrocephalum</i>	<i>Argyroxiphium sandwicense</i> ssp. <i>macrocephalum</i>	Endangered	Plant
Maui, Moloka'i, O'ahu	<i>Asplenium dielirectum</i>	<i>Asplenium dielirectum</i>	Endangered	Plant
O'ahu	<i>Asplenium dielfalcatum</i>	<i>Asplenium dielfalcatum</i>	Endangered	Plant
Hawai'i, Maui	<i>Asplenium peruvianum</i> var. <i>insulare</i>	<i>Asplenium peruvianum</i> var. <i>insulare</i>	Endangered	Plant
O'ahu	<i>Asplenium unisorum</i>	<i>Asplenium unisorum</i>	Endangered	Plant
O'ahu	<i>Bidens amplexens</i>	<i>Bidens amplexens</i>	Endangered	Plant
Maui	<i>Bidens campylothea</i> ssp. <i>pentamera</i>	<i>Bidens campylothea</i> ssp. <i>pentamera</i>	Endangered	Plant
Maui	<i>Bidens campylothea</i> ssp. <i>waihoiensis</i>	<i>Bidens campylothea</i> ssp. <i>waihoiensis</i>	Endangered	Plant
Maui	<i>Bidens conjuncta</i>	<i>Bidens conjuncta</i>	Endangered	Plant
Hawai'i	<i>Bidens micrantha</i> ssp. <i>ctenophylla</i>	<i>Bidens micrantha</i> ssp. <i>ctenophylla</i>	Endangered	Plant
Maui	<i>Bidens micrantha</i> ssp. <i>kalealaha</i>	<i>Bidens micrantha</i> ssp. <i>kalealaha</i>	Endangered	Plant
Moloka'i	<i>Bidens wiebkei</i>	<i>Bidens wiebkei</i>	Endangered	Plant
Hawai'i, Maui, Moloka'i, O'ahu	<i>Bonamia menziesii</i>	<i>Bonamia menziesii</i>	Endangered	Plant
Maui, Moloka'i	<i>Brighamia rockii</i>	<i>Brighamia rockii</i>	Endangered	Plant
Maui	<i>Calamagrostis hillebrandii</i>	<i>Calamagrostis hillebrandii</i>	Endangered	Plant
Moloka'i	<i>Canavalia molokaiensis</i>	<i>Canavalia molokaiensis</i>	Endangered	Plant
Maui	<i>Canavalia pubescens</i>	<i>Canavalia pubescens</i>	Endangered	Plant
Hawai'i, Mui, O'ahu	<i>Cenchrus agrimonoides</i>	<i>Cenchrus agrimonoides</i>	Endangered	Plant
O'ahu	<i>Chasiempis ibidis</i>	<i>Chasiempis ibidis</i>	Endangered	Vertebrate
O'ahu	<i>Chrysodracon forbesii</i>	<i>Pleomele forbesii</i>	Endangered	Plant
Hawai'i	<i>Chrysodracon hawaiiensis</i>	<i>Pleomele hawaiiensis</i>	Endangered	Plant
Hawai'i	<i>Clermontia drepanomorpha</i>	<i>Clermontia drepanomorpha</i>	Endangered	Plant
Hawai'i, Maui	<i>Clermontia lindseyana</i>	<i>Clermontia lindseyana</i>	Endangered	Plant
Moloka'i	<i>Clermontia oblongifolia</i> ssp. <i>brevipes</i>	<i>Clermontia oblongifolia</i> ssp. <i>brevipes</i>	Endangered	Plant
Maui	<i>Clermontia oblongifolia</i> ssp. <i>mauiensis</i>	<i>Clermontia oblongifolia</i> ssp. <i>mauiensis</i>	Endangered	Plant
Hawai'i	<i>Clermontia peleana</i>	<i>Clermontia peleana</i>	Endangered	Plant
Maui	<i>Clermontia peleana</i> ssp. <i>singuliflora</i>	<i>Clermontia peleana</i>	Endangered	Plant
Hawai'i	<i>Clermontia pyrularia</i>	<i>Clermontia pyrularia</i>	Endangered	Plant
Maui	<i>Clermontia samuelii</i> ssp. <i>samuelii</i>	<i>Clermontia samuelii</i>	Endangered	Plant
Hawai'i, Maui, O'ahu	<i>Colubrina oppositifolia</i>	<i>Colubrina oppositifolia</i>	Endangered	Plant
Hawai'i, Maui, Moloka'i, O'ahu	<i>Ctenitis squamigera</i>	<i>Ctenitis squamigera</i>	Endangered	Plant
O'ahu	<i>Cyanea acuminata</i>	<i>Cyanea acuminata</i>	Endangered	Plant
Maui	<i>Cyanea asplenifolia</i>	<i>Cyanea asplenifolia</i>	Endangered	Plant
O'ahu	<i>Cyanea calycina</i>	<i>Cyanea calycina</i>	Endangered	Plant
Hawai'i	<i>Cyanea copelandii</i> ssp. <i>copelandii</i>	<i>Cyanea copelandii</i> ssp. <i>copelandii</i>	Endangered	Plant
Maui	<i>Cyanea copelandii</i> ssp. <i>haleakalaensis</i>	<i>Cyanea copelandii</i> ssp. <i>haleakalaensis</i>	Endangered	Plant
O'ahu	<i>Cyanea crispa</i>	<i>Cyanea crispa</i>	Endangered	Plant
Moloka'i	<i>Cyanea dunbariae</i>	<i>Cyanea dunbariae</i>	Endangered	Plant
Maui	<i>Cyanea duvalliorum</i>	<i>Cyanea duvalliorum</i>	Endangered	Plant
Maui	<i>Cyanea glabra</i>	<i>Cyanea glabra</i>	Endangered	Plant
Moloka'i, O'ahu	<i>Cyanea grimesiana</i> ssp. <i>grimesiana</i>	<i>Cyanea grimesiana</i> ssp. <i>grimesiana</i>	Endangered	Plant
O'ahu	<i>Cyanea grimesiana</i> ssp. <i>obatae</i>	<i>Cyanea grimesiana</i> ssp. <i>obatae</i>	Endangered	Plant
Hawai'i	<i>Cyanea hamatiflora</i> ssp. <i>carlsonii</i>	<i>Cyanea hamatiflora</i> ssp. <i>carlsonii</i>	Endangered	Plant
Maui	<i>Cyanea hamatiflora</i> ssp. <i>hamatiflora</i>	<i>Cyanea hamatiflora</i> ssp. <i>hamatiflora</i>	Endangered	Plant
Maui	<i>Cyanea horrida</i>	<i>Cyanea horrida</i>	Endangered	Plant
Maui	<i>Cyanea kunthiana</i>	<i>Cyanea kunthiana</i>	Endangered	Plant
O'ahu	<i>Cyanea lanceolata</i>	<i>Cyanea lanceolata</i>	Endangered	Plant
Maui	<i>Cyanea lobata</i> ssp. <i>lobata</i>	<i>Cyanea lobata</i>	Endangered	Plant
O'ahu	<i>Cyanea longiflora</i>	<i>Cyanea longiflora</i>	Endangered	Plant

Table 3 Record of federally listed threatened and endangered species with designated critical habitat in the dry forests of the main Hawaiian islands (USFWS, 1977, 1983, 1984, 2001, 2003a,b,c, 2012, 2016b, 2018).—cont'd

<i>Island(s) designation</i>	<i>Scientific name</i>	<i>Current federal register name</i>	<i>Endangered species act status</i>	<i>Species group</i>
Maui	<i>Cyanea magnicalyx</i>	<i>Cyanea magnicalyx</i>	Endangered	Plant
Moloka'i	<i>Cyanea mannii</i>	<i>Cyanea mannii</i>	Endangered	Plant
Maui	<i>Cyanea maritae</i>	<i>Cyanea maritae</i>	Endangered	Plant
Maui	<i>Cyanea mceldowneyi</i>	<i>Cyanea mceldowneyi</i>	Endangered	Plant
Moloka'i	<i>Cyanea munroi</i>	<i>Cyanea munroi</i>	Endangered	Plant
Maui	<i>Cyanea obtusa</i>	<i>Cyanea obtusa</i>	Endangered	Plant
O'ahu	<i>Cyanea pinnatifida</i>	<i>Cyanea pinnatifida</i>	Endangered	Plant
Hawai'i	<i>Cyanea platyphylla</i>	<i>Cyanea platyphylla</i>	Endangered	Plant
Moloka'i	<i>Cyanea procera</i>	<i>Cyanea procera</i>	Endangered	Plant
Moloka'i	<i>Cyanea profuga</i>	<i>Cyanea profuga</i>	Endangered	Plant
Hawai'i	<i>Cyanea shipmanii</i>	<i>Cyanea shipmanii</i>	Endangered	Plant
Moloka'i	<i>Cyanea solanacea</i>	<i>Cyanea solanacea</i>	Endangered	Plant
Hawai'i	<i>Cyanea stictophylla</i>	<i>Cyanea stictophylla</i>	Endangered	Plant
O'ahu	<i>Cyanea superba</i> ssp. <i>superba</i>	<i>Cyanea superba</i>	Endangered	Plant
O'ahu	<i>Cyanea truncata</i>	<i>Cyanea truncata</i>	Endangered	Plant
Hawai'i, Moloka'i	<i>Cyperus fauriei</i>	<i>Cyperus fauriei</i>	Endangered	Plant
Hawai'i, Maui, O'ahu	<i>Cyperus pennatifolius</i> var. <i>pennatifolius</i>	<i>Cyperus pennatifolius</i>	Endangered	Plant
Moloka'i, O'ahu	<i>Cyperus trachysanthos</i>	<i>Cyperus trachysanthos</i>	Endangered	Plant
O'ahu	<i>Cyrtandra dentata</i>	<i>Cyrtandra dentata</i>	Endangered	Plant
Maui	<i>Cyrtandra ferripilosa</i>	<i>Cyrtandra ferripilosa</i>	Endangered	Plant
Maui, Moloka'i	<i>Cyrtandra filipes</i>	<i>Cyrtandra filipes</i>	Endangered	Plant
Hawai'i	<i>Cyrtandra giffardii</i>	<i>Cyrtandra giffardii</i>	Endangered	Plant
Maui	<i>Cyrtandra munroi</i>	<i>Cyrtandra munroi</i>	Endangered	Plant
Maui	<i>Cyrtandra oxybapha</i>	<i>Cyrtandra oxybapha</i>	Endangered	Plant
O'ahu	<i>Cyrtandra polyantha</i>	<i>Cyrtandra polyantha</i>	Endangered	Plant
Hawai'i	<i>Cyrtandra tintinnabula</i>	<i>Cyrtandra tintinnabula</i>	Endangered	Plant
O'ahu	<i>Delissea subcordata</i>	<i>Delissea subcordata</i>	Endangered	Plant
Hawai'i	<i>Delissea undulata</i>	<i>Delissea undulata</i>	Endangered	Plant
Maui, Moloka'i	<i>Diplazium molokaiense</i>	<i>Diplazium molokaiense</i>	Endangered	Plant
O'ahu	<i>Doryopteris takeuchii</i>	<i>Doryopteris takeuchii</i>	Endangered	Plant
O'ahu	<i>Dubautia herbstobatae</i>	<i>Dubautia herbstobatae</i>	Endangered	Plant
Maui	<i>Dubautia plantaginea</i> ssp. <i>humilis</i>	<i>Dubautia plantaginea</i> ssp. <i>humilis</i>	Endangered	Plant
O'ahu	<i>Eragrostis fosbergii</i>	<i>Eragrostis fosbergii</i>	Endangered	Plant
Moloka'i, O'ahu	<i>Eugenia koolauensis</i>	<i>Eugenia koolauensis</i>	Endangered	Plant
O'ahu	<i>Euphorbia celastroides</i> var. <i>kaenana</i>	<i>Euphorbia celastroides</i> var. <i>kaenana</i>	Endangered	Plant
O'ahu	<i>Euphorbia haelealeana</i>	<i>Euphorbia haelealeana</i>	Endangered	Plant
O'ahu	<i>Euphorbia herbstii</i>	<i>Euphorbia herbstii</i>	Endangered	Plant
O'ahu	<i>Euphorbia kuwaleana</i>	<i>Euphorbia kuwaleana</i>	Endangered	Plant
O'ahu	<i>Euphorbia skottsbergii</i> var. <i>skottsbergii</i>	<i>Euphorbia skottsbergii</i> var. <i>skottsbergii</i>	Endangered	Plant
Moloka'i	<i>Festuca molokaiensis</i>	<i>Festuca molokaiensis</i>	Endangered	Plant
Hawai'i, Maui, Moloka'i, O'ahu	<i>Flueggea neowawraea</i>	<i>Flueggea neowawraea</i>	Endangered	Plant
O'ahu	<i>Gardenia mannii</i>	<i>Gardenia mannii</i>	Endangered	Plant
Maui	<i>Geranium arboreum</i>	<i>Geranium arboreum</i>	Endangered	Plant
Maui	<i>Geranium hanaense</i>	<i>Geranium hanaense</i>	Endangered	Plant
Maui	<i>Geranium hillebrandii</i>	<i>Geranium hillebrandii</i>	Endangered	Plant
Maui	<i>Geranium multiflorum</i>	<i>Geranium multiflorum</i>	Endangered	Plant
Kaho'olawe, Maui, Moloka'i	<i>Gouania hillebrandii</i>	<i>Gouania hillebrandii</i>	Endangered	Plant
O'ahu	<i>Gouania meyenii</i>	<i>Gouania meyenii</i>	Endangered	Plant
Hawai'i, Maui, O'ahu	<i>Gouania vitifolia</i>	<i>Gouania vitifolia</i>	Endangered	Plant
Maui, Moloka'i, O'ahu	<i>Hesperomannia arborescens</i>	<i>Hesperomannia arborescens</i>	Endangered	Plant
Maui, O'ahu	<i>Hesperomannia arbuscula</i>	<i>Hesperomannia arbuscula</i>	Endangered	Plant
Hawai'i	<i>Hibiscadelphus hualalaiensis</i>	<i>Hibiscadelphus hualalaiensis</i>	Endangered	Plant
Moloka'i	<i>Hibiscus arnottianus</i> ssp. <i>immaculatus</i>	<i>Hibiscus arnottianus</i> ssp. <i>immaculatus</i>	Endangered	Plant
Hawai'i, Kaho'olawe, Maui, Moloka'i	<i>Hibiscus brackenridgei</i> ssp. <i>brackenridgei</i>	<i>Hibiscus brackenridgei</i>	Endangered	Plant
O'ahu	<i>Hibiscus brackenridgei</i> ssp. <i>mokuleianus</i>	<i>Hibiscus brackenridgei</i>	Endangered	Plant
Hawai'i, Maui	<i>Huperzia mannii</i>	<i>Huperzia mannii</i>	Endangered	Plant
Hawai'i	<i>Huperzia nutans</i>	<i>Huperzia nutans</i>	Endangered	Plant

(Continued)

Table 3 Record of federally listed threatened and endangered species with designated critical habitat in the dry forests of the main Hawaiian islands (USFWS, 1977, 1983, 1984, 2001, 2003a,b,c, 2012, 2016b, 2018).—cont'd

<i>Island(s) designation</i>	<i>Scientific name</i>	<i>Current federal register name</i>	<i>Endangered species act status</i>	<i>Species group</i>
Hawai'i, Maui, Moloka'i	<i>Ischaemum byrone</i>	<i>Ischaemum byrone</i>	Endangered	Plant
Hawai'i	<i>Isodendron hosakae</i>	<i>Isodendron hosakae</i>	Endangered	Plant
O'ahu	<i>Isodendron laurifolium</i>	<i>Isodendron laurifolium</i>	Endangered	Plant
O'ahu	<i>Isodendron longifolium</i>	<i>Isodendron longifolium</i>	Threatened	Plant
Hawai'i, Maui, Moloka'i, O'ahu	<i>Isodendron pyrifolium</i>	<i>Isodendron pyrifolium</i>	Endangered	Plant
Hawai'i	<i>Kadua cookiana</i>	<i>Kadua cookiana</i>	Endangered	Plant
Hawai'i, Maui, O'ahu	<i>Kadua coriacea</i>	<i>Kadua coriacea</i>	Endangered	Plant
O'ahu	<i>Kadua degeneri</i>	<i>Kadua degeneri</i>	Endangered	Plant
Maui, Moloka'i	<i>Kadua laxiflora</i>	<i>Kadua laxiflora</i>	Endangered	Plant
O'ahu	<i>Kadua parvula</i>	<i>Kadua parvula</i>	Endangered	Plant
Kaho'olawe	<i>Kanaloa kahoolawensis</i>	<i>Kanaloa kahoolawensis</i>	Endangered	Plant
Moloka'i	<i>Kokia cookei</i>	<i>Kokia cookei</i>	Endangered	Plant
Hawai'i	<i>Kokia drynarioides</i>	<i>Kokia drynarioides</i>	Endangered	Plant
O'ahu	<i>Korthalsella degeneri</i>	<i>Korthalsella degeneri</i>	Endangered	Plant
O'ahu	<i>Labordia cyrtandrae</i>	<i>Labordia cyrtandrae</i>	Endangered	Plant
Moloka'i	<i>Labordia triflora</i>	<i>Labordia triflora</i>	Endangered	Plant
O'ahu	<i>Lepidium arbuscula</i>	<i>Lepidium arbuscula</i>	Endangered	Plant
Maui	<i>Lipochaeta kamolensis</i>	<i>Melanthera kamolensis</i>	Endangered	Plant
O'ahu	<i>Lipochaeta lobata</i> var. <i>leptophylla</i>	<i>Lipochaeta lobata</i> var. <i>leptophylla</i>	Endangered	Plant
O'ahu	<i>Lipochaeta tenuifolia</i>	<i>Melanthera tenuifolia</i>	Endangered	Plant
O'ahu	<i>Lobelia monostachya</i>	<i>Lobelia monostachya</i>	Endangered	Plant
O'ahu	<i>Lobelia niihauensis</i>	<i>Lobelia niihauensis</i>	Endangered	Plant
Hawai'i	<i>Loxioides bailleui</i>	<i>Loxioides bailleui</i>	Endangered	Vertebrate
Maui	<i>Lysimachia lydgatei</i>	<i>Lysimachia lydgatei</i>	Endangered	Plant
Moloka'i	<i>Lysimachia maxima</i>	<i>Lysimachia maxima</i>	Endangered	Plant
Hawai'i, Kaho'olawe, Maui, Moloka'i	<i>Manduca blackburni</i>	<i>Manduca blackburni</i>	Endangered	Invertebrate
Moloka'i, O'ahu	<i>Marsilea villosa</i>	<i>Marsilea villosa</i>	Endangered	Plant
O'ahu	<i>Megalagrion oceanicum</i>	<i>Megalagrion oceanicum</i>	Endangered	Invertebrate
Maui	<i>Melicope adscendens</i>	<i>Melicope adscendens</i>	Endangered	Plant
Maui	<i>Melicope balloui</i>	<i>Melicope balloui</i>	Endangered	Plant
Maui	<i>Melicope knudsenii</i>	<i>Melicope knudsenii</i>	Endangered	Plant
O'ahu	<i>Melicope lydgatei</i>	<i>Melicope lydgatei</i>	Endangered	Plant
O'ahu	<i>Melicope makahae</i>	<i>Melicope makahae</i>	Endangered	Plant
Maui, Moloka'i	<i>Melicope mucronulata</i>	<i>Melicope mucronulata</i>	Endangered	Plant
Moloka'i	<i>Melicope munroi</i>	<i>Melicope munroi</i>	Endangered	Plant
Maui	<i>Melicope ovalis</i>	<i>Melicope ovalis</i>	Endangered	Plant
O'ahu	<i>Melicope pallida</i>	<i>Melicope pallida</i>	Endangered	Plant
Moloka'i	<i>Melicope reflexa</i>	<i>Melicope reflexa</i>	Endangered	Plant
O'ahu	<i>Melicope saint-johnii</i>	<i>Melicope saint-johnii</i>	Endangered	Plant
Hawai'i	<i>Melicope zahlbruckneri</i>	<i>Melicope zahlbruckneri</i>	Endangered	Plant
Hawai'i	<i>Mezoneuron kavaense</i>	<i>Mezoneuron kavaense</i>	Endangered	Plant
Maui	<i>Mucuna sloanei</i> var. <i>persericea</i>	<i>Mucuna sloanei</i> var. <i>persericea</i>	Endangered	Plant
Maui	<i>Myrsine vaccinioides</i>	<i>Myrsine vaccinioides</i>	Endangered	Plant
O'ahu	<i>Neraudia angulata</i> var. <i>angulata</i>	<i>Neraudia angulata</i>	Endangered	Plant
Hawai'i	<i>Neraudia ovata</i>	<i>Neraudia ovata</i>	Endangered	Plant
Kaho'olawe, Maui, Moloka'i	<i>Neraudia sericea</i>	<i>Neraudia sericea</i>	Endangered	Plant
Maui	<i>Newcombia cumingi</i>	<i>Newcombia cumingi</i>	Endangered	Invertebrate
Hawai'i	<i>Nothoctrum breviflorum</i>	<i>Nothoctrum breviflorum</i>	Endangered	Plant
Maui, O'ahu	<i>Nototrichium humile</i>	<i>Nototrichium humile</i>	Endangered	Plant
Hawai'i	<i>Ochrosia kilaueaensis</i>	<i>Ochrosia kilaueaensis</i>	Endangered	Plant
Maui, Moloka'i	<i>Palmeria dolei</i>	<i>Palmeria dolei</i>	Endangered	Vertebrate
Hawai'i	<i>Panicum fauriei</i> var. <i>carteri</i>	<i>Panicum fauriei</i> var. <i>carteri</i>	Endangered	Plant
Maui	<i>Peperomia subpetiolata</i>	<i>Peperomia subpetiolata</i>	Endangered	Plant
Maui, Moloka'i, O'ahu	<i>Peucedanum sandwicense</i>	<i>Peucedanum sandwicense</i>	Threatened	Plant
Maui	<i>Phyllostegia bracteata</i>	<i>Phyllostegia bracteata</i>	Endangered	Plant
Maui, Moloka'i	<i>Phyllostegia haliakalae</i>	<i>Phyllostegia haliakalae</i>	Endangered	Plant
O'ahu	<i>Phyllostegia hirsuta</i>	<i>Phyllostegia hirsuta</i>	Endangered	Plant

Table 3 Record of federally listed threatened and endangered species with designated critical habitat in the dry forests of the main Hawaiian islands (USFWS, 1977, 1983, 1984, 2001, 2003a,b,c, 2012, 2016b, 2018).—cont'd

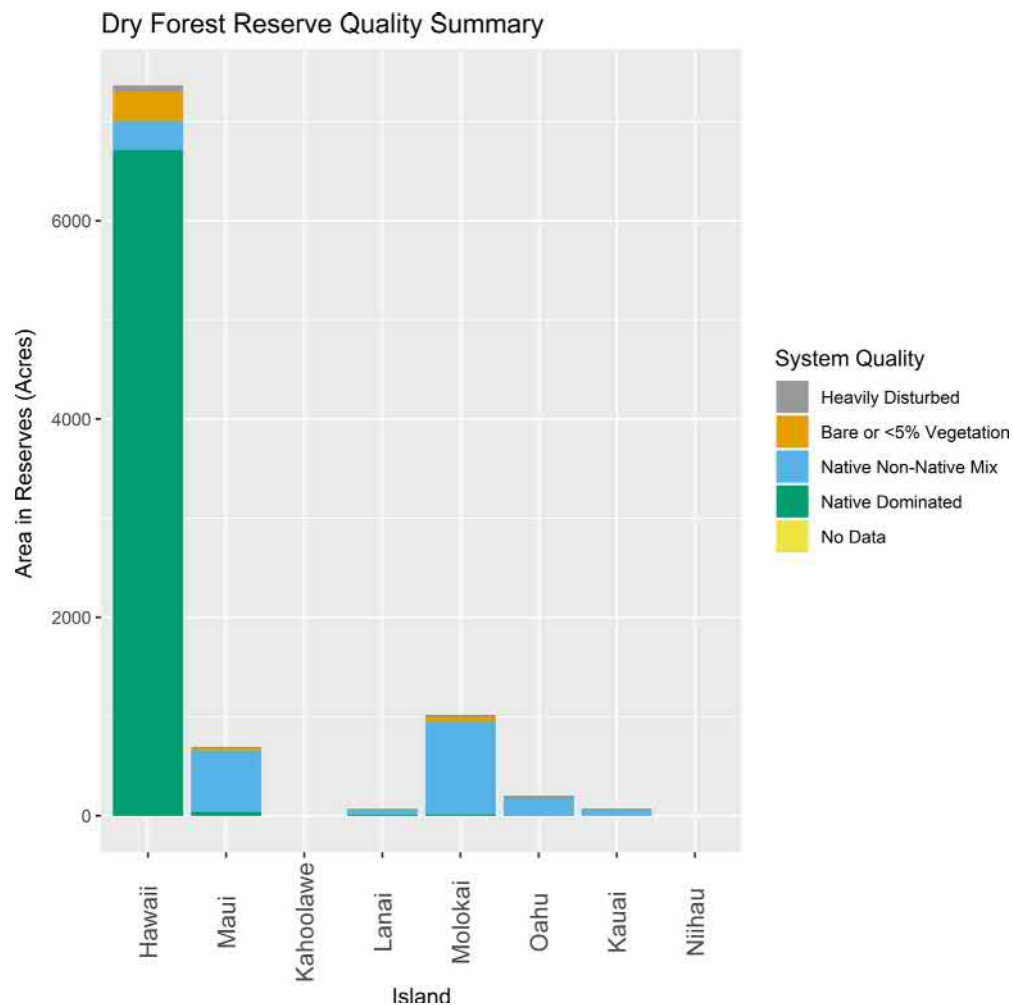
<i>Island(s) designation</i>	<i>Scientific name</i>	<i>Current federal register name</i>	<i>Endangered species act status</i>	<i>Species group</i>
Moloka'i	<i>Phyllostegia hispida</i>	<i>Phyllostegia hispida</i>	Endangered	Plant
O'ahu	<i>Phyllostegia kaalaensis</i>	<i>Phyllostegia kaalaensis</i>	Endangered	Plant
Maui, Moloka'i	<i>Phyllostegia mannii</i>	<i>Phyllostegia mannii</i>	Endangered	Plant
O'ahu	<i>Phyllostegia mollis</i>	<i>Phyllostegia mollis</i>	Endangered	Plant
O'ahu	<i>Phyllostegia parviflora</i> var. <i>parviflora</i>	<i>Phyllostegia parviflora</i>	Endangered	Plant
Maui, Moloka'i	<i>Phyllostegia pilosa</i>	<i>Phyllostegia pilosa</i>	Endangered	Plant
Hawai'i	<i>Phyllostegia racemosa</i>	<i>Phyllostegia racemosa</i>	Endangered	Plant
Hawai'i	<i>Phyllostegia velutina</i>	<i>Phyllostegia velutina</i>	Endangered	Plant
Hawai'i	<i>Phyllostegia warshaueri</i>	<i>Phyllostegia warshaueri</i>	Endangered	Plant
Moloka'i	<i>Pittosporum halophilum</i>	<i>Pittosporum halophilum</i>	Endangered	Plant
Hawai'i	<i>Plantago hawaiiensis</i>	<i>Plantago hawaiiensis</i>	Endangered	Plant
O'ahu	<i>Plantago princeps</i> var. <i>anomala</i>	<i>Plantago princeps</i>	Endangered	Plant
Maui, Moloka'i	<i>Plantago princeps</i> var. <i>laxiflora</i>	<i>Plantago princeps</i>	Endangered	Plant
O'ahu	<i>Plantago princeps</i> var. <i>princeps</i>	<i>Plantago princeps</i>	Endangered	Plant
Maui, Moloka'i	<i>Platanthera holochila</i>	<i>Platanthera holochila</i>	Endangered	Plant
O'ahu	<i>Platydesma cornuta</i> var. <i>decurrens</i>	<i>Platydesma cornuta</i> var. <i>decurrens</i>	Endangered	Plant
O'ahu	<i>Polyscias gymnocarpa</i>	<i>Polyscias gymnocarpa</i>	Endangered	Plant
O'ahu	<i>Polyscias lydgatei</i>	<i>Polyscias lydgatei</i>	Endangered	Plant
Hawai'i	<i>Portulaca sclerocarpa</i>	<i>Portulaca sclerocarpa</i>	Endangered	Plant
Hawai'i	<i>Pritchardia maideniana</i>	<i>Pritchardia maideniana</i>	Endangered	Plant
Hawai'i	<i>Pritchardia schattaueri</i>	<i>Pritchardia schattaueri</i>	Endangered	Plant
Maui, Moloka'i	<i>Pseudonestor xanthophrys</i>	<i>Pseudonestor xanthophrys</i>	Endangered	Vertebrate
O'ahu	<i>Pteralyxia macrocarpa</i>	<i>Pteralyxia macrocarpa</i>	Endangered	Plant
Maui, Moloka'i	<i>Pteris lidgatei</i>	<i>Pteris lidgatei</i>	Endangered	Plant
Maui	<i>Remya mauiensis</i>	<i>Remya mauiensis</i>	Endangered	Plant
O'ahu	<i>Sanicula marivera</i>	<i>Sanicula marivera</i>	Endangered	Plant
Maui	<i>Sanicula purpurea</i>	<i>Sanicula purpurea</i>	Endangered	Plant
Maui, Moloka'i	<i>Santalum haleakalae</i> var. <i>lanaiense</i>	<i>Santalum haleakalae</i> var. <i>lanaiense</i>	Endangered	Plant
Maui, Moloka'i, O'ahu	<i>Schenkia sebaeoides</i>	<i>Schenkia sebaeoides</i>	Endangered	Plant
Maui	<i>Schiedea haleakalensis</i>	<i>Schiedea haleakalensis</i>	Endangered	Plant
O'ahu	<i>Schiedea hookeri</i>	<i>Schiedea hookeri</i>	Endangered	Plant
Maui	<i>Schiedea jacobii</i>	<i>Schiedea jacobii</i>	Endangered	Plant
O'ahu	<i>Schiedea kaalae</i>	<i>Schiedea kaalae</i>	Endangered	Plant
O'ahu	<i>Schiedea kealiae</i>	<i>Schiedea kealiae</i>	Endangered	Plant
Moloka'i	<i>Schiedea laui</i>	<i>Schiedea laui</i>	Endangered	Plant
Moloka'i	<i>Schiedea lydgatei</i>	<i>Schiedea lydgatei</i>	Endangered	Plant
O'ahu	<i>Schiedea nuttallii</i>	<i>Schiedea nuttallii</i>	Endangered	Plant
O'ahu	<i>Schiedea obovata</i>	<i>Schiedea obovata</i>	Endangered	Plant
Maui	<i>Schiedea salicaria</i>	<i>Schiedea salicaria</i>	Endangered	Plant
Moloka'i	<i>Schiedea sarmentosa</i>	<i>Schiedea sarmentosa</i>	Endangered	Plant
O'ahu	<i>Schiedea trinervis</i>	<i>Schiedea trinervis</i>	Endangered	Plant
Hawai'i, Kaho'olawe, Maui, Moloka'i, O'ahu	<i>Sesbania tomentosa</i>	<i>Sesbania tomentosa</i>	Endangered	Plant
Hawai'i	<i>Sicyos albus</i>	<i>Sicyos albus</i>	Endangered	Plant
Moloka'i	<i>Silene alexandri</i>	<i>Silene alexandri</i>	Endangered	Plant
Hawai'i	<i>Silene hawaiiensis</i>	<i>Silene hawaiiensis</i>	Threatened	Plant
Hawai'i, Moloka'i, O'ahu	<i>Silene lanceolata</i>	<i>Silene lanceolata</i>	Endangered	Plant
O'ahu	<i>Silene perlmanii</i>	<i>Silene perlmanii</i>	Endangered	Plant
Hawai'i, Maui	<i>Solanum incompletum</i>	<i>Solanum incompletum</i>	Endangered	Plant
O'ahu	<i>Solanum sandwicense</i>	<i>Solanum sandwicense</i>	Endangered	Plant
Kaua'i	<i>Spelaorchestia koloana</i>	<i>Spelaorchestia koloana</i>	Endangered	Invertebrate
Hawai'i, Maui, Moloka'i, O'ahu	<i>Spermolepis hawaiiensis</i>	<i>Spermolepis hawaiiensis</i>	Endangered	Plant
Moloka'i	<i>Stenogyne bifida</i>	<i>Stenogyne bifida</i>	Endangered	Plant
O'ahu	<i>Stenogyne kanehoana</i>	<i>Stenogyne kanehoana</i>	Endangered	Plant
Maui	<i>Stenogyne kauaulaensis</i>	<i>Stenogyne kauaulaensis</i>	Endangered	Plant
Hawai'i	<i>Tetramolopium arenarium</i>	<i>Tetramolopium arenarium</i>	Endangered	Plant
Maui	<i>Tetramolopium capillare</i>	<i>Tetramolopium capillare</i>	Endangered	Plant
O'ahu	<i>Tetramolopium filiforme</i> var. <i>filiforme</i>	<i>Tetramolopium filiforme</i>	Endangered	Plant

(Continued)

Table 3 Record of federally listed threatened and endangered species with designated critical habitat in the dry forests of the main Hawaiian islands (USFWS, 1977, 1983, 1984, 2001, 2003a,b,c, 2012, 2016b, 2018).—cont'd

<i>Island(s) designation</i>	<i>Scientific name</i>	<i>Current federal register name</i>	<i>Endangered species act status</i>	<i>Species group</i>
O'ahu	<i>Tetramolopium lepidotum</i> ssp. <i>lepidotum</i>	<i>Tetramolopium lepidotum</i> ssp. <i>lepidotum</i>	Endangered	Plant
Maui	<i>Tetramolopium remyi</i>	<i>Tetramolopium remyi</i>	Endangered	Plant
Moloka'i	<i>Tetramolopium rockii</i> var. <i>rockii</i>	<i>Tetramolopium rockii</i>	Threatened	Plant
O'ahu	<i>Urera kaalae</i>	<i>Urera kaalae</i>	Endangered	Plant
Hawai'i, Kaho'olawe, maui, Moloka'i, O'ahu	<i>Vigna o-wahuensis</i>	<i>Vigna o-wahuensis</i>	Endangered	Plant
O'ahu	<i>Viola chamissoniana</i> ssp. <i>chamissoniana</i>	<i>Viola chamissoniana</i> ssp. <i>chamissoniana</i>	Endangered	Plant
Maui	<i>Wikstroemia villosa</i>	<i>Wikstroemia villosa</i>	Endangered	Plant
Hawai'i	<i>Zanthoxylum dipetalum</i> var. <i>tomentosum</i>	<i>Zanthoxylum dipetalum</i> var. <i>tomentosum</i>	Endangered	Plant
Hawai'i, Maui, Moloka'i	<i>Zanthoxylum hawaiiense</i>	<i>Zanthoxylum hawaiiense</i>	Endangered	Plant

Word from Reeves, M.K., and Amidon, F. (2018). Habitat status assessment methods—Hawai'i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439. Medeiros, A.C., Loope, L.L., and Chimera, C.G. (1993). Kanaio natural area reserve biological inventory and management recommendations. Prepared for the natural area reserve system, State of Hawai'i, pp. 35 + appendices. Hawai'i Department of Land and Natural Resources (HDLNR). (2015). Hawai'i's state wildlife action plan. Prepared by H. T. Harvey and Associates, Honolulu, Hawai'i.

**Fig. 10** Quality of dry forests designated as reserve areas in the main Hawaiian islands. Word from Reeves, M. K., and Amidon, F. (2018). Habitat status assessment methods—Hawai'i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439.

the State, and 106,703 ha (263,670 ac) are actually classified as dry forests in the State, indicates a need to implement additional measures to increase the public's awareness of the remaining gap between unprotected versus protected dry forests.

National parks

Lands managed by the National Park Service (NPS) (land ownership is summarized in [Fig. 8](#)) have benefited from ongoing management programs, which include invasive species control, research, and species-specific management. See [Table 4](#) for a list of protected dry forests in the NPSs and see [Table 5](#) for examples of conservation efforts being applied at each NPS. Protected parks include Haleakalā National Park on east Maui, which was established by Congress in 1916. The Park now protects > 33,000 ac of land on the island of Maui ([Haleakalā National Park, 2016](#)). Kalaupapa National Historical Park on Moloka'i is home to Kauhakō Crater, which contains the only known low elevation native/pristine dryland forest in the state ([HDLNR, 2015](#)). Hawai'i Volcanoes National Park (HVNP) was established by Congress in 1916. Hawai'i Volcanoes National Park encompasses diverse environments that range from sea level to the summit of Mauna Loa at 13,677 ft. and includes the active Kīlauea volcano ([National Park Service, 2015](#)). Some of the lowlands at HVNP contain small scattered stands of dry forest species on cliff faces, which are described in the dry cliff subtype of the Hawai'i's Dry Shrublands and Grasslands chapter.

National wildlife refuges

National Wildlife Refuges (NWR) are a national network of lands and waters managed by the USFWS for the conservation of fish, wildlife, and plant resources and their habitat. See [Table 4](#) for a list of protected dry forests in the NWRs in Hawai'i and [Table 5](#) for examples of conservation efforts being applied at NWRs.

State

Natural area reserves system

The Natural Area Reserves System (NARS) was established in 1970 with the intent to preserve in perpetuity specific land and water areas which support communities, as relatively unmodified as possible, of the natural flora and fauna, as well as geological sites, of Hawai'i. Natural Area Reserves (NAR) are State lands that are administered by the Division of Forestry and Wildlife (DOFAW) within the Department of Land and Natural Resources (DLNR). The State conducts some conservation management actions on these lands and provides access to others who are conducting such activities. See [Table 4](#) for a list of protected dry forests in the NARS of Hawai'i and [Table 5](#) for examples of conservation efforts being applied within each NAR.

Forest reserve system

The Forest Reserve System (FRS) was created by the Territorial Government of Hawai'i in 1903 as early foresters recognized the need to protect forests to provide water for agriculture and surrounding communities. This represented a public-private partnership to protect and enhance forested lands that is carried on today through the management of DOFAW as they focus their resources to protect, manage, restore, and monitor the natural resources of the FRS ([DOFAW, 2018a](#)). The FRS and Wildlife Sanctuaries contains over 274,624 ha (678,612 ac) of land of which approximately 11,201 ha (27,680 ac) or 4% are classified as dry forest. See [Table 4](#) for a list of protected dry forests in the FRS and Wildlife Sanctuaries, and [Table 5](#) for examples of conservation efforts being applied within each of these protected areas.

Landowner assistance programs

DOFAW implements a variety of landowner assistance programs for landowners willing to protect forest, wildlife, and watershed resources ([DOFAW, 2018b](#)). The Forest Stewardship Program (FSP) provides technical and financial assistance to private landowners to protect, manage, and restore important forest resources on their properties. The Conservation Reserve Enhancement Program (CREP) was created as an initiative under FSP to expand financial assistance to landowners and focuses on the restoration of agricultural lands and protection of sensitive habitats. Projects under these programs that include dry forest include the Waikoloa Dry Forest Initiative on the island of Hawai'i and a developing project in Palehua on O'ahu ([Waikoloa Dry Forest Initiative, 2015](#)). See [Table 5](#) for examples of conservation efforts being applied at Waikoloa Dry Forest.

Department of Hawaiian Home Lands

The Department of Hawaiian Home Lands (DHHL) was created by the Hawai'i State Legislature in 1960 and is governed by the Hawaiian Homes Commission Act of 1920. DHHL views its responsibility as a landowner to manage and protect native lands "to support both cultural and resource management activities and create homesteading opportunities for the future" ([DHHL, 2009](#)). Thus, the 'Āina Mauna Legacy Program was created to protect native forest on the slopes of Mauna Kea on the island of Hawai'i. The program specifically includes the lands of Humu'ula and Pi'ihonua, which contain tracts of dry forest. See [Table 5](#) for examples of conservation efforts being applied by the 'Āina Mauna Legacy Program.

Office of Hawaiian Affairs

The Office of Hawaiian Affairs (OHA) is a public agency responsible for improving the well-being of Native Hawaiians. OHA accomplishes this by collaborating with various organizations to strengthen community resources, including natural and cultural resources. One example is OHA's role as a funder for a dryland forest restoration project in Ka'ūpūlehu on the island of Hawai'i.

Table 4 Protected dry forest in the main Hawaiian Islands.

<i>Island</i>	<i>Ownership</i>	<i>Location</i>	<i>Protected dry forest acreage (ha(ac))^{a,b}</i>	<i>Dry forest conservation importance^{a,b,c,d}</i>
Moloka'i	National Park Service	Kalaupapa National Historical Park	159 ha (~392 ac)	Kauhakō Crater; 1 ha (3 ac) of closed 'ōhi'a dry forest, 84 ha (206 ac) of kiawe dry forest; 1 ha (3 ac) of mixed native and nonnative dry forest; 73 ha (180 ac) of nonnative dry forest
Hawai'i	National Park Service	Hawai'i Volcanoes National Park	2083 ha (5147 ac)	1 ha (2 ac) kiawe dry forest; 1267 ha (3132 ac) mixed māmane-naio and other native trees; 4 ha (10 ac) nonnative dry forest; 119 ha (293 ac) open koa-māmane dry forest; 692 ha (1710 ac) of open 'ōhi'a dry forest
Hawai'i	National Park Service	Kaloko-Honokōhau National Historical Park	35 ha (87 ac)	35 ha (87 ac) of kiawe dry forest
Hawai'i	National Park Service	Pu'u'honua o Hōnaunau National Historical Park	8 ha (19 ac)	4 ha (10 ac) of closed 'ōhi'a dry forest; 4 ha (9 ac) of kiawe dry forest
Kaua'i	Fish and Wildlife Services	Kilauea Point National Wildlife Refuge	5 ha (13 ac)	5 ha (13 ac) of kiawe dry forest
Kaua'i	Fish and Wildlife Services	Hanalei National Wildlife Refuge	2 ha (6 ac)	2 ha (6 ac) of kiawe dry forest
O'ahu	Fish and Wildlife Services	James Campbell National Wildlife Refuge	61 ha (149 ac)	13 ha (31 ac) of kiawe dry forest; 48 ha (118 ac) of nonnative dry forest
O'ahu	Fish and Wildlife Services	Pearl Harbor National Wildlife Refuge Kalaeloa Unit	8 ha (20 ac)	6 ha (16 ac) of kiawe dry forest; 2 ha (4 ac) of nonnative dry forest
Moloka'i	Fish and Wildlife Services	Kakahai'a National Wildlife Refuge	4 ha (11 ac)	4 ha (11 ac) of kiawe dry forest
Maui	Fish and Wildlife Services	Kealia Pond National Wildlife Refuge	4 ha (10 ac)	4 ha (10 ac) of kiawe dry forest
Hawai'i	Fish and Wildlife Services	Hakalau Forest National Wildlife Refuge and South Kona Section	51 ha (124 ac)	11 ha (26 ac) of mixed māmane-naio and other native trees; 40 ha (98 ac) of open koa-māmane dry forest
Kaua'i	State Department of Land and Natural Resources	Nāpali Coast State Wilderness Park	22 ha (54 ac)	4 ha (9 ac) of kiawe dry forest; 18 ha (45 ac) of nonnative dry forest
O'ahu	State Department of Land and Natural Resources	Ka'ena Point Natural Area Reserve	2 ha (5 ac)	2 ha (5 ac) of kiawe dry forest
O'ahu	State Department of Land and Natural Resources	Hāmākua Marsh Wildlife Sanctuary	2 ha (4 ac)	2 ha (4 ac) of nonnative dry forest
O'ahu	State Department of Land and Natural Resources	Pouhala Marsh Wildlife Sanctuary	1 ha (3 ac)	1 ha (3 ac) of nonnative dry forest
Moloka'i	State Department of Land and Natural Resources	Oloku'i Natural Area Reserve	17 ha (41 ac)	17 ha (41 ac) of kiawe dry forest
Maui	State Department of Land and Natural Resources	Kanaio Natural Area Reserve	10 ha (~25 ac)	In a 1993 survey, contained lama dry forest and wiliwili dry forest. 10 ha (25 ac) of kiawe dry forest
Maui	State Department of Land and Natural Resources	West Maui Natural Area Reserve	8 ha (20 ac)	8 ha (20 ac) of nonnative dry forest
Maui	State Department of Land and Natural Resources	'Āhihi-Kīna'u Natural Area Reserve	34 ha (84 ac)	30 ha (75 ac) of kiawe dry forest; 4 ha (9 ac) of nonnative dry forest
Hawai'i	State Department of Land and Natural Resources	Kīpāhoehoe Natural Area Reserve	48 ha (119 ac)	11 ha (28 ac) of mixed māmane-naio and other native trees dry woodland; 26 ha (63 ac) of open koa-māmane dry forest; 11 ha (28 ac) of open 'ōhi'a dry forest
Hawai'i	State Department of Land and Natural Resources	Mauna Kea Ice Age Natural Area Reserve	1 ha (~2 ac)	1 ha (2 ac) of mixed māmane-naio and other native trees
Hawai'i	State Department of Land and Natural Resources	Kīpuka 'Āinahou Nēnē Sanctuary	42 ha (105 ac)	41 ha (102 ac) of mixed māmane-naio and other native trees; 1 ha (3 ac) of open koa-māmane dry forest
Hawai'i	State Department of Land and Natural Resources	Manukā Natural Area Reserve	580 ha (1433 ac)	187 ha (462 ac) of closed 'ōhi'a dry forest; 56 ha (139 ac) of kiawe dry forest; 70 ha (173 ac) of mixed māmane-naio and other native trees; 4 ha (10 ac) of nonnative dry forest; 13 ha (32 ac) of open koa-māmane dry forest; 250 ha (617 ac) of open 'ōhi'a dry forest

Table 4 Protected dry forest in the main Hawaiian Islands.—cont'd

<i>Island</i>	<i>Ownership</i>	<i>Location</i>	<i>Protected dry forest acreage (ha(ac))^{a,b}</i>	<i>Dry forest conservation importance^{a,b,c,d}</i>
Hawai'i	State Department of Land and Natural Resources	Pu'u Wa'awa'a Wildlife Sanctuary	6 ha (> 14 ac)	6 ha (14 ac) of mixed māmane-naio and other native trees. Tracts of montane dry and lowland dry forest
Hawai'i	State Department of Land and Natural Resources	Pu'u Maka'ala Natural Area Reserve	67 ha (166 ac)	66 ha (164 ac) of mixed māmane-naio and other native dry forest trees; 1 ha (2 ac) of open koa-māmane dry forest
Moloka'i	The Nature Conservancy	Kamakou Preserve	3 ha (7 ac)	3 ha (7 ac) of kiawe dry forest
Moloka'i	The Nature Conservancy	Pelekunu Preserve	18 ha (44 ac)	18 ha (44 ac) of kiawe dry forest
Moloka'i	The Nature Conservancy	Mo'omomi Preserve	211 ha (521 ac)	211 ha (521 ac) of kiawe dry forest
Lāna'i	The Nature Conservancy	Kānepu'u Preserve	29 ha (72 ac)	5 ha (13 ac) of kiawe dry forest; 23 ha (57 ac) of nonnative dry forest; 1 ha (2 ac) of open 'ōhi'a dry forest
Maui	The Nature Conservancy	Waikamoi Preserve	1 ha (3 ac)	1 ha (3 ac) of kiawe dry forest
Hawai'i	The Nature Conservancy	Kīholo Preserve	1 ha (3 ac)	1 ha (3 ac) of kiawe dry forest
Hawai'i	The Nature Conservancy	Kamehame Preserve	2 ha (6 ac)	2 ha (6 ac) of kiawe dry forest
Hawai'i	The Nature Conservancy	Kona Hema Preserve	26 ha (63 ac)	11 ha (26 ac) of mixed māmane-naio and other native dry forest; 15 ha (37 ac) of open koa-māmane dry forest
Hawai'i	The Nature Conservancy	Kīpuka a 'Umi Preserve	2 ha (4 ac)	2 ha (4 ac) of mixed māmane-naio and other native dry forest
Maui	National Park Service	Haleakalā National Park	6614 ha (~16,343 ac)	810 ha (2000 ac) of lowland dry forest; 5649 ha (13,960 ac) of montane-subalpine dry forest; 137 ha (339 ac) of kiawe (<i>Prosopis pallida</i>) dry forest; 18 ha (44 ac) of nonnative dry forest

^aReeves, M. K., and Amidon, F. (2018). Habitat status assessment methods—Hawai'i, current condition summaries. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 439.

^bU.S. Fish and Wildlife Service (USFWS). (2016). Endangered and threatened wildlife and plants; designation and nondesignation of critical habitat on Moloka'i, Lāna'i, Maui, and Kaho'olawe for 135 species; final rule. *Federal Register* **81** (61), 17790–18110.

^cMedeiros, A. C., Loope, L. L., and Chimera, C. G. (1993). Kanaio natural area reserve biological inventory and management recommendations. Prepared for the natural area reserve system, State of Hawai'i, pp. 35 + appendices.

^dHawai'i Department of Land and Natural Resources (HDLNR). (2015). Hawai'i's state wildlife action plan. Prepared by H. T. Harvey and Associates, Honolulu, Hawai'i.

OHA awarded \$172,262 to the Hawai'i Forest Institute to support the restoration of native dryland lama forest in Ka'ūpūlehu. The project aims to foster relationships between community and 'āina (land) through utilizing educational stewardship, traditional knowledge, and scientific methods ([Hawai'i Forest Institute, 2017](#)).

Private

The Nature Conservancy

The mission of The Nature Conservancy (TNC) is to protect the lands and water on which all life depends. The Nature Conservancy of Hawai'i (TNCH) has 11 preserves in the State of Hawai'i encompassing > 16,187 ha (40,000 ac) ([TNCH, 2015](#)). See [Table 4](#) for a list of protected dry forests found within TNCs Preserves and [Table 5](#) for examples of conservation efforts being applied within each of the Preserves.

Kamehameha Schools

Kamehameha Schools (KS) is the largest private landowner in the State of Hawai'i with landholdings of over 147,710 ha (365,000 ac). Approximately 99% of this land is designated for agricultural (71,585 ha (176,890 ac)) or conservation (73,521 ha (181,675 ac)) purposes ([Kamehameha Schools, 2014](#)). In addition, roughly 19,425 ha (48,000 ac) or 13% is classified as dry forest with the majority located on the Kona side of the island of Hawai'i. Kamehameha Schools partners with many other conservation organizations to enhance stewardship of their resources. For example, KS has collaborated with the Three Mountain Alliance and the Hawaiian Silversword Foundation to protect montane-subalpine dry forest in Lupea (Kona side) on the island of Hawai'i ([Kamehameha Schools, 2011](#)). Examples of conservation efforts being applied at Kamehameha Schools are found in [Table 5](#).

Table 5 Examples of conservation efforts in dry forests.

<i>Organization/agency name</i>	<i>Location, island</i>	<i>Organization type</i>	<i>Conservation efforts^a</i>	<i>Target stressor(s)</i>
National Park Service	Hawai'i Volcanoes National Park, Hawai'i	Federal	Fencing, ungulate control, restoration	Invasive species
National Park Service	Kalaupapa National Historical Park, Moloka'i	Federal	Fencing, invasive plant and ungulate control, restoration, outplanting	Invasive species
National Park Service	Haleakalā National Park, Maui	Federal	Fencing, ungulate removal, invasive predator and plant control, surveys for listed species	Invasive species
National Park Service	Kaloko-Honokōhau National Historical Park, Hawai'i	Federal	Habitat restoration, research, invasive plant control, monitoring	Invasive species
National Park Service	Pu'uhonua o Hōnaunau National Historical Park, Hawai'i	Federal	Habitat restoration, invasive plant control, monitoring	Invasive species
US Fish and Wildlife Service	Hanalei National Wildlife Refuge, Kaua'i	Federal	Invasive plant control, endangered species management, habitat enhancement, predator control, monitoring	Invasive species
US Fish and Wildlife Service	Kilauea Point National Wildlife Refuge, Kaua'i	Federal	Invasive plant control, endangered species management, habitat enhancement, predator control, monitoring, outreach and education, predator-proof fence	Invasive species
US Fish and Wildlife Service	James Campbell National Wildlife Refuge, O'ahu	Federal	Habitat restoration and endangered species protection, predator and invasive plant control, monitoring	Invasive species
US Fish and Wildlife Service	Pearl Harbor National Wildlife Refuge, Kalaeloa Unit, O'ahu	Federal	Habitat restoration and endangered species protection, predator and invasive plant control, monitoring	Invasive species
US Fish and Wildlife Service	Kakahai'a National Wildlife Refuge, Moloka'i	Federal	Education, habitat restoration, invasive species control	Invasive species
US Fish and Wildlife Service	Hakalau Forest National Wildlife Refuge and South Kona Section, Hawai'i	Federal	Habitat restoration, fencing, ungulate and invasive plant control, propagation and outplanting, vegetation monitoring	Invasive species
Hawai'i Department of Land and Natural Resources	Pu'u Wa'awa'a Wildlife Sanctuary, Hawai'i	State	Fencing, invasive plant and ungulate control, fire control, removal of livestock, prevention of illegal logging	Invasive species, fire
Hawai'i Department of Land and Natural Resources	Kipāhoehoe Natural Area Reserve, Hawai'i	State	Fencing, invasive plant and ungulate control	Invasive species
Hawai'i Department of Land and Natural Resources	Manukā Natural Area Reserve, Hawai'i	State	Fencing, invasive plant and ungulate control, fire control, monitoring	Invasive species, fire
Hawai'i Department of Land and Natural Resources	Pu'u Maka'ala Natural Area Reserve, Hawai'i	State	Fencing, invasive plant and ungulate control, restoration, monitoring, outreach and education	Invasive species, fire
Hawai'i Department of Land and Natural Resources	Kanaio Natural Area Reserve, Maui	State	Fencing, invasive plant and ungulate control, restoration and outplanting	Invasive species
Hawai'i Department of Land and Natural Resources	West Maui Natural Area Reserve, Maui	State	Fencing, invasive plant and ungulate control, monitoring, public education, volunteer recruitment	Invasive species
Hawai'i Department of Land and Natural Resources	'Āhihi-Kīna'u Natural Area Reserve, Maui	State	Fencing, outreach	Invasive species
Hawai'i Department of Land and Natural Resources	Oloku'i Natural Area Reserve, Moloka'i	State	Aerial and ground monitoring for ungulates and invasive plants	Invasive species
The Nature Conservancy	Kamakou Preserve, Moloka'i	Private	Fencing, invasive plant and ungulate control, monitoring, fire prevention, outplanting, community outreach	Invasive species, fire
The Nature Conservancy	Pelekunu Preserve, Moloka'i	Private	Fencing, invasive plant and ungulate control, monitoring	Invasive species
The Nature Conservancy	Mo'omomi Preserve, Moloka'i	Private	Fencing, invasive plant control, monitoring, community outreach, native plant reestablishment	Invasive species

Table 5 Examples of conservation efforts in dry forests.—cont'd

<i>Organization/agency name</i>	<i>Location, island</i>	<i>Organization type</i>	<i>Conservation efforts^a</i>	<i>Target stressor(s)</i>
The Nature Conservancy	Kānepu'u Preserve, Lāna'i	Private	Fencing, invasive plant and ungulate control, monitoring, outplanting	Invasive species
The Nature Conservancy	Waikamoi Preserve, Maui	Private	Invasive plant and ungulate control, research and monitoring, outreach	Invasive species
The Nature Conservancy	Kona Hema Preserve, Hawai'i	Private	Fencing, ungulate control, restoration, research	Invasive species
Department of Hawaiian Home Lands	ʻĀina Mauna Legacy Program, Hawai'i	State	Invasive species removal, reforestation and restoration, conserving endangered species, providing educational and cultural opportunities	Invasive species
Waikoloa Village Association	Waikoloa Dry Forest Initiative, Hawai'i	Private	invasive species control, outplanting and restoration, providing educational and cultural opportunities, native plant propagation and planting, fuels management	Invasive species, fire
Kamehameha Schools	Lupea, Hawai'i	Private	Fencing, invasive species control, outplanting and restoration	Invasive species
Kamehameha Schools	Ka'ūpūlehu, Hawai'i	Private	Fencing, ungulate removal, invasive plant and predator control, fire management, outplanting and restoration	Invasive species, fire
ʻUlupalakua Ranch	Auwahi Forest Restoration Project, Maui	Private	Fencing, invasive plant and predator control, outplanting and restoration, providing educational and cultural opportunities,	Invasive species
Pūlama Lāna'i	Lāna'i	Private	Invasive plant and animal control, fire management, propagation and outplanting	Invasive species, fire
Hawai'i Association of Watershed Partnerships—Leeward Haleakalā Watershed Restoration Partnership	Makawao Forest Reserve to Kaupō, Maui	Multi-agency Partnership	Fencing, invasive plant and ungulate control, surveys and monitoring, reforestation	Invasive species
Hawai'i Association of Watershed Partnerships—Wai'anāe Mountains Watershed Partnership	Mākua Kea'au Forest Reserve, O'ahu	Multi-agency Partnership	Invasive plant and predator control, fire management	Invasive species, fire
Invasive Species Committees—O'ahu Invasive Species Committee and Big Island Invasive Species Committee	Various locations, O'ahu and Hawai'i	Multi-agency Partnership	Invasive plant and predator control, fire management	Invasive species, fire
Hawaiian Islands Land Trust—Nu'u refuge	Nu'u refuge, Maui	Nonprofit 501(c)(3)	Restoration, protect cultural sites, educational outreach	Invasive species

^aHawai'i Department of Land and Natural Resources (HDLNR). (2015). Hawai'i's state wildlife action plan. Prepared by H. T. Harvey and Associates, Honolulu, Hawai'i.
 Word from Hawai'i Department of Agriculture (HDOA). (2009). Plant guidelines for importation to Hawai'i. Available at <http://hawaii.gov/hdoa/pi/pq/plants>.

Auwahi Forest Restoration Project

The Auwahi Forest Restoration Project began in 1997, as a collaboration between ʻUlupalakua Ranch, US Fish and Wildlife Service (USFWS), US Department of Agriculture (USDA), regional scientists, and volunteers to develop technologies for restoration of nonnative pastoral lands back to native dry forest. Examples of conservation efforts being applied at Auwahi Forest are found in **Table 5**.

Hawaiian Islands Land Trust

The Hawaiian Islands Land Trust (HILT) is a nonprofit 501(c)(3) land conservancy organization. It was formed in 2011 and helps to protect >7284 ha (18,000 ac) on Maui, Kaua'i, O'ahu, Moloka'i, and the island of Hawai'i. These conservation easements held in perpetuity by HILT help to conserve scenic views, agricultural resources, wildlife habitats, water resource areas, cultural and historical values, and outdoor recreation opportunities ([Hawaiian Islands Land Trust, 2018a](#)). On Maui, >32 ha (80 ac) of lowland dry forest and wetlands are protected at Nu'u refuge on east Maui through lands owned by the HILT ([Hawaiian Islands Land Trust, 2018b](#)). See **Table 5** for examples of conservation efforts being applied at Nu'u refuge.

Lānaʻi

The island of Lānaʻi is almost entirely under private ownership but does have conservation partnerships with the USFWS, the state of Hawaiʻi, and The Nature Conservancy. Currently the land manager, Pūlamā Lānaʻi, is implementing actions that benefit dry forests (USFWS, 2016b; Lānaʻi Resorts et al., 2015, in litt.). See [Table 5](#) for a list of these actions.

Multiple agency partnerships

Association of watershed partnerships

Watershed Partnerships are voluntary alliances of public and private landowners committed to protecting over 809,371 ha (2 million ac) of the most important watershed lands in Hawaiʻi of which approximately 52,487 ha (129,700 ac) is dry forest. Individual watershed partnerships have been established on five islands (island of Hawaiʻi, Maui, Molokaʻi, Oʻahu, and Kauaʻi) and jointly form the Hawaiʻi Association of Watershed Partnerships, to support statewide needs. A list of conservation actions happening through these partnerships are found in [Table 5](#).

Invasive species committees

Invasive species committees (ISCs) are voluntary partnerships of government, private and nonprofit organizations, and concerned individuals working to address invasive species issues in Hawaiʻi. These committees have been formed on individual islands (island of Hawaiʻi/Big Island [BIISC], Maui [MISC], Molokaʻi [MoMISC], Oʻahu [OISC], Kauaʻi [KISC]) and focus on the specific issues of their island. The overall goal of the ISCs is to “prevent, eradicate, or control priority incipient plant and animal species that threaten Hawaiʻi’s most intact federal, state, and private conservation lands” (HDLNR, 2015). For example, fountain grass has been identified as a target species for OISC and cooperative project species (work with others to control) for BISC (BISC, 2018; OISC, 2018). See [Table 5](#) for a list of conservation actions undertaken by ISCs.

Laws and regulations

Inadequate protection from introduction of nonnative species

Currently, four agencies are responsible for inspection of goods arriving in Hawaiʻi (CGAPS, 2009): Hawaiʻi Department of Agriculture (HDOA), US Department of Homeland Security-Customs and Border Protection (CBP), US Department of Agriculture-Animal and Plant Health Inspection Service-Plant Protection and Quarantine (USDA-APHIS-PPQ), and USFWS. A summary of each agencies responsibility can be found in [Table 6](#).

The State of Hawaiʻi’s unique biosecurity needs are not recognized by Federal import regulations. Under the USDA-APHIS-PPQ’s commodity risk assessments for plant pests, regulations are based on species considered threats to the mainland United States and do not address many species that could be pests in Hawaiʻi (Hawaiʻi Legislative Reference Bureau (HLRB, 2002; USDA-APHIS-PPQ, 2010; CGAPS, 2009). Interstate commerce provides the pathway for invasive species and commodities infested with nonfederal quarantine pests to enter Hawaiʻi. Pests of quarantine concern for Hawaiʻi may be intercepted at ports in Hawaiʻi by Federal agents but are not always acted on by them because these pests are not regulated under Federal mandates. Hence, Federal protection against pest species of concern to Hawaiʻi has historically been inadequate. It is possible for the USDA to grant Hawaiʻi protective exemptions under the “Special Local Needs Rule,” when clear and comprehensive arguments for both agricultural and conservation issues are provided; however, this exemption procedure operates on a case-by-case basis and is extremely time-consuming to satisfy. Therefore, that avenue may only provide minimal protection against the large diversity of foreign pests that threaten Hawaiʻi.

Adequate staffing, facilities, and equipment for Federal and State pest inspectors and identifiers in Hawaiʻi devoted to invasive species interdiction are critical biosecurity gaps (HLRB, 2002; USDA-APHIS-PPQ, 2010; CGAPS, 2009). State laws have recently been passed that allow the HDOA to collect fees for quarantine inspection of freight entering Hawaiʻi (e.g., Act 36 (2011) H.R.S. 150A-5.3). Legislation enacted in 2011 (H.B. 1568) requires commercial harbors and airports in Hawaiʻi to provide biosecurity and to facilitate cargo inspections.

Nonnative Vertebrate Species: The laws in the State of Hawaiʻi prohibit the importation of all animals unless they are specifically placed on a list of allowable species (HLRB, 2002; CGAPS, 2011). The importation and interstate transport of invasive vertebrates is federally regulated by the USFWS under the Lacey Act as “injurious wildlife” (Fowler et al., 2007); the current list of vertebrates considered as “injurious wildlife” is provided at 50 CFR 16. The existing vertebrate pest species previously mentioned are already well established and therefore not responsive to these biosecurity measures. However, the law in its current form has limited effectiveness in preventing new invasive vertebrate introductions into the State of Hawaiʻi.

Nonnative Invertebrate Species: The introduction of most invasive invertebrate pests to the State has been and continues to be accidental and incidental to other intentional and permitted activities. Although Hawaiʻi State government and Federal agencies have regulations and some controls in place (see above), the introduction and movement of invasive invertebrate pest species between islands and from one watershed to the next continues. For example, an average of 20 new nonnative invertebrate species were introduced to Hawaiʻi per year since 1970, an increase of 25% over the previous totals between 1930 and 1970 (TNCH, 1992). Existing regulatory mechanisms therefore appear inadequate to ameliorate the threat of introductions of nonnative invertebrates, and we have no evidence to suggest that any change to this situation is anticipated in the future. The introduction of nonnative invertebrates to the State of Hawaiʻi is a significant risk to dry forests.

Table 6 Examples of conservation efforts related to laws and regulations in dry forests.

<i>Conservation method</i>	<i>Target stressor</i>	<i>Summary of actions^a</i>
Hawai'i Department of Agriculture (HDOA)	Inadequate protection from introduction of nonnative species	Inspects domestic cargo and vessels and focuses on pests of concern to Hawai'i, especially insects or plant diseases not yet known to be present in the State
US Department of Homeland Security-Customs and Border Protection (CBP)	Inadequate protection from introduction of nonnative species	Inspecting commercial, private, and military vessels and aircraft and related cargo and passengers arriving from foreign locations. Quarantine issues involving nonpropagative plant materials (processed and unprocessed); wooden packing materials, timber, and products; internationally regulated commercial species under the Convention in International Trade in Endangered Species (CITES); federally listed noxious seeds and plants; soil; and pests of concern to the greater United States., such as pests of mainland United States. forests and agriculture
US Department of Agriculture-Animal and Plant Health Inspection Service-Plant Protection and Quarantine (USDA-APHIS-PPQ)	Inadequate protection from introduction of nonnative species	Inspects propagative plant material, provides identification services for arriving plants and pests, conducts pest risk assessments, trains CBP personnel, conducts permitting and preclearance inspections for products originating in foreign countries, and maintains a pest database that, again, has a focus on pests of wide concern across the United States
US Fish and Wildlife Service	Inadequate protection from introduction of nonnative species	Inspects arriving wildlife products, enforces the injurious wildlife provisions of the Lacey Act (18 U.S.C. 42; 16 U.S.C. 3371 et seq.), and prosecutes CITES violations

^aHawai'i Department of Agriculture (HDOA). (2009). Plant guidelines for importation to Hawai'i. Available at <http://hawaii.gov/hdoa/pi/pq/pq.plants>.

Word from Miller, S. E. (2018). Defining the foreseeable future for Pacific Islands habitat status assessments. June 2018 technical report. U.S. Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI, pp. 13.

Nonnative Plant Species: The State of Hawai'i allows the importation of most plant taxa, with limited exceptions, if shipped from domestic ports (HLRB, 2002; USDA-APHIS-PPQ, 2010; CGAPS, 2009). Hawai'i's plant import rules (H.A.R. 4–70) regulate the importation of 13 plant taxa of economic interest; regulated crops include pineapple, sugarcane, palms, and pines. Certain horticultural crops (e.g., orchids) may require import permits and have pre-entry requirements that include treatment or quarantine or both either prior to or following entry into the State. The State noxious weed list (H.A.R. 4–68) and USDA-APHIS-PPQ's Restricted Plants List restrict the import of a limited number of noxious weeds. If not specifically prohibited, current Federal regulations allow plants to be imported from international ports with some restrictions. The Federal Noxious Weed List (see 7 CFR 360.200) includes few of the many globally known invasive plants, and plants in general do not require a weed risk assessment prior to importation from international ports. The USDA-APHIS-PPQ is in the process of finalizing rules to include a weed risk assessment for newly imported plants. Although the State has general guidelines for the importation of plants, and regulations are in place regarding the plant crops mentioned above, the intentional or inadvertent introduction of invasive plants outside the regulatory process and movement of species between islands and from one watershed to the next continues. In addition, government funding is inadequate to provide for sufficient inspection services and monitoring. Therefore, the potential for invasive plants to adversely impact the dry forests due to a lax in State and Federal regulations will continue until the regulatory process is revised and additional funding is provided to support inspection services and monitoring at our ports.

General invasive species control actions

The Hawai'i Invasive Species Council (HISC), which was created by gubernatorial executive order in 2002, to coordinate local initiatives for the prevention and control of invasive species by providing policy level direction and planning for the State departments responsible for invasive species issues. In 2003, the Governor signed into law Act 85, which conveys statutory authority to the HISC to continue to coordinate approaches among the various State and Federal initiatives for the prevention and control of invasive species (HDLNR, 2003; HISC, 2009; H.R.S. 194–2(a)). Some of the recent priorities for the HISC include interagency efforts to control nonnative species such as naio thrips (HISC, 2009). In early 2009, HISC projected that, due to a tighter economy in Hawai'i and anticipated budget cuts in State funding support of up to 50%, there will be a serious setback in conservation achievements, and the loss of experienced, highly trained staff (HISC, 2009).

In 1995, the Coordinating Group on Alien Pest Species (CGAPS), a partnership comprised primarily of managers from every major Federal, State, County, and private agency and organization involved in invasive species work in Hawai'i, was formed in an effort to improve communication, increase collaboration, and promote public awareness (CGAPS, 2009).

Future Scenarios

The condition of dry forests in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are as follows:

1. *Conservation Values*: stakeholder involvement and public opinion determine the formulation, implementation and funding of natural resource conservation within laws and development plans.
2. *Laws and Biosecurity*: national, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented (e.g., hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.).
3. *Development or Conservation Planning*: national, state, county, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

These conservation management parameters are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The year 2035 is the extent of the “foreseeable future,” and is based on the projected divergence of IPCC Representative Concentration Pathway (RCP) climate change scenarios (van Vuren et al., 2011a,b; Miller, 2018).

The four foreseeable future scenarios considered in this assessment are:

Future Scenario One, Status Quo—the most likely foreseeable future; no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues through the foreseeable future.

Future Scenario Two—a slight increase in natural resource conservation in the CMPs marginally improves conservation management.

Future Scenario Three—a slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management.

Future Scenario Four—a moderate to large increase in conservation actions in the CMPs substantially improves conservation management.

The future condition of Dry Forests in Scenario One, the status quo, was characterized from an assessment of change over time in Dry Forest land cover obtained from existing land cover maps (Amidon and Reeves, 2018). Based on these land cover maps, an annual rate of change for Dry Forest was estimated, and a projected change (in acres/ha) was calculated for the year 2035. The resulting information on changes in land cover by 2035, as derived from existing land cover change estimates, is the extent of the Dry Forest that is expected in the foreseeable future under Scenario One where conservation efforts remain unchanged and the current rate of change in land cover is also unchanged.

The future conditions of Dry Forest for Scenarios Two, Three, and Four cannot be quantitatively (acres/ha) estimated. However, the Scenario One estimate can provide a “baseline” for a qualitative characterization of changes in the future condition of Dry Forest under Scenarios Two, Three, and Four.

Changes in human population are captured only by the changes in the “developed” land cover footprint derived from land cover map analysis (Amidon and Reeves, 2018). Impacts from other sources of human activities or human-caused ecotype stressors (e.g., plant and animal diseases, wildfires, invasive species, etc.) are not well characterized in the land cover changes, but significantly contribute to increases in the land cover area dominated by nonnative vegetation.

Also, note that island-wide implementation of the CMPs is unlikely to have a significant effect on climate-related stressors (temperature, precipitation, and severe weather) resulting from global warming by 2035. This lack of CMP climate effects is due to the global lag in climate response to changes in greenhouse gas emissions which occurs on the order of centuries rather than years (Solomon et al., 2009; Gillett et al., 2011; Jevrejeva et al., 2012). Evidence of climate effects is also confounded by the large annual variation in the Pacific islands climate parameters, which is much greater than projected climate change by 2035. Although impacts from climate-related ecotype stressors do not change across the four scenarios, they were included in this analysis because of their overall magnitude of potential importance to future ecotype viability.

Future Scenario One—Status Quo.

Under Scenario One there is no change in the implementation of the three CMPs between 2018 and 2035. A continuing current rate of change in land cover through this foreseeable future results in a slow but continuous change in dry forest subcategories. See Table 7 for responses of Dry Forest stressors under Scenario One and Table 8 for a summary of change in quality and quantity of each dry forest subtype under Scenario One.

Redundancy is defined as the ability to withstand catastrophic events and is measured by the number and distribution of dry forests across representative areas. In this scenario, native dry forests would have a continued decline in size and distribution, and therefore a decrease in redundancy. Human-caused stressors will have a small increase overall and continue to reduce the

Table 7 Responses of dry forest stressors in foreseeable future scenarios

Conservation Management Parameters (CMPs)				
Conservation Values	Stakeholder involvement and public opinion influence the formulation, implementation, and funding of natural resource conservation and biosecurity (NRC/B) within laws and development or conservation plans.			
Laws and Biosecurity	National, state, county, and city laws and regulations are the means by which NRC/B are supported and implemented.			
Planning for Development or Conservation	National, state, county, city, and private development plans or conservation plans define actions that result in losses or gains in NRC/B (impacts realized at implementation).			
Foreseeable Future Scenarios and the resulting Dry Forest conditions				
Use Foreseeable Future	Scenario One:	Scenario Two:	Scenario Three:	Scenario Four:
Scenario One as a “baseline” to characterize changes in Conservation	CMPs: unchanged in support for NRC/B.	CMPs: small increase in support for NRC/B.	CMPs: small to moderate decrease in support for NRC/B.	CMPs: moderate to large increase in support for NRC/B.
Actions and Habitat Conditions in Future Scenarios Two, Three and Four.	Conservation Actions: no change; current rate of land cover change continues through the foreseeable future. Habitat Condition: habitat area, quality, and sustainability slowly decrease through the foreseeable future.	Conservation Actions: marginal increase. Habitat Condition: habitat area is unchanged through the foreseeable future; habitat quality and sustainability are slightly enhanced through the foreseeable future.	Conservation Actions: substantial decrease. Habitat Condition: urban and agricultural uses are prioritized over conservation; habitat area, quality, and sustainability substantially decrease through the foreseeable future.	Conservation Actions: substantial increase. Habitat Condition: robust, sustained effort to restore, manage, and expand conservation; habitat area, quality, and sustainability substantially increase through the foreseeable future.
Habitat stressors				
Development	small to moderate increase	no change (redevelop)	moderate to large increase	small to moderate decrease
Invasive Species	small increase	small increase	larger increase	small decrease
Plant Diseases	small increase	small increase	larger increase	no change to small decrease
Fire	small increase	small increase	larger increase	no change to small increase
Climate				
Temperature	small to moderate increase	small to moderate increase	small to moderate increase	small to moderate increase
Precipitation	small decrease	small decrease	small decrease	small decrease
Storms	small increase	small increase	small increase	small increase

Table 8 Summary of change in quality and quantity of dry forest subtypes in foreseeable future scenarios.

<i>Subtype</i>	<i>Scenario One: status quo</i>	<i>Scenario Two: slightly improved</i>	<i>Scenario Three: substantially decreased</i>	<i>Scenario Four: substantially improved</i>
Lowland native dry forests	Decrease	Slightly decrease	Severely decrease	Increase
Montane-subalpine native dry forests and woodlands	Decrease	Slightly decrease	Severely decrease	Increase
Introduced dry forests	Slightly increase	Slightly increase	Decrease	Decrease
Managed tree plantations	Slightly increase	Unchanged	Increase	Unchanged

size and quality of native dry forests. Ecological function is predicted to be reduced due to the ability of invasive plants and animals to outcompete native plants for water and space, subsequently resulting in a reduction in native biodiversity. Degradation of native dry forests will continue to increase as remaining areas become more fragmented, thus reducing their resiliency and representation.

Introduced dry forests are predicted to increase in size and distribution (redundancy) as a result of the overall small increase in human-caused ecotype stressors. Introduced dry forests are likely to expand as invasive species replace native-dominated communities, resulting in an increase in resiliency, redundancy, and representation.

The Tree plantations are predicted to slightly increase in size and distribution due to the assumed expansion of the human population and continued development pressure for forest products (lumber, fuel), horticulture, and agriculture (coffee, fruit, nut orchards resulting in a slight increase in resiliency, redundancy, and representation.

Future Scenario Two—there is a slight increase in the CMPs that marginally improves conservation management.

Under Scenario Two, conservation agencies and stakeholders work with increased but limited resources to slow or stop the degradation of landscape areas. Scenario Two is essentially ‘status quo’ with minor improvements in the three CMPs. This scenario is expected to have the second highest likelihood of occurring into the foreseeable future, being slightly less likely than Scenario

One. The anticipated changes, under Scenario Two, for each ecotype stressors important to Dry Forests are given in [Table 7](#). A summary of the change in quality and quantity of each dry forest subtype under Scenario One can be found in [Table 8](#).

Future Scenario Three—there is a small to moderate decrease in conservation actions in the CMPS that substantially decreases conservation management.

All natural resource management actions in the CMPs are set aside in deference to land use for economic development. With extensive localized management, some native species may persist in park-like settings or in areas where land development is not possible. This scenario has substantial declines in natural resource conservation within the three CMPs. An increasing human population is supported in its use of land for economic development over the conservation of native ecotypes. Areas that cannot support development become the only areas of free-living native species. The anticipated changes, under Scenario Three, for each ecotype stressors important to Dry Forests are given in [Table 7](#).

Overall, this scenario would severely degrade and fragment native dry forest and result in reduced resiliency, redundancy, and representation. However, this scenario, along with Scenario Four, has the lowest likelihood of occurring in the foreseeable future. See [Table 8](#) for a summary of change in quality and quantity of each dry forest subtype under Scenario Three.

Future Scenario Four—There is a moderate to large increase in conservation actions in the CMPS that substantially improves conservation management.

For this scenario, substantial improvements to the three CMPs and a general decrease in human-caused habitat stressors would increase the size and quality (resiliency) of lowland native dry forests and montane-subalpine native dry forests. Although this increase in native forest subtypes would be gradual at first it will become more noticeable by 2035 as the substantial improvements to the three CMPs will help keep these subtypes from declining (see [Table 8](#)).

Based on this analysis, the substantial improvements in restoration for native dry forest would result in increased resiliency, redundancy, and representation. However, as mentioned above, this scenario and Scenario Three have the lowest likelihood of occurring in the foreseeable future. The anticipated changes, under Scenario Four, for each ecotype stressors important to Dry Forests are given in [Table 7](#).

Conclusion

In summary, the conservation efforts by Federal, State, private, and multiple agency partnerships have been beneficial in helping to conserve and protect the remaining dry forests in Hawai'i. The restoration of dry forests cannot be accomplished solely on Federal lands because their range occurs primarily on non-Federal lands. To achieve restoration of these non-Federal dry forests requires cooperative conservation efforts on private and State lands. However, increasing funding sources remains a high priority, to accomplish the goals of expanding and actively managing the remaining dry forests.

The primary stressors to dry forests include habitat destruction and modification by invasive ungulates, competition with invasive species, natural disasters (hurricanes), fire, drought, agriculture and urban development, and climate change. These stressors, as described in more detail above, are serious and ongoing, act in concert with other stressors to dry forests, and are expected to continue or increase in magnitude and intensity into the future without effective management actions to control or eradicate them. In addition, the combined effects of ungulate, rodent, and invertebrate predation on dry forests suggests the need for immediate implementation of restoration and conservation methodologies. Without active management, dry forests will continue to be degraded and destroyed.

Finally, the condition of dry forests in the foreseeable future favors Scenario One, which has the highest likelihood of occurring in the foreseeable future relative to the other scenarios. Under Scenario One there is no change in the implementation of the conservation management parameters (CMPs). Scenario Two is based on a slight increase in the implementation of the CMPs, which marginally improves conservation management. Thus Scenario Two is expected to have the second highest likelihood of occurring into the foreseeable future, being slightly less likely than Scenario One. Scenario Three is based on a slight to moderate decrease in conservation actions in the CMPs which substantially decreases conservation management. Because there is a decrease in the implementation of the CMPs, Scenario Three would severely degrade and fragment native dry forest eco-types and result in reduced resiliency, redundancy, and representation. In Scenario Four, the substantial improvements in restoration for native dry forest eco-types would result in increased resiliency, redundancy, and representation. However, this scenario and Scenario Three have the lowest likelihood of occurring in the foreseeable future.

Overall, the CMPs are critical factors that drive the direction and magnitude of natural resource conservation and determine the foreseeable future scenarios. Any increase in the implementation of the CMPs will result in the greatest conservation returns for native dry forest (Scenario's Two and Four). Conversely, any decrease in the implementation of the CMPs will result in the least conservation returns for native dry forest (Scenario's One and Three). Thus, realistic expectations of the implementation of the CMPs were considered when determining the likelihood of occurrence for each scenario in the foreseeable future.

See also: Physical Geography of the Hawaiian Islands; Hawai'i's Dry Grasslands and Shrublands.

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In Litt

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Hawaiian Islands Wet Forest

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Published by Elsevier Inc.

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Abstract

Forest description, historic and current status, stressors, conservation efforts, and projection of potential future scenarios are analyzed for quality and quantity of wet forests across the Hawaiian islands. The wet forest ecosystem occurs on the windward sides of all the main Hawaiian islands except Ni'ihau and Kaho'olawe. Hawaiian islands wet forest is comprised of three native-dominated and one introduced plant communities: lowland rainforest, montane rainforest, montane cloud forest, and managed tree plantation. Stressors of wet forests include invasive plant and animal species, plant diseases and increased tropical cyclones from climate change. The keystone species of wet forests in Hawai'i is 'ōhi'a (*Metrosideros polymorpha*). 'Ōhi'a colonize new lava flows in the form of cohorts. In the later part of the wet forests lifecycle, the 'ōhi'a canopy breaks down in synchrony, a natural forest regeneration phenomenon known as *ōhi'a dieback*. Recently 'ōhi'a has experienced widespread mortality on the island of Hawai'i as a result of two novel species of the fungal genus *Ceratocystis*. This phenomenon is referred to as rapid 'ōhi'a death (ROD) and has had significant impacts on lowland rainforests. Once the canopy is opened either from 'ōhi'a dieback or ROD, invasive plants have greater potential to become established and disrupt the natural succession back to closed 'ōhi'a forest. Analysis under various "best" and "worst" case future scenarios show the continued decline of lowland rainforest except under the best case scenario of an increase in quantity and quality of rainforest compared to current conditions. Substantial improvements to laws, biosecurity, and implementation of intensively managed, fenced conservation areas are required to conserve this forest type in the future. Montane rainforest and montane cloud forest fair better under the future scenarios but are still vulnerable to decline if existing management actions are not maintained. Managed tree plantations are expected to increase as the human population increases.

Hawaiian Islands Wet Forest Description

Defining Hawaiian Wet Forest

A forest is a plant community characterized by vegetation dominated by trees (woody plants) generally 5–35 m in height, and often including a canopy, subcanopy, shrub, and an herbaceous layer (composed of nonwoody plants). The forest canopy is dense with 60–100% cover. The classification of Hawaiian wet forest is based on elevation, moisture, and physiognomy (look, aspect, or appearance). Physiognomic classes of wet forest are based on percentage cover of the dominant plant life-form in the uppermost vegetation layer. Those classified as “wet forest” have more than 2,500 mm annual rainfall and >25% cover in trees (Gagné and Cuddihy, 1999). Hawai'i wet forest include lowland rainforest, montane rainforest, and montane cloud forest.

Geology

Substrates for Hawai'i wet forest vary from very weathered soils on older islands to rocky substrates on recent lava flows on younger islands. There are two broad classes of soil substrates formed from basalt lava which support wet forests: undeveloped or geomorphologically recent soil substrates found on Hawai'i and Maui and well developed soils in humid climates. Within each of these classes there are a large number described soil types (Mueller-Dombois and Fosberg, 1998). Soils vary throughout the island chain, from gray acidic clays on older islands to thin organic mucks over lava flows and ash beds on Hawai'i.

Vegetation structure, composition, and subunits

Wet forests can be very tall exceeding 15 m but also shorter and scrubby in nature. Rainfall and persistent cloud cover is sufficient to support lush growth of vegetation comprised of many types of plant forms including lianas (long-stemmed, woody vines that are rooted in the soil), mosses, lichens, and ferns. Distinguishing characteristics among the different types of wet forest or subunits include elevation, precipitation, presence of clouds, vegetative structure, and plant communities. Wet forests contain discrete patches and mosaics of plant communities which occur across the landscape with spatial variation.

Lowland rainforest

Lowland rainforest occurs from 100 to 1,200 m elevation on all of the main islands except Ni'ihau and Kaho'olawe. Lowland rainforests typically have at least two tree layers, an upper one composed of *Meterosideros polymorpha* ('ōhi'a) alone or mixed with a codominant tree species such as *Cheiodendron* spp. ('olapa) or *Antidesma platyphyllum* (hame) and an understory of diverse lower-statured tree species including tree ferns—*Cibotium* spp. (hapu'u). Lowland rainforests are also home to lianas such as *Freycinetia arborea* ('ie'ie) and the ground is usually covered with mosses, sedges and a diverse array of fern species (Cuddihy, 1989; Gagné and Cuddihy, 1999).

Montane rainforest

Montane rainforest is found on the islands of Hawai'i, Maui, Moloka'i, Lāna'i, O'ahu, and Kaua'i between 823 and 2,200 m elevation. The boundary between the lowland and montane rainforests is not generally agreed upon by all botanists and ecologists, and it may be variable on the different islands. At lower elevations on the island of Hawai'i, montane rainforests merge with lowland rainforest. At upper elevations on Hawai'i and Maui, they quickly grade into mesic forests. The dominant tree species of montane rainforests is most often 'ōhi'a. A distinct type of forest with tall *Acacia koa* (koa) and 'ōhi'a occurs in areas with deep soil above the elevations of 900–1,200 m. Montane rainforests are multilayered, below the canopy of 'ōhi'a (or koa and 'ōhi'a) is a layer of diverse lower-statured trees in which no one species is dominant. Epiphytic mosses, liverworts, lichens, ferns and hapu'u are abundant on tree trunks and fallen logs. Fallen logs serve as nurse logs for seedling germination of wet forest species. On the island of Hawai'i a layer composed almost entirely of hapu'u is present, this occurs on other islands as well but to a lesser extent. As with lowland rainforest the ground cover consists of mosses, sedges and a diverse array of fern species (Cuddihy, 1989; Gagné and Cuddihy, 1999).

Montane cloud forest

Montane cloud forests occur between 750 and 1,830 m elevation on all the main Hawaiian islands except for Ni'ihau and Kaho'olawe. Hawaiian montane cloud forests are forests which receive a substantial amount of additional precipitation from fog drip on a regular basis. The division between montane rainforest and montane cloud forest can be hard to define as there is no exact qualitative or quantitative criteria to separate them. Medeiros et al. (1993) describes cloud forests on Moloka'i and Lāna'i in the same zone as others describe montane rainforest. Juvik and Nullet (1993) describe three zones of wet montane cloud forest and a fourth zone which is considered dry montane cloud forest. Wet montane cloud forests which face northeast trade winds on exposed mountain ridges and peaks consist of dwarf elfin forests with abundant mossy epiphytes. Wet montane cloud forests which occur on geologically young volcanic mountains at Haleakalā, Maui and Mauna Kea and Mauna Loa, Hawai'i are taller in stature and do not have a huge biomass of mossy epiphytes. The dominant tree species of montane cloud forests are 'ōhi'a and 'olapa. Koa is a codominant species in the taller stature montane cloud forests on young volcanic islands. Montane cloud forests are multilayered, species rich and host a diverse array of over 30 species of trees, 30 species of shrubs, and more than 60 species of ferns (Mueller-Dombois and Fosberg, 1998).

Sustainability

Wet forests need volcanic substrates, nutrient availability, light and to be situated high enough on the windward sides of the main islands to intercept moisture-laden trade winds for adequate rainfall ($> 2,500$ mm) to develop and sustain themselves (Gagné and Cuddihy, 1999). Adequate distribution across the landscape of wet forest contributes to its ability to perpetuate after a catastrophic event in one area by having a redundant or similar forest in another area.

Hawaiian wet forests start on new lava flows. Plants, lichens and mosses colonize in 1–2 years, and 'ōhi'a in 4 years (Smathers and Mueller-Dombois, 1972). Plant growth leads to leaf litter which provides organic matter to aid in the further development of the forest. The most common native plant in wet forests other than 'ōhi'a is a fern known as uluhe (*Dicranopteris linearis*). Uluhe forms dense mats which can be impenetrable, 'ōhi'a trees and other plants will eventually cover over and shade out uluhe and form a forest or re-form one. Haup'u, another dominant species of wet forests, are shade tolerant and able to colonize the understory of closed canopy mature 'ōhi'a forests. Haup'u cover declines after 3,000 years to be replaced by woody plants. In the later part of the wet forests lifecycle, the 'ōhi'a the canopy guild breaks down often in synchrony, a natural forest regeneration phenomenon known as 'ōhi'a dieback. The trigger is hypothesized to be climatic in nature. Five types of dieback are recognized and vary by substrate; dryland dieback, wetland dieback, displacement dieback and gap and bog formation dieback. The rainforest develops from young 'ōhi'a forests to mature diverse forests with inclusions of bog and stream ecosystems as it progresses through the stages of dieback (Mueller-Dombois and Boehmer, 2013).

Many of the relationships between plants, and their environment are reciprocal: rain, temperature, humidity, soil fertility influence plant growth, while plants affect microclimate and soil moisture, structure, acidity, and fertility. Mineral nutrients, such as nitrogen and phosphorus, cycle between the living and nonliving compartments of the forest. When Hawaiian wet forests are younger nutrients are rock-derived. As they age and the nutrients are leached and weathered away from high rainfall, nutrients are supplied to the forest by the atmosphere via dust from the deserts of central Asia. The atmosphere becomes the dominant source of all major biological nutrients apart from phosphorus in less than 100,000 years. Phosphorus is still the primary limiting factor for biological activity in older wet forests since the weathering source of phosphorus is depleted but also because atmospheric inputs of phosphorus are very low (Chadwick et al., 1999).

Biodiversity

Biodiversity is high in lowland rainforests, specialized plants, and animals occur there, such as tree snails (e.g., *Achatinella* and *Partulina* spp.) and endemic *Cyrtandra* spp. Biodiversity is moderate to high in montane rainforests and montane cloud forests. Specialized plants and animals which occur there include predatory caterpillars (*Eupithecia*) and lobeliads (Campanulaceae). The montane wet system is important habitat for forest birds (Hawaiian honeycreepers, thrushes, and flycatchers) and seabirds (Newell's shearwater and Hawaiian petrel) (The Nature Conservancy, 2006).

Cultural Significance

In ancient Hawai'i, lowland rainforests were a source of native plants used for fiber, weaving, clothing, medicines, and wood. This zone is referred to as *wao kanaka*, the realm of man. Montane rainforests and montane cloud forests were not for casual visitation as they were remote and difficult to access and considered the realm of Hawaiian gods or *wao akua*. Only priests and medicine men ventured into these forests for healing herbs or to collect forest birds for feather work worn by the ruling chiefs (HDLNR, 2003; Pratt and Gon, 1998).

Montane rainforests are considered sacred for the Hawaiian people as they are the primary sources of the island's freshwater. The montane rainforest is highly efficient at capturing and retaining water. The wet forest captures rainfall through the multiple layers of canopy, subcanopy, shrub, and an herbaceous layer which includes mosses and ferns. These layers and the leaf litter slow the rainfall down and act like a giant sponge, absorbing water and allowing it to drip slowly underground and into streams and aquifers. The forest can also pull moisture from passing clouds (The Nature Conservancy, 2006). Wetforests continue to see to the practical and spiritual needs of the people of Hawai'i.

Pre-Human Condition

Before the modern era, wet forests occurred on windward (northeastern) slopes above the coastal zone on the main Hawaiian islands (except for Ni'ihau and Kaho'olawe) and extended to the summits of Kaua'i, the Wai'anae Range of O'ahu and eastern Moloka'i, as well as the windward slopes of Maui and Hawai'i, where wet forest extended well above 1,650 m elevation, and included a narrow band on the Kona side of the island of Hawai'i (Figs. 1–4). The Nature Conservancy (2006) estimates the total prehuman extent of wet forest to be 455,833 ha.

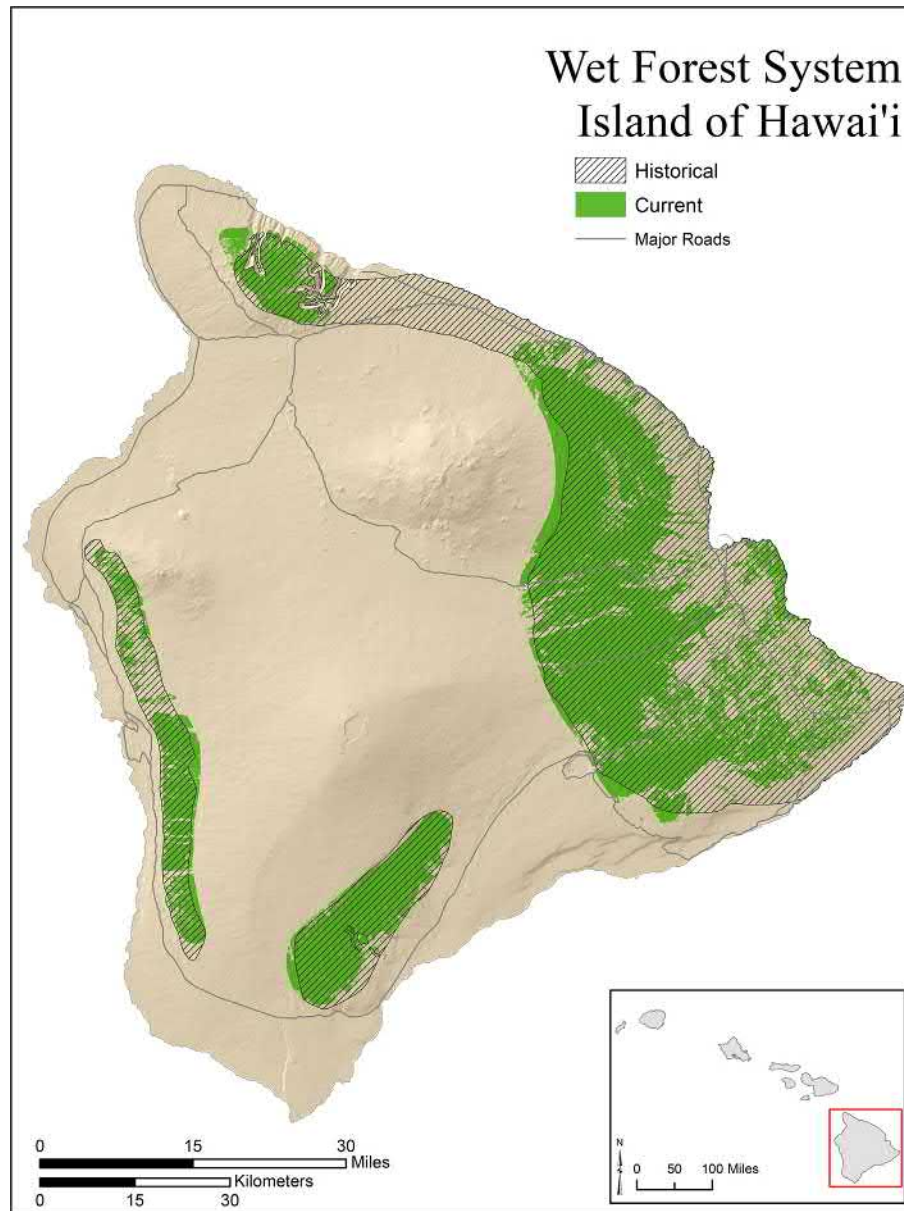


Fig. 1 Map of historical and current extent of wet forests on the island of Hawai'i (Reeves and Amidon, 2018).

Prior to the arrival of the Polynesians to the main Hawaiian islands the vegetation cover may be inferred from existing vegetation, remnants in disturbed areas, patterns of climate and substrates, and a few fossilized remains (Cuddihy and Stone, 1990). Table 1 below lists plants that were found in prehuman times in wet forests by subunit type.

Lowland rainforest is thought to have been the predominant original vegetation of the windward lowlands on the larger main islands (Cuddihy and Stone, 1990). In prehuman times, a lowland rainforest dominated by *Acacia koa* (koa) was probably widespread below 1,000 m on the larger islands in windward areas with deep soils. A clear picture of prehuman vegetation in montane rainforests is complicated by the extreme disturbance the lowlands have suffered. However relatively intact high-elevation montane rainforest currently cover large expanses in the same locations as they did in prehuman times. Pollen samples indicate similar dominant species in prehuman times that occur at present in montane rainforests and montane cloud forests including, hapu'u, 'ōhi'a and 'olapa (Cuddihy and Stone, 1990).

Pre-human wet forest resilience

The wet forest system was redundant across multiple islands, distributed over a broad geography, and able to withstand catastrophic events. During the prehuman period, wet forests were resilient due to the large extent, diversity of species and ability of species to

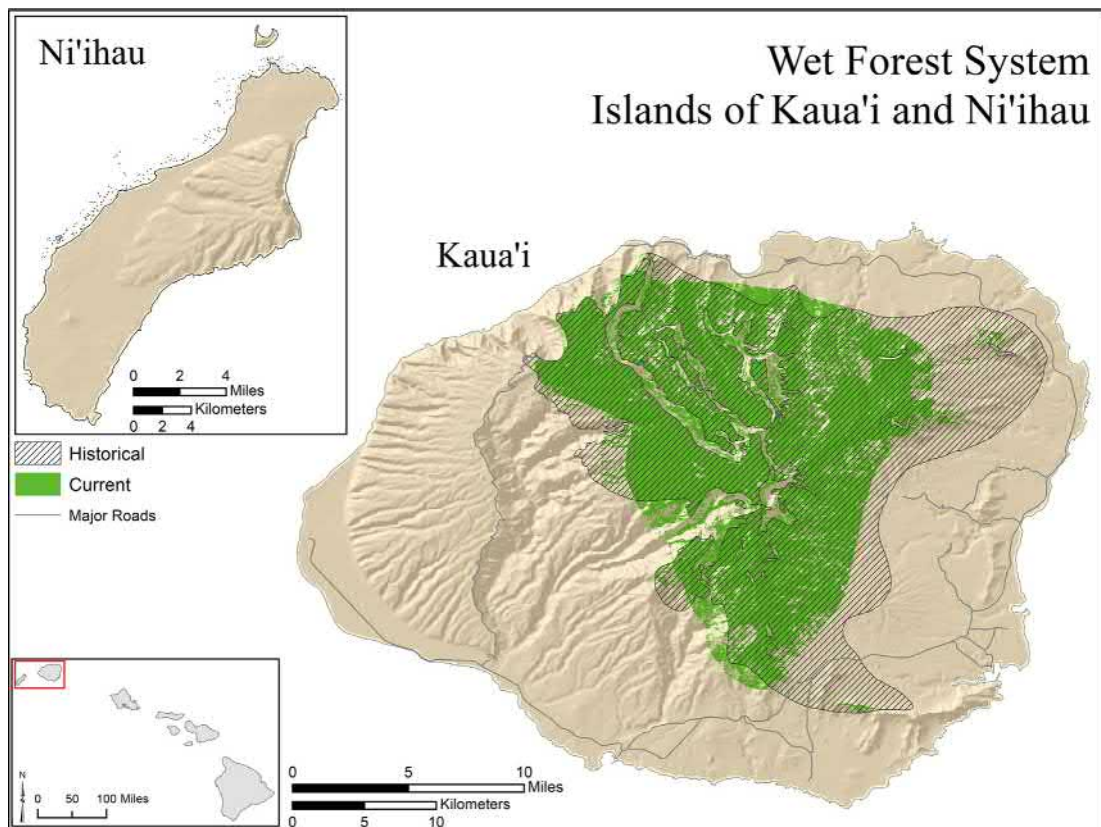


Fig. 2 Map of historical and current extent of wet forests on the islands of Kaua'i and Ni'ihau (Reeves and Amidon, 2018).

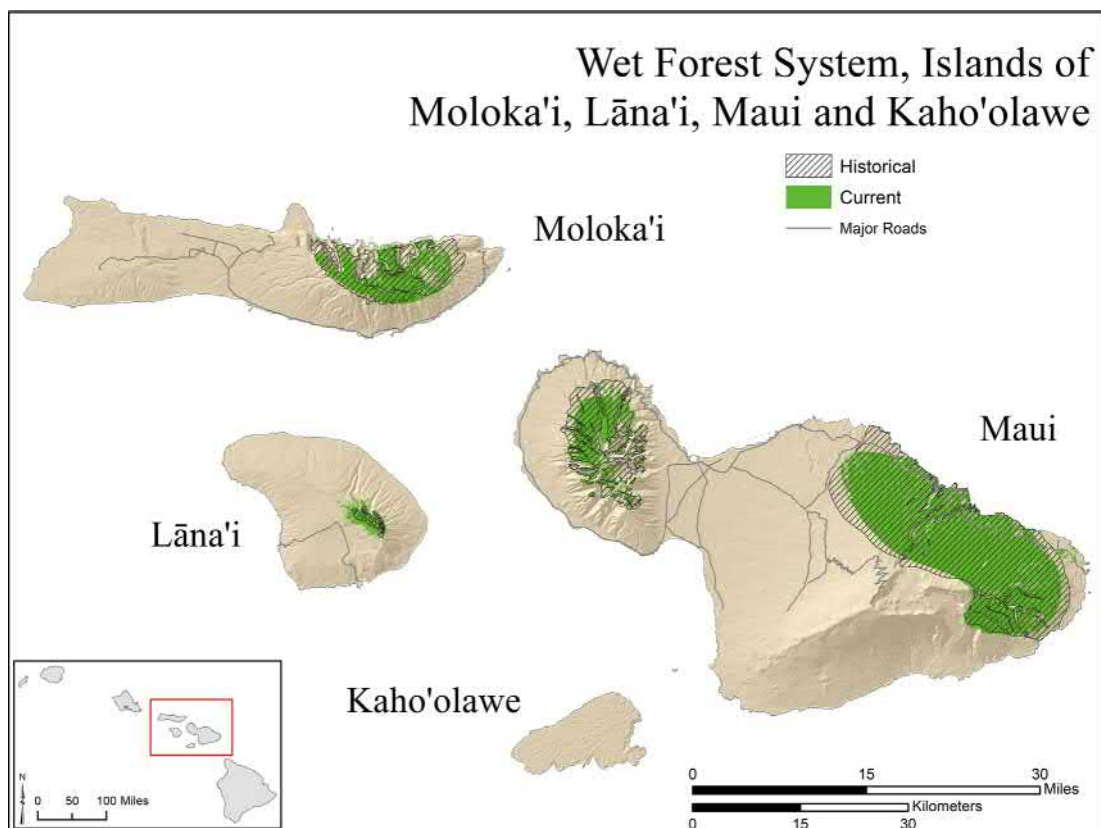


Fig. 3 Map of historical and current extent of wet forests on the islands of Moloka'i, Lāna'i, Maui and Kaho'olawe (Reeves and Amidon, 2018).

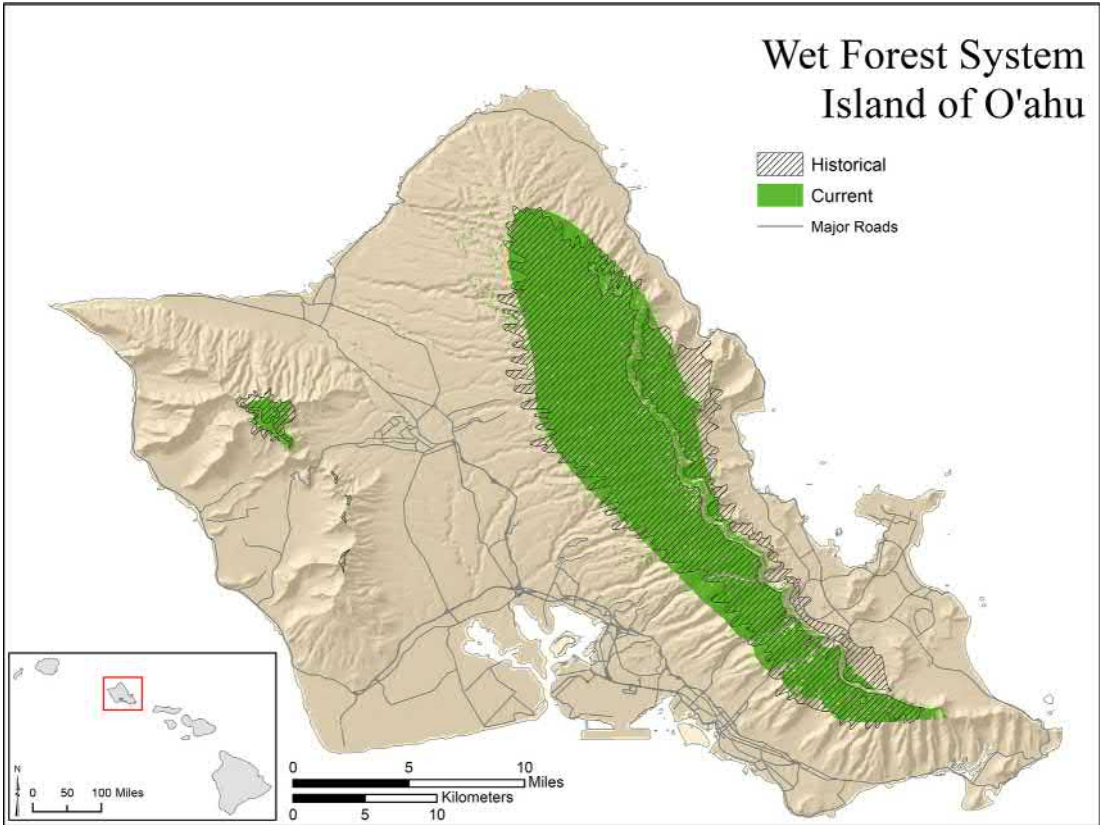


Fig. 4 Map of historical and current extent of wet forests on the island of O'ahu (Reeves and Amidon, 2018).

Table 1 Plant species found in Hawaii wet forest in pre-human times by subunit (Gagné and Cuddihy, 1999; Landfire, 2016; Cuddihy, 1989).

Wet forest subunits	Characteristic plants
Lowland rainforest	<i>Acacia koa</i> , <i>Adenophorus</i> spp., <i>Alyxia stellata</i> , <i>Antidesma platyphyllum</i> , <i>Astelia menziesiana</i> , <i>Bobea elatior</i> , <i>Broussaisia arguta</i> , <i>Cheirodendron</i> spp., <i>Cibotium</i> spp., <i>Coprosma</i> spp., <i>Cyrtandra</i> spp., <i>Dicranopteris linearis</i> , <i>Diospyros sandwicensis</i> , <i>Diplopterygium pinnatum</i> , <i>Elaphoglossum</i> spp., <i>Freycinetia arborea</i> , <i>Hedyotis</i> spp., <i>Huperzia</i> spp., <i>Ilex anomala</i> , <i>Korthalsella</i> spp., <i>Leptecophylla tameiameiaie</i> , <i>Machaerina</i> spp., <i>Melicope</i> spp., <i>Metrosideros polymorpha</i> , <i>Myrsine</i> spp., <i>Peperomia</i> spp., <i>Perrottetia sandwicensis</i> , <i>Pipturus</i> spp., <i>Pittosporum</i> spp., <i>Polyscias</i> spp., <i>Pritchardia</i> spp., <i>Psychotria</i> spp., <i>Sadleria</i> spp., <i>Smilax melastomifolia</i> , <i>Sticherus owhyensis</i> , <i>Urera glabra</i> , <i>Vaccinium</i> spp.
Montane rainforest	<i>Acacia koa</i> , <i>Adenophorus</i> spp., <i>Alyxia stellata</i> , <i>Anoectochilus sandwicensis</i> , <i>Astelia</i> spp., <i>Athyrium</i> spp., <i>Broussaisia arguta</i> , <i>Bobea brevipes</i> , <i>Carex alligata</i> , <i>Cheirodendron</i> spp., <i>Cibotium</i> spp., <i>Clermontia</i> spp., <i>Coprosma</i> spp., <i>Cyrtandra</i> spp., <i>Cyanea</i> spp., <i>Dicranopteris linearis</i> , <i>Diplopterygium pinnatum</i> , <i>Dubautia</i> spp., <i>Elaphoglossum</i> spp., <i>Eurya sandwicensis</i> , <i>Hedyotis</i> spp., <i>Huperzia</i> spp., <i>Ilex anomala</i> , <i>Korthalsella</i> spp., <i>Leptecophylla tameiameiaie</i> , <i>Lobelia</i> spp., <i>Machaerina</i> spp., <i>Melicope</i> spp., <i>Metrosideros polymorpha</i> , <i>Myrsine</i> spp., <i>Peperomia</i> spp., <i>Perrottetia sandwicensis</i> , <i>Pittosporum</i> spp., <i>Polyscias</i> spp., <i>Pritchardia</i> spp., <i>Psychotria</i> spp., <i>Rubus hawaiiensis</i> , <i>Sadleria</i> spp., <i>Scaevola</i> spp., <i>Smilax melastomifolia</i> , <i>Stenogyne</i> spp., <i>Vaccinium</i> spp.
Montane cloud forest	<i>Acacia koa</i> , <i>Adenophorus</i> spp., <i>Alyxia stellata</i> , <i>Anoectochilus sandwicensis</i> , <i>Astelia</i> spp., <i>Broussaisia arguta</i> , <i>Cheirodendron</i> spp., <i>Cibotium</i> spp., <i>Clermontia</i> spp., <i>Coprosma</i> spp., <i>Cyrtandra</i> spp., <i>Cyanea</i> spp., <i>Dubautia</i> spp., <i>Dryopteris</i> spp., <i>Elaphoglossum</i> spp., <i>Huperzia</i> spp., <i>Ilex anomala</i> , <i>Korthalsella</i> spp., <i>Leptecophylla tameiameiaie</i> , <i>Lobelia</i> spp., <i>Machaerina</i> spp., <i>Melicope</i> spp., <i>Metrosideros polymorpha</i> , <i>Myrsine</i> spp., <i>Peperomia</i> spp., <i>Pittosporum</i> spp., <i>Phyllostegia</i> spp., <i>Sadleria</i> spp., <i>Smilax melastomifolia</i> , <i>Stenogyne</i> spp., <i>Trematolobelia</i> spp., <i>Vaccinium</i> spp.

recolonize after stochastic events such as landslides, tropical cyclones, lava flows, and fires. When new lava flowed on older rainforests, the forest began the process of regeneration. Islands of remnant vegetation separated by new lava flows were formed. These remnant islands of vegetation are known as kipuka, the seeds and spores from kipuka colonize new lava flows. Older landscapes subjected to fires, tropical cyclones or landslides were recolonized by native plant species in neighboring valleys and watersheds. Uluhe colonized areas which were denuded, 'ōhi'a trees and other plants eventually cover and over shade uluhe and form/reform the forest (Carlquist, 1980).

Representation, the number or percent of ecological settings across the range, was high in wet forests. Each subunit contained riparian areas, natural clearings, wetlands and bogs of mosses, sedges, grasses, and shrubs. These inclusions were common and they supported a variety of species, some of which are specific to a subhabitat type (e.g., wetland or bog obligate species). During prehuman times species diversity and endemism was high in each subunit of wet forest (The Nature Conservancy, 2006). High biodiversity increases the resiliency and representation of wet forests.

Current Condition

Current extent/range

The extent of Hawaiian islands wet forest today is largely similar across all islands as the prehuman condition, except for substantial loss of lowland rainforest on the islands of O'ahu and Kaua'i (Figs. 1–4). There are 373,764 ha of wet forest (all subunits combined) in the Hawaiian islands with 65% on the island of Hawai'i (Fig. 5). Seventy-eight percent (235,819 ha) is native species dominated (> 50% native species), the remaining portion of wet forest is nonnative species dominated (> 50% invasive species) (Fig. 6). There are nine vegetation classes of wet forest based on canopy height and cover and dominant tree species (Fig. 7). They are closed hala (*Pandanus tectorius*), closed koa-ōhi'a forest, closed 'ōhi'a wet forest, low stature 'ōhi'a wet forest, mixed native nonnative wet forest, nonnative wet forest, open koa-ōhi'a wet forest, open 'ōhi'a wet forest and plantation forest. Dominant native species are mostly the same in lowland rainforest, montane rainforest and montane cloud forests as in prehuman times (Table 1). Nonnative species are listed below in the subunit descriptions. A fourth subunit of wet forest, Hawai'i managed tree plantation, is also described.

Lowland rainforest

Lowland rainforest became invaded during the 20th century in many areas by ecosystem altering nonnative plants including but not limited to: *Psidium cattleianum* (strawberry guava), *Albizia moluccana* (Albizia), *Melastoma candidum*, *Clidemia hirta* (Coster's curse), *Rubus* spp., *Aleurites moluccana* (kukui nut tree) and *Syzygium malaccense* (mountain apple). Though lowland rainforest is still widespread throughout Hawai'i, invasive trees have significantly impaired the system's ability to perpetuate itself. In fact many areas where native lowland rainforest used to occur are completely dominated by alien species. Other dominant alien species in these forests include but are not limited to: *Mangifera indica* (mango), *Psidium guajava* (common guava), *Syzygium cumini* (Java plum), *S. jambos* (rose apple) and *Phyllostachys nigra* (bamboo) (Gagné and Cuddihy, 1999).

Montane rainforest and montane cloud forest

Hawai'i montane rainforest and montane cloud forest were minimally affected prior to western contact, largely because these upper elevation wet forests are remote and difficult to access. Hawaiians ventured primarily to lower elevation forests for koa and other forest products (Cuddihy and Stone, 1990). Early in the 18th century with the introduction of cattle and more efficient logging of koa and 'ōhi'a, some montane cloud forests on Maui, Moloka'i, and Hawai'i were converted to pasture lands, a process that was accelerated by the introduction of nonnative forage grasses (Cuddihy and Stone, 1990; Pratt and Jacob, 2009). In addition to nonnative grasses, other nonnative species which invade montane wet and montane cloud forests include Himalayan ginger (*Hedychium gardnerianum*), Australian tree fern (*Cyathea cooperi*), and mules foot fern (*Angiopteris evecta*).

Hawai'i managed tree plantation

During the early 20th century large private forest reserves (protected areas) were created in response to the damage caused to native forests from grazing, logging, and feral animals. Mostly nonnative trees were planted above sugar plantations at Lihu'e, Kaua'i (4,050 ha) and Pahala, Hawai'i (20,240 ha), and on Maui and O'ahu for watershed protection (Cuddihy and Stone, 1990). Tree plantings for forest restoration consisted of introduced, fast-growing tropical species such as, *Eucalyptus globulus*, *E. robusta* (swamp mahogany), *Melaleuca quinquenervia* (paperbark), *Ficus* spp. (banyan) among others. Native species and commercially valuable timber were avoided so that future generations would not be tempted to harvest the trees that would result in damage to the watershed (Cuddihy and Stone, 1990). The emphasis on forest reserves as protected watersheds began to change during the 1940s and 1950s. Experimental planting of introduced trees accelerated, and large-scale plantings of timber species began in forest reserves (Hosmer, 1959). Currently, managed tree plantations are of commercially valuable trees harvested for lumber and fuel. Introduced trees planted for lumber and fuel include, *Araucaria columnaris*, *Araucaria heterophylla*, *Eucalyptus* spp., *Pinus elliottii*, *Pinus radiata*, and *Sequoia sempervirens*. Plantations are often at the lower elevation edge of current forest reserves (Landfire, 2016). There are 10,645 ha of wet forest managed tree plantations (see Table 2). Commercial koa forestry on deforested lands emerged in recent decades to supply demand for this valuable hardwood (Skolmen and Fujii, 1980; Baker et al., 2009). Koa silviculture is practiced on old pasturelands in wet areas.

Wet forest land ownership

Fifty-eight percent (176,943 ha) of Hawaiian islands wet forest is owned by Federal, State, local and Hawaiian homelands government, except for island of Lāna'i, which is entirely privately owned (Fig. 8). Lāna'i contains 1,291 ha of wet forest. On the island of Hawai'i there are 521,900 ha of conservation district lands, that include large areas of wet forest. Housing development and intensive agriculture (planting of field crops) are not permitted on lands zoned for conservation (County of Hawai'i, 1970).

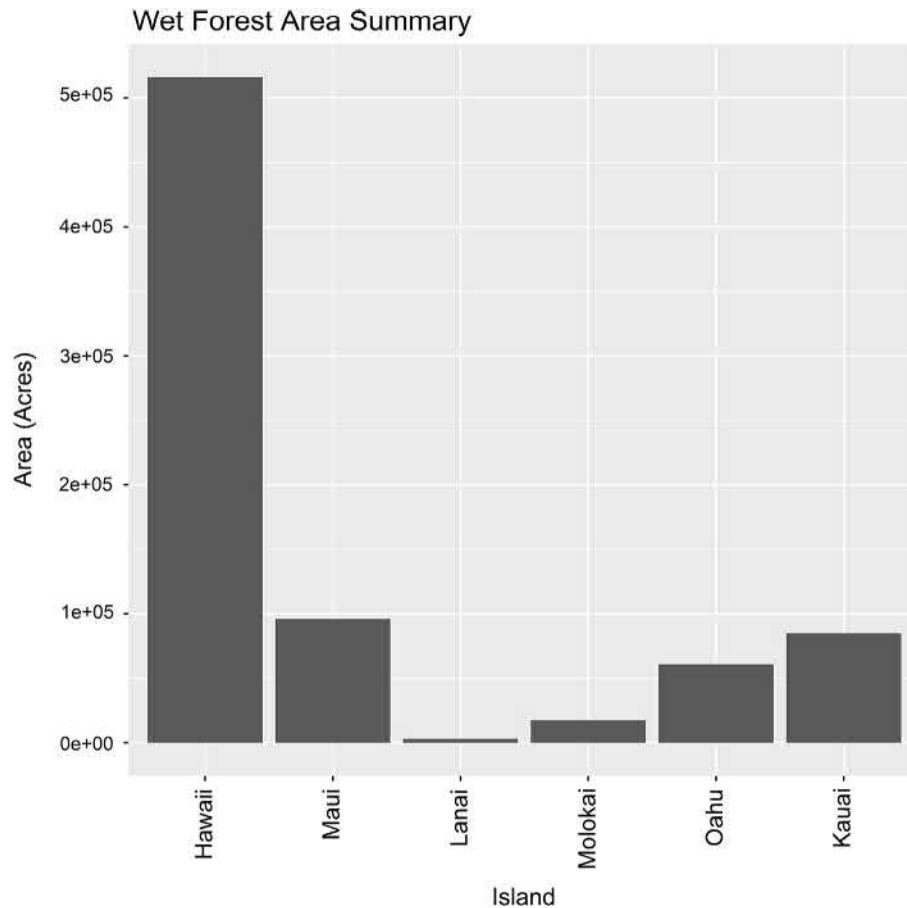


Fig. 5 Wet forest area summary (Reeves and Amidon, 2018).

Stressors

The health and distribution of Hawaiian islands wet forest is affected by natural and nonnative processes and agents. These stressors include introduced ungulates, plants, predators (rats, cats, and mongoose), herbivores (slugs, rodents, and insects), and plant disease. Fire, drought, natural disasters, climate change, agriculture, and urban development also threaten and degrade wet forests. The most significant stressors are discussed below.

Invasive ungulates

Hawaiian wet forests are currently threatened by the destruction or degradation of habitat due to invasive ungulates, including pigs, goats, deer, and cattle. The mild climate of the islands, combined with the lack of competitors or predators, led to the successful establishment of large populations of these invasive mammals, to the detriment of native Hawaiian species and ecosystems. The wet forests are exposed to both direct and indirect negative impacts of invasive ungulates. The effects of ungulates include the destruction of vegetative cover; trampling of plants and seedlings; direct consumption of native vegetation; soil disturbance; dispersal of invasive plant seeds on hooves and coats, and through the spread of seeds in feces; and creation of open disturbed areas conducive to further invasion by invasive plant species. All of these impacts can lead to the subsequent conversion of a native plant community to one dominated by invasive species (Nogueira-Filho et al., 2009). In addition to these direct effects, because ungulates inhabit terrain that is often steep and remote, foraging and trampling contributes to severe erosion of watersheds and degradation of streams (Cuddihy and Stone, 1990). As early as 1900, there was increasing concern expressed about the integrity of island watersheds due to effects of ungulates and other factors, leading to the establishment of a professional forestry program emphasizing soil and water conservation.

Invasive plants

Invasive plants adversely affect microhabitat in the forest by modifying availability of light and nutrient cycling processes, and by altering soil-water regimes (Smith, 1985). Some invasive plants may release chemicals that inhibit growth of other plants. These competitive advantages allow invasive plants to convert native-dominated plant communities to nonnative plant communities. Native vegetation on all of the main Hawaiian Islands has undergone extreme alteration because of past and present land

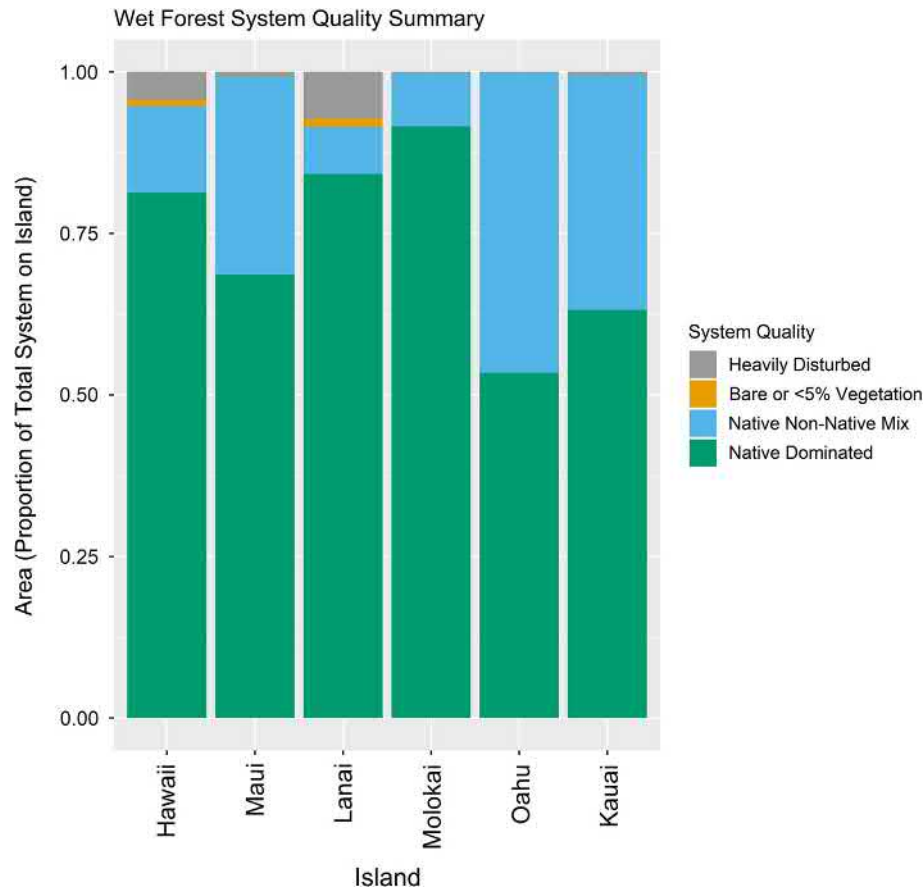


Fig. 6 Wet forest habitat quality summary (Reeves and Amidon, 2018).

management practices, including ranching, the deliberate introduction of nonnative plants and animals, and agricultural development (Cuddihy and Stone, 1990). The original native flora of Hawai'i (species that were present before humans arrived) consisted of about 1,000 taxa, 89% of which are endemic (species that occur only in the Hawaiian Islands). Over 800 plant taxa have been introduced from elsewhere, and nearly 100 of these have become pests (e.g., injurious plants) in Hawai'i (Smith, 1985; Gagné and Cuddihy, 1999). A smaller subset of species have attributes which degrade native wet forest ecosystems. These relatively few species, however, are capable of serious and irreversible damage.

Although 'ōhi'a dieback is considered a natural forest regeneration phenomenon, now widespread invasive plant species such as strawberry guava and albizia, are having negative impacts on the natural regeneration of the native Hawaiian wet forest following 'ōhi'a dieback occurrences. Strawberry guava spreads clonally and by seeds, it forms dense thickets which do not allow any other species to grow. Albizia is a nitrogen-fixing tree which grows very fast, it overgrows the otherwise dominant 'ōhi'a. Wherever this overgrowth occurs 'ōhi'a dies from lack of light under the canopy of the trees (Mueller-Dombois, 2008). Feral ungulates exacerbate the spread of strawberry guava and other nonnative weeds and negatively impact the regeneration of native 'ōhi'a lowland rainforests (Murphy et al., 2014; Mueller-Dombois and Boehmer, 2013).

Plant disease

The primary plant disease that impacts wet forests are two species of the fungal genus *Ceratocystis* which cause mortality in 'ōhi'a, referred to as rapid 'ōhi'a death (ROD). 'Ōhi'a is Hawai'i's most common and widespread native tree, occurring from sea level to 8,200 ft (2,500 m) elevation and is often a dominant species in lowland, montane wet, and montane cloud forest. It is an ecologically important species that defines native forest succession and ecosystem function, provides habitat to many native species, and is also culturally significant (Keith et al., 2015).

Rapid 'ōhi'a death was identified in 2012 on the island of Hawai'i and discovered in 2018 on the island of Kaua'i. The disease causes browning in the crowns of 'ōhi'a trees and ultimately leads to mortality. By the end of 2014, it was reported that approximately 2,428 ha of forest stands from Kalapana to Hilo showed greater than 50% mortality (Friday et al., 2015). By 2017 approximately 30,351 ha showed symptoms of ROD, including areas in Kona where dry forest habitat occurs. Once a stand is infected, nearly 100% of the trees can succumb to the disease within 2–3 years. Humans are thought to be a primary vector of transmission by moving infected wood, or contaminated tools, gear, and vehicles from one location to another. In addition, research has

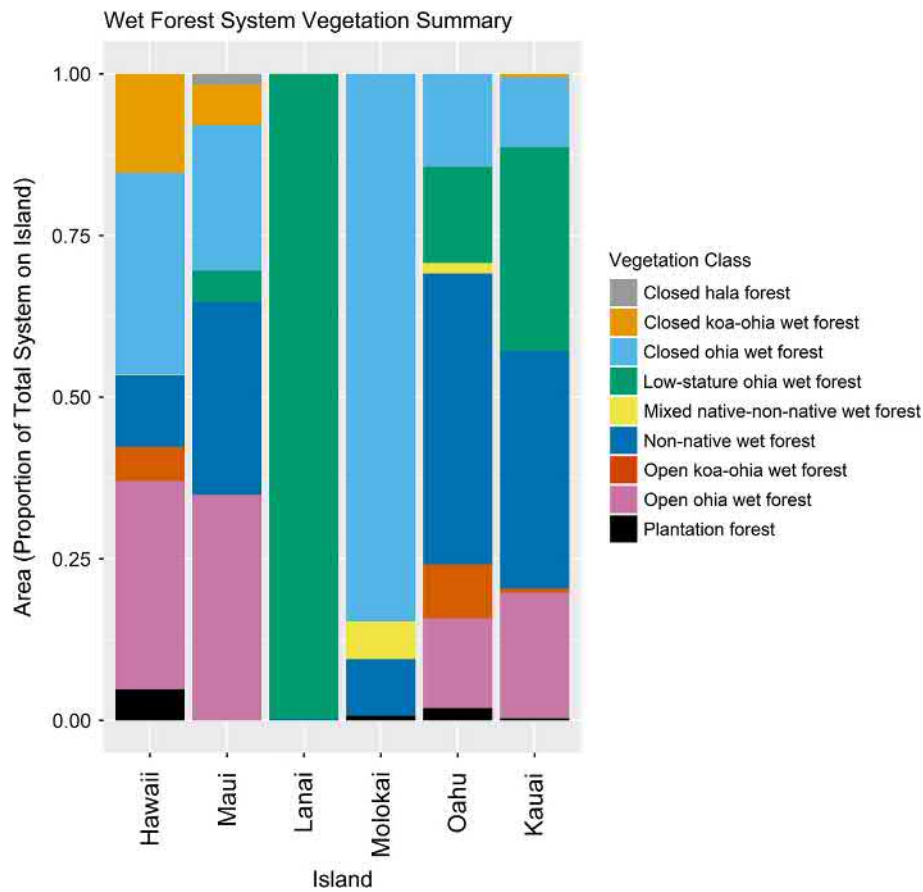


Fig. 7 Wet forest vegetation summary (Reeves and Amidon, 2018).

Table 2 Hawaii managed tree plantation wet forest extent by Island (Reeves and Amidon, 2018).

<i>Island</i>	<i>Acres/hectares of managed tree plantation</i>
Kaua'i	276/112
O'ahu	1156/468
Moloka'i	119/48
Hawai'i	24,753/10,017

identified a nonnative ambrosia beetle as another likely vector. The beetles bore into trees and create a fine dust, referred to as frass, that can be carried by the wind and enter 'ōhi'a through wounds (CTAHR, 2018). Stands which are affected by ROD in areas where invasive plants such as strawberry guava and albizia occur, as mentioned above regarding 'ōhi'a dieback, are not likely to recover to native species dominated forests.

Natural disasters

In addition to their direct effects on plants, tropical cyclones (tropical storms and hurricanes) exacerbate the impacts from other threats such as habitat modification and destruction by ungulates and competition with invasive plants. By destroying vegetation, tropical cyclones open the forest canopy, thus modifying the availability of light, and create disturbed areas conducive to invasion by invasive plants (Asner and Goldstien, 1997; Harrington et al., 1997). Two hurricanes (Iwa and Iniki respectively) struck Kaua'i in 1982 and 1992 causing much damage to the montane wet forest of the Alakai Wilderness Preserve. Several species of endangered honeycreepers have not been sighted since Hurricane Iniki in 1992 despite intensive bird surveys in formally occupied areas within the preserve (USFWS, 2006).

Climate change

The Hawaiian Islands Climate Vulnerability and Adaptation Synthesis evaluated wet forests as having overall moderate vulnerability to climate change with moderate-high sensitivity to climatic factors and disturbance regimes such as tropical cyclones,

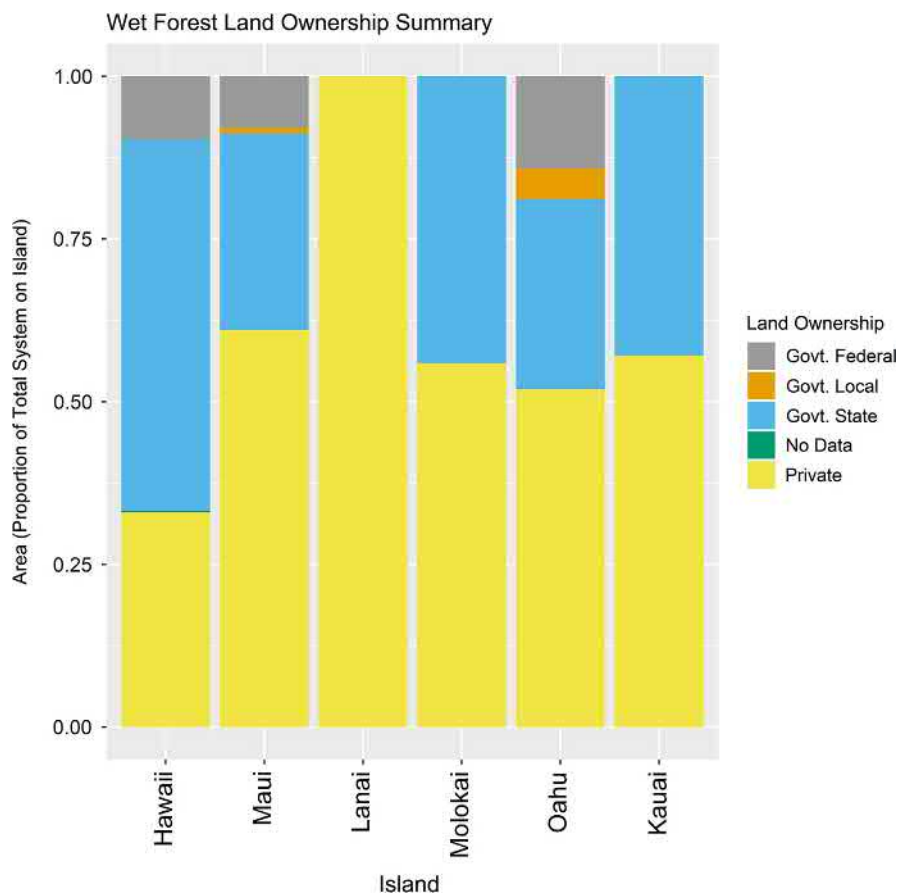


Fig. 8 Wet forest land ownership summary (Reeves and Amidon, 2018).

drought, and fire (Gregg, 2018). Wet forests are sensitive to factors that alter moisture gradients. Alteration of moisture gradients may impact species composition and forest distribution and potentially reduce habitat extent. The synthesis predicts that wet forests in remote areas will remain relatively intact but lower elevation forests will become more degraded.

Conservation Efforts

Active conservation is conducted by Federal and State agencies, nonprofit organizations, and private landowners. In Table 3 below, existing conservation areas that contain wet forests are listed by island. Efforts by conservation organizations may include invasive plant and animal control, and native forest restoration. Invasive plant control includes the use of herbicides, hand tools, and in some instances, biocontrol methods to reduce the numbers and distribution of invasive plants in mesic forests. For example, the Brazilian scale (*Tectococcus ovatus*) has been introduced to control strawberry guava. Reintroduction of native plants is also used to control the spread of invasive plants. Ungulates are controlled through the use of exclusion fences, trapping, and hunting. Predator control for rats, mongoose and cats (via rodenticide and/or trapping) is occurring in wet forests which are important for forest-birds and seabirds (HDLNR, 2016).

Reserves

Twenty percent (10,769 ha) of wet forest in the state of Hawai'i is protected in reserves. Reserves that benefit wet forests are found throughout the state of Hawai'i and exist in national parks, national wildlife refuges, State natural area reserves, State forest reserves, and on private preserves. The State of Hawai'i's Forest Reserve System (FRS) from its inception represented a public-private partnership for the protection of upland forests needed to provide water requirements for lowland agriculture demands and use by surrounding communities (Cuddihy and Stone, 1990). There are 274,625 ha in the FRS on the islands of Kaua'i, O'ahu, Moloka'i, Maui, and Hawai'i, protecting large areas of Hawai'i wet forest (HDLNR, 2018). The State of Hawai'i's Natural Area Reserve System (NARS) was established to preserve and protect representative samples of Hawaiian biological ecosystems and geological formations. There are 21 natural area reserves that have been designated statewide (HDLNR, 2016). Several of these reserves contain

Table 3 Wet forest conservation areas in the Hawaiian Islands (HDLNR, 2018; Reeves and Amidon, 2018).

<i>Island</i>	<i>Wet forest subcategory</i>	<i>Name of reserve</i>	<i>Landowner</i>	<i>Number acres (hectares) protected</i>
Kaua'i	Lowland and montane wet	Hono O Nā Pali Natural Area Reserve	State	2286 (925)
Kaua'i	Montane wet	Alakai Wilderness Preserve	State	1953 (790)
Kaua'i	Lowland wet and montane wet	The Nature Conservancy-Wainiha Preserve	Private	5405 (2187)
Kaua'i	Lowland wet	National Tropical Botanical Garden-Limahuli Preserve	Private	459 (186)
Kaua'i	Lowland wet	Blue Hole, Lihue Koloa Forest Reserve	State	30 (12)
O'ahu	Lowland wet	Kaluanui Natural Area Reserve	State	367 (149)
O'ahu	Montane wet	Mt. Ka'ala Natural Area Reserve	State	224 (91)
Maui	Montane wet and montane cloud	Hanawi Natural Area Reserve	State	4820 (1951)
Maui	Montane wet	West Maui Natural Area Reserve	State	357 (144)
Maui	Montane wet and montane cloud	The Nature Conservancy-Waikamoi Preserve	Private	3496 (1415)
Maui	Lowland wet and montane wet	Haleakalā National Park	Federal	7388 (2990)
Moloka'i	Montane wet	Pu'u Ali'i Natural Area Reserve	State	858 (347)
Moloka'i	Montane wet and lowland wet	Oloku'i Natural Area Reserve	State	1284 (520)
Moloka'i	Montane wet	The Nature Conservancy-Pelekunu Preserve	Private	1639 (663)
Moloka'i	Montane wet	The Nature Conservancy—Kamakou Preserve	Private	1197 (484)
Hawai'i	Lowland and montane wet	Kahauale'a Natural Area Reserve	State	16,292 (6593)
Hawai'i	Lowland wet	Kipahoehe Natural Area Reserve	State	2800 (1133)
Hawai'i	Lowland and montane wet	Laupahoehoe State Natural Area Reserve	State	7968 (3225)
Hawai'i	Lowland and montane wet	Pu'u Maka'ala Natural Area Reserve	State	17,169 (6948)
Hawai'i	Montane wet	Kamehameha Schools-Kilauea Forest	Private	2955 (1196)
Hawai'i	Lowland and montane wet	Ka'ū Forest Reserve	State	12,000 (4856)
Hawai'i	Lowland and montane wet	The Nature Conservancy-Ka'ū	Private	3561 (1441)
Hawai'i	Lowland and Montane Wet	Kamehameha Schools Ka'ū Forest	Private	2883 (1167)
Hawai'i	Montane wet and montane cloud	Pu'u O 'Umi Natural Area Reserve	State	10,122 (4096)
Hawai'i	Lowland and montane wet	Hakalau National Wildlife Refuge	Federal	28,109 (11,376)
Hawai'i	Lowland and montane wet	Hawaii Volcanoes National Park	Federal	21,774 (8812)

wet forest habitat. The Hono O Nā Pali, Kaluanui, Mt. Ka'ala, Pu'u Ali'i, Oloku'i, Hanawi, West Maui, Kahauale'a, Kipahoehe, Laupahoehoe, Pu'u Maka'ala, and Pu'u O 'Umi Natrual Area Reserves contain large areas and excellent examples of lowland wet, montane wet and montane cloud forest. There are several other reserves throughout the state which benefit wet forests. The Nature Conservancy of Hawai'i has 11 preserves in the State of Hawai'i encompassing more than 16,187 ha, including 9,195 ha of wet forest. On Kaua'i, the State of Hawaii manages the Alaka'i Wilderness Preserve, portions of which are fenced to exclude invasive ungulates and invasive plant control efforts are ongoing. On Maui, large areas of native wet forest are fenced to exclude feral ungulates at Haleakalā National Park and The Nature Conservancy's, Waikamoi Preserve. On Moloka'i, The Nature Conservancy's, Pelekunu and Kamakou Preserves, are fenced and ungulates have been removed. On Hawai'i Island, large areas of wet forest are protected in Hawai'i Volcanoes National Park, the Hakalau Forest National Wildlife Refuge and in the The Nature Conservancy's Ka'ū Preserve. Ongoing invasive plant control is also occurring in many of these areas.

Watershed partnerships

Watershed partnerships are voluntary alliances of public and private landowners and water municipalities committed to protecting over 809,371 ha of the most important watershed lands in Hawai'i. Individual watershed partnerships have been established on five islands (Hawai'i, Maui, Moloka'i, O'ahu, and Kaua'i) to support statewide watershed protection needs (see Fig. 9 and Table 4). The first watershed partnership formed in 1991 (East Maui Watershed Partnership) and in 2003 on the 100th anniversary of Hawai'i's Forest Reserve System, Governor Linda Lingle signed a Memorandum of Understanding (MOU) with the watershed partnerships formally recognizing the states dedication to watershed protection and established the Hawai'i Association of Watershed Partnerships (HAWP) (HAWP, 2018). Typical management activities implemented by watershed partnerships which protect wet forests include landscape scale ungulate proof fencing, ungulate and invasive plant removal and rare species protection. Several partnerships manage large scale active restoration projects which plant native plants back into degraded areas. In addition to on the ground work, watershed partnerships play an important role in community outreach, education, and engagement.

Rain Follows the Forest Initiative

The State of Hawaii, HDLNR launched the "Rain Follows the Forest" or Hahai no ka ua i ka ululā'au Plan in November 2011. The goal of the plan is to double the amount of protected watershed area for the purpose of securing water supply by 2021. The plan recognizes that the most efficient way to secure island water supply is by protection of the source, montane rainforests.

Hawai'i Watershed Partnerships

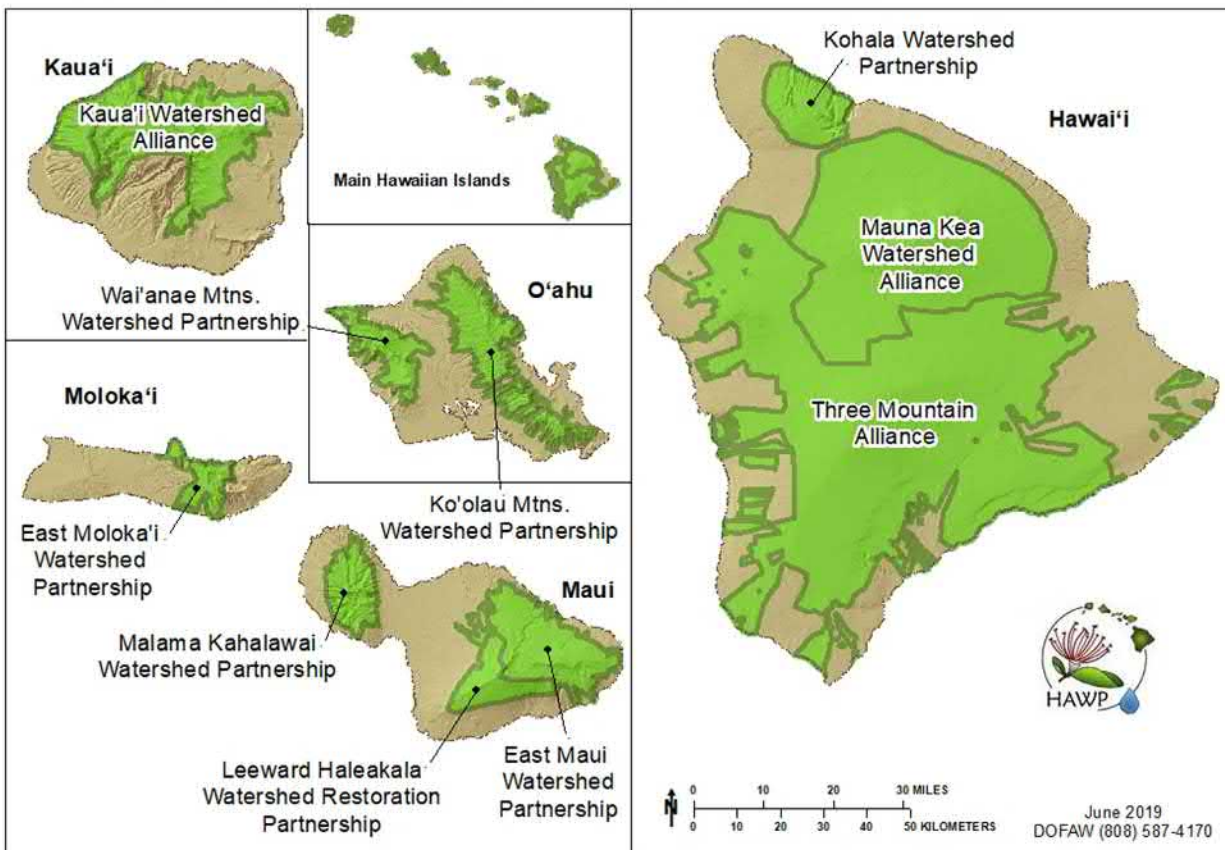


Fig. 9 Map of the distribution of the Hawai'i Association of Watershed Partnerships. Adapted from Hawai'i Association of Watershed Partnerships [HAWP]. (2018). *Watershed Partnerships*. <http://hawp.org/>.

Table 4 Watershed Partnerships, number of partners, hectares managed, and wet forest protection in the Hawaiian Islands (HAWP, 2018).

Island	Watershed partnership	Number of partners	Total management area/wet forest Ha
Kaua'i	Kaua'i Watershed Alliance	11	58,276/4,088
O'ahu	Ko'olau Mountains Watershed Partnership	16	40,469/4,452
O'ahu	Wai'anae Mountains Watershed Partnership	8	18,963/405
Maui	East Maui Watershed Partnership	9	48,360/16,544
Maui	West Maui Mountains Watershed Partnership	13	19,150/8,824
Moloka'i	East Moloka'i Watershed Partnership	15	16,862/4,047
Hawai'i	Three Mountain Alliance	10	445,154/111,289
Hawai'i	Mauna Kea Watershed Alliance	8	103,700/11,376
Hawai'i	Kohala Watershed Partnership	11	29,947/2,428

Consequently several thousand acres of montane rainforests have been protected and several thousand additional acres are targeted for protection across the state, see Fig. 10 below. HDLNR works with watershed partnerships to implement the plan.

Laws and Biosecurity

Biosecurity

Control of introduction and spread of invasive species is critical to protect the integrity of wet forest ecosystems. Executive orders 11987 (1977), 13112 (1999), and 13751 (2016) direct federal and encourage other agencies, councils, and processes to coordinate efforts to prevent the spread of invasive species.

Watershed Priority Areas

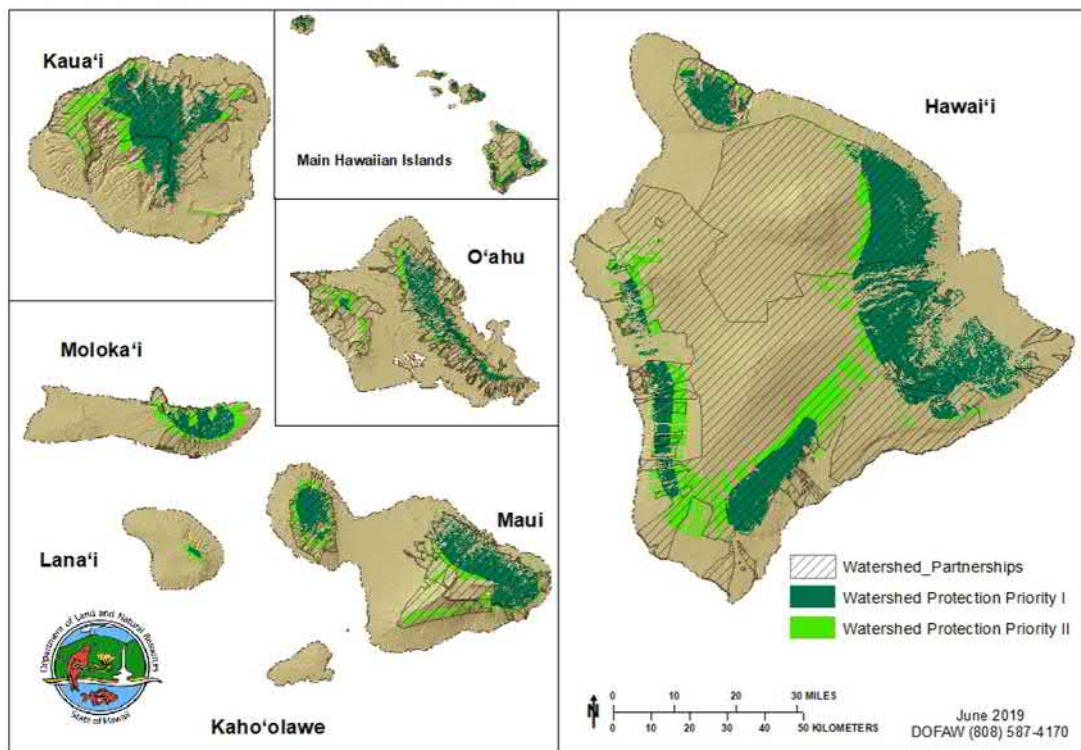


Fig. 10 Rain Follows the Forest Initiative priority areas for protection (HDLNR, 2011).

Prevention and management of invasive species helps prevent the further incursion of invasive species into Hawai'i that can establish and outcompete native wet vegetation or destroy seedlings and regeneration, especially after disturbance events. Invasive species are a primary stressor for wet forest and therefore prevention and management across the State of Hawai'i is essential to protect the remaining wet forest.

The Hawai'i Invasive Species Council (HISC) is a State of Hawai'i body that provides funding and is responsible for the Hawai'i Interagency Biosecurity Plan that guides the state's biosecurity implementation and tracking Hawai'i's biosecurity comprises many components and is the work of multiple state, federal, and county agencies and partners. Although the Hawai'i Department of Agriculture (HDOA) is the only agency with a mandated biosecurity program, this biosecurity plan recognizes that HDOA is not alone in protecting Hawai'i's agriculture, environment, and people from the impacts of invasive species. Key players in Hawai'i's biosecurity include the Hawai'i HDLNR, Hawai'i Department of Health (DOH), and University of Hawai'i (UH).

Endangered Species Act

Wet forests in Hawai'i provide habitat for many endangered plant, insect, and forest bird species. The Endangered Species Act of 1973 (ESA) aims to provide a framework to conserve and protect endangered and threatened species and their habitats. As habitat loss is the primary threat to most imperiled species, the ESA allows the Fish and Wildlife Service (FWS) and National Marine Fisheries Service (NMFS) to designate specific areas as protected critical habitat zones. In 1978, Congress amended the law to make critical habitat designation a mandatory requirement for all threatened and endangered species. Twenty percent (80,980 ha) of wet forest habitat in the state of Hawai'i is designated as critical habitat for several endangered species including forest birds, plants, and invertebrates (Fig. 11). Section 4 of the ESA refers to the section of the act pertaining to the determination of threatened and endangered species, as well as the establishment of critical habitat. Critical habitat is the regulatory link between habitat protection and recovery goals, it requires the identification and protection of all lands, water and air necessary to recover endangered species. The need for individual and population growth including food, water, light, nutritional requirements, breeding sites, seed germination, seed dispersal, and lack of disturbances are all considered in determining critical habitat.

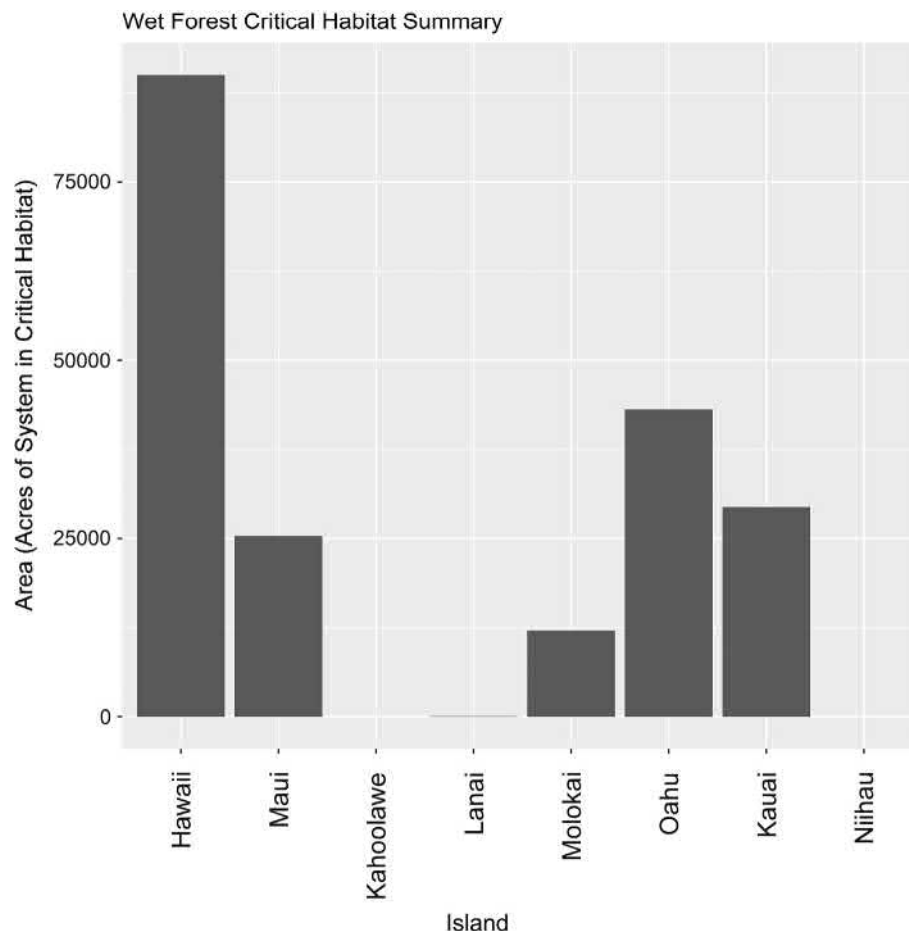


Fig. 11 Federally designated critical habitat on the main Hawaiian Islands composed of wet forest habitat (Reeves and Amidon, 2018).

Summary of Interactions of Stressors and Conservation Efforts

The extent of Hawai'i wet forest today is largely similar across all islands as the prehuman condition, except for substantial loss of lowland rainforest on the islands of O'ahu and Kaua'i. Loss of lowland rainforest is due to invasion by feral ungulates, invasive plants, agriculture and development. Effects of tropical cyclones before the introduction of invasive plants to Hawai'i were likely short lived, and areas damaged soon recolonized by native plants. With large areas of wet forest now partly invaded by invasive plants, tree canopy removal by tropical cyclones have been shown to accelerate the process of invasion. Loss and degradation of lowland rainforest results in decline in distribution and therefore decreases redundancy. Invasive plants and animals displace native species which decreases the quality and size and native lowland rainforests which decreases resiliency. Representation, the unique ecological features within the forest, is also decreased as invasive species out-compete native species which causes declines in species richness and genetic range.

Montane rainforests and cloud forests have been degraded but to a lesser extent than lowland rainforests. Montane rainforests and cloud forests still dominated by native species have shown to be more resilient to stressors as shown by the fact that intact native high-elevation wet forests are redundant in remote and central regions of all of the main islands. Representation is still high in montane rainforests and montane cloud forests, as these forests still contain riparian areas, natural clearings, wetlands and bogs of mosses, sedges, grasses, and shrubs. These forests have been the focus of conservation efforts through the watershed partnerships since the early 1990s and are receiving additional support from HDLNR's *Rain Follows the Forest Plan*. Conservation measures will need to be maintained into the future which can prove challenging with limited resources. Increased biosecurity measures could limit the spread of plant diseases such as ROD and prevent further introduction and spread of invasive species.

Hawaii managed tree plantations are expected to increase as the human population grows throughout the islands, increasing the demands for fuel and forest products, carbon storage, horticulture, and agriculture (coffee, fruit, nut orchards). **Table 5** summarizes the impacts of these interactions on the sustainability (resiliency, representation, and redundancy) of wet forest habitats.

Table 5 Summary of interactions of stressors and conservation efforts.

<i>Wet forest subunit</i>	<i>Redundancy</i>	<i>Resiliency</i>	<i>Representation</i>
Lowland rainforest	Decrease	Decrease	Decrease
Montane rainforest and montane cloud forest	Stable	Stable	Stable
Hawaii managed tree plantation	Increase	Increase	N/A

Future Scenarios

The condition of wet forests in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are as follows:

- (1) Conservation values: stakeholder involvement and public opinion determine the formulation, implementation, and funding of natural resource conservation within laws and development plans.
- (2) Laws and biosecurity: national, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented (e.g., hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.).
- (3) Development or conservation planning: national, state, county, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

These conservation management parameters are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The year 2035 is the extent of the “foreseeable future,” and is based on the projected divergence of IPCC Representative Concentration Pathway (RCP) climate change scenarios (van Vuuren et al., 2011; Miller, 2018).

The four foreseeable future scenarios considered in this assessment are:

Future Scenario One, Status Quo—the most likely foreseeable future; no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues throughout the foreseeable future.

Future Scenario Two—a slight increase in natural resource conservation in the CMPs marginally improves conservation management.

Future Scenario Three—a slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management.

Future Scenario Four—a moderate to large increase in conservation actions in the CMPs substantially improves conservation management.

The future condition of wet forest in Scenario One, the status quo, was characterized from an assessment of change over time in wet forest land cover obtained from existing land cover maps (Amidon and Reeves, 2018). Based on these land cover maps, an annual rate of change for wet forest was estimated, and a projected change (in hectares) was calculated for the year 2035. The resulting information on changes in land cover by 2035, as derived from existing land cover change estimates, is the extent of the wet forest that is expected in the foreseeable future under Scenario One, the status quo, where conservation efforts remain unchanged and the current rate of change in land cover is also unchanged.

The future conditions of wet forest for Scenarios Two, Three, and Four cannot be quantitatively (hectares) estimated. However, the Scenario One estimate can provide a “baseline” for a qualitative characterization of changes in the future condition of wet forest under Scenarios Two, Three, and Four.

Changes in human population are captured only by the changes in the “developed” land cover footprint derived from land cover map analysis (Amidon and Reeves, 2018). Impacts from other sources of human activities or human-caused stressors (e.g., plant and animal diseases, wildfires, invasive species, etc.) are not well characterized in the land cover changes, but significantly contribute to increases in the land cover area dominated by nonnative vegetation.

Also, note that island-wide implementation of the CMPs is unlikely to have a significant effect on climate-related stressors (temperature, precipitation, and severe weather) resulting from global warming by 2035. This lack of CMP climate effects is due to the global lag in climate response to changes in greenhouse gas emissions which occurs on the order of centuries rather than years (Solomon et al., 2009; Gillett et al., 2011; Jevrejeva et al., 2012). Evidence of climate effects is also confounded by the large annual variation in the Pacific Islands climate parameters, which is much greater than projected climate change by 2035. Although impacts from climate-related stressors do not change across the four scenarios, they were included in this analysis because of their overall magnitude of potential importance to future habitat viability.

Future Scenario One—Status Quo: Scenario One is considered the most likely future scenario, and serves as a “baseline” for comparing among the four future scenarios. There is no change in the implementation of the three CMPs between 2018 and 2035. A continuing current rate of change in land cover throughout this foreseeable future results in a slow but continuous change in wet forest as described below.

Scenario One will result in small increases of stressors. All wet forests have the potential for degradation under this scenario at varying extents. Lowland rainforest are expected to continue to decline in redundancy, resilience, and representation due to development, agriculture and invasive species. Montane rainforests and montane cloud forests will be less impacted than lowland rainforests by small increases of stressors since much of the montane wet forests are in relatively good condition. Montane rainforests and montane cloud forests which are being managed for ungulates and nonnative plants will continue to be sustainable. Hawaii managed tree plantation will continue to increase as the human population increases.

Future Scenario Two: there is a slight increase in the CMPs that marginally improves conservation management.

Under Scenario Two, lowland rainforests are expected to continue to decline. Removing the pressures of development will provide some benefit but invasive species will continue to degrade lowland wet forests. A small increase in CMPs will provide some benefit to lowland wet forests but not enough to stem the spread of existing invasive species. Active restoration, removal of invasive species and reintroduction of native species, is required to preserve remaining lowland rainforests. These activities require a substantial amount of resources and commitment from government agencies and local communities. Scenario Two will have little impact on montane rainforest and montane cloud forests as these areas are in remote and inaccessible areas and are not suitable for development. As in Scenario One, montane rainforests and montane cloud forests which are being managed for ungulates and nonnative plants will continue to be sustainable. Hawai'i managed tree plantation will continue to increase but at a slower rate due to limited development.

Future Scenario Three: there is a small to moderate decrease in conservation actions in the CMPs that substantially decreases conservation management.

All natural resource management actions in the CMPs are set aside in deference to land use for economic development. With extensive localized management, some native species may persist in park-like settings or in areas where land development is not possible.

Under Scenario Three, lowland rainforests are expected decline at a significantly faster rate. Current areas of native lowland rainforest may become developed or converted to agriculture and managed tree plantations. Setting aside natural resource management actions and CMPs will increase the spread of invasive species in lowland wet forests. Scenario Three would negatively impact montane rainforests and montane cloud forests as current management would likely be abandoned. Ungulates and invasive plants will degrade these forests. Hawaii managed tree plantation will significantly increase to fuel economic development.

Future Scenario Four: there is a moderate to large increase in conservation actions in the CMPs that substantially improves conservation management.

Under Scenario Four, lowland rainforests will increase. Current areas of native lowland forest will be prioritized for conservation. Increased support for control of invasive species and active restoration, planting native vegetation rather than only addressing stressors, will lead to an increase in native lowland wet forest. Montane rainforest and montane cloud forests will increase. Areas that are currently managed will continue to be managed ensuring sustainability of montane rainforests and montane cloud forests into the future. Additional montane rainforests and montane cloud forests that are not currently managed for invasive species will be fenced and ungulates and invasive plant species will be removed. Hawaii managed tree plantation will increase to meet the demands for forest and orchard products for the growing human population.

Conservation Implications

Under the most likely future scenario, lowland rainforest are expected to decrease in resiliency, redundancy, and representation. Alien species dominated lowland rainforests are predicted to increase. Substantial improvements to laws, biosecurity, and implementation of intensively managed, fenced conservation areas are required to conserve this forest type in the future. Montane rainforest and montane cloud forest fare better since they have been actively managed through various states, federal and private initiatives but are still vulnerable to decline if existing management actions are not maintained. Resiliency, redundancy and representation are expected to remain stable if management initiatives continue for montane rainforest and montane cloud forests. Managed tree plantations are expected to increase as the human population increases. [Table 6](#) summarizes the overall condition for wet forest under the future scenarios.

Table 6 Summary of overall condition for wet forest in the future scenarios.

<i>Wet forest subunit</i>	<i>Scenario 1: Status quo</i>	<i>Scenario 2: Slightly improved</i>	<i>Scenario 3: Substantially decreased</i>	<i>Scenario 4: Substantially improved</i>
Lowland rainforest	Decrease	Decrease	Significantly decrease	Increase
Montane rainforest	Stable	Stable	Decrease	Increase
Montane cloud forest	Stable	Stable	Decrease	Increase
Hawaii managed tree plantation	Increase	Slowly increase	Significantly increase	Increase

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Hawai'i: Mesic Forests

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Published by Elsevier Inc.

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Abstract

This paper is an assessment of the Hawaiian Islands mesic forests, including the current status, stressors, and future viability. Mesic forests in Hawai'i generally receive between 1200 and 2500 millimeters (mm) of rainfall annually and are found on leeward and windward sides of the islands in lowland or in montane-subalpine zones (Cuddihy and Stone, 1990). These zones are differentiated by elevation and climate, which primarily dictate which species can exist in them (Gagne and Cuddihy, 1999). Historically, mesic forests in Hawai'i were located on all of the main Hawaiian Islands. These forests were distributed across the islands of O'ahu, Maui, Kaua'i, and Hawai'i, and to a lesser extent, on Moloka'i and Lāna'i. Currently, mesic forests are still found on all of the main Hawaiian Islands. However, the quality of these forests are largely composed of a mixture of native/nonnative vegetation. In addition to the native lowland and montane-subalpine mesic forests that characterized mesic forests historically, introduced mesic forests and managed tree plantations are now classified as mesic forests in the main Hawaiian Islands. Our assessment of mesic forest viability, defined as the likelihood of persistence over the long term, is based on the concepts of representation, redundancy, and resiliency. The main stressors to mesic forests are invasive ungulates, invasive plants, plant disease, invasive herbivores, wildfires, drought, natural disasters (i.e., hurricanes), and agriculture and human development. Ongoing conservation efforts are helping to protect mesic forests in Hawai'i. The conservation of mesic forests depends largely on combined efforts of State, Federal, multiagency organizations, nonprofit organizations, and the voluntary support of private landowners.

Introduction

The Hawaiian archipelago is the most isolated landmass in the world and is composed of eight large, "main" islands (Hawai'i, Maui, Lāna'i, Moloka'i, Kaho'olawe, O'ahu, Kaua'i, Nī'ihau), and 124 smaller islands, islets, atolls, and shoals. Nearly the entire land area is concentrated on the eight largest Hawaiian Islands (Wagner et al., 1999). The geography, geology, climate, hydrology, and descriptions of the islands in the Hawaiian archipelago are described in the chapter on Physical Geography of the Hawaiian Islands by Harrington in this work. We provide an overview of the Mesic Forest biome in the Hawaiian archipelago and describe the ecological factors that have influenced this biome over time and into the future.

Description

A forest is a plant community characterized by vegetation dominated by trees (woody plants) generally 5–35 meters (m) in height, and often including a canopy, subcanopy, shrub, and an herbaceous layer (composed of nonwoody plants). The classification of Hawaiian mesic forest is based on elevation, moisture, and physiognomy (aspect or appearance). Physiognomic classes of mesic forest are based on percentage cover of the dominant plant life-form in the uppermost vegetation layer. A mesic forest is a forest type that is neither wet nor dry (Sailer, 2006). Those classified as "mesic forest" have a moderate amount of moisture and greater than 25% forest cover (Gagne and Cuddihy, 1999).

Geology

Mesic forest substrates are highly variable but are generally well-drained and include rocky, shallow, organic muck soils, steep rocky talus (accumulation of rock debris) soils, shallow soils over weathered rock in steep gulches, and deep soils over soft weathered rock and gravelly alluvium (soils composed of clay, silt, sand, and gravel) (Gagne and Cuddihy, 1999).

Vegetation Structure and Composition

Vegetation structure and composition is variable throughout the mesic forests. Structure ranges from open to dense and mostly evergreen tree layer ranging from 2 to 35 m tall (Gagne and Cuddihy, 1999).

Other Biotic Components

Many of the relationships between trees and their environment are reciprocal: rain, temperature, humidity, and soil fertility influence tree growth, while trees affect microclimate, and soil moisture, structure, acidity, and fertility. Among the most important and well-studied tree-soil relationships are nutrient cycles, whereby plants take up the mineral elements essential for growth from the soil solution and return those elements to the soil via litterfall and root decay. Nitrogen (N-fixing) is particularly important in providing nutrients essential for growth and regeneration for plants and trees (Rowe et al., 2017). As a dominant and N-fixing canopy tree species in many Hawaiian mesic forests, native *Acacia koa* (koa) adds substantial benefits to soils by increasing nitrogen (Baker et al., 2009).

Biodiversity

The biodiversity in mesic forests is high compared to other ecosystems in the Hawaiian Islands (USFWS, 2016). Mesic forests contain areas with many microclimates that support a high species diversity. Diverse native mesic forests support many native bird and invertebrate species, and Hawai'i's only terrestrial mammal, the Hawaiian hoary bat, or 'ōpe'ape'a (*Lasiurus cinereus semotus*) (TNCH, 2006; Sailer, 2006).

Physical/Life History Components

Water availability

Rainfall influences the availability of water for plants and is a critical component of mesic forests. Tree species and vegetation typically found in mesic forests require moist conditions throughout the year. If water availability changes substantially, the biome may no longer be favorable for mesic forest vegetation that prefer a moist environment, and the altered biome may shift to a drier or wetter biome classification if the species shift is substantial. The density and diversity of tree species found in lowland mesic forests tends to increase with elevation and rainfall and decreases in lower elevations that receive less rainfall (Gagne and Cuddihy, 1999). The montane-subalpine mesic forests are found in regions that lack sufficient rainfall to support a wet forest, but that do not suffer moisture deficits for prolonged periods (Gagne and Cuddihy, 1999). Water can be a major limiting factor for the growth of some dominant native tree species in mesic forests, particularly koa, especially toward the drier end of its climatic range (Baker et al., 2009).

Viability of mesic forests

The viability of Hawaiian mesic forests depends on maintaining multiple and distributed populations (redundancy) of sufficient quality and size (resiliency) with species richness and genetic range (representation) to survive across the biome over time.

We define redundancy by the number, distribution, and connectivity of subunits that make up a biome. By resiliency we refer to the overall health, stability, quality and quantity of subunits that compose a biome. We define Representation, by the range of variation that exists within subunits that make up a biome, including environmental conditions and features (geographic, ecological, and climatic).

Adequate distribution across the landscape of mesic forests contributes to its ability to perpetuate after a catastrophic event in one area by having a redundant population in another area. Natural recruitment in the mesic forest is driven by dispersal, rainfall, light, and nutrient availability. Forest birds provide a vital role in seed dispersal in mesic forests to maintain and establish new forested areas (Culliney, 2011). Native invertebrates also serve an important role in the pollination of plant species found in mesic forests (Magnacca, 2007). Seabirds contribute an important source of marine derived nitrogen to the mesic forests through deposition of guano at their nesting sites (Rowe et al., 2017).

Conditions needed by mesic forests to develop are influenced by numerous factors including disturbance (fires, volcanism, storms, pathogens, and insect pests) as well as by rainfall, light, and nutrient availability. Shade limits the recruitment of some dominant mesic forest tree species, particularly koa, which grow best in forest clearings (Baker et al., 2009).

The quality and quantity of mesic forest contributes to its resiliency in the face of stochastic events. Most native species in this biome are not specifically fire-adapted, however, many species regenerate after disturbance if environmental conditions are optimal. Fire can reset the successional clock of this system by removing a substantial amount of plants. Some seeds will survive and be able to germinate following the fire, however, others rely on dispersal from other sources such as the wind or animals.

Diversity within and among locations of mesic forest is necessary to enhance its ability to adapt to change. Mesic forests are best represented when there is geographic and genetic diversity across the range. Representation considerations for mesic forests include presence on each of the main Hawaiian Islands spanning across both leeward and windward slopes, and from lowland to montane elevations.

The mesic forest ecosystem occurs throughout the State on most of the main Hawaiian Islands including Hawai'i, Moloka'i, Maui, Kaua'i, O'ahu, and Lāna'i on slopes ranging from 30 to 2000 m in elevation. Annual rainfall ranges from 1200 to 2500 millimeters (mm) per year (Gagne and Cuddihy, 1999). Price et al. (2007) further classified the mesic zone into "Moist-mesic" and "Seasonal-mesic" categories based on precipitation and elevation. Mesic forest stands are found in the mesic seasonal zone between the dry leeward and wet windward climates. These sites are considered too dry to support rainforests but typically do not experience extended periods of drought like the dry forests (Cuddihy and Stone, 1990).

Mesic forest subtypes include two native and two introduced communities: lowland mesic montane-subalpine mesic, introduced wet-mesic, and introduced managed tree plantation.

Prehuman Condition

Historically the lowland and montane mesic forests were found on the islands of O'ahu, Maui, Kaua'i, and Hawai'i, and to a lesser extent, on Moloka'i and Lāna'i. Although mesic forests were found historically on all of the main Hawaiian Islands, the majority occurred on the islands of Hawai'i and Maui (Figs. 1–4).

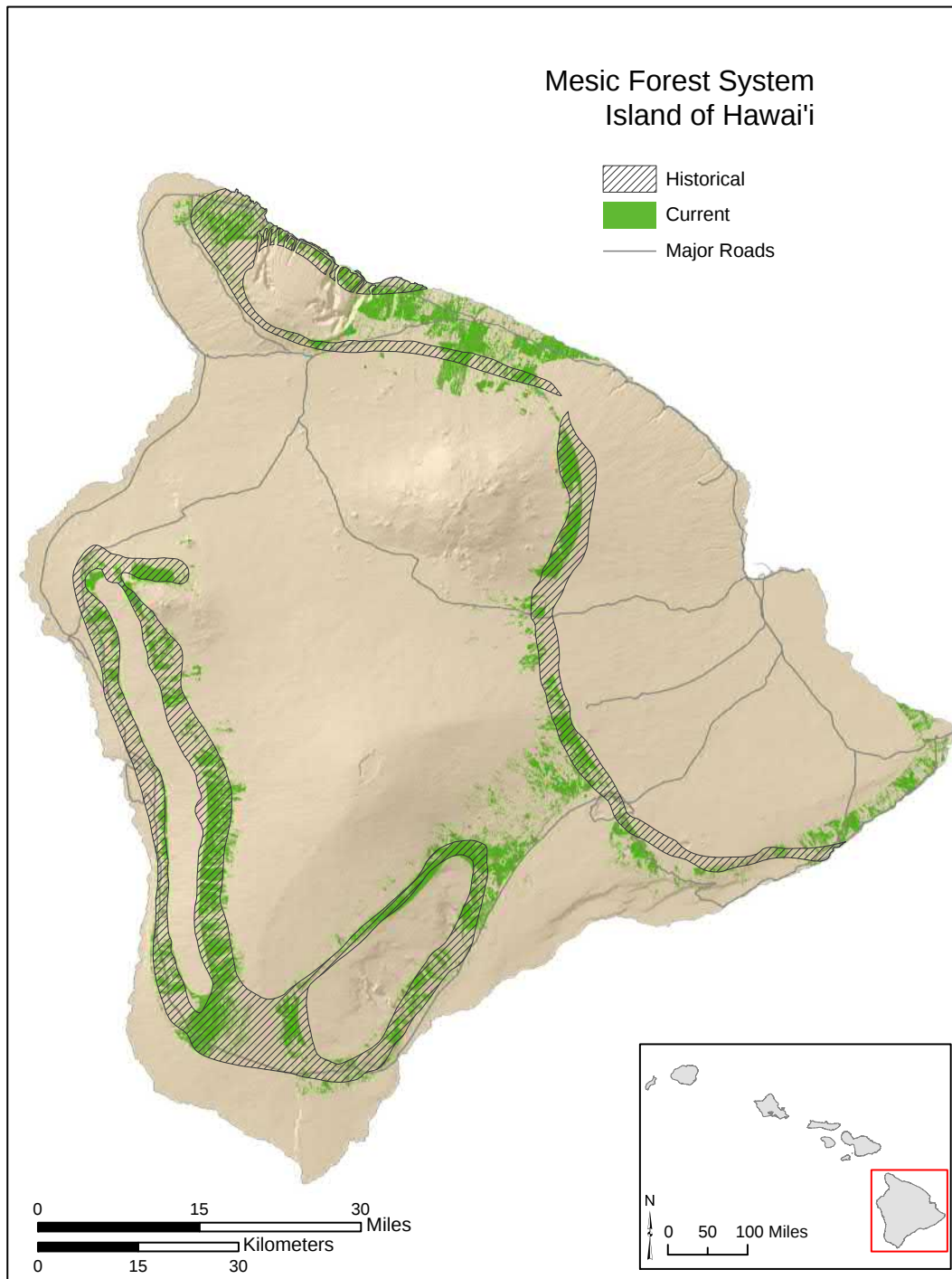


Fig. 1 Historical and current extent of the mesic forest system on the island of Hawai'i. Reeves, M.K. and Amidon, F. (2018). *Habitat Status Assessment Methods—Hawaii, Current Condition Summaries*. Technical Report from United States Fish and Wildlife Service. Honolulu, HI: Pacific Islands Fish and Wildlife Office, pp. 439, August 2018.

The original vegetation cover prior to the arrival of the Polynesians to the main Hawaiian Islands may be inferred from existing vegetation, remnants in disturbed areas, patterns of climate and substrates, and a few fossilized remains. Forests were and are the natural vegetation of most of the main Hawaiian Islands. On the six main Hawaiian islands with elevations exceeding 1000 m, the climate promotes forest development except in the alpine zones and in the driest parts of the leeward lowlands (Cuddihy and Stone, 1990). The mesic forest zone occupied both windward and leeward slopes. It occurred in regions transitional between wet and dry areas, in rain shadows, or at elevations above a temperature inversion layer on the higher islands, usually between 1525 and 2135 m elevation (Cuddihy and Stone, 1990).

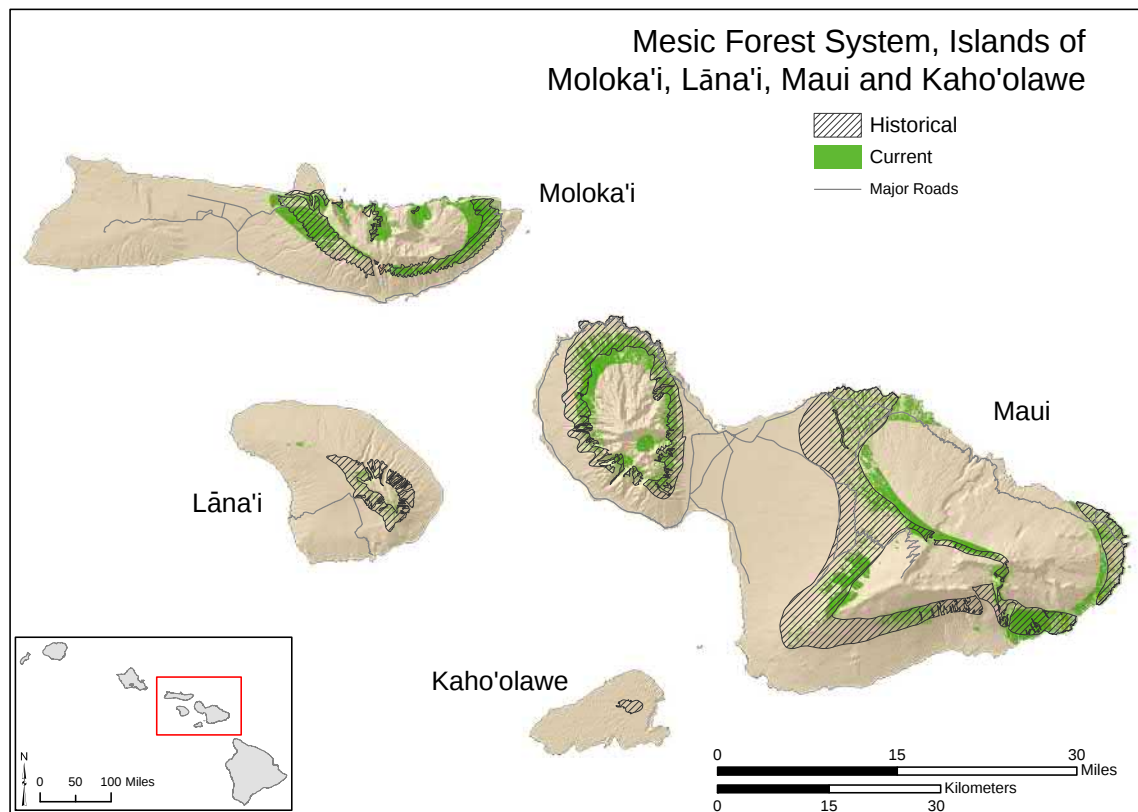


Fig. 2 Historical and current extent of the mesic forest system on the islands of Moloka'i, Lāna'i, Maui and Kaho'olawe.

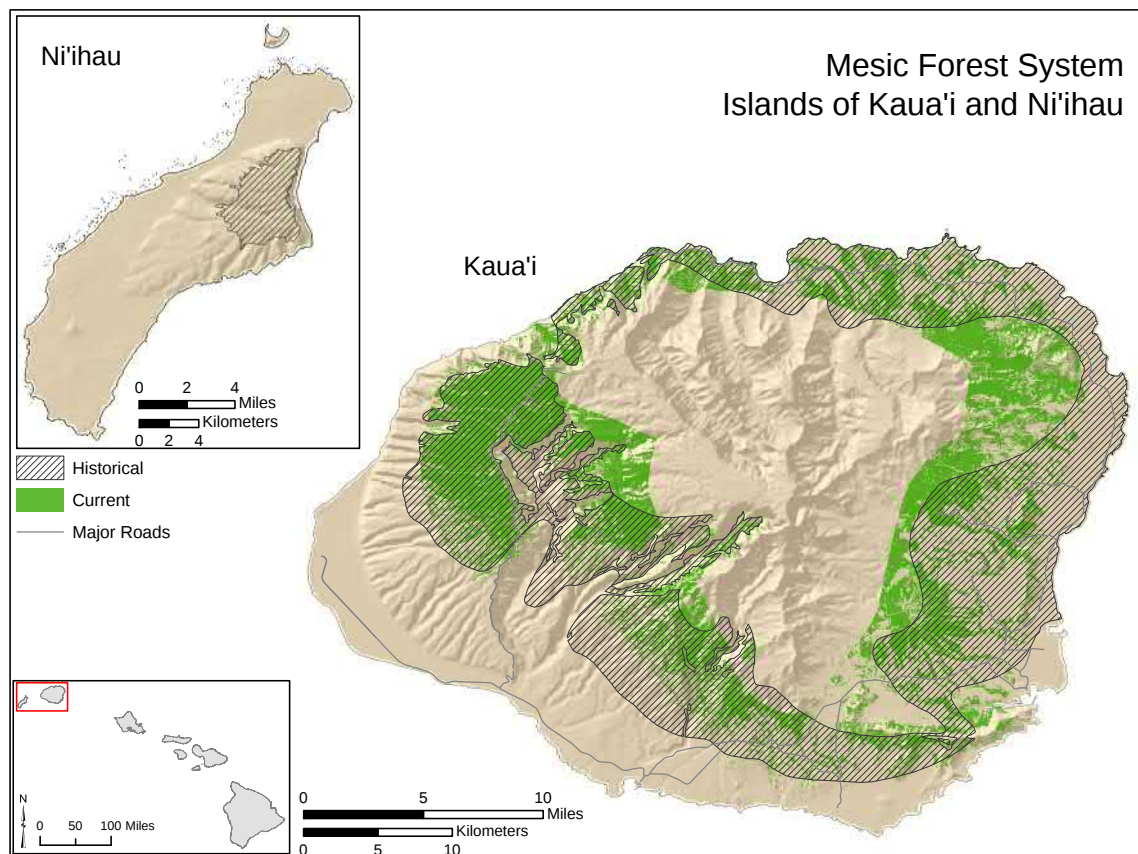


Fig. 3 Historical and current extent of the mesic forest system on the islands of Kaua'i and Ni'ihau.

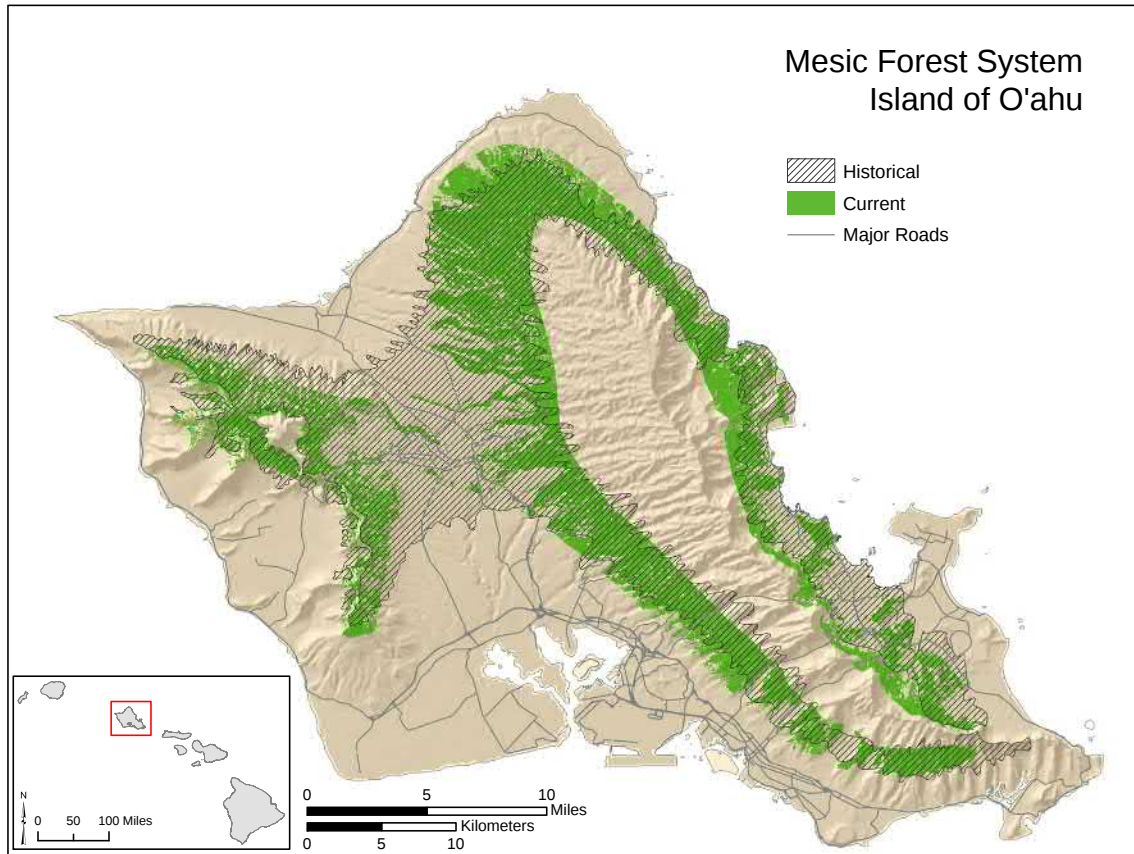


Fig. 4 Historical and current extent of the mesic forest system on the island of O'ahu.

Mesic forests were more extensive historically, particularly in the lowlands, and contained inclusions of native grasslands and shrublands throughout the areas they occurred. Prior to human contact this biome encompassed an area up to 297,074 ha (734,086 ac) as indicated (cross-hatched) in Figs. 1–4.

Prehuman Mesic Forest Subtypes

Before the arrival of humans, mesic forest included two subtypes: lowland mesic forests and montane-subalpine mesic forests. Vegetation commonly found in these subtypes are included in Table 1.

Table 1 Diagnostic species found in prehuman mesic forest subtypes in Hawai'i.

Lowland mesic forest	Montane-subalpine mesic forest
<i>Acacia koa</i>	<i>Acacia koa</i>
<i>Alectryon macrococcus</i>	<i>Coprosma</i> spp.
<i>Antidesma pulvinatum</i>	<i>Dryopteris</i> spp.
<i>Charpentiera</i> spp.	<i>Leptecophylla tameiameia</i>
<i>Chrysodracon</i> spp.	<i>Metrosideros polymorpha</i>
<i>Cryptocarya mannii</i>	<i>Myoporum sandwicense</i>
<i>Ctenitis squamigera</i>	<i>Myrsine</i> spp.
<i>Diospyros sandwicensis</i>	<i>Nestegis sandwicensis</i>
<i>Doodia</i> spp.	<i>Pelea</i> spp.
<i>Flueggea neowawraea</i>	<i>Pipturus albidus</i>
<i>Metrosideros polymorpha</i>	<i>Pleomele</i> spp.
<i>Nestegis sandwicensis</i>	<i>Rubus hawaiiensis</i>
<i>Pisonia</i> spp.	<i>Sadleria</i> spp.
<i>Pritchardia kaalae</i>	<i>Sapindus</i> spp.
<i>Rhus sandwicensis</i>	<i>Santalum</i> spp.
<i>Strongylodon ruber</i>	<i>Uncinia uncinata</i>

Hawai'i lowland mesic forest: This mesic forest subtype occurred on the islands of Hawai'i, Moloka'i, Maui, Kaua'i, and O'ahu. Stands occurred in the mesic zone between the dry leeward and wet windward climates. Vegetation composition was variable, ranging from an open to dense tree layer. There was often a diverse canopy, subcanopy, and tall-shrub layers with lianas (Gagne and Cuddihy, 1999). These forests would usually grade into lowland wet forests upslope. At their lower limits they would grade into either lowland mesic shrublands, lowland dry shrublands, or lowland dry forests, depending on topography, and moisture (Gagne and Cuddihy, 1999). Seven subcategories of native lowland mesic forests are recognized: 'Ōhi'a lowland mesic forest, Koa lowland mesic forest, Olopuia lowland mesic forest, Lama/'Ōhi'a lowland mesic forest, Diverse lowland mesic forest, Loulu lowland mesic forest, and Pāpala kēpau/Pāpala lowland mesic forest (Gagne and Cuddihy, 1999; Table 2).

Hawai'i montane-subalpine mesic forest: This subset of the mesic forest system occurred on the montane and subalpine slopes of Kaua'i, Maui, and Hawai'i. Montane mesic forests occurred above the 'Ōhi'a lowland wet forest, below montane wet forests, and leeward of koa/'Ōhi'a montane wet forests (Gagne and Cuddihy, 1999). The understory was variable and composed of sedges, ferns, and shrubs (Gagne and Cuddihy, 1999). Four subcategories are recognized under the mesic montane-subalpine subtype: 'Ōhi'a montane mesic forest, Koa/'Ōhi'a montane mesic forest, Koa/'Ōhi'a/A'e mesic forest, and Olopuia montane mesic forest (Gagne and Cuddihy, 1999; Table 2).

Redundancy, Representation, and Resiliency

Redundancy

Both lowland mesic and montane-subalpine mesic forests were widely distributed historically across a broad range in the main Hawaiian Islands (Figs. 1–4). This redundancy made mesic forests less susceptible to catastrophic events such as an occasional hurricane or volcanic eruption. In the case of lava flows, these were localized events affecting only some populations of mesic forests across the biome. The distribution of mesic forest in multiple units across the landscape and across the islands provided redundancy, which provided the ability to withstand events only affecting smaller areas of mesic forests on individual or a few islands (e.g., single volcanic eruptions or hurricanes affecting multiple islands).

Representation

Historically, mesic forests were found throughout the main Hawaiian islands (Hawai'i, Moloka'i, Maui, Lāna'i, Kaua'i, and O'ahu) and across multiple watersheds (representation). They occurred on both windward and leeward slopes as well as across a broad range of substrates from the oldest on Kaua'i to the youngest on Hawai'i. Since mesic forests were found across a diversity of subunits historically it is likely that natural stochastic events (fires, hurricanes, etc.) did not severely impact the biome. Greater representation of mesic forest subunits would have provided more opportunity for the biome to adapt and evolve under changing conditions.

The diversity of tree species found within mesic forests historically also contributed to high representation (the ability to adapt to changing environmental conditions and is measured by the variation across the landscape) found in this ecotype. Prior to human arrival, all plants, animals, and invertebrates arrived in Hawai'i by accident or by drift. Because of this isolation, species were able to fill empty niches not already occupied by other species that lead to speciation (adaptive radiation) and a high rate of endemism. This endemism and diversity existed across the pre-human mesic forest subtypes, thus leading to high representation.

Resiliency

Lowland mesic and montane-subalpine mesic forests were historically found in multiple areas containing high quality subunits with a wide range of species and diversity. Healthy and stable high quality mesic forest areas would have enabled the biome to withstand natural, annual variations in the environment and recover from periodic disturbances (i.e., floods, minor fires, etc.). Should a natural disturbance have occurred, the amount and quality of mesic forest, and the range and diversity of species composing the seed bank, would have allowed the mesic forest to recover, making it resilient.

Intact, high quality, native mesic forests are resilient and are able to recover after natural stochastic events. Koa and 'Ōhi'a, both dominant mesic forest tree species, have been observed to regenerate following stochastic disturbances such as lava flows, fires, and hurricanes. The principal natural ignition sources of fires in Hawai'i before human settlement were lava flows and lightning but these events were infrequent and did not have major impacts on mesic forests (TMA, 2007; Abrahamson, 2013).

A number of native plant species are fire-tolerant, although no native plant is fire-resistant (Smith and Tunison, 1992). Koa, like other *Acacia* species, has many traits of a fire-adapted species, such as seeds that persist for years or decades in the soil and require scarification for germination. Although koa trees may be killed by high-intensity fires, disturbance by fire has been shown to stimulate their germination (Scowcroft and Wood, 1976; Baker et al., 2009). Other species found in mesic forests that are fire-tolerant, include naio (*Myoporum sandwicense*), 'ō'hia, tree ferns (*Sadleria cyatheoides*), and the native grasses, *Deschampsia nubigena*, and *Eragrostis* spp. (Mueller-Dombois, 1981; Mueller-Dombois and Fosberg, 1998; Smith and Tunison, 1992; Baker et al., 2009).

It is reasonable that mesic forests prior to human contact showed similar or higher resiliency. Mesic forest regeneration likely occurred through transportation of seeds by wind and native birds (Carlquist, 1980). Native forest birds and insects were also important pollinators (Cox and Elmqvist, 2000) while seabirds contributed an important source of nitrogen through deposition of guano (Rowe et al., 2017).

Table 2 Characteristics of current mesic forest subtypes in Hawai'i (Gagne and Cuddihy, 1999; Landfire, 2016).

Mesic forest subtypes (and subcategories)	Precipitation (mm)	Elevation (m)	Characteristic plants
Lowland mesic forest <i>Subcategories of lowland mesic forests</i> <i>Native:</i> • 'Ōhi'a • Koa • Olopuā • Lama/'Ōhi'a • Diverse • Loulu • Pāpala kēpau/Pāpala <i>Nonnative:</i> • Kukui • Christmas berry • Guava • Ironwood Silk oak	Between 1200 and 3800 mm	Between 30 and 1600 m	Native species: <i>Metrosideros polymorpha</i> ('ōhi'a), <i>Acacia koa</i> (koa), <i>Diospyros sandwicensis</i> (lama), <i>Nestegis sandwicensis</i> (olopua), <i>Chrysodracon</i> spp. (halapepe), and <i>Pritchardia kalae</i> (loulu), <i>Antidesma pulvinatum</i> (hame), <i>Cryptocarya mannii</i> , <i>Alectryon macrococcus</i> (māhoe), <i>Charpentiera</i> spp. (pāpala), <i>Flueggea neowawraea</i> (mēhamehame), <i>Rhus sandwicensis</i> (neneleau), <i>Pisonia</i> spp., <i>Canthium odoratum</i> (alaha'e), <i>Ctenitis squamigera</i> (pauoa fern), <i>Doodia</i> spp. ('ōkupukupu fern), <i>Strongylodon ruber</i> (nuku'i'iwi), and <i>Freyinetia arborea</i> ('ie'ie). Nonnative species: <i>Schinus terebinthifolius</i> (Christmas berry), <i>Aleurites moluccana</i> (kukui), <i>Psidium guajava</i> (common guava), <i>Psidium cattleianum</i> (strawberry guava), <i>Syzygium</i> spp. (roseapple), <i>Casuarina equisetifolia</i> (ironwood), <i>Grevillea robusta</i> (silk oak), <i>Alocasia macrorrhiza</i> (giant taro), <i>Nephrolepis</i> spp. (sword fern), <i>Passiflora suberosa</i> (passionfruit), <i>Cordyline fruticosa</i> (Ti), <i>Rubus rosifolius</i> (thimbleberry), and <i>Clidemia hirta</i> (Koster's curse)
Montane-subalpine mesic forest <i>Subcategories of montane-subalpine mesic forests</i> <i>Native:</i> • 'Ōhi'a • Koa/'Ōhi'a • Koa/'Ōhi'a/A'e • Olopuā	Between 1000 and 3800 mm	Between 900 and 2000 m	<i>Metrosideros polymorpha</i> ('ōhi'a), <i>Acacia koa</i> (koa), <i>Sapindus saponaria</i> (a'e), <i>Nestegis sandwicensis</i> (olopua), <i>Coprosma</i> spp. (pilo), <i>Myrsine</i> spp. (kōlea), <i>Pisonia</i> spp., <i>Myoporum sandwicense</i> (naio), <i>Sophora chrysophylla</i> (māmane), <i>Leptecophylla tameiameia</i> (pūkiawe), <i>Pipturus albidus</i> (māmaki), <i>Rubus hawaiiensis</i> ('ākala), <i>Strongylodon ruber</i> (nuku'i'iwi), and ferns such as <i>Dryopteris</i> spp., and <i>Sadleria</i> spp. Nonnative species: <i>Cenchrus clandestinus</i> (Kikuyu grass), <i>Ehrharta stipoides</i> (meadow rice grass), and <i>Tropaeolum majus</i> (garden nasturtium)
Introduced wet-mesic forest	Generally between 1200 and 1900 mm	Generally below 1000 m, but occasionally higher elevations	<i>Bambusa</i> spp. (bamboo), <i>Casuarina</i> spp. (ironwood), <i>Psidium</i> spp. (guava), <i>Grevillea</i> spp. (silk oak), <i>Melaleuca leucadendra</i> (paper bark tree), <i>Melastoma candidum</i> , <i>Melochia umbellata</i> , <i>Miconia calvescens</i> , <i>Moluccan albizia</i> , and <i>Morella faya</i> (firetree)
Managed tree plantation	Generally between 1000 and 1900 mm	Generally between 30 and 1600 m	<i>Araucaria columnaris</i> (Cook pine), <i>Araucaria heterophylla</i> (Norfolk pine), <i>Eucalyptus</i> spp. (gum tree), <i>Pinus</i> spp. (pine), <i>Sequoia sempervirens</i> (redwood); horticulture; or agriculture (coffee, fruit, nut orchards). <i>Casuarina</i> spp. (ironwood), <i>Paraserianthes</i> spp. (albizia), <i>Fraxinus</i> spp. (tropical ash), <i>Melaleuca</i> spp., <i>Psidium</i> spp. (guava), <i>Grevillea</i> spp. (silk oak), and <i>Acacia koa</i> (koa)

Current Condition

Mesic forests are still found across multiple watersheds on all of the main Hawaiian Islands (Figs. 5–8). It is estimated that only 40% of the original mesic forest biome in the Hawaiian Islands currently remains (State of Hawai'i DLNR, 2016). Between ~400 and 1800 CE, Hawaiians settled, colonized, and reshaped much of the vegetation of the lowlands, including mesic communities, on all the major Hawaiian Islands (Kirch, 1982). In these ecosystems, Hawaiians used fire to clear land for agriculture (i.e., slash and burn). By the time of European contact in the late 1700s, most of the native mesic communities below 760 m were converted from forest and open woodlands to open grasslands (Cuddihy and Stone, 1990; Kirch, 1982). Much of the lowland mesic forest have since been converted to pasture, military or agricultural use, or have been lost to urbanization or fire (Cuddihy and Stone, 1990; State of Hawai'i DLNR, 2016). Intensive human disturbance in the lowlands has resulted in the majority of intact native mesic forests remaining only at higher elevations (The Nature Conservancy (TNC), 2006).

Mesic forests now include mixed native-introduced forests, highly disturbed mesic forests, and introduced plantations (Table 2). Many areas in the lowland and montane mesic forest zone have been cleared for timber logging, and have been invaded by invasive grasses brought in by early ranchers to support grazing animals (Juvik et al., 2008). Ranching activities and the subsequent increase and spread of invasive grasses has been the most important disruption of the montane mesic forests. Large expanses of koa/'ōhi'a montane mesic forest have been converted to cattle ranches after logging of koa. Browsing by feral pigs, goats and sheep, fires, and

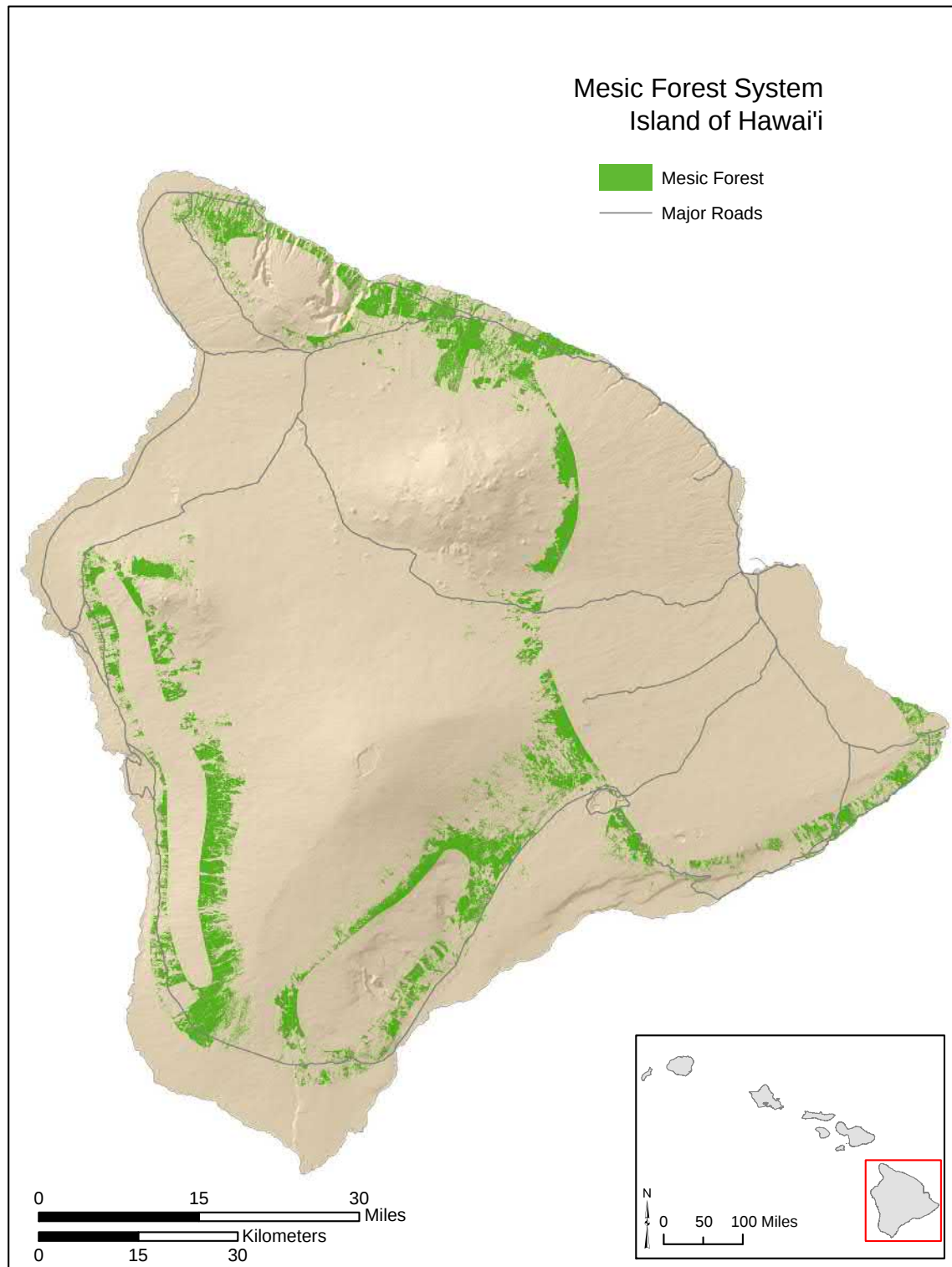


Fig. 5 Current distribution of the mesic forest system on the island of Hawai'i.

clearing of land for commercial tree planting and harvest have also reduced the quality and extent of the mesic forests (Gagne and Cuddihy, 1999).

Because mesic forests are restricted in range and have been highly modified by human activity and introduced species, the ability of this ecotype to recover from stochastic events in unmanaged forest areas is greatly reduced, particularly in areas that have been

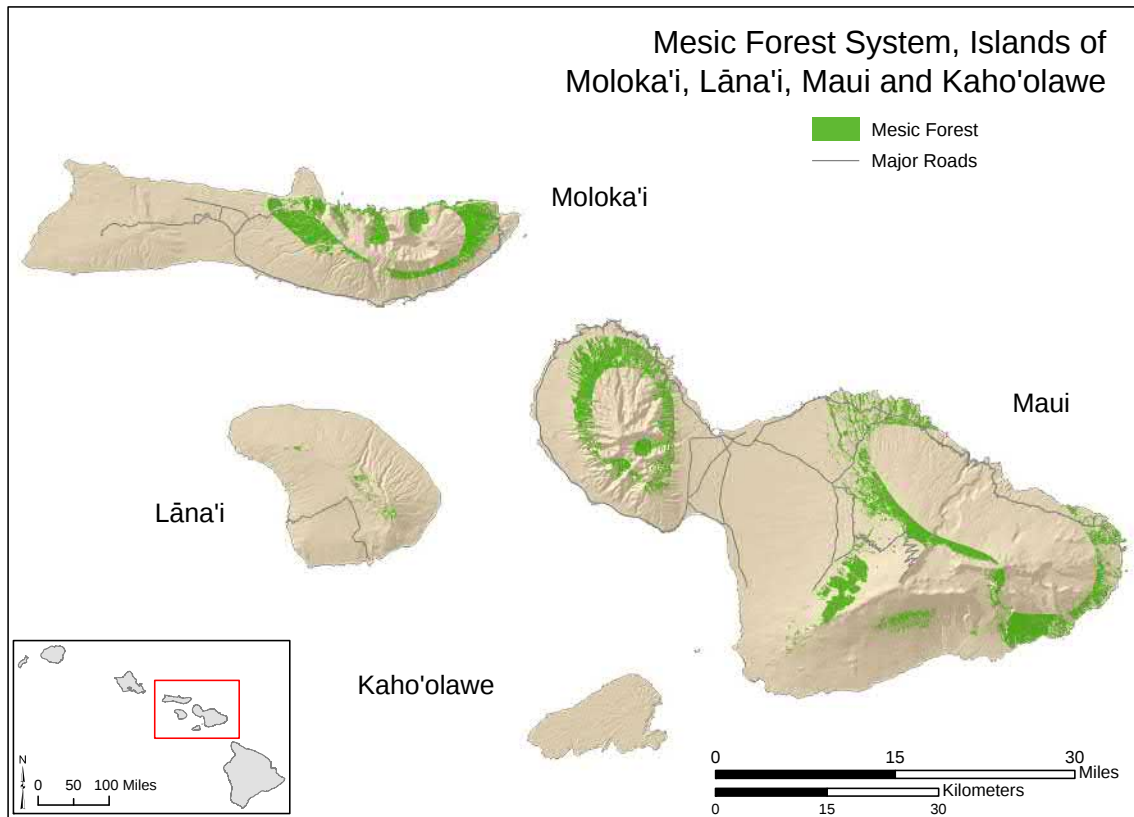


Fig. 6 Current distribution of the mesic forest system on the islands of Moloka'i, Lāna'i, Maui, and Kaho'olawe.

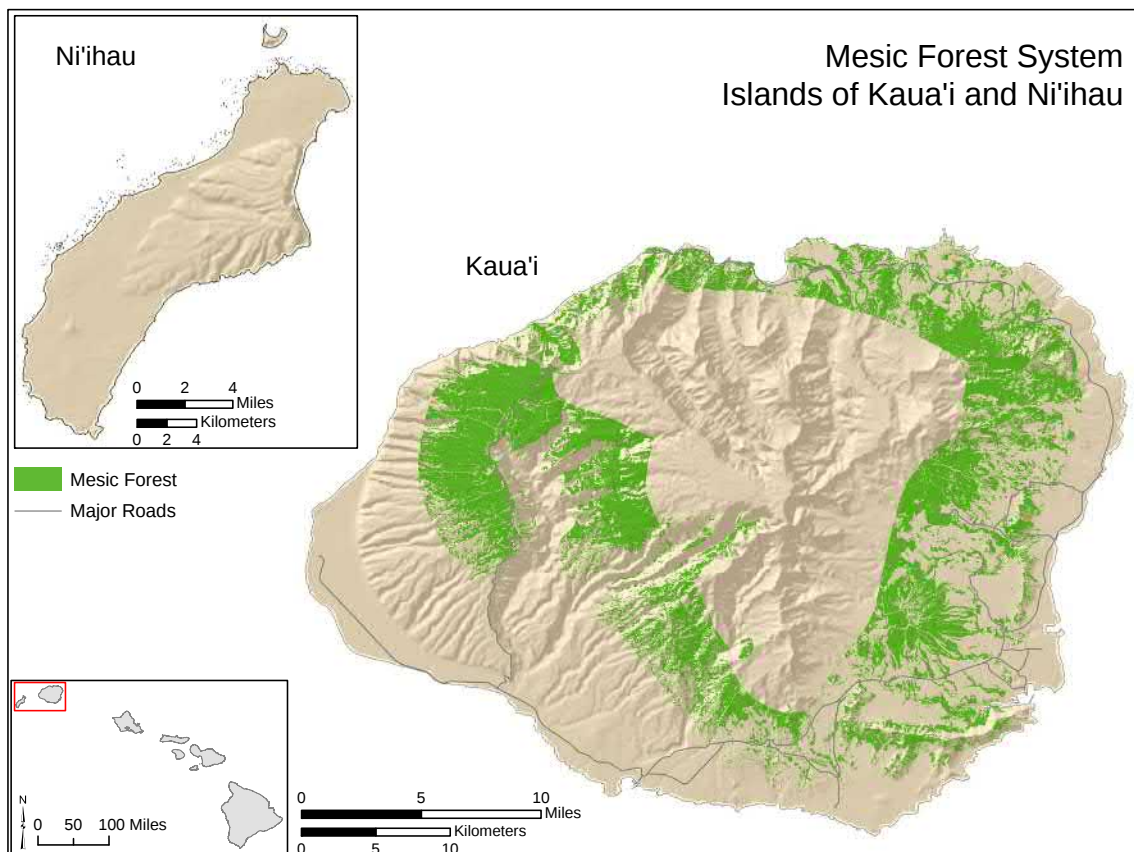


Fig. 7 Current distribution of the mesic forest system on the islands of Kaua'i and Nī'ihau.

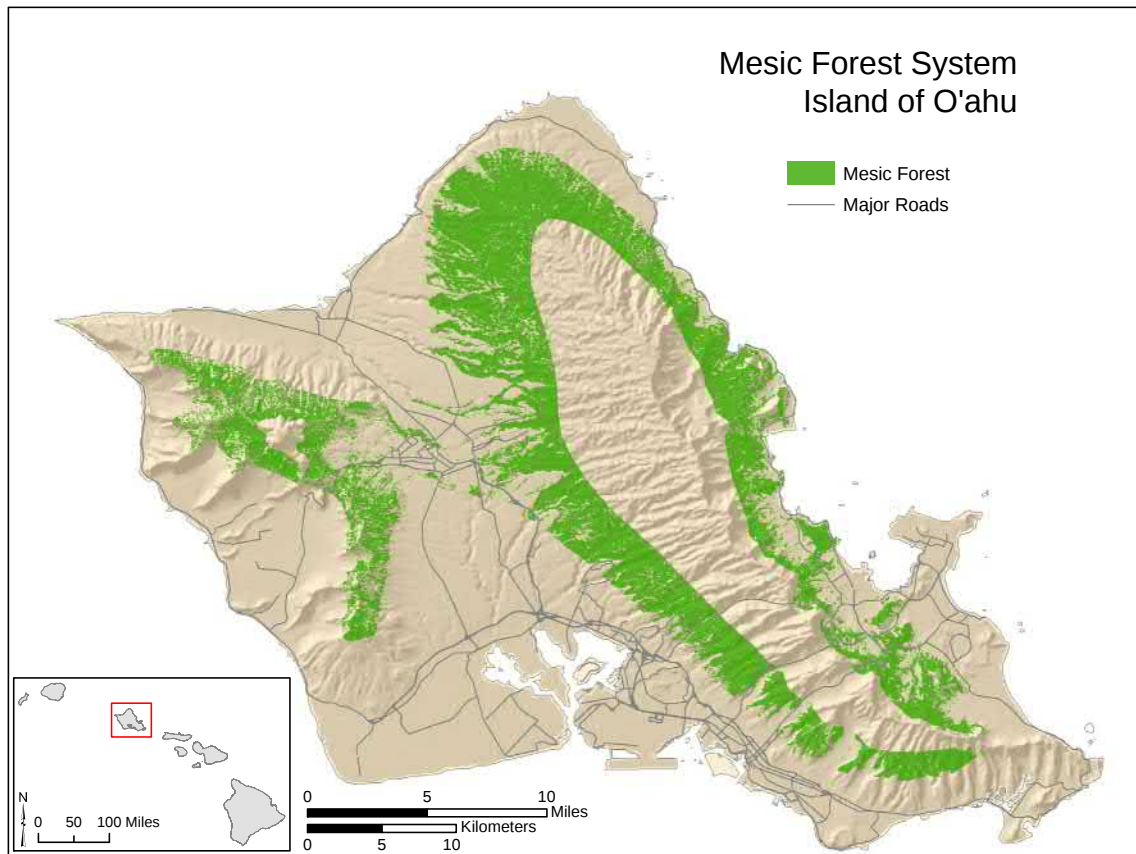


Fig. 8 Current distribution of the mesic forest system on the island of O'ahu.

fragmented by timber extraction and conversion of forests to cattle pasture. Wildfires are also a serious threat to both lowland and montane mesic forests.

Mesic forests currently include two native dominated subtypes: lowland mesic forest and montane-subalpine mesic forest, and two introduced subtypes: introduced wet-mesic forest, and introduced mesic managed plantations. Characteristics of the forest subtypes are described in [Table 2](#).

Current Mesic Forest Subtypes

Hawai'i lowland mesic forest: This subset of the mesic forest system still occurs on the mesic slopes of Hawai'i, Moloka'i, Maui, Kaua'i, and O'ahu. Lowland areas have been heavily impacted by disturbance and displacement, leaving remnant native areas at higher elevations ([The Nature Conservancy, 2006](#)). Seven native and five introduced lowland mesic forest communities are identified and are defined by dominant and codominant species ([Table 2](#)). The native communities include: 'Ōhi'a (*Metrosideros polymorpha*) lowland mesic forest, Koa (*Acacia koa*) lowland mesic forest, Olopua (*Nestegis sandwicensis*) lowland mesic forest, Lama/'Ōhi'a (*Diospyros/Metrosideros*) lowland mesic forest, Diverse lowland mesic forest, Loulu (*Pritchardia*) lowland mesic forest, and Pāpala kēpau/Pāpala (*Pisonia/Charpentiera*) lowland mesic forest ([Gagne and Cuddihy, 1999](#)). Introduced lowland mesic forest communities include: Kukui (*Aleurites*), Christmas berry (*Schinus*), Guava (*Psidium*), Ironwood (*Casuarina*), and Silk oak (*Grevillea*) lowland mesic forests ([Gagne and Cuddihy, 1999](#)). The diversity of native species that remain in the introduced forests is likely related to the level of human disturbance ([Gagne and Cuddihy, 1999](#)). Most of the remaining native mesic lowland forests are dominated by lama (*Diospyros sandwicensis*) or 'ōhi'a (*Metrosideros polymorpha*) where they may occur in mixed stands. They are generally found in areas with rocky or steep slopes, or in gulches where human development is limited by terrain.

Hawai'i montane-subalpine mesic forest: This mesic montane-subalpine forest system still occurs on Kaua'i, Maui and Hawai'i. The island of Hawai'i contains the majority of this subtype while the islands of Maui and Kaua'i contain only a few thousand acres each ([Cuddihy and Stone, 1990](#)).

Four native communities are recognized as subcategories under the mesic montane-subalpine subtype: 'Ōhi'a montane mesic forest, Koa/'Ōhi'a montane mesic forest, Koa/'Ōhi'a/ A'e forest, and Olopua montane forest ([Gagne and Cuddihy, 1999](#)). Characteristics of these forests are described in [Table 2](#).

Hawai'i introduced wet-mesic forest: This introduced vegetation cover type is common on lower elevation wet-mesic sites. It has developed in areas that would have been dominated historically by native vegetation found in lowland mesic forests. Introduced

forests are a result of human activity including land conversion due to agricultural practices, development, and due to the introduction and establishment of nonnative species. The tree canopy is typically dominated by a variety of introduced wet or mesic tree species (Gagne and Cuddihy, 1999; Landfire, 2016) (Table 2).

Hawai'i managed tree plantation: The Hawai'i managed tree plantation typically consists of stands of introduced trees planted for forest products (lumber and fuel); horticulture; or agriculture (coffee, fruit, nut orchards) (Landfire, 2016; Table 2). Many of the plantations were also planted on converted agricultural land (sugarcane) to provide soil and water conservation benefits (State of Hawai'i DLNR, 2017). Plantations typically occur at lowland and montane, wet-mesic to mesic settings, often at the lower elevation edge of forest reserves (Landfire, 2016).

With awareness in the late 19th and early 20th century of the damage caused to native forests from grazing, logging, and feral animals, and the importance of forest cover to provide water for the sugar industry, large private forest reserves (planted mostly in nonnative species) were established at Līhu'e, Kaua'i 4050 ha (10,008 ac), and Pāhala, Hawai'i 20,240 ha (50,014 ac), and plantings for watershed protection on Maui and O'ahu (Cuddihy and Stone, 1990). At the beginning of the 20th century, in the early days of the territorial forest reserve, tree plantings for forest restoration were primarily of introduced fast growing tropical species. Native species and commercially valuable timber trees were avoided so that future generations would not be tempted to harvest trees (Cuddihy and Stone, 1990). Today managed tree plantations are commercially valuable trees harvested for lumber and fuel and total 12,379 ha (30,589 ac) statewide (Reeves and Amidon, 2018). The vast majority of plantations found within mesic forests are categorized as mixed (7321 ha; 18,090 ac) and contain stands of both native and introduced tree species. Mesic plantations categorized as "disturbed" total approximately 4449 ha (10,994 ac), and those containing less than 5% vegetation total ~2.4 ha (6 ac) statewide. Native tree plantations (primarily koa) are still at an experimental stage in Hawai'i. In spite of being a high-quality wood with high demand in local and foreign markets, native koa plantations have not gone through a full rotation (State of Hawai'i DLNR, 2017; Inman-Narahari, 2015). Native-dominated koa plantations total ~607 ha (1500 ac) statewide and compose a small proportion (<1%) of the available mesic forest plantations (Reeves and Amidon, 2018).

Interest in koa silviculture has grown in recent decades on deforested lands to supply demand for this valuable hardwood. These native dominated plantations often support an under story of native species (Skolmen and Fujii, 1980; Baker et al., 2009). Koa silviculture practiced on old pasturelands has resulted in increased habitat for some native species including endangered and common Hawaiian forest birds (Pratt and Jacobi, 2009).

Extent/Quantity of Mesic Forests

The extent of Hawai'i mesic forest today is similar across all islands to the prehuman condition, except for substantial loss of lowland mesic forests on the islands of O'ahu, Kaua'i, and Lāna'i (Figs. 6–8), and intrusion of lowland mesic forests by invasive trees, shrubs, and nonnative grassland communities. In total, there are approximately 175,175 ha (432,867 ac) of mesic forest currently found in the main Hawaiian Islands (Table 3). Although mesic forest is found on all of the main Hawaiian Islands, over half occur on the island of Hawai'i (Table 3). Thirty-eight percent (66,335 ha; 163,917 ac) of Hawai'i's mesic forest is native species dominated (i.e., greater than 50% native) (Fig. 10). The remaining portion (52%) is composed of nonnative species mixed forests (90,963 ha; 224,774 ac), or in a system described as heavily disturbed or bare, (containing <5% vegetation cover) (17,874 ha; 44,168 ac) which accounts for ~10% of the current vegetation quality found in Hawai'i mesic forests (Reeves and Amidon, 2018). Managed tree plantations compose 12,380 ha (30,592 ac) of mesic forests in Hawai'i. This constitutes ~7% of all mesic forests. The large majority of mesic forest plantations occur on the island of Hawai'i (8538 ha; 21,098 ac) with smaller plantations on O'ahu (2340 ha; 5782 ac), Moloka'i (811 ha; 2004 ac), and on Kaua'i (691 ha; 1707 ac) (Fig. 9).

Native dominated mesic forests are still found on the islands of Hawai'i (46,590 ha; 115,126 ac), Kaua'i (6001 ha; 14,829 ac), Maui (4317 ha; 10,667 ac), Moloka'i (4670 ha; 11,540 ac), O'ahu (4677 ha; 11,557 ac), and Lāna'i (79 ha; 195 ac). The greatest percentage of native dominated mesic forests occur on the islands of Hawai'i and Moloka'i (>50% remain on both islands) (Fig. 10).

There are eight vegetation classifications for Hawai'i mesic forest based on canopy height and dominant tree species (Reeves and Amidon, 2018). These are closed koa-ōhi'a mesic forest, closed 'ōhi'a mesic forest, mixed native non-native mesic forest, native

Table 3 Current distribution of mesic forest in the main Hawaiian Islands (Reeves and Amidon, 2018).

Island	Area in acres (hectares)	Area (% of Island)	Area (% of state of Hawai'i)
Lāna'i	952 (385)	1	< 1
Moloka'i	19,987 (8088)	12	< 1
Kaua'i	74,124 (29,997)	21	2
O'ahu	80,344 (32,514)	22	2
Maui	54,152 (21,914)	12	1
Hawai'i	203,304 (82,274)	8	5
Total	432,867 (175,175)	NA	12

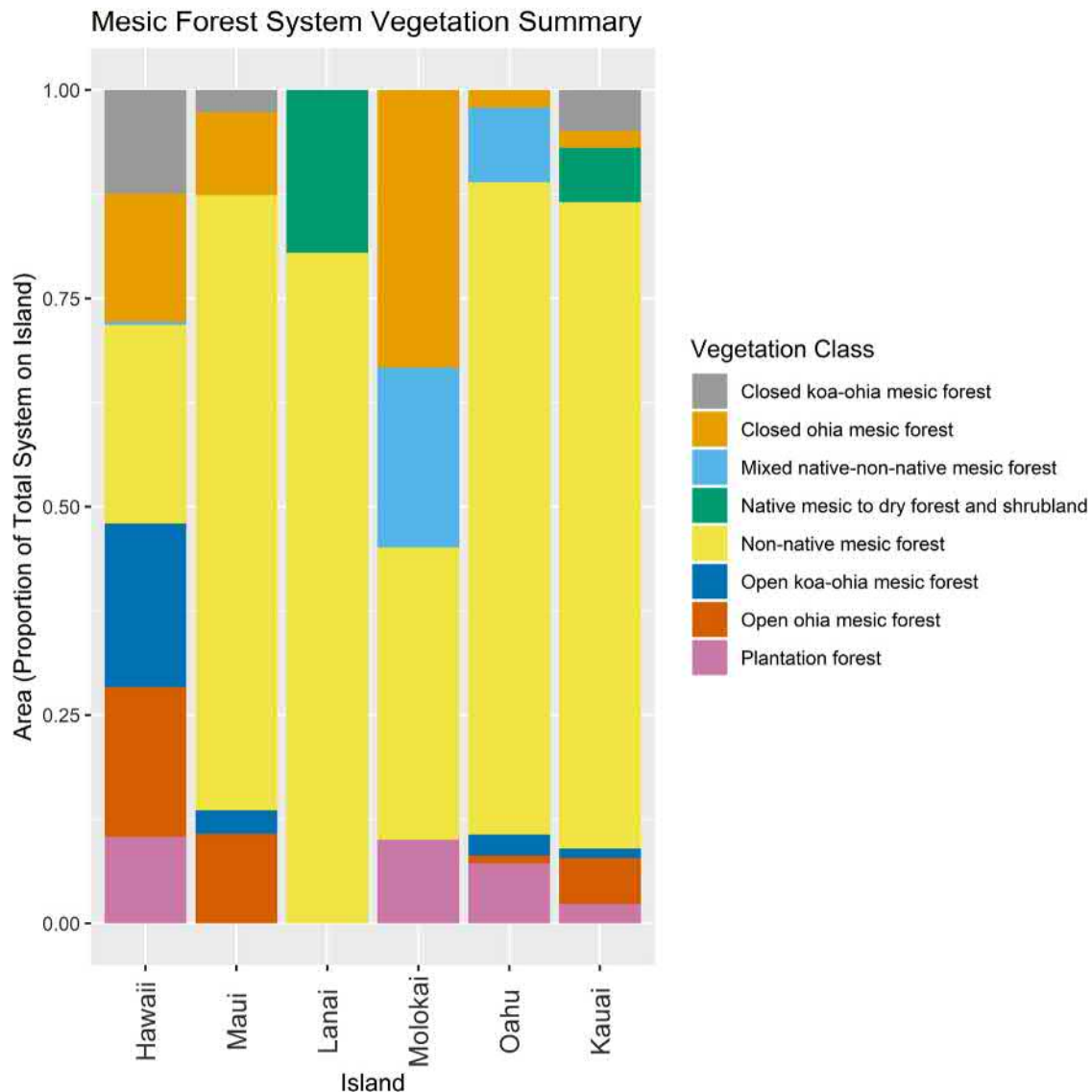


Fig. 9 Summary of mesic forest vegetation classifications.

mesic to dry forest and shrubland, nonnative mesic forest, open koa-‘ōhi’a mesic forest, open ‘ōhi’a mesic forest, and plantation forest (Fig. 9).

Land Ownership

Over 46% (80,715 ha; 199,451 ac) of mesic forest in the Hawaiian Islands is owned by the federal, state, and local government. The remaining mesic forests exist on private land (Fig. 11; Table 4; Reeves and Amidon, 2018).

Stressors

Hawaiian mesic forest ecosystems are highly vulnerable to impacts of stressors due to climate change as well as nonclimate stressors since they are sensitive to biotic and abiotic factors associated with both (Hilberg et al., 2018). Table 5 lists the climate and non-climate stressors for mesic forests which are described in further detail below.

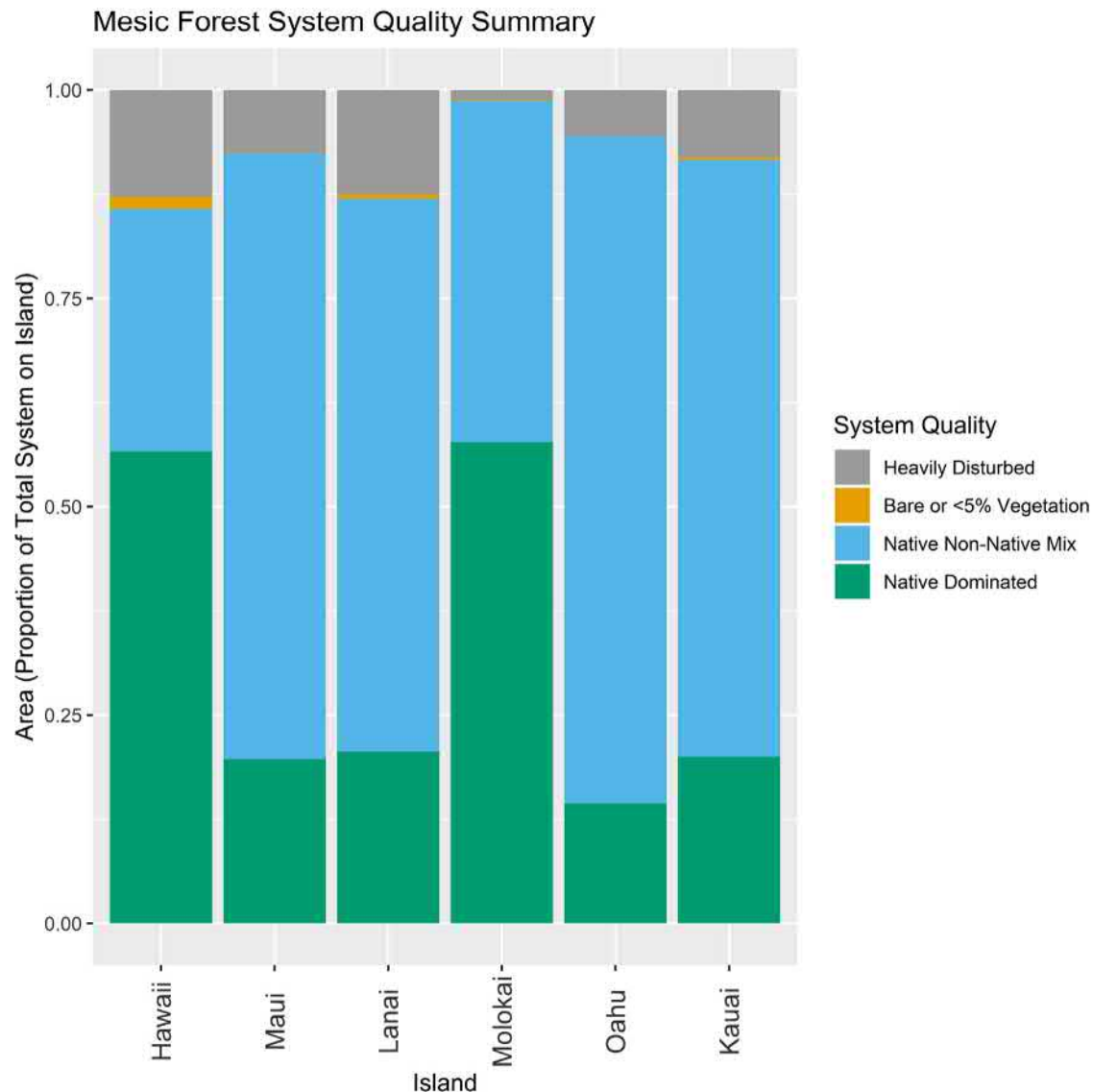


Fig. 10 Quality of mesic forest system.

Climate Stressors

Precipitation, wind, drought, soil moisture, air temperature, and storms

Mesic forests are susceptible to hurricanes, high winds, and landslides that may affect vegetation, alter succession, and create conditions more favorable to invasive species growth resulting in an altered vegetation community (Hilberg et al., 2018). Tree species found in mesic forests are somewhat wind-resistant but koa, which have shallow root systems, are vulnerable to snapping and uprooting in extremely high winds associated with storms (Baker et al., 2009). Storm related flooding and landslides can destroy mesic forests and alter succession, particularly in areas with poor drainage or on steep ridges and valleys (Restrepo and Vitousek, 2001; Walker, 1999). One of the most sensitive climatic components for mesic forests is water availability as a function of precipitation, soil moisture, drought, air temperature, and presence of trade winds. For example, reduced or increased water availability can directly alter vegetation composition and distribution in these communities by favoring growth and germination of invasive plants with higher tolerance for drier or wetter conditions (Hilberg et al., 2018).

A primary question regarding the possible impacts of rising temperatures on local climate in Hawai'i is whether the trade wind inversion layer will be affected. If the height or frequency of the inversion changes due to warming, significant hydrological, and ecological changes can be expected (Loope and Giambelluca, 1998; Krushelnycky et al., 2016). The impact of climate on mesic forests varies across the main Hawaiian Islands. On Maui and Hawai'i where higher elevation environments exist, continued warming may result in an upslope shift of mesic forests (Vorsino et al., 2014).

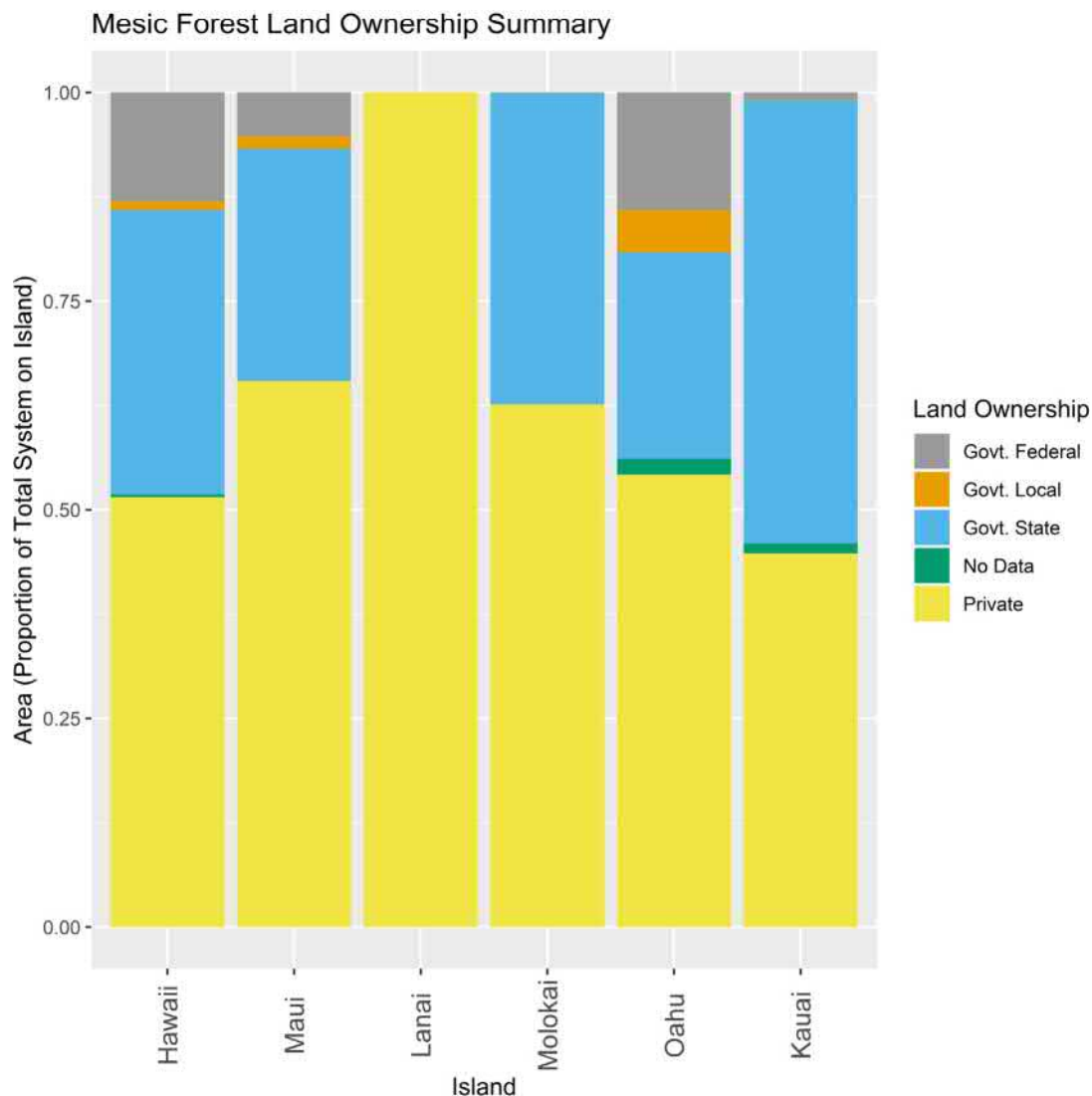


Fig. 11 Summary of mesic forest land ownership.

Nonclimate Stressors

Invasive species

Invasive species are nonnative organisms whose introduction causes or is likely to cause economic or environmental harm or harm to human health. They are a prominent stressor for the Hawaiian mesic forest ecosystem as many of the native species evolved in isolation on the islands in the absence of mammalian herbivores and plant competitors (Weller et al., 2011; Dunkell et al., 2011). Some invasive plants are less susceptible to drought and less palatable to invasive herbivores and therefore may thrive when disturbance events occur and outcompete the native mesic forest vegetation (Weller et al., 2011). Nonnative grass competition reduces recruitment of native tree and shrub species in mesic forests and also reduces the availability of water and nutrients to native trees and shrubs (Denslow et al., 2006). Depredation of seeds and seedlings by invasive rodents including rats (*Rattus rattus*, *R. norvegicus*, and *R. exulans*), and mice (*Mus musculus*) can also inhibit growth and regeneration of native species (Shiels, 2010). Feral ungulates (pigs, goats, cattle, and deer) consume and trample new growth and seedlings of native vegetation, and also promote the spread of invasive plant seeds through fecal matter causing further degradation of mesic forests (Dunkell et al., 2011).

Primary threats to lowland mesic forests are caused by feral animals (pigs, goats, deer, and cattle), fires, and subsequent invasion of weeds and grasses including *Andropogon virginicus*, *Panicum maximum*, *Cenchrus clandestinus*, *Schizachyrium condensatum*, *Clidemia hirta*, *Melastoma candidum*, *Psidium cattleianum*, and *Psidium guajava* (Gagne and Cuddihy, 1999).

Agriculture, grazing, and urban development

Since the 19th century Hawaiian forests have undergone severe stress from grazing by cattle and livestock and other agriculture uses on the landscape. Many of the mid-elevation mesic forests have been transformed into grassland pastures composed of invasive

Table 4 Land ownership of mesic forest in Hawai'i (Reeves and Amidon, 2018).

<i>Island</i>	<i>Land ownership</i>	<i>Area in acres (hectares)</i>	<i>Area (% of Island)</i>	<i>Area (% of state of Hawai'i)</i>
Lāna'i	Private	952 (385)	1	<1
Moloka'i	Govt. Local	6 (2.4)	<1	<1
Moloka'i	Govt. State	7467 (3022)	5	<1
Moloka'i	Private	12,515 (5065)	8	<1
Kaua'i	Govt. Federal	595 (241)	<1	<1
Kaua'i	Govt. Local	61 (25)	<1	<1
Kaua'i	Govt. State	39,401 (15,945)	11	1
Kaua'i	No Data	893 (361)	<1	<1
Kaua'i	Private	33,175 (13,425)	9	1
O'ahu	Govt. Federal	11,307 (4576)	3	<1
O'ahu	Govt. Local	4096 (1658)	1	<1
O'ahu	Govt. State	19,853 (8034)	5	<1
O'ahu	No Data	1537 (622)	<1	<1
O'ahu	Private	43,552 (17,625)	12	1
Maui	Govt. Federal	2829 (1145)	1	<1
Maui	Govt. Local	820 (332)	<1	<1
Maui	Govt. State	15,060 (6095)	3	<1
Maui	No Data	9 (3.6)	<1	<1
Maui	Private	35,433 (14,339)	8	1
Hawai'i	Govt. Federal	26,464 (10,710)	1	1
Hawai'i	Govt. Local	2137 (876)	<1	<1
Hawai'i	Govt. State	69,354 (28,067)	3	2
Hawai'i	No Data	614 (248)	<1	<1
Hawai'i	Private	104,736 (42,385)	4	3

Table 5 Climate and nonclimate stressors for mesic forests in Hawai'i.

<i>Climate stressors</i>	<i>Nonclimate stressors</i>
Precipitation	Invasive species
Wind	Urban development
Drought	Agriculture, grazing
Soil moisture	Insects/disease
Air temperature	Wildfire
Storms	Natural disasters
	Biological

species after timber has been harvested. Mesic pasture conversion has occurred across 69,483 ha (171,696 ac) in the main Hawaiian Islands. The largest proportion of mesic forest pasture conversion is seen on the island of Hawai'i (23,916 ha; 59,098 ac) and Maui (3296 ha) (NOAA, 2018).

It was recognized as early as the mid-1800s that cattle grazing impacted many types of native vegetation and especially egeneration of koa (Cuddihy and Stone, 1990). The consumption of seedlings and saplings by cattle directly prevents the successful regeneration of mesic forests (Blackmore and Vitousek, 2000; Mueller-Dombois, 1992) and competition with nonnative pasture grasses impedes the germination of native seeds (Baker et al., 2009). Continued grazing, soil compaction, and loss of the canopy trees has resulted in persistence of the grasslands rather than regeneration of the native mesic forests (Denslow et al., 2006).

Continued human population growth on all of the main Hawaiian Islands has increased the need for additional housing and development (State of Hawai'i, 2016). Additional development threatens destruction of the mesic forest biome where it occurs on private land (Fig. 11).

Much of the lowland mesic forest has been converted to pasture or agricultural use (crops and timber production), or has been lost to urbanization or fire (Cuddihy and Stone, 1990; SABP, 2015). Military training activities have also impacted mesic forest areas through live-fire training, large-scale troop movements, and heavy equipment operations. These activities impact mesic areas at United States Army training facilities on O'ahu. Training operations have resulted in vegetation clearing, increases in wildfire frequency, and the introduction and spread of unwanted alien species (State of Hawai'i DLNR, 2016).

Insects and disease

The nonnative acacia psyllid (*Psylla uncatoides*) breeds and feeds on the new terminal growth of koa and infestations by this insect can cause terminal growth dieback in mesic koa stands (Baker et al., 2009).

In early 2005, a fungal disease was found in 'ōhi'a trees on O'ahu. The disease, named 'ōhi'a rust (*Puccinia psidii*), has since spread to all the main Hawaiian Islands, where it affects other Myrtaceae taxa. In severe infections, terminal growth will die back (TMA, 2007).

Another significant threat, koa wilt disease, caused by *Fusarium oxysporum*, threatens the health of koa (*Acacia koa*), one of the two dominant tree species in Hawai'i's native forests. This soil-borne disease causes dieback and decline of koa in native forests by compromising the tree's vascular system (State of Hawai'i DLNR, 2016). Young trees less than 15 years old seem to be affected more often than old trees, and the disease is more often seen on trees planted below 760 m elevation than on trees growing in the forest at higher elevations. Koa wilt has been observed on the islands of Hawai'i, Maui, O'ahu, and Kaua'i (TMA, 2007; Baker et al., 2009).

Rapid 'Ōhi'a death is a disease that was first identified on the island of Hawai'i in 2010. The disease is caused by two fungal pathogens, *Ceratocystis lukuohia* and *Ceratocystis huliohia*. Both fungal pathogens kill 'ōhi'a which is a significant component of mesic forests (Barnes et al., 2018). Since 2010 the disease has spread to over 30,300 ha (75,000 ac) on the island of Hawai'i with some stands showing a greater than 90% mortality within 2–3 years. In 2018 the disease was also detected on the island of Kaua'i. The primary path for *Ceratocystis* to enter 'ōhi'a plants is through a wound which can occur following an injury due to cutting, pruning, sawing, breakage, strong winds, root abrasion, ungulate damage, and root trampling (CTAHR, 2018).

Wildfire

The proliferation of invasive grasses adapted to fire and the increased incidence of human ignited fires have resulted in an altered fire regime that is more frequent and severe, and increasing as much as fivefold in frequency since the 1970s (Abrahamson, 2013).

Throughout much of the state, particularly in lowland mesic areas, highly flammable nonnative grasses have replaced less flammable native communities (Abrahamson, 2013). The fire potential is greatest in areas subjected to seasonal drought, particularly in native ecosystems below 1400 m, in areas invaded by alien grasses and previously affected by fire (Smith and Tunison, 1992).

The montane parkland mesic ecosystem has shown some adaptation to fire (Mueller-Dombois, 1981), with rapid recovery of some native mesic forest species, particularly koa. Fire potential is relatively high in the montane mesic zone because of the continuous arrangement of grasses and abundance of shrubs. The invasion of alien grasses is increasing the fire potential in this ecological zone (Smith and Tunison, 1992; USFWS, 2010).

Postfire regeneration of native species is also impaired by invasive grasses which compete with native seedlings for water, light, and nutrients, and serve as fuel for future fires (Baker et al., 2009).

Natural disasters

Mesic forests are susceptible to natural disasters such as volcanic eruptions that remove vegetation and alter succession (Hilberg et al., 2018). These events can cause extensive damage over short time periods but are localized in their extent and occur only on the volcanically active island of Hawai'i. Regeneration of native mesic forest plants and trees is slow, beginning with the growth of lichens and pioneer species. Substrate age, climatic moisture, and elevation are the primary drivers of rates of succession. Succession in the mesic zone is slower than in wet areas but faster than in dry and arid regions (Carlquist, 1980; Price et al., 2007).

Biological

The recent and continued significant population decline of seabirds has a negative impact on mesic forests. Seabirds contribute marine derived nutrients, especially nitrogen, to the mesic forest ecosystems through deposition of guano (Rowe et al., 2017). In addition, the loss of native forest birds and pollinators has reduced the pollination of native plant and tree species resulting in lower rates of regeneration of native species (Aslan et al., 2013; Price and Wagner, 2004).

Conservation Efforts

Reserves

Approximately 25,683 ha (63,464 ac) of mesic forests are protected in reserve areas across the main Hawaiian Islands (Fig. 12). Reserve areas may include areas designated as a national park, national wildlife refuge, Natural Area Reserve (NAR), private reserve, or Nature Conservancy preserve (Reeves and Amidon, 2018). The amount of mesic forest protected in reserve areas varies by island, with 18,292 ha (45,200 ac) on the island of Hawai'i, 3615 ha (8933 ac) on Maui, 1867 ha (4613 ac) on Kaua'i, and 1384 ha (3420 ac) on Moloka'i (Fig. 12). Of 18,292 ha (45,200 ac) protected in reserves areas on the island of Hawai'i, roughly 15,304 ha (37,817 ac) (84%) are classified as native dominated habitat (Fig. 12). Lāna'i and O'ahu contain the least amount of mesic forest protected in reserve areas in the State with 49 ha (121 ac) on Lāna'i and 482 ha (1191 ac) on O'ahu (Fig. 12). Knowing that less than 25,683 ha (63,464 ac) of mesic forests are protected in reserve areas in the state, and 175,175 ha (432,867 ac) are actually classified as mesic forests in the state, indicates a need to implement additional measures to increase the public's awareness of the remaining gap between unprotected versus protected mesic forests. Conservation areas that contain mesic forests in the state are listed in Table 6. Management efforts within reserve areas may include wildfire threat control, invasive plant and animal control, and native forest restoration.

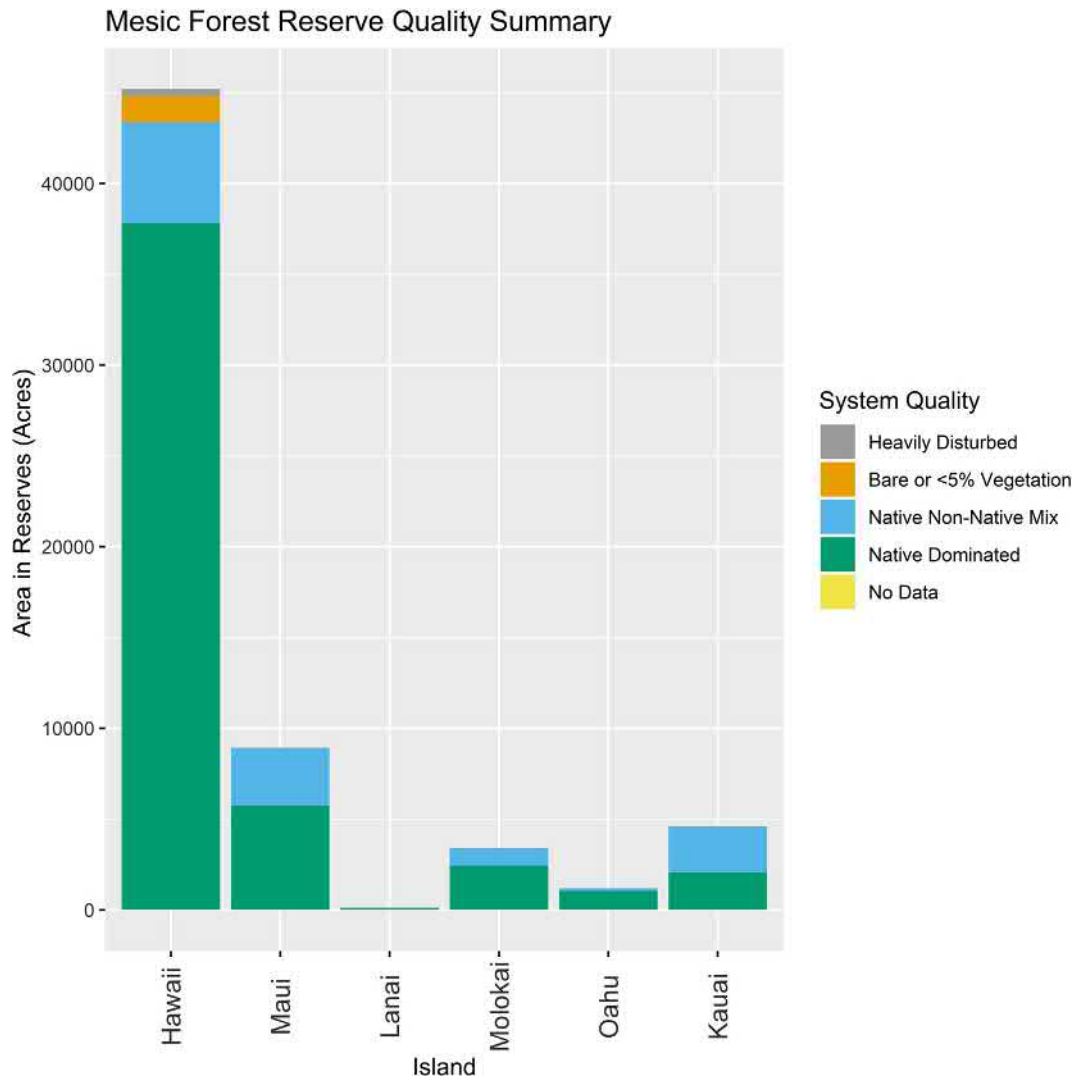


Fig. 12 Quality of mesic forests in reserves.

Table 6 Mesic forest conservation areas in Hawai'i.

<i>Island</i>	<i>Mesic forest subcategory</i>	<i>Name of reserve</i>	<i>Landowner</i>	<i>Number acres (hectares) protected</i>	<i>Year established</i>
O'ahu	Lowland mesic	Pahole Natural Area Reserve	State	658 (266)	1981
O'ahu	Lowland mesic	Mt. Ka'ala Natural Area Reserve	State	1100 (445)	1981
O'ahu	Lowland mesic	O'ahu Forest National Wildlife Refuge	Federal	4525 (1831)	2000
Kaua'i	Lowland and montane mesic	Ku'i'a State Natural Area Reserve	State	1636 (662 ha)	1981
Maui	Montane mesic	Nakula State Natural Area Reserve	State	4441 (1797)	2011
Maui	Montane mesic	Haleakalā National Park	Federal	33,265 (13,462)	1961
Hawai'i	Montane mesic	Hawai'i Volcanoes National Park	Federal	207,634 (84,027)	1916
Hawai'i	Montane mesic	Hakalau Forest National Wildlife Refuge	Federal	32,733 (13,247)	1985
Hawai'i	Montane mesic	Kona Refuge	Federal	5300 (2145)	2005
Hawai'i	Montane mesic	The Nature Conservancy—Kona Hema Preserve	Private	8089 (3274)	2003
Hawai'i	Montane mesic	Keauhou Forest—Kamehameha Schools, Three Mountain Alliance	Private	32,570 (13,181)	1985
Hawai'i	Montane mesic	Pu'uwa'awa'a State Forest Bird Sanctuary	State	3806 (1540)	2003
Hawai'i	Montane mesic	Manukā State Natural Area Reserve	State	25,714 (10,406)	1983

Laws and Biosecurity

Endangered species protections and biosecurity and invasive species laws, regulations, coordination, and authority aid in conservation efforts for mesic forests by preventing the introduction of invasive plants and providing legal protections for rare native species (Table 7).

Biosecurity

In addition to federal biosecurity laws (Executive Orders 11,987, 13,112, 13,751), the Hawai'i Invasive Species Council (HISC) adopted Resolution 17-1 endorsing the Hawai'i Interagency Biosecurity Plan. This Interagency Biosecurity Plan is the state's guiding document for biosecurity improvements over the coming decade.

Endangered species act (ESA)

The Endangered Species Act of 1973 (ESA) aims to provide a framework to conserve and protect endangered and threatened species and their habitats. As habitat loss is the primary threat to most imperiled species, the ESA allows the U.S. Fish and Wildlife Service (USFWS) and National Marine Fisheries Service (NMFS) to designate specific areas as critical habitat zones. In 1978, Congress amended the law to make critical habitat designation a mandatory requirement for all threatened and endangered species.

Nineteen percent (30,942 ha; 76,459 ac) of mesic forest habitat in the state of Hawai'i is designated as federal critical habitat for 305 threatened and endangered species in the main Hawaiian islands (Fig. 13). The majority of designated critical habitat that is also classified as mesic forest is located on the islands of Hawai'i (11,932 ha; 29,484 ac) and O'ahu (8291 ha; 20,487 ac) (Fig. 13). Species listed under the ESA are automatically added to the State of Hawai'i list of endangered species, and are thus also protected by State regulations.

Table 7 Laws and regulations

<i>Title</i>	<i>Year implemented</i>	<i>Authority</i>	<i>Intent/purpose</i>
Endangered Species Act	1973	Federal	Protects critically imperiled species from extinction
50 CFR 16	1974	Federal	Implements the Lacey Act (18 USC 42), which prohibits importation of injurious species
Convention on International Trade in Endangered Species	1975	International	Ensures that international trade in specimens of wild animals and plants does not threaten the survival of the species in the wild
Executive Order 11987	1977	Federal	Charges executive agencies with restricting the introduction of exotic species into the natural ecosystems on federal lands; and encourages States to do the same
Hawai'i Administrative Rules, Title 4, Subtitle 6, Chapters 68 and 70	1981	Hawai'i (Department of Agriculture, DOA)	Rules/amendments for noxious weeds, plant and nondomestic animal quarantine, plant import, and bromeliad import
Executive Order 13112	1999	Federal	Requires that a Council of Departments dealing with invasive species be created to prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause
HRS 194-2	2002	Hawai'i (Department of Land and Natural Resources, DLNR)	Establishes Hawaii Invasive Species Council (HISC)
Act 85	2003	Hawai'i (HISC)	Conveys statutory authority to HISC to continue to coordinate approaches among the various State and Federal initiatives for the prevention and control of invasive species
Act 36 (2011) HRS 150A-5.3	2011	Hawai'i (DOA)	Imposes a fee for the inspection, quarantine, and eradication of invasive species contained in any freight brought into the State
HB 1568	2011	Hawai'i (DOA)	Requires commercial harbors and airports in Hawai'i to provide biosecurity and to facilitate cargo inspections
HRS 174C Hawaii State Water Code	2013	Hawai'i (CWRM)	Establishes Commission on Water Resource Management (CWRM) and Water Resource Management Fund
Executive Order 13751	2016	Federal	To prevent the introduction of invasive species and provide for their control, and to minimize the economic, plant, animal, ecological, and human health impacts that invasive species cause (amends EO 13112)
7 CFR 360.200	2018	Federal	Designates certain plants as noxious weeds

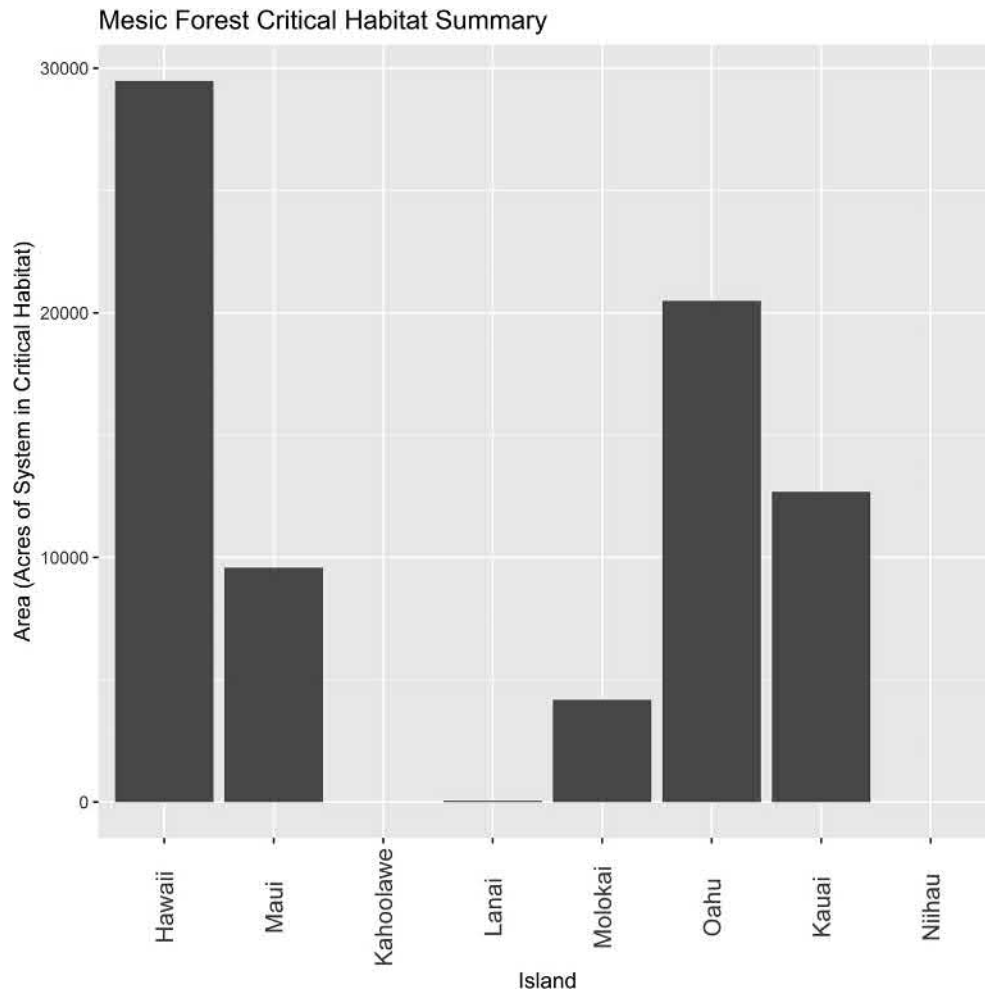


Fig. 13 Federally designated critical habitat on the main Hawaiian islands containing mesic forest.

Stakeholder Engagement

National parks and national wildlife refuges

A total of 16,671 ha (41,195 ac) of mesic forests exist on federal lands in the Hawaiian islands (Table 4). Of this, approximately 64% are found on the island of Hawai'i within Hawai'i Volcanoes National Park and in the Hakalau Forest and Kona National Wildlife Refuges (Table 6). Haleakalā National Park also contains native mesic forest resources on Maui (Tables 4 and 6). Management actions by these federal agencies include fencing, ungulate removal, and invasive weed control (USFWS, 2010; NPS, 2015; U.S. DOI, 1999).

State of Hawai'i

Approximately 61,162 ha (151,135 ac) of mesic forests occur on lands managed by the state of Hawai'i. They are found on all of the main Hawaiian Islands except Lāna'i (Fig. 11 and Table 6).

These native and nonnative forests are found within State Forest Reserves (FRS), parks, sanctuaries, and in Natural Area Reserves (NARS) (Table 4). The state forest reserves were created by the Territorial Government of Hawai'i in 1903 as early foresters recognized the need to protect forests to provide water for agriculture and surrounding communities. The Reserves encompass over 274,624 ha (678,611 ac) of land statewide. The Department of Land and Natural Resources (DLNR), Division of Forestry and Wildlife (DOFAW) manage the forest reserves and focus their resources on protection, management, restoration, and monitoring.

The Natural Area Reserves System (NARS) was established in 1970 with the intent to preserve in perpetuity native flora and fauna, as well as geological sites, of Hawai'i. The Natural Area Reserves are also administered by the DLNR, Division of Forestry and Wildlife (DOFAW). Lowland mesic forests are found within the Mt. Ka'ala and Pahole NAR on O'ahu and in the Ku'ia NAR on Kaua'i. Montane-mesic forests are found in the Ku'ia NAR on Kaua'i, Nakula NAR on Maui, and also in the Manuka NAR on the island of Hawai'i (Table 6). NARS management activities include construction of conservation fencing, ungulate management, weed control, and restoration of native species.

Department of Hawaiian Home Lands

The Department of Hawaiian Home Lands (DHHL) was created by the Hawai'i State Legislature in 1960 and is governed by the Hawaiian Homes Commission Act of 1920. The act set aside a land trust for native Hawaiians to maintain their traditional ties to the land. The primary responsibility of DHHL is to serve its beneficiaries and manage its land trust. DHHL also views its responsibility as a landowner to manage and protect native lands "to support both cultural and resource management activities and create homesteading opportunities for the future" (DHHL, 2009). Thus, the 'Āina Mauna Legacy Program was created to protect native forest on the slopes of Mauna Kea on the island of Hawai'i. The program specifically includes the lands of Humu'ula and Pi'ihonua, which contain tracts of mesic forest. Management goals include removal of invasive species, koa silviculture, native forest protection and restoration, conserving endangered species, and providing educational and cultural opportunities (DHHL, 2009).

Watershed partnerships

The Hawai'i Association of Watershed Partnerships (HAWP) comprises ten island-based statewide watershed partnerships that work collaboratively with more than 74 public and private partners on five islands to protect over 890,000 ha (2.2 million ac) of vital forested watershed lands (Hawai'i Association of Watershed Partnerships, 2018).

The HAWP's mission is to increase the effective management and protection of upper elevation watershed areas. Watershed partnerships undertaking conservation efforts to protect and manage large areas of mesic forest include the Three Mountain Alliance, Mauna Kea Watershed Alliance, East Maui Watershed Partnership, West Maui Watershed Partnership, Leeward Haleakalā Watershed Restoration Partnership, and East Moloka'i Watershed Partnership.

Safe harbor agreements

The Federal and State Safe Harbor programs encourage proactive conservation efforts by non-Federal landowners while providing them certainty that future property-use restrictions will not be imposed if those efforts attract species listed as endangered or threatened to their property, or result in increased populations of endangered or threatened species already present. In return for voluntary conservation commitments, the Agreement gives the landowner assurances covered by agency permits that allow for future alteration or modification of the enrolled property back to its original condition. These cooperative efforts provide landowners with a way to manage their lands to support the conservation of listed species while conducting approved land-use practices. Without this cooperative government/private effort, the private property would be less valuable to the recovery of endangered or threatened species (State BLNR, 2018).

A Safe Harbor Agreement between Kamehameha Schools, the State Department of Land and Natural Resources, and the U.S. Fish and Wildlife Service was finalized in June of 2018. The total area covered by the agreement is 13,034 ha (32,208 ac) on lands owned by Kamehameha Schools on the island of Hawai'i. The area covered by the SHA includes mesic forest resources. The 50-year agreement will contribute to the recovery of 32 endangered species and the agreement is part of an ongoing watershed partnership effort within the State of Hawai'i managed by the Three Mountain Alliance Watershed Partnership. Management activities covered by this agreement include outplanting of native plant species, control of invasive plants, koa silviculture, predator control, fencing and ungulate removal, fire threat management, response efforts to rapid 'Ōhi'a Death, and other land management activities that assist in the maintenance and enhancement of native forest (TMA, 2007; State BLNR, 2018; KS, 2014).

Pulama Lāna'i

The island of Lāna'i is privately owned but does have conservation partnerships with the U.S. Fish and Wildlife Service, the State of Hawai'i, and The Nature Conservancy. Currently the land manager, Pulamā Lāna'i, is implementing actions that benefit mesic forests inside its Lāna'ihale unit (Increments 1 and 2). The management unit encloses a total of 890 ha (2199 ac) and ongoing management actions within the unit include the control of invasive ungulates and weeds. Three smaller fenced units, totaling less than 6 ha (15 ac) have been constructed for the purposes of protecting individual rare plant and snail populations that occur in mesic forests (Lāna'i Resorts et al., 2015, in. litt.).

Invasive species committees

The Invasive Species Committees (ISC's) are voluntary island-based partnerships on Kaua'i (KISC), O'ahu (OISC), Maui (MISC), Moloka'i (MOMISC), and the Big Island (BIISC) that work with government agencies, nonprofit organizations, and private businesses and landowners to protect each island from the most threatening pests with a proactive approach. The ISC's target species that have high potential to severely impact the economy, environment, agriculture, human health, and quality of life (HDLNR, 2015).

Work done by these committees contributes directly to the conservation of mesic forests through removal and reduction of invasive plants and animals in mesic forests and in restoration of sites across the Hawaiian Islands. In addition, the ISC's helps generate public education that in turn enhances conservation of mesic forests.

Ranching and farming easements

Land eligible for agricultural easements that overlaps with the mesic forests are generally composed of rangeland, grassland, pastureland, and nonindustrial private forest land. The Natural Resources Conservation Service (NRCS) prioritizes the protection of agricultural uses and related conservation values of the land and those that maximize the protection of contiguous acres devoted

to agricultural use. Private landowners and lessees may enroll land through agricultural land easements through NRCS. Easements are contingent on the development of an agricultural land easement plan that promotes the long-term viability of the land (USDA, 2018). The Natural Resources Conservation Service currently have no dedicated land through such easements currently in the state of Hawai'i.

The NRCS Healthy Forests Reserve Program (HFRP) also helps landowners restore, enhance and protect forestland resources on private lands through easements and financial assistance. The HFRP aids the recovery of endangered and threatened species under the Endangered Species Act, improves plant and animal biodiversity, and enhances carbon sequestration (USDA, 2018).

The Healthy Forests program is not yet available in the NRCS-Pacific Islands Area (PIA). This program could assist landowners with mesic forest restoration and protection in the future.

Military

The United States Army has instituted an ecosystem management program to mitigate environmental impacts of their military training activities. This is an active and well-funded management program for native systems occurring within military managed lands. The United States Army and other military branches in Hawai'i also provide acquisition buffer programs that have played important roles in acquiring important threatened and endangered species habitat (State of Hawai'i DLNR, 2016). The O'ahu Army Natural Resources Program conducts research and conservation efforts in mesic forest areas to promote reduction in invasive species and reduce fire occurrence. These efforts collectively help to support conservation, restoration, and protection of native mesic forests across the main Hawaiian Islands.

Hawai'i Wildfire Management Organization

Since 2002, the Hawai'i Wildfire Management Organization (HWMO) has worked with communities throughout the state of Hawai'i to implement dozens of projects mitigating wildfire hazards and protecting natural and cultural resources. HWMO partners work closely with varied organizations from the United States Forest Service, United States Army, and University of Hawai'i, to the grassroots small community associations of Hawai'i's towns and villages. They sponsor community wildfire preparedness workshops, and have conducted wildfire hazard assessments for every community in the State. These assessments provide a more thorough understanding of wildfire hazards that can be addressed by communities, decision makers, fire responders, and natural resource managers. This organization directly supports the conservation of mesic forests through preparation and education efforts to minimize destruction of mesic forests by wildfires (HWMO, 2018, in litt.).

Others

Several groups have organized and taken action to address native species and ecosystem level conservation issues. The Hawaiian Forest Bird Recovery Team is an example where the group assisted in developing the Draft Revised Recovery Plan for Hawaiian Forest Birds that includes efforts to conserve and protect mesic forests where endangered populations of birds occur (Hawai'i Resource Strategy, 2010). The Maui forest bird recovery project has also undertaken large-scale forest restoration efforts in the mesic forest of the Nakula NAR on Maui.

Future Scenarios

The condition of Mesic Forests in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are as follows:

- (1) *Conservation values*: Stakeholder involvement and public opinion determine the formulation, implementation and funding of natural resource conservation within laws and development plans.
- (2) *Laws and biosecurity*: National, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented (e.g., hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.).
- (3) *Development or conservation planning*: National, state, county, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

These conservation management parameters are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The year 2035 is the extent of the "foreseeable future," and is based on the projected divergence of IPCC Representative Concentration Pathway (RCP) climate change scenarios (van Vuuren et al., 2011a,b; Miller 2018).

The four foreseeable future scenarios considered in this habitat assessment are:

- Future Scenario One, Status Quo*—The most likely foreseeable future; no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues through the foreseeable future.
- Future Scenario Two*—A slight increase in natural resource conservation in the CMPs marginally improves conservation management.

Future Scenario Three—A slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management.

Future Scenario Four—A moderate to large increase in conservation actions in the CMPs substantially improves conservation management.

The future condition of Mesic Forests in Scenario One, the status quo, was characterized from an assessment of change over time in Mesic Forest land cover obtained from existing land cover maps (see [Amidon and Reeves 2018](#) for a description of land cover change assessment methodology.). Based on these land cover maps, an annual rate of change for Mesic Forests was estimated, and a projected change (in acres/ha) was calculated for the year 2035. The resulting information on changes in land cover by 2035, as derived from existing land cover change estimates, is the extent of the Mesic Forest ecotype that is expected in the foreseeable future under Scenario One, the status quo, where conservation efforts remain unchanged and the current rate of change in land cover is also unchanged ([Amidon and Reeves, 2018](#)).

The future conditions of Mesic Forests for Scenarios Two, Three, and Four cannot be quantitatively (acres/ha) estimated. However, the Scenario One estimate can provide a “baseline” for a qualitative characterization of changes in the future condition of Mesic Forests under Scenarios Two, Three, and Four.

Changes in human population are captured only by the changes in the “developed” land cover footprint derived from land cover map analysis ([Amidon and Reeves, 2018](#)). Impacts from other sources of human activities or human-caused habitat stressors (e.g., plant and animal diseases, wildfires, invasive species, etc.) are not well characterized in the land cover changes, but significantly contribute to increases in the land cover area dominated by nonnative vegetation. For an assessment of island-by-island changes in human population see [Amidon and Reeves, 2018](#).

Also, note that island-wide implementation of the CMPs is unlikely to have a significant effect on climate-related stressors (temperature, precipitation, and severe weather) resulting from global warming by 2035. This lack of CMP climate effects is due to the global lag in climate response to changes in greenhouse gas emissions which occurs on the order of centuries rather than years ([Solomon et al., 2009](#); [Gillett et al., 2011](#); [Jevrejeva et al., 2012](#)). Evidence of climate effects is also confounded by the large annual variation in the Pacific islands climate parameters, which is much greater than projected climate change by 2035. Although impacts from climate-related habitat stressors do not change across the four scenarios, they were included in this analysis because of their overall magnitude of potential importance to future habitat viability.

Future Scenario One—Status Quo

Summary: Under Scenario One there is no anticipated change in the implementation of the three CMPs between 2018 and 2035. A continuing current rate of change in land cover through this foreseeable future results in a slow but continuous change in mesic forest subcategories ([Table 8](#)).

Native mesic forests would have a continued decline in size and distribution, and therefore a decrease in redundancy. Human-caused stressors will have a small increase overall and continue to reduce the size and quality of native mesic forests. Ecological function is predicted to be reduced due to the ability of invasive plants and animals to outcompete native plants for water and space, subsequently resulting in a reduction in native biodiversity. Degradation of native mesic forests will continue to increase as remaining areas become more fragmented, thus reducing their resiliency and representation.

Introduced mesic forests are predicted to increase in size and distribution (redundancy) as a result of the overall small increase in human-caused ecotype stressors. Introduced mesic forests are likely to expand as invasive species replace native-dominated communities, resulting in an increase in their resiliency, redundancy, and representation ([Table 9](#)).

The managed tree plantations are predicted to increase in size and distribution due to the assumed expansion of the human population and continued development pressure for forest products (lumber, fuel), horticulture, and agriculture (coffee, fruit, nut orchards) resulting in an increase in their resiliency, redundancy, and representation ([Table 9](#)).

Future Scenario Two

There is a slight increase in the CMPs that marginally improves conservation management.

Conservation agencies and stakeholders work with increased but limited resources to slow or stop the degradation of native mesic forest areas. Introduced mesic forests will continue to increase. Scenario Two is essentially “status quo” with minor improvements in the three CMPs. This scenario is expected to have the second highest likelihood of occurring into the foreseeable future, being slightly less likely than Scenario One ([Table 9](#)).

Future Scenario Three

There is a small to moderate decrease in conservation actions in the CMPs that substantially decreases conservation management.

All natural resource management actions in the CMPs are set aside in deference to land use for economic development. With extensive localized management, some native species may persist in park-like settings or in areas where land development is not possible. This scenario has substantial declines in natural resource conservation within the three CMPs. An increasing human population is supported in its use of land for economic development over the conservation of native ecotypes. Areas that cannot

Table 8 Responses of mesic forest habitat stressors in foreseeable future scenarios (Amidon and Reeves, 2018).

Conservation management parameters (CMPs)				
Conservation values	Stakeholder involvement and public opinion influence the formulation, implementation, and funding of natural resource conservation and biosecurity (NRC/B) within laws and development or conservation plans			
Laws and biosecurity	National, state, county, and city laws and regulations are the means by which NRC/B are supported and implemented			
Planning for development or conservation	National, state, county, city, and private development plans or conservation plans define actions that result in losses or gains in NRC/B (impacts realized at implementation)			
Foreseeable future scenarios and the resulting mesic forest conditions				
Use foreseeable future Scenario One as a “baseline” to characterize changes in <i>Conservation Actions</i> and mesic forest <i>Conditions</i> in future Scenarios Two, Three, and four	Scenario One: <i>CMPs</i> : unchanged in support for NRC/B <i>Conservation actions</i> : no change; current rate of land cover change continues through the foreseeable future <i>Mesic forest condition</i> : ecotype area, quality, and sustainability slowly decrease through the foreseeable future	Scenario Two: <i>CMPs</i> : small increase in support for NRC/B <i>Conservation actions</i> : marginal increase. <i>Mesic forest condition</i> : ecotype area is unchanged through the foreseeable future; habitat quality and sustainability are slightly enhanced through the foreseeable future	Scenario Three: <i>CMPs</i> : small to moderate decrease in support for NRC/B <i>Conservation actions</i> : substantial decrease <i>Mesic forest condition</i> : urban and agricultural uses are prioritized over conservation; ecotype area, quality, and sustainability substantially decrease through the foreseeable future	Scenario Four: <i>CMPs</i> : moderate to large increase in support for NRC/B <i>Conservation actions</i> : substantial increase <i>Mesic forest condition</i> : robust, sustained effort to restore, manage, and expand conservation; ecotype area, quality, and sustainability substantially increase through the foreseeable future
Stressors	Responses of mesic forest stressors			
Development	Small to moderate increase	No change (redevelop)	Moderate to large increase	Small to moderate decrease
Altered hydrology	No change to small increase	No change	Larger increase	Small decrease
Recreation/access	Small increase	Small increase	Larger increase	Larger increase
Invasive species	Small increase	Small increase	Larger increase	Small decrease
Plant diseases	Small increase	Small increase	Larger increase	No change to small decrease
Fire	Small increase	Small increase	Larger increase	No change to small increase
Erosion	Small increase	No change	Larger increase	Small decrease
Climate				
Temperature	Small to moderate increase	Small to moderate increase	Small to moderate increase	Small to moderate increase
Precipitation	Small decrease	Small decrease	Small decrease	Small decrease
Storms	Small increase	Small increase	Small increase	Small increase

Table 9 Summary of overall condition for mesic forest biome subtypes in the future scenarios.

<i>Mesic forest subtype</i>	<i>Scenario One: status quo</i>	<i>Scenario Two: slightly improved</i>	<i>Scenario Three: substantially decreased</i>	<i>Scenario Four: substantially improved</i>
Montane-subalpine mesic forest	Decrease	Slowly decrease	Decrease	Significantly increase
Lowland mesic forest	Decrease	Slowly decrease	Decrease	Significantly increase
Introduced mesic managed tree plantation	Increase	Slightly increase	Significantly increase	Slowly decrease
Hawai'i introduced wet-mesic forest	Increase	Slightly increase	Significantly increase	Slowly decrease

support development become the only areas of free-living native species. The anticipated changes, under Scenario Three, for each of the ecotype stressors important to Mesic Forests are given in [Table 8](#).

Overall, this scenario would severely degrade and fragment native mesic forest habitat and result in their reduced resiliency, redundancy, and representation. Introduced mesic forest subtypes would significantly increase in resiliency, redundancy, and representation under this scenario. This scenario, along with Scenario Four, has the lowest likelihood of occurring in the foreseeable future ([Table 9](#)).

Future Scenario Four

There is a moderate to large increase in conservation actions in the CMPs that substantially improves conservation management.

For this scenario, substantial improvements to the three CMPs and a general decrease in human-caused ecotype stressors would increase the size and quality (resiliency) of native lowland mesic forests and montane-subalpine mesic forests. Although this

increase in native forest sub-types would be gradual at first it will become more noticeable by 2035 as the substantial improvements to the three CMPs will help keep these subtypes from declining. The introduced mesic forest subtypes would slowly decrease in resiliency, redundancy, and representation under this scenario (Table 9).

Based on this analysis, the substantial improvements in restoration for native mesic forest ecotypes would result in increased resiliency, redundancy, and representation and introduced subtypes would slowly decrease. This scenario, and Scenario Three have the lowest likelihood of occurring in the foreseeable future.

Conservation Implications

Under the most likely future scenario, the native mesic forests are expected to decrease in resiliency, redundancy and representation while the introduced subtypes are predicted to increase (Tables 9 and 10). Conservation efforts by Federal, State, private, and multiple agency partnerships have been beneficial in helping to conserve and protect native mesic forests. Without increased effort the current level of conservation is insufficient to conserve the native subtypes of this biome. The continued spread of invasive plants and browsing ungulates is rapidly degrading native dominated mesic forests decreasing their resiliency and representation while the introduced subtypes continue to increase (Table 10). The managed tree plantations are also increasing in representation, redundancy and resiliency as interest in tree plantations for forest products (lumber and fuel) grows (Landfire, 2016). Additionally, the loss of marine derived nutrients from seabirds, insect pollinators, and seed dispersing native birds, adds to a decrease in resiliency of the native forest subtypes. All of these impacts combined with changes in fire regime, climate, and water availability are more favorable to the introduced mesic forest subtypes than they are to the native mesic forests which are decreasing in resiliency, representation, and redundancy (Table 10).

Mesic Forests Conclusion

In summary, the conservation efforts by Federal, State, private, and multiple agency partnerships have been beneficial in helping to conserve and protect the remaining mesic forests in Hawai'i. The protection and restoration of mesic forests cannot be accomplished solely on Federal lands however, because their range occurs primarily on non-Federal lands. To achieve conservation objectives these non-Federal mesic forests require cooperative conservation efforts on private and State lands. Increasing funding sources remains a high priority, to accomplish the goals of expanding and actively managing the remaining mesic forests.

The primary stressors to mesic forests include habitat destruction and modification by invasive ungulates, competition with invasive plant species, insects, forest disease, natural disasters (storms, landslides hurricanes), fire, drought, agriculture and urban development, and climate change. These stressors act in concert with other stressors on mesic forests, and are expected to continue or increase in magnitude and intensity in the future without effective management actions to ameliorate threats.

Finally, the condition of mesic forests in the foreseeable future favors Scenario One, which has the highest likelihood of occurring in the foreseeable future relative to the other scenarios. Under Scenario One there is no change in the implementation of the conservation management parameters (CMPs). Scenario Two is based on a slight increase in the implementation of the CMPs, which marginally improves conservation management. Thus Scenario Two is expected to have the second highest likelihood of occurring into the foreseeable future, being slightly less likely than Scenario One. Scenario Three is based on a slight to moderate decrease in conservation actions in the CMPs which substantially decreases conservation management. Because there is a decrease in the implementation of the CMPs, Scenario Three would severely degrade and fragment native mesic forest eco-types and result in reduced resiliency, redundancy, and representation. In Scenario Four, the substantial improvements in restoration for native mesic forest eco-types would result in increased resiliency, redundancy, and representation. However, this scenario and Scenario Three have the lowest likelihood of occurring in the foreseeable future.

Overall, the CMPs are critical factors that drive the direction and magnitude of natural resource conservation and determine the foreseeable future scenarios. Any increase in the implementation of the CMPs will result in the greatest conservation returns for native mesic forest (Scenario's Two and Four). Conversely, any decrease in the implementation of the CMPs will result in the least conservation returns for native mesic forest (Scenario's One and Three). Thus, realistic expectations of the implementation of the CMPs were considered when determining the likelihood of occurrence for each scenario in the foreseeable future.

Table 10 Summary of interactions of current stressors and conservation efforts on redundancy, resiliency, and representation in the mesic forest subtypes.

<i>Mesic forest biome subtype</i>	<i>Redundancy</i>	<i>Resiliency</i>	<i>Representation</i>
Introduced mesic managed tree plantation	Increase	Increase	Increase
Introduced wet-mesic forest	Increase	Increase	Increase
Lowland mesic forest	Decrease	Decrease	Decrease
Montane-subalpine mesic forest	Decrease	Decrease	Decrease

See also: Physical Geography of the Hawaiian Islands.

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Mariana Islands Forest

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Published by Elsevier Inc.

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Abstract

We present a status assessment of the Mariana Islands archipelago (Marianas) forests, including the current status, stressors, and future viability. Forests in the Marianas generally receive moderate to high rainfall during distinct wet and dry seasons

and are associated with limestone or volcanic substrates. Prior to the arrival of humans in the Marianas approximately four centuries ago, native forest was the dominant forest type. As a result of natural and anthropogenic disturbance, a proportion of native forest was converted to three additional forest sub-types: secondary, monoculture, and *Leucaena* forests. Forests were defined and characterized using the classification of landcover types for the Mariana archipelago developed by Amidon et al. (2017). Currently, forests occur on all islands in the archipelago, except for Farallon de Medinilla due to extensive bombing during military operations and continuing volcanic activity on Uracas. The main stressors to forests are invasive species, development, volcanic eruptions, typhoons, and fire. Ongoing conservation efforts include biosecurity measures, protected area and species management, invasive species control, and existing laws and regulations. Forest viability, defined as the likelihood of persistence over the long term, is described based on the concepts of representation, redundancy, and resiliency. We developed four plausible future scenarios, each differing in levels of natural resource management, to evaluate the status of forests into the foreseeable future. Two of the scenarios, which are based on no change in conservation actions (Scenario One; status quo) and a slight increase in conservation actions (Scenario Two) have the highest likelihood of occurring in the foreseeable future while the other two, which are based on a slight to moderate decrease in conservation actions (Scenario Three) and a moderate to large increase in conservation actions (Scenario Four) do not. Scenario One would continue to degrade and fragment native forests and result in reduced resiliency, redundancy, and representation. In Scenario Two, the slight improvements in conservation actions would result in a moderate increases in resiliency, redundancy, and representation.

Mariana Islands Forest

Introduction

The Mariana archipelago consists of 15 main islands and various small islets spanning a north-south distance of 890 kilometers (km) in the western Pacific Ocean between latitudes 21° and 13°N and longitudes 144° and 146°E. The vast majority of the archipelago's land area is concentrated in the larger, southern main islands, including Saipan, Tinian, Rota, and Guam.

We provide an overview of the forest ecoregion in the Mariana archipelago and describe the ecological factors that have influenced this biome over time and into the future. Forests occur on all islands in the archipelago, except for Farallon de Medinilla due to extensive bombing during ongoing military operations and continuing volcanic activity of Uracas. A thorough introduction of the geography, geology, climate, hydrology and descriptions of the islands in the Marianas archipelago are described in the chapter on Physical Geography of the Mariana Archipelago by Harrington in this work.

Description

Here we use the definition of a forest as a plant community characterized by vegetation with >25% cover in trees (a woody perennial that usually has a single trunk) (Gagne and Cuddihy, 1999). We defined and characterized Mariana forests using the landcover types for the Mariana archipelago described by Amidon et al. (2017). The 2017 study incorporated existing classification systems by the National Oceanic and Atmospheric Administration (NOAA) and U.S. Forest Service (Liu and Fisher, 2006a,b; NOAA, 2017) with additional imagery data to delineate a total of 23 vegetation types in six major landcover types (biomes). Ten vegetation types associated with the forest biome were then grouped into the four Marianas forest sub-types: native, secondary/mixed, monoculture, and *Leucaena leucocephala* or tangantangan, hereafter referred to as "*Leucaena*" described in the Current Condition section.

Geology

The six southern islands are geologically older than the nine northern islands, and due to complex plate uplifting, contain large areas of limestone substrate and areas volcanic in origin. The islands are characterized by plateaus ringed by a series of steep escarpments (Young, 1989). Limestone areas have shallow, highly weathered soils with an abundance of calcium (Donnegan et al., 2011). Guam, Rota, Aguiguan, Tinian, and Saipan exhibit well-developed, deep soils where the underlying volcanic parent materials have been exposed and weathered. The abundance of calcium in the limestone and coral sand on these landscapes creates soils that are inherently more fertile than volcanic soils (Donnegan et al., 2011).

All of the northern islands, from Anatahan to Uracas, are stratovolcanoes comprised mostly of hardened lava, tephra and volcanic ash, and are characterized by steeply sloping topography, both above and below the ocean's surface (Brainard et al., 2012). Periodic, explosive volcanic eruptions occur on the islands, with the most recent major eruptions occurring at Uracas in 1967, Pagan in 1981, and Anatahan in 2003 (Global Volcanism Program, 2013). While deep, soil developed on volcanic parent materials has low fertility, most of which resides in the topsoil.

Physical/life history components

Water availability and climate

Climate in the Mariana archipelago is classified as "tropical rainforest" (according to the Koeppen climate classification) with seasonal monsoons (Ohba, 1994). Moderate temperatures, ranging between 30 °C and 22.8 °C and constant trade winds create stable conditions. Precipitation averages 96 in (218 cm) per year, dependent in part on elevation, with a rainy season between July and October, and a drier season from November through June, with April characteristically being the driest month of the year (Ohba, 1994; Mueller-Dombois and Fosberg, 1998). During the dry season, brisk east and northeast trade winds dominate

the western Pacific Ocean (Eldredge, 1983), while slower east and southeast trade winds occur during summer months. An average of at least one tropical cyclone per year impacts the Mariana archipelago, typically during the summer months as they move from east to west.

Vegetation structure and composition

Forests in the Marianas are characterized by a closed canopy of broadleaf trees with an understory of younger trees, vines, epiphytic ferns, and orchids (Stone, 1970; Vogt and Williams, 2004). It is usually composed of tall trees (10+ meters (m)) that comprise the upper canopy, small to mid-size trees (3–10 m) as a mid-story, and shrubs and herbs that form the understory (Falanruw et al., 1989a,b). Undergrowth can be sparse in densely shaded areas but may contain ground herbs, shrubs, ferns, and small trees of varying heights in areas with more open canopy.

The Marianas are one of the highest risk areas in the world for typhoons (Marler, 2001). Many plant species evolved to avoid catastrophic damage from these storm events by having leaves which are easily removed during high wind. This is far less damaging than uprooting or the breaking of major branches. Most native woody perennial plants recover fairly rapidly following typhoon damage, provided that they remain well-rooted and the major scaffold system of the canopy remains intact (Marler, 2001).

Biodiversity/biotic components

The Marianas, situated in Micronesia, lies within the Polynesia-Micronesia bioregion recognized as a global biodiversity hotspot (Conservation International, 2019). A comprehensive study of the endemic plant species in Micronesia indicate that the region contains the highest percentage of plant endemism per kilometer out of globally recognized insular biodiversity hotspots (Costion and Lorence, 2012). The combination of old age and close proximity to continental land masses of some of the Micronesian islands has enabled them to accumulate a very high richness of distinct plant lineages compared to more remote archipelagos such as Hawaii. The Marianas possess a level of richness measured by endemic plants per square kilometer (5%; 54 endemics/1007 total species) somewhat below the average for the region (14%; 364/2628), but on par with other island groups recognized for their biodiversity (Hawaii at 4%, Fiji and Samoa at 5%, and Marquesas and Society Islands at 6%).

Forests in the Marianas provide habitat for several endemic vertebrate species including the Mariana fruit bat (*Pteropus mariannus mariannus*), Micronesian megapode (*Megapodius laperouse*), and the Mariana crow (*Corvus kubayari*). Many of these native vertebrate species are known to be important pollinators and/or dispersers of seeds for the native forest plant species. Without seed dispersing vertebrates, plants would deposit their seeds directly below themselves with little expectation of successful reproduction due to low light, competition with more established plants and high seed density.

Several endemic invertebrate species such as the fragile tree snail (*Samoa fragilis*), humped tree snail (*Partula gibba*) and Guam tree snail (*Partula radiolata*) occur in the cool, shaded forest habitat with high humidity and reduced air movement (USFWS, 2015a). These invertebrates feed primarily on dead or decaying plant material recycling nutrients near the bottom of the food chain (Cowie, 1992). This recycling creates chemical nutrients that are released back into the soil, air and water and become available for new growth.

Pre-Human Condition

Forest Sub-types

Marianas forests likely began as strand vegetation (small plants that hold the soil and are tolerant of wind, salty air, and waves) that dispersed from elsewhere to isolated shores via the sea, and inland plant species blown by air currents to the islands' slopes and mountains. These initial plant species evolved to create distinct species adapted for newly encountered niches including the limestone substrate. In addition, seed dispersers such as bats or migrating birds are likely responsible for carrying some species to the islands, and during the evolution of the plant fauna, new species were continually making their way to the island chain (Berger et al., 2005).

Before human settlement occurred on the Marianas, forests had probably reached their climax of primary succession. Forested areas were likely well distributed on the southern islands of Guam, Rota, Aguiguan, Tinian, Saipan, and Farallon de Medinilla, and likely covered the majority of the landmass (Reeves and Amidon, 2018). Conversely, the northern islands are much younger geologically, and many have large areas of barren lava or lack the kind of soils needed to support forests (Ohba, 1994). The species found in the pre-human forest in the southern islands included, but were not limited to: *Ficus*, *Elaeocarpus*, *Mammea*, *Guamia*, *Cynometra*, *Aglaia*, *Premna*, *Pisonia*, *Ochrosia*, *Neisosperma*, *Intsia*, *Melanolepis*, *Eugenia*, *Pandanus*, *Artocarpus*, *Hernandia*, and others (Engbring et al., 1986). In the native forest found on the northern islands, predominant plant genera included *Aglaia*, *Pandanus*, *Terminalia*, *Trema*, *Morinda*, and *Erythrina* (Liske-Clark, 2015). Several of the trees and shrubs within these groups, including *Artocarpus mariannensis*, *Pandanus tectorius*, and *Terminalia catappa* are endemic or indigenous and produce fruit that provide food for wildlife such as the Mariana fruit bat (Vogt and Williams, 2004).

Forest Viability of Pre-Human Conditions

The viability of Mariana forests depended on maintaining multiple and distributed occurrences (redundancy) of sufficient quality and size (resiliency) with species richness and genetic diversity (representation) to survive across the Mariana archipelago over time.

Native forests likely recovered quickly from storms and were widespread across many islands and appeared to be well-represented. The ecologically healthy, or viable, forests that existed throughout the Marianas prior to human contact likely maintained natural connections between system components. Native biota that was historically characteristic of Mariana forests filled environmental niches necessary to sustain the habitat. It can be assumed that in the less volcanically active southern islands, forests reached their carrying capacity and were spread across the islands with a high level of land coverage. Conversely, in the northern volcanic islands, the frequency and intensity of volcanic eruptions likely had catastrophic impacts to forest vegetation and replaced suitable soils with volcanic rocks which made it difficult for new forest plants to colonize. This delayed or prevented succession into native forest as seen on areas of all of the northern islands.

Reproductive strategies of forest species, such as fruit and seed dispersal by birds and fruit bats, encouraged representation on all islands that supported those dispersing species. In addition, the presence of fruit-eating animals such as birds and fruit bats benefited plant recruitment by increasing germination during gut passage and moving seeds away from conspecifics, thereby creating more resilient forest systems (Egerer et al., 2018). Overall, the high diversity of plant species and seed dispersers within native forests in the Marianas likely improved the ability of these forests as a whole to survive stochastic or even catastrophic events.

Table 1 summarizes the viability of Mariana forests in its pre-human condition based on what is known about these forests in their native state.

Current Condition

Forest Sub-types

Prior to the arrival of humans approximately four centuries ago, native forest was the dominant forest type in the Marianas. As a result of natural and anthropogenic disturbance, a proportion of native forest was converted to three additional forest sub-types: secondary, monoculture, and *Leucaena* forests. A summary of current Mariana forest sub-types, dominant canopy species, and distribution across the archipelago follows in **Table 2** (Fig. 1).

Current Forest Extent/Range

Native forest

In its current condition, native forest covers approximately 38,288 ac (15,495 ha) or 15% of the land area in the Marianas (Reeves and Amidon, 2018). In the southern islands, native forest is predominantly restricted to limestone substrate (25,347 ac (10,258 ha)) with the exception of native volcanic forest on Guam (8576 ac (3471 ha)). In the northern islands, native forest is represented only by volcanic forest (3542 ac (1433 ha)) and hibiscus thicket (590 ac (239 ha)). The impacts of nonnative species and human colonization have greatly influenced the quality and quantity of native forests throughout a majority of the archipelago. Only the islands of Guguan, Asuncion, Uracas, and Maug have been left relatively undisturbed, however relatively recent volcanic eruptions has limited the amount of native forest established on these islands.

Southern Islands

Approximately 90% (13,821 ha) of native forest can be found in the southern islands with the most area on Guam (8769 ha) and Rota (4068 ha), followed by Tinian (432 ha), Aguiguan (380 ha), and Saipan (173 ha). Native forest represents a significant portion of the islands of Rota (47%) and Aguiguan (55%), but less than 17% of Guam, less than 5% of Tinian and 2% of Saipan. The decline in the quantity of native forests on Guam, Tinian, and Saipan largely occurred from clearing for agriculture, residential, commercial and military development (Liske-Clark, 2015; USFWS, 2015a,b). Nevertheless, native forest still occurs along the edges and tops of cliff sides, in steep ravines, and other rugged karst terrain.

Although Rota and Aguiguan still contain large tracts of native forest, the high number of feral ungulates on both islands impedes recruitment of native plants by browsing on new growth and seedlings. The reduction in new growth and recruitment makes the native forests on these islands less able to recover from stochastic and catastrophic events (decreased resiliency and redundancy). The introduction of the brown tree snake had a profound effect on the forests of Guam by preying on and completely wiping out a majority of the forest birds on the island, which served as important pollinators and seed dispersers for the forests. Some native forest seeds need to pass through the gut of a bird to germinate, therefore islands with healthy bird populations (Rota, Tinian, and Saipan) have more intact forests than Guam (Rogers, 2011). A decline in fruit bat populations may have had an impact on the recruitment of forest trees with large seeds such as *Cycas micronesica*. Feral pigs and deer have also been found to act as seed dispersers, although feral ungulates have been found to selectively disperse native species (Gawel et al., 2018).

Table 1 Assessment of native forest resiliency, redundancy, and representation of forests in the Mariana Islands prior to human contact.

Forest type	Resiliency	Redundancy	Representation
Native forest	High	High	High

Table 2 Mariana archipelago forest subtypes with associated vegetation types, dominant species, and brief descriptions (Amidon et al., 2017; Reeves and Amidon, 2018).

Forest subtype	Vegetation Types	Dominant species (Common name)	Characteristics	Island															
				Agr	Agu	Ala	Ana	Asu	FDM	Gua	Gug	Mau	Pag	Rot	Sai	Sar	Tin	Ura	
Native	Native Limestone Forest	Canopy species include: <i>Elaeocarpus joga</i> (joga), <i>Pisonia grandis</i> (umumu or umomo), <i>Hernandia labyrinthica</i> (oschal), <i>Hernandia sonora</i> (nonak or nonag), <i>Ficus prolixa</i> (nunu), <i>Macaranga thompsonii</i> (pengua), and <i>Intsia bijuga</i> (ifit)	Forest on limestone substrate with a canopy dominated by native tree species. Includes forests of varying age classes. Dominant canopy species can vary by island and region of island.																
	Native Volcanic Forest	Canopy species include: <i>Pisonia grandis</i> (umumu or umomo), <i>Hernandia sonora</i> (nonak or nonag), <i>Barringtonia asiatica</i> (putting), <i>Pandanus tectorius</i> (kafu), and <i>Terminalia catappa</i> (talisai).	Forest on volcanic soil substrate with a canopy dominated by native tree species. Includes forests of varying age classes and is primarily found in the northern volcanic islands of the CNMI and volcanic soil regions of southern Guam.																
	Hibiscus Thicket	<i>Hibicus tiliaceus</i> (pago)	Found throughout the archipelago around wetlands, along streams, and in interior areas																
Secondary	Mixed Introduced Forest	Canopy species can include combinations of coconut, ironwood, tangantangan, <i>Spathodea campanulata</i> (African tulip tree), <i>Delonix regia</i> (flame tree), <i>Acacia confusa</i> (sosugi), <i>Albizia lebbbeck</i> (trongkon-kalaskas), <i>Pithecellobium dulce</i> (kamachile), and <i>Samanea saman</i> (trongkon-mames or monkeypod)	All forests dominated by non-native species. May include components of other forest subtypes. Mixed in composition, not dominated by a specific non-native species.																
	Vitex Forest	<i>Vitex parviflora</i>	Large stands occur in northern Guam																

(Continued)

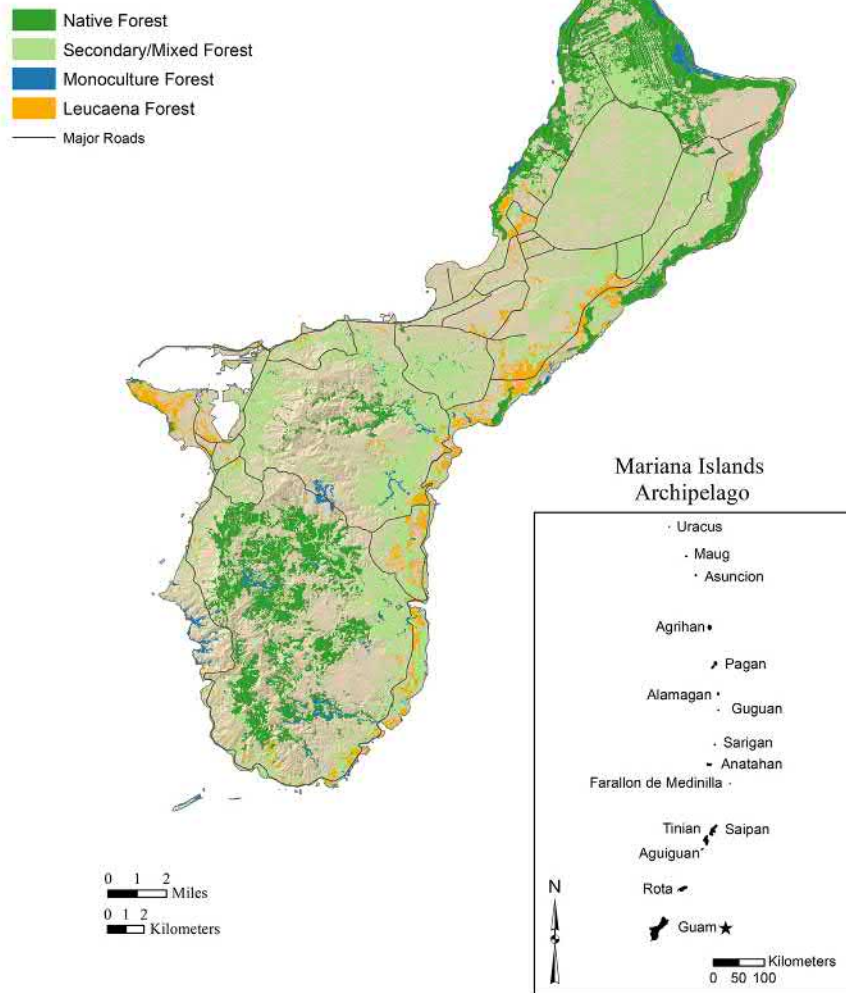
Table 2 Mariana archipelago forest subtypes with associated vegetation types, dominant species, and brief descriptions (Amidon et al., 2017; Reeves and Amidon, 2018).—cont'd

Forest subtype	Vegetation Types	Dominant species (Common name)	Characteristics	Island														
				Agr	Agu	Ala	Ana	Asu	FDM	Gua	Gug	Mau	Pag	Rot	Sai	Sar	Tin	Ura
Monoculture	Coconut Forest	<i>Cocos nucifera</i> (coconut)	Former coconut plantations. Found on limestone and volcanic substrates.															
	Casuarina Forest	<i>Casuarina equisetifolia</i> (ironwood)	Along shorelines and throughout the interior of an island. Found on volcanic and limestone substrates.															
	Bamboo Thicket	<i>Bambusa vulgaris</i> (bamboo)	Along streams and near wetlands, however, can also occur throughout the interior of an island.															
	Acacia Forest	<i>Acacia auriculiformis</i> and <i>Acacia mangium</i>	Found on volcanic substrates in the badlands on southern Guam.															
Leucaena	Leucaena Thicket	<i>Leucaena leucocephala</i> (tangantangan)	Associated with previously cleared areas and often forms monotypic stands. Found on limestone and volcanic substrates.															

Shading indicates occurrence of forest.

Island abbreviations: *Agr*, Agrihan; *Agu*, Aguiguan; *Ala*, Alamagan; *Ana*, Anatahan; *Asu*, Asuncion; *FDM*, Farallon de Medenilla; *Gua*, Guam; *Gug*, Guguan; *Mau*, Maug; *Pag*, Pagan; *Rot*, Rota; *Sai*, Saipan; *Tin*, Tinian; *Ura*, Uracas.

Guam, Mariana Islands



Rota, Mariana Islands

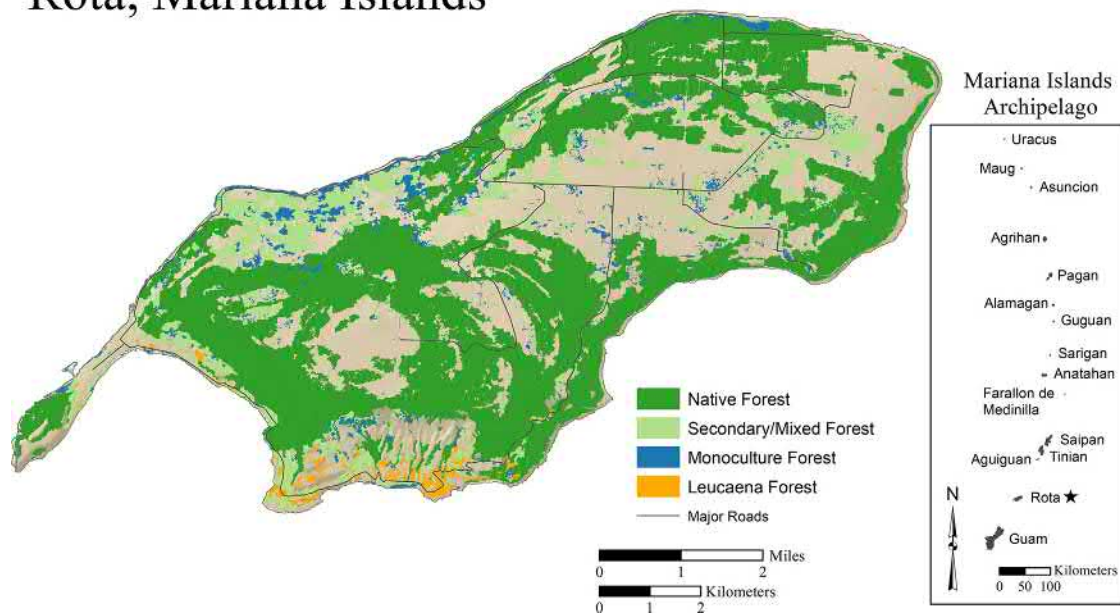


Fig. 1 (A–F) Current distribution of forests in the Mariana archipelago (Reeves and Amidon, 2018).

Tinian and Saipan, Mariana Islands

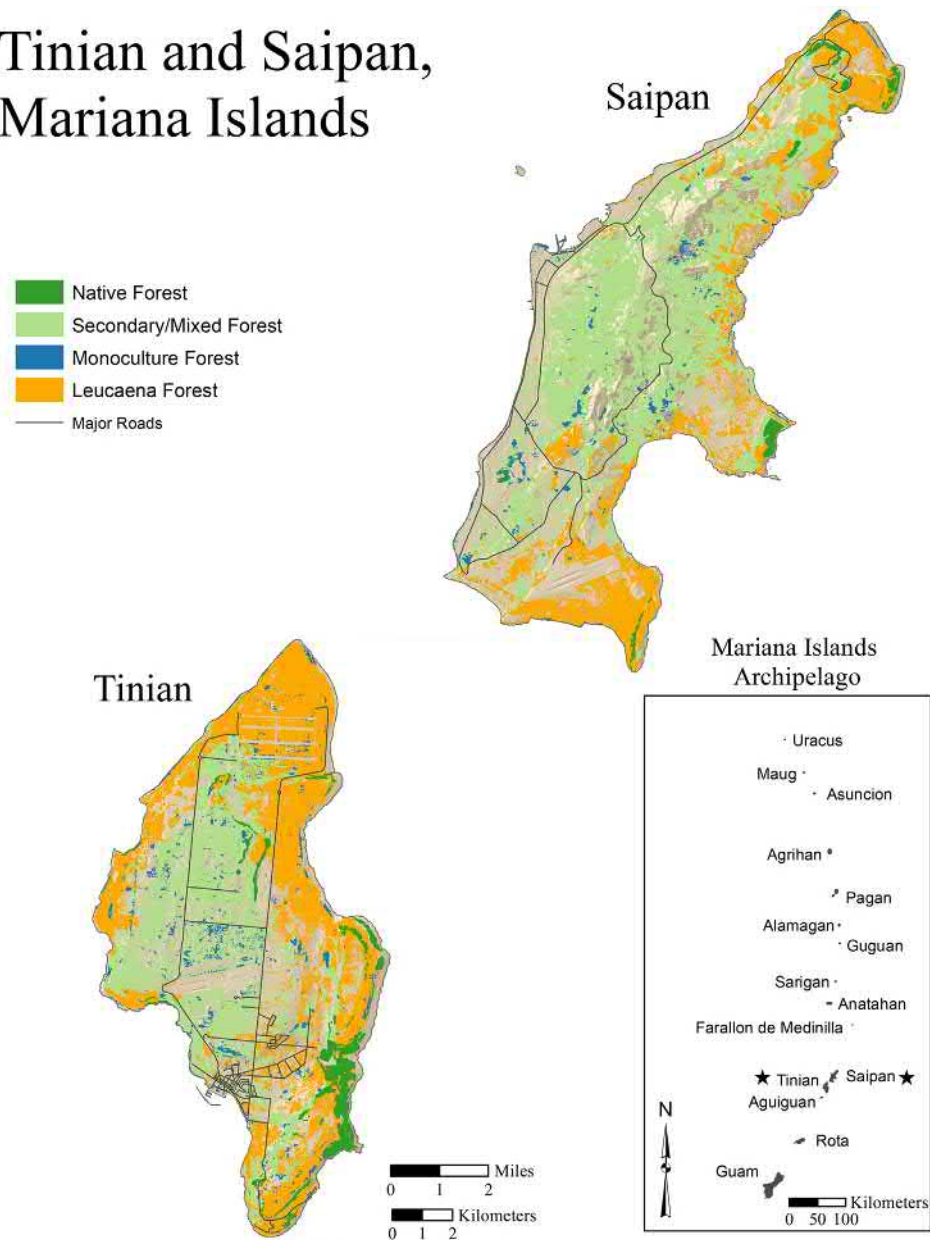


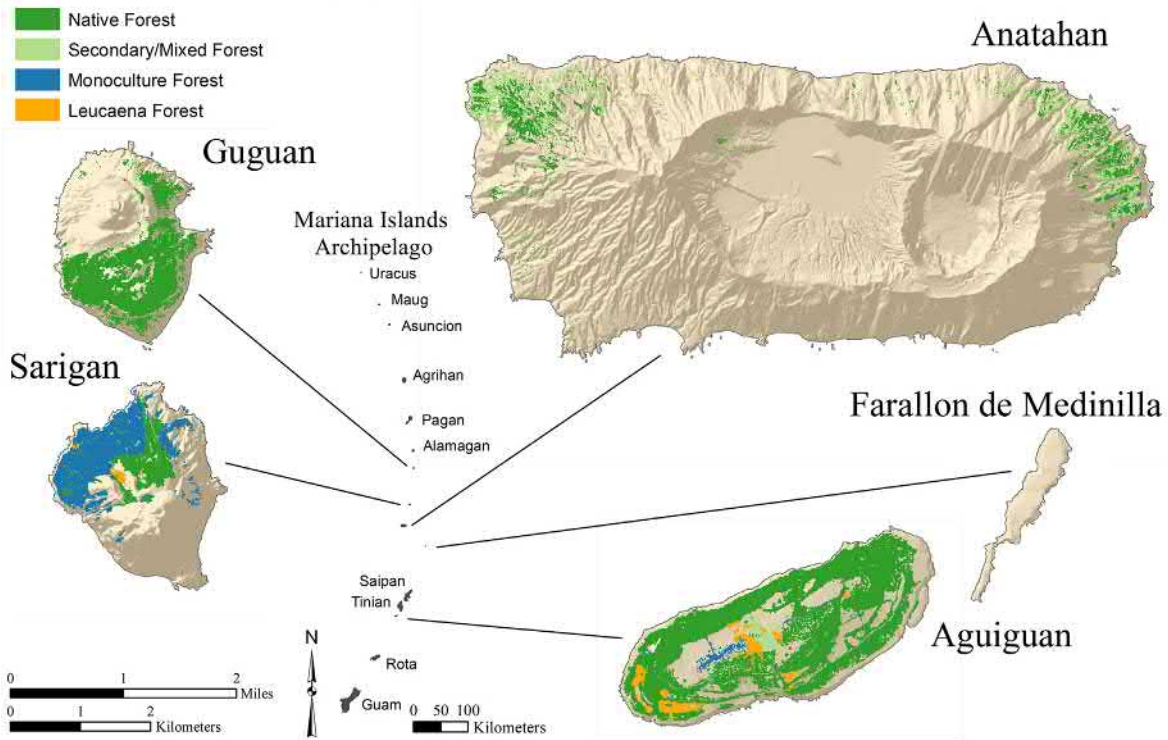
Fig. 1 (continued).

There are now several nonnative tree, shrub, and vine species that are found in native forests that colonize the forest edge and become established in disturbed areas. The colonization of these plants into the native forests has reduced the habitat quality and converted large swaths of the native forests in the islands most disturbed by humans further reducing resilience and redundancy of native forests (Figs. 2 and 3).

Northern Islands

Approximately 10% of native forest (1672 ha) in the Marianas can be found in the northern islands, comprised of 1433 ha of volcanic forest and 239 ha of hibiscus thicket. Native forest distribution, abundance, and quality varies among the northern islands largely based on the level of impacts from feral ungulates, copra production, and volcanic activity. Forests on islands such as Anatahan, Sarigan, Alamagan, Pagan, and Agrihan have been greatly affected by the introduction of ungulates. The recent volcanic eruptions on Anatahan and Pagan resulted in the loss of large tracts of native forest. Guguan, Asuncion and Maug did not have ungulates introduced and remain relatively unaffected by volcanism as well leaving their forests relatively intact.

Aguiguan, Farallon de Medinilla, Anatahan, Sarigan, and Guguan, Mariana Islands



Alamagan, Pagan, and Agrihan, Mariana Islands

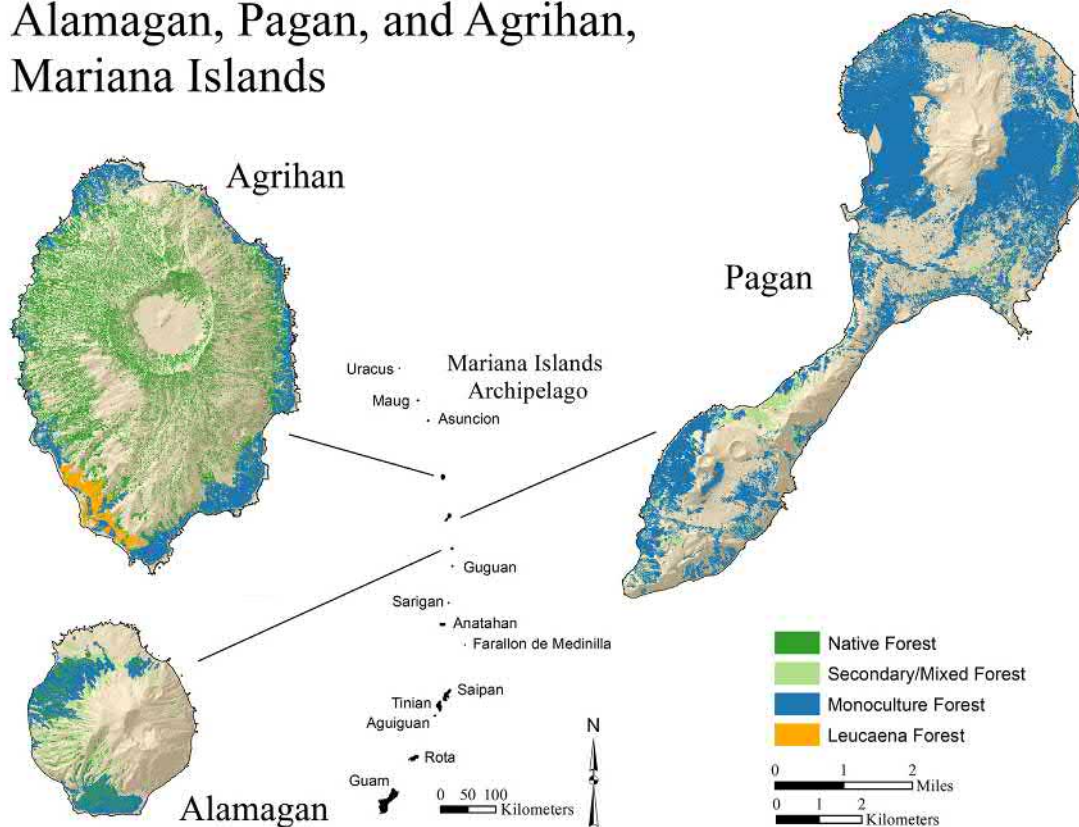


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Asuncion, Maug, and Uracus, Mariana Islands

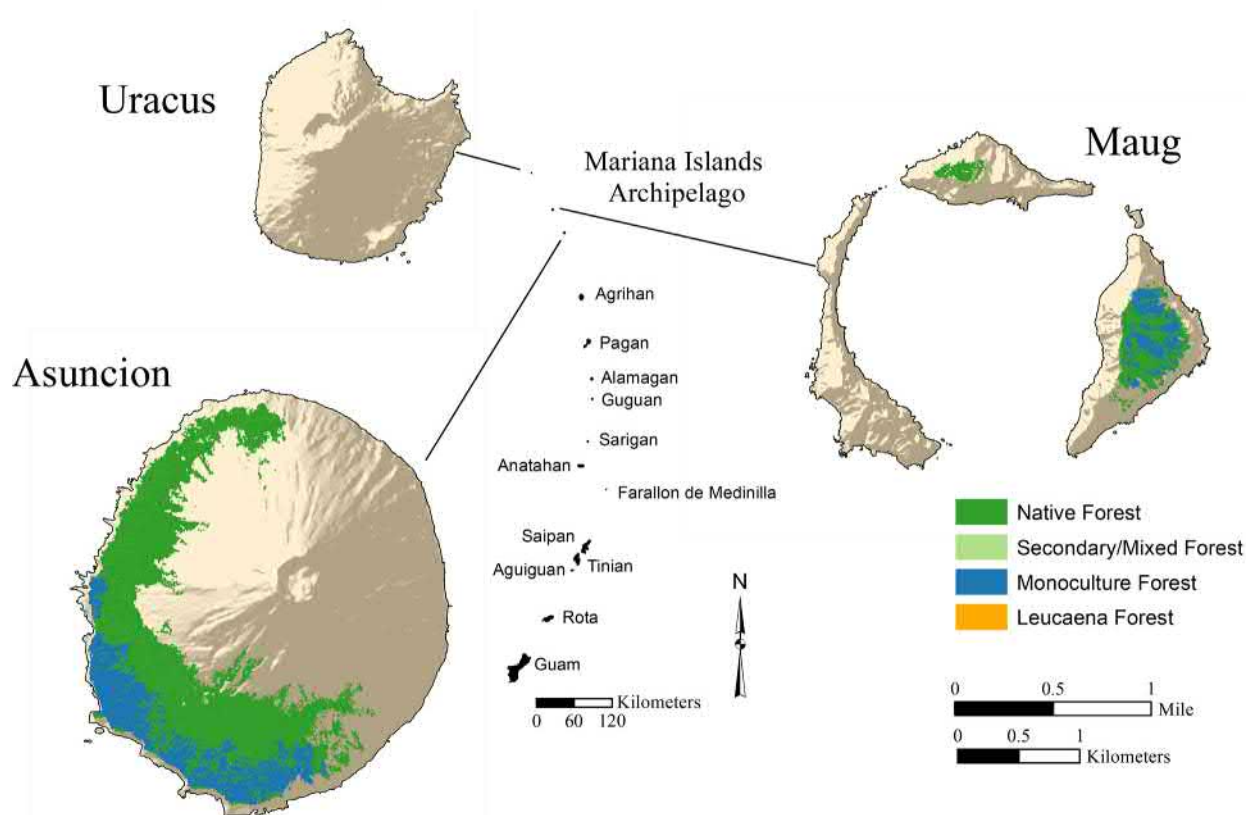


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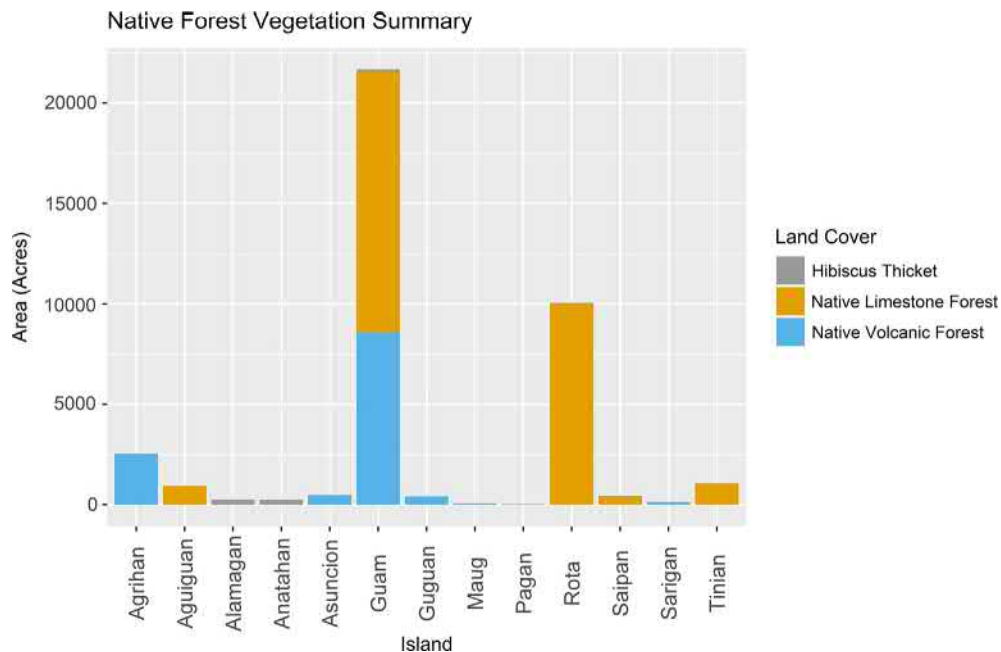


Fig. 2 Native forest vegetation summary with land cover types (Reeves and Amidon, 2018).



Fig. 3 Native forest on karst limestone terrain, Marpi, Saipan. Photo by Tyler Willsey.

Secondary forest

Secondary forest presently covers approximately 21,231 ha or 21% of the land area in the Marianas (Reeves and Amidon, 2018). Secondary forest is one of the most common forest types on the more developed southern islands such as Guam, Tinian, and Saipan due to a history of disturbance by humans. Aguiguan, Rota, and some of the northern islands (Anatahan, Alamagan, and Pagan), have smaller areas of secondary forest, while the islands that were not colonized by humans have little to none.

Secondary forest is composed of a mixture of native and nonnative species representing forests recovering from disturbance; native forests invaded by nonnative species or forests that are establishing in disturbed areas from a mix of seed sources (Liske-Clark, 2015). As such, secondary forests are generally dominated by nonnative species, but may include components of other forest types. Natural disturbances such as typhoons or drought can result in the loss of mature trees but the understory often remains intact, while man made disturbances such as land clearing and fire usually result in conversion to bare ground. During World War II, large portions of Guam, Tinian, and Saipan were destroyed during intense bombing or cleared for the development of military infrastructure. This resulted in major losses to native forest. Following disturbance, hardy and low-growing grasses and herbs colonized this bare ground. In time, shrubs, small trees, and seedlings of tall forest trees grow and soon overtop the grasses and herbs, forming a secondary forest. Major forest loss during World War II, and the introduction of nonnative plant species which outcompete natives led to the establishment of secondary forest currently found on large portions of Guam, Tinian, and Saipan.

Secondary forest tends to have a more open canopy, generally below 10 m in height, and a dense understory. Secondary forest is often composed trees such as *Albizia lebbbeck*, *Cynometra ramiflora*, *Ficus prolixa*, and a thick understory of native and introduced shrubs, vines, and grasses (Falanruw et al., 1989a,b) (Figs. 4 and 5).

Monoculture forest

Monoculture forest presently covers approximately 4688 ha or 5% of the land area in the Marianas (Reeves and Amidon, 2018). Monoculture forests are described as those planted by people for agricultural purposes or areas solely consisting of ironwood trees (*Casuarina equisetifolia*). Historically, large plantations of coconuts, for copra production (kernel of the coconut where oil is extracted), were planted and managed on several islands, including Anatahan, Sarigan, Alamagan, and Agrihan until the 1940s. It is likely that all areas of coconut monocultures were man-made, and not formed by coconuts being washed ashore in great numbers (Mueller-Dombois and Fosberg, 1998). In addition to coconut monoculture forests, mango (*Mangifera*), betel nut (*Areca catechu*), and citrus (*Citrus* sp.) monoculture forests are found on the islands where larger human populations exist such as Guam, Rota, Tinian, and Saipan. In these forests, the trees tend to all be the same height, as they were usually planted at the same time, and in rows. If the farm is actively being worked, the understory will typically be solely small herbaceous plants and grasses. The ground within coconut plantations is often filled with thick cordlike roots that prevent most other large woody plant species from growing (Mueller-Dombois and Fosberg, 1998).

In addition to agricultural monoculture forest, other monoculture forests in the Marianas exist because of allelopathic properties of certain species of trees such as ironwood (*Casuarina equisetifolia*). The long needle shaped leaves cover the forest floor, smothering

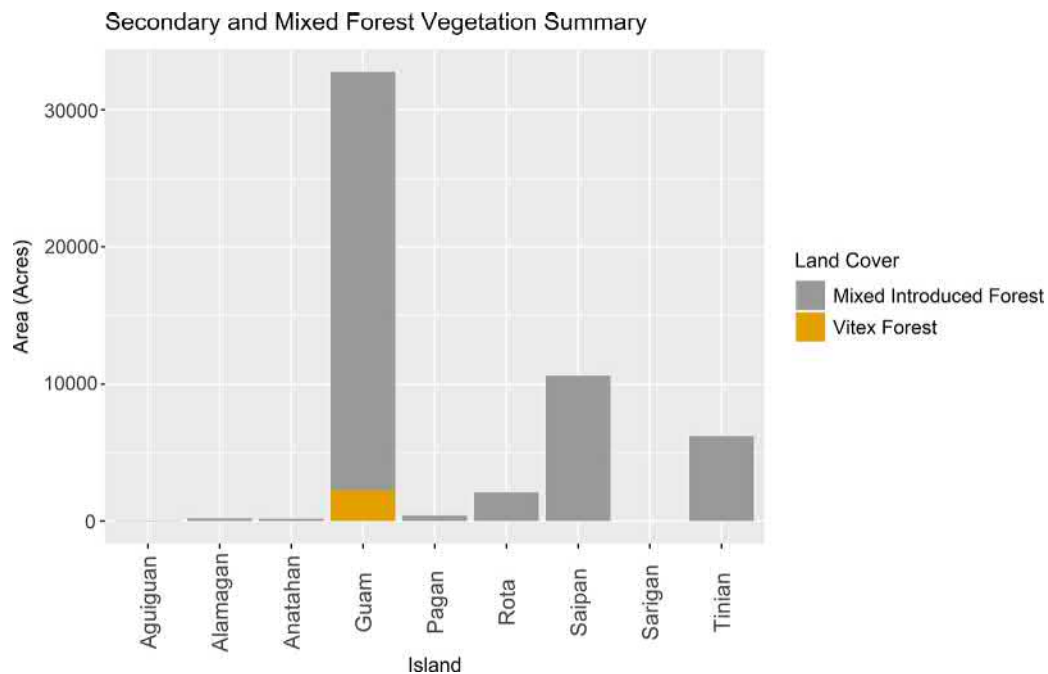


Fig. 4 Secondary forest vegetation summary with land cover types (Reeves and Amidon, 2018).



Fig. 5 Secondary forest in Navy Hill, Saipan. Photo credit: Tyler Willsey.

other plants, and have been found to have allelopathic tendencies to prevent other species' seeds from germinating (Wheeler et al., 2011). An ironwood forest typically has a single tree species and very limited understory. Currently, large expanses of iron wood monoculture forest occur on the islands of Guam, Tinian, and Pagan (Figs. 6 and 7).

Leucaena forest

Leucaena or tangantangan (*Leucaena leucocephala*) forest presently covers approximately 7768 ha or 8% of the land area in the Marianas (Reeves and Amidon, 2018). The southern islands of Guam, Tinian, and Saipan have vast areas of *Leucaena* forest, while

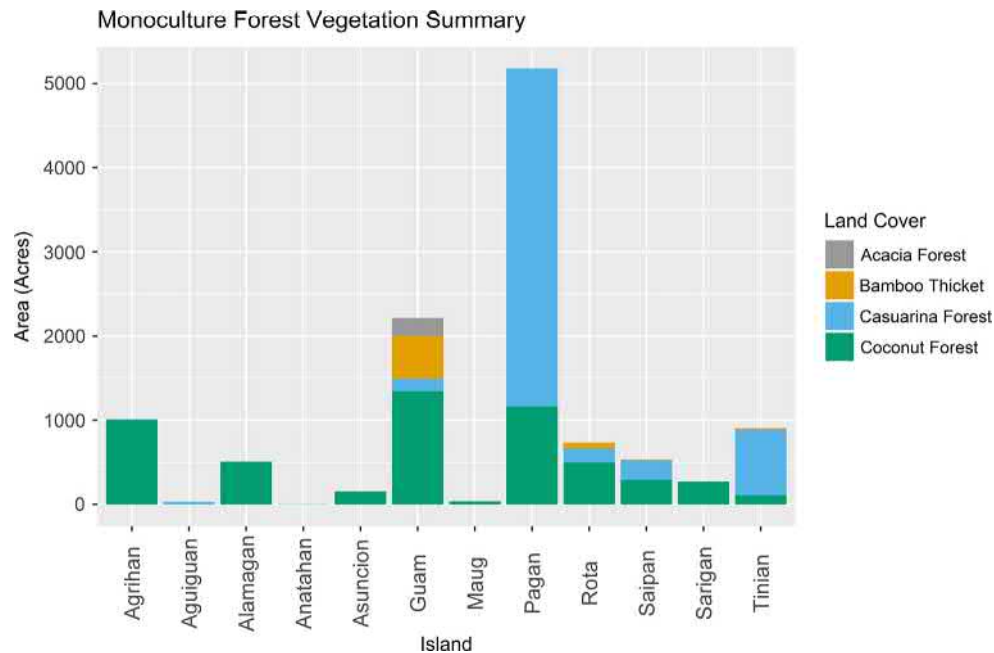


Fig. 6 Monoculture forest vegetation summary with land cover types (Reeves and Amidon, 2018).



Fig. 7 Betel nut (*Areca catechu*) monoculture forest on the island of Saipan. Photo credit Tyler Willsey.

Rota and Aguiguan only have a few stands (Vogt and Williams, 2004). *Leucaena* was not introduced to the northern islands so *Leucaena* forests do not exist north of Saipan. *Leucaena* was first observed on Tinian in 1946, although it is uncertain exactly when and how *Leucaena* was introduced to the Marianas and Tinian or whether it was intentional or inadvertent (Fosberg, 1980, unpublished report, as quoted in Hawaiian Agronomics 1985). It is possible that the U.S. military broadcast seeds of *Leucaena* and other plants from planes in an attempt to reduce erosion (Guam Division of Aquatic and Wildlife Resources (DAWR), 2006, Marler and Moore, 2011). Because of its rapid growth, and possibly allelochemical attributes (the ability to inhibit surrounding, competing plant growth) once established, it quickly forms dense thickets that crowd out native vegetation (Little and Skolmen, 1989). Consequently, *Leucaena* is considered highly invasive in many parts of the world including in the tropical Pacific

and the Hawaiian Islands. On some islands, *Leucaena* has formed large areas of dense forest which, due to its small leaves which allow bright sunlight to reach the forest floor, produces a xeric (containing little moisture) understory (Hopper and Smith, 1992) (Figs. 8 and 9).

Stressors

Historic Habitat Loss and Destruction

Since the arrival of humans in the Mariana archipelago, there has been ongoing degradation and impacts to native forests from hundreds of nonnative plants and animals, resulting in various rates of conversion to secondary, monoculture, and *Leucaena* forests in many areas. Archeological excavations indicate aboriginal human populations, including the Chamorro peoples, arrived in Micronesia 2000–4000 years ago and initiated major alterations to the native forests through a variety of activities such as the clearing of lands for agriculture. The human population during this initial period was relatively high compared to the islands' populations today and may have reached 20,000 on Tinian alone (Farrell, 1992). Studies of the pollen record strongly suggest human activities had transformed native forest into savanna over broad areas of the interior upland areas of Guam as early as 2000 years ago (Athens and Ward, 2004).

The arrival of Europeans in the 16th century also caused widespread damage to the forests. Reports from the 1700s indicate that Tinian's original forests were largely destroyed during early efforts to develop cattle ranching (Fosberg, 1960; Barratt, 1988). Later, during the 18th century, Spanish governors depopulated residents from the island to maintain it as a large pasture for cattle used to supply meat to the Guam garrison (Farrell, 1992).

During the German occupation of the Marianas from 1899 to 1917, native forest on several islands was converted to copra (*Cocos nucifera*) production. Several of the northern islands including Anatahan, Sarigan, Alamagan, Pagan, and Agrihan were likely dominated by native forests, but much of the lower coastal slopes were converted to copra plantations during this time (Spoehr, 1957). Extensive copra plantations likely existed in the southern islands as well but those areas were cleared by war time activities or development so little evidence of the plantations remain. Between the years of 1917 and 1944, large swaths of land were converted to sugarcane (*Saccharum* spp.) on the southern islands of Rota, Aguiguan, Tinian and Saipan during the Japanese colonization of those islands (Spoehr, 1957).

Changes in forest distribution and composition continued during the considerable destruction that occurred during World War II. During this time, Guam, Rota, Tinian, and Saipan were heavily bombed prior to the landing of Allied forces in 1944. Following the initial bombings and weeks-long battles in the Marianas, the U.S. military quickly began to develop the islands to maximize their strategic potential. Extensive military infrastructure was constructed on Guam, Tinian, and Saipan. Although the full extent of habitat loss during WWII is difficult to determine, photos from the time period show extensive alteration to the landscape and native forests in general. For example, based upon some reports, between only 3% and 5% of Tinian's forest was estimated to remain on the island following the conclusion of wartime activities (Engbring et al., 1986).

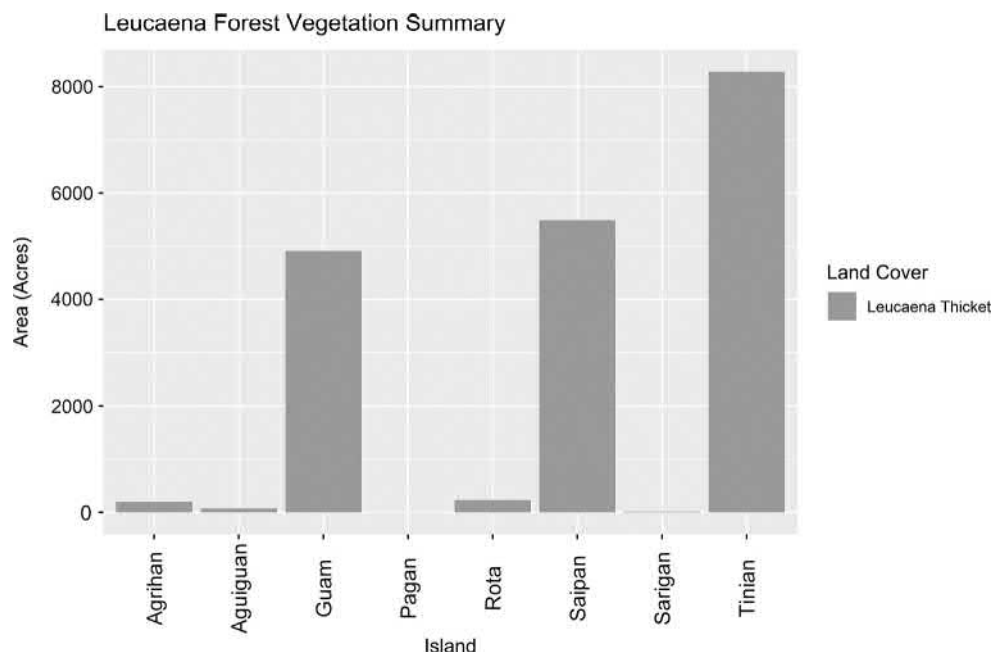


Fig. 8 *Leucaena* Forest Vegetation Summary with vegetation types (Reeves and Amidon, 2018).



Fig. 9 *Leucaena* forest on the island of Saipan, CNMI. Photo credit: Tyler Willsey.

Invasive Species

Invasive species have had tremendous impacts upon the habitats in the Marianas. [Table 3](#) lists the key invasive species known to be established in the Marianas that impact forests.

Forest degradation by invasive animals

Following the end of WWII, the widespread introductions of nonnative plants and animals accelerated with the advent of new and additional human activity and commerce. The brown tree snake (*Boiga irregularis*) (BTS) ([Savidge, 1987](#)) was inadvertently introduced to Guam following WWII and has caused the extirpation or extinction of forest birds on Guam ([Savidge, 1987](#)). The loss of the birds has caused significant effects within the forest, most notably the loss of a major seed dispersers ([Egerer et al., 2018](#)). Seeds from native trees that depend upon the birds for dispersal are no longer being moved. Therefore, seeds fall directly from the parent tree and sprout beneath, but the high density of seedlings causes almost complete mortality ([Rogers et al., 2017](#); [Egerer et al., 2018](#)).

Native forests have also been severely degraded by the introduction of ungulates including cattle, deer, goats, and pigs on the islands of Guam, Rota, Aguiguan, Tinian, Saipan and several of the northern islands ([Liske-Clark, 2015](#)). On all of these islands, populations of feral ungulates browse the forest understory impeding recruitment and leading to increased erosion ([Kessler, 2011](#)). Aerial photos from before and after the introduction of pigs and goats on Sarigan and Anatahan illustrate the tremendous impacts of the browsing to forests ([Kessler, 2011](#)). Pigs were already established on Anatahan during the late 1890s ([Fritz, 1902](#)) and goats are thought to have been introduced in about 1960 ([Reichel, 1988](#)). From 1890 until 2002, approximately 2153 ha of forest was converted to swordgrass or bare ground by browsing ungulates on the island of Anatahan ([CNMI, DFW, 2000](#)). On Guam, invasive pigs and deer are known to have species-specific negative effects on seedling dispersal and recruitment. On Rota, deer in particular, are responsible for high seedling mortality rates thereby playing a major role in forest species structure and composition ([Gawel et al., 2018](#)).

Forest degradation by invasive insects

Coconut Rhinoceros Beetles (CRB) primarily impact coconut palms by boring into the crowns or tops of the tree damaging growing tissue and feeding on tree sap, potentially destroying the trees ([CNAS, 2016](#)). The CRB also feeds on a variety of other plant species including other palms, banana, pineapple, and sugarcane. Coconut trees have been heavily decimated on Guam where the CRB was first detected in 2005 and has since been found in Rota ([CNAS, 2016](#)). The loss of coconut palms may have direct negative consequences such as overall loss of forest cover.

The nonnative cycad aulacaspis scale (*Aulacaspis yasumatsui*) quickly causes mortality of all life stages of *Cycas micronesica* or fadang, an endemic species that was once dominant in the native limestone forests on Guam ([USFWS, 2015a](#)). It was introduced to Guam in 2003, possibly via importation of the landscape cycad, *Cycas revoluta* ([Marler and Lawrence, 2012](#)). In 2002, prior to the scale infestation, *C. micronesica* was the most abundant tree species on Guam ([Donnegan et al., 2002](#)). By 2005, the cycad aulacaspis

Table 3 Invasive species of concern in Mariana Islands forests.

Common name	Scientific name	Primary species affected	Impacts to forest	Island impacted
Coconut rhinoceros beetle (CRB)	<i>Oryctes thinoerosrhin overos</i>	Coconut palms	Loss of forest and brush cover and edible flowers (i.e., fruit bat)	Guam
Cycad aulacaspis scale	<i>Aulacaspis yasumatsui</i>	Cycads	Loss of dominant native forest component	Rota
Vines (Ivy Gourd, Bitter Melon, Mile-a-Minute, Mikania, Woodrose, Chain of Love)	<i>Coccinia grandis</i> , <i>Momordica charantia</i> , <i>Mikania scandens</i> , <i>Mikania micrantha</i> , <i>Merremia tuberosa</i> , <i>Antigonon leptopus</i>	Native vegetation	Highly degraded forest by outcompeting other plants for resources such as water and sunlight. If left unchecked vines can smother full grown trees and prevent recruitment	Guam
Feral ungulates (goats and pigs, deer)	(<i>Capra hircus</i> , <i>Sus scrofa</i> , <i>Rusa marianna</i>)	All forest types	Dig up soils, facilitating erosion, compete with native species for resources, consume or otherwise destroy natural resources, spread pest species through moving seeds, soil compaction	Rota
Rodents (black rats)	<i>Rattus rattus</i>	Native vegetation, prey on native and non-native fauna, including birds	Prevents recruitment, damage to crops, compete with forest birds for seeds/fruit	Guam
Brown tree snake	<i>Boiga irregularis</i>	Prey on birds, reptiles	Without birds, the vegetation has reduced dispersal ability and germination success	Guam
Other non-native plants Lantana, Fountain grass, tangantangan, Bidens, Koster's curse, and Wedelia	<i>Lantana camara</i> , <i>Cenchrus setaceus</i> , <i>Leucaena leucocephala</i> , <i>Bidens alba</i> , <i>Clidemia hirta</i> , <i>Sphagneticola trilobata</i>	Native vegetation	Competition with native vegetation for space, light, water, and other resources	Guam

scale had spread throughout the forests of Guam causing more than 90% mortality in once healthy populations in certain areas (Marler and Lawrence, 2012). To date, release of biocontrols to abate the scale infestation have been unsuccessful (USFWS, 2015a). In addition, three other insects a nonnative butterfly (*Chilades pandava*), a nonnative leaf miner (*Erechthias* sp.), and a native stem borer (*Dihammus marianarum*), opportunistically feed on *C. micronesica* weakened by the cycad aulacaspis scale, compounding its negative impacts (Marler, 2013). The significant ongoing loss of this once dominant component could result in a negative cascading effect for native limestone forests (Marler and Lawrence, 2012).

Forest alteration by invasive plants

The negative impacts of nonnative plants on forests are seen throughout a majority of the Marianas. The impacts include the alteration of the wildfire regime and the creation of large swaths of monotypic stands of nonnative species that outcompete and crowd out native forest plant species. Historically and presently, the most likely source of introduction of nonnative plant species is inadvertent or intentional transport of soil, seeds, or plants intended for ornamental or farm use, often without knowledge of their deleterious effects (Space and Falanruw, 1999).

Over 100 plant taxa have been introduced to the Marianas, and at least one-third of these have become pests (i.e., injurious plants) (Stone, 1970; Mueller-Dombois and Fosberg, 1998). Of these approximately 30 nonnative pest plant species, at least nine species are known to be habitat-altering, including trees such as lantana (*Lantana camara*), grasses such as fountain grass (*Cenchrus* (= *Pennisetum*) *setaceus*), and tangantangan (*Leucaena leucocephala*) (Space et al., 2000).

The greatest risk posed by nonnative plant species in the Marianas is aggressive displacement of native species. One of the most invasive plants in the Marianas is lantana, a branched shrub up to 10 ft. (3 m) tall, first brought to the Marianas as an ornamental plant and first reported as naturalized on Tinian in 1930 (Space and Falanruw, 1999). Lantana is aggressive, thorny, and forms thickets, crowding out and preventing the establishment of native plants (Davis et al., 1992; Wagner et al., 1999). Recognized as a serious pest species in Micronesia by the 1940s (Denton et al., 1991), lantana was reported as abundant and widespread on the islands of Tinian and Aguiuan in the 1990s (Denton et al., 1991; Space and Falanruw, 1999). Ungulates can exacerbate the spread of lantana and other nonnative plants as has occurred on the island of Aguiuan, where goats facilitate lantana's spread by eating nearly everything else with the exception of lantana (Thaman, 1974; Denton et al., 1991).

Another nonnative plant species of concern is tangantangan, widely considered invasive in many parts of the world. Native to the neotropics, tangantangan is a nitrogen-fixing shrub and an aggressive competitor that often forms the dominant element of the vegetation (Geesink et al., 1999). It alters the chemistry of soils to its own benefit and this competitive advantage has allowed it to now cover approximately 29% of Tinian (Marler et al., 2016).

Additional invasive plant species are located on Rota, Tinian, Saipan, and Guam including ivy or scarlet gourd (*Coccinia grandis*), molasses grass (*Melinis minutiflora*), and fountain grass (*Pennisetum setaceum*) (Space et al., 2000), all of which often cause harm to forests where they are introduced through military or civilian activities. In 2004, more than one third of all trees in Saipan, Tinian, and Rota were affected by invasive vines which can grow into dense patches that smother and kill host trees by blocking out sunlight (Liske-Clark, 2015). Invasive vines also reduce light availability under the canopy, impacting understory plant species composition and the rate of forest regeneration. Furthermore, many nonnative species including lantana, molasses grass, and fountain grass alter fire ecology (Space and Falanruw, 1999) with detrimental effects on forests.

Forest Loss From Volcanic Activity

As noted previously, volcanism has historically caused periodic destruction of forests of the northern islands. For example, Anatahan's eruption in 2003 and Pagan's eruption in 1981 caused major alterations to the island's forests (Kessler, 2011). In particular, the large amount of ash and cinder produced by these events completely wiped out large sections of forest which are just now recovering by colonization from early successional species. At the north end of the archipelago, the island of Uracas still lacks native forest (or forest of any kind) due to being one of the most active volcanoes of the western Pacific. Additionally, the islands of Asuncion, Agrigan, and Guguan have all experienced eruptions since 1900 resulting in significant forest loss (Tanakadate, 1940).

Development

Development is a major factor impacting forests throughout the Mariana Islands. Since humans first arrived in the islands, forests and other land cover types have been cleared and modified for human activities. The U.S. military claimed nearly one-third of the lands on Guam after World War II and have modified large areas of former forest. Forest destruction continues with the military build-up, as roughly 862 ha of native and secondary forest are being converted into a Cantonment and a Live Fire Training Range (USFWS, 2017). As part of the rebalancing of military forces to the Asia Pacific region, the northern portion of Pagan Island and the northern two-thirds of Tinian Island are being considered for live fire ranges and training as part of the Commonwealth Joint Military Training (CJMT). The area leased by the military for CJMT is 6195 ha and contains roughly 4593 ha of forests (U.S. Navy 2017). Based on preliminary planning documents, the military does not intend to develop or clear the entirety of the area and large tracts of land will be preserved or even enhanced for wildlife usage. The CJMT build-up is still in its planning stage and areas of proposed development or clearing will likely change making it difficult to determine the amount of forests that will be impacted.

Commercial and residential development continues to have a significant impact on all land cover types in the southern inhabited islands. The direct clearing of land for both large and small scale projects often results in the permanent loss of forests. Guam is the most populated and developed of the islands. The increase in population from the military build-up will likely result in a corresponding increase in commercial and residential development which may impact forests. In the CNMI, there have been several periods of rapid development coinciding with increased tourism. Several large-scale resorts are proposed on both islands in areas that are primarily forested. On Rota, small scale development for homes or agriculture is common. The islands north of Saipan are either uninhabited or contain very small populations, however infrastructure in the northern islands has begun to allow for people to reside on Alamagan, Pagan, and Agrihan.

Typhoons

Typhoons and super typhoons have had major impacts on forests in the Marianas. Intense winds can defoliate trees, break primary branches, and uproot or topple trees. Forests can take several years to recover and during this time the habitat is susceptible to encroachment from invasive trees, shrubs, and vines (Marler, 2001). "Dry" typhoons have very little rainfall, causing salt water to be carried by the wind and deposited far inland. This causes the leaves on most dicot trees to wither and fall within 2 days of a storm and can cause mortality (Kerr, 2000). While some coastal land cover types are adapted to salt spray, native, secondary, monoculture, and *Leucaena* forests in the Marianas are heavily impacted. The salt spray kills large amounts of vegetation, which may not regenerate until rains have washed away the salt (Kerr, 2000). Most forest types typically recover and are refoliated within 1 year (Kerr, 2000), but the temporary change in canopy cover can allow for the encroachment of invasive plants.

Fire

Wildfire is very rare in the Marianas as most fires are typically caused by humans either intentionally for the clearing of land or unintentionally from improper disposal of lit cigarettes. In addition, some hunters on the southern inhabited islands start grassland fires to attract deer since deer forage on the new grass shoots following a fire, the exposure making them easier to hunt. The lack of rainfall during the dry season desiccates grasses, trees, and leaf litter providing additional fuel for fires. These fires, which are often set in the dry season, can spread and cause significant damage to adjacent forests converting these forests to bare ground and facilitating the colonization of invasive plants.

Climate Change

Climate change related stressors (i.e., increased precipitation, sea level rise, increased typhoon intensity and frequency) cause ongoing impacts to this and other land cover types. However, the magnitude of the impacts are not discrete events but occur continuously on a longer time scale. Therefore, we do not see climate change related stressors as the primary threat to the forests at this time.

Conservation Efforts

Impacts from stressors are addressed through various management approaches such as active (on-the-ground) management (i.e., predator and invasive species control, fencing, reintroduction, etc.), land protections, laws and regulations, and education and outreach. These approaches are implemented by numerous government agencies (federal, territorial, and commonwealth), private organizations, and non-governmental organizations (NGOs).

Federal

Endangered species act

The Endangered Species Act of 1973 (ESA) aims to provide a framework to conserve and protect endangered and threatened species and their habitats. As habitat loss is the primary threat to most imperiled species, the ESA allowed the U.S. Fish and Wildlife Service (USFWS) and National Marine Fisheries Service (NMFS) to designate specific areas as critical habitat zones. In 1978, Congress amended the law to make critical habitat designation a mandatory requirement for all threatened and endangered species.

Approximately 3355 ha has been designated as critical habitat on Guam and Rota for four species (Mariana crow, Mariana fruit bat, Guam Micronesian Kingfisher, and the Rota bridled white-eye) under the ESA. On Guam, 152 ha of critical habitat was designated for the Mariana crow, Micronesian kingfisher, and Mariana fruit bat and is comprised of 97 ha of native forest and 30 ha of monoculture forest. On Rota, approximately 3059 ha of native forest, 83 ha of secondary forest, 51 ha of monoculture forest, and 35 ha of *Leucaena* forest was designated for the Mariana crow and Rota bridled white-eye.

Sikes act and the integrated natural resources management plan

The Sikes Act (16 U.S.C. 670) was originally passed in 1960 to direct the United States Department of Defense (DoD) to carry out conservation and natural resource rehabilitation projects on military installations in coordination with local and federal fish and wildlife agencies. Installations are required to create an Integrated Natural Resources Management Plan (INRMP) which describes future and ongoing conservation projects on military lands. In the Mariana Islands, the DoD manages large tracts of lands on Guam, Tinian, and Farallon de Medinilla (FDM). Many of the projects proposed in the INRMP are required or recommended by other laws and regulations, including the Endangered Species Act and Clean Water Act. The U.S. military owns nearly 7689 ha of forests on Guam and roughly 4047 ha of forest on Tinian which are included in several conservation actions proposed in their INRMPs.

Table 4 below shows the forest types on DoD lands on Tinian and Guam.

Guam Micronesian kingfisher memorandum of agreement (MOA)

In 2015, the U.S. Fish and Wildlife Service (USFWS) entered into an agreement with the Department of the Navy (DON) on conservation efforts to protect habitat (which includes forest habitat) in northern Guam for the benefit of the Guam Micronesian kingfisher. For the kingfisher to be recovered in Guam, 4659 ha of habitat is needed, with 3309 ha of that on DoD lands. Through the Integrated Natural Resources Management Plan (INRMP) the DON plans to restore and manage 2118 ha to offset the loss of 540 ha of kingfisher habitat due to the planned military relocation from Okinawa to northern Guam (USFWS, 2015a,b). Projects include fencing in large areas of forest, removing ungulates, replanting native trees (including threatened and endangered species), and removing invasive plants.

Local Permitting

In Guam, Public Law 25–152 was put in place to control accelerated soil erosion and manage nonpoint source pollution. This regulation allows for the Guam Department of Agriculture (GDOA), Division of Aquatic and Wildlife Resources (DAWR) to review all development projects which will involve the clearing of forest (and other) habitat prior to the start of project activities to ensure there are no negative impacts to protected species or resources.

Table 4 Forest types on Department of Defense (DoD) lands on Guam and Tinian (Reeves and Amidon, 2018).

Forest subtype	Acres on Guam	Acres on Tinian
Native	11,735	183
Secondary	5203	4198
Monoculture	1208	5375
<i>Leucaena</i>	18,698	10,537

In the CNMI, the Northern Mariana Islands Administrative Code (NMIAC) Chapter 65-30, § 65-30-101 details the permit requirements for any land clearing activities. It states “No person shall commence or continue any earthmoving activity including grading, filling, or clearing of vegetation without a DEQ Earthmoving and Erosion Control Permit issued in accordance with the regulation.” In order for land clearing to commence, CNMI DFW, historic preservation, coastal resource management, and zoning must all approve the permit. It is the role of CNMI DFW to review all land clearing projects and determine whether locally or federally protected species or resources will be impacted. This mechanism was put in place to ensure no unauthorized clearing of forest (or other) land cover types occurs in the CNMI.

Protected Lands

There are several categories of protected lands in the Marianas including conservation areas, national parks, a national wildlife refuge, and the only mitigation bank in the Pacific islands. These lands were designated by federal or local governments for the conservation of natural resources and have protections regarding development, hunting, fishing, wildlife-oriented recreation, and other uses. Regulations vary among protected areas, as each area has a distinct history and purpose for protection (Liske-Clark, 2015).

There are conservation areas established on Guam, Rota, Tinian, and Saipan. These areas are set aside by the local government or the DoD to restrict the activities in an effort to minimize impacts to natural resources. In the CNMI, these lands are designated through the passage of a congressional bill and are under the ownership of the CNMI Department of Lands and Natural Resources. On Guam, lands are placed under the ownership of the Government of Guam or DoD.

Conservation lands comprise 22% of Rota, 4% of Tinian, and 9% of Saipan. Of the northern islands, the entire island of Sarigan is regulated by the Division of Fish and Wildlife and Guguan, Asuncion, Maug, and Uracas are designated wildlife conservation areas. No people are allowed on these islands without prior approval from the Director of the CNMI DFW, so human impact to forest lands is minimal. CNMI conservation lands total approximately 5560 ha, representing 12% of the total land area (Liske-Clark, 2015).

Approximately 10,182 ha of forest are classified as reserves or protected areas across the Mariana archipelago including 7263 ha of native forest, 2103 ha of secondary forest, 466 ha of monoculture forest, and 349 ha of *Leucaena* forest (Reeves and Amidon, 2018). Table 5 summarizes the protected areas in the Marianas (Figs. 10–13).

Invasive Species Management and Control

Biosecurity

A major biosecurity focus within the Mariana Islands is preventing the spread of BTS to the Northern Mariana Islands from Guam. In this effort, federal agencies support local capacity both in Guam and the CNMI. On Guam there are extensive efforts to keep BTS out of the transportation chain, effectively reducing the potential for BTS to be accidentally transported from the island (Brown Tree Snake Technical Working Group (BTSTWG), 2015). In the CNMI, efforts are undertaken to ensure that high risk cargo and craft arriving from Guam are inspected to reduce risks of BTS accidentally arriving and establishing. These efforts include inspection of all arriving cargo from Guam to the CNMI by BTS detection dogs as well as specialized trapping around all major ports of entry. Control and management activities in regards to the BTS are highly effective and since enacted, credible BTS encounters outside of Guam and its native range have been reduced and at present there are no known populations established outside of its native range and Guam (Brown Tree Snake Technical Working Group (BTSTWG), 2015). Nevertheless, biosecurity mechanisms rarely eliminate the risk and the situation with the BTS on Guam needs to be continually monitored, enforced and adjusted as needed to best ensure that BTS do not accidentally become established in the CNMI or elsewhere.

The University of Guam and the College of the Northern Mariana Islands provide research and extension services which in part support invasive species management. Activities include CRB monitoring and management and research programs (Brown Tree Snake Technical Working Group (BTSTWG), 2015). Similarly, both the CNMI and Guam governments have staff which support management of various established pest species and provide natural resource management, conservation and restoration efforts. The DoD on military lands also has active natural resource programs including BTS management, feral ungulate control, habitat restoration and fencing (Brown Tree Snake Technical Working Group (BTSTWG), 2015).

These efforts to reduce the presence or impact of invasive species offer the potential to protect both the quality and quantity of vegetation within any habitat, including forests, as well as species that depend on the vegetation.

Partnerships

Micronesia Challenge

In 2006 the Republic of Palau, the Federated States of Micronesia, the Republic of the Marshall Islands, the U.S. Territory of Guam, and the U.S. Commonwealth of the Northern Mariana Islands committed to conserve at least 30% of the near-shore marine resources and 20% of the terrestrial resources across Micronesia by 2020. This pledge has become known as the Micronesia Challenge. The Challenge aims to preserve these resources for the benefit of future generations, to sustain livelihoods, and to sustain each island's unique biodiversity (Micronesia Challenge, 2012).

Table 5 Conservation areas of the Marianas (Berger et al., 2005; Guam Division of Aquatic and Wildlife Resources (DAWR), 2006; SWCA Environmental Consultants, 2010a,b; U.S. Fish and Wildlife Service (USFWS), 2007; Cogan et al., 2013; Reeves and Amidon, 2018).

<i>Conservation area (forest subtypes)</i>	<i>Location</i>	<i>Purpose</i>	<i>Enabling law or agreement</i>
Sabana heights wildlife conservation area (N S M L)	Rota, Sabana plateau	Terrestrial, for wildlife conservation	Rota Local Law 9-1 and regulations promulgated under Public Law 2-51
I Chenchon Park Wildlife Conservation Area and Bird Sanctuary (N S M)	Rota, cliffs along eastern coast	Terrestrial, for wildlife conservation and especially for sea birds	Rota Local Law 9-1 and regulations promulgated under Public Law 2-51
Wedding Cake Mountain Wildlife Conservation Area (N S M L)	Rota, Taipingot Peninsula on southwest end of island	Terrestrial, for protection of all wildlife, plants, and soils	Rota Local Law 9-3 and regulations promulgated under Public Law 2-51
Saipan Upland Mitigation Bank (N S L)	Saipan, upland areas of Marpi region on north end of island, encompassing the Marpi Commonwealth Forest	Terrestrial, to provide “credits” for sale to developers as a mitigation measure for the take of Nightingale Reed Warblers; and for preservation of wildlife	CNMI Public Law 10-84; Saipan Upland Mitigation Bank Agreement between CNMI and USFWS; and regulations promulgated under Public Law 2-51
Bird Island Wildlife Preserve (N S L)	Saipan, lands on Saipan island to the west of Bird Island	Terrestrial, for preservation of wildlife	CNMI Public Law 10-84
Bird Island Sanctuary (N S L)	Saipan, lands and waters surrounding and including Bird Island (N L)	Terrestrial and marine, no-take zone for all natural resources; natural laboratory for educational purposes	CNMI Public Law 12-46
Kagman Wildlife Conservation Area (N S M L)	Saipan, lands on eastern side of Kagman Peninsula	Terrestrial, for preservation of wildlife	CNMI Public Law 10-84
American Memorial Park National Park (N S M L)	Saipan	To commemorate those who lost their lives on the Mariana Islands in military campaigns during World War II. Protects several historical and cultural sites and provides recreational areas for the public	P.L. 95-348 (1978)
CNMI Mitigation Area (N S M L)	Tinian, north of airport	Compensate for loss of Tinian monarch habitat as a result of airport expansion	Biological Opinion (1-2-98-F-06) for the Federal Aviation Administration
Asuncion Island (N M)	Asuncion Island	Terrestrial, to be maintained as an uninhabited place and used only for the preservation and protection of natural resources, including but not limited to bird, wildlife and plant species	CNMI Constitution, Article XIV, Section 2 and CNMI Public Law 14-49
Guguan Island (N)	Guguan Island	Terrestrial, to be maintained as an uninhabited place and used only for the preservation and protection of natural resources, including but not limited to bird, wildlife and plant species	CNMI Constitution, Article XIV, Section 2 and CNMI Public Law 14-49
Maug Island (N M)	Maug Island	Terrestrial, to be maintained as an uninhabited place and used only for the preservation and protection of natural resources, including but not limited to bird, wildlife and plant species	CNMI Constitution, Article XIV, Section 2 and CNMI Public Law 14-49
Uracas Island (None)	Uracas Island	Terrestrial, to be maintained as an uninhabited place and used only for the preservation and protection of natural resources, including but not limited to bird, wildlife and plant species	CNMI Constitution, Article XIV, Section 2 and CNMI Public Law 14-49
Anao Conservation Area (N M)	Northeastern Guam	Wildlife, species conservation, outdoor recreation	Guam PL 16-62
Bolanos Conservation Area (N M)	Southern Guam	Hunting, outdoor recreation, species conservation	Guam PL 16-62
Cotal Conservation Area (S M)	Southern Guam	Species conservation	Guam PL 16-62

Table 5 Conservation areas of the Marianas (Berger et al., 2005; Guam Division of Aquatic and Wildlife Resources (DAWR), 2006; SWCA Environmental Consultants, 2010a,b; U.S. Fish and Wildlife Service (USFWS), 2007; Cogan et al., 2013; Reeves and Amidon, 2018).—cont'd

<i>Conservation area (forest subtypes)</i>	<i>Location</i>	<i>Purpose</i>	<i>Enabling law or agreement</i>
Guam National Wildlife Refuge (Ritidian Unit) (N M)	Northern Guam	Conservation of threatened and endangered plants and wildlife and their ecosystems, migratory birds, wildlife-oriented recreation	Proposed Guam NWR and Finding of No Significant Impact (USFWS, 1993)
Guam National Wildlife Refuge Overlay—Air Force (N S M)	Northern and southern Guam	Conservation of threatened and endangered plants and wildlife and their ecosystems, wildlife-oriented recreation, Air Force mission responsibilities	Cooperative Agreement between USFWS and Navy (March 10, 1994)
Guam National Wildlife Refuge Overlay—Navy (N S M L)	Northern and southern Guam	Conservation of threatened and endangered plants and wildlife and their ecosystems, wildlife-oriented recreation, Navy mission responsibilities	Cooperative Agreement between USFWS and Navy (March 4, 1994)
Haputo Ecological Reserve Area (N M)	Northwestern Guam	Preserving examples of ecosystems and genetic diversity while providing opportunities for scientific research. Mitigation for construction of Kilo Wharf, Outer Apra Harbor; part of Guam NWR Overlay	Chapter 15, OPNAVINST 5090.1; Chapter 17 of the NAVFAC P-73 Real Estate Manual; 36 CFR 251.23; 40 FR 38; and HR 5602, The National Heritage Policy Act of 1979 (March 15, 1984)
Orote Ecological Reserve Area (N S L)	Southern coast of Orote Peninsula, western Guam	Same as Haputo Ecological Reserve Area	Same as Haputo Ecological Reserve Area
War in the Pacific National Park (N S L)	Guam, 7 units Asan Beach, Asan Inland, Agat, Piti, Mt Alifan, Mt. Tenjo/Mt. Chachao, Fonte Plateau	To commemorate the bravery and sacrifice of those participating in the campaigns of the Pacific theater of World War II and Conserve and interpret outstanding scenic and historic values and objects for the benefit of present and future generations	Public Law 95-348, 92 Stat. 492, 16 USC 460dd (1978)

Interactions of All the Above

The primary stressors to forests include habitat loss and destruction caused by development and the introduction of invasive plants and animals. These stressors are significant and ongoing, act in concert with other stressors, and are expected to continue or increase in magnitude and intensity into the future without effective management actions to control or eradicate them.

Current conservation efforts taken by Federal, State, private, and agency partnerships combined with laws and regulations limit some of the effects of the stressors on forests, but do not eliminate them. Without active management, forests will continue to be degraded and destroyed. Increased levels of restoration and conservation efforts such as invasive species management, restoration of lands to native dominated forests and a reduction in the level of development have the potential to limit the degradation or loss of forests or even reverse any ongoing degradation occurring for these forest subtypes.

In summary, all forest sub-types across the Marianas are moderately resilient, aside from *Leucaena* forests which are highly resilient. Their rapid growth, and possibly allelochemical attributes allows it to form dense thickets that crowd out other vegetation making it highly resilient (Little and Skolmen, 1989). Development and invasive species have negatively impacted the quantity and quality of native forests and to some degree secondary forests. Development has reduced the quantity of native forests primarily on the southern islands. However, all forest types remain distributed across several islands throughout the Marianas (moderate redundancy). The current stressors or conservation actions do not seem to have significantly reduced the species richness or genetic variation, therefore representation remains moderate (Table 6).

Future Scenarios

The condition of Mariana Islands Forests in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are as follows:

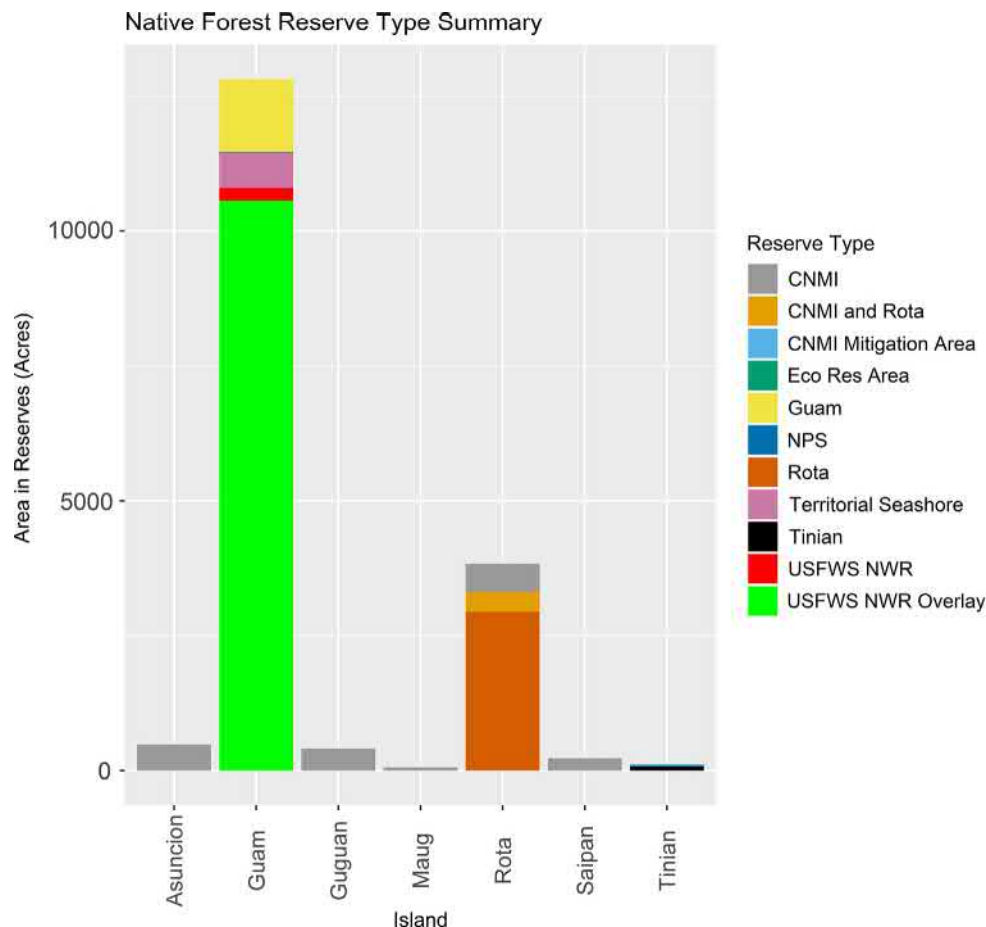


Fig. 10 Native forest reserve type summary (Reeves and Amidon, 2018).

1. *Conservation Values*: stakeholder involvement and public opinion determine the formulation, implementation, and funding of natural resource conservation within laws and development plans.
2. *Laws and Biosecurity*: national, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented (e.g., hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.).
3. *Development or Conservation Planning*: national, state, county, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

These conservation management parameters are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The year 2035 is the extent of the “foreseeable future,” and is based on the projected divergence of IPCC Representative Concentration Pathway (RCP) climate change scenarios (van Vuuren et al., 2011; Miller, 2018).

The four foreseeable future scenarios considered in this assessment are:

Future Scenario One, Status Quo—the most likely foreseeable future; no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues through the foreseeable future.

Future Scenario Two—a slight increase in natural resource conservation in the CMPs marginally improves conservation management.

Future Scenario Three—a slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management.

Future Scenario Four—a moderate to large increase in conservation actions in the CMPs substantially improves conservation management.

The future condition of Marianas Forests in Scenario One, the status quo, was characterized from an assessment of change over time in Forest land cover obtained from existing land cover maps (Reeves and Amidon, 2018). Based on these land cover maps, an annual rate of change for each forest subtype was estimated, and a projected change (in acres/ha) was calculated for the year 2035 (Amidon and Reeves, 2018). The resulting information on changes in land cover by 2035, as derived from existing land cover

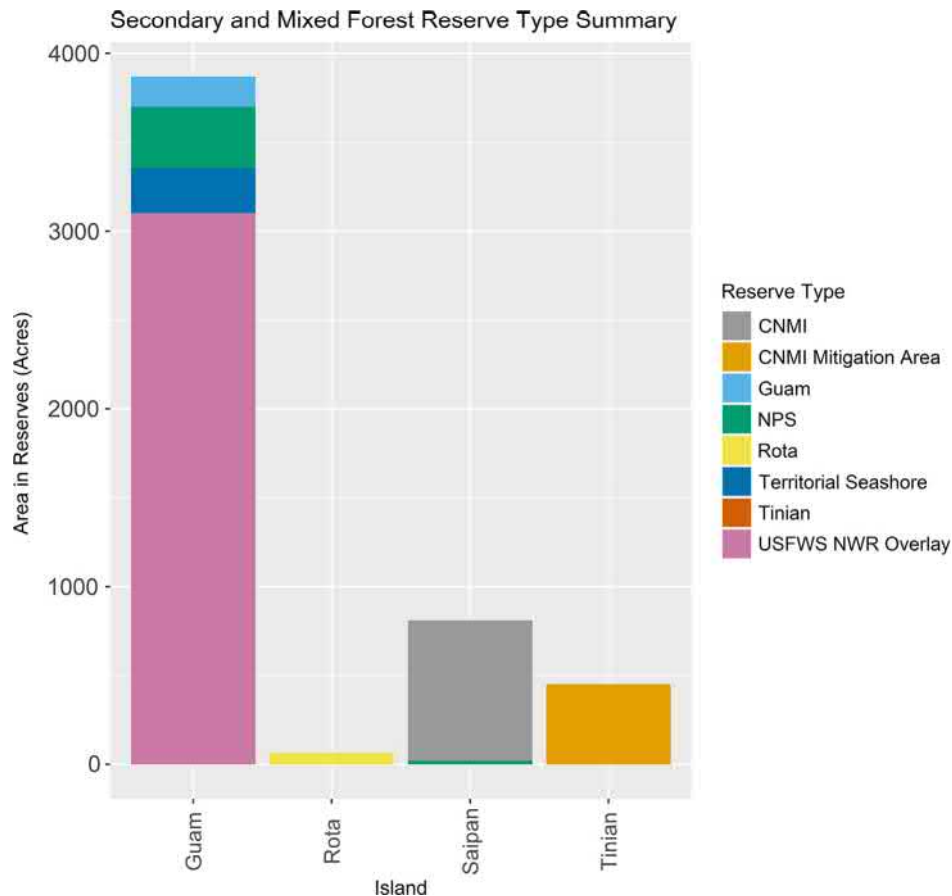


Fig. 11 Secondary forest reserve type summary (Reeves and Amidon, 2018).

change estimates, is the extent of Marianas Forest ecotypes that is expected in the foreseeable future under Scenario One, the status quo, where conservation efforts remain unchanged and the current rate of change in land cover is also unchanged.

The future conditions of Marianas Forests for Scenarios Two, Three, and Four cannot be quantitatively (acres/ha) estimated. However, the Scenario One estimate can provide a “baseline” for a qualitative characterization of changes in the future condition of Mariana Forests under Scenarios Two, Three, and Four.

Changes in human population are captured only by the changes in the “developed” land cover footprint derived from land cover map analysis (Amidon and Reeves, 2018). Impacts from other sources of human activities or human-caused stressors (e.g., plant and animal diseases, wildfires, invasive species, etc.) are not well characterized in the land cover changes, but significantly contribute to increases in the land cover area dominated by nonnative vegetation. For an assessment of island-by-island changes in human population, see Amidon (2018).

Also, note that island-wide implementation of the CMPs is unlikely to have a significant effect on climate-related stressors (temperature, precipitation, and severe weather) resulting from global warming by 2035. This lack of CMP climate effects is due to the global lag in climate response to changes in greenhouse gas emissions which occurs on the order of centuries rather than years (Solomon et al., 2009; Gillett et al., 2011; Jevrejeva et al., 2012). Evidence of climate effects is also confounded by the large annual variation in the Pacific islands climate parameters, which is much greater than projected climate change by 2035. Although impacts from climate-related stressors do not change across the four scenarios, they were included in this analysis because of their overall magnitude of potential importance to future ecotype viability.

Future Scenario One: Status Quo

Under Scenario One there is no change in the implementation of the three CMPs between 2018 and 2035. A continuing current rate of change in land cover through this foreseeable future results in a slow but continuous change in Mariana forest subtypes. The anticipated changes, under Scenario One, of each stressor important to the four Mariana forest subtypes are given in Table 7. The summary of the change in quality and quantity of the four Mariana forest subtype under Scenario One can be found in Table 8.

Under Scenario One, an expanding human population and increased development and general land use on all inhabited islands is anticipated (Amidon, 2018; Amidon and Reeves, 2018), and therefore Mariana forest stressors are expected to increase at a small

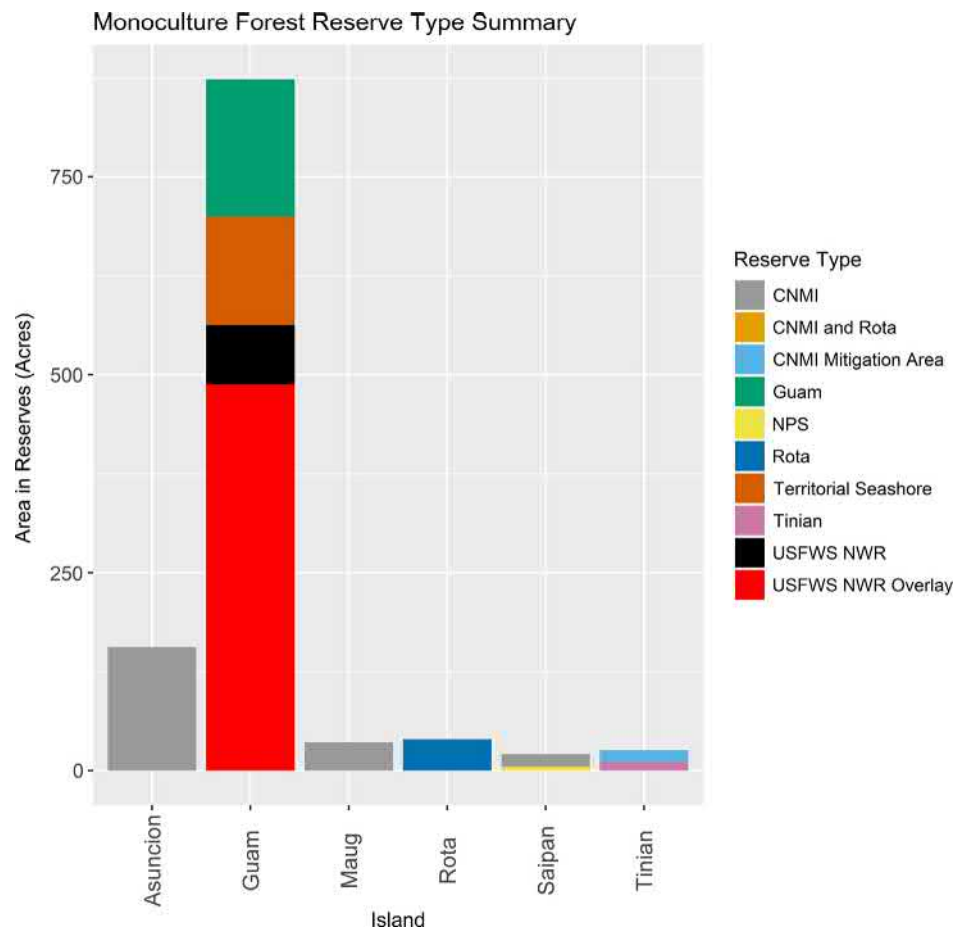


Fig. 12 Monoculture forest reserve type summary (Reeves and Amidon, 2018).

annual rate. Exceptions are a small to moderate annual rate of increase for development, wild fires, and surface air temperature, and a small annual rate of decrease for precipitation. On average, the percentage of land developed for residential, commercial, and agricultural purposes on the inhabited islands is expected to increase by 25% from 2016 to 2035. This rate is only true for the southern inhabited islands of Guam, Rota, Tinian, and Saipan. Data on rates of development for the remaining islands does not exist at this time. Based on the rate of development and land cover data, estimates of the amount and percent change in each forest sub-type from 2016 to 2035 on the southern inhabited islands of Guam, Rota, Tinian under Scenario One were calculated.

Overall, the continued gradual decline of all forest subtypes in the Marianas is predicted under Scenario One. Most development (agricultural, commercial, military, or residential) occurs within forests, resulting in ongoing forest loss and fragmentation reducing resilience and redundancy of all forest types. No change in native forest is expected on Guam (<1%) and a moderate decrease is expected on Rota (28%) as areas identified as homestead sites continue to be cleared. Secondary forest is projected to remain stable on Guam (1% decrease) and Rota (2% increase), and decline on Tinian (26%) and Saipan (40%) as forests are converted to scrub/grass and developed land cover types. Monoculture forest is projected to remain stable in the foreseeable future on these islands. *Leucaena* forest is projected to increase slightly on Guam (5%) and decline modestly on Tinian (9%) likely tied to increases scrub/grass and developed land cover types.

Future Scenario Two: There Is a Slight Increase in the CMPs That Marginally Improves Conservation Management

Under Scenario Two, conservation agencies and stakeholders work with increased but limited resources to slow or stop the degradation of landscape areas. Scenario Two is essentially 'status quo' with minor improvements in the three CMPs. This scenario is expected to have the second highest likelihood of occurring into the foreseeable future, being slightly less likely than Scenario One. The anticipated changes, under Scenario Two, of each stressor important to the four Mariana forest subtypes are given in Table 7. The summary of the change in quality and quantity of the four Mariana forest subtypes under Scenario Two can be found in Table 8.

Though there is an expanding human population in Scenario Two, development is not expected to substantially increase. A slightly improved biosecurity effort should help reduce invasive species and plant diseases but increases are still expected. The small

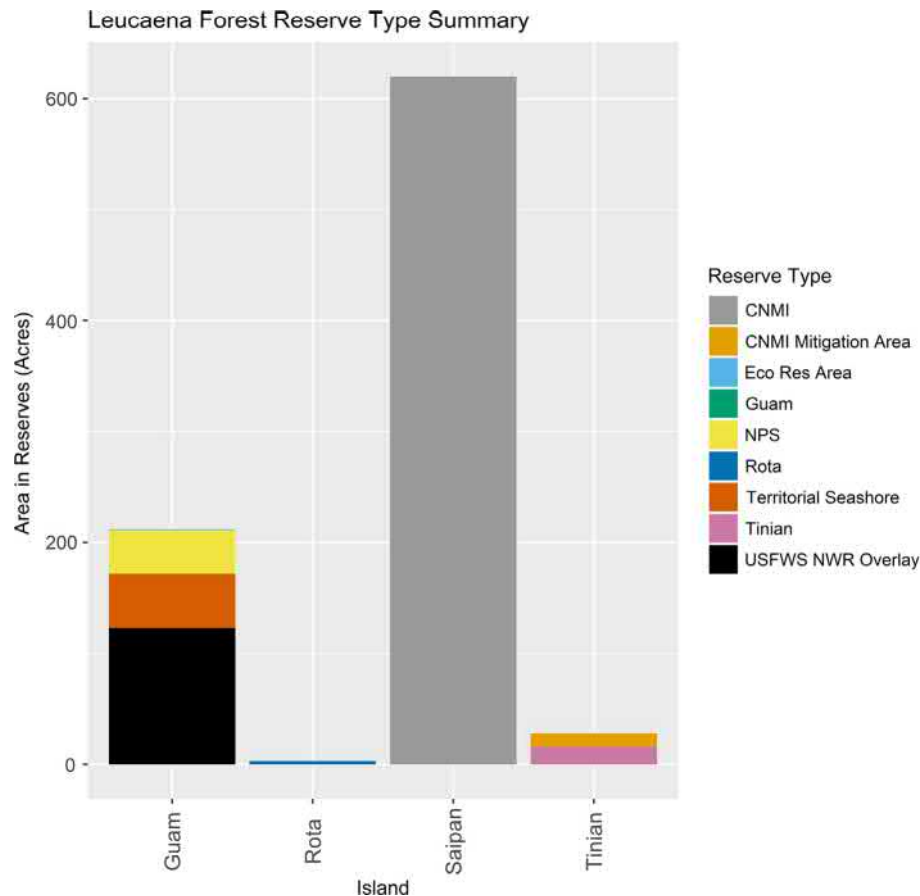


Fig. 13 Leucaena forest reserve type summary (Reeves and Amidon, 2018).

Table 6 Assessment of native forest resiliency, redundancy, and representation of forests in the Mariana Islands in their current condition.

Forest sub-type	Resiliency	Redundancy	Representation
Native forest	Slightly reduced but still moderate	Slightly reduced but still moderate	Slightly reduced but still moderate
Secondary forest	Moderate	Moderate	Moderate
Monoculture forest	Moderate	Moderate	Moderate
Tangantangan forest	High	Moderate	Moderate

increased support of natural resource management in the CMPs is not expected to greatly alter wildfire frequency and intensity, but these might (lower slightly) compared to Scenario One. The CMP supported conservation will not prevent, mitigate, or reverse the impacts of climate change-related stressors.

Under this scenario the decline of native and secondary/mixed forest subtypes in the Marianas is predicted to decrease or halt. Whereas, development (residential, commercial, or agricultural) in the past and present occurred largely within native forest, a slight increase in planning could target development to areas of past development or disturbance. Disturbed open fields or abandoned buildings could be developed to accommodate an increase in population allowing for tracts of all forest types to remain undeveloped and possibly move through successional stages towards native or secondary forest on the islands with functional seed dispersal systems.

Future Scenario Three: There Is a Small to Moderate Decrease in Conservation Actions in the CMPs That Substantially Decreases Conservation Management

Under Scenario Three, all natural resource management actions in the CMPs are set aside in deference to land use for economic development. With extensive localized management, some native species may persist in park-like settings or in areas where land development is not possible. The anticipated changes, under Scenario Three, of each stressor important to the four Mariana forest subtypes are given in Table 7. The summary of the change in quality and quantity of the four Mariana forest subtypes under Scenario Three can be found in Table 8.

Table 7 Responses of Mariana Forest stressors in foreseeable future scenarios.

Conservation management parameters (CMPs)				
Conservation values	Stakeholder involvement and public opinion influence the formulation, implementation, and funding of natural resource conservation and biosecurity (NRC/B) within laws and development or conservation plans			
Laws and biosecurity	National, state, county, and city laws and regulations are the means by which NRC/B are supported and implemented			
Planning for development or conservation	National, state, county, city, and private development plans or conservation plans define actions that result in losses or gains in NRC/B (impacts realized at implementation)			
Foreseeable Future Scenarios	and the resulting Mariana Forest conditions			
Use Foreseeable Future Scenario One as a “baseline” to characterize changes in <i>Conservation Actions</i> and <i>Forest Conditions</i> in Future Scenarios Two, Three, and Four	<i>Scenario One:</i> CMPs: unchanged in support for NRC/B <i>Conservation Actions:</i> no change; current rate of land cover change continues through the foreseeable future <i>Forest Condition:</i> area, quality, and sustainability slowly decrease through the foreseeable future	<i>Scenario Two:</i> CMPs: small increase in support for NRC/B <i>Conservation Actions:</i> marginal increase <i>Forest Condition:</i> area is unchanged through the foreseeable future; quality and sustainability are slightly enhanced through the foreseeable future	<i>Scenario Three:</i> CMPs: small to moderate decrease in support for NRC/B <i>Conservation Actions:</i> substantial decrease <i>Forest Condition:</i> urban and agricultural uses are prioritized over conservation; area, quality, and sustainability substantially decrease through the foreseeable future	<i>Scenario Four:</i> CMPs: moderate to large increase in support for NRC/B <i>Conservation Actions:</i> substantial increase <i>Forest Condition:</i> robust, sustained effort to restore, manage, and expand conservation; area, quality, and sustainability substantially increase through the foreseeable future
Stressors	Responses of Mariana Forest stressors			
Development	Small to moderate increase	No change (redevelop)	Moderate to large increase	Small to moderate decrease
Altered hydrology	No change to small increase	No change	Larger increase	Small decrease
Recreation/access	Small increase	Small increase	Larger increase	Larger increase
Invasive species	Small increase	Small increase	Larger increase	Small decrease
Plant diseases	Small increase	Small increase	Larger increase	No change to small decrease
Fire	Small to moderate increase	Small increase	Larger increase	No change to small decrease
Erosion	Small increase	No change	Larger increase	Small decrease
Climate:				
Temperature	Small to moderate increase	Small to moderate increase	Small to moderate increase	Small to moderate increase
Precipitation	Small decrease	Small decrease	Small decrease	Small decrease
Storms	Small increase	Small increase	Small increase	Small increase

Under this scenario the quality and quantity of all forest types in the Marianas is expected to rapidly decline. Development (residential, commercial, or agricultural) will increase substantially and continue to disproportionately impact Mariana forests relative to other land cover types. Overall, this will result in fragmentation and degradation of forests reducing resiliency, redundancy, and representation across all forest types.

Future Scenario Four: There Is a Moderate to Large Increase in Conservation Actions in the CMPs That Substantially Improves Conservation Management

Under Scenario Four, an overt and robust, active, ongoing effort is made to engage partners and stakeholders in identifying and prioritizing landscape areas needed for the conservation of native ecosystems, and to actively restore and expand these areas. A substantial emphasis on natural resource conservation is present in the three CMPs, reflecting increased societal concern for declines in natural habitats and biodiversity. Active and well-supported natural resource management begins to restore these habitats and ecosystems and expand their landscape areas. The anticipated changes, under Scenario Four, of each stressor important to the four Mariana forest subtypes are given in [Table 7](#). The summary of the change in quality and quantity of the four Mariana forest subtypes under Scenario Four can be found in [Table 8](#).

Under this scenario the rate of decline of all forest types in the CNMI is expected to halt allowing forests to regenerate and expand. The BTS will continue to hinder the natural regeneration of forests lost due to the absence of seed dispersers, but active restoration efforts by DOD and conservation agencies will aid in the creation of native forest habitat. Whereas, development (residential, commercial, or agricultural) in the past and present occurred largely within forest habitat, with a robust increase in

Table 8 (A–D). Estimated acreages and percent of island in each forest sub-type currently (2016) and in the foreseeable future (2035) for the islands of Guam, Rota, Tinian, and Saipan.

Island	Current (2016)		Future (2035)		% Change 2016 to 2035
	Acres	% of Land	Acres	% of Land	
Native forest ^a					
Guam	21,668	16%	21,681	16%	< 1%
Rota	10,052	47%	7,207	34%	– 28%
Tinian	1067	4%	471	2%	– 56%
Saipan	427	1%	637	2%	49%
Secondary forest ^b					
Guam	33,270	25%	32,946	25%	– 1%
Rota	2163	10%	2212	10%	2%
Tinian	6202	25%	4594	18%	– 26%
Saipan	10,656	36%	6369	22%	– 40%
Monoculture forest ^c					
Guam	1709	1%	1701	1%	0%
Rota	667	3%	772	4%	16%
Tinian	888	4%	1676	7%	89%
Saipan	526	2%	741	3%	41%
Leucaena forest ^d					
Guam	4914	4%	5137	4%	5%
Rota	229	1%	34	0%	– 85%
Tinian	8279	33%	7567	30%	– 9%
Saipan	5492	19%	5709	19%	4%

Percent (%) change is the difference between the % of land in 2035 and 2016. No data is currently available for projecting habitat change in the foreseeable future for the remaining islands in the archipelago (Amidon and Reeves, 2018).

^aNo change in Native Forest is expected on Guam, a moderate decrease is expected on Rota, a large decrease is expected on Tinian, and a large increase is expected on Saipan. The increase on Saipan is likely due to inconsistencies in classification. Native forest on Saipan is highly fragmented and has not been mapped well over the various assessments. Therefore, we consider that increases in native forest on Saipan are unlikely. The decline on Tinian is also likely to be due, in part, to classification inconsistencies. However, some decreases may occur on Tinian. Declines in native forest are expected on Rota as areas identified for homestead sites continued to be cleared.

^bSecondary forest is projected to remain stable on Guam and Rota and decline on Tinian and Saipan. A decline on Saipan is expected as a large proportion of the island is secondary forest and the increases in developed land cover is likely associated with losses in this forest sub-type. A decline on Tinian is also expected as approximately a quarter of the island is in this forest sub-type and increases in scrub/herbaceous and developed habitats are likely related to the loss of this forest sub-type.

^cBased on the analysis, monoculture forest is projected to remain stable on Guam and increase on the remaining islands. However, the increases on Rota, Tinian, and Saipan in this habitat are likely related to mapping error and inconsistent classification as new plantings of monoculture forest are not regularly encountered on these islands. The changes on Saipan and Rota are relatively small and consistent with mapping error. The increase on Tinian is substantial. However, review of the imagery from 2005 and 2016 indicates that the increase in this forest sub-type is likely due to misclassification. The monoculture forest in the 2016 map was present in the 2005 imagery and was likely misclassified due to the lower resolution of the imagery. Therefore, we conclude that changes in monoculture forest are unlikely under the status quo scenario.

^dThe analysis indicates that *Leucaena* Forest is projected to remain stable on Saipan, increase slightly on Guam, and decrease on Rota and Tinian. The projected decline on Rota is likely related, in part, to mapping and classification errors. Review of the imagery from 2016 and 2005 indicate that the extent of this forest type was consistent between both images and that the decline may be related to over estimates in the 2005 maps. The decline on Tinian is expected as approximately 1/3rd of the island is classified as this habitat and increases in Developed and Scrub/Herbaceous land cover types (see associated sections in Amidon and Reeves, 2018) on this island are likely related to the loss of this forest sub-type.

planning, development in forest habitat will be virtually non-existent and almost entirely occur in areas of past development or disturbance. Disturbed open fields and impaired forests will then be actively targeted for reforestation and restoration resulting in an increase in the quality and quantity of forested habitat.

Conclusion

Prior to the arrival of humans in the Mariana archipelago, native forest was likely widespread, contained a high amount of diversity, and recovered quickly from storms; thereby exhibiting high levels of resiliency, redundancy, and representation. As a result of natural and anthropogenic disturbance since the arrival of humans, a significant proportion of native forest was converted to three additional forest sub-types: secondary, monoculture, and *Leucaena* forests resulting in the current condition of Mariana forests.

Currently, the primary stressors to Mariana forests include invasive species, development, volcanic eruptions, typhoons, and fire. These stressors are serious and ongoing, and are expected to continue or increase in magnitude and intensity into the future. Without changes in current laws or regulations, biosecurity will continue to be an issue and continuing the spread and introduction of invasive plants, animals, and insects and their impacts throughout the archipelago. In addition, the threat of introduction of the BTS to the CNMI is ongoing, and will also continue to prevent the recovery of seed dispersing avian species hindering native forest

restoration on Guam. And without active management to halt or reduce the impacts of development and invasive species, the quantity and quality of Mariana forests will continue to decline and result in reduced resiliency, redundancy and representation.

Native and secondary forests are biologically important as they support native species and provide the conditions needed for their survival. The majority of remaining native (90%) and secondary forests (99%) are found on five of the southern islands (Guam, Rota, Tinian, Saipan, Aguiguan) which underscores the importance of these areas for biodiversity conservation in the Mariana archipelago. However, these islands also support the highest concentration of the human population and military activities which presents a greater risk of forest degradation and destruction as result of the ongoing impacts of development and invasive species.

Though conservation efforts by Federal, Territorial, Commonwealth, and multiple agency partnerships have been beneficial in helping to conserve and protect some of the remaining forests in Marianas, without increased efforts to address biosecurity, development, and invasive species, a decrease in the viability of Mariana forests is expected. Because the remaining native and secondary forests and reserve areas occur across public, private, and Department of Defense lands (including the USFWS Overlay Refuge), conservation of these areas will require continued efforts by all stakeholders.

Finally, in the foreseeable future, Scenario One, has the highest likelihood of occurring in relative to the other scenarios. Under Scenario One there is no change in the implementation of the conservation management parameters (CMPs). Scenario Two is based on a slight increase in the implementation of the CMPs, which marginally improves conservation management. Thus Scenario Two is expected to have the second highest likelihood of occurring into the foreseeable future, being slightly less likely than Scenario One. Scenario Three is based on a slight to moderate decrease in conservation actions in the CMPs which substantially decreases conservation management. Because there is a decrease in the implementation of the CMPs, Scenario Three would severely degrade and fragment native and secondary forest subtypes and result in reduced resiliency, redundancy, and representation. In Scenario Four, the substantial improvements in restoration for native and secondary forest subtypes would result in increased resiliency, redundancy, and representation. However, Scenario Three and Four have the lowest likelihood of occurring in the foreseeable future.

Overall, the CMPs are critical factors that drive the direction and magnitude of natural resource conservation and determine the foreseeable future scenarios. Any increase in the implementation of the CMPs will result in the greatest conservation returns for native and secondary forests (Scenario's Two and Four). Conversely, any decrease in the implementation of the CMPs will result in the least conservation returns for native and secondary forests (Scenario's One and Three). Thus, realistic expectations of the implementation of the CMPs were considered when determining the likelihood of occurrence for each scenario in the foreseeable future.

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Seeing the Freshwater Among the Trees: The Little-Recognized Aquatic Resources of Canada's Boreal Forest Region

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Abstract

Much world attention has been given to engineering solutions to the increasing threats of water scarcity and pollution in regions where aquatic systems have been lost or degraded. However, government leaders and decision-makers must acknowledge that this crisis cannot be solved without giving equal attention to protection of the Earth's remaining pristine lakes, rivers, wetlands and peatlands. Canada's Boreal Forest region encompasses some of the world's largest intact freshwater ecosystems, contains the highest concentration of wetlands—which hold billions of tons of carbon—with countless pristine lakes and free-flowing rivers and streams. The aquatic systems of the region benefit the lives of billions of people across the world by stabilizing climate, supporting ocean health, enhancing food security, protecting wildlife and influencing the global economy. Protection of Canada's Boreal Forest region and its waterways and wetlands, along with limiting greenhouse gas emissions, should be among the top global conservation priorities.

Introduction to the Globally Significant Aquatic Features of the Boreal

While most of the world is focused on water scarcity and pollution, a few places on earth still retain pristine and abundant water resources maintained by large areas of intact forests and wetlands (Fig. 1; Keddy et al., 2009). Canada's Boreal Forest (Fig. 2) is one of these regions. Canada contains, by some estimates, more than 20% of the world's wetlands (Scott and Jones, 1995; Webster et al., 2015) and the largest amount of surface freshwater within a single country (Minns et al., 2008), most of it within the Boreal Forest region (Fig. 3). Also within Canada's Boreal Forest are North America's most significant undammed rivers (Figs. 4 and 5A, B; Dyne-sius and Nilsson, 1994), millions of lakes (Fig. 4 and 5C) including some of the world's largest (Minns et al., 2008), and the world's most extensive peatland systems (Abraham and Keddy, 2005; Tarnocai, 2009; Keddy et al., 2009). All of these are embedded within a matrix of forested habitat, still largely unfragmented by industrial development, representing the world's largest intact forest ecosystem maintained for millennia by Indigenous communities who still rely on Canada's Boreal Forest for food, health and livelihoods (Karst, 2010).

Canada's Boreal Forest and its wetlands and waterways have an integral influence on the planet's climate and marine productivity in ways that impact hundreds of millions of people across the world in relation to global warming, food security, and economics (Dai and Trenberth, 2002; Dai et al., 2009). The value that Canada's Boreal Forest provides to the world in total ecosystem services has been estimated at 700 billion dollars annually, with more than half of that attributable to services provided by wetlands including carbon storage, water filtration, and flood control (Anielski and Wilson, 2009). This is 14 times greater than the value of natural resources (mining, forestry, oil and gas, hydroelectric generation) extracted annually from the region. Industrial resource extraction is also expected to decrease the ability of Canada's Boreal Forest to provide ecosystem services to society.

The rivers (Fig. 4) that drain Canada's Boreal Forests' 5.8 km² (1.4 billion acres) are among the earth's most significant in providing freshwater flow and nutrients to northern marine systems including the Arctic Ocean, Bering Sea, and Hudson and James Bay (Stewart and Lockhart, 2005). This input is critical in the formation of sea ice that cools the atmosphere through the reflection of solar radiation (Loeng et al., 2005) and provides the substrate for much of the biodiversity of that unique marine ecosystem including marine algae, plankton, fish, seals, whales, and polar bears (Stewart and Lockhart, 2005). Flows from Canada's Boreal Forest rivers also are key drivers in the dynamics of large deep ocean currents that link cold northern Polar waters with warmer tropical waters and have a major influence on global weather and future climate change (Dai and Trenberth, 2002; Dai et al., 2009).



Fig. 1 Wetlands of all shapes and sizes make up much of the landscape within Canada's Boreal Forest region like these in (A) northern Ontario, (B) northern Quebec, and (C) the Northwest Territories. Photos by Jeff Wells.

Peatlands (Fig. 6) and the sediments of lakes and river deltas of Canada's Boreal Forest are one of the world's largest stores of carbon (Wells et al., 2010). Canadian peatlands store an estimated 147 billion tonnes of carbon (Tarnocai, 2009) while the sediments in the delta of the Mackenzie River contain 41 billion (Tarnocai et al., 2009). The 208 billion tonnes of carbon estimated to be stored overall within Canada's Boreal Forest represent the equivalent of 26 years worth of world carbon emissions from the burning of fossil fuels as measured in 2006 (Carlson et al., 2009, 2010).



Fig. 2 North America's Boreal Forest biome (in *green*) as delineated by Brandt (2009). Canada's portion of the biome extends from the Alaska-Yukon border east to Newfoundland and Labrador.

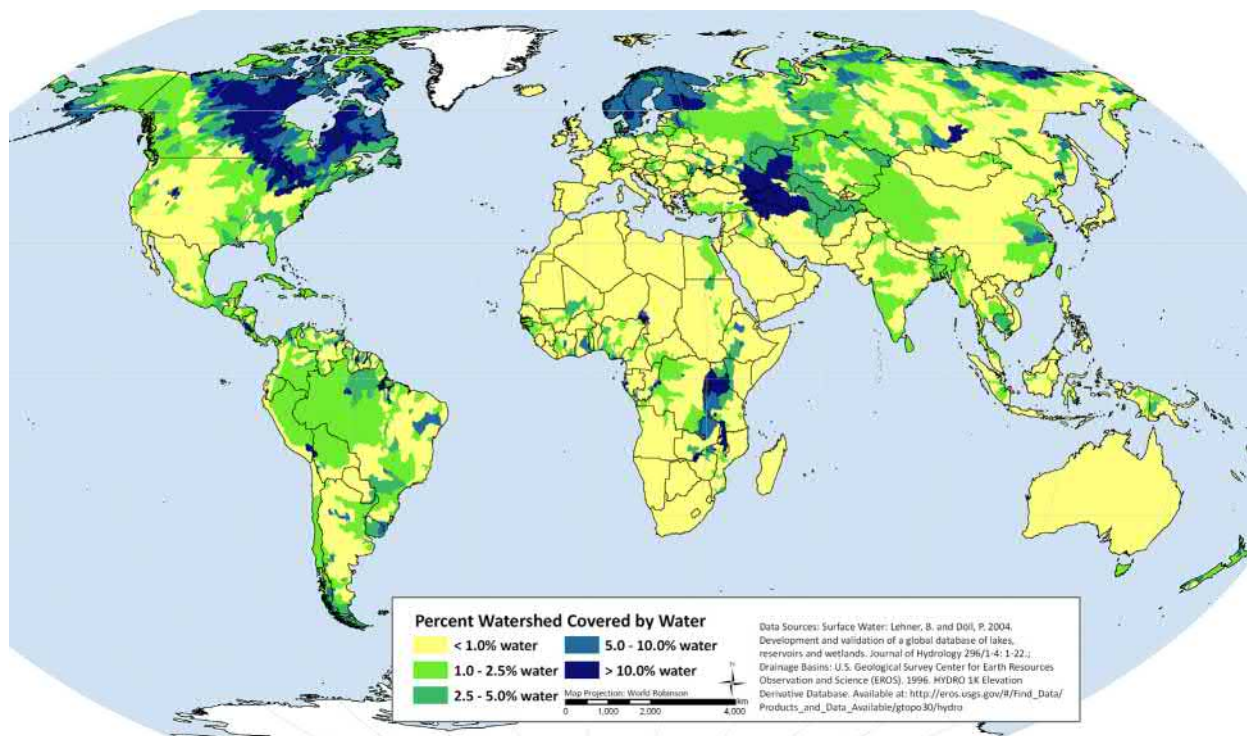


Fig. 3 Canada's Boreal Forest contains the highest concentration of surface freshwater in the world with millions of lakes and ponds.

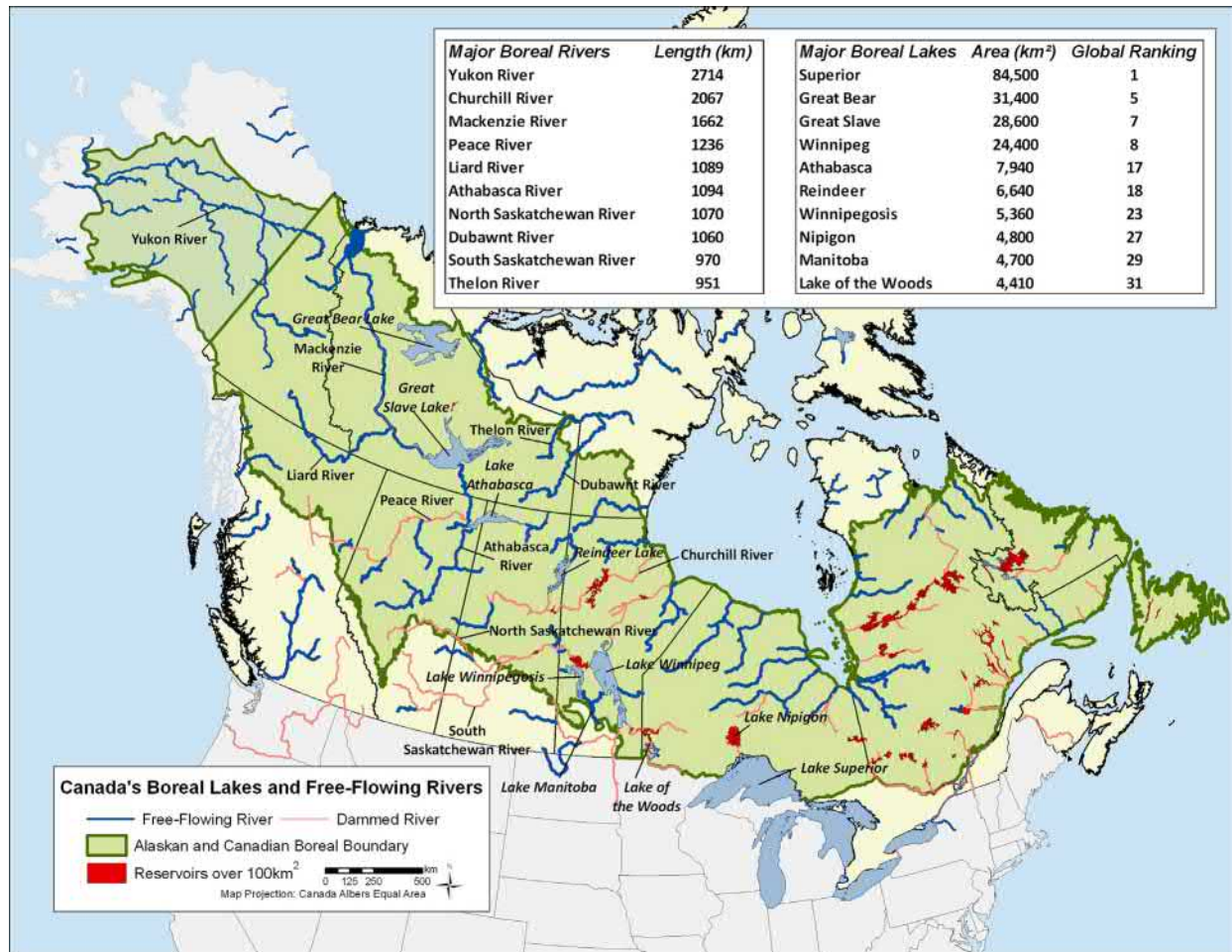


Fig. 4 Canada's Boreal Forest hosts more free-flowing rivers than anywhere else in North America although mega-hydro projects have been developed on many river systems as well. Four of the world's largest lakes are found wholly or partly in Canada's Boreal Forest region.

Globally Significant Biodiversity in Canada's Boreal Forest

The biodiversity supported by the wetlands and waterways of Canada's Boreal Forest is nationally and globally significant (Wells et al., 2010). Its large and long undammed rivers have become the last refuges for many of the world's sea-run migratory fish including species that have been lost or reduced in vast portions of their former range. For example, half of the remaining healthy populations of North America's Atlantic salmon (*Salmo salar*) are found in rivers within Canada's Boreal Forest (Fig. 7) and some of the most significant populations of Pacific salmon species occur in Canada's Boreal Forest rivers including the Yukon and the Stikine (Scott and Crossman, 1973; Augerot and Foley, 2005; Wells et al., 2010). The low human population density and lack of overexploitation of many of Canada's Boreal Forest lakes and rivers has permitted freshwater ecosystems to retain many natural qualities lost throughout most of the world including very large and long-lived fish. The sportfishing world record largest lake trout (*Salvelinus namaycush*) was a 72-pound individual taken on Great Bear Lake and the world record largest brook trout (*Salvelinus fontinalis*), Arctic grayling (*Thymallus arcticus*), and round whitefish (*Prosopium cylindraceum*) are all from waters within Canada's Boreal Forest (International Game Fish Association, 2010).

The 1–3 billion birds that breed in Canada's Boreal Forest are highly dependent on its wetlands and waterways (Cheskey et al., 2011; Wells and Blancher, 2011; Slattery et al., 2011). Some of the world's largest concentrations of waterfowl and shorebirds nest and feed in Canada's Boreal Forest wetlands including RAMSAR designated sites like the Polar Bear Provincial Park in the Hudson Bay Lowlands, the Peace Athabasca Delta, and Yukon's Old Crow Flats (Cheskey et al., 2011; Wells et al., 2013). The intact nature and remoteness of Canada's Boreal Forest watersheds has also shielded the region from the large numbers of invasive plants and animals that are causing major ecosystem degradation in much of the world.



Fig. 5 Within Canada's Boreal Forest biome are major free-flowing rivers like the Mackenzie River (A) in the Northwest Territories and the George River (B) in Quebec and the world's fifth largest and perhaps most pristine lake, Great Bear Lake (C) in the Northwest Territories. Photos by Jeff Wells.

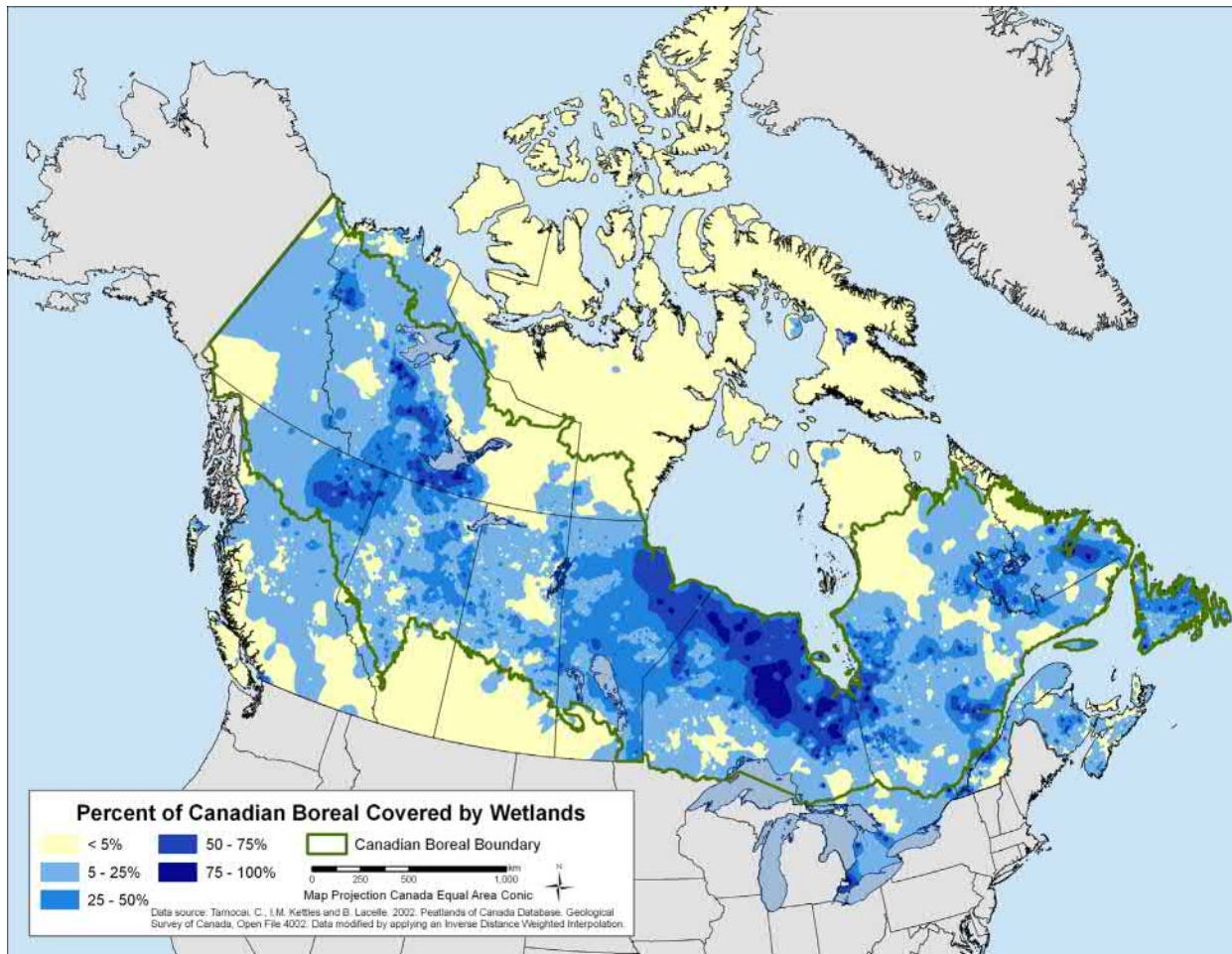


Fig. 6 Wetlands dominate within Canada's Boreal Forest including some of the largest peatland systems in the world, some of the largest inland deltas, and major lakeshore freshwater marshes along its many large lakes and marine marshes and estuaries as well.

Large-Scale Industrial Activity Is Increasing

Although Canada's Boreal Forest is globally significant in the conservation values it still retains, the region is becoming increasingly impacted by large-scale industrial activities (Kreutzweiser et al., 2013). Already the footprint of industrial activity within Canada's Boreal Forest encompasses 730,000 km² (180 million acres) including logging, road building, mining, oil and gas extraction, and hydropower (Wells et al., 2010). A third of Canada's Boreal Forest region has been allocated by provincial governments for logging (Fig. 8A and B) and approximately 10% was under mining claims in 2008. There are 7000 abandoned mines (Fig. 8C) within Canada's Boreal Forest with 3000 of these within 1 km of a waterway (Wells et al., 2010) and over 230,000 of the active and abandoned oil and gas wells in Canada's Boreal Forest are within 5 km of a waterway. Ten thousand new oil and gas wells were drilled annually from 1999 to 2009 (Wells et al., 2010). There are over 600 dams generating hydropower across Canada with the largest in Canada's Boreal Forest region (Lee et al., 2012). Impoundments behind dams are estimated to have inundated 52,000 km² (12.9 million acres) of wildlife habitat (Wells et al., 2010) and over 130,000 km (80,778 miles) of river have been affected by flow regulation from dams in Canada (McAllister, 2000). At least 20 new large hydropower projects are planned or proposed and hundreds more identified as potential projects across Canada (Lee et al., 2012). The rapidly increasing effects of climate change are already manifesting themselves across Canada's Boreal Forest ecosystems, especially in wetlands and waterways through the melting of permafrost and drying of wetlands in the western part of the region (Schindler, 2001; Schindler and Lee, 2010). Industrial activities lessen the adaptability of natural habitats to adapt to these climate change impacts, especially because much of the water in Canada's Boreal Forest systems is not recharged on an annual basis but is the result of years of accumulation in ice and snow (Schindler, 1998a,b).

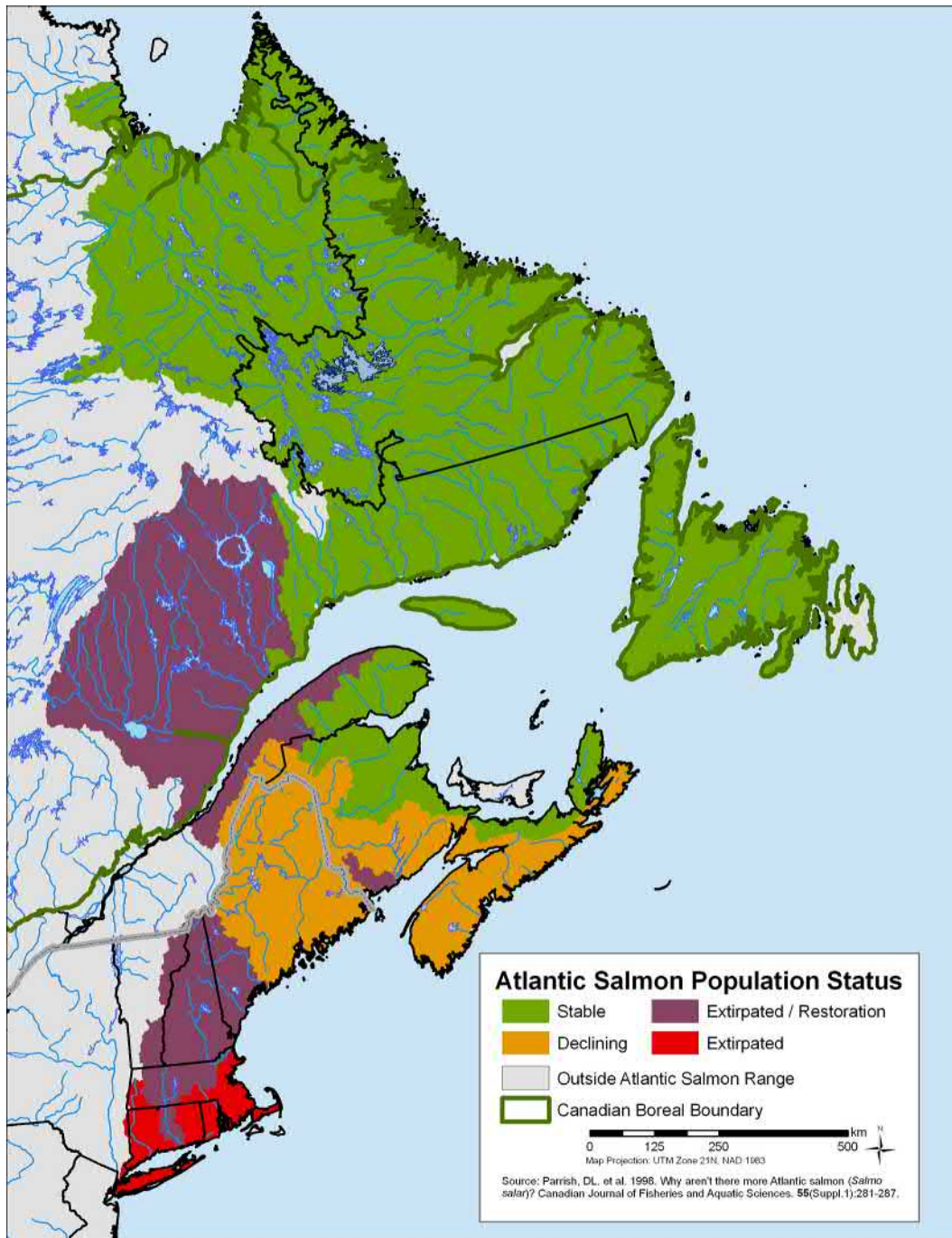


Fig. 7 Atlantic Salmon (*Salmo salar*) populations are now endangered in the United States, largely as a result of dams prohibiting access to upstream spawning grounds and pollution. But healthy populations remain in the undammed, free-flowing, and pollution-free rivers within Canada's Boreal Forest (shown in green).

A Bold Conservation Vision

Modern conservation science principles now recommend much higher protected areas benchmarks are required in order to have a reasonably high probability of retaining a region's species diversity and ecosystem functions (Noss et al., 2012; International Boreal Conservation Science Panel, 2013; Locke, 2013; Wilson, 2016; Dinerstein et al., 2017; Watson et al., 2018). These principles have been applied to Canada's Boreal Forest region and a resulting vision articulated that calls for the establishment of a series of large, interconnected protected areas that encompasses at least half of the region's 5.8 million km² and with industrial natural resource extraction activities that occur outside of these protected areas carried out with leading edge responsible development practices to ensure the retention of biodiversity and ecosystem function (International Boreal Conservation Science Panel, 2013).



Fig. 8 Examples of some types of industrial activity in Canada's Boreal Forest include road-building and forestry (A and B), these from northern Ontario, and mining (C), this the now abandoned Pine Point mine south of Great Slave Lake in the Northwest Territories. Photos by Jeff Wells.

The Canadian Boreal Forest Conservation Framework describes this vision and was endorsed by the Boreal Leadership Council, a coalition that includes First Nations, leading industries from many sectors, and environmental organizations (Carlson et al., 2015).

World-Leading Stewardship of Aquatic Resources

Major progress has been made in some jurisdictions toward protecting and maintaining their northern aquatic resources as a result of public support for increased land conservation efforts, particularly led by Indigenous governments. The provinces of Ontario and Quebec have each committed to protecting half of their northern regions, an area in total of more than 858,000 km² (Carlson et al., 2015; Wells et al., 2015). Indigenous governments throughout Canada's Boreal Forest region have been especially efficient in implementing conservation initiatives (Indigenous Circle of Experts (ICE), 2018). In 2012, the Indigenous Inuit and Cree governments in partnership with the Government of Quebec, established Tursujuq National Park, a 26,000-km² pristine network of rivers and streams along the northern shores of Hudson Bay in northwestern Quebec that weave together a wetland fabric of marshes, peatlands, ponds, and lakes (Wells et al., 2013; Carlson et al., 2015). The park encompasses at least three river systems totaling more than 300 km in length with headwater to mouth protection. These culminate with some of Quebec's most unique lakes: Lacs des Loups Marins (Seal Lakes) and Quebec's second largest lake, Lacs à l'Eau-Claire (Clearwater Lake), which was formed by an ancient massive meteor strike. The waterways and wetlands further upstream are home to a remarkable number of water-dependent species. The most surprising is its resident race of freshwater harbor seals (*Phoca vitulina mellonae*). Apparently landlocked for thousands of years, these seals somehow find enough open water and food through the winter for survival (Wells et al., 2010).

In Manitoba and Ontario, four Indigenous governments (Bloodvein River First Nation, Little Grand Rapids First Nation, Pauingassi First Nation, and Poplar River First Nation) in partnership with both provincial governments, have protected 30,000 km² of primary forest within the Pimachiowin Aki World Heritage Site that includes virtually the entire lengths of four free-flowing rivers (Fig. 9) with a total length of over 1200 km and that discharge 6.9 million m³ of freshwater into Lake Winnipeg, the world's 10th largest lake (Davidson-Hunt et al., 2012; Wells et al., 2014) and one suffering from polluted waters flowing into the lake from agricultural landscapes to its south and west (Schindler and Vallentyne, 2008).

In Labrador, the Innu Nation worked with the provincial government to establish the Mealy Mountains National Park and the Eagle River Waterways Provincial Park, two adjoining protected areas totaling over 13,000 km² (Carlson et al., 2015) and including headwater to mouth protection for the 200 km Eagle River which supports one of the area's largest runs of anadromous Atlantic salmon.

In the Northwest Territories, indigenous government land-use planning together with federal government initiatives has led to the establishment of more than 425,000 km² (105 million acres) of protected areas and interim protected areas (Wells et al., 2015). This includes the 30,000 km² (7.4 million acre) Nahanni National Park Reserve and adjoining 4850 km² (1.2 million acre) Náát-s'ihch'oh National Park Reserve that includes over 25,000 km of rivers and streams, the Thaidene Nene Indigenous Protected Areas that encompasses 2847 km² of wetlands and nearly 14,000 km of rivers and streams and the Edézhíe Indigenous Protected Area that encompasses 370,000 ha of wetlands and nearly 10,000 km of streams and rivers.

In the Sahtu Settlement Area of the Northwest Territories, the 93,300 km² (23 million acre) Tsá Tué Biosphere Reserve was established in 2016. The area is the homeland of the Sahtuto'ine, the "Bear Lake People." It encompasses Great Bear Lake, the world's



Fig. 9 The 300 km Blood Vein River flows unimpeded from headwaters in western Ontario to the east shore of Lake Winnipeg in Manitoba within the Pimachiowin Aki World Heritage Site. Photo by Jeff Wells.

eighth largest lake and perhaps the world's most pristine large lake, and most of its watershed. Within the Tsá Tué Biosphere Reserve are 992,000 ha of wetlands, 49,000 km of streams and rivers, and over 139,000 lakes.

In the Yukon, the final land-use plan for the 67,431 km² (16 million acres) Peel River Watershed was approved in 2019, requiring 55,858 km² (13.8 million acres) of new protected areas. The Peel River watershed includes six major river tributaries—the Snake, Wind, Bonnet Plume, Hart, Ogilvie, and Blackstone rivers that flow north into the Mackenzie Delta. The protected areas within the plan encompass 179,000 ha of wetlands, 62,000 km of streams and rivers, and 18,000 lakes. The watershed includes the traditional territories of four Indigenous governments, the Na-Cho Nyk Dän, Tr'ondëk Hwëch'in, Vuntut Gwitchin, and Teetl'it Gwich'in, all of whom led the initiative to protect the watershed.

The Government of the Northwest Territories initiated a water stewardship strategy for the Mackenzie River watershed in 2009 that involves collaborative planning with Indigenous governments, community based water monitoring, and the negotiation of transboundary water agreements with three provinces (Alberta, British Columbia, and Saskatchewan) and one territory (Yukon) with which the Northwest Territories share the Mackenzie River watershed ([Government of the Northwest Territories, 2010](#); [Webster et al., 2015](#)).

More to be Done

Protecting and maintaining the water resources of Canada's Boreal Forest will clearly require more attention and effort than ever before. The pace and scale of protected area establishment within Canada's Boreal Forest will have to reach unprecedented levels in coming years, including headwater to mouth protection for the world's last, large unfragmented rivers and their entire watersheds ([Lertzman and MacKinnon, 2013](#)). Land-use planning that is ongoing across many jurisdictions within Canada's Boreal Forest will have to more explicitly consider and integrate water and aquatic conservation values including maintaining intact waterways ([Schindler and Lee, 2010](#)).

New incentives will be needed to maintain the vast stores of carbon in Canada's Boreal Forest peatlands, forests, and waterways so they do not contribute to global warming. Large waterways and wetlands within Canada's Boreal Forest, especially the Mackenzie River Basin, the Yukon River Basin, the Hudson Bay-James Bay Lowlands, Labrador, and the Great Lakes-St. Lawrence Basin must also be the focus of renewed attention by Indigenous, provincial federal, and international leaders to develop joint protection and management strategies that recognize the global uniqueness and influence of these ecosystems.

A Last Great Conservation Opportunity

As governments around the world strive to enact the U.N. Sustainable Development Goals, including Goal 6—"Ensure availability and sustainable management of water and sanitation for all"—many are understandably focused on the twin issues of water scarcity and pollution that already impact billions of people. But equal attention must be given to another of the targets embedded within Goal 6—protecting and maintaining the Earth's last, large remaining pristine waterways and wetlands. As the human industrial footprint expands and global warming escalates, protection of these intact watershed will be absolutely critical to ensure both safe and adequate water for all but also to maintain ecosystem services and biodiversity, a goal of another U.N. convention, the Convention on Biological Diversity (the so-called Aichi Treaty). Maintaining the wetland and waterways of Canada's Boreal Forest in pristine, unfragmented and fully functioning condition should be a world priority.

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Grassland and Shrublands—An Overview

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Abstract

This section of the *Encyclopedia of the World's Biomes* covers the grassland, shrubland and savanna biomes through the individual regional ecosystems by which these biomes are expressed across the globe. Grasslands, shrublands, and savannas occupy upwards to 40% of the terrestrial surface of the earth, excluding Greenland and Antarctica. They occur on every continent except Antarctica and are found across the temperate and tropical zones of the world, as well as in the Arctic. Grasslands are defined as terrestrial ecosystems dominated by herbaceous plants, mainly graminoids in the Poaceae family (grasses) and related families, and which lack a considerable cover of woody plants. Shrublands are vegetation communities dominated by shrubs or short statured trees generally less than 5 m tall, often in a single canopy layer. Additional definitions used to define and describe grasslands, shrublands, and savannas are discussed. This overview article provides a brief introduction to the grassland, shrubland and savanna biomes with a focus on their global patterns of diversity, general ecology, and relationships to climate, disturbance and geology. The paleoecological origins of grassland, shrubland and savanna biomes and the evolution of important physiologic traits in ecosystem defining taxa are also explored. A review of the major grassland, shrubland and savanna ecosystems of the globe not covered by the articles in this section of the *Encyclopedia*, as well as references for further investigation, are provided. The articles in this Grasslands and Shrublands section, written by an accomplished set of authors, cover major grassland, shrubland, savanna, and woodland ecosystems in North America, South America, Europe, Asia, Africa, Australia, Micronesia, and Polynesia.

Introduction

Grasslands, shrublands, and savannas occupy upwards to 40% of the terrestrial surface of the earth, excluding Greenland and Antarctica (White et al., 2000). They occur on every continent except Antarctica and are found across the temperate and tropical zones of the world, as well as in the Arctic. Grasslands and shrublands are highly diverse in their vegetation structure and floristic composition, and in many cases their biodiversity, owing in large part to their broad range of climatic zones, widespread global distributions, and often long and complex geologic and evolutionary histories. In a broad sense, grasslands and shrublands are identified by a moderate to dense vegetation cover (> 10%) and a lack of a continuous and/or multi-layered tall tree canopy (i.e., non-forest). However, many different definitions exist for grasslands, shrublands, savannas, and woodlands (White et al., 2000; Dixon et al., 2014; Török and Dengler, 2018).

In general, a grassland is a terrestrial ecosystem that is dominated by herbaceous plants, mainly graminoids in the Poaceae (grasses), Cyperaceae, Restionaceae, and related families, and which lacks trees or a considerable cover of woody plants (White et al., 2000; Gibson, 2009; Dengler et al., 2014). A shrubland is vegetation that is dominated by shrubs or short statured trees, generally < 5 m tall, often in a single canopy layer. Shrub cover may be very dense to fairly open with considerable grass cover, but with shrubs common and evenly distributed throughout (Dixon et al., 2014). As with grasslands, shrublands also lack considerable tall tree cover (< 10%). Grasslands and shrublands may occur as distinct from one another, the physiognomy of each characterizing vast ecoregions. However, grasslands and shrublands also co-occur in a variety of ways; intermixed in distinct grassland or shrubland patches, as grassy shrublands, or grasslands with a sparse cover of shrubs.

Definitions for savanna vary considerably, as they exist along a continuum between forest and woodland on one side of the spectrum and treeless grasslands on the other. Definitions also differ for savannas of temperate versus tropical regions. In general a savanna is defined as vegetation comprised of continuous grass cover with scattered trees, with some definitions including vegetation with shrub understories. Savannas are visually recognizable by their simple two layered structure: a single layer of scattered trees over top a continuous low statured understory layer of grasses or shrubs (Dixon et al., 2014). Tree cover thresholds can range from 10% to 60% (and as high as 75%) among savanna definitions in the literature (Dixon et al., 2014; Faber-Langendoen et al., 2016), although these upper limits exceed tree cover thresholds used to define woodlands. Faber-Langendoen et al. (2016) settle on

a threshold of 10–25% tree cover, while recognizing higher tree cover in the definition of tropical savannas. [Dixon et al. \(2014\)](#) and [Faber-Langendoen et al. \(2016\)](#) distinguished temperate savannas as those having 10% cover of trees < 5 m in height, from tropical savannas that have between 10% and 40% cover of trees < 8 m in height.

Woodlands are also described in several articles of this section, as these plant communities often occur among grasslands, savannas, and/or shrublands in a complex mosaic of different vegetation structural types and often share many ecological affinities and species with these adjacent communities. Woodlands are terrestrial ecosystems with a significant cover of trees but at lower densities than forests, often allowing enough sunlight through the canopy to support an abundant herbaceous or shrub ground layer of sun-loving plants. Where significant ecological similarities exist, woodland biomes are sometimes referred to as grassy woodlands or densely wooded savannas to highlight their relationships with grassy biomes ([Ratnam et al., 2011](#); [Rehwinkel, 2020](#)).

Grasslands and shrublands are often further defined through terminology that explain their ecological origins and persistence. Zonal grasslands and shrublands are those that occur in climates too dry (e.g., steppes) or too cold (e.g., alpine or arctic tundra) to support forests ([Dengler et al., 2014](#); [Török and Dengler, 2018](#)). These grasslands and shrublands are often referred to as climato-genic. Azonal and extrazonal grasslands and shrublands are those that persist due to edaphic (i.e., soil) conditions (azonal) or local climate extremes (extrazonal), sometimes in conjunction with disturbances, in regions and climates that otherwise support forests ([Dengler et al., 2014](#); [Török and Dengler, 2018](#)). Primary grasslands and shrublands are natural grasslands and shrublands that have formed spontaneously as a result of climate, soil conditions, and possibly a predominant natural disturbance regime. Secondary grasslands and shrublands are those that resulted from human land uses that converted previous natural vegetation types to anthropogenic, but semi-natural grasslands and shrublands (e.g., cleared forest, drained wetlands).

Despite being globally widespread and extensive, grasslands and shrublands are often regarded as among some of the least studied ecosystems on the planet ([Gibson, 2009](#); [Rundel et al., 2018](#)). They are also some of the most negatively impacted ecosystems from recent human activities. Several major temperate grassland regions of the world have been largely converted to industrial agriculture, most of the Mediterranean-type ecosystems coincide with rapid urban development due in part to the favorable weather, and tropical savannas of sub-Saharan Africa are succumbing to desertification due to intensifying human land uses and a warming global climate.

Scope of the Grasslands and Shrublands Section

The articles in this section of the *Encyclopedia of the World's Biomes* cover a wide range of the different grassland and shrubland ecosystems that occur across the globe, from grasslands, shrublands and savannas that occur on remote islands of Oceania, to the most extensive temperate grassland region in the world—the Eurasian steppe. However, they are by no means comprehensive of all the grassland, shrubland, and savanna ecosystems on planet earth (see below for a discussion on the major grasslands, shrublands and savannas of the world not treated in this publication). This section of the Encyclopedia includes articles from the tropical, temperate and Mediterranean climate type regions of the world. Not covered in this section are the herbaceous, succulent, or shrub dominated ecosystems of the world's major desert regions, herbaceous and shrub dominated wetlands, and the extensive areas of low shrub and herbaceous dominated vegetation of the arctic tundra above the Arctic circle and, to a smaller extent, the alpine zones at the tops of high elevation mountain ranges. Also not treated in this section are croplands and intensively managed grasslands consisting of pasturelands that are plowed and intentionally seeded with improved varieties of forage species.

Biogeography and Ecology

Grasslands and shrublands occur within nearly every temperate and tropical terrestrial region of the globe. They occur as broad ecotypes spanning large swathes of entire continents, such as the Great Plains grasslands and sagebrush shrub-steppe of North America or the tropical grasslands and savannas of sub-Saharan Africa, but also as smaller insular habitats among regions largely dominated by forests or deserts. Three main environmental factors explain the existence, development, and persistence of grasslands, shrublands, and savannas: climate, physical disturbance and soil conditions, all of which are described in detail below. Depending on the biome, the region, or the specific location, the role of each of these three environmental factors can vary from exclusive to highly interactive in determining the presence and extent of grasslands and shrublands. More often than not, two or more of these environmental factors intersect and act synergistically in producing conditions conducive for the development and maintenance of grasslands and shrublands. A fourth important factor at play that is touched upon throughout this overview is the evolutionary traits of the diagnostic plants that not only allow them to persist and proliferate in these environments but also reinforce disturbance regimes and structural characteristics that maintain areas as grasslands, shrublands or savannas (e.g., hemi-cryptophytic life form, below ground buds, epicormic sprouting, abundant post-fire germination, flammable resins, etc.).

Climate

One of the most important factors determining the global distribution of the major grassland, shrubland and savanna ecosystems of the world is climate, namely aridity in the form of low or highly seasonal annual precipitation and/or low humidity ([Lugo et al., 1999](#); [Bredenkamp et al., 2002](#); [Gibson, 2009](#)). In temperate and desert regions of the world, large grassland or grass-shrub

environments occur in drier regions, often towards the interior of continents not influenced by maritime climates. In cooler dry climates, these grasslands and grass-shrub ecosystems are referred to as steppes, whereas in warmer dry climates, they are referred to as desert grasslands and semi-arid shrublands. In moister climates, where annual rainfall is adequate to support woodlands and forest, periodic landscape scale fires are central to maintaining these areas as grasslands and shrublands. In tropical regions, relatively low annual rainfall is an important contributing factor to the existence of grasslands, shrublands, and savannas. However, in many tropical environments, fire appears to play a critical role in the maintenance of grasslands, shrublands, and savannas, with the abundance of C_4 grasses and their fine fuels aiding in promulgating fires.

Mediterranean type climates, that mainly persist in five major regions of the world (California, central Chile, the Cape Region of South Africa, southern and southwest Australia, and the Mediterranean Basin) present unique environmental conditions where grasslands, shrublands and woodlands are widespread and often floristically distinctive with high plant species endemism. These regions have a pronounced winter wet/summer drought climate. Due to their coastal positions on the western edge of continents that receive westerlies that reliably brings winter rain, allowing abundant plant growth in late winter and spring, and persistent summer time high pressure systems causing summer drought and high temperatures, these regions, with the exception of Chile, have been highly prone to wildfires for millennia. This has led to the development of vegetation and species persistence strategies that are highly adapted to drought and wildfire, most notably expansive evergreen sclerophyll shrublands, as well as savannas, grasslands, and broadleaf evergreen woodlands, with forest vegetation often restricted to more mesic and/or fire protected sites. The sclerophyll shrublands and woodlands that predominate in all five regions superficially appear very similar but are from often distinct or distantly related evolutionary lineages. All five Mediterranean climate type regions possess exceptionally high plant species diversity and are considered biodiversity hotspots.

Disturbance

While most natural grasslands and shrublands owe their origins and existence in large part to climate (i.e., seasonal drought), and in some cases to soil conditions (e.g., infertile soils, ultramafic geology, highly saline soils, or shallow soils), for many grasslands and shrublands their continued persistence and maintenance can be attributed to periodic disturbances. As alluded to above, the most important of these in many parts of the world are fire and, to a lesser extent, animal herbivory. This is particularly important in tropical savannas at locales where the monsoonal climate and seasonal precipitation patterns may otherwise favor the development of forest or woodland vegetation, but where a warm moist growing season that supports high biomass production is followed by a dry season accompanied by lightning (Keeley and Rundel, 2005). The presence of a continuous grass cover, with its annual accumulation of fine dry biomass (i.e., low fuel bulk density), is easily ignitable during dry seasons and can carry fires throughout the savanna or grassland and sometimes into neighboring vegetation types (Hoffman et al., 2012; Dantas et al., 2015; van Nes et al., 2018), thereby maintaining open, grass dominated vegetation. Summer rain along with intermittent dry periods and lightning ignited fires has a similar impact on many temperate grassland biomes. Shrublands in semi-arid or seasonally dry (e.g., Mediterranean type climate) environments, while not as readily flammable as grasses, can promulgate wildfires in a similar way through an extensive canopy of interlocking shrubs that, once ignited, can carry expansive fires that consume above ground biomass and eliminate trees.

Herbivory by large grazing animals plays a significant role in many grassy biomes, particularly where their populations are high or had been in the past. In some cases pastoralism with domesticated livestock has replaced the role indigenous ungulates had on grasslands and savannas. Herbivory exerts a considerable influence on the structure and species composition of the herbaceous layer and limits establishment of woody plants within grassy biomes. Both herbivory and fires influence species composition and contribute to the openness and grass dominance in these systems, however, these two consumers of biomass impact grassy biomes in different ways (Bond and Keeley, 2005; Gibson, 2009; Archibald and Hempson, 2016). The comparative importance and interactive effects of these two disturbances varies depending on the region and grassy biome where they occur.

Other types of disturbances can also be highly consequential for the maintenance of some grasslands and shrublands, such as in the case of periodic inundation through landscape level seasonal floods (in the Pantanal of central South America and the Zambesian flooded grasslands of central Africa) and, in mountainous areas, heavy snow loads and avalanches. Along major riverine systems, periodic flooding and river scour create and maintain open or non-forested vegetation types in otherwise forested landscapes. Another important disturbance that maintains some grasslands and shrublands are disturbances initiated by humans, through intentionally set fires, livestock grazing, and mowing, or through historic clearing for agriculture and present day abandonment. In addition, all aforementioned types of physical disturbance can contribute to grasslands and shrublands occurring as temporary successional stages in forests.

Soils

In distinct locations on earth large areas exist where soil conditions are so harsh to plant life that they largely override the influence of climate and favor the evolution and development of generally herbaceous, shrubby, and otherwise low statured non-forest species, ecotypes and vegetation cover. Still, dry climatic intervals and natural disturbance regimes (e.g., fires) can intersect and further promote the development and persistence of grassland and shrublands in such areas.

Large areas with exposed ultramafic geology (magnesium and iron rich rock often commonly referred to as serpentine) occur across the globe near present or ancient convergent plate boundaries where oceanic plates were pushed down into the mantle

and later thrust onto continental plates. Ultramafic derived soils are deficient in the essential plant nutrients phosphorus, potassium and calcium, have low calcium to magnesium ratios that inhibits calcium uptake resulting in weak cell wall development, and have high concentrations of phytotoxic minerals, particularly nickel and chromium (Alexander et al., 2007; Tashakor et al., 2013; Galey et al., 2017). Herbaceous or low statured woody growth forms are more advantageous to overcoming these limitations on plant growth and nutrient uptake. Regionally extensive exposures of ultramafic surfaces, such as those found in the Klamath-Siskiyou mountains in northern California and southwest Oregon, the Gaspé Peninsula of eastern Canada, New Caledonia, and Sulawesi in Indonesia, as well as smaller insular ones elsewhere, often support extensive grasslands, shrublands, savannas, and stunted woodlands whose floras are composed of species that specifically evolved to only occupy these harsh soil environments (serpentine endemics), as well as populations of adapted individuals of common species from the adjacent non-serpentine influenced, habitat generalist floras.

Hopper (2009) describes old, climatically buffered, infertile landscapes (OCBIL theory) that occur in southwestern Australia, South Africa's Greater Cape Region and Venezuela's Pantepui Highlands. These are land surfaces where rejuvenation through glaciation, volcanism, uplift and mountain building have been absent for tens to hundreds of millions of years and have been sufficiently weathered so that soils are nearly devoid of essential nutrients for plant growth, particularly phosphorus. Here again, unfavorable soil conditions lead to the development of grasslands, shrublands and woodlands while constraining development of forest vegetation. Many of these regions with either ultramafic geology or old infertile landscapes harbor some of the world's highest plant species richness, in part due to speciation and evolution of traits for persistence driven by soil infertility and toxicity, and in the case of OCBILs, though the retention of relic species and families from ancient lineages (i.e., paleo-endemics).

What these aforementioned environments have in common is that soil infertility (i.e., oligotrophic soils), and its resulting growth limitations and drought stress on plants, severely constrained the development of arboreal plant growth forms and instead favored herbaceous and lower statured woody plants that characterize grasslands, shrublands, savannas and woodlands. Furthermore, areas of high soil salinity, such as those found in endorheic drainage basins, support halophytic flora often in the form of succulent or scrub vegetation.

While not significant nurseries for the evolution of plant species as the environments mentioned above, excessively drained and highly mobile substrates such as sands on stabilized sand dunes, talus slopes, and pumice fields, as well as areas of shallow bedrock (e.g., limestone and dolomite grasslands of southeast United States) and salt spray influenced coastal fringes, similarly make tall tree and forest growth difficult and tend to support herbaceous, shrub, savanna, or low statured woodland communities.

Origins of Grasslands and Shrublands

While the early terrestrial biota of the earth following the evolution of large land plants (e.g., horsetails, ferns and gymnosperms) is often thought of as vast forests growing in a warm wet world, large areas of herbaceous and low statured woody vegetation may have existed as far back as the middle/late Triassic Period (230 Ma). At this time the vast continental interior of the supercontinent Pangea harbored the arid conditions, seasonality of rainfall, and resulting accumulation of dry biomass susceptible to wildfires that favored the evolution and expansion of herbaceous and low statured woody plants from among the ferns and gymnosperms (Bredenkamp et al., 2002). Fossil evidence also shows that fires were common during the earlier Permian and Carboniferous Periods (Falcon-Lang, 2000; Jasper et al., 2013) and may have affected the development of vegetation in similar ways.

Grasses and grasslands emerged only recently relative to other major plant lineages and biomes of the earth. The hemicyptophytic life form (i.e., herbaceous plants with perennating buds at or near the soil surface) that is so prevalent in contemporary grassland taxa evolved early in the monocotyledons in response to harsh environmental conditions. This important trait most likely originated in oxygen deprived aquatic habitats (Takhtajan, 1969), only later becoming advantageous to withstanding defoliating disturbances and drought. The common ancestor that gave rise to the Order Poales, which contains Poaceae (i.e., true grasses) as well as similar families such as Juncaceae, Cyperaceae and Restionaceae that also can form the major component species of grasslands, diverged in the middle Cretaceous Period more than 100 Ma (Janssen and Bremer, 2004). Early grasses evolved in forest environments under shade or in forest openings (Bredenkamp et al., 2002; Gibson, 2009). The early lineages of the two main clades that comprise the bulk of Poaceae emerged during the Eocene Epoch between 55 and 34 Ma, with fossil evidence pointing to an even earlier emergence of a component subfamily, Ehrhartoideae, in the late Cretaceous (Prasad et al., 2011).

The appearance of grasslands, extensive areas dominated by herbaceous angiosperms mostly in the family Poaceae and its related families, was largely associated with the spread of open habitats that formed when arid, or at least seasonally dry, conditions took shape over portions of continents. The first expansive grass-dominated ecosystems likely appeared in South America around the Eocene-Oligocene boundary 34 Ma (Coughenour, 1985; Jacobs et al., 1999). This expansion of grasslands continued through the Oligocene and by the Miocene Epoch (23–5 Ma), grasslands were globally widespread, occurring on all the large continents except for Antarctica (Stebbins, 1981; van der Hammen, 1983; Strömberg, 2002; Kamelin, 2017). It was during the mid-Miocene period that the major diversification of the grass family coincided with this widespread, worldwide development of grasslands (Kellogg, 2001).

Adaptation to drought appears to be the key development in grasses that allowed them to spread into these newly created open habitats that had been expanding during the Eocene and onward. Some of the most important of these traits, as summarized by Gibson (2009), include basal meristems, small stature, deciduous shoots, below ground nutrient reserves, and rapid transpiration and growth in response to irregular moisture availability. Ability to survive drought is often regarded as the main environmental

factor selecting for low stature in plants and the herbaceous habit is general. In grasses, this selection pressure has often come in combination with disturbances, such as animal grazing or trampling and fires, that defoliate and otherwise destroy above ground biomass of individual plants. The intercalary meristem, which allows growth from both the base of leaves and internodes of stems, is also an important trait that evolved in grasses, allowing them to respond to defoliation by wildfires or herbivory.

Although grasses existed for a long time before large mammalian grazing ungulates evolved, there is a strong conjunction between the emergence of a diverse array of large grazing mammals with hypsodont teeth and the widespread expansion of grass dominated ecosystems (Stebbins, 1981; Coughenour, 1985). Their emergence coincided so closely that it is widely regarded as an example of co-evolution, with the grazing by these animals reinforcing the spread and maintenance of grasses and grasslands.

Another important development within the evolutionary history of the grasses, as well as the spread of grasslands, is the evolution of C_4 photosynthesis. C_4 photosynthesis evolved independently and multiple times in several eudicot and monocot plant lineages in response to arid climate conditions, with a significant proportion of these C_4 lineages emerging from within a portion of the Poaceae family. C_4 photosynthesis is therefore considering one of the most overwhelming examples of convergent evolution among life on earth (Sage et al., 2011). It is a metabolic pathway that, through the process of concentrating CO_2 in bundle sheet cells, allows the plant species that possess it to maintain a high photosynthetic rate while stomata are nearly or entirely closed. This affords these plants considerable water conservation abilities, while allowing them to produce considerably higher biomass under high temperatures and arid conditions than they otherwise could. This ability was highly consequential for the expansion of grasslands during the late Miocene. Climate changes during this time brought about drier conditions (including monsoonal summer rainfall and abundant lightning), throughout large portions of the tropical and sub-tropical regions of the world (Keeley and Rundel, 2005; Bond, 2015). The C_4 grasses that existed in these regions were well suited to take advantage of these climate conditions, and they produced high amounts of biomass during the wetter portions of the year that were then easily ignited during the drier periods. This resulted in the rapid, wildfire facilitated spread of grassland and savanna environments throughout the tropical and subtropical regions of the world during the late Miocene (Keeley and Rundel, 2005), because this process not only reinforces the maintenance of large grassland and savanna environments, but also allows their expansion into areas that would otherwise support forests (Keeley and Rundel, 2005; Hoffman et al., 2012; Bond, 2015; van Nes et al., 2018).

The appearance of widespread shrubland biomes on earth is potentially far more difficult to ascertain within the geologic record than is the arrival of grasslands. This is because of the considerable variability in plant growth forms within plant families and their lineages, particularly in the angiosperms, and because the component low statured woody taxa are derived from a large number of angiosperm lineages that also include tall woody taxa. Therefore, it is difficult to determine the presence of widespread shrublands from limited fossil evidence such as pollen or small fossilized remains, as compared to the relative ease of identifying the pollen and fossil signatures of just a few characteristics plant lineages (i.e., Poaceae) that indicate the first arrival and widespread presence of grasslands.

However, many of the same extreme environmental pressures that drove the development of the first grasslands (i.e., arid or semi-arid climate, fires, grazing and trampling by large animals) very likely resulted in the spread of shrubland ecosystems, and they could conceivably have appeared much earlier in the earth's history than did grasslands. Additionally, the advantage that small-statured woody plants have over tall woody plants to persist on shallow or nutrient poor soils would have made possible the existence of shrublands over these edaphic controlled areas. Possessing a low stature affords a considerable advantage in meeting evapotranspiration evaporative demand when exposed to periodic or persistent drought as compared to the high water demand involved with maintaining a tall structure. Therefore, it is likely that low statured woody plants formed shrublands and low statured woodlands in arid and semi-arid environments after species from the regional species pool evolved the ability to persist and spread through those environments.

Furthermore, most angiosperms possess the ability to re-sprout from above ground or below ground parts following exposure to environmental stresses that damage or destroy above ground biomass, whereas gymnosperms (conifers) rarely have this trait. In most angiosperms, dormant, protected, or adventitious buds are grown during a plant's development or are later differentiated from superficial tissue that allow sprouting from stems through epicormic buds. Re-sprouting of the whole above ground plant body can also occur from re-sprouting stumps or below ground lignotubers. New meristem growth, initiated by low auxin and high cytokine levels (i.e., death of the terminal end of a stem), readily commences from these pre-existing or newly created buds, enabling the surviving part of the plant to recover from damage or loss to above ground biomass. While it is unclear whether these re-sprouting traits evolved in response to drought or disturbance (Hopper, 2009), they are certainly strategies of resistance against loss of biomass and are critical traits that allow woody angiosperms to survive defoliation from herbivory, wildfire, and other destructive above ground disturbances (Zeppel et al., 2014). Woody plants that possess strong re-sprouting abilities can proliferate in areas with regular disturbances. Plant species with strong re-sprouting abilities and other persistence strategies coupled with a low stature, can also reinforce disturbance regimes such as fire, thereby maintaining areas of shrubland and low statured woodland. Exemplars of this can be found in the evergreen sclerophyll shrublands and woodlands that predominate in the Mediterranean type climates of the world (California, the Mediterranean Basin, central Chile, the Cape Region of South Africa, and southern and southwest Australia). While these shrubland and woodland communities are profoundly shaped by this distinct Mediterranean type climate regime, which appeared in its present day locations during the Miocene (Rundel et al., 2016), there is a great deal of evidence that evergreen sclerophyll vegetation existed much earlier than the onset of Mediterranean type climates and under different climate conditions, being particularly widespread across North America and Southern Eurasia (Madrean-Tethyan regions) during the Eocene Period (Axelrod, 1975; Valiente-Banuet et al., 1998; Verdú et al., 2003). Many modern Mediterranean plant clades in California, the Mediterranean Basin, and central Chile diversified in the Miocene following the onset of Mediterranean

type climates (Rundel et al., 2016, 2018; Vargas et al., 2018), whereas the South African Cape Region and southwest Australia possess many older lineages (Hopper and Gioia, 2004; Carpenter et al., 2015).

During the Cretaceous Period, evergreen sclerophyll shrublands existed on oligotrophic soils and other challenging soil conditions that some authors have termed “edaphic ghettos” (very shallow soils, heavy clays, etc.). These soil conditions limited tree growth at a time when warm humid climates mostly supported forests worldwide (Rundel et al., 2016). However, molecular-dated phylogenies and fossils of the currently extant fire adapted family Proteaceae, which contains a great deal of shrub and low statured tree species, show the appearance of strongly fire adapted traits in the late Cretaceous (Lamont and He, 2012; Carpenter et al., 2015). This evidence of strongly fire adapted species suggests that fires, and therefore fire sculpted shrublands and woodlands were somewhat common and not only restricted to edaphic controlled areas during this time period, at least in parts southern Africa and Australia. Fires were common over portions of the globe during the Cretaceous Period (Bond, 2015) and therefore it is probable that expansive shrublands were also prevalent.

Shrublands may have lost ground to forest in the still warm and humid climate of the Eocene when fire activity diminished considerably, becoming restricted to resource poor or shallow substrates, dry interiors of continents, and areas of frequent river scour. But, there was a marked increase in fire activity in the mid to late Miocene (Bond, 2015) and at the same time there was an ongoing cooling and drying climate, which had been occurring throughout the Tertiary Period. These conditions once again promoted the formation or expansion of widespread shrublands, and by this time grasslands as well. These global trends in climate and fire activity have continued to the present day.

The origins of present day grasslands and shrublands are likely different wherever they currently exist across the globe. However, most will owe their origin to the widespread occurrence of drought and fire. As a general pattern, many modern day grassland and shrubland biomes had their beginnings in the Tertiary Period as an increasingly cooler and arid climate took shape over large portions of the planet in the Paleogene and Neogene Periods and continuing to this day, and expanded significantly as fires became much more prevalent across the globe roughly 10 Ma (Bond, 2015). The position of the continents and distribution of arid and semi-arid climates, and therefore early analogs to present day grasslands and shrublands, began to settle in their current locations in the late Miocene and Pliocene. However, most present day grassland and shrubland biomes, particularly those in the higher (and therefore less climatically buffered) latitudes, developed during the more recent Quaternary Period.

Important Grasslands, Shrublands and Savannas Not Covered in This Section

The articles in this Grasslands and Shrublands section of the *Encyclopedia of the World's Biomes* largely cover the array of grassland, shrubland and savanna ecosystems that occur across the northern hemisphere. However, some types are missing from the southern hemisphere. A few important grassland, shrubland and savanna biomes from South America and Australia are not included and, except for the Mediterranean Basin region of northern Africa and the temperate grasslands of southern Africa, the vast diversity of grasslands, shrublands, and savannas of Africa are largely uncovered. I describe those missing types briefly in the following section.

Africa contains the most extensive area of tropical savannas of any continent on earth and otherwise possesses a wide array of dry woodlands, bushlands, temperate and montane grasslands, and Mediterranean scrublands. It is therefore regrettable that so few chapters on Africa's grasslands, shrublands and savannas are presented in this section.

Tropical savannas are very widespread across Africa, covering roughly 50% of its land area (Shorrocks and Bates, 2015). The vegetation composition therefore varies considerably between the different regions where they occur. The Sahelian and Sudanian savannas, characterized (often sparsely so) by trees in the *Acacia* genus to the north and *Combretum* and *Terminalia* shrub and tree species to the south, stretch across sub-Saharan Africa south of the Sahara desert and north of the Equatorial forest regions. In the east, the tropical savanna biome wraps around the Congo and Lake Victoria Basins going south through East Africa in the form of the *Acacia* and *Commiphora* tree and shrub savannas and bushlands that spread across the Horn of Africa countries and southward through Kenya and Tanzania. This region includes the Masai xeric grasslands in Kenya and the iconic Serengeti grasslands in Tanzania. South of the Congo rainforests, throughout much of southern Africa north of the deserts and temperate region, are the Miombo and Mopane savannas and woodlands, two extensive vegetation types broadly defined by the dominance of miombo (*Brachystegia boehmii*) and mopane (*Colophosphermum mopane*) trees respectively. Shorrocks and Bates (2015) provide a thorough treatment of the tropical savanna biome of Africa, while Scholes and Walker (1993), and White (1983) also offer useful overviews.

There exists several good references for the vegetation of southern Africa that include descriptions of the region's grasslands, savannas and shrublands not already covered in this section, including Cowling et al. (1997), Born et al. (2007), Mucina and Rutherford (2006), and Bergh et al. (2014). Dean and Milton (1999) provide an in-depth treatment of the extensive Karoo shrubland biome of southern Africa. Cowling and Pierce (1999) give a detailed description of a component of the Karoo biome known as Namaqualand, or Succulent Karoo. In addition, Cowling and others (Cowling, 1992; Cowling and Richardson, 1995; Rebelo et al., 2006) provide several thorough accounts of the South African Cape Mediterranean Scrub, collectively the Fynbos and renosterveld, the only one of the five Mediterranean climate type shrubland biomes not covered in this section. Another unique shrubland of the South African Cape, Albany thickets, are described by Cowling et al. (2005) and Hoare et al. (2006). Jacobs and Schloeder (2002), Williams et al. (2004), and Kidane et al. (2012) are all suitable references for understanding the montane grasslands of Ethiopia. An introduction to the grasslands and dry thickets and woodland of Madagascar can be found in Vorontsova et al. (2016), Gautier and Goodman (2003), and Koechlin (1972).

There are many articles in this section from South America that cover a great deal of the continent's grassland, shrubland, and savanna vegetation cover. However, due to its great topographical diversity and latitudinal span, several important grasslands and shrublands were missed. [Veblen et al. \(2007\)](#) give overviews of the major regional environments of the continent. Within this volume [Rundel et al. \(2007\)](#) and [Paruelo et al. \(2007\)](#) cover the Monte region and the Patagonian steppe respectively. [Gaitán et al. \(2020\)](#) also describe the vegetation of the Monte and Patagonian steppe in the Deserts section of this Encyclopedia. [Young et al. \(2007\)](#) describe the alpine and montane shrubland, sub-shrub, and grassland communities of the puna, páramo and southern Andean steppe found in the northern and central Andes. Further information on these ecosystems can be found in [Villagrán et al. \(1981\)](#), [Carilla et al. \(2018\)](#), and [Lambrinos et al. \(2006\)](#). In the central lowlands of Venezuela and Colombia lies a significant tropical grassland and savanna biome known as the Llanos that is described in [Blydenstein \(1967\)](#), [Medina and Silva \(1990\)](#), [Ramia \(1967, 1974\)](#), [Behling and Hooghiemstra \(1999\)](#), and [Berroterán et al. \(1998\)](#). [Larrea-Alcázar et al. \(2011\)](#), [Langstroth \(2011\)](#), and [Haase and Beck \(1989\)](#) give focused treatments of the Beni savanna of northeast Bolivia.

In Australia, not covered in this section of the Encyclopedia are the semi-arid shrublands and spinifex grasslands that cover vast portions of the interior of the continent and its central west coast south of the tropical regions. The book by [Keith \(2017\)](#) provides an overview of these vegetation formations, as well as a review of all of Australia's vegetation. It also presents a comprehensive account of all the heathlands of Australia ([Lamont and Keith, 2017](#)) that includes the heath communities not treated in the articles in this section. In addition, [Keith \(2017\)](#) covers the montane grasslands of the Australian Alps. Also from this part of the globe, [Mark and others \(Mark, 1993; Mark et al., 2013\)](#) describe the prominent montane and temperate grasslands of New Zealand's South Island.

Introduction to the Grasslands and Shrublands Chapters

The Grasslands and Shrublands section is organized by the continents and as best as possible covers the major grassland, shrubland, savanna and steppe ecosystems from all the continents of the globe, including Oceania and excluding Antarctica. Tropical, Temperate, and Mediterranean Grasslands of the World ([Faber-Langendoen, 2020](#)), which includes descriptions of savannas and most shrubland ecosystems, starts off the section by providing a global overview through the lens of The International Vegetation Classification.

For North America, [Comer and Hoagland \(2020\)](#) describe the temperate grasslands of the Great Plains and Chihuahuan Desert that stretch from central Canada to northern Mexico. The grasslands and savannas of the southeastern United States are reported on by [Noss \(2020\)](#). [Parker \(2020\)](#), [Tyler and Stahlheber \(2020\)](#), and [Dunwiddie and Alverson \(2020\)](#) provide overviews of the chaparral of California, the oak savannas and grasslands of California, and the prairies, savannas, and oak woodlands of the Pacific Northwest, respectively. In the North American western interior, [Shinneman \(2020\)](#) gives an account of the North American sagebrush steppe and shrubland, while [Muldavin and Triepke \(2020\)](#) cover the Pinyon-Juniper Woodlands. Lastly, [Valiente-Banuet and Verdú \(2020\)](#) discuss the Mexical shrubland of central Mexico with a special focus its ancient relationship with the modern evergreen sclerophyllous vegetation of several Mediterranean climate-type regions of the world.

Moving to South America, [Silva and Lacher \(2020a,b\)](#) present two chapters, one on the savannas of the Cerrado and the other on the Caatinga woodlands, which together cover a great deal of the eastern half of Brazil. [Fernández et al. \(2020\)](#) summarize the grasslands and open savannas of the Dry Chaco of northern Argentina, southern Bolivia and western Paraguay, while [Oyarzabal et al. \(2020\)](#) cover the temperate subhumid grasslands that surround the Río de la Plata estuary in central-eastern Argentina, Uruguay and southern Brazil. [Meserve et al. \(2020\)](#) describe the Mediterranean-type shrubland of central Chile, known as the Chilean matorral, along with the neighboring thorn scrub communities to the north.

[Vargas \(2020\)](#) discusses the Mediterranean floristic region, which covers the Mediterranean Basin (southern Europe, northern Africa, and western parts of the Middle East and Asia Minor), touching on explanations for its exceptionally high diversity of plants.

Dr. Jürgen Dengler and Dr. Peter Török very graciously organized 13 articles for this section from multiple author teams from across Europe and Asia on the various grasslands and shrublands of the Palaearctic Realm (encompassing the temperate regions of Europe and Asia as well as North Africa) on behalf of the European Dry Grasslands Group (<https://edgg.org/>). They present a comprehensive and unifying overview of the Palaearctic grasslands and shrublands ([Dengler et al., 2020b](#)) and introduce the following chapters from Palaearctic Realm: Grasslands and shrublands of the Mediterranean Region ([Guarino et al., 2020](#)), Heathlands of temperate and boreal Europe ([Loidi et al., 2020b](#)), Shrublands of temperate Europe ([Loidi et al., 2020a](#)), Grasslands of Western Europe ([Boch et al., 2020](#)), Grasslands of Northern Europe and the Baltic countries ([Dengler et al., 2020a](#)), Grasslands of Eastern Europe ([Török et al., 2020](#)), Grasslands and shrublands of the Middle East and the Caucasus ([Ambarli et al., 2020](#)), Grasslands and shrublands of Russia ([Tishkov et al., 2020](#)), Grasslands and shrublands of Kazakhstan and Middle Asia ([Wagner et al., 2020](#)), Grasslands and Shrublands of Mongolia ([Pfeiffer et al., 2020](#)), Grasslands of China ([Li et al., 2020](#)), and Grasslands and shrublands of Japan ([Ushimaru et al., 2020](#)).

For the subtropical and tropic regions of Asia, [Wikramanayake et al. \(2020\)](#) present the chapter on grasslands and savannas of South Asia. [Brown and Bezuidenhout \(2020\)](#) provide a treatment of the temperate grasslands of southern Africa.

[Woinarski et al. \(2020\)](#) provide an overview of the tropical savannas of northern Australia while [Rehwinkel \(2020\)](#) outlines the South-eastern Australian temperate grasslands and grassy woodlands. The Mediterranean climate-type shrubland ecosystems of Australia are treated in two separate chapters: Sclerophyll shrublands of southwestern Australia ([Lamont, 2020](#)) and Mallee and maalok ecosystems of southern Australia ([Keith et al., 2020](#)). Representing Polynesia and Micronesia, several teams of United States

Fish and Wildlife Service scientists describe Hawai'i's dry, wet and mesic grasslands and shrublands (Pe'a et al., 2020; Nelson et al., 2020; Ball et al., 2020, respectively), as well as the savannas of the Mariana Islands Archipelago (Frager et al., 2020).

As stated above, the articles in this Grasslands and Shrublands section of the *Encyclopedia of the World's Biomes* are by no means a comprehensive accounting of all the grassland, shrubland, savanna and steppe ecosystems that currently exist on earth. The diversity of these habitats is as vast and variable as their distributions across the planet is broad. However, these articles provide a starting point for individual students and researchers to discover and build their knowledge of these important ecosystems, as well as the context and framework for the continued exploration, inquiry and scientific research of the grassland and shrubland biomes of the globe.

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Tropical, Temperate, and Mediterranean Grasslands of the World

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Abstract

Grasslands of the world span the tropics to temperate regions. We first define grasslands in general, then we use the International Vegetation Classification (IVC) to characterize the vegetation, climate, soils, disturbances and geographic range of the four major grassland biomes (IVC formations): Tropical Lowland Grassland, Savanna, and Shrubland, Tropical Montane Grassland and Shrubland, Mediterranean Scrub and Grassland, and Temperate Grassland and Shrubland. We recognize 54 biogeographically based continental grassland biomes (IVC divisions) and summarize their spatial distribution by WWF ecoregions. We highlight various patterns of grassland productivity, ecosystem services and climate change. In conclusion, we briefly describe a number of tools that can assist the conservation of these critically imperiled biomes.

Introduction

Natural grasslands may, at a casual glance, seem somewhat monotonous and simple, little different than an overgrown pasture, or easily replicated by planting. Yet a closer look shows a diversity of species that reach up to the sun and quiver in the wind, flatten with rain, disappear in a fire, slump through winter, and reemerge fresh in the spring. And unlike almost any other system, grasslands contain large animals that tower over the system they are in, introducing plant-animal dynamics rarely found in other biomes. Indeed, in what other biome would Aldo Leopold's quote be so applicable, as he wondered "what a thousand acres of silphiums looked like when they tickled the bellies of the buffalo."

Here we introduce in broad strokes the major grassland (including savanna) biomes that comprise a large portion of the globe. We focus on four major global grassland biomes: Tropical Lowland Grassland, Savanna, and Shrubland, Tropical Montane Grassland and Shrubland, Mediterranean Scrub and Grassland, and Temperate Grassland and Shrubland. We then turn to look at the diversity within these biomes across and within continents. We conclude by briefly describing some important aspects of grasslands, including their productivity, ecosystem services, climate change and conservation.

Defining Grasslands—An Ecological Vegetation Perspective

Following [Dixon et al. \(2014\)](#), we define natural or semi-natural grassland by the following typical characteristics:

1. a non-wetland, natural formation,
2. vascular vegetation has at least 10% cover,
3. graminoids have at least 25% cover (but if <25% cover, graminoids exceed that of other herbaceous and shrub cover),
4. broad-leaved herbs (forbs) may have variable levels of cover and dominance,
5. shrubs have <25% canopy cover,

6. and trees:

- (i) in temperate zones, typically have <10% canopy cover, are <5 m tall and single-layered,
- (ii) in tropical regions, typically have <40% canopy cover, are <8 m tall, and single layered.

Several aspects of this definition deserve additional comment (see also [Dixon et al., 2014](#)). First, the term “grassland” often has a broad meaning when defining a comprehensive set of ecological vegetation types (such as grassland versus forest, desert, tundra, or wetland). In this context, the grassland biome concept emphasizes dominance by grasses or grass-like plants (graminoids) and the lack of trees, but also includes other narrow-leaved grass-like herbs (i.e., non-woody graminoids) and even forbs (broad-leaf herbs) ([Veldman et al., 2015](#)). In his comprehensive review of major grasslands regions of the world, [Coupland \(1979\)](#) defined “grassland” as referring to “ecosystems in which the dominant vegetation is comprised of herbaceous species.”

From a biome perspective, natural grasslands are typically separated from other related types, including cultural grasslands, wetlands and woodlands. For example, the *Ecosystems of the World* project provided separate descriptions for natural grasslands ([Coupland, 1992](#)) and managed grasslands ([Breyer, 1987–1990](#)). Grassland often form an ecotone with woodlands. Our thresholds for distinguishing grasslands from woodlands are adapted to tropical and temperate conditions (see [Dixon et al., 2014: Table 1](#) for a comparison between American and African definitions). We reserve the term savanna for tropical grasslands, with or without a scattered woody layer, but not sufficiently dense or tall to qualify as woodland. Grasslands grade into wetlands which are characterized by wetland growth forms (including aquatic plants, forbs, and mosses) that comprise various open wetland biomes, such as ponds, bogs, fens, salt and freshwater marshes.

We limit our review here to Tropical, Temperate and Mediterranean Grasslands, the most common and dominant of grassland types. Grassland-dominated stands can also occur in deserts and in alpine or tundra biomes, and they are described elsewhere.

Types of Grasslands

We present four major biome types, following our grassland types defined in the International Vegetation Classification:

- Tropical Lowland Grassland, Savanna, and Shrubland
- Tropical Montane Grassland and Shrubland
- Mediterranean Scrub and Grassland
- Temperate Grassland and Shrubland

We include shrublands in the name of the types, because even though they are typically a relatively minor component at higher hierarchical (biome-scale) levels, they may form distinct plant community types at lower levels.

Tropical Lowland Grassland, Savanna, and Shrubland

Summary: Tropical Lowland Grassland, Savanna & Shrubland is characterized by shrubs and herbs with mesomorphic growth forms (including *broad-leaved*, *small-leaved*, *sclerophyllous*, and *palm shrubs*, and *forb* and *graminoid herbs*). Annual precipitation is seasonal to monsoonal and typically varies from 50 to 150 cm. In the driest climates, the herbaceous cover is annual and/or sparse. Vegetation structure varies from open grasslands, with very few woody growth forms to closed-canopy shrubland. Spatially patchy vegetation structure is typical for this type, especially the savannas with clumped or irregular horizontal canopy spacing and variable height. Neotropical and paleotropical savannas are included here as well as lowland shrublands or scrub, such as the Neotropical Cerrado. Savannas represent the vast majority of the area covered by this type and they are characterized by a layer of perennial herbaceous plants, mainly C₄ grasses and sedges, and C₃ forbs, with varying degrees of shrubs, and with low trees (<8 m) ranging up to 40% cover. This type is found widely throughout lowland and montane habitats of the tropical latitudes, from the equator to about 23°N and S ([Whittaker, 1975](#); [Woodward, 2008](#); [Faber-Langendoen et al., 2016](#)).

Climate: This formation occurs typically within an annual precipitation range of 100–150 cm, with lower and upper extremes around 40 and 200 cm, respectively. The rainfall is seasonal, with either a short (1–3 months) dry season or a long one (5–7 months). Mean annual temperature is about 22–25 °C but can reach 6 °C in winter at the edges of the tropical distribution range (e.g., southern limit of Cerrado in Brazil), with very occasional frosts. Even though a close correlation exists between tropical savannas and the Tropical Wet and Dry Climate (Aw in the Koeppen climate classification system), climate does not seem to be the main reason most savannas are found where they are; rather, as [Woodward \(2008\)](#) notes, “repeated burning, low-nutrient soils, iron-rich hardpans close to the surface, and the impacts of large grazing and browsing mammals are also factors in the presence and maintenance of many of the world’s tropical grasslands.”

Soil/substrate/hydrology: Tropical savanna usually develops on nutrient-deficient, acidic soils (Oxisols, Ultisols) with aluminum toxicity and pronounced alternation of wet and dry conditions. Soils in humid tropical climates are exposed to high rates of leaching, and the amount of leaching is related to the age of the land surface. Thus, in Brazil and western Africa, the savannas lie on very ancient surfaces that for millions of years have been affected by high temperatures and relatively high amounts of rainfall, whereas over much of eastern and southern Africa, the savannas lie on younger, less leached surfaces, and soils are less acidic (pH = 6.2) and

Table 1 Tropical, Mediterranean and Temperate Grassland Biomes, as classified using the International Vegetation Classification (IVC) at the formation and division levels. See [Faber-Langendoen et al. \(2019\)](#) for more details on the IVC and its relation to biome concepts.

<i>IVC formation (Global Biome)</i>	<i>IVC division (Continental Biome)</i>
Tropical Lowland Grassland, Savanna and Shrubland (2.A.1) (17 Continental Biomes)	<i>Neotropical</i> • 2.A.1.Ea. Caribbean-Mesoamerican Lowland Grassland, Savanna and Shrubland (D094) • 2.A.1.Eb. Amazonian Savanna and Shrubland (D124) • 2.A.1.Ed. Brazilian-Parana Lowland Grassland, Savanna and Shrubland (D126) • 2.A.1.Er. Colombian-Venezuelan Lowland Grassland, Savanna and Shrubland (D249) • 2.A.1.Es. Guianan Lowland and Upland Grassland, Savanna and Shrubland (D250) <i>African</i> • 2.A.1.Ff. West-Central African Mesic Woodland and Savanna (D128) • 2.A.1.Fg. Eastern and Southern African Dry Savanna and Woodland (D129) • 2.A.1.Fh. Mopane Savanna (D130) • 2.A.1.Fi. Sudano-Sahelian Dry Savanna (D131) • 2.A.1.Fn. Miombo and Associated Broadleaf Savanna (D164) • 2.A.1.Fo. Eastern African Moist Woodland and Savanna (D165) • 2.A.1.Fp. Malagasy Dry Forest and Scrubland (D166) • 2.A.1.Fq. Malagasy Subhumid Woodland & Savanna (D167) <i>Indo-Malayan</i> • 2.A.1.Ij. Indo-Malayan Mesic Savanna and Grassland (D132) <i>Australian</i> • 2.A.1.Lk. Australian Tropical Savanna (D133) <i>Oceania</i> • 2.A.1.Ol. Polynesian Lowland Shrubland, Grassland and Savanna (D074) • 2.A.1.Om. Eastern Melanesian Lowland Shrubland, Grassland and Savanna (D075)
Tropical Montane Grassland and Shrubland (2.A.2) (10 Continental Biomes)	<i>Neotropical</i> • 2.A.2.Ea. Tropical Andean Grassland and Shrubland (D134) • 2.A.2.Eb. Caribbean-Mesoamerican Montane and High Montane Grassland & Shrubland (D135) • 2.A.2.Ek. Guianan Montane Grassland and Shrubland (D252) • 2.A.2.El. Brazilian-Parana Montane Grassland and Shrubland (D253) <i>African</i> • 2.A.2.Fe. African Montane Grassland and Shrubland (D138) • 2.A.2.Fj. Malagasy Montane Thicket and Sclerophyllous Shrubland (D168) <i>Indo-Malayan</i> • 2.A.2.If. Indo-Malayan Montane Meadow (D139) • 2.A.2.Lg. New Guinea Montane Meadow (D140) <i>Oceania</i> • 2.A.2.Oh. Polynesian Montane Shrubland, Grassland and Savanna (D076) • 2.A.2.Oi. Eastern Melanesian Montane Shrubland, Grassland and Savanna (D077)
Mediterranean Scrub and Grassland (2.B.1) (10 Continental Biomes)	<i>Neotropical</i> • Chilean Mediterranean Scrub, Grassland and Forb Meadow • Chaco-Espinal Scrub and Grassland (D274) <i>African</i> • South African Cape Mediterranean Scrub (D107) <i>Australian</i> • Australian Mediterranean Scrub (D108) <i>Californian</i> • Californian Scrub and Grassland (D327) <i>Mediterranean Europe</i> • Mediterranean Basin Scrub (D103) • Mediterranean Basin Montane Grassland and Scrub (D105) • Mediterranean Basin Dry Grassland (D104) • Northern African Mediterranean Scrub (D302) • Mediterranean Alpine Grassland and Scrub (D304)

Table 1 Tropical, Mediterranean and Temperate Grassland Biomes, as classified using the International Vegetation Classification (IVC) at the formation and division levels. See Faber-Langendoen et al. (2019) for more details on the IVC and its relation to biome concepts.—cont'd

IVC formation (Global Biome)	IVC division (Continental Biome)
Temperate Grassland and Shrubland (14 Continental Biomes)	<i>Neotropical</i> • 2.B.2.Ek. Pampean Grassland and Shrubland (D141) • 2.B.2.En. Madrean Grassland and Shrubland (D275) • 2.B.2.Eo. Patagonian Grassland and Shrubland (D144) <i>African</i> • 2.B.2.Fm. Southern African Montane Grassland (D143) <i>Australian</i> • 2.B.2.Li. Australian Grassland and Shrubland (D112) • 2.B.2.Lj. New Zealand Grassland and Shrubland (D113) <i>North American</i> • 2.B.2.Na. Western North American Grassland and Shrubland (D022) • 2.B.2.Nb. Central North American Grassland and Shrubland (D023) • 2.B.2.Nc. Eastern North American Grassland and Shrubland (D024) • 2.B.2.Nd. Western North American Interior Chaparral (D061) • 2.B.2.Ne. Southeastern North American Grassland and Shrubland (D102) <i>Palaearctic</i> • 2.B.2.Pf. European Grassland and Heath (D109) • 2.B.2.Pg. Western Eurasian Grassland and Shrubland (D110) • 2.B.2.Ph. Eastern Eurasian Grassland and Shrubland (D111)

Modified from the Dixon, A., Faber-Langendoen, D., Josse, C., Morrison, J. and Loucks, C.J. (2014). Distribution mapping of world grassland types. *Journal of Biogeography* 41, 2003–2019. publication by John Wiley and Sons.

somewhat more fertile. Savannas that flood seasonally are common in the tropics, especially in South America (the Llanos, Beni, and Pantanal). There they occur in a complex spatial mosaic of upland and seasonally flooded types, with waterlogged soils grading into drained soils within very short distances. (Woodward, 2008).

Natural disturbances: Fires play a critical role in tropical grasslands and, whereas drought may prevent tree establishment in part of the savanna range, fires may override climatic conditions favorable to tropical woodlands and forests in other parts of the range (Bond et al., 2005). Lightning is the most common source of natural fires, but humans have long played a role in increasing the fire frequency throughout the tropics.

Animals: The role of large animals in savanna structure and function can be quite substantial. For example, in eastern and southern Africa, herds of large mammals are conspicuous, including zebras (*Equus* spp.), wildebeest (*Connochaetes taurinus*), antelope (*Hippotragus equines*), elephant (*Loxodonta africanus*), rhinoceroses (*Diceros bicornis* and *Ceratotherium* spp.), and giraffes (*Giraffa* spp.). But elsewhere, the most characteristic animals may be small mammals, including rodents, rabbits, and hares. Though not typically seen, termites (*Macrotermes* spp.), play a substantial role in savanna soil processes, and are conspicuous through their above ground mounds or termitaria (Woodward, 2008).

Human disturbances: Humans have had a long history in shaping tropical savannas. In tropical southeast Asia and India, savannas are most likely derived from human activities such as logging, burning, and the grazing of livestock, any or all of which altered tropical dry (or deciduous) forests that once grew in the area (Woodward, 2008). Caribbean pine savannas have a more complicated history, with stands being derived from both natural and human processes.

Geographic range: This formation type, or biome, is found in northern South America, western and southwestern Amazon Basin, Guiana Shield, Brazilian Shield, Western Africa (Guinea-Congolia/Sudania regional transition zone), sub-Sahel (Sudanian regional center of endemism), the Central African Plateau (Guinea-Congolia/Zambezia regional transition zone and the Zambezan regional center), and Eastern Africa (Somali-Masai regional center of endemism), northern Australia and Indomalaysia. It is typically located poleward of the Tropical Rainforest and Tropical Dry Forest biomes and form a transition between those forests and the deserts of the subtropics. The boundary between forest and savanna is often abrupt.

Tropical Montane Grassland and Shrubland

Summary: Tropical Montane Grassland & Shrubland is dominated by shrubs and herbs with mesomorphic growth forms, predominantly tussock grasses, large rosette plants, shrubs with evergreen coriaceous and sclerophyllous-*ericoid* leaves, and cushion plants. Vegetation structure varies from grasslands, with few short woody growth forms, to a closed canopy of shrubs usually not taller than 1–2 m high. Spatially patchy vegetation structure is typical due to both substrate heterogeneity and human influence characterized by periodic burning and grazing. The majority of the area covered by this vegetation corresponds to types that occur on tropical mountains within or above the limit of continuous, closed-canopy forest or forestline and below the sub-nival elevations, from

3000 to 4500 m (i.e., *páramo* and *puna*). Annual precipitation varies with the site and aspect of the location, from 50 to 300 cm, and seasonality is related to the rainfall rather than to temperature. The main environmental difference between this formation and its temperate counterpart is the diurnal fluctuation of temperature, which can be of 20 °C or more in tropical high mountains (e.g., Andes, Africa), with no growth limiting season. Shrub and herbaceous vegetation of smaller tropical ranges (e.g., Central America, Southeast Asia and New Guinea) and on the summits of mountains of the Guyana Shield and the Brazilian *planaltos* (plateaus) are included here because they occur above the forest line (about 1600 m in the latter). True cryomorphic vegetation, super-*páramo* and higher elevation *puna*, are treated in the tropical alpine biome. They grow above 4300 m elevation up to the permanent snowline, with mean annual temperatures < 3 °C, and soils have cryomorphic features (such as cryoturbation). Physiognomic distinctions are mostly based on the ground, which is continuous here as compared to the low, semi-open coverage of the tropical alpine biome.

Climate: The majority of the area covered by this vegetation corresponds to types that occur on tropical mountains near or above the limit of continuous, closed-canopy forest or forestline and below the sub-nival elevations, from 3000 to 4500 m (i.e., *páramo* and *puna*). The elevational range varies depending on the location, but it is the correlation between elevation and a decrease in temperature that, in natural conditions, generates the replacement of forested vegetation with grasslands and shrublands. There are other factors, such as the effect of recent glaciation periods, and anthropogenic disturbance. The variability in elevation range is associated with greater variation in climate among locations, but in general, the mean annual temperature for this type is between 3° and 12 °C, with lower locations reaching a maximum of 18 °C average annual temperature. The greatest fluctuation in temperature occur daily rather than seasonally. Due to the mountain setting, precipitation is highly variable as well, both in the annual amount and the distribution, with some locales having a marked dry season and others more humid throughout the year.

Soil/substrate/hydrology: Given the volcanic origin of several tropical mountains, they have volcanic ash soils, with very high organic content and a high water-holding capacity. Other uplifts have formed metamorphic, sandstone or limestone ranges, with soils varying from shallow to deep, highly humic and forming clayish peat in locations with permanently high moisture.

Geographic range: Tropical Montane Grassland & Shrubland occurs in the tropical mountain regions of Central and South America, Africa, Malaysia, including New Guinea, Hawaii, lower ranges in the Caribbean, and Brazil.

Mediterranean Scrub and Grassland

Summary: Mediterranean Scrub and Grassland includes sclerophyllous scrub and herbaceous vegetation that develops in (moderately dry, warm-temperate, maritime climates with little or no summer rain). It occurs in the Mediterranean Basin, southwestern California in the United States, west-central Chile, the western Cape Province of South Africa, and southwestern and southern Australia. Sclerophyll-leaved growth forms prevail, but facultatively drought-deciduous “soft chaparral” forms may also occur. Mixed annual and perennial grasslands and non-grass “forblands” may also occur, with only scattered scrubby trees and shrub. Shrub growth forms range from low, open subshrubs (< 1 m) to arborescent (2–5 m tall) shrubs with a closed canopy, in response to moisture, fire and other factors. Dominant plants are affected by frequent fires, except for in Chile. Sclerophyll woodlands and forest are excluded from this classification of Mediterranean Scrub and Grassland. Grasslands are a mix of annual and perennial growth forms. (Whittaker, 1975; Faber-Langendoen et al., 2016).

Physiognomy and structure: There is a complex variation of growth forms, depending on the interactions of rainfall, soil texture, and type and intensity of natural processes such as fire, browsing/grazing, and bioturbation. Broad-leaved evergreen, sclerophyllous shrubs dominate the vegetation in areas with higher and more predictable winter rainfall, while facultatively deciduous shrubs occur in areas that are drier and rainfall is less predictable. Perennial herbaceous vegetation such as bunchgrasses occur in areas with relatively high precipitation. Perennial geophytes (bulbs, corms, etc.) are especially common in South Africa. Above-ground portions of perennial grasses dry and wither, or annuals set seed and die by mid-spring to early summer. Small numbers of summer annuals also occur, which take advantage of lingering deep soil moisture by having evolved long taproots. The vegetation tends to produce the highest biomass in the cool rainy winter and becomes dormant in the summer drought.

Climate: The Mediterranean climate is characterized by dry summers and mild, humid, sometimes rainy winters. Annual precipitation averages 25–100 cm. Freezing temperatures are relatively rare. Wherever mountains and predominant wind directions cause orographic effects (for example the rainfall increases on the windward side), and annual precipitation at the higher elevations may be sufficient to support a change from scrub to woodland or forest. With increasing latitude, rainfall totals and length of the rainy season also increase, causing a comparable shift to woodland or forest (Kuennecke, 2008). Many Mediterranean climate areas have been “invaded” by exotic annual grasses and other species that can modify natural disturbance patterns such as fire (Faber-Langendoen et al., 2016).

Geographic range: This formation or biome occurs in the Mediterranean Basin, and in the Mediterranean climate regions of southwestern California in the United States, west-central Chile, the western Cape Province of South Africa, and southwestern and southern Australia, at latitudes between 31° and 46°N in the Northern Hemisphere and between 28° and 42°S in the Southern Hemisphere. These areas form on the western or southern margins of continents where warm-season high pressure tends to settle offshore driving all precipitation to the north or south of the adjacent shore areas. Each region of Mediterranean scrub has developed unique names for the type, including in California, *chaparral* and *coastal scrub*; in Chile, *matorral* and *espinal*; in Spain, *tomillares*; in France or French-speaking countries, *maquis* or *garrigue*; in Greece, *phrygana*; in Israel, *bath’a* or *goresh*; in South Africa, *fynbos* and *strandveld*; and in Australia, *kwongan* and *mallee* (Kuennecke, 2008).

Temperate Grassland and Shrubland

Summary: Temperate grasslands are dominated by mesomorphic to somewhat xeromorphic perennial grasses with a variable amount of perennial forbs. Trees are scattered to largely absent (typically <10% cover), often controlled by drought, cold or fire. Grasses and forbs grow to different heights at maturity, depending on climate, soil and other factors. Grasses may be either tussock (bunch) forming or sod forming (forming a carpet on the ground), with bunchgrasses increasingly common in droughty conditions. Both C3 and C4 grasses are found, with C3 increasingly common toward the poles. Grasses and perennial forbs are well-suited to withstand cold seasons and tolerate grazing and fire because of the position of their buds near or below the ground surface.

Climate: Temperate grasslands occur in regions with a semi-arid to moist climate (mostly BSk in the Koeppen climate classification). Semi-arid climate regions receive 25–50 cm of precipitation a year; moist regions receive 50–90 cm. Snow may occur in some areas, including mid-continental prairie of North America and the East European steppes of Eurasia. The continental location of grasslands in both North America and Eurasia creates wide annual range in temperatures, with winters having temperatures well below freezing and summers very hot, and the growing season extending from 5 to 7 months (Woodward, 2008).

Continental precipitation gradients shape the distribution of regional temperate grassland biomes. In some instances, such as in North America, longitudinal zones dominate and replace each other in an east-west direction across the mid-continent (i.e., tallgrass prairie to shortgrass prairie). In other areas, such as Eurasia, latitudinal zonation is more prominent, with biomes changing in a north-south direction. Still other natural grasslands are a consequence of rainshadows on the lee sides of major mountain ranges or of high elevation, or of specialized droughty substrates (Woodward, 2008).

Soil/substrate/hydrology: Temperate grasslands are often found on soils that are highly fertile and productive, though large expanses of sandy soils may also occur. Soils are built from the combination of dense roots and the annual die-off of above ground vegetation. More living biomass exists below ground than above. The highly fertile soils are classified as mollisols (USDA Soil Taxonomy, also called chernozems) and are rich in humus in both the A and B horizons. The soils often contain loess material, rich in carbonates (Woodward, 2008).

Animals: Herbivorous mammals play an important role in regulating vegetation structure and composition in temperate grasslands. They may either be migratory ungulates, such as pronghorn or bison, that move in either small or large herds, or they are burrowing rodents, such as prairie dogs, that live in colonies. Insects are also key herbivores, with grasshoppers especially abundant. Animal diversity is relatively low, especially in comparison to the animals of some tropical grasslands (Woodward, 2008) (Fig. 1).

Geographic range: Temperate grasslands and shrublands occur in the middle latitudes (25–55°) of the northern and southern hemispheres. The largest expanses are found in North America (“prairies”) and Eurasia (“steppe”), with smaller but substantial areas in South America (“pampas”) and southern Africa (“veld”) (Woodward, 2008).

Boreal variant: Poleward of the temperate grassland are minor areas of Boreal Grassland and Shrubland, dominated by mesomorphic perennial grasses and forbs, with shrubs of varying dominance. Mosses and lichens play a larger role than in other grasslands. This type is associated with cold semi-arid to moist climates, with extended cold winters and short mild summers, and geographically occurs mixed with boreal forests and wetlands. The climate generally favors establishment of forest vegetation; thus, the absence of forest vegetation is a result of local conditions related to water regime, soil parameters (including thin, rocky sites),

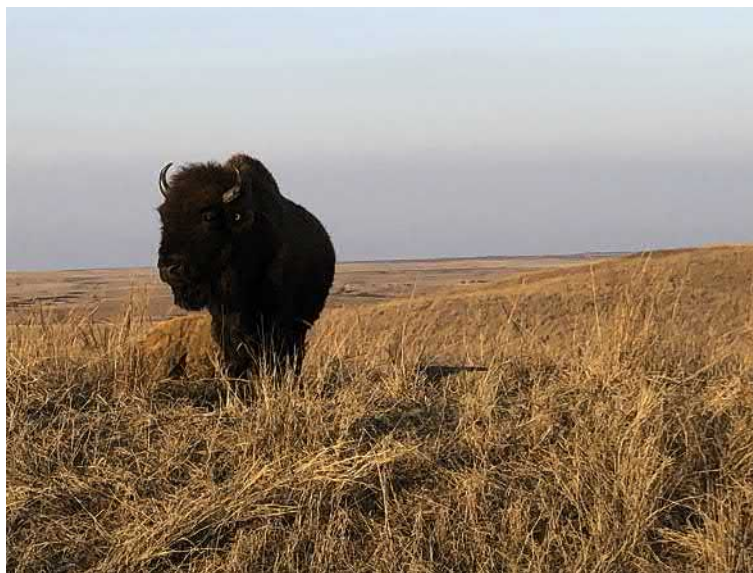


Fig. 1 American bison (*Bison bison*) are large herbivores that shape Central North American grasslands, including at the Tallgrass Prairie Preserve in Oklahoma. Photo by Don Faber-Langendoen.

or disturbance regimes. There are lengthy periods of freezing temperatures with the coldest month isotherm of -3°C , and the growing season generally averaging <100 days, occasionally interrupted by nights of below-freezing temperatures. Snow may be present for extended periods (7–10 months) and soils are frozen in winter. Annual precipitation is 38–50 cm (15–20 in.). The northern and southern boundary of these boreal grasslands may be similar to that of boreal forest. This formation is found in the northern mid-latitude regions of North America and Eurasia, extending through much of the boreal region between 55° and 70°N latitude.

Biogeographic Distribution of Tropical, Temperate, and Mediterranean Grasslands

To show the grassland types and their distribution, two systems were integrated: the International Vegetation Classification (IVC) at the Division level to help characterize global and continental biome types (Faber-Langendoen et al., 2014), and Terrestrial Ecoregions of the World (TEOW) (Olson et al., 2001; Dinerstein et al., 2017) to show their distribution. By integrating these two systems, we generated a systematic, spatially-explicit framework that broadly accounts for grassland biodiversity (as continental biome or IVC division types) and the spatial ecoregion within which these grassland types occur (Dixon et al., 2014).

In the IVC, a formation (akin to a global biome) represents combinations of dominant and diagnostic growth forms that reflect macroclimatic factors such as altitude, seasonality, substrates, and hydrologic conditions. Nested within each formation are a set of divisions (akin to continental biomes), which describe broadly uniform growth forms and a broad set of diagnostic plant species at large biogeographical scales, reflecting continental gradients in ecological factors (Faber-Langendoen et al., 2014). At both the formation and division levels, the ecological and vegetation types include a range of grassland and related shrubland types. For example, the IVC division Patagonian Grassland and Shrubland (Table 1) includes reference to both grassland and shrubland because they strongly overlap in floristic composition, growth forms, and biogeography. However, within the hierarchy, a lower level plant community distinction may eventually be made between the grassland and shrub types.

The IVC defines 51 distinct tropical, mediterranean, and temperate grassland division types, creating a new global biogeographical representation of earth's grassland types (Fig. 2). Divisions are mapped by ecoregion, for all ecoregions where they historically occupied at least 10% of the ecoregion (see Dixon et al., 2014 for details, including Appendix S2 for a list of all TEOW ecoregions where a grassland type occupied at least 10% of the given ecoregion). This map capitalizes on the use of both the IVC and TEOW to develop a platform for global grassland conservation policies. Furthermore, describing grasslands and their spatial distribution in this way provides decision makers with robust information on global grassland biodiversity patterns (Dixon et al., 2014).

The maps demonstrate how unique levels of biodiversity, particularly species biogeographic differentiation, emerge at the division level. For example, within the temperate grassland formation, there is little to no species overlap between the Eastern Eurasian Grassland and Shrubland division and the Great Plains Grassland & Shrubland division. At this division level, species attributes such as richness, abundance, and endemism may begin to be used, facilitating management and policy decisions. Development

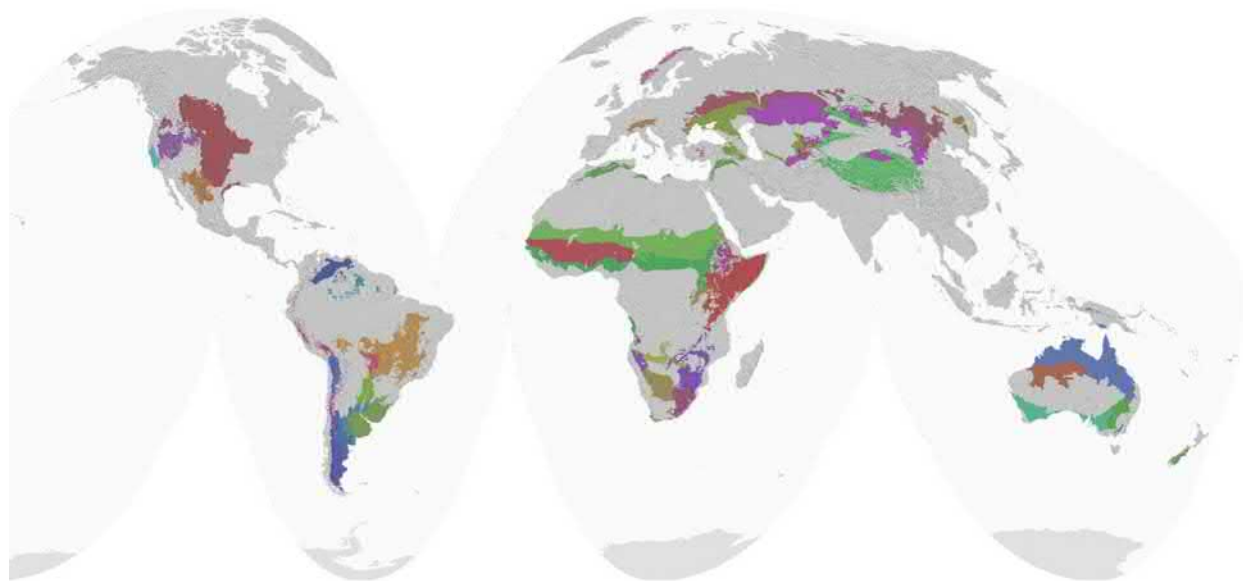


Fig. 2 Diversity of continental-scale grassland types based on the division level of the International Vegetation Classification. From Dixon, A., Faber-Langendoen, D., Josse, C., Morrison, J. and Loucks, C.J. (2014). Distribution mapping of world grassland types. *Journal of Biogeography* 41, 2003–2019. and reproduced with permission from John Wiley and Sons.

of levels below division, such as that of macrogroup and group, would further enhance the application of the grassland types, because these levels are more comparable to types used by other widely used regional classifications (Dixon et al., 2014).

Other aspects of grassland processes may emerge at somewhat broader biogeographic scales. For example, Lehmann et al. (2014) found that although a common set of environmental drivers shape tropical savannas across the globe, there are important differences in how these drivers interact at the continental level. These differences include response of woody biomass to climate change, e.g., climate change could lead to increased woody biomass in Africa because the woody species that have evolved on that continent respond differently to fire-temperate interactions than do the species on other continents.

Biodiversity of Grasslands

Grasslands are notable for their contribution to biodiversity, both in terms of species diversity and the diversity of crop cultivars. The major cereal crops of the world are grasses, and their origins are in grasslands. The genetic diversity of wild stock continues to be a means for improving cereal and forage cultivars. Gibson (2009) noted that 40 of the world's 234 Centres of Plant Diversity (CPD) identified by the International Union for Conservation of Nature and Natural Resources (IUCN) and World Wildlife Fund-US occur in grasslands, with an additional 70 CPDs containing some grassland habitat. To qualify as a CPD, mainland areas must contain 1000 vascular plants with 10% endemism. Gibson also notes that perhaps the biologically richest grassland worldwide is that of the Agulhas Plain, part of the Cape Floristic Province of South Africa. This region, considered as one of the world's 25 biodiversity hot-spots for conservation contains a flora of 1751 species, including 23.6% regional endemics and 5.7% local endemic in a landscape of shrubland, savannah, and fynbos. Other regions, particularly in the northern hemisphere, are of more recent origin and do not contain the same levels of diversity.

From a very different angle, Veldman et al. (2015) approach the biodiversity of grasslands from an "old-growth" perspective; namely, that grasslands, despite their apparent ephemeral above ground structure, are ancient ecosystems with high herbaceous species richness, high endemism and unique species composition (as reflected in our division/continental biome types).

Grassland Productivity, Ecosystem Services and Climate Change

Grasslands have both intrinsic (non-use) and economic (use) values. Intrinsic values focus on the aesthetic, cultural, and ecological values that grasslands provide, irrespective of any direct benefit to humans. Economic values include grazing livestock, harvesting native or cultivated plants, hunting wildlife, recreational activities (e.g., hiking, bird watching, photography), educational activities, erosion control, water quality control, and research activities. Some of these economic values may degrade or even destroy the grasslands, and for that reason, there has been growing interest in pricing ecosystem functions, goods, and services based on the persistence of native grasslands. We consider several here: carbon storage, agriculture and biofuels.

Carbon Storage and Agriculture

Grasslands are an important contributor to global carbon storage because of the high levels of carbon accrual and sequestration below ground in the soil. According to Gibson (2009), up to 90% of grassland biomass is below ground and levels of soil carbon are higher in grasslands than in forests, agroecosystems, or other ecosystems. Temperate grasslands in particular have high storage rates, because decomposition rates are generally low and soil organic matter has accumulated over thousands of years. By contrast, tropical grasslands have high above ground production because of the warmer temperatures, but below-ground storage is low. In both cases, grasslands are a potentially important sink for carbon in the terrestrial biosphere. For these reasons, there is concern that their role as a carbon sink could be lost in response to global climate change.

The effects of climate change on carbon storage may be small relative to the large impacts cause by conversion of grasslands for agricultural production. Many regions of the world have lost substantial portions of the grasslands (e.g., as much as 98% in North American tallgrass prairie), and many agricultural uses have led to soil erosion and loss of organic matter. Improved agricultural methods could minimize loss of soil organic matter, but for degraded soils, recovery is slow, taking 50 or more years. Gibson (2009) notes that other causes of carbon loss from grasslands include fire, grazing, and exotic species. Burning tropical grasslands, for example, releases carbon to the atmosphere, and contributes up to 42% of gross CO₂ to global emissions.

Agricultural Grazing

Natural grasslands have a long history of use by human, including production of domestic livestock principally mammalian herbivores: cattle, sheep, goats, horses, water buffalo, and camels. According to Gibson (2009), the densities of livestock in grasslands range from 1 to 100 head/km⁻², with the highest densities in the world in the Middle East, Asia, and Australia. Densities may still be on the rise, with the potential for overgrazing and a degraded grassland range.

Biofuels

In the quest of sustainable energy sources, researchers have turned to perennial grasses and native grasslands. Mixtures of native grassland perennials, referred to as low-input high-diversity (LIHD) biofuels, were shown to exhibit bioenergy yields 238% greater than monocultures (Gibson, 2009). Moreover, these LIHDs are particularly valuable because they sequester more CO₂ in the soil and roots than released during conventional biofuel production. But there are tradeoffs because the ecological traits of a grass species bred for biofuel production are also known to contribute to invasiveness, prompting concerns regarding the ecological risks involved in introducing and planting them (Palik et al., 2016). Many grassland biofuel species are invasive outside their native range.

Grasslands in Crisis—Conservation Strategies

Grasslands have historically been subject to a wide variety of human uses, including conversion to crops or other types of farming. Temperate grasslands are considered among the most threatened biomes worldwide (Hoekstra et al., 2005), but increasing pressures on tropical grasslands from agricultural expansion, heavy grazing and continued population growth may soon make them equally threatened. These threats challenge governments, business, and civil society to develop policies that address conversion pressures on global grassland ecosystems and seek to balance development with conservation. However, decision makers currently lack a framework to monitor global grassland biodiversity for both biological uniqueness and total historic distribution. One promising initiative is the International Union for the Conservation of Nature's (IUCN) proposed Red List of Ecosystems, where the likelihood that an ecosystem will persist into the future is assessed (Keith et al., 2013). Another is the increased focus on national reporting of progress toward "Aichi Targets" under the United Nations Convention on Biodiversity (CBD). Aichi Target 11 states that "By 2020, at least 17 percent of terrestrial and inland water areas... especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures and integrated into the wider landscape and seascape." Tools are being developed to measuring progress in meeting these targets based on a suit of indicators (Han et al., 2017), which can help conservationists and policy makers assess priorities for grassland conservation.

Acknowledgments

This review of grasslands would not have been possible without the legwork of the Hierarchy Revisions Working Group that completed the Faber-Langendoen et al. (2016) publication. In particular, for the grasslands work summarized here, I thank Carmen Josse and Todd Keeler-Wolf. This work was also informed by the popular but comprehensive work of Susan Woodward's (2008) Grassland Biomes book and by David Gibson's (2009) book on grasslands. Finally, Adam Dixon provided the lead on linking the International Vegetation Classification with the Ecoregions of the World map, and I thank him for the high-quality maps that became part of our Dixon et al. (2014) paper.

See also: Perspectives on Terrestrial Biomes: The International Vegetation Classification.

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- <https://php.radford.edu/~swoodwar/biomes/>—Woodward Biomes of the World.

North American Temperate Grasslands: Conservation at the Center of the Continent

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Glossary

Bunchgrass Perennial grass species that usually grow as singular plants in clumps, tufts, hummocks, or bunches, rather than forming a sod or lawn.

Cool Season Grass Grass species that reach maximum growth and flower later from spring to early summer using a C_3 photosynthetic pathway.

Mixedgrass Prairie Grassland communities with plant species that tend to grow above waist height, thus they are middling in height between the shortgrass prairie to the west and the tallgrass prairie to the east, and hence the name mixed grass prairie.

Semi-Desert Grassland Grassland communities, often of irregular or sparse vegetative cover, of warm deserts that are dominated by bunchgrasses and succulent plants.

Shortgrass Prairie Grassland communities with plant species that tend to grow well below waist height, and hence the name shortgrass prairie.

Sod-forming Grass Grass species that spread by means of a specialized structure known as a rhizome, which is a modified root. When the rhizomes grow into dense mats, they are referred to as sod forming.

Tallgrass Prairie Grassland communities with plant species that tend to grow well above waist height, and hence the name tallgrass prairie.

Warm Season Grass Grass species that reach maximum growth and flower later from mid to late summer using a C_4 photosynthetic pathway (common to most plants) that enables plants to reduce moisture stress.

Nomenclature

International Vegetation Classification Provides a comprehensive multi-level structure to describe and classify the world's vegetation. The classification is based on vegetation and ecological criteria, including vegetation growth forms and structure, plant species, and ecological characteristics such as site, disturbance, bioclimate, and biogeography.

IVC Group A relatively narrow set of diagnostic plant species (including dominants and codominants), broadly similar composition, and diagnostic growth forms that reflect regional mesoclimate, geology, substrates, hydrology, and disturbance regimes.

NatureServe Terrestrial Ecological System A terrestrial ecological system is defined as a group of plant community types that tend to co-occur within landscapes with similar ecological processes, substrates, and/or environmental gradients.

Abstract

Grasslands dominate the central regional landscape of the North America, extending from the Canadian prairies south across the Chihuahuan Desert. We describe this grassland diversity, discussing common forms of ecological classification, and highlight the International Vegetation Classification. We then report on a series of analyses and a Landscape Conservation Design for temperate grassland conservation. We targeted 12 major grassland ecosystem types that occur across this region.

Component analyses included: (a) documenting long-term trends in extent by grassland type, (b) assessing landscape intactness among grassland areas, and (c) identifying Grassland Potential Conservation Areas to advance grassland conservation. Most severe declines in grassland extent have occurred in tallgrass prairie types, followed by mixed-grass, shortgrass, and semi-desert grasslands. Similar trends by type were documented for landscape intactness and connectivity. A total of 177 Grassland Potential Conservation Areas (GPCAs) were identified to represent grassland type diversity in areas least likely to conflict with other land uses. Within identified GPCAs, type-specific representation varied from a low of just 1% of historic extent for Texas Blackland Tallgrass Prairie to a high of 27% for Western Great Plains Sand Prairie. Combined across all 12 grassland types, 15% of historic extent is represented.

Introduction

The North American grassland biome occupies a large expanse of the continental interior. The types of grassland are typically differentiated based on the height of the predominant species (tallgrass, mixed or mid grass and shortgrass) or the prevailing climate (desert grassland). The region is also known for a gently rolling landscape that is punctuated by rugged badlands. The words grassland or prairie, however, evoke images in the popular imagination; herds of massive American bison (*Bison bison*) grazing beneath dazzling blue skies, nomadic Native American peoples encamped along clear streams, and a west bound Prairie Schooner navigating the Great Ocean of grass. But this is an ancient landscape. The earliest grass fossils date from roughly 19 million years before the present. At that time, the vegetation was a mosaic of savannah vegetation and open grassland.

Humans have influenced the structure of the grasslands since their arrival 15,000 years ago. But the changes in human population density, technology, and land use in the 19th century, initiated decades of profound changes to the grasslands. Because of rich and abundant soils, grassland conversion for agricultural purposes has been an ongoing process for centuries. Arguably, the pace of conversion was slow following arrival of Euro-American settlers seeking the independence of an unfettered agrarian life. Their cultivation of western lands, however, followed practices that were appropriate in the humid east, but unsuitable in the semi-arid Great Plains. The pace of grassland loss accelerated with the invention of the steel plow. First introduced by John Lane in 1833 and later modified and manufactured by John Deere, thousands of plows pulled by oxen began to break the prairie soil. As the steel blade cut the dense, intertwined network of roots in the prairie sod, the sound was likened to that of a zipper. Those soils have long since eroded away. The arrival of railroads also facilitated agricultural intensification by providing rapid transport of commodities to distant markets, thus increasing the strain on native grasslands. Although some of these lands were retired from crop production following the Dust Bowl of the 1930s, more recent trends in agricultural intensification of the Chihuahuan Desert (Pool et al., 2014), biofuel production (Wright and Wimberly, 2013), and energy development (Pruett et al., 2009; Fargione et al., 2012), have introduced pockets of rapid change across the region (Drummond et al., 2012).

In this article, we discuss the following topics: how do ecologists distinguish and classify grassland vegetation? How can the past distribution of grasslands be mapped and compared with the current extent of grassland vegetation? Do “intact” remnants of grassland vegetation exist and how are place-based conservation priorities set?

Classifying the Grassland Biome

Classifying vegetation (defined here as “plant cover, including both floristic composition and vegetation structure, documented at a specific location and time, under specified ecological conditions, and preferably described at an optimal time during the growing season”) requires careful consideration of the species present and their proportions relative to one another and the physical environment that they inhabit. The species composition and grassland vegetation in the Great Plains reflects three major environmental gradients. The first is a marked increase of average annual and monthly temperatures from north to south. The second is an increase in annual precipitation from west to east, the product of both a rain shadow, created by mountains to the west, and the location of much of the region near the center of the continent. And finally, elevation which increases from east-to-west because of the Rocky Mountain uplift. When developing descriptions of vegetation, ecologists include adjectives that reflect these environmental factors.

Ecologists also incorporate species traits to distinguish units of vegetation. All plants exhibit adaptations to regional climatic factors. In the case of grassland plants, drought and high sunlight can affect the efficiency of photosynthesis. Thus, range managers and ecologists speak of cool season grasses as adapted to cool-moist conditions and reach maximum growth and flower during the spring and early summer. Warm season grasses are those that are adapted to hot-dry conditions and reach both maximum growth and flower later from mid to late summer. Underlying these distinctions is a difference in the mode of photosynthesis utilized. The C_3 photosynthetic pathway is typical of cool season grass species (Ehleringer and Cerling, 2002). But under hot and dry condition, plants experience water loss and hot temperatures that cause a decline in photosynthetic efficiency. The adaptations of C_4 photosynthesis alleviates much of this stress.

Grasses can also be categorized as rhizomatous grasses (or sodding forming) versus bunchgrasses. Rhizomatous grasses spread through the soil by a specialized structure known as a rhizome, essentially a modified root. When the rhizomes grow into dense mats, they are referred to as sod forming (Weaver, 1954). Euro-American settlers learned that the dense prairie sod could be cut into blocks and used like bricks to construct house, known as “soddies” (Thornthwaite, 1941). Bunch grasses grow in clumps, producing space between individuals of the same species.

Table 1 International Vegetation Classification Hierarchy, example from Temperate North America including the number of natural types in the conterminous United States as of 2019.

Level no.	Level name	Defining characteristics	No. types	Example
1	Class	Life form Physiognomy	6	Grassland and shrubland
2	Subclass	Global physiognomy	11	Temperate and Boreal grassland and shrubland
3	Formation	Global physiognomy	24	Temperate grassland and shrubland
4	Division	Continental floristics	51	Great plains grassland and shrubland
5	Macrogroup	Subcontinental floristics	121	Great plains tallgrass prairie
6	Group	Regional floristics	319	<i>Northern Great Plains Tallgrass Prairie</i> <i>Schizachyrium scoparium—Bouteloua curtipendula</i>
7	Alliance	Subregional floristics	1201	Northern Grassland <i>Schizachyrium scoparium—Bouteloua curtipendula—Hesperostipa spartea—(Pascopyrum smithii) Grassland</i>
8	Association	Local floristics	5794	

The International Vegetation Classification (IVC) provides a hierarchical framework for the classification and description of vegetation types (Faber-Langendoen et al., 2014). The IVC draws upon bioclimatic, biogeographic, and soils data to develop coherent classification units at each scale. It is important to emphasize that an IVC unit represents existing vegetation (i.e., a suite of species that are present currently at a given location), and not potential natural vegetation (i.e., the species that might be present in a location in the absence of human action) (Zerbe, 1998). The IVC is organized into eight levels (Table 1). The three upper levels (Formation Class, Formation subclass, Formation) segregates vegetation into units based upon the dominant and diagnostic growth forms as a reflection of the macroclimatic as modified by altitude, seasonality of precipitation, substrates, and hydrologic conditions. These levels are too generalized for our needs here but note that the North American Temperate Grasslands fall within the Shrub and Herb Formation Class, the Temperate and Boreal Grassland and Shrubland Formations Subclass and the Temperate Grassland and Shrubland Formation. Vegetation often referred to as “shrub steppe” such as big sagebrush (*Artemisia tridentata*)-dominated steppe in Montana, is classified in the “Cool Semi-Desert Scrub and Grassland” Formation, the “Western North American Cool Semi-Desert Scrub and Grassland” Division, and the “Great Basin-Intermountain Tall Sagebrush Steppe & Shrubland” Macrogroup. Shrub steppe is intermediate between more dense shrublands and temperate grasslands. They are widespread across the western Great Plains and intermountain region, but are not treated here with the predominant temperate grasslands.

Our discussion of the North American Temperate Grasslands will be center on the “Group” in the mid-level (Division, Macrogroup, and Group) of the IVC, defined as a “relatively narrow set of diagnostic plant species (including dominants and codominants), broadly similar in composition, and diagnostic growth forms that reflect regional mesoclimate, geology, substrates, hydrology, and disturbance regimes.” Thus, each unit in the mid-level is defined based on four criteria: characteristic taxa, physiognomy, ecology, and biogeography. Naming conventions for all categories in the IVC require that both a scientific and a common name be provided to facilitate utility among broad groups of users. For example, the scientific name *Andropogon gerardii—Heterostipa spartea—Muhlenbergia richardsonis* Grassland Group corresponds with the common name Northern Mesic Tallgrass Prairie. Group common names will be used in this article. The lower levels of the classification (e.g., alliance and the association) will not be discussed here.

The North American Temperate Grasslands fall within the Central North American Grassland and Shrubland Division and are distributed among four macrogroups: Great Plains Mixedgrass and Fescue Prairie, Central Lowlands Tallgrass Prairie, Great Plains Sand Grassland and Shrubland, and Western Great Plains Shortgrass Prairie. Of the several hundred Groups in the IVC, 24 occur in the Great Plains, nine of which are grasslands. The remaining 15 Groups represent wetland, shrubland, and riparian vegetation. Several more semi-desert grassland types occur in the Chihuahuan Desert in temperate to subtropical latitudes of the southwest United States and adjacent Mexico. The descriptions of the grassland Groups that follow will begin at the northern extent of this biome and proceed southward, thus highlighting changes in species composition as related to changing temperatures.

The Great Plains Mixedgrass & Fescue Prairie macrogroup consists of four units: the Central Great Plains Mixedgrass Prairie, Northern Great Plains Dry Mixedgrass Prairie, Northern Great Plains Mesic Mixedgrass Prairie, and Northern Great Plains Rough Fescue Prairie. The distribution of these grasslands has been impacted either directly or indirectly by glacial history. Over a time-span of 2.5 million to 11,000 years ago, the region was subject to four major glacial episodes which forced plant and animal species south and obliterated or restructured soils. Since the last glaciation, soil development on gently rolling to flat terrain and influenced by the cool climate have developed into deep silty loam Mollisols, which are some of the most agriculturally productive soils on earth. As a result, much of the natural vegetation has been replaced by row crop agriculture.

Because temperatures in this region are cool, the predominate grasses are cool season species. Warm season grass species are present, particularly in the southern portion of the region, but they are low in abundance. The term mixedgrass refers to the stature of the predominant grasses; midway or a mix in height between those of the tallgrass and shortgrass prairies.

The Northern Great Plains Rough Fescue Prairie is reported only from the western Canadian provinces of Alberta, Manitoba, and Saskatchewan. Grasslands within this Group are dominated by Hall’s Fescue (*Festuca hallii*) with Timber Oatgrass (*Danthonia*

intermedia), Thick-spike Wheatgrass (*Elymus lanceolatus*), Needlegrass (*Hesperostipa* spp.), Ricegrass (*Achnatherum* spp.) as codominants. Hall's Fescue is limited to very high latitudes in North America and high elevations in the United States.

The Northern Great Plains Dry Mixedgrass Prairie is reported from Alberta, Saskatchewan, Montana, North Dakota, and Wyoming. The vegetation is characterized shortbristle needle and thread (*Hesperostipa curtipendula*), thickspike wheatgrass (*Elymus lanceolatus*), bluebunch wheatgrass (*Pseudoroegneria spicata*), western wheatgrass (*Pascopyrum smithii*), needle and thread (*Hesperostipa comata*), Idaho fescue (*Festuca idahoensis*), and sun sedge (*Carex inops* ssp. *heliophila*). Western wheatgrass and thickspike wheatgrass are rhizomatous species, while the others are considered bunchgrasses.

The Northern Great Plains Mesic Mixedgrass Prairie occurs from Alberta, Saskatchewan, and Manitoba, south to Nebraska, and Wyoming. It typically occupies narrow valleys, stream terraces, and rolling uplands and mesic slopes. The soils are loams with well-developed profiles. Although it overlaps geographically with the Northern Great Plains Dry Mixedgrass Prairie, the two differ on the basis of moisture regimes and the secondary species present. The number of warm season grass species increases in this Group, such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and Indiangrass (*Sorghastrum nutans*). Green needlegrass (*Nassella viridula*) and western wheatgrass, both cool season species, are also common components of this Group.

The Central Great Plains Mixedgrass Prairie Group covers the widest geographic extent of the Groups considered here, extending from New Mexico, Oklahoma and Texas, north to southern Nebraska. Warm season grasses predominate on all sites. In addition to big bluestem, little bluestem, and Indiangrass, blue grama (*Bouteloua gracilis*), hairy grama (*Bouteloua hirsuta*), and sideoats grama (*Bouteloua curtipendula*) are common co-dominant species. The area is a mosaic of grasslands interspersed with woody vegetation. On sandy soils, sandsage (*Artemisia filifolia*) shrublands are common and less frequently, shiner oak (*Quercus havardii*) woodlands. The mixedgrass prairie is intensively utilized for the cultivation of winter wheat, cotton, milo, and livestock. Due to suppression of fire, overgrazing, and land abandonment, eastern red cedar (*Juniperus virginiana*) had replaced grassland cover in overgrazed pastures and abandoned fields and represents an economic and ecologic threat in many areas.

Central Lowlands Tallgrass Prairie macrogroup consists of four Groups; the Northern Tallgrass Prairie, Central Tallgrass Prairie, Southern Tallgrass Prairie, and Blackland and Coastal Tallgrass Prairie. These grasslands tend to receive more rainfall and experience greater humidity relative to the western grasslands. They occur on a wide variety of soils, ranging from deep, well-formed mollisols and shallow soils and outcrops over limestone. Big and little bluestem and Indiangrass are predominant species in these Groups. On dry, shallow soils, hairy and sideoats grama are co-dominants. In lowland prairies, switchgrass (*Panicum virgatum*) is a dominant species, as was prairie cordgrass (*Spartina pectinata*), but its abundance has been greatly reduced in areas by cattle grazing.

The Northern Tallgrass Prairie Group extends from Manitoba, Ontario and Minnesota south through Nebraska, South and North Dakota, and east into Iowa and northern Missouri. Like the Northern Mixedgrass Prairie Groups described above, vegetation distribution and patterns were affected by glacial cycles. Although the warm season grasses big and little bluestems, and sideoats grama are predominant grasses, several cool season species such as porcupine grass and western wheatgrass also characterize these grasslands.

The Central Tallgrass Prairie and Southern Tallgrass Prairie Groups share many features. Of the two, the Central Tallgrass Prairie covers the greatest geographic area, ranging from the Great Plains into the Prairie Peninsula of Ohio, Indiana, and Illinois (Transeau, 1935). The Central Tallgrass Prairie of Kansas, Nebraska, and South Dakota is within the region considered here. Southern Tallgrass Prairie occupies a smaller range that includes Kansas, Oklahoma, and Texas, with extension into Arkansas and Missouri. Unlike the Northern Tallgrass and portions of the Central Tallgrass, the Southern Tallgrass Prairie was not directly affected by glaciation.

Of the Blackland and Coastal Tallgrass Prairie Group, only the Blackland Prairie occurs in the region under consideration. The soils have developed over limestone and tend to have high pH. Both Alfisols and Vertisols are present with the inclusion of mima mounds. Little bluestem and Indiangrass are frequently the dominant species. Silveus' dropseed (*Sporobolus silveanus*) is prevalent in Blackland Prairies on Alfisols. Mead's sedge (*Carex meadii*) and prairie bishop (*Bifora americana*) are also characteristic species.

The Great Plains Sand Grassland & Shrubland macrogroup consists of the Great Plains Sand Grassland and the Great Plains Sand Shrubland. Soils tend to be nutrient poor, weakly developed, and well drained. Vegetation is sparse and a mix of grass and forb species on large sand dunes. Plant species in this Group must be adapted to these rather extreme conditions. Although the Great Plains Sand Grasslands occur throughout the region (Manitoba and Saskatchewan, south through the Montana and the Dakotas to Oklahoma and Texas), it interdigitates or is locally restricted within the grassland Groups described above. Sand bluestem (*Andropogon hallii*) is a predominant species, with prairie sand reed (*Calamovilfa longifolia*) as a co-dominant in northern locations, and giant sand reed (*Calamovilfa gigantea*) as a co-dominant in the south. The Nebraska Sandhills, a mosaic of wetland and grassland vegetation, is the best-known region with this Group (Loope and Swinehart, 2000).

The Great Plains Shortgrass Prairie is the only Group in the Western Great Plains Shortgrass Macrogroup. The Shortgrass Prairie intergrades with foothill vegetation of the Rocky Mountains in Colorado and New Mexico and extends east to the Colorado border, the Oklahoma Panhandle, and southwest Texas. Soils formed over the Ogallala outwash, and Permian period sandstones, with scattered outcroppings of earlier Paleozoic Era formations. The soils range from shallow and rocky to deep Mollisols. The predominant grasses and forbs are of short stature relative to species of the eastern grasslands, hence the name shortgrass. The iconic species of the shortgrass prairie are blue grama and buffalograss (*Bouteloua dactyloides*). The occurrence and abundance of these two species varies with soil type. On sites with shallow soils, side oats grama (*Bouteloua curtipendula*) and hairy grama (*Bouteloua hirsuta*) are codominant or dominant species. Much of the shortgrass prairie has been converted to the production of winter wheat, which is irrigated, or grazed by livestock.

The shortgrass prairie region is associated with one of the greatest environmental disasters to strike the United States, the Dust Bowl. A combination of drought and inappropriate land use practices resulted in the mobilization of soil by high winds, which in

one instance carried the dust to the Halls of Congress and into the Atlantic Ocean (McLeman et al., 2014). In the years following the disaster, ecologists documented an increased in geographic extent of the shortgrass prairie. In fact, a challenge for modern ecologists is determining which vegetation types are an expression of human mediated changes and which represent species assemblages in the absence of human influence.

Semidesert grasslands fall within the North American Warm Desert Scrub & Grassland Division, and Chihuahuan Semi-Desert Grassland Macrogroup. These grasslands may include sparsely vegetated patches as well as succulent shrubs or scattered small trees; all occurring along a transition to desert scrub or subtropical thornscrub. Some variation among four IVC Groups are reflective of grassland composition along elevation (from lower montane to foothill elevations) or by soils, with some types more strongly associated with sands, loams, and gypsum. Plant species such as bullgrasses (e.g., *Muhlenbergia emersleyi* and *Muhlenbergia setifolia*), New Mexico Feathergrass (*Hesperostipa neomexicana*), black grama (*Bouteloua eriopoda*), sotal (*Dasyllirion* spp.), side-oats grama (*Bouteloua curtipendula*), mesa dropseed (*Sporobolus flexuosus*), hairy crinklemat (*Tiquilia hispida*), Torrey yucca (*Yucca torreyi*), and tobosa grass (*Pleuraphis mutica*) variously characterize these IVC Groups.

Conservation Status and Trends

To determine the changing extent of grasslands in the Great Plains and Chihuahuan Desert, Comer et al. (2018) employed spatial technologies to compare distributions of targeted grasslands. They used spatial data layers consisting of a “biophysical setting” layer (potential/historical distribution) and “existing vegetation type” layer (current distribution) developed by LANDFIRE. That effort used inductive modeling with satellite imagery, climate, landform, and soil data (Rollins, 2009) to map the distribution for each major grassland type at spatial resolutions of approximately 5-ha minimum map unit. These maps use the NatureServe terrestrial ecological system classification (Comer et al., 2003), that align closely with either the Group or Alliance levels of the IVC hierarchy described above. From the map of potential or historic distribution of grassland ecological systems, 12 that exceeded 8000 km² in extent were selected for further analysis (Fig. 1). Of these, the Northwest Great Plains Mixed-grass Prairie had the greatest historical extent (~630,000 km²) and the Chihuahuan Sandy Plains Semi-Desert Grassland had the lowest (8100 km²) (Table 1).

Next, Comer et al. (2018) determined long-term change in extent by comparing the mapped distribution of grasslands (circa 2003) against the potential or historical extent from the previous analysis (Table 2). Direct conversion of grasslands for agriculture explained much of the change in areal extent for most types. Three types experienced a loss of greater than 90%: Texas Blackland Prairie (98%), Northern Tallgrass Prairie (96%), Central Tallgrass prairies (92%). These grasslands occur on productive soils in areas with significant summer rainfall, which enhances agricultural productivity. Based upon the “historic long-term trends in extent” criterion of the International Union for Conservation of Nature (IUCN) Red List Ecosystems (Keith et al., 2013), three grassland types would be considered Critically Endangered, four types Endangered, and three types Vulnerable (Table 2). If the 12 types are considered collectively, the loss would total 62% and qualify as Vulnerable.

Grassland Landscape Condition

Land conversion and subsequent land protection tell only part of the story of trends in temperate grassland biodiversity. A common factor in landscape design for biodiversity conservation is documentation of the relative condition or intactness, and key ecological processes such as connectivity, in any given area in order to inform conservation action (Groves, 2003). High condition or intact vegetation retains expected composition, structure, and dynamic process characteristics of sites that have not been altered by prior human land uses (Parrish et al., 2003). Substantial environmental degradation—due to wildfire suppression, soil compaction, overgrazing, and climate change—or alteration of biotic composition (i.e., invasive species introductions, landscape fragmentation and inhibition of dispersal by native species) and processes (i.e., wildfire suppression) have had substantial (albeit varying) impact on each grassland type (Samson et al., 2004).

Fragmentation of natural habitat by human activities can be mapped and used to identify intact core areas. Hak and Comer (2017) designed the NatureServe landscape condition model to calculate an index of relative intactness for the vegetation. The model integrates data layers representing roads, land uses, and maps of altered vegetation. The result is a grid layer of landscape condition with values falling between 0.0 and 1.0, where values close to 1.0 imply relatively little ecological impact from surrounding land use. The product is a wall-to-wall grid surface of landscape condition values falling between 0.0 and 1.0 (Fig. 2). For North American grasslands, it is clear that large proportions occur in some of the most intensively converted and fragmented landscapes. But one can also see that in western and drier portions of the region, more extensive and contiguous grassland areas remain.

Landscape Conservation Design

The United Nations Convention on Biodiversity (CBD), held in Nagoya, Aichi Prefecture, Japan in 2010, set five strategic goals consisting of 20 biodiversity targets, known collectively as the Aichi Targets. Strategy C strives to “improve the status of biodiversity by

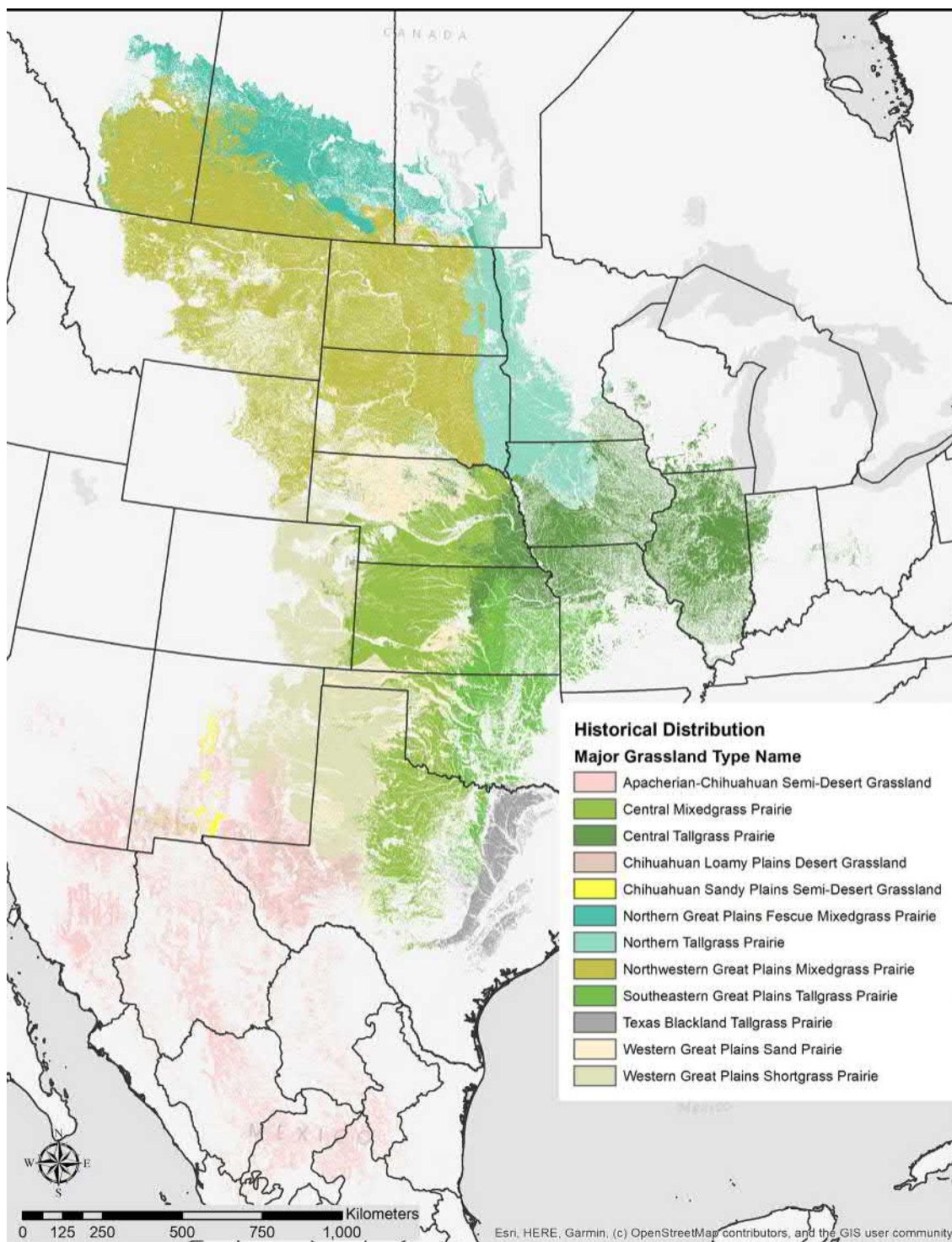


Fig. 1 Potential or approximate historical location and extent of 12 major grassland types across the central interior of North America.

Table 2 Long-term trends in extent and at-risk status of 12 major grassland types.

Major temperate grassland type	Historical extent estimate (km ²)	Current extent estimate I (km ²)	Percent loss to conversion
Texas Blackland Tallgrass Prairie	41,400	670	98
Northern Tallgrass Prairie	157,200	6500	96
Central Tallgrass Prairie	242,000	20,100	92
Northern Great Plains Fescue Mixedgrass Prairie	137,000	18,000	87
Chihuahuan Sandy Plains Semi-Desert Grassland	8100	1600	80
Southeastern Great Plains Tallgrass Prairie	108,000	31,400	71
Central Mixedgrass Prairie	259,000	77,000	70
Western Great Plains Sand Prairie	107,300	38,000	65
Chihuahuan Loamy Plains Desert Grassland	38,300	14,400	62
Northwestern Great Plains Mixedgrass Prairie	620,900	307,500	50
Apacherian-Chihuahuan Semi-Desert Grassland and Steppe	249,400	152,200	39
Western Great Plains Shortgrass Prairie	259,000	188,000	27
Total	2,227,600	855,370	62

safeguarding ecosystems, species and genetic diversity,” and Target 11, a component of this strategy, states that “By 2020, at least 17 per cent of terrestrial and inland water, and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes.” But how can we determine if this goal has been reached?

Grassland Priority Conservation Areas (GPCAs) is one vehicle to measure progress toward Target 11. Although GPCA analyses exist for grasslands in the Great Plains and Chihuahuan Desert (PCAP, 1998; Gauthier et al., 2003; Pool and Panjabi, 2011), all predate the CBD. Comer et al. (2018) completed a GPCA analysis to determine if the Target 11 goals might be achieved in grasslands. The analysis consisted of a grid of approximately 48,000 hexagons (each 100 km² in size). Although the area of the hexagon may seem large, it is a defensible choice given the geographic extent of the trinational region. A comparison was made of grassland extent and landscape intactness score. Hexagons with high areal grassland extent and high landscape intactness scored highest were then analyzed with consideration of existing managed/protected areas, land use intensity and connectivity, and the presence of at-risk species. The analysis produced 177 distinct GPCAs, with units in all 12 grassland types, which if conserved could achieve or surpass the Aichi Target 11 (Fig. 3 and Table 3).

The Western Great Plains Sand Prairie in the Nebraska Sandhills had the greatest modern extent within what was the historic range identified within GPCAs. At 27%, this far surpasses the 17% set in Target 11. Six additional major grassland types met or surpassed the 17% milestone of Aichi Target 11; Northwestern Great Plains Mixed-grass Prairie (21%), Chihuahuan Loamy Plains Desert Grassland (19%), Central Mixed-grass Prairie (18%), Southeastern Great Plains Tallgrass Prairie (18%), Western Great Plains Shortgrass Prairie (17%), and Apacherian-Chihuahuan Semi-Desert Grassland (17%). These types dominate the relatively dry-to-arid portions of the western Great Plains and extending throughout the Chihuahuan Desert. Of the tallgrass prairie ecological systems, only the Southeastern Great Plains Tallgrass Prairie achieved the 17% target. The majority of GPCAs in this grassland type were located on relatively shallow soils with extensive rock outcrops, areas with limited potential for cultivation, such as in the Flint Hills of Oklahoma and Kansas. GPCAs in the Chihuahuan Sandy Plains Semi-Desert Grassland were relatively small and fragmented areas and as a result, fell below the 17% milestone. Other grasslands that fell below the milestone were the Central Tallgrass Prairie (only 4% in GPCAs), Northern Great Plains Fescue Mixed-grass Prairie (4%), Northern Tallgrass Prairie (2%), and Texas Blackland Tallgrass Prairie (1%). When considered collectively, approximately 15% of all 12 major temperate grassland types occurred in identified GPCAs (Table 3). While just below the 17% Aichi Target 11 milestone, the selection of GPCAs still represents all major grassland types in areas most likely to support successful conservation.

Conclusions

Major grasslands of the Great Plains and adjacent Chihuahuan Desert span a vast region of high floristic diversity, and an array of temperature, humidity, and soil moisture regimes. The product is a variety of grassland vegetation types variously dominated by bunchgrasses or sod-forming species that are tall, medium, and short in stature. Dense and tall grasslands historically dominated the eastern, more humid margins of the Great Plains. In northern and central portions of the region, mixedgrass prairies remain dominant. To the southeast, shortgrass prairie dominates increasing warm and dry terrain, and semi-desert grassland becomes dominant further south extending across northern Mexico.

Given the severe impact of land conversion and fragmentation on most grassland types, we demonstrated a systematic approach, focusing on grassland type distributions, to advance toward global conservation targets such as Aichi Target 11 under the global Convention for biodiversity. Grassland Potential Conservation Areas can serve as one important focus for collaborative conservation action to build landscape resiliency in the face of accelerating environmental change.

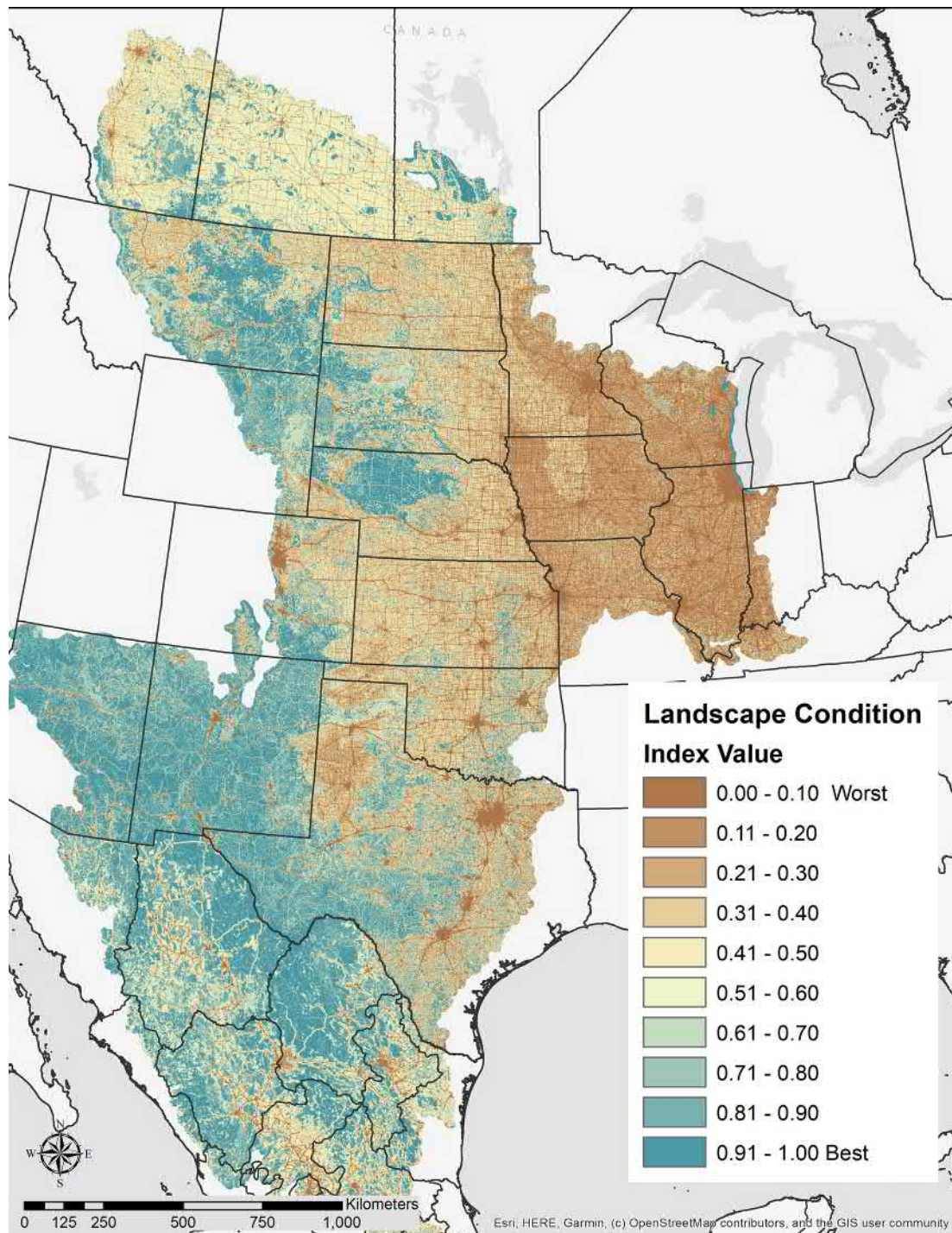


Fig. 2 NatureServe landscape condition model applied to ecoregions currently supporting major grassland types, predicting a range of grassland quality.

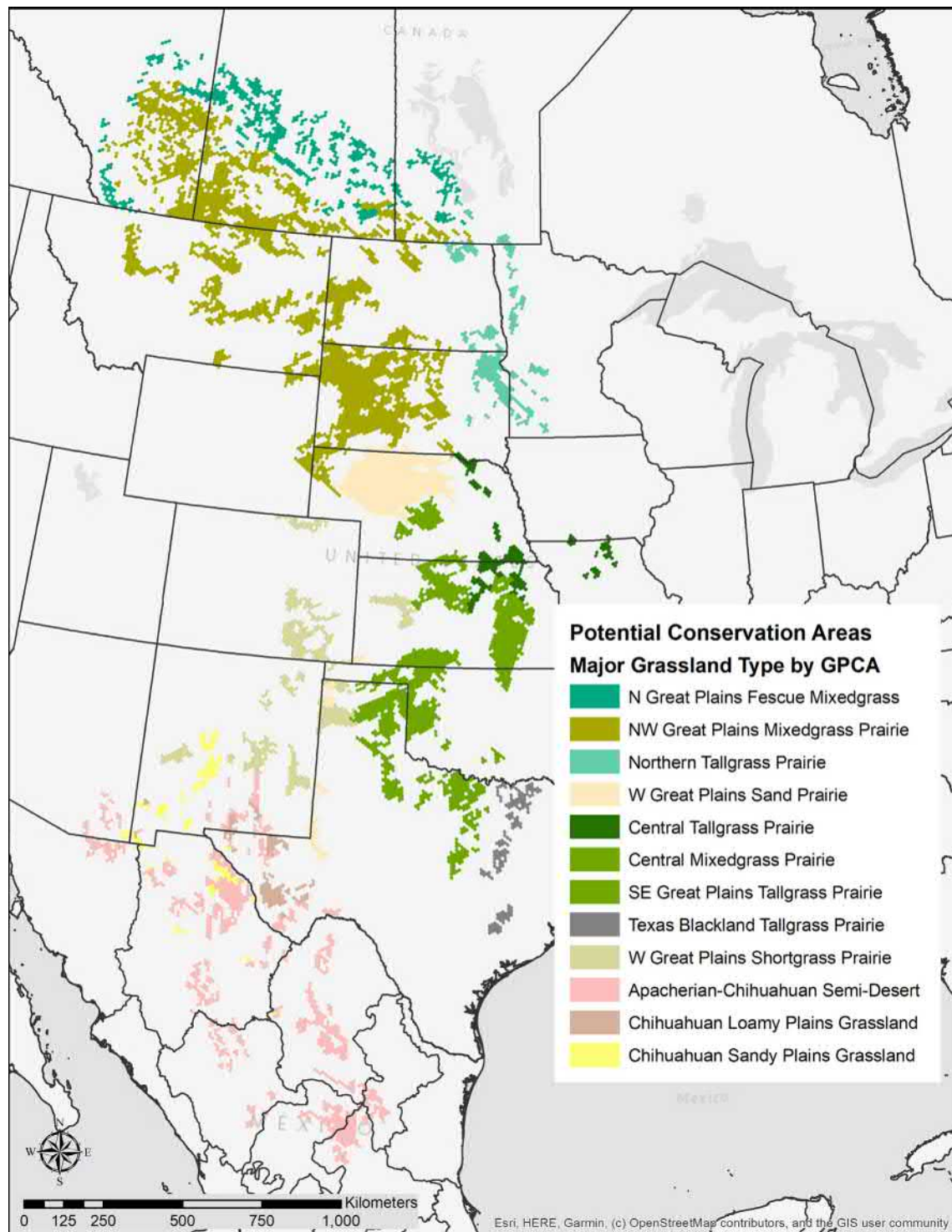


Fig. 3 Grassland Potential Conservation Areas (GPCAs) based on representation of 12 major temperate grassland types (ordered north to south).

Table 3 Proportion of historical extent of each major grassland types represented in identified Grassland Potential Conservation Area (GPCA).

Grassland type	Historic extent estimate (km ²)	Current extent estimate (km ²)	Number of GPCAs	Km ² within in GPCAs	% Historical extent in GPCAs
Western Great Plains Sand Prairie	107,300	38,000	7	29,200	27
Northwestern Great Plains Mixedgrass Prairie	620,900	307,500	26	128,400	21
Chihuahuan Loamy Plains Desert Grassland	38,300	14,400	10	7300	19
Central Mixedgrass Prairie	259,000	77,000	9	39,200	18
Southeastern Great Plains Tallgrass Prairie	108,000	31,400	5	19,300	18
Western Great Plains Shortgrass Prairie	259,000	188,000	14	50,700	17
Apacherian-Chihuahuan Semi-Desert Grassland and Steppe	249,400	152,200	34	42,000	17
Chihuahuan Sandy Plains Semi-Desert Grassland	8100	1600	16	1000	12
Central Tallgrass Prairie	242,000	20,100	8	10,000	4
Northern Great Plains Fescue Mixedgrass Prairie	137,000	18,000	29	5400	4
Northern Tallgrass Prairie	157,200	6500	15	3500	2
Texas Blackland Tallgrass Prairie	41,400	670	4	400	1
Total	2,227,600	855,370	177	342,400	15%

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Grasslands and Savannas of the Southeastern USA

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Abstract

Much of the southeastern United States was covered by grassland vegetation (including savannas, woodlands, glades, and other open vegetation) prior to EuroAmerican settlement. This was particularly true for the southeastern Coastal Plain, where pine savanna/woodland covered roughly two-thirds of the landscape. However, grasslands were also prominent in other subregions of the Southeast. Collectively, these grasslands held a large proportion of the biodiversity of the Southeast, but they have suffered more serious declines than forests, estimated as around 90% for all types combined. This article summarizes major types of grassland in the region, factors responsible for creating and maintaining them, factors contributing to high levels of biodiversity in these communities, and prospects for the future.

Introduction

An old and widely repeated myth regarding the vegetation of the eastern United States is that a squirrel could travel from the Atlantic coast to the Mississippi River without ever once touching the ground, so dense were the forests (Matthiessen, 1959). Particularly in the southeastern United States, however, that squirrel would have had to take a very circuitous route. The southeastern United States, from the southern tip of Florida northward to Delaware, Maryland, and West Virginia, westward through the Ohio Valley, across the Mississippi and through Arkansas south of the Ozark Plateau, and including southeastern Oklahoma and eastern Texas, held large areas of prairies, savannas, open woodlands, glades, and other grasslands prior to EuroAmerican settlement (Noss, 2013; Fig. 1). Both historically and today, Florida contains more grassland vegetation than any other southeastern state.

Because converting grassland to crop fields is much easier than for forests, much of the grassland of the Southeast was lost before the first botanists or other naturalists in this region could describe them. These losses of grassland to agriculture escalated as the region became more settled, and they continue today. A considerable amount of grassland loss also was caused by fire exclusion. Both lightning (originally) and Native Americans were important ignition sources for fires in the region. Following an early Euro-American settlement period when fires actually increased in some parts of the Southeast due to frequent burning by settlers, the exclusion of fire caused many remnant grasslands to convert to forest. This fire exclusion was both deliberate and passive, the latter due to the effects of barriers such as agricultural fields and roads, which stopped the natural flow of fire across landscapes (Noss, 2018). Elimination of large grazing and browsing herbivores such as bison and elk facilitated replacement of grasslands by forest. Today the rampant urbanization of this region is eliminating most grasslands that are not secured within protected areas.

Despite the severe loss of native grassland ecosystems in the southeastern United States, those that remain hold an enormous portion of the region's biodiversity, especially endemic species (i.e., those found within a particular region but nowhere else in the world). Although most of the remnant grasslands exist only as small patches, some large grassland landscapes still remain, especially in the



Fig. 1 The southeastern United States, as defined in this article. The boundary is approximate. From *Forgotten Grasslands of the South*, by Reed F. Noss. Copyright © 2013 Island Press. Reproduced by permission of Island Press, Washington, D.C.

southeastern Coastal Plain. Moreover, active restoration can bring many former grasslands back. If second-growth forests on former grassland sites are logged or thinned, for example, and enough grass or other flammable material in the ground layer allows for controlled burning, grassland plants will often spring up from the seed bank where they've been buried for sometimes more than a century.

The purpose of this article is to summarize the major types of grasslands across the southeastern United States; briefly discuss the physical and ecological factors that created and maintained them; examine some reasons why these communities have such high and distinctive biodiversity; and consider what the future may hold for these communities in the face of rapidly changing climate and land use.

Types of Grasslands in the Southeastern United States

Many grassland ecologists favor an inclusive definition of grasslands, which takes into consideration the important role of the graminoid-dominated groundcover in the ecology of the community. Hence, grasslands may be treeless or treed, shrubby or not shrubby. For the purposes of this article, a grassland is any community in which the grass or graminoid layer, with its associated forbs, is the dominant layer in terms of plant cover, biomass, species richness, or at least two of these three. In the southeastern United States, natural community types that meet this definition include: prairies (which are treeless or nearly so); grassy balds (mountaintop prairies of the southern Appalachians); savannas and woodlands (typically with 10–80% tree canopy cover); barrens, glades, and outcrops (highly variable, often occurring in mosaic patterns and with considerable bare soil or rock); herbaceous wetlands; and canebrakes (dominated by species of *Arundinaria*, the American bamboo). As tree canopy cover approaches 80% or so, an ecosystem begins to behave ecologically more like a forest than a savanna/woodland, in the sense that the tree layer begins to shape the ecological processes, interactions, and dynamics of the system more than the ground (herbaceous) layer.

Table 1 lists some types of grasslands in the southeastern United States that fall into the general categories listed above. Examples of these community types are discussed in more detail below, though limited space precludes a detailed treatment.

Prairies

Prairies are ecological communities dominated by grasses and other herbaceous plants and with few or no trees. Some prairies are relatively shrubby, particularly if fire is excluded for a period of time. Trees also become more abundant with reduced fire frequency in many prairies, for example cabbage palms (*Sabal palmetto*) invading Florida dry prairie. Prairies occur on a variety of soils in the southeastern United States, including mollisols, clays, sands, and loams. Some southeastern prairies occur on deep mollisols or loams similar to those of the Central Tallgrass Prairie region, although more typically calcareous clays or sands are the primary soil types of southeastern prairies. Dominant grasses of southeastern prairies include little bluestems (*Schizachyrium* spp.), big bluestems (*Andropogon* spp.), three awns/wiregrasses (*Aristida*), and Indiangrasses (*Sorghastrum* spp.). There are also many species of prairie forbs, such as blazing-stars (*Liatris*), purple coneflowers (*Echinacea*), prairie clovers (*Dalea*), and prairie docks (*Silphium*).

Table 1 Examples of some “ecological systems” of the southeastern United States, as classified by NatureServe, which fit into the categories of grassland types considered in this chapter.*Prairies*

Pennyroyal Karst Plain Prairie and Barrens
 Cumberland Riverscours
 Arkansas Valley Prairie and Woodland
 Lower Mississippi Alluvial Plain Grand Prairie
 Southern Coastal Plain Blackland Prairie and Woodland
 West Gulf Coastal Plain Southern Calcareous Prairie
 Texas-Louisiana Coastal Prairie
 Florida Dry Prairie

Grassy Balds

Southern Appalachian Grass and Shrub Bald

Savannas and Woodlands

Eastern Serpentine Woodland
 Bluegrass Savanna and Woodland
 Cumberland Wet-Mesic Meadow and Savanna
 Atlantic Coastal Plain Upland Longleaf Pine Woodland
 Ozark-Ouachita Shortleaf Pine-Bluestem Woodland
 West Gulf Coastal Plain Wet Longleaf Pine Savanna and Flatwoods
 Central Florida Flatwoods
 South Florida Pine Rockland

Barrens, Glades, and Outcrops

Cumberland Sandstone Glade and Barrens
 Nashville Basin Limestone Glade and Woodland
 Alabama Ketona Glade and Woodland
 Ouachita Shale Glade and Barrens
 South-Central Saline Glade
 East Gulf Coastal Plain Dry Chalk Bluff
 West Gulf Coastal Plain Catahoula Barrens
 Panhandle Florida Limestone Glade

Herbaceous Wetlands

Southern and Central Appalachian Bog and Fen
 Interior Low Plateau Seepage Fen
 Southern Ridge and Valley Seepage Fen
 Ozark-Ouachita Fen
 Central Florida Wet Prairie and Herbaceous Seep
 Atlantic Coastal Plain Embayed Region Tidal Freshwater Marsh
 Floridian Highlands Freshwater Marsh
 South Florida Wet Marl Prairie

Canebrakes

Atlantic Coastal Plain Peatland Pocosin and Canebrake
 Mississippi River High Floodplain (Bottomland) Forest^a

Ecological systems are defined as “mid- to local-scale ecological units useful for standardized mapping and conservation assessments of habitat diversity and landscape conditions. Each ecological system type describes complexes of plant communities influenced by similar physical environments and dynamic ecological processes (like fire or flooding)” (<http://www.natureserve.org/conservation-tools/terrestrial-ecological-systems-united-states>). See also Noss (2013). Data from NatureServe Explorer.^b

^aCanebrake can exist as alternative stable state to forest in these bottomlands, especially on higher ground (“ridges”).

^b<http://explorer.natureserve.org/>.

These plant genera typically have greater species richness in the Southeast than in the more extensive prairies of the Great Plains, underscoring the antiquity of southeastern grasslands (Noss, 2013).

Major prairie regions of the southeastern United States include the Grand Prairie of the Mississippi Alluvial Plain of Arkansas; the Pennyroyal Karst Plain of Kentucky and Tennessee; the Coastal Prairie of Louisiana and Texas; the Black Belt Prairie (a type of blackland prairie) of Mississippi, Alabama, and a small portion of southern Tennessee; and the Florida Dry Prairie landscape of south-central Florida (Fig. 2). Most of these regions have lost the vast majority of their grasslands, on the order of 90–99.99% decline. Prairies and other grasslands in the unglaciated Southeast typically have higher plant species richness and a higher proportion of endemic species than prairies of the Great Plains, probably mostly because the more stable climate of the Southeast reduced extinction rates. However, geological and soil diversity are also high in the Southeast, species colonized the region from several other



Fig. 2 Florida dry prairie, Kissimmee Prairie Preserve State Park, Florida. This community is more accurately called a hyperseasonal subtropical grassland. Photo by Reed Noss.

regions, and disturbance was frequent enough to prevent competitive exclusion by dominant species—all of these factors likely contributed to high species richness.

At least three *Bison* species (going back to the Pleistocene) once roamed many southeastern prairies, most abundantly west of the Mississippi River. Animals and plants more typical of the western United States occur as disjunct populations in many southeastern grasslands. For example, in south-central Florida, the dry prairie and other grasslands contain the characteristically western bird species crested caracara (*Caracara cheriway*), burrowing owl (*Athene cunicularia*), and white-tailed kite (*Elanus leucurus*).

Grassy Balds

Grassy balds are essentially mountain-top prairies (Fig. 3), but their unique origins and histories suggest recognition as a separate class of communities. Communities of this general type occur in only a few places on Earth, most notably the southern



Fig. 3 A grassy bald, Roan Mountain, along the Tennessee-North Carolina border. This community is thought to have been maintained by a mixture of climatic factors and the activities of large herbivores. Photo by Reed Noss.

Appalachians (north to Virginia and West Virginia, and in the Cumberland Mountains along the Virginia-Kentucky line) at elevations of around 1500 m to nearly 1900 m, as well as in the Oregon (USA) Coast Range and the East Carpathian Mountains in the Czech Republic and Romania. The grassy balds of the southern Appalachians have cool temperatures most of the year and average annual precipitation approaching 250 cm. Dominant and characteristic plants include mountain oat-grass (*Danthonia compressa*), common hairgrass (*Avenella flexuosa*), bluejoint (*Calamagrostis canadensis* var. *canadensis*), mountain-cinquefoil (*Sibbaldia retusa*), Pennsylvania sedge (*Carex pensylvanica*), Gray's lily (*Lilium grayi*), mountain angelica (*Angelica triquinata*), Appalachian bluet (*Houstonia serpyllifolia*), and green alder (*Alnus crispa*).

Although fires occasionally occur on balds in drought years, fire is not a dominant factor in the origin and maintenance of these communities, given their generally moist and cool conditions. Indeed, the origin of these communities has been hotly debated for decades, with extreme exposure, fire, clearing by Native Americans or white settlers, grazing, and other factors suggested as most important. The currently best accepted explanation for the existence of grassy balds is the climate-herbivore hypothesis of [Weigl and Knowles \(2014\)](#). This hypothesis suggests that grassy tundra occupied these communities during the late Pleistocene, and megaherbivores such as mammoths, mastodons, horses, and ground sloths would migrate from the lowlands to graze and browse there during the summers. Nearby fossil sites document numerous species of Pleistocene megaherbivores in this region. When these herbivores were driven extinct, there were still native elk, deer, and bison in the area to maintain the grazing and browsing pressure. When these species were extirpated or greatly reduced by over-hunting by the late 18th century, the domestic livestock brought up the mountains by settlers to graze these balds in the summer continued the process of herbivory, but less effectively than the native megaherbivores. This likely explains, in part, the reduction in the size and number of grassy balds over time ([Weigl and Knowles 2014](#)).

Savannas and Woodlands

This category of communities is very diverse in the southeastern United States and constitutes the matrix or dominant vegetation over large portions of the region, particularly the Atlantic and Gulf Coastal Plains but also in some other subregions. Important community types included longleaf pine savannas across the Coastal Plain ([Fig. 4](#)), and savannas and woodlands with other pine species such as slash (*Pinus elliotii*), South Florida slash (*P. densa*), loblolly (*P. taeda*), pond (*P. serotina*), and shortleaf (*P. echinata*) pines. Savannas of shortleaf pine and bluestem grasses are major community types in the Ouachita Mountains of Arkansas and eastern Oklahoma, and shortleaf pine-post oak (*Quercus stellata*)-bluestem (*Andropogon gerardii*/*Schizachyrium scoparium*) savannas were characteristic of plateaus and ridges on the Cumberland Plateau of Tennessee and other parts of the Southeast.

Oak savannas and woodlands, including post oak, blackjack oak (*Q. marilandica*), and, especially in Kentucky, burr oak (*Q. macrocarpa*), were abundant, especially north and west of the Coastal Plain, for example in the Arkansas Valley ([Fig. 5](#)) and in Kentucky (Bluegrass Savanna and Woodland) and into the Midwest. These are among the most depleted of all ecosystem types in North America ([Noss et al., 1995](#)). Unusual savanna/woodland types in the Southeast include serpentine woodlands of the Piedmont and Blue Ridge provinces, the pine rockland communities of South Florida (primarily Miami Rock Ridge and Lower Keys),



Fig. 4 A longleaf pine savanna, also known as pine flatwoods. Forever Florida Preserve, near Holopaw, Florida. Pine savannas and woodlands of various types once covered approximately two-thirds of the southeastern Coastal Plain. Photo by Reed Noss.



Fig. 5 Post oak savanna, Camp Robinson State Wildlife Management Area, in the Arkansas Valley, 30 miles northwest of Little Rock, Arkansas. Photo by Reed Noss.

where limestone pinnacles are commonly exposed on the surface, as well as dwarf cypress (dwarfed pond cypress, *Taxodium ascendens*) savannas in the Everglades and Big Cypress regions.

Fire was the primary factor that maintained most savannas and woodlands in the Southeast and prevented their conversion to closed forests. The frequency of cloud-to-ground lightning strikes is higher in the southeastern Coastal Plain than in any sizeable region of North America, and peaks in central Florida. In this region lightning was more important for igniting fires than Native Americans, presumably for millions of years and up to the time of EuroAmerican settlement (Noss, 2018). To the north and further from the coasts, lightning activity is lower, and at the time of EuroAmerican settlement most fires were probably lit by Native Americans.

Barrens, Glades, and Outcrops

This is one of the most heterogeneous categories of grasslands in the Southeast, further confused by the terms “barren” and “glade” being used in a variety of ways by different authors. As considered here, these communities range along a gradient from shallow-soil prairies (barrens), to sparsely vegetated communities with abundant exposed rock or bare soil (glades), to primarily rock with patches of grasses and other plants (outcrops, including flatrocks and domes). Given their generally harsh, primarily physically-controlled conditions, these communities are edaphic, meaning produced by the soil—of which there is often little. Examples of these communities include herbaceous serpentine barrens and woodlands, ranging from eastern Maryland and adjacent Pennsylvania to parts of the southern Appalachian Mountains and Piedmont in North Carolina and Georgia; limestone and dolomite glades and barrens from southern Ohio and Indiana, through Kentucky and Tennessee to Virginia and south to Alabama; sandstone glades and barrens on the Cumberland Plateau; shale barrens of the central and southern Appalachians, as well as the Ouachitas; granitic flatrock communities of the southern Piedmont, best developed east of Atlanta, Georgia (Fig. 6); and saline glades or barrens in Texas, Louisiana, and Arkansas. All of these communities, and others on more unusual substrates, have harsh physical or chemical conditions that are unfavorable to growth of woody plants. In some cases, such as some saline barrens and shale barrens on steep southwest-facing slopes, edaphic conditions are so extreme that fire does not appear necessary to maintain their grassland condition. In other cases, tree growth is impaired, but fire or other disturbances are necessary to prevent woody encroachment.

Given that barrens, glades, and outcrops are islands of distinct edaphic conditions in a sea of dissimilar geology and soils, one might expect that their isolation would provide ample opportunities for evolution of new species. And it often did. Southeastern glades and barrens are often packed with endemic species, some of which have their closest relatives a great distance away. An extreme example of high single-site endemism is the Ketona glades along the Little Cahaba River in central Alabama (Fig. 7). The shallow soil of this generally steep site is derived from Ketona dolomite, which has concentrations of magnesium high enough to be toxic to plants. Since the Ketona glades were discovered in 1992, nine new species and subspecies of endemic plants have been described from this site. All apparently evolved here in isolation. Throughout the southeastern United States, edaphic grasslands—often found only on very small sites—are of high priority for protection due to their unique biodiversity.



Fig. 6 A granitic flatrock community, Mt. Arabia, in the Georgia Piedmont east of Atlanta. The Precambrian granitic schists and gneisses support patches of grasses and other plants among abundant bare rock. Photo by Reed Noss.

Herbaceous Wetlands

Herbaceous wetlands generally lack tree cover and are dominated by grasses, sedges, rushes or other graminoid and herbaceous plants. Some of these communities are spatially extensive, such as freshwater, brackish, and salt marshes near the coast and the extensive sawgrass (*Cladium jamaicense*) sloughs and marl prairies of the Everglades, whereas others are usually small patch communities such as isolated bogs and fens. The hydroperiod—the annual duration of inundation—of a herbaceous wetland determines its ecology and species richness to a great extent. Longer hydroperiods usually result in lower species richness. For example, in the Florida Everglades, various marshes have hydroperiods of 6–12 months and typically fewer than 20 species on a site, whereas marl prairie (Fig. 8) has a hydroperiod of 2–4 months in most years and often more than 100 species on a site (Florida Natural Areas



Fig. 7 Ketona Dolomite Glades in Bibb County, Alabama. The dolomite bedrock contains extremely high levels of magnesium and supports only sparse plant cover over most of the area of exposed rock. Nine new species and subspecies of plants have been described, so far, on these glades since 1992. They exist nowhere else in the world. Photo by Reed Noss.



Fig. 8 A marl prairie in Big Cypress National Preserve, Florida. These prairies are usually inundated between 2 and 4 months of the year, during the summer wet season, so are not true wetlands. They have many more species of plants than the longer-hydroperiod marshes. Photo by Reed Noss.

Inventory, 2010). Some herbaceous wetlands, such as seepage slopes, are usually saturated but rarely inundated—i.e., there is little or no standing water. Herbaceous wetland communities are of many types and occur throughout the southeastern United States. Their inundated or saturated soil conditions, often in addition to frequent fire, prevent or reduce tree encroachment.

Canebrakes

Canebrakes often do not resemble grasslands, but they qualify as such because they are dominated by any of three species of cane or American bamboo, *Arundinaria*, which are in the grass family. They occur (or occurred) in seepage areas of pine savannas, in raised areas (“ridges”) of river floodplains, and a few other locations. On some sites fire alone may be adequate to maintain canebrakes, but in other cases, such as in bottomlands, a combination of disturbances appears to be required. Gagnon and Platt (2008) determined that canebrakes in floodplain/bottomland forest are maintained by fire or flood following a large canopy disturbance, such as a hurricane, tornado, or ice storm. The extinct passenger pigeon (*Ectopistes migratorius*) probably also helped maintain canebrakes (Noss, 2013). Their immense flocks roosted in bottomlands, especially in winter, and were reported to break apart tree canopies from their weight. They also produced abundant fertilizer, which favors cane. Passenger pigeons and large canebrakes disappeared together over the course of the 19th century; less than 1% of the historic canebrake area remains, with giant canebrakes (*A. gigantea*) especially depleted. Remnant canebrakes are distributed from the Ohio River Valley south to the Gulf of Mexico coast and central Florida.

Factors that Create and Maintain Southeastern Grasslands

Climate

One of the fundamental generalizations of biogeography is that grassland biomes occur along a climatic gradient between desert and forest (Coupland, 1991). This rule does not apply to grasslands of the southeastern United States. Whereas the Prairie Region of the Great Plains receives mostly between 30 and 76 cm of rain annually, the southeastern United States generally receives between 76 and 254 cm (https://nationalmap.gov/small_scale/printable/images/pdf/precip/pageprecip_us3.pdf)—quite enough to support dense forest virtually everywhere. Therefore, climate alone cannot explain the existence or distribution of southeastern grasslands. Nevertheless, historical periods of hot, dry weather appear to have promoted the eastward spread of grassland vegetation in the region (Transeau, 1935). Today, sites with hotter and drier microclimate, such as south- or southwest-facing slopes, often feature patches of grassland within a matrix of forest (Noss, 2013). Thus, modern climate does have an effect on grassland distribution in the Southeast, but mostly on a local scale. For an explanation of grassland occurrence across the region, we must look to other factors (below).

Fire

Fire is the paramount factor explaining the existence of grassland worldwide in regions with precipitation sufficient to support forest (Bond et al., 2005). Essentially, fire overrides the influence of climate in determining the distribution and abundance of vegetation types in regions such as the Southeast. Most types of grassland in the southeastern United States depend on at least occasional fire. Some grassland types—such as longleaf pine (*Pinus palustris*) savannas—require very frequent fire, on the order of every 1–3 years, to maintain their characteristic structure, composition, and species richness. Several independent lines of evidence suggest that fire has a long evolutionary history in this region: (1) charcoal in sediment layers of lake bottoms—although absence of charcoal does not indicate absence of fire; (2) fire-derived chemicals in ancient soils; (3) paleoclimate proxies such as sediment deposition patterns indicating dry/wet seasonal cycles, which favor frequent fire; (4) ancient fossils of plants found today in fiery habitats; (5) ancient fossils of vertebrates with morphologies adapted to savannas or other fire-maintained ecosystems; (6) high species endemism in fire-maintained ecosystems; and (7) high incidence of fire-adapted traits, such as thick bark, smoke-stimulated germination, underground organs for carbohydrate storage, and rapid resprouting after fire (Noss, 2018).

In fire-dependent grasslands, reduced frequency of fire results in invasion and increasing growth and dominance of woody plants and other plant species that lack traits adapted to frequent fire. Hardwood trees and shrubs, for example, increase in abundance and cover relative to grasses, long-needled pines, and other plants typical of savannas and other grasslands. The increased levels of fine fuels (e.g., grass thatch, fallen pine needles) and small woody stems after fire exclusion may lead to unusually intense conflagrations when fire finally returns. If a site continues to go without fire for many years, however, it may undergo what ecologists call a regime shift, transitioning to an alternative steady state such as hardwood forest, which is relatively non-flammable due to absence of flammable fine fuels. Only during a period of extreme drought may fire finally enter the community, but usually only some distance from an edge, and full recovery to the original frequent-fire community may be essentially impossible (Noss, 2018).

Substrate and Landform

As noted earlier under the discussion of barrens, glades, and outcrops, extreme or unusual geology or soils can favor grassland over woody vegetation. Edaphic grasslands may or may not require fire or other disturbances to prevent tree encroachment. For example, serpentine grasslands are found on ultramafic soils rich in magnesium, iron, and other metals such as nickel and chromium. These soils reduce effective moisture availability; have low amounts of the essential nutrients calcium, potassium, and phosphorus; high amounts of magnesium that further inhibits calcium uptake resulting in weak cell wall development; and have toxic effects on some plants (Tashakor et al., 2013). Many grasses and grassland forbs, though, thrive under these conditions of reduced competition. However, serpentine grasslands in the relatively wet southeastern United States cannot be maintained by soil properties alone—trees still invade, albeit more slowly than on less toxic soils. A combination of fire and harsh soils maintain southeastern serpentine grasslands.

In some cases, however, edaphic conditions can maintain grasslands in the Southeast even in the absence of fire. Many sandstone, limestone, and other glades have soils so thin that they are wet only for brief periods after rains but then dry completely (i.e., they are hydroxeric). This harsh condition in combination with the limited space available for tree roots assures relatively open-canopy conditions; whatever trees invade are usually killed during subsequent droughts. A type of shale barren, known as shale ridge bald, occurs primarily in Virginia on south- and southwest-facing slopes of mountains. The thin, shaly soils in combination with the hot, dry microclimate produced by maximum sun exposure prevents tree encroachment, apparently even in the absence of fire. As a final example, the saline barrens of Louisiana, southern Arkansas, and eastern Texas have such extreme alkali soils that woody plants cannot survive, except on small patches of more favorable soil, such as elevated mounds (“pimple mounds”) of wind-deposited soils.

Hydrology

Hydrology affects plant communities and limits tree encroachment and survival in many ways. In low-lying landscapes prone to seasonal flooding, a good way to assess the effects of hydrology is through consideration of hydroperiod, which as noted earlier is the period of time during a year that a site is inundated. Hydroperiod is usually expressed as a range because of interannual variability in precipitation. Different plant communities experience different hydroperiods, with those at lower elevations usually being inundated for longer periods. Long periods of inundation or tidal cycles exclude most tree species. In the southeastern United States, herbaceous wetlands with long hydroperiods are marshes of many types, which are often zoned along elevational gradients. A depression marsh, for example, may be inundated almost all year in its deepest, central zone, but only for a short period in the outermost zones. The mostly flat topography of Florida creates conditions for large floodplain marshes to be inundated from 120 to 350 days per year. Artificial drainage of marshes typically results in invasion by woody species (Florida Natural Areas Inventory, 2010). Most marshes in the Southeast also depend on frequent fire (which can burn through a marsh even while it is partially inundated) to prevent tree and shrub encroachment.

Herbaceous wetlands with short hydroperiods in the Southeast might be better considered grasslands than wetlands. A marl prairie (Fig. 8), with its short hydroperiod of 2–4 months, is at least as much upland as wetland. The so-called Florida dry prairie (Fig. 2) might be better called a hyperseasonal subtropical grassland, because its lower portions are usually inundated for a few weeks of the year. The interacting stresses of fire in the early rainy season (May–June) followed by inundation later in the rainy season effectively exclude trees from this ecosystem under natural conditions (Platt et al., 2006).

Some herbaceous wetlands in the Southeast have no true hydroperiod—they have saturated soils due to groundwater seepage but are rarely or never inundated. Prominent among these communities are seepage slopes (especially in Florida) and various types of bogs and fens across the region. Insectivorous plants such as pitcher plants, sundews, bladderworts, butterworts, and the Venus fly-trap (within its small native range in the Carolinas) are characteristic species in these communities.

Herbivores

Large herbivores may be second only to fire as a dominant ecological factor maintaining grassland vegetation worldwide. The hypothetical but highly probable role of grazing and browsing herbivores in maintaining the high-elevation grassy balds of the southern Appalachians was discussed earlier. To the west and north of this region, Pleistocene megaherbivores created and maintained a complex network of trails connecting salt licks where they gathered to consume the minerals, but often got mired in the mud and left their remains as fossils. These trails, called “Buffalo traces” by white settlers because they were used by bison at that time, extended beyond salt licks and allowed the herbivores to make seasonal migrations across a large region. The combination of grazing, browsing, and trampling by these animals created unique short-stature grassland conditions, in which endemic plants such as Short’s goldenrod (*Solidago shortii*), running buffalo-clover (*Trifolium reflexum*), and some other species apparently evolved. These plants have persisted in part in heavily grazed pastures adjacent to ancient buffalo traces (Noss, 2013).

The combination of fire and grazing may be particularly important to the maintenance of high species richness in southeastern grasslands. In the Great Plains, this “pyric herbivory” produces higher species richness of plants and several animal groups than either fire or grazing alone (e.g., Fuhlendorf et al., 2008). Either bison or cattle (properly managed) appear able to play this keystone role. Pyric herbivory is not yet well documented in the Southeast, but given the long history of large herbivore activity in this region, it is highly likely to occur here.

Other Disturbances and Combinations

Most grasslands are disturbance-prone communities, and disturbance helps keep them free of trees or with open as opposed to closed tree canopies. Besides fire, many other disturbances damage tree canopies and promote a grass-dominated ground cover. Windstorms (hurricanes, tornadoes, etc.) and ice storms play this role frequently in the southeastern United States. As noted earlier, canebrakes in floodplains may require a combination of large canopy disturbances followed by fire or flooding. Besides the canopy disturbances produced by windstorms and ice storms, the extinct passenger pigeon probably facilitated canebrake development (Noss, 2013).

Along rivers, occasional flooding and ice scour also can maintain grasslands. These riverscours prairies or glades are well developed in several parts of the Southeast, including along the Potomac River in the vicinity of Washington, DC, on rivers of the Allegheny Plateau of West Virginia and Pennsylvania, on some rivers in the Blue Ridge province, in the Ohio River Valley (e.g., Adams County in southern Ohio), on the Cumberland Plateau and Interior Plateaus, and in the Ouachita Mountains of Arkansas and Oklahoma.

Why Are Southeastern Grasslands So Biologically Diverse?

The grasslands of the southeastern United States are some of the most species-rich and endemic-rich grasslands in the world, especially in the temperate and subtropical zones. At a fine scale, a near-record-high richness of 52 vascular plant species in one square meter was recorded in a longleaf pine savanna in the Green Swamp of North Carolina (Walker and Peet, 1984). On a broader scale, several regions of the Southeast are among the biologically richest regions in North America. In particular, the originally grassland-dominated Coastal Plain is now recognized as a global biodiversity hotspot because it meets the criteria of having at least 1500 endemic plant species (it has 1816) and suffering at least 70% loss of its original vegetation (it has lost 86%) (Noss et al., 2015). Some 85% of the plants endemic to the Coastal Plain are associated with pine savannas and embedded communities such as depression wetlands; these are mostly herbaceous grassland plants dependent on frequent fire.

Some factors that explain the high biodiversity of southeastern grasslands are the following:

- Relative climatic stability for long periods of time in this unglaciated region reduced extinction rates and fostered the retention of ancient lineages (paleoendemics) and survival of recently-evolved taxa (neoendemics).
- In the Coastal Plain, sea-level fluctuations promoted allopatric speciation on higher elevation sites surrounded by ocean during high sea-level stands (as did isolation by rivers).

- Several regions contributed species to the Southeast over time, including regions as distant as the western United States, Mexico, Central America, and the Caribbean.
- Frequent disturbance, especially by fire, wind, or large herbivores, prevents competitive exclusion (e.g., in pine savannas, maximum plant species richness occurs at the highest fire frequencies).

Southeastern Grasslands and Carbon Storage

People concerned and knowledgeable about climate change now recognize that in addition to reducing emissions of greenhouse gases, we must also increase the capture and storage of carbon in natural ecosystems. Therefore, protection and restoration of natural areas on vast scales is a necessary component of climate change mitigation. Most attention has been given to forests in this regard. Some plans even include afforestation, which involves planting trees in native grasslands and does more harm than good from a biodiversity conservation perspective. On a global scale, grasslands potentially store as much or even more carbon than forests. Moreover, more of the stored carbon in grasslands is belowground, where it is secure from fire and other disturbances that release carbon.

In grasslands dependent on disturbance to reduce tree encroachment, which most are, fire and large herbivores maintain herbaceous plant cover and diversity. Although fire releases carbon to the atmosphere, this loss of carbon is temporary, since the rapid and prolific plant regrowth after fire quickly takes up carbon dioxide from the atmosphere. In addition, the dung produced by herbivores and the charcoal produced by fires store abundant carbon.

Besides the legendary long roots of prairie grasses, which are often longer and contain much more biomass than the aboveground parts, many grassland plants have generalized or specialized underground storage organs. These fascinating structures store abundant, concentrated carbohydrates, which the plants utilize to resprout after disturbances remove their aboveground parts. Underground storage organs are best developed in plants of tropical and subtropical grasslands. In the southeastern United States, the subtropical grasslands of peninsular Florida are the center of abundance of these “underground forests.”

What Is the Future for Southeastern Grasslands?

As noted earlier, the grasslands of the southeastern United States have suffered devastating declines—greater than 90% for most types. The forces that reduce grasslands, most importantly agricultural and urban development and fire exclusion, show little sign of abating. On the other hand, although traditionally conservationists in the United States have been far more interested in forests than grasslands, a grasslands conservation movement has been steadily growing over the last several decades. Although this movement was initially confined mostly to the Great Plains and Midwest, and to some extent California, it has spread to the Southeast. For example, the Southeastern Grasslands Initiative “aims to preserve, restore, and promote native grasslands of all types throughout the Southeast” (<https://www.segrasslands.org>).

What does the future hold for southeastern grasslands? The most vulnerable grasslands in the region, in general, are probably coastal grasslands, which are threatened by a combination of increasing coastal development and rapid sea-level rise. Elsewhere, all else being equal, the current trend toward a warmer and drier (or more droughty) climate in the region should favor grasslands over forests, as has happened during many similar climatic intervals in the past (Noss, 2013, 2018). Moreover, some models predict greatly increasing lightning activity (Romps et al., 2014), which should benefit grasslands if at least some of the additional fires are not suppressed. However, humans now control land use across the region and are perfectly capable of suppressing most fires and preventing any widespread recovery of grasslands. In the end, the fate of grasslands rests on how we treat them—protection, restoration, and management versus continued destruction.

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- <https://www.segrasslands.org>—Southeastern Grasslands Initiative.
- <http://www.natureserve.org/conservation-tools/terrestrial-ecological-systems-united-states>—NatureServe Explorer (Terrestrial Ecological Systems).
- <https://islandpress.org/books/forgotten-grasslands-south>—Forgotten Grasslands of the South (Island Press).

Chaparral of California

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Abstract

California is one of five biological “hotspots” in the terrestrial temperate zone, all of which occur in Mediterranean-type climate regions. Chaparral is a dominant vegetation type in California, dominated by evergreen sclerophyllous shrubs. This vegetation occurs throughout the California Floristic Province, from northern Baja California to southern Oregon, and contains more than 20% of the flora of California, mostly as postfire herbaceous annuals. Chaparral occurs on poor shallow, soils, and often on steep slopes. Summer drought and fire, along with poor soils, are the main selective agents on the vegetation.

What Is Chaparral?

Chaparral is a shrub-dominated ecosystem in western North America (Keeley and Davis, 2007; Parker et al., 2016). Tough, evergreen shrubs and small trees characterize chaparral in California that makes up over 9% of the wildland vegetation in California (Parker et al., 2016). This nearly impenetrable (to humans) vegetation is one of the most biologically diverse ecosystems in California with numerous animals and over 1400 plant species (over 20% of the California flora) (Parker et al., 2016; Halsey and Keeley, 2016; Jennings, 2018). Many of these species are of limited distribution and are considered rare or endangered (Vasey and Parker, 2014; Keeley, 2018). Principally found on thin, rocky soils in topographically diverse mountains, chaparral dominates much of the coastal regions, southern California, and Sierra Nevada mountain landscapes (Fig. 1).

Chaparral is a dominant vegetation type in the California Floristic Province, an area encompassing most of the nondesert areas of California, as well as northern Baja California and southern Oregon. The region experiences a Mediterranean-type climate with mild wet winters and warm but rain-free summers. The consequence is strong selection for drought tolerance and adaptations to fire. The leaves of the dominant shrubs are usually small and strongly sclerophyllous. Plants exhibit a variety of adaptations to fire regimes. Analogous vegetation types occur in the four other similar climatic regions; *maquis* or *garrigue* in the Mediterranean basin, *fynbos* in the Cape Region of South Africa, *kwongan* in western and southern Australia, and *matorral* in central Chile (Rundel, 2011; Rundel et al., 2016). These five Mediterranean-type climate areas are recognized as areas of high biological diversity, with their floras totaling around one-sixth of the global flora in only about 2.2% of the land area (Cowling et al., 1996; Rundel, 2018). Each region is characterized not only by high diversity, but also by high endemism in multiple lineages. Within North America, chaparral-like shrub-dominated ecosystems extend into Mexico and the mountains of the western United States, but these areas have more summer rainfall and their species and dynamics differ in many characteristics (e.g., Keeley et al., 2012a).

Chaparral varies in species dominance among sites consistent with its extensive geographic distribution. More than 100 shrub species can be found in chaparral but any single site generally contains only a few. Variation in soil types and local climatic conditions are major drivers of composition and dominance shifts among locations. One species, *Adenostoma fasciculatum* (Rosaceae), is widespread and can be found in almost all lower elevation sites (Fig. 2). Two shrub genera have radiated within chaparral, *Arctostaphylos* (Ericaceae) and *Ceanothus* (Rhamnaceae). Shrub oaks (*Quercus* species, Fagaceae) and silk tassel bushes (*Garrya* species, Garryaceae) also have multiple species restricted to chaparral. At higher elevations *Adenostoma* species drop out, but species from the other common genera continue to dominate. Small trees from the genera *Hesperocyparis* (Cupressaceae) and *Pinus* (Pinaceae) are common members of lower elevation chaparral, and other trees may invade chaparral between fires. In more northerly stands and at higher elevations, chaparral is usually found in mosaics with mixed evergreen or conifer forests across the landscape (Fig. 3). Annuals, herbaceous perennials and suffrutescents make up a majority of species in chaparral, but they are common only in the first few years after fire and generally decline rapidly as the shrub canopy closes postfire.

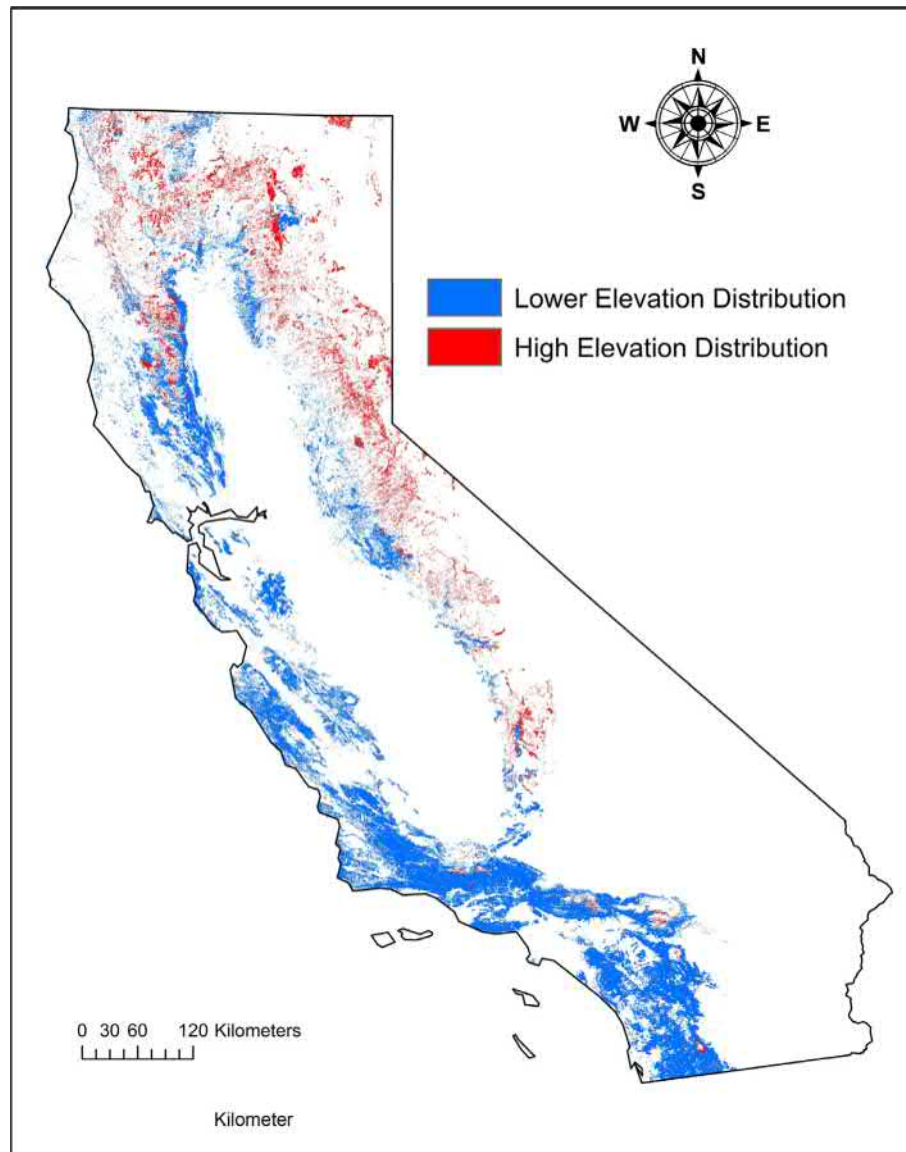


Fig. 1 Distribution of chaparral in California (chaparral also extends into SW Oregon to the north, and into Baja California to the south). Chaparral is divided into a lower elevation vegetation that also exhibits the high diversity postfire annuals and herbaceous perennials. The higher elevation chaparral contains similar woody species but the postfire display is low in diversity. Figure based on data from Cal Fire, Fire Resource and Assessment Program (FRAP) and modified with permission from a figure in Parker, V. T., Pratt, R. B. and Keeley, J. E. (2016). Chaparral. In Mooney, H. and Zavaleta, E. (eds). *Ecosystems of California—A source book*, pp. 479–508. Berkeley: University of California Press.

Origins of Chaparral

Fossil floras indicate that most chaparral shrub taxa trace their origins to at least the Eocene epoch. These floras were mostly east of California as geological processes were still actively forming a terrestrial California. By the middle Miocene, typical genera of chaparral dominants were found in fossil floras in western Nevada and eastern California. The combination of species now observed in chaparral is presumed to have depended on the origin of a Mediterranean-type climate. The timing of when this climate was established in California has been argued to be as early as the mid-Miocene (Keeley et al., 2012b; Rundel et al., 2016) or as late as the Pliocene or early Pleistocene (Axelrod, 1989). Regardless, a Mediterranean-type climate undoubtedly sorted the floras and enabled those genera with evergreen sclerophyllous leaves and other adaptive traits to expand (Axelrod, 1989; Ackerly, 2004; Keeley et al., 2012b). The Mediterranean-type climate varies considerably in California (Fig. 4) (Abatzoglou et al., 2017), acting as one of the driving processes for the variation observed in chaparral. Northern California (e.g., Marin County, Fig. 4) experiences considerably more precipitation due to a higher frequency of winter frontal systems. Southern California (e.g., Los Angeles County, Fig. 4) experiences higher average temperatures than regions to the north. There is also a gradient in maritime conditions; these are coastal fog or relatively low elevation cloud cover with much cooler temperatures in summer only a few kilometers from hotter



Fig. 2 *Adenostoma fasciculatum* dominated chaparral from Southern California. Other species include *Quercus berberidifolia* and others.



Fig. 3 Montane chaparral at over 2200 m in the northern Sierra Nevada on volcanic soils. Chaparral at higher elevations forms dense stands dominated by different mixtures of *Arctostaphylos patula*, *A. nevadensis*, *Quercus vaccinifolia*, *Garrya fremontii*, *Ceanothus cordulatus*, *C. velutinus*, *C. prostratus*, *Prunus emarginata*, and others. These sites are well above the winter permanent snowline and experience a more condensed growing season than lower elevation sites.

inland conditions. Such maritime conditions are frequent in the summer in northern and central California, declining generally southward down the coast. A high proportion of Marin County's land area directly experiences summer fog or moderated temperature (Fig. 4) such that, even with a range of summer temperatures in different locations, the county average temperature is considerably reduced in summer. Areas with breaks in the north-south ranging coastal mountains permit maritime condition to penetrate farther inland in areas like the San Francisco Bay, Monterey Bay, and Morro Bay. South of Point Conception, where ocean currents shift, maritime conditions persist, but are much more limited in impact. Considerable variation thus exists in California's Mediterranean-type climate.

Many of the species found in chaparral appear to have arisen prior to the development of a Mediterranean climate and are consider paleo-endemic taxa in chaparral, such as the widespread dominant *Adenostoma*, but also other genera like *Pickeringia*

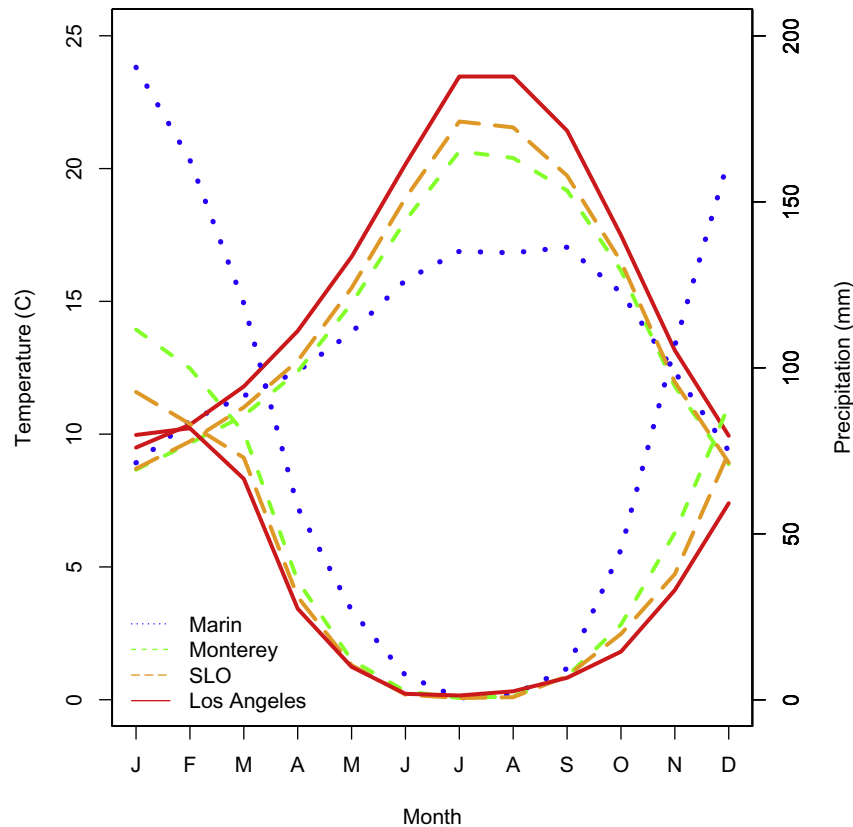


Fig. 4 Temperature and precipitation profiles for four counties in California. The counties, from north to south, are Marin, Monterey, San Luis Obispo, and Los Angeles Counties. The data are average monthly temperature and average monthly precipitation. The lines peaking in the summer represent temperatures (*left y-axis*), while the lines at zero in the summer represent precipitation (*right y-axis*). Temperatures are higher in southern California and decline to the north, especially in summer. Note that the summer lacks precipitation in all locations. Precipitation peaks in the winter and is higher in the northern regions. Data are from Abatzoglou, J. T., McEvoy, D. J., and Redmond, K. T. (2017). The west wide drought tracker: Drought monitoring at fine spatial scales. *Bulletin of the American Meteorological Society*. doi:10.1175/BAMS-D-16-0193.1.

(Fabaceae) and *Dendromecon* (Papaveraceae). The modern chaparral flora represents combinations of these older lineages, along with considerable and more recent immigration from regional floras. The high levels of endemism in chaparral are principally found in the postfire herbaceous flora as only two shrub genera have extensively diversified, *Arctostaphylos* (Ericaceae) (Boykin et al., 2005; Wahlert et al., 2009) and *Ceanothus* (Burge et al., 2011).

Drought and Wildfire: Key Processes of Ecology and Evolution

California averages a much smaller amount of summer rain than other Mediterranean-climate regions (Keeley et al., 2012b), suggesting greater selection for drought-tolerating traits that can aid plant survival. When researchers point out the lack of summer rain in Mediterranean-climates, one aspect that frequently lacks emphasis is the small total amount of precipitation. Most areas in California with chaparral average only around 400–600 mm annual precipitation. Because annual patterns can vary 20% or more between years, in dry years water stress can be considerable, while in wet years, total precipitation can still be less than most temperate regions. Rather than rare events, then, normal fluctuation in aspects of climate can be significantly stressful, occurring multiple years in every decade (Cowling et al., 2005; Cayan et al., 2008; Dettinger, 2016).

Physiology and Drought Stress

As a consequence of the lack of summer rain, drought-adapted shrubs dominate chaparral (Mooney, 1989). The lack of summer moisture constrains the growth and productivity of these species. Precipitation, however, falls in the winter and spring when temperatures are relatively low and days are shorter in photoperiod. Growth and metabolism of these plants then is regulated by low soil moisture in the summer and fall, shifting photoperiod, and temperature (Mooney et al., 1975, 1977; Davis and Mooney,

1986). These factors create a strong seasonal cycle with assimilation peaking in spring and early summer, and water conservation emerging as a constraint in late summer and fall (Parker et al., 2016).

The presence of evergreen leaves of the dominant shrubs allows photosynthesis to occur throughout the year. More active rates of photosynthesis occur following rains in the fall and winter, although the daylight periods are shorter and temperatures are cooler. Even with cooler temperatures, photosynthesis continues near optimally during winter and early spring (Oechel et al., 1981; Mooney and Miller, 1985; Parker et al., 2016). Chaparral shrubs are able to photosynthesize at relatively maximal rates over a broad range of temperatures (10–30°C) (Mooney et al., 1975; Oechel et al., 1981). Consequently, rates of photosynthesis and growth are moderate in winter and tend to increase throughout the moist spring as temperatures warm along with longer day lengths. Leaf structure is compromised between maximizing rates of carbon assimilation versus water conservation and survival of low water potentials. Leaves are low in specific leaf area (SLA), which makes them mechanically strong and better able to tolerate water stress. Sclerophyllous leaves, however, limit the maximum potential rates of carbon assimilation and summer drought can further restrict photosynthesis as plants reduce transpiration by stomatal control (Pratt et al., 2007) (Fig. 5).

Chaparral principally occurs in shallow, rocky soils on equator-facing slopes. Rooting depth becomes a major organizing concept with respect to species distribution patterns within chaparral and what types of adaptive characteristics they may exhibit. Species with deeper roots as adults can avoid water stress for longer time periods, but tend to be distributed in more mesic sites, like polar-facing slopes or ravines. Constraints on seedling establishment are probably responsible for this initially counterintuitive pattern. *Heteromeles arbutifolia* and *Rhus laurina* (Anacardiaceae) are good examples. Species dominating ridges or equator-facing slopes tend to have shallower rooting systems but with vascular structures able to withstand lower water availability (Jacobsen et al., 2007); *Ceanothus* and *Arctostaphylos* species are typical of this group. Most species tend to fall between the extremes, but using the extremes as representatives of different sets of adaptations, chaparral species have diverged in a number of ways. The more shallow-rooted species will experience much drier soils in the late summer and early fall and experience much greater minimum water potentials (Jacobsen et al., 2007; Pratt et al., 2007). They also tend to have strong stem cavitation resistance, close their stomata at much lower water potentials, and have denser and stronger xylem (Jacobsen et al., 2007; Pratt et al., 2007, 2008). These plants also have tracheids associated with vessels (vasicentric tracheids) (Carlquist, 1989), thought to provide an adaptive back-up water source for leaves should cavitation occur in the main vessels. Species with deeper roots tend to have larger, slightly more mesic leaves and be more sensitive to dry conditions, especially as seedlings (Parker et al., 2016).

Fire and Adaptive Responses

A consequence of the seasonal droughts is a fire regime. The relatively low stature of chaparral (generally 2–6 m) and continuous canopy structure means that fire will carry through the canopy and consume nearly the entire above-ground biomass. Consequently, these are fairly intense fires, but vary in intensity within and among fires depending on environmental conditions. Multiple dimensions make up the chaparral fire regime (Keeley and Safford, 2016). The frequency of fire is variable but generally occurs



Fig. 5 Close up of the sclerophyllous leaves of *Ceanothus cuneatus*. These leaves are only about 2 cm in length and provide an example of some of the leaf type most chaparral species exhibit. Some species have leaves that are more needle-like, in others the leaf blade is larger; some are cupped upward, others flat or rolled in on the lower surface.

between 30 and 100 or more years. Historical records are lacking for vegetation of this type, but given the presence of serotinous conifers and other types of data, together they indicate this is a natural range, especially given the climatic variation in distribution for chaparral (van Wageningen and Cayan, 2008; Van de Water and Safford, 2011; Safford and Van de Water, 2014; Parker et al., 2016; Syphard and Keeley, 2016; Keeley and Syphard, 2017). Fires historically tended to peak in September at lower elevations as the vegetation began to dry. This follows fruiting and dispersal for most species. Fire severity is moderate to high, and variations in local severity can favor different sets of species arising from the seed bank. Other aspects can sometimes be important, depending on environmental conditions. Historically lightning was the primary source of ignition, but with the expansion of human infrastructure and population densities, accidental ignitions by people are now the most common ignition sources (Keeley and Syphard, 2018). In the past century, as population density increased, so too did fire ignitions. Since around 1980, however, ignitions have begun to decrease while area burned has stayed relatively constant (Keeley and Syphard, 2018).

Chaparral dynamics therefore reflects the pattern of fire, postfire recovery, and maturation, all in the context of fluctuating drought conditions. Variation in fire frequency, intensity and other conditions within the normal fire regime favor different sets of species. The first postfire year is characterized by a diverse group of annuals, suffrutescents, and species with bulbs and corms. Fire also stimulates their postfire germination or emergence due to both the fire's heat pulse into the soil or due to chemicals from smoke that the first winter rains wash into the soil (Keeley, 1987, 1991; Keeley et al., 2012b). The annual populations remain for one to several years; the seed produced during those years remains dormant in the soil until the next fire (Figs. 6 and 7). The herbaceous perennials and suffrutescents persist until the dominant shrubs close the canopy of the vegetation (Fig. 8). Many of these herbaceous perennials and suffrutescents also produce dormant, persistent seed banks. These are very diverse groups of species, with representatives from a number of plant families like Fabaceae, Lamiaceae, Polemoniaceae, Onagraceae, Papaveraceae, Hydrophyllaceae, Liliaceae, and Melanthiaceae among others (Keeley and Davis, 2007; Parker et al., 2016; Keeley, 2018).

Most woody plants in chaparral are capable of surviving fire due to underground stems, root crowns, or enlarged woody bases containing a high density of dormant buds (burls). In the first postfire year, surviving shrubs resprout and grow rapidly so that within a few years the stand has closed the canopy again and a continuous layer of vegetation covers the landscape. Most of these shrubs recruit new individuals only in the shade of older stands so their persistence requires their ability to survive fires. These shrubs are referred to as obligate sprouters and examples are species from *Grassia*, *Heteromeles*, *Frangula* (Rhamnaceae), and *Quercus* among others (Fig. 9) (Table 1). Three chaparral shrub genera, *Adenostoma*, *Arctostaphylos*, and *Ceanothus*, have developed seed that partially or completely remain dormant until stimulated by fire, either due to a heat pulse into the soil or from chemicals found in smoke (Keeley, 1987, 1991, Parker and Kelly 1989). In the first postfire year, shrubs resprout and seed from the soil seed bank germinate and recruit new individuals; these plants have been referred to as facultative seeders (Table 1; Fig. 9). A different life history has also developed in some species in the latter two of these genera, *Arctostaphylos* and *Ceanothus*. In these species the adults are killed by fire and the population is completely dependent on seedling recruitment emerging from the soil seed bank to maintain their populations. Because of this pattern, these species have been referred to as obligate seeders (Table 1; Fig. 10). A similar life history occurs in some of the conifers associated with chaparral. The cones of some lineages of *Pinus* and *Hesperocyparis* remain closed after maturation and are opened by the heat of the fire, a condition referred to as serotiny. The adults of these trees are killed and the population recruits from the postfire dispersal from the cones. They are also obligate seeders but utilize their closed, serotinous cones as aerial seed banks. Chaparral also occurs in landscape mosaics with other vegetation types, especially a variety of forests. In those circumstances, trees may invade chaparral during fire-free periods, but are usually eliminated by canopy fires unless they are able to resprout (Table 1).



Fig. 6 *Chorizanthe pungens* var. *hartwegiana* (Ben Lomond spineflower), a rare species except after fire, an example of the annual diversity in the postfire years.



Fig. 7 *Phacelia suaveolens* (sweet scented phacelia) is a pyrophyte in the sense that you see it after fires and then it remains only as seed in the soil until the next fire. A number of *Phacelia* species throughout the range of chaparral are abundant in the postfire years.



Fig. 8 *Xerophyllum tenax* (bear grass) is a herbaceous perennial species in the Melanthiaceae, a family of the Liliales. This plant can rarely be found flowering except in the years following a fire. Native Americans would burn areas with this plant because the leaves in the first year or two following fire can be used for baskets (hence the other common name, basket grass).

Among these species, aspects of physiology diverge with respect to characteristics of the habitat for germinating seed and seedling establishment. This is clear when examining woody species. Those taxa that are obligate sprouters establish seedlings in the shade of mature chaparral, their physiology matches the requirement of seedlings being somewhat shade tolerant and more mesic (Pratt et al., 2010). Obligate and facultative seeders establish seedlings in open, postfire habitat with high light and variable temperatures; they are generally shade-intolerant. These seedlings have to grow roots rapidly to survive and indeed most seedlings do not survive the first summer-fall dry period. Overall, then, chaparral illustrates a range of species with respect to fire regimes, from those with no obvious adaptations but exploit fire free periods, to those whose populations are adapted to and dependent on fire to recruit new individuals.



Fig. 9 Chaparral response in the first growing season following a fire. Shrubs here are resprouting, with most of the site dominated by *Quercus wislizenii* var. *frutescens*, an obligate sprouter, with *Arctostaphylos glandulosa*, a facultative seeder, in the right foreground appearing a little grayer.

Biological Diversity of Chaparral

Chaparral is one of the most diverse vegetation types in California, with over 20% of the flora comprising part of chaparral. The majority of species are seen only in postfire circumstances, either their regeneration being tied to fire stimulation of germination or their abundance limited by the closed canopies of the dominant shrubs prior to fire (Keeley and Davis, 2007; Parker et al., 2016). Thus variations in fire regimes are fundamental drivers of diversity found in chaparral and as human populations increase and modify fire regimes, such changes may be a large influence on future chaparral diversity as we will focus on later.

The postfire arena exhibits over three-quarters of the chaparral flora, principally as annuals or herbaceous perennials. Many of these are essentially endemic to chaparral, such as a variety of species from the Hydrophyllaceae (e.g., *Emmenanthe penduliflora*, *Phacelia brachyloba*, *P. grandiflora*, *P. sauevolens* among others), Papaveraceae (e.g., *Ehrendorferia chrysantha*, *E. ochroleuca*, *Papaver californicum*), Polemoniaceae (e.g., *Allophyllum glutinosum*, *A. giliodes*, *Saltugilia australis*) among others (Keeley and Davis, 2007, Parker et al., 2016). These species generally occur patchily across the landscape and are dependent on local and historical conditions; local referring to site fire severity, and current patterns of precipitation and temperature, while historical mainly refers to dispersal patterns of fires in the past and the climatic conditions associated with past postfire environments.

Suffrutescents, or subshrubs as they are sometimes called, are also common in postfire areas. Most of these have dormant seed banks stimulated by fire. Their rapid growth rates permit their establishment and temporary dominance in the postfire circumstances, slowly being eliminated by woody shrub canopies shading them out through time. Typical species vary among sites, but *Crocianthemum* (*Helianthemum*) *scoparium* and other species in the Cistaceae are widespread; other local dominants include *Eriocameria arborescens* (Asteraceae), *Eriodictyon californicum* (Hydrophyllaceae), *Acmispon glaber* (*Lotus scoparius*) (Fabaceae), *Lepechinia calycina* (Lamiaceae), *Salvia mellifera* (Lamiaceae), *Diplacus* (*Mimulus*) *aurantiacus* (Phrymaceae), and *Eriogonum fasciculatum* (Polygonaceae).

Two woody shrub species have radiated in California chaparral, *Arctostaphylos* and *Ceanothus*. *Arctostaphylos* has about 104 taxa, almost all of which are found in the California Floristic Province (Parker et al., 2012) (Fig. 11). About two thirds of the taxa are obligate seeders while the rest are facultative seeders. The resprouting individuals have large burls, a character lacking in *Ceanothus*. A similar diversity pattern is found in *Ceanothus* comparing facultative versus obligate seeding, with nearly two thirds or more being obligate seeders (Fig. 12). Within *Ceanothus*, however, there is less clarity about whether a species is an obligate seeder or not, and in some lineages, there is a shift in the proportions of individuals among populations that are killed versus those that resprout after fire. *Ceanothus thyrsiflorus*, for example, has a higher proportion of individuals that resprout in its southern distribution, for example, San Luis Obispo County, while almost all individuals are obligate seeders toward northern California. Another species, *Ceanothus tomentosus*, has resprouting populations in the Sierra Nevada foothills, but populations in coastal San Diego County are obligate seeders (Schwilk and Ackerly, 2005). This divergence may result from specialization in different types of habitats, with obligate seeders being favored under different conditions from facultative seeders (Keeley et al., 2016).

Much of the diversity in *Ceanothus* and *Arctostaphylos* is comprised of local endemics, often restricted to areas with maritime influence of moderated temperatures and some frequency of coastal fog (Fig. 13). In the area around the northern San Francisco Bay, for example, a series of species of *Ceanothus* occur on a range of soil types and climatic conditions. *Ceanothus jepsonii* var. *jepsonii*

Table 1 Common plant life form and life history types in California chaparral.

Life form	Life history	Occurrence	Example species	Common name
Tree	<i>Survives only surface fires</i> (no canopy fires)	Generally trees in coast ranges, especially in the more northerly areas or higher elevations in mountains, invades chaparral over time	<i>Pseudotsuga menziesii</i> <i>Pinus ponderosa</i> <i>Abies concolor</i>	Douglas-fir Ponderosa pine White fir
	<i>Obligate sprouter</i>	Coast ranges in central California and more mesic regions; one restricted species in Southern California	<i>Quercus agrifolia</i> <i>Notholithocarpus densiflorus</i> <i>Pseudotsuga macrocarpa</i>	Coast live oak Tanbark oak Big-cone Douglas-fir
	<i>Serotinous or semiserotinous</i> (adults dying, population reestablishes from seed dispersed postfire) (obligate seeder)	In more mesic regions of chaparral environmental gradients, mostly coast ranges, Sierra foothills	Multiple pine species, especially <i>Pinus attenuata</i> , <i>P. radiata</i> , <i>P. muricata</i> , <i>P. sabiniana</i> ; Multiple cypress species, especially: <i>Hesperocyparis sargentii</i> <i>H. macnabiana</i>	Knobcone pine Monterey pine Bishop pine Gray pine Sargent's cypress MacNab's cypress
Shrub	<i>Obligate sprouters</i> (species regenerating later on in fire-free periods in the shade of mature stands)	Widespread and common throughout	Multiple species of shrub oaks, especially: <i>Quercus berberidifolia</i> <i>Q. durata</i> <i>Q. vaccinifolia</i> <i>Q. wislizenii</i> var. <i>frutescens</i> Multiple other species like: <i>Heteromeles arbutifolia</i> <i>Pickeringia montana</i> <i>Garrya elliptica</i> <i>Frangula californica</i> <i>Cercocarpus betuloides</i> <i>Rhus integrifolia</i> <i>Rhus ovata</i> <i>Malosma laurina</i>	California scrub oak Leather oak Huckleberry oak Interior live oak Toyon Chaparral pea Silt tassel Coffee berry Mountain mahogany Lemonade berry Sugar bush Laurel sumac
	<i>Facultative seeders</i> (species resprouting after fires, but recruiting new individuals in the first year or two postfire from dormant, fire-stimulated soil seed banks)	Widespread and common throughout	<i>Adenostoma fasciculatum</i> Several species of manzanitas, especially: <i>Arctostaphylos glandulosa</i> <i>A. tomentosa</i> <i>A. crustacea</i> <i>A. patula</i> Several species of California lilac, especially: <i>Ceanothus leucodermis</i> <i>C. cordulatus</i>	Chamise Eastwood manzanita Woolyleaf manzanita Brittleleaf manzanita Greenleaf manzanita Chaparral whitethorn Mountain whitethorn
	<i>Obligate seeders</i> (species whose adults are killed by fire and recruit new individuals in the first year or two post-fire from dormant, fire-stimulated soil seed banks)	Widespread and common throughout	In California only two shrub genera represent this life history. The majority of species in both genera are obligate seeders, with many local endemics. <i>Arctostaphylos</i> , especially: <i>A. canescens</i> <i>A. glauca</i> <i>A. pungens</i> <i>A. manzanita</i> <i>A. stanfordiana</i> <i>A. viscida</i> <i>Ceanothus</i> , especially: <i>C. cuneatus</i> <i>C. crassifolius</i> <i>C. perplexans</i> <i>C. jepsonii</i> <i>C. thyrsiflorus</i> <i>C. papillosus</i> <i>C. oliganthus</i>	Hoary manzanita Big berry manzanita Mexican manzanita Common manzanita Stanford manzanita White leaf manzanita Buckbrush Hoaryleaf Ceanothus Cupped leaf Ceanothus Musk brush Blue blossom Wartleaf Ceanothus Hairy Ceanothus/Jim brush.

is a serpentine endemic found in one area just north of San Francisco, while closer to the coast and under more summer fog *C. decoratus* is another highly restricted serpentine endemic (Parker, 2014). Along the immediate coast are three varieties of *C. gloriosus* that range from highly restricted endemics to spottily distributed populations up the coast. To the east and north, another highly restricted serpentine endemic, *C. sonomensis* occurs, but farther north being replaced by *C. jepsonii* var. *albiflorus*. On other soil types, *C. purpureus* dominates volcanic soils in the Napa Range, while to the west of the Napa Range, *C. divergens* and *C. confusus* can be found (Parker, 2014). In central and southern California, other examples of local endemism in *Ceanothus* can also be found (Burge et al., 2017). *Arctostaphylos* demonstrates similar patterns of diversity and restricted endemics (Fig. 14). In the San Luis Obispo region of the central coast a series of local endemics are found on diverse soil types (Wells, 1962). In the maritime region around Monterey and San Francisco Bay, jumping down the coast to islands off Santa Barbara are a series of species with leaves unique in the genus having auriculate shapes. These include *A. auriculata* and *A. pallida* in the north, to *A. imbricata*, *A. montaraensis*, *A.*



Fig. 10 Seedlings of *Arctostaphylos andersonii* emerging from a rodent cache in the first postfire spring. This provides an example of both germination of dormant seed that were stimulated by chemicals from the fire, as well as illustrating the mutualistic role of rodents in caching the seeds to a depth sufficient to keep them below the killing heat pulse in the soil during a fire.



Fig. 11 *Arctostaphylos* (manzanita) dominated chaparral from Mt. George, Napa County, Northern California. In the foreground are two different species of *Arctostaphylos* (*A. canescens*, grayish, *A. stanfordiana*, green). On the left foreground several individuals of *Adenostoma fasciculatum* are visible, with very small, needle-like leaves. The landscape in the background is dominated by manzanita chaparral.

andersonii, and others going south to *A. viridissima* on Santa Cruz Island (Parker et al., 2012). In both genera, some of these taxa may have evolved due to hybridization or by ancestral variability constrained by strong edaphic conditions, permitting different genetic combinations to parse local soil and climate conditions (Wells, 1968, 1969; Burge et al., 2011, 2013, 2017, 2018; Parker and Vasey, 2004, 2016; Vasey and Parker, 2014).

Chaparral animals also represent a diverse group. California has considerable mammal diversity including within chaparral areas (Parker et al., 2016; Halsey and Keeley, 2016; Jennings, 2018). While many of these mammal species frequent multiple habitats, some are essentially restricted to chaparral or similar shrub habitats, like *Peromyscus californicus*. These animals can



Fig. 12 *Ceanothus cuneatus* (buckbrush) dominated chaparral in the Sierra Nevada foothills. This *Ceanothus* species and close relatives occupy lower elevation chaparral in the foothills of the Sierra Nevada on a variety of soil types. This figure illustrates chaparral in the Red Hills region where soils are principally serpentine. The site also contains *Pinus sabiniana*, a semiserotinous species, *Adenostoma fasciculatum*, and a few other shrub species sparsely. A number of rare annuals are present during the growing season.



Fig. 13 Maritime chaparral on sand dunes in Monterey County. This site is only a few km from the Pacific Ocean and is dominated by *Arctostaphylos tomentosa*, *A. pumila*, *Ceanothus rigidus*, and *Quercus agrifolia*. Annuals dominate available sandy openings during the growing season.

represent critical ecological processes, such as seed predation and dispersal (Warzecha and Parker, 2014; Parker, 2015), burying seed in some cases to depths and in manners ensuring seed survival (Parker, 2015; Peterson and Parker, 2016) (see Fig. 10). Invertebrates are especially important in chaparral, as key pollinators and components of mineral and energy flow. Over 500 invertebrates, for example, have been found on one species alone of montane chaparral, *Arctostaphylos patula* (Valenti et al., 1997). These are principally herbivores, predators and parasitoids. Coastal plant species also appear to harbor considerable diversity, with over 200 insect taxa found on 26 coastal manzanita species, most of which were foliovores (Andres and Connor, 2003). At least two invertebrate genera have radiated in chaparral. One aphid genus, *Tamalia*, has multiple species, all of which are apparently restricted to *Arctostaphylos* species (Miller III, 2005). *Timena* is a genus of walking-stick insects that have evolved variations in cryptic coloration relating to their host plants, species of *Ceanothus* and *Adenostoma* (Crespi and Sandoval, 2000). Other lineages are richly diverse in chaparral, for example, over 300 bee species are found in chaparral in San Diego County (Halsey and Keeley, 2016).



Fig. 14 Serpentine chaparral in the Laguna Mountain ranges of San Benito County. This inner coast range site is dominated by soils derived from serpentinite. These soils are poor in nitrogen and phosphorus, generally have an imbalance between magnesium and calcium, and are rich in heavy metals. *Arctostaphylos glauca*, *A. pungens*, and *Quercus durata* are the shrub dominants at this site. The pine is *Pinus sabiniana*, a semiserotinous species.

Ecosystem Services

Chaparral is often perceived generally as “worthless brush” or a major fire hazard (Sterling, 1904; Love et al., 1952; Doman, 1967; Rundel, 2018), but much less often as the valuable ecosystem that it actually is. Without trails, chaparral is nearly impenetrable and difficult for people to enjoy. Chaparral does provide considerable ecosystem services, however. The Millennium Ecosystem Assessment (MA) (2003, 2005) defined such services as benefits that people obtain from the functioning of ecosystems. One is clearly the cultural services most natural areas provide to people; the aesthetic of mountain slopes and views, the slopes coming into flower and fruit in different seasons from mid-winter to late summer is something many enjoy.

More critically, functioning chaparral provides all four of the service categories indicated by the Millennium Assessment, including provisioning (such as food, fuel), regulating (such as air and water purification, climate stabilization, hazard mitigation), cultural (such as spiritual, aesthetic and educational enjoyment of nature), and supporting services (such as soil formation, nutrient cycling, biomass production) (Chaplin-Kramer et al., 2016; Parker et al., 2016; Rundel, 2018).

For example, a large proportion of areas dominated by chaparral are moderate to steep slopes, the kind that are subject to erosion, mudslides and debris flows. Chaparral shrubs with their various shallow to deep rooting systems are able to mitigate and constrain these processes, such that danger from debris flows are limited to occasional postfire years with heavy rains (Gabet and Dunne, 2002; Ren et al., 2011; Rundel, 2018).

Stands of chaparral also filter water and produce watersheds that can reduce N pollution and other hazards from precipitation and air pollution. Downstream these services reduce eutrophication in reservoirs and adjacent near-shore regions (Rundel, 2018). At the same time, chaparral is a relatively productive vegetation, even in older stands, and consequently provides considerable biomass and carbon sequestration. The shrub canopies also mitigate the heat island effect of adjacent developed regions, a critical feature as climate change predicts increasing temperature (LaDochy et al., 2007; Rundel, 2018).

In addition to these types of ecosystem processes, chaparral vegetation is a habitat for a large number of fungal and animal species. Extensive chaparral provides significant pollination services beyond its own boundaries (Kremen et al., 2004). The large number of organisms indicates extensive food webs, which provide wildlife value for birds and mammals not restricted to chaparral.

Threats to Chaparral Conservation

Mediterranean climate ecosystems globally are highly threatened for diversity loss due to increasing habitat loss and climate change (Sala et al., 2000; Stein, 2002; Underwood et al., 2009). In California, urban and agricultural expansion has replaced roughly 75% of all natural vegetation, including considerable chaparral (Brooks et al., 2004). Currently, most chaparral management practices are focused on fire and fire hazard rather than on practices that would sustain or enhance this ecosystem and its services. Many people seem to have a perspective that they are separate from natural processes, and when something is a negative or threatening feature of the region, they desire to reduce it as much as is possible. Treating chaparral only as a fire hazard is a principal issue today.

One critical threat is the over-generalization of fire-type vegetation. Chaparral is resilient to fire within a range of frequencies, severities, and timing that it has historically experienced, a pattern that varies among locations such as the foggy maritime chaparral along the coast, to drier inland sites, to higher elevation montane chaparral above the winter snowline. When articles appear in the press concerning fire, chaparral is frequently lumped with forests and the whole state of California is seen in a homogeneous perspective. The reality, however, is that fire regimes vary considerably among vegetation types (Keeley and Safford, 2016) and considerably within those different vegetations (Syphard and Keeley, 2016; Keeley and Syphard, 2017; Parker et al., 2016). The application of a single fire concept and ignoring locally and regionally unique responses in such a variable ecosystem is destructive. For example, poor timing of management, like reducing fuel load by burning chaparral under moist and cool conditions when it is safer to control, considerably reduces the ability of chaparral to recover, especially from the persistent soil seed bank (Doman, 1967; Parker, 1987, 1989, 1990, 1993; Le Fer and Parker, 2005). Not recognizing variation in species composition also threatens chaparral recovery from fire. Increases in fire frequency eliminates obligate seedling species and permits non-native annual plants to invade, degrading the system function (Zedler et al., 1983; Haidinger and Keeley, 1993). Similarly, introducing large scale fire breaks provides a corridor for invasive annuals that limit chaparral postfire recovery (Keeley, 2006; Halsey and Keeley, 2016). These are issues throughout global Mediterranean-type climate shrub ecosystems (Keeley et al., 2012b).

Fire hazard concern also emphasizes one of the greatest threats to chaparral, which is increasing population and encroachment of communities into wildland areas. Increased frequencies of fires associated with human expansion and strong desert winds in Southern California has resulted in type conversions in a number of sites. Because people are the most common source of ignitions in California (Syphard et al., 2007, 2017; Keeley and Syphard, 2018), increased fire frequency has been followed by calls for intensive (mis)management of chaparral. The total number of fires has been declining for the past 50 years (Keeley and Syphard, 2018), but the eight of the largest and mostly deadly fires have been in the past decade. Human ignitions in the context of climate change in chaparral areas adjacent to exurban and urban housing is an increasingly unsafe and ecologically destructive combination.

Climate change thus may represent a significant threat as well. A narrowed rainy season combined with higher summer temperatures means the potential for fire increases from 4 to 6 summer to early fall months, to nearly year-round conditions. Changes in ocean temperatures and currents along the California coastline may reduce the frequency and persistence of coastal fog (Johnstone and Dawson, 2010). Such a modification of coastal environments potentially threatens California's maritime chaparral in these regions (Vasey et al., 2012). These maritime habitats contain a majority of the woody rare and endemic chaparral species (Vasey et al., 2014; Vasey and Parker, 2014). Finally, impacts on mutualisms may be substantial, such as for populations of pollinators (Memmott et al., 2007).

Recent decades have also witnessed the introduction of multiple pathogens, particularly species in the genus *Phytophthora*, which can injure and sometimes kill numerous chaparral species. The genus *Arctostaphylos*, the most diverse woody plant genus in chaparral, may be particularly sensitive to some *Phytophthora* (Swiecki et al., 2003, 2017). While these pathogens are management problems in protected areas, habitat loss and destruction due to fire hazard management remain the principal issues.

Animals within chaparral are also increasingly at risk as development encroaches on natural areas. In addition to the direct loss of habitat that results from the clearing of chaparral to make way for developments, development adjacent to and human activity within wild areas appears to change the distribution and reduce the richness of wildlife (Sauvajot et al., 1998; Ordeñana et al., 2010; Šálek, 2014). In some cases it results from domesticated animals that prey on birds or rodents (Crooks and Soulé, 1999). Recent research indicates human development causes substantial changes in mesopredator distribution and temporal responses, and also shifts in their feeding niches (Wang et al., 2015; Gaynor et al., 2018; Smith et al., 2018).

Future of Chaparral

Climate change and increasing population density in California make predicting the future of chaparral difficult (Parker et al., 2016). Recent dieback from extended droughts in southern regions of California (Paddock III et al., 2013) indicate that fluctuations in future climate may impact chaparral considerably (Hayhoe et al., 2004; Cayan et al., 2008; Dettinger, 2016). Shortened rainy season and increases in temperature will extend the fire season for most areas of the region. Changes in climate and fire regimes will combine to drive changes in the composition and distribution of chaparral (Keeley and Syphard, 2016). Management practices that treat chaparral primarily as a fire hazard and increases in invasive species will further alter fire regimes and distribution patterns, cascading into the food webs of the ecosystem and the services provided.

Chaparral is a biotically diverse and abundant vegetation in California. The fact that fire regimes are a critical aspect of the dynamics and regeneration of the ecosystem leads to conflicts with human occupation on the landscape. No policies have yet been produced and implemented that balance conservation of chaparral with safety for urban and exurban developments. Recognition of the ecosystem services provided by chaparral, as well as the biodiversity spread across the state, will aid in a future accommodating both chaparral and human development. Considering current management practices in a context absent of fire crises will be necessary to achieve such balance.

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California Oak Savannas and Grasslands

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Abstract

California's oak savannas and associated grasslands occupy roughly 3 million ha. They are defined by the presence of scattered oak trees, in monospecific or mixed stands, with an herbaceous ground cover, composed predominantly of annual grasses and forbs. Supporting natural communities rich with native flora and fauna, oak savannas and grasslands contribute significantly to the designation of the California Floristic Province as a "biodiversity hotspot". These systems also provide numerous benefits to humans: in the past sustaining indigenous cultures who depended on oak acorns for food, and in the more recent past and present as a source of wood, timber, livestock grazing, and recreation. Climate in California's oak savannas is Mediterranean, with cool, wet winters and hot, dry summers. Both climate and soil type exert broad control on the distribution of grasslands and co-occurring woody vegetation in California. At a finer scale, plant and animal interactions strongly influence community structure and dynamics, as do human impacts such as livestock grazing and the use of fire. Two of the most significant threats to the longterm sustainability of California's oak savannas and grasslands are land-use conversion to agriculture and residential development, compounded by low rates of natural regeneration in extant stands of oaks.

Introduction

Savannas are generally defined as open woodlands, composed of scattered trees over an herbaceous ground layer. In California's oak savannas the tree canopies are generally not overlapping, and oak trees comprise between 10 and 30% of the vegetative cover (Griffin, 1977; Grossman et al., 1998; Allen-Diaz et al., 1999; Sawyer et al., 2008). Grassland, characterized by herbaceous graminoid and forb species (Grossman et al., 1998; Sawyer et al., 2008), dominates in the intervening spaces between the trees and extends under the oak canopies. Thus, California oak savannas include components of both tree-dominant woodland and herbaceous-dominant grassland. In some oak savannas the understory may also include shrubs associated with chaparral or coastal sage scrub plant communities.

As has been described for other savanna ecosystems (Taft, 1997; Anderson et al., 1999), California oak savannas lie on a continuum from grassland to forest, and they often occur in a mosaic of grassland, shrubland, and woodland communities (Fig. 1). Depending on the spatial and temporal scale that observations are made, the boundaries of those community-types may not always be clearly demarcated. While some attributes, such as species composition and climate conditions, of the continuum “end points” described above (distinct grassland and oak forests) overlap with oak savanna, this article primarily focuses on savannas and their corresponding grassland communities.

Distribution

Oak dominated landscapes (forests, woodlands, and savannas) occupy roughly 4.5 million ha, or approximately 11% of the state of California (Davis et al., 1998). The more open landscapes—oak woodlands and savannas—have generally been considered a single “type” (e.g., 10–60% tree canopy cover) in hardwood inventories and wildlife assessments (Davis et al., 2016). However, it has been estimated that between 2.1 million ha (Davis et al., 2016) and 3.8 million ha (Allen-Diaz et al., 1999) in California are classified as oak savanna/grassland (i.e., 10–30% tree canopy cover).

The five species of arborescent oaks that are predominant in California’s oak savannas are blue oak (*Quercus douglasii* Hook. & Arn.), valley oak (*Q. lobata* Née), coast live oak (*Q. agrifolia* Née), interior live oak (*Q. wislizeni* A. DC.) and Englemann oak (*Q. engelmannii* Greene) (Fig. 2). These may be present in monospecific or mixed stands. Several previous articles characterize oak savannas as distinct vegetation communities or types (e.g. valley oak savanna, blue oak savanna, mixed oak savanna) (see Allen et al., 1991, and Allen-Diaz et al., 1999). Many of the key species co-occur (e.g., blue oak savanna, dominated by blue oak, may also include valley oak, interior live oak, and coast live oak) or are present in nearly all sites (e.g., many species of nonnative annual grasses). In addition, many of the ecological characteristics are similar among all these types. Thus in this article, we will focus on the distributions of each of the dominant tree species, with their common co-dominants and ranges, and elsewhere describe factors that are similar across all of these savannas.

Oak savannas dominated by blue oak, valley oak, and interior live oak, are found in a ring around the Central Valley along the inner Coast and Transverse Ranges and Sierra Nevada foothills. Coastal oak woodlands and savannas are dominated by coast live oak. Englemann oak savannas occur in a more geographically restricted distribution in the Peninsular Ranges. All occur primarily within an elevation range of 60–700 m (Allen-Diaz et al., 1999).

Although not the subject of this article, the unique oak woodlands found on the California Channel Islands ought to be mentioned, as they occasionally occur in relatively open settings, similar to the savannas on the mainland. Island oak (*Q. tomentella* Engelm.) is an evergreen tree and an insular endemic (Sawyer et al., 2008). Most often in north-facing slope and moist canyon habitats, island oak is present in dense groves and woodlands, co-occurring with coast live oak (*Q. agrifolia*), canyon live oak (*Q. chrysolepis*), and Catalina ironwood (*Lyonothamnus floribundus* A. Gray). The endemic island scrub oak (*Q. pacifica* Nixon & C.H.



Fig. 1 Mosaic of oak savanna, grassland, and shrubland at the University of California Sedgwick Reserve, Santa Barbara County. Photograph by C. Tyler.

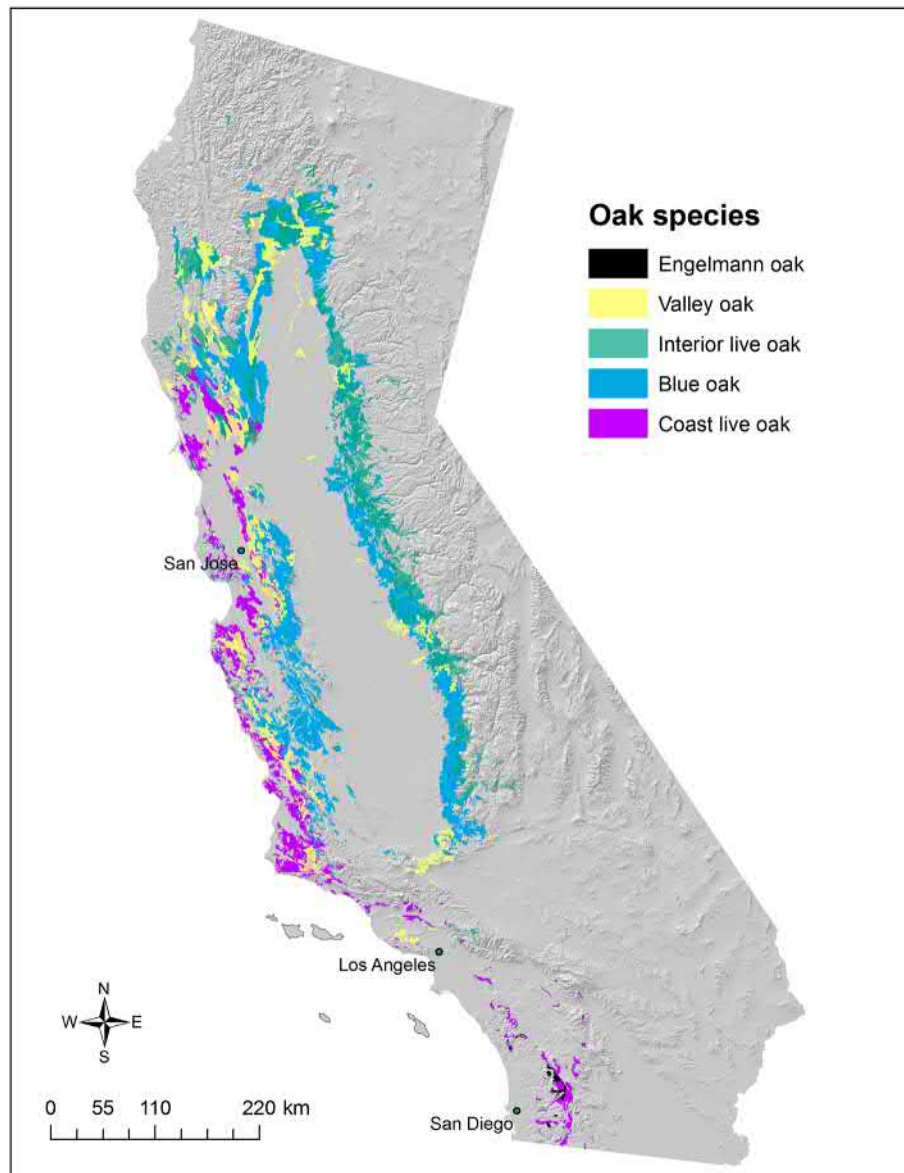


Fig. 2 California oak savanna and woodland landscapes as mapped by the California Gap Analysis Project (Davis et al., 1998). Characteristic dominant or co-dominant oak species are shown. Species may occur in mixed oak or oak-pine savannas but for legibility only one characteristic oak species is shown. The mapped species may also occur in less extensive areas beyond those mapped here. Map produced by F. W. Davis.

Mull.) can form woodland and savanna-like communities where individual shrubs reach treelike stature, especially on the uplands of Santa Catalina and the isthmus of Santa Cruz (Junak et al., 2007).

Climate and Soils

The climate in California's oak savannas is Mediterranean, with cool, wet winters and hot, dry summers. Over 90% of precipitation falls between December and March, with an extended summer drought. Foothill savanna oak species occur in locations that experience 40–80 cm of winter rainfall, and mean annual temperatures of 14–17°C (Davis et al., 2016).

The various oak species occur in many ecological settings including slopes, alluvial terraces, valley floor and some ridge-top environments. Oak savannas may be found on a wide variety of soil-types from rich loams in the valleys to thin, rocky or sandy soils on upland slopes, with the different oak species tending to occupy different settings and soil-types. For example, valley oak tends to occupy deep, relatively fertile valleys or canyon bottoms, while blue oak may be more common on drier slopes with rocky soils, but there are sites where these species co-occur.

Biodiversity: Key Species

Rich in both flora and fauna, California's oak woodlands and savannas support thousands of understory and grassland plant species, thousands of invertebrate species, and over 300 species of vertebrates. They contribute significantly to the designation of the California Floristic Province as a "biodiversity hotspot" (Myers et al., 2000). Some of the key species and the interactions that structure these communities are described below.

Trees

The oaks themselves literally and functionally define the structure of oak savanna, and are best described as the foundation species in these ecosystems. They influence the composition of the understory vegetation, and most of the animal species in these systems depend on the resources that oaks provide, directly or indirectly.

California oak savannas primarily contain oak trees belonging to five different species, two deciduous, one semi-deciduous, and two evergreen. As described above, while there can be overlap in these species distributions, and they may co-occur within stands, many oak savannas in California are dominated by one tree species. Thus we describe here the key tree species and unique attributes of the community in which it predominates, and follow with discussion of some of the common herbaceous plant and the animal species that may be found across many of these savanna habitats.

Blue oak (*Quercus douglasii* Hook. & Arn.) is a winter-deciduous, California endemic species that occupies dry slopes and foothills bordering interior valley grasslands (Fig. 2). Individual blue oaks are small- to medium-sized trees (to 20 m in height) with waxy, bluish-gray leaves (Fig. 3). The density of trees in blue oak savannas ranges from wide spacing with larger trees to more closely packed small trees (Allen-Diaz et al., 1999). In both woodland and savanna settings, blue oak can be the only overstory species present over large areas. However, other tree species present in these habitats can include foothill pine (*Pinus sabiniana*), California buckeye (*Aesculus californica*), valley oak, interior live oak, and coast live oak (Pavlik et al., 1991; Sawyer et al., 2008). This species is the most abundant and widespread of California's oaks, covering nearly 1.3 million ha (Table 1).

Valley oak (*Q. lobata* Née) is another winter-deciduous, California endemic, and is among the largest and longest lived of the North American oaks. Trees are large (up to 32 m in height), with massive spreading limbs and leaves with deep, blunt lobes (Pavlik et al., 1991; Allen-Diaz et al., 1999) (Fig. 4). It occurs in savannas along valley bottoms, foothills, and riparian areas and can co-occur with coast live oak, interior live oak, or blue oak (Pavlik et al., 1991; Sawyer et al., 2008). The distribution of valley oak appears as a discontinuous ring around the Central Valley (Fig. 2). It is far less abundant than blue oak, with an estimated extent of approximately 35,000 ha (Table 1).

Engelmann oak (*Q. engelmannii* Greene) is described as semi-evergreen or semi-deciduous, because it generally retains its leaves until they are replaced in the spring by new foliage (Pavlik et al., 1991). The trees are medium-sized, rarely reaching 18 m in maturity, with thick, muted blue-green leaves. Also known as mesa oak, this species is most abundant on the western foothills and mesas of the Peninsular Ranges; in savanna and woodland settings there it co-occurs with coast live oak. It has been described as ecologically homologous to blue oak in the north (Holland and Keil, 1995). Engelmann oak has the narrowest geographic range of the savanna oaks in California, extending just over 8000 ha (Table 1, Fig. 2). The present Engelmann oaks in the savannas of southern California occur as relict populations, having been relatively widespread in the past (Pavlik et al., 1991).



Fig. 3 Blue oak (*Q. douglasii*) on north facing slope with foothill pine (*P. sabiniana*) and coastal sage scrub. Santa Barbara County. Photograph by C. Tyler.

Table 1 Distribution and extent of foothill oak woodlands and savanna in California. Based on data from Gaman and Firman, 2008.

Dominant species	Hectares (ha)	# oaks (1–10' dbh) per ha	# oaks (> 10' dbh) per ha	General distribution
Blue oak <i>Quercus douglasii</i>	1,289,076	152	9	Interior foothills of the Coast Ranges and Central Valley
Valley oak <i>Q. lobata</i>	34,770	81	7	Interior valleys, foothills, and riparian zones, Santa Monica Mountains north to Oregon
Engelman oak <i>Q. engelmannii</i>	8,246	10	11	Peninsular Ranges, mainly San Diego and Riverside Counties
Coast live oak <i>Q. agrifolia</i>	376,734	251	21	Coastal plain, valleys, and foothills of the Central Coast Ranges, Transvers Ranges, and Peninsular Ranges
Interior live oak <i>Q. wislizeni</i> var. <i>wislizeni</i>	351,976	333	10	Foothill to lower montane zones surrounding the Central Valley, and in southern ranges from upper Sacramento Valley to northern Baja peninsula

**Fig. 4** Valley oak (*Q. lobata*). Photograph by C. Tyler.

Coast live oak (*Q. agrifolia* Née) is evergreen, with dark green, tough leaves, which are convex and have spiny margins. When one is within 50 miles of the coast, both the dark color of the foliage and the dense hemispherical canopy distinguishes this species from the other savanna trees even from a distance. It is one of the largest savanna trees reaching heights of 25 m, but also often has very wide spreading limbs (Fig. 5), up to 40 m wide (Hickman, 1993), with complex branching architecture (Fig. 6). This species is the only oak that flourishes along the coast (from Mendocino County south into Baja California) (Fig. 2), and it can form monospecific stands there, from scattered savanna trees to dense woodland (Pavlik et al., 1991). Further inland, it may co-occur with valley oak and Engelman oak, as well as bay laurel (*Umbellularia californica*), madrone (*Arbutus menziesii*) and toyon (*Heteromeles arbutifolia*). In drier sites, it is associated with blue oak and foothill pine (Holland and Keil, 1995). Coast live oak is the second most widely distributed savanna oak with nearly 377,000 ha (Table 1).

Interior live oak (*Q. wislizeni* A. DC.) can occur in savannas, most often in the northern part of its range, where it is frequently mixed with blue oak and foothill pine (Fig. 2; Allen-Diaz et al., 1999). It is one of the two evergreen oak species found in savannas and, like coast live oak, its leaves are dark green and tough, but they are distinctly flat rather than convex (Pavlik et al., 1991;



Fig. 5 Coast live oak (*Q. agrifolia*). Note that tree breadth exceeds the height. Nonnative annual grasses, especially *Bromus diandrus* in the foreground. Photograph by P. Slaughter.



Fig. 6 Under the canopy of the coast live oak (*Q. agrifolia*) shown in Fig. 5, illustrating the complex branching architecture. Photograph by C. Tyler.

Allen-Diaz et al., 2007). However, hybridization with coast live oak and the scrub oak *Q. parvula* Greene in the lower elevation of the northern Coast Range can produce individuals with intermediate characteristics (Nixon, 2002). In the southern part of the state, it rarely attains the full height of a tree and instead forms part of shrubby chaparral communities. Interior live oak is widely distributed with over 350,000 ha within California (Table 1).

Herbaceous Plants

The understory in oak savannas is typically made up of herbaceous species that are shared with neighboring grasslands, although shrubs may also be present as well as poison oak (*Toxicodendron diversilobum* (Torr. & A. Gray) Greene). Nonnative winter annual grasses and forbs frequently dominate the herbaceous community, particularly species with European or Mediterranean origins (Allen-Diaz et al., 1999). Dominant, exotic grasses include soft chess (*Bromus hordeaceus* L.), rip-gut brome (*B. diandrus* Roth), compact brome (*B. madritensis* L.), wild oats (*Avena barbata* Pott ex Link and *Avena fatua* L.), annual fescue (*Festuca myuros* L.), and foxtail (*Hordeum murinum* L.). These species are pervasive across most savanna communities and along with other annual grasses, likely arrived with Spanish colonists 250 years ago (Bartolome et al., 2007; Hendry, 1931). More recent arrivals include medusa head (*Elymus caput-medusae* L.) and barbed goatgrass (*Aegilops triuncialis* L.). Common forbs, introduced during the same period as the dominant annual grasses, include annual stork's-bills (*Erodium* spp.), mustards (*Brassica* sp. and *Hirschfeldia incana*), and introduced clovers (*Trifolium* spp.) (Hendry, 1931). The deep-rooted summer-annual yellow starthistle (*Centaurea solstitialis* L.) is also widespread in savannas, and is a more recent arrival. Other nonnative thistles, such as italian thistle (*Carduus pycnocephalus* L.) and milk thistle (*Silybum marianum* (L.) Gaertn.), are often located at or near the canopy drip line of the oak trees (Marañón and Bartolome, 1994; Tyler et al., 2007; Stahlheber et al., 2015).

Native herbaceous species are much more variable in their distribution and cover across savannas and grasslands. At six different well-studied grassland sites, native species made up 28–73% of the cover (Bartolome et al., 2007). Perennial bunchgrasses such as purple needle-grass (*Stipa pulchra* Hitchc.) (Fig. 7) are more common on coastal terrace savannas, becoming rarer in interior habitats. Other perennial grasses include prairie Junegrass (*Koeleria macrantha* (Ledeb.) Schult.), squirreltail grass (*Elymus elymoides* (Raf.) Swezey), blue wild rye (*Elymus glaucus* Buckley), pine bluegrass (*Poa secunda* J. Presl) and California brome (*Bromus carinatus* Hook. & Arn.). Some of these native grasses can be found in association with the oak canopy and appear to benefit from the cooler, more fertile microhabitat in the savanna understory (Stahlheber and D'Antonio, 2014; Stahlheber et al., 2015).

The canopy is also strong influence on the diverse community of native herbaceous forbs (Stahlheber et al., 2015). Fiesta flower (*Pholistoma auritum* (Lindl.) Lilja), hoary bowlesia (*Bowlesia incana* Ruiz & Pav.), common bedstraw (*Galium aparine* L.) and miner's lettuce (*Claytonia perfoliata* Donn ex Willd.) are associated with the understory of deciduous and evergreen oaks in savannas (Parker and Muller, 1982; Marañón and Bartolome, 1993; Stahlheber et al., 2015). Native forbs common in the open spaces between the trees and in larger grassland patches are also diverse, including California poppy (*Eschscholzia californica* Cham.) (Fig. 8), lupines (*Lupinus* spp.), lotuses/trefoils (*Acmispon* spp.), owl's clover (*Castilleja exserta*) (Fig. 9), goldfields (*Lasthenia* spp.) and clovers (*Trifolium* spp.) just to name a small selection.

Not much is known about the composition of the herbaceous plant community prior to the arrival of Europeans and their novel plants. Surveys and reports from explorers and missionaries in California before 1900 offer some insight into the general kinds of plants present in these habitats, but are too sparse to offer much to our understanding of species composition. Although many ecologists have historically assumed *S. pulchra* was a dominant member of the herbaceous community (Clements, 1934; Holland and Keil, 1995), there is little direct evidence for complete dominance of perennial bunchgrasses throughout the state (Hamilton, 1997; Bartolome et al., 2007). Instead, close examination of these early accounts and study of soil phytoliths (microscopic particles of biogenic silica that have different characteristics for grasses and broadleaf plants) suggests that much of California's Central Valley was not dominated by perennial grasses but rather by forbs (Minnich, 2008; Fick and Evett, 2018). Therefore, like the Central Valley grasslands, more interior oak savannas also likely had a substantial component of annual and perennial forb species.

Animals: Invertebrates

Thousands of invertebrate species are associated with California's oak woodland habitats, including an estimated 5000 arthropod species—mainly insects (Swiecki et al., 1997). Some depend on and affect oaks directly and thus are found associated with the savanna trees (described below), while others are more common in the open grassland. Included in the latter group are



Fig. 7 Native perennial bunchgrass, *Stipa pulchra*. Photograph by C. Tyler.



Fig. 8 California poppies (*Eschscholzia californica*) in the grassland between oaks. Photograph by C. Tyler.



Fig. 9 Native annuals, including purple owls' clover, *Castilleja exserta*. Photograph by C. Tyler.

grasshoppers, which are important herbivores impacting both herbaceous annual and perennial plants. In California there are over 200 species of grasshoppers, and more than half are native to the state and found nowhere else (Schiffman, 2007).

One of the noticeable, yet relatively harmless, groups of insects found on oaks is the gall-inducing cynipid wasps. There are over 200 species of cynipid gall wasps, which specialize on either the white oak or black oak group of California oaks (Russo, 2006). Complex communities of insects are associated with the galls themselves, including predators, parasites, competitors and mutualists, attracted to the developing wasp larvae (Russo, 2006) (Fig. 10).



Fig. 10 Valley oak gall, induced by the California gall wasp, *Andricus quercuscalifornicus*. Photograph by C. Tyler.

Other species directly dependent on the oaks are the California oak worm (*Phryganidia californica*), which is the larval stage of the California oak moth, and filbert weevil (moth larva, *Curculio* sp.) and filbertworm (beetle larva, *Cydia latiferreana*), which are the most common invertebrate consumers of acorns. In addition to the impacts these herbivores have on the vegetation, they also are important food sources for vertebrate consumers.

Animals: Vertebrates

Reptiles and amphibians benefit from shelter provided by leaf litter, downed wood or hollows in oak trunks, as well as abundant food sources—especially insects and small mammals (Block and Morrison, 1998; Tietje and Vreeland, 1997; Tietje et al., 1997). Lizards and snakes are important predators in oak communities and species represented include skinks (*Plestiodon* spp.), western fence lizard (*Sceloporus occidentalis*), California legless lizard (*Sceloporus occidentalis*), alligator lizards (*Elgeria* spp.), racers (*Coluber* spp.), common king-snake (*Lampropeltis getula*), gopher snake (*Pituophis catenifer*) and western rattlesnake (*Crotalus oreganus*). Amphibian abundance and diversity vary considerably with site conditions; most species depend on moist microsites under downed logs, litter, riparian elements or vernal pools (Block and Morrison, 1998). Among the most common amphibian species are slender salamanders (*Batrachoseps* spp.), ensatinas (*Ensatina* spp), and chorus frogs (*Pseudacris* spp.) (Tietje and Vreeland, 1997; Block and Morrison, 1998).

Birds are the most diverse vertebrate group in these habitats, with over 100 species represented. Some rely on acorns for food, including the acorn woodpecker (*Melanerpes formicivorus*), western scrub-jay (*Aphelocoma californica*), and the yellow-billed magpie (*Pica nuttalli*). Others, such as phainopepla (*Phainopepla nitens*) and western bluebird (*Sialia mexicana*), rely on food sources associated with oaks, such as mistletoe fruits or insects. Raptors such as red-tailed hawk (*Buteo jamaicensis*), red-shouldered hawk (*Buteo lineatus*), Cooper's hawk (*Accipiter cooperii*), great horned owl (*Bubo virginianus*) and golden eagle (*Aquila chrysaetos*), though not restricted to oak habitats, nest in these woodlands and can play a major role in the community trophic structure as predators on small mammal populations (Tietje et al., 1997). Turkey vultures (*Cathartes aura*) are an ever-present and important scavenger, consuming carrion in these habitats.

Mammals that are found in oak savanna habitats include consumers of insects, seeds, or herbs such as bats, brush rabbit (*Sylvilagus bachmani*), California ground squirrel (*Otospermophilus beecheyi*), Botta's pocket gopher (*Thomomys bottae*) and other rodents. The distribution and abundance of rodent species vary with microhabitat such as shrub and downed wood cover: for example, dusky-footed woodrats (*Neotoma fuscipes*) are more abundant where there is shrub cover, whereas a sparsely vegetated ground cover is associated with higher numbers of deer mice (*Peromyscus* spp.) (Tietje and Vreeland, 1997). Large mammals here include omnivores and browsers such as American black bear (*Ursus americanus*) and mule deer (*Odocoileus hemionus*), as well as carnivores such as cougar (*Puma concolor*), bobcat (*Lynx rufus*), American badger (*Taxidea taxus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and long-tailed weasel (*Mustela frenata*).

Factors Affecting Species Distributions and Community Composition

Climate

Climate imposes one of the broadest controls on the distribution of grasslands and co-occurring woody vegetation in California. The ranges of precipitation and temperature experienced by the savanna and grasslands described here would fall into the climate zone, described by Whittaker (1975), "in which either grassland, or one of the types dominated by woody plants may form the

prevailing vegetation". In addition, climate exerts finer scale influences on the dynamic patterns at the grass-tree boundaries, as well as the seasonal and annual variation in productivity, seed production, and biodiversity.

Interannual variation in precipitation and the timing of the first germinating rain in fall can cause major changes in the composition of the herbaceous plant community in oak savannas (Slade et al., 1975; Bartolome, 1979). Shifts between "grass years" and "forb years" are common in response to environmental conditions, including lag times in the response of wildflowers (Pitt and Heady, 1978; Reeve Morghan et al., 2007). Increased rainfall tends to favor the exotic annual grasses, often at the expense of native plant species richness and invertebrate food webs (Suttle et al., 2007).

In addition to the effects of climate on the distribution and range of individual oak species (see section on Distribution), climate also has effects on oak populations. Rainfall can have profound implications for oak seedling emergence and initial survival, although established seedlings are less likely to be killed by drought (Griffin, 1971; Borchert et al., 1989; Tyler et al., 2008; Mahall et al., 2009; Davis et al., 2019). Competition for soil water between oak seedlings, nonnative annual grasses and established adults can constrain early growth of oak trees (Gordon and Rice, 2000), especially in the driest parts of their range.

Weather is a primary factor driving masting for oak species, including those in California (Koenig et al., 2016, 2017). In particular, rainfall and temperatures during the spring and summer are key drivers of acorn production, especially for evergreen species (Koenig et al., 2016). Studies in valley oak have suggested considerable local adaptation of populations to climate, which could have important implications for the future of oak savannas as the regional climate changes (Sork et al., 2010, 2016).

Over the past 50 years the major trends in changing climate in these systems have been: an increase in mean annual temperature and minimum nighttime temperatures, and increased interannual variation in temperature and rainfall (Christy et al., 2006; LaDochy et al., 2007). Global climate models are consistent in predicting that California will continue to warm over the next century (Cayan et al., 2008). As described above, climate influences oak savanna and grasslands in multiple ways, from seed production, seedling establishment and survival, and community species composition. It has been suggested that grasslands, which are dominated by annual species, may experience changes in the relative abundance of native compared to nonnative grass species due to predicted changes in the timing and duration of rain events (Suttle et al., 2007; Eviner, 2016). The establishment and ultimately the overall ranges of savanna oak species has been predicted to decline with warming climate (Kueppers et al., 2005; McLaughlin and Zavaleta, 2012; Davis et al., 2016). Thus climate will continue to play a major role in determining the distribution and make-up of California's oak savanna and grassland ecosystems.

Soil Type

Oak savannas are most often found on noncalic Mollisols typical of grasslands, with medium-heavy texture and moderate organic matter. As mentioned previously, valley oak savannas are commonly located on deep, fertile valley bottom and riparian soils, whereas blue oak savannas occupy sandier, rockier soils typical of slopes. The parent materials underlying these savannas have a variety of origins, chemistries and physical properties. In general, blue, valley and coast live oak occupy sites with sandstones and shales, along with granitic parent materials north and east of the Central Valley (Allen-Diaz et al., 1999). Interior live oak savannas on the other hand frequently are found on mafic, metamorphic and deep igneous parent materials (Allen-Diaz et al., 1999).

The presence of the oak canopy in savannas creates patchiness in soil properties, as the oak trees can create "islands of fertility" beneath their canopy. Soil organic matter, cation-exchange capacity, inorganic nitrogen and nitrogen turnover rates are often higher below the canopy (Parker and Muller, 1982; Jackson et al., 1990; Frost and Edinger, 1991; Dahlgren et al., 1997; Herman et al., 2003; Stahlheber et al., 2015), likely contributing to the effects of oaks on productivity and understory composition.

Tree-Grass Interactions

The oak canopy exerts a strong influence on the productivity and community composition in the understory relative to neighboring open grassland. Interactions between the understory and blue oak trees range from facilitative to competitive, leading to trees that have higher or lower productivity beneath them relative to the surrounding grassland (Callaway et al., 1991). Climate, precipitation, and/or root distribution likely all contribute to whether a tree will positively or negatively affect understory production (Callaway et al., 1991; McClaran and Bartolome, 1989; Frost et al., 1997). Legacy effects of oak trees are persistent, although more so in terms of composition than productivity. Both evergreen and deciduous oak canopies favor growth and establishment of ripgut brome (*B. diandrus*) thus it is often abundant in the understory whereas other grasses (*B. hordeaceus* and *Avena* spp) are favored in open spaces (Parker and Muller, 1982; Marañón and Bartolome, 1993; Rice and Nagy, 2000; Stahlheber et al., 2015). These dominant, productive populations of ripgut brome can persist more than 30 years following the death of the tree; therefore legacy effects of a former canopy may be important sources of patchiness in composition of savanna herbaceous communities (Holland, 1980; Bartolome et al., 1994; Stahlheber et al., 2015).

Plant-Animal Interactions

Oaks Providing Food and Habitat for Animals

Many of the animals residing in oak savanna rely on the food or shelter that oaks provide (California Department of Fish and Wildlife, 2008). Acorns are a carbohydrate-rich food resource for many species. This resource varies considerably from year to year,

especially in white and red oak species like blue oak, valley oak and coast live oak, whose acorns mature in 1 year (Koenig and Knops, 2013; Koenig et al., 1994). Oak mast seeding behavior has been found to drive population dynamics of animals dependent on them and throughout the food webs (Koenig and Knops, 2005; Koenig et al., 2009; Ostfeld et al., 2006).

Other resources provided by the oaks include leaves, twigs, sap, leaf litter, and a complex physical structure including canopy, shaded and open branches, cavities, bark, and standing, dead or downed logs. These serve as either food or shelter to a variety of animal species.

Oak savannas, which are by definition diverse in structure—with elements of both woodlands and grasslands—sustain diverse communities that include species generally found in one or the other habitat, but here overlap in their distributions.

Mutualist Seed-Dispersers

Though oaks do not require that their acorns are dispersed or buried by animals, this “service” provided by birds or small mammals greatly increases the likelihood that acorns will successfully germinate and become established seedlings. Most acorns that drop under the adult oak trees are eaten, and those that are left on the soil surface are killed by desiccation or heat stress. Acorns that are shallowly buried have a higher probability of producing emergent seedlings (Borchert et al., 1989; Tietje et al., 1991). While some acorns may be buried naturally (e.g., by falling into deep leaf litter), acorn-hoarding animals play an important role in getting the acorns to microsites that promote their survival and germination. One of the most important acorn “planters” is the western scrub-jay (*Aphelocoma californica*), which may scatter-hoard, or “plant”, up to 5000 acorns in a season but only recover and consume half (Carmen, 1988), leaving thousands of buried acorns across the landscape. Other acorn-caching or hoarding animals include yellow-billed magpie (*Pica nuttalli*) and California ground squirrel (*Otospermophilus beecheyi*).

Ecosystem Engineers

Ecosystem engineers are organisms that impact the availability of resources to other species by causing physical changes to the environment (Jones et al., 1994). Residing in oak savannas and woodland are several animal species that play this role (Schiffman, 2007). Botta’s pocket gopher (*Thomomys bottae*) function as “soil engineers” because their burrowing causes high rates of soil turnover and their tailings cause disturbances that, among other impacts, mediate competition between annual and perennial plant species (Hobbs and Mooney, 1995; Stromberg and Griffin, 1996; Seabloom and Richards, 2003). California (or Beechey) ground squirrel (*Otospermophilus beecheyi*) similarly impacts the soil environment with their extensive burrowing. Badgers (*Taxidea taxus*) are impressive soil excavators, tunneling sparse but extensive underground burrows, which may be as far as 3 m below the surface with up to 10 m of tunnels. Nonnative wild pigs (*Sus scrofa*) are an important agent of soil disturbance in many oak woodlands and grasslands, but, unlike other animals that may foster higher biodiversity by creating heterogeneity in the soil environments, pig activities are usually associated with increases in nonnative plant species that recover from pig disturbance faster than native species (Tierney and Cushman, 2006). All of these ecosystem engineers influence the composition of soil biota, herbaceous vegetation, and potentially the establishment of oaks by moving or removing acorns.

Animals Contributing to the Oak Regeneration Problem

As has been reported for other oak woodlands around the world, California’s oak savannas are generally composed of large, old adults with few individuals in the smaller, younger classes, raising concerns that there is an oak regeneration problem, that is, that natural recruitment of the oaks may be insufficient to balance adult mortality. Among the factors often cited as limiting oak recruitment are acorn and seedling predation, and herbivory of established seedlings and saplings (Tyler et al., 2006). Predation by small mammals, including mice, gophers, voles, and ground squirrels has been shown to be a major source of acorn and seedling mortality for most California tree oaks (Griffin, 1971, 1980; Borchert et al., 1989; Callaway, 1992; Tyler et al., 2008).

Herbivory and browsing of seedlings and saplings also strongly limits oak establishment in some sites. Leaf defoliation by grasshoppers, root damage by pocket gophers and voles, and bark girdling by mice have all been reported to cause mortality or severe damage to established oak seedlings and saplings (Griffin, 1976; McCreary and Tecklin, 1994; Bernhardt and Swiecki, 1997; Tyler et al., 2008). In addition, browsing by deer has been noted to significantly reduce growth of oak saplings and limits their transition to larger size-classes (White, 1966; Griffin, 1971; Davis et al., 2011, 2019). The commonly-observed associations of natural oak seedlings with shrub canopies (Callaway and D’Antonio, 1991; Callaway, 1992) are likely a result of protection provided by shrubs from herbivory and browsing by mammals.

Human Impacts

Early Uses, Tree-Cutting, and Firewood Harvesting

Oaks served an important function to California’s indigenous cultures by providing sustenance; acorns were a staple in the diet of most native American tribes residing among the oaks woodlands and savannas in the region (Rossi, 1980; Keator, 1998). Because of this dependence on an important food source, it is unlikely that tree-cutting would have been prevalent in that time period (Rossi, 1980).

Following European exploration and settlement, oaks were harvested for several uses, including fuel for heating and cooking, timbers for mine supports or fencing, and for the production of charcoal. Since oaks were less desirable compared to pines in producing strong, straight lumber, historically there were no large-scale forestry operations initiated in California oak savannas and woodlands (Rossi, 1980).

In the present day, cutting of oak trees for firewood still occurs, but at a relatively low rate. A 4-year, state-wide survey of firewood harvesting in California found that there was annual harvest of approximately 2400 ha, representing <0.1% of the total hardwood rangeland (Standiford et al., 1996). This harvesting took place primarily in just two counties, and in most locations growth surpassed harvest, in terms of oak tree volume. The authors concluded that firewood harvest of oaks was not a dominant factor impacting these woodlands.

Fire

Lightning ignitions in the coastal and lower-elevation foothill habitats occupied by oak savannas and woodlands are rare, among the lowest rates in the southwestern United States (Keeley, 2002; Davis et al., 2016). Convective lightning storms are relatively rare in the summer, when fuels are dry and in the winter, fuel moisture is high enough to resist ignition (Keeley, 2002). Human and lightning ignitions are difficult to separate in the paleoecological record, but the occurrence of large, catastrophic fires does suggest some naturally-ignited fire (Keeley, 2002; Mensing et al., 1999). Today, humans are the source of almost all ignitions in these habitats (Keeley, 2002; Davis et al., 2016).

The southern and central Coast ranges of California have been settled since at least the late Pleistocene/early Holocene (Erlandson, 1997). By the late Holocene, even without engaging in agriculture, the complex hunter-gatherer societies of indigenous Californians had some of the highest population densities in North America (Lightfoot and Parrish, 2009). They managed the wild plant communities they inhabited with fire, and given the density of human settlement in oak savanna habitats, it is likely that Native American fire had significant impacts on these communities (Keeley, 2002; Anderson, 2005; Mensing, 2006). Indeed, the expansion of oak habitat throughout California following the last glaciation coincided with the first appearance of people, so environmental modification may have been central to their success along with a changing climate (Mensing, 2005). Burning (as often as every 1–3 years) would have enhanced the abundance of hunted game, the production of seeds from desirable herbaceous plants, as well as increased the abundance of corms and bulbs (Keeley, 2002; Lightfoot and Parrish, 2009; Bartolome et al., 2007). Van de Water and Safford (2011) collected available literature on Pre-European fire return intervals in California vegetation and estimated a mean return interval of 12 years for oak woodlands and savannas with a range from 5 to 45 years. Current fire return intervals in oak-dominated habitats in the Los Padres National Forest range from 13 to 103 years, with a mean of approximately 41 years (an average departure of almost 30 years from the likely historical fire regime) (USFS FRID database; <http://www.fs.fed.us/r5/rs/clearinghouse/r5gis/frid/>).

As shown in coastal oak habitats, wildfire can mediate transitions between oak woodland/savanna communities, open grassland and shrubland phases by reducing establishment of woody plants into grassland or shrubland (Callaway and Davis, 1993). Seedlings and saplings of oaks can be killed by high-intensity fires, slowing recruitment of trees (Mensing, 1998; Swiecki and Bernhardt, 2002; Bartolome et al., 2002). On the other hand, adult oak trees are generally resilient to the effects of fire; their thick bark protects them from cambial damage and coast live oak, blue oak and valley oak often vigorously resprout from the crown and interior live oak can resprout from the base (Fry, 2008; Haggerty, 1994). Prescribed fire has only rarely been used in these habitats, partly due to the fact that >80% of oak savannas and woodlands are privately owned, and many have been, and still are, used for livestock grazing (Huntsinger et al., 2010).

Changing climate may significantly alter the role of fire in structuring these systems. As a result of warming temperatures it is likely that oak savannas and grasslands will experience new fire regimes and longer fire seasons. More frequent fire may increase the relative cover of grassland and decrease abundance of oaks. Such a change would have cascading impacts through the plant and animal communities.

Livestock Grazing

Most of the large (>200 acres) properties with oak woodland and savanna are used for livestock grazing, and the owners tend to live on their properties, participate in voluntary land conservation programs and are often concerned about the effects of oak on forage (Huntsinger et al., 2010). Oak thinning has been common in grazed landscapes, often for “rangeland improvement” (Frost et al., 1997). However, more landowners have come to value multifunctionality and diverse ecosystem services from their oak properties, viewing them as important “working landscapes” (Huntsinger et al., 2010). Along with this change in perspective is an interest in using grazing as a land management tool, both to reduce fire hazard for human dwellings and maintain a diverse herbaceous plant community (Huntsinger et al., 2010; Stahlheber and D’Antonio, 2013; Bartolome et al., 2014).

Continuous grazing at high stocking rates is frequently implicated in the invasion of California grasslands by nonnative annual species and the loss of perennial grasses (Bartolome et al., 2007). Large animals reduce dominance of tall grasses, break up litter layers and favor short, broad-leaved plants (Díaz et al., 2007). Grazing used as a conservation or management tool is most often applied by rotating cattle through smaller pastures during the wet/grass-growing season (November to May). A recent meta-analysis

of grazing studies in California grasslands (some including oak savanna habitat) found that across the state, grazing tended to increase the richness and abundance of exotic forbs (Stahlheber and D'Antonio, 2013). There were also positive impacts on native forbs, especially in arid, inland sites compared to those in the Coast Ranges (Stahlheber and D'Antonio, 2013). The response of native grasses appeared to be much more variable.

Oak understory and open grassland habitats do not necessarily respond the same way to grazing. Trees can change the behavior of grazers, causing them to congregate in shade or seek out the more nutritious forage present in the understory (Senft et al., 1985; Frost et al., 1991; Treydte et al., 2010). Most studies of grazing in oak woodland or savanna habitats have not separated understory and intertree locations when considering the effects on native and exotic plant populations. A recent study that did compare understory to open grassland locations found that in open sites outside the canopy (> 5 m from the edge) of valley oaks, cattle grazing breaks up litter layers formed by *B. diandrus* and other annual grasses, increasing species richness and facilitating native species (Stahlheber et al., 2017). By contrast, the understory of coast live oak and valley oak had higher species richness and cover of native species when grazing was removed (Stahlheber et al., 2017). These results suggest that implementing grazing to benefit native species will have highly variable outcomes in oak savanna depending on tree density, livestock behavior and the species already present in understory and open habitats.

Grazing can also have effects on attributes beyond the herbaceous plant community, including oak regeneration, soil attributes and the abundance of animals. Cattle may reduce the success of oak recruitment, however, small mammals can have much larger effects (Tyler et al., 2008; Davis et al., 2019). These small mammals such as gophers and ground squirrels can themselves be affected by cattle grazing (Stromberg and Griffin, 1996, but see Fehmi et al., 2005). Most studies have also found relatively muted effects of grazing on oak understory soils outside of a small increase in bulk density and some changes in soil phosphorus availability (Dahlgren et al., 1997; Tate et al., 2004; Stahlheber et al., 2017).

Current Threats

Regeneration Problem

As described above, in California's oak woodlands and especially in oak savannas, researchers have observed low recruitment rates, even as early as the 1990s (Sudworth, 1908; Jepson, 1910). Stands of trees that are dominated by old adults raises concerns about potential population decline, or an "oak regeneration problem". Field surveys of California oak species, including those important to savanna ecosystems, indicate that in many sites there are very low numbers of oak seedlings and young saplings present (Bolsinger, 1988; Tyler et al., 2006; Allen-Diaz et al., 2007). The degree to which oak populations are declining, stable, or increasing appears to vary among species and to vary regionally. For example, live oaks may be increasing in some regions, blue oak populations appear to be regenerating adequately in many locations, but valley oak populations in Central California and Engelmann oak in Southern California appear to be declining (Tyler et al., 2006).

There are many physical and biotic factors that can limit establishment of oaks in savanna habitats. These include: low rainfall in some years, acorn diseases, acorn predation, herbivory of established seedlings and saplings, competition between oak seedlings and nonnative annual grasses for water, soil compaction by cattle, and low adult tree population density. Any one of these factors can prevent the establishment of seedlings and the subsequent transition to sapling and tree (Tyler et al., 2006).

Predicted changes in climate, including increased temperatures and increased variability in rainfall may well impact oak recruitment in multiple ways. As described previously, climate affects acorn production: spring temperature and humidity impact pollen production and dispersal. Higher temperatures at ground level may reduce acorn and seedling survival. Reduced availability of water-requiring vegetation may also drive higher rates of browsing and herbivory on existing saplings. The few studies that have examined potential impacts of climate change on oaks support the prediction that oak establishment will become more limited with warming conditions (Kueppers et al., 2005; McLaughlin and Zavaleta, 2012), thereby exacerbating regeneration problems already reported in some savanna habitats.

Habitat Loss and Degradation Due to Land-Use Conversion

Arguably the most significant threat to California oak savannas is the outright clearing of oak trees and conversion of the land for residential development and agriculture. Although oaks themselves provide multiple benefits to both humans and other organisms as a natural resource, as of the mid-1980s between 3 and 5 million of California's original 10–12 million acres of oak woodland habitats had been lost largely due to rangeland clearing, agricultural conversion and urban development (Bolsinger, 1988). Most lowland oak woodland conversion to cropland and orchards occurred in the latter half of the 19th century, primarily in valleys and floodplains that could support growth of crops, such as open sites around the Central Valley. By the 1880s, much of the state's grassland had been plowed, and 75% of the area within the Central Valley had been converted to production. Even hillsides that today do not appear plowed probably once were during this period. Stromberg and Griffin (1996) found that cultivation has large impacts on present day composition; native perennial bunchgrasses in particular appear to be mostly restricted to unplowed sites.

In the last quarter of the 20th century another wave of agricultural conversion took place, with the burgeoning wine industry in California; vineyard acreage expanded by nearly 300% just between 1976 and 2010 (Davis et al., 2016).

Residential development in both suburban and rural areas has heavily impacted oak woodlands and savannas since the 1950s. Even where development has occurred on relatively large lots—those between 5 and 20 acres—the habitat becomes fragmented by roads and fencing, and environmentally degraded due to changes in understory vegetation, disruptions to animal communities, and impacts to air and water quality. Such impacts are likely to continue as demands for new housing accompany projected increases in the state's population.

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Relevant Website

https://ucanr.edu/sites/oak_range/.

Prairies, Savannas, and Oak Woodlands of the Pacific Northwest

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Abstract

Grasslands, woodlands, and associated communities comprise a biologically diverse ecoregion in western Oregon, Washington, and British Columbia. These habitats contrast conspicuously with the coniferous forests that largely surround them and were historically strongly shaped by a pronounced summer-dry Mediterranean climate together with frequent fires set by Native Americans. Agricultural development, urbanization, and forest encroachment have resulted in the loss over 90% of these habitat types in most areas. Remnants are mostly small and highly fragmented. Conservation efforts focus on restoring native species diversity, managing invasive species, and enlarging acreages to enhance ecological resilience.

Introduction

Conifer forests largely dominate the vegetation of the middle latitudes along the Pacific Coast of North America. Yet within portions of this region, substantial areas of nonforested vegetation occur. These areas have many affinities in life form and climate with grassland, savanna, and woodland biomes elsewhere in the world, and are generally regarded as falling within a single ecoregion (Floberg et al., 2004, EPA website). In this article, we follow Floberg et al.'s (2004) delineation and refer to these habitats as comprising the Willamette Valley-Puget Trough-Georgia Basin (WPG) ecoregion. They lie west of the Cascade Mountains in northwestern Oregon, western Washington, and southwestern British Columbia, and extend nearly 800 km, from about 44–50°N latitude. A disproportionate amount of the region's biodiversity is associated with these vegetation types, and the connections to human influences—past, present, and future—are a source of significant ecological and conservation interest. Botanical nomenclature follows Hitchcock and Cronquist (2018).

History and Physical Setting

Historical Extent and Distribution

Grasslands, savannas, and open woodlands are closely related habitat types that overlap and intergrade. Historically, they were most commonly found in the lowlands west of the Cascade Mountains and east of the Coast Ranges and Olympic Mountains, within the area known as the Willamette Valley-Puget Trough-Georgia Basin (WPG) ecoregion (Floberg et al., 2004; Fig. 1). Different terms are sometimes used within the ecoregion to refer to these communities. Grasslands are widely referred to as “prairies” throughout much

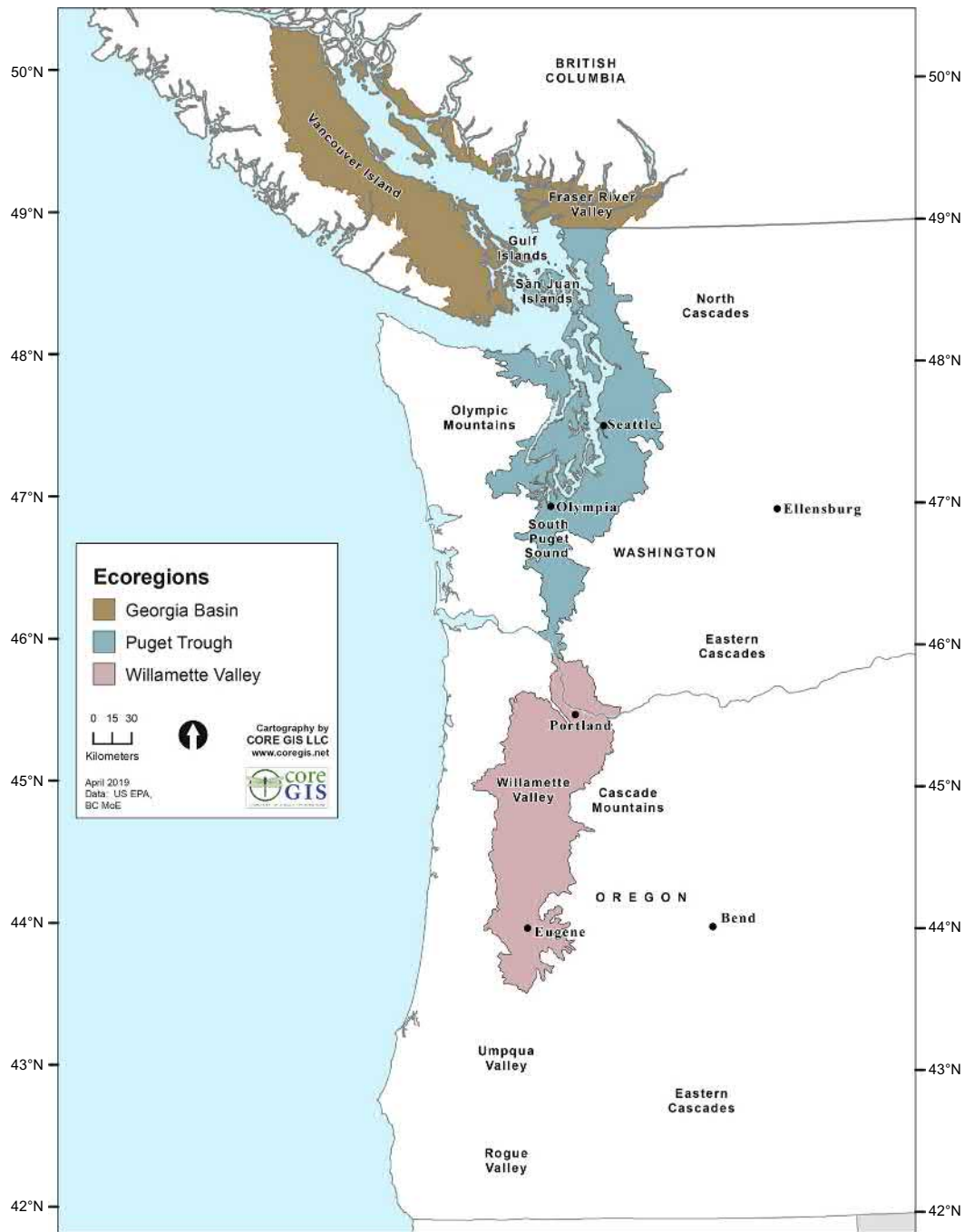


Fig. 1 Map of the Willamette Valley-Puget Sound-Georgia Basin ecoregion in western Washington, Oregon, and British Columbia.

of the range, although the term “balds” is frequently used in the San Juan archipelago (Chappell, 2006) and “meadows” in southwestern British Columbia. The overall range of these habitats is fairly well tracked by occurrences of the native oak, *Quercus garryana* var. *garryana*, a dominant species of both savannas and woodlands. This species is known as Oregon white oak or Garry oak, the latter name being applied in British Columbia to describe the suite of grasslands and woodlands of high conservation value—the “Garry oak ecosystem” (GOERT, n.d.). Its range extends somewhat beyond that of the WPG, reaching south into California and crossing the Cascades slightly in southern Washington.

The historical extent of these habitat types at the time of Euro-American settlement (ca. 1850) has been documented from early land surveys, as well as inference based on occurrences of grassland soils. They were most extensive in the Willamette Valley, with over 400,000 ha of prairie, 200,000 ha of savanna, and 250,000 ha of woodland (Christy and Alverson, 2011). These habitats were less extensive in the lowlands of western Washington and British Columbia, and detailed estimates of the historical acreages of the

different habitat types are less certain. Chappell et al. (2001, 2003) estimated grasslands in presettlement times occupied about 73,000 ha in western Washington, with the majority occurring south of Puget Sound. Mixed oak-conifer savannas and woodlands were often associated with these prairies, but their historical extent in Washington is less certain. In British Columbia, prairies and associated oak habitats were most extensive on southeastern Vancouver Island, the adjacent Gulf Islands, and in the lower Fraser River Valley. Approximately 12,000 ha of presettlement prairies, savannas, and balds have been mapped (Lea, 2006), but this does not include areas of historically fire-influenced woodland, or balds that lacked an extensive oak component.

Paleoecology

Across most of the region, the present-day vegetation only developed in the Holocene following the climatic and environmental changes accompanying the end of the Ice Age. Numerous fossil pollen records from sediment cores throughout the WPG ecoregion generally show species with xerophytic affinities, including *Quercus*, reaching their maximum abundance in the Hypsithermal, 5–8000 years ago, suggesting that prairie and savanna habitats were also at their maximum extent during this time (Whitlock, 1992; Leopold and Boyd, 1999; Leopold et al., 2016). Walsh et al. (2008) and others also describe fossil charcoal records during the Hypsithermal that suggest frequent low to moderate severity fires, which may in part reflect human ignitions of these habitats.

Various origins for individual elements of the flora can be posited. *Quercus garryana* itself belongs to a lineage with a long history in the fossil record in western North America that extends back to the Miocene species *Quercus prelobata* (Retallack, 2004). In some cases, important herbaceous elements in the vegetation belong to lineages or genera endemic to the Pacific Northwest or western North America (e.g., *Camassia*), while other important taxa are widespread across the northern hemisphere (e.g., *Deschampsia cespitosa*).

Climate

The present-day climate in prairie and savanna areas throughout the WPG ecoregion shows a Mediterranean-type pattern of seasonal precipitation, with warm, dry summers and mild, wet winters (Table 1). Unlike most temperate grasslands, where most of the precipitation occurs in late spring and early summer, 75–90% of annual precipitation typically occurs from October through April. However, total precipitation varies by a factor of two to three times across the WPG ecoregion. At the north end of the region, precipitation in the San Juan and Gulf Islands averages only 40–65 cm due to their location within the rain shadow of the Olympic Mountains of western Washington. Farther south, average annual precipitation is considerably greater, reaching 130 cm in southern Puget Sound and 100–120 cm in the Willamette Valley. The Willamette Valley and southern Washington sites are significantly wetter than most temperate grasslands elsewhere in the world, which typically average 50–90 cm annually (UC-Berkeley website). Overall, temperatures tend to be more moderate in the WPG ecoregion than most other grasslands due to the oceanic influence. Winter temperatures are relatively mild for the latitude; frosts are common but hard freezes less so, and winter snowfall is uncommon and rarely persists for long. Summer temperatures are similarly moderate, with average August maxima ranging from 20°C in the north to 28°C in the Willamette Valley.

Soils

Soil parent materials generally are of late-Pleistocene and Holocene age throughout the WPG ecoregion, although they vary considerably in origin. The northern half of the region (Thurston County, Washington northward) was impacted by the most recent extent of the continental ice sheets. As a consequence, soils are often derived from glacial deposits, particularly outwash, which are often

Table 1 Average annual and summer (June–August) precipitation, maximum August temperature, and minimum January temperature for stations in prairie habitat types in the WPG ecoregion from the southern Willamette Valley (Eugene) to southwestern British Columbia (Victoria).

Location within WPG ecoregion		Annual precip. (cm)	Summer precip. (cm)	Aug max. temp (°C)	Jan min. temp (°C)
Eugene, OR	Southern Willamette V.	117	6.70	28	1
Salem, OR	Central Willamette V.	101	6.20	28	2
Centralia, WA	Southern Puget Sound	119	8.78	27	2
Olympia, WA	Southern Puget Sound	127	8.48	26	1
Sequim, WA	Olympic Peninsula	41	5.38	21	0
Coupeville, WA	Whidbey Island	54	7.62	23	3
Victoria, BC	Vancouver Island	58	13.20	20	2
Bismarck, ND	X	45	21.18	83	2
Valentine, NE	X	51	22.7	87	11
Wichita, KS	X	87	32.38	91	22

Comparable data from grassland habitats in the Great Plains are listed for comparison.
<https://www.usclimatedata.com/climate/>.

excessively drained mixtures of sand, silt, and gravel. Bedrock outcrops occur frequently in the San Juan and Gulf Islands, where grasslands often are associated with shallow soils on bedrock and on dry coastal bluffs.

South of the limit of the continental glaciation, some prairie areas have developed on older deposits, but most are found on fine sediments dropped by the massive late-glacial Missoula floods, which scoured materials from western Montana, Idaho, and eastern Washington. These sediments were deposited across the entire Willamette Valley below an elevation of about 120 m (O'Connor et al., 2001).

Hydrology

Prairie and savanna vegetation may be found in association with a wide range of hydrologic conditions. While most remnants of these habitats on the landscape today occur in droughty, well-drained uplands, extensive prairies historically occurred on deeper, more mesic soils that were rapidly converted to agriculture by early Euro-American settlers (Boyd, 1999; Lea, 2006). Wet prairies also were frequent, especially along rivers and on poorly-drained substrates, but have been virtually extirpated by hydrological alterations, agriculture practices, and encroachment of invasive species. In many portions of the WPG ecoregion, prairies and savannas are associated with azonal soils characteristic of sites—both wet and dry—where conifers (particularly Douglas-fir—*Pseudotsuga menziesii*) are poorly adapted or less competitive.

Biota

Community Types

Grasslands, savannas, and woodlands in the WPG ecoregion often transition gradually from one type to another rather than changing abruptly in structure and species composition. While grasslands are readily recognized by a dominance of herbaceous species and only a minor presence of shrubs or an occasional tree, savannas and woodlands are less clearly distinguished from each other, being defined primarily on the basis of tree density and canopy cover. Savannas are generally considered to have a canopy < 25–30%, with woodlands defined by a denser canopy between 30% and 70%, above which they usually are considered to be forest. Some authors have further distinguished between open and closed oak woodlands (Altman, 2011).

Grasslands

Grass-forb dominated communities vary along gradients of seasonal hydrology, substrate composition, and soil depth and texture. Prairies on deep soils with adequate drainage were historically among the most extensive community types, but were also among the first areas to be converted to agriculture. As a result, examples of these habitat types in good condition are scarce today throughout the region. Regardless of the total precipitation received, the herbaceous vegetation dominating these habitats tends to be of low to moderate stature (generally < 50 cm tall). This is unlike most other temperate grasslands, where areas with higher annual precipitation generally support bunchgrasses and forbs that may reach 1.5–2 m or more in height. The short stature may result from the pronounced summer drought limiting growth for most species, particularly in July and August.

Numerous herbaceous-dominated plant associations have been described across the ecoregion, although it is generally recognized that historically, many others likely occurred as well. In Washington, Chappell (2004) described 10 grassland associations. In British Columbia, few native grasslands remain, and descriptions of Garry Oak Ecosystem community types largely include plant associations that include *Quercus garryana* as an important component (Erickson, 2002). The Oregon Natural Areas Program has described several Willamette Valley grassland ecosystems along gradients of soil depth and winter hydrology (Oregon Natural Areas Program, 2015).

The species composition of these plant associations varies considerably across the ecoregion. Soil composition, depth and fertility, together with seasonal moisture stress are likely some of the more important factors that contribute to this variability. Appendix A lists the more common native species (i.e., those present in > 70% of sites in at least one ecoregional sector) that are frequently encountered in the upland grassland/savanna habitat types in major sectors of the ecoregion. These data are drawn from the remnants of these habitats that still survive, which are often small and thus may not be entirely representative of the historical occurrences of the species.

In general, the flowers of diverse forbs are conspicuous in the spring (April–May), with bulbous species, particularly *Camassia quamash* or *C. leichtlinii*, often abundant (Fig. 2). Considerably fewer forbs flower in summer or autumn, likely reflecting the pronounced summer drought. Native annual grasses are minimally represented in the flora. Although annual forbs are inconspicuous in today's prairies, this may be due to the lack of fire over the last 150 years (Dunwiddie et al., 2014). Frequent burning consumes accumulated litter and moss, a conspicuous groundcover in many regional prairies. This produces larger gaps among the perennial plants where annuals can flourish. In addition, burning tends to increase forb abundance over the native grasses (Fig. 3). In contrast to the diversity of forbs, remarkably few species of native bunchgrass are dominant. Roemer's fescue (*Festuca roemerii*) occurs throughout the WPG ecoregion, and is thought to have historically been the primary native grass in many dry, upland prairies in the Willamette Valley and southern Washington (Titus et al., 1996). Red fescue (native forms of *Festuca rubra*) tends to be the more common bunchgrass farther north in the San Juan and Gulf Islands,



Fig. 2 Abundant *Camassia quamash* in a South Puget Sound prairie, with *Quercus garryana* in the background. Photography by P. Dunwiddie.



Fig. 3 Postfire flowering in a forb-rich bald in the San Juan Islands dominated by *Ranunculus occidentalis*, *Castilleja hispida*, and *Camassia leichtlinii* spp. *suksdorfii*. Photography by P. Green

with very few other grasses (*Danthonia californica*, *Elymus glaucus*, *Elymus trachycaulis*, *Koeleria macrantha*, and *Bromus carinatus*) conspicuous in some areas.

Due to many decades of livestock grazing and other disturbance, the prairie remnants that still persist generally are significantly degraded. Many native species almost certainly have been extirpated from most sites. For example, in a study of 15 of the largest prairie remnants in South Puget Sound, 40% of the native plant species occurred in only 1 or 2 prairies (Dunwiddie et al., 2006). Sites also have been greatly altered by the introduction of a large number of nonnative plant species. The same study of South Puget Sound prairies found 39% of the species are nonnative. A similar 36% were recorded in grasslands in the San Juan Islands (Dunwiddie, 2018). These figures are likely representative of habitat degradation in other sectors of the WPG ecoregion as well.

Wet prairies are a distinctive variant most commonly found in the southern half of the ecoregion, but historically present to a smaller extent in the northern half as well. Wet prairies occur where the water table is at or near the soil surface, at least in the winter, creating conditions for hydrophytic vegetation. *Deschampsia cespitosa* is the dominant grass in many wet prairies in Oregon, along with species of sedge (*Carex*) and other graminoids. Vast acreages of wet prairies have been drained and converted to pasture and cropland, or have been overrun by *Phalaris arundinacea* and other nonnative grasses.



Fig. 4 Prairie and *Quercus garryana*–*Quercus kelloggii* savanna in the southern Willamette Valley. Photography by E. Alverson.

Savannas and Woodlands

Savannas consist of an understory comprised largely of prairie grasses and forbs with an open tree canopy. The arboreal component generally is comprised of Oregon white oak, Douglas-fir, or other fire-tolerant conifers which vary regionally, but include *Calocedrus decurrens*, *Pinus ponderosa*, or *Pinus contorta*. Other drought-tolerant trees that occur in savannas include *Quercus kelloggii* (southern Willamette Valley only), *Fraxinus latifolia*, *Arbutus menziesii*, and *Juniperus maritima* (San Juan and Gulf Islands only). To a large degree, the herbaceous understory of savannas historically was similar to prairies, but with a greater representation of shrubs and shade tolerant woodland species (Fig. 4).

Woodlands are often found near prairies and savannas, and may in part have developed in response to interactions between topography, soils, and fire frequency. Prairie fires tend to become more patchy and die out as they enter the shadier, cooler, and moister conditions under trees, thereby greatly reducing the burn frequency to perhaps every 10–30 years. This would have inhibited survival of regenerating conifers while favoring oaks and shrubs such as *Corylus cornuta* var. *californica*, *Symphoricarpos albus*, *Rosa* spp., and (in the Willamette Valley) *Toxicodendron diversilobum*, all of which resprout after fire. These taller woody species would have shaded out many grasses and forbs, further reducing the fine fuels that carried frequent fires in more open vegetation.

In the absence of fire since settlement, savannas and woodlands have largely succeeded to forest, and considerable uncertainty exists about their understory composition in pre-settlement times when they were being frequently burned. Today, remnant open-grown oak trees surrounded by younger forest-grown trees are an indicator of a former savanna that has converted to forest. In some areas where fire frequencies may have been higher, oak forests often include many multitemmed trees. These likely were denser stands of stump-sprouted oak brush at the time of settlement which were released to develop into forest in the absence of fire. Because the oaks are less shade tolerant, slower growing, and smaller statured than Douglas-fir trees, in many areas oaks have been overtopped by conifers and are dying out beneath a Douglas-fir forest canopy.

Oak woodlands and forests are still relatively extensive in the Willamette Valley. However, in many cases they occupy sites that were savanna at the time of Euro-American settlement, and which developed as a result of a reduction in fire frequency (Fig. 5). Such sites now have a depauperate native herbaceous flora and may not be representative of their historical composition or structure. Patches of oak woodland are part of the landscape mosaic in western Washington and British Columbia, in some cases persisting on sites where saturated soils in the winter preclude establishment of Douglas-fir.

Oak-dominated plant associations or community types have been variously described across the WPG ecoregion. In Oregon, two oak-dominated savanna types and three woodland types were described by Buechling et al. (2008), whereas in Washington, Chappell (2004) described three savanna types dominated by *Quercus garryana*, *Pseudotsuga menziesii*, and *Pinus ponderosa*, respectively, and an additional 11 oak-dominated woodland types. At the northern end of the range of *Quercus garryana*, a finer community taxonomy has been described in British Columbia, where Erickson (2002) examined the relationship between 26 oak-dominated community types and various environmental variables. However, no single system for characterizing these associations has emerged that can be readily applied throughout the ecoregion.

Biogeography and Floristics

Overall, about 716 native vascular plant taxa have been documented from grasslands, savannas, and woodland habitats in the WPG ecoregion. 554 of these show high or moderate fidelity to at least one of these three habitats. The remaining 162 taxa are more typical of other habitats, such as conifer forests, riparian forests, or wetlands. Many species are widespread across the ecoregion; of the high and moderate fidelity taxa, 53% are documented from most of the WPG, although very few are dominant throughout



Fig. 5 Late summer view of a Willamette Valley oak woodland showing an open grown presettlement oak surrounded by dense younger oaks, which likely established due to a reduction in fire frequency. The red foliage belongs to the liana form of *Toxicodendron diversilobum*. Photography by E. Alverson.

(see [Appendix A](#)). Nevertheless, there is considerable variability in the composition of similar communities in different areas. For example, 25% of the taxa are documented from only one portion of the ecoregion.

The high and moderate fidelity species are represented by 68 vascular plant families and 259 genera. The top species-rich families (with the number of native taxa represented) are Asteraceae (76), Poaceae (44), Fabaceae (39), Plantaginaceae (21), Apiaceae (20), and Saxifragaceae (20). The most species-rich genera are *Trifolium* (14 taxa), *Carex* (13 taxa), *Lupinus* (11 taxa), and *Lomatium* (9 taxa). Bulbous monocots, formerly assigned to Liliaceae but now divided among Amaryllidaceae, Asparagaceae, Liliaceae, and Melanthiaceae are particularly conspicuous in the flora, and are represented by 29 taxa.

Twenty-nine species, subspecies, or varieties of vascular plants are endemic or nearly endemic to the WPG ecoregion and occur exclusively or predominantly in oak or prairie habitats ([Table 2](#)). Many of these are species of conservation concern due to their rarity throughout the ecoregion. Of the 27 endemics that have been ranked according to NatureServe's methodology, 20 (74%) are considered to be at risk, with a Global Status of G3 or lower. Six taxa (22%) are ranked G1, which is defined as "critically imperiled." Listing of some of these species under federal and state/province endangered species laws has helped to focus conservation attention and reduced the likelihood of them becoming extinct. For example, *Castilleja levisecta* had been extirpated in Oregon and reduced to about 12 sites globally before it was federally listed as threatened in the United States in 1997. Since then, it has been established in over 40 sites throughout its historical range, with some populations exceeding 50,000 flowering plants (Dunwiddie, unpublished data).

Like *Quercus garryana*, many of the prairie and woodland species in the WPG ecoregion have the center of their geographic distribution in northern California and southwestern Oregon, and thus represent a northern extension of the Californian flora. However, some taxa are more widely distributed east of the Cascades and may have arrived via long-distance dispersal. A few examples these eastern disjuncts include *Iris missouriensis*, *Lomatium grayi*, *Shepherdia canadensis*, and *Balsamorhiza hookeri*. Others, such as *Bistorta bistortoides*, *Carex aurea*, *Oxytropis campestris* var. *spicata*, *Micranthes oregana*, and *Vaccinium cespitosum*, are more typically found at high elevations in the mountains in the Pacific Northwest, and may be persistent relics from late-glacial times.

Fauna

The grassland and woodland habitats of the WPG ecoregion do not support the diversity of large ungulates characteristic of many other similar temperate biomes. Black-tailed deer and Roosevelt elk are the main large herbivores in these habitats. Historically, the Columbian white-tailed deer was present in the Willamette Valley, though it was extirpated following Euro-American settlement. Historically, gray wolves were present, as well as grizzly bears in the Willamette Valley; cougars, black bears, and coyotes are predators that are still present ([Vesely and Rosenberg, 2010](#)). Various smaller mammals are present in many areas, including rodents

Table 2 Endemic and near-endemic vascular plants of the Willamette Valley-Puget Trough-Georgia Basin ecoregion associated with prairie and oak habitats.

Scientific name	Family	Global rank	US ESA status	COSEWIC status
<i>Camassia quamash</i> spp. <i>maxima</i> ^a	Asparagaceae	4		
<i>Cardamine penduliflora</i>	Brassicaceae	4		
<i>Castilleja levisecta</i>	Orobanchaceae	2	Threatened	Endangered
<i>Castilleja victorae</i>	Orobanchaceae	1		Endangered
<i>Delphinium leucophaeum</i>	Ranunculaceae	2	Sp. of concern	
<i>Delphinium nuttallii</i> ^a	Ranunculaceae	4		
<i>Delphinium oregonum</i>	Ranunculaceae	2	Sp. of concern	
<i>Delphinium pavonaceum</i>	Ranunculaceae	1	Sp. of concern	
<i>Erigeron decumbens</i>	Asteraceae	1	Endangered	
<i>Eucephalus vialis</i> ^a	Asteraceae	3	Sp. of concern	
<i>Grindelia integrifolia</i> ^a	Asteraceae	5		
<i>Horkelia congesta</i> spp. <i>congesta</i> ^a	Rosaceae	2	Sp. of concern	
<i>Iris tenax</i> var. <i>gormanii</i>	Iridaceae	1		
<i>Juniperus maritima</i> ^a	Cupressaceae	3		Candidate (low)
<i>Lathyrus holochlorus</i>	Fabaceae	2	Sp. of concern	
<i>Limnanthes macounii</i>	Limnanthaceae	2		Threatened
<i>Lomatium bradshawii</i>	Apiaceae	2	Endangered	
<i>Lupinus oregonus</i> ^a	Fabaceae	2	Threatened	Extirpated
<i>Navarretia willamettensis</i>	Polemoniaceae	1		
<i>Penstemon hesperius</i>	Plantaginaceae	1		
<i>Sericocarpus rigidus</i>	Asteraceae	3	Sp. of concern	Special concern
<i>Sidalcea campestris</i> ^a	Malvaceae	4		
<i>Sidalcea cusickii</i> ^a	Malvaceae	4		
<i>Sidalcea nelsoniana</i> ^a	Malvaceae	2	Threatened	
<i>Sisyrinchium hitchcockii</i> ^a	Iridaceae	2	Sp. of concern	
<i>Sisyrinchium idahoense</i> var. <i>macounii</i>	Iridaceae	(not ranked)		
<i>Sisyrinchium idahoense</i> var. <i>segetum</i> ^a	Iridaceae	(not ranked)		
<i>Symphyotrichum hallii</i> ^a	Asteraceae	4		
<i>Trillium albidum</i> spp. <i>parviflorum</i>	Melanthiaceae	2		

Global ranks, US Endangered Species Act (ESA) status, and Committee on the Status of Endangered Wildlife in Canada (COSEWIC) status provided by NatureServe Explorer (explorer.natureserve.org/) and Oregon Biodiversity Information Center (2016).

^aNear-endemic.

(mice, voles, woodrats, and introduced rats), squirrels, rabbits, and pocket gophers. Among these species, several are of particular conservation concern. The western gray squirrel (*Sciurus griseus*) is common in Oregon but is extremely rare in western Washington, where it is limited to a few mixed oak-conifer woodlands near Olympia. The gray-tailed vole (*Microtus canicaudus*) and camas pocket gopher, (*Thomomys bulbivorus*) are endemic to Willamette Valley prairies and savannas, and several subspecies of the Mazama pocket gopher (*Thomomys mazama*) found in WPG grasslands are considered rare, while two appear to be extinct.

Forty-nine species of birds are highly associated with prairie and oak habitats of the WPG ecoregion (Altman, 2011). Twenty-one have exhibited notable declines in range and/or population size, and three have been extirpated as breeding populations—burrowing owl (*Speotyto cunicularia*), Lewis's woodpecker (*Melanerpes lewis*), and Say's phoebe (*Sayornis saya*). Two subspecies are endemic to the habitats—the streaked horned lark (*Eremophila alpestris strigata*) and Oregon vesper sparrow (*Pooecetes gramineus affinis*), and a third, the slender-billed white-breasted nuthatch (*Sitta carolinensis aculeata*) is a near-endemic.

Overall, the invertebrate fauna of these habitats is poorly known. Butterflies are among the best-studied groups, with approximately 81 taxa currently known to occur in the WPG ecoregion (Appendix B). Sixteen species are of conservation concern, thirteen of these are endemic or near-endemic to the ecoregion (Table 3), and four are the focus of considerable conservation efforts, including Taylor's checkerspot (*Euphydryas editha taylori*), mardon skipper (*Polites mardon*), island marble (*Euchloe ausonides insulanus*), and Fender's blue (*Icaricia icarioides fenderi*) (Schultz et al., 2011). Interest in the native bees and other pollinators of these habitats in the ecoregion is increasing, but data summarizing species, abundance, and distribution is lacking. Additional research documenting the conservation and habitat management needs of native invertebrates would be beneficial.

Ecological Processes

Grasslands in the Pacific Northwest frequently occur on substrates that are too droughty for trees to readily establish. However, moisture stress is not sufficient to maintain these open, herbaceous-dominated ecosystems in most areas. Conditions suitable for tree establishment frequently arise, and once started, woody species from the surrounding forests—most commonly

Table 3 Endemic butterflies in the WPG ecoregion.

Scientific name	Common name	Location	Status
<i>Atlides halesus corcorani</i>	Great purple hairstreak	WV	
<i>Cercyonis pegala incana</i>	Common wood nymph	PT, GB	
<i>Coenonympha tullia insulana</i>	Island ochre ringlet	GB	
<i>Euchloe ausonides insulana</i>	Island marble	GB	C (US); EX (Can.)
<i>Euphydryas editha taylori</i> ^a	Taylor's checkerspot	WV, PT, GB	E (US); E (Can.)
<i>Oeneis nevadensis gigas</i>	Great arctic	GB	
<i>Phyciodes pulchella nr pulchella</i>	Field crescent	WV, GB	
<i>Icaricia icarioides blackmorei</i>	Puget blue	PT	
<i>Icaricia icarioides fenderi</i>	Fender's blue	WV	
<i>Icaricia saepiolus insulana</i>	Island blue	GB	E (Canada)
<i>Polites sonora siris</i>	Sonora skipper	WV, PT	
<i>Speyeria cybele pugetensis</i> ^a	Great spangled fritillary	WV, PT	
<i>Speyeria zerene nr bremneri</i> ^a	Valley silverspot	WV -X, PT, GB	

Location: WV = Willamette Valley, PT = Puget Trough, GB = Georgia Basin (including San Juan Islands). Status: C = Candidate, E = Endangered.

^aNear-endemic.

Douglas-fir, oaks, and various shrubs—are able to thrive and often grow more rapidly than in the forest. As with most temperate grasslands, fire historically played a major role in limiting tree encroachment. In the WPG ecoregion, fires were largely ignited by indigenous tribes for at least the last several millennia and perhaps much longer (Whitlock, 1992; Storm and Shebitz, 2006; Weiser and Lepofsky, 2009). Such burning limited encroachment of woody vegetation, thereby maintaining the prairies as openings in the extensive conifer forests of the region despite the high precipitation in many areas that favors growth of trees. Frequent prairie fires enhanced the diversity and growth of numerous plants that provided Native Americans with important food and medicinal resources. Storm and Shebitz (2006) report that 83% of 153 species in southwestern Washington prairies had cultural uses, with 35% of these used for food. Camas bulbs were especially valued, and along with salmon, served as a primary dietary staple for most tribes in the region. Most ethnographic evidence suggests that prairies were ignited in the late summer or fall throughout the ecoregion (Boyd, 1999; Storm and Shebitz, 2006). Storm and Shebitz suggested that prairies were ignited every 1–2 years, but the patchiness of vegetation and fuels resulting from such frequent burning likely produced a longer fire rotation for any particular patch of prairie, perhaps burning every 3–5 years or longer.

The large-scale harvesting of roots, rhizomes, and bulbs such as *Camassia*, *Lomatium*, *Fritillaria*, and *Pteridium* would have resulted in significant soil disturbance and creation of gaps in the prairie vegetation matrix. Similarly, burrowing animals likely were historically more abundant and widespread, further adding to soil disturbance. These activities, together with the regular ignition of fires, would have combined to significantly shape the vegetation composition, as well as influence ecological processes such as pollination, pest impacts, and nutrient cycling. Today's prairies may differ in important ways from their historical antecedents due to alteration or absence of these processes.

Savannas and woodlands, which often occur immediately adjacent to prairies, were also strongly influenced by fire. Fires ignited in the grasslands would regularly burn into the surrounding forests, killing smaller trees and shrubs and helping to maintain the more open character of the savannas and woodlands. As in the prairies, burning released nutrients and stimulated growth that enhanced berry production and vigor of plants with edible leaves, shoots, roots, and rhizomes. Where oaks were present, fall burns also cleared brush and litter, facilitating acorn collection by indigenous people (Turner, 1999).

Fire is a common element limiting ecological succession and maintaining vegetation in a seral state in many temperate grasslands worldwide. However, the grasslands of the WPG ecoregion differ from those of the Great Plains and many other regions in their lack of large herds of grazing ungulates. Although black-tailed deer and occasionally elk were present in many areas, they did not occur in the numbers that would have impacted the ecology of these systems to the extent seen in similar grasslands elsewhere. Thus, it is not surprising that trees and other woody vegetation have rapidly and extensively increased in these communities, frequently transforming them into different vegetation types since Euro-American settlers brought an end to the fires set by Native Americans.

Threats

Remnants of prairie, savanna, and oak woodland can be found throughout most of the WPG ecoregion. However, throughout the region these habitats have declined by 90–99% from three main causes: conversion for agriculture, urban development, and succession to forest in the absence of fire (Noss et al., 1995; Crawford and Hall, 1997; Lea, 2006; Christy and Alverson, 2011; Dunwiddie and Bakker, 2011).

In the 1.2 million ha Oregon portion of the WPG ecoregion, remaining oak-dominated vegetation occupies ca. 44,000 ha, though most is in a highly altered state (Alverson, 2011). The same study found a similar amount (ca. 42,000 ha) of

grassland types. Although higher quality prairies were not distinguished, they probably do not exceed 1–2% of the historical extent. Of the original extent of prairie in the Willamette Valley, ca. 70% is now utilized for agriculture, 15% has converted to conifer forest through ecological succession, and 10% has been lost to urbanization and other development. In savanna habitats, 45% is utilized for agriculture, 35% is forest, and 10% has been developed (Hulse et al., 2002). Nearly half of the remaining acreage of these habitats occurs in parcels exceeding 25 ha, but only about 9% occurs on lands under some type of conservation ownership. In South Puget Sound, Crawford and Hall (1997) reported that of the 60,000 ha with grassland soils, only 3% were dominated by native prairie species. Present day extent of savannas and oak woodlands is not as well documented, but the Spanaway-Lakewood area of Pierce County, which historically supported the most extensive savannas, has largely been urbanized.

In the northern Puget Sound region, prairies are restricted to small remnants, field corners, and roadsides, but are still important refuges for endangered prairie species such as golden paintbrush. Herbaceous balds, particularly in the San Juan and Gulf Islands, have been less affected by habitat loss due to their unsuitability for cultivation, although many have been negatively impacted by grazing, resulting in loss of native species diversity and invasion of nonnative plant species. Some of the highest quality remnants are located on small islands that were too small to be subject to regular grazing by domestic livestock (Dunwiddie, 2018). Studies by Lea (2006) in British Columbia show similarly extensive losses, with ca. 1600 ha (less than 5%) of these ecosystems remaining, largely limited to only a few small fragmented remnants. Overall, urbanization and forest encroachment likely remain the primary threats, as nearly all areas that were potentially important for agriculture have already been converted.

Invasive nonnative species have had a major impact in reducing ecological function and native species abundance. Nonnative grasses, mostly Eurasian in origin, predominate in many remnants due to historical agricultural conversion and grazing. Native forbs have also declined, many being desired forage for livestock, or because of an inability to compete with nonnative herbaceous species in disturbed areas. While not all nonnative plant species are invasive, Dennehy et al. (2011) listed over 100 species that are currently or potentially invasive in prairie and oak habitats. Important or noteworthy nonnative grasses include *Agrostis capillaris*, *Arrhenatherum elatius*, *Brachypodium sylvaticum*, *Schedonorus arundinaceus*, and *Phalaris arundinacea* (in wet prairies). Important nonnative forbs include *Centaurea* spp., *Daucus carota*, *Geranium lucidum*, *Hieracium pilosella*, *Hypericum perforatum*, *Hypochaeris radicata*, *Leucanthemum vulgare*, *Potentilla recta*, and *Senecio jacobaea*. Prominent nonnative woody species, which have colonized prairie and oak remnants and altered ecological function in major ways, include *Cytisus* spp. (largely *C. scoparius*), *Crataegus monogyna*, *Daphne laureola*, *Pyrus communis*, *Prunus avium*, *Rosa* spp., and *Rubus bifrons* (= *R. armeniacus*). Most of these species are native to temperate regions of Eurasia, where they have evolved under the influence of agriculture and grazing of domestic livestock, and thus have been able to respond better than native species to grazing and agricultural management in WPG prairies, savannas, and oak woodlands. And while some invasive nonnative plants can be fairly readily managed by fire (e.g., *Cytisus scoparius*), many respond positively to burning (Nuckols et al., 2011).

Anticipating how prairie and oak habitats will respond to climate change is challenging. Climatic models for the Willamette Valley project hotter and likely drier conditions (Shafer and Bartlein, 2015), which might be expected to favor oaks over conifers, but may also favor grassland habitats over forests (Michalak et al., 2017). Yet considerable uncertainties remain not only regarding the extent and rate of predicted environmental changes, but also how numerous other factors will change in response. Fire frequency and severity, CO₂ fertilization, species interactions, introduction of invasive taxa and new pathogens, increased habitat fragmentation, and human responses, are just a few critical factors that are likely to have not only significant direct effects, but complex and often unpredictable interactions as well. Extant prairies and savannas represent remnants of habitats that reached their peak extent during the Hypsithermal, when the climate was warmer and drier than today, and have survived for millennia in a dynamic world. Whether these systems and the species that comprise them have the ecological, genetic, and physiological capacity to adapt to a rapidly-changing environment and landscape remains uncertain.

Conservation and Research

There are few large acreages of predominantly native grassland remaining in the WPG ecoregion. The main exceptions are on a military base in South Puget Sound (Joint Base Lewis-McChord), where nearly 5000 ha of prairies remain, including several over 1000 ha. In most areas, prairies that once extended for thousands of hectares have been reduced to small, highly fragmented remnants. Most of these remnants are less than a few hundred hectares, and often much smaller. Many of these have already been protected from development by conservation organizations and government agencies, so there are relatively few opportunities to preserve significant acreages of native prairie. Instead, future acquisitions of land for prairie conservation are likely to focus on undeveloped farmland (Dunwiddie and Bakker, 2011; Sinclair et al., 2006). Although native species may be largely absent in such areas, the presence of prairie soils offer important conservation opportunities by providing locations where native prairie species can be planted, beginning the long process of recreating the complex associations of plants, pollinators, and ecological processes that comprise viable prairie communities.

In native prairie remnants that have been protected, conservation efforts are largely directed in two main areas—removing and managing invasive non-native plants, and reestablishing and introducing native species to increase diversity and enhance ecological resilience of the prairie communities. Managers use a variety of tools to achieve these restoration objectives, such as setting fires and applying selective herbicides to treat invasive plants and create favorable conditions in which to sow seed of native species

(Stanley et al., 2011a,b). Because many of these sites are small and isolated, managers are constrained in terms of the ecological functionality that can be restored. For example, prescribed fires in prairie remnants burn much smaller areas than historical fires would have consumed, or cannot be ignited when these historical fires were set due to air quality or safety concerns. It may be difficult or impossible to sustain populations of some nesting birds that require territories larger than a preserve. Butterflies that rely on recolonizing locally extirpated populations by dispersal of individuals from nearby sites may be difficult to maintain on isolated sites.

As a result of these constraints, managers of natural areas that include remnants of prairie, savanna, and woodland habitats have come to recognize that most sites require frequent and intensive intervention, and cannot simply be left alone to let nature take its course. To retain rare species, minimize the impact of invasive species, and sustain healthy populations of a large diversity of species, active restoration is required. The science of ecological restoration is still evolving, with much that remains to be learned about how to effectively and efficiently maintain and restore these systems and their biota. Academic and agency scientists often collaborate with land managers across the region to research questions that advance conservation objectives in two main areas. First, much research is directed toward understanding the biology and ecology of individual species, particularly rare species that are primarily found in the WPG habitats. Preventing the extinction of species such as golden paintbrush, Taylor's checkerspot, or streaked horned larks relies on recognizing key vulnerabilities in their life cycle, understanding what comprises optimal habitat, and helping managers integrate this information into conservation actions. Second, extensive research also is focused on the habitat management process itself—how best to reduce invasive species, establish native species, and maintain healthy communities over the long term. The process of creating and maintaining prairies and woodlands in a landscape that is rapidly urbanizing, within a changing sea of newly arriving, often invasive species, and in a climate that is presenting new and still uncertain challenges, will require continued new insights, creativity, and perseverance by WPG researchers and conservationists.

Future

In recent decades, the prairie and savanna habitats of the WPG ecoregion have become the focus of a remarkable network of conservation programs. The inherent synchrony of natural and human systems that have come into play to create these vibrant ecosystems has inspired citizens, practitioners, and researchers to apply a hands-on approach to conserving, managing, and restoring these ecosystems. While efforts to date have led to many successes, questions remain as to how successfully managers can mitigate the numerous threats prairies and savannas and their biota face in the coming decades. Extreme habitat loss is further eroded by fragmentation, reduced habitat quality, invasive species, and loss of appropriate fire regimes. Despite thousands of hectares of remnant prairies and savannas being under conservation management, this acreage still represents only a small fraction of the historical extent.

Today's prairie and savanna species are inexorably altered from their condition when the first Euro-American explorers and settlers were arriving a mere two centuries ago. Numerous species of nonnative plants, animals, and fungi have become permanent residents. Meanwhile, it is unclear how well the resulting novel ecosystems will be able to sustain the remaining native biodiversity. It is possible that current levels of extinction debt, together with extensive and rapid changes in future climate and habitat, may doom many species unless conservationists are able to greatly expand available habitat, enhance connectivity, and facilitate dispersal of species to more favorable environments (Dunwiddie et al., 2009; Dunwiddie and Rogers, 2017). While hotter temperatures and increased moisture stress in the future may expand prairie and savanna habitats by reducing tree density in transitional sites, it is also possible that the species that are capable of moving into newly created openings will largely be nonnative unless proactive steps are taken to assist in the establishment of less vagile native species.

As the community of conservation practitioners moves to take on these challenges, new perspectives will be valuable to help improve prospects for success. Developing restoration implementation strategies that use the most effective treatments and maximize the likelihood of restoration success through staged restoration or other hedging methods may be key (Bakker et al., 2018). Ultimately, in an ecoregion that has been so heavily modified, ecological restoration in the Pacific Northwest may depend on the degree to which it can be closely integrated with cultural restoration—that is, sustaining native ecosystems as a social and cultural goal (Dunwiddie and Bakker, 2011). Working collaboratively to incorporate the values of native cultures—such as reviving camas harvesting and use of native plant materials—may be an especially integral part of future conservation success.

Appendix A

Common vascular plants of Pacific Northwest prairies. Species recorded in >70% of prairie/oak sites for four sectors within the WPG ecoregion. Percent frequency of species in each sector was calculated based on comprehensive species lists for multiple sites. The total number of sites used to calculate percentages in each sector are: South Willamette Valley (20), South Puget Sound (15), San Juan Islands (62), and Vancouver Island and adjacent Gulf Islands of southwestern BC (31). x = Species present but documented from <70% of inventoried sites in that subregion.

Scientific name	Family	Grass/Forb/Shrub	Peren/Ann.	S. Will. Valley	S. Puget Sound	San Juan Islands	SW BC
<i>Achillea millefolium</i> (var. <i>borealis</i>)	Asteraceae	F	P	95%	100%	90%	94%
<i>Acemisson parviflorus</i>	Fabaceae	F	A	75%	87%	x	81%
<i>Allium acuminatum</i>	Amaryllidaceae	F	P	x		77%	97%
<i>Allium amplexans</i>	Amaryllidaceae	F	P	70%	x	x	x
<i>Amelanchier alnifolia</i>	Rosaceae	S	P	90%	x	81%	92%
<i>Aphanes occidentalis</i>	Rosaceae	F	A	x	x	73%	x
<i>Apocynum androsaemifolium</i>	Apocynaceae	F	P	x	87%	x	x
<i>Arctostaphylos uva-ursi</i>	Ericaceae	S	P		93%	x	x
<i>Balsamorhiza deltoidea</i>	Asteraceae	F	P	x	73%		x
<i>Berberis aquifolium</i>	Berberidaceae	S	P	80%	x	79%	97%
<i>Brodiaea coronaria</i>	Asparagaceae	F	P	x	80%	x	97%
<i>Bromus sitchensis</i> var. <i>carinatus</i>	Poaceae	F	A	x	x	x	97%
<i>Calochortus tolmiei</i>	Liliaceae	F	P	100%			
<i>Camassia leichtlinii</i> spp. <i>suksdorfii</i>	Asparagaceae	F	P	70%	x	73%	86%
<i>Camassia quamash</i> spp. <i>maxima/azurea</i>	Asparagaceae	F	P	x	93%	x	86%
<i>Campanula rotundifolia</i>	Campanulaceae	F	P		80%	x	
<i>Cardamine nuttallii</i>	Brassicaceae	F	P	80%	x		x
<i>Carex inops</i> spp. <i>inops</i>	Cyperaceae	G	P		100%	x	89%
<i>Carex tumulicola</i>	Cyperaceae	G	P	70%	x		x
<i>Cerastium arvense</i> spp. <i>strictum</i>	Caryophyllaceae	F	P	x	73%	94%	92%
<i>Claytonia perfoliata</i>	Montiaceae	F	A	75%	X	79%	94%
<i>Collinsia parviflora</i>	Plantaginaceae	F	A	x	X	73%	92%
<i>Danthonia californica</i>	Poaceae	G	P	80%	93%	x	92%
<i>Delphinium menziesii</i>	Ranunculaceae	F	P	95%	X	x	83%
<i>Dichelostemma congestum</i>	Asparagaceae	F	P	95%	X		
<i>Dodecatheon hendersonii</i>	Primulaceae	F	P	75%	73%		78%
<i>Elymus glaucus</i> spp. <i>glaucus</i>	Poaceae	G	P	85%	X	84%	86%
<i>Eriophyllum lanatum</i> var. <i>leucophyllum</i>	Asteraceae	F	P	90%	100%	x	81%
<i>Erythranthe alsinoides</i>	Phrymaceae	F	A	x		x	83%
<i>Erythronium oregonum</i> spp. <i>oregonum</i>	Liliaceae	F	P	x	x	x	86%
<i>Festuca roemerii</i> var. <i>roemerii</i>	Poaceae	G	P	70%	100%	x	x
<i>Festuca rubra</i> , native spp./vars	Poaceae	G	P		73%	95%	78%
<i>Fragaria vesca</i> spp. <i>californica</i>	Rosaceae	F	P	85%		x	x
<i>Fragaria virginiana</i> spp. <i>glaucia</i>	Rosaceae	F	P	100%	93%	x	x
<i>Fritillaria affinis</i>	Liliaceae	F	P	x	93%	76%	94%
<i>Grindelia integrifolia</i>	Asteraceae	F	P	x		87%	x
<i>Heuchera micrantha</i> var. <i>diversifolia</i>	Saxifragaceae	F	P	x		71%	x
<i>Hieracium scouleri</i>	Asteraceae	F	P	x	87%		x
<i>Iris tenax</i> var. <i>tenax</i>	Iridaceae	F	P	90%			
<i>Koeleria macrantha</i>	Poaceae	G	P	75%	93%	x	x
<i>Lathyrus nevadensis</i> var. <i>nevadensis</i>	Fabaceae	F	P	x	x	x	83%
<i>Ligusticum apiifolium</i>	Apiaceae	F	P	80%	x		
<i>Lithophragma parviflorum</i>	Saxifragaceae	F	P	80%	x	x	81%
<i>Lomatium nudicaule</i>	Apiaceae	F	P	70%	x	x	x
<i>Lomatium utriculatum</i>	Apiaceae	F	P	75%	93%	x	78%
<i>Lonicera hispidula</i>	Caprifoliaceae	S	P	x		x	75%
<i>Lupinus albicaulis</i>	Fabaceae	F	A	x	73%		
<i>Lupinus lepidus</i> var. <i>lepidus</i>	Fabaceae	F	P	x	73%		x
<i>Luzula comosa</i> s.l. (native taxa)	Juncaceae	G	P	85%	87%	x	x
<i>Micranthes integrifolia</i>	Saxifragaceae	F	P	x	x	x	83%
<i>Microseris laciniata</i> spp. <i>laciniata</i>	Asteraceae	F	P	x	100%		x
<i>Pentagramma triangularis</i> spp. <i>triangularis</i>	Pteridaceae	F	P	x		x	81%
<i>Perideridia montana</i>	Apiaceae	F	P	70%	x		x
<i>Plectritis congesta</i>	Caprifoliaceae	F	A	75%	x	71%	86%
<i>Potentilla gracilis</i> var. <i>gracilis</i>	Rosaceae	F	P	90%	73%		x
<i>Prunella vulgaris</i> spp. <i>lanceolata</i>	Lamiaceae	F	P	95%	87%	x	x
<i>Ranunculus occidentalis</i> var. <i>occidentalis</i>	Ranunculaceae	F	P	95%	93%	x	94%

(Continued)

Scientific name	Family	Grass/Forb/Shrub	Peren/Ann.	S. Will. Valley	S. Puget Sound	San Juan Islands	SW BC
<i>Sanicula bipinnatifida</i>	Apiaceae	F	P	85%		x	x
<i>Sedum spathulifolium</i>	Crassulaceae	F	P			x	83%
<i>Sericocarpus rigidus</i>	Asteraceae	F	P	x	100%	x	x
<i>Sidalcea virgata</i>	Malvaceae	F	P	90%	x		
<i>Symphotrichum hallii</i>	Asteraceae	F	P	85%	x		
<i>Toxicodendron diversilobum</i>	Anacardiaceae	S	P	90%			x
<i>Toxicoscordion venenosum</i> var. <i>venenosum</i>	Melanthiaceae	F	P	70%	93%	x	92%
<i>Trifolium microcephalum</i>	Fabaceae	F	A	x	x	75%	x
<i>Trifolium willdenowii</i>	Fabaceae	F	A	x	x	x	86%
<i>Triteleia hyacinthina</i>	Asparagaceae	F	P	80%	x	x	97%
<i>Vicia americana</i> var. <i>americana</i>	Fabaceae	F	P	85%	73%	81%	x
<i>Viola adunca</i>	Violaceae	F	P	x	93%		x
<i>Wyethia angustifolia</i>	Asteraceae	F	P	75%	x		

Appendix B

Butterflies of the prairies, savannas, and oak woodlands of the Willamette Valley-Puget Trough-Georgia Basin ecoregion. X = present, H = historic (extirpated). Data sources: Dana Ross (WV); Ann Potter, Jon Pelham, Robert M. Pyle (SPL); [Hinchliff \(1996\)](#), Ann Potter, James Miskelly (SJ, G, VI). Nomenclature follows ([Pelham et al., 2019](#) and [Warren 2005](#)).

Family	Taxon	Willamette Valley	South Puget Lowlands	San Juan/Gulf/Vancouver Isl.
Hesperiidae	<i>Epargyreus clarus californicus</i>	X	X	X
	<i>Thorybes pylades</i>		X	H?
	<i>Erynnis icelus</i>	X	X	X
	<i>Erynnis propertius</i>	X	X	X
	<i>Erynnis persius</i> spp.	X	X	
	<i>Pyrgus ruralis ruralis</i>	X	X	X
	<i>Pyrgus communis</i> spp.	X		
	<i>Carterocephalus palaemon</i> spp.	X	X	X
	<i>Thymelicus lineola</i>			X
	<i>Amblyscirtes vialis</i>	X		X
	<i>Hesperia juba</i>	X	X	X
	<i>Hesperia colorado</i> nr. <i>oregonia</i>	X		
	<i>Hesperia colorado</i> "Salish segregate"		X	X
	<i>Polites mardon mardon</i>		X	
	<i>Polites sonora siris</i>		X	
	<i>Polites sonora</i> spp.	X		
	<i>Atalopedes campestris campestris</i>	X		
	<i>Ochlodes sylvanoides sylvanoides</i>	X	X	X
	<i>Euphyes vestris vestris</i>	X	X	X
Papilionidae	<i>Parnassius clodius claudianus</i>	X	X	X
	<i>Papilio zelicaon</i>	X	X	X
	<i>Papilio rutulus</i>	X	X	X
Pieridae	<i>Papilio eurymedon</i>	X	X	X
	<i>Colias eriphyle</i>	X	X	
	<i>Colias eurytheme</i>	X	X	X
	<i>Colias occidentalis</i>		X	H?
	<i>Anthocharis julia flora</i>	X	X	X
	<i>Euchloe ausonides insulanus</i>			X
	<i>Neophasia menapia tau</i>	X	X	X
	<i>Pieris marginalis marginalis</i>	X	X	X
	<i>Pieris rapae rapae</i>	X	X	X
	<i>Pontia occidentalis occidentalis</i>	X		X

(Continued)

Family	Taxon	Willamette Valley	South Puget Lowlands	San Juan/Gulf/Vancouver Isl.
Lycaenidae	<i>Lycaena arota</i> spp.	X		
	<i>Lycaena xanthoides nigromaculata</i>	X		
	<i>Lycaena helloides</i>	X	X	X
	<i>Atlides halesus corcorani</i>	X		
	<i>Satyrus sylvinus nootka</i>	X	X	
	<i>Callophrys dumetorum</i> nr. <i>dumetorum</i>	X	X	
	<i>Callophrys gryneus plicataria</i>	X	X	X
	<i>Callophrys augustinus iroides</i>	X	X	X
	<i>Callophrys mossii</i>	X		X
	<i>Callophrys polios</i> "Salish segregate"		X	
	<i>Callophrys eryphon sheltonensis</i>		X	X
	<i>Callophrys eryphon</i> spp.	X		
	<i>Strymon melinus</i>	X	X	X
	<i>Celastrina echo echo</i>	X	X	X
	<i>Glaucopteryx lygdamus columbia</i>		X	X
	<i>Glaucopteryx lygdamus incognitus</i>	X		
	<i>Cupido comyntas sissona</i>	X		
	<i>Cupido amyntula amyntula</i>	X	X	X
	<i>Icaricia saepiolus insulanus</i>			X
	<i>Icaricia icarioides fenderi</i>	X		
	<i>Icaricia icarioides blackmorei</i>		X	X
	<i>Icaricia acmon acmon</i>	X		
	<i>Icaricia acmon</i> "Juan de Fuca segregate"			X
	<i>Plebejus anna</i>			H?
Nymphalidae	<i>Danaus plexippus plexippus</i>	X	X	X
	<i>Boloria epithore chermocki</i>	X	X	X
	<i>Speyeria cybele pugetensis</i>	X	X	
	<i>Speyeria zerene bremnerii</i>	H?	X	X
	<i>Speyeria callippe</i> spp.	H?		
	<i>Speyeria hydaspe</i>	X	X	X
	<i>Limenitis lorquini ilgae</i>	X	X	X
	<i>Adelpha californica</i>	X		
	<i>Vanessa virginiensis</i>	X	X	X
	<i>Vanessa cardui</i>	X	X	X
	<i>Vanessa annabella</i>	X	X	X
	<i>Vanessa atalanta rubria</i>	X	X	X
	<i>Aglais milberti subpallida</i>	X	X	X
	<i>Nymphalis californica californica</i>	X	X	X
	<i>Nymphalis antiopa antiopa</i>	X	X	X
	<i>Polygonia satyrus neomarsyas</i>	X	X	X
	<i>Polygonia oreas silenus</i>	X	X	X
	<i>Polygonia faunus rusticus</i>	X	X	X
	<i>Euphydryas editha taylori</i>	X	X	X
	<i>Euphydryas chalcedona</i>			H?
	<i>Euphydryas colon colon</i>	X		
	<i>Phyciodes mylitta mylitta</i>	X	X	X
	<i>Phyciodes pulchella</i>	X		X
	<i>Coenonympha tullia eunomia</i>	X	X	
	<i>Coenonympha tullia insulana</i>			X
	<i>Cercyonis pegala incana</i>		X	X
	<i>Cercyonis pegala ariane</i>	X		
	<i>Oeneis nevadensis gigas</i>			X
	Total	66	56	59
	Historical	2		4

Acknowledgments

We are grateful to the many researchers that have generously contributed data used in the summaries of plants and butterflies found across the ecoregion. In addition to our own plant species lists for many sites, we also drew on datasets made available by Joe Bennett, Patrick Lilley, Jenny McCune, and James and Kristen Miskelly. Information and lists for butterflies were contributed by James Miskelly, Jonathan Pelham, Ann Potter, Robert M. Pyle, and Dana Ross.

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North American Sagebrush Steppe and Shrubland

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Published by Elsevier Inc.

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Abstract

The sagebrush (*Artemisia* spp.) biome extends throughout arid and semi-arid environments in the western U.S., stretching northward into southwestern Canada and eastward to the western Great Plains. The sagebrush biome primarily consists of sagebrush-steppe, with relatively abundant perennial bunchgrasses, and sagebrush shrublands that are generally more desert-like with sparser herbaceous cover. Big sagebrush (*A. tridentata*) is the most widely distributed species, but other sagebrush species are found throughout the biome, some in relatively distinct environments. Sagebrush communities range from almost pure sagebrush to a diverse mix of shrubs, grasses, and forbs, often with complex biological soil crust communities. Sagebrush ecosystems provide habitat for hundreds of species of conservation concern, including sagebrush-obligate wildlife such as the greater sage-grouse (*Centrocercus urophasianus*), a widely distributed species that is declining across most of its range, primarily due to deteriorating habitat quality. Roughly ~45% of the historical area of sagebrush steppe/shrublands has been lost due to human activities, including: over-grazing by livestock, clearing to enhance rangeland forage, energy development, roads, cropland conversion; altered fire regimes driven by invasive, fire-prone, annual plant species; and expansion of woodlands caused by land use and climate variability. Climate change will likely have significant future impacts on sagebrush ecosystems. Conservation of sagebrush ecosystems is critical for the myriad species supported, ecological services provided, and the iconic character of western U.S. landscapes, and will likely require enhanced efforts to restore and protect sagebrush habitat from detrimental land uses and wildfire. Scientific research can provide a better understanding of how interactions among various stressors affect sagebrush communities, and how to best manage and prioritize sagebrush habitats for conservation.

What Are Sagebrush Steppe and Sagebrush Shrublands?

“Sagebrush” are woody shrub or subshrub species contained within the genus *Artemisia*, mostly within the subgenus *Tridentatae*, and all of which are endemic to North America. There have been numerous taxonomic revisions, but approximately 12 sagebrush species in the subgenus *Tridentatae* are currently recognized (depending on the taxonomic authority), with a similar number of subordinate taxa; however, several allied species are also generally considered “sagebrush” (McArthur and Sanderson, 1999; Shultz, 2009, 2012; Garcia et al., 2011). Most sagebrush species are evergreen, and the leaves persist on the plant through the winter for several years, permitting winter photosynthesis; however, many species produce both ephemeral and persistent leaves which can vary in size and shape (Shultz, 2012). Sagebrush do not have showy flowers common to other members of the Asteraceae family to which they belong, but they are known for their distinctive, aromatic “sage” odor derived from volatile compounds, especially in the glands of their leaves, which helps to reduce herbivory by insects and grazing animals. However, sagebrush are a valuable and nutritious food source for many insect and wildlife species, especially in the fall and winter when leaf concentrations of volatile compounds are lower (Rosentreter, 2005).

Sagebrush ecosystems are commonly classified into either a shrub-steppe type or a shrubland type, with sagebrush-steppe generally characterized by the potential for co-dominance of perennial bunchgrasses, and sagebrush shrublands typically defined as more desert-like and containing a dominant shrub overstory with relatively sparse cover of grasses and forbs. The dominant species vary greatly among specific sagebrush community types (Table 1) depending on environmental setting and disturbance history, but sagebrush steppe communities are typically dominated by one of three subspecies of big sagebrush (*A. tridentata*), including basin big sagebrush (*A. t. tridentata*), Wyoming big sagebrush (*A. t. wyomingensis*), and mountain big sagebrush (*A. t. vaseyana*). Other common sagebrush ecosystems are dominated by “low” or “dwarf” forms of the species, often growing on shallow, rocky, or poorly drained soils (West and Young, 2000), including low sagebrush (*A. arbuscula*) and black sagebrush (*A. nova*). Other sagebrush species (e.g., *A. pygmaea*, *A. rothrockii*) grow in more limited habitats, often reflecting dry locations and unique soil environments (McArthur, 2000).

Table 1 Some of the most common and dominant sagebrush species and subspecies of the sagebrush steppe and sagebrush shrublands, with summaries of their distribution, key characteristics, and environmental settings.

Species/subspecies	Common name	Description and environmental settings
<i>Artemisia arbuscula</i>	Low (little) sagebrush	This widespread, short-statured sagebrush species occurs in a wide variety of habitats, and the four recognized subspecies often exist in unique soils conditions among big sagebrush communities, including poorly drained clayey soils in alkali basins and on dry, high-elevation, windy ridges. Elevations range from < 1000 m to over 3500 m, and annual precipitation ranges from 20 cm to > 50 cm
<i>A. cana</i>	Silver sagebrush	The three recognized subspecies of this low sagebrush occupy distinct habitats, ranging from areas with relatively high moisture/precipitation areas (e.g., near streams rivers, snowmelt) often at high elevations (up to 3300 m), to lower elevation basins and playas, and eastward into the grasslands of the Great Plains
<i>A. nova</i>	Black sagebrush	A short-statured sagebrush species typically located in warmer, drier sites with shallow, rocky, and often calcareous soils throughout much of the interior mountain west. Annual precipitation ranges from 15 cm to 50 cm; typical elevation is 1200–2400 m
<i>A. rigida</i>	Scabland (rigid) sagebrush	A low-growing sagebrush species found primarily on volcanic, often shallow rocky soils, mostly in the Columbia Basin (Washington and Oregon). Annual precipitation ranges from 20 cm to 40 cm, and elevation 230–2100 m
<i>A. tridentata</i>	Big sagebrush	Most widespread of the sagebrush species (with several recognized subspecies), ranging from Sierra Nevada and Cascade Mts. east to the Great Plains, and from southern Canada to Arizona, New Mexico, and northern Baja Mexico. Big sagebrush is the dominant shrub species in much of the sagebrush steppe and shrublands, and often on the northwestern Great Plains. Big sagebrush taxa are found on a wide variety of soils, with annual precipitation ranging from 20 cm to > 75 cm, and elevations ranging from 600 m to > 3000 m. Three primary subspecies with broad geographical ranges are described below
<i>A. t. ssp. tridentata</i>	Basin big sagebrush	Deep rooted subspecies of big sagebrush found on lower elevation (600–2000 m) sites with deep, fertile soils (loamy to sandy) and annual precipitation 20–40 cm. Plants can exceed 3 m in height, with spreading, irregularly-shaped crowns
<i>A. t. ssp. vaseyana</i>	Mountain big sagebrush	A big sagebrush subspecies commonly found at higher elevations (typically 1000–3200 m) on mountain slopes and meadows, often more mesic and productive than other sagebrush sites; with annual precipitation ~35–45 cm
<i>A. t. ssp. wyomingensis</i>	Wyoming big sagebrush	Common and widespread big sagebrush subspecies that forms extensive communities in the interior western U.S., found on generally well-drained, loamy soils (but shallower than for <i>A. t. ssp. tridentata</i>) across dry sites (18–30 cm precipitation per year) at low- to mid-elevations (800–2200 m)
<i>A. tripartita</i>	Threetip sagebrush	There are two recognized subspecies, one reaching up to 2 m in height and occurring on igneous-derived soils, and a less common low-growing subspecies (< 40 cm in height). The former, more common threetip subspecies is found throughout the sagebrush steppe where annual precipitation is generally 30–40 cm and elevation ranges from 900 m to 2400 m. This is one of the few sagebrush species that resprouts after disturbance, including fire
<i>A. bigelovii</i>	Bigelow sage	A short- to mid-sized sagebrush found primarily in the Colorado Plateau region and the desert grasslands and scrublands of the southwest

Primary information sources: McArthur, E. D. (2000). Sagebrush systematics and distribution. In Entwistle, P. G., DeBolt, A. M., Kaltenecker, J. H., Steenhof, K. (comps.) *Proceedings: Sagebrush Steppe Ecosystem Symposium; 1999 June 23–25; Boise, ID*. BLM/ID/PT-001001 + 1150. Boise, ID: USDI Bureau of Land Management, pp. 9–14; Miller, J. E. D., Rossman, A., Rosentreter, R. and Ponzetti, J. (2011a). Lichen ecology and diversity of a sagebrush steppe in Oregon: 1977 to the present. *North American Fungi* 6, 1–14.; Miller, R. F., Knick, S. T., Pyke, D. A., et al. (2011b). Characteristics of sagebrush habitats and limitations to long-term conservation. In Knick, S. T. and Connelly, J. W. (eds.) *Greater sage-grouse: Ecology and conservation of a landscape species and its habitats*. Berkeley, CA: University of California Press, pp. 145–184; Shultz, L. M. (2012). Pocket guide to sagebrush. PRBO Conservation Science. Available: http://www.sagestep.org/pubs/pubs/sagebrush_pock_guide.pdf; NRCS PLANTS Plant Guides, available at <http://plants.usda.gov>.

Where Are Sagebrush Ecosystems Found?

Sagebrush ecosystems are commonly found throughout the interior western U.S., generally occurring in arid to semi-arid climates, with wide distribution across the plateaus and basins that exist between and surrounding mountain ranges, and often forming the dominant vegetation type over vast landscapes. The sagebrush biome extends from southwestern Canada (British Columbia, Alberta, and Saskatchewan) southward into northern New Mexico and Arizona, and stretches from the eastern slopes of the Sierra Nevada and Cascade Mountains to western North Dakota, South Dakota and Nebraska (Fig. 1). Prior to EuroAmerican settlement, ecosystems with sagebrush taxa as a significant component likely extended over more than 1 million square kilometers (km²) (Beetle, 1960), although estimates vary depending on how sagebrush ecosystems are defined and delineated (Welch and Criddle, 2003). Based on distribution of potential natural vegetation types (Küchler, 1970), sagebrush-steppe habitat (including the wheatgrass-needlegrass steppe of the Wyoming Basin) covers ~450,000 km² and sagebrush shrublands (delineated here as generally coinciding with the Great Basin sagebrush type) cover ~180,000 km² (West and Young, 2000), with hundreds of thousands of

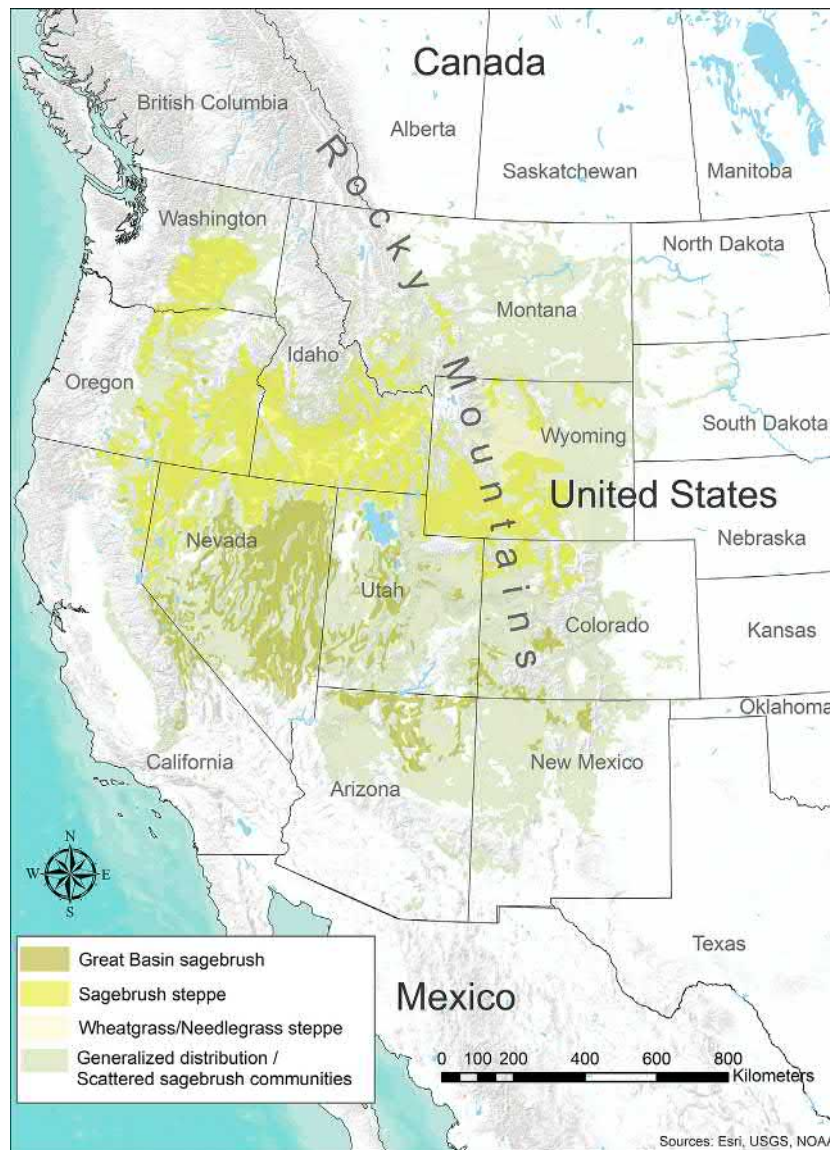


Fig. 1 The distribution of the sagebrush steppe and sagebrush shrubland ecosystems as defined by potential natural vegetation type (Küchler, 1970), and set within the context of a generalized distribution of extant sagebrush ecosystems that are often scattered among other natural community types (e.g., grasslands, woodlands) or human-developed landscapes (e.g., agricultural lands).

additional square kilometers containing scattered sagebrush communities or areas in which sagebrush is an important component but not necessarily dominant (Fig. 1).

Sagebrush communities generally occur where winters are long, with cool to cold temperatures, and summers are hot and dry (McArthur, 2000). Sagebrush community composition and structure vary along broadly-defined bioclimatic gradients, but can also vary abruptly with changes in topography, geology, elevation, and soils that affect growing conditions (e.g., plant-available water). The primary sagebrush taxa generally occur where annual precipitation averages 18–35 cm, usually occupying elevations below woodlands and forests, but above salt-desert shrub communities. However, mountain big sagebrush (*A. t. ssp. vaseyana*) can form extensive communities at higher elevations with generally wetter environments (35–45+ cm precipitation per year) and species such as silver sagebrush (*A. cana*) also occur at higher elevations or in moist habitats near streams, in meadows, or in areas with more persistent snowpack (McArthur, 2000; Miller et al., 2011a,b).

In the western portion of the sagebrush biome, most precipitation arrives as winter snow or rain, summers are hot and dry, and deeper soil water storage favors deep-rooted woody species such as sagebrush. Within these “cold desert” ecoregions, the sagebrush shrubland type is coarsely delineated from sagebrush-steppe by generally occurring south of a climate transition zone in which warmer temperatures and seasonal changes in precipitation limit the abundance and productivity of perennial bunchgrasses (Miller et al., 2011a,b; Chambers et al., 2017). As a result, the Northern Basin and Range, Snake River Plain, Wyoming Basin, and Columbia

Plateau ecoregions generally support shrub-steppe communities, while the Colorado Plateau, Central Basin and Range, and Arizona/New Mexico Plateau generally support sagebrush shrublands with sparser herbaceous cover. The proportion of annual precipitation arriving during warmer months also increases toward the eastern edge of the sagebrush biome, where shrublands converge with prairie grasslands, and silver sagebrush and sand sagebrush (*A. filifolia*) may be co-dominant with grasses, or grass-dominated prairie landscapes contain scattered Wyoming big sagebrush communities, characteristic of much of the northwestern Great Plains. Sagebrush communities are also found throughout the valleys, foothills, and southerly-facing slopes of the western mountain ranges that separate cold desert ecoregions (Chambers et al., 2017).

Ecological Attributes

Structure and Composition

Sagebrush communities can range from almost pure sagebrush, especially on more xeric sites, to a diverse mix of shrubs, grasses, and forbs, especially on more mesic sites. Sagebrush community types classified at the alliance or association level within the International Vegetation Classification system (Reid et al., 2002) are those in which sagebrush species are typically either dominant or co-dominant in the overstory, sometimes with other shrub species, such as bitterbrush (*Purshia tridentata*) or snowberry (*Symphoricarpos* spp.), and often further delineated by prevalent herbaceous species, especially tussock forming “bunchgrasses” that occur in the understory or spaces between shrubs in much of the sagebrush biome. In northern portions of the sagebrush biome and at higher elevations, diagnostic bunchgrasses for classification include species such as bluebunch wheatgrass (*Pseudoroegneria spicata*) or Idaho fescue (*Festuca idahoensis*), while broadly-adapted species and those that tolerate drought conditions, such as Sandberg bluegrass (*Poa secunda*) or bottlebrush squirreltail (*Elymus elymoides*), become more dominant in warmer and drier areas. There is also a transition from cool-season bunchgrasses that dominate much of the sagebrush steppe to increasing presence of warm-season or sod-forming grasses (e.g., *Bouteloua* spp., *Sporobolus* spp.) in sagebrush shrublands in more southerly portions of the biome. In the northwestern Great Plains, needlegrasses (e.g., *Hesperostipa* spp., *Achnatherum* spp.), wheatgrasses (e.g., *Pascopyrum smithii*, *Elymus* spp.), grama grasses (*Bouteloua* spp.), and bluestem species (e.g., *Andropogon gerardii*, *Schizachyrium scoparium*) tend to dominate. At higher elevations, sagebrush species can form understory components of mountain shrub and woodland communities (e.g., *Purshia tridentata*, *Cercocarpus* spp., *Juniperus* spp., *Pinus* spp.), while at lower elevations, sagebrush often interperse with salt-desert shrub communities (e.g., *Atriplex* spp., *Sarcobatus* spp., *Krascheninnikovia lanata*).

The size and dominance of sagebrush plants varies with sagebrush species, environmental setting, and disturbance history. For instance, in the sagebrush steppe, shrub cover varies widely (~10–80%) depending on site conditions and disturbance history (West and Young, 2000). The overstory shrub layer in most sagebrush steppe and shrublands is typically 0.3–1.0 m tall; however, basin big sagebrush can exceed 3 m in height. Understory layers of grasses and forbs are typically <0.4 m tall, and the relative cover and production of herbaceous species varies greatly depending on community type, growing season moisture availability, site conditions and disturbance history. There is often greater density and shorter stature of sagebrush plants on xeric sites where sagebrush can comprise more than 70% of relative plant cover (West and Young, 2000). Biological soil crusts or bare ground may dominate inter-spaces between shrubs, especially within more arid sites where herbaceous species are found mostly under or near shrubs (Miller et al., 2011a,b). Biological soil crusts are considered good indicators of rangeland ecosystem health, and often include complex assemblages of lichens, mosses, cyanobacteria, green algae, and micro-fungi that can protect soil surfaces from erosion, regulate nutrient availability, and provide sites with favorable conditions for germination of native plant species (Belnap et al., 2001).

Biological Diversity Supported by Sagebrush Ecosystems

Sagebrush ecosystems provide habitat for over 350 plant and animal species of conservation concern (Wisdom et al., 2005), including several sagebrush-obligate wildlife species that depend on sagebrush habitat for part or nearly all of their life-history needs. These sagebrush-obligate species include the pygmy rabbit (*Brachylagus idahoensis*), sagebrush lizard (*Sceloporus graciosus*), pronghorn (*Antilocapra americana*), sagebrush vole (*Lemmyscus curtatus*), Brewer’s sparrow (*Spizella breweri*), sage thrasher (*Oreoscoptes montanus*), sagebrush sparrow (*Artemisiospiza nevadensis*), greater sage-grouse (*Centrocercus urophasianus*), and Gunnison sage-grouse (*C. minimus*) (Rowland et al., 2006; Wisdom et al., 2011). Although many sagebrush landscapes are not considered particularly floristically diverse (West and Young, 2000), intact or lightly-impacted sagebrush landscapes in some regions can support relatively species-rich plant communities, with high levels of diversity found both within and among individual sites (e.g., Seipel, 2006; Shinneman et al., 2008). Forb species richness is generally higher, but typically with less cover and biomass, compared to grasses. Other species groups are not as well studied across the sagebrush biome; however, some sagebrush communities have been shown to support a rich diversity of insect, lichen, and fungal species (Welch and Criddle, 2003; Miller et al., 2011a,b; Pilliod and Rohde, 2016).

The greater sage-grouse—a charismatic species of the sagebrush biome

The greater sage-grouse is a sagebrush-obligate species considered at risk throughout its range (Fig. 2). This large grouse species is perhaps best known for its flamboyant mating displays on lek sites, on which the males “strut” to attract female grouse, fanning their tail feathers and puffing their chests to inflate two bulbous air sacs that produce popping and whistling noises. In general, sage-grouse select relatively large, undisturbed sagebrush landscapes with minimal human activity (Aldridge et al., 2008). Greater sage-grouse depend on sagebrush for food, cover, nesting and brood rearing (Beck et al., 2009; Connelly et al., 2000, 2011). Optimal shrub cover

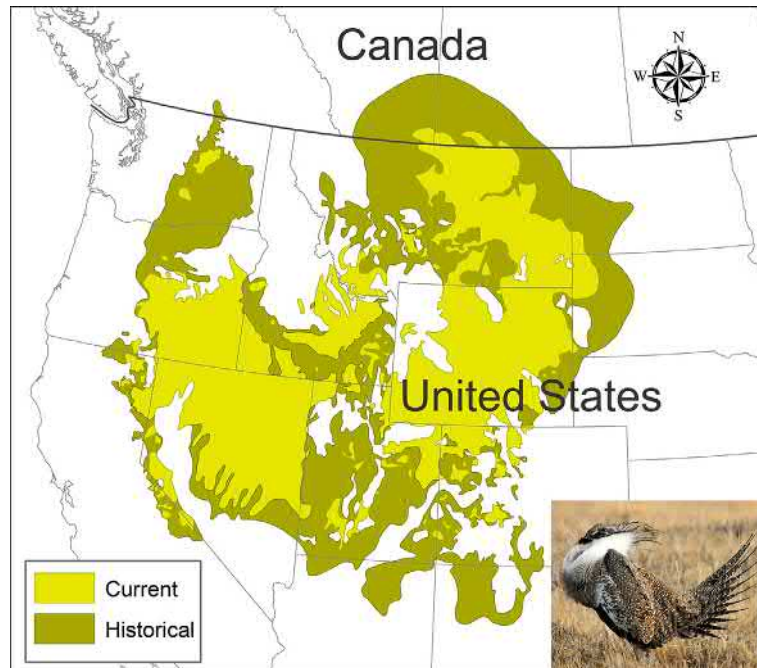


Fig. 2 The estimated historical distribution of the greater sage-grouse (*Centrocercus urophasianus*) and Gunnison sage-grouse (*C. minimus*) before EuroAmerican settlement and the approximate range distribution of contemporary sage-grouse populations. The sagebrush biome has been altered by fire, invasive species, cropland conversion, and human development (e.g., energy extraction, roads, housing, and powerlines) causing substantial declines in sage-grouse populations. Photo: U.S. Fish and Wildlife Service.

for greater sage-grouse is ~15–25% for nesting and early-season brood-rearing habitat (Stiver et al., 2015), but sagebrush cover and other structural requisites vary with seasonal life requirements and among populations in different parts of the distribution.

The greater sage-grouse has experienced substantial population declines and contraction of its historical range, prompting several (unsuccessful) petitions to list the bird for legally protected status under the U.S. Endangered Species Act. Human activities, such as energy development, roads, shrub removal, and conversion of habitat to cropland have fragmented or destroyed habitat, and currently, loss from fire is a predominant threat, especially in the western half of the sage-grouse range (Brooks et al., 2015), where increasing wildfire activity over recent decades is linked to dramatic sage-grouse population declines (Coates et al., 2016). As a result, land management agencies have recently developed sagebrush ecosystem management goals that focus on conserving sage-grouse habitat, including minimizing effects of wildfire (Chambers et al., 2017; see below). Because the greater sage-grouse is a wide-ranging, often migratory species that uses different sagebrush habitats during different seasons, it has been considered a potential “umbrella” species, whereby conservation of its broad extent and diversity of habitats would likely benefit numerous other sagebrush-associated species (Rowland et al., 2006).

Ecological Processes

Long term fluctuations in climate have influenced the distribution of sagebrush communities in western North America over many thousands of years, as well as the relative abundance of associated grass, forb, shrub, and tree species (Nowak et al., 1994; Mensing et al., 2013). Extreme climate events (e.g., drought) and disturbances operating over much shorter time scales, including fire, disease, and herbivory pressure, also influence the relative abundance of sagebrush species. Fire is particularly relevant to contemporary management and conservation of sagebrush ecosystems. Before EuroAmerican settlement, fire was infrequent in most sagebrush ecosystems, varying with climatic influence on fuel availability, fuel moisture, and ignition rates. Large portions of the pre-settlement sagebrush biome were likely affected by infrequently occurring large fires, resulting in landscapes characterized by large patches of mature sagebrush and some large grass-dominated areas (i.e., recovering from fire), with a superimposed, fine-scale mosaic of community structural conditions created by more frequent but smaller disturbance events (Bukowski and Baker, 2013). Historically, the average time between fires (i.e., mean fire return interval) ranged from a few decades in more productive, mesic sagebrush ecosystems near forest and woodlands (Miller and Heyerdahl, 2008) to hundreds of years or more in fuel-limited, hotter and drier sagebrush ecosystems or where summer precipitation limited fire spread (Baker, 2013). Most sagebrush species reestablish slowly after fire, as they lack capacity for re-sprouting or long-distance seed dispersal, and sagebrush seed viability is generally of short duration (Young and Evans, 1989). As a result, several decades or more may be required for full recovery to mature sagebrush habitat after fire (Shinneman and McIlroy, 2016), and trends of increasing fire frequency threaten the persistence of many sagebrush ecosystems, as discussed below.

Threats and Anthropogenic Stressors of Sagebrush Ecosystems

Since EuroAmerican settlement began during the mid-1800s, sagebrush ecosystems have undergone rapid and often irreversible conversion to human-developed landscapes and nonnative ecosystems that threaten the long term persistence of these communities and the myriad species they support. Historically, sagebrush was not a valued rangeland plant species, and conversion using fire or chemical and mechanical treatments were commonly imposed to increase forage for domestic livestock and improve water yields (Welch and Criddle, 2003). Sagebrush ecosystems are considered one of the most imperiled major ecosystems in North America (Noss and Peters, 1995), due to historical widespread over-grazing by domestic livestock, clearing of sagebrush to enhance livestock forage, conversion to cropland, urban expansion, and extensive fragmentation caused by energy development, road networks, and fuel treatments (Table 2). It has been estimated that ~45% of the historical area of sagebrush steppe and sagebrush shrublands has been lost (Miller et al., 2011a,b), mostly due to agriculture, but also from ecosystem type conversion (described below). Sagebrush communities of the Great Plains have also experienced substantial loss, particularly from cropland conversion and energy development.

Altered wildfire regimes coupled with the spread of invasive plant species pose a major threat to many sagebrush habitats (Knick, 2011), especially in drier sagebrush ecosystems in the western portion of the biome (Brooks et al., 2015) that have inherently low resilience to disturbance (i.e., slow recovery) and low resistance to invasion (Chambers et al., 2014). Nonnative annual plants, especially cheatgrass (*Bromus tectorum*), readily invade many sagebrush landscapes, establish quickly in burned areas, outcompete native perennials, and form continuous fine fuels that are highly ignitable and facilitate wildfire spread. The resulting “invasive plant–fire regime cycle” (Fig. 3) is characterized by both greater fire frequency, which retards shrub and perennial grass recovery, and promotes expansion of fire-prone, nonnative plant communities (Brooks et al., 2004). During a recent 30-year period (1984–2013), about 8.4 million ha burned in Great Basin rangelands alone, including areas that burned multiple times, some with mean fire return intervals <7.5 years (Brooks et al., 2015). Cheatgrass already dominates vast acreages in the Great Basin (Bradley and Mustard, 2005; Boyte and Wylie, 2016), and evidence suggests this nonnative species is contributing to increasingly larger fires (Balch et al., 2013), some of which have exceeded 200,000 ha in size (Brooks et al., 2015). Recent wildfire activity suggest these trends are likely to continue (Fig. 4), and future climate change could bring even more wildfire, as discussed below.

Effects of Climate Change

Directional trends in climate over the past several decades are evident across the sagebrush biome and throughout much of the western United States, including increasing temperatures, a longer frost-free season, and a declining snowpack (Kunkel et al., 2013; Mote et al., 2018). However, broad-scale trends in precipitation are difficult to discern and generally more variable across the region. Estimates derived from global circulation models (GCMs) project continued warming for the region throughout the next century. However, projected temperature increases vary among GCMs and are further dependent on the radiative forcing (greenhouse gas concentration) trajectories being modeled, as depicted in the representative concentration pathways (RCPs) developed for the Intergovernmental Panel on Climate Change [IPCC] (2014) to reflect future potential warming scenarios. Chambers et al. (2017) summarized climate projections from an ensemble of 11 GCMs across the sagebrush biome through the end of the 21st century, and found that average temperatures are expected to increase over the recent past (1980–2010) by a range of 2–5 °C to 3–7 °C using RCP pathways representing eventual stabilization (RCP4.5) versus steadily increasing (RCP8.5) radiative forcing, respectively, while precipitation projections ranged from a slight decrease (~10% decline) to substantial increases (up to 50%) over the long-term, reflecting considerable variability among models concerning future precipitation trends. Although climate change and its effects are expected to vary spatially, even if portions of the sagebrush biome receive more precipitation on average, less of it is predicted to fall as snow (Klos et al., 2014) and higher evapotranspiration rates are expected due to longer and hotter growing seasons (Palmquist et al., 2016). Thus, seasonal interactions between shifts in temperature and precipitation may effectively increase aridity and reduce plant available soil water, resulting in possible elevational or latitudinal range shifts by big sagebrush (Schlaepfer et al., 2015), or possibly an overall loss in climatically suitable habitat (Still and Richardson, 2015). A recent multi-model analysis by Renwick et al. (2018) suggested big-sagebrush in cooler and more mesic location might actually benefit from climate change, while big sagebrush in warmer locations, that are generally less resistant to invasion and less resilient after disturbance, are likely to decline.

In addition to directly affecting the distribution and abundance of individual sagebrush species, climate change may also impact sagebrush ecosystem composition and function by further altering disturbance regimes. More fire activity is likely if climate change increases the duration of fire-prone weather or enhances growing conditions for fire-prone species (Abatzoglou and Kolden, 2011). Indeed, some models predict climate-enhanced wildfire activity in the future, including higher probabilities of large fires, across much of the arid and semiarid portions of the western U.S. (Barbero et al., 2015). Over the near-term, warmer temperatures combined with wetter early growing-seasons could promote the productivity of cheatgrass and other nonnative annuals (Boyte et al., 2016), affecting the distribution of fine fuels that increase the potential for large and frequent fires (Bradley et al., 2018). Under frequent-fire dynamics, carbon storage would likely be reduced across the sagebrush biome and could convert the region from a carbon sink (net storage) to a carbon source (net loss/emission) (Bradley et al., 2006). However, complex, long-term future interactions between climate, fire, and vegetation remain difficult to predict with great certainty, and some areas could eventually experience less fire over time if fuels become increasingly limited under increasingly arid conditions. Ongoing research and observations are needed to better address this uncertainty and to facilitate management adaptation to changing conditions.

Table 2 Anthropogenic stressors that threaten the health or persistence of sagebrush ecosystems, and associated management and conservation actions that may alleviate these ecologically negative consequences.

<i>Threat/stressor description</i>	<i>Primary causes/sources</i>	<i>Potential management and conservation actions</i>
Human development: Human development can reduce or degrade sagebrush habitat, and threaten the viability of sagebrush-dependent wildlife, such as sage-grouse. Development impacts may occur individually or collectively, and include direct habitat conversion or indirect impacts via habitat fragmentation or by facilitating spread of invasive species	• Energy/mineral extraction and exploration • Conversion to cropland • Urban and exurban expansion • Infrastructure (e.g., roads, powerlines) • Associated human activity (e.g., increases in vehicle traffic, human-caused fires, recreation)	• Manage activities to minimize fragmentation, maintain landscape-scale connectivity, and limit risk of unintentional ecological change (e.g., exotic species invasions) • Limit or prohibit damaging activities in most sensitive habitats • Restore habitat and connectivity from past activities where feasible • Utilize minimum impact resource extraction technologies and methods • Utilize public land management planning, conservation designations, and cooperative arrangements among land-owners across boundaries to protect habitat and landscape-scale ecological processes
Livestock grazing: Livestock grazing impacts vary widely over time and space (i.e. environmental settings) and can be relatively benign, but heavy grazing by domestic livestock (cattle, sheep), especially without adequate rest, can reduce native herbaceous composition, structure, and productivity; damage biological soil crust; and increase the probability of exotic, annual grass invasion, especially at mid- to low-elevations. Effects can also vary regionally, as prior to EuroAmerican settlement, large ungulate grazing was relatively uncommon in the western portion of the sagebrush biome. Grazing intensity can also interact with limited and variable precipitation in sagebrush ecosystems, resulting in slow or delayed recovery / regrowth of plants	• Domestic livestock grazing is ubiquitous across federal, state, and private lands in the sagebrush biome • Unregulated grazing that began in the mid- to late-1800s and continued until after passage of the U.S. Taylor Grazing Act in 1934 likely had substantial and persistent impacts on sagebrush communities, especially where it damaged biological soil crusts and facilitated the historical expansion of cheatgrass	• Utilize ecologically sustainable stocking levels, rest periods, and seasonal rotation across landscapes • Minimize or restrict grazing in the most ecologically sensitive habitats, and after fire to promote recovery • Manage grazing animals to promote healthier ecosystems or to minimize adverse ecological consequences, including using strategically placed and timed grazing to reduce fuel loads in exotic species-invaded, fire-prone environments • Manage timing and placement of livestock to support post-grazing recovery of important seasonal wildlife habitats
Nonnative plant species: Nonnative plant species have invaded vast areas throughout the sagebrush biome, threatening habitat for native species, decreasing forage quality, and altering important ecological processes, including nutrient cycling and fire regimes	• Spread and dominance of exotic annual grasses (e.g., cheatgrass) and forbs, especially in drier-warmer environments that are less resistant to invasion • Intentionally introduced nonnative perennial grasses meant to improve forage for livestock that persist as dominant communities and can displace native plant species	• Utilize resistance and resilience concepts to prioritize and design effective restoration treatments for areas most in need and most likely to have successful outcomes • Prioritize postfire seeding and planting treatments in areas with high potential for exotic species invasions • Minimize future invasions through enhanced wildfire suppression efforts and land use management practices (see below)

(Continued)

Table 2 Anthropogenic stressors that threaten the health or persistence of sagebrush ecosystems, and associated management and conservation actions that may alleviate these ecologically negative consequences.—cont'd

Threat/stressor description	Primary causes/sources	Potential management and conservation actions
Altered wildfire regimes: Fire regimes across much of the sagebrush biome are no longer within their historical ranges of variability, with larger fire sizes and higher fire frequency, creating conditions that can eventually prevent recovery of native sagebrush communities	• Fire-prone, nonnative annual grasses that provide continuous fine fuels that drive larger and more frequent fires (invasive plant–fire cycle, Fig. 3) • Increasing rates of human ignited fires, especially near roads and populated areas • Changing climate that enhances fire-weather conditions, fire-prone species dispersal, and fuel loadings	• Where feasible, prioritize wildfire suppression activities to protect remaining intact sagebrush communities and wildlife habitat • Utilize fuel reduction treatments (targeted grazing, planting fire-resistant plants, mechanical reduction of biomass) where ecologically beneficial (e.g., avoid disturbing intact sagebrush communities), including carefully planned and constructed fuel break networks • Restore fire-prone, annual-grass invaded sagebrush communities, using native species where feasible • Control invading trees caused by past land use with low-impact mechanical treatments (e.g., individual tree removal) that permit retention of sagebrush cover valuable to wildlife • Prioritize treatments in or near essential wildlife habitat or where tree invasion elevates risk of altering ecological processes (e.g., increasing fire severity) • Avoid treatments in persistent and old-growth woodlands (that also have high value to wildlife) or where woodland removal enhances risk of nonnative species invasions
Native woodland expansion: Woodland tree species, particularly piñon pines (<i>Pinus</i> spp.) and junipers (<i>Juniperus</i> spp.) have expanded into adjacent sagebrush communities in portions of the sagebrush biome or have become denser, particularly in higher elevation sagebrush communities. While woodlands are an important native habitat, this shift in native ecosystem boundaries can result in loss of habitat for sagebrush-dependent wildlife, altered fire regimes, changes in composition and cover of plants, and altered hydrologic processes	• Natural, climate-driven expansion of woodland-shrubland ecotone over time • Influence of land uses that favor tree establishment and dominance, including livestock grazing and fire exclusion • Recovery from historical clearing of woodlands during early EuroAmerican settlement • Changing climate and enhanced atmospheric CO₂ that enhance tree species establishment and growth	• Recognize potential changes to sagebrush, including identifying systems that may become less resistant to invasion or less resilient to disturbance with climate change • Prioritize conservation/protection of important habitats (e.g., where future restoration under climate change may be most challenging) • Recognize potential for shifts in wildlife habitat utilization based on shifts in plant community composition and structure • Use climate forecasts and expected shifts in vegetation-fuel conditions to plan for wildfire control • Carefully manage livestock grazing intensity to reflect changing sensitivity of ecological conditions under climate variability/change
Climate Change: Variations in climate over space and time, especially water availability, are important determinants of sagebrush species distributions and abundance. Timing of precipitation can affect the relative abundance of shrubs vs. grasses, as well as contribute to the spread and dominance of invasive plants. Warming temperatures and altered precipitation regimes create new variations in plant composition and can affect the abundance and condition (e.g., moisture) of fuels that drive wildfires. Droughts limit forage available for wildlife and livestock	• Anthropogenic climate change caused by enhanced atmospheric CO₂ and other green-house gas concentrations • Climate variability occurring over different time periods (seasonal, annual, decadal) • Climate-driven disturbance events (e.g., fire, drought) • Ecophysiological response of plants to climate variability and long-term climate shifts (e.g., sagebrush shrubs typically take advantage of deep soil-water provided by winter precipitation—changes in the timing and type of precipitation may change soil hydrology and sagebrush community patterns)	• Recognize potential changes to sagebrush, including identifying systems that may become less resistant to invasion or less resilient to disturbance with climate change • Prioritize conservation/protection of important habitats (e.g., where future restoration under climate change may be most challenging) • Recognize potential for shifts in wildlife habitat utilization based on shifts in plant community composition and structure • Use climate forecasts and expected shifts in vegetation-fuel conditions to plan for wildfire control • Carefully manage livestock grazing intensity to reflect changing sensitivity of ecological conditions under climate variability/change

Multiple stressors can interact to push sagebrush ecosystems past ecological thresholds, making natural recovery unlikely and restoration efforts difficult, expensive, and uncertain.

Primary information sources: Chambers, J. C., Beck, J. L., Bradford, J. B., et al. (2017). *Science framework for conservation and restoration of the sagebrush biome: Linking the Department of the Interior's integrated rangeland fire management strategy to long-term strategic conservation actions*. Gen. Tech. Rep. RMRS-GTR-360. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.; Beck, J. L., Connelly, J. W. and Reese, K. P. (2009). Recovery of greater sage-grouse habitat features in Wyoming big sagebrush following prescribed fire. *Restoration Ecology* **17**, 393–403.; Davies, K. W., Boyd, C. S., Beck, J. L., Bates, J. D., et al. (2011). Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* **144**, 2573–2584.; Knick, A. T. (2011). Historical development, principal federal legislation, and current management of sagebrush habitats: Implications for conservation. In Knick, S. T. and Connelly, J. W. (eds.) *Greater sage-grouse: Ecology and conservation of a landscape species and its habitats*. Berkeley, CA: University of California Press, pp. 13–31.; Manier, D. J., and Hobbs, N. T. (2007). Large herbivores in sagebrush steppe ecosystems: Livestock and wild ungulates influence structure and function. *Oecologia* **152**, 739–750.; Miller, J. E. D., Rossman, A., Rosentreter, R. and Ponzetti, J. (2011a). Lichen ecology and diversity of a sagebrush steppe in Oregon: 1977 to the present. *North American Fungi* **6**, 1–14.; Miller, R. F., Knick, S. T., Pyke, D. A. et al. (2011b). Characteristics of sagebrush habitats and limitations to long-term conservation. In Knick, S. T. and Connelly, J. W. (eds.) *Greater sage-grouse: Ecology and conservation of a landscape species and its habitats*. Berkeley, CA: University of California Press, pp. 145–184.

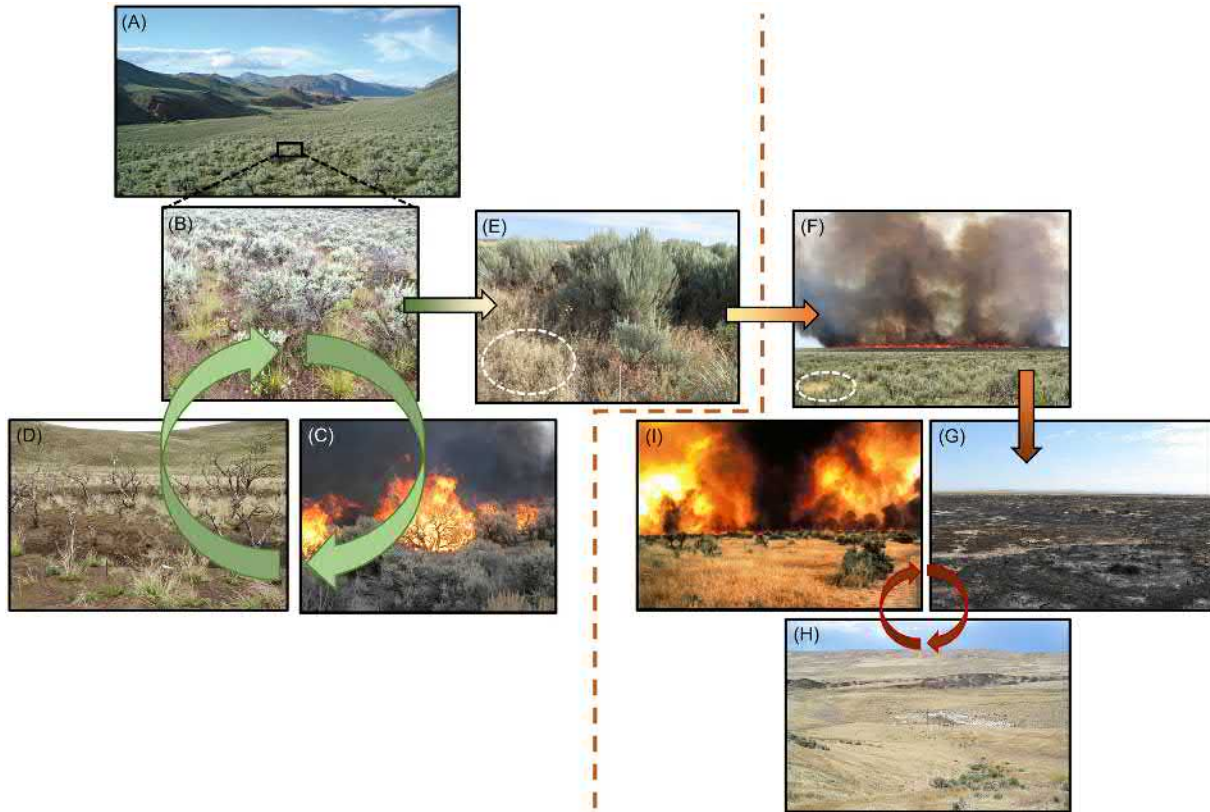


Fig. 3 Schematic illustration of the transition from a native sagebrush community (A–D) to an annual grassland (E–I) via the “invasive grass-fire regime cycle.” Historically, landscapes dominated by sagebrush ecosystems (A) often had relatively discontinuous fuel loadings, with sparse bunchgrasses and native forbs in the interspaces (B), that burned relatively infrequently (C), and required up to several decades or more to recover from loss of shrub cover (D) and eventually back to mature shrub conditions (B). Exotic, fire-prone, annual grasses (especially cheatgrass) and forbs have invaded much of the sagebrush biome, filling the interspaces and providing continuous fine fuel loadings (E) that dry early in the growing season and facilitate large fires (F). With mortality of native species after fire (G), these fire-adapted nonnative species rapidly germinate, dominate the seed-bank, and spread in the postfire environment (H), outcompeting slower-recovering native species. These highly-flammable annual grasslands are prone to frequent fires (I) that prevent native species reestablishment, especially shrubs, without intensive and expensive restoration efforts (many of which are either unsuccessful or only partially restore native ecosystem structure and function). The exotic annual grass community does not provide suitable habitat for sagebrush-obligate wildlife species, such as the greater sage-grouse. Direction and color (transitioning from *green* to *yellow* to *orange*) of the straight arrows represent the annual plant invasion process, with *white-dashed circles* showing the transition from native bunchgrasses to nonnative annual grasses (i.e., increasing cover of *Bromus tectorum*) in the shrub interspaces. The downward (*dark-orange*) arrow indicates facilitation of the invasion process via fire, representing complete ecosystem type conversion. The size of the fire cycle-succession circles roughly correspond to the proportional difference in the mean fire return interval between the historical fire regime (in *green*, decades to hundreds of years between fires) relative to the invasive grass fire regime cycle (in *dark-orange*, < 15 years between fires). The dashed-orange line represents the crossing of an ecological threshold, after which conversion back to a native community condition becomes prolonged, improbable, or even impossible. Photos: USGS, BLM.

Conservation Strategies

Conservation of sagebrush ecosystems is critical for the myriad species they support (Wisdom et al., 2005; Rottler et al., 2015). Various mechanisms for conservation of sagebrush ecosystems exist, ranging from implementing sagebrush-favorable land use policies and designations, protecting intact sagebrush habitat from wildfire, and restoring degraded and disturbed sagebrush habitat, especially after fire, to prevent the continued spread and dominance of cheatgrass and other nonnative species (Table 2). Although about two-thirds of sagebrush landscapes fall on federally-managed lands, most are managed for multiple uses that are not necessarily compatible with conservation goals (Knick, 2011). Moreover, < 3% of the land area of sagebrush ecosystems and < 1% of sage-grouse habitat fall within more strictly protected designations, such as national parks and federally designated wilderness areas, and even many of these protected areas permit livestock grazing or other activities (e.g., mining) that may be counterproductive to certain sagebrush habitat conservation objectives (Knick et al., 2003; Knick, 2011).

Protected areas also do not prevent the devastating effects of invasive-grass wildfire interactions that continue to threaten ecologically valuable sagebrush habitat for sagebrush obligate species such as sage-grouse. Between 2015 and 2017 alone, more than 1.3 million ha of sage-grouse habitat burned in the western U.S. (U.S. Department of the Interior, 2017). Restoration of burned sagebrush ecosystems is not easily achieved in harsh, arid climates and across remote landscapes, and post-fire rehabilitation and restoration outcomes do not always meet the habitat needs of sagebrush-dependent species (Arkle et al., 2014). Thus, one

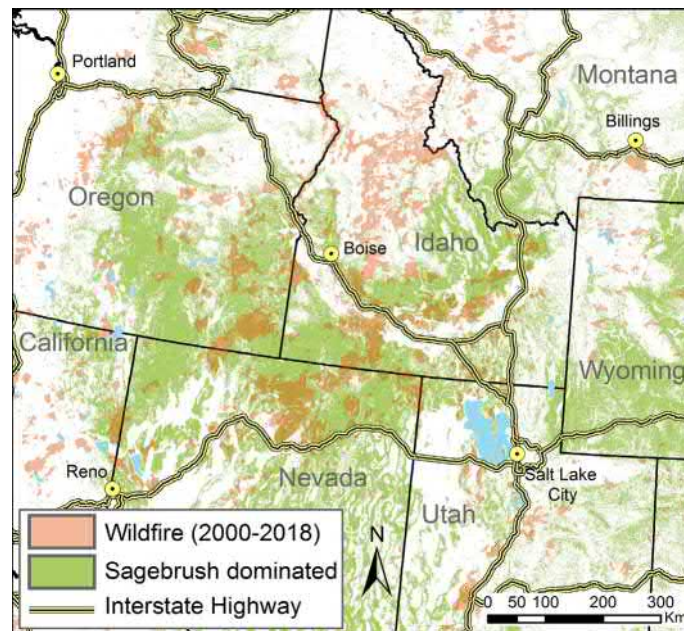


Fig. 4 Recent (2000–18) wildfire activity in the central-western portion of the sagebrush biome shown in relation to sagebrush-dominated landscapes.

strategy being promoted and implemented by federal land managers in the Great Basin is the construction of tens of thousands of kilometers of “fuel-breaks” (i.e., strips of land regularly cleared or mowed to reduce fuel loads, or planted with fire-resistant nonnative species) that are intended to limit the spread of wildfire in sagebrush landscapes. Unfortunately, the benefits of fuel breaks are uncertain, in part because their potential negative effects on sagebrush-dependent wildlife, including fragmentation of habitat, are largely unknown (Shinneman et al., 2019).

Ultimately, there are no easy solutions to conserving remaining sagebrush habitat across the vast reaches of the sagebrush biome. However, obtaining a better understanding of land use and management effects on sagebrush communities, estimating potential future risks, and seeking greater cooperation among state, federal, and private land owners to protect the sagebrush biome will be critical. Scientific research can facilitate these objectives, by investigating and elucidating the complex and dynamic interactions occurring among climate, wildfire, invasive species, and land use within sagebrush communities. This enhanced scientific understanding will improve our capacity to prioritize sagebrush landscapes for restoration and conservation action, protect important wildlife habitat they provide, and anticipate management outcomes under future climate change.

Acknowledgments

Special thanks to D. Manier and S. McIlroy for helpful review comments that benefited this chapter. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

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North American Pinyon–Juniper Woodlands: Ecological Composition, Dynamics, and Future Trends

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Abstract

Pinyon and juniper woodland is a major biome type centered on the Basin and Range and Colorado Plateau physiographic regions of interior western North America. It covers over 40 million ha from western Oregon in the northwest United States, eastward to Wyoming and southward to northern Chihuahua in Mexico, then westward to Baja California. Climatically, these woodlands lie within both the warm and cold temperate zones of North America but at the wetter and cooler portion of the semiarid realm where precipitation seldom exceeds 400 mm. This biome occupies a unique environmental envelope within North America, and with it comes a diverse complement of plant and animal species with the center of their ranges within its confines, and a wide variety of vegetation communities. The communities are characterized by low-statured woodlands and forests dominated by pinyon (nut pines) in combination with juniper trees. At lower elevations junipers tend to prevail and typically form very open-canopied woodlands of scattered trees in a shrubland or grassland matrix (shrubby woodlands and grassy woodlands or savannas, respectively). With increasing elevation, pinyons become more prevalent and co-dominate with junipers to form moderate-canopied woodlands and closed-canopied forests. Fire is integral to the dynamics of these woodlands ranging from high-frequency, low-intensity surface fires in grassy woodlands to low-frequency, high severity canopy fires in the forest communities. Across their domain, pinyon–juniper woodlands have been economically important in the lives of the people of western North America for millennia, from the harvesting of pinyon nuts and hunting to fuel wood gathering and livestock grazing. But now, given a growing human population in the region, increased landscape fragmentation, and potential climate change impacts, particularly on water availability, this biome is on the cusp of a transformation not yet seen in its history.

Introduction

Pinyon and juniper woodland is a major biome type centered on the Basin and Range and Colorado Plateau physiographic regions of interior western North America (Fig. 1). It covers over 40 million ha from western Oregon in the northwest United States, eastward to Wyoming and southward to northern Chihuahua in Mexico, then westward to Baja California (Kyllo, 2016). These are

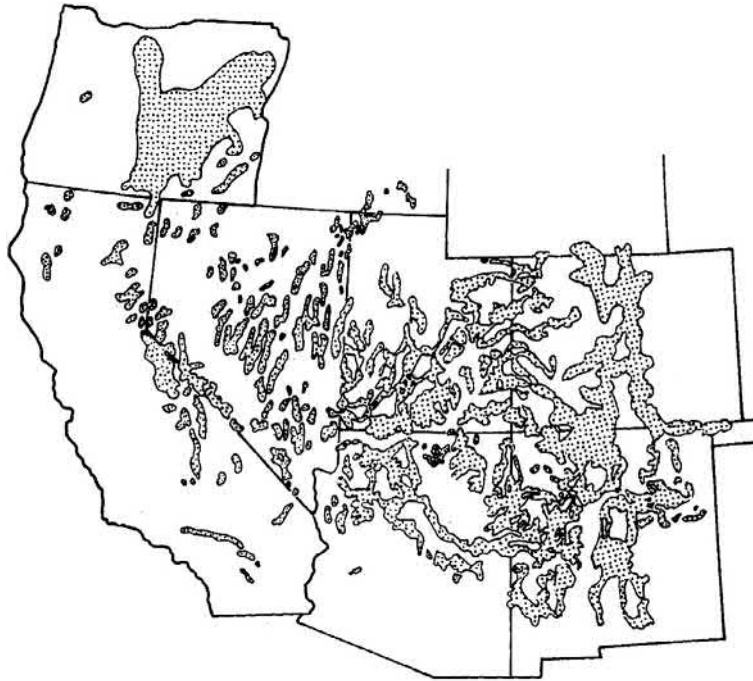


Fig. 1 Distribution of pinyon-Juniper woodlands in the United States. From Evans, R. (1988). *Management of pinyon-juniper woodlands*. General technical Report INT-249. Ogden, UT: Intermountain Research Station.

low-statured (<10 m) woodlands dominated by pinyon, or nut, pines in combination with juniper trees (Fig. 2). At the lower elevations of valley plains, plateaus, and foothills, junipers tend to prevail and typically form very open-canopied (>10%–25% canopy cover) stands consisting of scattered trees in a shrubland or grassland matrix (colloquially known as “juniper savannas,” although the use of “savanna” is a recent adoption of a term originally used to describe tropical and sub-tropical grassland plains with trees, which have different ecological context for their structure than those in N. America). With increasing elevation, pinyons become more prevalent and co-dominate with junipers to form moderate-canopied woodlands between 25% and 70% cover. Farther up mountain slopes, pinyons clearly dominate with junipers in the sub-canopy forming nearly closed-canopied forests that border on montane forests dominated by tall pines and firs.

Climatically, these woodlands lie within the wetter and cooler portion of the semiarid realm where precipitation seldom exceeds 400 mm. While summer precipitation becomes predominant in the eastern portion of the distribution, winter precipitation stored in the soil profile is crucial to sustaining these tree species throughout their ranges, particularly during summer drought years. Increasing temperatures at lower elevations leads to greater evaporative demand and limits the lower-elevation range of the type while extreme cold and competition from more mesic and productive species may limit the woodlands at upper elevation. Within this semiarid framework, fire plays a complex role in ecological dynamics from the tree to landscape level, varying in intensity and frequency with differences in composition and structure across the woodland domain. For example, following fires where shrubs were prevalent in the understory, successional communities dominated by shrubs such as mountain mahogany or oaks may prevail as long-standing elements of pinyon-juniper woodland landscape. Similarly, under natural conditions repeated fires in open-woodlands with a grassy matrix may prevent successful pine and juniper reproduction that would otherwise lead to expansion of the biome.

Overall, this biome occupies a unique environmental envelope within North America, and with it comes a diverse complement of plant and animal species with the center of their ranges within its confines. For example, 90% of the range of Pinyon Jays, a bird species dependent on nut-producing conifers, lies within the distribution of the four pinyon pine species. In turn, the birds are important dispersers of pinyon pine nuts leading to tree regeneration (Boone et al., 2018). Similarly, gray vireos are tied to the range of juniper species within the biome. The flora is diverse, with its share of endemics (43 species; Siviniski and Knight (1996) and Goodrich et al. (1997)) as well as a wide range of vegetation communities across the biome (150 plant associations; see Pinyon-Juniper Types section below).

Across their domain, pinyon-juniper woodlands have been economically important in the lives of the people of western North America. Pinyon nuts were not only nutritionally valuable, they have played a central cultural role among indigenous peoples and later in colonial Euro-American communities. Similarly, while the woodlands provide limited timber resources, they have provided fuel wood to all communities over the centuries into the present day. Beyond this, livestock grazing has been a nearly constant element of the landscape since European settlement and has a significant influence on land management practices. But now, given a growing human population in the region, increased landscape fragmentation, and potential climate change impacts, particularly on water availability, this biome is on the cusp of a transformation not yet seen in its history.



Fig. 2 Pinyon-juniper woodlands have a broad range of structure and composition across the biome including: (A) open grassy savanna-like woodlands with short trees in a grassy matrix; (B) open shrubby woodlands (or wooded shrublands) with shrubby inter-tree spaces; (C) closed-canopy long-lived, persistent forests with relatively tall trees with a mix of shrubs, grasses, and forbs in the understory; and (D) very open, often sparse woodlands on cliffs, escarpments and other rocklands. Photos: A, C, and D by E. H. Muldavin; B by F. A. Martin.

Types of Pinyon–Juniper Woodlands

Given its wide distribution and environmental complexity, the pinyon–juniper (P-J) woodland biome offers a wide diversity of vegetation types (some 150 plant associations have been identified across the P-J domain). Using the International Vegetation Classification (IVC) framework (Faber-Langendoen et al., 2014, 2017), P-J woodlands occur in both warm-temperate and cool-temperate forest and woodland formations that reflect climates with relatively warm winters versus cold winters, respectively (Table 1). Within the warm-temperate formation, the woodlands are further subdivided geographically into California and Madrean-Balconian divisions corresponding to west coast versus southwestern United States and Mexican distributions, respectively. The California P-J woodlands are dominated by California juniper (*Juniperus californica*) and four-needled or Parry's pinyon (*Pinus quadrifolia*) whose distribution is strongly influenced by the Mediterranean-like winter precipitation-dominated climate of southern California, southwestern Arizona, and adjacent Baja California in Mexico. In contrast, in Madrean-Balconian woodlands, monsoonal summer precipitation is predominant and P-J woodlands fall within Madrean Lowland Evergreen Woodlands dominated by a different set of pinyons—border pinyon (*P. cembroides* and *P. discolor*) and to a limited degree two-needled pinyon (*P. edulis*)—along with junipers such as redberry juniper (*Juniperus coahuilensis*), alligator juniper (*J. deppeana*), dropping juniper (*J. flaccida*), and Pinchot's juniper (*J. pinchotii*).

The cool-temperate P-J woodlands are represented by the Western North American Pinyon–Juniper Woodland and Scrub Division and are further divided into Intermountain Pinyon–Juniper versus Southern Rocky Mountain Two-needle Pinyon–Juniper Woodland macrogroups. The former includes woodlands of Great Basin, Colorado Plateau, and Colorado Plateau regions where winter precipitation is dominant and the winters can be very cold; summer precipitation is dependent on the extension of the “Arizona” monsoon from the south, which can be erratic. These woodlands are dominated by either singleleaf pinyon (*P. monophylla*) to the west or two-needle pinyon to the east in combination with Utah juniper (*Juniperus osteosperma*). Western juniper (*J. occidentalis*) occurs in the far northwest of the domain usually without pinyons. Included here are also curl-leaf mountain-mahogany (*Cercocarpus ledifolius*) shrubby woodlands which can be prevalent across the Great Basin. At lower elevations, these P-J woodlands can border on cold-desert shrublands and grassland communities while at upper elevations they grade to pine and mixed-conifer forests.

Table 1 A classification of pinyon-juniper woodlands following the International Vegetation Classification hierarchy (see Faber-Langendoen et al., 2014, 2017 for definitions of the hierarchy elements). For each level there is a database code per the US National Vegetation followed by the type name (complete descriptions of each element are available at the US National Vegetation Classification website: <http://usnvc.org/>).

1 Forest & Woodland Class			
1.B Temperate & Boreal Forest & Woodland Subclass			
1.B.1 Warm Temperate Forest & Woodland Formation			
D007	1.B.1.Nc Californian Forest & Woodland Division		
M009	Californian Forest & Woodland Macrogroup		
	G198	Californian Conifer Forest & Woodland Group	
		A3353	Transmontane Desert Pinyon–Juniper Woodland Alliance
D060	1.B.1.Nd Madrean-Balconian Forest & Woodland		
M010	Madrean Lowland Evergreen Woodland Macrogroup		
	G487	Madrean Juniper Open Woodland Group	
		A3134	Madrean Juniper/Grass Open Woodland Alliance
		A3133	Madrean Juniper/Shrub Open Woodland Alliance
	G200	Madrean Pinyon–Juniper Woodland Group	
		A3131	Madrean Pinyon–Juniper/Shrub Woodland Alliance
		A3132	Madrean Pinyon–Juniper/Grass Woodland Alliance
1.B.2 Cool Temperate Forest & Woodland			
D010	1.B.2.Nc Western North American Pinyon–Juniper Woodland & Scrub		
M896	Intermountain Pinyon–Juniper Woodland Macrogroup		
	G900	Colorado Plateau Pinyon–Juniper Woodland Group	
		A3571	Foothill & Lower Montane Pinyon–Juniper/Shrub Dry-Mesic Woodland Alliance
		A4371	Colorado Plateau Utah Juniper Shrubby Woodland Alliance
		A3573	Colorado Plateau Two-needle Pinyon–Utah Juniper Open Woodland Alliance
		A3572	Two-needle Pinyon–Utah Juniper Grassy Open Woodland Alliance
		A3497	Utah Juniper Grassy Open Woodland Alliance
	G248	Columbia Plateau Western Juniper Open Woodland Group	
		A3500	Western Juniper Grassy Open Woodland Alliance
		A3499	Western Juniper Shrubby Woodland Alliance
	G899	Great Basin Pinyon–Juniper Woodland Group	
		A4370	Great Basin Utah Juniper Shrubby Woodland
		A2108	Great Basin Singleleaf Pinyon–Utah Juniper Shrubby Woodland Alliance
		A2109	Great Basin Singleleaf Pinyon–Utah Juniper Grassy Open Woodland Alliance
	G249	Intermountain Basins Curl-leaf Mountain-mahogany Woodland & Scrub	
		A0828	Curl-leaf Mountain-mahogany Scrub Alliance
		A3570	Curl-leaf Mountain-mahogany Grassy Woodland Alliance
		A0586	Curl-leaf Mountain-mahogany Shrubby Woodland Alliance
M897	Southern Rocky Mountain Two-needle Pinyon–Juniper Woodland Macrogroup		
	G252	Southern Rocky Mountain Juniper Open Woodland Group	
		A3575	One-seed Juniper Wooded Grassland Alliance
		A3574	One-seed Juniper Shrubby Woodland Alliance
	G253	Southern Rocky Mountain Pinyon–Juniper Woodland Group	
		A3577	Southern Rockies Pinyon–Juniper Grassy Woodland Alliance
		A3576	Two-needle Pinyon–One-seed Juniper Shrubby Woodland Alliance

To the southeast, the Southern Rocky Mountain Two-needle Pinyon–Juniper Woodland macrogroup prevails along the flanks of the southern Rocky Mountains and among the mountains, plains, and mesa tablelands of Arizona and New Mexico. In this summer-precipitation-dominated climate, singleleaf pinyon and Utah juniper drop out and two-leaf pinyon and one-seed juniper (*J. monosperma*) dominate the woodlands (singleleaf pinyon at higher elevations and one-seed juniper at lower). At lower elevations to the east these woodlands border on grasslands of the southern Great Plains, and to the south they can intermix with Chihuahuan Desert grasslands and scrub.

Detailed Pinyon–Juniper Woodland Descriptions

The following are summary descriptions of pinyon–juniper woodlands at the group level of the IVC (detailed descriptions of each group and its constituent alliances can be found at the US National Classification webpage (USNVC.org). Descriptions are ordered by the hierarchically in Table 1.

G198 Californian Conifer Forest & Woodland Group

Californian Conifer Forest & Woodland Group includes a variety of cypress and pine forests and woodlands along with pinyon–juniper woodlands of the Transmontane Desert Pinyon–Juniper Woodland Alliance.

Environment: These woodlands are found in the montane regions of southern California extending to the western edge of the Mojave Desert and southward into northern Baja California, Mexico. Stands occur on ridges, slopes, valleys, alluvial fans, valley bottoms at elevations ranging from 600 to 2450 m. Soils are porous, rocky, coarse, sandy or silty, and often very shallow.

Vegetation structure and composition: This alliance consists of scrub woodlands, generally < 5 m in height, where *Juniperus californica* is codominant with Parry pinyon or singleleaf pinyon. In some stands, the junipers are open-grown trees over grassy understories. In others, the junipers form mixed stands with pinyon. The understory often has Mojave Desert shrubs such as blackbrush (*Coleogyne ramosissima*), Mormon tea (*Ephedra* spp.), and scrub oaks such as Muller oak (*Quercus cornelius-mulleri*).

G487 Madrean Juniper Open Woodland Group

Environment: This Madrean juniper woodland and savanna occurs at lower-elevations within the range of the macrogroup from northern Mexico into the southwestern United States. Savanna-like stands occur primarily on loamy rolling plains, alluvial fan piedmonts, plateaus, and lower foothill slopes while the more closed-canopied woodlands are found on cooler aspects of steeper slopes with generally shallow rocky soils.

Vegetation structure and composition: These savannas and woodlands have open to moderately closed tree canopies (10%–60% cover). The lack of pinyon trees and the dominance of the Madrean junipers redberry juniper or alligator juniper are diagnostic. At the northern end of the range, one-seed juniper may replace redberry. Madrean oak trees may be present but do not dominate the tree canopy.

The woodland understories are usually dominated by species with Sierra Madrean affinities. Some communities are distinctly shrubby and make up the Madrean Juniper /Shrub Open Woodland Alliance of associations that may include chaparral species (e.g., manzanita, ceanothus, mountain mahogany, yuccas, and scrub oaks) or warm desert scrub elements (e.g., creosote bush, lechuguilla and mesquite). In contrast, the associations of Madrean Juniper/Grass Open Woodland Alliance have often luxuriant grassy understories and a high mix of forbs and few shrubs. Common Madrean grasses include bull muhly, curlyleaf muhly (*M. setifolia*), and Texas bluestem (*Schizachyrium cirratum*), but elements from more northern woodlands and plains may be prevalent such as blue grama (*B. gracilis*), hairy grama (*B. hirsuta*), or sideoats grama (*B. curtispendula*).

G200 Madrean Pinyon–Juniper Woodland Group

Environment: This P-J woodland group is common in higher foothills, mountains and plateaus within the range of the southwestern United States and northern Mexico. Sites range from gentle to steep slopes. Ground cover often has high cover of rock or bare ground. Elevations range from 1700 to 2200 m. Substrates are variable, but soils are generally shallow, dry and rocky often with rock outcrops.

Vegetation structure and composition: These vegetation communities are characterized by open to moderately closed tree canopies (10%–60% cover and occasionally greater) dominated by Mexican pinyon (*Pinus cembroides* and its variations) and juniper trees that can range from 2 to 10 m in height. Alligator juniper (*Juniperus deppeana*), drooping juniper (*J. flaccida*), or redberry juniper (*J. coahuilensis*) may be common or co-dominant. Two-leaf pinyon and one-seed juniper may become the dominants in the northern distribution of the group. Madrean oak trees may be present but do not dominate the tree canopy.

The understories are usually dominated by species with Sierra Madrean affinities. Some communities are distinctly shrubby and may include chaparral species such as manzanita (*Arctostaphylos* spp.), desert ceanothus (*Ceanothus greggii*), mountain mahogany (*Cercocarpus montanus*), yuccas, and scrub oaks and belong to the Madrean Pinyon–Juniper /Shrub Woodland Alliance. In contrast, the Madrean Pinyon–Juniper/Grass Woodland Alliance has associations that often have luxuriant grassy understories and a high diversity of forbs and few shrubs. Common Madrean grasses include bull muhly (*Muhlenbergia emersleyi*), New Mexico muhly (*M. pauciflora*), and pinyon ricegrass (*Piptochaetium fimbriatum*).

G900 Colorado Plateau Pinyon–Juniper Woodland Group

Environment: This P-J woodland group occurs in dry mountains and foothills of the Colorado Plateau region including the western slope of Colorado and the Wasatch Range, south to the Mogollon Rim, and east into the northwestern corner of New Mexico. Winter precipitation in the form of snow predominates while summers can be warm to hot. Elevations range from 1500 to 2440 m. Sites often have high cover of rock or bare ground and soils are generally shallow, dry and rocky often with rock outcrops.

Vegetation structure and composition: These communities are characterized by stands with moderate to closed tree canopies (30%–60% cover and occasionally greater) which are dominated by twinleaf pinyon and Utah juniper trees that can range from 2 to 10 m in height.

A suite of communities are distinctly shrubby and make up the Foothill & Lower Montane Pinyon–Juniper/Shrub Dry-Mesic Woodland, Colorado Plateau Utah Juniper Shrubby Woodland, and Colorado Plateau Two-needle Pinyon–Utah Juniper Open Woodland alliances representing over 40 plant associations. These associations may include montane chaparral species such as manzanita (*Arctostaphylos* spp.), desert ceanothus (*Ceanothus greggii*), mountain mahogany (*Cercocarpus montanus*), yuccas, and scrub oaks, or cold desert shrubs such as sagebrush (e.g., *Artemisia tridentata*, *A. nova*) and antelope bitterbrush (*Purshia tridentata*).

In contrast, Two-needle Pinyon–Utah Juniper Grassy Open Woodland and Utah Juniper Grassy Open Woodland alliances are made up of associations with grassy understories that are commonly dominated by cool-season (C3) grasses. These thrive on winter moisture and the cooler temperatures of early summer, e.g., needle and thread grasses (*Hesperostipa comata*; *H. neomexicana*), bluebunch wheatgrass (*Pseudoroegneria spicata*) and Indian ricegrass (*Achnatherum hymenoides*). Cheat grass (*Bromus tectorum*) is also a cool-season grass that is nonnative and invasive that has become important in these communities, altering fire regimes and competitive relationships among the native grasses.

G248 Columbia Plateau Western Juniper Open Woodland Group

Environment: This P-J woodland group is found on the Columbia Plateau and extends to the northern and western margins of the Great Basin, from southwestern Idaho along the eastern foothills of the Cascades south to the Modoc Plateau of northeastern California. Elevations range from 200 to 1500 m. Soils are generally medium-textured, with abundant coarse fragments, and derived from volcanic parent materials.

Vegetation structure and composition: Western juniper is typically the only tree species and pinyons are absent. The tree form of curl-leaf mountain mahogany (*Cercocarpus ledifolius*) may also occasionally co-dominate. In Western Juniper Shrubby Woodland Alliance associations, the spaces between trees are dominated by tall shrubs such as big sagebrush or curl-leaf mountain mahogany along with rabbitbrush (*Chrysothamnus viscidiflorus*, *Ericameria nauseosa*) and antelope bitterbrush with a scattering of cool-season grasses. In contrast, the Western Juniper Grassy Open Woodland Alliance communities are dominated by cool-season grasses such as Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrasses, and Sandberg bluegrass (*Poa secunda*) in the inter tree spaces and occasionally co-dominate with shrubs.

G899 Great Basin Pinyon–Juniper Woodland Group

Environment: This P-J woodland group occurs on dry mountain ranges of the Great Basin region and eastern foothills of the Sierra Nevada, and south in scattered locations throughout southern California. They are typically found at elevations from 1500 to 2600 m. Stands occur on warm, dry sites on mountain slopes, mesas, plateaus and ridges.

Vegetation structure and composition: The vegetation is characterized by stands with open to moderately dense tree canopy typically composed of a mix of singleleaf pinyon and Utah juniper. In some regions of southern California, Utah juniper is replaced by California juniper. There are two alliances where shrubs dominate the inter-tree spaces with or without a grass layer: Great Basin Singleleaf Pinyon–Utah Juniper Shrubby Woodland and Great Basin Utah Juniper Shrubby Woodland that lacks the singleleaf pinyon. The most common shrub dominants are big sagebrush, black sagebrush, little sagebrush (*Artemisia arbuscula*), curl-leaf mountain mahogany, littleleaf mountain mahogany (*Cercocarpus intricatus*), blackbrush (*Coleogyne ramosissima*), and antelope bitterbrush among others that are also elements of cold-desert communities found at lower elevations. Those associations that lack a strong shrub component belong to the Great Basin Singleleaf Pinyon–Utah Juniper Grassy Open Woodland where cool-season grasses such as basin wild rye (*Leymus cinereus*), needle and thread grass, and bluebunch wheatgrass tend to dominate between the trees.

G249 Intermountain Basins Curl-leaf Mountain-mahogany Woodland & Scrub

Environment: Stands of this woodland and shrubland group occur in hills and mountain ranges of the Intermountain West basins from the eastern foothills of the Sierra Nevada northeast to the foothills of the Bighorn Mountains of Wyoming. It typically occurs from 600 m to over 2650 m in elevation on rocky outcrops or escarpments and forms small- to large-patch stands in forested areas. Most stands occur as shrublands on ridges and steep rimrock slopes, but they may be composed of small trees in steppe areas.

Vegetation structure and composition: This woodland and shrubland group includes stands dominated by either the tree or shrub form of curl-leaf mountain mahogany. Scattered junipers or pines may also occur. Curl-leaf Mountain-mahogany Shrubby Woodland and Curl-leaf Mountain-mahogany Scrub alliances are typically co-dominant with other Great Basin cold-desert shrubs such as big sagebrush, antelope bitterbrush or more montane elements such as Gambel oak (*Quercus gambelii*), snowberry (e.g., *Symphoricarpos oreophilus*), or rockspirea (*Holodiscus dumosus*). The Curl-leaf Mountain-mahogany Grassy Woodland associations tend to have a high cover of cool-season grasses such as basin wild rye, Idaho fescue, and bluebunch wheatgrasses under the curl-leaf mountain mahogany.

G252 Southern Rocky Mountain Juniper Open Woodland Group

Environment: This P-J woodland and woodland-savanna group occurs along the eastern and southern foothill slopes of the southern Rocky Mountains and mesa tablelands, and plains of the southeastern Great Plains. They occur on a range of sites from steep, colluvial slopes of escarpments with rocky soils to lower toeslopes and valley bottoms and plains with loamy soils.

Vegetation structure and composition: Stands of this group typically have open tree canopies (10%–60% cover) that are dominated by short-statured (2–5 m) one-seed juniper (*Juniperus monosperma*). Two-needle pinyon may be present but usually growing within the canopy of the juniper. On plains, tablelands, and gentle foothill slopes, savanna-like stands develop with widely spaced juniper trees with lush perennial grass cover between trees (One-seed Juniper Grassy Woodland Alliance). Grasses tend to be warm-season

species that are prevalent in the adjacent plains and desert regions such as blue grama, sideoats grama, or galleta (*Pleuraphis jamesii*), but occasionally cool-season grasses such as needle and thread grass can dominate the sites. On the rockier, steeper sites, stands tend to have a strong shrub component, particularly scrub oak (e.g., *Quercus x pauciloba*) or mountain mahogany and belong to the One-seed Juniper Shrubby Woodland Alliance. In addition, yuccas and prickly pear or cholla cacti (e.g., *Opuntia phaeacantha* and *Opuntia imbricata*) can be common.

G253 Southern Rocky Mountain Pinyon–Juniper Woodland Group

Environment: This P-J woodland group occurs on dry mountains and foothills in southern Rocky Mountain in Colorado east of the Continental Divide down through the mountains and plateaus of northern New Mexico extending east into the southeastern Great Plains (on limestone and shale breaks, escarpments and hills). Stands are found on warm, dry sites on mountain slopes, mesas, plateaus, and ridges. Elevations range from near 1500 to 2900 m with high-elevation stands restricted to relatively warm, dry ridges and south and west aspects. Lower-elevation stands are often restricted to cooler north- and east-facing slopes. Soils vary in texture ranging from stony, cobbly, gravelly or sandy loams to clay loam or clay.

Vegetation structure and composition: The vegetation is characterized by two-needle pinyon that dominates or codominates the tree canopy with one-seed juniper. Rocky Mountain juniper (*Juniperus scopulorum*) may codominate or replace *Juniperus monosperma* at higher elevations. At higher elevations on mountain slopes stands can have the stature (> 10 m tall) and canopy closure (> 60% canopy cover) of forests. In contrast, at lower elevations tree size diminishes to as low as three meters and canopies become very open, forming woodland savannas. The forest-like woodlands have a mixture of grasses and shrubs in the understory and overall cover can be sparse. Most these communities belong to the Two-needle Pinyon–One-seed Juniper Shrubby Woodland Alliance where Gambel oak, mountain mahogany, and cool-season grasses such as Scribner needle and thread grass (*Achnatherum scribneri*) are prevalent. In contrast, the P-J woodland savannas of this group have a predominantly grassy inter-tree space and belong to the Southern Rockies Pinyon–Juniper Grassy Woodland Alliance. Grasses tend to be warm-season species that are prevalent in the adjacent plains and desert regions such as blue grama, sideoats grama, or galleta, but occasionally cool-season grasses such as New Mexico needle and thread grass can dominate the sites.

Ecological Dynamics in Pinyon–Juniper Woodlands

Fire Regimes

Fire is integral and a natural element in most pinyon–juniper woodlands, but the regimes vary depending on the environmental context and vegetation composition and structure. Among the types described above, three basic structural types emerge primarily at the alliance level: those woodlands with open canopies and grassy interspaces, those with moderate canopies and well-developed shrub strata, and those with near-closed, forest-like canopies with understories that are a mix of shrubs and grasses at low to moderate cover. These correspond roughly to three P-J fire regimes types described by [Romme et al. \(2009\)](#) as grass-dominated savanna, shrubby woodland (or wooded shrubland), and persistent woodland (the last also includes the woodlands of rocklands with little or no understory). These structural types are primarily driven by the amount of precipitation and its seasonality whereby winter precipitation that results in deep soil moisture storage will tend to favor trees and other deep rooted woody species while transient shallow summer moisture tends to favor more shallow-rooted grasses and forbs ([Fig. 3](#)). Accordingly, they have different proportions of tree, shrub, and grass fuels that generate different types of fire of frequencies and intensities. In general, under normal conditions savanna woodlands are likely to have low intensity fires that kill only small seedlings and sapling trees, keeping the stands open, but the fires can be spatially extensive since the stands commonly occur in gentle terrains of rolling hills and plains (fire regime type I). They also tend to happen more frequently than other P-J types because of the rapid recovery of grasses to a fire-ready state—every 10–30 years depending on the plant association ([Wright et al., 1979](#); [West and Young, 2000](#)).

Woodlands with significant shrub cover typically have mixed to high-severity regimes with some tree torching and top-killing of shrubs ([Fig. 4](#)). This is followed by a longer recovery period leading to somewhat lower frequencies, (perhaps 25–80 years; [Gori and Bate, 2007](#)). Spatially, under extreme conditions they can reach landscape scale, but more commonly they are small to large patch fires. Persistent woodlands with near-closed canopies tend to have moderate surface to high-intensity canopy fires that occur at frequencies from 60 to > 100 years or more, usually as small to medium patches, but extreme events can reach landscape scale ([Fig. 5](#)). There are also persistent woodlands of escarpment rocklands where fire is very rare or absent because of the spacing of trees and the lack of surface fuels.

Fire in P-J woodlands has been impacted by human activities, and particularly following European settlement beginning in the early 17th century ([Jacobs, 2008](#)). Historical fire regimes were disrupted following the introduction of livestock. Grazing passively suppresses fire by removing fine fuels needed to carry surface and low to mixed-severity fires that likely maintained the structure and composition of pinyon–juniper savannas and pinyon–juniper shrub woodlands historically. Active fire suppression was also practiced by the Federal government during the last 100 years ([Swetnam and Baisan, 1996](#)). As fire became less frequent, pinyon and juniper trees became denser and subsequent fires became more severe. Over the last century, a reduction in fire frequency has caused a conversion of some juniper savanna to juniper woodland, as well as invasion of juniper trees from areas of naturally low fire frequency, (e.g., rocky ridges) into adjacent communities, especially sagebrush steppe ([Wright et al., 1979](#); [West and Young, 2000](#); [Romme et al., 2009](#)). In contrast, nonnative grasses such as annual cheatgrass can quickly invade and promote increased fire frequencies, particularly in the western regions dominated by winter precipitation.

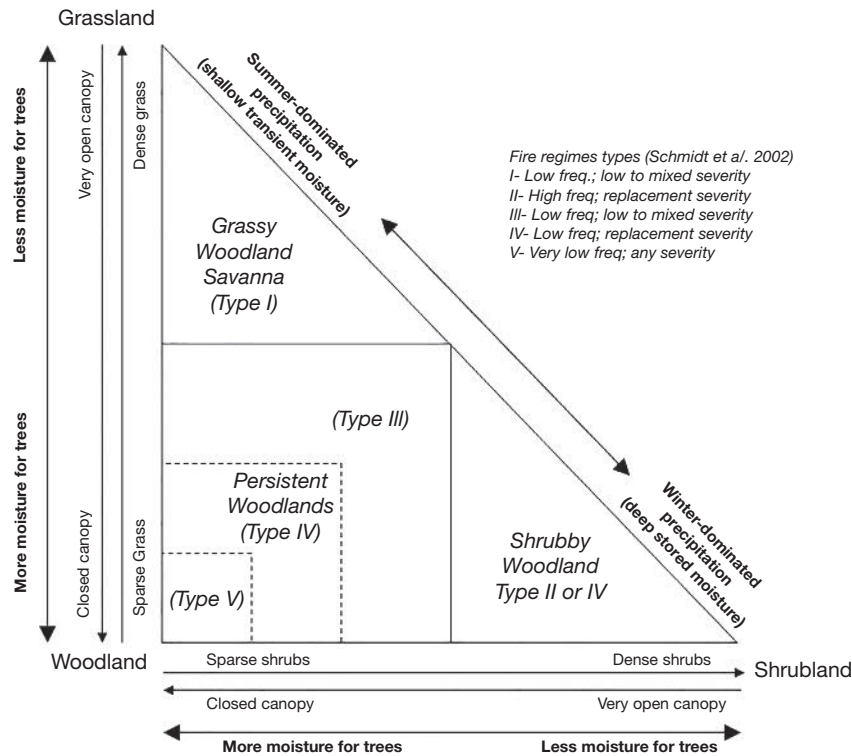


Fig. 3 A general framework for the distribution of three broad types of western pinyon-juniper woodlands with respect to soil moisture gradients and associated fire regimes. Fire regime classes adapted from Schmidt, K. M., Menakis J. P., Hardy C. C., Hann W. J. and Bunnell D. L. (2002). Development of coarse scale spatial data for wildland fire and fuelmanagement. *General Technical Report RMRS-87*. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.



Fig. 4 A firefighter crew hiking out from a wildland fire burning in a pinyon-juniper woodland along the Utah-Nevada border. Photo: Dan Jimenez, U.S. Forest Service.

Given a site's land use history and woodland type, post-fire responses can vary. Woodland savannas are likely to recover quickly if grass cover was not reduced by increased density of trees from fire suppression. That is, with increased density and more extreme fire events, burned sites will require a longer period for grasses to colonize bare zones left by dead trees and return the site to an optimal grassy fire-ready state. In shrubby woodlands where large patch or landscape-scale canopy fires have occurred, shrubs, particularly those that resprout after fire, can come to dominate the landscape and slow the tree recolonization process because

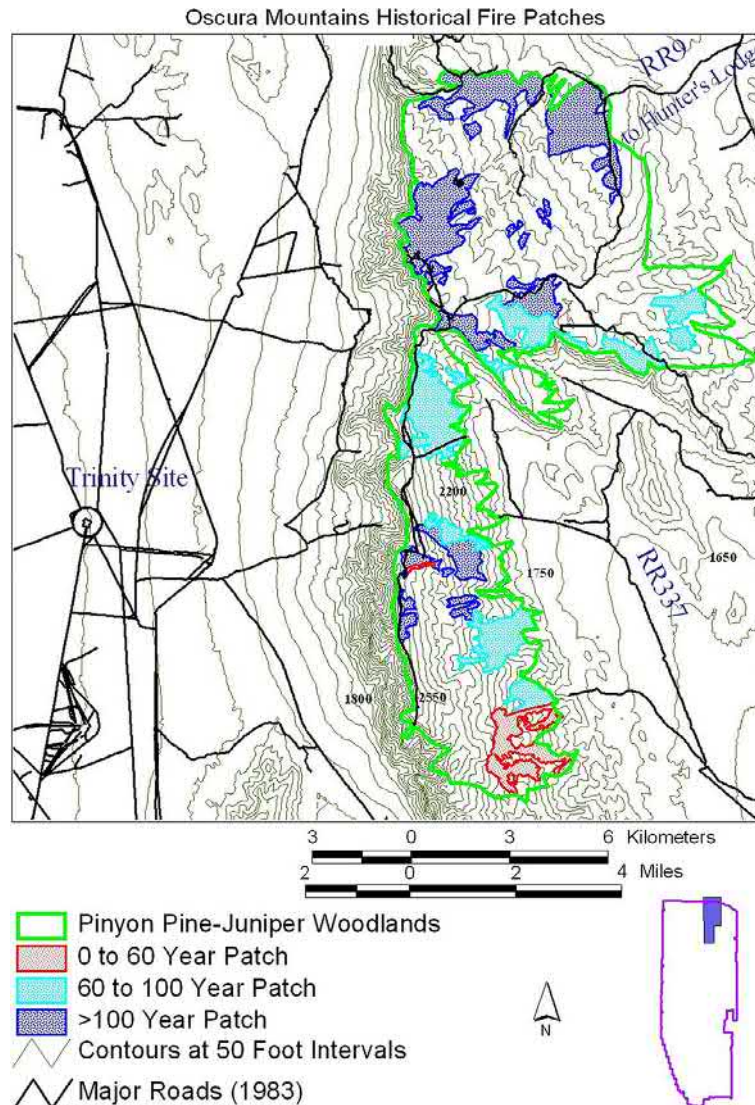


Fig. 5 Fire-patches in the Oscura Mountains of southern New Mexico based on comparative aerial photo analysis. Adapted from Muldavin, E., Baisan, C., Swetnam, T. DeLay, L. and Morino, K. (2003). *Woodland fire history studies in the Oscura and Northern San Andres Mountains, White Sands Missile Range, New Mexico*. Natural Heritage New Mexico Publ. No. 03-GTR-256. Albuquerque, NM: Natural Heritage New Mexico, University of New Mexico.

of seed source loss and competitive exclusion of those tree seedlings that do germinate. Response to extreme fire events in persistent woods may be similar, but localized seed sources may be more common and therefore likely provide more sites for successful seedling establishment to speed recovery to mature woodland.

Insect Pathogens

Although pinyon pines and junipers are drought tolerant, prolonged droughts can weaken trees and promote mortality by secondary agents. For example, trees play host to a set of endemic insect pathogens such pinyon bark beetle (*Ips confusus*) or cypress bark beetle (*Phloeosinus cristatus*), and associated fungal agents such as blackstain root-rot (*Leptographium wageneri*) that can cause whole stand die-offs that are often correlated with droughts (Clifford et al., 2008) (Fig. 6). These mortality events may be localized or widespread but can result in 50%–90% mortality of pinyon in affected areas (Harrington and Cobb 1988). Yet die-offs can be patchy even in local landscapes and there is more to be learned about the underlying mechanism of spread and specific triggers of outbreaks (Meddens et al., 2015).



Fig. 6 Pinyon pines in New Mexico in 2002, stressed from drought and an associated bark beetle outbreak. Photo by Craig D. Allen, US Geological Survey.

Ecosystem Services and the Changing Land Use of Pinyon–Juniper Woodlands

The diversity of land use and ecosystem services in pinyon–juniper is as varied as the ecology, composition, and structure of these woodlands (Comer et al., 2003; Moir and Carlton, 1986; Romme et al., 2009). While we acknowledge the wide range of services that have supported subsistence and livelihood, including watershed function, plant production, and drinking water, we focus on some of the most important socioeconomics of woodlands and their land use legacies involving pine nut gathering, livestock use, and fuelwood. This narrow set of uses are broadly applicable to North American woodlands and are in large part the same uses that have affected their environmental conditions and trends, sometimes in positive feedbacks. Carbon storage is another key ecosystem service of pinyon–juniper that we consider in a later section on climate.

History and Land Use Impacts (e.g., Involving Herbivory, Changes in Fire Regime)

Pinyon nuts

In North America humans have a long history of exploiting pinyon–juniper woodlands for raw materials for building, medicine, and food that continues to this day (Cartledge and Propper, 1993; Mayes et al., 1989; Scurlock, 1998). Pinyon nuts are usually collected in early autumn directly from the tree by dislodging cones or seeds or by picking seeds from mature cones that have fallen to the ground (Gillihan, 2006). The brown nut shells within cones must be opened to expose the small nut inside. Immature cones can be opened by heating and the seeds roasted. The nuts are also eaten raw or boiled and were historically ground into paste or cooked in soups (Janetski, 1999). Roasted nuts lend themselves to long-term storage and were a key source of protein and fats to native people going back at least a couple of millennia (Bettinger, 1976; Lanner, 1981).

There is some evidence that the amount of pinyon nuts as a staple, and pinyon–juniper resources in general, fluctuated considerably in the southwestern United States. For instance by the 13th century AD, after hundreds of years of occupation, Puebloans had abandoned the Four Corners region perhaps as a result of deforestation of pinyon–juniper woodlands (Lekson and Cameron, 1995; Flint-Lacey, 2003). Archeological evidence indicates a time of widespread clearing of woodlands near the end of this period of Four Corners occupation (Litzinger, 2003). To the southeast, at present-day Bandelier National Monument in New Mexico, available evidence reveals significant changes to pinyon–juniper leading up to peak occupation of the area at about 1500 AD (Gottfried et al., 1995). Still, pinyon nuts remained important to native peoples of the Four Corners region for nutrition, medicine, and for ceremonial purposes (Mayes et al., 1989).

Today, nut gathering represents a pastime for some and an important cash crop for others, adding to the need for the sustainable management of woodland resources (Gottfried and Severson, 1994). Pound-for-pound pinyon nuts are by far the most value product of pinyon–juniper woodlands. By one estimate, the crop production in the species of two-needle pinyon alone is over 900,000 kg, though in some years commercial crops are nearly nonexistent (Ronco Jr, 1990). Commercial-scale crops occur on cycles of three to five years. Resource management that integrates permitting ensures that users can harvest what they need while preventing nuts from being over-collected and impacting the pinyon's ability to furnish other services such as tree regeneration and food for wildlife forage (Vander Wall and Balda, 1977; Stone, 1993).

Livestock use

The most widespread use of pinyon–juniper woodlands has been livestock grazing, especially for cattle and sheep (Aro, 1971; Gottfried et al., 1995). In many areas these woodlands offer essential spring and fall range resources for grazing animals. Though

consensus is lacking, there may also be some noneconomic advantages to light to moderate grazing of woodland understories including nutrient cycling, simulated gap disturbance, and stimulation of plant production (Milchunas, 2006). Economic and subsistence benefits to rural communities are clearly linked to the availability and quality of forage available to livestock in woodlands and other vegetation types, an ecosystem service dependency going back centuries (Allred, 1996; Scurlock, 1998).

Livestock grazing and fire suppression are the two most regarded agents of 20th-century change in pinyon–juniper, including increased tree densities through ingrowth along with the expansion of woodland into neighboring grasslands (Ronco Jr, 1990). Fire suppression coupled with land use patterns that are ubiquitous to fire-adapted woodlands of Mexico and the western United States have substantially reduced the frequency of fire. Past decades of overgrazing by livestock, and now management for uncharacteristically high levels of wild ungulates, has reduced grass competition to favor woody ingrowth of trees and shrubs. As a result, overutilization by both native and nonnative herbivores is often a component within a feedback system involving fewer fine fuels to facilitate fire spread that, in turn, promotes higher tree densities and decreased grass growth and forage availability (Allen, 2007; Gori and Bate, 2007). A notable effect of these agents in combination has been a major increase in juniper savannah cover types as grasslands submit to tree growth and woodland succession, expanding the pattern of reduced livestock forage. Increasing tree density in juniper savannah, and in fire-adapted pinyon–juniper generally, promote a positive feedback with elevated tree seed sources. While changes to woodland structure and composition have been linked to climate, there is some evidence to suggest that climate forcing is secondary to grazing and that the effects of grazing can be exacerbated by climate (Fuhlendorf and Smeins, 1997).

Resource managers and land owners have sought ways to reduce tree cover in pinyon–juniper, including woodland types where fire was infrequent and tree densities were characteristically elevated. In recent decades the drive for additional big game habitat has furthered efforts for woodland-to-grassland conversion. Among the approaches used to clear trees, the process of “chaining” began in earnest in the 1950s as a means to convert woodlands to enhance forage production. Though approaches vary, chaining often involves two bulldozers pulling a large chain, such as from a ship anchor, between them to knock down and uproot trees (Fig. 7). In recent years chaining has become more targeted and fallen out of use because of issues with soil erosion and habitat loss among other concerns (O’Meara et al., 1981).

While some woodlands have been converted to grassland, on balance the extent and density of pinyon–juniper has increased considerably, with pollen evidence suggesting that these woodlands are more abundant now than at any time in the past 5000 years (Miller and Wigand, 1994). The most remarkable changes in the structure of woodlands are concentrated in fire-adapted types that were historically more open and less connected. The over 40 million hectares occupied by pinyon–juniper in the intermountain United States represents an important resource for livestock management to be managed sustainably (Miller and Wigand, 1994).

Fuelwood

In Mexico and the western United States, pinyon–juniper woodlands have long been a major source of fuel for heating, cooking, and other uses. In the southwestern United States and Mexico the wood is still the main fuel in many rural communities. Pinyon–juniper woodlands have been used as a fuelwood source longer than any other of its provisioning services (Barger and Ffolliott, 1972; Ffolliott et al., 1999) and these tree species have exceptional heat content. On a given hectare there are about 58 cubic meters of wood volume (6.5 cords per acre). In the state of Nevada alone there are an estimated 125 million cubic meters of wood volume in pinyon–juniper woodlands (Born et al., 1992).



Fig. 7 Chaining of pinyon-juniper trees in southern Colorado, circa 1958. Note the chain is attached to a bulldozer on the left and one out of sight on the right. Photo by Jack Rottier, USDI Bureau of Land Management.

Beginning in the 19th century, these woodlands became a source of materials for many products including railroad ties, and a source of materials for mining operations, especially as fuel for processing metals but also for building materials for adits, shafts, and operations and processing facilities (Ffolliott et al., 1999). It follows that notable episodes of unsustainable use were concentrated near geologic resources and near human communities, as was likely the case with the decline of woodlands in the Four Corners region near the middle of the last millennium (Lekson and Cameron, 1995; Flint-Lacey, 2003). In the Chaco Canyon area of New Mexico, Samuels and Betancourt (1982) determined that human demography and fuelwood use of the time infers that woodlands would have been driven to depletion in about 200 years.

By the mid-20th century the demand for pinyon–juniper trees as a domestic fuel source gave the woodlands commercial value that peaked in the early 1980s (Born et al., 1992). Harvesting is done by commercial operators and by individuals for personal use, with private use representing the majority of cutting permits sold for federal lands (Wagstaff, 1987). Commercial woodyards exist in many urban centers of the western United States and on many tribal reservations, making the sale of fuelwood important for income and economies. In recent decades public land agencies have been driven to implement sustainable harvest policies with permitting and designated harvest areas. Such policies prevent local depletion of woodland resources despite that, in general, there has been a pronounced increase in the density and extent of pinyon–juniper woodlands (Gedney et al., 1999; Miller and Tausch, 2000). These woodlands collectively represent a vast resource capable of sustaining the production of fuelwood as a byproduct of the restoration and maintenance of ecosystem function.

Pinyon–Juniper Woodlands and Climate

A changing climate is altering the types and amounts of ecosystem services from pinyon–juniper. The vulnerability of these woodlands and the biodiversity and human communities that depend on them is based on their exposure to changing climate at a given location, their sensitivity to change, and their ability to adapt (USGCRP, 2011). Climate vulnerability is uneven across the extent of pinyon–juniper in North America due to the varying magnitude of projected change, the intrinsic sensitivity of human and natural systems in a given place, and their adaptive capacity (Hand et al., 2018). These factors and human interventions will determine how the provision of ecosystem services may be modified.

Pinyon–juniper woodlands, particularly in the southwestern United States, have become hotspots for a changing climate and warmer temperatures (Notaro et al., 2012; Garfin et al., 2013; Thorne et al., 2017). Expected changes include increased summer temperatures and enhanced variability of precipitation and temperature (Seager et al., 2007; Gutzler and Robbins, 2010). Because pinyon–juniper woodlands are inherently moisture-limited they are especially vulnerable to extended drought and higher temperatures (Allen and Breshears, 1998).

Tree Mortality and Plant Composition Changes

Marked change in the distribution and composition of pinyon–juniper systems is anticipated in the coming decades, especially at lower ecotones where conversion to juniper savannahs and grasslands is expected (Allen and Breshears, 1998). Vulnerability forecasts coupled with spatial information on tree density for Arizona and New Mexico (Mellin et al., 2008; Triepke et al., 2019) suggest that shifts are already occurring, with high vulnerability areas seeing a decline in the amount of tree cover and low vulnerability sites remaining on an overall trajectory of increased tree density (Table 2).

Ironically, the woodlands that are forecast to be the most vulnerable to future climate may be the least at risk to mortality from fire (Triepke et al., 2019). There is some evidence indicating that decreased plant productivity from warmer and more arid conditions may be associated with decreased fuel levels and reduced fire risk (Rocca et al., 2014).

The lower warm-dry woodland ecotones of pinyon–juniper communities are inherently vulnerable to periods of warmer temperatures and drought (Allen and Breshears, 1998; Maestas et al., 2016) (Fig. 8). The difference between upper and lower ecotones is reflected by ecosystem resilience in the face of long-term temperature increases that drive the upward expansion of woodlands into montane forest zones and the expansion of grassland and shrubland systems into areas previously occupied by woodlands (Clifford et al., 2011).

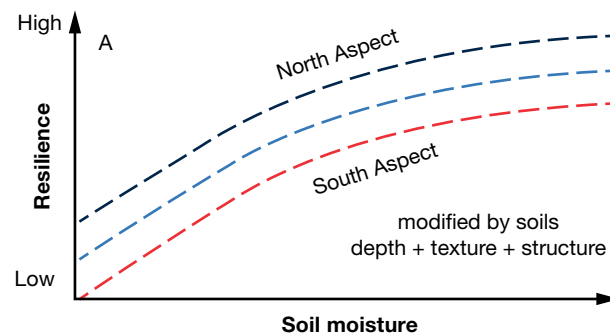
It stands to reason that warmer temperatures likewise favor changes in woodland understory vegetation, including trends in shifts from C3 to C4 grasses with increasing aridity. In addition to tree mortality, summer heat events have resulted in widespread mortality of many species of grasses, shrubs, and even cacti (Allen, 2007). Climate controlled changes in overstory and understory vegetation composition and plant productivity ultimately impact ecosystem and human communities that rely on the services of pinyon–juniper.

Carbon Storage as an Ecosystem Service

Vegetation biomass is an integral component of woodland carbon cycling. Through the process of photosynthesis atmospheric carbon dioxide is converted to carbohydrates as *carbon fixation* (Archer, 2011). Carbohydrates are used by plants to grow both belowground tissue in the form of roots and tubers and aboveground tissue in the form of stems and leaves. These components together with standing dead vegetation, downed woody debris, and the litter-duff surface make up woodland *biomass*, about half of which is *carbon stock* (USDA Forest Service, 2015). In pinyon–juniper woodlands there are approximately three to 55 metric

Table 2 Chi-square test evaluating the relationship of tree density and projected climate vulnerability, where high-vulnerability areas reflect less tree cover in comparison to background levels and low-vulnerability areas express greater tree cover.

Tree density	Deviation from expected		Sample number and significance
	Low vulnerability	High vulnerability	
<i>All Pinyon–Juniper</i>			
Stands with low tree cover (10%–29.9%)	–9.6%	12.1%	$n = 255,047$
Stands with high tree cover (30%+)	10.7%	–13.5%	$P\text{-value} < .00000$
<i>Juniper Grass (savannah)</i>			
Stands with low tree cover (10%–29.9%)	–17.6%	2.0%	$n = 19,143$
Stands with high tree cover (30%+)	38.2%	–4.4%	$P\text{-value} < .00000$
<i>Pinyon–Juniper–Evergreen Shrub</i>			
Stands with low tree cover (10%–29.9%)	–11.5%	9.5%	$n = 89,233$
Stands with high tree cover (30%+)	9.8%	–8.2%	$P\text{-value} < .00000$
<i>Pinyon–Juniper with Grass</i>			
Stands with low tree cover (10%–29.9%)	–15.5%	14.3%	$n = 40,367$
Stands with high tree cover (30%+)	14.2%	–13.0%	$P\text{-value} < .00000$
<i>Pinyon–Juniper Persistent Woodlands</i>			
Stands with low tree cover (10%–29.9%)	–2.0%	6.4%	$n = 98,286$
Stands with high tree cover (30%+)	2.8%	–8.8%	$P\text{-value} < .00000$
<i>Pinyon–Juniper with Sagebrush</i>			
Stands with low tree cover (10%–29.9%)	–28.6%	34.0%	$n = 8018$
Stands with high tree cover (30%+)	24.1%	–28.7%	$P\text{-value} < .00000$

**Fig. 8** Conceptual model showing the variation in ecosystem resilience to stress between upper and lower ecotones according to aridity, elevation, and soil properties. The middle line is the resilience as related to elevation and moisture, whereas the upper and lower lines show adjustments for aspect and soil properties. Adapted from Maestas, J., Campbell, S., Chambers, J., Pellant, M. and Miller, R. (2016). Tapping soil survey information for rapid assessment of sagebrush ecosystem resilience and resistance. *Rangelands* **38**, 1–9.

tons per hectare of biomass carbon depending on the type of pinyon–juniper and the stage of succession (Fernandez et al., 2013; Weisz et al., 2010). Soil organic carbon makes up an additional 40–85 metric tons per hectare depending on soil type (Strenger et al., 2007). The amount and kind of soil organic carbon represents and controls soil development and woodland productivity (Van Cleve and Powers, 1995). Carbon can be conversely released from these woodlands to the atmosphere through decomposition and burning. Pinyon–juniper woodlands provide an important carbon storage service by their considerable extent, biomass, and soil reserves which are constantly changing through natural succession and disturbance.

As implied by the discussion on woodland expansion and ingrowth, the balance of carbon stock has increased significantly in pinyon–juniper (Strand et al., 2008; Neff et al., 2009; Fernandez et al., 2013) despite localized carbon losses linked to tree dieback, woodland clearing, stand replacement fire, and erosion. Carbon increases are the likely result of fire suppression and are especially concentrated in fire-adapted types. Trends in the levels of soil organic carbon are mostly influenced by the growth of vegetation, by activities that remove biomass from the soil surface, and by climatic factors of temperature and moisture that influence weathering and decomposition. Causes of carbon loss from woodland soils include fire and erosion from grazing, land conversion, and development. Losses in woodland vegetation cover coupled with climate-induced increases in the intensity of rain lead to reductions in soil aggregate stability and an increase in erosion rates (Allen and Breshears, 1998). For the moment, land use patterns and carbon accumulation appear to be offsetting the effects of climate forcing on the reduction in woodland extent and density (Table 2). There is some debate on the probable effects of 21st-Century climate on decomposition rates and the stability of soil organic carbon (Davidson and Janssens, 2006). But the net effect of climate forcing and land use on pinyon–juniper may be continued increase in total carbon storage.

Conclusion—Climate and Carbon

Increasing temperatures and drought conditions in the interior western United States will likely lead to further tree mortality in woodlands, in turn affecting disturbance processes of soil erosion, insect outbreaks, fire, and additional mortality (Allen, 2007). Climate vulnerability forecasts for pinyon–juniper woodlands in North America (e.g., Comer et al., 2012; Rehfeldt et al., 2006; Triepke et al., 2019) likewise infer vulnerability to plant and wildlife habitat along with risks to provisioning services including pinyon nut production, livestock grazing, and fuelwood.

Future Trends and Conservation

Because P-J woodlands are so extensive in the western United States and northern Mexico, significant efforts are being made to install effective management prescriptions to meet the challenges of conserving biodiversity and natural resources in a rapidly changing world (Aldon and Shaw, 1993; Gottfried et al., 2008). Given increasing frequency of droughts, fire, insect outbreaks, and changes in resource use and management, managers are faced with complex scenarios in their attempt to maintain P-J woodlands in optimal conditions. For example, pinyon jays (*Gymnorhinus cyanocephalus*) have a range that is strongly tied to P-J woodland distribution (across all that shown in Fig. 1 with some minor extension into neighboring forest biomes), but despite their wide range their numbers are significantly declining (Boone et al., 2018). Management strategies implemented to uniformly increase fire frequency across all types through tree thinning or the mechanical treatment to create more open, grassy stands for grazing coupled with increased tree die-off caused by droughts and insect outbreaks may be collectively altering the woodland structure that may be driving downward trend in species populations. This type of scenario likely applies to other animals and plants, each with their unique niche, and where there competing needs for biodiversity and society that managers must address. Looking to the future there is a growing awareness that an integrated ecosystem management approach will increasingly be needed to solve these issues at site to landscape scales across this widely distributed and diverse ecosystem.

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Relevant Website

<http://explorer.natureserve.org/servlet/NatureServe> or <http://usnvc.org/>—For detailed descriptions of vegetation types according to the International Vegetation Classification (IVC) system.

Mexical Shrubland

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Abstract

The vegetation named Mexical inhabiting areas with warm wet summers and dry winters represents the same vegetation associated to Mediterranean climates, characterized to share common characteristics such as evergreen sclerophyll leaves and the ability to resprout after fires. Preliminary evaluations indicate that this vegetation occupies at least 1.8 million of hectares in Mexico, distributed along the rain-shadowed mountain chains of the country, at elevations between oak and pine forests (above), and the xerophytic communities (below). We present a synthesis focusing on historical, paleobotanical and palaeoecological analyses showing that Mediterranean type ecosystems and the Mexical, have a common origin. The archetypal evergreen sclerophyllous vegetation of modern Mediterranean-type vegetation is relictual of the Madrean-Tethyan vegetation of the Paleogene and Neogene periods, which originally existed in a belt around North America and Eurasia when the climate was warm and wet. During a general palaeoclimatic trend towards greater aridity, the Mediterranean climate appeared in the Quaternary when summer precipitation decreased because the oceans became colder and the lands became hotter. The change from tropical to Mediterranean climate led surviving taxa to seek refuge in today's current Mediterranean areas, whereas Mexical did not experience this climatic transition and refuted along the principal mountain chains of Mexico. All these historical effects have been the basis for the analyses about plant ecophysiological studies mostly related to the water economy of evergreen species inhabiting semiarid environments; regeneration niche and community organization; and fire responses of Mexical species. Based on these studies we propose different areas for future research.

Introduction

The Mexical Shrubland and its Similitude with the Mediterranean Shrublands

Plant species assemblages from four continents of the world have traditionally been pointed out to share common characteristics such as evergreen sclerophyll leaves and the ability to resprout after fires (Barbour and Minnich, 1990). This is the case of Mediterranean ecosystems inhabiting areas with warm, dry summers and cool, wet winters (Rundel et al., 2016). These ecosystems constitute iconic examples of hotspots of biodiversity, as they occupy ca. 5% of the Earth's surface, but harbor almost 20% of the known vascular plant species of the world (Cowling et al., 1996). The vegetation in these ecosystems are constituted by evergreen sclerophyllous species, mostly low-stature shrubs and trees (1–3 m high) and broad-leaved species with 40 to more than 100% coverage by woody vegetation. Distributed in five different Mediterranean regions of the world, these ecosystems have been named “maquia” in the Mediterranean basin, “mallee” in the south and south-western Australia, “chaparral” in California, “fynbos” in the Cape Province of South Africa, and “matorral” in Chile (Cody and Mooney, 1978).

Since the 1970s, their study was marked by the convergent model of Mooney and Dunn (1970) generating a fruitful research program in the different Mediterranean areas of the world. Accordingly, the similarities in the characteristics of plant species living in such distant areas would be explained by invoking common adaptations to the Mediterranean climate, high frequency of periodic fires, drought, high temperatures, rainfall unpredictability, and soil oligotrophy (Mooney and Dunn, 1970; Cody and Mooney, 1978; but see Lloret et al., 1999; Verdú, 2000).

However, since the 1930s, different reports of evergreen sclerophyllous vegetation sharing the same or congeneric species with similar “convergent” traits were reported for different parts of Mexico under a tropical climate of summer rains (Muller, 1939, 1947; Shreve, 1939; Le Suer, 1945; Miranda, 1948, 1952; Martin, 1958; Miranda and Hernández, 1963; Rojas-Mendoza, 1965; Rzedowski,

1966, 1978; Rzedowski and Mac Vaughn, 1966; González-Quintero, 1968; Puig, 1970; Axelrod, 1975, 1989; Quero, 1977; Cruz-Cisneros and Rzedowski, 1980; Hiriart, 1981; García, 1983; Valiente-Banuet et al., 1998; Rivera-Hernández et al., 2019). Moreover, the presence of “convergent” plant traits were reported from sclerophyllous taxa in areas of summer and winter precipitation in Arizona-New Mexico, and eastern Mediterranean; as well for summer rain and winter drought in eastern Mexico and northwestern India, as well as in the northern coast of Turkey where rainfall is well distributed throughout the year (Axelrod, 1975). Moreover, the studies of Vankat (1989), in which different responses in seasonal patterns of stem-water potentials for plants inhabiting Arizona (with summer rainfall) and California chaparrals; and the assessment of the degree of convergence among the different Mediterranean-type ecosystems (Barbour and Minnich, 1990) were the basis to claim for a revision of the Mooney and Dunn’s (1970) long-standing paradigm.

Sclerophyllous vegetation under tropical climate in Mexico, named Mexical to differentiate from the Mediterranean vegetation, was described by Valiente-Banuet et al. (1998) showing that species that comprise this vegetation type have many similar characters to vegetation from Mediterranean climate areas. These authors hypothesized that the presence of Mexical, sharing “convergent” traits could respond to historical processes that occurred since floristic elements evolved during the Paleogene, when climate was warm and wet and later on when climate changed since the Oligocene when climatic deterioration with cooler and dryer conditions prevailed until present (Axelrod, 1958, 1975). This initial study (Valiente-Banuet et al., 1998) expanded the convergence paradigm of the chaparral under a more integrative view, in which biogeographic, paleobotanical, and ecological patterns might explain floristic, adaptive, and community organization processes occurring in these environments.

In this article we present a synthesis of these different aspects centered in the Mexical shrubland focusing in: (1) a historical paleobotanical and palaeoecological analysis about its origin and its relationship with the Mediterranean type ecosystems, (2) current geographical distribution; (3) floristic composition and plant traits in order to test whether the characters at the community and population level that have been claimed to converge under Mediterranean climates all over the world are the same as those in these plant communities, as well as a comparative analysis of vegetation across Mediterranean regions, including Mexical, in order to compare between historical and convergence hypotheses (i.e. common history of Paleogene and Neogene taxa vs. adaptations evolved under Mediterranean climates in Quaternary taxa); (4) plant ecophysiological studies mostly related to the water economy of evergreen species inhabiting semiarid environments; (5) regeneration niche and community organization; (6) fire responses of Mexical species; and (7) areas for future research.

Palaeobotanical and Palaeoecological Evidence and the Origin of the Mexical Shrubland

The evolution of Mediterranean-type ecosystems is well studied (Axelrod, 1958, 1975; Palamarev, 1989; Herrera, 1992; Keeley, 1992; Cowling et al., 1996; Ackerly, 2003; Verdú et al., 2003; Rundel et al., 2016). As in other ecosystems, Mediterranean-climate communities are the result of historical effects and sorting processes occurring in different geological times and different ecological scenarios (Herrera, 1992; Verdú et al., 2003; Valiente-Banuet et al., 2006). Many extant taxa in Mediterranean climates originated in the Paleogene and the Neogene (66 to 2 million years (Myr) B.P.) (Axelrod, 1975; Cowling et al., 1996) and are now mixed with recent taxa that evolved at the end of Neogene and the beginning of the Quaternary (2 Myr B.P., post-Pliocene) during a period when global climate became much more arid and cooler (Verdú et al., 2003). In fact, the current Mediterranean climate emerged during the Quaternary (see Rundel et al., 2016), corresponding with the extinction of a substantial component of Paleogene and Neogene taxa, but also providing a strong stimulus for the evolution of new taxa. Based on paleobotanical evidence (Axelrod, 1975; Palamarev, 1989), the archetypal evergreen sclerophyllous vegetation of modern Mediterranean-type vegetation is relictual of the Madrean-Tethyan vegetation of the Paleogene and Neogene, which originally existed in a belt around North America and Eurasia where the climate was wet and warm. Relictual Madrean-Tethyan taxa, or the Laurisilva, can be observed today in the isolated northern Atlantic Canary archipelago (Axelrod, 1975; Juan et al., 2000), and preliminary observations indicate that it can be observed also in different forests of Oaxaca, Mexico, which allows visualizing the magnitude of the occurred climatic change when these forests shifted to shrublands in the transition from Neogene to Quaternary. During most of the Paleogene/Neogene, sclerophyllous shrubs constituted the understory of a rich oak-laurel-madrone woodlands, and these shrubs expanded geographically in response to the drying climate during the transition between the Eocene (55 Myr B.P.) and the Oligocene (36 Myr B.P.) (Axelrod, 1975; Palamarev, 1989). Despite the wave of extinctions that occurred with increasing cooling and aridity, the fossil record shows that large taxonomic components of this ancient flora remained in contemporary communities of Mediterranean regions (Axelrod, 1975; Palamarev, 1989; Herrera, 1992), as well as in tropical non-Mediterranean regions (Valiente-Banuet et al., 1998; Flores-Hernández et al., 1999; Verdú et al., 2003) around the world and include some of the most abundant modern genera. This is the case of the Mexical located in the Tehuacán-Cuicatlán Valley, in which floristic elements such as *Rhus*, some Rosaceae, *Quercus*, and *Fraxinus* have been reported for the Tehuacan Formation of Middle Miocene by Ramírez-Arriaga et al. (2014).

According to Herrera (1992), pre-Pliocenic and Quaternary taxa of the Mediterranean Andalusian vegetation differ substantially in life-history-reproductive traits showing that these differences have a strong historical component that was set before the Mediterranean climate appeared. Similarly, Verdú et al. (2003) analyzed pre-Pliocenic and Quaternary taxa in the Mexical showing two contrasting life-history and reproductive traits of woody genera. Mexical did not experience a climatic transition from tropical to Mediterranean climates because it has always been in a tropical climate (Raven, 1973; Rzedowski, 1978).

Both studies agree that the most important traits distinguishing old and Quaternary syndromes are fruit type (fleshy vs. non fleshy fruits) and seed size, which are directly related to the regeneration niche. By integrating biogeographic, paleobotanical, and ecological relationships among species in these plant communities, Valiente-Banuet et al. (2006) showed that during recruitment, facilitative ecological interactions among plant species depend on the evolutionary histories of taxa (periods and environment in which species evolved). Thus, facilitation, as a positive interaction in which one species enhances the establishment of other species and no harm is caused to either; or even possibly being a mutualism (Stachowicz, 2001), is much more important

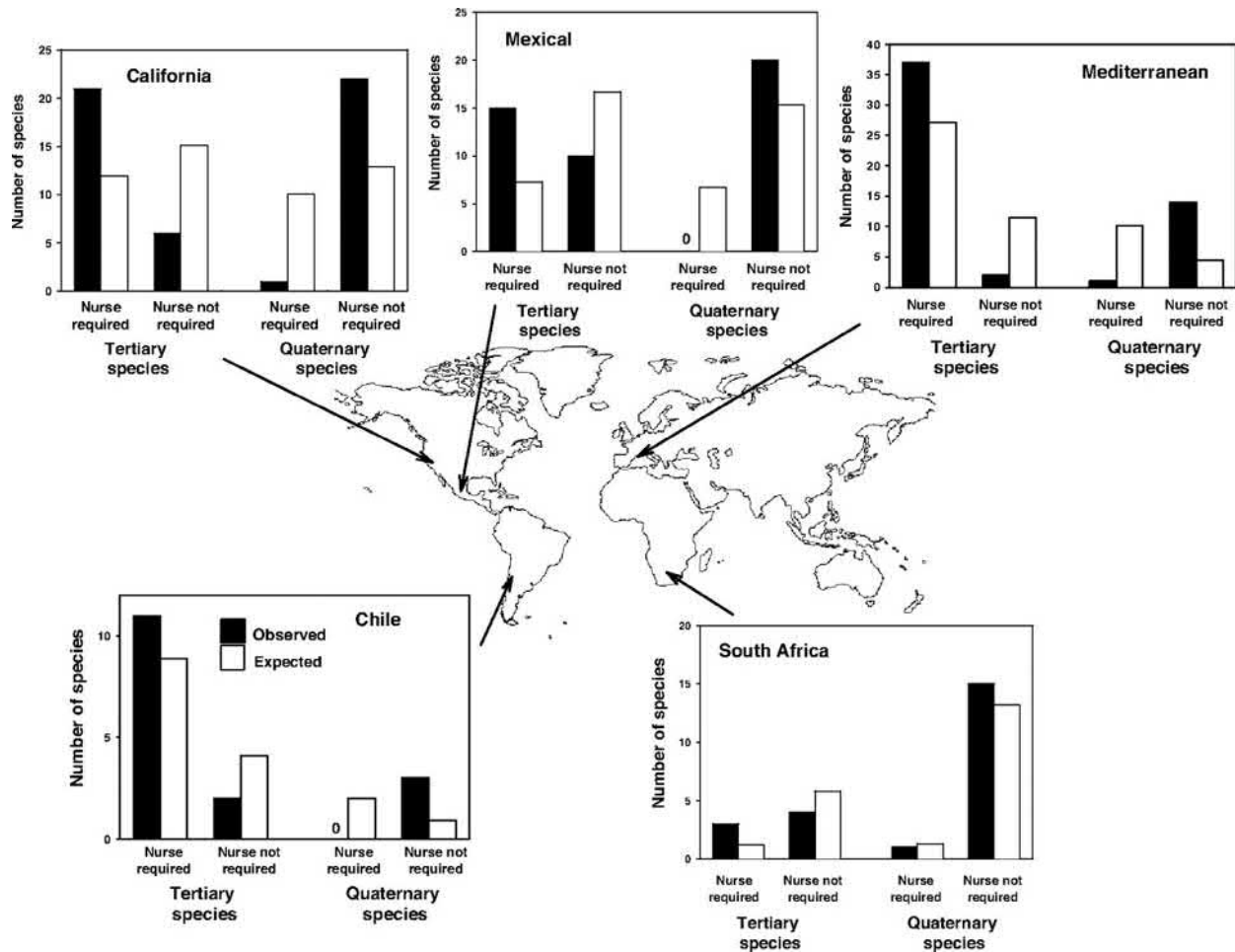


Fig. 1 Regeneration-niche requirements of Tertiary (Paleogene and Neogene) and Quaternary lineages, based on the fossil record, in the five Mediterranean areas of the world and in the Mexical shrubland of central Mexico. Filled bars show the observed numbers of species from each lineage reported in the literature that occupy particular regeneration niches, and open bars show the expected numbers of species of each lineage. Copyright (2006) National Academy of Sciences, U.S.A.

for the recruitment of species that evolved in the Paleogene and Neogene periods than for the recruitment of species that evolved in the Quaternary period (Fig. 1). In sum, modern regeneration niches and recruitment life history strategies of taxa derived from the ancient Madrean-Tethyan flora and the recent Quaternary are highly correlated with the time and environment in which these taxa evolved. This can be seen during succession in which Quaternary species are the most common early colonizers of open areas in Mediterranean climate vegetation (see supporting information Table 2 in Valiente-Banuet et al., 2006). In contrast, most late successional species identified in the literature were pre-Pliocene elements. These patterns are reinforced by experimental facilitative studies (Gómez-Aparicio et al., 2004), which demonstrated that pioneer (i.e., Quaternary) shrubs facilitate the establishment of woody, late-successional (i.e., pre-Pliocene) Mediterranean species. Likewise, old lineages seldom recruit by seed in the first several decades after fire, and, therefore, these taxa require long fire-free periods for establishment, which occur almost exclusively after closed-canopy stands have developed (Keeley, 1992). Once prepliocenic elements dominate the vegetation seedling establishment use to occur through facilitation among these old lineage elements. All this evidence supports the idea that species which evolved under more mesic environments than today require facilitation for establishment, suggesting that facilitation mimics the Paleogene/Neogene niche, a process that played a crucial role in maintaining biological diversity through evolutionary time (Valiente-Banuet et al., 2006). In other words, community-scale facilitation appears to have been a crucial historical sorting process sustaining ancient species in semiarid plant communities as the globe became more arid (Valiente-Banuet et al., 2006). This regeneration niche conservatism is a central aspect to analyze community assembly processes in these ecosystems (see the niche conservatism and community organization processes section below).

Geographical Patterns of the Mexical

The distribution of the Mexical is concentrated along the mountain chains of Mexico (Fig. 2), occupying an intermediate position between oak and pine forests (above), and the xerophytic communities (below), although in many cases it occupies the mountain-tops. Altitudinally the Mexical ranges between 1800 and 2800 m.a.s.l. Climatically, the Mexical ranges from arid to dry-temperate climates, which corresponds to types Bs and Cw, respectively (García, 1988). Its distribution includes the states of Aguascalientes,

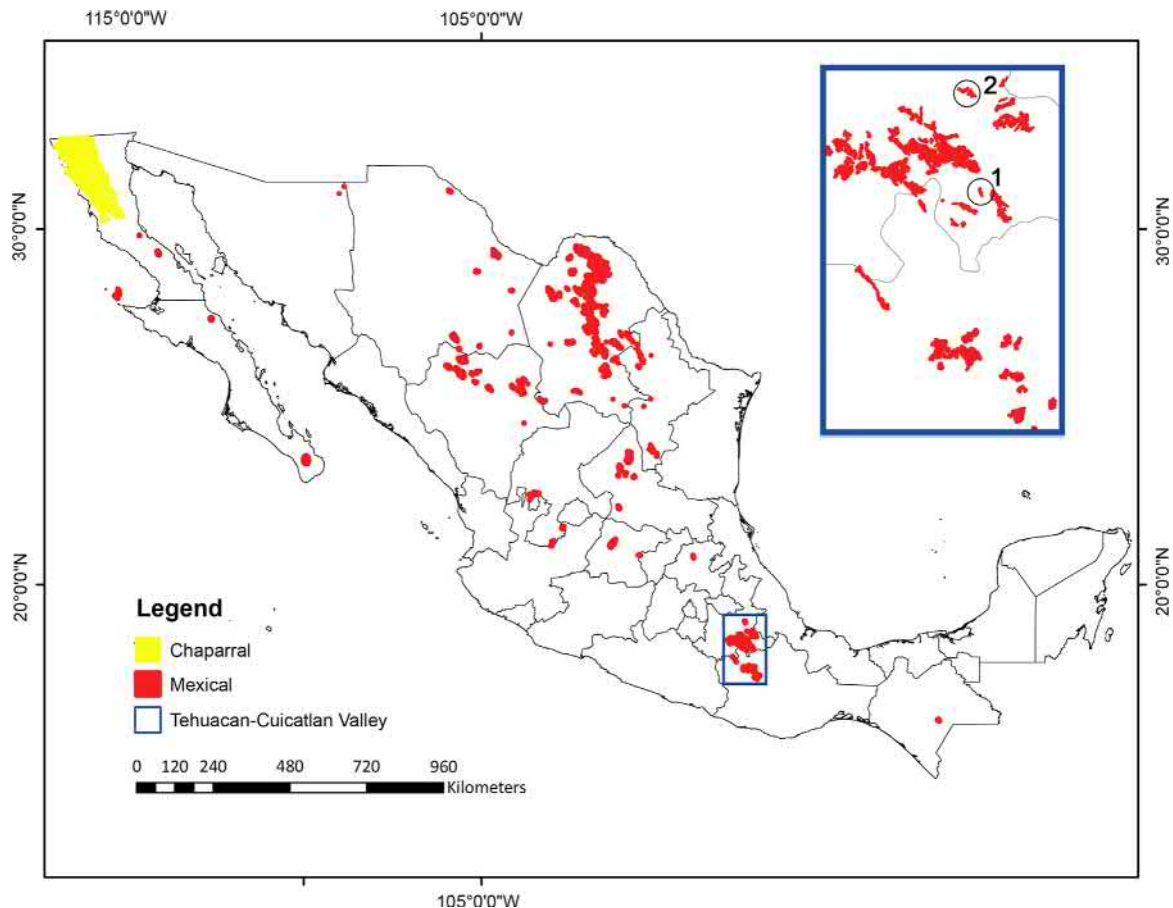


Fig. 2 Distribution of the Mexical (red-dotted marks) under wet-summer climates in México. The yellow-delimited zone in the North West of Mexico indicates the chaparral distribution under Mediterranean climate.

Baja California Sur, Coahuila, Chihuahua, Durango, México, Guanajuato, Guerrero, Hidalgo, Jalisco, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tamaulipas, Tlaxcala, and Zacatecas (Figs. 3–5). In all cases, the Mexical is located along the dry (rain-shadowed) aspects of different mountain chains including the Sierra Madre Oriental, Sierra Madre Occidental, Neovolcanic belt, and Oaxacan mountains.

Floristic Composition, Vegetation, and Plant Traits of Mexical

Floristically, the Mexical shrubland shares common genera with all the Mediterranean shrublands. For example, some of the genera of the Mexical have the same species or close relatives of those present in the Californian Mediterranean ecosystem (i.e., *Arbutus*, *Ceanothus*, *Garrya*, *Juniperus*, and *Rhus* (Table 1). In addition, the Mexical share common genera with the Mediterranean ecosystems of Chile, the Mediterranean Basin, or Australia (i.e., *Acacia*, *Gochnatia*, *Baccharis*, *Satureja*, *Rhus*, *Juniperus*, *Arbutus*, *Comarostaphylis* (= *Arctostaphylos*), *Quercus*, *Pistacia*, *Salvia*, *Stevia*, *Lithospermum*, *Linum*, *Aristida*, *Dodonaea*, etc. (Valiente-Banuet et al., 1998). A summary of floristic composition of different studies conducted in Mexico, shown in Table 2, indicates that mexical shrubland occupies altitudes ranging between 1800 and 2800 m.a.s.l. with many common genera and species among the different localities, being Anacardiaceae, Fagaceae, Rosaceae, Asteraceae, Ericaceae, and Fabaceae, the most well represented taxonomic families.

Based on floristic records and field samplings in two localities of the Tehuacán-Cuicatlán Mexical (Fig. 2), Valiente-Banuet et al. (1998), reported a total of 225 species and plant diversity of 90 ± 6 species of vascular plants per 1000 m² sample in two study zones. Also, from these samplings, they obtained for each woody species information of relative cover, maximum and minimum height, and frequency (%) as the proportion of times each species was found in the 15 lines. From these data the Relative Dominance Index (R.D.I.) per species was obtained, such that $R.D.I. = \text{relative cover (\%)} \times \text{frequency (\%)} \times \text{relative density}$, where relative density = number of individuals in 50 m². They found that the Mexical is a broad-leaved evergreen sclerophyllous shrubland constituted mainly by shrubs (47%), ephemerals (39.2%), chamaephytes (10.8%) and trees (7.41%). In both cases plant coverage ranged from 105 to 187% (Table 3), although many areas in which soils present a well-developed petrocalcic horizon plant cover is ca. 40–60%.

Also, a comparative analysis of plant characters of the dominant woody species from different Mediterranean areas and the Tehuacán-Cuicatlán mexical was conducted by Valiente-Banuet et al. (1998). To do so, information from Mediterranean areas were obtained from the Specht (1988) databook. The importance of the species within their studied communities was confirmed from studies of Wilson and Vogl (1965), Hanes (1977), and Mooney et al. (1977) for the Californian chaparral; Mooney et al. (1977) and Rundel (1981) for the Chilean matorral; Beadle (1981) and Specht (1981) for the Australian mallee; and Tomaselli (1981), Quezel (1981),



Fig. 3 Mexical shrubland in the Puebla State, ca. 2000 m elevation. A large number of shrubs and some trees are present and include: *Brahea nitida*, *Amelanchier denticulata*, *Dodonaea viscosa*, *Garrya ovata*, *Quercus sebifera*, *Dasyllirion serratifolium*, among others.



Fig. 4 Mexical shrubland in the Oaxaca State, ca. 2200 m elevation. A large number of shrubs and trees are present and include: *Amelanchier denticulata*, *Dodonaea viscosa*, *Fourcraea* sp., *Garrya ovata*, *Quercus obtusata*, *Comarostaphylis polifolia*, *Opuntia* sp., among others.

and Romane and Terradas (1992) for the Mediterranean Basin vegetation of France, Spain, and Greece (Valiente-Banuet et al., 1998). Fourteen characters regarding plant form, photosynthetic organs, and leaf characteristics characterizing typical Mediterranean traits were used in the comparative analysis (Table 4). The role of the characters was weighted by means of the number of species scored in each area and then ordinated by a Simple Correspondence Analysis (Valiente-Banuet et al., 1998). As a reference, the spiny shrubland vegetation adjacent to mexical was considered in the analysis, which is distributed close to the mexical, with an altitude ranging from 1380 to 1800 m.a.s.l. (Valiente-Banuet et al., 2000) and an average annual rainfall around 425 mm (Dávila et al., 1993; Valiente, 1991). The inclusion of this external group into the analysis was considered to test the similarity with the mexical situated within the same region and just below the altitudinal belt of the sclerophyllous vegetation. A total of 121 dominant species were included in the analysis: 28 for the Tehuacán region, 18 for the Tehuacán spiny shrubland, 23 for the Californian chaparral, 13 for the Chilean matorral, 24 for the Mediterranean Basin, and 15 for the Australian mallee. The correspondence analysis showed two different groups (Fig. 6). The first corresponds to the areas of evergreen sclerophyllous vegetation (Chilean matorral, Tehuacán mexical, Californian chaparral, Australian mallee, and Mediterranean Basin vegetation) and the second to the Tehuacan spiny shrubland. Both groups were differentiated on the basis of leaf seasonality, consistency, and angle. In all five evergreen sclerophyllous vegetation areas of the analysis, the character states “evergreen” and “sclerophyllous” and “vertical leaf angles” were dominant. In contrast, in the



Fig. 5 Mexical shrubland in the Tamaulipas States in North East Mexico, ca. 2000 m elevation. A large number of shrubs and trees are present and include: *Rhus virens*, *R. chondroloma*, *R. pachyrrhachis*, *Garrya ovata*, *Quercus* spp., *Pinus* sp.

Table 1 Common genera between mediterranean-type ecosystems and the Tehuacán Mexical.

Family of seed plants	Tehuacán Valley mexical	California chaparral	Chilean matorral	Mediterranean Basin	Australian mallee
Agavaceae	Yucca	x			
Anacardiaceae	Rhus	x		x	
Anacardiaceae	Pistacia			x	
Cupressaceae	Juniperus	x		x	
Ericaceae	Arbutus	x		x	
Ericaceae	Comarostaphylis	x		x	
Fagaceae	Quercus	x		x	
Garryaceae	Garrya	x			
Lamiaceae	Salvia	x		x	
Rhamnaceae	Ceanothus	x			
Rosaceae	Amelanchier	x		x	
Rosaceae	Cercocarpus	x			
Rosaceae	Vauquelinia	x			
Scrophulariaceae	Penstemon	x			
Mimosaceae	Acacia		x		
Asteraceae	Gochnatia		x		
Asteraceae	Baccharis		x		
Lamiaceae	Satureja		x	x	
Asteraceae	Stevia			x	
Boraginaceae	Lithospermum			x	
Convolvulaceae	Ipomoea			x	
Crassulaceae	Sedum			x	
Oleaceae	Fraxinus			x	
Linaceae	Linum			x	x
Poaceae	Aristida				x
Sapindaceae	Dodonaea				x

Modified from Valiente-Banuet, A., Flóres-Hernández, N., Verdú, M., and Dávila, P. (1998). The chaparral vegetation in Mexico under non-Mediterranean climate: Convergence and Madrean-Tethyan hypotheses reconsidered. *American Journal of Botany* 85, 1398–1408. Rights Link License Number: 4638360309620.

Tehuacan spiny shrubland the character states “deciduous,” “malacophyllous,” and “horizontal leaf angles” were the dominant traits. Two of these discriminatory characteristics (evergreen and sclerophyllous) correspond to those found by Barbour and Minnich (1990) as consistently similar among the five Mediterranean-type ecosystems. The other factor, steep leaf angles, has been reported as an adaptation of Mediterranean sclerophyllous plants to reduce radiation absorption during extended drought periods (Ehleringer and Comstock, 1989; Valiente-Banuet et al., 2010). Considering the second axis in the correspondence analysis, the number of stems is a significant discrimination factor. This character can be considered as an architectural characteristic related to resprouting ability, and is represented by a significant number of species in the Chilean matorral not so frequently observed in other Mediterranean regions. Mediterranean-type ecosystems have been matched with natural fires and therefore typical features of shrubs, such as

Table 2 Environmental and vegetation characteristics of Mexical under wet-summer climates.

Mexican state (Source)	Altitude (masl)	Climatic type (García, 1988)	Dominant woody species	Vegetation height range (m)
Chiapas (Miranda, 1952)	1530	Cb	<i>Amelanchier denticulata</i> , <i>Dodonaea viscosa</i> , <i>Garrya laurifolia</i> , <i>Harpalyce macrobotrya</i> , <i>Quercus sebifera</i> , <i>Rhus schiedeana</i> , <i>Temstroemia tepezapote</i> , <i>Ximenia americana</i> , <i>Xylosma flexuosa</i>	2–4
Coahuila (Muller, 1947)	> 2000	Between Bs and Cw	<i>Acacia greggii</i> , <i>Amelanchier denticulata</i> , <i>Arbutus xalapensis</i> , <i>Arctostaphylos pungens</i> , <i>Berberis trifoliolata</i> , <i>Ceanothus greggii</i> , <i>Ceanothus lanuginosus</i> , <i>Cercocarpus mojadensis</i> , <i>Cercocarpus</i> sp., <i>Cowania plicata</i> , <i>Dasyllirion</i> sp., <i>Fraxinus cuspidata</i> , <i>Fraxinus greggii</i> f. <i>nummularis</i> , <i>Garrya ovata</i> , <i>Juniperus flaccida</i> , <i>Juniperus pachyphloe</i> , <i>Lindleyella</i> sp., <i>Microrhamnus ericoides</i> , <i>Mimosa biuncifera</i> , <i>Nolina erumpens</i> , <i>Ptelea trifoliata</i> , <i>Quercus hypoxantha</i> , <i>Quercus intricata</i> , <i>Quercus intricata</i> , <i>Quercus invaginata</i> , <i>Quercus laceyi</i> , <i>Quercus pringlei</i> , <i>Quercus pungens</i> , <i>Rhus microphylla</i> , <i>Rhus microphylla</i> , <i>Rhus trilobata</i> , <i>Rhus virens</i> , <i>Yucca carerosana</i>	0.30–0.60
Distrito Federal (Rzedowski, 1954)	2500–2800	Cw	<i>Quercus rugosa</i> , <i>Eupatorium glabratum</i> , <i>Baccharis conferta</i> , <i>Q. mexicana</i> , <i>Q. crassipes</i> , <i>Q. centralis</i> , <i>Buddleia americana</i> , <i>Salvia mexicana</i> , <i>Lamoureauxia rhinanthifolia</i> , <i>Arbutus</i> sp.	1–3
Guanajuato (Quero, 1977)	2300–2600	Cw ₀ –Cw ₁	<i>Quercus potosina</i> , <i>Q. eduardii</i> , <i>Q. grisea</i> , <i>Arctostaphylos pungens</i> , <i>A. oaxacana</i> , <i>Baccharis heterophylla</i> , <i>Ageratina calaminthaefolia</i> , <i>Brickelia scoparia</i> , <i>B. veronicifolia</i> , <i>Dalea argyrostachya</i> , <i>Eupatorium espinosarum</i> , <i>E. glabratum</i> , <i>Eysenhardtia polystachya</i> , <i>Garrya laurifolia</i> , <i>Dasyllirion</i> , <i>Dodonaea viscosa</i> , <i>Arbutus glandulosa</i> , <i>Prunus serotina</i> , <i>Amelanchier denticulata</i> , <i>Havardia elachystophylla</i> , <i>Comarostaphylis glaucescens</i> , <i>C. polifolia</i>	1–4
Hidalgo (González-Quintero, 1968; Hiriart, 1981)	2150–2300	Bs	<i>Quercus mexicana</i> , <i>Agave lecheguilla</i> , <i>Amelanchier denticulata</i> , <i>Arbutus glandulosa</i> , <i>Dasyllirion longissimum</i> , <i>Nolina nelsonii</i> , <i>Cercocarpus fothergilloides</i> , <i>C. pringlei</i> , <i>Arctostaphylos arguta</i> , <i>Berberis ilicina</i> , <i>Salvia ballotaeflora</i> , <i>S. hidalgensis</i> , <i>Clethra pringlei</i> , <i>Juniperus monosperma</i> var. <i>gracilis</i> , <i>Krugiodendron ferreum</i> , <i>Lindleya mespiloides</i> , <i>Mimosa aculeaticarpa</i> , <i>Myrtus ehrenbergii</i> , <i>Pistacia mexicana</i> , <i>Rhus andrieuxii</i> , <i>R. mollis</i> , <i>R. trilobata</i> , <i>Vauquelinia corimbosa</i> , <i>Wimmeria concolor</i> , <i>Croton hypoleucus</i> , <i>Lippia berlandieri</i> , <i>Tecoma stans</i> , <i>Thryallis glauca</i> , <i>Zexmenia gnaphalioides</i>	0.20–3
México (Rzedowski et al., 1964)	> 2000		<i>Quercus microphylla</i> , <i>Nolina parviflora</i> , <i>Agave atrovirens</i> , <i>Bouvardia longiflora</i> , <i>Dalea tuberculata</i> , <i>Dasyllirion acrotriche</i> , <i>Ageratina calaminthifolia</i> , <i>A. scorodonioides</i> , <i>Helianthemum glomeratum</i> , <i>Bouvardia longiflora</i> , <i>Rhus standleyi</i> , <i>Verbesina hypomalaca</i>	0.20–2
Nuevo León (Muller, 1939; Rojas-Mendoza, 1965)	2000–2800	BSkw	<i>Agave americana</i> , <i>Agave falcata</i> , <i>Amelanchier nervosa</i> , <i>Arbutus xalapensis</i> , <i>Arctostaphylos novae-angliae</i> , <i>A. pungens</i> , <i>Ceanothus ovata</i> , <i>C. ferox</i> , <i>C. lanuginosus</i> , <i>Cercocarpus majodensis</i> , <i>Cowania plicata</i> , <i>Garrya glaberrima</i> , <i>Garrya ovata</i> , <i>Juniperus mexicana</i> , <i>Mahonia fremontii</i> , <i>Nolina microcarpa</i> , <i>Philadelphus argenteus</i> , <i>Pinus cembroides</i> , <i>Quercus clivicola</i> f. <i>dentata</i> , <i>Q. cordifolia</i> , <i>Q. errans</i> f. <i>Graciliramis</i> , <i>Q. flocculenta</i> , <i>Q. porphyrogenita</i> f. <i>macropetiolata</i> , <i>Q. pringlei</i> , <i>Q. saltillensis</i> , <i>Rhus microphylla</i> , <i>Rhus pachyrrhachis</i> , <i>Rhus trilobata</i> , <i>Rhus virens</i> , <i>Yucca carerosa</i>	0.30–1.5
Oaxaca (Cruz-Cisneros and Rzedowski, 1980; García, 1983)	2000–2450	Cw ₀ –Cw ₁	<i>Rhus standleyi</i> , <i>R. dukeri</i> , <i>Amelanchier denticulata</i> , <i>Calliandra grandiflora</i> , <i>Perymenium discolor</i> , <i>Gymnosperma glutinosum</i> , <i>Lindleya mespiloides</i> , <i>Mortonia diffusa</i> , <i>Arctostaphylos polifolia</i> , <i>A. pungens</i> , <i>Juniperus flaccida</i> , <i>Quercus microphylla</i> , <i>Arbutus xalapensis</i> , <i>Ceanothus greggii</i> , <i>Cercocarpus fothergilloides</i> , <i>Dodonaea viscosa</i> , <i>Eupatorium spinosarum</i> , <i>Eysenhardtia polystachya</i> , <i>Leucaena sculenta</i> , <i>Tecoma stans</i> , <i>Prunus serotina</i> , <i>Vauquelinia australis</i>	1–4
San Luis Potosí (Rzedowski, 1966)	> 2000	Between Bs and Cw	<i>Quercus crassifolia</i> , <i>Amelanchier denticulata</i> , <i>Arbutus xalapensis</i> , <i>Arctostaphylos pungens</i> , <i>Ceanothus depressus</i> , <i>Ceanothus greggii</i> , <i>Cercocarpus paucidentatus</i> , <i>Comarostaphylis polifolia</i> , <i>Garrya ovata</i> , <i>Rhus pachyrrhachis</i> , <i>Salvia regla</i> , <i>Yucca filifera</i> , <i>Brahea decumbens</i> , <i>Casimiroa pringlei</i> , <i>Citharexylum oleinum</i> , <i>Gochnatia hypoleuca</i> , <i>Persea</i> sp.	1.5–3

Table 2 Environmental and vegetation characteristics of Mexical under wet-summer climates.—cont'd

Mexican state (Source)	Altitude (masl)	Climatic type (García, 1988)	Dominant woody species	Vegetation height range (m)
Tamaulipas (Martin, 1958; Puig, 1970)	> 1700	Between Bs and Cw	<i>Arbutus</i> sp., <i>Quercus opaca</i> , <i>Q. grisea</i> , <i>Bauhinia coulteri</i> , <i>Cercocarpus fothergilloides</i> , <i>Yucca</i> sp.	± 1.8
Veracruz (Rivera-Hernández et al., 2019)	1900–2500	Between Bs and Cw	<i>Quercus sebifera</i> , <i>Quercus mexicana</i> , <i>Quercus repanda</i> , <i>Nolina parviflora</i> , <i>Rhus pachyrrhachis</i> , <i>Comarostaphylis polifolia</i> , <i>Lindleya mespilioides</i> , <i>Ceanothus caeruleus</i> , <i>Pistacia mexicana</i> , <i>Cercocarpus macrophyllus</i> , <i>Cercocarpus fothergilloides</i> , <i>Malacomeles denticulata</i> , <i>Brahea</i> sp., <i>Galphimia speciosa</i> , <i>Desmodium orbiculare</i> , <i>Eysenhardtia polystachya</i> , <i>Rhus standleyi</i> , <i>Tecoma stans</i> , <i>Bouvardia ternifolia</i>	1.5

Modified from Valiente-Banuet, A., Flóres-Hernández, N., Verdú, M., and Dávila, P. (1998). The chaparral vegetation in Mexico under non-Mediterranean climate: Convergence and Madrean-Tethyan hypotheses reconsidered. *American Journal of Botany* 85, 1398–1408. Rights Link License Number: 4632160463589.

Table 3 Summary of vegetational measurements obtained by the line intercept in the study areas (E, evergreen; D, deciduous).

Area species	Percent cover	Height max.	Height min.	Relative frequency	Relative dominance	Leaf seasonality
Cerro Viejo (see Fig. 2)						
<i>Quercus sebifera</i>	24.92	2.90	0.10	100.00	646.29	E
<i>Citharexylum oleinum</i>	8.52	3.50	0.15	88.87	56.41	E
<i>Rhus virens</i>	7.46	2.00	0.20	88.87	90.91	E
<i>Garrya ovata</i>	7.29	3.50	0.20	66.63	44.88	E
<i>Dasyllirion serratifolium</i>	6.70	2.00	0.35	100.00	47.79	E
<i>Havardia elachistophylla</i>	5.95	0.80	0.05	100.00	54.51	D
<i>Ageratina espinosarum</i>	5.02	2.00	0.30	55.53	69.11	D
<i>Quercus obtusata</i>	4.82	4.00	3.50	33.33	9.64	E
<i>Brahea nitida</i>	4.22	6.00	0.15	55.53	36.83	E
<i>Comarostaphylis polifolia</i>	4.04	1.40	0.14	55.53	49.76	E
<i>Salvia candicans</i>	3.68	1.00	0.10	88.87	55.18	E
<i>Krameria cytoides</i>	3.20	1.30	0.50	55.53	8.66	E
<i>Litsea glaucescens</i>	2.80	1.10	0.18	55.53	3.71	E
<i>Ceanothus greggii</i>	2.77	1.80	0.50	44.43	19.29	E
<i>Bouvardia longiflora</i>	1.98	0.70	0.20	33.30	0.91	D
<i>Phyllanthus subcuneatus</i>	1.56	1.00	0.16	22.20	6.90	D
<i>Dodonaea viscosa</i>	1.51	2.40	0.50	33.33	7.04	E
<i>Nolina longifolia</i>	1.17	2.00	0.40	33.33	5.45	E
<i>Rhus standleyi</i>	1.08	1.10	0.25	66.63	2.05	E
Others	79.76					
Total	105.2					
Cerro Zotoltepec (see Table 2)						
<i>Quercus sebifera</i>	32.20	4.32	0.60	100.00	774.32	E
<i>Ageratina espinosarum</i>	22.99	2.40	0.28	100.00	542.35	D
<i>Amelanchier denticulata</i>	22.51	2.50	0.33	83.30	794.29	E
<i>Rhus virens</i>	12.89	3.40	1.10	83.30	79.29	E
<i>Forestiera rotundifolia</i>	11.90	2.76	0.46	83.30	137.88	D
<i>Salvia candicans</i>	11.09	1.64	0.12	100.00	199.68	E
<i>Salvia thymoides</i>	10.85	1.30	0.08	83.30	224.06	E
<i>Garrya ovata</i>	7.68	4.10	1.05	66.65	79.64	E
<i>Lindleya mespilioides</i>	7.48	4.48	0.66	50.00	64.81	E
<i>Mimosa lacerata</i>	7.26	3.02	0.53	83.30	44.05	D
<i>Citharexylum oleinum</i>	6.92	2.52	0.30	100.00	46.01	E
<i>Dodonaea viscosa</i>	4.33	3.95	0.70	50.00	37.50	E
Others	29.23					
Total	187					

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Table 4 Morphological attributes reported for species of mediterranean-type ecosystems (Hanes, 1971; Specht, 1988), Tehuacán mexical and spiny shrubland (Valiente-Banuet et al., 1998).

Zone	Leaf seasonality		Leaf consistency		Leaf angle		Photosynthetic organs		Leaf size		Number of stems		Resprouting stems	
	0	1	0	1	0	1	0	1	0	1	0	1	0	1
Tehuacan mexical	18	82	79	21	93	7.1	3.6	96	11	89	93	7.1	3.6	96.4
Tehuacan spiny shrubland	89	11	0	100	39	61	0	100	5.6	94	44	56	77.7	22.3
California chaparral	35	65	74	26	70	30	4.3	96	13	87	87	13	50	50
Chile matorral	38	62	54	46	0	100	7.7	92	15	85	69	31	41	75.6
Mediterranean Basin	0	100	79	21	92	8.3	0	100	0	100	38	63	62.5	37.5
Australia mallee	0	100	100	0	67	33	6.7	93	6.7	93	60	40	69.3	30.7

Numbers indicate % of species bearing the morphological trait: leaf seasonality: 0 = summer and winter deciduous 1 = evergreen; leaf consistency: 0 = semi-sclerophyll, sclerophyll 1 = malacophyll; leaf angle: 0 = mainly vertical 1 = mainly horizontal; photosynthetic organs: 0 = phyllodes, cladodes, both leaves and stems, absent 1 = leaves; leaf size: 0 = microphyll (12.25 cm²)-mesophyll (180.25 cm²) 1 = subleptophyll (<0.10 cm²)-nanomicrophyll (12.25 cm²); stem number: 0 = several 1 = single; sprouting stems: 0 = no 1 = yes.

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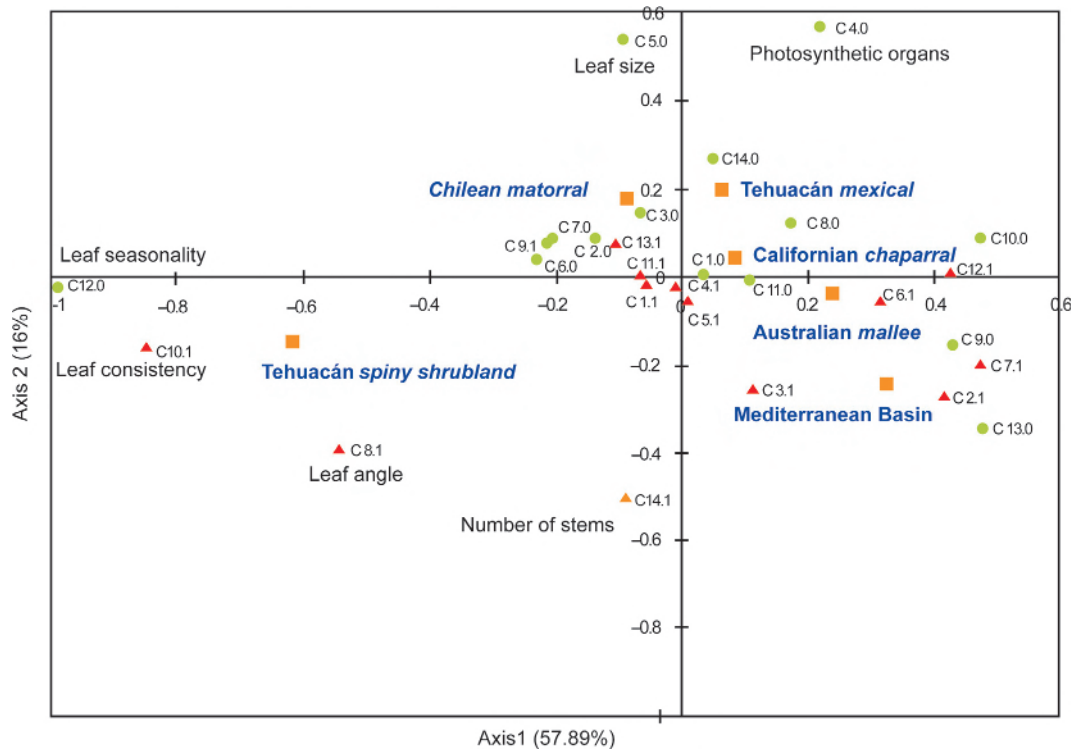


Fig. 6 Correspondence analysis graph of the structural comparative analysis between the Tehuacán-Cuicatlán Mexican and the Mediterranean-type ecosystems of California, Chile, Australia, and the Mediterranean Basin. The Tehuacán spiny shrubland was used as an outgroup. The first axis explains 58% of variance and the second axis explains 16% of variance. Modified from Valiente-Banuet, A., Flóres-Hernández, N., Verdú, M., and Dávila, P. (1998). The chaparral vegetation in Mexico under non-Mediterranean climate: Convergence and Madrean-Tethyan hypotheses reconsidered. *American Journal of Botany* 85, 1398–1408. Rights Link Licence Number: 4613741487587.

lignotubers and burls at the root crown/stem base, have been associated with postfire resprouting ability (James, 1984; Kummerow and Ellis, 1989). These woody structures and resprouting ability are present in the shrubs of the Tehuacan mexican where there is no evidence of periodic fire, indicating that their presence can be better considered as an ancient preadaptation to fire inherited from ancestors belonging to laurophyllous forests (Axelrod, 1975).

Trait similarity not only among plant species from different Mediterranean ecosystems but also from Mexical species challenged the convergence hypothesis. [Verdú et al. \(2003\)](#) showed that the similarities among Mediterranean (including Mexical taxa) were explained by common ancestry because similarities in the character syndromes vanished when common genera were excluded from the analysis.

Plant Physiological Studies

Limited water represents a major stress affecting plant performance within both Mediterranean-type and Mexical ecosystems. Since leaf temperatures usually increase plant water stress, steep leaf angles contribute to a reduction in leaf solar radiation absorption (Smith and Ullberg, 1989) (Fig. 7). Functionally, the predominance of steeply inclined foliage in water-limited environments has been considered as a strategy to cope with water limitations and high radiation loads (Falster and Westoby, 2003). Steep leaf angles with respect to the horizontal plane considerably reduce heat loads particularly at midday, decreasing the risk of over-heating and photoinhibition (Valladares and Pugnaire, 1999). Likewise, species with steep leaf angles may be able to maintain increased levels of photosynthesis during high radiation periods (Falster and Westoby, 2003) increasing water use efficiency (King, 1997). Different studies have considered that such leaf architecture may have adaptive value in arid environments due to its positive effects on reproduction output (Smith and Ullberg, 1989; Pearcy et al., 2005). In the Tehuacan mexical, 93% of the species present leaf angles ranging between 45 and 90 degrees with respect to the horizontal axis, which suggests that evergreen-sclerophyllous species are responding mainly to water stress. Valiente-Banuet et al. (2010) quantified leaf angle in 28 dominant species under a phylogenetic framework and evaluated the functional implications of the observed range of leaf angles in terms of leaf temperature, water potentials, and transpiration. In addition, they combined manipulative experiments restraining leaves horizontally with microclimatic and stomatal conductance measurements in five species. Leaf angles were experimentally manipulated to restrain leaves horizontally by inserting an inert epoxy material between the leaf petiole and the branch. A control branch of the same height and with a similar number of leaves as the experimental branch was labeled on the same individual. In all cases, branches with horizontally restrained leaves presented significantly lower water potentials than control branches in all of the five species studied: *Citharexylum oleinum* (Verbenaceae), *Comarostaphylis polifolia* (Ericaceae), *Garrya ovata* (Garryaceae), and *Quercus sebifera*. Because phylogenetic analyses showed that steep leaf angles evolved in a correlated fashion in evergreen species, they concluded that it is an adaptive trait allowing evergreen species to cope with dry conditions to persist within the mexical community.



Fig. 7 *Arctostaphylos pungens* in the Tehuacán-Cuicatlán Mexican showing its almost vertical leaves.

A comparative study between the California chaparral and the Mexical shrubland was conducted by Bhaskar et al. (2007) to analyze the adaptive significance of traits governing plant water use. By comparing closely-related species pairs in these two geographic localities, they examined whether evolutionary contrasting divergences in hydraulic conductivity were associated with contrasting seasonality of the rainy season. Evolutionary correlations were examined also by using phylogenetically independent contrasts, considering a suite of hydraulic traits, including stem and leaf specific conductivity, resistance to embolism, wood density, inverse Huber value, and minimum seasonal water potential. Despite the seasonal climatic differences between California and Tehuacán (high summer temperatures and high vapor pressure deficit in the former, and summer rain regime and annual period of soil water deficit coinciding with the cooler months in the latter), predrawn water potentials at the end of the dry season did not differ between localities. In addition, although evolutionary divergences in hydraulic traits among the selected species pairs were expected to be correlated with the precipitation conditions at each locality, sapwood specific conductivity (K_s), did not differ between sites. In contrast, leaf-specific conductivity was higher in California which may be adaptive where soil and atmospheric droughts coincide during summer. Finally, a significant correlation was found between divergencies in xylem resistance to embolism and minimum seasonal water potential, but surprisingly, no evolutionary trade-off was found between resistance and stem conductivity.

Plant Phenology

Plant phenology in Mediterranean type ecosystems is also a trait that had been hypothesized to have converged under the selective pressure imposed by the typical summer stress (Mooney and Kummerow, 1981). In contrast, Mexical shrubland has not experienced summer drought because of its tropical climate. While spring flowering is the typical phenology of Mediterranean plants, nonseasonal flowering is typically produced in tropical communities. To test the weight of the evolutionary history in the phenological response of plants to climatic conditions, Verdú et al. (2002) compared flowering phenology of Mexical plants to that of Mediterranean ecosystems. Flowering phenology in the Mexical strongly differed from that of Mediterranean ecosystems because it was not as seasonal and the flowering peak was produced in summer. Phenological differences were not only shown at the community level but also between Mexical and their Mediterranean congeneric species. These findings suggest that despite sharing common ancestors, current climatic conditions drive different phenologies. At what extent such phenological response is a product of plasticity deserve further research (see Vanderplank and Ezcurra, 2015).

Regeneration Niche Conservatism and Community Organization

The growing evidence that closely related species with disjunct distributions have maintained their fundamental niche features through evolutionary time (Wiens and Graham, 2005) supports the hypothesis that the niche evolves in a conserved manner. This pattern, known as phylogenetic niche conservatism constitutes a central aspect for understanding the mechanisms that organize communities (Wiens and Graham, 2005; Valiente-Banuet and Verdú, 2007). Actually, interspecific interactions that comprise a substantial part of the species niche, and the organization of biological systems through evolutionary time is mediated by a marked conservatism of ecological interactions across the entire Tree of Life (Gómez et al., 2010). On this vein, Valiente-Banuet et al. (2006) hypothesized that there should be a correlation between the characteristics of the environment in which individual taxa evolved and the contemporary features of the regeneration niche of these species. They found that in Mediterranean climate and Mexical communities most woody Paleogene/Neogene floristic taxa tend to recruit through facilitation, whereas Quaternary elements do it in open spaces. As a way to test whether regeneration niche evolves in a conserved manner, Valiente-Banuet and Verdú (2007) analyzed the regeneration niche in a large worldwide database in which Mediterranean and Mexical taxa were included and shown to be strongly conserved (Valiente-Banuet and Verdú, 2007). The salient picture of regeneration niche conservatism is that nurse species facilitate distantly related species, suggesting that at the community level, facilitation increases the phylogenetic diversity of the plant community. This hypothesis has been already tested in Mediterranean Basin shrublands (Verdú et al., 2009) and in Mediterranean Basin grasslands (Soliveres et al., 2012) showing that effectively, facilitation occurs between distantly related species

and that observed phylogenetic distance between nurses and facilitated species were significantly higher than the expected from a null expectation in the community (Valiente-Banuet and Verdú, 2013).

Fire Responses of Mexical Species

In Mediterranean-type ecosystems, fire has been recognized as an important factor determining vegetation dynamics (Hanes, 1971; Moreno and Oechel, 1994). Regenerative mechanisms that allow populations to recover after fire are widespread in Mediterranean-type vegetation (Mooney and Dunn, 1970; Keeley and Zedler, 1978; Gill, 1981; Trabaud, 1987). For example, these mechanisms include fire-stimulated germination, or resprouting from stumps, lignotubers, or burls (James, 1984). For obligate seeders, fire has been proposed as a major selective force leading to the acquisition of this character associated with post-fire regeneration (Gill and Groves, 1981; Keeley, 1986). The hypothesis of the adaptive significance of resprouting due to recurring fire (Mooney and Dunn, 1970; Biswell, 1974; Naveh, 1975; Shmida, 1981) has often been rejected because the resprouting habit is common among the dicotyledons, and several authors have proposed resprouting to be a preadaptive character resulting from anatomical features and herbivory pressures (Trabaud, 1987; Zedler and Zammit, 1989; López-Soria and Castell, 1992; Lloret et al., 1999).

In the Mexical, fire in the past has been absent or very rare (Valiente-Banuet et al., 1998). However, in the last decades, some human-caused fires have occurred but in the last few years, this type of disturbance has increased its frequency in different parts of Mexico as a consequence of long drought periods. Consequently, it is important to know the ability of these communities to regenerate after burning (Lloret et al., 1999). Valiente-Banuet et al. (1998) reported plant responses after a fire occurred in the Mexical shrubland in south-central Mexico. In June 1995, a wildfire burned 2 ha of mexical shrubland in Cerro Viejo mountain (Mexico, Tehuacán Valley, 18°15' N, 97°26' W; 2450 m.a.s.l.). In April 1997, five 25 × 2 m transects were established and all stump diameters of dead and resprouting plants for each species were measured (Valiente-Banuet et al., 1998). A total of 14 species resprouted: *Ageratina spinosarum* (Asteraceae), *Amelanchier denticulata* (Rosaceae), *Comarostaphylis polifolia* (Ericaceae), *Citharexylum oleinum* (Verbenaceae), *Croton hypoleucus* (Euphorbiaceae), *Gochmatia smithii* (Asteraceae), *Havardia elachystophylla* (Mimosaceae), *Lindleya mespiloides*, *Quercus sebifera* (Fagaceae), *Rhus standleyi*, *Rhus virens* (Anacardiaceae), *Salvia aspera*, *Salvia candicans* (Lamiaceae), and *Xerospirea hartwegiana* (Rosaceae). Reproduction from seeds was recorded only for *Croton hypoleucus*, *Gymnosperma glutinosum* (Asteraceae), *Ceanothus greggii* (Rhamnaceae), and *Phytolacca icosandra* (Phytolaccaceae).

Moreover, an experimental study on the resprouting response to fire that considers the development stage of the plants and the biogeographical origin of the species was conducted by Lloret et al. (1999) in the Tehuacán-Cuicatlán mexical. A total of 24 plants of eight dominant species were selected at Cerro Zotaltepec (Mexico, Tehuacán-Cuicatlán Valley (Fig. 2; 18°38' N, 97°27' W; 2350 m a.s.l.). Four of these species which belong to relict genera of the Madro-Tertiary Geoflora, with close relatives in the Californian chaparral were able to resprout after fire (Axelrod, 1975; Valiente-Banuet et al., 1998) (*Quercus sebifera*, *Rhus standleyi*, *Garrya ovata*, and *Comarostaphylis polifolia* subsp. *polifolia*). In contrast, the other four species, *Xerospirea hartwegiana*, *Coutaportia ghiesbreghtiana*, *Mortonia diffusa*, and *Krameria cytisoides*, having Neotropical affinities (Rzedowski, 1978; Gentry, 1982; Henrickson, 1985; Maberley, 1997) showed less ability to regenerate after fire, and small plants were more likely to die after disturbance than in the Madro-Tertiary group. They found that resprouting is a widespread trait in the Mexical species characterized by the presence of lignotubers and burls. Resprouting can be considered an ancient trait, probably linked to losses of aboveground biomass, that became a preadaptation in Mediterranean fire-prone communities. They concluded that the resprouting feature and the seeder strategy of other species after a fire in the Mexical shrubland are similar to Mediterranean-type ecosystems, emphasizing their common origin and the relevance of phylogenetic and biogeographical studies to explain current patterns of vegetation.

Areas for Future Research

Undoubtedly, Mexical shrubland is the least studied ecosystem of Mexico. Accordingly, complete biodiversity studies are needed in order to assess the Mexical contribution to the world's biodiversity considering its closeness to the tropics. As we have pointed out, the study of the Mexical shrubland under a more integrative approach, including biogeographic, paleobotanical, and ecological patterns, has opened the possibility to explain floristic, adaptive, and community organization processes occurring in these environments.

Moreover, pollination studies are needed in relation to the pre-Pliocene syndrome proposed by Herrera (1992) which has been validated for the Mexical by Verdú et al. (2003) and the potential role of bees on pollination success. In addition, no studies have been conducted involving seed dispersal in the Mexical, mostly for the pre-Pliocene floristic elements which depend on facilitation for seedling establishment. All these aspects open the possibility to unravel coevolutionary processes if plant-animal interactors have been interacting for long periods of time.

Finally, global climate change, is an urgent task to consider in the Mexical shrubland. Although it distributes along the principal mountains of Mexico, our observations indicate that in many cases this vegetation occupies the mountaintops. Historical information shows that this vegetation had altitudinal or geographical shifts as a result of the climatic fluctuations occurred in the Southern and Northern hemispheres during the Quaternary (Betancourt et al., 1990; Markgraf et al., 1995), which emphasize its vulnerability to the increase of temperatures and the intensity and duration of droughts. Currently, an increase of severe droughts in Mexico has been documented for the last two decades (Cruz, 2011; Neri and Magaña, 2016; Murray-Tortarola et al., 2018).

Ecophysiologically, most of the Mexical plants that are C3, sclerophyllous and evergreen species will have to deal with the problem that the increase in droughts will pose in terms of low water availability and loss of moisture due to stomatal opening during the day. Accordingly, analyzing the mechanisms of resistance to water stress of these taxa, mainly those related to the susceptibility of embolisms in vascular ducts, is crucial to understand the near future of the Mexical shrubland under the ongoing climate change.

Acknowledgments

The authors thank Tania Sánchez Ortiz and Noé Flores Hernández for the elaboration of figures and tables as well as the search for information to elaborate this article. This work was carried out thanks to the support of the DGAPA-PAPIIT project (IN-210117).

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Cerrado—South America

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Abstract

The Cerrado Biome is considered one of the most important savanna biomes in the world, due to its high species richness, endemism, and source of multiple valuable ecosystem services. The Cerrado landscape is diverse, with a mixture of open grasslands, shrub lands, open woodland, and closed canopy woodlands as the dominant ecosystems. The region also harbors ecologically important habitats more restricted in area, such as gallery forests, tropical dry forests, marshes, palm groves, and high elevation rocky grasslands, all of these important contributors to the overall diversity of the region. Many of Brazil's most important rivers originate in the Cerrado highlands and plateaus. The Cerrado also is home to a diverse and evolutionary distinctive flora and fauna, with multiple major sub-regions each with distinctive plant and animal species. Some of the diversity is evolutionarily quite old. The Cerrado has recently become a focal region for the expansion of Brazilian agriculture, and vast areas have been modified in the past 50 years. In addition, the population in the region has grown dramatically of the past five decades, placing additional demands on water resources. Although there are a number of important protected areas, the region is still under protected and more conservation effort needs to be applied to the protection of the biodiversity of the Cerrado in order to save this unique global resource.

What Is Cerrado?

The Cerrado covers 2 million km² in central South America (Fig. 1). It encompasses most of Central Brazil (most of Mato Grosso, Mato Grosso do Sul, and Tocantins; western Minas Gerais and Bahia; southern Maranhão and Piauí; all Goiás and Distrito Federal; and small portions of São Paulo and Paraná), northeastern Paraguay (departments of Amambay, Canindeyú, Concepción, San Pedro, and Alto Paraguay) and eastern Bolivia (provinces of Itenez, Guarayos, Ñuflo de Chávez, Velasco, Chiquitos, and Ángel Sandoval). Cerrado is a morphoclimatic domain because it shows a unique combination of geomorphology, geology, soils, vegetation, and climate (Ab'Saber, 1977). Cerrado is an ecoregion when all of these unique biological and ecological features are considered together (Olson et al., 2011). When only species distributions are taken into account, the Cerrado is a dispersal center (Müller, 1973), an area of endemism (Cracraft, 1985; Haffer, 1985), a phytogeographic province (Rizzini, 1976), and a biogeographical province (Cabrera and Willink, 1980; Morrone, 2017; Udvardy, 1975). Cerrado has even classified as a biome for legislation purposes in Brazil (IBGE, 2004), but the use of this term has been criticized in the literature (Batalha, 2011). In overall, there is a general consensus that Cerrado is one of the most distinct South American biogeographic regions regardless of the information and criteria used to demarcate it (Fig. 2).

Cerrado has borders with all major South American lowland biomes (Silva and Bates, 2002): The Amazon (on the north), the Chaco and Pantanal (on the west), Caatinga the (on the northeast), and the Atlantic forest (on the east and the south). As is common in South American biogeography, the boundaries between Cerrado and other major ecological regions are not well defined (Ab'Saber, 1977). Instead, these regions are separated by transition zones where vegetation mosaics create fascinating landscapes found nowhere else. These ecotonal regions have a complex interplay of species from various biomes resulting in a high combined regional species richness and unique communities of species in contact zones (Bezerra et al., 2009; Bueno et al., 2018; Lacher and Alho, 2001).

The Landscapes of Cerrado

The core of Cerrado is located on the large blocks of crystalline or sedimentary plateaus in Central Brazil. The continuity of these plateaus is only broken by a network of peripheral or intermontane depressions (Brasil and Alvarenga, 1989). The flat, gently rolling surfaces of the plateaus (500–1820 m of elevation) were mostly molded from the Upper Cretaceous to the Mid-Tertiary, during the South-American cycle of erosion (Braun, 1971; Cole, 1986). Then, the resulting peneplain (Sul-Americana surface) was uplifted during the Plio-Pleistocene, with associated subsidence leading to the formation of the peripheral depressions, which has altitudes



Fig. 1 The Cerrado Biome is located in Central South America.



Fig. 2 General appearance of the Cerrado landscape, showing the complex mosaic of different Cerrado vegetation.

ranging from 2 to 600 m (Brasil and Alvarenga, 1989). Peripheral depressions have been continuously transformed during the Quaternary by the most recent cycles of erosion (Braun, 1971). Geomorphological evidence suggests that during the cyclic global climatic fluctuations in the Pleistocene and Holocene, peripheral depressions were much more unstable and prone to ecological changes than the plateaus (Ab'Saber, 1983).

The tops of the plateaus are covered mostly by cerrado *sensu lato* (s.l.), a xeromorphic vegetation that grows on the deep, well-drained, and nutrient-poor soil (Eiten, 1972; Furley and Ratter, 1988). Cerrado s.l. is composed of two layers: a woody layer that includes trees and large shrubs, and a ground layer, which is composed of subshrubs and herbs. The flora of these two layers have possibly different origins, but both are well adapted to poor soils and frequent fires (Rizzini, 1976). There are five structural types for



Fig. 3 Broad savannas on the uplands bordering a stream-side gallery forest. (Photo credit: T. Lacher).

the cerrado s.l. (Eiten, 1972): (a) campo limpo (“clean field”), dry grassland with few or no shrubs or taller woody plants (Fig. 3); (b) “campo sujo” (“dirty field”), grassland with scattered shrubs and small trees (2–3 m tall); (c) campo cerrado (“closed field”), an open scrubland (3–6 m tall) with few trees and a large proportion of grassland; (d) cerrado (sensu stricto), a woodland (3–8 m tall) with closed scrub and more trees but still with herbaceous vegetation between them; and (e) cerradão (“tall cerrado”), a dense woodland (8–15 m tall) that often has a completely closed canopy and a ground layer much reduced (Fig. 4). Soil fertility and fire regime are the two most common factors used to explain the structural variation in cerrado s.l. (Bueno et al., 2018).

In a few places where the ecological conditions in the tops of the plateaus are not suitable for cerrado s.l., other vegetation types are found (Bueno et al., 2018; Eiten, 1972). These are: (1) veredas, valley-side marshes with palm groves of buriti-palm (*Mauritia flexuosa*) that dominates areas with a large fluctuation in the water table; (2) riverine and valley forests, 20–30 m tall semi-deciduous to evergreen forests with a humid understorey that harbors many ferns, epiphytes, as well as palms, and are found on cambisols or hydromorphic soils rich in organic matter along the streams or covering a wide valley floor; (3) seasonally tropical dry forests that grow on a few, small and scattered areas where limestone rocks were exposed due to erosion; (4) campo rupestre (rocky grasslands), a vegetation rich in endemic species that are found in high altitudes on the tops of the ancient plateaus and mountain ridges where soils are shallow.

In contrast with the plateaus, the peripheral depressions are generally flat pediplains associated with the channels of the region’s major rivers (Brasil and Alvarenga, 1989). Because the landscapes of depressions include both the pediplains and the scarps of the plateaus, they are much more heterogeneous than those found on the top of plateaus. As a consequence, peripheral depressions are covered by vegetation mosaics that include riverine forests, seasonally tropical dry forests, cerrado s.l., and grasslands. Riverine forests are found only along with the courses of the large rivers in the Cerrado. They are semi-deciduous to evergreen forests with trees 20–30 m tall. In contrast, seasonally tropical dry forests (“matas secas” in Portuguese) are deciduous or semi-deciduous forests with canopy height averaging 20–45 m that grow on patches of mesotrophic soils derived from basic rocks such as limestone



Fig. 4 Cerradão, the dense high canopy physiognomy associated with deeper soils and higher soil fertility.

(Bueno et al., 2018; Ratter et al., 1978). In some depressions (e.g., the Paran  River valley), tropical dry forests are the dominant vegetation type. Floodplain grasslands are a seasonally flooded vegetation found on areas of flat topography along the large rivers; they can be the dominant vegetation in a depression, such as the ones found in the Bananal Island in the Araguaia River valley.

In addition to terrestrial ecosystems, the Cerrado is home of important freshwater ecosystems (Innoc ncio, 1989). In fact, the Cerrado is the region where some of the longest South American rivers have their headwaters. The rivers and their affluents that originate on the high plateaus of the Cerrado flow to almost all neighboring ecological regions. Among the rivers that have headwaters in Cerrado are the Xingu, S o Francisco, Tocantins-Araguaia, Parna ba, Tapaj s, tributaries to the right margin of the Paran  River and all rivers forming the Pantanal. Little is known about the evolution of the present-day drainage system of the Cerrado Region. It has certainly had a long and dynamic history associated with the geological changes in central Brazilian plateaus since the Paleozoic (Innoc ncio, 1989). However, most of its modern features developed more recently, possibly in association with the Plio-Pleistocene uplift (Brasil and Alvarenga, 1989; Braun, 1971).

The climate of the Cerrado is tropical seasonal. The dry period, from May through September or October, coincides with the coldest months of the year (Nimer, 1989). The average annual rainfall ranges from 759 to 2245 mm, and the average annual temperature from 15.4  C to 27.8  C. Extremes of minimum temperature vary from 4.4  C to 14.7  C whereas extremes of maximum temperature ranges from 23.6  C to 36.5  C. In the context of the ecoclimatic zones of the Earth (Bailey, 2014), the Cerrado is part of the savanna division of the humid tropical domain that includes around 20.6 million km² of South America, Africa, Asia, and Oceania. The degree of seasonality in the Cerrado varies dramatically throughout the biome, with regions closer to the Amazon or Atlantic forest having longer periods with an excess of precipitation over evapotranspiration, generally in October through April (Camargo, 1971). This wetter period is somewhat shorter in the core areas of the Cerrado, and grades to semiarid conditions, with declining surplus of moisture, where the Cerrado grades into the Caatinga of northeastern Brazil. During the dry season grasslands become dry and brown and fire susceptibility increases dramatically. Woody Cerrado vegetation is highly resistant to fires, and many seeds of Cerrado plants have higher germination rates post-fire. A number of other Cerrado plants exhibit post-fire flowering (Miranda et al., 2002).

The Biodiversity of Cerrado

The Cerrado vegetation in Brazil is represented by a core area and a number of disjunct Amazonian Cerrados. There are some clear phytogeographic patterns observed across this vast savanna region (Ratter et al., 2006). The pockets of *Disjunct Amazonian Sites* are located in small isolated regions in the states of Roraima, Amap , and Par , with a more isolated region on the border between Amazonas and Rond nia. These are depauperate and quite distinct floristically. There is another small but distinctive region, *Far-Western Mesotrophic Sites*, in Rond nia located on more mesotrophic soils. The core region of the Cerrado is further divided into four geographic regions which have pronounced heterogeneity in species composition. These four regions, *North and North-Eastern*, *Central and South-Eastern*, *Southern*, and *Central-Western*, all have species restricted to their regions, ranging from 57 of 333 in the North and North-Eastern region to 162 of 557 total species in the Central-Western region (Ratter et al., 2006). These strong phytogeographic patterns contribute to the overall diversity of plants in the Cerrado.

Similar patterns of heterogeneity in species composition across the broad Cerrado landscape are observed in animal groups as well. Lepidopterans (moths and butterflies) show a strong influence of larger landscapes and vegetation on moth community composition, but geographic clustering in butterflies (Brown and Gifford, 2002). The biogeography of birds in the Cerrado is influenced by Amazonian and Atlantic Forest elements, given more mobile birds are able to colonize the Cerrado along the mesic gallery forests of the main Brazilian rivers (Silva, 1995a,b). The Atlantic Forest influence, however, is stronger than that of the Amazon (Silva, 1996). Mammalian species richness in the Cerrado is third in Brazil compared to the Amazon and Atlantic Forest biomes. One of the interesting aspects of the mammalian fauna of the Cerrado is the dominance of small bodied mammals and the low species richness of large grazing herbivores, in contrast to the African savannas (Marinho-Filho et al., 2002).

During the 1970s, the biota of Cerrado was considered as having both a low number of species as well as a low percentage of endemic species. However, intensive field surveys conducted since the 1980s have rejected both hypotheses. To date, scientists have identified in the region 12,097 species of plants (Zappi et al., 2015), 800 of fishes (Mittermeier et al., 2011), 209 of amphibians (Valdujo et al., 2012), 76 of lizards (Nogueira et al., 2011), 158 of snakes (Nogueira et al., 2011), 33 of amphisbaenians (Nogueira et al., 2011), 856 of birds (Silva and Santos, 2005), and 251 of mammals (Paglia et al., 2012). The percentage of endemic species ranges from 3.6% in birds to 60.6% in amphisbaenians (Table 1). Because large areas of Cerrado have never been sampled for any group of organisms (Silva, 1995a,b), it is possible that the actual regional species richness and percentage of endemic species are even higher than the ones presented in Table 1. Despite knowledge gaps, the Cerrado is currently considered as the world's most biodiverse tropical savanna.

The ranges of endemic species can cover a small portion or the entire Cerrado. The ranges of the endemic species found across the region define Cerrado as a distinctive biogeographic region. In contrast, the overlap of the ranges of endemic species found only in a small portion of Cerrado define biogeographical sub-regions. Such sub-regions are, in turn, termed areas of endemism. The number of areas of endemism varies according to the taxonomic group, ranging from four among birds (Silva, 1997), to 13 when ranges of amphibians lizards, snakes, and amphisbaenians are combined (Azevedo et al., 2016). The number of areas of endemism within Cerrado is expected to be larger for plants than any vertebrate groups because plants are limited by edaphic factors (i.e., chemical, physical, and biological properties of soils), microclimate, and dispersal modes (Major, 1988). Some areas of endemism are

Table 1 Number of species and percentage of endemic species of Cerrado in eight biological groups.

Biological group	Number of species	% Endemics
Plants ^a	12,097	35.1
Fishes ^b	800	25.0
Amphibians ^c	209	51.7
Lizards ^d	76	42.1
Snakes ^d	158	32.3
Amphisbaenians ^d	33	60.6
Birds ^e	856	3.5
Mammals ^f	251	8.8

^aZappi et al. (2015).^bMittermeier et al. (2011).^cValdujo et al. (2012).^dNogueira et al. (2011).^eSilva and Santos (2005).^fPaglia et al. (2012) and Gutiérrez and Marinho-Filho (2017).

common to all biological groups, such as the ones found along the Espinhaço Range, where the top of the plateau is dominated by rocky fields that have a unique set of species found nowhere else (Conceição et al., 2016).

Cerrado endemic species have accumulated over time, indicating a continuous process of biotic assemblage associated with the environmental changes that have been occurring in the region since the Miocene. Among birds, old endemic vertebrate species (i.e., that originated before Pliocene) are restricted to the top of the plateaus whereas evolutionarily young vertebrate species (i.e., originated during the Quaternary) are found mostly on the depressions (Silva, 1997). This pattern seems to be found also among other groups of organisms (Deus Vidal et al., 2019).

Threats and Conservation

The major threat to Cerrado biodiversity is the expansion of commercial agriculture across the region due to the ever-growing global demand for food. Until the 1970s, agriculture in the Cerrado was restricted only to regions with nutrient-rich soils found in the peripheral depressions (Mesquita, 1989). The plateaus, despite their level topography, deep well-drained soils, favorable climate, and a vegetation (cerrado s.l.) that can be easily cleared for farming or cattle ranching, were considered unfit for crop production because of their nutrient-poor, acidic soils. In 1970, only 10.6% of the Cerrado natural vegetation had been cleared (Klink and Moreira, 2002).

Things began to change when the Brazilian Institute for Agricultural Research (EMBRAPA) developed a set of new technologies that helped farmers circumvent the natural obstacles that existed for large-scale commercial agriculture in the Cerrado plateaus (Klink and Moreira, 2002). These technologies include soil fertilization with phosphate and lime; *Rhizobium*-based nitrogen fixation; new crop varieties; heavy use of pesticides and herbicides; “no-till” agriculture (in which crops or pastures are grown from year to year without disturbing the soil through tillage); forest, agriculture and livestock integration (in which fields are used alternately for crops and livestock but windbreak lines of trees are also planted in between the fields, where cattle can forage); and the adoption of modern machinery. In addition to new technology, the Brazilian national government improved road and energy infrastructure and provided very generous government subsidies to farmers (Mesquita, 1989). As a result, large-scale commercial agriculture focused on soybeans, rice, coffee, wheat, maize, sugarcane, and cotton has expanded exponentially in the Brazilian Cerrado with spillovers to Cerrado regions of Bolivia and Paraguay. In 2010, around 53% of the native vegetation of Cerrado in Brazil had been replaced by agriculture fields or other types of land use (Beuchle et al., 2015).

The expansion of agriculture across the Cerrado has caused many environmental transformations that currently threaten the region’s biodiversity. Land use changes have led to habitat fragmentation and isolation, reducing the area available for populations of several species of organisms (Rocha et al., 2018). Soil mechanization of large areas of agriculture exposed bare soil, leading to soil erosion and compaction (Merten and Minella, 2013). Freshwater systems have been affected by pollution caused by the use of fertilizers and pesticides, the establishment of dams for energy production, as well as continuous and unsustainable water withdrawals for irrigation (Nogueira et al., 2010). Finally, although cerrado species and ecosystems are adapted to fire, fire frequency has intensified drastically across the region due to human actions (Durigan and Ratter, 2016).

Cerrado is considered as poorly protected in general, but there are some important differences among countries. In Bolivia, the Noel Kempff National Park (15,230 km²) was gazetted in 1988 with 5412 km² and expanded in 1996 to its current size to protect the country’s largest cerrado area. Because of the park’s remoteness and Bolivia’s comparatively low human population density (especially in the country’s eastern lowlands), the most substantial human threats to this area come from burning associated with ranching operations in neighboring Brazil (Silva and Bates, 2002). In Paraguay, Cerrado is protected in the following public

protected areas: Cerro Corá National Park (55.3 km²), Paso Bravo National Park (1100 km²), Río Negro National Park (1237 km²), Serranía de San Luis National Park (102.8 km²), Cerro Chovoreca Natural Monument (1009 km²), and Cabrera-Timane Natural Monument (1258 km²). In Brazil, there are 418 public protected areas in Cerrado. Altogether these protected areas cover 176,173 km², they represent only 8.6% of the region. The ten largest protected areas with strict protection in the Brazilian Cerrado are: Nascentes do Rio Parnaíba National Park (7498 km²), Serra Geral do Tocantins Ecological Station (7163 km²), Araguaia National Park (5577 km²), Mirador State Park (5000 km²), Chapada dos Veadeiros National Park (2406 km²), Grande Sertão Veredas National Park (2310 km²), Araguaia State Park (2231 km²), Iquê Ecological Station (2159 km²), Serra da Canastra National Park (1978 km²), and Chapada das Mesas National Park (1599 km²).

The lack of balance between use and conservation has increased the extinction risk of many species of animals and plants. According to the most recent estimates there are 1267 threatened species for the Cerrado, of which 979 are plants (Martins et al., 2018) and 288 animals (ICMBIO, 2018).

Changing Climatic Conditions

There is very little doubt that the Cerrado is going to be drastically affected by climate change. For instance, Torres and Marengo (2014) synthesized a large number of climate model projections and found that a large portion of Cerrado can be considered as a persistent climate change hotspot throughout the different forcing scenarios and Global Circulation Model datasets. More specifically, the Brazilian Panel on Climate Change (PBM, 2013) projected that: (1) temperatures will increase by between 1 °C and 5.8 °C in the region, with a drier and warmer period by 2070; (2) flows of all river basins with significant tributaries rivers in the center-west (Tocantins/Araguaia, Paraná, São Francisco, Paraguay and Amazonas) will be reduced for the period 2071–2100, relative to the historical average (1961–90); (3) temperature rises will result in a reduction of the photosynthetic process, which over time can lead to a decrease in plant biomass and a reduction in primary productivity; (4) the increase in the length of the dry period can potentially result in increased vulnerability to fire in the Cerrado, leading to more frequent burning and decreasing precipitation across the region.

The implications of climatic change on the regional ecosystems is still a question open to debate. Studies using techniques of ecological niche modeling indicate that species of plants (de Siqueira and Peterson, 2003; Velazco et al., 2019) and birds (Marini et al., 2009) will lose a substantial portion of their ranges.

The Future of Cerrado

A detailed spatial plan for the prioritization of conservation efforts in the Cerrado has been developed by the Brazilian Ministry of the Environment (<http://areasprioritarias.mma.gov.br/>), and this map recently has been used in developing conservation plans for both plants (Amaral et al., 2017) and vertebrates (Silvano et al., 2016). In addition, the Critical Ecosystem Partnership Fund has developed a detailed ecosystem profile for the Cerrado, to best guide conservation investment in the region (<https://www.cepf.net/sites/default/files/cerrado-ecosystem-profile-summary-english-revised-2017.pdf>). Thus there is an excellent baseline database and scientifically justified planning information for future conservation actions.

However, the Cerrado is home of 25–30 million people who live mostly in large and mid-size cities. These cities, in turn, depends on the natural and agriculture systems that surround them. Climate change threatens both systems and therefore can have a negative impact on the wellbeing of future generations of people living in the region. Hence, Cerrado requires an adaptation plan that is ambitious enough to transform the way by which human development has occurred across the region. Instead, to follow the traditional frontier development model, in which natural resources are perceived as infinite and focus is on short-term gains, societies should pursue a sustainable development model, in which improvements in biodiversity conservation, agriculture production, and social inclusion are enabled by effective governance. The transition to a sustainable Cerrado requires the following urgent actions: (1) conserve all region's natural vegetation remnants; (2) move current agriculture systems to a more sustainable path, by finding ways to increase significantly the productivity while reducing GHG emissions, soil loss, water consumption and pollution; (3) end poverty; and (4) adopt transparent, effective, and participatory decision-making processes across all government levels, from local to national.

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Caatinga—South America

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Abstract

The Caatinga is a large semi-arid biome located entirely within the northeastern quadrant of Brazil. It is a region with patterns of anomalous precipitation, and with occasional multi-year droughts, which has earned it the label the “Polygon of Drought.” This has affected the adaptations of species within the region as well as the livelihoods of human populations. The major ecosystem types within the Caatinga biome include open canopy thorn scrub woodlands on shallow soils with an abundance of cactus, taller semi-arid forests on sedimentary soils, and tall deciduous and semi-deciduous forests on more nutrient rich substrates. The Caatinga also has a varied topography or small rocky ranges and plateaus. Caatinga biodiversity was once thought to be species poor with low levels of endemism, but recent research has demonstrated a rich flora and fauna with high levels of endemism. The Caatinga, however is highly threatened by poor land use practices and expanding large-scale development, resulting in growing rates of deforestation. This is exacerbated in times of drought, resulting in very low indicators of human development. Although a number of important protected areas currently exist in the Caatinga, they represent a small proportion of the biome and are poorly interconnected.

What is Caatinga?

Caatinga is a natural region that lies in the hinterland of northeastern Brazil (Fig. 1). The term caatinga means “white forest” in Tupi, the language used by the Amerindians that lived in the region (Prado, 2003). Caatinga extends over 900,000 km² and encompasses part of the areas of 10 Brazilian states: Piauí, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia, and Minas Gerais (Silva et al., 2018a,b). The region is surrounded by the Amazon (on the east), Atlantic forest (on the west), and Cerrado (on the south). In the north, Caatinga reaches the Atlantic Ocean. As is common among biomes everywhere, Caatinga is separated from the adjacent terrestrial biomes by transition zones where types of vegetation with distinct ecological requirements can be found side by side (Eiten, 1972).

Caatinga is one of the most highly distinctive natural regions in South America. Based on the range overlaps of their endemic species, it has been recognized as a dispersal center (Muller, 1973), an area of endemism (Cracraft, 1985; Haffer, 1985), a phytogeographic province (Rizzini, 1976), a phytogeographic domain (Queiroz et al., 2018), and a biogeographical province (Cabrera and Willink, 1980; Udvardy, 1975; Morrone, 2014). Caatinga has also been considered as an ecoregion (Olson et al., 2011), a biome (IBGE, 2004), or a morphoclimatic domain (Ab'Saber, 1973) because it has a unique combination of physical and biological features.

The Landscapes of Caatinga

Caatinga is a heterogeneous region where seasonally dry tropical forest and woodlands (STDFWs), gallery forests, wetlands, tropical rain forests, savannas and rupestrian grasslands compose an intricate mosaic (Queiroz et al., 2018). Caatinga's environmental heterogeneity is, in turn, a consequence of the interaction of geomorphological, soil, and climate factors (Andrade-Lima, 1981). Around 71.4% of Caatinga lies on Precambrian crystalline basement, 23.8% on Paleozoic and Mesozoic sedimentary basins, and 4.7% in Quaternary sedimentary basins. Most of Caatinga (42.3%) is formed by peripheral depressions (0–600 m) that are large flattened or undulating surfaces shaped in both crystalline and sedimentary rocks (Cole, 1986). These depressions are separated by plateaus (600–2200 m) that are locally known as “*serras*,” “*planaltos*,” “*tabuleiros*,” “*chapadas*” or “*brejos*” and that represent residual formations of old erosion cycles (Cole, 1986). Sometimes, intermediate and mid-altitude surfaces locally known as “*patamares*” link the depressions with the plateaus. Regional soils are diverse and several types have been described to the region. The most common soil classes according to the Brazilian Soil Classification System (Santos et al., 2018) are Neosols (18.7%), Latosols (17.1%), Argisols (14.1%), and Luvisols (12.8%). Most Caatinga has a semiarid climate, but there are also patches of semi-humid climate due to orographic effects (Nimer, 1989). The average minimum temperature is 14.8 °C (range = 7.6 °C–28.1 °C), the average mean



Fig. 1 The Caatinga biome is restricted to northeastern Brazil.

temperature is 21.9°C (range = 15.6°C – 28.1°C), and the average maximum temperature is 29.7°C (range = 23.0°C – 36.3°C). The average annual rainfall is 1026 mm a year (range = 346 mm/year–1733 mm/year), but 11% of the region receives less than 500 mm/year and 70% receives less than 1000 mm/year. Rainfall is higher from November to April, but it usually is concentrated in 2 or 3 months within this period (Nimer, 1989). The number of dry months varies from six to eleven, with the length of the dry season declining from the region's center to its edges (Nimer, 1989). Caatinga has a high interannual variability in rainfall (sometimes more than 50%), and droughts, defined usually as those years in which the annual rainfall is less than 30% of the average, can sometimes last for years (Sampaio, 1995). These droughts can have devastating effects on both the ecology of the region and the human population, and the region is referred to as the "Polygon of Drought." Periodic droughts exacerbate the poverty of the region and are part of its history, and a frequent theme in the literature and music of northeastern Brazil.

The dominant vegetation in Caatinga is a SDTFW termed locally as "caatingas" (Andrade-Lima, 1981; Prado, 2003) because it shows a wide variation in structural forms ranging from open cactus scrub (mostly on rock outcrops in the driest areas or areas deeply transformed by human activities; Fig. 2) to tall, semi-deciduous forests on moister sites with nutrient-rich soils



Fig. 2 General appearance of the Caatinga landscape, dominated by cacti, thorn scrub vegetation.

(Andrade-Lima, 1981; Queiroz et al., 2018). From a floristic perspective, there are three subgroups of caatingas: (1) crystalline caatingas, (2) sedimentary caatingas, and (3) caatinga forests. The crystalline caatingas are the most widespread, as they cover 73% of the region (Queiroz et al., 2018). They grow on shallow and very stony soils associated with the crystalline basements that do not retain water for a long time (Fig. 3) and have a flora (Fig. 4) associated with other Neotropical SDTFWs (Queiroz et al., 2018). In contrast, the sedimentary caatingas grow on deep, nutrient-poor sandy soils of the sedimentary depressions and are found as islands in three major patches: The Ibiapaba and Araripé plateaus, the tableland surfaces of the Tucano-Jatobá sedimentary basins, and the sandy dunes of the São Francisco valley (Queiroz et al., 2018). The flora of sedimentary caatingas seems to be more recent and associated with other vegetations on sandy soils in eastern South America (Queiroz et al., 2018). These two groups of caatingas have different phenological patterns, as sedimentary caatingas are not so strongly linked with rainfall patterns, and their floras have different biogeographic connections with other South American biomes (Queiroz et al., 2018). The caatinga forests is the third and most distinctive subgroup among caatingas (Prado, 2003). It can be deciduous or semideciduous and is found on nutrient-rich soils derived from limestone rocks along the valleys of the rivers São Francisco e Gurgéia, on the upland Chapada do Araripe, the Potiguar basin, and along the slopes of the high plateaus of the Chapada da Diamantina (Prado, 2003). These forests are 20–30 m tall and dominated by exuberant trees of the genera *Tabebuia*, *Anadenanthera*, *Myracrodunon*, *Cavanillesia*, and *Schinopsis* (Andrade-Lima, 1981; Prado, 2003). Some studies suggest that this type of vegetation was once more widespread across the region and that it was replaced by open physiognomies and woodlands as a consequence of human disturbances (Coimbra-Filho and Câmara, 1996).

In addition to caatingas, patches of other types of vegetation are found in Caatinga and contribute to increase the regional environmental diversity. For instance, wetlands and seasonally flooded grasslands are found along the main rivers (Siqueira Filho, 2012). Gallery forests with carnauba palm (*Copernicia prunifera*) are found in the riverbeds near the crystalline caatingas (Queiroz et al., 2018). Tropical rain forests with strong floristic connections to Atlantic Forest are found along the slopes of Chapada da Diamantina as well as small and isolated plateaus in the states of Pernambuco, Paraíba, and Ceará (Andrade-Lima, 1982). On the



Fig. 3 Example of the dense thorn scrub understory typical of Caatinga (Photo credit: T. Lacher).



Fig. 4 *Cnidoscolus urens*, a thorny and spiny member of the family Euphorbiaceae. Many Caatinga plants.

top of the Chapada da Diamantina, the Araripe Plateau, and small plateau islands within the region, it is possible to find patches of cerrados, the tropical xeromorphic savanna that dominate the extensive plateaus of Central Brazil, Bolivia, and Paraguay (Eiten, 1972). Rupestrine grasslands are restricted to the most ancient geomorphological surfaces of the Chapada da Diamantina and are a vegetation type rich in species and endemism of plant families with unique adaptations that allow them to thrive in very poor soils (Queiroz et al., 2018).

Caatinga is also a region with unique freshwater ecosystems (Silva et al., 2018a,b). The region has a dense river network composed of both perennial and intermittent rivers. Perennial rivers are few, and their headwaters are generally outside the Caatinga (Steffan, 1977). The São Francisco is the largest and most important perennial river in the region, forming a set of unique aquatic ecosystems along its course. In contrast, intermittent rivers, such as Jaguaribe, are the ones that cease to flow every year or at least twice every 5 years (Steffan, 1977). They can experience flash floods and prolonged droughts, both of which act as agents of hydrologic disturbance and have a strong influence on aquatic biological communities (Silva et al., 2018a,b).

The Biodiversity of Caatinga

In the past, the Caatinga biota was thought to be composed mostly of widely distributed species with few being restricted to the region (Mares et al., 1985). However, recent studies have rejected this hypothesis. In fact, the Caatinga harbors an astounding diversity of native species with a high proportion of endemic species (Table 1), making it one of the world's more diverse and unique tropical drylands (Tabarelli et al., 2018).

In a region with so many endemic species, it is difficult to pinpoint a set of flagship species that can be used as symbols for the region's conservation efforts. Nevertheless, Aguiar et al. (2002) proposed two birds and two mammals as flagship species for Caatinga. The two birds are Lear's macaw (*Anodorhynchus leari*) and Spix's macaw (*Cyanopsitta spixii*), both of which are endemic to Caatinga. Lear's macaw is an impressive metallic blue macaw, superficially similar to the hyacinth macaw (*Anodorhynchus hyacinthinus*), but slightly smaller (75 cm long), with a larger head, and lighter in color. This species is known from two colonies at Toca Velha and Serra Branca, south of Raso da Catarina, Bahia (Collar et al., 2019a). Because of intensive recent conservation efforts, the population of this species has increased from 140 in 1994 to 1123 in 2010 (Collar et al., 2019a). As a consequence, it has been downlisted from Critically Endangered to Endangered in the International Union for Nature Conservation (IUCN) Red List.

In contrast with Lear's macaws, Spix's macaws seems to be extinct in wild (Collar et al., 2019b). This small blue macaw (55–57 cm) with pale greenish blue crown and blackish gray bare facial area once lived in the gallery woodlands dominated by caraíba (*Tabebuia caraiba*) along the river São Francisco valley (Collar et al., 2019b). However, because the destruction of its habitat as well as illegal trapping, its population declined fast. When it was rediscovered in nature, its population had only five individuals. The last known wild individual disappeared in 2000 from near Curacá, Bahia (Sick, 1993). The fate of this species depends on a successful introduction of a few captive individuals in nature.

The two species of mammals that can be proposed as flagship species are the rock cavy (*Kerodon rupestris*) and the Brazilian three-banded armadillo (*Tolypeutes tricinctus*). The rock cavy is a large (700 g) rodent endemic to Caatinga that is distantly related to guinea pigs and that occupies rock outcrops where it lives in crevices and forages on foliage (Lacher, 1981; Lacher et al., 1982). With numerous adaptations to its rocky habitat, the rock cavy has many morphological, ecological, and behavioral similarities to the hyraxes and gundis of Africa (Mares and Lacher, 1987). It also climbs well and often forages high in trees. When disturbed, it gives a rapid, trilling alarm call and flees deep into crevices in the boulder piles. The species is heavily hunted but it is considered as least concern by IUCN Red List (Lacher, 1981).

Different from the rock cavy, the Brazilian three-banded armadillo is considered as vulnerable by the IUCN Red List and its populations are declining because of heavy hunting. It was once thought to be extinct, but Silva and Oren (1993) rediscovered populations in tropical deciduous forest remnants in the state of Bahia. Although it has been observed in the Cerrado (Marinho-Filho et al., 1997; Oliveira 1995), it is largely a Caatinga species. This armadillo has the ability to completely roll itself into a tight ball as a defensive posture (Silva and Oren, 1993). Because of that behavior, it was selected to be the mascot of the 2014 Soccer World Cup. In 2015, scientists demanded that the Brazilian government set aside 1000 ha of protected areas in Caatinga for each goal scored in the tournament (Melo et al., 2014). The Associação Caatinga, an important regional conservation organization, carries on a program to protect the species.

Table 1 Number of species and proportion of endemics in Caatinga for selected biological groups.

Groups	Number of species	% Endemic species	Source
Flowering Plants	3150	23.0	Queiroz et al. (2018)
Fishes	386	54.1	Lima et al. (2018)
Amphibians	98	20.4	Garda et al. (2018)
Reptiles	79	30.8	Mesquita et al. (2018)
Birds	548	23.0	Araujo and da Silva (2018)
Mammals	183	28.0	Carmignotto and Astúa (2018)

The biota of Caatinga has been assembled as a consequence of three biogeographic processes: species production, biotic exchange, and regional mass extinction (Araújo and da Silva, 2018). Species production is the origin of species within the region, biotic exchange is the flow of species between regions, and regional mass extinction occurs when many species disappear within a region as a consequence of regional-scale environmental changes. The relative contribution of each one of these processes seems to vary across biological groups. Because of the high proportion of endemic species within these groups, species production is more important in flowering plants (Queiroz et al., 2018), fishes (Lima et al., 2018), amphibians (Garda et al., 2018), and reptiles (Mesquita et al., 2018). In contrast, because many species living in Caatinga have most of their ranges in adjacent regions, biotic exchange seems to be more prevalent among birds (Araújo and da Silva, 2018) and mammals (Carmignotto and Astúa, 2018). The contribution of the regional mass extinction on the present-day composition of the Caatinga's biota needs still to be investigated, but recent studies indicate that this process could be important at least among mammals (Castro et al., 2014). In the past, it was suggested that species endemic to the Caatinga were evolutionarily young and derived from other regions, such as Atlantic Forest or Chaco (Rizzini, 1976; Andrade-Lima, 1981). However, this hypothesis has been rejected by phylogenetic studies using molecular markers (Queiroz et al., 2018). The estimated ages of the endemic species of the Caatinga range from the early Holocene to Mid-Miocene, indicating that species production has been continuous within the region (Tabarelli et al., 2018). In addition, Caatinga endemic species are related to species that live in different South American regions, indicating a complex network of biogeographic relationships for the region and a very fascinating biogeographic history (Araújo and da Silva, 2018; Queiroz et al., 2018).

As important as an understanding of the biogeographical processes that generated the current Caatinga biota is the identification of the ecological processes that help to maintain the current biodiversity of the Caatinga. Among the several factors suggested in the literature, environmental heterogeneity seems to be the most important. A region with high environmental heterogeneity is expected to maintain more species at local and regional scales than a region with less environmental heterogeneity. The Caatinga is heterogeneous from an environmental perspective. For instance, Rodrigues e Silva et al. (2000) recognized at least 135 geo-environmental units and Velloso et al. (2002) recognized nine ecoregions. Although dominated by caatingas, the presence of enclaves of other vegetation types contributes to sustaining a significantly high number of species across the region. For instance, among birds, almost 60% of the species require forests (a habitat that covers less than 15% of the region) for their life cycles (Araújo and da Silva, 2018). The region's environmental heterogeneity shapes the distribution of the species, forming environmental gradients. These gradients, in turn, are fundamental in providing mesic refuges and migratory corridors during the long dry season for several species that are able to move between habitats within landscapes and between landscapes within the region (Silva et al., 2003). Ecological gradients can also facilitate the speciation among some groups of organisms that have low dispersal, and enable the evolution and the maintenance of complex and unique types of plant-animal interactions (Leal et al., 2018).

Threats and Conservation

Human activities have been documented within the Caatinga since at least the Late Pleistocene and Early Holocene (Bueno and Dias, 2015). When the first Europeans disembarked in Brazil in 1500, the indigenous population in the Caatinga was roughly estimated at 100,000 people (Hemming, 1987). At this time, human impacts on the natural ecosystems of the Caatinga were possibly restricted to the patches of humid ecosystems found along the few perennial rivers and on the plateau slopes, as crops were restricted to a few small plots. During the 1600s and 1700s, European colonizers supported by their African slaves slowly colonized the Caatinga from their coastal settlements. By using the major rivers as routes, they slowly opened up space for settlements that had cattle ranching and subsistence agriculture as their major economic drivers (Hemming, 1987). This expansion of the colonizers led to escalating conflicts with the native peoples, who resented their forcible exclusion from ancient hunting and fishing grounds. The clashes eventually led to the annihilation of the native resistance and the relocation of the few survivors to the harshest zones of the region (Puntoni, 2002). Since then, human settlements have spread out across the whole region and set the basis for the modern cities. In 2010, the Caatinga was home to 28.6 million people, and the region had some of Brazil's lowest human development indicators (Silva et al., 2018a,b). The human footprint can be detected everywhere across the region as traces of pastures, agriculture fields, roads, fire, reservoirs, cities, and other human infrastructure have accumulated over time as a palimpsest (Silva and Barbosa, 2018).

Tabarelli et al. (2018) identified three major types of human disturbances in the Caatinga. The first is acute disturbance caused by the rapid conversion of large areas of native vegetation into human-made ecosystems, dominated by roads, reservoirs, and commercial agriculture (Silva and Barbosa, 2018). The second type is chronic disturbance caused by the slow but continuous overexploitation of the native vegetation, such as through establishing slash-and-burn agriculture, collecting firewood, and browsing by livestock (Albuquerque et al., 2018; Melo, 2018). Finally, the third type consists of the introduction of exotic species of plants and animals (Almeida et al., 2015). These three types of disturbance together are leading to an irreversible loss of biodiversity, biomass, and ecological processes that, over time, reduce the provision of critical ecosystem services (e.g., food, freshwater, and firewood) that local human populations need to survive (Silva et al., 2018a,b). The problem is even larger if one considers that one-third of the Caatinga has a high potential for desertification and that all attempts to control the expansion of the existing four desertification nuclei have not been successful (Sá and Angelotti, 2009; Vieira et al., 2015).

Most of the Caatinga currently is covered by anthropogenic rather than natural ecosystems. Silva and Barbosa (2018) combined the impacts of road expansion, fires, as well as native vegetation loss and estimated that 63.3% of the Caatinga is composed of anthropogenically altered ecosystems. Human impact is higher in the humid and more productive ecoregions than among those

ecoregions where climate and nutrient-poor soils have always constrained human occupation (Velloso et al., 2002). Yet, even the ecoregions that are less amenable to humans have more than 40% of their areas disturbed. In general, the distribution of the natural vegetation across the region shows that most of the remnants are becoming small and isolated and that opportunities to protect large and roadless areas within the Caatinga are quickly becoming scarce (Silva and Barbosa, 2018).

Caatinga is one of the few drylands in the world that has a large-scale science-based conservation plan that was designed together with stakeholders (Silva et al., 2003) and that has been updated by using new datasets and modern decision-making methods (Fonseca et al., 2018). In addition, the region has two large and comprehensive conservation initiatives that have been formally recognized by the Brazilian government: (a) the Caatinga Biosphere Reserve designated in 2001 with 19.9 million hectares and (b) the Caatinga Ecological Corridor announced in 2006 with 11.7 million hectares. However, despite all this effort, the Caatinga continues to be poorly protected (Leal et al., 2003). In fact, only 7.4% of the region is within protected areas and most of these protected areas are not properly funded (Oliveira and Bernard, 2017). If national priorities do not change and more protected areas are not added to the regional system, the future of the Caatinga would inadequately rely on a few large national parks and ecological stations that have areas above 50,000 ha. These protected areas are: the National Park Serra das Confusões (823,435 ha), National Park Boqueirão da Onça (347,557 ha), National Park Chapada Diamantina (152,000 ha), National Park Serra da Capivara (100,000 ha), Ecological Station Raso da Catarina (99,772 ha), National Park Catimbau (622,300 ha), National Park Cavernas do Peruaçu (56,800 ha), and State Park Caminho dos Gerais (56,237 ha).

Changing Climatic Conditions

Because of its current interannual rainfall variability, climate is already a major driver of the Caatinga's socio-ecological systems (Marengo et al., 2016). The situation is projected to get worse because scenarios of future climate suggest that the near surface air temperature will increase between 1 °C and 4 °C and rainfall will reduce by about 0.3 mm day⁻¹ by the end of the 21st century (Torres et al., 2018). In addition, the IPCC (2013) projected with medium to high confidence the following climatic stressors over the Caatinga: (1) surface soils are projected to dry out; (2) both annual evapotranspiration and runoff are projected to decrease; (3) days and nights are projected to be warmer; (4) more frequent intense rainfall episodes will be followed by dry and warm periods without rain; and finally, (5) dry spells are projected to be longer with the possibility of triggering droughts. Climate change associated with desertification make Caatinga one of the world's most vulnerable regions to climate change, with potential adverse impacts on its rich biodiversity, water resources (Andrade et al., 2018), and, consequently, its human population (Torres et al., 2018).

The Future of Caatinga

What is the future of the Caatinga? It is hard to project, however the current indicators are not promising. Despite some progress in the last decades, the region still has very low indicators of human development (Silva et al., 2018a,b). Therefore, social inclusion continues to be a regional issue. From an environmental viewpoint, loss of native ecosystems continues at a fast pace, biodiversity conservation policies are still poorly elaborated, and all efforts to constrain the desertification frontiers have not been successful. Projections about the impact of future climate change on the region are grim and the adaptive capacity available at the regional level to face such changes is limited. A better future for the Caatinga requires the adoption of a development model in which environmental conservation, social inclusion, economic prosperity and good governance go together (Sachs, 2015). A shift toward this model demands visionary leaders, persistence, creativity, innovative science and technology, consistent financial and political support, and a robust and evident connection between the improvement of human livelihoods and the conservation of natural landscapes (Leal et al., 2005). These basic enabling conditions for change have never been in place during the last several decades and, unfortunately, are unlikely to be put in place in the near future.

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Grasslands and Open Savannas of the Dry Chaco

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Abstract

The Dry Chaco is mostly known as a forested ecosystem. However it includes natural grasslands, savannas, scrublands, and wetlands. With one of the highest global deforestation rates in the last two decades and only 12% of the area protected, the concern about land-use change in this ecoregion has raised exponentially; but conservation initiatives developed in last years almost exclusively targeted forests whereas natural grasslands and savannas remain as neglected ecosystem within scientific and governmental agendas. While currently the distribution of natural grassland and savanna area encompasses over 20,000 km², historical records and spatial models indicate that natural grassland and savannas were more widespread in pre-European era. Two main reasons drove this reduction in natural grasslands and savannas: woody encroachment by fire suppression and overgrazing, and conversion to agriculture and implanted pastures. In this article, through a combination of analyzes and bibliographic revisions, we describe biotic and abiotic components of natural grassland and savannas of the Dry Chaco. We also present the current distribution and conservation status of these ecosystems, and describe the process of change and the ecological consequences for biogeochemical cycles and biologic interactions. To provide basis for management, we estimate current grazing stocking rates on natural grasslands and savannas of Argentine Dry Chaco and we propose an alternative approach to sustainably intensify the use of these ecosystems and improve cattle rancher livelihoods. Despite the existent knowledge about natural grasslands and savannas in the region, we believe that is necessary to motivate the scientific community and national institutions to increase efforts to reconcile the restoration and conservation of these particular rangelands.

Introduction

The Dry Chaco is, for the most part, a vast sedimentary plain, essentially modeled by the action of rivers that cross it in a northwest-southeast direction. Expanding from 33.8 to 22°S and from 67.5 to 59.2°W, this ecoregion is mostly known for its forests. However,

it includes natural grasslands, savannas, scrublands, and wetlands (Adamoli et al., 1990; Navarro et al., 2006). With one of the highest global deforestation rates in the last two decades (Baumann et al., 2016; Grau et al., 2005), and only 12% of the area protected, the concern about land-use change has raised exponentially, and some governmental initiatives for conservation have been taken, such as the promotion of a national forest conservation law in Argentina. However, agriculture does not only expand into forests but also into natural grasslands and savannas with less energy to plow up and convert them, representing a major conservation challenge for the scientific and governmental agendas (Grau et al., 2014).

Albeit the introduction of European livestock into South America started in the 16th century (Bishko, 1952; Kunst et al., 2003), it was not until the beginning of the 20th century that cattle ranching began to spread into the Chaco rangelands (Adamoli et al., 1990). By 1930, the excessive stocking rate had degraded the herbaceous forage resources, and started its own decay (Morello and Saravia Toledo, 1959). As with other semi-arid regions of the world (Smith, 1899; Griffiths, 1904; Wooton, 1908), such overabundant cattle for many years favored scrubland expansion while herbaceous cover and productivity decreased in natural grasslands and savannas.

Domestic livestock-driven degradation of semiarid rangelands remains controversial in climates with high annual rainfall variability (von Wehrden et al., 2012) as some areas of the Dry Chaco. But, a sum of evidence, including historic registers, town names, and distributions models, indicates that the extension of natural grasslands and savannas was much larger prior to domestic livestock expansion in the early 20th century (Grau et al., 2014; Kunst et al., 2003). The degradation process of natural grasslands could have been reinforced by the sedentary character of the main cattle grazing production system in that period: the “puestos,” in which cattle is managed centered around a water source (commonly near the center of ranch) shaping a 70–150 km² “piospheres,” and without transhumance in periods of fodder shortage (Adamoli et al., 1990) contributing to the overgrazing process.

There are still many information gaps at different scales in natural grasslands and savannas of the Dry Chaco. For example, we do not know the pre-European distribution of these natural rangelands, since such knowledge would require detailed paleo-ecological research inexistent to date. Neither the current state of degradation, nor even knowledge of the physiognomy and distribution of the “old-growth” grasslands (see Veldman et al., 2015), which could represent the most valuable information in terms of conservation, is known. The role of these ecosystems in biological interactions, biogeochemical cycles and the provision of ecosystem services has been superficially explored to date. The sum of these information gaps represents the first obstacle to determine conservation areas and apply restoration practices in these natural areas with the least impacts on the well-being of local communities.

Currently Dry Chaco presents multiple challenges, with large undeveloped reserves of natural resources (principally native forest), widespread poverty, extensive livestock supporting the subsistence of thousands of small farmers, and one of the most active agricultural frontiers with the associated conflicts for land tenure, nature conservation, and regional development. This chapter revises the existent knowledge about natural grasslands and savannas in the region, as a way to motivate the scientific community to increase efforts in understand these ecosystems to reconcile the restoration, conservation and sustainable development. Although we aim at addressing the entire ecoregion in this article, the discussed analyses mostly involve the Argentine Dry Chaco (which encompasses 69% of the region), due to the paucity of information for the Bolivian and Paraguayan areas.

Specifically, in this article we (1) describe the current distribution and typologies of grasslands of the Dry Chaco; (2) discuss the recent and historical drivers that resulted in present-day patterns; (3) describe the soils, climate, and floristic composition of natural savannas; (4) discuss the current drivers of natural grassland transformations, their management, and their impact in ecosystem services; (5) estimate the cattle stock grazing for the Argentinean part of the region to explore opportunities for sustainable intensification to conserve these ecosystems; and (6) describe the role of native grasslands for biodiversity conservation in relation to the current conservation status of the region.

Natural Grassland and Savannas Typologies and Distribution

Using Landsat TM and ETM+ image composites and identifying different spectral signatures (Baumann et al., 2016) we mapped natural grasslands in the entire Dry Chaco (i.e., including Argentina, Bolivia and Paraguay) (Fig. 1). However, it was not possible to discriminate among the different types mentioned below, as well as to discriminate old-growth natural grassland and savannas (Veldman et al., 2015) from grasslands generated in post agriculture early successional stages of vegetation. Based on this analysis, we estimate that natural grasslands area extends over 20,369 km² (Table 1).

The majority of natural grasslands and savannas are located in the southeast limit of the region, towards drier and colder conditions in Cordoba, and southern Santiago del Estero provinces, representing near 60% of the total. In Bolivia and Paraguay, grasslands are more scattered than in Argentina. In the west of Santa Cruz (Bolivia) exist a concentration of edaphic natural grasslands associated with sandy soils representing near 10% of the total area of the region.

We briefly describe four main types of grasslands and savannas of the Dry Chaco region and mapped the distribution of natural grassland and savannas for the entire area (Fig. 1). More detailed descriptions of vegetation physiognomies can be found for Bolivian Chaco (Navarro and Fuentes, 1999), Paraguayan Chaco (Navarro et al., 2006), and for the Argentinean Dry Chaco region (Morello et al., 2013). Based on these, we identify the following typologies:

1. Grassland and savannas located in lowlands close to rivers and permanent waters bodies; typically with poorly drained clay, high water table and recurrent flooding, often with high salt content. These grasslands and savannas are mainly concentrated in the Dulce river basin or wetlands as Bañado del Izozog or Bañado de la Estrella. These areas are not suitable for agriculture and are

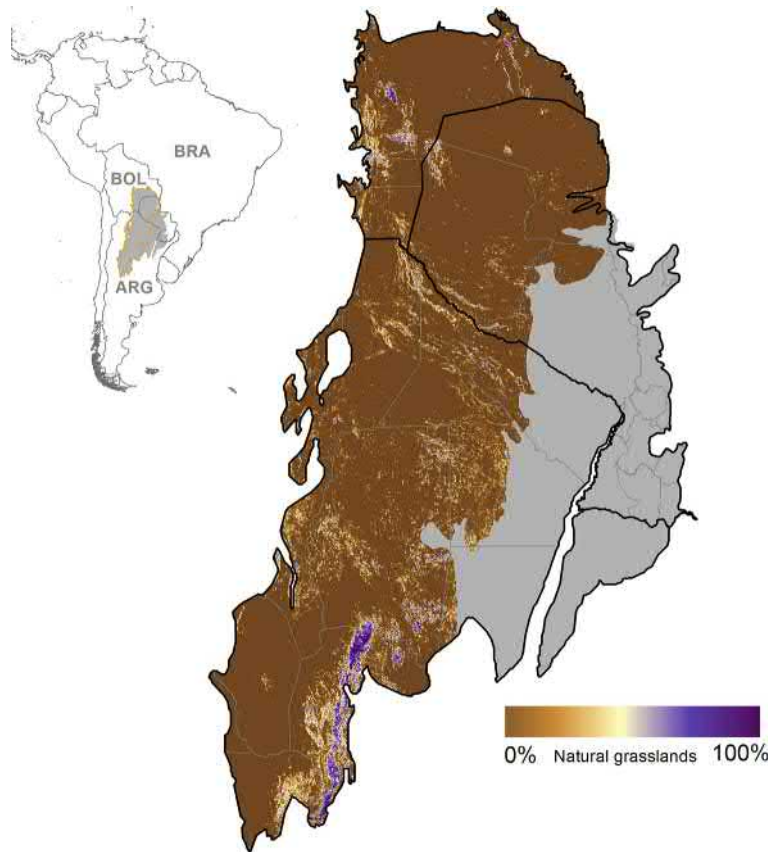


Fig. 1 Current distribution of natural grasslands and savannas in the Dry Chaco region (Argentina, Bolivia and Paraguay). In gray, the ecoregion of Humid Chaco.

Table 1 Estimated extension of natural grasslands by first order national subdivision for 2013.

Country	First order national subdivision	Natural grassland area (km ²)	Relative extension (%)
Argentina 16,595 km ² (81.5%)	Córdoba	7040	34.6
	Santiago del Estero	3945	19.4
	Chaco	1228	6.0
	Salta	1134	5.6
	San Luis	1049	5.1
	Formosa	829	4.1
	Catamarca	511	2.5
	Tucuman	367	1.8
	Santa Fe	337	1.6
	Jujuy	78	0.4
	La Rioja	74	0.4
	San Juan	2	0.0
Bolivia 2548 km ² (12.5%)	Santa Cruz	2033	10
	Chuquisaca	261	1.2
	Tarija	253	1.2
Paraguay 1226 km ² (6%)	Boquerón	862	4.2
	Alto Paraguay	182	0.9
	Presidente Hayes	182	0.9
Total		20,368	

mainly used by extensive traditional grazing livestock. In the area comprising northern Argentina and southwestern Paraguay and southern Bolivia, they include palm savannas dominated by *Trithrinax schizophylla* and *Copernicia alba* as tree components (Fig. 2).

2. Edaphic grassland and savannas. They are situated in low fertility sandy soils associated with ancient river meanders ("paleo-cauces"). They are found in the northwest of the Bolivian Chaco; and Argentina (center of Santiago del Estero province) and the



Fig. 2 Poor drained and regular flooded Savanna with a *Copernicia* palm woody component (Formosa province, Argentina). Photo by courtesy of Alejandro Brown.

area of influence of the Juramento, Bermejo and Pilcomayo rivers (Salta and Formosa provinces). They are also used mostly for low-intensity grazing. Recurrent fires maintain the herbaceous cover of grasslands dominated by *Elionurus muticus*, with isolated trees of the genera *Prosopis* ("Algarrobos") and *Aspidosperma* ("Quebrachos blancos").

3. Mesic grasslands and savannas. Commonly located in deep and fertile soils. They are concentrated in the east of Santiago del Estero province and west of Chaco provinces, Argentina. To persist, they need recurrent fires generating in a positive feedback associated with high flammability and post-fire resprouting capacity of the dominant grasses. Given their high agriculture potential, most of them have been converted into croplands and implanted pastures.
4. Montane grasslands located in the south and western borders of the ecoregion (Cordoba and San Luis province in Argentina; Sierra San Miguel in Bolivia). Commonly dominated by *Festuca hieronymi*, they can alternate with short grasslands in shallow rocky soils patches. These grasslands are used in extensive cattle ranching, as topography limits croplands in these fertile soils. In the Cordoba provinces they have also been replaced for pine plantations in extensive areas.

Historic Land-Use Changes Affected Dry Chaco Grassland Present Day Distribution

In 1950, the geographer Carl Sauer claimed that all the world's grasslands had coevolved with humans and fire for some 200,000 years (Sayre et al., 2017). In South America, before the expansion of European land uses, descriptions indicate regular use of fire by indigenous communities to hunt and to preserve open areas (Jolis, 1972).

The Chaco was not the exception, and indigenous uses likely persisted for most the 19th century, since the region was mostly outside the colonial influence (Métraux, 1946). However, with the introduction of cattle following the colonization by "Criollos" people in Argentina and Mennonites in Paraguay and Bolivia, a process of overgrazing and depletion of fine fuel in grasslands changed fire regimes and reduced herbaceous cover, and shrub encroachment spread over natural grasslands and savannas. Such processes took place mostly from 1890 to 1950, according to different authors (de Maurice et al., 1919; Muello, 1926; Morello and Saravia Toledo, 1959). The restoration of herbaceous productivity began to be done through the implantation of exotic and more productive pastures. For example, in the early 1950s, Robert Unruh, an agronomy engineer, introduced the first exotic grass (*Pennisetum ciliaris*) in the Paraguayan Dry Chaco, starting the expansion of implanted pastures in the region (Glatzle, 1999). In Bolivia, the British Mission in Tropical Agriculture started the shift from natural grasslands to implanted pastures, introducing many of the most successful cultivated pastures in the 1970s (Killeen et al., 2008). In the montane grasslands of Cordoba natural grasslands have been used for cattle ranching for at least 400 years (Díaz et al., 1994), with well-documented processes of overgrazing and soil erosion (Menghi et al., 1978).

The historical importance of natural grasslands and savannas in the Dry Chaco has been analyzed particularly for northern Argentina by Grau et al. (2014), combining approaches as historical assessments, environmental modeling, and toponyms that refer to natural grassland. Such analyses consistently shows that, in the past, many sectors of the northern Argentine Dry Chaco (mainly towards the limit between Formosa and Salta provinces and the east sector, covering areas of Chaco, Formosa and Santiago del Estero provinces) likely included extensive areas of natural grasslands and savannas as part of the pre European landscape.

Environmental Characteristics

Climate and Soils

In the Dry Chaco, the presence of pronounced climatic gradients together with heterogeneous geomorphological characteristics, generate a diversity of environments reflected in vegetation physiognomies (dry and flooded savannas, estuaries, marshes, salters, and a great extension and diversity of forests and shrublands) (Adamoli et al., 1990). Despite such heterogeneity, the Dry Chaco plains host one of the largest global reserves of fertile soils that are still uncultivated (Lambin et al., 2013), which in combination with flat terrain and low population density facilitates the expansion of large-scale mechanized agriculture.

In Koppen's classification for South America (Peel et al. 2007), the Dry Chaco region is included within three climatic regions: subtropical humid, warm semiarid, and cold semiarid. Subtropical humid host the South American "heat pole," defined as the territory where absolute maximums exceed 47 °C (e.g., Rivadavia district in Argentina or 44 °C in Filadelfia department in Paraguay). In the southern portion of the region, mean annual temperatures range from 23 °C to 18 °C (in La Rioja and San Luis), with absolute minimum temperatures as low as −10 °C/−15 °C (GTZ, 2006 Atlas Gran Chaco). Inter-annual rainfall is highly variable and occurs mainly during the warmer months, and about 80% is concentrated between October and March (Capitanelli, 1979). However, in years during the "El niño" phase of the climatic southern oscillation, autumns and winters tend to be rainy (Glatzle, 1999). Rainfall ranges from 800 mm to 200–300 mm per year. The wettest areas are located in eastern sector, close to the Humid Chaco, and in the western sector in transition with the Yungas ecoregion; and driest areas are located towards the south, in San Luis and La Rioja provinces (Boletta, 1988).

All the permanent fluvial systems, such as Pilcomayo, Bermejo, Juramento-Salado and Salí-Dulce, are allochthonous; i.e., they do not receive affluent in their journey through the ecoregion (Burkart et al., 1999). There are at least two important intermittent rivers for the subfluvial flows, the Del Valle and the Dorado. With the exception of these rivers, permanent water bodies are strange in the Dry Chaco, constituting the principal limitation to rural population and livestock (Glatzle, 1999). The shallow subterranean water is commonly briny, for which rainwater harvesting constitutes a key technology in the region (Magliano et al., 2015).

The Dry Chaco region lies in a structural environment of sedimentary basin, and as a unit of relief it transcends regional boundaries and extends between the crystalline massif of Brasilia, and the Andes mountain range. The behavior of the sedimentary basin is governed by a tendency to sink, at very slow speeds, but continued from the Paleozoic until today which has led it to remain depressed with respect to its peripheral areas, and to receive as sediments the eroded materials of those. With exceptions of mountains in the south and northwestern borders (including mountain ranges up to 2000 m.a.s.l.), topography is mostly flat, and elevation rarely exceeds 200 m.a.s.l., in a gentle regional slope from northwest to southeast (Moretti et al., 2018). In the region there is a diversity of parental materials due to different areas of contribution and sedimentary processes, which determined the composition and particle size in soils. However, the dominant materials are fluvial sediments, and to a lesser extent area, lacustrine and eolian (Moretti et al., 2018).

The dominant order soils are Mollisols and Alfisols; and to a lesser extent, Entisol, Inceptisol and Aridisol (Moretti et al., 2018; SAGYP-INTA, 1990). A huge proportion of soils has moderate to well-developed profiles. Mollisols are mostly developed from loess sediments. They have thick surface A horizons rich in organic matter, and show varying degrees of development in accordance with drainage conditions and their moisture regimen: the presence of an argillic subsurface horizons (Bt) (Argiustoll or Argiudoll) in the humid areas, but in slightly drier areas dominate Haplustoll (A- AC-C or incipient Bw). In this situation accumulations of calcium carbonates in depth are common (Ck). The Alfisols are present in the plains, and they were developed from fine-textured materials, generally associated with the original forest and shrub vegetation. They are deep soils with thick clayey Bt horizons. In general, the soils of the region have high percentages of base saturation, neutral to basic pH and medium values of CEC, and the mottles and gley features are common.

Floristic Composition and Diversity

In poorly drained and regularly flooded grassland and savannas, the woody stratum is commonly dominated by the presences of *Prosopis ruscifolia*, finding also species such as *Bulnesia bonariensis* or *Bulnesia sarmientoi*, *Capparis retusa* or *Capparis tweddiana* and *Acacia cavens* or *Acacia monacantha*, *Loncocharpus fluvialis*, *Tabebuia nodosa*, *Parkinsonia aculeata* and palms such as *Trithrinax schizophylla* or *Copernicia alba* (Fig. 2). The herbaceous stratum is dominated by the grasses *Cenchrus pilcomayensis*, *Schizachyrium condensatus*, *Sporobolus phleoides* and *Heteropogon contortus*; and other common herbaceous species of the genus *Eupatorium* (Asteraceae) and *Solanum* (Solanaceae). Halophytic vegetation appears in soils with high level of salt, such as the floodplain of the lower Dulce river, and it is mainly represented by *Allenrolfea vaginata*, *Atriplex* spp., *Stetsonia coryne*, *Prosopis ruscifolia*, *Maytenus vitis-idea*, and *Spartina argentinensis*.

In edaphic natural grassland and savannas (Fig. 3), grasses are dominated by *Elionorus muticus* (syn. *Aibe*, *Espartillo* or *Paja amarga*), which can reach 30–90% of grass cover. These species are very flammable, with terpenes in foliage that reach maximum concentration in spring, in coincidence with environmental conditions predisposing to fires in the region (Bravo et al., 2001a; Hess et al., 2007). Bucher (1982) defined these landscapes as pyrogenic savannas. *Pennisetum frutescens*, *Heteropogon contortus*, *Pappophorum pappiferum*, *Digitaria californica*, *Schizachyrium tenerum*, *Trichloris pluriflora*, *Bothriochloa laguroides* are other grass species of pyrogenic savannas, and the later three have high tolerance to fires due to survival of underground parts and high re-sprouting capacity. Some herbaceous *Fabaceae* species, such as *Rynchosia senna* and *Indigofera parodiana*, enhance grassland forage potential due to nitrogen content. *Asteraceae* species, such as *Bacharis pingraea* and *Baccharis trimera* are common in *E. muticus* savannas; and fires



Fig. 3 Edaphic savanna in lowlands of Dry Chaco (Northwest of Santiago del Estero, Argentina). Photo by courtesy of Sandra Bravo.

can promote the recruitment of rare species, such as *Dimerostemma hieronymi*. Rhizomatous and perennial species vegetate successfully in these disturbed environments, reestablishing through underground organs. *Lippia turbinata*, *Aloysia gratissima*, and *Lantana* sp. are *Verbenaceae* species containing aromatic components that can feedback fire recurrence, increasing grassland flammability. Isolated trees of *Aspidosperma quebracho-blanco*, *Prosopis nigra*, *Prosopis kuntzei* and small shrubby patches of *Vachellia aroma*, *Schinus bumeloides*, *Schinus fasciculatus* and *Celtis ehrenbergiana* are scattered across these savannas. In Bolivia appear *Schinopsis cornuta* trees.

In mesic grassland with deep and fertile soils (Fig. 4), herbaceous strata are dominated by the Poaceae species *Trichloris crinita*, *Trichloris pluriflora*, *Gouinia paraguariensis*, *Gouinia latifolia*, *Setaria argentina*, *Setaria gracilis*, *Digitaria sanguinalis*, *Pappophorum pappiferum*, *Pappophorum mucronulatum* (Herrera et al., 2003). *Acacia caven*, *Senegalia gilliesii*, *Larrea divaricata*, *Celtis ehrenbergiana* and *Condalia microphylla* are the most common woody invaders in these grasslands (Cabido et al., 2018).

In the montane environments, pure grasslands are rare and dominated by C4 species below 1000 m.a.s.l. Above this elevation ground cover dominance turns towards C3 species up to close to 2000 m.a.s.l. (Cabido et al., 1997, 1998) and grasslands become a common physiognomy. As altitude increases and temperature decreases, grasses of the genera *Nassella* and *Festuca* take over the landscape from 1000 to 1850 m.a.s.l. The most common physiognomy is *Festuca hieronymi* tussock communities that alternate with short grasslands and grazing lawns (Fig. 5). Short grasslands are found in shallow, rocky and dry soil patches. Grasses *Nassella* spp., *Aristida spagazzinii*, *Schizachyrium spicatum*, *Eustachys retusa* and forbs *Dichondra sericea*, *Margyricarpus pinnatus*, *Acalypha communis*, *Baccharis* spp., *Galactia glaucophylla*, *Lucilia acutifolia* are common. Grazing lawns are found in terrain concavities with poor drainage. These are the flattest areas in the landscape and are crossed by permanent or temporal water courses, both factors that improves habitat condition for cattle, increasing grazing pressure. *Paspalum notatum*, *P. dilatatum*, *Steinchis mahians*, *Sporobolus indicus*, *Axonopus fissifolius*, *Cyperus* spp., *Bulbostylis* spp. and *Trifolium repens* thrive here. Short grasslands and lawns are found in the extremes of both soil depth and soil moisture gradients, in between the landscape is dominated by *Festuca hieronymi* tussocks, accompanied by climbing or shade tolerant species such as *Cologania broussonetii*, *Tragia geraniifolia*, *Oxalis conorrhiza*, *Chevreulia sarmentosa*, *Pfaffia gnaphalioides*, *Eryngium horridum* and *Dichondra microcalyx* among others.

Ecosystem Management and Properties

Rangelands provide multiple ecosystem services, but only few of them have market value (Sala and Paruelo, 1997). Further, the demands and perceptions on these ecosystem services vary among stakeholders (Lamarque et al., 2011), and geographical regions (Anadon et al., 2014). In the case of the Chaco's ranchers, the use of herbaceous biomass as fodder constitutes the main demand.



Fig. 4 Mesic grassland in deep and fertile soil (Northwest of Santiago del Estero province, Argentina). Photo by courtesy of Sandra Bravo.



Fig. 5 Montane grassland dominated by *Festuca hieronymi* (Northern Cordoba province, Argentina, 1600 m.a.s.l.). Photo by courtesy of Torcuato Tessi.

When agriculture is possible, as in the mesic and mountain natural grasslands, the major threat to such ecosystems has been an accelerated conversion to crops in mesic grasslands or to pine plantations in mountain grasslands. However, most natural grassland and savannas of the Dry Chaco have undergone two major transformation processes: the degradation by overgrazing and the increasing of productivity with exotic grasses. Both processes probably have been propelled by the demand for herbaceous forage and resulted in changes in ecosystem structure and function. Below, we discuss the patterns emerging from the local literature, and contrast them with global patterns described in international rangeland literature. In addition, we highlight regional information gaps and outline an avenue to restoration of these singular ecosystems.

In natural grasslands and savannas of the Dry Chaco, differences in vegetation structure and functionality are driven by hierarchically organized factors, including climate, topography, soil development and textures. However, these differences are blurred by past vegetation management, principally carrying capacity and disturbances regimes (Kunst et al., 2006).

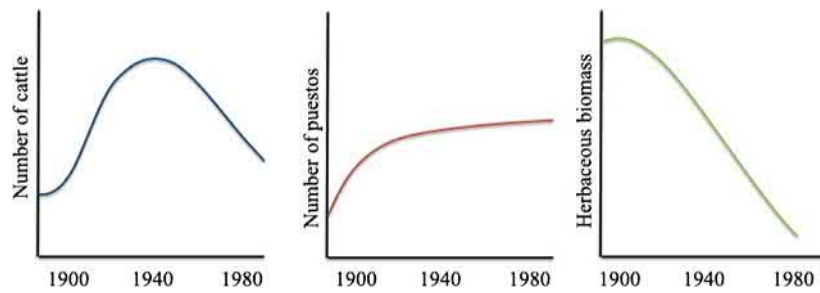


Fig. 6 Cattle, puestos and herbaceous biomass dynamic during the 20th century. Adapted from Adamoli, J., Sennhauser, E., Acero, J.M., Rescia A., 1990. Stress and disturbance: Vegetation dynamics in the Dry Chaco region of Argentina. *Journal of Biogeography* 17, 147–156.

Mismanagement of carrying capacity often leads to an increase in woody species (Fig. 6) (Adamoli et al., 1990; Bucher and Huszar, 1999; Kunst et al., 2006). Woody encroachment has been described as a global phenomenon (Sala and Maestre, 2014), occurring at similar rates across different continents (0.1–1.1% of cover/year) (Barger et al., 2011; Stevens et al., 2017), but faster in rangelands with high rainfall variability, as in the case of the Chaco, as the resulting lower predictability makes optimization of the carrying capacity more difficult (Kiage, 2013). Sedentary pastoralism (as opposed to transhumance strategies) has been mentioned as a sociological driver of rangeland degradation worldwide (Sayre et al., 2017). In the Dry Chaco rangelands, particularly in areas with limited bodies of water, sedentary pastoralism has been a predominant system across different scales of cattle ranching systems: smallholders in puestos, with the establishment of a ranch near a water body; and large scale producers with fences and different grazing managements. In addition, an increase of fire frequency from the 1970s and the resulting nitrogen volatilization (Archer and Predick, 2014) and increased atmospheric CO₂ might also be drivers of the increase of woody cover (Grau et al., 2014).

With the aim of restoring herbaceous productivity, active woody encroachment controls such as prescribed fire and mechanical controls have been used in the region (Blanco et al., 2005; Kunst et al., 2012; Ledesma et al., 2018). These practices commonly include the seeding of exotic C4 grasses: *Megathyrsus maximum* in the wettest areas, *Pennisetum ciliare* in the driest areas (Houspannosian et al., 2016), or *Chloris gayana* in halomorphic soils. Despite their similar physiological pathway (i.e., C4, as with many native grasses), exotic grasses often become dominants in basal cover, multiplying up to four times grassland productivity (Blanco et al., 2005; Kunst et al., 2012), but reducing biodiversity in the herbaceous community. This increase of productivity by a monodominant species implies a stronger phenological seasonality than multispecies natural grasslands leading to changes in ecosystem functionality and in some cases constituting “novel” ecosystems (Hobbs et al., 2009).

The consequences of the mentioned replacement for biogeochemical cycles and biological interactions are understudied but potentially important aspects that should be addressed. For example, Macchi et al. (2013) found characteristic bird assemblages in natural grasslands that differed from that found in *Megathyrsus* pastures. However, the interaction of wild primary consumers (i.e., mammals and insects) needs to be much better understood. While carbon losses in soil storage by woody encroachment in natural grasslands and savannas are a process documented at global scale for rangelands (Eldridge et al., 2011), is a poorly understood process in the Chaco.

Ecosystem degradation or restoration are context specific and non-linear processes in rangelands, making difficult general management decisions. In contrast, adaptive management practices to restoring herbaceous productivity while maintaining a broad set of ecosystem services should be carried out contemplating differences in ecological sites, production systems and socioeconomic characteristics across different grasslands typologies of Dry Chaco.

State and transitions models plus the definition of ecological sites has been adopted in the northwest of Santiago del Estero province in Chaco region (Kunst et al., 2006) and should be considered as a promising framework for tackling rehabilitation of natural grasslands and savannas with less impacts in biodiversity while still maintaining social and economic values (Fig. 7). To make a regional assessment of the states of the grassland and savannas of the region, the map generated in this article (Fig. 1), in combination with soil maps and vegetation surveys and field validations, could be helpful in the evaluation of the state of degradation in different ecological sites of the region (Bestelmeyer et al., 2009). The next step should be to elucidate the management practices or the intrinsic conditions that drive the changes of states with respect to the references sites across the diversity of natural grassland and savanna types. Finally, it is necessary to monitor effects of restoration and management practices (including fire and mechanical woody control, and different stocking rates) on biodiversity and productivity. Participatory approaches among stakeholders could make a more effective and integrated assessing and monitoring regime for a large region such as the Dry Chaco, as occur in other regions as in United States rangelands where this approach is improving the capacity to make regional assessments (Bestelmeyer et al., 2017).

Conservation and restoration initiatives should also match with economic incentives for ranchers. Alternatives include subsidies for meat or milk produced in these natural grasslands and savannas, tax reductions, certification schemes to facilitate ecosystem stewardship to conserve multiple ecosystem services while they are still being economically productive. The increase in the awareness of the variety of ecosystem services provided by these rangelands would help for the conservation of these ecosystems. For example, the partial replacement of montane grasslands by pine plantations in Córdoba province has been affecting the magnitude and temporal distribution of stream and river flows, with the water yield in afforested watersheds being 48% less than in

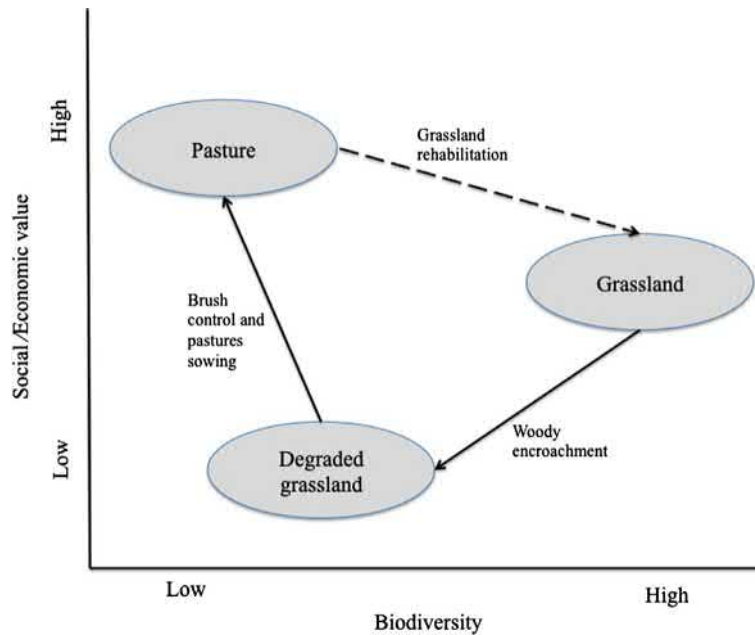


Fig. 7 The common transitions of natural grasslands in Dry Chaco and their relation with biodiversity and social economic value. In dotted lines is the unusual transition of rehabilitation.

grassland watersheds (Jobbágy et al., 2013). In the end, the principles of rangeland management would be more appropriately portrayed as those of the science of managing trade-offs among ecosystem services, and negotiating among stakeholders with competing interests. Thus, as Dry Chaco natural grasslands and savannas will become more valued as singular ecosystems and suppliers of broad ecosystems services for the society, interest on its research and conservation will increase (Fig. 7).

Fire Regime

Fire is one of the main disturbances in Dry Chaco grasslands and savannas. The fire regime (i.e., extent, frequency, severity and intensity) defines the role that fire plays in the ecosystem, affecting soil and plants. The fire season in Chaco region coincides with the prolonged dry season between April and October. Studies about historical fire regimes in grasslands and savannas of the region are scarce, due to the absence of fire records. However, paleo-environmental evidences suggest the natural occurrence of fire events at least over the last 4500 years, with fluctuations in their frequency and intensity related to climatic changes (Di Lello and Linscoug, 2018; Linscoug, 2016).

Under current environmental conditions, grasslands and savannas dominated by natural grass can produce 1000–6000 kg DM ha⁻¹, depending on growing season rainfall. These loads of fine fuels can generate medium to high intensity fire events, with flame height reaching three meters (Kunst and Bravo, 2003). The positive association between fine fuel availability, fuel desiccation, and fire severity was confirmed in manipulative studies using experimental burns and controlled fine fuel loads in Chaco environments (Bravo et al., 2014; Ledesma et al., 2018). Higher fine fuel loads, low moisture content, and higher temperatures during the end of the fire season generate more severe fires. Most fires are concentrated in open areas managed for livestock, where fires are intentionally set with the aims of promoting palatable grass regrowth and woody encroachment control. The ecosystem stresses of overgrazing, excessive use of fires (and a consequent nitrogen volatilization), and droughts facilitate woody encroachment with significant losses in biodiversity and forage productivity both for wild and domestic herbivores.

Historical dendroecology descriptions of fire regimes indicate that water availability in the previous growing season, and subsequent fuel desiccation, controlled fire frequency and extension and resulted in a mean fire interval (MFI) of 3.3 years over the 1925–2000 period with a significant increase in fire frequency from the 1970 decade, attributed to greater water availability at the regional level (Bravo et al., 2010). Before 1970, mean annual precipitation was 496 mm and MFI was 5.63 years. An increase in ~100 mm above such mean annual precipitation reduced MFI to 2 years, and more extensive fires occurred. Other dendroecological studies using fire scar height as an indicator of fire severity indicate that fires were more severe after 1970, and fires scars in trees were identified up to 4.30 m heights (Bravo et al., 2001a,b). These historic data suggest a high frequency fire regime of medium to high severity occurring in the last several decades in the Dry Chaco.

Fires usually increase herbaceous species diversity in natural grasslands and savannas during the 3–4 years after fire, when natural grasslands and savannas gradually recover their initial biodiversity (Kunst et al., 2003). The date of fire occurrence can modify its effect on herbaceous biodiversity, due to pre and post fire environmental conditions and species phenological status.

Experimental burns at the mid-fire season (June to July) generated higher diversity than during early (April to May) or late (October) fires, probably due to better post fire environmental conditions close to spring. Late experimental burns are usually of high severity; thus, prescribed burns at the mid-fire season could be desirable to restore herbaceous species diversity in Chaco natural grasslands and savannas.

Isolated trees of *Aspidosperma quebracho-blanco*, *Prosopis nigra*, *Prosopis kuntzei*, or small shrubby patches of *Vachellia aroma*, *Schinus bumeloides* and *Celtis ehrenbergiana* are scattered across these savannas. The effects of fires on the tree components of Chaco savannas depend on species adaptations and regeneration strategies. Traits such as bark thickness, bud bank size, and reproductive mature age determine woody species maintenance in savannas. For example, *A. quebracho-blanco* is one of the most fire-resistant tree species in Chaco savannas, due to its thick bark (Bravo et al., 2008). Fabaceae species such as *Prosopis nigra*, *P. kuntzei*, *Vachellia aroma*, and *Schinus* sp., among others, have an important aerial bud bank, which allows these species to resprout from aerial organs after low-intensity fire events. Certain species also exhibit buds in underground organs, and can thus reestablish after high-intensity fires through basal resprouts (Bravo et al., 2014; Ledesma et al., 2018). The maintenance of tree habits in these species depends on bark thickness increase rate, and on the fire intervals in natural grasslands or savannas (Bravo et al., 2018).

Assessing the Role of Natural Grasslands in Cattle Grazing, and Exploring Sustainable Intensification Opportunities

Assessing cattle stock rates that can graze in natural grassland and savannas is an initial step to design restoration processes on natural grasslands and savannas with lower impacts on ranchers' livelihoods. At a regional scale, natural grasslands and savannas do not seem to be crucial for cattle diet, since their currently extension is $\sim 20,000 \text{ km}^2$ (less than 0.5% of the region). With an average productivity of $3500 \text{ kg ha}^{-1} \text{ year}^{-1}$ of DM, the total share of natural grasslands could be enough to feed 2 millions of animal unit equivalents ($3600 \text{ kg of DM year}^{-1} \cdot \text{a.u.}^{-1}$, this is an average of c. 1 cattle per hectare). This amount could be enough to satisfy the requirements of 15% of the total stock of the entire Dry Chaco (around 12 million of cattle heads for Argentina, Paraguay and Bolivia). However, this rough number does not reflect diversity in herbaceous productivity or cattle management, and analyses at farm level could be key to understanding the role of these ecosystems in ranchers' livelihoods. In this section, we explore for the Argentinean Dry Chaco, the stocking rate of natural grasslands and savannas and simulate different scenarios of beef production exploring the possibility of sustainable intensification of cattle ranching.

Cattle Grazing in Natural Grasslands and Savannas

We estimate how much cattle can graze in natural grasslands and savannas, exploring the cattle density in these ecosystems for the Argentinean Dry Chaco (80% of Dry Chaco natural grassland and savannas), where we have more detailed information. This rough estimate does not reflect the real current use by ranchers, the state of degradations, nor the role of natural grasslands in relation to other components of the productive system. To refine the analysis we selected $1 \times 1 \text{ km}$ grid cells of the above-presented map (Fig. 1), with more than 50% of natural grassland share; and considered them as centers of a 3-km radius buffer for which we computed cattle stock using explicit geospatial cattle distribution data provided by foot and mouth disease vaccination of the Servicio Nacional de Sanidad y Calidad Alimentaria (SENASA) for 2017. Combining these data, we summed the potential maximum number of cattle heads that could be using natural grasslands and savannas as a forage source. Our results showed that near 720,000 cattle heads occur at less than 3-km of radius for the total extension of $16,000 \text{ km}^2$ of natural grassland and savannas in the Argentinean Dry Chaco (Fig. 8). This stock represents 13% of the total stock for Argentine Dry Chaco.

Assessing Potential for Cattle Intensification

We also explored the possibilities for sustainable intensification (e.g., Garnett et al., 2013; Thomson et al., 2019) for cattle ranching. To do so, we performed dynamic simulations on 42 theoretical farms of cow-calf systems (i.e., productions systems oriented to production of calf to later finishing) across an extension of 14 millions of hectares with different landscape composition, soil (i.e., dominant texture) and climate, using a calibrated and evaluated biophysical cattle management model developed by Nasca et al. (2015). For each of these theoretical farms, we evaluated the following four scenarios in a gradient of intensity: M0 (baseline) cattle ranching developed on natural grasslands fodder sources with conventional management and low technological level; M1, which applies changes in cattle management (adjust of carrying capacity with climate variations, management of service in cows, strategic supplementation for rearing heifers, etc.), on the same landscape and fodder sources as M0; M2, which incorporate implanted pastures as fodder source, and includes same management as M1; and M3, equal to M2, but incorporating corn silage in cows diet. The interannual variability of carrying capacity of M0 was taken as the maximum acceptable threshold to select the outputs of M1, M2 and M3. For these, we carried out five simulations for each scenario modeled, selecting the one that fulfilled the highest productivity and less variability than M0. This condition was fundamental to evaluate resilient stocking rates through climatic variations.

In general, the results showed an increase in beef production (that range from 80% to 2000%) in all scenarios in relation to the baseline (M0), indicating broad opportunities to increase beef production in Dry Chaco (Fig. 9). This increase varied across different edaphic-climatic conditions, showing the environmental constrain for beef production improvements. For example, the drops in beef production in M3 are explained by a dominance of sandy soils and consequent limitations to produce corn silage (Fig. 9).

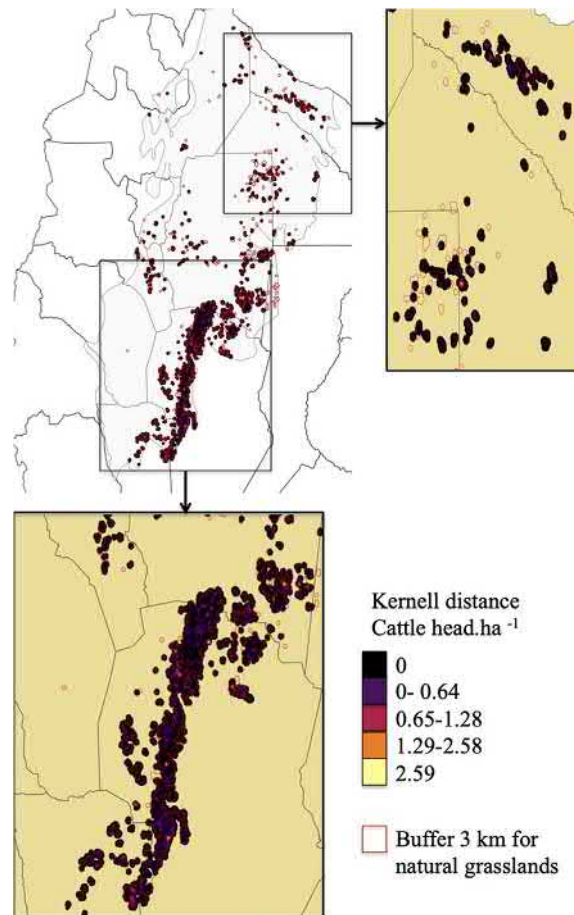


Fig. 8 Cattle density in natural grasslands and savannas of Argentinean Dry Chaco. Red limits represent the 3-km buffer area from the center of pixels with more 50% of natural grasslands; the gradient between black and yellow inside each buffer is a kernel distance representing density of cattle head ha^{-1} .

In M2 scenario (which incorporate implanted pasture in their fodder resources) average beef production was 10 times higher than in M0; and 3 times higher than M1. The M3 scenario represents the higher productive potential in situations of increasing intensification, obtaining average increases of 3100% in relation to M2 (Fig. 9). In conclusion, sustainable intensification provides many opportunities for increase beef production in the Dry Chaco, across diverse edaphic-climatic conditions. As many of the cattle ranching production in the region occur at small production scales (i.e., 85% of producers and 50% of cattle stock remain in farms with less than 250 heads; INTA, IER, SENASA, 2016) conservation practices which include the exclusion of grazing for prolonged times could impact the subsistence of local farmers. We argue with these results that there exists a broad opportunity to increase beef production through management decision. Governmental initiatives targeting to conserve natural grasslands and savannas or forests in this region, should consider the implementation of processes that improve cattle ranching production, as long as they release pressure on natural environments.

Livestock-Wildlife Interactions

The Chaco hosts an important biological diversity (Bucher and Huszar, 1999; TNC et al., 2005), with around 500 species of birds, 150 species of mammals, 120 species of reptiles and around 100 of amphibians; in addition to 3400 plant species (TNC et al., 2005). It also has a long history of colonization, land-use changes and interactions with wildlife, from subsistence hunting by native people to more intensified practices that expanded in the last decades (Eva et al., 2004; Hoyos et al., 2013). The combination of these practices has resulted in the mentioned replacement of natural grasslands and woodlands with shrubs and eroded areas of bare soil (Baldi and Jobbágy, 2012). Thus, many species occupying the region are in fact mostly associated to open vegetation (Macchi et al., 2013; Marinaro et al., 2015; Torres et al., 2014). However, conservation strategies almost exclusively focus on forests conservation, to the point that protected areas include fire suppression as a management policy, with the consequent woody encroachment (Cardozo et al., 2011; Grau et al., 2014).

Medium-large mammal species of the Argentine Chaco are particularly sensitive to anthropogenic changes, and their sharp decline is mostly attributed to habitat loss and hunting pressure (Periago et al., 2015). Among these species, many seem to prefer

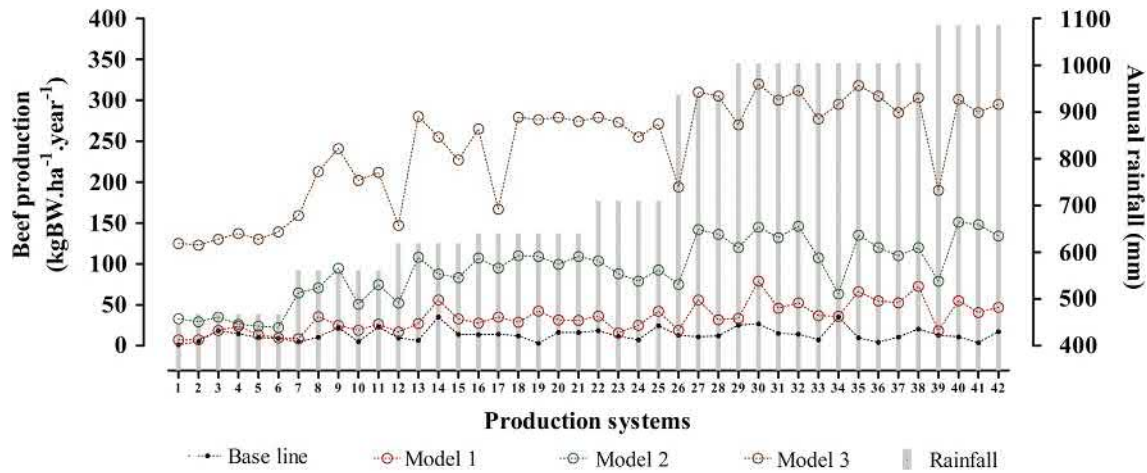


Fig. 9 Beef production ($\text{Kg BW ha}^{-1} \text{ year}^{-1}$) across annual rainfall gradient (gray bars) for different production systems and management scenarios. Base line: Scenario without management practices. Model 1: Scenario including adjusting carrying capacity. Model 2: Scenario including implanted pastures. Model 3: Scenario including corn silage supplementation.

open habitats (e.g., giant anteater, guanaco, manedwolf, large rhea) and their populations may thus be further threatened by forest-centered policies. Medium-large mammals play important, yet understudied functional roles in Chaco ecosystems (Periago et al., 2015). For example, preferential utilization of woody plants by wild browsers (Staver et al., 2009), or seed and seedling predators (Weltzin et al., 1997) may help maintain grassland and savanna communities. The behavior of these herbivores can prevent shrubs and trees from establishing and exerting dominance, and maintain them at a stature vulnerable to fire. On the contrary, woody plants may be in advantage where livestock are effective dispersers of their seeds. In addition, livestock introductions can cause displacement of native browsers and seed predators, releasing woody plants from top-down controls. Preserving populations of native herbivores in systems managed for livestock grazing may help maintain grass-woody populations in desired configurations, while concurrently enhancing biodiversity.

The introduction of cattle early in the 20th century not only affected the balance between woody and herbaceous cover, with several indirect effects on many species, but also gave place to other issues that threaten medium-large mammal communities, such as human-carnivore conflicts due to actual or perceived livestock depredation (Quiroga et al., 2014). The combined effect of traditional hunting and retaliatory/preventive hunting by livestock breeders has already caused the ecological extinction of jaguars in the Argentine Chaco (Quiroga et al., 2014) and is possibly behind the low population densities of the puma, the only other apex predator of the region (Quiroga et al., 2016). Because top-predators have strong top-down effects, the marked decrease in their populations in the Chaco may cause far-reaching changes in the dynamics of its ecosystems.

Conservation and Representation in Protected Areas

Human population is projected to increase from the current ~7 billion people, to ~10 billion people by 2050 (United Nations, 2017). This population growth, translated into an increasing global food demand, strongly threatens natural areas worldwide; particularly in regions such as the Dry Chaco, with strong potential for agriculture expansion (Lambin et al., 2013). However, conservation policies have focused on the threats exerted to forests, at the extreme of neglecting natural grasslands as a specific, and fundamental conservation target (Grau et al., 2014). In addition, these policies may even result in increased pressure over non-forested landscapes, such as natural grasslands (Miles and Kapos, 2008).

The Dry Chaco ecoregion as a whole is rather under-protected. The protected area represents 11.1% of the entire ecoregion, with large differences among the three encompassed countries. Whereas 35.7% of the area is protected in the Bolivian Chaco, the Paraguayan and Argentine Chaco portions barely reach values of 11.8% and 4.8%, respectively. In addition, forests mostly represent these percentages. In the Argentinean portion, only 4.1% of the protected area encompasses natural grasslands, while in Bolivia this value reaches only 0.18%; and in Paraguay, 1.7%. Regarding the relative extension of protected natural grasslands, only 10.1% of Argentine Dry Chaco natural grasslands are protected. In turn, Bolivian native grasslands are protected in a similarly low proportion (9.8%), while in Paraguay this amount increases, with 16.5% of the natural grasslands under protection. We argue that natural grasslands need to be specifically targeted by biodiversity conservation planning, which is not the case in current forest-based initiatives.

Biodiversity in the region is likely very-well adapted to, and even dependent on, natural grasslands and savannas (Grau et al., 2014). Protected areas do not ensure grassland conservation; rather, fire suppression policies that favor woody encroachment are applied, which potentially leads to the disappearance of the grasslands with the highest conservation value (Cardozo et al., 2011). Further, the Native Forest Law of Argentina also ignores the importance of grasslands for many animal species, including species

with high conservation concerns (Grau et al., 2014; Marinaro and Grau, 2015). Identify the “old-growth” natural grassland and savannas (i.e., ancient ecosystems characterized by high herbaceous species richness, high endemism, and unique species compositions) (Veldman et al., 2015) represent an urgent task to identify priority areas of conservation related to natural grasslands and savannas of different typologies.

Future Research and Conclusions

Natural grasslands and savannas are singular components of the Dry Chaco geography spread in different environments and diverse physiognomies, but during the last century they have been seriously reduced and transformed by different human activities that resulted in their replacement by both woody vegetation and agriculture. They have been neglected by the scientific community, in the understanding of their contribution to biodiversity and human livelihoods. Governments, on the other hand, neglected these ecosystems in terms of conservation and management policies. Albeit we elucidate that cattle stocking rates supported by natural grasslands and savannas, particularly in Argentine Chaco, would not represent a major obstacle in terms of production cost at regional scales, the impact of removing the cattle of such areas in terms of livelihoods and rural and indigenous populations' subsistence is not understood and has not been addressed to date. In addition, knowledge of the biological composition, ecological interactions and biogeochemical cycles of natural grassland and savannas transitions (novel ecosystems of implanted pastures, and encroached natural grasslands) should be intensified. The reintroduction of prescript fires not only as a production but also as a conservation tool, the alternatives of restoration practices, and the promotion of ecotourism as sources of income are alternatives whose costs and benefits should also be addressed. We believe that studies in this particular landscape are in initial stages and we encourage continuing understanding these singular ecosystems.

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Temperate Subhumid Grasslands of Southern South America

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Abstract

Temperate subhumid grasslands extend in the eastern part of South America. This region represents one of the most diverse, largest and less transformed grassland areas in the world. The grasslands occupy the vast and continuous plains of central-eastern Argentina, Uruguay and southern Brazil that surround the Río de la Plata estuary. For this reason, they are referred to as the Río de la Plata grasslands. These grasslands, despite its apparent physiognomic homogeneity, hold high diversity of species, having grasses as the dominant life form except for few scattered shrubs and trees, and show a year-round photosynthetic activity. In this article we describe structural and functional characteristics of the vegetation of the Río de la Plata grasslands. We give an overview on biogeography, ecosystem functioning and services, human appropriation of primary production, disturbances, land use change, biological invasions and conservation status.

Introduction

Temperate subhumid grasslands extend in the eastern part of South America from 28 to 38° Latitude S and from 50 to 66.5° Longitude W. They cover about 760,000 km² and represent one of the most diverse, largest and less transformed grassland areas in the world. They occupy the vast and continuous plains of central-eastern Argentina, Uruguay and southern Brazil that surround the Río de la Plata estuary. For this reason, they are referred to as the Río de la Plata grasslands (Soriano et al., 1992). These grasslands are bordered by deciduous xerophytic forest to the west, and deciduous tropical and subtropical humid forests to the north (Overbeck et al., 2007; Andrade et al., 2018; Oyarzabal et al., 2018). Due to the influence exerted by the Atlantic Ocean, climatic conditions are less extreme than in other regions of the world located at similar latitudes (Paruelo et al., 1995). Average annual temperature varies from 20 °C in the north to 13 °C in the south. The total annual rainfall varies from 1500 mm in the northeast to 400 mm in the southwest, with a lack of seasonal variation and a marked increase tendency in the last decades (Royo Pallarés et al., 2005; Paruelo et al., 2007; Barros et al., 2015).

The grasslands are physiognomically uniform, hold high diversity of species, have grasses as the dominant life form except for few scattered shrubs and trees, and show a year-round photosynthetic activity. Grasslands co-dominated by C₃ and C₄ species are the most abundant physiognomic type, combined with shrublands and forests (Figs. 1 and 2; Boldrini, 1997; Overbeck et al., 2007; Perelman et al., 2001, 2017; Oyarzabal et al., 2018; Lezama et al., 2019a). Steppes occur mainly in the drier western part of the region (Oyarzabal et al., 2018). Prairies and meadows may be locally important under particular topographic and/or edaphic conditions (Burkart et al., 1990; Batista and León, 1992; Perelman et al., 2001; Aragón and Oesterheld, 2008). Savannas become important only in the north ecotones of the regions (Batista et al., 2014). Shrub encroachment may occur, mainly, because of changes in the grazing regime (Altesor et al., 2006; Andrade et al., 2015; Buisson et al., 2019). Forests are mainly restricted to



Fig. 1 Winter aspect of a humid prairie (sensu [Perelman et al., 2001](#)) of the Flooding Pampa, Río de la Plata grasslands. Planted trees of *Casuarina* sp., *Eucalyptus* sp., *Maclura pomifera*, *Robinia pseudo-acacia* and *Ulmus* sp. are seen in the background (see [Appendix 2 of Supplementary material](#)). Photo credit: Sofia Campana.



Fig. 2 Savanna of *Butia odorata* in the Southern Campos, Río de la Plata grasslands. Photo credit: Mauricio Bonifacino.

riparian corridors along the large Paraná and Uruguay rivers and their tributary streams, to rocky hills and ravines, and to azonal soils formed on top of shell debris deposits ([Lewis and Collantes, 1973](#); [Cabrera, 1976](#); [León et al., 1979](#); [Morello et al., 2012](#)).

In this article we describe structural and functional characteristics of the vegetation of the Río de la Plata grasslands. We give an overview on biogeography, ecosystem functioning and services, human appropriation of primary production, disturbances, land use change, biological invasions and conservation status.

Biogeography

Pampa and Campos are the two sub-regions that can be distinguished according to physiognomic, geomorphologic and edaphic features (Soriano et al., 1992). Pampa occurs exclusively in the Argentinean territory, while Campos corresponds to Brazil, Uruguay and a small portion of Eastern Argentina (Fig. 3). From a physiognomic point of view, Pampa has few trees, while Campos includes gallery forests along rivers and woodlands dispersed on hilly areas (Soriano et al., 1992). From a geomorphology standpoint, the Pampa has been formed by thick quaternary loess deposits that have experienced varying degrees of local reworking (Anderson et al., 1999; Ortiz-Jaureguizar and Cladera, 2006). Exceptions to this general pattern are a few isolated uplands in Argentina. In contrast, Campos has been formed of more modern strata on crystalline and basaltic basements, merging or lying near the surface. Here, diverse arrays of older and stable rocks as Precambrian granite, Carboniferous sandstone, and Jurassic basalt have been not fully buried by eolic sediments and exposed to surface and soil-forming processes. In respect to edaphic features, soils in Pampa shift along a west-east gradient, from mollic Entisols with incipient horizon differentiation to well-developed Mollisols with high clay accumulation, high organic matter content and base saturation, very suitable for agriculture (INTA, 1990; Rubio et al., 2019). The lower and flat portions of the landscapes are characterized by the presence of sodic and/or hydromorphic soils, with greater crop restrictions (Lavado and Taboada, 1988; Paruelo et al., 2007). In Campos, the complex array of parent materials and topographic forms has resulted in higher soil heterogeneity than in Pampa (Duran, 1991). This fact probably explains the greater general diversity of plants and number of endemic species in Campos than in Pampa. In Campos, well-developed Mollisols are the predominant soils. Toward the north and east they are associated with Alfisols, Inceptisols, Oxisols, Vertisols and Ultisols, and towards the west with Entisols (Duran, 1991; Paruelo et al., 2007; Streck et al., 2008).

In spite of the apparent uniformity of the vegetation, Pampa and Campos sub-regions can in turn be subdivided in “vegetation units” (Soriano et al., 1992; Oyarzabal et al., 2018; Fig. 3). Vegetation units are areas with relatively homogeneous physiognomy and floristic composition, sharing geomorphic, hydrologic, and edaphic features. Such characterization into vegetation units summarizes and integrates information of the flora at both regional and local scales, generated in the region by more than three generations of botanists and ecologists. We only summarized here the vegetation units based mainly on the seminal description of Rolando León (in Soriano et al., 1992; Oyarzabal et al., 2018). All vegetation units are now partially covered by annual crops, sown pastures or tree plantations (Baldi et al., 2006; Baeza et al., 2014; Baeza and Paruelo, 2018; Andrade et al., 2015; Volante et al., 2015; Modernel et al., 2016). Where land cover has almost completely changed to cultivated cover types, original vegetation can only be inferred from a few isolated remnants of unconverted vegetation and from early, but postcolonial, botanical descriptions. The Pampa sub-region can be subdivided into six vegetation units: Rolling Pampa, Mesopotamic Pampa, Flat Inland Pampa, West Inland Pampa, Flooding Pampa and Austral Pampa (Fig. 3; see more details of each vegetation unit in Soriano et al., 1992 and Oyarzabal et al., 2018). The Campos sub-region has two vegetation units: Northern Campos and Southern Campos (Fig. 3), though this separation is under revision considering the high geomorphological diversity in this region (Hasenack et al., 2010).

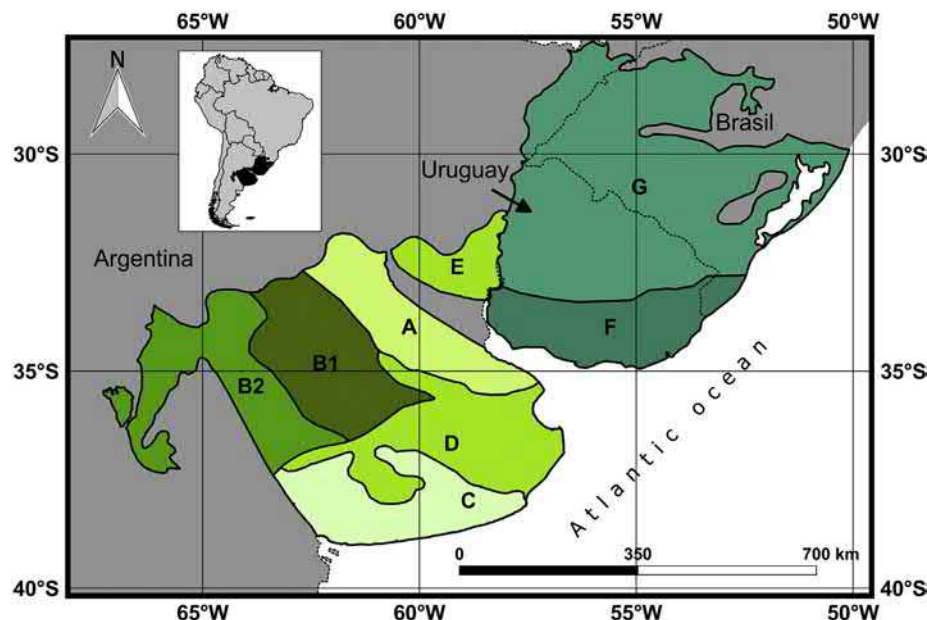


Fig. 3 Río de la Plata grasslands region. Letters denotes vegetation units as subdivisions of subregions Pampas (A, B1, B2, C, D and E) and Campos (G and F). (A) Rolling Pampa, (B1) Flat Inland Pampa, (B2) West Inland Pampa, (C) Southern Pampa, (D) Flooding Pampa, (E) Mesopotamic Pampa, (F) Southern Campos, (G) Northern Campos. *Dash lines* are international boundaries (see vector files available in [Appendix 1 of Supplementary material](#)).

Río de la Plata grasslands have high species richness, including many endemic species. The list of all vascular plant species for Río de la Plata grasslands region comprises 4836 species, belonging to 1324 genera and 194 families (Andrade et al., 2018). This total number of species is higher than average per unit area when compared to the entire Southern Cone region (Argentina, Chile, Paraguay, south Brazil and Uruguay), and almost equal to numbers of the savannas in the central region of Brazil, the *Cerrado*. Such high species richness is probably due to its location in a transition zone (Burke et al., 1998). The species richness follows a latitudinal trend. The Brazilian and Uruguayan part hold about twice as many species per unit area as the Argentine part. For every thousand km², there are 20 species in Brazil, 17 species in Uruguay and 9 species in Argentina. About 40% of all species found for the region relies on five families: Asteraceae (659 species; Fig. 4), Poaceae (645; Fig. 5), Fabaceae (399), Cyperaceae (184) and Orchidaceae (149). The endemic species of the Río de la Plata grasslands are 403, corresponding to 159 genera and 49 families (Andrade et al., 2018). Asteraceae and Poaceae are also the two families with the highest number of endemic species, but others much smaller also present a high number of plant endemism: Cactaceae, Iridaceae, Fabaceae, Euphorbiaceae and Amaryllidaceae. Alstroemeriaceae, Bromeliaceae, Erythroxylaceae, Lamiaceae, Passifloraceae have records of endemic species restricted to the Brazilian limits, while Araceae, Caryophyllaceae, Onagraceae and Orobanchaceae were restricted to Uruguay, and just Brassicaceae and Cannaceae presented endemic species only found in Argentina (Andrade et al., 2018).



Fig. 4 *Senecio pulcher* Hook. & Arn., a native species belonging Asteraceae family, growing in humid prairie (sensu Perelman et al., 2001) of the Flooding Pampa, Río de la Plata grasslands. Photo credit: Pedro M. Tognetti.



Fig. 5 *Chascolytrum subaristatum* (Lam.) Desv. and *Melica brasiliana* Ard., two native grass species growing in the Flat Inland Pampa, Río de la Plata grasslands. Photo credit: Pedro M. Tognetti.

Vegetation surveys allowed identifying grassland communities within the vegetation units. Starting with the pioneer work of León (1975) and León et al. (1979), different studies characterized floristic heterogeneity of portions of Campos and Pampa sub-regions (Lewis, 1981; Lewis et al., 1985, 1990; Batista et al., 1988; Burkart et al., 1990, 1998, 2011; Fontana, 1996; Lezama et al., 2006, 2011, 2019a). For the Brazilian region of the Campos, three grassland vegetation types and 10 subtypes were classified based on species dominance pattern (Andrade et al., 2019). The classification confirmed the existence of a sharp upper north limit between the Río de la Plata grasslands region and the Highland grasslands, the subtropical grassland ecosystems found in the south and southeast part of Brazil (Andrade et al., 2019). These results give support to an earlier study based on quantitative forest-composition data (Oliveira-Filho et al., 2013). In the Uruguayan portion of the Campos (Fig. 6), the main floristic gradients were associated to edaphic and topographic factors that control water availability. Five communities were identified (Lezama et al., 2019a). Three of the communities correspond to densely-vegetated grasslands associated to medium and deep soils. The remaining two communities were defined as sparsely-vegetated grasslands and were typical of shallow soils (Lezama et al., 2019a,b; Table 1). Such communities presented significant differences in total C gains and in its seasonal dynamics (Baeza et al., 2010; Guido et al., 2014). In the Pampa, 11 communities were identified by Perelman et al. (2001), based on more than 749 relevés. Such communities were in turn classified in five community groups associated to a particular landscape position and soils: mesophytic meadows, humid mesophytic meadows, humid prairies, halophytic steppes and humid halophytic steppes (Table 2; Perelman et al., 2001).

Fossil evidence suggests grazing is not a novel factor in the Río de la Plata Grasslands, considering that grassland ecosystems in South America coevolved with large grazers since ~25 million years (MacFadden, 2006). Further, pollen and charcoal data show that grassland vegetation had dominated during late Quaternary, with forest ecosystems expanding only during the second half of the Holocene. After the large grazer extinctions by the end of the Pleistocene, fire has likely had an important role in maintaining grassland vegetation (Behling et al., 2005; Behling and Pillar, 2007).

Thus, it is expected that, depending on initial conditions and primary productivity, domestic herbivore grazing maintains or changes grassland structure and functioning (Sala et al., 1986; Rodríguez et al., 2003; Altesor et al., 2005, 2006; Semmartin and Oesterheld, 2001; Semmartin et al., 2007; López-Mársico et al., 2015, 2016; Lezama et al., 2014; Fischer et al., 2019). Grazing's effect on vegetation heterogeneity was recognized in the Pampa (Anderson et al., 1970, 1978; León and Marangón, 1980; León and Movia, 1981; León and Anderson, 1983; León and Oesterheld, 1991). As a way to summarize structural and functional changes associated with grazing, several state and transition models were proposed for the region (e.g., Bestelmeyer et al., 2003; Andrade et al., 2015; Buisson et al., 2019). For the humid mesophytic meadows of the Flooding Pampa (Perelman et al., 2001), a model described that changes in plant functional types (prostrated dicots, tall grasses and prostrated grasses) resulted from the combined effects of grazing and floods (Oesterheld and Sala, 1994). For the five communities identified in the Uruguayan Campos (Lezama et al., 2019a), state and transition models were also developed (Altesor et al., 2019). Communities presented an internal heterogeneity associated with changes in total cover, stratification, and proportion of plant functional types. Different states within the same community presented different responses to extreme climatic events. The stocking rate, sheep/cattle ratio, and grazing method are key grazing management strategies that promote the transition among states and phases (Altesor et al., 2019; Fischer et al., 2019).



Fig. 6 Grassland landscape in the Uruguayan portion of the Northern Campos. Photo credit: Mauricio Bonifacino.

Table 1 Synoptic table of grassland vegetation in Uruguay at sub-community level.

Community	Sub-community	Physiognomy	Geomorphologic region
I	a. <i>Portulaca papulosa</i> - <i>Selaginella sellowii</i>	One stratum, 2–5 cm tall, dominated by forbs and grasses	Basaltic “Cuesta”
	b. <i>Lippia coarctata</i> - <i>Oenothera parodiana</i>	Two stratus: 5 cm tall, dominated by forbs and grasses; 11–30 cm tall, erect grasses and subshrubs (<i>Baccharis coridifolia</i>)	Basaltic “Cuesta”
II	a. <i>Glechom marifolia</i> - <i>Jarava filifolia</i>	Two stratus: 5 cm tall, forbs and grasses; 30 cm tall, subarbusts and erect grasses (<i>Aristida filifolia</i> and <i>Jarava filifolia</i>)	Eastern Hills
	b. <i>Oxalis conorrhiza</i> - <i>Chascolytrum erectum</i>	Two stratus (typical): 5 cm tall, dominated by forbs and grasses; 30 cm tall, subshrubs (<i>Baccharis</i> sp.)	Eastern Hills
	c. <i>Stenachaenium campestre</i> - <i>Andropogon ternatus</i>	Two stratus (typical): 5 cm tall, dominated by forbs and grasses; 30 cm tall, subshrubs (<i>Baccharis</i> sp.)	South Central region, Eastern Hills, North Eastern Sedimentary Basin
	d. <i>Aira elegantissima</i> - <i>Micropsis spathulata</i>	One stratum, 5 cm tall, dominated by forbs and grasses	Eastern Hills, North Eastern Sedimentary Basin
	e. <i>Paspalum leptoneuron</i> - <i>Hypoxis decumbens</i>	Two stratus (typical): 5 cm tall, dominated by forbs and grasses; 30 cm tall, subshrubs (<i>Baccharis</i> sp.)	North Eastern Sedimentary Basin
III	a. <i>Mecardonia procumbens</i> - <i>Eleocharis dunensis</i>	Two stratus: 5–10 cm tall, grasses; 20–30 cm tall, grasses	Basaltic “Cuesta”
	b. <i>Ruellia morongii</i> - <i>Steinchisma hians</i>	Two stratus: 5–10 cm tall, grasses; 20–30 cm tall, grasses	Basaltic “Cuesta”
IV	a. <i>Eryngium horridum</i> - <i>Danthonia rhizomata</i>	Two-three stratus: 5–10 cm tall, forbs and grasses; 20–30 cm tall, erect grasses and subshrubs. Occasionally, one additional stratum: 100 cm, shrubs.	Eastern Hills (occasionally: South Central region, North Eastern Sedimentary Basin)
	b. <i>Senecio selloi</i> - <i>Nassella pauciciliata</i>	Two-three stratus: 5–10 cm tall, forbs and grasses; 20–30 cm tall, erect grasses and subshrubs. Occasionally, one additional stratum: 100 cm, shrubs.	North Eastern Sedimentary Basin (occasionally: South Central region, Eastern Hills)
	c. <i>Chevreulia sarmentosa</i> - <i>Danthonia montevidensis</i>	One stratum: 5 cm tall, dominated by forbs and grasses. Occasionally, one additional stratum: 30 cm tall, subshrubs.	South Central region, Eastern Hills, North Eastern Sedimentary Basin
	d. <i>Lolium multiflorum</i> - <i>Nassella charruana</i>	Two stratus: 5–10 cm tall, dominated by grasses; 20–30 cm tall, dominated by erect grasses (<i>N. charruana</i>)	(occasionally: Eastern Hills, North Eastern Sedimentary Basin)
V	a. <i>Paspalum pumilum</i> - <i>Chascolytrum poomorphum</i>	Three stratus: 5–10 cm tall, dominated by grasses; 20–30 cm tall, dominated by erect grasses; 50 cm tall, grasses	South Central region, Eastern Hills, North Eastern Sedimentary Basin

Modified from Lezama, F., Pereira, M., Altosor, A. and Paruelo, J. M. (2019b). Cuán heterogéneos son los pastizales naturales en Uruguay? In Altosor, A., López-Mársico, M. and Paruelo, J. M. (eds), *Bases Ecológicas y Tecnológicas para el manejo de pastizales II*. 1st edn., pp. 15–26, Montevideo: Instituto Nacional de Investigación Agropecuaria.

Table 2 Landscape and soil characteristics of the main five community groups of the Flooding Pampa, Río de la Plata grasslands.

Community group	Position in the landscape and soil description	Predominant soil types
I: Mesophytic meadows	Positive and convex terrains, highest areas. Deep, well drained soils, acidic, non-saline, poligenic soils	Typic Argiudolls and Poligenetic Thaptoargic Hapludols
II: Humid mesophytic meadows	Flat areas. Intermediate topographic position. Acidic, nonsaline A1 horizon and saline, highly alkaline B2 horizon	Typic Natraquolls with natric B2 horizon Natralbolls
III: Humid prairies	Extended lowlands, with groundwater near the surface, subject to flooding. Soils range from acidic throughout the profile to acidic in the upper and alkaline in the deeper layer Small depressions in flat areas, or rings surrounding humid areas	Argiacuic Argiallbolls Argiacuolls
IV: Halophytic steppes	Very shallow, alkaline soils with very high salt content in the upper layer	Mollic Natraqualls
V: Humid halophytic steppes	Negative positions on fluvial valleys, tidal areas poorly drained. Alluvial, saline sodic soils	Typic Natraqualls

Modified from Perelman, S., León, R. J. C. and Oesterheld, M. (2001). Cross-scale vegetation patterns of flooding Pampa grasslands. *Journal of Ecology* **89**, 562–577.

Ecosystem Functioning

Ecosystem functioning varies according to the environmental heterogeneity and gradients in vegetation structure described above. Net primary production and its seasonal dynamics have been identified as key ecosystem attributes able to integrate different aspects of ecosystem functioning, e.g., the exchange of matter and energy between biota and the abiotic environment. Paruelo et al. (2010) summarized different studies on C gains on the Río de la Plata grasslands based on field data, remote sensing techniques and modeling. Aboveground net primary production, as suggested by remote sensing proxies, decreased from NE to SW following the dominant precipitation gradient. Across the precipitation gradient two-fold differences in aboveground net primary production may be expected, from 30 to 750 g DM m⁻² y⁻¹ (Oesterheld et al., 1992). Estimates of belowground net primary production were more variable than aboveground net primary production, and field estimates ranged from 660 to 1420 g DM m⁻² y⁻¹. Total Carbon ranged from 5004 to 15,008 g C m⁻². The largest plant C stock corresponded to belowground biomass. Aboveground green biomass represented less than 7% of the plant C. Soil organic carbon was concentrated in the slow and passive compartments of the organic matter. Active soil pool represented only 6.7% of the soil organic carbon (Fig. 7).

Vegetation units of the Río de la Plata grasslands showed three general patterns of seasonal change of the fraction of the photosynthetic active radiation absorption (fAPAR) as estimated from remotely sensed data (Paruelo et al., 2010). fAPAR is basically determined by the dynamics of leaf area index. The northern most vegetation units (Northern and Southern Campos and Mesopotamic Pampa) showed a relatively low intra-annual variability of fAPAR. A spring peak of fAPAR was evident in these three vegetation units. Inland and Rolling Pampas showed a delayed fAPAR peak and a more marked seasonal variation. The remaining vegetation units (Austral and Flooding Pampas) presented two clear peaks of fAPAR (Paruelo et al., 2010). Photosynthetic active radiation (PAR) presented a well-defined December maximum which determined that the two peaks of some of the vegetation units disappear when absorbed PAR is calculated. Empirical estimates of the radiation use efficiency showed that this coefficient presents minima in summer and maxima in winter (Paruelo et al., 2010, 2019). The seasonal dynamics of radiation use efficiency determined a reduction in the contrast of aboveground net primary production throughout the year. The ratio between maximum and minimum absorbed PAR ranged between 5.45 and 3.12, and between 4.12 and 2.47 for aboveground net primary production (Paruelo et al., 2010).

Regional patterns of primary production are matched by strong patterns of livestock biomass and, consequently, of the proportion of aboveground net primary production consumed by herbivores (Fig. 8). Livestock biomass, a major determinant of

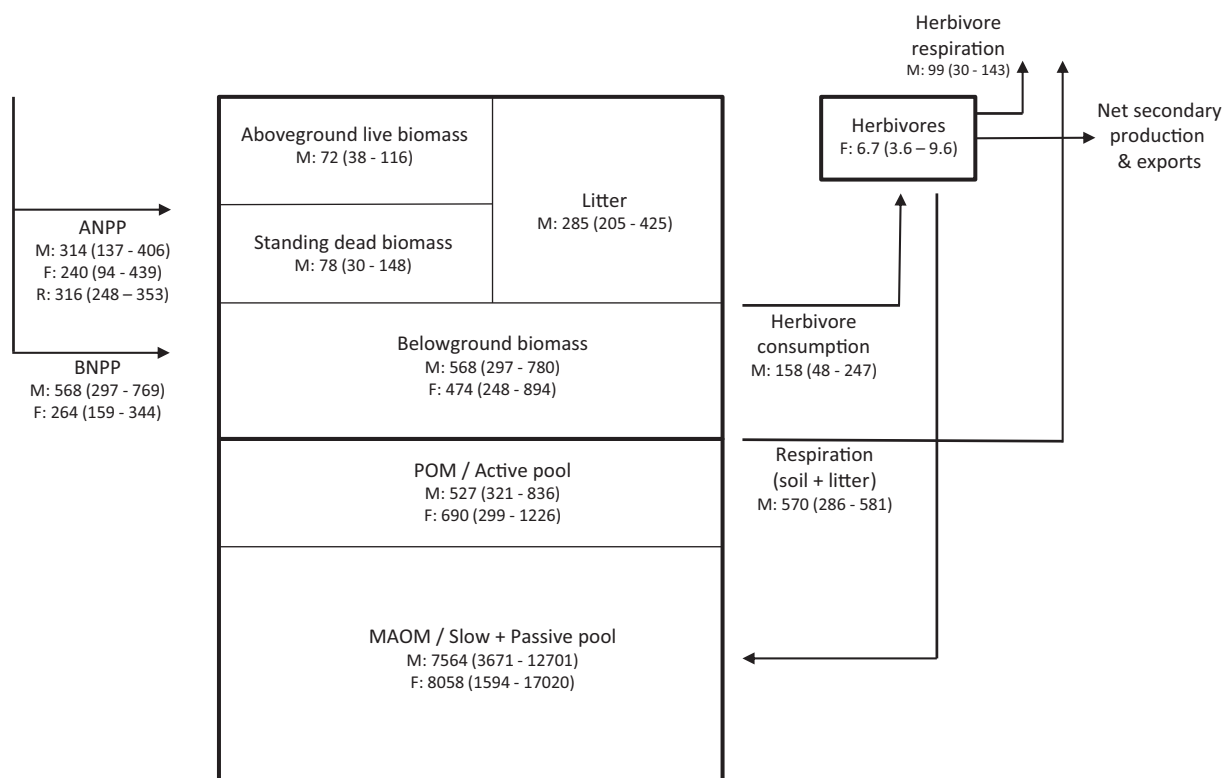


Fig. 7 Carbon balance for the Río de la Plata grasslands. Estimates based on modeling (M), field studies (F), and remote sensing techniques (R) are presented. The values are expressed in g C m⁻² (stocks) and g C m⁻² y⁻¹ (fluxes). Values in parentheses corresponded to the range of observed/simulated values. Abbreviations: ANPP, aboveground net primary production; BNPP, belowground net primary production; POM, particulated organic matter; and MAOM, mineral-associated organic matter. Paruelo, J. M., Piñeiro, G., Baldi, G., Baeza, S., Lezama, F., Altesor, A. and Oesterheld, M. (2010). Carbon stocks and fluxes in rangelands of the Río de la Plata Basin. *Rangeland Ecology & Management* 63(1), 94–108.

net secondary production across the Río de la Plata grasslands, increases more than proportionally as aboveground net primary production increases (Oesterheld et al., 1992). Livestock biomass is six times greater and 0.4 times less variable between years than that observed in natural ecosystems with similar primary production (McNaughton et al., 1989; Irisarri et al., 2014).

Ecosystems Services

Early in the 1990s, the importance of native grasslands on the supply of ecosystem services was highlighted (Sala and Paruelo, 1997). Such ecosystem services include provisioning (e.g., livestock production), regulation (e.g., water, climate and air quality regulation; pollination) and supporting services (e.g., primary production, soil formation). Recently, an integrative index of ecosystem services provision was developed (Paruelo et al., 2016). The index is based on the aboveground net primary production seasonal dynamics assessed through remotely sensed data. The index allows describing the spatial variability of the supply but also temporal trends (Fig. 9). The analysis of the absolute values of the trends over the period 2001–14 showed that almost a third of the



Fig. 8 Livestock in the Flooding Pampa, Río de la Plata grasslands. Photo credit: Pedro M. Tognetti.

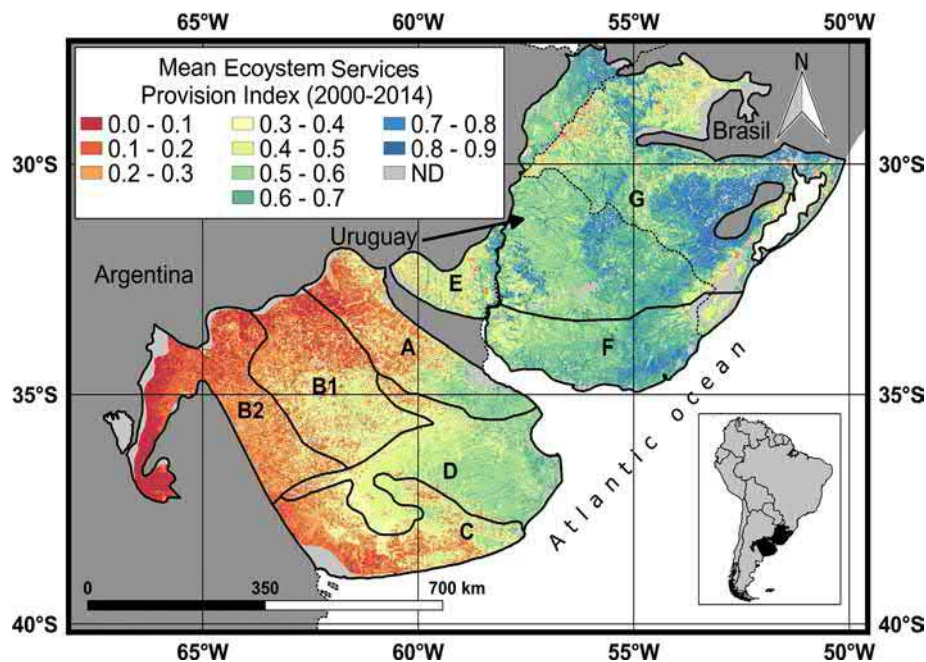


Fig. 9 Mean values of the Ecosystem Services Provision Index for Río de la Plata grasslands. Letters denotes vegetation units as subdivisions of subregions Pampas (A, B1, B2, C, D and E) and Campos (G and F). (A) Rolling Pampa, (B1) Flat Inland Pampa, (B2) West Inland Pampa, (C) Southern Pampa, (D) Flooding Pampa, (E) Mesopotamic Pampa, (F) Southern Campos, (G) Northern Campos. *Dash lines* are international boundaries. Modified from Paruelo, J. M., Texeira, M., Staiano, L., Mastrángelo, M., Amdan, L. and Gallego, F. (2016). An integrative index of ecosystem services provision based on remotely sensed data. *Ecological Indicators* **71**, 145–154.

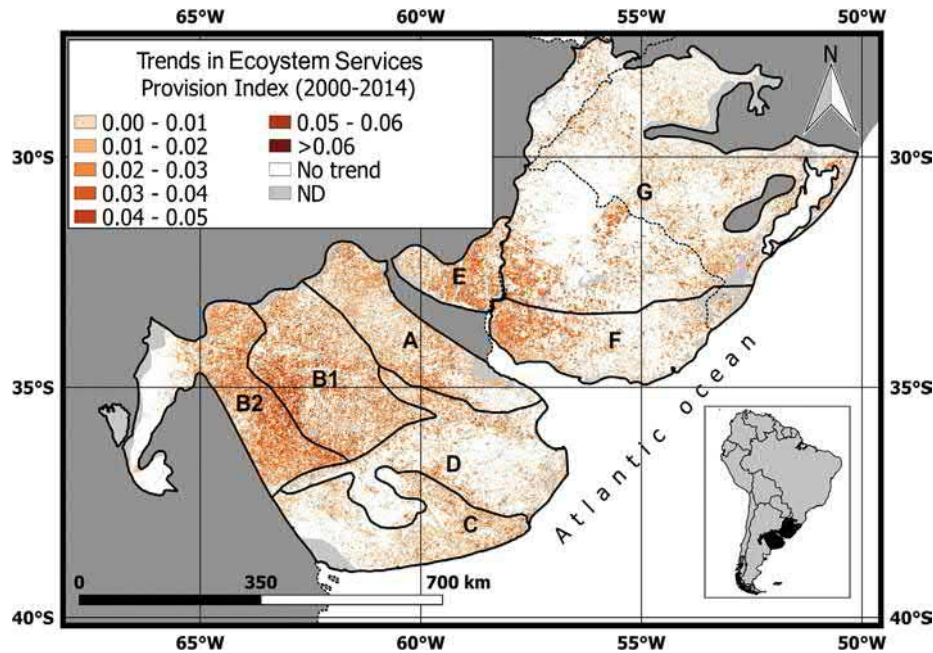


Fig. 10 Absolute values of the Ecosystem Services Provision Index trends (slope of the regression Index vs. time) for Río de la Plata grasslands. Letters denotes vegetation units as subdivisions of subregions Pampas (A, B1, B2, C, D and E) and Campos (G and F). (A) Rolling Pampa, (B1) Flat Inland Pampa, (B2) West Inland Pampa, (C) Southern Pampa, (D) Flooding Pampa, (E) Mesopotamic Pampa, (F) Southern Campos, (G) Northern Campos. *Dash lines* are international boundaries. Modified from Paruelo, J. M., Teixeira, M., Staiano, L., Mastrángelo, M., Amdan, L. and Gallego, F. (2016). An integrative index of ecosystem services provision based on remotely sensed data. *Ecological Indicators* **71**, 145–154.

Río de la Plata grasslands presented changes in ecosystem services provision (Fig. 10), most of the trends were negative (Paruelo et al., 2016). Many of those areas corresponded to the agricultural foci identified in both regions (Paruelo et al., 2016). The index of ecosystem services supply presented a negative relationship with a human development index (Paruelo and Dieguez, 2019). It reflects the impact of human activities on ecosystem services.

Human Appropriation of Primary Production

Human impact on the Río de la Plata grasslands is altering ecosystem energy flows, biodiversity, atmospheric composition and the ecosystem capacity to provide services. Human impact on net primary production provides a comprehensive quantification of both aspects of agricultural intensification: increases in cultivated area and crop yield. It quantifies the portion of ecosystems net primary production used directly or indirectly by humans (Vitousek et al., 1986), reflecting changes in available energy for the trophic web (Field, 2001). Forty-two percent of the potential net primary production was appropriated by humans in 2001/2002 in the Río de la Plata grasslands (Baeza and Paruelo, 2018), a value higher than the 15.2% world average estimated by Vitousek et al. (1986). Such percentage in the Río de la Plata grasslands increased 4.5% during the last year due to land use changes.

Disturbances

Four types of disturbances are particularly important in shaping the structure and functioning of Río de la Plata grasslands. First, the type and magnitude of herbivore load determines a pattern of biomass removal, trampling, defecation, and urination with profound consequences for the entire system (Oesterheld et al., 1999). Lezama et al. (2014) analyzed paired grazed and ungrazed plots across a productivity gradient. Compositional dissimilarity between grazed and ungrazed plots, as well as grazing induced differences in plant richness and beta-diversity, all increased across productivity gradient. Plant species richness increased with grazing in high-productive grasslands. Altesor et al. (2006) found that, in contrast with other grasslands worldwide, the absence of grazing promoted shrub encroachment in the Campos subregion. Dominant species were more strongly suppressed by grazing in the most productive grasslands (Lezama et al., 2014).

Continuing with grazing, it may increase or decrease net primary production and soil carbon content in the Río de la Plata grasslands. In the Flooding Pampa, grazed plots presented lower aboveground net primary production than paired ungrazed areas (Rusch and Oesterheld, 1997). In contrast, in the Southern Campos, grazed areas produced more than the ungrazed ones (Altesor et al., 2005). When the initial biomass was the same, ungrazed areas were 29% more productive. Species and plant functional type

composition or biomass vertical distribution promoted by grazing may explain such differences through changes on resource availability, mainly light. Grazed areas showed higher belowground biomass, belowground net primary production and turnover than ungrazed areas (López-Mársico et al., 2015). Studying a network of grazed and ungrazed sites, Altesor et al. (2006) detected a differential effect on the labile and recalcitrant fraction of the soil organic matter due to grazing. Grazing increases superficial soil carbon content, mainly due to the higher belowground biomass in grazed areas. In the deeper soil layer, ungrazed sites showed higher soil C content because of an increase in the more recalcitrant organic matter pool. Piñeiro et al. (2009) hypothesized that changes in soil organic matter content between grazed and ungrazed stands resulted from the balance between root N retention and N loss. Root N retention is due to changes in belowground N allocation patterns. N loss is related to the ability of the soil to retain the extra N available after the exclusion of herbivores and the cessation of volatilization and leaching from urine and dung patches.

Second, the frequency and intensity of fires determines a pattern of biomass removal, nutrient volatilization, and ash deposition which affect the whole ecosystem (Oesterheld et al., 1999; López-Mársico et al., 2019). Spatial distribution of fire events is influenced by the predominant vegetation type and land use in different magnitudes depending on the region. In savannas and prairies, fire density was lowest in areas with a high proportion of agriculture due to the addition of irrigation and fuel reduction practices (Di Bella et al., 2006). Particularly, in the West Inland Pampa, fire as a management practice is excluded by agriculture (Fischer et al., 2012). In the Uruguayan Campos, mainly occupied by grasslands and even when fires are used to improve forage quality, the detected number of fires was insignificant (Di Bella et al., 2006). In contrast, in the Mesopotamic Pampa and in the Argentinean portion of the Campos, fire density was positively associated with the uncultivated land coverage, mainly represented by grasslands (Di Bella et al., 2011).

Third, year-to-year changes, and even larger-scale trends in climate variables, can affect water availability, a major driving force of these systems (Oesterheld et al., 1999). In the Uruguayan Campos, the year-to-year variability in precipitation was higher than the variation in aboveground primary production (Texeira et al., 2019a). The temporal response of carbon gains to precipitation was strong and positive for all land uses (Texeira et al., 2015; Pagnanini et al., 2019). Although there were not clear trends in precipitation, there was a strong negative trend in carbon gains through time, particularly in rangeland of the Northern Campos of Uruguay. These trends represent a decrease of 10–25% of the annual aboveground net primary production (Texeira et al., 2015). Most of these negative trends were associated to seasonality increase and vegetation loss (Texeira et al., 2019b). On the other hand, positive trends in carbon gains through time were associated to grassland afforestation and native forests (Texeira et al., 2015).

Finally, the type and magnitude of nutrient additions generates nutrient concentration, volatilization and lixiviation with effects on the whole system. Nutrient additions are frequent in the Río de la Plata grasslands (García et al., 2002). In the Flooding Pampa, N addition increased the growth of grasses and P addition increased plant P content (Ginzo et al., 1982, 1986; Ginzo, 1983; Collantes et al., 1998; Semmartin et al., 2007). A season $\times$ environment factorial experiment explored the relative importance of mowing, shading and N and P addition as single factors of aboveground net primary production and nutrient dynamics. N addition during spring and summer had the largest and most extended impact on productivity and N and P uptake, whereas P addition, mowing and shading had a lower effect. Three species groups differentially accounted for these responses (Semmartin et al., 2007).

Land Use Change

The Río de la Plata grasslands experienced a profound transformation through the last four centuries. Starting with European colonization, agriculture expanded, mainly since the early years of the 20th century due to European immigration. The main land-use changes that took place in the region include the replacement of grasslands by annual and forage crops, the replacement of grasslands by tree-plantations, and grazing intensification in native grasslands (Paruelo et al., 2007). Though summer drought restricted in the past annual crops expansion in the western edge of the area, nowadays the spatial variability in cropped area is associated with soil restrictions, particularly salinity and soil drainage in the Flooding Pampa and soil depth in the Campos. Grassland cover was reduced from 67.4 to 61.4% between 1985 and 2004 (Baldi and Paruelo, 2008). During the first decades of the 21st century this trend accelerated (Baeza and Paruelo, 2018; Fig. 11). The increase observed was associated, mainly, to the expansion of double-crops systems (Volante et al., 2015). Afforested area with exotic species, mainly of *Eucalyptus* and *Pinus* genera, also expanded in the Río de la Plata grasslands, mainly in the Northern and Southern Campos and the Mesopotamic Pampa (Baldi and Paruelo, 2008). From 1984 to 2004 tree plantations increased the area occupied from 6.7% to 8.6%. With climatic change, even more critical scenarios are expected for the next decades, due to the growing pressure for food production, particularly soybean (Caetano et al., 2018).

Floods can be one of the consequences of replacing perennial vegetation by annual crops. The replacement of perennial alfalfa pastures by annual crops in the Inland Pampa changes the hydrology functioning. Perennial pastures had higher annual transpiration rates (1075 mm y^{-1}) than double winter/summer crops (778 mm y^{-1}) and single summer crop (679 mm y^{-1}). Significantly deeper water-table levels in pastures compared to single and double cropping (4, 1.5 and 2.1 m, respectively) were suggested by hydrological modeling and confirmed by field observations (Noseto et al., 2015). Field studies suggested enhanced groundwater recharge in croplands and direct groundwater discharge by pastures. Soil profiles, being notably drier under pastures (316 vs. 552 mm stored at 0–3 m depth), prevented the recharge episodes experienced by agricultural plots after an extraordinary rainy

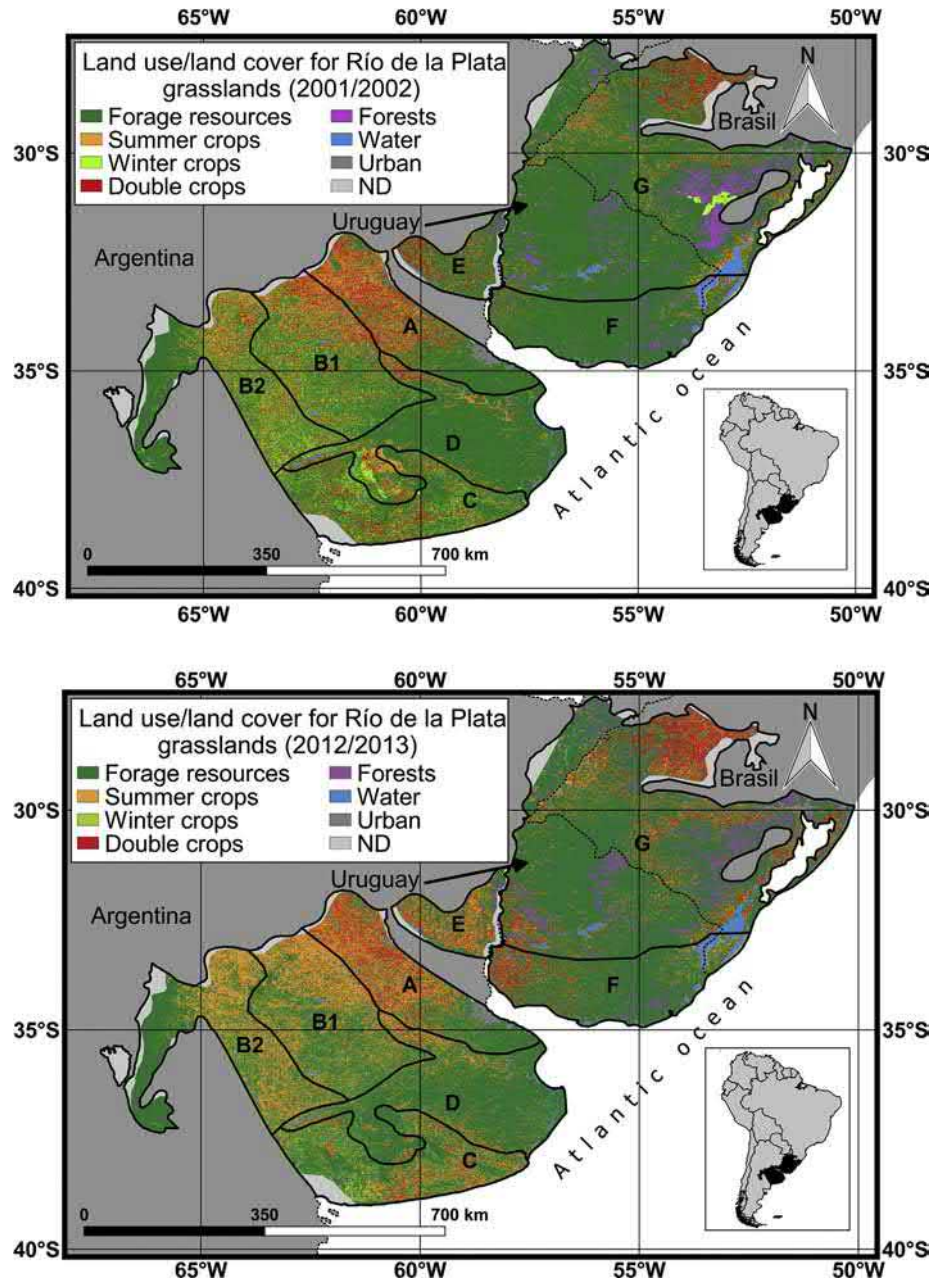


Fig. 11 Land use/land cover maps for Río de la Plata grasslands in two periods. Letters denotes vegetation units as subdivisions of subregions Pampas (A, B1, B2, C, D and E) and Campos (G and F). (A) Rolling Pampa, (B1) Flat Inland Pampa, (B2) West Inland Pampa, (C) Southern Pampa, (D) Flooding Pampa, (E) Mesopotamic Pampa, (F) Southern Campos, (G) Northern Campos. Forage resources are perennial and Forests include afforested areas and native forests. *Dash lines* are international boundaries. Modified from Modified from Baeza, et al. (2018). Spatial and temporal variation of human appropriation of net primary production in the Río de la Plata grasslands. *ISPRS Journal of Photogrammetry and Remote Sensing* **145**, 238–249.

period. The studies from [Noseto et al. \(2015\)](#) indicated that land-use has a direct impact on the hydrology of the subhumid hyperplains of the Pampa, supporting the linkage of groundwater level raises and flood frequency and severity increases with the expansion of grain production systems in the region ([Fig. 12](#)). Floods reduced thermal range and longer frost-free periods ([Houspanossian et al., 2016](#)).

Compared to grasslands, tree plantations had higher primary production ([Vassallo et al., 2013](#)). This production increase was accompanied by higher evapotranspiration rates ([Nosetto et al., 2005](#)) and a lower water yield, responsible of halving stream flow in afforested watersheds ([Jobbágy et al., 2006](#)). In some areas of the Pampa, trees used groundwater increasing the salinity of deep soil and the water table ([Jobbágy and Jackson, 2004](#)).

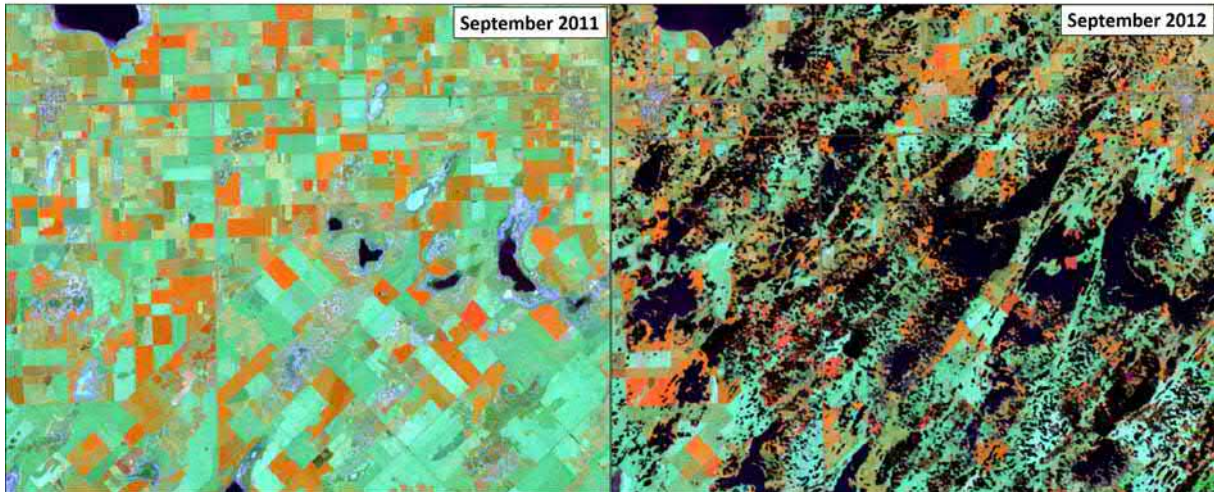
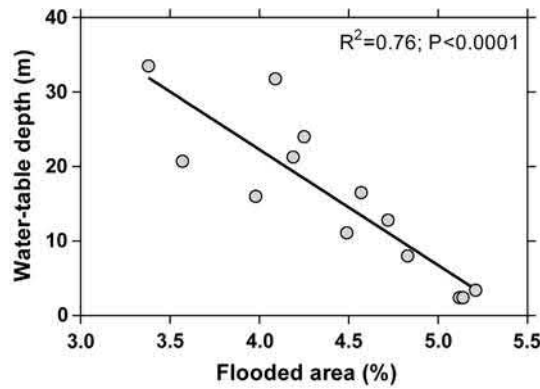


Fig. 12 Relationship between water-table depth and flooded area (top), and Landsat images showing the flooded area in two contrasting dates (bottom), in the core of the Flat Inland Pampa, Río de la Plata grasslands. Modified from Noseto, M. D., Paez, R. A., Ballesteros, S. I. and Jobbágy, E. G. (2015). Higher water-table levels and flooding risk under grain vs. livestock production systems in the subhumid plains of the pampas. *Agriculture, Ecosystems and Environment* 206, 60–70.

Biological Invasions

Of the entire 4864 species of the Río de la Plata grasslands flora, 496 species are exotic (10%) (Andrade et al., 2018). Poaceae, Asteraceae and Fabaceae were the families with the highest number of invasive species, and herbs were the most common life form (Fonseca et al., 2013). Most invasive plants originated from Europe, Asia and Africa, and almost one-quarter of the species are associated with some human use, especially gardening (Fonseca et al., 2013; Poggio et al., 2015). Some invasive species have a very wide distribution, such as *Eragrostis plana* Nees. (capimannoni 2) in the Campos (Medeiros and Focht, 2007; Barbosa et al., 2013; Guido et al., 2016; Caetano et al., 2018) and *Festuca arundinacea* Schreb. (tall fescue) in the Pampa (Scheneiter et al., 2015). In the Pampa, 18–32% of the species are exotic (Fig. 13), while only 4–7% are in the Northern Campos (Chaneton et al., 2002; Lezama et al., 2006; Perelman et al., 2001, 2007, 2017; Bresciano et al., 2014).

Different communities could present a different degree of vulnerability to invasion. In the Northern Campos, the level of grassland conversion into agriculture at the surrounding landscape is one of the main factors driving invasion in grassland remnants (Guido et al., 2016). In the hydromorphic prairies and halomorphic steppes of the Flooding Pampa, the invasion resistance of these communities may be related to flooding events, since there are few exotic species that arrived to the region adapted to conditions so extreme. Consequently, it is observed that the richness of exotic species decreases with the stress level of the soil environment: higher electrical conductivity or lower depth of the surface horizon (Perelman et al., 2007; Fig. 14). In contrast, in the humid mesophyte meadows, where the abiotic conditions are more benign, the resistance to the invasion is generated by a group of native species, the summer perennial grasses (Perelman et al., 2007; see also Bresciano et al., 2014). Most exotic species that invade these grasslands correspond to annual cool-season species, for which it is not expected that their adult individuals will be displaced by the competition of summer perennial grasses. However, towards the end of summer, the large biomass produced by summer grasses interferes with germination and installation of exotic annual cool-season species (Perelman et al., 2007).

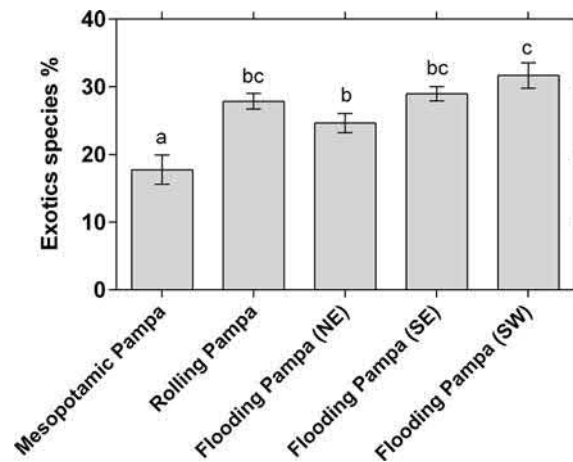


Fig. 13 Mean percentage number of exotic species for five latitudinal grassland areas belonging three vegetation units of the Río de la Plata grasslands. Bars are SE. Means labeled with different letters differ at $P < .05$ (Tukey test after ANOVA). Perelman, S., Burkart, S., Oyarzabal, M., Bagnato, C. and Batista, W. (2017). Climatic and land use drivers along a latitudinal gradient: Species diversity in temperate grasslands on agricultural soils. *Journal of Vegetation Science* **28**(6), 1097–1269.

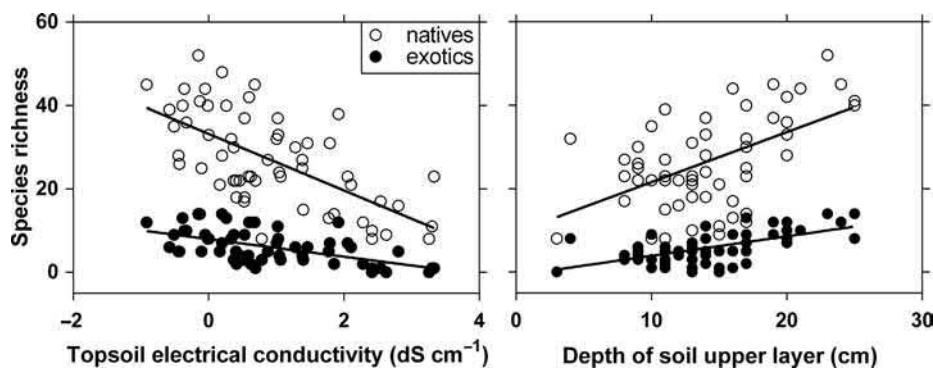


Fig. 14 Relationship of native and exotic species richness with (A) topsoil electrical conductivity (ln-transformed), and (B) depth of soil upper layer. All regressions are significant at $P < .001$. Perelman, S. B., Chaneton, E. J., Batista, W. B., Burkart, S. E. and León, R. J. C. (2007). Habitat stress, species pool size, and biotic resistance influence exotic plant richness in the flooding Pampa grasslands. *Journal of Ecology* **95**, 662–673.

Conservation Status

Four aspects evidence that conservation initiatives in the Río de la Plata grasslands are insufficient. First, most of grassland remnants are located in private properties and under immediate threat of conversion to other land use (Pillar and Vélez, 2010; Bilenca and Miñarro, 2014). Second, despite the vast tradition in botanic and floristic studies (Cabrera, 1976; Perelman et al., 2001, 2017, 2018; Lezama et al., 2006, 2019a, 2010), a red list of grassland species and communities is lacking in Uruguay and Argentina (Berg et al., 2014). Third, the number of protected areas is low, 38 in the Pampa and 61 in the Campos. Such areas covered 3.7% and 6.8% of each subregion area (UNEP-WCMC, 2019), figures below the proportion recommended (10–15%). The selection of these protected areas has been fundamentally opportunistic, based on preexisting and low cost public areas (Overbeck et al., 2007; Baldi et al., 2017, 2019). Finally, grazing and fire disturbances are essential part of the dynamics of grassland ecosystems as described above (Fig. 15). These disturbances contribute to the maintenance of its high biological diversity (Pillar and Vélez, 2010). However, this subject is yet a taboo in conservation of grassland ecosystems (Overbeck et al., 2015), and consequently conservation practices could be ineffective.



Fig. 15 Cows, and *Coleataenia prionitis* tussocks re-growing post-fire in the Southern Campos, Rio de la Plata grasslands. Photo credit: Mauricio Bonifacio.

Appendix: Supplementary Material

Supplementary material related to this chapter can be found on the accompanying CD or online at <https://doi.org/10.1016/B978-0-12-409548-9.12132-3>.

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The Chilean Matorral: Characteristics, Biogeography, and Disturbance

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Abstract

The matorral or Mediterranean scrub biome occurs within a narrow band of central Chile between approximately 30 and 38°S latitude. Bounded on the east by the Andean Cordillera and on the west by the Pacific Ocean, the area is characterized by a winter-wet, summer-dry climate, generally frost-free winters, and prolonged summer drought. A diverse flora includes many sclerophyllous shrubs, some drought-deciduous ones, and an herbaceous understory during winter and spring months. However, within the latter, exotic species which have become naturalized now make up a substantial proportion of the ephemeral flora. Matorral perennial shrub vegetation displays considerable endemism, and is structurally convergent with Mediterranean scrub in California, Spain, and the Mediterranean Basin. Among higher vertebrates, herptiles, birds and small mammals exhibit broad geographic ranges in the matorral and lower species turnover between habitats (β -diversity) than in other Mediterranean scrub areas. Despite low taxonomic affinity, similar to perennial shrubs, there is convergence in major body types, feeding guilds and foraging techniques. Due to anthropogenic disturbance including clearing, fire, and extensive overgrazing/browsing, there are relatively few intact examples of undisturbed matorral left, and greater effort needs to be expended to preserve this highly unique biome. Long-term studies at a thorn scrub site on the northern edge of the matorral suggests that altered rainfall patterns have led to changes in the small mammal assemblage composition. Over time, such effects may also become manifest in the central Chilean matorral.

Introduction

The Chilean Mediterranean shrubland or matorral occurs in a narrow band of the central part of the country between approximately 30° and 38°S latitude from sea level to ca. 1500 m (Rundel, 1981; Armesto et al., 2007). The term “matorral” is used in a broad sense, as it encompasses a wide variety of vegetation assemblages resulting from plant responses to the great diversity of environmental gradients that can be found along the Mediterranean region of Chile (central Chile). This environmental diversity is determined by the combination of high topographic heterogeneity (with the Andean Cordillera to the east, the western Pacific shore, and the intervening Central Valley), a latitudinal aridity gradient (with the Atacama desert at the northern limit and temperate forest at the southern limit), and the presence of the cold Humboldt Current (Rundel, 1981; Luebert and Plissock, 2006; Armesto et al., 2007).

The climate here is characterized as Mediterranean-type with winter-rain summer-drought seasons and generally frost-free conditions (Mooney et al., 1977). The Humboldt Current results in typically dry conditions except in winter; the lack of convective thunderstorms in summer as well as the presence of the high Andes as a rain-shadow is a further hindrance to moisture, especially in summer months. Similar to the structurally convergent chaparral of California and Baja California, the Chilean matorral is strongly influenced by aperiodic episodes of high rainfall as a consequence of the El Niño Southern Oscillation (ENSO) (Armesto et al., 2007). In Chile during such periods, the cold Humboldt Current is displaced vertically resulting in warmer onshore winds and more rainfall during the winter.

The matorral is characterized by a mixture of drought-deciduous and evergreen sclerophyllous shrubs and trees, and a diverse herbaceous plant assemblage (Fig. 1; Armesto et al., 2007). Much of the original biome has been extirpated, and degraded matorral or *espinal* characterizes much of the Central Valley where the terrain now is dominated by thorn acacia (*Vachellia caven*) forming extensive savannas (Rundel, 1981). Many exotic weeds have been introduced due to human activities (Arroyo et al., 2000). In central Chile, 18% of the flora is composed by naturalized species and in some matorral communities alien plants can reach 80% of the total herb abundance (Arroyo et al., 2000; Gómez-González et al., 2011).

As a consequence of a long history of land use change, frequent wildfires and plant invasions, today the matorral has serious conservation problems; less than 30% remains intact, and only 10% is protected (Myers et al., 2000). Well-preserved examples



Fig. 1 Typical matorral with xerophytic species on north-facing slopes and sclerophyllous woodlands on south-facing ones. Photo: F. Ojeda.

of matorral occur in isolated areas (e.g., Parque Nacional Las Palmas de Cocalán near Valparaíso, Parque Nacional La Campana, Reserva Puquén in Los Molles); on the northern edge of the matorral, a notable intact thorn scrub community occurs in Parque Nacional Bosque Fray Jorge (henceforth Fray Jorge). Although not strictly matorral, it may provide insight into the ongoing processes there.

Herein, we review the history, biogeography, and composition of Chilean matorral, the role of anthropogenic disturbance, and conservation status with particular emphasis on its flora and vertebrate fauna. Finally, we discuss salient patterns that have emerged at a well-studied site in Fray Jorge.

History and Geography

The location of the matorral in central Chile is a product of two important geographical features which affect all communities on the west coast of South America: proximity to the Pacific Ocean, and the Andean cordillera. Running N to S in a narrow strip no more than 120 km wide, the biome occupies a region whose climate is strongly influenced by the offshore flow of the Humboldt Current bringing extremely cold Antarctic water northward. This has the effect of cooling eastward-flowing air (which is accentuated by strong seasonal upwellings; [Escribano et al., 2003](#)), thus reducing its moisture capacity—particularly in warm summer seasons—and leading to a single rainy season in winter ([Armesto et al., 2007](#)). The orogeny of the Andes was initiated in the late Mesozoic, but the greatest uplift has been in the past 30 Mya ([Orme, 2007](#)). Beginning about 14 Mya, the Andes isolated present-day Chile from the rest of South America and created the Arid Diagonal (sensu [Abraham et al., 2000](#)). This determined the appearance of the Atacama Desert on the west side of the Andes in northern Chile (one of the driest and oldest deserts in the world; [Rundel et al., 2007](#)) and of the Mediterranean region further south with the development of the sclerophyllous vegetation ([Hinojosa and Villagrán, 1997](#)). It has been proposed that many plant species of the matorral have their origins in drought-adapted vegetation similar to that in the Chaco, the Monte and the Andean PrePuna ([Hinojosa and Villagrán, 1997](#); [Armesto et al., 2007](#)). Some genera were already present during the Tertiary, under a tropical climate (e.g., *Peumus*, *Lomatia*), while others resulted from evolutionary processes that occurred after the Andes uplifted (e.g., *Schinus* and *Puya*) ([Hinojosa and Villagrán, 1997](#); [Rundel et al., 2016](#)). For some faunal elements such as terrestrial mammals, the Andes have been at once a barrier, a center of diversification, and a dispersal corridor ([Raven, 1973](#); [Meserve and Glanz, 1978](#); [Meserve, 2007](#)).

Flora

The Chilean matorral has high floristic richness and a diversity of plant communities due to its environmental heterogeneity ([Arroyo et al., 1999](#)). This heterogeneity is a result not only of the presence of two mountain ranges running N-S (i.e., the coastal range and the Andes), but also the relatively broad latitudinal range of the biome. There is a high degree of endemism, especially at the generic level, as a consequence of the age and geographic isolation of this biome ([Fuentes et al., 1995](#)).



Fig. 2 Arid matorral at Reserva Puquén de Los Molles, Punta Los Molles, Chile. The community here includes many succulents as well as sclerophyllous shrubs and cacti in protected areas. Photo: P. L. Meserve.

According to [Luebert and Plissock \(2006\)](#), the Mediterranean zone of Chile includes six different ecosystem types from north to south (with many subtypes depending on the distance to the shore and altitude), but we can summarize them in three main types: (1) the arid matorral ([Fig. 2](#)), located in the Coastal Range from the south of Coquimbo to Valparaíso, dominated by endemic xerophytic shrubs such as *Flourensia thurifera*, *Bahia ambrosioides*, *Heliotropium pycnophyllum*, and *Colliguaja odorifera*, cacti (e.g., *Copiapoa* and *Eulychnia* spp.) and bromeliads (e.g., *Puya chilensis*); (2) the thorny matorral ([Fig. 3](#)), composed of spiny trees like *Vachellia caven*, and *Prosopis* spp., and xerophytic shrubs (e.g., *Trevoa* and *Baccharis* spp.); and: (3) the sclerophyllous matorral ([Fig. 1](#)), which contains the most typical matorral shrubs and trees, such as *Cryptocarya alba*, *Lithraea caustica*, *Peumus boldus*, *Schinus latifolius*, *Quilaja saponaria*, *Maytenus boaria*, *Kageneckia angustifolia*, and *Azara integrifolia*, among others ([Luebert and Plissock, 2006](#)). In the northern part of the Mediterranean region (31–35°S), thorny scrublands alternate with sclerophyllous woodlands (and relict populations of the Chilean palm, *Jubaea chilensis*, in the Valparaíso region; [Figs. 1 and 3](#)), while in the southernmost zone (36–38°S), sclerophyllous forests mixed with broadleaf evergreen and deciduous forests can be found forming a highly diverse ecotone in the Mediterranean-temperate climatic transition ([Luebert and Plissock, 2006](#)).



Fig. 3 Thorny matorral dominated by *Vachellia caven* and a relict population of the Chilean palm (*Jubaea chilensis*), in Parque Nacional La Campana. Photo: J. Pausas.

There are strong physiognomic similarities among sclerophyllous shrubs in Chile and California, as well as in southwest Africa, Australia, and the Mediterranean Basin (Mooney et al., 1977; Young et al., 2007), but these are due to convergent evolution in similar climates rather than taxonomic affinity (Arroyo et al., 1995). However, the geographic isolation and the virtual absence of fires in Chile has resulted in a relatively less species richness (~3000) in the matorral compared to other Mediterranean-type ecosystems (Rundel et al., 2016). This isolation has generated a high degree of endemism at the generic level (Fuentes et al., 1995).

Floristically, the perennial shrubs and native ephemerals in the Chilean matorral are among the most distinctive in South America, with almost 60% endemism (Young et al., 2007). Although some notable congeners appear in both North and South America (e.g., *Larrea* spp., *Prosopis* spp., *Vachellia* spp.) none are dominant elements in the matorral except for *Vachellia* in the *espinal*. The evergreen shrub *Porlieria chilensis* (guyacán), which dominates the thorn scrub community in Fray Jorge at the northern end of the Chilean matorral, is believed to be of Andean origin (Solbrig et al., 1977) and is in the same family (Zygophyllaceae) as the widespread *Larrea* spp. of northwestern Argentina and southwestern United States.

Fauna

Three faunal groups—reptiles, birds, and small mammals—are particularly useful for illustrating the effects of isolation and spatial heterogeneity on their distributions and local (α or alpha) diversity in the Chilean matorral. While all three groups received a pulse of research activity in the 1970s, subsequent work on reptiles and birds has been surprisingly limited.

Continental Chile hosts five species of snakes and about 120 species of lizards (Ruiz de Gamboa, 2016), the vast majority of which (about 96) are in the extremely diverse genus *Liolaemus* (Liolaemidae). Of these, two snake and about 23 lizard species occur in Mediterranean Chile (Cody et al., 1977; Fuentes et al., 1995; Ruiz de Gamboa, 2016; Uetz, 2019). Fuentes (1976) showed that lizards occurring in the Mediterranean scrub of Chile and California exhibit strong convergence in habitat use, diet, and species turnover between habitats (β -diversity). In particular, he described strong one-to-one matches in the niches of taxonomically-unrelated lizards across these regions. In Fray Jorge, up to 6–8 lizard species occur sympatrically, occupying both the thorn scrub and higher elevational shrub communities in the park (Minn, 2000; Albiñana, 2005). These species range in diet from carnivory (*Callopistes maculatus* [Chilean iguana or tegú]) to insectivory and herbivory (*Liolaemus* spp.). Remarkably, *Callopistes* were more numerous in experimental plots from which avian and mammalian predators were excluded, and they appear to depress numbers of smaller (prey) lizards (Minn, 2000). These observations were not repeated in a second field season, but they comprise a compelling call for further research.

Of about 315 terrestrial bird species known from Chile (Vilina and Cofré, 2006; Jaramillo and Barros, 2013; Couve et al., 2016; Remsen et al., 2019), 108 to 127 (Jaramillo, 2003; Couve et al., 2016) occur in the Mediterranean region. The Chilean matorral has fewer birds than Mediterranean scrub in California (Cody et al., 1977), although α -diversity is similar, indicating that Chilean birds occur in a broader range of habitats, such that species turnover (β -diversity) among habitats is distinctly lower (Cody et al., 1977). Longer-term studies in Fray Jorge (Kelt et al., 2012, 2016) reported 63 species from triennial surveys, suggesting that earlier estimates for the matorral were a significant underestimate due to failure to incorporate periods when birds migrate in from Andean foothills, and during periods of high rainfall associated with ENSO events, and on-going climatic change. In spite of intriguing ecological comparisons between birds of Chile and rather distantly related passerine species in the Northern Hemisphere (e.g., tit-spinetails (Furnariidae, *Leptasthenura*) and tit-tyrants (Tyrannidae, *Anairetes*) versus holarctic parids (Paridae, e.g., tits, *Parus*, or chickadees, *Poecile*) or regulids (Regulidae, *Regulus*); (Ridgely and Tudor, 1994; Jaramillo, 2003), very little comparative behavioral work has been pursued (but see Engilis and Kelt, 2009, 2011). Another intriguing parallel with other arid/semiarid regions is the mutualism between the endoparasitic mistletoe *Tristerix aphyllus*, two species of columnar cacti (*Echinopsis chilensis* and *Eulychnia acida*), and the Chilean mockingbird (*Mimus thenca*; see Kelt et al., 2016). Unlike many other bird-mistletoe associations, however, the *Tristerix-Mimus* relationship is highly asymmetric as the Chilean mockingbird retains a relatively diverse diet and is not tightly bound to the mistletoe for food (cf. Watson and Rawsthorne, 2013).

Cody et al. (1977) and Fuentes et al. (1995) reported on small mammal trends in Chilean matorral; 5–10 species may occur in different matorral habitats resulting in similar α -diversity as in California. However, as is the case for birds, small mammal species in Chile occur in a wider variety of habitats, resulting in lower β -diversity. Also, small mammals show dispersion of feeding specializations (granivory, herbivory, insectivory, omnivory; Glanz, 1976; Meserve, 1981), and in most instances where multiple species share similar diets, one is much more common than the other (Meserve and Le Boulengé, 1987).

The ecological equivalent of fossorial gophers (*Thomomys*, Geomyidae) in California Mediterranean scrub is the endemic cururo (*Spalacopus cyanus*, Octodontidae) in coastal range matorral and Fray Jorge. This rodent specializes on geophytic bulbs, and its colonial activities can alter significantly the composition of the herbaceous community by generating important soil disturbances at the landscape scale (Contreras and Gutiérrez, 1991; Torres-Díaz et al., 2012).

Disturbance

The current physiognomy and composition of the Chilean matorral cannot be understood without considering the role of human disturbance. The landscape of central Chile has been dramatically transformed since Spanish colonization, particularly from the 19th century to the present. After many years of intensive grazing, vegetation removal, and burning, vast areas of matorral have



Fig. 4 Invasion of *Eschscholzia californica* in a disturbed matorral in the Central Valley near Til-Til. Photo: P. L. Meserve.

been converted to degraded habitats, highly susceptible to alien plant invasion and erosion (Arroyo et al., 2000; Fig. 4). Land use change has significantly reduced the distribution of native sclerophyllous shrublands in central Chile since it is a key region for agriculture, livestock, and forestry, and supports ca. 80% of the total population (Heilmayr et al., 2016; Miranda et al., 2017). A consequence of this elevated human pressure and the Mediterranean-type climate is the occurrence of wildfires, which are increasing in frequency and magnitude with climate change (González et al., 2018). Unlike the other Mediterranean-type biomes of the world, natural fires are rare in Chilean matorral, and fire adaptations are less frequent in the flora (Montenegro et al., 2004; Gómez-González et al., 2017). Although the most common woody species are able to resprout after fire (e.g., *Lithraea caustica*, *Quilaja saponaria*, and *Peumus boldus*), post-fire germination and seedling recruitment is scarce (Muñoz and Fuentes, 1989; Segura et al., 1998). Many fire-intolerant species are endemic and therefore carry important conservation value (e.g., *Azara petiolaris*, *Cryptocarya alba*, *Kageneckia angustifolia*, and *Podanthus mitiqui*; Gómez-González et al., 2017). Therefore, fire reduces woody plant diversity (Armesto and Gutiérrez, 1978) and favors the development of annual grasslands dominated by alien species (Gómez-González et al., 2011).

Besides wildfires, the matorral is subjected to high pressure from exotic herbivores (livestock and naturalized European rabbits [*Oryctolagus cuniculus*] and hares [*Lepus europaeus*] Holmgren, 2002). These herbivores can also favor alien plant invasion and limit the establishment of the seedlings of native woody species in open microhabitats (Fuentes et al., 1984; Holmgren, 2002). Therefore, active restoration has been recommended to overcome the recruitment limitations of native species in the matorral (Armesto et al., 2009). Currently, a national restoration program is needed to recover the biodiversity and generate more sustainable landscapes that improve social adaptation to frequent wildfires and climate change.

Conservation

As noted previously, the Chilean matorral is considerably reduced in area due to its location near the most populated and accessible parts of central Chile. Historically, with relatively little montane vegetation there, much of the sclerophyllous woodlands were rapidly cleared for construction material, and matorral was burned for charcoal production in colonial times (Rundel, 1998). Further, many remaining areas were greatly altered by goat overgrazing resulting in extensive *espinal* savannas today in the Central Valley. On the north end of the region known as the “Norte Chico,” extensive areas of denuded shrublands now exist with little prospect of recovery (Bahre, 1979). A concerted effort for “reforestation” of such areas by the Chilean government and conservation/park agencies (e.g., CONAF) has resulted in a monotonous landscape dominated by exotic saltbush (mostly *Atriplex nummularia*) which supports few birds or mammals (Kelt and Meserve, 2016). On the other hand, extensive forest plantations of *Eucalyptus* spp. and *Pinus* spp. have contributed significantly to the loss of native vegetation in the Mediterranean zone of Chile, particularly in the Coastal Range of the Maule Region, where the matorral and the temperate rain forest meet to form a highly diverse ecotone (Heilmayr et al., 2016; Miranda et al., 2017). In the current scenario of warming and drought, the transformation of native forests into plantations and agricultural areas is increasing fire risk and damage at landscape scale (González et al., 2018; McWethy et al., 2018; Gómez-González et al., 2019), contributing to the degradation of contiguous natural areas of elevated conservation value.

Without a concerted effort to set aside significant new areas for preservation, the prospects for conservation of the matorral's biota are dim, especially given the high degree of endemism and increasingly endangered plants and animals there (e.g., [Squeo et al., 2001](#)). Further, with increasing evidence of the impact of climate change on Mediterranean-type ecosystems (e.g., [Oechel et al., 1995](#); [Hilbert and Canadell, 1995](#)), there is great urgency for such efforts.

Fray Jorge, a Sentinel Site

Since 1989, a long-term field manipulation has been in progress at a thorn scrub site on the northern edge of the Chilean matorral ([Fig. 5](#)). This experiment has focused on identifying and quantifying factors influencing community dynamics including biotic interactions (i.e., vertebrate predation, herbivory, interspecific competition) and abiotic factors (i.e., rainfall, climate change). Results from this multifaceted project have been reported elsewhere (e.g., [Kelt et al., 2016](#); [Meserve et al., 2016a,b](#)), and are only briefly summarized here. They highlight the importance of long-term studies in this region, and the increasing evidence for, and impact of, ongoing climate change.

The initial focus of this research was on the role of biotic interactions in small mammal populations, and indeed, evidence for strong predator effects on elements of the small mammal assemblage have been demonstrated, but these effects were transitory in nature and predation neither prevented small mammal increases nor accelerated their decline. At the same time, important effects of a small mammal herbivore (the degu, *Octodon degus*) on Mediterranean scrub vegetation have been documented (e.g., [Gutiérrez et al., 1997](#); [Gutiérrez and Meserve, 2000](#)) and we tested the effects of food addition on this and other small mammal species ([Meserve et al., 2001](#)). In the latter study, food addition did not elicit responses by *O. degus* and another herbivore, Darwin's pericote (*Phyllotis darwini*), during a high rainfall year, but did induce increases in a drought year. Overriding these results, however, is the importance of background climatic events such as ENSOs on the majority of small mammals of this community. In 2000–02, a prolonged high rainfall event led to record increases in degu populations, and degu numbers and biomass have remained high in ensuing years instead of returning to previously lower numbers ([Meserve et al., 2016a](#)). This suggests that a fundamental shift may have occurred in the small mammal assemblage, leading to a new stable point; [Scheffer \(2009\)](#) has termed this a "critical transition." We suggest that the pattern of somewhat lower average annual rainfall with markedly reduced interannual variation may be responsible for this shift. Long-lived small mammal species such as *O. degus*, formerly unable to increase cumulatively because of long intervals between high rainfall events and periodic drought periods, were able to maintain high populations because of more predictable (albeit lower) annual rainfall. On the other hand, recent accentuation of differences in mean annual rainfall may indicate a return to previously existing conditions.

Whether other community elements will experience such a transition in the near future remains to be seen, but we have seen evidence for increased interactions between native and exotic ephemerals as well as between native small mammals and exotic lagomorphs (*Lepus europaeus* and *Oryctolagus cuniculus*) at this site. These novel interactions are playing out a period of dramatic climate change in the region, and it remains uncertain how these will play out in the coming decades. Ongoing work at Fray Jorge, now in its 32nd year, continues to provide surprises and insight as we monitor this system.



Fig. 5 Thorn scrub community in Parque Nacional Bosque Fray Jorge. Dominant shrubs include *Portieria chilensis*, *Adesmia bedwellii*, and *Proustia pungens*. This site has been protected from disturbance since about 1940. Photo: P. L. Meserve.

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The Mediterranean Floristic Region: High Diversity of Plants and Vegetation Types

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Abstract

One of the richest hotspots of the world is the Mediterranean floristic region with over 24,000 species distributed in the large territory (2,300,000 km²) of the Mediterranean Basin. High numbers of genera (around 2000) and families (around 200) have been recorded, which gives this region the richest figures of the five mediterranean floristic regions of the world. All these taxa group together into numerous habitats (c. 150) and vegetation types brought about by main abiotic (climate, soil types and altitudinal gradients) and biotic (autoecology and ecological interactions) characteristics. This chapter summarizes floristic and vegetation richness over the last geological epochs, considering historical biogeography and past climatic events, which have shaped the distribution of plants in southern Europe and northern Africa. Time-calibrated phylogenies and the fossil record help interpret a long period of extinctions of Tertiary lineages in the Neogene giving the opportunity of speciation to other plant groups. Vegetation arranged into five vegetation belts (thermo-Mediterranean, meso-Mediterranean, supra-Mediterranean, oro-Mediterranean, cryoro-Mediterranean) is understood as a dynamic ecological succession in which vegetation transition occurs in a predictable series of grasslands, shrublands and woodlands.

Predictable Climate

There exist some seasonal characteristics that make any mediterranean climate predictable. Since the establishment of the mediterranean climate in the Old World about 2.8 millions of years ago, a long hot summer is expected every year. Any mediterranean-type biome of the world is located in southwest territories of most continents (California, Chile, South Africa, Australia and the Mediterranean Basin) and characterized by a long drought when temperatures are the highest (summer) (Fig. 1A). This is why fire is particularly lethal during summer months. Strategies of fire persistence in woody shrubs, annuals and geophytes are common, albeit less remarkable than those of other Mediterranean floristic regions such as South Africa (Rundel et al., 2018). Main rainfall occurs in autumn, winter or spring depending on country location. Indeed, rainfall and temperature regimes are not homogeneous across a large territory such as the Mediterranean Basin (Fig. 2). On the one hand, temperatures significantly vary depending on proximity of the areas to the Mediterranean Sea that always buffers low temperatures in winter, while inland areas suffer from more extreme day/night and winter/summer changes in temperatures. On the other hand, rainfall is also related to sea and ocean proximity where precipitation is generated by favorable atmospheric currents. Western areas have a strong oceanic (Atlantic) influence that diminishes eastwards. Eastern areas are influenced by precipitation primarily generated from the Mediterranean Sea and occasionally after the monsoon season (Giannakopoulos et al., 2011; Lionello and Sanna, 2005).

The elevational gradient in mountains consists of a decrease in temperature at increasing elevation (about 0.8°C mean average every 100 m.a.s.l.). Mountains provide not only lower temperatures but also higher rainfall, which give high altitude areas more similar conditions to those of the Eurosiberian floristic region (Fig. 1). In contrast, numerous mountains bring about rain shadows producing drylands on southern slopes (e.g. the Spanish Almería desert and the Moroccan Anti-Atlas) and extreme deserts out of the Mediterranean floristic region (e.g. south of the Mediterranean Basin). Lack of sufficient rainfall because of the influence of the largest desert of the world (Saharan dessert) also makes extreme deserts in some African areas nearby the Mediterranean coast (Fig. 2). Capes and islands buffer temperatures because they are embedded in the influence of the Mediterranean Sea.

All these characteristics make significant differences in a large territory such as the Mediterranean Basin, even though a summer drought takes place every year in every country. Indeed, climate is highly predictable in terms of both temperature and rainfall at a local scale. However, the effects of climate change on plants have been already detected (Aguilera et al., 2015). Flowering phenology is one of the variables most used to assess quick plant response to climate change. Although precipitation is involved in flowering variation, temperature affects the most plant species in flowering phenology across the Mediterranean Basin (Petanidou et al., 1995; Gordo and Sanz, 2010).

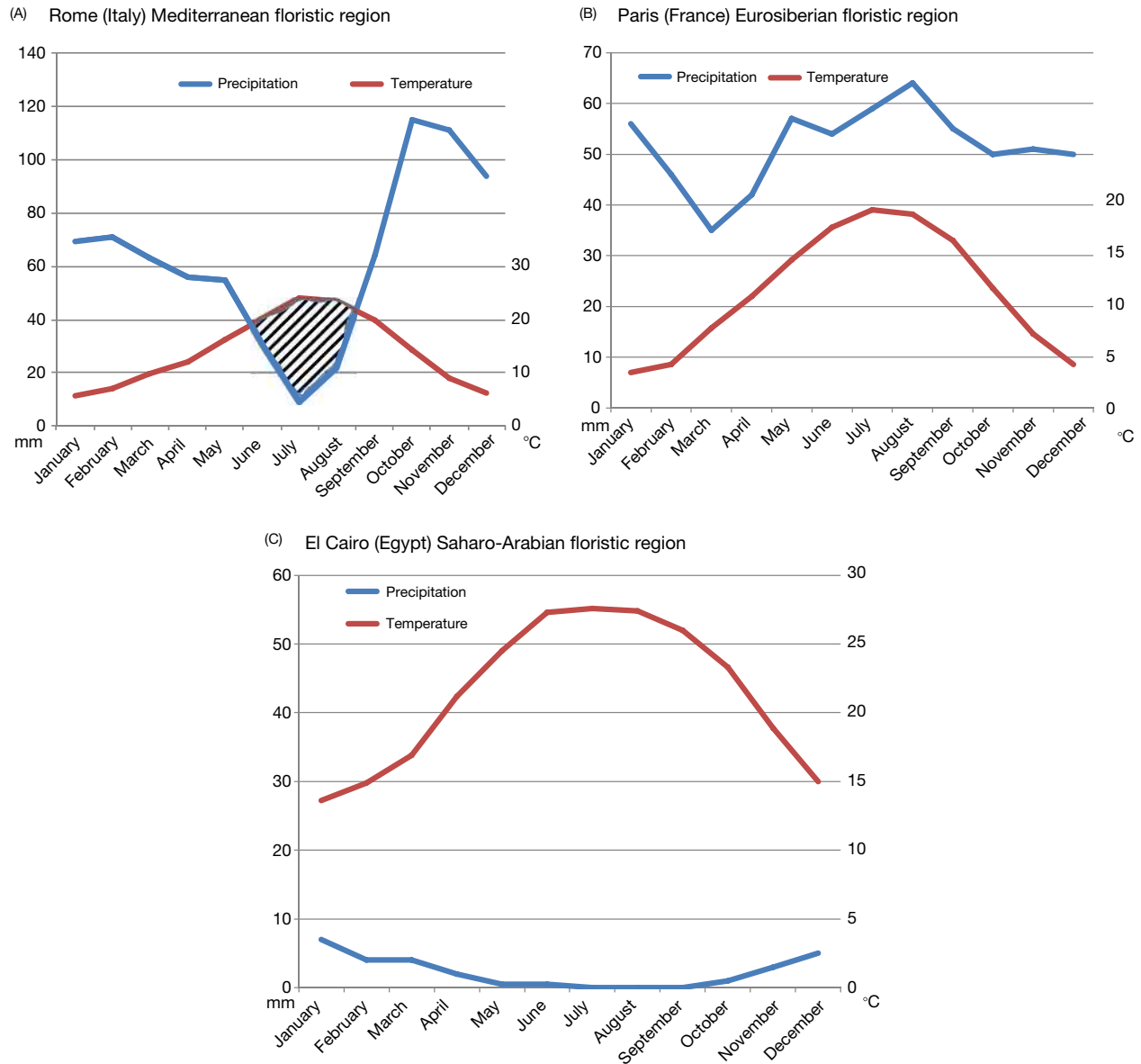


Fig. 1 Climographs (ombrothermic diagrams) for a locality (Rome) of the Mediterranean floristic region, a locality (France) of the Eurosiberian floristic region and a locality (El Cairo) of the Irano-Saharan floristic region. Each climograph displays data for monthly average precipitation and monthly average temperature. The scale of temperature is half of the value of the rainfall scale. Notice that only the Mediterranean locality (Rome) has an intersection of lines (shadowed), i.e. the station has a long dry season in summer.

Biodiversity Primarily Shaped by Geography and Soils

Geographic speciation is predominant in the evolution of plants, which is particularly exacerbated when a territory has numerous geographic features (Fontdevilla, 2014). Indeed, geographic isolation has been particularly effective in the Mediterranean Basin, where numerous islands, peninsulas and high mountains are broadly distributed (Rundel et al., 2016; but see ecological speciation in Fernández-Mazuecos and Vargas, 2010). As a result, a high number of narrow endemics are observed across countries of southern Europe and northern Africa because of strong spatial isolation (Fernández-Mazuecos et al., 2014). Over 10,000 islands (and islets) distributed across the Mediterranean Basin illustrate significant areas for geographic isolation (de Montmollin and Strahm, 2005). The number of capes is even higher (Fig. 2). Abundant opportunities for species isolation have been also provided by high mountains that built up since the Paleogene (Rosenbaum et al., 2002). Species isolation by altitude is also remarkable because mountains about 2000 m above sea level are scattered across southern Europe as a result of plate collision of the three main peninsulas (Iberia, Italian and Balkan) and the European plate in the Tertiary (Hewitt, 2011). Interestingly, these three peninsulas harbored a great deal of plant lineages that became relicts after the glaciations of the Quaternary. In northern Africa, the largest mountain range is the

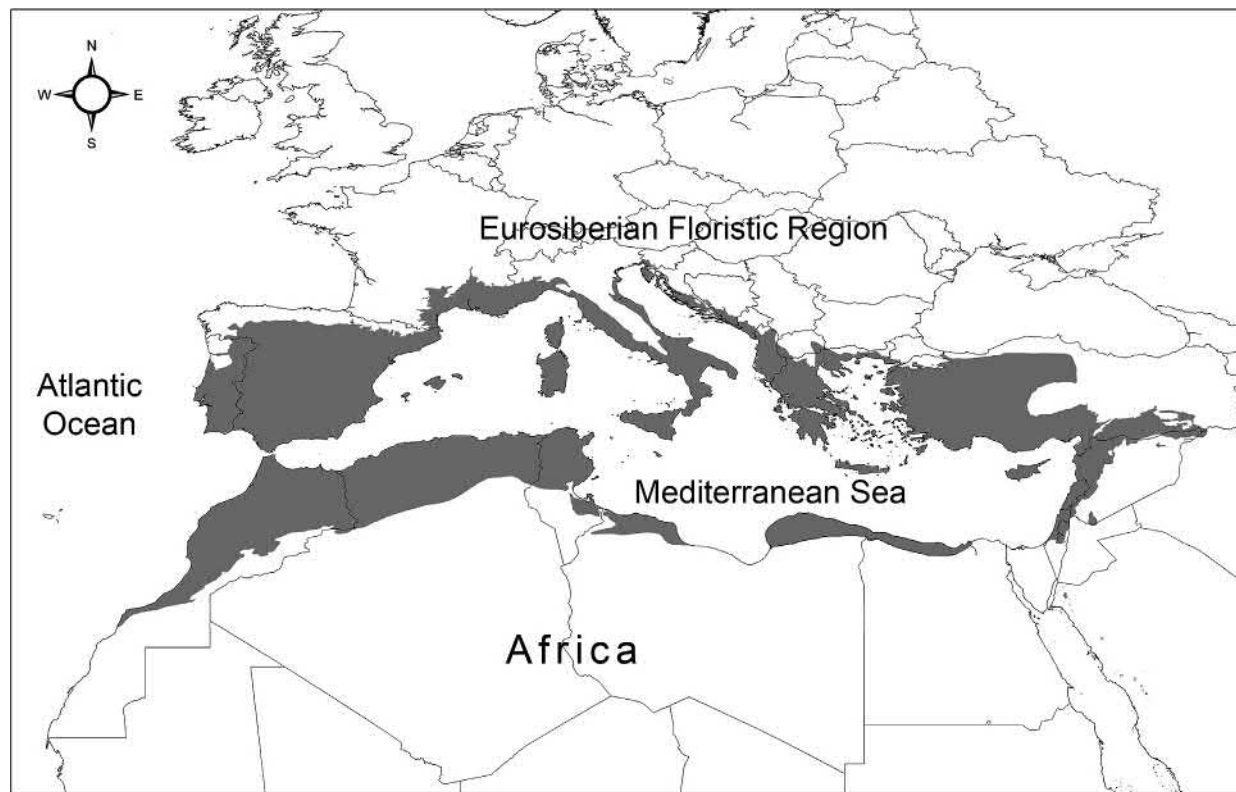


Fig. 2 Map of the Mediterranean floristic region (shadowing). This map is based on Ecoregions 2017 © *Resolve* (<https://ecoregions2017.appspot.com/>) with some modification from Vargas and Kadereit (2001).

Atlas, which is the result of orogenic movements finally uplifted in the Miocene (Babault et al., 2008). The east–west orientation of most of these mountain ranges hindered north–south migrations during glaciations in most of the territory except for central Italy and Greece. Additionally, the east–west orientation of the Mediterranean Sea has also been a significant geographical barrier for plant dispersal between North Africa and Europe, with exceptions of land proximity on the straits of Gibraltar and Tunisia–Sicily (Rodríguez-Sánchez et al., 2008; Rodríguez-Sánchez and Arroyo, 2011).

As a result of the Mediterranean geographic setting, most narrow endemics are found either on islands or medium-high mountains (Lavergne et al., 2004; Fernández-Mazuecos et al., 2014; Jiménez-Mejías et al., 2015). Indeed, migration barriers have been responsible for patterns of isolation, including recent-most differentiation of subspecies inferred by phylogeographic analyses (Vargas, 2003). Species (phylogenetic) differentiation is associated with geographic isolation over longer periods of time (Vargas et al., 2018). Therefore, taxonomic ranks (genera, species, subspecies) appear to be a reliable proxy to generate evolutionary hypotheses.

Speciation of Mediterranean plants is also clearly linked to soil types, which determine geographic occurrence of plants (Thompson, 2005). Botanists consider two basic soil types related to plant distribution. On the one hand, Cenozoic deposits of calcareous sediments resulted in extensive plains and coastal mountains. On the other hand, inland mountains are primarily made of acid soils derived from granites, shales and sandstones. Indeed, the majority of species are well adapted mainly to limestone (calcareous) or acidic soils (granites, shales, sandstones), while a lower number of species are competitive on both substrates (soil tolerant plants). Therefore, the two main soil types (calcareous vs. siliceous) are good predictors of plant distribution. Plants are also adapted to saline soils (halophilous species) extensively found along the 46,000 km of Mediterranean coast, which offers an interesting linear system to test evolutionary and phylogeographic hypotheses (Kadereit et al., 2005). Adaptation to gypsum soils is particularly interesting in the Mediterranean region given that many edaphoendemics are found narrow in areas of northern Africa, the Iberian Peninsula and Anatolia (Escudero et al., 2015). Soil requirements are exacerbated in Mediterranean (vs. Eurosiberian) conditions because nutrient uptake is limited by lack of water, which primarily occurs in the 2–4 months of summer (Lamont, 1982). The same is true for serpentine soils (Oyornate, 2008), although speciation is low because they are scarce in the Mediterranean Basin. Given that plant isolation is related to both edaphic adaptation and geographic confinement, the question remains as to whether geography or soils have been the most significant drivers of speciation (Molina-Venegas et al., 2013).

Pollination is one of the most developed disciplines in the search for ecological factors promoting diversity of Mediterranean flowering plants because insect diversity parallels that of flowering plants. Although the Mediterranean Basin mostly lacks vertebrate pollinators, unlike in other Mediterranean floristic regions (primarily South Africa), abundance and diversity of insect pollinators entail intense evolutionary pressures as revealed by a considerable range of flower forms and differential phenologies (Herrera, 1992). Flowers with a high level of generalization are common in Mediterranean areas (Gómez et al., 2007) coexisting with



Fig. 3 Snapdragons (*Antirrhinum*) show the most occluded corolla of angiosperms, and bees are the main pollinators of the 24 snapdragon species. Photo of *A. graniticum* pollinated by *Xylocopa violacea* in Colmenar Viejo (Spain).

some of the most specialized flowers of angiosperms such as *Ophrys* and *Antirrhinum* (Vargas et al., 2017) (Fig. 3). Numerous reproductive systems and flower morphologies suggest that pollination shifts are responsible for a significant part of plant diversity in the Mediterranean Basin.

Mediterranean Floristic Richness

The Mediterranean Basin harbors a rich flora of over 24,000 species (Greuter, 1991) in a large territory that accounts for 75% (2,300,000 km²) of global Mediterranean-type floristic regions (Rundel et al., 2016). Using floristic of data, we estimated a total of around 2000 genera and 200 families for the native species of the Mediterranean floristic region (Euro+Med, 2006; Greuter et al., 1986–1989; Tutin et al., 1964–1980). At the genus level, species diversity is also deeply uneven with a great deal of monospecific genera co-occurring with hyperdiverse genera. For example, botanists recognize 27 monospecific angiosperm genera of a total of around c. 1132 genera (c. 5537 species) for the Iberian Peninsula (Aedo et al., 2017). In contrast, some other genera are hyperdiverse in the Mediterranean Basin: *Astragalus* (429 spp.), *Centaurea* (533 spp.) (Fig. 4), *Hieracium* (547 spp.), *Satureja* (124 spp.), among others (data from Greuter et al., 1986–1989; Greuter and Raab-Straube, 2008).



Fig. 4 The genus *Centaurea* with over 500 species is one of the most diverse in the Mediterranean Basin. Photo of *C. ornata*, Madrid, Spain.

About 700 woody species are distributed across the Mediterranean Basin (Fady and Conord, 2010). The Fabaceae, Lamiaceae, and Cistaceae provide the highest number of shrub species, while trees are mostly found in the Fagaceae, Pinaceae, Rhamnaceae, Rosaceae and Salicaceae. The diversity of tree species is, however, low (c. 220 species) in comparison with other biomes at similar latitudes (Médail et al., 2019). Numerous annual herbs (up to 50% in some local floras) are found in the Asteraceae, Brassicaceae, Caryophyllaceae, Lamiaceae and Poaceae (Fiz et al., 2002). The high number of endemic species (6318 spp.) indicates successful isolation of populations relatively long-term (Greuter, 1991). A low number of species (2.5%) are introduced, which indicates that the Mediterranean flora is really competitive against aliens.

Proportional levels of vascular plant diversity have been recorded in countries of the eastern (Greece, 5000 spp.), middle (Italy, 5600 spp.) and western (continental Spain, 5050 spp.; Morocco 3675 spp.) Mediterranean Basin (Davis et al., 1994). A detailed analysis shows similar levels of species–area relationship between Spain and Greece, which have medium levels in comparison to the other four Mediterranean floristic regions (Cowling et al., 2015). The Mediterranean region shows richer levels of species diversity than nearby floristic regions. However, the highest diversity is found when the Eurosiberian and the Mediterranean regions meet on the northernmost limit (Fig. 2). This boundary is easier to be established when mountain ranges shape more extreme climatic conditions that fit into Eurosiberian (cold winter, rain all year round) and Mediterranean (rainy winter, dry summer) conditions. However, botanists do not always agree about the boundary at lowland areas.

Two floristic topics still under investigation are: (i) delimitation of the Mediterranean region boundaries, and (ii) addition of peripheral territories to the Mediterranean floristic region. On the one hand, boundaries of the Mediterranean region with the Euro-siberian region on the north (Europe) and the Saharan region on the south (Africa) have been fluctuating over the last millions of years as a result of climate change (Fig. 2 for estimated limits). On the other hand, the floras of Macaronesian islands challenge the classification of floristic regions of Europe and Africa (Takhtajan, 1986). While Azores has a strong European (Atlantic) floristic connection, the Canary Islands close affinities with the Mediterranean floristic region and the Cape Verde islands with the Sahara. Recognition of Macaronesia as a group of archipelagos conforming its own floristic region, rather than each archipelago included in continental floristic regions, is still under debate (Takhtajan, 1986; Finnie et al., 2007; Rivas-Martínez, 2009).

Plant relationships between floras as well as key species help delimit floristic regions. In particular, presence of the Mediterranean olive tree (*Olea europaea* L. subsp. *europaea*) is considered by paleobotanists as the best indicator of mediterraneity in natural areas of the Mediterranean Basin (Carrión et al., 2010). The natural range of this olive is indeed used to define the extent of the mediterranean climate (Besnard et al., 2013; Carrión et al., 2010). Interestingly, *Olea europaea* is also distributed in Madeira (subsp. *cerasifomis*) and the Canary Islands (subsp. *guanchica*), which indicates relatively old climatic connection between Mediterranean and Macaronesian lowland areas. Additional signal of mediterraneity is given by the fact that countries of the other four Mediterranean floristic regions of the world easily cultivate the olive tree and other Mediterranean crops. One more example is given by the holm oak (*Quercus ilex*) and relatives (*Q. rotundifolia*, *Q. calliprinus*, *Q. coccifera*) (Fig. 5), which are dominant trees in lowland areas and suggest historical mediterranean conditions (Ochando et al., 2019). All these trees have played a central role in both diet and vegetation of human cultures over millennia.



Fig. 5 The genus *Quercus* has numerous species dominant in Mediterranean vegetation types. Photo of *Q. coccifera*, Madrid, Spain.

Biogeography at the Cross-roads of Three Continents

Historical biogeography reveals that the flora of the Mediterranean region is a melting pot of plant lineages from Europe, Africa and Asia that survived and differentiated primarily as a result of geography and recent climatic events. The four last glaciations that took place in the Pleistocene not only drove numerous lineages of plants to extinction but also vegetation communities. As a result, the Mediterranean Basin harbors numerous floristic lineages of Pliocene and Quaternary origin coupled with a few ancient lineages from pre-mediterranean epochs (Vargas et al., 2018). Four waves of extinction during the Cenozoic and Quaternary took a toll on many lineages: tropical elements by emergence of strong seasonality in the middle Miocene (16–14 Ma); tropical and subtropical elements by aridification during the Messinian Salinity Crisis (6–5 Ma); and mesic elements by cool temperatures and drying during Quaternary glaciations (<2.5 Ma) (Postigo-Mijarra et al., 2009; Barrón et al., 2010). Thus, descendent lineages of the Cenozoic paleoflora that once occupied wide areas of warm temperate rainforests and swamp forests of the Northern Hemisphere compose only a small part of the modern flora (Rundel et al., 2016). Intensification of seasonality and the onset of a full Mediterranean-type climate in the Pliocene and Pleistocene were associated with the disappearance of many paleotropical and mesic temperate forest taxa and gave way to the Mediterranean-type vegetation that exists today. Indeed, there is paleobotanical and phylogenetic evidence for early mediterranean conditions in some areas of southern Europe during the Miocene (Vargas et al., 2018), followed by the establishment of a mediterranean climate across the Mediterranean basin in the last 2.8 million years (Suc, 1984). This, together with extinctions during Quaternary glaciations, gave plants new environment opportunities to differentiate. The lack of angiosperm families endemic to the Mediterranean Basin, with the exception of the monotypic carnivorous *Droserophyllaceae*, supports the explanation of failure of long-term isolation and relatively recent immigration of many lineages. Nevertheless, several paleotropical lineages—for example, *Myrtus* (Myrtaceae) (Fig. 6), *Phillyrea* (Rhamnaceae), and *Pistacia* (Anacardiaceae)—overcame the environmental and climatic challenges of the late Cenozoic and remained as widespread components of the modern flora in the region (Barrón et al., 2010).

Plant connection between the northern (Europe) and southern (Africa) sides of the Mediterranean region has been challenged by dispersal biogeography. Current studies of biogeography test two competing hypotheses when analyzing plant disjunctions: vicariance as a result of the opening of the Strait of Gibraltar and subsequent refilling of the Mediterranean Basin (Zanclean flood) and long distance dispersal (Sanmartín, 2014). Phylogenetic and phylogeographic studies indicate that the Mediterranean Sea has been a permeable barrier for many plants (Rodríguez-Sánchez et al., 2008) irrespective of diaspore dispersal syndromes (Guzmán and Vargas, 2009).

Historical biogeography helps understand the geographic distribution of plants in an evolutionary framework, in which ecological requirements are also analyzed (Sanmartín, 2014). The woody flora of the Mediterranean region shows that not only adaptation but also phylogenetic constraints and lineage age are of substantial importance for explaining covariation among life-history traits and associated ‘character syndromes’ in plant communities (Herrera, 1992). Ecological results reveal that many key traits considered as plant response to mediterranean climates are found in leaves (Paula and Pausas, 2006; Guzmán et al., 2009). Indeed, one of the distinctive features of Mediterranean-type plants of the world is sclerophylly: thick, tough leaves with thick cuticles and small, thick-walled cells (Paula and Pausas, 2006). Although phylogenetic evidence of rapid speciation associated with the non-sclerophyllous plants (herbs) was found, a syndrome-driven local diversification has also been described for shrublands under mediterranean conditions (Verdú and Pausas, 2013). Rapid diversification has been referred to as plant radiation, which should be reflected in a greater morphological and/or physiological divergence among species in brief periods of rapid diversification from a single



Fig. 6 Despite the family Myrtaceae has a single species in the Mediterranean floristic region, time-calibrated phylogenies reveal that the myrtle (*Myrtus communis*) forms a paleotropical lineage. Photo taken in Chipre (by M. Luceño).



Fig. 7 Representatives of the adaptive radiation of rockroses (*Cistus* spp.): (A) *C. clusii* (Spain); (B) *C. ladanifer* (Spain); (C) *C. laurifolius* (Spain); (D) *C. monspeliensis* (Spain); (E) *C. creticus* (Morocco); (F) *C. crispus* (Morocco).

ancestor. Some of the best examples have been found in herbaceous plant groups well represented in the Mediterranean Basin (*Astragalus*, *Centaurea*, *Dianthus*, *Silene*, *Ophrys*), rivaling or exceeding the fastest known global plant radiations (Valente et al., 2010; Breitenkopf et al., 2015). Geographic speciation is closely associated with plant ‘radiation’ in the Mediterranean, while ecological factors are considered responsible for species ‘adaptation’, i.e. both together meet the conditions for ‘adaptive radiation’ (Schluter, 2000). The first example of adaptive radiation of Mediterranean plants was described in *Cistus* (Guzmán et al., 2009) (Fig. 7), one of the most characteristic bushes in vegetation dynamics after Mediterranean woodland deforestation.

Vegetation Dynamics

The vegetation of the Mediterranean floristic region is dominated by evergreen trees and shrubs adapted to survive long hot summers without rainfall. Rich floristic regions have historically challenged a practical classification of plant communities (Dallman, 1998). Indeed, plant richness across the Mediterranean Basin region not only outnumbers that of the other mediterranean floristic regions of the world given that it covers a territory that is 75% of all Mediterranean-climate countries, but also entails a greater number of habitats (c. 150) (Sundseth, 2009). Similarly to plant evolution, the three main drivers of plant community

assemblages are geography, topography and soil types. Indeed, vegetation across the Mediterranean Basin is clearly determined by base- or acid-rich soils that filter species distributions (Oyonarte et al., 2008).

Early phytogeographers of the 18th century such as Linnaeus and Soulavié described the distribution of European plants into altitudinal patterns of vegetation (vegetation belts) (Egerton, 2018). Subsequent description of plant distributions and altitudinal zonation was applied to any mountainous territory of the world (Humboldt, 1807). In particular, there is agreement in recognizing five vegetation belts in the Mediterranean region: (1) coastal scrub (maquis/garrigue/phrygana) and conifer-oak woodlands on inland hills (thermo-Mediterranean vegetation belt); (2) sclerophyll woodland on plains and piedmont (meso-Mediterranean); (3) oak and pine woodlands up to the altitudinal timberline (supra-Mediterranean); (4) high-altitude bush communities (oro-Mediterranean); and (5) alpine communities of herbs (cryoro-Mediterranean).

Thermo-Mediterranean vegetation belt—Coastal scrub called *maquis* (dense shrubs) and *garrigue* (scattered shrublets) in western countries (Fig. 8) and *phrygana* in Greece (Fig. 9) is dominant, although the climax is believed to be reached when woodlands of the olive tree (*Olea europaea*), the carob tree (*Ceratonia siliqua*) and pine trees (*P. halepensis*, *P. pinea*) find optimal conditions. Communities at this altitude are analogous to those of the basal belt of the Eurosiberian region. Most representative plants are classified mainly in eight angiosperm families of bushes that are distributed in patchy patterns after tree deforestation: Anacardiaceae (*Pistacia* spp.); Cistaceae (species of *Cistus*, *Halimium*, *Helianthemum* and *Fumana*); Euphorbiaceae (*Euphorbia acanthothamnus*, *Euphorbia dendroides*); Fabaceae (species of *Genista*, *Ulex*, *Stauracanthus*, *Calicotome*); Lamiaceae (*Rosmarinus officinalis*, *Thymus* spp., *Salvia* spp.); Myrtaceae (*Myrtus communis*); Palmaceae (*Chamaerops humilis*); Rhamanceae (*Rhamnus* spp.); and Rosaceae (*Sarcopoterium spinosum*). Despite human deforestation, some woodland areas of conifers (*Pinus pinea*, *Pinus halepensis*, *Juniperus phoenicea*, *Juniperus oxycedrus*) are still preserved and even favored because human activities for timber. Many herbaceous species in the Asteraceae (e.g. *Asteriscus maritimus*, *Pallenis spinosa*, *Carlina corymbosa*, *Centaurea alba*), Poaceae (e.g. *Brachypodium pinnatum*, *Hyparrhenia hirta*, *Lamarckia aurea*, *Aira caryophyllea*, *Vulpia bromoides*) and Euphorbiaceae (*Euphorbia characias*) are widespread. The oleander (*Nerium oleander*) and tamarisks (*Tamarix* spp.) occur when ravines cross the coastal scrub of the phrygana (east) and maquis (west).

Meso-Mediterranean vegetation belt—The altitude zone between 300 and 800 m.a.s.l. is dominated by evergreen trees and shrubs. They form sclerophyll woodlands on mountain foothills analogous to the lower montane belt of the Eurosiberian region. These woodlands are less patchy than coastal groves because of dominance of particular trees such as the helm oak (*Quercus ilex*/*Q. calliprinos*) in drier areas (Fig. 10), while other *Quercus* species are predominant in western oceanic areas (*Q. suber*) (Fig. 11) and gypsum soils (*Q. coccifera*) (Fig. 5). They group together with some other small trees such as the Judas tree (*Cercis siliquastrum*), the Christ's thorn (*Paliurus spina-christi*) (Fig. 12), the smoke tree (*Cotinus coggygria*) (Fig. 13) in eastern Mediterranean areas. Ecological succession at this vegetation belt includes numerous species of heathers (*Erica* spp.) and rockroses (*Cistus* spp.) on acidic soils, while legume scrub (*Ulex minor*, *Genista scorpius*, *Spartium junceum*), a rockrose (*Cistus albidus*) and a blue-flowered shrublet (*Aphyllanthus monspeliensis*) find optimal conditions on basic soils. The plane tree (*Platanus orientalis*) in the east, poplars (*Populus* spp.) in the west and the elm tree (*Ulmus minor*) across the Mediterranean Basin are dominant trees when streams cross this vegetation belt.

Supra-Mediterranean vegetation belt—Few tree species dominate in high mountains between 800 and 1700 m.a.s.l., which form extensive woodlands analogous to the upper montane belt of the Eurosiberian region. Almost monospecific forests of pine trees (*Pinus sylvestris*, *P. nigra*, *P. uncinata*, *P. heldreichii*) accompanied by some other conifers (*Cedrus atlantica*, *C. libanii*, *Abies pinsapo*, *A. nebrodensis*, *A. cephalonica*, *Cupressus sempervirens*) are observed at high altitudes of Mediterranean mountains, which reach



Fig. 8 Coastal vegetation in the thermo-Mediterranean vegetation belt of the western Mediterranean (Almería, Spain).



Fig. 9 Herbivorism, together with fire and human activities, has shaped the landscape of the phrygana and other vegetation types since time immemorial. Photo taken in Crete (eastern Mediterranean Basin).



Fig. 10 The meso-Mediterranean vegetation belt is well recognised by the presence of the helm oak tree (*Quercus ilex*). Photo taken in Sierra de Guadarrama, Spain.

timberline around 1700 m.a.s.l (Fig. 14). There is a mixed temperate forests of conifers, oaks (*Quercus pyrenaica*, *Q. pubescens*, *Q. macrolepis*), strawberry trees (*Arbutus unedo*, *A. andrachne*) and a prickly juniper (*Juniperus oxycedrus*). When degradation occurs, the ecological succession shows numerous legume bushes (*Genista* spp., *Cytisus* spp.), rockroses (*Cistus laurifolius*) (Fig. 7C), the common box (*Buxus sempervirens*) and heathers (*Erica* spp.), followed by numerous herbaceous species after further degradation (Fig. 15). The herbaceous layer is often dominated by a cosmopolitan fern (*Pteridium aquilinum*), numerous sedges (*Carex* spp.) and grasses (Poaceae). Although ravines and valleys harbor also tree species of lower altitudes, some trees (*Alnus glutinosa* on acidic soils; *Aesculus hippocastanum* in the east) and several species of willows (*Salix* spp.) form dense riparian vegetation.



Fig. 11 The cork tree (*Quercus suber*) is distributed in mesic areas exclusively of the western Mediterranean region.



Fig. 12 Some endemic species, such as the Christ's thorn (*Paliurus spina-christi*), are distributed in the eastern Mediterranean Basin in the meso-Mediterranean vegetation belt. Photo taken in Mount Parnassus (Greece).

Oro-Mediterranean vegetation belt—Tall trees cannot cope with climatic conditions at altitudes between 1700 and 2100 m.a.s.l. Therefore, groups of bushes and dwarf trees are the biggest plants. Monospecific dense scrub is common in all Mediterranean mountains, which delimits a vegetation belt analogous to the subalpine belt of the Eurosiberian region. Legume bushes (*Genista cinerea*, *Cytisus* spp., *Echinopartum* spp.) are common in the west, while spiny *Astragalus* species and the barberry (*Berberis* spp.) form the scrub in the east (Fig. 16). Degradation of bushes leads to pastures, which is often the result of natural fires (storm lightning) that brought about herbaceous species adapted to burnt soils. Mediterranean grasslands of the oro-Mediterranean belt are dominated by species of fescues (*Festuca*) in dry soils and matgrass (*Nardus stricta*) in humid habitats.

Cryoro-Mediterranean vegetation belt—High-mountain plants at altitudes over 2100 m form part of communities analogous to those of the alpine belt of the Eurosiberian region. Dominant prairies on the top of the mountains have perennial species of herbs (Fig. 17), of which many are shared with Eurosiberian mountains because some ecological characteristics in common. However, herbs of Mediterranean mountains suffer from environmental uncertainty given that scarce snow does not help protect plant tissues from deep temperature variation including frost. A high number of endemics of a few genera are found in this vegetation belt together with numerous species shared in many Mediterranean and Eurosiberian mountains (*Agrostis*, *Alchemilla*, *Androsace*, *Carex*, *Hieracium*, *Linaria*, *Minuartia*, *Saxifraga*, *Silene*, *Viola*).



Fig. 13 Not all species that form characteristic vegetation types are endemic to the Mediterranean Basin. For instance, the smoke tree (*Cotinus coggygria*) is distributed from the eastern Mediterranean to the Himalayas. Photo taken in Mount Olympus (Greece).



Fig. 14 Some conifers such as the Heldreich's pine (*Pinus heldreichii*) reach timberline in Mount Olympus (Greece).

Conservation

When woodlands are dramatically altered by fire or human activities, the ecological succession at low and medium altitudes takes place from pastures, followed by shrubs and then woodlands after about a century of natural restoration. Monospecific woodlands or mixed forests appear to be the climax in the three lower vegetation belts of the Mediterranean floristic region. Trees cannot survive at high elevations, which results in a shorter ecological succession from grassland to bush communities (oro-Mediterranean) or even



Fig. 15 Predictable ecological succession occurs after degradation of oak woodlands (*Quercus pyrenaica*) of the Iberian Peninsula, and then legume bushes (*Genista florida*) and rockroses (*Cistus laurifolius*) take over. Photo taken in Miraflores (Spain).



Fig. 16 The oro-mediterranean vegetation belt of Sierra de Gredos (central Iberia) shows large areas of legume scrub (*Cytisus oromediterraneus*).

shorter from a type of alpine prairie to another (cryoro-Mediterranean). At lower elevations, the floras and vegetation types observed today have been dramatically shaped by long human activity, more than in any other Mediterranean floristic region of the world because of more than 10,000 years of domestication, plant cultivation, livestock spread and fire. Natural fires have been a significant agent of driving plant evolution since the Miocene, although current landscapes shaped by fire in the Mediterranean has been recently favored by human activities (Rundel et al., 2018). Conservation of pristine Mediterranean woodlands is one of the priorities by the European Commission (Natura, 2000).



Fig. 17 Neither trees nor bushes are found in the cryoro-Mediterranean vegetation belt (*Sierra de Guadarrama*, central Iberia), where short herbs and cushion-like plants can cope with extreme climatic conditions, including environmental uncertainty brought about by short-lasting snow cover.

Despite human pressure during millennia, conservation of numerous species and areas is still feasible and should be urgently prioritized (Nature and Biodiversity, 2019). On the one hand, it has been estimated a relatively low number of extinctions (32 species in the Mediterranean Basin), although most countries report about a fourth of floras threatened as applying IUCN criteria (Greuter, 1994). Some of the Critically-Endangered species of the Mediterranean belong to monospecific genera such as the five Iberian genera (*Avellara*, *Castrilanthemum*, *Gadoria*, *Gyrocarum*, *Naufraga*), which have been considered as ‘endangered living fossils’ that need the most urgent conservation measures (Vargas, 2010; Vargas et al., 2019). On the other hand, eight large hotspots have been found across the Mediterranean Basin: Moroccan Atlas, Baetic-Rifaen complex, Tyrrhenian islands, Greece, Crete, Anatolia and Cyprus, Syria-Lebanon-Israel and Mediterranean Cyrenaic (Médail and Quézel, 1997). Most of the 52 putative refugia within the Mediterranean region obtained from the analysis of the phylogeographical patterns of 82 plant species are included in these eight large hotspots (Médail and Diadema, 2009). Floristic and genetic data provide suitable tools to propose conservation of particular areas as a priority given that human pressure still increases every year.

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Grasslands of the Palaearctic Biogeographic Realm: Introduction and Synthesis

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This chapter was solicited and edited by Jürgen Dengler and Péter Török on behalf of the Eurasian Dry Grassland Group (EDGG).

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Abstract

Grasslands are spontaneously occurring herbaceous vegetation types that are mostly dominated by grasses or other graminoids and have usually > 10% herb-layer cover, while woody species are absent or have a significantly lower abundance than the herbs. In the Palaearctic biogeographic realm, natural and secondary grasslands (76% and 24% of all grasslands, respectively) cover about 10.0 million km², i.e., 18% of its territory, which constitute 41% of global grasslands—more than any other biogeographic realm. In “The encyclopedia of the world’s biomes,” the Palaearctic grasslands are placed in the section “Grasslands and shrublands,” where we defined 10 regions, which are treated in individual chapters: Western Europe, Northern Europe and Baltic States, Eastern Europe, Mediterranean Region, Middle East and Caucasus, Russia, Kazakhstan and Middle Asia, Mongolia, China, and Japan. These regions cover the huge majority of the realm and about 98% of its grasslands. Each chapter describes the extent, physiogeography, origin, biodiversity and typology of the grasslands in the region, the threats for grassland diversity and extent, as well as grassland management and conservation. Grasslands are important habitats for many groups of taxa. Dry calcareous grasslands and steppes constitute habitat of most of Europe’s butterfly and *Orthoptera* species, and they host significant number of European endemic plants. In small spatial scales (i.e., below 100 m²) Palaearctic grasslands, especially meso-xeric ones, can hold even higher species diversity of plants than tropical rainforests. However, Palaearctic grasslands are also among the most intensively and negatively human-impacted habitats. Changes in grassland management, like overgrazing or other types of intensification as well as abandonment were assessed as the most important recent and future threats. Other important reasons of decline in grassland diversity are habitat loss and altered site conditions. The negative impact of climate change and invasive species is predicted to be stronger in the future. In the last years, various conservation efforts to monitor, maintain and promote grassland extent and diversity were made. However, to counteract the negative trends, these efforts urgently need to be intensified and their efficiency needs to be improved.

Introduction

The Palaearctic biogeographic realm is the largest terrestrial realm on Earth (Olson et al., 2001; see Fig. 1), and grasslands cover a substantial fraction of its territory. The grasslands of the Palaearctic are of diverse type and origin, i.e., natural, semi-natural or anthropogenic. They are a major basis for human food supply and at the same time host a high biodiversity. In this article, we provide an overview on the major grassland types of the realm, including information on origin, spatial extent, and biodiversity.

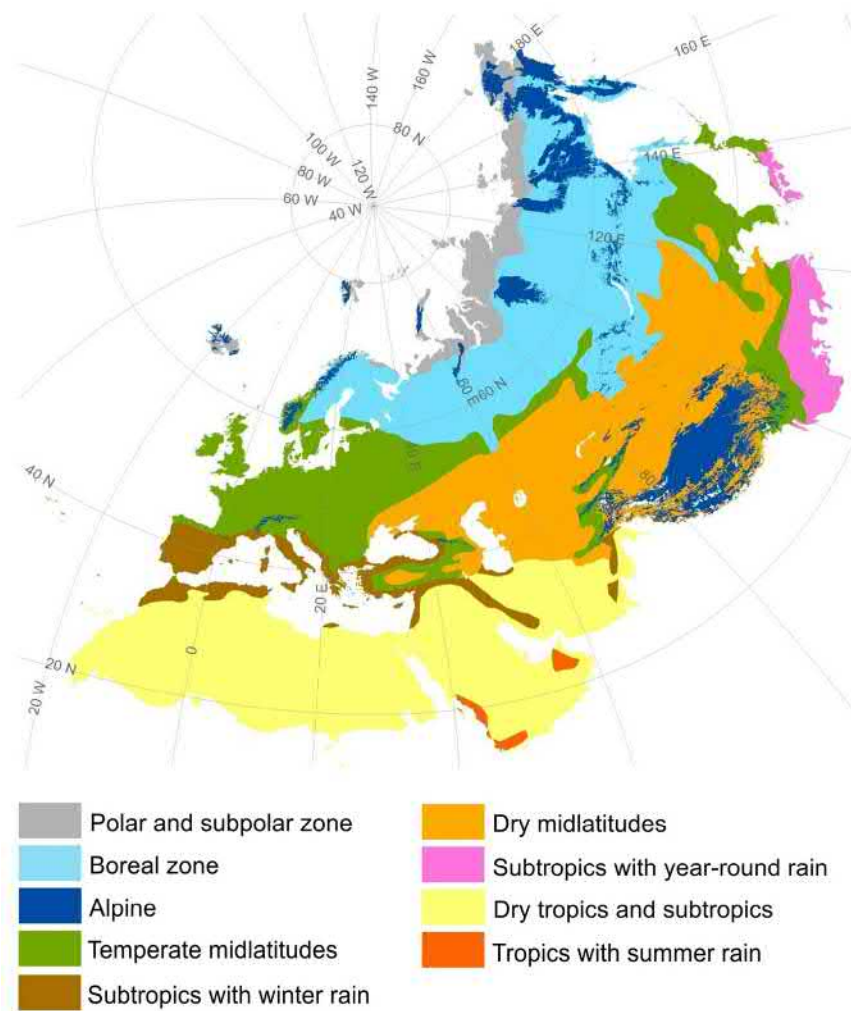


Fig. 1 Delimitation of the Palearctic biogeographic realm according to [Olson et al. \(2001\)](#) combined with the biome classification of [Bruehlheide et al. \(2019\)](#), largely based on [Schultz \(2005\)](#) (map kindly provided by C. Marcenò). Note that according to other concepts, the “Subtropics with year-round rain” do not reach as far north and, for example, most of Japan would belong to the Temperate midlatitudes.

In addition, we outline the causes of regional differences among these factors including the major drivers of biodiversity loss. We largely summarize the knowledge assessed for ten specific chapters on grasslands in different regions of the Palearctic and some previous syntheses (e.g., [Dengler et al., 2014](#); [Wesche et al., 2016](#); [Török and Dengler, 2018](#)). Both the individual chapters and the synthesis have been organized by the Eurasian Dry Grassland Group (EDGG), an international organization dealing with ecology and conservation of all types of natural and semi-natural grasslands of the Palearctic (**Box 1**).

In “The encyclopedia of the world’s biomes,” the Palearctic grasslands are placed in the section “Grasslands and Shrublands.” We defined ten regions, which are treated in individual chapters (Western Europe: [Boch et al., 2020](#); Northern Europe and Baltic States: [Dengler et al., 2020b](#); Eastern Europe: [Török et al., 2020](#); Mediterranean Region: [Guarino et al., 2020](#); Middle East and Caucasus: [Ambarlı et al., 2020](#); Russia: [Tishkov et al., 2020](#); Kazakhstan and Middle Asia: [Wagner et al., 2020](#); Mongolia: [Pfeiffer et al., 2020](#); China: [Li et al., 2020](#); Japan: [Ushimaru et al., 2020](#)). The regions cover the huge majority of the Palearctic biogeographic realm and about 98% of its extant grasslands (**Fig. 2** and **Table 1**). For practical reasons, we delimited the chapters mostly based on political borders, i.e., by combining countries with similar physical geography and/or land-use history. Only the chapter of the Mediterranean Region ([Guarino et al., 2020](#)) and partly the one of Western Europe ([Boch et al., 2020](#)) apply a more biogeographic delimitation by including some countries only partly (**Fig. 2**).

The focus of the grassland chapters are natural and semi-natural grasslands and largely exclude arctic-alpine grasslands. However, to provide a comprehensive overview and for consistency reasons, in this synthesis we also cover intensified as well as arctic-alpine grasslands.

Box 1 The Eurasian Dry Grassland Group (EDGG).

The Eurasian Dry Grassland Group (EDGG; <http://www.edgg.org>), an official working group of the International Association for Vegetation Science (IAVS), was founded in 2008. It has 1314 members, both scientists and conservation practitioners, from 64 countries over the whole Palaearctic (September 2019). With a membership free of any charge, the EDGG coordinates international research on the biodiversity, ecology and conservation of all natural- and semi-natural grasslands of the Palaearctic and initiates respective policy actions. The EDGG is governed by an Executive Committee currently with eight chairs, elected by the membership for 2-years terms. The EDGG facilitates the communication between members by using its mailing list and its open-access electronic journal *Palaearctic Grasslands* with editorial peer review that currently appears in five issues annually. The EDGG organizes yearly conferences (Eurasian Grassland Conferences, EGCs) and Field Workshops (Research Expeditions) for its members. The EDGG is strongly involved in facilitation the establishment of national grassland databases and started the realm-wide database GrassPlot (<https://bit.ly/2HvVkgu>) with the aim of joining standardized multi-scale datasets collected during the Field Workshops with comparable datasets from other projects to support grassland research and macroecological studies in grassland biodiversity. The EDGG is very active in organizing and publishing thematic issues and special features in and with internationally recognized journals and publishers.

Delimitation and Physical Geography of the Region

According to the biogeographic classification by Olson et al. (2001), the Palaearctic biogeographic realm comprises > 52 million km² on three continents, Europe, Asia, and Africa (Fig. 1 and Table 1). It extends over > 20,000 km from west to east (30°W on the Azores to 170°W in the Russian Far East) and over 7000 km from north to south (81°N on Franz-Josef Land in the Arctic Ocean to 17°N on the Arab Peninsula). Thus, the highest (Mt. Everest, 8846 m a.s.l.) and the lowest point (shores of the Dead Sea; 431 m b.s.l.) of the terrestrial surface of the Earth are covered.

The Palaearctic biogeographic realm comprises all terrestrial biomes (Bruehlheide et al., 2019) except the “Tropics with year-round rain” (Fig. 1). While the “Subtropics with year-round rain” only occur in East Asia and the “Tropics with summer rain” can only be found in the Southern part of the Arab Peninsula, the other seven biomes are widely distributed: the “Boreal zone,” the “Temperate midlatitudes,” the “Dry midlatitudes” and the “Dry tropics and subtropics” are the most extensive, the “Polar and subpolar zone,” the “Alpine biome” and the “Subtropics with winter rain” (also known as “Mediterranean biome”) cover a smaller area. The climate in the Palaearctic biogeographic realm is very diverse. According to the Köppen–Geiger climate classification system the continental climates (group D) prevail in the realm, mostly warm-summer humid continental climate (Dfb) and subarctic climate (Dfc), that are present from Central Europe to the Bering Sea (respectively in the western and in the eastern most parts of the realm). In Western Europe and within several areas of south-eastern borders of the Palaearctic realm, and in South Japan also temperate climates occur (group C). Dry climates (group B) dominate major parts of Central Asia, Mongolia, north-western China, the Middle East, the Arab Peninsula and North Africa (Kottek et al., 2006). The Eastern part of the realm is influenced by the monsoon circulation resulting in large seasonal precipitation variability. In the northernmost regions and in mountain ranges of the realm also polar and alpine climates occur (group E). Mean annual temperature ranges from −29.3 °C to +31.0 °C, and mean annual precipitation from close to 0–3722 mm (Hijmans et al., 2005). Given the huge latitudinal and elevational gradients, it is not surprising that bedrocks and soils are highly variable.

Origin and Extent of the Grasslands

Definition and Types of Grasslands

There are many different definitions of grasslands from ecological, physiognomic, agronomic or remote-sensing points-of-view (Gibson et al., 2009; Dixon et al., 2014; Wesche et al., 2016; Török and Dengler, 2018), which in turn have considerable impact on measuring the spatial extent of grasslands. Here, we follow a slightly modified version of the definition of Török and Dengler (2018), based on earlier suggestions by Janišová et al. (2011) and Dengler et al. (2014):



Fig. 2 Subdivision of the Palearctic biogeographic realm into regions corresponding to chapters in this “Encyclopedia” and/or used in tables and figures of this chapter. The 10 colored regions correspond to one of the EDGG-edited grassland chapters in the “Encyclopedia,” while the *white* and *gray* regions are not treated in a specific chapter (map prepared by I. Dembicz).

Grasslands are spontaneously occurring herbaceous vegetation types that are mostly dominated by grasses (*Poaceae*) or other graminoids (*Cyperaceae*, *Juncaceae*) and have a relatively high herb-layer cover (usually > 10%), while woody species (dwarf shrubs, shrubs and trees), if present at all, have a significantly lower cover than the herbs.

With “spontaneously occurring,” we exclude artificial grasslands that are reseeded every year, such as cereal fields (which otherwise would meet the definition). Deviating from Török and Dengler (2018), we lowered the minimum vegetation cover in the definition from 25% to 10% to match the definition used by FAO (2019). This means that now also desert steppes are fully covered.

Based on their origin, there are two main and five subordinate categories of grasslands (Dengler et al., 2014; Török and Dengler, 2018; see Fig. 3):

- (1) *Natural grasslands* (occurring in places where the natural vegetation would also be a grassland, though the current grasslands are potentially modified through human land use)
 - (1a) *Steppes* (climatogenic grasslands in climates that are too dry to sustain forests and are affected by frost) (Fig. 3A).
 - (1b) *Arctic-alpine grasslands* (climatogenic grasslands in climates that are too cold to sustain forests) (Fig. 3B).
 - (1c) *Azonal and extrazonal grasslands* (pedogenic or topogenic grasslands that occur under special soil or topographic conditions that, at small spatial scales, allow grassland to exist in climates that otherwise would support forests, shrublands or deserts; azonal grassland types are those that nowhere form the zonal vegetation, but occur in similar form across two or more biomes, whereas extrazonal grasslands in one biome are similar to zonal grasslands, i.e., steppes or arctic-alpine grasslands, in another biome). Examples of azonal grasslands are salt marshes and coastal dunes (Fig. 3C), while a typical example of extrazonal grasslands are the steppic grasslands that occur on steep south-facing slopes in the forest climate of central Europe (Fig. 3D).

Table 1 Overview of areas covered by grasslands in the different regions of the Palearctic biogeographic realm.

<i>Region</i>	<i>Western Europe^a</i>	<i>Northern Europe and Baltic States</i>	<i>Eastern Europe</i>	<i>Mediterranean Region</i>	<i>Middle East and Caucasus</i>	<i>Sahara and Arab Peninsula</i>	<i>Russia^b</i>	<i>Kazakhstan and Middle Asia</i>	<i>Mongolia</i>	<i>China (Palearctic part)</i>	<i>Himalayas south of China</i>	<i>Korean Peninsula</i>	<i>Japan</i>	<i>Total</i>
<i>Chapter</i>	Boch et al. (2020)	Dengler et al. (2020b)	Török et al. (2020)	Guarino et al. (2020)	Ambarlı et al. (2020)	–	Tishkov et al. (2020)	Wagner et al. (2020)	Pfeiffer et al. (2020)	Li et al. (2020)	–	–	Ushimaru et al. (2020)	
Number of countries included	17	9	16	19	9	20	1	5	1	1	5	2	1	99
- Fully included	13	9	16	10	9	7	1	5	1	–	1	2	1	87
- Partly included	4	–	–	9	–	13	–	–	–	1	4	–	–	12
Total area included [km ²]	1,607,947	1,484,419	1,982,849	1,672,102	3,985,900	11,258,219	17,075,400	4,008,139	1,565,000	8,748,897	779,125	220,755	369,700	54,758,452
Total extant grasslands [km ²]	375,000	103,000	277,500	303,000	1,305,000	60,000	1,790,000	1,480,000	1,210,000	2,911,000	125,000	10,500	24,000	9,974,000
- Fraction of territory	23%	7%	14%	18%	33%	1%	10%	37%	77%	33%	16%	5%	6%	18%
- Proportion of natural grasslands	5%	49%	7%	6%	67%	100%	79%	87%	100%	87%	80%	14%	25%	76%
- Proportion of HNV grasslands	31%	45%	71%	63%	77%	NA	91%	76%	77%	74%	NA	NA	NA	ca. 76%
(1) Natural grasslands (extant) [km ²]	20,000	50,500	18,500	19,000	868,000	60,000	1,420,000	1,290,000	1,210,000	2,545,000	100,000	1500	6000	7,608,500
- As fraction of their original area	75%	89%	8%	NA	NA	NA	50%	63%	100%	95%	NA	NA	NA	ca. 72%
(i) Steppes [km ²]	0	0	11,000	14,000	740,000	55,000	500,000	1,120,000	1,090,000	745,000	65,000	0	0	4,340,000
(ii) Arctic-alpine grasslands [km ²]	10,000	46,500	4500	3000	100,000	0	820,000	100,000	100,000	1,198,000	30,000	0	500	2,412,500
(iii) Azonal + extrazonal grasslands [km ²]	10,000	4000	3000	2000	28,000	5000	100,000	70,000	20,000	602,000	5000	1500	5500	856,000

(Continued)

Table 1 Overview of areas covered by grasslands in the different regions of the Palearctic biogeographic realm.—cont'd

<i>Region</i>	<i>Western Europe^a</i>	<i>Northern Europe and Baltic States</i>	<i>Eastern Europe</i>	<i>Mediterranean Region</i>	<i>Middle East and Caucasus</i>	<i>Sahara and Arab Peninsula</i>	<i>Russia^b</i>	<i>Kazakhstan and Middle Asia</i>	<i>Mongolia</i>	<i>China (Palearctic part)</i>	<i>Himalayas south of China</i>	<i>Korean Peninsula</i>	<i>Japan</i>	<i>Total</i>
<i>Chapter</i>	Boch et al. (2020)	Dengler et al. (2020b)	Török et al. (2020)	Guarino et al. (2020)	Ambarlı et al. (2020)	–	Tishkov et al. (2020)	Wagner et al. (2020)	Pfeiffer et al. (2020)	Li et al. (2020)	–	–	Ushimaru et al. (2020)	
(a) In good state [km ²]	17,500	49,000	12,500	4500	600,000	NA	1,278,000	950,000	930,000	1,909,000	NA	NA	NA	ca. 77%
(b) Strongly degraded [km ²]	2500	1500	7000	14,500	268,000	NA	142,000	340,000	280,000	636,000	NA	NA	NA	ca. 23%
(2) Secondary grasslands [km ²]	355,000	52,500	259,000	284,000	437,000	0	370,000	190,000	0	366,000	25,000	9000	18,000	2,365,500
- As fraction of their maximum area (in the past)	60%	34%	55%	60%	NA	NA	NA	NA	100%	100%	NA	NA	50%	ca. 64%
(a) Semi-natural grasslands [km ²]	100,000	11,500	184,000	187,000	400,000	NA	347,000	170,000	0	244,000	NA	NA	5500	ca. 71%
(b) Strongly intensified grasslands [km ²]	255,000	41,000	75,000	97,000	37,000	NA	23,000	20,000	0	122,000	NA	NA	12,500	ca. 29%

The delimitation of the 13 regions is shown in Fig. 2. Ten of the regions are covered in regional chapters, except the three regions set in italics. Note that the areas covered in the articles "Mediterranean Basin" and "Middle East and the Caucasus" slightly overlap; for this synthesis, however, the complete territories of Turkey, Syria and Jordan are treated under the latter despite they also have a share of the Mediterranean Basin. Likewise, the Western Balkan countries Slovenia, Croatia, Bosnia and Herzegovina, Montenegro and North Macedonia in this table are fully counted under "Eastern Europe," despite they have significant areas in the Mediterranean Region. The numbers provided in this table are mostly rough estimates by the authors of the ten regional chapters and other experts because for the majority of presented facts there are no or no easily accessible hard data. The different grassland categories concerning origin and quality are defined in detail in the text. Fractions of original and maximum areas, respectively, refer roughly to the past 500 years, not to geological time scales. HNV grasslands = High Nature Value grasslands, i.e., natural grasslands in good state and semi-natural secondary grasslands combined. The threshold between the quality categories (a) and (b) is a biodiversity loss of 50%, both for natural and secondary grasslands.

^aAreas given here deviate from Boch et al. (2020) as these authors based their stats on FAO MODIS (FAO 2019), while we, in agreement with Dengler and Tischew (2018), use FAO CCI_LC (FAO, 2019), which corresponds better to other published stats (Smit et al., 2008; Eurostat, 2015).

^bAreas for Russia were taken from Reinecke et al. (2018).



Fig. 3 Examples of major grassland categories of the Palaeartic biogeographic realm (A–D: natural grasslands; E–H: semi-natural grasslands): (A) Steppe in Southern Ukraine; (B) Arctic-alpine grasslands form an extensive belt above the timberline in most Palaeartic mountains, here in the Swiss Alps; (C) coastal dune grassland in Sicily, Italy; (D) extrazonal steppic grasslands on steep slopes above the Rhone valley, Switzerland; (E) semi-dry basiphilous grassland in Transylvania, Romania, holding two small-scale world records of vascular plant species richness (see [Table 2](#)); (F) eutrophic, wet meadow, Slovenia; (G) extensive semi-natural grasslands, together with arable fields and hedgerows, are part of the traditional cultural landscapes in many parts of Europe, as here in Central Slovakia; (H) in East Asia, semi-natural grasslands are much less extensive, as here on Jeju Island, South Korea (photos by J. Dengler).

- (2) *Secondary grasslands* (occur in places where the natural vegetation is forest, shrubland, heathland or wetland; these grasslands developed under human land use like mowing, grazing, burning or abandoning arable fields)
- (2a) *Semi-natural grasslands* (secondary grasslands in which site conditions except for removing woody species remained more or less unaltered, e.g., no or very little artificial fertilization, no regular reseeding) (Fig. 3E–G).
- (2b) *Strongly intensified grasslands* (secondary grasslands in which the site conditions were altered strongly compared to the natural stage; in particular, with high land-use intensity to increase yield enabled through (artificial) fertilization).

In natural and secondary grasslands high levels of human impact generally reduces biodiversity and conservation value. However, initial, low-level intensification can even increase the biodiversity of certain grasslands, e.g., relatively species-poor extrazonal steppes in the Swiss inneralpine valleys have been transformed to species-rich meso-xeric grasslands by irrigation (in line with the loss of steppe-specialist species); also a very low level of fertilization or liming of very nutrient-poor and/or acidic secondary grasslands might increase species richness. However, any further land-use intensification (fertilization, higher stocking rates, more cuts per year, drainage, plowing and reseeding, removal of small-scale heterogeneity) will ultimately lead to a strong loss of biodiversity across taxonomic groups (Allan et al., 2014). To capture this process, we differentiate among the *natural grasslands* those “in good state” from those that are “strongly degraded” and in *secondary grasslands* the “semi-natural grasslands” from the “strongly intensified grasslands.” The natural grasslands in good state and the semi-natural secondary grasslands together are the so-called “High Nature Value” grasslands (HNV grasslands; Veen et al., 2009; Oppermann et al., 2012; Török and Dengler, 2018). As the loss of “nature value” is a gradual process, we reduced this concept and only distinguish High Nature Value grasslands from grasslands with low nature value. The threshold to distinguish between the two categories was the loss of 50% or more of the original biodiversity. The author teams of the chapters were asked to assess the situation in their particular region based on this definition. While we are not aware of any other definition that connects the concept of “High Nature Value” grasslands (or of the semi-natural grasslands within the secondary grasslands) with clear numbers of biodiversity loss, it is evident that some other publications used much stricter thresholds. When Bullock (2011) reports a loss of 97% of semi-natural grasslands in England and Wales (United Kingdom) since the mid-20th century, this evidently refers to a higher, yet undefined threshold. Definitions of semi-natural grasslands can also refer to other factors than biodiversity, e.g., in Estonia to the fact that a site has never been plowed (S. Rusina, Riga, pers. comm.). Instead of a dichotomy as we apply it here, other systems might use finer delimitations, e.g., Stevens et al. (2010) distinguished “unimproved,” “semi-improved,” and “improved” grasslands of which the first two approximately correspond to HNV grasslands in our sense. It is important to keep these different delimitations of HNV grasslands in mind when interpreting our Table 1.

Grasslands can also recover after cessation of arable fields, other human disturbance or the removal of afforestations. Actually this is a process that happened repeatedly in many regions of the Palaearctic (Poschlod, 2015; Brinkert et al., 2016; Kämpf et al., 2016) and nowadays is often assisted by restoration measures. For the sake of simplicity, we assign such recovered grasslands depending on their sites to either natural grasslands or secondary grasslands and depending on their quality to either HNV grasslands or non-HNV grasslands (to be kept in mind when interpreting Table 1).

Spatial Extent of Grasslands in the Palaearctic

Quantifying the extent of grasslands in the Palaearctic and its subunits is a major challenge, not only because of the different grassland definitions used in different sources (see above). Even when using the same FAO definition “area dominated by natural herbaceous plants (grasslands, prairies, steppes, and savannahs) with a cover of 10 per cent or more, irrespective of different human and/or animal activities, such as grazing or selective fire management. Woody plants (trees and/or shrubs) can be present, assuming their cover is less than 10 per cent,” values for individual countries vary sometimes strongly, depending on whether one refers to the one or the other remote-sensing based product provided by FAO (2019). Sometimes the grassland areas based on MODIS (Moderate-resolution imaging spectroradiometer) are much higher than those based on CCI_LC (Land Cover project of the European Space Agency Climate Change Initiative) (e.g., Turkmenistan: 93,722 MODIS vs. 27,083 km² CCI_LC), and sometimes the other way around (e.g., France: 48,791 km² MODIS vs. 121,408 CCI_LC); rarely both values are close together (e.g., Italy: 35,357 km² MODIS vs. 37,732 km² CCI_LC). Similar unexplained inconsistencies, albeit not as strong, were already recorded by Dengler and Tischew (2018) for Western and Northern European countries based on one FAO statistics and two other sources. We tried to use as far as possible national sources to overcome these unexplained inconsistencies, and, when such were not available, averaged the CCI_LC and MODIS-based values of FAO (2019).

According to our compilation (Table 1), there are about 10.0 million km² grasslands in the Palaearctic, corresponding to 18% of its territory. In our last, less detailed assessment (Török and Dengler, 2018), we had estimated 9.7 million km² and 22%, i.e., the first value is quite similar and the difference in the second can easily be explained by the fact that Török and Dengler (2018) excluded the Arab Peninsula, which hardly contains any grasslands but largely belongs to the Palaearctic biogeographic realm. Comparing these values with the FAO stats for the whole terrestrial surface of Earth (FAO, 2019: mean of MODIS and CCI_LC), it appears that the Palaearctic biogeographic realm comprises approx. 41% of the global grasslands (24.5 million km²), and thus more than any other biogeographic realm, while the fraction of grasslands here is slightly lower than the global average of 19%. The fractions of grasslands in the 13 regions distinguished range from 1% in the Sahara and Arab Peninsula to 77% in Mongolia (Table 1).

Overall, natural grasslands prevail with 76% vs. 24% secondary grasslands, but in the Europe, the Mediterranean Region, Korea and Japan secondary grasslands dominate, while natural ones often contribute < 10% (Table 1). Natural grasslands consist of 57% steppes, 32% arctic-alpine grasslands and 11% azonal and extrazonal grasslands (Table 1). Slightly less than three-fourths of their

original extent is still covered by grasslands, but in two regions the loss was particularly dramatic, Eastern Europe with 92% and Russia with 50% (Table 1). The remaining natural grasslands are predominantly (77%) considered as in good state. In those regions, where secondary grasslands nowadays prevail, they were even more widespread in the past, with area losses of typically 40%, but up to 75% in Northern Europe and the Baltic States (Table 1). More than two-thirds of the remaining secondary grasslands belong to our category “semi-natural grasslands,” i.e., they still contain at least half of their former biodiversity (Table 1). However, in three of the regions (Western Europe, Northern Europe and the Baltic States, Japan) meanwhile a clear majority of grasslands has been strongly intensified with severe negative impacts on their biodiversity (Table 1).

Biodiversity of Palaearctic Grasslands

Biodiversity Hotspots and Diversity of Taxa in General

Palaearctic grasslands have a significant share of the overall biodiversity of the Earth (for some examples, see Fig. 4). Among the 34 biodiversity hotspots recognized globally (among others defined by the presence of at least 1500 endemic vascular plant species; Mittermeier et al., 2004), six are located in the Palaearctic biogeographic realm: Mediterranean Basin, Caucasus, Irano-Anatolian, Mountains of Central Asia, Himalaya and Japan. All six comprise significant areas of natural and semi-natural grasslands which contribute largely to the overall biodiversity.

Grassland-dominated landscapes are rather young ecosystems in the geological history of the Earth. They originated and expanded in the Cenozoic (from ca. 40 million year), as the effect of the co-evolution of grasses and grazers (Retallack, 2001). In the past, Eurasian steppes supported large herds of wild ungulates such as the saiga antelope, the Przewalski's horse, the Asiatic wild ass, and the Bactrian camel. However, due to human activities most of these species have been extirpated in the wild or survive in only small herds in the Eastern Steppe (Visconti et al., 2018). Grazers typical for alpine grasslands, like ibex, chamois and wild sheep still exist in many mountain ranges in the Palaearctic realm. Other important consumers of plant biomass in grasslands that often play a role of ecosystems engineers in this Palaearctic grasslands are pikas and rodents (Wesche and Treiber, 2012), e.g., ground squirrels, marmots (Fig. 4H), voles, zokors, mole rats, hamsters, gerbils, and jerboas.

Grasslands are also very important for other groups of taxa. It was assessed that in Europe 29% (152 out of 526) of all bird species is associated with grasslands habitats (Nagy, 2014). Dry calcareous grasslands and steppes constitute habitat of 63% of Europe's butterfly species (274 out of 436, van Swaay et al., 2006; Fig. 4E), while in the case of *Orthoptera* (Fig. 4F) even 74% of the species occurring in Europe are dependent on open habitats, mostly grasslands (Hochkirch et al., 2016). European grassland areas also host many species of endemic terrestrial mollusks (Neubert et al., 2019). In the floras of vascular plants of Palaearctic countries, typically the grassland species are the largest group (e.g., Korneck et al., 1998, for Germany); and among the >6000 endemic vascular plant species of Europe those of grasslands (18.1%) constitute the second-largest group after rock-dwelling species (Hobohm and Bruchmann, 2009).

Exceptional Biodiversity at Small Spatial Scales

At small spatial scales (i.e., below 100 m²) Palaearctic grasslands can hold higher species diversity of plants even than tropical rain-forest (Wilson et al., 2012). Meso-xeric grasslands are the most species-rich grasslands (Fig. 3E) in the Palaearctic realm for most spatial scales, both regarding mean and maximum values (Fig. 5 and Table 2). Only at the smallest grain size, 1 cm², wet grasslands and mesic grasslands show higher means for vascular plants and total vegetation, i.e., including bryophyte and lichen species, respectively. Maximum richness values of vascular plants correspond specifically to meso-xeric grasslands in Eastern Europe for grain sizes larger than 0.1 m² (Table 2), with an outstanding value of 82 species in 1 m² (White Carpathians, Czech Republic), 98 in 10 m² (Transylvania, Romania; Fig. 3E) and 133 in 100 m² (White Carpathians, Czech Republic). Roleček et al. (2019) reported 106 vascular plant species in 10.89 m² (3.33 × 3.33 m) in the mentioned grassland from Transylvania and 119 vascular plant species in 16 m² from the Chernivtsi Mts. in Ukraine. For smaller grain sizes, meso-xeric grasslands still show the highest maximum richness for 10 cm², but in this case in Western Europe (Navarre, Spain), while a wooded meadow from the Baltic States and a wet grassland from Eastern Europe hold the maximum richness for 100 cm² (Estonia) and for 1 cm² (Poland), respectively (Table 2). Fig. 6 shows the differences across grain sizes and subregions of mean species richness of vascular plants of the richest vegetation type. Highest means change from Western and Northern Europe in the grain sizes up to 0.1 m² to Eastern Europe and Russia in the largest sizes (Fig. 6).

However, bryophytes and lichens exhibit different richness patterns than vascular plants, i.e., being more diverse in other grassland types (Fig. 7). Their fraction changes across the grain sizes, but rocky grasslands and sandy dry grasslands are usually the vegetation types with their highest proportion, with bryophytes normally more abundant in the former and lichens in the latter. Outstanding are the mean bryophyte richness values in wet grasslands (6.4) at 10 m² and Mediterranean grasslands (8.1) at 100 m², where they constitute 18.3% and 16.1% of the total richness, respectively (Fig. 7). As regards the maximum richness values, rocky grasslands from the Baltic islands (both in Sweden and Estonia) hold the bryophyte records for all grain sizes, as well as the lichen records for most grain sizes, except 1 cm² and 100 m², for which a sandy dry grassland and a meso-xeric grassland from Germany show the maximum values (Tables 3 and 4). However, Boch et al. (2016a) reported an outstanding value of 36 lichen species on 16 m² in a calcareous grassland in Germany (Baden-Württemberg; see dataset Boch et al., 2016b). It is worth to indicate that the fraction of bryophytes and lichens in total vegetation is changing even within particular vegetation types depending on the region.

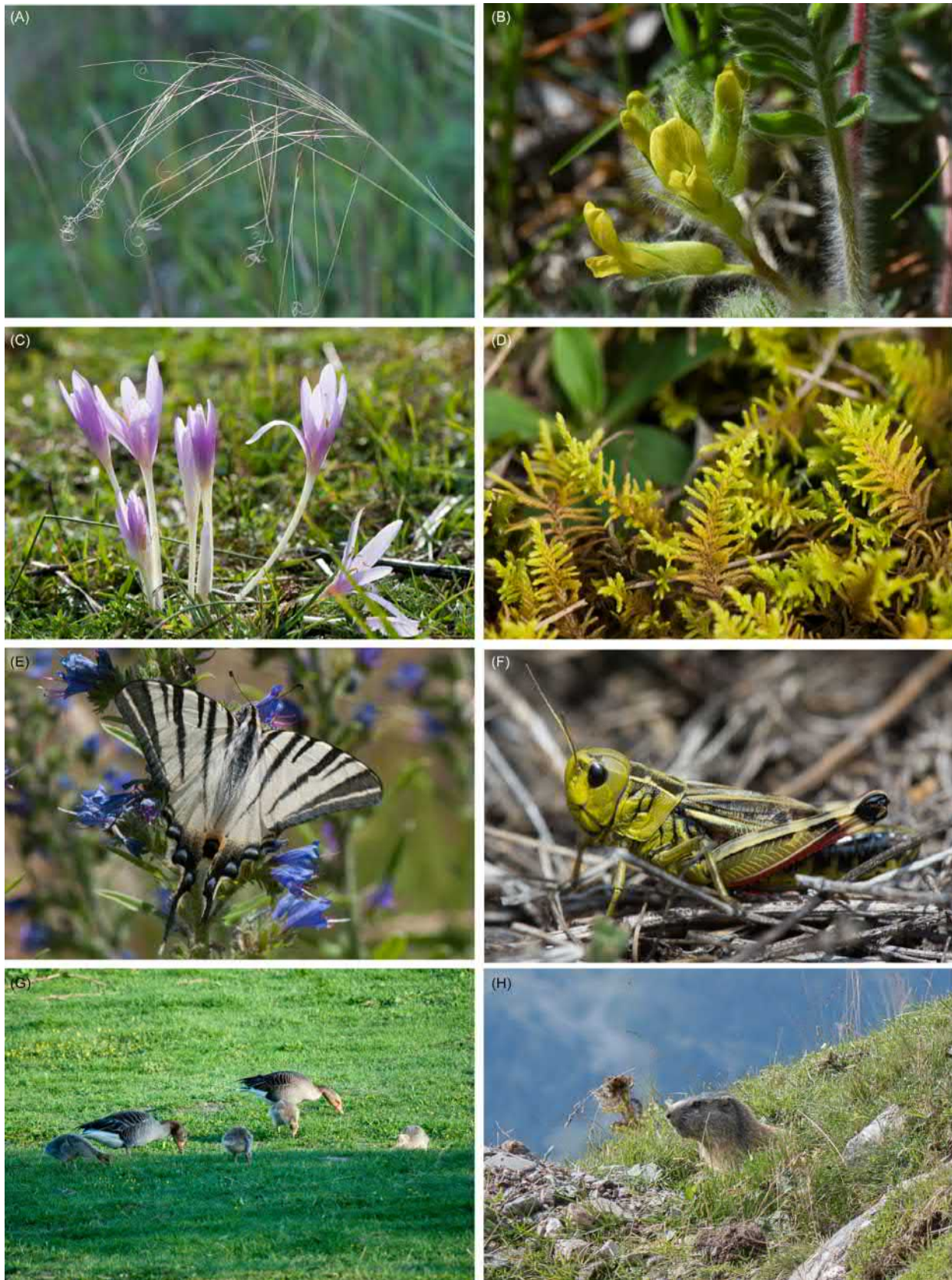


Fig. 4 Examples of typical taxa of Palearctic grasslands: (A) *Stipa capillata*, a representative of one of the most-widespread drought-adapted tussock grass genera of the realm; (B) *Astragalus exscapus*, representing one of the most species-rich genera of Palearctic forbs and dwarf shrubs; (C) geophytes, like *Colchicum autumnale*, play a lesser role in only some grassland types; (D) *Abietinella abietina* is a widespread moss species of dry grasslands; (E) *Iphiclides podalirius* is a typical butterfly of dry grasslands throughout most of the Palearctic; (F) *Arcyptera fusca* is a herbivorous *Orthoptera* species grazing in dry grasslands; (G) family of Greylag geese (*Anser anser*) feeding in a wet grassland; (H) Alpine marmot (*Marmota marmota*), a grazer from the genus *Marmota*, which occurs with several medium-sized species in alpine grasslands as well as steppes (photos by J. Dengler).

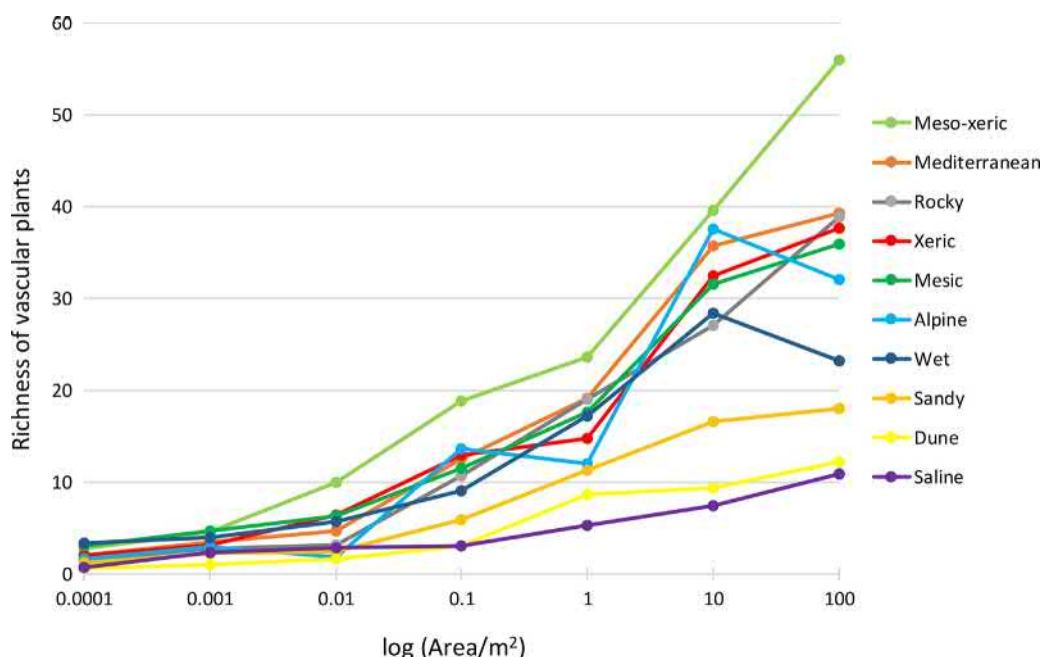


Fig. 5 Vascular plant richness of Palearctic grasslands across grain sizes and 10 major grassland types. The values are means of all plots in each grain size across the Palearctic biogeographic realm that were contained in version 2.00 of the GrassPlot database (Dengler et al., 2018; Biurrun et al., 2019).

Table 2 Maximum richness of vascular plants across regions of the Palearctic realm, as considered in the Encyclopedia.

Area (m ²)	Western Europe	Northern Europe and Baltic States	Eastern Europe	Mediterranean Region	Middle East and Caucasus	Russia	Kazakhstan and Middle Asia	Mongolia	China	Japan	Place and grassland type of Palearctic maximum
0.0001	9	5	11	8	3	5	5	–	–	–	Poland: wet grassland
0.001	19	12	13	12	4	9	15	–	–	–	Spain: meso-xeric grassland
0.01	23	25^a	22	24	20	17	17	–	–	–	Estonia: meso-xeric grassland in a wooded meadow
0.1	34	35 ^b	43^c	37 ^b	34	28	28	–	–	–	Romania (shoot; Fig. 3E) and Czech Republic (rooted) ^c : meso-xeric grassland
1	53	49	82^c	48	48	52	37	11	59	58	Czech Republic: meso-xeric grassland
10	86	49 ^b	98	71	65	76 ^d	50	–	71 ^b	–	Romania: meso-xeric grassland (Fig. 3E)
100	110	70	133^c	99	85	109 ^d	67	34	76	–	Czech Republic: meso-xeric grassland

Richness is provided for the grain sizes from 1 cm² to 100 m². Data from version 2.00 of the GrassPlot database (Dengler et al., 2018; Biurrun et al., 2019), except for values marked by superscript numbers. Palearctic maximum richness values are indicated in bold.

^aChytrý et al. (2015).

^bRecords are for 10% smaller areas, i.e., 0.09 and 9 m², respectively.

^cWilson et al., 2012.

^dUnpublished data provided by M. Chytrý.

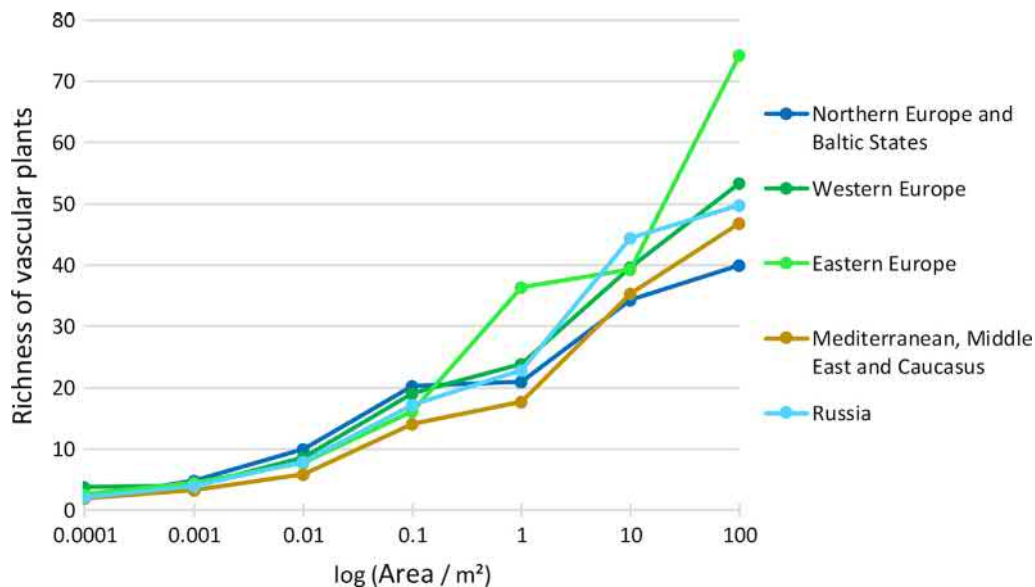


Fig. 6 Mean vascular plant richness of meso-xeric grasslands across grain sizes and Palearctic regions. Note that the Mediterranean Region and Middle East and Caucasus were joined to get sufficient number of plots in some grain sizes. Japan and Korea, Kazakhstan and Middle Asia, China and Mongolia are not included, because there are not data of meso-xeric grasslands at any grain size, or only at one.

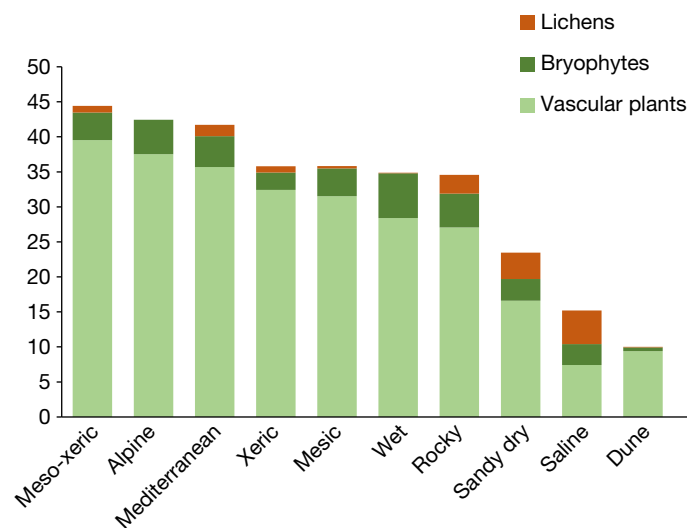


Fig. 7 Species richness and taxonomic composition of the vegetation of 10 major grassland types. The values are means of all the 10-m² plots across the Palearctic biogeographic realm that were contained in version 2.00 of the GrassPlot database (Dengler et al., 2018; Biurrun et al., 2019). Mean richness values of bryophytes and lichens are calculated only for those plots in which they were recorded. Note that the relatively high fraction of non-vascular plants in saline grasslands is due to the fact that non-vascular plants were recorded only in a small subset of these that is not typical for saline grasslands in general.

As an example, Fig. 8 (left) shows the fraction of vascular plants, bryophytes and lichens of meso-xeric grasslands across subregions at 10 m². Meso-xeric grasslands from northern Europe hold the highest fraction of both bryophytes and lichens, as well as the highest mean richness values of these taxonomic groups. This pattern is conserved in rocky grasslands, which hold the highest fraction of bryophytes and lichens at the level of the Palearctic realm. Once again, Fig. 8 (right) shows that at 10 m² rocky grasslands from Northern Europe hold by far the highest fraction and highest mean values of both bryophytes and lichens, followed by rocky grasslands from Western Europe.

The species richness of other taxa than vascular plants are only rarely reported in the literature. We therefore analyzed data of the Biodiversity Exploratories, a large-scale and long-term functional biodiversity research project (www.biodiversity-exploratories.de/1/home/) where many taxa were sampled on the same plots in 150 differently managed grasslands in three regions of Germany and used for synthesis analyses (e.g., Allan et al., 2014; Blüthgen et al., 2016; Gossner et al., 2016; Soliveres et al., 2016a,b). In plots with a size of 50 × 50 m, on average 3.5 bird species (max. 19; for methodological details see Wells et al., 2011) and 3 bat species (max. 10; years

Table 3 Maximum richness of bryophytes across regions of the Palaearctic realm, as considered in the Encyclopedia.

Area (m ²)	Western Europe	Northern Europe and Baltic States	Eastern Europe	Mediterranean Region	Middle East and Caucasus	Russia	Kazakhstan and Middle Asia	China	Place and grassland type of Palaearctic maximum
0.0001	4	5	4	5	1	3	1	–	Estonia: rocky grassland and Italy: Mediterranean grassland
0.001	6	9^a	7	8	1	4	2	–	Estonia: rocky grassland
0.01	7	18	10	9	1	5	2	–	Sweden: rocky grassland
0.1	10	24^a	10	10	2	9	2	–	Sweden: rocky grassland
1	13	31	11	18	2	11	3	–	Sweden: rocky grassland
10	27	40^a	18	19	2	13 ^a	7	–	Sweden: rocky grassland
100	23	38	17	23	3	19	9	2	Estonia: rocky grassland

Richness is provided for the grain sizes from 1 cm² to 100 m². Data from version 2.00 of the GrassPlot database (Dengler et al., 2018; Biurrun et al., 2019). Palaearctic maximum richness values are indicated in bold. For Mongolia and Japan, GrassPlot 2.00 does not contain plots with records of bryophytes.

^aRecords are for 10% smaller areas, i.e., 0.0009, 0.09 and 9 m², respectively.

Table 4 Maximum richness of lichens across regions of the Palaearctic realm, as considered in the Encyclopedia.

Area (m ²)	Western Europe	Northern Europe and Baltic States	Eastern Europe	Mediterranean Region	Russia	China	Place and grassland type of Palaearctic maximum
0.0001	4	2	2	1	3	–	Germany: sandy grassland
0.001	4^a	6^a	2	1	2	–	Sweden: rocky grassland
0.01	7	8	3	3	6	–	Sweden: rocky grassland
0.1	10 ^a	15^a	4	5	8	–	Sweden: rocky grassland
1	11	21	8	5	17	–	Sweden: rocky grassland
10	16 ^a	24^a	12	10 ^a	20	–	Sweden: rocky grassland
100	31	25	15	15	28	3	Germany: meso-xeric grassland

Richness is provided for the grain sizes from 1 cm² to 100 m². Data from version 2.00 of the GrassPlot database (Dengler et al., 2018; Biurrun et al., 2019). Palaearctic maximum richness values are indicated in bold. For Middle East and Caucasus, Kazakhstan and Middle Asia, Mongolia and Japan, GrassPlot 2.00 does not contain plots with records of lichens.

^aRecords are for 10% smaller areas, i.e., 0.0009, 0.09 and 9 m², respectively.

2008–2012; for methodological details see Heim et al., 2015; Treitler et al., 2016) occurred. Sweep netting along transects in these plots (Simons et al., 2014, 2015, 2016; Neff et al., 2019), revealed on average 19.8 *Hemiptera* (max. 34) and 1.6 *Orthoptera* species (max. 5). As sweep netting largely excludes most ground-dwelling species, e.g., *Araneae* species (spiders) and *Coleoptera* species such as most carabid beetles, the sweep netting approach was combined with pitfall trapping in a subset of 27 plots (Lange et al., 2011; Allan et al., 2014). This resulted in 7.5 and 8.5 times higher mean numbers of *Coleoptera* species (mean 13 vs. 98.1, max. 34 vs. 153 species) and *Araneae* species (mean 3.6 vs. 30.6, max. 11 vs. 56 species), respectively, than the pure sweep-netting approach.

Factors Influencing Alpha Diversity of Grasslands

As in all other biogeographic realms and biomes, biodiversity of Palaearctic grasslands is shaped simultaneously by many environmental factors. Therefore it is impossible to point out only one or two major predictors of species diversity. Moreover, the main drivers of biodiversity can be properly indicated only for a given spatial scale (Huston, 1999) and for different taxonomic groups the observed patterns can be opposite (Mateo et al., 2016).

Coarse-scale diversity patterns of plants in Palaearctic grasslands are determined mostly by climate and geological history (Antonelli et al., 2018). With regard to climatic factors, evapotranspiration as a climatic parameter that combines some of the effects of precipitation, temperature, solar radiation, and other factors in a single value seems to be the most important (Huston, 1999), but this still needs to be confirmed for Palaearctic grasslands. The geological history, like formation of mountain ranges, past climate changes and glaciations greatly impacted the current distribution of species. Exceptionally diverse regions, rich in endemic plant species, usually occur in mountainous regions, former glacial refugia, and especially in places with calcareous bedrock (Smyčka et al., 2017; Noroozi et al., 2018; Večeřa et al., 2019).

In a more local scale, plant diversity in grasslands is determined e.g., by primary productivity, fertility and pH of soil, as well as management or natural disturbance regime. In general, primary productivity influences plant species richness according to a unimodal relationship (Fraser et al., 2015). Productivity in grasslands is mostly determined by climate (precipitation, temperature and length of growing season) in case of natural, climatogenic grasslands, while in semi-natural grasslands it also strongly depends on soil fertility. Palpurina et al. (2019) found that the type of nutrient limitation can affect the plant species richness-productivity

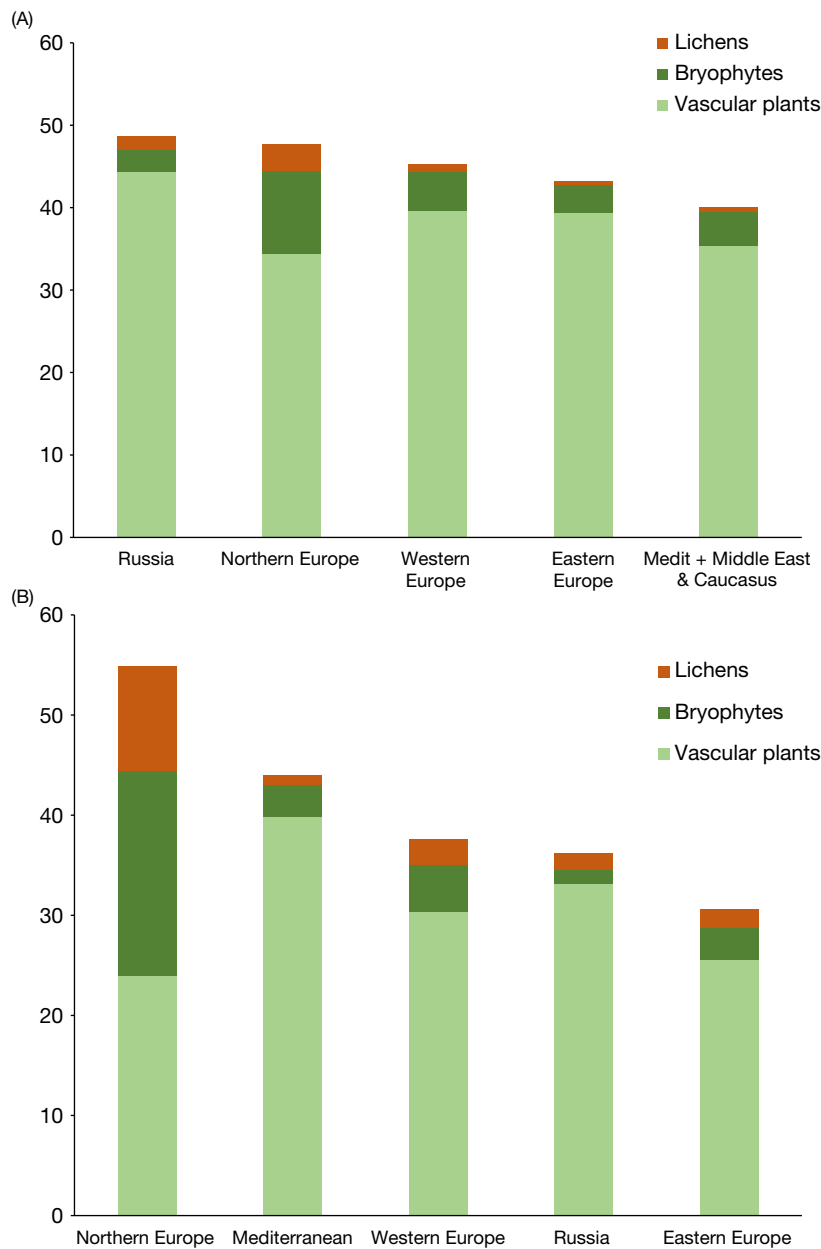


Fig. 8 Species richness and taxonomic composition of the meso-xeric grasslands (*left*) and rocky grasslands (*right*) across Palearctic subregions. Displayed are means of all 10-m² plots contained in version 2.00 of the GrassPlot database (Dengler et al., 2018; Biurrun et al., 2019) in which all three taxonomic groups were recorded. Note that Mediterranean and Middle East & Caucasus were joined for meso-xeric grasslands to get a sufficient number of plots. Japan and Korea, Kazakhstan and Middle Asia, China and Mongolia are not included because of lack of data.

relationship in Palearctic dry grasslands: species richness increased more steeply and peaked higher under elevated productivity levels at nitrogen and phosphorus co-limited sites. Similarly to productivity, a hump-shaped relationship was found for soil pH and plant diversity at the regional scale, with highest richness in neutral or slightly basic pH, but in drier conditions this relationship became negative or was not significant (Palpurina et al., 2017).

Management is a particularly important driver of species richness in semi-natural grasslands, as abandonment usually is followed by secondary succession towards shrubland or forest communities. Traditional, extensive management, like grazing or mowing, usually supports high diversity of grasslands, while intensification through excessive application of fertilizers, frequent mowing, sowing of highly productive species of grasses and/or legumes, and also too intensive grazing often lead to biodiversity decline (e.g., Socher et al., 2012; Török et al., 2016; Boch et al., 2018). It should be noted that in case of natural grasslands, the natural factors shaping their diversity quite often are disrupted by human activities, thus their biodiversity can also decline if there is no active conservation measure, e.g., replacing grazing by wild animals (that are locally extinct) or natural fires (Havrylenko, 2011).

Species-Area Relationships and Beta Diversity

Extensive multi-scale sampling conducted on Palaearctic grasslands in recent years with application of standardized methodology (Dengler et al., 2016) and other data stored in the GrassPlot database (Dengler et al., 2018; Biurrun et al., 2019) revealed other interesting macroecological patterns. Analyses of data coming from 2057 nested plot series in Palaearctic grasslands (with at least seven grain sizes varying from 1 cm² to 1024 m²) confirmed that the power function $S = c A^z$ (where S is the species number, A represents area and c and z are fitted parameters of the function) describes species-area relationships (SARs) in Palaearctic grasslands best (Dengler et al., 2020a).

Moreover, the exponent z of the power function, which describes how fast species richness increases with increasing area, can give valuable ecological information, i.e., on the fine-scale beta diversity. Such beta diversity (called multiplicative beta diversity; Jurasinski et al., 2009) is calculated according to the formula $z = \log_{10}(S_\gamma/S_\alpha)/\log_{10}(A_\gamma/A_\alpha)$, where S_i is the species richness and A_i the area at the α - and γ -level, respectively. Fine-scale beta-diversity is useful in comparing the rate of spatial species turnover between different ecological situations. Analyses performed on 4546 nested plot series in Palaearctic grasslands showed that taxonomic groups significantly differ in this respect with bryophytes having the lowest, and lichens the highest beta diversity (Dengler et al., unpublished). Fine-scale beta diversity of Palaearctic grasslands can be controlled by environmental factors, that can have positive impact like habitat heterogeneity (Polyakova et al., 2016; Dengler et al., unpublished), negative impacts like heat load (proxy of the drought stress) and productivity (Chiarucci et al., 2006; Turtureanu et al., 2014), or unimodal effect as in annual precipitation (Polyakova et al., 2016; Dengler et al., unpublished).

Threats and Conservation

Overall Threat Assessment

In the Palaearctic region, grasslands are important habitats for many species of global conservation concern (Habel et al., 2013; Török et al., 2016; Török and Dengler, 2018). These type of terrestrial habitats are among the most intensively and negatively human-impacted ones, characterized by a strong declining trend in habitat extent (see Table 1) and intactness as well as species diversity and abundance since the second half of the 20th century (Visconti et al., 2018). Because of that, a high proportion of grassland types (e.g., Janssen et al., 2016) and associated species are endangered today (Visconti et al., 2018). Alarming losses of species abundances in a rather short time period and the homogenization of species communities by supporting generalist species at the expense of habitat specialists were reported for well-monitored taxa such as farmland birds (57% population decrease) and grassland butterflies (45% population decrease) in Western and Central Europe (Visconti et al., 2018). Mollusk abundance and diversity has also declined with grassland intensification or conversion to arable land (Neubert et al., 2019).

In Table 5, we summarize the major threats to grassland biodiversity in the 10 regions of the Palaearctic biogeographic realm, separated in drivers of biodiversity loss during the past decade and projected change of the impact of these drivers in the next decade. The table was mainly based on expert assessments by the author teams of the ten regional chapters, combined with the findings of the IPBES regional assessment report on biodiversity and ecosystem services for Asia and the Pacific (Karki et al., 2018) as well as for Europe and Central Asia (Rounsevell et al., 2018). We used a comprehensive classification of drivers with 16 threat categories, arranged in six main groups, updated from Török and Dengler (2018).

Generally, the drivers of the category “changes in grassland management” were considered as the most negative ones (Table 5). While in Mongolia and China, overgrazing is the major cause of biodiversity loss, in the more oceanic areas (with prevailing secondary grasslands), the “twin threats” of abandonment/underuse and other forms of intensification than overgrazing have this role (Table 5). Habitat loss generally is the second most important driver of biodiversity loss of grasslands, with built-up areas, arable fields and afforestation being seen as similarly important, but with regional differences (Table 5). Up to now, on average 28% of the natural grasslands and 38% of the secondary grasslands got completely lost that way, but regionally losses are much more dramatic, with up to 92% for natural grasslands (Eastern Europe) and 75% for secondary grasslands (Northern Europe and Baltic States). Altered site conditions in general were of only moderate impact on biodiversity currently, with the exception of eutrophication, which is one of the most important drivers in Western Europe, and to a lesser extent in Northern Europe and the Baltic States. In Europe formerly also drainage of wet grasslands was a major course of biodiversity loss (Wesche et al., 2009), but the large-scale drainages are largely history, while nowadays locally even re-wetting projects are performed. The three other driver groups, climate change, invasive species and direct impact of humans and their infrastructure were generally considered of lesser importance, but also with some regional differences (Table 5). When projecting the current trends into the future, the regional author teams largely assumed that the same drivers that cause biodiversity loss today will continue to do so at a similar level in the next 10 years (Table 5). The only two drivers where a significant proportion of regional author teams predicts stronger negative impact in the future are climate change and invasive species.

Individual Threat Factors

Land-use change (including changes from intensification to the complete abandonment) was identified as the major driver of habitat degradation, large-scale biodiversity loss and homogenization of species assemblages by the IPBES assessment (Visconti et al., 2018), consistent with our own assessment (Table 5). On the one hand, intensification of land use aims to increase the productivity of grasslands; it is mostly achieved with the addition of organic or inorganic fertilizers and the broadcast of high-

Table 5 Overview of the main drivers of grassland biodiversity loss, their current impact (i.e., rate of biodiversity loss caused by them 2010–2019) and its anticipated future change (i.e., change in the rate of biodiversity loss in 2020–2029 compared to the situation in 2010–2019).

Driver	Western Europe		Northern Europe and Baltic States		Eastern Europe		Mediterranean Region		Middle East and the Caucasus	
	Current impact	Future change	Current impact	Future change	Current impact	Future change	Current impact	Future change	Current impact	Future change
Habitat loss										
Conversion to arable land	High	± Constant	Low	± Constant	Medium	± Constant	Low	± Constant	Low	± Constant
Afforestation	Medium	± Constant	Medium	± Constant	Medium	± Constant	Low	± Constant	High	± Constant
Mining and energy production ^a	Low	Decrease	Low	± Constant	Low	± Constant	Low	± Constant	Medium	Increase
Settlements and other infrastructure	Medium	± Constant	Low	± Constant	Low	± Constant	Medium	± Constant	Medium	± Constant
Changes in grassland management										
Abandonment and underuse	High	± Constant	High	Increase	Very high	± Constant	Medium	Increase	High	± Constant
Overgrazing	Medium	± Constant	Medium	± Constant	Low	± Constant	Medium	± Constant	Low ^b	± Constant
Other forms of intensification ^c	Very high	± Constant	High	± Constant	Medium	Increase	Low	± Constant	Low	± Constant
Altered site conditions										
Eutrophication (direct and indirect) ^d	Very high	± Constant	Medium	± Constant	Low	± Constant	Low	± Constant	None	± Constant
Altered water regime ^e	Medium	± Constant	Low	± Constant	Low	± Constant	Low	± Constant	Low	NA
Climate change	Low	± Constant	Low	Increase	Low	Increase	Medium	Increase	Low ^f	Increase
Invasive species	Medium	± Constant	Low	± Constant	Medium	Increase	Medium	± Constant	Low	Increase
Direct impact of humans and their infrastructure										
Military and armed conflicts	None ^g	± Constant	None ^g	± Constant	Low	± Constant	Low	± Constant	Medium	± Constant
Recreation activities	Low	± Constant	Low	± Constant	Low	Increase	Low	± Constant	Low	± Constant
Collecting wild plants and hunting	Low	± Constant	Low	± Constant	Low	± Constant	Low	± Constant	Medium	± Constant
Wildlife loss due to electrocution, wind farm collision or traffic	Low	± Constant	Low	± Constant	Low	± Constant	Low	± Constant	None	NA
Wildfires caused by humans	None	NA	None	NA	None	NA	Medium	± Constant	None	NA
Driver	Russia		Kazakhstan and Middle Asia		Mongolia		China		Japan	
	Current impact	Future change	Current impact	Future change	Current impact	Future change	Current impact	Future change	Current impact	Future change
Habitat loss										
Conversion to arable land	Medium	± Constant	Medium	± Constant	Low	± Constant	Low	± Constant	None	± Constant
Afforestation	Low	± Constant	Low	± Constant	None	± Constant	Low	± Constant	Low	± Constant
Mining and energy production ^a	Low	± Constant	Low	± Constant	Medium	Increase	Medium	± Constant	None	± Constant
Settlements and other infrastructure	Low	± Constant	Low ⁱ	± Constant	Medium	Increase	Medium	± Constant	Medium	Increase
Changes in grassland management										
Abandonment and underuse	High	± Constant	Medium ^h	± Constant	Low	± Constant	Low	± Constant	High	Increase
Overgrazing	Medium	± Constant	Medium	Increase	High	Increase	High	± Constant	Low	± Constant ⁱ
Other forms of intensification ^c	Medium	± Constant	Low	± Constant	Low	± Constant	Low ^j	± Constant ^j	High ^k	Increase ^k
Altered site conditions										
Eutrophication (direct and indirect) ^d	Low	± Constant	Low	± Constant	None	± Constant	Low	± Constant	Low ^l	± Constant
Altered water regime ^e	Medium	± Constant	Medium	± Constant ^m	None	Increase	Low	± Constant	None	± Constant
Climate change	Low	± Constant	Low	± Constant	Medium	Increase	Medium	Increase	Low	Increase
Invasive species	Medium	Increase	Low	Increase ^l	None	± Constant	Low	± Constant	Low ⁿ	± Constant
Direct impact of humans and their infrastructure										
Military and armed conflicts	Low	± Constant	Low	± Constant	None	± Constant	None	± Constant	None ^o	± Constant
Recreation activities	Low	Increase	Low	± Constant	Low	Increase	Low	± Constant	Low ^p	± Constant
Collecting wild plants and hunting	Medium	± Constant	Medium	± Constant	Medium	± Constant	Medium	± Constant	Low	± Constant ^q
Wildlife loss due to electrocution, wind farm collision or traffic	Medium	± Constant	Medium ^r	± Constant ^r	Low ^s	± Constant ^s	NA	NA	Low ^t	Increase
Wildfires caused by humans	High	Increase	Medium ^u	Increase ^u	Low	± Constant	Low	± Constant	None	± Constant

"Current impact" is given on a five-step ordinal scale (none—low—medium—high—very high), while "Future change" was assessed on a three-step ordinal scale ("decrease"—"± constant"—"increase"), where "± constant" means that the biodiversity loss due to this driver is expected to continue in the next decade at the same level as in the previous decade ($\pm 10\%$). Please note that in order to get an assessment of the expected impact during the next decade, both columns have to be combined: for example, if the current impact is "medium" and the future change is predicted to be an "increase," the future impact would be "high" (or even "very high"). Likewise, even if the importance of a driver is predicted to decrease, it will in most cases still cause additional biodiversity loss during the next decade. "NA" = not assessed.

^aThis includes area loss due to open-cast mines and water dams for energy production.

^bOvergrazing is not widespread but in some places it is an important driver of biodiversity loss.

^cThis includes high cutting frequency, pesticide application, re-seeding and homogenization of grasslands/removal of heterogeneity.

^dThis refers to direct fertilization, spill-over from neighboring fields and airborne nitrogen input.

^eThis refers both to drainage and irrigation.

^fExcept for the sprawling city of Almaty and its satellite towns ("high").

^gIn the absence of war, military training areas had in the past even a positive or very positive effect on grassland biodiversity, but during the past decade the diversity in these areas remained $\pm$ constant.

^hAbandonment and underuse "high" in steppes of Kazakhstan but "low" in remaining regions.

ⁱOvergrazing by livestock is not widespread but biodiversity loss by wild deer browsing will increase in semi-natural grasslands.

^jHay making ("low"/"± constant"), use of pesticides ("none"/"± constant").

^kPaddy consolidation and increased sown pastures.

^lGenerally "none" to "low," but "high" in some meadows.

^m± Constant because of recent dam reservoir constructions in Pamir-Altay and surroundings.

ⁿGenerally "none" to "low," but "high" in oceanic islands.

^oTraining grounds for the Japan Self-Defense Forces have maintained semi-natural grassland biodiversity.

^pSki slope grasslands have maintained semi-natural grassland biodiversity whereas off-road vehicle recreation degrades coastal and riparian grasslands.

^qHunting pressure on wildlife will decrease due to aging of hunters.

^rElectrocution ("high"/"± constant") and wind farm collisions ("low"/"increase," but "low"/"± constant" in Kirgystan and Tajikistan).

^sElectrocution ("moderate"/"± constant"), wind farm collisions ("none"/"± constant").

^tWind farm construction has negative effects on coastal grassland biodiversity in the northern part of the country.

^uWild fires variable by region: "very high"/"increase" in steppes of Kazakhstan to "low"/"± constant" in remaining regions.

production grass and forb cultivars. Productive grasslands are mown more frequently or grazed at higher stocking densities compared to extensively managed grasslands (Blüthgen et al., 2012). Intensive management promotes a few mowing-tolerant species (e.g., Socher et al., 2012) or leads to diversity loss due to overgrazing (Török et al., 2016). The conversion of a large proportion of semi-natural to intensified grasslands caused a large-scale landscape simplification and homogenization, especially in Western and Central Europe (Visconti et al., 2018). This is resulting in a multi-trophic homogenization of grassland communities, the loss of specialist species and ecosystem multifunctionality (Gossner et al., 2016; Soliveres et al., 2016a,b). On the other hand, the cessation of grassland management in general leads to litter accumulation, increased competition by community generalists and woody encroachment on the long-run. In the future, woodland increase and further grassland declines are particularly projected for Western and Central Europe (Harrison et al., 2018). The cessation of traditional land use is associated also with the loss of indigenous and local knowledge and practices (Elbakidze et al., 2018). However, effects of abandonment might differ among vegetation types, regions and taxa (Kämpf et al., 2016; Valkó et al., 2018). There is evidence for particularly strong negative effect of the cessation of grassland management on the biodiversity in semi-natural grassland systems of temperate regions (Dengler et al., 2014; Rotherham, 2015) and mountain areas (MacDonald et al., 2000; Valkó et al., 2012; Boch et al., 2019). This is in accordance with our evaluation, as the threat group “Changes in grassland management” was identified as the most negative one (Table 5). In addition, abandonment and underuse was identified as an important driver of biodiversity loss in Europe (Western Europe, Northern Europe and Baltic States, and Eastern Europe), but also in the Middle East and Caucasus, Russia or Japan. Also the negative impacts of abandonment were assessed to remain constant or even increase in some regions (Table 5). Another important driver was intensification of land use in form of overgrazing (Mongolia and China) and other forms of intensification mostly for hay making (Western Europe, Northern Europe and the Baltic States and Japan; Table 5).

Habitat loss in the form of conversion to arable land, afforestation, mining and energy production or urbanization (settlements and other infrastructure) was assessed to have a high impact in Western Europe (conversion to arable land) and in the Middle East and the Caucasus (afforestation). In most regions, however, its current impact was assessed from low to medium with a remaining trend for the future. Abandonment of crop production in marginal or low-production cropland areas promotes the recovery of landscape-scale biodiversity, as on the abandoned areas in case of proper sources of propagules available in the landscape grasslands spontaneously regenerates. This type of large-scale recovery was typical for Central Asian steppes after the dissolution of the USSR (Brinkert et al., 2016; Kämpf et al., 2016). This recovery was further associated with increased ecosystem functioning because of increased soil carbon sequestration (Kurganova et al., 2015). In contrast, in Western Europe the reuse of fallow lands is typical – which also resulted in the conversion of spontaneously recovered grasslands. The eutrophication was identified as an important threat for grassland biodiversity in Western Europe (by fertilizer application, aerial nitrogen deposition and run-on of fertilizers from neighboring fields), but having only low impact in most of the other regions. Altered water regime was assessed having currently no to medium impact (but had strong negative impact in some regions in the past).

Negative effects of invasive alien species encroachment include suppression of native species, gene drift, homogenization of species assemblages and modifications of habitats and ecosystem functions. Moreover, invasive alien species might have negative economic and human health consequences (Nentwig et al., 2016, 2018; Elbakidze et al., 2018). Western European countries have the highest numbers of invasive alien species in the Palearctic realm due to trade and colonial histories, the invasion rates continuously increasing in all environments, taxonomic groups (except mammals), and subregions and there is no sign of reversing or slowing down this trend. However, there are data limitations in large parts of the region outside Europe (Karki et al., 2018; Rounsevell et al., 2018). Although the invasion threat during the 21st century is expected to be medium to very high in most parts of Europe and Central Asia (except Northern regions), the negative impact of invasive alien species on Palearctic grasslands so far has been evaluated as low to moderate (Török and Dengler, 2018). In the current assessment a medium impact of invasive species were assessed in Europe (excluding Northern Europe and Baltic States where it was low) and Russia, but was low and even negligible (Mongolia) in other regions. This might be because of the low number of high-impact invasive aliens that are actually associated with grasslands (see Nentwig et al., 2018). However, effects of invasions are expected to increase in future (Table 5) and might be particularly accelerated by climate change, but the outcome will largely depend on effective management and policy measures (Elbakidze et al., 2018).

Climate change is expected to come along with increased temperatures, reduced precipitation and increased numbers of extreme weather events in large parts of the Palearctic realm. Projected habitat changes can lead to transitions in species composition and diversity loss. While desertification risk is particularly high in Asian steppe regions (Faridah-Hanum et al., 2018; Visconti et al., 2018), mountain and northern grasslands are affected by northwards and upwards shifting thermophilous species, which can cause a decline of cold-adapted, high-elevation species (Gottfried et al., 2012; Steinbauer et al., 2018). Moreover, climate change might accelerate the negative effects of other major drivers of biodiversity loss (Faridah-Hanum et al., 2018; Visconti et al., 2018). In the present assessment, we found the current impact of climate change from low to medium but in most regions an increasing impact was assumed for the future. With climate change spontaneous wildfires and arsons will likely increase, which can have high impact on the biodiversity (we assessed its current impact to be high in Russia).

Further direct human impacts such as military and armed conflicts vary among the regions: In absence of war, for example in Western Europe, Northern Europe and the Baltic States or Japan, military training areas are associated with extensive land use and low accessibility, which is highly promoting grassland diversity. In contrast, grassland biodiversity is threatened by armed conflicts in regions such as Eastern part of Ukraine, the Middle East and Central Asia (Török and Dengler, 2018, Table 5). In most parts of Asia and the Middle East and Caucasus the collecting of wild plants and hunting was assessed to have medium impact on grassland biodiversity. Impact of recreation activities, wildlife loss due to electrocution and wildfires (for the latter two in exception of Russia where they were assessed as medium and high, respectively) was assessed to be low or not present in most regions.

Conservation and Restoration of Grasslands

In the last decades, much attention has been given to the conservation and restoration of biodiversity in natural and semi natural habitats, including grasslands of the Palaearctic realm and elsewhere (Brudvig, 2011; Török et al., 2018). Conservation authorities seek cost-effective ways to restore and sustain grassland biodiversity by considering theoretical findings on dispersal, species pool, community assembly rules and biodiversity patterns (Laughlin, 2014; Török and Helm, 2017). In the last years, various conservation efforts to monitor, maintain and promote grassland extent and diversity were made. This includes large national biodiversity monitoring programs (e.g., Bergamini et al., 2019), subsidies to farmers and restoration efforts. In Europe, there are many landscape-scale grassland restoration programs funded by the EU. Browsing the LIFE program database searching for themes of “Habitats-Grasslands” with the keyword “restoration measure” retained 101 projects in the 1993–2017 timeframe (European Union, 1995–2019). However, a large proportion of subsidies within the EU common agricultural policy (CAP) is still misleading as they often promote productive grasslands and do not conserve HNV grasslands and their diversity (Sutcliffe et al., 2015). A rethinking and the development of appropriate tools to reverse negative trends are urgently needed. This aspect is of particular importance in current nature conservation planning, as the European Union’s CAP assigns outstanding importance to permanent grassland for species protection. Permanent grassland is an agricultural term that is generally defined as “land used by sowing or self-seeding for the cultivation of grasses or other forage plants and not used as arable land for at least five years” (Bundesamt für Naturschutz, 2014). However, the basic EU guidelines on the promotion and conservation of permanent grasslands do not only lack specific management recommendations, but do not distinguish between extensively and intensively managed permanent grasslands with regard to their impact on environmental and biodiversity protection, which to our opinion also should be considered in the revision of the CAP for the next funding period (see Péter et al., 2014, 2019). However, at a specific level there are various management-related instruments for achieving environmental objectives in the common European agricultural policy (e.g., agri-environmental and climate measures, organic farming and animal welfare measures; see Bundesministerium für Ernährung und Landwirtschaft, 2015).

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Grasslands and Shrublands of the Mediterranean Region

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Glossary

Acidophilous Thriving in an acidic environment.

Basiphilous Thriving in an alkaline environment.

Biocoenosis Biotic community.

Chamaephyte Woody plant bearing its dormant vegetative buds up to 30 cm above the ground level.

Geliturbation Frost-driven movements of unconsolidated, superficial material.

Hemicryptophyte Herbaceous perennial plant bearing its dormant vegetative at the ground level.

Oligotrophic Thriving in an nutrient-poor environment.

Phytosociology Classification of plant communities based on compositional data.

Thermoxerophilous Thriving in a warm and dry environment.

Therophyte Herbaceous annual plants, surviving the adverse season in the form of seeds.

Abstract

The Mediterranean Region extends to the 1.6% of the world's land surface and more than the half of the Mediterranean-type ecosystems of the world. The remarkable species richness in the Mediterranean Region mainly originates from an exceptional habitat diversity and the presence of several natural barriers facilitating the segregation and differentiation of local taxa and biocoenoses. In this article, we deal with the habitats characterized by grasslands and shrublands that clearly show the adaptations to what could be called "the Mediterranean syndrome", i.e., the intrazonal Mediterranean grasslands and shrublands (MG&S). The main driving forces of the adaptive radiation and high biodiversity that characterize the MG&S are geographical segregation and appearance of new lands, climatic variability, substrate heterogeneity, species-specific plant-animal interactions and short generation times. MG&S are of paramount importance for delivering a wide array of ecosystem services. Apart from their importance for the maintenance of biodiversity, they play a major role in providing high quality forage for both livestock and wild animals; they support communities of insects with major roles in the ecosystem services of control and pollination; they sustain apiculture, and contribute to the prevention of erosion processes and maintenance of the water cycle; they buffer the negative impacts from fertilizers and pesticides and display highly significant aesthetic and recreational values. However, major threats to the provision of ecosystem services mostly originate from climate change, and recent land use changes (such as: "coastalization," unbalanced grazing activities and abandonment of traditional

practices). To mitigate the adverse effects of land use changes, the management of MG&S may be based on four principles; (a) ecosystem sustainability, (b) natural regeneration, (c) multifunctionality, and (d) protection.

Delimitation and Physiogeography

The Mediterranean Region consists of thousands of differently sized islands and peninsulas, surrounded by the Mediterranean sea. The most important ecological feature of the Mediterranean Region is a very peculiar climate: despite its proximity to the sea, the warmest season is also the driest. This requires from terrestrial sessile or low vagile organisms several morphological and physiological adaptations to tolerate or to avoid the summer drought stress. On the other hand, winter is the rainiest season and the relatively mild temperatures of wintertime make the Mediterranean Region “wintergreen,” at least close to the sea, because the Mediterranean mountains can impose a severe winter cold stress to their living organisms (Guarino, 2001).

The Mediterranean Region extends on 2,073,806 km² (Olson et al., 2001), i.e., 1.6% of the world’s land surface and more than the half of the Mediterranean-type ecosystems of the world (Fig. 1; Esler et al., 2018). The distribution ranges of the genus *Cistus*, as well as that of species like *Quercus ilex* and *Olea europaea*, outline quite well the boundaries of the Mediterranean Region.

The biological diversity of the Mediterranean Region is very high, currently estimated in 400,000–600,000 different species of living organisms, sea included (Hofrichter, 2001). Among them, about 25,000 are vascular plants, half of which are endemic to the whole Region or to smaller parts of it. Additionally, the fauna of the Mediterranean biogeographical region shows a great variety; 75% of the total European insect fauna are found here (Balletto and Casale, 1991). Similarly, levels of endemism are high for most groups of insects (Blondel and Aronson, 1999).

In spite of the high rate of endemism at the genus and species level in the vascular flora of the Mediterranean Region, high-rank endemics are rare (no endemic families, with the exception of the monotypic carnivorous *Drosophyllaceae*; few endemic subfamilies, such as *Aphyllanthoideae*). This testifies the relatively short evolutionary history of the Mediterranean flora and fauna (Cowling et al., 1996; Rundel et al., 2016). As we will see, the beginning of the speciation processes featuring the present-day Mediterranean biodiversity can be fixed in the mid-Pliocene.

The remarkable species richness in the Mediterranean Region is mainly caused by an exceptional habitat diversity and to the occurrence of several natural barriers facilitating the segregation and differentiation of local taxa and biocoenoses. The landscape heterogeneity and the natural fragmentation of habitats did not only have a direct influence on the local biodiversity, but also on the human land use and cultural diversity. In the last 12,000 years, human practices contributed to increase the patchiness of the Mediterranean landscapes and favored the establishment of grasslands and shrublands to the detriment of pristine forests. According to FAOstat (2014), grasslands cover 21.3% and shrublands 24.0% of the Mediterranean Region. (CCI LC data set limited to the Mediterranean part of the following countries: Albania, Algeria, Bosnia and Hercegovina, Croatia, Cyprus, France, Gibraltar, Greece, Holy See, Italy, Israel, Lebanon, Malta, Monaco, Montenegro, Morocco, Palestine, Portugal, San Marino, Slovenia, Spain, Spain, Tunisia.)

The topographic diversity may exasperate or alleviate the main climatic driver of the Mediterranean ecosystems, which is summer aridity. Therefore, in azonal vegetation under generically mesic or wet conditions, it often happens that the microclimatic and edaphic conditions favor a vegetation that is structurally and floristically quite similar to that of the European temperate ecosystems. In this article, we will only deal with the habitats characterized by grasslands and shrublands that clearly show the adaptations to

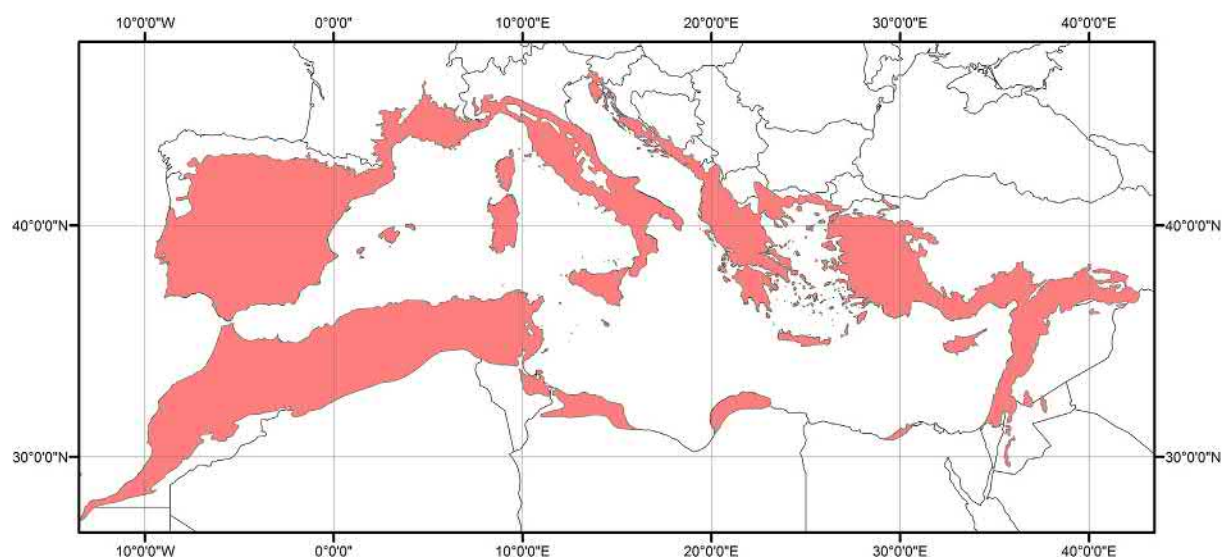


Fig. 1 Approximate delimitation of the Mediterranean Region covered by this article. Adapted from Olson, D. M., Dinerstein, E., Wikramayake, E. D., et al. (2001). Terrestrial ecoregions of the world: A new map of life on earth. *BioScience* 51, 933–938.

Table 1 Synopsis of the main adaptive responses to the environmental stresses of the plant species of MG&S.

<i>Environmental stress</i>	<i>Functional trait</i>	<i>Functional consequence</i>
Winter cold	Winter dormancy	Tolerance to low temperatures
	Low stature of plants	Reduced physical stress and frost damage
	Persistent dead leaves	Seasonal isolation of the buds
Summer drought	Epidermal trichomes, waxes, thick cuticle	Reduced evapotranspiration
	Sunken stomata, conduplicate leaves	Increased boundary layer resistance
	Reduced leaf area	Reduced water loss
	Summer loss of the leaves	Reduced evapotranspiration
	Aromatic oils in the stomatal chambers	Decreased evapotranspiration
	Thorny, hairy pulvinate architecture	Effective captation of the air moisture
	High root/shoot ratio	Increased absorptive area
	Deep rooting	Access to perennial water
	Dimorphic root system	Access to dew and deep water
	Poikilohydry	Tolerance to extreme drought
Summer heat	Therophytic/Geophytic habit	Avoidance of extreme drought
	Rapid root growth of seedlings	Adequate water supply
	Reduced or dissected leaves	Reduced heat loading
	Open canopy architecture	Sensible heat removal
	Epidermal trichomes, waxes, thick cuticle	Increased reflectance
Wildfires	Succulence	Increased thermic inertia
	Precocity/serotiny	Fire avoidance
	Myrmecochochory	Maintenance of viable populations
	Persistent, soil-stored seeds	Maintenance of viable populations
	Resprouting rootstocks	Vigorous post-fire regeneration
Nutrient limitation	Geophytic habit	Rapid re-establishment
	Secondary flammable compounds	Limited fire damage
	Bacterial symbioses	Facilitation of nutrient uptake
	Fungal symbioses	Facilitation of nutrient uptake
	Pulvinate architecture	More effective retention of the organic matter
	Slow growth at maturity	Reduced nutrient requirements
	Cluster roots	Increased exchange surface
	Big rootstocks	Nutrient sequestration
	Cumulative set of persistent seeds	Slow build-up of seed store
	Entomogamy	Optimization of resources
Predation	Spines and/or secondary aromatic/toxic compounds	Unpalatability
	Sclerophylly	Little nutrient content for herbivores
	Anemochory	Minimization of predator resource base
	Low seed set	Minimization of predator resource base
	Prolific seed set	Predator satiation
Wind	Myrmecochochory	Avoidance of post-fire predation
	Reduced/slender leaves and/or stems	Reduced physical resistance and damage
	Low stature of plants	Reduced mechanical stress
Ionic imbalance/toxicity	Anemochory	Optimal dispersal strategy
	Ion exclusion at the surface of the roots	Tolerance of salinity
	Cytoplasmatic compartmentalization	Tolerance of salinity
Physiological drought	Salt extrusion through specialized glands or bladders	Tolerance of salinity
	High osmotic pressure in the tissues	Adequate water supply

From Guarino, R. (2006). On the origin and evolution of the Mediterranean dry grasslands. *Berichte der Reinhold Tüxen Gesellschaft* **18**, 195–206; Guarino, R., Giusso del Galdo, G. and Pignatti, S. (2006). The Mediterranean dwarf shrubs: Origin and adaptive radiation. *Annali di Botanica N. S.* **5**, 93–101.

what could be called “the Mediterranean syndrome”, i.e., the intrazonal Mediterranean grasslands and shrublands (MG&S). Relevant physiognomic, adaptive and floristic differences are featuring in these vegetation types. The main structural and functional traits of the plants growing in the MG&S are reported in **Table 1** and will be summarized in the following sections, in which the taxonomic nomenclature follows Euro + Med PlantBase (accessed in September 2019, www.emplantbase.org) and the syntaxonomy of vegetation types follows the EuroVegChecklist (Mucina et al., 2016).

Typology of Mediterranean Dry Grasslands

In the Mediterranean Region, three main structural and functional types of zonal dry grasslands can be recognized (Guarino, 2006), i.e., those dominated by large caespitose hemicryptophytes (wintergreen perennial dry grasslands), those dominated by

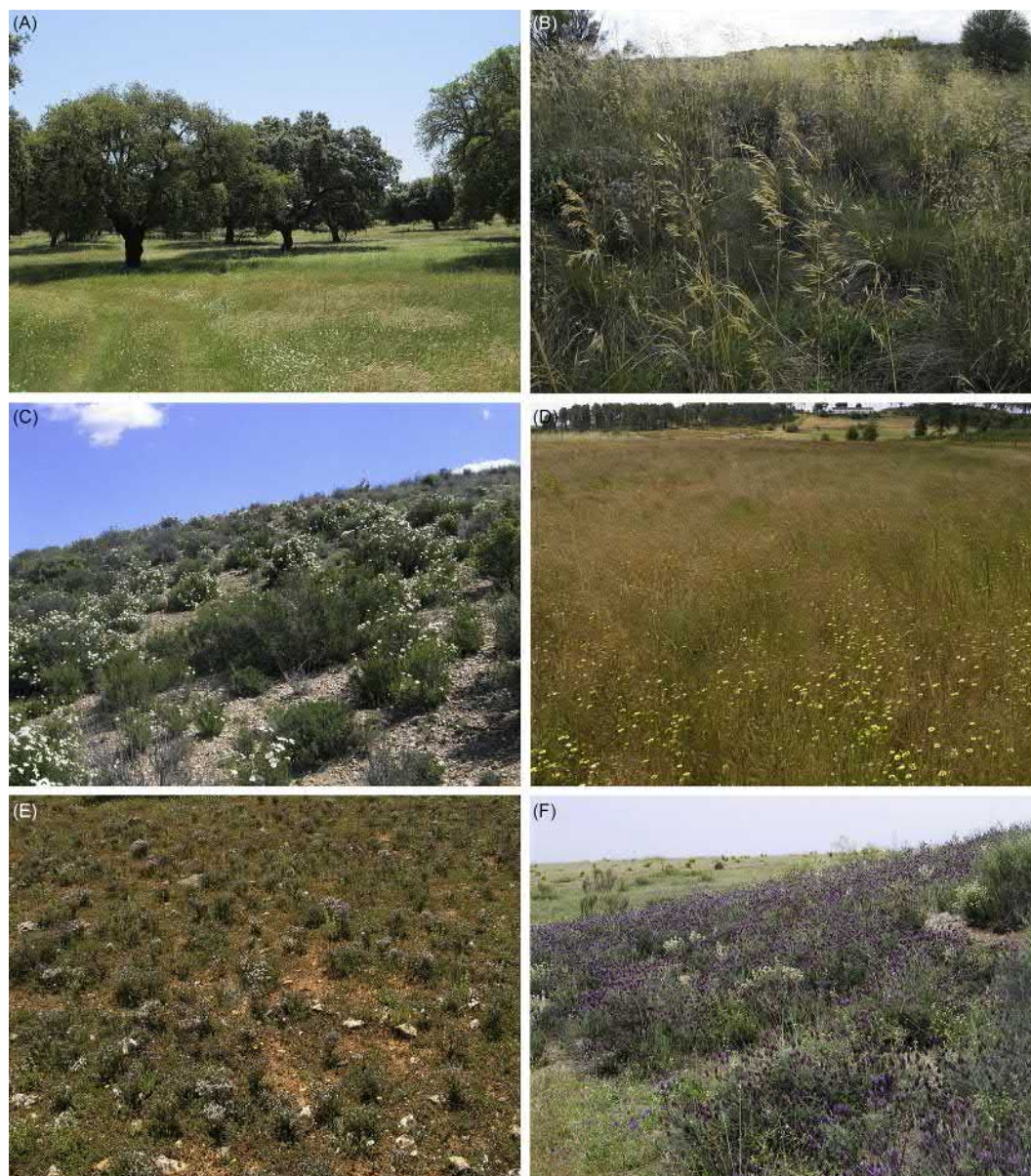


Fig. 2 Characteristic Mediterranean grasslands and shrublands; (A) Dehesa (Córdoba, Spain), (B) dry perennial grasslands of *Celtica gigantea* (*Stipo giganteae-Agrostietea castellanae*) (Toledo, Spain), (C) dwarf shrublands of *Cistus clusii* and *Rosmarinus officinalis* (*Ononido-Rosmarinetea*) (Cuenca, Spain), (D) grasslands of *Agrostis castellana* (vallicares), (E) shrublands (scrubs) of *Thymus vulgaris* (*Ononido-Rosmarinetea*), (F) shrublands (scrubs) of *Lavandula pedunculata* and *Thymus mastichina* (*Cisto-Lavanduletea stoechadis*) Toledo (Spain). Photos by María Pilar Rodríguez Rojo.

thermoxerophilous therophytes (wintergreen ephemeral dry grasslands), those dominated by relatively small chamaephytes and hemicryptophytes, occurring at higher elevations but below the timberline (summergreen perennial dry grasslands) (Figs. 2 and 3).

Wintergreen Perennial Dry Grasslands

Vegetation widely distributed in the most xeric habitats of the Mediterranean Region, under a rather long (usually over 3 months) summer drought period (San Miguel et al., 2016). With reference to the bioclimatic classification by Rivas-Martínez (2004), these grasslands are linked mainly to thermo- to supramediterranean thermotypes (i.e., from sea-level up to ~900 m a.s.l.), with dry-subhumid ombrotypes.

Perennial bunchgrasses, such as *Brachypodium retusum*, *Hyparrhenia hirta*, *Macrochloa tenacissima*, *Ampelodesmos mauritanicus* and *Lygeum spartum* are the most frequent and typical representatives of this vegetation, classified by phytosociologists within the class *Lygeo sparti-Stipetea tenacissimae*.



Fig. 3 Characteristic Mediterranean grasslands and shrublands: (A) *Hyparrhenia hirta* grassland (*Hyparrhenion hirtae*, *Lygeo sparti-Stipetea tenacissima*), with *Asphodelus ramosus* in the foreground (E-Sicily), (B) *Lygeum spartum* grassland (*Moricandio-Lygeion sparti*, *Lygeo sparti-Stipetea tenacissima*) (S-Sicily), (C) annual dry grassland (*Trachynion distachyae*, *Stipo-Trachynietea distachyae*) with *Trachynia distachya* and *Lagurus ovatus* (SE-Apulia), (D) maquis of *Juniperion turbinatae* (*Pistacio lentisci-Rhamnetalia alaterni*), with *Juniperus phoenicea* and *Euphorbia dendroides* (SW-Sardinia), (E) early summer view of a coastal maquis with *Euphorbia dendroides* and *Periploca angustifolia* (*Periplocion angustifoliae*, *Pistacio-Rhamnetalia halepensis*) (W-Sicily), (F) submontane garrigue of *Armerio sardoae-Genistion salzmannii* (*Cisto-Lavanduletea stoechadis*), with *Cistus salviifolius*, *Erica scoparia*, *Genista desoleana*, *Tuberaria lignosa*, *Vincetoxicum hirundinaria* (NW-Sardinia). Photos by Riccardo Guarino.

In the meso-supramediterranean (and submediterranean) vegetation belts of the West Mediterranean Region, on siliceous cambic soils, *Stipa* and *Festuca* species form dense and bunchy grasslands, classified into the class *Stipo giganteae-Agrostietea castellanae*. These grasslands are dominated by *Celtica* (*Stipa*) *gigantea* on dry to subhumid lands and shift towards *Festuca merinoi* grasslands on northern and humid territories.

At mid-montane altitudes of the same region, geliturbate shallow soils are colonized by hemicrypto-chamaephytic communities, which can be classified in two main groups based on the type of substrate; acidophilous grasslands dominated by *Festuca indigesta*, *F. summilusitana*, *Koeleria crassipes* and *Plantago subulata*; basiphilous grasslands dominated by *Festuca hystris* and *Poa ligulata*. They are classified in the phytosociological orders *Jasiono sessiliflorae-Koeleretalia crassipedis* (*Festucetea indigestae*) and *Festuco hystricis-Poetalia ligulatae* (*Festuco hystricis-Ononidetea striatae*).

Semi-natural grasslands of *Poa bulbosa* ("majadales"), classified within the class *Poetea bulbosae*, are dense and short perennial grasslands resulting from the intense and continuous grazing of all the above mentioned grasslands. Besides the dwarf perennial grasses, the *Poetea bulbosae* include many legumes (mainly *Trifolium*, *Astragalus*, *Medicago*) and rosulate species (*Plantago*, *Echium*, etc.). These Mediterranean grasslands dry up in early summer but from the beginning of the autumnal rainy season they grow fast and remain green and fertile during winter. They are more frequent in the western Mediterranean, but also have been recognized in southern Italy and Greece.

The primary habitats of wintergreen perennial dry grasslands are rocky ledges and steep sunny slopes, where edaphic and microclimatic conditions favor the vigorous growth of the perennial bunchgrasses. Seasonal grazing, along with periodical early summer burning, has been traditionally adopted by the Mediterranean shepherds to create and maintain grasslands on the cheap. Secondary dry grasslands obtained in this way are one of the most common elements of the Mediterranean landscape. They are characterized by more or less dense tussocks of perennial grasses with interstitial space occupied by annual grasses. The density of perennial vs. annual grasses is greatly influenced by the soil compaction; excessive grazing pressure during the rainy season compacts the soil near the surface, which reduces infiltration, percolation, and water holding capacity, and concentrates roots near the surface (Menke, 1989). Differences in germination time and early seedling vigor may determine the competitive ability of one functional group against the other (Joffe, 1990; Garnier, 1992). Overgrazing, frequent burning and soil erosion can favor poisonous geophytes and hemicryptophytes belonging to the genera *Asphodeline*, *Asphodelus*, *Cachrys*, *Carlina*, *Drimia*, *Ferula*, *Iris*, *Mandragora*, *Narcissus*, *Ornithogalum*, *Thapsia*, etc. They occur throughout the southern, central and eastern Mediterranean Region and have their optimum under thermo-mesomediterranean bioclimate (Guarino and Pasta, 2017).

Wintergreen Ephemeral Dry Grasslands

Circum-Mediterranean thermo- to supramediterranean annual vegetation, which occurs sporadically also in temperate and Atlantic Europe, Macaronesia and the Saharo-Sindic region. It is dominated by small, poorly competitive annual grasses, colonizing nutrient-poor and seasonally dry soils. This vegetation is ascribed to the phytosociological classes *Helianthemetea guttati* (acidic grasslands) and *Stipo-Trachynietea distachyae* (calciphilous grasslands) (Rivas-Martínez, 1978; Brullo, 1985; de Foucault, 1999). Through ruderalisation, this vegetation may shift toward *Brometalia rubenti-tectorum* (*Chenopodietea*) communities.

Therophytic dry grasslands can develop on a variety of edaphic conditions, from loose sands to skeleton-rich shallow soils and heavily eroded slopes. The spatio-temporal changes in the composition and structure of the above-ground vegetation are closely related to those of the soil seed bank. Many annual plants show efficient germination at low temperatures, seed and fruit heteromorphism, as well as variation in seed dormancy among plant species and populations.

Disturbance plays a fundamental role in creating or maintaining the site conditions suitable for these ephemeral assemblages. Grazing, prolonged drought, and competition for limited soil resources may favor the annual strategy (Westoby, 1980). Frequent fires can be considered good allies of the perennial dry grasslands (see Bradshaw et al., 2011) but have an ambivalent effect on the establishment of annual dry grasslands, by reducing the chances of a viable seed bank establishment for many therophytes.

In spite of their limited resilience and functional stability, Mediterranean annual dry grasslands play a relevant ecological role by preventing the soil from rill erosion during the rainy season and by producing resources for a wide spectrum of seed eaters, pollinators and herbivores (Harper, 1977; Naveh, 1991; Guarino et al., 2005; Sánchez et al., 2017). Biological soil crusts dominated by annual plants, cyanobacteria, lichens and mosses are conspicuous in gypsum environments worldwide, and are important drivers of Mediterranean ecosystem processes such as carbon and nitrogen cycling, water infiltration and run-off and soil stability (Escudero et al., 2015).

Summergreen Perennial Dry Grasslands

In the Mediterranean Region, summergreen perennial grasslands can occur under a transition to temperate climate or wherever edaphic and topographic situations favor a later and longer-lasting vegetation period. Basiphilous summergreen grasslands are frequently found on mid-montane altitudes of the Iberian Massif (Serranía de Cuenca, Sierra de Gúdar) along the Apennines (up to Mt. Pollino; but see Gianguzzi et al., 2018) and the Balkans (up to northern Greece). These are species-rich grasslands, whose most conspicuous species in the Mediterranean are *Bromopsis erecta* and *Brachypodium rupestre*. Basiphilous grasslands dominated by *Brachypodium phoenicoides* may grow on meso-supramediterranean territories on deep clayey soils that retain soil moisture through the summer season. These grasslands are classified within the Eurosiberian class *Festuco-Brometea*, whose representatives, being well adapted to tolerate short periods of intense heat and drought stress, stretch into the North-Mediterranean Region. (In *Festuco-Brometea* vegetation on steep stony slopes of Southern Prealps, Lederbogen (1996) measured thermic peaks up to 50 °C and negative water balances up to –250 mm, due to the combined action of wind, solar radiation and limited water holding capacity of the soil.) On acidic and oligotrophic substrates, in the Iberian Peninsula, summergreen grasslands (“vallicares”) can grow on deep soils with occasional groundwater uplift, forming a dense and productive pasture that keeps green until midsummer. These meso-supramediterranean grasslands, characterized by *Agrostis castellana*, *Festuca ampla*, *Gaudinia fragilis*, are transitional to mesic grasslands of the class *Molinio-Arrhenatheretea*.

Typology of Mediterranean Shrublands

In the Mediterranean Region, four main structural and functional types of zonal shrublands can be recognized (Guarino et al., 2006), i.e., the semi-desertic halo-nitrophilous scrub in hyperarid coastal habitats and inland salt basins, the thermo-xerophilous dwarf shrublands, the thermo-xerophilous tall shrublands and the oromediterranean thorny cushion-like vegetation above the timberline (Fig. 3). The latter is not treated here.

Halo-Nitrophilous Shrublands

Under remarkably thermo-xeric climatic conditions, evaporitic sediments and marly to clayey substrata in the Mediterranean, Saharan-Atlantic and Macaronesian regions are colonized by open shrublands characterized by succulent *Chenopodiaceae* with a chamaephytic to nanophanerophytic habit, frequently growing together with representatives of the genera *Artemisia*, *Capparis*, *Peganum*, *Reaumuria* and *Limonium*.

These shrublands are ascribed to the phytosociological class *Pegano-Salsotea* (Brullo et al., 2012) and play an important ecological role against desertification in very dry and saline substrata, where the role of soil mesofauna in the decomposition of vegetation debris is limited. The soil organic carbon and total nitrogen pools of drylands are largely depending on symbiotic, nitrogen fixing bacteria associated with the rhizosphere and root endosphere of *Zygophyllaceae*, *Chenopodiaceae*, *Capparaceae*, *Tamaricaceae*, and others (Ahmad et al., 2006; Berendsen et al., 2012; El-Sayed et al., 2014), which can supply N for the plant growth. Individual shrubs can create areas of elevated soil nutrients and microbial activity, facilitated by the accumulation of wind-borne organic material under the shrubs and by the accumulation of ions next to the soil surface due to the evaporation. Nitrification runs fast under warm temperatures, neutral to alkaline pH and coarse soil texture. Therefore, it can be speculated that the immobilization of N during relatively wet and productive periods in winter and the mineralization of N during drier times, can contribute N for relatively rapid plant uptake as the system shifts to drought conditions.

Many species typical to the *Pegano-Salsotea* vegetation have succulent leaves, with big vacuoles where large quantities of ions can be accumulated, in order to facilitate the water uptake from a soil solution that has a low water potential. These morpho-anatomic and physiologic adaptations enable the plants dominating these communities to accumulate salts internally, or to excrete salts from cells and tissues (McKell, 1994). Although precise measurements are missing, it is likely that these plants need an intense solar radiation, because high levels of energy are required to keep the ionic pump efficient for the intracellular compartmentalization. Therefore, for these plants, an obligatory heliophily can be postulated.

Thermo-Xerophilous Dwarf Shrublands

The thermo-xerophilous Mediterranean dwarf-shrubs are locally named with different vernacular terms such as "tomillar," "matorral," "garrigue," "phrygana" or "bath'a." They are classified into the phytosociological classes *Ononido-Rosmarinetea*, related to base-rich substrates, and *Cisto-Lavanduletea stoechadis*, related to acidic siliceous and ultramafic substrates. This fire-resilient vegetation constitutes one of the most characteristic features of the Mediterranean landscapes. Matorrals or shrublands on base-rich soils bear a large number of species belonging to the *Lamiaceae* (*Nepeta*, *Salvia*, *Satureja*, *Sideritis*, *Teucrium*, *Thymus*), *Cistaceae* (*Helianthemum*, *Fumana*), and *Fabaceae* (*Anthyllis*, *Astragalus*, *Genista*, *Ononis*) families. On acidic siliceous soils, dominant plants mostly belong to the genera *Cistus*, *Lavandula*, *Genista*, *Halimium*, and *Ulex*. This vegetation displays several adaptations to tolerate both summer drought and heat stress, eventually ensuring a vigorous post-fire regeneration. Adaptations include deep rooting, persistent seeds, flammable secondary compounds, epidermal trichomes, sunken stomata, reduced leaf area, seasonal leaf dimorphism, and loss of leaves during the driest months (Orshan, 1972; Margaris, 1981; Christodoulakis, 1989; Christodoulakis et al., 1990; Kyparissis and Manetas, 1993; Gratani and Bombelli, 1999; Aronne and De Micco, 2001).

Many Mediterranean thermo-xerophilous dwarf-shrubs are used for the fragrance of their foliage. Aromatic oils have a threefold effect; they protect the plant against grazing, facilitate the ignition of wildfires, and reduce the loss of water vapor, as oils evaporate into the stomatal chambers (Margaris and Vokou, 1982; De Lillis, 1991). The root system, as well, helps these shrubs to cope with wildfires and summer drought: many species have deep roots and their young seedlings, typically germinating in autumn or winter, have fast-growing taproots that ensure an early root development away from the soil surface, thus limiting the effects of the summer drought. Moreover, most of the Mediterranean thermo-xerophilous dwarf-shrubs developed several symbioses with fungi and bacteria, so to increase the efficiency of nutrient-uptake (Kummerow, 1981; Puppi and Tartaglini, 1991).

Thermo-Xerophilous Tall Shrublands

The dense and tall woody assemblages belonging to this vegetation type are named with several different regional vernacular terms such as "madroñal," "maquis," "makia," or "ajmatan." (The thorny mantle communities (class *Crataego-Prunetea*) and the Balkan tall shrublands named "shibljak" deserve to be treated separately, because they host plenty of summergreen deciduous shrubs, small trees and lianas belonging to the temperate element) Most of these plant communities are placed in different orders of the class *Quercetea ilicis*, like *Quercetalia calliprini* in the East Mediterranean area, *Pistacio lentisci-Rhamnetalia alaterni* in western and central Mediterranean countries and *Pinetalia halepensis* in the arid sectors of South and East Mediterranean territories (Quézel and Médail, 2003).

Maquis communities are dominated by several small to medium-sized evergreen sclerophyllous and few lauriphyllous trees with sympodial growth (*Arbutus*, *Ceratonia*, *Juniperus Olea*, *Phillyrea*, *Pinus*, *Pistacia Quercus*, *Rhamnus Tetraclinis*, *Viburnum*, etc.), often tied together by lianas (*Asparagus*, *Clematis*, *Lonicera*, *Rosa*, *Rubia*, *Smilax*, etc.). The leaves of these species share many morpho-anatomical adaptations to Mediterranean climate. In fact, they are evergreen, sclerophyllous (coriaceous) and/or microphyllous, with the upper surface covered by hairs and/or waxes and the lower surface hairy and revolute. These traits help to mitigate the potential damages of solar radiation, to reduce water loss and to capture some overnight humidity. In areas prone to extremely severe and long-lasting

drought, species able to lose their leaves entirely during the summer months (like *Euphorbia dendroides*, *Periploca angustifolia*, *Rhus tripartita*, *Ziziphus lotus*) may prevail.

Thanks to effective resprouting and seed-dispersal strategies (Bond and Midgley, 2001; Higgins et al., 2008; Traveset et al., 2014), these woody species are able to recover after fire within few decades. The speed of woody encroachment and the “final” stage of local vegetation dynamics are strongly affected by the size, species richness and frequency of wooded nuclei and individual woody plants within the patchy and open landscapes (La Mantia et al., 2019). The intensity and frequency of disturbance shape the structure and the floristic composition of such communities, too. In many cases, frequent burning leads to species-poor and dense communities, dominated by a few resilient resprouters, like *Chamaerops humilis*, *Erica arborea*, *Phillyrea* spp. and *Quercus coccifera*, or the most stress-tolerant species, like *Euphorbia dendroides*, *Olea europaea*, *Pistacia lentiscus* and *Rhamnus oleoides*. Conifers—especially pines (*Pinus* spp.)—tend to dominate in areas subject to edapho-climatic drought stress (warm and arid areas, steep and S-facing slopes, well drained, base- and/or skeleton-rich thin soils) and moderately frequent fire disturbance, but may be completely wiped off if burning occurs too frequently.

The current distribution and the floristic patterns of Mediterranean maquis communities originate from millennia of anthropogenic disturbance and land use. Past human activities not only destroyed, altered and impoverished Mediterranean woodlands and shrublands (Henne et al., 2015), but also drove local vegetation dynamics towards results that are different from those expected according to local climatic conditions. For example, the thick soil layer accumulated over centuries on dry stone wall terraces may change the direction and enhance the speed of local vegetation dynamics (Rühl and Pasta, 2008).

The sides and beds of the seasonal and often large braided streams, mostly under thermo-mediterranean bioclimate, are characterized by species-poor thermo-hygrophilous shrublands ascribed to the class *Nerio-Tamaricetea*. These communities are dominated by few pioneer shrubs or small trees such as *Nerium oleander*, *Spartium junceum*, *Tamarix* spp., *Vitex agnus-castus*. These woody species are adapted to resist—or to rapidly respond by resprouting—the intense mechanical disturbance during the rainy season and to face extreme thermic conditions (up to 70 °C on the gravelly streambeds during summer) and long-lasting drought periods (up to 4–5 months). Most of them are poisonous and perform long-distance wind-dispersal.

On acidic soils, the hilly and submontane portions of the main mountain ranges of the West Mediterranean Region host dense tall shrublands dominated by several broom species (*Fabaceae* tribe *Genisteae*) of the genera *Adenocarpus*, *Cytisus* (incl. *Calicotome*), *Genista* (incl. *Teline*), *Retama* and *Ulex*. These communities are ascribed to the West Mediterranean-Atlantic class *Cytisetia scopario-striati* and form species-poor and dense communities on deforested areas as first seral stages, mostly linked to locally humid and cool mesoclimatic conditions. Most of the dominant species are poisonous and/or thorny, fast-growing, behave as seeders and/or resprouters after burning and play a major role in soil evolution thanks to N-fixing symbiotic rhizobia.

Origin of Mediterranean Grasslands and Shrublands

With the exception of the most archaic lineages (the so-called Tethysian and Palaeo-Mediterranean relict elements) and of the most recently immigrated species (i.e., those introduced by the human activities), all of the Mediterranean living organisms passed through massive and relatively recent adaptive radiations and speciation processes, which started in the late Miocene and are still ongoing. The biological history of the MG&S has been especially influenced by the Messinian salinity crisis (5.96–5.33 Ma), the formation of the Isthmus of Panama (around 2.8 Ma) and the Pleistocene climatic oscillations combined with glacial events (ongoing since 2.58 Ma).

Many of the thermo-xerophilous fire-resistant Mediterranean dwarf shrubs and tussock grasses derive from the so-called “Mediterranean flora.” They originated from a local adaptive radiation triggered by the gradual shifting from subhumid to semiarid climatic conditions, at the boundary between the tropical and the temperate zone, under evolutionary trends that probably begun during the Messinian disruption and exacerbated when the setup of the Isthmus of Panama changed the patterns of the oceanic currents and sharpened the seasonal climatic drought stress in the Mediterranean lands (Vargas et al., 2018).

The events associated to the Messinian age can be resumed as follows: due to the periodical obstruction of the Gibraltar Strait, part of the Mediterranean Sea dried up and reflooded several times. In the most critical periods, the sea was up to 1250 m shallower than today. Part of the continental slopes emerged, the bathyal floor turned into a patchy mosaic of sebkhas (salty drylands), salt-marshes and hypersalted, highly alkaline lakes (Hsu, 1973). Erosion increased everywhere, diverse rocks became rapidly exposed. The indirect uplift of mountain ranges gave rise to huge rockfalls and massive debris flows. The topographic diversity increased and, as mountain ranges were rapidly rising up, hundreds of new canyons and gorges were incised into them, steep slopes came into existence and divergent localized microhabitats developed everywhere. Plenty of new ecological niches were ready to be colonized by pioneer plants with different adaptations (Bertolani-Marchetti and Cita, 1975; Bocquet et al., 1978; Thompson, 2005). For instance, the *Pegano-Salsolitea* vegetation derives from Irano-Turanian and Saharo-Arabian chorotypes, whose pristine elements spread into the Mediterranean Basin during the Messinian salinity crisis (Suc et al., 2018).

As a consequence of the Messinian age and of the subsequent climatic changes, which increased the seasonal aridity on the Mediterranean lands, the ancestors of the MG&S passed through a new adaptive radiation. The driving forces of the speciation wave, which is still characterizing the Mediterranean flora, are the following (Raven, 1973):

- *Geographical segregation and appearance of new lands*: as the level of Mediterranean Sea fluctuated several times during last 6 Ma, many currently isolated lands have been repeatedly connected to the mainland. Some plant species growing in the MG&S are

- neoenemics, deriving from the splitting of a formerly continuous distribution range; some examples are provided by the phylogenetic groups named *sensu lato* after *Anthyllis vulneraria*, *Bromopsis erecta*, *Brachypodium pinnatum*, *Centaurea deusta*, *Heli-anthemum nummularium*, *Stipa pennata*, *Thymus serpyllum*.
- *Climatic variations*: the Mediterranean climate is not only depending on the latitude, but also on the cyclonic circulation of the oceanic air masses (Azores High), whose influence and effects are ranging year by year. Annual climatic variations and major climatic changes may locally lead to the severe reduction and splitting of metapopulations. Several noticeable disjunctions in the distribution ranges of plant species growing in the Mediterranean dry grasslands can be attributed to these climate changes. For example, the disjunct Sicilian populations of *Heteropogon contortus*, *Artemisia alba*, *Sesleria nitida* subsp. *sicula*, *Koeleria splendens* and *Helictotrichon convolutum*, have probably reached the island in the Pleistocene, during the dry interglacial periods. Moreover, long periods of high climatic variability can favor an evolutionary trend towards the adoption of annual life strategies.
 - *Substrate heterogeneity*: in the Mediterranean lands, several outcropping rock types are represented. Due to the few or no frost days and the relatively scarce rainfall, soils reflect quite precisely the chemical composition of the parental rock material. Different soil chemistry and texture select different floras; noticeable examples are provided by the phytosociological classes *Ononido-Rosmarinetea* and *Stipo-Trachynieta distachyae*, related to base-rich substrates, versus *Cisto-Lavanduletea stoechadis* and *Heli-anthemetea guttati*, related to calcium-poor acidic siliceous and/or ultramafic substrates.
 - *Rich fauna of pollinators*: the fauna of pollinators is far richer in the Mediterranean Region than in the neighboring temperate and semiarid ones. We know that many insects are quite precise in their flower-visiting habits, and in the Mediterranean dry grasslands and shrublands several examples of coevolution between flowers and insects are known, especially among representatives of the families *Fabaceae*, *Lamiaceae*, *Plantaginaceae* and *Orchidaceae* (Galloni et al., 2007; Bradshaw et al., 2010; Vargas et al., 2017).
 - *Short generation time*: the intense gene flows characterizing short-lived organisms may easily promote random gene fixation and subsequent divergent genotypes, which can efficiently occupy new niches in the patchy mosaic of the Mediterranean landscapes, particularly in ecologically marginal or geographically peripheral populations. Noticeable examples of micro-evolutionary processes promoting population differentiation at local scale are provided, for instance, by the species complexes of *Senecio* sect. *Senecio* (Comes and Abbott, 2001), *Silene* sect. *Coloratae* (Valsecchi, 1995; Brullo et al., 2015), *Rumex bucephalophorus* (Press, 1988) and *Dianthus* sect. *Sylvestris* (Bacchetta et al., 2010).

These evolutionary trends in Mediterranean dry grasslands overall lead from long-lived, big-seeded, monochorous plant species toward short-lived, small-seeded, polychorous species (Pignatti, 1978, 1979). Some examples of primitive plant species, still showing ancestral features, are found in the *Lygeo-Stipetea* vegetation of some isolated Mediterranean districts; this is the case, for instance, of *Astragalus huetii*, endemic to a small area of inner Sicily, *Astragalus verrucosus*, endemic to a small area of SW Sardinia, and *Asperula crassula* restricted to Crete. Many species typical of the *Lygeo-Stipetea* derive from the paleotropical Paleogene flora and are often characterized by very disjunct, sometimes amphi-Saharan distribution ranges. For example, it is likely that the *Lygeum spartum* grasslands of Southern Crete and northern Egypt, representing the easternmost disjunct outposts of the *Lygeum spartum* distribution range, remained isolated in those districts since the end of the Messinian age (Marcenò et al., 2019).

The already mentioned, evolutionary trend toward short-lived life strategy often coincide with the tendency towards rewardless, species-specific pollination strategies and high investment in seed productivity (Dafni, 1987). Obligate seeders have greater numbers of sexually produced generations, resulting in greater genetic recombination, which in turn contributes to more rapid speciation processes. This could explain why the Mediterranean Region has such a high diversity of plant and insect species if compared with the temperate European ecosystems (Médail and Quézel, 1997).

Examples of how the ancestors of Mediterranean therophytes could have looked like, are quite rare in the perennial dry grasslands; yet grasslands are ruled by competition and intense dynamism. Instead, woody ancestors of present-day herbaceous species occur on Mediterranean cliffs; *Linum arboreum* looks probably rather similar to the ancestors of the Mediterranean yellow-flowered annual flaxes; the same holds true for *Bupleurum dianthifolium* versus *B. baldense*, *B. fontanesii* and allied taxa; *Tuberaria lignosa* vs. *T. guttata*, and other similar examples reported by Pignatti (1979). As a matter of fact, secondary woodiness may also represent a recently acquired trait which has been triggered repeatedly in insular and insular-like realms, thus enabling annual and biennial herbs to better fit with recently colonized habitats (Nürk et al., 2019).

The Mediterranean *Festuco-Brometea* vegetation is derived from Holarctic and Eurasian elements that probably reached and colonized the Mediterranean Region during the Pleistocene glacial events, together with herds of wild herbivores. During the glacial maxima, the North-Mediterranean territories experienced a non-Mediterranean or feebly Mediterranean climate, and they acted as refugia for several species coming from the north (Feliner, 2011). Migratory patterns of plants and animals along latitudinal gradients became established, and new ecological niches became available for a new adaptive radiation. Therefore, the Mediterranean patches of *Festuco-Brometea* vegetation are the last shreds of a vegetation type that was probably much more widely distributed during the dry interglacial periods. In the Mediterranean Region, this vegetation is nowadays restricted to the main mountain ranges of the southern European countries, especially where the fully Mediterranean climatic conditions are buffered by the condensation of orographic moisture, as it happens along the Apennines. In some cases, the postglacial isolation of *Festuco-Brometea* species on the Mediterranean uplands originated new endemic taxa, such as *Phleum ambiguum*, *Sesleria nitida*, *Astragalus sirinicus*, and *Crepis lacera*.

Similarly, in the case of Mediterranean shrublands, some elements are related to the humid palaeotropical Paleogene flora coming from the African plate, whereas others are related to the cool temperate so-called “Arcto-Tertiary flora” (Raven, 1973; Axelrod, 1975; Quézel, 1995; Rundel et al., 2016).

Representatives of the first group are the “desert disjunct” genera, which evolved in the African plate during the Cretaceous and moved northwards through the Saharan Region during the early Paleogene, when the Sahara was not as desertic as today. This is the case of genera like *Ceratonia*, *Chamaerops*, *Cotinus*, *Erica*, *Laurus*, *Myrtus*, *Olea*, *Paliurus*, *Phillyrea* and *Phoenix*, which now have in the Mediterranean shrublands the north-western limit of their distribution range (Palamarev, 1989).

Representatives of the second group are the so called “Laurasian” genera, whose representatives are also found in Eurasia and North America. This is the case of species belonging to genera like *Acer*, *Arbutus*, *Cercis*, *Clematis*, *Crataegus*, *Cupressus*, *Fontanesia*, *Fraxinus*, *Juniperus*, *Liquidambar*, *Lonicera*, *Pinus*, *Platanus*, *Prunus*, *Quercus*, *Rhamnus*, *Rosa*, *Rubus*, *Salvia*, *Smilax*, *Styrax*, *Viburnum*, *Vitis*, *Zelkova*, etc., which often meet in the Mediterranean shrublands the southern limit of their distribution range.

Some evolutionary trends associated to the species growing in the Mediterranean shrublands are quite coherent to those observed in the Mediterranean dry grasslands; from evergreen to drought-deciduous, from long to short life cycle, from dioecy to hermaphroditism, from fleshy few-seeded fruits to dry many-seeded ones (Herrera, 1992; Aronne and Wilcock, 1994). All these trends can be seen as the result of a local evolution, triggered by the progressive increase of both summer drought and fire occurrence, under the selective pressure of limited soil nutrient and water availability.

Until recent times, the scientific community is still lively debating whether the opening and the fragmentation of natural landscape across Mediterranean Region was mostly climate-driven (e.g., Di Rita et al., 2018) or more due to anthropogenic pressure (e.g., Tinner et al., 2016). The truth is probably in the middle; although many recent researches point out that human impact was able to cause deep and sudden changes in tree cover, and even the local destruction of entire forest ecosystems, the extension of Mediterranean forest habitats prior to human disturbance has probably been overestimated; grasslands and shrublands being more common than expected even before the onset of the first human communities (Feurdean et al., 2018).

Ecology and Biodiversity Patterns

The Mediterranean Region stretches over approximately 3800 km west-east and 1000 km north-south (Fig. 1). This creates a very strong biogeographic contrast between the western and the eastern halves of the Mediterranean. A marked biogeographic boundary runs north-south through the Sicily-Tunisian “sill”. Indeed, it has been recognized a western “Atlantic-Mediterranean” subregion, and an eastern “Ponto-Mediterranean” subregion, strongly influenced by immigration of Irano-Turanian elements. Historical and current-day differences in climate, in particular rainfall and seasonal aridity, are more extreme from east to west than they are in a north-south direction (Thompson, 2005). The water deficit ranges from an average of 2 months in the west Mediterranean to 5 months in the southeast Mediterranean Region (Blondel et al., 2010). Though this is an overall pattern, even within the Iberian Peninsula aridity is very contrasted from the proximity to the Atlantic Ocean toward the Southeast, with some scattered areas under a Mediterranean desertic bioclimate (0.17% of total area of Iberian Peninsula and Balearic Islands; Rivas-Martínez et al., 2017). Biogeographically, in addition to the Western and Eastern Mediterranean, a North African Mediterranean subregion, can be recognized (de Foucault, 1993; Valdés et al., 2002; Rivas-Martínez, 2007; Taleb and Fennane, 2018). However, the floristic and ecological differences between northern and southern Mediterranean lands become less evident in the west, due to the similarity of the southern Iberian Peninsula to the Moroccan Rif, resulting from a common geological history (Valdés, 1991).

Though the summer drought stress is the essence of the Mediterranean climate, another important climatic constraint is the winter cold stress, whose length and intensity depends on the altitude and exposure (Guarino, 2001). These climatic factors limit the plant species distribution and also determine the floristic composition of MG&S along the gradient from the infra-mediterranean to the cryo-oromediterranean vegetation belts.

Also, continentality influences the vegetation distribution at local scales. Remarkable differences in the daily and seasonal temperature ranges occur in the largest Mediterranean mainland, such as the Iberian and Balkan Peninsulas, in which the peripheric disposition of the mountains limits the oceanic influence of the sea on the interior territories. For instance, the difference between the warmest and coldest month can reach 22 °C in central Spain (La Mancha).

The strong seasonality is a main environmental driver conditioning the insect populations of dry grasslands. The number of individuals is subject to seasonal fluctuations (Stamou, 1998). The temporal distribution of the main food resources (sprouts, leaves, flowers, seeds) allows most insects of these habitats to develop only one generation per year. For example, in synchronism with the abundant production of pollen by many herbaceous plants, there is a clear spring peak of abundance of flower-visiting beetles. The peaks of abundance of the herbivory correspond to those of the predators such as the spiders; in particular the wandering spiders, which do not build webs (e.g., *Salticidae*).

Substrate plays a primary role in the composition of regional grasslands and shrublands, more important than in Mediterranean forests. Most of the Mediterranean mainland is covered by calcareous sedimentary rocks. Magmatic and metamorphic siliceous (acidic) rocks dominate in Iberian-Atlantic region, Corsica and Sardinia, while these are less common in the rest of the Mediterranean Region. Overall, a wide range of substrates, from crystalline (granite, gneiss, quartzite, schists, sandstones, etc.), to calcareous (limestones, dolomites) and sedimentary rocks (marls, gypsum, etc.), turns into a high community diversity. The floristic affinity of silicicolous Mediterranean Iberian-Atlantic and calcicolous eastern-Iberian grasslands and shrublands is weaker than that between the western and eastern Mediterranean calcicolous ones. Many more vegetation units occur on base-rich substrates than on acidic substrates (Mucina et al., 2016), probably because of the larger extension and varied lithology of Mediterranean limestones, but nutrient-poor acidic soils support a high level of regional endemism throughout the Mediterranean Region (Rivas-Martínez, 2011).

The ancient Mediterranean civilization is largely known as a main determinant in shaping the Mediterranean vegetation landscape and biodiversity. However, before arrival of humans, the Mediterranean landscape was already a natural mosaic. It is known that fires have occurred naturally at least since the Miocene. From the onset of Neolithic, burning was a constant practice as humans learnt how to use fire to create pastures and prepare soils for cultivation. The use of fire began earlier in the Mediterranean than elsewhere in Europe (Thompson, 2005). Also, there was an abundance of native populations of wild herbivores, including deers (*Cervus elaphus*, *Dama*, *Capreolus capreolus*), large bovids, such as the aurochs (*Bos primigenius*), the European bison (*Bison bonasus*), and also of the Eurasian wild horse (*Equus ferus*) (Casinello, 2012). This resulted in a high grazing pressure and a long history of a continuous adaptation of plants to grazers.

Extensive livestock rearing has been an essential economic activity for millennia in the Mediterranean Region, especially on acidic nutrient-poor soils, rocky and rugged areas, whereas fertile soils were predominantly used as arable fields. One specific Mediterranean landscape is the “dehesa” or “montado,” very extended in Sardinia and in the western and southwestern quadrants of the Iberian Peninsula, consisting of open oak woodlands occupying gently sloping or flat areas. In the understorey, there can be crops, pastures and shrublands. Pastures comprise a mosaic of acidophilous annual ephemeral grasslands, subnitrophilous Mediterranean grasslands, *Poa bulbosa* grasslands and “vallicares.” Shrublands comprise tall broom-like communities (*Cytisetea scopario-striati*) and garrigues (*Cisto-Lavanduletea*). Dehesa and montado are associated to an agro-sylvo-pastoral system resulting from the co-evolution of man and nature in a difficult environment (San Miguel, 1994) and promotes a high biological diversity (Eichhorn et al., 2006; Díaz and Pulido, 2009).

Ecosystem services

Mediterranean grasslands and shrublands are of paramount importance for delivering a wide array of ecosystem services. (According to the Millennium Ecosystem Assessment (2005), there are four main classes of ecosystem services: Provisioning services are those related to the products people obtain from ecosystems, such as food, fuel, fiber, fresh water, and genetic resources. Regulating services are the benefits people obtain from the regulation of ecosystem processes, such as air quality maintenance, erosion control or water purification. Cultural services are the non-material benefits people obtain from ecosystems through spiritual enrichment, cognitive development, recreation, and aesthetic experiences. Supporting services are those that are necessary for the production of all other ecosystem services, such as primary production and soil formation.) They sustain not only economies and societies but also many elements of the local biodiversity. Apart from their importance for the maintenance of biodiversity, they play a major role in providing high quality forage for both livestock and wild animals; they support communities of insects with major roles in the ecosystem services of control and pollination; they sustain apiculture, and contribute to the prevention of erosion processes and maintenance of the water cycle; they buffer the negative impacts from fertilizers and pesticides and display highly significant aesthetic and recreational values (Vrahnakis et al., 2013).

Provisioning services obtained by MG&S are the most prominent, with grazing-related goods being at the top of these values. From the onset of livestock husbandry, MG&S were offering their natural resources for feeding animals and humans as well. It is believed that during the Paleolithic age there was a positive interplay between humans and Mediterranean grasslands; the shift of human population generated greater disturbances on grasslands, which in turn controlled competitive advantages and increased the human ecological fitness (Pignatti, 1978). The intensity of this interplay was getting higher when an extensive selection and domestication of the most productive breeds was taking place during the Neolithic age. It seems that there was a triple co-evolution of grazing systems, human systems and the capacity of MG&S to provide their goods and services. For example, the traditional grazing system of nomadism, which is still practiced in some places of the Mediterranean (e.g., in Sierra de Gredos (center of Spain); in northern Pindus mountain (Greece); in Molise, Apulia and Abruzzo (southern Italy)), played an important role for the development of human cultures in sites unsuitable for sedentary settlement (Ispikoudis et al., 2004).

The provisioning service of grazing still plays an important role in the Mediterranean societies. In terms of animal units, the south-European Mediterranean lands (Spain, Italy, France, Greece, Malta and Portugal) hold more than 15 million cattle, 9 million goats, 30 million sheep and 0.5 million horses, while north-African Mediterranean lands (Algeria, Egypt, Libya, Morocco and Tunisia) hold 10 million cattle, 15 million goats, 60 million sheep, and 0.2 million horses (roughly estimated by data provided by FAO, 2014). These animals use extensively the feeding resources provided by almost 100 million ha of land occupied by MG&S. Grazing produce a series of meat and dairy products benefits, quite often of high nutritive qualities, certified by European Community as products of “Protected Denomination of Origin” (PDO), “Protected Geographic Indication” (PGI) and “Traditional Specialties Guaranteed” (TSG). Such products are linked to cultural heritage for consumers and sustain social cohesion, by connecting rural and urban populations (Zander et al., 2014). Also, high natural value farming (HNVF) that takes place in dehesas and montados produces a variety of (a) economic benefits, such as increase in farm income through multiple uses of natural resources, increase security against market perturbations; (b) social benefits, such as employment stability in the expense of depopulation; (c) environmental benefits, such as mitigation of desertification, contribution to the resilience of the ecosystem against climate change, decreasing fire risk, ecological corridors and refuges for large mammals and birds of prey (Sequeira, 2008). For example, the threatened Spanish Imperial Eagle (*Aquila adalberti*) and Black Vulture (*Aegypius monachus*), nest in montados and dehesas and meet their feeding demands in the open grasslands (Bugalho and Abreu, 2008; Vrahnakis et al., 2009).

MG&S play also a crucial role in preventing land degradation. They operate against soil loss due to water and wind erosion, with soil retention capacity generally lower than arable land (Cerdan et al., 2010). The tussock grasses typical to the wintergreen thermo-

xerophilous grasslands provide suitable microclimatic conditions (shade, water through overnight dew accumulation, etc.) for many annual plants and play an essential role for soil organic carbon storage (Novara et al., 2013). In addition, Mediterranean grasslands serve as fire breaks, so reducing fire risk (Úbeda et al., 2005).

Although MG&S largely contribute to the overall Mediterranean carbon balance, there are few available studies concerning the biomass and the net ecosystem exchange capacity of MG&S communities. Additionally, the above- and below-ground biomass of such communities shows a wide variation, which depends on the intensity of local stress factors and on the nature, intensity and frequency of disturbance (Pasta et al., 2015).

Apart from the above-mentioned ecosystem services, the cultural value of MG&S is of great importance for the Mediterranean people, traditions and history. Quite often rural civilizations are based on the use of natural resources provided by MG&S. For instance, the traditions of “Sarakatsani,” traditionally transhumant shepherds in continental Greece, were deeply influenced by the phenology of MG&S, determining livestock keeping activities. Traditional Sarakatsani settlements were located on or near dry grasslands and their life centered year-round on the needs of their flocks (Clogg, 2002). Nowadays, the revival of old traditions of Sarakatsani take place during their annual meetings (αντάμωμα = antamoma), in specific areas of open semi-natural dry grasslands, thus reflecting their strong cultural bonds with this vegetation type.

Threats

According to the homeorhetic hypothesis, there is a dynamic equilibrium of human and natural perturbations and climatic fluctuations in Mediterranean (Waddington, 1975; Guarino, 2006). This triplet of perturbations may form the possible sources of threat for MG&S, i.e., human, climate and natural (biotic, abiotic) environment. For MG&S, the dynamic equilibrium happens at the expense of soil stability and productivity, in cases when human—via uncontrolled pastoral activities—uptake nutrients rapidly, while the return rates are very low. Coupled with increased erosion risks, the new equilibriums are characterized by low energetic rates, and soil degradation lead to desertification, which poses severe threats for MG&S (Waddington, 1975; Guarino, 2006; Ambarlı et al., 2018).

Climate change is an important threat for MG&S. In particular, the Mediterranean is expected to experience more intense dry-heat conditions by further increasing atmospheric temperature and reducing precipitation (Hulme, 1999), thereby reducing soil moisture (Déqué et al., 1998). The available soil moisture affects the growth and survival of plants, affects the carbon and nitrogen cycle and, consequently, affects the floristic composition of ecosystems (Cheddadi et al., 2001). Ecosystems in areas with dry heat conditions are the most vulnerable to these climate changes (Schröter et al., 2005). Of course, it is difficult to distinguish in practice the effects of climate change from those of long-term disturbances of these ecosystems, such as overgrazing, fires, logging, and air pollution (Naveh, 1995; Pausas, 1999). Degradation, area and species loss, currently observed in many MG&S, is largely a result of overgrazing (Asner et al., 2004). Climate change, coupled with intense grazing, can threaten the biodiversity, productivity and stability of MG&S, and increase the risk of desertification (Scheffer et al., 2001).

It is well established that in order to withstand soil degradation and combat desertification, grazing capacity must be in balance with livestock density (Holeček et al., 2004). The overgrazed MG&S dominated the Mediterranean open landscape in the past, and still dominate where communal grazing is taking place (Roukos et al., 2013; Kairis et al., 2015). However, this is not the case in the present. It is rather the undergrazed aspect of vegetation that characterizes the MG&S nowadays (Ambarlı et al., 2018). This is mainly attributed to the decline of the mountain rural communities and to the abandonment of traditional practices, resulting in shrub encroachment, biodiversity loss and consequent accumulation of organic flammable material (Peco et al., 2006; Zomeni et al., 2008; Metera et al., 2010).

MG&S co-evolved with humans. In the past, the level of human intervention in the spatio-temporal distribution of MG&S was adjusting to the increased needs. However, the uptake of productivity was taking place in a way that a balance was kept in favor of nature's resilience. For example, given the restricted availability of palatable green biomass in the xerothermic periods, when animal feeding demands were increasing, rangelands were burnt every 5–10 years in the past, so to control the density and spreading of unpalatable chamaephytes of *Ononido-Rosmarinetea*, and *Cisto-Lavanduletea stoechadis*. While fire-controlled areas experienced the short-term catastrophic effect of fire, the medium-term effect is considered beneficial for nature (floristic diversity) and man (increased quality of regenerated forage material), as well (Vrahnakis et al., 2004). In addition, shrub and tree encroachment is prevented, as fire and subsequent grazing by goats control the expansion of woody species (Noy-Meir, 1995).

Shrub and tree encroachment are indirectly supported by the economic framework that often is set by state agricultural strategies. One of the major driving forces for recent alterations may be found in European Commission's system of subsidies that favor agricultural intensification and expansion of arable lands (Chouvardas and Vrahnakis, 2009). For example, in recent year, large areas of the formerly used summer pastures have been abandoned and the subsidies provided to halt this trend are used by the local communities to make the mountain pastures more accessible. Therefore, shepherds are indirectly encouraged to move from the pastures to the villages carrying hay and concentrates to feed their stocks during the critical periods. Such practice facilitates the turn of an extensive production process into a more productive, but more restricted and intensive exploitation of the land. As a result, large parts of the Mediterranean former rangelands are nowadays shifting toward shrublands and woodlands, if abandoned, or toward *Onopordetea acanthii* vegetation through overgrazing (Bauer and Bergmeier, 2011; Bianchetto et al., 2015).

The recent demographic changes that occurred in Mediterranean Region have often detrimental effects on natural vegetation of high value. Urban sprawl processes taking place in European cities constitute an important problem opposing sustainable growth

and environmental protection. This is particularly evident in the Mediterranean, where intense tourism development and “coastalization” continuously impose urban land pressures on agricultural areas and natural land (Cori, 1999; Ivanov et al., 2009). For example, coastalization has severe impact on the vegetation of *Pegano-Salsoletea*, which is represented by several interesting and well differentiated phytosociological units. Also, most of the sites colonized by this vegetation have an outstanding stratigraphic and geo-morphological interest for Quaternary/Pleistocene lower boundary and the early stage of Pleistocene (Gibbard et al., 2010). The proximity of high value MG&S to areas of rapid population growth and urban development is a source of increasing concern, also because the naturalistic and scientific value of such vegetation is ignored by most, and the public access to sensitive habitats/biotopes is totally uncontrolled. For example, it is estimated that in the last three decades, 80% of the *Limonio opulenti-Salsolietum oppositifoliae* habitat was lost, even if some floristic reminiscences of the former vegetation can still be found in the town of Porto Empedocle (southern Sicily). The same holds true for the many “badlands” that, due to the waterproof properties of the clay, have been transformed into landfills for the urban solid waste. This is the case, for instance, of the habitat formerly occupied by the *Capparido siculae-Salsolietum oppositifoliae*, near the town of Adrano, Italy (Brullo et al., 2012).

Impacts from human activities are resulting in a severe habitat loss and declining environmental quality. Roads, dust, pollution, industrial activities, uncontrolled off-road access, are limiting factors in the population dynamics of the most sensitive species of MG&S. Moreover, the overall disturbance can increase the competitiveness of nonnative species, opening the way to multiple problems, such as the potential to out-compete native species, habitat alteration and alteration of the trophic levels.

Conservation, Sustainable Management and Restoration

The close relation of the historical evolution of MG&S vegetation and human societies supports their consideration as socio-ecosystems (Hutsinger and Oviedo, 2014). Within these mutually-dependent socio-ecosystems, characterized by a variety of management, ecosystem services provided by MG&S appear along a gradient of intensity of their resource use.

The majority of MG&S are maintained by a combination of natural and human caused disturbances, such as extensive historical clearings, seeding, flooding, fertilization, burning, grazing (Papanastasis, 1999; La Mantia et al., 2007) and would succeed to natural shrublands in the absence of such disturbances. If an extensive grassland management is abandoned, the natural succession will favor shrubs. According to Fuhlendorf (1997), shrubs exhibit specific characteristics that support significant competitive advantages over herbaceous species, like exponential growth rate, higher tolerance to nutrient or water stress, chemical or physical deterrents to browsing, vegetative reproduction, extended longevity. It is well-documented that as shrub assemblages of the Mediterranean Region become thicker, total biodiversity declines (Vrahnakis et al., 2005). Thus, grazing seems to be a valuable tool in controlling shrub and tree invasion and must be incorporated into management plans.

The European Red List of Habitats assessed that 60% of dry grassland habitats are threatened to some degree, and it includes some Mediterranean types, while only one Mediterranean shrubland habitat is threatened (Thermomediterranean scrub) (Table 2). With few exceptions, the large majority of the aforementioned MG&S are protected by the 92/43 “Habitats” EU Directive. Additionally, many species living in these habitats are listed in the Annexes of international and European conventions and/or figure within national and regional red-lists compiled according to IUCN criteria.

On the other side, those legal measures are often neglected and unattended. As a consequence, wide areas covered by grasslands and nonforest woody communities, especially on the plains, near the cities and along the coasts, currently suffer from urban sprawl and land use intensification (e.g., expansion of greenhouse agriculture wiped out large surfaces covered with grasslands and shrub communities along the coasts of S Spain, SE Sicily, SE Crete, etc.). The conservation of such plant communities should go beyond the administrative limits of the Mediterranean countries. Scientists, politicians and other stakeholders should try to interact in order to set up internationally shared measures aiming at maintaining the best preserved patches of grassland and shrubland.

In order to verify the short- to medium-term effect of land use changes, an international scientific network should be built up in order to perform regular and accurate monitoring of the impact of the main disturbance factors (e.g., overgrazing/undergrazing, fire regime, plant invasion) on the aforementioned ecosystems. In our opinion, the most effective way to conserve Mediterranean ecosystems is the adoption of dynamic and flexible management strategies. On this purpose, we should learn from (and teach once again) the past extensive land use practices. In fact, moderate (low-intensity- and low-frequency-) disturbance induced by extensive land use allows the self-maintenance of mosaic-like landscapes where frequent patches of tall and dwarf shrublands may co-exist with grasslands. Hence, extensive land use practices should be legally and financially supported by Mediterranean countries in order to obtain dynamic, yet steady habitats and landscapes. To do this, ad hoc legal and political strategies should be developed in order to maintain sustainable farming and agro-forestry activities, like transhumance, dehesas and montados, which allow extensive grazing fitting with the carrying capacities of local pastures, tree exploitation and grassland improvement through the sowing of forage species; extensive cultivation of drought-tolerant crops and fruit trees, providing plenty of suitable habitats for many thermo-xerophilous annual and biennial herbs and grasses; rational (cyclic) coppicing of tall shrublands to provide precious ecotones. By creation of clearings, the local biodiversity can be enhanced. For example, flower visiting insects, are observed above all where ecotonal vegetation develops, with a high diversity of flowering plants, especially herbaceous ones. This means that the structure of these insect communities, in the forest/shrubland/garrigue mosaic of evergreen vegetation, is based on a dynamic balance that is continually renewed through natural mechanisms such as fire and grazing. Moreover, as urbanization is increasingly affecting the plains and the coasts of all Mediterranean countries, more efforts should be addressed in order to find out the best technical “nature-based” solutions to create networks of functionally interdependent plant communities (e.g., *Lygeo-*

Table 2 Mediterranean grassland and shrubland types and their relationships to habitats of the European Red List (RL; Janssen et al., 2016), phytosociological units (Mucina et al., 2016) and Annex I of the “Habitats” 92/43 EU Directive.

Vegetation type	Habitat type in the European Red List	Phytosociological unit	RL code	RL status (EU28+)	Annex I
Annual dry grasslands	Mediterranean annual-rich dry grassland	<i>Stipo-Trachynietea distachyae</i>	E1.3c	NT	6220 ^a Pseudo-steppe with grasses and annuals of the <i>Thero-Brachypodietea</i>
	Mediterranean to Atlantic open, dry, acid and neutral grassland	<i>Helianthemetea guttati</i>	E1.A	VU	—
	Mediterranean closely grazed dry grassland	<i>Poetea bulbosae</i>	E1.3a	LC	6220 ^a Pseudo-steppe with grasses and annuals of the <i>Thero-Brachypodietea</i>
	Mediterranean tall perennial dry grassland	<i>Lygeo sparti-Stipetea tenacissimae</i>	E1.3b	LC	—
	Iberian summer pasture (vallicar)	<i>Stipo giganteae-Agrostietea castellanae</i>	E2.4	NT	—
	Open Iberian supramediterranean dry acid and neutral grassland	<i>Jasiono sessiliflorae-Koeleretalia crassipedis (Festucetea indigestae)</i>	E1.8	LC	—
	Iberian oromediterranean basiphilous dry grassland ^a	<i>Festuco hystricis-Poetalia ligulatae (Festuco hystricis-Ononidetea striatae)</i>	E1.5b	LC	6170 Alpine and subalpine calcareous grasslands
	Perennial rocky calcareous grassland of subatlantic-submediterranean Europe	<i>Festuco-Brometea (p.p)</i>	E1.1i	VU	6210 Semi-natural dry grasslands and scrubland facies on calcareous substrates (<i>Festuco-Brometalia</i>)
	Dry steppic, submediterranean pasture of South-Eastern Europe	<i>Scorzoneretalia villosae (Festuco-Brometea)</i>	E1.1j	NT	62A0 Eastern sub-Mediterranean dry grasslands
					6210 Semi-natural dry grasslands and scrubland facies on calcareous substrates (<i>Festuco-Brometalia</i>)
Perennial dry grasslands	Semi-dry perennial calcareous grassland	<i>Festuco-Brometea (p.p)</i>	E1.2a	VU	6310 Dehesas with evergreen <i>Quercus</i> spp.
Other grasslands	Mediterranean wooded pastures and meadows	—	E7.3	NT	—
	Western basiphilous garrigue	<i>Ononido-Rosmarinetea (p.p.)</i>	F6.1a	LC	2260 <i>Cisto-Lavanduletea stoechadis (p.p.)</i>
	Western acidophilous garrigue	<i>Cisto-Lavanduletea stoechadis (p.p.)</i>	F6.1b	LC	—
	Eastern basiphilous garrigue	<i>Ononido-Rosmarinetea (p.p.)</i>	F6.2	LC	—
		<i>Ononido-Rosmarinetea (p.p.)</i>			—
		<i>Festuco hystricis-Ononidetea striatae (p.p.)</i>	F6.6	LC	—
	Supramediterranean garrigue				5320 Low formations of <i>Euphorbia</i> close to cliffs
					5410 West Mediterranean clifftop phryganas (<i>Astragalo-Plantaginetum subulatae</i>)
					5420 <i>Sarcopoterium spinosum</i> phryganas
					5430 Endemic phryganas of the <i>Euphorbio-Verbascion</i> p.p. (only the western subtypes)
Dwarf shrublands	Western Mediterranean spiny heath	<i>Ononido-Rosmarinetea (p.p.)</i> <i>Helichrysetalia italici (p.p.) (Crithmo-Staticetea)</i> <i>Lavandulo stoechadis-Hypericetalia olympici (Cisto-Lavanduletea stoechadis)</i>	F7.1	LC	5420 <i>Sarcopoterium spinosum</i> phryganas 5430 Endemic phryganas of the <i>Euphorbio-Verbascion</i> p.p. (only the western subtypes)
	Eastern Mediterranean spiny heath (phrygana)	<i>Hyperico empetrifolii-Genistetalia acanthocladae (Ononido-Rosmarinetea)</i>	F7.3	LC	

(Continued)

Table 2 Mediterranean grassland and shrubland types and their relationships to habitats of the European Red List (RL; Janssen et al., 2016), phytosociological units (Mucina et al., 2016) and Annex I of the “Habitats” 92/43 EU Directive.—cont’d

Vegetation type	Habitat type in the European Red List	Phytosociological unit	RL code	RL status (EU28+)	Annex I
					5210 Arborescent matorral with <i>Juniperus</i> spp.
					5230 Arborescent matorral with <i>Laurus nobilis</i>
					5310 <i>Laurus nobilis</i> thickets
					5330 Thermo-Mediterranean and pre-desert scrub
					5220 Arborescent matorral with <i>Ziziphus</i>
					5330 Thermo-Mediterranean and pre-desert scrub
					5330 Thermo-Mediterranean and pre-desert scrub—only <i>Retama shrublands</i>
					92D0 Southern riparian galleries and thickets (<i>Nerio-Tamaricetea</i> and <i>Securinegion tinctoriae</i>)
Tall shrublands	Mediterranean riparian scrub	<i>Nerio-Tamaricetea</i>	F9.3	LC	1430 Halo-nitrophilous scrubs (<i>Pegano-Salsoletea</i>)
Halo-nitrophilous shrublands	Mediterranean halo-nitrophilous scrub	<i>Pegano harmalae-Salsoletea vermiculatae</i>	F6.8	LC	

EN, endangered; LC, least concern; NT, near threatened; VU, vulnerable.

^aIt also includes upper supramediterranean levels, below the timberline.

Stipetea and *Helianthemetea guttati*) by exploiting the suburban brownfields and the roofs of the buildings of expanding cities (Catalano et al., 2013).

Sustainability of ecosystem services should be the main target of MG&S management (Varela and Robles, 2016). To achieve sustainability, a balanced interplay between all aspects of ecosystem services, and especially the control of the impact of human and climate constraints that may alter regulating and supporting services, must be well incorporated in management plans (Cavender-Bares et al., 2015). In addition to sustaining socio-economic systems that are based on MS&G, the natural capital is needed to maintain them. In that sense, issues related to property rights, land tenure, policies aimed at promoting the sustainable use of MS&G and resilience of socio-ecosystems must be adequately incorporated and discussed in the framework of management plans. Integrated management plans (IMPs) are urgently needed. They should include on the one hand a zoning framework to protect key habitats and species from detrimental human activities, as well as to allow (and suggest) appropriate sustainable uses, and on the other hand adequately address the socioeconomic relations expected to develop with the other aspects of local and regional or even state economies. Moreover, the abandonment of traditional management practices may deprive sustainable ways of human intervention in MG&S. Thus, such traditional practices must be detected and included (thus preserved) in the IMPs. It is to be hoped that, in the future, people and resources will be found in order to make more resolvable the conflict between human activities and conservation needs.

The management of MG&S may be based on four principles; (a) ecosystem sustainability, (b) natural regeneration, (c) multiple purposes, and (d) protection (Papanastasis, 2009). Advances in research into the ecological characteristics, structure and functioning of MG&S ecosystems, new socio-economic conditions and new trends and proven practices are upgrading or enhancing this four-principle management framework. Ecosystem sustainability has its roots in American forestry practice (Chapin et al., 1996). An ecosystem is considered sustainable when, during the natural cycle of disturbances, it maintains (a) the characteristic diversity of its major functional groups, (b) soil fertility and productivity, and (c) effective biogeochemical nutrient cycles. According to this concept, it is necessary to safeguard and protect the structural and functional characteristics of MG&S, in order to ensure the sustainable outcome of their operation, i.e., their productivity. The principle of natural regeneration requires measures to enhance the natural continuity of vegetation in space, but mainly over time. This principle is of particular importance nowadays, as the continuous underuse of MG&S (e.g., undergrazing, cease of firewood collection) over the last decades has resulted in the natural expansion and thickening of woody vegetation at the expense of grasslands (Zomeni et al., 2008). The multipurpose principle calls for the multifunctional role of MG&S to be highlighted. In line with this principle, as well as the ecosystem perception, the adoption of specific principles and criteria for the certification of products and services based on the MG&S is expected to highlight their important multifunctional role. The principles for Forest Stewardship (FSC, 2002) can be used as a template for this certification. Finally, the principle of protection requires the adoption of all those institutional measures, in particular, which will help to reduce the impact of the causes of degradation on the MG&S.

See also: Shrublands of Temperate Europe.

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Heathlands of Temperate and Boreal Europe

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This chapter was solicited and edited by Jürgen Dengler and Péter Török on behalf of the Eurasian Dry Grassland Group (EDGG).

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Abstract

Scrub communities dominated by heathers are called heathlands and are frequent in western and central Europe and in the subalpine belts of the mountains. They are diversified into seven subtypes along a wide geographic span along the entire Atlantic countries of Europe, from the Cape North to the Strait of Gibraltar as well as the Azorean islands, and penetrate in some areas of central Europe. They always grow on siliceous soils poor in bases and require high moisture during the growing season. The organic matter produced by heathlands is acidic and favors the podsolization of the soils. Most of them are linked to the human activity based on traditional land use: extensive grazing, harvesting and fire, which supported an agrarian economy based in livestock: sheep, goats, cattle. They started expanding from the Neolithic on at the expense of the forests that existed before. With the current rural abandonment, heathlands are severely diminishing and being replaced by newly growing forests or other human induced vegetation types such as grasslands, tree plantations or fields.

Delimitation and Physiogeography [Topography, Climate, Soils] of the Region

Heathlands have been considered one of the most genuine European landscape types (Gorissen, 2004), being particularly widespread in its Atlantic zone (Gimingham, 1972). The word heathland is used to name a treeless area covered by heath, a term used to name an evergreen scrub vegetation formed mostly by heathers, i.e. dwarf-shrubby species of the *Ericaceae* family, basically of the genera *Arctostaphylos*, *Erica*, *Calluna*, *Daboecia*, *Empetrum*, *Loiseleuria*, *Rhododendron* and *Vaccinium*. A number of woody legumes may add to them, mostly of the genera *Ulex* and *Genista*, as well as some grasses, bulbs, mosses and lichens. Heathlands are particularly frequent in the western part of Europe where they encompass both its northern and southern extremes, being also found in many areas of the center of the continent. In many European territories they play an important role in the landscape, where they occupy a substantial share of the surface. Depending on the dominant shrub species and the treatment, heathlands size can vary from a mid-sized shrubland up to 2 m dominated by gorses (*Ulex* species) to a dwarf scrub of a few centimeters high rich in cryptogams and grasses. More frequently they adopt an intermediate size between 20 and 80 cm in a dense formation of woody ericoid plants covering large parts of the soil surface.

Soils

Typical heathlands grow on a range from dry, well-drained acidic and oligotrophic soils on ridges and slopes and sandy plains to moderately hydromorphic or slightly peaty soils in poorly-drained depressions prone to water accumulation. The ericaceous vegetation causes acidification and even podsolization in the soil. This is due to the acidity of its organic matter and the humidity of the climate which induces several processes in the upper layers of the soil profile: the formation of organic-mineral complexes of iron and aluminum oxides with the acidic compounds from the organic matter known as chelates. These chelates are leached and transported to deeper horizons (illuvial), where they accumulate. This loss of organic-mineral complexes eventually results in a bleached ash-gray color eluvial horizon which is rich in quartz, depending on bedrock and climate conditions. This edaphic process is known as podsolization and can end in the formation of true podzols derived by degeneration of brown soils (Fig. 1), but similar to those originated under the boreal conifer forest (Gimingham, 1972). Usually heaths are found on siliceous rocks such as granite, schists,



Fig. 1 Podzolic soil under a heathland in the Basque Country, northern Spain. (J. Loidi).

slate, sandstone or even sand dunes. In some cases, if the rainfall is high enough, cation weathering is so active that they can thrive even on base-rich bedrocks. Basiphilous heaths in such environments have a high number of calcicolous species and are classified in different plant communities than the genuine acidic heaths, and are dominated by species like *Erica vagans*.

Climate

Heathlands mostly are distributed in the Atlantic countries of Europe, where oceanic climate conditions prevail. They expand inland to some regions of central Europe under sub-Atlantic conditions, where they require a high moisture provision. In the north, under a long winter season climate, the short summer is cool and rainy and the vegetation does not experience any shortage of water. Southwards, summer becomes longer and warmer and even in winter vegetative activity is not suppressed. Such conditions demand more rain to sufficiently provide water the heather species require. For that reason, heathlands refuge in wet mountain slopes in west and southwest Iberia, as well as in their most southern part of their distribution range, in the highly rainy western slopes of the Rif range in north Morocco.

Ecology, Typology of the Communities Flora and Fauna

With the exception of topographic positions in which soils are shallow and rocky, impeding succession toward the establishment of a forests, such as coastal cliffs and mountain ridges, the great majority of the heathlands of Europe are intermediate steps in the successional series ending in the Potential Natural Vegetation (Fagúndez, 2012), i.e. seral stages of degradation of ancient forests (Fig. 2). They are strongly related to a severe and recurrent disturbance regime responsible for arresting the natural succession. Such disturbance regime consist fundamentally in burning, mowing and/or grazing, thus, most of the today existing heaths are secondary (Webb, 1998). Exceptions are primary stands on coastal cliffs and on windswept plateaus and ridges of mountains, especially in the boreal region.

Heathlands are found all along the western edge of the European continent, from North Cape to the Gibraltar strait, in all areas influenced by the ocean (Fig. 3); this includes Norway, western Sweden, Denmark, NW Germany, Benelux, France, Ireland, the United Kingdom, north and western Iberia and NW Morocco. In the interior areas of the European continent, i.e. central and eastern France, Germany, Poland, Czech Republic, the Alps, and the Carpathians, impoverished or subalpine versions of the heathlands are found on siliceous bedrock. Heathlands have a basic set of species which are present in most of its range and of its variants: *Avenella flexuosa*, *Calluna vulgaris*, *Carex pilulifera*, *Festuca* sp. pl., *Juniperus communis*, *Potentilla erecta*, *Pteridium aquilinum*, *Solidago virgaurea*, *Vaccinium myrtillus*, and some others. Such a broad geographic scope entails a strong diversification into several main subtypes. The following typology reflects the main vegetation synthesis have been published for Europe or its Atlantic countries (Böcher, 1940, 1943; Díaz González, 1998; Géhu, 1975; Mucina et al., 2016; Rivas-Martínez, 1979).

1. The first subtype corresponds to the boreal areas and subalpine-alpine levels of the temperate mountains and is submitted to relatively cold climatic conditions. It is extended in arctic-boreal regions and the subalpine belts of the European mountains (Pyrenees, Alps, Carpathians, Balkans) and is characterized mostly by cold-adapted species such as *Arctostaphylos uva-ursi*,



Fig. 2 Heathland on siliceous bedrock in Asturias, northern Spain. (J. Loidi).

Arctostaphylos alpinus, *Bruckenthalia spiculifolia*, *Empetrum hermaphroditum*, *Erica carnea*, *Loiseleuria procumbens*, *Rhododendron ferrugineum*, *Rhododendron hirsutum*, *Rhododendron myrtifolium* and *Vaccinium gaultherioides*, while more widespread ericoid species like *Calluna vulgaris*, *Erica cinerea*, *Vaccinium myrtilis* and *Vaccinium vitis-idaea* may dominate as well. They are natural and semi-natural acidophilous close stands of dwarf-shrub heaths, mostly on siliceous bedrock, sometimes on neutral or base-rich soils. These heaths are usually dominated by one or few heathers and are quite species-poor in terms of vascular plants, in which representatives of the *Ericaceae* and *Empetraceae* families play an important role. The plant diversity is mainly found in mosses and lichens. *Hylocomium splendens* is a typical moss species that may dominate, while many *Cladonia* and *Cetraria*-species may form a lichen-rich moss layer. There are substantial differences in the floristic composition between the northern areas (boreal-arctic) and the subalpine-alpine levels of the southern mountains. In the temperate mountains, *Rhododendron*-heaths occupy sheltered sites with deep long-lasting snow cover, while *Loiseleuria*-heaths are found on snow-free ridges, exposed to the severe cold of the winter. In the boreal region, *Arctostaphylos* and *Vaccinium* grow on more sheltered or lower sites, while the moss *Racomitrium lanuginosum* may dominate the highest and most windswept areas. Such differences are the result of the higher amount of snow in subalpine-alpine areas in comparison to the boreal region and in different conditions during summer, with long and cold nights in the subalpine-alpine areas in contrast to the almost permanent daylight of the boreal-arctic growing season. This variant is mainly classified within the class *Loiseleurio-Vaccinieta* for arctic-boreal tundra dwarf shrubland and alpine acidophilous heaths and *Vaccinio-Piceetea* for the subalpine and boreal heaths. Information about this type can be found in Rodwell (1991), Fremstad (1997), Delarze and Gonseth (2008), and Čarni and Šibik (2016).

2. A second subtype is the northern and central-European heath, submitted to a climate with cold winters due to latitude or to continentality. Its vascular plant flora is relatively poor in comparison to the southern heathlands: we can only mention *Empetrum nigrum* (for north Europe), *Genista germanica*, *Genista pilosa* and the rare *Diphysastrum tristachyum* as characteristic species, while *Calluna vulgaris* and *Vaccinium* species are common shrubs, substituted by *Erica tetralix* in younger stages. Also here, the main diversity consists of mosses and lichens, and one can see a shift in species-composition of these cryptogams during succession. A specific variety are the very open, young *Calluna*-heathlands on inland sand dunes. They are found in large open, drift-sand areas, the so-called Atlantic deserts, which are the result of degradation of the landscape in historical times. These young heathlands are rich in lichens, especially of the genera *Cetraria*, *Cladina*, *Cladonia* and *Stereocaulon*. Older stages, especially in *Empetrum nigrum* dominated heaths, can be rich in large foliose hepatics of the genera *Barbilophozia*, *Lophozia*, and *Bazzania*, the later especially on loess. These northern and central heathlands inhabit the subatlantic and continental territories of western Europe, ranging from the northern foothills of the Pyrenees, central-eastern France, Germany, till the Alps and Bohemia and expanding northwards to the British Isles, the Benelux, NW Germany, Denmark and southern Norway (Böcher, 1943; Nordhagen, 1921). The alliances *Empetrium nigri* (restricted to coastal dunes), *Calluno-Genistion pilosae* and *Genisto pilosae-Vaccinion* group these heaths. Information about this type can be found in Rodwell (1991), Fremstad (1997), and Janssen (2016a).
3. A third subtype is the western Atlantic heath with *Ericaceae* and gorses spread across NW Iberia, western France and the western part of the British Isles. The characteristic species of this subtype are *Agrostis curtisii*, *Avenula marginata* subsp. *sulcata*, *Carex asturica*, *Daboecia cantabrica* (Fig. 4) *Euphorbia polygalifolia*, *Glandora prostrata*, *Halimium lasianthum*, *Erica cinerea* (Fig. 5A and B), *Erica mackaiana*, *Erica scoparia*, *Erica vagans* (Fig. 6), *Ulex europaeus* (Fig. 7), *Ulex gallii*, *Ulex minor*, *Pseudarrhenatherum longifolium*, *Simethis mattiazzi*, *Viola lactea*, *Xolantha globulariifolia*, among others. Most of these characteristic plants are restricted to the southern section of the territory. Going northwards, the floristic composition impoverishes significantly. Information about this type can be found in Géhu (1975), Géhu and Géhu-Franck (1975), Loidi et al. (1997), and Rivas-Martínez (1979).

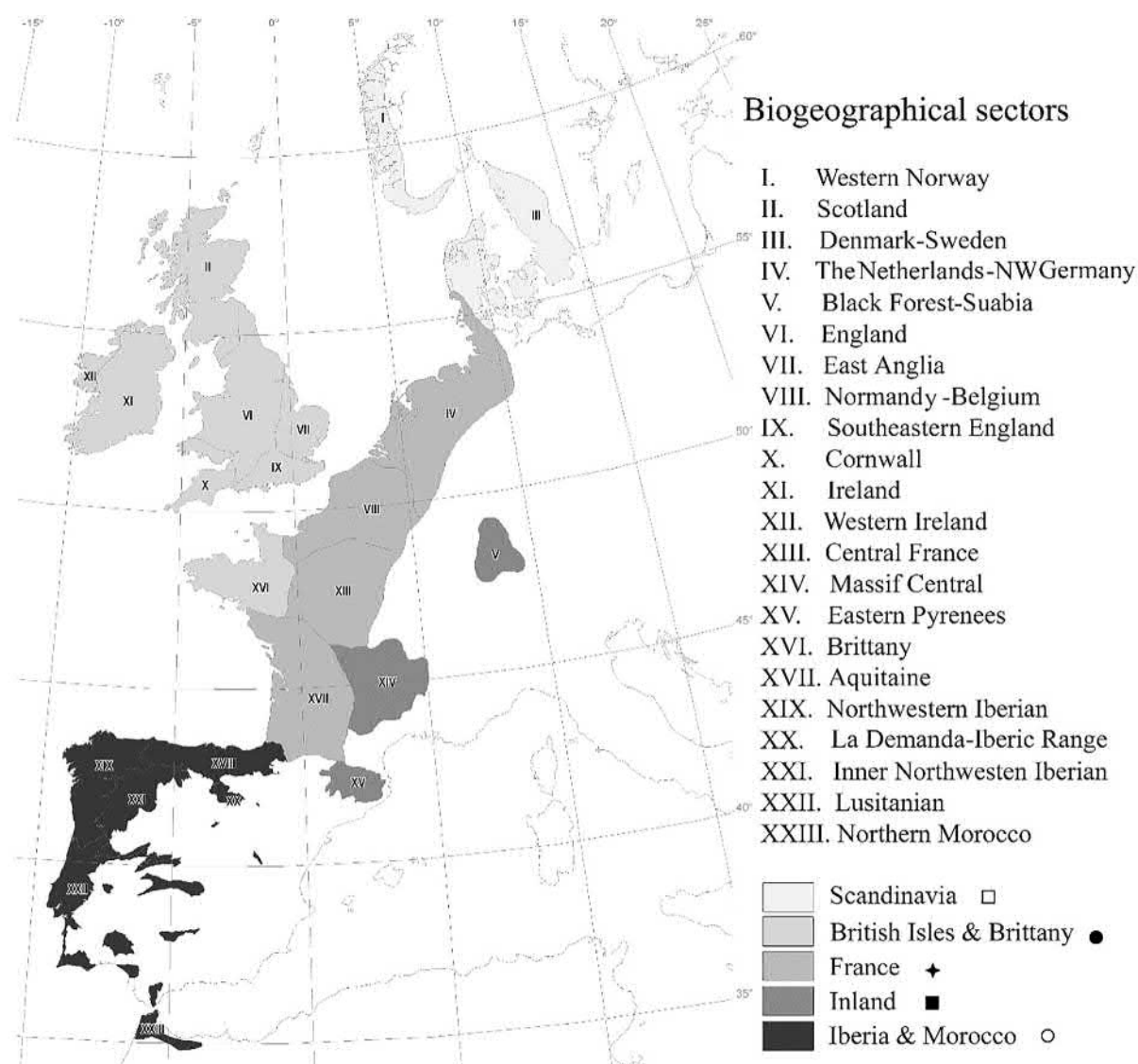


Fig. 3 European distribution of Atlantic heathlands. From Loidi, J., Biurrun, I., Campos, J.A., García-Mijangos, I. and Herrera, M. (2010). A biogeographical analysis of the European lowland heathlands. *Journal of Vegetation Science* **21**, 832–842.



Fig. 4 *Daboecia cantabrica* (J. Loidi).



Fig. 5 (A). *Erica cinerea* (J. Loidi). (B). *Erica cinerea* (J. Loidi).



Fig. 6 *Erica vagans* (J. Loidi).

4. A fourth subtype is the wet heath which appears in depressions where water accumulates and remains there for most of the year, giving way to a clear hydromorphy accompanied by low pH. They are represented in many regions of western Europe, from the Baltic countries to SW Iberia (Doñana), being particularly frequent in the wettest parts of the range: Northwest-Iberia, Ireland and the United Kingdom. The most indicative plants of this variant are *Erica ciliaris* (Fig. 8) and *Erica tetralix* (Fig. 9), which use to be accompanied by other hydrophilic plants such as *Carex panicea*, *Drosera rotundifolia*, *Juncus squarrosus*, *Gentiana pneumonanthe*, *Lycopodiella inundata*, *Molinia caerulea*, *Myrica gale*, *Narthecium ossifragum*, *Sphagnum compactum*, *Sphagnum molle*, *Sphagnum tenellum*, and *Trichophorum cespitosum* among others. In the edges of ponds of oligotrophic waters some wet grassland species appear in the heath, such as *Dactylorhiza maculata*, *Molinia caerulea* and *Pedicularis sylvatica*. In the warmer and more oceanic areas of the south Atlantic, particularly Iberia, *Cirsium filipendulum*, *Cirsium welwistchii*, *Euphorbia uliginosa*, *Genista ancistrocarpa*, *Genista anglica*, *Genista berberidea*, *Genista micrantha* and *Thymelaea coridifolia* subsp. *dendrobryum* characterize these wet heaths. The alliance *Ulici-Ericion ciliaris* includes these wet heaths, although Iberian stands have been grouped into the *Genistion micrantho-anglicae*. In the northern areas of Europe there are also *Erica tetralix* and *Calluna vulgaris* dominated fens, grouped in the *Ericion tetralicis* alliance. Information about this type can be found in Rodwell (1991) and Janssen (2016b).
5. A fifth subtype is formed by the coastal cliffs heaths (Fig. 10) of the Atlantic shores between NW Iberia and the British Isles (Fernández Prieto and Loidi, 1984). They are influenced by the saline spray of the sea wind and consequently several forms of wind-adapted cushion-shaped gorses and heathers dominate in the scrub, such as of *Ulex europaeus* f. *humilis* and *Ulex gallii* f. *humilis*. Plants adapted to salinity such as *Angelica pachycarpa*, *Anthyllis vulneraria* subsp. *iberica*, *Dactylis marina*, *Daucus carota* subsp. *gummifer*, *Festuca rubra* subsp. *pruinosa*, *Leucanthemum vulgare* subsp. *crassifolium*, *Plantago maritima*, *Pulicaria odora*, *Rumex acetosa* subsp. *biformis* or, *Silene uniflora*, are common in the vegetation, in addition to the common *Calluna vulgaris*, *Erica cinerea*, *Erica vagans* and *Glandora prostrata*. These coastal cliff heaths are considered as permanent communities, because succession is prevented by the saline and windy conditions. For that reason, they could be some of the primary stations of all the Atlantic European heaths, which survived during the cold phases of the ice-ages and existed before humans expanded heathlands since



Fig. 7 *Ulex europaeus* (J. Loidi).



Fig. 8 *Erica ciliaris* (J. Loidi).

the early Neolithic times by means of their land-managing procedures (Gimingham, 1972). Information about this type can be found in Fernández Prieto and Loidi (1984), Rodwell (1991), and Janssen (2016a).

6. A sixth subtype is the southern Atlantic heaths are widespread in W-SW Iberia (and actually reaching NW Morocco, Deil, 1984), inside the Mediterranean region (Fig. 11). They are found on the wet slopes of hills and mountains and on sandy humid depressions in the dunes and palaeodunes of the coastal strip. Climatically they thrive under conditions of severe summer drought but the high windward precipitations or the edaphic water table offset this shortage and this highly water-demanding vegetation can survive. This influence is shown by a high number of characteristic plants with a Mediterranean distribution: *Cistus crispus*, *Cistus psilosepalus*, *Cistus salviifolius*, *Drosophyllum lusitanicum*, *Erica andevalensis*, *Erica australis* (Fig. 12), *Erica scoparia*, *Erica umbellata*, *Genista triacanthos*, *Genista tridens*, *Glandora lusitanica*, *Halimium umbellatum*, *Halimium ocymoides*, *Hypericum linariifolium*, *Lavandula viridis*, *Luzula lactea*, *Polygala microphylla*, *Pterospertum tridentatum*, *Stauracanthus boivinii*, *Thymelaea broteriana*, *Thymelaea villosa*, *Thymus villosus*, *Ulex airiensis*, *Ulex jussiaei*, *Ulex micranthus*, and some others. In some areas where fire



Fig. 9 *Erica tetralix* (J. Loidi).



Fig. 10 A coastal cliff heathland (J.A. Campos).

and soil degradation is very intense, stands of *Cistus ladanifer* and *Cistus populifolius* can appear in the heathlands. Information about this type can be found in [Janssen \(2016a\)](#).

7. A particular subtype of European heathlands are those from the Azores Islands ([Lüpnitz, 1975](#)). They inhabit in the mid and high-elevation areas of the archipelago's volcanoes where the almost permanent fog soaks the vegetation constantly. A number of Macaronesian endemics, such as *Daboecia azorica* ([Fig. 13](#)), *Diphasiastrum maderense*, *Huperzia dentata* or *Huperzia suberecta*, together with *Calluna vulgaris*, form these heathlands. Information about this type can be found in [Capelo \(2016\)](#).

Fauna

For fauna species most heathlands are an extreme and dynamic environment, with strong fluctuations in temperature and water supply and limited availability of nutrients. The larger fauna usually operates on a landscape scale, and characteristic species in



Fig. 11 A western Iberian heathland (J. Loidi).



Fig. 12 *Erica australis* subsp. *aragonensis* (J. Loidi).

heathlands may prefer mosaics with open soil, grassland, tall-herb vegetation and forest. Typical birds related to such heathland landscapes are among others Black Grouse (*Tetrao tetrix*), Common Stonechat (*Saxicola rubicola*), Dartford Warbler (*Sylvia undata*), European Curlew (*Numenius arquata*), European Golden Plover (*Pluvialis apricaria*), Northern Wheatear (*Oenanthe oenanthe*), Whinchat (*Saxicola rubetra*) and Wood lark (*Lullula arborea*). The European Nightjar (*Caprimulgus europaeus*) is a ground breeder of the transition zone between forest and heathlands. Smaller animals often prefer a mosaic of different vegetation structures within the heathlands, and in many cases they require different (micro)habitats in different life stages. Typical reptiles are among others Slowworm (*Anguis fragilis*), Viviparous lizard (*Zootoca vivipara*), Sand lizard (*Lacerta agilis*), Smooth snake (*Coronella austriaca*), and in wet heathland Common European viper (*Vipera berus*). Amphibians are always related to wet heathlands or fens within the heathland landscape, including the Moor frog (*Rana arvalis*) and Natterjack Toad (*Epidalea calamita*).

The highest diversity of insects seems to be related with diversity in vegetation structure rather than in species diversity (Usher, 1992; Stuijzand et al., 2004), although some species depend on one plant species or genus in their larval stage. Many butterflies, spiders, grasshoppers, beetles, wasps, bees and ants have concentrations of their distribution in heathland areas. Some examples are the butterflies Silver-studded Blue (*Plebejus argus*), Green Hairstreak (*Callophrys rubi*), Grayling (*Hipparchia semele*), Silver-spotted Skipper (*Hesperia comma*), Tree Grayling (*Hipparchia statilinus*), Grizzled Skipper (*Pyrgus malvae*) and—characteristic for wet heathlands—Alcon Blue (*Phengaris alcon*), which larvae live on *Gentiana pneumonanthe*. In the Alps Asian Fritillary (*Hypodryas intermedia*) is characteristic, while in subalpine and boreal heathlands Cranberry blue (*Plebeius optilete*) is a typical butterfly species. Among the



Fig. 13 *Daboecia azorica* (P. Arsenio).

grasshoppers we mention Wart-biter (*Decticus verrucivorus*), Heath-bush Cricket (*Gampsocleis glabra*), Blue-winged Grasshopper (*Oedipoda caerulescens*) and the Field Cricket (*Gryllus campestris*). It is also worth mentioning the ground beetle *Callisthenes reticulatus* which lives in the west European heathlands. A last species that should be mentioned in particular is the Heather Beetle (*Lochmaea suturalis*). Both larvae and adults eat heather (leaves, stem apices and bark) and cause regular outbreaks that may destroy entire dry heath patches (Gillingham et al., 2015). The beetle occurs in the dry *Calluna* dominated heaths of Western Europe.

Biogeography and Biodiversity Patterns

The biodiversity of European heathland is expressed by the variety in subtypes described above, and these subtypes show clear patterns of geographic distribution of their plant species and communities. These patterns can be explained by the history of the Quaternary and its climatic oscillations on one hand (Loidi et al., 2010), and by the history of the human influence during the Holocene, on the other hand.

Concerning the origin of the flora of the European heathlands, we can distinguish two sets: one is formed by species that were differentiated by adaptation to a cold climate, the Arctic-Boreal set, and the second by species that were differentiated by being adapted to a warm-temperate to subtropical rainy climate. The former was likely formed during the Pleistocene when the temperatures experienced dramatic descents in the high and mid latitudes. The latter is an older group, probably differentiated along the Tertiary in an area now including NW Iberia, the Gulf of Biscay and surrounding territories. Several phylogeographic surveys carried out so far and the current distribution of the heathland species are in favor of this hypothesis (Gil-López et al., 2017; Hornoy et al., 2013; Mahy et al., 1999). The small group of species with mainly a boreal and alpine distribution are the characteristic plants for the first subtype of our classification. The “subtropical” species are clearly concentrated in Iberia, where they likely originated and diversified and later refuged during the ice-ages, as is documented for heathers, gorses and other taxa. This group has a broad representation in the Atlantic areas, such as western France and the British Isles, where some of the heathers show a significant disjunct distribution, as is the case for *Daboecia cantabrica* (Beatty and Provan, 2013) and *Erica mackaiana*. The subtropical group constitutes the floristic core of these European heathlands, which has expanded over the northern and central European territories during the warm phases of the Pleistocene and during the Holocene.

The Azores archipelago rose from the ocean bottom (Azores Platform) due to volcanic activity and reached the sea surface in a period when the Atlantic Ocean was substantially narrower than it is now. The first island, Santa María, emerged about 8.12 million years ago. Thus, Europe, now at a distance of 480 km, was likely closer to the archipelago than it is now. That means that the heathers that occurred in SW Europe could colonize this archipelago creating a back and forth migratory relationship helped

by a system of “stepping stone islands” (Fernández-Palacios et al., 2011). Later, the Azores became more isolated due to the separation of Europe from North America, driven by the plate tectonics and, due to this isolation, the flora differentiated, having a large set of endemic plants.

The other driver explaining current distribution patterns of heathlands across Europe is human intervention. Land use has functioned only as a driving force since early to mid Holocene (8000–6000 years ago), when Neolithic cultures, with agriculture and animal husbandry, spread over Europe. Such activities have a high impact on vegetation and in a traditional way of land use, they intensely favor the expansion of heathlands. For that reason, many of the current heaths are considered anthropogenic and likely many regions in Europe were invaded by heathlands due to human land use, particularly in areas with siliceous bedrock.

Natural vs. Anthropogenic Communities

For a long time it was thought that heathland has always existed as the landscape we know today. However, insights from land-use history, archeology, palynology and vegetation science completed our understanding of the processes that determine occurrence and development of the current plant communities.

In Norway, the lowland heath region along the west coast was completely forested until 5000 years BP (Kvamme et al., 2004). From then on, small-scale forest clearance started and continued for more than 4000 years. Pollen analyses made clear that the reduction of the tree cover was accompanied by the establishment and increase of a *Calluna* dominated heath vegetation plus an increase of peat formation. The existence of charcoal remnants at the stratigraphical border between forest and heather peat and of charcoal dust in all the subsequent layers, strengthen the arguments that the development and spread of lowland heath was induced by man, mainly by intentional burning (Kaland, 1986).

On the British Isles a comparable evolution took place. Changes in the pollen signature of peat and in soil development (podsolization) make clear that from the Atlantic period on, when the climate became more oceanic, the impact of man on the landscape became prominent. The original forest cover was disturbed, leading to the spread of heathland which was encouraged by the increased leaching of the soils that followed the deforestation. At the Late Bronze age (3000 BP) heathlands extended to become a dominant land cover over in major parts of the British Isles (Rackham, 1997; Webb, 1986).

In the Iberian Peninsula similar palynological observations have been made. The expanse of *Calluna vulgaris* and *Erica* species coincided with evidence of extended grazing areas, originated from severe fires (for instance Abel-Schaad et al., 2014). Frequent severe fires hindered the complete recovery of forests while shrubland and grasslands established. From 5800 to 5400 BP on, heathlands developed and became the dominant vegetation type in vast areas with suitable soil and climatic conditions. They were maintained by fires, most likely associated with human activities (Morales-Molino et al., 2013). There are plenty of evidences showing that forest vegetation preceded heaths almost universally and that human settlements and land cultivation and grazing frequently are associated with the decline of forest and increase of heath (Gimingham, 1972). Human induced disturbance regimes that created most of the European heathlands have persisted so far.

Although rapid re-growth of forest after clearance was prevented because of all-year-round grazing of heath, made possible by the oceanic climate and because of the harsh environmental conditions, agriculture in the Atlantic domain of Western Europe had to cope for thousands of years with the same environmental constraints (Gimingham and de Smidt, 1983; Webb, 1986). This resulted in a comparable landscape pattern from the Lofoten Islands in Norway to the Serra da Estrêla in Portugal (Haaland, 2002). The solutions and techniques used to overcome the natural factors that limited production in these regions, gave rise to the same organization and use of the land: a combination of large ‘outfields’ -the heathlands- and ‘infields’ -the cultivated land- (Webb, 1998). Management of the outfields had the purpose of maintaining and optimizing them as a crucial source in the local agricultural economy (De Blust, 2007; Diemont et al., 2013). The outfields served as grazing land for horses, cattle, goats and sheep, which were crucial natural resources on the farm, not least as producers of manure and other valuable products that could be marketed. To ensure a sufficient quality and quantity of fodder for grazing animals, the main management of these outfields was to burn them regularly (Niemeyer, 2005). *Ulex* and *Sarothamnus* were harvested for an additional valuable fodder. Cut *Calluna* and turfs served as bedding in the stables and, saturated with manure, became valuable fertilizers for the permanent infields. In some regions, fertilization of temporary fields was achieved by sowing *Sarothamnus*. In the Ardennes (Belgium) and in Brittany (France), after collecting the useful fodder and bedding, the remaining dried litter and crumbled humus layer was submitted to controlled burning and the ashes and clay were spread over the parcel of former heath to provide a new, temporary field for rye and buckwheat. This was the practice of ‘écobuage.’ All these uses of the heathland, resulted in a continuous flux of minerals and energy, from the outfields to the infields, a key process that this farming system and the landscape depended on (Haaland, 2002).

400–200 years ago, lowland heath was at its greatest extent in Europe. In many places however, despite strong traditions and regulations (De Moor et al., 2002), exploitation had reached and surpassed the limits of sustainability. Productivity fell to a minimum and in sandy regions shifting dunes expanded and threatened farms and covered the heath. The decline and transformation of heathland was inevitable when in the 18th century changing economic conditions, improved technology, population growth and the interests of foreign rulers, challenged its traditional use and functions. Heath no longer fitted with the ever-growing human society and it was cultivated as permanent agricultural land, planted with pine or *Eucalyptus* forest, reclaimed for urbanization or made productive for the emerging industries.

Threats

The area of heathland that has remained until today, is only rarely still part of the current (local) agricultural system. This has huge consequences for the functioning of this ecosystem. In former days, the agricultural use led to a continuous flux of energy and minerals out of the heath which resulted in an impoverishment of the system. Today, because of the cessation of traditional management, and especially because of the substantial increase of atmospheric deposition, the flow is inverted and nutrients accumulate (Terry et al., 2004). As a result, natural succession toward forest is not hindered by intensive grazing or other management interventions anymore and altered environmental conditions facilitate potentially dominant plant species, especially grasses, to rapidly spread and become dominant in the vegetation (Aerts and Heil, 1993). Development toward more homogeneous and grass dominated vegetation is further intensified by desiccation of the wet heath due to drainage and ground water pumping activities. This favors the mineralization of the organic soil layer which leads to increased nutrient availability. Species dependent on groundwater are becoming increasingly rare and species richness of communities decreases. Finally, in large parts of Europe changes in pH have affected the heathland ecosystems in various ways; by altering the balance and availability of minerals in the soil and water, by causing direct toxic or lethal effects, and by hindering successful reproduction and seedling establishment. Again, some species become extinct while others find favorable conditions to spread, or even may invade the heathland communities.

Where heathlands became part of nature reserves the management changed as well. More large-scale grazing, burning and sod-cutting resulted in a more homogeneous vegetation structure, and this is especially problematic for the insect and reptile fauna of heathlands. Besides, atmospheric deposition causes soil acidification and eutrophication, which alter the mineral balance (high nitrogen amounts, low concentrations of Calcium and other elements)—resulting in lower food quality for fauna (Vogels et al., 2013)—and stimulate the dominance of grasses—resulting in reduction of bare soil and lowering of vegetation structure diversity. Together with fragmentation of remaining heathland patches, these are the main causes for many characteristic animal and plant species in heathlands to be endangered. In areas with high amounts of atmospheric deposition, sod cutting has been a management practices since the 1980s, aiming at removing nutrients and dominance of grasses. However, the large scale at which this management has been practiced, has resulted in a low proportion of heathlands with undisturbed humus profiles. Especially such older and more stratified soils have better water and buffer capacity, and need conservation from that perspective (Bijlsma et al., 2013). One of the unwanted by-effects of large-scale sod-cutting is the loss of foliose hepatics which are dependent on undisturbed humus profiles. Since their dissemination abilities are poor, the recolonisation of heathlands is hampered once they disappeared.

Fagúndez (2012) deals about the dynamics of heathlands identifying 5 drivers of change which operate at different scales and have diverse prevalence and intensity. In order of the importance of their currently visible effects we could quote: (1) Habitat destruction and fragmentation due to land use change; (2) Natural vegetation dynamics enhanced by rural abandonment; (3) Air pollution and eutrophication mostly by atmospheric N deposition; (4) Climate change with temperature increases and changes in precipitation amount and distribution; (5) The spread of invasive exotic species. These drivers interact among themselves and make up a summary scheme of elements and relationships that determine the changes experienced by heaths today.

Conservation, Restoration and Sustainable Management

Heathlands have received a great attention from the European Union in its nature law, the Habitats Directive (EU, 2013), as a logical consequence of the multiple pressures which lead to a decrease in their abundance and diversity. There are eight habitat types which are included in Annex 1 of that Directive, three of them of priority conservation (*): Dry sand heaths with *Calluna* and *Genista* (2310), Dry sand heaths with *Calluna* and *Empetrum nigrum* (2320), Northern Atlantic wet heaths with *Erica tetralix* (4010), Temperate Atlantic wet heaths with *Erica ciliaris* and *Erica tetralix* (4020*), European dry heaths (4030), Dry Atlantic coastal heaths with *Erica vagans* (4040*), Endemic macaronesian heaths (4050*), and Alpine and Boreal heaths (4060). As the majority of these heathlands are secondary and linked to human management, their conservation is only guaranteed by maintaining the traditional exploitation regime that prevents succession toward forest. Some type of disturbance has to be applied: mowing, grazing, burning or a similar management which keeps the vegetation in a scrub state (Figs. 14 and 15). Prescribed and controlled fires following a low frequency temporal pattern is a reasonable and low cost option when no other actions can be taken. Currently a European Dry Heath Action Plan is under development, initiated by the European Union.

It is however important to carry out management practices at a small scale, whenever possible within financial, social and practical prerequisites, as large-scale management leads to homogeneity in vegetation structure and micro-climates, and this causes loss of flora and fauna diversity. One should be aware that in the sandy plains of Northwestern Europe, historically, the heathlands on more productive soils have been transformed into agricultural land in an early stage and at a much larger scale, leaving behind mainly heathlands on very poor soils. Especially on such soils, atmospheric deposition is a huge problem, and no solution has been found yet to alter the misbalance between nutrients and loss of minerals. At an experimental scale, the addition of rock dust has been applied, aiming at restoring the balance of minerals in the soil and plants.



Fig. 14 Mown heathland in northern Spain (J. Loidi).



Fig. 15 Burned heathland in northern Spain (J. Loidi).

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Shrublands of Temperate Europe

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This chapter was solicited and edited by Jürgen Dengler and Péter Török on behalf of the Eurasian Dry Grassland Group (EDGG).

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Abstract

Shrublands are largely represented in Europe being diversified into several types. They are found in primary stations, usually on shallow soil sites of rocky places and steep slopes, in which they were differentiated along history and evolution. However, the overwhelming majority of the currently existing shrublands are in secondary stations, as seral stages of forests, being favored by humans by means of the traditional land use systems, particularly extensive husbandry and farming. They often form hedgerows for fencing rural properties, most of them by spiny shrubs such as brambles, roses and blackthorns. This vegetation produces abundant organic matter and keeps the soil in good conditions of fertility. Shrublands also host a large number of small animals, particularly butterflies, and provide abundant fleshy fruits for seed dispersal which fodder many birds. The conservation of the reticulated hedgerows landscape, known as bocage, is a relevant issue for the preservation of the structural complexity and biodiversity of the terrestrial ecosystems in temperate Europe. The modern tendency towards more technological exploitation systems in some regions, parallel to the rural abandonment in others, is leading to the reduction of this habitat type all over Europe.

Delimitation and Physiogeography of the Region

In the progressive succession towards the forests starting from abandoned fields, grasslands or heathlands, there is a stage formed by shrubs which precedes mature forest. They represent the previous stage before the potential natural vegetation, which is a summergreen deciduous forest in most of the European territories under a temperate climate. These shrublands replace forests after disturbance, whereas in stable disturbance-free situations, they also constitute their edge communities. The forest patches are surrounded by a linear fringe of shrub sealing them and, for that reason, they are often called mantel or forest-edge communities. By sealing the border of the forest patch, the conditions proper of the forests ecosystem (shade, temperature, humidity and a tempered wind), are preserved. In addition to this secondary position as seral stages and forests edges, shrublands have a primary position in rocky places with shallow soils unable to sustain true forests, such as crests, ridges and steep slopes. Also in severe wind exposed sites or under very dry or very wet conditions, where trees are unable to grow, shrubland may form the potential vegetation.

Mantel shrubs produce a high amount of organic matter which is usually easy degradable (mull) and to intermingle with the mineral fraction, being able to keep the soils built under the forest in good conditions of depth and fertility. This is an important point as regards their appraisal for conservation, particularly in areas where soil degradation is a threat. In the Mediterranean they are replaced by macchia or garrigue, in the north and in the upper altitudinal belts in the mountains by cold adapted heathlands.

Ecology and Biodiversity Patterns; Typology of the Communities, Flora And Fauna

The vegetation is formed by shrubs of diverse size, from humble scrubs of a few tens of centimeters, to small trees like hazel or dwarf forms of hornbeams or cherry trees. Many shrub species are spiny and have fleshy fruits adapted to animal dispersal—endozoochory- (Fig. 1). Especially in the Mediterranean, leafless woody legumes with green photosynthetic stems dominate, having the ability to fix atmospheric nitrogen, thus enhancing the fertility of poor soils.

Temperate forests are considered the climax or potential natural vegetation in most of Europe, representing the ecosystem optimum in terms of naturalness and complexity, but shrublands, which usually are a subordinate vegetation type, have important features referring the forest, particularly due to their capacity to build structured soils and to cast intense shade on the soil surface. In forest edges, where shrublands form a transition from grassland to forest (Fig. 2), these mantles may be very species rich, combining species of both the open and the wooded habitats, apart from the edge specialists. In the form of hedgerows, the combination of species preferring shady conditions and sunny conditions may also cause high diversity. Shrublands also harbor



Fig. 1 Blackthorn (*Prunus spinosa*) fleshy fruits (J.Loidi).



Fig. 2 The edge of the forest is sealed by a thorny species shrub mantle (J.Loidi).

many (apomictic) micro-species of plants, especially within the family of *Rosaceae*, like in the genera *Rubus* (Fig. 3), *Rosa* and *Crataegus*. These micro-species contribute largely to the plant diversity in temperate regions.

We can distinguish eight main subtypes of this vegetation in temperate Europe.

1. Deciduous spiny shrubland. The most extensive subtype is that of the deciduous -often spiny- shrublands. They are found over deep soils with medium to high fertility and nutrient richness. They are related to the temperate summergreen deciduous broadleaved forests of the class *Querc-Fagetea*. Very frequently, these shrublands are formed by thorny shrubs of the *Rosaceae* family, with the genera *Amelanchier*, *Crataegus*, *Prunus*, *Pyrus*, *Rosa* (Fig. 4), *Rubus*, etc. being largely represented. Other genera are *Berberis*, *Cornus*, *Corylus*, *Euonymus*, *Ligustrum*, *Rhamnus*, *Ribes*, *Ulmus*, *Viburnum*, etc. Due to their spinosity, these shrublands have been transformed into living semi-natural hedges separating rural parcels (Fig. 5) and bordering countryside roads. In addition to its impenetrability, they shelter many small vertebrates and insects, many of them pollinators of plants of the neighboring lands often crops or meadows. Additionally, the fleshy fruits, abundant from late summer to early winter, provide an important resource for many animal populations, especially birds. Both the hedges and the forest edges form important migration routes for different groups of animals, like small mammals, bats and butterflies. Besides, hedgerows function as corridors between different forests patches for such species, especially in fragmented landscapes. the typical European farmland landscape of the "bocage" (a french term for a landscape in which hedgerows are a characteristic feature) is the paradigm of the use of these spiny shrubs to build a linear grid of hedges that frames and includes meadows and fields. The most common and characteristic species of these spiny shrublands are: *Acer campestre*, *Acer monspessulanum*, *Acer tatarica*, *Amelanchier ovalis*, *Berberis aetnensis*, *Berberis hispanica*, *Berberis vulgaris* subsp. *cantabrica*, *Berberis vulgaris* subsp. *vulgaris*, *Cornus mas*, *Cornus sanguinea*, *Corylus avellana*, *Corylus colurna*, *Cotinus coggygria*, *Cotoneaster granatensis*, *Cotoneaster integerrimus*, *Cotoneaster nebrodensis*, *Cotoneaster tomentosus*, *Crataegus granatensis*, *Crataegus laciniata*, *Crataegus laevigatus*, *Crataegus monogyna*, *Crataegus orientalis*, *Crataegus transalpina*,



Fig. 3 Bramble (*Rubus ulmifolius*) flower (J.Loidi).



Fig. 4 Wilde rose (*Rosa canina*) flower (J.Loidi).

Euonymus europaeus, *Euonymus verrucosus*, *Hippophae rhamnoides*, *Ligustrum vulgare*, *Paliurus spina-christi*, *Prunus avium*, *Prunus institia*, *Prunus mahaleb*, *Prunus ramburii*, *Prunus spinosa*, *Pyrus elaeagrifolia*, *Pyrus pyraster*, *Malus sylvestris*, *Rhamnus alpinus*, *Rhamnus catharticus*, *Rhamnus intermedia*, *Rhamnus saxatilis*, *Ribes alpinum*, *Ribes uva-crispa*, *Rosa agrestis*, *Rosa canina* agg., *Rosa dumalis*, *Rosa micrantha*, *Rosa montana*, *Rosa obtusifolia*, *Rosa pouzinii*, *Rosa pendulina*, *Rosa rubiginosa*, *Rosa sherardii*, *Rosa sicula*, *Rosa tomentosa*, *Rosa villosa*, *Rosa vosagiaca*, *Rubus bifrons*, *Rubus caesius*, *Rubus canescens*, *Rubus dalmaticus*, *Rubus egregius*, *Rubus elegantispinosus*, *Rubus geertii*, *Rubus geniculatus*, *Rubus grabowskii*, *Rubus lindleianus*, *Rubus macrophyllus*, *Rubus montanus*, *Rubus phyllostachys*, *Rubus polyanthemus*, *Rubus praecox*, *Rubus radula*, *Rubus raduloides*, *Rubus rubercadaver*, *Rubus rufescens*, *Rubus senticosus*, *Rubus steracanthos*, *Rubus ulmifolius*, *Rubus vestitus*, *Rubus wahlenbergii*, *Rubus winteri*, *Sambucus nigra*, *Sorbus aria*, *Syringa vulgaris*, *Viburnum lantana*, *Viburnum opulus*, etc. In the southern section of the area of this shrubland type, from Iberia to the Balkans, some evergreen species appear, such as *Buxus sempervirens*, *Phillyrea latifolia* or *Ruscus aculeatus*, combined with some submediterranean deciduous species: *Acer monspessulanum*, *Ostrya carpinifolia*, or *Quercus pubescens*. These shrublands may be distinguished as a submediterranean variety.

Thorny shrublands find their optimal area in temperate central-western Europe. Northwards, they lose most of the thermophilic species and become impoverished, whereas in continental areas of Europe most Atlantic taxa are missing. In the Mediterranean territories, they are represented by species-poor communities confined to riverbanks and to some mountain areas under a rainy climate, always on deep nutrient-rich soils.

Thorny shrublands are grouped into the class *Rhamno-Prunetea spinosae* (Tüxen, 1952, Arnaiz, 1983, Géhu et al., 1983, 2003, Weber, 1998, Bergmeier, 1990, Janssen, 2016b, Haveman and de Ronde, 2019).

2. Hazel calcareous scrub. A subtype (more-or-less) differentiated from the previous one is the *Corylus avellana* scrub. It comprises relatively stable shrublands dominated by hazel, growing basically on limestones in regions of temperate climate, from the British Isles to Central Europe, Central Italy and northern Spain. It establishes in situations where the shallow soils (crests, steep



Fig. 5 Hedgerow fencing a hay meadow (J.Loidi).

slopes), sometimes helped by strong winds, prevent the development of the forest. The associated species vary across the geographic range of this type, being mostly herbs typical of forests and grasslands. Grazing and browsing, usually by sheep or goats, open up the *Corylus* canopy and introduce more grassland species in the understory, preventing the regeneration of the hazel and other shrubs and trees. Under this management it is produced a kind of parkland in which old hazel individuals form a discontinuous canopy covering a shaded grassland. This is adapted to a pastoral exploitation system combined with the harvesting of the hazel branches and fruits (nuts), important items in the traditional rural economy. Under such management, the conservation of this shrubland type is ensured (Janssen, 2016c).

3. Atlantic bramble shrub. In Atlantic and sub-Atlantic regions of Europe a subtype of shrubland dominated by brambles (*Rubus* sp. pl.) is found in places under a cool microclimate on acidic soils submitted to intermediate moisture conditions. This vegetation includes bramble species-rich formations forming forests edges and extensive scrub in open landscapes, mostly on sandy soils, with a broader distribution in northwestern Europe and submontane areas in Central Europe (Central France-Germany-Bohemia-Poland). They are formed basically by *Rubus* species, many of them endemics such as *Rubus adpersus*, *Rubus amiantinus*, *Rubus ammobiis*, *Rubus bertramii*, *Rubus calvus*, *Rubus contractipes*, *Rubus discors*, *Rubus distractus*, *Rubus divaricatus*, *Rubus drenthicus*, *Rubus flexuosus*, *Rubus frederici*, *Rubus glandithyrus*, *Rubus gratus*, *Rubus integribasis*, *Rubus laciniatus*, *Rubus laevicaulis*, *Rubus lasiandrus*, *Rubus mucronulatus*, *Rubus mycrophyllus*, *Rubus nemoralis*, *Rubus nessensis*, *Rubus passionis*, *Rubus phoenicacanthus*, *Rubus plicatus*, *Rubus pyramidalis*, *Rubus scissus*, *Rubus schlechtendalii*, *Rubus silvaticus*, *Rubus sprengelii*, *Rubus taxandriae*, *Rubus trichanthus*, and *Rubus vigorosus* amongst others. These bramble scrubs are included in the class *Lonicero-Rubetea plicati*, alliance *Lonicero-Rubion silvatici* (Haveman et al., 1999; Weber, 1990, 1997, 2003; Janssen, 2016d; Haveman and de Ronde, 2019).
4. Forest gaps bramble shrub. In the colline and submontane belt (and rarely in the lowlands) of central and western Europe, another type of bramble-shrub is found, formed by low-growing, glandular, forest-dwelling *Rubus* species. This type occupies smaller or larger gaps in the forest-canopy (e.g. tree felling caused by storms) and is confined to humus-rich and not too nutrient-poor soils within the tempered microclimate of mainly broad-leaved forests of the class *Querceto-Fagetea*. Although they might facilitate tree-sapling establishment, there are examples that massive bramble-vegetation hampers the regeneration of the forest canopy. Species composition of these 'silvicolous' bramble-scrubs is yet poorly known, since they are recognized only recently. These 'silvicolous' bramble-shrubs are characterized by *Salix caprea*, *Sambucus racemosa*, and many (mainly only regionally distributed) bramble species, amongst which *Rubus bellardii*, *Rubus foliosus*, *Rubus hirtus*, *Rubus hypomalacus*, *Rubus idaeus*, *Rubus igoratus*, *Rubus iuvenis*, *Rubus loehrii*, *Rubus lusaticus*, *Rubus melamporphyrus*, *Rubus mucronipetalus*, *Rubus negatus*, *Rubus oreades*, *Rubus pallidifolius*, *Rubus pallidus*, *Rubus picearum*, *Rubus rosaceus*, *Rubus rudis*, *Rubus schleicheri*, *Rubus serpens*, *Rubus sulcatus* and *Rubus teretiusculus*. Phytosociologically, these scrubs are assigned to the alliance *Athyrio felicis-feminae-Rubion idaei* Passarge ex Haveman and De Ronde 2014, class *Rhamno-Prunetea spinosae* (Passarge, 1982; Haveman and de Ronde, 2014; Haveman et al., 2017c; Weber, 2003).
5. Steppic central-eastern scrub. There is a steppic low scrub occurring in central-east Europe centered in the Pannonian Basin and reaching Ukraine and Russia. It is a scrub of usually less than 1 m tall, common in the forest-steppe and steppe zones, developing on both shallow soils (leptosols) near rock outcrops and on deep soils (chernozems, kastanozems, phaeozems, cambisols or luvisols). Frequently it forms stands of clonally growing dominant shrubs on relatively mesic sites in relation with the dry grasslands. It also forms forests edges in form of tall scrub or dry woodland. In places with shallow soils it is a permanent natural vegetation type, while in others with deeper soils is a successional stage replacing the dry grassland after abandonment. The most

typical flora is formed by: *Caragana frutex*, *Cotoneaster integerrimus*, *C. melanocarpus*, *Elymus hispidus*, *Festuca rupicola*, *F. valesiaca*, *Fragaria viridis*, *Geranium sanguineum*, *Melica ciliata*, *M. transsilvanica*, *Poa angustifolia*, *Polygonatum odoratum*, *Prunus x eminens*, *Prunus fruticosa*, *Prunus tenella*, *Rosa gallica*, *Rosa pimpinellifolia* (= *R. spinosissima*), *Spiraea chamaedryfolia*, *Spiraea crenata*, *Spiraea media*, etc. These scrubs are gathered into the Alliance *Prunion fruticosae* Tx. 1952 (Tüxen, 1952; Chytrý, 2013; Doniță et al., 2005; Bită-Nicolae, 2016).

6. Western broom legume shrubland. A sixth subtype formed by leafless shrubby legumes (brooms) of the genera *Adenocarpus*, *Cytisus*, *Genista*, *Retama* and occasionally *Ulex*. These plants have photosynthetic stems and are very active in fixing atmospheric nitrogen. This evergreen vegetation, from 0.6 up to 3 m high, is the first seral stage and mantel of temperate forests of *Quercus pyrenaica*, *Q. robur*, *Q. petraea*, *Fagus sylvatica* being also represented in the domains of *Q. rotundifolia* and *Q. suber*, in part of the Mediterranean region, particularly in western Iberia (Fig. 6). The highest diversity and representation of these mantel shrublands are in W and NW Iberia, although there is an important penetration towards central and NW Europe by means of the *Cytisus scoparius* communities. In the area of its optimal development and diversity, they are mostly found on siliceous nutrient-poor and low pH substrates, replacing the thorny mantel of the previous subtypes that are more exigent in moisture and in soil nutrients. Due to its particular morphology, this scrub receives several names in Spain: piornal, escobonal or retamal, depending the geographic area and the dominance of one or other species. This vegetation is not so useful for the farmers to build efficient hedges because it is a non-thorny vegetation. For that reason it is very rare to find hedgerows made of them. However, it is very frequent to find it in form of scattered individuals covering extensive areas under agro-pastoral management in a pattern resulting from the specific and ancient model of human management. It is notorious to remark that shepherds know empirically that these plants “enrich” the soils and promote its fertility. For that they avoid a complete deletion of these communities in the grazing areas, even conserve a regularly scattered pattern of these retamoid individuals intermingled with the heathland or the grassland. Often the green branches and seeds of these species can be used as an additional fodder for the livestock in periods of shortage of available pasture. This shrubby broom-like vegetation easily catches fire and suffers from frequent burning in the areas where it is abundant. Fires, if repeated with high frequency, lead to the establishment of heathland, which is accompanied by soil degradation. A regime of frequent fires has been induced historically, to most of the present day heaths of western Iberia and Europe. If fires are not so frequent, broom shrublands, are resilient and recover in a few years without fire from the surviving roots or from seed, thanks to the high germination capacity of their seeds. Fire frequency determines whether heathland or shrubland is the dominant plant community in the landscape. The plant species of this subtype are: *Adenocarpus anisochilus*, *Adenocarpus argyrophyllus*, *Adenocarpus aureus* subsp. *aureus*, *Adenocarpus complicatus* (subsp. *brutius*, subsp. *complicatus*), *Adenocarpus decorticans*, *Adenocarpus hispanicus* (subsp. *gredensis*, subsp. *hispanicus*, subsp. *neilense*), *Adenocarpus lainzii*, *Adenocarpus telonensis*, *Cytisus cantabricus*, *Cytisus commutatus*, *Cytisus ingramii*, *Cytisus scoparius* (subsp. *scoparius*, subsp. *bourgaei*), *Cytisus grandiflorus* subsp. *cabezudo*, *Cytisus multiflorus*, *Cytisus striatus* (subsp. *eriocarpus*, subsp. *striatus*), *Echinopartum ibericum* subsp. *ibericum*, *Genista cinarescens*, *Genista cinerea* subsp. *speciosa*, *Genista florida* (subsp. *florida*—Fig. 7 and subsp. *polygaliphylla*), *Genista obtusiramea*, *Genista polyanthos*, *Orobancha rapum-genistae*, *Retama monosperma*, *Retama sphaerocarpa*, *Ulex europaeus* (subsp. *europaeus*, subsp. *latebracteatus*). The core of the broom genistoid shrublands is the Iberian Peninsula, from where it expands northwards and eastwards over large areas of western and central Europe until Denmark, Italy and Croatia. In this expansion, most of the species remain in Iberia and only *Cytisus scoparius*, *Ulex europaeus* and *Orobancha rapum-genistae* are broadly distributed on sandy or loamy soils. These shrublands are framed into the class *Cytisetea scopario-striati* widespread across



Fig. 6 Broom shrubland in central Spain (F. Fernández-González).



Fig. 7 *Genista florida* in central Spain (F. Fernández-González).

western Europe (Rivas-Martínez, 1974; Gavilán et al., 2011; Pinto-Gomes et al., 2012; De Foucault et al., 2013; Janssen, 2016a; Haveman et al., 2017b).

7. Atlantic coastal dune buckthorn shrub. Along the coast of north-western Europe, including the British Isles, France, Belgium, The Netherlands and Denmark, Sea-buckthorn forms pioneer shrublands on calcareous dune-sand, following *Ammophila* and dune grassland communities in the succession (Fig. 8). Both species can inhabit moist dune slacks as well as dry dune complexes. Like the species in the retamoid scrubs of the previous type, Sea-buckthorn is able to fixate atmospheric nitrogen, stimulating the soil development in this pristine environment. Natural soil acidification through leaching and infestation with nematodes



Fig. 8 *Hippophae rhamnoides* shrubland and grassland of *Ammophila* on fixed dunes at Baltrum island, northern Germany, North Sea shore (J.Loidi).

eventually causes the dying-off of the scrubs, and depending on the soil development, higher, spiny shrublands (subtype 1), or grasslands replace the Sea-buckthorn shrubs. In many dune areas, encroachment with Sea-buckthorn is considered a problem, since the expanding, species poor shrubs threaten to overgrow large areas of species rich dune grasslands. This shrub-encroachment has several causes, amongst them a decrease of natural (geomorphological) dynamics and the decrease of grazing. The serious decline of rabbits in large parts of the dune areas in north-western Europe caused by several subsequent diseases was followed by a large scale increase of dune scrubs with Sea-buckthorn. The most important species in this coastal scrub type are *Hippophae rhamnoides* subsp. *rhamnoides* and *Salix repens* and (mainly subsp. *arenaria*); these species are accompanied by *Ligustrum vulgare*, *Rosa rubiginosa*, *Rosa spinosissima*, and *Sambucus nigra*. Sea-buckthorn shrubs are comprised in the class *Salicetea arenariae* Weber, 1999 (Tüxen, 1952; Géhu and Géhu-Franck, 1983; Weber, 1999; Haveman et al. 2017).

8. Juniper shrubland. A last subtype can be recognized in a broad region encompassing temperate and submediterranean Europe: it is the shrubland dominated by *Juniperus communis*, widespread in old pastoral landscapes and dependent on extensive grazing. These juniper populations distribute in scattered populations forming patchy mosaics with a grassland or heathland matrix. They are distributed on low- to mid-elevation areas from Scandinavia to Italy and from France to the Baltic Countries (Janssen 2016d). Substrates can be base-rich, in which case *Juniperus* populations coexist with the *Festuco-Brometea* communities, or on siliceous acidic bedrock, usually sandy, in which case the accompanying community will be one of the *Calluno-Ulicetea* class. On neutral and calcareous soils the main associate shrubs are *Cornus sanguinea*, *Crataegus monogyna*, *Prunus spinosa*, *Rosa canina* and several *Rubus* species. The high dependence of this shrubland type with the extensive grazing makes its conservation particularly difficult in the modern times; if abandoned and neglected, the succession will lead to woodland (Barkman, 1985; Cooper et al., 2012; Janssen, 2016e; Rejmánek and Rosén, 1988).

Fauna

The already mentioned function of shrubland for fauna is revealed by several animal species which are heavily dependent on this habitat. Forest edges and hedgerows provide shelter and food for many small mammals. Specific shrubland mammals are Garden Dormouse (*Eliomys quercinus*), found in forest edges on good soils, and the related Hazel Dormouse (*Muscardinus avellanarius*), which builds nests in *Rubus* scrub. Many common bird species breed in shrubland, for example Bluethroat (*Luscinia svecica*), Lesser Whitethroat (*Sylvia curruca*), Willow Warbler (*Phylloscopus trochilus*), Hedge Sparrow (*Prunella modularis*), Whitethroat (*Sylvia communis*), Grasshopper Warbler (*Locustella naevia*), Red Backed Shrike (*Lanius collurio*) and Nightingale (*Luscinia megarhynchos*). For amphibians, shrubland is a place to hibernate, but European Tree frog (*Hyla arborea*) and the Stripeless Tree Frog (*Hyla meridionalis*) mainly live in shrubland in the vicinity of ponds and pools. Many insects use forest edges and hedges for migration and foraging. Some of the typical butterfly species are Purple Emperor (*Apatura iris*), White Admiral (*Ladoga camilla*), Southern White Admiral (*Ladoga reducta*), Poplar Admiral (*Limenitis populi*), Camberwell Beauty (*Nymphalis antiopa*), Brown Hairstreak (*Thecla betulae*), Purple Hairstreak (*Quercusia quercus*), Sloe Hairstreak (*Nordmannia acaciae*), Ilex Hairstreak (*Nordmannia ilicis*) and Comma (*Polygonia c-album*).

Natural vs. Anthropogenic Communities. Threats

In a natural ecosystem grazing by herds may result in a patchy landscape in which shrubland occurs in small patches and in and along forests, scattered through the landscape. In Europe such landscapes may have existed thousands of years ago, but for many centuries the landscape patterns are largely the result of human land-use. This is certainly the case for shrublands, which—besides for small stands in waterlogged or extreme dry, rocky or steep conditions—are secondary vegetation types. Hedgerows are the result of long-term human management, and in their form sometimes have a medieval or even older origin. The optimum of this shrubland in western Europe is assumed to have been reached in the 19th century, when large parts of the landscape were heathlands, and forests occupied relatively small areas. In those times the landscape consisted of many small fields owned by different farmers who used shrubs for fencing. With the introduction of modern technology in the exploitation procedures of the farmland, the abundance of thorny hedgerows, particularly of subtypes 1, 3 and 4 described above, has diminished dramatically all over Europe during the 20th century, especially after 1960 in the Atlantic European landscape. This was realized amongst other reasons by removal of hedges. It has been demonstrated that the length of hedge structures declined drastically in several regions during the second half of the 20th century (see for example Petit et al., 2003). This process started earlier though, when barbed wire was introduced for fencing the property limits and many farmers decided to install them replacing the hedges. The advantages were evident, a substantial surface of land was freed to be used as meadow or crop land. This led to a massive replacement of thorny hedgerows by barbed wire fences. Another element in this retreat history has been the concentration of plots belonging to the same owner, in order to get to a much larger average field size for farmland, more suitable for larger machines. This led to the disappearance of many limits between plots, simplifying the reticular web they formed in the landscape and homogenizing it.

With the loss of hedgerows, the habitat for many fauna species disappeared as well, for example the nesting habitat for many farmland birds. Besides the loss of shrubland structures, also a decline in quality occurred, especially in the agricultural landscape. Eutrophication resulted in dominance of a few, robust plant species in the herb-layer, while the use of herbicides and fertilizers lead to a strong decline in insects and other animals. Also more natural stands of shrubland have declined during the last century, partly

due to transformation of semi-natural areas to agricultural land, and partly by the construction of plantations of trees. On the other hand, natural stands of shrubland have increased a lot in the last decades, mainly in continental Europe, due to abandonment of traditional management of grasslands. In fact, in these areas the natural succession towards shrubland and forest is a severe threat to biodiversity. Summarizing, the loss of a big part of the hedgerows has had a negative impact on the function and diversity of the bocage landscape. More recently, in large parts of western Europe the floristic composition of undergrowth of the remaining shrublands changed and impoverished due to hypertrophication. In this process, many characteristic woodland-remnant species are replaced by nitrophillous species, like *Galium aparine* and *Urtica dioica*, and it is reported that even narrow-endemic *Rubus* species fall prey to expanding *Urtica dioica*.

Symmetrical to the retreat of these hedgerows in the farmlands, is its expansion in plots of abandoned land, formerly field or grassland, where it develops rapidly (Fig. 9). This phenomenon is due to the generalized rural abandonment of the peasant population, which release many areas from the land exploitation. In these cases, secondary succession triggers and this thorny shrubland encroaches the area as the previous stage before the forest. A similar story can be told about the juniper shrubland of subtype 8, in which a decreasing tendency is observed in most of the sites where it is present (Janssen, 2016e).

Conservation, Restoration and Sustainable Management

Being a temporal succession-stage in a cultural or semi-natural landscape, shrublands need some type of management for sustainable survival. Ceasing of management leads to succession, in this case the encroachment of trees and higher shrubs, leading towards the development of forest communities. The recovery of the thorny hedges is difficult in the conditions reigning in the current industrial and post-industrial society. This means that some areas should be intentionally preserved from the loss of this vegetation mosaic in regards to the ecosystem services they provide. Restoration can be spontaneous as many of the plants forming these hedges are very dynamic, particularly some *Rubus*, *Crataegus* and *Prunus* species, which are efficiently dispersed by birds and easily germinate in degraded areas facilitating their colonization (Fig. 10). The most common management practices to preserve this vegetation are (extensive) grazing, selective or cyclic cutting of trees, and burning. Also removal of non-native species may be needed in some places. Replanting and even re-establishment of hedgerows is an important restoration practice in some countries, especially in the United Kingdom. An important aspect of restoration is the use of autochthonous plant material for the involved shrubs and trees.

In the case of the hazel dominated shrublands of subtype 2, their cultural forms grazed by sheep or goats suffer from a general abandonment while the primary stands maintain their situation stable.

The broom like shrublands of subtype 6 present the most progressing situation as they are covering large areas that have been abandoned from livestock in Iberia. The occurrence of fires, if not too frequent, favors the maintenance of this vegetation.

These types of shrublands are not included in Annex 1 of the Habitat Directive of the European Union (European Commission, 2013), thus they have not usually been taken into account for any protection policy. In spite of this, the protection and increase of this vegetation types are recommended as they favor ecosystem structural and functional complexity and the soil maintenance.



Fig. 9 Shrubland growing in a patch after abandonment (J.Loidi).



Fig. 10 Thorny shrubland in autumn (J.Loidi).

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Grasslands of Western Europe

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This article was solicited and edited by Jürgen Dengler and Péter Török on behalf of the Eurasian Dry Grassland Group (EDGG).

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Abstract

In Western Europe forests are the natural climax vegetation and only about 14% of the total area are grasslands. The largest part of Western European grasslands below the alpine zone are therefore secondary grasslands, originating from human land use. The floristic composition of the region's grasslands was largely shaped by repeated glaciations during the Pleistocene and is today mainly composed of perennial herb species. Grasslands of Western Europe can be placed in 18 phytosociological classes, and joined into nine broadly defined grassland types. These grasslands harbor a rich diversity of different taxa, including many endemic species. Moreover, seminatural grasslands of the region were repeatedly highlighted for their high vascular plant species densities. However, natural and seminatural grasslands are among the most negatively human-impacted terrestrial habitats in Western Europe with a strong long-term declining trend in habitat extent and integrity as well as species diversity and abundance since the industrial and agricultural revolutions but especially from the second half of the 20th century onwards. This resulted in a high proportion of threatened grassland types and species. Major direct drivers negatively affecting grasslands across the region were the large-scale conversion of seminatural grasslands to crops, the expansion of urban and industrial areas, the intensification of seminatural grassland to more productive meadows and pastures as well as the abandonment of traditional land-use regimes. Substantial subsidies for increasing agricultural productivity have greatly worsened such damage. A rethink and the development of appropriate tools to reverse this trend are urgently needed. Recently, various conservation and restoration efforts have been undertaken to maintain, promote and restore grassland extent and diversity.

Delimitation and Physiogeography of the Region

The Western Europe region, as defined here, encompasses nine entire countries (plus the Channel Islands and the Isle of man) as well as temperate parts of France, Italy, Portugal and Spain. The countries included vary greatly in land area, population density and grassland extent. The total land area covered here is 1,607,947 km² (Table 1). The region extends from approximately 41 to 60 degrees northern latitude, from 10 degrees western to 17 degrees eastern longitude and from below sea level in coastal areas of the Netherlands to 4810 m a.s.l. in the Alps.

The climate is mainly temperate to warm temperate with warm summers and without extensive drought, though recent years have seen more climatic extremes and uncertainty. In the Alps, the Pyrenees and low mountain ranges such as the Vosges and the Bavarian forest regions a sub-montane climate can be found (Peel et al., 2007; Klötzli et al., 2010).

Repeated glaciation during the Pleistocene involved the relocation and deposition of glacial and fluvio-glacial sediments and loess. Because of this, Western Europe is dominated by rather young soil types which developed by the dominant soil-forming processes typical for humid temperate climates, namely humus formation, leaching, weathering, clay migration, clay destruction and podsolization on well-drained parent materials, as well as gley and peat formation in poorly-drained areas. The most

Table 1 Included countries of the Western European region and basic statistics on total and grassland area (FAO, 2019) and population size (UN, 2019).

Country	Total area (km ²)	Grassland area (km ²)	Grassland fraction of total area (%)	Grassland fraction of agricultural area (%)	Population (million)	Population density (persons/km ²)
Austria	83,879	13,004	15.5	47.1	8.68	105.3
Belgium	30,530	2,826	9.3	35.4	11.29	372.8
Channel Islands	198	17	8.5	56.4	0.17	834.9
France (only temperate part)	531,418	46,846	8.6	32.6	63.53	117.7
Germany	357,580	34,629	9.7	28.2	81.79	234.6
Ireland	70,280	24,167	34.4	89.9	4.65	67.5
Isle of Man	572	172	30.1	41.0	0.08	146.0
Italy (only temperate part)	125,000	14,757	11.8	28.8	25.00	206.0
Liechtenstein	160	32	19.9	58.1	0.04	234.2
Luxembourg	2,590	363	14.0	51.4	0.57	218.8
Netherlands	41,540	6,493	15.6	40.6	16.94	502.3
Portugal (only temperate part)	5,300	1,267	23.9	51.9	0.60	113.0
Spain (only temperate part)	74,000	19,798	26.8	35.2	6.83	93.6
Switzerland	41,290	12,449	30.1	72.0	8.30	210.0
United Kingdom	243,610	51,114	21.0	65.0	65.86	272.2
<i>Western Europe total</i>	<i>1,607,947</i>	<i>227,934</i>	<i>14.2</i>	<i>42.8</i>	<i>294.31</i>	<i>189.8</i>

Values for "Grassland fraction of agricultural area (%)" is the fraction of permanent pastures and meadows of the agricultural area. Area and population values for "France (only temperate part)," "Italy (only temperate part)," "Portugal (only temperate part)" and "Spain (only temperate part)" are estimates, and assuming that grasslands and human population are similarly distributed over the whole country. Values for grassland area are based on FAO MODIS (FAO, 2019) and therefore deviate from Dengler et al. (2020) who used FAO CCI_LC (FAO, 2019).

widespread soil type in Western Europe is therefore Cambisol. However, also leached soils like Albeluvisols and Podzols, ground-water saturated Gleysols, as well as periodically flooded deposit soils like Fluvisols in alluvial or marine areas occur (Jones et al., 2005).

Biogeography, Flora and Fauna

Within the Palaearctic realm, Western Europe comprises the Atlantic and Central European floristic regions (Frey and Lösch, 2004). The biogeography of the region was largely shaped by repeated glaciations during the Pleistocene. These cyclic changes between cold and warm periods favored two completely different plant and animal groups: while populations of species of the first group expanded during warm and retreated during cold periods, the second group acted conversely (Taberlet and Cheddadi, 2002; Varga and Schmitt, 2008). In particular low-growing species which overwinter on or below the soil surface were better adapted to survive these harsh and fluctuating climatic conditions than woody species. Because of this 51% of the 4500 vascular plant species of Central Europe and the Alps are perennial herbs with above-ground buds (chamaephytes, hemicryptophytes), 29.3% are herbs without above-ground parts in winter (geophytes, therophytes) and only a very small proportion are woody (15%) or aquatic species (4.6%) (Leuschner and Ellenberg, 2010). During the cold periods, many organisms survived in Southern European mountain ranges, which provided different topography and microclimates (Bennett et al., 1991; Taberlet and Cheddadi, 2002). In addition, numerous grassland plants expanded after glacier recession from Central Asian and Southeastern European steppes and were able to disperse across Western Europe because of the lack of geographical barriers (Pärtel, 2002; Ewald, 2003) or were intentionally or unintentionally introduced by humans (Leuschner and Ellenberg, 2010).

Origin of the Grasslands

The temperate to warm and humid climate in Western Europe allows forest development. Without humans, different forest types would cover most of the region as potential natural climax vegetation and natural grasslands below the timberline would constitute only about 2% (Bohn et al., 2004). Therefore, the largest part of Western European grasslands below the alpine zone are secondary grasslands, originating from human timber harvesting, forest burning to establish arable fields or grazing of woodlands (Török and Dengler, 2018). Secondary grasslands include both seminatural grasslands and anthropogenic grasslands, the latter also called improved or intensively used grasslands. Azonal and extrazonal grasslands are natural grasslands in areas where forest growth is limited by particular soil or topographic conditions, i.e. salt marshes and dunes, as well as rocky slopes, sandy skeletal soils and naturally disturbed sites (Dengler and Tischew, 2018). In this chapter the focus is on both seminatural secondary and natural azonal and extrazonal grasslands, excluding anthropogenically improved grasslands and wetlands.

Typology of the Communities

Grasslands of Western Europe below can be placed in 18 phytosociological classes (Mucina et al., 2016), and joined into nine broadly defined grassland types (Fig. 1), as defined in the GrassPlot database (Dengler et al., 2018). Table 2 summarizes the relationships of these vegetation types and phytosociological units with the habitat types of the European Red List (Janssen et al., 2016). In the following section, the described grassland types are arranged according to the typology provided by Dengler et al. (2014).

Primary or Natural Grasslands

Alpine grasslands

Grasslands above the timberline in western European mountains are natural zonal grasslands in those areas which are too cold to support forest growth (Fig. 1A). These alpine grasslands are not treated in this chapter.

Azonal and extraazonal grasslands

Natural grasslands occurring locally at small scale within the forest biome on soils that are too wet, too dry, too saline, too shallow and too instable to allow tree growth.

- a. *Rocky grasslands*. Natural grasslands on shallow rocky substrates of the order *Stipo pulcherrimae-Festucetalia pallentis* (class *Festuco-Brometea*) are regularly found at small scale in the both lower mountain ranges of Central Europe as well as in valleys of the Alps (France, Austria, Germany and Switzerland), although they are quite common in Central-eastern and Eastern Europe. In the south-western Alps, Apennines, Cevennes, Pyrenees and Cantabrian mountains, the rocky grasslands belong to the class *Festuco-hystrix-Ononidetalia striatae*. The pioneer vegetation on shallow soils on rocky outcrops is included in the class *Sedo-Scleranthetea*, and is rich in succulents, therophytes and cryptogams (Fig. 1B,C).
- b. *Inland dunes and sandy dry grasslands*. Natural or seminatural dry grasslands on sandy soils are sparsely distributed in Western Europe (Fig. 1D). They are included in the class *Koelerio-Corynephoretea canescentis*, developed mostly as tussock grasslands on inland sand dunes (order *Corynephoretalia canescentis*), although fescue sandy steppes of the order *Festucetalia vaginatae* are also locally present in the Pannonian part of Austria. Also local is the presence of the alliance *Hieracio castellani-Plantaginion radicatae* (class *Festucetalia indigestae*) on south-facing siliceous gravel slopes of the Cantabrian range in Spain.
- c. *Saline communities*. Grass- and herb-dominated communities in coastal areas of Western Europe belong to the class *Juncetea maritimi* (Fig. 1E). Intermixed with these natural perennial grasslands and rushes, we can find pioneer vegetation of annual succulent halophytes included in the class *Thero-Salicornietea*. These pioneer succulents are also occurring in inland salt marshes, which are quite scarce in Western Europe. Even more local in Western Europe are the natural continental inland salt steppes (class *Festuco-Puccinellietea*), which are only present in a small area of Austrian Pannonia.
- d. *Coastal dunes*. Atlantic coastal dunes of Western Europe are colonized by vegetation types of the classes *Ammophiletea*, which includes tall-grass perennial swards on mobile dunes (Fig. 1F), and *Helichryso-Crucianelletea maritimae* on stabilized gray dunes. Traditional land use in this system, especially of gray dunes in the Netherlands and Germany and machairs of Ireland and the Scottish isles, is extensive grazing.

Secondary Grasslands

Xeric grasslands

These dry grasslands occur in the xeric zone of the hydrological gradient, and can occur both as secondary and natural grasslands. They belong to the class *Festuco-Brometea*. In west and south-west Europe, these grasslands are mostly placed to the orders *Artemisio albae-Brometalia erecti* and *Brachypodietalia phoenicoidis*. The order *Festucetalia valesiacae*, which is zonal in the steppe and forest-steppe zone of Europe, occurs extraazonally in Austria, eastern France, Germany, Italy and Switzerland. It is mainly restricted to south-facing slopes in xerothermic mountain valleys (Fig. 1G). Only in the Pannonian area of northeast Austria they might be considered zonal grasslands. In north-eastern Italy the dry steppe grasslands of the order *Scorzonetalia villosae*, which are widespread in SE Europe, extend to their north-western distribution border.

Meso-xeric grasslands

Dry grasslands growing on meso-xeric soils. Most meso-xeric calcareous grasslands of Western Europe belong to the order *Brachypodietalia pinnati*, in the broad class *Festuco-Brometea*. These seminatural grasslands are maintained by extensive grazing, but also by mowing or sometimes burning (Fig. 1H).

Mesic grasslands

Meadows and pastures on humid but well-drained soils. The most widespread is the class *Molinio-Arrhenatheretea*, which includes seminatural grasslands on nutrient-rich soils maintained by mowing and/or grazing. Two orders correspond to mesic grasslands: *Arrhenatheretalia elatioris*, on low- to mid-elevations (Fig. 1I), and *Poo alpinae-Trisetetalia*, on mountain ranges. This vegetation type also includes most secondary mat-grass swards included in the class *Nardetea strictae*, typically on nutrient-poor soils, and optimally developed in temperate Atlantic areas and the Alps. Finally, also included in this group of mesic grasslands are the upper



Fig. 1 Impressions of grassland vegetation types occurring in Western Europe: (A) alpine grassland in North Italy, (B) rocky grassland in South Germany, (C) rocky grassland in Switzerland, (D) sandy grassland in South Germany, (E) saline grassland in North Germany, (F) coastal dune grassland in France, (G) xeric grassland in Switzerland, (H) meso-xeric grassland in Switzerland, (I) mesic grassland in South Germany, (J) wet grassland in South Germany. Photos: Jürgen Dengler.

Table 2 Grassland types and their relationships to habitats of the European Red List (RL; Janssen et al., 2016) and phytosociological units (Mucina et al., 2016).

Grassland type	Habitat type in the European Red List	Phytosociological unit	RL code	RL status
Alpine grasslands	Iberian oromediterranean siliceous dry grassland	<i>Festucetalia indigestae</i> (<i>Festuco hystricis-Ononidetea striatae</i>)	E1.5a	NT
	Vegetated snow patch	<i>Salicetea herbaceae</i>	E4.1	VU
	Boreal and arctic acidophilous alpine grassland (Scotland)	<i>Juncetea trifidi</i> (p.p.)	E4.3a	LC
	Temperate acidophilous alpine grasslands (alpine communities)	<i>Juncetea trifidi</i> (p.p.)	E4.3b	LC
	Arctic-alpine calcareous grasslands (alpine communities)	<i>Carici rupestris-Kobresietea bellardii</i> , <i>Seslerietalia caeruleae</i> (<i>Elyno-Seslerietea</i>) (p.p.)	E4.4a	LC
Rocky grasslands	Alpine and subalpine calcareous grassland of the Balkan and Apennines (alpine communities)	<i>Seslerion apenninae</i> (<i>Elyno-Seslerietea</i>) (p.p.)	E4.4.b	LC
	Cryptogam- and annual-dominated vegetation on siliceous rock outcrops	<i>Sedo-Scleranthetalia</i> (<i>Sedo-Scleranthetea</i>)	E1.1b	VU
	Cryptogam- and annual-dominated vegetation on calcareous and ultramafic rock outcrops	<i>Alysso-Sedetalia</i> (<i>Sedo-Scleranthetea</i>)	E1.1d	VU
	Perennial rocky grasslands of Central Europe and the Carpathians	<i>Stipo pulcherrimae-Festucetalia pallentis</i> (<i>Festuco-Brometea</i>)	E1.1g	LC
	Iberian oromediterranean basiphilous dry grassland	<i>Festuco hystricis-Ononidetea striatae</i> (p.p.)	E1.5b	LC
Inland dunes and sandy dry grasslands	Submediterranean xeric open grassland of skeletal calcareous and ultramafic soils	<i>Festuco hystricis-Ononidetea striatae</i> (p.p.)	E1.1e	VU
	Pannonian and Pontic Sandy steppe	<i>Festucetalia vaginatae</i> (<i>Koelerio-Corynepherea</i>)	E1.1a	CR
	Oceanic to subcontinental inland sand grasslands on dry acid and neutral soils	<i>Corynepherea canescens</i> (<i>Koelerio-Corynepherea</i>) (p.p.); <i>Sedo-Scleranthetea</i> (p.p.)	E1.9a	EN
	Inland sand drift and dunes with siliceous grasslands	<i>Corynepherea canescens</i> (<i>Koelerio-Corynepherea</i>) (p.p.)	E1.9b	EN
	Mediterranean to Atlantic open, dry, acid and neutral grasslands	<i>Helianthemetea guttati</i>	E1.A	NT
Saline communities	Atlantic coastal salt marsh	<i>Juncetea maritimi</i> (incl. <i>Saginetea maritima</i>)	A2.5c	VU
	Continental inland salt steppe	<i>Festuco-Puccinellietea</i>	E6.2	VU
Coastal dunes	Temperate inland salt marsh	<i>Juncetea maritimi</i> (incl. <i>Saginetea maritima</i>)	E6.3	EN
	Atlantic and Baltic shifting coastal dune	<i>Ammophiletea</i>	B1.3a	NT
Xeric grasslands	Atlantic and Baltic coastal dune grasslands (gray dune)	<i>Helichryso-Crucianelletea maritima</i>	B1.4a	VU
	Machair	<i>Ammophiletea</i> , <i>Koelerio-Corynepherea</i> (p.p.)	B1.9	LC
	Perennial rocky calcareous grasslands of subatlantic-submediterranean Europe	<i>Artemisio albae-Brometalia erecti</i> (<i>Festuco-Brometea</i>)	E1.1i	VU
Meso-xeric grasslands	Dry steppic, submediterranean pasture of South-Eastern Europe	<i>Scorzonetalia villosae</i> (<i>Festuco-Brometea</i>) (p.p.)	E.1.1j	VU
	Continental dry steppe	<i>Festucetalia valesiacae</i> (<i>Festuco-Brometea</i>)	E1.2b	NT
	Semi-dry perennial calcareous grasslands	<i>Brachypodietalia pinnati</i> (<i>Festuco-Brometea</i>)	E1.2a	VU
Mesic grasslands	Mesic permanent pastures of lowlands and mountains	<i>Arrhenatheretalia elatioris</i> (<i>Molinio-Arrhenatheretea</i>) (p.p.)	E2.1	VU
	Low and medium altitude hay meadows	<i>Arrhenatheretalia</i> (<i>Molinio-Arrhenatheretea</i>) <i>elatioris</i> (p.p.)	E2.2	VU
	Mountain hay meadows	<i>Poa alpinae-Trisetetalia</i> (<i>Molinio-Arrhenatheretea</i>)	E2.3	VU
	Lowland to submontane, dry to mesic <i>Nardus</i> grasslands	<i>Nardetea strictae</i> (p.max.p.)	E1.7	VU
	Temperate acidophilous alpine grasslands (subalpine communities)	<i>Juncetea trifidi</i> (p.p.)	E4.3b	LC
	Arctic-alpine calcareous grasslands (subalpine communities)	<i>Seslerietalia caeruleae</i> (<i>Elyno-Seslerietea</i>) (p.p.)	E4.4a	LC
	Alpine and subalpine calcareous grassland of the Balkan and Apennines (subalpine communities)	<i>Seslerion apenninae</i> (<i>Elyno-Seslerietea</i>) (p.p.)	E4.4.b	LC
	Moist or wet mesotrophic to eutrophic hay meadows	<i>Molinietalia caeruleae</i> (<i>Molinio-Arrhenatheretea</i>) (p.p.)	E3.4a	EN
	Moist or wet mesotrophic to eutrophic pastures	<i>Molinietalia caeruleae</i> (<i>Molinio-Arrhenatheretea</i>) (p.p.)	E3.4b	EN
	Temperate and boreal moist or wet oligotrophic grasslands	<i>Molinietalia caeruleae</i> (<i>Molinio-Arrhenatheretea</i>), <i>Nardo-Juncion squarrosi</i> (<i>Nardetea strictae</i>)	E3.5	EN
Wet grasslands	Mediterranean tall humid inland grassland	<i>Holoschoenetalia</i> (<i>Molinio-Arrhenatheretea</i>) (p.p.)	E3.1a	LC
	Mediterranean short moist grassland of lowlands	<i>Holoschoenetalia</i> (<i>Molinio-Arrhenatheretea</i>) (p.p.)	E3.2a	LC
	Submediterranean moist meadow	<i>Trifolio-Hordeetalia</i> (<i>Molinio-Arrhenatheretea</i>)	E3.3	LC

CR, Critically endangered; EN, Endangered; LC, Least concern; NT, Near threatened; VU, Vulnerable.

montane and subalpine occurrences of the high mountain classes *Juncetea trifidi* on acidic soils and *Elyno-Seslerietea* on calcareous soils, which comprise natural grasslands in the alpine zone.

Wet grasslands

Temporarily wet and floodplain meadows. Wet meadows and rushes of the order *Molinietalia caeruleae* (class *Molinio-Arrhenatheretea*) are frequent in Western Europe (Fig. 1J), but this grassland type also includes hygrophilous oligotrophic meadows on peaty soils of the alliance *Nardo-juncion squarrosi* (class *Nardetea strictae*). Submediterranean amphiadriatic wet meadows of the order *Trifolio-Hordeetalia*, are widespread in the Balkans, but also occur in the Apennines, while Mediterranean humid grasslands of *Holoschoenetalia* are present in the submediterranean areas of Spain and France. These mainly seminatural grasslands are maintained by grazing or mowing.

Ecology and Biodiversity Patterns

Grasslands cover about 14% of Western Europe (Table 1). Natural grasslands below the timberline would constitute less than 2% of the potential natural vegetation (Bohn et al., 2004). However, grasslands are very important for the biodiversity of many taxonomic groups, such as butterflies (WallisDeVries and van Swaay, 2009), spiders (Polchaninova et al., 2018), grasshoppers (Detzel, 1998), reptiles (Laufer et al., 2007), birds (Nagy, 2009), vascular plants, bryophytes and lichens (Visconti et al., 2018).

European grasslands harbor 18.1% of the 6200 European vascular plant endemics and particularly Western European grasslands host a relatively high proportion of range-restricted species, with a higher proportion of basiphytic endemics (Hobohm and Bruchmann, 2009). According to Grime (1973), European grassland communities on acidic soils are generally characterized by lower species numbers than those on calcareous soils. Ewald (2003) explains this by the theory that in Southwest Asia and Southeast Europe extensive steppe areas existed on calcareous soils. In the course of the species formation process during evolution, numerous plant species have adapted to these conditions. These species were able to spread according to Pärtel (2002) and migrate to Europe via the “renewed” areas with calcareous soils during the Pleistocene. For this reason, according to Ewald (2003), basiphytes now account for a much larger share of the total species inventory in Europe than acidophytes.

Seminatural grasslands of Europe have been highlighted as global record holders in small-scale vascular plant diversity for areas larger than 100 m² (Wilson et al., 2012). In Western Europe, the maximum richness values are not far from the global records, and for the 10 cm² size, the global record is located in Western Europe, specifically in Navarre (Spain), in a Pyrenean valley, with 19 vascular plant species (Table 3). Particularly meso-xeric grasslands are the richest in vascular plants for all area sizes regarding both maximum values and mean values (data extracted from the GrassPlot database; Dengler et al., 2018).

Similar patterns can be observed for bryophytes, with maximum richness values in meso-xeric grasslands, although mean values are distributed among several grassland types: the highest means are once again for meso-xeric grasslands, except for the sizes 10 m², where wet grasslands have the highest values (6.6 ± 4.0), and for 0.1 m² in rocky grasslands with a mean of $2.9 (\pm 2.9)$. Diversity patterns change completely when considering lichens: the highest species densities occur in sandy dry grasslands except for 100 m², where a meso-xeric grassland from Brandenburg (Germany) holds the Western European record, with 31 species. Boch et al. (2016a) reported an outstanding value of 36 lichen species on 16 m² in a calcareous grassland in Germany (Baden-Württemberg; see dataset Boch et al., 2016b). As regards mean values, sandy grasslands are also the richest, except for the 1 and 100 m² large areas, where the richest are rocky grasslands.

Threats

Grasslands of Western Europe are among the most negatively human-impacted terrestrial habitats, which has led to a strong long-term declining trend in habitat extend and intactness as well as species diversity and abundance since the second half of the 20th century (Visconti et al., 2018). Habitat destruction and degradation by the conversion of grasslands to built-up areas and arable

Table 3 Western European maxima of vascular plant species richness per area (shoot presence; Dengler et al., 2018).

Area (m ²)	Max. species number Western Europe	Vegetation type	Location	Max. species number Europe	Max. species number global
0.0001	9	meso-xeric	ES (Navarre)	11	11
0.001	19	meso-xeric	ES (Navarre)	19	19
0.01	23	meso-xeric	ES (Navarre)	25	25
0.1	34	meso-xeric	ES (Navarre) DE (Bavaria)	43	43
1	53	meso-xeric	DE (Bavaria)	82	89
10	82	meso-xeric	ES (Navarre)	106	106
100	110	meso-xeric	(IT) Apennines	133	233

fields (e.g. to grow crops for biogas production), as well as land-use intensification and abandonment were considered being the major past and current drivers of grassland threat in Western Europe (Visconti et al., 2018; Dengler et al., 2020). Apart from those which occur in very dry situations, seminatural grasslands depend not only on particular combinations of climate and soil but also on repeated defoliation through herbivory by stock and wild animals and/or by mowing for crops of herbage. Any process which frustrates such relationships poses a threat and two main dangers impact strongly and widely on European grasslands at this time (Janssen et al., 2016; Dengler and Tischew, 2018; Török and Dengler, 2018). First, especially with more mesic and certain wet grasslands, the need for increased agricultural productivity has seen a shift from manuring with dung to the liberal use of chemical fertilizers or concentrated liquid animal manure in slurry (Fig. 2). This has enabled more intensive stocking of pastures for meat and milk production (Fig. 3) and the change from traditional meadow management to cutting of silage rather than hay for forage or indoor feed (Török et al., 2016). Such change began early in the more industrial parts of Europe but has been much encouraged in recent



Fig. 2 Liquid manure fertilization of an intensified meadow in Germany. Photo: Valentin Klaus.



Fig. 3 Intensified pasture with high stocking rate in Germany. Photo: Steffen Both.



Fig. 4 Species poor intensified meadow in Germany. Photo: Frank Suschke.

decades by financial incentives, more universally available through the EU Common Agricultural Policy. These “improved” grasslands now provide the mainstay of European pastoral agriculture (Fig. 4).

The eutrophication of soils has often been accentuated by atmospheric nitrogen deposition and ground-water enrichment from farming itself and from industrial and domestic effluents, especially in the lowlands of more populous regions (Stevens et al., 2010). With land-use intensification, these changes have resulted in a dramatic loss of overall grassland biodiversity (Allan et al., 2014; Visconti et al., 2018), among vascular plants themselves (Socher et al., 2012), bryophytes (Boch et al., 2018a,b), lichens (Boch et al., 2016a), but also in soil microbial populations (Bardgett et al., 1999) and associated invertebrate and bird fauna (Heim et al., 2015). In addition, the land-use intensification strongly affects associations among taxa (Manning et al., 2015), changes species composition and community stability with a loss of specialist species, leading to homogenization of communities (Blüthgen et al., 2016; Gossner et al., 2016). This further negatively affects ecosystem multifunctionality (Soliveres et al., 2016a,b). The great variety of highly distinctive grasslands adapted to particular local soil and climate conditions and long histories of traditional management has converged into a few impoverished types of intensive pastures and leys. Such changes have often been accompanied by a disintegration of cultural features and practices associated with traditional farming: e.g. change of use in traditional buildings, loss of memory of landscape names, abandonment of seasonal festivals (Rodwell, 2015).

A second major threat has come from abandonment of grassland management, sometimes with a shift into arable cultivation, but more widely because of a reduction or withdrawal of grazing or mowing of naturally less productive grasslands (Visconti et al., 2018). Such changes in pasturing or abandonment of mowing have often been a consequence of wider demographic, socio-economic and cultural shifts leading to the extensive spread of heath, scrub and woodland (e.g. Valkó et al., 2018; Boch et al., 2019a,b). More recently, programs of “rewilding” and tree-planting for biofuels or carbon capture have exacerbated this second major threat across Europe.

Of more localized impact, but especially important for wetter seminatural grasslands dependent on regular regimes of seasonal flooding or ground-water supply, have been changes in hydrographic regimes because of water abstraction or in flood-control schemes within river basins (García-Baquero et al., 2016). In other situations, draining of species-poor wet grasslands can diversify plant species composition, provided there is not too intense eutrophication by fertilizers.

Grasslands on stable coastal dune sands have also suffered from lowering of the water table through water abstraction but more widespread losses have occurred through urbanization and the spread of tourist infrastructure. Upper salt-marsh grasslands have been reduced by industrialization on coasts and in estuaries (Janssen et al., 2016).

Invasion of nonnative plant species tends to be limited in the closed swards of grasslands where management has been stable (Visconti et al., 2018) but in lowland meadows of the northern Iberian Peninsula, the South American dallis grass (*Paspalum dilatatum*) has established very widely (Campos et al., 2013). In addition, also in sand dunes and heathlands the rapid colonization of the invasive moss *Campylopus introflexus* suppresses other species such as vascular plants, bryophytes and lichens in 21 European countries (Essl and Lambdon, 2009; Essl et al., 2013).

Impacts of climate change on these grasslands are at present limited (van Oijen et al., 2018) but disruptions in the regular patterns of temperature and rainfall (e.g. longer growing seasons, more frequent drought, irregular flooding) might be expected to affect plant species composition and productivity of grasslands and associated populations of pollinating insects, either directly or through shifts in styles of farming.

Conservation, Restoration and Sustainable Management

The European Red List of Habitats assessed that over 50% of seminatural grasslands were threatened in some way, with many in Western Europe in the Endangered or Vulnerable categories (Table 2). Many such grasslands figure as Priority Habitats in the EU Habitats Directive, are regarded as in urgent need of conservation by many country statutory agencies and often figure in campaigns of wildlife NGOs. However, most farm subsidies continue to favor high-productivity grasslands and biodiversity benefits can be offset against intensive farming.

In addition to overall loss of biodiversity and extent, many surviving grasslands now remain as fragments within highly intensive landscapes presenting additional problems of maintenance and restoration. Even when these remnants are well conserved, connectivity within a wider landscape presents challenges for plant and animal populations and for scenic value. The importance of larger-scale tracts of grasslands has been recognized in the concept of High Nature Value Landscapes (Akeroyd et al., 2014).

The conservation of seminatural pastures and meadows demands a maintenance or reinstatement of existing methods of management or some replacement treatments that mimic such regimes. Traditional management was often an integral part of farming cultures that are now uneconomic, with skills like stock rearing and hay-making becoming lost and traditions such as the naming of fields and community celebrations of harvest losing their meaning.

With huge and continuing loss of seminatural grasslands and continuing threats, restoration is now widely undertaken using a variety of methods (Mora and Bueno, 2018; Warwickshire County Council, 2018). Crucial to all of these is the availability of sites with generally low fertility (particularly of phosphates); some source of suitable herbage or seed; appropriate aftercare; long-term commitment of participants; and effective monitoring. Where, as often, fertility of donor sites is high, some technique of nutrient-stripping is essential, either by top-soil removal or soil inversion using deep plowing or, generally slower, by hard-grazing and repeated cutting of herbage (Kiehl and Pfadenhauer, 2007; Török et al., 2011).

On sites with lower fertility, species-enrichment of existing swards can be undertaken. A variety of restoration approaches has been tried. Translocation is the moving of vegetation and soils, preferably as intact turfs, from a donor to a receptor site where habitat conditions are as similar as possible. It is usually regarded as a last resort when it is impossible to protect a threatened site and, even when more successful, cannot avoid disrupting ecological processes and the historical landscape continuity of the original grassland. Current best practice (Box and Stanhope, 2010) recommends that cutting should use lightweight equipment, transfer should be quick, turfs laid tightly and in the same arrangement as when cut, then rolled and watered.

Where intensive farming of pastures and meadows has not been too damaging, elements of a seminatural seedbank may remain within the soil and be able to contribute to establishment of a more diverse flora (Klaus et al., 2018a,b). Natural colonization of prepared sites by seed is usually slow but may be successful if new locations are adjacent to established grasslands and there is some means of spreading of seed by stock or machinery movement. Sowing seed mixtures, with appropriate composition mimicking that of the target grassland type and of local provenance, has sometimes proved successful particularly where the sward is disturbed and opened up (Klaus et al., 2017; Schäfer et al., 2019). Strewing green hay cut from established meadows is also now widely used and often effective in enriching existing grasslands.

In the early stages of restoration, stress-tolerating specialists, often the distinctive species of the target grassland, perform rather poorly while more competitive generalists can quickly gain an advantage, further limiting specialists or new recruitment from seed by the occlusion of microsites. The presence of an appropriate microbial flora may also prove crucial (Walker et al., 2004).

In all restoration programs, there needs to be a commitment to long-term management and adequate monitoring of benefits. Even in meadows where mowing is an essential part of aftercare, grazing before and after cutting a hay crop has been shown to be essential for effective restoration. Most studies from seven European countries have shown that positive results took more than 10 years to appear (Conservation Evidence, 2019).

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Grasslands of Northern Europe and the Baltic States

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This chapter was solicited and edited by Jürgen Dengler and Péter Török on behalf of the Eurasian Dry Grassland Group (EDGG).

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Abstract

This chapter deals with the grasslands of Northern Europe (Denmark, Faroe Islands, Finland, Iceland, Norway, Sweden) and the Baltic States (Estonia, Latvia, Lithuania), with a focus on natural and semi-natural grasslands of the lowlands, thus treating arctic-alpine and strongly intensified types only marginally. At present, grasslands cover ca. 7% of the study region, half of which are natural grasslands (mostly arctic-alpine, to a smaller extent also azonal and extra-zonal) and the other half secondary grasslands created by human land use (livestock grazing or haymaking). Both grassland categories have high importance for biodiversity in many taxa. However, particularly the secondary grasslands are profoundly negatively affected by area loss (conversion to other land uses) and quality loss (mainly due to intensification and to abandonment). Conservation measures typically try to mimic traditional low-intensity land uses that are agronomically not profitable anymore.

Delimitation and Environmental Conditions of the Region

We define “Northern Europe and the Baltic States” here based on political territories: Iceland, Faroe Islands, Norway, Sweden, Finland, Denmark, Lithuania, Latvia and Estonia. With the exception of the British Isles which are treated in the Western European grassland chapter of the “Encyclopedia of the World’s Biomes” (Boch et al., 2020), this definition corresponds to “Northern Europe” in the UN Geoscheme. This geographic unit comprises the northern parts of the “Western and Northern European” treatise (Dengler and Tischew, 2018) in the global grassland book (Squires et al., 2018) together with the three Baltic States, which in the book were included in the Eastern European chapter (Török et al., 2018). In this chapter, “Nordic-Baltic region” or “the region” refers to Northern Europe and the Baltic States combined. “Northern Europe” (sometimes also called “Nordic countries”: Denmark, Faroe Islands, Finland, Iceland, Norway, Sweden) and “Baltic States” (Estonia, Latvia, Lithuania) are used to address the two subregions, respectively. Ecologically, the subregions are similar (with differentiation mainly following a North-South gradient), but they differ in land-use history during the 20th century as the Baltic States were part of the communist Soviet Union. In the following, we use “Fennoscandia” to refer to the three countries on the Fennoscandian Peninsula (Norway, Sweden, Finland) but excluding the Russian territory on the peninsula because this is addressed in Tishkov et al. (2020).

The overall territory of the study region is 1.484 million km², extending from 54 to 81° northern latitude and from 25° western to 32° eastern longitude (Table 1). The territory is inhabited by nearly 30 million people but population density varies tremendously from as high as 135 persons/km² in Denmark in the south to only 3.5 persons/km² in Iceland in the north (Table 1). Most parts of the territory are flat to hilly lowland, with the only exception of Iceland, which is a volcanic island with a maximum elevation of 2110 m a.s.l., and the Scandes, covering most of Norway and the westernmost parts of Sweden and reaching an elevation of 2469 m a.s.l.

Table 1 Overview of the region covered in this chapter with its eight political entities, their area and population, grassland area and grassland types.

Region	Denmark ^a	Faroe Islands ^b	Iceland ^b	Norway (including Svalbard and Jan Mayen) ^c	Sweden ^b	Finland ^d	Estonia ^e	Latvia ^f	Lithuania ^g	Total
Total area included [km ²]	43,075	1399	102,820	385,155	440,940	337,030	45,100	63,700	65,200	1,484,419
Number of inhabitants	5,814,000	52,000	360,000	5,328,000	10,291,000	5,521,000	1,325,000	1,920,000	2,794,000	33,405,000
Population density [inhabitants/km ²]	135.0	37.2	3.5	13.8	23.3	16.4	29.4	30.1	42.9	22.5
Total extant grasslands [km ²]	1750	1000	35,650	19,900	21,850	2900	2950	8700	8300	103,000
Fraction of territory	4%	71%	35%	5%	5%	1%	7%	14%	13%	7%
Proportion of natural grasslands	29%	50%	87%	65%	23%	9%	5%	< 1%	1%	49%
Proportion of HNV grasslands ^h	46%	NA	NA	NA	NA	NA	44%	NA	NA	ca. 45%
(1) Natural grasslands (extant) [km ²]	500	500	31,000	12,950	5000	250	150	50	100	50,500
as fraction of their original area	20%	95%	95%	90%	90%	60%	75%	NA	75%	ca. 89%
(i) Steppes ⁱ [km ²]	0	0	0	0	0	0	0	0	0	0
(ii) Arctic-alpine grasslands ^j [km ²]	0	450	29,000	12,800	4000	200	0	0	0	46,450
(iii) Azonal + extrazonal grasslands ^k [km ²]	500	50	2000	150	1000	50	150	50	100	4050
(a) In good state ^l [km ²]	250	NA	NA	NA	NA	NA	150	NA	NA	NA
(b) Strongly degraded ^l [km ²]	250	NA	NA	NA	NA	NA	0	NA	NA	NA
(2) Secondary grasslands [km ²]	1250	500	4650	6950	16,850	2650	2800	8650	8200	52,500
as fraction of their maximum area (in the past)	10%	95%	95%	NA	NA	NA	NA	33%	NA	ca. 34%
(a) Semi-natural grasslands ^m [km ²]	550	NA	NA	400	NA	400	1150	2150	2050	ca. 22%
(b) Strongly intensified grasslands ⁿ [km ²]	700	NA	NA	6550	NA	2250	1650	6450	6150	ca. 78%

The categorization of grasslands follows the definitions in the "synthesis" chapter by Dengler et al. (2020). The values are rounded expert estimates, only partly supported by hard GIS data. HNV = high nature value; NA = not available.

^aAssessed by H. H. Bruun based on national statistics.

^bTotal grassland area from FAO (2019), based on CCI_LC for the year 2015; subcategories are rough estimates based on ecological knowledge.

^cAssessed by H. Sickel based on national statistics.

^dAssessed by T. Birge based on national statistics.

^eBased on data from Török et al. (2018).

^fSemi-improved grasslands (included here in semi-natural grasslands s. l.) make up 15%–20% of all secondary grasslands, in addition to 7.9% semi-natural ones in the stricter sense. Moreover, 1740 km² of temporal grasslands were counted under grasslands following the definition of Dengler et al. (2020), while in other land use classifications they might be included in arable lands.

^gAssessed by V. Rašomavičius based on national statistics.

^hHNV grasslands = natural grasslands in good state + semi-natural secondary grasslands.

ⁱSteppes = climatogenic grasslands in regions where the climate is too dry to sustain forests.

^jArctic-alpine grasslands = climatogenic grasslands in regions where the climate is too cold to sustain forests.

^kAzonal + extrazonal grasslands = pedogenic grasslands in forest climates, e.g. coastal dunes, salt marshes or grasslands of rocky outcrops, such as alvars.

^lIn good state vs. strongly degraded is roughly separated at a biodiversity loss of 50% (Dengler et al., 2020).

^mSemi-natural grasslands are those secondary grasslands that still contain at least 50% of the original biodiversity (Dengler et al., 2020), which is less strict than other definitions. Accordingly, also semi-improved grasslands as well as some grasslands that recovered or were restored from former arable fields and early successional stages of abandoned grasslands belong here.

ⁿStrongly intensified grasslands are those secondary grasslands that host less than 50% of the typical biodiversity of "good" semi-natural grasslands (Dengler et al., 2020). Accordingly, also most temporary and frequently re-seeded grasslands belong here.

The climate of the region is very mild for its latitude due to the Gulf Stream and the North Atlantic Drift, as well as due to dominating southwesterly winds. The climate is humid as there is cyclonic rain in all the seasons, with a maximum in late summer and autumn (Dahl, 1998). According to the Köppen climate classification, most parts of Scandinavia experience a cold climate with cold summers and no drought (Dfc type and, in the far north, tundra climate ET type). However, most of Denmark, the southern parts of Finland and Sweden, and the Baltic States have cold climate with warm summers and no drought (Dfb type). Additionally, Southern Denmark lies in the temperate climate zone with warm summers (Cfb) (Peel et al., 2007).

During the last (Weichselian) glaciation, the vast majority of the territory was covered by the Eurasian ice sheet complex and the separate Icelandic and Faroese ice sheets, with the exception of southwestern Denmark and tiny areas in southern Lithuania (Patton et al., 2017). From the last glacial maximum at 23 ka BP, the ice shield retreated to reach the current status with only a few remaining mountain glaciers approx. 8.7 ka BP (Patton et al., 2017). However, the post-glacial rebound is still affecting the region today (Patton et al., 2017) particularly the Bay of Bothnia, where post-glacial land uplift at a maximum rate of more than 5 mm relative to sea level creates new terrestrial surfaces. Glaciation has influenced geomorphology of the region significantly and has created considerable diversity in the landscape.

Grasslands have developed on a variety of soils from calcite-bearing parent soils to acidic soils developed from sandstone, gneiss or granite. Mesic grasslands occur on deep soils formed on quaternary deposits. Fertile types of mesic meadows and pastures occur mostly on Luvisols, while poor pastures rather inhabit Planosols or Podzols, the latter being the most widespread soil type in Fennoscandia. Semi-dry and rocky grasslands most commonly develop on shallow calcareous soils (Leptosols) which reach their greatest coverage in the Baltic Sea islands, southern Sweden, and western Estonia. Arenosols support dry sandy grasslands and mesic nutrient-poor *Nardus* grasslands across the region but they are the most widespread in Sweden and in parts of Latvia, Lithuania, and Denmark. Floodplain grasslands grow mostly on Fluvisols, which are common in Baltic States but less frequent in Fennoscandia. Moist and wet grasslands are commonly found on Gleysols, Estonia being the richest in such areas, and Histosols (Reimann et al., 2003; Jones et al., 2005; Tóth et al., 2008).

Biogeography, Flora and Fauna

Due to the humid climate, forests form the zonal vegetation in most of Northern Europe and the Baltic States. Regions with short periods of frost (Denmark, southernmost tip of Norway and Sweden) belong to the nemoral zonobiome (ZB VI), which are naturally dominated by broad-leaved forests (Walter and Breckle, 1986). Regions further north with longer winters and cooler summers (most of Sweden and Finland) are classified as boreal zonobiome (ZB VIII) and naturally covered by coniferous forests (Walter and Breckle, 1986). Between both zonobiomes, a transition zone, the so-called boreonemoral zone (zonoecotone VI–VIII) occurs where broad-leaved and coniferous trees jointly form the tree layer (Baltic States, south Finland, south Sweden, non-alpine parts of Norway). In the northernmost tip of Fennoscandia, the Scandes and Iceland, the tundra biome prevails (ZB IX sensu Walter and Breckle, 1986).

The study region comprises four floristic provinces (Finnie et al., 2007). The Northern European province coincides with the boreal zonobiome. The border of Central European and Eastern European province runs through the territory of Baltic States. The western parts of Denmark and the most southwestern tip of Norway belong to Atlantic European province. Phytogeographers of the Baltic States argue for the delimitation of a separate Baltic province. The southwestern boundary of the Baltic province coincides with the boundary of the boreonemoral zone. The northern boundary of the continuous *Carpinus betulus* distribution range is the outline of the transition of the Baltic province into the Central European province. The distributional boundary of several continental species, such as *Koeleria glauca*, *Astragalus arenarius*, *Pulsatilla pratensis*, *P. patens* and *Silene chlorantha*, marks the southeastern boundary with the Eastern European province (Eilart, 1975).

The flora and fauna of the region is “under-saturated” with species because of the recent glaciations, which “reset” the biota. Immigration of species after the retreat of glacial sheet is still ongoing, and the limited duration of the postglacial period has provided limited opportunity for in-situ speciation (Dahl, 1998). The floristic elements of northern Europe tend to be composed of wide-ranging species and include only a low proportion of European endemics (Finnie et al., 2007). The endemics of the region are mostly infraspecific taxa in apomictic polymorphous groups or allopolyploids, with only a few being accepted at the rank of species (Dahl, 1998; Jonsell and Karlsson, 2004). Grasslands comprise several such endemics, especially on the islands of the Baltic Sea. They are, for instance, *Helianthemum oelandicum* subsp. *oelandicum*, *Galium oelandicum*, *Festuca oelandica*, *Crepis tectorum* subsp. *pumila*, and *Allium schoenoprasum* var. *alvarensense* (Dengler et al., 2006). A second “hotspot” of endemism are the Baltic shores, mostly with grassland taxa (Jonsell and Karlsson, 2004). In Finland, seashore meadows are a habitat type for which the country has an international responsibility. The seashore meadows are important for endemic species, and Finland’s international responsibility stems from the uniqueness of the post-glacial land uplift quality of the seashore meadows (Lehtomaa et al., 2018).

The biota outside the glacial limits were also affected by cold and arid climate during the Pleistocene. Nevertheless, the lack of glaciation in southwestern Denmark and southern Lithuania (Patton et al., 2017) resulted in comparatively high species richness there (Lawesson and Skov, 2002). Similarly, the dune heath of the Atlantic province is a special responsibility for Denmark, harboring a few endemic species, such as *Euphrasia dunensis* (see Jonsell and Karlsson, 2004) and the grasshopper *Corthippus jutlandica*.

Origin of the Grasslands

In the region, natural arctic-alpine grasslands are widespread in the tundra biome. Azonal and extraazonal natural grasslands, including steppe-like semi-dry grasslands, heathlands, and coastal grasslands on saline to brackish wet soils, occur throughout the region in areas where edaphic factors or natural disturbance hamper tree growth. However, grazing by large herbivores or surrogates thereof, nowadays livestock grazing and mowing, is essential for long-term stability of such grasslands. Semi-dry grasslands with floristic elements of steppe are especially abundant on the islands of Öland (Fig. 1E), Gotland and Saaremaa in the Baltic Sea. These islands are arguably the best candidates in the region for a zonoecotone between the nemoral and the arid-temperate continental zonobiome (ZB VII; Walter and Breckle, 1986). Secondary grasslands, both semi-natural and intensified types, prevail in the two forest biomes and their zonoecotone. They have been created by clearing of forests and need regular mowing, livestock grazing or burning for their maintenance.

The origin of temperate grasslands in the Nordic-Baltic region is disputed. There are two main lines of reasoning. Habitats for the grassland biota may be naturally present in sufficient area coverage in mosaic with dominant forest and woodland (Svenning, 2002), or—alternatively—grasslands of the region owe their existence entirely to human pastoralism and shifting agriculture from the Neolithic and onwards (Iversen, 1973; Pott, 1995). There is no doubt that human land use has radically expanded grassland habitats through the last few millennia, hence the term “semi-natural grassland” (Marquer et al., 2014). Likewise, there is little doubt that entirely open landscapes devoid of trees are cultural products. However, different lines of evidence suggest a long-term existence of habitat for grassland biotas in the region. Evidence from the Eem interglacial and earlier is very scarce, due to the resetting effects of the later Weichselian glaciation, almost entirely covering the region at its maximum (Patton et al., 2017). However, pollen assemblages in Eemian palaeosols from western Jutland have been found to contain a certain grassland element (Andersen, 1965; Björck et al., 2000). It is thought that large herbivores—interacting with local climate and soil conditions—have influenced vegetation structure to allow a significant grassland element in the biotas (Svenning, 2002; Sandom et al., 2014; Schweiger and Svenning, 2018). The decline of the megafauna was already in an advanced state by the onset of the Holocene (Barnosky et al., 2004). Nonetheless, several palaeoecological studies have found that open vegetation persisted throughout the period in the Nordic-Baltic region (Nielsen et al., 2012; Theuerkauf et al., 2014; Hjelle et al., 2018) and the wider Western Palearctic (Sommer et al., 2011; Holm and Svenning, 2014). However, palaeoecological methods have limited power in discrimination between open forests with a closed field layer (“savanna”) or a mosaic of open grassland patches within dense forests (“forest steppe”).

Just like under current conditions, grasslands or grassland-forest mosaics may have been more likely on certain soil types, such as more drought-prone calcareous and sandy soils (e.g. Theuerkauf et al., 2014), under certain conditions of topography, such as on steep slopes and potentially in places prone to wind-throw or wildfires (Kuosmanen et al., 2018). Furthermore, the isostatic land uplift in the Baltic region has continuously through the Holocene provided new land to become colonized by grassland biotas (Zobel and Kont, 1992; Auffret and Cousins, 2018).

The grassland flora of the Nordic-Baltic region is made up of plant species with an overall distributional center of gravity in Central Europe (Pärtel et al., 2005). Thus, the species of the current flora seem to have survived the Weichselian glacial maximum in Central and Eastern Central Europe and have re-immigrated from there. Recent reviews of landscape openness during the Holocene in Central Europe suggest the continuous presence of grassland habitat throughout the Holocene, as grasslands and open woodlands, and that the Neolithic pastoralism probably first expanded in landscapes that were already somewhat open (Hejman et al., 2013; Kuneš et al., 2015).

Hay meadows came into existence much later. Animal husbandry started in Eastern Baltics only around 2900–2400 BCE (Piličauskas et al., 2018), and the first scythes come from the Iron Age and are dated to the 3rd–4th century in the southeastern part of the Baltic region (Apals et al., 1974), and also Sweden, where the first finds of hay rakes date from the 3rd to 4th century (Pedersen and Widgren, 2011).

Types of Grasslands

Overall, the spatial extent of natural vs. secondary grasslands is similar, with approx. 50,000 km² in each group (Table 1). Natural grasslands are found at large extents on Iceland but cover only rather small areas in the other countries (Table 1; see also Helgadottir et al., 2014). Among the natural grasslands, arctic-alpine types prevail (Figs. 1A and B), while azonal and extraazonal types contribute less than 10% of the total area (Figs. 1C–E) and true steppes (in the sense of climatogenic grasslands in climates that are too dry for forests) are absent from the region (Table 1). Among the secondary grasslands, a majority nowadays are strongly intensified (Fig. 2B), while species-rich, so-called semi-natural grasslands (Figs. 1E–H, 2A, 2C–E) have become a minority (Table 1).

Most of the countries in the region have national classification schemes for their grassland types. Norway, for example, recently adopted a new system called “Nature types in Norway” (NiN; <https://artsdatabanken.no/Pages/135563>), which distinguishes 25 semi-natural grassland types along the three main gradients, soil pH, soil moisture and management (weak–strong). Finland, as another example, distinguishes 12 main types of semi-natural grasslands and grazed woodlands, which are collectively referred to in the country as traditional rural biotopes. These are: heaths, rock meadows, dry meadows, mesic meadows, moist meadows, freshwater meadows, seashore meadows, alluvial meadows, fen meadows, pollard meadows, wooded pastures and grazed woodlands (Kontula and Raunio, 2018). In total, 42 sub-types of traditional rural biotopes were assessed in Finland for the 2018 Red List



Fig. 1 Different grassland types in the Nordic-Baltic region: (A) natural arctic-alpine grassland in Iceland; (B) natural arctic-alpine grassland (habitat type E4.3b in Table 2) in Norway with willow ptarmigan (*Lagopus lagopus*) as a typical bird species; (C) coastal salt marsh (A2.5b) as a natural azonal grassland in Western Estonia; (D) coastal dune grassland (B1.4a) as a natural azonal grassland on Saaremaa, Estonia; (E) alvar vegetation on Southern Öland, Sweden—alvars are calcareous flatrocks with a mixture of natural vegetation on rocky outcrops (E1.1d) in the foreground, semi-natural meso-xeric grasslands on deeper soils (E1.2a) in the background, fens and shrublands; sometimes alvars are considered as extrazonal

of Habitats (Lehtomaa et al., 2018). The Estonian vegetation site type classification includes four main grassland types (dry and fresh, floodplain, coastal, and paludified grasslands) with 14 subtypes (Paal, 1997). In Latvia and Lithuania, grassland classification follows phytosociological approach (Rašomavičius, 1998; Rūsiņa, 2007). In Latvia, 16 habitat types at the alliance level are distinguished (Kabucis, 2001), among which the dry and mesic grasslands include 23 associations (Rūsiņa, 2007).

For the sake of comparability, we provide here an overview of the main grassland types in the region based on the refined EUNIS grassland typology (Table 2), which can now be applied consistently across national borders via an electronic expert system (Schaminée et al., 2016). The same system also underlies the first Red List of Habitats in Europe (Janssen et al., 2016) and clearly connects to the priority habitats of the Habitats Directive of the European Union (European Commission, 2013).

Management and Agricultural Policy

During the period of traditional agriculture, the area of meadows was often greater than that of arable fields within the resource area of each village or isolated farm. The primary management of semi-natural grasslands in Northern Europe was through grazing and hay-making to provide winter fodder. In many cases in traditional agriculture in the Nordic and Baltic countries, animals were turned out to graze meadows only after hay was collected. Pollarding was once a common form of fodder collection in the Nordic countries and produced distinctive features in e.g. wooded pasture and grazed woodlands. Swiddening was practiced in some areas, leading, for example, to treeless heaths (Berglund et al., 2014). Collection of reeds for winter fodder was also practiced and was instrumental in keeping coastlines open. The grazing and fodder collection under traditional agriculture in Northern Europe created mosaic landscapes and is thought to have had a primarily positive impact on biological diversity at least up until the end of the 19th century (Pykälä, 2001; Berglund et al., 2014). The existing semi-natural grasslands are the most important feature for biodiversity associated with farmlands in the Nordic-Baltic region.

Traditional farming in Scandinavia (lasting until approximately the end of the 19th century) was based on an infield-outfield landscape, where inlands (often fenced) were used as field and hay meadow and outlands (unfenced) were used as pasture (Berglund et al., 2014). In the Baltic States, meadows were located mainly in river flood plains where spring floods ensured natural enrichment of soils. Outside flood-plains, meadows were situated in areas which were not suitable for arable land (e.g. too poor or too wet). The poorest land not suitable even for mowing was used as pasture land. Fallow-lands, fens, forest edges and forests were also grazed (Gustiņa, 2016). Traditionally in Estonia wooded meadows and alluvial meadows were mown, wooded pastures, alvars, and coastal grasslands were used as pastures (Sammul et al., 2000).

Semi-natural grasslands are the result of centuries with domestic animals grazing natural vegetation types and the harvest of wild growing plant material used as fodder for cattle, sheep, horses and goats in the winter months (Emanuelsson, 2009). The animals were normally kept indoors during cold winter months with snow, but were let out to graze as early in the spring as possible. The winter feed was often limited and nutritionally deficient. Thus, it was important to give the animals fresh plant material as soon as possible after the winter. Grazing often took place near the farms in the spring and autumn, but in the summer it was important to save the hay meadows so that they could be harvested for winter fodder. In Finland and the Baltic States, animals were usually allowed on to the hay meadows only after the hay had been harvested. Generally, the animals were herded into forests, heathland, mountain pastures, wetland or other natural vegetation. In Norway and Sweden, it was normal to move the husbandry to summer farms, situated in the subalpine vegetation zone of mountains or in woodland, where grazing resources were almost unlimited. On the summer farms, milk products such as cheese, butter and sour cream were produced, and winter fodder such as grasses, herbs, sedges, lichen, leaves and branches from bushes and trees were harvested (Reinton, 1955). A huge amount of wood was needed as firewood on the summer farms and the landscape surrounding these farms were often open and treeless.

In an effort to make agriculture more efficient, governments replaced the traditional parceling systems for fields and meadows with land ownership based on contiguous property, starting, for example, already in the 18th century in Sweden and Finland. Policy encouraging specialization has played a significant role in the decline of biodiversity-rich semi-natural meadows in the Nordic and Baltic countries, with the loss of mixed farming and decline in small-holdings with a small number of ruminants leading to abandonment, afforestation, or conversion to arable fields. This process happened earlier in the Nordic countries compared to the Baltic countries, and the regions and countries have different histories. Accession to the European Union promoted intensification of grasslands but has also provided countries with financial support for conservation of low-input semi-natural grasslands and wooded meadows.

Once essential to the food production of Northern Europe and the Baltic States, the value of semi-natural grasslands to farm income nowadays is relatively low or non-existent for most farmers. The cost of fodder collection on these sites is viewed by many farmers as too costly for too little return. Hay collection on uneven surfaces is slower, fodder quality is more variable, and fencing more challenging compared to cultivated (intensified) grasslands. Thus, agricultural subsidies are important sources of

← occurrences of the forest-steppe zonoecotone; (F) secondary, semi-natural, meso-xeric grassland (E1.2a) on a coastal limestone cliff (B3.4a) in NW Jutland, Denmark, with the rare plant species *Tephrosia integrifolia*; (G) secondary, semi-natural mesic grasslands (E2.1a or E2.2) in Norway; (H) secondary, semi-natural, wet grassland (E3.4) in Latvia. (A) Photo: T. Birge; (B) Photo: I. Dembic; (C) Photo: J. Dengler; (D) Photo: I. Dembic; (E) Photo: I. Dembic; (F) Photo: H. H. Bruun; (G) Photo: H. Sickel; (H) Photo: S. Rūsiņa.



Fig. 2 Management, threats, conservation and restoration of Nordic-Baltic grasslands: (A) traditional sheep grazing on secondary, semi-natural mesic grassland (habitat type E2.1a in [Table 2](#)) on Vågsøy island, Norway; (B) Species-poor, secondary, strongly intensified mesic grassland in Lithuania; (C) the famous wooded meadow (E7.2) of Laelatu, Western Estonia, which holds two small scale species-richness world records; (D) wooded pasture (E7.2), grazed by dairy cattle in Finland; (E) conservation management of semi-natural, mesic grasslands (E.2.2) in the Koli National Park, Finland—to support insects, strips of grasslands remained unmown; (F) machinery used to mimic traditional haymaking management

income enabling farmers to manage semi-natural grasslands in the region. As a result, cultivated (intensified) grasslands, including grass leys in rotation, now by far exceed managed semi-natural grasslands in the Nordic countries (Helgadottir et al., 2014)—and this process is continuing throughout the region (I. Herzon et al., unpublished material).

Ecology of the Semi-Natural Grasslands of the Region

The activity of grazing and harvesting winter fodder and firewood changed the natural ecosystems and the species composition in them and created semi-natural vegetation types dominated by grasses and forbs. Many grassland plant species have clonal and horizontal growth (e.g. *Knautia* and *Pilosella* species), leaves placed near the ground (e.g. *Primula*, *Pilosella* and *Leontodon* species) or growth nodes located at the lower parts of the plants (e.g. grass species). Even if upper parts of the plants are removed, plants survive and continue growing. Some plants have properties that deter grazing mammals, such as spines (e.g. *Rosa* and *Cirsium* species). Removal of trees and shrubs, mowing and grazing result in increased light conditions and a changed microclimate. Grasslands are therefore also characterized by many small, drought-tolerant and light-demanding plants. Typical plants in grasslands tolerate disturbances and stress, but are rather poor competitors (Grime, 2001). The majority of grassland organisms are adapted to relatively nutrient-poor conditions, under which the competitive strategy is ill-adapted. Also, trampling, grazing and mowing reduce the power of competitive plants. In nutrient-poor grasslands, mycorrhizae are common, in which the fungal partner secures plant nutrient uptake and co-existence (Dostálek et al., 2013).

Grazing and mowing increase the availability of gaps allowing seed germination and establishment. Grazing animals disperse seeds of many plant and animal species - for plants not the least because many grassland plants have seeds tolerating ingestion and gut passage or stick to fur and hoofs. Seeds are also dispersed via transported hay and mowing machines.

Biodiversity: Patterns and Drivers

Semi-natural grasslands are known to be very species rich compared to most other vegetation types in the Nordic-Baltic region (Kull and Zobel, 1991; Austrheim et al., 1999; Eriksson et al., 2002). There are many plants, insects, fungi and birds that live in these open landscapes that are moderately affected by human activity (Artsdatabanken, 2018).

At small spatial scales, Nordic-Baltic grasslands can be very rich in vascular plant species. Among the scale-dependent world records of vascular plant species richness in any habitat reported by Wilson et al. (2012), there are three entries from the study region: 12 species on 0.001 m² in a limestone grassland on Öland, Sweden, as well as 25 and 42 species of a wooded meadow in western Estonia, on 0.01 and 0.04 m², respectively (see Kull and Zobel, 1991). However, for areas of 0.1 m² and larger, mean and maximum richness values of vascular plants in the Nordic-Baltic region more and more lag behind similar grasslands in other regions of the Palaearctic biogeographic realm, such as Eastern Europe, Western Europe, Russia or the Mediterranean Region, the Middle East and the Caucasus (Dengler et al., 2020). For meso-xeric grasslands, the mean richness on 100 m² in the Nordic-Baltic region is “only” about 40 species, while in Eastern Europe, the average is around 75 species (Dengler et al., 2020).

However, one peculiarity of the Nordic-Baltic grasslands is that bryophytes and lichens play a bigger role than in any other Palaearctic region studied (Dengler et al., 2020). This is true across grassland types, but it is particularly pronounced in rocky grasslands where terricolous bryophytes and lichens together on average contribute more species than vascular plants (Ejrnæs and Poulsen, 2001; Boch and Dengler, 2006; Löbel and Dengler, 2008; Dengler et al., 2020). When considering also the bryophytes and lichens growing on other substrata than soil (e.g. saxicolous and epiphytic species), total species richness of the vegetation in rocky outcrop communities of Saaremaa, Estonia, can be as high as 140 species on 100 m² (Dengler and Boch, 2008). However, already when taking only terricolous species into account, the richness of bryophytes and lichens in the rocky grassland communities of the alvars of Öland (Sweden) and Saaremaa (Estonia) are higher for most of the analyzed grain sizes than in any other known Palaearctic grassland type (Dengler et al., 2020).

In a study of a wide range of dry grassland types in Southern Öland, Sweden, Löbel et al. (2006) found that among the studied environmental factors, soil pH was the most important for all three taxonomic groups in the vegetation: it had a positive effect on plot-scale species richness of bryophytes and lichens and a unimodal one on that of vascular plants. Other important factors were microrelief (positive for all taxa, vascular plants and bryophytes) and size of the dry grassland area (positive for all taxa, bryophytes and lichens). Across a wide range of Danish semi-natural grasslands from dry to wet, Moeslund et al. (2013) found that soil moisture (represented by the topographic wetness index) had a strong negative impact on plot-scale vascular plant species richness.

on a semi-natural grassland of high conservation value in Norway; (G) restoration of an alvar site in Western Estonia through removal of woody (*Juniperus* and *Pinus*) encroachment; (H) afforestation (here with spruce) is one of the threats low-productive grasslands (here an acidic semi-natural grassland with *Nardus stricta*; E1.7) are subject to. (A) Photo: I. Dembic; (B) Photo: V. Rašomavičius; (C) Kull K and Zobel M (1991) High species richness in an Estonian wooded meadow. *Journal of Vegetation Science* 2: 711–714; Wilson JB, Peet RK, Dengler J, and Pärtel M (2012) Plant species richness: The world records. *Journal of Vegetation Science* 23: 796–802; (D) Photo: T. Birge; (E) Photo: I. Dembic; (F) Photo: H. Sickel; (H) Latvia; photo: S. Rüsiga.

Table 2 Natural and semi-natural grassland types of the Nordic-Baltic region, the corresponding vegetation types (syntaxa) and habitat types of the Habitats Directive and the threat status in the European Red List of Habitats.

Code	Name in red list	Corresponding vegetation type(s)	Corresponding habitat type(s)	RL
<i>Coastal habitats (A, B)</i>				
A2.5a	Arctic coastal salt marsh	<i>Juncetea maritimi</i>	1330	NT
A2.5b	Baltic coastal meadow	<i>Juncetea maritimi</i>	1630*	EN
A2.5c	Atlantic coastal salt marsh	<i>Juncetea maritimi</i>	1320, 1330	VU
B1.3a	Atlantic and Baltic shifting coastal dune	<i>Ammophiletea</i>	2110, 2120	NT
B1.4a	Atlantic and Baltic coastal dune grassland (gray dune)	<i>Koelerio-Coryneporetea (Coryneporetalia canescentis, Sedo acris-Festucetalia)</i>	2130*	VU
B3.4a	Atlantic and Baltic soft sea cliff	various	1230	LC
<i>Grassland (E)</i>				
E1.1a	Pannonian and Pontic sandy steppe	<i>Koelerio-Coryneporetea (Sedo acris-Festucetalia)</i>	2340/ 6120*	CR
E1.1b	Cryptogam- and annual-dominated vegetation on siliceous rock outcrops	<i>Koelerio-Coryneporetea (Sedo-Scleranthetalia)</i>	8230	VU
E1.1d	Cryptogam- and annual-dominated vegetation on calcareous and ultramafic rock outcrops	<i>Koelerio-Coryneporetea (Alyso alyssoidis-Sedetalia)</i>	6280*, 8240*	VU
E1.2a	Semi-dry perennial calcareous grassland	<i>Festuco-Brometea (Brachypodietalia pinnati)</i>	6210(*), 6270*	VU
E1.7	Lowland to submontane, dry to mesic <i>Nardus</i> grassland	<i>Nardetea strictae (Nardetalia strictae)</i>	6230*	VU
E1.9a	Oceanic to subcontinental inland sand grassland on dry acidic and neutral soils	<i>Koelerio-Coryneporetea (Trifolio arvensis-Festucetalia ovinae)</i>	2330	EN
E1.9b	Inland sanddrift and dune with siliceous grassland	<i>Koelerio-Coryneporetea (Coryneporetalia canescentis)</i>	2330, 6270*	EN
E2.1a	Mesic permanent pasture of lowlands and mountains	<i>Molinio-Arrhenatheretea (Arrhenatheretalia elatioris)</i>	6270*, 6510	VU
E2.2	Low and medium altitude hay meadow	<i>Molinio-Arrhenatheretea (Arrhenatheretalia elatioris)</i>	6270*, 6510	VU
E2.3	Mountain hay meadow	<i>Molinio-Arrhenatheretea (Poa alpinae-Trisetetalia)</i>	6520	VU
E3.4a	Moist or wet mesotrophic to eutrophic hay meadow	<i>Molinio-Arrhenatheretea (Molinietalia caeruleae)</i>	6410	EN
E3.4b	Moist or wet mesotrophic to eutrophic pasture	<i>Molinio-Arrhenatheretea (Molinietalia caeruleae)</i>	6410	EN
E3.5	Temperate and boreal moist or wet oligotrophic grassland	<i>Molinio-Arrhenatheretea (Molinietalia caeruleae)</i>	6410, 6430, 6440, 6450	EN
E4.1	Vegetated snow patch	<i>Salicetea herbaceae</i>	–	VU
E4.3a	Boreal and arctic acidophilous alpine grassland	<i>Juncetea trifidi</i>	6150	LC
E4.4a	Arctic-alpine calcareous grassland	<i>Saxifrago cernuae-Cochlearietea groenlandicae, Carici rupestris-Kobresietea bellardii, Elyno-Seslerietea</i>	6170	LC
E5.2a	Thermophilous woodland fringe of base-rich soils	<i>Trifolio-Geranietea sanguinei</i>	–	NT
E5.2b	Thermophilous woodland fringe of acidic soils	<i>Trifolio-Geranietea sanguinei</i>	–	LC
E5.3	<i>Pteridium aquilinum</i> stand	<i>Trifolio-Geranietea sanguinei</i>	–	LC
E5.4	Lowland moist or wet tall-herb and fern fringe	<i>Epilobietea angustifolii</i>	6430	VU
E5.5	Subalpine moist or wet tall-herb and fern fringe	<i>Mulgedio-Aconitetea</i>	–	LC
E7.2	Hemiboreal and boreal wooded pasture and meadow	various	6530*	CR

"Code" and "Name in the Red List" are according to Janssen et al. (2016) and Schaminée et al. (2016); the latter also contains distribution maps. "Corresponding vegetation type(s)" refer to phytosociological classes and in four widespread classes of semi-natural grasslands to phytosociological orders (in brackets). Classification is generally based on Mucina et al. (2016), but modified for the class *Koelerio-Coryneporetea* s. l. according to Dengler (2003). Orders (O.) are given only for the four widespread classes of semi-natural grasslands. "Corresponding habitat type(s)" lists the corresponding habitat types that are protected in European Union by the Habitats Directive (European Commission, 2013), with * indicating priority habitats. "RL" finally gives the Red List status at European scale (EU28+; Janssen et al., 2016): CR = Critically Endangered, EN = Endangered, VU = Vulnerable, NT = Near Threatened, LC = Least Concern.

While in the study of Löbel et al. (2006), land use was no influential variable (probably because all the land uses occurring there were of low intensity), many other studies found pronounced effects of land use and land use history. Finnish cattle pastures were most diverse at plot scale when continuously grazed, intermediate when grazing had been restarted 3–8 years ago and lowest in pastures that were abandoned for more than 10 years (Pykälä, 2004). The loss of species in Finnish grassland started almost immediately after abandonment, reached a plateau between year 15 and 40, followed by a second strong decrease afterwards (Pykälä et al., 2005). Swedish calcareous and coastal pastures at the 0.001-m² scale showed a humpbacked relationship to grazing intensity with the moderately grazed plots being richest and the heavily grazed and long abandoned ones being poorest (Dupré and Diekmann, 2001). However, this effect vanished more and more towards larger plot sizes and was absent at 1000 m², meaning that abandoned grasslands did not lose species at larger grain sizes, but just became more patchy, i.e. had higher beta-diversity (Dupré and Diekmann, 2001). One must also consider that there can be a considerable time-lag in the extinction of species when environmental conditions become worse. Helm et al. (2006) demonstrated for alvar grasslands on Saaremaa and Muhu, Estonia, that the negative effects of grassland fragmentation became visible at the plot scale only with decades of delay ("extinction debt").

Semi-natural grasslands are structurally relative simple, but highly biodiverse ecosystems. Co-existence of many different species is governed by many ecological processes, including large mammal grazing, often replaced by extensive human use (e.g. mowing), which interacts with other biotic as well as abiotic factors. Resource limitation is a key factor in maintaining the high diversity and coexistence between plant species in semi-natural grasslands (Pykälä, 2005).

Threats

Among the threat factors of grassland biodiversity, in the Nordic-Baltic region clearly those related to changes in grassland management prevail, in particular abandonment and general intensification, to a lesser extent also overgrazing of un-improved grasslands (Table 3). While natural grasslands lost only a small proportion of their original area to other land uses, secondary grasslands lost about 2/3 compared to their maximum extent, which is the worst situation in all assessed regions of the Palaearctic biogeographic realm (Dengler et al., 2020). However, currently and in the near future further habitat losses due to land use conversions are of subordinate importance. Likewise, altered site conditions, climate change, invasive species and direct impacts of humans and their infrastructure have no or low impact. Only eutrophication is considered of medium importance (Table 3). For the majority of drivers no major change in severity is expected for the next decade, while for abandonment and climate change impacts, we predict an increase in severity (Table 3).

The main threats to grassland ecosystems result from the lack of intact native grazer faunas and the changed agronomic frame around semi-natural grasslands as socio-ecological systems. Grasslands depend on grazing or similar disturbances. However, semi-natural grasslands have a much lower productivity than agriculturally improved grasslands (intensified grasslands in Table 1). Thus, they are the first ones that are either excluded from economic activity of farms by abandonment or intensified to increase their economic value (I. Herzon et al., unpublished material). Accordingly, abandonment and underuse are among the most important drivers of biodiversity and habitat loss during recent decades (Raatikainen et al., 2007; Rüşina, 2017; Lehtomaa et al., 2018; Dengler and Tischew, 2018; Török et al., 2018; see Table 3). Abandonment results from changes in agricultural practices, namely the simplification of farm structure and farming systems. A similarly negative factor is agricultural intensification (Fig. 2B), namely high frequency of cutting, re-seeding, fertilizing and drainage (see Table 3 under “Other forms of intensification” and “Altered water regime”). Generally, intensification affects comparatively fertile grasslands on flat terrain, but abandonment is a bigger threat for dry and wet grasslands, which are located in difficult terrain with harder access for agricultural management. Ultimately, both drivers lead to habitat loss, which in turn results in high fragmentation levels—a threat of grassland maintenance and restoration of its own. The utmost limit of intensification is the conversion of permanent to temporary grasslands, which are reseeded regularly. It results not only in loss of biodiversity but also in decreased chances for restoration of semi-natural grasslands in the future as

Table 3 Overview of the main drivers of grassland biodiversity loss across the Nordic-Baltic region, their current impact (i.e. rate of biodiversity loss caused by them 2010–19) and its anticipated future change (i.e. change in the rate of biodiversity loss in 2020–29 compared to the situation in 2010–19).

<i>Driver</i>	<i>Current impact</i>	<i>Future change</i>
<i>Habitat loss</i>		
Conversion to arable land	Low	± Constant
Afforestation	Medium	± Constant
Mining and energy production	Low	± Constant
Settlements and other infrastructure	Low	± Constant
<i>Changes in grassland management</i>		
Abandonment and underuse	High	Increase
Overgrazing	Medium	± Constant
Other forms of intensification	High	± Constant
<i>Altered site conditions</i>		
Eutrophication (direct and indirect)	Medium	± Constant
Altered water regime	Low	± Constant
<i>Climate change</i>	Low	Increase
<i>Invasive species</i>	Low	± Constant
<i>Direct impact of humans and their infrastructure</i>		
Military and armed conflicts	None	± Constant
Recreation activities	Low	± Constant
Collecting wild plants and hunting	Low	± Constant
Wildlife loss due to electrocution, wind farm collision or traffic	Low	± Constant
Wildfires caused by humans	None	NA

“Current impact” is given on a five-step ordinal scale (none–low–medium–high–very high), while “Future change” was assessed on a three-step ordinal scale (“decrease”–“± constant”–“increase”), where “± constant” means that the biodiversity loss due to this driver is expected to continue in the next decade at the same level as in the previous decade (± 10%). Please note that in order to get an assessment of the expected impact during the next decade, both columns have to be combined: For example, if the current impact is “medium” and the future change is predicted to be an “increase”, the future impact would be “high” (or even “very high”). Likewise, even if the importance of a driver is predicted to decrease, it will in most cases still cause additional biodiversity loss during the next decade. “NA” = not assessed.

restoration in arable land is less successful due to high nutrient levels. A comparison of the Baltic States with three Nordic countries (Norway, Sweden, Finland) showed that the temporary grassland share was as high as 70%–90% in Finland and Sweden, but less than 60% in the Baltic States and Norway (I. Herzon et al., unpublished material). Conversion to arable land and afforestation (Fig. 2H) is also a common threat throughout the region (Table 3). In Norway, habitat loss due to the building of new homes, holiday houses in mountain regions, and roads threatens semi-natural grasslands. Specific threats to wooded pastures and meadows are imbalanced tree stand age structure that causes a lack of trees of certain age brackets, thus reducing the habitat conditions for long-term survival of tree-dependent species (Bergmeier et al., 2010).

Invasive species and climate change are reported as minor threats at present but with potential to increase in the near future (Table 3; see also Dengler and Tischew, 2018; Török et al., 2018). Mostly species-poor grasslands, for instance semi-improved grasslands and grasslands with high disturbance levels, are prone to invasions. The tall forbs *Solidago canadensis* and *S. gigantea* as well as *Impatiens glandulifera*, *Fallopia sachalinensis*, *F. japonica*, in Latvia and Lithuania also *Echinocystis lobata*, *Rumex confertus*, *Bunias orientalis*, and the shrubs *Amelanchier spicata* and *Rosa rugosa* are currently the most widespread neophytes that tend to form dominant stands in former grasslands (Dengler and Tischew, 2018; Gudžinskas et al., 2014). As a result of abandonment and eutrophication, native species such as *Calamagrostis epigejos* and *Pteridium aquilinum* are gaining ground, leading to species-poor mono-dominant stands (Dengler and Tischew, 2018). Other winner species resulting from land-use change are *Anthriscus sylvestris*, *Aegopodium podagraria*, *Arrhenatherum elatius*, *Chaerophyllum aromaticum*, *Galium aparine*, *Urtica dioica*, *Phragmites australis* (in wet grasslands) and *Deschampsia flexuosa* (in dry sandy grasslands) (e.g. Rūsiņa, 2017).

Continuous warming has been documented during spring and summer in the southern parts and during autumn and spring in the northern parts of the Baltic Sea basin (BACC II Author Team, 2015). The duration of the cold season has decreased, duration of precipitation periods has increased and there is an increased risk of extreme precipitation events. For the Baltic States, there has been a significant increase in the number of hot days and nights and the number of heat waves, as well as a significant decrease in the number of frost days. Similar tendencies are projected also in the future (BACC II Author Team, 2015). Widespread increase in atmospheric temperatures and moisture content seems to have rather positive direct effects on vascular plant species richness in grasslands of the region (Dengler and Tischew, 2018). Increased plant species diversity at mountain tops (Kullman, 2010) and alpine insect diversity as a response to glacier retreat (Franzén and Öckinger, 2012) are reported. Still, the high-altitude fauna is expected to be out-competed when temperatures rise (Franzén and Öckinger, 2012). Higher temperatures will promote northward and upward shifts in the boundaries of species occurrence, sometimes at the cost of the original species in that area. For instance, the range of *Lolium perenne*, which is a non-native species in the northern part of the region, will expand. It will change species composition, as it is a competitive species commonly dominating the sward of semi-natural pastures in Central Europe (Höglind et al., 2013). Wet grasslands of the Northern Europe can experience negative impacts due to less ice and snow cover, leading in changing moisture regime during spring. Floodplain grasslands will experience less spring flooding (Apsīte et al., 2013), meaning also less possibilities for dispersal of grassland flora and fauna which is facilitated by floods. It could partly be mitigated by greater water availability as precipitation is forecasted to increase for Northern Europe, thus offering opportunities to restore or create new wet grasslands from intensively managed drained grasslands or croplands (Joyce et al., 2016).

While the negative effects of eutrophication are considered overall as medium (Table 3), there are strong regional differences regarding the atmogenic nitrogen deposition, which for semi-natural grasslands usually is the main source of eutrophication. Denmark is highly affected, Lithuania moderately, Latvia and the southernmost parts of Norway and Sweden at a low level, while this driver is not relevant at all in the majority of the region (Sutton et al., 2011).

Conservation and Restoration

As natural and semi-natural grasslands are highly important for biodiversity conservation in the region, while at the same time many of their types are threatened (Janssen et al., 2016; see Table 2), various grassland types are protected nationally in the countries of the region. Moreover, the European Union, via its Habitats Directive (European Commission, 2013), protects 24 grassland types of the region as of “community importance” (Table 2). Of these, nine are priority habitats, subject to a particular strict protection and monitoring across the countries: “Boreal Baltic coastal meadows” (Habitat type 1630 in Table 2), “Fixed coastal dunes with herbaceous vegetation (grey dunes)” (2130), xeric sand calcareous grasslands (6120), important orchid sites among the “Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*)” (6210), “Species-rich *Nardus* grasslands, on siliceous substrates in mountain areas (and submountain areas, in Continental Europe)” (6230), “Fennoscandian lowland species-rich dry to mesic grasslands” (6270), “Nordic alvar and precambrian calcareous flatrocks” (6280), “Fennoscandian wooded meadows” (6530) and “Limestone pavements” (8240).

Semi-natural grasslands and wooded meadows are maintained through appropriate grazing and haying pressure. Clearing of scrub is an essential practice for restoration and for management in areas where grazing pressure is insufficient. In the case of seashore meadows, clearing of reeds at the shoreline is frequently necessary for meadow restoration and may be needed periodically even in grazed seashore meadows. Substantial tree felling and clearing of shrubs, such as *Juniperus communis*, is necessary for restoration of afforested and abandoned sites, respectively. As a way of combating abandonment of grasslands, alternative management strategies and uses for biomass beyond fodder have been explored. Since 2010, Estonia has used hay and reed biomass from the extensive semi-natural grasslands of Matsalu National Park to heat the Lihula District, an area of 384 km² (Kask, 2014).

The European Union supports semi-natural grasslands through agri-environment-climate schemes for management and non-productive investment to improve the condition of semi-natural grasslands. Each member country applies these mechanisms, along with own country funds and programs, to support grasslands conservation and restoration according to their agriculture programs

and biodiversity strategies. Additionally, there are specific schemes to support cultivated (intensified) grasslands. Payment amounts, requirements for management and minimum area and type of grassland included in schemes vary across the countries.

The main principles of management for the semi-natural grasslands is no external inputs and sufficient grazing pressure or other management to retain the characteristics that define the habitat type. Development and implementation of site-specific management plans are increasingly being recognized as important parts of sustainable conservation of semi-natural grasslands but are not yet universally practiced. In Finland, for example, site-specific management plans are a requirement for farmers or landowners to receive the agri-environment-climate measure for semi-natural grasslands. Latvia began training farmers in making management plans for their grasslands in 2016. Agri-environment-climate schemes are primarily actions-based, while schemes based on management outcomes, such as those reported from Baden-Württemberg, Germany (Russi et al., 2016), and the Burren, Ireland (Dunford, 2016) are mainly lacking (Herzon et al., 2018), although Finland has a two-tier payment system, with the higher payment reserved for sites deemed nationally or regionally valuable. Countries use obligatory annual management practices and management diaries, along with inspections, as a way to assure that management is carried out. An outcome of support payments being action rather than results-based is that remedial actions such as ploughing to combat invasive species and reseeding are generally proscribed in the schemes.

Land use history affects the biodiversity of sites and their restoration potential, and research supports that grasslands (semi-natural pastures and meadows) have a measurable positive effect on biodiversity compared to other farmland land-use types (Santangi et al., 2019). The most valuable semi-natural grasslands have been under continuous management for hundreds of years, but these are increasingly rare. Commitment to management and restoration varies across the Nordic-Baltic region. Estonia has implemented a large-scale restoration of its seashore meadows and alvars and revitalized associated grazing in recent years (<https://life.envir.ee/english-project-life-alvars>; Kasari et al., 2018). The primary concern for semi-natural grasslands in Latvia is finding ways to make the low-input hay-making and pasturing viable for farmers. Finland recognizes the dire state of its semi-natural grasslands and grazed forests, collectively known as traditional rural biotopes, as the country's most threatened habitat type but has been unsuccessful in increasing the overall area under management (Lehtomaa et al., 2018). In Norway, semi-natural mown grasslands (hay meadows) are critically threatened (CR, Artsdatabanken, 2018), and are a "selected habitat type" according to the Norwegian Act on Natural Diversity. Since 2009, Norway has run an Action Plan for Hay Meadows (Direktoratet for naturforvaltning, 2009), through which it has organized management of approximately 700 hay meadows. Financial support is provided to landowners and farmers who carry out management of the hay meadows according to a plan made by biologists (Miljødirektoratet, 2016).

Fodder potential of the semi-natural grasslands is largely determined by the northern conditions and the variation in fodder quality and quantity according to habitat type. In the cases of seashore meadows and other lush grasslands, grazing, which should start as soon in the season as possible, is often delayed by the wet spring, which can result in decreased palatability of plants and decreased grazing when the animals are eventually turned out to pasture. Dry summers with extreme drought events will be more pronounced in southern part of the region (BACC II Author Team, 2015), and may also negatively affect fodder quality and regrowth. Along the Baltic Sea coast, occurrence of blue-green algae may result in animals having to be removed from the coastal meadows altogether because the grazing animals cannot drink the contaminated water.

Acknowledgments

We are grateful to Iwona Dembicz (University of Warsaw and Zurich University of Applied Sciences) for providing nice photos from various locations in the study region.

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Grasslands of Eastern Europe

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This chapter was solicited and edited by Jürgen Dengler and Péter Török on behalf of the Eurasian Dry Grassland Group (EDGG).

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Abstract

Grasslands cover around 282,000 km², corresponding to 14.6% of the total area in the countries of Eastern Europe, here defined as East Europe, Eastern Central-Europe, and the non-Mediterranean part of the Balkan Peninsula. Primary (steppes, alpine grasslands, azonal and extrazonal grasslands) and secondary grasslands (created mostly by forest cuts) provide a wide range of ecosystem services, such as biomass production and food for grazing animals and other herbivores, carbon storage and sequestration, home for pollinators as well as for migratory and breeding birds, water infiltration, purification and storage, erosion prevention and recreation. Both primary and secondary grasslands in Eastern Europe harbor a rich flora and fauna, but they are threatened by area loss, the twin threats of intensification and abandonment, invasive species encroachment, and climate change. Large areas of grasslands in the lowland regions have been converted to croplands, and the remaining grassland fragments are in general degraded by intensified use. Intensified use and application of tillage, drainage, intercropping, high intensity grazing or the use of pesticides, mineral and organic fertilizers have a detrimental effect on flora and fauna. In contrast, low accessible areas in mountains, foothills or other marginal areas, the traditional grassland management is abandoned. To recover or improve grassland biodiversity, in many countries, the re-introduction of traditional management regimes by mowing or grazing have been suggested. In case of completely destroyed grasslands, restoration of grassland vegetation and diversity by spontaneous succession and/or technical reclamation are necessary. While in large-scale restoration programs successes were often reported, it was also noted by the authors that the success of restoration was strongly influenced by the availability of high-quality grasslands in the landscape, acting as donor sites or spontaneous sources of propagules. High quality grassland fragments act as hotspots of biodiversity in landscapes dominated by agriculture; thus, their preservation should be prioritized in conservation actions.

Delimitation and Physiogeography

Grasslands in Eastern Europe cover around 282,000 km², approximately 14.6% of the total area of the countries in Eastern Europe, Eastern Central-Europe and the non-Mediterranean part of the Balkan Peninsula (Fig. 1). With high differences between countries or

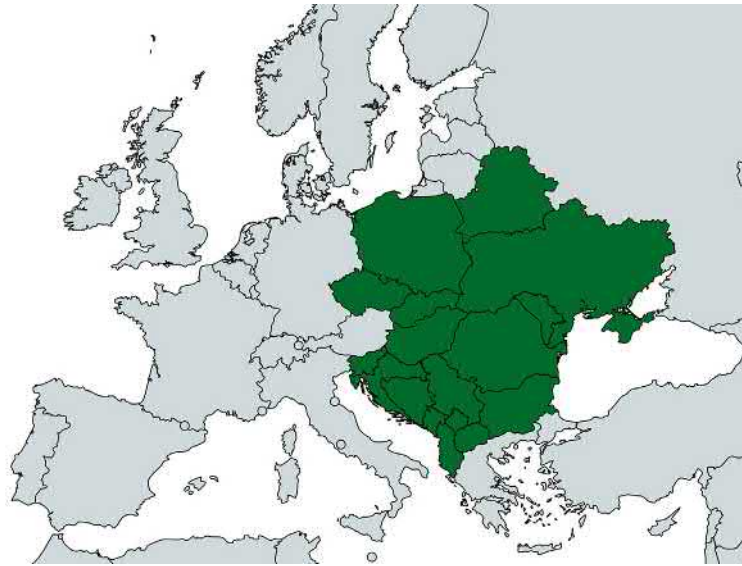


Fig. 1 The Eastern European region. The region covers countries of East Europe, Eastern Central-Europe, and the non-Mediterranean part of the Balkan Peninsula. The map was created by Map Chart (<https://mapchart.net/>).

subregions, the proportion of high natural value grasslands can be up to 70% of permanent grassland area (Török and Dengler, 2018; Török et al., 2018).

The Eastern European region is characterized by a cool continental climate with an increasing Mediterranean influence in the south (Peel et al., 2007). The region clearly divides into two main subregions: Central European highlands and mountain chains (the Carpathians, Balkan- and Crimean Mountains) with their intermountain basins (e.g., Great Hungarian Plain) in the South and Southwest and Central and Eastern European Lowlands in the North and Northeast. While the landscape of the southern part of the region is related to the older (Paleozoic or Mesozoic) bedrock or Holocene alluvial deposits, the surface of the lowlands in the north was shaped mostly during the Pleistocene. Young glacial landscapes with lakes are only present in the northernmost part of the region; the vast areas more to the south were glaciated earlier and are covered with older, denudated and transformed tills or glacio-fluvial deposits. Moreover, south of the glaciation borders, a thick loess cover accumulated during the Pleistocene, dominating the landscape and masking older landforms. The region is characterized by the presence of many large rivers (e.g., Vistula, Danube, Dnieper, Dniester, Siverskyi Donets and tributaries), the valleys of which are environmentally rich and harbor valuable grassland sites.

Eastern Europe is the western border of the Eurasian steppe and forest steppe zones, primary steppe grasslands and forest-steppe mosaics historically covered large areas in Bulgaria, Hungary, Moldova and Ukraine (Wesche et al., 2016; Török et al., 2018). A considerable part of the region is situated in the zones of deciduous forests and forest-steppes, where the primary vegetation consists of deciduous and mixed forests or forest-steppe mosaics (Metzger et al., 2005; Erdős et al., 2018a). These areas are dominated mostly by secondary grasslands, created after forest cuts and maintained by regular mowing and/or livestock grazing (Dengler et al., 2014).

Origin and Biodiversity of Grasslands

The grass family appeared almost 90 million years ago, but its diversification and the development of grassland ecosystems happened much later (Gibson, 2009). Grassland ecosystems in South America appeared about 34 million years before present (BP), whereas in Europe the steppe-like grasslands occurred probably 5 million years BP. Natural grasslands have existed continuously since the Pleistocene (2.4 million years BP), and during glacial periods they covered the majority of the European continent in form of steppe-tundra in the north and xerothermic grasslands in the south. It is assumed that present steppes and steppe grasslands in the forest steppe zone (i.e., primary grasslands) originated in the Holocene from the near glacial steppe-tundra (also called “tundra-steppe” or “mammoth steppe”), which dominated the landscape of the region in cold periods of the Pleistocene (Binney et al., 2017; Chytrý et al., 2017). In Ukraine, the steppe range was slightly changing after the last glaciation according to climate fluctuations, being more mesophilous during the relatively warm and humid Holocene Climate Optimum (9000 to 5000 BP; Kremenetski, 1995). Simultaneously, the migration of species from Mediterranean and Asian glacial refugia enriched the steppe species pool during the Holocene, leading to the development of the current European steppe (Korotchenko and Peregrin, 2012). Recent paleoecological research has revealed that, during the climatic optimum, when the large-scale

expansion of dense, deciduous forests occurred in the region, patches of natural grassland ecosystems survived in favorable locations even outside of what is traditionally regarded as steppe and forest-steppe zone (Moskal-del Hoyo et al., 2018; Pokorný et al., 2015). Those isolated refugia, as well as the continuous steppe zone, served as important sources of species for many types of semi-natural grasslands created by humans in the forest zone (Kajtoch et al., 2016).

In the north of the region the biodiversity of the more humid semi-natural grasslands probably originates from both the open forests and from wetlands (mostly fens and floodplains). It is believed that the large ungulates which lived there, including the aurochs and wisent, had a potential to create gaps or maintain openings in the forest resulting from natural disturbances such as windthrows or flooding. Moreover, beaver activity could create treeless areas around watercourses (Hejcman et al., 2013). Noticeably, there is a large number of grassland species with distributions related primarily to the forest zone of Eurasia, indicating the existence of open habitats long before the Neolithic revolution (Pärtel et al., 2005). Such species include *Iris sibirica*, *Gladiolus imbricatus*, *Maculinea teleius*, and *Maculinea alcon*. During interglacial periods their areas decreased because of forests spreading (Pärtel et al., 2007). During the last glaciations in the Holocene, 7500–6800 years BP, neolithic people developed agricultural practices, mainly by introducing grazing, which resulted in the alteration of forests towards semi-natural grasslands (Hejcman et al., 2013).

Palaecological studies validated that some semi-natural grasslands in Eastern Europe already existed between 8500 and 6000 BP (Price, 2000; Barczy et al., 2006), but most of the grasslands of secondary origin were established much later, in the Middle Ages. These secondary grasslands were mostly created by clear-cutting of various types of forests, and reached their largest extent during the last 200 years (Török et al., 2018). For example, it is thought that mesophilous meadows of the *Arrhenatherion elatioris* have developed after medieval times (Poschlod et al., 2009; Hejcman et al., 2013); however, they are among the most widespread meadows today. Pastures are in general older than mown meadows as in most regions the scythe appeared much later than the livestock grazing systems. Also, the age of grasslands is increasing from the North to the South, because regions with drier and warmer climate favoring grassland vegetation are more frequent in the Southern part of the region, while in the North spontaneous shrub and tree encroachment highly suppressed grassland vegetation (Török et al., 2018).

As the steppes and forest-steppes of Eastern Europe constitute the western border of these biomes, many species of the steppe fauna have their distribution limits in the region, like the bobak marmot (*Marmota bobak*), the great jerboa (*Allactaga major*), the thick-tailed three-toed jerboa (*Stylodipus telum*), the gray dwarf hamster (*Cricetulus migratorius*), the steppe lemming (*Lagurus lagurus*), the greater mole-rat (*Spalax microphthalmus*), the northern mole vole (*Ellobius talpinus*), the steppe polecat (*Mustela eversmannii*), the marbled polecat (*Vormela peregusna*), and the steppe ratsnake (*Elaphe dione*) (Akimov and Radchenko, 2009; IUCN, 2019). However, the ranges of some species are limited to Eastern European steppes and semi-natural grasslands, e.g., that of the Podolsk mole-rat (*Spalax zemni*), the sandy mole rat (*S. arenarius*), the Balkan mole-rat (*S. graecus*), and the European ground squirrel (*Spermophilus citellus*; the range of this species extends to Austria). For the speckled ground squirrel (*Spermophilus suslicus*) Eastern Europe together with the European part of Russia constitute the whole distribution range of the species. Especially rich in endemic species, mostly invertebrates, are the steppes of the Crimean Peninsula (Akimov and Radchenko, 2009).

The natural and the semi-natural grassland flora of the lowlands in the region is dominated by species with wide Euro-Siberian distribution. However, there is a group of species, also referred to as Pannonian species, which have most of their range within the described region. They include such important grassland specialists as *Rhinanthus borbasii*, *Festuca vaginata*, *F. wagneri*, *Colchicum arenarium*, *Dianthus diutinus*, *Iris arenaria*, *Pulsatilla pratensis* ssp. *hungarica*, and *Linum hirsutum*. Much more species with limited distributions are related to the mountain ranges in the south of the region, especially those of the Balkan Peninsula, e.g., in Central Serbia and Kosovo (41% of the total number of 490 Balkan endemic plants were recorded in the class Festuco-Brometea (Ácić et al., 2015)).

Like in other parts of Europe, the flora and fauna of semi-natural grasslands contribute much to the overall biodiversity of the region. However, the diversity of these ecosystems is strongly shaped by management regime and human-controlled landscape factors (e.g., a large proportion of grasslands in the surrounding landscape supports the biodiversity of the given grassland area; Janišová et al., 2014). The oligo- to mesotrophic, traditionally managed, semi-natural, temperate grasslands of Eastern and Central Europe hold world-records for vascular plant diversity at small spatial scales (Vassilev et al., 2011; Wilson et al., 2012; Chytrý et al., 2015).

In Romania, 43 species were recorded in a plot of 0.1 m², and 98 within a 10-m² plot (Dengler et al., 2009), while in the White Carpathians, a mountain range on the border between the Czech Republic and Slovakia, there were 67, 88 and 131 vascular plant species in plots of 1, 4 and 49 m², respectively (Merunková et al., 2012). Semi-natural grasslands are important not only for plant biodiversity but also for other organisms. It is, for example, estimated that around 74% of European grasshopper species depend on open habitats (Hochkirch et al., 2016). Semi-natural grasslands seem to be equally important for butterflies (Skórka et al., 2007) and birds (Hoste-Danyłow et al., 2010). Despite recently observed negative trends, eastern European semi-natural grasslands are still hosting higher biodiversity when compared to their western counterparts (Batáry et al., 2010; Żmihorski et al., 2016).

Typology of Grasslands

Grasslands in Eastern Europe can be classified as primary (natural) and secondary (semi-natural) grasslands. Primary grasslands cover sites that are in general unfavorable for the establishment of trees. The most important types are the following:

Steppes and Steppe Grasslands in Forest Steppe Mosaics

Steppes are primary climatogenic grasslands on dry habitats, which are not suitable for the establishment of trees in hilly regions, foothills, and lowlands (Fig. 2A). Steppes are very diverse and mosaic-like habitats characterized by perennial graminoids of *Bromus*, *Elymus*, *Agropyron*, *Festuca*, and *Stipa* species. They are in general rich in forbs, the most frequent genera being *Achillea*, *Artemisia*, *Aster*, *Astragalus*, *Centaurea*, *Inula*, *Linum*, and *Salvia*. There is an early spring aspect characterized by several early flowering species from the genera *Adonis*, *Gagea*, *Ornithogalum*, *Pulsatilla*, and *Tulipa*. Steppe grasslands in Eastern Europe are the westernmost localities of their Eurasian distribution. (Wesche et al., 2016; Török et al., 2016a). In the steppe zone, historically extended steppe grasslands were typical for loess deposits, mostly on chernozemic soils. In the forest-steppe zone, steppe grasslands are components of forest-



Fig. 2 Grassland types of the region: (A) steppe grassland on chalk outcrops, Dvorichansky National Nature park, Kharkiv oblast, Ukraine; (B) steppe grassland patch in a forest-steppe of Northern Hungary; (C) inland saline grassland, Oril river floodplain, Poltava oblast, Ukraine; (D) coastal halophyte vegetation, Dzharylhach Island, Kherson oblast, Ukraine; (E) sand steppe, Oleshkivsky Sands National Nature park, Kherson oblast, Ukraine; (F) rocky grassland, Svydovets ridge, Carpathian Mountains, Ukraine; (G) dry secondary grassland on limestone, Bükk Mountains, Hungary; (H) mesic secondary grassland, Lower Dnieper floodplain, Kherson oblast, Ukraine. Photos by Anna Kuzemko (A, C, D, E and H), Roman Kish (F), and Péter Török (B and G).

grassland complexes (Fig. 2B, Erdős et al., 2014; Erdős et al., 2018a,b). In the region, remaining stands of this grassland type are typical in the Czech Republic, Hungary, Moldova, Poland, Romania, Ukraine, and the countries of the Northern Balkan. Based on recent estimates, the overall extent of this type of grasslands in the region is around 1.1 million hectares (Török and Dengler, 2018).

Alpine Grasslands

Alpine grasslands are climatogenic grasslands occurring in regions that are too cold for the establishment of trees. Based on a recent estimate, there are 500,000 ha of these grasslands in the Eastern European region (Török and Dengler, 2018), but this grassland type is not discussed in detail in this article.

Azonal and Extrazonal Grasslands

Pedogenic or topogenic grasslands, where special habitat properties prevent the establishment of trees. The extent of this grassland type is estimated to be about 400,000 ha in Eastern Europe (Török and Dengler, 2018). There are several subtypes within this grassland type:

Coastal and inland saline grasslands

Pedogenic grasslands in lowland regions, where the astatic water availability and high salt content of the soil prevents the establishment of trees (Fig. 2C and D). These grassland types are the most well-preserved in Eastern Europe, as their soil is unsuitable for agricultural production and can be utilized only with extensive pasture management. The most typical inland saline vegetation occurs in large extents in Hungary and Ukraine, but small fragments are present in all countries with dry lowland regions like Slovakia, Serbia, Bulgaria or Macedonia (Eliáš et al., 2013). These types of grasslands are characterized by a high cover of tussock-forming fescue species (*F. pseudovina*, *F. rupicola*, *F. regeliana*), and several *Puccinellia* and *Juncus* species are also typical, especially in wet places at slightly lower elevations. Characteristic forbs are halophytes or other salt-tolerant species in the genera *Artemisia*, *Aster*, *Limonium*, *Plantago*, *Podospermum*, *Salicornia*, *Salsola*, *Spergularia*, and *Suaeda*.

Sand steppes and coastal sand grasslands

These pedogenic grasslands cover acidic to calcareous sands which are in general unsuitable to sustain trees (Fig. 2E). Their vegetation is characterized by tussock-forming grasses, including fescues (*Festuca vaginata*, *F. pseudovina*, *F. psammophila*, *F. polesica*, *F. beckeri*), *Corynephorus canescens*, *Koeleria glauca*, *Stipa capillata*, and *S. borysthena*. Also, several small clonally spreading *Carex* species are typical (e.g., *C. stenophylla*, *C. praecox*, *C. supina*, and *C. colchica*). Many short-lived forbs are characteristic in the spring, including the genera *Arenaria*, *Cerastium*, *Draba*, *Erophila*, and *Veronica*. Cryptogamic species (mosses and lichens) can reach considerable cover in this type of grasslands. Sand grasslands occurring in the lowlands of the Eastern European region are typical in the countries of Belarus, Croatia, the Czech Republic, Hungary, Poland, Serbia, Slovakia, Slovenia, and Ukraine.

Grasslands on shallow rocky substrates

Because of the steep slopes, high erosion enables only the development of shallow and rocky soils (skeletal soils), which is in general unsuitable for the establishment of trees. This topogenic grassland type typically occurs in small patches near the top of hills and middle mountains (Fig. 2F). The species composition is characterized by xerophytes, and the species composition and richness is strongly influenced by the type of the bedrock (the most species rich grasslands are on limestone or dolomite bedrock; grasslands formed on volcanic or metamorphic bedrock are less species rich). Typical graminoids are *Festuca*, *Bromus*, *Poa*, and *Stipa* species. Frequent forb genera are *Campanula*, *Cerastium*, *Inula*, *Potentilla*, *Spergula*, and *Veronica*. In addition, many species of the Brassicaceae family, as well as several succulent species from the genera *Jovibarba*, *Saxifraga*, *Sedum*, and *Sempervivum* occur in these grasslands.

Secondary grasslands

Secondary grasslands were created by the anthropogenic suppression of phanerophytes and are sustained by regular management—mostly mowing and/or livestock grazing. They can be formed on various substrates from fine alluvial deposits to solid bedrock. Their secondary origin does not necessarily mean that they are less important in biodiversity conservation. In many cases, they are valuable and species rich habitats, sustained by several hundreds of years of extensive management. Secondary grasslands can be classified into the following subtypes:

Dry and Semi-Dry Grasslands

The most valuable meso-xerophytic secondary grassland types, which occur on shallow to deep soils, formed mostly on calcareous or volcanic bedrocks in the whole region, from lowlands to mountains (Fig. 2G). Especially the calcareous types harbor many steppe elements and are extremely species-rich habitats, threatened in many countries by woody encroachment (Eliáš et al., 2018). Dry grasslands are also characterized by high cryptogam diversity. Characteristic graminoids are tussock-forming and rhizomatous species like *Brachypodium pinnatum*, *Elymus hispidus*, *Bromus erectus*, *Danthonia alpina*, *Sieglingia decumbens*, *Avenula pubescens*, *Nardus stricta*, *Festuca ovina*, *Melica altissima*, *M. transylvanica*, *Carex caryophyllea*, and *C. montana*. Characteristic forbs are in the genera

Allium, *Campanula*, *Centaurea*, *Clinopodium*, *Cirsium*, *Geranium*, *Inula*, *Lathyrus*, *Origanum*, *Peucedanum*, *Salvia*, *Thymus*, *Trifolium*, *Verbascum*, and *Vicia*.

Mesic to Wet Grasslands

These types of secondary grasslands are the most common in the region from lowlands to mountain areas. In general they cover medium to deep, in most cases nutrient-rich mesic to wet soils (Fig. 2H). Most characteristic species are generalist graminoids and forbs. Typical tussock forming and rhizomatous graminoids include *Arrhenatherum elatius*, *Alopecurus pratensis*, *Agrostis tenuis*, *Anthoxanthum odoratum*, *Briza media*, *Bromus inermis*, *Cynosurus cristatus*, *Festuca pratensis*, *F. rubra*, *F. arundinacea*, and *Poa pratensis*. Small-growing *Carex* species like *C. pallescens*, *C. panicea*, and *C. tomentosa* are also important. More moist types harbor *A. stolonifera*, *Molinia arundinacea*, *Deschampsia caespitosa*, *Poa trivialis*, further *Carex* species including *C. nigra*, *C. flava*, and *C. flacca*, and *Juncus* species (e.g., *J. conglomeratus*, *J. effusus*). They harbor several forb species from the genera *Achillea*, *Chrysanthemum*, *Dactylorhiza*, *Gentiana*, *Leontodon*, *Lychnis*, *Medicago*, *Mentha*, *Orchis* s.l., *Ranunculus*, *Rhinanthus*, *Stellaria*, *Trifolium*, and *Veronica*.

Ecology and Biodiversity Patterns

As it was mentioned earlier, natural grasslands of the region are usually climatogenic (steppes, steppe grasslands in forest steppe mosaics, and alpine grasslands), pedogenic (sand steppes and coastal sand grasslands), or topogenic (grasslands on shallow rocky substrates). However, besides the crucial role of climate and extreme habitat conditions which prevent woody encroachment, the maintenance of ecosystem functioning, high biodiversity and typical species composition of natural grasslands can also be driven by other factors. For example, in the steppe ecosystem large mammal herbivores and fires are consumers of vegetation, preventing steppe ecosystems from reaching their climatic potential, and thus preventing the accumulation of litter and subsequent changes towards more mesophilous grasslands or shrublands. Many steppe nature reserves face the risk of losing biodiversity due to the implementation of fire prevention measures and the lack of important wild ungulates such as horses and saiga (the latter of which became locally extinct because of hunting and habitat fragmentation) (Havrylenko, 2011).

Microclimatic gradients are important for both natural and semi-natural grasslands. Vegetation typical for more northern zones or more mesophilous sites are occupying northern exposition, while more xerophytic grasslands occupy south-facing slopes (Sudnik-Wójcikowska and Moysiienko, 2008; Sutcliffe et al., 2016). Soil and bedrock gradients are also important in both natural and semi-natural grasslands. The main drivers of species composition are soil pH (e.g., *Nardus* dominated grasslands occur on acidic bedrock), soil depth (e.g., *Festuca pallens* grasslands occur on rock outcrops), and soil texture (sand grasslands on coarse sediments and more steppe-like grasslands on loess). Moisture gradient is important predominantly in semi-natural grasslands, but its role can also be recorded in natural steppes, with depressions being occupied by more mesic vegetation or being prone to salinization. Besides the amount of available moisture, its seasonal variation is also important (e.g., the inundation time or its temporal fluctuations).

However, the most crucial driver of species composition in semi-natural grasslands is the management regime. Mowing promotes graminoids, while grazing usually suppresses them. Furthermore, grazing allows more forb species to develop and replenish (small disturbances and open soil surfaces created by trampling are crucial for the germination of many grassland species). The type of grazing livestock can also be an important factor. Cattle and horses eat the taller grasses while sheep prefer forbs and short grasses (Tóth et al., 2018). Goats, which are browsers, can reduce shrub encroachment into the grassland (Elias et al., 2018). Mowing regime can also influence species composition; for example, early mowing favors early-flowering species. The importance of the fertility gradient should also be emphasized. It is especially important in semi-natural grassland types as natural primary productivity is controlled by moisture deficit. Recent studies point out the role of limiting nutrients in shaping the species composition of grasslands, with different species adapted to N and P limitation (Roeling et al., 2018).

Biodiversity patterns (especially of plants) can be controlled by the same gradients as the species composition of grasslands. In general, the biodiversity of various groups of organisms inhabiting grasslands (especially drier, more xerothermic types of grasslands) is decreasing from south to north in the region, mostly due to the climate and the geological history (glaciation and later the expansion of forests), as well as the mountain ranges forming a barrier for the migration of species from the south (like the Sudety and the Carpathian Mts). However, at regional scales, the patterns can be opposite. For example, in natural steppes in Ukraine plant diversity decreases from the forest-steppe zone to the south, along with the drought stress becoming more intensive. Management type is another important driver of species richness in grasslands, in particular in semi-natural ones. Traditional management usually supports biodiversity, while too intensive management leads to its decline (Cremene et al., 2005). The highest fine-scale richness of vascular plants occurs in semi-natural mown grasslands (Turtureanu et al., 2014), but grazing and small disturbances created by animals can also be important for the diversity of this taxonomic group (Enyedi et al., 2009). It is worth mentioning that the plant richness of natural grasslands, like steppes, is enhanced by grazing and fires (Kuzemko et al., 2016).

Typically, the relationship of pH with fine-scale plant diversity in the region seems to be hump-shaped, with the highest richness occurring under neutral or slightly basic conditions, although under drier conditions the relationship may be negative or non-existent/non-detectable (Palpurina et al., 2017). Well known is the hump-shaped relationship between primary productivity and plant species richness (Fraser et al., 2015). As it was mentioned before, in natural grasslands primary productivity is controlled by

climate (with the resulting pattern of richness in steppe), but in semi-natural grasslands it depends on fertility. Limiting nutrients can influence the richness or the richness-productivity pattern (Palpurina et al., 2019).

The relationship between biodiversity and productivity in grassland ecosystems was much studied (e.g., Grime, 2001; Kelemen et al., 2013; Cerabolini et al., 2016; Sonkoly et al. 2019). The most important factors affecting the productivity of grassland communities are water and nutrient availability, which influence the biodiversity of the community. High values of phosphorus, nitrogen and potassium decrease the biodiversity of grasslands (Merunková and Chytrý, 2012). Bernhardt et al. (2010) reported some data on grassland productivity from different parts of the EU. The regions with the lowest productivity are located in the Mediterranean, with annual yields limited to 1.5 t per ha or even less; slightly higher yields are obtained for mountain areas, which are more mesic, e.g., the Pyrenees and the mountains of the Balkan Peninsula. The Central EU countries (Poland, the Czech Republic and Slovakia) reach fairly high yields, around 4 t per ha, while in the steppe conditions of Hungary, Bulgaria and other southeast European countries, the yields are much lower—about 1.5 t per ha, because of unfavorable water regime and drought.

Ecosystem Services and Threats

Natural and semi-natural grasslands provide a wide range of ecosystem services, such as biomass production and food for grazing animals and herbivores, carbon storage and sequestration, home for pollinators as well as for migratory and breeding birds, resources for flood reduction, water infiltration, purification and storage, erosion prevention and recreation (Peciña et al., 2019). The conversion of grassland into arable land decreases soil carbon because of the reduced carbon input from litter and the loss of carbon by tillage (Jones and Donnelly, 2004). Plant diversity and soil organic carbon pools are thought to be the major factors for the provision of several ecosystem services, mainly pollination, herbs for traditional medicinal use, nutrient cycling, nutrient retention and biomass production (Peciña et al., 2019). In addition to cultural and aesthetic values, grasslands play an important role in nutrient cycling, balancing of the local climate and soil erosion, and sustaining pollinators and biological control agents (e.g., Fantinato et al., 2018). Grassland ecosystems have also attracted substantial scientific and policy interest because of their potential role as sinks or sources for atmospheric carbon dioxide. Conversion of arable land into permanent grassland is one measure that is believed to have a considerable carbon sequestration potential (Ammann et al., 2007). The supply of multiple ecosystem services is decreasing significantly worldwide because of pressures of climate change and other anthropogenic factors, including overgrazing, intensive agricultural production, deforestation, and urbanization (Costanza et al., 2014). Both climate change and grazing exert great influence on the supply and interrelation of ecosystem services (Hao and Yu, 2018). However, modern agricultural practices, mainly referring to intensive agriculture, as well as fragmentation and land-use abandonment in recent decades, have caused a biodiversity loss and consequent conservational concerns, due to negative effects of value and provision of grassland ecosystem services.

Area Loss

The most alarming threat for most of the natural communities including grasslands is area loss. Important causes of area loss are the (i) conversion to croplands and other agricultural areas, (ii) afforestation, establishment of tree plantations and spontaneous forest succession, (iii) and urbanization. The most threatened grasslands are in the lowlands, embedded into intensively managed croplands. Recent estimates suggest that in the last 200 years at least 50% of all grassland area has vanished in the Eastern European region (Török and Dengler, 2018). The area loss is strongly variable between grassland types and/or regions. Bíró et al. (2018) summarized the area loss of 8 natural and semi-natural grassland types in Hungary. They found that the lowest decrease in area occurred in saline grasslands (39%), which are unsuitable for agricultural production, while other grassland types displayed 85–98% decrease in area. A similarly high decrease was reported for the western part of steppes and forest steppes (Deák et al., 2016; Wesche et al., 2016; Erdős et al., 2018b).

One of the consequences of habitat loss is high fragmentation and the isolation of remaining grassland patches, which are exceptionally severe in Eastern European steppes. For example, in the Lugansk region (Ukraine) the formerly continuous steppe vegetation has survived in 2000 fragments that are mostly surrounded by intensive agricultural landscapes (Parnikoza and Vasiluk, 2011). The increasing fragmentation and isolation of semi-natural grasslands is a serious threat for grassland biodiversity in many other countries in the region. Isolation can lead to local extinctions (while immigration from other patches has low probability) and can negatively influence the genetic structure of the populations, as was found in steppe enclaves of southern Ukraine (Dembicz et al., 2016; Wódkiewicz et al., 2016).

Changes in Management: Intensification and Abandonment

Management changes can be considered the most important threats for grassland biodiversity in the Eastern European region. The cessation of former management became typical in the last 50 years in Eastern Europe affecting mostly grasslands in mountainous areas, foothills and other areas with low accessibility (Török and Dengler, 2018). Land abandonment in these regions resulted in the decrease of grassland biodiversity and increased woody encroachment (Valkó et al., 2011, 2012). Land abandonment was especially intensive in the 1960s, when traditional herding management was replaced in many places by the intensive forms of animal husbandry. A second wave of abandonment happened after the fall of the Socialist regimes and the collapse of collective farms.

However, land abandonment also result in a slight increase of grassland areas in lowlands because of the spontaneous recovery of grasslands following cropland abandonment (Ramankutty and Foley, 1999). The access of EU subsidies in countries such as the Czech Republic, Slovakia, Romania and Hungary, impacted grassland biodiversity controversially. In some foothill regions shrub encroachment was suppressed and many grassland sites were cleared from shrubs, which affected grassland biodiversity positively. In other grasslands, subsidies enabled the farmers to improve the management of grasslands and provided a source for intensification, which resulted in the decrease of farmland biodiversity (Sutcliffe et al., 2015). For example, in Romania the subsidies increased the amount of grazing livestock, which, in most cases, meant an increased sheep grazing in high diversity grasslands historically maintained by low-intensity cattle grazing and/or mowing. The process proved detrimental to grassland biodiversity (Roman et al., 2019).

Invasive Species Encroachment

Grasslands were considered in a recent evaluation of invasion threat by Pyšek et al. (2010) as habitats characterized with intermediate levels of invasion and low invasion risk. However, grassland habitats are subjected to highly different levels of invasion and invasion risk. Botta-Dukát (2008) found that there are grassland types that can be characterized by low levels of invasion (e.g., rocky grasslands and saline grasslands), while others like sand grasslands are highly invaded. Plant invasions are strongly associated with the management changes of grasslands. In general, the overuse of grasslands (e.g., overgrazing or improper management) can create many establishment gaps in the vegetation and can facilitate the invasion. Climate change can also interact with this process, e.g., extreme weather events can create bare-soil patches in the vegetation, and increased frequency of droughts and fire favor the establishment of fire-adapted and drought-tolerant C4 grasses (Walther et al., 2009; Török and Aradi, 2017).

Climate Change

An emerging future threat is climate change, which can considerably affect grassland biodiversity in the forthcoming decades. According to the last predictions, (1) the yearly mean temperature will rise by about 1–3 °C, (2) precipitation patterns will be reshaped, as winter precipitation is expected to increase at the expense of summer precipitation, (3) the frequency of extreme weather events (e.g., extreme droughts, wildfires, extreme frosts, heavy rains) will increase in the future (Anders et al., 2014; Wesche et al., 2016). These effects jointly reshape the composition of grasslands by favoring drought-tolerants and ephemeral species, and increasing the proportion of Mediterranean species in the southern and central part of the region (Thuiller et al., 2005).

Some Further Drivers of Grassland Biodiversity

In many countries in Europe, grasslands assigned to the military are well-preserved and sustained because of the limited access and other restrictions in management (Elias et al., 2018). However, recent military conflicts (e.g., in Ukraine) had devastating impact on the subjected regions and embedded grasslands (e.g., uncontrolled fires by explosives, demolition by artillery fires, armored vehicle maneuvers, Vasyliuk et al., 2017). In Western Europe, among the most important threats are nitrogen deposition and aerial eutrophication (Dengler and Tischew, 2018). In the Eastern European region this threat can be considered to be of much lower importance. It was found that the nutrient enrichment of nutrient-limited grassland types (e.g., dry grassland types on shallow soils) can facilitate the increase in the cover of generalist graminoids and, due to their increased biomass production, can also decrease the beneficial effects of management on the grassland biodiversity (Kelemen et al., 2014; Habel et al., 2013).

Conservation, Sustainable Management and Restoration

Conservation

The most valuable grassland habitats can be found in protected areas, most cases in national parks and other nature reserves (e.g., Askania-Nova Biosphere Reserve, Carpathian Biosphere Reserve, Ukrainian Steppe Reserve, Oleshkivski Sands National Nature Park, Slovenský Raj National Park). In general, the active protection of semi-natural grasslands only began in the late 20th century when the approach of nature conservation shifted from absolute non-intervention to active conservation. Until then, the emphasis was mainly placed on species conservation, sometimes not even considering or misunderstanding habitat ecology and the requirements of the species. While due to the non-intervention approach, although there were a very few grasslands in protected nature areas preserved, it made possible to save particularly valuable virgin steppes from plowing (extensive stands were destroyed in the so called “virgin steppe” campaign in the 50s).

One of the main legislative instruments that regulates the protection of grassland ecosystems in Europe, is the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), which principal aims are to ensure conservation of wild plant and animal species and their natural habitats. This Convention provides the basis for development of the Emerald network of areas of special conservation interest. In EU Member States, this type of network is called Natura 2000. Natura 2000 is based on two directives: the Birds Directive and the Habitats Directive. There are more than 4000 Natura 2000 sites, in which there is a noticeable cover of grasslands. Within the Natura 2000 and the Emerald network, management plans are fine-tuned to take into account the environmental requirements of certain habitat types of certain rare or endangered species.

Sustainable Grassland Management and Restoration

In the Eastern European region several grasslands were created and later sustained by extensive forms of management mostly by mowing or grazing (Dengler et al., 2014). Large areas of grasslands in the lowland regions has been converted to croplands, and the remaining grassland fragments are in general degraded by intensified use. Intensified use and application of tillage, drainage, intercropping, high intensity grazing or the use of pesticides, mineral and organic fertilizers have a detrimental effect on flora and fauna (McLaughlin and Minneau, 1995). In contrast, low accessible areas in mountains, foothills or other marginal areas, the traditional grassland management is abandoned (van Dijk et al., 2005). In lowland regions of Eastern Europe, natural and semi-natural grasslands are embedded as small islands in the sea of intensified landscape. These patches also often key elements of High Nature Value (HNV) farmland systems, which are low-input farming systems in terms of biodiversity and management practices. The sustainable management of species-rich grasslands in EU countries of Eastern Europe is made achievable under the Common Agricultural Policy (Oppermann et al., 2012). In Eastern Europe, a high proportion of extensively managed remnants of the traditional rural areas are present (Oppermann et al., 2012). In many countries, the re-introduction of traditional management by mowing or grazing as a restoration tool has been suggested (Török et al. 2016b, Galvánek and Lepš, 2008; Valkó et al., 2011, 2012). Low intensity grazing by herded livestock (local breeds) or free grazing (by wild horses and cattle) are often recommended (Török et al., 2016b,c; Tóth et al., 2018). In many regions the re-introduction of traditional management is not feasible or sustainable; thus, conservation authorities and site managers are seeking substitute management practices (e.g., prescribed burning during the dormant season, Valkó et al. 2014). Instead of a single type of management by mowing or grazing adopting a whole scheme of traditional land use may be required for many grasslands to sustain the extraordinary grassland diversity in a particular region (Babai and Molnár, 2014).

In degraded grasslands, the decrease of management intensity is often recommended, but in case of completely destroyed grasslands (e.g., converted grassland areas), restoration of grassland vegetation and diversity by spontaneous succession and/or technical reclamation are necessary. There were several large-scale grassland restoration programs in Eastern Europe. Most publications were related to grassland restorations in the Czech Republic and lowland regions of Hungary (Halassy et al., 2016; Kövendi-Jakó et al., 2019; Török et al., 2011; Prach et al., 2014; Lengyel et al., 2012). While in large-scale restoration programs successes were often reported, it was also noted by the authors that the success of restoration was strongly influenced by the availability of high-quality grasslands in the landscape, acting as donor sites or spontaneous sources of propagules. These facts underline that the preservation of natural and semi-natural high-quality grassland fragments should be prioritized in conservation actions (Török and Helm, 2017).

Acknowledgments

P.T. was supported by the ‘Momentum Program’ of the Hungarian Academy of Sciences, and by NKFIH (Grants: K 119225 and KH 129483) during manuscript preparation. We are indebted to Judit Sonkoly and László Erdős for kindly checking the manuscript for errors and typos.

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Grasslands and Shrublands of the Middle East and the Caucasus

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This chapter was solicited and edited by Jürgen Dengler and Péter Török on behalf of the Eurasian Dry Grassland Group (EDGG).

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Abstract

The Middle East and the Caucasus grasslands and shrublands host a high diversity of habitats, species and land management practices. It is the homeland of the earliest agriculture and many ancient civilizations following it. The land extends across more than 2 million km², spanning the majority of nine countries with 269 million people living within. The variety of climate types, orography and position with respect to four floristic regions (Mediterranean, Euro-Siberian, Irano-Turanian and Saharo-Sindian) play an important role in the diversification and distribution of the vegetation. Major vegetation zones of interest are steppes, forest-steppes and related shrublands. The steppe zone is marked with *Artemisia* steppes of the plains, tragacanthic/thorn-cushion steppes of the mountains and scattered intrazonal saline vegetation. Forest-steppes and related shrublands are dominated by *Pistachio-almonds* in dry foothills and by oaks-junipers on the mountains. The region is one of the richest in terms of biodiversity: the Irano-Anatolian biodiversity hotspot covers most of the Middle East and neighbors the Caucasus hotspot. It is an endemism center pronounced with more than 4000 endemic plants and some butterfly genera. Furthermore, it supports populations of several endangered large herbivores as well as top predators such as the leopard. Livestock keeping is the major land-use activity on grasslands. Grasslands are mostly managed extensively around villages and in the form of large-scale transhumance in highlands. Shrubs and trees are harvested for fuel, construction material for local use and charcoal production. Unregulated (unsustainable) grazing, conversion to croplands, afforestation with non-native tree species, mining and energy production projects are the major threats that cause habitat degradation, fragmentation and loss. The protected areas cover ca. less than 15% of each country and their efficiency to fulfill conserve priorities are under question.

Delimitation and Physiogeography

The region in the focus of this article is the Middle East (ME) and the Caucasus (C). Although a wide range of delimitations is applied for the ME, we adopt a common approach which also provides consistency in ecological conditions: In this article, ME extends in Asia, from the Anatolian Peninsula of Turkey in the north to Syria, Lebanon, Palestine, Israel, Jordan and Saudi Arabia in the south; and Iran and Afghanistan to the east. Among those countries, we focus on the ones with a large area of grasslands and shrublands of non-Mediterranean origin; therefore we focus on the land within the borders of Iran, Iraq, Afghanistan, Jordan, Syria, and Turkey (Fig. 1). The Caucasus region, on the contrary, is well agreed to extend from northeast Turkey, Georgia and neighboring lands of Russia, Armenia to Azerbaijan. Within those countries, we focus on steppes and related vegetation and further exclude the land covered by Mediterranean, desert, closed-canopy temperate forest and alpine vegetation. With a rough estimate, this land covers 2 million km² (Fig. 1, based on ecoregions in Olson et al., 2001).

The region lies like a bridge between the Mediterranean Sea, Black Sea, Caspian Sea, Persian Gulf and Red Sea. The Turkish-Iranian Plateau, from East Anatolia to Caucasus, is lifted from the Neo-Tethys Sea after the Middle Miocene following the initial Paleogene Arabia-Eurasia collision and since then shaped by mantle-derived collision magmatism (Neill et al., 2015). The elevation is above 500 m in depressions, between 1000 and 3000 m in high plateaus but more than 4000 m at the peaks. The region is lined with several mountain chains of the Alpine-Himalayan orogenic belt: North Anatolian and Taurus, Lesser Caucasus and Greater



Fig. 1 The Middle East and the Caucasus with countries on the focus of this article labeled. Country borders were shown in red. The map was colored to show lowlands (green), plains and rolling hills (yellow), mountains (brown) and mountain peaks (white) and water bodies (blue). The lake layer (in turquoise color with black lining) was obtained from NatureEarth. The map shows an area between ca. 23°–43° latitudes and 25°–73° longitudes in north orientation. Scale:1:16,000,000.

Caucasus, Zagros and Alborz Mts. aligned on the north and west borders of Iran and finally Hindu Kush of Afghanistan. Rolling hills and scattered mountains are common as well. Long rivers (e.g., Euphrates, Tigris, Çoruh, Amu Darya, and Helmand) fracture the topography. The region is rich in water bodies with many scattered lakes but few large ones such as Van Gölü (3755 km²) of Turkey, Urmia (5200 km²) and Bakhtegan (3500 km²) of Iran, most of which are saline lakes. In the central parts of the basins, the accumulation of evaporitic minerals led to the formation of vast expanses of salt soils and permanent or ephemeral salt lakes.

The region has a complex geological structure, leading to high plant diversity. The geological formations are very different in origin (plutonic, volcanic, sedimentary, metamorphic), age (Precambrian to Quaternary) and composition. The major bedrock types are soft bedrock-chalk, clay marl in central Anatolia, basic igneous rocks in eastern Anatolia, neritic limestones and undifferentiated continental clastic from Southeastern Anatolia to the north of the Arabian Peninsula (Okay, 2008; General Directorate of Mineral Research and Exploitation, 2015), various limestones in western and NE Iran; calcareous, siliceous and volcanic rocks in central Iran and the Alborz; flysch in the Makran Range of southeastern Iran and volcanic complexes in NW Iran. The soils of the ME&C, generally of low productivity, represent six major soil types: soils of arid regions with low organic content dominate central Anatolia and Mesopotamia (xerosols). Lithosols, less than 10 cm deep on coherent hard rocks, dominate the Turkish-Iranian Plateau and Afghanistan (FAO/UNESCO, 1971–1981). Highlands of this zone on the south are covered with calcic and luvic kastanozems: humus rich brown soils of the arid zone but not as productive as chernozems of the Russian steppe belt. Cambisols cover relatively small area at alluvial zones. They lack a layer of accumulated clay, humus, soluble salts and iron. Along the Black Sea Coast where semi-natural grasslands do occur, vertic luvisols dominate. Luvic arenosols, sandy-textured soils that lack any significant soil profile development, cover southwest of Afghanistan.

According to Köppen-Geiger classification, three major climate types occur in the region—excluding deserts (Kottek et al., 2006): (i) a warm Mediterranean-like temperate climate dominates the region. It prevails in most of the Anatolian periphery, extending to western Syria and western Iran. The summers are dry and hot and winters are rainy and mild. (ii) An arid climate with less precipitation and harsher winter conditions prevails in depressions of the ME and Azerbaijan. (iii) On the highlands of east Anatolia, Iran and Afghanistan, a colder climate prevails which is called “snow zone.” Summers are comfortably cool and there is a permanent snow cover on mountains. In Lesser and Greater Caucasus, a fully humid snow climate is experienced. Toward east of Afghanistan, the climate is affected by monsoons. Having said that, we should also mention that Rivas-Martínez et al. (2011) classify the whole region under the effect of Mediterranean macro-climate except northeast Anatolia, Lesser and Greater Caucasus and southern coasts of the Caspian Sea, where a temperate climate prevails.

Origin of Grassland and Shrubland Communities

World-wide expansion of grasslands was associated with increased aridity between 8 and 6 MaBP, a decline in woodlands due to fires, and coevolution of mammals adapted to grazing and open habitats (Anderson, 2006). Those enabled grassland to replace once-forest covered habitats. Onwards, grasslands and forests replace one another due to climatic oscillations and human interventions. During the last glacial period (30,000–15,000 calibrated years before present) in Anatolia for example, the climate was generally cold and humid and therefore the northern Anatolia was covered by forests of *Pinus* spp. in cool places but of *Fagus*, *Alnus*,

Quercus, and *Pistacia* under warmer conditions. But under cold and dry conditions, steppes of *Artemisia*, Chenopodiaceae and Poaceae dominated the land (Şenkul and Doğan, 2013).

Under current climatic conditions, it is expected that sites with more than ca. 500 mm annual precipitation are covered by closed-canopy forests. Within this zone, mesophilic semi-natural grasslands are found in sites of forest clearance or depending on edaphic conditions. Areas with less than 300 mm annual precipitation are expected to be covered naturally by treeless steppes and desert-steppes (Fig. 1). Following the definition in Wesche et al. (2016), steppes are the vegetation types dominated by herbs, mainly grasses and other graminoids, sometimes with a significant admixture of chamaephytes, in arid and semi-arid climates. In transition between natural steppes and closed-canopy forests, forest-steppes cover large areas as exposure- or soil-related mosaics or open woodlands (Erdős et al., 2018). In steppes and forest-steppes; scrublands composed of dwarf-shrubs of *Artemisia* or of thorn-cushions as well as shrubby forms of trees belonging to the forest-steppes are common. Today, vegetation types of the region show distribution patterns different from naturally limited: steppes of the ME and Caucasus cover larger areas than naturally limited due to continuous deforestation and grazing activities. As a result, the vegetation has many elements resistant to grazing. Furthermore, the dwarf-shrub communities of *Artemisia*, naturally making up desert-steppes of very dry areas on depressions, are more widespread due to grazing. Oak woodlands are one of the most common type of forest-steppes. Based on pollen records, Asouti and Kabukcu (2014) claim that low-diversity, even aged shrubby oak woodlands of the ME are actually not natural but replaced natural semi-arid savannah grasslands by sheep grazing and harvest practices. Furthermore, forest-steppes have shrunk due to deforestation activities. Wild orchards, scattered fruit trees on rocky outcrops or arable fields, are very common in the region. They were thought to be remnants of preceding forest-steppes but it was shown that they were there before oak expansion and the dominant shrubs of the wild orchards are not common in forest-steppes (Woldring and Cappers, 2000). As a summary, most of the vegetation has been largely shaped by human activities.

Typology of Communities

The vegetation types in the focus of this article are major natural and semi-natural grassland and shrublands. We excluded Mediterranean vegetation, wetlands, sparsely vegetated areas (less than 10% cover), humid forests, alpine vegetation, intensified grasslands, ruderal and segetal vegetation. We put emphasis on steppes and forest-steppes but also briefly mention saline and semi-natural grasslands. We classify grasslands and shrublands of the region into five major groups: intrazonal saline vegetation in lowland depressions, three zonal vegetation types: plain steppes, montane steppes, forest-steppes and related shrublands, and azonal mesophilic semi-natural grasslands (Figs. 2 and 3). Of those; primary or secondary origin is common in the region. The elements of those different vegetation types can be seen together in transition zones as well as in many other places due to human effects.

Saline Vegetation

Salty hydromorphic alluvial soils around saline lakes have high salt content (up to 10% NaCl and Na₂SO₄) and support halophytic vegetation (Fig. 2C). Salinity and moisture are two important ecological drivers shaping halophytic vegetation (Akhani, 2004, 2006). The saline vegetation is species poor with mean number of species 6–15 per 64–100 m² area but can be rich in endemic species (personal observations). Soils with moderate salt and low moisture content are dominated by grasses (*Puccinellia koeieana* and to a lesser extent *P. convoluta*), or annual forbs (e.g., *Suaeda cucullata*, *S. carnosissima*) and accompanied by succulent forbs. In hypersaline places close to both permanent water and salt crust, *Frankenia hirsuta* becomes dominant together with *Petrosimonia brachiata*, *Salsola* spp. (e.g., *S. stenoptera*) and *Limonium* spp. Perennial forbs are generally absent and perennial grasses have underground organs to survive (e.g., *Cynodon dactylon*). Plant communities of high water tables are *Juncetea maritime* (halophytic grassland and herbaceous perennial sedge communities belonging to genera *Puccinellia* and *Juncus*), *Tamaricetea ramosissimae* (*Tamarix* communities) and *Haloxylon-Salsoletea tomentosae* (halophytic shrubby communities on salty and dry soils) (Akhani, 2004). As the salinity increases, the share of perennial forbs decreases; and annual grasses and succulent plants increase (Çetik, 1985).

Plain Steppes

We focus on steppes on plains (ca. 900–1200 m elevations) and group them into desert-steppes and treeless steppe grasslands. Desert steppes occur in the driest depressions of the region and lowlands neighboring the desert zones. Desert-steppe vegetation is dominated by *Artemisia*; herbs or dwarf-shrubs of Asteraceae that are usually aromatic and bluish-silvery in appearance (Fig. 2A). Naturally confined to steppe zone, this vegetation type extends to mountains as a response of grazing eliminating natural perennial grasses and other herbs (Zohary, 1973; Walter and Breckle, 1985; Frey and Probst, 1986). Density and floristic composition of these scrublands are influenced by edaphic factors, annual precipitation and duration of the dry season, elevation and erosion (Frey and Probst, 1986). Some dominant species are *Artemisia fragrans* in central Anatolia (Çetik, 1985); *A. sieberi* (referred as *A. herba-alba* s.l. in the old literature), *A. kopetdaghensis*, *Seriphidium quettense* (valid name for *A. quettensis*), *A. lehmaniana* and *A. santolina* in southeast Anatolia, Iran to Afghanistan (Breckle, 2007). In rainy years and particularly toward mountains, species richness of these steppes is increased to around 45 species in each 25 m² plots in Iran (Akhani, 1998). In plain steppes, the



Fig. 2 Grassland communities of the region. (A) *Artemisia* steppes in Taftan Mts. SE of Iran; (B) Grass-forbs steppes with *Smymiospis armena*, Selim pass, Armenia. (C) Hypersaline vegetation with *Limonium iconicum* and *Halocnemum strobilaceum*, Konya, Turkey. (D) Thorn-Cushion *Onobrychis cornuta* grasslands in Damavand, Alborz Mts, 3400 m a.s.l. (A) Photo by A. Naqinezhad. (B) Photo by A. Aleksanyan and G. Fayvush. (C) Photo by M. Vural. (D) Photo by A. Talebi.

dominant *Artemisia* is accompanied by common species of treeless steppe grasslands such as *Thymus* and *Stipa* spp., *Poa bulbosa*, *Festuca valesiaca* and *Noaea mucronata* (Akhani, 1998).

Treeless steppe grasslands naturally occur in sites with ca. 300 mm annual precipitation but can extend in more humid lands due to anthropogenic influences. This vegetation is mostly destroyed and highly degraded except in protected areas. It is dominated by perennial grasses of *Bromus tomentellus*, *Festuca valesiaca*, *Stipa* (*S. lessingiana*, *S. pulcherrima*, *S. hohenachkeriana*, *S. holosericea*, *S. tirsia*, *S. pennata*), *Koeleria pyramidata* (valid name for *Koeleria cristata*), *Elymus hispidus* accompanied by *Thymus* spp. (e.g., *T. leucostomus* var. *leucostomus*, *T. sipyleus* ssp. *rosulans*, *T. longicaulis*, *T. kotschyanus* var. *kotschyanus*, *T. pubescens*, *T. transcaucasicus*) and forbs from a diversity of plant genera e.g., *Achillea*, *Alyssum*, *Ajuga*, *Anthemis*, *Convolvulus*, *Euphorbia*, *Fumana*, *Galium*, *Genista*, *Hedysarum*, *Helianthemum*, *Hypericum*, *Linum*, *Marrubium*, *Nepeta*, *Onosma*, *Onobrychis*, *Phlomis*, *Silene*, *Salvia*, *Scutellaria*, *Teucrium*, *Veronica*, etc. (Fig. 2B as an example). A peculiar steppe type of the Lesser Caucasus is dominated by wild wheat species, i.e., *Triticum boeoticum*, *T. araraticum* and *T. urartu*. Overgrazed sites are marked with presence of many unpalatable, spiny or grazing-resistant species such as *Noaea mucronata*, *Peganum harmala*, *Gundelia tournefortii*, *Eryngium campestre* and several species of *Verbascum*. In Georgia, the dominant species of steppe vegetation is *Bothriochloa ischaemum*, a representative of the subtropical-tropical *Bothriochloa* genus. Typologically, they are very diverse and include vegetation units of *Glycyrrhizieto-Bothriochloeta*, *Bothriochloeta ephemerosa*, *Festuceta-Bothriochloeta*, *Stipa-Bothriochloeta*, etc. (Nakhutsrishvili, 2013).

Montane Steppes

Montane steppes are the natural vegetation of wind-swept slopes of above timberline to subalpine zone (1800–3500 m a.s.l.) (Kürschner, 1986), today they occur extensively in the montane zone (1200–1800 m a.s.l.) and replace forest-steppes, i.e. the potential vegetation of the zone, following disturbances. It is dominated by tragacanthic (thorny cushion-forming dwarf shrub form) or soft-leaved plant species (Zohary, 1973; Djmalali et al., 2011). Montane steppes can have a substantial amount (up to 30% cover) of shrubs and trees of the forest-steppes. Tragacanthic shrubby vegetation is one of the most important features of high mountains zone throughout the Middle East and SW Asia and very species-rich (Fig. 2D) (Zohary, 1973; Frey and Probst, 1986). The most common genera are *Astragalus* (e.g., *A. gummifer*, *A. microcephalus*, *A. lagopoides*), *Acantholimon*, *Acanthophyllum*, *Onobrychis cornuta*, *Gypsophylla*, *Minuartia*, *Ononis*, and *Arenaria* spp. On some volcanic highlands of Iraq, east Anatolia and Armenia, giant umbellifers

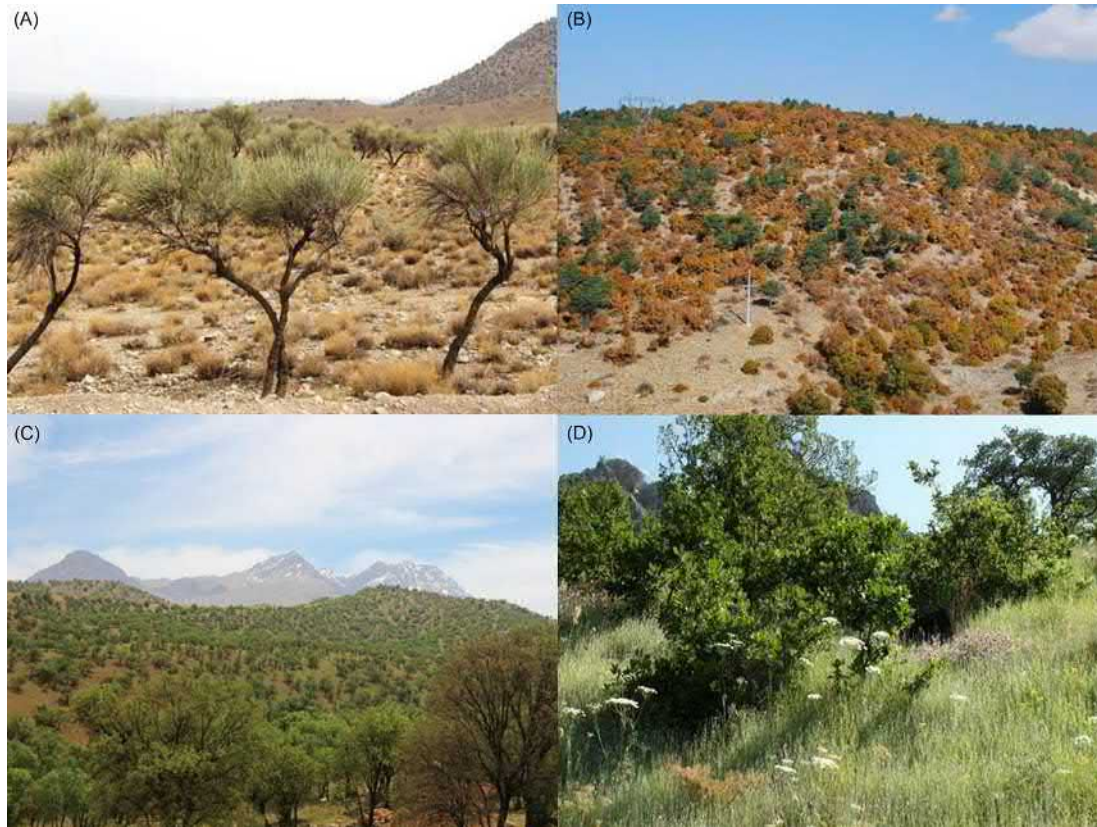


Fig. 3 Shrublands of the region. (A) Woodlands in south of Iran (a mixture of pistachio and almond vegetation). (B) Oak-juniper shrubland, Kayseri, Turkey. (C) Zagros forest-steppes of oaks, Iran. (D) Open woodlands in south of Armenia with *Quercus araxina*. (A) Photo by A. Naqinezhad. (B) Photo by D. Ambarli. (C) Photo by A. Naqinezhad. (D) Photo by A. Aleksanyan.

becomes dominant or co-dominant such as *Prangos* spp. (Prangeto-Astragaletum) accompanied by *Eryngium* sp., *Eremopoa persica*, *Thlaspi* spp., and *Alyssum* spp.. Protection from grazing pressure was shown to decrease the cover of tragacanthic species and increase the grasses such as *Festuca valesiaca* and *Dactylis glomerata*. Some examples of common forb genera are *Thymus*, *Salvia*, *Phlomis*, *Achillea* and *Verbascum*. Wild fruit trees (*Pyrus elaeagnifolia*, *Crataegus monogyna*, *Prunus cerasus*, *Rosa* spp. etc.) scattered in arable fields are common in montane steppes and rocky outcrops.

Forest-Steppes and Related Shrublands

The potential vegetation of sites with more than ca. 400 mm annual precipitation is forest-steppes which lost most of its natural vegetation due to destruction for cropland and hunting, and extraction of fuel and construction material. For example, forest-steppes in inner Anatolia cover 0.7% (2369 km²) of the land which is less than half of its potential area (Ambarli et al., 2016). The vegetation corresponds to one out of nine forest-steppe types of the Palearctic: the Middle East (Erdős et al., 2018). Within that, we differentiate two major vegetation types: xerophytic communities dominated by pistachio-almond communities mostly in lower elevation and oak-juniper communities on more humid parts. The communities can occur in the form of woodland, i.e. woody vegetation in which tree cover is between 10–40% due to aridity or degradation. Degradation causes those two plant community types to occur also in shrub form, i.e. woody plants with less than 2 m height in general and with several stems growing from ground level. Furthermore, shrublands of *Rhododendron*, typical for forest understory, cover large areas in subalpine zone of the Caucasus and the Black Sea region.

Pistachio-almond shrubby steppes occur between lowland *Artemisia* dominated semi-desertic steppes and thorn-cushion formations of the upper mountains (Zohary, 1973). The dominant species are *Prunus scoparia* (valid name of *Amygdalus scoparia*), *Pistacia khinjuk*, *P. atlantica*, *P. terebinthus* subsp. *palaestina* (SE Anatolia), *P. vera* (Afghanistan), *Amygdalus bucharica* (Afghanistan), *Cercis griffithii* (west Afghanistan) and *Crataegus* spp., *Pyrus* spp., *Cotoneaster* spp., *Rhamnus pallasii*, *Daphne mucronata*, *Acer monspessulanum* and *Fraxinus angustifolia* (in the Caucasus).

Oak and juniper formations, on the other hand, are widespread on the mountain zone (Mayer and Aksoy, 1998; Sagheb-Talebi et al., 2003, 2014; Breckle, 2007). Dominant species are *Quercus pubescens*, *Q. infectoria*, *Quercus brantii*, *Quercus petraea* subsp. *pin-natiloba*, *Q. libani*, *Juniperus oxycedrus* and *J. excelsa* (Zohary, 1973; Assadi, 1989; Sagheb-Talebi et al., 2003; Breckle, 2007; Kürschner

and Parolly, 2012; Akan, 2019). Wild orchards (sensu stricto Woldring and Cappers, 2000) are common. Carpet like formations of *Juniperus communis* and *J. sabina* cover montane and subalpine zones (Ravanbakhsh et al., 2016; Assadi, 1989; Akhani, 1998). Those are accompanied by shrubs like *Berberis integerrima*, *Rubia florida*, *Lonicera nummulariifolia*, *Cotoneaster ellipticus* (valid name for *C. nummularius*), *Cerasus microcarpa*, and *Rhamnus pallasii* in the Caucasus. Oak-juniper woodlands are mixed with pine trees (*Pinus nigra* subsp. *pallasiana* and *Pinus sylvestris*) at high elevations in Turkey. Xeric woodlands merge with *Quercus baloot* or *Pinus gerardiana* evergreen woodlands in east Afghanistan (Breckle, 2007). Human intervention results in lower canopy cover and height and changes in vegetation structure, e.g. shrubby form, and composition (Akman, 1974; Çetik, 1985).

Forest-steppes can include a diversity of trees. Elements of Mediterranean vegetation or of humid forests are found under special micro-climatic conditions. It is common to see open shrublands of *Acer*, *Lonicera*, *Cerasus* and *Cotoneaster* in mesic valleys. Caucasian forest-steppes occur with *Acer monspessulanum* subsp. *ibericum*, *Celtis glabrata*, *Pyrus salicifolia*, *Prunus fenziiana*, *Punica granatum*, several wild fruit trees and many other Mediterranean elements (Aleksanyan, 2012; Fayvush and Aleksanyan, 2016). Succession scrubs of *Paliurus spina-christi*, *Jasminum fruticans*, *Rhamnus* are common features of dry foothills in valleys and along some seasonal rivers and streams (Memariani et al., 2016). In Armenia, they get the special name *shibliak* and occur almost in every mountain belt, except in the highlands. About 25–30 species contribute to the formation of *shibliak* including both mesophilic and xerophilic species such as *Berberis vulgaris*, *Cotinus coggygia*, *Punica granatum*, *Carpinus orientalis*, *Crataegus orientalis*, *Lonicera iberica*, *Rhamnus pallasii*, *Caragana grandiflora*, *Atraphaxis spinosa*, *Ephedra major* subsp. *procera* (Aleksanyan, 2012). *Rhus coriaria* communities occur sporadically in forest-steppes of Iran as well as inner Anatolia (Sabeti, 1976). Even Saharo-Sindian species occur in a subtropical, savanna like ecosystem along the Persian Gulf and the Sea of Oman (see Zohary, 1973; Léonard, 1989; Djamali et al., 2011): Its woody members are *Acacia* spp., *Albizia lebbekii*, *Calotropis procera*, *Capparis decidua*, *Dalbergia sissoo*, *Moringa peregrina*, *Nannorrhops ritchieana*, etc. (Assadi, 1989; Sagheb-Talebi et al., 2014).

Mesophilic Semi-Natural Grasslands

Semi-natural grasslands occur in the humid zones under the effect of the Black Sea and Caspian Sea. Anthropogenic managed pastures, meadows and tall-herb meadow fringes on fertile deep soils at low and mid-elevations (rarely also high elevations), humid grass-rush meadows, tall-rush wetlands, patchy green wet meadows and fens in mountain slopes and riverbanks are among types of such grasslands (Ambarlı et al., 2018). Although grasslands were degraded as a result of millennia of overgrazing, they still are of great importance in the high montane and subalpine zones, like in northern parts of Alborz Mts slopes in north Iran. Meadows and pastures are present in the northern slopes of Alborz Mts where the potential natural vegetation is the montane or submontane forests. Kelardasht, Kojour area and Golestan National Park are important examples. They can also occur due to abandonment of the cultivated lands or settlements within the forest (Akhani, 1998, 2005). In some areas of Iran, a well-developed vegetation dominated by *Elymus hispidus*, *Elymus elongatiformis*, *Cephalaria microcephala* and *Carex melanostachya* covers higher mountains and subalpine areas, where scattered *Acer* or *Crataegus* shrubs can also be seen (Akhani, 1998, 2005; Memariani et al., 2016). Grasslands of the northeast Anatolia which is used mainly for hay-cutting host tens of rare butterfly species and therefore they are prime butterfly areas of the country as well as Europe (Karaçetin and Welch, 2011).

Biogeography and Biodiversity

The ME and the Caucasus are in the Western Palearctic biogeographically. During the last Ice Age, species of the western Palearctic found refuges there: especially the Caucasus and the periphery of the Taurus Mountains of Turkey were refuge areas and then centers of adaptive radiation for several taxonomic groups such as grasshoppers, hedgehogs and brown bears (Hewitt, 2000). Several relict species do occur in the region such as *Rhodothamnus sessilifolius* and *Rhododendron caucasicum*. Owing to the diversity of abiotic conditions, land-use practices (see below), unique geological history and large size; the ME and the Caucasus host remarkable plant and animal diversity. The region lies at the intersection of three biodiversity hotspots (Regions with remarkably high percentage of endemic vascular plants (>1500) and low percentage of its original vegetation (<30%): Irano-Anatolian, covering most of the region, the Caucasus on the northeast, and the Mediterranean on the west (Mittermeier et al., 2011). Those are also part of the Global 200 Ecoregion network because of specific evolutionary processes and unique historical floral and faunal development (Nakhutsrishvili, 2013). The hotspots overlap with phytogeographical regions, i.e., regions with distinctive climate and flora (Takh-tajan et al., 1986): The Irano-Turanian region, marked with continental climate, covers most of the inner land. The Mediterranean region along the sea has a substantial effect on the flora. The Euro-Siberian region shapes the flora of the Black Sea and Caspian Sea coasts, and the Caucasus. Additionally, the Saharo-Sindian region covers southern parts of Iran and Iraq, extending to Saudi Arabia and Pakistan.

The Irano-Turanian region is a center of evolution and endemism for many plant genera (Kürschner, 1986; Manafzadeh et al., 2017) such as *Astragalus*, *Verbascum*, *Salvia*, *Acantholimon*, *Acanthophyllum*, *Cicer*, *Cousinia*, *Dianthus*, *Onosma*, *Echinops*, *Euphorbia*, *Gypsophila*, *Minuartia*, *Noaea*, *Onobrychis*, *Oxytropis* and *Scorzonera* (Zohary, 1973). Among those are the tragacanthic plants e.g., many *Astragalus* sp. and *Onobrychis cornuta*. Furthermore some endemic genera of the Irano-Turanian region are monotypic (i.e., genus with only one species), such as *Azilia*, *Mozaffariania*, *Kalakia*, *Elburzia*, *Zerdana* and *Zhumeria* (Noroozi et al., 2019). The grasslands of the ME have high cover of herbaceous species adapted to arid conditions; i.e., xerophytes e.g., *Thymus spathulifolius* (Fig. 4). The steppes represent a center for secondary adaptive radiation, giving rise to numerous groups of closely related, often vicarious,



Fig. 4 A selection of steppic species. (A) Steppe fritillary *Euphydryas orientalis* endemic to Turkey, (B) *Thymus spathulifolius* endemic to Turkey, (C) Chukar partridge *Alectoris chukar*, (D) Asia Minor ground squirrel *Spermophilus xanthopyrmnus*. Photographers: Didem and Hüseyin Ambarlı.

neoendemic species, explained with the recent neogenesis of Anatolia (Pils, 2013). As expected, the countries of the Irano-Turanian region hold the richest flora of the northern temperate zone compared to their sizes. Turkey has 9753 vascular plant species, ca. 30% of which are endemics (Güner et al., 2012). It is estimated that at least half of those endemics live in semi-arid inner part. More than 8100 vascular plant species are present in Iran with almost 30% endemics (Noroozi et al., 2019). Afghanistan is estimated to have 5000 vascular plant species with 25–30% endemic to the country (Breckle, 2007). The number of vascular plants in the Caucasus is as follows: 3800 for Armenia, 4500 for Azerbaijan and 4310 for Georgia (Ministry of Ecology and Natural Resources Republic of Azerbaijan, 2014; Ministry of Environment Protection and Natural Resources of Georgia, 2015; Ministry of Nature Protection of Republic of Armenia, 2014) with endemism ratios between 3% and 7%. The region is also a world center for agro-biodiversity, hosting wild relatives of many legume and cereal crops such as einkorn, emmer, barley and rye (Willcox, 2005).

The region is important not only for the floral elements but also for the fauna (Fig. 4): The ME&C is an endemism center for the genus *Erebia*, one of the most diverse butterfly genus of the Palearctic (Peña et al., 2015). Furthermore, Iran-Turan region is the center of diversification of a group of Lycenids, *Agrodiaetus*, with more than 120 species. The group has one of the highest interspecific karyotypic diversities known in the animal kingdom with an explosive speciation rate of 1.6 species per million years (Kandul et al., 2007). The countries hold extremely high diversity of butterflies, remarkably the Lycaenids (Blues). For example, Turkey is the richest in Europe with more than 380 species, 81 of which are endemics such as the steppe fritillary *Euphydryas orientalis* (Fig. 4) (Karaçetin and Welch, 2011).

The region holds the breeding bird fauna of a majority of the Western Palearctic habitats from semi-deserts to Caucasian forests (Rosalea, 1995). Furthermore, every year it hosts millions of migrating birds of the Palearctic as it has important passages: Flyways from East Asia to East Africa, Palearctic-African and central to South Asia pass through Bosphorus, Caucasus and over the Black Sea. More than 30 Ramsar sites, wetlands of global importance, serve as stopover or wintering grounds for birds (Ramsar Information Centre, 2019). The region is a home for several steppic bird species distinguished by cryptic coloring, ground nesting, tendency to walk or run and aerial displays such as several species of larks, Chukar partridge *Alectoris chukar* (Fig. 4), great bustard *Otis tarda* and little bustard *Tetrax tetrax*. The Caucasus hosts a regional-endemic bird species, the Caucasian Grouse (*Lyrurus mlokosiewiczi*) which lives in alpine and subalpine grasslands and humid shrublands of *Juniper* and *Rhododendron*.

ME&C is remarkable in wildlife: hosted lions, wild oxes, elephants a few centuries ago; it is still possible to see small herds of wild ungulates such as the Mouflon (*Ovis orientalis*), the ancestor of the domestic sheep, and more than 10 gazelle species, some of which are endemic to region e.g., Cuvier's Gazelle (*Gazella cuvieri*). Habitats support populations of large carnivores such as gray wolf (*Canis lupus*), brown bear (*Ursus arctos*) and leopards (*Panthera pardus*) that are extinct in neighboring biomes. Not only large mammals but also small mammals are abundant. Taurus Ground Squirrel (*Spermophilus taurensis*), Asia Minor Ground Squirrel (*Spermophilus xanthopyrmnus*, Fig. 4D) and Williams's Jerboa (*Allactaga williamsi*) are among many endemic small mammals of the region.

Land Use

Birth of agriculture is probably one of the major critical advancements in human history. The Fertile Crescent is one of four major centers of first farming where several cereal and legume crops were domesticated (Brown et al., 2009). This land extends from Palestine to Turkey and Syria; covering valleys and adjacent hills of Jordan, Tigris and Euphrates rivers. It is also the earliest for animal domestication, as early as 11,000 calibrated years BP for cattle and sheep (Zeder, 2008). Since then, the region hosts the oldest civilizations of the Palearctic such as the Hitites, Romans, Seljuks, Persian, Byzantine and Ottoman. The oldest sanctuary of the world, Göbekli Tepe, where hunter-gatherers worshipped during the stone age, was discovered in the Fertile Crescent a few years ago (Schmidt, 2012). As a result, the habitats and its biodiversity are the earliest to be exposed to the anthropogenic effects of agriculture, domestication and settled life. The vegetation has continuously been shaped by humans: destruction by fires for opening croplands, hunting grounds and grassland management purposes; wood cutting for fuel and construction material, wars etc. Not only the locals but also migrating populations and trade along the Silk Road contributed to this effect.

The countries of the region have small economies except developing conditions in Turkey and Iran (Table 1). The share of labor in agriculture varies between 2% in Jordan and 79% in Afghanistan where most of the labor works in agriculture. Low productivity due to semi-arid conditions and prolonged summer droughts allow only for rangeland grazing in lowland steppes. In the more humid and productive highlands, hay making and transhumance grazing are also commonly practiced. A total of 35 million cattle held in countries of the region represent ca. 2.3% of the world total (Table 1). The ME region is a milk exporter with the total production of 25 million tons in 2008 (Maitah and Smutka, 2013). Livestock keeping is usually coupled with cereal and pulse production for subsistence or semi-subsistence in family farms, except for areas with very cold winters or dry summers (Karagöz, 2006). Today, most of the grazing takes place around settlements. Sheep is the common livestock of the lowland plains and it is replaced by cattle on highlands and by goats in rocky mountains. Nomadic life, disappeared in Turkey, is still common in Iraq, Iran and Afghanistan. Transhumance grazing, seasonal migration of livestock on fixed historical routes to productive meadows, is common in the highlands.

Shrublands in the focus of this article are accepted to be of low wood productivity due to arid conditions. Today, they are mostly used by local people for fuel and construction material. Another common use of oaklands is charcoal production for ovens and barbecue: Coppice oak stands are cut rotationally, e.g., every 20 years, by wanderer families. This activity maintains the oaks in a shrubby stage. Oak nuts are used to make some local bread, so-called "Kalg." It is specifically eaten for stomach pains and gastrointestinal problems (Mosaddegh et al., 2012).

There are other common extractive uses of grasslands and shrublands. Those are hunting areas especially for small game animals such as hares, partridges and foxes, although some of such activities can be illegal. Collecting wild plants for medicinal or commercial purposes is common among local people. Bulbous plants are the target of illegal collection e.g., *Orchids* for ice-cream making and other bulbous plants for flower markets. An extractive use of steppes is removal of tragacanthic *Astragalus* species e.g., *A. microcephalus*. Those species have multiple uses: They are widely collected for fuel, fodder, medicinal plants, and even cleaning stuff. They are burned to heat shepherds during cold nights in rangelands. Tragacanth gum produced by *A. gummifer* (Milkvetch) is collected widely to be used as thickener in confections, salad dressings, sauces or for medicinal purposes (Kadioğlu et al., 2008). As a result, *Astragalus* steppes are degraded and open to erosion and desertification. Bee keeping is a non-extractive land use widely practiced in grasslands as well as forests. A kilogram of honey of average quality is worth more than 20 Euros and the same amount of honey produced in traditional ways in the sup-alpine meadows of the Black Sea region costs as much as 200 Euros.

Table 1 Population, labor force and its share in agriculture sector, gross domestic product (GDP) and cattle numbers for the Middle East and the Caucasian countries in focus of this article.

Country	Area (km ²)	Population (millions)	Labor force (millions)	Agriculture in labor force (%)	GDP (billion US\$)	Cattle number
Afghanistan	652,860	33.3	7.9	79	21	5,349,000
Armenia	29,743	2.9	1.4	18	11	661,003
Azerbaijan	86,600	9.9	5.0	6	53	2,442,373
Georgia	153,910	3.7	2.0	9	14	1,128,800
Iran	1,745,150	80.8	27.4	16	386	8,670,000
Iraq	435,050	32.6	9.7	22	177	2,780,000
Jordan	89,320	7.9	2.5	2	38	69,100
Syria	185,180	18.0	4.8	17	40	NA
Turkey	785,350	79.8	31.9	18	860	13,916,924
Total	4,163,163	269	93	–	1600	35,017,200

Note that only countries with large share of non-Mediterranean grasslands and shrublands are included.

Sources: <https://datacatalog.worldbank.org/> and <http://www.indexmundi.com/> accessed: 30 June 2019.

Threats and Conservation

Due to various unsustainable land-use activities acting on the biodiversity of the ME&C, many species are threatened: for example, among the 10,930 species of vascular plants, birds, butterflies, mammals and herptiles distributed in Turkey, 1130 species were found to be living predominantly in steppic environments and being classified either as threatened, near-threatened or data deficient at the national level, if not globally (Ambarlı et al., 2016). In Armenia, from 3800 vascular plants, 452 are included in Red Book of Armenia among which many species are adapted to grasslands (Tamanyan et al., 2010). Among the major threats acting in recent times are overgrazing, afforestation, illegal harvest and over-exploitation of wild plants and animals, climate change and unsustainable exploitation of minerals and fossil fuels. Those threats act in similar ways in different countries.

Overgrazing is a major problem throughout the region. Almost half of the land is not suitable for livestock production and local livestock densities are usually too high for low-productivity pastures (see country summaries in Table 1), except highlands in the eastern Anatolia, Iran and the Caucasus. For example, by the beginning of the 1990s due to plowing the mountain steppes and intensive grazing on the remaining, steppes of the Caucasus, which occupy from 1200–1300 to 1800–2000 m above sea level and higher, were limited mostly to steep and strongly stony slopes (Fayvush, 2000; Fayvush and Aleksanyan, 2016). As a result, more than 60% of the land here was more or less eroded. Natural populations of wild relatives of crop species are threatened due to deterioration and fragmentation of their habitats, overgrazing and desertification. The indigenous breeds and populations of domestic animals are also threatened due to hybridization with non-indigenous breeds, transfer of diseases and shrinkage of populations due to abandonment of grazing in some places. E.g., Hybridizing with Swiss and American breeds causes erosion of genetic resources of Caucasian gray cattle breeds and threatens the local populations (Food and Agriculture Organization of the United Nations, 2019).

The most important factors affecting the structure of the grasslands in the Middle East are grazing and fuel collection. They allow penetration and expansion of many ruderal, shrubby and tragacanthic vegetation in natural communities (Zohary, 1973). Over the millennia a change of species composition has occurred. Desertification, i.e., decrease in total vegetation cover, disappearance of perennial grasses and herbs but increase in dwarf shrubs as a response to grazing, is a common problem of the ME. The nomadic grazing of herds over millennia has markedly changed the face of the vegetation of Iran. The present broad distribution of vegetation units dominated by thorn shrubs, dwarf scrub, or thorn cushions is assumed to have resulted from overgrazing. The original vegetation was shrunk, leading to the dominance of poisonous and unpalatable species like thorn cushions (antipastoralism, antipyrism). As Zohary (1973) pointed out, two processes of “ruderalization” and “tragacanthization” of the steppe is perhaps one of the most striking features in the dynamics of the *Artemisia* communities in most parts of Iran. This formation becomes more species rich (particularly with grass species like *Stipa hohenackeriana*), when protected from grazing and human interference. Conservation of some steppes and other grasslands provide the opportunity for developing original grasslands with less proportion of thorn-cushion plants due to grass species increasing competitive advantage. This situation is well observed in places like Golestan National Park or some long-time protected regions of northern slopes of Alborz (e.g., Golestanak Protected Area) (Akhani, 1998, 2005, personal observations). In Golestan National Park with a long history of protection, only few thorn-cushion species like *Onobrychis cornuta* and *Acantholimon raddeanum* occur along with many grass species such as *Festuca valesiaca*, *Stipa lessingiana*, *Poa densa*, *Poa bulbosa*, *Bromus tomentellus* and *Koeleria macrantha*.

Afforestation is a popular trend in areas that were formerly forest-steppes. Usually trees that do not occur naturally in a site are planted, not the native trees. Some examples are *Pinus nigra*, *Pinus sylvestris*, *Acacia* spp., and *Ailanthus altissima*. As a result, sites with rare plant and animal populations are destroyed. For example, in Turkey, the Forestry Department planted more than 24,000 km² only between 2008 and 2012, and most of the afforestation sites were steppes where several endemic plant and butterfly species live (Ambarlı et al., 2016). Planting non-native plants such as *Ailanthus altissima*, *Populus* spp., *Pinus* spp., *Cupressus* spp. and more recently *Paulownia tomentosa* for ornamental purposes is starting to cause invasive species to be an issue in forest-steppes of Iran.

Conversion to cropland was a threat in the past which replaced steppes and forest-steppes. Irrigation maintained by several dams promoted large-scale conversions in the Mesopotamia. But this trend is not in increase any more. Land abandonment is reported to be a threat in neighboring European countries due to shrub encroachment and disappearance of the grasslands. Such a negative impact of land abandonment has not been reported from the ME&C. On the contrary, one study shows that abandonment allowed natural restoration of the overgrazed lands and supported richer biodiversity (Ambarlı and Bilgin, 2014). The Middle East has one of the highest rates of emigration due to harsh living conditions, impoverishment and armed conflicts. Since 2011, the world has witnessed the fleeing of millions from Syria, seeking refuge. The consequences of armed conflicts for nature have not been documented yet.

The region is among the most vulnerable to climate change (Lelieveld et al., 2012): Compared to the period between 1961 and 1990, it is estimated that the maximum summer temperatures will increase 3.5 °C–5 °C at the north of the region but 1.5 °C–3.5 °C at the south in the period between 2040 and 2069. In the same period, number of dry days will increase by 5–20 days. This suggests strong shifts in species distributions and community composition, already stressed by existing growing conditions but also even harsher conditions for natural resource extraction and production.

Facing a wide range of threats, the steppes and forest-steppes of the region are under-represented in the network of protected areas. In Turkey, effective protected areas cover only 1.5% of those habitats and only 16.2% of the threatened and near-threatened species fall within the borders of protected areas of different categories (Ambarlı et al., 2016). Biodiversity conservation in Caucasian countries is implemented mainly in protected areas referred as specially protected nature areas, where 60–70% of the species composition of the flora and fauna is concentrated, including the overwhelming majority of rare and endemic species. In

Armenia the total territory covered by protected areas (3 state reserves, 4 national parks, 27 state sanctuaries and 232 natural monuments) is 387,054 ha, which comprises 13.1% of the total territory. Besides, there are also 2 protected landscapes and 1 biosphere reserve (Ministry of Nature Protection of Republic of Armenia, 2014). In Georgia, protected areas (14 state reserves, 11 national parks, 19 managed nature reserves, 41 natural monuments, 2 protected landscapes) occupy 600,597 ha area (about 8.6% of the country) (Ministry of Environment Protection and Natural Resources of Georgia, 2015). In Azerbaijan protected areas (9 national parks, 24 nature sanctuaries, 11 nature reserves) occupy 892,546 ha area (about 10.3% of the country) (Ministry of Ecology and Natural Resources Republic of Azerbaijan, 2014). Iran has a total of 203 protected sites, covering 10% of Iranian territory and types of grasslands and forests (Department of Environment, 2017). In Syria, there are 14 rangeland protected areas (Barkoudah et al., 2000). In general, effectiveness of the conservation in the protect areas of the ME&C it is not clear. In addition to the state protected areas, several sites are indicated as conservation areas of international importance such as important bird areas, important plant areas, key biodiversity areas, prime butterfly areas, Ramsar sites and sites of EMERALD network. There are national and international conservation efforts targeting specific species and habitats. For example, several FAO projects target strengthening protected areas with grasslands in the region. But evidence is needed for effectiveness of such projects. As the region itself is a biodiversity hotspot, further attempts are needed.

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Temperate Grasslands and Shrublands of Russia

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This article was solicited and edited by Jürgen Dengler and Péter Török on behalf of the Eurasian Dry Grassland Group (EDGG).

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Abstract

For Northern Eurasia and, consequently, for Russia, temperate grasslands and shrublands are an obligatory element of a forestless landscape. They are present in all plain and montane biomes, forming natural and secondary (anthropogenic) communities, and occupy forestless spaces in the bounds of both the forest and steppe zones. In the forest zones, they are predominantly anthropogenic, locating in sites naturally occupied by forests (*Molinio-Arrhenatheretea* grasslands are specifically extensive and diverse here). Conversely, in the steppe zone, they are natural (*Festuco-Brometea* grasslands prevail). The total area of temperate grasslands is 920,000 km², of which 680,000 km² are used as pastures and 240,000 km² as hay meadows), and they are widely spread in all natural zones of Russia, especially within the forest zone (250,000 km²) and steppe zone (500,000 km² including steppes in mountain areas). The main distinctive features of their spread are small contour; diffusiveness; a strong anthropogenic transformation (of the steppe); and proneness to fires, desertification, etc. Biogeographically, the regions are so different that zonal-provincial variants can be identified. Grasslands are both zonal (steppes) and intrazonal (floodplain meadows). They are mainly composed of graminoids and forbs in different proportions, the composition and production of which change annually (fluctuations) and in perennial autogenous cycles (for example, “a year of grasses” or “a year of legumes”). A spatially extensive and diverse group comprises post-forest or post-agrarian watershed meadows, representing perennial stages of a progressive succession, which follow the pioneer stages. Their conservation (economically and sustainably optimal maintenance) depends on man, who has included them in the cycle of agrarian use as hay fields or pastures and, less often, uses for recreation and for conserving historical landscapes. A similar picture is observed for shrublands, which form both zonal (at watersheds) and intrazonal complexes with herbaceous vegetation. The most stable and spatially extensive shrublands are represented by two types. The first type are arctic and alpine thickets formed by Siberian dwarf pines (*Pinus pumila*), dwarf birches (*Betula rotundifolia*, *B. fruticosa* and others), and *Alnus alnobetula* subsp. *fruticosa*. The second type are steppe shrub thickets dominated by many species of genera such as *Caragana*, *Spiraea*, *Chamaecytisus* and *Prunus*. Shrublands on floodplains or clearing and burn sites are relatively quickly replaced with other kinds of vegetation during succession. The first inventory of grasslands in Russia was performed back in 1932–1938 by the outstanding vegetation scientist Leonty Ramensky (1884–1953), who was the first in the world to create so-called ecological scales (ecological indicator values), which, using data on the contribution of plant species in a community's composition, make it possible to assess habitat parameters (humidity, soil wealth, salinity, etc.). According to a recent phytosociological overview, the diversity of temperate grasslands and shrublands of Russia's plains comprises 18 classes, 35 orders, and 92 alliances for grassland communities and 4 classes, 5 orders, and 8 alliances for steppe shrublands. We highlight distinctive features of meadow and steppe ecology as well as the contribution of these habitats to the conservation of biodiversity, global climate regulation, and the formation of various ecosystem services, including use as hayfields, pastures, recreation and historical sites. Grassland and shrubland conservation and restoration in Russia are associated with the prospects to create a network of protected areas and with the restoration of steppe and meadow animal husbandry.

Boundary Delimitation and Area Physiography

Russia is situated in the Northern Hemisphere, surrounded by seas of the Pacific (the Bering Sea, the Sea of Okhotsk, and the Sea of Japan), Atlantic (the Baltic and Black seas and the Sea of Azov), and Arctic (the Barents, White, Kara, East Siberian, Laptev, and Chukchi seas) oceans, and has the longest coastline in the world (37,653 km). It lies in the North of Eurasia, occupying the larger part of Eastern Europe and the entire northern part of Asia. The conventional border between the country's European and Asian parts runs along the Urals.

The northernmost point of Russia is Rudolf Island (Franz Josef Land, 81°51' N); the easternmost, Big Diomed Island in the Bering Strait (169°0' W); the southernmost is at the border with Azerbaijan (41°11' N); and the westernmost is on the Vistula Spit of Gdańsk Bay of the Baltic Sea (19°38' E). The extent of the country from west to east is 10,000 km and from north to south, over 4000 km. The national area is a little more than 17,000,000 km².

According to some estimates the area of Russia's temperate grasslands is 7–10% of the national territory (White et al., 2000). It is quite concurring with official data of the land statistics of Russia (Rosreestr, 2013). Officially, grasslands in Russia occupy an area of 920,000 km² (ca. 5.5% of the national territory), including 680,000 km² counted as natural pastures and 240,000 km² as hay meadows. Large shrub thickets in the Russian land statistics are included in the "forest lands" category and occupy about 750,000 km² of the Forest Fund lands (Governmental Report, 2017).

The diffused character of the current distribution of natural shrub and grass vegetation is obvious from its reflection by variously scaled maps. On the map of Russia (see Map 2), for example, it occupies a continuous area within the steppe biome only in the Caspian Depression and in the south of Siberia. In the forest biome, meadows and shrublands are represented as large blocks mostly in the periphery of the area at the northern and southern boundaries, where their postforest character is obvious.

More than 70% of Russia's territory consists of upland and lowland plains. The western part of the country is within the vast East European Plain with its lowlands (the Upper Volga Lowland, Caspian Depression, etc.) and uplands (the Valdai Hills, Central Russian Upland, Volga Upland, etc.). The Ural Mountains separate the East European Plain from the West Siberian Plain; east of it lies the Central Siberian Plateau, continuing into the Central Yakut Lowland and then the Kolyma and Yana-Indigirka lowlands. Low mountains and foothills of Caucasus, Ural, Altai, Sayans, Baikal and Transbaikalia, and Far East constitute the main part of other Russian areas.

Extensive areas of temperate grasslands and shrublands formerly were presented on all the plains and low mountains in the zone of temperate climate (Figs. 1–3, Map 1). However, the actually existing tracts of grasslands and shrublands cover no more than 10% of the area of the forest and steppe zones (Map 2). Their area and spread within the forest zone vary from year to year and in perennial cycles owing to two major causes: progressive successions and involvement in economic use (ploughing and so on).

Significant areas of wet grasslands and shrublands are associated with rivers and wetlands. Russia has the world second largest (next after Brazil) amount of fresh water (FAO, 2003). Surface waters occupy 12.4% of primarily plain part of the country's territory, with 84% of surface waters being concentrated east of the Urals. Large tracts of floodplain ecosystems are scattered over the forest and steppe biomes in the floodplains of the Volga, Pechora, Kama, Ural, Ob', Irtysh, Yenisei, Angara, Lena, Yana, Kolyma, Indigirka, Anadyr, and other rivers.

Soils on plains are arranged in accordance with latitudinal zonality, as well as vegetation. Characteristic of the transitional tundra-forest zone (south of the northern boundary of the forest) are gleys and low podzolic or gley-taiga-cryogenic soils. About 65% of Russia's territory is within the forest zone. In its northern part, the soils are podzolic, and east of the Yenisei taiga-cryogenic soils. In the taiga subzone (especially in West Siberia), there are many bogs, primarily raised bogs (oligotrophic), and boggy forests. Peaty cryogenic soils often are presented here under grasslands and shrublands. Soddy podzolic soils underlie coniferous-broadleaved forests on the East European Plain, and gray forest soils underlie broad-leaved forests. They are also developed under oak forests in the forest-steppe subzone.

Characteristic of the steppe zone are chernozem soils (with a thick humus horizon of up to 1 m with humus content 4–10%). Dark chestnut (kastanozem), light chestnut, and brown soils, while saline soils are typical for more arid steppe subzones (dry steppe and deserted steppe). Over 50% of the global chernozem area is located in Russia.

Characteristic soils of intrazonal floodplain grasslands and shrublands are alluvial (i.e., affected by river, lake, or sea floods) and different in terms of duration. They are highly fertile due to annual silt ingress. This favors the development of highly fertile communities of meadows and shrublands (willow thickets) in floodplains.

The territory of Russia mostly lies north of 50° northern latitude (but about 8° more south in both the western and eastern ends of the country, in the Caspian shore of Caucasus and Far East). All the national territory south of the Polar Circle (N66.5°) is situated in the temperate climate, mainly belonging in the Köppen-Geiger climate types Dfb, Dfc, Dfd, BSk, Dwa, Dwb, Dwc, and to a lesser extent Cfa, Cfb, and BWk (Beck et al., 2018). Average January temperatures vary by region from +6 to –50 °C, and July temperatures, from 8° to 25 °C; precipitation is from 250 to 1000 mm per year. Permafrost (northernmost part of European Russia, Siberia, and the Far East) occupies 65% of the Russia's territory.

Climate diversity is determined by the zonal gradient, continentality gradient, and relief. The fullest spectrum of natural zones characterizes European Russia, where Arctic desert, tundra, forest tundra, taiga forest, mixed and broad-leaved forest, forest steppe, steppe, and semi-desert zones and subzones succeed one another from north to south. Almost the same climatic gradient (excluding semi-desert) can be found in the Far East. Moving inside of the Asian landmass, to Siberia and Central Asia, the climate becomes increasingly continental, and the number of natural zones decreases. The diversity of climatic conditions for the temperate grassland and shrubland area within the forest and steppe zones is shown in Table 1.

Biogeography, Flora, and Fauna

Biogeographically, the region lies entirely within the Boreal Kingdom, the Palearctic realm with sub-areas such as the Euro-Siberian taiga, European nemoral, East Siberian (Angarian), Eurasian steppe, Irano-Turanian, and Mediterranean regions.



Fig. 1 Upland meadows of Russia: (A) Novgorod Province, Photo by A. Tishkov; (B) Novgorod Province, Photo by E. Belonovskaya; (C) Primorsky Province (every year burning), Photo by S. Titova. Floodplain meadows of Russia: (D) Novgorod Province, Photo by E. Belonovskaya; (E) Tver' Province, Photo by A. Tishkov; (F) Kursk Province, Photo by S. Titova.

According to M. Udvardy's classification (Udvardy, 1975), the following biomes are presented in Russia: tundras, temperate coniferous forests, temperate broadleaf forests, grasslands (steppes), deserts, and cold mountains of East Siberia. Cox and Moore (1993) identify only five biomes here: Arctic tundras, northern coniferous forests, temperate forests, temperate grasslands, and deserts. WWF recognizes six biomes: tundra; boreal forests/taiga; temperate broadleaf and mixed forests; temperate grasslands, savannas, and shrublands; deserts and xeric shrublands; and montane grasslands and shrublands (Olson et al., 2001). Steppes alone (without other temperate grasslands) often are considered as an entire biome (Wesche et al., 2016).

The biodiversity of Russia's temperate grasslands and shrublands is determined by their high landscape diversity, represented by the northern, middle, and southern taigas; larch forests and woodlands; coniferous–broad-leaved forests; broad-leaved forests;



Fig. 2 Plain steppes of Russia: (A) Belgorod Province, Photo by S. Titova; (B) Orenburg Province, Photo by A. Chibilev; (C) Altai Territory, Photo by I. Smelansky; (D) Transbaikalian Territory, Photo by I. Smelansky.

forest steppes; and meadow, typical, dry, and deserted steppes in zonal variant and specific variants on chalky, sandy, rocky, and salty substrates (Map 1), as well as by intrazonal ecosystems, such as different wetlands, floodplain and halophytic meadows. This is the reason for their exceptional landscape and ecosystem diversity, which is *a priori* the “receptacle” of high species diversity and the region’s biogeographic characteristic.

In regional floras of Russia’s forest and steppe biomes, vascular plants of grasslands and shrublands make up from 40–50 (taiga) to 80% (the subzones of meadow and typical steppes). In absolute values for a local flora (per 100 km²), there may be from 250 to 600–700 species, predominantly from the families (using the Takhtajan’ system of flowering plants taxonomy—Takhtajan, 2009) *Asteraceae*, *Poaceae*, *Brassicaceae*, *Fabaceae*, *Lamiaceae*, and *Ranunculaceae*; in floodplains additionally, *Cyperaceae*, *Polygonaceae*, *Juncaceae*, and *Chenopodiaceae*; and in xeric conditions (in steppes), *Scrophulariaceae*, *Caryophyllaceae*, and *Rosaceae* (Table 2). Among characteristically diverse genera in grassland communities are both graminoids (including such grasses as *Festuca*, *Poa*, *Stipa*, *Elytrigia*, *Bromopsis*, *Alopecurus*, *Dactylis*, *Deschampsia*, *Agrostis*, *Calamagrostis*, *Phleum*, *Bothriochloa*, *Koeleria*, *Milium*, *Hierochloa*, *Leymus*, *Arrhenatherum*, and also *Carex* and *Kobresia*), and forbs (such as *Centaurea*, *Trifolium*, *Lathyrus*, *Galium*, *Achillea*, *Crepis*, *Veronica*, *Filipendula*, *Thymus*, *Potentilla*, *Campanula*, *Rumex*, etc.). At the extreme positions of ecological gradients, grasses are replaced by other taxonomic groups: under high humidity, by sedges of the family *Cyperaceae*, and under growing salinization, by species from the family *Chenopodiaceae*. The alternation of the positions of families with the largest species diversity in the structure of the floras reflects the ecotopes of grassland communities by the gradients of humidity, soil wealth, and salinity. High requirements on the light regime are obligatory, distinguishing the ecosystems under consideration and their floristic composition from forests (Tables 2 and 3).

Bryophytes within grassland and shrubland communities are represented by the entire spectrum of the ecological groups of Russia’s mosses and liverworts: meadow (*Climacium dendroides*, *Thuidium recognitum*, *T. philibertii*, *Rhytidiadelphus squarrosus*), steppe (*Thuidium abietinum*, *Tortula desertorum*, *T. ruralis*), forest (*Pleurozium schreberi*, *Hylocomium splendens*, *Mnium* spp., *Rhodobrym roseum*, *Dicranum* spp., *Polytrichum* spp., *Hypnum* spp., *Mnium* spp.), and bog (*Sphagnum* spp., *Calliergon* spp., *Drepanocladus* spp., *Tomenthypnum nitens*, *Aulacomnium palustre* and others) species. Heliophilous and moderately hydrophilic moss species dominate, except for some steppe species, which can resist summer droughts.



Fig. 3 Shrublands of Russia: (A) steppe shrubs, Belgorod Province. Photo by S. Titova; (B) *Prunus sibirica* shrubs (“kharganaty”), Trans-Baikal Territory. Photo by I. Smelansky; (C) *Betula rotundifolia* shrubs (“ernik”), Altai Republic. Photo by I. Smelansky; (D) floodplain shrubs, Arkhangelsk Province. Source: www.pohody2.narod.ru.

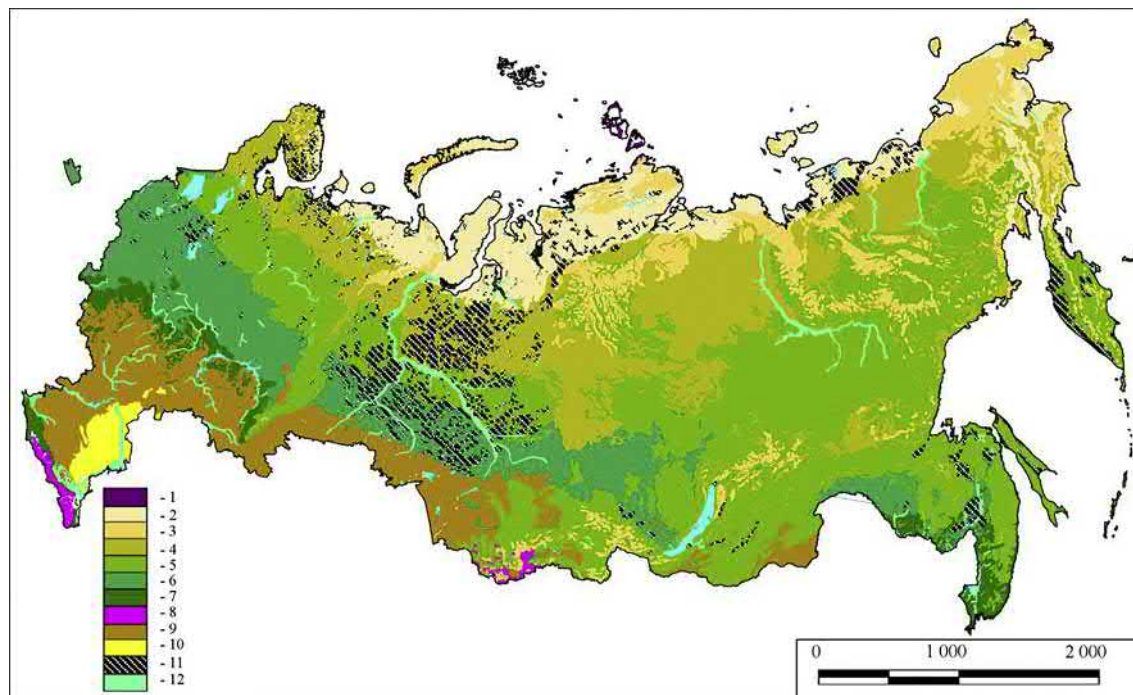
Fungi of Russia’s meadows, steppes, and shrublands are also exceptionally diverse. Dominating among them are *Basidiomycota*: *Agaricus campestris*, *A. arvensis*, *A. bitorquis*, *A. xanthoderma*, *Coprinus comatus*, *C. atramentarius*, *Phaeolepiota aurea*, *Agrocybe dura*, *Marasmius oreades*, *Lepista saeva*, *Bovista nigrescens*, *Langermannia gigantea*, and others. In steppes, *Clavaria* species are also observed—*Clavaria argillacea*, *C. falcata*, *C. fragilis*, *Clavulina cinerea*, *C. coralloides*, *Clavulinopsis corniculata*, *Ramaria* spp., *Ramariopsis* spp., *Typhula* spp., and others. Their spatial distribution, as well as that of other groups of the biota, corresponds to the zonal gradient of heat and moisture (Shiryayev, 2018) (Table 3).

Based on floristic composition, Russia (excluding high mountains) is divided into the following floristic regions: Circumboreal, including the Northern European, Central European, Euxinian (the Black Sea coast), Caucasian (the Caucasus foothills), Eastern European, West Siberian, Altai-Sayan (the Altai foothills), Central Siberian, Transbaikalian, Northeastern Siberian, and Okhotsk-Kamchatkan Provinces; East Asian, including Manchurian (the Amur basin, Primorski Territory) and Sakhalin-Hokkaido provinces; Mediterranean, including the Crimea-Novorossiysk province; and the Irano-Turanian, including Turanian province (the Caspian Depression).

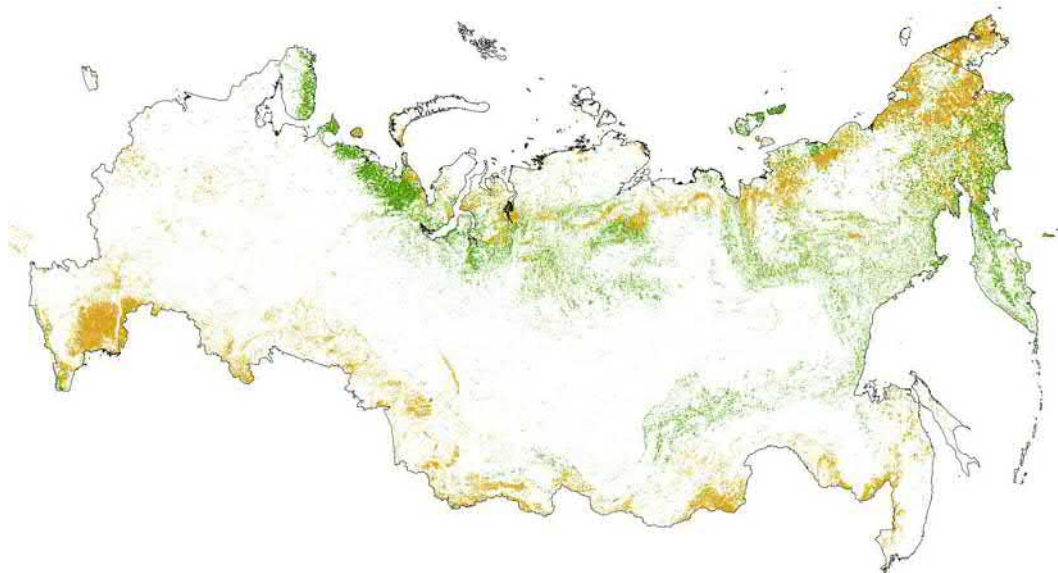
In different geographical units grasslands and shrublands occupy from 2% to 3% (steppes of central part of Russian plain or meadows of the northern taiga of European Russia) to 50–60% (the steppes, secondary meadows, and shrublands of the south of Siberia and the Far East) of the total area of the region.

Specific fauna of “open spaces” is characteristic for Russia’s grasslands and shrublands. Among insects the orders *Orthoptera*, *Homoptera*, *Heteroptera*, *Coleoptera*, *Lepidoptera*, *Hymenoptera*, and *Diptera* are dominating. Many of the insect species are obligatory associated with herbaceous forage plants and some of them lead in the elimination of grasslands primary production on large areas (for example, some locusts in steppes). Some of the typical steppe insects penetrate deep in the forest zone in Northeastern Siberia in the specific cold (cryo-arid) steppe habitats.

The characteristic mammals of steppe grasslands and shrublands of Russia’s plains are long-distant migrating antelopes—Saiga (*Saiga tatarica*) and Mongolian Dzeren (*Procapra gutturosa*). But these two species are surviving in small areas only, on the opposite ends of the steppe belt in Russia, Saiga in Caspian Lowlands and Dzeren in Transbaikalia. Actually widespread ungulates in



Map 1 Natural biomes and ecosystems of the Russia: (1) Polar deserts; (2) plain Arctic and subarctic tundras; (3) alpine tundras; (4) forest tundra, northern taiga, and larch woodlands; (5) middle taiga; (6) southern taiga and coniferous-broad-leaved forests; (7) plain and alpine broad-leaved forests; (8) ecosystems of middle mountains and highlands (subalpine and alpine meadows, shrublands, petrophytic groups, barren); (9) steppes; (10) desert steppes and deserts; (11) bogs; (12) floodplain complexes of large rivers.



Map 2 Map of the actual distribution of grasslands and shrublands on Russia's territory. Based on the analysis of ASTER, SPOT-Vegetation (1999–2012), and PROBA-V (2013–2015) images, a resolution of 300 m. Yellow means grasslands, mosaic herbaceous cover (> 50%); green, shrublands evergreen and deciduous (more than 15%).

grassland and shrubland habitats are the Roe Deer, *Capreolus capreolus* and *C. pygargus*, and common in Siberia is the Elk, *Cervus canadensis* (formerly Siberian Elk was considered as subspecies of *C. elaphus*). Ungulates are considered as keystone species in grassland ecosystems, their grazing and trampling forming grasslands in both evolutionary and ecological scales.

Other mammal grazers play a key role as ecosystem engineers in the grasslands, the colony-forming burrowing rodents and lagomorphs. In Russian grasslands the guild includes many species of the Sousliks (*Spermophilus suslicus*, *S. pygmeus*, *S. major*, *S. erythrogenys*, *S. dauricus*, *S. undulatus*), Marmots (*Marmota bobak*, *M. baibacina*, *M. kastschenkoi*, *M. sibirica*), Steppe Lemming (*Lagurus*

Table 1 Climatic characteristics of plain grasslands and shrublands of forest and steppe biomes in Russia (along zonal transects from the North to the South).

<i>Region</i>	<i>Zonal and intrazonal vegetation</i>	<i>Mean annual temperature (°C)</i>	<i>July mean long-term temperature (°C)</i>	<i>January, mean long-term temperature (°C)</i>	<i>Mean annual amount of precipitation (mm)</i>
European transect					
Kola Peninsula, the White Sea shores, the lower Pechora-river	Forest tundra, the northern taiga	−4.0 to −9.0	+7.0 to +10.0	−8.0 to −20.0	300–450
Karelia, the north of the Russian plain	Northern taiga	+0.5	+15.0	−11.0 to −15.0	350–400
Central Russian plain	Middle and southern taiga, swamps	+2.0	+17.0 to +18.0	−10.0 to −12.0	570–620
The Ural taiga	Middle and Southern taiga	+1.0 to +2.0	+16.0 to +18.0	−13.0 to −17.0	550–650
Dnieper-Volga interfluvium	Mixed and deciduous forests, forest-steppe	+3.0 to +4.0	+17.5 to +18.0	−9.0 to −11.0	650–750
Vyatka-Kama interfluvium	Mixed and deciduous forests, forest-steppe	+3.5	+19.0	−11.0 to −13.0	500–600
Trans Volga-river steppes	Deciduous forests, steppes	+2.5 to +4.5	+20.0 to +21.0	−12.5 to −15.0	550–600
Crimean-Caucasian steppes	Open oak woodland, steppes	+10.0 to +12.0	+21.5 to +24.0	−0.5 to +1.0	420–700
Black Sea–Ciscaucasian plain steppes	Steppes	+7.0 to +9.0	+22.0 to +24.5	−3.0 to 9.0	300–400
Caspian desert steppe	Steppes, Northern deserts	+8.0 to +10.0	+23.0 to +27.0	−10.0 to −15.0	200–250
West Siberian transect					
The North of Western Siberia	Forest-tundra, northern taiga	−2.0 to −5.0	+11.0 to +15.0	−20.0 to −25.0	500–600
Ob-Irtysh rivers interfluvium	Northern and middle taiga, swamps, floodplains	−1.5 to −2.0	+16.0 to +18.0	−15.0 to −20.0	450–600
Tobol-Ob rivers interfluvium	Birch woods, pine forests, forest-steppe, steppes	−0.1 to +2.0	+19.5	−15.5 to −19.0	380–520
The South of Western Siberia	Birch woods, forest-steppes, swamps	+0.9	+18.5	−15.0 to −17.0	480–550
Trans Volga-river-Kulunda steppes	Birch woods, steppes	+0.5 to +4.0	+20.0 to +23.0	−14.0 to 20.0	250–350
Middle Siberian transect					
The North of Central Siberia	Forest-tundra, Northern taiga, open woodlands, the dwarf birch	−12.0 to −14.0	+11.5 to +12.5	−28.0 to −31.0	300–350
The Olenyok-river basin	Open larch woodlands	−12.0 to −14.0	+11.0 to +13.0	−33.0 to −40.0	250–300
The South of Central Siberia	Middle and southern taiga, forest-steppe	+0.5 to −3.0	+17.5 to +19.0	−17.0 to −23.0	350–400
East Siberian and Far Eastern transect					
The lower Kolyma-river	Open larch woodlands	−11.0 to −15.0	+11.0 to +15.0	−35.0 to −39.0	250–300
The western part of Kamchatka peninsula	Northern taiga, dwarf birch	−0.5 to −3.0	+10.0 to +13.0	−12.0 to −18.0	600–1100
The upper Vilyui-river	Open woodlands, middle taiga, middle taiga, dwarf birch, floodplains	−5.0 to −6.0	+17.0 to +22.0	−25.0 to −30.0	320–420
Central Yakutia	Open woodlands, middle taiga, dwarf birch, “alases”	−8.0	+17.0 to +19.0	−35.0 to −42.0	250–300
The North of Sakhalin island	Middle taiga, dwarf birch	+1.5 to +2.0	+14.0 to +15.0	−17.0 to −20.0	500–700
Amur-Zeya rivers interfluvium	Southern taiga, dwarf birch, floodplains	−3.0 to −4.0	+17.0 to +19.0	−23.0 to −28.0	420–600
Amur-Ussuri rivers interfluvium	Coniferous-deciduous forests, meadows, swamps	+0.5 to +2.5	+18.5 to +21.0	−19.5 to −22.0	580–700
Zeya-Bureya rivers interfluvium	Deciduous forests, forest-steppe, steppes	−2.0 to +3.0	+20.0 to +21.0	−15.0 to −25.5	460–660
Daurian steppes	Birch and larch woods, steppes	−2.0 to −3.0	+16.0 to +20.0	−21.0 to −26.0	290–340

Data from <http://meteo.ru/data>—for 518 meteorological stations of Russia.

Table 2 Characteristic species of vascular plants in grasslands and shrublands of the forest and steppe biomes on the plains of Russia.

Region	Biomes and ecosystems	Characteristic graminoid and forb species	Characteristic shrub and dwarf shrub species
European transect			
Kola Peninsula, the White Sea shores, the lower Pechora River	Forest tundra, northern taiga, swamps, marches, floodplain meadows	<i>Agrostis straminea</i> , <i>A. alba</i> , <i>Castilleja lapponica</i> , <i>Carex norvegica</i> , <i>C. salina</i> , <i>C. limosa</i> , <i>Festuca rubra</i> , <i>Puccinellia capillaris</i> , <i>P. pulvinata</i> , <i>P. coarctata</i> , <i>Sedum acre</i> , <i>Rumex pseudonatronatus</i> , <i>Rhodiola rosea</i> , <i>Tripleurospermum subpolare</i>	<i>Betula nana</i> , <i>Juniperus communis</i> , <i>Salix</i> spp.
Karelia	Northern taiga, swamps, floodplain meadows	<i>Achillea millefolium</i> , <i>Calamagrostis canescens</i> , <i>Carex acuta</i> , <i>Dactylis glomerata</i> , <i>Deschampsia cespitosa</i> , <i>Elymus repens</i> (= <i>Elytrigia repens</i>), <i>Filipendula ulmaria</i> , <i>Galium album</i> , <i>Heracleum sibiricum</i> , <i>H. umbellatum</i> , <i>Knautia arvensis</i> , <i>Lathyrus pratensis</i> , <i>Leucanthemum ircutianum</i> , <i>Phleum pratense</i> , <i>Poa pratensis</i> , <i>Scutellaria galericulata</i> , <i>Veronica longifolia</i>	<i>Betula tortuosa</i> , <i>B. nana</i> , <i>Salix</i> spp.
European taiga	Middle and southern taiga, swamps, watershed and floodplain meadows	<i>Alopecurus pratensis</i> , <i>Elymus repens</i> (= <i>Elytrigia repens</i>), <i>Bromopsis inermis</i> , <i>Poa pratensis</i> , <i>Carex cespitosa</i> , <i>C. loliacea</i> , <i>Filipendula ulmaria</i> , <i>Leucanthemum vulgare</i> , <i>Deschampsia cespitosa</i> , <i>Geum rivale</i> , <i>Veronica longifolia</i>	<i>Juniperus communis</i> , <i>Salix</i> spp.
Urals taiga	Middle and southern taiga, watershed and floodplain meadows, willows thickets	<i>Poa angustifolia</i> , <i>Festuca rubra</i> , <i>F. pratensis</i> , <i>Bromopsis inermis</i> , <i>Agrostis tenuis</i> , <i>A. stolonifera</i> , <i>A. gigantea</i> , <i>Phleum pratense</i> , <i>Alopecurus pratensis</i> , <i>Dactylis glomerata</i> , <i>Deschampsia cespitosa</i> , <i>Carex vulpina</i> , <i>C. acuta</i> , <i>C. praecox</i> , <i>Cirsium setosum</i> , <i>Sanguisorba officinalis</i> , <i>Dianthus pratensis</i> , <i>Fragaria viridis</i>	<i>Juniperus communis</i> , <i>Salix</i> spp.
Dnieper-Volga interfluvium	Mixed and deciduous forests, forest-steppe, steppe shrubs, watershed and floodplain meadows, willows thickets	<i>Agrostis gigantea</i> , <i>A. tenuis</i> , <i>Alopecurus pratensis</i> , <i>Anthoxanthum odoratum</i> , <i>Bromopsis inermis</i> , <i>Bunias orientalis</i> , <i>Calamagrostis epigeios</i> , <i>Campanula glomerata</i> , <i>Carex acuta</i> , <i>C. praecox</i> , <i>Cerastium arvense</i> , <i>Dactylis glomerata</i> , <i>Elymus repens</i> (= <i>Elytrigia repens</i>), <i>Festuca rubra</i> , <i>F. pratensis</i> , <i>Glechoma hederacea</i> , <i>Lathyrus pratensis</i> , <i>Leontodon autumnalis</i> , <i>Medicago falcata</i> , <i>Phalaroides arundinacea</i> , <i>Phragmites australis</i> , <i>Poa palustris</i> , <i>P. pratensis</i> , <i>P. trivialis</i> , <i>Taraxacum officinale</i> , <i>Trifolium hybridum</i> , <i>Vicia cracca</i>	<i>Chamaecytisus ruthenicus</i> , <i>Prunus tenella</i> (= <i>Amygdalus nana</i>), <i>Prunus fruticosa</i> (= <i>Cerasus fruticosa</i>), <i>Prunus spinosa</i> , <i>Rhamnus cathartica</i> , <i>Salix</i> spp., <i>Spiraea crenata</i>
Vyatka-Kama interfluvium	Mixed and deciduous forests, forest-steppe, steppe shrubs, watershed and floodplain meadows	<i>Achillea millefolium</i> , <i>Agrostis tenuis</i> , <i>A. vinealis</i> , <i>Alopecurus pratensis</i> , <i>Anthoxanthum odoratum</i> , <i>Carex rostrata</i> , <i>C. vesicaria</i> , <i>C. vulpina</i> , <i>C. cespitosa</i> , <i>C. praecox</i> , <i>Deschampsia cespitosa</i> , <i>Festuca rubra</i> , <i>F. valesiaca</i> , <i>Filipendula ulmaria</i> , <i>Nardus stricta</i> , <i>Poa palustris</i> , <i>P. pratensis</i> , <i>P. angustifolia</i> , <i>Potentilla anserina</i> , <i>Tanacetum vulgare</i> , <i>Trifolium arvense</i> , <i>T. pratense</i> , <i>T. montanum</i> , <i>Veronica chamaedrys</i>	<i>Chamaecytisus ruthenicus</i> , <i>Prunus tenella</i> (= <i>Amygdalus nana</i>), <i>Prunus fruticosa</i> (= <i>Cerasus fruticosa</i>), <i>Prunus spinosa</i> , <i>Salix</i> spp., <i>Spiraea crenata</i>
Trans-Volga steppes	Deciduous forests, floodplain meadows, steppes, steppe shrubs	<i>Aconitum septentrionale</i> , <i>Alopecurus pratensis</i> , <i>Centaurea sibirica</i> , <i>Dactylis glomerata</i> , <i>Echinops ruthenicus</i> , <i>Festuca valesiaca</i> , <i>F. rubra</i> , <i>F. pratensis</i> , <i>Filipendula vulgaris</i> , <i>Fragaria viridis</i> , <i>Origanum vulgare</i> , <i>Phlomis tuberosa</i> , <i>Poa angustifolia</i> , <i>Salvia stepposa</i> , <i>Stipa capillata</i> , <i>S. pennata</i> , <i>Trifolium montanum</i>	<i>Caragana frutex</i> , <i>Rhamnus cathartica</i> , <i>Rosa cinnamomea</i> , <i>Prunus stepposa</i> , <i>Prunus tenella</i> (= <i>Amygdalus nana</i>), <i>Prunus fruticosa</i> (= <i>Cerasus fruticosa</i>), <i>Salix viminalis</i> , <i>S. triandra</i>

Table 2 Characteristic species of vascular plants in grasslands and shrublands of the forest and steppe biomes on the plains of Russia.—cont'd

Region	Biomes and ecosystems	Characteristic graminoid and forb species	Characteristic shrub and dwarf shrub species
Crimean-Caucasian forest steppe	Open oak woodland, steppes, steppe shrubs, floodplain meadows	<i>Adonis vernalis</i> , <i>Aegilops biuncialis</i> , <i>A. triuncialis</i> , <i>Asphodelina taurica</i> , <i>A. lutea</i> , <i>Bothriochloa ischaemum</i> , <i>Briza australis</i> , <i>Bromus riparius</i> (= <i>Bromopsis riparia</i>), <i>Carex humilis</i> , <i>Festuca valesiaca</i> , <i>Filipendula vulgaris</i> , <i>Galium verum</i> , <i>Helianthemum canum</i> , <i>Hordeum bulbosum</i> , <i>Jurinea stoechadifolia</i> , <i>Koeleria cristata</i> , <i>Onosma taurica</i> , <i>Paeonia tenuifolia</i> , <i>Phleum phleoides</i> , <i>Poa pratensis</i> , <i>Salvia stepposa</i> , <i>Scutellaria orientalis</i> , <i>Stipa pulcherrima</i> , <i>S. pontica</i> , <i>S. tirsia</i> , <i>Teucrium polium</i> , <i>Thymus</i> spp., <i>Trifolium montanum</i>	<i>Acer campestre</i> , <i>Crataegus</i> spp., <i>Prunus spinosa</i> , <i>Prunus tenella</i> (= <i>Amygdalus nana</i>), <i>Swida australis</i>
Black Sea-Ciscaucasian steppes	Steppe, steppe shrubs	<i>Stipa zalesskii</i> , <i>S. lessingiana</i> , <i>S. pennata</i> , <i>S. tirsia</i> , <i>S. pulcherrima</i> , <i>S. ucrainica</i> , <i>Festuca valesiaca</i> , <i>Koeleria cristata</i> , <i>Bromopsis riparia</i> , <i>Poa angustifolia</i> , <i>Leymus ramosus</i> , <i>Agropyron cristatum</i> , <i>Artemisia hololeuca</i> , <i>A. salsoloides</i> , <i>Thymus roegneri</i> , <i>T. tauricus</i> , <i>Hedysarum tauricum</i> , <i>Astragalus reduncus</i> , <i>A. calycinus</i> , <i>Iris pumila</i> , <i>I. halophylla</i> , <i>Adonis vernalis</i> , <i>A. wolgensis</i> , <i>Paeonia tenuifolia</i> , <i>Filipendula vulgaris</i> , <i>Phlomis tuberosa</i> , <i>Trifolium montanum</i> , <i>Salvia nutans</i> , <i>Tulipa suaveolens</i> (= <i>Tulipa schrenkii</i>), <i>T. biebersteiniana</i> , <i>Gagea pusilla</i> , <i>Crocus reticulatus</i> , <i>Ferula orientalis</i> , <i>F. caspica</i> , <i>Limonium bungei</i> , <i>L. sareptanum</i>	<i>Calophaca wolgarica</i> , <i>Caragana frutex</i> , <i>Prunus stepposa</i> , <i>P. spinosa</i> , <i>Prunus tenella</i> (= <i>Amygdalus nana</i>), <i>Prunus fruticosa</i> (= <i>Cerasus fruticosa</i>), <i>Prunus mahaleb</i> (= <i>Cerasus mahaleb</i>), <i>Rosa canina</i>
Caspian lowland	Steppe, steppe shrubs, northern desert	<i>Agropyron desertorum</i> , <i>A. pectinatum</i> , <i>Anisantha tectorum</i> , <i>Artemisia lerchiana</i> , <i>A. santonica</i> , <i>A. marschalliana</i> , <i>A. nitrosa</i> , <i>A. pauciflora</i> , <i>A. taurica</i> , <i>Bassia</i> (= <i>Kochia</i>) <i>prostrata</i> , <i>Bothriochloa ischaemum</i> , <i>Bromus squarrosus</i> , <i>B. mollis</i> , <i>Camphorosma monspeliaca</i> , <i>Elymus repens</i> (= <i>Elytrigia repens</i>), <i>Euphorbia uralensis</i> , <i>Festuca valesiaca</i> , <i>Galium ruthenicum</i> , <i>Galatella villosa</i> , <i>Iris pumila</i> , <i>Leymus ramosus</i> , <i>Phlomis pungens</i> , <i>Poa bulbosa</i> , <i>Stipa sareptana</i> , <i>S. capillata</i> , <i>S. lessingiana</i> , <i>S. pennata</i> , <i>S. ucrainica</i> , <i>Tanacetum achilleifolium</i> , <i>Tulipa</i> spp.	<i>Caragana frutex</i> , <i>Prunus spinosa</i> , <i>Rhamnus cathartica</i> , <i>Spiraea hypericifolia</i> , <i>Tamarix meyeri</i> , <i>T. ramosissima</i>
West Siberian transect North of Western Siberia	Forest-tundra, northern taiga, dwarf birch, floodplain meadows	<i>Alopecurus alpinus</i> , <i>Bromus sibiricus</i> , <i>Calamagrostis neglectus</i> , <i>C. langsдорffii</i> , <i>Crepis nigrescens</i> , <i>Deschampsia borealis</i> , <i>Equisetum arvense</i> , <i>Festuca rubra</i> , <i>F. criophila</i> , <i>Geranium albiflorum</i> , <i>Hierochloa odorata</i> , <i>Koeleria asiatica</i> , <i>Parnassia palustris</i> , <i>Poa alpigena</i> , <i>P. alpina</i> , <i>Polemonium acutiflorum</i> , <i>Polygonum laxmannii</i> , <i>Roegneria turuchanensis</i> , <i>Rumex thyrsiflorus</i> , <i>Tanacetum bipinnatum</i> , <i>Trollius asiaticus</i> , <i>Veratrum lobelianum</i>	<i>Alnus alnobetula fruticosa</i> (= <i>Duschekia fruticosa</i>), <i>Betula nana</i> , <i>Salix glauca</i> , <i>S. pulchra</i> , <i>S. phylicifolia</i> , <i>S. dasicladus</i> , <i>S. lapponum</i>
Ob-Irtysh interfluve	Northern and middle taiga, swamps, floodplain meadows and willow thickets	<i>Carex aquatilis</i> , <i>C. acuta</i> , <i>Calamagrostis epigeios</i> , <i>Milium effusum</i> , <i>Melica nutans</i>	<i>Salix</i> spp.

(Continued)

Table 2 Characteristic species of vascular plants in grasslands and shrublands of the forest and steppe biomes on the plains of Russia.—cont'd

Region	Biomes and ecosystems	Characteristic graminoid and forb species	Characteristic shrub and dwarf shrub species
Tobol-Ob' interfluve	Birch woods, pine forests, steppes, steppe shrubs, floodplain meadows	<i>Agrostis alba</i> , <i>Artemisia pontica</i> , <i>Brachypodium pinnatum</i> , <i>Calamagrostis epigeios</i> , <i>Carex riparia</i> , <i>C. caespitosa</i> , <i>Elymus repens</i> (= <i>Elytrigia repens</i>), <i>Festuca pseudovina</i> , <i>Filipendula ulmaria</i> , <i>Filipendula vulgaris</i> , <i>Galatella hauptii</i> , <i>Helictotrichon schellianum</i> , <i>Heracleum sibiricum</i> , <i>Koeleria cristata</i> , <i>Medicago falcata</i> , <i>Phlomis tuberosa</i> , <i>Pleurospermum uralense</i> , <i>Stipa pennata</i> , <i>S. capillata</i> , <i>S. zaleskii</i> , <i>Artemisia dracunculus</i> , <i>A. glauca</i> , <i>Achillea millefolium</i> , <i>Pulsatilla patens</i> , <i>Poa angustifolia</i>	<i>Prunus spinosa</i> , <i>Prunus tenella</i> (= <i>Amygdalus nana</i>) (= <i>Cerasus fruticosa</i>), <i>Rosa cinnamomea</i> , <i>R. majalis</i> , <i>Spiraea crenata</i> , <i>S. hypericifolia</i>
South of Western Siberia	Birch woods, forest-steppes, floodplain meadows and willow thickets, swamps	<i>Agrostis gigantea</i> , <i>Alopecurus arundinaceus</i> , <i>Calamagrostis canescens</i> , <i>C. langsdorffii</i> , <i>Carex omskiana</i> , <i>C. riparia</i> , <i>C. caespitosa</i> , <i>Filipendula ulmaria</i> , <i>F. vulgaris</i> , <i>Galium verum</i> , <i>Iris ruthenica</i> , <i>Lythrum salicaria</i> , <i>Phleum phleoides</i> , <i>Phlomis tuberosa</i> , <i>Pulsatilla flavescens</i> , <i>Saussurea amara</i> , <i>Seseli libanotis</i> , <i>Trifolium lupinaster</i> , <i>Veronica incana</i> , <i>Veronica longifolia</i>	<i>Salix cinerea</i> , <i>S. rosmarinifolia</i> , <i>S. pentandra</i>
Trans-Volga-Kulunda steppes	Birch woods, steppes, solonchaks	<i>Allium hymenorhizum</i> , <i>Artemisia nitrosa</i> , <i>Bassia</i> (= <i>Kochia</i>) <i>prostrata</i> , <i>Bromopsis inermis</i> , <i>Calamagrostis epigeios</i> , <i>Carex humilis</i> , <i>C. supina</i> , <i>Delphinium dictyocarpum</i> , <i>D. uralense</i> , <i>Dianthus uralensis</i> , <i>Elymus bungeanus</i> (= <i>Elytrigia pruinifera</i>), <i>Festuca valesiaca</i> , <i>Filipendula vulgaris</i> , <i>Gypsophila altissima</i> , <i>Helictotrichon schellianum</i> , <i>H. desertorum</i> , <i>Koeleria cristata</i> , <i>Leymus paboanus</i> , <i>Medicago romanica</i> , <i>Peucedanum alsaticum</i> , <i>P. morisonii</i> , <i>Phleum phleoides</i> , <i>Poa stepposa</i> , <i>Pulsatilla multifida</i> , <i>Salvia stepposa</i> , <i>Stipa zaleskii</i> , <i>S. capillata</i> , <i>S. tirsia</i> , <i>S. lessingiana</i> , <i>S. pennata</i> , <i>S. korshinskyi</i> , <i>Thymus marschallianus</i>	<i>Caragana frutex</i> , <i>C. pumila</i> , <i>Chamaecytisus ruthenicus</i> , <i>Prunus tenella</i> (= <i>Amygdalus nana</i>), <i>Rosa majalis</i> , <i>Spiraea crenata</i> , <i>S. hypericifolia</i>
Middle Siberian transect			
The Olenyok River basin	Open larch woodlands, dwarf birch, floodplain meadows, willow shrubs	<i>Carex melanocarpa</i> , <i>Dianthus repens</i> , <i>Euphorbia discolor</i> , <i>Festuca kolyensis</i> , <i>Hedysarum alpinum</i> , <i>Limnas stelleri</i> , <i>Papaver nudicaule</i> , <i>Phlox sibirica</i> , <i>Potentilla arenosa</i>	<i>Alnus alnobetula fruticosa</i> (= <i>Duschekia fruticosa</i>), <i>Betula exilis</i> , <i>B. nana</i> , <i>B. fruticosa</i> , <i>Salix alaxensis</i> , <i>S. bogdanidensis</i> , <i>S. glauca</i> , <i>S. pulchra</i> , <i>S. lanata</i> , <i>S. pyrolifolia</i>
Angara River basin	Middle and southern taiga, forest steppe, floodplain meadows	<i>Achnatherum sibiricum</i> , <i>Alopecurus glaucus</i> , <i>Artemisia tanacetifolia</i> , <i>A. latifolia</i> , <i>Aster alpinus</i> , <i>Bupleurum scorzoniferifolium</i> , <i>Calamagrostis epigeios</i> , <i>Festuca supina</i> , <i>F. lenensis</i> , <i>F. jensseensis</i> , <i>F. pseudovina</i> , <i>Filifolium sibiricum</i> , <i>Gentiana barbata</i> , <i>Helictotrichon desertorum</i> , <i>Iris ruthenica</i> , <i>Onobrychis sibirica</i> , <i>Phleum phleoides</i> , <i>Phlojodicarpus sibiricus</i> , <i>Poa stepposa</i> , <i>Pulsatilla flavescens</i> , <i>Sanguisorba officinalis</i> , <i>Saussurea controversa</i> , <i>Senecio integrifolius</i> , <i>Thalictrum petaloideum</i> , <i>Trifolium lupinaster</i>	<i>Alnus alnobetula fruticosa</i> (= <i>Duschekia fruticosa</i>), <i>Juniperus communis</i> , <i>Rhododendron dahuricum</i> , <i>Rosa acicularis</i> , <i>Spiraea media</i>
East Siberian and Far Eastern transect			
Lower Kolyma River	Open larch woodlands, dwarf birch, elfins	<i>Androsace septentrionalis</i> , <i>Artemisia tilesii</i> , <i>Astragalus alpinus</i> , <i>Bistorta vivipara</i> , <i>Dianthus repens</i> , <i>Draba juvenilis</i> , <i>Festuca rubra</i> , <i>Galium densiflorum</i> , <i>Parnassia kotzebuei</i> , <i>Pedicularis sudetica</i> , <i>Poa alpigena</i> , <i>Poa glauca</i> , <i>Wilhelmsia physodes</i>	<i>Alnus alnobetula fruticosa</i> (= <i>Duschekia fruticosa</i>), <i>Betula exilis</i> , <i>Pinus pumila</i> , <i>Salix glauca</i> , <i>S. lanata</i> , <i>S. pulchra</i>

Table 2 Characteristic species of vascular plants in grasslands and shrublands of the forest and steppe biomes on the plains of Russia.—cont'd

Region	Biomes and ecosystems	Characteristic graminoid and forb species	Characteristic shrub and dwarf shrub species
North-Eastern Siberia	Open woods, valley forests and meadows, cold steppes, elfins	<i>Artemisia borealis</i> , <i>Carex duriuscula</i> , <i>C. pediformis</i> , <i>Chamaenerion latifolium</i> , <i>Deschampsia brevifolia</i> , <i>D. borealis</i> , <i>Elymus maritimus</i> , <i>Equisetum arvense</i> , <i>Helictotrichon krylovii</i> , <i>Koeleria asiatica</i> , <i>Senecio congestus</i>	<i>Alnus alnobetula fruticosa</i> (= <i>Duschekia fruticosa</i>), <i>Betula exilis</i> , <i>Pinus pumila</i> , <i>Salix alaxensis</i> , <i>S. pulchra</i> , <i>Rubus arcticus</i>
Western part of Kamchatka peninsula	Northern taiga, dwarf birch, high-grass meadows, elfins	<i>Calamagrostis langsdorffii</i> , <i>Filipendula camtschatica</i> , <i>Leymus mollis</i> , <i>Urtica platyphylla</i>	<i>Salix</i> spp.
Upper Vilui River	Open woodlands, middle taiga, middle taiga, dwarf birch, floodplain meadows	<i>Alopecurus pratensis</i> , <i>Anemone sylvestris</i> , <i>Astragalus schumilovae</i> , <i>Cacalia hastata</i> , <i>Calamagrostis langsdorffii</i> , <i>Elymus reflexiaristatus</i> (= <i>Elytrigia jacutorum</i>), <i>Elymus repens</i> (= <i>Elytrigia repens</i>), <i>Festuca pratensis</i> , <i>Lilium dahuricum</i> , <i>Senecio erucifolius</i> , <i>Serratula coronata</i> , <i>Thymus reverdattoanus</i> , <i>Veratrum lobelianum</i>	<i>Betula fruticosa</i> , <i>B. exilis</i> , <i>B. divaricata</i> , <i>Juniperus sibirica</i> , <i>Potentilla</i> (= <i>Pentaphylloides</i>) <i>fruticosa</i>
Central Yakutia	Open woodlands, middle taiga, dwarf birch, alases	<i>Alopecurus arundinaceus</i> , <i>Arenaria saxatilis</i> , <i>Artemisia frigida</i> , <i>Bassia</i> (= <i>Kochia</i>) <i>prostrata</i> , <i>Bromus irkutica</i> , <i>Calamagrostis langsdorffii</i> , <i>Carex juncella</i> , <i>C. juncella</i> , <i>Cerastium arvense</i> , <i>Festuca jacutica</i> , <i>F. kolymensis</i> , <i>F. lenensis</i> , <i>Helictotrichon krylovii</i> , <i>Helictotrichon schellianum</i> , <i>Koeleria</i> spp., <i>Limnas stelleri</i> , <i>Poa angustifolia</i> , <i>P. attenuata</i> , <i>Puccinellia tenuiflora</i> , <i>Salsola ruthenica</i> , <i>Scolochloa festuacea</i> , <i>Silene repens</i> , <i>Stipa sibirica</i> , <i>S. krylovii</i> , <i>Thymus serpyllum</i>	<i>Alnus alnobetula fruticosa</i> (= <i>Duschekia fruticosa</i>), <i>Rhododendron dahuricum</i>
Sakhalin island	Middle taiga, dwarf birch, elfins, high-grass meadows, <i>Sasa kurilensis</i> thickets	<i>Angelica gmelinii</i> , <i>A. ursina</i> , <i>Calamagrostis langsdorffii</i> , <i>Carex appendiculata</i> , <i>C. schmidtii</i> , <i>C. minuta</i> , <i>Deschampsia sukatschewii</i> , <i>Filipendula kamtschatica</i> , <i>Lathyrus pilosus</i> , <i>Ligusticum scoticum</i> , <i>Petasites amplus</i> , <i>Polygonum sachalinense</i> , <i>Sanguisorba parviflora</i> , <i>Senecio palmatus</i>	<i>Alnus alnobetula fruticosa</i> (= <i>Duschekia fruticosa</i>), <i>Alnus maximowiczii</i> , <i>Betula exilis</i> , <i>B. divaricata</i> , <i>Juniperus sibirica</i> , <i>Ledum macrophyllum</i> , <i>Myrica tomentosa</i> , <i>Pinus pumila</i> , <i>Rhododendron aureum</i> , <i>R. parvifolium</i> , <i>Salix saxatilis</i> , <i>Sasa kurilensis</i> , <i>Spiraea salicifolia</i>
Amur-Zeya interfluvium	Southern taiga, dwarf birch shrubland, floodplain meadows	<i>Agrostis trinii</i> , <i>Calamagrostis langsdorffii</i> , <i>C. epigeios</i> , <i>C. neglecta</i> , <i>Carex duriuscula</i> , <i>C. lasiocarpa</i> , <i>C. limosa</i> , <i>C. korshinskyi</i> , <i>Clematis hexapetala</i> , <i>Filifolium sibiricum</i> , <i>Koeleria cristata</i> , <i>Poa angustifolia</i> , <i>P. attenuata</i> , <i>Potentilla chinensis</i>	<i>Alnus hirsuta</i> , <i>Betula fruticosa</i> , <i>B. divaricata</i> , <i>Crataegus pinnatifida</i> , <i>Rhododendron parvifolium</i> , <i>R. dauricum</i> , <i>Ribes rubrum</i> , <i>Rosa acicularis</i> , <i>Salix pierotii</i> , <i>S. miyabeana</i> , <i>S. udensis</i> , <i>S. nipponica</i> , <i>S. schwerinii</i> , <i>Spiraea salicifolia</i> , <i>S. sericea</i>
Amur-Ussuri interfluvium	Coniferous-deciduous forests, meadows, swamps	<i>Adenophora verticillata</i> , <i>Agrostis trinii</i> , <i>Arundinella anomala</i> , <i>Calamagrostis langsdorffii</i> , <i>Carex cespitosa</i> , <i>Clematis fusca</i> , <i>Filipendula palmata</i> , <i>Fimbripetalum radians</i> , <i>Geranium vlassovianum</i> , <i>Hierochloa glabra</i> , <i>Iris ensata</i> , <i>I. orientalis</i> , <i>Lathyrus komarovii</i> , <i>Lysimachia davurica</i> , <i>Patrinia scabiosifolia</i> , <i>Poa pratensis</i> , <i>Senecio campestris</i> , <i>Thalictrum contortum</i> , <i>Trifolium lupinaster</i> , <i>Valeriana alternifolia</i> , <i>Vicia amoena</i>	<i>Alnus alnobetula fruticosa</i> (= <i>Duschekia fruticosa</i>), <i>Alnus hirsuta</i> , <i>Betula ovalifolia</i> , <i>Corylus heterophylla</i> , <i>Spiraea salicifolia</i> , <i>Myrica tomentosa</i> , <i>Salix myrtilloides</i> , <i>S. brachypoda</i> , <i>S. bebbiana</i>
Zeya-Bureya interfluvium	Deciduous forests, steppes	<i>Arenaria juncea</i> , <i>Arundinella anomala</i> , <i>Bupleurum scorzonifolium</i> , <i>Calamagrostis langsdorffii</i> , <i>Clematis hexapetala</i> , <i>Festuca jacutica</i> , <i>Filifolium sibiricum</i> , <i>Helictotrichon schellianum</i> , <i>Koeleria cristata</i> , <i>Miscanthus sacchariflorus</i> , <i>Patrinia rupestris</i> , <i>Potentilla chinensis</i> , <i>Scabiosa comosa</i> , <i>Schizonepeta multifida</i> , <i>Scutellaria baicalensis</i> , <i>Spodiopogon sibiricus</i> , <i>Stipa baicalensis</i>	<i>Betula ovalifolia</i> , <i>Caragana manshurica</i> , <i>Corylus heterophylla</i> , <i>Crataegus pinnatifida</i> , <i>Lespedeza bicolor</i> , <i>L. juncea</i> , <i>Prunus</i> (= <i>Cerasus</i>) <i>glandulosa</i> , <i>Prunus</i> (= <i>Armeniaca</i>) <i>mandshurica</i> , <i>Ulmus pumila</i>

(Continued)

Table 2 Characteristic species of vascular plants in grasslands and shrublands of the forest and steppe biomes on the plains of Russia.—cont'd

Region	Biomes and ecosystems	Characteristic graminoid and forb species	Characteristic shrub and dwarf shrub species
Daurian steppes	Birch and larch woods, forest-steppes	<i>Agropyron cristatum</i> , <i>Artemisia frigida</i> , <i>A. laciniata</i> , <i>Carex duriuscula</i> , <i>C. pediformis</i> , <i>Cleistogenes squarrosa</i> , <i>Clematis hexapetala</i> , <i>Festuca lenensis</i> , <i>Filifolium sibiricum</i> , <i>Galium ruthenicum</i> , <i>Hemerocallis minor</i> , <i>Hetheropappus altaicus</i> , <i>Hierochloa odorata</i> , <i>Koeleria cristata</i> , <i>Leymus chinensis</i> , <i>Phlojodicarpus sibiricus</i> , <i>Ph. dauricum</i> , <i>Poa botryoides</i> , <i>P. attenuata</i> , <i>Pulsatilla turzaninovi</i> , <i>Scabiosa comosa</i> , <i>Scutellaria baicalensis</i> , <i>Serratula centauroides</i> , <i>Stellera chamaejasme</i> , <i>Stipa baicalensis</i> , <i>S. krylovii</i> , <i>S. sibirica</i> , <i>Thalictrum minus</i> , <i>Thalictrum petaloideum</i>	<i>Caragana microphylla</i> , <i>C. stenophylla</i> , <i>Rhododendron dauricum</i>

Table 3 Families of vascular plants with the greatest species diversity in the main types of grasslands of Russia.

Steppes	Meadows		
	Halophytic	Upland	Floodplain
<i>Asteraceae</i>	<i>Asteraceae</i>	<i>Asteraceae</i>	<i>Poaceae</i>
<i>Poaceae</i>	<i>Fabaceae</i>	<i>Brassicaceae</i>	<i>Asteraceae</i>
<i>Brassicaceae</i>	<i>Lamiaceae</i>	<i>Poaceae</i>	<i>Fabaceae</i>
<i>Fabaceae</i>	<i>Poaceae</i>	<i>Fabaceae</i>	<i>Cyperaceae</i>
<i>Lamiaceae</i>	<i>Chenopodiaceae</i>	<i>Laminaceae</i>	<i>Polygonaceae</i>
<i>Caryophyllaceae</i>		<i>Ranunculaceae</i>	<i>Brassicaceae</i>

lagurus), Brandt's and Mandarin Voles (*Lasiopodomys brandti*, *L. mandarinus*), and Pikas (*Ochotona pusilla*, *O. pallasi*, *O. daurica* and few more species in montane steppes). Another and even more specific guild of grasslands burrowing mammals are totally underground rodents what in Russia includes several species of Blind Mole Rats (*Spalax microphthalmus*, *S. giganteus*), Zokors (*Myospalax altaicus*, *M. aspalax*, *M. psilurus*), and the most widespread in steppes the Northern Mole Vole (*Ellobius talpinus*). Burrowing, grazing, and food storing of these mammals are crucially important for forming grasslands soil and vegetation structure, removing primary production, and constructing micro-habitats for many invertebrates and even vertebrates. These mammals also are specifically important for functioning food webs in grassland and shrubland ecosystems.

Formerly the diversity of Russia's grassland mammals used to be much richer. For a long time after glaciations, the steppes and meadows of the temperate zone preserved remnants of the Late Pleistocene mammoth fauna: Mammoth, Bison, Musk Oxen, Saiga, Reindeer, Asiatic Lion, Cheetah, and others. The last typical inhabitants of the grasslands of the steppe and forest biomes of Eurasia—Aurochs *Bos primigenius*, Tarpan *Equus ferus ferus* and Przewalski's Horse (*E. f. przewalskii*) and Onager *Equus hemionus*—became extinct as late as the 17–19th century. A program on the restoration of the semi-wild population of Przewalski's Horse is being implemented since 2015 in the Orenburg Nature Reserve. The horses were brought from France and Hungary. In July 2018, the first foal was born in the Reintroduction Center and now, in 2019, 40 horses lived in the reserve on the grassland area of 165 km². The next group of the horses will be brought from the Minnesota Zoo.

Other mammal orders also have some specific representatives in Russian grasslands and shrublands, such as the Steppe Fox *Vulpes corsac*, Steppe Polecat *Mustela eversmanii*, Marbled Polecat *Vormela peregusna*, Steppe Cat *Felis lybica ornata*, and the Pallas's Cat *Otocolobus manul* among carnivores, and Long-Eared Hedgehog *Hemiechinus auritus* among Eulipotyphla, and *Lepus tolai* among Lagomorpha. Nevertheless most of these species in Russia are not numerous and/or have limited distribution near the boundaries of their ranges. Numerically dominating and widespread mammals in the Russian grasslands and shrublands are the common Palaearctic and Holarctic species like *Vulpes vulpes*, *Canis lupus*, *Mustela nivalis*, *M. ermynea* among carnivores, *Erinaceus romanicus*, *Sorex* spp., and *Crocidura suaveolens* among insectivores (Eulipotyphla), *Lepus europeus*, *L. timidus* among lagomorphs, etc.

Russian grasslands and shrublands serve as specific open habitats for many birds. Probably the most characteristic insectivorous and granivorous songbirds in the Russian steppe and meadow habitats are several species of Larks (*Alauda arvensis*, *Alauda leucoptera* [formerly *Melanocorypha leucoptera*], *Melanocorypha yeltoniensis*, *M. calandra*, *M. mongolica*, *Eremophila alpestris*, and some others), Wheatears (*Oenanthe oenanthe*, *O. pleschanka*, *O. isabellina*), Buntings (*Emberiza hortulana*, *E. calandra*, *E. citronella*, *E. cia*, *E. cioides* and some others) and several others. Typical for steppe grasslands are large ground-nesting birds, like Demoiselle Crane (*Grus virgo*), Little Bustard (*Tetrax tetrax*), and Great Bustard (*Otis tarda*; this species faces risk of extinction in Russia). A very characteristic and ecologically important bird guild in open habitats is raiding raptors hunting ground-dwelling small mammals, reptiles, birds, and

large arthropods. The guild includes Steppe Eagle (*Aquila nipalensis*), Imperial Eagle (*A. heliaca*), Buzzards (*Buteo rufinus*, *B. hemilasius*), Harriers (*Circus cyaneus*, *C. pygargus*, *C. macrourus*, and *C. spilonotus*), large and small Falcons (*Falco cherrug*, *F. tinnunculus*, *F. naumanni*) and some others. Most of the raptors are nesting on the ground but a few of them need trees or bushes for building nest. Another characteristic ecological group is birds of steppe wetlands which include many species of Waders, Pelecan, Herons, Grebes, and few very specific ducks (*Tadorna ferruginea*, *T. tadorna*, *Oxyura leucocephala*). Shelducks (*Tadorna* spp.) nest in the mammal burrows far away from water bodies.

Reptiles are not divers and numerous in Russian grasslands and shrublands in general but occur in several local regions (such as Caucasus foothills, Lower Volga, and Far East meadows). Characteristic for the entire Russia's grasslands are only few species of snakes and lizards: *Lacerta agilis*, *Eremias velox*, *E. arguta*, *Coronella austriaca* (west of Urals only), *Elaphe dione*, *Vipera renardii*, *Gloydius halys*. Meanwhile, grasslands and shrublands of some southern regions of Russia comprise up to 15–20 species of reptiles, including many Turanian and Mediterranean taxa (including representatives of *Gekkonidae*, *Agamidae*, *Scincidae*, *Boidae*, *Testudinidae*, and some other families which are absent from most of the Russian territory).

In general, the highest biogeographic units (as Mediterranean, Caucasian, Siberian, Far Eastern, Beringian, and others) differ in the distribution and composition of temperate grassland and shrubland communities. While the Ural Range is of no significance in this respect, the wide valley of the Yenisei River is an important boundary both for many of the inhabitants of open spaces and for their communities. In fact, the western meadow class *Molinio-Arrhenatheretea* is replaced here by the eastern class *Calamagrostietea langsfordii* (see [Appendix 1](#)). Also, the boundary between western steppes of the *Festuco-Brometea* vs. the eastern steppes of the *Cleistogenetea squarrosae* (see [Appendix 1](#)) runs here. The steppe fauna demonstrates effects of species vicariance from west to east. A good example is the sequence of the *Sciuridae* rodents: *Marmota bobak*—*M. baibacina*—*M. sibirica* and *Spermophilus suslicus*—*S. pygmaeus*—*S. erythrogenys*—*S. dauricus* replacing one another from the western edge of the Russian steppe belt to the eastern one.

Natural and Anthropogenic Communities (Including the Origin of Meadows)

The areas of *secondary grasslands* ([Fig. 1](#)) and *shrublands* ([Fig. 3](#)) of the forest zone are included in the summation of forest cover area. The forest cover of Russia's territory totals 45.4% (7,962,000 km²). Deforestation due to clearcuts and wild fires, which significantly increased in the 20th and 21st centuries, is a great challenge for Russia. Over the last decades, also a neutralizing process has been observed, namely abandonment of farming lands with further spontaneous afforestation. As a result, the forest area in Russia over the past decades only slightly decreased, by 5000–6000 km² nationwide.

Natural grasslands in Russia include zonal and extra-zonal steppes ([Fig. 2](#)), floodplain meadows along rivers and around lakes ([Fig. 1](#)), specific grasslands (meadows) of alase habitats (in thermokarst depressions of Yakutia), halophytic communities of continental and coastal salt marshes and other saline habitats. The genesis of natural grasslands of Russia is determined by the presence of specific conditions of climate, ecotopes, and soils, able to prevent the formation of tree canopy for a long time. For zonal *steppes*, for example, of importance is the value of the aridity coefficient, the ratio of precipitation (mm) to evapotranspiration or potential evaporation (the amount of moisture evaporated in a given climate from water surface), which is 0.6–0.9 in meadow steppe and >0.6 in typical and dry steppes (up to 0.1–0.3 is characteristic for deserts). Steppe grasslands on loess loams and clays form chernozems, dark soils containing a high percentage of humus, wash-resistant even under strong precipitations. Chernozem is one of the most fertile soils in the world. The northeast of Siberia is represented by cryo-arid relict (Pleistocene) steppes ("mammoth steppes"), and the slopes of thermokarst depressions (alases), by meadow steppe communities with *Calamagrostis neglecta*, *Hordeum brevisubulatum*, *Stipa krylovii*, *Festuca lenensis*, *Carex pediformis* and so on.

Floodplain meadows ([Fig. 1](#)) are natural intrazonal ecosystems that form on the flooded (for 15–45 days) part of river or lake floodplains on alluvial soils, annually enriched with silt. They are interspersed among any zonal biome in temperate climate. Among usual species, there are grasses, such as *Glyceria fluitans*, *Festuca pratensis*, *Elymus repens* (= *Elytrigia repens*), *Poa pratensis*, *Bromus inermis*, *Calamagrostis epigeios*, and others, as well as several species of *Carex*. Abundances of the specific dominating species depend on the dates and duration of the floodwater overflow.

The runoff of most large and middle-sized rivers of Russia's temperate belt, especially in the European part, is regulated by levees and dams of hydroelectric power plants. As a result, significant areas of floodplain communities, including meadows, have disappeared or changed, becoming dependent on the anthropogenic regime of dams' operation. A bright example is the Volga basin, where, as a result of runoff regulation, reservoir construction, deforestation, and continuous plowing of watersheds, about 30% of watercourses and large areas of floodplain meadows have disappeared over the last millennium. The river itself has turned into a cascade of nine large shallow reservoirs. One of them, the Rybinsk Reservoir (about 4580 km²) flooded floodplain meadows and willow thickets along the Volga itself on a distance of 110 km; along the Mologa River, 226 km; and along the Sheksna River, 328 km. Before 1940, this was one of the Europe's largest ranges of floodplain hay meadows, which supplied hay to a significant part of Russia's cavalry.

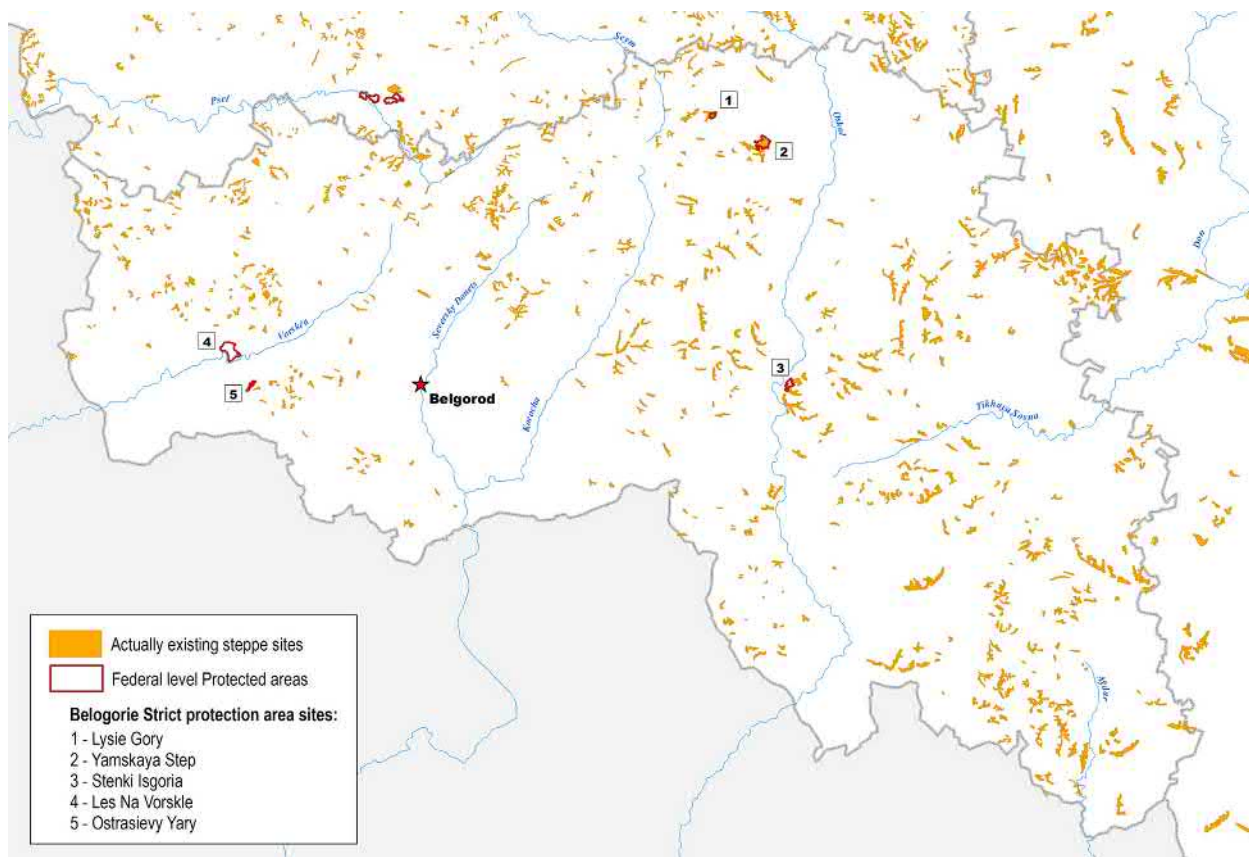
In the plains of Russia's temperate zone there are also some natural shrubland communities: in the forest biome, these are *erniks* in Siberia and the Far East with *Betula nana* (incl. subsp. *rotundifolia*), *B. fruticosa*, *B. exilis*, and *B. divaricata* (incl. subsp. *middendorffii*) and, less frequently, with *Salix* spp., *Rosa* spp., *Potentilla* (= *Pentaphylloides*) *fruticosa*, and *Alnus alnobetula* subsp. *fruticosa* (= *Duschekia fruticosa*); in floodplains, willow (*Salix* spp.) thickets; and in the steppe biome, thickets of *Genista tinctoria*, *Chamaecytisus ruthenicus*, *Caragana frutex* and other *Caragana* spp., *Prunus stepposa*, *Prunus tenella* (= *Amygdalus nana*), *Prunus* (= *Cerasus*) *fruticosa*, *Rhamnus cathartica*, *Crataegus* spp., *Rosa* spp., *Tamarix meyeri*, *T. ramosissima* and other shrubs.

The grasslands of the forest biome's plain watersheds (meadows and weed brushes) are exclusively of anthropogenic origin. They represent early stages of the progressive succession, which form after (1) logging, (2) drainage of bogs, (3) forest fires, (4) abandonment of farmlands, and so on. The main condition of their long-standing existence without trends toward afforestation and changes in the structure, flora composition, and productivity is intentional or spontaneous human control over their dynamics. The succession may be blocked, which excludes the start of the forest stage, due to annual or periodic mowing, continuous grazing by livestock, and periodic burns (in spring or fall) with a frequency excluding the formation of a forest cover. Upland post-forest meadows in many regions of the East European Plain are results of millennia-long evolution of the temperate agricultural landscape. They are relatively stable subclimax communities with a "conservative" flora composition, a soil seed pool corresponding to the actual flora composition, and other mechanisms to exclude alien species invasion.

Similar properties are typical for secondary (anthropogenic) steppes, which formed on set-asides after long-standing plowing, on degraded steppe pastures, and on eroded lands. With the area of the steppe zone of about 1,370,000 km² (8.0% of the Russia's territory), preserved parts of the steppes and natural steppe and shrubland communities proper are represented in European Russia (Belgorod, Voronezh, Kursk, Saratov, and other provinces) on 3%–15% of the region's area and in Siberia (Buryatia, Altai, Tyva, Novosibirsk oblast, Transbaikalia, etc.), on 30%–50% (Map 2). The exceptions are Kalmykia where desert steppes occupy about 50,000 km², Orenburg oblast with 20,000 km² (including two large blocks of over 1000 km²), Tyva with 27,000 km², and Transbaikalia with almost 20,000 km². The most disastrous situation with plowing and degradation of steppe vegetation occurs in the provinces of Voronezh, Kursk, and Belgorod, where fragments of secondary steppes are preserved on 1.0%, 1.3%, and 1.7% of the region's area, respectively (Map 3). Overall, following the results of the implementation of the UNDP/GEF (United Nations Development Programme/Global Environmental Finance) project of 2010–2016 "Improving the Coverage and Management Efficiency of Protected Areas in the Steppe Biome of Russia," 10,178 tracts of steppes were identified in the 29 provinces of Russia (Table 4). Their area totaling 179,700 km² and the average area of an individual steppe tract is 17.65 km² (Rogova and Skvortsov, 2016).

The Classification of Grasslands and Shrublands of Russia

The problems of the typology of grasslands and shrublands on the plains of Russia's forest and steppe biomes are associated, on the one hand, with the anthropogenic origin of many of them and, on the other, with their combination with upland and floodplain



Map 3 The actually existing steppe sites in Belgorod oblast, identified by the 2011–2016 inventory (<http://savesteppe.org/ru/maps>).

Table 4 Areas of the actually existing plain steppes in some provinces of Russia.

Province (oblast, krai, republic)	Area of the province (km ²)	Number of identified steppe sites	Area of steppe (km ²)	Share of the area of the region (%)
Astrakhan	58,265	163	14,765	25.3
Belgorod	27,151	702	471	1.7
Chelyabinsk	88,637	245	4510	5.1
Kalmykia	72,105	196	48,377	67.1
Kursk	30,002	1088	388	1.3
Lipetsk	24,066	1079	449	1.9
Novosibirsk	177,850	84	2246	1.3
Omsk	141,256	23	936	0.7
Orel	24,648	290	427	1.7
Orenburg	124,305	2437	22,869	18.4
Penza	43,394	254	321	0.7
Rostov	102,838	1202	8092	7.9
Samara	53,881	895	1649	3.1
Saratov	101,182	2502	5993	5.9
Stavropol	66,178	443	5889	8.9
Tambov	34,456	1296	1305	3.8
Tatarstan	68,013	383	348	0.5
Transbaikal	432,070	278	17,159	4
Ul'yansk	37,227	254	459	1.2
Volgograd	112,871	2612	16,814	14.9
Voronezh	52,248	257	522	1

Based on inventory by remote sensing data with further field verification 2011–2016.

woodlands, wetlands, halophytic vegetation, and so on. Shrub layer also affects the composition and classification status of steppe herbaceous communities. In other cases, the shrubs form shrublands which would be classified as a specific type, not a variant of grassland. The classification on dominants might introduce corrections and could allow a more deterministic classification of these plain communities within the forest and steppe biomes. However, the dynamic character of their composition (owing to successional variation and the temporary existence of grasslands and shrublands themselves) does not allow a correct use of approaches and methods other than floristic classification. The background and bibliography of the Braun-Blanquet approach, used to classify vegetation, including grasslands and shrublands, in Russia and neighboring countries, were presented in [Solomestch et al. \(1994\)](#) and [Mirkin and Ermakov \(2010\)](#).

To reflect higher units of the classification of grasslands and shrublands of Russia's plains, we used the prodromus prepared by [Ermakov \(2012\)](#). For temperate grasslands, it includes 18 classes, 35 orders, and 92 alliances; for steppe shrubland communities, four classes, five orders and eight alliances ([Appendix 1](#)).

Of special interest is the typology of plain variants of dwarf birch, willow, and *Duschekia fruticosa* communities in Siberia and the Far East. Most of them within the forest zone form primary and secondary thickets (*ermiks*). A similar situation is observed with *Pinus pumila* communities, which form at the foothills and on the plains of Siberia and the Far East, including on Kamchatka's coastal plains, which are included in the class of boreal forests Vaccinio-Piceetea. No doubt, in terms of spread and the organization of the communities themselves, they are thickets of large shrubs, which, in the boreal conditions of the northern taiga and continental *Larix* spp. woodlands, extend to the plains. This allowed Ermakov and colleagues ([Ermakov et al., 2002](#)) to attribute the alliance *Vaccinio-Pinion pumilae* to the class *Loiseleurio-Vaccinietea* of shrub heathlands, which can also form on plains in temperate climate.

Ecology and Biodiversity

Ecologically, temperate grasslands and shrublands of Russia's plains are mesophytic, xeromesophytic, and mesoxerophytic communities. Absence of tree cover affects all aspects of their ecology. First, these are communities of heliophilous plants and animals, which prefer open spaces and can find refuge within the herbaceous or shrub horizon (within a range of 0.5–2.5 m). Second, the leading role in their functioning and dynamics is played by small burrowing mammals and, overall, soil fauna. They ensure active soil-building processes, a deeper rainfall penetration, the development of the biogenic microrelief, and the spatial mosaic of the communities. Third, these are ecosystems with domination of grazing-based food web (not detritus-based ones), i.e., functionally oriented at the active consumption of phytomass in the annual cycle and the exclusion of excessive litter accumulation.

By climatic parameters (attitude to heat), these ecosystems have a unique, exceptionally wide range: by average annual temperature, from −15.0 to +12.0 °C; by average July temperature, from +7.0 to +25.0 °C; by average January temperature, from +0.0 to −42.0 °C; and by annual precipitation, from 250 (in the Caspian steppes) to 1100 mm in Kamchatka's valleys. The reaction norm of these ecosystems is one of the widest and occupies wide "portions" of physical gradients of life, "within" climatic ranges of zonal biomes, which testifies to their anthropogenic genesis and existence as a forestless subclimax: pyrogenic, pascual, agrogenic, and

floodplain. A part of the range of the ecosystems under consideration is developed in continental climate conditions. For example, in Yakutia with its extensive representation of meadows, alases, cold steppes, and shrublands, the difference between the maximal (+38.4 °C) and minimal (−64.4 °C) temperatures is more than 100 °C.

An important ecological factor for the grasslands and shrublands of Russia's temperate belt is their formation on permafrost, where the active layer can vary from 20–30 cm to 1.5–2.0 m. However, typical of floodplain meadows and shrublands are floodplain and lake taliks and of marshes, submarine taliks. Within the forest zone in Siberia, widespread are anthropogenic taliks with secondary meadow vegetation on frozen grounds.

The soil pH, content of Cl, Na, and Ca ions in soils vary widely under Russia's grasslands and shrublands. Meadows, marshes, and steppes represent the entire spectrum of halophilous and calciphilous ecosystems, including such extremely calciphilous ones as steppes on chalk deposits and limestone outcrops. Examples of widespread of halophilous grasslands and shrublands can be found in the Caspian Depression and in Southern Urals where halophilous communities are represented by following syntaxonomical classes (*Festuco-Puccinellietea*; *Scorzonero-Juncetea gerardii*; *Nerio-Tamaricetea*) (see [Appendix 1](#)).

The ecological features of grasslands and shrublands also include their biological and economic productivity ([Titlyanova et al., 2018](#)). The productional potential of their seasonal use as natural forage lands (hay fields and pastures) is sufficiently high. Biological productivity in zonal (steppes) and intrazonal (floodplain meadows) grasslands vary widely ([Table 5](#); [Tishkov, 2005a](#); [Titlyanova et al., 2018](#); [Bazilevich et al., 1986](#); [Tsarevskaya, 1989](#)). [Table 5](#) does not present numerous assessments for meadows and shrublands of the Far East, the Kamchatka Peninsula, Sakhalin, and the Kuril Islands with *Filipendula camchatica*, *Angelica ursina*, *Reynoutria sachalinensis*, *Petasites amplus*, *Sasa kurilensis*, where extremely high figures of both total phytomass (up to 57–90 t ha^{−1}) and net primary production (35–57 t ha^{−1} year^{−1}) are recorded.

The annual primary production in upland post-forest meadows is close to those of the zonal forests on the same territory. However, the proportion of above-ground and below-ground phytomass depends on the position in the relief and the slope exposure, i.e., on water supply, arriving heat, and the conditions of the transit and accumulation of nutrients ([Table 6](#)). Studies on the productivity of meadows in the Valdai National Park (southern taiga of European Russia) have shown that the both total phytomass and net primary production increase top-down along the slope ([Table 6](#)).

Plain grasslands are the economically most important biome of Russia. They serve as a natural base for both arable farming and animal husbandry. For example, the steppe zone yields over 85% of the total Russian grain harvest, feed over 70% of cattle, and produce over 90% of sheep and goat wool. Their ecosystem services, including long-term and reliable carbon depositing, are critically important for human life and the economy. The preserved natural grasslands provide for the survival of globally endangered and vulnerable species of mammals and birds and, at the national level, for more than 100 rare species of plants and animals ([Smelansky and Tishkov, 2012](#)).

Ecosystem services of grasslands can be assessed in both physical and monetary values ([Table 7](#)). Carbon storage is a significant part of their total value. For example, the total carbon storage in steppe soils of Russia's plains is estimated at more than 100 million tons in the uppermost 1 m of depth (under the total area of the zone: 2232 km²). This is about 25% of the total carbon storage deposited in Russia's soils and it is held in the soils occupying only about 13.5% of the country's area ([Smelansky and Tishkov, 2012](#); [Romanovskaya et al., 2019](#)). Generalized assessments of ecosystem services of grasslands and shrublands are presented in the national report on ecosystem services of Russia ([Bobylyev et al., 2018](#)).

The total area of actually existing steppe ecosystems in Russia is estimated at about 500,000 km² ([Smelansky and Tishkov, 2012](#)). Assuming the above-mentioned evaluation of the total amount of carbon, its total stock for Russia's steppe biome can be estimated at 35 billion tons. The total long-term average annual potential of carbon deposition in steppe ecosystems is estimated at 75 million tons per year.

In the soil of protected meadow steppe on the East European Plain (Kursk Province) the amount of bound organic carbon is estimated at 462 t ha^{−1} (at a soil depth of 2 m) ([Table 7](#)). On the neighboring annually mowed steppe plot the carbon storage is a bit smaller, 451 t ha^{−1} ([Mikhailova and Post, 2006](#)). For the soils of meadow steppes, the share of carbonates is estimated at about 30%. Therefore, the total carbon storage in the chernozem underlying unused meadow steppe is about 700 t ha^{−1}, only 3.5% of which has a turnover period of about 300 years, while for the rest of the pool this period is estimated at thousands

Table 5 The average phytomass and production of the grasslands and shrublands in Russia.

Zonal and azonal ecosystem	Phytomass (t ha ^{−1})	Litter (t ha ^{−1})	Net primary production (t ha ^{−1} year ^{−1})
Floodplain meadows	6.0–55.0	1.0–5.0	5.0–45.0
Meadow steppes	15.0–30.0	10.0–20.0	18.0–25.0
Steppes	10.0–30.0	10.0–15.0	15.0–20.0
Dry steppes	8.0–15.0	8.0–12.0	6.0–15.0
Desert steppes	5.0–10.0	10.0–12.0	4.0–8.0
Shrublands of the forest and steppe zones	25.0–60.0	3.0–6.0	10.0–15.0

From Bazilevich NI, Grebenshchikov OS, and Tishkov AA (1986) *Geographicheskie zakonomernosti struktury i funktsionirovaniya ekosistem* [Geographical regularities of ecosystems' structure and functioning]. Moscow: Nauka. 297 p. (In Russian); Tishkov AA (2005) *Biosfernye funktsii prirodnikh ekosistem Rossii*. [Biosphere functions of natural ecosystems in Russia]. Moscow: Nauka. 309 p. (In Russian); www.biodat.ru/db/prod/index.htm.

Table 6 Phytomass and production of the upland hay meadows in the Valdai National Park.

Position on the slope	Dominant species	Phytomass ($t\ ha^{-1}$)			Production ($t\ ha^{-1}\ year^{-1}$)		
		Above-ground	Below-ground	Total	Above-ground	Below-ground	Total
Upper part of the south-west slope ^a	<i>Poa angustifolia</i> , <i>Anthoxanthum odoratum</i> , <i>Briza media</i> , <i>Centaurea jacea</i>	3.3	5.1	8.4	4.8	5.0	9.8
Middle of the south-west slope	<i>Briza media</i> , <i>Phleum pratense</i> , <i>Alchemilla</i> spp.	3.6	5.7	9.3	5.4	5.5	10.9
Lower part of the south-west slope	<i>Deschampsia caespitosa</i> , <i>Carex vesicaria</i> , <i>Crepis sibirica</i> , <i>Geranium</i> spp.	5.1	8.2	13.3	7.5	8.0	15.5
Lower part of the south slope	<i>Alopecurus pratensis</i> , <i>Agrostis tenuis</i> , <i>Festuca pratensis</i> , <i>Dactylis glomerata</i> , <i>Phleum pratense</i> , <i>Trifolium pratense</i>	3.8	10.2	14.0	5.9	8.6	14.5

^aAccording repeated mowing for above-ground phytomass and calculated for underground phytomass.

From Tsarevskaya NG (1989). Produktivnost i struktura fitomassy lugov lesnoi zony. [Productivity and phytomass structure of forest zone meadows]. *Proceedings of the USSR Academy of Sciences, series geographical* 6, 60–69. (In Russian) With permission.

Table 7 Volumes and estimated monetary values of some groups of ecosystem services in the meadow steppe of Central Chernozem Zapovednik (Nature Reserve), Kursk Province.

Some groups of ecosystem services	Central Black Earth Nature Reserve	
	Absolute values for calculation	Estimated monetary value ($USD\ ha^{-1}\ year^{-1}$)
Climate-regulating services (including carbon depositing)	Humus content in the upper 10 cm of the soil is 9%–12%, while the stock in the 2 m depth layer is 540 t/ha. Carbon sink can be 1.5–2.5 t/ha per year	75–125
Water-regulating services (runoff provision and decreasing water losses; calculation through compensation)	Compensation (substitution) is calculated through possible costs of the runoff-regulating “activity” of oak forests and steppes	30–50
Assimilative services (neutralization of pollutants and excessive biogens; calculation through compensation)	Assimilative properties of chernozems	10–15
Soil protection services (erosion risk decrease, through costs of eroded land restoration)	Amount to 2.0–4.0% of restoration costs at a steppe secondary succession rate of 40–60 years	20–40
Production and biological resource services (costing hay yield; value of wild berries, mushrooms, medical and aromatic plants, and wildlife, including the function of its reproduction for neighboring areas)	Hay yield is up to 0.4–0.6 t/ha (at about \$50 per ton); primary production in steppe pasture is up to 1.5–2.0 t/ha of herbage per grazing season (at a carrying capacity of 0.3–0.5 head per hectare); and honey yield, 20–80 kg/ha per season	40–120
Information services	Unique biodiversity, monitoring of biota, a museum, a visiting center, a weather station. Assessed through the costs of inventory, natural object mapping, scientific studies, and arrangements for ecological monitoring	25–50
Recreational services (use for tourism and ecological education)	The reserve is annually visited by about 4000 persons (primarily excursions by ecological routes and visits to the museum)	5–10
Total		200–410

Data from Estimates and calculations of A. Tishkov specifically for this review.

of years. Hence, in terms of carbon “binding” effectiveness and global climate regulation, the role of Russia’s grasslands is comparable with that of boreal forests (taiga).

According to Costanza et al. (1998), the specific value of grasslands is about $232\ USD\ ha^{-1}\ year^{-1}$ and their global estimated monetary value reaches 906 billion USD per year (higher than that of boreal and temperate forests). What is the share of Russia’s grasslands in the figure? We estimate it at about 12% of the volume of potential ecosystem services of the global grassland biomes. In addition to the unique role of chernozems as carbon stock and its influence on the greenhouse gas concentration in the atmosphere, the following aspects can be specifically important (Tishkov, 2005a,b): (1) river runoff regulation (for example, the restoration of steppe vegetation in the region increases the river runoff by up to 10.0%), (2) grassland radiation balance is 20–30% higher than that of barren soil, and (3) the substitution of primary steppe vegetation by its anthropogenic modifications changes albedo by 3–9%.

Threats

Threats to floodplain meadows and shrublands of Russia are largely associated with plain river runoff regulation and dam construction. Many floodplain areas have been flooded with shallow waters of the reservoirs (constituting 20–70% of the aquatic area), while meadows and shrublands downstream of the dams dry and transform because of the lack of normal floods. The threat of fires is lower here, although it is annual burns that have become a real threat, for example, for the grasslands of the Amur River basin.

The threat of invasive alien plant species has become characteristic of the last decades. The Black Book of European Russia (Vinogradova et al., 2010) among the 100 most aggressive invasive species identifies many ones usual for floodplains, such as *Echinocystis lobata*, *Heracleum sosnowskyi*, *Acer negundo*, *Bidens frondosa*, *Impatiens parviflora*, *Hippophaë rhamnoides*, *Phragmites altissimus*, *Zizania latifolia*, and others.

The current threats to upland meadows of the forest zone are associated with the following processes: (1) decrease of traditional farming and drop in the livestock number what lead to dramatic decrease of mowing and grazing areas; (2) amelioration, which can include changes in the drainage, leveling, boulder clearance, weed control, fertilization, forage herb seeding, and so on; (3) local over-grazing in and around large farms and villages; (4) increase of burns which kill a part of the land biota and form weed brushes in places of complex invasion-resistant meadows; and (5) alien species invasions.

Main threats to natural steppes follow from the agricultural value of steppe soils. Historically turning grasslands into arable was the worst threat for steppes in Russia (Chibilev, 1998; Moon, 2013; Smelansky and Tishkov, 2012). The total steppe area turned into arable land is assessed at almost 1,000,000 km² nationwide (for 1990, the peak value). Meadow steppes and typical steppes in European Russia (west of Volga R.) have disappeared on almost 95% of their area. The collapse of the USSR has resulted in massive cropland abandonment followed by spontaneous restoration of grasslands and then partial re-plowing 15–20 years later (Prishchepov et al., 2012; Schierhorn et al., 2013; Alcantara et al., 2013; Reinecke et al., 2018).

Actual threats were analyzed under framework of the UNDP/GEF project “Improving the Coverage and Management Efficiency of Protected Areas in the Steppe Biome of Russia” (2010–2016). The primary threat is still a direct destruction of natural and semi-natural steppes by plowing for permanent crops (not only for food production but also for forage and biofuel). Conversion into cropland is specifically dangerous for secondary steppes nationwide and for meadow steppes and typical steppes of European Russia where natural steppe sites are in peril.

Destruction of steppe grasslands by mining, oil and gas industries is now the next most important threat. The oil and gas industry is an important driver of fragmentation, degradation, and pollution of steppes in Volga-Urals region while mining is specifically important in South Urals, Altai, Khakassia, and Transbaikalia.

Overgrazing and undergrazing both threaten Russian steppes. The livestock number in Russia decreased dramatically after 1990. During the decade 1990–2000 the cattle number had dropped to half of the 1990 figure, and sheep and goats' number did to a third of the 1990 level. Currently overgrazing is an important threat for dry and deserted steppes of the Caspian and Caucasus regions (specifically Dagestan, Kalmykia, and Stavropol) and steppes of Altai and Tuva (Fig. 4) where livestock numbers are high and continue to rise (Smelansky and Tishkov, 2012; Reinecke et al., 2018). At the same time, undergrazing is especially important in the meadow steppes and typical steppes of European Russia and several provinces of Southern Siberia, driving deterioration of grasslands, spontaneous afforestation, and disappearance of many specific grassland species (Reinecke et al., 2018).

Undergrazing also is important as a driver causing a rise of steppe fires. Wild fires that became numerous and frequent after 2000 are an important threat for steppe grasslands and shrublands causing deterioration of habitats and direct destruction of some steppe species (Smelansky, 2015). Currently wild steppe fires have a huge spatial extent in Russia but their ecosystem effects are contradictory (Fig. 4). Steppe fires are specifically extensive and frequent in Pre-Caucasian, Volga-Urals, West Siberia, Khakassia, and Transbaikalia regions.

Fragmentation with infrastructure (roads, pipelines) is a threat to small steppe sites, specifically in European Russia. Afforestation projects are potentially dangerous but have little extent and are generally rare in Russia. Encroaching of weeds and invasive plant species is a threat attracting special attention in recent years.

Conservation, Restoration, and Sustainable Management

A big problem for Russia's steppes is an absence of any clear governmental policy regarding their use and conservation. The Russian legislation does not distinguish steppes as a specific object of regulation and conservation management. Meanwhile, several types of steppes are currently considered among the most imperiled ecosystems in Russia (Smelansky and Tishkov, 2012). The main conservation instrument for protecting steppes in Russia is federal and provincial systems of protected areas (PAs). As assessed by the end of 20th century, only 0.11% of the area of steppe biome in Russia was formally covered with federal protected areas (PAs). Such assessment for provincial PAs at that time could not be made due to lack of available information (Smelansky and Tishkov, 2012). During the last two decades the area of steppe ecosystems under protection and number of PAs protecting steppes increased tenfold and even more at both federal and provincial levels. Also information on provincial PAs became available for assessment. In 2018 the area of steppe ecosystems under protection in Russia reached 2.4–2.5 million hectares and makes a solid figure of 4.3–7.7% of the national area of the steppe biome (depending which assessment of the biome area we use). This protected steppe area is divided almost equally into federal and provincial PA systems. Steppe grasslands and shrublands are conserved in about 600 sites within about 550 PAs (including 84 sites of 51 PAs belonging to federal level). Meanwhile, the steppe biome is still among



Fig. 4 Turning grassland into arable: (A) just re-plowed secondary steppe, Altai Territory. Photo by I. Smelansky; (B) just re-plowed secondary steppe, Samara Province. Photo by I. Smelansky. Grazing in natural pastures of Russia: (C) grazing in dry steppe, Altai Republic. Photo by I. Smelansky; (D) winter grazing in overgrazed dry steppe, Khakass Republic. Photo by I. Smelansky. Wildfires in grasslands of Russia: (E) spring fire in the typical steppe, Orenburg Province. Photo by I. Smelansky; (F) just burnt typical steppe with *Caragana microphylla* shrubs, summer fire, Transbaikalia Territory. Photo by I. Smelansky; (G) post-forest meadow, Primorsky Territory. Photo by K. Kobayakov; (H) "pyrogenic savanna," Territory Primorsky kray. Photo by K. Kobayakov.

the least protected in Russia and needs more protection (Smelansky and Titova, 2018). In total, temperate grasslands comprise not more than 2% of the total area of the federal PA system. Also, often the PAs provide steppes with only formal protection as their regimes are not optimal for long-term conservation of grasslands.

Conservation of floodplain meadows and shrublands is also important since they are both forage lands and valuable ecotopes of floodplain fauna, including wetlands, because plain river runoff regulation has changed the flooding schedule of floodplains. Many floodplains found themselves under reservoirs' water, and their extents lying downstream of dams stopped functioning as floodplain ecosystems and partially lost their typical biota. Floodplain grasslands and shrublands are conserved only in the Khopersky, Volga-Kama, and Oksky nature reserves; in the Nyzhne-Kamsky and Ugra national parks; and in the Volg-Akhtubinsky "floodplain" Nature Park.

In the context of the large-scale cutback in agricultural production in Russia's forest zone, the recently formed pool of set-asides and abandoned hay meadows and pastures (according to different estimates, up to 300,000 km²) is gradually becoming covered with small-leaved forests (*Betula* spp., *Alnus incana*, *Populus tremula*, *Salix* spp.) and, on sandy soils, with pine forests (*Pinus sylvestris*). The conservation of, for example, the ancient Russian forest-field-meadow landscape in European Russia, in which the share of upland meadows reached 20–30% of its area, requires supporting by traditional agricultural production oriented at dairy husbandry, implying hay making and seasonal grazing. This problem is especially acute for the networks of protected areas of the forest and meadow-steppe zones, where the introduction of the conservation regime often has resulted in the afforestation of meadows and steppes.

In recent years, Russia has encountered a relatively new problem, the conservation of forest zone grasslands. For the numerous waterfowl birds of the Arctic (geese, cranes, sandpipers), grasslands in the agricultural landscape are the key territories of concentration and rest during migrations. The GPS-GSM-supported Russian-German studies on the migration of geese within the international ICARUS program (Wikelski and Terbitski, 2016) show that changes in the structure of agricultural lands, the decrease in the livestock, the reduction of the tillage area, and the foresting of meadows and set-asides have shifted the birds' migration routes from the center of the East European Plain toward the Baltic Sea coast.

For saving the most destroyed ecosystems, meadow steppes and dry meadows of European Russia, conservative methods probably are not sufficient, they need restoration. The restoration measures include active and passive methods. Active methods using seeds from natural vegetation locations were developed for various regions of the Old World (Dudar, 2000; Dzybov, 2010; Tishkov, 2000). The main limiting factor here is an absence of special seed nurseries, "wildflower farms." To create stable seeded meadow or meadow steppe with a balanced species composition and high productivity, the Fodder Institute developed new technologies (Trofimova and Kulakov, 2012; Kosolapov and Trofimov, 2014). An important element of these technologies is their adaptation to various climatic, soil, and landscape conditions and testing within long-standing experiments at the zonal stations of the Fodder Institute of Russian Academy of Sciences.

Passive methods of grassland restoration include protection against burns, a decrease in pasture loads, temporary isolation of large ranges from grazing, and the creation of protected areas on degraded lands for the development of a progressive succession.

Anyway, the overwhelming majority of the Russian grasslands area cannot be covered with protected areas and will stay as productive landscape. Obviously these grasslands should be saved by management methods.

Management to maintain the stability of Russia's grasslands includes (1) choosing optimal technologies, loads, periodicity, and grazing seasonality; (2) choosing a mowing regime optimal in terms of time, frequency, and the use of technical means; (3) conserving the biodiversity and forming regional networks of protected grassland localities with different management regimes; (4) preventing and combating grass fires and agricultural burns; (5) the ecological restoration of eroded and disused agricultural lands; (6) measures on fertilization and amelioration of ecosystems used in farming; and (7) strategic actions aimed at the reproduction and reintroduction of animal species important for the functioning of grasslands.

Management in agricultural use is a powerful driver of the conservation and maintenance of the sustainability of ecosystems, both meadows and steppes. Under the influence of grazing and mowing (for floodplain meadows, of seasonal floods as well), there formed stable, long-term ecosystems, diverse in composition and productivity.

As was shown above, on the forest zone plains the grasslands used for agriculture occupy 250,000 km². Their average economic yield (in dry weight) is 1.0–1.1 t ha⁻¹ (on watersheds) and 2.0–2.5 t ha⁻¹ in the floodplain. The forage reserve on natural forage lands of the forest zone is 25–35 million tons. In the forest-steppe and forest zones, controlled grasslands occupy 340,000 km². Due to the high plowing (50%–75%), inarable (slope) lands are used for grazing. Hay fields are primarily in floodplains and lowlands. The average economic yield on a watershed is 0.7–0.8 t ha⁻¹ and in a floodplain, two to three times higher. The forage reserve on natural forage lands of the forest-steppe and steppe zones is 20–25 million tons. In dry and desert steppes of Russia, there are 93,000 km² of herbal pastures with an average yield of 0.25–0.35 t ha⁻¹ and a forage reserve of 2.0–4.0 million tons on dry basis.

Livestock usually spend 130–160 days on pastures in the forest zone; in the forest-steppe zone, 160–200 days; in meadow steppes and typical steppes, 180–200 days; and in dry steppes and desert steppes, 220–280 days. Pasture herbage and good hay have always been the cheapest and biologically most complete feed. Their share in animals' ration should not decrease. For their production, 200,000–250,000 km² of natural and seeded hay fields and pastures are annually mowed in Russia. The optimal management mode in using pastures and hay fields requires (1) shredding and mowing plants in a state that can ensure a maximal yield from the animals; (2) feeding a maximal number of animals; and (3) preserving the yields of pastures and hay fields and the forage composition of their plants at a high level during the entire period of use and, at the same time, creating conditions for a further increase in the yield. All this can be attained considering the needs of animals and the response of plants to the usage mode.

The management of the dynamics of grasslands involved in agricultural production, consists of the following elements: (1) establishing an optimal height, time, and frequency of the use of the herbs; (2) choosing methods of use during the pasture season and by years; (3) using grazing and mowing rotations; (4) equipping the pasture territory, making up a herd, and choosing a pasture-day order; and (5) daily pasture and hay-field farming.

The regime of using grasslands as pastures (Fig. 4) corresponds to the composition of herbage: in the forest zone, three to four shredding cycles per season; in steppes, five to seven cycles. On average, one conditional head requires from 1.2–1.5 to 2.5–3 ha of pastures (Kosolapov and Trofimov, 2014).

Control over grasslands in the agricultural sector, which conflicts with the tasks of biodiversity conservation, is associated with the introduction of low-cost technologies of simplified improvement and progressive succession stimulation up to the stage when it becomes possible to maintain and even increase the share of valuable forage species in the stand by regulating grazing and mowing. Another result of the introduction of this technology will be the creation of everlasting pasture and hayfield phytocoenoses.

The long-standing experience of the conservation of grasslands on the plains of Russia's temperate zone shows that prospects here are associated exclusively with the restoration of beef (steppes) and dairy and meat (meadows of forest zone) husbandry. They should occupy the leading place in the traditional agricultural landscape and fulfill not only feeding but also environment-forming, protective, and recreational functions. Strategically, natural grasslands and their anthropogenic modifications can become a buffer between urbanized territories and intensive agriculture, dairy farms, and tillage, relieving the latter from some of the loads related to forage growing. In combination with the development of a network of protected territories, the area of which, according to the Goals of Sustainable Development in Russia, must be no less than 17%, grasslands in the steppe zone should constitute the ecological framework of the country's temperate belt.

Appendix 1: Syntaxonomic Prodrum of the Meadows, Steppes and Shrublands of Russia (Largely Following Ermakov (2012)) (Presented in the Ecological Order: Meadows, Steppes, Communities of Forest Edges, Communities of Inland Continental Saline Territories)

Class Molinio-Arrhenatheretea TX. 1937 – Secondary post-forest meadows of the temperate zone of the Western Eurasia on fairly rich non-saline lands

Order Althaeetalia officinalis Golub & Mirkin in Golub 1995a – Meadows of steppe and deserted steppe zones of Southeast Europe on lightly saline and moderately saline soils of river valleys, which are flooded for a long time

All. Althaeion officinalis Golub & Mirkin in Golub 1995b – Meadows of the Middle Volga valley on slightly saline and moderately saline soils, flooded during the spring-summer floods for a long time

All. Euphorbion palustris Ageulov & Golub in Golub 1995c – meadows of the river Ural valley, flooded during spring floods for 1–1.5 months, on slightly saline and moderately saline soils

Order Arrhenatheretalia Pawlowski et al. 1928 – Mesophytic meadows on well-drained mineral soils. Temperate zone of the Western Eurasia

All. Festucion pratensis Sipailova et al. 1985a – Meadows on well-drained, relatively rich mineral soils in Eastern Europe and Western Siberia

All. Cynosurion cristati TX. 1947a – Low grass meadows of the forest zone of the European part of Russia with hay-pasture use on poor, slightly acidic soils

Order Carici macrourae-Crepidetalia sibiricae Ermakov, Maltzeva & Makunina 1999a – Natural and semi-natural post-forest meadows of the forest-steppe and south of the forest zone of Southern Siberia and the Southern Urals

All. Polygonion krascheninnikovi Kashapov 1985b – Mesophytic post-forest meadows of the Southern Urals

All. Crepidion sibiricae Mirkin ex Ermakov, Maltzeva & Makunina 1999b – Post-forest meadows of humid well-drained habitats of plains and mountains of Southern Siberia

All. Aconito barbati-Vicion unijugae Ermakov, Maltzeva & Makunina 1999c – Post-forest meadows of moderately humid and moderately dry habitats of plains and mountains of Southern Siberia

Order Galietalia veri Mirkin & Naumova 1986a – Steppe meadows of Eastern Europe and Western Siberia, forming in a continental climate

All. Trifolion montani Naumova 1986b – Steppe meadows of forest-steppe and steppe zones of Eastern Europe and Western Siberia

All. Artemision ponticae Golub & Savelyeva in Golub 1995d – Steppe meadows in the valley of the Lower Don river and its tributaries

All. Seselion libanotis Ageulov & Golub in Golub 1995e – Steppe meadows in the valley of the Lower Ural and its tributaries

All. Scabioso ochroleucae-Poion angustifoliae Bulokhov 2001a – Steppe upland meadows of the southern forest part of the forest zone (subzone of deciduous forests) and forest-steppe zones within the Central Russian Upland

All. Agrostion vinealis Sipailova et al. 1985c – Dry meadows on sandy soils in the floodplains of southeastern Europe, transitional to the class of pioneer vegetation

All. Trifolion lupinastri Mirkin in Tuzhilin 1988a – Mesoxerophytic meadows of the northern Baikal region (Central Siberia)

- All. *Vicio-Hemerocallion lilio-asphodeli* Mirkin in Alimbekova & Mirkin 1989a – Rich meadows of the floodplains of the Lena and Yenisei rivers (Central Siberia)
- Order *Molinietalia* Koch 1926a – Wet meadows on mineral soils, Eastern Europe and Western Siberia
- All. *Caltion palustris* Tx. 1937 – Wettest meadows of the order, Eastern Europe and Western Siberia
- All. *Deschampsion cespitosae* Horvatić 1930 – Wet meadows of rich mineral floodplain soils, Eastern Europe and Western Siberia
- All. *Lythro-Euphorbion* Mirkin & Naumova 1986c – Wet meadows on floodplain soils of variable moisture regime in the lower parts of the river valleys in the deserted steppe zone of the European part of Russia
- All. *Molinion caeruleae* Koch 1926b – Wet meadows on mineral and peaty soils, with signs of transition to swamps
- All. *Anemonidion dichotomae* Mirkin in Iljina et al. 1988b – Wet meadows of the river valleys of the Western Siberia
- All. *Alopecurion arundinacei* Kononov in Kononov et al. 1986d – Swampy meadows on permafrost and bog soils
- Order *Potentillo-Polygonetalia* Tx. 1947b – Temporarily flooded disturbed meadows:
- All. *Potentillion anserinae* Tx. 1947c – Wet meadows of pasture use with a predominance of undersized hygrophilous species
- All. *Puccinellio-Agrostion stoloniferae* Gogoleva et al. 1987a – Communities of waterlogged, trampled solonchek habitats of Eastern Siberia.
- Class *Calamagrostetia langsdorffii* Mirkin in Achtjamov et al. 1985d – Communities of swampy floodplain meadows, East Asia
- Order *Calamagrostietalia langsdorffii* Achtjamov et al. 1985e – Floodplain meadows of northeastern Asia
- All. *Calamagrostion langsdorffii* Achtjamov et al. 1985f – Reed floodplain meadows of northeast Asia
- All. *Caricion schmidtii* Achtjamov et al. 1985g – True and swampy meadows in conditions of strongly variable water regime
- Class *Arundinello anomalae-Agrostietea trinii* Ermakov & Krestov 2009a – Dry land stepped meadows and meadow steppes, East Asia.
- Order *Artemisietalia mandshuricae* Achtjamov et al. 1985h – Driest type of meadows of deciduous forest and forest-steppe zones of Southern Primorye, Amur Region and Eastern Transbaikalia
- All. *Arundinellion anomalae* Achtjamov et al. 1985i – Meadows of Southern Transbaikalia and Mongolia;
- All. *Polygono alopecuroidis-Anemonastrion criniti* Arbuzova 1990 – Steppe meadows of Southern Transbaikalia and Mongolia
- Order *Carici schmidtii-Agrostietalia trinii* Ermakov & Krestov 2009b prov. – communities of medium-humid real meadows, common both in watersheds and in river valleys
- All. *Agrostion trinii* Achtjamov et al. 1985j – communities of real watersheds and river valleys meadows under the conditions of a variable regime of atmospheric humidification of the monsoon climate
- Class *Festuco-Brometia* Br.-Bl. & Tx. ex Soo 1947d – Xerothermic and hemixerothermic steppes of the Western Palearctic
- Order *Brometalia erecti* Koch 1926c – Subatlantic and sub-Mediterranean semi-xerophytic grassland communities on plain, Kerch peninsula (Crimea)
- All. *Bromion erecti* W. Koch 1926d – Subatlantic and sub-Mediterranean semi-xerothermic grass communities dominated by *Bromus* species
- All. *Cirsio-Brachypodion pinnati* Hadač & Klika in Klika & Hadač 1944a – More xerothermic subcontinental herbal communities of the Central and Southeast Europe
- Order *Festucetalia valesiacae* Br.-Bl. & Tx. ex Br.-Bl. 1949 – Subcontinental and continental meadow steppes of Central, Eastern Europe and Western Siberia:
- All. *Festucion valesiacae* Klika 1931a – Subcontinental and continental meadow steppes of Eastern Europe and Western Siberia
- All. *Poo urssulensis-Artemision glaucae* Saitov & Mirkin 1991a – Xeromesophytic steppes of the Ob riverside in the south of Western Siberia
- All. *Amygdalion nanae* Golub in Iljina et al. 1991b – Continental shrub steppes of Eastern Europe and Siberia
- All. *Galatellion biflorae* Korolyuk 1993a – Steppe meadows on slightly saline solonchek chernozem-like soils of the steppe zone of Western Siberia
- Order *Stipetalia sibiricae* Arbuzova & Zhitlukhina ex Korolyuk & Makunina 2001b – Meadow steppes of the Altai-Sayan mountain region
- All. *Aconito barbati-Poion transbaicalicae* Korolyuk & Makunina 2001c – Meadow steppes and steppe meadows of the Altai-Sayan mountain region
- All. *Veronico incanae-Helictotrichion desertorum* Korolyuk 2010a – Steppes and their petrophytic variants of the Altai-Sayan mountain region
- All. *Rosion pimpinellifoliae* Korolyuk 1997 – shrub steppes of the foothills of the Western Altai.
- Order *Helictotricho-Stipetalia* Toman 1969a – Continental steppes of Northern Kazakhstan, the Southern Urals and Western Siberia
- All. *Helictotricho desertori-Stipion rubentis* Toman 1969b – Continental steppes of Northern Kazakhstan, the Southern Urals
- All. *Plantagini-Calamagrostion epigei* Royer 1991c – Steppes of forest-steppe zone of Trans-Urals and Western Siberia;
- All. *Stipion korshinskii* Toman 1969c – Continental dry steppe of Northern Kazakhstan and South Urals;
- All. *Agropyron pectinati* Golub & Uzhmetskaya 1991d – Desert steppes on slightly saline soils of the Middle Volga

- Class *Helianthemo-Thymetea* Romashchenko, Didukh & Solomakha 1996a – Xero- and mesoxerothermic evergreen shrub communities are usually dominated by *Lamiaceae* species on dry, stony, non-saline and nitrate-poor calciferous soils in the southwestern part of the Central Russian Upland
- Order *Thymo cretacei-Hyssopetalia cretacei* Didukh 1989b – Xerothermic shrub communities on chalk outcrops in the southwestern part of the Central Russian Upland
- All. *Artemisio hololeuca-Hyssopion cretacei* Romashchenko et al. 1996b – Communities on chalk outcrops in the southwestern part of the Central Russian Upland
- All. *Centaureo carbonatae-Koelerion talievii* Romashchenko et al. 1996c – Grasslands of the Central Russian Upland
- All. *Euphorbio cretophilae-Thymion cretacei* Didukh 1989c – Cretaceous outcrop communities in the lower part of the Seversky Donets river basin
- Class *Festucetea vaginatae* Soo ex Vicherek 1972a – Continental psammophytic steppes and dry meadows
- Order *Festucetalia vaginatae* Soo 1957 – Continental psammophytic steppes and dry meadows of Europe
- All. *Festucion beckeri* Vicherek 1972b – Grass communities on sandy and sandy loam soils of the steppe zone of southeast Europe
- Class *Koelerio-Coryneporetea* Klika in Klika & Novak 1941 – Pioneer vegetation on dry poorly developed sandy soils and outcrops of acidic habitats.
- Order *Coryneporetalia canescentis* Klika 1934 – Pioneer psammophytic communities on poorly developed sandy soils
- All. *Corynephorion canescentis* Klika 1931b – the same characteristic as for the order
- Order *Trifolio arvensis-Festucetalia ovinae* Moravec 1967 – Subcontinental and continental psammophytic steppes of Europe and Western Siberia:
- All. *Koelerion glaucae* Volk 1931c – Xerophytic communities on neutral, stabilized sands
- All. *Armerion elongatae* Pötsch 1962a – Dry psammophytic meadows on sandy soils
- Class *Sedo-Scleranthetea* Br.-Bl. 1955 – Succulent communities on unformed soils underlain by weathered rocks
- Order *Sedetalia hybridi* Ermakov prov. – Succulent communities in Altai-Sayan mountain region
- All. *Sedion hybridi* Ermakov, Chytrý & Valachovic 2006a – Communities of succulents of forest-steppe and steppe belts
- Class *Calluno-Ulicetea* Br.-Bl. & Tx. ex Klika & Hadač 1944b – Heathlands on poor acidic soils of plains and low mountains of Europe.
- Order *Nardetalia strictae* Preising 1950 – the same characteristic as for the class
- All. *Violion caninae* Schwickera 1944c – Acidic pastures in the plains and low mountains
- All. *Deschampsio-Anthoxanthion* (Du Rietz 1942) Dahl 1957 – Chionophytic meadows and shrub-grass communities of places with late melting snow in the mountain and zonal tundra of Fennoscandia
- All. *Nardo-Caricion rigidae* Nordhagen (1936) 1943 – Chionophytic meadows of the timberline of the mountain and zonal tundra of Fennoscandia
- Class *Trifolio-Geranietea sanguinei* T. Müller 1962b – Meadow communities of forest edges and woodlands
- Order *Origanetalia vulgaris* T. Müller 1962c – Mesophilic meadow communities of forest edges and woodlands
- All. *Trifolion medii* T. Müller 1962d – Mesophytic forest edge communities
- All. *Geranion sanguinei* Tx. in T. Müller 1962e – Xeromesophytic communities of thermophilic herbaceous plants of the forest edges and woodlands open to the sun
- Class *Cleistogenetea squarrosae* Mirkin & al 1992 – Steppes of Eastern Siberia, Central and East Asia.
- Order *Festucetalia lenensis* Mirkin in Gogoleva et al. 1987b – Moderately dry meadow steppes of Southern Siberia and Inner Asia
- All. *Helictotrichion sellelliani* Hilbig 2000a – Typical meadow steppes of Transbaikalia and Eastern Mongolia
- All. *Stellerion chamaejasmeae* Korolyuk 2002a – Petrophytic meadow steppes of Transbaikalia and Eastern Mongolia
- All. *Filifolion sibirici* Akhtyamov ex Korolyuk 2002b – Meadow steppes of Lesser Khingan
- All. *Pulsatillion flavescens* Mirkin in Gogoleva & al 1987c – Meadow steppes of Central Yakutia
- All. *Elytrigio jacutori-Dracocephalion palmati* Sinelnikova 2009c – Extrazonal meadow steppes of the Far North-East of Asia
- All. *Festuco valesiaca-Caricion pediformis* Ermakov, Larionov & Polyakova 2012
- All. *Eritrichio pectinati-Selaginellion sanguinolentae* Ermakov, Chytrý & Valachovic 2006b – Petrophytic meadow steppes of the steppe and forest-steppe zones of the Altai-Sayan mountain region.
- Order *Stipetalia krylovii* Mirkin in Gogoleva et al. 1987d – Floristically extremely poor extrazonal steppes of the middle taiga subzone of Central Yakutia
- All. *Stipion krylovii* Mirkin in Gogoleva et al. 1987e – the same characteristic as for the order
- All. *Psatyrostachion juncea* Mirkin et al. 1987f – Dry steppes on eroded slopes in Central Yakutia
- Order *Cleistogenetalia squarrosae* Mirkin et al. ex Ermakov 2012b – Steppes of Southern Siberia and Central Asia
- All. *Poo attenuatae-Cleistogenion squarrosae* Mirkin et al. ex Ermakov 2012c – Daurian and Eastern Mongolian moderately dry steppes;
- All. *Thymion gobici* Mirkin in Kashapov et al. ex Hilbig 2000b – Petrophytic steppes of Transbaikalia and Eastern Mongolia.
- Order *Kochio prostratae-Stipetalia krylovii* Ermakov 2012d – Dry and desert steppes of Southern Siberia and Mongolia
- All. *Kochio prostratae-Stipion krylovii* Ermakov 2012e
- All. *Stipion orientalis* Korolyuk & Makunina 2009d – Petrophytic dry and desert steppes of the Altai-Sayan mountain region
- All. *Convolvulo ammannii-Stipion krylovii* Mirkin et al. ex Ermakov 2012f – Dry steppes of Southern and Eastern Mongolia

- Class *Stipetea glareosae-gobicae* Hilbig 2000c – Desert steppes of Central Asia
 Order *Allietalia polyrrhizi* Hilbig 2000d – the same characteristic as for the class
 All. *Allion polyrrhizi* Hilbig 2000e – the same characteristic as for the order
- Class *Artemisio santolinifoliae-Berberidetea sibiricae* Ermakov, Chytrý & Valachovic 2006c – Mountain communities of rocky screes of the steppe and forest-steppe zones of Central and North Asia
 Order *Artemisio santolinifoliae-Berberidetalia sibiricae* Ermakov, Chytrý & Valachovic 2006d – the same characteristic as for the class
 All. *Artemision rutifoliae* Ermakov, Chytrý & Valachovic 2006e – Rocky communities of steppe and desert-steppe zones
 All. *Ulmion pumilae* Mirkin et al. ex Hilbig 2000f – Shrubs on screes in the steppe belt of Southern Transbaikalia and Eastern Mongolia
- Class *Brometea korotkyi* Hilbig & Korolyuk 2000g – Xerophytic sand steppes of the Ulsu-Nur Basin
 Order *Brometalia korotkyi* Hilbig & Korolyuk 2000h – the same characteristic as for the class
 All. *Bromion korotkyi* Hilbig & Korolyuk 2000i – the same characteristic as for the order
 All. *Oxytropidion lanatae* Chytrý, Pesout & Anenkhonov 1993b – Sand steppes of the Baikal region
- Class *Festuco-Puccinellietea* Soo ex Vicherek 1973a – Halophytic communities
 Order *Festuco valesiacae-Limonietalia gmelinii* Mirkin in Golub & V. Solomakha 1988c – Halophytic steppes of Northern Eurasia
 All. *Festuco valesiacae-Limonion gmelinii* Mirkin ex Golub & V. Solomakha 1988d – Halophytic steppes of Southern Ural and Northern Kazakhstan
 All. *Artemision nitrosae* Korolyuk in Korolvuk & Kipriyanova 1998 – Halophytic steppes of south of the West Siberian Plain
 All. *Limonion tomentelli* Agafonov & Golub in Golub 1994a – Halophytic steppes of chernozem regions of the European part of Russia
 All. *Psathyrostachyo-Limonion Saitov* ex Golub et al. 2001d – Halophytic steppes of forest-steppe zone of the Middle Irtysh
- Order *Artemisietalia pauciflorae* Golub & Karpov in Golub et al. 2005a – Halophytic communities of the Volga-Ural region
 All. *Artemisio pauciflorae-Camphorosmion monspeliacae* Karpov 2001e – Floristically poor halophytic steppe of the Orenburg region
 All. *Artemision pauciflorae* Grebenyuk, Golub, Yuritsyna in Golub et al. 2005b – Relatively floristically rich halophytic steppes of the Volga-Ural region, as well as the right bank of the Volga river
- Order *Glycyrrhizetalia glabrae* Golub & Mirkin in Golub 1995f – Subhalophytic alluvial communities of the lower Volga and Don rivers
 All. *Glycyrrhizion echinatae* Golub & Savelyeva in Golub 1995g – Subhalophytic meadows of the lower Don river valley
 All. *Glycyrrhizion glabrae* Golub & Mirkin in Golub 1995h – Subhalophytic meadows of the lower Volga and Ural rivers valleys
 All. *Glycyrrhizion korshinskyi* Lysenko 2010b – Subhalophytic meadows of the steppe zone of the Volga and Ural rivers valleys
- Class *Scorzonero-Juncetea gerardii* Golub et al. 2001f – Halophytic wet meadows of the interior of Eastern Europe and North Asia.
 Order *Suaedetalia corniculatae* Golub 1994b – Halophytic meadows of Siberia and Mongolia
 All. *Suaedo corniculatae-Puccinellion tenuiflorae* Mirkin ex Golub 1994c – Saline meadows of thermokarst depressions (the alasses) of Central Yakutia, river valleys of Mongolia, peripheral parts of lakes and waterlogged depressions in the south of the West Siberian Plain
 All. *Suaedion corniculatae* Golub 1993c – Halophytic meadows in thermokarst depressions of Yakutia
- Order *Halerpestetalia* Mirkin et al. ex Holub 1994d – Halophytic meadows of Central Yakutia
 All. *Halerpeston salsuginosae* Mirkin et al. ex Holub 1994e – the same characteristic as for the order
- Order *Scorzonero-Juncetalia gerardii* Vicherek 1973b – Continental wet halophytic meadows of Eastern Europe and Western Siberia
 All. *Cirsion esculenti* Golub 1994f – Saline meadows on solonetz-solonchak soils of the forest-steppe and steppe zones from central Russia to the south of Western Siberia and East Kazakhstan
 All. *Cirsio-Hordeion* Mirkin ex Golub 1994g – Meadow communities of valleys of small rivers of the Southern Ural foothills and plain on saline soils with a fairly stable moisture regime
 All. *Juncion gerardii* Wendelberger 1943 – Wet meadows of river floodplains and shores of lakes in Central and Eastern Europe, on salt marshes with a variable type of moisture
 All. *Agrostio stoloniferae-Beckmannion eruciformis* Mirkin in Barabash et al. 1989d – Subhalophytic floodplain meadows and pastures of rivers of the steppe zone of southeastern Europe
- Class *Achnatheretea splendentis* Mirkin et al. 1988e – Communities with dominance of *chii* on slightly saline metabolic habitats of the continental regions of the steppe zone of southern Siberia and Mongolia
 Order *Achnatheretalia splendentis* Mirkin et al. 1988f – the same characteristic as for the class
 All. *Achnatherion splendentis* Mirkin et al. 1988g – the same characteristic as for the order
- Class *Nerio-Tamaricetea* Br.-Bl. & O. Bolos 1958 – Gallery forests and valley shrub communities of arid and subarid regions of Southern Europe and Central Asia
 Order *Tamaricetalia ramosissimae* Borza & Boscaiu 1965 – the same characteristic as for the class

- All. *Agropyro fragilis*-*Tamaricion ramosissimae* Golub & Kuzmina 1996d – Communities with dominance of *Tamarix ramosissima* on deserted habitats and lower Volga-river valleys
- All. *Galio humifusi*-*Tamaricion ramosissimae* Golub & Kuzmina 1996e – Xero-mesophytic communities dominated by *Tamarix ramosissima* and *Elaeagnus angustifoliae* in the lower Volga-river valley

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Grasslands and Shrublands of Kazakhstan and Middle Asia

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This article was solicited and edited by Jürgen Dengler and Péter Török on behalf of the Eurasian Dry Grassland Group (EDGG).

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Abstract

Kazakhstan and Middle Asia comprise 4 million km² of plains, uplands and tall mountain ranges in the core of the Eurasian continent. The region's semi-arid climate, grazing pressure by wild and domestic ungulates, and long pastoral tradition, have given rise to a variety of open habitat types and a distinct flora and fauna. Grasslands and shrublands are a natural and dominant vegetation type in the forest-steppe and steppe zone of northern and central Kazakhstan, as part of the Eurasian grassland biome. In Middle Asia, grasslands and shrublands are widespread habitat types in the Tian Shan, Pamir-Alai and Pamir—mountain systems that have been recently acknowledged as a global biodiversity hotspot. Here, grasslands and shrublands are often semi-natural, formed by a long practice of logging, burning and domestic livestock grazing, and comprise a variety of vegetation types, including Eurosiberian meadows and steppe, Irano-Turanian semi-savanna and thermophilous shrublands. The most serious threats to grassland biodiversity and ecosystem functioning are habitat degradation, including conversion to cropland, pollution, urban development, under- and overgrazing, and illegal hunting. Notwithstanding these threats, Kazakhstan and Middle Asia still harbor vast areas of public, unfenced grasslands and shrublands that are traditionally managed and often embedded in regions with low human density. This makes the region a globally important area for biodiversity conservation.

Delimitation and Physiogeography of the Region

Kazakhstan and Middle Asia form a continental area of 4 million km² (1.5 million square miles), with 97% of the territory belonging to the Asian and 3% to the European continent. The region borders on Russia in the north, China in the east, the Caspian Sea in the west, and Pakistan and Afghanistan in the south, and spans approximately 2000 km of latitude and 2900 km of longitude. In political terms, the region is divided among the countries of Kazakhstan, Kyrgyzstan, Tajikistan, Turkmenistan, and Uzbekistan. Middle Asia has been defined by Soviet geographers as a region comprising the four latter countries and southern Kazakhstan (approximately south of the 48° latitude, stretching from the Caspian Sea to the border of China; [Rachkovskaya et al., 2003](#)). In the last three decades, the term Central Asia has been increasingly used to describe the region covered here and neighboring western China and Mongolia. However, we restrict the term Central Asia more narrowly to the latter region (in line with [Rachkovskaya et al., 2003](#)), which is not treated in this article and separated from Middle Asia by the Dzhungar Alatau and Tian Shan mountains.

The northern plains and gentle uplands of Kazakhstan are dominated by forest-steppe and steppe (dry grasslands), while Middle Asia encompasses lowland deserts and tall mountains, such as the Altai, Tarbagatai, and Dzhungarian Alatau in the east, and the Tian Shan, Pamir-Alai, and Pamir in the south. The mountains of Middle Asia are among the tallest worldwide, with some peaks exceeding 7000 m.

The runoff from the region's uplands and mountain systems drains into rivers that discharge into the Arctic Sea or the endorheic basins of the Aral and Balkhash Seas. The Zhetisu region north of the Tian Shan, and the Amu Darya and Syr Darya rivers west of the Tian Shan form large floodplains. However, the two latter have been strongly reduced in size due to intensive crop-irrigation further upstream ([Peterson, 1993](#)). The plains and uplands of Kazakhstan are rich in freshwater and saline wetlands.

The region's climate is strongly continental and shaped by its landlocked position in the heart of the Asian continent. In general, it is characterized by high solar insolation, relatively low precipitation and a strong amplitude of daily and seasonal temperatures. According to the recent Köppen global climate classification (Beck et al., 2018), the plains and uplands of Kazakhstan, and central mountains of Middle Asia, have cold semi-arid (climate zone code: Bsk) and desert (Bwk) climates. The outer northern and western mountain ranges of the Altai, Tian Shan, Pamir-Alai, and Pamir intercept precipitation carried by Westerlies and show a humid continental climate (Dsa, Dsb, Df). The foothills of the western Tian Shan and south-western Pamir-Alai are the only areas in the region with a Mediterranean climate (Csa). By comparison, the innermost and tall mountain ranges that stretch from the Altai in the north-east to the Pamir in the south display tundra (ET) climate with low temperatures year-round.

Biogeography, Flora and Fauna

Forest-Steppe and Steppe Zones

The grasslands of northern and central Kazakhstan are part of the Eurasian steppe biome and the Black Sea-Kazakhstan steppe sub-region (Lavrenko et al., 1991; Bragina et al., 2018). They span two biogeographic zones that are aligned as latitudinal belts (Rachkovskaya et al., 2003). The forest-steppe zone comprises the northern tip of Kazakhstan. As part of the West Siberian Lowlands, it is made up of gentle topography covered by a mosaic of steppe grasslands, shrublands, meadows, and woodlands. In a recent overview of forest-steppe zones, Erdős et al. (2018) assigned northern Kazakhstan to the West Siberia and North Kazakhstan forest-steppe region. A total of 48 species of mammals occur here (Rodentia: 21, Carnivora: 10, Insectivora: 7, Chiroptera: 5, Artiodactyla: 3, Lagomorpha: 2), including Siberian roe deer (*Capreolus pygargus*), moose (*Alces alces*), northern white-breasted hedgehog (*Erinaceus roumanicus*), northern birch mouse (*Sicista betulina*), and bank vole (*Myodes glareolus*). A total of 167 nesting bird species (most of which are bound to woodlands, shrublands, and lakes) and seven reptile species (mostly snakes) inhabit this region. Common amphibians are European green toad (*Bufo viridis* complex), moor frog (*Rana arvalis*), common frog (*Rana temporaria*), and Siberian newt (*Salamandrella keyserlingii*). Due to the region's fertile chernozem soils and moderate climate, approximately 60–90% of grasslands have been plowed (Semenov, 2012; Kraemer et al., 2015).

The adjacent and more arid steppe zone is found further south, approximately at latitudes 48°–52°. Its vegetation is dominated by drought-tolerant steppe and—more rarely—shrublands on chernozem and kastanozem (chestnut) soils. This zone is home to 73 species of mammals (Rodentia: 35, Carnivora: 13, bats: 9, Insectivora: 7, Artiodactyla: 5, Lagomorpha: 4 species). Characteristic species of mammals are saiga antelope (*Saiga tatarica*), marmots (*Marmota bobak*, *M. baibacina*), sousliks (*Spermophilus pygmaeus*, *S. major*, *S. erythrogenys*), mole vole (*Ellobius talpinus*), steppe lemming (*Lagurus lagurus*), steppe fox (*Vulpes corsac*), steppe polecat (*Mustela eversmanii*), and steppe and kazakh pikas (*Ochotona pusilla*, *O. opaca*). Characteristic birds are little bustard (*Tetrax tetrax*), demoiselle crane (*Anthropoides virgo*), steppe eagle (*Aquila nipalensis*), long-legged buzzard (*Buteo rufinus*), several species of *Calandrella* and *Melanocorypha* larks (including sub-endemic black lark *Melanocorypha yeltoniensis* and white-winged lark *Melanocorypha leucoptera*; the latter considered as *Alauda leucoptera*—Alström et al., 2013), wheatear species (specifically isabelline wheatear, *Oenanthe isabellina*, pied wheatear, *O. pleschanka*), and red-headed bunting (*Emberiza bruniceps*). The Naurzum Nature Reserve, a protected area in the steppe zone of northern Kazakhstan, provides habitat for 316 bird species, of which 168 are nesting (Bragin and Bragina, 2014, 2017). Six species of amphibians and 14 species of reptiles are found in the steppe zone of Kazakhstan. Rain-fed crop agriculture and animal husbandry dominate the regional land-use.

In the past, the forest-steppe and steppe of Kazakhstan have been grazed by many wild ungulates, rodents, and lagomorphs, which have likely been keystone mutualists and ecological engineers in steppe ecosystems (Murdoch et al., 2009; Abaturov and Kulakova, 2010). Common ungulates included wild horse (now extinct), kulan (extinct), saiga antelope (critically endangered), and the argali wild sheep (near threatened). Populations of ungulate grazers have strongly decreased in the last three centuries due to hunting, grassland conversion into crop land, and competition with livestock for pastures. While the populations of wild ungulates have decreased, those of many rodents and lagomorphs have stayed viable (Kamp et al., 2016).

About 2000 vascular plants are known to grow in the forest-steppe and steppe zones of Kazakhstan, with about 1.5% of the total flora endemic to the region (Rachkovskaya and Bragina, 2012; see below for a more detailed outline of prevalent species). The steppe zone borders on the desert zone further south (not covered in this article).

Middle Asia

The biogeographic make up of Middle Asia is shaped by strong differences in topography and macroclimate. The plains are dominated by South Turanian deserts (not covered here), which border on an extensive mountain region with a wide range of different habitat types, including grasslands, meadows, semi-savanna, and shrublands. Based on the prevalent flora, the mountain region of Middle Asia can be divided into four provinces (Rachkovskaya et al., 2003; the Kopet Dag is not covered here).

- (1) The Dzhungar-North Tian Shan province includes the northern ranges of the Tian Shan and parts of the Dzhungar Alatau and central Tian Shan. These ranges intercept moist air from the Westerlies and are characterized by *Picea schrenkiana* forests (sometimes only as fragments), Eurosiberian meadows on northern slopes and gentle shoulders in the mid-altitudinal belts, and steppe grasslands with Eurasian bunchgrasses in the foothills and on southern exposed slopes (Rachkovskaya et al., 2003).

- (2) The Middle Asian mountain province encompasses the western Tian Shan, the Karatau mountains, the western central Tian Shan, and the mountains of western Tajikistan. Being mostly oriented to the west, they similarly intercept precipitation from the Westerlies. Bedrock is dominated by limestone. The montane belt is commonly formed by open juniper forests while spruce is rare. The mountains of the Fergana valley (Chatkal and Fergana ranges), and the Gissar and Darvaz ranges, are covered by wild fruit forests with walnut (*Juglans regia*), Turkestan maple (*Acer turkestanicum*), and wild apple (*Malus sieversii*). The low mountains and foothills are dominated by semi-desert that encompasses many annuals and geophytes with a peak growing and flowering season in late winter and spring. Steppe vegetation is rare (Rachkovskaya et al., 2003).
- (3) The Central Asian mountain province is found at the south-eastern edge of the region covered in this article and includes the high mountains and plateaus of the eastern central Tian Shan and eastern Pamir. This region is characterized by strong aridity since precipitation carrying winds are blocked from this region by mountain chains further north, west and south. Forest vegetation is almost absent. Instead, mountain deserts play an important role at the lowest and middle altitudinal belts. Cryophytic cushion communities are found at the highest elevations (Rachkovskaya et al., 2003).
- (4) The North Hindukush Province comprises the south-western Gorno-Badakhshan region in southern Tajikistan and some neighbouring territories outside of the chapter's focus. Lower altitudes are covered by semi-desert and xerophytic shrublands, in which sagebrush species play an important role. They are replaced by cryophytic cushion communities at higher elevations (Rachkovskaya et al., 2003).

The mountains of Middle Asia and southern Kazakhstan are a global biodiversity hotspot ("Critical Ecosystem Partnership Fund," www.cepf.net/our-work/biodiversity-hotspots). Approximately 10,000 vascular plant species can be found here (Kamelin, 2017). Although detailed data on species numbers across habitats are missing, we assume that a large portion of taxa grows in open habitat types because they are widespread in this region and occur over a wide variety of bedrock and soil types. Regional plant endemism is high: approximately half of the species pool and approximately 100 genera of flowering plants are endemic (Kamelin, 2017). Regional studies report endemism rates of 14% (Aksu-Jabagly Nature reserve, calculated from Karmysheva, 1973), 10% (Uzbekistan, Tojibaev, et al. *in prep*, cited in Sennikov et al., 2016) and approx. 30% (Nowak et al., 2011). Some plant genera are particularly rich in endemics, such as *Allium*, *Astragalus*, *Cousinia*, and *Oxytropis*. The high rate of endemism in the mountain regions of Middle Asia is probably due to niche diversification in the Pleistocene when environmental conditions repeatedly shifted between dry and humid (Bagheri et al., 2017).

Vascular plants with an Irano-Turanian distribution make up a large percentage of the regional flora (c. 60% of the total regional species pool, e.g. *Acantholimon diapsenioides*, *Carex pamirensis*, *Ranunculus badachschanicus*). Mediterranean species (10%) grow mainly in lowlands and montane belts of the western and south-western ranges, and include species like *Avena meridionalis*, *Cressa cretica*, and *Parietaria serbica*. Euro-Siberian species are particularly common in the northern ranges of the Tian Shan and Dzhungar Alatau (e.g. *Dactylis glomerata*, *Fragaria viridis*, *Stipa capillata*). The remaining part of the species pool is made up of circumpolar (e.g. *Parnassia palustris*), East Asian (Oriental) (e.g. *Eucommia ulmoides*), Indo-Chinese (e.g. *Sphenoclea zeylanica*), tropical and subtropical (e.g. *Ludwigia perennis*), Saharo-Sindian (e.g. *Nanorrhinum ramosissimum*), arctic-alpine (e.g. *Carex microglochin*, *Lloydia serotina*) and Himalayan plants (e.g. *Aconitum rotundifolium*, *Alopecurus himalaicus*).

Middle Asia has a rich fauna. A total of 543 migratory and non-migratory bird species are known from the area, including the rare white pelican (*Pelecanus onocrotalus*), Egyptian vulture (*Neophron percnopterus*), and Asian paradise flycatcher (*Terpsiphone paradisi*; Ryabitshev, 2019). The Aksu-Jabagly Nature Reserve, Middle Asia's oldest protected area, lists 44 mammal species, including the Indian crested porcupine (*Hystrix indica*), argali (Marco-Polo sheep, *Ovis ammon polii*), Himalayan brown bear (*Ursus arctos isabellinus*), and the critically endangered snow leopard (*Uncia uncia*) (Beg, 2009). A mixture of crop agriculture and pastoralism has been practiced for millennia in the fertile foothills and lowlands (Spengler et al., 2014) and the region has been traversed by the Silk Road network in the past (Spengler, 2019). Today, the western and northern Tian Shan has a disproportionately high human density and includes large metropolitan areas, like Almaty, Bishkek, and Tashkent. Despite the recent growth in urban areas, pastoralism still plays an important role in mountainous Middle Asia.

Grassland Origin

The Kazakh forest-steppe and steppe are considered to be of natural origin, attributed to the region's semi-arid climate that established since the Indian and Eurasian tectonic plates collided in the Cenozoic. The relatively young mountains of the Tian Shan, Pamir-Alai, and Pamir cut the region off from the moist southern monsoon (Kamelin, 2017). Wild ungulates have likely also played an important role in reducing shrub and tree encroachment. After the emergence of mobile pastoralism approximately 5000 years before present (BP), the roaming herds of wild ungulates were replaced by domestic ungulates (Frachetti, 2012). Today, the vegetation of forest-steppe and steppe is still affected to a large degree by livestock grazing and wildfires.

The origin of grasslands in the mountain regions of eastern and southern Kazakhstan and Middle Asia is more complex and likely of both anthropogenic and natural origin. Here, open coniferous and deciduous forests prevail in the montane belt, especially in the outer mountain ranges that receive the highest amounts of precipitation in the region. Local nomads burned and logged forests and shrublands in mountains to expand grasslands (Elenevskiy, 1940; Dakhsleyger, 1980). Although exact data are missing, we can assume that a high percentage of hay meadows and pastures in the foothills and the mid-elevational zone are of

anthropogenic origin. However, the steppe communities on southern-exposed slopes and alpine grasslands are likely of natural origin, favored by a microclimate that limits tree growth.

Typology of Communities

Forest-Steppe and Steppe Zones

Grasslands are a dominant vegetation type in the forest-steppe and steppe zones of northern Kazakhstan (Fig. 1). The forest-steppe zone is a transitional region between the Siberian taiga in the north and steppe in the south and is comprised of a mixture of grasslands, meadows and woodland groves. As precipitation decreases further south in the steppe zone, tree growth becomes limited and open habitats—most importantly dry grasslands—dominate the landscape.

Temperate-dry rich forb—feathergrass meadow steppes on haplic chernozem are located along the southern periphery of the West Siberian Lowland. These communities are rich in forbs (e.g. *Filipendula vulgaris*, *Iris ruthenica*, *Lathyrus pratensis*, *Peucedanum*



Fig. 1 Grasslands and shrublands of the plains and uplands of Kazakhstan. (A)—Steppe with *Stipa capillata* on sandy soils (B)—Shrubland with prostrate *Juniperus sabina* in the steppe zone (both in the Naurzum Nature Reserve) (C)—Desert steppe with *Stipa lessingiana* and *S. sareptana* (Mugodzhary Hills, western Kazakhstan) (D)—Dry steppe with *Spiraea hypericifolia* (Central Kazakhstan Upland, Karaganda region) (E)—Desert steppe with *Stipa sareptana* and *Agropyron desertorum* (Sub-Urals Plateau, western Kazakhstan) (F)—Dry xeric forb—bunchgrass steppe with *Caragana pumila* shrubs (Dogalan Hills, east Kazakhstan Uplands). Photos by V. Wagner (A), T. Bragina (B), and I. Smelansky (C–F).

morisonii, *Phlomis tuberosa*, *Veronica spuria*) and feathergrasses (e.g. *Stipa pennata*, *S. zaleskii*). Further south, in the plains of the West Siberian Lowland, the Trans-Ural Plateau and the northeast Kokshetau uplands, steppe is dominated by dry forb—feather grass communities with *Stipa zaleskii* and *Festuca valesiaca* as dominant plants, and *Koeleria cristata* as a co-dominant. On calcareous soils, *Stipa korshinskiyi* is a characteristic dominant plant and *Stipa lessingiana* a co-dominant. Temperate dry-bunchgrass steppes on dark chestnut soils are common on the plains of the Sub-Ural and Turgay Plateau, in the eastern periphery of the West Siberian Lowland, and the plains among the hills of the Central Kazakhstan. Here, *Stipa lessingiana* prevails with an admixture of small forbs. Dry xerophytic forb—bunch grass steppes on chestnut soils are widespread in the Sub-Ural and Turgay Plateau (with *Festuca valesiaca*, *Galatella divaricata*, *G. tatarica*, *Phlomis agraria*, *Stipa lessingiana*, *Tanacetum achilleifolium*). Steppe on sandy soils are characterized by *Stipa capillata*, *S. borysthenica*, and *Helichrysum arenarium*.

The most southern zonal steppe grasslands are made up of desert sagebrush—bunch grass steppes on light chestnut soils. They are dominated by the drought resistant *Stipa sareptana* and are found in the Caspian Lowlands, the Sub-Ural and Turgay Plateaus, the Mugodzhary Hills, the Central Kazakhstan Uplands, and the Kulunda Plain. Desert steppe is the most xeric among zonal steppe grasslands. It is found between latitudes N48–49° to N46–47° and is associated with light kastanozem soils. Its communities are dominated by *Stipa sareptana* and *S. kirghisorum* on sandy and clay-rich soils and *Stipa caucasica* and *S. orientalis* on rocky soils and bedrock outcrops. These grasslands can occur interspersed with dwarf shrub deserts (dominated by *Artemisia* and *Chenopodiaceae* species). They are distributed as a solid belt on plains and uplands from the Caspian Lowland in the west to the Zaisan Depression in the east. Dry saline habitats with deep water horizons on river and lake terraces are occupied with specific *saz* steppe communities commonly dominated by giant bunchgrass *Neotrinia* (= *Achnatherum*) *splendens*, *Leymus* spp. (on sandy soils: *Leymus racemosus*, giant grass), and *Iris halophila*.

Depressions and riparian corridors are covered by reed beds with rhizomatous grasses, sedges, rushes and mesic to wet meadows with e.g. *Filipendula ulmaria* and *Sanguisorba officinalis*. As salinity increases, meadows become dominated by more salt-tolerant species such as *Glycyrrhiza uralensis*, *Hordeum brevisubulatum*, *Limonium gmelinii*, and *Puccinellia distans* (Kalinina, 1961). Compared to steppe grasslands, reed bed and meadow vegetation in the forest-steppe and steppe zones of Kazakhstan has not been well studied.

Shrubs can occur interspersed as single individuals in grasslands or can form communities corresponding to the grassland types outlined above. For instance, thickets with *Rosa* spp., *Cytisus* spp., *Lonicera tatarica*, *Spiraea crenata*, and *Padus racemosa* are characteristic for meadow steppe. *Spiraea hypericifolia* and *Caragana frutex* form extensive shrublands in dry steppe. Several species of *Atraphaxis* (*A. decipiens*, *A. spinosa*, *A. laetevirens*) and *Caragana* (e.g. *C. balchaschensis*, *C. bongardiana*, *C. leucophloea*, *C. pumila*) are characteristic for desert steppe shrublands. Steppes with the sub-endemic *Calophaca soongorica* shrub are typical for the Tarbagatai foothills in eastern Kazakhstan. Rocky habitats in uplands and foothills can have a high cover of steppe shrublands, including communities with *Cotoneaster melanocarpa*, *Lonicera microphylla*, *Juniperus sabina*, or *Ephedra* species (e.g. *E. equisetina*). Saline depressions and river and lake terraces of the southern half of the steppe zone are often dominated by *Halimodendron halodendron* and *Tamarix* spp. shrublands.

Middle Asia

The grasslands and shrublands of Middle Asia display a rich array of different habitat types due to the region's pronounced differences in climate and topography (Fig. 2). The foothills of the western Tian Shan and Pamir-Alai are covered by ephemeral semi-desert on thick loam deposits, dominated by annual grasses (e.g. *Bromus danthoniae*, *B. tectorum*, *Poa bulbosa*) and sedges (e.g. *Carex pachystylis*) (Korovin, 1961). With increasing elevation, it transitions into a taller drought tolerant vegetation type dominated by grasses (*Agropyron trichophorum*, *Bothriochloa ischaemum*, *Hordeum bulbosum*, *Lolium persicum* and *Trachymia distachya*) or Apiaceae species (*Ferula tenuisecta*, *Prangos pabularia*), often interspersed with shrubs (e.g. *Rosa kokanica*) or small trees (e.g. *Celtis caucasica*). This vegetation comprises various open and thermophilous plant community types on xeric sites, such as on rocky soils and southern or western slopes. This habitat type is not related to the Eurasian dry grasslands and meadows but is rather Irano-Turanian vegetation, being found only in the western mountain ranges of Middle Asia, Afghanistan, Iran and Turkey. The high cover of tall and drought tolerant Apiaceae species and grasses, combined with interspersed shrubs or trees, has puzzled Soviet botanists as it did not match their concept of a typical grassland, as exemplified by the Eurosiberian steppe or meadow. Hence, they used different names for this vegetation type, e.g. "savannoides," "semi-savanna," or "turanian steppe" (Korovin, 1962; Karmysheva, 1973; Pavlov, 1980).

Wind-exposed slopes in the northern and western mountain ranges are often covered by steppe with tussock grasses (e.g. *Festuca valesiaca*, *Helictotrichon hookeri*, *Koeleria cristata*, *Stipa krylovii*). This vegetation type closely resembles the steppes of the northern plains of Kazakhstan and is used foremost for livestock grazing (Korovin, 1962).

The precipitation-rich northern and western ranges of the Tian Shan are also home to meadow-steppe and meadows on deep brown soils in the montane and subalpine belts, dominated by Eurosiberian species, like *Bromus inermis*, *Dactylis glomerata*, *Galium verum*, and *Poa angustifolia* (Karmysheva, 1961; Wagner, 2009). Given their productivity and prevalence of palatable species, these mesic grasslands are often used for traditional hay making.

Shrublands are widespread in the mountains of Middle Asia. They encompass thermophilous communities (referred to as "shiblyak" in Slavic languages), low-growing juniper shrublands, and dwarf shrub communities (Korovin, 1962). Shiblyak vegetation occurs primarily in the western Tian Shan and Pamir-Alai, on rocky soils from lower elevations to the lower montane belt. Common shrubs include wild pistachio (*Pistacia vera*), elm-leaved sumach (*Rhus coriaria*), jujube (*Ziziphus jujuba*), thorny almond (*Amygdalus*



Fig. 2 Grasslands and shrublands of Middle Asia. (A)—Mesic meadows and *Picea schrenkiana* forests (Trans-Ili Alatau, northern Tian Shan, Kazakhstan) (B)—Semi-savanna with *Ferula tenuisecta* (western Pamir-Alai, Tajikistan) (C)—Mountain steppe interspersed with *Picea schrenkiana* fragments (eastern Kyrgyzstan) (D)—Mountain steppe with *Stipa drobovii* (Fon Mountains, western Pamir-Alai) (E)—Shiblyak vegetation with *Rhus coriaria* (Hissar mountains, western Pamir-Alai) (F)—Haymaking in the southern Naryn region (Kyrgyzstan). Photos by V. Wagner (A), A. Nowak (B, D, E), and K. Vanselow (C, F).

spinosissima), wild pomegranate (*Punica granatum*), and Jerusalem thorn (*Paliurus spina-christi*). Shiblyak is rich in annuals and geophytes and occurs interspersed with semi-deserts and semi-savanna (see above). It has been suggested that these shrublands, together with open deciduous woodlands, are the potential natural vegetation of the lower montane and colline belt in the western Tian Shan and Pamir-Alai, and that their spatial extent has been much reduced due to wood removal (Karmysheva, 1982).

Shrublands at higher elevations comprise thickets of procumbent *Juniperus pseudosabina*, especially in the northern and western Tian Shan. Rose thickets are common in the Tian Shan, Pamir-Alai and western Pamir (e.g. with *Rosa begeriana*, *R. divina*, *R. ecae*, *R. fedtschenkoana*, or *R. maracandica*). The western Pamir is also home to shrub communities with *Amygdalus bucharica* associated with tall herbs (e.g. *Eremurus stenophyllus*) and other shrubs (e.g. *Lonicera persica*), rose communities (e.g. *Rosa kokanica*, *R. webbiana*), associated with *Exochorda alberti*, *Lonicera korolkowii* and tall herbs (e.g. *Aconogonon coriarium*), and *Cotoneaster* communities dominated by *Cotoneaster uniflorus* and *C. multiflorus* associated with *Lonicera microphylla*. Thickets with *Ephedra* spp. can be dominant in more arid mountain ranges (e.g. with *Ephedra intermedia*, *E. glauca* or *E. equisetina* accompanied by shrubs of *Atraphaxis pyrifolia*, *A. seravschanica* and *Sageretia laetevirens*). Dwarf shrub communities are found at high elevations throughout the region's arid mountains (not covered here).

Moist meadows are limited to riparian sites with a high ground water table or accumulations of melting snow. These meadows are dominated by species of sedges (*Carex* spp.) and bog sedges (*Kobresia* spp.) and often degraded due to grazing.

Threats

Habitat degradation and loss is the most serious threat to grasslands and shrublands in the region. This is particularly true for the forest-steppe and steppe zones of Kazakhstan. This area has been traditionally inhabited by mobile pastoralists. When the country became part of the Soviet Union in the first half of the 20th century, the government enforced sedentarization of its nomads. About 254,000 km² of steppe was converted to crop land (foremost for wheat farming) under the Virgin Land Campaign (Peterson, 1993; Semenov, 2012; Kraemer et al., 2015). This land-use transformation resulted in large-scale loss of two zonal types of steppe ecosystems, rich forbs—grass steppe and dry steppe (meadow steppe had been destroyed even earlier, in the start of 20th century). It has contributed to the decline of many steppe species, including the saiga antelope (*Saiga tatarica*, critically endangered), marmots (*Marmota bobac*, *M. baibacina*), many steppe raptors, and great bustard (*Otis tarda*, vulnerable). After the cessation of the Soviet Union, the region experienced a strong economic depression and rural exodus. It is assumed that this trend has fostered undergrazing of steppe grasslands as many wild ungulates are extinct and cannot fill the niche (Kamp et al., 2016). Undergrazing in turn has led to extensive wildfires that became a significant factor in steppe grasslands and shrublands after the year 2000 (Smelansky et al., 2015; Kamp et al., 2016). Many steppe species, including feathergrass (*Stipa* spp.), demoiselle crane (*Grus virgo*), and different larks (Alaudidae), benefited from this land-use change. Some others, meanwhile, faced new threats. Populations of red-cheeked sousek (*Spermophilus erythrogenys*) and sociable lapwing (*Vanellus gregarius*, critically endangered since 2004) have almost collapsed in 1990–2000s, and the steppe eagle (*Aquila nipalensis*, recognized as endangered in 2015) has declined significantly (Kamp et al., 2011, 2016; Sheldon et al., 2013; Karyakin, 2013, 2018).

The official lists of rare and endangered species of Kazakhstan include 370 species of vascular plants, three bryophyte species, one lichen species, 13 fungus species, and 224 taxa of animals, including 18 fish, three amphibian, 10 reptile, 57 bird, and 40 mammal species (128 vertebrate species in total), and 96 invertebrate species (2 annelid, 6 mollusc, 1 crustacean, 2 arachnid, and 85 insect species) (Annexes No. 5 and 6 to 2012 Government Resolution No. 1413).

In Middle Asia, grasslands and shrublands face a multitude of threats and pressures. The rise in human population and associated urban development, coupled with land conversion and organized hunting programs, lead to the extinction of keystone species, like the Caspian tiger (*Panthera tigris virgata*) and Asiatic cheetah (*Acinonyx jubatus venaticus*) in the desert lowlands. Land conversion also resulted in soil erosion and salinization, a decline of groundwater levels, and the disappearance of the Aral Sea. Rural population numbers are still high. For instance, 73.6% of the population in Tajikistan lives outside of cities (Kamoliddinov et al., 2012). Here, direct human impacts, such as overgrazing, soil erosion or failures in irrigation are major environmental threats, with 30–35% of land being extremely degraded (Safarov et al., 2014). Pressure on natural resources and human induced land cover change strongly increased in the recent past, especially after the collapse of the Soviet Union and the associated demand for fuel and agricultural products (Vanselow et al., 2012; Mislimshoeva et al., 2013; Kraudzun et al., 2014; Yu et al., 2019). In the West Pamir, for example, the number of cattle increased since 1990 (Qonunov, 2010), which resulted in overstocking and an expansion of unpalatable and harmful plants (Akhmadov et al., 2006). For the same region, Breckle and Wucherer (2006) report a human-induced decline of juniper woodland and steppes during the last decades. This trend will be intensified by climate change. For example, Seim et al. (2016) disclose that in the northern Pamir-Alai and Tian Shan mountains in Kyrgyzstan and eastern Uzbekistan increasing temperatures and changing precipitation patterns during the past eight decades led to increased drought stress in juniper trees. Several other studies discuss increased severity of weather conditions, such as erratic rainfall, or changes in the hydrology due to increased snowmelt with torrential runoff as an impact, in particular for riparian ecosystems and adjacent settlements (Narama, 2001; Breu et al., 2005; Khromova et al., 2006; Kassam, 2009; Kayumov and Rajabov, 2010). Recent persistent threats in some regions of Kazakhstan and Middle Asia encompass uncontrolled pollution by toxic waste released by industry and mining (Peterson, 1993).

Conservation, Restoration and Sustainable Management

Long before the onset of modern conservation, locals had practiced a traditional form of nature conservation in the region through assigned “kuruk” (pronounced “koorook”) areas. Until the 19th century, kuruks were public land where ordinary land use was prohibited, and grasslands reserved for occasional future needs like grazing of cavalry horses for a war campaign or mass hunting (Drobyshev, 2014; Pochekaev, 2016). Modern and science-based conservation was established in the region in the 1920s by the Soviet government (Ziegler, 1990). After their proclamation of independence at the beginning of the 1990s, all countries have maintained a system of protected areas that differ in the degree of protection, with Zapovedniks as the most strictly protected areas (IUCN category I). However, protected areas are not evenly distributed across the region, with major gaps in the western part (Bragina et al., 2018). In the steppe and forest-steppe zones of Kazakhstan the protected area network currently includes five national parks (480,644 ha in total), two strict nature reserves (Zapovedniks, 734,552 ha in total), three state nature reserves (in total 1,429,894 ha), and several wildlife sanctuaries. Most protected areas were established after the year 2000. However, although many are located in the steppe zone, only a small part of these protected areas is covered by grasslands and shrublands. Instead,

most of their area are covered by azonal forests, wetlands, sand and saline deserts, and other habitat types. In addition, vast areas of montane steppe and desert steppe in East Kazakhstan are protected through the recently established Tarbagatai National Park (143,550 ha) and Arganaty Wildlife Refuge (c. 187,000 ha).

The region comprises three World Natural Heritage Sites: Saryarka—Steppe and Lakes of Northern Kazakhstan (including Naurzum and Korgalzhyn State Nature Reserves, Kazakhstan), Western Tian Shan (a network of protected areas, including 13 in Kazakhstan, Kyrgyzstan, and Uzbekistan), and Tajik National Park (Mountains of the Pamirs) (Tajikistan). The three sites include large areas of mesic, semi-arid, and arid grasslands and shrublands.

The grasslands and shrublands of Kazakhstan and Middle Asia have not been subject to any major restoration efforts because the region still maintains relatively undisturbed ecosystems, thanks to their large area, public ownership and a traditional management regime (Fig. 2F). The collapse of agriculture in the early 1990s in Kazakhstan resulted in abandonment of approximately 12 million hectares of cropland, mainly in the steppe zone, and millions of hectares of rangelands in the both steppe and desert zones (Kamp et al., 2011). Approximately within a decade, the abandoned grasslands spontaneously restored to their optimal conditions and abandoned croplands underwent a succession to secondary steppe-like grasslands. After 2005, a significant part of the spontaneously recovered grasslands was re-plowed or returned into pastoral use. Nevertheless, vast areas of secondary and recovered grasslands and shrublands are still relatively intact.

All countries of Middle Asia have legislations for rangeland use (adopted in 2009 in Kyrgyzstan, and in 2019 in Uzbekistan) based on the principles of sustainable land-use. Although far from being perfectly implemented, this legislation provides an important framework for sustainable rangeland use in the region. Furthermore, wildlife conservation has also received increased attention. The Turkmenian kulan (*Equus hemionus kulan*) has been recently reintroduced and several efforts are being carried out in support of saiga, birds, and snow leopard conservation.

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Grasslands and Shrublands of Mongolia

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This chapter was solicited and edited by Jürgen Dengler and Péter Török on behalf of the Eurasian Dry Grassland Group (EDGG).

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Abstract

Mongolian grasslands and arid rangelands cover 80% of the country's area at an estimated 1.2 million km². They are still relatively intact, with largely natural environmental conditions and natural structure, and the country has declared >17% of its territory as conservation area. The region has an extremely continental climate with absolute temperatures fluctuating between –50 °C and +45 °C, and <350 mm rainfall per year. Botanically, Mongolia is located at the intersection between three different subkingdoms (i.e., the Boreal, Tethyan, and East Asian subkingdoms) of the Holarctic realm. Nomadic herders use these pastures since the Bronze Age and livestock grazing has been the dominant human impact in Mongolian grasslands until now, with the national herd comprising >65 Mio. animals in 2018. Overgrazing has become a major problem in parts of the steppe ecosystem, impacting fauna and flora and leading to a higher vulnerability of herds to mass mortality in harsh winters. Global warming is another major global change impact in Mongolia.

Topography, Climate and Soils

Located between the Russian Federation and the People's Republic of China in the heart of the Asian continent, land-locked Mongolia extends between the latitudes of 41°35'N and 52°09'N (1,259 km) and the longitudes of 87°44'E and 119°56'E (2,392 km). Mongolian steppes span between the Siberian taiga in the north and Gobi Desert in the south, and are part of the largest natural grassland in the world, which Mongolia hosts together with China (Pfeiffer et al., 2018). The Mongolian grasslands and arid rangelands cover 80% of the country's area at an estimated 1.2 million km² (Suttie, 2005). They lie at altitudes between 500 and 2300 m a.s.l. with an average of about 1580 m a.s.l., and comprise several types of grasslands in the main ecoregions: forest steppe, steppe and desert steppe (Table 1). The seemingly "endless" steppes of Mongolia are still relatively intact, with largely natural environmental conditions and natural structure (Batsaikhan et al., 2014). Mongolia's unique location, its pristine ecosystems, and the low population still practicing ancient traditions and the culture of nomadic livestock breeding make it a priority country for the conservation of temperate grasslands, which are at the brink of extinction in many other regions (Henwood, 1998). They are key habitats for threatened animal and plant species and for the sustainable coexistence between humans and nature (Fig. 1).

Three large mountain ranges run through the Mongolian plateau: in the west and in the south the alpine Altai Mountains with their snow-capped peaks reach >4000 m a.s.l. The Khangai Mountains are a broadly arched mountain range stretching 800 km from west to east in central Mongolia. The Khentii Mountains are smaller and lower than the other mountain ranges and extend from northeastern Mongolia to Siberia. The mountains are surrounded by vast steppes that extend into the Gobi Desert in the south, which embraces mosaic patterns of dry vegetation types.

Mongolia has an extremely continental climate with very little rainfall. The temperature fluctuations are enormous, both daily and annually. Seasons change quickly and both spring and autumn are rather short. Winters are long and last from the beginning of November to April, with absolute temperatures between –30° and –40 °C in many regions and as low as –48 °C in the mountains (Dulamsuren and Hauck, 2008). In summer absolute temperatures rise sharply and can reach over +40 °C in the South Gobi. While yearly average temperatures in the whole of Mongolia are around zero degrees, they increase along a north to south gradient e.g., from 1.1 °C in Ulaanbaatar to 4.3 °C in Dalanzadgad (South Gobi) (Pfeiffer et al., 2003).

Table 1 Ecoregions with natural grasslands of Mongolia, and their key environmental, climate and land use characteristics (median and interquartile range based on Hijmans et al. (2005)).

<i>Ecoregion</i>	<i>Forest steppes</i>	<i>Typical steppes</i>	<i>Desert steppes</i>
<i>Estimated grassland extent (Mio. km²)</i>	0.3	0.3	0.4
<i>Elevation (m a.s.l.)</i>			
Median	1850	1100	1400
25–75% quartile	1400–2300	850–1300	1150–1700
<i>Mean annual temperature (°C)</i>			
Median	–2.4	0.4	1.4
25–75% quartile	–5.1 to –0.7	–0.3–1.0	–1.8–3.3
<i>Mean annual precipitation (mm)</i>			
Median	260	220	130
25–75% quartile	200–330	190–250	110–170
<i>Mean precipitation warmest quarter (mm)</i>			
Median	170	150	90
25–75% quartile	120–220	140–180	80–110

Not listed are relatively small areas of alpine steppes in Mongolia (<0.1 Mio. km²). Based on original area estimates for TEOW (Terrestrial Ecosystems of the World Olson et al. (2001)) weighted by an estimated share of grasslands in the TEOW.

**Fig. 1** A Mongolian herder crosses the steppes in winter time. Photo by Nyamsuren Batsaikhan.

The mountain ranges of the Altai, Tien Shan, the Himalayas and the Tibetan Plateau as well as the Great Khingan shield off precipitation from west, south and east. Moisture thus comes in from the northern part of the country, which receives more rainfall (200–350 mm per year) than the central and southern areas at 100–200 and even below 100 mm, respectively. These steep gradients in precipitation and temperature shape a north to south sequence of latitudinal vegetation belts, namely tundra, taiga, forest-steppe, steppe, semi-desert and desert (Lavrenko and Karamysheva, 1993). Tree growth is restricted to the northern borders of Mongolia, and to mountain as well as water surplus areas. In the transition zone of forest steppes trees are only growing on the northern slopes where evaporation is reduced.

More than 50% of the yearly average precipitation falls in summer between early June and late August, resulting in mean monthly precipitation sums of >30 mm, which is enough to sustain grasslands, even in areas with much <150 mm rainfall per year (Pfeiffer et al., 2018). In recent years stratiform rains that provide continuous precipitation that can be absorbed by the ground and become plant available have decreased, while frequency of convective (showery) rains increased; the latter cause intense, short-lasting rainfalls with increased surface runoff and risk of erosion (Vandandorj et al., 2017). High inter-annual variability of the summer rainfall at a local scale limits the continuous use of pasture by herders, who are thus forced to movements and mobile livelihoods. From year to year, annual precipitation totals can change by 100% or more at a given site. A few dozens or hundreds of

kilometers away the situation may be completely different, prompting herders to move. Winter rainfall can fluctuate greatly as well—in extreme years cold temperatures and high snow cover, often in combination with previous summer drought and (consequential) overgrazing, can result in *dzuud*, the Mongolian word for a mass mortality of herds that can affect most of the livestock in large areas (Nandintsetseg et al., 2018b; Middleton et al., 2014).

Due to the cold continental climate and severe winters the southern border of the Siberian permafrost is running through Mongolia: 67% of its area, including most of the steppe region, is classified as permafrost area (Tumurbaatar and Mijiddorj, 2006) with continuous, discontinuous or sporadic permafrost or at least isolated patches of it. These permafrost layers are important for the preservation of local ecosystem functions, because permafrost keeps soil moisture in upper layers accessible for roots by preventing rain from seeping into deeper soil layers. In such regions, top soils remain wet even under low annual precipitation (Ishikawa et al., 2018). While current permafrost temperatures are between 0° and –1 °C, an increase in temperatures and active layer thickness has been observed in the context of global warming (Sharkhuu et al., 2008).

Long winters, high altitudes and low precipitation are impacting Mongolian soils. Soil formation in the steppes is characterized by (1) slow processes of chemical weathering and clay formation, (2) slow biological element cycling and short annual period of biological activity, (3) soil formation at mean temperatures around zero degrees, and (4) a shallow humus layer and short soil profile (Dorzgotov, 2003; Tamura et al., 2013). In congruence with the ecological zonation of Mongolia, soil distribution changes from north to south in the following order (1) cryomorphic taiga soils in the mountain taiga, (2) Chernozems, dark Kastanozems, Derno taiga soils and forest darkcolored soils in the mountain forest-steppe, (3) Kastanozems dominate in dry-steppe, (4) brown semidesert soils in semidesert, and (5) gray-brown desert soil and extra-arid desert “borzon” soils in the desert zone (Dorzgotov, 2003; Tamura et al., 2013).

Biogeography and Ecology

Flora and Typology of Communities

A total of 3127 vascular plant species belonging to 683 genera, 112 families, 39 orders and 14 classes are recognized for the flora of Mongolia (Urgamal et al., 2014).

Mongolia's vegetation is dominated by different types of steppe ecosystems, which are part of the Palaearctic steppe biome (Wesche et al., 2016). They are of natural origin and can be classified according to Dengler et al. (2014) mostly as zonal steppes and in a few cases as arctic-alpine grasslands. These steppes have been used for mobile pastoral livestock husbandry at least since the Bronze Age. The original population densities of wild herbivores are not known, but Gorshkova and Lobanova (1972) and Abaturov (2001) suggested that at moderate grazing pressure the grazed steppe grasslands might resemble the original grassland communities existing before the wild herbivores were displaced by livestock. Therefore, it can be assumed that Mongolia's steppe ecosystems belong to those ecosystems on earth which are not much affected by anthropogenic transformation into other ecosystem types, and which still exist as near-natural vegetation despite their long-standing land use history. Strongly increasing livestock numbers since the 1990s (Lkhagvadorj et al., 2013b) have resulted in local or regional overgrazing and might cause steppe vegetation to get increasingly dissimilar from its original state (Bazha et al., 2012).

Biogeographically, Mongolia is located at the intersection between three different subkingdoms (i.e., the Boreal, Tethyan, and East Asian subkingdoms) of the Holarctic realm (Kamelin, 2010). The position at this phytogeographical transition zones creates a unique and diverse flora. According to a recent phytogeographical classification by Kamelin (2010), 10 floral provinces and 23 floral districts are completely or partly located on the territory of Mongolia (Fig. 2). Different types of steppe vegetation in a broader sense occur nearly everywhere in these phytogeographical units, except for three of the provinces (i.e., the dry Dzungarian, Alashan-Ordos, and Transaltai-Beishan floral provinces) or the respective four districts (Shargyn Gobi, Nom, North Alashan Gobi, and Transaltai Gobi) that comprise desert vegetation.

The occurrence of steppe vegetation across most of Mongolia's phytogeographical districts, reflecting the wide range of climate types and soil conditions, corresponds to a high diversity of steppe formations and a considerable species turnover between the different vegetation types. The major zonal grassland types basically follow a gradient of decreasing precipitation and increasing potential evaporation from north to south, including mountain meadow and meadow steppes in the north, typical and dry steppes at intermediate positions of the gradient, and desert steppes in the south (Table 2 and Fig. 3). In addition to the zonal grassland types at medium elevation, mountain steppes and alpine steppes are found in high mountain systems (Table 2).

The most productive grassland formations are montane meadow steppes, which intermingle with forests in the forest-steppe ecotone (Fig. 3A). While the moistest sites in the forest steppe support boreal forests of Siberian larch (*Larix sibirica*) and other conifers (or birch, *Betula platyphylla* at disturbed sites), the drier parts of the landscape are dominated by meadow steppes and (at climatically and edaphically more extreme sites) mountain steppes (Dulamsuren, 2004). This setting results in a vegetation mosaic of forests on north-facing slopes and grasslands on south-facing slopes and in dry valleys (Hilbig, 1995). The plains of eastern Mongolia receive relatively high amounts precipitation and thus are covered with tall grass steppes (Fig. 3C), which is floristically different from the meadow mountain steppe of the forest-steppe ecotone. Central and western Mongolia receive less precipitation and are covered by vast grasslands of typical and dry steppes. The typical steppes mark the moister sites; therefore, the typical steppe follows the meadow and mountain meadow steppes along the moisture gradient from north to south. The dry steppes receive less precipitation and thus occur south of the typical steppe. In large typical steppe areas of eastern and central Mongolia, the feather grass *Stipa baicalensis* is dominant alone or together with *S. krylovii* (Fig. 3D). In the dry steppe, the former species increasingly loses

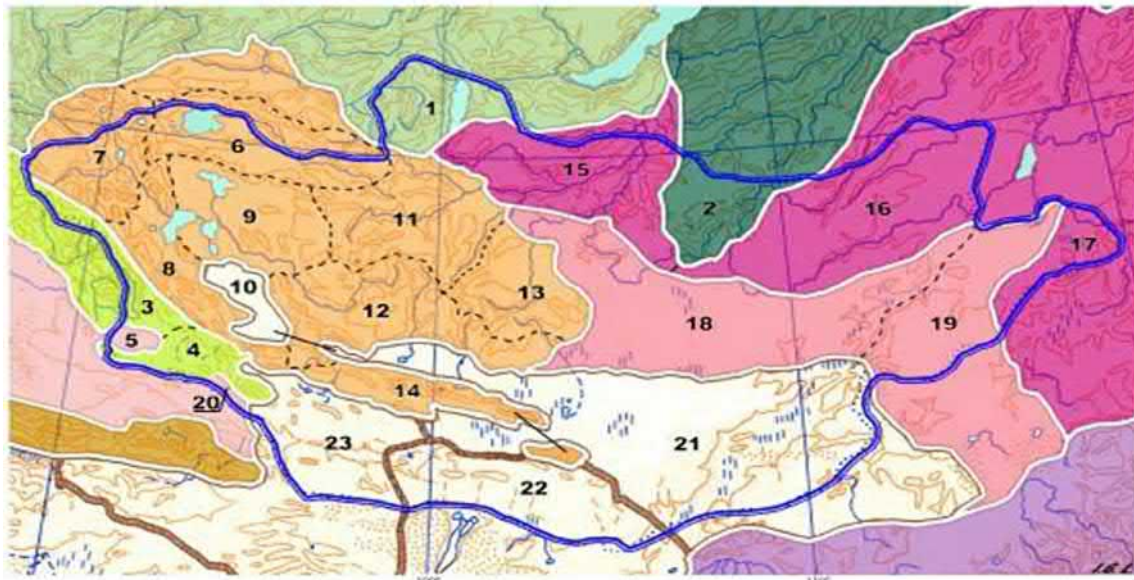


Fig. 2 Map of the phytogeographical regions of Mongolia. Holarctic realm: (I) Boreal subkingdom: *Altai-Sayan floral province* (1. Southern Sayan floral district); *Baikal-Dzhugzhur floral province* (2. Khentey floral district), (*Kazakhstan*)-*Altai-Dzhungarian floral province* (3. Dzhungaria-Altai floral district, 4. Southern Mongolian Altai floral district, 5. Barun-Khurai exclave); *Tuvanian-Mongolian floral province* (6. Ubsanuur, 7. Chui-Achit Nuur, 8. Khovd, 9. Depression of Lakes, 10. Shargyn Gobi exclave, 11. Northern Khangai, 12. Southern Khangai, 13. Eastern Khangai, 14. Gobi Altai); (II) East-Asian subkingdom: *Daurian-(Mongolian)-Manchurian floral province* (15. Selenge-Daurian floral district, 16. Onon-Kherlen-Daurian floral district, 17. Central Khingan floral district); *Khalkh-East Mongolian transitive floral province* (18. Khalkh floral district, 19. Darigang-East Mongolian floral district); (III) Tethyan subkingdom: *Dzhungarian floral province* (20. Nom floral district); *North-eastern Gobi floral province* (21. Northern Gobi floral district); *Alashan-Ordos floral province* (22. Northern Alashan-Gobi floral district); *Transaltai floral province* (23. Transaltai-Beishan floral district). Figure with permission from Kamelin, R. V. (2010). Mongolia on the map of the phytogeographical division of Palaearctics. Turczaninowia 13, 5–11, <https://creativecommons.org/licenses/by/3.0/de/deed.en>.

Table 2 Main steppe types of Mongolia and selected characteristic plant species.

Steppe type	Characteristic species
<i>Zonal vegetation of lower elevations</i>	
Meadow steppe	<i>Stipa baicalensis</i> , <i>Allium senescens</i> , <i>Filifolium sibirica</i> , <i>Stellera chamaejasme</i>
Typical steppe	<i>Leymus chinensis</i> , <i>Stipa baicalensis</i> , <i>S. krylovii</i> , <i>Agropyron cristatum</i>
Dry steppe	<i>Stipa krylovii</i> , <i>Cleistogenes squarrosa</i> , <i>Koeleria cristata</i> , <i>Carex duriuscula</i> , <i>Caragana microphylla</i> , <i>C. stenophylla</i>
Desert steppe	<i>Stipa glareosa</i> , <i>S. gobica</i> , <i>A. polyrhizum</i> , <i>A. mongolicum</i> , <i>Caragana korshinskii</i> , <i>C. pygmaea</i>
<i>Steppes of high mountains</i>	
Alpine steppe	<i>Kobresia</i> sp., <i>Carex macrogyna</i> , <i>C. stenocarpa</i> , <i>C. orbicularis</i>
Montane meadow steppe	<i>Festuca sibirica</i> , <i>Stipa sibirica</i> , <i>S. grandis</i> , <i>Koeleria macrantha</i> , <i>Carex pediformis</i> , <i>Helictotrichon schellianum</i> , <i>Thalictrum petaloideum</i>
Mountain steppe	<i>Carex korshinskyi</i> , <i>Poa attenuata</i> , <i>Festuca lenensis</i> , <i>Potentilla sericea</i> , <i>Thymus gobicus</i> , <i>Artemisia commutata</i> , <i>Alyssum lenense</i>

ground with increasing aridity, whereas *S. krylovii* and *Cleistogenes squarrosa* become dominant components of the vegetation. The dry steppes of western Mongolia share the occurrence of *Stipa krylovii* and *Cleistogenes squarrosa* with dry steppes of eastern Mongolia, but additionally comprise species with western distribution ranges, like *Stipa capillata*, *S. sareptana*, and *S. orientalis*. *Stipa klemenzi*, which is another characteristic feather grass of the dry steppes in western Mongolia, is regularly associated with shrubs of different *Caragana* species (Grubov, 1963).

Desert steppes form the transition between dry steppes and the Gobi desert. The gradient from meadow to desert steppes parallels a gradient of decreasing productivity and biomass, and is associated with an increasing share of xerophytic species in the vegetation from north to south. The desert steppes are widely dominated by *Stipa glareosa* and *S. gobica* (Tuvshintogtokh, 2014; von Wehrden et al., 2009). Mongolia's desert steppes are usually a mixture of grasslands and shrublands, including, for instance, *Artemisia xerophytica*-*Stipa glareosa* or *Caragana bungei*-*Stipa glareosa* communities in western Mongolia (Grubov, 1963). Some species of onions (*Allium mongolicum* and *A. polyrhizum*) are also characteristic members of the desert steppe flora (Fig. 3E).

The boreal floral subkingdom of the Holarctic realm occurs with four floral provinces in Mongolia. Three of them (all belonging to different floral regions) only extend with small proportions of their total areas onto Mongolia's territory; this applies to the Altai-Sayan, Baikal-Dzhugdzhur, and Altai-Dzhungar provinces (Kamelin, 2010). The dominant grassland formations of the Altai-Sayan and Baikal-Dzhugdzhur provinces include alpine steppe, montane meadow steppe and mountain steppe with continental

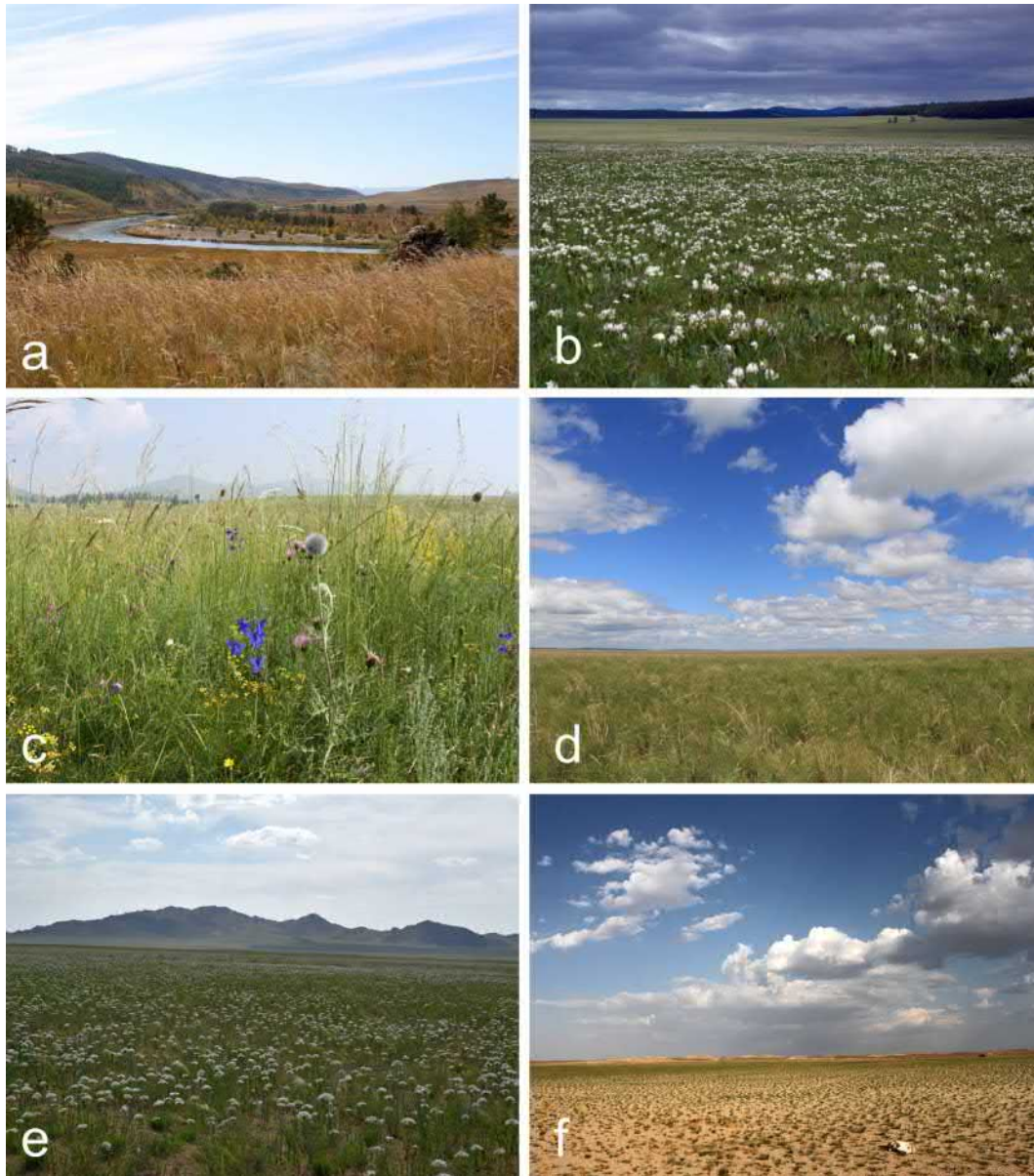


Fig. 3 Steppe types in Mongolia from north to south. (A) Forest steppe, a mosaic of forest and meadow steppe, with forests restricted to the north-facing mountain slopes, Ulaan-Azargana, Onon river. (B) *Oxytropis*-meadow steppe in the northern Mongolian Khuvsugul district. (C) Meadow steppe in eastern Mongolia. (D) Typical steppe in eastern Mongolia, with *Stipa* grasses. (E) Desert steppe with flowering *Allium*. (F) Desert steppe in Dornogovi province. Photos (A,C,D, and F) photographed by Nyamsuren Batsaikhan, photos (B and E) by Shukherdorj Baasanmunkh.

mountain and high mountain species (e.g., *Carex orbicularis*, *C. ledebouriana*, *Aster alpinus*, and *Festuca lenensis*). This floral element has strong ties to the flora of other mountain systems of the central Siberian-Dahurian flora, which includes the flora of the Altai, Sayan and the Transbaikalian mountains.

The Tuvan-Mongolian province constitutes the fourth boreal floral province of Mongolia; it is largely restricted to Mongolia's territory with only small parts extending northward into Russia in Tuva and the south-eastern part of the Russian Altai. The Tuvan-Mongolian floral province covers large parts of western Mongolia and is highly diverse from the biogeographical point of view. Floristically, the steppes of the western part of Tuvan-Mongolian floral province share the virtual lack of East Asian plant species as common character. Different types of mountain steppes are found at high elevations in both the forest steppe and the desert steppe. The flora and vegetation of these mountain steppes is further diversified by the marked elevation profiles of the Altai, Kharkhiraa, Khan-Khuhii and Khangai mountains (Beket, 2009). Alpine steppes are dominated by *Carex* and the closely related (and nowadays often included) *Kobresia* in the Tuvan-Mongolian province. In the north-westernmost part of this floral province in Mongolia, in the Mongolian Altai, the alpine steppes are more species-rich, since plant species which are more widely distributed in the Russian Altai (e.g., *Deschampsia koeleroides* and *Oxytropis altaica*) enrich the vegetation. By contrast, the mountain steppes in the

Tuvan-Mongolian province are characterized by the occurrence of species from the Tien Shan Mountains. These steppes differ in their flora from the dry steppes and desert steppes of the plains between the mountain systems. Subdominant species include the dwarf-shrubs *Anabasis brevifolia* and *Chenopodium frutescens*; the latter is subendemic to western and north-western parts of the Tuvan-Mongolian province as well as Tuva and the Russian Altai. Furthermore, numerous species of the Dzungarian-Turanian floral element occur in the Tuvan-Mongolian desert steppes, including *Carex soongorica*, *Londesia eriantha*, *Arnebia decumbens*, *Eremostachys molucelloides*, *Asperula humifusa*, and *Serratula alata* (Grubov, 1963).

In the Khangai Mountains, an altitudinal zonation of steppe types up to the alpine belt is found. Mountain steppes represent the most common grassland type of the Khangai Mountains with, for example, *Koeleria cristata*, *Festuca lenensis*, *Poa attenuata*, *Oxytropis filiformis*, *Arenaria capillaris*, and *Potentilla sericea*. The steppe flora in the eastern part of the Khangai Mountains is more strongly influenced by the central and partly even by the eastern Mongolian flora, whereas the flora of the western Khangai Mountains is more influenced by the western Mongolian flora element.

The East Asian floral subkingdom is formed by the Dahurian-Mongolian-Manchurian and the Khalkh-East Mongolian provinces. It occupies large parts of eastern Mongolia. The borders of the East Asian floral subkingdom are primarily determined by the western distribution limits of plant species with Dahurian-Mongolian-Manchurian and Dahurian-Manchurian-North Chinese distribution ranges, or more rarely by species with an East Siberian-North-East Asian distribution (Kamelin, 2010). The East Asian floral element distinguishes the Mongolian steppes from the grasslands west of the Altai in Kazakhstan, southern Russia and eastern Europe, where precipitation is more or less evenly distributed over the year. By contrast, the Mongolian climate is characterized by a marked peak of precipitation in summer. East Asian plant species are also absent from the steppes of western Mongolia as well as from the country's southern, south-western, and south-eastern desert steppe regions. In central Mongolia, the East Asian floral element is still present, but thins out westward. The restriction of the East Asian floral element to East and Central Asia, sporadically also to central and eastern Siberia, can only be explained by the seasonal precipitation patterns. The share of the summer months (June to August) in the total annual precipitation amounts to 80–95% in Mongolia east of 100°E, 35% west of 100°E in the Depression of the Great Lakes, 40–60% in the Mongolian Altai, and 25% in Dzungaria. Species with wide distribution ranges across the entire Eurasian steppe belt (e.g., *Koeleria gracilis*) need to be highly plastic to deal with the contrasting water relations in the eastern and western parts of the steppe region.

The Khalkh-East Mongolian floral province comprises the meadow steppes and typical steppes of central and eastern Mongolia and extends into north-eastern China. The flora is formed by elements of typical, dry, and desert steppes. In the East Asian floral subkingdom, the landscape is dominated by vast plains with zonal meadow, typical, and dry steppes. This contrasts with the more mountainous western and southern parts of Mongolia. Montane meadow steppes and few mountain steppes occur in the north and desert steppes in the south of this subkingdom. In the large steppe landscapes of eastern Mongolia, a sequence of different feather grasses is found along the moisture gradient from the mountain meadow and meadow steppes in the north (with *Stipa sibirica*, *S. grandis*, and *S. baicalensis*), over the typical steppe (*S. baicalensis*, *S. krylovii*) and the dry steppe (*S. krylovii*) to the desert steppe (*S. gobica*). The steppes of eastern Mongolia are characterized by the occurrence of Dahurian-Mongolian and Manchurian-Mongolian floral elements. Examples from meadow steppes for these floral elements include *Filifolium sibiricum*, *Hemerocallis minor*, *Iris dichotoma*, and *Thalictrum squarrosum* (Dmitriev and Jargalsaikhan, 2018). Usually, the vegetation of the eastern Mongolian steppes is formed by several codominant species, such as *Stipa krylovii*, *S. grandis*, *Cleistogenes squarrosa*, *Leymus chinensis*, *Poa attenuata* subsp. *botryoides*, and *Koeleria cristata* in the dry steppe (Dmitriev and Jargalsaikhan, 2018). A further characteristic feature of the eastern Mongolian steppes is the occurrence of several *Allium* species, which can reach high cover values. *Allium senescens* is typically found in meadow steppes, *A. anisopodium*, *A. ramosum* in typical and dry steppes and *A. polyrrhizum* and *A. mongolicum* in desert steppes. *Allium bidentatum* is typical of both dry and desert steppes.

The Tethyan floral subkingdom is represented in Mongolia by four provinces. Three of them, however, are only found in the Gobi Desert and lack steppe vegetation. The fourth one, the North-eastern Gobi province, is partly covered with desert steppe, which is characterized by the occurrence of *Stipa gobica*, *Allium mongolicum*, and *Asparagus gobicus*.

Apart from mere grassland communities where grasses and herbs are mixed in different ratios, shrub-rich steppe communities are a characteristic feature of Mongolia's vegetation (Yunatov, 1950; Karamysheva and Khamtsov, 1995). *Caragana* and *Artemisia* are two genera of high significance, which contribute as shrubs (*Caragana*) or dwarf shrubs (*Artemisia*) to the steppe vegetation. Mountain steppes are the habitat of *Spiraea aquilegifolia*, *Armeniaca sibirica*, *Amygdalus mongolica*, *Amygdalus pedunculata*, *Potentilla fruticosa*, *Ribes diacanthum*, *Grossularia acicularis* and species of *Rosa*, *Cotoneaster*, and *Salix*. The dwarf shrub *Artemisia frigida* is found in mountain steppes as well as typical and dry steppes. *Caragana* plays an important role in typical, dry, and desert steppes. The typical and dry steppes of central and eastern Mongolia host *Caragana microphylla* and *C. stenophylla*, which often occur as subdominant species (Ogureeva et al., 2009). Characteristic *Caragana* species of Mongolia's desert steppes include *C. leucophloea*, *C. pygmaea*, and *C. korshinskii*. Other typical shrub and half-shrubs of the desert steppe are *Anabasis brevifolia*, *Salsola passerina*, *Kalidium gracile*, and *Reaumuria soongorica*, the latter typically occurring on saline soils.

Like in other parts of the world, high livestock densities were observed to increase the shrub cover to the disadvantage of grasses and herbs (Bazha et al., 2012). The dwarf shrubs *Artemisia frigida* and *A. adamsii* are typical examples that increase in degraded steppes. Another disturbance indicator are high proportions of *Carex duriscula* in the vegetation. The share of *Allium polyrrhizum* in the vegetation has increased, whereas that of *Stipa* and other grasses has decreased in the dry steppes of southern central Mongolia as the result of increasing aridity and increased livestock densities (Gunin et al., 2010).

Mongolia's ultracontinental climate with its dry winters has no parallels with other places on earth. Therefore, neophytes only play a small role in the Mongolian flora. Even the ruderal and segetal flora is thus formed by native species (e.g., *Chenopodium album*, *Axyris hybrida*).

Fauna

Mongolia's fauna includes 138 mammal species, 417 species of resident bird, 75 fish species, 22 reptile species, 6 amphibian species, 516 mollusk species and probably over 13,000 insect species (Batbold et al., 2015, Sundev and Leahy, 2019).

Mongolian steppes, however, are dominated by large herds of domestic livestock tended by the traditional nomads (Fig. 4A). The cultural origins of dairy pastoralism in the region date back to the Late Bronze Age ~2900–3300 years ago (Orlando, 2018). Nomadic animal husbandry has been the dominant form of agriculture all over Mongolia for thousands of years, and has continued even during the age of communistic economy.

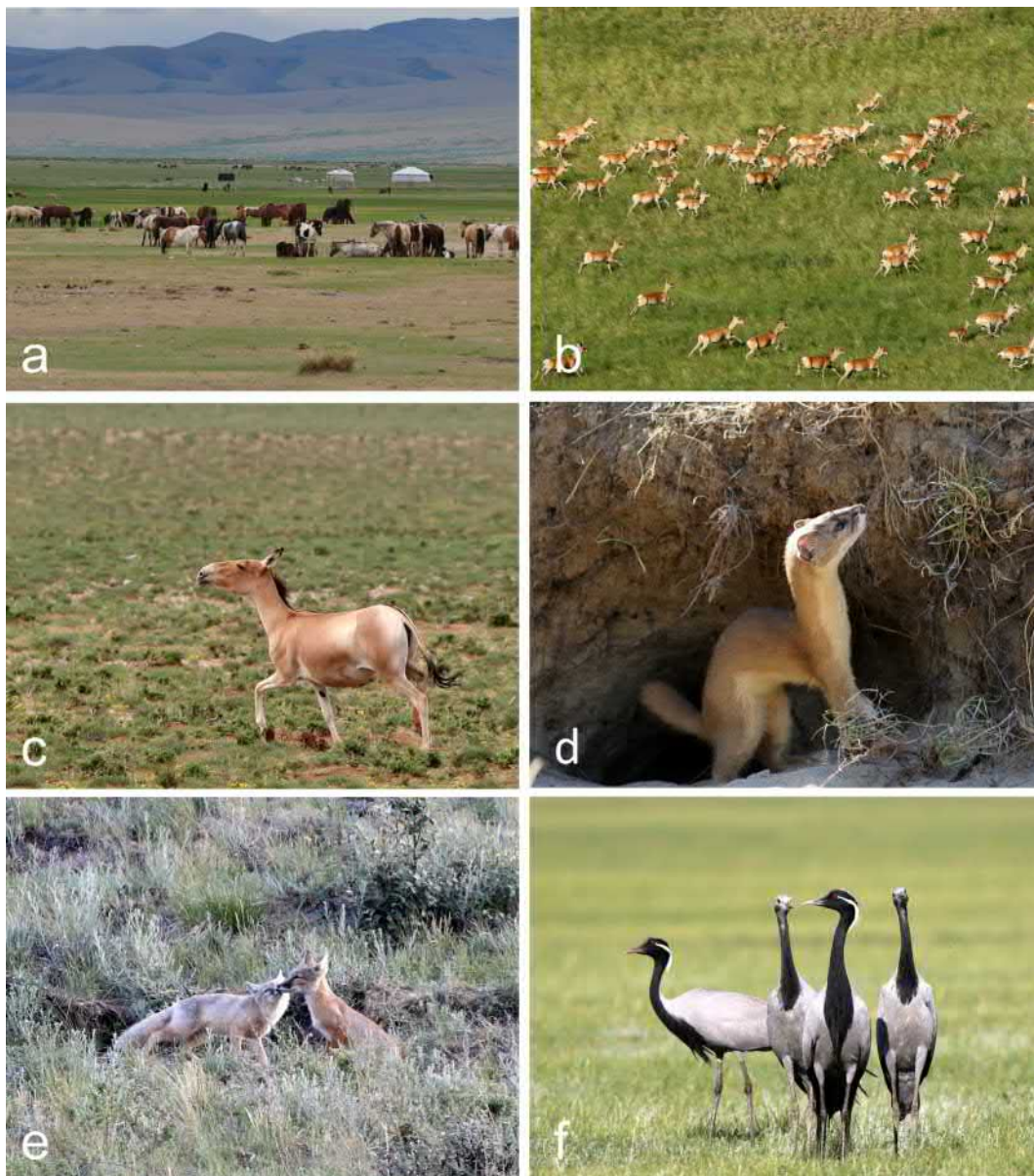


Fig. 4 Fauna of the Mongolian steppes. (A) Mongolian steppes are dominated by the herds of the nomads. (B) A herd of Mongolian gazelles roams the steppe in Toson Khulstai, northern Kherlen River basin. (C) A wild ass or khulan, in southern Mongolia. (D) A mountain weasel *Mustela altaica*—preparing to hunt small mammals, Degree River valley, eastern Mongolia. (E) Two corsac foxes *Vulpes corsac* in mountain steppe at the northern slope of Bogd Khan mountain. (F) Demoiselle cranes (*Anthropoides virgo*) are frequent inhabitants of the Mongolian steppe. Photo (A) by M. Pfeiffer, photos (B–F) by N. Batsaikhan.

Despite this immense ecological impact, steppes and rangelands of Mongolia are still home to large herds of freely migratory ungulates (Batsaikhan et al., 2014; Mallon and Jiang, 2009). Ten species or subspecies of large ungulate herbivores live in the steppes and drylands of Mongolia, many of them highly threatened (Table 3) due to hunting, habitat change and diseases.

Mongolian gazelles (*Procapra gutturosa*) are estimated at still over 1 million animals that roam through the Daurian steppe in eastern Mongolia (Fig. 4B) (Batsaikhan et al., 2014; Olson et al., 2009). The Mongolian goitered gazelle (*Gazella subgutturosa hillieriana*) is under severe pressure from poachers who wiped out all the large herds and reduced numbers by 50% (IUCN, 2017), yet large populations survived in the Gobi and in the Eastern Mongolian steppes. The Mongolian saiga (*Saiga tatarica mongolica*) underwent a harsh genetic bottleneck: only 200 individuals had been left due to poaching in 1977, but due to active conservation and favorable climate the population increased to 11,000 in 2016. However, the population declined again when the majority of the population died in an outbreak of peste de petits ruminants (PPR, or Ovine rinderpest) that struck livestock in western Mongolia. Currently, only 3750 mature individuals are left (IUCN, 2018).

The Mongolian khulan or wild ass (*Equus hemionus hemionus*), which is ranging through southern Mongolia, lost 75% of its former habitat and is nowadays mainly restricted to the most arid areas of the Gobi (Fig. 4C) (Lkhagvasuren et al., 2018). The population is viable and stable with over 40,000 mature individuals (Buuveibaatar et al., 2017; Kaczensky et al., 2015).

Przewalski's horses (*Equus przewalskii*) are related to a horse lineage herded by the eneolithic Botai culture in northern Kazakhstan about 5500 years ago (Gaunitz et al., 2018), and are only weakly related to the modern domestic horse (Gaunitz et al., 2018) that is still of unknown origin (Fages et al., 2019). They are an enigmatic species of national importance for Mongolia. In cooperation with European zoos, *E. przewalskii* has been reintroduced to the steppes since 1992 after almost 50 years of being extinct in the wild, and still occurs only as managed populations in conservation areas (Kaczensky et al., 2003).

The argali (*Ovis ammon*), the mountain sheep, is confined to steep, jagged habitats, similar to the Siberian ibex (*Capra sibirica*), a wild goat inhabiting arid mountain areas over 1000 m a.s.l. The lower mountain forest steppe is home to red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*).

Burrowing small mammals are keystone species in the Mongolian grasslands with a remarkably species diversity and abundance (Fig. 4D) (Samiya and Mühlenberg, 2006). Many species, e.g., the lagomorph pikas (*Ochotona pallasi*), are eco-engineers that increase the diversity and heterogeneity of their habitats and impact ecosystem services, e.g., by improvement of water drainage and soil fertility, establishment of new habitats for plants and provision of dens and prey for other animals (Wesche et al., 2007). Burrowing species are also most of the 64 species of rodents that are documented for Mongolia (Batsaikhan et al., 2010). These include ground squirrels (*Spermophilus* spp.), chipmunks (*Tamias* spp.), zokors (*Myospalax* spp.), hamsters (*Phodopus* spp.), dwarf hamsters (*Cricetulus* spp.), marmots, lemmings and voles that all are abundant in the grasslands. Being exceptional in that sense, most species of gerbils (*Meriones* spp.) and jerboas (*Allactaga* spp.) prefer more arid areas. The Siberian marmot (*Marmota sibirica*) is a widespread dweller in steppe, although its conservation status is "endangered" as marmots are hunted for their meat and fur, despite their status as nationally protected. Marmot burrows are often also used by corsac foxes that take advantage from the burrowing activities of these large rodents (Murdoch et al., 2009). Together with a variety of small mammals, marmots represent natural reservoirs for the plague, a vector-borne disease caused by the Gram-negative bacterium *Yersinia pestis* that is transmitted by fleas to local hunters. The main vector is the marmot flea (*Oropsylla silantiewi*), causing yearly outbreaks of the disease in rural Mongolia (Galdan et al., 2010).

Some rodents, such as the Brandt's vole (*Lasiopodomys brandti*), undergo extreme population fluctuations and can compete with livestock for food at high densities. Their cyclical rapid population growth, which increases pasture degradation, is often triggered by overgrazing (Zhang et al., 2003).

The top predators in the Mongolian steppes are wolf (*Canis lupus*), Eurasian lynx (*Lynx lynx*), bear (*Ursus* spp.) and snow leopard (*Panthera uncia*), all of them are endangered by (illegal) hunting. Especially wolves and snow leopard are under pressure as their attacks on livestock can cause considerable economical losses to herder communities and often result in reactive or preventive killing (Mijiddorj et al., 2018). Red fox (*Vulpes vulpes*) and Corsac fox (*Vulpes corsac*), as well as martens (*Martes* spp.) and other Mustelidae are among the small carnivores of the grasslands (Fig. 4E).

Table 3 Main species of wild ungulates in Mongolian steppes and arid lands, and their regional Red List status (species level) according to IUCN (2016, 2017, 2018).

Species	Scientific name	Family	Regional Red List status
Siberian Ibex	<i>Capra sibirica</i> (Pallas, 1776)	Bovidae	Least Concern (LC)
Mongolian Goitered Gazelle	<i>Gazella subgutturosa hillieriana</i> Heude, 1894	Bovidae	Vulnerable (VU)
Altai Argali	<i>Ovis ammon ammon</i> (Linnaeus, 1758)	Bovidae	Near Threatened (NT)
Gobi Argali	<i>Ovis ammon darwini</i> Przewalski, 1883	Bovidae	Near Threatened (NT)
Mongolian Gazelle	<i>Procapra gutturosa</i> (Pallas, 1777)	Bovidae	Least Concern (LC)
Mongolian Saiga	<i>Saiga borealis mongolica</i> Bannikov, 1946	Bovidae	Endangered (EN)
Red Deer	<i>Cervus elaphus</i> Linnaeus, 1758	Cervidae	Least Concern (LC)
Przewalski's Horse	<i>Equus (equus) przewalskii</i> Poliakov, 1881	Equidae	Endangered (EN)
Mongolian Kulan	<i>Equus (asinus) hemionus hemionus</i> Pallas, 1775	Equidae	Near Threatened (NT)
Wild Boar	<i>Sus scrofa nigripes</i> Blanford, 1875	Suidae	Near Threatened (NT)

Birds of prey also benefit from the abundant rodents in the steppes (Gombobaatar et al., 2009); these include upland buzzard (*Buteo hemilasius*), steppe eagle (*Aquila nipalensis*), common kestrel (*Falco tinnunculus*) and saker falcon (*Falco cherrug*), as well as owls (*Athene* spp., *Asio* spp.). Lacking roosting or perching sites in steppe areas force raptors to utilize electricity distribution pole lines, resulting in high electrocution risk (Ganbold et al., 2018). Black vultures (*Aegypius monachus*) feed on carrion of wild and native ungulates. A famous group of steppe birds are cranes (*Grus* spp.; Fig. 4F) and pheasants, as well as larks (Alaudidae) that have a high species richness and abundance in steppe environments (Wesche et al., 2016). In spring and autumn, a rich diversity of migrant birds crosses the steppes. The Mongolian bird fauna, including all residents, migrants, and vagrants, comprises 503 species (Sundev and Leahy, 2019) with diversity peaking in forest steppe and around the great lakes that are internationally important wetlands protecting threatened species and migratory waterfowls (e.g., the white-headed duck *Oxyura leucocephala*) (Sundev and Leahy, 2019).

Amphibians are rare in the steppes due to the dry climate; only six species of two orders are known for the country. They distribute along open waters and are under pressure due to the drying of surface water points (Terbish et al., 2013). Four of these species are listed as vulnerable in the red list, e.g., the Siberian salamander (*Salamandrella keyserlingii*) (Batbold et al., 2014). Two species of snakes, namely Halys (Pit) viper (*Gloydius halys*) and steppe's rat snake (*Elaphe dione*) are widely distributed over Mongolia, while *Vipera* species are mainly restricted to the mountain areas. Generally, reptiles are more common in the Gobi area.

Mongolia's steppe zone comprises a variety of lakes and rivers that include some of the least impacted freshwater ecosystems on the planet (Karthe et al., 2017). They are home to a rich fish fauna including the Siberian taimen (*Hucho taimen*), the sharp-snouted lenok (*Brachymystax lenok*), and the Baikal grayling (*Thymallus baicalensis*). These species live in sympatry throughout the country's two major river basins and are targets of a quickly growing recreational fishery (Kaus et al., 2019).

Mongolia is home to a rich insect fauna (Bayartogtokh et al., 2016). Ants (Formicinae) are abundant everywhere and important as predators and eco-engineers (Bayartogtokh et al., 2014; Pfeiffer et al., 2003). Darkling beetles (Tenebrionidae) are exceptional rich in species and well adapted to the dry climate; their radiation is strongly shaped by the steep climate gradient that provides a north-south zonation for this thermophilic taxon (Paknia et al., 2013). Copronecrophagous dung beetles (Scarabaeinae) are essential for the recycling of cattle droppings and expanded their populations in response to livestock domestication in Mongolia, as demonstrated for the telecoprid beetle *Gymnopleurus mopsus* (Kang et al., 2018). Overgrazing by cattle can impact diversity and species composition of invertebrate herbivores, e.g. moths, that compete with vertebrate grazers (Enkhtur et al., 2017). Similarly, fly communities change in their species composition and decrease in diversity in response to overgrazing (Clement et al., 2018).

Bacteria

A recent study on diversity of soil bacteria in the semi-arid steppe region of central Mongolia yield highly diverse bacterial communities dominated by the phyla or classes Bacteroidetes, Acidobacteria, Alphaproteobacteria, and others (Kim et al., 2013). Diversity in this study was closely linked to soil texture and was—presumably due to extreme climatic conditions—much higher than the diversity of comparative samples from tropical Malaysia.

Threats of Changing Land Use and Climate

Nomadic pastoralism has been the by far most important form of land use over millennia, and has changed remarkably little up to the present. Meat and milk have always been provided by sheep, goat and cattle in the moister parts, and by yaks in the cooler regions, while camel and horses have been the main animals kept for transport until very recently. Typically, herders have moved several times per year in search of fresh forage, and only winter camps were used for longer periods of time (Lkhagvadorj et al., 2013b). There were modifications to this basic scheme (Fernández-Giménez, 1999), and the advent of socialist economy resulted in herds becoming state-owned. The rangelands, in contrast, have never been under formal ownerships of private households. Livelihoods did not change fundamentally, and livestock numbers have also been stable over most of the 20th century, fluctuating between 20 and 30 million animals from the 1920s to the 1990s (Lkhagvadorj et al., 2013b). Livestock numbers varied in response to droughts and snow disasters.

In 1992, after the breakdown of socialism, livestock was privatized and since then the number of domestic animals in Mongolia has more than doubled. It was almost 66.5 million by 2018 (National Statistics Office of Mongolia, <https://www.en.nso.mn/>), including 30.5 million sheep, 27 million goats, 4.3 million cattle, 3.9 million horses and about 460.000 camels. Growth was brought about by a two to threefold increase in small livestock sheep and cashmere goats (von Wehrden et al., 2015), the latter reared for the international market. Numbers of larger livestock were stable, camels did even decline, but taken together, animal numbers converted to the standard Mongolian livestock units rose from 80 Mio. in the 1990s to over 120 Mio. today (Pfeiffer et al., 2018).

Recent rates of change were, however, very uneven across the country, and were also accompanied by changes in livelihoods. Herds increasingly concentrate in the central parts of the country around the major cities, especially Ulaanbaatar. There, but also elsewhere in the country mobility declined, with herders staying more and longer near larger settlements or at other sites with favorable infrastructure (Fernández-Giménez et al., 2017). In consequence, rangelands are increasingly degraded in the central parts of the country (Bazha et al., 2012; Hilker et al., 2014) and overgrazing has become a major problem, leading to a higher vulnerability of herds to mass mortality during dzuud (Nandintsetseg et al., 2018a) and impacting fauna and flora (Oyuntsetseg

et al., 2019). For other, especially the drier parts of the country, resampling studies and grazing experiments show mixed results with respect to grazing degradation in steppes (Khishigbayar et al., 2015; Wesche et al., 2010). Based on monitoring data collected at 1516 long-term monitoring sites all over Mongolia in 2016, about 42% of the sites were non-degraded, 14% slightly degraded, 21% moderately degraded, 13% heavily degraded and 10% in fully degraded state, while the degree of degradation of the two most heavily degraded levels has increased since 2014 by about 4% and 6%, respectively (Densambuu et al., 2018).

In comparison to grazing, other land use types have more spatially limited effects. Arable farming is practiced on <1% of the area (John et al., 2018). After large-scale fallowing in the 1990s, farming has now intensified again, but that still remains on a low level with basically local effects.

In terms of total land directly affected, large-scale mining is at a similar order of magnitude as arable farming. Effects of resource extraction extend, however, far beyond the extraction sites (Batbayar et al., 2015). In addition to mining areas, oil fields cover increasingly large regions, especially in the east. Apart from direct impact, the associated infrastructural development, especially with respect to development of traffic lines, dissects and thus affects huge parts of the steppe (Batsaikhan et al., 2014). Effects are even more pronounced as proper road infrastructure is still missing in most parts of Mongolia, where mainly unpaved roads interconnect the country. Increasing traffic, open terrain and communal land tenure have created a web of dirt track corridors, sometimes up to 4 km width, concentrating around the villages and river crossings (Keshkamat et al., 2013). Dirt tracks promote desertification by impacting plant life, facilitating erosion, soil compaction and increasing water run off; heavy dust problems may occur in mining areas with intensive traffic (Jackson, 2015). Fragmentation is the key problem here, as roads and railroads as well as settlement building have already disrupted migration patterns of Eastern Mongolia's remaining large gazelle herds (Olson et al., 2011) and wild asses (Ito et al., 2013).

Fragmentation thus adds to the direct pressure exerted by livestock herding. The high dietary diversity of sheep and goats and their overlap with wild species (Retzer et al., 2006) render increasing livestock numbers a potential risk for the survival of wild ungulates (Sugimoto et al., 2018). Recent land use changes thus have started to affect the Mongolian steppes. Not surprisingly, effects differ across the vast and environmentally heterogeneous rangelands. Grazing, as the spatially most relevant impact, interacts with climate (Liu et al., 2013), and grazing effects tend to be more pronounced in moister and thus more productive regions (Khishigbayar et al., 2015; Wesche et al., 2010). In that sense, climate change may not only have direct effects, but also indirect effects via land use change.

Climate is the overwhelmingly dominant control over most of Mongolia's ecosystems, and thus ecosystems are particularly sensitive to climate change. The highly continental climate results in relatively rapid changes, which have immediate effects on the "open-air" land use system of nomadic pastoralism (Lkhagvadorj et al., 2013a). The vulnerability of pastoralism is aggravated by the lack of stables and the scarcity of external forages sources such as hay or concentrated feed. Global warming is more intensive in Mongolia than in many other parts of the world, with the annual average temperature having increased by 2.2 °C (or 0.3 °C decade⁻¹) between 1940 and 2008 (Batbold et al., 2014). Rise of air temperature in the permafrost region in Mongolia from 1901 to 2014 has been higher than in other permafrost regions of the world, with a trend of 0.18 °C decade⁻¹, while in the period 1979–2014 temperatures rose even at a rate of 0.31 °C decade⁻¹ (Guo et al., 2018). These results have been corroborated by extensive tree ring analyses, which suggest that warming in the recent years exceeds any other time since 931 C.E. (Davi et al., 2015). Strongly rising temperatures affect permafrost and glaciers in Mongolia (Walther et al., 2017). Glacier area has decreased by 28% in the past 70 years, snowmelt occurs around 1 month earlier, and evaporation of surface water has increased largely (Batbold et al., 2014). Moreover, climate change has led to reductions in the productivity, vitality and regeneration of conifers and birch trees in Mongolia's boreal forests, which occur in close neighborhood to steppe grasslands in the forest steppe (Dulamsuren et al., 2010a,b; Liu et al., 2013; Khansaritoreh et al., 2017). Increasing dryness may also increase the probability of wild fires that impact forests and grassland, especially in eastern Mongolia (Nasanbat and Lkhamjav, 2016).

The high natural variability of precipitation in both space and time renders analysis of trends difficult, because potential long-term changes at scales of mm year⁻¹ are dwarfed by interannual variability (Pfeiffer et al., 2018). This makes statistical derivation of trends very difficult and for many stations no clear trend is discernible. Geographical factors such as the pronounced relief make modeling of large-scale climate a difficult task, and climate models show limited congruence with respect to future changes. Moreover, timing of precipitation in terms of seasonality is even more difficult to model, yet is crucial for ecosystem functioning. Shifts in the onset of precipitation can have direct effects on growing season length, and several authors described a shift from summer to spring or winter precipitation (Dagvadorj et al., 2009). Whether this will result in increased snow cover and more frequent Dzuud disasters (Middleton et al., 2014), or in higher moisture availability in spring and thus longer growing season is not clear yet. Even the locally apparent trend towards fewer but more intense rain events (Nandintsetseg and Shinoda, 2013) may prove beneficial for the drier grasslands, that often benefit less from modest rain events with respect to productivity (Heisler-White et al., 2009) or recruitment (Gunin et al., 2003; Ronnenberg et al., 2008).

Net effects of climate change are thus not easily derived and will certainly differ across the vast and diverse region of Mongolia. Aridity indices showed a decreasing tendency for the period of 1961–2015, especially in central and north east Mongolia (Nyamtseren et al., 2018; Batbold et al., 2014; Tao et al., 2015). While Mongolia has a very low number of river stations, river discharge showed a sharp decreasing trend at all stations since 1995 (Dorjsuren et al., 2018). As mining operations in Mongolia are increasing, especially underground water use is likely to increase. Similarly, the ever-growing number of livestock adds pressure on water resources.

Attributed to climate change 551 rivers, 483 lakes and 1587 springs/wells dried up in 2011 (Batbold et al., 2014). However, given the high intra-annual and interannual variations in precipitation in arid areas, long term data were needed to draw reliable

conclusions and to avoid misinterpretation of seasonal changes. Based on all available Landsat images of the Mongolian plateau from 1991 to 2017, a recent study revealed a significant decrease in area and numbers of lakes $>1 \text{ km}^2$ until 2009, followed by a partly recovery until 2013 and a further decrease in current years (Zhou et al., 2019). Rising grazing intensity could be identified as a driver of lake shrinkage in Mongolia in the first period ($r^2 = 0.45$), while rainfall had a positive effect on lake numbers and area in the second period. Altogether between 1991 and 2013 lake numbers decreased from 338 to 257 and total area of lakes $>1 \text{ km}^2$ decreased by 355 km^2 (2.6%). (Zhou et al., 2019). Earlier studies corroborated the total decline of lakes on the Mongolian plateau (Tao et al., 2015; Zhang et al., 2017).

Remote sensing studies on primary productivity are not fully conclusive. A decrease in NDVI due to decreasing precipitation and increase of temperature has been reported for the period from 1982 to 2016 (Filei et al., 2018), yet a number of previous studies showed high spatial differences or failed to find evidence for widespread decline of plant productivity (Sternberg et al., 2015; Fernández-Giménez et al., 2017).

Conservation, Restoration and Sustainable Management

In terms of sheer numbers, Mongolia perhaps has of the most well developed system of protected areas across the Eurasian steppes. The country prides itself to host one of the oldest reserves of all, the Bogd Uul range south of Ulaanbaatar being essentially in place since the late 18th century (Banzragch, 1998). After large scale gazetting in the last two decades, there are currently 99 special state protected areas covering $272,000 \text{ km}^2$ area or 17.4% of Mongolia's territory, including important steppe areas. Besides the state protected areas, there are 911 locally protected areas altogether occupying 10.3% of total territory (Batbold et al., 2015). Hustai National Park hosts the world's most viable populations of wild horses and is a role model in terms of conservation effectiveness, mediation of land use conflicts and ecotourism development (Wit and Vegten, 1998; Tserendulam et al., 2018). Formerly neglected, the Ikh Nart reserve in southeastern Mongolia has also become a well functioning reserve (Reading et al., 2016). Most other parks are far less effective, partly owing to their sheer size with reserves like Great Gobi A or Gobi Gurvan Saykhan covering $25,000 \text{ km}^2$ or even more. Many of these larger reserves are, however, situated in the country's drylands, where climate constraints limit human impact and result in relatively pristine dry steppes still occurring.

Given that larger-scale degradation is a relatively recent phenomenon in Mongolia, steppe restoration has so far not been a major topic. While the literature on grassland and dryland restoration in China is vast (e.g., Akiyama and Kawamura, 2007; Hao et al., 2014), specific restoration studies on Mongolia are lacking. There are, however, studies on population ecology of key plant species that are relevant in this context. Reproduction and germination ecology have been studied for keystone feather grass species of steppes and desert steppes in Mongolia (Ronnenberg et al., 2008, 2011). Persistence is mainly by vegetative tillering within grass bunches, while reseeding is rare and takes place in exceptional years with e.g., high-intensity rainfall events. On average, seedling establishment occurs at intervals of some decades in key grasses, and may even need centuries in woody chenopods such as saxaul (Gunin et al., 2003). Annual species germinate more easily (Ronnenberg et al., 2007; Wesche et al., 2006) and similar experiences have been made in neighboring China (Akiyama and Kawamura, 2007). Yet, the overwhelming number of key species in intact steppes is perennial, and prospects for restoration of natural vegetation types are thus at best uncertain. Clearly, restoration should be an ultimate response only, and the focus should lie on sustainable management preventing degradation and destruction of habitats.

Improved grazing management may be a pathway for recovery of highly degraded pastures. Since 2011 Mongolian government, NGOs, herders and local authorities cooperate to implement a new comprehensive approach called *resilience-based rangeland management* in order to sustain rangeland health (Densambuu et al., 2018). A nationwide network of 1516 long-term monitoring sites and 4200 photo monitoring sites has been established for rangeland assessment according to core indicators (biomass, plant height, species composition, etc.). A central database serves as platform for decision making on rotational grazing, fodder preparation, animal breeding, animal health and quality management as well as product marketing. By 2018, $>15,000$ herder families using 16 million hectare pasture land have already been organized in 740 Pasture User Groups (PUGs) by the condition of Rangeland Use Agreements (RUAs) that enforce community-led grazing schedules and herd management plans, including stocking rates adjustments (Densambuu et al., 2018). They agree to achieve a resilient carrying capacity of the grasslands and a sustainable pastoral production that is needed for food security in Mongolia and the future of its nomadic lifestyles under climate change conditions.

Acknowledgments

We thank Dr. Sci. O.P. Kamelina for her permission to use a map from an article by her late husband Rudolf Vladimirovich Kamelin. We thank Mr. Batsaikhan, N. senior lecturer at the Department of Biology, School of Arts and Sciences, National University of Mongolia, Mongolia, and Mr. Baasanmunkh, Sh. Ph.D. student at the Department of Biology & Chemistry, Changwon National University in South Korea for providing photographs for this book chapter.

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Grasslands of China

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This chapter was solicited and edited by Jürgen Dengler and Péter Török on behalf of the Eurasian Dry Grassland Group (EDGG).

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Abstract

The grasslands in China cover 3.26 million km², 86% of which are the “Northern Grasslands” in the Palearctic realm, occurring primarily on the (Inner) Mongolia Plateau, the Loess Plateau and the Tibetan Plateau, and in the within-desert mountain areas in northwestern China. Vast steppes, including meadow steppes, typical steppes, desert steppes and alpine steppes, as well as alpine meadows are the zonal grassland types. Typical meadows and marshy meadows occur in azonal and extrazonal habitats on mountains and lowlands, and secondary grasslands grow in relatively humid areas in both temperate and tropical regions. The Northern Grasslands are rich in plant species and host large herds of emblematic freely migrating ungulates. These grasslands are predominantly in intact natural conditions. Grassland regions represent not only rangelands or pastures for animal production, but also are “green barriers” and “water towers,” critically important for the ecological security of Asia. These grasslands are under the threats of increasingly strong human activities such as overgrazing, conversion, collecting, hunting, open pit mining, development of infrastructures (fences, traffic lines), grassland fragmentation, as well as climate change. Distinguishing between the main grassland regions, implementing different land-use policies in these regions, and increasing the mobility and flexibility of wildlife and livestock are keys for the conservation and sustainable use of these grasslands.

Delimitation and Physiogeography

The temperate grasslands on the Eurasian continent are characterized by a vast range, mainly extending across longitudes from west to east. There is, however, a southwesterly turn at the eastern end in China. The conspicuous turning starts at the southern edge of the Mongolian Plateau and extends across the entire Loess Plateau and throughout the Qinghai-Tibet (QT) Plateau, spanning 23.8 degrees of latitude from 28° to 51.8°N (Li et al., 1980a). The hydrothermal conditions within the range of temperate grasslands in China are semi-arid to semi-humid, as the changes in thermal and moisture conditions imposed by the southward shifts are counteracted largely by the rise in relief. The temperate grassland region in China is divided into two distinct biogeographic regions, that is, the temperate steppe region and the alpine vegetation region (Wu, 1980). The temperate steppe region encompasses the large continuous blocks of the Song-Liao Plains (mostly between 120 and 500 m a.s.l.) in northeastern China, the Inner Mongolian Plateau and the Loess Plateau (mostly between 800 and 2000 m a.s.l.) in northern China, and the extensive mountain areas (mostly between 600 and 2200 m a.s.l.) in northwestern China. The alpine vegetation region mainly occupies the QT Plateau with an altitude mostly above 4000 m a.s.l. (Li et al., 1980a) (Fig. 1).

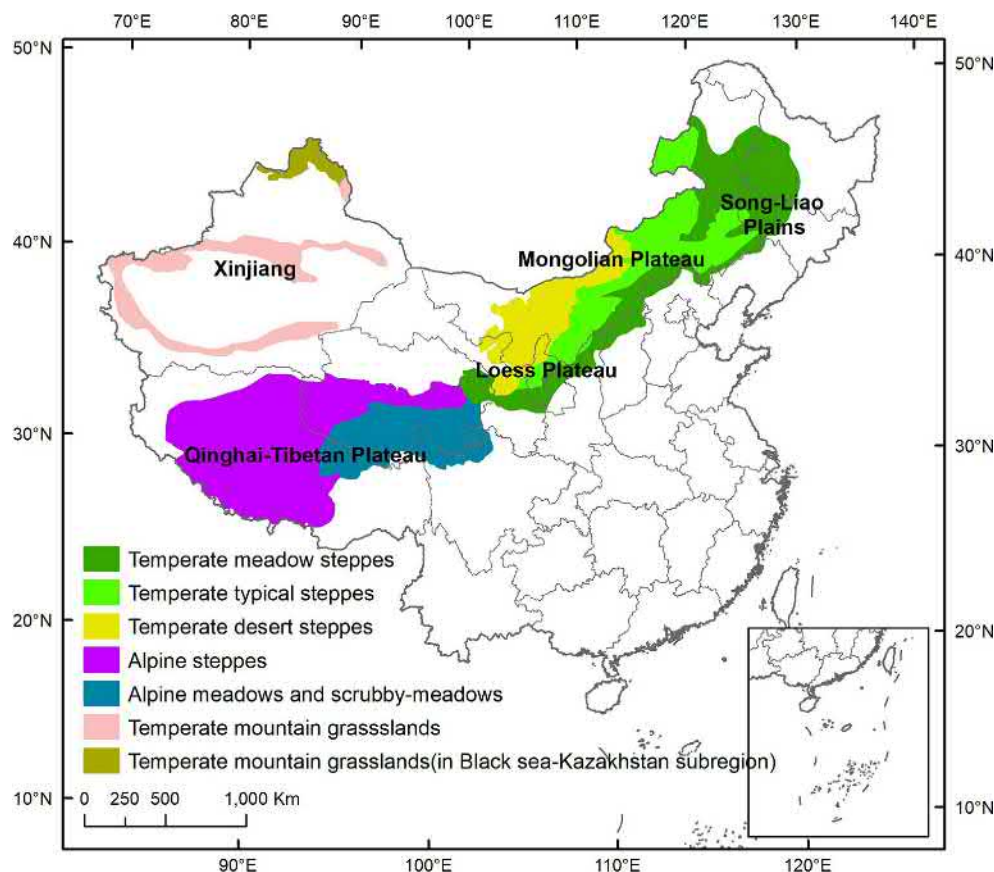


Fig. 1 Grassland biomes in China, derived primarily from “Vegetation Regionalization Map of China (1:6,000,000)” (Zhang, 2007). The zones marked as temperate mountain grasslands are actually vegetation complex with various steppes and meadows in different elevation zones, and admixed with other vegetation types. The grasslands with small or noncontinuous distribution areas, either steppes or meadows in mountainous areas or low lands, or secondary grasslands in forest regions are not shown.

The eastern Eurasian steppe region is primarily controlled by the Mongolian high-pressure anticyclone system during the winter, thus being cold, dry and windy. Yet, these steppes are also influenced by the southeasterly maritime monsoonal system in summer, when conditions are warm and relatively humid. The mean annual temperature ranges from -3 to 5°C depending on locality, with the coldest and warmest month means from -7 to -29°C (January) and 18 to 26°C (July), respectively. The annual precipitation varies mostly between 200 and 500 mm; inter-annual variability is pronounced, and about 70% of rains fall in the plant growing season, beneficial to plant growth (Li et al., 1980b). Temperate grassland soils are of several types (Li et al., 1980b). The black soil, Chernozem soil, Chestnut soil and brown soil are sequentially distributed along a gradient of increasing climatic aridity from south-east to northwest on the Inner Mongolian Plateau, or on the mountains from low to high altitudes in the arid regions in Xinjiang. The black soil occurs mainly in the piedmont hilly plains, being rich in organic matter, and has a pH of 5.6 – 6.6 but no calcium accumulation, and supports forb meadows. The Chernozem, Chestnut and brown soils have a pH ranging from 7.5 to 9.5 , an organic matter content from 6% to 1% in top soil layer, and calcium accumulation at depths from 70 to 25 cm in soil profile. These are soils support meadow steppes, typical steppes and desert steppes (Li et al., 1980b).

The alpine steppes and meadows occur dominantly on the QT Plateau, which is under a typical plateau continental climate characterized by humid summers controlled by the South Asian and East Asian monsoons and cold and dry winters influenced by the Westerlies and the Siberian High (An et al., 2001). Patterns in mean annual temperatures are more directly controlled by topography; most areas have an annual mean from -5.8 to 3.7°C , and the means of the coldest and warmest months range from -17 to -8.0°C and 5.5 to 13.6°C , respectively. The alpine grasslands include the vast continuous steppes in the north and the west, and the meadows or scrubby meadows in the south and the east, reflecting a decreasing precipitation gradient from southeast (above 400 mm) to northwest (below 100 mm; Wang et al., 1980a). The water systems on the QT Plateau comprise both exterior and interior ones. Exterior rivers are primarily in the wide marginal areas, being the headwater and upper reaches of several big rivers in China and Southern Asia, such as Yangtze River, Yellow River, Lancang River (Mekong River in Southeast Asia), Yarlung Zangbo River (Brahmaputra-Jamuna Rivers in India and Bangladesh) and Gar Zangbo River (Indus River in Kashmir and Pakistan). The interior rivers flow into lakes of various sizes in the central part of the QT Plateau, most of which are salty due to the intense water evaporation under the arid continental climate. Alpine steppe soils are variants of the temperate steppe soils on the

Inner Mongolian Plateau, having developed under cold conditions from a high diversity and variety of substrates and associated geomorphologic processes. Leptic Cambisols and Leptosols occur mainly on steep upper slopes, while Gleysols are often found close to rivers or lakes. Alpine meadow soils are mainly Gelic Gleysols, Gelic Cambisols and Permagelic/Gelic Histosols (Baumann et al., 2009). They are rich in organic matter and their surface layer is full of compact root networks resulting in a high resilience against mechanical disturbance.

The Chinese grasslands in the Palearctic realm cover 2.82 million km², including temperate steppes at 0.75 million km², alpine steppes at 0.58 million km² and alpine meadows at 0.64 million km². Mountain and lowland meadows extent over 0.42 million km², secondary grasslands over 0.18 million km², and other scattered grasslands over 0.25 million km² in azonal and extrazonal habitats (Ministry of Agriculture, 2006). The grasslands in southern China cover 0.45 million km² including small areas of savanna. The grassland distribution is well presented in the vegetation map of China (Edition Board of Vegetation Map of China, 2007) and the maps of the Terrestrial Ecoregions of the World (TEOW; Olson et al., 2001; Pfeiffer et al., 2018).

Biogeography and Ecology

The temperate steppe region in China, along with that of Mongolia, constitutes the eastern most part of the Eurasian steppe zono-biome, and the majority of the steppe region belongs to the Central Asian steppe subzonobiome (Li et al., 1980a). However, the most northwestern part of the steppe region in the western Altay Mts. and the Tarbagatay Mts. as well as their piedmont sloping plains, is delimited as a separate “Western steppe sub-region” in “Vegetation Regions of China” (Li et al., 1980a), and considered as the easternmost part of the Black Sea-Kazakhstan steppe subzonobiome, as the steppes in this sub-region contain characteristic species of Kazakh steppes, such as *Stipa sareptana* and *S. kirghisarum*. The grasslands on the QT Plateau, including alpine steppes and meadows, are delimited as one alpine vegetation region (Wang et al., 1980a). The alpine steppes are distributed across the larger part of the QT Plateau, and are connected to the steppes on the Loess Plateau and the Mongolian Plateau, whereas the alpine meadows occur mainly on the southeastern parts, typically above 4000 m a.s.l.

Flora

Incomplete statistics show that some 4100 vascular plants can be found in the temperate steppe region, which are affiliated to ca. 800 genera and 140 families (Li, 1995). Phytogeographically, the region belongs to the Tethys Sea floristic realm (Wu and Wang, 1983; Li, 1995). The Central Asian steppe species, especially the Mongolian ones, are most prevalent in the flora, especially in the typical and desert steppes. The meadow steppes in the Northeast China plains also have many temperate Asian species.

The QT Plateau vegetation region has a very rich, diverse and often endemic flora. It comprises species of Central Asian (semi-) deserts, as well as temperate East Asian and Himalayan elements. The dominant herbaceous species are not typically grasses, but are frequently sedges of genera *Kobresia* and *Carex*, especially in alpine and subalpine meadows. Recent studies (Global Carex Group, 2015) suggest that the genus *Kobresia* should be included into *Carex*, but here we still keep the traditional nomenclature to allow comparison to most of the relevant literature. A total of 5766 plant species have been documented for the Tibetan Autonomous Region (Wu, 1983; Li, 1995). More than 2000 of these species are recorded for the grassland region, of which 86% are forage plants and occur mainly in the humid and sub-humid pastures of eastern Tibet, while 540 species occur in the arid and semi-arid rangelands (Gu, 2000). The flora of alpine steppes consists of Eurasian steppe species (*Festuca kryloviana*, *F. pseudovina*, *Stipa glareosa*, *S. krylovii*, *S. bungaena*), as well as Central Asian alpine (*S. subsessiliflora*), Pamir-QT Plateau (*S. purpurea*, *S. roborowskyi*, *F. olgae*, *Carex moorcroftii*), and QT Plateau endemics (*S. subsessiliflora* var. *basiplumosa*, *S. capillacea*; Wang et al., 1980a).

Fauna

The faunal diversity in the temperate grassland region in China (and Mongolia) was recently reviewed by Pfeiffer et al. (2018). The temperate steppes and arid lands in Inner Mongolia, QT Plateau and Xinjiang host large herds of freely migrating ungulates (Mallon and Jiang, 2009), including 12 species of large herbivores, emblematic of different rangeland systems in the region (Fig. 2). Mongolian gazelle (*Procapra gutturosa*), Mongolian Saiga (*Saiga tatarica mongolica*), goitered gazelle (*Gazella subgutturosa*), Mongolian argali (*Ovis ammon*), Asian wild ass (*Equus hemionus*), Asiatic ibex (*Capra sibirica*), wild camel (*Camelus ferus*), and Przewalski's horse (*Equus przewalskii*) occur mostly on the temperate steppes and nearby arid lands. Several unique mammals are found in Tibetan steppes, such as Tibetan antelope (*Pantholops hodgsonii*), Tibetan gazelle (*Procapra picticaudata*), Przewalski's gazelle (*Procapra przewalskii*), Tibetan wild ass (*Equus kiang*) and wild yak (*Bos mutus*). Some species prefer mountain habitats, e.g., white-lipped deer (*Cervus albir-ostriis*), blue sheep (*Pseudois nayaaur*) and Tibetan argali (*Ovis ammon hodgsoni*). The majority of these ungulates are threatened migratory species. Przewalski's horses have recently been reintroduced in Xinjiang after they had been extinct in the wild for decades (Mallon and Jiang, 2009; Pfeiffer et al., 2018).

Small herbivorous mammals on the steppes include marmots (*Marmota bobak*), ground squirrels (*Spermophilus* spp.), hares (*Lepus* spp.), plateau pikas (*Ochotona* spp.), voles (*Microtus* spp.) and Zokors (*Myospalax baileyi*). The burrowing of these herbivores has profound effects on the patterns and processes of grassland ecosystems (Wesche et al., 2007). Small carnivores include Tibetan steppe foxes (*Vulpes ferrilata*), red foxes (*Vulpes vulpes*), martens (*Martes* spp.), while the top predators are wolves (*Canis lupus*), lynx (*Lynx lynx*), bears (*Ursus* spp.) and snow leopards (*Panthera uncia*) (Pfeiffer et al., 2018).



Fig. 2 Typical wild animals on Tibetan grasslands. (A) Tibetan wild ass (*Equus kiang*); (B) Tibetan steppe fox (*Vulpes ferrilata*); (C) Tibetan gazelle (*Procapra picticaudata*); (D) Tibetan antelope (*Pantholops hodgsonii*); (E) black-necked crane (*Grus nigricollis*); and (F) Plateau pika (*Ochotona curzoniae*). Photos credit: J. Schmidt and Huaben Duo.

Steppe eagles (*Aquila nipalensis*) and Saker falcons (*Falco cherrug*) are threatened avian raptors, while Cinereous vultures (*Aegypius monachus*) live on carrion of ungulates on the steppes. Larks (*Alaudidae* spp.) are the dominant birds with high species richness and abundance (Wesche et al., 2016). Other bird species include upland buzzards (*Buteo hemilasius*), goshawks (*Accipiter gentilis*), black kites (*Milvus migrans*) and some waterfowl, such as black-necked cranes (*Grus nigricollis*), bar-headed geese (*Anser indicus*) and ruddy shelducks (*Tadorna ferruginea*). The steppes are also rich in invertebrates including grasshoppers (*Orthoptera*), moths and butterflies (*Lepidoptera*), ants (*Formicinae*), and ground-dwelling beetles (*Coleoptera*), which play an important role in grassland ecosystem functioning (Pfeiffer et al., 2018).

Origin of the Grasslands

Much of the contemporary natural grassland region in China was covered by subtropical forests and savanna woodlands during the Tertiary period. The grasslands formed as a consequence of the region getting drier with the uplift of the QT Plateau since the Tertiary, especially after the repeated glacial periods in the Quaternary, during which the region became progressively arid and continental (Dinesman et al., 1989; Pfeiffer et al., 2018). This led to the gradual development of xerophilous steppes replacing the former mesophilous vegetation. Thus, the flora is relatively young in the region, though certain older relict species can still be found (Li et al., 1980a).

The extensive natural steppes and high-altitude grasslands have been grazed over evolutionary time-scales as proven by the rich native grassland fauna. Human land use dates back to the early Holocene, when hunter-gatherers roamed the grassland region. Nomadic pastoralism has expanded on the Mongolian Plateau since the Bronze Age, yet livestock keeping left major imprints on the dry steppes of the Mongolian Plateau not earlier than 900–600 years ago (Dinesman et al., 1989; Pfeiffer et al., 2018). The impact of human activities has dramatically increased over the last decades; some temperate meadows or steppe meadows have been converted into cultivated lands (Wu et al., 2015), and some grazing land has been seriously degraded. Yet, the temperate steppes are still in relatively intact conditions.

The evolutionary history of biodiversity and endemism on the QT Plateau is still under debate, depending on differing hypotheses on highland uplift and climate history. Similarly, the history and intensity of human impact on Tibetan grasslands are under discussion based on evidence from diverse disciplines (Miehe et al., 2019). The most recent proposal suggests that long-term

residential groups of hunters, probably early pastoralists, had settled in this region between 8 and 5 ka BP, which is supported by genomic evidence from yak domestication (Qiu et al., 2015). However, as a consequence of increased animal husbandry and fires, forests had undoubtedly disappeared although the climate conditions were relatively favorable for their development.

Typology of Plant Communities

The natural grasslands in China are classified into temperate grasslands, including temperate steppes and meadows, and alpine grasslands including alpine steppes and meadows (Wu, 1980; Guo et al., 2018). There are also secondary grasslands in the humid and semi-humid temperate regions, and secondary grasslands and savannas in the humid or dry tropical and subtropical regions. We present mainly the temperate and alpine grasslands of the Palearctic realm in this article, but also briefly describe those of tropical and subtropical regions.

The temperate steppes (Fig. 3) include meadow steppes, typical steppes and desert steppes, which are mainly distributed on the Inner Mongolian Plateau and the northern and western part of the Loess Plateau spreading from east to west along a gradient of climatic aridity, and on the uplifted zones on the within-desert mountains in Xinjiang region. Alpine steppes are found mostly on the QT Plateau (Li et al., 1980b; Sun, 2005; Kang et al., 2007).

Meadow steppes occur on relatively moist and fertile sites among the temperate grassland habitat, typically in areas with annual precipitation around 450 mm and soils of high organic content. The dominant species are mostly mesoxerophilous, xeromesophilous or pan-xerophilous (i.e., adapted to a relatively moist part of dry habitats, or relatively dry condition of medium moist habitats, or a wide range of dry habitats), including the bunchgrasses *Stipa baicalensis*, *S. kirghisorum*, *Cleistogenes mucronata*, *Bothriochloa ischaemum*, *Pennisetum flaccidum*; the rhizomatous grasses *Leymus chinensis* and *L. angustus*; and forbs such as *Filifolium sibiricum*. Meadow steppes usually lack dwarf semi-shrub species.



Fig. 3 Main grassland types on the Mongolian Plateau. (A) desert steppe dominated by *Stipa klemenzii*; (B) typical steppe dominated by *Stipa krylovii*; (C) typical steppe dominated by *Stipa grandis*; (D) meadow steppe dominated by *Leymus chinensis* and *Achnatherum sibiricum*; (E) meadow steppe dominated by *Leymus chinensis* with diverse forbs (*Iris dichotoma* in the front); (F) meadows dominated by *Sanguisorba officinalis* and *Bromus inermis*; (G) Przewalski's horses reintroduced on the steppe; (H) a pastoral household on the steppe; (I) degraded grassland dominated by *Artemisia frigida* and *Potentilla acaulis*. The photos (A)–(F) were taken along a climate gradient from dry to humid regions; and photos (G)–(I) were taken in the typical steppe region. Photo credit: F.Y. Li.

Typical steppes occur under a semi-arid climate with annual precipitation around 350 mm. Plant species are typically drought-tolerant. The most common communities are dominated by bunchgrasses such as *Stipa grandis*, *S. krylovii*, *S. bungeana*, *S. capillata*, *Festuca sulcata*, *F. ovina*, *Cleistogenes squarrosa*, *Agropyron cristatum*, *Koeleria cristata*, *Poa botryoides* and *Aristida trisetia*, and semi-shrubs and dwarf semi-shrubs, such as *Artemisia frigida* and *Thymus mongolicus*.

Desert steppes occur under the most arid and continental climate, with annual precipitation between 150 and 250 mm. The species are predominantly strongly xerophilous grasses, usually accompanied by super-xerophilous dwarf semi-shrubs in large numbers. The common dominant species include the bunchgrasses *Stipa klemenzi*, *S. gobica*, *S. breviflora*, *S. glareosa*, *S. orientalis*, *S. caucasica*, *Cleistogenes songorica*, rhizomatous forbs like *Allium polyrrhizum*, and the dwarf semi-shrubs *Ajanina achilloides*, *Hippolytia trifida* and *Artemisia dalailamae*.

Alpine steppes are mostly found at elevation between 3300 and 5300 m a.s.l. on the QT Plateau. The common dominant species are extremely cold- and drought-tolerant grasses and dwarf shrubs, with a more or less pronounced admixture of cushion plants. The dominants include locally distributed species such as *Stipa subsessiliflora* var. *basiplumosa*, *S. roborowskyi*, *Festuca olgae*, *Carex moorcroftii*, *Orinus thoroldii* and *O. kokonorica* and *Artemisia salsoloides* var. *wellbyi*; yet there also are common plants of Eurasian steppes such as *Festuca kryloviana* and *F. pseudovina*.

Meadows in classic European understanding are agriculturally managed grasslands regularly mown for livestock forage (UNESCO classification; Ellenberg and Mueller-Dombois, 1965/1966). In China, meadow refers to natural grasslands primarily composed of mesophilous perennial herbs that thrive under moderate moisture conditions. The meadows naturally occupy vast continuous areas with moderate moisture conditions that derive from atmospheric precipitation, and with relatively low temperature that limits the growth of trees, such as alpine meadows on the QT Plateau. However, in most other cases meadows are azonal, occurring in the montane, alpine, plain and coastal areas of the temperate zones, with moisture originating from groundwater, runoff, or melted snow and ice; these meadows are classified into typical, marshy and salt meadows, based on the ecological traits of their constituent species, that is, the dominance of mesophilous, xero-mesophilous, hygro-mesophilous or halo-mesophilous species in their composition (Wang et al., 1980a, b).

Alpine meadows occur mainly on the eastern QT Plateau (Fig. 4) and in part on the high mountains of northwestern China and northern China, under an alpine cold climate with intermediate humidity, adequate sunshine, intense solar radiance, and strong

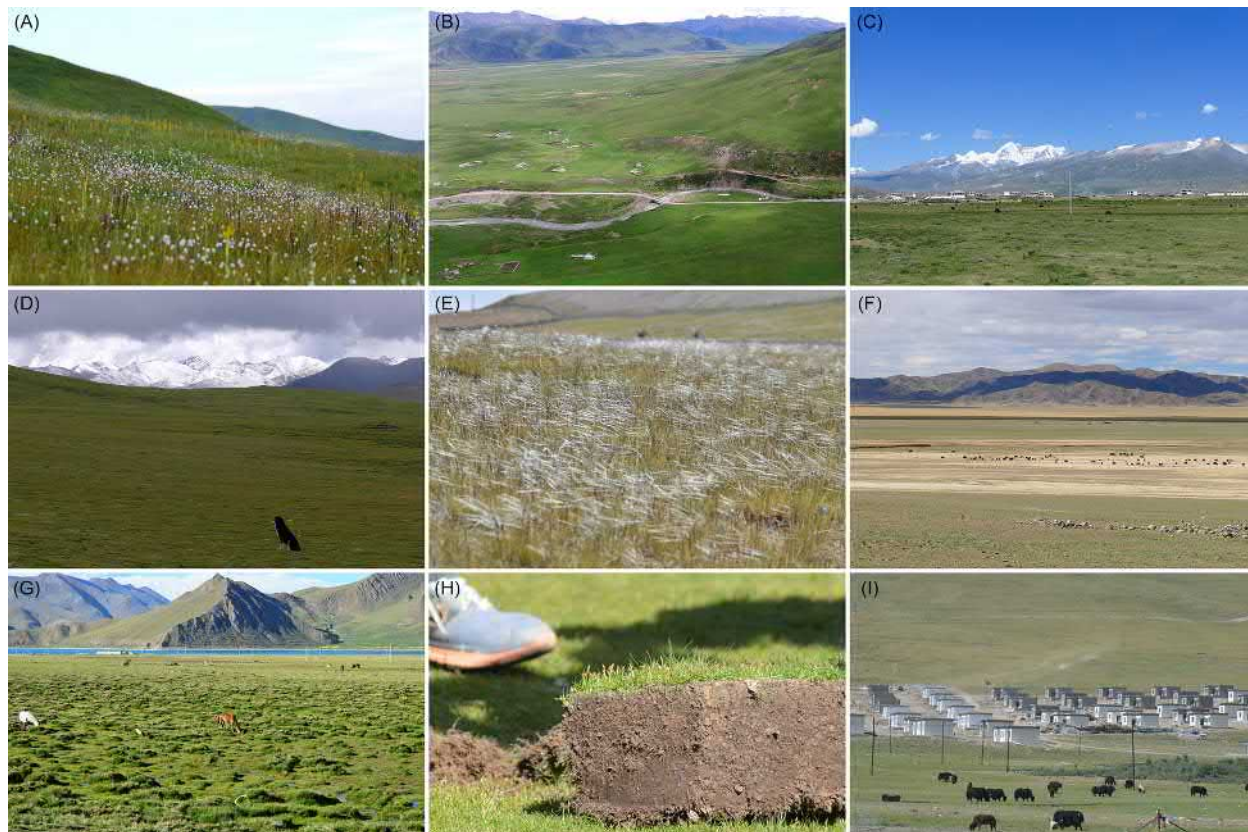


Fig. 4 Main grassland types on the QT Plateau. (A) moist alpine meadows dominated by *Kobresia setschwanensis* and *Polygonum macrophyllum* (the white flowers) in Maqu, Gansu province; (B) winter pastures dominated by *K. royleana* and *K. pygmaea* in Yushu, Qinghai province; (C) moist alpine meadows in Dangxiong, central Tibet; (D) alpine meadows dominated by *K. pygmaea* in Namco, central Tibet; (E) alpine steppe dominated by *Stipa purpurea* in Qumahe, Qinghai province; (F) alpine steppe dominated by *Orinus thoroldii* in Gaize, western Tibet; (G) alpine marshy meadow dominated by *K. schoenoides* in Linzhou, eastern Tibet; (H) large root/shoot ratio from *K. pygmaea* turf; (I) newly built winter settlements from sedentarization project in Qinghai province. Photo credit: Y. Jäschke.

winds. Here the word “alpine” does not strictly refer to mountain climate, which is not warm enough to allow for tree growth, but only indicates high-elevation distribution. Alpine meadow soils are shaped by intense sod-forming processes during pedogenesis, and are characterized by the occurrence of semi-decomposed residual turf, closely-interwoven root mats, and a poorly-intermingled humus layer. The *Kobresia* alpine meadows are the most typical and most widespread of the alpine meadows in China. *Kobresia* species are both mesophilous and cold- and drought-tolerant. There are about 40 *Kobresia* species, dominant ones include *K. pygmaea*, *K. humilis*, *K. capillifolia*, *K. graminifolia*, *K. setchuanensis*, *K. prattii*, *K. royleana*, *K. smirnovii* and *K. bellardii*. There are also alpine meadows dominated by typical sedges such as *Carex scabriostriis*, *Blysmus sinocompressus*, bunchgrasses such as *Festuca ovina*, *Poa alpina*, *Anthoxanthum odoratum*, and forbs such as *Polygonum viviparum*, *P. sphaerostachyum*, *Ligularia virgaurea* and *Alchemilla japonica*.

Typical meadows occur mainly in the temperate forest and steppe regions, and on the high mountains of the desert and subtropical forest regions. They are particularly abundant in ecotone areas from the forest to the steppe regions, or in subalpine belts of high mountains, usually in or above the forest belt and on black soils. They are primarily dependent on precipitation, and dominated by mesophilous forbs. Typical meadows also occur at low-lying sites of valleys and river plains that are controlled by groundwater and dominated by grasses. The dominant meadow species include forbs *Sanguisorba officinalis*, *Phlomis alpina*, *Iris ruthenica*, *Medicago falcata*, *Melilotus albus* and *Trifolium repens*; the rhizomatous grasses *Calamagrostis epigejos*, *Bromus inermis*, *Brachypodium* spp., *Hierochloa glabra*, *Agrostis mongolicus*, *A. alba*, and *Elytrigia repens*; the bunchgrasses *Dactylis glomerata*, *Trisetum sibiricum*, *Deyeuxia arundinacea* and *Elymus nutans*; and the sedge *Carex stenophylla*.

Marshy meadows are primarily composed of hygrophilous herbs and have transitional characteristics between a typical meadow and a marsh. Their occurrence is generally associated with high soil moisture regulated by special topographic factors, most often at poorly drained sites, thus with humid and poorly-aerated soil. The existence of a permafrost layer is also a major cause for association of humid soil conditions and marshy meadows, such as on the QT Plateau. Massive layers of humus and even peat or a semi-peat layer accumulate in soils of marshy meadows due to slow decomposition of plant residuals. Examples of alpine marshy meadows include those dominated by *Kobresia tibetica* along streams or waterlogged areas over permafrost in the catchments of the Yellow River, Yangtze, Mekong and Salween. *Kobresia schoenoides* is, however, dominant along the Yarlung Zangbo River. *Carex schmidtii* or *Sanguisorba parviflora* dominate at the river flats adjacent to forest stands in Hinggan Mts.

Saline meadows are mainly composed of mesic perennial halophytes, that is, salt-tolerant or otherwise adapted species, and occur on salinized low-lying sites, wide valleys, fringes of lake basins and river flats within steppe and desert regions. Most widely distributed saline meadows include those dominated by *Achnatherum splendens*, *Leymus dasystachys*, *Phragmites communis*, *Sophora alopecuroides*, *Crypsis aculeata* and *Suaeda* spp.

Secondary grasslands occur mainly in warmer, southern or south-eastern forest regions. They are in the serial succession stages of original forest vegetation under disturbance, such as the temperate grasslands dominated by *Bothriochloa ischaemum* and *Themeda japonica*, with or without admixtures of shrubs such as *Vitex negundo* var. *heterophylla* or *Ziziphus jujuba* in northern China, and the tropical and subtropical grasslands dominated by *Miscanthus sinensis* in southern China.

Savannas in tropical and subtropical China are primarily confined to the dry and hot valleys in Yunnan province where the *Heteropogon contortus*, *Woodfordia fruticosa* and the *Bombax malabarica* community occur, to the seashores of Guangdong province, and on the basaltic plain in the northern portion of the Hainan Island, such as the *Heteropogon contortus*, *Flacourtia indica* and *Streblus asper* community. The savannas are mostly secondary in nature, thus having a noncontinuous, scattered distribution range.

Biodiversity Patterns

The temperate steppes border with the Gobi deserts at the dry end, and the temperate forests at the humid end. The steppe plants, especially dominant *Stipa* species, have xeric structural traits such as reduced leaf area, leaf involution, stomatal subsidence, and well-developed root system. Many plants (e.g., *Stipa*, *Festuca* and *Allium*) form dense clumps with shoot bases being thickly clothed by persistent dead leaf sheaths to avoid overheating of the ground in summer and to protect regenerative buds in winter (Li et al., 1980b).

Plant species richness and biomass production increases with the climatic humidity from desert steppes via typical steppes to meadow steppes (Li et al., 1994; Bai et al., 2009). The species density surveyed using nested quadrats increases from 8 species on 1 m², 12 species on 16 m² and 16 species on 256 m² in desert steppe sites with precipitation around 150 mm, via 14 species on 1 m², 21 species on 16 m² and 29 species on 256 m² in typical steppe sites with precipitation around 350 mm, to 20 species on 1 m², 32 species on 16 m² and 42 species on 256 m² at meadow steppe sites with precipitation around 500 mm (Fig. 5A). The density recorded in these 1-m² quadrats is similar to that reported by Ma and Fang (2006) for the Inner Mongolian steppes, that is, 10 (range 4–23), 12 (5–25) and 20 (10–35) species on 1 m² for desert steppes, typical steppes and meadow steppes, respectively based on a survey at 207 sites. The ecological turnover of steppe species of the same genera is very pronounced along the climate gradient, especially for the genera *Stipa* (Fig. 5B), *Astragalus* and *Caragana*, and the same holds true for *Kobresia* species (Zhang et al., 1995).

The species richness of alpine, semi-arid steppes is similar to that of temperate, semi-arid steppes. Alpine meadows are generally more diverse than steppes, having 45, 35 and 23 species in average for the communities dominated *Kobresia pygmaea*, *K. humilis* and *K. tibetica* (marshy), respectively, recorded in 20 quadrats of 0.5 m² in a survey at representative sites of these alpine meadows in the northeastern QT Plateau (Wang et al., 1999).

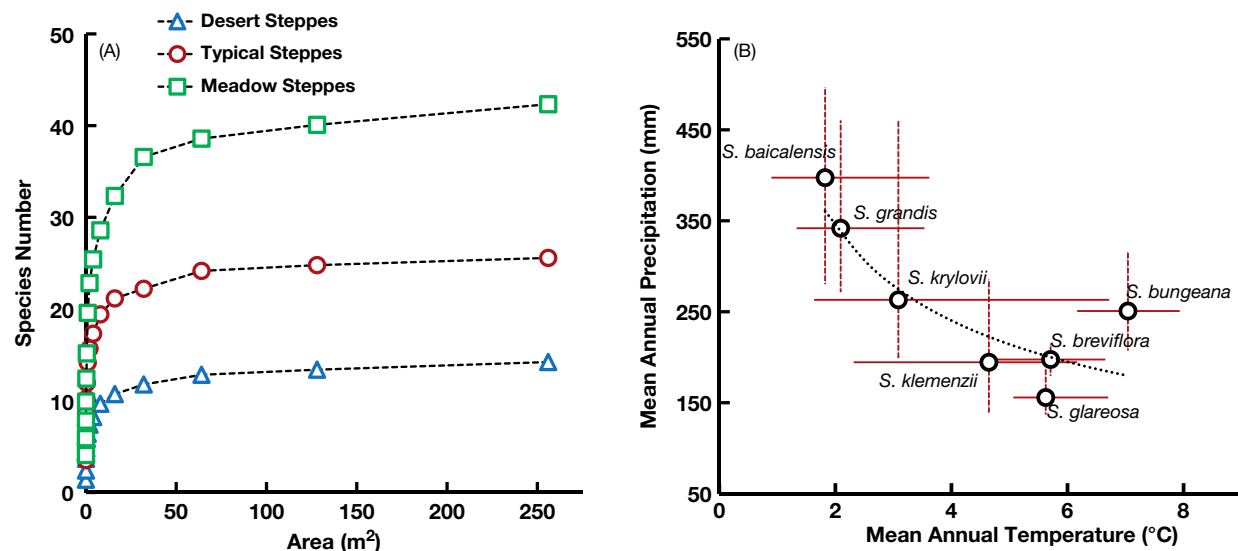


Fig. 5 (A) Species density of desert steppes, typical steppes and meadow steppes recorded using nested quadrats of 0.125 to 256 m². The values are the averages of 18, 18 and 13 nested quadrats respectively for the desert steppes, typical steppes and meadow steppes. (B) Substitution of *Stipa* species along the temperature-precipitation gradient (the means and ranges of temperature and precipitation of their distribution sites surveyed) on the Mongolian Plateau. Original Data of F.Y. Li.

Ecosystem Services and Threats

The temperate and alpine grasslands in China are still relatively intact in structure. The grassland ecosystems have been traditionally used as grazing land by nomadic herders for animal production. Regulating ecological services such as prevention of wind erosion and sand fixation, conservation of water and soil resources, carbon sequestration, biodiversity conservation, as well as cultural services such as ecotourism, have received increasingly attention during the past three decades. The temperate steppe regions in Inner Mongolia and Xinjiang are recognized as a major “green barrier” for ecological security, with major importance for prevention of wind erosion and reduction of dust storms in northern China. The alpine grassland region on the QT Plateau is another “green barrier” for ecological security of China. The area in the eastern part of the QT Plateau harbors the headwaters of three major rivers (Yellow, Yangzi, and Lancang) in Asia, and is considered as the Asian “water tower.” The Three River Headwater National Park, with an area of 123,100 km², has been gazetted for conservation purpose (NDFC [National Development and Reform Commission of China], 2018). Ecological health of these grassland ecosystems is critically important not only for a sustainable pastoral society in these regions but also for the ecological security of whole China and beyond. The shift of the grassland administration from the Ministry of Agriculture to the National Forestry and Grassland Ministration (under the Ministry of Natural Resources) in 2018 also indicates a shift of the government’s primary goal for grassland management, from animal husbandry production to ecological services. The total values of ecosystem products and services for human welfare and sustainable development, in terms of Global Ecosystem Products (GEP), has been crudely estimated in China (Ouyang et al., 2016). A recent estimate of the GEP for Inner Mongolia suggests that only 7% of its total GEP is from product provision, and 76% is from ecological regulation (Inner Mongolia Academy of Agriculture and Animal Husbandry, unpublished report, 2019), indicating the important role of grasslands in terms of ecological services. New estimates based on an intensive field survey shows that the grasslands in China contains 25.4 Pg C, representing 28.3% of the total carbon pool in China’s terrestrial ecosystems (Tang et al., 2018). Another estimate suggests that about half of the grassland carbon pool in China is in alpine grasslands (Schleuss et al., 2015). However, a series of inappropriate human activities and climate change is exerting great threats to the grasslands.

Overgrazing

The grasslands have been traditionally used as grazing land by nomadic herders. Land use has significantly changed since the 1950s through a series of government policies, including collectivization of land and livestock in 1950s and decollectivization in 1980s (*Household responsibility system*), a shift from nomadic to sedentary systems, and an increase in human population and associated livestock numbers (Thwaites et al., 1998; Ptackova, 2011; Hua and Squires, 2015; Wu et al., 2015; Li and Li, 2016). The social change induced overgrazing and, less importantly, over-mowing (Li et al., 2008; Harris, 2010; Baoyin et al., 2014), at least locally resulting in serious grassland degradation. Estimates show that about 47% of grassland areas are severely to moderately degraded in China (State Environmental Protection Administration, 2000). Grassland degradation leads to declines in plant species diversity, productivity and soil carbon storage (Li et al., 2008; Zhao et al., 2017). The current stocking rates on the Inner Mongolia grasslands are estimated to exceed its carrying capacity by 3.2 times (Briske et al., 2015). On the QT Plateau, although grasslands are also

considered widely degraded by overgrazing (most frequently quoted number is 30% of grassland estimated to be degraded), the extent and causes of degradation are still under debate (Harris, 2010). A summary of a larger number of case studies across Chinese grasslands suggests that locally increased grazing intensity indeed has negative effects on vegetation cover and aboveground biomass, but does not necessarily reduce plant species richness, while effects on soil conditions vary also among grassland types and are site-dependent (Fig. 6, Wang and Wesche, 2016). The nonconsistent grazing effects reflect abiotic interactions, particularly with precipitation. In semi-humid alpine meadows, grazing effects on vegetation are more obvious than in semi-arid steppes (Wang et al., 2017, 2018). This suggests that managing stocking rates is important in relatively stable alpine meadow systems, while developing management regimes adaptive to the highly variable environment is more important in the steppes that represent examples of nonequilibrium systems.

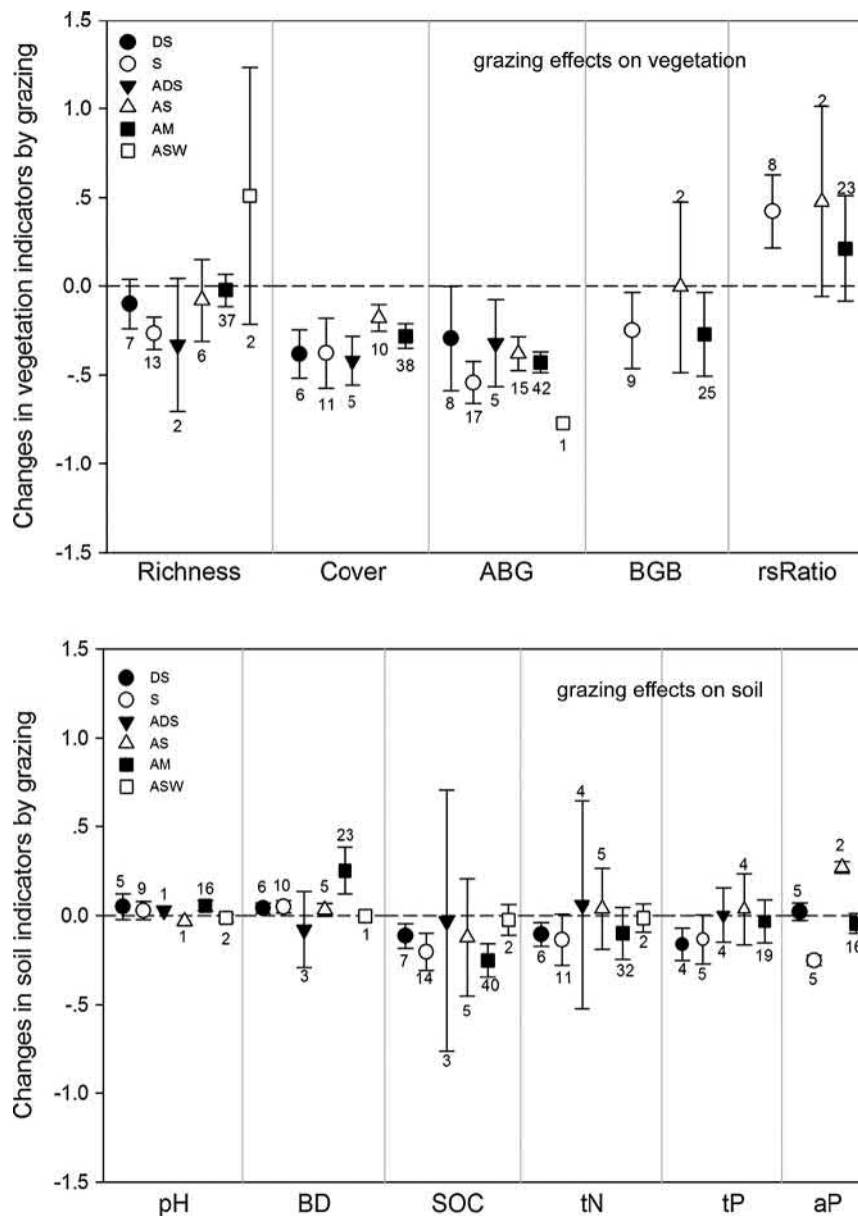


Fig. 6 Relative grazing effects on (A) vegetation, (B) soil indicators from different grassland types based on available studies across Chinese grasslands between 2000 and 2014 (Wang and Wesche, 2016). Error bars indicate standard deviation and numbers close to the error bars represent sample sizes. Abbreviations for grassland types: DS, desert steppe; S, steppe; ADS, alpine desert steppe; AS, alpine steppe; AM, alpine meadow; AS, alpine swamp. Abbreviation for the indicators: AGB, aboveground biomass; BGB, belowground biomass; rsRatio, root/shoot ratio; BD, soil bulk density; SOC, soil organic carbon; tN, soil total nitrogen; tP, soil total phosphorus; aP, plant available phosphorus in soils.

Land conversion

Conversion of grasslands into arable lands for crop or forage production is limited to meadow and meadow steppe areas. More than 10% of grasslands are estimated to be converted in Inner Mongolia (Wu et al., 2015), and the proportion is greater on the Loess Plateau and Northeastern China Plains. However, the extreme conditions put severe constraints on further conversion. Grasslands in the oasis in the Hexi corridor and the Junggar and Tarim basins in northwest China are largely converted, yet this land conversion is a local phenomenon in the vast grassland region. On the QT Plateau, converting land for crop production is not reasonable due to the short growing season at the generally high altitudes and under the extreme climate conditions. Tibet's only large agricultural regions are located in the central and the southern parts, along the Yarlung Zangbo River valley and also the main river valleys in western Sichuan and eastern Qinghai.

Plant Collecting and Animal Hunting

Collection of wild species, including medical and edible plants, fungi and "algae" has exerted profound effects on these species and the grassland environment. Collection of the edible cyanobacterium *Nostoc flagelliforme* has largely damaged the soil crust and induced soil erosion in desert steppe areas. Excavating the roots of various medical plants such as *Glycyrrhiza uralensis*, *Saposhnikovia divaricata* and *Bupleurum scorzoniferolium* as well as the Chinese caterpillar fungus *Ophiocordyceps sinensis* has not only markedly reduced the abundance of these species but also damaged the soils. The (illegal) hunting is still a pressure for native ungulates and small mammals, though poaching declines with the increasingly strong implementation of the laws and regulations for nature conservation.

Mining, Urbanization and Development of Infrastructure

The development of the roads and railways, the rapid expansion of open pit mining, and the fencing schemes in the course of sedentarization and privatization of land-use rights (Li and Li, 2016) lead to obvious fragmentation of Chinese grasslands (Squires and Hua, 2017), which hampers migration of wild ungulates, reduces mobility of livestock, and affects the sustainability of grassland use. The large-scale barrier formed by the fence that runs along much of the Chinese-Mongolian border has blocked the migration of wild ungulates.

Climate Change

The greatest climate warming trend was observed in the semi-arid region in China, with the climate becoming warmer and drier at an accelerated rate (Huang et al., 2015, 2019). The significant warming trend and large inter-annual variation in precipitation has started to constrain plant growth in temperate and alpine steppe grasslands, and also affects the pastoralism in natural grassland regions. This happens in spite of a slight increase in precipitation in the alpine steppe region over the past three decades (Qian et al., 2012; Haung et al., 2016). However, increased temperature and precipitation levels are generally favorable to plant growth in meadows in the QT Plateau (Haung et al., 2016). Aboveground biomass of an alpine meadow was shown to increase with increased precipitation rather than with experimental warming (Fu et al., 2018). Chen et al. (2013) reviewed the impacts of climate change and human activities on biogeochemical cycles on the QT Plateau, suggesting that warming increased net primary production as well as soil respiration, and resulted in significant permafrost thawing and glacier melting, which lead to substantially increased methane consumption of meadows. The variation and change in climate subsequently affects grassland and animal production, and financial and environmental outcomes of herders households. Thus, adaptive management must be addressed in devising policies (Smit et al., 1996). The management measures to adapt to climate variability and changes in the steppe region include selling livestock, buying forage, reserving pastures for extreme climate events, housing livestock and looking for other alternative jobs to compensate for economic losses (Hou et al., 2012). Local ecological knowledge and community-based institutions are beneficial to improve resource availability and distribution and to reduce risks caused by climate change (Fu et al., 2012).

Conservation, Restoration and Sustainable Management

A series of policies have been implemented to prevent grassland degradation and to restore degraded sites in China. Formal conservation of grasslands has been implemented by setting up a series of natural reserves or protected areas. The protected areas in the grassland region in China account for some 15% of the total area, which is higher than in other grassland regions of the world (Wesche et al., 2016). Reserves are, however, not balanced among grassland types or regions. The protected areas in Inner Mongolia account for 11.7% of the total area with typical and desert steppes being under-represented (Ma et al., 2016); while a single complex of 11 reserves on the QT Plateau accounts for 0.8 million km². Outside their typically small core zones, livestock grazing is allowed in almost all reserves in the grassland region.

Several major policies have been implemented in the grassland region with the objectives to reduce overall grazing pressure and restore the degraded grassland, including "Retire Livestock to Restore Rangeland" (RLRR; 2003), and "Ecological Subsidy and Award System" (ESAS; 2011). The latter aims to maintain the ecological services while improving herder livelihoods through providing

subsidies for the year-round “grazing-ban” area (approx. 14.0 USD per ha) or “forage-livestock balance” area (approx. 3.5 USD per ha), and through increasing subsidies for livestock production system and infrastructure improvement, as well as providing training to facilitate diversification of herders’ livelihoods (Li and Li, 2016). The large-scale application of these policies, involving fencing of rangeland, year-round or seasonal removal of grazing livestock, and encouraging pastoralists to move out from degraded rangelands among other have improved the overall health of grassland ecosystems. Especially vegetation cover has improved and thus capability of grassland to prevent soil erosion and desertification (Piao et al., 2015). Nonetheless, grassland management strategies such as fencing, grazing bans or rearing livestock in stables have been questioned from an ecological and social point of view (Li and Huntsinger, 2011; Wang et al., 2014; Hua and Squires, 2015). The fences cause a loss of flexibility and increase the vulnerability of the pastoral system to global changes, and they also block the passage of migratory ungulates. The challenge is to optimize management practices that result in “win-win” outcomes for grasslands, the environment, and households. This is possible by reducing animal numbers considerably using an energy-balance/market-based approach while improving household incomes (Kemp et al., 2013), with the “Ecological Subsidy and Award System” and other policies to foster restoration of degraded grassland. To restore mobility and flexibility of both native and livestock animals and to develop multiple ecosystem services are recommended key measures for sustainable pastoralism (Shang et al., 2014; Wang et al., 2014; Wu et al., 2015). Regional planning encompassing multiple goals of grassland management through implementation of the ecological red-line policy (Xu et al., 2018) and design of ecological corridors including those across Chinese-Mongolian borders, are recommended strategies towards conservation and sustainable use of the grasslands.

Acknowledgment

FYL and KG acknowledge support of the Inner Mongolia Department of Science and Technology for Mongolian Plateau project (201503001), the Chinese Academy of Sciences for the Strategic Priority Research program (XDA19050402) and the Chinese Ministry of Ecology and Environment for the Red List of Ecosystems project. YJ and KW acknowledge support of the German Federal Ministry of Education for the MoreStep project within the BioTip funding scheme. Thanks to Xianguo Qiao for assistance in preparation of Fig. 1.

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Grasslands and Shrublands of Japan

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This chapter was solicited and edited by Jürgen Dengler and Péter Török on behalf of the Eurasian Dry Grassland Group (EDGG).

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Glossary

Chagusaba Meadows maintained by annual mowing specially for green tea production.

Houbokuchi (or maki) Pastures that have been maintained by grazing and annual burning.

Karishiki Green manure produced in *shibakusachi*. *Kari* and *shiki* mean mowing plants and spreading to fields, respectively.

Kayaba *Miscanthus* or *Phragmites* dominated meadows that have been maintained by mowing and annual burning for thatch roofing.

Kurobokudo The Japanese black soil, which indicates long history of semi-natural grassland vegetation.

Saisochi Meadows managed by mowing and burning for winter fodder production.

Satokusachi (or keihansochi) Meadow strips around paddy and vegetable fields. They have usually been managed by frequent mowing.

Shibakusachi Meadows producing green manure for paddy and crop fields.

Abbreviations

AGRC ASO Grassland Restoration Committee

BP Years before present

FAO Food and Agriculture Organization

GHIAS Globally Important Agricultural Heritage systems

NGO Non-governmental organization

NPO Non-profit organization

Abstract

Natural or semi-natural grasslands and shrublands are small but widely distributed throughout Japan, although the forest vegetation is the potential climatic climax under the humid climates in the most parts of the country. Grasslands and shrublands have been formed by natural and anthropogenic disturbances and/or specific soil conditions in the Japanese archipelago. Since the last century, however, grasslands, especially semi-natural ones, have decreased in the area continuously, mostly due to land-use changes (abandonment, intensified use, afforestation and urban development) driven by socioeconomic growth in Japan. The rapid declines, along with fragmentation and degradation, of semi-natural grasslands have caused significant biodiversity loss as in the other Palaearctic regions but most of those grasslands and shrublands are not well protected. Natural grasslands and shrublands, on the other hand, have been protected from anthropogenic developments in general, but their area may decrease by climate changes in the future. The anti-disaster development, such as dams and embankments, reduced natural disturbances and have caused reduction and degradation of grasslands and shrublands in riparian and coastal areas. In some oceanic islands, feral goats have had significant negative impacts on grassland and shrubland vegetation. Some grasslands and shrublands on limestone and serpentine soils and on oceanic islands are often hotspots of endemic species whereas semi-natural, riparian and coastal grasslands harbor many plant and animal species which used to be found throughout Japan but now at high risk of extinction. Thus, in Japan, recent human activities largely degraded and reduced Japanese grasslands and shrublands which have high conservation values. To protect these invaluable ecosystems, a suite of activities have been initiated to promote biodiversity conservation and restoration in Japanese grasslands and shrublands.

Delimitation and Physiogeography of the Region

Japan is an island country located at the eastern edge of the Eurasian continent. The Japanese archipelago consists of more than 6800 islands, most of which are continental but some are oceanic, stretching c. 3000 km long from the Philippine Sea to the Sea of Okhotsk in the western Pacific Ocean region (20°25'–45°31' N, 122°56'–153°59' E). The total land area is approximately 378,000 km², and over 97% of the area are of the four main continental islands, Hokkaido, Honshu, Shikoku and Kyushu islands (Fig. 1). The terrain is mostly mountains and the highest elevation is 3776 m a.s.l. at the summit of Mt. Fuji. The current population of Japan is 126.2 million and most population is concentrated in urban areas near the coast, plains and valleys.

In Japan, the climate is strongly governed by seasonal winds (i.e., monsoon) and latitudinal extent. The climate mostly belongs to temperate (e.g., Tokyo: mean temperature 5.2 °C in January, 26.4 °C in August) but varies largely from subtropical in the south (e.g., Naha: mean temperature 17.0 °C in January, 28.9 °C, July) to subarctic in the north (e.g., Utoro: mean temperature –5.6 °C in January, 19.0 °C in August). The monsoon strongly influences precipitation patterns throughout the country. Winter monsoon brings cold and wet air from the Eurasian continent and results in heavy snows to the coastal parts of Sea of Japan, while summer monsoon and typhoon brings hot and wet air from the Pacific Ocean to the most parts of Japan, providing high annual precipitation (c. 1000–3500 mm per year) over the country (Numata, 1961). The climatic climax vegetations are a variety of forests and currently primary and secondary forests cover approximately 67% of terrestrial areas of the country (Ministry of the Environment of Japan, 2016). Meanwhile, natural grasslands and shrublands below sub-alpine zones are distributed very narrowly in the areas with wind-swept, heavy snow and/or avalanche areas, in riparian and coastal areas, in relatively small islands with high permeability and in the areas on limestone and serpentine soils and volcanic materials (Kitamura, 1956; Hayakawa, 1993; Koizumi, 1996, Fig. 1). Currently, semi-natural grasslands are distributed in very limited areas as well (Fig. 2).

Major soil types are Andsols (Japanese black soils or *kurobokudo*, c. 31% of the lands), Brawn forest soils (c. 30%) and Lowland soils (mostly alluvial soils, c. 14%) in Japan, although the estimate percentages differ depending on the soil categorization systems (Obara et al., 2016): total estimated area of Andsols used to be estimated as approximately 17% of the Japanese land surface (Ushimaru et al., 2018). Riparian and coastal natural grasslands and shrublands establish on lowland soils or Sandy Regosols (c. 0.7%) whereas semi-natural grasslands are distributed primarily on Andsols (Ushimaru et al., 2018). Andsols typically contain many grass phytolith and charcoal particles, indicating long historical use of semi-natural grasslands associated with fire (Kawano et al., 2012; Miyabuchi et al., 2012). In contrasts to the general rarity of Andsols (< 1% of that in the world, IUSS Working Group WRB, 2015), this soil type is very widely distributed throughout Japan but is concentrated to the montane areas of Kyushu, Shikoku and Honshu (including the foot of Mt. Fuji) as well as lowlands of Kanto plain and the south-eastern Hokkaido. Dark red soils, which are developed on limestone and serpentine bedrocks, are narrowly scattered over the montane areas of the whole country (c. < 0.5%, Obara et al., 2016). Immature soils originated from volcanic materials, serpentine and coral reefs are found in c. 7% of the land surface whereas podosols covers only 2% and are mainly found in hills and lithic plains and partly sand dunes (Obara et al., 2016).

Biogeography, Flora and Fauna

The Japanese Archipelago had begun to separate from the eastern edge of the Eurasian Continent since 20 Ma in the Miocene (Isozaki, 2019). This geological event caused the biogeographic separation of flora and fauna between the islands and the continent. Throughout the duration since this period to the present, most parts of the islands have been covered with various types of forests, although constituting flora have changed depending on climatic conditions in the geological time scale (Yabe, 2019).

During repeated glacial periods in the Quaternary, formations of land bridges led to biogeographic exchanges between the Japanese peninsulas and the mainland of the continent. Three routes on the land bridges allowed the exchanges of species: (1) the northern route through Sakhalin or the Kuril islands which connected Hokkaido and Russia, (2) the western route through the Korean Peninsula which connected Kyushu and the north-eastern China, (3) the southern route through Taiwan, Ryukyu islands which connected Kyushu and the south-eastern China (Tojo et al., 2017). Most of the present grassland and shrubland species in Japan are considered to have immigrated into this area through the northern route or the western route during the ice ages in the Quaternary. The Japanese islands and north-eastern Eurasia have lots of grassland herb and butterfly species in common at present, although multiple immigrations of these species could have occurred during the repeated glacial periods. Recent molecular phylogeographic studies partly supported the scenario (Uchida et al., 2016b; Takaishi et al., 2019). Meanwhile, subtropical island flora and fauna have been suggested to immigrate from the southern route.

In the present biogeographic regions of the world, most of the Japanese Archipelago is assigned to the Palaearctic region, whereas Ryukyu islands are assigned to the Oriental region. As a sub-division of the Palaearctic region, the Sino-Japanese region is commonly recognized in studies on the biogeography of plants (Hotta, 1974) and butterflies (Hiura, 1984; Saigusa and Araya, 2015). Majorities of plants and butterflies in the Japanese grasslands have the Shino-Japanese or the Palaearctic distributions.

Several dozens of herb and woody species in semi-natural grasslands of Japan are also distributed in the Korean Peninsula, the north-eastern China and the Russian Far East (Murata et al., 1998; Tabata, 1997; Igari, 2012). The greater part of these species inhabit Honshu and Kyushu, but not in Hokkaido. This pattern of distribution suggests the importance of the western route of immigration in the glacial periods for the grassland herbs (Murata et al., 1998). Tabata (1997) argued the possibility that these species dispersed from the continental temperate meadows which still exist at present in north-eastern China (The Editorial Board of Vegetation Map of China, Chinese Academy of Science, 2001). Similar arguments are also proposed on the immigration routes of grassland insect species including Lepidoptera, Coleoptera, Hemiptera and Orthoptera (Hiura, 1984).

The majority of the mammals of Japan mainly inhabit forests. Only a few species of mammals, such as a harvest mouse *Micromys minutus* (Palaearctic) and the Japanese grass vole *Microtus montebelli* (endemic) prefer grassland habitats, although mammals utilize both forests and grasslands include the sika deer *Cervus nippon* (Sino-Japanese), the Japanese hare *Lepus brachyurus* (endemic), the red fox *Vulpes vulpes* (Holarctic) and dozens of other species (Tsukada, 2007). The sika deer prefer to eat herb species and recently often inflict damages on biodiversity of semi-natural grasslands, even though they keep using forests as their hiding places. Japanese breed horses, constituted of several strains, are found in several locations in Japan but are considered to be descendants of populations transported by humans from Mongolia through the Korean Peninsula during the period of the 3rd–5th centuries (Nozawa et al., 1998). As of today, there is no evidence that the horse inhabited Japan during the earlier parts of the Holocene. Among 417 species of birds in Japan, 20–30 species, including the Japanese skylark *Alauda arvensis japonica* and the Chestnut-eared bunting *Emberiza fucata*, are considered to inhabit grasslands (Tojo, 2007).

Origin of the Grasslands and Shrublands

After the last glacial period (during the Holocene), the temperate and humid climate would have facilitated the succession to forest vegetation over the Japanese islands. Various natural grassland and shrubland types, however, still exist narrowly under timberlines of Japan (Figs. 1 and 3, Table 1). Natural grasslands and shrublands are maintained by heavy snow, frequent avalanches, strong winds and landslides in subarctic (subalpine) and cool temperate zones. In lowland floodplain and coastal areas, natural grasslands have been maintained by frequent natural disturbance agents, such as flooding, waves and strong winds. Some chemical and physical soil conditions, which are provided from limestone and serpentine bedrocks, can limit tree growth and often facilitate the establishment of herbs and shrubs as well (Kitamura, 1956; Hayakawa, 1993; Koizumi, 1996). In small continental and oceanic islands, such as Nansei, Oki, Izu and Bonin (Ogasawara) islands, natural grasslands and shrublands are often developed on highly jointed basalt or limestones originated from coral reefs creating high soil permeability resulted in dry soil conditions (Shimizu, 1991; Hayakawa, 1993). Around active volcanos, grasslands and shrublands are often established around solfataras and on lava flows and pyroclastic materials throughout Japan (Ministry of the Environment of Japan, 1999).

Anthropogenic activities such as burning, grazing and mowing have created and maintained various types of semi-natural grasslands in hilly and montane areas and often in lowland floodplains, coasts and small islands (Fig. 4). The beginning of Japanese semi-natural grasslands, indicated by the start of Andosols formation, may date back to c. 10,000–40,000 BP in the Aso area, Kyushu (Sakaguchi, 1987; Kawano et al., 2012; Miyabuchi et al., 2012; Hosono and Sase, 2015). Semi-natural grasslands from the Jomon period (13,000 BC–300 BC) to the Yayoi period (~250 CE) are hypothesized to have been maintained for hunting by burning, but this hypothesis has rarely been examined archeologically (Sakaguchi, 1987; Suka et al., 2012).

During the 3rd–5th centuries, pastoralism (horse and cattle grazing) was introduced to the Japanese islands from the Eurasian continent. Since then, pastures increased from the 8th to mid–19th centuries, and become widely distributed in Japanese islands (Ushimaru et al., 2018). In contrast, historical transition in meadow distributions is largely unknown in Japan, but the strong association with the development of cultivated fields has been suggested (Ogura, 2006; Mizumoto, 2015). Indeed, several types of meadow have been maintained for thatch roofing, winter fodder for livestock, and grass-compost (green manure). Until a hundred years ago, meadows were widely maintained all over the country (Ogura, 2006).

However, since the late 19th century, the semi-natural grasslands have continuously decreased in areas (only 1–3% of the national land area today) and were heavily fragmented (Ogura, 2006; Suka et al., 2012; Ushimaru et al., 2018). Some pastures

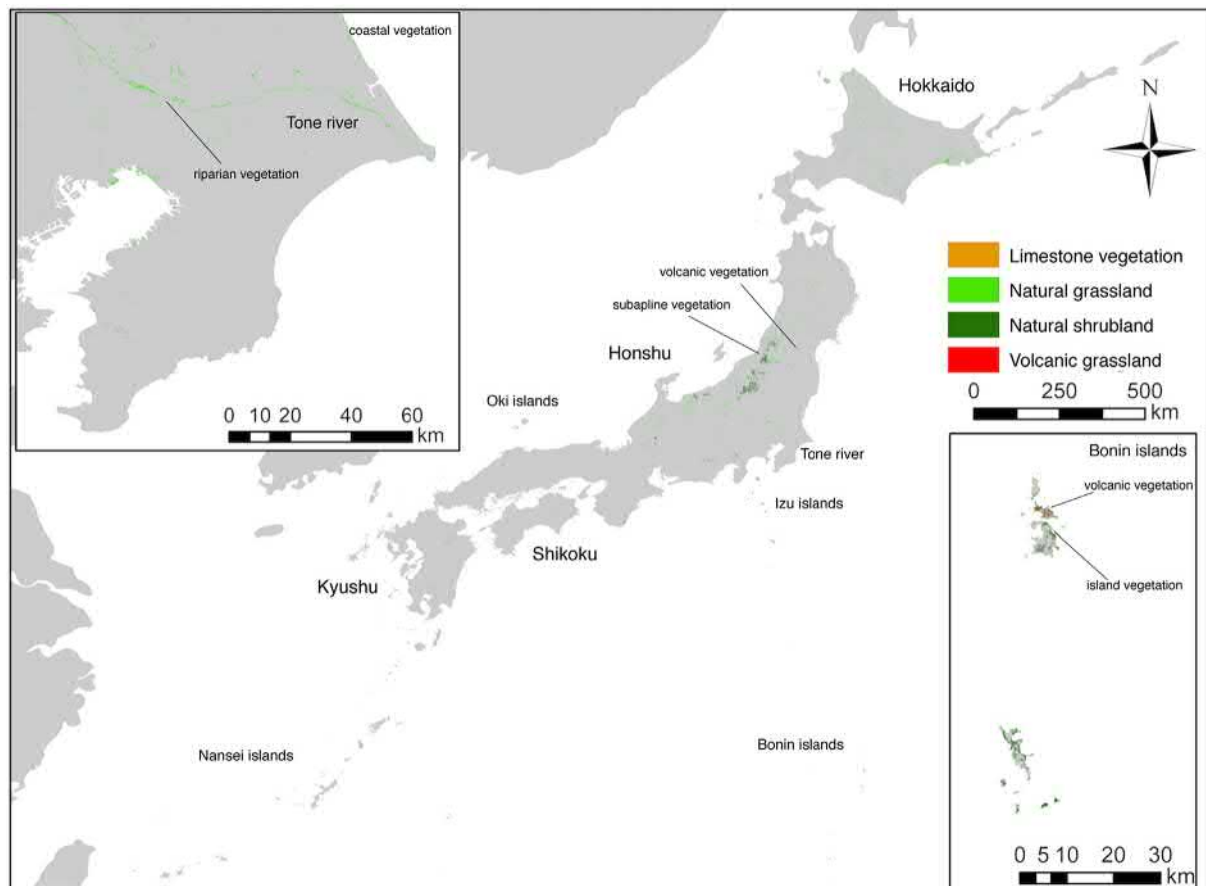


Fig. 1 Distribution map of Japanese natural grassland and shrubland vegetation. The map was drawn based on the 5th vegetation survey (1988–96) by Japanese Ministry of the Environment.

and meadows are still actively managed for husbandry or for sightseeing and tourism (Japanese Society of Grassland Science, 2010), but most remaining semi-natural grasslands have been abandoned (Nagata and Ushimaru, 2016; Uchida et al., 2016a; Koyama et al., 2017). Currently, only a small fraction of the “semi-natural” pastures have been maintained whereas some fractions were converted into artificial sown pastures: eastern Hokkaido, northeastern Honshu and Aso areas in Kyushu are the main areas of current husbandry (Ushimaru et al., 2018).

Typology of the Communities

Natural Grasslands and Shrublands

Here, we refer to grasslands and shrublands maintained or temporally established by natural disturbances and specific soil conditions as “natural grasslands and shrublands” whereas those maintained by continuous anthropogenic managements are referred as “semi-natural grasslands” (Table 1). Grasslands and shrublands established temporally or maintained continuously after land-use changes and grazing animals are called as “secondary grasslands and shrublands” in this paper. Dengler et al. (2014) classified Palaearctic grasslands into four types: steppes, Arctic-alpine grasslands, azonal and extrazonal grasslands and secondary grasslands. According to the classification, all Japanese natural grasslands (and shrublands) which are introduced in this chapter are azonal and extrazonal whereas both semi-natural and secondary grasslands (and shrublands) are included in secondary types: arctic-alpine grasslands and shrublands are outside the scope of the chapter. Because natural grasslands and shrublands are often next to each other and are maintained by similar disturbance agents in various ecosystems, we describe them together for each ecosystem. The following categorization was based on the modification of the 5th vegetation survey by Ministry of the Environment of Japan (1999).

Windswept grasslands and shrublands

From subalpine (subarctic) to cool temperate montane zones, natural grasslands and shrublands are maintained by strong winds, heavy snow, frequent avalanches and/or landslides (Fig. 1). Windswept grasslands are primarily established on the mountain

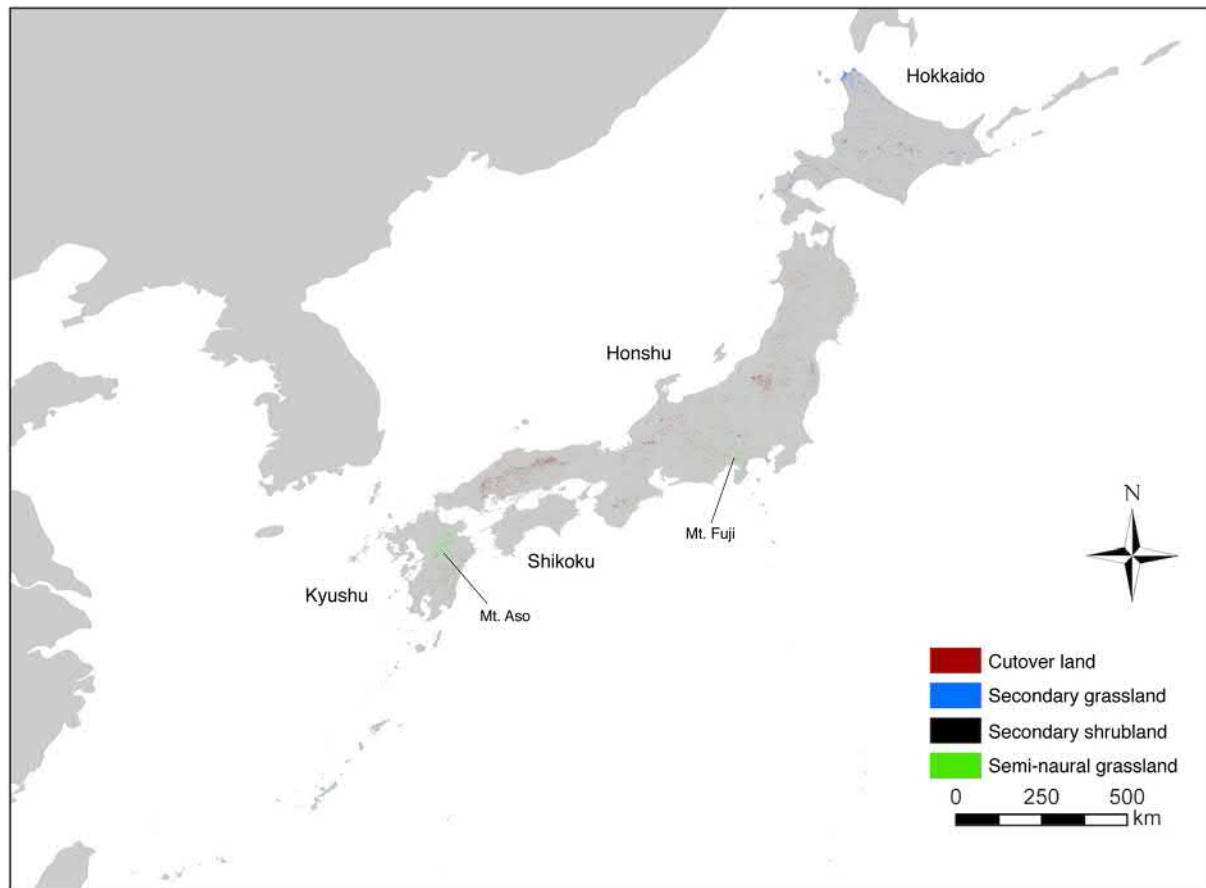


Fig. 2 Distribution map of Japanese semi-natural and secondary grassland and shrubland vegetation. The map was drawn based on the 5th vegetation survey (1988–96) by Japanese Ministry of the Environment.

summits and ridges whereas those maintained by frequent avalanches and landslides are found on steep slopes and valleys (Fig. 3A). In these grasslands, dwarf bamboos (*Sasa* spp.) are often dominant throughout the country whereas tall forbs, such as *Ranunculus acris* var. *nipponicus*, *Veratrum* and *Reynoutria* spp. are often abundant in heavy snow areas of Hokkaido and Honshu. Similarly, natural shrublands are also established due to heavy snow, frequent avalanches, strong winds, landslides and rocky environments in subalpine and cool temperate zones (Fig. 3B). In windswept and rocky shrublands, diverse shrub species (e.g., *Sorbus commixta*, *Rhododendron pentaphyllum* var. *nikoense*, *R. quinquefolium* and *Enkianthus campanulatus*) can be dominant. Meanwhile, in areas with frequent avalanches, shrublands dominated by *Weigela hortensis*, *Alnus pendula* and *Rhododendron trinerve* have been established.

Riparian grasslands and shrublands

In riparian zones, *Phragmites*-, *Miscanthus*- and annual plant-dominated grasslands and willow-dominated shrublands have been maintained by frequent flooding (Washitani, 2001; Osawa et al., 2010). *Phragmites japonicus* is a dominant grass species in upstream riparian areas whereas *P. australis* and *M. sacchariflorus* are dominant species in downstream areas. In temperate riparian areas shrublands dominated by *Salix gracilistyla* and *S. triandra* subsp. *nipponica* are maintained in up- to mid-stream and mid- to downstream, respectively, throughout the main islands (Ministry of the Environment of Japan, 1999). Grasslands on riparian levees are often managed by mowing to keep grassland landscape and sometimes harbor endangered species (Fig. 3C).

Coastal grasslands and shrublands

Because Japan is an island country with total coastal lines of over 30,000 km, several types of natural coastal grasslands and shrublands maintained by strong wind and wave disturbances and/or high salinity (Ishikawa et al., 1995) are found throughout the country. Coastal grasslands and shrublands are roughly divided into four types: those on sand dunes, cliffs, uplifted coral reefs and subtropical coastal shrublands (Figs. 3D and E). Coastal sand dune grasslands and shrublands are usually continuously (and often mixedly) distributed, such that grasslands establish in the front of coastal lines and shrublands behind them (Miyawaki, 1991). *Imperata cylindrica* var. *koenigii* (Fig. 3D) and *Carex kobomugi* and *Vitex rotundifolia* widely dominate in coastal sand dune grasslands and shrublands, respectively. In addition to these species, *Mertensia maritima* subsp. *asiatica* and *Rosa rugosa* are typical



Fig. 3 Natural grassland and shrubland types in Japan. (A) *Sasa*-dominated windswept grasslands, (B) windswept shrublands on an avalanche area, (C) an endangered species, *Arisaema heterophyllum* in a riparian grassland, (D) coastal sand dune grasslands dominated by *Imperata cylindrica* var. *koenigii*, (E) coastal sand dune and cliff shrublands with orange flowers (*Lilium maculatum*), (F) serpentine grasslands, (G) *Miscanthus condensatus*-dominated island grasslands on the Minami-iou island, (H) island dry scrub. Photos by A. Ushimaru (A, C-D), T. Suka (B), Daichi Funamoto (F) and Kazuto Kawakami (G, H).

Table 1 Grassland (GL) and shrubland (SL) types and their dominant species in Japan.

Types	Climatic zone		Factors influencing establishment	Dominant species
<i>Natural</i>				
Windswept	GL	Subalpine (subarctic)–cool temperate	Wind, snow, avalanches, landslides	<i>Sasa</i> , <i>Veratrum</i> and <i>Reynoutria</i> spp.
	SL	Cool temperate		<i>Sorbus commixta</i> , <i>Rhododendron</i> spp., <i>Weigela hortensis</i>
Riparian	GL	Temperate	Flooding	<i>Phragmites japonicus</i> , <i>P. australis</i> , <i>Miscanthus sacchariflorus</i>
	SL	Subalpine (subarctic)–temperate		<i>Salix gracilistyla</i> , <i>S. triandra</i> subsp. <i>nipponica</i>
Coastal sand dune	GL	Temperate-subtropic	Wind, high salinity, sandy soils	<i>Imperata cylindrica</i> var. <i>koenigii</i> , <i>Carex kobomugi</i>
	SL	Temperate-subtropic		<i>Rosa rugosa</i> , <i>Vitex rotundifolia</i> , <i>Juniperus chinensis</i> var. <i>procumbens</i>
Coastal cliff	GL	Temperate-subtropic	Wind, rocky soils	<i>Miscanthus condensatus</i> , <i>M. sinensis</i> , <i>Libanotis coreana</i> f. <i>ugoensis</i>
	SL	Temperate-subtropic		<i>Euonymus japonicus</i> , <i>Pittosporum tobira</i> , <i>Quercus phillyreoides</i>
Uplifted coral reef	GL	Subtropic	Lithic soil conditions	<i>Zoysia pacifica</i> , <i>Sporobolus virginicus</i> , <i>Lepturus repens</i>
	SL	Subtropic		<i>Artemisia chinensis</i>
Coastal	SL	Subtropic	High salinity	<i>Hibiscus</i> spp., <i>Scaevola taccada</i> , <i>Pandanus odoratissimus</i>
	GL and SL	Subalpine (subarctic)–temperate		Diverse depending on climatic and other conditions
Serpentine and Limestone Island	GL	Temperate–subtropic	Dry soil conditions	<i>Zoysia tenuifolia</i> , <i>Miscanthus condensatus</i>
	SL	Subtropic	Dry soil conditions	<i>Distylium lepidotum</i> , <i>Pouteria obovata</i>
Volcanic	GL and SL	Subalpine (subarctic)–subtropic	Specific soil conditions	Diverse depending on climatic and other conditions
<i>Semi-natural</i>				
Pasture	GL	Subalpine–subtropic	Grazing and/or burning	<i>Zoysia</i> spp., <i>M. sinensis</i> , <i>Pleiolablastus</i> spp.
Meadow	GL	Subalpine–subtropic	Mowing and/or burning	<i>M. sinensis</i> , <i>Sasa</i> spp., <i>Pleiolablastus</i> spp., <i>P. australis</i>
<i>Secondary</i>				
Cutoverland	GL and SL	Subalpine (subarctic)–subtropic	Clear cutting of timber	Diverse grass, forb and shrub species
Animal grazing	GL	Subalpine (subarctic)–subtropic	Wild deer or feral goat grazing	Unpalatable species, alien species

species distributed in the temperate regions and *Thuarea involute*, *Ipomoea pes-caprae* and *Scaevola taccada* are in subtropical regions. Windswept grasslands and shrublands on coastal cliffs are usually neighboring each other and often found just beside dune vegetation (Fig. 3E). Cliff grasslands are dominated by forb species, such as *Libanotis coreana* f. *ugoensis*, *Lilium maculatum*, *Cyrtomium falcatum*, *Peucedanum japonicum* var. *japonicum* as well as grasses (e.g., *Miscanthus condensatus* and *M. sinensis*) whereas shrublands are dominated by *Euonymus japonicus*, *Pittosporum tobira*, *Quercus phillyreoides* and *Eurya emarginata* both in warm temperate and subtropical zones. In subtropical island coasts, natural grassland and shrubland vegetations, which are dominated by *Zoysia pacifica*, *Sporobolus virginicus*, *Lepturus repens* and *Artemisia chinensis*, are established on uplifted coral reef-originated flat plain, plateau and cliffs. In a special case, subtropical rocky or cliff grasslands are established around seabird nesting areas in some oceanic islands. Subtropical coastal shrublands, whose dominant species are *Hibiscus hamabo*, *H. tiliaceus*, *Scaevola taccada* and/or *Pandanus odoratissimus* are often established in brackish water areas at estuaries and on sand dunes and uplifted coral reefs of southern islands.

Grasslands and shrublands on specific soil conditions

In Japan, natural grasslands and shrubland and their complex are occasionally found on dark red soils (on serpentine or limestone bedrocks), likely owing to their specific soil chemical and physical conditions (Kitamura, 1950, 1956; Hayakawa, 1993; Koizumi, 1996, Fig. 3F), as in the other Palaearctic regions (Whittaker, 1954). The species composition, sometimes containing endemic herb and shrub species that are predominantly distributed in the vegetation, usually vary depending on climatic and physiographic conditions (Kitamura, 1956, 1957; Yamanaka, 1960).

In oceanic and small continental islands, such as Bonin, Izu, Sado, Nansei, Iki and Oki islands, dry soil conditions often facilitate establishment of natural grasslands and shrublands (Shimizu, 1991; Hayakawa, 1993; Yoshida et al., 2002, Figs. 3G and H). Island natural grasslands have often been used for pastures where *Zoysia tenuifolia* and *Miscanthus condensatus* are dominant species



Fig. 4 Semi-natural and secondary grasslands and shrublands in Japan. (A) Pasture, (B) lithic grassland used as pasture, (C) *saisochi* meadow, (D) *satokuschi* meadow, (E) ski slope grassland, (F) a training ground of the Japan Self-Defense Force, (G) grassland herbs in a cutover land, (H) secondary grasslands 15 years after feral goat eradication in the Yomejima island (H). Photos by A. Ushimaru (A, D–G), Daichi Funamoto (B), Yuko K. Nagata (C) and Kazuto Kawakami (H).

(Hayakawa, 1993). Dry scrub dominated by *Distylium lepidotum* and *Pouteria obovata* is established owing to extreme dry soil conditions in summer in Bonin islands (Shimizu, 1991; Yoshida et al., 2002, Fig. 3H).

Volcanic activities have created grasslands and shrublands with relatively sparse vegetation covers around solfataras, on lava flows and on pyroclastic materials throughout Japan (Ministry of the Environment of Japan, 1999). In solfataras grasslands and shrublands, species composition often differs depending on the climatic zones (Tsujimura, 1977). Diverse plant species such as *Carex angustisquama*, *Ledum palustre* subsp. *diversipilosum* var. *nipponicum*, *Avenella flexuosa*, *Miscanthus sinensis* and *Sasa kurilensis* are often abundant in the solfataras vegetation (Tsujimura, 1977). *Rhododendron kiusianum*, *Avenella flexuosa*, *Reynoutria japonica* var. *compacta*, *Reynoutria japonica* var. *terminalis*, and *Nephrolepis cordifolia* often form sparse vegetation on lava flows. *Campanula punctata* var. *hondoensis* and *Cirsium purpuratum* constitute vegetation on denuded lands of active Mt. Fuji.

Semi-Natural Grasslands

Semi-natural grasslands are distributed from lowland to subalpine zones and can be roughly divided into pastures and meadows (Fig. 4A–D). At present, relatively wide semi-natural grasslands are distributed in the Aso-Kuju area of Kyushu, around Mt. Fuji, the center (Nagano Prefecture) and the northeastern areas of Honshu, although most semi-natural grasslands have become shrunk, fragmented and isolated (Ogura, 2006, Fig. 2). The distribution of pastures and meadows largely overlaps with the Andosol distribution (Ushimaru et al., 2018). In addition, some riparian and coastal, limestone and island grasslands (e.g., Akiyoshi-dai, Shikoku-Karst and Oki) have often been maintained as pastures and meadows by burning, grazing and/or mowing (Hayakawa, 1993; Washitani, 2001; Tsuda et al., 2002; Obata et al., 2012, Fig. 4B), although their distributions could not often be precisely distinguish in the map (Figs. 1 and 2) due to limited nation-wide information.

Pastures

Today, pastures (*hobokuchi* or *maki*, Fig. 4A and B) are distributed very narrowly within the country (such as in Toimisaki, Aso, Sanbe, Oki and Shiriya-zaki). Pastures have traditionally been managed by combining spring burning and grazing (Koyanagi et al., 2013), but currently many pastures are maintained only by grazing. *Zoysia japonica*-dominated pastures are usually found in cool-temperate (central) regions whereas those dominated by *Miscanthus sinensis* and/or *Pleiblastus* spp. are in warm-temperate (southern) regions (Numata, 1969).

Meadows

Several meadow types have been maintained for various uses in Japanese traditional rural livelihood (Ushimaru et al., 2018). *Sasa* spp., *M. sinensis* and *Pleiblastus* spp. are dominant grasses in northern, central and southern meadows, respectively (Numata, 1969). Meadows usually have higher vegetation heights than pastures and exhibited higher diversity of forbs, sometimes including many endangered species, such as *Lithospermum erythrorhizon*, *Polemonium kiusianum*, *Echinops setifer*, *Platycodon grandifloras* and *Vincetoxicum pycnostelma*.

In the past, *M. sinensis*- (or sometimes other *Miscanthus* spp.-) and *Phragmites australis*-exclusively-dominated meadows (*kayaba*) for thatch production were widely found in hilly and riparian areas, respectively, throughout the country. The meadow type is usually managed by spring burning and grass harvest during October to December. Today, due to the housing modernization, only a very small fraction of them remain in places such as in the Aso region and around Mt. Fuji.

Traditionally, stock breeders have managed meadows for winter fodder production (*saisochi*, Fig. 4C). In the mid-17th century, expansive meadows that produced green manure for rice and crop cultivated fields (*shibakusachi*) were maintained in foothills near villages (Ogura, 2006). However, the meadows of this type were mostly abandoned after the invention of chemical fertilizers in the 20th century. In the Aso region, meadows for green manure production are still actively managed but in very limited areas. These meadow types are usually commons and have been managed with both burning and mowing by local communities (Nagata and Ushimaru, 2016; Uchida et al., 2016a; Koyama et al., 2017).

In addition to the above meadow types, relatively narrow private meadows (*satokusachi* or *keihansochi*, Fig. 4D) have been maintained by individual farm families around paddy and crop fields. Around cultivated fields, belt-like meadows on levees are maintained by frequent (1–7 times per year) mowing rarely combining with spring or winter burning for insect/pathogen control as well as for fodder and green manure production in the past, but today only for keeping landscape (Uematsu et al., 2010; Uematsu and Ushimaru, 2013; Koyanagi et al., 2014; Uchida and Ushimaru, 2014). Dominant grass species of *satokusachi* meadows are known to change from *Pleiblastus* spp., *M. sinensis*, *Imperata cylindrica* var. *koenigii* to *Z. japonica* as mowing frequency increases. As paddy and other fields cover c. 18.4% of the total land area (c. 68,000 km²), the total area of this meadow type was estimated up to c. 1850 km² in 2010 (Ministry of Agriculture, Forestry and Fisheries of Japan, 2016).

Miscanthus sinensis- or *Pleiblastus chino*-dominated narrow meadows producing green manure for tea fields (*chagusaba*) have been managed to improve the tea quality in green tea production areas in Shizuoka Prefecture (Kusumoto and Inagaki, 2016). Farmers usually mow once during autumn and winter to maintain these meadows. As the ratio of *chagusaba* area to tea plantation area is estimated 0.71 in the Higashiyama district of Kakegawa city, the total area of this meadow type is considered to be significant in the tea producing areas (Kusumoto and Inagaki, 2016).

As modern land uses, ski and golf course development have maintained kinds of semi-natural grassland since the early 20th century. Ski slope grasslands are often dominated by *M. sinensis* under typical management only by annual mowing in autumn (Fig. 4E). Some ski grasslands developed on old pastures have harbored diverse endangered grassland species (Nakahama et al.,

2018; Yaida et al., 2019). Other ski grasslands developed by forest clear-cutting are dominated by introduced *Festuca rubra*, *Pteridium aquilinum* var. *latiusculum* and some woody species (Tsuyuzaki, 1995). Golf courses usually host a very low plant diversity, because the alien grasses (e.g., *Zoysia* spp.) are predominantly used, but some courses have maintained diverse grassland species just besides the courses by mowing management (Ushimaru et al., 2018). Moreover, relatively large-scale semi-natural grasslands have been maintained by spring burning as training grounds for the Japan Self-Defense Forces (Fig. 4F). These grasslands are scattered distributed within the country and share similar species compositions to meadow vegetation and host many endangered species (c.f. Ohwaki, 2018).

Secondary Grasslands and Shrublands

At cutover lands, secondary grasslands and shrublands are established and maintained for several years after clear-cutting in secondary forests and conifer plantations (Ministry of the Environment of Japan, 1999). Despite their short time periods, cutover lands are widely distributed from subalpine to warm temperate regions throughout the country (Fig. 2) and harbor many shrub, grassland herb and insect species (Inoue, 2003; Ushimaru et al., 2008). In cutover lands, *Sasa* spp., *M. sinensis*, *Cirsium* spp. *Rubus* spp., *Aralia elata* and *Stephanandra incisa*, are often abundant (Inoue, 2003, Fig. 4G).

In subalpine and temperate zones, recently increasing deer grazing has facilitated the establishment of secondary grasslands dominated by toxic plant species, such as *Senecio cannabifolius*, *Ligularia dentata* and *Hypolepis punctata*. In Bonin and Izu islands, grazing by feral goats have maintained alien herb-dominated secondary grasslands (Shimizu, 1991; Hayakawa, 1993, Fig. 4H).

Ecology and Biodiversity Patterns

For biodiversity conservation, natural and semi-natural grasslands and shrublands are essential ecosystems. Japan harbors more than 2800 endemic terrestrial plant species (including endemic subspecies and varieties) and is designated as a global biodiversity hotspot: 36% of vascular plant species are endemic to Japan (Kato and Ebihara, 2011). Grasslands and shrublands on serpentine and limestone areas (Mt. Apoi, Mt. Yubari and Mt. Shibutu) and those in oceanic (Bonin and Izu) islands are regional hotspots of endemic herb and shrub species (Ebihara, 2011). Riparian gravel bar grasslands have many river-side specialist species such as *Potentilla chinensis*, the endemic *Anaphalis margaritacea* subsp. *yedoensis*, *Artemisia capillaris*, *Eusphingonotus japonicus* and *Omophron aequalis* (Washitani, 2001; Yoshioka et al., 2010; Ministry of the Environment of Japan, 2014). Riparian grasslands often harbor non-endemic but endangered plant species as well (Fig. 4C). Coastal grassland and shrubland vegetation exhibit high endangered plant diversity: 23% of the coastal-specialist species are listed in the national red list (Sawada et al., 2006). Riparian and coastal grasslands sometimes share the same species with semi-natural grasslands.

As for Japanese semi-natural grasslands, a lower endemism in plant species composition are known: the same species are distributed in grasslands of the Korean Peninsula and meadow steppes of northeastern China (Kadota, 2011). Despite a low endemism at the species level, semi-natural grassland butterflies exhibit a higher endemism at the subspecies level (Ohwaki, 2018). Moreover, many semi-natural grassland plant and animal species are now at risk of extinction in Japan (Koyanagi and Furukawa, 2013; Uematsu and Ushimaru, 2013; Nakahama et al., 2016; Uchida et al., 2016a,b,c; Koyama et al., 2017). Large semi-natural grassland areas (e.g., Aso and Mt. Fuji areas) are considered as regional or local hotspots, which harbor numerous endangered species (Fig. 1 in Kadota et al., 2014; Kitahara and Sei, 2001; Kubo et al., 2009; Ministry of the Environment of Japan, 2014; Uchida et al., 2016a). Narrow meadows around cultivated fields have maintained a high endangered species diversity as well (Kusumoto and Inagaki, 2016; Uchida et al., 2016c). Traditional extensive land-management practices have played as kinds of disturbance to maintain diverse endangered and common grassland plant and animal species, but recently the biodiversity has rapidly decreased due to various land-use changes (see detail in Threat). Thus, the Japanese grasslands and shrublands are local or regional hotspots of endemic or endangered species.

Threats

The flora of subalpine and island grasslands and shrublands is mostly protected within national parks. Although these vegetation have been protected from anthropogenic activities in general, the future climate changes may degrade the vegetation (Hotta et al., 2014; Ministry of the Environment of Japan, 2012). In Mt. Apoi-Dake, grassland area have declined owing to a rapid expansion of Japanese stone pine (*Pinus pumila*) to higher altitude (Ministry of the Environment of Japan, 2012). Reduced snowfall is also the potential driver of the degradation of subalpine grassland and shrubland vegetation by facilitating browsing impacts of sika deer (Takatsuki, 2009). In Bonin islands, feral goats have caused drastic vegetation changes and loss of endemic grassland and shrubland species (Shimizu, 1991).

Riparian grasslands and shrublands have undergone rapid changes to willow-dominated forests in recent decades (Nakamura et al., 2016). Large dams and consolidated river banks, which have been constructed to guard against large disasters by flooding after typhoon events, heavily reduce river disturbance events. This, in turn, has promoted successions from grasslands and shrublands to forest vegetation in riparian zones (Washitani, 2001; Nakamura et al., 2016). In addition, coastal vegetation maintain many endangered species that rapidly declined during recent decades (Sawada et al., 2006). The major driver of the declines is coastal

development. Currently, 41% of Japan's coastal lines have been "developed" with concrete to counteract tsunamis or big waves associated with typhoon-induced surges.

As for semi-natural grasslands, the areas have decreased during the last century, mainly due to land-use changes in Japan. After World War II, drastic population migration from rural to urban (industrial) areas has occurred within the country under very rapid economic growth, in which industrial structure shifted from agriculture to manufacturing during the late 1950s to the early 1970s. The situation caused various land-use changes in semi-natural grasslands, which in turn resulted in rapid loss and degradation of semi-natural grasslands in Japan (Ministry of the Environment of Japan, 2016). Over the past 80 years (c. 1920–2000), semi-natural grassland areas have largely declined throughout Japan: approximately 38,000 km² of semi-natural grasslands existed at the beginning of the 20th century (c. 10.1% of Japan's total lands), but only c. 4300 km² grassland (c. 1.1% of total land area) remained in 2000 (Ogura, 2006). Based on our own estimation using the 5th vegetation survey data, the total area of semi-natural grasslands including ski and training ground grasslands is c. 5600 km² (c. 1.5% of the total land surface) (Fig. 2). Although the estimates were different, there is agreement that only a small fraction of the grasslands has remained today. Additionally, *satokusachi* meadows have rapidly declined after World War II: total *satokusachi* meadow area was of 3090 km² in 1956, but they decreased to 1850 km² in 2010 (Ministry of Agriculture, Forestry and Fisheries of Japan, 2016).

Major drivers of semi-natural grassland loss have been abandonment, intensified use, afforestation and urban development in Japan as in other Palaearctic areas (Török and Dengler, 2018). After World War II, the energy and green revolutions in rural areas have promoted abandonment of husbandry and green manure production, and subsequently the conversion of grasslands into other land uses (Ministry of the Environment of Japan, 2012). Depopulation and aging farmers in rural areas further have accelerated this trend (Normile, 2016; Osawa et al., 2016b).

Land abandonment that promotes subsequent vegetation succession to forests is the most influential driver of declines in grassland specialist species in Japan (Suka et al., 2012; Nagata and Ushimaru, 2016; Uchida et al., 2016a). Huge semi-natural grassland areas are considered to have changed to secondary forests, although there were no reliable data on how much grasslands have been abandoned to date (Ministry of Environment of Japan, 2016). Paddy field abandonment has caused not only endangered species declines but also decreases in almost of all grassland species diversity in Japan (Fukamachi et al., 2005; Uematsu et al., 2010; Uchida and Ushimaru, 2014; Osawa et al., 2016b; Uchida et al., 2016c).

Management method changes in remaining semi-natural grasslands have often occurred during recent decades due to labor-saving and/or loss of local traditional knowledge, causing grassland biodiversity loss (Suka et al., 2012). For example, in Kiso area, a central part of Honshu, abandonment of the traditional practice has caused plant and butterfly species declines (Nagata and Ushimaru, 2016; Uchida et al., 2016a). Recent changes in mowing timing were responsible for declines in reproductive success and genetic diversity of an endangered grassland plant species, *Vincetoxicum pycnostelma* in meadows (Nakahama et al., 2016). The knowledge of traditional practices is diminishing year by year via new socioeconomic drivers such as the introduction of large machinery agriculture and aging farmers (Uchida and Ushimaru, 2014; Uchida et al., 2018a). Because traditional practices are very diverse depending on grassland type and region, we need to find ways to pass down these practices to the next generations.

The effects of intensified use (i.e., land consolidation and nitrogen input) are conspicuous in *satokusachi* meadows around paddy fields in Japan. Paddy consolidation, which converts narrow, irregular and poorly drained paddy fields into wide, quadrangular and well-drained fields to improve productivity and to allow mechanized farming, rarely leads to grasslands that resemble the original ones in composition and structure (Matsumura and Takeda, 2010; Uematsu et al., 2010). More than 65% of paddy fields are now consolidated (Ministry of Agriculture, Forestry and Fisheries of Japan, 2019), which largely reduced plant and herbivorous insect diversity via changing management frequency and characteristics of the surrounding landscape (Uchida and Ushimaru, 2014). The effects of nitrogen input on biodiversity of pastures have not been conspicuous in Japan, although the negative effects are well known to cause biodiversity loss in European semi-natural grasslands (Kleijn et al., 2009; Dengler and Tischew, 2018; Török et al., 2018). Pastures and meadows are usually established on *kurobokudo*, which typically consists of volcanic ash and humus and is very acidic (pH < 5.7) and oligotrophic (<200 mg P₂O₅/kg) (Hiradate et al., 2008; Nagata and Ushimaru, 2016; Koyama et al., 2017). Manuring had always failed to effectively improve productivity of Japanese pastures due to the oligotrophic soil conditions and had been gradually discouraged (Numata, 1961). Nutrient input and neutralization of the formerly acidic soil in consolidated paddy fields can cause declines in rare plant species (Uematsu and Ushimaru, 2013) and increases of invasive alien plants, such as *Andropogon virginicus*, *Erigeron annuus* and *Solidago altissima* (Hiradate et al., 2008). For areas promoting intensified livestock farming, farmers improved pastures via replacing native grass and herb species by introducing alien ones (Numata, 1961). For example, large semi-natural grassland areas in Aso were converted to sown pastures by the national grassland improvement project. Similarly, huge semi-natural grassland areas of eastern Hokkaido were "improved" into sown pastures, dominated by non-native grass *Poa pratensis* from Europe, until the 1960s (Numata, 1961).

Moreover, conversion of pastures and meadows to conifer plantations have been promoted for post-World War II rebuilding since the 1950s. The total area of plantations drastically increased from c. 49,700 km² in 1952 to c. 102,900 km² in 2012 according to various data from the Ministry of Agriculture, Forestry and Fisheries. However, there are no reliable statistics on how much semi-natural grasslands have been converted to plantation in Japan.

Rapid urbanization since the 1960s has also caused drastic decreases in lowland paddy and vegetable fields and riparian floodplain grasslands (Washitani, 2001; Tsuji et al., 2011). Current assessments of the effects of urbanization on biodiversity of *satokusachi* meadows indicate significant negative impacts on grassland plants and animals via habitat loss and degradation (Tsuji et al., 2011; Uchida et al., 2018b).

Overall, areas of natural and semi-natural grasslands and shrublands are rapidly lost owing to diverse human impacts. As a consequence of the widespread loss and fragmentation of natural and semi-natural grasslands and shrublands, plant and herbivorous insect diversity has declined drastically (Suka et al., 2012; Koyanagi and Furukawa, 2013).

Conservation, Restoration and Sustainable Management

As above stated, grassland and shrubland biodiversity has been rapidly threatened by various drivers in Japan. On that account, a variety of biodiversity conservation and restoration activities have been conducted to meet differentiated necessities. Currently, subalpine (subarctic) and island grasslands and shrublands and those on specific soils are mainly protected in national parks, so the national (Ministry of the Environment of Japan and the Forestry Agency and the Cultural Agency of Japan) and local governments direct the conservation planning, to which researchers and local organizations contribute as well. Similarly, the national (Ministry of Land, Infrastructure, Transport and Tourism of Japan and Ministry of the Environment of Japan) and/or local governments manage conservation and restoration of grasslands and shrublands in riparian and coastal areas, with consultation of academic societies and local organizations. Meanwhile, many different stakeholders, including governments, citizens, local committees, non-profit organizations (NPOs) and scientists (for details, see below) have conducted conservation and restoration of semi-natural grasslands, which are predominantly private lands or local commons.

Legal Conservation and Restoration Status

The principal parts of the natural and several expanses of the semi-natural grasslands and shrublands are conserved as parts of the national and quasi-national parks in Japan. Feeding damage on rare plant species by sika deer, however, has become serious in some subalpine areas (natural grasslands and shrublands of the South Japan Alps and the semi-natural grasslands in Kirigamine). In such areas, deer fences have been constructed to protect the vegetation. In Bonin islands, a World Heritage site, eradication of feral goats has been conducted by the Tokyo Metropolitan government to restore natural grasslands and shrublands. In several islands, all the goats were successfully eradicated and natural grasslands and shrublands have been restored (Hata et al., 2010), although long-lasting negative effects of goat grazing and trampling on soil conditions have limited full restoration of natural grasslands and shrublands (Osawa et al., 2016a; Hata et al., 2019, Fig. 4H). In addition, a small area of semi-natural grassland, which has been maintained in the Kaida Plateau, Nagano prefecture, is conserved as a reserve for some endangered species of plants and insects by the local prefectural government (Nagata and Ushimaru, 2016; Uchida et al., 2016c). As special cases, several endangered semi-natural grassland plants and insects (e.g., *Polemonium kiushianum*, *Agapanthia japonica* and *Celes akitanus*) as well as island grassland and shrubland species (e.g., *Patrinia triloba* var. *kozushimensis*, *Symplocos kawakamii* and *Parnara ogasawarensis*) are protected under the Law for the Conservation of Endangered Species of Wild Fauna and Flora and similar local regulations.

Although global warming is believed to significantly influence grasslands and shrublands, especially those in subalpine (subarctic) zones and islands, the expected impacts have been poorly investigated (Ministry of the Environment of Japan, 2012). The national government has promoted the enhancement of scientific knowledge on global warming impacts and how to adapt to them under Climate Change Adaptation Act which were enacted in 2018.

Semi-natural Grassland Conservation

To conserve semi-natural grasslands, support measures as well as regulatory measures should play an important role under the current socioeconomic situations. Regarding an international approach, GIAHS designation by FAO encourages semi-natural grassland conservation activities of local communities in the Aso area and in the tea plantation areas of Shizuoka. In the light of national and local approaches, ASO Grassland Restoration Committee (AGRC) has been established under the Act on the Promotion of Nature Restoration. The AGRC is facilitating local activities for conservation and restoration of semi-natural grasslands by engaging in promotions of sustainable use of the grasslands, biodiversity conservation, environmental education, ecotourism and adding of values to grassland resources by supporting scientific researches (AGRC, 2017). Some subsidy schemes for conservation of semi-natural ecosystems to farmers by national and local governments exist but are operating insufficiently for grassland conservation.

During the last decades, people have realized the values of semi-natural grasslands in the terms of low-cost resources for modern husbandry and biodiversity and cultural landscape conservation (Japanese Society of Grassland Science, 2010). These social backgrounds have promoted a variety of public and private activities for conservation and restoration of Japanese semi-natural grasslands (Japanese Society of Grassland Science, 2010; Ushimaru et al., 2018). Abandoned or unmanaged semi-natural grasslands have usually been restored by reintroduction of burning, grazing and/or mowing: Reintroduction of traditional management schemes combining spring burning and autumn mowing successfully restored plant richness in Aso (Koyama et al., 2017). Although burning is an unfamiliar restoration measure in European counties (Valkó et al., 2014), it is very effective together with use of mowing for meadow biodiversity maintenance in Japan (Nagata and Ushimaru, 2016; Koyama et al., 2017) like in North America (Valkó et al., 2014). Reintroduced extensive cattle grazing has resulted in an increase in autumn-blooming species and in population size of an endangered *Pulsatilla cernua* in an abandoned pasture (Japanese Society of Grassland Science, 2010). To restore meadow biodiversity, reintroduction of mowing is effective as well. Removal of the tall grasses, *Miscanthus sinensis* and *Pleioblastus chino* var. *viridis* from abandoned meadows by reintroduced mowing effectively increased species richness or a population of

endangered species (Japanese Society of Grassland Science, 2010; Hashimoto et al., 2012). Reintroduction of mowing should also be suitable to restore narrow meadows around abandoned paddy fields (Ushimaru et al., 2018). Yet, only a handful of restoration projects have examined the effects of management reintroduction on restoration of abandoned or degraded pastures and meadows in Japan. Therefore, no clear recommendations can be made currently. For example, in Koshimizu Nature Reserve, Hokkaido an experimentally introduced combination of burning and grazing management unexpectedly increased the alien plant dominance, suggesting the importance of continuous monitoring and adaptive management strategy (Tsuda et al., 2002). Thus, accumulating knowledge of semi-natural grassland management through studying grassland restorations is needed to establish the modern ways of grassland managements.

Acknowledgments

We thank Jürgen Dengler and Péter Török for inviting us to write the chapter and giving us constructive advice. This work was supported by grants-in-aid for A. Ushimaru from The Japan Science Society for the Promotion of Science (Nos. 20770015, 23570024, 17K07557, 16H02993 and 19H03303) and Ichimura foundation for New Technology (26-10, 27-9, 28-12).

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Grasslands and Savannas of South Asia

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Glossary

Deccan Plateau Deccan Plateau is the large, inverted triangle-shaped plateau that comprises the Indian Peninsular.

Ecoregions Ecoregions are relatively large units of land or water containing a distinct assemblage of natural communities sharing a large majority of species, dynamics, and environmental conditions (definition from [Olson et al., 2001](#)).

Relict species Relict species is a taxon that was once widespread and diverse, but where the current occurrence has been reduced to a relatively more restricted area, usually through geological time and events.

Succession Succession is an ecological process of change of an ecological community or vegetation composition. The process will include several seral or intermediate communities until it reaches a stable state, or climax community, determined by the interactive environmental variables in the area. The process can include several associated states as defined below:

- Climax stage is the stable ecological community achieved at the end of the succession process, and will remain relatively unchanged in the absence of disturbances.
- Deflected succession is a process where a vegetation community is maintained in a quasi-stable by continuous or frequent human activity that prevents the system from achieving a climax state.
- Disclimax is a vegetation community which is maintained in a stable but subclimax state due to constant or frequent disturbances.
- Edaphic climax is a vegetation community that is maintained primarily by substrate conditions, such as soil type, moisture, depth, topography, etc.

Abstract

Grasslands have an ancient history in South Asia. Reconstructions of geological history and biogeography indicate that grasslands spread through South Asia after the northward drifting Deccan Plate collided with the northern Laurasian continent about 40 million years ago. The larger, distinctive patches of grasslands in South Asia are the Terai-Duar alluvial grasslands and savanna along the floodplains of the Ganges River system, the large shola grasslands on the high elevation hill slopes and plateaus of the Western Ghats mountains, the *Banni* and *Vidi* grasslands of Gujarat in northwestern India, the plateau and valley grasslands along the Satpura and Maikal mountain ranges in north-central India, the dry grasslands of Andhra Pradesh and Tamil Nadu plains in the south and central regions of the Indian peninsula, and the montane patana grasslands on the southeastern slopes of the central mountains of Sri Lanka. Most South Asian grasslands are disclimax or edaphic climax communities. Some scientists consider these to be interim 'stable' states, maintained through 'deflected succession' due to continuous disturbances that keep setting back successional processes, preventing the ecosystems from attaining a 'climax stage.' Some grasslands, are, however, maintained by edaphic conditions, where the soil conditions prevent growth of trees, and the grasslands are considered to be an 'edaphic climax' community. These South Asian grasslands now harbor a rich biota, with many faunal species having adapted their behavior to the ecological dynamics of grasslands. For example, several birds time their nesting and mating periods to coincide with grassland dynamics drive by seasonal floods and fires. The South Asian grasslands are also especially important for grazing herbivores that include large deer, Asian elephant, and Greater One-horned Rhinoceros. Where ungulate prey gather predators follow; thus, the grasslands support high densities of Asia's largest predator, the Tiger.

What Are Grasslands? Back to Basics

A grassland is easy enough to identify by sight as an area dominated by grasses. But it's a challenge to define ecologically because the ecosystem processes that determine its physiognomy are complex. As a result, there are several definitions of grasslands that focus on structure, function, and even on the absence of specific features, such as woody plants and trees (Gibson, 2009). But there are three characteristics that unite most of these definitions (Gibson, 2009). The first is the dominance of grasses, or members of the plant Family Poaceae. Second, is the low abundance of wood vegetation; usually trees. Third is a generally arid climate. Other characteristics that are included in the range of definitions include deep and fertile soils, frequent disturbances from fires and floods or grazing, and soil types. This general inability among scientists to define what seems to be a fairly simple ecosystem actually hides the highly dynamic and responsive nature of grasslands that are maintained by various drivers of environmental change or conditions that attain different levels of importance based on where the grasslands are. White et al. (2000) simplified this conundrum by providing a working definition of grasslands as "terrestrial ecosystems dominated by herbaceous and shrub vegetation and maintained by fire, grazing, drought and/or freezing temperatures." This straightforward-sounding definition then includes the physiognomy and the drivers that maintain the grasslands.

Grasslands occur in every continent on Earth, except for Antarctica (White et al., 2000). They cover an estimated 40% of the Earth's land area, although this is based on a broad inclusion that of savannas, shrublands, and tundra (Gibson, 2009; White et al., 2000). Grasslands support rich ecological communities—visualize the Serengeti Plains of East Africa with teeming herds of wildlife. They are critically important habitats for breeding, migrating, and wintering birds, support rich and diverse soil faunas, and are feeding grounds for diverse ecological communities of wild ungulates that in turn support some of the most charismatic mega-predators on Earth.

Grasslands also provide a multitude of ecosystem goods and services to support human communities and have done so for millennia. Over the centuries they have been extensively cleared for agriculture, but they are also the storehouses for source pools of grains such as wheat, corn, rice, rye, millet, and sorghum that have supported civilizations. Even now, grasslands are the primary source of genetic resources for improving agricultural crops. They have been pastures for livestock tended by ancient and present pastoral communities. Grasslands are important to cycle water and nutrients, and they help to store below-ground carbon, contributing to limit global warming.

Unfortunately, grasslands the world-over are highly threatened by various drivers of change, especially from conversion to agriculture, urbanization and human settlement, desertification, exotic invasive species, and fragmentation (Gibson, 2009; White et al., 2000).

Biogeographic Origins of South Asia and South Asian Grasslands

South Asia, consisting primarily of the Indian Subcontinent, is the geographical reference to the landmass to the south of the Himalayan Mountain range, and bordered on the east and west by the Ganges and Indus River valleys, respectively. The region is represented by seven countries, namely Bangladesh, Bhutan, India, Maldives, Nepal, Pakistan, and Sri Lanka. In addition to these political entities, there are 55 terrestrial ecoregions represented in this region, including those that extend into the high Himalayas (Fig. 1). With the exclusion of the alpine meadows along high elevations of the Himalayan range, the only extent of grasslands that are large enough to qualify as an ecoregion in spatial scale (see Olson et al., 2001 for treatise on ecoregions), is the Terai-Duar Grasslands and Savannas ecoregion, which extends as a long, narrow swathe from northwestern India, through the southern regions of Nepal and Bhutan and eastern India (Fig. 1, Wikramanayake et al., 2002). Most of the other terrestrial ecoregions in South Asia belong to dry deciduous forests, thorn scrub forests, or tropical and subtropical broadleaf forests.

Despite the relatively less predominance and representation in South Asian ecoregions, grasslands have relatively ancient histories in South Asia, and date back several million years, as reconstructed by multiple sources of circumstantial evidence. The biogeographic origins of the present-day South Asia region are traced back to the southern supercontinent known as Gondwanaland, which comprised of an amalgamation of the African, Antarctic, Indo-Australian, and South American tectonic plates during the late Jurassic period. When this continent broke up during the Cretaceous period, about 100 million years ago, the tectonic plate bearing the area that now forms much of the Indian Subcontinent, began a slow drift northward, until it collided with the northern Laurasian continent that is now Central Asia. The collision, about 40 million years ago (Bouilhol et al., 2013), created violent geological uplifts that formed the Himalayas, that contain the highest mountain peaks on Earth. The Indian subcontinent, or the plate which contains most of the Deccan Plateau and Sri Lanka, thus harbors relict species of the ancient southern flora and fauna with links to Africa and Madagascar (Srivastava, 2011; Prasad et al., 2013).

The grasslands of South Asia likely spread through the subcontinent long after the collision, following the long continental voyage. The evolutionary history of grasslands throughout the world can be broken down into distinct stages in paleobiogeographic history, covering a period known as the Paleogene, which began 66 million years ago and lasted for about 43 million years, and the subsequent Neogene period that lasted until about 2.5 million years ago (Strömberg, 2011). During the Paleogene, the Earth's climate shifted from warm and humid conditions to a cooler and drier environment. This was the period when the Indian Subcontinent was closer to its current position, and in the process of colliding with the northern continent of Laurasia. This was also the period when mammals began their great diversification, during the latter part of the Paleogene, an era known as the Oligocene,

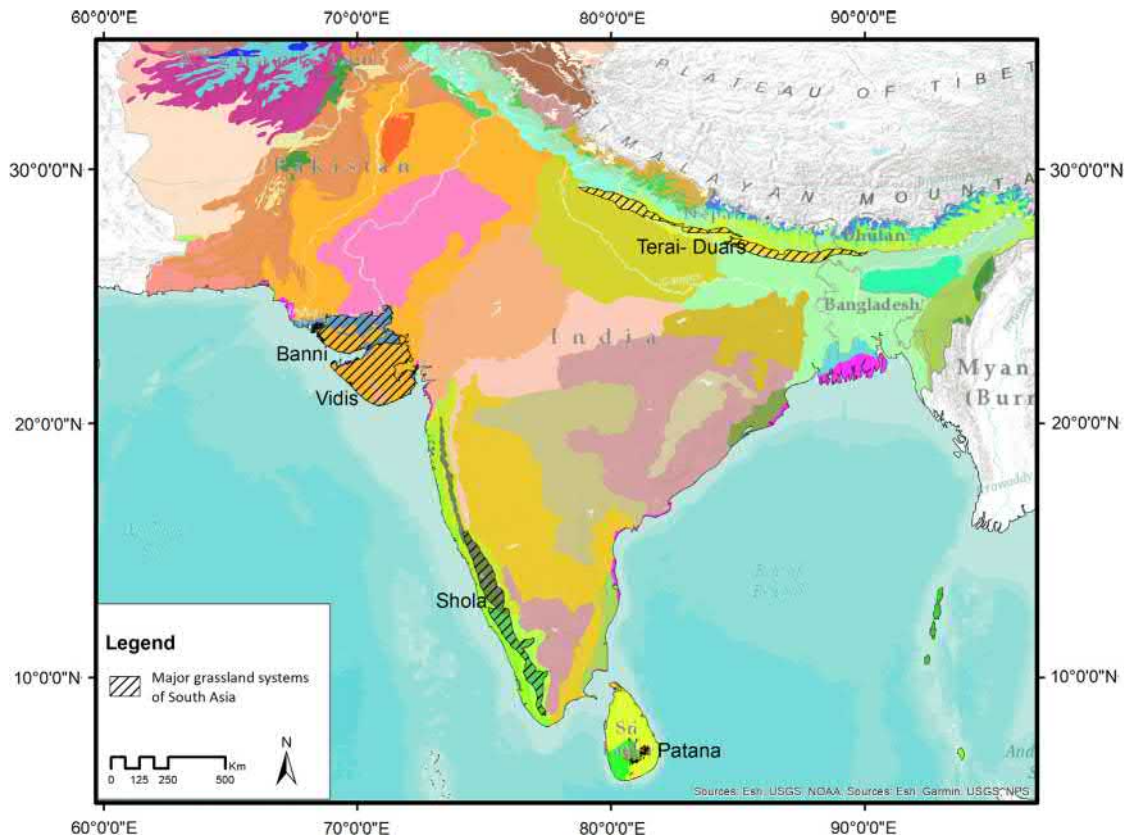


Fig. 1 The locations of the major grassland ecosystems of South Asia, in relation to the ecoregions of South Asia. More details about the ecoregions can be found in Wikramanayake et al., 2002, and at <http://ecoregions2017.appspot.com/>. The grasslands occur as scattered vegetation types or ecosystems within the ecoregions that represent regional-scale ecosystems. The only distinctive grassland ecosystem to be recognized as an ecoregion is the Terai-Duars along the base of the Himalayan mountains, where annual flooding of the Ganges and Brahmaputra rivers scours the alluvial floodplains, creating conditions that encourage and maintain grasslands.

about 32 million years ago. This diversification of mammals and the fossil teeth they left behind provides one line of evidence to trace the history of grasslands, another being pollen counts (Strömberg, 2011 and references therein).

As the climate continued to cool there was a shift in vegetation. Many of the larger tropical plants began to die off and became replaced by grasses and herbs. Thus, the Paleogene period saw the emergence of grasslands. The initial grassland communities included both C_3 and C_4 grasses, adapted to open habitats, but with continued atmospheric cooling, the environment favored C_3 grasses, which began to dominate the grasslands, until the late Neogene, when warming trends turned the tide back in favor of C_4 grasses that spread southwards into the tropical-subtropical latitudes. The C_4 photosynthetic pathway allows grasses to fix carbon more efficiently under high temperatures, aridity, and low atmospheric CO_2 conditions than the C_3 pathway, and favor their growth in tropical and subtropical lowlands and areas with warm-season precipitation (Ehleringer and Cerling, 2002).

Grasslands of South Asia. Where They Are

Although not large enough to be considered ecoregions on their own, there are several areas with relatively extensive grasslands in South Asia (Fig. 1). All are considered to be disclimax or edaphic climax communities. The most extensive is, of course the alluvial grasslands and savanna along the base of the Himalayan mountain range, which has been recognized as an ecoregion (Wikramanayake et al., 2002). These grasslands—considered to be the tallest in the world because of the wild sugar cane (*Saccharum spontaneum*) grasses that can grow to over seven meters tall and effectively tower over elephants that wander through them—grow in the floodplains of one of Asia's largest and most revered river systems, formed by the Ganges and Brahmaputra Rivers.

Other less extensive, but nevertheless significantly large areas of grasslands occur in the Indian Subcontinent; estimates derived from satellite imagery indicate that about 17% of the land area of India is covered by grasslands (White et al., 2000), but these include the alpine meadows of the high Himalaya, the alluvial grasslands along the base of this mountain range, and the scattered grasslands further south in the Deccan Plateau. The more extensive of the latter grasslands are found on the high elevation rocky hill slopes and plateaus of the Western Ghats mountain range that runs parallel to the western coast of the Indian peninsula, or Deccan

Plateau, the 'Banni' and 'Vidi' grasslands of Gujarat, the plateau and valley grasslands along the Satpura and Maikal mountain ranges in the north-central regions of the Indian peninsula, and the dry grasslands of Andhra Pradesh and Tamil Nadu plain in the south and central regions of the Indian peninsula (Rawat and Adhikari, 2015). Further south, the island of Sri Lanka has several grasslands on the southeastern slopes of the central mountains (Pemadasa and Mueller-Dombois, 1979; Mueller-Dombois, 1968).

Ecological Dynamics of South Asian Grasslands. How Are They Maintained?

What maintains the grasslands of South Asia is an important question to explore because there are many different points of view proposed on whether these grasslands are 'climax' ecosystems, or an interim stage in the 'successional process.' A climax community represents the 'stable' 'end point' along the process of recovery of an ecosystem that has been disturbed. Some scientists consider the South Asian grasslands as being an interim 'stable' state and maintained through a process termed 'deflected succession,' where the grasslands maintained by relatively continuous or frequent disturbances or forces that keep setting back the successional processes, thus preventing the ecosystems from attaining the 'climax stage.' The disturbances that set back succession can be floods, fire, frost, or even diseases that can kill trees and cause widespread changes to the ecosystem composition. Or they can even be anthropogenic forces such as unsustainable harvesting of trees for a variety of purposes, from construction to firewood, as well as grazing livestock or fires set to create pastures or hunting grounds. Some grasslands, are, however, maintained by edaphic conditions, where the soil depth or composition prevent growth of trees, and the grasslands are considered to be an 'edaphic climax' community. However, with time, as the top soils begin to develop through weathering, these grasslands can succeed into forests or savannas.

For example, research and analyses of human settlement patterns in the Western Ghats point to frequent fire set by early pastoral and agricultural communities as the primary driver that maintains the grasslands, known as *Shola*, in the hills of this mountain range (Thomas and Palmer, 2007). More recent analyses have also shown that topography and bioclimatic variables such as ambient and soil temperature regimes, moisture and precipitation determines the configuration of the grasslands and forests in the matrix, with slopes that are more affected by insolation and lack of moisture and greater proneness to fires being clothed with grasslands, while forests grew in shaded valleys (Das et al., 2015). Thus, ecological dynamics of grasslands are complex and complicated.

In Sri Lanka, the origin and maintenance of the montane *Patana* grasslands are also under contention, with some researchers pointing to a 'disclimax' state, or a 'stable state' maintained below a climax state, due to frequent burning (Holmes, 1951), while others argue for an ecosystem maintained by edaphic conditions (De Rosayro, 1946); however, this conflict has not been resolved (Pemadasa, 1990).

Biodiversity of South Asian Grasslands

The grasslands of South Asia harbor a rich biota, with many faunal species having adapted their behavior to the ecological dynamics of grasslands through the millennia. Several birds time their nesting and mating periods to coincide with grassland dynamics. Species such as the Great Indian Bustard (*Ardeotis nigriceps*) and Lesser Florican (*Sypheotides indicus*) are now highly threatened because of loss of grasslands and disruption of the seasonality of the dynamics that maintain grasslands. The South Asian grasslands are also especially important for the grazing herbivores that include large deer such as Sambar (*Rusa unicolor*), Spotted Deer or Chital (*Axis axis*), Blue bull or Nilgai (*Boselaphus tragocamelus*), Blackbuck (*Antelope cervicapra*), as well as Asian elephant (*Elephas maximus*), and Greater One-horned Rhinoceros (*Rhinoceros unicornis*). Where ungulate prey gather in numbers, the predators will follow; thus, the grasslands support some of the highest densities of Asia's biggest and most charismatic predator, the Bengal Tiger (*Panthera tigris*). Other predators such as Striped Hyena (*Hyaena hyaena*) and Indian Wolf (*Canis lupus pallipes*) also use these grasslands and the high prey densities they offer. Over the ages, species like Blackbuck (Fig. 2) and Swamp deer (*Rucervus duvaucelii*) (Fig. 3) have evolved and adapted to specific grassland types. Larger carrion seeking birds such as vultures also gather in the grasslands. The Indian grasslands have a rich assemblage of vultures that include Red-headed vulture (*Sarcogyps calvus*), White-backed vulture (*Cyps africanus*), Long-billed Vulture (*Cyps indicus*), Slender-billed Vulture (*Cyps tenuirostris*), and Egyptian Vulture (*Neophron percnopterus*). The isolated patches of montane grasslands have also been recognized as centers of endemism, and adaptation (Das et al., 2015; Rodgers and Panwar, 1988).

Terai Duar Grasslands and Savanna of India, Nepal and Bhutan

These grasslands cover the floodplains of the rivers that cascade down from the Himalayan Mountains into the lowlands and inner valleys and bring down large silt loads that are deposited in the floodplains. Large silt loads are also carried far by the two major rivers, the Ganges flowing from the west and Brahmaputra from the east and become confluent, to the Bay of Bengal where they sustain the largest mangrove in the world, the Sunderbans.

These grasslands extend as a narrow swathe from northwestern India's Himachal Pradesh, through southern Nepal into Bhutan and Arunachal Pradesh further east in India (Fig. 1). The ecoregion name is derived from the colloquial name for these grasslands, known as the *Terai* in the western range and *Duars* in the east.



Fig. 2 Blackbuck, *Antelope cervicapra*, are adapted to live in short grasslands and are now found in isolated populations in northwest India and western Nepal, where they live in a semi-captive state. They are fast runners enabling them to escape predation by the Asiatic Cheetah, *Acinonyx jubatus venaticus*, which is now extinct in India. Courtesy: E. Wikramanayake.

The climate is hot and humid in the summer months, especially immediately before the torrential monsoon rains begin, when temperatures can exceed 40 °C. But the winters are cool, dropping low enough to form morning ground frost. A blanket of fog and low clouds in the winter overlies the grasslands and can remain until late morning, adding to the winter chill. It is this extreme



Fig. 3 Swamp deer or *barasingha*, *Rucervus duvaucelii*, are adapted to live in marshy alluvial grasslands of the Terai Duar Savanna and Grasslands ecoregion. This species is now mostly confined to a few protected areas along the base of the Himalayan Mountain range in southern Nepal and Northern India. Courtesy: E. Wikramanayake.



Fig. 4 The monsoon clouds darken the skies over the Terai grasslands in southern Nepal. The mature flower stalks of wild sugar cane, *Saccharum spontaneum*, will shed seeds that will regenerate the grasslands after the floods scour the alluvial plains, resetting succession. Courtesy: E. Wikramanayake.

monsoonal seasonality that maintains the *Terai-Duar* grasslands (Fig. 4). The combination of annual floods from the gushing, silt-laden mountain rivers and to a lesser extent, fires set back succession by flushing and burning the floodplains and clearing the saplings and seedlings from the encroaching forest trees, but the grasses regenerate rapidly after the floods and fires. But scattered trees *Bombax ceiba* or silk cotton trees, or smaller patches of evergreen and deciduous broadleaf forests can survive, adding some savanna-like definition to the landscape vegetation.

The grassland communities are also quite variable, with the species compositions determined by the fluvial and fire-related disturbances, edaphic conditions, moisture, and the hydrological and hydraulic processes from floods. For instance, as the rivers change course from alluvial deposition and water flow intensities, they can leave behind isolated ox-bow lakes, abandoned channels, and new alluvial depositions, all of which can support different grassland communities in this highly dynamic landscape.

The alluvium replenishes the floodplains and enhances the productivity of the grasslands, which provide nutrition to a rich assemblage of small to large herbivores. The latter that includes some of Asia's largest terrestrial animals, such as Asian elephants, Greater One-horned Rhinoceros, Wild Water Buffalo (*Bubalus arnee*), Guar (*Bos gaurus*), Sambar, and Swamp Deer. The high densities of these ungulates also support high densities of predators, including Asia's largest, the charismatic Bengal Tiger. Great Hornbills (*Buceros bicornis*), Sarus Crane (*Grus antigone*), Bengal Florican (*Houbaropsis bengalensis*), several species of vultures, and Lesser Adjutant Stork (*Leptoptilos javanicus*) add to the charismatic avian community, while the rivers support mugger crocodiles (*Crocodylus palustris*), gharial (*Gavialis gangeticus*), Gangetic river dolphins (*Platanista gangetica*) and large mahseer fish (*Tor* spp.).

Grazing is another ecological process that contributes to the grassland structure and composition. Historically, most grazing was by the diverse community of ungulates, from small Muntjak or barking deer (*Muntiacus muntjac*) and Hog deer (*Axis porcinus*) to the larger sambar, swamp deer, water buffalo, rhinoceros and elephants. But now herds of domestic cattle also contribute to grazing intensity and influence the vegetation community diversity and distribution, and contribute to the degradation of grasslands, setting back the disclimax state even further.

The early studies of the Terai grasslands conducted by Lehmkühl (1994) and Peet et al. (1999) describe several grassland vegetation assemblages, including different successional stages. In general, the grassland assemblages are influenced by moisture levels and disturbance. The grasslands in permanently wet or seasonally inundated areas are dominated by tall grasses such as *Phragmites karka* and *Saccharum spontaneum*, while drier areas are dominated by *Narenga porphyrocoma* and *Themeda arundinacea*. Abandoned agricultural sites are characterized by the shorter *Imperata cylindrica*. Grazing lawns with short grasses and forbs are interspersed amidst the large patches of tall grasslands (Karki et al., 2000), and are dominated by *Imperata cylindrica*, *Saccharum spontaneum*, *Vetiveria zizanioides*, and *Desmostachya bipinnata*, but kept cropped down by the community of grazing mammals, including included Chital, Swamp deer, Hog deer, Greater one-horned rhinoceros, and Muntjak.

Peet et al. (1999) went further, and described nine grassland vegetation communities from the Terai, based on sampling in protected areas in Nepal, which now support the remaining refuge remnants of these grasslands. Community composition was described on the basis of the dominant species, which were generally represented by five or less species that contributed to the total vegetative cover. The assemblages are:

1. *Typha elephantina* assemblage that grows in permanently water-logged sites
2. *Phragmites karka*-*Saccharum spontaneum* assemblage that grows in seasonally inundated and heavily grazed areas
3. *Phragmites karka*—*Saccharum spontaneum*—*Saccharum arundinaceum* assemblage
4. *Phragmites karka* assemblage, a tall, dense riverine grassland community that grows in seasonal and permanent marshes
5. *Saccharum spontaneum* assemblage, which is a phase that can include a mixed *Saccharum spontaneum*—*Dalbergia sissoo* association in the floodplain grasslands and alluvial soils that are often inundated
6. *Imperata cylindrica* assemblage that grows in dry areas with well-developed soils and usually have been previously cultivated.
7. *Imperata cylindrica*—*Narenga porphyrocoma* assemblage, where the *Imperata cylindrica* dominated assemblage is invaded by the taller grasses
8. *Narenga porphyrocoma* assemblage, which are tall, dense grasslands that grow along old river terraces and wetter sites that are also influenced by fire
9. *Themeda arundinacea* assemblage, which is a tall, dense grassland usually found along the forest edge and on well-developed soils and influenced by fire.

The Banni and Vidis Grasslands of Gujarat, India

The Banni and Vidis grasslands are located along the northern border of Kachchh district and in the Saurashtra peninsular region of Gujarat, respectively, and form some of the largest areas of contiguous grasslands in India (Kumar et al., 2015, Mehta, 2015, Figs. 5 and 6). The term 'Banni' is derived from the local Kachchhi dialect for 'Bannai,' which means 'freshly made' in reference to the land that has been formed by detritus and sediments brought down by the Indus, Luni, Banas and Saraswati rivers which flowed through this region in the recent geological past (Kadikar, 1994 – in Kumar et al., 2015).

The Banni grasslands consist of a matrix of wetlands and grasslands and are considered to be mid-successional or subclimax grasslands (Roy and Singh, 2013). Over 37 species of grass belonging to the genera *Sporobolus*, *Dichanthium*, *Lasiurus*, *Cenchrus* and *Eragrostis* have been recorded in these grasslands.

The Banni grasslands were once managed under a traditional rotational livestock grazing system, which has now broken down, causing the grasslands to degrade under intense and continued grazing by domestic livestock. Consequently, the grasslands are being invaded by *Prosopis juliflora*, a robust, highly invasive colonizing tree species. Water scarcity is also driving the grasslands to desertification.

The Vidis grasslands in Saurashtra, in the western peninsular region of Gujarat state grow under semi-arid and hot conditions. The vegetation is described as scrub savanna, with a high proportion of graminoids (Mehta, 2015). Despite the low productivity and sparse vegetation cover, the Vidis have been traditionally used by local pastoral communities for livestock grazing. The grasslands used to be continuous, with a relatively rich grass cover, but with the expansion of agriculture, human settlements, industries, and subsequent invasion by *Prosopis julifera*, by the second half of the 20th century the grassland landscape has been heavily fragmented.



Fig. 5 Banni grasslands of the dry and arid regions of northwestern India include wetlands that support species associated with wetlands, such as the common crane (*Grus grus*). Courtesy: Manoj Dholakia.



Fig. 6 *Vidis* grasslands in the western peninsular region of Gujarat are home to the Asiatic lion (*Panthera leo*). Smaller species such as the Four-horned antelope or *chinkara* (*Gazella bennetti*) can survive these semi-arid, hot conditions without drinking water for several days, depending on moisture from plants and morning dew. Courtesy: Shikha Bisht/G.S Rawat.

About 58 species of grasses have been recorded from these grasslands, defining nine recognizable grassland communities, which are determined by different habitats, micro-geomorphic conditions among other factors. For instance, the hilly to mild undulating terrain on gravel soil and basalt are characterized by a *Sehima-Dichanthium* dominated community, while *Sehima-Aristida* characterize the piedmont slopes and foothills. A *Bothriochloa*—*Aristida* dominated community grows on dry hills and hillocks with mild grazing, while the low-lying heavy soils and alluvial plains consists of a *Cenchrus*—*Dichanthium* community, and an *Eragrostis-Aristida* community dominates highly degraded grasslands with sandy soils. Xerophytic thorny trees such as *Acacia* spp., *Zizyphus nummularia*, *Commiphora wightii*, *Maytenus emarginata*, *Balanites aegyptica*, and *Euphorbia* spp. grow scattered throughout.

The *Vidis* grasslands are home to the small, isolated population of Asiatic lion (*Panthera leo*). Other mammals of note in the *Vidis* and *Banni* grasslands include ungulates such as Four-horned antelope or *chinkara* (*Gazella bennetti*), Blue bull, and Blackbuck. The community of predators that are sustained by these ungulates include Indian wolf, Striped hyena, Golden jackal (*Canis aureus*), Jungle cat (*Felis chaus*), Indian fox (*Vulpes bengalensis*), and Common leopard (*Panthera pardus*). The grasslands also support over 250 species of birds including critically endangered grassland specialist birds such as the Great Indian bustard and Lesser Florican.

Shola Grasslands of the Western Ghats, India

The *Shola* grasslands occur as a matrix of montane grasslands and stunted montane forests on the high plateaus and slopes of the 1600 km long Western Ghats mountain range (Fig. 7). The grasslands of Eravikulam National Park, Mukurti Sanctuary, Kodajadri, Bababudangiri, Agastyamalai, and Poochipara in Silent Valley National Park are all examples of *shola* grasslands.

The Western Ghats region is classified as a distinct biogeographic zone of India based on its unique species assemblage (Rodgers and Panwar, 1988). The *shola* grasslands are found atop the highest plateaus, above 1500 m, of the Niligiri, Palini and Anamalai Hills along the mountain range. Phytogeographical analysis has shown that the vegetation, especially of the *shola* forests of the Western Ghats share more similarity to those of the Western Himalayas. This is likely due to the presence of a biogeographic corridor between the Western Ghats and the Western Himalayas along the Vindhya and Satpura mountain ranges of Central India that allowed migration and exchange of species (Gupta, 1990). With the more recent warming trends, the temperate species in the lower mountain ranges would likely have disappeared. Because of these differences, Thomas and Palmer (2007) have suggested that the *sholas* of the Western Ghats and the *patana* grasslands of Sri Lanka should not be clustered as a singular biogeographic unit.

The origins of the *shola* forests and grasslands are also contested. One theory suggests that these grasslands have been in existence long before human occupation in the Western Ghats, and the grasslands evolved due to climatic conditions, with the strong monsoon winds and frost in the winter months stunting the growth of trees in the region (Thomas and Palmer, 2007; Srinivasan et al., 2015). The other theory suggests that the grasslands have originated and remain in a state of permanent flux due to biotic



Fig. 7 Shola grasslands of the Western Ghats Mountains of India. This mosaic of grasslands and forests represent sky islands, where some species that are adapted to the grassland and forest habitats remain isolated in the respective patches. Over time, some species can evolve into endemic species. Courtesy: K. Karunakaran/G.S Rawat.

pressures such as fire, cattle grazing and the extraction of forest products. Humans have inhabited the Western Ghats since the Paleolithic or Old Stone Age, more than 12,000 years ago (Chandran, 1997), and these millennia of human interaction with the landscape have allowed for the evolution of the grasslands in the Western Ghats to remain without turning into the woody vegetation (Pemadasa, 1990; Thomas and Palmer, 2007). Interestingly, experimental research has indicated that burning the land in winter helps curtail the spread of woody plants while also reducing damage to endemics like the *Strobilanthes kunthiana* or *Neelakurinji*, the shrub that blooms once every 12 years to impart a purple-blue hue across the grasslands from which the mountains get their name; Nilgiri, which literally means the blue mountains (Thomas and Palmer, 2007).

The shola grasslands harbor many herbaceous species with a limited geographic distribution (Blasco, 1970). Most grasses are perennial C_4 tussock grass varieties. Characteristic species include *Eulalia phaeothrix*, *Dichanthium polyptychum*, *Themeda tremula*, *Ischaemum indicum*, and species of *Chrysopogon*, *Agrostis*, *Andropogon*, *Arundinella*, *Garnotia*, *Jansnella*, *Eragrostis*, *Poa* and *Helictotrichen* (Chandran, 2015; Srinivasan, 2011).

A flagship species for the shola grasslands is the endemic Nilgiri tahr (*Nilgiritragus hylocrius*), an endangered mountain goat that inhabits the high elevation cliffs and grasslands of the Western Ghats. The presence of this endemic mountain goat in the Nilgiris, should be considered indicative of the importance of developing a deeper understanding of these grasslands (Thomas and Palmer, 2007). Other important species that use the grasslands include the Tiger, Asiatic wild dog or dhole (*Cuon alpinus*), and Gaur (*Bos gaurus*).

The Nilgiri hills in the Western Ghats harbors the best existing example of a shola grassland ecosystem and has been identified as an important center of speciation in southern India, as indicated by the exceptionally high endemism and diversity among floristic and faunal species when compared with the Palni and Anamalai hill plateaus (Blasco, 1970; Srinivasan et al., 2015). In most likelihood many of the species that evolved in the Nilgiris never left this hill top.

Humans have lived in the Western Ghats range for over 12,000 years, with the first recorded evidence of the landscape having been altered due to farming happening around 3000–5000 years ago (Thomas and Palmer, 2007). However, this historic interaction with the landscape was environmentally sustainable and beneficial for the regeneration of the sholas. It was during British colonial rule in India that the landscape of the Western Ghats became vulnerable consequential to human actions, in particular monoculture plantations had a detrimental impact upon the ecosystem. The original swathes of grassland have become converted and fragmented due to agricultural expansion for commercial crops such as tea, Black wattle (*Acaia mearnsii*) and pine (*Pinus patula*) (Srinivasan et al., 2015). The grasslands are also being invaded by exotic species such as Scottish broom (*Cystisus scoparius*), which has destroyed the diversity of the native plant community. Expansion of monoculture plantations of *Acacia mearnsii* and *Eucalyptus globulus* continue unabated. These changes to the landscape have in turn caused changes in the volume and rate of streamflow, and

negatively impacted soil conditions, with increased levels of salinity and acidity (Srinivasan et al., 2015). Such changes to the ecosystem affect the productivity of the landscape for local biodiversity and the people who depend upon it for their livelihoods. Hence, the restoration of the grasslands should be encouraged as it will restore ecosystem services.

Grasslands and Savannas of Sri Lanka

The grasslands of Sri Lanka can be classified into three general groups; the montane grasslands, savannas, and lowland grasslands (Pemadasa, 1984, 1990). The montane grasslands, locally known as *Patana*, cover the slopes of the south-central highlands of the island, above 500 m (Pemadasa, 1990), mainly in the Montane Intermediate Floristic Zone, Horton Plains Floristic Zone, with smaller patches in the Eastern Intermediate Floristic Zone and Knuckles Floristic Zone (Fig. 8). There are different views on the drivers that maintain these *patana* grasslands, with some researchers pointing to historic anthropogenic activities that have removed the forest vegetation (Holmes, 1951), while others attribute it to edaphic conditions that prevent tree growth (De Rosayro, 1946).

A characteristic feature of all *patanas* is their occurrence on mountain slopes (Fig. 9); however, there are also phytosociological and physiognomy dissimilarities as well as other biotic and abiotic differences that makes these grasslands ecologically fascinating and floristically diverse (Pemadasa, 1984). Using complex multivariate analyses, Pemadasa and Mueller-Dombois (1979) were able to distinguish five different types of *patana* grasslands:

1. Humid-zone dry *patanas* that grow predominantly in the western slopes of the island (Kandy, Gampola, Pussellawa and Ramboda), with an annual rainfall of over 2100 mm, with a single dry spell in February. These *patanas* are characterized by the dense bunch-grass species *Cymbopogon nardus* at lower elevations (500–700 m) but transitioning into tussock grasses (*Themeda tremula*) higher up, above 90 m. Other noteworthy species in the humid-zone dry *patanas* include the grasses *Dimeria gracilis*, *Eulalia trispicata*, *Imperata cylindrical* and herbaceous species such as *Desmodium heterocarpum* and *Vernonia* spp. (Pemadasa, 1990).
2. Summer dry zone dry *patana* are confined to the Uva basin, in the south-eastern slopes (Pemadasa, 1984). Climatically, the region is distinguishable for having a long and intense dry spell from June through September, followed by convectional-cyclonic weather that brings over 1500 mm of rainfall between October and November. These *patana* grasslands are characterized for having creeping perennial grasses such as *Alloteropsis cimicina*, *Bracharia distachya*, and *Eragrostiella secunda* (Pemadasa, 1990).
3. Intermediate *patanas* grow on the steep hills between 1500 and 2000 m, in Hakgala, Ohiya and Haputale areas (Pemadasa, 1984), with an average annual rainfall of 2000 mm. These grasslands are characterized by grasses such as *Arundinella villosa*, *Chrysopogon zeylanicus*, *Cymbopogon nardus* and *Themeda tremula* (Pemadasa, 1990).
4. Lower wet *patana* grasslands are found between 2000 and 2330 m in Ambewela, Sita Eliya, Moon Plains and Elk Plains with rainfall similar to the humid zone dry *patana*. These grasslands are heavily grazed by cattle, which creates a stubble-like short turf characterized by *Arundinella villosa* and *Chrysopogon zeylanicus* (Pemadasa, 1984).
5. The Upper wet *patana* are found on the Horton Plains plateau, above 2330 m in elevation, and are distinguished from the lower wet *patanas* as they are cooler and develop overnight ground frost, which is considered an important determinant of vegetation type (Pemadasa, 1984). Some of the dominant species in these grasslands are *Dichanthium polypicum* and *Tripogonbromoides*.

The *patana* ecosystems are now under severe threats from various drivers of environmental change, ranging from mining, agricultural expansion, invasive species, and climate change. Many of the lower wet *patanas* are considered totally extirpated (MoMD&E, 2019). Therefore, urgent interventions are needed to conserve and manage these montane grasslands, especially since several faunal species, especially birds, reptiles, and insects, have evolved their natural histories to adapt to the grassland ecosystems and dynamics. However, for this to happen a better understanding of the ecological dynamics of the grasslands is necessary; many of the previous studies have been descriptive, rather than focused on the ecological processes and dynamics that are critical for management.

Sri Lanka's savannas occur to the north and east of the Uva Basin, between 300 and 500 m, in the Eastern Intermediate Floristic Zone and Hill Savannah Dominant Floristic Zone (Fig. 8). Smaller, scattered patches occur in the Montane Intermediate Floristic Zone, mixed with the *patanas*. These ecosystems are characterized by the presence of fire tolerant tree species, notably *Careya arborea* and *Phyllanthus emblica*. The savannas have been categorized into two types; the upland and lowland savannas, based upon topographic, edaphic, floristic and physiognomic dissimilarities. The upland savannas are comprised of tall grasses that grow up to 1.5 m, dominated by *Cymbopogon polyneuros*, *Themeda tremula* and *T. triandra* Forsk.

The lowland savannas, locally known as *talawa* and *damana* grow in valleys and plains of the eastern and southeastern hillsides around Bibile and Moneragala. These savannas are comprised primarily of *Imperata cylindrica* with scattered trees of *Pterocarpus marsupium* and *Syzygium cumini*.

The savannas are utilized for multiple ecosystem services such as cattle grazing, shifting cultivation, and firewood collection, but are also being converted with urban expansion (MoMD&E, 2019). The spread of the exotic *Megathyrsus maximus*, commonly known as elephant grass, is of considerable concern because it is displacing the native savanna grasses (MoMD&E, 2019).

The lowlands grasslands surround the central highlands and are referred to as pastures by Pemadasa (1984) due to the utilization of these grasslands for grazing. Climatically these grasslands are diverse, and four main lowland pasture types have been described by Pemadasa (1990):

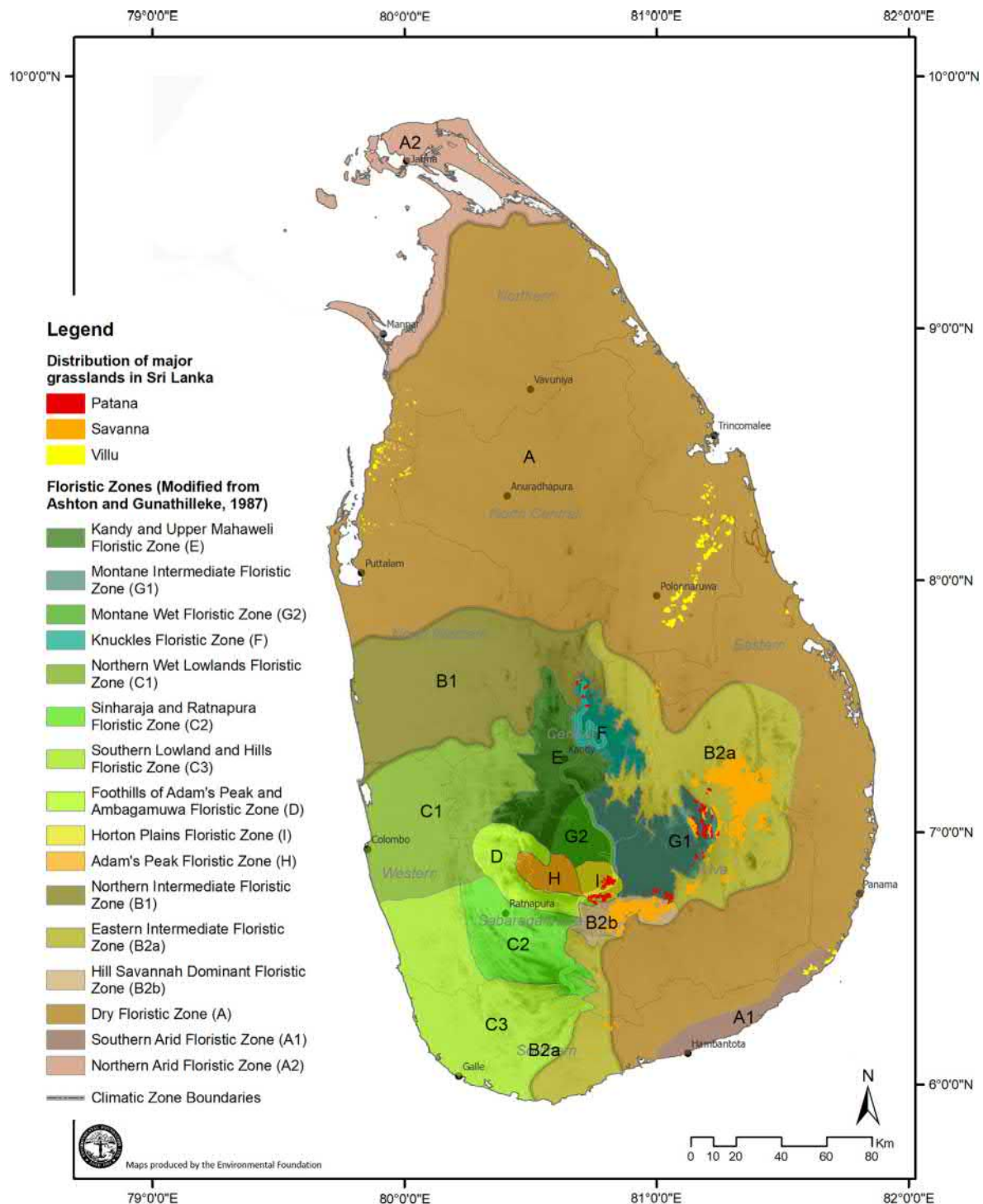


Fig. 8 Distribution of major grassland ecosystems in Sri Lanka. The floristic zones from MoMD&E (2019).

1. Wet pastures that are found extensively within coconut cultivations in the western, south-western and southern lowlands, a region characterized for its perennial rainfall and receiving an annual rainfall of over 2300 mm. These pastures are predominantly comprised of carpet grass species such as *Axonopus compressus* and *Chrysopogon aciculatus* which are popular choices for animal fodder. These grasslands are maintained by intensive management to prevent succession.



Fig. 9 The rolling *patana* grasslands of the montane regions of Sri Lanka are believed to be maintained by fire. The grasslands that grow on steeper slopes are likely in an edaphic climax state, where the thin topsoil cannot support woody plants. Over millennia, several birds, reptiles and insects have adapted their life histories to this cycle of fire and other disturbances. Loss of these grasslands could also affect the survival of these faunal species. Courtesy: Kithsiri Gunawardena.

- Intermediate pastures are maintained by forest clearing for coconut plantations in the north-western lowlands, where rainfall is around 2000 mm. The pastures are used for cattle grazing. Floristically the pastures are comprised of both wet and dry pastures species such as *Aristida setacea*, *Axonopus compressus*, *Chrysopogon aciculatus* and *Cyrtococcum trigonum*.
- Dry pastures in the northern, north-central and north-eastern lowlands of Sri Lanka are largely disclimax ecosystems that have been maintained as grasslands by frequent anthropogenic disturbances since the abandonment of cultivated land during ancient times. These areas receive about 1400 mm of annual rainfall during the North-eastern monsoon period. Floristically, species variation occurs depending upon edaphic conditions. *Imperata cylindrica* dominates alluvial areas, while the dense-tufted *Aristida setacea* grows in areas with less human interference. *Chloris inflata* is found in areas with moist soil conditions, and *Cyrtococcum trigonum* is spread out on the floors of forested landscapes (Pemadasa, 1990). Wild elephants and buffalo are recognized as two species that have a close relationship with this grassland ecosystem, and their grazing helps to maintain these grasslands (MoMD&E, 2019). The *villu* ecosystems (Fig. 10) that dot the landscape in the northwest and along the lower reaches of the Mahaweli River in the northeastern regions of Sri Lanka are also examples of these dry lowland grassland habitats. The *villu* are a reference to the shallow humus-rich depressions that collect rain or flood waters and form isolated wetlands that provide important water sources for wildlife. The *villu* vegetation is dominated by species such as *Iseilema laxum*, *Paspalidium flavidum* and *Fimbrystili* spp. (Pemadasa, 1990).
- Arid pastures are found along the northwestern and southeastern coasts, in Sri Lanka's arid zones, where annual rainfall is less than 1000 mm, interspersed with prolonged droughts. Despite the hostile climate, these are important grazing grounds for both domestic livestock and wildlife. The sandy and muddy flats of Hambantatota and Yala in the southeast and Puttalam and Mannar in the northwest are examples of these arid pastures. The floristic composition is characterized by grasses such as *Cynodon dactylon*, *Eragrostis tenella*, *Zoysia matrella* and the tree species *Acacia eburnean*, *A. planifrons* and *Salvadora persica*.

Other Grasslands of South Asia

In addition to the larger patches—now mostly remnants—of grasslands there are other, less extensive areas of grasslands that occur elsewhere in the Indian subcontinent (Chandran, 2015). These include the grasslands along the Eastern Ghats mountain range, which run parallel to the eastern coast of the Deccan Plateau. These grasslands are drier and occur at lower elevations of around 700 m in the Shevroy hills of Yercaud, Javadi hills and Malkanagiri. The vegetation communities are dominated by species such as *Arundinella setosa* in the higher elevations and *Aristida adscensionis*, *Heteropogon contortus*, and species of *Sporobolus*, *Themeda*, *Chrysopogon* in the lower elevations.

The northeastern hill States of India support several grasslands that are characterized by a unique species community represented by floral elements from the Himalayan region, Southeast Asia, and peninsular India. These grasslands occur in Dzukou Valley in



Fig. 10 The villu grasslands that dot the dry forest landscape of Sri Lanka's dry zone are created around the shallow, humus-rich depressions that collect rainwater and form saucer-like wetlands. As the water evaporates the grasses emerge around the peripheral areas, and form important grazing grounds for the large herbivores, such as spotted deer (*Axis axis*) and Asian elephants (*Elephas maximus*). Courtesy: Devaka Seneviratne.

Nagaland and Manipur, the Ukhrul grasslands of Manipur, Saramati grasslands of Nagaland, and the rolling downs of Shillong. These grasslands are dominated by species of *Festuca*, *Bromus*, *Arundinella*, *Agrostis*, *Cyathopus*, *Coix*, *Tripsacum*, *Cymbopogon*, *Themeda*, *Microstegium*, *Glyceria*, and *Gymnopogon*. The lower hill slopes are also rich in species of *Microstegium*, *Erianthus*, *Narenga fallax*, *Thysanolaena maxima* and several montane bamboos (Chandran, 2015).

The Central Highlands of the Indian Peninsular support grasslands that are interspersed among tropical dry deciduous forests, grow on the rocky patches, and in sparse, open forests. The vegetation is generally comprised of *Manisuris forficulata*, species of *Arthraxon*, *Pennisetum*, *Diectomis*, *Schizachyrium*, *Cymbopogon*, *Themeda*, *Eragrostis* and *Dimeria*. Further south in the Deccan Plateau, the scattered grasslands are dominated by *Sehima nervosum*, *Dichanthium annulatum*, *Eremopogon foveolatus*, *Pollinia fimbriata*, and species of *Bothriochloa*, *Cymbopogon*, *Mnesithea*, *Rottboelia*, *Sorghum*, *Triplopogon*, *Dimeria*, and *Eulalia*.

Concluding Remarks

South Asia's grasslands have existed for millions of years and are considered to be sustained as successional disclimax ecosystems by human activities and natural disturbances such as fire, floods and grazing. In this state these ecosystems provide habitats for a range faunal species, including species that are now adapted to these ecosystems and have even evolved into endemic species. However, intensive use for agriculture, livestock grazing, human settlement, and invasion by exotic invasive species is rapidly changing natural grasslands that will eventually place the survival of grassland adapted species, and the ecosystem services provided by grasslands at risk. Further, shifts in the monsoon seasons, reflected by intense rainfall events and long periods of droughts, are likely to have impacts on the structure and dynamics of grasslands across South Asia (Ratnam et al., 2016).

Finally, it is important to note that the impacts of these various disturbances in driving community and ecosystem dynamics within South Asian grasslands are largely understudied, and the current knowledge of the functional role of herbivores and fires remain mostly limited. Thus, if these important ecosystems are to be sustained, especially under uncertain weather patterns and expanding anthropogenic influences, better understanding of these ecosystems should be gained to formulate effective grassland management strategies.

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Grassland Vegetation of Southern Africa

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Abstract

Southern African grasslands occur on mid to high altitudes and originated due to environmental conditions becoming drier and colder towards the end of the Eocene. The cool climatic conditions with incidences of frost together with fire are regarded as one of the most important driving forces that prevent woody species from establishing. The grassland biome of southern Africa comprises close to a third of the total landscape of the region. When compared to other biomes, grasslands have the second highest species richness after the Fynbos biome. The biome contains more than 640 red listed species and provide habitat for a large number of plant and animal species. A total of 34 grass taxa and 67% of the orchid species present in the biome are endemic. The highveld grassland in the north-eastern part of the region contains various centers of diversity with up to 4000 different plant species recorded. Mining, urbanization and agriculture have the greatest negative impact on the total suite of grassland ecosystem services and are responsible for irreversible changes in the biome in terms of species composition and ecosystem functioning. Climate change is expected to impact on the size, structure, and species richness of the area.

History of Southern African Grasslands

In terms of vegetation, grasslands are relative newcomers to the world and only evolved about 30 million years ago ([McCarthy and Rubidge, 2005](#)). Before grasses established the vegetation of the low to moderate rainfall areas of the Earth was characterized by either bare soil patches or small dwarf shrubs. The higher rainfall areas comprised tall forests ([McCarthy and Rubidge, 2005](#)). Southern Africa was characterized by subtropical forests and woodlands (savanna) before climate changes took place that led to the establishment of grassland vegetation ([Bredenkamp et al., 2002](#)). The earliest grasses occurred in the dry areas and competed with dry woodland species ([McCarthy and Rubidge, 2005](#)). Later other grasses became established in wetter and cooler areas. According to [Retallack \(2001\)](#) grasslands played a major role in cooling the environment over the past 30 million years. This is as a result of their relative lighter color compared to woodlands and forests which means they reflect a greater proportion of solar radiation into space. That causes cooler soil temperatures while more water is retained in the soil due to the dense cover of the grassland vegetation. Research has established that grassland vegetation is closely associated with geology, soil, and climate ([Bezuidenhout, 1993](#)).

Southern African grasslands are located at mid to high altitudes (1200–3400 m) and originated due to the environmental conditions becoming drier towards the end of the Eocene as well as the cooler conditions caused by continental uplift. The cooler conditions are regarded as one of the most important driving forces that prevent woody species from establishing ([Bredenkamp et al., 2002](#)). According to [Anderson \(1999\)](#) the climatic change that took place during the Oligocene caused southern Africa to become 5% colder which provided ideal conditions for the establishment of primary grasslands.

What Is the Scope of Southern African Grasslands?

Southern African grasslands form part of the world temperate grassland biome which comprises the steppes of Russia, Mongolia and China, the north American prairies, the South American pampas, temperate grasslands of Australian Alps and the tussock grasslands of New Zealand ([Mucina and Rutherford, 2006](#); [Van As et al., 2012](#)).

When defining the grasslands of southern Africa, the following definition refers: “Herbaceous vegetation dominated by the family Poaceae with various other forb and dwarf woody species in-between.” Grasslands are diverse in terms of species composition and vegetation structure. In terms of species richness there are more individual forb species recorded than individual grass species. In simple terms it is estimated that only one in every six plant species in grassland is a grass species. It is, however, interesting to note that the forb species (short-leaved herbaceous plants and ferns) are mostly inconspicuous due to the dominance of the taller grass species. Grasslands have a relatively high canopy cover and biomass production compared to woodland plant communities (O'Connor and Bredenkamp, 1997). The average annual rainfall of southern African grassland areas ranges between 250 and 900 mm depending on the region. They are mostly associated with wet summer rainfall period followed by a relatively dry winter period. Summer temperatures are warm (up to 38 °C) and the winters cold (sometimes as low as –4 °C) with frost and snow a common occurrence (Van As et al., 2012).

The grassland biome of southern Africa comprises 28% of the land surface and is the second largest biome after the savanna biome (Carbutt et al., 2011). The grasslands occur mostly on the high central plateau (also known as the Highveld region), the mountainous inland areas of KwaZulu-Natal and extends to the central parts of the Eastern Cape Province (Fig. 1) (Mucina and Rutherford, 2006). These include both warm-temperate and cool-temperate grasslands. In the high-lying altitude mountainous areas of the Maluti-Drakensberg range sub-alpine grasslands are present. The warm-temperate grasslands of southern Africa comprise C4-dominated grasses and occurs both under dry and mesic conditions while the high-altitude grasslands are dominated by C3 grasses (Van Oudtshoorn et al., 2011). The latter is rich in endemics and has mountain summit affinities with East African grasslands as well as Fynbos lineages, such as *Ehrharta* spp. (Verdoorn et al., 2003). The grassland biome of southern Africa interfaces with the Nama-karoo biome in the dry western and south-western boundary, indigenous Afromontane forests along its south-eastern boundary and the bushveld and savanna regions in the north. Although smaller grassland patches, referred to as satellite grasslands, do occur within other biomes of southern Africa, they are not considered as belonging to the grassland biome as per the above definition. These satellite patches are part of the natural herbaceous layer of these different biomes. The boundaries between the grasslands and adjacent biomes are not always clearly defined. In most cases the changes from grassland vegetation to that of another biome is gradual with an overlap between species of the two biomes (Van As et al., 2012).

Mucina and Rutherford (2006) has described a total of 72 different grassland vegetation types based on their floristic composition. According to Scholes and Von Maltitz (2015) they can be grouped into five broad categories: Dry Highveld (between 400 and 550 mm of rain), Mesic Highveld (> 550–800 mm of rain), High-Altitude or sub-alpine grasslands on the Drakensberg (> 800–2000 mm of rain), Sub-Escarpment on foothills of the escarpment, and the Coastal grassland.

The grassland biome of southern Africa is also one of the most impacted and as a result, degraded areas of the region (Bezuidenhout, 1993). This is ascribed to the geology, topography soil, and climate that makes these areas suitable for mining, agriculture and urbanization (Brown and Du Preez, 2014).

The grassland biome of southern Africa occurs within South Africa, Lesotho and Swaziland and comprises 46,653,419 ha (Table 1). The largest proportion, 91% (42,553,492 ha) occurs in South Africa with 9% (4,053,122 ha) occurring in Lesotho and 1% (46,805 ha) in Swaziland. The Mesic Grassland vegetation type occurs in all three countries and comprises an area of 15,889,414 ha. The Sub-escarpment Grassland vegetation type is 10,159,429 ha in size and occurs only in Swaziland and South Africa, while the Drakensberg vegetation type occurs only within South Africa and Lesotho and are more or less equal in size comprising 2,873,824 and 2,801,325 ha respectively. The Dry Highveld grassland vegetation type only occurs on the higher-lying escarpment of South Africa on more than 15 million hectares of land.

Ecosystem Modifiers

Various environmental and anthropogenic influences play a significant role in the species composition, richness and structure of the various landscapes of the grassland biome.

Geology, Soil, and Terrain

Geologically the largest part of the grassland biome of southern Africa is located on the Karoo Supergroup which is underlain by the Witwatersrand, Ventersdorp and Transvaal Supergroups. The latter has been deposited during the Archaean period (between 3100 and 2000 million years ago) with the Karoo Supergroup being deposited on top during the Phanerozoic period (60 million years ago) (McCarthy and Rubidge, 2005). Various metamorphic and igneous rocks intruded into sections of the Karoo Supergroup which resulted in the forming of the so-called African super swell. Furthermore, the Limpopo, Kalahari and Karoo river systems were responsible for eroding large sections of the Karoo Supergroup strata giving rise to the higher-lying escarpment areas of the grasslands of southern Africa (McCarthy and Rubidge, 2005; Mucina and Rutherford, 2006).

Within these supergroups some of the most important economically valuable minerals in the world are found. In particular southern African grasslands have the largest gold, manganese and platinum reserves in the world, which is augmented by large deposits of other similarly important commodities such as diamonds, coal and iron ore. Most of these mineral deposits have been the backbone of the region's economic growth for many years (Cairncross, 2004) and have been responsible for various anthropogenic changes in the grassland vegetation in terms of species composition and structure.

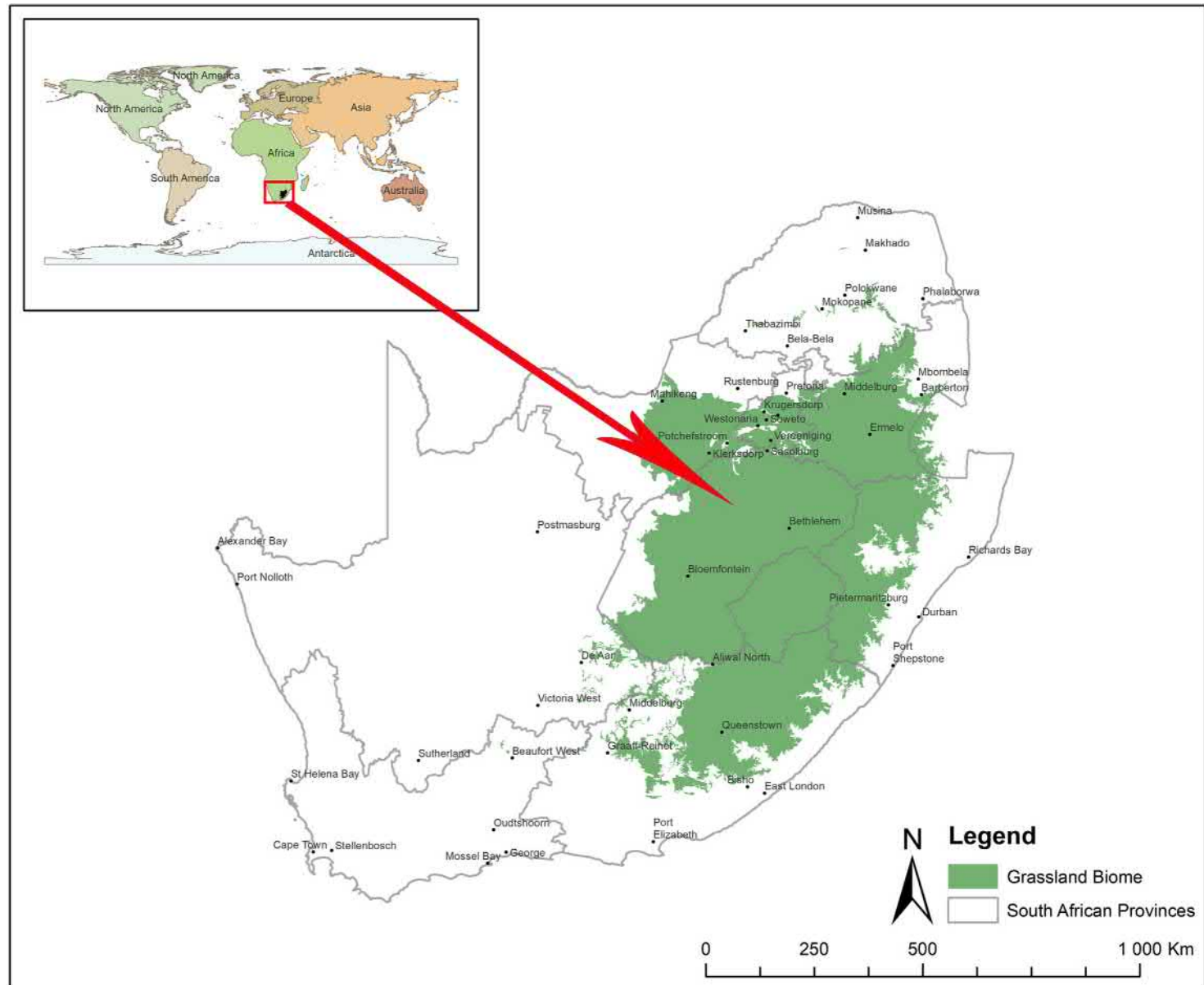


Fig. 1 Location of the grassland vegetation of southern Africa. Adapted from Mucina, L. and Rutherford, M.C. (eds.) (2006). *The vegetation of South Africa, Lesotho and Swaziland: Strelitzia 19*. Pretoria: South African National Biodiversity Institute.

Table 1 Sizes of the different grassland types within southern Africa.

Country	Grassland type	Area size (ha)	Total (ha)
Swaziland	Mesic Highveld Grassland	378716	46805
	Sub-Escarpment Grassland	46805	
Lesotho	Mesic Highveld Grassland	1251796	4053122
	Drakensberg Grassland	2801325	
South Africa	Mesic Highveld Grassland	14258902	42553492
	Dry Highveld Grassland	15308142	
	Sub-Escarpment Grassland	10112624	
	Drakensberg Grassland	2873824	
	Total		46653419

In terms of topography and soil the area consists of relatively large homogeneous landscapes. Most of the grassland biomes' in situ soil forming has caused differences in inorganic nutrients in the soil throughout the biome. The soil nutrient content is delimited by soil depth, texture, and rainfall (Hillel, 1971). Weathering of the rocks caused by wind and water erosion has given rise to various Land Types, Terrain Units, and Soil Forms (Soil Classification Work Group, 1991; Land Type Survey Staff, 1986).

Fire

The grassland biome of southern Africa has a high lightning strike density making the incidence of fires a regular occurrence in these ecosystems (Mucina and Rutherford, 2006). According to O'Connor and Bredenkamp (1997) fire is vital in the maintenance of the structural and specific species composition of grassland areas. Although fires are naturally caused by lightning strikes and, in rare instances, by rock falls (Van As et al., 2012), anthropogenic fires have become more prevalent in southern Africa. Fire plays an important role in maintaining the grassland structure and species composition. According to Midgley et al. (1997) regular fires in grasslands are regarded as the main cause of abrupt boundaries between grassland and forest since it inhibits the establishment of seedlings of woody species in the grassland areas (Fig. 2).

Natural fires occur mostly from late winter to early spring within the summer rainfall areas. The fire intensity is dependent on the amount of fuel available, the fuel moisture, air temperature and wind speed (Mucina and Rutherford, 2006). Fire is in most cases beneficial to the ecosystem and the plants and wildlife occurring in fire prone areas are adapted to these conditions. Fire can have direct or indirect impact on vegetation and wildlife. Direct impacts depend on the type of plant species and organism. In cases where the plant species and/or wildlife is not adapted to fire, they will in all likelihood be killed (Van As et al., 2012). Where grasses are not regularly defoliated by grazers it could lead to the vegetation becoming moribund. In such a case the fire removes all moribund material and stimulates the growth of the vegetation (Trollope, 1999). When fire removes vegetation cover more light is available that stimulate grassland geophytes to grow and flower before the grasses resprout or recover. Regular fire in grasslands also kill seedlings of woody plants encroaching into these areas thereby maintaining the grassland species composition (Van As et al., 2012).

**Fig. 2** Normal surface fire within the grassland vegetation of southern Africa. Photo: LR Brown.

The incorrect use of fire could cause ecosystem degradation that results in a loss of plant species, erosion, decreased water infiltration as well as woody species encroachment.

In southern Africa fire is used effectively as a management tool in natural areas as well as cultivated grasslands to maintain and/or enhance grazing (Trollope, 1999). One of the most common practices of fire in land management is to use fires regularly to prevent accumulation of dry material that could cause high intensity wild fires (Whelan, 2002).

Climate

Grasses are well adapted to withstand cold temperatures as well as overgrazing. That is due to their meristematic tissues being located close to the ground level. Grasses are furthermore dormant during the dry winter season which allows them to withstand frost and even snow. In contrast broad-leaved savanna woody species are not adapted to the longer periods of extreme cold temperatures and can therefore not establish in these areas.

Different grass plant species grow during different times of the growing season. The dominance of the grass species in a specific grassland community is influenced by the season and the amount of rainfall received (Bezuidenhout et al., 2018). Grasslands are regarded as event-driven resilient ecosystems. During drought times or as a result of overgrazing the grass biomass is greatly reduced resulting in a greater visibility of perennial forbs and dwarf shrubs. However, during high rainfall events the grass layer recovers rapidly with a significant increase in biomass and less visibility of the perennial forbs and dwarf shrubs.

In the sub-alpine grasslands at high altitudes, the cold temperatures and shallow high clay content basalt derived soil results in grasses having a stunted bonsai-like growth form.

Southern Africa does not have cold resistant trees that can withstand continued low temperatures and incidences of frost as found in the northern hemisphere. Very few savanna species have developed a tolerance to cold, dry conditions and frost that is prevalent in the grassland biome of southern Africa. Only woody species that have developed a tolerance to cold conditions are found scattered in some grassland sections. One such species, the tree *Vachellia karroo*, is regarded as a forerunner in the woody encroachment of grassland areas especially where overgrazing has taken place (Bredenkamp et al., 2002).

Thus, cold temperatures and fire are important ecosystem modifiers responsible for the maintenance of the structure and species composition of grasslands.

Grazing

Grasses are well adapted to being defoliated due to their meristematic tissues being located at the base of the leaf. That means that if the aboveground leaf material of young leaves is removed the plant will continue to produce new leaf material. According to Bredenkamp et al. (2002) the establishment of grasses together with grazers is a remarkable case of symbiotic co-evolution. Grazing of grasslands affect the plant species composition and production of the grass plant. Koerner and Collins (2014) found that grazing of grasslands increased diversity while decreasing grass cover. They also found that both the production and below ground biomass decreased as a result of grazing. The effect of leaf removal of the grass is dependent on the amount and parts of the leaf removed (Wolfson, 1999). The removal of part or the whole leaf will reduce the photosynthetic capacity of the grass that could result in lower production. However, if the grasses are moderately grazed it will lead to a compensatory increase in photosynthetic efficiency in the remaining leaves (and culms) that would not significantly reduce the production of the grass (Wolfson, 1999). Thus, there is mostly a temporary and short-term decline in photosynthetic capacity and production under normal grazing conditions. De Klerk et al. (2001) estimate that grazed areas might only achieve the same production of non-grazed areas after 4 years of normal grazing. According to O'Connor (2005) the stocking rate of livestock and wildlife in grassland areas are currently 6–20 times higher than before humans settled in these areas. This is one of the main reasons for the decline in grass production and change in species composition of grassland vegetation in southern Africa. Overgrazed grassland areas are also prone to woody species encroachment which not only causes a shift in species composition, vegetation structure, but also a loss in valuable grazing land. Grazing is, however, a natural phenomenon of healthy grassland ecosystems in order to maintain the vitality of the grass plants. If a grass is not moderately defoliated on a regular basis, it could lead to the grass becoming moribund and eventual death of the plant. Therefore, properly planned and executed grazing strategies will maintain the grassland ecosystem patterns and processes.

Biodiversity

The term biodiversity refers to the diversity and number of viable plant and animal species present in an area (Brown and Du Preez, 2014). The grassland biome of southern Africa contains a variety of aesthetically pleasing landscapes with a high biodiversity value. According to Cowling et al. (1989) data on plant species richness and diversity for the total grassland biome of southern Africa is not readily available. Between 9 and 29 plant species have been recorded in 100 m² vegetation sample plots within high-altitude grasslands of the Eastern Cape and KwaZulu-Natal (Eckhardt et al., 1996). According to Van Oudtshoorn (2008) it is estimated that southern African grasslands contain between 55 and 100 species per 1000 m². According to Siebert (2011) southern African grasslands has a mean plant species richness of 61 species per 100 m². Cowling et al. (1989) found that grasslands have a high alpha diversity and a moderate gamma diversity with the highveld grassland region containing various centers of diversity with up to 4000 different plant species recorded in this area. When compared to other biomes in southern Africa, grasslands have the second highest

Table 2 Mean species richness per 1000 m² for selected biomes of southern Africa.

<i>Biome</i>	<i>Number of species</i>
Fynbos	86
Grassland	82
Succulent karoo	74
Forest	51
Nama karoo	47

Adapted from Van Wyk, A.E. (1998). *Grassland: The most threatened Biome in South Africa*. Pretoria: Unpublished report.

species richness after the Fynbos biome (Table 2). The grassland biome of southern Africa contains more than 640 red listed species of which 136 are threatened by extinction while six are already extinct. Of these red listed species only nine are grass species (Mucina and Rutherford, 2006). A total of 34 grass taxa are endemic to the southern African grasslands (Steenkamp et al., 2002). In addition, Linder et al. (2005) states that of the 161 orchid species found within the grassland biome, a total of 67% are endemic.

In terms of animal species, the grassland biome provides suitable habitat for ungulates, birds, insects, and amphibians.

Ecosystem Services

Apart from providing valuable grazing to wildlife, southern African grasslands play an important role in terms of water production, purification and retention in this water scarce region (O'Connor, 2005). Egoh et al. (2011) state that grasslands also provide ecosystem services in terms of soil conservation and carbon storage. Grasslands effectively remove carbon from the atmosphere and where woody species store the carbon in their organs, grasses store it in the soil. Thus, the grassland soils are far richer in carbon than forest soils (McCarthy and Rubidge, 2005). This can be partially ascribed to regular fires in grasslands that result in a large number of carbon rich ash being produced. This carbon rich ash is not easily decomposed by soil bacteria and therefore contributes to the higher carbon concentrations in grassland soil (McCarthy and Rubidge, 2005). Other ecosystem services include forage production, medicinal resources, biodiversity, erosion regulation, tourism, bird-watching, and hunting. According to Scholes and Von Maltitz (2015) it is estimated that the value of the ecosystem services from grassland is in excess of \$650 million.

Threats to the Grasslands of Southern Africa

Urbanization, agriculture, rural settlements, and mining have had the most severe negative impacts on the biodiversity of grassland ecosystems (O'Connor and Kuyler, 2009; Cilliers et al., 2004). The largest areas affected by urbanization include the Johannesburg-Pretoria region in the northern parts of the biome as well as the eastern and central parts of the biome (Fig. 3). Urbanization causes the establishment of impermeable surfaces, landscape fragmentation, habitat loss and a loss in natural resource pathways and biodiversity (Van der Walt et al., 2015).

Most grassland areas are prime land for agricultural practices such as grazing and planting of crops (Fig. 4). The largest concentration of agricultural practices is conducted within the grassland biome. Compared to the rest of southern Africa the grassland biome is the most impacted and therefore under threat (Fig. 3). The planting of crops results in the total destruction of the natural vegetation and alters the soil profile, while the long-term application of fertilizers and herbicides has a negative effect on the soil nutrients and micro-organisms of the system.

Overutilization in terms of grazing combined with the effect of trampling degrades the grassland habitat making it susceptible for invasion by alien plants and woody species encroachment. Thus, incorrect grazing practices and stocking rates combined with drought events can alter the structure, composition and ecosystem functioning of the grassland areas. Moderate to heavy grazing by domestic animals causes a decrease in forb species richness of up to 84% and even leads to the extirpation of certain perennial forbs (Scott-Shaw and Morris, 2014). In areas where land is left fallow it seldom if ever returns to its original vegetation structure. Breidenkamp and Brown (2003) found that natural grasslands in the Highveld region of South Africa that are degraded due to anthropogenic influences become dominated by thatch grasses (*Hyparrhenia* spp.). These *Hyparrhenia*-dominated grasslands tend to be stable for a very long time (up to 50 years or more) and mostly have low species richness and diversity. In the high-altitude sub-alpine grasslands of Lesotho uncontrolled and ill-managed grazing programs have resulted in the degradation of the grasslands as well as its associated peatlands where large-scale erosion occurs. This has negative impacts on the larger and very important water catchment that is regarded as the most important water catchment area of southern Africa (Du Preez and Brown, 2011).

The mining of the significant mineral deposits and urbanization contribute to the continued degradation of the ecosystem (Bezuidenhout 1993). More than 40% of the country's mining activities are located in this biome (Scholes and Von Maltitz, 2015) (Fig. 5). Various coal, diamond, gold and bentonite mining activities to name a few occur throughout the grassland biome

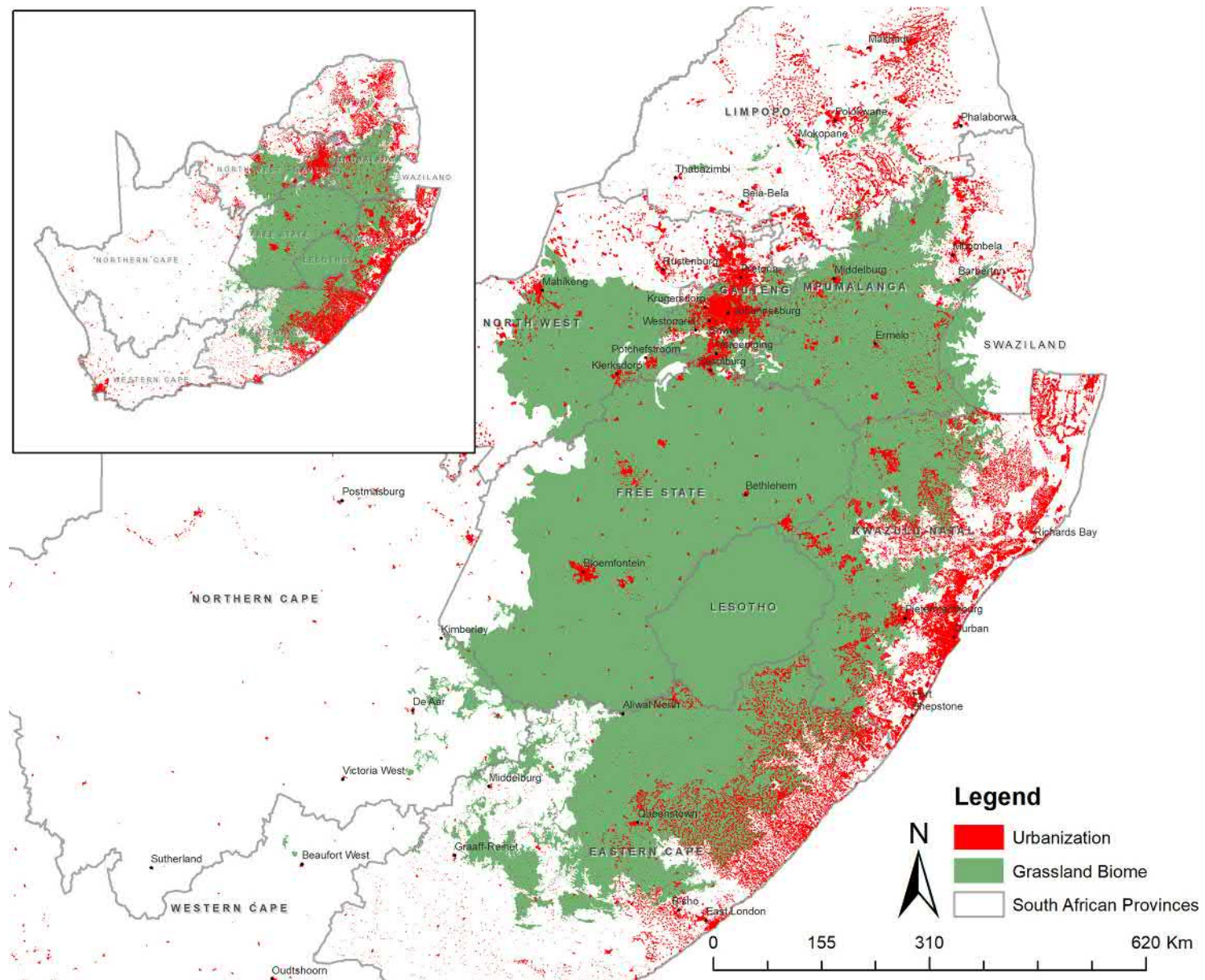


Fig. 3 Urbanization within the grassland biome compared to the rest of the region (no data is available for the country of Lesotho and is therefore not indicated in the figure).

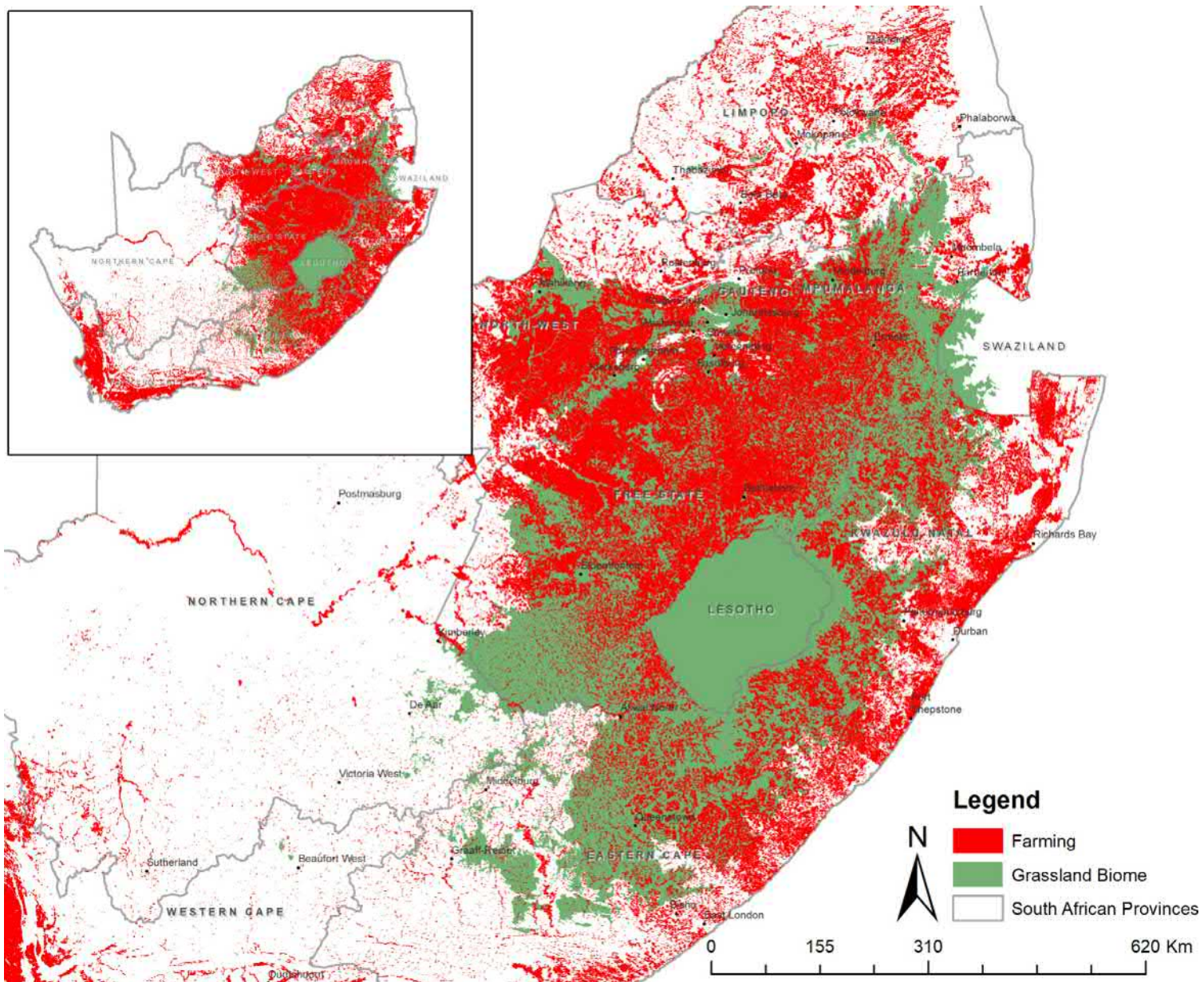


Fig. 4 Agricultural practices within the grassland biome compared to the rest of southern Africa (no data is available for the countries of Lesotho and Swaziland and is therefore not indicated in the figure).

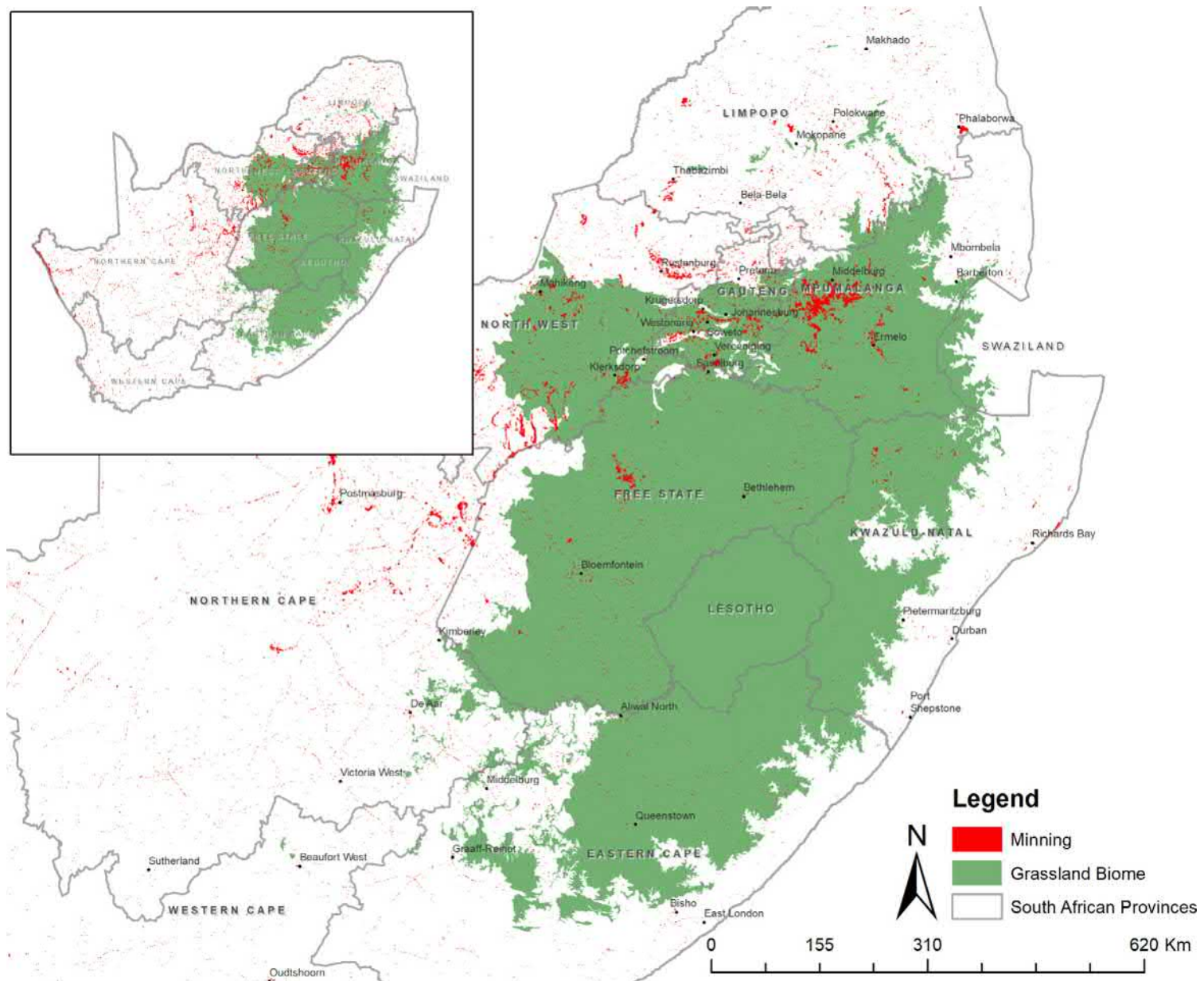


Fig. 5 Mining activities within the grassland biome compared to the rest of southern Africa (no data is available for the countries of Lesotho and Swaziland and is therefore not indicated in the figure).

(Brown and Du Preez, 2014). These activities normally result in the total destruction of the natural ecosystem and cause a loss of natural grasslands. In order to prevent the large-scale loss of these ecosystems current government legislation requires mining companies to obtain similar natural areas that could be used as offset areas to conserve specific grassland ecosystems (Bull et al., 2013).

The spread of alien invasive plants threatens the diversity and functioning of natural ecosystems worldwide (Van Wilgen et al., 2001). These alien plants have the ability to outcompete the natural grassland vegetation thereby displacing the natural species of the area. That leads to a loss of diversity and habitat for many plant and animal species. Alien plants also use more water than indigenous grass species and contribute to the drying up and degradation of the land (Forsyth et al., 2012).

Incorrect burning strategies, continuous overgrazing and general mismanagement of grasslands results in a loss of vegetation cover and a change in species composition. The consequence of these actions results in larger evapotranspiration and therefore loss of water from these ecosystems (O'Connor, 2005). In addition, the loss of vegetation cover results in a greater surface water runoff and less infiltration that causes large scale erosion and poorer water quality of these landscapes.

Connectivity between different natural landscapes is important to ensure natural ecosystem processes and patterns. The fragmentation of the natural habitat is an important factor that contributes toward the loss of and isolation of vegetation thereby creating smaller natural vegetation patches (Fahrig, 2003). Connectivity between different landscapes in the grassland biome is hampered due to different land use practices such as planting of crops, mining, urbanization, and afforestation. This has had a negative impact on the grassland species composition, richness, and general vegetation structure. The farming practices in southern Africa where fences have been erected to manage the land use has also largely contributed to the loss of connectivity between grassland landscapes and their associated wildlife. Although connectivity measurements have not been widely used in habitat fragmentation determinations in southern Africa, it is gradually gaining momentum as a conservation planning tool (Fourie et al., 2015).

Fuggle and Rabie (1992) developed a matrix whereby the various anticipated impacts of any anthropogenic activity on the ecosystem can be assessed. Table 3 presents an adapted analysis of different threats on the ecosystem services of the grassland biome.

According to Table 3 mining and urbanization have the greatest negative impact on the total suite of grassland ecosystem services. Almost all the impacts of these activities on the ecosystem are highly significant and irreversible. Cultivation activities is the third most significant impact on the grassland ecosystem services with more than 50% of the activities resulting in irreversible changes to the ecosystem. Alien plant invasions have significant negative effects on grassland processes and patterns, as well as water purification and retention. Alien plants are well-known to use more water and lose it through transpiration than indigenous species (Le Maitre et al., 1996). Fragmentation of the grassland environment has negative effects on the grassland processes and patterns while also possibly having a negative effect on climate change. Incorrect management practices are regarded as having significant negative effects on the grassland ecosystem, however if correctly managed and detected early it could be mitigated by implementing correct management strategies. If this is not done it would most probably have the same negative impact as mining and urbanization.

Conservation

Grassland areas are important in terms of plant and wildlife biodiversity as well as a water resource. Large sections of the grassland biome of southern Africa have been degraded or transformed due to human activities (e.g., agriculture, mining, urbanization, overgrazing, etc.). It is estimated that close to 33% of the biome has already been irreversibly transformed primarily as a result of anthropogenic influences (Carbutt et al., 2011). A further 7% has been severely degraded due to soil erosion and poor land management, while it is estimated that 30% of the remaining grassland areas are secondary grasslands on previously degraded areas (Mucina and Rutherford, 2006).

Afforestation of the grassland biome has resulted in the large sections of the grassland being destroyed (Fig. 6). Although this practice is declining with some plantations being terminated, it is of utmost importance that these areas are restored by scientifically defensible and well-informed restoration plans. Degraded (ploughed, overgrazed, mined) grassland areas do not naturally recover to its original climax condition. Whereas the degraded grasslands of western Europe become overgrown by woody species, degraded southern African grasslands remain grass dominated (Bredenkamp et al., 2002) and develop into a species poor grassland normally dominated by secondary successional grasses such as *Hyparrhenia hirta*, *Eragrostis rigidior*, *Hyperthelia dissoluta*, and *Eragrostis curvula* together with a variety of pioneer weedy forbs.

Although sections of the grassland biome are conserved in smaller nature and private reserves, they only account for 2.2% of the grassland biome. Furthermore, not all areas of the biome are equally protected, with the highveld grasslands especially poorly conserved (Low and Rebelo, 1996). Apart from the highveld grassland areas, the northern parts of the grassland biome are characterized by the lack of formally protected conservation areas. According to Zunckel (2003) the establishment of the Maluti-Drakensberg Transfrontier Park which encompass grasslands that are found in Lesotho, KwaZulu-Natal and the Golden Gate Highland National Park is one of the most important grassland biome conservation initiatives in the region. The National Grasslands Biodiversity Programme (NGBP) which aims to ensure sustainable long-term management, research and conservation of the grassland biome, hosted by the South African National Biodiversity Institute (SANBI) is another initiative to protect the grassland biome.

Table 3 An analysis of the different threats on grassland ecosystems in southern Africa (Color coding were given to the different categories based on their significance: *Red*, high; *Orange*, Medium; *Yellow*, Low; *Gray*, undetermined).

Activities	Urbanisation	Mining	Cultivated lands	Incorrect management practices: grazing, fire and bush encroachment	Alien invasive species	Fragmentation	Assessment Entries in Matrix Cells (Fuggle & Rabie, 1992)
Grassland ecosystem services							Qualities
Grassland processes and patterns	L 1 C F 5 R	L 1 C F 5 R	L 1 C F 4 R	L 1 P S 3 R	L 1 P S 3 R	D 1 P F 3 R	Symbol
Water purification and retention	D 1 P ? 5 R	L 1 U S 4 R	D 1 U S 3 R	D 1 U T 1 N	L 1 C S 5 R	D 1 U T 2 R	Meaning
Soil conservation	L 1 C F 4 R	L 1 C F 5 R	D 1 C F 4 R	D 1 P T 3 N	D 1 P T 3 R	L 1 U T 1 N	Position in Cell
Carbon storage	L 1 P F 2 R	L 1 C F 5 R	L 1 C F 4 R	D 1 P S 2 N	D 1 P S 2 R	D 1 P S 2 N	
Climate change	L 1 C F 5 R	L 1 C F 5 R	D 1 P S 3 R	D 1 P S 2 N	D 1 C S 3 R	D 1 P S 2 R	

Importance Risk	5 4 3 2 1 ?	Major Medium Minor Unable to assess	5
Probability	C P U ?	Certain Probable Unlikely Unable to assess	C
Time of Occurrence	I D L ?	Immediate effect Delayed effect Long term Undetermined	D
Duration	T S F ?	Transient Short / Temporary Final / Permanent Unknown	T
Influence	+ - ?	Positive Negative Unable to determine	+
Risk	R N ?	Great risk Not a great risk Unknown	N

Adapted from Fuggle, R.V. and Rabie, M.A. (1992). *Environmental management in South Africa*. Cape Town: Utah and Co Ltd.



Fig. 6 Large areas of the grassland biome have been planted with forest plantations for commercial purposes thereby destroying the natural grassland ecosystem. Photo: LR Brown.

With the advent of anthropogenic climate change it is predicted that the extent of the grassland biome may become reduced by up to 55% with a significant change in plant species composition and vegetation structure. The areas that are most likely to be affected are the north-western portion of the current grassland biome (Mucina and Rutherford, 2006). Changes in abundances and species are predicted to occur with a heightened risk of extinction for many species as a result of climate change (Huntley and Barnard, 2012). The loss of suitable habitat for various animal species (mammals, insects, and birds) could also have far-reaching effects in terms of ecosystem functioning since these species play a role in pollination, seed dispersal, and maintaining general grass vitality.

The grasslands of southern Africa as a result of its ongoing transformation due to the various threats listed above is regarded as one of the most threatened biomes (Scholes and Von Maltitz, 2015). It is imperative that conservation efforts in southern Africa are properly planned and implemented to ensure the long-term functioning of this highly important and diverse biome. The increase in human population in southern Africa together with an increase in management pressures in terms of agricultural and urbanization demands as well as climate change will place more pressure on the natural grassland vegetation and its biodiversity. Biodiversity conservation not only refers to the protection of specific species, but also habitats, ecosystems, and landscapes (Van As et al., 2012). The solutions to the conservation of grasslands will mostly depend on the decisions and actions in the socio-political arena (Watkinson and Ormerod, 2001).

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The Tropical Savannas of Northern Australia

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Abstract

Tropical savannas comprise the main environment across the 2 million km² of monsoonal northern Australia. As with savannas world-wide, Australian tropical savanna vegetation is characterized by a dense C₄ grass layer and variably open tree layer. Vegetation structure and composition vary across the gradient of annual rainfall from c. 2000 mm (in the coastal north) to c. 500 mm (inland), with tree cover and height greatest in higher rainfall areas. Unlike most tropical savannas globally, in the Australian tropical savannas, most canopy trees are evergreen, with eucalypts (*Eucalyptus* and *Corymbia* species) dominating. Influenced by a long annual dry season, fire is frequent and is a major influence on vegetation, particularly shaping the extent of a shrubby understorey layer. The fauna is highly distinctive—for some groups it is extremely rich and with high levels of endemism, but it lacks native megaherbivores. The Australian tropical savannas have remained extensive and largely intact, with relatively low human population density, little habitat loss, and no known extinctions over the c. 200 years since European settlement. However, some native species are now declining, many invasive species have become pests or weeds, and there is ongoing pressure to modify habitats to allow more intensive development.

Introduction

Tropical savannas occur in the seasonal tropics of Africa, South America, Asia and Australia. A dense grass layer is a defining feature, but vegetation structure varies from essentially grasslands with sparse trees, especially on cracking-clay soils, to open forests with a mixed understorey of shrubs and grasses, typically on deep sandy loams with high annual rainfall. Australia's tropical savannas occur extensively as the dominant vegetation type across the northern quarter of the continent. Intermixed with the tropical savannas are smaller areas of other biomes, including rainforest patches, treeless floodplains, and heathlands, with the latter occurring on some sandy coastal soils (especially on Queensland's Cape York Peninsula: Fig. 1A) and on skeletal or sandy soils in rugged rocky areas. Here we treat the Australian tropical savannas as a single ecoregion, despite the presence of numerous non-savanna vegetation types.

Biogeography

Australia's tropical savannas occupy about 2 million km² of the north Australian mainland (Fig. 1A) and many nearby islands including three of Australia's largest: Melville (5786 km²), Groote Eylandt (2285 km²) and Bathurst (1693 km²). The southern limit of the tropical savannas is loosely delineated by the limit of strongly seasonal monsoon influence, with gradational shift to the semi-arid and arid environments of inland Australia, down to mean annual rainfall of about 250–500 mm. In the wet tropics of North Queensland, the savannas abut tropical rainforest, and small patches of rainforest are embedded in tropical savanna throughout northern Australia, especially along rivers and creeks and around permanent springs.

Similar environments, with many shared plant and animal species, also occur in the Trans-Fly area of southern New Guinea, which was connected to Australia during periods of lower sea levels in the Pleistocene (Nix and Kalma, 1972), as well as in most of Timor and elsewhere in eastern Indonesia, outside the Australian continent.

The Australian tropical savannas extend largely uninterrupted across an east–west arc of about 3000 km (Fig. 1A). Given this continuity, many plant and animal species occur throughout this environment. However, there are some notable landscape breaks and barriers that have served as variably effective evolutionary divides (Potter et al., 2012). Areas of rugged terrain in the Kimberley, the Arnhem Plateau in the Northern Territory and parts of Cape York Peninsula have a long history of differentiation from the lowland environments, and harbor many species that are either endemic or with relictual distributions (Woinarski et al., 2009).

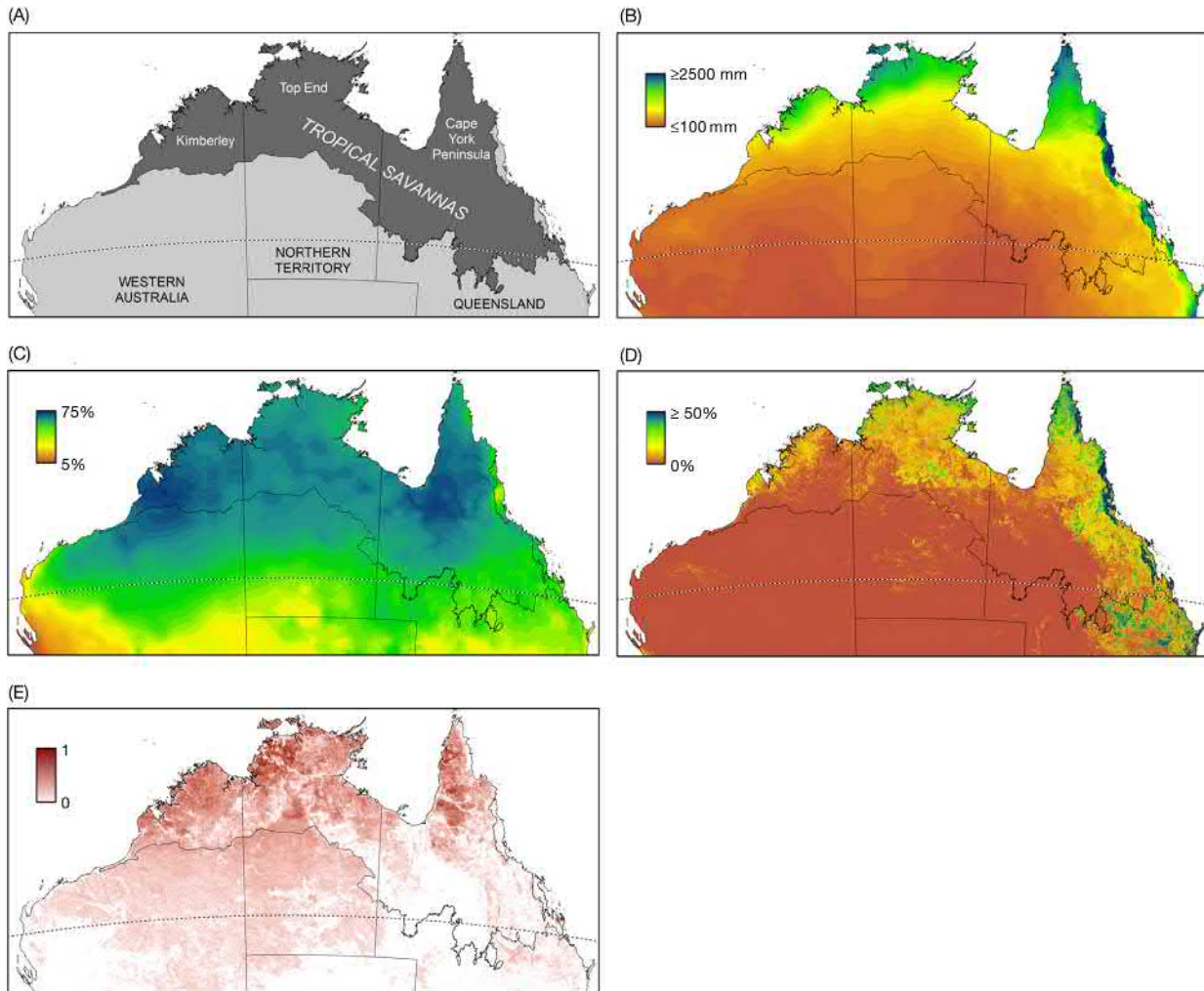


Fig. 1 (A) The extent of the tropical savannas in northern Australia (Fox et al., 2001), across three states, with (B) mean annual rainfall (modified by authors from data held by Australian Bureau of Meteorology), (C) the proportion of mean annual rainfall that falls during the summer months (December–February, inclusive) (modified by authors from data held by Australian Bureau of Meteorology), (D) tree cover, based on MODIS satellite imagery (Hansen et al., 2003); and (E) annual fire frequency, based on the MODIS satellite record (2000–2017) (Giglio et al., 2016). The dashed lines indicate the Tropic of Capricorn.

Vegetation and Environmental Setting

The Australian tropical savannas comprise a range of open forests, woodlands and open woodlands dominated by eucalypts (i.e. trees from the closely related genera *Eucalyptus* and *Corymbia*) over an understorey of C_4 grasses. The two most widespread and dominant eucalypt species are Darwin stringybark (*Eucalyptus tetrodonta*) and Darwin woollybutt (*E. miniata*), especially in savannas with mean annual rainfall exceeding 700–800 mm. The most common non-eucalypt overstorey species is the legume Cooktown ironwood (*Erythrophleum chlorostachys*), which also occurs across the savanna zone where annual rainfall exceeds 700 mm. Beneath the eucalypt-dominated canopy, a range of non-eucalypt species may form a conspicuous midstorey. These tend to be from pantropical genera such as *Terminalia*, *Buchanania* and *Planchonella*. While the overstorey eucalypts are typically evergreen, many of the midstorey species are deciduous. The Australian tropical savannas are exceptional in the dominance of evergreen trees despite extreme rainfall seasonality. The overstorey eucalypts are also remarkable in their extreme fire tolerance, with juvenile eucalypts able to survive repeated burning, and grow rapidly to fire-resistant sizes between fires. Non-eucalypt species of the midstorey tend to be more fire-sensitive, and often only persist in frequently burnt savannas as suppressed juveniles in the understorey. Remarkably, many non-eucalypt species of the midstorey are able to complete their life cycle (i.e. flowering and fruiting) while suppressed, effectively living as shrubs, within the flame zone. A conspicuous component of the upper understorey to lower midstorey of many eucalypt open forests and woodlands are arborescent species such as sand palms (*Livistona* spp.) and cycads (*Cycas* spp.). The understorey of the Australian tropical savannas is a variable mix of C_4 grasses and shrubs, mainly depending on tree cover. Typically, as tree cover increases, grass biomass decreases, given the shade-intolerance of C_4 grasses.

The structure and floristic of Australian tropical savannas are strongly influenced by a strong north–south rainfall gradient, from about 1800 mm annually at the most northern coastal regions, to 250 mm annually in western Queensland (Fig. 1B). The mesic coastal savannas of the north have higher tree biomass, higher tree densities, larger trees (especially in terms of tree height), and greater canopy cover, compared to the arid savannas of the south (Fig. 2). Like savanna regions elsewhere, the climate of the Australian tropical savannas is characterized by intense rainfall seasonality, with the vast majority of rainfall falling in the summer monsoon months (Fig. 1C), typically December to April. The length and intensity of the dry season promotes high frequencies of fires. In the long-term absence of fire, much of the higher-rainfall savannas experience an increase in tree density sufficient to exclude C_4 grasses and switch to non-savanna biomes, such as dry forests—although the long-term absence of fire is exceptionally rare in natural settings.

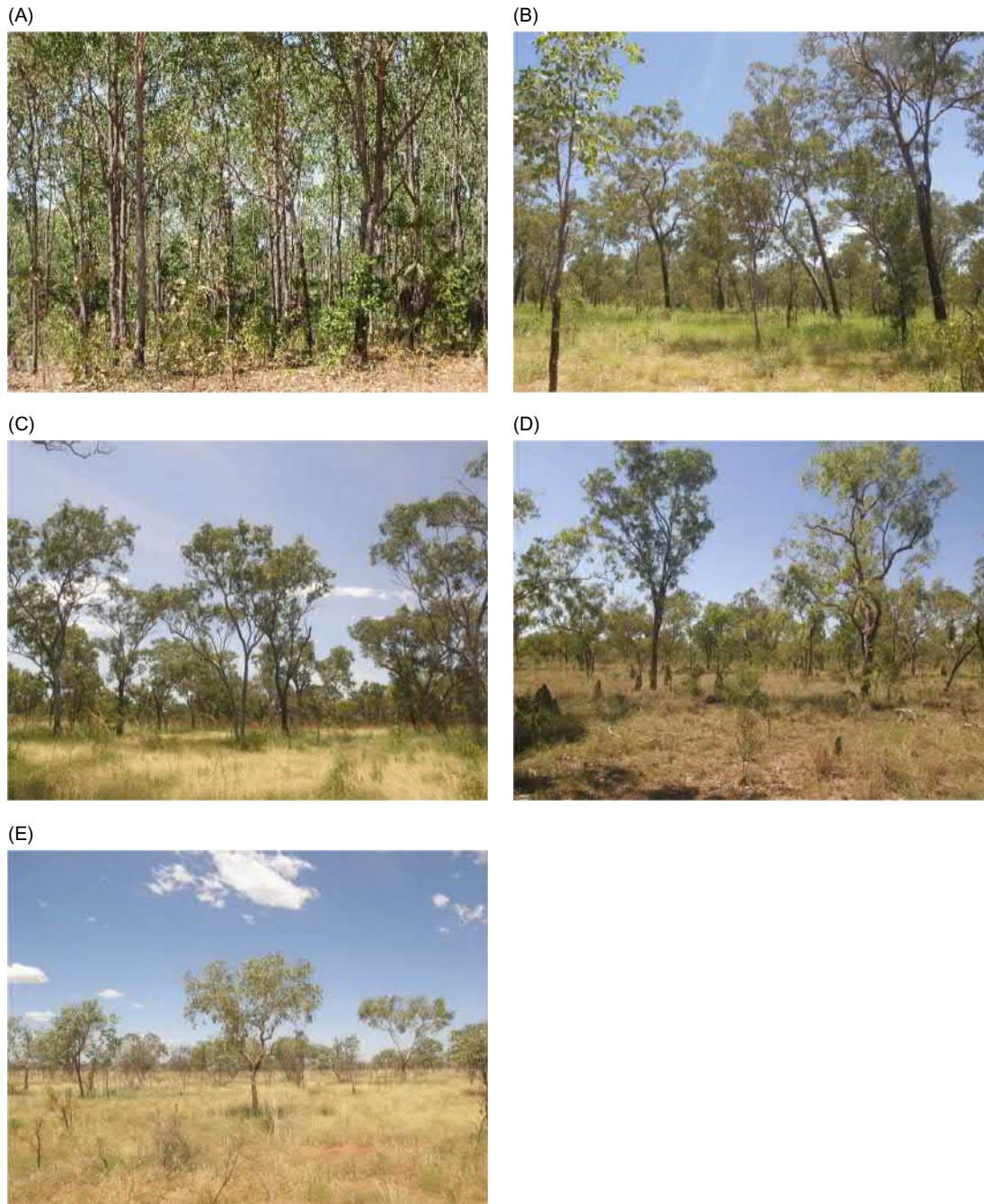


Fig. 2 Variation in savanna structure with decreasing mean annual rainfall in the Northern Territory. Panel (A) is near the north coast, near Darwin, and (E) is about 600 km south, near the southern, arid margin of the tropical savannas. (A) Darwin: 1700 mm. (B) Southern Kakadu: 1320 mm. (C) Mataranka: 950 mm. (D) Maryfield: 800 mm. (E) Newcastle Waters: 550 mm. (A) Photo by John Woinarski. (B–E) Photo by Alan Andersen.

In addition to climate, soils and topography exert strong control over the tree stand structure of the tropical savannas. Deep soils tend to hold more water, especially throughout the dry season, and typically support higher tree basal area, and taller trees. Skeletal soils, such as on sandstone plateaux, support very low tree basal area. In such areas, savanna woodlands grade into heathlands. Hence, the general positive relationship between mean annual rainfall and tree abundance (e.g. basal area, canopy cover; Fig. 2) tends to be highly variable.

Within the broad savanna matrix (Fig. 1A), there are a number of more-restricted non-savanna biomes, including: seasonally inundated treeless floodplains; swamps, including seasonally flooded *Melaleuca* forests; rainforest patches, both evergreen and deciduous; and heathlands. Extensive treeless floodplains occur adjacent to many large rivers in coastal areas, and support a range of grass and sedge species. Floodplains and rivers are often fringed by *Melaleuca* swamps and riparian forests. Heathlands predominantly occur on rocky, sandstone landforms, where the skeletal, infertile soils prevent the development of a tree canopy. The largest areas of sandstone heathland are on the Arnhem Plateau in the Northern Territory and in the Kimberley, Western Australia (Fig. 1A), with high levels of plant endemism and species richness of fire-sensitive shrub species. The tropical sandstone heathlands have floristic similarities with southern Australian heathlands, including diverse shrubs of the families Myrtaceae, Proteaceae and Fabaceae.

Fauna

Australia's tropical savanna fauna is highly distinctive and—for at least some groups—extremely rich and with high levels of endemism. They are home to about 75 frog species of which about 50 are endemic to the area, 400 reptiles (240 endemic), 340 birds (excluding marine species and occasional visitors, and including about 30 endemic species) and 135 mammals (60 endemic). Local vertebrate richness can be high: for example, the c. 20,000 km² Kakadu National Park supports about 140 reptile and 65 mammal species. Even the vertebrate fauna is far from comprehensively known, with many recent studies, especially those incorporating genetic analysis, substantially adding to the known species tally and discovering hitherto unrecognized local-scale endemism, especially for reptiles.

Diversity and endemism are particularly high in the invertebrate fauna. The best-known groups taxonomically are butterflies (132 species) and day-flying moths (31 species; Braby et al., 2019). Levels of endemism in these groups are relatively low (10%) at the species level, but this figure rises to 31% if sub-species are considered. The ecologically dominant faunal group in terms of biomass and energy flow are ants, which are poorly known taxonomically but their diversity and distribution have been extensively studied (Andersen, 2000). Australian savannas support some of the world's richest known ant faunas, rivaling those of the Amazon Basin. More than 1500 species are likely to occur in the savanna environments of the Northern Territory alone (Fig. 1A), with 60% of these occurring nowhere else (Andersen et al., 2018). Levels of ant diversity and endemism are similarly high in the Kimberley, and this is also very likely the case on Cape York Peninsula. Other important insect groups are termites and grasshoppers, but their levels of diversity and endemism have been poorly documented.

The Australian savanna fauna has dichotomous biogeographic origins, consisting of both autochthonous taxa with Gondwanan heritage and Indomalayan elements that have colonized over the past 20 million years as the Australian continent neared the Sunda Plate. Such a dichotomy is clearest for non-flying mammals, which comprise both marsupials (Gondwanan; about 40 species) and placentals (Indomalayan; about 20 rodent species). Other important Indomalayan elements of the vertebrate fauna include varanid lizards and colubrid snakes. The savanna ant fauna includes many highly diverse genera of Afrotropical/Indomalayan origin, including *Monomorium*, *Meranoplus* and *Tetramorium*, along with dominant autochthonous genera such as *Iridomyrmex* and *Melophorus* (Andersen, 2000).

Assemblages of bird and mammal species and species-groups occurring in the Australian tropical savannas share many similarities with assemblages occurring in the temperate woodlands of eastern and south-western Australia. Many faunal species, including the iconic frilled lizard (*Chlamydosaurus kingii*), agile wallaby (*Notamacropus agilis*) and northern meat ant (*Iridomyrmex sanguineus*), have extensive distributions across Australian savannas. However, many others have highly restricted ranges, often associated with isolated regions of rugged sandstone environments: examples include the rough-scaled python (*Morelia carinata*) and black grass-wren (*Amytornis housei*) from the Kimberley, and the black wallaroo (*Osphranter bernardus*) and very large Oenpelli python (*Simalia oenpelliensis*) from the Arnhem Plateau.

For most faunal groups in Australian savannas, richness and total abundance decreases from areas of higher to lower rainfall (Woinarski et al., 1999). Ants are a notable exception, with very high diversity maintained throughout the rainfall gradient (Andersen et al., 2015). Faunal composition varies with climate, soils, topography, disturbance history and vegetation structure within tropical savanna environments. The most marked contrasts are between treeless grasslands and open forest savannas. The grasslands at the low-rainfall inland edge of the savannas have a distinctive fauna, with characteristic species including the flock bronzewing (*Phaps histrionica*)—a highly nomadic species occasionally occurring (albeit mostly formerly) in immense flocks—and Spencer's monitor (*Varanus spenceri*), one of Australia's largest lizards. Typical of grassy environments world-wide, granivorous birds (comprising many species of pigeons, doves and finches, including the spectacular Gouldian finch [*Erythrura gouldiae*]), are a major component of the vertebrate fauna in Australia's tropical savannas, especially in open woodland savannas in relatively low rainfall areas. Many vertebrate species occur only in those savanna environments with greater tree density and height. This is particularly so for hollow-dependent species (such as cockatoos, kookaburras, owls, possums, tree-rats, tree frogs and some monitor lizards), which comprise about 25% of the terrestrial vertebrate fauna of Australia's tropical savannas, with another c. 20% being occasional

users of hollows (Taylor et al., 2003). In contrast to their relatively rich floristic diversity, the small areas of heathlands scattered across the Australian tropical savannas have relatively few vertebrate species associated with them, although a small set of highly restricted grass-wrens occur in heathland and hummock grassland environments in the Kimberley (black grass-wren [*Amytornis housei*]), western Arnhem Land (white-throated grass-wren [*A. woodwardi*]) and the Gulf hinterland (Capentarian grass-wren [*A. dorotheae*]).

Most other tropical savannas in the world, and particularly in Africa, have diverse assemblages of large mammalian herbivores and associated predators. In contrast, the largest extant native mammals of the Australian tropical savannas are a small number of kangaroo and wallaby species, all < 50 kg in body mass. These typically occur at low densities and have relatively low biomass. The largest predator is the dingo (*Canis dingo*/*C. familiaris*) at about 15 kg, which was introduced by IndoMalayan people about 4000 years ago. A diverse suit of megafauna was present in the Australia tropical savannas until the Late Pleistocene. The cause of their extinction is controversial, but most likely due to overhunting by humans, natural climate change, or a combination of both.

The tropical savannas of northern Australia are highly seasonal environments, and animal species respond in diverse ways to this marked temporal change in climate and resource availability. Many disperse widely across savanna environments, tracking spatial and temporal variation in food availability. Others, such as the channel-billed cuckoo (*Scythrops novaehollandiae*) and eastern koel (*Eudynamis orientalis*), are long-distance migrants whose occurrence in Australia's tropical savannas is largely restricted to the wet season, when the resources on which they primarily feed are most abundant. Many other species have very well-defined breeding seasons, timing their reproductive output to match the climate-influenced variation in resource availability.

Land Use and Human Population

Northern Australia has been occupied by humans for at least 65,000 years (Clarkson et al., 2017), and the present-day landscape owes much to this continuous occupation and management, particularly to Indigenous fire management. Indigenous people continue to maintain a major presence in the area, owning much of the land and maintaining responsibility for fire management across large swathes of it.

European settlement of the area began in the 19th Century, with military and trading outposts, for mining and for extensive pastoralism, with the latter land use in particular resulting in the usurpation of Indigenous land ownership across extensive areas. However, in notable contrast to the tropical savannas of other continents, the northern Australian landscape remains sparsely populated. Outside the few major towns, human population density is very low: more than 99% of the tropical savannas has a population density less than 0.1 person km⁻², and the total population in the region is about 620,000.

In contrast to the rest of the savanna world, there is—to date—very little intensive agricultural development in Australian tropical savannas, and consequently only a tiny proportion (c. 1%) of the landscape has been cleared. Pastoralism continues to be the major land use, occupying about 70% of the land area (Fig. 3). Conservation reserves occupy about 16%, with the majority of this reserved area comprising Indigenous Protected Areas, a tenure of rapidly increasing extent in which Aboriginal land-owners enter formal contracts with the Australian government to manage the cultural and natural values of their lands. The establishment of these Indigenous Protected Areas and their associated Indigenous ranger groups has led to some notable improvements in conservation management, and to health, education, and employment outcomes in otherwise impoverished remote communities. Other Indigenous landholdings comprise about 8% of northern Australia.

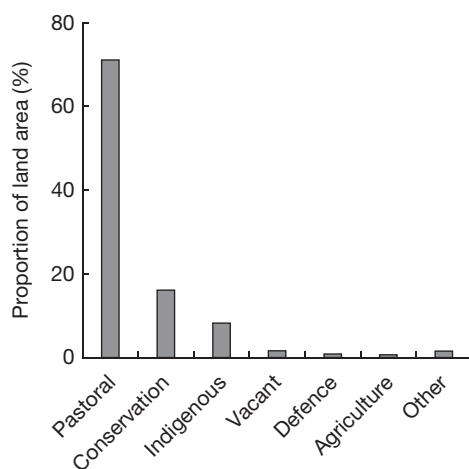


Fig. 3 Major land uses of the tropical savannas in northern Australia. Conservation reserves include Indigenous Protected Areas.

Incidence and Impacts of Fire

Tropical savanna is the most fire-prone biome on Earth, and northern Australia's savannas landscapes burn with extremely high frequencies. High fire frequencies are driven by the annual cycle of high summer rainfall (Fig. 1B)—which fuels rapid grass growth—followed by an intense dry season—when the grass dries out. Although humans are now the primary source of ignitions of fires in the savannas, even in the absence of humans there is an ample supply of ignitions due to the frequency of lightning storms at the end of the dry season, when the moisture content of grasses is low. Fire frequency is highest in the high-rainfall coastal regions of the monsoon tropics (Fig. 1B and E)—in such regions, typical intervals between fires can be as low as 1–2 years. Moving south into the more arid parts of the tropical savannas, fire frequency declines, driven by declining grass production. In the more arid savannas, fire activity is more temporally variable, following a 'boom–bust' cycle. In these areas, extensive fires occur when fuel has accumulated to sufficient levels to carry fire, especially after high rainfall associated with La Niña events.

Fire has shaped the Australian biota for at least 40–60 million years, long before the development of the northern Australia monsoon, and hence the tropical savannas, over the last 10 million years. Plants and animals of the Australia's tropical savannas possess an incredible diversity of adaptations to cope with frequent fire, attesting to the importance of fire as an evolutionary force in this region. For most species, populations are able to quickly recover after fire, given either high survival rates (especially for vertebrate animals and woody plants), or high post-fire recruitment (especially for herbaceous plants and shorter-lived woody plants). Fire-sensitive species and communities—especially those that are sensitive to short intervals between fires—tend to be concentrated in isolated, fire-protected areas, such as rugged, rocky landforms (e.g. sandstone heathlands, rainforests) or on islands and peninsulas (coastal vine thickets).

Fire in northern Australia has been intensively managed by humans for millennia. Australian Aborigines have traditionally used landscape fire for a wide range of purposes, including hunting and maintenance of forage for game, as well as protection of fire-sensitive plant resources (e.g. yams). The extent to which Aboriginal people deliberately used landscape fire to manage resources led to the coining of the term 'fire-stick farming'. The dispossession of Aboriginal people of their lands in the 19th and 20th Centuries led to a widespread breakdown of traditional fire management across most of northern Australia. It is widely believed that the loss of traditional fire management has led to a significant increase in the frequency of large, intense wildfires, typically late in the dry season when fire weather conditions are most severe, across the tropical savannas.

The loss of traditional fire management, and resultant increase in the frequency of high-intensity fires, is likely to have led to the decline of a number of fire-sensitive plant and animal species, as well as some plant communities embedded within the savanna matrix. Most notably, frequent high-intensity fires are thought to be contributing to the decline of small mammals and a range of granivorous birds, although compelling evidence is limited. Frequent high-intensity fires have driven the widespread decline of the native tree, northern cypress-pine (*Callitris intratropica*), especially in lowland savannas. Plant communities within the savanna matrix listed by the Australian Government as Endangered, with the key threat being frequent high-intensity fires, include the sandstone heathlands of the Arnhem Plateau and coastal vine thickets of the Dampier Peninsula in the Kimberley.

In recent decades, there has been an increasing use of extensive prescribed burning (i.e. the deliberate lighting of fires under relatively mild fire weather conditions) to reinstate more benign fire regimes, typical of those that prevailed under traditional Aboriginal management. In particular, prescribed burning is applied with the intention of shifting the predominant season of fire to the early dry season when fire weather conditions are less severe, so that the resultant fires are less intense, as well as smaller and patchier. Such fire regimes are widely *perceived* as being more conducive to the maintenance of biodiversity, although some researchers have argued that a greater emphasis on reducing overall fire frequencies, and increasing the extent of longer-unburnt areas, is required.

Threats, Conservation Challenges and Management

Due to low human population density and little intensive agricultural development, the tropical savannas of northern Australia have survived as one of the world's most intact extensive natural ecosystems (Woinarski et al., 2007). The total extent of habitat loss is relatively minor (only 1% has been cleared), the conservation reserve system is extensive and reasonably comprehensive (comprising 16% of land area) and, in contrast to most of Australia, no endemic species are known to have become extinct since European settlement about 200 years ago. Furthermore, Australia's tropical savanna environments have retained many vertebrate species and species-groups that have been lost from elsewhere in the continent, including, for example, the rabbit-rats (*Conilurus* spp.), nail-tailed wallabies (*Onychogalea* spp.) and magpie goose (*Anseranas semipalmata*).

However, there are some substantial conservation challenges. Over the last c. 100 years, there have been extirpations of many native mammal species from many locations within the tropical savannas, especially in lower rainfall areas, and severe and rapid losses of native mammals continue, even in the most significant conservation reserves. Although causality remains difficult to circumscribe, much of this ongoing decline is likely to be due to predation by feral domestic cats (*Felis catus*), habitat degradation due to cattle and feral herbivores, and changed fire regimes (Ziembicki et al., 2015); and recent targeted management of these factors has led to some recovery of at least some species in some areas (Legge et al., 2019).

Many introduced species are now widespread and abundant and exert major pressures on native species: in most areas of the tropical savannas, the biomass of introduced vertebrates (especially livestock) now far exceeds that of native vertebrate species (Woinarski, 2014), and high densities of introduced herbivores are continuing to transform and degrade many environments. The cane toad (*Rhinella marina*) was introduced in the 1930s to north-eastern Australia, and has subsequently expanded its range across most of Australia's tropical savannas. The toad has toxins that kill a range of native species that prey on it, and its continuing spread has precipitated severe declines of the northern quoll (*Dasyurus hallucatus*) and many other predators, including snake and goanna (monitor) species. In turn, the marked declines of these previously abundant native predators has destabilized some food webs and led to increases and decreases of many other native species. In much of the tropical savannas, introduced pigs (*Sus scrofa*) are now widespread, and these have become a major threat to many species, including plants, ground-nesting birds and freshwater turtles. Largely because of the pervasive occurrence of introduced species across much of the north Australian mainland, the many islands of northern Australia—that often have not yet been reached by these introduced pests and weeds—are important refuges for many species.

In many areas, the pastoral industry has attempted to increase productivity through the establishment of exotic grasses as forage for cattle. Some of these introduced plants, most notably African gamba grass (*Andropogon gayanus*), have become serious environmental weeds, extending from their initial plantings in pastoral holdings to lands of all tenures (including conservation reserves), out-competing native grasses, fuelling fires that are of far higher intensity and frequency than those typical of native vegetation, and consequently transforming environments from savanna woodlands with a high diversity of native species to a grassland monoculture (Setterfield et al., 2013).

There have been repeated attempts to intensify the resource use and development of Australia's tropical savannas, especially for mining, horticulture and more intensive pastoralism (Cook, 2009). The momentum for development is strong, although often not tempered by the capacity and constraints of the environment or by the risks to the region's natural assets. Consequently, the pace of loss and degradation of native environments (and the biodiversity dependent upon them) is likely to increase.

Australia is the only country to include emissions from wildfires in its national greenhouse gas accounts, and most of such emissions come from savanna burning. This has led to the emergence of a new land-use and economy in savannas that is unique to Australia: a carbon market has been established to trade in reductions in greenhouse gas emissions through prescribed burning in the early dry season that reduces the overall extent of fire and particularly that of higher-intensity fires later in the dry season (Russell-Smith et al., 2013). This has been of particular benefit to remote, economically disadvantaged Aboriginal communities, promoting cultural connection to traditional lands along with employment opportunities and improved health and education. It has also led to the more-purposeful management of fire, a major factor affecting savanna biodiversity. A significant proportion of the high-rainfall (≥ 1000 mm) tropical savannas, mostly Aboriginal lands, are now managed as part of fire/carbon abatement projects. There remains some uncertainty about the extent of overlap between fire regimes managed for the carbon market and optimal fire regimes for biodiversity, although there is likely to be considerable convergence.

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South-Eastern Australian Temperate Grasslands and Grassy Woodlands

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Abstract

South-eastern Australian grassy ecosystems include a variety of grassland, grassy woodland and related vegetation types. Prior to European settlement, grassy ecosystems existed in a mosaic, alongside extensive forests and other vegetation types. Some fauna species of grassy ecosystems are distinctive. Australian grassy ecosystems have a history of land-use by Aboriginal

peoples. Since European colonization, grassy ecosystems have been adversely impacted upon, including agricultural transformations, infrastructure development and invasion by pest animals and plants. Many grassy communities are now legislatively recognized as endangered. Recognition of native grassy ecosystems by government ecologists and conservation managers has emerged, with grassland and grassy woodland conservation reserves, off-reserve measures and engagement programs established. There is growing public interest, with community organizations and some landholders being particularly active. In the agricultural sector, there is growing application of sustainable use of native grassy systems. The conservation status of these systems remains poor, particularly that of grasslands, and government policies and legislative enforcement lag.

Description of the Ecosystems

South-eastern (SE) Australian grassy ecosystems include a variety of grassland, grassy woodland and related vegetation types, which prior to European settlement existed in a mosaic, alongside extensive forests on the ranges, and lesser areas of heathlands, wetlands and riparian systems (Keith, 2004; Armstrong et al., 2013; Keith and Pellow, 2015). SE Australian grassy ecosystems have been impacted by post-settlement land-uses since colonization, including agricultural transformation and urban and other infrastructure development (Benson, 1994; Gott et al., 2015; Kirkpatrick et al., 1995; Williams and Morgan, 2015). Many are now legislatively recognized as endangered ecological communities (Australian Government, 2006, 2008, 2009a,b,c, 2016, 2019; NSW Government, 2005a, 2011a,b). Greater interest in these communities emerged in the late 1980s with increased efforts to understand them and application of conservation actions (Kirkpatrick et al., 1995; Williams and Morgan, 2015).

Distribution

Grassy ecosystems are widely distributed throughout continental Australia. Here I focus on grassy ecosystems of temperate south-eastern New South Wales (SE NSW), the Australian Capital Territory (ACT), Victoria and Tasmania. The grassy ecosystems of the following bioregions (Environment Australia, 2000) are described: South Eastern Highlands, NSW South Western Slopes, Sydney Basin and South East Corner in NSW, Victorian Midlands, Southern Volcanic Plain and South East Coastal Plain in Victoria, and Ben Lomond, Northern Midlands, Northern Slopes, South East, King, Flinders, Central Highlands and Southern Ranges in Tasmania. On the mainland, the systems merge with related vegetation types at the northern and western boundaries of these regions.

Definitions

SE Australian grasslands are defined as vegetation dominated by grasses, Poaceae, and forbs of various families, with <10% projected tree and shrub cover (Benson, 1996). Lowland grasslands are defined as those occurring at elevations <1200 m (Australian Government, 2016). Grassy woodlands are defined as vegetation composed of well-spaced trees (10–30% projected foliage cover), the trees with single trunks, with canopy depth of individual trees usually greater than the length of the trunks and mature heights >5 m, with a groundlayer predominately grassy, containing a variety of forbs, and with a variable shrub-layer (Howling, 1996).

Major Systems

Temperate grasslands

NSW temperate grasslands occur throughout the South Eastern Highlands bioregion, with minor occurrences in the following neighboring bioregions: NSW South Western Slopes, South East Corner and Sydney Basin Bioregions (Australian Government, 2016). Studies in SE NSW have defined grassland associations or communities, with Armstrong et al. (2013) describing eight communities defined by dominant grass species, their location within the region and association with either topographical position or geological substrates. The Armstrong et al. (2013) grassland communities, including one occurring on ephemeral wetlands, are dominated by grass species in various combinations. Dominant grasses are kangaroo grass (*Themeda triandra*, Figs. 1 and 2) snow grass (*Poa sieberiana*), several wallaby-grasses (*Rytidosperma*) and speargrasses (*Austrostipa*), and with a number of other taxa being prominent, including redgrass (*Bothriochloa macra*), purple wiregrass (*Aristida ramosa*), nine-awn grass (*Enneapogon nigricans*), wind-mill grass (*Chloris truncata*), hairy panic (*Panicum effusum*) and several species of plume grass (*Dichelachne* spp.) and lovegrass (*Eragrostis* spp.). The communities are generally forb-rich in their undisturbed states, with herbaceous species of the families Fabaceae, Orchidaceae, Asparagaceae, Asteraceae, and Anthericaceae well represented, alongside species from numerous other families (Armstrong et al., 2013) (Fig. 3). Regionally restricted grassland communities have species of grasses, forbs and woody plants similarly restricted in their ranges (Armstrong et al., 2013). Sedges and rushes (Cyperaceae, Juncaceae and several minor families) occur locally in moist patches. A grassland community of low-lying sites with poor drainage is dominated by river tussock (*Poa labillardierei*). Trees and shrubs in the following genera occur in low densities: *Eucalyptus*, *Acacia*, *Melicetyus* and *Bursaria*. Low sub-shrubs in Ericaceae and Fabaceae occur (Armstrong et al., 2013).

Additional NSW grassland types are the maritime grasslands occupying either rocky coastal headlands or unconsolidated beach sands (Keith, 2004), with the exposed headland community dominated by *Themeda triandra*. It resembles *T. triandra*-dominated



Fig. 1 A grassland dominated by kangaroo grass (*Themeda triandra*) at Turallo Nature Reserve, NSW. Photo: R. Rehwinkel.



Fig. 2 Kangaroo grass (*Themeda triandra*), NSW. Photo: R. Rehwinkel.



Fig. 3 Bulbine lily (*Bulbine bulbosa*, Anthericaceae), a grassy ecosystem forb, NSW. Photo: R. Rehwinkel.

communities of the adjacent highlands, differing in having a distinctive forb and shrub component characterized by species typical of the Sydney Basin and South East Corner bioregions (NSW Government, 2005a).

In Victoria, temperate grasslands occur predominately on the Volcanic Plain bioregion, with pockets in the Victorian Midlands and South-east Coastal Plain bioregions (Australian Government, 2008). Two ecological sub-types are recognized: plains grassland, containing three associations, and creekline tussock grassland (Australian Government, 2008). These grasslands, like those in NSW, contain *T. triandra*, but differ from NSW grasslands in having a greater occurrence of semi-arid elements, such as *Ptilotus* spp. and a number of species in Chenopodiaceae. Grasslands occupying low-lying sites with poor drainage are dominated by *Poa labillardierei* (Australian Government, 2008), like those in SE NSW.

Lowland grasslands of Tasmania occur principally in the Tasmanian Midlands, Derwent Valley, the east coast and the southeast, with localized areas in the northwest and on islands in Bass Strait, with two variants defined by their dominant grass species (Australian Government, 2009a). Tasmanian grasslands resemble those on the mainland, with drier sites dominated by *T. triandra* and low-lying sites by *P. labillardierei*. Forbs and associated plants resemble those of the mainland, with some semi-arid elements of the western Victorian grasslands co-occurring with species common to those in SE NSW (Kirkpatrick, 1988; Kirkpatrick et al., 1995).

Temperate grassy woodlands

In temperate SE NSW, and ranging beyond the boundaries of the regions covered here, are a set of grassy woodlands typified by trees of various *Eucalyptus* species, and a forb-rich grassy groundlayer (Australian Government, 2006; Keith, 2004). The groundlayer resembles adjacent grassland communities, often having a similar floristic composition, though a number of forb and shrub species only occur or are more common in woodlands and adjacent dry forests (Armstrong et al. 2013).

In SE NSW, several broad woodland types occur (Keith, 2004). In the Sydney Basin and South East Corner bioregions of NSW, woodlands dominated by forest red gum (*Eucalyptus tereticornis*) occupy deep soils of river flats and granite landscapes (Keith, 2004; NSW Government, 2011a). These have groundlayers dominated by *T. triandra*, and, like the sometimes adjacent coastal headland grasslands, have forb and shrub components typical of their bioregions. A similar woodland type occurs on the Gippsland Plains of Victoria (Australian Government, 2009b).

In the NSW South Eastern Highlands, two main grassy woodland types occur. Most widespread, occurring especially in warmer, low-altitude regions, as well as on the NSW South Western Slopes bioregion and beyond, are the so-called box-gum grassy woodlands. Several distinct communities occur (Armstrong et al., 2013; Australian Government, 2006; Keith, 2004), with most co-dominated by yellow box (*Eucalyptus melliodora*) and Blakely's red gum (*E. blakelyi*). A variety of other eucalypts occur, commonly including apple box (*E. bridgesiana*) and candlebark, (*E. rubida*). Additionally, a number of mid-stratum *Acacia* species occur, along with minor occurrences of she-oaks (*Allocasuarina* spp.), kurrajong (*Brachychiton populneus*) and a variety of other midlayer shrubs, including species in Fabaceae, Asteraceae, Pittosporaceae, Ericaceae and Myrtaceae (Armstrong et al., 2013). Woodlands on the NSW South Western Slopes have white box (*E. albens*) as a co-dominant (Australian Government, 2006), and shrubs in Chenopodiaceae occur more frequently, as these woodlands merge with grassy and shrub-dominated woodlands dominated by gray box (*E. microcarpa*) and white cypress-pine (*Callitris glauca*) on the plains in the far west of the region (Keith, 2004).

Occurring in cooler, higher-altitude regions of the SE NSW highlands are woodlands dominated by cold-tolerant eucalypts, including snow gum (*E. pauciflora*, Fig. 4), ribbon gum (*E. viminalis*), swamp gum (*E. ovata*), black sallee (*E. stellulata*), black gum (*E. aggregata*), and *E. rubida* (Keith, 2004; NSW Government, 2011b). Midlayer and groundlayer components resemble the



Fig. 4 A cool-climate grassy woodland dominated by snow gum (*Eucalyptus pauciflora*) at Rows Lagoon, NSW. Photo: R. Rehwinkel.

adjacent grassland communities, with shrubs locally more common than in the grasslands, and with additional shrub species in Myrtaceae, Fabaceae, Proteaceae, Ericaceae, and Asteraceae (Armstrong et al. 2013).

Box-gum grassy woodlands also occur in the Victorian Midlands bioregion of Victoria (Australian Government, 2006), while woodlands dominated by cold-adapted species, particularly *E. viminalis* and associated species, are also widespread in cooler parts of Victoria and in Tasmania (Australian Government, 2009a,b, 2019). In each state, co-occurring tree, shrub, and forb components vary according to the flora of each bioregion, though many species occur throughout the SE, while others turn over in north-south or east-west gradients (Cosgrove, 2014; Eddy et al., 1998; Falconer, 2004; Kirkpatrick, 1988; Lunt et al., 1998; Marriott and Marriott, 1998; Sharp et al., 2015a; Walker et al., 2001).

Minor Systems

Ephemeral wetlands, bogs, and fens

Areas occupied by shallow waterbodies during wet periods in highland SE NSW transform into grasslands during extended dry spells (Armstrong et al., 2013). The largest of these, Lake George and Lake Bathurst, are, when dry, occupied by a grassland-forbland dominated by species restricted to this community (Armstrong et al., 2013). Smaller ephemeral wetlands on the Monaro basalt plains behave like the larger wetlands to their north (Armstrong et al., 2013; Benson and Jacobs, 1994). A set of grassy ecosystems known as bogs and fens occur at higher elevations bordering the montane regions of the Australian Alpine bioregion and along the Great Eastern Escarpment; these are typified by mosaics of grasses, sedges, rushes and forbs, often with emergent trees and shrubs, and in some high-altitude sites, sphagnum (*Sphagnum cristatum*) (Armstrong et al., 2013; Australian Government, 2009c; Thomas et al., 2000).

Adjoining Grassy Ecosystems

Semi-arid grasslands and woodlands

To the west and north of the above-listed grasslands and grassy woodlands in NSW and Victoria, in semi-arid climates and on flatter landscapes, occur several grassland and grassy woodland formations and vegetation classes that are similar to the those in the SE; however, these generally have different dominants, including more arid-adapted grasses, shrubs, especially those in Chenopodiaceae, and *Eucalyptus* spp. Forbs also differ, with many being annual, rather than the perennials characteristic of the SE (Keith, 2004). Some woodlands in these regions are dominated by *Acacia* spp. (Keith, 2004).

Montane and alpine grasslands, shrublands and woodlands

NSW, Victorian and Tasmanian lowland grassy communities give way to distinctive communities in the montane and alpine regions at the highest elevations. Some of these communities are characterized by grassy groundlayers, others are shrubby; in most of the

montane communities and all of the alpine communities, the grass, forb, shrub and tree components are distinctive, relative to lowland communities (Keith, 2004).

Tableland dry forest communities

On the tablelands and slopes, grassy woodlands give way to a variety of dry open forest communities, mostly occupying steeper terrain with shallow soils (Keith, 2004). These communities are dominated by *Eucalyptus* spp., with *Acacia* and *Allocasuarina* spp. and black cypress-pine (*Callitris endlicheri*) common, and have a greater variety and density of shrubs in Myrtaceae, Asteraceae, Fabaceae and Proteaceae (Armstrong et al., 2013). Where present, the grassy groundlayers may resemble those of the adjacent grassy woodlands occurring on gentler terrain, though some are dominated by the shade-loving weeping grass (*Microlaena stipoides*) or robust tussocks of red-anthered wallaby-grass (*Rytidosperma pallidum*) and spiny-headed mat-rush (*Lomandra longifolia*) (Armstrong et al., 2013).

Adjoining Non-Grassy Ecosystems

In higher rainfall areas or sheltered parts of the ranges and coastal plains, dry forests give way to increasingly wetter eucalypt forests, with shrubby midlayers, some with ferny groundlayers, and soft tree-fern (*Dicksonia antarctica*) and burrawang (*Macrozamia communis*) as occasional midlayer dominants (Keith, 2004; Armstrong et al., 2013). The wettest, most sheltered areas support rainforest types, with distinctive floras and largely lacking *Eucalyptus* spp. (Keith, 2004). Wet forests generally lack grass-dominated groundlayers, though *Microlaena stipoides* may be common.

Secondary Grasslands

Clearing of trees and shrubs from any woody vegetation community, with the retention of a native grassy groundlayer, results in so-called secondary or derived grassland (Australian Government, 2006, 2016; Benson, 1996; Rehwinkel, 2015). Where grassy woodland and dry forest communities are cleared, grasslands resembling the natural communities result, with *T. triandra*, *Austrostipa* spp. and *Rytidosperma* spp. dominating. Where wet forest communities are cleared, novel grassland communities may result, dominated either by *M. stipoides* or *P. labillardierei*, species that prefer higher-nutrient soils resulting from addition of fertilizers for pasture management (Langford et al., 2004).

Ecological Conditions Determining Grassy Ecosystems

Kirkpatrick (1988), Kirkpatrick et al. (1995), and Rehwinkel (1997) reviewed conditions determining SE Australian grasslands, with the following contributing, either alone or interactively:

1. deep, mineral, fertile soils;
2. seasonal drought excluding trees and shrubs;
3. competitive exclusion of woody vegetation by grass roots and sward;
4. attraction by grazing animals to grassland, destroying seedlings of woody plants;
5. severe frosts, particularly low-probability, low-temperature events;
6. wildfires, particularly in combination with grazing;
7. periodic waterlogging, particularly in low-lying sites and in combination with frosts;
8. basaltic or alluvial soils, regardless of climatic conditions;
9. heavy clay soils that crack in summer, causing death of newly established tree seedlings;
10. pre-European settlement burning patterns of the Aboriginal peoples (firestick farming); and
11. previous climates, particularly the colder and drier climates of the Holocene glacials.

Major grassland areas in SE Australia are mapped in Williams and Morgan (2015).

Similar conditions to those that determine presence of grasslands, though generally less severe, determine presence of woodlands (Howling, 1996; Rehwinkel, 1997). Lowland woodlands occur on flat to undulating terrain and fine-textured soils of moderate fertility, with rainfall between 500 and 900 mm p/a, or in rainshadow valleys on the coast receiving rainfall between 700 and 1000 mm p/a (Keith, 2004). The various grassy woodland formations and communities occur on landscapes with varying combinations of the above set of influences (e.g., Keith, 2004; Armstrong et al., 2013).

Fauna of Grassy Ecosystems

The fauna of grassy ecosystems generally shows affinities to fauna across the Australian continent, though there are some species-level differences. Amongst the most iconic of the Australian fauna, the macropods (kangaroos and wallabies, Macropodidae) are represented by the eastern gray kangaroo (*Macropus giganteus*), a large, gregarious grazer of grasslands, open woodlands and dry forests. It is one of the largest kangaroos and adapted to survive on poor quality grasses in open country in

SE Australia (Hume et al., 1989). The Tasmanian Midlands are that state's strongholds for *M. giganteus* (Australian Government, 2009a). Other, smaller macropods and macropod allies (Potoroidae) occur in grassy ecosystems, including the eastern bettong (*Bettongia gaimardi*), which was extirpated in SE mainland grasslands soon after European colonization (Costin, 1954), but survives in Tasmania, where it too has its stronghold (Australian Government, 2009a). In Victoria, the eastern barred bandicoot (*Parameles gunnii*) is confined to one grassland site (Wynyard, 2014), though it remains common in Tasmania ("Eastern Barred Bandicoot" website).

Other marsupials found in grassy ecosystems include, very sparingly in woodlands in NSW, the koala (*Phascolarctos cinereus*) (NSW Government, 2011c) and squirrel glider (*Petaurus norfolcensis*) (Australian Government, 2006), very commonly throughout the SE, the common wombat (*Vombatus ursinus*) (Australian Government, 2009a, 2016), and the three carnivorous marsupials, Tasmanian devil (*Sarcophilus harrisii*), eastern quoll (*Dasyurus viverrinus*) and spotted-tailed quoll (*Dasyurus maculatus*), common now only in Tasmania (Australian Government, 2009a). One of the three surviving monotremes, the short-beaked echidna (*Tachyglossus aculeatus*) remains common in grassy woodlands throughout the SE, as do a number of bats (order Chiroptera). Less common are native rodents (Muridae).

Avifauna of grassy ecosystems include emu (*Dromaius novaehollandiae*), which is now locally rare in the SE mainland, and Australian bustard (*Ardeotis australis*), which has been extirpated there (Menkhorst et al., 2017). The most distinctive grassy ecosystem birds are cockatoos (Cacatuidae) and parrots (Psittacidae), specifically those in the genera *Cacatua*, *Eolophus*, *Platycercus*, *Polytelis*, *Psephotus*, and *Neophema*, which feed principally on seeds of grasses, and *Eucalyptus* and *Acacia* spp. in dry forests, woodlands and grasslands (Menkhorst et al., 2017). Other distinctively SE Australian grassy ecosystem birds include magpie-lark (*Grallina cyanoleuca*), Australian robins (Petroicidae), thornbills, gerygones and weebill (Acanthizidae), whistlers and shrike-thrushes (Pachycephalidae), pardalotes (Pardalotidae, Fig. 5), some honeyeaters (Meliphagidae) and most of the woodswallows, butcherbirds and Australian magpies (Artamidae) (Menkhorst et al., 2017). Grassy ecosystem birds of distinctly non-Australian bird families, i.e., those with a greater distribution outside Australia, include many hawks (Accipitridae), falcons (Falconidae), two quails (Phasianidae), a lark (Alaudidae), a pipit (Motacillidae) and several corvids (*Corvus* spp. in Corvidae) (Menkhorst et al., 2017).

Reptiles include several threatened species that are all but confined to grassy ecosystems in SE Australia, including grassland earless dragon (*Tympanocryptis lineata*), striped legless lizard (*Delma impar*), pink-tailed worm-lizard (*Aprasia parapulchella*) and little whip snake (*Suta flagellum*) (Australian Government, 2016). Other herpetofauna common in lowland grasslands include eastern common froglet (*Crinia signifera*), spotted marsh frog (*Limnodynastes tasmaniensis*), eastern brown snake (*Pseudonaja textilis*), eastern blue-tongued skink (*Tiliqua scincoides*), shingleback (*T. rugosa*, Fig. 6) and Cunningham's skink (*Egernia cunninghami*).

Some invertebrates are closely tied to grassy habitats. On the SE mainland, golden sun moth (*Synemon plana*), Canberra raspy cricket (*Cooraboorama canberrae*) and perunga grasshopper (*Perunga ochracea*), are three threatened grassland specialists, while the rare Key's matchstick grasshopper (*Keyacris scurra*) is tied to species of family Asteraceae in grassy woodlands (Australian Government, 2016). Grassland-insect relationships are similarly close in Tasmania, where a skipper butterfly (*Anisynta dominula*) and Ptunnarra brown butterfly (*Oreixenica ptunnarra*) both feed on *Poa* spp., and the Tunbridge looper moth (*Chrysolarentia decisaria*) is restricted to one grassland site (Australian Government, 2009a).

Human Interactions: Indigenous Connections and European Exploitation

Indigenous Land-Uses: Pre1788

The interactions of Aboriginal peoples with SE Australian grassy ecosystems were given scant recognition in early 20th century literature (e.g., Costin, 1954). Writing of the Monaro region of SE Australia, Hancock (1972) said it was thought that Indigenous



Fig. 5 Striated pardalote (*Pardalotus striatus*), a grassy woodland belonging to a typical Australian family. Photo: R. Rehwinkel.



Fig. 6 Shingleback (*Tiliqua rugosa*), a common grassy woodland reptile, NSW. Photo: R. Rehwinkel.

peoples only arrived there some 15,000 b.p., and, while focussing on their hunting practices, particularly the harvesting of Bogong moths (*Agrotis infusa*), Hancock acknowledged that some observers thought that grasslands and open woodlands did not merely result from prevailing climate-soil conditions and plant-animal interactions, but some may indeed be partly anthropogenic, resulting from Aboriginals' firesticks.

In recent years, an increasing body of literature emerged, putting the Indigenous inhabitants of Australia firmly in the picture. It is now generally recognized that Aboriginals had a longer tenure of the continent, by as much as 50,000 years b.p. (Gott et al., 2015). Chief amongst those who have written about Aboriginal land-uses, Gammage (2011) argued that Aboriginals shaped Australian grassland and woodland systems in a highly complex manner by careful land-management techniques, including use of firestick farming. Gott et al. (2015) and Pascoe (2018) present evidence of sophisticated agricultural practices of the Aboriginal cultures in grassy ecosystems, citing instances of cultivation of root crops, including, amongst others, the murrnong (*Microseris lanceolata*, Fig. 7), a grassy ecosystem forb that was once super-abundant and widespread throughout the SE mainland, but is now rare. Pascoe (2018) also cites instances of large-scale harvesting and storage of grain crops from native grasses and even irrigation and sowing of grain crops, though Gott et al. (2015) suggests that this occurred mainly in arid regions, rather than in the south-east. Aboriginals established permanent or semi-permanent settlements in some temperate grassland areas (Gott et al., 2015; Pascoe, 2018).

Early European Land-Uses: 1788 to 1950s

European colonization started with establishment of the Sydney penal settlement in 1788. It was not until the early 19th century that country west of Sydney, occupied by extensive grasslands and grassy woodlands, attracted the European explorers, who were



Fig. 7 Murrnong (*Microseris lanceolata*), an important staple of pre-European cultures. Photo: R. Rehwinkel.



Fig. 8 Grassy woodland transformed into productive croplands, at the expense of the ground flora, South-western slopes, NSW. Photo: R. Rehwinkel.

followed by colonists and their stock. It is often said, referring to Australia's agricultural wealth, that "Australia rode on the sheep's back" (Gott et al., 2015), but it is rarely acknowledged that wealth generated from wool resulted because the sheep grazed exclusively on native grasses and forbs. The grasslands in the SE were progressively opened up by colonists (Fig. 8): in NSW, firstly in the Bathurst region by 1813 (Keith, 2004), then the Goulburn to Canberra region by 1823, the Monaro by 1824, the Tasmanian Midlands by 1825, and Victoria, starting in 1835 (Gott et al., 2015).

The early phases of agriculture in SE Australia were marked by rapid growth of flocks of sheep and herds of cattle, which led to, or co-occurred with:

1. overgrazing of native grasslands;
2. the beginnings of substantial soil erosion;
3. massive stock losses due to droughts;
4. European rabbit (*Oryctolagus cuniculus*) plagues that followed their introduction and expansion of their populations;
5. "ring-barking" to expand pastures by deliberate destruction by cutting of the cambium layer of trees; and
6. declines of some productive native grasses to be replaced by exotic annual species (Costin, 1954; Benson, 1994; Gott et al., 2015).

SE Australian grassy ecosystems now contain a significant number of introduced plant and animal species, resulting from either deliberate or accidental introductions. The misguided introduction of European red fox (*Vulpes vulpes*) was to introduce the British sport of fox-hunting to Australia ("Fox Scan" website), and other species, such as European starling (*Sturnus vulgaris*) were introduced to control crop pests ("PestSmart" website). Other species were introduced deliberately for their role as important pasture plants; examples include the European grasses cocksfoot (*Dactylis glomerata*), phalaris (*Phalaris aquatica*), fescues (*Festuca* spp.), rye-grasses (*Lolium* spp.) and clovers (*Trifolium* spp.). Though now important economically, they are considered invasive in SE Australian grasslands. Other species, including the European St John's wort (*Hypericum perforatum*), serrated tussock (*Nassella trichotoma*) and Chilean needle-grass (*N. neesiana*) from South America, and African lovegrass (*Eragrostis curvula*), now considered to be amongst the most intractable of invaders in grasslands and woodlands, were accidental introductions (Armstrong et al., 2013; Australian Government, 2016; Eddy et al., 1998).

Agricultural and Infrastructure Development Post-World War II

Historical adverse changes to grassy ecosystems were likely the result of widespread misunderstanding of Australian conditions (soils, climates, plant responses), though there had been early warnings of caution (Costin, 1954; Benson, 1994; Gott et al., 2015). The early transformations were intensified with the advent of modern technologies from the time of World War II: increasing use of motorized farm equipment and state-sponsored schemes, including increased tree-clearing, introduction of exotic pasture

species and subsidized chemical fertilizer use, though irrigation was generally limited in the SE (Costin, 1954; Hancock, 1972; Benson, 1994; Gott et al., 2015). Towards the end of the 20th century and after, establishment of commercial non-native pine plantations and other forms of intensive agriculture (olives, vineyards) impacted on native grassy ecosystems (Australian Government, 2016).

Alongside agricultural impacts on natural ecosystems were increases in urban populations, resulting in increased infrastructure development in the form of widening of highways, pipeline developments and urban intensification, including rapid increases in urban, suburban and rural residential development, all of which impacted on grasslands and grassy woodlands (Australian Government, 2016; Fallding, 2002; Friends of Grasslands, 1998; Gott et al., 2015). Anthropogenic climate change is also recognized as a threat to grassy ecosystems (Australian Government, 2009a, 2016). Estimates of the extent remaining of some grassy ecosystems communities are provided in the following examples:

- of the box-gum grassy woodlands in SE NSW, <4% are estimated to remain (Thomas et al., 2000); and
- of the approximately 890,000 ha of natural grassland that existed in SE Australia pre-European settlement, now only 34,000 ha are estimated to remain, which is a 96.2% decline (Australian Government, 2016; Williams and Morgan, 2015).

Recognition of the decline of the extent and condition of grasslands and grassy woodlands, and an emerging interest in conservation or sustainable use of these systems in SE Australia, coincided with the introduction of the first state-level vegetation protection regulations in the early 1990s (NSW Government, 1997), which was followed by introduction of Australian Government legislation to recognize many grassy communities as endangered (Australian Government, 2006, 2008, 2009a,b,c, 2016; NSW Government, 2005a, 2011a,b). State and Commonwealth funds were made available to initiate research and conservation activities and non-government agencies and state and territory governments increased efforts in conservation actions, including establishment of formal nature reserves, off-reserve conservation measures and community engagement programs. Community groups and non-government agencies assist in many aspects of this conservation effort. Sustainable agricultural use of native grasslands has also emerged.

Human Interactions: Greater Understanding, Targeted Conservation, Research, Community Engagement, and Sustainable Land-Use

Due to the volume of actions undertaken over the last three decades in SE Australia, and the necessity for brevity, the following sections focus on actions undertaken in SE NSW and the ACT, with references to Victoria and Tasmania to illustrate specific points, where necessary.

Research

Classification and mapping

Grassland and woodland communities were subjected to ever-more refined classifications in SE NSW, beginning with Costin (1954), and proceeding with Benson (1994), Thomas et al. (2000), and finally Armstrong et al. (2013), and in the ACT, by Pryor (1938), Ingwersen et al. (1974), Sharp (1997), and Bains et al. (2013). Grasslands were classified throughout SE Australia by Kirkpatrick et al. (1995). Kirkpatrick et al. (1995) defined 28 communities ranging from South Australia through Victoria, NSW and Tasmania. Following the rationale and methodologies as in Thomas et al. (2000), which focussed on forest ecosystems in NSW for the Comprehensive Regional Agreements, a Victorian study (Victorian Government, 1996) led to the comprehensive mapping of all vegetation communities there, including grasslands and grassy woodlands ("Bioregions and EVC benchmarks" website). Tasmania also has a comprehensive vegetation classification (Kitchener and Harris, 2013).

In a project including the ACT and surrounding Southern Tablelands region of NSW, Fallding (2002) presented pre-European and contemporary mapping, and a broad-scale review of ecosystems focussing on grasslands and grassy woodlands. Remote-sensing modeling was undertaken for grassy ecosystems covering SE NSW and the ACT (ERIC, 2001; Rehwinkel, 2005; Walter and Schelling, 2004, 2005). Region-wide vegetation surveys were undertaken for the NSW South-western Slopes bioregion followed by classification, mapping and remote-sensing modeling of grassy ecosystems there (Benson 2008; Priday 2005; Rehwinkel and Priday, 2003; Rehwinkel, 1998). Keith (2004) maps all NSW vegetation formations.

Research on ecology, genetics, management and restoration

Early grassland research focussing purely on conservation management, rather than economic use, was pioneered in Victoria (Stuwe, 1986) and Tasmania (Kirkpatrick, 1993), and later, with a broadening focus throughout the south-east (Craigie and Hocking, 1998; Kirkpatrick et al., 1995).

Research was carried out in the ACT, initially as a result of conflicts between development and conservation of grasslands, to assess potential sites for conservation, undertake flora and fauna surveys, and ultimately, once reserves had been established, on the ecology and genetics of threatened grassland reptiles, invertebrates and plants, followed by fine-scale assessments, mapping of sites and management trials (Friends of Grasslands, 1998; ACT Government, 2005, 2015). The ACT Government commenced long-term monitoring of grassland sites in 1993; this is proposed to continue until 2112 (Sharp and Dunford, 1996).

In SE NSW, similarly reacting to conflicts between the development industry and conservation interests, more limited grassland research was undertaken (Fallding, 2002), with the exception of more extensive site-surveys covering SE NSW region for the Grassy Ecosystems Database (GEDB) (Rehwinkel, 1997; “NSW BioNet” website), which resulted in development of remote-sensing modeling of grasslands and grassy woodlands and a regional grassland community classification (Armstrong et al., 2013). Research in grassy woodlands, principally in the NSW South-western Slopes bioregion focussed on understanding aspects of woodland functioning and management (Lindenmayer et al., 2010; McIntyre et al., 2014; Michael et al., 2018; Prober and Thiele, 1995, 2004; Prober et al., 2002, 2004a,b; Prober, 1996). Woodland research undertaken in SE Queensland is accepted as being applicable to grassy ecosystems in SE Australia (McIntyre et al., 2002).

Research on the genetics of grassy ecosystem flora species (e.g., Prober and Thiele, 1993; Young, et al., 2000; Broadhurst et al., 2012, 2015) focussed on threatened species and others with potential for rehabilitation or restoration of grassy communities. Research into taxonomy of a grassland reptile has yielded answers to questions that are important for conservation of threatened species: the formerly considered single taxon, *Tympanocryptis pinguicollis*, has been split into four taxa: *T. pinguicollis* from Victoria, *T. lineata* from the Canberra region, *T. osbornei* sp. nov. from the Monaro and *T. mccartneyi* sp. nov. from Bathurst (Melville et al., 2019). This work postulated that the Victorian species may be the first Australian mainland reptile species to become extinct, and also highlights the critical conservation status of the other three taxa, with particularly the Bathurst species, known from only two specimens.

Research on the ecology and functioning of grasslands has been undertaken to understand management (Antos and Williams, 2015; Morgan and Williams, 2015; Morgan, 2015; Reid, 2015; Robinson, 2015; Sharp et al., 2015b; Williams and Morgan, 2015). Management trials have been undertaken in grassland and woodland nature reserves by NSW National Parks Service, though these tend not to be well-documented. Research focus on connectivity has developed planning and spatial modeling, in some cases undertaken specifically for grassy ecosystems, and at ever-decreasing scales, from the national scale (e.g., Doerr et al., 2013) to the regional (Barrett and Love, 2012; Love et al., 2014a,b).

Formal Conservation

Early efforts: National parks pre-1990

Few lowland grasslands and woodlands were conserved in formal conservation reserves in SE Australia, although montane and alpine systems, including bogs, fens, montane woodlands and grasslands and the Tasmanian buttongrass moors were protected in parks such as Kosciuszko in NSW (NSW Government, 2014), the Greater Alpine National Parks in Victoria (Victorian Government, 2016), and in the Tasmanian Wilderness World Heritage Area (Tasmanian Government, 2016). In the ACT, Namadgi National Park and some of the reserves surrounding Canberra protected areas of grassland and woodland that are now recognized as endangered communities (ACT Government, 1999, 2010; Armstrong et al., 2013; Bains et al., 2013).

Recent efforts: National parks and nature reserves post-1990

On the mainland, the ACT Government was an early adopter of the need to target the conservation of lowland grassy communities, with the gazettal of the first set of nature reserves specifically for grasslands in the mid-1990s as a result of studies that identified rare fauna, flora and communities that were potentially to be impacted on by development of suburbs in the Gungahlin district, and other reserves were subsequently gazetted elsewhere (ACT Government, 2005, 2015).

Conservation of grassy ecosystems in the ACT culminated in the establishment of Mulligans Flat Sanctuary, a collaboration between ACT Government, two non-government agencies, and researchers at Australian and international institutions, with the aims not only to conserve grassy woodland, but also to undertake intensive research and woodland restoration programs, and reintroduce woodland fauna species that have become regionally extinct within predator-proof fencing (ACT Government, 2016; McIntyre et al., 2014).

Specifically targeted woodland conservation in NSW was initiated by the Regional Forest Agreement (RFA) process (NSW Government, 2001), which comprehensively identified under-represented vegetation communities; several grassy woodland reserves were established resulting from this and subsequent similar processes (NSW Government, 2006). The RFA processes, however, failed to identify grasslands, and in NSW, the first set of reserves specifically gazetted to conserve lowland grasslands in SE NSW were identified through specific project work or through planning processes as a result of conflicts with infrastructure development (Fallding, 2002; NSW Government, 1999, 2007, 2009a; Rehwinkel, 1996a, 2003a). Kuma NR was amongst the first large areas set aside as to offset loss of a smaller area following development pressures.

Formal grassland conservation reserves are also established in Victoria (Victorian Government, 1998), though a promised 15,000 ha offset reserve is still awaiting formal protection (“The Age” website). Lowland grasslands remain poorly reserved in the formal Tasmanian reserve network (Australian Government, 2009a; “Township Lagoon” website).

Despite the above efforts, of the natural grassland in pre-European highlands NSW, only 600 ha, or 0.1% of the former extent are formally conserved (Australian Government, 2016). In the ACT, an estimated 2200 ha of native grassland are protected within the formal reserve network or are otherwise managed for conservation (Australian Government, 2016), which is proportionately greater relative to its pre-settlement extent than that of the other three states.

Conservation Planning

Developing strategies for planning, acquiring and managing grassland and grassy woodland reserves, and also to set priorities for off-reserve conservation and sustainable multi-use of sites, generally falls either to the Australian or state or territory governments, often in partnership with each other, and usually in concert with non-government agencies, community groups and the wider community. Examples of plans and strategies include region-wide plans for biodiversity or general ecosystems (Fallding, 2002; Murray CMA and OEH, 2012), or the plans focussing on specific grassy ecosystems, including ACT woodland and grassland strategies, national recovery plans for natural temperate grassland and box-gum woodland, and species-related recovery or action plans (ACT Government, 2005, 2015; Australian Government, 2006, 2008; “ACT Action Plans” website; “EPBC Recovery Plans” website).

ACT operates an on-line mapping tool that enables infrastructure planning for significant vegetation types and species, including grassy ecosystems and a suite of associated threatened flora and fauna, amongst other assets (“ACT Mapi” website). Fine-scale plans have been developed for each threatened grassy ecosystem species in NSW; these are accompanied by defined projects and funding for projects is available (“Saving Our Species program” website).

At the landscape-scale, Local Lands Services (LLSs) have developed catchment management plans for natural resources in their areas of concern; these have invariably marked grasslands and grassy woodlands for attention because of their threatened status, and as such, LLSs have prioritized actions and directed funding to landholders and community groups for off-reserve conservation (“South East Local Land Services” website). South East LLS was responsible for developing connectivity plans for the region (Love et al., 2014a) and have contributed in the recovery planning processes (Australian Government, 2008). The LLSs occur throughout NSW, and equivalent agencies occur throughout Victoria and Tasmania.

In NSW, the LLSs have other responsibilities relating to conservation of grassy ecosystems, including management responsibility for the system of traveling stock reserves (TSRs), which are parcels of land set aside by legislation in the early 1900s to ensure herds of cattle and sheep could be walked across the landscape for drought relief or to markets (Phillips, 2000). Because these reserves generally had limited grazing and little if any pasture modification since their establishment, they retain excellent examples of endangered grassy ecosystems and many have populations of threatened flora and fauna (Australian Government, 2006, 2008; O’Loughlin et al., 2017; Rehwinkel, 1996a). The LLSs have worked with ecologists from NSW State Government and community organizations since the mid-1990s to refine management planning and mapping of TSRs (“Australian Government TSR” website; “South East Local Land Services” website; “TSR map” website).

Other roles of LLSs that assist landholders in conservation of grassy ecosystems include farm planning, capacity building via workshops, field days and landholder engagement, administering and servicing native vegetation legislation, and providing advice on pest animal and invasive plant control (“South East Local Land Services” website).

Off-Reserve Conservation

Covenants and stewardships

The NSW Government initiated a system that applies in-perpetuity conservation agreements to private land sites, a number of which have areas of significant grasslands or woodlands. While remaining in private ownership, these sites fall under the responsibility of the NSW Biodiversity Conservation Trust (BCT) (“NSW Biodiversity Conservation Trust” website), which monitors the agreements and provides management assistance to the site’s owners. BCT operates a revolving fund that enables purchase and subsequent sale to conservation managers and some significant grassy ecosystem sites have been protected (e.g., “Bunhybee Grasslands” website). A similar revolving fund occurs in Victoria, where over 3000 ha of grassland are conserved (Williams and Morgan, 2015; “Trust for Nature” website).

The Australian Government introduced the Environmental Stewardship Program to provide support for landholders with box-gum woodlands throughout SE Australia. This program employed a competitive tendering process, delivering funded contracts to landholders to assist management of sites (Burns et al., 2016). Some landholders subsequently entered in-perpetuity agreements with the NSW Government and in 2018, the NSW Biodiversity Trust introduced a stewardship fund specifically for grasslands in the NSW Monaro region (“NSW Biodiversity Conservation Trust” website).

Informal reserves on state-owned and private lands

In addition to the NSW National Parks and Wildlife Service, which manages the formal reserve network in NSW (NSW Government, 1999, 2014), other NSW Government agencies play a part in conserving native grassy sites (Friends of Grasslands, 2000). NSW Department of Lands work alongside community groups, developing Crown land (State-owned public land) reserves with the aims of environmental protection and passive recreation (see Fig. 9), or additionally, to maintain common grazing at some town commons (Brooks Hill Reserve Trust, 1997; Rehwinkel and Treweek, 2012; Sharp, 2012). Several public land sites in NSW with grassland or woodland values await conservation action (“Greening Australia” website) with some identified as priority sites for threatened species projects subject to funded works (“Saving Our Species program” website).

Paralleling actions undertaken by state agencies in NSW and ACT are efforts undertaken solely by landholders, community groups and local government and non-government agencies, either to establish informal grassland and woodland reserves on lands of various tenures, or to assist government agencies in a voluntary capacity, including on government-owned and private lands in SE NSW and the ACT (Kosciuszko to Coast, 2013a; Robertson and Parker, 2018; “Friends of Grasslands” website). Bush Heritage



Fig. 9 Awaiting effective conservation action: a floristically diverse grassland on a Crown land reserve at Bibbenluke, NSW. Photo: R. Rehwinkel.

Australia manages a reserve with significant areas of grassland and woodland (*"Scottsdale Reserve" website*), and a private land site is being developed as a reserve with a predator-proof fence (*"Wandiyali Restoration Trust" facebook site*).

Informal private land conservation, where there is no formal protection afforded by an agreement between a federal, state, territory or non-government agency and the landholder, has been initiated by private individuals, with or without funding assistance. Private individuals conserving patches of grassland or grassy woodland largely remain undocumented ([Rehwinkel, 1996b,c, 2001](#)). I have visited sites where landholders have fenced areas containing grassy ecosystem remnants, some of which exceed 30 ha, which is larger than some formal grassland reserves managed by state agencies ([NSW Government, 2009a,b](#)). Some sites were established as early as the 1960s, predating the period when grassland conservation had become a part of the priorities and policies of state and territory governments. Areas were fenced for protection from grazing, and some receive management in the form of control of invasive plants and feral animals.

While private and local government land sites contain valuable remnants of grassy vegetation, their long-term security is not assured, unless owners or managers enter into formal protection agreements, without which, such remnants are vulnerable to loss or degradation, due to factors that would mostly include changing economic pressures. For example, the fences around remnants fall into disrepair, the owners are forced to graze sites more heavily, or there may be increased invasive plant or feral animal pressures that managers cannot afford to control.

Examples exist of grassland reserves that are owned and managed by a local government in Tasmania ([Jerry deGryse Pty Ltd., 1990](#)) or a non-profit, non-government agency in Victoria (*"Graigieburn grasslands" website*).

Conservation on traveling stock reserves and country cemeteries

NSW government agency ecologists, along with a number of non-government and community groups, including World Wide Fund for Nature, managers and associates of conservation management networks and Friends of Grasslands ([Eddy, 2007](#); [Rehwinkel, 1996a, 1998, 2003b](#); *"South East Local Land Services" website*, *"Friends of Grasslands" website*), undertook conservation assessments of traveling stock reserves (TSRs) in the south-east of the state, beginning in 1995 and continuing through to the time of writing. Data from assessments (the 'Grassy Ecosystems Database' (GEDB)), together with those from surveys undertaken by other workers beyond the SE, are collated in NSW and Australian Government databases (*"ALA" website*; *"Australian Government TSR" website*; *"NSW BioNet" website*). Project-workers consulting with TSR management bodies and other government and non-government groups with interests in conservation of TSRs sought to ensure that TSRs with identified high conservation values are managed to retain those values ([Eddy, 2002](#); [Rehwinkel, 1996a](#)). The TSR managers have, as a result, recognized the special values of the TSRs (*"TSR map" website*). At many TSRs, their managers have responded with application of increasingly sympathetic conservation management, often having sourced funding, and in some cases, erecting interpretive signage outlining the sites' values.

Many cemeteries in regional towns have retained high conservation values because of the benign neglect that they have received ([Jones, 1998](#); [Rehwinkel, 1996a](#)). The surrounding rabbit-proof fencing of most cemeteries, lack of stock grazing, the occasional

slashing or mowing applied over parts of the sites to enable access, and often, lack of any treatment to some areas of grassy vegetation beyond the aprons of gravesites have contributed to retention of values. Conservation gains have been made in collaboration with government and non-government groups, with conservation management actions applied to a number of sites in SE NSW and the ACT, including erection of interpretive signs to outline values of sites, application of defined mowing regimes and invasive plant control ("Friends of Grasslands" website; "Hall cemetery" website; "Sydney Morning Herald" website).

Education and Community Engagement

Recovery planning and other formal programs

Many Australian, state, territory and local government departments, non-government agencies and community groups have played significant roles in communicating with each other and the broader community, disseminating information on conservation of endangered grassy ecosystems and their component threatened species in SE Australia; I describe these here under the broad fields of education and community engagement (Fig. 10). NSW and ACT government ecologists have played roles in public consultation, education and community engagement, with sections in the departments now devoted to that aspect of conservation, focussing on providing technical assistance and support for actions on private lands and promoting voluntarism (Rehwinkel, 2003d; "ACT volunteering" website, "Saving Our Species program" website). Community engagement in Victoria is reviewed in Williams (2015) and Reid (2015).

Recovery planning for threatened flora, fauna and endangered ecological communities has guided voluntary activities. Recovery planning depends on collaborative approaches, invariably relying on land-managers with responsibilities for conservation assets on various tenures. If from public agencies, land-managers frequently rely on community groups to assist in conservation efforts. Land-managers or community groups acting on behalf of landholders rely on funding sources that include the Australian, state, territory and local governments, and less commonly, from philanthropic organizations. Community organizations that assist in these activities include Catchment Management Groups, Friends of Grasslands, Greening Australia, and Landcare and ParkCare groups ("ACT Landcare" website; "ACT volunteering" website; "Friends of Grasslands" website; "Ginninderra Catchment Group" website; "Greening Australia" website; "Molonglo Conservation" website). In NSW and the ACT, community-facilitated management and restoration works have been undertaken for a number of threatened flora and fauna species ("ACT Action Plans" website; "EPBC Recovery Plans" website; "Saving Our Species program" website).

In efforts to ensure that information on threatened flora, fauna and endangered ecological communities, the Australian, state and territory governments developed online profiles for each threatened entity, which include amongst them many from grassy ecosystems ("ACT Government threatened species and ecological communities" website; "Australian Government species profile and threats database" website; "NSW threatened species profile search" website; "State wide integrated flora and fauna teams" website; "Tasmanian Government threatened species link" website). In some cases, profiles rely on information sourced through engagement with community members, industry consultants and researchers.

In NSW, threatened species profiles were further developed to provide a link from each threatened entity's profile to a program that has developed species- or threatened ecological community-specific project-planning; this program enables individuals or community groups to select a project for a species or threatened ecological community, and to source specifically targeted funding to complete tasks on one or more of a set of identified sites for each species or community (NSW Government, 2016, 2017; "Saving Our Species program" website).



Fig. 10 Community engagement in NSW. Photo: R. Rehwinkel.

Flora and management guides

Inter-agency government and community collaboration in community engagement to assist grassland managers in NSW and the ACT resulted in the publication of a grassland flora field guide (Eddy et al., 1998), enabling farmers, land-managers and interested members of the public to identify grassland flora species in SE Australia. A number of other field guides have been developed in NSW, ACT, Victoria and Tasmania (Cosgrove, 2014; Falconer, 2004; Kirkpatrick, 1988; Lunt et al., 1998; Marriott and Marriott, 1998; Sharp et al., 2015a; Walker et al., 2001; "Field guide to plants of the Molonglo Valley" website).

Inter-agency and community collaboration was instrumental in the development of material to guide management and to assist conservation efforts of landholders and managers of grassy ecosystem sites (Eddy, 2002; Grassy Box Woodland CMN et al., 2011; Rawlings et al., 2010; Rehwinkel, 2013; Ross, 1999; Sharp et al., 2005; Stol and Prober, 2015), or to guide in the assessment of sites for their values and monitoring of the outcomes of management actions (Sharp and Gould, 2014; Rehwinkel, 2015).

Conservation management networks

The establishment of conservation management networks (CMNs) was a community engagement effort to assist with conservation of grassy ecosystems (Eddy, 2007; Lunt et al., 2010; McLeish et al., 2013; Rehwinkel, 2003b; Rehwinkel, 2003c,d; "Far South Coast CMN" website). A CMN is a network of remnants of native vegetation, their owners or managers and other interested individuals. CMNs usually focus on a single ecosystem type, because the management needs of each are usually relatively uniform. CMNs are managed by coordinators, who assist land managers to learn about the ecosystems, their fauna and flora, and how to manage them according to the goals of either conservation or production. The coordinators' role is to communicate with members of the CMN through newsletters, forums and field days, and to put members in touch with ecologists, botanists and fauna specialists and others with particular management expertise, including other members of the CMN. CMN coordinators also enable sourcing of funding for project work, and perform other supporting roles, including development and maintenance of site databases. CMNs relied on government funding, and unfortunately, when government priorities shifted, funding ceased and three CMNs for grassy ecosystems in NSW dissolved (McLeish et al., 2013). CMNs continue to operate, with one in SE NSW and several in Victoria ("Far South Coast CMN" website; "Victorian CMNs" website), with continuing funding from various sources. The surviving CMNs are now rarely concerned exclusively with grassy ecosystems, for which the original model was devised; rather they have a more tightly restricted regional focus than that of some of the now defunct CMNs.

Connectivity partnerships

Falling under the umbrella of the Great Eastern Ranges Initiative, a continental-scale landscape connectivity partnership, are several SE NSW regional partnerships with grassy ecosystems as amongst their connectivity targets (Pulsford, et al., 2013; "Bush Heritage K2C" website; "Great Eastern Ranges" website; "K2C" website; "Slopes to Summit" website). An unforeseen outcome of the regional partnerships, which include government and non-government groups that previously worked together only minimally, has been greater coordination, less duplication of conservation effort and improved communication to landholders and land managers. The Kosciuszko to Coast partnership undertook a number of grassy ecosystems conservation projects ("K2C" website; Kosciuszko to Coast, 2013a).

Community groups

Locally-based community groups have contributed significantly to grassy ecosystem conservation in SE Australia, and one with an emphasis on education and advocacy is Friends of Grasslands (FOG) ("Friends of Grasslands" website). This group hosts forums, conferences and field trips, and as part of its advocacy roles, submits comments to formal Australian, ACT and NSW government consultation processes. FOG also undertakes monitoring of grassland recovery at a Bush Heritage Australia reserve and undertakes on-ground works at sites in the ACT and NSW ("Friends of Grasslands" website).

A major government-funded program, Landcare, has delivered government funds to communities for works on private and public lands since the 1980s ("ACT Landcare" website; "Landcare Australia" website). While much effort in Landcare's early years was expended on tree-planting, soil erosion works and other on-farm programs, increasingly, efforts have assisted landholders protecting conservation assets, including grassy ecosystem sites, by providing funding for exclusion fencing and other management assistance, including hosting workshops and field days for information dissemination. Land for Wildlife ("Land for Wildlife" website), a voluntary property registration scheme, also receives government funding to assist landholders wishing to conserve grassy ecosystem sites.

Greening Australia provides assistance to landholders and communities ("Greening Australia" website). Receiving funding from donations and Australian, state and territory governments, Greening Australia (GA) draws on the resources of community volunteers (Fig. 11). GA was also initially principally concerned with returning trees to degraded agricultural landscapes but it too is increasingly assisting landholders with sites with grassy ecosystems. Greening Australia's has a role in providing education and training ("Greening Australia" website), and published a bird field guide (Taws, 2007).

In recent decades, GA used its considerable intellectual capital in developing propagation and establishment techniques in the field of grassland and grassy woodland restoration and has applied these widely. Examples include programs throughout the SE and at the Cumberland Plains near Sydney (ACT Government, 1999, 2016; Kosciuszko to Coast, 2013a; NSW Government, 2005b, 2009b; Rehwinkel, 2013; "Greening Australia at Scottsdale" website). In Victoria GA and others have established seed orchards for grassland species and have undertaken extensive experimental trials and successful establishment of restored sites (Gibson-Roy and Delpratt, 2015; Delpratt and Gibson-Roy, 2015).



Fig. 11 Grassy ecosystems restoration often depends on community volunteers. Photo: R. Rehwinkel.

Several other groups are active in grassy ecosystems conservation. Voluntary community groups assist the ACT Government in managing grassy woodland sites ([“Friends of Mt. Majura” website](#); [“Red Hill Regenerators” website](#)). Ginninderra Catchment Group (GCG) is active in grassland restoration trials, using fire to enhance diversity in a volunteer-led, government-funded project ([“Ginninderra Catchment Group” website](#); [“Ginninderra Catchment Group burning trials” website](#)). GCG has produced interpretive materials for engaging with the wider community, including a flora guide ([“Ginninderra Catchment Group flora guide” website](#)) and catchment planning strategies ([Ginninderra Catchment Group; 2000](#)). Molonglo Conservation, similarly, has developed a planning strategy and programs for community engagement, and is undertaking a Saving Our Species project ([“Molonglo Conservation”, website](#)).

Indigenous engagement

Focus in recent years has turned to Indigenous peoples’ interactions with grassy ecosystems. Examples include application of traditional land management techniques and recognition of indigenous values ([Kosciuszko to Coast, 2013a](#); [Kosciuszko to Coast, 2013b](#); [Natural Resources Advisory Council, 2010](#)), promotion of traditional plant use ([ACT Government, 2014](#); [Williams and Sides, 2008](#)), programs undertaken by Greening Australia ([“Greening Australia Indigenous culture” website](#)), and an on-ground project to reintroduce yamfields, using murrnong, (*Microseris lanceolata*), and other species ([“Bundian Way Yamfields” website](#)).

Grassy ecosystems in art and horticulture

Artists have engaged with grassy ecosystems and their managers to bring them to a wider audience; examples are the fine art by James ([“Christine James art” website](#)), line drawings of grassland species by Bedingfield (e.g., [Friends of Grasslands, 1998](#)); woodland photographs in [Lindenmeyer et al. \(2005\)](#) and grassland photography in [Young and McIntyre \(2018\)](#).

Considerable interest in recent years has turned to indigenous grassy ecosystem flora species for use in home gardens and public landscaping ([Fig. 12](#)). This is reflected in development of a grassy ecosystems garden at the Australian National Botanic Gardens, and the Southern Tablelands Ecosystems Park, devoted to locally indigenous plants including grassy ecosystem species, at the National Arboretum, Canberra ([“Australian National Botanic Gardens” website](#); [“National Arboretum Canberra” website](#)). These gardens function as places of engagement with grassy ecosystems flora for residents and tourists that otherwise would not be exposed to grasslands and woodlands in natural settings. Many local nurseries now stock grassy ecosystems plant species.

Towards More Sustainable Land-Use in the Agricultural Landscape

Sustainable land-use

Native grasslands, grassy woodlands and their flora and fauna have become the focus not only for conservation, but in sustainable agriculture ([McIvor, 2005](#); [Barlow and Thorburn, 1999](#); [O’Dwyer and Hamilton, 2003](#); [“Stipa” website](#)). [Massey \(2017\)](#), a grazier from the Monaro grasslands, exemplifies a trend towards ‘regenerative agriculture’ in SE NSW. Research has focussed on sustainable use of native grasslands ([McIntyre et al., 2002](#); [Wong and Dorrough, 2015](#)). Guides have been developed for farmers to enable management of native pastures ([Eddy, 2002](#); [Grassy Box Woodland CMN et al., 2011](#); [Kahn and Heard, 1997](#); [Langford et al., 2004](#); [Mokany et al., 2006](#); [Natural Resources Advisory Council, 2010](#)), and there is material focusing on conservation of flora



Fig. 12 Grassland plants are increasingly popular in the home garden; in the author's garden, Bungendore NSW. Photo: R. Rehwinkel.

and wildlife in the agricultural landscape (Barrett, 2000; Clarke et al., 1999; Dorrough et al., 2008; Lindenmayer et al., 2003; Michael et al., 2018).

Landcare, catchment groups and Local Land Services deliver information resources and advice to the agricultural sector on sustainable agriculture, often focussing on native grasslands as part of the farm landscape ('Ginninderra Catchment Group rural landcare' website; 'Molonglo Conservation sustainable land management' website; 'South East Local Land Services' website). GA's Whole of Paddock Rehabilitation program focuses on private grazing lands (Streatfield et al., 2010).

Conflicts between legislation and the agriculture sector

Clearing of woody vegetation including woodlands is continuing, despite legislation designed to limit this, and although data on clearing rates of grasslands is deficient, it is likely that grassland clearing is also continuing (Evans, 2015; 'Audit Office of NSW Managing native vegetation' website). Conflicts between threatened species and native vegetation policies and the agriculture sector have led to a review of the Australian Government legislation (Craik, 2018; 'The Land' website).

Conclusion

Grasslands and grassy woodlands remain amongst the most threatened ecosystems in SE Australia. Recognition of native grassy ecosystems by government agency ecologists and conservation managers has emerged, as has growing public interest, with community organizations and some landholders being particularly active. However, the conservation status of these systems remains poor, particularly that of grasslands. Australian and state government policies and legislative enforcement lag in some areas, with amongst SE Australian jurisdictions, perhaps only the ACT Government heading towards comprehensive grassland and grassy woodland conservation.

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https://www.swift.net.au/cb_pages/conservation_management_networks_cmns.php—Victorian CMNs.
<https://www.givenow.com.au/wandiyalirestorationtrust>—Wandiyali Restoration Trust.

Sclerophyll Shrublands of Southwestern Australia

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Abstract

The sclerophyll shrublands of southwestern Australia are a blend of graminoids, forbs, subshrubs and shrubs mostly < 2 m tall. They are renowned for their high species richness and endemism and spectacular floral displays in spring. The array of remarkable adaptations among root systems, leaves, flowers and fruits to the nutrient-impovertised soils, severe summer droughts and heat, intermittent crown fires and presence of unique pollinators, herbivores, granivores and dispersers matches the high species diversity. Phenology of the flora is controlled by both the mediterranean climate and the incidence of fires. Conservation of this special biome is threatened by land clearing in particular and the side effects of climate change.

Introduction

Vast areas of sclerophyll shrublands occur in the more coastal areas of southwestern Australia (Fig. 1). They stretch from just south of Shark Bay, 650 km north of Perth, to Cape Arid National Park, 800 km south-east of Perth, and (more patchily) 300 km east to Southern Cross, and cover about 13 million hectares (Lamont and Keith, 2017). These shrublands are a major repository of some of the world's rarest and most charismatic plants and animals in the presence of some of the world's poorest soils with extreme summer droughts and fires. They exhibit spectacular flora displays, have exceptional levels of species richness, turnover and endemism, and are the end product of tens of millions of years of nutritional poverty, episodic drought, recurrent fire and unique microbe-plant-animal interactions. They are of international significance for their contribution to biodiversity of the Earth, are an essential part of Australia's natural and cultural heritage, and are a unique resource for the biological sciences as human interference has remained minimal. In addition, they have utilitarian values in ecotourism, mineral sands, beekeeping, wildflower trade, source of propagules for rehabilitation and ornamental horticulture, and stabilizing greenhouse gases.

The sclerophyll shrublands thrive on nutrient-impovertised sands, sand over rock and among rock outcrops under a typical Mediterranean-type climate. The vegetation comprises exceptionally species-rich low heath to scrub/mallee heath, especially in the so-called northern and southern sandplains (Lamont et al., 1977). This vegetation type has been given the aboriginal name "kwongan," though it has not been widely adopted, with just heathlands or shrublands, or, more popularly, "wildflower country," generally used to describe this biome. The scrub-heath rises to low sclerophyll woodland with a heathy understorey in the Perth Coastal Plain that has a higher winter rainfall than the northern and southern sandplains (Tsakalos et al., 2019). Freshwater lakes are dotted through the biome and it is traversed by many creeks and a few rivers, notably the Moore, Swan and Kalgan, that only flow in winter-spring. Much of the area has been cleared for farming since 1960, despite the poor soils, and, to a lesser extent, for housing, roads, light industry, and mining for heavy minerals. However, this unique flora is still well represented in reserves and national parks and much intact Crown land remains.

Climate and Soils

The climate is a typical Mediterranean-type, with long hot summers and mild wet winters (Fig. 2). Cloudless skies are typical over summer. Snow is unknown (it is rarely recorded in the peaks of the Stirling Ranges in the south of the biome). The weather is milder in the south (moderate mediterranean, with pan evaporation typically exceeding rainfall by four times) and more extreme in the north and east (dry warm mediterranean, with evaporation exceeding rainfall by about eight times) (Table 1). Rainfall is typically 300–600 mm pa but can rise to 1200 mm in the uplands (Darling Scarp, Stirling Range). Mean rainfall has declined by 15% since 1970 and is not taken into account by these figures. Minimum temperatures average a minimum of 6(south)-12(north)°C in the winter months of June-August and a maximum of 25(south)-37(north)°C in the summer months of January-February

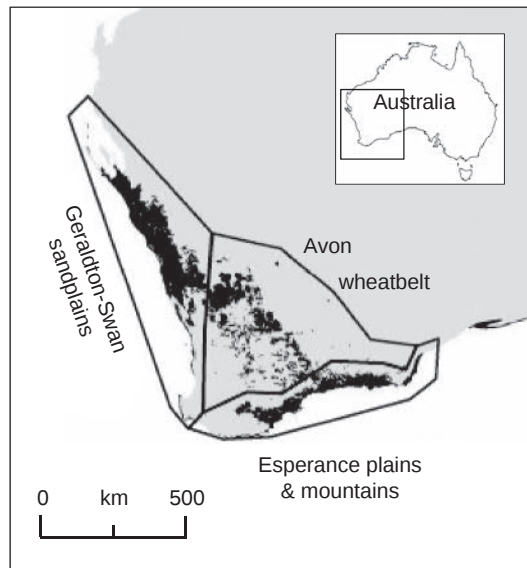


Fig. 1 Distribution of sclerophyll shrublands in SW Australia (in black) framed by the three major biogeographic regions, with the northern and southern sandplains characteristic of the upper and lower regions respectively. The inset shows the area highlighted (square) relative to the rest of Australia. Adapted from Lamont, B. B. and Keith, D. A. (2017). Heathlands and associated shrublands. In: Keith, D. A. (ed.) *Vegetation of Australia*, 3rd edn. Cambridge: Cambridge University Press. pp. 339–368, reprinted with permission.

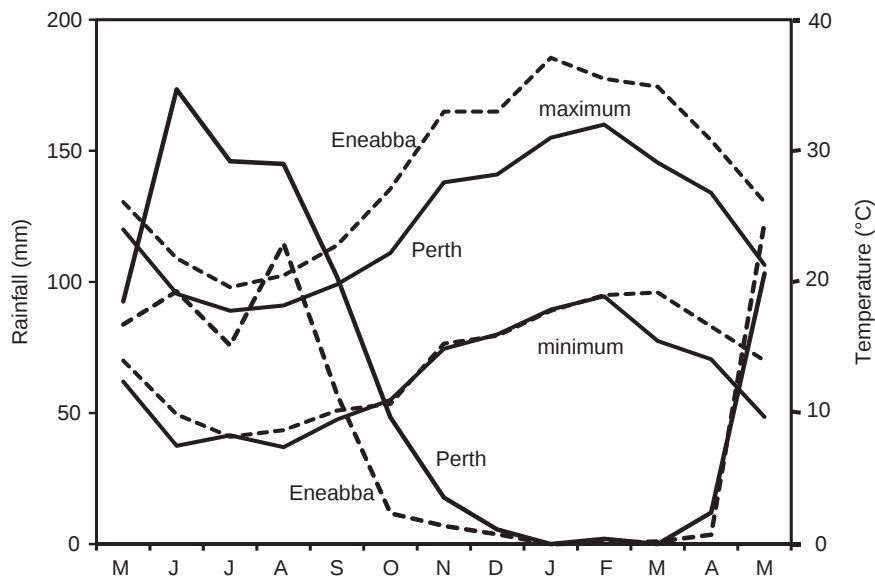


Fig. 2 Monthly rainfall and minimum and maximum temperatures (May 2006 to May 2007) for Perth (29.92°S 115.87°E) (solid line) and Eneabba (29.82°S 115.27°S) (dashed line), 300 km north of Perth, for two sandplain locations in southwestern Australia. Data obtained from the Bureau of Meteorology, Australia (www.bom.gov.au) and plotted by B. B. Lamont.

(Fig. 2). The mean relative humidity at 15.00 h in January is 60(coastal)-30(inland)%. Several days above 40°C are common in summer with relative humidity reaching < 15%. Most areas have < 50 days of mild frost a year, but it may reach 100 days inland (data collated from Lamont and Connell, 1996).

The mediterranean climate in Western Australia probably first arose 1000 km north of its current center as the Australian continent gradually drifted toward the equator after separating from Antarctica 34 million years ago (Lamont and He, 2017). It then migrated south as Australia continued north so that a mediterranean climate was already widespread in the southwest by 20–10 million years ago. However, it is likely that sclerophyll shrublands long preceded the mediterranean climate, as many typical plant groups originated in the Cretaceous period over 50 million years earlier. Thus, the environmental conditions would have been uniformly wet, hot and fire-prone (due to the high oxygen levels prevailing then) but, as now, located in the most nutrient-impovertished sites, leached sands, and laterites and rock outcrops (see under "Fire").

Table 1 Sclerophyll shrublands within the natural regions of southwestern Australia including their climates, annual rainfall, length of growing season (for crops), and dominant vegetation.

Natural region	Climate	Annual rainfall (mm)	Length hot dry season (months)	Dominant vegetation
Northern sandplains	Dry warm mediterranean	300–500	7–8	Scrub-heath interspersed with mallees, dominated by sclerophyllous Myrtaceae, Proteaceae, Fabaceae, Ericaceae, Restionaceae; <i>Acacia-Allocasuarina</i> thickets inland
Swan coastal plain	Warm mediterranean	600–1000	5–6	<i>Banksia</i> low woodland with sclerophyll shrub understorey, <i>Melaleuca</i> swamps in lowlands, eucalypt woodlands on coast and eastern edge
Wheatbelt	Dry warm mediterranean	300–650	7–8	Eucalypt woodlands, <i>Acacia-Allocasuarina</i> thickets, patches of scrub-heath
Mallee	Dry warm mediterranean	300–500	7–8	Eucalypt scrub-heath and woodland, understorey of sclerophyllous shrubs
Southern sandplains	Moderate mediterranean	500–700	5–6	Scrub-heath or mallee-heath dominated by sclerophyllous Myrtaceae, Proteaceae, Fabaceae, Ericaceae, Restionaceae

Collated from Groom, P. G. and Lamont, B. B. (2015a). Evolution and diversity of the flora. In *Plant Life of Southwestern Australia: Adaptations for Survival*. pp. 6–29. Warsaw: De Gruyter Open.

The landforms are usually undulating dunes rising little more than 5 m above the flat swales, sometimes interspersed with prominent uplands of laterite, sand over laterite, tamala limestone, sand over limestone, quartzite, metaschists or gneissic granite. The deep sands are well drained but because they store so much water they support the tallest vegetation with the greatest biomass per unit area (Fig. 3). The rock outcrops too are well drained but the restricted availability of soil, as a source of water and nutrients, means that they can only carry low heath. Shallow sand over a hardpan of clay-silt in lowlands or uplands with sand over laterite, limestone or granite too are resource-stressed and can also only support low heath. Some lowland swales or local depressions, some spring fed, are waterlogged bogs in winter-spring that are water-stressed in summer and again can only support low vegetation, often bearing endemic species, such as *Beaufortia squarrosa* (Myrtaceae).

Soils are typically slightly acid (pH 5.8–6.5) but may exceed a pH of 7.0 on calcareous dunes and outcrops. The sands are renowned for their nutrient impoverishment, especially the low levels of phosphorus ($1\text{--}4\text{ mg kg}^{-1}$), considered among the lowest in the world, but also nitrogen, potassium and the micronutrients, especially zinc, copper, boron, and sometimes molybdenum (Table 2). This has resulted from millions of years of fires and leaching without landscape rejuvenation. In a three-way interaction trial, wild oats failed to thrive unless phosphorus, nitrogen and potassium were added to Eneabba sand (Lamont, 1995) that supports scrub-heath which is equally renowned for its high species diversity (Table 2; Lamont et al., 1977). Note the tendency

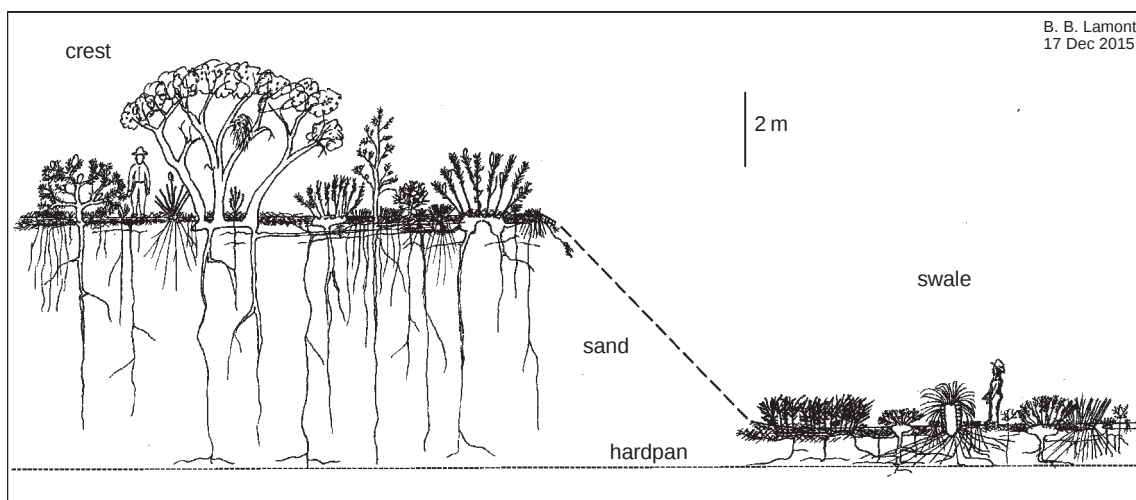


Fig. 3 Stylized vegetation profile, including root systems, of sclerophyll vegetation on deep sandy dunes (crest, left) and shallow sands over clay-silt associated with a deeper laterite deposit (swale, right). This interspersed of scrub-heath and low heath is typical of the dune complex in the northern sandplains. Even though two such sites (on which the above profile is based) were just 300 m apart, only 41% of their species were in common (Table 2). From Lamont, B. B. and Keith, D. A. (2017). Heathlands and associated shrublands. In: Keith, D. A. (ed.) *Vegetation of Australia*. 3rd edn. Cambridge: Cambridge University Press. pp. 339–368, reprinted with permission.

Table 2 Details on the shrubland floras present in five representative plots in the Eneabba Plain, southwestern Australia.

Substrate	Coastal limestone	Laterite upland	Low dune (flat)	Interdune lowland (swale)	High dune (crest)
Shrubland type	Scrub-heath	Low heath	Scrub-heath	Low heath	Scrub/mallee heath
Perennial species in 40 × 40 m ²	72	93	101	109	114
Unique species (%)	47	26	8	15	9
Mean plant density (m ⁻²)	6.7	15.2	8.8	14.3	6.6
Mean species density (m ⁻²)	5	10	8	11	6
Species diversity based on cover (H')	1.41	1.47	1.60	1.66	1.53
Most abundant species (family) based on cover	<i>Hibbertia hypericoides</i> (Dilleniaceae) (14.7%)	<i>Ecdeiocolea monostachya</i> (Restionaceae) (11.3%)	<i>Banksia attenuata</i> (Proteaceae) (15.7%)	<i>Lepidobolus preissianus</i> (Cyperaceae) (5.9%)	<i>Banksia hookeriana</i> (Proteaceae) (15.0%)
Next most abundant species	<i>Acacia spathulifolia</i> (Fabaceae)	<i>Georgeantha hexandra</i> (Restionaceae)	<i>Melaleuca leuropoma</i> (Myrtaceae)	<i>Ecdeiocolea monostachya</i> (Restionaceae)	<i>Banksia attenuata</i> (Proteaceae)
Next most abundant species	<i>Melaleuca leuropoma</i> (Myrtaceae)	<i>Allocasuarina microstachya</i> (Casuarinaceae)	<i>Hakea polyanthema</i> (Proteaceae)	<i>Mesomelaena stygia</i> (Cyperaceae)	<i>Hibbertia</i> aff. <i>hypericoides</i> (Dilleniaceae)
Next most abundant species	<i>Banksia leptophylla</i> (Proteaceae)	<i>Hibbertia hypericoides</i> (Dilleniaceae)	<i>Desmocladius semiplanus</i> (Myrtaceae)	<i>Beaufortia elegans</i> (Myrtaceae)	<i>Adenanthos cygnorum</i> (Proteaceae)
Next most abundant species	<i>Labichea cassioides</i> (Fabaceae) (8.7%)	<i>Melaleuca scabra</i> (Myrtaceae) (3.3%)	<i>Cassytha pubescens</i> (Lauraceae) (8.2%)	<i>Banksia (Dryandra) shuttleworthiana</i> (Proteaceae) (3.3%)	<i>Xylomelum angustifolium</i> (Proteaceae) (6.0%)
Postfire resprouting species (%)	67	88	79	81	69
Interfire annuals (%)	17	1	2	4	2
Species with plant-held seeds (%)	19	24	25	28	26
Species with soil-stored seeds (%)	81	76	75	71	73
Surface soil pH (in water)	6.7	6.1	6.0	6.2	6.2
Colwell's available P (mg kg ⁻¹)	4.0	4.0	2.8	3.7	2.9
Available NO ₃ + NH ₄ (mg kg ⁻¹)	7.4	4.8	2.5	4.5	3.5
Available K (mg kg ⁻¹)	55.6	50.8	30.0	36.9	31.3
Exchangeable Ca (mg kg ⁻¹)	34.1	19.6	8.6	8.1	8.9
Total S (mg kg ⁻¹)	6.5	4.7	3.8	4.4	4.0

Data obtained from Enright, N. J., Mosner, E., Miller, B. P., Johnson, N. & Lamont, B. B. (2007). Soil versus canopy seed storage and plant species coexistence in species-rich shrublands of southwestern Australia. *Ecology* 88, 2292–2304.; Perry, G. L. W., Enright, N. J., Miller, B. P. and Lamont, B. B. (2008). Spatial patterns in species-rich Mediterranean-type shrublands of southwestern Australia. *Journal of Vegetation Science* 19: 705–716; Herath, D. N., Lamont, B. B., Enright, N. J. and Miller, B. P. (2009). Comparison of postmine rehabilitated and natural shrubland communities in southwestern Australia. *Restoration Ecology* 17, 577–585; Herath, D. N. and Lamont, B. B. (2009). Persistence of resprouting species after fire in natural and post-mine restored shrublands in southwestern Australia. *Applied Vegetation Science* 12: 451–458. The three exotic species present overall have been omitted from the numbers. See the original papers for variation about the means given here. Compiled by B.B. Lamont.

for species richness to increase as availability of all nutrients declined in the studies reported in Table 2. The porous sands and moderate rainfall ensure that dryland salinity is unknown here, unlike the silty loam soils to the east of the region.

Vegetation and Flora

The vegetation can be divided into: (a) low heath, species-rich sclerophyllous subshrubs, broad-leaved creepers and leafless graminoids to a height of 0.5 m, (b) heath, similar but shrubs reach a height of 1.5 m, and (c) scrub/mallee heath, heath with some emergent shrubs (scrub) and occasional trees (mallees) reaching 4 m tall but typically < 2 m. Families that are represented elsewhere as



Fig. 4 Selected examples of sclerophyll shrublands in southwestern Australia (sites proceed from north to south to east). (A) Spring flowering of low heath in Kalbarri National Park in the most northerly sandplains with *Melaleuca* aff. *scabra* (Myrtaceae, red) and *Conospermum stoechadis* (Proteaceae, 1 m tall, white) in flower; (B) bird-pollinated *Banksia hookeriana* (Proteaceae), 1.3 m tall, flowering from seed 5 years after fire in Yordanogo Reserve, northern sandplains, showing a positive edge effect beside the road (Lamont et al., 1994); (C) scrub-heath in Trigg Point (hill on right) Reserve, Eneabba with *Banksia attenuata* (Proteaceae, left), and *Lambertia formosa* (Proteaceae, right), 1.6 m tall, with *Xylomelum angustifolium* (Proteaceae) with white fruits held on plant in midground until opened by fire heat; (D) Scrub-heath on calcareous coastal dune (outcropping limestone in foreground) at Jurien Bay, with *Melaleuca huegelii* (Myrtaceae, white), 1.6 m tall, and *Banksia* (*Dryandra*) *sessilis* (Proteaceae, yellow) in foreground, with planted marram grass (*Ammophila arenaria*) in midground; (E) low heath with emergent grasstrees (*Xanthorrhoea acanthostachya*, Asphodelaceae), 1–1.5 m tall, sand-covered sandstone downslope from lateritic breakaway on left (where crouching person can be seen) in the

shrubs and trees (Myrtaceae, Proteaceae, Fabaceae) exist here as numerous subshrubs and ground creepers, some even clonal. Images of representative shrubland sclerophyll types are given in Fig. 4 and show the profound effect of substrate, climate and landscape location on the type of vegetation that can be supported. Even adjacent dunes and the intervening swales can have quite different physiognomies and floristics because of substrate effects. These vegetation types are best represented in the so-called northern and southern sandplain country (Table 1). The shrubland continues beneath the banksia and eucalypt woodlands and forests where soils are more fertile and the rainfall is higher. The sclerophyll shrublands are the heart of the high species diversity of southwestern (the SouthWest) Australia: although they cover only 10% of its area, these shrublands account for over 4250 (50%) of its plant species. The SouthWest in turn covers only 5% of Australia yet accounts for 30% of its species.

The major plant families in Australia reach their peak representation in the sandplain country. These include the woody Myrtaceae, subfamily Leptospermoideae, especially *Melaleuca* that has now been enlarged to 440 species Australia-wide; Proteaceae, especially *Grevillea* and its sister *Hakea* (together comprising 300 species in the SouthWest) and *Banksia* with 80 species. Paraphyletic rules indicate that *Banksia* should include *Dryandra*, endemic to the SouthWest with an additional 100 species, although there has been resistance to such lumping as they are easily distinguished in the field. This is followed by the legumes, especially *Acacia* (subfamily Mimosoideae, 440 species in the SouthWest) and *Gompholobium* (subfamily Faboideae), and Ericaceae (subfamily Epacridoideae), especially the essentially endemic *Leucopogon* with 210 species here. Mallee eucalypts, with gigantic lignotubers, are widespread, especially in the southern sandplains.

The grass-like Restionaceae and Cyperaceae are prominent although the true grasses, Poaceae, are not. Creeping undershrubs, such as *Dampiera* (Goodeniaceae), are also conspicuous. The geophytic terrestrial orchids, especially *Caladenia* with 150 species in the SouthWest, are widespread though many species are highly localized. Small herbs, such as the trigger plants, *Stylidium* (210 species), and carnivorous droseras (> 100 species), are nowhere better represented on a world scale. Annuals, essentially the daisies, Asteraceae, and the tiny Centrolepidaceae contribute little to species diversity or biomass but persist, and are especially evident after fire. Most notable is the annual kangaroo grass, *Austrostipa compressa*, that may form a sward in the first year after fire and be virtually absent by the next year. Herbaceous weeds, especially from South Africa and the Mediterranean Basin, have spread throughout the metropolitan and farming areas, though nature reserves and unallocated lands remain weed free (Table 2).

While species richness is exceptional at the broad scale (gamma diversity), it is also exceptional at the fine scale (alpha diversity). Despite the fact that 95% of the species in a stand of vegetation are evergreen perennials, every square meter of the interdunal low heaths typically contains 14 evergreen plants and these belong to 11 species (up to 37 plants and 21 species per individual m²), so that an area of just 40 × 40 m² contains 23,000 plants and 109 species (Table 2). This is because of the small growth form of most plants (graminoids, herbs, and subshrubs) that allows for high species packing given a large species pool (Perry et al., 2009; Lamont and Keith, 2017). In addition, their low projective cover [few leaves (or none) and these leaves are small (leptophylls), needle-like or vertically oriented] such that their crowns readily overlap and plants can intermingle. Of course, in taller vegetation the number of plants reduces accordingly but not necessarily species richness because some large plants, such as *Eucalyptus tottiana*, can facilitate the presence of others, such as *Stachystemon axillaris* (Groom and Lamont, 2015a,b). Another feature of this flora is the prodigious diversification that has occurred in selected, well-adapted genera. Thus, for the five 40 × 40 m² plots in representative shrubland types in the Eneabba sandplain described in Table 2, *Banksia* (mostly in the form of *Dryandra*) is represented by 14 species, *Hakea* by 11, *Leucopogon* by 10, *Stylidium* by 10, *Lepidosperma* (Cyperaceae) by 10, and *Conostylis* (Haemodoraceae) by 6 species. We located one site in the Fitzgerald River National Park that contained 7 *Hakea* species within an area of just 10 × 10 m² (Lamont and Groom, unpublished). See Table 2 for other well-represented species in this subbiome.

Fire

Sclerophyll shrublands are highly flammable in the dry season, summer-autumn (Fig. 5). They currently burn at 10–20-year intervals but they can carry a fire again within 5 years while stands that escape fire for 40 years or more are almost unknown. Anthropogenic causes have taken over from lightning as the main ignition source. All species have some traits that enable them to survive fire as a result of their lineage's long history of fire-proneness. It has been shown that fire itself (in the form of heat, source of

← Gairdner Range, Mt. Lesueur National Park—the plants here have the smallest growth forms and by the far the highest species density among the eight sites shown here; (F) spring flowering of heath on Cenozoic laterite with outcropping Precambrian gneissic granite (right) at Crystal Brook Reserve, 15 km east of Perth; over 80% of species seen flowering in the image (*Grevillea*, *Hemigenia*, *Acacia*, *Diplopeltis*, *Burchardia*) regenerated 7 years ago from soil-stored seeds; the remainder [*Hakea*, *Allocasuarina*, *Isopogon*, *Banksia* (*Dryandra*)] recovered from plant-stored seeds; the one exception is *Xanthorrhoea preissii*, still showing spike remnants from its fire-stimulated flowering at that time, whose seeds must germinate the first winter after flowering or perish; (G) thick scrub to 4 m tall that suppresses smaller growth forms on neutral sands Milyearup, Scott River with *X. preissii*, *Banksia grandis* and the rare *Lambertia orbifolia* (Proteaceae) in the midground, with scattered trees of *Agonis*, *Melaleuca* and *Eucalyptus* (all Myrtaceae) and *Acacia*; the conical dunes in the background support low heath with some scrub-heath (this area is poorly known botanically); (H) scrub-heath near Cheynes Beach, 160 km north-east of Albany, on sand over gneissic granite with low mallee eucalypt (foreground), *Melaleuca*, *Calothamnus* (Myrtaceae) and *Adenanthos sericeus* (Proteaceae, upper left), 2 m tall; note pruning of *Banksia praemorsa* on the right that is otherwise protected from the salt-laden winds by the pinnacle of granite in the almost absence of soil. The water visible in the backgrounds of C–E is the Indian Ocean, and that in H is the Southern Ocean. Photos taken by B. B. Lamont, except A, donated by J. S. Beard.



Fig. 5 (A) Crown fire in scrub-heath at Yardanogo Reserve, southwestern Australia. Flames are consuming a 2-m tall, fire-killed *Banksia hookeriana*—note the cones, which have retained their highly combustible florets, are igniting and they will later release their seeds stored in the heat-resistant follicles. (B) *Banksia menziesii*, 0.9 m tall and at the same location, recovering from fire 3 years ago via its massive lignotuber and already producing bird-pollinated flower heads. Note the open follicles (arrowed) on cones retained on the dead prefire stems and white indumentum on the stomate-bearing underside of the leaves and their highly reflective upper surfaces. Photos taken by B. B. Lamont.

mutagenic organic chemicals or by concentrating mutagenic chemicals already in the environment) may be a potent mutagenic agent with the potential to induce trait change and species diversification (He and Lamont, 2018). There is increasing evidence that the presence of fire and the origin of fire-related traits among many prominent shrubland families can be traced back to the Mid-Upper Cretaceous Period (100–70 million years ago) (Lamont et al., 2018). This means that pockets of sclerophyll shrublands/woodlands may have existed in the Southwest, and through much of Australia, at that time. While it is likely that a uniform rainfall, perhaps with a summer maximum, prevailed then, seasonality would not have controlled the incidence of fires like today because atmospheric oxygen levels were so high that plant matter was much more combustible. Sclerophylly would have been promoted by poor soils and rocky substrates even then. The slow rates of decay would lead to considerable fuel buildup, and the frequent lightning strikes associated with the high rainfall, especially in the exposed drier uplands, together with the high oxygen, were a combination of selective forces that would have promoted the evolution of many fire-adapted traits.

Of particular interest are the fire-stimulated resprouters that account for 65–90% of species in local floras (Table 2). These resprout from the major stems via numerous sunken epicormic buds among taller plants, from a swollen rootstock (lignotuber, Fig. 5) or root crown via sunken accessory buds among most shrubs and subshrubs, and from creeping underground stems (rhizomes) via axillary buds among graminoids and herbs, or suckering from lateral roots among a few shrubs and herbs (Pausas et al., 2018). An exception are the widespread grass-trees, *Xanthorrhoea* (Asphodelaceae) and *Kingia australis* (Dasypogonaceae): their terminal buds are well insulated from fire heat by the mantle of leaves wrapped around the apex and they just keep growing at an accelerated rate after fire. With their slow generation times, 300–500 years or more, and low seed production, it is surprising that speciation of resprouters has kept pace with fire-killed species (a new generation every time there is a fire and high seed production) in the sandplains. Clonal plants are the longest lived and it has been estimated that the creeping shrub, *Banksia candolleana*, for example, may survive for 1100 years. Although controversial, there is increasing evidence that nonsex-related mutations, which are more likely to occur in older plants, may not only cause low seed set in the first place but may sometimes lead to genetically distinct offspring (Fowler et al., 2018).

On-plant seed storage is called serotiny. Not only is southwestern Australia the world center of diversification for this reproductive trait, but it also peaks in the sclerophyll shrublands. The most prominent species in shrublands are serotinous and it accounts for 20–30% of local floras (Table 2). The seeds are retained in woody fruits (Proteaceae—*Banksia* (follicles held in cones, Fig. 5), *Hakea*, *Xylomelum*, Myrtaceae—*Eucalyptus*, *Melaleuca*, *Leptospermum*, *Beaufortia*, *Calothamnus*) or cones (Cupressaceae—*Callitris*) or winged, single-seeded fruits in cones (Casuarinaceae—*Allocasuarina*, Proteaceae—*Petrophile*, *Isopogon*, Restionaceae—*Lyginia*). Fire heat from summer-autumn fires releases seeds from their supporting structures and they arrive on an ideal surface for germination and recruitment following winter-spring rains. Nutrients build up in the seeds while stored on the plant. While the seeds stored by *Banksia hookeriana* only account for 0.5% of its aboveground biomass, they contain 48% of its phosphorus, 24% of its nitrogen and 4% of its potassium (Lamont and Groom, 1998). This gives the seedlings a head start once the seeds are released into the nutrient-depleted sands following fire.

The remaining species (70–80%) release their seeds once they are mature and they are stored in the soil until the next fire (Table 2). They are either stimulated to germinate by heat (hard seeds of the Fabaceae, such as *Acacia*, *Daviesia*, *Hovea*, *Gompholobium*, *Bossiaea*, *Oxylobium*, *Albizia*, *Templetonia*, and other families, such as Surianaceae—*Stylobasium*, Polygalaceae—*Comesperma*) or smoke (softer seeds of grasses in *Austrostipa* and Restionaceae—*Desmocladius*, *Lepidobolus*, *Stylidium*; Anthericaceae; Haemodoraceae—*Anigozanthos*, Iridaceae; Dilleniaceae; Euphorbiaceae—*Stachystemon*; Ericaceae; Goodeniaceae; Proteaceae—*Grevillea* only; Rutaceae—*Pimelea*; Violaceae—*Hybanthus*). Only 1–2% of species release their seeds at maturity that must germinate the first winter or perish but do include the ecologically important grasstrees—*Xanthorrhoea* and *Kingia*, the unique *Nuytsia floribunda* (Loranthaceae)—the only mistletoe with winged fruits and one of the world's outstanding flowering small trees, and *Macrozamia*—typical of other cycads, its emu-dispersed seeds must germinate in the second year after release or die. These shrublands are also centers of diversification for ants and the world's greatest concentration of ant-dispersed/buried seeds exists here.

Another feature of this flora is fire-stimulated flowering (FSF): about 10% of species flower only in the 1–2 years after fire (obligate) or peak at that time (facultative). FSF is particularly well represented among geophytes, especially terrestrial orchids and droseras, but, unlike fire-prone floras in other climate types and continents, resprouting woody shrubs and subshrubs are also prominent. With 24 species so far recorded with FSF, *Caladenia* (Orchidaceae) is the best represented genus but other speciose orchid genera are *Diuris*, *Cyanicula*, and *Prasophyllum* (Lamont and Downes, 2011). Graminoids include *Lomandra* and *Dasyopogon* (Dasyopogonaceae) and a few rhizomatous grasses, geophytes such as *Drosera* (eight species), *Burchardia* (Colchicaceae), *Thysanotus* (Asparagaceae), *Haemodorum* and *Conostylis* (Haemodoraceae), forbs include clonal *Anigozanthos* and *Macropidia* (Haemodoraceae) and a few *Stylidium*. (Sub)shrubs include the floriferous *Pileanthus* and *Verticordia grandis* (Groom and Lamont, 2015b) (Myrtaceae), *Stirlingia* and *Conospermum* (Proteaceae). The cycads (*Macrozamia*) also show fire-stimulated coning that is almost obligate. The most conspicuous group with FSF are the grasstrees, *Xanthorrhoea* and *Kingia*. The most remarkable of all is the clonal small tree, *Nuytsia floribunda*, emergent in all types of heath, whose masses of orange blooms emerge in late spring from blackened trunks before leaf production has commenced (called protanthly) (Lamont and Downes, 2011).

Phenology

Seeds germinate the first winter after summer-autumn fires and seedlings grow rapidly over spring until summer heat and drought settle in. Small-seeded species produce small seedlings that are drought tolerant and have small or needle leaves that reduce the heat load. Large-seeded (> 20 mg) species produce large seedlings that develop a long taproot at the expense of laterals: by summer, a 15-cm tall plant may possess a root system exceeding a depth of 200 cm that helps it maintain contact with soil water. Nevertheless, almost all young plants spend some months below the wilting point and survival by autumn seldom exceeds 50%, including fitful herbivory by kangaroos and grasshoppers (Lamont and Groom, 1998). Attrition continues over the years so that eventually self-replacement by 15 years (when the next fire is likely) may have taken 50–200 seeds from the original parent plants. Once established, forbs and subshrubs can only flower then grow vegetatively during the wet season, while deep-rooted shrubs and small trees continue to flower then grow well into summer, some showing negligible drought stress at this time. Annuals and geophytes, such as droseras, are the first to appear in winter and to dieback by early summer. *Xanthorrhoea* is unusual as it never stops growing and leaf growth may even accelerate in response to summer rains (Lamont et al., 2004).

Fire-surviving plants break this cycle by starting to recover immediately postfire so that substantial regrowth may have occurred by up to 6 months before the wet season begins. Geophytes and some forbs and shrubs may even be stimulated to flower in response to fire, though most flowering is retarded by a few years as growth and flowering gradually increase up to an asymptote some 15–20 years after the fire. Some subshrubs and forbs may only survive for 5–10 years, but those reaching 2 m or so typically survive for 40–50 years. Unless strongly serotinous, all species release their seeds in response to the drying conditions of summer. Some species benefit from the stronger winds of autumn to lift the seeds or winged fruits from their supporting structures (*Nuytsia*, *Xylomelum*, *Hakea*) while others require the wet-dry cycles associated with autumn rains to open the valves or scales sufficiently to release their contents (*Banksia*, *Petrophile*, *Allocasuarina*).

Roots only grow in the wet season. Root growth in the surface humus layer is early and prolific. The Proteaceae (except *Persea*, although this genus has rootlets with exceptionally long root hairs) and some legumes develop hairy root clusters (proteoid roots, Fig. 6B) that adhere to the decomposing litter and soil particles, a major source of phosphorus and micronutrients in these highly leached sands (Lamont, 2003). They act by secreting organic acids and enzymes that solubilize inorganic phosphates in particular. As a result, an estimated 80% of the root system lies in the uppermost 10 cm of soil (Lamont and Keith, 2017). The remaining 70–90% of species usually possess fungal threads attached to their rootlets (mycorrhizas) that enhance nutrient uptake in a similar way. The most important groups of plants are the Myrtaceae (*Eucalyptus*, *Melaleuca*) and some legumes (*Gastrolobium*) with ectomycorrhizas associated with higher (puffball) fungi. Almost all other plants possess endomycorrhizas, notably *Hibbertia* (Dilleniaceae), *Caladenia* (Orchidaceae), and *Leucopogon* (Ericaceae), all associated with different, but less advanced, fungal partners. Fixation of soil-stored free nitrogen, especially in response to the extra nutrients released by fire that promotes vegetative growth, occurs among all faboid and mimosoid legumes here via perennial root nodules (rhizobacteria), cycads via coralloid roots (cyanobacteria) and waterlogged casuarinas via actinorhizas (*Frankia* fungi). It has long been known that the belowground nutrient uptake mechanisms and their associated microflora in the sclerophyll shrublands are as diverse as the aboveground macroflora (Lamont, 1982).



Fig. 6 With 100 species and 7 extra subspecies, including four species yet to be named and all but 4 endemic to the sclerophyll shrublands/woodlands of southwestern Australia, *Hakea* (Proteaceae) is the archetype genus in this biome. It is also regarded as the world's most sclerophyllous clade (Lamont et al., 2015). (A) *Hakea francisiana* showing its 12-cm long raceme held on a strong stem produced the previous year that enables meliphagid birds to perch while probing for nectar (visible as beads in the image) and inadvertently picking up pollen from the protruding presenters (most are still in the “looped” condition here) or depositing pollen once the stigmatic cleft emerges the next day. Typical of bird-pollinated flowers, the inflorescence is reddish and high in cyanoglycosides that deter herbivory from other birds such as cockatoos and emus (Hanley et al., 2009). Note the upward-pointing, isobilateral leaves that have twisted vertically and serve to limit light reception during the hottest part of the day. (B) Surface lateral root of *Hakea incrassata* bearing a sequence of three proteoid root clusters (all hakeas and all taxa, but *Persoonia*, in the Proteaceae produce these bottlebrush clusters of hairy rootlets). They are ephemeral, absorbing water and poorly mobile nutrients, especially phosphates and molybdenates, during the wet season, and take the place of mycorrhizas common in other plant groups here (Lamont, 2003). Photos taken by B. B. Lamont.

Flowering

Some flowering occurs throughout the year in the sclerophyll shrublands but they are renowned for their spectacular displays of flowers in spring (Figs. 4–7). This coincides with high demand from insect pollinators that are most active in moderately warm weather and the breeding season of bird and mammal pollinators. The range of adaptations to the presence of these three groups of pollinators is perhaps unparalleled in the world, the three syndromes sometimes even present in the same genus (Fig. 7). Visitors to the flora comment on the abundance of blue-mauve flowers, including *Dampiera* such as *D. wellsi* (Goodeniaceae, 60 species in SW Australia), *Lechenaultia floribunda* (Goodeniaceae), *Cyanicula* (Orchidaceae), *Trachymene caerulea* (Araliaceae), *Patersonia occidentalis* (Iridaceae) and *Hakea lehmanniana*. These attract insect pollinators that see well in the ultraviolet range, but many small-flowered species with little nectar production have other colors (white, pink, yellow, orange, red, green). The mammal-pollinated species tend to have inflorescences concealed in the crown, and are dull-colored (honey yellow, brown, Fig. 7) consistent with their rodent and marsupial pollinators that tend to be active only at night, and emit a musky odor and so much nectar that it often drips to the ground acting as a trail to the inflorescences. The bird-pollinated inflorescences are usually brightly colored, especially red, and held above the crown or away from the stem, lack any odor and also produce copious nectar.

The terrestrial orchids have produced the most bizarre pollination syndromes, varying from the nonrewarding blue flowers of several *Thelymitra* species that mimic rewarding blue flowers in other families, to the fungal-gnat-pollinated underground orchid, *Rhizanthella gardneri*, that emits a putrid odor thought to mimic the spore-bearing bodies of mycorrhizal fungi. Of special interest are the wasp-pollinated orchids, *Drakaea*, *Paracaleana*, *Cryptostylis* and *Spiculaea*, that emit pheromones attractive to particular male thynnid or ichneumonid wasps that attempt to copulate with the head of the labellum whose appearance mimics the corresponding female wasp—the labellum is articulated and it is then triggered to swing the wasp back to the androgynoeium where pollen is either received or donated. (All these pollination syndromes are fully described in Groom and Lamont, 2015c).

Other special features of this flora include: (a) protandry—the anthers mature before the stigma that promotes outbreeding and is universal in such major families as Myrtaceae, Proteaceae, Goodeniaceae, Stylidiaceae (SW Australia is the world center of distribution of the “trigger” plants with 210 species, predominantly in the heathlands), Myoporaceae and Thymelaeaceae; (b) flower color change (usually cream to red) as they mature that promotes pollination efficiency; (c) though most species accept a wide range of pollinators because of their high nectar production that attracts the three pollinator groups, there are



Fig. 7 Three species of *Banksia* adapted to the three types of pollinators present in SW Australian shrublands: left: *B. lemanniana* (bloom 12 cm long) with *Cryptocheilus* wasps; middle: *B. prionotes* (bloom 15 cm long, tree present in moister sites in northern sandplains) with white-cheeked honeyeater that uses the flower head as a landing platform; right: *B. tricuspis* (bloom 15 cm long, restricted to the Lesueur National Park) with honey possum [the only mammal (marsupial) with a specially constructed tongue for gathering pollen as well as nectar]—note the hooked styles that hold pollen at their tips and scrape against the head of this tiny marsupial. Photos taken by B. B. Lamont, Jiri Lochman and S. van Leeuwen respectively.

many species with pollinator-specific flowers, such as bee-pollinated verticordias; and (d) the presence of poisonous compounds (cyanide-bearing glycosides—*Hakea*, *Grevillea*, fluoroacetate—*Gastrolobium*) within inflorescences exposed to bird pollinators (and hence bird florivores) versus small inflorescences concealed among spinescent foliage that are insect-pollinated and lack such compounds (Hanley et al., 2009).

Leaves

The distinctive, leathery-stiff texture of leaves (sclerophylly) is characteristic of this biome (70% of species). Indeed, SW Australia has the most sclerophyllous flora in the world, attributed to both the nutrient scarcity and severe summer droughts, so that the level of sclerophylly is highest in low heath and in the northern sandplains (Lamont et al., 2002). *Hakea*, with 100 species here, is the world's most sclerophyllous genus. Notable species include *H. clavata*, occurring on granite outcrops near Esperance, whose leaves are up to 5 mm thick (no hard-leaved species anywhere is thicker)—thickness is a drought adaptation. *H. oldfieldii* has the highest dry leaf density at 1.0 mg mm^{-3} (no species anywhere has a harder leaf due to its high concentration of lignified tissues that stop leaf collapse when below turgor)—density is a low-nutrient adaptation. For comparison, hardwood timbers have a dry density of about 0.8 mg mm^{-3} . Winter deciduous plants, characterized by their low leaf hardness, are unknown, though most plants drop some or all of their old leaves at the start of summer (aestivation) that reduces the transpirational surface. Even so, the low nutrient availability means that leaf turnover risks the loss of nutrients already absorbed so that again this flora is renowned for its leaf longevity (40% greater than 2 years), with a record of 13 years in the prostrate *Banksia gardneri* whose highly divided vertical leaves act like stems. Nevertheless, many annuals, geophytes, forbs and some shrubs have relatively mesomorphic leaves (30% of species) and the oldest are dropped annually (20%). Leaf succulence is rare (3%), and includes the creeping *Carpobrotus* (Aizoaceae) on calcareous soils. (A full discussion on leaf properties is given in Groom and Lamont, 2015d).

The leaves are also known for their small size: about 50% of the species in a typical heath site have leaves under an area of $5 \times 5 \text{ mm}^2$ (leptophylly) with almost no species exceeding $75 \times 75 \text{ mm}^2$ (mesophylly). Odd leaf shapes include scale-like (10%), needle-like (25%), strap-like (35%), and highly dissected (10%). Loss of the leaf blade retaining just the petiole (phyllode) is the norm among legumes, with the phyllodes continuing down the flattened green stem (phylloclade) in a few species that is possibly unique to this flora. Absence of leaves is notable: species of *Daviesia* and *Jacksonia* (Fabaceae) and *Exocarpos* (Santalaceae), all Casuarinaceae (20 shrubland species) and all Restionaceae, the most prominent graminoid in the flora. It is interesting to note that most taxa without normal leaf lamina development contain higher than average levels of nutrients and this might reduce their attractiveness to herbivores as well as reduce their heat load and need for nutrient cycling. Another remarkable feature is the preponderance of heterophylly (different leaf types within the same plant) that is essentially a heteroblastic process, with juvenile leaves tending to be more mesomorphic and the adult leaves (associated with flowering) more sclerophyllous. This process is usually repeated among branches resprouting after fire. Heterophylly is best known among the legumes, especially *Acacia*, and eucalypts and almost universal in the Proteaceae. Heteroblasty may also occur on an annual basis, of which the most outstanding example

is *Hakea trifurcata* (Proteaceae) that does not commence production of its broad, highly incurved leaves until it is able to flower. Its alternating seasonal broad-needle leaf sequence has been used to support other evidence that a mediterranean climate has existed in southwestern Australia since the Miocene, though greatly restricted during the ice ages of the Pleistocene (Lamont and He, 2017). This species is one of at least 12 hakeas whose leaves appear to mimic or shield the fruits from granivores. They appear to be ineffective against black cockatoos (unlike the exceptionally large woody fruits produced by some other species in this genus) and may instead to be aimed at insect granivores (beetles, moths) that are usually night active and have poor eyesight so that they are less likely to oviposit on the more vulnerable fruits that remain green (Lamont et al., 2016).

Conservation and Management

The major threats to the distribution and biodiversity of the sclerophyll shrublands in SW Australia are land clearing with habitat fragmentation, weed invasion, climate change, suboptimal fire regimes, plant pathogens, wildflower picking, and eutrophication. Land clearing is the most significant but could easily be controlled through appropriate legislation. Consider the charismatic *Banksia hookeriana*, restricted to a 15 × 120 km area in the northern sandplains and whose biology/ecology are possibly the best understood for any plant species in Australia. Records show that this species range has contracted by 40% in area, and 26% latitudinally, through the loss of outlier and marginal populations since 1960. In addition, 22% of shrublands within the core distribution of *B. hookeriana* have been further lost over this period through clearing for farming, infrastructure, and mining. The area of shrublands declined at a rate of 0.3% per year in 1990–2001. At this rate, and a mean fire frequency of 14 years (equivalent to its mean generation time), *B. hookeriana* habitat is being lost at a rate of 4% per generation (Lamont et al., 2007). *B. hookeriana* may be absent from a further 10% of suitable habitat because recurrent fires are at intervals < 8 years that is too short for population survival (insufficient time for adequate seed production). Eighteen percent of the sandplain area lies within conservation/nature reserves, but a large, heavy mineral sand mine within one reserve reduces the effective conservation area to 16%. These reserves include 25% of the known populations and, as the two largest populations are among these, they represent 75% of individuals. Most of the remaining populations occur on vacant Crown land, and some in small fragments of vegetation in roadside reserves that tend to become heavily infested with exotic grasses over time. Population fragmentation also results in decreased seed set (the Allee effect).

The declining rainfall and possibly increasing fire frequency (at least in the short term) in this biome associated with climate change will, and is, exacerbating these trends, especially among serotinous, fire-killed species such as *B. hookeriana* (Enright et al., 2014). The heathlands are particularly vulnerable to the root pathogen, *Phytophthora cinnamomi*, especially the vegetation-defining Proteaceae, Fabaceae, Ericaceae, and *Xanthorrhoea*. This disease has devastated some stands in the southern sandplains and uplands of the Stirling Range. Concerted rehabilitation efforts following mining for heavy minerals has had considerable success at returning species richness but less so at restoring species composition and physiognomy. The restored vegetation is more vulnerable to fire as the resprouting species are less fire-tolerant. This is because they grow much faster and recruitment is lower as the silty surface soil inhibits root development (Herath and Lamont, 2009; Herath et al., 2009). Commercial flower and seed harvesting can have a severe effect on seed available for recruitment postfire as well as depleting the habitat of scarce nutrients. It has been noted that the greater growth and fecundity of plants along road verges, because of greater access to nutrients and water, may have conservation value. However these also act as pathways for the advancement of weeds, especially following fire and stray fertilizer from farms. Restricting harvesting to older stands, longer prescribed burning intervals and even hand-sowing have been recommended as improving the viability of targeted species. Research has not supported the expected adverse effects of spring rather than autumn burning on plant recruitment though possible effects on breeding animals has yet to be investigated. Encroachment by saline groundwater beneath coastal shrublands on highly porous sands as sea level rises and groundwater extraction escalates is a future threat.

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Mallee and Maalok Ecosystems of Southern Australia

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Abstract

Mallee related maalok ecosystems are unique to southern Australia, having no direct analogue on other land masses. They straddle the interface between the Mediterranean-type and arid climate zones. The key environmental factors that shape mallee ecosystem functions and traits are severe summer water deficits, nutritional poverty, and fire regimes. These processes interact with herbivores, which are critical to regeneration of woody perennials in the postfire period. Approximately 30% of mallee ecosystems were converted to cropping and exotic pasture in the past 200 years. Future sustainability depends on a more representative protected area network, regulation of land use change, conservative livestock management, avoidance of short fire-return intervals, minimizing risks of recruitment failure, and approaches that build resilience to climate change.

Introduction

A distinctive suite of ecosystems stretches across almost the entire continental breadth of southern Australia, straddling the subhumid “Mediterranean-type” and semi-arid climate zones. This chapter focusses on mallee ecosystems in that bioclimatic region, which is dominated almost exclusively by eucalypts in sections *Bisectaria* and *Dumaria* largely on unconsolidated sandy substrates, excluding those of more humid regions on lithic substrates, and dominated by mallee eucalypts from other sections of the genus. The term “mallee” derives from indigenous languages in southeastern Australia, and refers to the distinctive growth form of dominant trees, characterized by multiple stems arising from a woody subterranean regenerative organ or lignotuber (Yates et al., 2017). Maalok differs from mallee vegetation in this respect because the dominant eucalypts are single-stemmed, nonlignotuberos and killed by fire, yet many of them have putative sister species with mallee growth forms (Gosper et al., 2019), and all belong to section *Bisectaria* of the genus *Eucalyptus*, as do most mallees. Mallee vegetation varies in height usually from 3 to 9 m tall, but exceptional sites support trees > 15 m tall (Parsons, 1994), and maalok reaches the upper part of this height range. Mallee tree densities vary from 1 to > 200 per hectare (Keith unpublished data), but densities in maalok may be much greater. Understorey vegetation varies physiognomically, structurally and compositionally in relation to regional climatic and edaphic gradients, fire regimes and biogeographic legacies.

Mallee ecosystems occupy a significant segment of a major regional climatic gradient extending from the southern coast of Australia, where mean annual rainfall may exceed 1000 mm with a prominent winter maximum, to the inland, where rainfall declines to 150 mm per annum, with aseasonal occurrence and very high interannual variability. Mallee ecosystems occur predominantly in a zone bounded by the 200 and 500 mm annual rainfall isohyets (Fig. 1), and are largely associated with unconsolidated aeolian sands. In subhumid temperate climates to the south, they transition to sclerophyll shrublands and eucalypt woodlands characterized by single-stemmed trees. With increasing aridity, they transition to desert shrublands dominated by chenopods or acacias, and hummock grasses. Mallee ecosystems are home to an endemic fauna including the mallee fowl (*Leipoa ocellata*) and mallee dragon (*Ctenophorus fordi*), as well as several fossorial mammals that went extinct, regionally or globally, in the modern era.

On a global scale, mallee ecosystems are biogeographically, climatically and functionally unique. Mediterranean-type climates in Europe, South Africa, Chile and California host sclerophyll shrubland and woodland systems that share a number of ecological

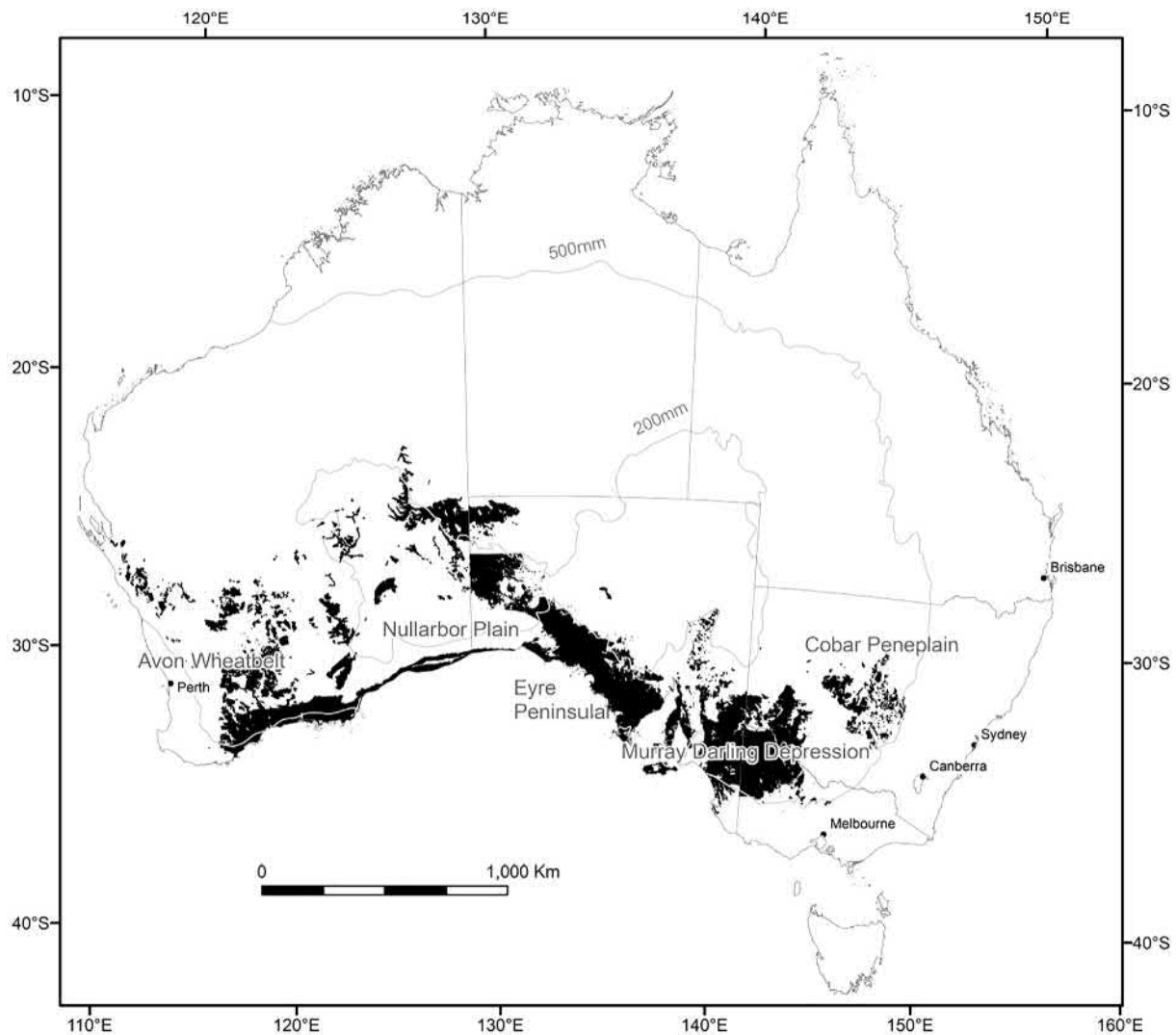


Fig. 1 Mapped distribution of mallee ecosystems in southern Australia (data from National Vegetation Information System, major vegetation subgroups version 5.1, <https://www.environment.gov.au/land/native-vegetation/national-vegetation-information-system/data-products#mvsg51>, downloaded 15/08/2019) in relation to 200 mm and 500 mm isohyets (data from Bureau of Meteorology, http://www.bom.gov.au/jsp/ncc/climate_averages/rainfall/index.jsp, downloaded 14/08/2019).

convergences with those in southern Australia (Rundel et al., 2016), but none of those systems are dominated by trees with subterranean regenerative organs. Similarly, chenopod shrublands are widespread in arid and semi-arid climates of the temperate Americas, Eurasia and southern Africa, as well as Australia. Mallee woodlands and shrublands, by contrast, seem to have no direct analogues in other parts of the world.

Mallee ecosystems appear to have mid Miocene origins (c. 15 million years ago) as the Australian continent underwent aridification. Diversification in *Bisectaria* and *Dumaria* clades accelerated from about 10 million years ago (Thornhill et al., 2019), apparently radiating from west to east as new aeolian substrates developed and became vegetated in the Murray-Darling depression (Yates et al., 2017). Other key components of mallee ecosystems, such as the hummock grass genus *Triodia*, have progenitors that arrived by long-distance dispersal from Asia in the mid Miocene, and spread from the south across the arid interior and into the tropics (Toon et al., 2015). Mallee ecosystems are core habitat for ancestral taxa of the genus, including *Triodia scariosa* and *Triodia irritans*.

This article examines current knowledge on the distribution and varied expressions of mallee ecosystems, the evolutionary biogeography of key taxa, gradients in major environmental drivers that shape their ecological features, and the traits of plants and animals that occupy these unique systems.

Distribution and Types of Mallee Ecosystems

Mallee ecosystems are distributed in a belt extending almost 3000 km, 400–600 km wide, from the Avon wheatbelt in southwestern Australia, through the south coastal hinterland, southern deserts and the Eyre and Yorke peninsulas to the Murray-Darling

depression and the eastern edge of the Cobar peneplain in central New South Wales (Fig. 1). The Nullarbor Plain, dominated by chenopod shrublands on heavy calcareous clay soils, imposes a major gap in the distribution, but mallee ecosystems occur semi-continuously both to its north and south.

Yates et al. (2017), building on a regional floristic analysis for mallee in the Murray-Darling region (Haslem et al., 2010), proposed five major types of mallee ecosystem based on contrasting understorey features and environmental associations (Fig. 2; Table 1).

Heathy Mallee

Heathy mallee marks the transition to sclerophyll shrublands in the more humid southern part of the distribution (Fig. 2), where annual rainfall exceeds 300 mm and has a winter maximum (Table 1). Soils are coarse-textured white sands and more siliceous than those of other mallee types or, more rarely, deeply weathered laterites of the southwest. The relative importance of reliable winter rains and siliceous sands in delimiting heathy mallee are difficult to evaluate because the latter are essentially replaced by calcareous sands as rainfall diminishes towards the continental interior. Heathy mallee typically occurs throughout the catenary sequence of these dune-swale landscapes. Lignotuberous mallee eucalypts dominate the vegetation, but there may be an appreciable component of nonlignotuberous trees, particularly *Callitris* and *Banksia*. The understorey flora includes conspicuous heathland plant families, such as Proteaceae, Ericaceae, Myrtaceae, Dilleniaceae, Rutaceae, and Rhamnaceae (Fig. 3A). Grasses and forbs are less conspicuous than sclerophyll shrubs and wiry graminoids. Recruitment of trees and shrubs is closely cued to fire. Western occurrences of heathy mallee in the Avon wheatbelt and south coast of Western Australia differ substantially in the species composition of both overstorey trees and understorey shrubs from eastern occurrences on the central-southern Eyre Peninsula and in the Ngarkat—Big Desert area to the south of the Murray River. Post-Miocene isolation is a likely cause of these differences, as the arid climate and heavy-textured soils of the Nullarbor Plain impose a dispersal barrier to many sclerophyll taxa.

Shrubby Mallee

Shrubby mallee occurs on calcareous sandplains receiving ~200–300 mm mean annual rainfall (up to 350 mm in some areas) through the entire east-west range of the mallee (Yates et al., 2017). It is commonly associated with extensive plains or swales, but is replaced by *Triodia* mallee on dunes and other areas of light-textured soils (Table 1). Lignotuberous mallee eucalypts are often the sole dominants and may exceed 10 m in height. Nonlignotuberous trees are typically absent but, amongst the eucalypts, other less frequent resprouting trees may include *Alectryon* and *Myoporum*. The most conspicuous shrubs are nonsclerophyll genera such as *Eremophila*, *Senna*, *Acacia*, *Olearia*, and *Maireana* (Fig. 3B), although a few sclerophyll shrubs may also be present (mainly *Acacia*, *Grevillea* or *Hakea*). Most of these species are widespread across Australia's arid zone. Shrubs tend to be long-lived (multiple decades) and most have subterranean regenerative organs, such as woody rhizomes or lignotubers. The non-woody component of the understorey is usually sparse, except after substantial rains, which tend to stimulate emergence and dominance of ephemeral forbs (mostly Asteraceae with Portulacaceae, Crassulaceae) and/or ephemeral grasses (mostly *Austrostipa*), depending on the contributions of autumn-winter and spring-summer rains (Robertson, 1988; Dwyer et al., 2015). Soils are generally calcareous red sandy loams, with greater silt and clay content in the subsoil, becoming very hard when dry. The soil surface is often consolidated by biological crusts comprising lichens, algae and bacteria, especially where surface water is slow to percolate or run-off after rains. These crusts have important roles in soil stability, moisture retention and nutrient cycling (Eldridge and Koen, 1998).

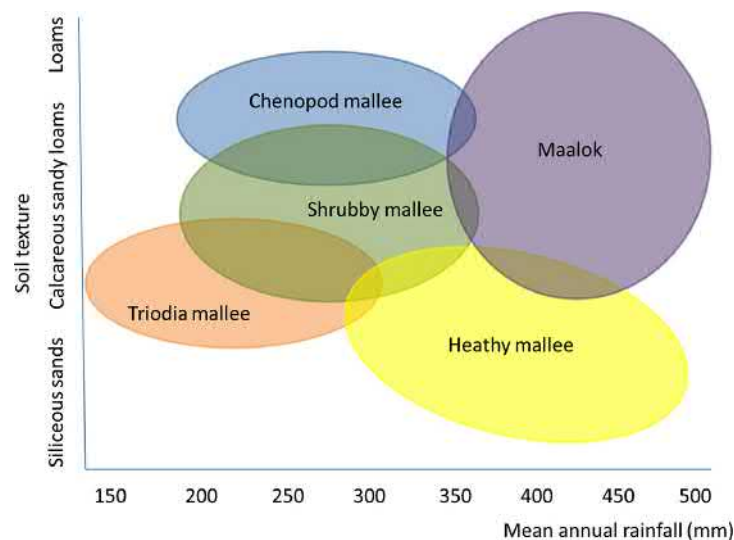


Fig. 2 Hypothesized relationships of different mallee ecosystems to regional climatic gradients and landscape edaphic gradients in southern Australia.

Table 1 Characteristic of mallee and maalok ecosystem types.

	<i>Heathy mallee</i>	<i>Shrubby mallee</i>	<i>Chenopod mallee</i>	<i>Triodia mallee</i>	<i>Maalok</i>
Mean annual rainfall	300–500 mm	200–350 mm	200–350 mm	150–350 mm	300–600 mm
Rainfall seasonality	Winter maximum	Aseasonal	Winter maximum—aseasonal	Aseasonal	Winter maximum
Substrate	Siliceous white sands	Red sandy loams sands	Red sandy loams sands	Deep red sands	Loams
Fire regime	Decadal to multidecadal scale summer canopy fires	Multidecadal to century scale summer canopy fires	Multidecadal to century scale summer canopy fires	Multidecadal to century scale summer canopy fires	Multidecadal to century scale summer canopy fires
Maximum tree height	< 10 m	> 10 m	> 10 m	< 10 m	> 10 m
Mallee trees	Dominant	Dominant	Dominant	Dominant	Absent
Fire-killed trees	Present	Absent	Absent	Present	Dominant
Sclerophyll shrubs	Dominant	Present	Absent	Uncommon	Present
Nonsclerophyll sprouter shrubs	Uncommon	Dominant	Present	Uncommon	Absent
Nonsclerophyll fire-killed shrubs	Uncommon	Uncommon	Common	Common	Absent
Chenopod shrubs	Uncommon	Present	Dominant	Uncommon	Absent
Perennial forbs	Present	Present	Present	Absent	Very sparse
Annual forbs	Uncommon	Common	Common	Present	Very sparse
Hummock grasses	Uncommon	Absent	Absent	Common	Absent
Tussock grasses	Uncommon	Present	Common	Present	Very sparse
Biological soil crusts	Uncommon	Common	Common	Uncommon	Uncommon

Chenopod Mallee

Chenopod mallee dominates plains with subdued topography and red calcareous sandy loams, finer in texture than those supporting other mallee types (Table 1). It marks an edaphic transition to clay-dominated soils that support *Casuarina* (Belah) woodlands or treeless chenopod shrublands. Chenopod mallee occurs more extensively in the eastern and central parts of the mallee distribution than in the southwest (Fig. 1), mostly where rainfall averages 200–300 mm per annum (rarely up to 350 mm). Lignotuberous mallee eucalypts are the sole dominants or may be interspersed with rhizomatous *Casuarina* and *Alectryon*. The shrub stratum is characterized by subsucculent “chenopods” (family Amaranthaceae), *Maireana*, *Atriplex*, *Rhagodia*, *Sclerolaena*, and *Chenopodium* (Fig. 3C). Tussock grasses may be abundant, depending on rainfall and herbivore activity, sometimes more conspicuous than chenopod shrubs, while communities of ephemeral forbs vary interannually depending on autumn–winter rains. As for shrubby mallee, soil crusts of lichens, mosses, algae and bacteria play a prominent role in ecosystem processes. Perennial plant recruitment, at least in the understorey, appears to be regulated primarily by rainfall variability and herbivore activity. While grass-dominated areas of chenopod mallee are fire-prone, chenopod-dominated fuels are likely to be less flammable than those of other mallee systems.

Triodia Mallee

Triodia mallee extends from the Cobar penplain to the Avon wheatbelt across extensive red calcareous sand dune landscapes. It marks the dry extremity of the mallee climatic gradient (Fig. 2), where mean annual rainfall diminishes to 150 mm towards the interior, and rainfall patterns are aseasonal and highly variable between years (Table 1). Surface-soils are unconsolidated sands, with loamy subsoils occurring one to several metres below the surface. Mallee eucalypts dominate the tree canopy, occasionally with nonlignotuberous species (*Callitris*, *Codonocarpus*). Shrubs are spatially and temporally variable in density, with nonsclerophyll foliage and recruitment cued to fire. Common genera include *Beyeria*, *Olearia*, *Acacia*, *Eremophila*, *Halgania*, and *Duboisia*, many of which are short-lived (< 20 years), deep-rooted with persistent soil seedbanks. Long-lived hummock grasses (*Triodia*) are distinctive features of the ground layer (Fig. 3D), but there are few other perennial nonwoody plants in the system. Ephemeral grasses (*Austrostipa*) and forbs (Asteraceae, Portulacaceae, Crassulaceae) may be common after rains and may be critical to the spread of fires (Noble and Vines, 1993), which occur at multidecadal intervals, and become less frequent with aridity.

Maalok

Maalok is confined to southwestern Australia extending from the semi-arid zone to wetter climates than mallee vegetation (300–600 mm per annum), although they may occupy depressions between sand dunes or very weathered lateritic rocky sites, juxtaposed with heathy mallee on coarser-textured white sands (Beard, 2015; Yates et al., 2017). As noted earlier, the dominant eucalypts are single-stemmed, nonlignotuberous and killed by fire (Table 1). Maalok eucalypts may grow in high densities (Fig. 3E), and hence



Fig. 3 (A) Healthy mallee in with *Eucalyptus dumosa*, sclerophyll shrubs of *Leptospermum*, *Melaleuca lanceolata*, *Hibbertia* and scattered *Triodia irritans* and *Amphipogon caricinus* in the ground layer. Note bleached white sand heaped into a nesting mound by mallee fowl. Hambidge Wilderness Protection Area (Eyre Peninsula). (B) Shrubby mallee in a dune swale with *Eucalyptus socialis* (center) and *Eucalyptus gracilis* (background, left), a prominent mostly nonsclerophyll shrub layer of *Senna petiolaris*, *Eremophila glabra*, *Dodonaea angustifolia*, *Acacia burkittii*, and *Acacia colletioides* and a soil crust of alga and mosses interspersed with depositional sands. Tarawi Nature Reserve, Murray-Darling depression. (C) Chenopod mallee on a flat sand plain with *Eucalyptus oleosa* (commonly a dominant tree species of chenopod mallee), *Maireana sedifolia* (pearl bluebush, most abundant shrub), *Olearia muelleri* (a daisy bush with bright green foliage) and an algal soil crust. Tarawi Nature Reserve, Murray-Darling depression. (D) Triodia mallee on a red dune crest with *Eucalyptus socialis* (foreground) with *Eucalyptus costata* (background, a characteristic species of Triodia mallee) with scattered shrubs of *Beyeria opaca*, *Acacia ligulata*, *A. rigens*, *Eremophila glabra* and *Olearia subspicata* and the hummock grass, *Triodia scariosa* (right) with loose sand and leaf litter on the surface. Tarawi Nature Reserve, Murray-Darling depression. (E) Maalok with a high density of single-stemmed nonlignotuberous *Eucalyptus platypus* and a sparse understorey with high cover of leaf litter. Sclerophyll shrubs are likely represented in the soil seed bank. Ravensthorpe Range, Southern Avon wheatbelt, Western Australia. (F) Postfire regeneration of Triodia mallee showing fire-killed prefire mallee stems and new postfire stems emerging from lignotubers in *Eucalyptus dumosa* (left). Other regenerating plants include shrub seedlings and resprouting Triodia hummocks. Dangdali Conservation Park, Reserve, Murray-Darling depression, 2 years after a fire in 2010. (A): Source: David Keith; (B) Source: David Keith; (C) Source: David Keith; (D) Source: David Keith; (E) Source: Cristina Ramalla; (F) Source: David Keith.

their sclerophyll shrub understories may be quite sparse. Common shrub families include Myrtaceae, Fabaceae, Rutaceae, and Proteaceae. Grasses and forbs are not major components of maalok vegetation. The characteristically sparse ground fuels and lack of ladder fuels limit the spread of fires through mature stands, which may experience fire-return intervals exceeding 100 years. Fires nonetheless play profound roles in tree regeneration, vegetation structure and composition of maalok vegetation (Gosper et al., 2018).

Key Drivers of Mallee Distribution and Ecology

Summer water deficit, nutritional poverty and fire regimes are key drivers of mallee ecosystem dynamics and have a key role in shaping ecosystem traits and functions. Herbivores have important roles in trophic functions and plant regeneration in some mallee systems (chenopod mallee, *Triodia mallee*), less so in others (heathy mallee, maalok).

Summer Water Deficit

Mallee ecosystems experience a severe summer water deficit due to low annual rainfall, a winter-maximum/summer-minimum seasonal pattern of occurrence, and extreme summer temperatures which promote high rates of evapotranspiration (Keith and Tozer, 2017). Summer water deficits are exacerbated by low soil moisture retention associated with sandy texture.

Summer water deficit varies markedly between years due to interannual variation in weather driven by El Niño—Southern Oscillation and Indian Ocean Dipole climatic cycles (Meyers et al., 2007), and as well as summer monsoonal weather systems that penetrate occasionally from the tropics to the southern inland in some years. The effects of water deficit diminish with depth below the surface, and subsoils may retain surprisingly higher levels of moisture and undergo markedly less variation than those near the surface (Fig. 4). These effects vary with topography and soil texture (Fig. 4). This has implications for water acquisition in shallow-rooted plants, including seedlings of deep-rooted species.

Summer water deficits vary across regional climatic gradients, with rainfall declining towards the inland (Figs. 1 and 2), and through local catenary and edaphic gradients. Water run-on and infiltration in local depressions can greatly influence moisture accumulation, while soil texture influences water retention. Water deficits are expected to be most severe in *Triodia mallee* due to its position at the arid end of the mallee climatic gradient and its light-textured soils (Fig. 4). Heathy mallee occurs in wetter climates, but their lighter-textured soils may experience greater moisture loss due to both percolation and capillary rise. The higher

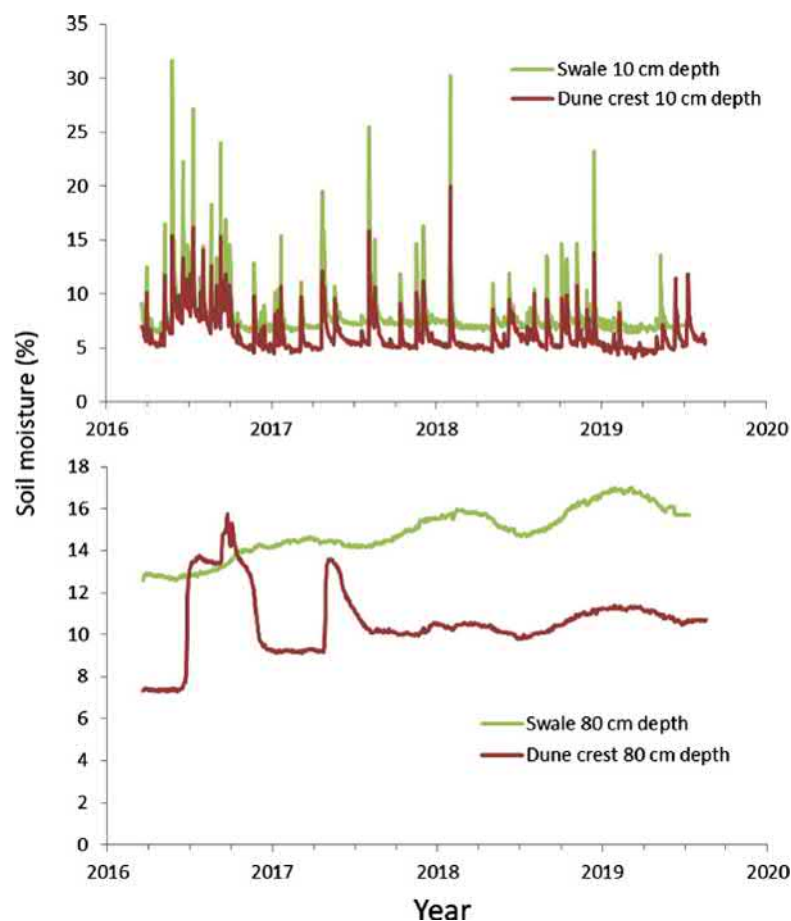


Fig. 4 Soil moisture traces at two depths (10 cm, 80 cm) for a dune crest supporting *Triodia mallee* and a swale supporting Shrubby mallee in Tarawi Nature Reserve. Moisture content at 10 cm depth is critical to germination, growth and survival of perennial seedlings and ephemeral plants. Moisture at 80 cm depth and below is accessible to established perennial shrubs and trees. Swale soils have smaller particle sizes than crest soils, especially in the subsoil. Swale soils, with rare exceptions, have higher moisture content than crest soils throughout the soil profile. Swale soils exhibit higher moisture variability than crest soils at the surface and lower moisture variability in the subsoil.

silt and clay content of subsoils beneath chenopod mallee, shrubby mallee and maalok may enable greater water retention, but it is not known whether clay content is high enough to cause reverse-texture effects (Noy-Meir, 1973).

Diverse traits associated with drought resistance and water conservation are evident in plants and animals that inhabit mallee ecosystems. Many plants exhibit reduced leaf forms including phyllodes (*Acacia*, *Senna*), cladodes (*Exocarpos*, *Logania*) and narrow or needle leaf shapes (*Acacia*, *Hakea*, *Triodia*). These, together with thick waxy cuticles, leaf vestiture and stomatal regulation and invagination reduce transpirational water loss through leaves. *Triodia* and some chenopods also have C_4 photosynthetic pathways, enabling them to fix CO_2 during night time and absorb light through photosynthesis during the day while stomatal pores are closed. Many vertebrates have analogous physiological traits enabling uptake of water from plant forage with reduced dependence of standing water, which becomes rare in mallee landscapes during summer. Behavioral traits also enable avoidance of high temperatures and reduce exposure to desiccation, including nocturnal activity cycles, common in mammals with small and medium body sizes, and resting in shady refuges or burrows. Macropods, emus and many other birds are able to move large distances to access available water. Many perennial plants have deep root architecture, enabling them to access reliable sources of moisture in subsoils. Roots of mallee eucalypts, for example, have been found at depths exceeding 25 m (Parsons, 1994). This is coupled either with rapid early growth enabling young winter germinants to access deep moisture before the first summer, or very long-lived adult life stages, which reduce the population-level impact of successive recruitment failures and exploit rare years when soil moisture remains at high levels through the summer. Conversely, many plants and animals (notably insects and some small mammals) have ephemeral life cycles, enabling them to complete their life cycles during periods of high moisture availability and persist through dry phases as dormant propagules (e.g., soil seed banks).

Although all mallee ecosystems routinely experience summer water deficits, large interannual variations influence both impacts on biota and opportunities for regeneration. Extreme mortality responses to century-scale drought events have been shown to leave transformative legacies on ecosystem identity and function across arid and semi-arid Australia, including mallee ecosystems (Godfree et al., 2019). Heat shock events, where afternoon summer temperatures exceed $50^\circ C$, may amplify the impacts of prolonged droughts, and both are expected to occur more frequently under future climates. Conversely, exceptionally large rainfall events may be critical to recharging resources, fuelling boom-bust productivity and trophic webs, and to long-term persistence of long-lived perennial plants, which rely on infrequent recruitment episodes to compensate attrition of established individuals (Morton et al., 2011; Wardle et al., 2013).

Nutrient Poverty

Mallee ecosystems have low stocks of phosphorus and nitrogen. Mapping by CSIRO suggests that surface soils contain 0.01–0.02% total phosphorus and 0.03–0.05% total nitrogen by weight (Keith and Tozer, 2017). Calcium dominates the cation exchange complex of most mallee soils. Vegetation accounts for 8 and 7 $kg \cdot ha^{-1}$ of phosphorus above- and below-ground, respectively, and 140 and 100 $kg \cdot ha^{-1}$ of nitrogen above- and below-ground, respectively (Burrows, 1976 cited in Parsons, 1994).

In general, mallee soils with greater clay content have higher nutrient levels than those with high sand content. In dune landscapes, soil phosphorus and cation exchange capacity may increase by a factor of 4 or 5 from the dune crest to the swale (Unkovich, 2014), indicating the substantial difference in nutrient availability between *Triodia* mallee on dunes and shrubby mallee in swales. The nutritional contrast between siliceous sands of heathy mallee and the loamy sands of chenopod mallee is likely to be even greater (Fig. 2).

Differences in nutrient status among mallee vegetation types are most evident in leaf traits of shrubs. The sclerophyll morphology of shrub leaves in heathy mallee and maalok likely reflect low levels of soil phosphorus, which in combination with abundant light and CO_2 and seasonally available moisture, result in production of excess carbohydrate directed into production of cellulose and lignin, rather than photosynthetic tissues (Orians and Milewski, 2007). Sclerophyll is virtually absent from shrubs in chenopod mallee, and less pervasively represented in the shrub floras of shrubby and *Triodia* mallee. The greater abundance and diversity of grasses in these latter vegetation types relative to heathy mallee and maalok may also reflect nutritional differences.

Fire Regimes

Patterns in fire occurrence

All mallee vegetation types and maalok are fire-prone. Murphy et al. (2013) predicted that mean fire return intervals for mallee vegetation varied from 20 to 100 years and fireline intensity varied from 1000 to 5000 $kW \cdot m^{-1}$, with extreme values up to 50,000 $kW \cdot m^{-1}$. Empirical estimates for heathy mallee in southwestern Australia reviewed by Gosper et al. (2016) were broadly similar, although typical intensities were slightly higher and fires occurred in summer-autumn, rather than spring-summer.

Models extrapolated from satellite image time series in the Murray-Darling depression estimate that time since last fire varies up to 110 years, with the oldest mallee distributed mainly in the northwest of that region where mean annual rainfall is lowest and landscapes are dominated by shrubby and *Triodia* mallee. Higher rainfall areas in the south, dominated by heathy mallee, generally had fires within the last 3 years.

Gibson et al. (2015) fitted failure time models to mapped fire history (1930s—present) to examine the influence of environmental covariables on fire regimes in the Murray-Darling Depression. They found that higher rainfall was consistently associated with shorter fire intervals, and that the probability of burning at a point was independent of time since fire, except in shrub-

dominated mallee communities at high rainfall (i.e., heathy mallee). They also found that higher-fertility sands were associated with shorter fire intervals in grass-dominated communities (i.e., chenopod mallee), whereas lower-fertility sands were associated with shorter fire intervals in shrub-dominated communities (heathy mallee cf. *Triodia* mallee).

Noble and Vines (1993) suggested that ephemeral fuels (primarily tussock grasses and forbs) promoted by antecedent rainfall were critical to extensive spread of fire, since these connected patches of eucalypt leaf litter and *Triodia*, fuel elements that otherwise remained discontinuous and unable to sustain fire spread except under strong winds. The limitations on fire spread in the absence of ephemeral fuels, irrespective of the age of perennial fuels, may explain Gibson et al. (2015) failure to detect a relationship between the probability of burning and time since fire in semi-arid mallee.

Plant traits and fire responses

The mallee flora is equipped with a number of morphological and life-history traits enabling persistence under a regime of canopy fires occurring at multidecadal frequencies during summer-autumn seasons. Morphological traits include subterranean woody regenerative organs, thick bark, canopy seedbanks and physical or physiological seed dormancy with fire-related germination cues (Gosper et al., 2012; Yates et al., 2017). Plant life histories vary from long-lived stress tolerators to fecund ruderals, with fires influencing survival, growth and reproduction in the former, and reproduction in the latter.

All mallee eucalypts have similar fire response traits (Fig. 3F). Their aerial stems have thin bark and are killed even by low intensity fires. New stems resprout from subterranean lignotubers, increasing in girth and height, and reducing in number with time since fire. Survival rates of established plants are typically high (>95%), but are much reduced under successive fires in spring (Noble and Diggle, 2013). Seeds are retained in woody fruits (serotinous seed banks) where they are insulated from the lethal heat during fire and subsequently released onto the ash bed. Seed bank turnover rates are high (c. 2 years) and fruit production is variable among years, so seed banks may be small or absent in some years (Keith and Tozer unpublished data). Seedling recruitment occurs almost exclusively after fire and is highly variable between fires. Recruitment failure may result from either small pre-fire seed banks, insufficient soil moisture to initiate germination, or high seedling mortality due to desiccation. As standing plants may live for several centuries (Wellington et al., 1979), even relatively rare recruitment events are sufficient to maintain stable populations. Maturation rates are slow. Although lignotuber development commences within the first year, it may take two or more decades for the majority of a cohort to develop sufficiently to survive their first fire. Flowering generally also commences within the third decade of life, although vigorously growing seedlings of *Eucalyptus costata* may produce their first seed crop within one decade.

With the exception of *Callitris*, fire-killed trees are uncommon in mallee, but dominate maalok (Table 1). Their growth and maturation rates are faster than those of mallee eucalypts, fecundity rates are greater and their serotinous seed banks persist for longer. Recruitment is closely associated with fires, which may result in high densities of seedlings. Nonetheless, population persistence is highly sensitive to short fire return intervals relative to maturation times and reestablishment of seed banks, which are entirely exhausted by a single fire (Bradstock and Cohn, 2002). They are also sensitive to recruitment failure associated with high interannual rainfall variability.

Fire-killed shrubs are especially prominent in *Triodia* mallee and may also be common in heathy mallee (Table 1). Unlike eucalypts and *Callitris*, most accumulate persistent soil seed banks that remain physically or physiologically dormant until fire-related germination cues (usually heat shock or smoke-associated chemicals) coincide with suitable temperature and moisture conditions. Seed bank longevity is poorly studied but anecdotal observations suggest it may extend to many decades or beyond a century. Standing plant longevity is shorter, with senescence occurring at 10–30 years of age for a range of species.

Resprouting shrubs are most common in shrubby mallee and heathy mallee (Table 1). While aerial stems are killed, they resprout from lignotubers or woody rhizomes. Their standing plants are slower-growing and longer-lived than fire-killed species, and they tend to be less fecund and may be expected to have smaller and less persistent soil seed banks due to reduced selection pressures on postfire recruitment. *Triodia*, although C₄ grasses, resemble resprouting shrubs in growth form and life history. Individuals form wiry, spiny hummocks and persist for more than a century, resprout from clustered underground rhizomes and recruit after fire from ostensibly short-lived soil seed banks. Interestingly, some populations are comprised entirely of fire-killed plants.

Unlike other shrub groups, seedling establishment occurs semi-continuously throughout the fire cycle in chenopod shrubs (*Maireana*, *Sclerolaena*, *Chenopodium*, *Atriplex*) and a few other species. When dominant in mallee understories (as in chenopod mallee, Table 1), they are less flammable than sclerophyll shrubs and *Triodia*, but standing plants are killed when burnt and population persistence relies on regeneration from seeds.

Ephemeral forbs and grasses are significant components of shrubby mallee and *Triodia* mallee. The forbs germinate and grow in the cool seasons of wet years, producing a seed crop before the onset of the fire season, and senescing in the warmer months. As noted above, emergence varies greatly between years with rainfall, but the magnitude of recruitment is generally enhanced by fire (Parsons, 1994). Ephemeral C₃ grasses (primarily *Austrostipa*) have similar life histories, but their phenology differs, with emergence occurring in spring, maximum growth and reproduction occurring in late spring-summer. Senescence and curing in mid-late summer contributes significantly to available fuels in years of high abundance (Noble and Vines, 1993).

At the community level, there is strong evidence of trends in plant species richness and composition with time since fire in *Triodia* mallee as standing plants of ephemerals and short-lived fire-killed shrubs decline in abundance and return to the soil seed bank (Parsons, 1994; Yates et al., 2017). Similar trends are less evident, or play out more slowly in heathy mallee (Gosper et al., 2012), as such life histories are not major components of those communities and standing plants are longer lived.

Pausas and Bradstock (2007) suggested that the relative proportions of fire-killed and resprouting woody plant species were related to a fire-productivity gradient in southeastern Australian mallee. They found that the proportion of fire-killed species

increased as mean annual rainfall and fire frequency declined from south to north. Subsequent work by Gibson et al. (2015) suggests that these relationships are more complex, however, as substrates interact with rainfall and fire regime gradients. In the low-rainfall regions, for example, most of the fire-killed shrubs are confined to light-textured soils on dunes (*Triodia mallee*), whereas resprouters dominate heavier-textured sandy loams in the swales (shrubby mallee).

Conservation

Major threats to mallee and maalok ecosystems include habitat loss and fragmentation related to land use intensification, invasive species, degradation of soils associated with cropping and livestock grazing, changes in fire regimes and climate change.

Mapping included in the National Vegetation Information System (Major Vegetation Subgroups version 5.1, <https://www.environment.gov.au/land/native-vegetation/national-vegetation-information-system/data-products#mvsg51>), estimates the pre-European extent of mallee ecosystems to be 400,000 km², of which about 30% has been cleared, primarily for dryland cropping in the wheatbelts of Victoria, South Australia and Western Australia. Earlier estimates suggest a smaller extent, but similar proportion cleared (DEWR, 2007). The impacts of these losses have fallen disproportionately in high rainfall areas (Yates et al., 2017) and on chenopod mallee, which has the most favorable soils for crop production. It is likely that clearing has eliminated much more than half of chenopod mallee distribution. Losses of shrubby and heathy mallee have also been appreciable, while *Triodia mallee* and maalok have been less affected, as their climate and soils are less suitable for agriculture.

Clearing has left ongoing legacies related to habitat fragmentation, which limits the viability of isolated populations of plants and animals in remnant patches (Luck et al., 1999a, 1999b), promotes incursions of invasive species, disrupts native animal movement and herbivory, and changes patterns of fire ignition and spread. Large protected areas have been established to limit the impacts of clearing and fragmentation, but their coverage is biased towards mallee vegetation types that are least at risk from clearing, notably *Triodia mallee*.

Invasive species have had major historical and ongoing impacts on mallee ecosystems. Feral foxes and cats are predators of a diverse range of native mammals, birds, reptiles, and insects. They are strongly implicated in regional and global extinctions of medium-sized mammals (Johnson and Isaac, 2009), including fossorial species that had major roles as ecosystem engineers in nutrient and carbon cycling, soil structure and plant recruitment (Eldridge and James, 2009).

Feral rabbits and goats, together with overgrazing by domestic livestock, have direct impacts on woody and nonwoody vegetation (Cohn and Bradstock, 2000), reducing vegetation cover and structural complexity, with implications for exposure of native animals to feral predators. Impacts on regeneration of native shrubs and trees are particularly severe in some areas. Domestic and feral herbivores also contribute to soil degradation through disruption of biological soil crusts, compaction and by mobilizing surface soils and increasing their exposure to erosive winds (Mallen-Cooper et al., 2018). Erosion and redeposition of soil several metres deep has been documented in a number of areas, for example, through burial of fence lines (Unkovich, 2014).

Landscape-scale and targeted control programs aim to abate these threats posed by invasive species. These include release of biological control agents for rabbits, targeted baiting, culling and habitat management programs directed at foxes, cats and rabbits, construction of large enclosures enabling elimination of feral animals within, as well as active restoration of soils and woody vegetation. Ongoing control of feral animals will be crucial to maintaining function and diversity of mallee ecosystems, as will implementation of conservative stocking regimes in pastoral areas, with responsive reduction of livestock densities early in drought cycles. Reestablishment and maintenance of perennial shrub strata are critical to sustainability of these systems.

Changes in fire regimes threaten mallee and maalok ecosystems through at least three different mechanisms. Firstly, increases in fire frequency may erode diversity by interrupting seed bank reaccumulation in fire-killed plants, especially those with long maturation times (Bradstock and Cohn, 2002; Gosper et al., 2013, 2018). Frequent fires also maintain a greater portion of the landscape in young age classes, unsuitable for animal species dependent on old mallee habitat features (Kelly et al., 2011). Secondly, changes in the timing of fires may increase the probability of recruitment failure associated with extreme postfire water deficit. This could occur through increased fire occurrence in autumn (Noble and Diggle, 2013) or increased fire frequency at any time of year, which increases the probability of drought conditions during the postfire period. Thirdly, fires may enhance foraging efficiency of feral herbivores and predators, increasing mortality of regenerating perennial plants and native vertebrates, respectively. More work is needed to identify fire regimes associated with these effects, but fire frequency and spatial pattern are expected to be important.

Fuel reduction burning has been central to fire management in the mallee to reduce the likelihood of extensive unplanned fires (Yates et al., 2017). These are sometimes applied in spring when there are significant risks to mallee biota. The poor relationship between the probability of burning and fuel age (Gibson et al., 2015), together with the potential for rapid accumulation of ephemeral fuels in wet years (Noble and Vines, 1993), and continued occurrence of large fires driven by extreme weather, raises questions about the effectiveness of extensive fuel reduction as a core management strategy in semi-arid climates. Future fire management strategies need to address the mechanisms underpinning risks to mallee ecosystems, given the developing understanding of life-history responses of mallee biota, with flexibility to adjust management to current ecosystem states (Yates et al., 2017).

Projections of future climate suggest increases in mean temperature and frequency of days exceeding 40 °C, declines in rainfall particularly in winter, and increased frequency of extreme fire weather, all consistent with a southward shift in Australia's arid and Mediterranean climate zones (IPCC, 2014). The implications of such changes for mallee and maalok ecosystems are diverse. Reduced reliability of rainfall is likely to result in reduced cropping yields (Anwar et al., 2007), with more prolonged periods of exposed soils and associated erosion, impacting remnant mallee vegetation in cropping landscapes. Ultimately, dryland cropping

may become economically and ecologically unviable in these areas, prompting a shift to grazing enterprises and some opportunities for reconstructing mallee ecosystems. Technological innovations, such as drought-resistant crop strains, may prolong this transition. Declining rainfall is also impacting pastoral land uses, with economic pressures driving lags in destocking during drought events, in turn driving further erosion of perennial plant cover and resilience of the system to drought. Increasing aridity, together with legacies of past soil degradation have also driven a shift from sheep or cattle farming to harvest of wild goats, which have lower water requirements, lower investment and maintenance requirements and greater impact on perennial vegetation due to their broader diet.

In more natural areas, climate change may be expected to drive increased frequencies of major plant and animal mortality events associated with heat waves and increased frequencies of plant recruitment failure. Over long time scales, these processes may drive transition of *Triodia* mallee to desert shrubland in some areas and more subtle transitions in others. Changes in fire regimes are difficult to predict and depend on human ignition patterns. However, maalok and some heathy mallee systems may be under pressure from 'interval squeeze' if increased frequencies of extreme fire weather are reflected in fire frequencies that promote declines in fire-killed plants that rely on seed-bank reaccumulation between successive fires for population persistence. Drier parts of mallee distribution, even if they experience reduced fire frequency as a consequence of rainfall-related declines in fuels, are likely to be subject to increased risks of recruitment failure related to postfire droughts.

Aside from mitigation actions to reduce global warming, sustaining mallee ecosystems under future climates will depend critically on maintaining and building resilience by reducing pressures related to clearing and fragmentation, overpopulation of domestic, feral and native herbivores, soil degradation and fire regimes.

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Hawai'i's Dry Grasslands and Shrublands

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Published by Elsevier Inc.

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Abstract

This paper is a status assessment of Hawai'i's dry grasslands and shrublands, including its pre-human condition; current status, stressors, and conservation efforts; and future viability. Dry grasslands and shrublands in Hawai'i, including dry cliffs, generally have a hot and dry climate with relatively low annual rainfall and are characterized by being located in lowland, montane-subalpine, or alpine zones. These zones are differentiated by elevation and climate, which primarily dictate which species can exist in them (Gagne and Cuddihy, 1999). Prior to human arrival, dry grasslands and shrublands occurred on all of the main Hawaiian islands as well as Nihoa and Mokumanamana (Necker) in the Northwestern Hawaiian islands. Currently, they are still found on the same islands. However, the extent of the native species-dominated parts of this ecotype has greatly reduced in size. In addition to native sub-ecotypes, introductions of nonnative species resulted in two new sub-ecotypes referred to as introduced dry grasslands and introduced dry shrublands, which have become widespread. Our assessment of dry grassland and shrubland viability, defined as the likelihood of persistence over the long term, is based on

the concepts of resiliency, redundancy, and representation. The main stressors to dry grasslands and shrublands have been identified as invasive ungulates, invasive plants, invasive herbivores, fire, drought, natural disasters, climate change, and human development. Conservation efforts help to protect and restore native areas of dry grasslands and shrublands, and largely depend upon the actions of Federal, State, private, and multi-agency partnerships. The level of these conservation efforts and their impact on stressors determines the future viability of Hawai'i's dry grasslands and shrublands.

Introduction

The Hawaiian archipelago is the most isolated landmass in the world, consisting of some 132 islands, including 8 larger islands, and numerous smaller islands, islets, atolls, reefs, and shoals. The entire archipelago stretches 1603 miles (mi) (2580 kilometers (km)) on a southeast-northwest line across the middle of the Pacific Ocean. More than 99% of the land area is concentrated within eight larger, younger islands on the southeastern end of the chain (Wagner et al., 1999). These are referred to as the main Hawaiian islands and are named as follows: island of Hawai'i, Maui, Moloka'i, Lāna'i, Kaho'olawe, O'ahu, Kaua'i, Ni'ihau. The remainder of the archipelago to the northwest is made up of a much older and smaller collection of islands and atolls known as the Northwestern Hawaiian islands (NWHI). The NWHI consists of Nihoa, Mokumanamana (Necker), 'Ōnūnui (Gardner Pinnacles), Lalo (French Frigate Shoals), Kamole (Laysan), Kapou (Lisianski), Manawai (Pearl and Hermes), Kuaihelani (Midway), and Hōlanikū (Kure). The existence of a diversity in climate, geography, hydrology, and other environmental factors has resulted in a variety of biomes (forests, grasslands, shrublands, wetlands, etc.) in the Hawaiian islands. This paper provides an overview of Hawai'i's dry grasslands and shrublands and describes the factors that have impacted them over time and that will into the future.

Description

Defining Dry Grassland and Shrubland Characteristics

A grassland is defined as a plant community that has greater than 40% cover in grasses (Gagne and Cuddihy, 1999). Similarly, a shrubland is defined as a plant community that has greater than 40% cover in shrubs (woody plants 1–10 feet (ft) (1–3 meters (m)) tall and often with multiple stems) (Gagne and Cuddihy, 1999). Dry grasslands and shrublands occur primarily on the leeward sides of the islands in hot, dry climates with relatively low annual rainfall and are found in lowland, montane-subalpine, or alpine zones. These zones are differentiated by elevation and climate, which primarily dictate which species can exist in them (Gagne and Cuddihy, 1999), and are described further in the Pre-human Condition and Current Condition sections below. Dry grassland and shrubland occurs on all of the main Hawaiian islands from 50 to 11,100 ft. (15 to 3400 m) elevation (LANDFIRE, 2016), with annual rainfall ranging between 4 and 69 inches (in) (10 and 175 centimeters (cm)) (Gagne and Cuddihy, 1999). This ecotype also includes dry cliffs, which are defined by their occurrence in areas with steep slopes (greater than 65 degrees) that are away from the direct influence of the shoreline.

Geology

Substrates are highly variable throughout this ecotype. In the lowlands, dry grasslands often occur on thin soils and old lava flows while dry shrublands vary from silty loams to relatively unweathered pāhoehoe (Gagne and Cuddihy, 1999). Montane dry grasslands have either a sandy loam soil or less developed cindery soil (Gagne and Cuddihy, 1999). Montane-subalpine dry shrublands occur on sandy-loamy soils derived from volcanic ash or sand, or weathered lava (Gagne and Cuddihy, 1999). Alpine dry shrublands are well-drained and gravelly, and are derived from cinder and ash (LANDFIRE, 2016). Dry cliff substrate includes sandy loam soils derived from cinder, volcanic ash, and weathered basaltic lava with little soil development (LANDFIRE, 2016).

Vegetation structure and composition

Dry grasslands and shrublands vary in vegetation structure and composition. The dry shrubland ranges from an open to dense shrub layer up to 2 m in height in lower elevational zones (LANDFIRE, 2016), to sparse and almost non-existent vegetation in the higher elevational alpine shrubland (Gagne and Cuddihy, 1999). In the alpine shrubland, only plant communities that are morphologically and/or physiologically adapted to extreme conditions can survive (Gagne and Cuddihy, 1999). Dry grasslands range from a moderate to dense layer of grass up to 1 m tall (LANDFIRE, 2016). Dry cliffs generally have sparse vegetation, composed of an open shrub or herbaceous layer that's restricted to ledges or less steep slopes (LANDFIRE, 2016).

Other biotic components

Dry grasslands and shrublands provide habitat to many birds and invertebrate species, which have a functional role in the ecological processes of this habitat. Birds, along with wind, are integral in the dispersal and pollination of plant species in dry grasslands and shrublands. Lowland dry grasslands and shrublands may support native birds such as large flightless geese and ducks (family Anatidae) and thrushes (family Turdidae) (Chimera and Drake, 2011). Native invertebrates also play an important role in pollinating plant species, particularly in dry shrublands (Magnacca, 2007).

Dry cliffs provide nesting habitat for some species of seabirds (HDLNR, 2015). Seabirds provide important nutrients from the marine environment such as nitrogen and phosphorus to the substrate, which are essential to vegetation recovery and health (Fukami et al., 2006; VanderWerf et al., 2014).

Physical/life history components

Natural recruitment in dry grasslands and shrublands is driven by numerous factors including disturbance from fires, drought, hurricanes, volcanism, storms, pathogens, diseases, and invertebrate pests. It can also be influenced by rainfall, light, and nutrient availability.

Water availability in dry grasslands and shrublands is dependent on rainfall and elevation. In the lowlands, rainfall is mostly restricted to winter months, while summers are hot and dry (Gagne and Cuddihy, 1999). Montane-subalpine areas have a seasonal climate with drought conditions during the summer months (May to October) and rainfall mostly in the winter months (November to March) (Gagne and Cuddihy, 1999). Alpine dry shrublands have an extremely dry and cold climate, with frequent frost that occurs even in the summer months. Rainfall in the dry, leeward sides of the Hawaiian islands most commonly occur as a result of frontal storm systems that are distributed over a large area and are broad; and convective storm cells, which are localized to a particular area and are small (Cordell and Sandquist, 2008). The sporadic appearance of rainfall during drought periods from convective storms, although small and for the most part do not account substantially to annual primary productivity in dry grasslands and shrublands, are important in the maintenance and existence of woody plants present in dry shrublands (Cordell and Sandquist, 2008).

Fire can act as a primary driver for change in dry grasslands and shrublands, and reset the successional clock by removing a substantial amount of plant biomass and significantly reducing the presence of several plant species. Some seeds will survive and be able to germinate following the fire, however, others rely on dispersal from other sources such as the wind or animals. Most native species in Hawai'i are not specifically fire adapted (Smith and Tunison, 1992), while invasive grasses (e.g., fountain grass) can be highly fire-adapted and regenerate quickly after fire (Fujioka and Fujii 1980 in Cuddihy and Stone, 1990; D'Antonio and Vitousek, 1992).

System Viability

The viability of dry grasslands and shrublands is defined as the likelihood of persistence over the long term. This depends on maintaining multiple and distributed populations (redundancy) of sufficient quality and size (resiliency), with species richness and genetic range (representation) to survive across their ecological environment over time.

Adequate distribution across the landscape contributes to its ability to perpetuate after a catastrophic event in one area by having a redundant population in another area. Regeneration of vegetation starts through succession and natural recruitment influenced by dispersal, rainfall, light, and nutrient availability. Dispersal mechanisms such as animals or wind, along with the optimal water availability mentioned above allow dry grasslands and shrublands to persist before and regenerate after catastrophic events.

The quality and size of dry grasslands and shrublands contributes to its resiliency in the face of stochastic events. Typical stochastic events for this ecotype include flooding or minor fires. Factors that affect the quality, and therefore the resiliency, of dry grasslands and shrublands include the pre-disturbance biodiversity and vegetation type (i.e., native or nonnative dominated). Dry grassland and shrubland stands that are composed of a higher proportion of native species have a greater likelihood to recover to predominantly native species cover whereas stands that were dominated by non-native species typically recover to non-native species dominance post-disturbance. Larger patch sizes of dry grasslands and shrublands typically harbor a larger number and greater abundance of native plant species and are therefore more resilient.

Diversity (e.g., geographic, genetic, and species diversity) within and among locations of dry grasslands and shrublands is necessary to enhance its ability to adapt to change. Dry grasslands and shrublands are best represented when there is geographic and genetic diversity across the range. Typical representation considerations include biodiversity and presence across a wide range of the islands; both on windward and leeward sides, and from lowland to alpine elevations.

Pre-Human Condition**Dry Grassland and Shrubland Sub-Types**

Before the arrival of humans, Hawai'i's dry grasslands and shrublands were represented by six sub-types: dry cliff, lowland dry grassland, lowland dry shrubland, montane-subalpine dry grassland, montane-subalpine dry shrubland, and alpine dry shrubland (Table 1).

Physical/life history components

The historical fire regime in Hawai'i was characterized by infrequent, low severity fires, as few natural ignition sources existed (Cuddihy and Stone, 1990; Smith and Tunison, 1992). It is believed that prior to human colonization, fuel was sparse in dry plant communities and most native vegetation had a low flammability (Cuddihy and Stone, 1990), Smith and Tunison, 1992). *Heteropogon contortus* (Pili grass), however, was adapted to survive fires and may have benefited from burnings (Cuddihy and Stone, 1990). Vogl (1969, in Cuddihy and Stone, 1990) proposed that naturally occurring fires may have been important in the development of some of the original Hawaiian flora adding to the species richness of ecotypes including dry grasslands and shrublands. As naturally occurring fires destroyed many woody species in forests, species in dry grasslands such as pili could persist.

Table 1 Pre-human dry grassland and shrubland sub-types.

Sub-type	Precipitation (cm) (Gagne and Cuddihy, 1999; LANDFIRE, 2016)	Elevation (m) (Gagne and Cuddihy, 1999; LANDFIRE, 2016)	Characteristic plants (Gagne and Cuddihy, 1999; LANDFIRE, 2016)
Dry cliff	50–150	15–3000	<i>Heteropogon contortus</i> (pili), <i>Peperomia tetraphylla</i> (kupali'i), <i>Trisetum glomeratum</i> (pili uka, mountain pili), <i>Artemisia mauiensis</i> (hinahina), and <i>Psydrax odorata</i> (alahe'e)
Lowland dry grassland	10–175	Generally 30 and sparingly up to 2000	Pili and <i>Eragrostis monticola</i> (kalamālō)
Lowland dry shrubland	50–170	100–600	alahe'e, <i>Dodonaea viscosa</i> ('a'ali'i), <i>Wikstroemia</i> spp. ('ākia), <i>Bidens</i> spp. (ko'oko'olau), <i>Sida fallax</i> ('ilima), <i>Waltheria indica</i> ('uhaloa), and <i>Sesbania tomentosa</i> ('ōhai)
Montane-subalpine dry grassland	40–50	1615–2300	<i>Eragrostis atropioides</i> (lovegrass) and <i>Panicum tenuifolium</i> (mountain pili)
Montane-subalpine dry shrubland	40–150	900–3000	'a'ali'i, ko'oko'olau, <i>Myoporum sandwicense</i> (naio), <i>Dubautia</i> spp. (na'ena'e), <i>Styphelia tameiameia</i> (pūkiawe), <i>Vaccinium</i> spp. ('ōhelo), <i>Chenopodium oahuense</i> ('āweoweo), and <i>Metrosideros polymorpha</i> ('ōhi'a)
Alpine dry shrubland	75–125	Mainly between 3000 and 3400 but can extend down to 2600 in arid zones	<i>Argyroxiphium sandwicense</i> ('āhinahina, silversword), <i>Dubautia arborea</i> (na'ena'e), and <i>D. menziesii</i> (kūpaoa)

Pre-Human Extent/Range

Prior to human arrival, dry shrublands and grasslands (including dry cliff) occurred on all of the main Hawaiian islands. They were found primarily on the leeward sides of the islands and often in lower elevations (Figs. 1–4). Specifically, they were distributed across northwest and southwest areas of the island of Hawai'i; west and central Maui, and the summit of Haleakalā; lower elevation areas across the islands of Lāna'i and Kaho'olawe; western and central parts of Moloka'i; the Kaiwi coastline, 'Ewa plains, and western parts of O'ahu; western parts of Kaua'i including valleys in the Waimea canyon; and western and eastern parts of Ni'ihau (Figs. 1–4).

In the NWHI, dry shrublands and grasslands were found on the islands of Nihoa and Mokumanamana (Necker). These islands contained a mix of lowland dry grasslands and shrublands; as well as dry cliffs. They were likely composed of primarily lowland native species such as *Sida fallax* ('ilima), *Chenopodium oahuense* ('āweoweo), and *Sesbania tomentosa* ('ōhai) (PMNM, 2008). Based on numerous descriptions of the islands from ships logs and studies (Bryan, 1978), we speculate that mixed lowland dry grasslands and shrublands, and dry cliffs covered the majority of Nihoa and Mokumanamana. There were also sparse pockets of coastal mesic forests containing species like *Pandanus tectorius* (hala) and *Pritchardia* spp. (loulou).

Viability of Pre-Human Dry Grasslands and Shrublands

Historically, dry grasslands and shrublands were distributed across all of the main Hawaiian islands, with smaller ranges across individual islands like Kaua'i, O'ahu, and the island of Hawai'i (Figs. 1–4). Dry cliffs and lowland dry grasslands and shrublands were widely distributed, however, montane-subalpine dry grasslands and shrublands and alpine shrublands were limited mostly to Maui. This smaller size and distribution left montane-subalpine dry grasslands and shrublands less redundant, and therefore less tolerant to withstand catastrophic events (i.e., wildfires, lava flows, hurricanes). However, due to the widespread distribution across all of the main Hawaiian islands, the ecotype as a whole was redundant and could have withstood events only affecting individual or a few islands.

Occurring primarily on the leeward sides of the main Hawaiian islands, dry grasslands and shrublands were represented in relatively large areas. In the NWHI, the size of this ecotype was much smaller, given the size of the islands (Nihoa and Mokumanamana). In addition, species richness was considered low to moderate so although it was composed entirely of native vegetation, it may not have been of the highest quality. However, the large size of this ecotype in the main Hawaiian islands made it resilient to stochastic events like flooding or minor fires. Dry grasslands and shrublands in the NWHI were less resilient due to their smaller size.

Given that pre-human dry grasslands and shrublands were found primarily on the leeward sides of islands and in lower elevations, the features of this ecotype (i.e., geographic, ecological, climatic) are not very representative of those found throughout the Hawaiian islands. Therefore the species richness and genetic variability needed to survive across their ecological environment over time (representation) would have been low.

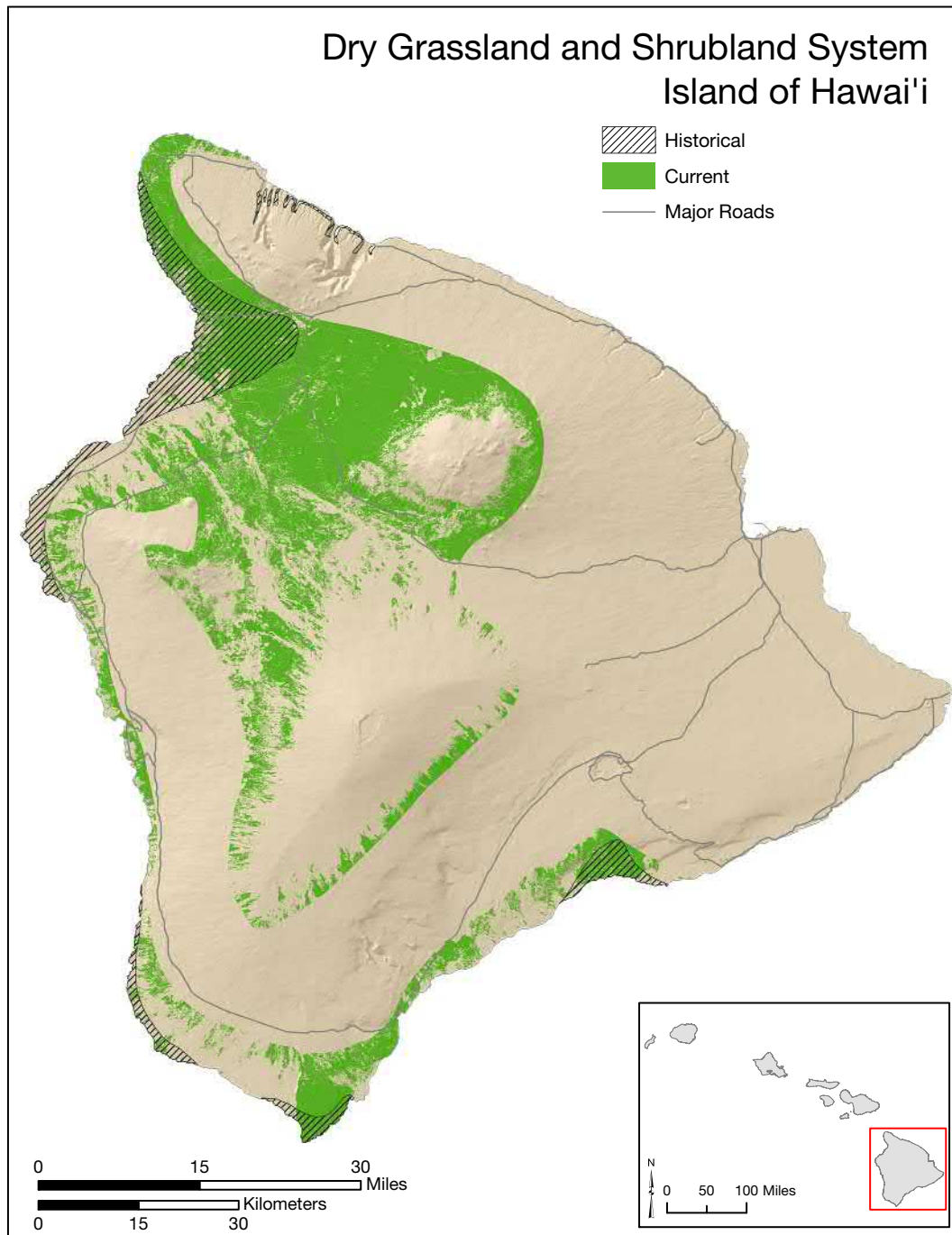


Fig. 1 Map of historic and current extent of dry grasslands and shrublands on the island of Hawai'i.

Current Condition

Dry Grassland and Shrubland Sub-Types

Before the arrival of humans, dry grasslands and shrublands were represented by six native sub-types. This is now further subdivided to include two more sub-types, which are introduced dry grassland and introduced dry shrubland. While five of the pre-human sub-types (lowland grasslands and shrublands, montane-subalpine grasslands and shrublands, and alpine shrublands) remain characterized by native species, dry cliff now includes introduced plant species. These changes and the two new sub-types are described in [Table 2](#) below.

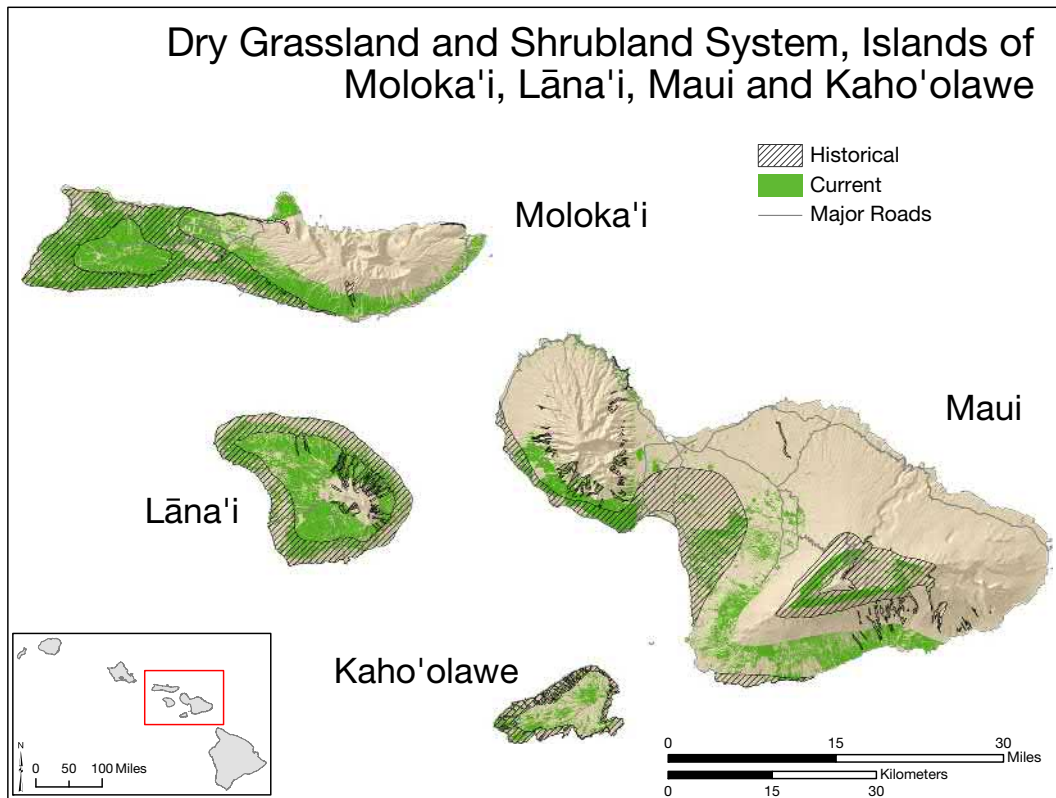


Fig. 2 Map of historic and current extent of dry grasslands and shrublands on the islands of Moloka'i, Lāna'i, Maui, and Kaho'olawe.

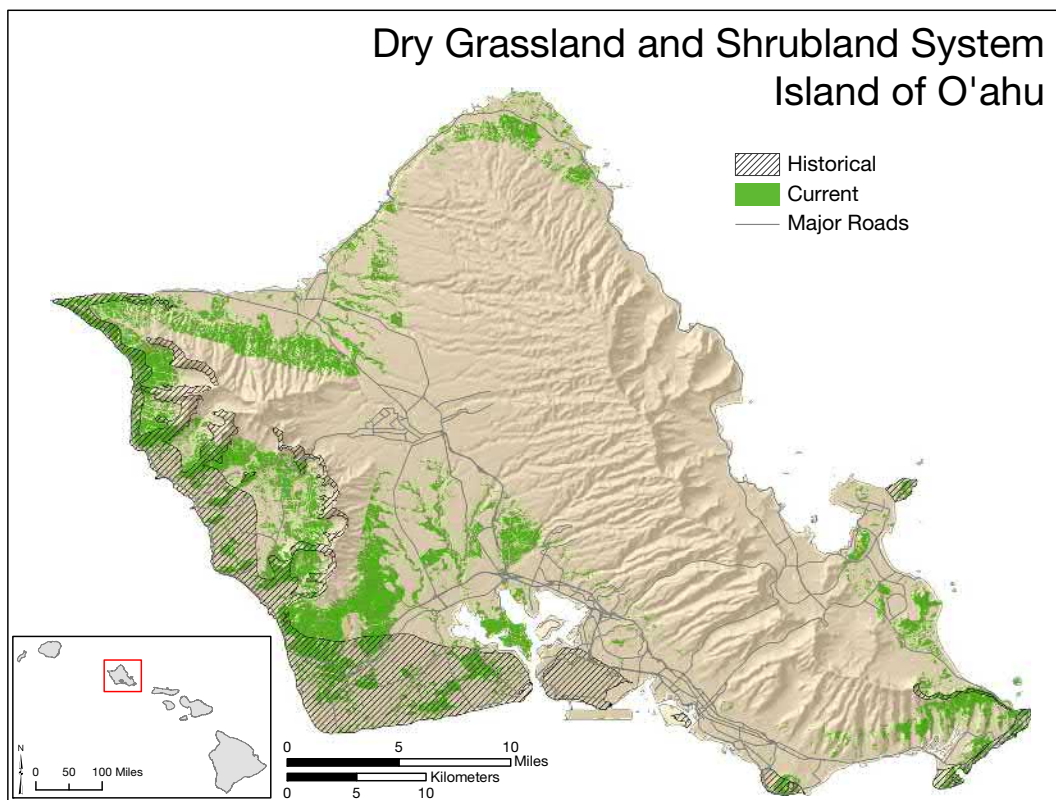


Fig. 3 Map of historic and current extent of dry grasslands and shrublands on the island of O'ahu.

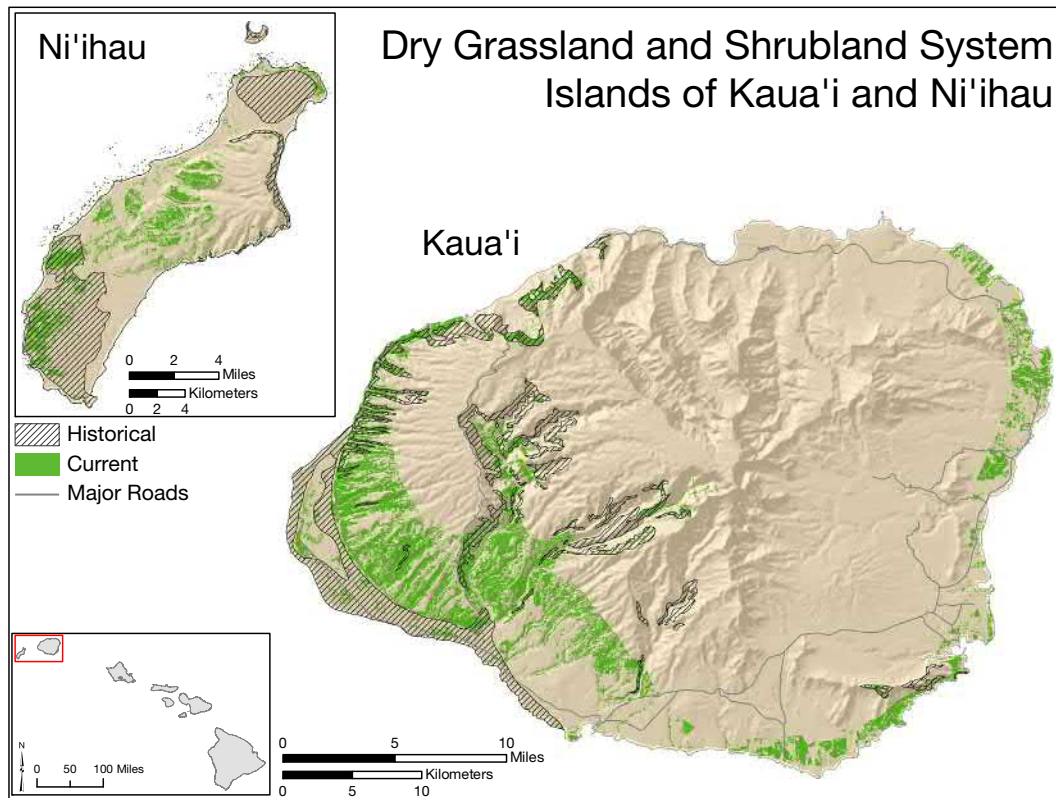


Fig. 4 Map of historic and current extent of dry grasslands and shrublands on the islands of Kaua'i and Ni'ihau.

Table 2 New current condition dry grassland and shrubland sub-types.

Sub-type	Precipitation (cm) (Gagne and Cuddihy, 1999; LANDFIRE, 2016)	Elevation (m) (Gagne and Cuddihy, 1999; LANDFIRE, 2016)	Characteristic plants (Gagne and Cuddihy, 1999; LANDFIRE, 2016)
Dry cliff	50–150	15–3000	Pili, kupali'i, pili uka (mountain pili), hinahina, alahe'e, <i>Melinis repens</i> (natal redtop), <i>Lantana camara</i> (lantana), <i>Leucaena leucocephala</i> (koa haole), and <i>Prosopis pallida</i> (kiawe)
Introduced dry grassland	Varies	Typically in lowlands, but extends to montane-subalpine areas	<i>Pennisetum setaceum</i> (fountain grass), <i>Cenchrus ciliaris</i> (buffelgrass), <i>Megathyrsus maximus</i> (guinea grass) <i>Andropogon virginicus</i> (broomsedge), <i>Schizachyrium condensatum</i> (beardgrass), natal redtop, and <i>Hyparrhenia rufa</i> (thatching grass); often mixed with kiawe in the overstory
Introduced dry shrubland	Varies	Lowlands through montane-subalpine	<i>Plantago lanceolata</i> (plantain), <i>Hypochoeris radicata</i> (cat's ear), <i>Heterotheca grandiflora</i> (telegraph weed), <i>Tagetes minuta</i> (marigold), and <i>Verbesina encelioides</i> (golden crownbeard)

Current Extent/Range

Distribution by sub-type

Dry cliff

Dry cliffs are currently found on all of the main Hawaiian islands except Ni'ihau, as well as Nihoa and Mokumanamana in the NWHI. Unlike their pre-human state of native vegetation, these sites are now often weedy and may contain introduced plant species like *Melinis repens* (natal redtop), *Lantana camara* (lantana), *Leucaena leucocephala* (koa haole), and *Prosopis pallida* (kiawe) (LANDFIRE, 2016).

Native dry grasslands and shrublands

Lowland native dry grasslands are found primarily on the dry leeward sides mostly on the islands of Lāna'i, Maui, Kaho'olawe, and Hawai'i (Gagne and Cuddihy, 1999). They are also found on Nihoa and Mokumanamana in the NWHI. The dominant native grass in this sub-type is pili which is fairly widespread in areas dominated by native species, including the understory of native dry shrublands (LANDFIRE, 2016). Most of the lowland dry grasslands are now primarily composed of nonnative species (Gagne and Cuddihy, 1999) and are characterized as introduced dry grasslands described below.

Lowland native dry shrublands occur on the leewards sides of all of the main Hawaiian islands, as well as Nihoa and Mokumanamana (LANDFIRE, 2016). Montane-subalpine native dry grasslands and shrublands are limited to dry slopes of high mountains like Haleakalā on Maui, and Mauna Kea, Mauna Loa, and Hualālai on the island of Hawai'i (LANDFIRE, 2016). Similarly, alpine native dry shrublands are found only on the high slopes of Maui and the island of Hawai'i (Gagne and Cuddihy, 1999; LANDFIRE, 2016).

Introduced dry grasslands and shrublands

Introduced dry grasslands and shrublands occur predominantly on the leeward sides of all the main Hawaiian islands (Gagne and Cuddihy, 1999; LANDFIRE, 2016). These sub-types are characterized as being dominated by introduced grasses or introduced shrubs.

Overall extent/range

Currently, native dry grasslands and shrublands still occur on all of the main Hawaiian islands, as well as Nihoa and Mokumanamana in the NWHI. However, the extent has changed since pre-human conditions (Figs. 1–4). One factor contributing to these changes are the introductions of nonnative species, which resulted in new sub-types referred to as introduced grasslands and shrublands that were likely once forest. There are still remnants of native-dominated dry grasslands and shrublands but they are greatly reduced in size, as introduced grasslands and shrublands have become very widespread (Fig. 6).

There is a total of 750,222 acres (ac) (303,604 hectares (ha)) of dry grasslands and shrublands in the main Hawaiian islands. The island of Hawai'i contains more than 462,000 ac (186,965 ha) of dry grasslands and shrublands, the most in the main Hawaiian islands, followed by Moloka'i with approximately 75,000 ac (30,351 ha) (Fig. 5 and Table 3). Roughly 164,090 ac (66,405 ha) or approximately 22% of dry grasslands and shrublands in Hawai'i are native dominated (greater than 50% of the total vegetation cover is native vegetation), with the majority (147,636 ac (59,746 ha)) located on the island of Hawai'i (Fig. 6). In comparison,

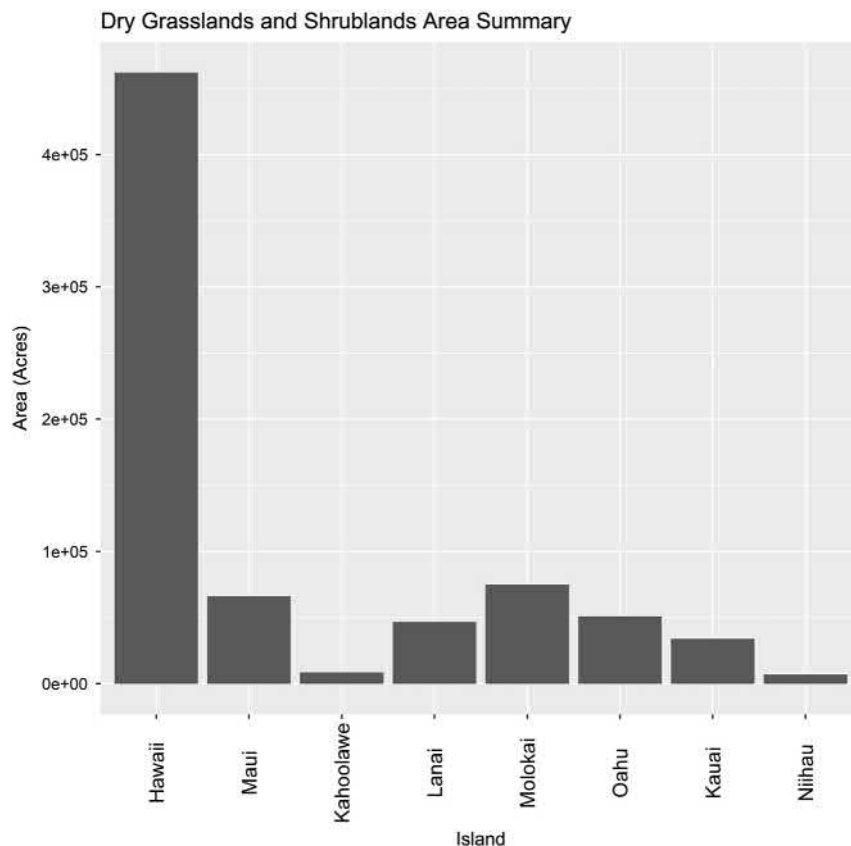
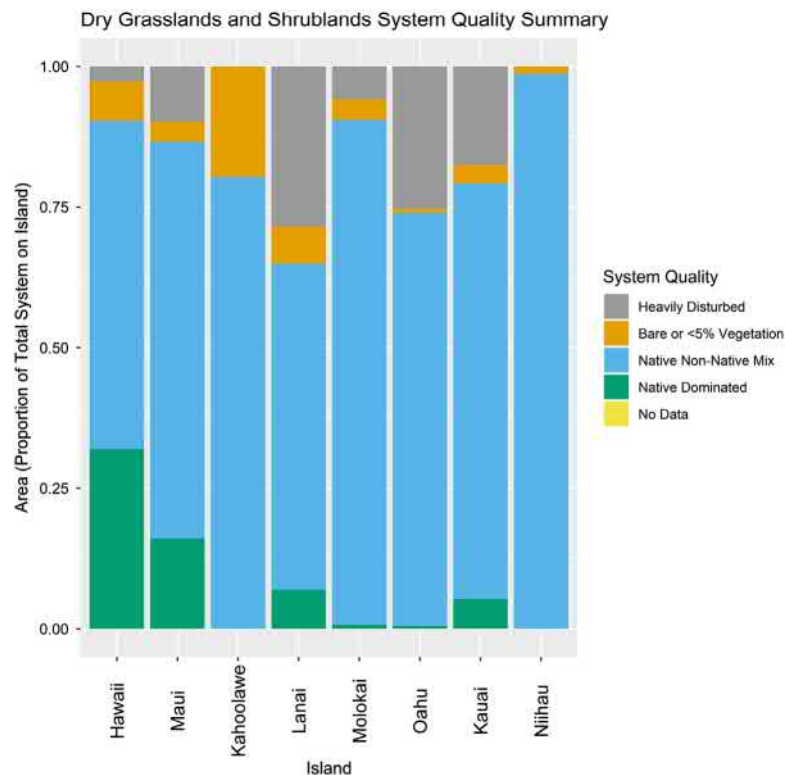


Fig. 5 Distribution of dry grasslands and shrublands in the main Hawaiian islands.

Table 3 Current distribution of dry grasslands and shrublands in the main Hawaiian islands (Reeves and Amidon, 2018).

Island	Area (Acres)	Percent of island	Percent of main Hawaiian islands
Kaho'olawe	8611	30	< 1
Ni'ihau	6948	15	< 1
Lāna'i	46,839	52	1
Moloka'i	74,744	46	2
Kaua'i	33,951	10	1
O'ahu	51,029	14	1
Maui	66,058	14	2
Hawai'i	462,042	18	11

**Fig. 6** Quality of dry grasslands and shrublands in the main Hawaiian islands.

approximately 486,958 ac (197,065 ha) or 65% of dry grasslands and shrublands in Hawai'i are native/nonnative mix and 55,113 ac (22,304 ha) or 7% are classified as heavily disturbed (Fig. 6).

In the NWHI, Nihoa and Mokumanamana are primarily made up of dry cliff and lowland dry grasslands and shrublands that are still dominated by native vegetation. These islands are highly significant in Hawaiian culture and are home to numerous cultural sites, suggesting they were visited by Hawaiians (PMNM, 2008). There is also evidence that habitation occurred for short periods of time, but most of the island, particularly on Nihoa, was unsuitable for cultivation. As a result, much of the natural ecosystem remained intact (USFWS, 1998).

Stressors

There are a number of stressors that impact dry grasslands and shrublands. Four of the most significant stressors are described below, followed by other less significant stressors.

Invasive ungulates

Introduced ungulates have greatly impacted the native vegetation of the Hawaiian islands. These impacts were accelerated following the arrival of Captain James Cook in 1778. The Cook expedition and subsequent explorers intentionally introduced a European race of pigs or boars and other livestock, such as goats (Tomich, 1986; Loope, 1998). Other ungulates now present in Hawai'i include

axis deer, black-tailed deer, mouflon, sheep, and cattle. The mild climate of the islands, combined with the lack of competitors or predators, led to the successful establishment of large populations of these invasive ungulates. The presence of these species is considered one of the primary factors underlying the alteration and degradation of native plant communities and habitats in the Hawaiian islands.

Dry grasslands and shrublands are exposed to both direct and indirect negative impacts of invasive ungulates. This includes the destruction of vegetative cover, trampling of plants and seedlings, direct consumption of vegetation, soil disturbance, dispersal of nonnative plant seeds, and creation of open disturbed areas conducive to further invasion by invasive plant species. All of these impacts lead to the subsequent conversion of a plant community dominated by native species to one dominated by invasive species, thus increasing the area of introduced grasslands and shrublands. In addition, because ungulates inhabit terrain that is often steep and remote, foraging and trampling contributes to severe erosion of watersheds and degradation of streams (Cuddihy and Stone, 1990).

Invasive plants

Native vegetation on all of the main Hawaiian islands has undergone extreme alteration because of past and present land management practices, the deliberate introduction of nonnative plants and animals, and agricultural development (Cuddihy and Stone, 1990). After human contact with Hawai'i, over 800 plant taxa have been introduced from elsewhere, and nearly 100 of these have become pests (Smith, 1985; Cuddihy and Stone, 1990). Some of the nonnative plants were brought to Hawai'i by various groups of people, including ranchers that intentionally introduced pasture grasses and other nonnative plants for agriculture, and sometimes inadvertently introduced weeds as well. These pasture grasses and invasive weeds often took over and dominated native dry grasslands and shrublands. As a result, much of the native plant species biodiversity was lost, while invasive plant species increased (Scott et al., 1986; Cuddihy and Stone, 1990).

Invasive plants can adversely affect microhabitat in dry grasslands and shrublands by modifying availability of light and nutrient cycling processes, altering soil-water regimes, altering fire characteristics of native plant habitat leading to incursions of fire-tolerant nonnative plant species, and outcompeting native plant species. Each of these effects can convert native-dominated plant communities to nonnative plant communities. Additionally, some invasive plants may release chemicals that inhibit growth of other plants (Cuddihy and Stone, 1990; Vitousek, 1992).

Invasive herbivores

The primary invasive herbivores that impact the dry grasslands and shrublands are rats. There are three species of rats, all of which are introduced, in the Hawaiian islands: the Polynesian rat (*Rattus exulans*), black rat (*Rattus rattus*), and Norway rat (*Rattus norvegicus*). Rats are omnivorous and eat almost any type of food (Nelson, 2012). They impact plants by eating fleshy fruits, seeds, flowers, stems, leaves, roots, and other plant parts (Atkinson and Atkinson, 2000), and by stripping bark and cutting small branches (twig cutting) in search of moisture and nutrients, seriously affecting vigor and regeneration (Abe and Umeno, 2011; Nelson, 2012). In the Hawaiian islands, rats may consume as much as 90% of the seeds produced by some native plants, and in some cases prevent regeneration of forest species completely (Cuddihy and Stone, 1990), which can result in the creation of barren areas that allow the spread of introduced grasslands and shrublands.

Fire and drought

Fires inadvertently or intentionally set by the Polynesian settlers probably contributed to the initial decline of native vegetation in the drier plains and foothills. These early settlers practiced slash-and-burn agriculture that created open lowland areas suitable for the opportunistic invasion and colonization of nonnative, fire-adapted grasses (Kirch, 1982; Cuddihy and Stone, 1990). Ranching and the creation of pasture lands in particular created highly fire-prone areas of nonnative grasses and shrubs (D'Antonio and Vitousek, 1992). Although fires were infrequent in mountainous regions, extensive fires have recently occurred in lowland dry areas, leading to grass-fire cycles that convert native dry forest to invasive grassland (D'Antonio and Vitousek, 1992).

Because of the greater frequency, intensity, and duration of fires that have resulted from the human alteration of landscapes and the introduction of nonnative plants, especially grasses, fires are now more destructive to native Hawaiian ecosystems (Brown and Smith, 2000), and a single grass-fueled fire often kills most native plants in the area (D'Antonio and Vitousek, 1992). Fire destroys dormant seeds of these native species, as well as the individual plants and animals themselves, even in steep, inaccessible areas or near streams and ponds. Successive fires remove habitat for native species by altering microclimate conditions, creating conditions more favorable to invasive plants. Invasive grasses (e.g., fountain grass), many of which may be fire-adapted, produce a high fuel load that allow fire to burn areas that would not otherwise burn easily, regenerate quickly after fire, and establish rapidly in burned areas, thus outcompeting native plants and inhibiting their regeneration (Fujioka and Fujii 1980 in Cuddihy and Stone, 1990, Tunison et al., 2002). Native woody plants may recover to some degree, but fire tips the competitive balance toward invasive species (National Park Service 1989 in Cuddihy and Stone, 1990). Due to the seasonal drought conditions in the dry grasslands and shrublands, the risk of fire and its associated impact is exacerbated and considered a significant stressor.

Other stressors

Natural disasters like hurricanes exacerbate the impacts from other threats such as habitat modification and destruction by ungulates and competition with nonnative plants. By destroying vegetation, hurricanes open the forest canopy, thus modifying the availability of light, and create disturbed areas conducive to invasion by nonnative pest species (Asner and Goldstein, 1997;

Harrington et al., 1997). Additionally, changes in environmental conditions that may result from global climate change include increasing temperatures, changing precipitation, and increasing storm intensities. These changes may lead to the loss of native species due to direct physiological stress, the loss or alteration of habitat, or changes in disturbance regimes (e.g., droughts, fire, storms, and hurricanes) (Fortini et al., 2013).

Past land use practices such as agricultural or urban development have resulted in little or no native vegetation below 2000 ft. (600 m) throughout the Hawaiian islands (TNCH, 2007), largely impacting lowland dry grasslands and shrublands. The development of irrigation systems has allowed for areas that were once dry grasslands and shrublands to be converted to farming and ranching lands. Although agriculture has been declining in importance, these large tracts of former agricultural lands are now being converted into residential areas or left fallow (TNCH, 2007). Forests were also converted to grasslands for ranching or grazing cattle (Cuddihy and Stone, 1990). In addition, the population in Hawai'i has increased almost 10% in the past 10 years, further increasing demands on limited land and water resources in the islands (HDBEDT, 2013).

Conservation Efforts

Conservation efforts attempt to provide some relief from stressors. These efforts are implemented by numerous government agencies (federal and State), private organizations, and non-governmental organizations (NGOs). Given that land ownership varies (Fig. 7), many partnerships are formed to collectively manage dry grasslands and shrublands. The goals of management vary by site, but may be to restore existing native dry grassland and shrubland or to restore sites back to dry forest. The following subsections describe some of the conservation efforts related to dry grasslands and shrublands, however they do not encompass all that exist (Table 4).

Federal

There are a number of federal agencies that are involved in the management of dry grasslands and shrublands (Table 4). Pōhakuloa Training Area (PTA) is a vitally important training area to the U.S. military in the Pacific and also home to large tracts of tropical subalpine dryland ecosystems and dozens of threatened and endangered plants, birds, and bats. Large-scale fences at PTA span > 37,298 ac (15,094 ha) which include montane-subalpine dry grasslands and shrublands (U.S. Army Garrison, 2016). The Kahuku Unit of Hawai'i Volcanoes National Park (HVNP) expands across lava fields, pastures, forests, shrubland and mesic, subalpine, alpine, and desert environments (National Park Service, 2015). Much of Haleakalā National Park contains montane-subalpine

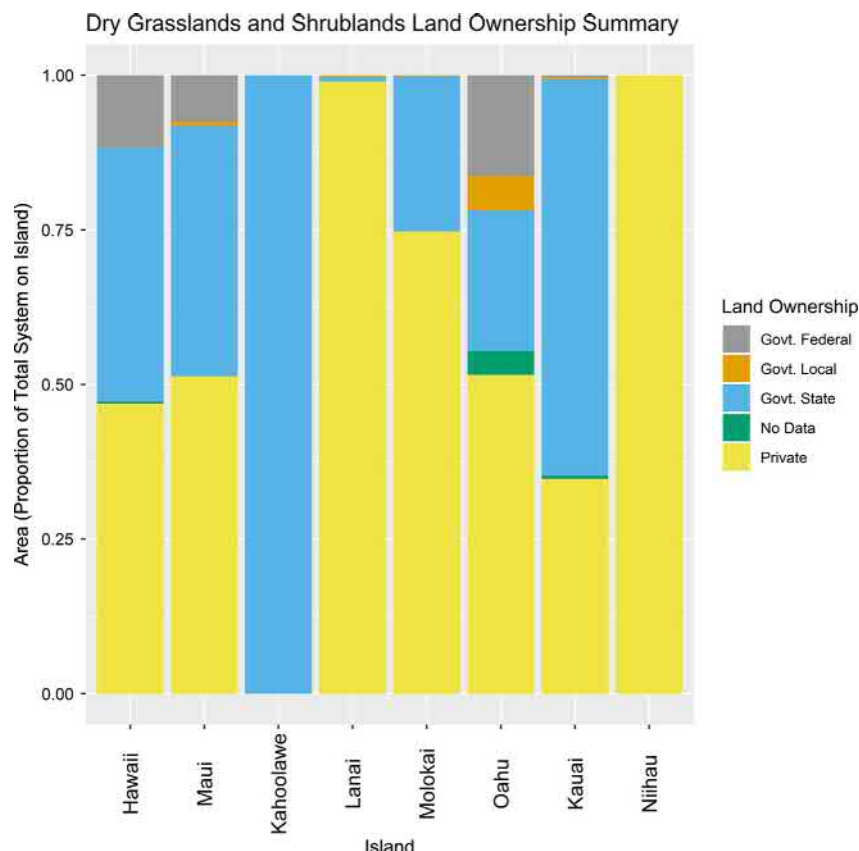


Fig. 7 Land ownership of dry grasslands and shrublands in the main Hawaiian islands.

Table 4 Examples of conservation efforts in dry grasslands and shrublands.

<i>Organization/agency name</i>	<i>Location, island</i>	<i>Organization type</i>	<i>Conservation efforts</i>	<i>Target stressor(s)</i>
U.S. Department of Defense	Pōhakuloa Training Area, Hawai'i	Federal	Fencing, invasive plant and ungulate management, fire prevention, propagation and outplanting	Invasive species, fire
National Park Service	Hawai'i Volcanoes National Park, Hawai'i	Federal	Fencing, ungulate control, restoration	Invasive species
National Park Service	Haleakalā National Park, Maui	Federal	Fencing, ungulate removal, invasive predator and plant control, surveys for listed species	Invasive species
U.S. Fish and Wildlife Service	Kalaeloa Unit of Pearl Harbor National Wildlife Refuge, O'ahu	Federal	Invasive plant control, fire break management, outplanting	Invasive species, Fire
Hawai'i Department of Land and Natural Resources	Mauna Kea Forest Reserve, Hawai'i	State	Fencing, invasive plant and ungulate control, fire control, surveys and monitoring, reforestation	Invasive species, fire
Department of Hawaiian Home Lands	Āina Mauna Legacy Program, Hawai'i	State	Invasive species removal, reforestation and restoration, conserving endangered species, providing educational and cultural opportunities	Invasive species
Kamehameha Schools	Lupea, Hawai'i	Private	Fencing, invasive species control, outplanting and restoration	Invasive species
Kamehameha Schools	Keauhou, Ka'ū, Hawai'i	Private	Fencing, ungulate removal, invasive plant and predator control, fire management, outplanting and restoration	Invasive species, fire
Pūlama Lāna'i	Lāna'i	Private	Invasive plant and animal control, fire management, propagation and outplanting	Invasive species, Fire
Hawai'i Association of Watershed Partnerships—Mauna Kea Watershed Alliance	Mauna Kea Forest Reserve, Hawai'i	Multi-agency Partnership	Fencing, invasive plant and ungulate control, fire control, surveys and monitoring, reforestation	Invasive species, fire
Hawai'i Association of Watershed Partnerships – Wai'anae Mountains Watershed Partnership	Mākaha Valley, O'ahu	Multi-agency Partnership	Invasive plant and predator control, fire management	Invasive species, fire
Invasive Species Committees – O'ahu Invasive Species Committee	Various locations, O'ahu	Multi-agency Partnership	Invasive plant and predator control, fire management	Invasive species, fire
Papahānaumokuākea Marine National Monument	Nihoa and Mokumanamana (Necker)	Multi-agency Partnership	Invasive plant management, research and monitoring	Invasive species

native dry grasslands and shrublands, as well as alpine shrublands. Restoration in the Nu'u parcel on the leeward slope of Haleakalā includes removal of feral ungulates and the construction of an ungulate-proof fence enclosing approximately 2115 ac (856 ha) ([Haleakalā National Park, 2016](#)). On O'ahu, the Kalaeloa Unit of the Pearl Harbor National Wildlife Refuge contains introduced dry grasslands in the lowlands along the coast. Weed control is often implemented for invasive grasses, as well as outplanting of native dryland shrub species like 'ilima.

State

The State of Hawai'i Department of Land and Natural Resources (DLNR) lands are made up of forest reserves, wildlife sanctuaries, Natural Area Reserves (NAR), State recreation areas, and a research reserve. The State conducts some conservation management actions on these lands and provides access to others who are conducting such activities. On the island of Hawai'i, the Mauna Kea Forest Reserve consists of dry subalpine and alpine communities and is just one example of an area where the State implements conservation efforts for this ecotype ([HDLNR, 2015](#)).

The Department of Hawaiian Home Lands (DHHL) was created by the Hawai'i State Legislature in 1960 and is governed by the Hawaiian Homes Commission Act of 1920. The act set aside a land trust for native Hawaiians to maintain their traditional ties to the land. DHHL views part of its responsibility as a landowner to manage and protect native lands "to support both cultural and resource management activities and create homesteading opportunities for the future" ([DHHL, 2009](#)). Thus, the 'Āina Mauna Legacy Program was created to protect habitat on Mauna Kea on the island of Hawai'i. The program specifically includes the lands of Humu'ula and Pi'ihonua, which contain tracts of dry grassland and shrubland ([DHHL, 2009](#)).

Private

Kamehameha Schools (KS) is the largest private landowner in the State of Hawai'i with landholdings of over 365,000 ac (147,710 ha). Approximately 99% of this land is designated for agricultural (176,890 ac) or conservation (181,675 ac) purposes. In addition, roughly 51,000 ac (20,640 ha) or 14% is classified as dry grassland and shrubland with the majority located in the Kona district and Keauhou, in the Ka'u district of the island of Hawai'i.

On the Kona side of the island of Hawai'i, KS implements active restoration and management of dry grasslands and shrublands in Lupea through collaboration with the Three Mountain Alliance and Hawaiian Silversword Foundation (*Kamehameha Schools, 2011*). In Keauhou, Ka'u, a Safe Harbor Agreement between KS, DLNR, and the U.S. Fish and Wildlife Service (USFWS) was signed in June of 2018. The total area covered by the agreement is 32,207 ac (13,034 ha) which includes dry grasslands and shrublands. The 50-year agreement will contribute to the recovery of 32 endangered species (17 endangered plants, 7 endangered animals, and one threatened animal). The agreement is part of an ongoing watershed partnership effort within the State of Hawai'i managed by the Three Mountain Alliance Watershed Partnership (*TMA, 2007*).

The island of Lāna'i is almost entirely under private ownership but does have conservation partnerships with the USFWS, the state of Hawai'i, and The Nature Conservancy. Currently the land manager, Pulamā Lāna'i, is implementing actions that benefit dry grassland and shrubland such as protecting the dry habitat within a designated Lowland Ecosystem Area totaling at least 2000 ac (809 ha) in size (*Lāna'i Resorts et al., 2015*).

Multiple agency partnerships

The Hawai'i Association of Watershed Partnerships (HAWP) are voluntary alliances of public and private landowners committed to protecting over 2 million ac (809,371 ha) of the most important watershed lands in Hawai'i. Individual watershed partnerships have been established on five islands (island of Hawai'i, Maui, Moloka'i, O'ahu, and Kaua'i) and jointly form HAWP, to support statewide needs. A number of watershed partnerships work to conserve dry grasslands and shrublands, some of which are included in *Table 4*.

Invasive species committees (ISCs) are voluntary partnerships of government, private and non-profit organizations, and concerned individuals working to address invasive species issues in Hawai'i. These committees have been formed on individual islands (island of Hawai'i/Big Island [BIISC], Maui [MISC], Moloka'i [MoMISC], O'ahu [OISC], Kaua'i [KISC]) and focus on the specific issues of their island. The overall goal of the ISCs is to "prevent, eradicate, or control priority incipient plant and animal species that threaten Hawai'i's most intact federal, state, and private conservation lands" (*HDLNR, 2015*). A typical approach taken by the ISCs is to identify the priority invasive species and then implement control and/or eradication.

Nihoa and Mokumanamana are located within the Papahānaumokuākea Marine National Monument (PMNM), which is managed by the following co-trustees: DLNR, USFWS, National Oceanic and Atmospheric Administration (NOAA), and Office of Hawaiian Affairs (OHA). Together, the co-trustees manage the dry grasslands, dry shrublands, and dry cliffs on these two islands. Access into the monument is very limited and visits to Nihoa or Mokumanamana are typically only for research, monitoring, or cultural purposes. In addition, both of these islands are designated as critical habitat for federally listed endangered plants (*HDLNR, 2015*).

Laws and regulations**Endangered Species Act**

The Endangered Species Act of 1973 (ESA) aims to provide a framework to conserve and protect endangered and threatened species and their habitats. As habitat loss is the primary threat to most imperiled species, the ESA allowed the U.S. Fish and Wildlife Service (USFWS) and National Marine Fisheries Service (NMFS) to designate specific areas as protected critical habitat zones. In 1978, Congress amended the law to make critical habitat designation a mandatory requirement for all threatened and endangered species listed under the Act.

Approximately 80,800 ac (32,700 ha) or 11% of dry grasslands and shrublands have been designated as federal critical habitat in the main Hawaiian islands (*Fig. 8*). The majority of designated critical habitat that is also classified as dry grasslands and shrublands is located on the island of Hawai'i at 53,408 ac (21,613 ha) (*Fig. 8*). Species listed under the Federal Endangered Species Act are automatically added to the State of Hawai'i list of endangered species, and are thus also protected by State regulations.

Biosecurity and invasive species control

As described above, invasive species are a major stressor to dry grasslands and shrublands. In addition to implementing invasive species control, biosecurity measures that prevent the introduction of invasive species are critical. *Table 5* provides a list of laws and regulations that address the issue of invasive species in Hawai'i. These laws and regulations not only benefit this ecotype, but all other ecotypes impacted by invasive species in Hawai'i.

Protected areas

Approximately 45,533 ac (18,426 ha) or 6% of dry grasslands and shrublands are protected in reserve areas in the main Hawaiian islands (*Fig. 9*). Reserve areas are defined as areas that are designated as parks or reserves such as a national park, national wildlife refuge, or NAR (*Reeves, 2018*). In the main Hawaiian islands, the island of Hawai'i has the most dry grasslands and shrublands in reserve areas with 33,641 ac (13,614 ha) or 7% of the total ecotype on the island (*Fig. 9*). This is followed by Maui with 7266 ac (2940 ha) or 11% of the islands ecotype (*Fig. 9*). In regards to the NWHI, Nihoa and Mokumanamana are protected within the PMNM.

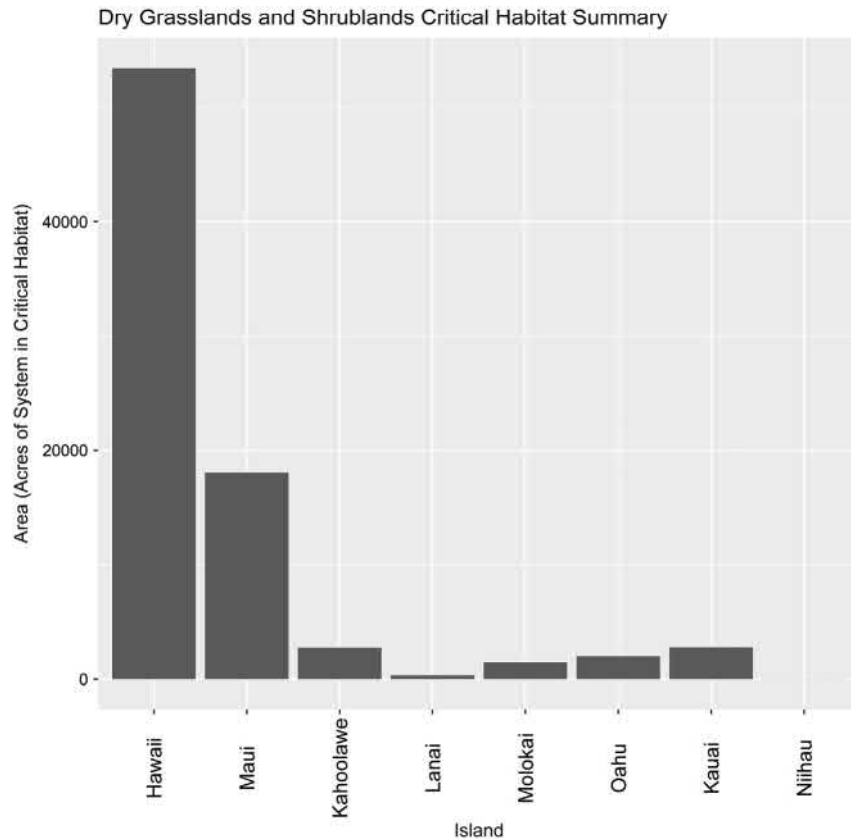


Fig. 8 Federally designated critical habitat in dry grasslands and shrublands across the main Hawaiian islands.

Viability of Current Dry Grasslands and Shrublands

Before the arrival of humans, dry grasslands and shrublands were distributed widely and covered relatively large areas in the main Hawaiian islands. These characteristics resulted in the ecotype as a whole being resilient and redundant. However, the features of this ecotype were not very widely distributed and biodiversity was low to moderate, which gave it low representation. Currently, the viability of the native sub-types have mostly decreased due to the stressors described above while introduced sub-types have been well established and continue to increase.

Lowland native dry grasslands and shrublands have reduced in size and distribution, and therefore have reduced in redundancy. The overall quality of this sub-type has also declined, resulting in a decrease in resiliency. Most of this reduction is a result of the spread of introduced dry grasslands and shrublands occurring mostly in the lowlands. Fragmentation from other stressors (as described above) has also led to a decrease in genetic range of variability and species diversity, and therefore a decrease in representation. This decrease in redundancy, resiliency, and representation has also occurred for dry cliff and montane-subalpine native dry grasslands and shrublands, but to a lesser extent.

Alpine native dry shrublands historically occurred only on Maui, and now occur on the island of Hawai'i as well (Figs. 1–4). This increased distribution has slightly increased its redundancy and representation compared to pre-human contact. However, as the stressors described above impact this sub-type, the size and distribution of this sub-type is decreasing, thus its redundancy and representation is also decreasing. In addition, the quality of this sub-type has also decreased due to the impact of human-caused stressors, which has reduced its resiliency.

Introduced grasslands and shrublands currently have the largest size and distribution among all of the sub-types. The stressors described above have resulted in the establishment and spread of these introduced sub-types throughout the main Hawaiian islands. Their large size and distribution throughout the range of islands has resulted in introduced grasslands and shrublands having the highest level of redundancy, resiliency, and representation among Hawai'i's dry grasslands and shrublands (Table 6).

Future Scenarios

The condition of dry grasslands and shrublands in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are as follows:

Table 5 Laws and regulations that address invasive species in Hawai'i.

<i>Title</i>	<i>Year implemented</i>	<i>Authority</i>	<i>Intent/purpose</i>
50 CFR 16	1974	Federal	Implements the Lacey Act (18 USC 42), which prohibits importation of injurious species
Convention on International Trade in Endangered Species	1975	International	Ensures that international trade in specimens of wild animals and plants does not threaten the survival of the species in the wild
Executive Order 11987	1977	Federal	Charges executive agencies with restricting the introduction of exotic species into the natural ecosystems on federal lands; and encourages States to do the same
Hawai'i Administrative Rules, Title 4, Subtitle 6, Chapters 68 and 70	1981	Hawai'i (Department of Agriculture)	Rules/amendments for noxious weeds, plant and non-domestic animal quarantine, plant import, and bromeliad import
Executive Order 13112	1999	Federal	Requires that a Council of Departments dealing with invasive species be created to prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause
HRS 194-2	2002	Hawai'i (Department of Land and Natural Resources)	Establishes Hawaii Invasive Species Council (HISC)
Act 85	2003	Hawai'i (HISC)	Conveys statutory authority to HISC to continue to coordinate approaches among the various State and Federal initiatives for the prevention and control of invasive species
Act 36 (2011) HRS 150A-5.3	2011	Hawai'i (DOA)	Imposes a fee for the inspection, quarantine, and eradication of invasive species contained in any freight brought into the State
HB 1568	2011	Hawai'i (DOA)	Requires commercial harbors and airports in Hawai'i to provide biosecurity and to facilitate cargo inspections
Executive Order 13751	2016	Federal	To prevent the introduction of invasive species and provide for their control, and to minimize the economic, plant, animal, ecological, and human health impacts that invasive species cause (amends EO 13112)
7 CFR 360.200	2018	Federal	Designates certain plants as noxious weeds

1. Conservation Values: stakeholder involvement and public opinion determine the formulation, implementation and funding of natural resource conservation within laws and development plans.
2. Laws and Biosecurity: national, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented. (e.g. hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.).
3. Development or Conservation Planning: national, state, county, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

These conservation management parameters are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The year 2035 is the extent of the "foreseeable future" (Miller, 2018), and is based on the projected divergence of IPCC Representative Concentration Pathway (RCP) climate change scenarios (van Vuren et al., 2011a,b).

The four foreseeable future scenarios being considered by federal, State, private and multiple agency partners are:

Future Scenario One, Status Quo—the most likely foreseeable future; no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues through the foreseeable future.

Future Scenario Two—a slight increase in natural resource conservation in the CMPs marginally improves conservation management.

Future Scenario Three—a slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management.

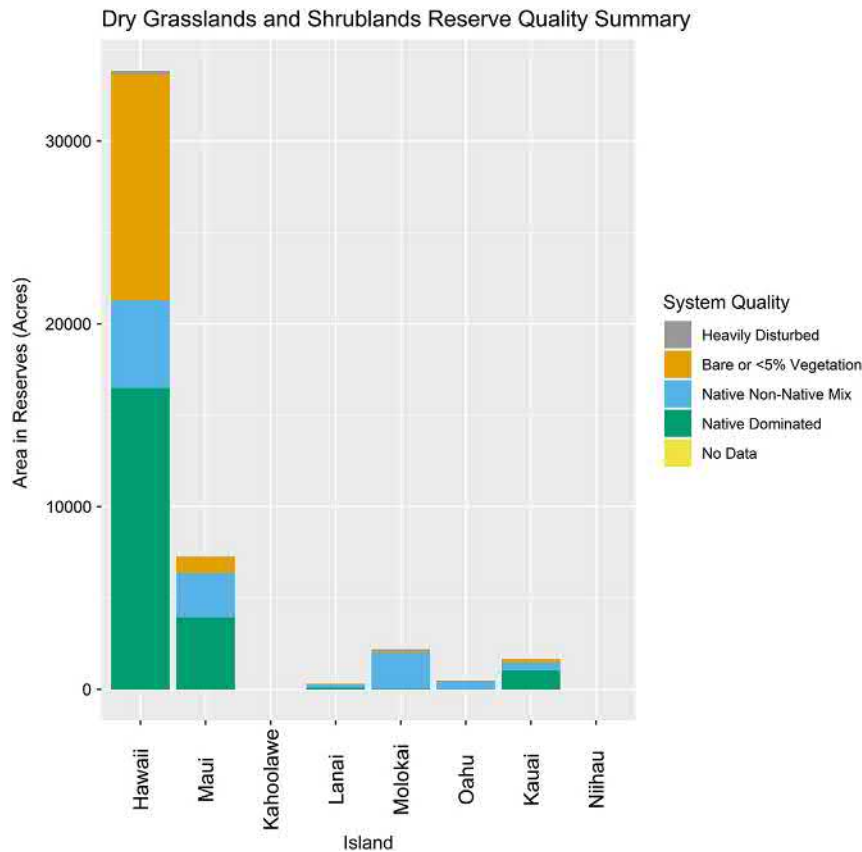


Fig. 9 Quality of dry grasslands and shrublands designated as reserve areas in the main Hawaiian islands.

Table 6 Summary of change in dry grassland and shrubland viability from pre-human to current.

<i>Sub-type</i>	<i>Redundancy</i>	<i>Resiliency</i>	<i>Representation</i>
Dry cliff	Decrease	Decrease	Decrease
Lowland native dry grassland	Decrease	Decrease	Decrease
Lowland native dry shrubland	Decrease	Decrease	Decrease
Montane-subalpine native dry grassland	Decrease	Decrease	Decrease
Montane-subalpine native dry shrubland	Decrease	Decrease	Decrease
Alpine native dry shrubland	Decrease	Decrease	Decrease
Introduced dry grassland	Increase	Increase	Increase
Introduced dry shrubland	Increase	Increase	Increase

Future Scenario Four—a moderate to high increase in conservation actions in the CMPs substantially improves conservation management.

We analyzed the future viability of the dry grasslands and shrublands in Hawai'i under these four future scenarios using a series of analyses of land cover maps and projected changes over time. The future condition of dry grasslands and shrublands in Scenario One, the status quo, was characterized from an assessment of change over time in dry grassland and shrubland land cover obtained from existing land cover maps (Amidon and Reeves, 2018). Based on these land cover maps, an annual rate of change was estimated, and a projected change (in acres/ha) was calculated for the year 2035. The resulting information on changes in land cover by 2035, as derived from existing land cover change estimates, is the extent of dry grasslands and shrublands that is expected in the foreseeable future under Scenario One, the status quo, where conservation efforts remain unchanged and the current rate of change in land cover is also unchanged.

The future conditions of dry grasslands and shrublands for Scenarios Two, Three, and Four cannot be quantitatively (acres/ha) estimated. However, the Scenario One estimate can provide a “baseline” for a qualitative characterization of changes in the future condition of dry grasslands and shrublands under Scenarios Two, Three, and Four. Changes in human population are captured only by the changes in the “developed” land cover footprint derived from land cover map analysis (Amidon and Reeves, 2018). Impacts

from other sources of human activities or human-caused stressors (e.g., plant and animal diseases, wildfires, invasive species, etc.) are not well characterized in the land cover changes, but significantly contribute to increases in the land cover area dominated by non-native vegetation. For an assessment of island-by-island changes in human population, see [Amidon and Reeves \(2018\)](#).

Also, note that island-wide implementation of the CMPs is unlikely to have a significant effect on climate-related stressors (temperature, precipitation, and severe weather) resulting from global warming by 2035. This lack of CMP climate effects is due to the global lag in climate response to changes in greenhouse gas emissions which occurs on the order of centuries rather than years ([Solomon et al., 2009](#); [Gillett et al., 2011](#)). Evidence of climate effects is also confounded by the large annual variation in the Pacific islands climate parameters, which is much greater than projected climate change by 2035. Although impacts from climate-related stressors do not change across the four scenarios, they were included in this analysis because of their overall magnitude of potential importance to future viability.

Future Scenario One—Status Quo

Scenario One is considered the most likely future scenario, and serves as a “baseline” for comparing among the four future scenarios. There is no change in the implementation of the three CMPs between 2018 and 2035. A continuing current rate of change in land cover through this foreseeable future results in a slow but continuous change in the dry grassland and shrubland sub-types ([Table 7](#)).

In Scenario One, the viability of all native sub-types of grasslands and shrublands (lowland, montane-subalpine, alpine) are predicted to decrease from their current state ([Table 8](#)). Since these sub-types are currently confined to the leeward sides of islands or the dry, high elevation areas on Maui and the island of Hawai'i, we predict their abundance will continue to decline in area (redundancy and representation). Human-caused stressors will increase overall ([Table 7](#)) and continue to reduce native composition. With the increased potential of invasive species, the ecological function of the native sub-types is expected to decrease due to the ability of invasive species to outcompete native species for water and space. As a result, native biodiversity in these sub-types including dry cliffs will also decrease ([Table 8](#)).

Table 7 Responses of dry grassland and shrubland stressors in foreseeable future scenarios.

Conservation management parameters (CMPs)				
Conservation values	Stakeholder involvement and public opinion influence the formulation, implementation, and funding of natural resource conservation and biosecurity (NRC/B) within laws and development or conservation plans			
Laws and biosecurity	National, state, county, and city laws and regulations are the means by which NRC/B are supported and implemented			
Planning for development or conservation	National, state, county, city, and private development plans or conservation plans define actions that result in losses or gains in NRC/B (impacts realized at implementation)			
Foreseeable future scenarios and the resulting dry grassland and shrubland habitat conditions				
Use Foreseeable Future Scenario One as a “baseline” to characterize changes in <i>Conservation Actions</i> and <i>Habitat Conditions</i> in Future Scenarios Two, Three and Four	Scenario One: <i>CMPs</i> : unchanged in support for NRC/B <i>Conservation actions</i> : no change; current rate of land cover change continues through the foreseeable future <i>Habitat condition</i> : habitat area, quality, and sustainability slowly decrease through the foreseeable future	Scenario Two: <i>CMPs</i> : small increase in support for NRC/B <i>Conservation actions</i> : marginal increase <i>Habitat condition</i> : habitat area is unchanged through the foreseeable future; habitat quality and sustainability are slightly enhanced through the foreseeable future	Scenario Three: <i>CMPs</i> : small to moderate decrease in support for NRC/B <i>Conservation actions</i> : substantial decrease <i>Habitat condition</i> : urban and agricultural uses are prioritized over conservation; habitat area, quality, and sustainability substantially decrease through the foreseeable future	Scenario Four: <i>CMPs</i> : moderate to high increase in support for NRC/B <i>Conservation actions</i> : substantial increase <i>Habitat condition</i> : robust, sustained effort to restore, manage, and expand conservation; habitat area, quality, and sustainability substantially increase through the foreseeable future
Stressors	Responses of dry grassland and shrubland stressors			
Development	Small to moderate increase	No change (redevelop)	Moderate to high increase	Small to moderate decrease
Invasive species	Small increase	Small increase	Higher increase	Small decrease
Plant diseases	Small increase	Small increase	Higher increase	No change to small decrease
Fire	Small increase	Small increase	Higher increase	No change or small increase
Climate				
Temperature	Small to moderate increase	Small to moderate increase	Small to moderate increase	Small to moderate increase
Precipitation	Small decrease	Small decrease	Small decrease	Small decrease
Storms	Small increase	Small increase	Small increase	Small increase

Table 8 Summary of change in dry grassland and shrubland viability in foreseeable future scenarios.

<i>Sub-type</i>	<i>Scenario One: status quo</i>	<i>Scenario Two: slightly improved</i>	<i>Scenario Three: substantially decreased</i>	<i>Scenario Four: substantially improved</i>
Dry cliff	Decrease	Slightly decrease	Severely decrease	Increase
Lowland native dry grassland	Decrease	Slightly decrease	Severely decrease	Increase
Lowland native dry shrubland	Decrease	Slightly decrease	Severely decrease	Increase
Montane-subalpine native dry grassland	Decrease	Slightly decrease	Severely decrease	Increase
Montane-subalpine native dry shrubland	Decrease	Slightly decrease	Severely decrease	Increase
Alpine native dry shrubland	Decrease	Slightly decrease	Severely decrease	Increase
Introduced dry grassland	Slightly increase	Slightly increase	Increase	Decrease
Introduced dry shrubland	Slightly increase	Slightly increase	Increase	Decrease

On the other hand, viability of introduced grassland and shrubland sub-types is expected to slightly increase (Table 8). The increase in introduced invasive species will add to the relative size and distribution of these sub-types. In addition, wildfires are expected to exacerbate these effects as introduced grasses and shrubs tend to recover quicker than native grasses and shrubs, therefore further contributing to a decrease in redundancy and representation of native sub-types. These stressors will essentially result in the continuation of introduced grasslands and shrublands replacing native sub-types and expanding in range.

Future Scenario Two—Slight Increase in CMPs Marginally Improves Conservation Management

In Scenario Two, conservation agencies and stakeholders work with increased but limited resources to slow or stop the degradation of landscape areas. Scenario Two is essentially 'status quo' with minor improvements in the three CMPs. The anticipated changes, under Scenario Two, for each of important stressor are given in Table 7.

In this scenario, native sub-types of dry grasslands and shrublands (lowland, montane-subalpine, alpine), and dry cliff are predicted to slightly decrease in viability from their current state (Table 8). This slight decrease will continue from its current state due to the difficulties of restoring these dry areas. Although there will be minor improvements in the three CMPs, restoration efforts are expected to be negligible as the response time of native vegetation is slow (i.e., reintroduction, augmentation). As a result, we predict the size and distribution of native sub-types will continue to decline in area, thus reducing its viability, but at a slower rate than in Scenario One.

The marginal improvements to conservation management will still result in slight increases to human-caused stressors, except for development (Table 7), as they did in Scenario One. For introduced grasslands and shrublands, the same effects of invasive species and wildfires will result in a slight increase in viability (redundancy, resiliency, and representation), but slightly less than in Scenario One. In addition, this scenario is expected to have the second highest likelihood of occurrence.

Future Scenario Three—Small to Moderate Decrease in CMPs Substantially Decreases Conservation Management

In Scenario Three, all natural resource management actions in the CMPs are set aside in deference to land use for economic development. With extensive localized management, some native species may persist in park-like settings or in areas where land development is not possible. This scenario has substantial declines in natural resource conservation within the three CMPs. An increasing human population is supported in its use of land for economic development over the conservation of native habitats. Areas that cannot support development become the only areas of free-living native species. The anticipated changes, under Scenario Three, for each of stressors are given in Table 7.

Due to the limited range (leeward or dry area, and high elevation slopes on Maui and the island of Hawai'i) of native dry grasslands and shrublands, substantial declines in the three CMPs will lead to high levels of degradation and fragmentation. This will result in a decline in the size and distribution of native sub-types at a much faster rate than in Scenario One. The higher increase in invasive species and wildfires will likely significantly alter their ecological structure and function, leading to their severe decrease in viability (Table 8).

The cumulative impacts of these stressors will also lead to an increase in the viability of introduced dry grasslands and shrublands (Table 8). Introduced grasslands and shrublands will continue to replace and outcompete native sub-types and generally expand in range, but at a much faster rate than in Scenario One. Additionally, the increase in development will reduce the overall size and distribution of all sub-types. This scenario will result in the highest impact to resiliency, redundancy, and representation of all future scenarios for all sub-types. However, this scenario, along with Scenario Four has the lowest likelihood of occurring in the foreseeable future.

Future Scenario Four—Moderate to High Increase in CMPs Substantially Improves Conservation Management

In this scenario, a substantial emphasis on natural resource conservation is present in the three CMPs, reflecting increased societal concern for declines in natural habitats and biodiversity. Active and well-supported natural resource management begins to restore these habitats and ecosystems and expand their landscape areas. The anticipated changes, under Scenario Four, for each of the stressors are given in [Table 7](#).

As conservation actions are identified, prioritized, and expanded, the size and abundance of native dry grassland and shrubland sub-types (including dry cliffs) will gradually increase over time, thus increasing its redundancy and resiliency. As stressors are reduced and managed, the ecological structure and function of native sub-types will be maintained in existing areas and increase as they expand. This will contribute to an overall increase in native biodiversity, and increase in representation. Thus, the overall viability of native dry grasslands and shrublands is expected to increase.

Scenario Four is the only future scenario that introduced grasslands and shrublands are predicted to decrease in viability ([Table 8](#)). The decrease in stressors and substantial increase in active restoration, will allow native sub-types to replace introduced grasslands and shrublands, resulting in an overall reduction in the size and distribution of introduced sub-types. In addition, development is expected to decrease, thus opening the potential for more restoration of native dry grassland and shrubland. However, like Scenario Three, this scenario has the lowest likelihood of occurring in the foreseeable future.

Conclusion

Conservation efforts by federal, State, private and multiple agency partnerships have been beneficial in helping to conserve and protect the remaining dry grasslands and shrublands in Hawai'i and the NWHI. While these efforts have helped to recover some of this ecotype through a combination of restoring back to native-dominated dry grasslands and shrublands and dry forests, more collaborative actions are likely needed to increase protection.

The primary stressors impacting dry grasslands and shrublands include habitat destruction and modification by invasive species (ungulates, plants, herbivores), and fire and drought. Despite protected areas and active management by numerous conservation groups to target these stressors, they are expected to continue or increase in magnitude and intensity in the future. It is likely that without continued or increased active management, native dry grasslands and shrublands will continue to be degraded or destroyed in the future while introduced dry grasslands and shrublands will likely stay stable or increase.

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Hawai'i Wet Grassland and Shrubland

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Published by Elsevier Inc.

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Abstract

This article provides an overview of the wet grassland and shrubland biome of the Hawaiian Islands, and includes an assessment of its current status, stressors, and future viability. Wet grassland and shrubland in Hawai'i generally have high rainfall and occur on the wet, windward sides of the main Hawaiian Islands in montane and lowland zones (Gagné and Cuddihy, 1990). Native wet grassland and shrubland consists of wet sedgelands and grasslands, dominated by different *Carex* species and native grasses, and native shrubland that occurs primarily on ridge crests and steep cliffs. The main stressors to this

biome are introduced ungulates (goats, pigs, and sheep), invasive plants, and natural disasters (i.e., hurricanes or landslide). With the introduction of ungulates and invasive plants in the 19th and 20th centuries some native wet grassland and shrubland biome became degraded, and communities of introduced grasses and shrubs became established. Conservation management to protect native grassland and shrubland include weed control, fencing, and ungulate removal, and depends on combined efforts of State, Federal, and multiagency organizations and nonprofit organizations and the voluntary support of private landowners. We base our assessment of wet grassland and shrubland viability in the future on the concepts of representation, redundancy, and resiliency, which we define in this article. We examine condition of wet grassland and shrubland biome in the foreseeable future (to year 2035) based on potential changes in three conservation management parameters: funding and public support for conservation management; conservation and biosecurity-related laws; and State/civic planning for conservation planning and land use and development.

Introduction

This article provides an overview of the wet grassland and shrubland biome in the Hawaiian Islands, the ecological factors that have influenced this biome over time and that will into the future, and a status assessment of wet grassland and shrubland that includes current status, stressors, and future viability. Grassland is defined as an area where vegetation is dominated by grass (Poaceae), sedge (Cyperaceae) and/or rush (Juncaceae) species. Shrubland is defined as an area where vegetation is dominated by woody plants generally less than 3 meters (m) in height. The Hawaiian archipelago is the most isolated landmass in the world. Because of this isolation, species were able to fill empty niches not already occupied by other species, which led to speciation (adaptive radiation) and a high rate of species endemism. Approximately 90% of the species in Hawai'i before arrival of humans were endemic (Cuddihy and Stone, 1990). The Hawaiian Islands in addition have remarkable differences in climate, precipitation, and hydrology over very short distances that contribute a wide diversity of biomes including alpine, desert, cloud forest, mesic and dryland forest, and many others (Gagné and Cuddihy, 1990). Invasive species introduced to Hawai'i are an important stressor on Hawai'i's native biomes, including invasive ungulates that cause damage to native plant communities by eating and trampling native plants, and invasive plants that out compete native plants. Hawaiian biomes sustain through redundancy, resiliency, and representation. Redundancy is a biome's ability to withstand a catastrophic event (e.g., hurricanes, catastrophic fire, earthquakes, volcanic eruptions, etc.) through multiple, distributed populations across the landscape (Smith et al., 2018). Resiliency is a biome's ability to withstand environmental stochasticity (random change in environmental conditions) and is related to the growth rate and size of species' populations (Smith et al., 2018). Representation is a biome's ability to adapt to a changing environment over time due to genetic and species diversity and amount of environmental variation within the biome (Smith et al., 2018). The condition of Hawai'i wet grassland and shrubland in the foreseeable future (to year 2035) is based on potential changes in conservation management parameters including conservation values, laws and biosecurity, and land development or conservation planning. These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out and are critical factors that drive the direction and magnitude of natural resource conservation in Hawai'i for in the foreseeable future.

Climate, Hydrology, and Soils

The entire Hawaiian archipelago consists of some 132 islands, including eight larger, younger islands, the "main islands" of Hawai'i, Maui, Kaho'olawe, Moloka'i, Lāna'i, O'ahu, Kaua'i, and Ni'ihau. These main islands are where the Hawai'i wet grassland and shrubland biome occurs. Climate in the Hawaiian archipelago is characterized by mild and equable temperatures year-round, low to moderate humidity, persistence of northeasterly trade winds, and for the main islands, remarkable differences in rainfall within short distances (Wagner et al., 1990). Most areas in the Hawaiian archipelago experience only two seasons. Warmer and drier "summer" weather occurs between about May and September, when the sun is more nearly overhead and the trade winds most persistent. Slightly cooler and wetter "winter" weather occurs between about October and April, when the sun is in the south and the trade winds are often interrupted by other winds and by intervals of widespread cloud cover and rainfall (Wagner et al., 1990). Depending upon their elevation, the mountains of the main Hawaiian Islands obstruct, deflect, and accelerate the flow of air, and due to a low inversion layer and moisture-laden trade winds, create a rainfall pattern known as the orographic effect that produces predictable and substantial precipitation on several of the main Hawaiian Islands. During the daytime and summer months, the tops of the higher Hawaiian mountains are almost constantly obscured by a band of clouds produced in this fashion (Wagner et al., 1990). In addition to rainfall, the primary factor driving the complexity and diversity of hydrological conditions observed in Hawai'i is the highly permeable nature of the islands' volcanic substrates, an attribute particularly prevalent on the younger islands of Hawai'i and Maui (Juvik and Juvik, 1998). Substrate permeability varies considerably and in some rift zones of the mountains of the main islands, very hard, dense, and highly impermeable dike rock formations capture and hold large volumes of groundwater. This trapped groundwater slowly percolates through the rock horizontally toward areas of greater permeability including geologic faults and down-thrusts, or where rivers have carved channels through the dike formations (Carlquist, 1992; Polhemus, 2007). This process often create conditions where wet grassland occurs. Hawai'i soils can be divided into three broad classes: (a) undeveloped or geomorphologically recent soil substrates, (b) well-developed soils in humid climates, and

(c) well-developed soils in seasonal or dry climates (Mueller-Dombois and Fosberg, 1998). Substrates for Hawai'i wet grassland and shrubland vary from very weathered soils on older islands to rocky substrates on recent lava flows on younger islands.

Physical Characteristics and Vegetation Composition

Native plants of wet grassland and shrubland are long growing and able to recolonize areas after disturbance from stochastic events, but are not able to outcompete many species of invasive plants (Gagné and Cuddihy, 1990). Introduced grasses and shrubs by contrast are disturbance adapted, produce copious numbers of seeds and many introduced grasses spread by rhizomes (underground stems). Because of these characteristics introduced grasses and shrubs rapidly invade disturbed areas of native vegetation and intrude within native plant communities. Hawai'i wet grassland and shrubland is comprised of four community subtypes: native wet sedge and grassland, native wet cliff and ridge crest shrubland, introduced grassland, and introduced evergreen shrubland. At a finer scale, these four subtypes are further differentiated into their constituent plant communities, based on dominant plant species or assemblages of cooccurring species present, and described below.

Native Wet Sedge and Grassland

Eragrostis lowland wet grassland: This plant community occurs below the summit crest of the Ko'olau Mountains on O'ahu, and on Moloka'i. This grassland may consist solely of *Eragrostis variabilis* (kāwelu) on sheer cliffs or on weathered basalt in steep drainages but native shrubs are often interspersed (Gagné and Cuddihy, 1990).

'Uki (Cladium) sedgeland: This plant community is dominated by *Cladium jamaicense* ('uki) and occurs on O'ahu and Hawai'i. Examples of the biome subtype occur within Ka'au Crater, O'ahu, and small occurrences of 'uki sedgeland in Kawai Nui Marsh on O'ahu and Waimanu Valley on Hawai'i. All examples of this community need active management to halt weed invasion (Gagné and Cuddihy, 1990).

Montane wet sedgeland: This plant community is dominated by sedges, including *Carex alligata*, *C. echinata*, *C. montis-eeka*, *Rhynchospora chinensis* (spp. *spiciformis*), and *Oreobolus furcatus*, and occurs both in open boggy areas as well as areas of mixed native-nonnative wet shrubs and grass/sedges in wet cliff and ridge crest areas, and inclusions within forest areas (Gagné and Cuddihy, 1990).

Carex alligata sedgeland occurs as treeless openings in montane wet forests in waterlogged sites and usually have standing water or water table just below the surface. This plant community occurs in wet forest of upper Hāna and upper Kīpahulu Valley in Haleakalā National Park, East Maui, and on Hawai'i in the Kohala Mountains and the Hāmākua region (Gagné and Cuddihy, 1990). Native *Deschampsia australis* (pili) grass occurs in *Carex alligata* sedgeland in high elevation bogs of east Maui (Vogl and Henrickson, 1971).

Carex echinata sedgeland occurs only on Maui in wet forest communities of upper Hāna at 1600–2100 m, on level, poorly drained sites (Gagné and Cuddihy, 1990).

Carex montis-eeka, *Rhynchospora chinensis* (spp. *spiciformis*), and *Oreobolus furcatus sedgeland* occurs in level high elevation bogs on Kaua'i and West Maui.

Native Wet Cliff and Ridge Crest Shrubland

Lowland wet shrubland: This plant community occurs on windswept ridge crests or in gulches on all of the main islands except Ni'ihau and Kaho'olawe at 200–900 m elevation.

Metrosideros polymorpha ('ōhi'a) shrubland occurs at summits and along ridge crests of the Ko'olau Mountains on O'ahu and is dominated by three species of *Metrosideros*: *M. polymorpha*, *M. rugosa* (lehua papa), and *M. tremuloides* (lehua 'āhihi).

Pipturus albidus (māmaki) riparian shrubland occurs in wet gulches on all the main islands except Ni'ihau and Kaho'olawe. Occasionally, this shrubland consists only of māmaki, but more frequently is mixed with other native members of the family Urticaceae such as *Touchardia latifolia* (olonā), *Boehmeria grandis* ('ākōlea), and *Urera glabra* (ōpuhe) (Gagné and Cuddihy, 1990).

Wet cliff and ridge crest shrubland: This community is characterized by different species of native shrubs, including *Dubautia* spp., *Lobelia* spp., *Vaccinium calycinum*, *Dicranopteris linearis* (uluhe) fern, and native sedges and occurs on crests, steep ridges and cliff faces on the islands of Kaua'i, O'ahu, Moloka'i, Maui, and Hawai'i. Annual rainfall is 250–500 cm year (Gagné and Cuddihy, 1990). This environment is characterized by regularly windy and usually foggy and wet conditions. Soils are generally thin over soft, highly weathered rock and thin mucky clays. Vegetation is windswept and variable, ranging from dense dwarf-shrublands to dominant sedges with few scattered shrubs to sparse rock with very little plant life. Wind-stunted trees and shrubs are 1–3 m in height, and are clothed with epiphytic cryptogams (plants which do not bear flowers or seeds) and there is a diverse array of native shrubs, vines, herbs, and ferns. Woody plants are so stunted in some sites that sedges and ferns form a continuous canopy with them. Dominant species vary according to island and terrain. Native species of wet cliff and ridge crest shrubland vary according to island but generally include wind-stunted species of *Metrosideros* ('ōhi'a), *Cibotium* (hapu'u or tree fern), and shrubs, *Melicope*, *Myrsine*, and *Vaccinium*. Other species include *Asplenium* spp. (ferns), *Astelia menziesiana*, *Bidens* spp., *Broussaisia arguta* (kanawao), *Cyrtandra* spp., *Diplopterygium pinnatum*, *Dicranopteris linearis* (uluhe) fern, *Dubautia* spp., *Eurya sandwicensis* (anini), *Freycinetia arborea* ('ie'ie), *Kadua terminalis* (manono), *Lycopodiella cernua* (wāwae'iole or staghorn clubmoss), *Lobelia* spp., *Machaerina angustifolia* ('uki), *Peperomia* spp., *Phyllostegia* spp. (mint), *Scaevola* spp., *Sadleria pallida*, and *S. cyatheoides* ferns ('ama'u), *Tetraplasandra* spp., *Trematolobelia*

spp., and several rare endemic species including the orchid *Anoectochilus sandwicensis* and *Brighamia insignis* (Gagné and Cuddihy, 1990; Landfire, 2016).

Mixed fern shrubland (uluhe ferns and native shrubs) is characterized by substantial land coverage by uluhe fern and native shrubs including *Dubautia* spp., *Lobelia* spp., *Styphelia tameiameia*, and *Trematolobelia* spp. (Gagné and Cuddihy, 1990).

Mixed native-nonnative wet shrubs and grass/sedges include both native species, as above, and invasive grasses and shrubs.

Introduced Wet Grassland

Introduced wet grassland is generally characterized by three species of invasive grasses: *Paspalum conjugatum* (Hilo grass), *Setaria palmifolia* (palm grass), and *Ehrharta stipoides* (meadow rice grass) (Cuddihy and Stone, 1990). These grasses rapidly invade disturbed areas, and form complete ground cover. Depending upon the dominant grass, they can tolerate mesic conditions and moderate shade. Other introduced species of grasses in this biome subtype include *Pennisetum clandestinum* (kikuyu grass), *Digitaria decumbens* (pangola grass), *Panicum maximum* (guinea grass), *Brachiaria mutica* (para grass), and *Cenchrus ciliaris* (buffle grass) (Urata, 1982). These five grasses are desirable forage for cattle and comprise managed pasture areas.

Introduced Evergreen Shrubland

Introduced evergreen shrubland is dominated by two species of invasive shrubs: *Schinus terebinthifolius* (Christmas berry) and *Ulex europaeus* (gorse).

Biome Extent and Range Prior Human Contact

Prior to human contact, Hawai'i wet grassland and shrubland consisted only of native wet sedge and grassland and native wet cliff and ridge crest shrubland, described above. Figs. 1–4 show what is thought to have been the extent of Hawai'i wet grassland and shrubland prior to Polynesian arrival ca. 500 AC (Cuddihy and Stone, 1990).

Biome Extent and Range After Human Contact

Nonnative grasses were introduced to Hawai'i after introduction of cattle in the late 18th and early 19th century, and many of these became invasive (Cuddihy and Stone, 1990). In the late 19th and early 20th century, gorse and Christmas berry were introduced, and quickly invaded native communities (Cuddihy and Stone, 1990). Currently, there are approximately 65,000 ha of wet grassland and shrubland (native and introduced) on the islands of Hawai'i, Kaua'i, Lāna'i, Maui, Moloka'i, and O'ahu (Figs. 5–8). Approximately 48% of wet grassland and shrubland biome today is native species dominated (defined by native species cover > 50%). Fig. 9 shows the relative proportion of vegetation classes of native and introduced wet grassland and shrubland by island.

Native Wet Sedge and Grassland

Within wet montane forest, the native wet sedge and grassland subtype occurs generally in small areas (< 1 to few ha area in size), and limited to areas with poor drainage and soils saturated with water preventing growth of trees and shrubs. Wet sedge and grassland occurs on east Maui and the Alakai Plateau on Kaua'i in large areas often many hectares in size. Areas of native wet sedge and grassland also occur in wet cliff and ridge crest shrubland, and mixed native-nonnative wet shrubs and grass/sedges in wet cliff and ridge crest areas.

Native Wet Cliff and Ridge Crest Shrubland

There are four vegetation communities within the wet cliff and ridge crest shrubland biome subtype, distributed across the islands of Hawai'i, Maui, Moloka'i, Lāna'i, O'ahu, and Kaua'i (Figs. 5–8). These are native wet cliff community; native wet shrubland; mixed fern shrubland; and mixed native-nonnative wet shrubs and grass/sedges (Fig. 9).

Native wet cliff community occurs over approximately 7800 ha on islands of Kaua'i, Moloka'i, Maui, and O'ahu. Extensive areas of native wet cliff community occur on cliff faces of the Ko'olau Mountains on O'ahu and Kaua'i.

Native wet shrubland is characterized by dwarf *Metrosideros polymorpha* ('ōhi'a) trees and native shrubs including *Broussaisia arguta* (kanawao), *Clermontia oblongifolia*, *Eurya sandwicensis*, *Hedyotis terminalis*, *Ilex anomala*, *Cibotium* spp. (hapu'u or tree fern), and various bryophytes (nonvascular land plants including liverworts, hornworts and mosses) (Gagné and Cuddihy, 1990). There is approximately 11,200 ha native wet shrubland on Hawai'i, Maui, Moloka'i, and Lāna'i. Examples of native 'ōhi'a montane wet shrubland occur within the State of Hawai'i Natural Area Reserves on West Maui and The Nature Conservancy, Kamakou Preserve on Moloka'i.

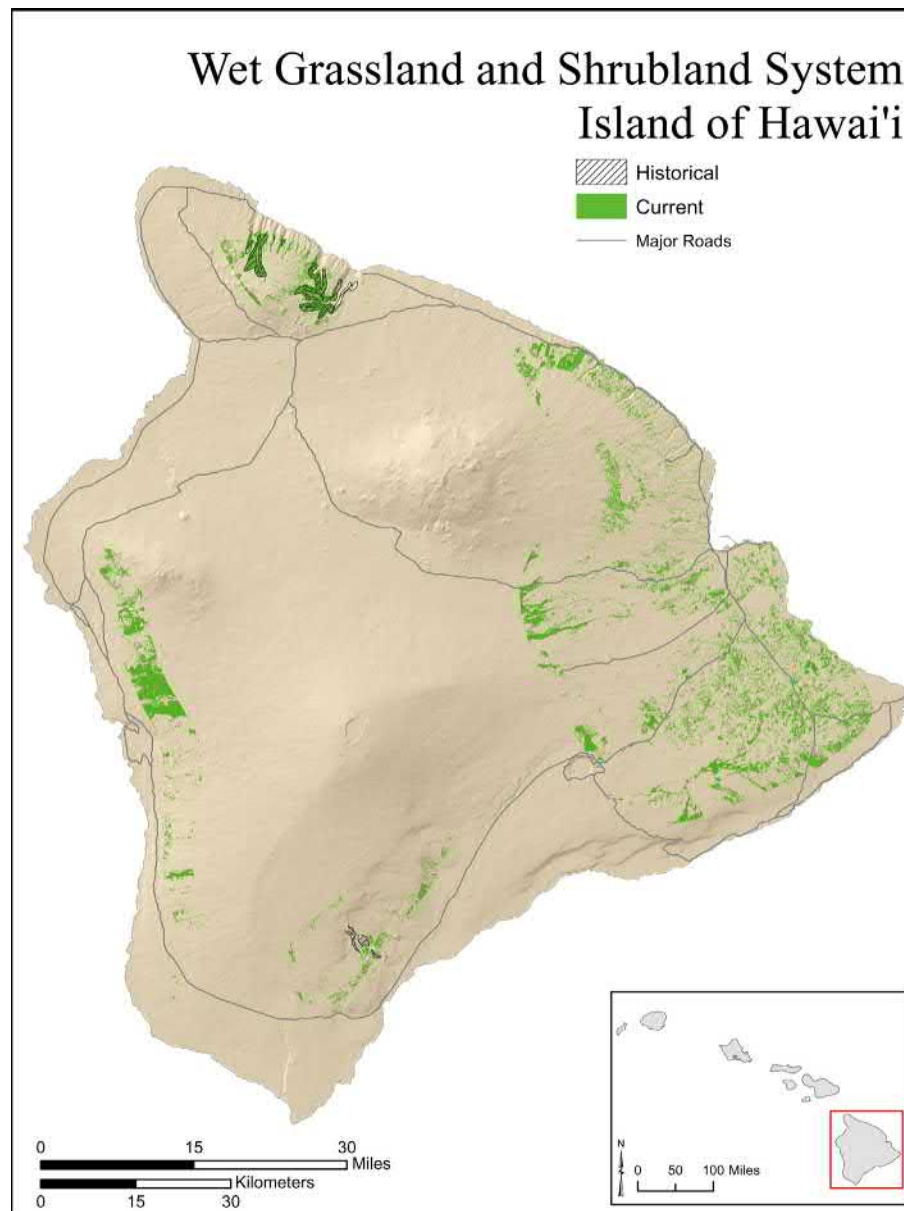


Fig. 1 Historic and current distribution wet grassland and shrubland, Island of Hawai'i.

Mixed fern shrubland (uluhe ferns and native shrubs): There is approximately 9600 ha mixed fern shrubland on the islands of Hawai'i, Maui, and O'ahu. Examples of native mixed fern shrubland occur within Mount Ka'ala Natural Area Reserve on O'ahu, and Kīpahulu Valley, Haleakalā National Park, Maui (Gagné and Cuddihy, 1990).

Mixed native-nonnative wet shrubs and grass/sedges: Approximately 2300 ha of this biome subtype occur on islands of Hawai'i and Moloka'i.

Introduced Wet Grassland

There are approximately 27,000 ha introduced wet grassland distributed across the islands of Hawai'i, Kaua'i, Lana'i, Maui, Moloka'i, and O'ahu (Amidon and Reeves, 2018). Many areas of introduced wet grassland is pasture and occurs in lowland areas (Figs. 5–8). Pasture grass improvement in Hawai'i in the 20th century has occurred largely by introduction of palatable grasses for livestock including *Pennisetum clandestinum* (kikuyu grass), *Digitaria decumbens* (pangola grass), *Panicum maximum* (guinea grass), *Brachiaria mutica* (para grass), and *Cenchrus ciliaris* (buffle grass) (Urata, 1982), and these forage grasses are dominant species of many introduced wet grassland areas.

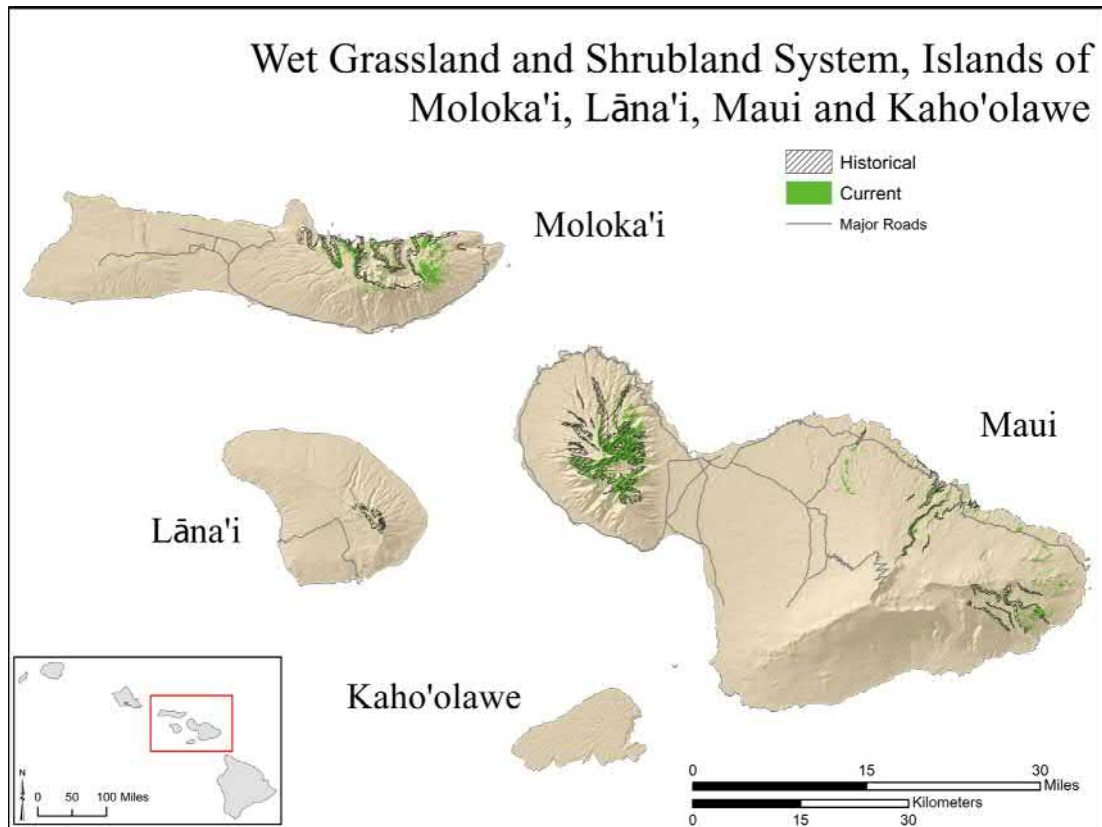


Fig. 2 Historic and current distribution wet shrubland and grassland, Islands of Moloka'i, Lāna'i, Maui and Kaho'olawe.

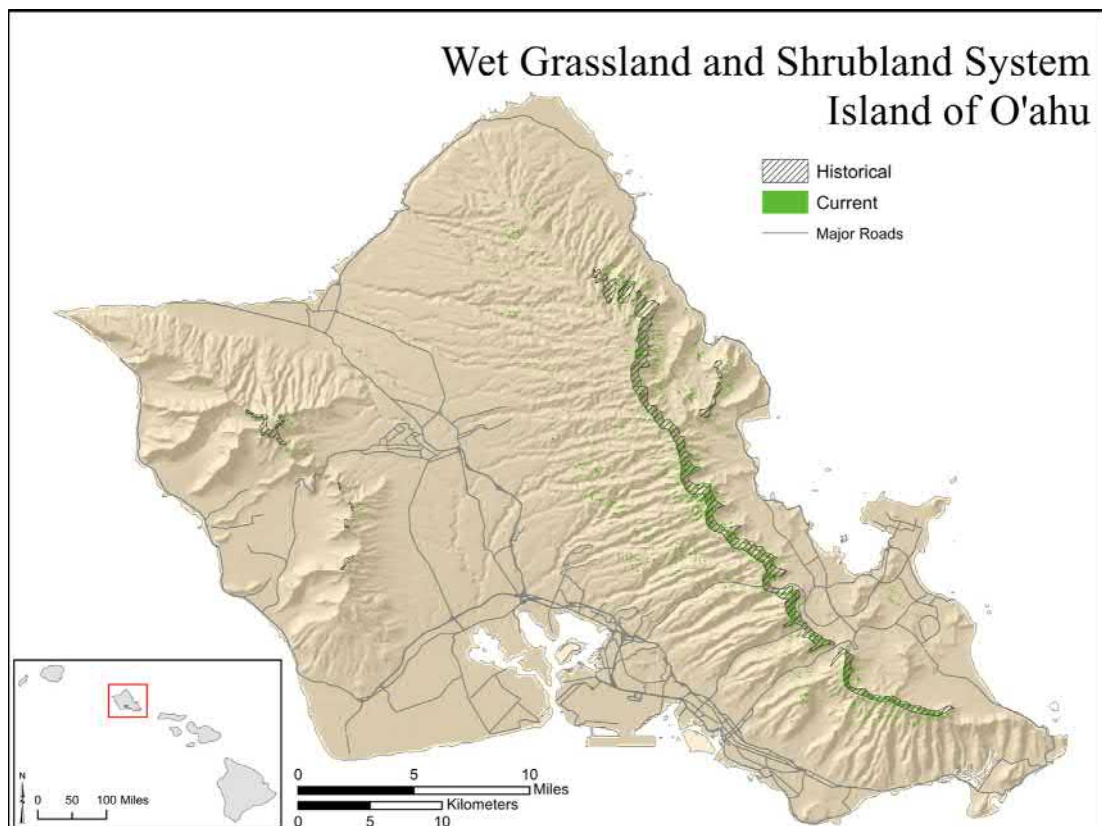


Fig. 3 Historic and current distribution wet shrubland and grassland, Island of O'ahu.

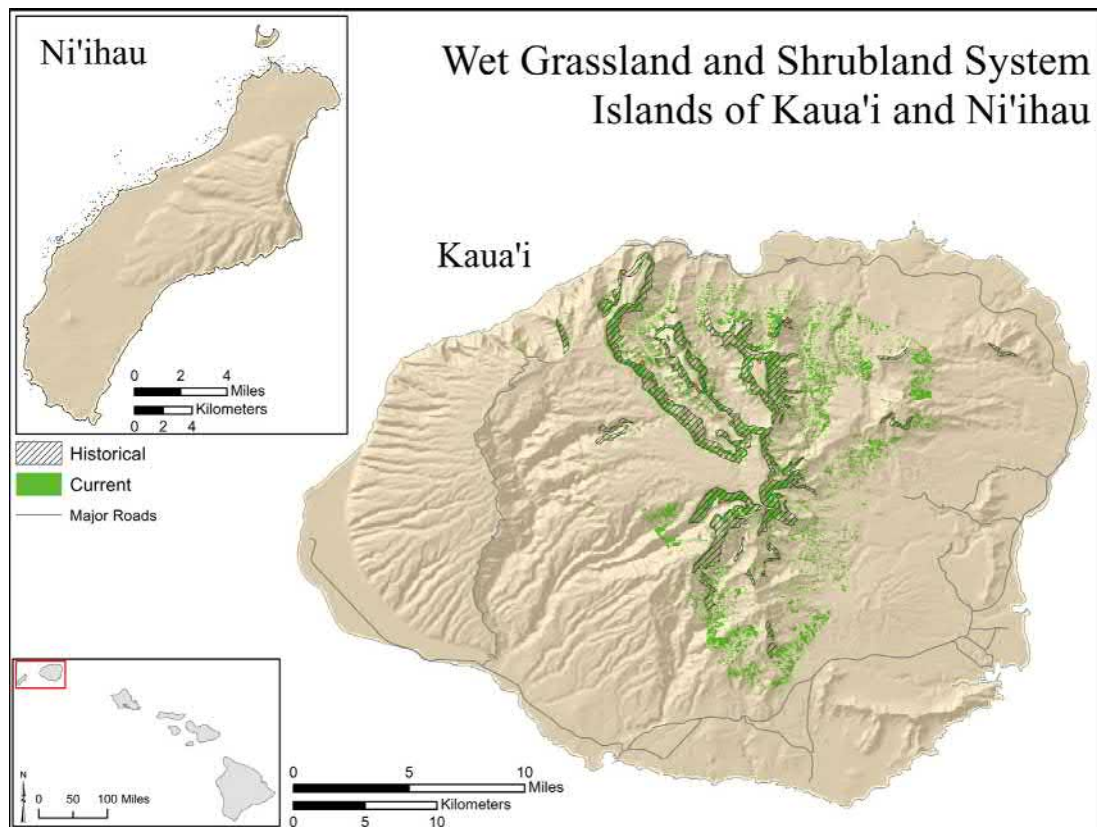


Fig. 4 Historic and current distribution wet shrubland and grassland, Islands of Kaua'i and Ni'i'hau.

Introduced Evergreen Shrubland

There are approximately 9000 ha nonnative wet shrubland distributed across the islands of Hawai'i, Kaua'i, Lana'i, Maui, Moloka'i, and O'ahu. This area is dominated by two invasive shrub species: *Schinus terebinthifolius* (Christmas berry) and *Ulex europaeus* (gorse). Both species also occur in mesic and dry areas.

Christmas berry evergreen shrubland: Christmas berry occurs over much of the southern half of the Wai'anae Mountains on O'ahu and is a threat to wet lowland plant communities on Maui and Hawai'i, in Haleakalā and Hawai'i Volcanoes National Parks, and Kalaupapa and Kaloko-Honokohau National Historic Parks (Cuddihy and Stone, 1990). A band of dense Christmas berry shrubland occurs at the lower margin of wet forest on the Kona side of Hawai'i Island.

Gorse evergreen shrubland: Although gorse is dry adapted, major infestations occur in mesic and wet areas adjacent to native forest on the islands of Hawai'i and Maui. Gorse is capable of invading native open upland forests and subalpine shrublands (Cuddihy and Stone, 1990). Gorse in mesic and wet areas covers over 8000 ha on the southeastern slopes of Mauna Kea, from 1981 to 2399 m elevation, and isolated pockets occur in wet forest down to 450 m elevation. Gorse occurs over nearly 6000 ha in mesic and wet areas on the northwestern slopes of Haleakalā, East Maui, between 631 and 2219 m elevation (Cuddihy and Stone, 1990).

Stressors

The health and distribution of Hawai'i native wet grassland and shrubland is affected by natural and nonnative processes and agents, including extreme weather events (hurricanes and tropical storms), climate change, drought, invasive ungulates, loss of plant pollinators, invasive rodents, invasive plants, and development (Table 1). Prior to human contact, native wet grassland and shrubland occurred on most cliffs and ridgelines, as inclusions within wet montane forest with the appropriate soil and hydrologic conditions, and open boggy areas with soil and hydrologic conditions that prevent forest establishment. Based on observation of current biome behavior in response to recent climate conditions, the wet grassland and shrubland biome likely was restricted prior human contact primarily by water availability and weather conditions (drought, tropical storms or hurricanes). After human contact, invasive ungulates and plants degraded native wet grassland and shrubland but these same stressors often benefit introduced wet grassland and shrubland.

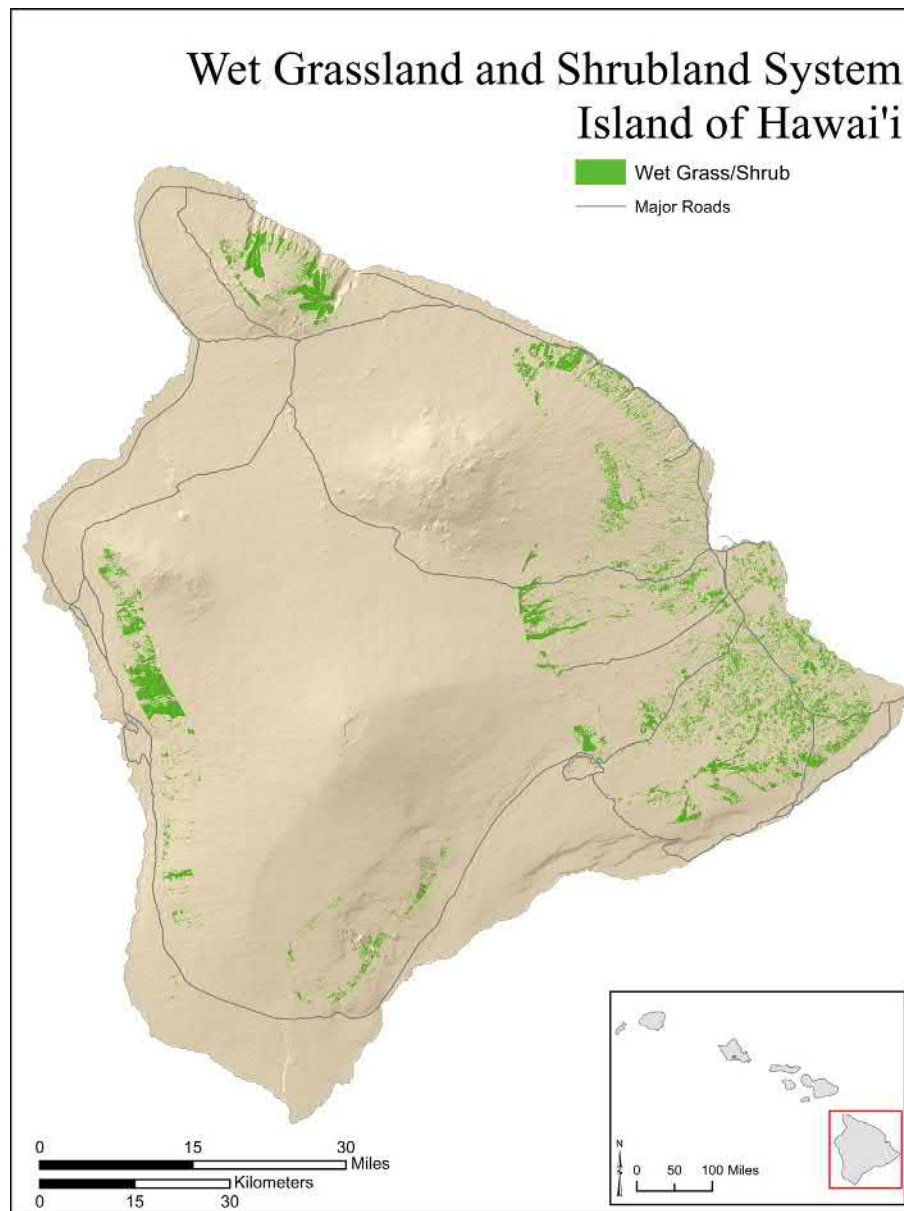


Fig. 5 Current distribution wet grassland and shrubland, Island of Hawai'i.

Extreme Weather Events

Hurricanes and tropical storms in the past 100 years have caused substantial damage to wet forest on Kaua'i, Maui and Hawai'i (Harrington et al., 1997; Businger, 1998) and presumably caused damage to wet cliff and ridge crest shrubland. Extended periods of heavy rainfall associated with extreme weather events, and rainfall runoff can cause erosion leading to destabilization of soils and landslides particularly in steep cliff and ridge crest areas, creating opportunities for disturbance adapted invasive grasses and shrubs to colonize eroded areas.

Climate Change and Drought

Effects of climate change on wet grasslands and shrublands include increasing air and ocean temperature and changes in precipitation. Effects of global climate change from the 1950s to 2007 in Hawai'i show an increasing number of consecutive dry days related to increased frequency of El Niño events (Smith and Reynolds, 2004; Chu and Chen, 2005; Giambelluca et al., 2008; Chu et al., 2010). Climate models predict continued drying climate during the wet winter season and dry leeward side of the islands through the 21st century (Timm and Diaz, 2009). Due to decreasing rainfall and increasing temperatures, drying climate has

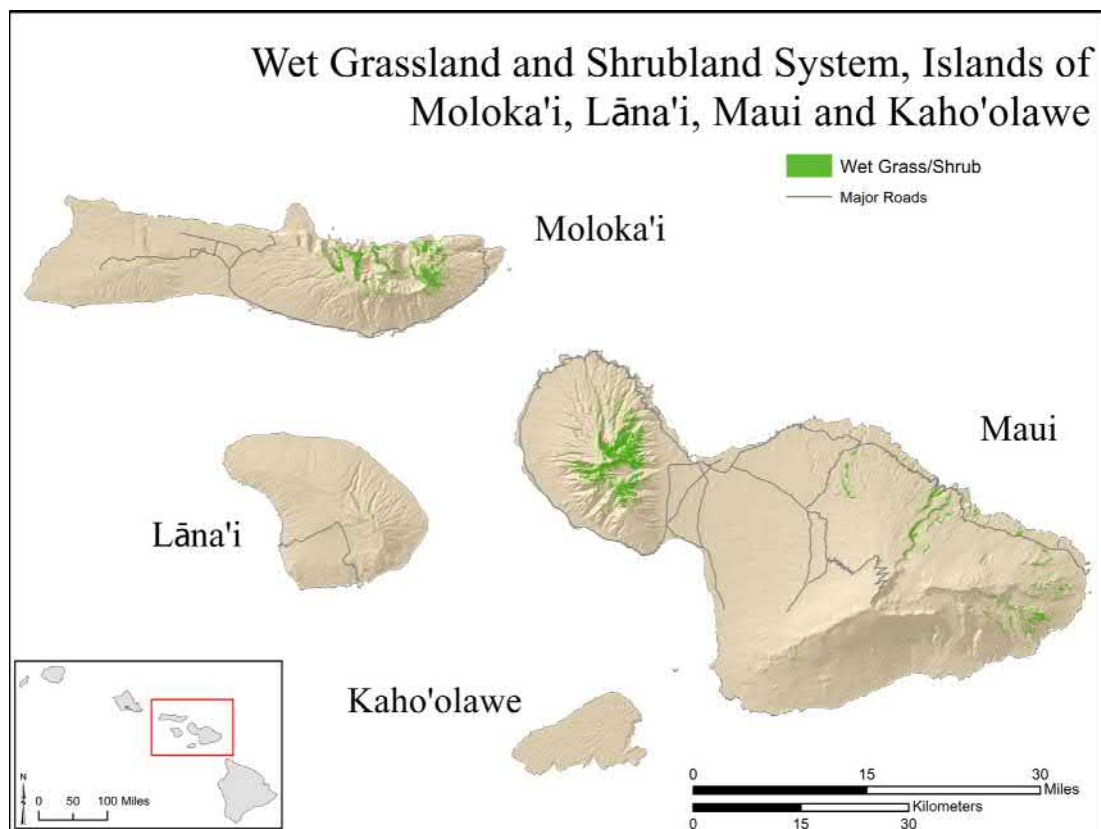


Fig. 6 Current distribution wet shrubland and grassland, Islands of Moloka'i, Lāna'i, Maui and Kaho'olawe.

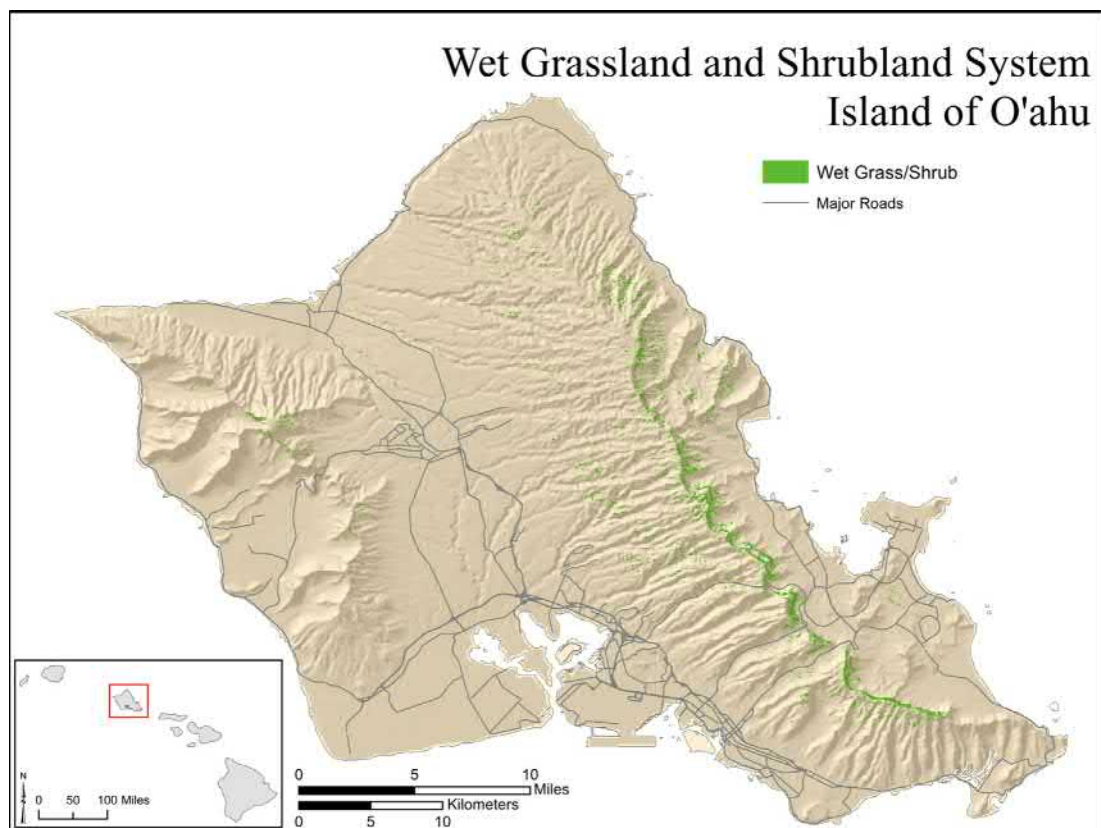


Fig. 7 Current distribution wet shrubland and grassland, Island of O'ahu.

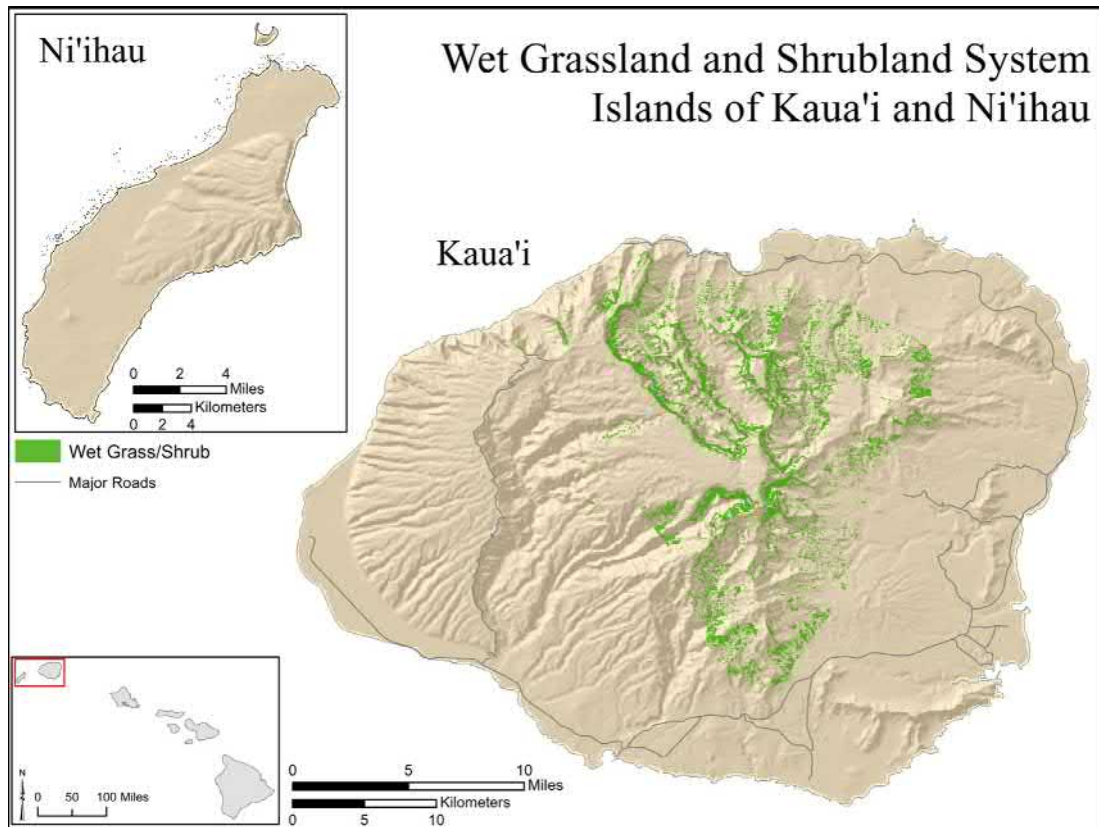


Fig. 8 Current distribution wet shrubland and grassland, Islands of Kaua'i and Ni'i'hau.

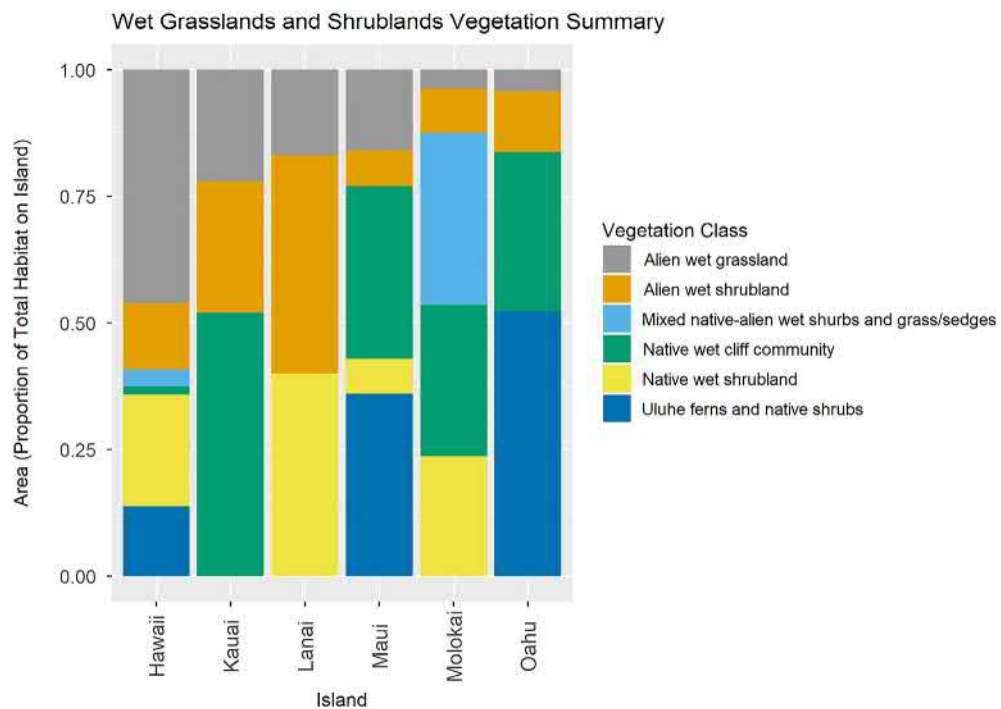


Fig. 9 Wet grasslands and shrublands vegetation summary.

Table 1 Stressors of Hawai'i wet grassland and shrubland by biome sub-type.

Stressor	Native wet grassland	Native wet shrubland	Introduced grassland	Introduced shrubland
Extreme weather events	x	x		
Climate change	x	x		
Drought	x	x		
Invasive ungulates	x	x		
Loss of plant pollinators	x	x		
Invasive rodents	x	x		
Invasive plants	x	x	x	
Development			x	x

contributed to increased drought stress of native plants throughout Hawai'i and increased fire occurrence (Dolling et al., 2005; Giambelluca et al., 2008; Frazier et al., 2012).

Invasive Ungulates

Feral pigs (*Sus scrofa*) and goats (*Copra hircus*) uproot and eat native plants and provide opportunities for disturbance-adapted invasive species to replace them (Gagné and Cuddihy, 1990). Feral pigs, goats, and sheep (*Ovis aries*), where these animals are able to reach cliffs and ridge crests, cause damage to wet cliff and ridge crest shrubland and grassland by consuming native plants, trampling, causing erosion through plant removal and soil compaction and spreading nonnative invasive plant seeds (Pratt and Jacobi, 2009).

Loss of Pollinators

Loss of pollinators is a stressor particularly for rare plant species such as *Brighamia insignis* and *Psychotria grandiflora* (kopiko) on Kaua'i that co-evolved with insect pollinators (Potenza, 2017). Once pollinated by the very rare, fabulous green sphinx moth (*Tinostoma smaragditi*), *P. grandiflora* now must be hand pollination by humans for the plants continued survival.

Invasive Rodents

Rats (black rat (*Rattus rattus*) and Polynesian rat (*Rattus exulans*)) eat the seeds and leaves of native plants in wet cliff and ridge crest shrubland, including kopiko (Potenza, 2017). Mice also eat seeds of Hawaiian plants although it is not known whether mice is a stressor for Hawai'i wet grassland and shrubland biome (Cuddihy and Stone, 1990).

Invasive Plants

The original native flora of Hawai'i (species that were present before humans arrived) consisted of about 1000 taxa, 89% of which were endemic (species that occur only in the Hawaiian Islands). Over 800 plant taxa have been introduced from elsewhere, and nearly 100 of these have become pests (i.e., injurious plants) in Hawai'i (Cuddihy and Stone, 1990; Gagné and Cuddihy, 1990). Of these 100 nonnative pest plant species, close to 70 species have altered native biomes. The most-often cited effects of nonnative plants on native plant species are displacement through competition. Competition may be for water or nutrients, or it may involve allelopathy (chemical inhibition of other plants). Nonnative plants may also displace native species by preventing their reproduction, usually by shading and taking up available sites for seedling establishment (Cuddihy and Stone, 1990). There are a number of invasive plants that out compete and displace native plants of Hawai'i wet grassland and shrubland. The introduced plants below share a number of characteristics. They produce numerous seeds easily and widely dispersed by animals, form dense stands or mats of vegetation, and are difficult to control once established. These species once established are capable of replacing native species of wet grassland and shrubland biome, and in some instances changing native biome to introduced forest.

Psidium cattleianum (strawberry guava): Since its introduction to the Hawaiian Islands in the early 19th century from its native range in Brazil, *Psidium cattleianum* (strawberry guava) has become invasive and has expanded into most of the native lowland forests of Hawai'i, becoming the dominant species in these areas (State of Hawaii, 2011). Strawberry guava regenerates both by seed and root sprouts; is able to regenerate in dense shade; is a prolific fruiter; and its seeds spread both by birds and feral ungulates (State of Hawaii, 2011). On O'ahu, strawberry guava is spreading along ridge crests into 'ōhi'a dominated lowland wet shrubland (Gagné and Cuddihy, 1990).

Clidemia hirta (Koster's curse): *Clidemia hirta* (Koster's curse or Clidemia) occurs in forest areas near wet cliffs, and some wet cliff and ridge crest shrubland (HERP, 1998). *Clidemia* grows between 1 and 5 m tall, depending on habitat, replaces native plants of the forest understory, overtops shorter vegetation and almost nothing can grow beneath its shade (Cuddihy and Stone, 1990; Smith, 1992). The purple-brown to blue-black berries each contains more than 700 tiny seeds that are widely spread by birds. In

undisturbed areas *Clidemia* levels remain low; however once an area is disturbed, colonization proceeds rapidly (Smith, 1992). Moloka'i has an infestation totaling more than 6000 ha, primarily in Wailau and Pelekunu Valleys of the North Shore, with some intrusion in wet cliff and ridge crest areas (Cuddihy and Stone, 1990; HERP, 1998). *Clidemia* is starting to invade the Koke'e/upper Alaka'i area on Kaua'i that abuts areas of native wet cliff shrubland.

Hedychium gardnerianum (Kahili ginger): *Hedychium gardnerianum* (Kahili ginger), and the very similar *H. coronarium* (white ginger) and *H. flavescens* (yellow ginger), are vigorous herbs capable of forming a very dense ground cover that excludes all other growth (Cuddihy and Stone, 1990). Kahili ginger typically achieves heights greater than 1 m and can displace all other understory plants in its vicinity (Cuddihy and Stone, 1990). Major infestations of Kahili ginger occur at Koke'e State Park, Kaua'i, and windward East Maui, and Hawai'i Volcanoes National Park, Hawai'i (Cuddihy and Stone, 1990). This very aggressive plant is able to form dense stands in open areas (forest margins, ravines or path sides) (Djedbour, 2008), and is a serious potential stressor to wet cliff and ridge crest habitat particularly areas on Kaua'i.

Cyathea australis (Australian tree fern): *Cyathea australis* (Australian tree fern) is a recent introduction into Hawai'i planted in private and hotel gardens at low elevations on O'ahu, Maui, and Hawai'i, and naturalized on O'ahu, Kaua'i, Maui, and Hawai'i (Cuddihy and Stone, 1990; Hawaii Invasive Species Council [HISC], 2019a,b, Australian Tree Fern). This large tree fern can grow to 12 m tall and windblown spores travel over 12 km from the parent plant. Fast growing, it aggressively out competes native plants in the forest understory and displaces native ferns including the slower growing hapu'u fern (Hawaii Invasive Species Council [HISC], 2019a,b, Australian Tree Fern). Australian tree fern occurs on Kaua'i in wet cliff areas at Wainiha and Lumahai Valleys (Long, 2007).

Tibouchina herbacea (cane Tibouchina): Native to Brazil, this shrub is semi-woody, can grow up to 3 m tall, a prolific seeder and spread by birds (Hawaii Invasive Species Council [HISC], 2019a,b, Cane Tibouchina). Cane Tibouchina has invaded some high elevation bogs on Maui (Kaiser, 2018).

Development

Ground breaking for development allows introduced grasses and shrubs to invade disturbed areas. Wet cliff and ridge crest habitat is almost entirely inaccessible to development. Development however causes ground disturbance in introduced wet grassland allowing the spread of undesirable grasses and shrubs, and pasture replacement by housing.

Conservation Efforts

Laws and Biosecurity

Protection of relatively intact natural areas and control of the introduction and spread of invasive species is critical for protecting the integrity of native wet grassland and shrubland (Gon and Olson, 2018). Endangered species protections and biosecurity and invasive species laws, regulations, coordination, and authority aid in conservation efforts for native wet grassland and shrubland by preventing introduction of invasive plants and providing legal protections for rare native species (Table 2).

Endangered species act: The Endangered Species Act (ESA) of 1973 aims to provide a framework to conserve and protect endangered and threatened species and their habitats. "Take" under the act has been broadly defined to include "harass, harm, pursue, hunt, shoot, wound, kill, trap, capture or collect." However, there is no take prohibition for plants. The U.S. Fish and Wildlife Service (USFWS) however has determined that "harm" includes "significant habitat modification or degradation" (USFWS, 2013). Thus, the habitat as well as the endangered animal may receive protection. As habitat loss is the primary threat to most imperiled species, the ESA allows the USFWS and National Marine Fisheries Service (NMFS) to designate specific areas as protected "critical habitat" zones. Seventeen percent (10,769 ha) of native wet grassland and shrubland in the state of Hawai'i are designated as critical habitat (Fig. 10) that provides native biome protection.

Biosecurity and invasive species control: A number of federal executive orders and State of Hawai'i conservation initiatives restrict introduction of invasive species to Hawai'i and are the basis of management frameworks for control of invasive species.

Federal executive orders. Executive Order 11987 (1977) requires Federal agencies, to the extent permitted by law to: restrict the introduction of invasive species into the natural ecosystems on lands and waters owned or leased by the United States. Order 11987 also encourages States, local governments, and private citizens to prevent the introduction of invasive species into natural ecosystems of the U.S. and the importation and introduction of invasive species into any natural U.S. ecosystems. Executive Order 13112 (1999) calls upon executive departments and agencies to take steps to prevent the introduction and spread of invasive species, to support efforts to eradicate and control invasive species that are established, and established a National Invasive Species Council (NISC) and the Invasive Species Advisory Committee (ISAC). Executive Order 13751 (2016) expanded the NISC membership, clarified NISC operations, and incorporated additional considerations including health, climate change, and emerging priorities. *State initiatives.* The Hawai'i Invasive Species Council (HISC) is a government body established by the Legislature of the State of Hawai'i with authority to provide funding and establish State policy for invasive species. In January 2017, the HISC adopted Resolution 17-1 endorsing the Hawai'i Interagency Biosecurity Plan and committing to its implementation. Key players in Hawai'i's biosecurity include the Hawai'i Department of Land and Natural Resources (DLNR), Hawai'i Department of Health (DOH), and University of Hawai'i (UH).

Table 2 Laws and regulations benefiting native wet grassland and shrubland subtypes.

<i>Title</i>	<i>Year implemented</i>	<i>Authority</i>	<i>Intent/purpose</i>
Endangered species act	1973	Federal	Protects critically imperiled species from extinction
50 CFR 16	1974	Federal	Implements the Lacey Act (18 USC 42), which prohibits importation of injurious species
Convention on International Trade in Endangered Species	1975	International	Ensures that international trade in specimens of wild animals and plants does not threaten the survival of the species in the wild
Executive order 11987	1977	Federal	Charges executive agencies with restricting the introduction of exotic species into the natural ecosystems on federal lands; and encourages States to do the same
Hawai'i Administrative Rules, title 4, subtitle 6, chapters 68 and 70	1981	Hawai'i (Department of Agriculture, DOA)	Rules/amendments for noxious weeds, plant and nondomestic animal quarantine, plant import, and bromeliad import
Executive order 13112	1999	Federal	Requires that a Council of Departments dealing with invasive species be created to prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause
HRS 194-2	2002	Hawai'i (Department of Land and Natural Resources, DLNR)	Establishes Hawaii Invasive Species Council (HISC)
Act 85	2003	Hawai'i (HISC)	Conveys statutory authority to HISC to continue to coordinate approaches among the various State and Federal initiatives for the prevention and control of invasive species
Act 36 (2011) HRS 150A-5.3	2011	Hawai'i (DOA)	Imposes a fee for the inspection, quarantine, and eradication of invasive species contained in any freight brought into the State
HB 1568	2011	Hawai'i (DOA)	Requires commercial harbors and airports in Hawai'i to provide biosecurity and to facilitate cargo inspections
HRS 174C Hawaii State Water Code	2013	Hawai'i (CWRM)	Establishes Commission on Water Resource Management (CWRM) and Water Resource Management Fund
Executive order 13751	2016	Federal	To prevent the introduction of invasive species and provide for their control, and to minimize the economic, plant, animal, ecological, and human health impacts that invasive species cause (amends EO 13112)
7 CFR 360.200	2018	Federal	Designates certain plants as noxious weeds

Stakeholder Engagement

Watershed partnerships: The Hawai'i Association of Watershed Partnerships (HAWP) comprises 10 island-based statewide watershed partnerships that work collaboratively with more than 74 public and private partners on five islands to protect over 890,308 ha of vital forested watershed lands (HAWP, 2018). The HAWP's mission is to increase the effective management and protection of mauka (upper elevation) watershed areas. Watershed partnerships undertaking conservation actions that protect and manage large areas of native wet grassland and shrubland include the East Maui Watershed Partnership, West Maui Watershed Partnership, East Moloka'i Watershed Partnership, Ko'olau Mountains Watershed Partnership, Wai'anae Mountains Watershed Partnership, and Kaua'i Watershed Alliance.

Invasive species councils: The State of Hawai'i created a group of invasive species councils (ISC's) to focus on priority threats identified by island. The invasive species councils are projects of the Pacific Cooperative Studies Unit and the Research Corporation of the University of Hawai'i (UH). The ISC's are voluntary island-based partnerships on Kaua'i (KISC), O'ahu (OISC), Maui (MISC), Moloka'i (MOMISC), and the Big Island (BIISC) (Hawai'i Island) that work with government agencies, nonprofit organizations, and private businesses and landowners to protect each island from the most threatening pests with a proactive approach. Each ISC has a staff that includes a field crew who works across thousands of hectares every year to rapidly respond to and control new invasive pests. The ISC's target species that have high potential to severely impact the economy, environment, agriculture, human health, and

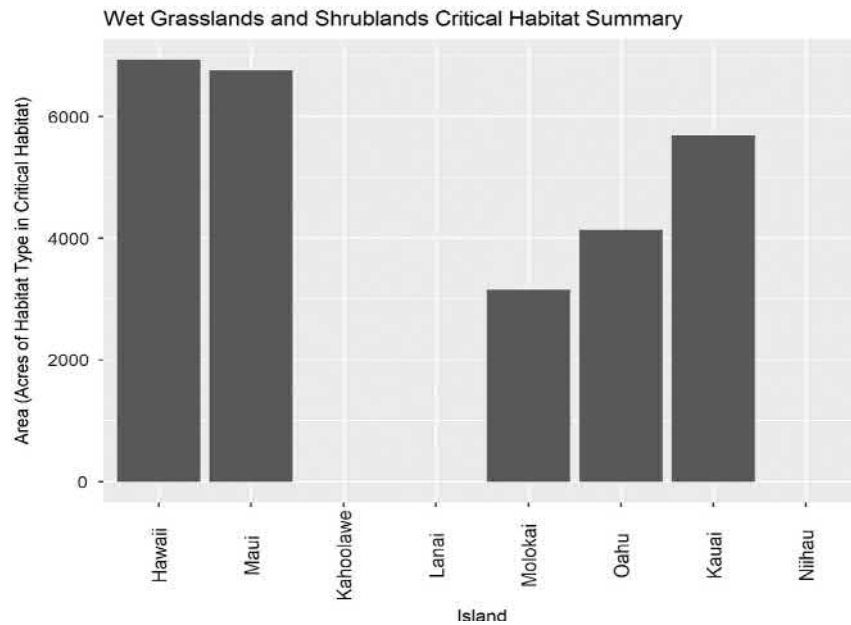


Fig. 10 Wet grasslands and shrublands critical habitat summary.

quality of life. Work done by these councils contributes directly to conservation by removal and reduction of invasive plants and animals in native wet grassland and shrubland areas and other Hawai'i biomes. In addition, the ISC's helps generate awareness and education to the public that in turn enhances this conservation strategy for wet grassland and shrubland biome.

Conservation Areas

Native wet grassland and shrubland occurs within conservation areas on Kaua'i, O'ahu, Moloka'i, Maui, Hawai'i, and Lāna'i. Nine percent (10,769 ha) of native wet grassland and shrubland is protected in reserves, defined as protected areas including national historic parks, national parks, national wildlife refuges, natural areas reserves, private preserve, state wilderness parks, The Nature Conservancy preserves, and wildlife sanctuaries (Reeves and Amidon, 2018).

On Kaua'i, the State of Hawai'i owns and manages the Alaka'i Wilderness Preserve that contains wet cliff and ridge crest shrubland and large areas of montane grassland and sedgeland. On O'ahu, portions of the Mount Ka'ala and Kaluanui Natural Area Reserves (NARs), owned and managed by the State of Hawai'i, contain wet cliff and ridge crest shrubland (HDLNR, 2016). On Moloka'i, wet cliff and ridge crest shrubland and native wet grassland occurs in portions of The Nature Conservancy's 2331 ha Pelekunu, and 1123 ha Kamakou Preserves (The Nature Conservancy of Hawai'i [TNCH], 2018a, 2018b), and the State of Hawai'i Pu'u Ali'i and Oloku'i NARs (Hawaii Department of Land and Natural Resources [HDLNR], 2016). On Maui, native wet grassland and shrubland occurs in Haleakalā National Park (NP), and the State of Hawai'i, West Maui NAR (Hawaii Department of Land and Natural Resources [HDLNR], 2016). On Hawai'i Island, the Pu'u O 'Umi NAR contains some wet cliff and ridge crest shrubland. On Lāna'i, Pūlama Lāna'i Company, is actively moving forward with projects for historical and cultural preservation and natural resource conservation including wet grassland and shrubland areas (Pūlama Lāna'i, 2014).

Conservation Activities

Conservation efforts to prevent degradation of native wet grassland and shrubland consist primarily of fencing and ungulate removal and weed control. These efforts have been effective at protecting and maintaining native wet grassland and shrubland where the biome subtype is minimally invaded by nonnative plants. Management of wet grassland and shrubland in areas already significantly impacted by ungulates and invasive plants has proven more difficult.

Fencing and ungulate control: Many areas of steep wet cliff and ridge crest scrubland are inaccessible to invasive ungulates (pigs, sheep and goats). In areas where ungulates can gain access to this biome subtype, fencing built across ridgelines helps prevent movements of ungulates into native wet grassland and shrubland areas. Ungulate exclusion fencing protects virtually all bog areas of native grasses and sedges (Honoluluadvertiser.com [HNLA], 2008; Kaiser, 2018).

Weed control: Control of invasive plants is ongoing by ISCs, Federal and State agencies and private landowners. Most effective for conservation of native grassland and shrubland is the exclusion of ungulates before substantial damage to native vegetation and introduction of weeds. Once invasive weeds establish in native grassland and shrubland methods available for their control may be inadequate to stem further invasion.

Strawberry guava: Strawberry guava currently occupies over 200,000 ha of lowland forest in Hawai'i (State of Hawaii, 2011). This extremely aggressive invader in areas where it is well established cannot be controlled using mechanical or chemical means. *Tectococcus ovatus* is a highly specific natural control agent producing leaf galls on strawberry guava that reduce its vigor and fruiting (Wikler and Smith, 2002; State of Hawaii, 2011). *T. ovatus* was first released in 2012 on Hawai'i Island in two demonstration plots and gall formation observed (Chaney and Johnson, 2013). It is too early however to know what effect releases of *T. ovatus* may have on strawberry guava on a regional scale.

Clidemia: Mechanical control of *Clidemia* is time consuming and even the leaves of pulled plants may form new roots and reestablish (Smith, 1992). Measures tested for biological control of *Clidemia* appear inadequate to control this species (Conant, 2002).

Kahili ginger: Although a number of diseases and insects are known to attack gingers, most promising for control of Kahili ginger is the bacterium *Ralstonia solanacearum*, which causes widespread plant death 16–20 weeks following inoculation (Anderson and Gardner, 1999). However, herbicidal control methods for ginger are not completely effective and are difficult to implement over large areas (Santos et al., 1986). Mechanical removal of ginger by digging up rhizome masses accomplished in small portions of Hawai'i Volcanoes National Park (HAVO), but this method of control is time consuming and labor intensive (Cuddihy and Stone, 1990).

Australian tree fern: On Kaua'i, Australian tree fern has invaded areas of pristine native forest and wet cliff habitats. Efforts to eradicate this noxious pest by aerial applied, targeted poisoning of individual plants are ongoing. Follow up surveys will indicate whether efforts to contain this pest in wet cliff areas on Kaua'i are effective (Sci-Tech Today, 2007; Borel, 2013).

Palm grass: Hawai'i Department of Forestry and Wildlife foresters on Kaua'i controlled palm grass where it had invaded native forest with drizzle applications of glyphosate at 0.75 lb/acre, but preventing reinvasion required continual monitoring and retreatment until the seed reservoir was exhausted. Hawai'i Volcanoes National Park (HAVO) staff reported control of palm grass in forest areas with foliar application of glyphosate at 1% of product (Motooka et al., 2003a,b, *Setaria palmifolia*).

Meadow rice grass: Glyphosate and imazapyr were used to suppress meadow rice grass at HAVO but with variable success depending upon amount of rainfall following herbicide application (Leary, 2009).

Christmas berry: Some biological controls for Christmas berry have been tried experimentally in Hawai'i but with limited success (Cuddihy and Stone, 1990). Herbicidal treatment or physical removal are the most common measures used to control Christmas berry. Physical removal however may result in greater stem densities if not followed by herbicide treatment to suppress repopulation from seeds in the ground (King, 2002).

Gorse: In 1926, in the 1950s, and beginning in 1984 researchers attempted biological control of gorse in Hawai'i (Markin et al., 1996). Of the more effective biocontrol agents released from 1984 to 1991, *Apion (Exapion) ulicis* (seed-pod-attacking weevil) and *Agonopterix ulicetella* (leaf-eating moth larvae) where successfully established, causing conspicuous damage to plants infected (Markin et al., 1996). Biocontrol for gorse may prevent the infested area from expanding but appears not to eliminate gorse in areas well established (Cuddihy and Stone, 1990).

Conservation of pasturelands: The Natural Resources Conservation Service (NRCS) is the technical agency of the U.S. Department of Agriculture that provides assistance to conservation districts and individuals in planning and carrying out conservation activities (Natural Resources Conservation Service [NRCS], 2018a,b). The NRCS provides financial and technical assistance to address farming and grazing operations concerns including water management, water quality, erosion control and fence management (Natural Resources Conservation Service [NRCS], 2018a,b). NRCS activities have improved pasture quality in introduced wet grassland by planting high quality forage grasses and use of herbicide application for control of invasive grasses. Hilo grass is controlled by introduction of taller forage grasses and grazing, and is sensitive to glyphosate and imazapyr, however both herbicides are nonselective, the latter with some residual soil activity (Motooka et al., 2003, *Paspalum conjugatum*).

Rodent control: Small-scale bait station grids in combination with rat traps have proven successful in reducing and/or eliminating predation on rare plant species by rats on O'ahu in an area containing dry and mesic forest (Mosher et al., 2010). Although rodent control of this scale has not been conducted in native wet grassland and shrubland it is expected it would be beneficial particularly for rare plants that are susceptible to seed predation by rodents.

Prior Human Contact: Redundancy, Resiliency and Representation

Biomes maintain ecosystem function through processes of *redundancy*, *resiliency*, and *representation*. We examine characteristics of redundancy, resiliency, and representation of wet grassland and shrubland prior to human contact and how these may change in the future under different management scenarios.

Redundancy is a biome's ability to withstand a catastrophic event (i.e., hurricanes, landslides, fire, earthquakes, volcanic eruptions, etc.) because multiple distributed communities exist across the landscape (Smith et al., 2018, p. 304). Before human arrival to Hawai'i, native wet grassland and shrubland occupied multiple watersheds on different islands. Because this system was broadly distributed across the island chain, localized catastrophic events, such as landslides, and more broad-scale events, such as landfall by a major hurricane, would not have affected the entire biome. Many of the plant species that comprise native wet grassland and wet cliff and ridge crest shrubland are common on all islands. However, there are plants within the community unique to individual islands. Before human contact, catastrophic events, even quite localized, could have had negative population effects on local species.

Resiliency is a biome's ability to withstand environmental stochasticity (random change in environmental conditions) and related to growth rate and size of species' populations, habitat quality and quantity, and demographic ability of populations to withstand stochastic disturbances (Smith et al., 2018). Before human contact the high species diversity of native wet shrubland would have helped this biome subtype tolerate natural, annual variations in the environment and recover from periodic disturbances (i.e., minor droughts, tropical storms, etc.).

Representation is a biome's ability to adapt to a changing environment over time due to genetic and species diversity and amount of environmental variation within the community type (Smith et al., 2018). Because of its extreme isolation from continental landmasses, species that arrived in Hawai'i were able to fill empty niches not already occupied by other species, which led to speciation (adaptive radiation) and high rate of endemism (Cuddihy and Stone, 1990). Representation prior to human contact however was limited compared to continents due to the few number of ancestral species that colonized the Hawaiian Islands. Environmental variation for native sedges is further limited due to species requirement for standing water or saturated soils.

Current Condition: Redundancy, Resiliency, and Representation

Native Wet Grassland and Shrubland

Native wet grassland and shrubland occupies multiple watersheds on different islands. Because this system is distributed across the island chain, localized catastrophic events, and more broad-scale events, such as landfall by a hurricane, will not affect entire biome, making it redundant. However although many of the plant species that comprise this system are common on all islands, there are rare plants within the community that are unique to individual islands and even watersheds. Therefore, catastrophic events, even quite localized, could seriously effect local species within this community type. Native plants of wet cliffs and ridge crest prior to human contact were resilient and able to recolonize areas after substantial disturbance. Native species are not able to outcompete many species of introduced invasive plants. Once broad areas of strawberry guava, *Clidemia*, Kahili ginger, Australian tree fern and other invasive plants have established, especially in extremely steep and difficult to access terrain, removal of these invasive plants may not be possible and native wet grassland and shrubland become fragmented. Therefore, the community has become less resilient over time.

Introduced Wet Grassland and Shrubland

Introduced wet grassland and shrubland is broadly distributed across the main Hawaiian Islands, making it redundant. This community quickly invades wet forest understory and native wet grassland and shrubland in disturbed areas. Plant species of this biome subtype produce copious numbers of seeds readily dispersed by birds and animals, and form dense stands of monotypic vegetation. The biome subtype responds positively to disturbance factors such as landslides that disrupt native communities, and invasive ungulates promote its establishment and expansion. Because of these characteristics invasive wet grassland and shrubland is strongly resilient. Species of introduced grassland and shrubland occur in mesic and even dry environmental conditions making it well represented due to wide environmental variation.

The Future of Hawai'i Wet Grassland and Shrubland

The condition of Hawai'i wet grassland and shrubland in the foreseeable future will be based on potential changes in conservation management parameters including conservation values, laws and biosecurity, and development or conservation planning. These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out and are critical factors that drive the direction and magnitude of natural resource conservation in the foreseeable future.

Foreseeable Future

The foreseeable future is used in the Endangered Species Act (ESA) as a criterion for determining when a species should be listed as threatened or endangered. The most commonly used factors to establish the "foreseeable future" involve species- or population-specific biological criteria, but also include nonbiological criteria (D'Elia and McCarthy, 2010). For the purposes of the foreseeable future in Biome Status Assessments (BSAs), using species-specific biological criteria will not suffice since the BSAs lack species information and are built upon assessments of ecosystem features that are not typically characterized with reference to specific species (Miller, 2018). As a solution to this unorthodox need, for BSAs the "foreseeable future" is in reference to Global Climate Models (GCMs) developed by the Intergovernmental Panel on Climate Change (IPCC) and other similar assessments. The major uncertainties in climate models are (1) the initial conditions of the climate that are used to set the starting point of the GCMs, (2) the greenhouse gas emission scenario that is used by the model, and (3) the parameterization of important but small-scale and often not-well understood climate processes such as clouds. Uncertainties in what society will do regarding greenhouse gas emissions is the greatest source of variance in the climate predictions. The dotted lines in Fig. 11 highlight the period of estimated least variance in the four climate models (Miller, 2018). Variance increases with increasing years from 2005, the last observed time plotted on the figure. From about 2018 through 2035, the lines for each of the GCM scenarios (RCPs—Representative

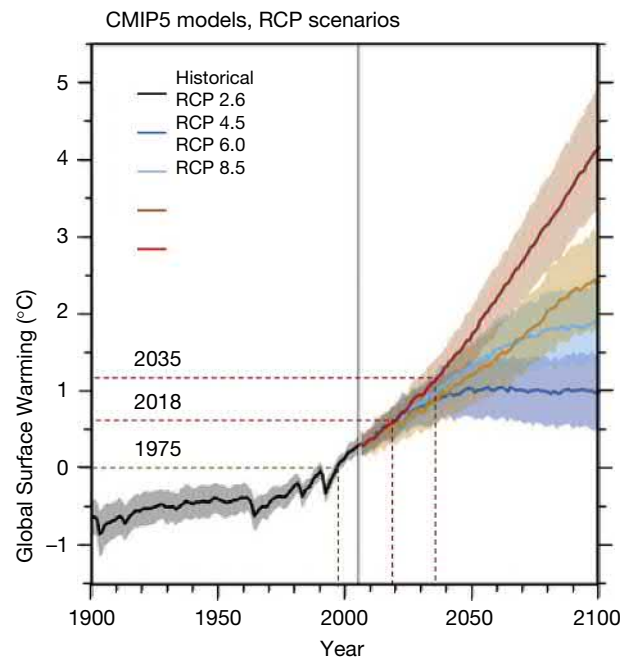


Fig. 11 The foreseeable future for global surface warming in reference to Global Climate Models (GCMs).

Concentration Pathways; Van Vuuren et al., 2011a,b) begin to diverge, but prior to 2035 the RCPs remain relatively similar. For the purposes of this BSA, the “foreseeable future” is defined as up to 2035, when the average values of each of the four RCP scenarios do not appear to differ “significantly” in the anticipated amount of global surface warming. The GCMs also provide projections of climate futures to the year 2100 and are downscaled to provide more focused information on the Hawaiian Islands (Table 3).

Conservation Management Parameters

The condition of wet grassland and shrubland biome in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out and are critical factors that drive the direction and magnitude of natural resource conservation in the foreseeable future: *Conservation values* describe stakeholder involvement and public opinion which determine the formulation, implementation and funding of natural resource conservation within laws and development plans. *Laws and biosecurity* encompass national, state, county, and city laws and regulations and are the means by which natural resource conservation and biosecurity are supported and implemented (e.g., hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.). *Development or conservation planning* encompass national, state, county, city, and private development plans or conservation plans which define specific actions that result in losses or gains in natural resource conservation and biosecurity.

Future Scenarios

We consider four foreseeable future scenarios in this BSA for the CMPs described above:

Future scenario one, status quo: The most likely foreseeable future; no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues through the foreseeable future.

Future scenario two: A slight increase in natural resource conservation in the CMPs marginally improves conservation management.

Future scenario three: A slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management.

Future scenario four: A moderate to large increase in conservation actions in the CMPs substantially improves conservation management.

Rates of change in human population for the four future scenarios is captured by the changes in the “developed” land cover footprint derived from land cover map analysis (Amidon and Reeves, 2018). Impacts from other sources of human activities or human-caused habitat stressors (e.g., plant and animal diseases, wildfires, invasive species, etc.) are not well characterized in the land cover changes, but significantly contribute to increases in the land cover area dominated by nonnative vegetation. Furthermore, island-wide implementation of the CMPs is unlikely to have a significant effect on climate-related stressors (temperature, precipitation, and severe weather) resulting from global warming by 2035. This lack of CMP climate effects is due to the global lag in

Table 3 Main Hawaiian Islands end-of-century^a and *Foreseeable Future* (2035) projections for select climate indicator variables.

Annual mean climate indicator	Projected change ^a by 2100 (unless noted)	Projected change in 2035 (17 years)
Air temperature	2055: Increase 3.0–3.5 °F (1.67–1.94 °C) 2085: Increase 4.5–5.0 °F (2.5–2.78 °C)	2035: Increase 1.5–2.0 °F (0.83–1.11 °C)
Precipitation ^{a,b}	Decrease 5–10% in wet season Increase 5% in dry season; NWHI: decrease 0–10%	Decrease 1.6–3.2% in wet season Increase 1.6% in dry season NWHI: decrease 0–3.2%
Sea level	Increase 1.48–2.69 ft. (0.45–0.82 m)	Increase 0.47–0.85 ft. (0.14–0.26 m)
Tropical cyclones ^{c,d}	Decrease frequency 4.8% Increased intensity 0.2% Increased duration 2.5% Increase precipitation 20% ^c	Decrease frequency 1.5% Increased intensity 0.06% Increased duration 0.8% Increase precipitation 6.3%

Note: All estimates for 2035 climate conditions in the table were done using linear extrapolations. The climate parameters do not change in a linear manner over time; they follow a concave upward path similar to a power function. Thus, the linear extrapolations will give values that are slightly higher than those obtained from analysis using a convex curved function. This should make any assessment of effects on biomes, ecosystems or federally listed species somewhat conservative and in favor of the biome or species. The four most important impacts (damages) of global climate change in the Pacific Islands are higher air and ocean surface temperatures; changing rain patterns; sea level rise; and ocean acidification.

^aAfter Keener et al., 2012.

^bTimm et al., 2015.

^cEmanuel et al., 2008.

^dKnutson et al., 2010.

climate response to changes in greenhouse gas emissions that occurs on the order of centuries rather than years (Solomon et al., 2009; Gillett et al., 2011; Jevrejeva et al., 2012). Evidence of climate effects is also confounded by the large annual variation in the Pacific islands climate parameters, which is much greater than projected climate change by 2035. The future condition of wet grassland and shrubland biome in scenario one, status quo, was characterized from an assessment of change over time in wet grassland and shrubland land cover obtained from existing land cover maps (Amidon and Reeves, 2018). Based on these land cover maps, an annual rate of change for wet grassland and shrubland biome was estimated, and a projected change (in hectares) was calculated for the year 2035. The future conditions of wet grassland and shrubland habitat for scenarios two, three, and four cannot be quantitatively estimated. However, the scenario one estimate can provide a “baseline” for a qualitative characterization of changes in the future condition of wet grassland and shrubland under scenarios two, three, and four. A large increase in land cover in pasture (introduced wet grassland) is predicted for Hawai'i Island, but little change in land cover for wet grassland and shrubland biome is predicted for other islands.

Future Scenario One, Status Quo

Summary: Scenario one is considered the most likely future scenario, and serves as a “baseline” for comparing among the four future scenarios. There is no change in the implementation of the three CMPs between 2018 and 2035. Using the current rate of land cover change, a large increase in land cover in pasture is predicted for Hawai'i Island (Amidon and Reeves, 2018). An expanding human population and increased development and general land use on all inhabited islands is anticipated, and therefore biome stressors are expected to increase at a small annual rate. Exceptions are a small to moderate annual rate of increase for development, wild fires, and surface air temperature, and a small annual rate of decrease for precipitation. Development will minimally effect native wet cliff and ridge crest shrubland and sedge and grassland areas because of the steep terrain and remoteness of these biome subtypes from human population areas. Because the scenario one biosecurity CMP remains unchanged while the population and development continue to grow there is an increased potential for new invasive species and new diseases (particularly those affecting native plants). The anticipated changes, under each of the scenarios for stressors important to wet grassland and shrubland biome are in Table 4.

Future Condition

Native wet grassland and shrubland. Native wet grassland and shrubland protected from invasive ungulates and with minimal presence of invasive weeds is expected to continue in its natural state. However, on Kaua'i, where Australian tree fern is well established, there will be continued invasion of this noxious pest in wet cliff and ridge crest areas. Native wet grassland and shrubland is expected to decline in quality in areas where ungulates are present due to ground disturbance, erosion and introduction of invasive plants. For the foreseeable future although reduction in hectares of this native biome subtype is not expected, negative effects of invasive plants in unmanaged areas will continue to occur as will native vegetation decline to a condition where current management tools can no longer prevent transition to biome subtype dominated by invasive species.

Table 4 Responses of wet grassland and shrubland habitat stressors in foreseeable future scenarios.

<i>Conservation management parameters (CMPs)</i>				
Conservation values	Stakeholder involvement and public opinion influence the formulation, implementation, and funding of natural resource conservation and biosecurity (NRC/B) within laws and development or conservation plans			
Laws and biosecurity	National, state, county, and city laws and regulations are the means by which NRC/B are supported and implemented			
Planning for development or conservation	National, state, county, city, and private development plans or conservation plans define actions that result in losses or gains in NRC/B (impacts realized at implementation)			
Foreseeable future scenarios	and the resulting wet grassland and shrubland habitat conditions			
Use foreseeable future scenario one as a "baseline" to characterize changes in <i>Conservation Actions</i> and <i>Habitat Conditions</i> in future scenarios two, three and four	Scenario one: <i>CMPs</i> : Unchanged in support for NRC/B <i>Conservation actions</i> : No change; current rate of land cover change continues through the foreseeable future <i>Habitat condition</i> : Habitat area, quality, and sustainability slowly decrease through the foreseeable future	Scenario two: <i>CMPs</i> : Small increase in support for NRC/B <i>Conservation Actions</i> : Marginal increase <i>Habitat condition</i> : Habitat area is unchanged through the foreseeable future; habitat quality and sustainability are slightly enhanced through the foreseeable future	Scenario three: <i>CMPs</i> : Small to moderate decrease in support for NRC/B <i>Conservation actions</i> : Substantial decrease <i>Habitat condition</i> : Urban and agricultural uses are prioritized over conservation; habitat area, quality, and sustainability substantially decrease through the foreseeable future	Scenario four: <i>CMPs</i> : Moderate to large increase in support for NRC/B <i>Conservation actions</i> : Substantial increase <i>Habitat condition</i> : Robust, sustained effort to restore, manage, and expand conservation; habitat area, quality, and sustainability substantially increase through the foreseeable future
Habitat stressors	Responses of wet grassland and shrubland habitat stressors			
Invasive ungulates	Small increase	No change	Moderate to large increase	Moderate decrease
Loss of plant pollinators	Small increase	No change to small increase	Moderate to large	Small to moderate decrease
Invasive rodents	Small increase	No change to small increase	Small to moderate increase	Small to moderate decrease
Extreme weather events	Small increase	Small increase	Small to moderate increase	Small increase
Invasive plants	Small increase	Small increase	Moderate to large increase	Small to moderate decrease
Drought	Small increase	Small increase	Small increase	Small increase
Development	Small increase	Small increase	Small to moderate increase	Small to moderate decrease
Erosion	Small increase	No change	Moderate to large increase	Moderate to large decrease
<i>Climate</i>				
Temperature	No change to small increase	No change to small increase	No change to small increase	No change to small increase
Precipitation	Small increase	Small increase	Small increase	Small increase

Introduced wet grassland. Current levels of funding, conservation protections, and methods for control of introduced wet grasses is expected to prevent the further spread of invasive wet grasses in managed native wet forest and wet grassland and shrubland. In unmanaged native biomes there will be no change in the current trajectory for introduced wet grassland's continued expansion in land area covered. Pasture grasses, including kikuyu grass, pangola grass, guinea grass, para grass, and buffle grass are expected to expand in area (Amidon and Reeves, 2018).

Introduced evergreen shrubland. Maintained levels of funding and current methods of weed control will continue to contain populations of introduced evergreen shrubland in areas currently managed. Unmanaged areas of introduced evergreen shrubland will expand in native wet forest. Of concern is the continued spread of Christmas berry by birds. The current effort to detect and remove incipient populations of Christmas berry from wet forest will be inadequate to prevent the establishment of new populations of this noxious shrub in intact wet forest communities. Control of gorse infestations adjacent to conservation areas at Hakalau Forest NWR and Haleakalā National Park will limit gorse from spreading further in these conservation areas.

Future Scenario Two

Summary: Conservation agencies and stakeholders work with increased but limited resources to slow or stop the degradation of native biomes. Scenario two is essentially "status quo" with minor improvements in the three CMPs. Though there is an expanding human population in scenario two, development is not expected to substantially increase. A slightly improved biosecurity effort should help reduce invasive species and plant diseases. The small increased support of natural resource management in the CMPs is not expected to greatly alter the rate of invasive species expansion, however this might lower it slightly compared to scenario one. The CMP supported conservation will not prevent, mitigate, or reverse the impacts of climate change-related stressors.

Future Condition

Native wet grassland and shrubland. With slightly improved conservation values, and laws and planning for development, somewhat greater funding will be available to manage invasive plants in native wet grassland and shrubland. Land managers will be able to prevent the decline of this biome subtype in managed areas by control of incipient populations of invasive plants. Continued decline of this biome subtype will occur in unmanaged areas. For the foreseeable future there will be little or no reduction in hectares of native wet grassland and shrubland however unmanaged areas will transition to a biome sub-type dominated by invasive species.

Introduced wet grassland. Somewhat greater funding will be available for control of invasive grasses, but because of the number of infestations throughout native wet forest and wet grassland and shrubland only a few additional high priority areas will be managed. Introduced wet grassland will expand in native wet forest and native wet grassland and shrubland biomes in unmanaged areas. With slightly improved conservation values, improved effort to remove unpalatable invasive grasses will allow more desirable range grasses to establish in pasture areas.

Introduced evergreen shrubland. Somewhat greater funding will be available for control of Christmas berry and gorse and improved pasture conditions will result. For large areas of these invasive shrubs, funding will be adequate only to prevent the continued expansion of established populations in native biomes. Slightly improved conservation funding will allow improved efforts to search and remove incipient populations of invasive shrubs in some areas of native wet forest and wet grassland and shrubland.

Future Scenario Three

Summary: All natural resource management actions in the CMPs are set aside in deference to land use for economic development. With extensive localized management, some native species may persist in protected areas where land development is not possible. Scenario three has substantial declines in natural resource conservation within the three CMPs. An increasing human population is supported in its use of land for economic development over the conservation of native biomes. Areas that cannot support development become the only areas of free-living native species. An expanding human population requires increased land use for agriculture and development with no encumbrance from natural resource management. Biosecurity controls are significantly weakened in this scenario leading to an increase in invasive species problems and new plant diseases. The substantial loss of CMP supported conservation may locally aggravate the impacts of climate change-related stressors of drought and extreme weather events in areas with increased invasive ungulates impacts.

Future Condition

Native wet grassland and shrubland. Under this scenario areas of native wet grassland and shrubland where ungulate fencing is needed to prevent erosion and weed invasion will suffer loss in quantity and quality due to a lack of fence maintenance and reduced effort to control invasive plants. Only the most remote wet cliff and ridge crest areas, impossible to access by invasive ungulates and with little or no invasive plants is likely to continue in its native condition. The reduction in effort to limit the introduction of invasive species to Hawai'i will lead to new invasive introductions, some likely harmful to this biome subtype. Compared to scenario one, more rapid decline in this biome subtype will occur due to increased effects of invasive ungulates and plants. There will be reduction in area of native wet grassland and shrubland as already moderately invaded areas transition to landscapes dominated by invasive species.

Introduced wet grassland. We expect Hilo grass, palm grass, and meadow rice grass to increase in pasture areas due to declines in funding for control of these introduced grasses. Increased development may result in loss of some pasture areas as housing development replaces agricultural lands. Declines in the three conservation management parameters will limit control of invasive grasses to only a few highest value conservation areas. Nonnative grasses will invade previously unaffected native wet forest and native wet grassland and shrubland.

Introduced evergreen shrubland. Areas of well-established evergreen shrubland will expand in size and invade adjacent wet forest and wet pasture. Gorse and Christmas berry, dispersed by water or carried by animals, will establish new populations in native biomes. Compared to scenario one, these effects will result in more rapid expansion of invasive shrubland in native forest and wet grassland and shrubland.

Future Scenario Four

Summary: An overt and robust, active, ongoing effort is made to engage partners and stakeholders in identifying and prioritizing landscape areas needed for the conservation of native biomes and to actively restore and expand these biomes. A substantial emphasis on natural resource conservation is present in the three CMPs, reflecting increased societal concern for declines in natural habitats and biodiversity. Active and well-supported natural resource management begins to restore ecosystems and expand their landscape areas. The needs of an expanding human population are addressed through more efficient land use governance based on redevelopment rather than development of undeveloped areas. Modern and novel agricultural practices focus on those that do not affect existing natural areas or areas needed for native biome restoration. Substantially improved biosecurity regulations decrease introductions of invasive species and plant diseases. The substantial increase in CMP supported conservation may locally mitigate the effects of climate change-related stressors, but climate change is expected to continue.

Future Condition

Native wet grassland and shrubland. With large increase in conservation management parameters, expected greater funding will allow increased management of invasive plants in native wet grassland and shrubland. This will reverse the degradation of areas of this biome subtype moderately affected by introduced plants. Remaining areas of this community will be fenced, protecting all areas of native communities from damage by invasive ungulates. With higher societal value of native species and ecosystems, there will be more acceptance of landscape-level removal of invasive species using traditional and new removal methods. Compared to scenario one, biome subtype resiliency will improve due to lower rates of intrusion and biome fragmentation by invasive species.

Introduced wet grassland. Increased funding for repeated treatments of invasive wet grassland with herbicide will reduce the area of this biome subtype in native forest and wet grassland and shrubland. Research may target development of more effective control measures for invasive grasses (such as biocontrol).

Introduced wet shrubland. Greater funding to control invasive Christmas berry and gorse adjacent natural areas and prevent new population establishment will reduce the area of this biome subtype. More research will target development of effective control measures including biocontrol. With higher societal value of native species and ecosystems there will be more acceptance of landscape-level removals of invasive species including introduced evergreen shrubland using traditional and new removal methods. Pasture quality will improve due to increased effort to remove Christmas berry and gorse.

Conclusion

Native Hawai'i wet grassland and shrubland biome since human contact has become less resilient primarily due to effects of invasive ungulates and invasive plants. Conservation measures to protect the native wet grassland and shrubland biome are effective in areas where ungulates are excluded and few invasive plants are present. However, some invasive plants, particularly strawberry guava and Australian tree fern, are able to spread into even protected and extremely remote areas of native wet cliff and ridge crest grassland and shrubland. Given current levels of conservation management, remote areas of native wet grassland and shrubland are likely to maintain redundancy, resiliency, and representation. Areas of moderately invaded native wet grassland and shrubland however are likely to experience gradual decline in ecological function and resiliency. Introduced wet grassland and shrubland by contrast is likely to expand in area under current levels of conservation management. Substantially improved conservation management will improve native biome resiliency due reduced biome fragmentation by invasive species and improve pasture areas through control of invasive grasses and shrubs.

See also: Physical Geography of the Hawaiian Islands.

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Hawai'i: Mesic Grasslands and Shrublands

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Published by Elsevier Inc.

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Abstract

This article provides an overview of the Hawaiian islands mesic grasslands and shrublands, including current status, stressors, and future viability. The mesic grassland and shrubland biome in Hawai'i receives between 1200 and 2500 mm of rainfall each year. It exists on both windward and leeward slopes of the main Hawaiian islands, and is found in both lowland and montane-subalpine zones (Gagne and Cuddihy, 1999). The lowland and montane mesic zones vary by elevation and climate which influences the composition of species within each of the mesic grassland and shrubland ecotypes (Gagne and Cuddihy, 1999). Mesic grasslands and shrublands were distributed across all of the main Hawaiian islands historically, with the majority occurring on the islands of Hawai'i and Maui. This biome is still found on all of the main Hawaiian islands however it is now composed of a mixture of both native and non-native grassland and shrubland ecotypes. Current ecotypes include, the native lowland and montane-subalpine mesic grasslands and shrublands, and three introduced ecotypes: perennial grasslands, evergreen shrublands and deciduous shrublands. Stressors to the mesic grasslands and shrublands are introduced weeds and ungulates, fire, natural disasters (i.e., hurricanes), climate (i.e., drought), plant diseases, and human development/agriculture. Ongoing conservation efforts are helping to protect the mesic grassland and shrubland biome in Hawai'i and depend on the combined efforts of the state and federal government, private landowners, and non-profit organizations. Management efforts are primarily focused on the removal of invasive species (weeds and ungulates) and protection of native grasslands and shrublands through the construction of fenced conservation areas. Our assessment of mesic grassland and shrubland viability is based on the likelihood of persistence over the long term, using the ecological concepts of representation, redundancy, and resiliency. We have evaluated the condition of the mesic grassland and shrubland biome in the foreseeable future (to year 2035) based on different scenarios involving the conservation management parameters of funding and public support for conservation management activities; conservation and biosecurity-related laws; and state/civic planning for conservation planning and land use and development.

Introduction

The Hawaiian archipelago includes eight large volcanic islands (Hawai'i, Maui, Lāna'i, Moloka'i, Kaho'olawe, O'ahu, Kaua'i, and Ni'ihau), as well as numerous offshore islets, shoals, and atolls set on submerged volcanic remnants at the northwest end of the island chain. The archipelago covers a land area of about 16,600 square kilometers (km) with the youngest and largest islands, Maui and Hawai'i, located in the southeast portion of the archipelago. Maui and Hawai'i are both unweathered shield volcanoes and contain the largest amount of land area in the main islands. The island of Hawai'i is still volcanically active. The older "main" Hawaiian islands (i.e., Moloka'i, Lāna'i, O'ahu, Kaua'i and Ni'ihau) are generally more heavily weathered, with steep cliffs and valleys, well developed streams, and gently sloped flood plains ([Gagne and Cuddihy, 1999](#); [Wagner et al., 1999](#)). The geography, geology, climate, hydrology and descriptions of the islands in the Hawaiian archipelago are described in the article on the Physical Geography of the Hawaiian islands by included in this work.

This article provides an overview of the mesic grassland and shrubland biome in the Hawaiian archipelago and describes the ecological factors that have influenced this biome over time and into the future.

Description

A grassland and shrubland is a plant community characterized by vegetation dominated by shrubs and grasses between 1 and 3 meters (m) in height. The classification of Hawaiian mesic grassland and shrubland is based on elevation, moisture, and physiognomy (look, aspect, and appearance). Physiognomic classes of mesic grassland and shrubland are based on percentage of cover of the dominant plant life and include subsets of native and introduced categories. The mesic zone of vegetation in the Hawaiian islands is defined as having an annual precipitation range from 1200 to 2500 millimeters (mm) per year ([Gagne and Cuddihy, 1999](#)). Mesic grassland and shrubland ecosystems are found in the mesic seasonal zone between the dry leeward and wet windward climates. Water availability is a critical component of the mesic grassland and shrubland biome. This biome exists where environmental conditions are less conducive to mesic forests due to shallower soils and more wind exposure ([Wagner et al., 1990](#)).

Mesic grasslands and shrublands occur on most of the main Hawaiian islands including Hawai'i, Moloka'i, Maui, Kaua'i, O'ahu, and Lāna'i on slopes ranging from 30 to 2300 m in elevation. They are found in the mesic seasonal zone between the dry leeward and wet windward climates and average 1000–2500 mm of rainfall annually ([Cuddihy and Stone, 1990](#)). These sites experience precipitation throughout the year but receive most rainfall during the winter months ([Landfire, 2016](#); [The Nature Conservancy \(TNC\), 2006](#)).

This biome is comprised of four native and three introduced plant communities: lowland mesic shrubland, subalpine mesic Shrubland, montane-subalpine mesic grassland, lowland mesic grassland, introduced perennial grassland, introduced deciduous shrubland, and introduced evergreen shrubland.

Biodiversity

Biological diversity is moderate in the mesic grassland and shrubland system relative to lower elevation systems ([The Nature Conservancy \(TNC\), 2006](#)). The lack of trees results in few microclimates created by this ecotype, however, there are several species of grass and shrubs that dominate or co-dominate in areas where this biome is found creating a moderate level of diversity.

Physical/Life History Components

Geological substrates are highly variable for this biome, but soils are generally shallow and often dry out regularly and may contain many rock outcrops ([Landfire, 2016](#)). The soils of mesic shrublands are much rockier than those of the mesic grasslands, and are generally much thinner than those of mesic forests ([Gagne and Cuddihy, 1999](#)).

Development of mesic grasslands and shrublands is influenced by numerous factors including disturbance (fires, volcanism, storms, pathogens, insect pests) as well as by precipitation, light, substrate, and soil availability. These ecotypes (sub-types) generally occur where forests cannot develop (due to a stressor limitation on tree growth), such as along gulch ledges, cliffs, ridges, or where there is regular exposure to strong winds on windward aspects ([Gagne and Cuddihy, 1999](#)).

Natural recruitment in the mesic grassland and shrublands is also driven by dispersal, pollination, and nutrient availability. Forest birds and the Hawaiian goose (Nēnē; *Branta sandvicensis*) provide a vital role in seed dispersal, allowing mesic grasslands and shrublands to maintain and establish in new areas ([Culliney et al., 2012](#)). Native invertebrates also serve an important role in the pollination of native plant species found in the native-dominated mesic grasslands and shrublands ([Magnacca, 2007](#)). Seabirds contribute an important source of marine derived nitrogen to the mesic shrublands through deposition of guano at their nesting sites ([Rowe et al., 2017](#)).

Vegetation Structure and Composition

Vegetation structure and composition varies among the seven subcategories included in the mesic grassland and shrubland category. It may consist of a closed-canopy ecotype dominated by ferns and small shrubs or an open grassland dominated by bunch grasses.

Water availability

Rainfall influences the availability of water for plants and is a critical component of mesic grasslands and shrublands. Shrubs and grasses typically found in mesic grasslands and shrublands require moist conditions throughout the year. Changes in the rainfall and water availability regime can lead to drier or wetter conditions that are not suitable to plants typically found in the mesic grassland and shrubland system. If water availability changes substantially, the area may no longer be favorable for mesic grassland and shrubland plants that prefer a moist environment, and the altered biome may shift to a drier or wetter biome classification if the species shift is substantial.

Viability of Mesic Grasslands and Shrublands (Redundancy, Resiliency, Representation)

The viability of Hawaiian mesic grasslands and shrublands depends on maintaining multiple and distributed populations (redundancy) of sufficient quality and size (resiliency) with species richness and genetic range (representation) to persist over time. We define redundancy by the number, distribution, and connectivity of subunits that make up a biome. By resiliency we refer to the overall health, stability, quality and quantity of subunits that compose a biome. We define representation, by the range of variation that exists within subunits that make up a biome, including environmental conditions and features (geographic, ecological, climatic).

Redundancy

The adequate distribution across the landscape of mesic grasslands and shrublands contributes to its ability to perpetuate after a catastrophic event in one area by having a redundant population in another area. Originally the mesic grass and shrubland communities were present on multiple islands and across multiple watersheds. They were found on both windward and leeward slopes and across a broad range of substrates from the oldest on the island of Kaua'i to the youngest on Hawai'i. Because of this redundancy in the mesic shrub and grassland biome, it is likely that natural catastrophic events such as large fires or hurricanes did not severely impact mesic grasslands and shrublands prior to human contact.

Resiliency

The quality and quantity of mesic grasslands and shrublands contributes to its resiliency in the face of stochastic events. Most native species in this biome are not specifically fire-adapted, however, many species regenerate after disturbance if environmental conditions are optimal. Fire can reset the successional clock of this system by removing a substantial amount of plants. Some seeds will survive and be able to germinate following the fire while others rely on dispersal from sources such as the wind or animals. It is reasonable to expect that mesic grasslands and shrublands were resilient prior to human contact having multiple, large, high quality areas composed of many ecotypes across the biome in the Hawaiian islands.

Representation

Diversity within and among locations of mesic grasslands and shrublands is necessary to enhance its ability to adapt to change. Mesic grasslands and shrublands are best represented when there is geographic and genetic diversity across the range. Representation considerations for this biome include presence on each of the main Hawaiian islands spanning across both leeward and windward slopes, and from lowland to montane elevations. Mesic grassland and shrubland communities prior to humans would have primarily been as inclusions in more tree dominated ecotypes, with limited species richness depending on the community (see discussion below on subtypes) (Cuddihy and Stone, 1990). Limited species richness in the native grassland and shrubland ecotypes may have reduced representation in the pre-human subtypes, making them less viable under changing conditions.

Pre-Human Condition

The original vegetation cover of the Hawaiian islands prior to the arrival of the Polynesians may be inferred from existing vegetation, remnants in disturbed areas, patterns of climate and substrates, and a few fossilized remains (Cuddihy and Stone, 1990). Because of the archipelago's historical isolation, the original vegetation has been characterized as biogeographically impoverished but secondarily enriched by evolution (Mueller-Dombois, 1992). Natural disturbances that shaped vegetation communities in pre-human Hawai'i included volcanic activity, hurricanes, lightning fires, and landslides (Mueller-Dombois, 1992).

Native mesic grasslands and shrublands present in pre-human times include four ecotypes: lowland mesic shrubland, subalpine mesic shrubland, montane-subalpine mesic grassland, and lowland mesic grassland. Dominant species found in pre-human mesic grasslands and shrublands are described in Table 1. These grassland and shrubland communities extended from the lowlands to the subalpine regions and were found on both the leeward and windward sides of the main Hawaiian islands (Cuddihy and Stone, 1990). They were found primarily on the islands of O'ahu, Maui, Kaua'i, and Hawai'i and to a lesser extent on Moloka'i and Lāna'i and were not known from the northwestern Hawaiian islands where vegetation communities are limited to lowland dry and coastal ecotypes (Cuddihy and Stone, 1990).

Prior to human contact the mesic grasslands and shrublands occurred as inclusions within mesic forests and encompassed an area up to 734,086 ac (297,074 ha) as indicated (cross-hatched) in Figs. 1–4. It is likely that shrublands and forests were found together throughout the lowlands, and even extended into coastal areas (Cuddihy and Stone, 1990). The montane grasslands

Table 1 List of dominant vegetation in the pre-human mesic grasslands and shrublands (Gagne and Cuddihy, 1999).

Lowland mesic shrubland	Subalpine mesic shrubland	Montane-subalpine mesic grassland	Lowland mesic grassland
<i>Dicranopteris linearis</i>	<i>Coprosma ernodeoides</i>	<i>Carex</i> spp.	<i>Bidens</i> spp.
<i>Dodonaea viscosa</i>	<i>Dryopteris wallichiana</i>	<i>Coprosma montana</i>	<i>Chamaesyce</i> spp.
<i>Leptecophylla tameiameiae</i>	<i>Lycopodium venustum</i>	<i>Deschampsia nubigena</i>	<i>Dodonaea viscosa</i>
<i>Lipochaeta</i> spp.	<i>Lysimachia remyi</i>	<i>Dubautia</i> spp.	<i>Eragrostis variabilis</i>
<i>Metrosideros polymorpha</i>	<i>Sadleria cyatheoides</i>	<i>Luzula hawaiiensis</i>	<i>Metrosideros polymorpha</i>
<i>Osteomeles anthyllifolia</i>	<i>Vaccinium calycinum</i>	<i>Leptecophylla tameiameiae</i>	
<i>Wilkesia</i> spp.	<i>Vaccinium reticulatum</i>		
<i>Eragrostis variabilis</i>			
<i>Tetramolopium lepidotum</i>			

are not believed to have been an important element in pre-human Hawai'i but the lowland kāwelu (*Eragrostis variabilis*) grasslands are thought to have been much more extensive (Cuddihy and Stone, 1990).

Although mesic grasslands and shrublands were found historically on all of the main Hawaiian islands, the majority occurred on the islands of Hawai'i and Maui, with Maui having the highest percentage of grasslands and shrublands represented (Reeves and Amidon, 2018).

Current Condition

Biome subtypes

Mesic grasslands and shrublands currently include four native and three introduced subtypes. Characteristics of these subtypes are described in Table 2.

Hawai'i lowland mesic shrubland

The Hawai'i lowland mesic shrublands are present on all of the main Hawaiian islands except Kaho'olawe. The remaining native lowland mesic shrublands include five sub-types: 'Ōhi'a (*Metrosideros*) Shrubland, Pūkiawe/'A'ali'i (*Leptecophylla/Dodonaea*) Shrubland, 'Ūlei (*Osteomeles*) Shrubland, Nehe (*Lipochaeta*) Shrubland, and Iliau (*Wilkesia* spp.) Shrubland (Gagne and Cuddihy, 1999). These shrublands occupy areas where forests cannot develop, such as along gulch ledges and on cliffs, ridges, and steep slopes, or where there is regular exposure to strong winds on windward aspects. The soils where this sub-type is found are generally shallow and easily dried out. These communities have open or closed canopies with little or no herbaceous layer development. Disturbance and displacement of the native communities has been greatest in the lowlands, leaving remnant native ecotypes at higher elevations or on ridgelines and cliff faces (Gagne and Cuddihy, 1999; The Nature Conservancy (TNC), 2006). In these areas the lowland mesic shrublands are often bounded below by dry or mesic forests, shrublands, or grasslands and above by 'ōhi'a/uluhe (*Metrosideros/Dicranopteris*) fern forest. An exception is the 'ūlei shrubland, which abruptly changes into 'ōhi'a lowland mesic shrubland and kāwelu (*Eragrostis*) lowland mesic grassland (Gagne and Cuddihy, 1999).

In some areas, lowland mesic shrublands are now surrounded by nonnative-dominated shrublands and forests that include Christmas berry (*Schinus terebinthifolius*), java plum (*Syzygium cumini*), and common guava (*Psidium* spp.) (Gagne and Cuddihy, 1999).

Hawai'i subalpine mesic shrubland

This community is represented by a single native ecotype on east Maui, the Ama'u/'Ōhelo (*Sadleria/Vaccinium*) Shrubland (Gagne and Cuddihy, 1999). This shrubland is known from the windward slopes of east Maui and within the adjacent Haleakalā Crater, primarily on ridges and upper slopes of rough, heavily dissected terrain. The substrate is composed of a thin soil with many rock outcroppings. Few herbs are present, but several species of ferns and mosses occur, and epiphytic lichens and bryophytes are abundant. At its lower elevational limits, this dense shrubland is two layered, with 'ōhelo (*Vaccinium* spp.) occurring above a layer of 'ama'u fern (*Sadleria*) and mixed shrubs. On the higher slopes and ridges, the shrubland layer is lower statured, dense, and single layered, with other *Vaccinium* spp. increasing in cover (Gagne and Cuddihy, 1999). Subalpine mesic shrubland is contained almost entirely within Haleakalā National Park or in preserves managed by The Nature Conservancy (Gagne and Cuddihy, 1999). Feral pigs and goats are the primary source of disturbance in the subalpine mesic shrublands. Invasive plants colonize disturbed areas and become established as a result of these animals (Gagne and Cuddihy, 1999). On the Nature Conservancy's Waikamoi preserve blackberry (*Rubus argutus*) and non-native grasses occur in disturbed areas adjacent to this subtype.

Hawai'i montane-subalpine mesic grassland

The Hawai'i montane-subalpine mesic grassland is represented by a single native community, the *Deschampsia* grassland. It is known from both the northeastern slopes of east Maui and on Mauna Loa volcano on the island of Hawai'i. On Maui, it occurs where the soil is thin with very little exposed rock surface. On Hawai'i, the substrate is a shallow ash soil over pāhoehoe. *Deschampsia* grasslands attain a very dense ground cover. Other native plants found in this community include rushes, sedges, and shrubs. On Maui,

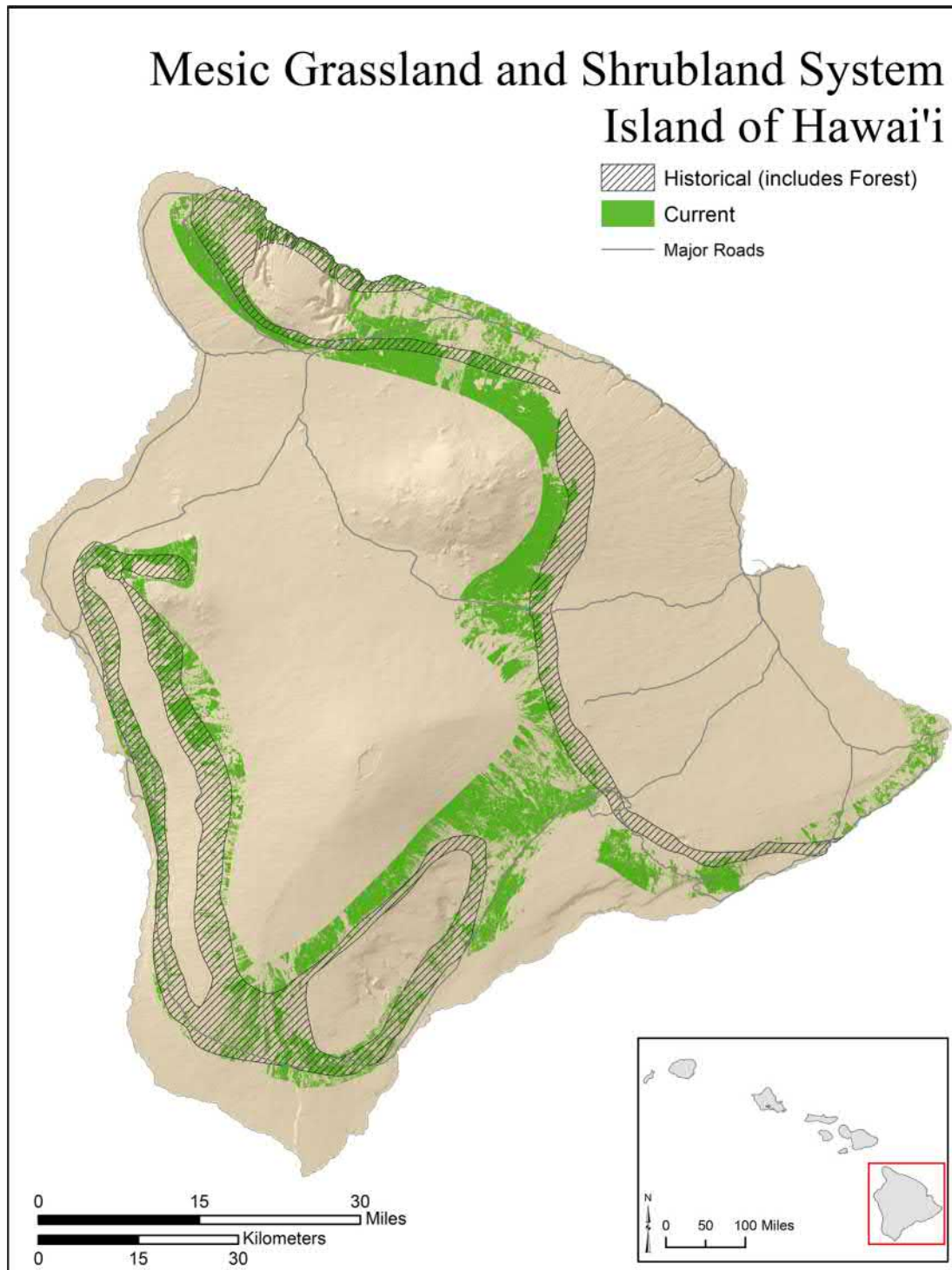


Fig. 1 Historical and current extent of the mesic grassland and shrubland system on the island of Hawai'i. Reeves, M.K. and Amidon, F. (2018). Habitat Status Assessment Methods—Hawaii, Current Condition Summaries. August 2018. Technical Report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI. 439 pp.

the community is bordered downslope by shallow gullies in which the vegetation is dominated by Ama'u/'Ōhelo (*Sadleria/Vaccinium*) Shrubland. *Deschampsia* grassland is also ecotonal below to treeline 'ōhi'a (*Metrosideros polymorpha*) forest on the slopes of Haleakalā. On Hawai'i, sites supporting this community are relatively small and often surrounded by open 'ōhi'a forest (Gagne and Cuddihy, 1999). *Deschampsia* grassland occurs primarily on state and federal lands. A good example is found inside Haleakalā National Park on Maui where over half of the remaining *Deschampsia* grassland in the state occurs. Feral pigs are the primary source

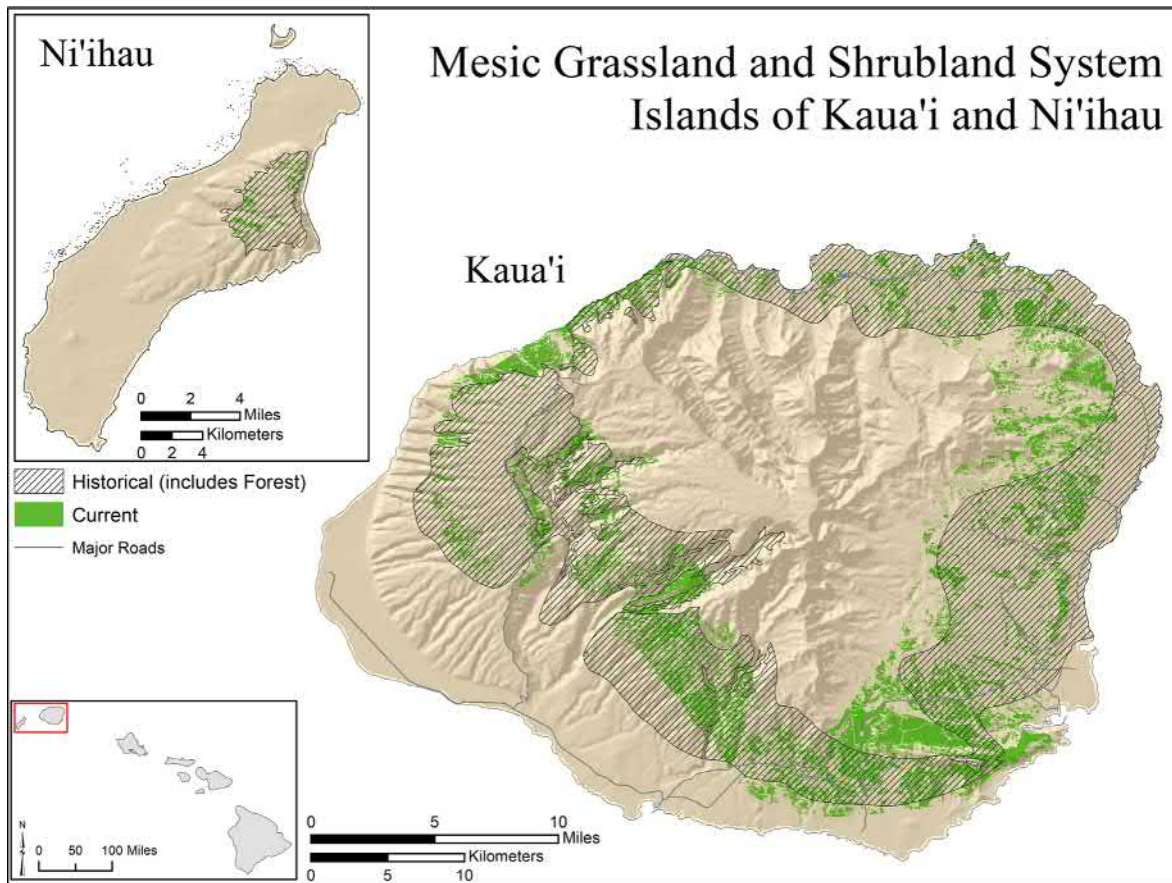


Fig. 2 Historical and current extent of the mesic grassland and shrubland system on the islands of Kaua'i and Ni'ihau.

of disturbance in the subalpine mesic grasslands. Invasive plants colonize disturbed areas and become established as a result of these animals (Gagne and Cuddihy, 1999).

Hawai'i lowland mesic grassland

Most of the vegetation in the lowland mesic shrublands and forests of the main Hawaiian islands has been changed from its original composition and is now composed mainly of mesic grasslands (Mueller-Dombois, 1992) that are floristically poor (Landfire, 2016) and may have originated from human-induced disturbance to the landscape. Native grassland communities generally remain only in areas that were unsuitable for agriculture and other habitat modifying activities by humans (Gagne and Cuddihy, 1999). Currently, there is one native lowland mesic grassland ecotype and two that are dominated by introduced species. The native Kāwelu grassland still exists on the islands of Kaua'i, O'ahu, Moloka'i, and Maui. It is dominated by *Eragrostis variabilis* and is located on moderate to steep slopes where it forms a continuous, dense ground cover. This mesic grassland subtype transitions into lowland mesic shrublands and forests, where 'ōhi'a (*Metrosideros polymorpha*) is present. The community may also extend downslope to coastal dry slopes (Gagne and Cuddihy, 1999). The Kāwelu grassland community is believed to have been much more extensive prior to human arrival (Cuddihy and Stone, 1990).

The introduced ecotypes include the Molasses grasslands (*Melinis minutiflora*) and Beardgrass grasslands (*Andropogon virginicus*/*Schizachyrium condensatum*). These communities have formed in areas that were once native grasslands and shrublands but that have since been disturbed by human activity, invasion by non-native weeds and browsing ungulates, and fire (Gagne and Cuddihy, 1999). Increased frequency of fire in the introduced grassland ecotypes is a result of the fire resilient, mat forming nature of the grass species that compose both ecotypes.

Hawai'i introduced perennial grassland

Introduced perennial grasslands have developed in areas that were once native dominated by lowland grasslands and shrublands but have since been replaced by introduced communities due to human activity. They are dominated by tall, medium, and/or a short statured herbaceous layer. Ecological changes to the community are primarily a result of introduced fire-adapted grasses and long term disturbance by browsing ungulates. The increased frequency of fire in the introduced perennial grasslands has led to the development of homogenous fire climax grass communities in some areas from coastal to subalpine environments (Gagne and Cuddihy,

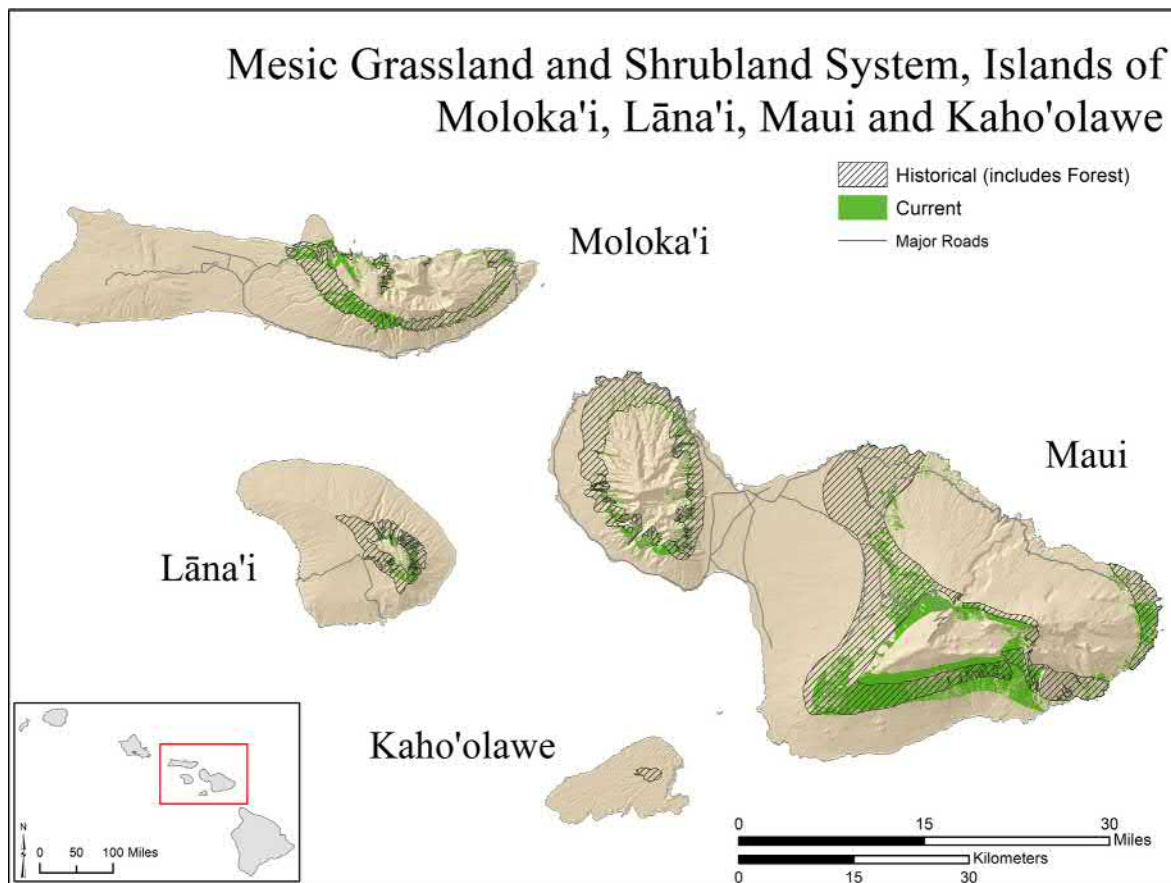


Fig. 3 Historical and current extent of the mesic grassland and shrubland system on the islands of Moloka'i, Lāna'i, Maui and Kaho'olawe.

1999). This community appears to be in secondary succession and requires continual disturbance for its maintenance (Gagne and Cuddihy, 1999).

Mesic pasture is distributed across 171,696 ac (69,483 ha) in the main Hawaiian islands. The largest proportion of mesic pasture exists on the islands of Hawai'i (59,097 ac; 23,916 ha) and Maui (8145 ac; 3296 ha) (NOAA, 2018). Many areas of pastureland occur within the introduced perennial grassland ecotype because the rainfall regime is optimal for growth of introduced pasture grasses.

Hawai'i introduced deciduous shrubland

The introduced deciduous shrubland cover type is dominated by haole koa (*Leucaena leucocephala*) and other introduced trees and shrubs. Haole koa are highly adaptable but prefer the mesic soil in low elevations. They are drought tolerant, fast growing, and produce a large amount of seeds forming dense thickets (Wildlife of Hawai'i, 2018). The introduced deciduous shrubland community overlaps in range with what was considered lowland mesic forests or lowland shrub and grassland communities historically. This ecotype often occurs throughout the main islands, especially on abandoned grazing lands (Gagne and Cuddihy, 1999). It has developed as a result of browsing by introduced goats and cattle and by processes driven by the increased frequency of fire due to introduced fire adapted grasses (Gagne and Cuddihy, 1999).

Hawai'i introduced evergreen shrubland

The Hawai'i introduced evergreen shrubland is dominated by introduced shrubs including Christmas berry (*Schinus terebinthifolius*) and gorse (*Ulex europaeus*). Christmas berry is fire resistant, drought tolerant, and flood tolerant, and can prevent or inhibit the growth of other plants by releasing chemicals (MISC, 2018). Gorse is a thorny shrub that is present on all of the main Hawaiian islands. It forms dense thickets which completely inhibits the regeneration of native species (USFWS, 2010). Seeds of gorse are adapted to germination after fires and the deep roots of this species make it resilient to fires (DLNR, 2018). In areas where the native vegetation no longer exists in lowland mesic grasslands, and fires have been curtailed, grasslands appear to be successional to shrublands dominated by introduced species such as Christmas berry (Gagne and Cuddihy, 1999). This community has replaced the native-dominated mesic lowland and montane forest, and native mesic shrublands and grasslands, as these native plant communities converted into an introduced shrubland following the introduction of fire tolerant shrub and grass species and as a result of disturbance by introduced ungulates and fire.

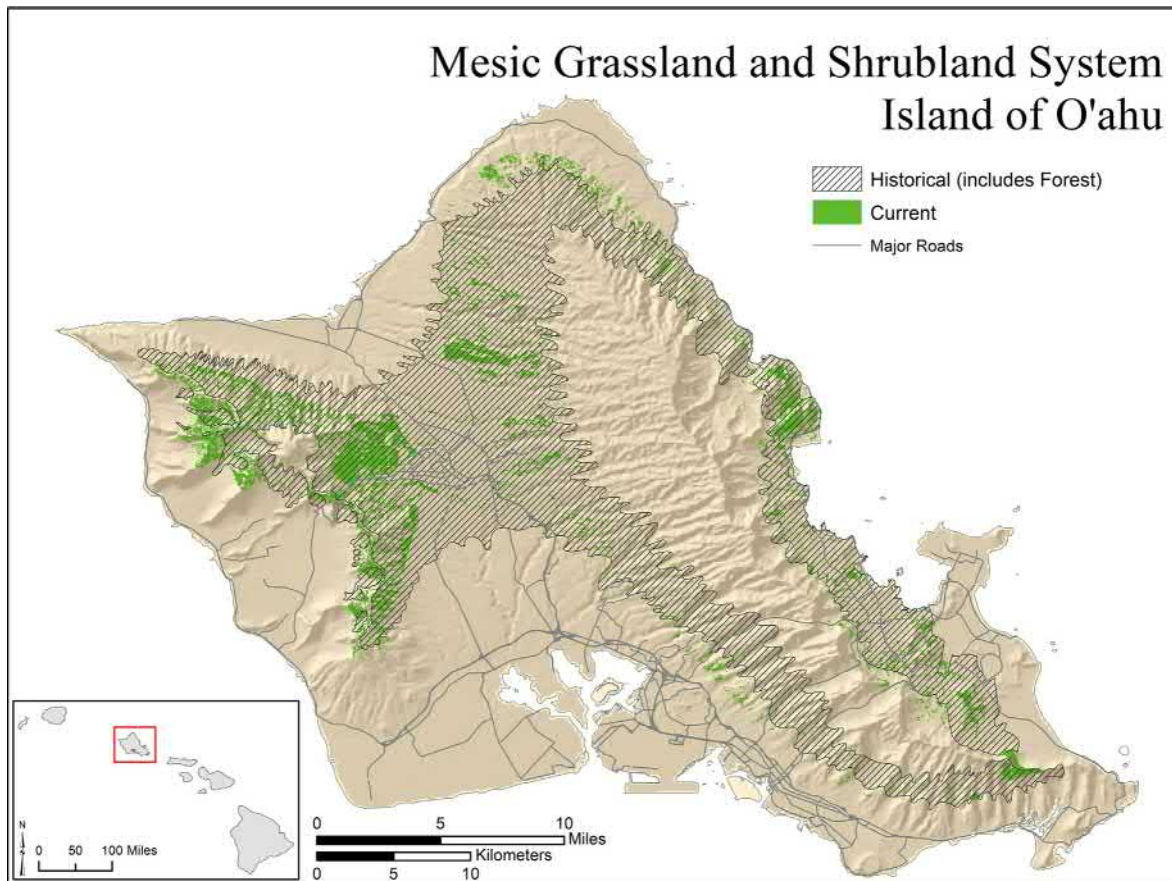


Fig. 4 Historical and current extent of the mesic grassland and shrubland system on the island of O'ahu.

Current distribution

Mesic grasslands and shrublands are found across multiple watersheds on all of the main Hawaiian islands. Between approximately 400 and 1800 CE, Hawaiians settled, colonized, and reshaped much of the vegetation of the lowlands, including mesic communities, on all the major Hawaiian islands (Kirch, 1982). In these ecosystems, Hawaiians used fire to clear land for agriculture (i.e., slash and burn). By the time of European contact in the late 1700s, most of the native mesic communities below 2500 ft (760 m) had been converted from forest, woodlands, and shrublands to open grasslands (Cuddihy and Stone, 1990; Kirch, 1982).

Since that time, native lowland mesic communities, including grasslands and shrublands, have been further converted to pasture, military or agricultural use, or have been lost to urbanization or fire (Cuddihy and Stone, 1990; State DLNR, 2016). It is estimated that <10% of the original native vegetation in lowland areas of the main Hawaiian islands currently remains (State DLNR, 2016). The majority of remaining native mesic grasslands and shrublands are found today at higher elevations and in areas where development, agriculture, and grazing have not been as intensive (Cuddihy and Stone, 1990; Figs. 5–8).

There are currently 457,929 ac (185,317 ha) of native and introduced mesic grasslands and shrublands distributed across Hawai'i, Moloka'i, Maui, O'ahu, Kaua'i, Lāna'i, and Ni'ihau (Reeves and Amidon, 2018). Over 70% of the biome occurs on the island of Hawai'i (Table 3; Fig. 5). Over half of the mesic grassland and shrubland biome in the state of Hawai'i occurs on private land. The remaining portion is owned by the federal, state and local government (Table 5, Fig. 10).

Native subtypes

Native grasslands and shrublands compose approximately 33% (148,895 ac; 60,256 ha) of all mesic grasslands and shrublands. Most of the native mesic lowland and subalpine shrublands occur on Hawai'i, Maui, Moloka'i, Lāna'i, and O'ahu. Of this, the majority occurs on Hawai'i (130,071 ac; 52,638 ha) and Maui (13,965 ac; 5651 ha). The remaining native shrubland occurs on Moloka'i (3116 ac; 1261 ha), Lāna'i (665 ac; 269 ha), and O'ahu (4 ac; 1.6 ha). The total amount of native *Deschampsia* grassland is 1074 ac (435 ha) occurring primarily on the island of Maui (Table 4, Fig. 9).

Introduced subtypes

Introduced grasslands and shrublands account for 67% (308,536 ac; 124,860 ha) of the available mesic grassland and shrubland biome statewide. A small amount of mixed native/introduced grassland and shrubland is also found on the island of Moloka'i (498 ac; 201 ha) (Table 4, Fig. 7).

Table 2 Characteristics of current mesic grasslands and shrublands in Hawai'i.

Mesic grassland and shrubland subtypes (subcategories)	Precipitation (mm)	Elevation (m)	Characteristic plants
Lowland mesic shrubland	1000–2000 mm	30–850 m	<i>Metrosideros polymorpha</i> ('ōhi'a), <i>Leptecophylla tameiameia</i> (pūkiawe), <i>Dodonaea viscosa</i> ('a'ali'i), <i>Eragrostis variabilis</i> (kāwelu), <i>Tetramolopium lepidotum</i> , <i>Dicranopteris linearis</i> , <i>Osteomeles anthyllidifolia</i> ('ūlei), <i>Lipochaeta</i> spp. (nehe), <i>Wilkesia gymnoxiphium</i> , <i>Wilkesia hobbdi</i> (iliau)
Subcategories: • 'Ōhi'a • Pūkiawe/'A'ali'i • 'Ūlei • Nehe • Iliau			
Subalpine mesic shrubland	1300–1900 mm	1950–2300 m	<i>Sadleria cyatheoides</i> (ama'u), <i>Vaccinium calycinum</i> , <i>Vaccinium reticulatum</i> ('ōhelo)
Montane-subalpine mesic grassland	1300–1900 mm	1680–2100 m	<i>Carex</i> spp., <i>Coprosma montana</i> (pilo), <i>Deschampsia nubigena</i> , <i>Dubautia</i> spp.
Subcategories: • <i>Deschampsia nubigena</i>			
Lowland mesic grassland	750–1000 mm	300–2000 m	<i>Luzula hawaiiensis</i> , <i>Leptecophylla tameiameia</i> (pūkiawe) Native: <i>Eragrostis variabilis</i> (kāwelu), <i>Bidens</i> spp. (ko'oko'olau), <i>Dodonaea viscosa</i> (a'ali'i), <i>Gouania hillebrandii</i> , <i>Metrosideros polymorpha</i> ('ōhi'a), <i>Metrosideros tremuloides</i> ('ōhi'a) Non-native: <i>Andropogon virginicus</i> (Broomsedge), <i>Melinis minutiflora</i> (Molasses grass) and <i>Schinus terebinthifolius</i> (Christmas berry), <i>Schizachyrium condensatum</i> (Beard grass)
Subcategories: • Kāwelu			
Non-native: • Molasses grass • Beardgrass			
Introduced perennial grassland	1300–1900 mm	Unrestricted	<i>Urochloa maxima</i> (guinea grass), <i>Pennisetum purpureum</i> (elephant grass) or <i>Hyparrhenia hirta</i> (thatching grass); medium-tall grasses like <i>Pennisetum setaceum</i> (fountain grass), <i>Brachiaria mutica</i> (California grass), <i>Panicum virgatum</i> (switch grass), or <i>Schizachyrium condensatum</i> (beard grass); or shorter grasses such as <i>Andropogon virginicus</i> (broomsedge), <i>Cymbopogon refractus</i> (barb wire grass), <i>Cynodon dactylon</i> (bermuda grass), <i>Melinis minutiflora</i> (molasses grass), <i>Melinis repens</i> (natal red top), <i>Paspalum conjugatum</i> (Hilo grass), <i>Pennisetum ciliare</i> (buffel grass), <i>Pennisetum clandestinum</i> (kikuyu grass)
Introduced deciduous shrubland	1300–1900 mm	Unrestricted	<i>Leucaena leucocephala</i> (haole koa), <i>Acacia confusa</i> , <i>Acacia mearnsii</i> , <i>Caesalpinia decapetala</i> , <i>Lantana camara</i> , <i>Rubus argutus</i> , and <i>Rubus discolor</i>
Introduced evergreen shrubland	1300–1900 mm	Unrestricted	<i>Schinus terebinthifolius</i> (Christmas berry) and <i>Ulex europaeus</i>

Gagne and Cuddihy, 1999; Landfire, 2016.

Non-native mesic grasslands, which include both introduced perennial and lowland mesic grasslands, account for 248,425 ac (100,534 ha) statewide and occur primarily on the islands of Hawai'i (175,670 ac; 71,091 ha), Maui (35,826 ac; 14,498 ha), Kaua'i (27,823 ac; 11,262 ha), O'ahu (7437 ac; 3010 ha), Moloka'i (1405 ac; 569 ha), and Lāna'i (264 ac; 107 ha). The non-native mesic shrubland, which includes both the introduced evergreen and deciduous shrubland sub-types, totals 60,111 ac (24,326 ha) statewide. These sub-types occur on Hawai'i (19,581 ac; 7924 ha), Kaua'i (17,593 ac; 7120 ha), O'ahu (13,599 ac; 5503 ha), Moloka'i (4004 ac; 1620 ha), Maui (3377 ac; 1367 ha), Lāna'i (1268 ac; 513 ha), and Ni'ihau (689 ac; 279 ha) (Table 4, Fig. 9).

Stressors

Hawai'i mesic grasslands and shrublands are vulnerable to impacts of stressors occurring from climate and non-climate threats since they are sensitive to biotic and abiotic factors associated with both of these (Hilberg et al., 2018). Table 6 lists the stressors for mesic grasslands and shrublands and the major stressors are described in further detail below.

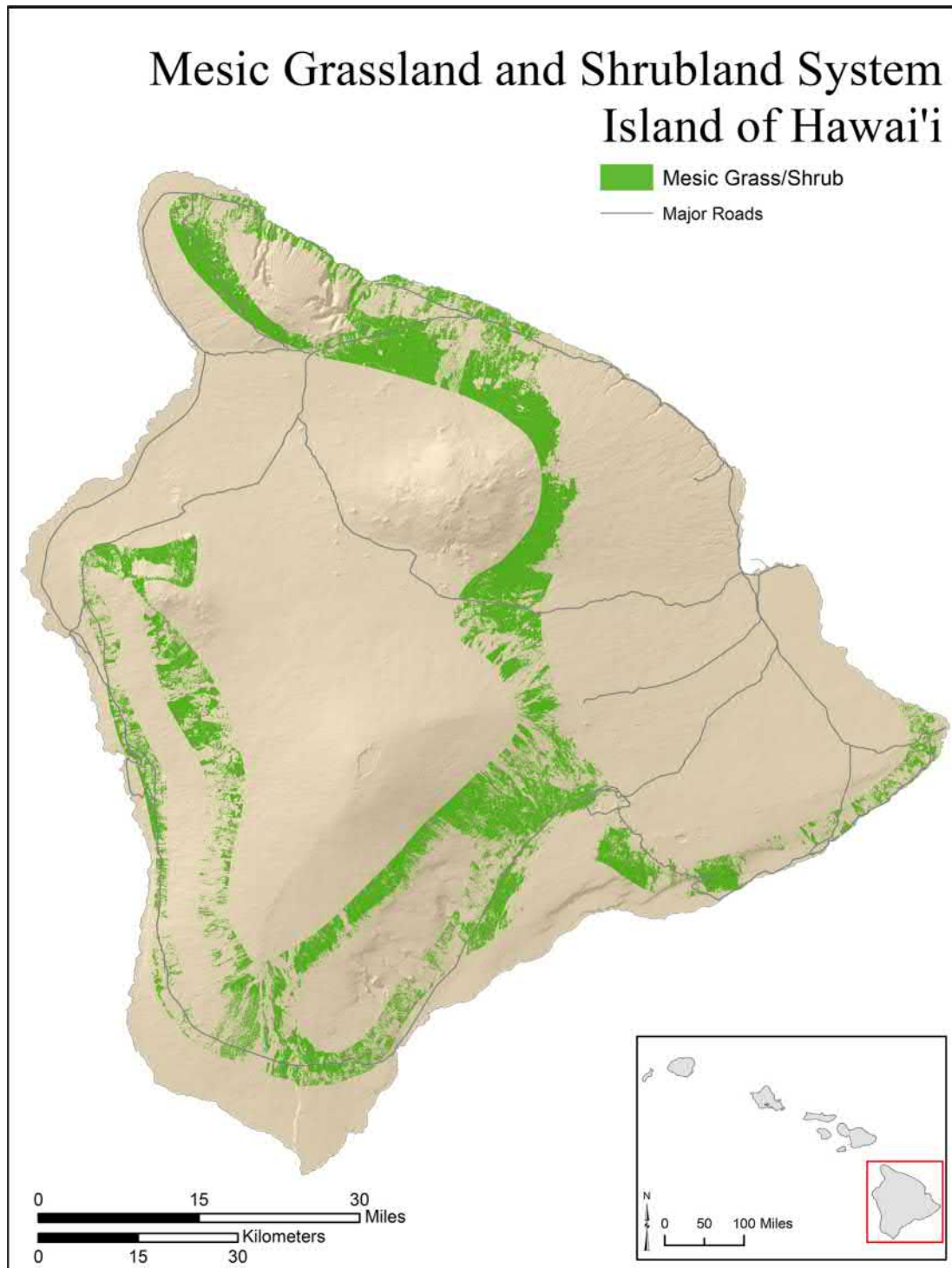


Fig. 5 Current distribution of the mesic grassland and shrubland system on the island of Hawai'i.

Climate stressors

Precipitation, wind, drought, soil moisture, air temperature, and storms

One of the most sensitive climatic components of the mesic grasslands and shrublands is water availability as a function of altered precipitation levels, soil moisture, drought, air temperature, and presence of trade winds. For example, reduced water availability can directly alter vegetation composition and distribution in these communities by favoring growth and germination of invasive plants with higher tolerance for drier or wetter conditions (Hilberg et al., 2018; Camp et al., 2018).

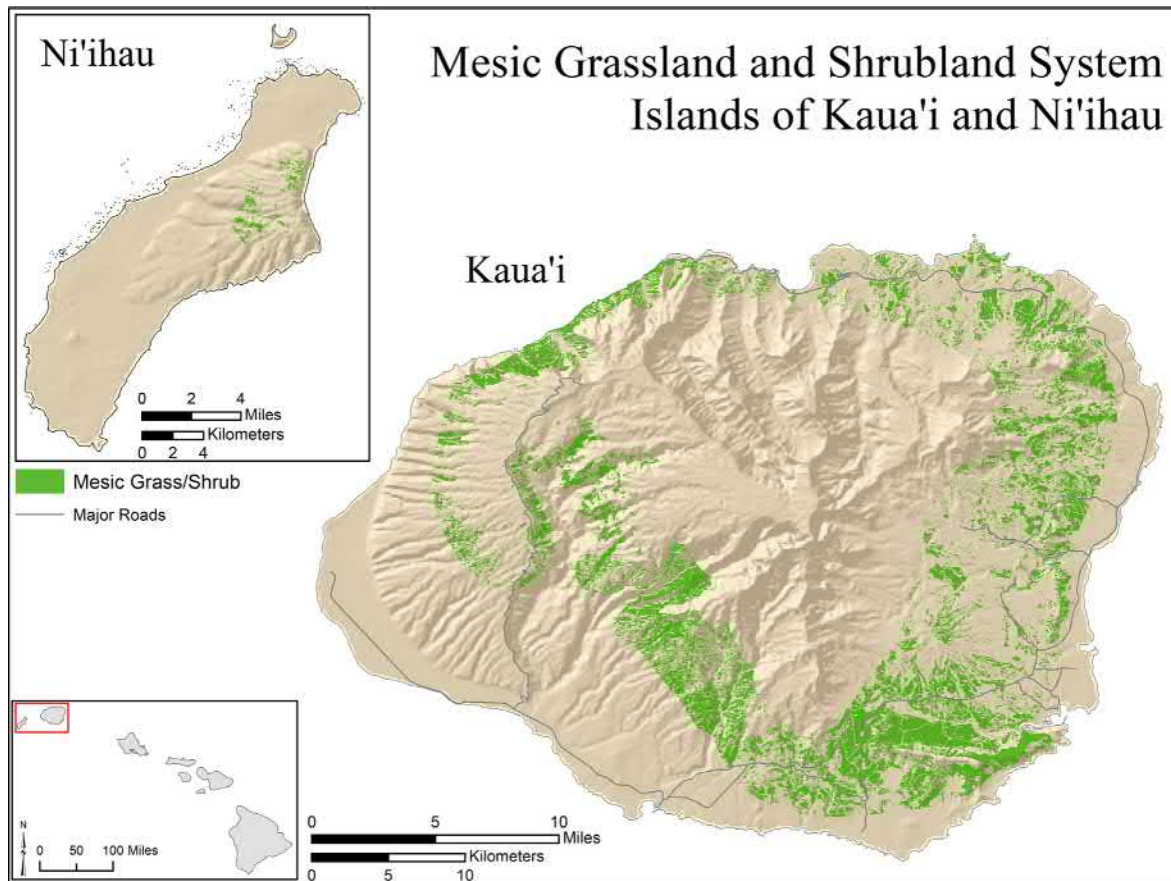


Fig. 6 Current distribution of the mesic grassland and shrubland system on the islands of Kaua'i and Ni'ihau.

The impact of changes in climate are likely to influence the distribution of native and introduced plant species ranges across the Hawaiian islands (Price et al., 2012). Climate modeling at Hawai'i Volcanoes National Park suggest that some native montane mesic grassland and shrubland species with narrow moisture requirements may diminish as components in mesic shrublands, or possibly migrate to wetter biomes. The same analyses found that dry biomes of the park may transition to more mesic biomes with changing climate (Camp et al., 2018). An increase in precipitation and flooding may also increase the frequency of landslides which can destroy mesic grasslands and shrublands and alter their succession, particularly in areas with poor drainage or on steep slopes and valleys (Restrepo and Vitousek, 2001; Walker, 1999).

One of the primary questions regarding the possible impacts of warming temperatures on climate in Hawai'i is whether the trade wind inversion layer will be affected. If the height or frequency of the inversion layer changes due to warming, significant hydrological and ecological changes to vegetation communities can be expected (Loope and Giambelluca, 1998; Krushelnycky et al., 2016).

Non-Climate stressors

Invasive species

Invasive species, including plants and animals, are a prominent stressor for the Hawaiian mesic grassland and shrubland ecosystem since many of the native species evolved in isolation in the absence of mammalian herbivores and plant competitors (Weller et al., 2011; Dunkell et al., 2011). Some invasive plants are less susceptible to drought and less palatable to invasive herbivores and therefore may thrive when disturbance events occur and outcompete the native mesic grassland and shrubland vegetation (Weller et al., 2011). Introduced grasses also impede the germination of native seeds (Baker et al., 2009). Invasive plants capable of modifying lowland mesic shrubland communities include *Psidium* spp., *Morella faya*, *Schinus terebinthifolius*, and *Melinis minutiflora*. Feral ungulates (pigs, goats, and deer) consume and trample new growth and seedlings of native vegetation, and also promote the spread of invasive plant seeds through fecal matter causing further degradation of the mesic areas (Dunkell et al., 2011; Gagne and Cuddihy, 1999). Feral pigs and goats are the primary source of disturbance in the subalpine mesic grasslands and shrublands, and both facilitate the spread of invasive plants in disturbed areas (Gagne and Cuddihy, 1999). Examples of the effects of introduced species on mesic grasslands and shrublands follow.

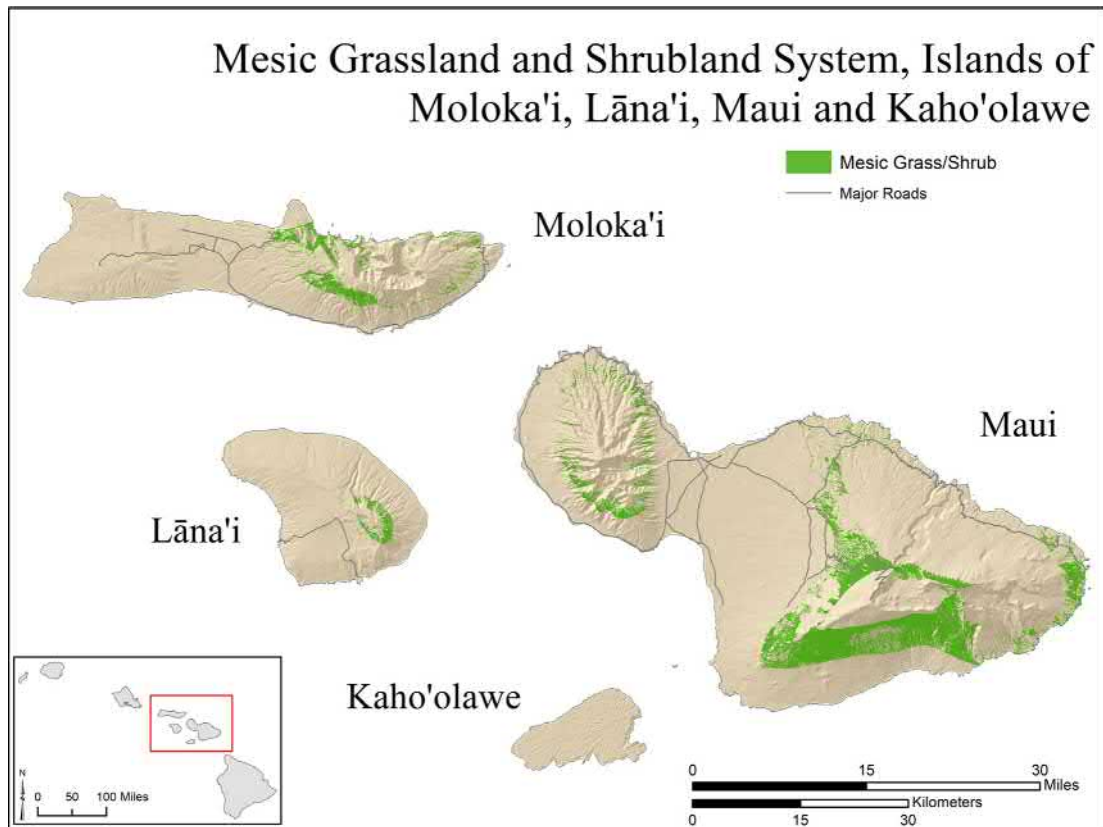


Fig. 7 Current distribution of the mesic grassland and shrubland system on the islands of Moloka'i, Lāna'i, Maui and Kaho'olawe.

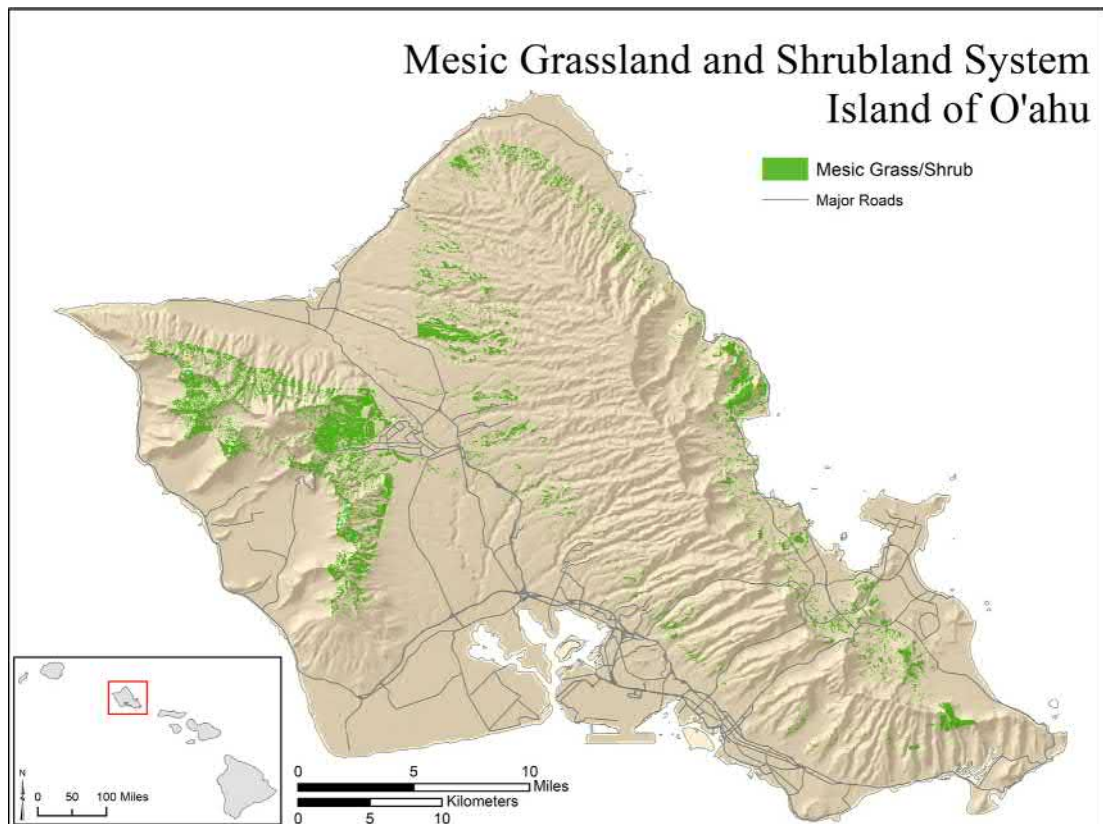


Fig. 8 Current distribution of the mesic grassland and shrubland system on the island of O'ahu.

Table 3 Distribution and area of mesic grassland and shrublands in the Hawaiian islands [Reeves and Amidon, 2018](#).

Island	Area in acres (hectares)	Area (% of island)	% of State of Hawai'i
Ni'ihau	689 (279)	1	< 1
Lāna'i	2198 (890)	2	< 1
Moloka'i	9022 (3651)	5	< 1
Kaua'i	45,416 (18,379)	13	1
O'ahu	21,043 (8516)	6	1
Maui	54,244 (21,952)	12	1
Hawai'i	325,322 (131,653)	13	8

Table 4 Current amount of mesic grassland and shrubland by subcategory [Reeves and Amidon, 2018](#).

Subcategory	Acres (hectares)
Mixed native-non-native mesic shrubs and grass	498 (202)
Native <i>Deschampsia</i> grassland	1074 (435)
Native mesic shrubland	147,821 (59,821)
Non-native mesic grassland	248,425 (100,534)
Non-native mesic shrubland	60,111 (24,326)
Total	457,929 (185,317)

- Lowland mesic grasslands are defined by two introduced sub-types: the Introduced molasses grass (*Melinis minutiflora*) and beardgrass (*Andropogon virginicus*) communities, both of which were primarily formed due to invasive species. These sub-types are present on most of the main Hawaiian islands and overlap with the native mesic shrublands and kāwelu grasslands. Lowland mesic grasslands, and more recently formed sub-types including introduced perennial grasslands, have been sculpted by human activity following the development of ranching, disturbance, and subsequent invasion of non-native weeds and browsing ungulates. In some lowland areas where native vegetation no longer exists and fires have been curtailed, mesic grasslands may be successional to introduced shrublands and forests, often composed of species such as Christmas berry (*Schinus terebinthifolius*) and firetree (*Myrica faya*) ([Gagne and Cuddihy, 1999](#); [MISC, 2018](#)).
- Introduced perennial grassland sub-types developed after the conversion of native lowland mesic forests and shrublands to grasslands following the arrival of humans in the Hawaiian islands ([Cuddihy and Stone, 1990](#); [Kirch, 1982](#)). The conversion from native-dominated ecotypes to entirely introduced grasslands is the result of human activity and disruptions brought by fire and introduced species, e.g., grazing ungulates. ([Gagne and Cuddihy, 1999](#)).
- Introduced evergreen and deciduous shrublands are defined by a dominant invasive vegetation community. In areas where the native vegetation no longer exists in lowland mesic grasslands, and fires have been curtailed, grasslands appear to be successional to introduced evergreen shrublands dominated by introduced species such as Christmas berry (*Schinus terebinthifolius*) ([Gagne and Cuddihy, 1999](#)). Christmas berry and gorse (*Ulex europaeus*) are both fire resilient and can prevent or inhibit the growth of other plants by releasing chemicals ([MISC, 2018](#)). Gorse is a thorny shrub that grows up to 6 ft. (2 m) tall and is only found on Maui, Molokai, and Hawaii. It forms dense thickets excluding almost all other species. This sub-type has also been shaped from browsing by invasive ungulates.

Agriculture, grazing, and urban development

Continued human population growth on all of the main Hawaiian islands has increased the need for additional housing and development ([State of Hawai'i, 2016](#)). Additional development threatens mesic grasslands and shrublands that exist primarily on private land across the islands ([Table 5, Fig. 10](#)).

Currently, most cattle grazing takes place on private and state-leased lands. However, cattle persist in many areas where inadequate or absent fencing has allowed them to wander into native-dominated areas. Unmanaged cattle are widely recognized as a major destructive agent in Hawai'i's ecosystems and have had a significant effect on montane mesic communities ([State DLNR, 2016](#)). Introduced pasture grasses brought to the Hawaiian Islands for the purpose of cattle ranching have also spread into native-dominated areas ([Cuddihy and Stone, 1990](#)).

Wildfire

The proliferation of invasive grasses adapted to fire and the increased incidence of human ignited fires have resulted in an altered fire regime that is more frequent and severe, and increasing as much as fivefold in frequency since the 1970s ([Abrahamson, 2013](#)). Fire is considered to be a primary threat to mesic grasslands and shrublands due to invasive grass fuels ([USFWS, 2010](#)). Some native plant

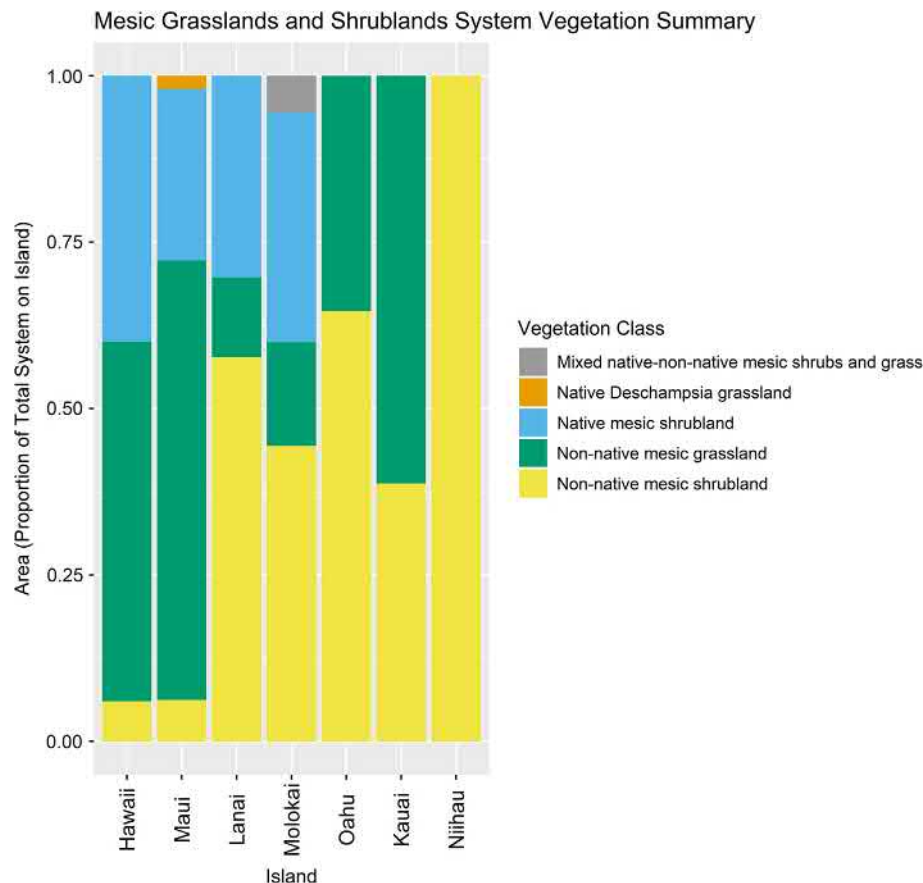


Fig. 9 Summary of mesic grassland and shrubland vegetation classifications.

species found in mesic grasslands and shrublands (e.g., ‘a‘ali‘i, ‘ōhi‘a, and ‘ūlei), show some tolerance of fire but most species (e.g., pūkiawe), are severely set back, killed, or compete poorly with alien vegetation when impacted by fire (Smith and Tunison, 1992).

Fire can create a cycle of spiraling degradation where cumulative effects of fire feed into the cycle of replacement with a greater percentage of invasive plants that are more susceptible to fire (leading to more frequent and severe fires and greater proportion of invasive plants). Fire affects the sub-types of the mesic grassland and shrubland differently. For example, the fire potential is considered to be relatively high in the montane mesic zone due to the continuous arrangement of grasses and abundance of shrubs (Smith and Tunison, 1992; USFWS, 2010). Fires in the lowland mesic grasslands have increased due to the presence of mat-forming and fire-adapted grasses (*Pennisetum clandestinum* and *Pennisetum setaceum*). The effect of fire on the introduced perennial grasslands has resulted in an increased fire frequency due to fire-adapted grasses and the development of secondary fire-climax grassland communities from coastal to subalpine environments (Gagne and Cuddihy, 1999). The introduced evergreen shrublands are able to recover from the effects of wildfire with fire adapted species such as gorse, whose seeds quickly germinate after fires (DLNR, 2018). Fire intensifies deciduous shrublands by increasing the cover of koa haole, which resprouts from the base and becomes established from seed (Smith and Tunison, 1992).

Natural disasters

Mesic grasslands and shrublands are susceptible to natural disasters such as volcanic eruptions and lightning fires that may remove vegetation and alter succession (Hilberg et al., 2018). These events can cause extensive damage over short time periods but are generally localized in their extent and occur only on the volcanically active island of Hawai‘i. Regeneration of native mesic grasslands and shrublands is slow on these newly created volcanic substrates, beginning with the growth of lichens and pioneer species. Substrate age, climatic moisture, and elevation are the primary drivers of rates of succession. Succession rates in mesic biomes are slower than in wet areas but faster than in dry and arid regions (Carlquist, 1980; Price et al., 2012).

Biological

The significant population decline of seabirds has likely had a negative impact on mesic biomes, including native mesic grasslands and shrublands. Seabirds contribute marine derived nutrients, especially nitrogen, to mesic areas through deposition of guano

Table 5 Land ownership of mesic grasslands and shrublands in Hawai'i (Reeves and Amidon, 2018).

Island	Land ownership	Area in acres (hectares)	Area (% of island)	Area (% of State of Hawaii)
Ni'ihau	Private	689 (279 ha)	1	<1
Lāna'i	Private	2198 (886 ha)	2	<1
Moloka'i	Govt. State	2857 (1156 ha)	2	<1
Moloka'i	Private	6166 (2495 ha)	4	<1
Kaua'i	Govt. Federal	243 (98 ha)	<1	<1
Kaua'i	Govt. Local	56 (23 ha)	<1	<1
Kaua'i	Govt. State	13,468 (5450 ha)	4	<1
Kaua'i	No data	1313 (531 ha)	<1	<1
Kaua'i	Private	30,336 (12,276 ha)	9	1
O'ahu	Govt. Federal	5493 (2223 ha)	1	<1
O'ahu	Govt. Local	1237 (501 ha)	<1	<1
O'ahu	Govt. State	5306 (2147 ha)	1	<1
O'ahu	No data	213 (86 ha)	<1	<1
O'ahu	Private	8794 (3559 ha)	2	<1
Maui	Govt. Federal	7850 (3067 ha)	2	<1
Maui	Govt. Local	394 (159 ha)	<1	<1
Maui	Govt. State	16,634 (6732 ha)	4	<1
Maui	No data	1 (0.4 ha)	<1	<1
Maui	Private	29,364 (11,883 ha)	6	1
Hawai'i	Govt. Federal	57,810 (23,395 ha)	2	1
Hawai'i	Govt. Local	1245 (504 ha)	<1	<1
Hawai'i	Govt. State	133,115 (53,870 ha)	5	3
Hawai'i	No data	1077 (436 ha)	<1	<1
Hawai'i	Private	132,076 (53,449 ha)	5	3

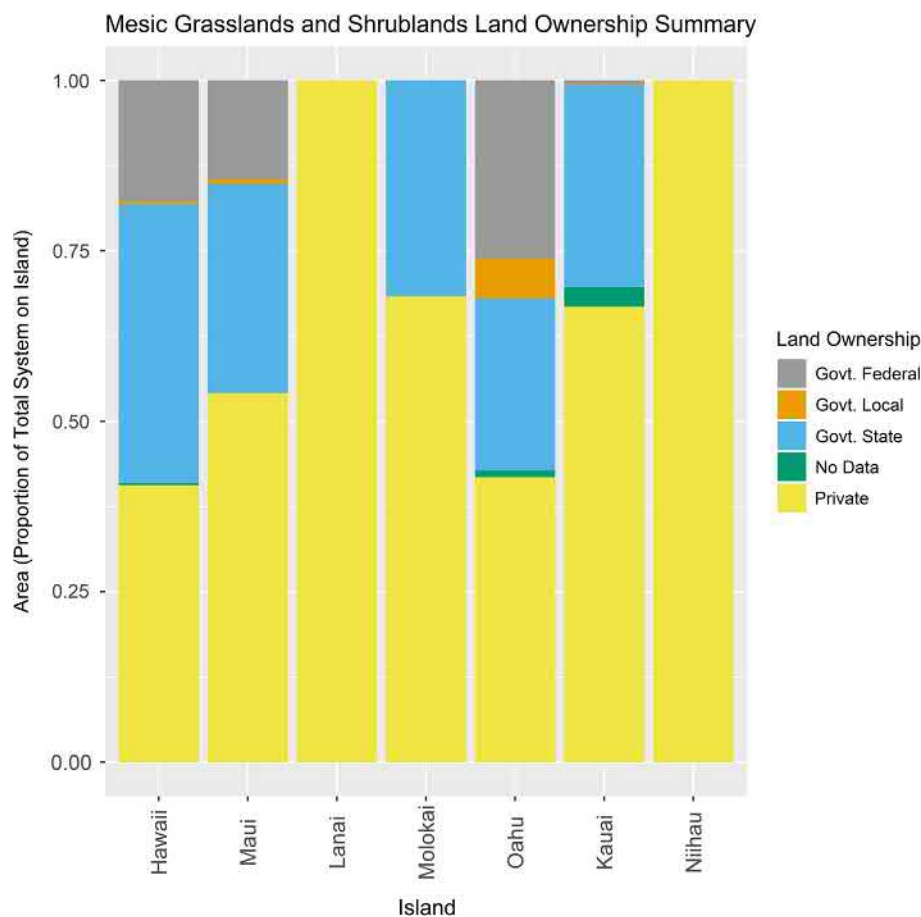
**Fig. 10** Summary of mesic grassland and shrubland land ownership.

Table 6 Climate and non-climate stressors of mesic grasslands and shrublands.

<i>Climate stressors</i>	<i>Non-climate stressors</i>
Precipitation	Invasive species
Wind	Urban development
Drought	Agriculture/grazing
Soil moisture	Insects/disease
Air temperature	Wildfire
Storms	Volcanic eruptions

Table 7 Reserves of high conservation importance for the native mesic grassland and shrubland biome.

<i>Protected area</i>	<i>Location information</i>	<i>Landowner/manager</i>	<i>Total protected acreage (ac)</i>
Haleakalā National Park	Maui	Federal	33,265 ac (13,462 ha)
Hawai'i Volcanoes National Park	Hawai'i	Federal	207, 635 ac (84, 027 ha)
Kamakou Preserve	Moloka'i	Nature conservancy	1220 ac (494 ha)
Waikamoi Preserve	Maui	Nature conservancy	5230 ac (2116 ha)
Kona Hema Preserve	Hawai'i	Nature conservancy	8107 ac (3281 ha)
Kona National Wildlife Refuge	Hawai'i	Federal	3737 ac (1512 ha)
Keauhou	Hawai'i	Private	22,723 ac (9196 ha)

Conservation importance refers to the protected areas relative priority and how it falls within resilience, representation, and redundancy.

Table 8 Laws and regulations.

<i>Title</i>	<i>Year implemented</i>	<i>Authority</i>	<i>Intent/purpose</i>
Endangered Species Act	1973	Federal	Protects critically imperiled species from extinction
50 CFR 16	1974	Federal	Implements the Lacey Act (18 USC 42), which prohibits importation of injurious species
Convention on International Trade in Endangered Species	1975	International	Ensures that international trade in specimens of wild animals and plants does not threaten the survival of the species in the wild
Executive Order 11987	1977	Federal	Charges Executive agencies with restricting the introduction of exotic species into the natural ecosystems on federal lands; and encourages States to do the same
Hawai'i Administrative Rules, Title 4, Subtitle 6, Chapters 68 and 70	1981	Hawai'i (Department of Agriculture, DOA)	Rules/amendments for noxious weeds, plant and non-domestic animal quarantine, plant import, and bromeliad import
Executive Order 13112	1999	Federal	Requires that a Council of Departments dealing with invasive species be created to prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause
HRS 194-2	2002	Hawai'i (Department of Land and Natural Resources, DLNR)	Establishes Hawaii Invasive Species Council (HISC)
Act 85	2003	Hawai'i (HISC)	Conveys statutory authority to HISC to continue to coordinate approaches among the various State and Federal initiatives for the prevention and control of invasive species
Act 36 (2011) HRS 150A-5.3	2011	Hawai'i (DOA)	Imposes a fee for the inspection, quarantine, and eradication of invasive species contained in any freight brought into the State
HB 1568	2011	Hawai'i (DOA)	Requires commercial harbors and airports in Hawai'i to provide biosecurity and to facilitate cargo inspections

Table 9 Responses of mesic grassland and shrubland stressors in foreseeable future scenarios (Amidon and Reeves, 2018).

Conservation management parameters (CMPs)				
Conservation values	Stakeholder involvement and public opinion influence the formulation, implementation, and funding of natural resource conservation and biosecurity (NRC/B) within laws and development or conservation plans			
Laws and biosecurity	National, state, county, and city laws and regulations are the means by which NRC/B are supported and implemented			
Planning for development or conservation	National, state, county, city, and private development plans or conservation plans define actions that result in losses or gains in NRC/B (impacts realized at implementation)			
Foreseeable Future Scenarios and the resulting mesic grassland and shrubland conditions				
Use Foreseeable Future Scenario one as a “baseline” to characterize changes in <i>Conservation actions</i> and <i>Ecotype conditions</i> in Future Scenarios Two, Three, and Four	Scenario One <i>CMPs</i> : Unchanged in support for NRC/B <i>Conservation actions</i> : No change; current rate of land cover change continues through the foreseeable future <i>Ecotype condition</i> : habitat area, quality, and sustainability slowly decrease through the foreseeable future	Scenario Two <i>CMPs</i> : Small increase in support for NRC/B <i>Conservation actions</i> : Marginal increase <i>Ecotype condition</i> : Habitat area is unchanged through the foreseeable future; habitat quality and sustainability are slightly enhanced through the foreseeable future	Scenario Three <i>CMPs</i> : Small to moderate decrease in support for NRC/B <i>Conservation actions</i> : Substantial decrease <i>Ecotype condition</i> : Urban and agricultural uses are prioritized over conservation; habitat area, quality, and sustainability substantially decrease through the foreseeable future	Scenario Four <i>CMPs</i> : Moderate to high increase in support for NRC/B <i>Conservation actions</i> : Substantial increase <i>Ecotype condition</i> : Robust, sustained effort to restore, manage, and expand conservation; habitat area, quality, and sustainability substantially increase through the foreseeable future
Stressors	Responses of mesic grassland and shrubland stressors			
Development	Small to moderate increase	No change (redevelop)	Moderate to high increase	Small to moderate decrease
Altered hydrology	No change to small increase	No change	Larger increase	Small decrease
Recreation/access	Small increase	Small increase	Larger increase	Larger increase
Invasive species	Small increase	Small increase	Larger increase	Small decrease
Plant diseases	Small increase	Small increase	Larger increase	No change to small decrease
Fire	Small to moderate increase	Small increase	Larger increase	No change to small increase
Erosion	Small increase	No change	Larger increase	Small decrease
Climate				
Temperature	Small to moderate increase	Small to moderate increase	Small to moderate increase	Small to moderate increase
Precipitation	Small decrease	Small decrease	Small decrease	Small decrease
Storms	Small increase	Small increase	Small increase	Small increase

Table 10 Summary of overall condition for mesic grassland and shrubland sub-types in the future scenarios.

<i>Sub-types</i>	<i>Scenario 1: Status Quo</i>	<i>Scenario 2: slightly improved</i>	<i>Scenario 3: substantially decreased</i>	<i>Scenario 4: substantially improved</i>
Lowland native mesic grasslands and shrublands	Decrease	Slowly decrease	Rapidly (severely) decrease	Significantly increase
Montane-subalpine native mesic grasslands and shrublands	Decrease	Slowly decrease	Rapidly (severely) decrease	Significantly increase
Introduced perennial grasslands, deciduous shrublands, and evergreen shrublands	Increase	Slight increase	Significantly increase	Slowly decrease

Table 11 Summary of interactions of stressors and current conservation efforts on redundancy, resiliency and representation in mesic grassland and shrubland sub-types.

<i>Sub-type</i>	<i>Redundancy</i>	<i>Resiliency</i>	<i>Representation</i>
Lowland mesic shrubland	Decrease	Decrease	Decrease
Lowland mesic grassland	Decrease	Decrease	Decrease
Montane-Subalpine mesic shrubland	Decrease	Decrease	Decrease
Montane-Subalpine mesic grassland	Decrease	Decrease	Decrease
Introduced perennial grassland	Increase	Increase	Increase
Introduced deciduous shrubland	Increase	Increase	Increase
Introduced evergreen shrubland	Increase	Increase	Increase

(Rowe et al., 2017). In addition, the loss of native insect pollinators has reduced the pollination of some native Hawaiian plant species resulting in lower rates of regeneration (Aslan et al., 2013; Price and Wagner, 2004). The overall decline of native birds, including seed dispersing native passerines and the Hawaiian goose (*Branta sandvicensis*) also limits the regeneration of native shrublands where these species once occurred (Culliney et al., 2012).

Conservation Efforts

Reserves

Approximately 82,477 (33,377 ha) of mesic grasslands and shrublands are protected in reserve areas across the main Hawaiian Islands (Fig. 11). Reserve areas are defined as those designated as parks and reserves. These may include areas designated as a national park, national wildlife refuge, Natural Area Reserve (NAR), or Nature Conservancy preserves (Reeves and Amidon, 2018). The amount of mesic grasslands and shrublands protected in reserve areas varies by island, with 66,012 ac (26,714 ha) on the island of Hawai'i, 11,040 ac (4468 ha) on Maui, 2702 ac (1093 ha) on Moloka'i, 2402 ac (972 ha) on Kaua'i, and 321 ac (130 ha) on O'ahu (Fig. 11). Of the 66,012 ac (26,714 ha) protected in reserves areas on the island of Hawai'i roughly 45,288 ac (18,327 ha) are classified as native dominated habitat (Fig. 11). Lāna'i and Ni'ihau contain the least amount of mesic grasslands and shrublands protected in reserve areas in the State with <3 ac (1 ha) on both Lāna'i and Ni'ihau (Fig. 11). Knowing that <82,477 ac (33,377 ha) of mesic grasslands and shrublands are protected in reserve areas in the State, and 457,929 ac (185,317 ha) are actually classified as mesic grasslands and shrublands in the State, indicates a need to implement additional measures to increase the public's awareness of the remaining gap between unprotected versus protected mesic grasslands and shrublands.

Active conservation efforts that benefit native mesic grassland and shrubland communities are underway in protected reserves and within watershed management areas. These efforts include wildfire threat control, invasive species management, exclusion fencing for ungulates, and removal of non-native ungulates and weeds. The islands of Hawai'i, Maui, and Moloka'i have the most intact areas of remaining native-dominated mesic grasslands and shrublands in the state (Fig. 12). Reserves of high conservation importance for the native mesic grassland and shrubland biome are included in Table 7.

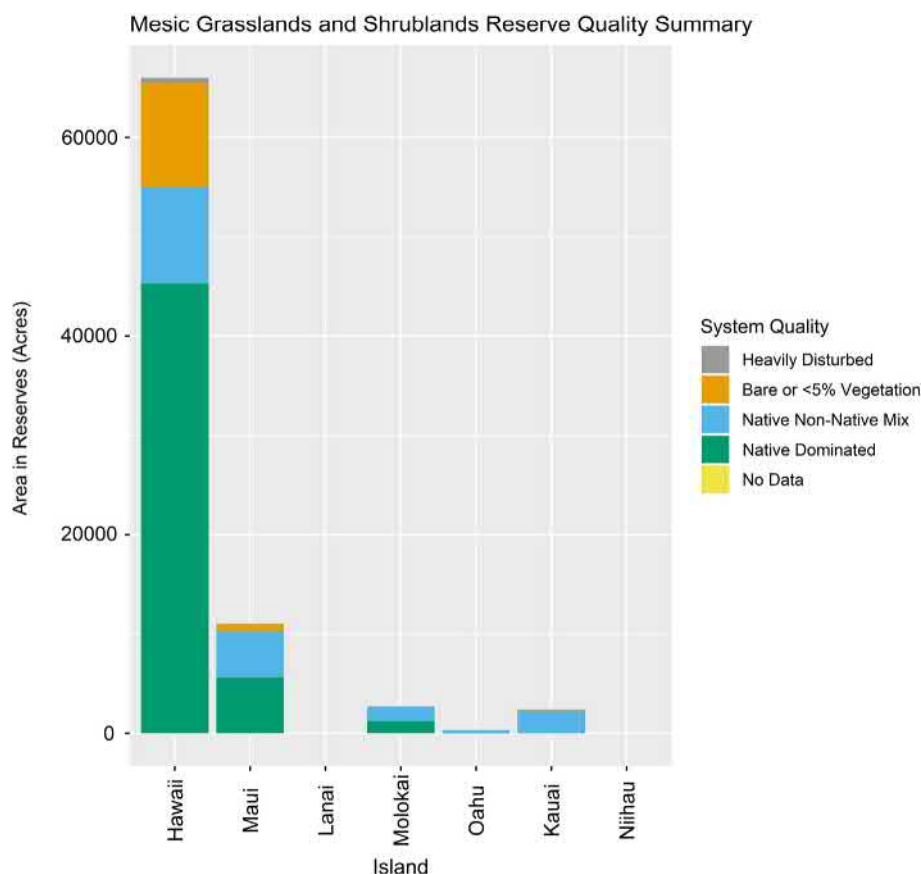


Fig. 11 Quality of mesic grasslands and shrublands in reserves.

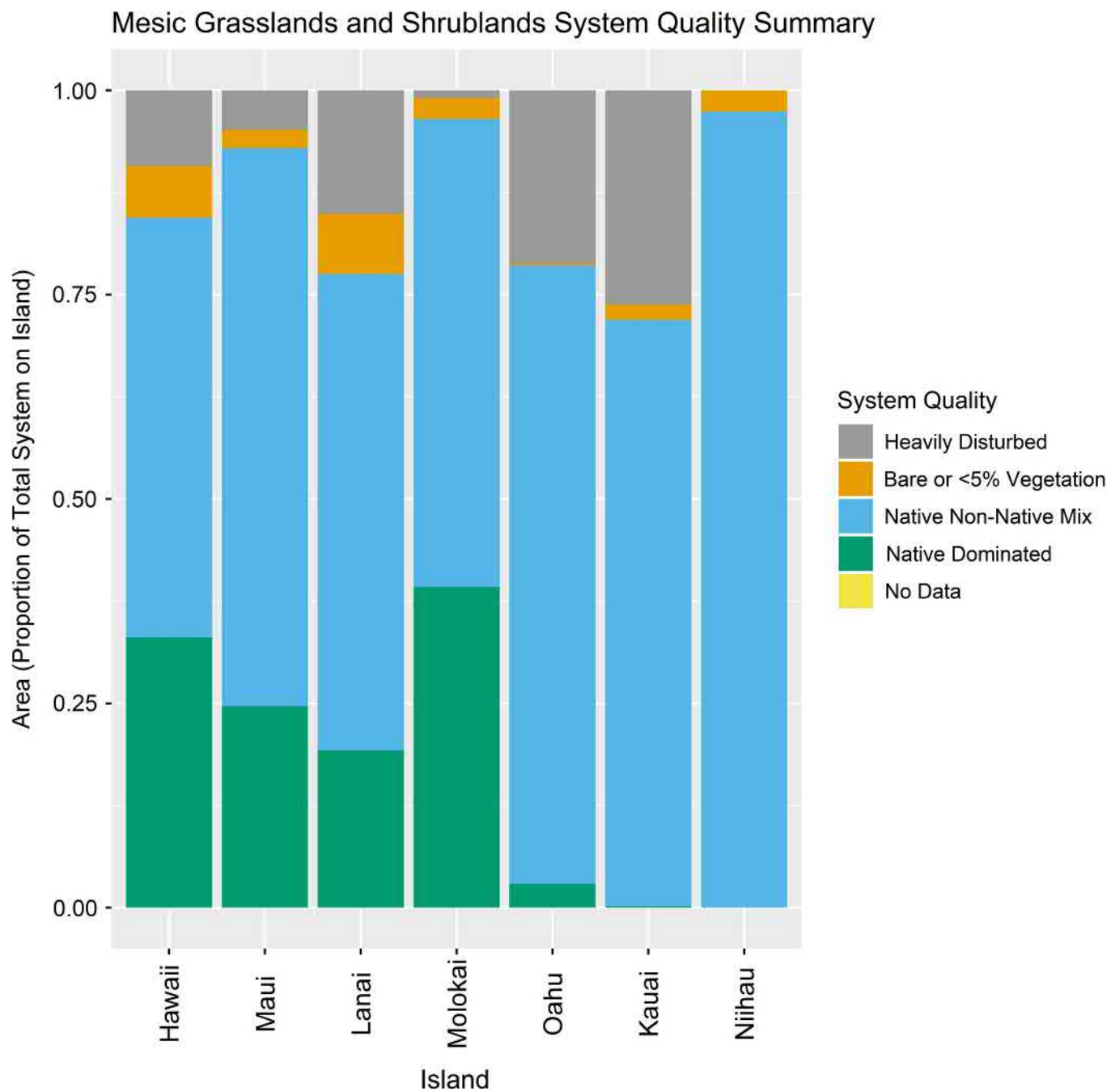


Fig. 12 Quality of the mesic grassland and shrubland system.

Laws and biosecurity

Endangered species protections and state and federal biosecurity laws, regulations, coordination, and authority aid in conservation efforts for native mesic grasslands and shrublands by preventing the introduction of invasive species and providing legal protections for rare native species (Table 8).

Biosecurity

In addition to federal biosecurity laws (Executive Orders 11,987, 13,112, 13,751), the Hawai'i Invasive Species Council (HISC) adopted Resolution 17-1 endorsing the Hawai'i Interagency Biosecurity Plan. This Interagency Biosecurity Plan is the state's guiding document for biosecurity improvements over the coming decade. Invasive species are a primary stressor for mesic grasslands and shrublands and therefore prevention and management across the state of Hawai'i is essential to protect the remaining mesic grasslands and shrublands.

Endangered species act

The Endangered Species Act (ESA) of 1973 and its amendments provides a framework to conserve and protect endangered and threatened species and their habitats.

The ESA prohibits "Take" (broadly defined to include "harass, harm, pursue, hunt, shoot, wound, kill, trap, capture or collect") endangered animal. Furthermore, the U.S. Fish and Wildlife Service (USFWS) has declared that "harm" includes "significant habitat modification or degradation." Thus, the habitat as well as the endangered animal is protected.

Critical habitat:

The ESA establishes "critical habitat" is a regulatory link between habitat protection and recovery goals for species. "Critical habitat" is defined as "all lands, water and air necessary to recover endangered species." To determine what exactly is critical habitat, the needs of open space for individual's and population's growth, food, water, light or other nutritional requirements, breeding sites, seed germination and dispersal needs, and lack of disturbances are considered (USFWS, 1998).

As habitat loss is the primary threat to most imperiled species, the ESA as enacted in 1973 allowed the USFWS and National Marine Fisheries Service (NMFS) to designate specific areas as protected "critical habitat." In 1978, Congress amended the law to make critical habitat designation a mandatory requirement for all threatened and endangered species. Fourteen percent (63,898 ac; 25,859 ha) of mesic grassland and shrubland habitat in the state of Hawai'i is designated as Critical Habitat (Fig. 13). Mesic grassland and shrubland in Hawai'i provide habitat for many endangered plant, insect, and forest bird species, and as a result receive protection through the ESA, and in particular, the protection of critical habitat for these listed species.

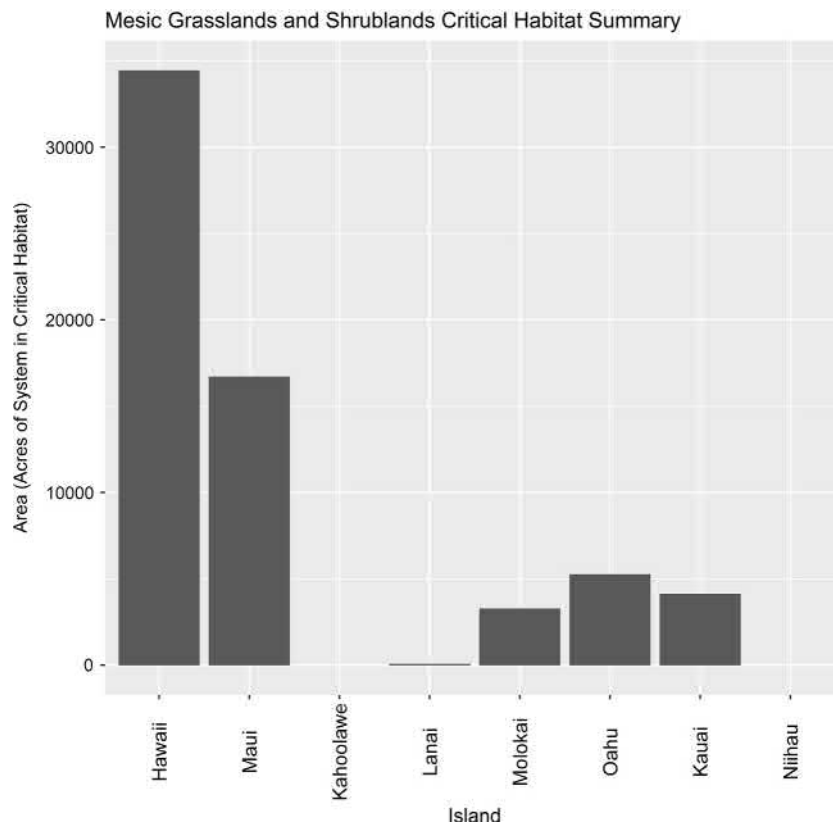


Fig. 13 Federally designated critical habitat on the main Hawaiian islands containing mesic grasslands and shrublands.

Stakeholder engagement

National parks

A total of 71,396 ac (28,893 ha) of mesic grasslands and shrublands exist on federal lands in the Hawaiian islands (Table 7). Of this, approximately 90% occurs on the islands of Hawai'i and Maui, primarily within Hawai'i Volcanoes and Haleakalā National parks (Tables 5 and 7). Management actions that benefit native mesic grasslands and shrublands within the national parks include fencing, ungulate removal, and invasive weed control (NPS 2015, 2016).

State of Hawai'i

A total of 171,380 ac (69,355 ha) of native and non-native mesic grasslands and shrublands exist on state lands, primarily within State Forest Reserves (FRS), state parks, and in Natural Area Reserves (NARS) (Table 5). The largest proportion of this biome occurring on state lands is found on the islands of Maui and Hawai'i (Fig. 10).

The Forest Reserve System (FRS) was created by the Territorial Government of Hawai'i in 1903 as early foresters recognized the need to protect forests to provide water for agriculture and surrounding communities. The FRS encompasses over 678,612 ac (274,624 ha) of land statewide, some of which includes lowland and subalpine mesic grasslands and shrublands. The Department of Land and Natural Resources, Division of Forestry and Wildlife (DOFAW) focus their resources to protect, manage, restore, and monitor the natural resources of the FRS (DOFAW, 2018).

The Natural Area Reserves System (NARS) was established in 1970 with the intent to preserve in perpetuity specific land and water areas which support communities, as relatively unmodified as possible, of the natural flora and fauna, as well as geological sites, of Hawai'i. The Natural Area Reserves are administered by the Division of Forestry and Wildlife (DOFAW) within the Department of Land and Natural Resources (DLNR). The Mt. Ka'ala and Pahole Natural Area reserves on O'ahu contain native lowland mesic shrublands. Some management actions taking place within the NARS include construction of feral ungulate exclosure fences, ungulate management, weed control, and outplanting of native species.

Department of Hawaiian Home Lands

The Department of Hawaiian Home Lands (DHHL) was created by the Hawai'i State Legislature in 1960 and is governed by the Hawaiian Homes Commission Act of 1920. The act set aside a land trust for native Hawaiians to maintain their traditional ties to the land. The primary responsibility of DHHL is to serve its beneficiaries and manage its land trust. DHHL also views its responsibility as a landowner to manage and protect native lands "to support both cultural and resource management activities and create homesteading opportunities for the future" (DHHL, 2009). Thus, the 'Āina Mauna Legacy Program was created to protect native forest (including shrublands) on the slopes of Mauna Kea on the island of Hawai'i. The program specifically includes the lands of Humu'ula and Pi'ihonua, which contain native mesic shrublands and introduced evergreen shrublands. Management goals include removal of invasive species (*Ulex europaeus*), native ecosystem protection and restoration, conserving endangered species, and providing educational and cultural opportunities (DHHL, 2009).

Watershed partnerships

The Hawai'i Association of Watershed Partnerships (HAWP) is composed of 10 island-based watershed partnerships that work collaboratively with >74 public and private partners on five islands to protect over 2.2 million ac (890,308 ha) of vital forested watershed lands (HAWP, 2018).

The HAWP's mission is to increase the effective management and protection of upper elevation watershed areas by raising the capacity of watershed partnerships, facilitating the sharing of watershed management expertise, building public support for protecting watershed values, and developing sustainable funding sources. Watershed partnerships undertaking conservation actions that protect and manage significant areas of native mesic grasslands and shrublands include the Three Mountain Alliance Watershed Partnership, Mauna Kea Watershed Alliance, Leeward Haleakalā Watershed Restoration Partnership, East Maui Watershed Partnership, West Maui Mountains Watershed Partnership, and the East Moloka'i Watershed Partnership.

Safe Harbor agreements

The Federal and State Safe Harbor programs encourage proactive conservation efforts by non-Federal landowners while providing them certainty that future property-use restrictions will not be imposed if those efforts attract species listed as endangered or threatened to their property, or result in increased populations of endangered or threatened species already present. In return for voluntary conservation commitments, the Agreement gives the landowner assurances covered by agency permits that allow for future alteration or modification of the enrolled property back to its original condition. These cooperative efforts provide landowners with a way to manage their lands to support the conservation of listed species while conducting approved land-use practices. Without this cooperative government/private effort, the private property would be less valuable to the recovery of endangered or threatened species (State BLNR, 2018).

A Safe Harbor Agreement between Kamehameha Schools, the State Department of Land and Natural Resources, and the USFWS was finalized in June of 2018. The total area covered by the agreement is 32,207 acres (13,034 ha) on lands owned by Kamehameha Schools on the island of Hawai'i. The area covered by the SHA includes mesic grasslands and shrublands. The 50-year agreement will contribute to the recovery of 32 endangered species and the agreement is part of an ongoing watershed partnership effort within the State of Hawai'i managed by the Three Mountain Alliance Watershed Partnership. Management activities benefiting mesic

shrublands and grasslands include control of invasive plants, fencing and ungulate removal, and fire threat management (TMA, 2007; State BLNR, 2018; KS, 2014).

Pūlama Lāna'i

The island of Lāna'i is privately owned but is developing an island-wide management plan in coordination with the USFWS and other partners. The land manager, Pūlama Lāna'i, is implementing actions that benefit mesic shrublands inside the Lāna'ihale unit (Increments 1 and 2). The management unit protects a total of 2200 ac (5436 ha) and ongoing management actions include the control of invasive ungulates and weeds (Lāna'i Resorts et al., 2015, in. litt.).

Ranching and farming easements

Land eligible for agricultural easements that overlaps with the mesic shrub and grassland communities are generally composed of rangeland, grassland, pastureland and nonindustrial private forest land. The Natural Resources Conservation Service (NRCS) prioritizes the protection of agricultural uses and related conservation values of the land and those that maximize the protection of contiguous acres devoted to agricultural use. Private landowners and lessees may enroll land through agricultural land easements through NRCS. Easements are contingent on the development of an agricultural land easement plan that promotes the long-term viability of the land (USDA, 2018).

Invasive species committees (ISC)

Invasive species are a prominent stressor for Hawai'i's native ecosystems, including mesic grasslands and shrublands. The State has developed a group of invasive species committees (ISC's) to focus on priority threats identified by each island. The ISC's are voluntary island-based partnerships on Kaua'i (KISC), O'ahu (OISC), Maui (MISC), Moloka'i (MOMISC), and the Big Island (BIISC) that work with government agencies, non-profit organizations, and private businesses and landowners to protect each island from the most threatening invasive species with a proactive approach. The ISC's target species that have high potential to severely impact the economy, environment, agriculture, human health, and quality of life (HDLNR, 2015).

The ISC's are invaluable to the protection and restoration of mesic grasslands and shrublands because of the significant impacts invasive plants and animals have on these communities. The ISCs work contributes directly to the conservation of mesic grasslands and shrublands through removal and reduction of invasive plants and animals in mesic grassland and shrubland areas and in restoration of these sites across the Hawaiian islands.

Hawai'i Wildfire Management Organization (HWMO)

The introduction and spread of invasive fire-adapted grasses and increased human-caused ignitions are important contributors to the increased incidence of fire, particularly in lowland mesic shrublands and perennial grasslands. Since 2002, the Hawai'i Wildfire Management Organization (HWMO) has worked with communities throughout the State of Hawai'i to implement dozens of projects mitigating wildfire hazards and protecting natural and cultural resources. They have also partnered extensively with a variety of organizations from the U.S. Forest Service, U.S. Army and University of Hawai'i, to the grassroots small community associations of Hawai'i's towns and villages (HWMO, 2018, in litt.). Their work includes sponsoring community wildfire preparedness workshops and conducting wildfire hazard assessments for every community in the state. These assessments provide a more thorough understanding of wildfire hazards that can be addressed by communities, decision makers, fire responders, and natural resource managers. This organization directly supports the conservation of mesic grasslands and shrublands through preparation and education efforts to minimize destruction of mesic grasslands and shrublands by wildfires (HWMO, 2018, in litt.).

Future Scenarios

We analyzed the future condition and viability of the mesic grasslands and shrublands in Hawai'i based on four possible future scenarios using a series of analyses based on land cover maps and projected changes over time (Miller, 2018). The condition of Hawai'i's mesic grasslands and shrublands in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are as follows:

- (1) *Conservation values*: Stakeholder involvement and public opinion determine the formulation, implementation and funding of natural resource conservation within laws and development plans.
- (2) *Laws and biosecurity*: National, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented. (e.g., hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.).
- (3) *Development or conservation planning*: National, state, county, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

These conservation management parameters are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The year 2035 is the extent of the "foreseeable future," and is based on the

projected divergence of IPCC Representative Concentration Pathway (RCP) climate change scenarios (van Vuuren, et al., 2011a,b; Miller, 2018) for a definition and description of the determination of the foreseeable future.

The four foreseeable future scenarios considered in this habitat assessment are:

Future Scenario One, Status Quo—The most likely foreseeable future; no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues through the foreseeable future.

Future Scenario Two—A slight increase in natural resource conservation in the CMPs marginally improves conservation management.

Future Scenario Three—A slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management.

Future Scenario Four—A moderate to large increase in conservation actions in the CMPs substantially improves conservation management.

The future condition of mesic grasslands and shrublands in Scenario One, the status quo, was characterized from an assessment of change over time in mesic grassland and shrubland land cover obtained from existing land cover maps by Amidon and Reeves (2018). Based on these land cover maps, an annual rate of change for mesic grasslands and shrublands was estimated, and a projected change (in acres/hectares) was calculated for the year 2035. The resulting information on changes in land cover by 2035, as derived from existing land cover change estimates, is the extent of the mesic grasslands and shrublands that is expected in the foreseeable future under Scenario One, the status quo, where conservation efforts remain unchanged and the current rate of change in land cover is also unchanged (Amidon and Reeves, 2018).

The future conditions of mesic grasslands and shrublands for Scenarios Two, Three, and Four cannot be quantitatively (acres/hectares) estimated. However, the Scenario One estimate can provide a “baseline” for a qualitative characterization of changes in the future condition of mesic grasslands and shrublands under Scenarios Two, Three, and Four.

Changes in human population are captured only by the changes in the “developed” land cover footprint derived from land cover map analysis (Amidon and Reeves, 2018). Impacts from other sources of human activities or human-caused habitat stressors (e.g., plant and animal diseases, wildfires, invasive species, etc.) are not well characterized in the land cover changes, but significantly contribute to increases in the land cover area dominated by non-native vegetation. For an assessment of island-by-island changes in human population, see Amidon and Reeves (2018).

Also, note that island-wide implementation of the CMPs is unlikely to have a significant effect on climate-related stressors (temperature, precipitation, and severe weather) resulting from global warming by 2035. This lack of CMP climate effects is due to the global lag in climate response to changes in greenhouse gas emissions which occurs on the order of centuries rather than years (Solomon et al., 2009; Gillett et al., 2011; Jevrejeva et al., 2012). Evidence of climate effects is also confounded by the large annual variation in the Pacific islands climate parameters, which is much greater than projected climate change by 2035. Although impacts from climate-related habitat stressors do not change across the four scenarios, they were included in this analysis because of their overall magnitude of potential importance to future habitat viability.

Future scenario one—status quo

Summary: Scenario One is considered the most likely future scenario, and serves as a “baseline” for comparing among the four future scenarios. There is no change in the implementation of the three CMPs between 2018 and 2035. A continuing current rate of change in land cover through this foreseeable future results in a slow but continuous change in mesic forest sub-categories (Table 9).

Under Scenario One, native mesic grasslands and shrublands would have a continued decline in size and distribution, and therefore a decrease in redundancy. Human caused stressors will have a small increase overall and continue to reduce the size and quality of native mesic grasslands and shrublands. Ecological function is predicted to be reduced due to the ability of invasive plants and animals to outcompete native plants for water and space, subsequently resulting in a reduction in native biodiversity. Degradation of native mesic grasslands and shrublands will continue to increase as remaining areas become more fragmented, thus reducing their resiliency and representation.

Introduced mesic grasslands and shrublands are predicted to increase in size and distribution (redundancy) as a result of the overall small increase in human-caused ecotype stressors. Introduced perennial grasslands and introduced shrublands are likely to expand as invasive species replace native-dominated communities, resulting in an increase in resiliency, redundancy, and representation (Table 10).

Future scenario two

There is a slight increase in the CMPs that marginally improves conservation management.

Under Scenario Two, conservation agencies and stakeholders work with increased but limited resources to slow or stop the degradation of native mesic grassland and shrubland areas. Introduced perennial grasslands and introduced shrublands will continue to increase. Scenario Two is essentially “status quo” with minor improvements in the three CMPs. This scenario is expected to have the second highest likelihood of occurring into the foreseeable future, being slightly less likely than Scenario One (Table 10).

Future scenario three

There is a small to moderate decrease in conservation actions in the CMPs that substantially decreases conservation management,

All natural resource management actions in the CMPs are set aside in deference to land use for economic development. With extensive localized management, some native species may persist in park-like settings or in areas where land development is not possible. This scenario has substantial declines in natural resource conservation within the three CMPs. An increasing human population is supported in its use of land for economic development over the conservation of native ecotypes. Areas that cannot support development become the only areas of free-living native species. The anticipated changes, under Scenario 3, for each of the ecotype stressors important to mesic grasslands and shrublands are given in [Table 9](#).

Overall, this scenario would severely degrade and fragment native mesic grasslands and shrublands and result in reduced resiliency, redundancy, and representation. Introduced mesic grassland and shrubland sub-types would significantly increase in resiliency, redundancy, and representation under this scenario. This scenario, along with Scenario Four, has the lowest likelihood of occurring in the foreseeable future ([Table 10](#)).

Future scenario four

There is a moderate to large increase in conservation actions in the CMPs that substantially improves conservation management.

For this scenario, substantial improvements to the three CMPs and a general decrease in human-caused ecotype stressors would increase the size and quality (resiliency) of native mesic grasslands and shrublands. Although this increase in native grassland and shrubland sub-types would be gradual at first it will become more noticeable by 2035 as the substantial improvements to the three CMPs will help keep these sub-types from declining. The introduced mesic grassland and shrubland sub-types would slowly decrease in resiliency, redundancy, and representation under this scenario ([Table 10](#)).

Based on this analysis, the substantial improvements in restoration for native mesic grasslands and shrublands would result in their increased resiliency, redundancy, and representation while the introduced grassland and shrubland sub-types would slowly decrease. This scenario, and Scenario Three have the lowest likelihood of occurring in the foreseeable future.

Conservation Implications

Under Scenario One (Status Quo), the most likely future scenario, the native mesic grasslands and shrublands are expected to decrease in resiliency, redundancy and representation while the introduced subtypes are predicted to increase ([Tables 10 and 11](#)). Conservation efforts by Federal, State, private, and multiple agency partnerships have been beneficial in helping to conserve and protect native mesic grasslands and shrublands. Increased funding and landowner incentives must be considered a high priority by agencies and partnerships in order to expand and manage remaining native mesic grassland and shrubland communities. Without increased effort the current level of conservation measures are insufficient to conserve the native subtypes of this biome. The continued spread of invasive plant species, particularly fire-adapted introduced grasses, and the proliferation of invasive ungulates is rapidly degrading native-dominated mesic grasslands and shrublands, reducing their representation and resiliency ([Table 11](#)). The decline in marine derived nutrients from seabirds, loss of insect pollinators, and loss of native birds for seed dispersal has resulted in less resilience in the native subtypes. All of these impacts combined with changes in fire regime, climate, and water availability are more favorable to increasing resiliency, redundancy, and representation in the introduced mesic grasslands and shrublands while the native-dominated subtypes will continue to decrease ([Table 11](#)).

See also: Physical Geography of the Hawaiian Islands.

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Savannas of the Mariana Islands Archipelago

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Published by Elsevier Inc.

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Abstract

This article provides an overview of the savannas of the Mariana island archipelago (Marianas) savanna biome, including current status, stressors, and future viability. Across the Marianas, savannas are typically found in mountainous areas formed by volcanic action. Tropical savanna are associated with the tropical wet and dry climate and develop in a seasonal forest of climax regions. However, edaphic conditions or disturbances prevent the establishment of species of trees associated with the climatic community (Woodward, 2012). Savanna in the Marianas generally receive between 50.8 and 127 cm (20–50 in.) of rainfall annually and are characterized by a predominance of grass and other herbaceous species with some small trees and shrubs (Webber et al., 2007). Currently, savanna ecotypes in the Marianas are experiencing severe erosion, forming badlands, which are challenging to control and restore back to native systems. Our assessment of savanna viability, defined as the likelihood of persistence over the long term, is based on the concepts of representation, redundancy, and resiliency. The main stressors to savanna in the Marianas are development, invasive species, erosion caused by recreational off-road vehicle use, fires, typhoons and drought. Current ongoing conservation efforts by Federal, State, and private entities and agency partnerships combined with certain laws and regulations limit some of the effects of stressors on the ecotype, but do not eliminate them. A stronger effort to engage partners and stakeholders in identifying and prioritizing landscape areas required for the conservation of native ecosystems, and to actively restore and expand these areas is needed for the successful conservation of savannas.

Introduction

The Mariana archipelago consists of 15 main islands and various small islets spanning a north-south distance of 553 miles (mi) (890 kilometers (km)) in the western Pacific Ocean between latitudes 21° and 13°N and longitudes 144° and 146°E. The Mariana

archipelago consists of the island of Guam and the Commonwealth of the Mariana Islands (CNMI), which consists of 14 islands located just north of Guam. The vast majority of the archipelago's land area is concentrated in the larger, southern main islands, including Saipan, Tinian, Rota, and Guam. Further information about the Mariana archipelago is described in Physical Geography of the Mariana Archipelago included in this work. This article provides an overview of the savanna in the Mariana island archipelago and describes the ecological factors that have influenced the habitat over time and into the future.

Description

The savanna community is characterized by grass and dispersed trees. Savanna are structurally simpler than forests, in that they do not provide the complexity of ecotypes above ground that forests do (Lobban and Lobban, 1997).

Climate is the most crucial factor in creating savanna. Therefore, savannas are typically found in warm or hot environments where the annual rainfall ranges from about 50.8 to 127 cm (20–50 in.) per year (Webber et al., 2007). Tropical savanna or grassland are also associated with the tropical wet and dry climate in regions where the climax community should be some form of seasonal forest or woodland, but edaphic conditions (e.g., availability of nutrients) or disturbances prevent the establishment of those species of trees associated with the climax community. Edaphic savannas are caused by soil conditions not entirely maintained by fire (Woodward, 2012).

A type of savanna that results from clearing of forest by farmers, hunters, or arsonists, either through manual clearing or setting fires, is known as derived savanna. As the grass takes over the bare ground (succession), wildfires can occur within a year of the initial human caused disturbance (Webber et al., 2007). Although seasonal fires play an important role in savanna's biodiversity, fire is not part of the Mariana's natural environment. In fact, the native plants and animals are poorly adapted to frequent burning while non-native plants thrive, altering biodiversity, an important component of ecosystem functioning (Loreau et al., 2002).

In the Northern Marianas, savanna/grasslands are typically found in mountainous areas formed by volcanic action but can also occur in limestone soils such as the Sabana Region of Rota and Mt. Tapotchau on Saipan (Falanruw et al., 1989; Liske-Clark, 2015). Savanna/grasslands also occur in the Talakhaya region of southern Rota. On Guam, savanna/grasslands are most common in the southern portion of the island where volcanic hills rise to about 1200 ft altitude. They can occur on hills or ridges where the soil is shallow, or in valleys where clay soils become waterlogged in wet weather (Stone, 1970).

"Inclusions," or sub-types, in the savanna include wetlands in depressions in the volcanic substrate that hold water; riverine systems within the savanna where natural drainage patterns hold enough moisture for native forest to grow; outplanted areas of *Acacia* forest from restoration activities, and badlands where severe erosion has stripped the soil to bare rock.

Geology

Savanna soils are red acidic clay and deeply weathered. They are usually volcanic but in a few small patches are composed of limestone (Fosberg, 1960). Volcanic soils often have a high aluminum content (Young, 1988) which restricts plant growth in acidic soils (Watanabe and Osaki, 2002). Due to the impermeable nature of the bedrock substrate under the soils, rainwater washes down the slopes and forms streams in river valleys, sometimes causing severe erosion and forming "badlands" (Young, 1988).

Badlands are highly degraded patches formed when soils and organic matter are washed off of steeply sloping terrain, exposing bare bedrock (Scheman et al., 2002; Golabi et al., 2005). Badlands usually form on heavily eroded Akina and Atate soils on Guam, Rota, and Saipan (Young, 1988, 1989). The soil of the Akina and Atate soil classification series are highly prone to erosion. Akina and Atate soils, which make up approximately 2266 acres of Guam, are found on volcanic uplands in very deep, well drained, and moderately slowly permeable terrain with slopes up to 45° (Young, 1988). Akina soils on Rota and Saipan make up approximately 203 and 1000 acres of those islands respectively, and are found on slopes ranging from 10% to 60% (Young, 1989).

Young (1988) described badlands on Guam as actively eroding areas of very deep, well-drained saprolite derived from tuff and tuff breccia. Saprolites (common in humid and tropical climates) are weathered rocks, in this case volcanic in origin, whose original textures and structures are preserved despite replacement of the fresh minerals by clay (Carroll et al., 1963). Saprolite is also strongly acidic and nutrient poor, creating a hostile environment for most plants.

Approximately 90% of Saipan's surface area is covered by limestone and calcareous sediments.

On Saipan, savanna vegetation types are supported by some relatively gray-white rocks from volcanic dacite (Raulerson and Rinehart, 1991). Dacite are 62–69% silica with moderate amounts of sodium and potassium (USGS, 2015).

Badlands are caused from sheet and rill erosion from wind and rain. Sheet erosion is caused when rain removes soil particles, leaving barren areas on the top layer of the soil. Rill erosion occurs when surface flow creates paths, sometimes leading to eroding channels. Badland soils have moderately low permeability and are vulnerable to impacts from both wind and rain, making them susceptible to severe sheet and rill erosion patterns. (Scheman et al., 2002).

Vegetation Structure

Rainfall, fire, and herbivory drive the structure and distribution of the savanna/grassland eco-type (Lehmann and Parr, 2016) (Fig. 1). The savanna/grassland of the Marianas is primarily composed of tall and short grasses, but many other shrubs, ferns,

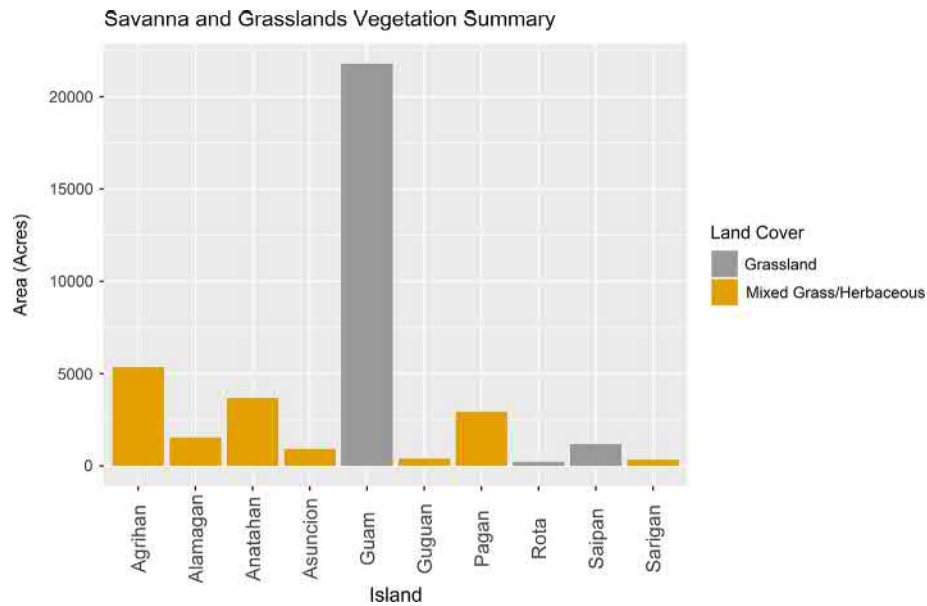


Fig. 1 Acres of grassland and mixed grass/herbaceous vegetation in the Marianas. From Reeves, M.K. (2019). Savanna and grassland vegetation summary.

and ground orchids can be found within the landscape (Fig. 2). Tall grasses can form dense thickets while areas dominated by short grasses have ferns and ground orchids scattered throughout. Many of the plants found in the volcanic geology-based savannas tolerate conditions that are inhospitable to most plants due to the high aluminum content and low pH in the soils (Raulerson and Rinehart, 1992). Some ferns, such as *Dicranopteris linearis*, and grasses, such as the invasive species *Miscanthus floridulus* and *Pennisetum polystachion*, are highly adapted to these soils and thrive in this environment (Minton, 2006). There are few trees in savannas and they tend to be short-statured due to destruction from fires or edaphic conditions. A summary of the vegetation in the Marianas is shown in Fig. 1 below.

Fosberg (1960) and Ohba (1994) described the following types of savanna/grassland communities for the Mariana Islands: *Miscanthus floridulus*, *Dimeria chloridiformis*, *Chrysopogon aciculatus*, and erosion scar. The *Miscanthus floridulus* type is dominated by *Miscanthus floridulus* but it can also include other grasses, sedges, ferns, shrubs, and herbs (Fosberg, 1960; Falanruw, 1989; Falanruw et al., 1989; Ohba, 1994). This community type forms a tall grassland and is found, at varying extents, on all the Mariana Islands



Fig. 2 Savanna in southern Guam, showing a small clump of Casuarina trees, low shrubs and ground orchids in the right foreground. From (USFWS) U.S. Fish and Wildlife Service. (2018). Savanna in southern Guam, showing a small clump of Casuarina trees, low shrubs and ground orchids in the right foreground. (USFWS unpubl. photo).

except *Uracus* (Fosberg, 1960; Ohba, 1994). However, the most extensive coverage of this community type occurs on Guam, Rota, Saipan, Anatahan, Alamagan, Pagan, and Agrihan. The *Dimmeria chloridiformis* community, which is dominated by *Dimmeria chloridiformis*, forms a low grassland on level and gentle sloping areas and appears restricted to Guam (Fosberg, 1960). The *Chrysopogon aciculatus* community forms a low grassland on ridges and appears restricted to the islands of Anatahan, Sarigan, and Guguan (Ohba, 1994). This community is dominated by *Chrysopogon aciculatus* but also includes other sedges, ferns, and shrubs. The erosion scar community is composed of a mixture of pioneer species that establish themselves in the heavily eroded areas of the savanna (i.e., the badlands; Fosberg, 1960). This community occurs on Guam, Rota, and Saipan and includes grasses, ferns, and shrubs (Fosberg, 1960). Table 1 summarizes the plant species recorded in savannas, by savanna type, if available.

Volcanic soils composed of decomposed volcanic ash have created the Akina soils on the slopes and ridgetops in Guam, Rota and Saipan creating red, silty, clay soils. When soil is loosened by actions of fires or vehicles or left unprotected by plant cover, soil particles are exposed to the forces of wind, gravity, and surface flow of water (Golabi et al., 2005). Soils are removed from the savanna leaving bare patches of red soil, referred to as badlands. Fig. 3 shows severe erosion in the savanna. The edges of badlands tend to be ringed by ferns tolerant of intense sunlight and high soil aluminum content (Raulerson and Rinehart, 1992).

Water Availability

On volcanic soils, vegetation in savanna depends on rainfall, which does not soak directly through the soil into a water table as it does in limestone-derived soils. Bedrock lined with very deep decomposed volcanic soils form a barrier to water entry. Rain soaks into the upper layers of soil where it is held by humus and available to plants. In areas where badlands have formed, rainwater washes soil directly away, leaving dry bare rock that plants cannot hold onto (Scheman et al., 2002). Fig. 4 shows an example of a typical savanna landscape in Guam.

Pre-Human Condition

Very few detailed studies on vegetation in the Marianas have been published. Brief descriptions of the lands and vegetation by early explorers and scientists exist for some of the islands, but not all (USGS report by Tracey et al. 1964; Gressitt in 1954). The vegetation of Guam has been the most researched, with botanical publications by Fosberg (1960), Stone (1970), and Safford (1905). Two publications from Raulerson and Rinehart (1991, 1992) as well as one by Mueller-Dombois and Fosberg (1998) covering vegetation for islands throughout the Pacific are the most extensive.

While not much is known about the prehistoric condition of the savannas in the majority of the Marianas, a study by Athens and Ward (2004) analyzed soil cores to study pollen and carbon deposits as signals of ancient human activities within the landscape such as gardening, burning, and other modification on Guam. The oldest soil cores include pollen from common forest tree genera such as *Aglaia*, *Pandanus*, and *Cycas*, while pollen of common grassland and savanna plants were absent. Charcoal from human burning activities and pollen from savanna plants such as *Lycopodium cernuum* and *Gleichenia linearis* began to appear in substantial amounts approximately 2500 years ago. Before humans arrived there was no evidence of a savanna landscape on Guam (Athens and Ward, 2004). It is unknown whether or not savannas on other islands in the Marianas were also anthropogenically influenced or naturally occurring.

Current Condition

Humans first came to the Mariana Islands approximately 4000 years ago, and at that time the savanna lands were significantly smaller than today, possibly existing as small fragments within a large forest ecotype. Human activities in the uplands of southern Guam, most probably burning to clear land for farming, combined with erosion and impoverished upland soils, created savannas where forests failed to regenerate (Athens and Ward, 2004).

Fosberg (1960) describes several plant communities in the Mariana Islands, four of which are included in the savanna: (1) *Miscanthus* community, (2) *Dimeria* community, (3) erosion scar community (badlands), (4) the *Phragmites* or reed community. The *Phragmites* community however, occurs in low spots with wetland characteristics, and therefore is not covered in detail in this article. While Fosberg describes the main constituents of each of his defined communities, he neglects to specify what smaller plants can be found within each. All of these communities can exist together in very close proximity in an area termed the “savanna complex” (Mueller-Dombois and Fosberg, 1998).

The *Miscanthus* savanna community of the Mariana Islands can form monotypic dense stands 2–3 m (6.5–9.8 ft) tall, while *Dimeria* forms shorter clumps (Fosberg, 1960). The thickness of *Miscanthus* stands generally crowds out other plant life, although some climbing ferns such as *Ctenitis subglandulosa* can be found. In *Dimeria* communities with mid to tall grasses, trees such as *Casuarina equisetifolia*, *Scaevola taccada*, and *Pandanus* spp. are scattered through the landscape. Other grasses may be found here such as introduced *Pennisetum* spp. or *Paspalum* spp. Small herbs and ferns can be found in the lower layers and wet depressions in the landscape may host phragmites marshes (Mafnas, 2010). Fig. 2 depicts a typical savanna community.

During World War II, large stands of *Casuarina* trees grew on the savannas of Guam because of movement and hunting restrictions placed upon activities of the local people. Fires were reduced and *Casuarina* was able to expand. After the war, fires resumed

Table 1 Plant species reported in Savannas by Savanna type, if available, in the Mariana Islands. Savanna types include: *Miscanthus floridulus* (MF), *Dimmeria chloridiformis* (DC), *Chrysopogon aciculatus* (CA), Erosion (ER), and Unknown (U) see text for details. Taxonomy follows [The Plant List \(2013\)](#).

Species	Savanna type	Source
<i>Ageratum conyzoides</i>	MF	Ohba (1994)
<i>Alyxia stellata</i>	ER	Fosberg (1960)
<i>Blechnum orientale</i>	ER	Fosberg (1960)
<i>Cajanus scarabaeoides</i>	U	Stone (1970)
<i>Calopogonium mucunoides</i>	U	Stone (1970)
<i>Cassytha filiformis</i>	CA	Ohba (1994)
<i>Casuarina equisetifolia</i>	MF	Fosberg (1960)
<i>Centella asiatica</i>	MF	Ohba (1994)
<i>Cheilosoria tenuifolia</i>	ER	Fosberg (1960)
<i>Christella dentata</i>	U	Stone (1970)
<i>Chrysopogon aciculatus</i>	CA,ER	Fosberg (1960) and Ohba (1994)
<i>Colubrina asiatica</i>	MF	Ohba (1994)
<i>Ctenitis subglandulosa</i>	MF	Fosberg (1960)
<i>Curculigo orchoides</i>	U	Stone (1970)
<i>Cyperus javanicus</i>	CA	Ohba (1994)
<i>Decaspermum fruticosum</i>	ER	Fosberg (1960)
<i>Desmodium incanum</i>	MF	Fosberg (1960)
<i>Desmodium triflorum</i>	CA	Ohba (1994)
<i>Dianella ensifolia</i>	U	Stone (1970)
<i>Dicranopteris linearis</i>	MF, ER	Fosberg (1960)
<i>Digitaria ciliaris</i>	MF	Ohba (1994)
<i>Dimeria chloridiformis</i>	DC	Fosberg (1960)
<i>Dicranopteris linearis</i>	ER	Fosberg (1960)
<i>Dodonaea viscosa</i>	CA	Ohba (1994)
<i>Elephantopus mollis</i>	MF	Ohba (1994)
<i>Emilia sonchifolia</i>	CA	Ohba (1994)
<i>Eurya japonica</i>	MF	Ohba (1994)
<i>Ficus prolixa</i>	MF	Ohba (1994)
<i>Fimbristylis tristachya</i>	U	Stone (1970)
<i>Geniostoma rupestre</i> var. <i>glaberrimum</i>	ER	Fosberg (1960)
<i>Glossocardia bidens</i>	U	Stone (1970)
<i>Hedyotis fruticulosa</i>	U	Stone (1970)
<i>Hedyotis laciniata</i>	U	Stone (1970)
<i>Hedyotis megalantha</i>	DC, ER	Fosberg (1960)
<i>Heteropogon contortus</i>	MF	Fosberg (1960)
<i>Hyptis capitata</i>	U	Stone (1970)
<i>Hyptis pectinata</i>	MF	Ohba (1994)
<i>Ipomoea pes-caprae</i> ssp. <i>brasiliensis</i>	CA	Ohba, 1994
<i>Ipomoea triloba</i>	U	Stone (1970)
<i>Lindsaea ensifolia</i>	U	Stone (1970)
<i>Lunathyrium bonincola</i>	MF	Ohba (1994)
<i>Lycopodiella cernua</i>	MF	Fosberg (1960)
<i>Melastoma malabarthicum</i>	MF, CA, ER	Fosberg (1960) and Ohba (1994)
<i>Miscanthus floridulus</i>	MF, DC, CA	Fosberg (1960), Stone (1970), and Ohba (1994)
<i>Myrtella bennigseniana</i>	MF, ER	Fosberg (1960)
<i>Nephrolepis hirsutula</i>	MF, CA	Ohba (1994)
<i>Ophioglossum nudicaule</i>	U	Stone (1970)
<i>Pandanus tectorius</i>	ER	Fosberg (1960)
<i>Paspalum conjugatum</i>	MF	Ohba (1994)
<i>Phyllanthus saffordii</i>	U	Stone (1970)
<i>Phymatosorus scolopendria</i>	MF	Fosberg (1960)
<i>Piper guahamense</i>	MF	Ohba (1994)
<i>Psilotum nudum</i>	CA	Ohba (1994)
<i>Psychotria mariana</i>	MF	Ohba (1994)
<i>Pteris fauriei</i>	MF, CA	Ohba (1994)
<i>Rhynchospora colorata</i>	CA	Ohba (1994)
<i>Rhynchospora rubra</i>	U	Stone (1970)
<i>Scaevola taccada</i>	ER	Fosberg (1960)

Table 1 Plant species reported in Savannas by Savanna type, if available, in the Mariana Islands. Savanna types include: *Miscanthus floridulus* (MF), *Dimmeria chloridiformis* (DC), *Chrysopogon aciculatus* (CA), Erosion (ER), and Unknown (U) see text for details. Taxonomy follows [The Plant List \(2013\)](#).—cont'd

Species	Savanna type	Source
<i>Selaginella ciliaris</i>	U	Stone (1970)
<i>Spathoglottis plicata</i>	CA	Ohba (1994)
<i>Sphaerostephanos unitus</i>	U	Stone (1970)
<i>Sphenomeris biflora</i>	MF	Ohba (1994)
<i>Sphenomeris chinensis</i>	U	Stone (1970)
<i>Sporobolus fertilis</i>	MF	Ohba (1994)
<i>Timonius nitidus</i>	ER	Fosberg (1960)
<i>Trema orientalis</i>	MF	Ohba (1994)
<i>Utricularia bifida</i>	ER	Fosberg (1960)
<i>Waltheria indica</i>	U	Stone (1970)
<i>Wikstroemia elliptica</i>	MF, ER	Fosberg (1960)
<i>Wollastonia biflora</i>	MF	Ohba (1994)
<i>Xylosma nelsonii</i>	ER	Fosberg (1960)

From (USFWS) U.S. Fish and Wildlife Service. (2018). Plant species reported in Savannas by Savanna type, if available, in the Mariana Islands.



Fig. 3 Savanna lands in southern Guam, showing hilly topography and areas of erosion due to off-road vehicle use. From (USFWS) U.S. Fish and Wildlife Service. (2018). Savanna lands in southern Guam, showing hilly topography and areas of erosion due to off-roading. (USFWS unpubl. photo).

and the savanna *Casuarina* forests were completely destroyed on Guam and in most of Saipan by 1946 ([Mueller-Dombois and Fosberg, 1998](#)).

Although there was very little historic information about savannas in the Mariana Islands, the available literature describes a decline in the quality of several vegetation types in the Marianas once humans arrived. Pressures caused by humans have increased as populations and technologies have advanced. Early settlers burned forests to create open fields for farming. The Spanish introduced deer, which were then hunted by setting fires to burn down vegetation. In modern times, hunters continue to hunt by setting fires ([Liske-Clark, 2015](#)). New human activities of off-roading and “mudding” exacerbate erosion. Intentionally set fires and damaging activities such as off-road vehicle use lead to severe erosion, causing the development of badlands. Carabao, goats, pigs, and deer have been found to be present in some of the highest densities in the world ([Knutson and Vogt, 2002](#)), and cause erosion through wallowing, rooting, or vegetation consumption.

Savanna on Guam was formed by anthropogenic influence ([Athens and Ward, 2004](#)), and it is unknown if savanna lands on other Mariana Islands were formed in a similar fashion. [Fig. 5](#) displays current occurrences of savanna ecotype on each island in the Mariana Islands.



Fig. 4 View across Guam's savanna lands, showing grassland and inclusion of riverine valley (Sigua River Valley). Exposed red soil erosion scars are visible on the ridge. Leo Palace sits in the distance. From (USFWS) U.S. Fish and Wildlife Service. (2018). View across Guam's savanna lands, showing grasslands and inclusion of riverine valley (Sigua River Valley). (USFWS unpubl. photo).

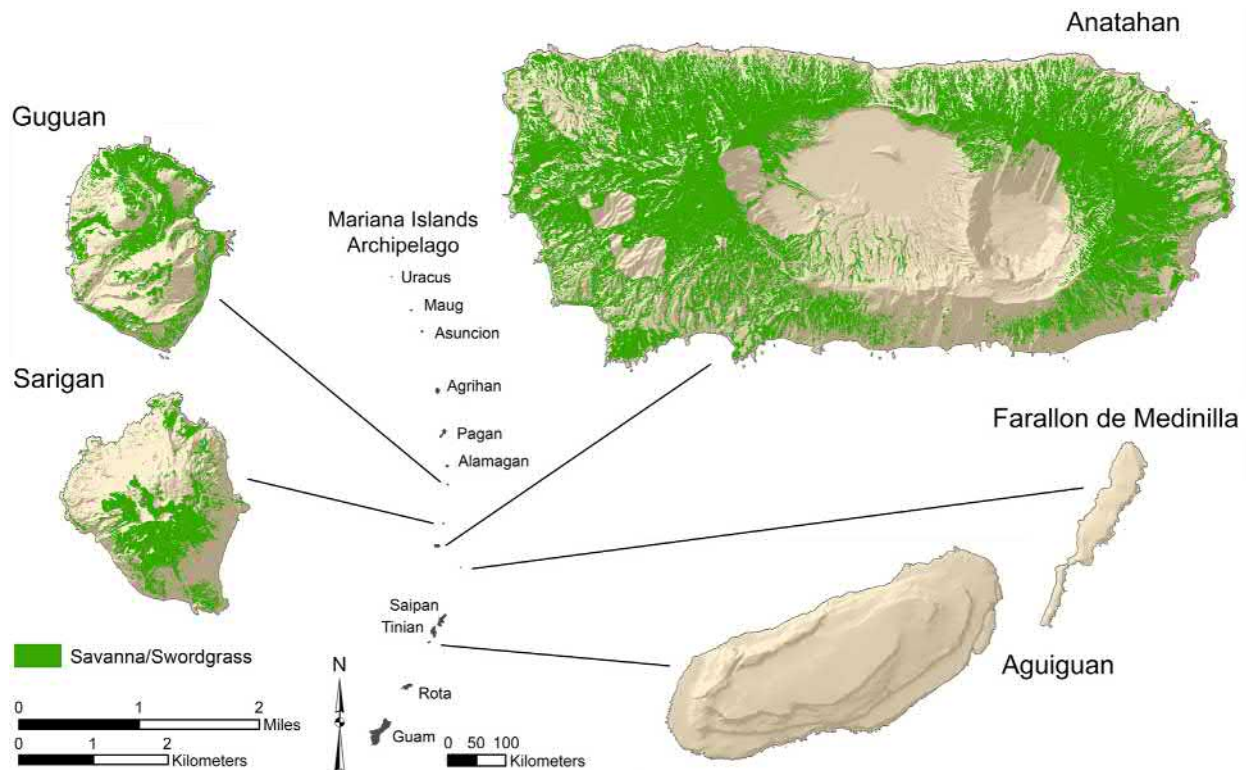


Fig. 5 Maps of savanna habitat occurrences in the Marianas. (A) Savanna/swordgrass system in Aguiuan, Farallon de Medinilla, Anatahan, Sarigan, and Guguan, Mariana Islands. (B) Savanna/swordgrass system in Guam, Mariana Islands. (C) Savanna/swordgrass system in Alamagan, Pagan, and Agrihan, Mariana Islands. (D) Savanna/swordgrass system in Rota, Mariana Islands. (E) Savanna/swordgrass system in Tinian and Saipan, Mariana Islands. (F) Savanna/swordgrass system in Asuncion, Maug, and Uracus in the Mariana Islands. From Reeves, M.K. and Amidon, F.A. (2018). Maps of savanna habitat occurrences in the Marianas.

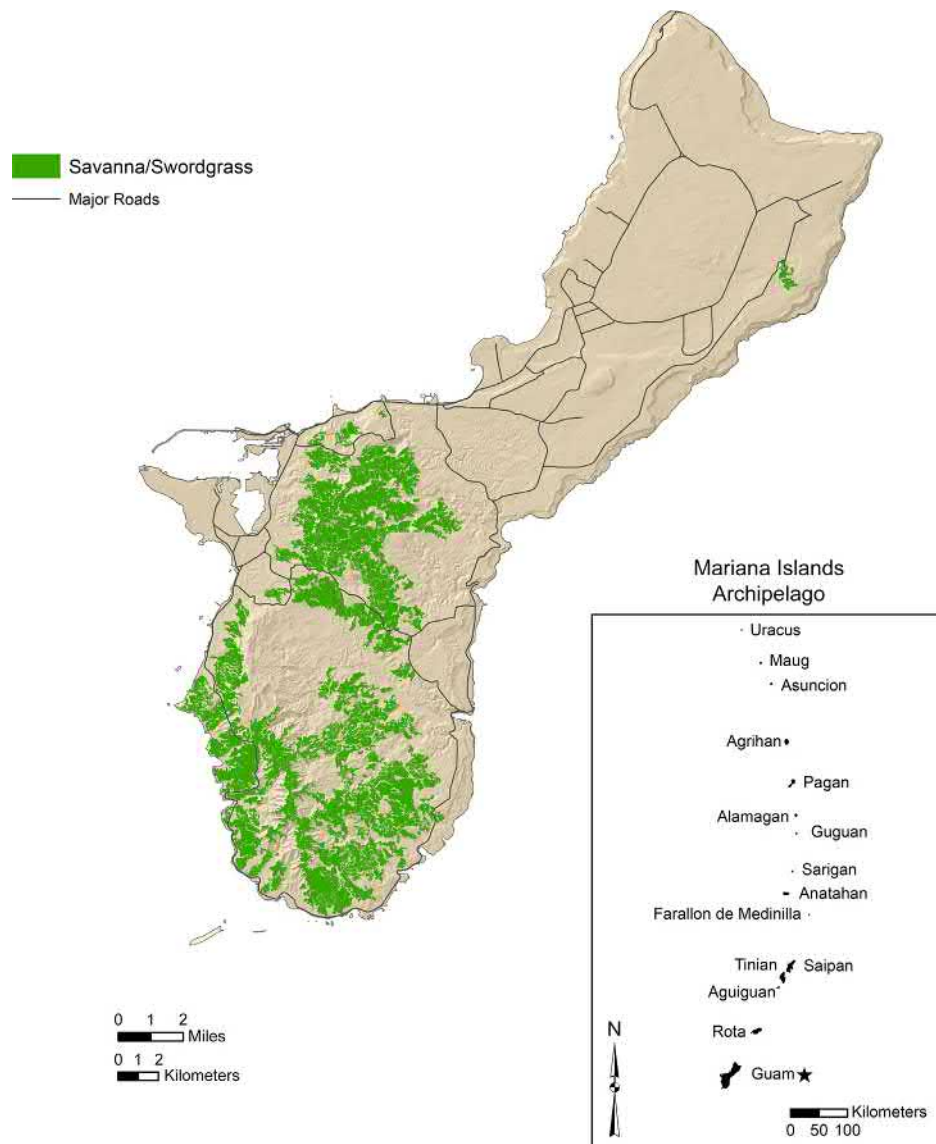


Fig. 5 (continued).

Nearly all savannas in the Mariana Islands occur on volcanic soils. However in the CNMI, a few small areas of savanna are found in limestone around Mt. Tapotchau on Saipan (Liske-Clark, 2015), which does not have the same problem of badland formation as found on Guam. On most islands in the Mariana archipelago, *Miscanthus* sp. is normally considered an indicator of volcanic soils, although on Saipan it is found in a few places on bare limestone (Mueller-Dombois and Fosberg, 1998).

Table 2 summarizes the acreage of savannas per island. Both Guam and Rota have savannas of primarily non-native invasive species.

Savannas throughout most of the Marianas are dominated by invasive species such as *Miscanthus floridulus*, which burns frequently. Savannas on Asuncion, Guguan and Saipan are dominated by native species. Although Saipan does have *Pennisetum polystachyon*, a nonnative species, it has not yet become dominant within the landscape (Figs. 6 and 7).

Sustainability

Ecotypes sustain through resiliency, redundancy, and representation. The viability of savanna ecotype depends on maintaining multiple and distributed ecotypes (redundant) of sufficient quality and size (resilient) with species richness and genetic range (representative) to survive across its ecological environment over time. Resilience is defined as the amount of disturbance that the system can absorb without a change in structure and composition (Holling, 1973; Carpenter et al., 2001). Disturbances include natural forces such as typhoons and droughts as well as anthropogenic forces such as wildfire or development. Redundancy refers to

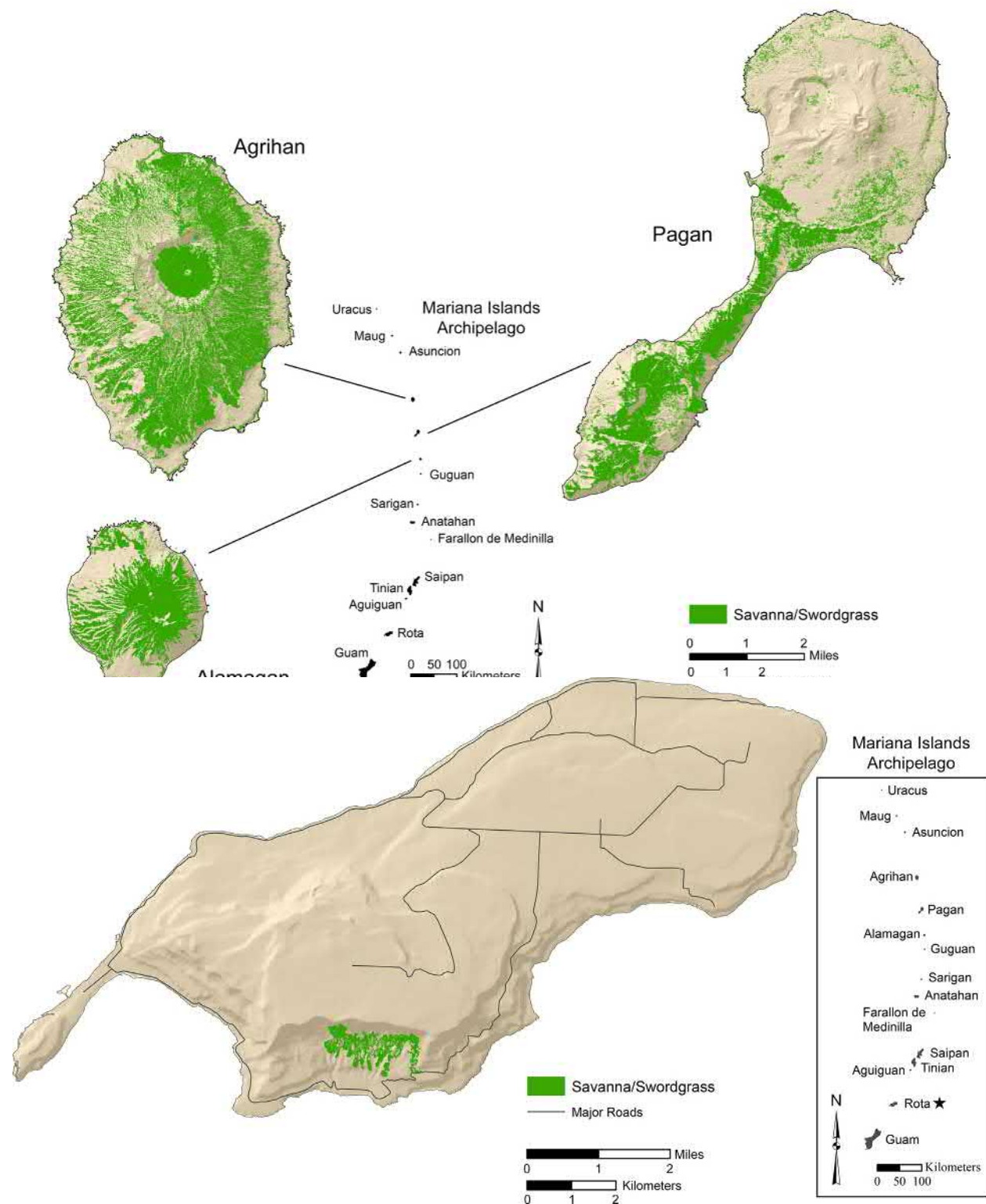


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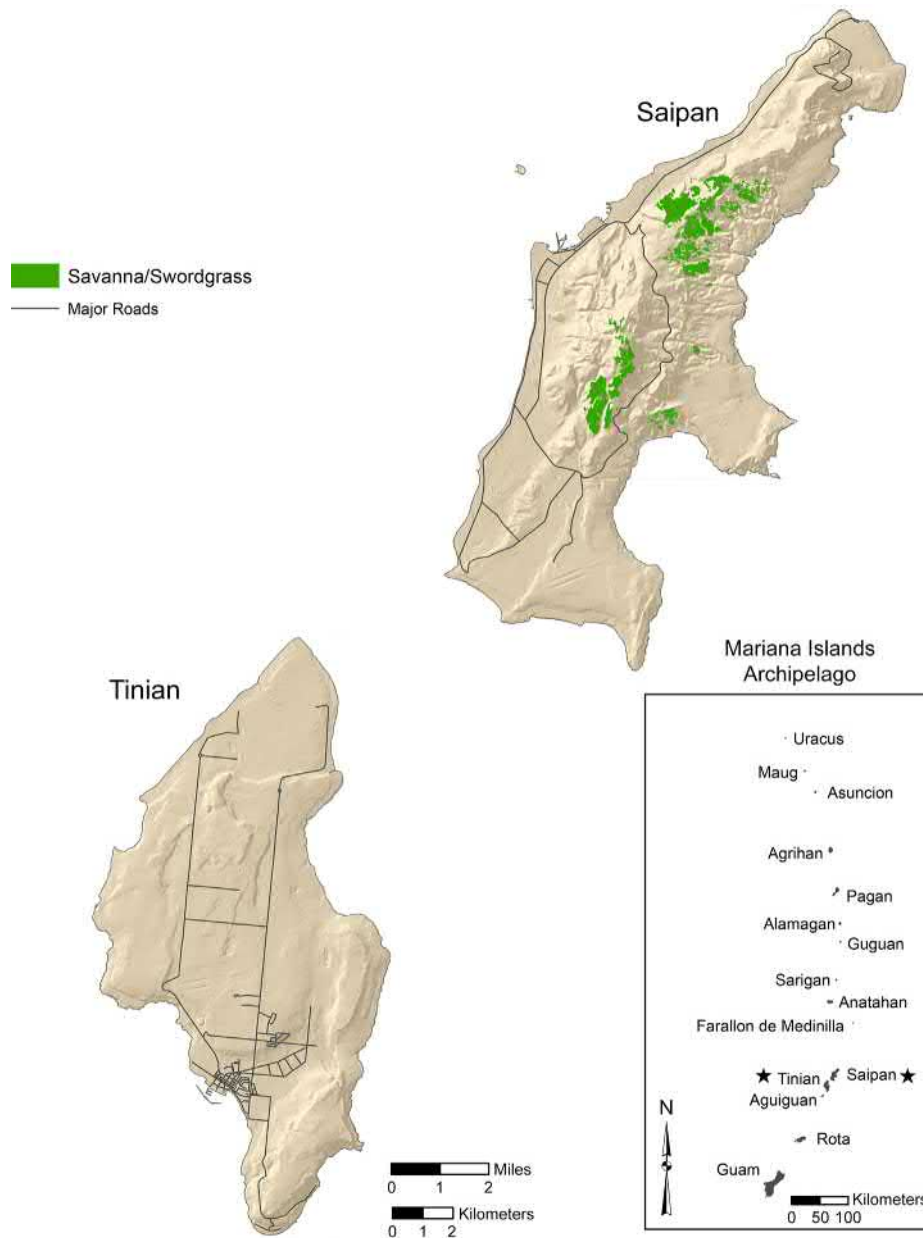


Fig. 5 (continued).

the extent and range of an ecotype across a given landscape. Redundancy from having multiple resilient ecotypes can decrease the risk of loss. Ecotypes with few occurrences across the islands are less resilient to catastrophic events that might otherwise have a relatively minor impact on widely-distributed ecotypes (Stacey and Taper, 1992). Representative ecotypes are those not restricted to particular locations but are scattered throughout due to diverse species that can occupy various ecotypes.

Stressors

Climate Change

While climate change related stressors (e.g., increased precipitation, sea level rise, increased typhoon intensity and frequency) cause ongoing impacts, they are not currently a significant factor in the Mariana Islands. Climate-related stressors, such as typhoons, can have an impact on the savanna by causing erosion (Kerr, 2000).

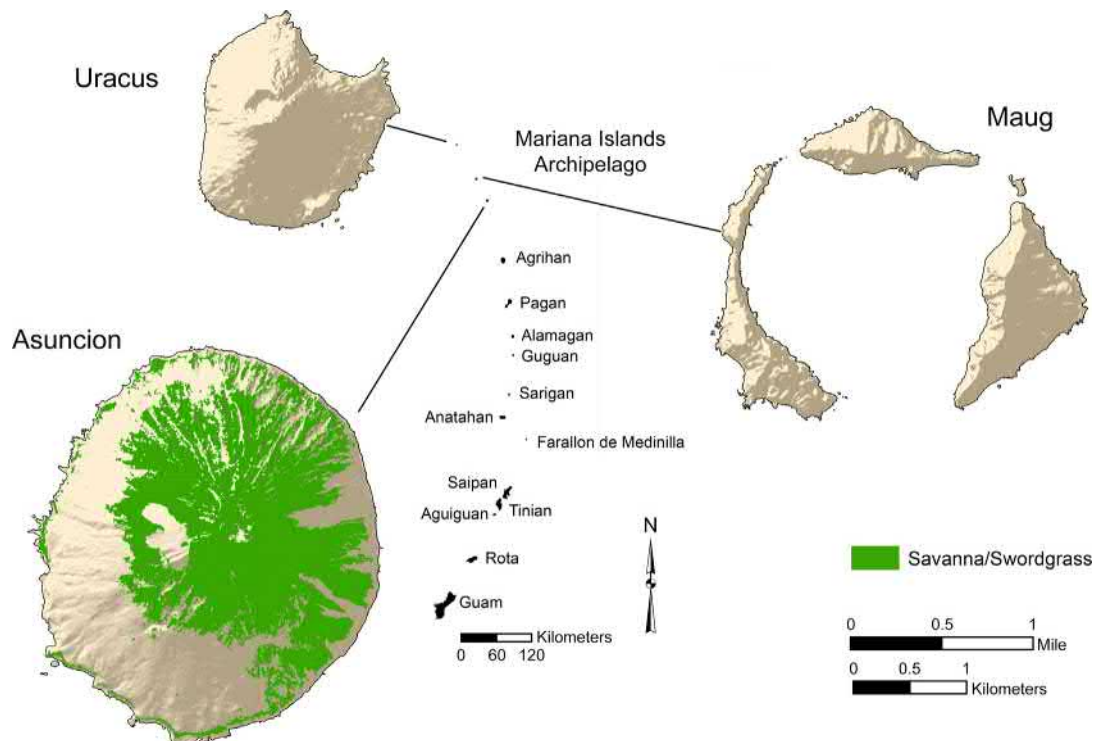


Fig. 5 (continued).

Table 2 Savanna lands across the Mariana Islands (Reeves and Amidon, 2018).

Island	Area (Acres)	Area (% of Island)	Area (% of Marianas)
Agrihan	5357	43	2
Alamagan	1530	39	1
Anatahan	3678	38	1
Asuncion	918	36	<1
	1453	1	1
	335	<1	<1
	8296	6	3
	5316	4	2
Guam	6371	4	2
Guguan	392	26	<1
Pagan	2928	21	1
Rota	26	<1	<1
	199	1	<1
	<1	<1	<1
Saipan	286	1	<1
	907	3	<1
	1	<1	<1
Sarigan	341	21	<1

From Reeves and Amidon (2018). Savanna lands across the Mariana Islands.

Typhoons

The Mariana archipelago lies in a typhoon belt and is regularly exposed to typhoons. Typhoons cause a variety of impacts to vegetation including pruned or downed vegetation from intense wind, defoliation and damage from wind, heavy rain and salt spray, and mortality by salt water inundation in low-lying areas (Kerr, 2000). Typhoons impact savannas primarily by causing erosion of loosened soils, which expand badland areas.

Increase in typhoon frequency and/or intensity are one of the factors in the increasing development of badlands. A study by Scheman et al. (2002) indicated that badlands across the steepest slopes of the watershed contribute an average of 65.90 tons/

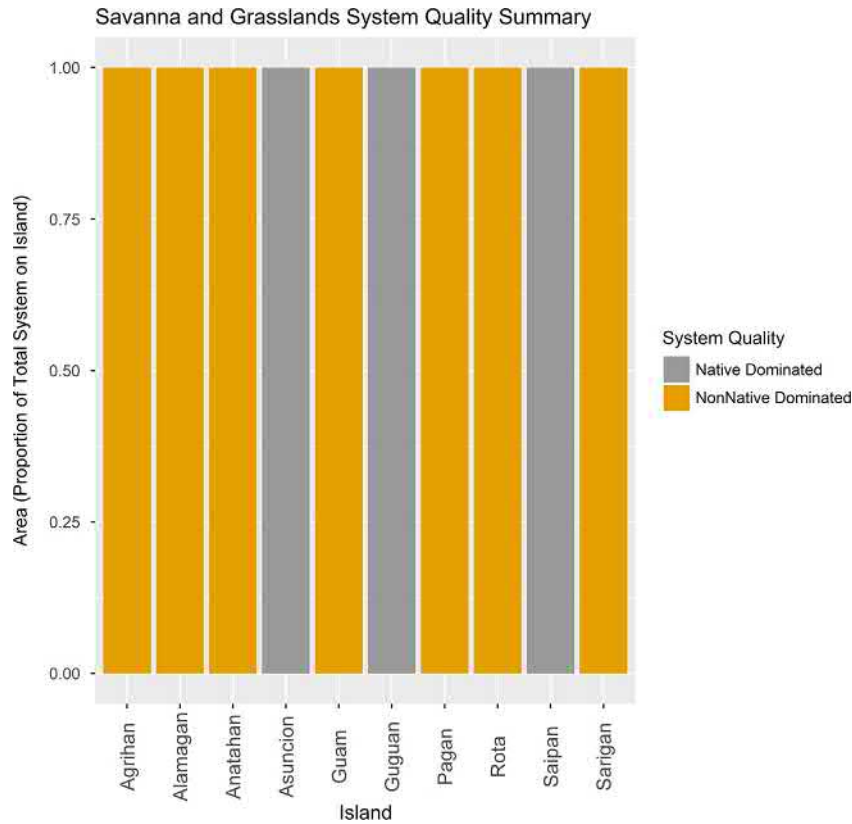


Fig. 6 Area of native and non-native dominated savanna and grassland in the Marianas. From Reeves, M.K. (2019). Savana and grasslands system quality summary.

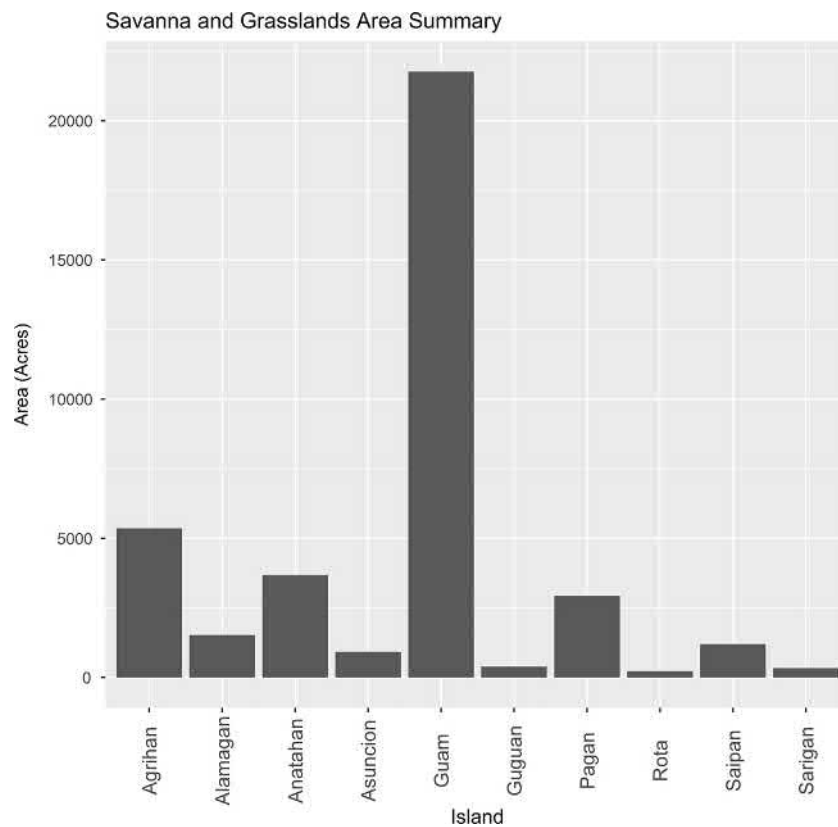


Fig. 7 Amount of savanna and grasslands across the Mariana Islands. From Reeves, M.K. (2019). Savanna and grasslands area summary.

acre/year in soil yield. Scheman et al. concluded that the accelerated erosion of the soil and increasing badlands in southern Guam can be blamed on human disturbance.

Fires

The frequency of grassland fires during the dry season have been a serious ecological problem in the Mariana Islands since the arrival of humans (Minton, 2006). Many fires are deliberately started to clear land or to drive wildlife for hunters. Fires burn quickly in the savannas due to the high flammability of grasses and the density of the fuel load. According to the Pacific Fire Exchange, there are an average of 730 fires per year on Guam that burn 4800 acres (1942 ha). While fire can help maintain the savanna, increased frequency of fires can result in increased erosion, further preventing revegetation (Minton, 2006).

Drought

Drought has caused major ecological harm in the Mariana Islands. The dry season occurs annually from January through June, and during years immediately following an El Nino year severe dry seasons can cause drought (Lander, 2004). During this time, large stands of *Miscanthus* becomes fuel for wildfires.

Off-Road Vehicle Use

Recreational use of the savannas exacerbates erosion. Off-road vehicles, dirt bikes, mountain bikes, and large trucks criss-cross the mountains, digging up vegetation and loosening the topsoil. One of the most damaging stressors to the savannas on Guam is off-road vehicle use (Kottermair et al., 2011). Neither Saipan nor Rota experience this stressor as the savanna lands are too small for this kind of recreation. Off-road use, along with some hiking and mountain biking, can cause erosion by damaging vegetation and weakening root systems, loosening soil particles or by compacting the soil causing an increased surface bulk and reduced infiltration rate or rain (Kottermair et al., 2011) When enthusiasts veer off of established trails new bare areas form. Fig. 8 depicts a popular off-roading area.



Fig. 8 Photo of savanna land on Guam, showing erosion scars from off-roading activities. From (USFWS) U.S. Fish and Wildlife Service (2018). Photo of savanna land on Guam, showing erosion scars from off-roading activities. (USFWS unpubl. photo).

Table 3 Key invasives species of concern in the Mariana Islands which impact savanna systems.

Common name	Scientific name	Primary species affected	How invasive affects the habitat	Island impacted
Ants (Yellow Crazy Ant, Little Fire Ant) ^a	<i>Anoplolepis gracilipes</i> , LFA: <i>Wasmannia auropunctata</i>	Native fauna (birds, reptiles, mammals, arthropods)	LFA: Tend or protect plant pests such as aphids and scale	Guam, Rota, Saipan LFA: Guam
Scale insects (e.g., Asian Cycad scale, Cycad Blue Butterfly) ^b	<i>Aulacaspis yasumatsui</i> , <i>Chilades pandava</i>	<i>Cycas micronesica</i>	Feed on plant, infest root systems	Guam Rota
Feral ungulates (goats and pigs, deer, carabao) ^c	(<i>Capra hircus</i> , <i>Sus scrofa</i> , <i>Rusa marianna</i> , <i>Bubalus bubalis</i>)	All vegetation	Dig up and compact soils, facilitating erosion, consume or otherwise destroy natural resources, spread pest species	Guam, Rota, Saipan
Rodents (black rats) ^d	<i>Rattus rattus</i>	Native vegetation, prey on native and nonnative fauna, including birds	Prevent tree or grass re-growth, destroy grass seeds	All Islands

^aBach (1991).^bMoore et al. (2013) and Marler and Muniappan (2006).^cKnutson and Vogt (2002) and Gawel et al. (2018).^dLiske-Clark (2015).

From (USFWS) U.S. Fish and Wildlife Service. (2018). Key Invasive species of concern in the Mariana Islands which impact savanna systems.

Invasive Species

Invasive ungulates such as deer, pigs, goats, and carabao increase rates of erosion through rooting and wallowing behaviors as well as by selectively preying upon native plants (Gawel et al., 2018). Also, the presence of ungulates on Guam attract both recreational and illegal hunting activities. Game trails created by hunters change the soil dynamics forming rills and possibly into an advanced stage called gully erosion. Table 3 describes impacts from invasive species on savanna systems in the Marianas.

Development

Development is a major factor negatively impacting savanna ecotype throughout the inhabited Mariana Islands. Most of the savanna lands on Saipan and Guam are located on volcanic slopes in the center of the islands (see Fig. 5). Increased housing demand has started to place development in the interiors of Guam and Saipan (ICF International, 2009). The Department of Defense holds large parcels of lands in the interior of Guam which include savanna. Continuing military development for training grounds, munitions storage, or personnel support facilities will convert savanna lands into developed lands.

Conservation Efforts

The Micronesia Challenge

In, 2006 the Republic of Palau, the Federated States of Micronesia, the Republic of the Marshall Islands, the U.S. territory of Guam, and the U.S. Commonwealth of the Northern Mariana Islands committed to conserve at least 30% of the near-shore marine resources and 20% of the terrestrial resources across Micronesia by 2020. This pledge has become known as the Micronesia Challenge. The Challenge aims to preserve these resources for the benefit of future generations, to sustain livelihoods, and to sustain each island's unique biodiversity (<http://www.micronesiachallenge.org>).

Examples of Micronesia Challenge projects in the Mariana Islands are described below.

- Rota's Talakhaya watershed, which contains areas of savanna has been revegetated with native grasses by local forestry staff. The staff is also educating local people on the fire impact to the savanna and how it can impact reef resources (Bickel and Mattos, 2015).
- On Saipan, the Laolao Bay watershed is being improved by revegetating badlands damaged by fire and illegal land clearings as well as conducting grassroots education campaigns (Bickel and Mattos, 2015).
- On Guam, the Humatak Project (Fig. 9), seeks to restore the watershed above Fouha Bay by implementing erosion control practices on the mountain slopes in the savannas and by educating the public about how erosion impacts coral reef resources. Sediment socks and vetiver grass (*Chrysopogon zizanioides*, a clumping grass species often used to stop erosion due to its thick root systems) were placed in areas displaying erosion and washouts. These erosion prevention measures resulted in both reduced erosion in the savanna and a reduction in reef sedimentation (Shelton and Richmond, 2016).

Several programs have been created to halt erosion in the savannas by replanting vegetation and covering badland areas with fiber mats to stimulate plant growth. Vetiver grass swales, trenches lined with grass, act as a soil trap and prevent soil transport. Fig. 9 shows the use of sediment traps on eroded slopes to stop soil loss. On Guam, the National Oceanic and Atmospheric



Fig. 9 Photo of Humåtak Project impacts on Guam's savannas in the Fouha Bay watershed. Image Courtesy of Austin Shelton, University of Guam Sea Grant.

Administration (NOAA) and the Center for Island Sustainability (CIS) have completed and ongoing projects to restore watersheds and coral health by stopping the spread of badlands in the savannas (NPS, 2017).

The CIS has also created initiatives to educate off-road motorists, bikers, and hikers about damages caused by improper use of trails and how this leads to badlands formation (Fig. 10). In 2018, a Guam-based Jeep dealer pledged to educate each new Jeep owner for responsible off-road use and an off-road adventure tour company pledged to encourage responsible use of trails. This program was announced at the Island Sustainability Conference in 2018 (Meno, 2018).

National Oceanic and Atmospheric Administration (NOAA)

NOAA's primary focus in the Marianas is on coral reef health, but as reef health is intertwined with upland health NOAA has created 10 Habitat Focus Areas (HFA) for watershed restoration to reduce erosion and runoff. On Guam, NOAA's HFA is the Manell-Geus watershed, which feeds into the southern lagoon. Restoration of the watershed has included replanting savannas with native vegetation, stopping erosion of badlands using fiber mats, and educating the public about responsible use of the land. National Oceanic and Atmospheric Administration partnered with Underwater World, the University of Guam, and Government of Guam agencies such as the Bureau of Statistics and Plans and the Department of Agriculture to complete the watershed restoration project. This project was created less than 2 years ago, and studies continue on its impacts to either the savanna or the reefs downstream.

Protected Lands

There are several protected areas found in the Marianas. These include conservation areas, national parks, critical habitat, a national wildlife refuge, and the only mitigation bank in the Pacific Islands. The Federal or local government designated these lands for the conservation of natural resources to protect them from development. Each area is regulated in regards to hunting, fishing, and other uses depending on the history and natural resources of area. The conservation areas in the CNMI are composed of all ecotypes aside from development but tend to prioritize forested areas (Liske-Clark, 2015).

Conservation lands in the CNMI comprise 22% of Rota, 4% of Tinian, and 9% of Saipan (Table 2 displays amounts of savanna ecotype). The entire islands of Guguan, Asuncion, Maug, and Uracas are protected by the CNMI constitution. The entire island of



Fig. 10 Severe erosion in Guam's savanna. (USFWS) U.S. Fish and Wildlife Service. Severe erosion in Guam's savanna. (USFWS unpublished photo).

Sarigan is owned by the Department of Public Lands but regulated by the Division of Fish and Wildlife. The CNMI conservation lands total 55.6 km² (21 mi²), representing 12% of the total land area. In the CNMI these lands are designated through the passage of a congressional bill and are under the ownership of the CNMI Department of Lands and Natural Resources or have been set aside by Department of Defense (DOD) to restrict activities permitted on the lands to minimize impacts to natural resources. On Guam, lands are placed under the ownership of the government of Guam or if they occur on DOD lands they remain under their ownership (Fig. 11) (Reeves and Amidon, 2018).

There are currently two national parks on Saipan and Guam. Both were designated to commemorate World War II and are comprised of primarily coastal ecotypes, although on Guam the National Park Service (NPS) has 688 acres (270 ha) of savanna in their Asan and Mt. Alifan units. These units are under the management of the NPS, which does basic vegetation management for the benefit of their visitors. There is a proposal under review by the NPS to designate a new park in Rota which may contain savanna lands but the status of that is unknown (NPS, 2017) (Fig. 12).

Critical habitat has been designated on Guam and Rota and contains some of the savanna ecotype. Critical habitat is defined as a specific geographic area that contains features essential for the conservation of a threatened or endangered species and that may require special management and protection. On Rota habitat was designated for the Mariana crow (Aga in Chamorro) and the Rota Bridled white-eye (Nosa Luta in Chamorro) and both are comprised primarily of forest habitat (see Fig. 13). Protection of designated critical habitat varies on land ownership.

In the CNMI, the Northern Mariana Islands Administrative Code (NMIAC) Chapter 65-30, § 65-30-101 details the permit requirements for any land clearing activities “to ensure no unauthorized clearing of any type of ecotype, including savanna, occurs in the CNMI.” Similarly on Guam, the Guam Administrative Rule (GAR) Chapter 3 Required Permits and Approvals under regulatory requirement 22 Guam Administrative Rules (GAR) 10,103, 10,106, 10,107 for any “development or construction activities that involve clearing, grading, filling, excavating, and other earth-moving operations.”

Protected Designations

Commonwealth of the Northern Mariana Islands Protected Lands

The government of the CNMI designated conservation lands located on the Sabana plateau and into the Talakhaya watershed in Rota in 1994 under local law 9-1. This land contains native forests, savannas (see Table 2 for acreage), coastlines, and coral reefs. All forms of take (meaning harassment or harm, including harvesting or hunting) of wildlife or plant life is prohibited, with the exception of traditional healing plants.

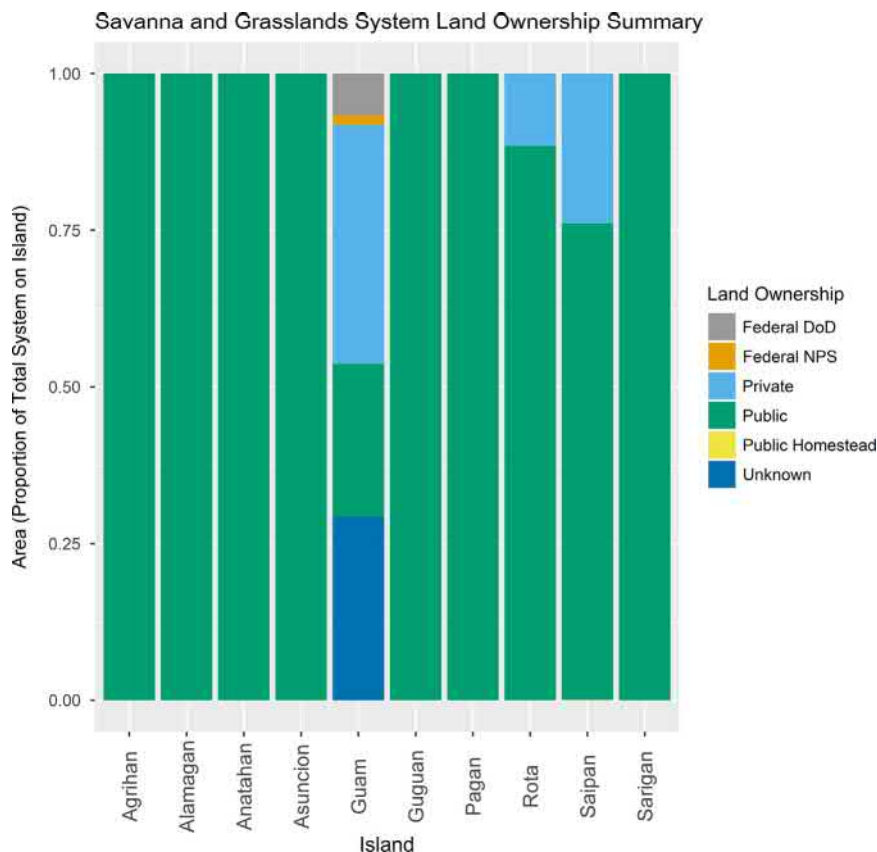


Fig. 11 Land ownership summary plot near here. From Reeves, M.K. (2019). Savanna and grassland system land ownership summary.

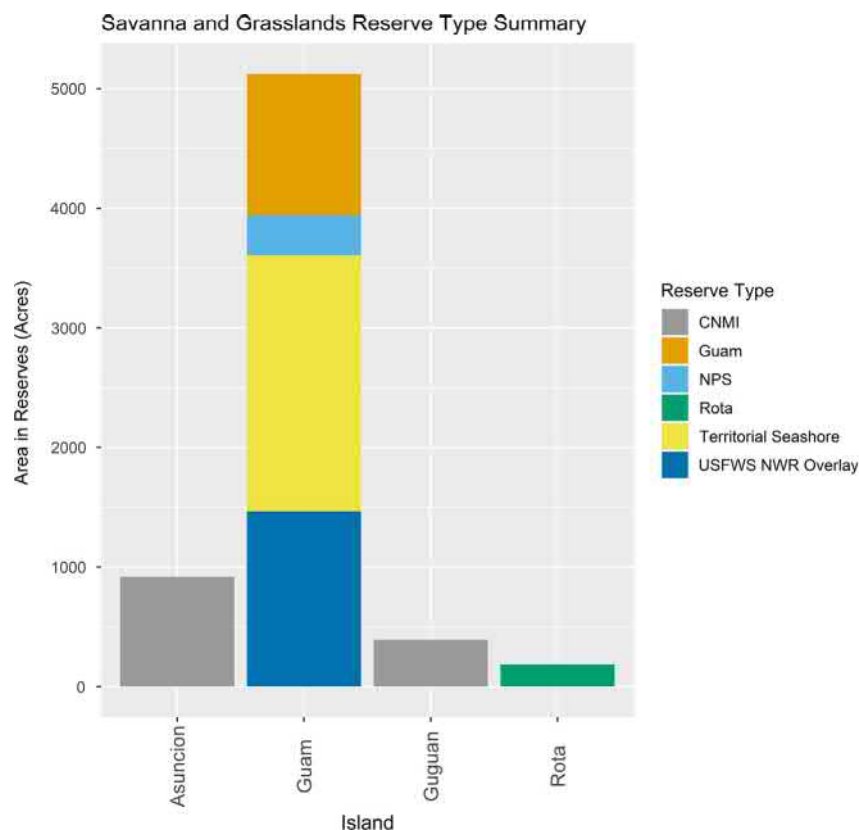


Fig. 12 Reserve type summary plot near here. From Reeves, M.K. (2019). Savanna and grasslands reserve type summary.

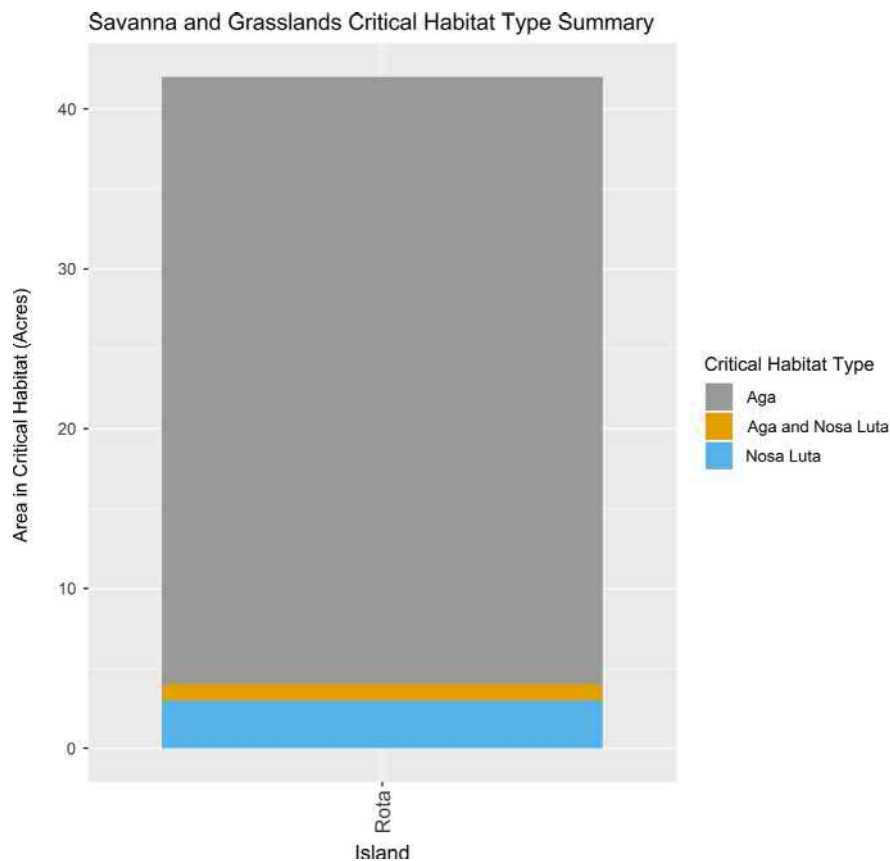


Fig. 13 Savanna and Grassland Critical Habitat Type Summary; describes the area in acres of critical habitat for Aga and Nosa Luta in Rota. From Reeves, M.K. (2019). Savanna and grassland critical habitat type summary.

Government of Guam Protected Lands

In 2004 the Government of Guam proposed a GovGuam Critical Habitat Alternative to the USFWS (DAWR, 2006). The stated objective was to establish four areas for the conservation of natural resources. The proposed areas were Anao (695 acres), Asdonlucas (471 acres), Cotal (552 acres), and Bolanos (2830 acres). Anao is primarily native limestone and secondary forest. Cotal is primarily savanna, badlands, and some secondary forests. Bolanos consists of savanna and forest. Asdonlucas was originally native limestone forest, but the area was leased to a private entity and has now become the Guam Raceway. Although the lands are all treated as conservation lands by the state wildlife agency, there are no binding legal protections for these lands. Cotal, which is primarily savanna ecotype, has had several acres removed for the construction of an experimental wind turbine by the Guam Power Authority. If successful, several more turbines may be built within the conservation area (Dumont-ol Daleno, 2016).

Stakeholder Engagement

Various awareness and engagement activities have been and/or are being undertaken to improve stakeholder engagement in reducing impacts from invasive species and reducing the threat from new species arriving and establishing. Existing efforts are mostly conducted by individual offices for specific activities and/or pest organisms. The University of Guam's CIS has worked with Jeep dealerships to educate buyers of the damages caused by off-road vehicle use (Meno, 2018). SeaGrant has worked with some villages in southern Guam to educate hunters of damage caused to the savanna by burning lands for hunting and how that causes damage to reefs (University of Guam Sea Grant Program, 2017). Guam Department of Agriculture, University of Guam, the Northern Marianas College as well as numerous others have all supported awareness activities.

Interactions of All the Above

The primary stressors to savannas include development activities and badland formations. These stressors are significant and ongoing, act in concert with other stressors, and are expected to continue or increase in magnitude and intensity into the future without effective management actions to control or eradicate them. Current conservation efforts taken by Federal, State, private, and agency partnerships combined with certain laws and regulations limit some of the effects of the stressors on the ecotype, but do not eliminate them. The stressors continue to contribute to the further increase of development and loss of species diversity. Development within the savannas is concentrated in southern Guam. The native plant and animal species have experienced reductions in numbers while invasive plants and animals take over. Without active management, badlands will continue to spread in the savannas of southern Guam.

Efforts to combat erosion have increased recently as part of an effort to protect the coral reefs. The protection of the savanna is not the primary reason for these restoration projects, but is necessary for protection of the reefs. Public education campaigns have periodically occurred to educate hunters and people who recreate off-road of how their activities cause erosion. Projects to prevent erosion by planting trees or laying vetiver swales must be maintained for a period of years, however, often once the trees are in the ground they are not monitored nor maintained. For any erosion control project to be successful on a long-term basis there should be monitoring and remediation for several years at least. This is not currently happening. While erosion control projects have had some protective effect on the savannas, large planned developments still threaten this ecotype.

Ecotypes in the Mariana Islands are experiencing stress from multiple sources. Many stressors are intertwined with each other. For example, increases in dry season severity can lead to increases in wildfires. Increases in development will require importation of more construction materials, leading to the potential for the introduction of more invasive species. Some stressors are beyond the ability of humans to control. Typhoons and volcanic eruptions will occur no matter what, and so it is important to ensure that ecotypes are as resilient as possible to bounce back from stochastic events.

The ultimate fate of savanna lands on each island will mainly depend upon its ownership. Savanna lands in protected areas, such as refuges or restricted-entry islands, will remain savanna due to the conservation missions of the owners. Savanna lands that are privately owned are more likely to be developed. See Table 4 for a chart of land ownership on each island.

In summary, the savanna across Marianas is highly resilient (Table 5) due to its ability to recover from disruptions such as fires or typhoons. Many grass species can regrow quickly from roots. Fire is not just a disruptor, but helps to maintain the savanna by preventing large trees from gaining a foothold. Savanna is highly redundant due to being present on 11 of the islands in the chain. A loss of savanna on one island may not be detrimental to the overall savanna across the Marianas and may be recovered because of the presence on other islands. Savanna ecotypes have medium representation due to the moderate diversity of grass, herb, and fern species present.

In the following sections we analyze future scenarios and their possible impacts for conservation in the Marianas.

Future Scenarios

The condition of savanna and grassland in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are as follows:

Table 4 Savanna land ownership by island.

<i>Island</i>	<i>Land Ownership^a</i>	<i>Area (Acres)</i>	<i>Area (% of Island)</i>	<i>Area (% of Marianas Islands)</i>
Agrihan	Public	5357	43	2
Alamagan	Public	1530	39	1
Anatahan	Public	3678	38	1
Asuncion	Public	918	36	<1
Guam	Federal DoD	1453	1	1
	Federal NPS	335	<1	<1
	Private	8296	6	3
	Public	5316	4	2
	Unknown ^b	6371	4	2
Guguan	Public	392	26	<1
Pagan	Public	2928	21	1
Rota	Private	26	<1	<1
	Public	199	1	<1
	Unknown	<1	<1	<1
Saipan	Private	286	1	<1
	Public	907	3	<1
	Public Homestead	1	<1	<1
Sarigan	Public	341	21	<1

^aPublic land includes homesteads (Public lands proposed for either village or agriculture homesteads), and lands in the CNMI leased to developers. DoD lands include lands owned by DoD and lands DoD leased and leased back to farmers on Tinian. NPS lands include lands owned by the NPS on Guam and leased by NPS on Saipan. USFWS is refuge land.

^bUnknown lands on Guam, Rota, and Tinian are lands with no associated GIS data layers for the determination of ownership. Most probably ownership is a combination of local government and privately owned lands.

From (USFWS) U.S. Fish and Wildlife Service. Savanna land ownership by island.

Table 5 Levels of resiliency, redundancy, and representation for savanna habitats that exist in the Marianas.

<i>Resilience</i>	<i>Redundancy</i>	<i>Representation</i>
High	High	Medium

Savanna and Grassland Habitat Status Assessment for the Mariana Islands.

From (USFWS) U.S. Fish and Wildlife Service. Levels of resiliency, redundancy, and representation for savanna habitats that exist in the Marianas.

- (1) *Conservation values*: Stakeholder involvement and public opinion determine the formulation, implementation and funding of natural resource conservation within laws and development plans.
- (2) *Laws and biosecurity*: National, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented. (e.g., hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.).
- (3) *Development or conservation planning*: National, state, county, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

These conservation management parameters are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The year 2035 is the extent of the “foreseeable future,” and is based on the projected divergence of IPCC Representative Concentration Pathway (RCP) climate change scenarios (van Vuuren et al., 2011; Miller, 2018).

The four foreseeable future scenarios considered in this assessment are:

Future Scenario One, Status Quo—The most likely foreseeable future; no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues through the foreseeable future.

Future Scenario Two—A slight increase in natural resource conservation in the CMPs marginally improves conservation management.

Future Scenario Three—A slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management.

Future Scenario Four—A moderate to large increase in conservation actions in the CMPs substantially improves conservation management.

The future condition of savanna and grassland ecotypes in Scenario One, the status quo, was characterized from an assessment of change over time in savanna and grassland land cover obtained from existing land cover maps (Amidon and Reeves, 2018). Based on these land cover maps, an annual rate of change for savanna and grassland ecotypes was estimated, and a projected change (in acres/hectares) was calculated for the year 2035. The resulting information on changes in land cover by 2035, as derived from existing land cover change estimates, is the extent of the savanna and grassland ecotype that is expected in the foreseeable future under Scenario One, the status quo, where conservation efforts remain unchanged and the current rate of change in land cover is also unchanged.

The future conditions of savanna and grassland ecotypes for Scenarios Two, Three, and Four cannot be quantitatively (acres/hectares) estimated. However, the Scenario One estimate can provide a “baseline” for a qualitative characterization of changes in the future condition of savanna and grassland ecotypes under Scenarios Two, Three, and Four.

Changes in human population are captured only by the changes in the “developed” land cover footprint derived from land cover map analysis (Amidon and Reeves, 2018). Impacts from other sources of human activities or human-caused stressors (e.g., plant and animal diseases, wildfires, invasive species, etc.) are not well characterized in the land cover changes, but significantly contribute to increases in the land cover area dominated by non-native vegetation.

Also, note that island-wide implementation of the CMPs is unlikely to have a significant effect on climate-related stressors (temperature, precipitation, and severe weather) resulting from global warming by 2035. This lack of CMP climate effects is due to the global lag in climate response to changes in greenhouse gas emissions which occurs on the order of centuries rather than years (Solomon et al., 2009; Gillett and Cullen, 2011; Jevrejeva et al., 2012). Evidence of climate effects is also confounded by the large annual variation in the Pacific islands climate parameters, which is much greater than projected climate change by 2035. Although impacts from climate-related stressors do not change across the four scenarios, they were included in this analysis because of their overall magnitude of potential importance to future ecotype viability.

Future Scenario One, Status Quo

Summary: Scenario One is considered the most likely future scenario, and serves as a “baseline” for comparing among the four future scenarios. There is no change in the implementation of the three CMPs between 2018 and 2035. A continuing current rate of change in land cover through this foreseeable future results in a slow but continuous change in the ecotype as described below.

Description: Using the current rate of change, the land cover for savanna was calculated for the year 2035. The projected change in land cover by 2035 is the only future scenario with quantitative values (acres or hectares). The anticipated changes, under Scenario One, for each of the ecotype stressors affecting savanna ecotype are given in Table 6.

An expanding human population and increased development and general land use on all inhabited islands is anticipated (Amidon, 2018; Amidon and Reeves, 2018), and therefore ecotype stressors are expected to increase at a small annual rate. Exceptions are a small to moderate annual rate of increase for development, wildfires, and surface air temperature, and a small annual rate of decrease for precipitation. On average, the percentage of land developed for residential, commercial, and agricultural purposes on the inhabited islands is expected to increase by 25% from 2016 to 2035. This rate is only true for the southern inhabited islands of Guam, Rota, Tinian, and Saipan. Data on rates of development for the remaining islands does not exist at this time. By island, estimated rates of change in savanna ecotype from 2016 to 2035 are: Guam – 1%, Rota 166%, Tinian 0%, and Saipan – 16%.

On Guam, off-roading is expected to continue to degrade the savanna, causing erosion and the spread of badlands. Current levels of typhoon events are not expected to impact savannas. Incidences of fires may remain at their current rate.

The island of Rota has seen a decrease in the human population (U.S. Census Bureau, 2010), most probably due to the collapse of the tourism industry. Farmlands and ranches have been abandoned and allowed to return to their natural state.

A few small conservation actions currently in place may slow the rates of erosion from small areas, but overall there will be a steadily increasing amount of erosion from the savannas on Guam and Saipan. Conservation will continue as small projects with a limited scale producing a limited overall benefit.

Because the Scenario One biosecurity CMP remains unchanged while the population and development continue to grow, an increased potential for new invasive species and new diseases (particularly those affecting native plants) exists. The introduction of additional plant diseases and invasive species may enhance the conditions that support wildfires.

Future Scenario Two—There is a slight increase in the CMPs that marginally improves conservation management.

Summary: Conservation Agencies and stakeholders work with increased but limited resources to slow or stop the degradation of landscape areas.

Description: Scenario Two is essentially “status quo” with minor improvements in the three CMPs. The anticipated changes, under Scenario Two, for each of important ecotype stressors for savanna are given in Table 6.

Though there is an expanding human population in Scenario Two, development is not expected to substantially increase. A slightly improved biosecurity effort should help reduce invasive species and plant diseases but increases are still expected. The small increased support of natural resource management in the CMPs is not expected to greatly alter wildfire frequency and intensity, but these might (lower slightly) compared to Scenario One. The CMP supported conservation will not prevent, mitigate, or reverse the impacts of climate change-related stressors.

The main stressor to savanna across the archipelago is development, which may see some controls in place to encourage development in existing cleared areas. Savannas on Guam may receive more conservation attention if outreach for damage due to off-roading is expanded.

Future Scenario Three—There is a small to moderate decrease in conservation actions in the CMPs that substantially decreases conservation management,

Summary: All natural resource management actions in the CMPs are set aside in deference to land use for economic development. With extensive localized management, some native species may persist in park-like settings or in areas where land development is not possible.

Description: Scenario Three has substantial declines in natural resource conservation within the three CMPs. An increasing human population is supported in its use of land for economic development over the conservation of native ecotypes. Areas that cannot

Table 6 Responses of Savanna and Grassland habitat stressors in foreseeable future scenarios.

Conservation Management Parameters (CMPs)				
Conservation values	Stakeholder involvement and public opinion influence the formulation, implementation, and funding of natural resource conservation and biosecurity (NRC/B) within laws and development or conservation plans			
Laws and Biosecurity	National, state, county, and city laws and regulations are the means by which NRC/B are supported and implemented			
Planning for Development or Conservation	National, state, county, city, and private development plans or conservation plans define actions that result in losses or gains in NRC/B (impacts realized at implementation)			
Foreseeable Future Scenarios and the resulting Savanna and Grassland habitat conditions				
Use Foreseeable Future Scenario One as a “baseline” to characterize changes in Conservation Actions and Habitat Conditions in Future Scenarios Two, Three and Four	Scenario One: CMPs: Unchanged in support for NRC/B Conservation Actions: No change; current rate of land cover change continues through the foreseeable future Habitat Condition: Habitat area, quality, and sustainability slowly decrease through the foreseeable future	Scenario Two: CMPs: Small increase in support for NRC/B Conservation Actions: Marginal increase Habitat Condition: Habitat area is unchanged through the foreseeable future; habitat quality and sustainability are slightly enhanced through the foreseeable future	Scenario Three: CMPs: small to moderate decrease in support for NRC/B Conservation Actions: Substantial decrease. Habitat Condition: Urban and agricultural uses are prioritized over conservation; habitat area, quality, and sustainability substantially decrease through the foreseeable future	Scenario Four: CMPs: Moderate to large increase in support for NRC/B Conservation Actions: Substantial increase. Habitat Condition: Robust, sustained effort to restore, manage, and expand conservation; habitat area, quality, and sustainability substantially increase through the foreseeable future
Habitat Stressors	Responses of Savanna and Grassland habitat stressors			
Development	Small to moderate increase	No change (redevelop)	Moderate to large increase	Small to moderate decrease
Altered hydrology	No change to small increase	No change	Larger increase	Small decrease
Recreation/access	Small increase	Small increase	Larger increase	Larger increase
Invasive species	Small increase	Small increase	Larger increase	Small decrease
Plant diseases	Small increase	Small increase	Larger increase	No change to small decrease
Fire	Small to moderate increase	Small increase	Larger increase	No change to small decrease
Erosion	Small increase	No change	Larger increase	Small decrease
Climate				
Temperature	Small to moderate increase	Small to moderate increase	Small to moderate increase	Small to moderate increase
Precipitation	Small decrease	Small decrease	Small decrease	Small decrease
Storms	Small increase	Small increase	Small increase	Small increase

From (USFWS) U.S. Fish and Wildlife Service. Responses of savanna and grassland habitat stressors in foreseeable future scenarios.

support development become the only areas of free-living native species. The anticipated changes, under Scenario Three, for each of the stressors important to savanna are given in [Table 6](#).

An expanding human population requires increased land use for agriculture and development with no encumbrance from natural resource management. Biosecurity controls are significantly weakened in this Scenario leading to an increase in invasive species problems and new plant diseases. Combined together, these factors will result in substantial increases of wildfire frequency and extent. The substantial loss of CMP supported conservation may locally aggravate the impacts of climate change-related stressors.

Future Scenario Four—There is a moderate to large increase in conservation actions in the CMPs that substantially improves conservation management.

Summary: An overt and robust, active, ongoing effort is made to engage partners and stakeholders in identifying and prioritizing landscape areas needed for the conservation of native ecosystems, and to actively restore and expand these areas.

Description: A substantial emphasis on natural resource conservation is present in the three CMPs, reflecting increased societal concern for declines in natural ecotypes and biodiversity. Active and well-supported natural resource management begins to restore these ecosystems and expand their landscape areas. The anticipated changes, under Scenario Four, for each of the ecotype stressors important for savanna are given in [Table 6](#).

The needs of an expanding human population are addressed through more efficient land use governance based on redevelopment rather than development of undeveloped areas. Modern and novel agricultural practices focus on those that do not affect existing natural areas or areas needed for native ecotype restoration. Substantially improved biosecurity regulations decrease introductions of invasive species and plant diseases. These improved land management actions result in decreased wildfire frequency and extent. The substantial increase in CMP supported conservation may locally mitigate the effects of climate change-related stressors, but climate change is expected to continue.

On Guam and Saipan, development is controlled. Durable conservation areas are created which then undergo enhancement to remove invasive plants and animals, returning the ecotype to its original state. Wildfires are no longer intentionally set and badland areas are reduced. Feral ungulates are controlled and no longer create wallows, ruts, or rubs on vegetation.

Conclusion

Conservation efforts by Federal, State, and private entities and agency partnerships have limited some of the effects of the stressors on savanna in the Marianas, but have not eliminated them. A stronger effort to engage partners and stakeholders in identifying and prioritizing landscape areas required for the conservation of native ecosystems, and to actively restore and expand these areas is needed for the successful conservation of savannas.

The primary stressors to savannas include development, invasive species, erosion caused by recreational off-road vehicle use, fires, typhoons and drought. Despite some protected areas and active management efforts to target stressors, they are expected to continue or increase in magnitude and intensity in the future. It is likely that without a greater shift in land ownership by refuges or other owners with a mission of conservation, and without an increase in active management to provide long-term monitoring and remediation, savanna in the Marianas will continue to be degraded or destroyed in the future.

See also: Physical Geography of the Mariana Archipelago.

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Freshwater: Oasis of Life—An Overview

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Glossary

Freshwater: A Glossary of Terminology Used in Freshwater Biology and Management (Suring, 2020d).

The definitions of terminology used to describe the ecological relationships and management of freshwater systems may vary

by geographical region and professional field of endeavor. This glossary of more than 220 terms used in reference to freshwater is provided to establish a common base of understanding among workers in this discipline.

Abstract

The freshwater biome is an essential life-sustaining element for the Earth which cannot be substituted for. Freshwater is indispensable for humans; water scarcity currently endangers food production throughout the Earth. It is also the foundation for substantial biological diversity and critical ecosystem functions. This review of the Freshwater Biome established the importance of freshwater to human life and enterprise by discussing the major uses of freshwater, including ecosystem services. We then provided an overview of the ecosystems that make up the Freshwater Biome, some elements of biogeography of the Freshwater Biome, and offered insights to the conservation and management of water resources in the Biome.

Introduction

The freshwater biome is an essential life-sustaining element for the Earth which cannot be substituted for (Koehler, 2008). Freshwater is indispensable for humans; water scarcity currently endangers food production throughout the Earth. It is also the foundation for substantial biological diversity and critical ecosystem functions. Over 10,000 fish species occur in freshwater (Lundberg et al., 2000) and when amphibians, aquatic reptiles, and mammals are included, perhaps as much as one third of all vertebrate species are associated with freshwater. When invertebrates are also considered, more than 10% of the described species on Earth occur in freshwater. Considering that surface freshwater contains about 0.01% of the Earth's water and covers only about 0.8% of the Earth's surface (Gleick, 1996), freshwater truly is an oasis of life.

Freshwater is a limited resource that is under significant anthropogenic threat. Ecosystems in the Freshwater Biome may be the most endangered ecosystems on Earth (Dudgeon et al., 2006). Indicators are revealing rapid population declines and a large extinction risk in freshwater organisms (Reid et al., 2019).

This review of the Freshwater Biome established the importance of freshwater to human life and enterprise by discussing the major uses of freshwater, including ecosystem services. We then provided an overview of the ecosystems that make up the Freshwater Biome using the basic classification system described by Fisher (2018) (i.e., lentic—still waters, lotic—flowing waters, riparian, aquifer/groundwater, glaciers). We used the established definition of freshwater (i.e., water that contains less than 1000 mg/L of dissolved solids [United States Geological Survey, 2019]) to guide what waters we included in this review. As such, we did not include brackish waters, estuaries, and mineral springs. We also only included natural water bodies, so we did not address water bodies created by human activity, such as reservoirs, stock ponds, canals, irrigation ditches, or rice paddies (Smith et al., 2002).

We provided a brief overview of some elements of biogeography of the Freshwater Biome and offered insights to the conservation and management of water resources in the Biome. We concluded with a glossary of terms associated with freshwater.

Why is Freshwater Important?

The Importance of Freshwater for Domestic Use (Padowski, 2020)

Of the many uses humans have for freshwater, water for domestic use is the most intimately understood by any given individual because it is the water we use each day. Domestic use includes all the water used in and around the home including water for indoor use, such as drinking, bathing, cleaning, preparing food, and outdoor use, such as maintaining lawns, livestock, and gardens. Due to its importance, understanding where and how much water is needed for domestic use continues to be a high priority for communities around the world. This is particularly true as rapid growth is expected to push the world population to 9.7 billion people by 2050. In most cases, this urban growth will occur in urban areas, and therefore particular attention is paid to the challenges and opportunities for meeting domestic water demands in urban areas. This article explores the importance of freshwater for meeting domestic use purposes in an increasingly human-dominated world. Included is an overview of how water for domestic purposes is used around the world, how domestic use impacts the freshwater resources that support communities, what the challenges and opportunities we as a society face as water becomes a more precious resource.

Importance of Freshwater for Irrigation (Edwards and Nehra, 2020)

The use of freshwater in irrigation arose in the world's first civilizations and remains critical to the planet's food supply today. This article first provides some historical context for irrigation before tackling the question of competing demands for water, discussing how coordination among irrigators is achieved and the complex relationship between irrigation and water conservation and reuse. The discussion focuses on four countries—the United States, India, China, and Chile—which provide insight into the importance of irrigation, as well as current challenges.

Importance of Freshwater for Livestock (El Mahdy, 2020)

Of the freshwater (blue footprint water) from rivers, lakes and groundwater 33–88%, is directed towards agriculture in varying proportions depending on the area. Only 0.6% is used for direct consumption by livestock or indirect activities associated with livestock. The distribution of livestock on the globe is dependent on existing water and the ability of animals to tolerate water deficiency and quality. In the animal body, water has multiple functions: metabolic, growth, breeding, and production. Deprivation or deficiency of freshwater affect these functions, but species from arid and semiarid areas have developed adaptations to these conditions. There are large differences between water requirements, for livestock in semi-arid and arid area of extensive and pastoral system, compared to livestock in the intensive farming system.

Dependent on the farming system, the type of rainfed agriculture and the distance to water source, the watering frequency is different. Water quality in many regions is poor in terms of salinity and contamination with toxic elements. In arid and semi-arid areas, water usually has a large amount of chloride, which is why research is directed to choosing the most resistant species to low quality water and to develop farms in these areas as well.

Importance of the Conservation and Management of Freshwater to Aquaculture (Goddard and Delghandi, 2020)

Inland fish farming contributes to the nutrition and livelihoods of many millions of people. Most fish are grown in constructed ponds or floating cages in natural or man-made water bodies. Freshwater fish farming is often integrated with the farming of crops, where wastes and by-products from one component are used as inputs for another. Developing technologies offer new opportunities to conserve water and increase the productivity of freshwater aquaculture.

Recirculating aquaculture systems (RAS) have been developed with the potential to greatly reduce the water requirements and environmental impacts of fish farms. Biofloc technologies (BT) utilize in situ bacterial processes to maintain water quality and provide food for filter-feeding species of fish and crustaceans. Full integration of fish and vegetable production can be achieved through aquaponics, which combines aquaculture and hydroponic plant production within a recycled water system. This article reviews current developments in water recirculation techniques, biofloc technology, and aquaponics against the background of increasing food security needs and water resource issues.

Mining and Water Resources (Mudd, 2020)

This article reviews the basics of mining and its interaction with water resources. While mining often requires a large amount of water, it can also present various risks to water resources, such as depletion or pollution (especially if acid and metalliferous drainage related to iron sulfide minerals occurs to the surface environment). Modern mining is typically regulated to address these risks, with statutory environmental reporting increasingly being made public to improve transparency and align with the need for industry-wide reporting on sustainable development performance. The article presents a concise overview of mining, its interactions with water resources, key risks to manage, and the principal regulatory and reporting approaches which can be used for sustainable management of both mining and water resources.

Freshwater and Industries (du Plessis, 2020)

Industries require large amounts of water which are used by various industries around the world at different rates and in different ways. Global water consumption has consistently been increasing since the 1980s and is expected to continue due to rising demands. Currently industrial water consumption is described as a major drain on the world's limited water supply and it is expected that the water demand will exceed current supply by 40% by 2030. The use of water for industrial processes as well as the discarding of wastewater can have various impacts if not properly managed and controlled.

The continued increase of industrial water use accompanied by continued population and socio-economic growth will consequently exacerbate current effects of industrial water use and cause greater future challenges. Industries are a huge source of pollution around the world as they produce pollutants which can be very harmful to both the environment and the human population. Freshwater resources around the world are faced with significant pollution problems, some more than others. The expanding industrial base with accompanied pollution have placed additional pressure on existing water and often causes water resources to no longer be suitable for human consumption or other uses. Water is at increased risk worldwide and industrial sectors will have to implement various strategies to minimize this risk in the future.

Importance of Freshwater for Electric Power Generation (Liao, 2020)

Global electric power generation relies heavily on water. Hydropower utilizes the potential and kinetic energy in running water and thermoelectric power plants, e.g., coal-fired, gas-fired and concentrated solar power, withdraw significant volumes of water for cooling purposes. Water is also used in various other stages of electric power generation's life cycle, such as coal mining, transportation, crop irrigation, and so forth. Consequently, water shortages and rising water temperature can lead to curtailment of electric power generations.

Climate change is expected to deteriorate water scarcities in some regions, which, compounded with rising water temperature, can exaggerate such electric power generation's water-related risks. Adopting air cooling systems, transforming the energy portfolio to gas, solar PV and wind, and utilizing alternative water sources, e.g., seawater and reclaimed water, can help reduce the electric power generation's reliance on freshwater resources in order to cope with future potential water-related risks.

The Importance of Freshwater for Providing Ecosystem Services (Apostolaki et al., 2020)

Freshwater ecosystems, whether surface, groundwater, or in the form of ice caps are fundamental for human life and for supporting the vast biodiversity, natural processes, and cycling. They provide ecosystem services, thus, benefits for humans and their societies obtained from nature, in all four categories: provisioning, regulating, cultural and supporting. The importance of sustaining ecosystem integrity via protecting ecosystem services is undeniable. However, it will be a big challenge as long as the human-induced degradation of the natural environment continues.

Lentic Freshwater

Ephemeral Wetlands (Deil, 2020)

Ephemeral wetlands (EW) are habitats with seasonal water body and ephemeral plant cover. Subtypes are shorelines of permanent rivers with fluctuating water level, seasonal pools in climates with variations in rainfall, and the ephemeral flush habitat on inselbergs. EW offer extreme environments, shifting from flooding to water shortage. Short-lived annuals, dwarfish perennials, and resurrection plants find a niche there. A permanent seed bank (and egg bank for crustaceans) buffers the year-to-year variability. Strong selective forces result in evolutionary processes like convergence, niche constancy, endemism, and vicariance of taxa. By sheltering rare and endemic species, EW are jewels of biodiversity.

Wetlands (Campbell, 2020)

Wetlands are globally diverse ecosystems that occur between terrestrial and aquatic environments. The degree of flooding is the main control on wetland vegetation, which varies from shallow water wetlands with submerged and floating-leaved plants, to emergent marsh, and treed swamp. Wetlands support unique flora and fauna, from duckweed to mangrove trees and from frogs to hippopotamus. Humans exploit them for water, rice, and fish, but wetlands also provide key services, such as flood attenuation, coastline protection, water purification, and carbon regulation. Despite these benefits, humans have drained or converted over half of global wetlands. Extensive wetlands remain, but many are threatened by altered flooding regimes, invasive species, nutrient enrichment, contamination, and climate change. Conservation efforts must focus on protecting wetlands and especially on maintaining key ecological processes on which wetlands rely.

Ponds (Lemmens and Pinceel, 2020)

Ponds are abundant landscape elements that provide vital ecosystem services and contribute disproportionately to biodiversity. Despite their importance for human society, they are threatened habitats and their protection and conservation is often neglected in current national and international legislation. We summarize a number of key aspects on pond ecology and biodiversity. In addition, we discuss current policy and highlight essential elements for the effective conservation of ponds.

Lakes (Suring, 2020a)

There are approximately 304 million freshwater lakes world-wide with the highest concentration, area, and perimeter of lakes located within boreal and arctic latitudes. The seven main formation processes of lakes are tectonic activity, volcanic activity, glacial activity, fluvial action, Aeolic action, anthropogenic action, and marine action. Lakes are generally characterized by low flow velocity and relatively low inflows and outflows. The primary parameters used to describe geomorphologic characteristics include lake length, lake width, lake depth, direction of major axis, shoreline length, lake area, lake volume, insulosity, and watershed to lake area/volume. Approximately 45% of photosynthesis on earth occurs in aquatic environments and photosynthesis supplies the primary source of organic matter for the growth and metabolic demand of all organisms in lakes.

Cultural eutrophication is thought to be the most widespread stressor of habitat in natural lakes. After eutrophication, acidification is the most important threat and stress factor for lake habitats. Above all, aquatic ecosystems are very vulnerable to climate change which influences the physical, chemical, and biological structure of lakes. These influences include fluctuating water levels, increased water temperature, shorter ice-cover periods, invasion of nonindigenous animal and plant species from tropical and subtropical regions, and structural changes in catchment areas.

The value of biological diversity in freshwater lakes and the need for its conservation is becoming more important world-wide. However, the challenges involved with the conservation of freshwater lakes are great. It is often difficult to decide what management

action to implement and what will be most effective. However, positive conservation action has brought real and sustained benefits across scales, from local to global, via a variety of mechanisms.

Lotic Freshwater

Springs (Suring, 2020b)

Springs are a unique resource from an ecological, economic, and cultural perspective. Springs harbor highly specialized and regionally restricted flora and fauna, often resulting in a unique freshwater biological diversity. Springs serve as evolutionary refugia, supporting concentrations of relict and endemic species that require habitat stability. Springs also provide a source of freshwater for personal human use and commercial sales. Major threats to springs include human draining and diversion of groundwater sources, pollution, habitat alteration, and invasive species. Moreover, restoration efforts are expensive and ecological responses to restoration are largely unknown. The safest management strategy is to refrain from potentially harmful land use within the vicinity of springs.

Stream Biomes of the World (McManamay and Jager, 2020)

Streams comprise only a small portion of Earth's terrestrial land surface area yet harbor a significant amount of the world's biodiversity. These ecosystems also support many competing human societal services, predisposing them to intense ecosystem alteration and leaving very a small percentage of streams in their natural state. Given their rarity and propensity for human disturbance, understanding stream structure and function, and how to conserve those properties, is extremely important. This article provides an overview of stream environments, their form and function, the organisms that inhabit them, and major ecological concepts and paradigms. An overview of major types of commercial uses is provided, which correlates with major anthropogenic stressors and the nature of ecosystem alteration. Finally, the article concludes with approaches and strategies for stream conservation and management.

Rivers (Wohl et al., 2020)

Ecosystems associated with rivers are intricately connected to their entire watershed. The river ecosystem includes the channel of active water flow, floodplain, and riparian and hyporheic zones. This ecosystem is shaped by interactions among the natural flow of water, sediments within the river and entering the river, and large wood regimes within the riparian zone. River integrity describes the ability of a river ecosystem to adjust to changes in these elements and through these adjustments maintain the habitat, disturbance regime, and connectivity necessary to sustain native biotic communities. Riverine food webs conceptualize the coupling between the physical environment and biotic communities and can be used to examine recovery from disturbance, variation in the structure of communities, and sources of energy that fuel metabolism within the ecosystem.

Riparian

Riparian Ecosystems (Capon, 2020)

Riparian ecosystems encompass a diverse suite of ecosystem types, including river banks, floodplains and wetlands, which are characterized primarily by being ecotones, or transitional zones, between adjacent terrestrial and aquatic realms. In general, riparian ecosystems represent wetter, cooler, and more heterogeneous habitats than adjacent upland areas and consequently tend to support biologically distinctive, productive, and diverse communities. Riparian ecosystems also provide a wealth of critical ecosystem functions and services of importance at local and catchment scales.

In particular, riparian vegetation plays a key role in: regulating microclimates and water quality; preventing riverbank erosion and promoting landform stability; subsidizing aquatic and terrestrial food webs; and providing habitat for a wide range of aquatic, amphibious, and terrestrial organisms. Despite these values, riparian ecosystems are also some of the most altered, degraded, and vulnerable ecosystems on Earth, due largely to their position in the landscape and hotspots of intensive human activity.

Effective management and restoration of riparian ecosystems is increasingly urgent, for both the conservation of much terrestrial and aquatic biota and the wellbeing and livelihoods of people throughout the world. Management approaches range from protection of intact riparian ecosystems to active revegetation of degraded riparian zones. Significant knowledge gaps exist in many places, however, regarding relationships between riparian ecosystem structure and function and the responses of these to disturbances and management interventions.

Groundwater and Aquifers

Groundwater and Aquifers (Suring, 2020c)

Groundwater and associated aquifers are considered essential resources for the maintenance of human life. However, the quality of groundwater and recharge rates has been diminished in many areas of the world. This poses a real threat to the health of aquifers and groundwater-dependent ecosystems such as springs, wetlands, streams, rivers, and lakes and the economies they support. Hydrological recharge of aquifers is complex and is affected by climate, geology, soil type, vegetation, and land use. Managers are becoming increasingly aware that aquifers are dynamic ecosystems rather than just water stored underground and that we need to identify and manage for the environmental values associated with groundwater. Sustainable groundwater management will allow groundwater to be maintained for an indefinite time without having unacceptable environmental, economic, or social consequences.

Glaciers and Ice Sheets

Glaciers and Ice Sheets (DeBeer et al., 2020)

Glaciers and ice sheets are masses of ice and snow that persist over many years formed by the accumulation and compaction of snow. They cover a significant amount of the Earth's land surface and store most of the world's freshwater. Glaciers flow under their own weight, carving out landscapes and transporting sediment and rocks as they move, and they advance and retreat in response to changes in the mass balance, or difference between annual accumulation and ablation.

Glaciers and glacierized river basins have unique hydrological characteristics. They serve as an important store of freshwater and influence the characteristics of annual and seasonal runoff downstream. Glaciers and ice sheets also represent an important biome with a rich diversity of life, from microbial communities to microscopic organisms and macroinvertebrates, and they influence ecosystem functioning well beyond their margins and termini. In recent decades, most glaciers worldwide have been losing mass and retreating in response to climatic variations, now primarily driven by human activity. The Greenland and Antarctic Ice Sheets have also begun to lose significant amount of mass and have exhibited an accelerating pattern of loss. This is expected to continue for many decades or more under current and expected future climate conditions, with the loss of much of the world's mountain glaciers, and significant changes in polar ice caps and ice sheets.

The loss of glaciers and ice sheets poses many problems and challenges, including sea level rise implications, regional changes in water availability, impacts on glacial and downstream ecosystems, release of legacy contaminants stored on and within glaciers, glacier-related hazards, feedback effects on regional and global climate, and many others that affect the well-being of people and communities. There is a need for more observations, better understanding and prediction of glacier dynamics, coordinated adaptation and mitigation strategies across multiple levels from local to international, and a coupled systems approach that integrates physical dimensions of changing ice environments with the human systems that engage with or depend upon them.

Biogeography

The Subtropical Everglades, Florida, USA (Sklar et al., 2020)

Everglades' restoration, the largest of its kind in the world, is expected to restore ecosystem functionality and community structure. Anthropogenic changes in peat elevations, water quality, hydrology, and habitat loss can make plant and animal recovery difficult. However, our understanding of the complexity of Everglades ecology and the spatial and temporal scales associated with plant and animal requirements for water, is putting the Everglades back on track. The knowledge base for this movement is summarized in this article.

The Wetland System of Hawai'i (Browning et al., 2020)

This article represents a status assessment of the Hawaiian archipelagos wetlands including the current status, stressors, and future viability. Wetlands in the Hawaiian archipelago encompass all fresh and saline lentic (standing or still water) ecotypes occurring from sea level to upper elevations. Wetlands can be separated into two categories: wetlands (bogs, upland marshes and swamps; lowland freshwater and saline marshes, and estuaries) and water bodies (ponds, fresh and saline lakes, anchialine pools, and artificial reservoirs). Historically, wetlands were located on all of the main Hawaiian Islands and a few of the Northwestern Hawaiian Islands (NWHI). Currently, wetlands are still found on all the main Hawaiian Islands and Midway and Laysan in the NWHI. However, the quality of many of these wetlands is now comprised of non-native vegetation, invertebrates, and fishes. In addition to naturally formed wetlands and water bodies, artificial reservoirs (i.e., wastewater treatment plants and stock ponds) are also classified as wetlands in the main Hawaiian Islands.

Our assessment of wetland viability, defined as the likelihood of persistence over the long term, is based on the concepts of representation, redundancy, and resiliency. The main stressors of wetland viability are development and altered hydrology, recreation and human access, water pollution, invasive animals and plants, sea level rise, flooding and erosions, natural disasters (i.e., hurricanes), and drought. Ongoing conservation efforts are helping to protect remnant patches of natural wetlands in the Hawaiian

archipelago. The conservation of these habitats depends largely on combined efforts of State, Federal, multiagency organizations, nonprofit organizations, and the voluntary support of private landowners. An analysis of four future scenarios identified a decline in wetlands viability in lieu of intensive management.

The Laurentian Great Lakes of North America (Collingsworth and Malloy, 2020)

The Laurentian Great Lakes of North America are a series of interconnected lakes that, collectively, comprise one of the largest freshwater ecosystems on the earth. Prior to large-scale European settlement, the largely forested watersheds of the Great Lakes Basin delivered few nutrients to the lakes and the lakes themselves maintained a trophic status that ranged from oligo- to mesotrophic conditions. The biotic community of the Great Lakes is relatively depauperate, which reflects the recent geological development of the ecosystem. Historically, there were two main biotic communities in the Great Lakes: those that occupied the biologically less-productive open waters of the upper Great Lakes, and another in nearshore areas and productive embayments.

Human activity in the Great Lakes Basin has brought with it a number of stressors, including land use changes, overfishing, altered nutrient loading, and invasive species. To help manage these stressors, the management communities of the Great Lakes, which represent two countries, eight states, two provinces, tribal governments, First Nations, and local public agencies, have developed a complex patchwork of governance in the Basin.

African Great Lakes (Ogutu-Ohwayo et al., 2020)

The African Great Lakes are ecologically and economically important. Their original biogeography was shaped by geological history but is being altered by habitat degradation, overfishing, invasive species, and climate change driven by the rapidly increasing human population. Most large near-shore species have declined or disappeared and become dominated by small pelagic fishes. Invertebrate and algal communities have changed and nutrients and pollutants increased with changes being more severe in lakes with high human population densities. These alterations are expected to continue. Countries sharing the lakes should, therefore, monitor and manage them to avoid reaching catastrophic levels.

The Biogeography of the Glacier Biome (Dial and Ditto, 2020)

If nutrients and a carbon source are available, life, as we know it, can actively reside nearly anywhere liquid water exists—even glacier ice and snow. Just as with tropical rainforests, temperate grasslands, and polar tundra, the worldwide collection of glacial ecosystems residing on permanent freshwater ice can be considered as a biological biome. In fact, all kingdoms of life have been found living on glacier surfaces, a land cover that extends over $1.6 \times 10^7 \text{ km}^2$, or 10% of the Earth's surface. The presence of these organisms living on glaciers leads to melting, and the melt-water they create is necessary for their existence, making the glacier biome important from a global warming perspective. While all of the Earth's glaciers have much microbial life in common, especially single-celled algae, the taxonomic orders of glacier-dwelling macroinvertebrates differ across continents.

Conservation and Management

Conservation Challenges to Freshwater Ecosystems (Reid et al., 2020)

Natural freshwater ecosystems represent the terrestrial phases of the global hydrological cycle and include rivers, streams, lakes, ponds, wetlands, as well as groundwaters. While freshwaters comprise only 0.01% of the water on Earth and constitute less than one-tenth of the global land surface area, they support > 10% of all recorded species including ~30% of all vertebrates. Freshwater ecosystems support the provision of numerous ecosystem services which range from natural flood management, to water supply, to health and mental being, to nurseries for important fish stocks. However, freshwater ecosystems, their biodiversity, and the services they provide are being jeopardized by a multitude of anthropogenic (human-mediated) stressors. Some of these threats are generated internally (habitat alteration, fragmentation, overexploitation) while others are external (invasive non-native species, climate change, atmospheric pollution). Fortunately, many options for freshwater ecosystem conservation exist and must be acted upon immediately.

Conservation of Temporary Wetlands (Boix et al., 2020)

Temporary wetlands are characterized by frequent drying resulting in a unique, highly specialized assemblage of often rare or specialized plant and animal species. They are found on all continents and in a variety of landscape settings. Although accurate estimates of the abundance of temporary wetlands are available in only a few countries, global estimations identify a decline in number and quality. The key environmental factors driving the structure of ecological communities in temporary wetlands are the duration, timing, frequency, and predictability of the aquatic and dry phases, which varies greatly with region and hydrogeomorphic setting.

Temporary wetlands have been historically neglected, but improved social awareness of the functions and values of, and increases in scientific interest, suggest that this is changing. They play a relevant ecological role in both global cycles (i.e., CO₂ emissions) and biodiversity (in proportion to their size, they contribute disproportionately to regional and global biodiversity).

Moreover, they provide valuable ecosystem services including wildlife habitat, nutrient flux to adjacent ecosystems, flood control, water filtration, and cultural services.

Three main current threats (i.e., inconsistent and inadequate regulatory protections; climate change; changes in land use) and three management challenges have been identified (i.e., management at both local and landscape scales; incomplete understanding of the ecosystem services provided by them; the need to enhance inventories). The most suitable approaches for conserving temporary wetlands include (1) regulations or other forms of protection; (2) sustainable management; (3) restoration and creation; and (4) collaborative conservation.

Wetlands of the Mariana Islands (Marshall et al., 2020)

This article represents an assessment of Mariana Island Wetlands that includes the current status, stressors, and future viability. Wetlands in the Mariana Islands are comprised of the following categories: estuarine wetlands, forest wetland/swamps, freshwater marshes, lakes, and artificial wetlands. Wetlands have been significantly impacted by human habitation in the islands, with many degraded, fragmented, or lost due to development, invasive species, fire, erosion, altered hydrology, agriculture, and pollution. Hydrophytic vegetation is primarily composed of species of grasses, reeds, ferns, and trees. Wetlands provide habitat for some species listed as endangered, while a couple of species reliant on wetlands have been extirpated.

Variables considered in analyzing current condition and future scenarios include stressors as well as conservation efforts. Considering the vulnerability of the wetlands and limited representation across the islands, as well as climate-related changes, it is anticipated that these habitats will continue to degrade in the absence of intensive or consistent management into the future.

Aquaculture Ponds (Boyd and Davis, 2020)

Capture fisheries production is no longer increasing, and production of fish, shrimp, and mollusks by aquaculture is necessary to meet the global demand for aquatic food animals. Aquaculture is conducted in freshwater areas, brackish water areas, and in the ocean. Most fish production from aquaculture is in freshwater areas, and freshwater fish are reared mainly in ponds. The global, freshwater pond surface area was estimated at 8.8 million ha in 2004. Since 2004, freshwater aquaculture production has doubled; but, because the intensity of production has increased, the global pond area in 2016 was estimated to only be around 11 million ha.

Nevertheless, the freshwater pond aquaculture area and volume is great enough for it to be included in the freshwater biome. The impact of aquaculture on the freshwater biome appears mostly negative, because aquaculture ponds tend to be eutrophic and of low biodiversity. Aquaculture pond effluents also are enriched in nutrients and organic matter and can cause eutrophication in receiving water bodies. As with agricultural production, which also has many negative environmental impacts, aquaculture production is necessary to supply the human population with food. Efforts to make food production more resource-use efficient and less harmful to the environment are critical to society.

Microplastics in Freshwater Environments (Rios Mendoza and Balcer, 2020)

The constantly increasing production and use of synthetic plastic materials are responsible for the global increase in plastic debris in freshwater environments. Microplastics (MPs) have been found in the water and sediments of lakes and rivers worldwide, with concentrations correlated with human population density. Wastewater treatment plants have been identified as one of the main point sources for MP release, including microbeads and clothing fibers. Synthetic polymers are identified by their chemical composition using Fourier Transform Infrared and Raman spectroscopies. In freshwaters, the primary synthetic polymers that have been detected are polyethylene, polypropylene, polyester, and polystyrene.

Field studies show that MPs are ingested by a variety of freshwater organisms, including clams, insects, and fish, but are retained at relatively low densities. Laboratory experiments document the effects that MPs can have on the metabolism, growth, survival, and reproduction of aquatic organisms, but usually at plastic particle concentrations that are orders of magnitude higher than those currently found in nature. The increased surface area of the small MP particles allows them to concentrate persistent organics pollutants from the aquatic environment. At this time there is limited information available on the concentration of toxic chemicals on freshwater MPs or the kinetics of the release of these compounds to organisms upon ingestion. Because MPs do not readily degrade, it is important for humans to reduce our reliance on plastic materials before their concentration in freshwater biomes reaches critical levels.

The Springs Ecosystem Biome, with Emphasis on Arid Regions (Stevens, 2020)

Springs ecosystems occur where groundwater reaches the Earth's surface, and are physically and biologically significant, complex, and highly socio-ecologically interactive ecosystems, particularly in arid regions. Nonetheless, springs are threatened by intensifying human appropriation, contamination of groundwater, and surface habitat destruction. This article reviews the literature and conceptual underpinnings of ecosystem ecology, springs distribution, typology, eco-evolutionary, and socio-cultural characteristics and processes in arid versus mesic/humid landscapes, and identify conceptual and data gaps.

This author estimates that the world's at least 2.3 million terrestrial springs produce at least 10.7 km³ of water/yr. Most ecohydrogeological characteristics and processes discussed apply to all terrestrial springs across latitude and elevation; however, aridland

springs differentially or more often have: (1) steeper environmental moisture and nutrient gradients between adjacent uplands; (2) distinctively different biotic assemblages; (3) higher occurrence of endemism and rare species in evolutionarily significant paleoregions; (4) interrupted, losing-stream springbrooks, disconnectivity that retards non-native species colonization; (5) lower levels of flow and increased ephemeral flow; (6) reduced resiliency and more dynamism in vegetation development following disturbance; (7) greater susceptibility to anthropogenic impacts that leads to (8) loss of springs habitat and increased probability and incidence of extinction of springs-dependent species.

These differences and greater conservation urgency elevate the need for improved stewardship of aridland springs. The study of aridland springs reveals much about the ecohydrology, distribution, ecological development and function, biogeography, ecological roles, and importance to humanity of springs everywhere, and the need and opportunities for enhanced stewardship of this highly endangered biome.

Headwater Streams (Richardson, 2020)

Headwater streams are the source streams at the initiation points of all river networks. These source streams may make up almost 80% of total stream length, but because of their small size and water volumes are extremely sensitive to the surrounding landscapes. Headwaters contribute to the characteristics of the downstream network in terms of water quality (nutrients, other solutes, and temperature), sediment transport, and organic matter supply.

These streams represent a distinct ecosystem as they support organisms that require relatively constant physical conditions, enemy-free spaces, or specific resources typical of source streams. The species found there are often unique to headwaters, and the key ecosystem functions usually differ from downstream in terms of being more dependent on organic matter sources from the surrounding terrestrial landscape, rather than in-stream primary production. Headwaters are also very sensitive to land use as they are strongly regulated by their surroundings, and often not protected.

Hawaiian Islands Streams (Valeros et al., 2020)

This document provides an overview of stream habitat in the Hawaiian archipelago and describes the ecological factors that have influenced the habitat over time and will influence it into the future. Stream habitats are found on the Northwestern Hawaiian Islands and all the main Hawaiian Islands. There is limited information about what stream habitats and their associated ecological communities looked like prior to human-contact. However, we assume that native flora and fauna were continuous, populations were larger than current populations with higher diversity and, as a result, were more resilient to stochastic events. These characteristics would have provided optimal canopy, good riparian zones, and limited erosion.

Currently, stream habitats are in decline, predominantly due to human-induced factors, such as channelization, development, recreation, and the introduction of invasive species. Despite this decline, there are federal, state, and private conservation efforts underway to purchase, protect, and manage these important stream habitats.

Streams of the Mariana Islands (Polhemus and Richardson, 2020)

This article provides a review of the flowing water, or lotic, ecosystems found in the Mariana Islands, with a particular emphasis on perennial streams. The geology, hydrology, and biota of these streams are discussed for the islands of Guam, Rota, and Saipan, the only islands in the archipelago which possess perennial stream ecosystems. Current integrity and future conservation of these ecosystems is also evaluated in the context of human-mediated stressors such as wildland fire, aquatic invasive species, and climate change. A provisional assessment is provided as to how the condition of such streams may change over time based on future climate scenarios.

Intermittent Rivers and Ephemeral Streams: A Unique Biome with Important Contributions to Biodiversity and Ecosystem Services (Vander Vorste et al., 2020)

The majority of flowing waterbodies throughout the world can be considered intermittent rivers or ephemeral streams (IRES) because at some point in time and space they stop flowing or dry. Despite their global abundance, less is known about this biome compared to perennial—permanently flowing—rivers. However, a recent surge in research has dramatically improved our understanding of how IRES function and what types of biodiversity and ecosystem services they support.

A cycle of terrestrial-aquatic habitat conditions caused by the periodic drying and rewetting creates a high temporal dynamic in the biogeochemistry, biodiversity, and ecosystem services of IRES. Vast amounts of accumulated sediment, organic matter, and organisms can be transported from IRES downstream to larger rivers or lakes, contributing to the global C cycle. The mosaic of aquatic and terrestrial habitats along IRES hosts high biodiversity including microorganisms, plants, invertebrates, reptiles, and mammals, with specialized strategies to resist to or recover from changes in habitat conditions. Although IRES provide a broad range of ecosystem services including provision of freshwater and cultural enrichment, there is a continued struggle to protect this dynamic and threatened biome.

Restoration of Riparian Habitats (Boisjolie et al., 2020)

Riparian areas are the terrestrial interface between freshwater and upland environments, encompassing important ecotones where aquatic and terrestrial biophysical processes intersect to create unique and dynamic habitats. Diverse riparian habitats support organisms adapted to variable hydrologic conditions associated with seasonal precipitation patterns and associated cycles of erosion and deposition. Riparian ecosystems encompass habitats for both aquatic and terrestrial species, making these areas biodiversity hotspots across river networks.

Riparian restoration is an effective conservation practice that can benefit terrestrial and aquatic organisms as well as promote water quality. Owing to their high conservation value, the protection and restoration of riparian areas has become a primary objective of land-management interests globally. Restoration practices include adjusting or targeting land- and water-management activities to meet conservation goals. Effective riparian restoration strategies will vary across biomes in response to distinct biophysical and social considerations at stream corridor, catchment, and regional scales.

Implications of Climate Change to Groundwater (Langridge and Fencel, 2020)

The net effect of climate change on groundwater depends not just on changing climatic conditions or the physical attributes of a region, but also on a wide range of human actions and management decisions. Researchers, managers, and policy makers involved with and responsible for groundwater stewardship are attempting to develop robust and innovative modeling tools, policies, and groundwater management strategies by building the capacity of individuals, groups, or organizations to adapt to the physical and social changes anticipated under climate change. These include the development of modeling tools, an increase in artificial recharge and recycled water, incentives to reduce demand, and the development of local drought reserves.

Glaciers and Ancient Carbon (Hågvær, 2020)

Glaciers participate in the global carbon cycle. They collect, produce, transform, store, and release carbon. A part of this carbon is ancient and is “captured” by the glacier in two ways. Firstly, a growing glacier may override an ecosystem and lock organic matter long enough to become ancient. Secondly, the surface of even remote glaciers “collect” aerosols containing ancient carbon. These aerosols are combustion products of fossil fuels such as coal, oil, or gas. Sooner or later, compounds containing ancient carbon are released from the glacier, and these compounds can be bioavailable. It has been shown that ancient carbon can be assimilated into food webs in glacier forelands, in glacial rivers, and in marine environments. Living invertebrates may achieve a radiocarbon age of several thousand years. Increased glacier melting due to climate change will increase the flow of ancient carbon to various food webs and may disturb radiocarbon dating of sediments.

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Freshwater: The Importance of Freshwater for Domestic Use

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Abstract

Of the many needs humans have for freshwater, water for domestic use is the most intimately understood by an individual because it is the water we use each day. Domestic use includes all the water used in and around the home including water for indoor use, such as drinking, bathing, cleaning, preparing food, and outdoor use, such as maintaining lawns, livestock, and gardens. Due to its importance, understanding where and how much water is needed for domestic use continues to be a high priority for communities around the world. This is particularly true as rapid growth is expected to push the world population to 9.7 billion people by 2050. In most cases, this urban growth will occur in cities, and therefore particular attention is paid to the challenges and opportunities for meeting domestic water demands in urban areas. This article explores the importance of freshwater for meeting domestic use purposes in an increasingly human-dominated world. Included is an overview of how water for domestic purposes is used, how use impacts the freshwater resources that support communities, and what the challenges and opportunities we as a society face are as water becomes a more precious resource.

Domestic Water Use Around the World

Globally, domestic water use makes up approximately 12% of the water used by humans (Fig. 1) (UN, 2018). While this is a relatively small amount compared to other water users (e.g. agriculture, industry), it represents a critically important portion of total water use. In 2015, this small but crucial use was $374 \text{ km}^3 \text{ y}^{-1}$, or roughly 129 L of water used per person per day (lpd) (FAO, 2019). However, the actual volume of water used around the world is highly variable. In countries such as Iceland, Australia, and the United States, per capita domestic water withdrawals are relatively high (600–700 lpd), while the mean reported water use can be much lower in other places, particularly Africa (e.g. Somalia, Rwanda, Benin) (Fig. 2). Of the nations that reported municipal water withdrawals for 2012, the 10 highest domestic water users withdrew on average 670 lpd per person, an order of magnitude more than the mean value of 17 lpd withdrawn by the 10 lowest users (FAO, 2019).

Differences in the volume of domestic water used are driven by a diversity of factors, including geography, cultural values, technological capacity, and wealth. Natural availability can play a major role in shaping local norms for domestic water use. For instance, arid locations or places with well-defined wet-dry seasonal patterns tend to foster communities that use water more conservatively. In contrast, communities in humid locations or with consistently available water sources often use water less conservatively (Padowski and Jawitz, 2012). Urbanization has also played an important role in altering the amount of water used in a home. Urban areas have higher population densities, which make it easier for water providers to set up efficient distribution networks that can be accessed by many people. Yet, while urban populations continue to grow many cities, particularly in the developed world, have seen overall total urban demands decrease over time. The underlying causes for this pattern are complex, but

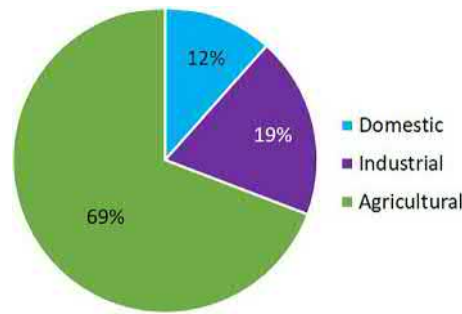


Fig. 1 Total water withdrawals by sector for the year 2010. Adapted from the FAO Aquastat database: <http://www.fao.org/nr/water/aquastat/>.

are often attributable to some combination of higher costs for urban water (Dalhuisen et al., 2003), a shift towards demand management by urban water providers (Baumann et al., 1998), and the limited outdoor use by people living in apartments or buildings with little or no outside space (Polebitski and Palmer, 2010).

However, strong correlations have also been found between per capita increases in domestic water use and national gross domestic product (GDP). Greater incomes and higher standards of living create opportunities to build more elaborate houses with indoor plumbing on larger, landscaped properties, which can raise domestic water use both indoors and outdoors. Higher standards of living also mean that more food, clothing, and other goods can be purchased, which can also increase the amount of water used for food preparation, laundry, and other activities around a home (WWAP, 2015). Conversely, in places where GDP is low and communities lack access to basic water infrastructure, water use can be substantially less. When water must be collected by hand from distant sources, the volume available is limited by the amount that can be gathered each day (mostly by women and children). In places where freshwater sources are distant (>1 km) or are inconsistently available, domestic water use can drop dangerously low, leading to major health concerns (Howard and Bartram, 2003). While the amount of water considered “adequate” for healthy living varies by region and culture, general consensus suggests a basic domestic water requirement of 50 lpd (Gleick, 1996). As of 2012, 30 of the 145 countries reporting national domestic water withdrawal data fell below the 50 lpd minimum threshold (FAO, 2019). Of those 30 countries, 96% were in Africa (80%) or Asia (16%), highlighting the continued importance of domestic water access issues in developing countries.

Sources of Water for Domestic Use

The water used in a home, whether for drinking, sanitation, food preparation, or irrigation (Fig. 3), generally comes from either surface water or groundwater sources. For many people in developed countries, domestic water is collected from one or more sources, and is provided by a water utility or water provider for a fee. Water is usually distributed through a network of pipes, reservoirs, and water towers or pump stations, and often delivered with some degree of chemical treatment. In less developed countries, water may come from a communal source, such as a protected well or tap stand, which is free or accessible for a nominal fee, or may be purchased from a vendor who sells water to individual households. In locations where water distribution infrastructure is lacking, water vendors may be an option for people who can afford to pay, but those who cannot are relegated to drawing water for their domestic needs from unprotected sources that are sometimes far away.

Which source is used for domestic supply depends in part on the proximity of the source, the quality of the water, and how easy it is to access. For communities near relatively clean rivers, lakes, or streams, surface water often is the primary source. When communities are not near surface water sources, residents have two options; if local groundwater is available, this can provide a relatively inexpensive and clean supply, but if neither surface water nor groundwater sources are available, then technological solutions are necessary to transport water long distances (e.g. aqueducts, regional water transfer pipelines) or desalinate ocean water. Each type of source has different strengths and weaknesses that a community needs to consider.

Surface Water

Globally, surface water is a commonly used source of domestic water, and is also the predominant source used by cities. It is estimated that nearly 78% of urban residents (1.2 billion people) rely on surface water sources, using approximately 504 billion liters per day (McDonald et al., 2014). Surface water, because it sits on the land surface, is relatively easy to access but the volume and quality available tends to vary more dramatically in response to climatic factors (e.g., precipitation, temperature) and human activity. Given the critical and consistent need for domestic water, variability in supply can be particularly problematic (Jackson et al., 2001). Streams, rivers, or lakes that experience large fluctuations in flow or volume may not be able to ensure a consistent supply. To help manage variability, many surface water sources have been modified to provide additional storage, such as by damming rivers. Depending on the size of the dam and the geology of the area, a reservoir can hold up to several years’ worth of demand. According to the International Commission on Large Dams (ICOLD; <https://www.icold-cigb.org/>), >7600 reservoirs have

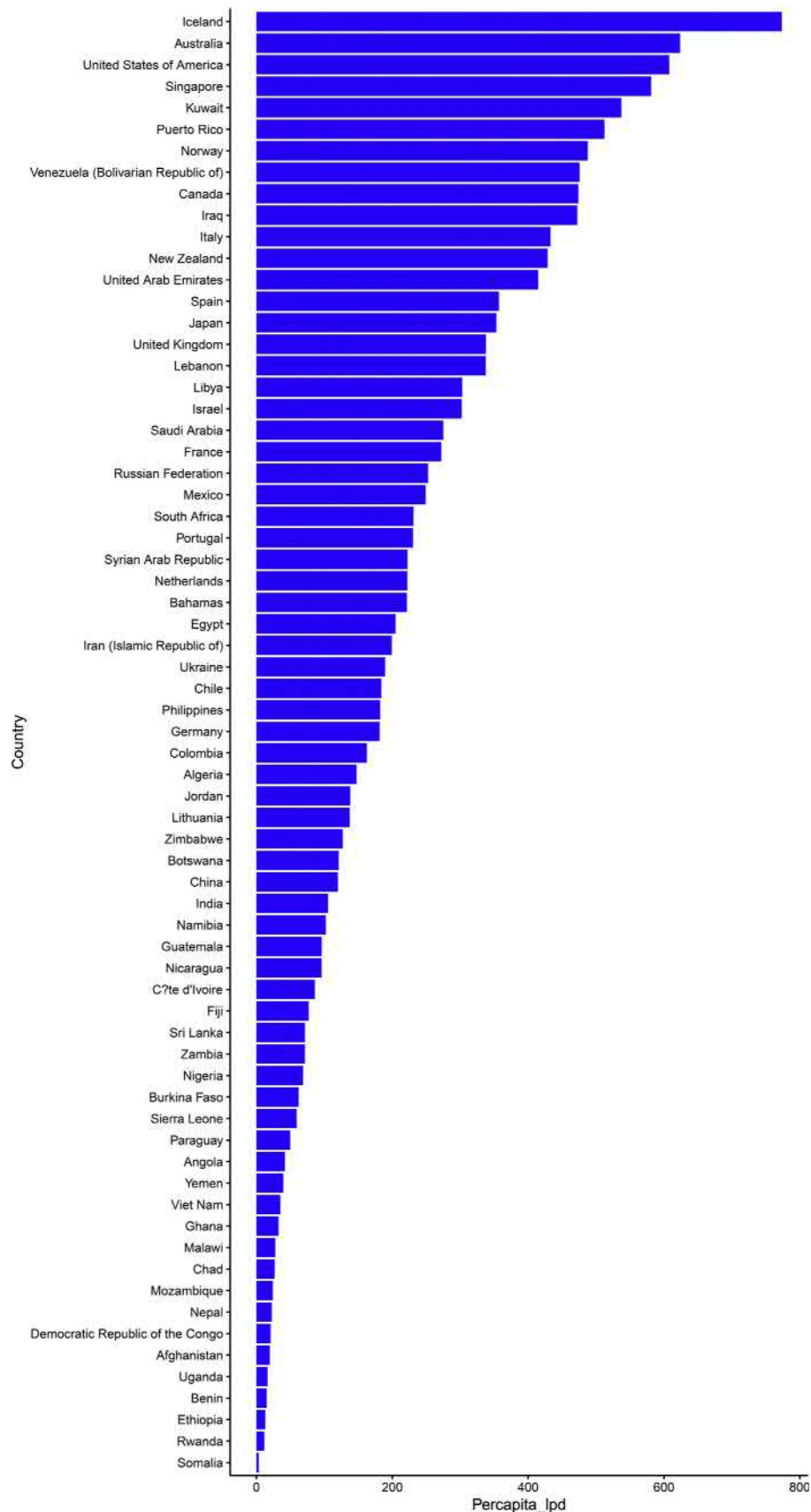


Fig. 2 Estimated national municipal per capita water withdrawals for selected countries for 2012. Data obtained from the Food and Agriculture Organization's AQUASTAT database (<http://www.fao.org/>).



Fig. 3 Different domestic water uses, including drinking (top left), bathing (top right), food preparation (bottom left) and landscape irrigation (bottom right).

been created to supply drinking water around the world since 1900. The volume each reservoir can hold varies depending on where they are and whether they serve a single purpose (e.g. domestic supply) or multiple uses (e.g., domestic supply, electricity production, agricultural irrigation, recreation). For example, the relatively small Lower Karori Dam in New Zealand holds $1 \times 10^5 \text{ m}^3$ of water while the Bratskoye Reservoir in Russia holds an impressive $1.69 \times 10^{11} \text{ m}^3$ (Lehner et al., 2011).

Groundwater

Groundwater is water that is stored below the land surface in large formations called aquifers and in other small pockets between soil particles, and accounts for nearly half of all drinking water worldwide (Smith et al., 2016). Unlike surface water sources, groundwater is found more ubiquitously across the landscape. The volume of groundwater on Earth has been estimated at an order of magnitude more than that of available surface water, and in general is a cleaner, more consistent source since it is more protected underground from evaporation and contamination. Being able to tap water in close proximity to where it is needed makes it a common source in areas that have no local surface water access. People who use groundwater for domestic purposes typically access an aquifer via a well or set of wells in a wellfield. The types of wells used to reach and withdraw water depend on the depth to water, the volume required, the local geology, and the financial and technological resources available. Shallow, hand dug wells are relatively easy and inexpensive to construct, but usually provide less water than wells that have motorized pumps to lift water to the surface. As such, deeper, larger volume wells are usually used to serve communities of people, whereas shallow, smaller volume wells may be suitable for single household use. While groundwater sources tend to be larger and less variable in response to climatic factors than surface water sources, they are susceptible to overuse and can take much longer to recover after declines or contamination. Withdrawing too much water from an aquifer can lower groundwater levels (Fig. 4), interrupt subterranean contributions to surface water sources, or lead to aquifer compaction and reduced storage. Monitoring groundwater withdrawals and aquifer response is a critical part of managing wells and wellfields for sustainable domestic use.

Other Sources

A small but important percent of the population lives in communities without adequate local surface or groundwater sources. In these communities, residents must depend on non-traditional sources to meet domestic water needs. In rural areas or communities where GDP is low, residents may pay water vendors to bring water to individual households or collect and store rainwater themselves. In urban areas or developed nations, residents may have the resources needed to invest in infrastructure or

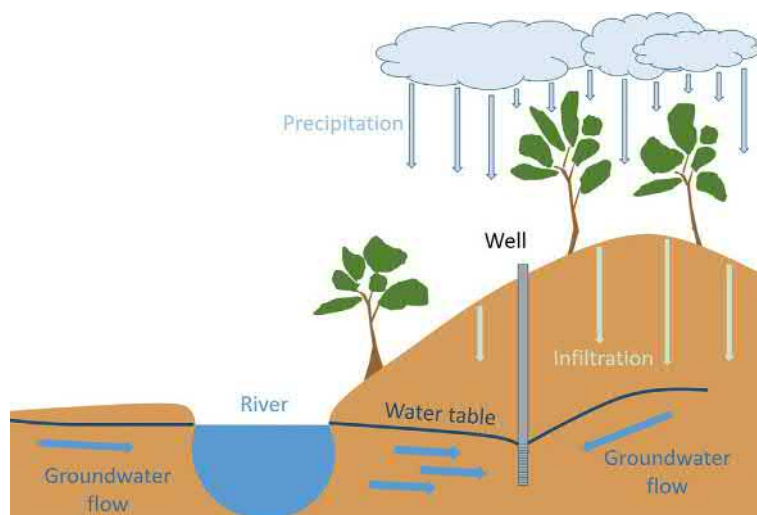


Fig. 4 Water that infiltrates the soil and rock below ground is called groundwater. When water is pumped from wells, the water table near the well is affected (as shown above). If water is withdrawn from the well at a rate faster than it can be replenished, either by infiltration or from surface water leakage, then groundwater levels will become lower. Adapted from USGS <https://water.usgs.gov/>.

new technology to bring water from distant sources, or treat low quality water to drinking water standards. Depending on their location and finances, communities with access to ocean water or brackish groundwater may choose to use desalination technology to remove impurities and purify water up to domestic use standards. In 2016, there were over 18,000 desalination plants in operation worldwide, most of which are located in the Middle East or Northern Africa, capable of producing up to 95 million $\text{m}^3 \text{day}^{-1}$ (Voutchkov, 2018). In other cases, cities have paid to have large aqueducts or pipelines built to bring water from distant sources to their residents. The city of Los Angeles in the United States is widely known for its 674 km aqueduct system that transfers water from Owens and Mono Lake to urban residents. While not all water transfers are across such far distances, cities relying on remote sources currently move up to 83 billion liters of water per day (McDonald et al., 2014).

Clean Water for Domestic Use

Domestic use makes up a small percentage of the total water used, yet the water quality standards are among the highest of any water use sector. Clean water is paramount for protecting human health, but most surface waters experience some degree of pollution, whether in the form of particulate matter, pesticides, or excess nutrients from agricultural runoff, oils and chemicals from urban roads, or bacteria and viruses from human and animal excrement washing into water sources. Groundwater sources tend to be cleaner, as water recharging aquifers must first filter through layers of soil and sediment that remove many potential contaminants. Ensuring that drinking and domestic use sources are of sufficiently high quality is critically important for supporting optimal human and environmental health. Part of ensuring clean water is available for domestic use lies in having the ability to protect, treat, and distribute water.

Protection

Protecting water sources has become more important as urbanization and land use change has converted natural areas, which previously helped purify water, into farmland, human settlements, or industrial sites. Protecting sources safeguards groundwater and surface water from contaminants and helps keep treatment costs down. As such, water managers have gone to great lengths in some areas to ensure water supplies come from pristine, protected environments. Some places, like the cities of Seattle, Portland, and New York City in the United States, have spent decades protecting and grooming large portions of their source watersheds, shielding them from development and human activity. Consequently, these systems produce high quality water that requires little to no filtering before use. Groundwater protection is also important, especially in rural areas where septic tanks and agricultural runoff may be able to infiltrate into drinking water aquifers, and in developing countries where bacteria from open defecation can run into poorly protected wells (Ivey et al., 2004; WWAP, 2017). Strategies for protecting the area around groundwater wells vary by location and community, but include actions such as establishing an off-limits buffer area around wellheads, adding above or below ground remediation filters to remove pollutants before they reach a well, and encouraging a change in land use or best management practices for land owners near the wellheads.

Treatment

When protection alone is inadequate, domestic water can be treated before use. Water treatment is common throughout the developed world, and comes in a variety of forms, ranging from filtration and reverse osmosis to chlorination, ozonation, and ultra violet disinfection. The type of treatment needed depends on the contaminants present, which can be metals, minerals, sediment, organic and inorganic compounds, and/or bacteria. The scale of treatment ranges from individual treatment systems that can be installed for a single private well or household, up to large water treatment facilities that process water for millions of people at a time. The cost of treating water varies depending on the volume of water that needs to be treated and the amount and type of pollutants that need to be removed. Globally, 9 in 10 large cities relying on surface water sources have seen their source watersheds lose significant areas of forested or natural land to development, leading to higher drinking water treatment costs for billions of people (McDonald et al., 2016). In places where treatment isn't available, waterborne diseases (e.g., parasites such as *Giardia*, *Cryptosporidium* or bacterial infections leading to typhoid or cholera) can exact heavy tolls on human health (Moe and Rheingans, 2006).

Delivery

Protecting sources and treating water are both important elements in providing safe water for domestic use. A final layer of protection comes from the protection afforded during delivery. The concept of protected delivery dates back centuries; water was delivered via Roman aqueducts to preserve water quality as it passed through human settlements, and qanats provided a protected subterranean water delivery system to ancient communities that currently would have been located in present day Syria (Lightfoot, 1996). Today, the type of delivery infrastructure relied upon by water users typically comes in the form of piped networks or vendors who deliver water, but making sure those pipes or vessels carrying the water are clean is critically important. Broken pipes, or parts of a distribution network that are compromised, can provide an opportunity for bacteria, sediment, and other pollutants to enter the delivery system with serious health consequences. For instance, in the city of Flint, Michigan in the United States, treatment by-products reacted with pipe materials to cause severe water pollution and illness in end users (Hanna-Attisha et al., 2015). However, when working properly, a piped water network distributes treated water from a centralized facility throughout a community, maintaining high water quality throughout the delivery process.

Challenges to Domestic Water Provision

Despite the major strides society has made in developing infrastructure and technology to improve water availability and quality, not all people have access to a safe domestic water supply. Estimates vary, but it is believed that 2–4 billion people live in areas with either a geographic (e.g., physical) or temporal (e.g., seasonal) mismatch between how and when water is needed and when it is available (Mekonnen and Hoekstra, 2016). Another 1.6 billion people live in places where water could be available, but isn't due to a lack of necessary infrastructure or technology (UN, 2018). Finally, there are many regions where water is still accessible and available, but supplies are being used at a faster rate than they can be replenished (Boithias et al., 2014). Each of these cases presents a critical challenge for communities, as it impacts not only the economic prosperity and health of the residents, but also has detrimental impacts on the environment which can hamper key ecosystem functions and services (e.g., soil retention, vegetative-induced cooling) that humans rely on.

Environmental Impacts

A major consequence of appropriating water for human use has been the changes in the timing and amount of water available for maintaining riparian and aquatic ecosystems (Mekonnen and Hoekstra, 2016). These changes bring a range of impacts for freshwater ecosystems, degrading breeding habitats of water-dependent species, altering water temperature, changing flow patterns, and impacting water quality. When water is scarce, rivers, lakes, and aquifers have often been drained for human needs or have become too polluted to use. Most river systems need to retain anywhere from 20% to 50% of their annual flow to maintain reasonably healthy freshwater-dependent ecosystems. Yet many basins in Asia and North Africa, and several basins in Australia, North America and Europe are currently withdrawing water at rates exceeding these levels, pushing their basins into high environmental water stress (Smakhtin et al., 2004). This stress is complicated by the fact that while dams and reservoirs have revolutionized water management around the world and made water more consistently available to millions of people, they have also had profound effects on local and regional hydrology and negative consequences for plant and animal species that depend on free-flowing rivers to survive. Concurrently, in locations where groundwater use is intensive, coastal aquifers are experiencing saltwater intrusion, while other groundwater sources see water levels drop, leading to land subsidence and aquifer compaction. Mexico City is a cautionary tale to other groundwater users, having experienced an 80 m decline in groundwater levels and a drop in land elevation of 30 m as large withdrawals have emptied aquifers (Werner et al., 2013). Despite the fact that over half of the world's population relies on groundwater, a third of the world's biggest groundwater systems are already in distress (Richey et al., 2015).

Health Impacts

Identifying and helping communities that lack safe drinking water and basic sanitation is one of the United Nation's Millennium Development Goals (WHO/UNICEF, 2017), which target over 2 billion people, mostly in Sub-Saharan Africa and Asia, who are still in need of assistance (Fig. 5). The WHO/UNICEF Joint Monitoring Programme for Water Supply, Sanitation, and Hygiene (JMP) assists in this goal by monitoring national, regional, and global efforts to develop safe and accessible drinking water and sanitation services (<https://washdata.org/>). Currently, the JMP estimates that only 89% of the global population has access to safe and affordable drinking water (UN, 2018); in the form of a nearby, improved water source that is free from contamination. Improved water sources can include boreholes or tubewells, protected dug wells, protected springs or rainwater collection vessels, or public taps or standpipes (WHO/UNICEF, 2017). These safe drinking water sources are easier to provide to urban residents, where high population density and relative economic prosperity allows governments to more easily establish and provide water services to residents. As a result, only two out of five people in rural areas use piped water supplies, whereas four out of five people in urban areas have access to piped water (WHO/UNICEF, 2017). Yet despite the progress made in urban communities, reports indicate that cities are increasingly finding difficult to keep pace with resident's water needs, particularly in the developing world (WWAP, 2015; WHO/UNICEF, 2017). Unplanned, rapid growth can contribute to increased eutrophication and bacterial contamination of local water sources. If these sources are the supplies for the urban community, their contamination can cost residents large sums of

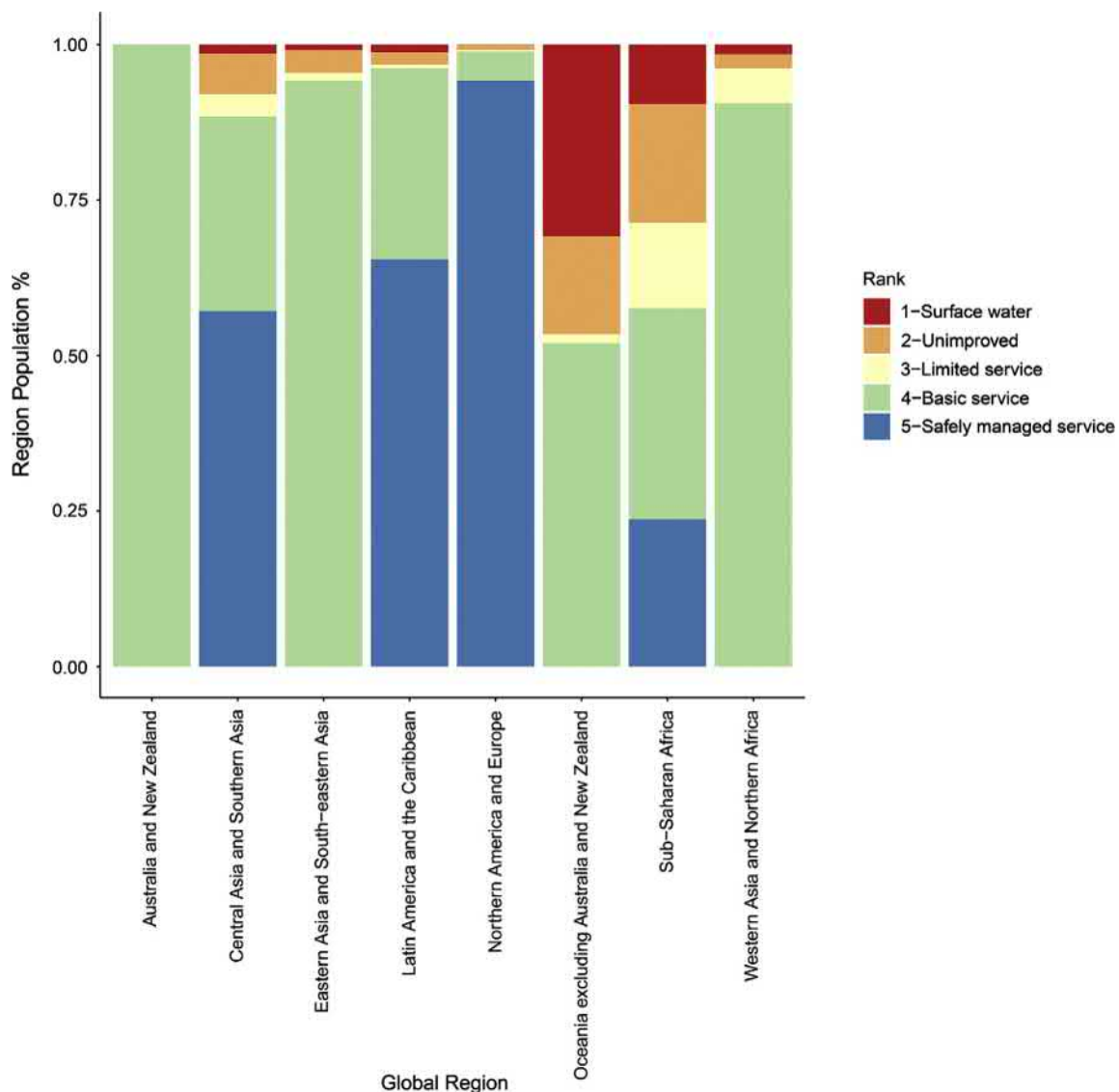


Fig. 5 Drinking water access by region. Safely managed sources are those from improved water sources located on premises, available when needed and free of contamination. Basic service is water from an improved source that takes <30 min to collect. Limited service is water from an improved source that takes >30 min to collect. Unimproved are sources obtained from an unprotected dug well or unprotected spring. Surface water is water drawn directly from a river, dam, lake, pond, stream or canal. Data compiled from JMP database: <https://washdata.org/data>.

money to treat, or force residents to develop a new source of water. The JMP estimates that to keep pace with current water supply and sanitation services at a 2015 standard, 700 million more people would need to be granted access to safe water (WHO/UNICEF, 2006). Yet, despite best efforts by global agencies, non-profits and local governments, water pollution and a lack of access persist.

Increased Competition

The mounting pressures society faces from rapid population growth are acutely expressed in how water is managed for human and environmental benefit. As populations grow, more water is needed not only for domestic uses, but for energy production, growing and processing food, and supporting more manufacturing and industry development. Yet the water resources available for these needs are finite and shrink as water is increasingly parsed across these sectors. As the volume of water available to meet these needs decreases, there is little buffer left to absorb instances where peak water needs co-occur across different water user sectors (Khan and Hanjra, 2009). As such, communities and water managers are more frequently seeing water needs fail to be met. This often happens in summer months, when indoor and outdoor water use is highest, farms are irrigating crops, and the water cooling systems at power plants are at full capacity as energy demands spike (Barnett et al., 2005). In places where this increased competition for water has already started, dramatic declines have been observed in the quality and health of environmental systems, which are usually the last to be considered when competing against uses that directly support human needs.

Climate Change

Water scarcity issues are further compounded by the growing impacts of climate change. Rising temperatures are creating new weather and atmospheric patterns that are altering water supply availability. These changes make it more difficult to predict the volume and distribution of rain and snow, and consequently how much water will be in rivers or will recharge to groundwater sources. While modeling efforts to understand this new “norm” are ongoing (Haddeland et al., 2014; Gosling and Arnell, 2016), water managers must rely on changing and incomplete information to make long-term decisions about how to meet growing demands for water while coping with current issues of acute water stress. The limited information available to decision-makers means that policies and strategies adopted for securing and maintaining existing water sources may not be sufficient for future needs, and the complexity of understanding the full range of biophysical, economic, and social impacts further complicates matters (Navarro-Ortega et al., 2015). By 2050, computer models suggest that the combined pressures of population growth and climate change will increase the number of people without regular access to water to >2 billion (Vörösmarty et al., 2000), and another 4.8–5.7 billion (64–76% of the global population) will face water scarcity at least one month per year (WWAP, 2018).

Future Opportunities

Freshwater systems are under acute strain from human use, including domestic water use. Where and why these systems are under pressure varies depending on a complex array of social, economic, and environmental factors. However, a water scarce future is not a predetermined fate. Recent estimates suggest that, while the number of people on the planet has increased dramatically, total water use per person is projected to decrease from a mean volume of 640 m³y⁻¹ to 580 m³y⁻¹ by 2025 due to water use efficiencies (Vörösmarty et al., 2000). In fact, water users have become increasingly aware of water scarcity issues and are collectively taking action to address the human and environmental impacts of increasing water demands. The actions being taken are range from individual to regional; from management and policy changes to implementation of new technology.

Improved Prediction

From a scientific and management perspective, one major advancement towards reducing water scarcity is being able to identify where and why it is occurring. Managers, scientists, and engineers are working together to better monitor, model, and predict how water availability and quality are changing at the local, regional, national, and global scale. Cheaper, smaller, and easier to deploy sensors are giving scientists and managers more precise and real-time information about how water resources used for household purposes are changing with time. These data in turn support increasingly sophisticated models that can more accurately assess how climatic, biochemical, economic, and policy changes alter current and future water availability and quality under a variety of possible future scenarios. This is particularly important in the face of climate change, where historically effective management strategies may no longer be economically or environmentally viable.

Water Conservation

From a community perspective, one of the most obvious pathways for addressing water scarcity issues worldwide is water conservation. Historically, community water providers would multiply expected population growth by current per capita domestic water demand to predict future water needs. If existing sources were not projected to be able to meet this future need, new sources of water were developed. Today, more water providers in developed countries are monitoring water use, and reporting a stabilization or reduction in total water demand, even as population increases (e.g., Rogers, 1993; Renwick and Green, 2000; Olmstead and

Stavins, 2009). This is due in part to the urbanization process, but is also due to water provider's increased focus on demand management through concerted customer education campaigns on how to reduce water use at home. In the US, Europe, and Australia many water providers offer rebates to replace old water-using appliances with newer models that use less water, and provide financial incentives to households to replace water-intensive landscaping with plants and features that require less water. As water conservation becomes ingrained in society, water demands are expected to continue to stabilize or decrease.

Technological Advancements

New technology is also relieving water scarcity issues. While desalination technology is not new, updated techniques and equipment have made the desalination process more efficient and less costly. Similar technology has allowed water recycling or water reuse to become more readily incorporated into water providers' portfolios of supply options (NRC, 2012). Recycled water is either filtered or decontaminated using processes similar to those used to desalinate water. While recycled water is still not widely used in the domestic sector one exception is in Singapore, where NEWater facilities use membrane technology to treat low quality water to drinking water standards. As of 2016, Singapore has five functional NEWater plants that are supplying 40% of the nation's domestic water needs (Lee and Tan, 2016). In the developing world, new technology is also being used to bring clean water to communities in need. Non-profit organizations like Engineers Without Borders (<https://www.ewb-use.org>) help low-income communities evaluate their water needs and options, and help communities construct solar pumps, boreholes, and simple filtration systems to access previously inaccessible sources.

Conjunctive Water Management

Thinking more strategically about where domestic use is overtaking source water supplies has become a critical preoccupation for water managers, particularly in the face of climate change and an increased uncertainty in the timing and availability of water. As such, some water providers are diversifying their source water portfolios, relying on not just a single sources, such as a reservoir, but rather a combination of water from different sources (Danilenko et al., 2010). Sometimes referred to as "conjunctive use", this strategy typically relies on a combination of surface and groundwater supplies, where one acts as a primary source, and the other can be tapped in times of high demand or when the primary source becomes overly stressed. However, conjunctive use can also refer not only to having the ability to access multiple different sources, but being able to move water between them. The concept of using groundwater as a refillable reservoir has been considered for decades, and some places have developed strategies for safely pumping surface water or highly treated wastewater into an aquifer as a means of enhancing or augmenting that groundwater source (Dillon, 2005).

Green Infrastructure

Finally, communities are also rediscovering the compounded benefits of creating spaces that work with the environment to provide critical ecosystem services. There has been a resurgence of interest in the idea of incorporating "green" infrastructure into towns and cities (Sandström, 2002; Benedict et al., 2012). Green infrastructure refers to soil and plant based structures that are able to capture, retain, remediate, and slowly release water that might otherwise have passed rapidly through an area (e.g., in periods of heavy rainfall, or runoff from paved surfaces). These structures can be large or small, ranging from backyard rain gardens that are designed to trap local runoff during rain events, up to large stormwater retention ponds that can hold thousands of liters of water. While often green stormwater infrastructure is not a direct solution to domestic water scarcity, it does provide a return to a more "natural" hydrologic state in places that have been developed by humans. In doing so, residents gain improvements in soil water retention and water purification, receive additional flood benefits from structures that trap water from rain events, and these natural structures often act as small wildlife refuges that bring birds, pollinators, and other beneficial species back into the area (Connop et al., 2016).

Drinking water is a critical and vital resource that warrants concerted attention to ensure that our water sources remain available and clean for generations after us. Ensuring that our water use habits are both equitable and environmentally friendly still remains a major challenge. While rapid population growth and urbanization have led to substantial declines in water availability and quality in many regions of the world, a greater societal awareness of this trend is inspiring new ideas, inventions, and attitudes towards water as a resource.

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Importance of Freshwater for Irrigation

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Abstract

The use of freshwater in irrigation arose in the world's first civilizations and remains critical to the planet's food supply today. This article first provides some historical context for irrigation before tackling the question of competing demands for water, discussing how coordination among irrigators is achieved and the complex relationship between irrigation and water conservation and reuse. The discussion focuses on four countries—the United States, India, China, and Chile—which provide insight into the importance of irrigation, as well as current challenges.

Introduction

Around 12,000 years ago, towards the end of the last ice age, the climate warmed and the first agricultural revolution began. In Egypt and Mesopotamia, access to low, flat floodplains provided moist, fertile soil ideal for cultivating cereals. Flood and drought, however, created huge variability in agricultural output, and the wealth of the societies themselves. Ever since, harnessing rivers, and much later aquifers, to provide water during shortage and store water during abundance has been one of the key challenges of civilization.

The amount of water needed to successfully grow crops varies, but staple cereals typically require somewhere between 450 and 700 mm per year. Fig. 1 shows that a good portion of the earth's land area is below this amount of precipitation, suggesting that the use of supplemental irrigation water is critical for food production in areas of every habitable continent. Through time, irrigation techniques and infrastructure have advanced, harnessing and moving huge volumes of water in the world's arid regions.

Yet key challenges remain. The intensification of water use has also increased water scarcity. Climate change will place pressure on the world's water infrastructure, and population growth in arid regions will strain water allocation institutions. If current trends continue, by 2025 up to a third of world's population will be living in regions where water withdrawals exceed 60% of the amount available, water primarily used for irrigation (Grafton et al., 2011). The increasing intensification of withdrawals will have profound effects on the water resources themselves, reducing flows for ecosystems and the services they provide. This article first provides some historical context for irrigation before tackling the question of competing demands for water, and key challenges in managing freshwater for irrigation across the globe.

A Brief History of Irrigation

The earliest archeological evidence of irrigation is dated circa 6000 BCE in the Jordan Valley. In the subsequent millennia, irrigation spread throughout Persia, the Middle East and westward along the Mediterranean, as well as to some parts of Asia (Bjorneberg et al., 2002). For instance, irrigation has existed in India for at least 5000 years in the form of minor irrigation works operated by households to irrigate small patches of land. Large-scale irrigation emerged much later, requiring coordination and investment that only a centralized state government could provide. For example, canals were introduced in India during medieval period (around 1220–1250).

Throughout ancient and medieval periods, irrigation has been linked to the growth and expansion of various empires (Reddy, 2017; Bjornlund and Bjornlund, 2009). In prehistoric America, the Hohokam people in the American Southwest built an estimated 850 miles of waterways in the 15th century (Nurzaman, 2017). This irrigation infrastructure supported the largest population in the

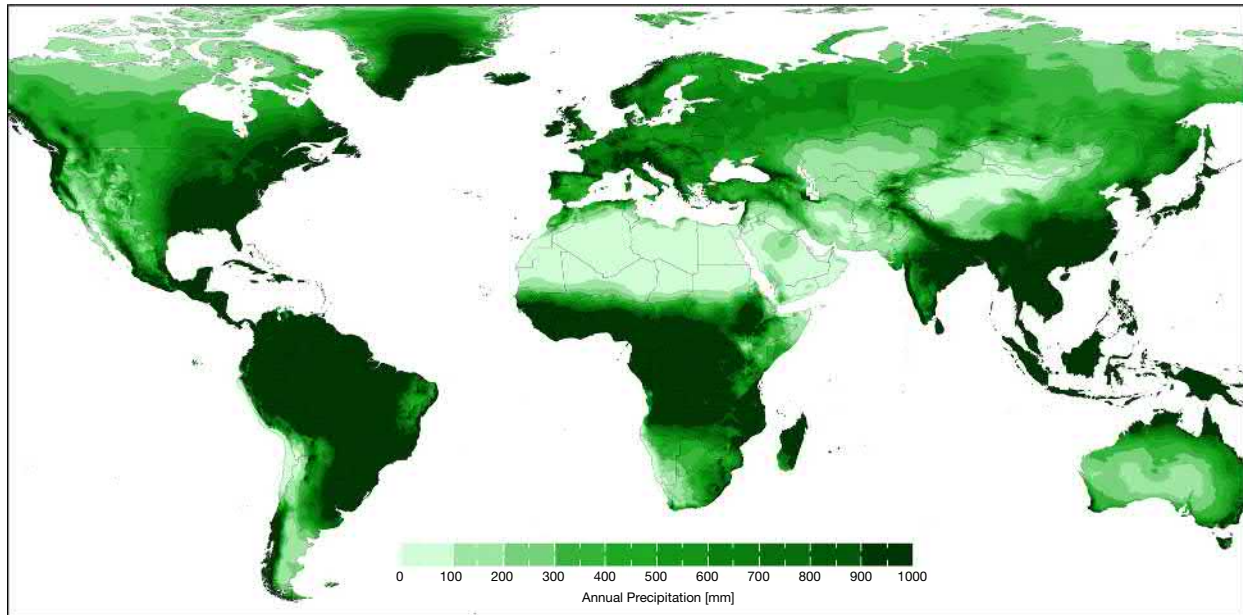


Fig. 1 Worldwide annual precipitation averages. Data from WORLDCLIMAP and ESRI.

present-day United States with 500 canals providing irrigation to around 80,000 people, the remains of which can be still found near Phoenix, Arizona (Rose, 2014).

In Europe, Spain has long history of irrigation spurred by its arid Mediterranean climate (Plusquellec, 2009). With a shortage of sites for constructing of dams, Spanish irrigation works focused on canals managed and financed by water user associations. The majority of irrigated land in Spain today is still based on the traditional systems and irrigator organizations, which have been recognized under revisions to the country's water law (Palerm-Viqueira, 2010; Plusquellec, 2009).

Where it has occurred, modernisation of irrigation took place at different times in different areas. In the American West, the late 19th century saw advanced irrigation development in California and Colorado, by Mormon settlers in present-day Utah, and Hispanic farmers in formerly Spanish areas of southern Colorado and New Mexico. Development of irrigation organizations, which started with co-ownership of irrigation networks and eventually evolved into county-sized irrigation districts, helped transform the American West into vital national and international food source (Nurzaman, 2017).

In Asia, the destruction of traditional irrigation systems and the exploitation of water and land resources during colonial rule led to delayed adoption of modern irrigation techniques. The adoption of widespread irrigation coincided with the Green Revolution in the 1960s, which also included the introduction of fertilizers, pesticides and high yield seed varieties. Combined with irrigation, these new practices led to a massive increase in food production. However, the associated ecological impacts, especially related to the ongoing decline and pollution of groundwater, remain a key challenge (Davies, 2003; Fitzgerald-Moore and Parai, n.d.).

The world's harvested land increased by about 24% from 1961 to 2003; out of which 28% was irrigated. Approximately 70% of the world's irrigated land is in Asia, where it accounts for almost 35% of cultivated land (Molden et al., 2007). Fig. 2 shows the intensity of irrigation in terms of how much of a one-kilometer grid is irrigated. That the majority of intensely irrigated land lies in India and China suggests just how critical irrigation is in feeding the world's two most populous countries. Growing reliance on irrigation led to physical changes in freshwater habitat, such as draining wetlands and building dams, and modification of water regimes through water extraction and pollution (Molden et al., 2007). In later sections we discuss the human and economic cost of India's reliance on groundwater for irrigation and China's recently completed South-to-North water transfer project.

Competing Demands

Increasing water diversions, especially for agricultural irrigation, have significantly affected the health of the world's saline lakes. Diversion in the Aral Sea watershed reduced lake area by 74% and volume by 90%, with significant environmental and economic impact. Salinity increases in the Aral Sea have led to the collapse of a commercial fishery that had once harvested 40,000 metric tons annually and provided around 60,000 jobs. Water development and river diversions by Mormon settlers, and later residents of the state of Utah, produced persistent reductions of flow into Great Salt Lake. Today, the lake's surface area is about 50% of what it was when settlers first arrived, and a 29% increase in inflows is required to restore fully-functioning ecosystems. In California, the City of Los Angeles diverted all inflow away from Owens Lake in eastern California, drying the lake and increasing air pollution.

Two approaches have been used to preserve saline lakes. First, as in the case of the Aral Sea, is the construction of a smaller lake to match the decreased flow into the lake. However, the costs of constructing the lake, together with the loss of ecosystem services and

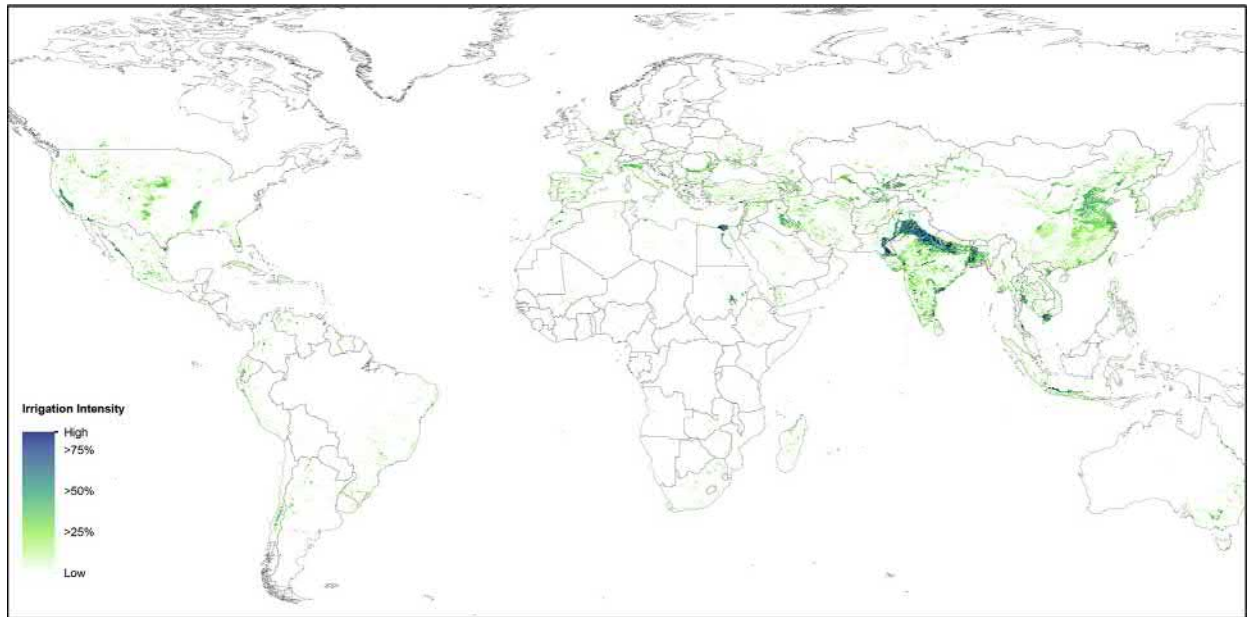


Fig. 2 Worldwide intensity of irrigated land. Data from the Food and Agriculture Organization of the United Nations and ESRI.

the cost of mitigating the dust impact, need to be included in evaluating the trade-offs between water withdrawals and reduction of lake area. Second, as in the case of Mono Lake in California, is the litigation of minimum water delivery needed to preserve the lake. The downside of this approach is cost of the projects and the loss of water for withdrawals and use in economic production (Wurtsbaugh et al., 2017). Absent preservation, a dry lake has large economic consequences; Los Angeles has spent billions of dollars to mitigate the effects of its drying of Owens Lake.

Irrigation Institutions

Irrigation moves water from where it is abundant to where it is needed. Doing so involves solving both technical and organizational challenges. When several irrigators utilize the same infrastructure, for instance a mutual canal, the organizational form matters as much as the technology. Irrigation systems in Nepal, as discussed by Ostrom et al. (1999), provide a clear example of the issues associated with ignoring the local governance aspect of irrigation. Nepal introduced a government-owned irrigation system in 1988 to replace some farmer-owned systems (Ostrom et al., 1999). The government systems provided technical improvements over the local systems, as they had concrete and steel head works which required less maintenance and worked more efficiently than the original mud and stone head works. However, the cropping intensity achieved by the farmer-managed irrigation system, which were coupled with social norms governing the allocation of water and maintenance labor, were substantially higher than was observed on the government systems (Hilton, 1992).

In the United States, irrigation was originally undertaken by individuals and private enterprise. For-profit canal companies and dams, however, soon faced difficulties because the canal works were linked directly to a fixed group of farmers. Farmers could withhold payment and canal owners could withhold water, leaving both vulnerable. Further, operating a canal required significant organizational capacity. As a result, private canal enterprises were soon replaced by mutual ditch companies, where irrigator-owners invested time and money in the construction of a ditch for a share of water. These enterprises solved the market power problem by combining the construction and operation of the canal infrastructure with the farmers themselves. However, small groups of farmers were still unable to compel participation and payments from unwilling participants, limiting the scale of irrigation enterprises. For this reason, the irrigation district, with governmental taxing authority to raise money for infrastructure, emerged as the dominant institutional structure. These districts solved the problems with large-scale coordination by electing boards and raising revenue sufficient to contract for water deliveries to irrigate hundreds of thousands of acres (Bretsen and Hill, 2007).

Another irrigation institution found in the US West, particularly in New Mexico, is the *acequia*. In place since the southwest United States was under Spanish and Mexican control, acequias are a decentralized but complex legal institution characterized by both Spanish and Anglo-American water law (Smith, 2016). These systems were generally replaced by irrigation districts in the early 20th century in order to centralize the organization of additional irrigated acres. However, where irrigation did not expand, acequias have worked as well as irrigation districts in coordinating irrigation (Smith, 2018).

Water Conservation and Reuse

With sites for storing additional surface supply dwindling, groundwater tables declining, and demand for in-stream water for ecological purposes increasing, competition for water resources is contentious. Most human use of freshwater across the globe is for irrigation, so improved technology has the potential to conserve a large volume of water, and to do so with little or no loss in crop yields. For instance, replacing flood irrigation, where water is allowed to flow out across a field, with sprinklers can save 10–35% of the applied water (Negri and Brooks, 1990). However, realized savings depend on the attributes of the system, the physical characteristics of the field, and the rules and institutions governing water use.

Implementing sprinkler irrigation has challenges. Sprinklers tend to save labor while gravity systems have lower upfront costs (Ge et al., 2018). Traditional gravity systems applied to land with high water holding capacity can achieve application efficiencies comparable to sprinklers. Conversely, land with porous soils or steep slopes is unsuitable for gravity systems because of deep percolation or runoff. Water saving irrigation technologies also include drip irrigation, where evaporation is limited by applying water via a buried hose, and tail water recovery systems which capture irrigation water for reuse. Drip irrigation is more expensive than sprinkler systems and it is relegated to small areas, generally devoted to specialty crops. The viability of a tail water recovery system is determined by soil texture, growing season length, and soil productivity. The cost of water, including pumping costs, affects the decision to adopt a water saving technology. Generally, however, water costs are low and irrigation efficiency improvements may not appear especially responsive to water prices (Negri and Brooks, 1990).

Even where adopted, the use of efficient irrigation technology is not enough to ensure more water availability. Termed the “irrigation efficiency paradox,” increased water use efficiency can actually lead to little gain in usable water. This is both an accounting and behavioral problem. Because non-consumptive water uses at a particular farm may be recovered and reused at the basin level, measuring water use at too fine a scale can overestimate the savings of efficiency improvements. Technologies that make crop production more efficient may induce farmers to switch to water-intensive crops or even apply more water to the same crop when a marginal yield response from additional water occurs. In Idaho, USA the reduction in groundwater recharge as a result of more efficient irrigation has reduced the Eastern Snake Plain Aquifer by about 30% since the mid-1970s, despite an increase in precipitation (Grafton et al., 2018).

Countries like the United States, Chile, and Australia have utilized markets to allocate water and create incentives for conservation. Property rights to water are separated from land and are traded in a market as a separate good. In opening the option for irrigators to sell conserved water, markets create incentives for investment in conservation without subsidies. However, while effective at incentivizing conservation, allowing irrigators to sell water still requires careful planning to avoid unanticipated issues, like those associated with the irrigation efficiency paradox. Grafton et al. (2018) suggest five actions to create effective policy for water conservation:

1. Development of physical water accounts from farm scale to basin scale with details on who gets what and where.
2. Establishment of a cap on water withdrawals or irrigated area.
3. Assessment of risk using accurate measurements from on-ground monitoring of flows.
4. Requirement of a payoff from subsidizing irrigation efficiency investments that includes the costs associated with reduced return flows.
5. Monitoring of the behavior of irrigators to ensure water extractions are consistent with established rules.

United States: The Value of Irrigation

In the United States, the 98th Meridian approximates the divide between the humid east and semi-arid west. A lack of adequate water for agricultural production is one of the defining characteristics of the American West. Early in the development of its agricultural economy, the western US saw two severe, prolonged droughts that led to significant political and social change. Drought from 1890 to 1896 led to a dramatic reversal of westward immigration trends and economic depression across the Great Plains. The drought was the primary impetus for the beginning of federal involvement in irrigation, leading directly to the Reclamation Act of 1902, although with limited impact initially. The Dust Bowl, a period of drought and wind erosion that occurred in portions of the Great Plains from 1930 to 1936 is perhaps the most important human-natural disaster in American history (Hansen and Libecap, 2004; Hornbeck, 2012). Compared to these early droughts, which transformed the social and economic lives of residents of western states and altered migration patterns, later droughts, similar in magnitude, appear to have been much less impactful. As Hansen and Libecap (2004) point out, droughts in the 1950s and 1970s did not result in the same levels of wind erosion, nor similar levels of economic or social upheaval.

The likely explanation is irrigation. Irrigated acreage remained relatively stagnant in the early 20th century. Beginning with the completion of the Hoover Dam in 1936, federal reclamation projects began to deliver water across the west and increased irrigation rates in many areas. Starting in the 1940s, technological innovation allowed for widespread adoption of groundwater irrigation on the Great Plains (Hornbeck and Keskin, 2014, 2015) and across the west (Edwards and Smith, 2018). As a result, irrigated acreage doubled from around 20 million acres in 1940 to 40 million acres by 1978.

In the Great Plains today, one of the world’s largest underground freshwater resources, the Ogallala Aquifer, provides significant water for irrigation. However, prior to the mid-1940s the aquifer had no impact on agriculture as the water was too deep to be

accessed. Following World War II, new irrigation technology and the availability of energy for pumping water made Ogallala groundwater available. Rates of irrigation increased from nearly zero to almost 20% of all farmland acres by 1997, leading to an increase in land value (Hornbeck and Keskin, 2014). In the entire western United States, including the Great Plains west of the 98th Meridian, areas with large streams or groundwater as irrigation sources increased crop production by \$19 billion after 1940, around 90% of the subsequent total increase in crop value in the western US (Edwards and Smith, 2018).

Areas where irrigation is present may be better able to better deal with weather variability, maintain harvest levels, and decrease failed acreage during periods of severe drought (Hansen et al., 2011; Edwards and Smith, 2018). However, increased access to irrigation has short- and long-run impacts. In the short run, farmers increase irrigation intensity, giving rise to higher productivity and less drought-sensitive crop yields. However, in the long run, this entails a movement towards more water intensive crops, potentially increasing drought sensitivity. On the Ogallala Aquifer, irrigation withdrawals after 1940 quickly surpassed the natural recharge rate; a phenomenon observed throughout the world. While agricultural land values remained lower in nearby counties, agricultural production adapted in a way so that counties with access to groundwater are actually more sensitive to drought (Hornbeck and Keskin, 2014).

India: Groundwater and Subsidies

Groundwater is critical, and problematic, in India, where high agricultural intensity combined with poorly planned energy subsidies create incentives for unsustainable irrigation water use. According to the World Bank, groundwater irrigation contributes up to 10% of India's GDP (Shah et al., 2004). Energy subsidies were introduced by the Indian government to allow poor farmers to access to water for irrigating high yield crops in the 1970s (Shah et al., 2004). After the implementation of the subsidy, the land with available groundwater increased by over 300% due to non-existent costs of pumping (Schoengold and Zilberman, 2007). As agriculture grew, it became increasingly difficult to install, monitor, or maintain meters for pumps. Hence, flat tariffs were implemented, which do not effectively incentivize water conservation.

Today, the lack of regulations on groundwater withdrawal threaten the viability of the electrical power sector and groundwater sustainability. Yet it is the impact of these subsidies on low income and rural households that is a roadblock to removing them. Irrigation has eliminated famine in India and groundwater is the backbone of Indian agriculture, supporting 70%–80% of irrigated output.

Shah et al. (2004) suggest that surface canal systems may be a viable alternative, and could be incentivized by raising the flat rate per hectare irrigated to a level that ensures the overall viability of the system. Alternatively, Indians could look to the groundwater-energy nexus, a framework for understanding the relationship between the consumption of water and energy, for a solution. The regulation of electricity for pumping could curtail wasteful use of groundwater through a direct tariff, or through restricting the availability or the electrical supply to pumps.

China: The Impacts of Moving Water

The majority of China's freshwater resources are located in the southern part of the country, whereas the key population and agricultural production centers are in the north and east (Jiang, 2009; Magee, 2011). Increasing groundwater depletion in arid northern China, where groundwater is the main source of supply, has given rise to issues like seawater intrusion and land subsidence. The Yellow River in the north has suffered completely dry periods in 22 of the past 28 years (Magee, 2011). Conversely, the Yangtze River in the south's rising water levels have threatened the lives and property of millions of people. In 1998, flooding on the river resulted in approximately 4000 deaths (Magee, 2011). To try and address these issues, the Chinese government has developed the South-North Water Transfer Project. The project aims to use a series of inter-basin transfer canals to move up to 48 billion cubic meters of water per year from the Yangtze basin to the Yellow River (Magee, 2011).

However, there are potential issues. One significant concern is the quality of water actually arriving in the Yellow River and ultimately Beijing and surrounding areas. Much of the canal system suffers from acute agricultural and industrial pollution. Because the transfer system is so large, intermediate river systems like the Han River could experience drying and water quality issues as a result of diversions. A major concern for the Yangtze River is the excessive withdrawals causing saltwater intrusion due to diminished volumes of freshwater, an issue the Yellow River is already facing. Finally, among the environmental concerns, potential impacts could include disruption of ecosystem integrity in all the rivers included in the diversion as a result of the construction of new dams, the creation of stagnant water where moving waters have been the norm, and the transfer of biological contaminants and invasive species between basins (Magee, 2011). In addition to its environmental issues, socio-economic impacts are also problematic. The resettlement of more than 300,000 people, mostly from the area around Danjiangkou reservoir on the Han River, offers an example of the scale of these issues.

Chile: Extreme Water Scarcity

The northern regions of Chile are perhaps the driest in the world. The Antofagasta Region receives less than 5 mm of water per year, but as a result of being the world's largest copper producer, also sees high water demand. Agriculture currently accounts for around 33% of the freshwater consumption in the region while mining uses about 56%. Since 2003, mining firms have been denied the use of purchased agricultural water rights to protect water access for small and indigenous farming communities. This has resulted in mining firms procuring water from desalination, an economically and environmentally costly solution (Edwards et al., 2018). The direct benefits of the policy include cultural values associated with indigenous water use, avoided relocation costs and agricultural production. Moreover, the costs of relocating entire villages may be much higher than the lost agricultural production.

The challenge that the Chilean government faces in allocating water is unique because the value of water is so high, but as populations grow in arid regions, the issue of extreme scarcity will remain: should water remain in irrigated agriculture or move to industry and urban users who are willing to pay more for it (Edwards et al., 2018)? Firms and farmers can work together reach mutually beneficial agreements, but often this will require compensation for the reduction in water in agricultural communities (Edwards and Libecap, 2015).

Conclusion

Irrigation has reshaped agriculture and societies in the arid regions of the world. However, growing demand and climate change pose a threat to the sustainability of world's freshwater resources. Addressing the competing demands for water is perhaps even more critical in the developing world, where governmental institutions may be weak. Lessons can be learned from the successes and failures of irrigation development in the United States, China, Chile, and India, where irrigation intensification has led to tremendous benefits, as well as costs. Because so much of the world's water is used in irrigation, the agricultural sector is key in balancing water use in cities, ecosystems, and food production systems. Allocating water across multiple valuable sectors is the key water management challenge of the 21st Century.

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Importance of Fresh Water for Livestock

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Abstract

Of the fresh water (blue footprint water) from rivers, lakes and groundwater 33–88%, is directed towards agriculture in varying proportions depending on the area. Only 0.6% is used for direct consumption by livestock or indirect activities associated with livestock. The distribution of livestock on the globe is dependent on existing water and the ability of animals to tolerate water deficiency and quality. In the animal body, water has multiple functions: metabolic, growth, breeding, and production. Deprivation or deficiency of fresh water affect these functions, but species from arid and semiarid areas have developed adaptations to these conditions. There are large differences between water requirements, for livestock in semi-arid and arid area of extensive and pastoral system, compared to livestock in the intensive farming system.

Dependent on the farming system, the type of rainfed agriculture and the distance to water source, the watering frequency is different. Water quality in many regions is poor in terms of salinity and contamination with toxic elements. In arid and semi-arid areas, water usually has a large amount of chloride, which is why research is directed to choosing the most resistant species to low quality water and to develop farms in these areas as well.

Water, “the Sap of Life on Earth” and Its Distribution

Rich in water, the “Blue Planet,” cannot satisfy the needs of fresh water even if is covered by huge surfaces of water (71%). The seas and oceans sum up about 97% of the surface occupied by water and only 3% belong to surface fresh water and underground water. Of this 3%, 2.5% is stored in glaciers that cannot be a viable source of fresh water, and 0.397% is polluted water. The remaining only 0.003% of all surface of water can be used as fresh water with a very uneven distribution (Balon and Dehnad, 2006; Naqvi et al., 2015).

The most disadvantaged regions are arid and semi-arid which occupy 30% of the total area in the world and extends into 80 countries, where, the degree of evaporation is greater than the amount of rainfall (200–250 mm rainfall/year, 250–600 mm/year evaporation). North Africa, South Asia, the Middle East and Mediterranean countries located in the arid and semiarid areas of Southern Europe are the most affected regions (Kammoun et al., 2018).

Fresh Water and Importance for Livestock

The water crisis enters into category of top 10, global risks. Worldwide, 70% of blue water from rivers, lakes and groundwater is directed to agriculture with quite remarkable differences between Europe, where the percentage is the lowest at 33% and Africa with the highest percentage at 88% (Appuhamy et al., 2016).

Providing fresh water for livestock has overwhelming importance for maintenance of their vital functions and production that depends on a number of factors, such as: species, body weight, physiological state, diet, temperature, frequency of water provision, type of housing and environmental stress (<http://www.fao.org/>, 2018). Water is also used in indirect activities that include: cleaning of animals, shelters, facilities, washing and preparation of fodder, slaughtering, processing of animal products and skin tanning. However, water requirements to satisfy the need for drinking water but also for the other services is only 0.6% of the fresh water used in agriculture (Ran, 2010).

The management of water resources for livestock production must take into account several aspects such as: the production system applied (grain—fed or mixed crop-livestock), the intensive or extensive breeding system of various animal species, taking

into account also the social and cultural aspects of animal husbandry in different countries. Water requirements are higher in the extensive system than in the intensive (industrial) system (Schlink et al., 2011).

Distribution of Livestock Dependent on the Rainfed Agriculture System

Of the total cultivated area in the world about 80% is integrated into the rainfed agriculture system divided into: highlands, dry tropics, humid tropics, subtropics and temperate. Accordingly, the distribution of livestock is different.

In dry tropics, which includes the Sudano-Sahelian zone of Africa, and India, small ruminants, goats and sheep are predominant. The cattle are common in southern Africa and in Latin America. Latin America and Asia are part of the humid tropics type, the predominant livestock are sheep or cows depending on the financial status of farmers.

Poorer farmers have as their main concern raising sheep and goats, while wealthier farmers raise cows. In the subtropics, cows are often the dominant species, with goats in the southern Mediterranean, sheep in Australia and pigs in China. Developed countries in Western Europe, the United States and Canada, are part of the temperate type of rainfed agriculture, where the predominant livestock is represented by pigs, poultry and cows reared in the industrial system (<http://www.fao.org/>, 2011).

The arid and semi-arid areas of China, Australia, and India experience scarcity in water, but these regions are raising one third of the total number of cattle on the globe and 30% of the sheep and goat population in the world (Avendaño-Reyes, 2012; Todaro et al., 2016; Araújo et al., 2010). In Sub-Saharan Africa, cattle, sheep, and goats account for about 1.2 billion tropical livestock units (1 TLU = 250 kg body weight), after Descheemaeker et al. (2010).

Quality of Fresh Water Sources

The main source of water for humans and livestock in the arid and semi-arid coastal areas of Southern Europe, the Middle East and the North African region is underground water, with a chemical composition rich in chlorides as a result of natural processes (Kammoun et al., 2018). The various sources of surface water pollution in the Sub-Saharan Africa results in water in an unsafe water category (<https://thelastwell.org/>, 2019).

A quote from Mandakini (2015) "Water, water, everywhere, nor any drop to drink," best describes the water situation in Asia, where water is contaminated with human fecal microorganisms and, in addition, contains large amounts of arsenic especially in shallow groundwater (Luby, 2008). In Kenya, large amounts of copper and nitrate are found in fresh water (Wayua, 2017). Water rich in sulphates can be found in the semi-arid rangelands of the western region USA, Minnesota's groundwater, river waters in western Canada, and in SW China (Kun et al., 2017; Cammack et al., 2012).

The Importance of Water for the Animal Body

Water in the body participates in all metabolic processes, growth and breeding, (e.g., it provides a fluid environment for the foetus). The placenta has a significant percentage of water that plays a role in preventing abortions and avoiding other problems in the reproductive sphere (Van Emon, 2015; Salah, 2018). It plays a role in lubricating joints and organs, maintaining blood volume, osmotic balance, regulating osmotic pressure and thermoregulation. Water assists in excretion of waste products such as urea from the cells for removal via the kidneys, but also from the lungs and gut. It also induces resistance against diseases. However, it may also be a favorable environment for the transport of unwanted elements, such as providing a growth medium for microorganisms. Limiting the intake of water results in reducing the amount of ingested feed with negative effects on productive and reproductive, because of retardation of ovarian follicular growth. Irregular water consumption affects production, reduces lactation and affect the animal's general health. For example, lack of water can affect vision and hearing (Patience, 2012; Grönvall, 2015; Chedid et al., 2014). Deprivation of fodder for a long period of time has as a consequence the loss of fat resources and almost all glycogen, half body protein and 40% of body weight. Compared to deprivation with feed, deprivation of water entails more serious repercussions. Loss of only 10% of body water can cause serious disorders, affect the production of milk, meat and eggs (Kubkomawa et al., 2015). However, sheep (Merino) in semi-arid or arid regions are adapted to losing about 5–7%/day of body weight daily and cows (Shorthorn) about 7–10% without being affected in any way at 40 °C, air temperature (Naqvi et al., 2015).

Livestock in semi-arid and arid areas have developed the ability to adapt to these harsh conditions through, the ability to carry water reserves in the rumen and extracellular fluid space; to adjust the amount of electrolytes in several fluid locations. Kidneys have the ability to conserve water and circulation does not have to suffer by reducing plasma volume; also, panting and sweating are lower (Constable et al., 2016).

Animal survival time with a lack of water is a few days dependent on climate and breed. Desert bighorn sheep can withstand water deprivation for 15 days, Australian Merino sheep survived for 10 days without water, while the Barki sheep in Egypt cannot survive water deprivation over a 3-day period (Naqvi et al., 2015).

Watering and Water Needs for Livestock in Different Regions

In intensive farming systems, ensuring access to water ad libitum is compulsory, as is providing the necessary water for cleaning. In low water areas, farmers administer water to cows, if not ad libitum, at least three times a day in semi-arid areas and two times a day in arid (Dhami et al., 2018).

In dry climate or drought seasons in south-central New Mexico, beef cattle on the pasture consume about 57 L/day⁻¹ fresh water. Through a single watering, they can provide 94% of their daily water consumption (Rouda et al., 1994). Black Bedouin goats, adapted to the conditions of the arid desert of Sinai, can consume the equivalent water of 45% of their body weight without haemolysis of the red blood cells (McGregor, 2004).

The amount of drinking water for livestock in Sub-Saharan Africa is estimated at 20–50 L⁻¹/day/tropical livestock unit TLU (1 TLU = 250 kg body weight (Descheemaeker et al., 2010). Cows kept in intensive systems benefit from access to water <15 m from food sources, while in arid and semi-arid areas, species of Sahelian livestock move long distances for watering without being affected the state of animal health: 6–10 km for cattle and 3–5 km for goats (Niyonzima et al., 2013). During the dry season in Kenya, livestock travel long distances even as much as 40 km, water sources (Kivunzya et al., 2018). Watering for cows in pastures in this area occurs every 3–4 days and 5–6 days for goats, which are more tolerant (Tolera and Abebe, 2007). Water consumption for a few days (4) does not negatively influence feed consumption or milk production (Naqvi et al., 2015). In contrast, high-productivity breeds will have the same requirements of the amount of water, similar to breeds grown in the intensive system, as can be seen from Table 1.

Factors That Influence Drinking Water Consumption

Factors that influence drinking water include: species, age, body condition, growing, pregnancy, lactation, fattening, individual behavior, injury and illness; or the environment: dry matter content, environmental conditions, water system and watering (discretionary or fractional), water quality, stress (Williams et al., 2016; Van Der Klis and De Lange, 2013).

Animals within the same genus may require different amounts of water. For example, *Bos indicus* cattle in northern Australia consume less water than *Bos taurus* breeds (Davis and Watts, 2016).

Feed content in dry matter affects the ingested water requirement. Animals that consume grass will drink less water because the grass has 80–85% water. Instead, grains and hay raise requirements for water consumption due to their low water content (i.e., 10–12%) (Spencer et al., 2017).

Table 1 Water intake and cleaning water requirement L day⁻¹.

Species	Water intake	Cleaning water	Species	Water intake L day ⁻¹	Wash water (L day ⁻¹)
Cattle	L day ⁻¹	requirement (L day ⁻¹)	Pigs		
Dairy cow	40–50	13–45	Dry sow	5–9	0.09
Bull	45–55		Lactating sow	18–23	Farrowing sows —5.63
Dairy cow	5/L milk		Boar	9	0.09
Yearling	25–40		Baconer	5–9	Growers (50 kg)—0.371
Calf	15–25		Piglet	4–5	Weaners (20 kg)—0.286
			(4–5 weeks)		
Sheep	Water intake L day ⁻¹		Poultry	Water requirement	Wash water (L m ⁻² floor
				(L day ⁻¹)	area)
Dry ewe	8		Laying hen cage	0.20	6
Ewe with	11		Laying hen non	0.22	6
lamb			cage		
Ram	11		Broilers	0.19	5
Lamb	2–4		Pullets	0.09	5.00
					12
Species, physiological stage, production			Water intake, depending on air temperature 15–35 °C (L day ⁻¹)		
African pastoral system-lactating 2 L milk/day			21–28.7		
Large beerd, dry cow 279 day pregnancy			44–102		
Large beerd, lactating 35 L/day			102.8–126.8		
Goat—lactating 0.2 L/day			7.6–11.9		
Sheep lactating 0.4 L/day			8.7–20.1		
Chicken, adult broilers/100 birds			17.7–62		
Laying eggs/100 birds			13.2–50.5		
Swine, lactating daily weight gain of pigs, 200 g			17.2–46.7		

From Brown, L. (2006). Livestock watering requirements, quantity and quality. Order No. 590.301.1, <https://www2.gov.bc.ca/assets/gov/>, Naqvi, S.M.K, Kumar, D., Kalyan, D., Veerasamy, S. (2015). Climate change and water availability for livestock: Impact on both quality and quantity in: climate change impact on livestock: Adaptation and mitigation, pp. 81–94, Springer India, New Delhi, India, and <http://randd.defra.gov.uk/>.

A high level of protein or salt in food rations increases the consumption of water in order to eliminate more urine required for the excretion of urea and salt. In poultry, higher water consumption is also observed in the case of rations with high content of fat or potassium (McKernan, 2012; Greg Lardy et al., 2008).

Water quality affects water consumption. For livestock, water with 1000–3000 mg TSD/L is considered satisfactory but, it can affect the faecal quality of poultry. Livestock can exhibit digestive disorders manifested by diarrhea if they are not accustomed with this kind of water (Ward, 2019).

High levels of sulphates affect the taste of water and high levels in cattle, sheep, and goats can lead to polio (Van Emon, 2015; El Mahdy et al., 2016). High amounts of magnesium sulphate can cause a drop in faecal quality in birds (Putnat, 2016). For nursery pigs, 2000–3000 ppm can cause a decrease in growth performance and increase fecal score (Flohr et al., 2014).

The most tolerant livestock to acid or alkaline water are laying hens and chickens. The maximum productive performances in broilers was recorded at pH 7.5, while, alkaline water had the most negative impact on performance (Khan et al., 2013). Treatments for pigs through the watering system may be ineffective at pH <5; 15 drugs precipitate below these values (Nyachoti and Kiarie, 2010). Large and small ruminants need to have water with a pH between 6.5 and 8.5 (Curran, 2014).

Fresh Water Requirements Depending on Physiological Stage

The state of gestation influences water consumption by increasing the amount of ingested water. In the last 4 months of gestation, dairy cows have 30–50% higher requirements for water consumption. Goats, during the advanced gestation period, have similar high requirements relative to the amount of ingested water (Brown, 2006; Ehrlenbruch et al., 2010). Water intake in sheep, progressively increases from the first to the 5th month of gestation, which means a 126% higher consumption.

A lamb's weight at birth for Magra and Marwari breeds which are adapted to desert conditions, does not suffer even if mothers are watered twice a week for long periods of time (Araújo et al., 2010; Naqvi et al., 2015). The water requirements of sows in lactation are 17–25 L⁻¹ of water per day (King, 2016).

Fresh Water Requirements for Livestock Production

A cow should normally drink about 7–10% of her weight a day. Water intake is influenced by many factors, including the type of production (e.g., milk, meat). A lactating beef cow will drink on average 95.92–56 L⁻¹/day (Lewandowski, 2015). The water requirements of most (80–90%) dairy cows are satisfied in by direct water intake. There is a linear relationship between the quantity of milk produced and the water requirements. In addition to the necessary water consumption to maintain vital functions, it is necessary to provide water to support milk production. Compared to non-lactating cows, those in lactation require a 25% higher water consumption and since the milk is 87% water it is necessary that, for each liter of milk produced, an intake of 2.5 L⁻¹ of water is required (Schroeder, 2015; Spencer et al., 2017). In dry tropics, the amount of water required for dairy cows is calculated taking into account that 1 L⁻¹ of water/10 kg of live weight, is added to the water requirement for milk production (i.e., 1.5 L⁻¹/L of milk produced) (Ibrahim, 2015).

Depending on the production system and the efficiency of red meat production, the amount of water required to produce 1 kg red meat is 180–540 L⁻¹/kg or 80 L⁻¹/kg—320 L⁻¹ in Southern Australia (Scholtz et al., 2013; Nason, 2018).

Water Consumption and Air Temperature

There is a direct proportional relationship between water consumption and air temperature. Increases in air temperature, result in increases in water consumption. In this regard, in cattle, for each additional degree higher than 40° F, water intake increases by 0.65 L⁻¹/day in dairy cows, 0.21 L⁻¹ in growing dairy bulls and 0.22 L⁻¹/day in feedlot cattle (Spencer et al., 2017).

The lactation period plays an important role in water consumption, cows at the middle and end of lactation being more susceptible to heat stress (Könyve et al., 2017). In warmer environments, the amount of water required is multiplied by 1.5 for gestating cows, and for those with calves the water intake increases by 0.87 L⁻¹ water/L milk (<http://www.fao.org/>).

After Brown (2006), the water requirement for a cow dependent on air temperature, below 15 °C or above 25 °C, varies between 4 L⁻¹ and 8 L⁻¹/45 kg animal weight.

Sows and finishing pigs are extremely sensitive to rising temperatures, which have, as a consequence, higher water consumption (Guthrie, 2011). In hot weather, rising temperatures change the patterns of drinking water of pigs, but also, the amount of water consumed, which will be 2–2.5 and even 4 times higher (King, 2016). For each additional degree of temperature compared to the comfort temperature, the water requirement rises by 0.1 L⁻¹/head/day (Schiavon and Emmans, 2000). In semi-arid and arid regions, drinking water required for the needs of animal is 4 L⁻¹/kg dry feed intake and increases by 50% in hot weather (Scholtz et al., 2013).

Bird water consumption expressed as: L⁻¹/bird/day can be an indicator of welfare and stress conditions to which birds are subjected. In addition, changes in daily water consumption may indicate health problems like enteritis and coccidiosis. It can also be a potential tool which indicates increased cases of foot pad dermatitis and deterioration of air quality due to wet litter (Manning

et al., 2007). The water consumption of broiler increases proportionally with raising the temperature. For each degree, above 20–32 °C, consumption is 6% higher. Parallel to the increase in water consumption, feed consumption decreases by 1.23% for each additional degree above the value of 20 °C (Williams et al., 2013).

Aspects Related With Water Quality

Due to either scarcity of water or poor water quality, especially in terms of the amount of total dissolved solids (TDS) or sodium chloride in different regions of the world, such as: Brazilian semi-arid region, Southern Tunisia and other regions, researches was undertaken to identify the most resistant species to these conditions, to the development of farms in these regions.

In a comparative study, Holstein cows in the semi-arid area of northern Mexico demonstrated that productive performances in cows were higher with lower feed consumption when they received water desalinated, by reverse osmosis compared with cows who received drinking water with $>1809 \text{ mg L}^{-1}$ TDS. In addition, the number of somatic cells and the percentage of cows with fat depression was lower with desalinization of water (García-Muñoz et al., 2015).

Crossbred goats from the Brazilian semi-arid region who received drinking water from the 30th day of lactation with TDS of 8326 mg L^{-1} did not show an affect in nutrient intake, digestibility or milk yield. Only water intake increases with increasing values for this parameter (Paiva et al., 2017).

In sheep, drinking water containing 1% NaCl does not affect feed consumption or growth performance of animals. In contrast, water with 1.5–2% NaCl negatively influences both; feed intake and weight gain. At concentrations above 2% NaCl, occasionally diarrhea occurred and sheep appeared is emaciated (Araújo et al., 2010). Barbarine sheep (Tunisia) who consumed drinking water with 11–15 g NaCl did show impeded growth, but, higher values (15 g NaCl), increased the creatinine and urea levels in the blood plasma, which suggested altered kidney function (Yousfi and Salem, 2017).

The milk yield of sheep who received drinking water with 10 g of NaCl over a period of 120 days was not significantly affected, but, there was a significant increase in salinity, conductivity and pH (ElGharbi et al., 2015).

Nguni goats grown in Southern Africa tolerated saline water with 5.477 g NaCl (Mdletshe et al., 2017). Adaptation of Boer Goats from the same area to water consumption with gradual increases in NaCl concentration to 1.5% NaCl led to conclusion that this method was effective to accustom the animals to the salinity of water (Runa et al., 2019).

Experimentally, it has been demonstrated that water intake with a progressive increase in the amount of NaCl up to 10‰, positively influenced the amount of ingested water in four castrated adult male goats from 2.0 to $3.2 \text{ L}^{-1}/\text{day}$, but decreased at the concentration of 20‰ NaCl. Increasing the salinity of water affects the concentration of sodium, glucose, urea, protein, osmolarity and creatinine in the blood plasma. However, potassium and body weight remained unaffected. So goats can survive with saline water for at least 2 weeks without negative repercussions (Zoidis and Hadjigeorgiou, 2017).

In desert areas, water containing 10 g sodium chloride, 20 g sulphates are considered safe for Marwari sheep and Parbatsar goats (Patil et al., 2012).

Conclusion

Water, with its multiple functions, maintains the body's homeostasis, and livestock, regardless of region, rich or poor in water, need fresh water for survival, production, breeding, even if the quantity, frequency of watering or water quality is not always the best.

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Importance of the Conservation and Management of Freshwater to Aquaculture

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Abstract

Inland fish farming contributes to the nutrition and livelihoods of many millions of people. Most fish are grown in constructed ponds or floating cages in natural or man-made water bodies. Freshwater fish farming is often integrated with the farming of crops, where wastes and by-products from one component are used as inputs for another. Developing technologies offer new opportunities to conserve water and increase the productivity of freshwater aquaculture. Recirculating aquaculture systems (RAS) have been developed with the potential to greatly reduce the water requirements and environmental impacts of fish farms. Biofloc technologies (BT) utilize in situ bacterial processes to maintain water quality and provide food for filter-feeding species of fish and crustaceans. Full integration of fish and vegetable production can be achieved through aquaponics, which combines aquaculture and hydroponic plant production within a recycled water system. This chapter reviews current developments in water recirculation techniques, biofloc technology and aquaponics against the background of increasing food security needs and water resource issues.

Challenges

Global population growth presents a major challenge in the provision of future food security. It has been predicted that by 2050 some 50% more food will be needed to feed a population exceeding 9 billion (Godfray et al., 2010). This will necessitate intensification of food production, more sustainable practices and more efficient use and protection of water and natural resources. Capture fisheries and aquaculture make a substantial contribution to global food security. Capture fisheries are fully exploited and

Table 1 Global fish production from aquaculture and capture fisheries. Estimates for 2016 and predictions for 2030.

	2016 ^a (million tonnes)	2030 Prediction ^b (million tonnes)
Aquaculture		
Inland	51.4	
Marine	28.7	
Total	80.1	93.6
Capture fisheries		
Inland	11.6	
Marine	79.3	
Total	90.9	93.2
Total global fish supplies	171	186.8

^aFAO (2018).^bWorld Bank (2013).

future increase in fish supplies will come from the expansion of aquaculture. Whilst the annual rate of increase in aquaculture production has declined from its peak in the 1980s it is predicted that aquaculture will continue to expand and by 2030 will contribute an annual 93 million tonnes of seafood to the global food supply (World Bank, 2013) (Table 1). Global food fish consumption per capita has grown from 9.0 kg in 1961 to 20.5 kg in 2017. This is an annual rate of increase of 1.5% (FAO, 2018). Fish currently represents 6.5% of all protein for human consumption where it represents a vital source of high quality protein and essential micronutrients, including various vitamins, minerals and polyunsaturated omega-3 fatty acids.

Freshwater Fish Farming

Inland fish farming is the major sector of global aquaculture producing 64% of the total global farmed fish in 2016. It has its origins in China and is most developed in China, South East Asia and Southern Asia. Diverse types of fish are produced with major emphasis on various species of carp and tilapia (Table 2; Picture 2). Freshwater crustaceans, including shrimp, crayfish and crabs are also produced in smaller quantities in inland waters.

Culture Methods

The majority of freshwater fish are farmed in extensive and semi-intensive pond systems and floating cages (Picture 1). Individual earth ponds are generally shallow (<1 m deep) and range in surface area from a few square meters to several hectares.

Extensive culture

In extensive pond systems fish feed on the natural production of algae, plankton, invertebrates and small fish. After filling and stocking the ponds with fish water exchange is kept to a minimum to retain natural food organisms. Fertilizers and animal manures may be used to promote natural productivity. A trophic web of natural food organisms offers the opportunity for farmers to grow several different fish species, which feed on different ranges of prey organisms within the same pond environment. This practice of polyculture increases the production capacity of ponds and improves the use of available resources.

Table 2 Global production of major farmed freshwater fish and shellfish species in 2016.

Common name	Scientific name	2016 production (million tonnes)	2016 production (% of total)
Finfish			
Grass carp	<i>Ctenopharyngodon idellus</i>	6.1	11
Silver carp	<i>Hypophthalmichthys molitrix</i>	5.3	10
Common carp	<i>Cyprinus carpio</i>	4.6	8
Bighead carp	<i>Hypophthalmichthys nobilis</i>	3.5	7
Nile tilapia	<i>Oreochromis niloticus</i>	4.2	8
Atlantic salmon	<i>Salmo salar</i>	2.3	4
Rainbow trout	<i>Oncorhynchus mykiss</i>	0.8	2
Shellfish			
Red swamp crayfish	<i>Procambarus clarkii</i>	0.9	12
Chinese mitten crab	<i>Eriocheir sinensis</i>	0.8	10
Freshwater prawn	<i>Macrobrachium rosenbergii</i>	0.2	3

Adapted from FAO (2018) *The state of world fisheries and aquaculture*. Rome: FAO.



Picture 1 Floating cages used for growing tilapia line the banks of an irrigation canal in central Thailand.

Extensive fish culture may be fully integrated with field crop production to increase overall food yields. Fish culture in rice paddies is a traditional and growing practice in China, South East Asia and India. Fish are grown deep-water rice paddies, which are variously modified with open water channels to facilitate fish movements and harvesting. The rice paddies provide a rich diversity of food and shade for the fish and farmers are able to use less fertilizer for the same grain output.

Semi-intensive culture

Farmers can increase fish stocking density and output from semi-intensive pond systems where natural food is supplemented with agricultural by-products, such as rice bran. These are either consumed directly by fish or break down within the ponds and serve as sources of carbon, nitrogen and essential minerals to support the primary growth of phytoplankton.

Intensive culture

In more intensive culture methods there is decreased dependency on the availability of natural food and greater or total dependence on the use of complete feeds, formulated to meet the nutritional requirements of a particular fish species. There is a global trend in intensifying production methods in ponds (FAO, 2018). Farmers use more food and water resources but are able to grow fish at higher stocking densities and increase their yields (Goddard, 1996).

Freshwater Resources

Fish are farmed in ponds, cages and raceways, which permit sufficient water exchange to remove harmful waste metabolites and maintain the required water quality. Water for freshwater farming is drawn from lakes, rivers and springs or pumped from aquifers (Boyd, 2005). Fish farms in tropical and subtropical areas are subject to significant water loss from seepage and evaporation. In carp ponds in India the water exchange requirement has been estimated as 10.3 m^3 water kg^{-1} of fish produced, of which 7.6 m^3 is lost to seepage and evaporation (Sharma et al., 2013). Traditional trout farms in Europe and North America, which operate on through-flow systems, use much higher quantities of water to meet the more demanding water quality and dissolved oxygen requirements of trout. Some 30 m^3 of water are used to produce 1 kg of rainbow trout (*Oncorhynchus mykiss*) (Bregnballe, 2015).

Freshwater resources are under pressure from increased levels of abstraction for industrial and agricultural use linked to population growth. This contributes to water pollution, habitat degradation, flow modification and threatens the biodiversity of aquatic organisms. Around one third of the Earth's surface is defined as desert or arid (<200 mm rain annually). These regions generally lack food security and are vulnerable to the effects of climate change. In arid regions freshwater aquaculture using traditional methods is a marginal activity, yet one which can benefit in the future from water reuse technology (Goddard and Al-Abri, 2018).

Fish Farm Effluent and Waste Products

Effluent from all traditional fish farms, whether seasonal drainage from ponds during maintenance or continuous outflow from floating cages and intensive farms, carries waste in the form of fish metabolites, primarily ammonia and solid waste. If not treated or used to fertilize field crops fish farm effluent will promote eutrophication in receiving waters. Discharge of farm wastes into the environment is a limiting factor in the future expansion of traditional fish farming and in most regions is subject to strict environmental regulation.



Picture 2 Common carp (*Cyprinus carpio*). A widely distributed species of freshwater fish farmed in both temperate and tropical environments. Photo courtesy of Water Farmers, Canada.

Recirculating Aquaculture Systems (RAS)

Growing fish in RAS has a number of advantages compared with traditional pond and floating cage methods. Typically <10% of the water is required and the systems occupy a small percentage of the space required for pond culture. Since there is less dependence on natural resources farms can be located closer to population centers and markets for fish. RAS operate as closed, contained units, usually within buildings. They provide opportunity to maintain year-round optimal water quality and temperatures for particular fish species and support culture at high stocking densities (Colt, 2006). Full measures of biosecurity can be applied to control transmission of fish diseases and parasites and to prevent escapes of fish into surrounding waters.

The application of RAS technology has demonstrated key advantages for fish production in a controlled environment.

- Improved fish quality
- Enhanced growth rates
- Improved food conversion efficiency
- Improved biosecurity
- Reduced transmittable disease problems
- Lower use of therapeutants
- Management of waste and reduction of environmental impact

RAS Applications

Water recirculation technology and its application in aquaculture has seen considerable progress in recent years with standard methods emerging and equipment supplies becoming more available and cost efficient (Martins et al., 2010). Most of the current 80 million tonnes of global farmed fish is produced in open pond or floating net cage systems. RAS are currently used to produce <5% of this total but this figure is predicted to rise to 40% by 2030. RAS are used in various applications where benefits are gained from growing fish in a controlled environment. These include research facilities, fish hatcheries and food fish production facilities.

RAS fish hatcheries

Control of temperature and photo-period can be used to regulate fish breeding cycles and enable farmers to produce eggs and young fish for sale beyond the normal spawning season. RAS freshwater hatcheries are used to grow a broad range of species, both for farming and restocking natural waters. They are widely used for producing juvenile Atlantic salmon (*Salmo salar*) for stocking into sea cages.

RAS food fish

Whilst there is a general focus on the production of high-value food fish species RAS are also used to grow cheaper commodity species. There is current interest in the development of large cold-water RAS Atlantic salmon farms using either seawater or freshwater and each capable of producing many thousands of tonnes of fish per year. Marine cage farms for Atlantic salmon production discharge waste directly into the ocean and are subject to increasing environmental controls and licensing costs,



Picture 3 Sampling Nile tilapia (*Oreochromis niloticus*) from a RAS fish tank.

which may limit future expansion. In comparison RAS salmon farms can manage their waste to advantage and also control problems with sea lice. These are crustacean ectoparasites which damage fish and are difficult to control in the open ocean.

Warm-water species grown in commercial freshwater RAS include tilapia and African catfish (*Clarias gariepinus*). These fish grow rapidly at optimum temperatures and are tolerant of high stocking densities. Production costs are generally higher than those for fish produced in open systems and farmers seek benefits from economies of scale and siting their farms in close proximity to favorable markets (Picture 3).

Water Treatment in RAS

Waste products and metabolites, including feces, ammonia and carbon dioxide are released by fish and must be treated in water-recycling systems to avoid the accumulation of potentially harmful and toxic compounds (Fig. 1). A full description and illustrations of modern RAS are given in Bregnballe (2015).

Removal of solids

Feces and any uneaten food contribute to particulate solids which dissolve and break up in water into particles, with sizes ranging from $<001\ \mu\text{m}$ (dissolved solids) to $>100\ \mu\text{m}$ (settleable solids). High levels of solids are damaging to the delicate gills of fish and may cause physical injury, increasing the risk of bacterial infection.

Settleable and supra-colloidal solids form the bulk of solids excreted by fish and can be removed by gravitational devices and micro-screens. Circular fish tanks with flat bottoms are generally used in large installations. Water circulates uniformly and centripetal forces transport solid wastes to the center from where they can be separated in a small separate drain pipe from the main flow of cleaner water. Additional suspended solids can then be removed by a combination of swirl separators, radial flow filters or rotating drum filters fitted with micro-screens ($40\text{--}100\ \mu\text{m}$). The cleanest water is returned to the fish tanks, whilst waste-rich water is diverted for further treatment.

Biological filtration

Nitrogenous waste resulting from the metabolism of protein is excreted primarily as ammonia from the gills of fish. On release the free ammonia (NH_3) molecules react in water to form ammonium hydroxide, which readily dissociates into ammonium (NH_4^+) and hydroxyl ions (OH^-).

Nitrogen in the form of free ammonia (NH_3) is toxic to fish and is oxidized in biofilter structures by nitrifying bacteria to harmless nitrate growing in films in biofilters. Two major groups of autotrophic bacteria are involved in the oxidative process. *Nitrosomonas* convert ammonia to nitrite and *Nitrobacter* convert harmful nitrite to more harmless nitrate.

1. $2\text{NH}_4^+ + 3\text{O}_2 \rightarrow 2\text{NO}_2 + 2\text{H}_2\text{O} + 4\text{H}^+$ (*Nitrosomonas*)
2. $2\text{NO}_2 + \text{O}_2 \rightarrow 2\text{NO}_3$ (*Nitrobacter*)

Biofilters typically contain plastic media which are light to handle and provide a large surface for bacterial films to colonize. Moving bed bioreactors are commonly used. These comprise tanks containing small plastic bio-balls ($2\text{--}3\ \text{cm}$ diameter) with sculpted surfaces to provide maximum surface area. The biofilter media is submerged in the recycling water which is heavily aerated.

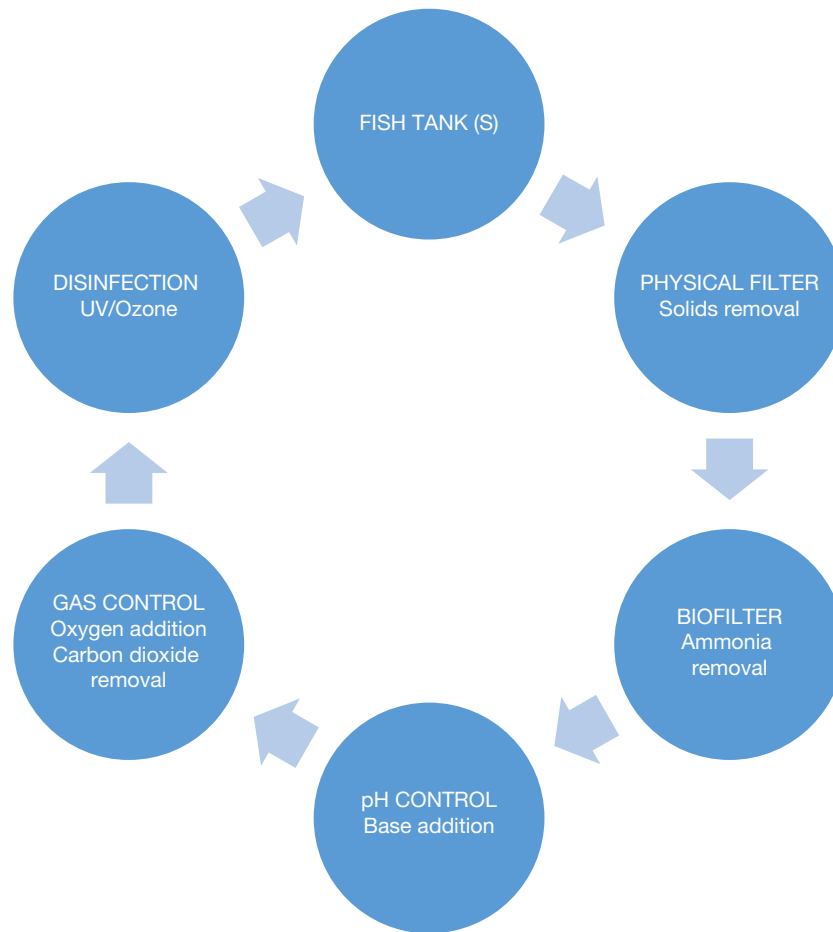


Fig. 1 Components and functions of a Recirculating Aquaculture System.

The size of biofilters is calculated based on various parameters. These include the total ammonia-nitrogen (TAN) released by the fish, hydraulic loading, water flow rates and the calculated surface area of the selected filter media. TAN calculations are based on the nitrogen content of the fish feed, daily food consumption, digestibility and nitrogen content of protein (Bregnballe, 2015).

Gas control

As water circulates through the fish tanks and biofilters oxygen is depleted and carbon dioxide accumulates. Aeration, using blown or compressed air linked to diffuser systems or airlifts can be used to increase oxygen levels. In RAS heavily stocked with fish oxygen gas is used to fully saturate the water with dissolved oxygen. Carbon dioxide is removed by heavy aeration in a process known as degassing.

pH adjustment

Within RAS the nitrification process produces acid which reduces the pH of circulating water. Water is dosed with a base compound, commonly sodium hydroxide, to restore pH to within the range 7.0–7.5.

Pathogen control

Ultra-violet light and ozone are used separately or in combination to reduce pathogen levels in the circulating water. UV tubes are commonly used and function by emitting light in wavelengths which destroy the DNA in biological organisms. Ozone functions by heavy oxidation of microorganisms and organic matter. Additionally it flocculates microparticles. These can be removed by physical filtration, clarifying the circulating water.

Waste water and sludge management

The solids separated from the circulating water can be de-watered and concentrated. Some 200 kg of solids (as dry matter) are produced for each tonne of food consumed by the fish. This waste can be used as an agricultural or garden fertilizer or as feed for biogas production.

Biofloc Technology

Extensive possibilities exist to conserve water through the novel application of biofloc technology (BT) (Avnimelech, 2009). Conventional RAS are mechanically complex and require significant amounts of energy. BT supports fish production in a much simpler system in which the harmful products of fish metabolism are processed by bacteria within the fish tanks or ponds (Avnimelech, 2007). BT enables farmers to minimize water exchange and water usage, whilst maintaining adequate water quality, through the balancing of carbon and nitrogen in the system (Crab et al., 2012). The technology is based on waste nutrient recycling, particularly nitrogen into microbial biomass. The biomass can be used directly as food by filter-feeding fish species such as tilapia and carp (Bossier and Ekasar, 2017) (Fig. 2).

Within ponds or tanks carbon: nitrogen ratios and dissolved oxygen levels are adjusted to provide optimal conditions for the growth of bioflocs. These are small aggregates (<1 mm diameter) of waste food, fecal material, phytoplankton, zooplankton and bacterial communities (Hargreaves, 2013). In well-balanced systems the bacterial communities take up the nitrogenous compounds, which are otherwise harmful to fish, and produce beneficial microbial proteins, lipids, vitamins and minerals.

Biofloc Farming Systems

Biofloc technology makes it possible to minimize water exchange and water use in fish farms; maintaining water quality whilst producing low-cost, protein-rich bioflocs. The practical application of biofloc technology in fish farming offers great potential for water conservation (Avnimelech, 2007). It is applied in static pond and tank systems and eliminates the requirement for water exchange in intensive culture systems. It is much simpler and less costly to operate than RAS. Microbial biomass contains 20–45% crude protein, 1–5% lipids (as dry matter), plus various bioactive compounds including essential fatty acids, carotenoids, vitamins and minerals (Kuhn et al., 2009). The availability of in situ nutrients has opened the way for reformulation of special aquafeeds for use in biofloc systems. Protein content can be reduced and fish meals can be replaced with plant meals. This improves sustainability and reduces cost (Martinez-Cordova et al., 2015). In practice Biofloc tanks or ponds must be continuously mixed and aerated and the carbon nitrogen ratio (C:N) carefully maintained (12:1-20:1) to support the formation and stabilization of a heterotrophic microbial community (Perez-Fuentes et al., 2016). Carbon content is balanced using readily available carbohydrate sources such as molasses or grain pellets. Total suspended solids content is monitored throughout the fish production cycle and maintained at optimal levels of 100–300 ppm. Excess biomass can be harvested and processed into feed ingredients (Kuhn et al., 2009).

Biofloc farming systems operate with zero or minimum water exchange and offer greatly enhanced biosecurity against the transmission of fish pathogens and parasites. Probiotics have been identified in bioflocs. These are microbial cells that have a beneficial effects on the health of a host organism, including growth promotion, increased immune response and inhibition of pathogenic microorganisms. The identification of natural probiotics and immunostimulants and their beneficial effects on fish survival and growth have been reported from recent studies on the microbial ecology of bioflocs (Rani et al., 2017).

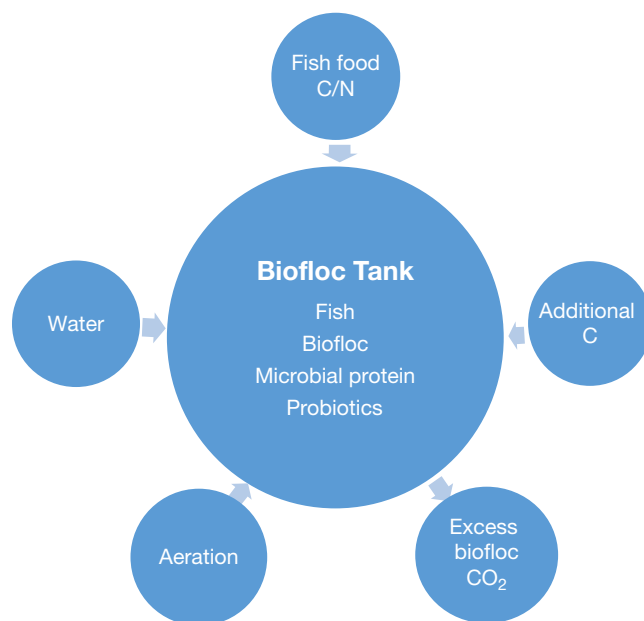


Fig. 2 Inputs and products in a Biofloc Technology System.

Aquaponics

Aquaponics combines the benefits of fish production in modified RAS systems with the soil-less production of plants (hydroponics) using the same water. It operates within a closed-loop system where fish feed provides most of the nutrients required for healthy plant growth. These nutrients, excreted directly by the fish, or generated by the microbial breakdown of organic wastes, are absorbed by growing plants. Aquaponics was first developed in its modern form by scientists researching novel methods for treating recycled water in fish culture systems (Love et al., 2015). In these studies edible plants, such as tomatoes and lettuce, were used to remove waste products from carp and tilapia production tanks (Naegel, 1977). Current research is generally aimed at refining methods for improved integration of fish and vegetable production (Rakocy et al., 2006).

Water consumption is <10% of normal levels for horticultural production and can be provided from potable supplies or pathogen-free groundwater (Somerville et al., 2014). There are no direct mineral or fertilizer costs since the primary mineral source is the fish feed provided to support fish growth. Some small additions of alkaline salts to maintain a stable, neutral pH and ferrous salts to maintain the necessary iron content are the only mineral additives used in aquaponics. The intensive nature of aquaponic production greatly reduces the amount of land necessary for commercial production units and there is no requirement for arable land. The combination of aquaponics with modified water recirculation technology has opened the way for aquaponic developments on large commercial scale (Picture 4).

Integrating Crops

A wide range of vegetables and fruits are grown in aquaponic systems, including include lettuce, chard, pak choi, spinach, kale, basil, tomatoes, peppers and micro-greens. Two types of grow bed are commonly used for plant production.

Media-filled systems

Crops are planted in shallow grow beds (50 cm) which contain gravel or clay balls. Water circulation through the grow beds is maintained by a flood and ebb system, driven by a pump and controlled by a bell siphon. Each bed is filled with nutrient-rich water and drained 2–3 times each hour. The media provides a large surface area which promotes biological filtration, reducing ammonia to nitrite and nitrate. The media also provides support to plant root systems and enables relatively tall plants to be grown. The overall productivity of plants is generally less than in floating raft systems, although a greater range of vegetable and fruit varieties can be grown.

Deep water culture systems

This method is used for smaller plants such as herbs and salads, which grow floating in a styrofoam raft. The plants are initially contained in small coir pots and receive their necessary minerals from the fish tank via the water which circulates around their exposed roots which grow below the floating rafts. The fish are held in a separate tanks and water from the fish tank circulates continuously through the system. Beneficial bacteria live throughout the system and the extra volume of water in the grow beds provides a buffer for fish, reducing stress and potential water quality problems (Picture 2).

Deep water culture and media-bed systems may be used singly or in combination. Deep water culture methods are typically used in large commercial units for the production of large quantities of mono-crops, such as lettuce, kale, salad greens and culinary herbs.



Picture 4 An aquaponic farm in a hot arid region in northern Oman producing Nile tilapia and a variety of vegetables (kale in the foreground). Treated effluent from the fish tanks (blue) supplies nutrients to plants growing in media beds and deep water culture tanks. Photo courtesy of Water Farmers, Canada.

Fish Production

A limited range of freshwater fish species is grown in aquaponics. Tilapia (*Oreochromis* spp.) is most commonly grown since they are hardy, readily available, grow rapidly under optimal conditions and are familiar to consumers (Bernstein, 2013) (Picture 4). Other warm-water species include Asian seabass (*Lates calcarifer*), catfish (*Clarias* sp.) and common carp, including ornamental varieties of koi carp (Picture 3). The volume and value of food fish grown in aquaponics is small in comparison with plant production. Plants reach harvest faster, which permits multiple plantings and have higher value per unit weight than fish. Typically, profits are gained on plant yield rather than fish production, where fish are sold as a secondary crop and are used as a source of bio-available plant nutrients. An aquaponics farm producing 50 t of fish year⁻¹ can readily produce in excess of 1000 t of vegetables year⁻¹.

Planning

A detailed review of planning, construction, operation and economics of small-scale aquaponic farms has been provided by FAO (Somerville et al., 2014). Capital costs can be high in relation to income and a recent survey suggests that the majority of aquaponic farms operate on small commercial scale (Love et al., 2015). The fish culture units are typically small in comparison with commercial fish farms. The majority produce <5 t of fish per year per year (Love et al., 2015). Fish units of this capacity lack the economies of scale seen in commercial-size fish farms, where production capacities range from 100 to 1000 plus tonnes per year. Production costs for aquaponic fish may be higher, which necessitates careful planning to manage capital and operating costs of the fish unit and pursuit of favorable farm prices for fresh, local product.

Water Reuse and Treatment

The essential requirements for treatment of recycled water depend primarily on the plant growing system selected. Media-filled grow beds will filter some solids and function as biofilters. In contrast deep water culture systems require additional solids separation and biofiltration. Water flows from the fish tanks in a cycle through solids separation equipment, followed by biofilters and the plant grow beds. It is then collected in a sump, aerated and pumped back to the fish tanks. Additional air is supplied to the water circulating in deep water culture beds to maintain dissolved oxygen levels around the plant roots.

Metrics based on feed use are fundamental to aquaponics. Determination of the quantity and quality of food used daily are used to calculate both scope of water treatment necessary and the scale of hydroponic plant production which can be supported by the treated effluent from fish tanks. Calculating biofilter size should also take into account the available surface areas of the grow beds and styrofoam floats which will be in contact with water and will also support the growth of bacterial films. Routine monitoring of water chemistry is vital to maintain a balanced water reuse system (Colt, 2006). Recycled systems accumulate acidity which must be adjusted by base addition to maintain optimal pH for fish, bacteria and plants growing in the same system.

Food Safety

Food safety is a vital component of food production and aquaponic farmers must follow available codes of good practice and apply biosecurity protocols for both aquaculture and horticulture components. The bacterium *Escherichia coli* is the most widely studied potential contaminant in aquaponics. This bacterium is found in the intestines of warm-blooded animals, including birds and cattle, and has been used in developing human health-based regulatory standards as a common indicator of fecal contamination and microbial water quality in agricultural water systems. Indicator microbes and pathogenic bacteria, such as *E. coli* and *Salmonella* spp., if present in aquaponic systems, most probably originate from warm-blooded animals, such as birds, since these enteric bacteria are transient in fish gut microflora (Sugita et al., 1996). As in all crop production systems cross-contamination is possible. However, the risk in aquaponics farming systems is low when compared with the traditional production of field crops (Sirsat and Neal, 2013). Extensive studies have reported negative tests from aquaponic farms for the food safety indicator organisms *E. coli* and *Salmonella* spp. (Chalmers, 2004, Fox et al., 2012).

Urban Aquaponics

Disused industrial space, including rooftops, is attracting aquaponics development in many European and North American cities. These typically use temperature and light-controlled greenhouse structures designed to support year-round production and incorporate space-saving stacked and vertical horticulture systems. Capital and operating costs are high but operators benefit from a large consumer base and demand for local, organically-produced fresh products. Urban projects play an important role in education and public awareness of food sources and security.

Prospects

Freshwater fish farming is predicted to expand into the future as farmers intensify their existing production methods. The annual rate of growth is slowing however, water resources are limited and new applications of more sustainable technologies are needed.

The sector faces the challenge of climate change. Erratic climate patterns of draught and flooding have direct physical impacts on traditional farms. Temperature changes, including heatwaves and abnormally cold events affect survival, reproduction and growth patterns of fish and may promote the spread of fish parasites and pathogens (Bueno and Soto, 2017). The development of closed systems, such as RAS, BT and aquaponic farms with enhanced biosecurity will help mitigate these risks.

It is important to control energy costs in closed-system aquaculture. Many farmers currently use renewable sources to power necessary equipment and it is expected that this practice will become universal within the next decade.

Integration of aquaponics with biofloc technologies has the potential to reduce the costs of water treatment, improve feeding efficiency and scale-up fish production. Early research indicates the bio-availability of plant nutrients in biofloc tanks and ponds (Pinho et al., 2017). Present systems will require modification for efficient handling of solids waste and excess biofloc.

Potential exists to apply aquaponic techniques in arid regions where salinization of ground water restricts traditional agriculture. Many farmed fish species are tolerant of low to medium salinities and their production can be combined with growing salt tolerant varieties of traditional crops at low salinities (Goddard et al., 2010) or edible halophytes at higher salinities (Pantarella and Bhujel, 2015).

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- www.was.org—World Aquaculture Society.
- www.aquaponicsassociation.org—Aquaponics Association, USA.
- www.aquaponics.org.uk—Aquaponics, UK.

Mining and Water Resources

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Abstract

This article reviews the basics of mining and its interaction with water resources. While mining often requires a large amount of water, it can also present various risks to water resources, such as depletion or pollution (especially if acid and metalliferous drainage related to iron sulfide minerals to the surface environment). Modern mining is typically regulated to address these risks, with statutory environmental reporting increasingly being made public to improve transparency and align with the need for industry-wide reporting on sustainable development performance. The article presents a concise overview of mining, its interactions with water resources, key risks to manage, and the principal regulatory and reporting approaches which can be used for sustainable management of both mining and water resources.

Introduction

Mining and water resources are intimately linked but have a complex and often fraught, poorly understood relationship. In simple terms, the process of mining requires significant amounts of water but can also manifest substantial risks to surface, marine and groundwater resources as well as the ecosystems and communities which depend on these water resources—analogueous to agriculture and other human activities. This complex picture for mining has been recognized for millennia, with the great Middle Ages mining scholar Georgius Agricola famously writing in his final treatise “De Re Metallica” that:

... the strongest argument of the detractors is that the fields are devastated by mining operations ... Further, when the ores are washed, the water which has been used poisons the brooks and streams, and either destroys the fish or drives them away. Therefore the inhabitants of these regions, on account of the devastation of their fields, woods, groves, brooks and rivers, find great difficulty in procuring the necessities of life, and by reason of the destruction of the timber they are forced to greater expense in erecting buildings. Thus it is said, it is clear to all that there is greater detriment from mining than the value of the metals which the mining produces. (Agricola, 1556, p. 8)

It has therefore been clear for centuries that mining can cause significant impacts to water resources, ecosystems and communities—that is, in more modern language, mining can lead to unsustainable outcomes if such risks are not identified, mitigated and managed well. This is the crux of mining in the 21st century but the scale is no longer very small scale mines affecting very localized catchments, as in Agricola’s Erzgebirge region (the “Ore Mountains” of Saxony) but rather often giant sized mines operating in almost every reach of the earth (Antarctica being the only exception where mining is banned by international treaty). In some parts of the world there are now great mining fields with numerous giant mines—such as the Mpumalanga coal province in South Africa, the lead-zinc and copper mines of Peru, the copper mines of the Atacama Desert in Chile, the iron ore mines of the Pilbara region in Australia or the Nevada gold fields of the United States (amongst many others). This leads to the need to consider not just one mine with respect to water resources but the cumulative effects of many mines in a geographic region or water catchment—effects which have to be considered alongside other activities in a catchment such as agriculture, environmental water flows, urban centers, and so on. There is also an increasing need to consider the climate change risks to water resources as well as the impacts of climate variability (which can be further exacerbated by climate change).

It is also important to remember, as the old saying goes, “if it aint grown, it’s mined”—meaning that society needs the materials provided by mining just as much as they need food and water. In the 21st century the modern world needs an ever-increasingly

complex suite of raw materials which mining provides—from the staples of iron (for steel) to light and base metals (e.g. aluminum, copper, zinc, nickel, etc.) to the so-called critical metals which are crucial for modern technology (e.g. rare earths, indium, lithium, tellurium, rhenium, etc.). When combined with population growth and economic development across the world (especially increased consumption and urbanization), this leads to an ever-growing demand for the raw materials which mining provides.

This article will review the basics of how mining works, the use of water in mining, the types of water resources impacts that mining can cause (especially water pollution), approaches to water management and reporting in mining, and finally present some important case studies. It is intended to present a broad coverage of the primary issues between water resources and mining, with greater detail found in the literature.

The Brief Basics of Mining

The extraction of raw materials from the earth, known as mining, typically involves several steps, depending on the element of interest. First, a sufficiently rich deposit must be located and explored to assess whether it is worth the costly process of mining. Second, assuming a deposit is considered economic and approved for extraction, a mine is built and operated. Typically, the products of a mine, such as a concentrate or saleable ore product, require further processing in a smelter and/or refinery to produce a metal suitable for sale to manufacturing. Smelters and refineries are commonly a long distance away from the mine (e.g. another country and often far away). Finally, after a deposit is exhausted or becomes uneconomic, a mine is expected to be rehabilitated to a suitable ecological standard. This is often known as the mining cycle, since there is a need to continually find more deposits to meet ever-growing global demand for raw materials.

Within a mine, there are typically two principal stages—mining and processing. The material with economic concentrations of metal(s) (or minerals) of interest is known as ore, which can be extracted through an open cut or underground mine. An open cut mine involves digging a large hole or void to access the ore, necessitating the extraction of large amounts of waste rock (sometimes called overburden) in the process. An underground mine uses shafts or tunnels to target and access ore, through a variety of methods (e.g. narrow vein, stoping, caving, etc.), leading to minimal amounts of waste rock. The processing stage involves using a particular technology to extract the metal or mineral of interest. Before any direct processing occurs, the ore is usually ground to a fine powder to increase the ability of separation. For base metals, such as copper, lead, zinc, nickel, a process known as flotation is used which preferentially concentrates the sulfide minerals containing the metals into a much smaller volume, with the product known as a concentrate. For certain metals, leaching processes can be used for direct extraction, such as using cyanide for gold or sulfuric acid for uranium. For bulk minerals, processes involving gravity or magnetic separation can be used to produce a saleable ore (e.g. iron ore, bauxite, manganese). The concentrates or saleable ores are then further processed at a smelter and/or refinery to produce a pure metal (or mineral in some cases).

Furthermore, there are also other techniques of mining which rely on the use of solutions directly in mining and their processing to produce a metal directly at the mine with no need for subsequent smelting or refining. For some metals, a mine can process ore using heap leaching, whereby ore is stacked into large piles, irrigated with a solution which has a chemical added to facilitate leaching and extraction (e.g. sulfuric acid or cyanide), and the rich solution from the bottom of the heap is then processed for the metal of interest. The use of heap leaching is widespread in the copper and gold mining sectors, with an increasing number of examples in other sectors (e.g. uranium, zinc, nickel). Alternatively, if the ore zone is sufficiently permeable, the reagent-rich solution can be directly injected into the ore to leach the metal(s) of interest and then pumped back to the surface for processing—a mining method known as “in-situ leaching” (ISL). Although there are some similarities between ISL and the petroleum industry, namely solution flow through a deposit of interest, there are also key differences. For example, conventional petroleum does not require primary chemicals to facilitate oil and gas extraction, although unconventional petroleum extraction from shales requires the use of hydraulic fracturing (aka “fracking”) and a range of chemicals to facilitate this.

Overall, the essential steps involved in mining include the extraction stage (via open cut or underground methods), the ore processing stage and finally the smelting and/refining steps to produce the metals (minerals) of interest. Alternatively, solution-based methods can also be used. It is therefore important to understand the exact configuration of any mining project, as this helps to identify and manage various risks to water resources.

As an example, the Chuquibambilla copper-molybdenum field in northern Chile is shown in Fig. 1, highlighting the various features of the mining complex.

Water Use in Mining

It is perhaps obvious to state that mining requires a significant amount of water to operate, but it is certainly not obvious that there is wide-ranging complexity and variability in how much water may be used for a given mining project—even for mines of similar scale and configuration. There are a variety of water needs in mining, such as:

- Mining—water for suppression of dust (especially for open cut mining);
- Crushing-Grinding of Ore—the crushing and grinding of ore to a fine powder generates vast amounts of dust which need control via water sprays;

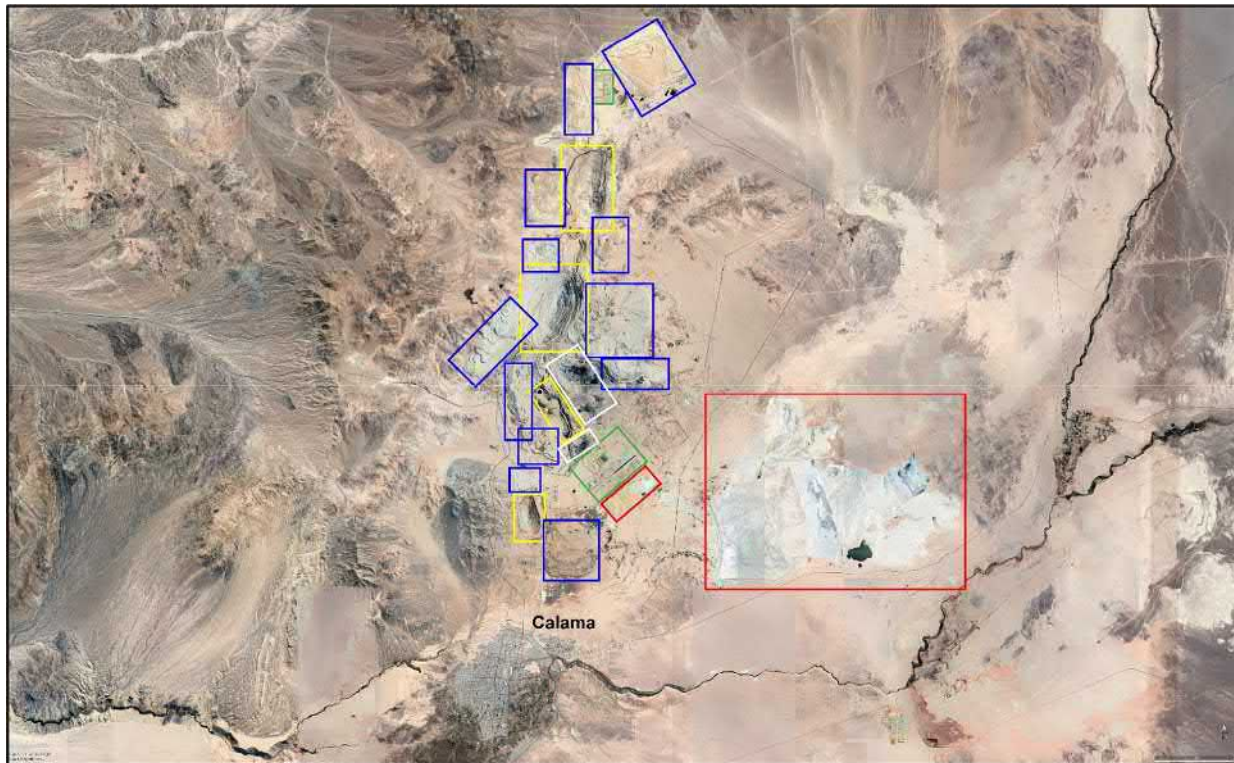


Fig. 1 The Chuquicamata copper-molybdenum-silver-gold field of northern Chile, showing the various mining features (*red*—tailings dams; *blue*—waste rock dumps; *yellow*—open cut mines; *green*—heap leach piles; *white*—processing facilities), the adjacent town of Calama (*bottom center*) and the River Loa (*right and along bottom*) (note the large tailings dam area is approximately 12 km wide). Figure adapted from Google Earth Service.

- Ore processing: finely sized ore is typically mixed with water to allow processing, such as flotation or leaching technology;
- Tailings disposal—after separation of metals (or minerals), the residual material is known as tailings and is commonly pumped as a slurry to an engineered tailings storage facility (or dam);
- Environmental management—including discharges of appropriate water to maintain environmental flows in streams, or for revegetation and rehabilitation works;
- Drinking water—for mine workers on site and sometimes the nearby mining town also.

The two dominant sources of water that a mine will access are surface water and groundwater, with sea (or marine) water used in rare cases (e.g. direct use or for a desalination plant to produce fresh water). Furthermore, it is important to consider the quality of different water sources, such as fresh, brackish, saline or hypersaline, as well as the interactions between the various water resources. All mines operate within a climatic context, such as temperate, tropical, arid or hyper-arid climates with widely varying seasonal temperature regimes (e.g. the Köppen-Geiger climate classification system). Finally, mines also operate within a regulatory context which will vary all over the world, and a mine's water management system will be tailored to meet these statutory requirements (such as the amounts, quality and timing of mine-related water discharges to streams, if allowed at all), as well as potentially any local social and environmental factors which need to be linked to a mine (e.g. maintaining environmental flows, protecting water quality, ensuring water availability for other users such as farmers, etc.). Overall, mining can be a very large user of water but the details are important and always very site-specific to assess and understand.

Water Resources Impacts From Mining

Surface Water Resources

Historically, mining was a modest affair and occupied a small extent of land—but modern mining can be vast in scale and occupy large tracts of land. With respect to surface water resources, this means that the risks and interactions are now much larger and more significant. There are many types of surface water impacts which mining can cause, such as (e.g. [Da Rosa et al., 1997](#); [Spitz and Trudinger, 2008](#)):

- *Stream diversions*—mining can necessitate the diversion of streams, ranging in scale from small creeks to large, long diversions (e.g. the McArthur River zinc and numerous coal mines in Australia);

- *Altered catchments*—mining causes significant geomorphological changes to hydrological catchments, due to open cut mines, waste rock dumps, ponds, tailings dams, process plants and infrastructure—leading to changes in runoff characteristics and surface water flows;
- *Extraction*—surface water can be extracted for use in mining, reducing stream flows;
- *Discharges*—a mine can sometimes discharge accumulated waters to adjacent streams, sometimes altering flow regimes and associated environmental and cultural values (e.g. Weeli Wolli Creek, Pilbara iron ore mines, Australia);
- *Contaminants*—waters (and sometimes sediment) leaving a mine site and entering a stream can carry contaminants which can cause impacts from short-term changes to water quality to severe pollution and aquatic ecosystem impacts, often associated with acid and metalliferous drainage (“AMD”, more commonly known as acid mine drainage).

All mines will have a water management plan which should address all of the above risks, meaning that the extent of actual impacts will vary considerably. For example, mines in tropical, high rainfall zones will have an excess amount of water which is often discharged. Conversely, mines in arid to hyper-arid climates will often face water deficits and need to manage water use very efficiently. In parallel, all mines will need to manage water quality, with criteria typically set by a government regulator and associated water resources policies or guidelines. In some cases, water with poor quality will need to be treated before it could be re-used or discharged. Various treatment methods are used across the industry for this, including reverse osmosis, engineered wetlands, land application (or irrigation), mixing with other water streams, or in some cases discharge to a nearby stream under strict criteria of high flows to maximize dilution (although this latter option does not address bioaccumulation risks from heavy metals or other contaminants).

Groundwater Resources

Groundwater is the water contained in saturated media below the ground surface, the study of which is a discipline known as hydrogeology. For groundwater, where it can be extracted from a geological layer or formation at a reasonable rate, this is called an aquifer (e.g. sands, sandstone, limestone). A geological layer or formation which limits the flow of water through it is called an aquitard (e.g. clays, shales). Given the often large extent of open cut mines and the scale and increasing depth of underground mining, groundwater presents various issues for mining, including:

- *Depletion*—open cut and underground mining require the extraction of groundwater, for both safety and access, with the amount depending on the scale of mining as well as the local and regional hydrogeological context, such as a productive aquifer (or the presence of aquitards);
- *Contaminants*—the seepage of waters from ponds and tailings dams (or in some cases direct injection) can carry contaminants into the underlying groundwater system, leading to impacts from short-term changes to water quality to severe pollution, often associated with AMD.

As with surface water, a mine should have a major focus on groundwater issues in its mine water management plan. For most mines the focus will be on monitoring the levels (or heads) and water quality groundwater to assess the impacts and risks from mining. For mines which use groundwater as their primary water source, they will also need to monitor this extraction carefully, which can often be at some distance away from the mine.

Marine Water Resources

Mining typically has very little interactions with marine water resources, mainly due to the fact that most mining occurs inland away from coasts and the marine environment. However, mining effects on stream flows and quality may reach the marine environment, especially if direct discharges occur. This remains a key concern for the coal mines of the Bowen Basin in central Queensland, Australia, as their collective discharges enter the Fitzroy River—which flows into the marine environment of the Great Barrier Reef (other impacts also need to be considered, such as agriculture, urban centers and other land uses which may also affect the Fitzroy River).

In some circumstances, mining can occur on the coast and impacts to marine water resources can be a real risk. For example, the Lihir mine in Papua New Guinea (PNG) mines a large gold deposit by open cut on the coast of a small island. Given the void is well below sea level, the mine induces the flow of sea water through the aquifer and this water is then discharged back to sea. Furthermore, waste rock from the mine is emplaced in the shallow harbor adjacent to the mine, with tailings discharged at depth to the marine environment (see later).

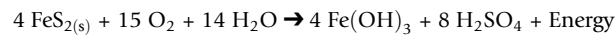
A frontier issue is the growing interest in the extraction of mineral resources from the deep-sea floor, ranging from volcanic sulfide vents, to manganese nodules or mineral rich sediments on seafloor mounts. The typical water depths can range from 1.5–2 km (e.g. vents, mounts) to 5–6 km (e.g. nodules). Deep sea mining has never been done before on a commercial scale, with trial mining recently completed in Japan’s deep marine waters and a proposed mining project at Solwara in PNG (which is currently in stasis given the lead company, Nautilus Resources, is working towards re-financing its debts). There are many complex issues which remain unresolved with potential deep sea mining, including marine biodiversity impacts—and especially the interaction of shallow, intermediate and deep sea biota, sedimentation issues from mine wastes, impacts to marine water quality and the difficulty of mine rehabilitation in deep waters.

Acid and Metalliferous Drainage (“AMD”)

The greatest water resources risk from mining is, without doubt, polluted mine water known as acid and metalliferous drainage (“AMD”)—commonly known as acid mine drainage. This is formed from the weathering of iron sulfide-related minerals in tailings or waste rock, and sometimes even from open cut mine walls or underground voids, leading to the formation of acidic, saline and/or heavy metal-rich waters which present a severe risk to aquatic ecosystems and human use of AMD-impacted waters. In recognition of AMD risks in particular, the US Environmental Protection Agency is attributed as stating in 1987 that (as cited by [EEB, 2000](#)):

... problems related to mining waste may be rated as second only to global warming and stratospheric ozone depletion in terms of ecological risk. The release to the environment of mining waste can result in profound, generally irreversible destruction of ecosystems.

The geochemistry of AMD is both simple and complex—in other words, although it can be simplified it is always site-specific with lots of factors to consider. In essence, AMD is caused by the exposure of iron sulfide minerals, such as pyrite and its close cousins, to water and oxygen. In general, AMD is considered to be a three-stage process, involving iron sulfide oxidation, then oxidation of ferrous to ferric iron (Fe^{2+} to Fe^{3+}) and the ferric iron either precipitating as ferrihydrite or further oxidizing sulfide minerals (e.g. [Lottermoser, 2010](#)). The overall reaction can be represented as:



(or in words : pyrite + oxygen + water goes to ferrihydrite (aka rust) + sulfuric acid + heat)

The sulfuric acid can then dissolve other salts and heavy metals, leading to extremely high concentrations in AMD-affected waters. In some cases, the acid can be buffered by alkaline minerals such as carbonates, leading to a pH neutral water but still rich in salts and heavy metals—hence AMD is more accurately called “acid and metalliferous drainage,” to reflect examples of neutral, saline and or/metalliferous drainage (e.g. [Taylor and Pape, 2007](#)). Examples of the chemistry of AMD at some mines are shown in [Table 1](#), including Australia’s water quality guidelines for high conservation value streams (Australia’s guidelines can be substituted for any equivalent national requirements or comparison to drinking water standards in the absence of specific environmental guidelines). Stark visual examples of AMD-impacted streams are shown in [Fig. 2](#).

Table 1 Selected examples of the chemistry of acid and metalliferous drainage (AMD) and comparison to Australia’s water quality guidelines (all mg/L, except pH; where given, number of samples on brackets).

Mine [Reference]	pH	Cu	Al	Fe	Zn	Mn	SO ₄
Redbank, Australia [1]							
Sandy Flat open cut	2.6	627.5	350.5	NR	NR	NR	NR
Hanrahan’s Creek	3.6	377.7	313.0	NR	NR	NR	NR
Mount Lyell, Australia							
Haulage Creek [2]	2.7	90	NR	421	9.3	120	3975
Mount Morgan, Australia [3]							
Open cut water	2.7 (1)	44.5 (1)	780 (1)	253 (1)	22.0 (1)	71.3 (1)	13,600 (1)
Sumps and waste rock dumps	3.1 (10)	64.0 (10)	1228 (10)	575 (10)	38.3 (10)	139 (10)	22,700 (10)
Dee River ~1 km upstream	6.9 (2)	0.01 (2)	BDL (2)	BDL (2)	BDL (2)	0.15 (2)	375 (2)
Dee River mine area	3.1 (6)	16.7 (6)	197 (6)	27 (6)	5.5 (6)	31 (6)	4415 (6)
Dee River ~20 km downstream	6.2 (1)	0.06 (1)	1.0 (1)	BDL (1)	0.01 (1)	0.6 (1)	340 (1)
Milluni Basin, Bolivia [4]							
Unimpacted Streams (wet season)	6.05 (53)	NR	0.28 (53)	0.26 (53)	NR	NR	24.3 (53)
Unimpacted Streams (dry season)	6.11 (53)	NR	0.11 (53)	0.10 (53)	NR	NR	25.5 (53)
Impacted Stream (wet season)	2.90 (52)	NR	6.4 (52)	160 (52)	NR	NR	856 (52)
Impacted Stream (dry season)	2.97 (52)	NR	4.1 (52)	245 (52)	NR	NR	160 (52)
Rio Tinto, Spain [5]:							
Upstream	1.8 (1)	240 (1)	NR	3500 (1)	130 (1)	NR	14,000 (1)
Downstream	1.7 (6)	127 (6)	NR	2805 (6)	209 (6)	NR	10,700 (6)
Tinto Estuary	7.6 (1)	0.05 (1)	NR	BDL (1)	0.3 (1)	NR	3400 (1)
Australian Guidelines [5]							
99% protection level	NR ^a	0.001	0.027 ^b	NR ^a	0.0024	1.2	NR ^a
80% protection level	NR ^a	0.0025	0.15 ^b	NR ^a	0.031	3.6	NR ^a

Notes: NR, not reported; BDL, below detection limits. References: [1] Table 6.3-2 ([EcOz, 2009](#)); [2] Table 5.1 ([Koehnken, 1997](#)); [3] Table 1 ([Edraki et al., 2005](#)); [4] Approximate averages from Table 1 ([Salvarredy-Aranguren et al., 2005](#)); [5] Upstream is site W1, Downstream the average of sites W2 to W7 ([Hudson-Edwards et al., 1999](#)); [6] Table 3.4.1 ([ANZECC and ARMCANZ, 2000](#)) (note these guidelines are being updated as of 2019).

^aAlthough no values are proposed, the typical approach would be to use baseline values (i.e. unimpacted or natural levels)

^bValues for pH > 6.5.

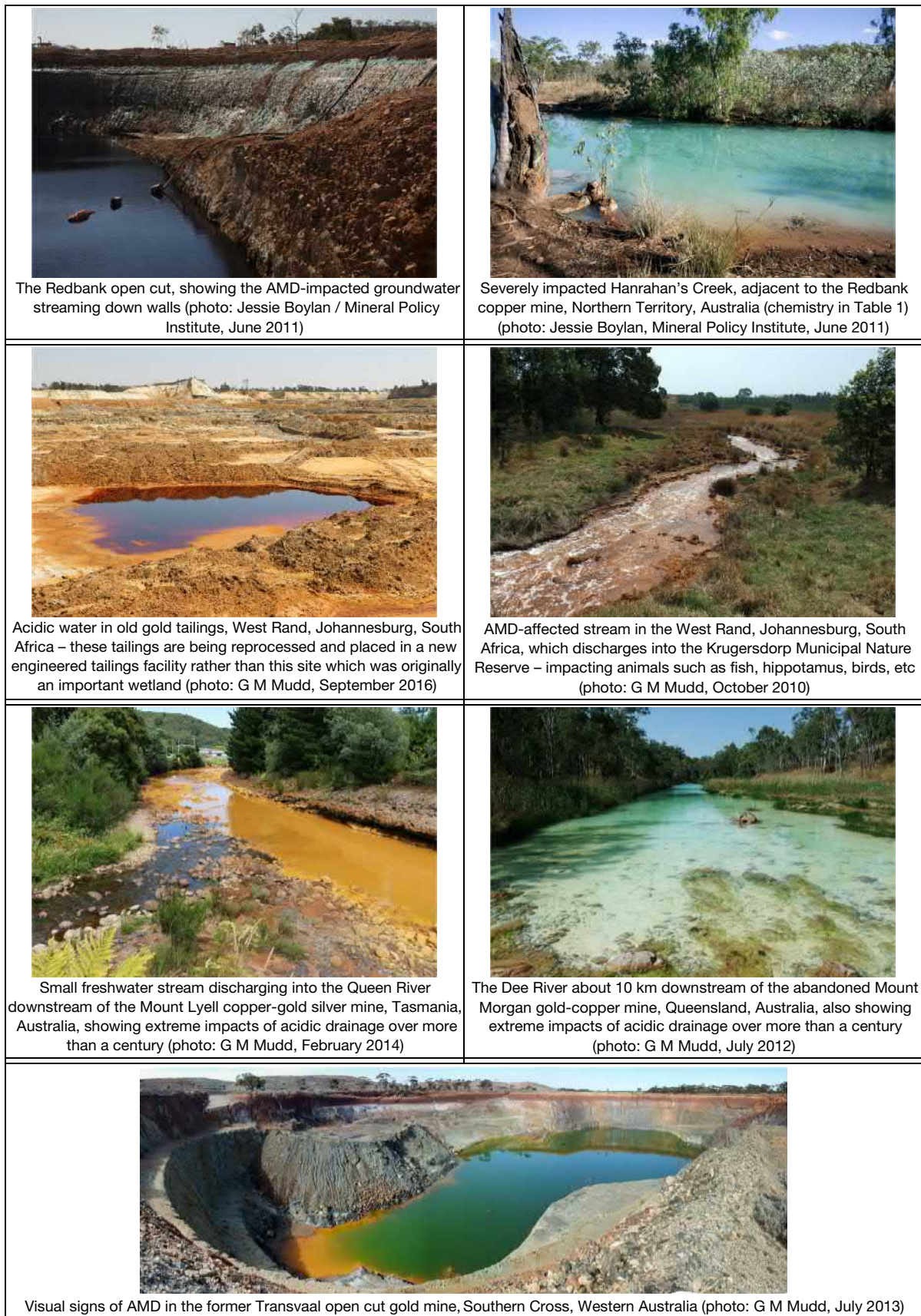


Fig. 2 Examples of acid and metalliferous drainage (AMD) impacts on water resources.

There are lots of site-specific factors to consider in assessing the risks of AMD generation, including particle and pore size of waste materials (e.g. coarse waste rock versus fine tailings), crystal and mineral structures (weaknesses increase oxidation), trace element substitution in sulfides (making it easier for oxidation), other mineralogy (especially other sulfides and alkaline minerals), temperature (hotter increases the oxidation rate), presence of microorganisms (especially acid- and heat-loving bacteria which thrive on iron oxidation, vastly speeding up sulfide oxidation rates), extent of oxygen and water availability (i.e. low availability limits the overall reaction progress), climate and hydrological seasons (e.g. wet/dry seasons), amongst others (see [Blowes et al., 2014](#); [Da Rosa et al., 1997](#); [Lottermoser, 2010](#); [Spitz and Trudinger, 2008](#); [Taylor and Pape, 2007](#)).

Across the world, there are many mines or regions which are now well recognized for their AMD-impacted catchments. An incomplete list includes the Witwatersrand gold and Mpumalanga coal fields of South Africa, the Tinto region of southern Spain (the namesake site for the Rio Tinto Ltd./Plc mining company), Mount Lyell, Mount Morgan and many others in Australia, the Sudbury Basin in Canada, Butte in Montana, USA, the Milluni Basin in Bolivia, amongst many, many others. Overall, there is (unfortunately) abundant field evidence to support the US EPA's statement of environmental risks from mine wastes—which largely revolve around AMD-related risks to water resources and aquatic ecosystems.

Water Management and Reporting in Mining

There have been a variety of approaches which have emerged since the late 1990s to facilitate reporting on the water aspects of mining—namely statutory environmental reporting or sustainability focussed reporting. While each approach has their merits, only the broad approaches are discussed here.

From about 1970 onwards, many countries around the world enacted legislation to protect the environment, led by the introduction of the National Environmental Policy Act 1969 in the United States which established the federal Environmental Protection Agency. In general, this limited the discharge of pollutants to the environment and allowed the establishment of standards for air, water and soil quality (especially for the remediation of formerly contaminated sites). From the 1980s to 1990s, this had evolved from licensing to monitoring and reporting on performance against environmental standards. That is, although a project may have an environmental permit for their discharges, they also needed to monitor the environment and ensure that their operations were not causing impacts which exceeded specific standards. This type of monitoring and reporting, typically done annually, has become known as statutory environmental reporting, and can be a very powerful mechanism to synthesize and publish monitoring data, especially over repeated years. For example, in the state of New South Wales, Australia, statutory environmental reports are required to be made publicly available for all mining projects by the company (e.g. their website). Over time, this allows evidence to be published about the actual impacts a mining project may or may not be having on the environment. Water resources remain a fundamental area of concern for such reporting (along with air quality, biodiversity, noise, mine waste, etc.).

In 1997, the Global Reporting Initiative (GRI) was developed to facilitate a more comprehensive reporting of the contribution to sustainable development by any type of organization as well as to give sustainability reporting the same profile and importance as statutory financial reporting. The GRI had metrics or indicators to report on various environmental, social, human rights, economic and financial aspects, evolving from the first “exposure draft” in 1999 through four formal editions to become a standard as of 2016. Although some global mining companies had pioneered the preparation of environmental progress-type reporting in the mid-1990s (which included energy, chemicals and water use and greenhouse gas emissions), following the 2002 United Nations Earth Summit in Johannesburg, South Africa, the global mining industry adopted the need for sustainability reporting—the basis of which quickly became the GRI. From large to small mining companies, GRI-based reporting is now becoming as prominent and common as financial reporting, helping to shine a light on the environmental, social and economic performance of mining companies.

Under the GRI, key aspects of water were reported, including water consumed, recycled water, water sources and discharges to water resources. Early water data reported for mines through GRI-based reports was highly variable and at times inconsistent (see [Mudd, 2008](#)), leading the Australian mining industry to develop the “Water Accounting Framework” (WAF) to facilitate standardized reporting that matched the GRI requirements ([SMI and MCA, 2012](#)). The WAF was recently extended to a global standard by the International Council on Mining and Metals (ICMM), ensuring global consistency on water data reported by the mining sector since ICMM members are required to implement such measures ([ICMM, 2017](#)). The example of detailed water reporting for the Diavik diamond mine in Canada is shown in [Fig. 3](#), highlighting the aspects reported and of concern to local indigenous communities.

Case Studies

Lady Annie Disaster, Australia

In early 2009, there was a very large environmental accident at the Lady Annie copper mine, about 200 km northwest of Mount Isa in western Queensland, Australia. The project was a new heap leach mine which used acid solutions passing through piles (or heaps) of copper ore to dissolve and extract the copper to be purified in a chemical refinery. Commercial operations started in October 2007, at the height of the mining boom. By late 2008, global metals prices had crashed, due to the evolving global financial

Water usage (m ³)*			
	2014	2015	2016
Fresh water used			
Fresh water for plant	428,018	404,206	369,534
Potable water	72,175	73,988	83,196
Dust management	50,494	47,512	69,622
Fresh water, other	0	50,826**	58,541***
Total	550,687	576,532	580,893
Underground dewatering			
	11,737,313	11,617,635	11,258,984
Effluent discharged to Lac de Gras			
Collection ponds to Lac de Gras (clean water)	0	0	0
North Inlet to Lac de Gras (water treated through north inlet water treatment plant)	11,438,537	11,903,811	13,832,886
Total	11,438,537	11,903,811	13,832,886
Recycled/reused water within plant			
Recycled processed kimberlite containment water	1,259,135	1,118,940	1,756,029
Recycled north inlet water**	1,190,855	1,124,851	670,884
Treated sewage effluent	70,945	71,261	81,632
Collection ponds to processed kimberlite containment (silty water)	201,558	288,817	310,136
Total	2,722,493	2,603,869	2,818,680

* 1 m³ = 1,000 litres ** drills *** drills and construction

Fig. 3 Example of detailed water reporting for the Diavik diamond mine, Canada (DDM, 2017).

crisis and the project became uneconomic, followed by bankruptcy placement for the operating company, CopperCo. Rainfall was high in the early months of 2009, leading to considerable local flooding onsite and eventually a structural failure of the solution ponds. Highly acidic and metal-rich solutions flowed into Saga and Inca Creeks, part of the headwaters for the Buckley River, one of the Lake Eyre Basin's major western river systems. At least 447 ML of mining waste water was accidentally released during two periods in early 2009, severely degrading water quality, biodiversity (killing fish in particular), pastoral grazing (including dissolving steel fences and cattle being put down) as well as recreational and indigenous values for the streams (Taylor and Little, 2013). The mining company was convicted of serious environmental harm and fined half a million dollars, with the additional responsibility of remediation and engineering costs of almost \$11 million. Although the mining company was explicitly alerted to this risk by the regulator before the accident, nothing was done to prevent it.

Cadia Valley Operations, Australia

The Cadia Valley Operations, just west of Sydney in central New South Wales, Australia, is a complex of three large gold-copper-silver mining projects and a central processing mill. The use of water and potential impacts on surface water and groundwater resources has always raised controversy since it began operations in August 1998. Newcrest Mining, the operator of Cadia, has been publishing the site's statutory environmental management reports for over a decade, and was an early pilot site for the WAF. The Cadia site has a comprehensive water management system, and includes surface water (licensed allocations), groundwater extraction from mine operations, treated effluent from nearby sewage treatment facilities as well as extensive recycling of water from the tailings dams. The extent of water from each source will vary each year depending on climatic conditions (e.g. drought), water needs and availability. The use of water in the processing mill is shown in Fig. 4, highlighting the seasonal variability (i.e. typically higher in summer months), the long-term very gradual increase in water use but also the difference in using monthly mill data (which effectively represents total water use) versus imported surface water (the dotted line). In May 2007, due to the decade-long severe drought across eastern Australia, the Cadia operations were almost forced to close due to lack of water security—with the rains in June 2007 breaking the drought.

Tailings Dams and Waste Rock Management

Tailings are the finely ground rock material remaining after the metals (or minerals) of interest have been extracted. Typically, tailings are pumped as a slurry to a storage dam, following similar engineering principles to water storage and hydroelectric dams. That is, a tailings dam has to be designed and engineered to address risks such as flooding (e.g. 1-in-100 or 1-in-1000 year storm events), seismic events (especially in some parts of the world), geology and geotechnical conditions (i.e. physical stability), seepage

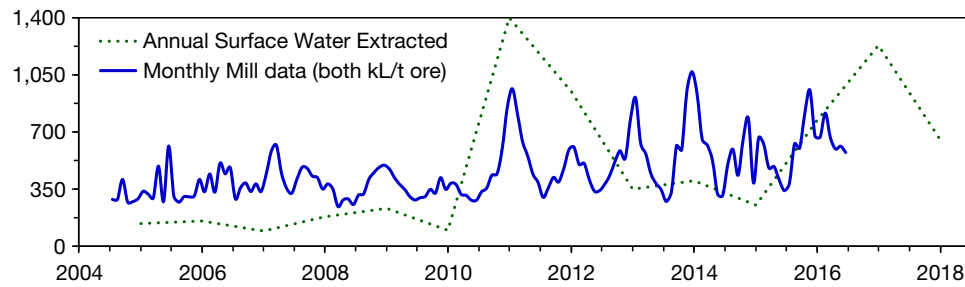


Fig. 4 Cadia water use per tonne of ore processed over time. Data from Newcrest Mining Ltd—Annual Environmental Management Reports (various years).

to groundwater and eventual closure and rehabilitation. In higher rainfall climates, tailings dams may need to incorporate a spillway to discharge excess waters and/or active water treatment (especially if reagents such as cyanide are used). A mine will typically build a tailings dam in stages, expanding the capacity as operations progress. Some tailings dams are now storing more than a billion tonnes already, meaning they can be truly giant facilities (as shown in Fig. 1 earlier). Waste rock is the material which has to be extracted to mine the metal-rich ores and is often multiples of the ore processed annually (see scale of waste rock areas in Fig. 1). The world currently produces at least eight and eighty billion tonnes of tailings and waste rock every year, respectively (author's estimates).

At a very select few sites around the world, tailings are allowed to be discharged into rivers or the marine environment—a practice which has largely been banned for many decades in most countries. At the Ok Tedi and Porgera (PNG) and Grasberg (Indonesia) mines, some 20, 6 and 60 million tonnes (Mt) of tailings, respectively, are discharged to rivers every year (plus a large fraction of about 40, 20 and 125 Mt./year of waste rock, respectively, either directly erodes or indirectly will erode also). The impacts of this practice are extreme, resulting in changed geomorphology and changed flooding regimes (especially on the floodplains downstream of the mines), significant impacts on the biodiversity as well as social impacts from the impacts on water resources. Alternatively, some mines deposit tailings directly into the marine environment (e.g. from 120 m depth) to avoid the impacts of riverine tailings disposal and costs and risks of engineered dams. At the Lihir mine (PNG), which sits on the edge of a remote and very small island, ~14 Mt./year tailings are now discharged to the deep sea while ~15 Mt./year of waste rock are emplaced in the shallow waters of Luise Harbour. At Batu Hijau, Indonesia, ~40 Mt./year of tailings are discharged to the deep sea. A small number of modest-scale mines in Norway and Turkey also practice marine disposal of tailings.

Unfortunately, there are many examples where tailings dams have failed and caused catastrophic disasters (e.g. environmental pollution, ecosystem damage, loss of life). The most high-profile examples are the two disasters in Brazil at the Samarco and Córrego do Feijão iron ore mines in 2014 and 2019, respectively, as well as the Mount Polley copper-gold mine in Canada in 2014. While the causes of each failure are always site-specific, common themes always emerge around poor site investigation, inappropriate engineering design, lack of risk assessment (especially consequence analysis) or deficient dam construction, operation and/or closure (often to save costs). Without doubt, all failures are absolutely preventable—but every tailings dam needs a comprehensive approach to all stages, from planning and design to construction and operation and eventually closure and rehabilitation (e.g. Franks et al., 2011). Recent disasters have highlighted the fundamental need for strong technical oversight, not just by mining companies and their consultants but especially government regulators.

Summary

Mining can be a large consumer of water and present significant and long-term risks to surface, marine and groundwater resources. Major pollution risks such as acidic and metalliferous drainage (AMD) have been observed for millennia, but it is only with the recent substantial growth in global mining that the scale has become so large that entire catchments may be affected. Modern mining is typically regulated by how much and what sources of water it can use as well as protecting water quality, with mines and companies adopting complex and varying water management approaches. The principal risks which need to be clearly identified for management include water depletion, groundwater and surface water interactions, water quality impacts but especially pollution risks from AMD which can continue for decades to centuries (or more in some cases). In addition, climate variability and the expected trends of climate change need to be factored into the water management system for a given mine and its environmental and social context. Finally, the digital age is facilitating public reporting and transparency around the ways that mines use water and may or may not impact water resources. This is crucial in modern, sustainable management of both mining and water resources as it helps to address community concerns and regulatory and investor or shareholder needs (especially in the context of ethical or responsible investment).

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Freshwater and Industries

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Abstract

Industries require large amounts of water which are used by various industries around the world at different rates and in different ways. Global water consumption has consistently been increasing since the 1980s and is expected to continue due to rising demands. Currently industrial water consumption is described as a major drain on the world's limited water supply and it is expected that the water demand will exceed current supply by 40% by 2030. The use of water for industrial processes as well as the discarding of wastewater can have various impacts if not properly managed and controlled. The continued increase of industrial water use accompanied by continued population and socio-economic growth will consequently exacerbate current effects of industrial water use and cause greater future challenges. Industries are a huge source of pollution around the world as they produce pollutants which can be very harmful to both the environment and the human population. Freshwater resources around the world are faced with significant pollution problems, some more than others. The expanding industrial base with accompanied pollution have placed additional pressure on existing water and often causes water resources to no longer be suitable for human consumption or other uses. Water is at increased risk worldwide and industrial sectors will have to implement various strategies to minimize this risk in the future.

Industrial Water Use

Industrial water use includes that used by economic entities such as mines, oil refineries, manufacturing plants, as well as energy installations using water for the cooling of power plants (WBCSD, 2006). It is mainly characterized by water being used in the production process (e.g. cooling purposes, cleaning/washing and employee use) and ultimately involves the manufacturing of a product. Water is vital in this sector as it helps machinery used in the production process to run efficiently and can also be a vital part of the product itself such as in the case of beverages. Industrial water is ultimately used for fabricating, processing, washing, diluting, cooling or transporting of a product. It is also used by smelting facilities, petroleum refineries, industries producing chemical products, food, paper and chemicals.

Industries require large amounts of water. Machinery requires cooling to a temperature which allows continuous manufacturing. The mining industry is also dependent on water in terms of washing of material brought up from underground to sort out the genuine product from the other particles. Water is also used for dust control as in the case of surface mining operations. Machinery and buildings are cleaned and in the case of the meat industry, water is used to process or trim animal carcasses.

Vast amounts of water are used in oil producing regions especially when oil wells are old and the underlying oil reserve has been tapped. Water is pumped down into the oil formation to push oil out. This industrial use of water has played a major role in this industry, without it oil and petroleum would be more scarce and expensive. Power generation also makes use of water through cooling equipment and to push turbines which forms the core of the electricity production process. Surface water resources are the most commonly used sources and much of the water is eventually returned to the environment for re-use. The pulp and paper industry also uses millions of liters of clean water especially in the papermaking process. Clean water is required to ensure that paper is smooth and that the machinery is not damaged by solid particles. Water may not play a key part in making the actual product in other industries however it is nevertheless required such as in the case of the steel making industry where water is used to cool equipment.

Water is therefore used by various industries around the world at different rates and in different ways. The following section will focus on the current and future observed trends of industrial water use in terms of consumption and withdrawal.

Current and Future Trends in Industrial Water Consumption and Withdrawal

Global water consumption has been increasing 1% per year since the 1980s and has been driven by a combination of continued population growth, socio-economic development as well as changing consumption patterns (Fig. 1). The global water demand is expected to continue to increase at a similar rate until 2050. An increase of 20–30% above the current level of water use is projected and is attributed to continuous rising demands in the industrial and domestic sectors (OECD, 2012; Burek et al., 2016; IEA, 2016). It is predicted that water use by the agricultural sector will likely fall in comparison with other sectors. However, it will remain the largest overall user in the coming decades in terms of both water withdrawal and consumption (WWAP, 2019).

Currently, industrial water use, which includes power generation, accounts for 20% of global water consumption and there are indications that this demand will rise. Although the industrial sector uses significantly less than the agricultural sector, the growth in water consumption has been rapid and global withdrawals quadrupled between 1950 and 1995 (Rosegrant et al., 2002; WWAP, 2019). Industrial water use is the second largest user of water globally and varies significantly from one type of industry to another. Water is used for energy in terms of hydro projects, cooling water for thermal power generation, process water, water for products and in some cases for waste disposal to name but a few. In the industrial sector, business is largely dependent on water, meaning that limiting water means limiting business (du Plessis, 2019).

Freshwater withdrawals have tripled over the past five decades with water demand increasing by 64 billion cubic meters per year. Currently industrial water consumption is described as a major drain on the world's limited water supply and it is expected that the water demand is expected to exceed current supply by 40% by 2030 (Schelmetic, 2012). The industrial era has mostly been characterized by water being viewed as a free and/or low-cost commodity. But, this perception is rapidly changing as communities across the globe are confronted by water supply limitations (Byers et al., 2010).

Industrial water use varies across the globe. Industrialized or developed nations are characterized by higher industrial water use, whereby they consume more than half of water available for human consumption. As much as 45% of water demand is generated by industries in advanced economies (Rosegrant et al., 2002). The percentage of industrial water use therefore varies significantly on a regional level according to the level of development (Fig. 2).

There is a current movement of more nations becoming more industrialized mainly attributed to global economic growth which is fuelling the expansion. Industrial water use will therefore grow much faster in developing countries than in developed countries and can have far reaching consequences. It is estimated that industrial water demand will increase to 121.7 cubic kilometers in 2025, seven cubic kilometers more than in the developed world. The intensity level of industrial water use is estimated to decrease on a global level as a result of improvements in water-saving technology and demand policy. However the absolute size of the increase in the world's production will still lead to a total increase in industrial water demand (Rosegrant et al., 2002).

The largest single use of water is for the cooling in thermal power generation. In terms of process water, the industry uses water to produce steam for direct drive power and for use in various production processes and chemical reactions. Other industries which use water for products include businesses like beverage and pharmaceutical sectors, consuming water by using it as an ingredient in finished products for human consumption (i.e., products delivered in liquid form). The term “virtual water” is consequently used to describe the water that is embedded in both agricultural and manufactured products as well as the water used in the growing or manufacturing process (WBCSD, 2006).

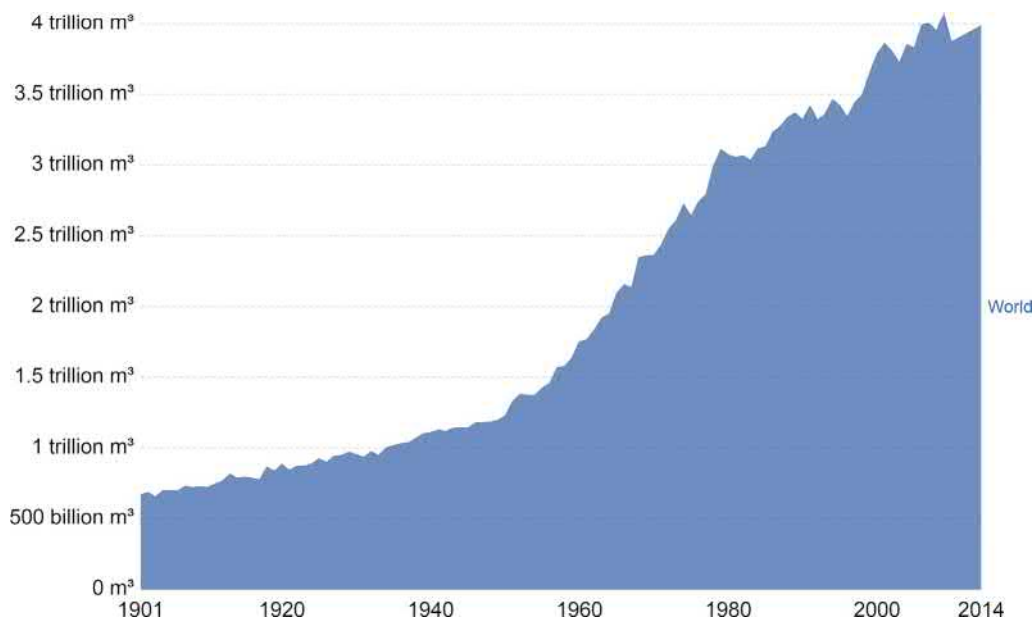


Fig. 1 Global water consumption since 1901 (Richie and Roser, 2019).

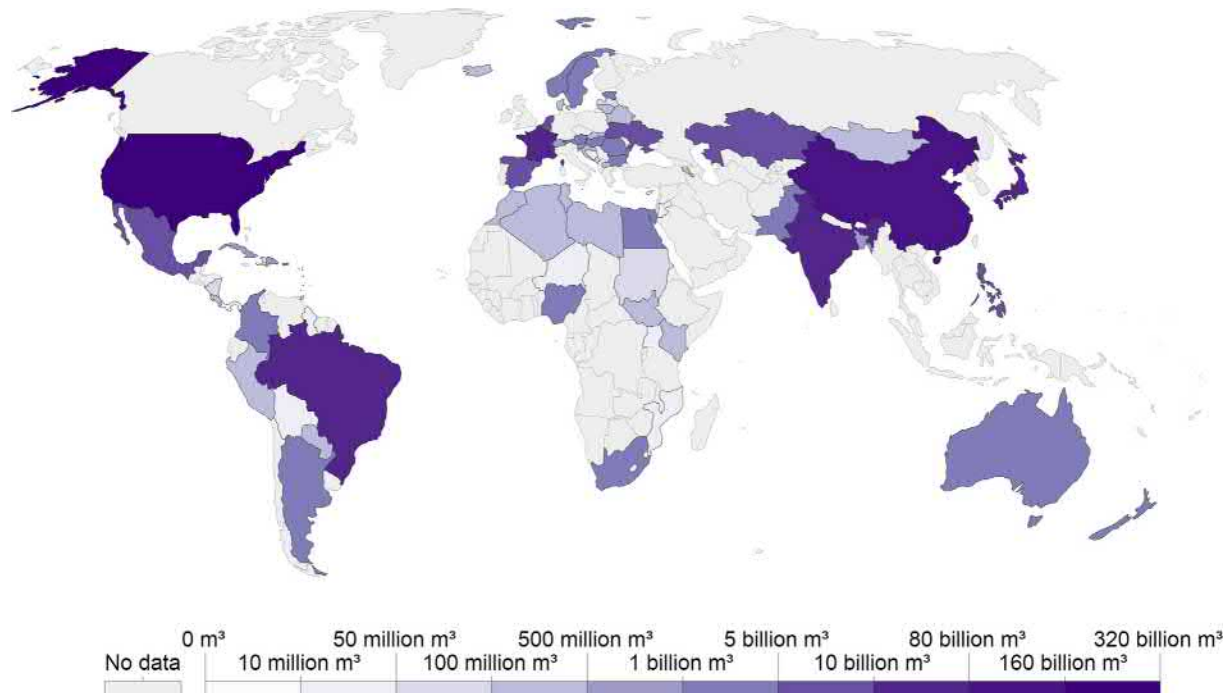


Fig. 2 Industrial water withdrawal for 2015 (Richie and Roser, 2019).

The overall demand for water is growing every day and surface as well as groundwater resources are facing more demand and in some instances, wells have become depleted. The world's population is estimated to reach 9.1 billion people by 2050 and with this growth comes a parallel rise in demand for clean water, food and energy. Water demand is already expected to exceed current supply by 40% by 2030 as indicated previously and many parts of the world are already facing increased water scarcity. The continuous increase in water demand together with climate change as well as current mismanagement of existing water resources in water intensive industries, especially agriculture, are exacerbating risk and unpredictability. The interlinked challenges have consequently also increased competition between communities and countries for scarce water and subsequently aggravated old security dilemmas, created new ones and in some instances hampered the achievement of fundamental human rights to food, water and sanitation (Manganello, 2019).

Industrial water usage is directly proportional to the average income level of its people. Industrial water withdrawals constitute 5% in low-income countries as opposed to the above 40% in some high-income countries. Furthermore, a number of countries in Asia are now also developing their economies around industrial development so that water usage in this sector will increase over subsequent years (Kibona et al., 2009; Lui et al., 2011). Industrial water use will, therefore, increase further across the globe, which may be accompanied with an increase of water-related risks such as increased competition for the resource as well as increased pollution if untreated wastewater is continually disposed of into surrounding water bodies.

The use of water for industrial processes as well as the discarding of wastewater can have various impacts if not properly managed and controlled. The additional increase of industrial water use accompanied by continued population and socio-economic growth will consequently exacerbate current negative effects of industrial water use and cause greater future challenges. Water is also used as a disposal site for wastewater into natural freshwater systems. Rivers and other water bodies can handle small quantities of waste broken down by nature, however, these limits are often exceeded and cause water quality to decline downstream causing it to be no longer useable without expensive treatment (du Plessis, 2019). The main contributing factors of industrial water pollution as well as the associated causes and effects follows.

Industrial Water Pollution: Contributing Factors, Causes and Effects

The start of the Industrial Revolution was accompanied by drastic changes in the social and economic lives of the world's population and the benefits of this are still experienced today. However, since the industrial revolution, industrial waste and pollution has become an increased major problem.

Industrial pollution can be described as different types of waste generated by various manufacturing or industrial processes. Industrial waste can be solid, liquid or gases held in containers. This waste can be toxic, ignitable, corrosive or reactive and if improperly managed, this waste can pose dangerous health and environmental consequences. The following sections will focus

on the contributing factors of industrial water pollution as well as the significant pollutants, causes and effects thereof on the human population and surrounding waterbodies.

Contributing Factors

Almost all of the water used in industries, ends up as industrial wastewater. Upon its release into the surrounding environment, it consequently creates a significant footprint and may be accompanied with various hazards (Ranade and Bhandari, 2014; O'Donnel, 2018). Chemical and allied process industries especially contribute to this negative water footprint. Industrial wastewater contains specific and readily identifiable chemical compounds. Water is mainly polluted by subsectors in the form of toxic wastes and organic compounds which can be largely traced to processing of industrial chemicals and to the food products industry.

Recent reports indicate that the total wastewater (combining sewage, industrial, and agricultural), being discharged globally is tens of millions of cubic meters per day (UN Water, 2008; Corcoran et al., 2010). It is believed that a very large portion of wastewater in developing countries is discharged untreated which have resulted in large-scale pollution of waterbodies and consequently endangering living species which include any surrounding population dependent on these water sources. It has been estimated that as much as 80–90% of all wastewater in developing countries is discharged directly into surface water bodies (UN Water, 2008; WWAP, 2009). Unfortunately, the discharge of untreated industrial wastewater is not limited only to developing countries but takes place in developed countries as well. The effects of industrial wastewater pollution can be vast and has been the cause of some of the most significant environmental disasters of all time. The main contributing factors of industrial pollution are extensive in nature however some of the major or top reasons include the following (Ranade and Bhandari, 2014; O'Donnel, 2018):

- *Unplanned Industrial Growth*—Established rules and regulations and standard practices are in some cases ignored by companies to facilitate rapid growth. Water and air pollution frequently occur due to unplanned developments.
- *Lack of Effective and Strict Policies/Enforcement thereof*—Numerous industries around the world have been able to disregard or bypass pollution laws as policies are either not valid or adequately enforced by relevant government departments or pollution control boards. This has resulted in significant pollution affecting both the environment and human populations.
- *The Large Number of Industries*—Since the industrial revolution the sheer number of industries and factories have increased significantly. Small sectors which rely on government for grants to enable them to keep operating, are often able to avoid adhering to environmental regulations. Most of these companies have been found to release significant amounts of toxic substances, increasing pollution to significant levels.
- *Use of Old and/or Outdated Technology*—New and updated technologies are often very expensive and there are numerous companies and factories which still rely on outdated technology to continue operating their business successfully. These old and outdated technologies often produce large amounts of waste.
- *Natural Resource Use*—A lot of industries make use of raw materials which requires the removal of these from underground. The process of removing raw materials is accompanied with the pollution of soil and may also be associated with oil leaks as well as spills which can be harmful to both the environment and the human population.
- *Improper Disposal of Waste*—The improper disposal of waste is the most common and significant form contributing to pollution. Most major industries should have treatment facilities for industrial effluents. Small-scale industries however in most cases cannot afford big investments in pollution control equipment as their profit margin is low.
- *Lack of Maintenance, Upkeeping and or Updating of Practices and Equipment*—In many instances, old equipment is continued to be used on a regular basis even though it may be faulty or not functioning properly. Equipment is not inspected on a regular basis and is left to fail or break which can then be accompanied by serious pollution events. An example of this was the Deepwater Horizon event. This happens regularly on a smaller scale in industries around the world.

The extent of industrial water pollution throughout the whole of Russia can be seen as a good example to illustrate the consequences of ineffective policies or regulations and a country driven by industry. Russia holds a quarter of the world's total freshwater supply and a large portion of this has been contaminated by industrial waste. It has been estimated that 35–60% of the total drinking water reserves do not meet sanitary standards and the industrial pollution now affects all corners of the country. Russia's Ministry of Natural Resources stated in 2017 that 74% of the country's population lives in environmental deterioration, and 40% of them consume water unhealthy to drink. Russia's Natural Resources Ministry has been charged by prosecutors of neglect as no environmental fines have been collected across the country. In 2016, an industrial company named Norilsk Nickel was fined a mere \$530 for contaminating an entire Siberian river with heavy metals. The Murmansk region located in the northwest of the country has suffered from widespread nuclear hazards and has been the dumping ground of ship skeletons. Currently, corporations do not have incentive to practice eco-friendly habits due to ineffective and unenforced fines and have consequently led to the country's rivers and lakes being flooded with waste runoff from factories. Russia has the means to enforce its own environmental regulations. However, its Natural Resource Ministry has neglected to collect on 132,075 instances of entire-river poisoning. The Russian federal budget has allocated US\$880,000 as a progressive move towards cleaning the unauthorized ship dumps out of Kola Bay. However, without proper enforcement of regulations, corporations will continue to abuse the environment and ignore eco-friendly habits or practices (Bramlett, 2018).

Both developing and developed nations are characterized by widespread industrial water pollution. The mentioned contributing factors all play a role at various intensities depending on the context. The description of significant pollutants, causes and effects of industrial water pollution now follows.

Significant Pollutants, Causes and Effects

Industries are a huge source of pollution around the world as they produce pollutants which can be very harmful to both the environment and the human population. Numerous industries use freshwater to transport waste away from the facility and into surrounding waterbodies, rivers and oceans. The significant pollutants from the mentioned industrial sources above include, but are not limited to, the following (Blacksmith Institute, 2007):

- *Lead and Mercury*: Metallic elements causing human health and environmental problems. They are nonbiodegradable and are very hard to remove from the environment once it is contaminated. They are harmful to both humans and animals. These pollutants are closely associated with mining, foundries and smelters, and other metal-based industrial operations.
- *Sulfur and Arsenic*: They are released most commonly by mining operations. Blasting and other mining processes expose surrounding waterbodies, especially groundwater, to high levels of these elements. Tailings dams which fail also causes mining wastewater containing these elements to spill into surrounding waterbodies.
- *Nitrates and Phosphates*: Increased fertilizer use have caused an increase of nitrates washed from soil into surrounding waterbodies. This causes eutrophication in both freshwater and marine environments which can be very problematic and is accompanied with serious environmental effects especially on aquatic species.
- *Oils and Petrochemicals*: Oil does not dissolve in water and forms a thick layer on the water's surface. Petrochemicals are formed from gas and petrol and can be toxic. Both of these pollutants are harmful and can be toxic to aquatic life.

The industrial activities which contribute the most to the degradation of freshwater sources, both surface and groundwater, include agriculture (fertilizer and pesticides); mining (blasting/extraction of materials and failure of tailings dams); fishing (regular use of boats releasing oil and petrochemicals); nuclear power plants (release of radioactive substances and thermal pollution); fuel industry (spills or leaks of petrochemicals); plastics (both production wastewater and dumping of plastics); textile manufacturing (production has a common by-product of asbestos); cleaning industries as well as commercial cleaning products (harsh chemicals and sewage and can also fall into this activity type); and lastly auto manufacturing (use of harsh chemicals and metals in production processes such as mercury and lead) (du Plessis, 2019). Most industries therefore have the potential to contribute to the degradation of waterbodies and ultimately cause damage to freshwater sources, the natural environment and human health.

Freshwater resources around the world are faced with significant pollution problems, some more than others. Water degradation in developed countries is mainly attributed to agriculture, industries, or factories as well as water pollution from fuel emissions especially in large metropolitan areas where human populations are growing at a constant pace. Developing countries, on the other hand, differ somewhat but the end result is relatively the same. The biggest culprit of water pollution in developing countries includes the lack of or inadequate waste management as well as primarily the lack of sewerage and septic systems (du Plessis, 2019).

Industrial water pollution has a dual effect as it has an impact both on the standard of living as well as the environment itself. The effects on the human population as well as aquatic communities are many and varied. The large amount of toxic materials which are released causes an overall reduction in human productivity but also affects biomass and diversity of communities of affected waterbodies. Human health is also affected. Drinking water is often negatively affected and can become a health hazard. The direct damage to aquatic environments also affect human health (Owa, 2013; du Plessis, 2019). Polluted water can become unsuitable for various uses especially in terms of drinking, recreation, agriculture, and industry.

The battle over industrial water pollution in Alabama, the United States of America (USA), can be used as a good example of how industrial water pollution can have widespread effects on both the environment as well as human health. Flint, Michigan is not the only city which has been experiencing severe issues related to safe drinking water in the USA. Other cities from Parkersburg, West Virginia, to Hoosick Falls, New York have also been experiencing this issue. Residents and a water authority in North Alabama are suing 3M, a maker of products from Scotchgard to Post-It Notes, in connection with chemical pollutants in the water supply. 3M has been manufacturing and discharging chemicals created to make non-stick surfaces into the Tennessee River for decades and the current pollution levels are three times what is considered safe by the Environmental Protection Agency. Residents have been experiencing a range of health issues, from cancer to high cholesterol due to long-term exposure (Douban, 2016).

Contaminated water therefore not only ultimately destroys aquatic life but creates short and long-term human health hazards which results in an overall decrease in productivity in all spheres. There are multiple sources of industrial water pollution however the end result is the same, namely the overall degradation of freshwater resources with varied effects on the environment and human health.

Current Challenges and Possible Risks, Solutions or Strategies

As highlighted in previous sections, the introduction of industrialization has been accompanied by various adverse effects especially in terms of water pollution. The expanding industrial base with accompanied pollution have placed additional pressure on existing water and often causes water resources to no longer be suitable for human consumption or other uses. Industries are therefore putting increased strain on the world's water resources in terms of increased demand as well as continued degradation.

The World Economic Forum has placed water crises third on the list of top world risks in terms of impact. It refers to the water crises as an interconnected world risk to other sectors. The intensity of the water crises is currently emphasized by approximately 36 countries around the world facing extreme levels of water stress. Water has also been consistently ranked as one of the top five risks

for seven consecutive years and the headlined threats to humanity and the planet over the next decade are all linked to water (World Economic Forum, 2017; World Resources Institute, 2017). Water is and will become an increased risk worldwide. The following sections will focus on the types of challenges and risks which industries currently face and may be exposed to in future as well as possible strategies which could be considered to manage or minimize these.

Current Challenges and Future Risks

The two major challenges which the world is facing are linked to consumption patterns. The supply of freshwater is already limited, however demand is consistently increasing and numerous countries are unable to meet basic water needs as well as provide sufficient quantities of water at an acceptable quality. Water shortages in terms of quantity is therefore already a serious challenge in many regions of the world. Some of the worst hit areas include, but are not limited to, southern Spain, the Maghreb, the Middle East, Central Asia, Pakistan, Southern India and Northern China (RobecoSAM, 2015). Water pollution exacerbates water scarcity around the globe even more as it limits the availability of clean water. As indicated previously, numerous countries are characterized by the dumping of non- or inadequately treated wastewater into waterbodies. Countries around the world are therefore increasingly faced with limited water availability as well as with the impacts associated with water degradation on human health as well as the environment. The global trends which primarily contribute to the current water challenges and which will continue to exacerbate these include continued growth in the global population, increasing urbanization, continued aging infrastructure and climate change.

The world's current population stands at an estimated 7.3 billion. Even though growth rates are expected to stabilize, the population will continue to increase over the next few decades. The world's population is expected to reach 9.6 billion by 2050 and the demand for water will consequently increase. However, the growth in population is not the only driver for an increase in water demand. The past couple of decades have shown that water consumption has grown faster than the population growth rate due to continuous improvement of living standards. This trend will most probably persist in future due to continuing increases in living standards especially in emerging markets (RobecoSAM, 2015; du Plessis, 2019).

Increased urbanization occurs concurrently with population growth. An increasing number of the world's population are leaving rural areas to live in cities. Rural–urban migration is usually driven by the real or perceived lack of employment opportunities in rural areas. It is estimated that 54% of the world's population currently live in urban areas and is forecasted to be 60% by 2030. Cities are growing in numbers but also in size, particularly in Asia, Africa and Latin America (RobecoSAM, 2015). The rapid growth in the amount as well as size of urban areas have consequently created an immense challenge for the water sector as the demand for water services have escalated exponentially. Major pressure has especially been placed on wastewater treatment and the challenge also extends to providing basic sanitation services, both of which require major investments.

Aging infrastructure in tandem with growing populations and urbanization has also become an increasing challenge especially in industrialized nations. In contrast to many developing nations which are still struggling to provide adequate access to safe drinking water, industrialized nations built most of their water infrastructure in the early 20th century. Most of these water supply and sewer systems have an average service life of 60–80 years and, in many cases, have reached the end of their lifespan. Additionally, water infrastructure has also not been properly maintained in some countries (RobecoSAM, 2015; du Plessis, 2019). Major investments in the repair and upgrade of aging infrastructure are therefore required in many areas to address this issue. The lack of improvement in this regard will consequently place additional pressure on water availability for all sectors as water of a suitable quality will decrease even further in quantity.

Climate change is also expected to have an increased and significant impact on water resources across the globe. It is anticipated that climate change-induced water scarcity and floods will intensify as concentrations of greenhouse gasses increase (IPCC, 2014). Climate change and increased climate variability is likely to vary at local and regional scales and over different seasons. The predominant trends indicate that dry areas will become drier and wet areas wetter and will most probably therefore exacerbate water stress in areas which are already the most affected (WWAP, 2019). Climate change in combination with the overexploitation and continued degradation of water resources is already affecting water supplies around the world and the effect will intensify if significant changes are not made.

Recently, many parts of the world are already feeling the “water crunch” to a great extent. Growing water stress across the globe results from substantial use of water resources with major impacts on resource sustainability and the rising potential of conflicts between water sectors. The world, as a whole, may not experience water scarcity. However, due to the uneven distribution of water across the globe, some parts of the world will experience more scarcity than others. The origin of water scarcity can be attributed to natural events such as reduced rainfall or climate variability. However, the human factor is the most critical as it consistently aggravates the problem through over-use, water wastage, continued pollution and/or inappropriate or flawed water management practices (du Plessis, 2019; WWAP, 2019).

Therefore, the core risk for the industrial sector is limited water supply in terms of availability and quality. Water plays a crucial role in industrial production such as paper, textile, electricity generation, mining operations, oil exploitation and pharmaceutical drugs. It was estimated in 2009 that industrial production consumed approximately 800 km³ and is projected to be 1500 km³ by 2030 (McGuire et al., 2009). Without water the industrial sector will not be able to continue production making increased water stress around the world a major challenge and risk.

The levels of physical water stress will ultimately increase in intensity and spread to other areas as populations and their demands grow and the effects of climate change intensify. Significant attempts should be made worldwide, especially in regions

already experiencing substantial water scarcity, to reduce water usage or demand as well as to treat wastewater to make it reusable or at least up to standard to discharge into the environment. It is also of importance to try and mitigate industrial impacts on water resources as well as the decline in water quality. Uncertain future conditions, especially in terms of unknown water inflows as well as diverse industrial activities, will require continuous innovative methods to support decision making especially in industrial water resources management systems. The following section will place focus on possible solutions or strategies which could be considered to lessen or reduce these challenges and risks.

Possible Solutions and/or Strategies

As highlighted in previous sections, water plays a vital role in numerous industrial processes from the extraction of natural resources in oil and gas or mining operations, to supplying the microelectronics and pharmaceutical sectors with ultrapure water. Water also needs to be adequately treated before it is discharged. The continued deterioration of water quality caused by industrial activities have emerged in many developing countries. This is of particular concern in India and China as the majority of industrial wastewater and effluents are discharged without adequate treatment into the surrounding environments posing serious threats to the population's health and the environment. The world is consequently faced by the dual challenges of water resource shortage and water quality degradation which will be further exacerbated by the continued increase in industrial water demands. The risk of water scarcity or decreased water supply is becoming more prominent across the globe.

The continual large gap between wastewater generated and the treatment thereof highlights the need for improved water management. Large investments are required to improve wastewater treatment especially in developing countries. The industrial wastewater treatment market has received increased attention as environmental regulations related to effluent discharge have become stricter. The declining availability of both surface and groundwater will require industries to look for alternative sources of water supply if they do not become self-sufficient through water recycling and reuse. The potential for water reuse and industrial wastewater treatment especially in the oil and gas industries, which is the fastest growing segment of the water market, has consequently become an attractive source of growth in terms of water technology companies (Ranade and Bhandari, 2014; RobecoSAM, 2015).

With the growing concern for the environment and increasing stricter government norms worldwide, it has now become necessary for industries to focus on increased pollution control. This includes adopting the most suitable technologies to treat their wastewaters and considering increased investment into wastewater treatment technologies to improve water use efficiency. This will ultimately reduce the risks of decreased water supply and possible conflicts with other water sectors such as agriculture. Some of the fastest growing areas in wastewater treatment technologies include the reverse osmosis and nanofiltration market. Ultrafiltration/microfiltration is also expected to grow while standard process equipment like aerators, screening and grit removal systems are likely to have low growth rates in the future. Zero-liquid discharge systems, including brine concentrators, crystallizers and evaporators are expected to have an above average growth rate due to the stricter regulatory restrictions related to effluent discharge (RobecoSAM, 2015; Wilkinson, 2017).

Industrial wastewater will have to undergo treatment to a suitable standard for discharge into surrounding waterbodies but will also need to be considered and highlighted as a useful and potential resource. Wastewater treatment, recycling, and reuse can have significant cost benefits mostly in the form of reduced water requirements. Process modifications can also substantially reduce the cost of wastewater treatment apart from a change of methodology for effluent treatment, land/space requirements, equipment costs, and legal binding legislation concerning pollution levels. Water efficient technologies therefore do not necessarily have to involve capital-intensive investments as existing systems and operations can be optimized. Full understanding through adequate monitoring and establishment of water use and disposal in the organization for each operation will be required. Buy-in from all sectors will also be necessary (Wilkinson, 2017).

A strong commitment at all levels will however be required from industry to government. Stricter and enforceable government regulations on pollution control and access to affordable and effective solutions are essential. Incentives in terms of economic tools and command as well as control tools will have to be created to support the creation of an enabling environment for water use optimization in the industrial sector. The creation of these incentives together with behavior changes can be difficult if results are not felt by the users. Awareness related to water efficient strategies and/or equipment among operators as well as the structuring of rewards can assist in changing current user behavior. For strategies related to water optimization and reduction of costs to be efficient in implementation, current water use and set global goals need to be assessed. The overall reduction of industrial water consumption can be seen as one means of reducing overall risk and addressing the global water crisis.

Conclusions

To be able to sustain the world's growing population, the world's economy will need to continue to grow. Water is critical for future growth and therefore can also be a major limiting factor for future growth. Water as a limiting factor has already become clear in businesses in water scarce regions which are facing risk. Investors are consequently increasingly considering water supply during their decision-making processes.

Industrial wastewater treatment especially in terms of recycling and reuse has become important themes in today's increasing water stress context. These measures are receiving increased attention, not just in an attempt to protect water resources from

continued degradation, but also to conserve water resources for water stress to be reduced or minimized. A number of technologies are available; however the selection will depend on the desired goals of wastewater treatment.

All water sectors, individuals and governments need to act as a collective to decrease water wastage and pollution, to reuse more industrial water, to increase effective management practices and become more water efficient. Higher water productivity levels can be achieved and water stress will ultimately be reduced. The continued evolution of technology and infrastructure improvements will hopefully enhance the world's overall water supply capacity and assist countries to deliver clean drinking water and sanitation services to both rural and urban populations. Political will however will be required on all fronts to promote future water efficiency to ultimately reduce the prominent risk of increased water stress and scarcity.

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Importance of Freshwater for Electric Power Generation

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Abstract

Global electric power generation relies heavily on water. Hydropower utilizes the potential and kinetic energy in running water and thermoelectric power plants, e.g. coal-fired, gas-fired and concentrated solar power, withdraw significant volumes of water for cooling purposes. Water is also used in various other stages of electric power generation's life cycle, such as coal mining, transportation, crop irrigation and so forth. Consequently, water shortages and rising water temperature can lead to curtailment of electric power generations. Climate change is expected to deteriorate water scarcities in some regions, which, compounded with rising water temperature, can exaggerate such electric power generation's water-related risks. Adopting air cooling systems, transforming the energy portfolio to gas, solar PV and wind, and utilizing alternative water sources, e.g. seawater and reclaimed water, can help reduce the electric power generation's reliance on freshwater resources in order to cope with future potential water-related risks.

Introduction

Modern human society runs on electricity (hereinafter referred to interchangeably with 'electric power' and 'power') that is consumed from agricultural and industrial productions to household consumption. It underpins humanity's development and prosperity. Higher electricity consumption level is correlated with higher human development and welfare indicators (Niu et al., 2013). Between 1990 and 2010, 1.7 billion people have gained access to electricity. Global electricity consumption has almost doubled from 11,894 TWh in 1990 to 21,481 TWh in 2010, and then 26,770 TWh in 2018 (IEA, 2019). It is worth noting that, in recent years, electricity consumption increased at an even faster rate than other energy products globally due to the proliferated electrification of various energy uses, e.g. air conditioning and electric vehicles. However, despite such impressive progress, 1 in 7 people living on this planet today still lacks access to electricity. The United Nations has proposed to ensure universal access to electricity by 2030 as a target of the 7th global Sustainable Development Goal (SDG) (United Nations, 2015).

There is a growing appreciation in the energy community that water is an important production factor for electricity generations. According to UN WWAP (United Nations World Water Assessment Program, 2014), about 90% of global electric power generation depends intensively on water. It is not difficult to understand that water is indispensable for hydro-electric power productions. In 2015, 150 countries had hydropower generations that made up 16.6% of the world's total electricity and 70% of all global renewable electricity. Apart from hydropower, many thermoelectric power plants, which provide over 80% of global electricity, require cooling water to cool and condense steam exiting the steam turbines and therefore withdraw significant volumes of water every year. Thermoelectric cooling is estimated to be responsible for around 43% and 50% of total fresh water withdrawals within the EU and the US, respectively (UN WWAP, 2014).

On the other hand, lack of water has been identified as one of the biggest risks facing humanity during the next decade (World Economic Forum, 2015). The fifth assessment report by the Intergovernmental Panel on Climate Change (IPCC) has anticipated that a changing climate is likely to change the spatio-temporal distributions of water resources by changing precipitation and evaporation patterns. Some already water-scarce regions may experience heightened drought risks, including increased drought periods and expansion of drought-affected areas, which will consequently amplify existing problems caused by water scarcity. UNESCO estimates that over half of the global population will face freshwater stress by 2025, and, by 2050, the number will increase to a worrying 75% (UN WWAP, 2003).

Water scarcity can have detrimental effects on the society and economy. Along with increased river water temperatures, water scarcity may lead to electricity production curtailments for instance. Numerous such incidents have been documented throughout the globe (McCall et al., 2016). For example, during the 2007 and 2012 droughts in western US, many thermal electric power

generators were exposed to water-related shut downs and curtailments, so were many nuclear electricity generators in France during the 2003 drought. Projections based on climate change modeling indicate reductions in usable capacity for 61–74% of the global hydropower and 81–86% for thermoelectric power from 2040 to 2069 depending on different climate change scenarios (Van Vliet et al., 2016). Overall, the water demand by the electric power sector is expected to increase with the growing economy and population, while climate change is expected to alter the spatiotemporal distributional pattern of water availability, e.g. low flows, thus reducing water security in some regions and raising freshwater for electricity generation as a global emergent challenge. Sadoff et al. (2015) have assessed the global water security and pointed out that China's water-scarce but relatively economically developed and densely populated north stands out as facing the highest water risk for its electricity generation.

Life-Cycle Water Use for Electric Power Generation

Water is required at different stages of the life cycle of electricity productions. Overall, the life cycle of electric power generation can be divided into three stages: upstream, power plant operation and downstream (Meldrum et al., 2013). Upstream stages include (1) fuel cycle, i.e. extraction, processing and transportation; (2) manufacturing of power plant components, e.g. steam turbines, wind turbines and solar PV panels; and (3) construction of power plants. Power plants operational water uses refer to on-site water usages that include water used for cooling, washing, and drinking etc. Downstream water uses primarily refer to water used in power plant decommissioning stage.

There are mainly two methods that can be used to quantify the life cycle water use for electricity productions: bottom-up process-based life cycle inventory analysis and top-down environmental-extended input-output analysis. With bottom-up life-cycle inventory analysis, (Mekonnen et al., 2015) estimated that 340 billion cubic meters (BCM) of water is consumed every year for the fuel extraction, power plant construction and power plant operation of global electric power generation's life cycle. Fthenakis and Kim (2010) estimated water intensities of both conventional and renewable electric power plants' life cycle in the U.S. based on data from the existing literature. They pointed out that, uranium enrichment, especially by gaseous diffusion, requires the largest share of nuclear power plants' upstream water usage. According to the US Department of Energy (1983), underground coal mining requires more water than surface mining for dust control inside the coal mines, which accounts for about 70% of the total on-site mining water use, while the rest is used for coal washing. Moreover, underground mining also requires more upstream water use than surface mining because of the extensive use of mine equipment that requires water inputs in their manufacturing stages. There are substantial variations in the exact values of water uses, depending on sources of the data, and conditions, such as heating value and seam thickness of the fuel (Fthenakis and Kim, 2010). Regarding renewable energies, water usages during the upstream stages are mainly related to device manufacturing and power plants construction, except for the biomass whose fuel cycle requires large amounts of water for irrigation. Grubert et al. (2012) found that replacing coal-fired power plants with natural gas combined cycle plants (NGCC) can reduce Texas coal power's water footprint by 60%, 0.2 BCM per year. Meldrum et al. (2013) broadened the study scope by including power plant decommissioning and harmonized literature estimates and concluded that (1) thermoelectric power productions are more water intensive than PV and Wind; and (2) Operational phase dominates electric power production's life-cycle water uses. The study of Feng et al. (2014) in China using hybrid Life-Cycle and Input-Output analysis also came to a similar conclusion, except they also included biomass and found that life-cycle water consumption of biomass tops the list, of which crop production accounts for 95%.

Another stream of scholarly work has used the Environmental-Extended Input-Output method to quantify the life cycle water uses for electric power production. Wan et al. (2016) found that Intended Nationally Determined Contributions (INDC) will lead to more life-cycle water consumption for the electric power sector in China, India and Russia because their renewable energy development requires substantial upstream water inputs. Chai et al. (2018) calculated that coal-fired power generation in China withdraws and consumes 35.46 and 17.67 m³, respectively, per MWh of electricity generated throughout the life cycle.

Operational Water Use for Electric Power Generation

Hydro-Electricity

Water carries a huge amount of energy that can be transformed into electricity. There are four types of technologies utilizing energy in water to generate electricity:

- (1) *Storage Hydropower Stations*: Storage hydro-electricity is generated from the potential energy of dammed water that is released in operation to drive a water turbine and generator;
- (2) *Run-of-the-River Hydropower Stations*: Some hydropower stations have small or no reservoir capacity are called Run-of-the-River hydroelectric stations so that only the water coming from upstream can be used for generation at that moment;
- (3) *Pumped storage hydropower stations* use excess electricity when electricity demand is low to pump water to higher reservoirs and release water when electricity demand is high;
- (4) *Offshore hydropower stations*: a less established group of technologies that are gaining market share generating electricity from seawater, which includes wave electricity that captures energy from ocean surface waves and tidal electricity that uses turbines to capture tides energy in the coastal areas.

Except offshore hydropower stations, hydroelectricity depends almost entirely on freshwater resources on earth. The power extracted from the water depends on the volume and the difference in height between the source and the water's outflow. This height difference is called the head. The capacity of hydro-electric plants can be calculated based on the equation below:

$$P = m \times g \times H_{\text{net}} \times \eta$$

where: P is power (Watts); m denotes water flow rate (kg s^{-1}); g refers to the gravitational constant, which is 9.81 m s^{-2} ; H_{net} is the net head and η is the product of efficiencies of all different components, including the turbine, drive system and generator. Net head is calculated as the gross head that can be measured at the site deducting any head losses, which is normally assumed to be 10%.

According to the [International Hydropower Association \(2018\)](#), an unprecedented amount of electricity, 4185 TWh, was generated from hydropower in 2017. Global hydropower capacity has reached 1267 GW, including 153 GW of pumped storage. The regional distribution of installed hydropower capacity is demonstrated in [Fig. 1](#).

It can be seen from [Fig. 1](#) that the largest amount of hydropower capacity is installed in the East Asian region. In 2017, 21.9 GW of new capacity was added globally and China, the world's largest hydropower producer, accounted for nearly half of the newly added capacity, at 9.1 GW. It was followed by 3.4 GW in Brazil, 1.9 GW in India, 1.1 GW in Portugal and 1.0 GW in Angola. [Fig. 2](#) demonstrates the countries with the largest hydropower productions whose national electricity productions are therefore highly dependent on freshwater resources.

Not only much less constrained by intermittence issues than other renewable energies, such as solar and wind, hydropower is also a much more flexible electricity source compared to conventional thermal electric power plants. Hydropower stations can be ramped up and down very quickly, normally around a few minutes, to adapt to different levels of electricity demands ([Robert, 2010](#)). Moreover, power generation at hydropower plants does not generate any greenhouse gases at the operational stage. Hence hydroelectricity is widely regarded as an ideal alternative to conventional fuel-combustion thermal power plants despite its various controversial social, environmental and ecological impacts. Global hydropower production is expected to continue growing against the backdrop of continuing economic development and climate change mitigation ([International Hydropower Association, 2018](#)). Human society's electric power generation's reliance on fresh water running in river systems is expected to elevate accordingly.

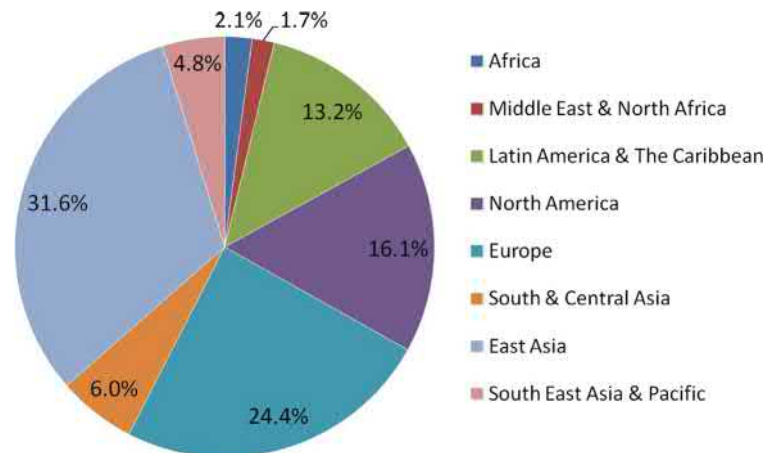


Fig. 1 Regional distribution of global installed hydropower capacity. Data source International Hydropower Association (2018). 2018 Hydropower Status Report. London, UK.

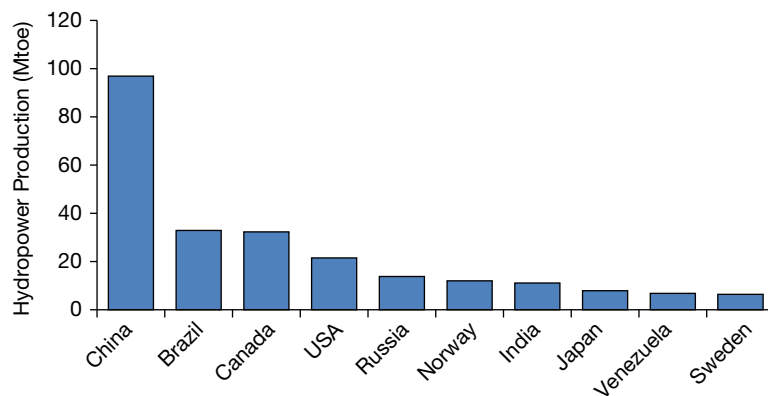


Fig. 2 Top countries with the largest hydropower productions. Data source: World Energy Council (2018). Data. London, UK.

Thermoelectricity

Coal-fired power plant

The largest share (40%) of global electricity is produced from coal. Water is often extensively used in coal-fired power plants as well. The water-using processes in a typical coal-fired power plant can be categorized as below:

- (1) *Industrial water use*: such as lime-ash removal and wet desulfurization, as well as cooling of the steam that drives the turbine and other auxiliary engines (including induced air fan, forced draft fan, primary air fan, and so forth). Cooling systems are needed to dissipate the residual heat of the steam exiting the turbine and water is often used as the medium. Cooling water constitutes the biggest part of thermoelectric power plants water uses.
- (2) *Domestic water use*: power plants workers require water to drink and for other domestic uses.
- (3) *Chemical water use*: Due to salinity enrichment, boilers need to be regularly emptied and replenished with demineralized water of the highest quality.

The abovementioned water flows and related energy flows are illustrated as in Fig. 3 below.

The amount of cooling water used depends largely on the cooling system employed. Water use may refer to both water withdrawal and water consumption. Water consumption is defined as water withdrawn from the environment but not discharged back into any water bodies. There are three types of cooling systems being used: open-loop and closed-loop wet cooling, and air-cooling:

Open-loop cooling systems, also called once-through, withdraw the largest amount of water but more than 99% is returned to the water source;

Closed-loop, or recirculated cooling, withdraws significantly less water; however a larger proportion is consumed due to evaporation, either in cooling ponds or cooling towers;

Air-cooling systems, also called dry cooling, have the lowest water consumption and withdrawal intensities as they do not need any water for cooling purposes. However, water is still required for other on-site uses, e.g. cleaning. Moreover, reducing water use by deploying air cooling systems comes at a price. As air cooling systems have lower cooling efficiencies, the steam leaving the turbine has a higher temperature, which creates a back pressure. As a result, power plants with air cooling systems face 5%–10% of thermal efficiency losses (Electric Power Research Institute, 2004).

Cooling technology affects the water consumption factors in two ways: first, nearly 100% of water abstracted by closed-loop cooling system evaporates during the cooling circles while only 3% of water withdrawal of open-loop system is consumed. Therefore, when compared to closed-loop cooling system, consumptive water use in an open-loop system is 70–80% lower than in a closed-loop system, but water withdrawal is 30–60 times higher (World Resource Institute, 2015). Secondly, since cooling systems marginally impact the plant's efficiency, power plants with an open-loop cooling system consume less water in other processes due to their higher efficiency. Due to the large share of ancillary water uses, air cooling systems' water consumption is on par with that of open-loop cooling systems.

Water consumption compositions of a typical coal-fired power plant equipped with open-loop cooling systems and closed-loop cooling systems are demonstrated in Tables 1 and 2 respectively (East China Electric Power Design Institute, 2012). It can be seen that 80% of water consumption in a power plant equipped with closed-loop cooling systems is used for cooling purposes.

Since water is used to dissipate any residual heat, improving boiler technology increases conversion efficiency and decreases residual heat and therefore lowers water requirements. Moreover, more water is needed if the intake water temperature is higher, for instance, during summer times, which is expected to happen under climate change together with drought situations and pose threat on coal-fired power plants water supplies.

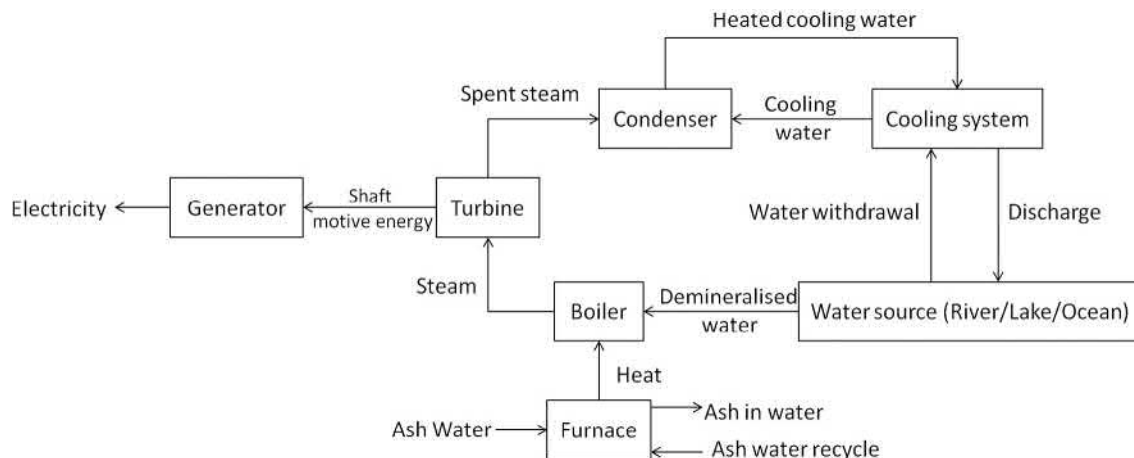


Fig. 3 Water and energy flows in a coal-fired power plant (Liao, 2018).

Table 1 Designed water consumption factor of power plants with open-loop cooling system of different capacities.

Capacity (MW)	Wet desulfurization (without GGH, m ³ /h)	Dry ash/lime-ash removal (m ³ /h)	Coal transport (m ³ /h)	Boiler make-up (m ³ /h)	Domestic water use (m ³ /h)	Total (m ³ /h)	m ³ /MWh
2 × 300	100–110	109–195	46–83	80–150	5–10	340–548	0.567–0.913
2 × 600	190–230	155–247	60–107	90–170	5–10	500–764	0.416–0.637
2 × 1000	270–320	265–380	77–146	150–270	5–12	767–1128	0.384–0.564

Source East China Electric Power Design Institute (2012). Investigation on designed water withdrawal and water consumption statistics of Shanghai's big thermal power plants. (Internal materials). Shanghai, China.

Table 2 Designed water consumption factor of power plants with closed-loop cooling system of different capacities.

Capacity (MW)	Wet desulfurization (without GGH, m ³ /h)	Dry ash/lime-ash removal (m ³ /h)	Coal transport (m ³ /h)	Boiler make up (m ³ /h)	Domestic water use (m ³ /h)	Cooling tower make-up (m ³ /h)	Total (m ³ /h)	m ³ /MWh
2 × 600	190–230	155–247	60–107	90–170	5–10	2092–2692	2592–3456	2.16–2.88

Source East China Electric Power Design Institute (2012). Investigation on designed water withdrawal and water consumption statistics of Shanghai's big thermal power plants. (Internal materials). Shanghai, China.

Natural gas electric power plants

There are primarily three types of natural gas-fired electric power plants: natural gas combined-cycle (NGCC) power plants, gas combustion turbines and gas-fired steam turbines. While gas turbines are directly driven by hot combustion gases, an NGCC plant first uses a gas combustion turbine to generate electricity and then uses the waste heat to create steam to generate more electricity in a steam turbine. Because gas combustion turbines require no cooling because there is no steam to be condensed, the overall combined cycle system requires much less water for cooling than traditional steam turbine technologies. According to Macknick et al. (2012), water use values (median) of a natural gas-fired power plants are as below in Table 3.

According to the US Energy Information Administration (2012), more than 80% of natural gas-fired power plants in the US are NGCC plants. Gas turbine and steam turbine power plants occupy 9% each. Utilizing natural gas is an effective way to reduce electric generation's reliance on freshwater resources at the operational stage.

Concentrated solar power (CSP) plants

CSP requires larger amounts of water at the operational stage compared to other commonly used renewable energies, i.e. Solar PV and Wind. Both CSP and solar PV require water to clean the mirrors and panels as dust can reduce the system efficiency. Water intensity for mirror and panel washing ranges from 0.08 to 0.15 m³ MWh⁻¹ (Bracken et al., 2015). Such variation depends on the frequency of cleaning which is decided by the site conditions, such as soil and dust properties, vegetation, air pollution, wind speed and direction, humidity, and temperature as well as precipitation characteristics, i.e. intensity, frequency, and duration. Other factors such as panel/mirrors orientation and angle of tilt, glazing properties also have impacts on the cleaning frequency (Sarver et al., 2013).

Apart from cleaning needs, the thermal cycle of Parabolic trough, linear Fresnel, and power tower CSP technologies are essentially the same as those used in coal and nuclear power plants and therefore require water for cooling purposes as well as boiler make-up as in a coal-fired power plant.

Dish systems do not generally require water for cooling, nor for steam cycle operations, but do require a small amount to wash the concentrators.

Macknick et al. (2012) conducted a review study on electric power plants in the US and consolidated the values of water withdrawal and consumption of different generating technologies and energy sources as displayed in Fig. 4.

Generally speaking, to generate a certain amount of electricity, gas-fired power represents the lower end of water usage while nuclear power presents the opposite.

Table 3 Water use at natural gas-fired power plants.

	Once-through		Closed-loop		Air cooling	
	Withdrawal	Consumption	Withdrawal	Consumption	Withdrawal	Consumption
NGCC	11,380	100	253	198	2	2
Steam	35,000	240	1203	826	2	2

Data source: Macknick, J., Newmark, R., Heath, G. & Hallett, K. C. (2012). Operational water consumption and withdrawal factors for electricity generating technologies: A review of existing literature. *Environmental Research Letters* 7: 045802.

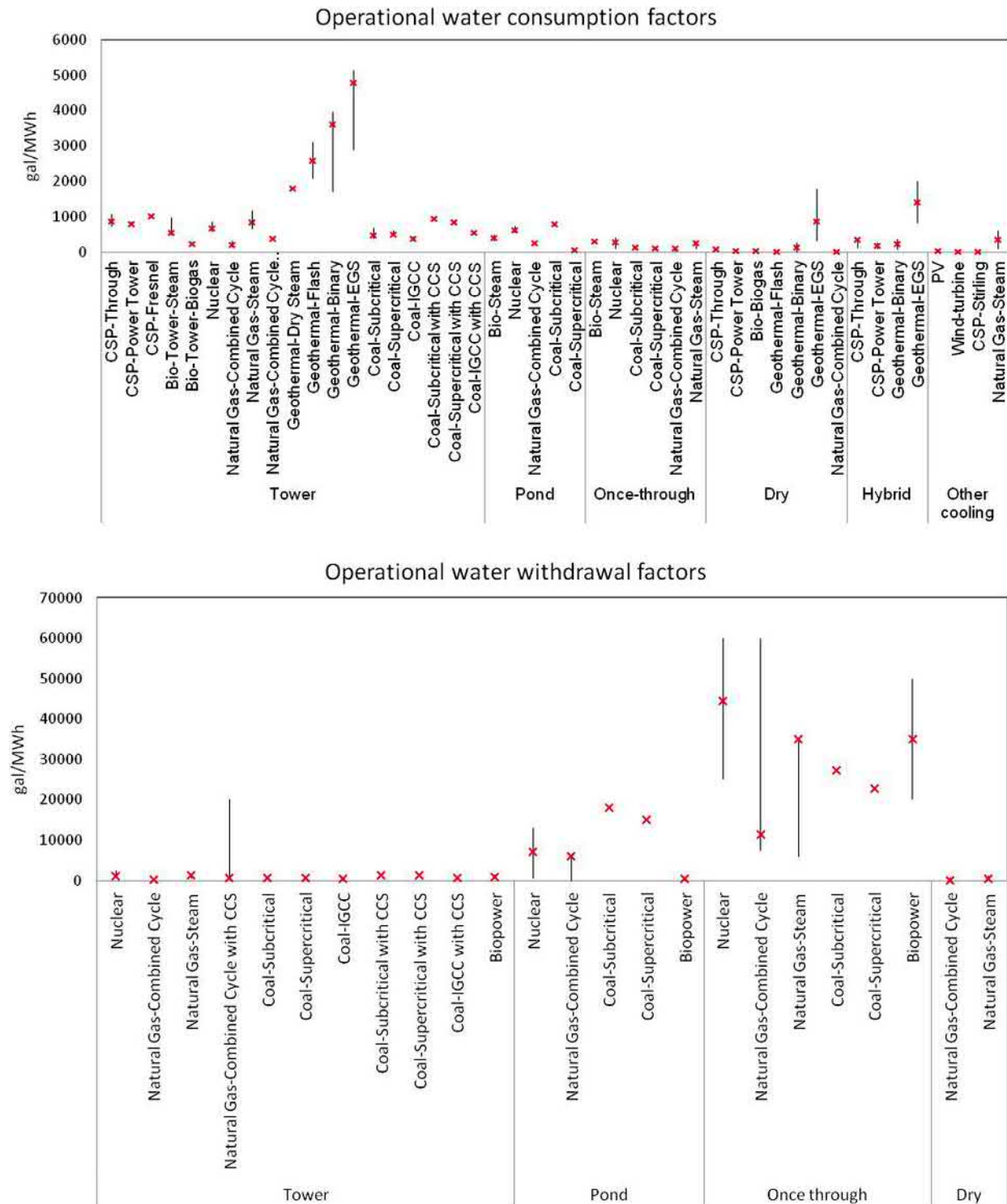


Fig. 4 Operational water consumption and withdrawal factors for different types of electric power productions. (Note: IGCC: Integrated gasification combined cycle; CCS: Carbon capture and sequestration; CSP: Concentrated solar power. Upper and lower ends represent maxima and minima, respectively; Red Cross represents median values). Data source: Macknick, J., Newmark, R., Heath, G. & Hallett, K. C. (2012). Operational water consumption and withdrawal factors for electricity generating technologies: A review of existing literature. *Environmental Research Letters* 7: 045802.

Water-Related Risks for Electric Power Generation

Electric power generation has been exposed to water-related risks worldwide, which has raised concerns in the global energy community in meeting the SDG7 providing universal access to reliable electricity. Water-related issues can affect electric power generation in several ways:

- (1) *Life cycle supply chain disruption*: Water-related natural hazards, e.g. flood, storm, drought, can disrupt the life cycle supply chain of electric power generation, e.g. bio-mass cultivation, coal transportation;
- (2) *Insufficient river discharge for hydropower production*: hydropower production capacity depends on the volume of water flowing in the river. Reduced river discharge can directly affect power plants capacity. It is projected that, due to reduced river flows brought by future climate change, 61–74% of global hydropower capacity may be compromised (Van Vliet et al., 2016);
- (3) *Insufficient river flows for thermoelectric cooling*: Low river discharge may fail to meet power plants water withdrawal requirement. For example, Byers et al. (2016) projected that, with Carbon Capture and Storage (CCS) development, water available in UK's river Trent is likely to fall short of cooling water demand for the basin's electricity generation by the 2030s–2040s; Tarroja et al. (2018) pointed out that water availability can also limit the development of thermally based renewable energies, e.g. geothermal and CSP, in water-stressed regions;
- (4) *High river water temperature for thermoelectric cooling*: Increased water temperature can reduce thermoelectric power plants' usable capacity due to legal thresholds for heat discharges (Van Vliet et al., 2012). The usable capacity of global thermoelectric power plants is projected to be reduced by 81–86% during 2040–2069 due to a compounded effect of changed water availability and increased water temperature (Van Vliet et al., 2016);
- (5) *Flood hazards on power infrastructures*: Flood hazards can generate damaging effects on power infrastructures in general. Flood hazards can lead to electricity brownout or blackout for various periods of time.

The situation is expected to worsen under a changing climate. The number of extreme weather events and natural hazards, e.g. flood, storm and drought, is likely to increase (IPCC, 2013). Air temperature and water temperature are expected to rise in hot summer days, which can reduce the cooling efficiency for thermoelectric power plants. On the other hand, human society is expected to have a higher demand for electricity for air conditioning and so forth.

Reducing Electric Power Generation's Reliance on Freshwater

Against the aforementioned backdrop, it is of vital importance to decouple the electric power sector with its freshwater requirements and thus lower the potential water risks for electric power generation. Liao and Hall (2018) have investigated the historical water use in China's electric power sector and concluded that transforming the energy structure to renewable energies and utilizing low-water technologies have contributed to reducing China's electric power sector's reliance on freshwater resources. Several ways for the electric power sector to adapt to future potential freshwater constraints are listed as below:

- (1) *Develop renewable energies that have lower water use intensities*, such as solar PV and wind power. Solar PV and wind power have the lowest operational water use intensities among all renewable energies. However, thermally based renewable energies, such as geothermal and CSP, should be developed cautiously based on water-sensitive planning;
- (2) *Develop gas-fired power as base load*: due to renewable energies intermittence issues and limited electricity storage, conventional fuel-based electric power production is still expected to dominate the energy portfolio to ensure electricity reliability. Compared to coal-fired power plants, gas-fired power plants not only have lower greenhouse gas emissions, but also significantly lower water dependencies. Developing gas-fired power production can have co-benefit of higher resiliency to water-related risks;
- (3) *Utilize alternative water supply systems*: limited by freshwater supplies, the electric power sector should make more use of alternative water sources, such as seawater, groundwater and reclaimed water etc. Developing electric power plants using seawater, such as tidal power and wave power, as well as coastal thermoelectric power plants that use seawater for cooling are all effective solutions to cope with potential freshwater shortages. In inland areas, utilizing groundwater and reclaimed water from industrial and municipal wastewater can also reduce the electric power sector's reliance on freshwater resources. Take China's dry north as an example, 30% and 15% of the region's thermal electric power sector's water use comes from groundwater and reclaimed water respectively (Liao et al., 2016). However, groundwater over-exploitation and reclaimed water's heavy energy use need to be taken into consideration in developing utilization plans for these alternative water sources;
- (4) *Adopt air cooling systems*: Since air cooling systems cool down the steam exiting the turbine using air and thus avoiding any water use for cooling purposes, retrofitting existing power plants with air cooling systems can significantly decrease the electric power sector's reliance on freshwater supplies. However, apart from the energy efficiency penalty mentioned above, capital cost of power plants with dry cooling systems is also much higher, can be at around 2.5 times of that of plants with wet cooling systems (Zhai and Rubin, 2010);
- (5) *Trade-off between open-loop cooling and closed-loop cooling*: It is worth mentioning that the trade-off between water consumption and withdrawal needs to be considered when choosing between open-loop cooling and closed-loop cooling systems. Open-loop cooling systems require a larger amount of water withdrawal and thus higher reliance on water supplies. However, most of the water withdrawn by open-loop cooling systems is returned back to the rivers and thus having lower water

consumption and impacts than closed-loop cooling systems. Water-sensitive plans should be made before any new power plant is proposed, planned and constructed incorporating future climate change in order to develop electric power generation that is resilient to any potential water-related risks.

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Freshwater: The Importance of Freshwater for Providing Ecosystem Services

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Abstract

Freshwater ecosystems, whether surface, groundwater or in the form of ice caps are fundamental for human life and for supporting the vast biodiversity, natural processes and cycling. They provide ecosystem services, thus, benefits for humans and their societies obtained from nature, in all four categories: provisioning, regulating, cultural and supporting. The importance of sustaining ecosystem integrity via protecting the ecosystem services, is undeniable. However, it comprises a big challenge provided the human-induced degradation of the natural environment that, in turn, affects the earth's natural capital: natural resources, associated services with the supporting processes.

Introduction

Freshwater ecosystems, whether surface, that is rivers, lakes, streams and wetlands, groundwater or in the form of ice caps are fundamental for human life and for supporting the vast biodiversity, natural processes and cycling. They provide ecosystem services, thus, benefits for humans and their societies obtained from nature, in all four categories: provisioning, regulating, cultural and supporting. The importance of sustaining ecosystem integrity via protecting the ecosystem services, is undeniable. However, it comprises a big challenge provided the human-induced degradation of the natural environment that, in turn, affects the earth's natural capital: natural resources, associated services with the supporting processes.

This article extensively presents the functionality of freshwater ecosystems that is inseparably linked to the ecosystem services provided by freshwater bodies and their importance for human and nature well-being. The ecosystem services provided by freshwater are of vital importance for supporting all life cycles, social processes and economic prosperity.

Fresh Water Bodies: Rivers & Streams, Wetlands and Ponds, Groundwater, Ice-Caps

Freshwater ecosystems, comprise only 2.5% of water on the planet, with most of it (68.7%) and (30.1%) being captured in ice caps and as groundwater, respectively. Most of the remaining 1.2% freshwater has the form of ground ice and permafrost (69.0%), 3% of it has the form of atmospheric moisture, while readily available surface water bodies, which comprise precious and critically important water resources add up to only 0.29%. A total of less than 0.01% of the Earth's freshwater is found in lakes, wetlands, swamps, and rivers (Shikomanov, 1996; Brown et al., 2014). The biggest freshwater abundance is found in the Americas (45% of total freshwater resources); Asia has significantly smaller freshwater system (28%), Europe has 16% and Africa just 9%. The small freshwater amounts and the unequal distribution of freshwater resources result in 45 countries to have been listed as "water scarce countries,"

in which water availability is at the maximum level of 500m³/inhabitant, and 44 countries to depend on other countries for more than 50% of their water use (Brown et al., 2014).

Life and people heavily depend on all types of freshwater. The importance of freshwater as an element of life, providing this unique service to the planet, is proven by and attributed to the unique properties of water due to hydrogen bonds in the water molecule which support cell and body structures and functions, such as water being liquid over large temperature range; slow changes in temperature; it has a high boiling point of 100 °C and a low freezing point 0 °C; it presents adhesion, cohesion and surface tension; it expands as it freezes; it is a good solvent and filters out harmful UV radiation. Freshwater bodies, therefore, directly support species, human survival and quality of life. They provide services linked to numerous life services through the support of biodiversity, the hydrological elements and processes, such as natural irrigation services through precipitation and climate regulation, as well as economic services such as water for industrial production, commercial uses and agriculture, with 86% of global water use being used in agriculture and processing of agricultural goods.

Surface Water Bodies: Rivers and Streams, Lakes, Ponds and Wetlands

Surface water bodies, although comprise a small portion of freshwater they form the most direct water resource due to its easiness in accessibility. Lakes host a volume of water of $0.125 \times 10^6 \text{ km}^3$ that is less than 0.01% of the total water volume on Earth, while rivers account for the tiny amount of $0.0017 \times 10^6 \text{ km}^3$, that is $0.0001 \times 10^6 \text{ km}^3$ of the total. The largest freshwater lakes such as Lake Superior (Canada and United States), Lake Victoria (Kenya, Tanzania and Uganda), Huron (Canada and United States), Michigan (United States), Tanganyika (Burundi, Democratic Republic of the Congo, Tanzania, Zambia), Baikal (Russia), comprise vital resources for natural, social and economic growth.

Lake, wetland and estuary ecosystems are particularly rich in biodiversity and they provide multiple services. They host about 10,000 fish species and about 90,000 species of invertebrates, the vast variety of which inhabit the littoral zone and the shores. The benthic zone, the bottom area of lakes and wetlands in transition between the actual water body, the sediment and substrate, are of high ecological significance in sustaining life cycles through invertebrates, amphibians, crustaceans and molluscs. Wetlands, in particular, are characterized by high primary productivity. Wetland vegetation follows particular patterns, such as emergent plants with roots, floating plants with roots, floating plants without roots, and submerged plants with roots. Macrophytes and angiosperms (flowering plants), algae (green, yellow-brown, red, and blue-green) and detritivores are found in high abundance; they support processes of unaccountable value such as, the photosynthetic process, community respiration, fast nutrient cycling and the food webs (Murphy, 1998).

Water flowing ecosystems, lotic, or else rivers and streams, whether permanent, intermittent or ephemeral, provide undeniable benefits. The water flowing ecosystems are the most common transboundary systems with obvious importance for national security. They may comprise fields of political dispute regarding water and territorial sharing or may act as connecting elements. The world's longest river, Nile (approx. 6853 km) serves as the only freshwater resource in proximity for most of the 12 countries within its river basin. The Amazon River is the world's biggest river in volume (219,000 m³/s discharge), drains eight countries, supports the Amazon rainforest and hosts a huge variety of species, including unique species such as the pink dolphins (*Inia geoffrensis*) and the Amazon giant otter (*Pteronura brasiliensis*). The shores of the Amazon are home to reptiles, mammals, birds, reptile, amphibians, invertebrates. Rivers comprise important water and food resources for the countries they serve, they provide rich habitats characterized by great biodiversity, and often are transboundary regions of high strategic importance for the countries they serve, they offer amenity and recreational areas.

Surface water bodies, whether rivers and streams or ponds and wetlands, offer nutritional products for the ecosystem and humans, food, fresh water, genetic resources and medicines, as well as habitat and biodiversity services through the creation of natural green and blue corridors connecting the, otherwise, disconnected or fragmented ecosystems. They offer supporting services, such as photosynthesis, oxygen provision, nutrient cycling, community respiration and they provide benefits through the regulation of life and ecosystem processes and cycles, that is, improvements in air quality, protection from shore erosion, climate regulation, CO₂ sequestration, flow attenuation and flood reduction. Flood prevention and increase in resilience to flooding are regulating services of great importance; surface water bodies are natural floodplains that provide flow attenuation and storm water management that result in flood control and collection of rainwater, while they reduce the pollutant load downstream (Grizzetti et al., 2016, 2019). Stormwater runoff management and flood prevention, also through the use of green infrastructure that aims to increase the potential for surface water accumulation have become priority concerns in urban planning (Chang et al., 2018; Berland et al., 2017) and in the ecosystem protection efforts. In addition, they act as carbon sinks as they have a high CO₂ absorption and storage capacity and offer obvious benefits in the efforts to combat climate change.

Surface water bodies, due to their high visibility to humans, have a significant contribution to human well-being through amenity and recreation (Arlinghaus, 2006; Pretty et al., 2007). Humans always tended to settle near water bodies, proof of that being the fact that 50% of the world population lives within less than 3 km from surface freshwater ecosystems (Kummu et al., 2011). The vicinity of surface open water bodies was always an attraction of increased amenity value, from early settlers to the proponents of urban design based on water features, such as the "Garden City Movement" of Ebenezer Howard, and the restoration actions of Niagara Falls (Apostolaki and Jefferies, 2009; Apostolaki and Duffy, 2017) to the latest decade that has seen explicit assessments of the importance of the water-human interactions in urban environments through numerous decision support tools aiming to quantify this relationship (Farrell et al., 2010; Braat and de Groot, 2012; Russi et al., 2013). Attractiveness of surface freshwater ecosystems and their biodiversity richness attract visitors, sport practitioners and nature lovers,

bearing clear benefits to their physical, mental and psychological well-being. The presence of surface water bodies and the contact with biodiversity are considered to provide health benefits, thus improve mental, spiritual, cultural, and physical health (Völker and Kistemann, 2013; McFarlane et al., 2019) and even increase property prices (Apostolaki and Jefferies, 2009; Venohr et al., 2018), at occasionally high levels.

Groundwater

Groundwater, the “unseen” part of the hydrological cycle, is in connection and constant exchange of water with surface water bodies; groundwater aquifers are formulated due to percolation from the bottom of rivers, lakes, wetlands, estuaries and in return surface water bodies are replenished by groundwater flows (West and Obling, 2014). Although “unseen,” groundwater comprises the most important source of usable freshwater at global scale. Groundwater aquifers are crucial for the provision of water to cover all needs and provision for agriculture. Most of the irrigation water comes from the groundwater aquifers. In addition, the underground water storage sustains rich soil ecosystems in support of soil formation, providing habitats for groundwater dwelling species and land surface formations.

Groundwater is a slowly replenished resource; in most instances replenishment rates are significantly lower than exploitation rates, often resulting in fast drop of the water table and drying up of the resource. Results are several: the surface water bodies in conjunction are affected and the condition of these surface resources degrade; the availability of groundwater aquifers reduces; there is subsidence of land resulting in land reformations and loss of services provided by land use; saltwater intrusion that pollutes the groundwater aquifer (salinization of the groundwater aquifer).

Ice Caps

Ice caps comprise the highest share of freshwater of earth. The ice coverage ranges from 4 million km² in each of the polar regions in the summer, to 16 million km² in the Arctic and nearly 20 million km² in Antarctica, in winter. The food webs and species forming the land and under-water ecosystems of the arctic regions differ significantly between them; from single-celled prokaryotes to large marine mammals in the former case, to Prokaryotes (Bacteria and Archaea) and eukaryotic trophic plankton, crustaceans and fish in the latter. Spring-summer phytoplankton bloom is affected by seasonal changes in the ice cover and in ice thickness, which in turn are regulated by air temperature, ablation rates and heat fluxes from the water column and they control spring-summer transmission of solar radiation through ice. The level of sunlight allowed to reach below the ice surface affects photosynthesis and consequently, biodiversity richness and food webs (Obryk et al., 2016).

The direct transformations of water through all its forms, from water into ice and vapor in the atmosphere, establish strong links between climate change and ecosystem stability; arctic ecosystems respond in uncontrolled and unpredicted ways in any loss of arctic ice.

Ice caps, although cannot be used as a direct source of drinking water, they affect the livelihood of all other ecosystems through the climate regulation service they provide. On the other hand, the melting of ice that has been recorded since 1978, and is constantly intensifying, affects the underlying aquatic ecosystems, global climate, and in extent the world ecosystems and the services provided by them.

Connecting Nature and Society: Ecosystem Services

The relationship between humans and the natural environment can be characterized via ecosystem services (Haines-Young and Potschin, 2010). Ecosystem services refer to the benefits (both in terms of goods and services) which people obtain from nature, and as such the production of ecosystem services is a result of the interplay between social and ecological systems (MEA, 2003; Bennett et al., 2015). The most widely accepted classification of these benefits is provided by the Millennium Ecosystems Assessment working group (2003), which divides ecosystem services into four main categories namely:

- Provisioning services
- Regulating services
- Cultural services
- Supporting services

Provisioning services: Refer to products provided by ecosystems, including food (derived from both plants and animal products), fuel, fresh water, genetic resources, biochemicals and pharmaceuticals etc. Materials such as wood, and minerals for construction, or ornamental products such as animal skins and fibers for clothing or decoration are also considered provisioning services.

Regulating services: Relate to benefits resulting from the regulation of ecosystem processes such as water purification, waste management, air purification, pest control, erosion and storm protection, climate regulation, water regulation and pollination (Fig. 1).

Cultural services: Refer to the intangible benefits offered by ecosystems, which relate to people’s use of ecosystems for recreational activities, intellectual and spiritual development, social cohesion, cultural heritage, and aesthetic value.



Fig. 1 Categories of ecosystem services. (Developed from MEA, 2003; TEEB, 2010.)

Supporting services: Are otherwise referred to as “Habitat Services” (TEEB, 2010), and encompass the services which ecosystems offer in terms of creating the conditions necessary to provide a basis for all other ecosystem services and maintain the conditions for life on Earth (MEA, 2003). This includes provision of natural habitats, water and nutrient cycling, soil formation, and oxygen generation through photosynthesis. The key difference between supporting services and provisioning or regulating services, is that while humans do not directly benefit from supporting ecosystem services such as soil formation, they do in contrast benefit directly from the food provided from the soil.

Ecosystem Services Approach to Natural Resource Management and Development

In recent years, the Ecosystem Services approach has been widely adopted within natural resource management (Daily et al., 2009; Plant and Ryan, 2013; Moore et al., 2017), as a useful framework which captures not just the monetary value of the natural environment, but also the intrinsic value locked within our rivers, seas, and landscapes. Here the concept of Total Economic Value (TEV) proves a useful tool, as it highlights the value that society derives from all natural capital (TEEB, 2010; Koundouri, 2015), thereby aiding decision-making in relation to resource allocation and management.

Furthermore, ecosystem services provide a critical link between the natural environment and human wellbeing (Akinsete et al., 2019) and offer a means to articulate the contribution of nature to human life, economic activity and societal development. Concepts such as the “cascade model” (Haines-Young and Potschin, 2010) seek to illustrate these relationships, charting the connections between ecosystems, the services they provide, and the benefits these afford society. In recent years, the discourse has expanded to incorporate the link between the benefits to society in the context of human well-being, as well as socio-political processes such as policy development, decision-making, and planning and implementation of management strategies. Such models provide vital frameworks, through which ecosystem services, and the value of nature to society, and be further embedded into crucial decision-making processes.

Initiatives such as the Natural Capital Project (a partnership between Stanford University, the Chinese Academy of Sciences, the University of Minnesota, the Stockholm Resilience Centre, The Nature Conservancy, and the World Wildlife Fund), aim to integrate the value nature provides to society (ecosystem services) into all major decision-making processes in order to improve human and natural wellbeing. World Resources Institute, has taken this mandate a step further, actively targeting decision-makers in order to raise awareness within this sector (World Resources Institute, 2008) (Fig. 2). Despite ecosystem services being increasingly identified as a key tool to nurture societal development with consideration for the natural environment, there is still a fundamental gap in the recognition of the concept in terms of its role in supporting sustainable development, and implementation of global agendas such as the Sustainable Development Goals (SDGs) (United Nations, 2016). While tools such as MESH (Mapping Ecosystem Services to Human well-being), developed by the Natural Capital Project, are working towards supporting ecosystem services-based decision-making in the context of the SDGs and the SDG indicators (Natural Capital Project, 2016), there are still calls for ecosystem services to undertake a more prominent role in the implementation of the SDGs and the drive towards sustainable development (Wood et al., 2017).

The Ecosystem Services of Freshwater Bodies

Freshwater is a cross-cutting element which in fact integrates several ecosystem services, providing multiple benefits to various aspects of human life. The type and number of ecosystem services provided are unique to each individual ecosystem, and different types of freshwater bodies offer a host of different ecosystem services depending on the type of water body as well as its location, and condition. The core ecosystem services provided by different types of water bodies, are presented below.



Fig. 2 Interactions between the natural environment and society. (Developed from: Haines-Young and Potschin, 2010.)

Surface Water Bodies: Rivers & Streams, Lakes, Ponds and Wetlands

Majority of the global population relies on rivers, streams and lakes for fresh water supply, providing access to water for drinking, domestic use, sanitation, agricultural and industrial use. Not only do these water bodies provide water for alternative uses such as hydropower production, and transportation, but they also provide food, materials and pharmaceuticals in the form of products derived aquatic organisms which live in these ecosystem habitats. This group of water bodies also play a key role in maintaining water quantity via nutrient filtration, and over the long term, in nutrient cycling and soil formation (Feld, 2013). In addition, rivers, streams and lakes along with floodplains and wetlands, are critical for the control of floods and erosion. Wetlands and floodplains, are a nexus point of the terrestrial and aquatic ecosystems, which play a unique and vital part in the provision of ecosystem services and are generally considered to be the most valuable ecosystems (UNEP-Secretariat of the Convention on Biological Diversity, 2015). As well as providing both agricultural and aquacultural produce for food, biofuel, fiber and raw materials, wetlands also carry out integral processes such as water purification, flood and erosion control, and nutrient cycling. Additionally, the riparian zones of wetland ecosystems serve as nature-based carbon capture facilities and thereby mitigate climate change. Arguably one of the most vital ecosystem services offered by wetlands is the support of vast amounts of biodiversity, providing habitat for a number of rare and endangered species as well as most of the world's migratory bird populations. This assortment of biodiversity in turn make wetlands particularly attractive locations for tourism and recreational activities such as hiking, fishing, bird watching, photography and hunting (Ramsar Convention on Wetlands, 2005; Millennium Ecosystem Assessment, 2005a,b).

Groundwater

With aquifers providing drinking water for up to 2 billion people, and irrigation for approximately 40% of the world's food, groundwater is essential for the storage and retention of clean water for domestic, industrial and agricultural uses (NRC, 1997; Morris et al., 2003; Bergkamp and Cross, 2006). Groundwater bodies and their systems are necessary for maintaining the hydrological cycle through discharge and recharge, thereby maintaining other freshwater bodies such as rivers and streams, while also mitigating against drought by straining freshwater flow during prolonged and extreme dry seasons. In cases where groundwater produces hot springs, they provide cultural ecosystem services such as therapeutic or recreational spas, and serve as heritage sites where such springs are considered sacred or of great aesthetic value (Griebler and Avramov, 2014).

Ice-Caps

While polar ice holds 68% of global fresh water, the least is known about the specific ecosystem services. It is known that polar ice, plays a key role in regulating global temperatures, by reflecting a greater amount of solar radiation and heat (180 W m^{-2} annually), than the annual solar input of 80 W m^{-2} (Nakamura and Oort, 1988). In addition, the polar ice provides a habitat for microbial organisms such as algae and bacteria, and serves as shelter and feeding ground for juvenile krill, along with larger animals like

Table 1 Various Ecosystem Services Provided by Different Freshwater Bodies. (Developed from Aylward et al., 2005; Bergkamp and Cross, 2006; Ramsar Convention on Wetlands, 2005; Millennium Ecosystem Assessment, 2005a,b; Palmer and Richardson, 2008; Feld, 2013; Schallenberg et al., 2013; Griebler and Avramov, 2014; CGIAR Research Program on Water, Land and Ecosystems, 2015; Mitsch et al., 2015; UNEP-Secretariat of the Convention on Biological Diversity, 2015; WWF Global Arctic Programme, 2015; Bock et al., 2018; Malinauskaite et al., 2019.)

		<i>Ecosystem services</i>			
		<i>Provisioning</i>	<i>Regulating</i>	<i>Cultural</i>	<i>Supporting</i>
Freshwater body	Rivers and Streams	• Water (quantity and quality) for consumptive use (for drinking, domestic use, and agriculture and industrial use) • Water for non-consumptive use (for generating power transport/navigation) • Aquatic organisms for food and medicines	• Maintenance of water quality (natural filtration and water treatment) • Buffering of flood flows, erosion control through water/land interactions and flood control infrastructure	• Recreation (river—rafting, kayaking, hiking, and fishing as a sport) • Tourism (river viewing) • Existence values (personal satisfaction from free-flowing rivers) • Cultural values (religious, historical or archeological value)	• Role in nutrient cycling (role in maintenance of floodplain fertility) • Soil formation • Predator/prey relationships and ecosystem resilience
	Wetlands	• Food (agriculture, aquaculture, fisheries) • Peat production for fuel and horticulture Furbearer and other animal harvesting Timber production	• Flood control groundwater replenishment • Shoreline stabilization and storm protection • Sediment and nutrient retention and export • Water purification • Climate change mitigation and adaptation (CO₂ capture)	• Cultural values (religious, historical or archeological value) • Recreation • Tourism (hiking, fishing, bird watching, photography and hunting) • Existence values • Landscape aesthetics • Sites for human relaxation • Ecology education	• Reservoirs of biodiversity • Habitat for rare and endangered species • Wetland functions such as hydric soil development, primary productivity, serving as chemical sources, sinks, and transformers, and water storage
	Groundwater	• Water (quantity and quality) for consumptive use (for drinking, domestic use, and agriculture and industrial use) • Water for non-consumptive us (geothermal and power production, hot springs for medical therapy) • Aquatic organisms	• Erosion and flood control • Climate change mitigation and adaptation (buffer against spatial variability in drought)	• Recreation (hot springs, mineral spas) • Historical/cultural value (sacred springs) • Spiritual knowledge and wisdom	• Maintenance of hydrological cycle (aquifer recharge and discharge)
	Ice-Caps	• Freshwater storage	• Climate change mitigation and adaptation (<i>albedo</i>—heat and solar reflection away from earth)	• Education and knowledge (record of the Earth's climate history preserved in ice cores)	• Habitat for microbial community (algae, bacteria, and small consumers) • Feeding ground for juvenile krill, penguins and seals

penguins and seals. Finally, polar ice is an invaluable source of knowledge and natural history, preserving a record of the Earth's climate in ice cores (Millennium Ecosystem Assessment, 2005a,b; WWF Global Arctic Programme, 2015) (Table 1).

Current Threats to Freshwater and Ecosystem Services

Although critical to natural and human communities, fresh water is threatened by a myriad of issues including overdevelopment, pollution, over abstraction and global warming. The threats to freshwater ecosystems strongly vary in space and time depending on both social and ecological contexts, with immediate impacts on ecosystem services. Needless to say, current concerns over freshwater, among others, focus on the fact that provisioning freshwater services are far from met on a global scale. Today, 748 million people worldwide remain without basic access to drinking water, 2.4 billion people lack access to basic sanitation services, 1 billion people practice open defecation and 1.7 billion people are currently living in river basins where water use exceeds recharge (UN Water, 2015; WWP, 2017).

Provided the increasing population, which is expected to reach 8 billion in 2025, water withdrawals are expected to increase; the business as usual scenario predicts increase in water withdrawals of 22% by 2025 while the crisis scenario foresees 37% increase.

Consequently, the stress to freshwater resources and the need to sustain ecosystem services, also as a means to achieve the targets set towards achieving the SDGs, are becoming increasingly pressing in the coming years (Aylward et al., 2005).

Freshwater bodies are experiencing declines in biodiversity at a far wider extent than the terrestrial ecosystems (Collen et al., 2014), affecting the vitality and survival of species, particularly of the most sensitive ones, like amphibians. The threats to freshwater biodiversity can be summed up to derive from: overexploitation, water pollution, flow modification that may degrade habitats, and human-induced invasion by non-native species. Protection of freshwater biodiversity, is therefore, prioritized but is still comprises a challenge as it is multi-dimensional. The trade-offs between conservation of freshwater biodiversity and human use of ecosystem goods and services, may impose additional threats for the ecosystems and may affect ecosystem functioning and resilience, human livelihoods and biodiversity.

Disturbances or even negative impacts to freshwater ecosystems derive even from recreational activities. The use of lakes and rivers have cumulative impacts on the ecology of the ecosystems and often contribute to high biodiversity losses that are notably higher at freshwater ecosystems in comparison to terrestrial and marine ecosystems. Rivers, in particular, seem to suffer the most by habitat alteration due to recreational activities, such as boating, swimming etc.; 56% of river water bodies were found to significantly suffer from habitat loss and habitat alterations in the E.U. (Fehér et al., 2012; EEA, 2015), with immediate impact on the social value of the ecosystem.

Wetlands, especially mangroves, are among the most threatened freshwater ecosystems. The shallow-water natural floodplains are facing degradation due to urbanization, land use changes, water abstraction and pollution. Wetland loss is associated with losses in biodiversity and decline of critically important ecosystem services of socio-economic significance that include, among others, the stormwater management element, prevention of coastal erosion, nutrient cycling, water purification and reduction of waste load, habitat provision (Sannigrahi et al., 2019). Climate extremes affect wetland vitality and result in increased risk of flooding in the built wetland shores. The ecosystem service beneficiaries, i.e., farmers, consumers, locals, domestic water supply to cover demand, tourists and visitors, face higher levels of uncertainty in relation to the access and availability of the resource (Gómez-Baggethun et al., 2019).

The groundwater aquifers comprise the most widely used water deposits, therefore, suffer severe depletion dropping groundwater aquifers at levels that are considered non-usable. Over-abstraction of groundwater is affecting surface freshwater flows in rivers and lakes, is causing lowering of the water table and land subsidence, increases the cost of abstraction. In coastal areas it is resulting in upwelling and mixing of brines with fresh groundwater, resulting in salinization of groundwater aquifers, the most common type on groundwater pollution (West and Obling, 2014). Although the balance between freshwater and saltwater tends to remain relatively stable, over-abstraction has resulted in massive contamination of groundwater and the linked surface water resources with salt. An estimated 12.9 km³ cubic kilometers of saline groundwater exists in comparison to about 10.5 km³ of fresh groundwater (Gleick, 1996), with direct impacts for water supply and socio-economic services of the resource.

Despite the low attention to sea-ice biomes degradation in relation to the terrestrial and marine biomes, as previously observed (Malinauskaite et al., 2019), today there is increasing concern over the threats to ice caps. The ecosystem services related to climate regulation and biodiversity provided by ice caps are becoming of vital importance for the planet. The threats to ice caps derive from the actual loss of ice extent and reduction of thickness due the average increase in temperature. Even small changes in the ice properties may have long-lasting effects on sea ice, freshwater ice and the dependent ecosystems. The rapidly developing climate change accelerates the impact on ice caps. The climate regulation and hydrological support of ice caps is, therefore, significantly reducing. The interactions of the underline aquatic ecosystems with atmospheric air and solar radiation are also reducing with immediate impacts in primary productivity and biodiversity.

Recommendations on Sustaining Ecosystem Services

Management of freshwater resources should address the multifunctional nature of water, should cover the water and ecosystem needs without jeopardizing the integrity of ecosystem services and the benefits deriving from them for human societies, economies and the environment. Holistic approaches are aiming at human well-being, at ensuring good ecological status and increase benefits to the society. Integration of knowledge, ideas and services are tools to achieve protection of freshwater ecosystems and to engage into holistic management approaches that can be proven beneficial in protecting and sustaining ecosystem services. A holistic management framework of this kind, needs to draw attention to the links between environmental (natural), recreational, socio-economic aspects of freshwater systems while it actively engages into participatory processes that are beneficial for the end users and protective for the local natural environment. On top, ecological restoration of freshwater bodies and of their services can provide multiple social and economic benefits (Rey Benayas et al., 2009).

The Ecosystem-based Approach is an approach that links the direct and indirect contributions of ecosystems to human well-being and emphasizes on the protection and value of ecosystem attributes (Millennium Ecosystem Assessment, 2005a,b). In extent, ecosystem-based water management is in support and sustenance of ecosystem services, thus, sustainable management in aquatic ecosystems that depend on policy integration, engagement and exchange of knowledge, targeting at the protection of natural ecosystems. This approach considers ecological integrity, biodiversity, resilience to change, it is carried out at the appropriate spatial scales, it develops and uses multi-disciplinary knowledge, it builds on social-ecological interactions, it involves stakeholder participation and transparency, it supports policy coordination and incorporates adaptive management concepts, thus, the ability to respond to a range of possible futures, weighting at the same time short-term actions against long-term benefits or alternative actions (Langhans

et al., 2019). Holistic ecosystem-based management allows for trade-offs between the Ecosystem Services while taking societal goals into account. Ecosystem services are engaged, within this framework, to map the impacts of ecosystem changes to human well-being, ultimately aiming at identifying mitigation options or actions for the sustainable use of ecosystems, able to adverse the effects of drivers and pressures and improve quality of life via meeting the sustainable development goals (Apostolaki et al., 2019). This framework works well provided it is initially well defined, it is based on extensive and consistent monitoring and on elaborate evaluation processes. Consistency on governance combined with innovative solutions are key to stakeholder engagement. The benefits deriving are related to open dissemination of processes, while conflicts of transboundary nature or of any other kind are resolved. The ecosystem-based approach comprises the basic tool towards ecological restoration, and action in response to environmental degradation caused by human activities. Restoration is seen as a tool towards regaining ecosystem services, re-establishing contact with nature and improving the well-being for humans and the natural environment.

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Ephemeral Wetlands

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Abstract

Ephemeral wetlands are habitats with seasonal water body and ephemeral plant cover. Subtypes are shorelines of permanent rivers with fluctuating water level, seasonal pools in climates with variations in rainfall and the ephemeral flush habitat on inselbergs. EW offer extreme environments, shifting from flooding to water shortage. Short-lived annuals, dwarfish perennials and resurrections plants find a niche there. A permanent seed bank (and egg bank for crustaceans) buffers the year-to-year variability. Strong selective forces result in evolutionary processes like convergence, niche constancy, endemism and vicariance of taxa. By sheltering rare and endemic species, EW are jewels of biodiversity.

What Are Ephemeral Wetlands (=EW)? Basic Characteristics and Questions

EW are habitats submerged only part of the year. Plant cover is appearing above-ground for a short period (ephemeral) and characterized by short living annuals and dwarfish perennials.

The following questions will be discussed: (1) How does the combination of abiotic factors change around the world? Can we distinguish different types of EW? (2) What are common ecological traits and which life forms are successful? (3) How do water depth, duration of inundation and time of emergence trigger small-scale vegetation patterns and the seasonal dynamic of pools? (4) What is the role of the seed bank for buffering the year-to-year variability? (5) Are EW colonized by cosmopolites or has each floristic kingdom evolved its own taxa? (6) Finally the impact of humans and conservation issues will be discussed.

Habitat Types According to Abiotic Factors

Fluctuations of the water level are the result of variations in precipitation, evaporation from the water surface, transpiration by plants, surface and groundwater inflow and outflow, infiltration rate, drainage intensity and seepage outflow. According to the combination of landform, hydrology, soil and climate, EW can be classified in three types (Fig. 1: shoreline habitat (=SHH), seasonal pool habitat (=SPH), and the ephemeral flush habitat (=EFH) (Deil, 2005). There is a clear geographical pattern (Fig. 2):

The *shoreline habitat* (=SHH) dominates in perhumid extratropical climates and in mountainous regions of the tropics. It occurs along the shores of permanent freshwaters (shallow lakes, ponds, rivers) with strong seasonal fluctuations of the water level (Photo 1). This water dynamic result from lower precipitation and reduced overland inflow in the dry season and from higher evapotranspiration in summer. With decreasing water level, the shoreline passes through a sequence of ecophases: hydrophase (limnic, deep water), littoral (shallow water), limosal (amphibious, semi-terrestrial) to terrestrial (Hejný, 1971; Hejný and Husák, 1978).

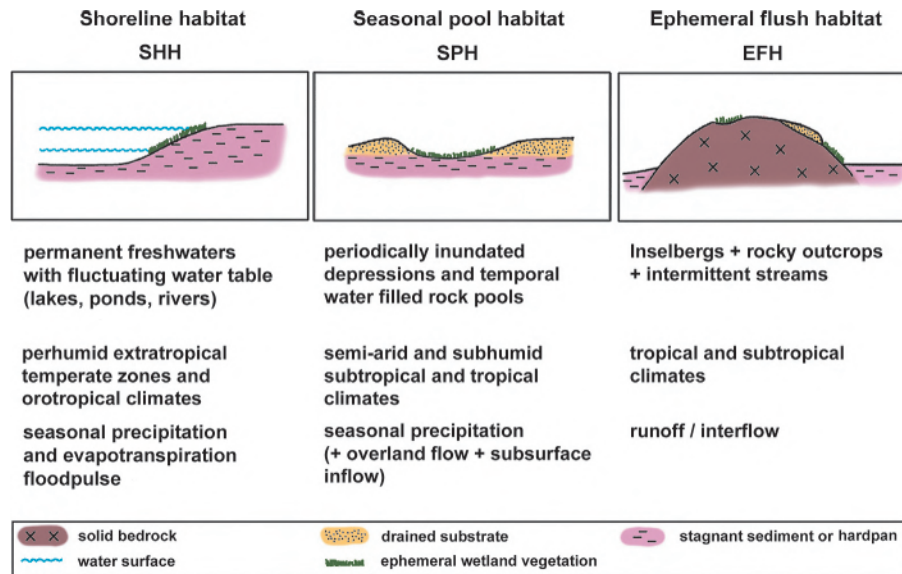


Fig. 1 Relief, soil, climate and hydrology of three types of ephemeral wetlands. Modified from Deil, U. (2005). A review on habitats, plant traits and vegetation of ephemeral wetlands—A global perspective. *Phytocoenologia* 35, 533–705. www.schweizerbart.de/journals/phyto.

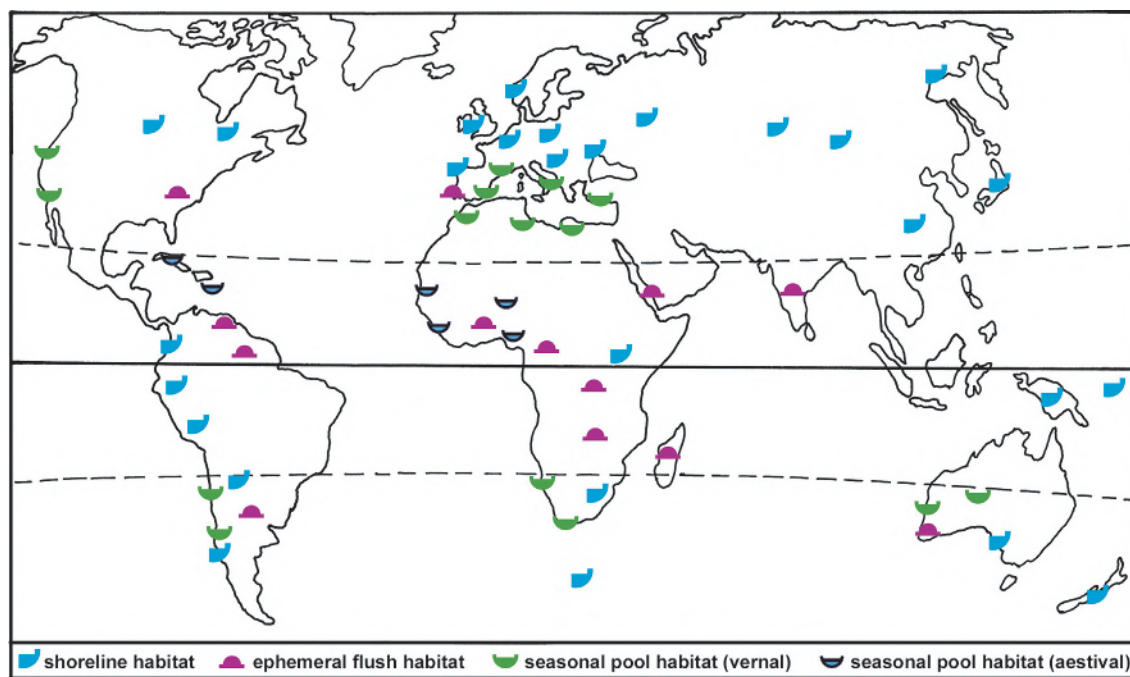


Fig. 2 Global distribution of ephemeral wetland habitats. From Deil, U. (2005). A review on habitats, plant traits and vegetation of ephemeral wetlands—A global perspective. *Phytocoenologia* 35, 533–705.

A special case of SHH are seasonal floodplains. The largest EW of this type is the Pantanal of Mato Grosso in South America. It covers about 200,000 square km during the maximum of the flood pulse (Heckman, 1998). A human-made case of SHH are fish ponds. Exposed pond bottoms offer a niche for ephemeral mud vegetation during summer drainage (Šumberová et al., 2006; Šumberová and Hrivňák, 2013).

The *seasonal pool habitats* (=SPH) are concentrated in the sub-humid areas on both sides of the Tropic of cancer. In climates with seasonal rainfall, rain fed ponds are seasonal too. In Mediterranean regions with winter rain maximum, shallow depressions over stagnant sediment and pools over impermeable rocks are ponded in winter (Photo 2). The pools desiccate completely in early summer. The widely used term “vernal pools” (=VP) refers to spring as amphibic phase and as the main season for plant growth and flowering. In the dry tropics the cycle is inverse with submersion in summer and an amphibic phase in autumn (aestival ponds).



Photo 1 *Marsilea quadrifolia*, colonizing amphibic shorelines of the rainfed fishpond Etang de la Grille, Sundgau, Upper Rhine Valley, Alsace, France.



Photo 2 Vernal pool in the aquatic phase with *Ranunculus peltatus* on the basalt plateau Giara di Gesturi, Sardinia, Italy.

VP landscapes occur in California (Holland, 1998), along the Atlantic coasts of Morocco (El Mahidi et al., 2017) and the Iberian Peninsula (Pinto-Cruz et al., 2009; Benavent-González et al., 2014), in Mediterranean Chile (Alvarez and Deil, 2015; Deil et al., 2011), South Africa and SW Australia. The size of the VP ranges from a few square meters in rock pools to several hectares in Moroccan depressions. One of the largest wetlands in the world are the millions of seasonal potholes in the prairie of North America (Van der Valk, 2005).

The catchment areas of SPH are local or the ponds are purely rain fed. The water budget of prairie potholes is dominated by precipitation (85% of water input) and evapotranspiration (78% of output) (Williams, 2006). Overland and subsurface inflow (16%) and seepage outflow (22%) are of minor importance.

Bauder (2005) studied pool hydrology over 20 years near San Diego: Water depth and hydroperiod are strongly correlated with the variability of rainfall. At site in the Great Valley, strong rainfall and high water levels result in outlet swales and seasonal streams,



Photo 3 Nave do Barão, Algarve, Portugal, Karstic depression flooded in April 2018.

overland and in the aquifer (Rains et al., 2006). VP hydrology is better described as mini-catchment than as a pure rainwater-evapotranspiration system. A special case of SPH is flooding by a raising karst water table after strong rainfall, as it occurs in depressions (dolines, poljes) of calcareous landscapes (Photo 3).

The *ephemeral flush habitat* (=EFH): In the perhumid tropics, EW are restricted to runoff-habitats. Ephemeral vegetation colonizes rock pools or occurs on the slopes of inselbergs, furthered by water seeping from mats with perennial plants (Photo 4). Richards (1957) coined the term ephemeral flush vegetation in Western Africa for a short-living plant cover, irrigated by water seeping from the adjacent *Afrotrilepis* mats. This term is now used to describe Inselberg vegetation (Porembski and Barthlott, 2000a). Inselbergs and EFH are common in West and East Africa, India, the Guyana shield (Fig. 2. Rare outliers occur in extratropical regions (SE United States, Southern Portugal, SW Australia).



Photo 4 Inselberg Mt. de Niangbo, Ivory Coast, with rock pools, Monocotyledonous mats and ephemeral flush vegetation. Photo: S. Porembski 1996.

Biological Characters and Plant Strategies

EW offer an extreme environment. Favorable conditions for growth and reproduction exist only within a short season and year-to-year variability is high. It is a life between inundation and desiccation, every year shifting from flooding to water shortage. The plants are dwarfish (a few centimeters high), above-ground biomass is ephemeral and the vegetation cover is open. Three plant strategy types predominate in EW:

1. *Dwarfish annuals with the ephemeroid syndrome*: They germinate from a permanent seed bank. Some species like *Limosella aquatica* germinate in shallow water and reproduce in the limose phase (amphiphytes); others like *Carex bohemica* germinate on mud in the littoral phase and complete their life cycle under terrestrial conditions (von Lampe, 1996). Characters of the ephemeroid syndrome (= co-evolved adaptive traits) are an extremely high phenological plasticity, a short life span, small growth form (nanism), rapid nutrient turnover, fructification a few weeks after germination and high reproductive effort. Representatives of the tiny annuals come from Cyperaceae, Lentibulariaceae and Scrophulariaceae (all floristic kingdoms), Juncaceae (Holarctic kingdom), Eriocaulaceae (Australia, East Asia), Centrolepidaceae (Australia), Callitrichaceae, Elatinaceae (most floristic kingdoms) (Photo 5) and other families. The ephemeral flush vegetation on Inselbergs is characterized by short living carnivorous succulents from the Lentibulariaceae and Droseraceae (Porembski and Barthlott, 2000a).
2. *Geophytic perennial herbs*: These species survive the dry phase with below-ground perennial organs (thick roots, tubers, bulbs, rhizomes). They resprout and develop leaves under submerged condition. In nutrient poor SHH and SPH dominate slow-growing, long-living stress-tolerators with the Isoetid syndrome (a rosette of long-lived terete leaves with lacunar air spaces, relatively high root biomass) like the fern *Isoetes*. Convergence in isoetid growth is stated by Keeley and Zedler (1998) for genera growing in Californian VP (*Orcuttia*, *Lilaea*, *Navarretia*, and *Eryngium*). In nutrient rich SHH and SPH in tropical climates, higher growing and productive hydro-geophytes such as *Nymphaea*, *Heteranthera*, and *Sagittaria* resprout from subterranean parts and develop floating leaves in the aquatic phase. Flowering and fruit setting happens in the limose phase.
3. *Poikilohydric vascular plants*: A special strategy to cope with water shortage is to desiccate passively, to lose more than 90% of the water content and to remain still alive in a dormant stage until water is again available. Water uptake and return in an active life (e.g., photosynthesis) occurs rapidly in these resurrection plants. Ninety percent of the worldwide species with this water budget strategy occur on Inselbergs in the tropics (Porembski and Barthlott, 2000b; Biedinger et al., 2000). Seasonal rock pools are the preferred habitat of desiccation-tolerant plants with representatives from Xyridaceae, Velloziaceae, Bromeliaceae, Cyperaceae in Southern Africa, resurrection plants are numerous in the genera *Craterostigma*, *Lindernia* (Scrophulariaceae), *Myriothamnus* (Myriothamnaceae), *Xerophyta* (Velloziaceae) a.o. On rock outcrops in Australia, the resurrection strategy is represented by *Borya*.

An extreme example of a resurrection plant is *Chamaejasme intrepidus*, the “fearless giant dwarf.” It colonizes rock pools in the Namib Desert, supports up to 20 desiccation-wetting-cycles per rainy period and can flower 2 days after resurrection (Heilmeyer et al., 2005). A “*Chamaejasme*-strategy” of desiccation tolerance and recovering within some minutes after re-flooding is recorded by McLachlan and Cantrell (1980) for Chironomid-larvae in tropical rock pools.

Fauna of EW and Strategy of Animals in SPH

The short favorable period for growth and reproduction of aquatic animals in SPH and EFH excludes long living predators and competitors like fish. EW however are not totally enemy free, because carnivorous aquatic insects such as larvae of Odonatae, amphibians and other active dispersers colonize VP in the wet season (Brendonck et al., 2002).



Photo 5 *Elatine gussonei* and *Crassula vaillantii* in rock pool on limestone plateau Cava Grande, Syracuse, Sicily, Italy.

The SPH faunal specialists are branchiopods and copepods (Crustacean) and Turbellaria, both passive dispersers (Jocque et al., 2010; Boix et al., 2016). They survive the dry period as eggs and cysts in a dormancy stage (diapause) (Williams, 1998). Branchiopod eggs can survive 20 years without ponding (Holland, 2009). The branchiopods produce enormous numbers of individuals during a short aquatic phase and are the most characteristic faunal element in VP (Guidicelli and Thiéry, 1998). Hundreds of Branchiopoda species live in SPH all over the world, many of them are endemic. One famous representative is the living fossil tadpole shrimp (*Triops cancriformis*). Observations in a pool network over decades are necessary to discover the complete species composition (Fahd et al., 2009).

To buffer the unpredictability of the time and length of the hydroperiod, only part of the egg bank is stimulated to hatching by submersion (diversified bet-hedging) (Simovich and Hathaway, 1997; Ripley et al., 2004). Some species need only a few days from hatching to reproduction. Like in the germination of vascular plants from the seed bank, delayed (by dormancy) and asynchronous hatching avoids depletion of the egg bank by rainfall shortly after desiccation of the pool. Offspring is spread over several years.

Bagella et al. (2010, 2011) studied crustaceans, amphibians, macroinvertebrates and vascular plants in VP on Sardinia over three seasons (filling, aquatic, drying). Each group of organisms has its own seasonal dynamic and beta-diversity pattern. There is low cross-taxon congruence: Vascular plants have high species-turnover rates between the ponds. The duration of the hydroperiod has a stronger impact on the crustaceans. Their beta-diversity is low: dispersal of the cysts and eggs by wind guarantees a meta-population in a pond landscape (Vanschoenwinkel et al., 2008).

Biomass Production, Photosynthetic Pathways and Heterophylly

SPH and EFH are exceptionally unproductive ecosystems, CO₂-limited in the aquatic phase and water-limited in the terrestrial phase (Keeley, 1999). Flat depressions are not filled up over the years by biomass accumulation. Biomass produced in the wet season is re-mineralized in the dry season (Collinson et al., 1995). Pure rainwater systems without lateral inflow of inorganic sediments can persist over thousands of years (Amami et al., 2013).

The variety of photosynthetic pathways used by aquatic and amphibic plants was studied by Keeley (1999) and Pedersen et al. (2011). CAM is recorded for a number of *Isoetes* and *Crassula*-species in Californian VP. It is not an adaptation to the scarcity of water, but to CO₂-shortage. The VP are poorly buffered and have an extreme diurnal fluctuation of carbon availability (Keeley, 1999). *Isoetes* has air chambers in the leaves, where endogenous CO₂ is accumulated at night. CAM enhances underwater photosynthesis and diminishes photorespiration (Pedersen et al., 2011). Semi-terrestrial *Isoetes* can switch from CAM to C₃ photosynthesis in the terrestrial stage.

Heterophylly and development of aerenchyma: Annuals as well as semi-terrestrial geophytes can change their morphology and histology under submergence and anoxic conditions. Shoot elongation, aerenchyma formation and heterophylly as response to flooding are typical for the amphibious fluctuation responders sensu Casanova and Brock (2000). An example is *Eryngium corniculatum* (Photos 6–8).



Photo 6 *Eryngium corniculatum*, aquatic form, Nave do Barão, Portugal.



Photo 7 *Eryngium corniculatum* amphibic form, Nave do Barão, Portugal.



Photo 8 *Eryngium corniculatum*, terrestrial form, Nave do Barão, Portugal.

Small Scale Zonation of Plant Communities

Abiotic ecological factors, which change over short spatial distance, are named ecological gradients. When they act as strong environmental filters for establishment and productivity of plants, the effect is a strong species turnover along this gradient and a small scale arrangement (= zonation) of different plant communities. Vegetation zonation according to water depth, length of inundation and time of emergence is a characteristic feature of temporary ponds (SPH) and emergent shorelines (SHH). Other differentiating gradients can be soil depth and duration of seepage water flow. These gradients determine repetitive patterns of plant communities. Three zonation examples with different climatical, hydrological and geomorphological situations are presented:

West Africa: The spatial sequence of plant communities according to water depth (hydrosere) in seasonal lakes in the Sahelian zone is illustrated in [Fig. 3](#) (from [Müller and Deil, 2005](#)) and [Photo 9](#). It starts in deep water with the free floating pleustophytic Lemno-Pistietum, characterized by duckweed (*Lemna* spp.), water ferns (*Salvinia*, *Azolla*, *Wolffia*), and water hyacinth (*Eichhornia natans*). In water of medium depth (150 to 20 cm) follow the Nymphaeion micranthae-communities. They are dominated by hydro-geophytes (rooting tubers, floating leaves) like water lilies (*Nymphaea* spp., *Nymphoides indica*) and bladderwort (*Utricularia* spp.). The shallow water and the amphibic zone are colonized by communities of the Rhamphicarpo fistulosae-Hygrophiletea senegalensis, a vegetation class of West-African distribution ([Müller and Deil, 2005](#)). The associations of the *Sagittario guayanensis*-Nymphaeion maculatae grow closer to the lake center (maximal 60 cm water depth), the grazing- and trampling-resistant swards of the *Brachiario muticae*-Cynodontion dactyli colonize the nutrient rich amphibic muddy lake margins with short-term

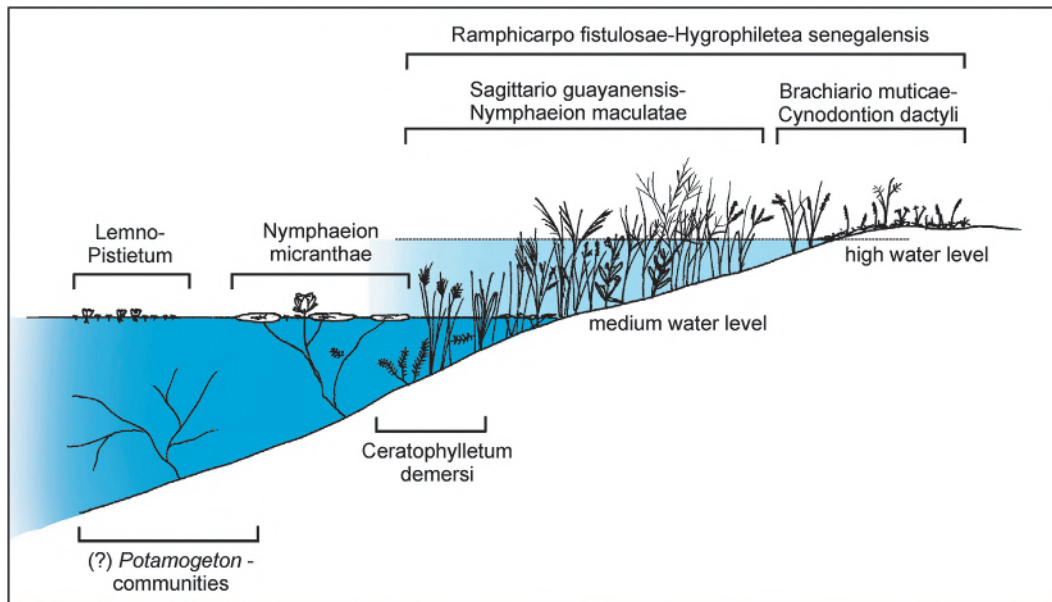


Fig. 3 Spatial sequence of plant communities according to water depth (Hydroseries) of a seasonal pond in the Sahel of West Africa. Modified from Müller, J. V. and Deil, U. (2005). The ephemeral vegetation of seasonal and semi-permanent ponds in tropical West Africa. *Phytocoenologia* **35**, 327-388.



Photo 9 Summer aspect of a Sahelian seasonal lake with ephemeral vegetation (*Nymphaea* div. spec., *Nymphoides indica*, *Ipomoea aquatica*), Mare d'Oursi, North Burkina Faso Photo: J.V. Müller

inundation. *Sagittario-Nymphaeion* is a very colorful vegetation type (**Photo 10**), dominated by hydro-geophytes (*Heteranthera*, *Sagittaria*, *Nymphaea*) and hemicryptophytic Cyperaceae (*Cyperus*, *Fuirena*, *Pycnus*), tolerating strong water level fluctuations.

Zonation in SPH in Mediterranean climates: Vegetation zonation in Californian VP in relation to inundation was studied in detail by Zedler (1987) and Bauder (2000). The sequence of the species according to weighted average inundation classes and inundation-frequency profiles are illustrated in Deil (2005; Fig. 17). The inundation in the pool Centre eliminates true terrestrial species. Only a small number of species is adapted to extended ponding. The desiccation in the terrestrial phase excludes obligate wetland taxa from the outer margin. The amphibic habitat in between offers a unique habitat quality, the evolutionary result is the VP-specific flora (Keeley and Zedler, 1998). Zonation in Moroccan VP was studied by Rhazi et al. (2001a), an example from Portugal is illustrated in Fig. 4.



Photo 10 *Sagittaria-guayanensis*-community with *Nymphaea maculata*, *Nymphoides indica*, *Sagittaria guayanensis*, *Schoenoplectus subulatus*, and *Ipomoea aquatica*, Mare de Kissi, Burkina Faso. Photo: J.V. Müller.

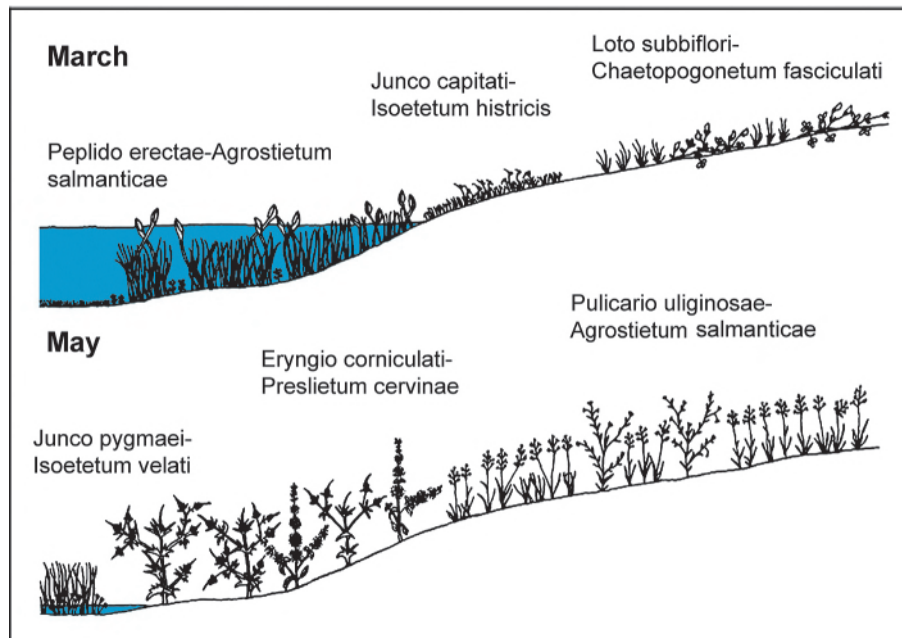


Fig. 4 Model of the seasonal and spatial distribution of vernal pool plant communities in Southern Portugal. From Espírito-Santo, D. and Arsénio, P. (2005). Influence of land use on the composition of plant communities from seasonal pond ecosystems in the Guadiana Valley National Park (Portugal). *Phytocoenologia* **35**, 267–281.

Zonation with EFH: The vegetation mosaic on inselbergs includes seasonal water-filled rock pools, water storing monocotyledonous mats and ephemeral flush vegetation. This spatial pattern was studied in French Guiana by Sarthou (2001). The water storing mats on the slopes are dominated by perennial grasses (*Axonopus ramosus*) and Bromeliaceae (*Pitcairnia geykesii*). On the water film soaking out of the mats develops an open and dwarfish turf, characterized by short-lived bladderworts (*Utricularia* spp.) and poikilohydric ferns (*Selaginella producta*).

Seasonal Dynamics, Year-to-Year Variability and the Role of Seed Bank

The dynamics of climate and flooding regime in SHH and SWH result in a high species turnover in the growing season and allow separating ecophases. The Mediterranean climate with the sequence of wet springs with fluctuating temperatures, and hot, dry

summers initiates a clear separation of cold and warm germinating/sprouting species. This is illustrated by an example from Southern Portugal: due to seasonal dynamic of VP vegetation and very different plant assemblages in March and May, [Espírito-Santo and Arsénio \(2005\)](#) distinguish a spring and a summer zonation. In March, the hydroseries is Peplido-Agrostietum (aquatic), Junco-Isoetum histricis (late emergent) and Loto-Chaetopogonetum (early emergent). In May, the long submerged Junco-Isoetum velati is surrounded by the Eryngio-Preslietum (amphibic) and the Pulicario-Agrostietum (terrestrial) ([Fig. 4](#)).

Year-to-year-variability is a prominent attribute of SHH and SPH. This is a consequence of between-year-fluctuations in precipitation, length of the flooding period and time of emergence of the shoreline. Plant response to drought is individualistic and depends largely on the timing of meteorological events in relation to life-stages ([Bauder, 2005](#)). Such a germination and sprouting ecology can explain the year-to-year-vegetation dynamic and spatial shift of vegetation zones. Inter-annual variability of the floristic composition and species abundance of Californian VP has been studied by [Bauder \(2000\)](#). The observation period included a normal, a wet and a dry year. "Pool species" were more static on the ponding gradient than "edge" species. "Non-pool" species moved in the dry year towards the pool centre and responded to the wet year by shifting towards the dry end of the moisture gradient ([Bauder, 2000](#)).

Permanent plot studies in Morocco by [Rhazi et al. \(2001b, 2009\)](#) confirm inter-annual variability in species diversity, composition and abundance and the spatial shift of the vegetation zones around vernal pools. *Myriophyllum alterniflorum*, abundant in the pool centre in wet years, is totally absent in dry years. *Pilularia minuta* was observed only in some years. Its sporocarps can persist over decades and wait for a good year ([Muller et al., 2009](#)). Enormous changes in population densities were observed for annuals (*Elatine brochonii*).

Time of emergence of shorelines and surface temperatures in the beginning of the amphibic phase can stimulate cold or hot germinating species ([von Lampe, 1996](#); [Pietsch, 1999](#); [Sumberová et al., 2006](#)) and results in different plant communities on exposed pond bottoms from year to year.

Seed bank and germination ecology: The seed bank makes the EW resilient to the inter-annual variability of ponding. A synopsis about seed bank, germination and dormancy, including data from EW, is presented by [Baskin and Baskin \(1998\)](#). VP species in Mediterranean areas were analyzed by [Carta \(2016\)](#), rock pool species in NW Australia by [Cross et al. \(2014\)](#). Inundation experiments and seed bank analysis ([Casanova and Brock, 2000](#) for SE Australia, [Bliss and Zedler, 1998](#) for California) show, that from an identical soil sample, different plant communities can be awakened by varying flooding regimes. Most species occur in the seed bank over a broader range of the inundation gradient and microrelief than in the above-ground vegetation ([Metzner et al., 2017](#); [Aponte et al., 2010](#)). In a certain year, only parts of the seeds are stimulated to germinate. The results are strong year-to-year changes in species composition and a spatial shift of the vegetation belts. The annuals shift around, the geophytes and the hemicryptophytes form a spatially constant matrix. The perennials react to the fluctuating water conditions with a changing sprouting rate and a different period and duration of above-ground appraisal ([Rhazi et al., 2001b, 2009](#)).

Major trends in seed bank characteristics and reproductive strategy are:

1. A persistent seed bank: Seeds are viable for decades or even more than one hundred years ([Poschod and Rosbakh, 2018](#)). Like seeds, the cyst stage of vernal pool shrimps can survive for decades ([Belk, 1998](#)). This is an adaptation to short-term availability and temporal unpredictability of the habitat. Ponding stimulates only part of the seed bank to germinate ([Brock, 2011](#)).
2. A high plasticity in germination: Secondary dormancy is enforced by unfavorable conditions like darkness or low oxygen level (imposed by water) ([Bliss and Zedler, 1998](#)). Physiological dormancy is the most common type of dormancy in amphibious plants ([Baskin and Baskin, 1998](#)). Soil perturbation and light are mobilizing seeds from deeper soil layers.
3. A high vegetative plasticity of adults, variability in plant size and in fruitset. Average and maximal seed output per plant vary enormously (*Anagallis minima* 250 to 6380 seeds; *Lythrum hyssopifolia* 2550 to 74,500) ([Salisbury, 1970](#)).

Evolutionary Processes and Large Scale Biogeographic Patterns

EW is a habitat occurring on all continents (except Antarctic) and in all biogeographic regions. When comparing the floristic composition of EW at the global scale ([Deil, 2005](#)), we can state three evolutionary processes: (1) convergent evolution of similar life forms and strategy types in different families, replacing each other in the same niche in several floristic kingdoms (niche equivalence). (2) A great number of phylogenetic lineages (mostly genera) entered the EW environment early in their evolution, spread globally, remained linked to this habitat (niche constancy) and evolved geographical vicarious species in different parts of the world. (3) A remarkable stock of taxa (most species), specialized to EW (stenoeious taxa), are restricted to a small area (stenochorous = endemic taxa). The latter species are an important contribution to global biodiversity. The evolution processes and the resulting biogeographical patterns will be presented now in more detail.

Convergence and Niche Equivalent Taxa

The niche of dwarf ephemeroid annuals is occupied by Juncaceae in the Holarctic kingdom, by Orcuttieae in California, Centrolepidaceae in Australia, Restionaceae in the Capensis, Eriocaulaceae in Australia and East Asia, and by Cyperaceae, Crassulaceae, Calitrichaceae, Ranunculaceae, Gentianaceae, Elatinaceae, and Apiaceae in all floristic kingdoms.



Photo 11 Poikilohydric plants in rock pools of the Yemeni Escarpment (SW Arabian Peninsula): *Craterostigma pumilum* and *Selaginella yemenensis*.

The niche for poikilohydric vascular plants with the xyroid syndrome occupy Xyridaceae (pantropical), Cyperaceae (*Afrotrilepis* in the Old World, *Trilepis* in the New World), Velloziaceae (*Xerophyta* in the palaeotropical, *Vellozia* in the neotropical region), Scrophulariaceae (*Craterostigma*, *Lindernia*, *Chamaegigas* in the palaeotropical region) (**Photo 11**), and *Borya* (Australian region). The xyroid families are not only niche-equivalent, but also have the same ecosystem function: These mat-forming taxa store the precipitation water and accumulate soil. The continuous supply of seepage water out of the mats on slopes of Inselbergs allows the development of the ephemeral flush vegetation below them (Porembski and Barthlott, 2000a).

Niche Constancy in EW Lineages and the Evolution of Geographical Vicarious Species

The database with floristic samples all over the world (Deil, 2005) shows clearly, that some phylogenetic lineages adapted quite early in geological time to seasonally wet conditions and later on evolved and speciated within this environment without radiating into other habitats (niche constancy). Some high ranked taxa (families, tribes, genera) are linked exclusively to EW and evolved geographically vicarious species. Examples are the families Isoetaceae, Marsileaceae, Centrolepidaceae, and genera like *Isoetes*, *Marsilea*, *Pilularia*, *Navarretia*, *Downingia*. A clear preference to the amphibic and limose environment is also expressed in generic names like *Amphibromus*, *Hygrophila*, *Limnophila*.

Moor (1937) was the first to underline that phylogenetically old taxa of trachaeophytes (*Isoetes*, *Marsilea*, *Pilularia*) are associated with EW. An explanation might be the extremely low productivity in SPH and EFH. At other sites, the dwarfish life form is outcompeted by advanced and more productive taxa. Branchiopoda as living fossils might have found a refugium in VP as habitat with low predation pressure (Zedler, 2003).

Isoetes (=quillwort =Merlin's grass) plays a major role in SPH all over the world. The genus is documented by fossils since the early Triassic (Jermy, 1990; Pigg, 2001). It is the oldest clade of CAM plants (Keeley and Rundel, 2003). 200 to 250 *Isoetes* species are known today (Photo 12). A pattern of geographical vicarious species in VP is recorded from the United States by Taylor and Hickey (1992) and from Spain by Molina (2005). When several species co-occur, they occupy different niches in the gradients of soil depth, soil fertility and inundation period. Geographical vicariance and niche partitioning can also be observed in *Marsilea* and *Pilularia* (Marsileaceae). Both genera are adapted to EW (Cook, 1990). They sprout from long-living (up to 100 years!) sporocarps. Juveniles are submerged, adults floating, emergent or terrestrial. Vicariance patterns occur in many other taxa specialized to EW (e.g., *Juncus*, *Limosella*, *Crassula*, *Hydrocotyle*, *Eriocaulon*, *Xyris*) (for details see Deil, 2005). The small size and the spatial isolation of the EW habitat reduce gene flow and favor allopatric speciation.

Regional Endemism and Biodiversity of SPH

Besides common genera and a very few species growing in EW in many continents, a classification of the available data set at the species level according to floristic similarity (the approach of Braun-Blanquet, 1964) results in clearly separated clusters (=classes), restricted to different floristic kingdoms. These classes have their own unique species, which contribute to the endemism of phytochorological areas. This pattern is demonstrated by the example of SPH (Fig. 5):

High ranked floristic-sociological clusters (classes) in the New World are the Downingio bicornutae-Lasthenietea fremontii in California (Barbour et al., 2003, 2005), replaced in Mediterranean South America by the Plagiobotryo pratensis-Navarretietea



Photo 12 *Isoetes hatrix* on rock outcrop with interflow, Serra de Monchique, Portugal.

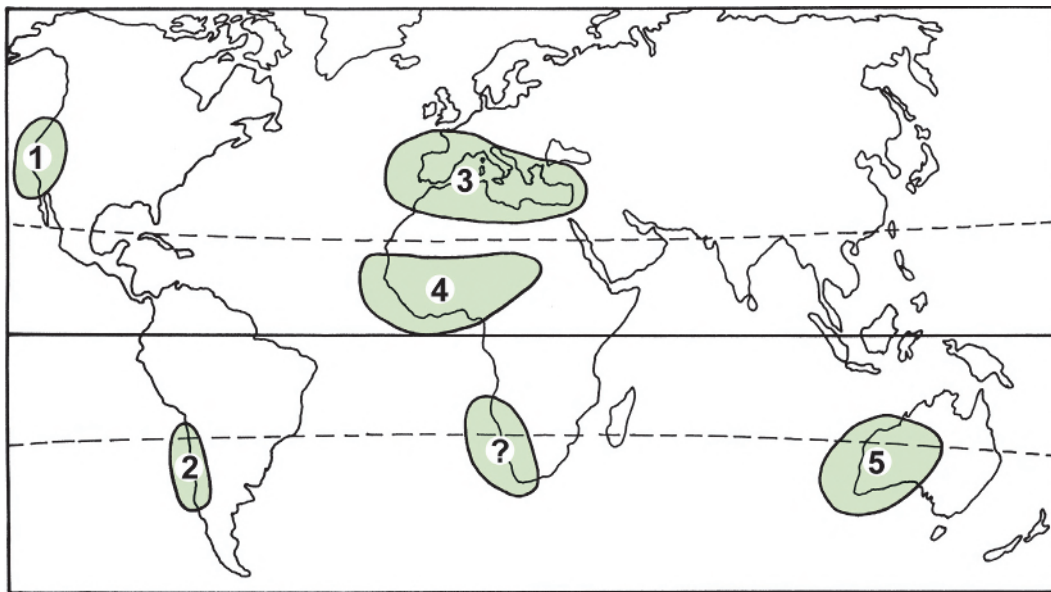


Fig. 5 Global distribution of phytosociological classes of seasonal pool vegetation. 1. *Downingio bicornutae*-*Lastenietea fremontii*. 2. *Plagiobotryo pratensis*-*Navarretietea involucretae*. 3. *Isoeto-Nanojuncetea/Isoetetalia duriei*. 4. *Rhaphicarpus fistulosae*-*Hygrophiletea senegalensis*. 5. *Centrolepidi aristatae*-*Hydrocotyletea alatae*. ?. undescribed class in South Africa and Namibia.

involucretae. Both classes are connected by a few species (amphi-neotropical elements sensu Raven, 1963) such as *Lasthenia kunthii*, *Psilocarphus brevissimus*, *Downingia pusilla*, *Navarretia involucreta*. Their high disjunct distribution is the result of long-distance dispersal by water birds.

Vernal pools are the state habitat of California (Keeley and Zedler, 1998). Fifty-five percent of the VP plant species are endemic to the Californian phytogeographical sector (Barbour et al., 2005). The *Downingio*-*Lastenietea* range from Oregon to Baja California. They are characterized by (1) *Downingia* spp. (Campanulaceae), a genus highly diversified in co-evolution with oligolectic bee species as pollinators (Thorp, 2007; Holland, 2009), by (2) *Orcuttia* spp., glandulous annual grasses with several genera, (3) by *Lasthenia* (18 species), *Limnanthes* (14 species), and by *Navarretia* spp. (Polemoniaceae) (Spencer and Porter, 1997).

The *Plagiobotryo pratensis*-*Navarretietea involucretae* (Deil and Alvarez, n.d.; Bliss et al., 1998; Deil et al., 2011) occur in Mediterranean Chile from 32 to 43°S (Alvarez and Deil, 2015) (Fig. 5) (Photos 13 and 14). The class is characterized by a number of *Plagiobotrys*, *Eryngium* and *Isoetes* species, by the endemic annuals *Blennosperma chilense*, *Centipeda elatinoides*, *Micropsis nana* a.o.



Photo 13 Vernal pool in a grazed *Acacia-caven* pseudo-savanna near Vilches, Prov. Maule, Chile.



Photo 14 *Plagiobotrys pratensis* (Boraginaceae), name giving species for VP vegetation in Chile; near Chillan, Prov. Biobio, Chile.

Because of their dwarfish and ephemeral character, some of these species have a hidden abundance and are often overlooked. Some were recently discovered for Chile (*Hydrocotyle cryptocarpa*) or rediscovered after some decades (*Lepuropetalum spathulatum*, [Alvarez et al., 2012](#)).

The plant communities of SPH in the Western Palaearctic belong to the class Isoeto-Nanojuncetea/order Isoetetalia, ([Mucina et al., 2016](#)). The Isoetetalia are of circum-mediterranean distribution ([Fig. 5](#)). Characteristic taxa are *Isoetes* spp., *Juncus* spp., *Crasula vaillantii*, *Scirpus cernuus*, *Lythrum* spp., *Marsilea strigosa*, *Pilularia minuta* a.o. ([Photo 15](#)). With the dominance of inconspicuous annual *Juncus* species from section *Tenageia* ([Photo 16](#)), European VP are less spectacular than Californian goldfields with blooming *Lastenia* spp. ([Holland, 2009](#)). By sheltering many rare and endemic species, they are however a botanic jewel of Southern Europe and Northern Africa ([Braun-Blanquet, 1935](#)).



Photo 15 *Illecebrum verticillatum*, *Ranunculus saniculifolius*, and *Isoetes velata* in vernal pool near Ben Slimane, Morocco.



Photo 16 *Juncus capitatus*, Monchique, Serra de Monchique, Portugal.

The SPH North (vernal pools) and South (aestival pools) of the Sahara (Fig. 2) have no species in common. The floristic contrast between Palaearctis and Palaeotropis is in the SPH as accentuated as in the flora in general. In sub-Saharan West Africa, the vegetation of SPH and SHH belongs to the Rhamphicarpo fistulosae-Hygrophiletea senegalensis (Müller and Deil, 2005). Hydrogeophytes from the Nymphaeaceae play a major role in amphibic mud vegetation. Details for zonation, life forms and dominant species are given in Fig. 3. The plant communities in the Mediterranean part of SW Africa (Capensis) are poorly studied but have their particular flora, different from NW and West Africa.

EW in SW Australia belong to the class Centrolepidi-Hydrocotyletea alatae (Pignatti and Pignatti, 1994, 2005). Fifty-six percent of its flora are SW-Australian endemics, characterized by Centrolepidaceae, Asteraceae, Apiaceae (*Hydrocotyle*), Cyperaceae, Juncaginaceae, and Stylidiaceae. Remarkable is the nearly total absence of Juncaceae. The dwarf rush niche is occupied by the Centrolepidaceae. The flora of seasonal flooded clay pans in SW-Australia is also characterized by a high endemism rate, with *Stylidium* (24 species), *Schoenus* (21), *Drosera* (18), *Isolepis* (13), and *Centrolepis* (9) (Gibson et al., 2000, 2005).

Major Anthropogenic Threats

Habitat Modification, Destruction, and Eutrophication

EW are rare and small-sized landscape elements, separated from each other and unpredictable in timing. With these characteristics, they are vulnerable habitats per se. EW are very sensitive to hydrological changes in their catchments (filling-in and drainage to avoid ponding respectively excavation and damming-up to achieve permanent water bodies). The main reason for the decline of SHH is the reduction of water table dynamics in lakes and old river beds by hydrological regulations and the direct destruction of the habitat by tourist resorts at shorelines. The SPH are threatened by drainage and transformation into arable land. In SW-Australia, 90% of VP and 95% of the clay pans were destroyed by agriculture (Pignatti and Pignatti, 1994; Gibson et al., 2000). Holland (2009) estimates the loss of grassland with VP in the Central Valley of California by urbanization and agriculture to 87%. A VP landscape in Morocco has lost 23% of the pools and 61% of pool surface in the period 1955–2001 (Rhazi et al., 2012).

The narrow geographical distribution of VP plants and animals and the small size of the populations make them vulnerable to extinction (Barbour et al., 2005). A survey of large branchiopods in SPH in Morocco showed an enormous decline in number of populations and species from 1987 to 2014 (Van den Broeck et al., 2015). The EFH is not so threatened, because inselbergs are holy places in many societies and in general of low economic interest (except exploitation by quarries).

Many VP taxa such as *Isoetes* spp. are specialized to oligotrophic conditions and need clear water bodies. Input of nutrients and sediments from the surrounding agricultural land is a great risk. Well conserved and species rich SPH in Japan and Morocco are restricted to ponds located in woodland (Rhazi et al., 2001a; Shimoda, 2005).

Expansion of EW Species and Shift Into Human-Made Habitats

An opposite trend to habitat loss and species extinction is the anthropogenous spread of EW taxa. There are two different processes: (1) an extension into similar habitats in other floristic kingdoms, (2) the shift from primary to human-made habitats.

An extension of the ephemeral wetland flora can be observed for example in annual *Crassula*-species. *C. tillaea* from Europe is naturalized in VP in Chile and South Africa. SPH in New Zealand have 13 native and 6 naturalized *Crassula* species (Johnson and Rogers, 2003). The “globalization” of the EW flora will result in the long term in a certain trivialization of the communities and a loss of floristic specificity of the floristic kingdoms. Sometimes are species, evaluated as threatened or vulnerable in their native area, classified as “aggressive neophytes” or “invasive species” in other regions. This concerns for example species of palaeartic origin like *Lythrum hyssopifolia* and *Ranunculus flammula* in New Zealand (Johnson and Rogers, 2003), or *Lythrum hyssopifolia* and *Anagallis minima* in California (Barbour et al., 2005; Gerhardt and Collinge, 2003).

Some EW species shift from primary to human-made habitats such as rice fields or fish ponds. In the tropics, amphibic shorelines and seasonal pools are often transformed into rice fields (Müller and Deil, 2005; Shimoda, 2005). Many annual SHH and SPH species like *Rhamphicarpa fistulosa* and habitat generalists among the fauna remained in this environment and became rice weeds (Lawler, 2001; Nowak et al., 2015; Rodenburg et al., 2014). *Heteranthera limosa* for example, originating from seasonally flooded playas in the Southern USA, became a troublesome weed in rice fields in the United States and in Europe.

In the temperate climate of Central Europe, fish and irrigation ponds can serve as secondary habitats for amphibic plants of SHH. Changes in fish pond management in the 20th century (extended submersion period, the abandonment of summer drainage, liming or herbicide spraying of the exposed pond bottom, eutrophication) have caused a decline of Isoeto-Nanojuncetea species in Carp ponds in Central Europe (Šumberová et al., 2006, 2012).

Climate Change and the Role of Grazing

EW systems are very sensitive to hydrological changes, but by a buffering seed/egg bank quite resilient to variations in precipitation. They shelter a wait-for-the-rain biodiversity. Every year is a good year for something in the pool. Pyke (2005) modeled the effect of climate change for VP in California. A broad spectrum of pools in nature reserves guarantees survival of rare Branchiopods. Shallow pools are more threatened by urbanization than by climate change. Pyke and Marty (2005) showed that cattle grazing can mediate climate change impact on SWH: It reduces transpiration by removing biomass and lowers infiltration rate by trampling. Inundation periods get longer despite higher temperatures. Excluding pasturing reduces the ponding period and favors invasive exotics versus native VP plants (Marty, 2015). These results from grazing experiments in California are confirmed by studies in VP in Morocco (Bouahim et al., 2010). Drainage, plowing and eutrophication of pools are greater threats for VP than grazing. EW support high disturbance frequencies, but suffer from intensive disturbance, which destroys the seed bank.

EW have always be submitted to grazing and trampling by large herbivores, searching for drinking-water (Photo 17). The plants are adapted to pasture pressure by nanism and creeping growth form (avoidance of grazing) or by a regeneration capacity (tolerance strategy) from subterranean parts and clonal growth. Moderate grazing reduces the competition of productive perennials. Trampling on wet surfaces creates open patches and germination niches for short-living ephemerals in permanent grassland. Ground disturbance by cattle grazing and rooting by pigs and wild boar is for example recommended for the maintenance of *Ranunculus revelieri* populations in mainland France and Corsica (Grillas et al., 2004). Pawing and wallowing by bison destroys the perennial plant cover in the Great Plains in North America. This creates ephemeral pools, deepens playa lakes, favors mudflat species and facilitates the establishment of *Marsilea mucronata* (Uno, 1989).



Photo 17 Horses grazing in vernal pool embedded into cork oak landscape, Plateau de Zaer, Ben Slimane, Morocco.

Conservation and Restoration

EW are included by the RAMSAR convention into vulnerable and protected wetland habitats. In the European Union, a certain conservation status is guaranteed by designating SPH as priority habitats.

Although seeds and resting eggs can be dispersed by wind, water and waterfowl, a remarkable regional endemism in plants and Crustacean can be stated. Beta diversity (dissimilarity in species composition from pool to pool) and year-to-year variability are high. Only many pools of different size, depth and hydroperiod and a network of nature reserves over a broad set of climatic variables can conserve the overall biodiversity of the VP flora and fauna (Pyke and Fisher, 2005; Alexander, 2007; Gómez-Rodríguez et al., 2009). An outstanding example is the network of about 3000 VP with different pool depth and hydroperiods, protected in the National Park Doñana in SW Spain (Díaz-Paniagua et al., 2010).

Restoration and mitigation projects of SPH in California have been quite successful. Inoculation by transfer of autochthonous soil and seed bank overcomes dispersal limitations and speeds up the trend towards natural pool characteristics after some years (Collinge et al., 2013). Aquatic invertebrates need more time to reestablish. Guidelines for VP restoration are presented by Schlatter et al. (2016).

EW as Model Ecosystems for Ecological Research

By their extreme low productivity (carbon limited in the aquatic phase, water limited in the terrestrial phase) EW are unique ecosystems. They offer a niche for dwarfish annual plants and for slow growing perennials with ephemeral above-ground biomass. Animals find a nearly enemy free habitat. SPH and EFH are islands in space and time. They are small and easy to manipulate for ecological experiments and can serve as model ecosystems in ecology, evolution, population and conservation biology. Various theories, concepts and models can be tested such as island biogeography, niche theory, connectivity, competition, dispersal limitation, founder effects, genetic drift, meta-population, speciation etc. (De Meester et al., 2005; Emery et al., 2008; Brendonck et al., 2010).

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Wetlands

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Abstract

Wetlands are globally diverse ecosystems that occur between terrestrial and aquatic environments. The degree of flooding is the main control on wetland vegetation, which varies from shallow water wetlands with submerged and floating-leaved plants, to emergent marsh and treed swamp. Wetlands support unique flora and fauna, from duckweed to mangrove trees and from frogs to hippopotamus. Humans exploit them for water, rice and fish, but wetlands also provide key services, such as flood attenuation, coastline protection, water purification and carbon regulation. Despite these benefits, humans have drained or converted over half of global wetlands. Extensive wetlands remain, but many are threatened by altered flooding regimes, invasive species, nutrient enrichment, contamination and climate change. Conservation efforts must focus on protecting wetlands and especially on maintaining key ecological processes on which wetlands rely.

What are Wetlands?

Wetlands, as their name suggests, occupy transitional zones between terrestrial environments and permanently-flooded or aquatic environments. They are dominated by wetland vascular plants, or macrophytes, and they occur where periodic or permanent flooding produces soils with low oxygen conditions, which forces the biota, particularly rooted plants, to adapt to flooding (Keddy, 2010). Wetlands have existed since vascular plants first evolved and colonized land, 430 million years ago in the early Silurian period (Greb et al., 2006).

We know wetlands by many names: bog, fen, peatland, moor, mire, muskeg, marsh, slough, prairie pothole, wet savannah, dambo, rice paddy, wet meadow, salt marsh, swamp, carr, pocosin, mangrove swamp, mangal, bottomland, and riparian zones, to give just a few names for wetlands in the English language. This list bears witness to the rich and regional language we use for wetlands. But this list also attests to the underlying diversity of wetland ecosystems.

Several regional systems categorize wetlands into different types, based on their landforms, flooding regimes, nutrient regimes, peat formation or their vegetation, but no global system exists to describe wetlands (Keddy, 2010; Mitsch and Gosselink, 2015). Two complementary approaches are commonly used to describe wetlands. The first considers their large-scale landscape setting, and the second considers their vegetation.

Wetlands occur in different broad landscape settings: slope wetlands, depression wetlands, extensive mineral flats, extensive organic flats or peatlands, riverine or floodplain wetlands, lacustrine fringe wetlands and tidal fringe or coastal wetlands; (Fig. 1; Brinson, 1993). Each wetland type occupies a distinct geomorphology setting, and each also has distinct water sources and patterns of water movement through the wetlands.

When wetland vegetation is considered, five broad wetland types are generally recognized: shallow water wetlands, marshes, swamps, bogs and fens.

1. Shallow water wetlands are the most aquatic wetland type. They occupy shallow riparian zones of rivers and littoral zones of lakes and ponds and are dominated by floating-leaved and submersed aquatic plants (Fig. 2A).
2. Marshes are mostly flooded but are occasionally exposed. They are dominated by rooted herbaceous plants with stems and leaves that emerge above the water level. They generally accumulate little peat (Fig. 2B). Freshwater marsh has distinct vegetation from salt marsh, a type of coastal wetland.
3. Swamps are at least periodically flooded but with less flooding than other wetland types. They are dominated by woody plants, either trees or shrubs. They also accumulate little peat (Fig. 2C). Mangrove swamps are a particular type of coastal wetland along protected subtropical or tropical coasts (Fig. 2D).

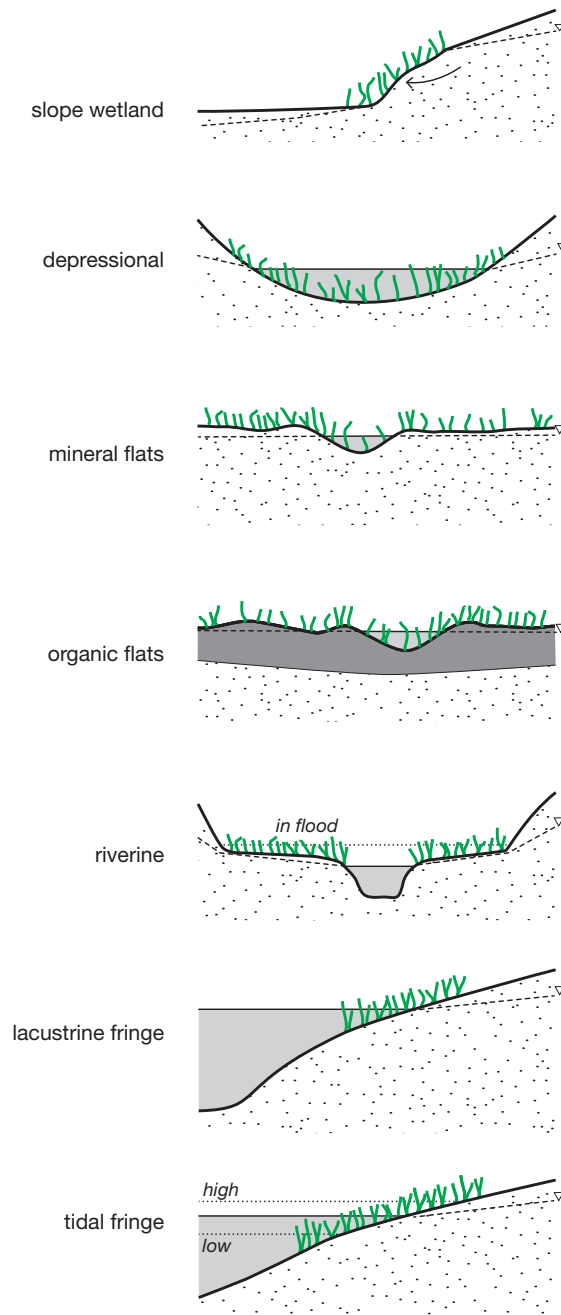


Fig. 1 General wetland landforms, following the hydrogeomorphic classification of wetlands (Brinson, 1993). The inverted triangle and dashed line indicates the water table in adjacent uplands.

4. Bogs are peat-accumulating wetlands, or peatlands, which are primarily rain-fed and are consequently nutrient-poor and acidic (pH 3–5.5). Bogs have a range of flooding environments and are dominated by peat mosses (*Sphagnum*), sedges, dwarf shrubs and scattered evergreen trees. Because they are rain-fed, bogs are also referred to as ombrotrophic peatlands (Fig. 2E).
5. Fens are another type of peatland that also receives groundwater inputs, and as such are less nutrient-poor and less acidic (pH > 5.5) than bogs. Again, a range of flooding conditions occur. They are dominated by other mosses, sedges, grasses, and scattered shrubs and trees. They are also referred to as minerotrophic peatlands (Fig. 2F).

Other wetland types could be added, such as wet meadows between marsh and swamps. Many wetlands also do not easily fit into these classes, as for instance tropical peat swamps, which are treed swamps that accumulate thick peat deposits.



Fig. 2 Examples of wetland habitats: (A) shallow water wetland with giant water lily in the Amazon basin, Colombia; (B) emergent marsh at the mouth of the Atchafalaya River delta, Louisiana, United States; (C) hardwood swamp with tupelo in Louisiana, United States; (D) mangrove swamp at low tide, Australia; (E) bog in the Hudson Bay Lowland, Canada; and (F) string fen with alternate pools and raised ribs in the Hudson Bay Lowland. Photo credits: Daniel Campbell, except 2d by H. Bieser.

Wetlands and Flooding

Flooding is the key factor that controls wetland ecosystems. It dictates the type of vegetation and key ecological processes such as decomposition and nutrient cycling. The extent of flooding is a function of the hydrology of the wetland, and more specifically the water balance. The water balance is a simplified way to view how water enters and exits wetlands (Fig. 3). For inland wetlands, inputs include precipitation, surface inflow and groundwater discharge, and outputs are from evapotranspiration, surface outflow

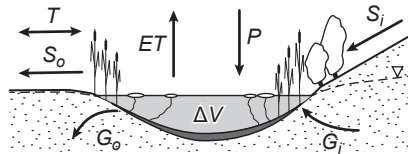


Fig. 3 Elements of a water balance in wetlands. Changes in water storage (ΔV) is a function of inputs of precipitation (P), surface runoff into the wetland (S_i) and groundwater discharge into the wetland (G_i), and outputs of evapotranspiration (ET), surface runoff out of the wetland (S_o) and groundwater recharge from the wetland (G_o). Where there is tidal influence, there are also tidal exchanges (T).

and groundwater recharge (Mitsch and Gosselink, 2015). Coastal wetlands also have tidal exchanges. When water inputs exceed outputs, flooding increases.

Oxygen diffuses 10,000 times slower in still water than in the air, and once a soil is flooded, oxygen diffuses even slower through the voids between the particles of wetland soils (Reddy and DeLaune, 2008). In consequence, once a wetland is flooded, the floodwaters and the surfaces of wetland soils are well-aerated, but oxygen below the soil surface is rapidly consumed by microbes and other biota (Fig. 4). Once flooded, wetland soils soon begin to suffer from low oxygen levels, a condition called hypoxia. With longer flooding duration, the oxygen becomes depleted, a state known as anoxia. Soil compounds of nitrogen, iron, manganese and sulfur also become chemically modified as flooding duration increases and oxygen is depleted (Ponnamperuma, 1972; Reddy and DeLaune, 2008). Methane gas is even produced from organic matter under anoxic conditions. Several of these modified compounds are toxic to plants (Kozłowski, 1984). As a result, plant roots and other wetland biota must not only survive through the low oxygen conditions found in flooded wetland soils, they must also contend with some toxic compounds produced by flooding.

Different wetlands have different duration of flooding, frequency of flooding and depth of the water table or the water level relative to the ground surface. The seasonal pattern of inundation above and below the soil surface is known as the hydroperiod (Reddy and DeLaune, 2008; Mitsch and Gosselink, 2015). However, sometimes the hydroperiod is defined more strictly as simply the duration of standing water in a wetland (Wellborn et al., 1996; Semlitsch, 2000; Batzer, 2013). The hydroperiod, along with the quality of soil organic matter and the availability of nutrients, determines the amount of oxygen that is available in wetland soils (Reddy and DeLaune, 2008). Plant roots, as discussed below, also strongly influence the amount of oxygen in wetland soils.

It is useful to contrast the seasonal hydroperiods of a few different wetland classes and consider the extent and timing of soil aeration with which wetland vegetation must contend.

Extensive organic wetlands, or large peatlands, such as bog and fen, have narrow water level fluctuations (Ingram, 1983; Fig. 5A). This produces extended anoxic conditions, which limit decomposition and the internal cycling of nutrients, and favor the accumulation of peat. Different flooding microhabitats occur in peatlands, from flooded pools >1 m deep to rarely flooded hummocks elevated 20–50 cm above the mean water table (Rydin and Jeglum, 2013), but all have relatively narrow water level fluctuations.

Lacustrine fringe wetlands, such as those along the Great Lakes of North America, are subject to wide seasonal water level fluctuations, with superimposed wind-driven short-term fluctuations, called seiches (Fig. 5B). Wetland vegetation types toward the upper end of this flooding gradient, such as swamp, wet meadow and, to a lesser extent, marsh, only have periodic flooding and consequently have respite from extended anoxic soil conditions. The water level fluctuations also allow more exchanges of nutrients and biota with the adjacent lake (Morrice et al., 2004).

Tidal fringe wetlands, or coastal wetlands, such as salt marshes or mangrove swamps, are subject to tides, with alternating flooded and exposed conditions once or twice each day (Fig. 5C; Friess et al., 2012; Van Loon et al., 2016). This flooding regime is superimposed upon longer-term water level fluctuations associated with lunar cycles, between neap tides and spring tides, and with those associated with occasional storm surges. Soils of tidal wetlands consequently alternate between hypoxic and more aerated

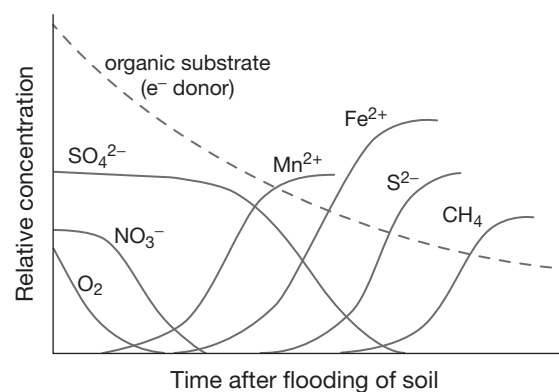


Fig. 4 Changes in relative concentration of soil compounds following flooding After: Reddy, K. R. and DeLaune, R. D. (2008). Biogeochemistry of wetlands: Science and applications, Boca Raton: CRC Press.

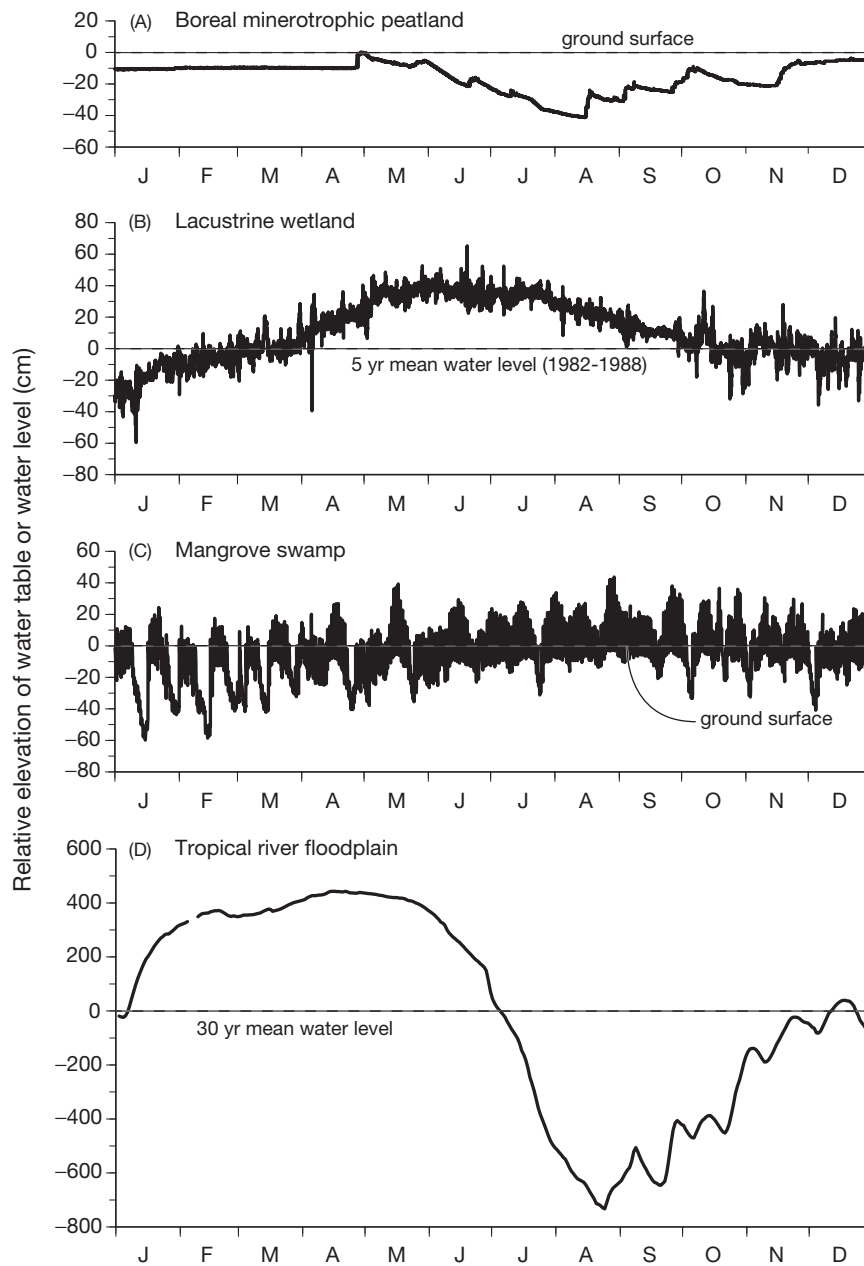


Fig. 5 Examples of annual hydroperiod curves in (A) a boreal minerotrophic peatland in Sweden in 2006 (Peichl et al., 2014); (B) a lacustrine wetlands along Lake Erie, USA/Canada, in 2017 (NOAA, 2018); (C) a microtidal mangrove swamp, in southern Florida, United States, in 2011 (Castañeda and Rivera-Monroy, 2018); and (D) a tropical floodplain along the Amazon River at Tabatinga, Brazil in 2017 (SO HYBAM, 2018). Elevations are relative to the ground surface or a local reference point, as indicated. Measurements were taken at hourly intervals (A–C) or daily intervals (D).

conditions on a frequent basis. The tides also allow for frequent exchanges of nutrients, organic matter and biota between the wetlands and the adjacent estuarine or marine environments.

Riverine wetlands are only inundated when the rivers flood. Extreme examples occur in the floodplain forests of the Amazon basin of South America, where water levels fluctuate over >12 m each year (Fig. 5D; Junk et al., 2011). These floodplain forests consequently shift from flooded anoxic environments to drained aerated environments, for several months at a time. The floods act as pulses that permit extensive exchanges of sediment, organic matter, nutrients and biota between the river channel and its floodplain (Junk et al., 1989).

Flooding and Wetland Vegetation

Flooding has profound but different impacts on different wetland plants (Sculthorpe, 1967; Hutchinson, 1975; Blom, 1999; Banach et al., 2009; Keddy, 2010). Consider an idealized transect along a water depth gradient bordering a river or lake, beginning from the most flooded to the least flooded wetlands sites (Fig. 6). Vegetation appears in zones depending on the extent of flooding.

Submerged aquatic macrophytes, such as milfoil (*Myriophyllum*) and bladderwort (*Utricularia*), and rooted floating-leaved macrophytes, such as water lilies (Nymphaeaceae), occur in shallow water wetlands, the most aquatic wetland habitats, which are predominantly to permanently flooded. Further upslope, in periodically exposed environments, is a zone of emergent macrophytes, such as cattail (*Typha*) and arrowhead (*Sagittaria*), rooted in wetland soils, but with their leaves extending above the water surface. This is marsh. Finally, shrubs, such as willows (*Salix*) or alders (*Alnus*), and trees, such as larch (*Larix*) or tupelo (*Nyssa*), occur toward the top of the flooding gradient in only periodically flooded environments, in swamp. Free-floating macrophytes, such as duckweeds (Lemnaceae) and water cabbage (*Pistia*), may occur across this flooding gradient. Algae also grow on plants and other surfaces across this gradient and can make up a substantial portion of primary productivity in some wetlands (McCormick et al., 1998; Adame et al., 2017). Bryophytes, such as peat mosses (*Sphagnum*) and brown mosses (Amblystegiaceae), are generally only abundant where water levels fluctuations are low, as in peatlands.

These different types of wetland plants have different adaptations to flooding. Submersed aquatic macrophytes are well adapted to completely aquatic environments. Their leaves lack a waxy cuticle, are thin and often have a large surface to volume ratio to facilitate the diffusion of oxygen and other substances between their tissues and the water column (Sculthorpe, 1967; Hutchinson, 1975). They can even use dissolved inorganic carbon during photosynthesis, instead of carbon dioxide, which makes them even more suitable to aquatic environments (Sculthorpe, 1967; Hutchinson, 1975; Pedersen et al., 2013).

Rooted floating-leaved macrophytes and emergent macrophytes extend their rhizomes and root systems into the flooded wetland soils. They can withstand some hypoxia in their roots and rhizomes, at least temporarily, through metabolic adaptations (Kozłowski, 1984; Blom, 1999). However, their principal strategy is to avoid hypoxia, through morphological adaptations. They have air channels within their stems and roots, called aerenchyma, which allow for air to circulate from leaves and stems above the water level to the rhizomes and roots in flooded wetland soils (Fig. 7; (Sculthorpe, 1967; Hutchinson, 1975; Jung et al., 2008; Sorrell and Hawes, 2010)). The aerenchyma not only provides oxygen to the roots and rhizomes, it also can aerate the flooded soils immediately around the plant roots (Reddy and DeLaune, 2008; Lai et al., 2012). This effect can facilitate the survival of less flood-tolerant species in the wetland soils nearby (Callaway and King, 1996). However, many emergent plants still prefer less flood duration (Campbell et al., 2016), and many will die back when they are continuously flooded for three or more years (Harris and Marshall, 1963; van der Valk, 1994). Seeds of many emergent plants also prefer to germinate under unflooded conditions (van der Valk, 1981), and as a result, periodic exposed conditions are needed to regenerate many species of emergent marsh vegetation.

Most woody plants lack any morphological adaptations to oxygenate their roots (Kozłowski, 2002; Parolin, 2009). They must rely on physiological adaptations to withstand flooding. They die after a year of continuous flooding, although a few woody wetland species can withstand flooding for 2–3 years (Valle Ferreira and Stohlgren, 1999; Kozłowski, 2002). This is why trees and shrubs are limited to swamps, the wetland type with the least flooding duration. Mangroves are exceptions. They are shrubs and small trees, but they can survive longer flooding because they have aerial roots known as pneumatophores, which transport oxygen to buried roots via aerenchyma (Srikanth et al., 2016).

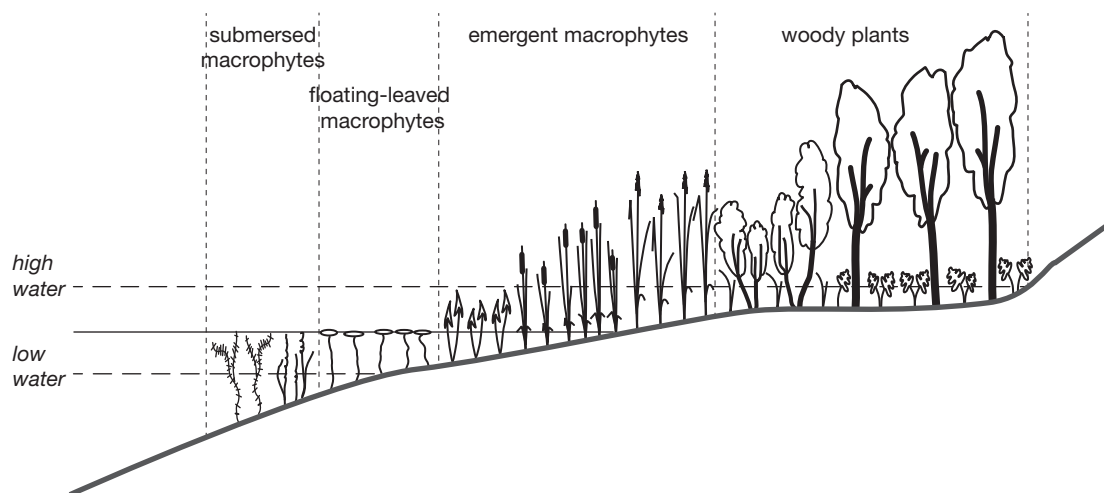


Fig. 6 An idealized transect across a wetland from shallow water wetlands through emergent marsh to swamp. The lower elevations are almost continuously flooded, while the upper elevations of the wetland are only periodically flooded during high water periods.

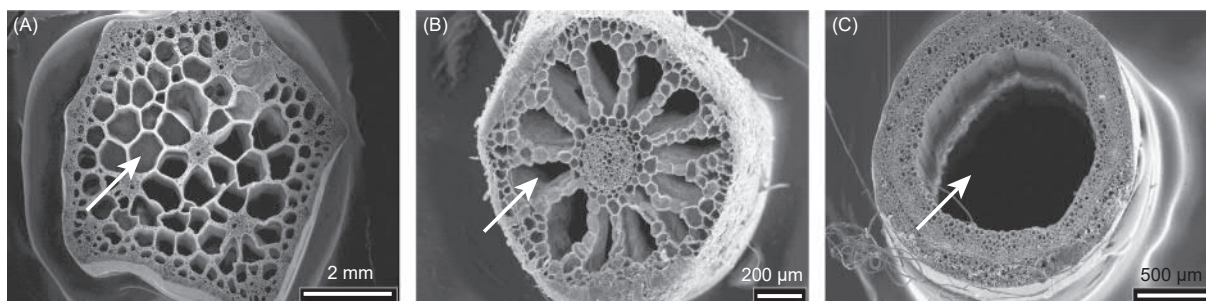


Fig. 7 Cross-sectional views of aerenchyma in shoots of wetland plants: (A) arrowhead, *Sagittaria sagitifolia* subsp. *Leucopelata* var. *edulis*, (B) water milfoil, *Myriophyllum spicatum* and (C) crowfoot, *Ranunculus cantoniensis*. The arrows indicate aerenchyma. After: Jung, J., Lee, S. C. and Choi, H. K. (2008). Anatomical patterns of aerenchyma in aquatic and wetland plants. *Journal of Plant Biology* **51**, 428–439.

Other Controls on Wetland Vegetation

Fertility is the second principal factor controlling wetland vegetation (Keddy, 2010). Many wetlands, such as salt marshes, freshwater marshes and swamps, are quite productive, with net primary productivity ranging between 1.5 and $>2 \text{ kg m}^{-2} \text{ year}^{-1}$ (Bradbury and Grace, 1983). Their productivity even exceeds that of intensively farmed agricultural land. However, not all wetlands are productive. Peatlands, for instance, have low net primary productivity, between 0.3 and $1 \text{ kg m}^{-2} \text{ year}^{-1}$. The supply of macronutrients, mainly nitrogen and phosphorus, is responsible for these differences in productivity among wetlands.

For instance, diverse infertile herbaceous wetlands exist in temperate regions, each with their own assemblage of wetland species (Fig. 8). Because of the low nutrient supply, these wetlands have low productivity and are dominated by short-statured species. In contrast, fertile herbaceous wetlands with high nutrient supply become dominated by only a few tall productive species, such as cattail (*Typha*) or common reed (*Phragmites*; Moore et al., 1989). When infertile wetlands receive increasing nutrient supply, the few taller competitive dominants replace the diverse short-statured species, in a process mediated by the competition for light. Many species of conservation concern are also short-statured, and are consequently restricted to infertile, unproductive wetlands (Moore et al., 1989).

Differences in vegetation between wetlands can also be a result of differing micronutrient supply. For instance, both macronutrients such as nitrogen and phosphorus are scarce across peatlands, but fens have a larger supply of calcium than bogs (Fig. 9). This is because bogs are only rain-fed, while fens also receive groundwater inputs. Fens, in consequence, have different species assemblages from bogs, have more rapid nutrient cycling and are more productive (Sjörs, 1950; Bridgman et al., 1996; Wheeler and Proctor, 2000; Keller et al., 2006).

Disturbances, defined as processes that substantially reduce the biomass of vegetation, also have profound influences on the vegetation of wetlands (Keddy, 2010). For instance, flooding by beaver damming is a disturbance because it drowns trees and shrubs. Other examples of disturbance include high river flows which erode river floodplains, ice which gouges shorelines in boreal regions, tropical cyclones which produce erosive waves and high salinity pulses in coastal wetlands, and fire in subtropical and tropical wetlands (Salo et al., 1986; Guntenspergen et al., 1995; Kotze, 2013; Lind et al., 2014). Many wetlands, such as emergent marshes, are adapted to these disturbances. They accumulate large banks of seed in the soil. These seeds consequently allow the vegetation to rapidly recover following severe disturbances (van der Valk, 1981; Keddy and Reznicek, 1986).

Grazing by herbivores is a more targeted type of disturbance that affects some wetlands (Bakker et al., 2016; Wood et al., 2017). Extreme examples include the overgrazing of subarctic coastal marshes by snow geese, or subtropical marshes by nutria, or constructed marshes by muskrat (Kerbes et al., 1990; Shaffer et al., 1992; Kadlec et al., 2007). These herbivores can efficiently transform productive emergent marsh to unvegetated mud flats. Wetland vegetation, at least submersed, floating-leaved and emergent macrophytes are more nutrient-rich, with a lower ratio of carbon to nitrogen than terrestrial vegetation, which explains why fauna prefer wetland plants as food (Bakker et al., 2016).

Other factors that control wetland vegetation include competition among plants, the burial of vegetation by sediment in floodplain and deltaic wetlands and salinity in coastal wetlands (Keddy, 2010).

Wetland Fauna

Many animals are dependent upon wetland environments at some point during their life cycle. An eclectic list could include species of mosquitoes, dragonflies, caddisflies, aquatic beetles, crayfish, crabs, snails, fish, frogs, salamanders, turtles, crocodilians, waterfowl, wading birds, rodents and a few large mammals.

One way to consider the animals in wetlands is to examine the wetland food webs (Montague and Wiegert, 1990). Herbivore-based food chains, where animals directly eat vascular plants, are important in some wetlands, as pointed out above for waterfowl and large rodents (Bakker et al., 2016; Wood et al., 2017). But in many wetlands, the food webs are based upon plant detritus and the bacteria and fungi that feed off it, or upon the microalgae attached to wetland surfaces (Fig. 10). Invertebrate animals feed from

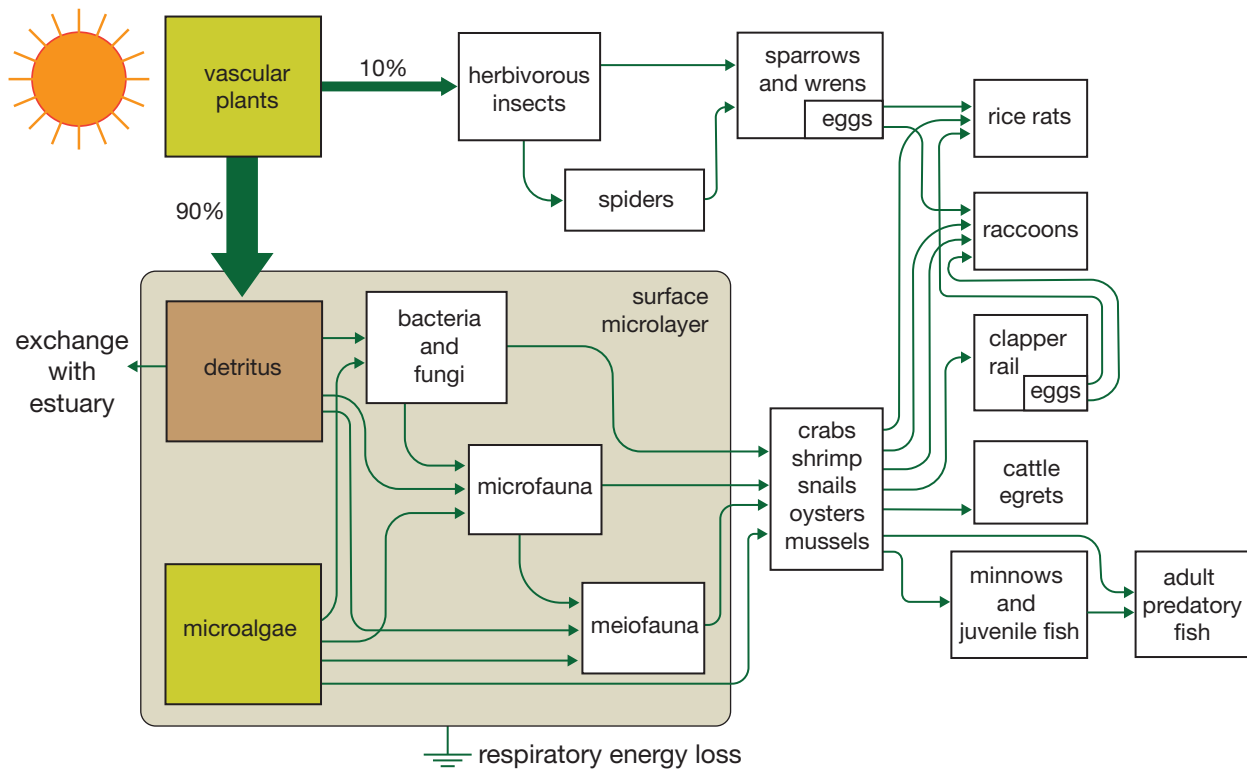


Fig. 10 Food web in a coastal salt marsh, with a grazing food chain along the top and a detrital and microalgal food chain on the bottom. After: Montague, C. L. and Wiegert, R. G. (1990). Salt marshes. In: Myers, R. L. and Ewel, J. J. (eds.) *Ecosystems in Florida*. pp 481–516. Orlando: University of Central Florida Press.

subtropical wet prairies, salt marshes, mangrove swamps and even peatlands (Murkin, 1989; Belicka et al., 2012; Jassey et al., 2013; Abrantes et al., 2015).

Fish utilize the more aquatic habitats found in wetlands. Different species use them as spawning grounds, nursery habitat for juveniles, or as feeding grounds for adult fish. Fish play important roles in the food webs of riverine wetlands, lacustrine wetlands, salt marsh and mangrove swamps (Minello et al., 2003; Petry et al., 2003; Junk et al., 2007; Nagelkerken et al., 2008; Lee et al., 2014; Trebitz and Hoffman, 2015). Fish also move from wetlands to more aquatic habitats. They consequently contribute to wider aquatic food webs in adjacent rivers, lakes, estuaries and nearshore marine ecosystems.

Amphibians are quintessentially associated with freshwater wetlands. They include frogs, toads, salamanders, newts, sirens, and amphiomas. Some amphibians use wetland habitats as larva and then inhabit more aquatic or terrestrial habitats as adults. Others, such as larger frogs, inhabit wetlands throughout their life cycle. Amphibian use of wetlands depends primarily on the duration of flooding and the presence of fish predators (Wellborn et al., 1996; Semlitsch, 2000; Baldwin et al., 2006). Small ephemeral depressional wetlands with only seasonal flooding can have high amphibian use and diversity, in part because they are fishless, whereas permanently flooded wetlands have different amphibian species, adapted to counter fish predation.

Several groups of birds depend on wetlands, including waterfowl, such as ducks, geese and swans, and wading birds, such as herons, cranes, flamingos, rails, jacanas, avocets, shorebirds and ibis (Batt et al., 1989; Sierszen et al., 2012; Holopainen et al., 2015). Many inland and coastal wetlands are globally recognized as Important Bird Areas for their role in providing nesting or migratory stopover habitat for wetland birds (<http://www.birdlife.org/>).

A few mammals are also emblematic of wetland habitats. For instance, beavers (*Castor* sp.) act as ecosystem engineers by damming small watercourses and creating wetlands in much of North America and parts of Eurasia (Naiman et al., 1988). Another noteworthy example, capybaras (*Hydrochoerus hydrochaeris*), the world's largest rodent, inhabit the vast floodplain wetlands in South America (Corriale and Herrera, 2014). Or consider hippopotamus (*Hippopotamus amphibius*) in sub-Saharan Africa, which, by means of their large bodies moving through wetlands, actually control the geomorphology of African wetlands (McCarthy et al., 1998). A less evident example would be the Bornean orangutan (*Pongo pygmaeus*), which has its last strongholds in the peat swamps of southeast Asia (Posa et al., 2011).

Where Are Wetlands Found?

Wetlands occur on all continents, except on Antarctica. They cover at least 12.1 million km² (Davidson et al., 2018), or roughly 9% of the global land area, excluding Antarctica (Fig. 11). Approximately 93% of wetland area occurs inland on the continents, while

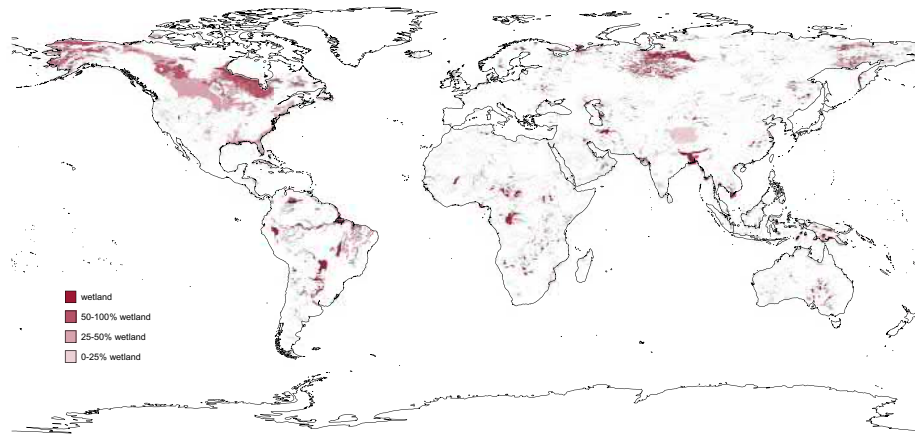


Fig. 11 World distribution of wetlands and wetland complexes. Data from the Global Lakes and Wetlands Database (Lehner and Döll, 2004).

the remaining 7% occurs along marine coasts or in estuaries (Davidson et al., 2018). A few wetlands are quite large, with the 11 largest wetlands or wetland complexes covering a total of 5.8 million km² (Fraser and Keddy, 2005; Keddy et al., 2009). The top four wetlands are representative and contrasting. They include two major boreal peatlands, the West Siberian Lowland in Russia and the Hudson Bay Lowland in Canada and two extensive tropical swamps in the Amazon River basin in South America and the Congo River basin in central Africa.

Wetland Ecosystem Goods and Services

Wetlands provide significant ecosystem goods and ecosystem services that support human well-being (Table 1; Millenium Ecosystem Assessment, 2005; Liqueite et al., 2013; Reis et al., 2017; IPBES, 2018; Ramsar Convention on Wetlands, 2018). Ecosystem goods include foods such as fish and grains, water, fuels and other biotic products. For instance, riverine, lacustrine and coastal wetlands support critical fisheries of fish and crustaceans, which provide essential protein for nearby settlements (Welcomme et al., 2010; Lee et al., 2014; Abrantes et al., 2015; Trebitz and Hoffman, 2015). Rice (*Oryza sativa* [Asian rice] or *Oryza glaberrima* [African rice]) is also widely cultivated in subtropical and tropical wetlands that have been converted to agricultural use (Gopal, 2013). It is a staple food that feeds billions of people. Another key ecosystem good from wetlands is water. Humans extract water near wetlands for drinking water, irrigation and other uses, although water extraction affects the flooding regimes upon which wetlands depend (McCartney and Acreman, 2009). Some wetlands also provide non-food goods, such as timber, thatching material, fuel wood, honey and waxes (Uddin et al., 2013).

Wetlands not only provide goods for human use, but they also provide key ecosystem services, for which we do not pay, that help to regulate and support broader ecosystems and human societies. For instance, headwater and riverine wetlands store water

Table 1 Principal ecosystem goods and services provided by wetlands

Ecosystem services	Examples in wetlands
<i>Ecosystem goods</i>	
Food provision	Fisheries (fish, mollusks, crayfish, crab, shrimp), waterfowl, rice, wild rice, sago palm, wild vegetables
Water storage and provision	Replenishment of groundwater resources, water for human consumption
Biotic materials and biofuels	Non-food uses, including timber, fibers, resins, medicines, genetic resources, fuel peat
<i>Regulating and supporting ecosystem services</i>	
Water flow regulation	Reduction of flood risks in rivers and consequent reduction in erosion and flood damage
Coastal protection	Wave attenuation and protection against storm surges in coastal wetlands
Water purification	Filtering and degradation of nutrients, organic wastes and pollutants
Climate regulation	Carbon regulation through uptake, storage and sequestration of CO ₂ as peat; release of methane
<i>Cultural services</i>	
Recreation and tourism	Birdwatching, ecotourism
Symbolic and aesthetic values	Spiritual and aesthetic enjoyment

Adapted from: Millenium Ecosystem Assessment (2005). *Ecosystems and human well-being: wetlands and water*, Washington, DC: World Resources Institute; Liqueite, C., Piroddi, C., Drakou, E. G., Gurney, L., Katsanevakis, S., Charef, A. and Egoh, B. (2013). Current status and future prospects for the assessment of marine and coastal ecosystem services: A systematic review. *PLoS One* **8**, e67737.

and slowly release it, as a sponge does, which allows these wetlands to moderate flows and reduce flood peaks and flood damage in water courses downstream (Fritz et al., 2018; Lane et al., 2018). Headwater wetlands also recharge and replenish the groundwater table (Lane et al., 2018).

Coastal wetlands, both salt marshes and mangrove swamps, act as barriers for coastal defense. They attenuate wave energy and floodwaters and stabilize the shorelines in estuarine and marine ecosystems (Shepard et al., 2011; Leonardi et al., 2018; Reed et al., 2018). However, sufficient sediment supply is required to maintain the coastal defense function of coastal wetlands (Boesch et al., 1994).

Wetland ecosystems purify water by filtering out sediments, nutrients, wastes and some pollutants (Verhoeven et al., 2006; Reddy and DeLaune, 2008). Some wetlands are even designed and constructed to treat nutrient-enriched waters in urban, industrial or agricultural settings (Kadlec and Wallace, 2009).

Wetlands are also key ecosystems for the control of climate change (Moomaw et al., 2018). Over millennia, wetlands, especially coastal wetlands and boreal peatlands, have sequestered and stored large quantities of carbon as organic enriched sediments and peat, making them key carbon sinks with the potential for mitigating the impacts of climate change (Mitsch et al., 2013; Sjogersten et al., 2014). However, methane, an important greenhouse gas, is also released from some wetlands (Bridgham et al., 2013; Mitsch and Gosselink, 2015).

Many wetlands provide significant cultural services, such as opportunities for ecotourism, recreation and even spiritual and aesthetic enjoyment. Consider mangrove swamps. They were once avoided as zones of danger, darkness and disease, at least to western eyes (Friess, 2016). Today, mangrove swamps not only provide recreation opportunities for tourists, such as birdwatching and nature enjoyment (Uddin et al., 2013), they also give spiritual and cultural meaning to those who visit them (Thiagarajah et al., 2015).

Threats to Wetlands

Wetlands face many threats, including drainage and conversion, changes in their hydrology, excess nutrients, invasive species and climate change.

The conversion or drainage of wetlands is the most important threat facing wetlands (Junk et al., 2013; van Asselen et al., 2013). Between 54% and 57% of natural wetlands are estimated to have been lost since 1700 AD, with a more rapid loss of between 64% and 71% since 1900 AD (Davidson, 2014). The most significant causes for these losses of wetlands are the expansion of arable land and the expansion of urban land, although the construction of dams, dykes and other infrastructure is also an important cause in some regions (van Asselen et al., 2013). Large urban population centres are often present in deltas and floodplains, which explains why wetland losses to urbanization are high. Some of the natural wetlands that are converted to agriculture, such as rice paddies, still provide some ecosystem services such as flood control and faunal habitat (Verhoeven and Setter, 2010; Gopal, 2013). Institutional and regulatory frameworks, such as the use of subsidies to convert natural wetlands to cropland, are also still responsible for substantial wetland losses in some regions (van Asselen et al., 2013).

The remaining wetlands are often affected by changes in flooding regimes (Junk et al., 2013). For instance, water control structures along rivers reduce species diversity in remaining wetlands downstream (Nilsson et al., 2005). In coastal wetlands, ditching and canalizing does not necessarily drain the wetlands, but they can lead to saltwater intrusion and consequent vegetation shifts (Gedan et al., 2009).

Although wetlands are valued for their ability to filter nutrient-enriched waters, excess nutrients can shift vegetation and ecosystem processes, especially in historically infertile ecosystems (Moore et al., 1989; Verhoeven et al., 2006). For instance, in the subtropical Everglades wetlands in the United States, oligotrophic marshes that have received nutrient-enriched agricultural runoff shift their species composition from sawgrass to cattail (McCormick et al., 2011). Atmospheric pollution also impacts infertile wetland ecosystems. For instance, peatlands subject to nitrogen-enriched atmospheric pollution shift toward non-peat accumulating wetlands (Bubier et al., 2007). Depending on their landscape position, wetlands may also receive high loads of contaminants from nearby land uses. For instance, wetlands that receive pesticide-enriched runoff from intensive agricultural land have higher incidences of limb malformations in the amphibians that breed there (Mann et al., 2009).

Invasive species, both animals and plants, are also a serious threat to wetlands by changing dominance of wetland species, the structure of their habitat and the food webs (Shaffer et al., 1992; Zedler and Kercher, 2004). A quarter of the most invasive species of plants are found in wetlands (Zedler and Kercher, 2004). Examples in wetlands include common reed (*Phragmites australis*) in wetlands of temperate North America, salt-cedar (*Tamarix* spp.) in floodplain wetlands of arid southwestern North America, and water hyacinth (*Eichhornia crassipes*) in tropical to sub-tropical wetlands outside of its native South American range (Shafroth et al., 2005; Villamagna and Murphy, 2010; Hazelton et al., 2014).

Climate change is also threat to wetlands, since it has the potential to change the water balance and the consequent flooding regime of wetlands (Mitsch et al., 2013). More importantly, climate warming could lower the water tables in peatlands and transform these peatlands from carbon sinks to sources of greenhouse gases, causing further climate warming (Moomaw et al., 2018).

Coastal wetlands are also threatened by sea level rise associated with climate change (Kirwan and Megonigal, 2013). However, recent research indicates that coastal wetlands can keep up with sea-level rise, if sufficient space is available for these coastal wetlands to migrate upgradient and inland as sea levels rise, and if they receive sufficient sediment supply (Schuerch et al., 2018).

However, where shoreline hardening inland restricts their upward and inland migration, coastal wetlands may be caught in a “coastal squeeze,” which limits their ability to migrate with sea level rise (Torio and Chmura, 2013).

Wetland Conservation and Restoration

Efforts to conserve and to restore wetlands have grown over the past half century. Arguments for their conservation are often based upon their high utilitarian value through the ecosystem goods and ecosystem services that they provide. But they are also intrinsically valuable as habitat for unique and often threatened biota. Both the utilitarian values and intrinsic values of wetlands should be considered in wetland conservation.

The Ramsar Convention on Wetlands was adopted in 1971 as an international treaty to promote the conservation and wise use of wetlands and their resources. Over 2300 wetlands, covering 2.5 million km² in 170 countries, are now designated as internationally important wetlands under this treaty (Ramsar Convention on Wetlands, 2018). Some countries, such as the United States and Canada, have few Ramsar sites, but they conserve wetlands through other protection systems. Nevertheless, only 10% of inland wetlands globally have protection status either as Ramsar sites or as other protected areas (Reis et al., 2017). Furthermore, few of these protected areas have safeguards to maintain their hydrology, their sediment dynamics and their water quality, upon which they depend (Reis et al., 2017). Wetland conservation must consider these key processes in order to retain the extent, quality and function of conserved wetlands.

A total of 73 countries have implemented national policies for wetland conservation (Ramsar Convention on Wetlands, 2018). The strength of these policies vary greatly, from countries with paper-only policies to countries with stringent policies where wetland loss is offset by the creation or restoration of wetlands elsewhere, as is attempted in the United States. Wetlands International (www.wetlands.org) is the primary non-governmental organization involved in the conservation of wetlands internationally, but national organizations operate in many countries toward the conservation of wetlands.

Wetland restoration or creation has increased substantially over the past half century as a strategy to mitigate the loss of wetlands, their ecosystem goods and services and their biodiversity (Darrah et al., 2019). However, data on the area of restored wetland are lacking in most regions. Restoration methods exist for several wetland types, including temperate swamps and marshes, bogs, vernal pools, floodplain wetlands, salt marshes and mangrove swamps (Broome et al., 1988; Quinty and Rochefort, 2003; Bosire et al., 2008; King et al., 2009; Calhoun et al., 2014; Biebighauser, 2015; Chimner et al., 2017). Further efforts are required to compile comprehensive restoration protocols across wetlands. Note that the biological structure and biochemical functioning of restored wetlands are lower than in natural wetlands nearby (Moreno-Mateos et al., 2012). This result, along with the high costs of wetland creation or restoration, suggest that the conservation and sound management of existing wetlands should take precedence over wetland creation and restoration, wherever possible. However, given the historical and current losses of wetlands, the restoration or creation of wetlands remains a useful strategy for wetland conservation.

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Ponds

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Abstract

Ponds are abundant landscape elements that provide vital ecosystem services and contribute significantly to biodiversity. Despite their importance for human society, they are threatened habitats and their protection and conservation is often neglected in current national and international legislation. We summarize a number of key-aspects on pond ecology and biodiversity. In addition, we discuss current policy and highlight essential elements for the effective conservation of ponds.

Key Characteristics

Despite the large variety of ponds around the world, efforts towards their classification have been limited so far, with a few exceptions in Europe (see for example [Kalettka and Rudat, 2006](#)). In the broad sense, ponds are small (1 m^2 to 5 ha), natural or man-made shallow lentic waterbodies that permanently or temporarily hold water ([Biggs et al., 2005](#); [Céréghino et al., 2008](#)). They are abundant ecosystems that occur in virtually all biogeographical regions ([Holgerson and Raymond, 2016](#)). Global estimates suggest that ponds represent approximately 90% of the standing waterbodies in the world and comprise up to 30% of the standing water by surface area ([Downing et al., 2006](#)). Despite their relatively small individual size, ponds are important ecosystems because they support global biogeochemical cycles ([Cole et al., 2007](#); [Downing et al., 2008](#); [Holgerson and Raymond, 2016](#)), provide vital ecosystem services ([Ipbcs, 2018](#)), and strongly contribute to biodiversity ([Williams et al., 2004](#); [Davies et al., 2008](#)).

The creation of natural ponds involves processes such as glacial activity in temperate and polar regions, the formation of oxbow ponds in alluvial areas, and the erosion of bedrocks. Natural ponds also arise in landscape depressions that permanently or temporally fill with water, as well as in periodically inundated floodplains. Animal activity, such as dam construction by beavers ([Johnston and Naiman, 1990](#)) or wallowing of large mammals ([Ayeni, 1977](#)) can also lead to the creation of ponds. In addition to the vast number of natural ponds, a considerable proportion of ponds is of anthropogenic origin ([Chester and Robson, 2013](#)) and has been created to fulfill a variety of human demands including fish production, sediment retention, recreation, and water supply ([Biggs et al., 2017](#)). In addition, multiple cases of unintentional pond creation also exist. For instance, ponds have formed in bomb craters ([Vad et al., 2017](#)) or mining quarries ([Dolný and Harabiš, 2012](#)). Many man-made ponds are now surrogate habitats for species of which the natural habitat has been lost ([Chester and Robson, 2013](#); [Lemmens et al., 2013](#); [Hill et al., 2017a](#); [Oertli, 2018](#)). In recent years, urban ponds are increasingly appreciated for their contribution to biodiversity and ecosystem services in anthropogenic landscapes ([Oertli and Parris, 2019](#); [Hassall, 2014](#); [Hill et al., 2016](#)) ([Fig. 1](#)).

Ponds are closely connected to their surrounding environment. This is definitely the case with respect to their water supply, which directly or indirectly depends on groundwater, precipitation, river connection or surface run-off. However, it also holds for their interaction with the soil and other ecotopes. Consequently, pond characteristics tend to differ extensively between ponds, both across and within climatological regions. While part of the variation among ponds is determined by differences in geology, soil typology, hydrology and landscape position, variation between ponds can also result from differences in pond morphology and internal processes that determine physical and chemical conditions. Furthermore, ponds are highly dynamic ecosystems in which the relative importance of environmental variables—and their interaction—varies considerably over time ([Hassall et al., 2012](#)). Therefore, pond age and pond history may also impact the abiotic and biotic characteristics of an individual pond at a given time ([Sferra et al., 2017](#); [Fairchild et al., 2000](#)). Finally, human interaction and disturbance have also become important factors, determining the characteristics and functioning of pond ecosystems.

Ponds share many characteristics with lakes ([Søndergaard et al., 2005](#)) and the distinction between both types of habitats is rather gradual ([De Meester et al., 2005](#)). Nevertheless, typical ponds are clearly distinguishable from typical lakes based on several functional aspects ([Oertli et al., 2002](#)). First, they have a smaller volume to edge ratio, which leads to a higher proportion of littoral zone and a more profound interaction with the surrounding terrestrial environment. Second, resuspension of sediments and internal eutrophication are generally less profound in ponds than in lakes because ponds are less exposed to wind and mostly lack dense fish populations that resuspend sediments. Third, ponds are relatively shallow (typically $< 3 \text{ m}$), which facilitates the development of aquatic vegetation over their entire water surface area and prevents profound thermal stratification of the water



Fig. 1 Examples of different types of ponds. *Top left*: Temporary floodplain pan from Karingani Game Reserve in Mozambique. *Top right*: Temporary rock pool on top of an inselberg in Western Australia. *Lower left*: Farmland pond in Belgium. *Lower right*: urban pond in a city park in Brussels, Belgium. *Top left*: Courtesy of Tom Pinceel. *Top right*: Courtesy of Tom Pinceel. *Lower left*: Courtesy of Mariuxi Peso, *Lower right*: Courtesy of Kristien Brans.

column (Scheffer, 1998). Fourth, ponds mostly have a much smaller catchment area (Davies et al., 2008). Finally, ponds have a higher probability to periodically dry out because of their relatively small size and shallow depth.

Biodiversity and Community Dynamics

Ponds harbor a significant proportion of global freshwater biodiversity (Dudgeon et al., 2006; Strayer and Dudgeon, 2010) and are important habitats for biodiversity conservation (Céréghino et al., 2014; Oertli et al., 2010). Indeed, ponds are often characterized by relatively high levels of local biodiversity and frequently contain multiple rare and endangered species (Davies et al., 2008; Williams et al., 2004). However, ponds are especially valuable because of their disproportionately strong contribution to regional biodiversity (Biggs et al., 2005; Williams et al., 2004; De Bie et al., 2010), which can largely be attributed to high spatial community turnover (Hill et al., 2018a) and the occurrence of unique species that are specific to small lentic waterbodies (Davies et al., 2008). Species turnover between ponds results from variation in local habitat characteristics, such as hydroperiod, succession stage and trophic structure, as well as from stochasticity in community assembly (Jeffries, 1994; Hill et al., 2017b; Hassall et al., 2012; Chase, 2007). The ecological importance of ponds is thus not exclusively linked to the value of individual ponds, but rather related to a network of ponds at the landscape scale ("pondscape"). Finally, ponds do not only sustain aquatic and semi-aquatic organism groups, but also support a variety of terrestrial taxa, including birds (Davies et al., 2016).

Ponds are highly dynamic habitats that show profound variation in community composition and diversity within and across years. Within-year variation in community characteristics can mainly be attributed to seasonal variation in climatological conditions and variation in biotic interactions (Brooks, 2000; Black and Hairston, 1988). Many pond systems become unfavorable or at least sub-optimal environments for their inhabitants during a certain period of the year (Williams, 2006). In temperate regions, this period is often associated with winter conditions of low temperatures and low sunlight radiation. Primary productivity is strongly reduced under these conditions, which can lead to nutrient limitation for consumers. Given that many pond inhabitants are ectothermic organisms, low temperatures imply strongly reduced metabolic rates and low activity (Clarke and Johnston, 1999). In order to bridge unfavorable episodes, organisms tend to react to cues that precede these and either move away (e.g., migratory insects), enter a state of metabolic rest (e.g., fish hibernation) or produce resistant dormant stages (e.g., phyto- and zooplankton cysts). Upon the return of favorable conditions for growth and reproduction, "active life" is resumed and dormant stages develop. Often, development is triggered by specific cues and not all organisms join the active community at the same time (Brendonck and

De Meester, 2003). Through such temporal niche segregation, competitive and predatory interactions may be avoided and organisms can tune their presence to the availability of specific resources that ensure optimal population performance (Jocque et al., 2007) (Fig. 2).

For temporary pond inhabitants the temporal variation in habitat suitability is even more extreme as their habitats sporadically disappear altogether due to drying. Local climate (rainfall and temperature) and near-surface geomorphology largely determine the frequency, length and variation in length of filling events (together defined as the hydroregime) of temporary waters (Williams, 2006; Hulsmans et al., 2007). Temporary waters may dry out as frequently as several times a month or as rarely as once every couple of years (Blaustein and Schwartz, 2001). Some habitats like the temporary Australian Lake Eyre, for instance, only fill a few times every century (Magee et al., 1995). Still, when filled, these systems are often home to a diverse community of aquatic organisms.

The fauna of temporary ponds comprises permanent residents, that bridge the dry phase in situ as drought resistant stages, and temporary residents that move away when the water evaporates (Williams, 2006). The length of the inundation (i.e., the hydroperiod) largely characterizes the habitat and the physicochemical environment its fauna and flora is exposed to (Wellborn et al., 1996; Schwartz and Jenkins, 2000). Rainfall is often stochastic, especially in (semi-)arid regions, which results in unpredictable variation in the hydroperiod of temporary pools, even between inundations of the same habitat (Philippi et al., 2001; Tuytens et al., 2014). Therefore, the hydroperiod and variation in hydroperiod can be one of the main determinants of variation in species richness and community composition, among temporary waters but also among years (Holland and Jenkins, 1998; Brendonck et al., 2017; Vanschoenwinkel et al., 2013). Not only do longer inundations allow for more extensive temporal niche segregation, they also allow for more extensive community dynamics and an increased opportunity for arrival of dispersers (Jocque et al., 2007).

Many ponds show profound changes in biotic and abiotic characteristics over subsequent years. A considerable fraction of this inter-annual variability can be attributed to successional change (Hassall et al., 2012), although several other factors can also be important (but see Korhonen et al., 2010). The process of succession in ponds is relatively fast because of their relative small size and shallow depth. Succession rates largely depend on the extent of primary production and the input of allochthonous material (Khan and Ansari, 2005). Eutrophication promotes primary production and thus accelerates succession. Pond succession typically involves major changes in the plant community (Ray et al., 2001; Arts et al., 1990), with vegetation dominated by open water species in the early successional stages and dominance of helophytes in late successional stages. However, pond succession also affects the community characteristics of other organism groups (see for example Fairchild et al., 2000; Raebel et al., 2010; Ruhí et al., 2011), and different taxa respond differentially to succession (Hassall et al., 2012). The rate of succession is generally faster in more shallow ponds because shallow water promotes helophytes of which the biomass is decomposed slower compared to



Fig. 2 Examples of pond inhabitants. Upper left: *Branchinella longirostris* is a dominant competitor in temporary rock pools across Western Australia. Upper right *Nothobranchius* killifish, such as *Nothobranchius furzeri*, are top predators in temporary ponds across Southeastern Africa. Like many zooplankton species, they bridge dry phases as resistant dormant eggs. Lower left: *Daphnia magna*, an important phytoplankton grazer in many ponds. Lower right: Adult female *Ischnura pumilio*, a semi-aquatic macro-invertebrate with an aquatic larval stage. Upper left: Courtesy of Tom Pinceel. Upper right: Courtesy of Aline Waterkeyn. Lower right: Courtesy of Robby Stoks.

organic material originating from submerged aquatic vegetation. In contrast, periodic drying slows down succession because it facilitates the remineralisation of organic material in pond sediments. Pond succession does not only affect biotic communities, but can also alter the chemical conditions of the water. Because succession gradually reduces the depth and volume of ponds, the end point of pond succession involves filling and terrestrialization, which finally results in the loss of ponds. Local biodiversity is expected to be highest in ponds at intermediate successional stages, but early and late successional communities have an important contribution to regional biodiversity (Hassall et al., 2012). Regional diversity can thus only be maximized by considering the dynamic nature of ponds with ponds in different successional stages.

Threats

Lentic freshwater systems belong to the most endangered ecosystems on the globe (Sala et al., 2000; Strayer, 2010; Carpenter et al., 2011; Gozlan et al., 2019). Habitat degradation and habitat destruction are considered major anthropogenic factors affecting the ecological integrity of ponds (Dudgeon et al., 2006; Strayer and Dudgeon, 2010). Additional concern arises from climate change (Moss, 2017). Ponds are especially vulnerable to environmental degradation because of their small size and volume (Boothby, 2003; Biggs et al., 2005).

Intensified land use practices and excessive application of fertilizers on agricultural lands have resulted in enhanced nutrient input in many regions on earth. As a result, an increasing number of pond ecosystems currently suffers from anthropogenic eutrophication (Smith and Schindler, 2009). Ponds are especially vulnerable to eutrophication (both phosphorus and nitrogen) because of their relatively small volume (Brooks, 2009; Biggs et al., 2005) and the intense interaction between the sediment and the water column, which facilitates internal eutrophication (Smolders et al., 2006). Eutrophication increases the primary productivity of pond ecosystems and can eventually cause a shift from a clear macrophyte dominated state to a turbid phytoplankton dominated state (Scheffer et al., 1993). Such state shifts are often difficult to reverse (Scheffer and Carpenter, 2003) and have a negative impact on biodiversity and the provisioning of ecosystem services (Hilt et al., 2017; Folke et al., 2004). Eutrophication also promotes toxic cyanobacteria blooms (Anderson et al., 2002). Eutrophicated ponds typically have low levels of biodiversity because of the absence of dense submerged vegetation. Submerged vegetation promotes aquatic biodiversity (Jeppesen et al., 1998; Hansson et al., 2010) by enhancing physical habitat complexity, increasing food availability and providing refuges for prey against predation (Kornijów et al., 1990; Warfe and Barmuta, 2004).

Land-use intensification has led to dramatic losses of ponds worldwide (Curado et al., 2011; Davidson, 2014). In Western Europe, for instance, approximately 50% of all ponds has been lost over the past century (Hassall, 2014). This is problematic because ponds typically form a pond network ("pondscape") in which individual pond communities interact via dispersal of organisms (e.g., the metacommunity framework, see Leibold and Chase, 2017). The loss of ponds can have direct negative effects on regional diversity by reducing the amount of suitable habitats (both the number of ponds and the total habitat area) (Gledhill et al., 2008), but can also reduce local and regional pond biodiversity through alteration of extinction-colonization dynamics by reducing landscape connectivity (Horváth et al., 2019).

Small freshwater bodies, such as ponds, are severely affected by climate change (Gozlan et al., 2019). Because of their typically small volume, temperature conditions tend to vary with atmospheric temperatures. Therefore, many pond systems experience more extreme temperatures and increasing daily temperature fluctuations (Carpenter et al., 1992; Stoks et al., 2014). While temperature changes may directly cause physiological stress to inhabitants (Jackson et al., 2016), altered temperatures may also indirectly affect organisms by, for instance, changing the solubility of gasses (e.g., oxygen) (Ficke et al., 2007). Increased temperatures are also associated with increased evaporation rates. For isolated ponds, increased evaporation results in higher concentrations of dissolved compounds including salts (Nielsen and Brock, 2009), and for temporary ponds it may result in early drying (Moss, 2012; Tuytens et al., 2014). Current climate change projections predict that rainfall will be reduced and more erratic in many regions (IPCC, 2014). Especially for temporary ponds, which are often directly dependent on rainfall for their inundation, this would imply changes in inundation regimes. Combined with higher evaporation rates due to increased temperatures, inhabitants of these systems would be faced with unpredictable drying and become increasingly time-stressed to complete the aquatic stages of their lifecycle (Moss, 2012). Climate change is at least partly caused by increasing greenhouse gas emission levels (IPCC, 2014). Following the industrial revolution in the 1750s, concentrations of carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O) have overall increased by 40%, 150%, and 20%, respectively (status in 2011; IPCC, 2014). While atmospheric CO₂ levels were around 278 ppm in 1750, currently the concentration is typically at 406 ppm and a further increase to up to 900 ppm is predicted by 2100 (Meinshausen et al., 2011). Although effects of increased CO₂ levels were long neglected for freshwaters, they may be far reaching and result, for instance, in acidification of aquatic systems and a higher carbon availability in aquatic food webs (Van de Waal et al., 2010). Combined with eutrophication, higher carbon availability could, in turn, directly increase phytoplankton productivity (Schippers et al., 2004).

Legislation and Conservation Management

With the definition of 17 sustainable development goals by the United Nations in 2015, the protection and the restoration of aquatic habitats were put high on the agenda (www.un.org/sustainabledevelopment). However, despite the high value of ponds for biodiversity conservation and the provisioning of vital ecosystem services, ponds are largely neglected in current national

and international policies and strategies (Biggs et al., 2017). In Europe for example, the Water Framework Directive is implemented to protect water quality of freshwater and shallow coastal waters. Yet in practice the focus lies almost entirely on river systems and large lentic waterbodies (> 50 ha) (EC, 2000). Unfortunately, the lack of direct legislative protection for ponds is also prevalent in most other regions, including Australia, Asia, and North-America (but see Hill et al., 2018b). Nature conservation legislation is currently the most important tool for the protection of ponds and their biodiversity (for example the Habitats Directive at EU-level and the Ramsar Convention at international level) (Hill et al., 2018b). Such legislations have definitely been successful, but their effectiveness is also limited because they largely focus on the protection of individual sites. Current knowledge on the drivers and dynamics of pond biodiversity suggests that legislations targeting pondscapes, rather than individual ponds, will be more effective in promoting biodiversity. This largely stems from the high spatial community turnover between ponds and the high temporal variation in the conservation value of individual ponds (Hassall et al., 2012). A focus on the pondscape level also allows improvement of the ecological connectivity of the landscape, which might be especially relevant in human-dominated landscapes that have been subjected to a profound loss of ponds, such as agricultural and urban areas.

Pond management is increasingly needed to conserve and enhance biodiversity. This is definitely the case in human dominated landscapes where biodiversity strongly depends on human interference (Biggs et al., 2005). Current restoration programs typically aim at the restoration of degraded ponds by promoting a clear-water-state with profound submerged vegetation (Usio et al., 2017; Sayer et al., 2012). Nevertheless, scientific evidence for the effectiveness of specific pond restoration measures based on biodiversity conservation is scarce. Empirical investigation suggests that adverse external influences to pond ecosystems from the surrounding environment can be mitigated most efficiently at small spatial scales (Declerck et al., 2006). For example, the presence of buffer strips with shrub vegetation around the shoreline can drastically reduce the input of nutrients, sediment run-off and pollution from the catchment (Joniak et al., 2017). Other management interventions include the removal of surrounding woody vegetation to increase insulation and promote the development of submerged aquatic vegetation (Sayer et al., 2012), and dredging to reset the successional stage of late-successional ponds (Hassall et al., 2012). Additional measures, such as changing the pond morphology or hydroperiod, might be relevant to target specific conservation goals (but see Williams et al., 2010a,b; Oertli and Parris, 2019).

Importantly, pond restoration measures should always be taken with care as some interventions might negatively affect local populations. The presence of regional species pools and the degree of habitat connectivity should definitely be considered prior to any radical management measure. Management at the pondscape level is the most effective approach to conserve biodiversity because it can promote landscape connectivity and can enhance habitat diversity (Oertli, 2018; Oertli and Parris, 2019; Hassall et al., 2012). Conservation programs targeting pondscapes, rather than individual ponds, also allow consideration of the dynamic character of pond ecosystems. With respect to this, the creation of new ponds has been proposed as an effective biodiversity conservation approach, especially in regions that have experienced a profound loss of ponds (see for example the Million Ponds Project, Williams et al., 2010a). Pond creation does not only enhance ecological connectivity of the landscape, but is also beneficial for regional diversity by providing early successional habitats. The latter might be especially relevant in regions that are dominated by late successional ponds since multiple studies highlight the importance of conserving a mosaic of pond successional stages within pondscapes. Resetting the successional stage of a subset of late successional ponds in the pondscape by dredging can be an effective measure to promote regional diversity in regions where the possibilities to create new ponds are limited.

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Lentic Freshwater: Lakes

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Abstract

There are ~304 million freshwater lakes world-wide with the highest concentration, area, and perimeter of lakes located within boreal and arctic latitudes. The seven main formation processes of lakes are tectonic activity, volcanic activity, glacial activity, fluvial action, aeolic action, anthropogenic action, and marine action. Lakes are generally characterized by low flow velocity and relatively low inflows and outflows. The primary parameters used to describe geomorphologic characteristics include lake length, lake width, lake depth, direction of major axis, shoreline length, lake area, lake volume, insulosity, and watershed to lake area/volume. Approximately 45% of photosynthesis on earth occurs in aquatic environments and photosynthesis supplies the primary source of organic matter for the growth and metabolic demand of all organisms in lakes.

Cultural eutrophication is thought to be the most widespread stressor in natural lakes. After eutrophication, acidification is the most important threat and stress factor for lakes. Above all, aquatic ecosystems are very vulnerable to climate change

which influences the physical, chemical, and biological structure of lakes. These influences include fluctuating water levels, increased water temperature, shorter ice-cover periods, invasion of nonindigenous animal and plant species from tropical and subtropical regions, and structural changes in catchment areas.

The value of biological diversity in freshwater lakes and the need for its conservation is becoming more important world-wide. However, the challenges involved with the conservation of freshwater lakes are great. It is often difficult to decide what management action to implement and what will be most effective. However, positive conservation action has brought real and sustained benefits across scales, from local to global, via a variety of mechanisms.

Introduction

The ability of lakes to retain, store, clean, and evenly provide water means they are an essential component of the hydrological and biogeochemical water cycles, and, as such, influence many aspects of ecological relationships and human well-being (Lehner and Döll, 2004). Lakes are generally defined as permanent bodies of still water (i.e., lentic water bodies) without direct connection to an ocean. They are formed by water filling geologic depressions (e.g., tectonic, volcanic, water or wind erosion) or by water being impounded behind a natural dam (e.g., glacial moraine, landslide) (Uhlmann et al., 2011). The size and shape of lakes is directly related to how they originated and how long they have been in existence. The resulting morphology of lakes (e.g., surface area, depth, shape, shoreline), regardless of how they were formed, determines their hydrological and biological characteristics (Kalff, 2002). Characteristics of lakes are also closely associated with characteristics of their drainage basin (Wetzel, 2001). Slope, soil, and vegetation influence the quality of water entering lakes (e.g., turbidity, organic matter). The area of drainage basins relative to the area of lakes is generally < 10:1 (Uhlmann et al., 2011).

There are ~8 million natural lakes world-wide with surface areas of > 1 ha (Ryanzhin et al., 2001) and about 304 million lakes ≥ 0.1 ha that cover 4.2 million km². (Downing et al., 2006; Downing and Duarte, 2013). The majority of them are freshwater lakes. This article provides broad insight to the contribution of lakes to the freshwater biome.

Biogeography

The highest concentration, area, and perimeter of lakes are located within boreal and arctic latitudes (i.e., 45°–75°N) while abundance of lakes is lower at southern latitudes where continental area is also lower (Verpoorter et al., 2014). Also, the total number, area, and perimeter of lakes decrease with increases in elevation (Verpoorter et al., 2014). Eighty-five percent of lakes, 50% of lake area, and 50% of total lake perimeter are located at elevations lower than 500 m above sea level.

Lakes of Europe

There is a great deal of variability in the characteristics of lakes in Europe. This variability is primarily a result of gradients in climate, geological history, land use, and atmospheric deposition, generally along a north–south axis. Lakes are also abundant in Europe, but similarly, numbers also decline from north to south (Weyhenmeyer et al., 2009). Stressors affecting lakes in Europe include climate change, intensive land use, increasing industrial activities, overfishing, invasive species, and atmospheric deposition of acids, metals, and organic pollutants (Weyhenmeyer et al., 2009).

A major issue facing lakes throughout Europe is decreasing quality of water resulting from human-induced increase of nutrient concentrations leading to heavy algal blooms. European countries are addressing these stressors by implementing the European Water Framework Directive to protect and enhance aquatic ecosystems and promote sustainable water use across Europe (Carvalho et al., 2019).

Lakes of Asia

The geological history and complex geomorphology of Asia has resulted in a large diversity of natural lakes that vary in age, area, depth, hydrology, water quality, and biodiversity (Gopal and Ghosh, 2009). For example, Asia has the world's largest lake (Caspian Sea), the oldest and deepest lake (Lake Baikal) as well as at the highest (~6000 m) and lowest elevations (Dead Sea, > 400 m below sea level), and with the highest salinity (> 400‰). Most of the natural lakes originated from tectonic activities over the past several million years.

This continent supports over half of the global human population, with consequent pressures on inland waters (including lakes), and a very significant part of the world's biological diversity (Dudgeon et al., 2006). Many lakes in Asia have been modified by human activities to create fishponds, including the introduction of exotic species (Dudgeon, 2000). As a result, there has been a loss in biological diversity and homogenization of the regional biota. Human livelihoods are a paramount consideration in Asia so reversal of these trends will be difficult (Gopal, 2005).

Lakes of Africa

North Africa

North Africa has considerable inland water resources with specialized aquatic flora and fauna. Lake environments are affected by conditions ranging from subhumid to arid so diversity of aquatic life shows much variation (Ramdani et al., 2009). Natural water resources like lakes have significant cultural importance in this area because of the general scarcity of water. Disturbance activities caused by agriculture and development have resulted in modified systems (Fouchy et al., 2019). Without active management that includes traditional methods as well as new innovations, these changes in natural systems will be exacerbated by climate change.

African Great Lakes

The African Great Lakes consist of large, deep rift valley lakes (e.g., Malawi and Tanganyika) and shallower lakes between the Eastern and Western Rifts (e.g., Victoria) (Coulter et al., 1986). Current management problems include over-fishing, increased input of sediment and nutrients, and, in the case of Lake Victoria, loss of endemic fish species and the proliferation of the introduced water hyacinth (*Eichhornia crassipes*). The great biological diversity in these lakes, and the recent loss of much of this diversity from Lake Victoria, present opportunities to examine the relationships between community structure and ecosystem functioning in natural settings (Bootsma and Hecky, 2003).

Lakes of Australia and New Zealand

Although these countries have different water resource concerns (i.e., generally dry Australia vs. wet New Zealand) many of their lakes have experienced similar changes since European colonization, including modified watershed land use, and the associated changes in hydrology, as well as deterioration of water quality (Brookes and Hamilton, 2009; Abell et al., 2019). Lakes in both countries reflect the major regional geological processes, hydrology, and climate leading to tremendous diversity of lakes. Glacial lakes are the most common lakes in New Zealand, and are generally the deepest lakes due to their formation in former glacial valleys.

Lakes in Australia and New Zealand have played important roles in ancient and recent cultural history (Brookes and Hamilton, 2009). Aboriginal and Maori settlements have focused around lakes and rivers. Subsequent European colonization drastically altered the landscape in both countries leading to a general deterioration of water quality. Nutrients, cyanobacteria, and pathogens are the principal water quality concerns (Verburg et al., 2010; Weeks et al., 2015). The main impact of human settlement on the area's shallow freshwater lakes, brackish lakes and lagoons, and deep lakes has been eutrophication along with changes in biological diversity, the introduction of nonnative species, and an increase in the vulnerability of lakes to regime shifts (Schallenberg and Sorrell, 2009; Schallenberg, 2019). Agriculture-related stressors such as sedimentation, nutrient enrichment, and flow regime changes are most pervasive, whereas other stressors either remain more localized (e.g., salinization and mining) or will be of growing concern in coming decades (e.g., climate change) (Matthaei and Piggott, 2019). Climate change will probably intensify stresses related to water scarcity due to hotter temperatures and lower, more variable rainfall.

Lakes of North America

North America contains 8 of the 20 largest lakes of the world, defined as having more than 10,000-km² surface area, all of which were formed by glaciers (Kalff, 2002). Five of these "Great Lakes" are in the Laurentian system, that is, the St. Lawrence River watershed (Superior, Huron, Michigan, Erie, and Ontario), and three others lie entirely in Canada (Great Bear, Great Slave, and Winnipeg) (Hansen et al., 2010).

The last continental glacier left North America with a large number of freshwater natural lakes that extended over the northern half of the continent, mostly north of 40° north latitude (Cole, 1994). Natural lakes are important resources throughout North America and contribute substantial economic benefits (Hansen et al., 2010). Recreational, commercial, and subsistence fisheries are among the most important social and economic values of natural lakes in North America.

Lakes of South America

South America is predominantly a rivers continent (Llames and Zagarese, 2009). As such, many floodplain lakes originate from rivers; particularly, from the Amazon, Orinoco, and Paraná-Plata rivers, which rank among the largest river systems of the world. As a result, the number of typical lakes is relatively small. The factors that determine the diversity of these lakes include geography, geomorphology, and climate.

Most Andean lakes were formed by tectonic activity, volcanism, or glaciers (Llames and Zagarese, 2009). Tectonic and volcanic events were most active in arid regions. Consequently, there are fewer tectonic lakes than glacial lakes in the Andes. Inland lowland lakes tend to be shallow fluvial lakes associated with floodplains of the large rivers of the region. The majority of these floodplains retain most of their natural hydrological characteristics.

Loss of habitat for indigenous plants and animals was the main concern identified for all South American lake ecosystems (Barletta et al., 2010). It may be caused by damming of rivers, deforestation, water pollution, mining, poor agricultural practice, or inadequate management practices. The biological diversity associated with lakes in South America is far from fully known. Continuing loss of habitat for associated species may result in losses of biological diversity before the full diversity of species is known.

Lakes of Antarctica

Despite temperatures well below the freezing point, the Antarctic continent possesses a wide variety of lakes that contain liquid water throughout the year, making them an oasis for life in what would otherwise appear to be an uninhabitable environment (Priscu and Foreman, 2009). Lakes in Antarctica are distributed on maritime islands, along the margins of the continent in ablation regions, and subglacially, beneath the ice sheet. More than 150 lakes exist beneath the ice sheet, many of which may be connected by large subglacial rivers. These lakes may harbor microbial ecosystems isolated from the atmosphere for as long as the continent has been glaciated (i.e., 20–25 million years).

Most of the 17 lakes on ice-free Signy Island lie in the valleys and plains of the narrow, coastal lowland which is usually snow free during the summer (Priscu and Foreman, 2009). The Schirmacher Hills contain several freshwater lakes formed by ice erosion and relict saline lakes formed as a result of the isolation of sea inlets and lagoons. These lakes are fed by melt water from snow beds and ice slopes during the summer. The lakes in Larsemann Hills may have formed from the exposure of basins after the retreat of the continental ice cap or after isolation due to the isostatic uplift following deglaciation.

Following the retreat of the continental ice sheet on the Vestfold Hills about 12,000 years ago, isostatic rebound occurred at a faster rate than sea level rise (Priscu and Foreman, 2009). As the land rose, it cut off fjords and trapped pockets of seawater, creating lakes. The lakes closest to the ice sheet are typically fresh, while those closer to the coast tend to be saline or hypersaline. Over 200 water bodies occur in the Bunger Hills, ranging in size from small, shallow ponds that freeze to the bottom during winter, to Algae Lake, one of the largest and deepest surface freshwater lakes in Antarctica (Priscu and Foreman, 2009). The McMurdo Dry Valleys contain eight relatively large lakes, all of which have permanent ice covers ranging in thickness from ~4 to 7 m (Priscu and Foreman, 2009). Coastal lakes and ponds are distributed around the margins of the Antarctic continent, and are particularly abundant around the ice free areas of McMurdo Sound (Priscu and Foreman, 2009).

Lakes of the Arctic

A major feature of Arctic landscapes is their large number of lakes and ponds, which in some regions can cover up to 90% of the total surface area (Pienitz et al., 2008). Although lakes in the Arctic are formed by nearly all of the processes that lakes are formed by, including the major categories of volcanic, glacial, and tectonic forces, most lakes in this area are formed by thermokarst processes (i.e., thermal erosion of permafrost soils) (Kling, 2009; Rautio et al., 2011). A feature of Arctic lakes is their low biological diversity of aquatic plants and animals, many of which are specialized toward extreme cold, low energy supply, and oligotrophy (Vincent et al., 2013).

Despite their generally isolated geographic locations, the freshwater lakes of the Arctic are subjected to a wide spectrum of environmental stressors (Schindler and Smol, 2006). High-latitude regions are especially sensitive to the effects of recent climatic warming. The depletion of stratospheric ozone over the north, together with the clarity of many Arctic lakes, renders them especially susceptible to damage from ultraviolet radiation. In addition, the long-range atmospheric transport of pollutants has led to elevated concentrations of many persistent organic pollutants (e.g., insecticides, which have never been used in Arctic regions) and other pollutants (e.g., mercury). Rapid development of gas and oil pipelines, mining for diamonds and metals, increases in human populations, and the development of all-season roads, seaports, and hydroelectric dams will also stress northern aquatic ecosystems.

Hydrologic and Geomorphologic Characteristics

The seven main formation processes of lakes are tectonic activity, volcanic activity, glacial activity, fluvial action, aeolic action, anthropogenic action, and marine action (Bek et al., 2019). Lakes are generally characterized by low flow velocity and relatively low inflows and outflows. Vertical stratification appears in deep lakes, while shallow lakes are considered well mixed in the vertical axis (Lewis, 2009). The main hydrodynamic processes in lakes are inflows and outflows, wind shear, vertical circulation, thermal stratification, and gyres and seiches.

The primary parameters used to describe geomorphologic characteristics include lake length, lake width, lake depth, direction of major axis, shoreline length, lake area, lake volume, insulosity, and watershed to lake area/volume (Timms, 2009).

Cael et al. (2017) estimated the volume of Earth's lakes to be 199,000 km³ (95% confidence interval 196,000–202,000 km³). This volume implies an overall mean depth (defined as total volume divided by total area) of 41.8 m. Lake depth has been used for decades as the best estimator of the sensitivity of lakes to nutrient loading (Vollenweider, 1975) and has been proven to be a reliable predictor for primary production and lake transparency (Canfield and Bachman, 1981). The existence of many shallow lakes indicates a large percentage of lakes could be susceptible to eutrophication via nutrient loading with increasing primary production and decreasing transparency.

Biological Characteristics

Photosynthesis is the biological conversion of light energy to chemical bond energy that is stored in the form of organic carbon compounds (Falkowski and Raven, 2013). Approximately 45% of photosynthesis on earth occurs in aquatic environments and

photosynthesis supplies the primary source of organic matter for the growth and metabolic demand of all organisms in lakes (Field et al., 1998; Falkowski and Raven, 2013). Photosynthetic organisms are the primary producers in lake ecosystems (e.g., cyanobacteria, algae, macrophytes) (Uhlmann et al., 2011). The biomass of primary producers is eaten by primary consumers (i.e., animals, from aquatic protozoa to many species of freshwater fish).

The resulting food webs are important characteristics of lake communities (Post et al., 2000). They influence community structure, ecosystem function, and contaminant concentrations in top predators. Geology, hydrology, and land-use have strong influences upon the lake community food web (Allan and Johnson, 1997). A variety of processes at multiple trophic levels create linkages among terrestrial, pelagic, and benthic energy pathways in lake food webs (Schindler and Scheuerell, 2002). Thus food webs provide an important conceptual link between population and community ecology in lakes (Woodward and Hildrew, 2002). Traditional models of lake food webs emphasized the importance of pelagic primary production. However, terrestrial and benthic primary production are equally or even more important than pelagic primary production for consumers in lakes (Solomon et al., 2011).

Plant Communities

Lake area, altitude, trophic state, and water quality have been found to be good predictors of macrophyte species richness for lakes (Murphy, 2002). Among aquatic macrophytes, there are emergent plants such as reeds (Gramineae), submerged vegetation such as milfoil (*Myriophyllum* spp.), and floating-leaved species such as water lilies (Nymphaeaceae) (Uhlmann et al., 2011). Some of the algae are filamentous; others are unicellular or grow in colonies. The richest world hotspots for aquatic macrophyte diversity all lie in the Neotropics (Murphy et al., 2019).

Loss of aquatic vegetation is accelerating in lakes throughout the world, especially submerged aquatic vegetation and particularly in lakes with an area larger than 50 km² (Zhang et al., 2017). Major threats to the survival of lake vegetation include eutrophication, algal blooms, land reclamation, aquaculture cultivation, and global climate change.

Animal Communities

Benthic Invertebrates

Benthic invertebrates are an abundant and diverse group of aquatic animals that are found on or in submerged substrates of lakes (Chaloner et al., 2009). Benthic invertebrate fauna includes representatives of nearly all animal phyla. However, aquatic insects are the most species-rich and abundant group of benthic invertebrates. The shallow littoral zone of lakes typically supports a more diverse invertebrate fauna than deeper water because of higher habitat heterogeneity, more abundant resources, and generally more favorable oxygen conditions. As participants in lacustrine food webs, benthic animals consume phytoplankton, aquatic plants, animals, bacteria, and detritus (Strayer, 2009). Benthic invertebrates are an important food resource for most freshwater fishes and are vital for decomposition of organic materials. Also, large populations of birds, bats, spiders, and other predators are drawn to lakes to feed on benthic animals, including emerging insects (Strayer, 2009).

Mammals

Although numerous mammals are associated with freshwaters and rely on wetland or aquatic vegetation for foraging (e.g., beavers [*Castor* spp.]) (Halley et al., 2012), very few depend on lakes exclusively. Baikal seals (*Pusa sibirica*) are endemic to Lake Baikal in Southern Siberia, Russia, are found only in this lake and connecting rivers, and are the only seals that live primarily in a freshwater lake (Miyazaki, 2018).

Other seals that live in freshwater include subspecies of ringed seals (*Pusa hispida*). The Ladoga seal (*Pusa hispida ladogensis*) is found entirely in Lake Ladoga in northwestern Russia and the Saimaa ringed seal (*Pusa hispida saimensis*) is found in Lake Saimaa, Finland (Sipilä and Hyvärinen, 1998). Colonies of harbor seals (*Phoca vitulina*) live in some lakes, such as Iliamna Lake, Alaska (Boveng et al., 2018) and the Ungava seal (*Phoca vitulina mellonae*) in Lacs des Loups Marins, Petit Lac de Loups Marins, and Lac Bourdel in northern Quebec (Seal, 2018).

Birds

Water birds provide a range of important ecosystem services associated with lakes (Whelan et al., 2008; Green and Elmberg, 2014). “Cultural services” such as providing human recreation, and “provisioning services” such as harvest for meat or feathers, have been in play throughout human history and continue to be important among cultures (Millennium Ecosystem Assessment, 2005; Wenny et al., 2011). “Regulating services” such as pest control, and “supporting services” such as maintaining connectivity for plants and invertebrates in isolated lakes by acting as vectors for dispersal, have received less attention but are also important.

Human influences on lakes can greatly alter the numbers and diversity of water birds (O’Connell, 2009). The total number of water birds on Earth is in decline, and many water bird species are threatened with extinction, although these declines are more acute in some parts of the world than others (Wetlands International, 2014). This will eventually result in reductions of their

positive ecological functions. The decline of water bird populations is likely to have significant negative consequences for lake ecosystems (Şekercioglu et al., 2004).

Fish

The number and diversity of fish species present in lakes generally increases with lake size in response to increases in habitat diversity (Matuszek and Beggs, 1988; Kalff, 2002). Species richness also responds to spatial, physical, chemical, and connection characteristics of lakes during their formation and development (Hansen et al., 2010). As a result, characteristic assemblages of fish are associated with specific type of lakes (e.g., cold water, cool water, warm water).

Recreational use of fisheries tends to predominate in lakes, especially in North America, but commercial and subsistence fisheries are also important uses of fish (Hansen et al., 2010). Recreational fisheries tend to rely on angling as the preferred method for securing fish. Commercial and subsistence fisheries rely on a greater variety of capture methods, including gill netting, trap-netting, angling, long-lining, and spearing.

Commercial Uses

Fisheries

Commercial fisheries in fresh water lakes have declined throughout Europe (Dill, 1993; Cowx, 2015). After slow expansion through the 1950s–1980s, catches have declined steadily over the past 25 years, more so in the north and west than in Eastern countries. For example, even though the commercial harvest of fish in fresh waters in Central and Eastern Europe (CEE) is declining, it continues to contribute to the livelihood of a large number of people (Aps et al., 2004). The total freshwater fish catches of all CEE countries decreased over 27% during the last decade of the 20th century.

Commercial fishing was an important industry during the settlement and development of the Laurentian Great Lakes region in North America (Brenden et al., 2013). From the late 1930s through the 1970s, the value of United States and Canadian commercial fisheries were relatively stable, with slight increases during the late 1940s and early 1950s due to increased yields of some species and increased demand following World War II. The value of harvested fish increased steadily from the 1970s through the early 1990s due to the recovery of native species, development of fisheries for exotic species, and worldwide increase in demand and prices for fishery products. Since the peak in 1992, value of commercial fishery yields have declined annually by 3.5% in the United States and 1.7% in Canada.

Lake Tanganyika, Africa's oldest and deepest (1470 m) lake, produces outstanding freshwater biological diversity and endemism (Cohen et al., 2016). It also provides up to 200,000 t of fish annually, comprising ~60% of regional animal protein consumed. Lake Malawi's fishes are a source of food for millions and provide a livelihood for thousands by encouraging tourism (Weyl et al., 2010). Lake Victoria (Tanzania side) accounts for over 60% of the total national inland fish production of Tanzania (Mgaya, 2012). However, declines in fish yields and shifts in species composition are serious concerns in the African Great Lakes of Tanganyika, Malawi (Nyasa/Niassa) and Victoria (Irvine et al., 2018). Despite management and regulatory structures, all the lakes remain as open-access fisheries, severely depressing yields, economic returns, and threatening biological diversity.

Shipping

Both lake vessels and ocean going vessels are used for international shipments in the Laurentian Great Lakes (Millerd, 2007). Lake vessels move grain and other agricultural products from Great Lakes ports to the lower St. Lawrence River and Gulf of St. Lawrence for trans-shipment. Both lake and ocean going ships move cargo into and out of the Great Lakes. Many ocean going ships will bring iron and steel products into the lakes and take out grain. Lake ships moving grain out of the lakes to the lower St. Lawrence River or Gulf of St. Lawrence will often take on a cargo of iron ore at a Gulf of St. Lawrence port for delivery to a Great Lakes steel mill.

Habitat Change

Eutrophication

Cultural eutrophication is thought to be the most widespread stressor of habitat for plants and animals in natural lakes (National Academy of Sciences, 1969; Hansen et al., 2010). This is particularly important because of its influence on health and food production associated with lakes in densely populated areas (Smith, 2003). About 30–40% of lakes worldwide are affected by unnaturally high nutrient concentrations leading to eutrophication (Uhlmann et al., 2011). Indications of eutrophication are high turbidity caused by algal blooms, dense macrophytes growths, food-web changes, mass development of toxin-producing cyanobacteria (i.e., blue-green algae), reduced species diversity, oxygen depletion, enrichment of reductive substances (e.g., toxic hydrogen sulfide), fish kills, and odors. Cultural eutrophication occurs when nutrients, primarily phosphorus and nitrogen, enter lakes from runoff or streams draining cattle feedlots, fields fertilized with chemicals or manure, sewage outfalls, or urban areas, at rates that exceed the decomposition rate in the lake (Kalff, 2002). The resulting oxygen deficit leads to kills of fish and other biota during

summer when stratification separates the hypolimnion from oxygen sources (photosynthesis and atmospheric oxygen) and in winter when ice and snow prevent photosynthesis and oxygen replenishment from the atmosphere.

Acidification

After eutrophication, acidification is the most important threat and stress factor for lakes (Uhlmann et al., 2011). Acid deposition has changed the natural water chemistry and the biological structure in 50,000–100,000 lakes and watercourses in Europe and North America. Acid rain is caused when burning coal produces sulfuric acid and nitric acid that are subsequently transported by wind to down-wind lakes (Haines, 1981). The vulnerability of lakes to acid rain is determined by their acid neutralizing capacity which is indexed by alkalinity. Areas underlain by limestone are less vulnerable to acidification even in the presence of acid rain (Hansen et al., 2010). Species richness in lakes is positively correlated to pH so acidification may negatively affect the number of species occupying lakes (Graham, 1993). Biota is also influenced by indirect consequences of acidification, such as increased release of potentially toxic metal ions (in particular aluminum, copper, cadmium, zinc, and lead) from soils and sediments (Uhlmann et al., 2011).

Shoreline Alteration

Alterations to shorelines of lakes through natural or anthropogenic forces may affect biological diversity in a variety of ways (Hansen et al., 2010). Human alterations to the riparian and littoral zones of lakes include aquatic and terrestrial vegetation removal, construction, dredging or filling on or near the shoreline, sand deposition, submerged woody debris removal, or seawall construction. Alterations such as these lead to accelerated rates of erosion and sedimentation, increased eutrophication, loss of aquatic plants and plant diversity, and invasion of nonnative plant species.

Invasive Species

Invasion of lakes by exotic species influences both physical and chemical environments in the littoral zone influencing abundance (Miranda and Pugh, 1997), survival (Miranda and Pugh, 1997), and growth (Olson et al., 1998) of native species.

Fish

Many lakes have experienced ecosystem changes due to invasive species (e.g., Smith et al., 2015). With their widespread distribution and likely more generalist habits, nonnative invasive fish may be contributing to the erosion of overall functional diversity of lacustrine fish assemblages (Kovalenko et al., 2019).

Invertebrates

Alien invertebrates are being discovered at increasing rates in large freshwater systems (Ricciardi, 2015). Multiple factors may be involved but human activities probably facilitate the majority of introductions. Rates of invasion by freshwater invertebrates in the Laurentian Great Lakes appear to be orders of magnitude greater now than before human influence (Ricciardi, 2006). Molecular evidence has shown that the current rate of invasion of North American lakes by European cladocerans is ~50,000 times greater than the prehistoric rate (Hebert and Cristescu, 2002).

Plants

Invasive plant species in lakes, and the associated large increase in biomass, strongly influences biological diversity in lakes (Hussner et al., 2009; Strayer, 2010). Invasive macrophytes can strongly modify local conditions in lakes, particularly water temperature, sediment chemistry, and nutrient cycling in the colonized area (Ribaudou et al., 2018).

Pollution

Contaminants of greatest concern in natural lakes, such as organochlorines, heavy metals, and mercury, are problematic because they are toxic, persistent, and often lipophilic, so they biomagnify and bioaccumulate in the biota (Kalff, 2002; Hansen et al., 2010). Contaminants have been linked to increased incidence of tumors in fish and possibly reproductive inhibition, but the most serious effects are felt in fish-eating birds and humans (Hansen et al., 2010). Therefore, birds and humans that eat contaminated fish are likely to suffer chronic effects related to toxicity of such substances.

Climate Change

Aquatic ecosystems are very vulnerable to climate change which influences the physical, chemical, and biological structure of lakes (Uhlmann et al., 2011). These influences include fluctuating water levels, increased water temperature, shorter ice-cover periods, invasion of nonindigenous animal and plant species from tropical and subtropical regions, and structural changes in catchment areas (e.g., soil erosion and land use). Most climate-change scenarios also show that the risk of eutrophication will increase due to a warmer climate.

Conservation and Management

Cultural Eutrophication

Methods for reducing nutrient levels that may cause cultural eutrophication include approaches that reduce (1) nutrient inputs (e.g., sewage treatment, wastewater diversion, wetland protection or construction, and buffer strips), (2) in-lake nutrient loads (inactivating phosphorus by adding aluminum sulfite, increasing phosphorus oxidation by adding lime, dredging nutrient-rich sediments, and harvesting aquatic macrophytes), or (3) oxygen-deficient water (pumping or aerating hypolimnetic water (Kalff, 2002; Hansen et al., 2010)).

Invasive Species

Many invasive species are invasive in a fraction of locales to which they are introduced, meaning that natural processes regulate their abundance at most sites (Bajer et al., 2019). It would be very valuable to understand what these limitations are and exploit them to design integrated pest management strategies based on natural processes.

Exotic plant species

Invasive aquatic plants may be removed or reduced by mechanical harvesting, application of herbicides, or stocking of plant-eating fish or invertebrates (Kalff, 2002). Target plants may be removed from all or selected areas of lakes using mechanical harvesters or herbicides, depending on objectives (e.g., beach esthetics, swimming) (Hansen et al., 2010). Mechanical harvesting has the advantage of removing plant biomass from the lake, while herbicides leave plant biomass in the lake for recycling of nutrients. Introducing plant-eating fish that feed on all plants, or plant-eating insects, that feed on single or a few target species of plants may be effective. However, introducing fishes and insects as biological agents for plant control may be risky because lakes are never closed systems, so introduced fish and insects, most of which are nonnative species, are likely to move to other lakes and rivers.

Invasive fish and invertebrates

Biological control is an approach to control populations of invasive species with other species. Means of biological control may include predators (Symondson et al., 2002), parasites or pathogens (Saunders et al., 2010), consumers (Malecki et al., 1993), or genetically modified organisms (Thresher et al., 2014). However, biological control of invasive fish and aquatic invertebrates remains rudimentary with only a few examples of success (Bajer et al., 2019). Control of invasives is still based primarily on physical removal by humans or predation by native species.

Acidification

Short-term treatment of acidification is possible through addition of lime (CaCO_3) directly to a lake (Clair and Hindar, 2005). Lime can be added to the entire lake surface but application of lime to specific areas of a lake may adequately increase pH enough to increase survival of organisms (Hasselrot and Hultberg, 1984). The only long-term solution to acidification is to reduce use of fossil fuels that produce acid constituents during combustion or to make combustion cleaner (Haines, 1981; Kalff, 2002).

Contaminants

The only apparent remedy is to eliminate sources, although aerial transport of contaminants makes elimination extremely difficult (Hansen et al., 2010).

Conclusions

Lakes world-wide are experiencing negative effects associated with increasing anthropogenic changes resulting from a growing human population and related development (Jeppesen et al., 2017). Consequently, many lakes are highly eutrophic and suffer from severe blooms of often toxic cyanobacteria and may become even more eutrophic in the future unless strong lake management actions are taken. Recent research has further shown that global warming and subsequent changes in water use will further

exacerbate eutrophication and invasive species in lakes. There is a growing need for expanded restoration of lakes and understanding and implementation of sustainable lake management.

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Lotic Freshwater: Springs

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Abstract

Springs are a unique resource from an ecological, economic, and cultural perspective. Springs harbor highly specialized and regionally restricted flora and fauna, often resulting in a unique freshwater biological diversity. Springs serve as evolutionary refugia, supporting concentrations of relict and endemic species that require habitat stability. Springs also provide a source of freshwater for personal human use and commercial sales. Major threats to springs include human draining and diversion of groundwater sources, pollution, alteration of habitat for associated flora and fauna, and invasive species. Moreover, restoration efforts are expensive and ecological responses to restoration are largely unknown. The safest management strategy is to refrain from potentially harmful land use within the vicinity of springs.

Introduction

In the early days of civilization, springs were regarded as sacred places (Williams, 1991). Springs provided refuges in arid landscapes and have been critical to the survival of indigenous peoples and also to European explorers and settlers (Scarsbrook et al., 2007). Springs were a reliable source of water for numerous human activities (e.g., irrigation, farming, mining, drinking) (Barquín and Scarsbrook, 2008).

Springs are unique from an ecological, economic, and cultural perspective (Rossi et al., 2015). Springs harbor highly specialized and regionally restricted flora and fauna, often resulting in unique freshwater biological diversity (Cantonati et al., 2012). Springs also serve as evolutionary refugia, supporting concentrations of relict and endemic species that require habitat stability (Davis et al., 2013).

Hydrologic and Geomorphologic Characteristics

Springs are formed when the water table intersects with the earth's surface, or groundwater rises to the surface through rock faults, fractures, or depressions (Death et al., 2004; Scarsbrook et al., 2007). Springs vary greatly in morphology and size, including minor seepages from bedrock faces, to resurgences in karst (e.g., the Bouillon de La Source resurgence, Albéric, 2004), up to very large vents discharging many thousands of liters per second (e.g., Homosassa Springs Group, Citrus County, Florida, USA). Thus, the main environmental drivers of spring ecosystems are the quantity and quality of groundwater inflow (Rossi et al., 2015). Natural variations in groundwater quantity and quality are controlled by a range of hydrogeological factors such as geology, topography, land cover, and recharge (Kresic and Stevanovic, 2009).

The distribution of springs is largely controlled by the volume and extent of groundwater recharge, the permeability of the geologic materials through which groundwater moves, geologic structure and faults, and topography (Cartwright and Johnson, 2018). A survey of 137 springs in the Crooked River subbasin of central Oregon revealed the hydrogeologic setting affects spring discharge type, temperature, and pH (Freed et al., 2019). Additional work in Iceland showed that spring type, temperature, and pH significantly subsequently influenced invertebrate community structure (Govoni et al., 2018).

Biological Characteristics

Springs provide stable habitats over years and even decades because their water comes from thermally buffered underground sources (Glazier, 2009; Kreiling et al., 2018). They are a transitional environment between cave conditions and surface stream

conditions. As such, springs provide benefits for a variety of aquatic and terrestrial organisms such as moisture, drinking water, food, minerals, shelter, thermal refuges, breeding sites, and travel corridors (Glazier, 2009; White, 2019).

Animal Communities

The relative constancy of the water temperature and flow rate of many springs affects the biotic composition in springs. Non emergent macroinvertebrates may have a competitive advantage over many insects in constant temperature springs because they can reproduce and maintain dense populations year-round, whereas insects must seasonally leave the water to breed as adults (Glazier, 2009). Non insect species are the most abundant macroinvertebrates in 78% of spring systems for which data are available. Macroinvertebrate abundance and diversity are influenced by consistent water flow, size of spring, substrate type and macrophyte density. The abundance and diversity of vertebrates may also be influenced by food availability; light conditions; substrate type; human influences; and water temperature, chemistry, and flow rate (Glazier, 2009).

Fish typically occur in large and persistent springs located on valley floors; few high-elevation springs are occupied by fish (Sada et al., 2001). These spring-dwelling fish are primarily threatened by establishment of nonnative fishes and macroinvertebrates and alteration of their habitat from water diversion for personal use and agriculture, excessive livestock grazing, and depletion of groundwater.

Commercial Uses

Springs have provided an obvious source of freshwater for human use (White, 2019). Villages and towns have grown up around springs because of the convenient supply of high-quality water. This has led to bottling and sale of spring water (LaMoreaux and Tanner, 2001). Some springs also attract thousands of tourists for sight-seeing (e.g., Silver Springs, Florida, USA) and bathing in warm, mineral waters.

Habitat Change

Springs throughout the world are not being properly managed and conserved and are disappearing rapidly, especially in arid regions (Glazier, 2009). Major threats to springs and their inhabitants include human draining and diversion of groundwater sources, pollution, alteration of habitat for associated species, and invasive species. Freed et al. (2019) found a high frequency of anthropogenic impacts on springs: 95% of diffuse-discharge springs and 79% of discrete-discharge springs they evaluated were disturbed by livestock grazing.

Pollution

Due to the rapid recharge and high velocities associated with karst aquifers, karst springs usually show high discharge dynamics. As a result, water quality often deteriorates very quickly following storm events due to the presence of contaminants such as pathogens, heavy metals, or pesticides (Schipperski, 2018).

Climate Change

As a result of climate change, hydrological cycles in many areas of the world have already been altered or soon will be (IPCC, 2014). Nevertheless, the groundwater supply to springs buffers surface and soil temperatures resulting in climate resilience of springs in some areas (Fernández-Pascual et al., 2015). Springs are potential hydrologic refugia from climate change (Cartwright and Johnson, 2018). Persistent wet or mesic microenvironments in springs that are relatively unassociated with regional climate could support climate resilience for natural communities (McLaughlin et al., 2017). Such hydrologic refugia may be particularly important in regions where droughts intensify (i.e., become more frequent or severe) as a result of climate change (Dai, 2012).

However, if water temperatures in springs do increase by several degrees there will likely be substantial impacts on biological diversity, causing regional extinctions of native, cold-stenothermal spring specialists (Jyväsjärvi et al., 2015). Even a slight (e.g., 1 °C) increase in water temperature may eliminate endemic spring species, thus altering bryophyte and macroinvertebrate assemblages of spring-fed streams.

Conservation and Management

Globally, springs suffer from groundwater depletion (Konikow and Kendy, 2005), contamination (e.g., nitrates, metals) (Laini et al., 2012), and anthropogenic disturbance (e.g., peatland drainage, livestock) (Aapala et al., 2013; Freed et al., 2019). Effective

conservation of spring-dependent ecosystems requires practical and cost-efficient means of identifying springs that are most likely to maintain their hydrologic and ecological functions within the landscape over time (Cartwright and Johnson, 2018). Because restoration efforts will be expensive and ecological responses to restoration are largely unknown, it may be necessary to emphasize springs that provide hydrologic refugia rather than those that may be influenced by climate change (Costelloe and Russell, 2014; Lehosmaa et al., 2017a,b). Restoration has been demonstrated to enhance the quality of habitats for species associated with springs; enhancement of biological diversity was detectable a few years post-restoration (Lehosmaa et al., 2017a,b).

Conclusions

Effective management of springs needs to consider the environmental and societal values associated with them, understand the threats to the sustainability of springs, and formulate strategies that provide a balance between potentially conflicting uses (Barquín and Scarsbrook, 2008).

Areas where spring ecosystems have been degraded by human alteration (Barquín and Scarsbrook, 2008; Ilmonen et al., 2013) will need restoration initiatives for long-term conservation of spring-dependent biological diversity. Without restoration measures that improve groundwater hydrology, the self-recovery potential of springs is very low. As little is currently known about the effectiveness of spring restoration in addressing the loss of biological diversity in springs, the safest management strategy is to refrain from potentially harmful land use within broad buffers around springs (e.g., > 40 m) (Selonen and Kotiaho, 2013; Lehosmaa et al., 2017a,b).

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Stream Biomes of the World

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Abstract

Streams comprise only a small portion of Earth's terrestrial surface area yet harbor a significant amount of the world's biodiversity. These ecosystems also support many services to human society predisposing them to ecosystem alteration and leaving a very small percentage of streams in their natural state. Given their rarity and propensity for human disturbance, understanding stream structure and function, and how to conserve those properties, is extremely important. This chapter provides an overview of stream environments, their form and function, the organisms that inhabit them, and ecological concepts and paradigms. An overview of major types of commercial uses is provided, which correlates with anthropogenic stressors and the nature of ecosystem alteration. Finally, the chapter concludes with approaches and strategies for stream conservation and management.

All streams flow into the sea, yet the sea is never full. To the place the streams come from, there they return again.
Ecclesiastes 1:7

Introduction

Freshwater is rare on planet Earth. The majority of the world's water is found within oceans, whereas only 0.01% of surface water occurs within rivers, lakes and wetlands. Despite the rarity of freshwater environments, these ecosystems support a disproportionate amount of the world's biodiversity, boasting 126,000 species or at least 7% of Earth's described species ([Dudgeon et al., 2006](#); [Balain et al., 2008](#)).

Lotic systems are even rarer than other freshwater environments, but they play important roles in connecting aquatic and terrestrial environments. Streams constitute over 88 million km of ribbons connecting upland areas to oceans yet these environments comprise < 0.6% of the Earth's land surface ([Downing et al., 2012](#)). Natural freshwater lakes constitute over 4 million km² ([Downing et al., 2006](#)), which is over six times more area than rivers. However, the cumulative length of rivers is 21 times longer than the total shoreline perimeter of world lakes and 46 times longer than the world coastline ([Downing et al., 2012](#)). Hence, streams and rivers likely play significant roles in freshwater's interaction with the terrestrial landscape, including the transportation and modification of materials from terrestrial sources.

The longitudinal directionality of moving water, in concert with dynamic lateral connections to the adjacent terrestrial environment, craft the uniqueness of stream ecosystems and the organisms that inhabit them; however, these properties also render streams challenging systems to study. Additionally, moving water provides many valuable ecosystem services, which have been over-exploited by humans and led to many of the world's river basins existing in highly altered states. Given the rarity of these systems, future protection and conservation of river environments will be critical for provision of future ecosystem services and sustaining aquatic biodiversity.



Fig. 1 Example of the variety of stream types and morphologies. (A) Stream in Canaan Valley State Park, West Virginia (photo: Ben Fertig), (B) Old Woman Creek, Ohio (photo: Alexandra Fries), (C) Cheakamus River, British Columbia (Photo: Adrian Jones), (D) Colorado River at Horseshoe Bend, Arizona (photo: Catherine Ward), (E) Sand dunes in Chippewa River, (photo: David Dean, USGS), (F) waterfall in Glacier National Park, Montana (photo: Ryan McManamay), (G) examples of gravel and cobble bars in the Middle Fork Flathead River, Montana (photo: Ryan McManamay). Photographs (A–D) were available from the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

What Is a Stream?

At a most basic level, a stream is a channel that carries water downhill from surrounding landscapes (Fig. 1). Streams range in size from small channels carrying occasional pulses of flow ($<0.03 \text{ m}^3 \text{ s}^{-1}$) during rainfall events to large systems, such as the Amazon River (Brazil), with discharges exceeding $200,000 \text{ m}^3 \text{ s}^{-1}$. Precipitation that falls on land evaporates, infiltrates the soil, or is shunted overland directly to streams (i.e., overland flow). Lateral flow refers to water that infiltrates the soil and flows downstream through the soil to a stream. Alternatively, water that infiltrates the soil may percolate to deeper soil horizons, where it enters groundwater (the water table).

Many streams carry surface water only a fraction of the time, and some only convey water during precipitation events. The latter type of stream is called an ephemeral channel, whereas streams carrying water at least a portion of year during the wet season are termed intermittent streams (Fig. 1B). Perennial streams, on the other hand, carry water year-round but can range dramatically in the duration of water conveyance. Some streams have continual wetted perimeters, whereas intermittent systems may have long periods of drying. Furthermore, sub-surface water flow may occur in streams where surface flow is not apparent. In karst terrain, “losing” reaches occur where streamflow decreases with downstream distance, only to re-emerge downstream.

Where groundwater intermixes with surface water is called the hyporheic zone. The hyporheic zone is the porous space beneath and alongside a stream bed, where shallow groundwater and surface water combine. Hyporheic flow is important for fish spawning and other biological processes. For example, salmonids build nests (“redds”) in upwelling and downwelling areas of stream gravel where eggs can incubate in a stable, groundwater-influenced thermal environment and metabolic wastes from developing eggs and larvae are removed by water fluxes into or from the sediment (Bjornn and Reiser, 1991; Groves and Chandler, 2005). For fall-spawning salmonids, the risk of freezing is lower in gravels with hyporheic exchange.

Physical Properties of Streams

Hydrology is the defining principle of stream environments, and accordingly, the amount of flow a stream carries has been used to classify different types of streams. To provide an inventory of streams in the landscape, however, it would be impossible to directly measure discharge ($\text{m}^3 \text{ s}^{-1}$) in all waterbodies. Horton (1945) and Strahler (1957) devised a classification for mapping streams based on identifying stream segments in maps; however, the granularity of such a system depends on the scale of each map. The smallest ephemeral streams are mapped as a 0-order streams, and where two ephemeral types join form a headwater stream—a 1st order stream, and the junction of two type 1 streams form a 2nd order stream, and so on (Fig. 2). However, each order is dependent upon the junction of two equally sized systems. For instance, the junction of a 1st and 2nd order system only results in a 2nd

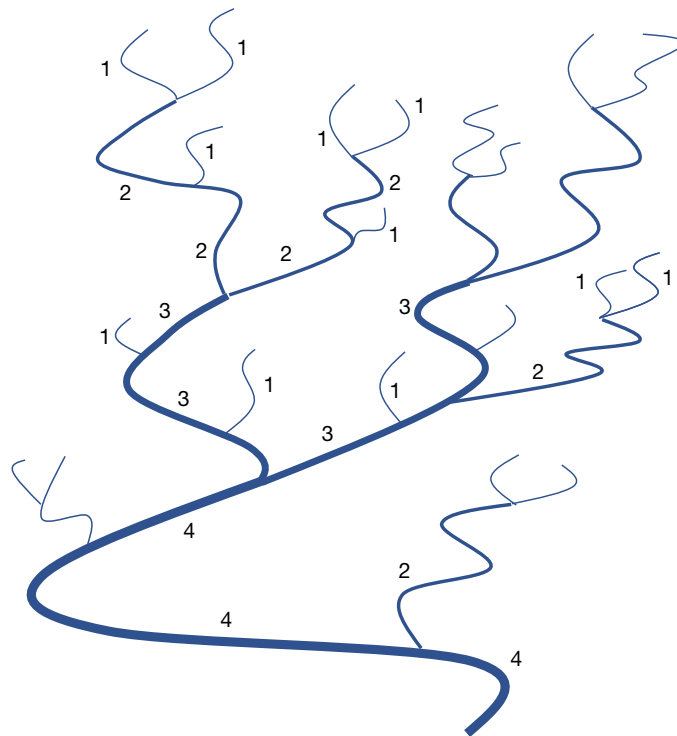


Fig. 2 Strahler stream order diagram.

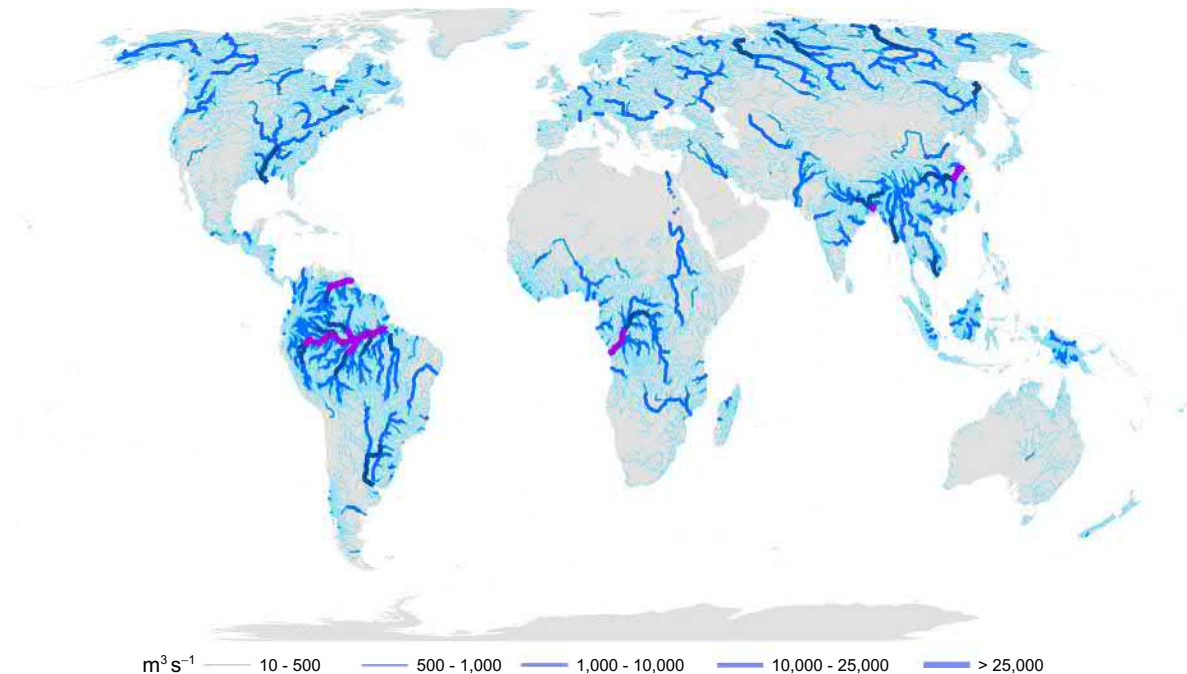


Fig. 3 Distribution of global rivers and their discharge. Data from Ouellet Dallaire et al. (2018).

order stream. The frequency of stream sizes in the landscape follows an exponential decay of abundance versus size, where headwaters are the most numerically abundant, comprising 52% of the total global stream length, and 12th order rivers are the rarest, comprising only 0.007% (Downing et al., 2012).

Each continent has a large river (Fig. 3) where size can be measured by total length or flow. Measuring the length of a river is challenging, and estimates remain uncertain. The Nile and Amazon Rivers are considered the two largest rivers. The Nile flows north across North Africa for 6650 km. Originating in the Andes Mountains on the South American continent, the Amazon River (~6400 km) is located mostly in Brazil and carries 7% of freshwater flow in the world ($209,000 \text{ m}^3 \text{ s}^{-1}$), more than any other river. Another major South American river is the Parana River (4880 km). The Chang Jiang (Yantze) River is 3rd longest in the world and the longest river on the Asian continent (6300 km). In North America, the fourth longest river is the Mississippi-Missouri River (5971 km). The Yanisei (5539 km) and Yellow Rivers (5454 km) are two major river systems on the Asian continent running through Mongolia and China, respectively. In Russia, the Ob River is a major river that runs 5463 km from the Altan Mountains to the Arctic Ocean. Australia is relatively dry continent. Its longest river is the Murray River (2508 km).

Streams are nested dendritic networks. Frissell et al. (1986) developed a hierarchical stream classification as a convenient way to represent the scale-dependence of stream habitats. At the coarsest level are watersheds or stream systems (10^3 m), representing the riverine landscape. The next levels are represented by stream segments (10^2 m), followed by stream reaches (10^1 m), meso-habitats (10^0 m , e.g., riffle, run, pool), and finally microhabitats (10^{-1} m).

Stream characteristics are determined by properties of the watersheds they drain and their hydrology reflects those characteristics (Hynes, 1975). Stream hydrology depends on the climate regime and properties of the watershed, such as topography and soil infiltration capacity. For instance, watersheds with low infiltration capacity (e.g., clay soils) shunt water quickly downhill and result in flashy, episodic hydrology, whereas watersheds with high rainfall and deep organic soils can store water and lead to high and stable baseflow conditions. A streams' hydrologic regime is quite specific, also referred to as its hydrologic signature (Fig. 4).

Streamflow is typically measured as discharge (e.g., $\text{m}^3 \text{ s}^{-1}$), which is a product of the stream's cross-section, its depth, and its velocity (Fig. 4). Flow regimes are partitioned into two main parts, baseflow (the sum of deep subsurface flow and delayed shallow subsurface flow) and event flow (elevated flows that occur following precipitation or snowmelt events). Flow regimes can be characterized by statistics including the magnitude, timing, duration, frequency, and rate-of-change of flow events. One controversial concept is that these statistics, when derived from unregulated rivers in pristine watersheds, comprises a stream's "natural flow regime" (Poff et al., 1997). A stream's flow regime influences material transport, channel and habitat structure, physiochemical characteristics, and the ecological communities that depend on these properties.

Fluvial geomorphology is largely governed by strong relationships among catchment area, discharge, stream width, slope, and sinuosity (Leopold, 1994; Frasson et al., 2019); hence, these relationships typically push streams toward a state of dynamic equilibrium, where changes in one geomorphic component result in changes to others (Leopold, 1994). Even so, a stream's hydrology interacts with the channel and surrounding floodplain in complex ways. In narrow valleys of mountainous terrain, streams are confined to a single channel (Fig. 5A), whereas in broad valleys streams are able to migrate laterally, even becoming braided

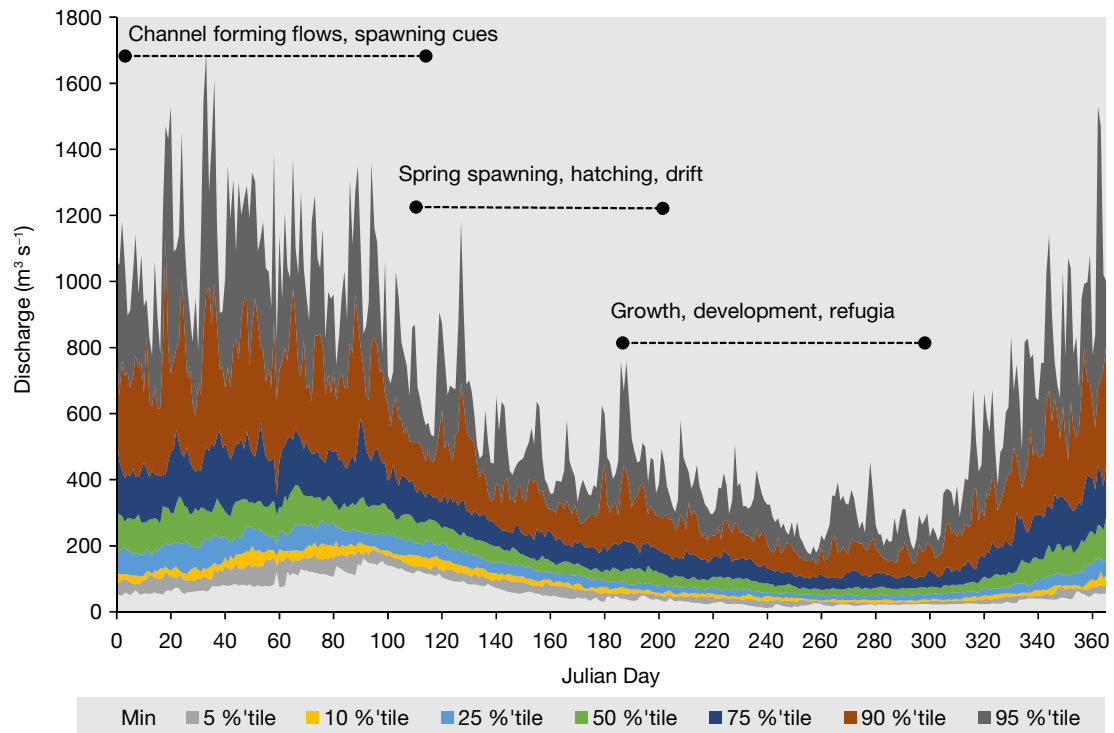


Fig. 4 Hydrologic regime for the Valley River, North Carolina, United States. Percentile statistics of discharge were calculated for each day of the year for US Geological Survey stream gage 03550000. Annual phases of the hydrograph are associated with life histories of many fish, especially spawning and recruitment.

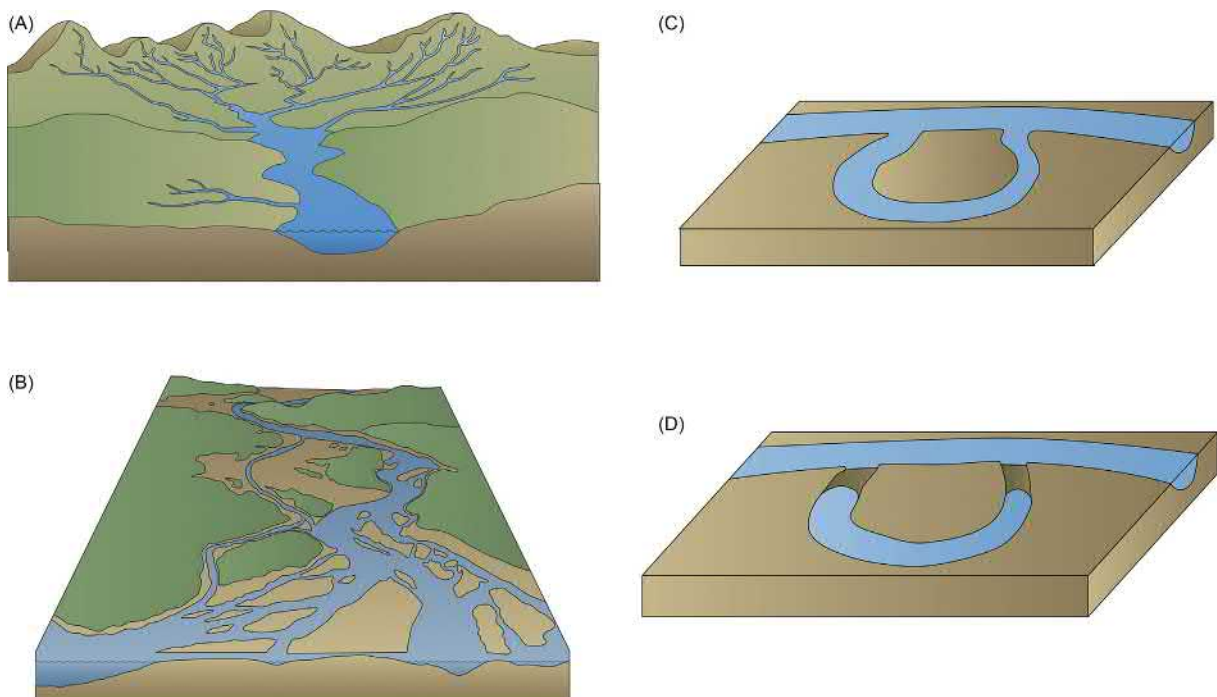


Fig. 5 Stream channel variation with respect to valley topography and floodplain interaction. (A) steep confined channels have less floodplain interaction, whereas in (B) coastal low-gradient rivers, floodplains are more extensive. (C) The initiation of oxbow formation occurs in highly sinuous rivers where bends become side channels, and eventually (D) are completely cut off from routine flows. Diagrams provided by Tracy Saxby, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

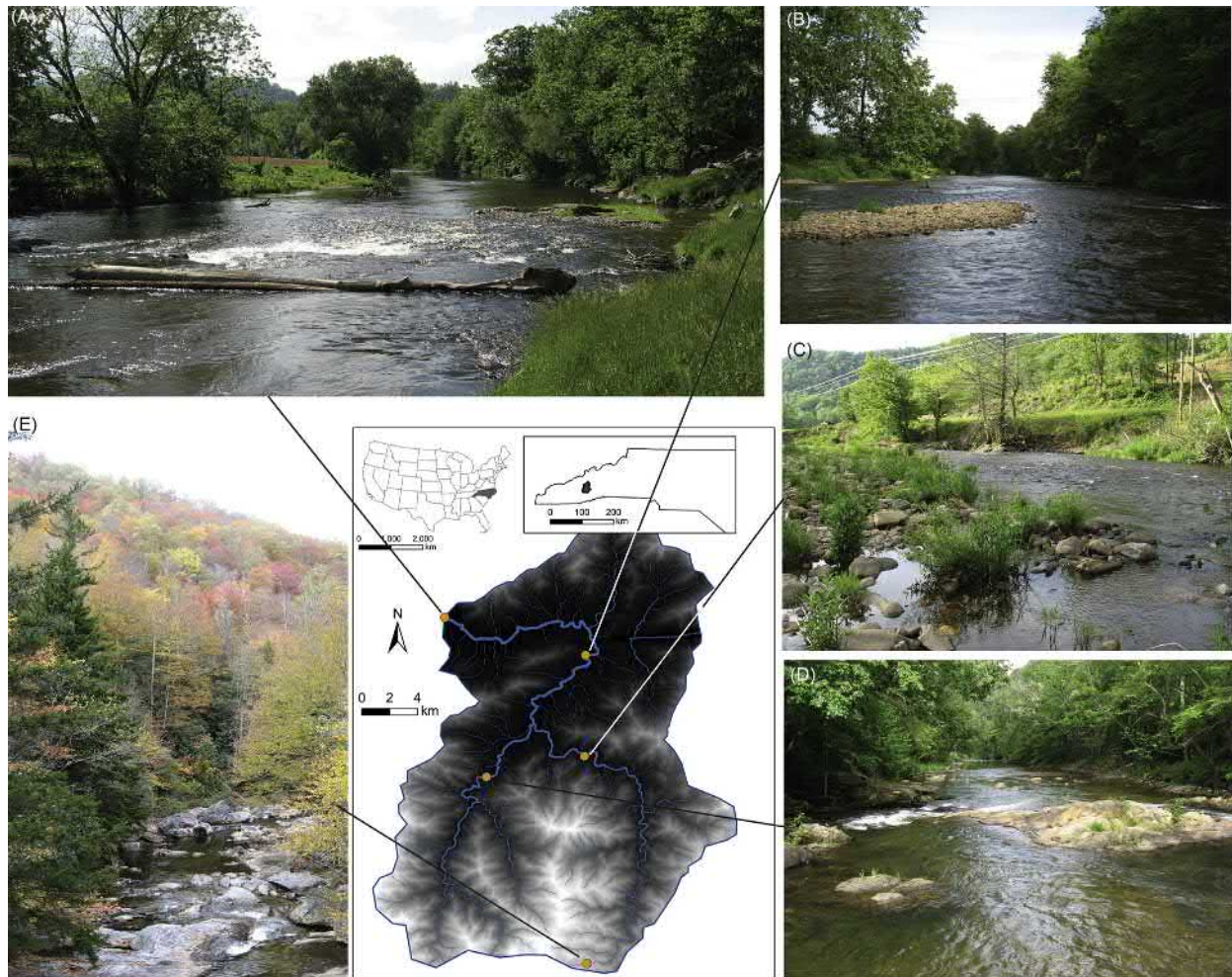


Fig. 6 Longitudinal variation in geomorphology of the Pigeon River, North Carolina (United States) from steep mountainous terrain to broad valley with high interaction between the channel and floodplain. A clear progression from narrow and confined channels dominated by boulder and bedrock substrate to wider channels with extensive floodplain interactions and finer substrates of gravel and sand. (A) Pigeon River near Clyde, (B) Pigeon River above Canton, (C) East Fork Pigeon River, (D) West Fork Pigeon River below Lake Logan, (E) headwaters of East Fork Pigeon River. Photographs by Ryan McManamay.

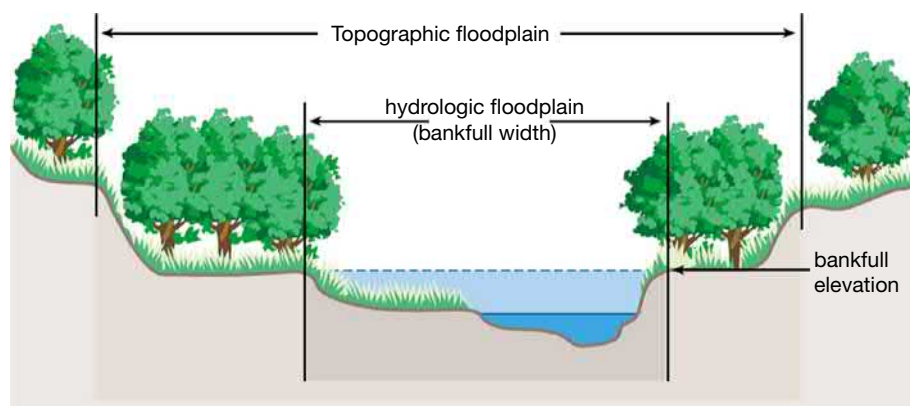


Fig. 7 Cross-section showing channel, bankfull width, and floodplain. Source: US Federal Interagency Stream Restoration Working Group. 1998. Stream Corridor Restoration: Principles, Processes, and Practices. GPO Item No. 0120-A; SuDocs No. A 57.6/2: EN3/PT.653. ISBN-0-034213-59-3.

with multiple channels (Fig. 5B). The longitudinal transition in geomorphology caused by confined valleys in mountainous terrain to unconstrained valleys can be observed in the Pigeon River Basin in western North Carolina, United States (Fig. 6).

When river flow is constrained within one channel (Fig. 7), the maximum discharge this channel can accommodate is termed the bankfull flow. The elevation of this flow within the channel can be determined based on morphometrics and physical marks on the stream bank (Fig. 7). Discharges exceeding the bankfull flow migrate into the floodplain. The frequency of bankfull flows (defined as inundating 1st floodplain) varies among streams and regions, although it typically re-occurs every 1.5–2 years. Bankfull flows are extremely important to maintaining channel dimensions and morphological units, such as the location of riffles and pools, their sequential pattern, and the location and extent of point and lateral bars (e.g., Fig. 1G, bars are deposits of stream material following high flow events) (Trush et al., 2000). Flows that inundate the floodplain may be constrained by a secondary channel. In this case, a secondary floodplain can exist (Fig. 7).

Stream channels and floodplains are dynamic (Fig. 8). Over time, stream channels evolve in response to physical disturbance regimes, such as changes in discharge (Fig. 8). The morphology of a stream depends on geomorphic properties of the surrounding valley, extreme flood events, and physical obstructions to flow, such as large woody debris (LWD). In steep tributaries, landslides caused by wildfire and/or high flows supply LWD and sediment, including large cobbles, to streams (Benda et al., 2004). At a local scale, LWD provides a focal point for deposition of fine sediments. Debris in channels creates roughness (i.e., resistance to flow), alters hydraulics, and tends to increase sinuosity and produce riffle-pool sequences. Rules describing the frequency of riffle and pools and relationships with sinuosity have been developed (Leopold, 1994). Typically, in broad valleys, channels increase in sinuosity over time and with distance downstream. They create slow-shallow habitats, such as oxbows and often become more braided in lower reaches (Fig. 5C). Over time, oxbows are eventually cut off from the main channel (Fig. 5D, Kramer and Wohl, 2017).

Streamflow is erosive and its ability to shape channel morphology depends on stream power (the magnitude of flow, along with gradient) and the particle size of substrates or roughness. Sand-dominated channels (e.g., Fig. 1E) will likely shift more than

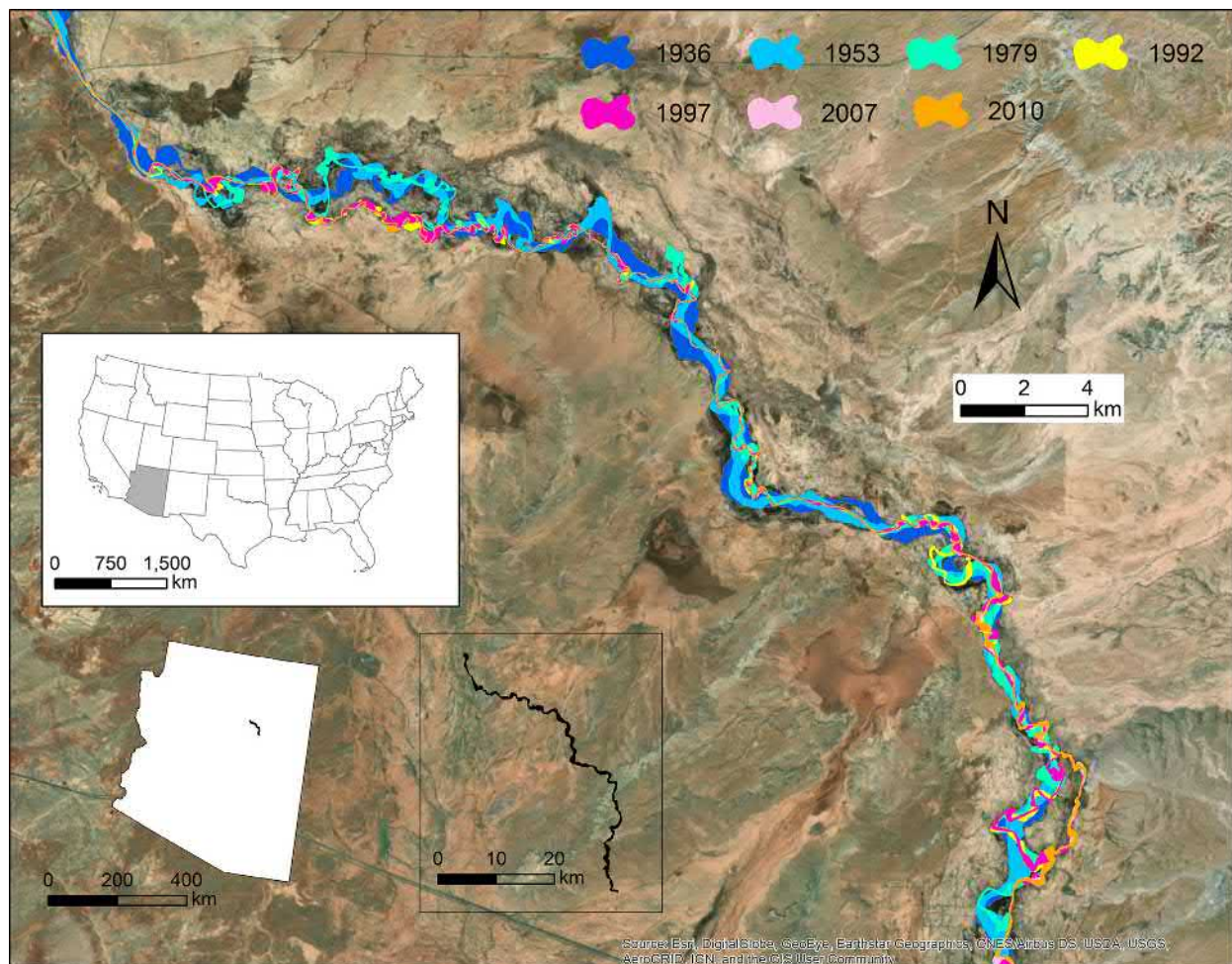


Fig. 8 Dynamic changes in the channel and floodplain in the Little Colorado River, Arizona from 1936 to 2010. Channel and active floodplain shift dramatically year to year. Dramatic reductions in discharge from human uses result in narrower and more sinuous channels over time. Map redrawn using data from [Bloom \(2014\)](#).

boulder-dominated systems (e.g., Fig. 1A and C), as the latter tend to have confined channels. In broad valleys, stream channels may migrate laterally over time. Unless modified by human activities, overall sinuosity of streams within valleys may remain constant yet riffle, run and pool sequences may shift in location, although the relative length of these units also tend to stay constant over time for a given system. Additionally, sediment budgets typically remain in a constant state of dynamic equilibrium where inputs to any point equal outputs. At some locations, sediment inputs may exceed outputs leading to aggradation of the channel and increases in bed elevation, whereas when the opposite is true, degradation of the channel occurs.

Several classification systems have been developed to describe the diversity of stream morphologies (e.g., Rosgen, 1994). These rely on metrics such as channel slope (rise/run), sinuosity (channel length versus straight line distance), width:depth ratios, median particle size of streambed substrates, and entrenchment ratio. Entrenchment ratio is the width of the floodplain at $2 \times$ bank full height divided by bankfull width. Large ratios (>2) indicate high interaction between stream channels and their floodplains. Confluences where tributaries enter larger mainstems are important features of rivers that help to determine river network properties. These also provide special habitat qualities for aquatic life. Naiman et al. (2008) developed principles to relate stream network structure to physical properties of confluences, including a series of testable hypotheses.

Many organisms adapted to living in streams have narrow ranges of physiochemical tolerances. Streams draining iron-rich soils will likely have lower pH than those in limestone-rich areas. Temperature in small streams is largely driven by groundwater, which remains stable at roughly the average of above-ground annual temperature and has low concentrations of dissolved oxygen. Additionally, shade from riparian vegetation plays a larger role in maintaining lower temperatures in small streams. As streams become wider downstream, channels widen and receive more solar radiation leading to increased temperatures (Caissie, 2006). As a rule of thumb, stream widths less than twice the height of the riparian tree canopy are effectively shaded. Water has high thermal inertia and larger river channels have lower surface-to-volume ratios; hence, rivers maintain cool temperatures for extensive distances downstream. Dissolved oxygen is dependent on temperature but also aeration from turbulence and exchanges between the surface film and atmosphere. Importantly, dissolved oxygen, which is required by aquatic life, can be consumed by bacterial respiration of decaying algal blooms.

Stream Ecology

Major Concepts

Because streams are highly complex systems, several concepts emerged to describe stream ecosystem behavior and formulate hypotheses regarding their responses to disturbance. Stream ecosystem metabolism is driven by two sources of energy (carbon): allochthonous inputs (organic matter from trees) and autochthonous inputs (from within-stream primary production from algae or periphyton). The relative contribution of these inputs to streams plays a large role in organizing ecosystem structure and composition. In small headwater streams draining forested watersheds with deciduous vegetation, the primary source of energy is through coarse particulate organic material (CPOM) inputs. CPOM is colonized and chemically conditioned by bacterial and fungal microbial communities, and then it is partially consumed and processed into fine POM (FPOM) by leaf-shredding macroinvertebrates. FPOM is then consumed by multiple other types of invertebrates, such as collector-gatherers and collector-filterers. As streams increase in size and channels widen, riparian shading decreases and elevated light penetration increases autochthonous production. In some non-forested systems, autochthonous production can be high even within small streams. Periphyton communities provide food resources for other types of organisms, such as scrapers and collector-gatherers.

Longitudinally, river systems display gradual shifts in their relative balance of energy inputs from primary production (internal) versus allochthonous (external) carbon sources (Fig. 9). The River Continuum Concept (RCC) originated to describe the longitudinal progression of shifts in the energy budget of river systems (Vannote et al., 1980; Fig. 9). In headwater systems, allochthonous inputs dominate organic inputs, and the ratio of carbon sequestration through photosynthesis (P) to carbon respiration (R) is <1 . However, as streams widen and autochthonous production increases, P:R ratios become >1 . As stream depth increases, light penetration through the water column lowers and P:R ratios again return to <1 . Thus, P:R ratios assume a parabolic function where P:R ratios maximize at intermediate-sized river systems. As mentioned above, the source of carbon influences the functional composition of ecological communities along the river continuum. For instance, in headwaters the RCC postulates that leaf-shredding invertebrates and collectors would dominate macroinvertebrate communities whereas, as system size increases, the relative abundance of collector filterers and scrapers increase (Fig. 9).

Once streams deepen, collector gatherers and predators predominate invertebrate communities. Similarly, insectivorous fish predominate headwater stream communities and omnivorous and piscivorous fish increase as system size increases. Piscivorous fish predominate large river communities (Fig. 9).

Challenges and refinements to the RCC have been articulated over time. For example, blackwater rivers become more dependent on heterotrophic respiration from processing allochthonous organic material as rivers become wider near the coast (Meyer, 1990; Meyer and Edwards, 1990; Mallin et al., 2004). Photosynthesis becomes limited by dark tannins produced in wetlands and floodplains that restrict penetration of light. Despite the lower incidence of algal blooms, heterotrophic respiration can produce eutrophic conditions in blackwater rivers (Jager et al., 2011).

The role of floodplain wetlands illustrates another important paradigm in river ecology, the food-pulse concept (FPC) (Junk et al., 1989). This paradigm suggested that river system structure and function were largely dependent upon lateral hydrologic connectivity, specifically periodic disturbance of overbank floods. Floods mobilize sediments and organic material, shift channel

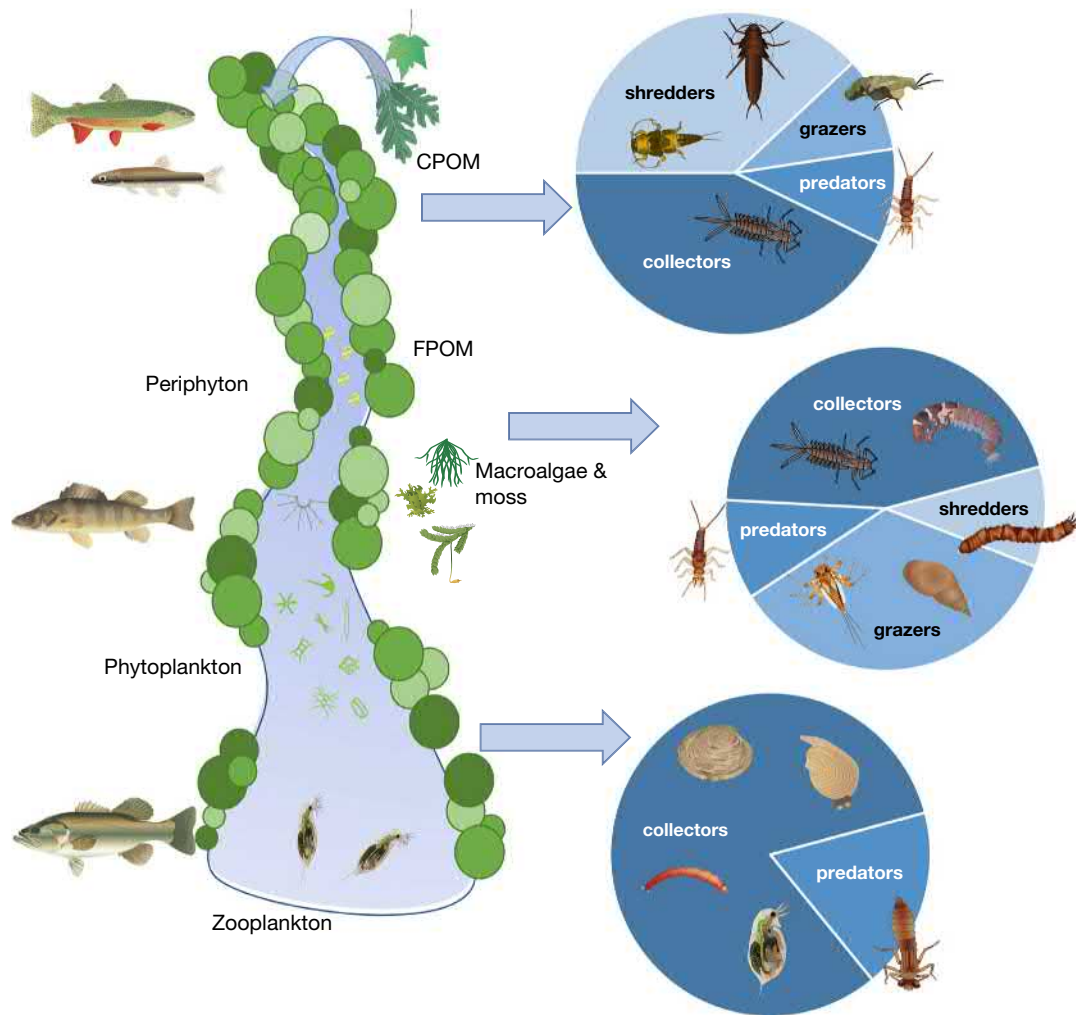


Fig. 9 The River Continuum Concept. Recreated from [Vannote et al. \(1980\)](#). Published with permission of NRC Research Press. Images of fauna and flora available from the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

morphology, maintain habitats, and shift organic material from the surrounding watershed to the stream ([Naiman et al., 2010](#)). Another concept, the Riverine Productivity Model ([Thorp and Delong, 1994](#)) suggests that riparian areas are important sources of organic matter inputs, specifically large autochthonous material such as large wood, which creates discrete areas of higher system productivity (e.g., fish abundance) as opposed to longitudinal progression in ecosystem balances between autochthonous and allochthonous resources. Geographic provinces vary in geology, which exerts controls on valley topography and geomorphic process in streams. The Process Domains Concept (PDC), postulates that geological landscapes or patches impose stronger controls than longitudinal processes on stream geomorphology and physiochemical characteristics, which then organize ecological communities ([Montgomery, 1999](#)). More recent frameworks emerged that built upon, or even cross-cut, these original paradigms. For instance, the Riverine Ecosystem Synthesis ([Thorp et al., 2006](#)) attempts to unify the longitudinal and lateral connectivity of riverine processes and networks with the broad discontinuous patterns of important landscape features.

Organisms Adapted to Living in Streams and Ecological Communities

Lotic systems induce very different selection pressures on organisms than their lentic counterparts. Among plants, special adaptations include hydrochory (life histories that depend on dispersal of seeds, fruits, and spores by water). Riparian woody species that colonize along rivers are pioneer species adapted to withstand and recover from floods. These include adaptations to counteract anoxic conditions during floods, flexible stems, floating seeds, and the ability to propagate from drifting stems ([Naiman and Decamps, 1997](#)).

Among aquatic animals, flowing water imposes energetic demands on organisms exerting effort to remain fixed or move upstream within the water column to feed or carry out their life history needs ([Fig. 10](#)). Body morphologies are evidence of



Fig. 10 Animals adapted for life in stream environments. (A) *Rhithrogena brunneotincta*, a species of flathead mayfly of the family Heptageniidae, (B) a caddisfly larvae in the genus *Cheumatopsyche* (family Hydropsychidae), (C) female *Acerpenna pygmaea*, a mayfly in the family Baetidae, (D) stripetail darter, *Etheostoma kennicotti*, (E) Tennessee dace, *Phoxinus tennesseensis*, (F) Blueside darter, *Etheostoma jessiae*, (G) largescale stoneroller, *Campostoma oligocephalus*, and (H) cartilaginous ridge on lower lip of *Campostoma* for scraping algae. Photo credits: (A) Donald Chandler, University of New Hampshire, (B and C) John Smith, Oak Ridge National Laboratory, (D–H) Trent Jett, Oak Ridge National Laboratory.

adaptation strategies to minimize drag in rapidly moving fluid environments. For instance, larval stages of Heptageniid mayflies have evolved very wide, dorsoventrally flattened bodies to minimize body exposure to swift currents and cling to substrates to feed on periphyton (Fig. 10A). As another example, pelvic fins of freshwater gobies in Hawaii (*Lentipes concolor* and *Sicyopterus japonicus*) evolved into suction disks to scale waterfalls in order to migrate. Other body morphologies show adaptations to feeding or reproduction strategies in streams. Fish of the genera *Camptostoma*, have a rigid cartilaginous ridge on their lower lip to scrape algae from substrate (Fig. 10G and H).

Animals also have very interesting behaviors adapted to living in flowing environments. Nearly all river biota perform an upstream migration during one life stage to counteract downstream passive drift during another life stage (usually an early life stage). We refer to this as a “conveyor-belt” life history. Migration distances vary, but typically involve movements to find habitats suitable for different purposes, such as reproduction, feeding/growth, and resting/cover. For instances, Tennessee dace (*Phoxinus tennesseensis*) are small minnows inhabiting 1st and 2nd order forested streams in the Tennessee River Basin, United States (Fig. 10E). During high flows in spring, they migrate into small headwaters to spawn. Long-distance migrations are classified as potamodromous (within river), amphidromous (to an estuary to feed or growth during short periods, followed by upstream migration), anadromous (marine to upstream spawning habitat), and catadromous (rear in freshwater and migrate to the marine environment to spawn) (Lucas and Baras, 2001). Salmon exemplify the anadromous life history, eels follow a catadromous life history, Hawaiian gobies (mentioned previously) follow the amphidromous life history, and different species of sturgeon (Acipenseridae) follow each of these spatial patterns.

At a local scale, biota have adaptations to flowing waters. For example, caddisfly larvae in the family Hydropsychidae, also known as “net-spinning” caddisflies (Fig. 10B), construct nets of silk for refugia and feeding by capturing particles of FPOM in transport, also called seston. Many fish species have adapted a variety of strategies for protecting eggs by depositing, burying, or hiding them within crevices of substrates (lithophils), depositing them on plants (phytolithophils), or broad casting them where they may drift downstream for up to hundreds of kilometers (Balon, 1975). Salmonids (trout and salmon) are an example of brood-hiding fishes where females will use their tails and bodies to prepare a nest called a “redd” by cleaning fine sediments from gravel and



Fig. 11 *Nocomis* chub mounds are elaborate nesting sites that provide spawning habitat for multiple other fish species. Top Image: A bluehead chub *N. leptoccephalus* guarding its completed mound nest. Bottom: Bluehead chub mound with (A) host male bluehead chub initiating a spawning clasp and six nest associate species, including (B) mountain redbelly dace *Chrosomus orea*, (C) rosyside dace *Clinostomus funduloides*, (D) central stoneroller *Camptostoma anomalum*, (E) white shiner *Luxilus albeolus*, (F) crescent shiner *L. cerasinus*, and (G) rosefin shiner *Lythrurus ardens*. Photos are from Toms Creek, Virginia, United States, by Emmanuel A. Frimpong. Image from Frimpong, E. (2018). A case for conserving common species. *PLoS Biology*, 16, e2004261 and used with permission from PLoS Biology, <https://doi.org/10.1371/journal.pbio.2004261.g001>.

cobble substrates. As females undulate their bodies and release the roe, a male will come alongside the female and fertilize eggs with milt, and the eggs settle within the interstitial spaces of substrates. Males of the genera *Nocomis*, known as the mound building chubs, develop elaborate mounds of gravel by carrying substrate particles in their mouth (Fig. 11). Eggs are fertilized and deposited within the mound following construction. *Nocomis* nests also provide important spawning habitat for other fish species, called nest associates (Fig. 11, Peoples and Frimpong, 2013, 2016; Frimpong, 2018). *Nocomis* mounds provide contiguous patches of highly porous gravel substrates, which would otherwise be unavailable in streams where they occur (Pendleton et al., 2012). It is believed that the relationship between mound-building chubs and nest associates is mutually beneficial, as *Nocomis* mounds are safeguarded by these other species (Fig. 11, Peoples and Frimpong, 2013; Frimpong, 2018).

Stream flow acts as a “master variable” (Power et al., 1995), controlling the geomorphology, physiochemistry, and habitat structure that sustain the ecological integrity of river systems (Poff et al., 1997). The specific natural flow regime signature of rivers (Poff et al., 1997) acts a template or filter of selective pressures, in which many organisms have adapted, and hence, require for carrying out their life history requirements (Fig. 4, Poff and Ward, 1989; Bunn and Arthington, 2002). For instance, discharge and water temperature must reach optimal ranges to induce spawning for many fish species, such as Chinese sturgeon (*Acipenser sinensis*) in the Yangtze River (Deguo et al., 2007), whereas the timing, duration, and magnitude of seasonal floods serve as cues for spawning for many species (Bunn and Arthington, 2002), but also provide cues for hatching and downstream drift of others (Næsjø et al., 1995). The frequency and intensity of flooding is important for scouring floodplains and reducing competition for non-native vegetation in favor of native riparian vegetation. For example, Virginia spirea (*Spiraea virginiana*), a rare and threatened perennial plant species of the Southern Appalachians of the United States, has fibrous clonal roots that can fragment and establish elsewhere. This species relies on floods of sufficient magnitude and frequency to scour and maintain floodplains while not dislodging the species.

General hypotheses linking hydrologic regimes and fish life histories have been useful for understanding the role of hydrology in organizing community structure. Fish life histories represent a tri-continuum of tradeoffs among three opposing endpoints, representing alternative strategies in life span, body size, fecundity, parental care, and number of spawning bouts within a season (Winemiller and Rose, 1992). On one endpoint, equilibrium species represent a K-strategy characterized by small-bodied fish with average life-span, low fecundity, only one spawning bout a year, and high parental care. Similar to other K-strategists, these species prefer stable conditions, like low-variant stream flows. Examples of stream-dwelling equilibrium fish species include small algal-grazing minnows, such as central stoneroller (*Camptostoma anomalum*). The other two endpoints split the r-strategy into two groups, periodic and opportunistic species. Periodic species, such as sturgeon, are long-lived, attain large sizes, have high fecundity, spawn no more than once per season, and invest very little in their progeny. These tend to be “capital-breeding” species that accumulate energy over multiple years before they invest in reproduction, for example, by making a long spawning migration (Jager et al., 2008). Periodic species prefer seasonally variant but predictable flows that provide suitable conditions for spawning every several years. Opportunistic species are short-lived, small sized, have average fecundity, and may have multiple spawning bouts per season. Opportunists, such as minnows within the genus *Notropis*, prefer highly variable flows and, at times, intermittent systems, as they can quickly colonize and re-establish populations once flows return.

Stream community structure and composition is dependent upon stream size, the primary productivity of the region, position within the stream network (e.g., near tributaries), and geographic radiation of species. The RCC postulates that the diversity of food resources (i.e., sources of energy) is maximized at intermediate stream sizes. Functional group diversity then should also maximize at intermediate-sized systems, and therefore, the RCC suggests that these medium-sized systems should harbor the highest diversity levels. However, fish species richness increases as a log-log relationship with river discharge where diversity is maximized at the largest system size (Xenopoulos and Lodge, 2006), as opposed to displaying a parabolic relationship with discharge.

Many complex relationships exist among species, such as competition, predation, parasitology, and symbiosis, are apparent in stream communities, as in other ecosystems. As mentioned earlier, an example of symbiosis is the utilization of *Nocomis* species spawning mounds by several fish species, whose recruitment may depend on the presence of *Nocomis*. Freshwater mussel life histories involve several phases and require a fish host. Male mussels release sperm, which is filtered by females to fertilize eggs. Larval mussels, called glochidia, are aggregated on a soft tissue, called a “lure”, which represent small fish or invertebrates. Fish bite the lures and parasitic glochidia attach to their gills and grow until attaining a sufficient size to release to the sediment, where they partially bury themselves.

Commercial Importance and Ecosystem Services

For thousands of years, humans have settled along rivers due to their provision of services (Böck et al., 2018). In North America, Indian tribes relied on rivers for fish food subsidies or areas that funneled large mammal crossings for hunting (Park et al., 2016), and as such, rivers were considered sacred places, providing sustenance for communities and a connective tissue linking distance lands supporting long-distance navigation and transport of commodities for trade (Marchand, 2013). Indeed, in the Corps of Discovery Expedition, commissioned by United States President Thomas Jefferson in 1804, rivers were envisioned as important routes for establishing new territory, connecting large land assets, and enabling trade. Rivers have served as sources of water for irrigation, boundaries of tribal lands, and eventually countries and states, whereas the junction of great rivers served as distinct landmarks for social meetings and eventual cities where major tributaries joined.

In modern day society, rivers still serve many of the same important purposes as they have for previous millennia, although many of these demands have become increasingly conflicted over limited resources. Rivers are a conundrum of jurisdictions and

shared resources. For instance, they provide sources of replenished drinking water while also serving as recipients of human waste. Because lotic systems dilute and metabolize contaminants, they have provided a convenient resource for handling treated and untreated waste from communities and transporting those materials downstream (Hardin, 1968). In under-developed countries, rivers still provide important food subsidies for local communities. For instance, indigenous peoples of the Amazon River basin and multiple nationalities of the Mekong River rely on these systems for protein. In developed countries, however, very few rivers still provide food subsidies at scales similar to resource provisions available to historical communities. To avoid overharvest, rivers in developed nations primarily consist of recreational fisheries. Rivers continue to be used for navigation, such as freight shipping, and the construction of locks and dams have expanded the transportation potential of rivers. Currently, over 275 million hectares are irrigated worldwide, accounting for 40% of total crop production (FAO, 2016a). The vast majority of the source water for irrigation comes from rivers. Rivers also provide an important source of water for thermoelectric facilities. Coal-fired power plants and nuclear power plants account for 40% and 11%, respectively (WEC, 2019), of electricity production, and these technologies typically rely on water for steam generation or cooling generators.

Rivers are also predisposed to human utilization because they provide a continual source of potential energy. Elevational gradients that precipitate downhill movement of water have been harnessed for conducting work for thousands of years. Small dams and diversions were developed to route water for powering or increase the elevation (i.e., potential energy) of water. Water-wheels and water-powered grist mills were in operation as early as the 4th century BC in the Persian Empire (Reynolds, 2002; Selin, 2013), but became commonplace worldwide by at least by the 10th century (Hill, 2013). Small hydropower dams were constructed to generate electricity as early as the late 19th century (DOE, 2008). Although a small fraction of historical grist mills are still in operation, hydropower continues to grow and currently supplies 16% of the world's electricity and over 70% of all renewable energy resources (WEC, 2019).

Anthropogenic Threats

As with much of the world's natural resources, human reliance on rivers has increasingly converted from a model of resource use to abuse. Earth's growing human populations and increasing demands for goods and services have left very few rivers in their natural state. Over half of Earth's accessible freshwater runoff is used by humans (Vitousek et al., 1997) and only one third of the world's great rivers flow freely to oceans without impoundment (Grill et al., 2019). Large rivers arguably bear most of burden of human demands—over 50% of large rivers ($\geq 1000 \text{ m}^3 \text{ s}^{-1}$) are significantly regulated by dams for water supply, flood control, navigation, and hydropower (Lehner et al., 2011). However, in the United States, 80% of streams, primarily comprised of small systems, show some sign of hydrologic alteration (McManamay et al., 2017). In the last century, global withdrawals have increased almost 7 times, a rate that is $1.7 \times$ that of population growth (FAO, 2016b). Forty-nine countries are currently classified as water stressed (FAO, 2016b), and this has been shown to increase the risk of armed regional conflicts (Mach et al., 2019).

One-third of all vertebrate species are confined to freshwater (Dudgeon et al., 2006). Given the rarity of these systems and their disproportionate role in sustaining biodiversity, the implications of human alterations to stream environments have been devastating to global biodiversity loss, the majority of which has occurred within the last few decades. From 1970 to 2014, freshwater populations have declined, on average, by 83% or by 4% per year (WWF, 2018). Currently, almost one in three freshwater species is threatened with extinction world-wide (Collen et al., 2014). For lotic environments, 34% of species are threatened (Collen et al., 2014), representing a higher proportion of species than in lakes or marshes. The likelihood of a species being in jeopardy is, in part, due to their life histories and requirements for habitats with greater propensity of human use and alteration. For instance, darters are typical of endemic freshwater species (Fig. 10D and F), which tend to have highly localized distributions in rugged landscapes (e.g., the Southern Appalachian Mountains) with small, relatively isolated watersheds. Other types of freshwater species that tend to be at risk include cave-dwelling fishes, gastropods, and mussels and spring-dwelling species. Similarly, the desert pupfish is now rare in arid environments where it was once common in the Southwestern United States and Mexico. Migratory species tend to be at higher risk because they require multiple habitats and safe corridors to pass between them. Although salmon are highly valued species, many runs of salmon are at risk in Western North America. Large-bodied species that are slow to mature, like sturgeons also tend to be at risk.

Dudgeon et al. (2006) lists five major categories of threats to freshwater biodiversity: overexploitation, water pollution, habitat modification, invasive species, and flow modification. Global-scale alterations, such as climate change, may influence multiple risks simultaneously and create compounding stressors, such as loss of thermal refugia (Isaak et al., 2012; Torgersen et al., 2001). Generally, overexploitation of river stocks is more common in underdeveloped countries where communities are highly reliant on freshwater fish as a source of protein. The United States and Canada, however, provided a globally important source of Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus*) meat and caviar during 1880–1900, and over-fishing is considered one of the major reasons for decline of the taxa (van Eenennaam et al., 2004). With the loss of other sources of caviar, paddlefish from North America became a premier source of caviar in 1980 and illegal harvests became rampant leading to declines in the species (Saffron, 2004).

Water pollution can be generally described as any change to the natural physiochemistry of waters. This includes pollutants, but also human-induced alterations to water temperature, conductivity, salinity, pH, and dissolved oxygen that may be outside or, in the least, constitute a stress to the physiological tolerance of aquatic organisms. Despite the improvement of water quality due technological advances in pollutant removal and imposed regulations, at least 80% of global human wastewater remains untreated (UN, 2017). Major classes of pollutants found in waters include wastewater, stormwater and non-point source pollution, nutrients,

sediments, metals, surfactants, organic pollutants, pharmaceuticals, endocrine disruptors, pesticides, petroleum hydrocarbons and polycyclic aromatic hydrocarbons (PAHs), ionic liquids, and nanomaterials (Pal et al., 2010; Choudri et al., 2017). Many of these compounds are persistent in stream environments and resistant to degradation via microbial community metabolism (Pal et al., 2010). Excess nutrients from agriculture runoff, sewage, and industrial wastewater have contributed to the increasing prevalence of cyanobacterial blooms, many of which produce toxins as a byproduct harmful to humans and wildlife (Cheung et al., 2013). Mercury is a globally abundant contaminant, acting as a neurotoxin to humans and wildlife. Humans have increased the atmospheric concentration of mercury 450% above natural levels, and land-use practices and point-source pollution are estimated to contribute 580 tons of mercury to aquatic environments annually (UN, 2019). Over 80% of fish samples and over 80% human hair samples across the world exceed US Environmental Protection Agency's reference dose values (BRI & IPEN, 2014).

Habitat and flow modifications in lotic environments occurs through direct (e.g., channelization) and indirect means (e.g., land use). Land transformation in upstream watersheds or in riparian areas alters hydrology, alters sediment regimes, and reduces shading from vegetation and organic matter contribution to streams. Deforestation reduces the forest canopy's interception of rainfall, reduces soil organic material, and increases soil erosion, all of which increases episodic runoff, sediment contributions to streams, and elevated air and water temperatures. Likewise, cultivation of the land surface for agricultural production increases sediment and nutrient contributions to streams, increasing siltation of streambeds and algal production. Conversion of permeable land cover to impervious surfaces in urban environments reduces the infiltration of precipitation, leading to increased stormflow magnitudes, loss of sediment and organic matter contributions, and elevated temperatures. Streams have been channelized and their banks armored to control lateral migration and prevent risk of human infrastructure failure. Over 160,000 km of levees have been constructed in the United States to constrain river flows and channel migration; however, the vast majority of these are outdated and need repair (AIR, 2014). In England, 65% of floodplains have been extensively altered due to agriculture leading to a virtual loss in fen, marsh, swamp and bog wetland habitats (Entwistle et al., 2019). Diversions for irrigation and water supply have left rivers with dramatically reduced flows. For instance, streamflow within the Colorado River at Hoover Dam, Arizona (United States) is reduced by at least 50% from pre-dam development periods and the river runs completely dry prior to entering the Pacific Ocean.

Arguably, dams induce the most dramatic alterations to river habitats (Petts, 1984), notably the conversion of lotic systems to lentic habitat. Many river organisms' life histories require flowing water; hence, these organisms are maladapted for life in reservoirs. Water storage in reservoirs alters downstream hydrologic regimes, traps sediment, and induces major shifts in temperature, dissolved oxygen, and other water quality parameters, leading to species declines. Depending on the size of the reservoir, these shifts in hydrology, sediment supplies, and water quality may be apparent for hundreds to thousands of kilometers downstream (Ward and Stanford, 1983; Schmidt and Wilcock, 2008). There are an estimated 16.7 million reservoirs worldwide which have increased the Earth's terrestrial surface water by 7.3% (Lehner et al., 2011). Of these reservoirs, approximately 57,000 are created by large dams (> 15 m height) (International Rivers, 2019). As of 2015, 3700 large dams at least 1 MW in size were either planned or under construction globally, and these facilities, once constructed, would increase global hydroelectricity capacity by 73% (Zarfl et al., 2015). Some of the world's great free-flowing rivers, such as the Amazon (Brazil), Congo (Africa), and Mekong (Asia) are at the highest risk of widespread dam development.

Invasive species are introduced through aquaculture, sport fishing, wild stock augmentation, aquarium trade, and biological control. Approximately 10,000 non-native species occur in waterways of the United States (USFWS, 2019). After establishment, invasive species often create new functional roles in aquatic ecosystems and communities, either directly, that is, competition/predation, or indirectly by changing habitat conditions (e.g., water quality) (Gallardo et al., 2016). In a global meta-analysis, effects of invasive species introductions resulted in predominately negative impacts on aquatic ecosystems, consistently reducing the abundance of native fish, benthic invertebrates, zooplankton, macrophytes, and phytoplankton; however, reductions in native species diversity were not consistently documented (Gallardo et al., 2016). Invaders tended to coincide with systems having higher organic matter and higher nutrient content, suggesting these habitats were typically altered by new functional roles by these species (Gallardo et al., 2016). Major alterations to habitat and flow regimes of rivers, such as impoundment and river regulation, create stable environments or new niche spaces that favor the establishment of invasive species.

Conservation and Management

Ecosystem conservation and management, particularly for streams, can be partitioned into two major strategies: (1) protection and/or prevention, or (2) mitigation and restoration. Regulations, legislative mandates, and policies may have application to one or both of these strategies and these vary widely among countries. We provide a brief overview of United-States (US)-centric federal protections of rivers, their protective provisions, and their lack thereof. In the United States, federal protections of river ecosystems are governed by the Clean Water Act (CWA), the Clean Air Act, the Endangered Species Act (ESA), the National Environmental Policy Act (NEPA), National Wild and Scenic River designations, and, for rivers influenced by non-federal hydropower facilities, the Federal Energy Regulatory Commission (FERC) licensing stipulations.

The US Federal Clean Water Act (CWA) commands the US Environmental Protection Agency (EPA) to pursue two policy goals. First, to restore and maintain the nation's waters; and second, to preserve each state's primary responsibility and right to prevent, reduce, and eliminate pollution. CWA was passed in 1972 (33 U.S.C. §1251 et seq.) and amended in 1975 (P.L. 95-217). Section 401 requires discharge permits for wastewater and pollutants, oil-spill prevention and response plans, and plans to clean up waters

that fail to meet state water-quality standards. The CWA has been very successful at improving water quality conditions in many industrialized and contaminated waterways in the US; however, here are several concerns about the ability of CWA to protect US rivers. First, a recent proposed ruling redefines “waters of the United States” or (WOTUS) to exclude headwaters, and therefore excludes the majority of reaches from protections (Federal Register 84 FR 4154, February 14, 2019). Secondly, agricultural and other “non-point” sources of pollutants are excluded from the law, and this has contributed to the serious degradation of water quality that manifests as algal blooms in lakes, reservoirs, and downstream estuaries.

Another piece of US legislation that has benefited rivers and streams in the United States is the Clean Air Act of 1963 (42 U.S.C. § 7401). This Act limited emissions of sulfate and nitrous oxides, and by doing so, it reversed freshwater acidification that affected rivers and streams. Sulfate concentrations declined from 30 million tons per year in 1970 to <5 in 2018, with similar reductions in nitrous oxides (Sullivan et al., 2018). Improved acid-base chemistry has been documented in hundreds of montane lakes throughout the northeastern United States (Strock et al., 2014). Reductions in mercury and lead deposition have also improved the safety of consuming freshwater fishes (Sullivan et al., 2018).

In the United States, the Endangered Species Act (ESA, 16 U.S.C. §1531 et seq.) was passed in 1973 and aimed to conserve threatened and endangered plants and animals and their habitats. The ESA is administered by the US Fish and Wildlife Service (USFWS) for freshwaters and by National Oceanic and Atmospheric Administration (NOAA) Fisheries for marine and anadromous fishes. The law requires federal agencies, in consultation with USFWS and/or NOAA to ensure actions they authorize, fund, or carry out are not likely to jeopardize the existence of listed species or result in harm to their environment. One of the first cases litigated (unsuccessfully) under the act was to prevent the building of Tellico Dam in East Tennessee, United States, to protect the snail darter (*Percina tanasi*), a species identified by taxonomist, David Etnier (Gilmer, 2013). For anadromous fishes in the western United States, the goal is to promote recovery of spawning “runs” to historical numbers and to preserve spatial diversity in salmon spawning habitat. Many fish and mussel species now listed under ESA are supported by artificial propagation in hatcheries because in-stream habitat is no longer adequate for reproduction. The goal of restoration efforts is to improve in-stream breeding habitat to eliminate the need for hatcheries.

The afore-mentioned regulations and policies are the primary driver behind a > 1 billion USD river restoration business within the United States (Bernhardt et al., 2005). Restoration approaches vary considerably in scale and type of applications (e.g., Fig. 12); however, the most cited objectives of projects were to improve water quality, manage riparian areas, enhance in-stream habitat,

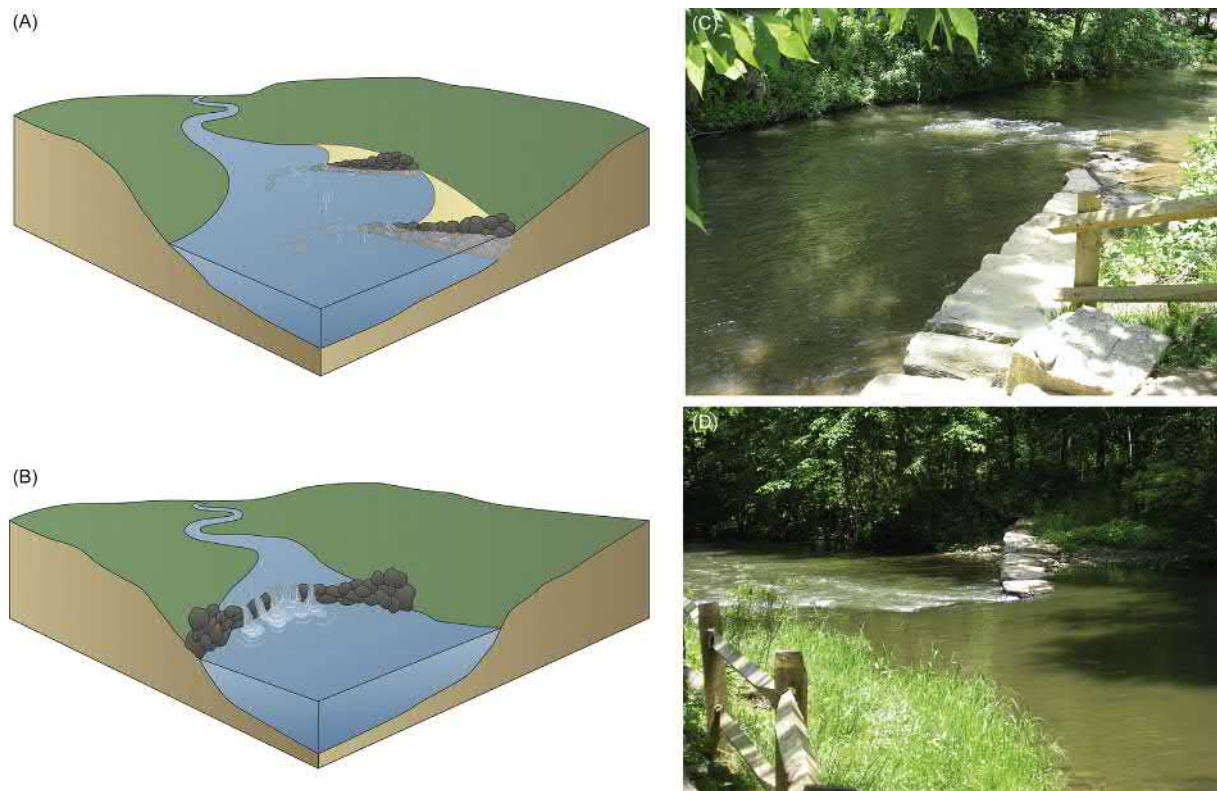


Fig. 12 Examples of river restoration specifically bank stabilization and habitat enhancement. Diagrams depicting (A) a cross vein to direct erosive flows away from outside meander of a channel, (B) a cross vein weir to direct flows to the center of the channel and prevent erosion, while also creating deeper run habitat, (C and D) photographs of a type of cross vein, termed a “J Hook”, installed in the Pigeon River, North Carolina. Diagrams A and B provided by Tracy Saxby, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/). Photographs taken by Ryan McManamay.

improve fish passage, or stabilize stream banks to prevent erosion (Fig. 12) (Bernhardt et al., 2005). Unfortunately, rates of success for restoration projects are quite low, and most projects are implemented without adequate monitoring (Palmer et al., 2010). Applications either fail to restore processes that sustain river ecosystem integrity (Roni et al., 2008) or there is a mismatch between the scale at which restoration project is implemented and the scale at which disturbances are operating (Bernhardt and Palmer, 2011).

Decades of growing expenditures to restore degraded rivers have emphasized a need for preventative measures and protection of rivers from human disturbance. Protection of land assets, especially floodplains and riparian areas, varies globally (Fig. 13A). For example, over 53% of lands within Venezuela, Slovenia, and Monaco are protected. Although Hong Kong is among the most densely populated countries in the world, over 40% of its lands are protected. In comparison, only 14% of US lands are protected; however, land protection does not complement river needs. Whereas the majority of species at risk occur in the Southeast United States, more watersheds are protected from development in the Western United States, causing a mismatch between protections and risk (Jenkins et al., 2015).

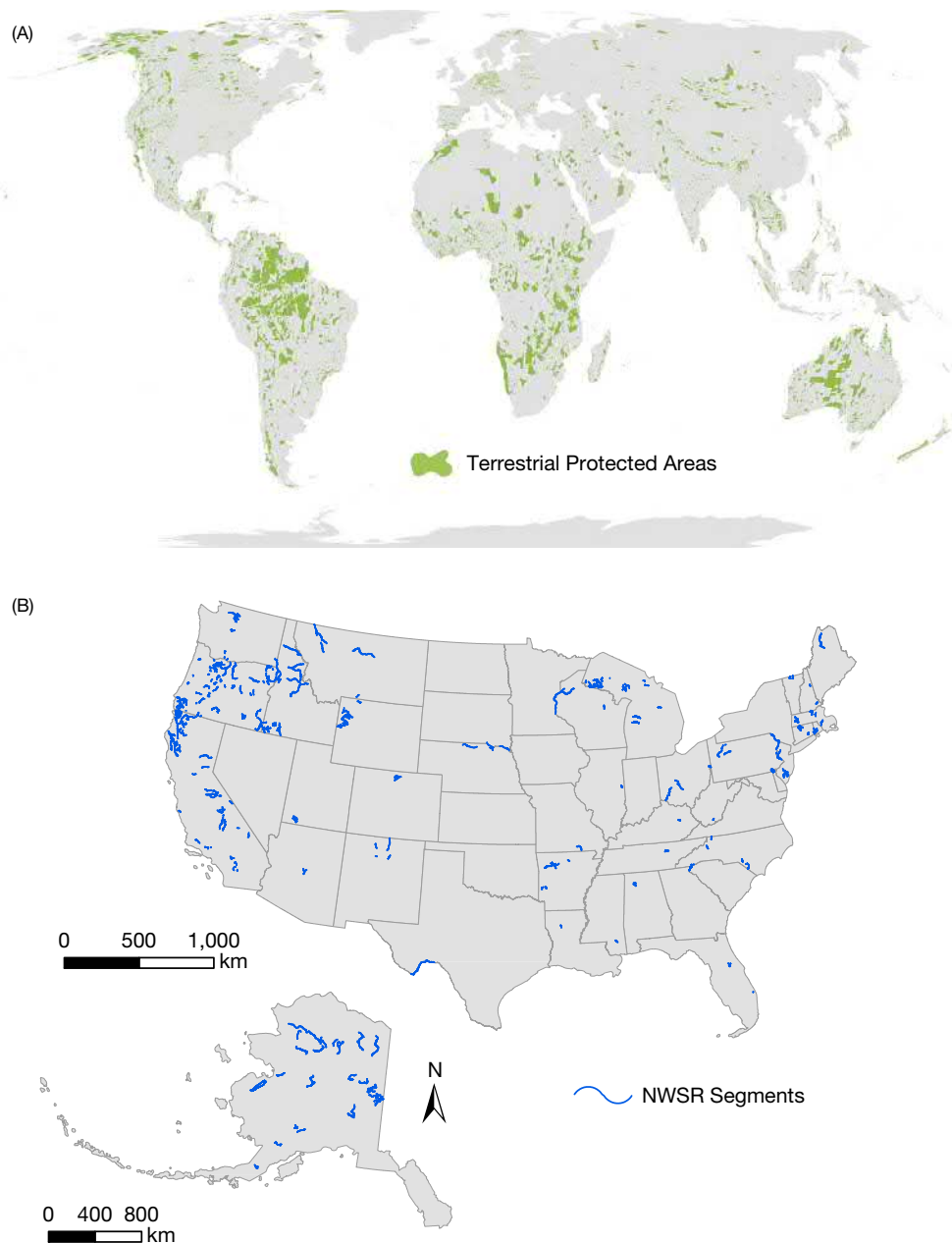


Fig. 13 (A) Global distribution of protected lands and (B) distribution of rivers protected under the National Wild and Scenic River System (NWSRS). Global protected lands provided by the IUCN World Database on Protected Areas. Data for NWSRS provided by the National Park Service.

Of course, land protection may not adequately protect rivers unless conservation provisions extend throughout the entire river corridor. The National Wild and Scenic Rivers System (NWSRS) was created explicitly for that purpose and is the highest level of protection provisioned to a river (Fig. 13B). The NWSRS was established in 1968 (Public Law 90-542; 16 U.S.C. 1271 et seq.) to preserve rivers with outstanding natural, cultural, and recreational values in a free-flowing condition for the enjoyment of present and future generations. The purpose of the act was to complement policies favoring dam and other development with preservation of other selected rivers sections to protect the water quality and fulfill other vital national conservation purposes. While the NWSRS ensures rivers under its jurisdiction will retain their legacy as free-flowing, < 0.25% of rivers in the United States are protected under the NWSRS. More research is needed to understand the best provision of protection for rivers while also balancing the needs of human society.

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Lotic Freshwater: Rivers

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Abstract

Ecosystems associated with rivers are intricately connected to their entire watershed. The river ecosystem includes the channel of active water flow, floodplain, and riparian and hyporheic zones. This ecosystem is shaped by interactions among the natural flow of water, sediments within the river and entering the river, and large wood regimes within the riparian zone. River integrity describes the ability of a river ecosystem to adjust to changes in these elements and through these adjustments maintain the habitat, disturbance regime, and connectivity necessary to sustain native biotic communities. Riverine food webs conceptualize the coupling between the physical environment and biotic communities and can be used to examine recovery from disturbance, variation in the structure of communities, and sources of energy that fuel metabolism within the ecosystem.

Introduction

Although rivers are sometimes regarded as relatively simple systems for downstream conveyance of water and other materials, rivers are most appropriately conceptualized as ecosystems that are intricately connected to the greater surrounding landscape and, eventually, the oceans. In this paper, we briefly discuss some of the principal physical and biological aspects of river ecosystems.

Basic Characteristics

Physical

A river corridor consists of some combination of the active channel(s), floodplain, riparian zone, and hyporheic zone (the area beneath the river bed and floodplain, in which surface and ground waters mix). Erosional and depositional forms created by river processes typically delineate the active channel, which in most regions is defined by that part of the river corridor that does not support mature woody vegetation (Osterkamp and Hedman, 1977; Arnaud et al., 2015). The upper elevation limit at which water is contained within a channel distinguishes the active channel from adjacent floodplain areas. A river corridor can have more than one active channel where multiple, subparallel channels branch and rejoin downstream, or where secondary channels are present. Secondary channels contain flowing water only during higher discharges (Fig. 1).

A floodplain is a relatively flat sedimentary surface adjacent to the active channel that is built by contemporary river processes and that is frequently inundated during floods (Nanson and Croke, 1992; Dunne and Aalto, 2013). The lateral extent of a floodplain can also be defined in a regulatory context based on the area inundated by a flow with a specific return interval: this



Fig. 1 Aerial view of a portion of the Kobuk River in interior Alaska, USA with multiple active channels. Flow direction is from upper right to lower left.

leads to definition of a 100-year floodplain, for example. River scientists typically describe a floodplain as the surface that is flooded on average at least once every 2 years. Rivers with highly variable flow, however, such as those in arid lands, can have flat surfaces adjacent to the channel which are composed of contemporary river sediments that are flooded only every few decades (Williams, 1978).

The riparian zone is the interface between terrestrial and aquatic systems (Naiman et al., 2005). The US Army Corps of Engineers, which oversees regulatory delineations for freshwaters in the United States, has defined riparian areas as “lands adjacent to streams . . . transitional between terrestrial and aquatic ecosystems, through which surface and subsurface hydrology connects riverine, lacustrine, estuarine, and marine waters with their adjacent wetlands, non-wetland waters, or uplands” (USACE, 2012). The lateral extent of the riparian zone can also be defined as the surface extent of frequent flooding and the subsurface extent of mixing of river, hyporheic, and ground waters (Wohl, 2014a), creating substantial overlap with the definition of floodplains. Riparian zones can occur in portions of the river network that do not have floodplains, such as steep sided, narrow canyons.

The hyporheic zone is the area in stream sediments where surface water and groundwater mix. This zone can extend several meters below large alluvial rivers (alluvial channels are those formed in unconsolidated sediments deposited by the river) and as far as 2 km laterally from the active channel in river corridors with broad floodplains underlain by gravel (Stanford and Ward, 1988; Gooseff, 2010).

Water and sediment inputs are the primary drivers of physical form and process in all rivers. In forested river corridors, large wood (typically defined as >10 cm diameter and 1 m length) historically formed an equally important component (Fig. 2). However, centuries of large wood removal in many river networks have reduced the influence of wood on channels and floodplains (Montgomery et al., 2003; Wohl, 2014b).

Water flowing downstream converts potential energy to kinetic energy, which is expended in overcoming frictional resistance, transporting sediment, and eroding the channel boundaries. The amount of stream energy available at any point in space and time reflects the volume of water flowing downstream and the valley and channel geometry, which influence downstream gradient and frictional resistance. The work exerted by the stream flow reflects the balance between available energy and the erosional resistance of the channel substrate. Substrate erosional resistance results from substrate composition and additional resistance created by living aquatic and riparian vegetation and dead vegetation in the form of instream and floodplain wood.

Understanding energy expenditure of stream flow is important in the context of river corridor stability. If stream flow energy increases substantially because of increasing discharge, such as during a flood, available energy can exceed the erosional resistance of the channel boundaries, resulting in erosion of the bed or channel widening. Conversely, if stream flow energy is insufficient to perform the work of transporting sediment supplied to the river corridor, sediment will accumulate along the river, causing bed sedimentation, floodplain aggradation, or abrupt lateral channel movement across the floodplain.

The natural flow regime refers to the characteristics of the hydrograph prior to intensive human alteration of a watershed (Poff et al., 1997) and is commonly described in terms of the magnitude, frequency, duration, timing, and rate of change of flow.

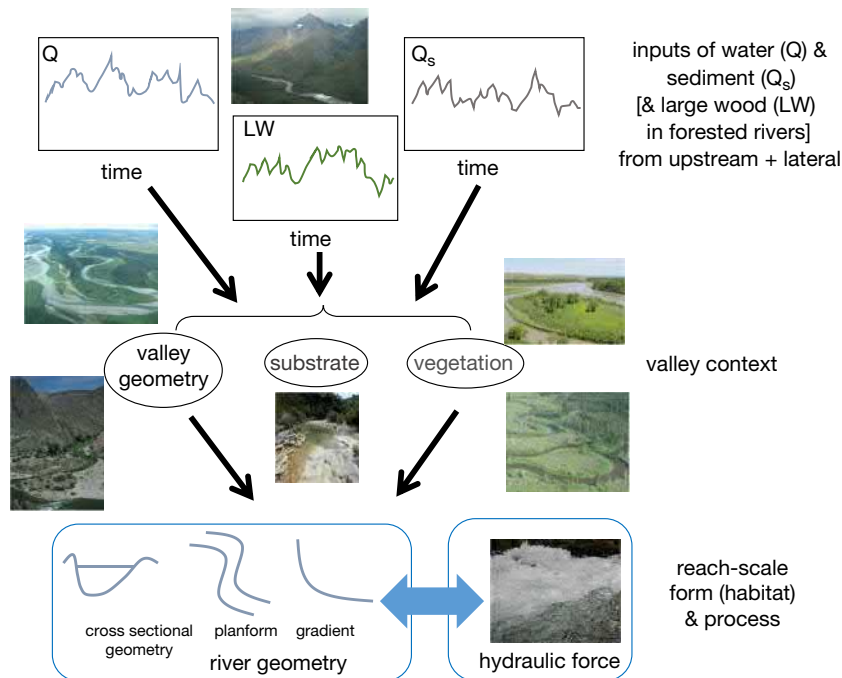


Fig. 2 Schematic illustration of how external inputs in the form of water, sediment, and large wood interact with the valley context to drive reach-scale response variables of river form and process.

Numerous methods exist for quantifying how much an altered watershed deviates from the natural flow regime (Richter et al., 1996; Poff et al., 2010).

Sediment entering the river corridor can serve multiple functions. Sediment in transport requires a minimum level of flow energy to remain mobile, but also acts as a tool to erode the channel bed and banks through abrasion if the sediment is sand-sized or larger (Sklar and Dietrich, 2004). High concentrations of suspended sediment can increase the viscosity of the stream flow and dampen turbulence and erosion (Kuhnle, 2013), and large amounts of coarse sediment supplied to the river corridor can exceed river transport capacity and form a depositional layer that covers the bed and protects underlying sediment and bedrock from erosion (Sklar and Dietrich, 2004). Sediment can come from adjacent uplands and enter the river corridor in abrupt, episodic mass movements such as landslides (Benda, 1990; Korup, 2013). Sediment can also move into the river corridor in a more gradual, diffuse fashion with widespread surface runoff or tributary inputs. Finally, sediment can be remobilized within the river corridor from the stream bed, banks, in-channel bars, and floodplain with subsequent increase in water discharge.

The natural sediment regime refers to the characteristics of sediment inputs, transport, and storage prior to intensive human alteration of a watershed (Wohl et al., 2015). Metrics for quantifying deviation from the natural sediment regime do not yet exist because of the extremely limited direct measurements of sediment transport and the greater difficulty in characterizing sediment inputs and transport relative to river discharge. Wohl et al. (2015) suggest focusing on a balanced sediment regime that involves managing for a desired balance between sediment supply and transport capacity in order to maintain specific physical processes and forms within the river corridor (Wilcock et al., 1996; Schmidt and Wilcock, 2008).

Large wood is recruited to the river corridor from uplands via hillslope failure (Abbe and Montgomery, 2003; May and Gresswell, 2003) and from floodplain forests via individual tree fall or mass mortality during blowdowns, insect infestations or blight, wildfires, and bank erosion (Benda and Sias, 2003). Once in the river corridor, large wood increases resistance to flow (Curran and Wohl, 2003; Hygelund and Manga, 2003) and creates obstructions that enhance hyporheic exchange (Hester and Doyle, 2008; Sawyer et al., 2011). Flow deflection around the wood drives local scour of the bed and banks, but also deposition of finer sediment and particulate organic matter in areas of lower velocity associated with the wood (Battin et al., 2008; Beckman and Wohl, 2014). Particulate organic matter ($>0.45 \mu\text{m}$ in size) is composed of materials such as fragments of leaves and twigs. Scour and deposition around large wood increase the abundance and diversity of aquatic habitat for a variety of organisms (Richmond and Fausch, 1995; Johnson et al., 2003). Logjams, in particular, facilitate formation of multithread channels (O'Connor et al., 2003; Wohl, 2011; Collins et al., 2012) and enhance channel-floodplain connectivity and patterns of overbank erosion and deposition (Jeffries et al., 2003). Floodplain large wood also influences flow resistance and patterns of erosion and deposition during overbank flows, as well as providing vital habitat for diverse types of plants and animals during periods of floodplain inundation and emergence.

A key point in understanding interactions in natural rivers is recognizing that the balance among flow energy, sediment supply, large wood, and channel erosional resistance changes across space and through time.

Biological

River ecologists conceptualize coupling between the physical environment and biotic communities via several means such as examining recovery of populations from disturbance, variation in community structure (the abundance and diversity of plants or animals living in a particular place), connectivity as a constraint on migration and dispersal of organisms, water quality, and sources of energy fueling metabolism. Food webs provide a means to link these topics. Food webs describe the processes by which solar energy is initially captured through photosynthesis and then transferred among organisms through herbivory, parasitism, and predation. Within river channels, energy flows among organisms start with either autochthonous or allochthonous production. Autochthonous production occurs within the channel via photosynthesis by bryophytes (mosses and lichens), attached algae, planktonic algae, and floating or rooted angiosperms (Ward, 1992). Allochthonous production is based on organic detritus from outside the channel in the form of dissolved and particulate organic matter. Much of this organic matter entering the channel comes from leaf litter and wood derived from terrestrial plants. Once in the stream, microbes, fungi, and aquatic invertebrates decompose this organic matter. In small streams, terrestrial organic matter can provide the basis for most of the animal production (the accrual of animal biomass over time) occurring within a stream (Wallace et al., 2015). Within floodplains, energy flows also start with allochthonous production by riparian terrestrial or wetland vegetation, although autochthonous inputs of dissolved and particulate organic matter during overbank floods can be very important (Fig. 3).

The primary consumers of organic matter within a channel are microbes living in biofilm assemblages, macroinvertebrates, and fish. Biofilms composed of attached algae, bacteria, fungi, protozoans, and micrometazoans (Lock et al., 1984) coat solid surfaces within the channel. Biofilms are of particular importance to stream food webs because they drive crucial processes within river ecosystems such as the cycling of organic matter and primary production (Battin et al., 2016). Many animals, such as aquatic invertebrates, specialize in scraping and consuming biofilms (Cummins, 1973; Benke and Jacobi, 1994).

Macroinvertebrates include aquatic insects, crustaceans, mollusks, leeches, amphipods, and nematodes, which collectively typically constitute 98% of animal biomass within the channel of some rivers (Ward, 1992). Different macroinvertebrate assemblages occupy the hyporheic zone, the streambed, the water column, and the air-water interface. Similarly, different species of fish, amphibians, or other aquatic organisms, or different life stages of a single species, occupy different portions of the river corridor.

Primary consumers of organic matter in the floodplain include terrestrial organisms and aquatic macroinvertebrates and fish that live within floodplain water bodies or migrate onto the floodplain during overbank flooding. Primary consumers also include species that live within the river corridor (e.g., beaver [*Castor canadensis* in North America, *Castor fiber* in Eurasia]) and those that move in and out of the river corridor (e.g., moose [*Alces alces*] or waterfowl).

Although distinctive biotic communities occupy hyporheic, channel, floodplain, and upland environments, the boundaries between these environments are leaky, with continual exchanges of matter and energy. Ecologists describe these exchanges as subsidies between aquatic and terrestrial environments. Examples include organic litter entering a channel or floodplain lake from the surrounding riparian forest (Cuffney, 1988); aquatic insects emerging from a water body, which are then eaten by riparian

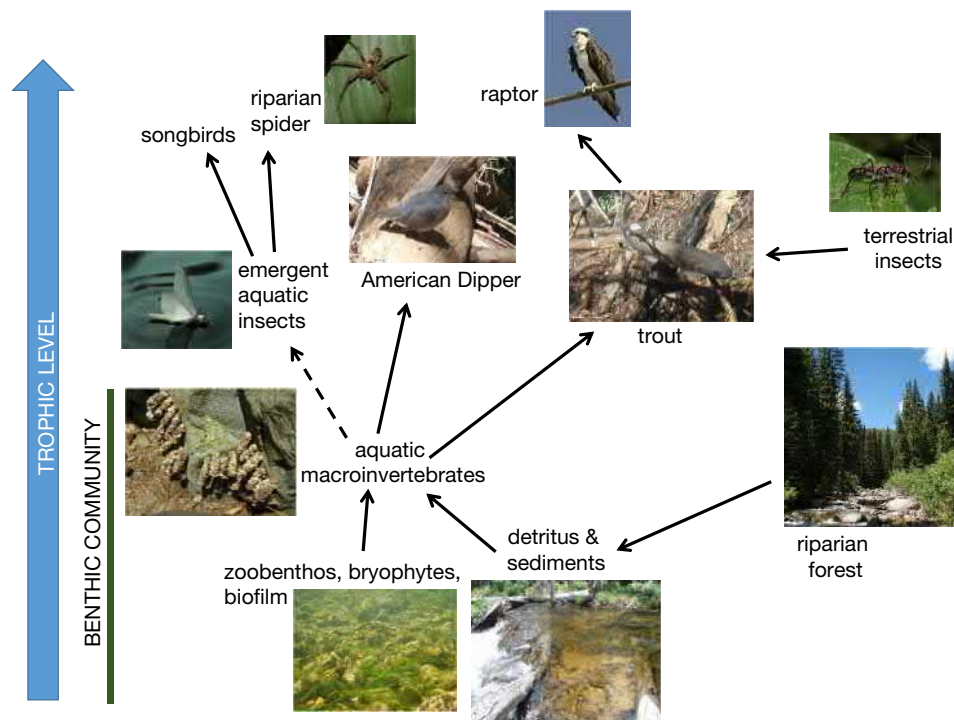


Fig. 3 Schematic illustration of a riverine food web for rivers in the Southern Rocky Mountains of Colorado, USA.

spiders or birds (Baxter et al., 2005); terrestrial insects such as wasps or ants that are eaten by fish (Nakano and Murakami, 2001); deer (*Odocoileus* spp.) that move into riparian zones to graze; and salmon (*Oncorhynchus* spp.) that migrate upstream to spawn and die, thereby transporting substantial nitrogen from the ocean to the river corridor via their decaying bodies (Gende et al., 2002).

A More Complete View of Rivers: Integrating Physical, Chemical and Biological Processes

Important examples of integrative river characteristics that combine physical and biological aspects are river integrity, connectivity, complexity, and context.

Physical integrity for rivers refers to a set of active river processes and landforms such that the river corridor adjusts to changes in water and sediment inputs within limits of change defined by societal values (Graf, 2001). Ecological integrity describes the ability of the river corridor to support and maintain a community of organisms with species composition, diversity, and functional organization similar to those within natural habitats in the same region (Parrish et al., 2003). River integrity combines these two definitions to describe the ability of the river ecosystem to adjust to changing water, wood, and sediment inputs (without constraints imposed by human manipulation such as dams or levees) and through these adjustments to maintain the habitat, disturbance regime, and connectivity necessary to sustain native biotic communities.

Connectivity describes movements of energy, material, and organisms between components of a system, which are typically spatially defined areas (Wainwright et al., 2011). Connectivity can be characterized in terms of spatial extent, magnitude, duration, timing, and frequency (Fig. 4). Connectivity also implies the presence of disconnectivity, some degree of which is important to many river ecosystem functions and communities. Downstream disconnectivity created by obstructions such as logjams, for example, can help to create fish habitat, retain particulate organic matter and nutrients, and promote fluxes of water between the surface and the hyporheic zone. Disconnectivity may also impede invasions of exotic organisms along river corridors (Rahel, 2013).

A river corridor has three primary dimensions of connectivity both within the corridor and between the corridor and adjacent environments (Ward, 1989; Pringle, 2001). Longitudinal connectivity describes the downstream movement of water, solutes, sediment, organic matter, and organisms, as well as upstream movement by animals (Vannote et al., 1980; Cote et al., 2009). Lateral connectivity can be bi-directional within the river corridor as high flows spread from the main channel into secondary channels and across the floodplain, and then recede back to the main channel (Junk et al., 1989). Lateral connectivity can also be unidirectional as materials and organisms move from uplands into the river corridor or when adult aquatic insects emerge from streams and disperse to riparian habitats. Vertical connectivity is also bidirectional above and below the river and floodplain. Water, gases, and organisms move upward into the atmosphere (Ward, 1989; Raymond et al., 2013). Wet and dry atmospheric deposition, as well as terrestrial insects, move downward into the river corridor. Water, solutes, microbes, and macroinvertebrates move vertically between the

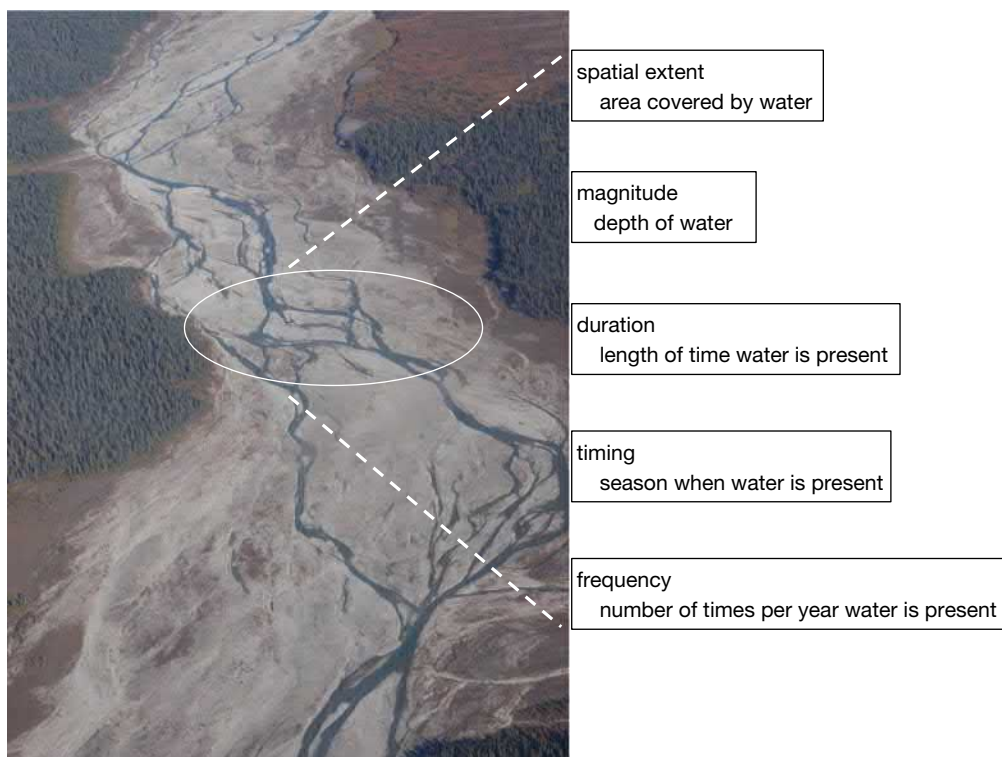


Fig. 4 Illustration of the five major components of hydrologic connectivity within a river corridor.

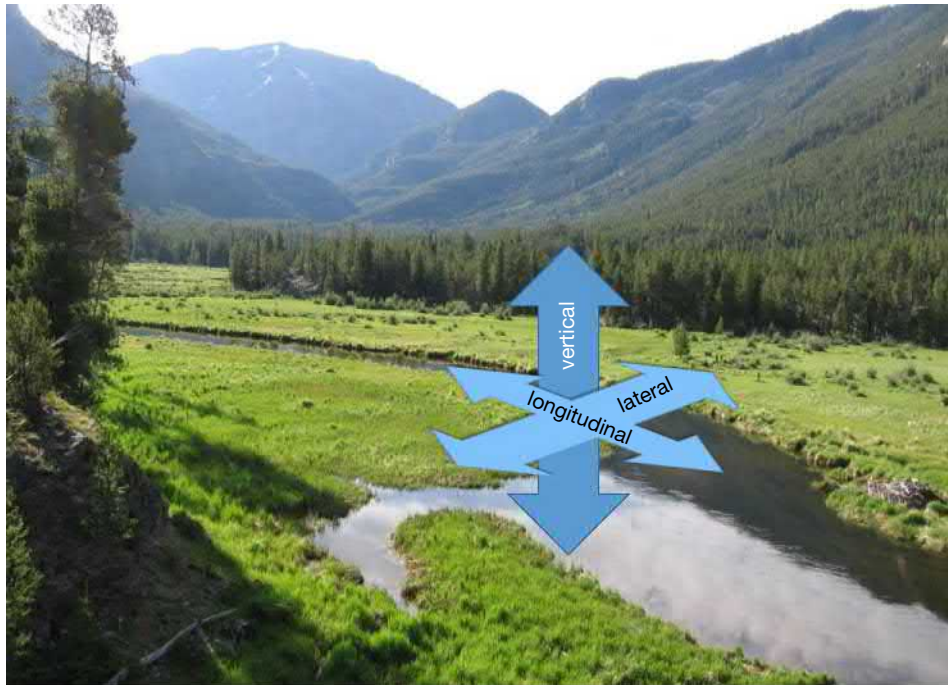


Fig. 5 Schematic illustration of the three primary dimensions of riverine connectivity. Longitudinal connectivity describes downstream movement of materials and upstream-downstream movements of organisms. Lateral connectivity refers to movement of material and organisms from uplands into the river corridor and between the channel and floodplain and riparian zone within the river corridor. Vertical connectivity describes movements between the river corridor surface and either the atmosphere or the underlying hyporheic zone and groundwater.

channel and the hyporheic zone, and water and associated solutes move vertically between the river corridor and the ground water (Fig. 5) (Brunke and Gonser, 1997).

Complexity has at least two meanings within river science. The first refers to natural systems that exhibit properties such as nonlinear dynamics, in which the change of the output is not proportional to the change of the input (Werner and McNamara, 2007; Phillips, 2014). The second uses complexity to describe spatial heterogeneity, or the degree to which a river corridor deviates from a straight, uniform canal (Wohl, 2016). Spatial heterogeneity in a river corridor occurs at diverse spatial scales from a channel unit or patch of sediment up to the entire longitudinal profile or river network (Fig. 6) (Frissell et al., 1986). At any of these scales, heterogeneity results from discrete patches with differing characteristics. These patches can be described in terms of patch richness (the number of patches present), patch frequency (the number of each patch type), patch configuration (patch arrangement in space relative to each other), patch change (which patches change and how they change), and a shifting mosaic (patch changes are spatially explicit and quantified) (Cadenasso et al., 2006), as well as spatial statistics and other metrics (Wohl, 2016).

Complexity is important for at least five reasons. (1) Complexity in the form of habitat diversity can correlate with biodiversity. Although other factors can constrain biodiversity, greater habitat diversity in river corridors correlates with greater biodiversity and biological productivity (Scott et al., 2003; Luck et al., 2010; Bellmore and Baxter, 2014; Greene and Knox, 2014). (2) Complexity attenuates downstream fluxes of water and elements. Diverse forms of complexity increase hydraulic resistance, reduce average downstream velocity, enhance hyporheic exchange, and facilitate at least transient deposition of organic matter and sediment (Jeffries et al., 2003; Brummer et al., 2006; Ensign and Doyle, 2006; Westbrook et al., 2006; Gooseff et al., 2007; Small et al., 2008; Wohl and Scott, 2017). (3) Complexity influences the resistance and resilience of river corridors to disturbance. A more complex river corridor can be more resistant and resilient to disturbance (Wohl, 2011; Collins et al., 2012). (4) Complexity both reflects and influences processes in rivers. The spatial heterogeneity present in the river corridor reflects the combined history of hydraulic force, sediment movement, and biotic colonization through time (e.g., Choné and Biron, 2016). Complexity influences river processes when bedforms or instream wood increase hydraulic resistance, which in turn influences hydraulic force and sediment movement (e.g., Yochum et al., 2012), or when logjams abandoned during channel migration and then buried in the floodplain form erosionally resistant points that limit subsequent channel migration (Collins et al., 2012). (5) Complexity reflects the inherent unevenness through time and space of processes within a drainage basin and river corridor, as indicated by the presence of ecosystem control points, that is, landscape features that disproportionately affect overall biogeochemical rates at certain times (Bernhardt et al., 2018).

Context refers to the environmental setting of the river corridor. Examples include the climate and precipitation regime, geology, topography, biome, position in the river network, land use, and land use history. Numerous classification systems have been proposed for rivers in recognition of these differences. Ecoregions, process domains, and river styles are examples of classification systems that are applied at relatively broad spatial scales within or between river networks. An ecoregion is a relatively large area of

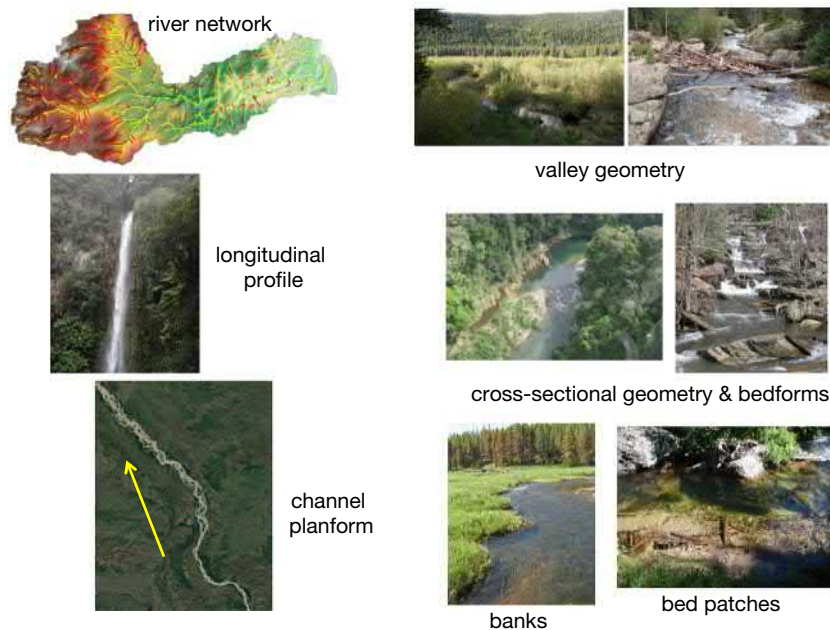


Fig. 6 Diverse spatial scales of heterogeneity within a river network. At the network scale, valley geometry can vary downstream between wide, low gradient reaches (upper left photo in right column) and narrow, steep reaches (upper right photo in right column). The map at upper left illustrates reach-scale variations in valley geometry: red indicates steep, narrow reaches; yellow indicates intermediate values; green indicates wide, low gradient reaches. The longitudinal profile of a river commonly includes heterogeneity associated with steeper reaches, including waterfalls. Channel planform can also vary downstream between straight, meandering, braided, and anastomosing patterns (yellow arrow in photo indicates flow direction). At the reach scale, cross-sectional geometry can vary between pools and riffles or straight segments and meander bends. The type and dimensions of bedforms present also vary among reaches. At smaller spatial scales, bank irregularities and patches of different streambed grain size create heterogeneity at the channel unit scale.

land or water that contains a geographically distinct assemblage of natural communities (WWF, 2013). Process domains (Montgomery, 1999) and river styles (Brierley and Fryirs, 2005) describe spatially discrete and internally homogenous portions of a landscape or river network characterized by distinct suites of geomorphic forms and processes (Fig. 7).

Ecological Relationships

Disturbance, Resistance, and Resilience

Inputs of matter and energy to a river corridor change through time and the river ecosystem responds to these changing inputs. Disturbance regimes characterize these fluctuations in inputs and resistance whereas resilience characterizes the nature of river ecosystem response.

A disturbance is any relatively discrete event in time that alters ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (White and Pickett, 1985). A flood is the preeminent example of a disturbance within a river ecosystem. Physical disturbances such as an annual flood commonly maintain habitat abundance and diversity and river connectivity that influence the survival of plants and animals in the river ecosystem (Junk et al., 1989; Bayley, 1991; Naiman et al., 1988b).

The disturbance regime is the spatial pattern and statistical distribution of disturbances with respect to magnitude, frequency, and duration of associated changes in the physical environment (Montgomery, 1999). Disturbance regime in river corridors reflects sources of water, sediment, nutrients, and other materials that originate outside of the river corridor, as well as disturbances within the river corridor. The characteristics of a disturbance and the response of the river corridor to the disturbance also vary within the river network in relation to spatial variations in disturbance and to the valley and channel geometry and substrate erosional resistance.

In a geomorphic context, resistance describes the ability of channel and floodplain substrate to remain physically unchanged by erosion or deposition. In an ecological context, resistance describes the ability of a river ecosystem to remain unchanged following a disturbance (Webster et al., 1975). Resilience is the persistence of the river ecosystem and the ability of populations and processes to return to initial conditions following a disturbance. Physical scientists also use resilience or sensitivity to describe the ability of a river corridor to return to its pre-disturbance configuration following disturbance (Brunsden and Thornes, 1979; Bull, 1991; Wohl, 2010; Reid and Brierley, 2015; Fryirs, 2016). In an ecological context, a resistant river corridor undergoes little change during disturbance and a resilient river corridor returns to its pre-disturbance configuration and relationships over a shorter time than the return interval of the disturbance.

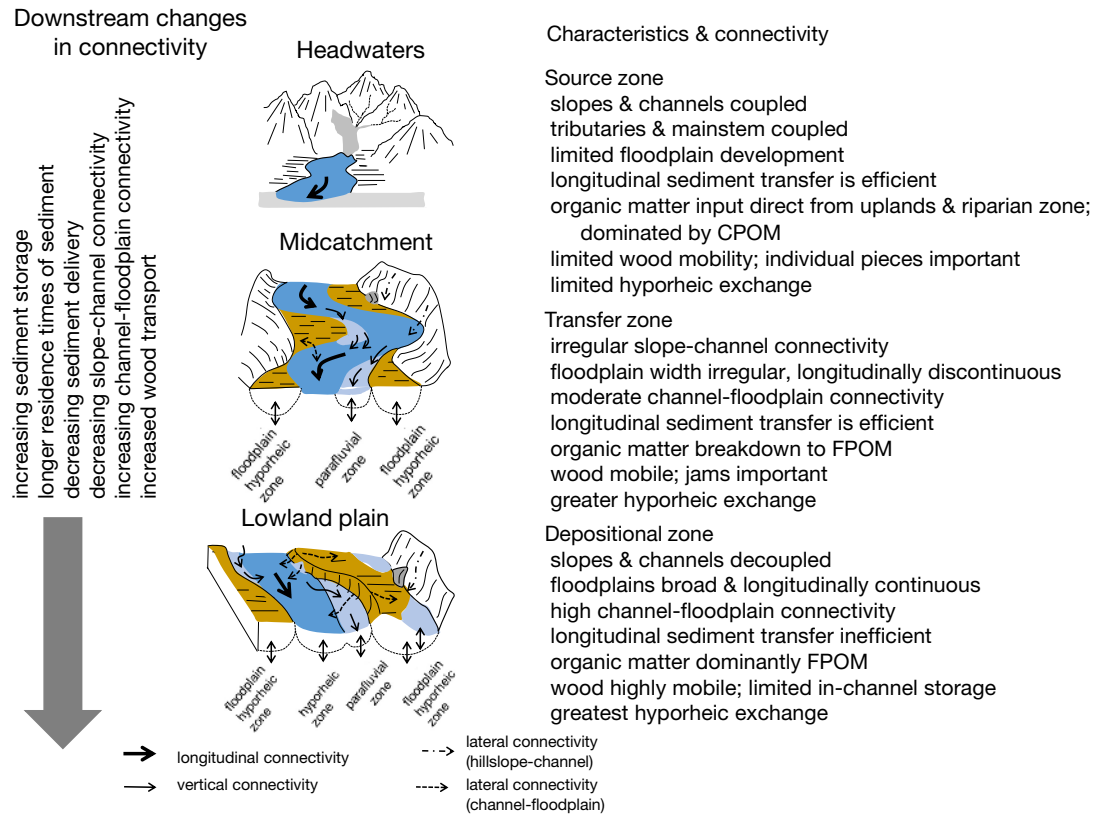


Fig. 7 An illustration of different river styles and characteristics common to headwater, mid-catchment, and lowland plain portions of a river network. In the description of characteristics, CPOM refers to coarse particulate organic matter (>1 mm in size) and FPOM (0.45 μm to 1 mm in size) refers to fine particulate organic matter. After Brierley, G. J. and Fryirs, K. A. (2005). *Geomorphology and River Management: Applications of the River Styles Framework*. Oxford: Blackwell, Figure 2.10.

An important aspect of understanding resistance and resilience is to explicitly recognize that physical characteristics of the river corridor and biotic communities are adjusted to the natural range of variability (Keane et al., 2009) in water, sediment, and large wood fluxes through time. For a river corridor, the natural range of flow variability, for example, describes the upper and lower magnitude limits of discharge, as well as the range of duration, frequency, rates of change, and seasonal timing of various components of the hydrograph in the absence of substantial human alteration of the watershed or manipulation of the flow (Poff et al., 1997).

Conceptual Models

River scientists use conceptual models to illustrate and explore interactions between physical processes and biotic communities and to describe patterns observed within river networks. Geomorphic conceptual models emphasize change through time, particularly in response to disturbances. These models include positive or self-enhancing feedback that occurs when an initial change creates a cascade of subsequent changes that amplify the initial change. These models also account for negative or self-arresting feedback that occurs when the response of the river corridor dampens an initial change. Response of the river corridor can lag changes in inputs, and change commonly occurs in an abrupt, nonlinear manner described via thresholds that separate distinct forms or modes of operation of a system. External thresholds refer to change forced by an external factor such as a flood, whereas internal or intrinsic thresholds describe abrupt changes in a river corridor in the absence of external change (Schumm, 1979).

When change occurs within morphologic features such as channel bars or floodplain wetlands, the affected morphologic feature can be described as transient or persistent (Brunsdon and Thornes, 1979; Bull, 1991). A transient form is created by a disturbance, but then returns to pre-disturbance conditions before the recurrence of a disturbance of similar magnitude. A persistent feature remains past the recurrence interval of the disturbance that created the feature. River metamorphosis describes an abrupt, sustained change in river form (Schumm, 1969; Wohl, 2013).

The most widely used river ecology conceptual models emphasize one of three characteristics: longitudinal patterns of process and form; lateral connectivity within river corridors; and changes through time. The river continuum concept (RCC) first described longitudinal patterns (Vannote et al., 1980). The RCC posits progressive downstream changes in the relative importance of primary production versus respiration and in the structure and function of aquatic communities (Fig. 8). Ward and Stanford (1983, 1995)

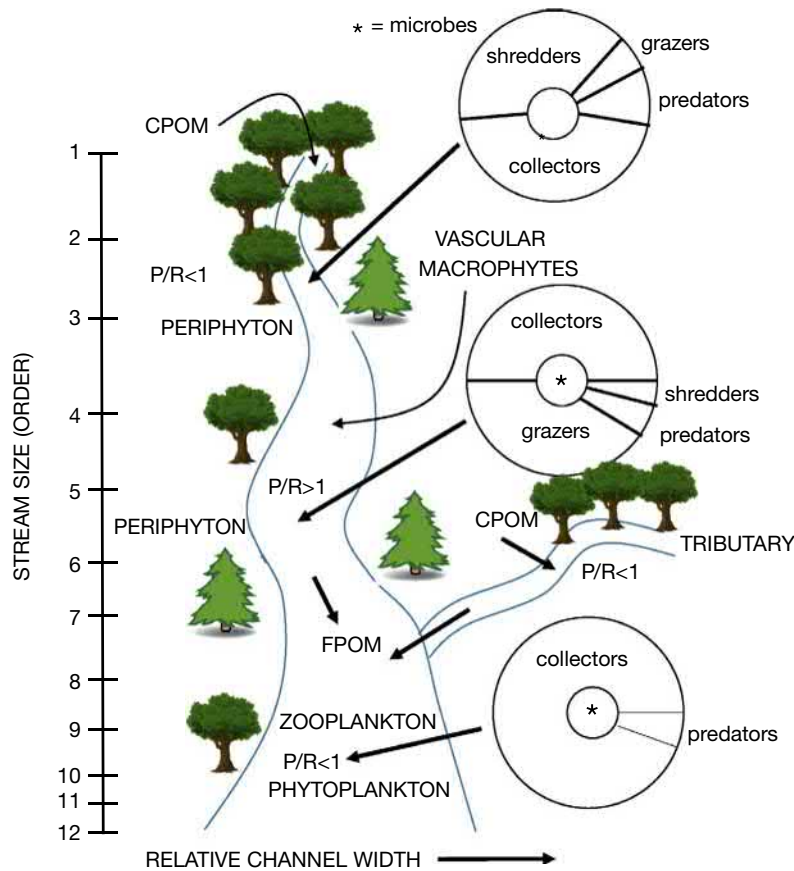


Fig. 8 Schematic illustration of the downstream changes in the relative importance of primary production (P) versus respiration (R) and in the structure and function of aquatic macroinvertebrate communities (shredder, grazer, predator, collector refer to functional groups of aquatic macroinvertebrates). After Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R. and Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130–137, Figure 1).

describe a variation in these downstream trends associated with the presence of dams and reservoirs that reset the downstream patterns, as described in the serial discontinuity model. Other studies emphasize hierarchical patch dynamics, which characterizes river corridors as consisting of relatively homogeneous patches from the scale of microhabitat up to channel reaches, with distinct changes in process and form between patches (Pringle et al., 1988; Poole, 2002; Thorp et al., 2006).

Longitudinal patterns of process can also be described in the context of nutrient spiraling. Nutrients such as nitrogen and phosphorus are displaced downstream as they complete a cycle (Webster and Patten, 1979) through the generalized compartments of water, particulates, and consumers (Newbold et al., 1981). Spiraling length refers to the downstream distance required for one complete cycle or, in the case of organic carbon, as the distance between its entry into the river corridor and its oxidation (Elwood et al., 1980). Spiraling length reflects the use of nutrients relative to the available supply as well as physical characteristics of the river corridor, such as the ability to at least temporarily retain solutes and particulates in areas of reduced transport capacity (Fisher et al., 1998; Battin et al., 2008; Baker et al., 2012).

Lateral connectivity within river corridors is the focus of the flood-pulse model (Junk et al., 1989), which describes the ecological influence of the seasonal flood pulse on large floodplain rivers such as the Amazon (Fig. 9). Water, sediment, nutrients, and organisms move from the channel onto the floodplain during peak flood flow and then return to the main channel and secondary channels during the receding limb and base flow. This repeated movement enhances nutrient availability, as well as habitat and biodiversity within the channel and the floodplain. A subsequent iteration of this model emphasizes flow pulses, which are smaller-scale fluctuations in discharge that change the extent of flow and standing water within a braided or multithreaded channel segment as well as flow levels along the margins of bars and islands within channels (Tockner et al., 2000).

Changes through time have been conceptualized in terms of river resistance and resilience, as described previously, and in terms of alternative states. Alternative stable states describe ecological systems that can exist in multiple, distinct, and self-reinforcing states in equilibrium under equivalent environmental conditions (Holling, 1973; May, 1977; Carpenter, 2003). This scenario relies on a disturbance or a threshold in response to ongoing changing conditions that is capable of driving the ecosystem into a new state from which it will not return. The ecosystem then takes a different pathway of recovery in response to the disturbance, which ultimately leads to a self-sustaining reorganization of ecosystem structure. The existence of alternative stable states has typically been

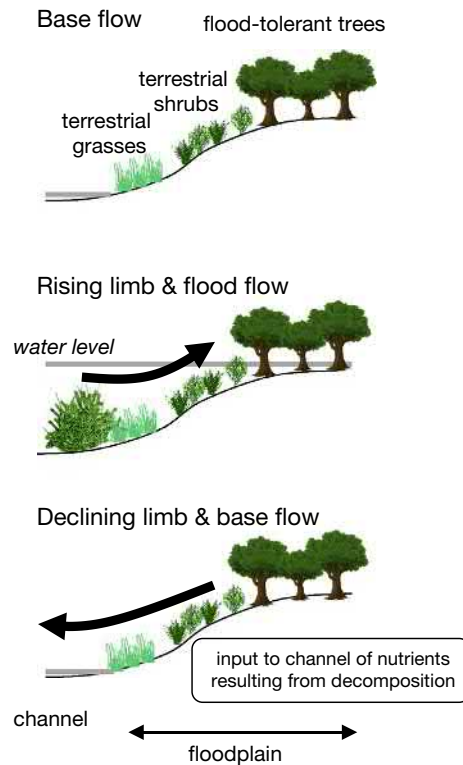


Fig. 9 Schematic illustration of the flood-pulse cycle and the associated lateral connectivity between the channel and floodplain. After Junk, W. J., Bayley, P. B. and Sparks, R. E. (1989). The flood-pulse concept in river-floodplain systems. *Canadian Special Publications in Fisheries and Aquatic Sciences* **106**, 110–127, Figure 2.

evaluated based on biotic community structure (e.g., Scheffer and Carpenter, 2003), although the concept is controversial because of the difficulty in demonstrating long-term stability (Schröder et al., 2005). This has led to the related concept of alternative states, which can be stable or transient over varying time scales (Suding et al., 2004).

Commercial Uses

The primary commercial uses of river channels include navigation, waste disposal, hydroelectric power generation, water storage, commercial fisheries, aggregate and placer mining, and diverse recreation (e.g., boating, fishing). Primary commercial uses of floodplains and riparian zones include agriculture and urbanization, which are commonly accompanied by land drainage and changes in land cover within the floodplain. These uses all have the potential to modify river corridors and the modifications can be categorized as consumptive/depletive (e.g., removal of water or organisms) or destructive (e.g., channelization or pollution) over diverse scales of time and space (Fig. 10), although human communities can benefit from these uses. The magnitude of physical and ecological changes resulting from individual commercial uses depend on factors such as the magnitude and duration of the commercial activity. Navigation, for example, can substantially alter river form, function, and process if the navigation is accompanied by channelization (channel straightening, dredging, bank stabilization, and levee construction) and if numerous large vessels generate waves that erode river banks and alternately expose and inundate portions of the river banks (Fig. 11) (Nanson et al., 1994).

The cumulative effects of diverse commercial uses have been to homogenize and simplify river corridors and to alter their connectivity. Dams and water diversions homogenize naturally variable flow regimes (Poff et al., 2007). Dams also fragment river networks thereby disrupting reproductive migrations of native fishes. Levees and channelization limit lateral connectivity between channels and floodplains and vertical connectivity between the surface and the hyporheic zone (e.g., Chovanec et al., 2004). These physical changes are reflected in massive loss of freshwater biodiversity and homogenization of river biota (Moyle and Mount, 2007; Peipoch et al., 2015). Within the United States, fewer than 2% of total river kilometers remain unaltered by flow regulation (Graf, 2001). More than half of the world's large river systems are altered by dams (Nilsson et al., 2005). Because of a long history of intensive and extensive commercial uses, river ecosystems can be regarded as a globally endangered ecosystem.

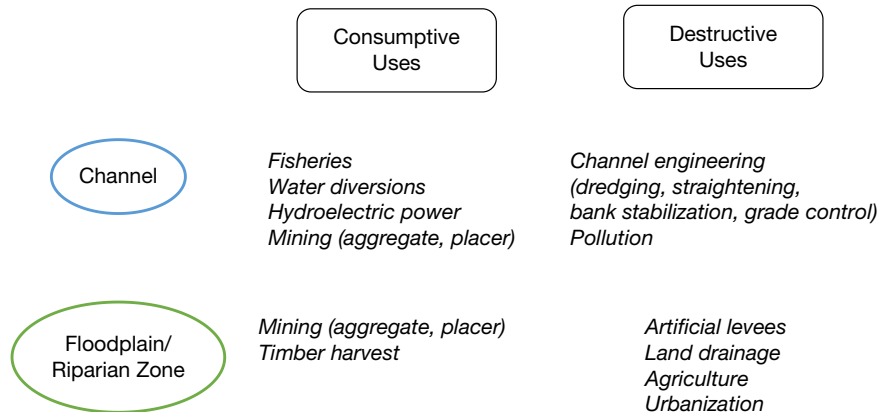


Fig. 10 Diverse types of consumptive and destructive commercial uses of the channel and floodplain/riparian components of river corridors. Any of the consumptive uses can become destructive if they are conducted in an unsustainable manner.



Fig. 11 Illustrations of commercial uses of river corridors. Aggregate mining of sand and gravel along the Rio Maipo, Chile (upper left). Channelization of a small channel in an agricultural region of Switzerland (upper right). Untreated urban sewage flowing into a river in Bogota, Colombia (lower right). Dry channel exposed downstream from a dam along the Vindel River in northern Sweden (lower left).

Major Anthropogenic Threats

Anthropogenic threats to river corridors include direct threats from activities occurring within the river corridor (e.g., channelization and flow regulation) and indirect threats from activities outside the river corridor that influence inputs of water, sediment, solutes, and large wood to the river corridor (e.g., changes in land use).

Habitat Modification, Fragmentation, and Destruction

River corridor habitat is modified, fragmented, and destroyed by most commercial uses. Channelization, levees, and bank stabilization simplify spatially heterogeneous channels and commonly increase longitudinal connectivity while reducing lateral

and vertical connectivity. Dams and diversions alter the fluxes of water and sediment that not only facilitate connectivity within river corridors, but also maintain habitat diversity. Floodplain drainage and changes in land cover within floodplains fragment or destroy floodplain habitat and connectivity. In-channel structures such as culverts, grade controls, and bridges alter channel geometry and stability and can limit aquatic organism passage (Cenderelli et al., 2011). Loss of headwater streams that are buried in pipes in both agricultural and urban areas significantly alters downstream fluxes of material and reduces habitat diversity for aquatic and riparian organisms (Fig. 12) (Elmore and Kaushal, 2008). Removal of instream large wood and beavers reduces habitat abundance and diversity, as well as lateral and vertical connectivity within river corridors (Naiman et al., 1988a, b; Burchsted et al., 2010; Pollock et al., 2014; Roni et al., 2014).

Mitigation strategies for habitat modification and fragmentation include: allowing rivers sufficient space to continue to adjust to changing water and sediment inputs by setting back levees and limiting infrastructure and urban encroachment on the river corridor (Dierauer et al., 2012); creating environmental flows that sustain longitudinal connectivity and habitat diversity (e.g., Opperman et al., 2018); and either actively reintroducing or allowing natural reintroduction of large wood and beavers to river systems (e.g., Pollock et al., 2014).

Invasive Species

Both aquatic and riparian invasive species can significantly modify river corridors in ways that reduce habitat and resources for native species, as well as directly competing with native species. Invasive plants in riparian zones can displace native species (Stromberg, 1998) and alter river morphology; for example, the invasion of tamarisk trees (*Tamarix* spp.) to riparian zones in rivers in arid regions can reduce channel width (Graf, 1978) and limit the lateral channel movement that creates habitat heterogeneity in the channel and floodplain. Invasive animals can change the aquatic food web, as in the example of invasive nonnative rainbow



Fig. 12 An example of stream burial. Here, a tributary draining the mountains adjacent to the city of Bogota, Colombia is diverted into a pipe before entering the city limits.

trout (*Oncorhynchus mykiss*) in Japan that usurped terrestrial insects falling into a stream, thereby causing native Dolly Varden charr (*Salvelinus malma*) to shift their foraging to insects grazing algae from the stream bed (Baxter et al., 2004). This indirectly increased algal biomass and decreased the biomass of adult aquatic insects emerging from the stream. Reduced insects entering the forest from the stream caused a decrease in riparian-specialist spiders in the forest.

The effects of animal invasions on streams are varied, ranging from having little effect to greatly affecting other animal populations via predation (Cucherousset and Olden, 2011) or interbreeding (Allendorf et al., 2001). Some invasive animal species in rivers can have extensive ecosystem-level effects due to high biomass of the invaders relative to native animals (Caraco et al., 1997; Hall et al., 2003). Past responses to invasive species have included attempted eradication; blocking migration routes; raising public awareness of, and attempting to limit, inadvertent human spread of invasive species; introducing other species that prey on or parasitize the original invasive species; and restoring riverine structure and function in a manner that favors native species. These responses can help, but there has been little success with completely eradicating invasive species once they are established in a river.

Environmental Pollution

As sites of concentrated human activity, river corridors receive diverse forms of pollutants. Major categories include heavy metals, mercury, nitrogen, phosphorus, pathogens, various persistent organic pollutants (POPs) such as polychlorinated biphenyls (PCBs) and pesticides, and sediment. Heavy metals such as Pb, Cu, and Zn are toxic to many aquatic animals, particularly invertebrates, and originate from natural and anthropogenic sources such as metal-rich mineral deposits, mining, chemical industries, fossil fuel combustion, and sewage waters (Bednarova et al., 2013). Mercury is a highly toxic natural element that enters rivers primarily via atmospheric emissions of inorganic mercury from coal combustion, waste incineration, and wildfire, as well as via discharge of industrial and municipal wastes (Fisher et al., 2012).

Nitrogen (Green et al., 2004; Galloway et al., 2004; Boyer et al., 2006) and phosphorus (Withers and Jarvie, 2008) become river pollutants at concentrations exceeding those of natural or background levels. This causes eutrophication, where high nutrients stimulate growth of algae and other aquatic plants. Excessive plant growth increases organic loading to rivers, which can in turn lead to oxygen depletion and animal die-offs (Mallin et al., 2006). Excess nitrogen and phosphorus result from agricultural and urban runoff, and nitrogen is also increased by fossil fuel emissions.

Pathogens include any microbial organism that can impair the health of humans or other organisms. Pathogens enter rivers from wastewater treatment effluent, sewage tanks, and agricultural operations, particularly those involving livestock (Varela and Manaia, 2013).

Persistent organic pollutants (POPs) are organic chemicals produced for a variety of agricultural and industrial uses. These chemicals are persistent because they degrade very slowly via natural processes and thus incur a long-term legacy of potential environmental exposures and effects. Many of these compounds are lipophilic ("fat loving") causing them to bioaccumulate in organisms and to biomagnify to potentially toxic levels in food webs (Walters et al., 2016). Polychlorinated biphenyls (PCBs), for example are a large class of persistent organic pollutants (POPs) that were widely used as additives in oils, industrial fluids, and other commercial products. PCBs cause a variety of health effects including cancer and remain one of the leading causes of organic pollution in riverine environments even though their production was banned in 1979 (National Research Council, 2001; USEPA, 2011). Other common types of organic pollutants in rivers include pesticides, polyaromatic hydrocarbons (PAHs), and brominated flame retardants among many others (Walters et al., 2016).

Mitigation strategies for pollutants include creating and enforcing water quality standards (e.g., Boyd, 2015); aggressively remediating contaminated sites (e.g., Sheng et al., 2013); and restoring and protecting riparian zones and in-channel heterogeneity that facilitate retention and biological uptake of excess nutrients (e.g., Aguiar et al., 2015). Sediment of sand size or smaller can be a pollutant in rivers because the sediment may carry adsorbed contaminants or because the sediment creates adverse impacts on water and channel properties. Adverse impacts include increased turbidity (a loss of water clarity) and the clogging of spaces between rocks on the stream bed that are important habitats for the survival of stream invertebrates, fish eggs, and some fishes. Excessive sediment deposition can lead to a loss of pool habitats themselves, which are also important habitats for many aquatic organisms. Beyond these obvious and direct effects on river habitats and organisms, excessive sediment increases the costs of drinking water treatment and stimulates growth of cyanobacteria that can produce chemicals toxic to other organisms. Owing to the myriad and pervasive negative effects of sediment on river ecosystems, the US Environmental Protection Agency lists sediment as the most common river pollutant (Owens et al., 2005). Mitigation strategies for pollution associated with excess fine sediment include protection and restoration of riparian zones that can retain fine sediment and enforcement of best management practices for construction, timber harvest, agriculture, and other activities that can result in erosion of fine sediment from uplands and transport into river systems (e.g., Aust and Blinn, 2004).

Climate Change

The details of climate change vary with geographic location, but changing climate affects the entire landscape and thus inputs of water, sediment, solutes, and large wood to river corridors, as well as transport and storage of material within the river corridor. These changes will in turn affect habitat abundance and diversity, disturbance regime, and connectivity within the river corridor. Climate warming is likely to disproportionately affect animals that depend upon cold-water habitats such as Bull Trout (*Salvelinus confluentus*) and the American Dipper (*Cinclus mexicanus*). These types of species will experience shrinking geographic ranges and

limited dispersal opportunities as the climate warms (Rieman et al., 2007). These effects are already apparent for certain cold-water taxa like high-alpine insects that are dependent upon glacial melt-water streams (Giersch et al., 2017). Climate warming is also likely to severely impact aquatic and riparian species in arid and semiarid regions, where the combined effects of decreasing precipitation and increasing human consumptive demands for water will lead to progressive drying of river corridors (Falke et al., 2011).

Changing climate can alter human consumptive demand, such as when depletion of groundwater aquifers and increasing drought result in greater water diversion from rivers. Finally, changing climate can increase hazards such as flooding, triggering additional human modifications of river corridors to enhance flood risk reduction.

Climate change is ongoing, but mitigation strategies for river systems can focus on: protecting connectivity that allows organisms to disperse to more suitable locations (Rahel et al., 2008), and on protecting and restoring characteristics that increase the resiliency of the river system to climate-associated disturbances such as floods, droughts, and wildfires. Restoring beaver populations and the high water tables and dense woody riparian vegetation that commonly accompanies beaver ecosystem engineering, for example, can help to mitigate the effects of droughts and wildfire (Hood and Bayley, 2008).

Conservation and Management

Traditional river management seeks to minimize natural disturbances and to constrain a river's ability to adjust its form in response to disturbance. This approach has harmed river biotic communities to the point that river management in many cases now seeks to restore disturbances, spatial heterogeneity, and diverse forms of connectivity (Wohl et al., 2015). Management and restoration of river corridors occur within the context of legal frameworks associated with legislation such as the 1972 Clean Water Act and the 1973 Endangered Species Act in the United States and the European Union's 2000 Water Framework Directive, each of which mandates levels of protection for water quality, habitat, and individual species. The Clean Water Act, for example, has been credited with substantial improvements in riverine water quality through regulation of point-source discharges, such as municipal water-treatment plants (EPA, 2000).

Research Needs

Among the primary research needs to enhance understanding and protection of river ecosystems are continued development of methods that quantify natural flow, sediment, and wood regimes, as well as necessary levels of restoration or mitigation where these regimes have been substantially altered. Bernhardt and Palmer (2011), for example, call attention to the fact that restoring riparian corridors along limited portions of a river network is unlikely to create enough retention and biological uptake of nitrogen to mitigate watershed-scale increases in nitrate inputs to river systems. Analogously, addition of a limited number of engineered logjams is unlikely to effectively mitigate historical river metamorphosis in which wood removal changed multi-channel, laterally mobile rivers with heterogeneous channels and floodplains to single-channel, laterally stable rivers with less habitat diversity (Collins et al., 2002). Mitigating changes to natural flow, sediment, and wood regimes also requires understanding how disturbances create and maintain desirable ecological processes and functions. The widespread tendencies to attempt to suppress natural disturbances such as floods or wildfires or to immediately reverse some of the effects of these disturbances (e.g., channel engineering designed to simplify channels and remove the habitat diversity created by flooding) suggest the need both to increase societal awareness of the importance of natural disturbances and to enhance scientific understanding of minimum thresholds of disturbance required to maintain the ecological integrity of river systems. We also need to develop methods allowing us to predict biotic responses to geomorphic changes in river form. This point is intentionally broad, in that what we need to predict depends on the research question or management objective. Predicting the response of species richness to river change is an example of a well-researched topic with obvious implications for river conservation (Hawkins et al., 2000). Some restoration efforts do not have the expected impact on biotic structure, e.g. increasing temperatures below a cold-water release dam did little to restore native invertebrate diversity (Vinson, 2001). Other approaches might be to predict ecosystem processes such as metabolism following river alteration or restoration (Bernhardt et al., 2018).

Acknowledgements

This research was subjected to USGS review and approved for publication. We appreciate insightful review comments by Robert B. Jacobson.

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http://ec.europa.eu/environment/water/water-framework/index_en.html—European Union Water Framework Directive.

<http://www.feow.org/>—Freshwater Ecoregions of the World.

<https://www.epa.gov/laws-regulations/summary-clean-water-act>—United States Clean Water Act.

Riparian Ecosystems

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Abstract

Riparian ecosystems encompass a diverse suite of ecosystem types, including river banks, floodplains, and wetlands, that are characterized primarily by being ecotones, or transitional zones, between adjacent terrestrial and aquatic realms. In general, riparian ecosystems represent wetter, cooler, and more heterogeneous habitats than adjacent upland areas and consequently tend to support biologically distinctive, productive and diverse communities. Riparian ecosystems also provide a wealth of critical ecosystem functions and services of importance at local and catchment scales. In particular, riparian vegetation plays a key role in: regulating microclimates and water quality; preventing riverbank erosion and promoting landform stability; subsidizing aquatic and terrestrial food webs; and providing habitat for a wide range of aquatic, amphibious, and terrestrial organisms. Despite these values, riparian ecosystems are also some of the most altered, degraded and vulnerable ecosystems on Earth, due largely to their position in the landscape and hotspots of intensive human activity. Effective management and restoration of riparian ecosystems is increasingly urgent, for both the conservation of much terrestrial and aquatic biota and the wellbeing and livelihoods of people throughout the world. Management approaches range from protection of intact riparian ecosystems to active revegetation of degraded riparian zones. Significant knowledge gaps exist in many places, however, regarding relationships between riparian ecosystem structure and function and the responses of these to disturbances and management interventions.

What Are Riparian Ecosystems?

The term *riparian* is derived from the Latin word *ripa*, meaning river bank. Indeed, riparian ecosystems are often considered to be limited to the relatively narrow borders of rivers and streams, e.g., gallery forests or fringing wetlands. In ecological terms, however, riparian ecosystems comprise a much broader suite of landforms that are characterized primarily by being zones of transition between terrestrial and aquatic (excluding marine) realms, the latter of which may comprise either lotic (i.e., flowing) or lentic (i.e., standing) waters (Naiman et al., 1998; Nilsson and Svedmark, 2002). As such, riparian ecosystems are examples of “ecotones,” i.e., transitions or boundaries between adjacent contrasting biomes (Naiman et al., 2005).

In a functional sense, riparian ecosystems can be defined as those areas which, due to their position fringing watercourses or waterbodies, exert a direct influence on adjacent aquatic ecosystems and, in turn, are themselves influenced by these (Naiman et al., 2005; Capon et al., 2013a,b). Consequently, riparian ecosystems include river and stream banks but also floodplains and the edges of lakes, including littoral zones, and other wetlands. Furthermore, dry river and lake beds as well as dry phases of intermittent wetlands can function as riparian ecosystems whose reciprocal interactions with their associated aquatic ecosystems are separated in time rather than space (Brock et al., 2006).

To some extent, the entire catchment of a watercourse or waterbody might be considered riparian, at least to some degree, in the sense that all areas within these may exert some influence on the aquatic ecosystems which they drain into—the degree of “riparian-ness,” i.e., the types, strength and significance of interactions that occur between neighboring terrestrial and aquatic ecosystems, declining with increasing distance. In practice, however, and particularly from legal and planning perspectives, riparian ecosystems are often only considered to comprise relatively narrow areas of land adjacent to watercourses (Verry et al., 2004).

Features of Riparian Ecosystems

As representatives of a biome that is widely distributed across every continent on Earth, riparian ecosystems are highly diverse, reflecting global and regional variation in climate, geology and geomorphology as well as the enormous range of terrestrial and aquatic ecosystems which they traverse. Because of their common low-lying position within the landscape, however, and the influences of the watercourses or waterbodies which they border, riparian ecosystems generally share numerous distinctive characteristics (Naiman et al., 2005).

First and foremost, riparian ecosystems tend to be wetter than surrounding terrestrial ecosystems. Depending on the permanence of water within adjacent aquatic systems, biota inhabiting riparian zones may have greater access to surface and shallow ground water and higher soil moisture levels. Humidity is also typically higher in riparian ecosystems (Pettit and Naiman, 2007). Additionally, riparian ecosystems are often subject to lower rates of evaporation and cooler temperatures than neighboring upland areas (Broszofski et al., 1997; Danehy and Kirpes, 2000; Dwire and Kauffman, 2003). As ecological edges, however, riparian zones can also have higher levels of light and more exposure to wind, waves and climatic events such as storms, cyclones and storm surge, particularly in areas immediately fringing open watercourses or waterbodies (Capon et al., 2013a,b).

Many riparian ecosystems (e.g., river banks, floodplains) are characterized by intermittent flooding which occurs as a result of overbank flows (Stromberg, 2001; Nilsson and Svedmark, 2002; Capon, 2003, 2005; Poff and Zimmerman, 2010). As well as temporarily increasing the extent and depth of surface waters (and topping up groundwaters), floods redistribute materials within a catchment. Flooding both deposits and scours fresh sediments (and nutrients) from riparian landforms which can consequently be quite dynamic, depending on the hydrological and hydraulic regimes to which they are subject (Gregory et al., 1991; Hupp and Osterkamp, 1996). Furthermore, at a landscape scale, riparian lands typically have more fertile soils than upland areas, at least in depositional areas, e.g., floodplains (Spink et al., 1998).

Flooding, as well as stream flow, provides an additional dispersal vector for propagules known as *hydrochory* (Nilsson et al., 1991). Biota in riparian ecosystems may therefore have more available dispersal vectors than organisms inhabiting terrestrial ecosystems because of the high potential for hydrochory as well as zoochory (i.e., dispersal via waterbirds and other animals that utilize the riparian corridor) and anemochory (i.e., dispersal via wind which may be enhanced by the openness of adjacent watercourses/waterbodies). Riparian organisms are also, however, subject to many stresses during periods of inundation including anoxia and the associated accumulation of toxic materials in the soil, reduced light in submerged areas and burial by deposited sediments (Blom and Voesenek, 1996; Nilsson and Svedmark, 2002; Capon, 2003). Furthermore, swiftly flowing surface waters, during floods as well as other times, can cause mechanical damage to in situ organisms, e.g., by snapping stems or uprooting plants (Bendix, 1999).

Overall, spatial and temporal variation in hydrological regimes across riparian ecosystems generates dynamic mosaics of habitat patches which differ in their availability of resources as well as the presence and intensity of stressors (van Coller et al., 2000; Capon, 2005; Brock et al., 2006). Consequently, riparian ecosystems are usually characterized by a high degree of habitat heterogeneity in space and time, both at local and larger (e.g., catchment) scales (Stromberg et al., 2007). Because of this, as well as their distinctive abiotic characteristics, riparian zones often support highly productive and species rich ecosystems (Capon and Pettit, 2018). In many places, more species occur in riparian ecosystems than in neighboring uplands, although this is not always the case (De'camps et al., 1987; Woinarski et al., 2000; Bennett et al., 2014). For the most part, however, riparian ecosystems enhance biodiversity at landscape and catchment scales by supporting different, if not more, species than surrounding terrestrial ecosystems (Sabo et al., 2005).

Riparian ecosystems typically comprise dynamic assemblages of aquatic, amphibious and terrestrial species, reflecting the range of conditions provided by these areas in space and time. Some species occurring in riparian ecosystems may have much broader distributions and only utilize riparian habitats at certain times or under particular conditions (e.g., aquatic organisms during flooding; King et al., 2003). Other species, however, can be restricted to riparian zones, either in certain locations or throughout their entire ranges (Rood et al., 2010). Such species might be considered to be riparian specialists if they possess traits that enable them to survive and flourish in riparian habitats (e.g., Machtans et al., 1996; Januschke and Verdonschot, 2016). Rheophytes, for example, are a group of plants adapted to swiftly flowing water (van Steenis, 1987).

As well as supporting high levels of biodiversity, riparian ecosystems are often characterized by greater structural habitat complexity than adjacent uplands (Capon, 2005). Riparian vegetation structure in particular tends to be very heterogeneous spatially, typically exhibiting lateral zonation along gradients of distance and/or elevation as a result of variation in exposure to surface water inundation or wave action (Hupp and Osterkamp, 1996; van Coller et al., 2000). Population structures of woody riparian species can similarly display lateral zonation with younger recruits (i.e., seedlings and saplings) often occurring at the edges of watercourses/waterbodies where there is greater exposure to light, soil moisture and freshly deposited, vacant sediments (e.g., Pettit et al., 2001; Boland, 2014).

The lateral extent (i.e., width) and differentiation of riparian ecosystems from the surrounding terrestrial landscape varies considerably both within and between catchments, largely in response to broad scale hydrological conditions. In areas of high precipitation, for example, such as tropical rainforests, riparian ecosystems bordering narrow streams might be relatively indistinguishable from adjacent upland forests, although some differentiation may occur where channels are wider as a result of greater light availability. In contrast, riparian ecosystems in arid landscapes are often very distinct from upland areas, even along narrow watercourses, reflecting marked differences in water availability (Capon et al., 2016a,b). Furthermore, riparian ecosystems in arid regions can support species with distributions that extend as "green tongues" from their more mesic distributions (Selwood et al., 2017). Indeed, in many arid regions, riparian vegetation represents the only major perennial plant life in otherwise relatively barren landscapes. Increasingly, riparian zones also tend to contrast starkly with their surrounding catchments because they are the only areas of significant vegetation remaining in human-dominated agricultural or urban landscapes (James et al., 2016).

Functions and Benefits of Riparian Ecosystems

Riparian ecosystems are critically important at both local and landscape scales and potentially even at much larger scales, e.g., by providing habitat along routes for migratory birds that travel between continents (Table 1; Capon et al., 2013a,b). Riparian vegetation, in particular, supports many key ecosystem functions that underpin ecological patterns and processes both within the aquatic ecosystems which they fringe as well as in the broader terrestrial landscape (Capon and Pettit, 2018). Significant functions of riparian ecosystems include the moderation of light and temperature within adjacent aquatic ecosystems, largely through shading by overhanging canopies, including those of trees, shrubs and herbaceous understorey plants. By reducing light availability, riparian vegetation can contribute to the regulation of aquatic plant growth, including green algae (Chauvet and Decamps, 1989). Shading also lowers water temperatures, providing refuges for aquatic organisms that are vulnerable to high temperatures (Stewart et al., 2013).

Riparian ecosystems serve as important buffers between aquatic ecosystems and their catchments and are therefore vital for regulating water quality (Mayer et al., 2007; Capon and Pettit, 2018; Luke et al., 2019). Riparian vegetation and soils play a particularly significant role by filtering terrestrial run-off and shallow groundwaters from catchments before these enter aquatic ecosystems, trapping sediments and nutrients via the physical presence of vegetation, litter and woody debris, as well as through plant nutrient uptake and soil microbial activity (Lowrance et al., 1984; Pinay and Decamps, 1988; Pinay et al., 1993). Riparian vegetation also has a significant influence on landform stability, especially that of river banks and beds in lotic systems (Malanson, 1993; Hubble et al., 2010; Solari et al., 2016; Krzeminska et al., 2019). Both deep and shallow rooted plants can reduce erosion and increase soil cohesion while surface vegetation and litter cover can protect top soils (Capon and Pettit, 2018). Riparian vegetation can further minimize bank erosion more indirectly by influencing surface water hydraulics, e.g., by roots or stems slowing down swiftly flowing waters (Pollen-Bankhead and Simon, 2010). Inundation patterns (e.g., flood extents) can similarly be affected by riparian ecosystems, especially their vegetation, soils and topography, which may therefore play an important role in flood mitigation and/or protecting upland areas from other disturbances such as storm surge (Capon et al., 2013a,b).

Riparian ecosystems provide significant habitat and food resources for both terrestrial and aquatic organisms, both directly and indirectly (Capon and Pettit, 2018). In aquatic ecosystems, overhanging branches or roots from riparian vegetation can provide vital habitat for a range of organisms (e.g., algae, invertebrates, fish), as can leaf litter or larger woody debris that enters watercourses from their riparian zones. Riparian leaf litter can play a particularly important role in some aquatic food webs where it is consumed by some groups of invertebrates, e.g., shredders (Cummins et al., 1989). In turn, riparian ecosystems support the supply of significant food contributions of aquatic origins to terrestrial food webs, e.g., adult aquatic insects such as dragonflies (Lynch et al., 2002). Because of their accessibility to water and other abiotic characteristics (e.g., lower temperatures), riparian ecosystems represent critical habitat for terrestrial fauna in many landscapes at certain times, e.g., as refuges from drought or heatwaves (Reside et al., 2014). Furthermore, riparian zones may provide corridors for the movement of organisms throughout the landscape, which may be particularly significant under climate change by allowing mobile species to migrate into cooler areas at higher elevations (Krosby et al., 2018).

Many riparian ecosystem functions are of direct benefit to people (e.g., water quality protection, erosion control, recreational values) while many others support crucial regulating ecosystem services (Table 1; Capon et al., 2013a,b). Many riparian ecosystem services (e.g., shading, flood mitigation) are also increasingly recognized as vital in relation to climate change adaptation (Capon et al., 2013a,b). The value of ecosystem services and benefits provided to people by riparian ecosystems is widely considered to be disproportionately high with respect to the surface area which they occupy.

Table 1 Critical ecological functions and associated ecosystem services provided by riparian ecosystems and some major factors influencing these

<i>Ecological functions</i>	<i>Ecosystem services</i>	<i>Key influencing factors</i>
Climatic regulation	Shading, provision of drought and heat refuges	Riparian canopy cover and height, channel width and aspect
Nutrient filtration and cycling	Water quality regulation	Riparian vegetation width and continuity, vegetation composition, root depth and structure, leaf litter, topography, hydrology, soil type
Sediment trapping Stabilization of channel banks and beds	Water quality regulation, landform stability	Riparian vegetation width and continuity, stem density, root structure, leaf litter, topography, hydrology, hydraulics, type of substrates
Food web subsidies Habitat structure	Support of biodiversity, e.g., fish Timber production, pasture growth, support of biodiversity, e.g., fish	Riparian vegetation composition and dynamics, hydrology, water quality Riparian vegetation composition and dynamics, hydrology, other disturbances (e.g., fire), surrounding landscape condition

Modified from Capon, S. J. and Pettit, N. E. (2018). Turquoise is the new green: Restoring and enhancing riparian function in the Anthropocene. *Ecological Management & Restoration* **19**, 44–53; Capon, S. J., Chambers, L. E., Mac Nally, R. et al. (2013a). Riparian ecosystems in the 21st plants. *Trends in Ecology & Evolution* **11**, 290–295; Capon, S. J., Chambers, L. E., Mac Nally R., et al. (2013b). Riparian ecosystems in the 21st century: Hotspots for climate change adaptation? *Ecosystems* **16**, 359–381.

Major Determinants of Riparian Ecosystem Structure and Function

While the regional species pools from which riparian assemblages are drawn are influenced by many factors, especially climate, the composition and structure of riparian ecosystems are typically governed primarily by hydrology (Power et al., 1995; Poff and Zimmerman, 2010). Riparian vegetation in particular is strongly influenced by hydrology and, to a lesser degree, geomorphology, and soils (Capon et al., 2016a,b). Patterns of water availability, flooding, and drying typically have an overarching effect on the condition, survival, reproduction and interactions of riparian plants and, therefore, the temporal and spatial patterns in vegetation communities of riparian landscapes (Capon et al., 2016a,b). Over short timeframes, key hydrological attributes influencing riparian ecosystems include the timing of flows/floods (e.g., seasonality), duration of flooding, magnitude (depth and extent) of flooding and the rates of rise and fall of floodwaters (Nilsson and Svedmark, 2002). Such factors act as environmental filters determining which species are able to tolerate the stresses generated by flooding and which are best able to capitalize on the associated opportunities for dispersal, growth and reproduction. Over longer time periods, patterns of flow/flood history (e.g., flood frequency) are also important (Capon, 2005). Spatial variation in riparian tree populations, for example, often reflect longer-term patterns in flood history (Friedman and Lee, 2002; Hultine et al., 2007; Stromberg et al., 2010). Many other factors can also exert significant influences on riparian vegetation dynamics depending on the nature of the ecosystems involved, e.g., hydraulics, salinity, fire. In most cases, however, such factors are themselves shaped by hydrological regimes (Capon et al., 2016a,b).

Riparian ecosystem function is strongly influenced, in turn, by the composition, structure and condition of riparian vegetation (Table 1; Capon and Pettit, 2018). Vegetation composition and structure, for instance, influences the presence and quality of habitats types and food resources available. Below ground, root density, architecture and composition affect groundwater filtration, nutrient uptake and landform stability. The width and density of riparian vegetation are particularly important with respect to its role as a buffer with wider, denser and more contiguous riparian vegetation typically having a greater capacity to trap sediments and nutrients (Mayer et al., 2007). Provision of habitat and food resources by riparian ecosystems to both terrestrial and aquatic organisms will also be determined by the extent of riparian vegetation, both laterally and longitudinally, as well as its spatial and temporal heterogeneity. The continuity of fringing riparian vegetation along watercourses, as well as in connection with upland vegetation patches, will especially contribute to its accessibility as refugial habitat for terrestrial fauna and its capacity to provide corridors for the movement of organisms through the landscape.

While riparian vegetation tends to play a fundamental role, complex interactions between hydrology, geomorphology and soils also influence riparian function. Riparian ecosystems with gently sloping landforms, shallow water tables and permeable soils, for example, may have a greater capacity to intercept and filter groundwaters (Mayer et al., 2007). Similarly, the width and orientation of adjacent aquatic landforms can determine the role and importance of some riparian ecosystem functions. The effects of shading by riparian vegetation, for example, might be expected to be more significant in narrow streams, although even partial shading of broad river reaches can provide some thermal refuges for aquatic organisms (Capon and Pettit, 2018).

Because of complex interactions between climate, hydrology and geomorphology, the composition, structure and function of riparian ecosystems vary considerably between regions as well as within catchments (e.g., upper vs. lower reaches) and over time in relation to hydrologic conditions. Furthermore, many riparian ecosystem functions (e.g., provision of drought refuge and corridors for fauna) can be expected to become more significant under climate change (Capon et al., 2013a,b).

Threats and Pressures

Riparian ecosystems are widely considered by to be amongst the most modified and degraded ecosystems in the world (Tockner and Stanford, 2002). Human activities and developments are often concentrated within and surrounding riparian zones in both urban and agricultural landscapes. Consequently, riparian ecosystems are frequently subject to a wide range of direct anthropogenic pressures including vegetation clearing, landform modification (e.g., channelization and armouring), water resources development, draining, harvesting, hunting, forestry, cropping, grazing, and infrastructure development. Many of these pressures result in significant reductions in the extent of riparian vegetation, including its width and longitudinal continuity, as well as changes to vegetation composition and structure with significant implications for critical ecosystem functions and services. Declining water quality in many human-dominated catchments around the world, for example, is often directly attributable to the loss and degradation of riparian vegetation (Sweeney et al., 2004; Lintern et al., 2018; Chua et al., 2019).

Because of their low-lying position in the landscape, riparian ecosystems are also exposed to the cumulative effects of pressures in their catchments, in both terrestrial and aquatic realms (Capon et al., 2013a,b). Changes to hydrological regimes due to upstream water resources developments, for example, can have dramatic effects on patterns of water availability and flooding in downstream riparian zones with significant implications for ecosystem structure and function (Nilsson and Svedmark, 2002). Changes to land cover and land use in upland areas can also have a substantial influence on the quantity and quality of surface runoff and groundwaters flowing into riparian ecosystems. In highly cleared agricultural and urban catchments, for instance, riparian ecosystems can be subject to much greater, flashier runoff bringing elevated sediment loads and pollutants.

Riparian ecosystems are additionally highly vulnerable to species invasions, especially by exotic plants (Richardson et al., 2007). Low resistance to plant invasion in riparian ecosystems is often attributed to their high levels of intrinsic (e.g., hydrological) and human disturbance, high edge to surface area ratios and the diversity of dispersal vectors available to colonizing plants (Capon and

Pettit, 2018). Changes to hydrological regimes are also widely associated with plant invasions in riparian ecosystems globally (Catford et al., 2011; Merritt and Poff, 2010). In turn, exotic plant invasions can have significant repercussions for ecosystem functions, e.g., the quality of leaf litter entering aquatic food webs.

Multiple direct and indirect pressures affecting riparian ecosystems interact with each other, often resulting in highly deleterious outcomes at both local and catchment scales. Climate change represents a further “umbrella” pressure that can affect the structure and function of riparian ecosystems both directly (e.g., by altering hydrological regimes) and more indirectly through its effects on other threats and pressures and the sensitivity of riparian ecosystems and biota to these. In general, riparian ecosystems are anticipated to be highly vulnerable to climate change impacts because of their high levels of exposure to altered climatic stimuli and disturbances as well as their high levels of sensitivity to these (Capon et al., 2013a,b). While riparian biota and ecosystems might also be expected to have relatively high levels of resilience and adaptive capacity in the face of climate change, having developed under conditions of environmental variability, this is likely to be significantly constrained in many places by the presence of intensive human threats and pressures. The capacity of riparian ecosystems and biota to adaptively respond to altered climatic disturbances such as extreme floods, for instance, is often severely limited due to the presence of hard infrastructure such as bank armouring or levee banks.

Conservation and Management

Historical approaches to managing riparian ecosystems have often tended toward the replacement or enhancement of certain ecosystem services through the construction of hard, engineered infrastructure, e.g., levee banks and bank armouring for flood mitigation. Recent decades, however, have seen growing appreciation of the importance of riparian ecosystem conservation and restoration at both local and catchment scales because of the disproportionate value and critical importance of the ecological functions and services which they support (Seavy et al., 2009; Capon et al., 2013a,b; Capon and Pettit, 2018). Conservation and restoration of riparian ecosystems have a high potential to generate multiple benefits across a range of scales with a relatively low risk of perverse outcomes. Indeed, riparian restoration now represents a multi-billion-dollar industry globally (Bernhardt et al., 2005; Brooks and Lake, 2007; Palmer et al., 2005), although appropriate approaches to this remain a matter for debate.

In general, protecting intact native riparian ecosystems should be prioritized at catchment scales. This can involve incorporation of riparian areas in reserve networks as well as the implementation of management strategies to minimize existing threats and pressures, e.g., limiting vegetation clearing, fencing to exclude grazing, prohibiting physical disturbances, etc. (Capon and Pettit, 2018). Where riparian ecosystems have been modified and degraded, restoration actions may also be necessary to restore ecosystem functions. Such interventions can include passive, open-ended approaches which seek to promote natural regeneration of vegetation by restoring hydrological regimes, removing armouring and dechannelizing watercourses or restoring physical habitat structure, e.g., returning boulders. More active restoration approaches typically involve direct seeding or planting, usually of native, often woody, species.

Control and eradication of exotic plants, by spraying herbicides or mechanical means, represents a particularly widespread focus of riparian restoration efforts globally. The effectiveness of weed control in riparian zones, however, remains poorly understood (Capon and Palmer, 2018). Furthermore, there is increasing evidence that exotic plants have the potential to support some crucial ecological functions and ecosystem services in degraded landscapes, especially under a changing climate and land use intensification (Capon and Palmer, 2018). Some (e.g., Davies, 2010), have further suggested that the increasing pressures of the Anthropocene era, along with the critical importance of riparian ecosystem functions, warrants consideration of over-restoration to enhance specific functions (e.g., shading) by planting targeted species (e.g., fast-growing, high shade species). Overall, such controversies reflect a rising interest in prioritizing conservation, restoration and environmental management actions in riparian landscapes in relation to their capacity to protect and restore critical ecosystem functions (e.g., bank stability, water quality regulation etc.). Rather than attempting to preserve or restore the historic composition and structure of riparian ecosystems, therefore, interventions may be favorable if they promote the spatial (and temporal) heterogeneity and connectivity of riparian landscapes which, in turn, support their capacity to supply so many vital ecosystem services.

Research Needs

Throughout the world, there is a plethora of significant knowledge gaps regarding the basic biology and ecology of riparian biota and ecological processes. Given the urgent need for robust scientific knowledge to inform planning and management of conservation and restoration strategies, however, a priority has emerged to better understand how riparian functions, services and values are underpinned by ecosystem composition and structure (Capon and Pettit, 2018). To design and implement effective and robust management strategies, it is also imperative that we improve our capacity to predict the ecological responses of riparian ecosystems to disturbances and interventions over multiple spatial and temporal scales.

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Freshwater: Groundwater and Aquifers

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Abstract

Groundwater and associated aquifers are considered essential resources for the maintenance of human life. However, the quality of groundwater and recharge rates has been diminished in many areas of the world. This poses a real threat to the health of aquifers and groundwater-dependent ecosystems such as springs, wetlands, streams, rivers, and lakes and the economies they support. Hydrological recharge of aquifers is complex and is affected by climate, geology, soil type, vegetation, and land use. Managers are becoming increasingly aware that aquifers are dynamic ecosystems rather than just water stored underground and that we need to identify and manage for the environmental values associated with groundwater. Sustainable groundwater management will allow groundwater to be maintained for an indefinite time without having unacceptable environmental, economic, or social consequences.

Introduction

Groundwater is the most important freshwater resource on earth (Bakker and Anderson, 2011). Water may be found in the ground almost everywhere but emphasis is usually placed on areas which contain and conduct substantial amounts of water groundwater (Bachmat, 2005). These areas are usually found in geological formations of permeable rock or loose material and are referred to as "aquifers." Aquifers of particular interest are those in which the water is renewable, in contrast to aquifers which contain fossil groundwater, a one-time, nonrenewable resource. It is a substantial resource making up approximately 37% of the Earth's non-ocean water, compared to 63% for ice and less than one half percent for surface water (e.g. rivers, lakes) (Trenberth et al., 2007; Beckie, 2013). More than two billion people world-wide rely on groundwater for their daily supply of drinking water (Griebler and Avramov, 2014).

A number of groundwater-dependent ecosystems rely on aquifers to maintain their composition, structure, and function (Kløve et al., 2011). Groundwater makes an essential contribution to other aquatic ecosystems including river, lakes, wetlands, and springs (Boulton, 2005). The aquifer itself is also an important ecosystem (Humphreys, 2006). In fact, aquifers are dynamic systems comparable in complexity to surface ecosystems (Tomlinson and Boulton, 2010). Groundwater is also an important source of water for public water supply, agriculture, and industry (Barlow and Leake, 2012; Sankarasubramanian et al., 2017; Seo et al., 2018). In the United States, groundwater supplies 25% of the fresh water used for all purposes; approximately 50% of the population relies on groundwater as its primary source of water for drinking (Zektser and Everett, 2004; Bachmat, 2005). The use of groundwater in the United States is increasing more rapidly than the use of surface water.

This increasing demand for groundwater resources has resulted in the need for better groundwater management (Danielopol et al., 2003; Humphreys, 2006). Managers are becoming increasingly aware that aquifers are dynamic ecosystems rather than just water stored underground and that we need to identify and manage for the environmental values associated with groundwater. The occurrence of little-known groundwater species delayed mining in Western Australia because of concerns the species would become extinct (Schmidt and Hahn, 2012). Groundwater ecological surveys are now required there by government legislation for developments that may impact aquifers (Tomlinson and Boulton, 2010; Stein et al., 2010).

Hydrologic and Geomorphologic Characteristics

Groundwater moves along established flow paths from recharge areas to discharge areas within springs, streams, lakes, and wetlands (Kløve et al., 2011). Recharge of the saturated part of the aquifer occurs whenever water from precipitation enters the ground. Actual

recharge pattern will vary locally depending on hydroperiod (defined as the duration of inundation in a year (Crase et al., 2013)) which is affected by water use, slope, topography, climate, and geology. Alfaro and Wallace (1994) described four types of hydroperiod: (1) periodic—A clear seasonal pattern dependent on precipitation and evapotranspiration, (2) intermittent—A large variability in flow patterns, (3) episodic—An irregular flow that occurs only when water levels are high, and (4) perennial—A continuous and consistent source year round.

Biological Characteristics

The environment in which aquifer ecosystems develop is characterized by darkness, consistency and persistence of habitat, and low energy and oxygen availability (Dresel et al., 2010). Most groundwater systems are characterized by low exchange (Humphreys, 2009) and low, if any, autotrophy (i.e., self-sustained production of organic matter from inorganic substances) (Schmidt and Hahn, 2012). As such, they have been traditionally considered as biological deserts (Gibert et al., 1994). Recent studies have shown that groundwater systems support a great variety of organisms (Deharveng et al., 2009), which provide important ecosystem services including water purification, bioremediation, water infiltration, and water transport (Boulton et al., 2008).

Groundwater carries a continuous flux of dissolved ions, nutrients, and organic matter that make an important contribution to linking the biological diversity of groundwater, surface water, and terrestrial ecosystems (Boulton, 2005; Barquin and Scarsbrook, 2008; Kløve et al., 2011). Lack of light in groundwater systems limits producers and grazers but dissolved organic matter and other nutrients support a food web of detritivores (Boulton, 2005). Groundwater systems often show gradients in organic carbon, oxygen, salinity, pH, and water chemistry along the groundwater flow path and with depth within the aquifer (Humphreys, 2006). Groundwater ecosystems are typically low in sources of energy (Huppopp, 2000; Humphreys, 2006). Subterranean biota usually rely on energy from particles of organic matter that was derived from surface plants and transported to subterranean habitats by water flow, percolation, or gravity (Deharveng and Bedos, 2000).

Animal Communities

Groundwater ecosystems support organisms from microbes such as bacteria to macro faunal crustaceans (Reiss et al., 2019). Many species are endemic to this ecosystem and are adapted to the low energy levels and lack of light (Griebler and Lueders, 2009; Marmonier et al., 1993). The organisms that inhabit these environments are often specialized morphologically and physiologically (Dresel et al., 2010). They are also predominantly invertebrates. These stable and confined environments result in high levels of endemism and high proportions of relict species in comparison to surface environments (Danielopol, 1989). Stygobites are obligate inhabitants of groundwater systems (Humphreys, 2006) and are generally crustaceans, but may include worms, snails, mites, insects, and fish (Humphreys, 2000, 2002; Humphreys and Harvey, 2001).

Commercial Uses

Aquifers can be used for storing surplus amounts of water (Bachmat, 2005). Subsurface storage of water saves losses of land and water lost through evaporation which occur with storage of water in surface reservoirs.

Among the many other services that groundwater ecosystems provide to humans (Boulton, 2009), the most valuable are drinking water supply (Van der Gun, 2012) and water used for irrigation for both traditional and intensive agricultures (Burke, 2003). Nearly all of the irrigation water in the United States is drawn from groundwater (Kenny et al., 2009). Consequently, groundwater extraction for irrigation in the high plains of the United States has depleted aquifer systems (Wada et al., 2010).

Habitat Change

The wellbeing of groundwater invertebrate communities increases with increasing associated surface area occupied by riparian forests and decreases under intensified agriculture use (Español et al., 2017). Also, key ecosystem services increased twofold with increasing area of forest. This is likely due to high concentrations of nitrates and sulfates associated with agriculture systems that affect the diversity of groundwater invertebrate communities.

An increasing human population results in an increasing demand for groundwater. As a result, groundwater resources are often being depleting faster than they can be replenished (Gleeson et al., 2012). Continued extraction of groundwater resources often leads to depletion of water in springs and wetlands and flows of streams and rivers since groundwater and surface water are a tightly coupled interconnected system (Mueller and Male, 1993; Winter et al., 1998; Sophocleous, 2002; Kumar et al., 2009).

Invasive Species

Invasive plant species can consume large amounts of groundwater, causing down-stream springs and wells to dry up (Calder and Dye, 2001; van Wilgen et al., 2008). However, limited work has been done on the effects of invasive plants on groundwater resources (Gorgens and Van Wilgen, 2004). The economy in arid regions of South Africa relies heavily on access to groundwater; many of these areas are also being invaded by mesquite (*Prosopis* species). Water use by these invaders is estimated to exceed 134 million m³ annually (Le Maitre, 2001). This could have a significant impact on the ability of these groundwater resources to continue to meet human demands (Gorgens and Van Wilgen, 2004).

Also, estimates of potential expected losses from an invasion of *Miconia calvescens* on Oahu, Hawaii, United States to groundwater recharge may be as high as \$137 million (USD) per year (Kaiser and Roumasset, 2002). Programs established to reduce the surface cover of alien invasive plant species and replacing these with native vegetation have reduced evapotranspiration and have contributed to recharge of shallow aquifers (Hayward, 2005).

Pollution

Contamination of groundwater occurs from point and nonpoint sources. Anthropogenic point sources include solid-waste dumps and landfills, mine-tailings, septic tanks, cesspools, injection wells of inferior-quality water, and aboveground and underground storage tanks of hazardous and nonhazardous waste materials (Bachmat, 2005). Anthropogenic nonpoint sources include application of agricultural chemicals, irrigation with poor-quality water, percolation of atmospheric pollutants, and urban runoff. Point sources are more easily identified than nonpoint sources and can be better managed and mitigated. Nonpoint sources tend to result in large-scale effects that are difficult to monitor and manage (Bachmat, 2005).

Once pollutants have reached the water table, their spread throughout the groundwater system is slow because water movement is generally very slow (Alley, 2009). Consequently, once contaminants have reached an aquifer, the time required for water quality to recover as a result of natural processes will likely be long after the sources of contamination have been removed. As a result, restoration of water quality in aquifers is generally very expensive and often only partly successful.

Climate Change

Climate change may be responsible for approximately 20% of projected world-wide increases in scarcity of water (Sophocleous, 2004). The challenges of understanding the effects of climate change on groundwater and aquifers are unique because climate change may affect hydrogeological processes and groundwater resources directly and indirectly, in ways that have not been fully realized (Dettinger and Earman, 2007; Green et al., 2011).

Extreme rainfall events resulting from the effects of climate change are expected to become increasingly more frequent in the northern hemisphere (Min et al., 2011; Taylor et al., 2013). Apart from the devastating impact on the economy and human livelihoods (Munro et al., 2017), flooding has the potential to detrimentally impact freshwater ecosystems, including groundwater and aquifers (Taylor et al., 2013; Reiss et al., 2019). During such extreme rainfall events, infiltrating water can potentially transport pollutants and nutrients, including carbon, from the surface to the aquifer (Taylor et al., 2013; Reiss et al., 2019), affecting groundwater ecosystems.

Others are anticipating that climate change will pose additional major threats to groundwater resources in the near future. Sandstrom (1995) suggested that a 15% reduction in precipitation, with no change in temperature, resulted in a 40–50% reduction in recharge of groundwater. Increased variability in precipitation, temperature, and evapotranspiration will thus significantly affect groundwater recharge and accessibility (Treidel et al., 2012). Riedel (2019) reported that aspects of groundwater quality change due to warming which may, in turn, increase the costs for purification when drinking water is produced from groundwater resources and may also result in some aquifers becoming uninhabitable for groundwater biota.

Further, the lowering of the groundwater table due to changes in precipitation patterns and rises in temperature may reduce irrigation well yield and increase pumping cost, which may seriously affect the livelihood of farmers in the regions where groundwater is used as the major source of irrigation (Salem et al., 2017). Mitigation of the impacts of climate change on groundwater resources to address increasing costs associated with irrigation and to maintain farmers' profits is likely to be a major challenge, particularly in developing countries whose economy is based on agriculture (Salem et al., 2018).

Conservation and Management

Subterranean sites present special conservation and protection problems (Culver and Pipan, 2013). Since they are out of sight, they are often overlooked during land management planning even though the groundwater–surface-water interface may be significantly degraded as a consequence of human activities (Bencala, 2011). Also, at the aquifer scale, a significant link between abundances, species richness, and composition of stygobite assemblages and human activities has been established (Marmonier et al., 2018). Groundwater is threatened by land-use practices, pollution, and extensive water use for irrigation (Kløve et al., 2011). Deforestation

and draining of wetlands can expedite surface runoff and reduce ground water recharge (Alley, 2009). Some agricultural tillage systems, impoundment of streams, and development of artificial wetlands can increase ground water recharge. Urbanization may either increase or decrease recharge. Protection of groundwater environments, and the species they support, requires protection from both excessive draw down and contamination of the aquifer (Culver and Pipan, 2013). This, in turn, requires greater public awareness and appreciation of groundwater environments.

Management measures to protect groundwater ecosystems should include the conservation, creation, and expansion of riparian forest corridors, especially in floodplains supporting intensive agriculture (Español et al., 2017). Also, reduction and careful application of agricultural fertilization and pesticides are needed to reduce contamination of groundwater and aquifer resources. Sustainable groundwater management will allow groundwater to be maintained for an indefinite time without having unacceptable environmental, economic, or social consequences (Alley et al., 1999).

Conclusions

"Ground water and surface water: A single resource." The recognition of this relationship has been established through the results of numerous field studies demonstrating the ongoing connections between groundwater aquifers and springs, wetlands, streams, rivers, and lakes (Bencala, 2011). However, groundwater and aquifers continue to be, for the most part, an unexplored aquatic ecosystem (Boulton et al., 2008). Their contribution to biological diversity and ecosystem services are generally undervalued, making their effective protection and wise management difficult. However, environmental policy and, in particular, European water legislation, in the framework of the EU Groundwater Directive, has started to consider groundwater not only as a resource but as a living ecosystem (Reichert, 2019).

Although there is a growing awareness of the complexity of groundwater ecosystems, increasing demands for water extraction and the associated declining availability and quality continue to generate threats (Millennium Ecosystem Assessment, 2005). Reliable evaluations of groundwater and aquifer ecosystem health are essential for the development and implementation of successful management and restoration strategies (Boulton, 2005; Griebler et al., 2014). Given the increasing threats and the general inaccessibility of groundwater environments, it is important to bring new conceptual designs and techniques to the field (e.g., Saccò et al., 2019). This will help to better inform management decisions affecting these ecosystems which are under pressure from climate change, overexploitation, and degradation.

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Glaciers and Ice Sheets

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Abstract

Glaciers and ice sheets are masses of ice and snow that persist over many years formed by the accumulation and compaction of snow. They cover a significant amount of the Earth's land surface and store most of the world's fresh water. Glaciers flow under their own weight, carving out landscapes and transporting sediment and rocks as they move, and they advance and retreat in response to changes in the mass balance, or difference between annual accumulation and ablation. Glaciers and glacierized river basins have unique hydrological characteristics. They serve as an important store of freshwater and influence the characteristics of annual and seasonal runoff downstream. Glaciers and ice sheets also represent an important biome with a rich diversity of life, from microbial communities to microscopic organisms and macroinvertebrates, and they influence ecosystem functioning well beyond their margins and termini. In recent decades, most glaciers worldwide have been losing mass and retreating in response to climatic variations, now primarily driven by human activity. The Greenland and Antarctic Ice Sheets have also begun to lose significant amount of mass and have exhibited an accelerating pattern of loss. This is expected to continue for many decades or more under current and expected future climate conditions, with the loss of much of the world's mountain glaciers, and significant changes in polar ice caps and ice sheets. The loss of glaciers and ice sheets poses many problems and challenges, including sea level rise implications, regional changes in water availability, impacts on glacial and downstream ecosystems, release of legacy contaminants stored on and within glaciers, glacier-related hazards, feedback effects on regional and global climate, and many others that affect the wellbeing of people and communities. There is a need for more observations, better understanding and prediction of glacier dynamics, coordinated adaptation and mitigation strategies across multiple levels from local to international, and a coupled systems approach that integrates physical dimensions of changing ice environments with the human systems that engage with or depend upon them.

Global Distribution and Physical Characteristics of Glaciers

Glaciers are masses of ice and snow that persist over multiple years and undergo deformation and flow under their own weight and the influence of gravity. They range in size and form, from the smallest mountain cirque and niche glaciers ($\sim 10^3$ – 10^0 km²) to the vast polar ice caps and the continental ice sheets of Greenland and Antarctica (10^4 – 10^6 km²), covering about 10% of the Earth's land surface and storing over 33 million km³ of freshwater (Benn and Evans, 1998). Glaciers form through the accumulation of multiple layers of snow, and are thus restricted to very cold regions and/or areas with heavy snowfall, such as high latitudes and high elevation mountainous regions. Aside from the Greenland and Antarctic Ice Sheets (1.7×10^6 and 14×10^6 km², respectively), there are roughly 216,000 glaciers worldwide. These cover an area of almost 706,000 km² (RGI Consortium, 2017; Fig. 1; Table 1), mostly in the Arctic and Antarctic polar regions, the mountainous regions of Alaska and western North America, southern and central Asia, the European Alps, and the South American Andes. The vast majority of the world's tropical glaciers are found in the Andes at elevations above 4000–5000 m, with the largest number in the Peruvian Andes (Schoolmeester et al., 2018). The recently updated Randolph Glacier Inventory (RGI) is a complete global inventory of glacier outlines, and provides information on their hypsometry (area–elevation distribution) for the different regions shown in Fig. 1 and for individual glaciers, as well as information on characteristics such as the surface slope, aspect, length, and other variables of each glacier (RGI Consortium, 2017).

Glacier ice is formed by the metamorphism and compaction of snow, a process that can take from several years to decades, or even centuries or more, depending on the temperature, occurrence and frequency of melt, and other factors (Patterson, 1994). Fresh snow (with a density of 50–200 kg m^{−3}) transforms into *firn* (400–830 kg m^{−3}) after it has lasted through a melt season and undergone significant change in crystal morphology and structure. As further compaction occurs under the growing weight of accumulating snow, ice crystals become larger, the pore volume decreases and air passages become smaller and more isolated, the *firn* transforms into dense glacial ice (830–910 kg m^{−3}) with a deep blue hue. In very cold environments with low snowfall rates, such as the polar regions, this process occurs very slowly and over depths of many tens of meters. Conversely, where snowfall rates

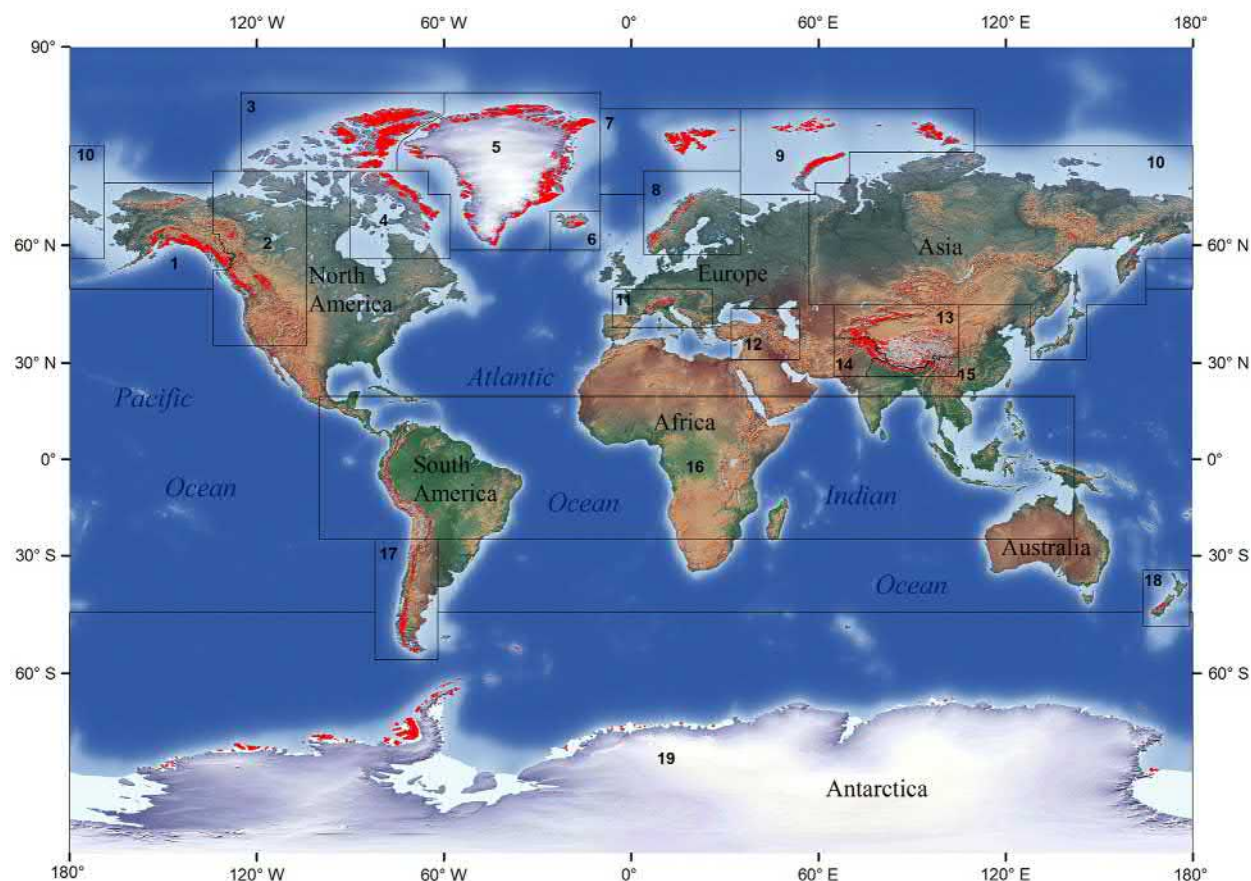


Fig. 1 Map of global glacier distribution (red polygons) and first order regions (listed in Table 1) of the Randolph Glacier Inventory version 6.0 (RGI Consortium, 2017). The topographic relief basemap is from Natural Earth (<http://www.naturalearthdata.com/>). RGI Consortium (2017) Randolph glacier inventory—A dataset of global glacier outlines: Version 6.0: Technical Report, Global Land Ice Measurements from Space. Colorado, USA: Digital Media. <https://doi.org/10.7265/N5-RGI-60>.

Table 1 Summary of regional glacier numbers and area, excluding the Greenland and Antarctic Ice Sheets.

Region	Region ID	Number of glaciers	Total area (km ²)	Percentage of world total area	Mean glacier elevation (m a.s.l.)
Alaska	1	27,108	86,725	12.3	1546
Western Canada and US	2	18,855	14,524	2.1	2129
Arctic Canada North	3	4556	105,111	14.9	994
Arctic Canada South	4	7415	40,888	5.8	992
Greenland Periphery	5	19,306	89,717	12.7	1018
Iceland	6	568	11,060	1.6	1204
Svalbard	7	1615	33,959	4.8	470
Scandinavia	8	3417	2949	0.4	1404
Russian Arctic	9	1069	51,592	7.3	443
North Asia	10	5151	2410	0.3	2491
Central Europe	11	3927	2092	0.3	3024
Caucasus and Middle East	12	1888	1307	0.2	3447
Central Asia	13	54,429	49,303	7.0	5052
South Asia West	14	27,988	33,568	4.8	5258
South Asia East	15	13,119	14,734	2.1	5391
Low Latitudes	16	2939	2341	0.3	5164
Southern Andes	17	15,908	29,429	4.2	1530
New Zealand	18	3537	1162	0.2	1888
Antarctic and Sub-Antarctic	19	2752	132,867	18.8	418
World		215,547	705,739	—	1565

From the Randolph Glacier Inventory version 6.0 (RGI Consortium (2017) Randolph glacier inventory—A dataset of global glacier outlines: Version 6.0: Technical Report, Global Land Ice Measurements from Space, Colorado, USA: Digital Media. <https://doi.org/10.7265/N5-RGI-60>).

are higher and melting occurs more frequently, such as in more temperate mountain environments, the process can be completed within a few years and at depths of several meters (Benn and Evans, 1998).

Snow accumulation and ablation rates vary over the surface of a glacier due to variations in air temperature, snowfall amount, net radiation, wind, and other factors. In steep and complex mountain terrain, processes such as avalanching and wind redistribution from surrounding slopes can significantly enhance the local accumulation over parts of the glacier surface. The upper portion of a glacier, where snowfall amounts are generally higher and air temperatures are cooler, is referred to as the accumulation zone. It is defined where annual net accumulation exceeds annual net ablation (i.e., melting and sublimation). The lower portion is referred to as the ablation zone (where net annual ablation exceeds net annual accumulation). These zones are separated by a line, along which annual accumulation and ablation are in balance, referred to as the equilibrium line. This generally coincides with the end-of-summer snowline. Fig. 2 shows an idealized schematic of these features. Averaged over the entire surface, the difference between the annual gains and losses of snow and ice is referred to as the glacier's annual net mass balance, which can be partitioned into winter and summer components, and is measured using various in situ, remote sensing, or proxy methods (Hubbard and Glasser, 2005; Cogley, 2017).

On some glaciers, the pattern of mass gains and losses is more complex than this idealized model. Where glaciers and ice sheets terminate in large water bodies (such as proglacial lakes, fjords, or the open ocean), a significant portion (or all) of the mass loss may occur through the calving of ice. A considerable amount of melt occurs on the underside of floating ice shelves and where ice is in contact with water bodies. *Dry calving* may also occur from smaller cirque and hanging glaciers in steep mountain areas, where masses of ice, or *seracs*, break away from glaciers and move downslope to eventually melt far below or accumulate on other ice masses. Debris-covered glaciers, which are characterized by a continuous and thick layer of rocks, sediment, and other material (from 0.03 m to as much as 2 m), are common in steep and erodible mountains, and the melt characteristics of such glaciers are highly complex due to the insulating properties of the debris (Kirkbride, 2011).

Under steady state conditions, net annual mass balance fluctuates around zero and any annual excess ice mass is transferred from the accumulation to the ablation zone by ice flow to maintain the glacier's longitudinal topographic profile (Fig. 2). This flow occurs by plastic deformation in cold-based glaciers that are frozen to the underlying substrate, but may also involve sliding at the ice–substrate interface and deformation of subglacial sediment and till in warm-based glaciers (i.e., where ice is at the pressure melting point at the glacier bed and liquid water is present at the base of the glacier) (Patterson, 1994). Rates of flow can vary tremendously, from very slow, cold-based glaciers with low accumulation rates (maximum velocities approximately several meters per year), to warm-based glaciers with high accumulation rates and/or topographic surroundings that funnel ice into ice narrow streams (with maximum velocities of over 8000 m yr⁻¹) (Benn and Evans, 1998). For most temperate glaciers, however, typical velocities are of the order of a few tens to hundreds of meters per year. This flow creates a variety of distinctive features, most notably crevasses, fractures in the glacier surface, which form due to tensile or shear stresses in the ice that are linked to velocity variations across the surface and at the margins of the glacier, and can be up to hundreds of meters in depth (Colgan et al., 2016).

Changes in climate that perturb glacier mass balance over long periods cause an adjustment in glacier form and flow toward a new equilibrium condition. This leads to progressive changes in glacier geometry, flow velocity, surface elevation, and terminus position, with the magnitude and timing of the response depending on factors such as the degree of change in mass balance, the size, shape, slope, velocity, and hypsometry of the glacier, and other morphological factors (Patterson, 1994). Changes in climate can also affect other properties, such as the ice temperature and deformation rate, the presence and distribution of meltwater at the glacier bed, and the interactions between glaciers and surrounding terrain and water bodies. In general, the characteristic response time for a temperate valley glacier to adjust is on the order of several decades (Raper and Braithwaite, 2009). Thus, at regional scales, the collective behavior of a region's glaciers can provide a useful indication of recent and contemporary climatic trends and variability. Other glaciers, such as ice caps in polar regions, can have response times on the order of centuries (Burgess and Sharp, 2004), while the large continental ice sheets adjust over periods of millennia or longer. However, they are also capable of rapid dynamic ice-marginal changes, as has been observed recently in Greenland and Antarctica, and are potentially subject to dynamic instabilities where they are grounded below sea level (Alley et al., 2005; Schoof, 2007; Hock et al., 2017; Fig. 2).

In regards to its influence on the land surface, the flow of glacial ice is one of the most significant geomorphic agents on Earth, eroding, transporting, and depositing rocks and sediment and shaping a wide variety of distinctive landforms and landscapes (Menzies, 2002, 2018). Over many centuries and millennia, the advance and retreat of glaciers and ice sheets has shaped the surface topography and geology of much of North America, Eurasia, and many of the world's mountain regions (Benn and Evans, 1998). The reader is referred to these other texts for a full description of the various glacier landforms and geomorphic processes.

Past and Future Glacier Changes

Throughout Earth's recent history, glaciers have advanced and receded in response to paleo-climatic variations, primarily as a result of well-understood cycles in the Earth's orbit and rotation (Solomina et al., 2015). At times in the Quaternary Period, referred to as glacial periods, up to one third of the Earth's land surface was covered by ice and global sea levels were over 100 m lower than at present (Alley et al., 2005; Cronin, 2012). During the height of the last glacial maximum (ca. 20,000 years ago) much of northern North America and significant parts of northern Europe and Asia were covered by the Laurentide and Feno-Scandian Ice Sheets, which were vast in size and up to several kilometers thick (Benn and Evans, 1998). Rapid retreat of these ice sheets began several thousand years after this, as a response to warmer climate conditions that marked the beginning of the present interglacial period,

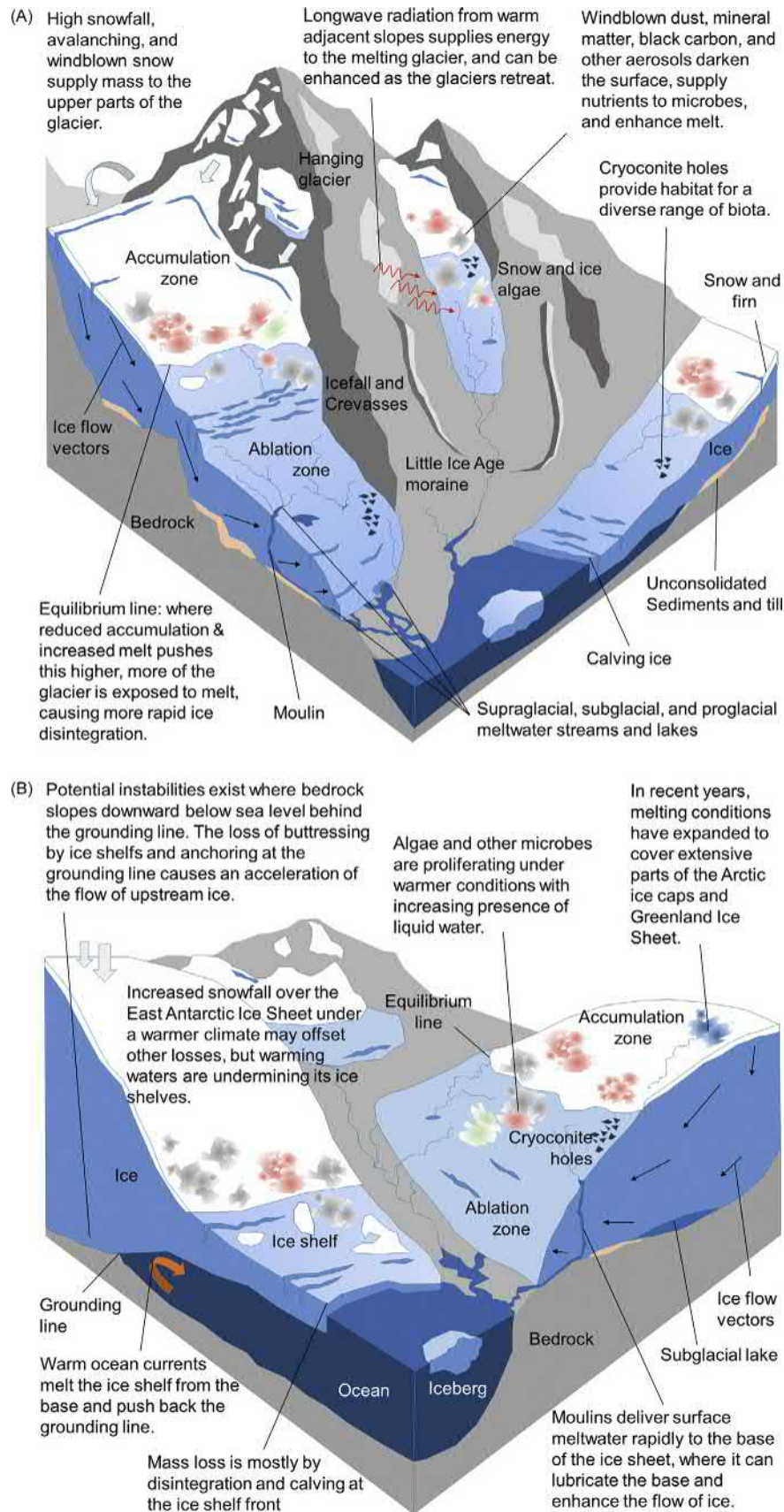


Fig. 2 Idealized schematic diagram of glacier form and flow, noting some of the characteristic features and describing some of the changes taking place for a) mountain glaciers, and b) polar ice caps and ice sheets. Not to scale.

but it took many thousands of years for them to disappear, leaving the present day glaciers and ice sheets as vestigial remnants of this former ice cover. There have been short-lived periods of glacier advance during the Holocene, the most recent and well-documented of which is the *Little Ice Age* (LIA), which occurred across the globe from about the 16th to the early 20th century and resulted in the advance of many glaciers by distances of up to several kilometers (Benn and Evans, 1998).

Since the end of the LIA, most glaciers worldwide have been losing mass and retreating. Clearly visible moraines and trimlines provide evidence of the recent maximum extents of these glaciers (Bolch, 2017; Paul and Bolch, 2019; Figs. 2 and 3), and photographic and anecdotal evidence documents their retreat. There have been some instances of glacier stability or even advance, for both individual glaciers and groups of glaciers. Surge-type glaciers, though uncommon, exhibit periodic sudden changes in flow rate and may advance in periods of rapid flow and then stagnate or retreat during slow phases of the surge cycle. However, recent changes in glacier extents have generally not approached the maximum positions reached in the LIA (Solomina et al., 2015).



Fig. 3 Little Ice Age moraines indicating the extent of former glaciation in (A) the Purcell Mountains of British Columbia, Canada, and (B) the Khumbu Mahalangur region of the Himalayas, Nepal. Photos: Chris DeBeer.

Remote sensing and in situ observations over the past several decades show a clear and coherent pattern of negative mass balances, glacier thinning and area loss, and terminal retreat, although there have been regional and inter-annual variations (Gardner et al., 2013; Vaughan et al., 2013; Zemp et al., 2015; DeBeer et al., 2016; Medwedeff and Roe, 2017; Schoolmeester et al., 2018; Bolch et al., 2019; Wouters et al., 2019; Hock et al., 2019). The rates of glacier shrinkage and mass loss have been accelerating over the past few decades (Zemp et al., 2019), and the proportion of the observed mass loss that is attributable to anthropogenic climate warming has increased dramatically, such that this is now the dominant driver of global glacier changes (Marshall, 2014; Marzeion et al., 2014a,b). Summer melt rates have increased greatly over the Greenland Ice Sheet and other Arctic ice caps, and melting of ice shelves in West Antarctica by warm ocean water has driven acceleration, thinning, and retreat of major outlet glaciers (Sharp et al., 2011; Meredith et al., 2019; Fig. 2). The current rates of glacier mass loss are unprecedented for the period of observations, and probably also for the Holocene (Zemp et al., 2015; Solomina et al., 2015). The recently released IPCC Special Report on The Ocean and Cryosphere in a Changing Climate (IPCC, 2019) provides an authoritative and comprehensive summary of these changes within both mountain and polar regions.

It is challenging to quantify glacier mass loss at regional and global scales due to the sparsity of direct measurements together with limitations of remotely sensed data such as the relatively short time period of observations, coarse resolution of gravity-based measurements from NASA's GRACE (Gravity Recovery and Climate Experiment; (https://www.nasa.gov/mission_pages/Grace/index.html), and other problems in deriving digital elevation models from optical and altimetric observations. Nevertheless there have been numerous recent studies using a variety of approaches to quantify trends in land ice mass and its contribution to sea level rise (e.g., Bamber et al., 2018). Based on in situ mass balance observations, the average cumulative mass balance of a set of 41 globally distributed reference glaciers indicates a collective loss of 23 m water equivalent over the glacier surfaces between 1960 and 2018 (WGMS, 2018; C3S, 2019) but with considerable variability among individual glaciers and regions. By extrapolating glaciological and geodetic observations, Zemp et al. (2019) found that glaciers distinct from the Greenland and Antarctic Ice Sheets contributed 27 ± 22 mm to global mean sea-level rise from 1961 to 2016, with approximately one third of this originating from Alaska. Although the potential contribution to sea level rise of mountain and polar glaciers is relatively small compared to that of the two major ice sheets (i.e., 0.3 m cf. 70 m, respectively; Alley et al., 2005; Farinotti et al., 2019), these glaciers have lost significant mass and they were the dominant contributor to sea level rise during the 20th century (Vaughan et al., 2013). Table 2 provides estimates of the sea level contribution from glacier mass loss in recent decades. In addition to the steadily rising contribution from mountain and polar glaciers, the contributions from the ice sheets have increased rapidly to become the dominant source of mass input to the oceans.

The future responses of glaciers to climate warming is of great scientific interest and societal importance. Already, anecdotal evidence is showing that many mountain glaciers are losing substantial mass due to melt under extremely warm summer conditions, and even higher winter snowfall is insufficient to compensate for the effects of heat waves and intense melting conditions in summer (e.g., see the news article by Harvey, 2019). Given their present configuration, most temperate glaciers are out of balance with current climate and will continue to recede to adjust their geometry to current conditions (Huss et al., 2017; Marzeion et al., 2018). Ongoing climate warming is expected to further exacerbate the current mass imbalance, leading to rapid and pronounced deglaciation over the remainder of this century. Model projections for mountain and polar glaciers indicate that they will lose from 25 to 48% of their current volume by the late-21st century, with sea level contributions that could range from 50 to 170 mm (Huss and Hock, 2015; Marzeion et al., 2018). For some regions, such as western Canada, projections show even greater relative losses of up to 90% or more by that time (Clarke et al., 2015). 21st century mass losses from the ice sheets could be potentially much more significant, contributing from 0.5 m to as much as 2 m or more to sea level rise by 2100 (Oppenheimer and Alley, 2016; Oppenheimer et al., 2019; Meredith et al., 2019). The future response of the ice sheets to ongoing climate warming remains very uncertain (see Section “Challenges and Priorities”).

Table 2 Contribution of glaciers and ice sheets to rates of global sea level rise for various recent time periods.

Source	Contribution rate (mm yr ⁻¹)			
	1961–2016	1992–2001	2002–2011	2012–2016
Mountain and polar glaciers ^a	0.48 ± 0.39	0.37 ± 0.12	0.52 ± 0.09	0.63 ± 0.08
Greenland Ice Sheet		0.02 ± 0.22	0.72 ± 0.06	0.68 ± 0.04
Antarctic Ice Sheet		0.18 ± 0.20	0.22 ± 0.07	0.55 ± 0.07
Total		0.57 ± 0.35	1.45 ± 0.14	1.85 ± 0.13

^aExcluding the Greenland and Antarctic Ice Sheets.

From Bamber JL, Westaway RM, Marzeion B, and Wouters B (2018) The land ice contribution to sea level during the satellite era. *Environmental Research Letters* 13(6): 063008. <https://doi.org/10.1088/1748-9326/aac2f0/meta>; IPCC (2019) Summary for policymakers. In: Pörtner H-O, Roberts DC, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, Mintenbeck K, Nicolai M, Okem A, Petzold J, Rama B, and Weyer N (eds.) *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. In press; and Zemp M, Huss M, Thibert E, Eckert N, McNabb R, Huber J, Barandun M, Machguth H, Nussbaumer SU, Gärtner-Roer I, and Thomson L (2019) Global glacier mass changes and their contributions to sea-level rise from 1961 to 2016. *Nature* 568(7752): 382.

Hydrological Characteristics and Importance

Glacial ice is an important store of freshwater that can significantly influence regional hydrological cycling, depending on the extent of glaciation in a river basin, and plays a major role in the global hydrological cycle (Jansson et al., 2003). Nearly 80% of the world's freshwater is stored in glaciers and ice sheets, with about 99% of this contained within the Antarctic and Greenland Ice Sheets and the remainder in mountain and polar glaciers worldwide (Vaughan et al., 2013; IPCC, 2019). Globally, the melting and loss of glaciers has major implications for sea level rise (see previous section), while regionally, glaciers provide seasonal runoff contributions to downstream river systems that can sustain discharge in summer after the melt of most of the seasonal snow cover. Glacier melting can also provide a buffering mechanism to help sustain discharge during unusually warm and dry periods. At the global level, 370 (140) million people live in river basins where glacially derived meltwater contributes at least 10% (25%) of river discharge on a seasonal basis (Schaner et al., 2012), but in many regions the relative contribution is much higher than this, especially in drought years.

Meltwater generation, the seasonal evolution of the glacier drainage system, and runoff are complex processes and highly dynamic over space and time, involving surface, englacial, and subglacial components (Nienow and Hubbard, 2005; Sharp, 2005; Irvine-Fynn and Hubbard, 2017). The hydrology of glaciers is closely tied to their dynamics and flow behavior, as water availability and drainage characteristics at the base of glaciers influence friction and sliding (Flowers and Clarke, 2002a,b; Anderson et al., 2004; Sharp and Tranter, 2017). Water enters the system from melting ice and snow, rainfall, and runoff from ice-free areas, and is stored throughout the glacier system in the snowpack, firn, supraglacial and ice-marginal lakes, englacial water pockets, subglacial cavities or lakes, and subglacial sediments (Fig. 2). Meltwater is predominantly generated at the surface and its runoff exhibits a distinct diurnal signal, but melt can also occur internally within the glacier and at the glacier bed if ice is at the pressure melting point (Patterson, 1994). Early in the melt season, water is transferred from storage in snow and firn and begins to flow across the glacier surface and into the glacier drainage system as it develops in response to the seasonal increase in meltwater fluxes. Early season runoff is slow and inefficient as flow through snow is attenuated and delayed, and the internal network of drainage channels and conduits has mostly closed down during the winter. With continuing melt and depletion of the snowpack, drainage reorganization occurs as runoff production increases, the channel and conduit network opens and expands, active drainage pathways connect to various storage sites on and within the glacier, and water is conveyed more rapidly and efficiently through the system. At the end of the melt season when water production and flow through the glacier decline, the drainage system begins to close as rates of ice deformation into now largely empty englacial channels increases.

The evolution and form of the drainage system is strongly controlled by the structure and temperature of the glacier ice. At the surface, water production is spatially distributed and runoff is focused by topography, forming a network of channels, ponds, and small lakes (Fig. 2). Crevasses and moulins intercept surface flow pathways, rapidly conveying water into the englacial system. The distribution of crevasses therefore controls the surface drainage density and the routing of supraglacial meltwater (Nienow and Hubbard, 2005; Colgan et al., 2016). Where the surface ice layer is cold, streams tend to flow for greater distances before entering the glacier or reaching its margins (Nienow and Hubbard, 2005). In some cases surface melt draining down into surface snow and firn may refreeze, forming thick ice layers. These ice layers may cause percolating water to pond above them, to the point that the snow becomes water saturated and starts to move downslope as slush flows and slush avalanches that can travel significant distances from their point of initiation. These slush flows may carve out surface channels that are subsequently occupied by seasonal meltwater streams.

Drainage through the glacier interior can occur through micro-scale channel networks and interstitial flow paths, but the bulk of the water flows through larger conduits and ice fractures, moving quickly toward the glacier bed and terminus. At the glacier bed, drainage occurs via both distributed (slow) and channelized (fast) systems (Sharp, 2005). Distributed systems involve thin films, linked cavities, and flow through sediment pore space and fracture systems. Channelized systems involve flow through ice-walled conduits (Röthlisberger or R-channels) that are kept open where the rate of wall melting exceeds the rate of conduit closure due to ice creep, or through channels incised into the underlying bedrock (Nye or N-Channels) or subglacial sediments. Distributed subglacial drainage systems often involve sections of channel incised into bedrock that act to link together larger cavities that form in the lee of bumps on the glacier bed and may become water-filled during the melt season. These distributed subglacial drainage systems may cover large areas of the glacier bed but are generally considered to be less efficient at transmitting water than channelized systems (which they may eventually connect to). Where channels are incised into subglacial sediments, deformation of those sediments in response to the shear stresses imposed on them by the overlying ice may result in deformable sediment periodically blocking the drainage systems, such that water spreads more widely across the bed than usual, and this may have feedback effects on water pressures at the ice-bed interface and on the rate of glacier flow.

Glacierized river basins have distinctive hydrological regimes with discharge characteristics that vary over a range of timescales (Willis, 2005). Seasonally, runoff is concentrated in the melt period, dominated by snow and ice melt, and at times rainfall-generated flows. At other times of the year, runoff is usually comprised of baseflow that is released from slowly draining reservoirs along with groundwater discharge. Basins with relatively high fractions of glacier coverage generally have lower inter-annual variability in runoff than in precipitation, due to the storage and release of water into and from glaciers (van Tiel et al., 2019). At synoptic timescales, meteorological conditions and the nature of the glacier surface control melt rates and runoff generation, which peak when there are high energy inputs to a low albedo surface (e.g., bare ice or dirty/algae-covered ice and snow; see next section). Summer snowfalls tend to raise the surface albedo and suppress melt. Runoff responses vary with the depth of snowpack

and the state of the glacier meltwater drainage system, becoming more rapid and pronounced later in the melt season when the system is well-developed. At daily timescales, melt and runoff vary in response to diurnal patterns of air temperature and radiation receipt, and the meltwater hydrograph is superimposed on a slowly-varying baseflow discharge. As the melt season progresses, the diurnal peak gets larger and more asymmetric, and the time of peak moves forward, reflecting changes in storage, flow pathways, and routing.

Over longer, decadal to century timescales, glacier runoff varies as a result of changes in the volume and area of ice in a river basin. In the current context of climate warming and global glacier loss, there are two competing effects: (1) warmer temperatures increasing the energy available for melt and increasing runoff for a fixed glacier geometry; and (2) negative mass balance causing glacier retreat, especially at lower elevations, reducing the ice-covered source area for melt and eventually glacier runoff volume. Thus, as glacier loss progresses, meltwater contributions to discharge will increase toward *peak water* (Huss and Hock, 2018; Hock et al., 2019)—or more specifically, peak glacier water, which is surplus runoff due to the release from long-term storage—followed by a decline in glacier runoff, even with further warming. Huss and Hock (2018) show that for many mountain regions globally, peak glacier water has already passed or will be approached in the coming several decades. For a few regions with very extensive and/or high elevation ice-cover, mainly in Alaska, the southern Andes, and the high mountains of central Asia, this is expected to occur in the more distant future (i.e., 50–70 years from now).

The loss of glaciers also impacts the variations in river flows, which can be important within the context of the timing of water demands and the need to meet basic domestic needs (generally taken to be 20 L per capita per day). For example, agricultural demands are highest in spring, but require regular water inputs throughout the growing season. Dams are optimized for historical peak flows and energy generation potential. Changes in timing and volume of flows may threaten the ability to meet these water requirements, or pose risks from high flows where glacier runoff contributions are still increasing. It is important to note, however, that river basin discharge and its interannual and seasonal variation depend strongly on this and other components of the hydrological cycle. Changes in precipitation and snow regimes, groundwater storage and cycling, vegetation characteristics, and evapotranspiration processes, which are themselves highly sensitive to climate change, may confound or subsume hydrological responses due to glacier loss alone (e.g., DeBeer et al., 2016). Some recent work has examined glacier change in context with changes in water storage and basin discharge, and found that groundwater can provide a limited and temporary buffering mechanism (Castellazzi et al., 2019; Somers et al., 2019).

Where glacial melt water forms supraglacial, subglacial, and ice-marginal lakes in mountain areas, glacier lake outburst floods, or *Jökulhlaups*, can pose a major hazard from the rapid release of large volumes of water (Roberts, 2005). These floods can be devastating for downstream communities, destroying houses and infrastructure and taking lives. Retreating glaciers have led to the formation and/or expansion of such lakes in many regions worldwide, and this is expected to continue in the coming decades (Hock et al., 2019). As these lakes develop in locations along mountain walls that are susceptible to landslides or where rapid ice disintegration and collapse might trigger outburst floods, there is concern about increasing flood hazard risks, particularly in the high and steep mountains of some developing countries (Schoolmeester et al., 2018; Bolch et al., 2019; Vaidya et al., 2019).

Ecological Characteristics and Importance

Despite extreme habitat conditions, low nutrient availability, and their mostly frozen state, glacier systems are biologically active ecosystems that host a diverse array of life and play an important role in the biogeochemical cycling of elements such as carbon and nitrogen (Barker et al., 2006; Hodson et al., 2008; Anesio et al., 2009; Sharp and Tranter, 2017). The ecology of glaciers is dominated by microbial communities that are adapted to low temperatures, comprised mainly of algae, bacteria, fungi, viruses, and protozoa (Anesio and Laybourn-Parry, 2012; Anesio et al., 2017; Hotaling et al., 2017a,b). Since the presence of liquid water is essential to sustaining microbial processes, habitat for these organisms is restricted primarily to where melting occurs and where water exists. Habitats include wet snow, bare ice surfaces, cryoconite holes (small, localized meltwater-filled holes on the glacier surface harboring bacteria, algae, and fungi; Fig. 4), and streams, ponds, and lakes throughout the glacier system. Micro-organisms have also been found in glacier ice, and sediment rich “basal ice” at glacier beds (Sharp et al., 1999), and as microbial biofilms on the walls of englacial meltwater channels. Only where extreme cold temperatures prevail year-round and melt is virtually non-existent, such as on the surface of the Antarctic polar plateau, are snow and ice surfaces truly sterile. Organisms are sustained by nutrients and organic matter supplied to glacier surfaces through wind transport of dust, minerals, and organic carbon, and at the base of glaciers where soils, sediments, and vegetation have been overridden during periods of previous glacial advance. Photosynthetic and other autotrophic organisms also produce organic matter that sustains heterotrophic organisms. Specially adapted, cold-tolerant microscopic organisms and macroinvertebrates are common on most glaciers worldwide, including insects (i.e. snow fleas, midges, and flies), worms, copepods, tardigrades, and rotifers (Takeuchi, 2011).

The supra-glacial environment is exposed to high solar radiation and large temporal and spatial variation in meteorological conditions, snow cover, liquid water and nutrient availability, and other factors. Life on glacier surfaces therefore tends to be transient and variable. The dominant primary producers here are snow and ice algae along with cyanobacteria (Anesio et al., 2017). Algae populations grow and cover extensive areas of wet snow and ice surfaces after the onset of melt, varying in color from green to shades of orange and red (Anesio et al., 2017), and together with windblown dust, mineral debris, and black carbon, this acts to significantly to reduce the surface albedo, often enhancing melt (Kintisch, 2017; Fig. 5). Cryoconite holes form locally due to darkening of the surface by a mixture of mineral and organic material, and harbor populations of cyanobacteria that have



Fig. 4 Cryoconite holes on the surface of the Peyto Glacier, Alberta, Canada. The size of these features is roughly of the order 10^{-2} – 10^0 m. Photos: Gennadiy Ivanov.



Fig. 5 Red algae, mineral matter and black carbon, and other organic material darken the ice surface of the Athabasca Glacier, Alberta, Canada. Photo: Mark Ferguson.

importance in sustaining heterotrophic communities where active biogeochemical cycling occurs (Fig. 4; Hodson et al., 2008; Anesio et al., 2017). Biota in these holes also include a diverse range of invertebrates (Zawierucha et al., 2015).

In contrast, the sub-glacial environment has a stable temperature regime, and despite the lack of light, it has several key advantages favorable to microbial life, including the presence of liquid water from surface meltwater and basal melting, and high contact with the glacier bed supplying nutrients and organic matter (Sharp and Tranter, 2017). There exists a range of conditions from well oxygenated to anoxic that creates diverse populations of organisms, from heterotrophic to chemoautotrophic, which further accelerate rock weathering and have major roles in biogeochemical cycling and production of greenhouse gases such as methane and carbon dioxide (Wadham et al., 2010, 2013). As the challenges of sampling in this environment are far greater compared to supra-glacial areas, the understanding and characterization of sub-glacial ecosystems is more limited but, in general microbial diversity deep within and at the base of glaciers is lower than at the surface (Anesio et al., 2017). The recent discovery of isolated hypersaline subglacial lakes under the Devon Ice Cap in the Canadian Arctic has opened up new scientific frontiers, since such lakes have never been observed previously, and these represent an extreme potential microbial habitat that might have extraterrestrial analogs (Rutishauser et al., 2018; see Pascoe, 2019).

Glaciers create distinctive habitats that are often havens for animals and plants, with many different specially adapted mammal, insect, and bird species living on and adjacent to glacier surfaces, and plants colonizing glacier-marginal and recently deglaciated foreland areas (Hambrey and Alean, 1994; Jones et al., 2001; Sale and Michelsen, 2018). Tidewater glaciers and glacier fronts are important foraging areas for terrestrial and marine predators (Descamps et al., 2017). Glacier runoff has an important role in nutrient delivery and influences ecosystem structure over multiple trophic levels in coastal and fjord environments (Arimitsu et al., 2016). Glaciers also influence local and regional climate conditions, maintaining low air temperatures and driving cold, dense

katabatic drainage winds, which affect vegetation growth and diversity. Their meltwater exerts a strong control on the flow and character of proglacial streams and rivers, including variations in volume of discharge, sediment load, redox conditions, electrical conductivity, pH, water temperature, and other characteristics. Therefore, aquatic and terrestrial ecosystems are influenced by glaciers far beyond and downstream from the ice margins (Brittain and Milner, 2001). Their role in moderating stream temperatures is particularly important for maintaining favorable habitat for salmonids and other fish species and invertebrates (Fellman et al., 2014; Milner et al., 2017).

With earlier and more frequent and extensive melt, and the ongoing recession and loss of glaciers under a warming climate, there are a number of anticipated changes to ecosystem functioning and biogeochemical cycling, which may have important feedback effects. Some recent reviews provide detailed insights and summarize the state of knowledge of these changes (Hodson et al., 2008; Hotaling et al., 2017a,b; Milner et al., 2009, 2017; Brighenti et al., 2019; Hock et al., 2019). Increasing availability of liquid water and nutrients across glacier surfaces favors the growth of algae and other microorganisms, both spatially and temporally, in turn reducing the surface albedo and enhancing melt (Hodson et al., 2008; Anesio et al., 2017; Kintisch, 2017; Williamson et al., 2019; Fig. 2). Reduced summer snow cover on glaciers leads to expansion of cryoconite habitats relative to snowpack habitats, and the increase in surface melting and resuscitation of near-surface microorganisms will increase supraglacial ecosystem productivity and organic carbon production (Hodson et al., 2008). The melting and loss of glaciers enhances the release of accumulated organic carbon and other nutrients (nitrogen, phosphorus), as well as anthropogenic contaminants deposited onto glaciers from the atmosphere over many decades (Sharp and Tranter, 2017), with major impacts on downstream aquatic ecosystems (Miner et al., 2017; Milner et al., 2017). With enhanced release of certain contaminants under climate warming, there is increased risk of emerging pollutants to freshwater sources (Chen et al., 2019) and the potential for bioaccumulation through organisms in the ecosystem. Together with shifts in discharge regime and water temperature, the effects of deglaciation are expected to result in a loss of regional biodiversity in microbial and macroinvertebrate communities (Hannah et al., 2007; Jacobsen et al., 2012; Wilhelm et al., 2013; Giersch et al., 2017; Milner et al., 2017; Hock et al., 2019).

Challenges and Priorities

Most glaciers are now responding more strongly to anthropogenic climate warming than to natural forcings (Marshall, 2014; Marzeion et al., 2014a,b). Thus, making reliable projections of future glacier change under different greenhouse gas emission and warming scenarios is a key challenge. There are a number of associated issues to be addressed, such as how fast and to what extent glaciers will change regionally and globally; how this will affect water availability (quantity and timing), water quality, glacier-related hazards, sediment transportation, and aquatic ecosystems; how this will alter global sea levels and their rate of rise, and nutrient fluxes to the oceans; how this will influence local, regional, and global biogeochemical cycles; and how this will feed back to the climate system regionally and globally. An equally important gap in our knowledge is the full range of consequences on people's health, livelihoods, cultures, and social fabrics.

The loss of glaciers is already impacting communities in many parts of the world, particularly in developing countries, prompting local adaptations and mitigation strategies to cope with changes in glacier runoff (see examples in Hock et al., 2019). In the European Alps, many ski and tourism resorts have been attempting to preserve glaciers by covering them with large sheets to insulate and protect the ice underneath, and through other measures such as snow traps and snow farming to supplement the glacier accumulation (see Hester, 2019; Miles, 2019). In other parts of the world, including Argentina and Chile, glacier protection laws have been enacted or considered in an attempt to safeguard against destructive activities such as mining or other resource extraction activities (Anaconda et al., 2018). But globally, further glacier loss cannot be prevented without international commitment and action on greenhouse gas reduction, and even then not likely for several decades or more.

Priorities include improving understanding of the links between glacier dynamics and climate variability, better representing these links in Earth system models, and expanding the observational data needed for assessing and predicting change (Hock et al., 2017). The importance of the ice sheets as a contributor to sea level rise has recently increased relative to that of mountain and polar glaciers (Reager et al., 2016; Bamber et al., 2018), and it is known that the ice sheets and their outlet glaciers are capable of rapid changes in flow speed and calving rate. In areas such as the West Antarctic Ice Sheet, the grounding of the ice below sea level creates an inherent instability that may lead to feedbacks and cascading responses. There is great uncertainty, however, over the future evolution of the ice sheets as measurements are sparse, ice sheet models lack realistic representations of some of the underlying physical processes and of interactions that take place at the ice–bed and ice–ocean interfaces, and there is low confidence in estimates of the warming thresholds required to trigger ice sheet instabilities (Oppenheimer and Alley, 2016; Hock et al., 2017; Meredith et al., 2019). Surface processes (accumulation and ablation) on glaciers and ice sheets are undergoing changes, and representing their spatial and temporal heterogeneity, especially in topographically complex mountain environments, is a challenge. Ablation processes are becoming increasingly affected by factors such as the deposition of dust and black carbon (especially as a result of large-scale wildfire events), as well as algal growth on glacier surfaces; all of which are very poorly handled in current generation models. Accumulation processes are significantly affected by changes in precipitation phase, the incidence of avalanching, snow redistribution by wind, and other factors that are all highly sensitive to changes in air temperature. It is essential that models for local, regional and global-scale projections of glacier mass balance and dynamics are based on physical process understanding as opposed to overly simple or empirical (e.g., temperature-index melt) approaches. This is necessary to capture the inherent process complexities, and sometimes unexpected interactions, feedbacks, and system responses. A further challenge is

in obtaining reliable projections of future climate, especially in mountain regions, at the scale needed to resolve heterogeneity in these processes due to limitations in the downscaling methods used to interpolate results from coarse-scale climate models to the glacier (or sub-glacier) scale (Hock et al., 2019).

Recent advances in remote sensing technologies and a rapid increase in new observations from satellites have greatly improved the monitoring of glaciers and ice sheets and provided much new information but, despite this, there remain significant challenges associated with a lack of adequate observational data (Hock et al., 2017, 2019; Meredith et al., 2019). In polar and high elevation mountain regions there is, in general, a very low density of climate monitoring stations which makes it difficult to assess trends in meteorological variables and to validate climate model outputs. In situ observations and mass balance measurements exist for only a very small fraction of global glaciers, and reference glaciers are typically chosen for reasons such as their accessibility, manageability, safety, and simplicity of their form (Østrem, 2006). As such they may not be representative of the broader regional set of glaciers, and several studies have demonstrated that these glaciers may exhibit notably different behavior than is observed in their regional surroundings (Fountain et al., 2009; Paul and Haeberli, 2008; Carturan et al., 2013; Menounos et al., 2019). This poses a challenge in relating sparse in situ glacier observations to regional scale changes and in explaining inter-glacier variability in behavior, particularly over historical time periods for which remotely sensed geodetic or altimetric observations are not available (Cogley et al., 2013).

Finally, a coupled systems approach is required that integrates physical dimensions of changing ice environments with the human systems that engage with or depend upon them. It is only through investment in coupled systems research and evidence generation that the urgent need for sustainable and appropriate adaptation and mitigation strategies and coordinated efforts demanded by the international community can be achieved, as specified in several recent frameworks including the Paris Agreement (<https://unfccc.int/process-and-meetings/the-paris-agreement/the-paris-agreement>), the UN 2030 Agenda and its Sustainable Development Goals (SDGs) (<https://sustainabledevelopment.un.org/post2015/transformingourworld>), and the Sendai Framework for Disaster Risk Reduction (<https://www.unisdr.org/we/cooordinate/sendai-framework>). Action is needed to build capacity, invest in infrastructure, and make communities more resilient and sustainable (see the call for action by the World Meteorological Organization at its recent High Mountain Summit (<https://highmountainsummit.wmo.int/en>)). Rural, remote, and otherwise marginalized communities, and women in particular, are the most vulnerable and least able to invest in prevention or solutions (Schuster-Wallace and Watt, 2015). Policy and practice therefore require input from these communities and must incorporate local tradition, knowledge, and beliefs to succeed (Schuster-Wallace et al., 2019). Ultimately solutions must involve joint activities and partnerships among researchers, stakeholders, practitioners, and decision makers, and these must utilize transdisciplinary approaches to addressing the complex challenges (Huss et al., 2017; Klein et al., 2019; Schuster-Wallace et al., 2019; IPCC, 2019).

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The Subtropical Everglades, Florida, USA

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Published by Elsevier Inc.

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Abstract

Everglades restoration, the largest of its kind in the world, is expected to restore ecosystem functionality and community structure. Anthropogenic changes in peat elevations, water quality, hydrology and habitat loss can make plant and animal recovery difficult. However, our understanding of the complexity of Everglades ecology and the spatial and temporal scales associated with plant and animal requirements for water, is putting the Everglades back on track. The knowledge base for this movement is summarized in this article.

Introduction

Freshwater wetlands all share similar ecosystem structure, functions, and services such as flood tolerant plants, carbon sequestration, and recreational value, respectively. However, the Everglades is one of the more unique wetlands in the world because of its semi-tropical geography, low nutrient biogeochemistry, and complex natural and anthropogenic histories. At the southern extent of the Everglades ecosystem, the value of Everglades National Park (ENP) is globally recognized as an International Biosphere Reserve, Ramsar wetland of international importance and a World Heritage site (with a conservation outlook recently rated as critical; IUCN, 2017). Alpert (2009) found that the Everglades contributes ~\$82 billion of ecosystem services annually, tied to freshwater marshes and associated with services such as water supply and treatment, wildlife habitat, ecotourism, environmental regulation, and land formation.

Historically encompassing 10,000 km², over the past 100 years, the spatial extent of the Everglades has been reduced by over 50% to accommodate the rapidly growing urban population and industrial agriculture in south Florida; dramatically altering the hydrology, chemistry, and biology of this ecosystem (Fig. 1). However, the remnant Everglades is still one of the world's largest wetlands and while in peril, remains a vast "river of grass" supporting a rich diversity of plants and animals, 47 of which are federally- or state-listed as threatened or endangered. Used for water supply, flood control, and environmental preservation, it is impossible to discuss this biome without including its well-documented anthropogenic influences.

The Everglades Historical Geography

The Everglades is comprised of a directionally patterned mosaic of tree islands, shrubs, sawgrass ridges, and aquatic sloughs (King, 1917a,b; Parker et al., 1955). Soil cores from freshwater tree islands (Gleason and Stone, 1994; Willard et al., 2006) document a relatively stable 5000-year-old system as well as very rapid community shifts associated with human encroachment and alterations of the basin hydrology beginning in the late 1800s (McVoy et al., 2011). The first major efforts to drain the Everglades began in 1880, and between 1906 to the 1920s had diverted approximately 2 billion m³ of water to the Atlantic Ocean and drained over 600,000 ha of wetland (Parker et al., 1955; Davis and Ogden, 1994; SFWMD, 1998). By 1940, water tables had declined as much as 3 m, large areas of organic soils had subsided, creating topographic changes of 0.5–2 m at an average rate of 2.5 cm year^{−1}

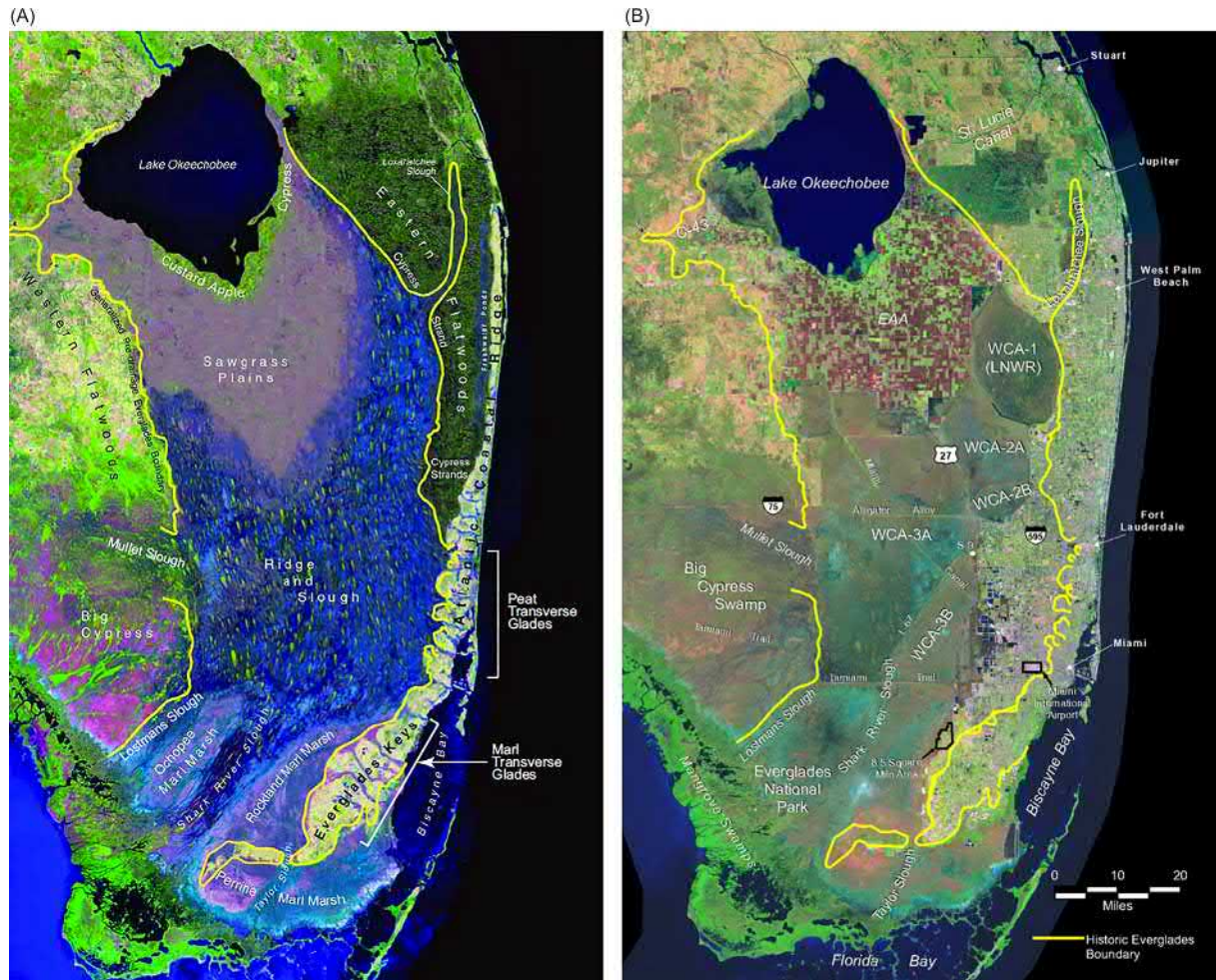


Fig. 1 Image on the left (A) is the estimated landscape structure of the predrainage (c. 1800) Everglades. Image on the right (B) is the present-day landscape structure. EAA—Everglades Agricultural Area. Modified from McVoy, C.W., Said, W.P., Obeysekera, J., Van Arman, J.A. and Dreschel, T.W. (2011). *Landscapes and hydrology of the predrainage Everglades*. Boca Raton, Florida, USA: University Press of Florida.

(Clayton, 1936; Clayton et al., 1942; Davis, 1943; Stephens and Johnson, 1951; Shih et al., 1979a,b). This extensive soil loss caused concern and led to the construction of levees to impound undeveloped lands (Allison, 1943; Advisory Committee, 1944). The Central and Southern Florida (C&SF) Project was authorized by the United States Congress in 1948 and by 1960 had compartmentalized the Everglades into separate hydrologic units—the Water Conservation Areas (WCAs) and ENP—and partitioned 283,000 ha for the Everglades Agricultural Area (EAA). From 1965 to 1973, additional changes were made in the C&SF Project to meet the Everglades' minimum monthly requirements of water that would have been expected in the 1940s and 1950s. Today the C&SF Project consists of approximately 3220 km of canals and levees, > 600 water control structures, 620 project culverts, and 77 pump stations to manage the water resources of south Florida (SFWMD, 2019). The discontinuous hydrologic subunits created by the C&SF Project (Fig. 1B) each have their own distinctive histories of water depths, flows, and ecological impacts. One of the key impacts has been a dramatic loss of peat. Using GIS data sets to calculate the difference between original and existing peat volumes over the past 150 - years, Hohner and Dreschel (2015) estimated that the historic Everglades had an average peat depth of 2 m, a peat volume of 20 billion m^3 , and a carbon content of 900 million metric tons. By contrast, the current Everglades, with half the original spatial extent and significant soil oxidation, has an average peat depth of only 0.75 m, a peat volume of 5 billion m^3 , and a carbon content of 200 million metric tons.

The Everglades Climate

The health and nature of the Everglades is closely tied to the volume, timing, and distribution of water inflows from rainfall, from Lake Okeechobee, and from agricultural and natural areas surrounding the Everglades. The National Oceanic and Atmospheric Administration (NOAA), United States Geological Survey (USGS), National Park Service, and South Florida Water Management

District (SFWMD) have collected and archived meteorological data in support of regional hydrologic modeling for south Florida (SFWMD, 2005; Brown, 2013), and are presented here as blended point measurements across the Everglades for each $3.22 \text{ km} \times 3.22 \text{ km}$ ($2 \text{ mi} \times 2 \text{ mi}$) grid cell. Climate in south Florida is classified as subtropical with two distinct seasons: a wet season from May to October and a dry season from November to April. The climatological start and end of the wet season are May 22 and October 12, with deviations of ± 3 weeks for the two dates (Swartz, 2019). Average monthly rainfall depths for a 70-year period of record (1948–2018) during the wet season and dry season are 44.5 and 15.2 cm (17.5 and 6.0 in.), respectively.

The primary mechanism producing rainfall are cyclones and wet season daily sea breezes. During the dry season, rainfall is mainly produced by large-scale frontal systems (Swartz, 2019). Fig. 2 is a time series of annual rainfall across three major subareas (WCA-1 and -2, WCA-3, and ENP). Annual average rainfall is 130 cm and can vary from 90 to 200 cm per year. On the average, 75% of the annual rainfall falls during the wet season, while the remaining 25% is accumulated during the dry season. Spatial variation in annual rainfall from one subarea to another can be as high as 50 cm, and decadal trends such as the below average rainfall of 1970 to 1990 have been observed (Fig. 2).

The seasonal pattern of monthly rainfall depths varies slightly across the three major regions (WCA-1 and -2, WCA-3, and ENP) of the Everglades. The northern region (WCA-1 and -2) tends to have slightly wetter dry season while the southern regions has a somewhat bi-modal wet season (June and September). The contrast between dry and wet season rainfall characteristics is well illustrated in Fig. 3, not only in terms of the amounts, but in variability and extreme monthly values. For wet season months, minimum precipitation for each one of the areas is substantially above zero. Of all the months, June tends to be the month with the highest monthly precipitation depth. The largest recorded June rainfall in the southern portion of the Everglades was in excess of 50.8 cm.

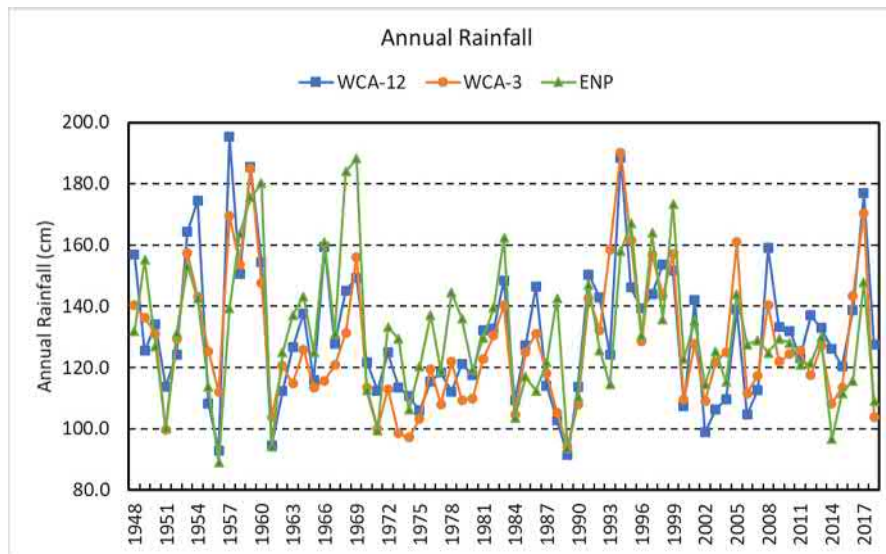


Fig. 2 Annual rainfall patterns across the Everglades (WCA-12 is for Water Conservation Areas 1 and 2) (see Fig. 1 for locations).

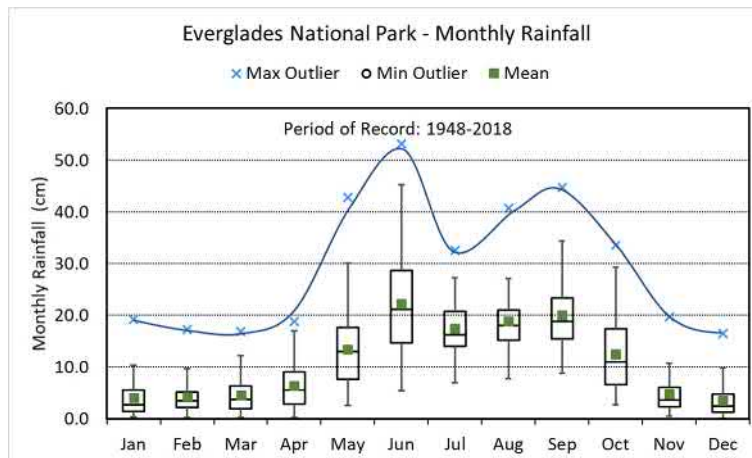


Fig. 3 Average monthly rainfall patterns for Everglades National Park using boxplot statistics (Helsel and Hirsch, 2002) (see Fig. 1 for locations).

During the winter months from November to March, temperatures can oscillate in the range of 5–28 °C. During the summer months daily temperatures can be as high as 38 °C. High temperatures in combination with wind and the availability of water generates high evapotranspiration (ET) rates, which in many cases equal or exceed rainfall at the annual time scale (Fig. 4). Potential evapotranspiration, computed for a reference crop under no limitations in the water available, helps to designate periods of time when rainfall cannot keep up with ET. Actual evapotranspiration, which is a function of actual vegetative cover and water availability, is much harder to calculate, especially for a system as large as the Everglades. Based upon this uncalibrated reference potential ET, the average annual surplus rainfall was estimated to be 21 cm and the average annual deficit rainfall was estimated to be 37 cm, indicating a small difference between surplus rainfall and deficit rainfall. Although upstream basin runoff keeps the Everglades wet every year, this small difference makes the Everglades sensitive to relatively small climatic changes.

Hydrology

Hydrology of the predrainage Everglades was unique due to the relationship between its topographic characteristics and climate. The slight slope of the topography, 5 cm per km, prevented central or tertiary drainage patterns from forming, which created an even distribution of water flow across the full width of the landscape. The flows were enough to create a multicomponent landscape (e.g. sloughs, sawgrass ridges, and tree islands) with stable elevation differences (McVoy et al., 2011; Said and Brown, 2013). The slope and flow meant that the predrainage Everglades was likely continually draining. The seasonal rainfall distribution meant the Everglades was a seasonally pulsed system. The balance between the seasonal inflow and outflow was such that each year's wet season arrived before the system dried out. The water depths within sloughs throughout the ridge and slough landscape (RSL) typically rose and fell each year from a low of about 30 cm to a high of about 90 cm (Fig. 5); an environment that could support long-lived aquatic organisms (McVoy et al., 2011; Said and Brown, 2013). Hydrologic characteristics of the predrainage

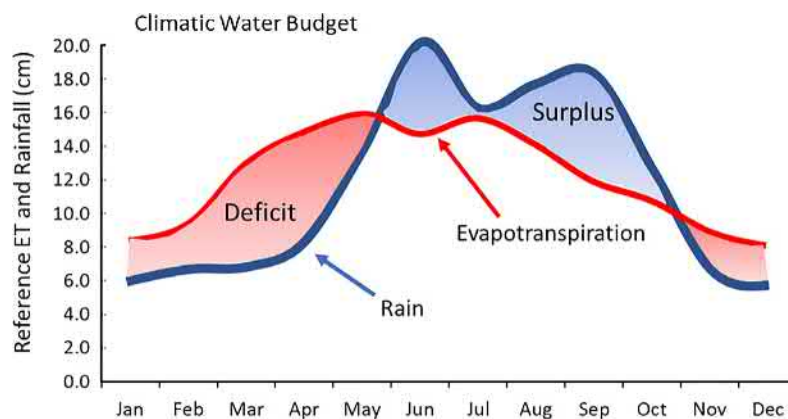


Fig. 4 Monthly rainfall patterns averaged across the WCAs and ENP from 1948 to 2018, compared to the average monthly rates of potential evapotranspiration indicating times of rainfall deficits and surpluses. Potential evapotranspiration was computed from measured temperature, relative humidity, solar radiation, and wind speed from a reference grass crop under no limitations in the water available.

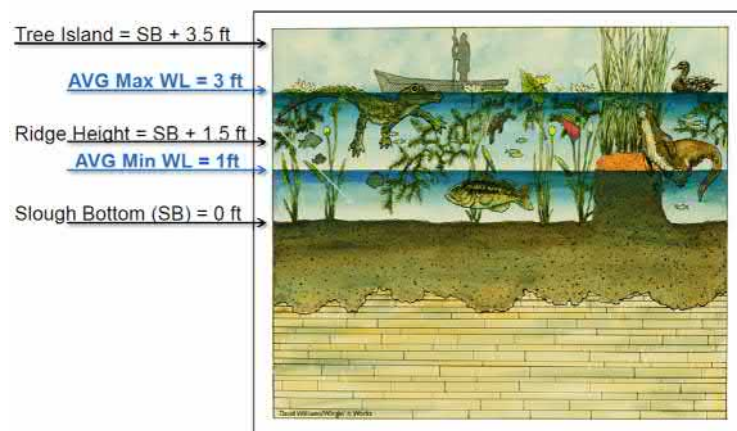


Fig. 5 An artistic view of relative water levels for three key Everglades landscape components. SB, slough bottom; WL, water level. A David Williams illustration, Everglades Hydrology. Charlotte, NC: <http://www.winginitworks.com/>.

Table 1 Hydrological ranges associated with the historic, predrainage Everglades landscapes (McVoy et al., 2011) and the current, modified Everglades compartments relative to slough bottom using an existing conditions baseline in the Glades-Lower East Coast Service Area (GL) of the Regional Simulation Model (RSM) used for restoration planning and design.

<i>Landscape</i>	<i>Hydroperiod (months)</i>	<i>Seasonal maximum depth (cm)</i>	<i>Seasonal minimum depth (cm)</i>
Predrainage Ridge & Slough (combined)	9.5–11	61.0	0.0
Predrainage Ridge (R)	9–10	45.7	–15.2
Predrainage Slough (S)	12	91.4	30.5
Historic Sawgrass Plains	9–10	45.7	–15.2
Current Northern WCA-3A	8–12	24–40	–24–9.1
Current Central WCA-3A	6–12	91–122	3.0–57.9
Current ENP (Shark River Slough)	2–12	33–73	–34–3.0

USACE and SFWMD (2014). Comprehensive Everglades Restoration Plan, Central Everglades Planning Project final integrated project implementation report and environmental impact statement. Jacksonville, Florida, USA: United States Army Corps of Engineers; and West Palm Beach, Florida, USA: South Florida Water Management District.

Everglades were synthesized into references ranges of inundation duration (hydroperiod) and seasonal range of minimum and maximum water depths or amplitude by McVoy et al. (2011) (Table 1).

The artificial infrastructure managing water in the remnant Everglades removes natural connectivity, creates preferential flowways and diverts upstream inflow, which all result in generally reduced water levels and greater frequency of drying and drought conditions within the Everglades marsh. The current flow and depth characteristics relative to the predrainage characteristics (Table 1) indicate that the extant Everglades is significantly drier (i.e., shorter hydroperiods) by 4–10 months, especially in ENP. The seasonal minimum water depths are also indicative of a drier extant landscape; they are lower than the historic ranges by 0.2–0.55 m in WCA-3A and by 0.3–0.6 m in ENP. The extant Everglades is also more variable than the historic Everglades. Due to impoundment, the current seasonal maximum water depth in central WCA-3A is much higher than the current ENP and is twice the depth of the historic RSL. At the same time, the minimum water depth varies between 0.03 and 0.6 m indicating that this region is often deeper than the historic landscape. A focus of Everglades restoration is to mimic the historical hydroperiod and seasonal maximum and minimum by increasing total flows from upstream watersheds to ENP.

Geology

Four main geological formations—Tamiami, Fort Thompson, Anastasia, and Miami—underlie the Everglades. The porosity of these formations to groundwater is spatially variable and contributed to their development and vegetation patterning. The northern section of the Fort Thompson underneath the historic sawgrass plain is less porous, while the southern section of the Fort Thompson under the RSL system is more porous and may have contributed to heterogeneous flow speeds and creation of Everglades iconic patterned system (Parker et al., 1955).

Limestone is the predominant bedrock of the Everglades, with some sandy areas on the eastern region. Therefore, groundwater has a higher ionic content than surface water, and in some cases extremely high if it encounters relict seawater (Renken et al., 2005; Harvey and McCormick, 2009). Dependent on the overlying soil characteristics, the karstic nature of the groundwater can influence the surface chemistry of the ecosystem. In the historically shallow sloping flat Everglades landscape, areas of continuous thick peat had a relatively high resistance to vertical water flow, allowing little exchange between the bedrock and surface soil layers (Gleason and Stone, 1994; Harvey and McCormick, 2009). In areas of shallow peat and on the western side of the Everglades, Newman et al. (2017) suggest that there is connectivity to the underlying bedrock, and surface waters and soils are influenced by the mineral rich groundwater.

In the remnant Everglades, the northernmost impoundment (WCA-1), is unique because in its interior it is a soft water, ombrotrophic system (i.e., most moisture and nutrients come from precipitation). Some believe that WCA-1 is ombrotrophic today because it is completely enclosed within the levees and canals and does not experience natural sheetflow (Willard et al., 2006). However, because of its location in the landscape, deeper peat deposits (depth 3 m) and resultant higher elevation, WCA-1 would naturally become isolated from surface and groundwaters, resulting in ombrotrophy (Harvey and McCormick, 2009). The paleoecological record suggests immediately downstream of WCA-1, WCA-2A was also soft water. Indicators of a more acidic environment were found in WCA-2A soils deposited prior to impoundment (1961), but were absent postimpoundment (Slate and Stevenson, 2000). Water entering WCA-2A, either through the canal system or via groundwater discharge under the levee system has become enriched in minerals, and the ecosystem switched to one where calcareous algae and cyanobacteria dominate, as opposed to soft water desmids (McCormick and O'Dell, 1996; McCormick et al., 2001; Gaiser et al., 2011; Hagerthey et al., 2011, 2012). Thus, the connectivity between surface water and groundwater in this karst system, whether through stage differentials or direct discharge, means increased water quantity for Everglades restoration in many areas will also be associated with increased mineral composition (Newman et al., 2017), unless decompartmentalization can eliminate some of these interactions.

Biogeochemistry

The historic Everglades primarily received nutrients via atmospheric deposition and with no source of phosphate from mineral rock weathering; it evolved as a phosphorus limited ecosystem (Noe et al., 2001). Any available phosphorus in the water column is rapidly cycled by the microbial community (Noe et al., 2003; Scinto and Reddy, 2003), before ultimately being stored in sediments. In areas with high mineral content, calcium-bound phosphate is the dominate inorganic form (Chambers and Pederson, 2006), but generally organic-bound phosphorus is the dominant form of phosphorus stored in the Everglades (Qualls and Richardson, 1995; Reddy et al., 1998, 2011).

Under low phosphorus conditions, organisms evolve strategies to acquire phosphorus when it is not typically available. For example, sawgrass and oligotrophic algal species produce phosphatase enzymes that enable the use of organic phosphorus compounds as sources of phosphate to support growth (Kuhn et al., 2002; Newman et al., 2003; Sharma et al., 2005). As a result, anthropogenically increased phosphorus loading has had a dramatic effect on the Everglades (Davis, 1994; Craft and Richardson, 1997; Crozier and Gawlik, 2002; McCormick et al., 2002; McCormick and Laing, 2003; Gaiser et al., 2005; Sklar et al., 2005; Hagerthey et al., 2008; Newman et al., 2017). Some of the most visual changes are the loss of phosphorus sensitive periphyton assemblages; particularly calcareous periphyton, and the replacement of the RSL by dense stands of southern cattail (*Typha domingensis*, Newman et al., 1998; Hagerthey et al., 2008; Fig. 6). While native to the ecosystem, cattail historically occurred in sparse stands or was associated with disturbed areas such as alligator holes (Davis, 1943, 1994; Loveless, 1959), it did not exist over tens of thousands of hectares of almost monotypic stands as it does today (Rutchey et al., 2008; Sklar et al., 2009, 2011).

With the first prototype completed in 1993 (Guardo et al., 1995), a series of stormwater treatment areas (STAs), constructed wetlands, were built on the boundaries of the Everglades, to remove phosphorus before it enters the ecosystem. Currently encompassing 23,000 ha of wetland treatment area, over the last 24 years, these STAs have treated ~6.6 trillion gallons of surface water and retained 2604 metric tons (Chimney, 2019), resulting in significant reductions in phosphorus inputs to the Everglades. While dense cattail stands are still prominent, there is evidence that the rate of expansion may be decreasing in response to phosphorus load reductions (Rutchey et al., 2008; Zweig and Newman, 2015).

Habitats

Ridge and Slough Landscape (RSL)

The Everglades RSL is a patterned/corrugated peatland with parallel drainage topography and is the dominant landscape type (Fig. 7). The RSL was created as a result of water flow, sediment dynamics, and differential production and decomposition, and has been relatively stable for thousands of years (Bernhardt and Willard, 2009). The RSL consists of long, linear ridges of sawgrass (*Cladium jamaicense* Crantz.); longer hydroperiod sloughs—open water areas with white water lily (*Nymphaea odorata*), submerged aquatic vegetation, and short-statured emergent species such as spikerush (*Eleocharis* spp.); and occasional tree islands oriented parallel to the slow-moving flow of water from northwest to southeast. The microtopography is very important (see Faunal



Fig. 6 Aerial image of WCA-2A showing dense cattail (forefront) transitioning to a patterned ridge and slough landscape with low phosphorus conditions found in areas distant from inflow structures. Photo credit: Mark Cook.



Fig. 7 Aerial image showing the parallel flow-oriented ridge-slough-tree island landscape within the central Everglades. Photo credit: Christa Zweig.

Communities) however, ridges are only 10–50 cm higher than sloughs. Historical microtopography was nearer to 1 m (McVoy et al., 2011). Fragmentation due to compartmentalization, impoundment, and reduced flows (Ogden, 2005) can explain this degradation (Wu et al., 2006; Nungesser, 2011; Zweig et al., 2011).

The RSL includes two types of wet prairie communities—marl and organic peat based (Fig. 8). Marl prairies are unique to the southern Everglades and are characterized by reduced hydroperiods, short-stature sawgrass, Muhly grass (*Muhlenbergia filipes*), and calcareous periphyton on marl or exposed limestone. The peat-based prairies occur in hydroperiods between marl prairies and sloughs and consist of the similar species to sloughs but in different densities. In peat-based prairies, the dominant plant is spikerush, followed by white water lily, maidencane (*Panicum hemitomon*) and Egyptian paspalidium (*Paspalidium geminatum*).

Tree Islands

Tree islands are a very distinctive, elevated Everglades feature (Fig. 9). Dominated by woody vegetation, this habitat currently rises some 30 cm above the surrounding marshes and although some islands rise more than 150 cm, most are 50 to 100 cm lower than they were historically (McVoy et al., 2011).

Although tree islands occupy only a small portion of the freshwater Everglades (3.8 to 14%, references in Wetzel et al., 2017) they are home to more than 50% of the animal biodiversity (Meshaka et al., 2002), especially birds (Table 2).

Tree islands come in two basic shapes (Fig. 10). Pop-up or battery islands have an elevation gradient radiating out from a high elevation center to low elevation peripheries. The elevation gradient on fixed or pedestal islands proceeds from a high elevation upstream head to a low elevation downstream tail (Fig. 10A).

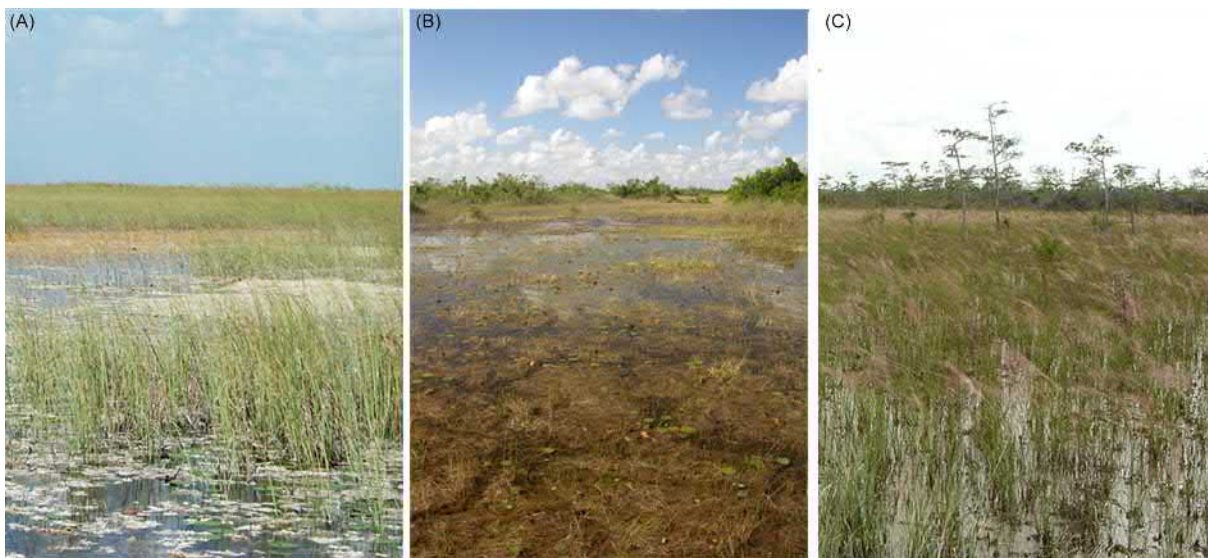


Fig. 8 (A) Ridge and slough habitat showing floating calcareous periphyton. (B) Soft water organic peat based wet prairie. (C) Marl-based wet prairie. Photo credits: Scot Hagerthey (A, B) and Todd Osborne (C).

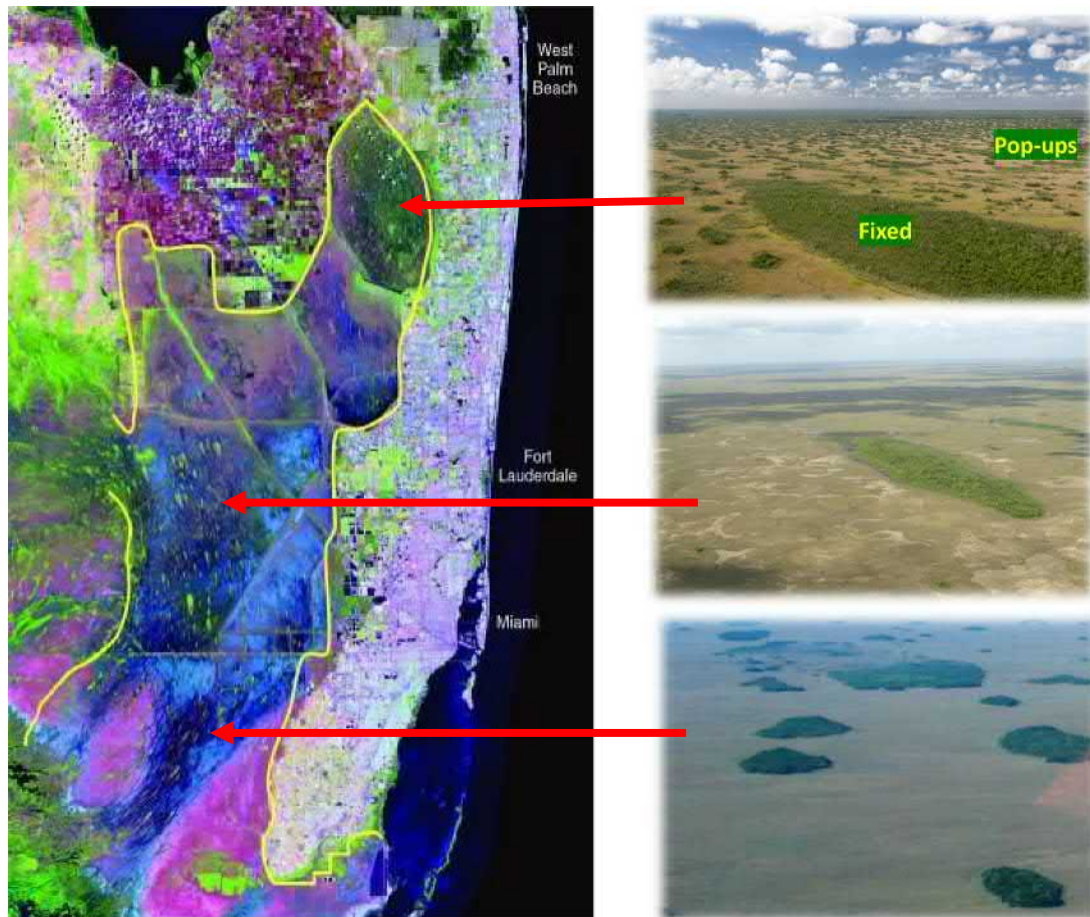


Fig. 9 The tree island habitats across the freshwater Everglades biome varies from thousands of pop-up islands in the north, to scattered and very wet large islands in the central region, to remnant dry islands in the south.

Table 2 Number of species associated with tree islands in the southern Everglades.

<i>Taxonomic group</i>	<i>No. Species</i>
Ants	52
Butterflies	29
Tree snails	2
Amphibians	10
Reptiles	34
Birds	137
Mammals	26
TOTAL	290

From Meshaka, W.E., Snow, R., Bass, O.L., and Robertson, W.B. (2002). Occurrences of wildlife on tree islands in the southern Everglades. In Sklar, F.H. and van der Valk, A. (eds.) *Tree islands of the Everglades*, pp. 391–428. Kluwer Academic: Dordrecht, The Netherlands.

In addition, the high elevation head is a significant zone of increased phosphorus storage and accumulation decreases toward the downstream tail (Fig. 11). Storage on tree islands is several-fold higher than the adjacent marsh, and it is postulated tree islands function as phosphorus sinks and thus regulators of Everglades oligotrophy (Wetzel et al., 2005, 2011; Ross et al., 2006).

Everglades tree islands exhibit a wide range of tolerances to fluctuating water levels (Fig. 12). Tree species, such as *gumbo limbo* (*Bursera simaruba*) and *white stopper* (*Eugenia axillaris*) are intolerant of high water levels and long hydroperiod; therefore, they are typically found in areas that are inundated only infrequently. On the other hand, species such as *willow* (*Salix caroliniana*) and *pond apple* (*Annona glabra*) tolerate high water levels and long hydroperiods; therefore, they are found in areas that are flooded

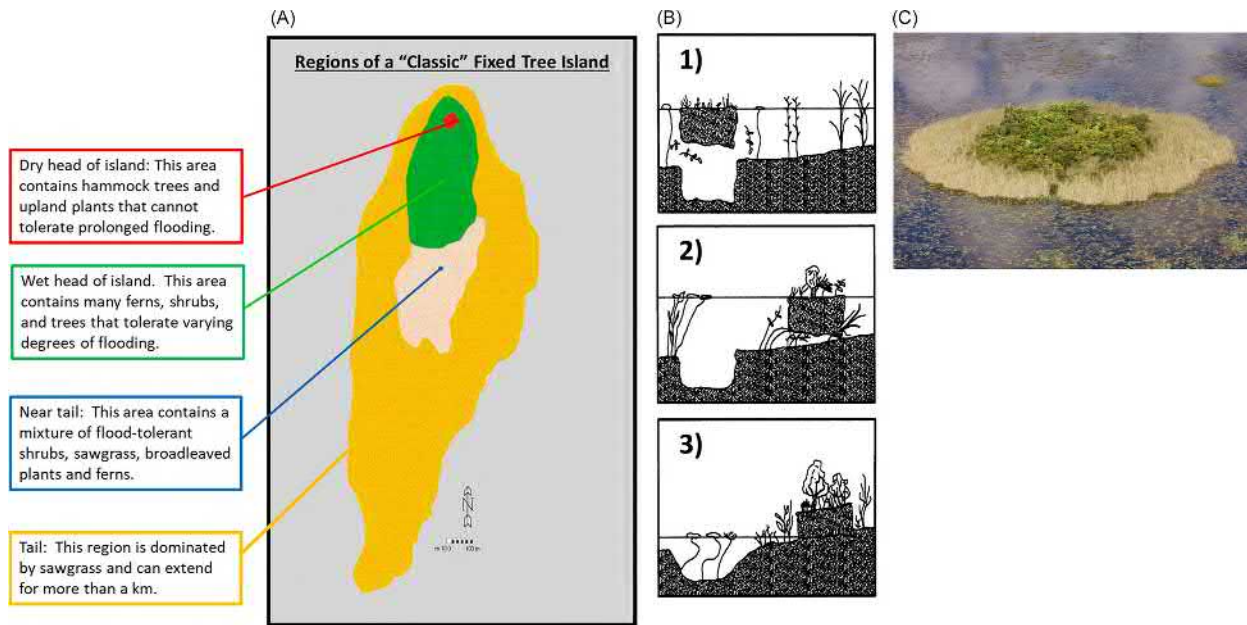


Fig. 10 (A) Regions of a typical pedestal tree island. (B) Development of a pop-up battery tree island: (1) peat detaches due to buoyancy provided by microbial gas, (2) peat battery drifts during periods of high wind and water, (3) floating battery islands rest slightly above the water's surface and are colonized by terrestrial plants. (C) Characteristic battery island with maximum elevation in the center of the island. Source: Wetzel, P.R. (2002). *Tree Island Ecosystems of the World*. In Sklar, F.H., and van der Valk, A. (eds.) (2002). *Tree Islands of the Everglades*, pp. 19–70. Boston, Massachusetts, USA: Kluwer Academic Publishers. Figs. 2–5, page 44.

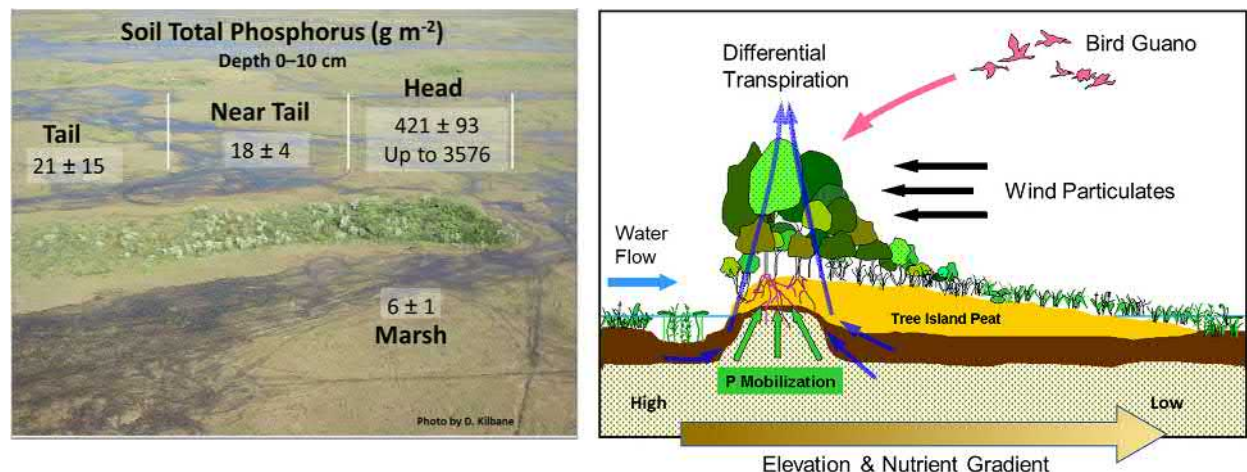


Fig. 11 (Left) Pedestal tree islands often have an irregular rock outcropping below the peat on the head of the island where nutrients accumulate more than 100 times that found in the surrounding marsh. (Right) The flow of nutrients on a fixed tree island is a function of surface and groundwater direction. The accumulation of nutrients is due to wildlife transference, particulate capture by dense trees on the head, and the ability of trees to transpire phosphorus from the underlying groundwater and limestone. Modified from Wetzel, P.R., van der Valk, A.G., Newman, S. et al. (2005). Maintaining tree islands in the Florida Everglades: Nutrient redistribution is the key. *Frontiers in Ecology and the Environment* 7(3), 370–376.

10–12 months a year. Species that are adapted to the wettest conditions can occur over relatively wider ranges of hydrologic conditions compared to less flood-tolerant species.

When hydrologic conditions on an island are altered for extended periods, the extant species lose their competitive advantage. The time required for a tree island community to significantly shift in response to altered hydrology is not clear but seems to vary from 10 to 25 years. In WCA-2A, initial over drainage from 1920 to 1950 caused a conversion of predrainage sloughs to shallower wet prairies (Loveless, 1959; Goodrick, 1974). The levees constructed between 1955 and 1964 increased water depths by some 0.75 m causing 90% of the tree islands in WCA-2A to “drown” due to excessive inundation, converting them to sawgrass ridges (Dineen, 1972; Worth, 1988; Sklar and van der Valk, 2003). Tree islands also “drown” when overgrown by invasive plants

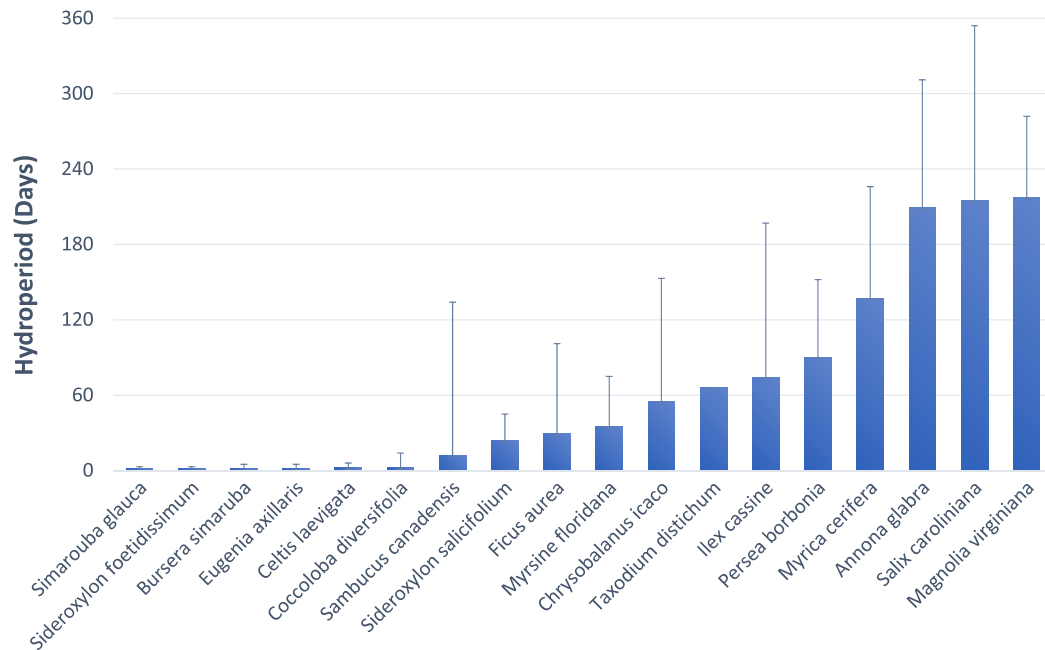


Fig. 12 The mean hydroperiod and hydroperiod range for dominate tree species from 73 tree islands from Everglades National Park and Water Conservation Areas 3A and 3B.

such as, *Lygodium microphyllum*, an invasive Old World climbing tree fern that can make a tree island uninhabitable. Some 50% of the islands in WCA-1 are infected by this fern (Volin et al., 2004).

Mangroves

Mangroves are a unique vegetation of forested tropical wetlands that dominate the tropical and subtropical coastal areas (Fig. 13), broadly between 25°North and 25°South latitude (Lugo and Snedaker, 1974; Tomlinson, 1986). While there are 10 species of mangroves in the New World (Smith, 1992), species richness in the Gulf of Mexico and Caribbean region is low, and only four mangrove species are commonly found in the Everglades at the transition between marine and freshwater biomes. They include red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), white mangrove (*Laguncularia racemosa*), and buttonwood (*Conocarpus erectus*) (Britton and Morton, 1989).

Mangrove forests in the Everglades are distributed along the southern extent of ENP (Fig. 14) covering an area of 144,447 ha with a total standing biomass of 5.6×10^9 kg (Simard et al., 2006). Unlike most mangrove forests of the world that receive significant inputs of terrigenous sediments and develop along deltaic gradients (Thom, 1982), Everglades mangroves receive extremely low upland sediments and nutrients (especially phosphorus) and develop along carbonate gradients (Woodroffe, 1992). In the Everglades, mangrove productivity is a function of freshwater flow and the organic content of the soil. Mangroves growing on historic freshwater peats of Shark River Slough are significantly larger, denser, and more productive than those growing on the low peat, carbonate soils of Taylor Slough (Fig. 14).

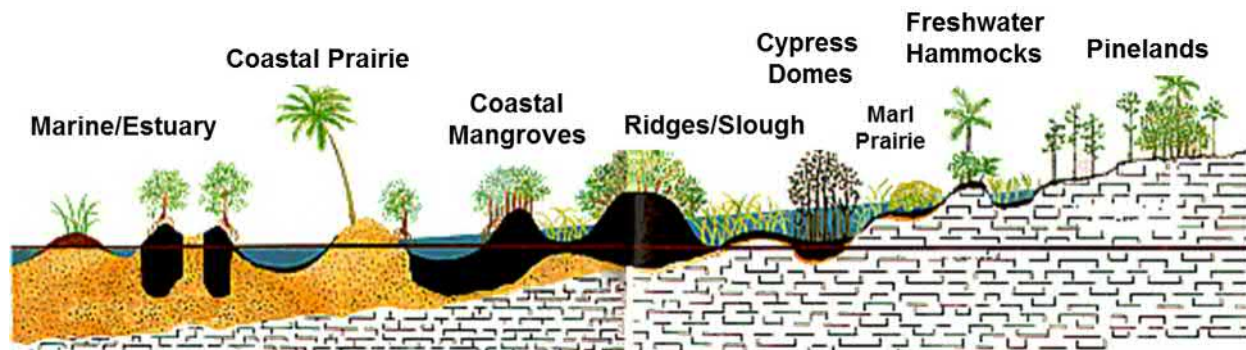


Fig. 13 Schematic marine-terrestrial transect showing the different plant communities, including mangroves, distributed along the transect. Figure was modified from a 1971 ENP brochure, Everglades Wild Guide Handbook, by Betty Fraser.

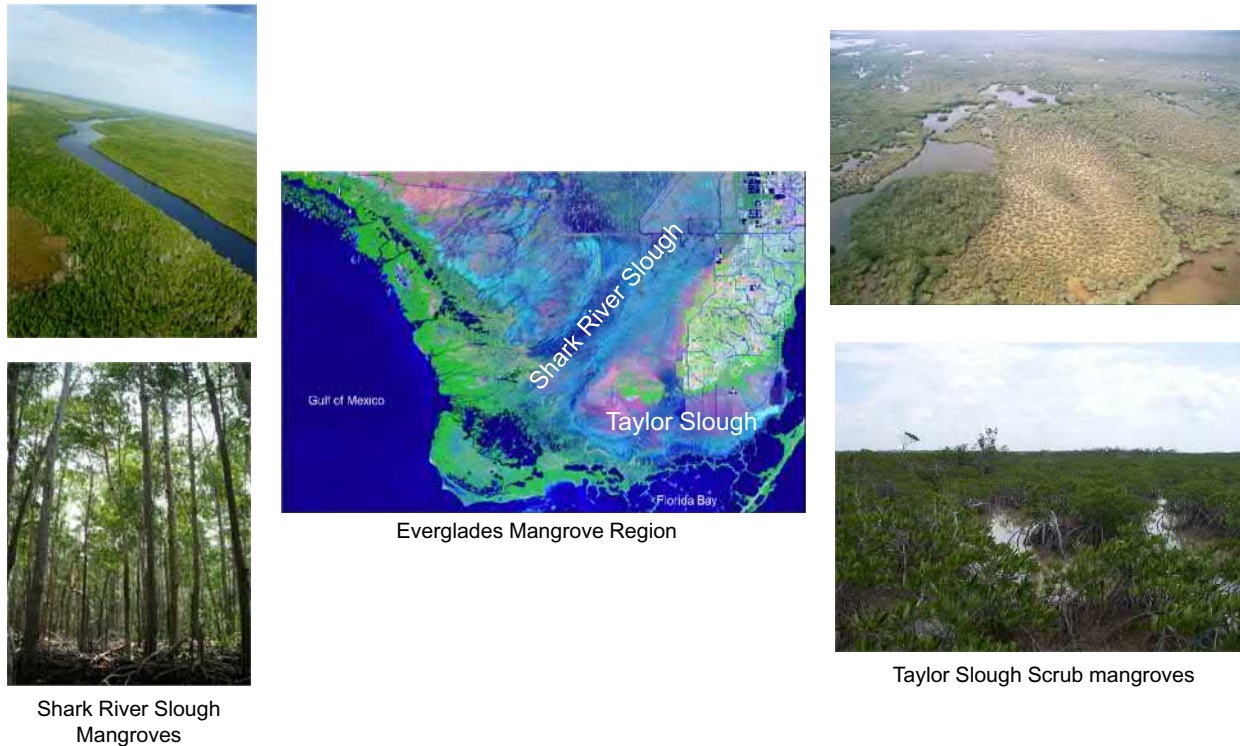


Fig. 14 Mangrove regions show up as a *green* fringe along the Gulf of Mexico and Florida Bay and include riverine-like forest distributed along Shark River Slough and the scrub mangroves distributed along northeastern Florida Bay and Taylor Slough.

The ability of these mangroves to compensate for sea level rise and maintain current shorelines has been compromised by freshwater diversions upstream (Ross *et al.*, 2000; Meeder and Parkinson, 2018). In southeast ENP, a broad band of mixed graminoid-mangrove and sawgrass communities has shifted inland by 3.3 km between 1940 and 1994 (Ross *et al.*, 2000), and using a combination of 1930s aerial photography and recent satellite imagery, Meeder and Parkinson (2018) measured an average rate of mangrove intrusion in the same region of 31 to 20 m year⁻¹, between 1938 and 1968. Projects designed to move more water to the southern part of the Everglades will hopefully prevent further migration and create conditions that allow mangroves to develop soil at a pace that keeps up with future sea level rise (Sklar *et al.*, 2019).

Faunal Communities

Though the Everglades is set climatically and geographically within the subtropics, its native faunal community is comprised largely of North American temperate species and few species from the adjacent Caribbean Basin. This is most notable for the terrestrial and freshwater taxa such that all freshwater fish species, and most species of freshwater invertebrates, amphibians, reptiles, terrestrial mammals (except for some species of bats), and breeding land birds originate from the coastal plain of the southeastern United States. Species that originate from the West Indies tend to belong to taxonomic groups that have the natural capacity to disperse across open water (Rader, 1999) either by flight (birds, bats, lepidopterans, odonates, and other terrestrial invertebrates), passive drifting by ballooning (spiders), or swimming (West Indian manatee *Trichechus manatus*). Only a limited number of terrestrial avian species from the West Indies are permanent residents, perhaps because of a lack of suitable upland habitat, but many species of waterbirds that breed in the Everglades are distributed throughout the neotropics (Robertson and Kushlan, 1984). The Everglades can clearly support freshwater species of neotropical origin as demonstrated by the large numbers of nonnative fauna that have become established in the Everglades through human assistance (e.g. Schofield *et al.*, 2009).

Animal species diversity in the Everglades is relatively low (except for some arthropods groups) and is typically characterized by a few dominant species for each taxonomic group. For instance, the number of species of freshwater fish (Loftus and Kushlan, 1987; Trexler, 1995), macroinvertebrates, and reptiles and amphibians (Means and Simberloff, 1987) are lower than in comparable habitats on the Florida Peninsula and elsewhere. The Everglades supports relatively high numbers of mammalian carnivore species but fewer bats and rodents compared to northern Florida (Layne, 1984). A similar pattern is evident for terrestrial birds, with southern Florida attracting fewer breeding land birds than northern Florida and about more than half the number of species of some northern states; however, numbers of species of breeding waterbirds are relatively high (Robertson and Kushlan, 1984). The Everglades is also characterized by relatively few endemic species. Notable subspecies include the Everglades snail kite

(*Rostrhamus sociabilis plumbeus*) and Everglades mink (*Mustela vison evergladensis*), which are found throughout southern Florida, and the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*), which has a far more limited distribution comprising just six subpopulations within ENP. Threatened or endangered species within the Everglades Biome include West Indian manatee, Florida panther (*Felis concolor coryi*), wood stork (*Mycteria americana*), Everglades snail kite, Cape Sable seaside sparrow, American crocodile (*Crocodylus acutus*), Bartam's hairstreak butterfly (*Strymonas bartrami*), and Schaus' swallowtail (*Heraclides aristodemus ponceanus*). The depauperate diversity and limited endemism are probably related to the isolated location of the Everglades at the tip of the 644 km long Florida peninsula (Means and Simberloff, 1987) and the young age of the Everglades (less than 6000 years old), which has provided a limited period of continuously favorable conditions necessary for speciation and immigration. Moreover, the extremes of temperature and frequent drying that occur in the Everglades' freshwater habitats and the limited availability of terrestrial habitats possibly preclude the establishment of many species (Layne, 1984; Robertson and Kushlan, 1984; Loftus and Kushlan, 1987).

Freshwater communities in the Everglades are dominated by macroinvertebrates (e.g. aquatic beetles, odonates, crustaceans, and planorbid snails), amphibians (i.e. frogs and salamanders), and small (< 4 cm; Poeciliidae and Cyprinodontidae) and large (Centrarchidae) fishes. Fish and crayfish play an especially important role in the food web by supporting some of the Everglades' most charismatic top predators such as alligators and wading birds (Boyle et al., 2012, 2014). Surprisingly, estimates for fish and invertebrate standing stocks in the Everglades are among some the lowest recorded for freshwater aquatic habitats despite the relatively high primary productivity of the periphyton (Turner et al., 1999). This is partly because of the physiological stress experienced by aquatic animals in the seasonally drying wetlands (Kushlan, 1976), but arguably more important is the inedibility of the calcareous periphyton mats (Browder et al., 1994; Geddes and Trexler, 2003; Chick et al., 2008). A significant proportion of the energy and nutrients moving through the food web appear to be transported via less efficient detrital pathways rather than consumption of primary producers (Williams and Trexler, 2006; Hagerthey et al., 2014).

Aquatic animals survive drying during the dry season either by moving to lower elevation aquatic refugia such as alligator holes and creeks (e.g., all freshwater fish), or by tolerating it through burrowing (crayfish), diapause (copepods and cladocerans) or aestivation (e.g. gastropods) (Gaiser et al., 2012). At least one crayfish species (*Procambarus fallax*) appears to use a joint strategy, first moving downslope from drying habitats to aquatic refugia and then burrowing when refugia are no longer available (Cook et al., 2014). The faunal community can experience high mortality depending on the severity and duration of the drydown (Trexler et al., 2005; Dorn and Cook, 2015). Recolonization rates vary by taxa, but population recovery typically take several years following reflooding (DeAngelis et al., 2005; Trexler et al., 2005).

Predator limitation on prey is a strong driver in the freshwater Everglades. Predatory sunfishes can limit small fish, crayfish and shrimp populations (Dorn et al., 2006). Dorn and Cook (2015) experimentally demonstrated that abundances of large predatory fish were seasonally reduced in marshes disturbed by moderate drying, and the response of small fish densities to this predator release was minimal, however slough crayfish (*P. fallax*) densities, which were similar across all wetlands before drying, increased almost threefold after the disturbance. The strength of predator control in the Everglades can shift through time and in space according to recent hydrological conditions. This creates variable environments for fish and crayfish population growth. This in turn, generates flexible food web reconfigurations that cascade upwards to provide variable foraging conditions for nesting wading birds. For example, whereas the Everglades' most abundant species of wading bird, the white ibis (*Eudocimus albus*), fuels its nesting colonies primarily with crayfish (Boyle et al., 2014), wood stork, snowy egret (*Egretta thula*), and tricolored herons (*E. tricolor*) almost exclusively feed fish to their young (Ogden et al., 1976; Boyle et al., 2012).

The Wading Bird Paradox

Although standing crops of small fishes and macroinvertebrates in the Everglades are relatively low, the Everglades can support unexpectedly large populations of top predators (Turner et al., 1999). Of note are the exceedingly large populations of nesting wading birds (orders Ciconiiformes and Pelicaniformes) that, in a given year, can exceed a hundred thousand nesting pairs (Ogden, 1994; Cook and Baranski, 2019). The key process limiting wading bird nesting in the Everglades is the availability of aquatic prey (Frederick and Ogden, 2001; Herring et al., 2011), which is a function both of prey production and how accessible prey are to capture by birds. The reason that the limited secondary production in the Everglades can support such large numbers of birds is because wetland topography and landscape-scale seasonal drying can interact to concentrate prey at extremely high densities and provide critical foraging conditions at the appropriate places during the winter/spring breeding season (Fig. 15).

Restoration Underpinnings

Impacts to the natural Everglades ecosystem resulted in a strong public desire to restore the Everglades and the implementation of the Comprehensive Everglades Restoration Plan (CERP) in 2000, with the goal of protecting, preserving and restoring this ecosystem. To support Everglades restoration, SFWMD developed a group of computer models to characterize the predrainage and postdrainage/managed Everglades system. These "Regional Simulation Models" (RSM) estimate the hydrology of



Fig. 15 Wading birds foraging in the Everglades ridge and slough on high densities of prey that became concentrated by landscape-scale seasonal drying. Photos credit: Mark Cook.

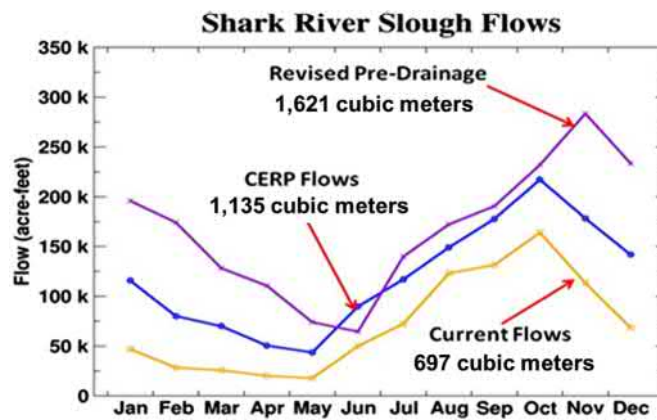


Fig. 16 Flow characteristics of the predrainage, postdrainage, and restored Everglades.

approximately 31,000 km² (3.1 million ha) of south Florida, including Everglades wetlands, in their current state and as they existed before drainage (ca. 1850). The model is used to indicate relative changes in hydrology between predrainage and current conditions and used in an adaptive management framework to help guide water management and project planning (Said and Brown, 2013). CERP changes to the south Florida infrastructure of canals, levees, and pumps is expected to increase the average volume of water to the parched Shark Slough of ENP by 63% (666.1 million m³) but is not expected to reach historic levels (Fig. 16).

Conclusion

The complexity and trade-offs required to ensure the anthropogenic and natural resource demands of the Everglades ecosystem are met can appear daunting (Sklar et al., 2005). Particularly given that in some cases even natural needs can be in conflict, e.g., low seasonal water requirements for the cape sable sparrow versus higher water needs for aquatic fauna. However, the ecosystem is resilient and while damaged, it can recover. In 2018, wading and migratory birds nested on scales seen over 100 years ago (Cook and Baranski, 2019).

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Hawai'i: The Wetland System of Hawai'i

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Published by Elsevier Inc.

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Abstract

This paper represents a status assessment of the Hawaiian archipelagos wetlands including the current status, stressors, and future viability. Wetlands in the Hawaiian archipelago encompass all fresh and saline lentic (standing or still water) ecotypes occurring from sea level to upper elevations. Wetlands can be separated into two categories: wetlands (bogs, upland marshes and swamps; lowland freshwater and saline marshes, and estuaries) (Polhemus et al., 1992) and water bodies (ponds, fresh and saline lakes, anchialine pools, and artificial reservoirs). Historically, wetlands were located on all of the main Hawaiian islands and a few of the Northwestern Hawaiian Islands (NWHI). Currently, wetlands are still found on all the main Hawaiian Islands and Midway and Laysan in the NWHI. However, the quality of many of these wetlands is now comprised of non-native vegetation, invertebrates, and fishes. In addition to naturally formed wetlands and water bodies, artificial reservoirs (i.e., wastewater treatment plants and stock ponds) are also classified as wetlands in the main Hawaiian islands. Our assessment of wetland viability, defined as the likelihood of persistence over the long term, is based on the concepts of representation, redundancy, and resiliency. The main stressors of wetland viability are development and altered hydrology, recreation and human access, water pollution, invasive animals and plants, sea level rise, flooding and erosions, natural disasters (i.e., hurricanes), and drought. Ongoing conservation efforts are helping to protect remnant patches of natural

wetlands in the Hawaiian archipelago. The conservation of these habitats depends largely on combined efforts of State, Federal, multi-agency organizations, non-profit organizations, and the voluntary support of private landowners. An analysis of four future scenarios identified a decline in wetlands viability in lieu of intensive management.

Introduction

This document is an overview in the wetlands and fresh and saline open water bodies in the Hawaiian archipelago and describes the ecological factors that have influenced the habitat over time. An introduction to the Hawaiian archipelago including geography, formation, climate, hydrology, island names and descriptions, can be found in the chapter on the Physical Geography of the Hawaiian Islands by Harrington included in this work. Other biome publications that influence wetlands and open water bodies in Hawai'i are "The Stream Systems of Hawai'i," "The Coastal Systems of Hawai'i," "The Wet Forest Systems of Hawai'i," and "Anthropogenic changes—The Developed System of Hawai'i."

Wetland and Open Water Body Description.

Wetlands and open water bodies occur in Hawai'i from sea level to elevations of at least 1525 meters (m) (Table 1). In general, wetlands and open water bodies in Hawai'i function (physically, chemically, and biologically) in similar manner as lentic ecotypes around the world. Similarly, they also do not function because of activities such as water diversions, groundwater withdrawals, and paving of nearby surfaces. The functions of wetlands and open water bodies in Hawai'i's are influenced by the tropical climate conditions (high year-round temperatures and precipitation), porous volcanic soil and steep terrain, which can increase rates of evapotranspiration, organisms respiration, soil weathers, and ground-water recharge. These differences suggest that relationships and models from temperate wetlands and open water bodies may not be uniformly applicable to wetlands in Hawai'i.

For this assessment, open water bodies, or "loko," are ponds, lakes, and any enclosed body of water with areas of open water (Pukui and Elbert, 1986; Apple and Kikuchi, 1975), with generally <25% cover of vegetation or soil (Polhemus et al., 1992). Also included are sub-types such as anchialine pools and artificial reservoirs that do not necessarily fit the standard definition of a wetland (i.e., little to no hydric soil). However, these have been included due to other "wet" similarities and also due to all habitat supporting similar organisms (e.g., aquatic insects, waterbirds, hydrophytes).

In the Hawaiian archipelago, naturally-formed bodies of open water occur in basins that are primarily volcanic in nature and substrate. In addition, there are a few naturally-formed open water bodies resulting from ancient climatic events such as lakes on nonporous coral islands and others created by melting of glaciers. They are also dependent on the same above and below ground water sources as wetlands. However, at higher elevation, along with precipitation and fog drip, snow melt also drains into alpine lakes. At lower elevations near the coast, storm or tidal waves and sea spray with continued evaporation may create a hypersaline condition (Schauinsland, 1899; Ziegler, 2002).

Naturally-formed wetlands and open water subtypes can have shoreline and substrates varying from solid rock to sandy, hydric soils. All of which can be influenced by climate, topography, organism in and around water bodies, time, and human manipulation.

In Hawai'i, the presence of hydric soils is a good indicator of wetland presence. However, it should be noted that not all areas containing hydric soils are considered wetlands. Other factors such as vegetation and hydrology must also be present. Some areas with hydric soils as shown on the maps are actually considered wet forest. The standard references for drainage classifications and permeability rates of soils in Hawai'i are contained in U. S. Department of Agriculture (USDA) Natural Resource Conservation Service's (NRCS) soil surveys.

Unlike wetlands which require hydric soils as a substrate, naturally-formed bodies of open water usually require a non-porous substrate like rock or coral. Anchialine pools are an exception, and are dependent on underground movement and flow of water and thus require porous volcanic or limestone substrates. In Hawai'i, the volcanic basalt parent material and derived minerals are extremely porous, and ancient limestone coral uplifts or karst material are full of cracks and crevices allowing water to drain to a water table, deep below the surface (Maciolek, 1969). At lower elevations, a water table near the surface can allow water to collect in an above ground basin. At high (alpine) elevations, Wentworth and Powers (1941 in Massey, 1978) have suggested naturally-formed basins were sealed by ice.

Plants and animals found in a particular wetland are also likely to be found in open water bodies that have similar topography, climatic conditions, salinity levels, shoreline and bottom substrate, surrounding habitat usage and water input. Exceptions to this are the anchialine pools. Due to the wide variety of locally unique algal and bacterial types these pools are generally the only open water bodies that provide habitat for individually unique assemblages of organisms (Yamamoto et al., 2015).

Pre-Human Condition

Information on the quality and extent of wetlands and open water bodies across the Hawaiian archipelago especially in NWHI prior to human settlement is limited to non-existent. While the main islands of Hawai'i were inhabited, eight of the ten NWHI have no physical evidence of habitation by native Hawaiians (Ziegler, 2002). Although the knowledge of islands northwest of Nihoa and Mokumanamana could be implied thru mo'olelo (stories) and mele (chants and songs) there is no record of settlements by native Hawaiians. Therefore, the wetlands and open water bodies on those islands remained unchanged by humans until contact with Westerners.

Due to the great long-term ecological stability in the Pacific islands prior to human contact (Steadman 1995 in Athens, 1997), it can be assumed that wetlands and open water bodies found in Hawai'i historically are the same as found today. The porous and permeable basalts substrate that forms the bulk of the main islands of Hawai'i facilitate infiltration and storage of groundwater. A large body of groundwater exists within these porous basalts at lower elevations throughout the interiors of the larger islands. In addition to this basal groundwater layer, smaller perched groundwater systems form at higher elevations, contained by dense geological features of low permeability. As such, many of the geographic locations for certain sub-types such as lakes, bogs, and upland marshes and swamps have remained the same. For instance, in 1982, Maciolek identified lakes in the Hawaiian archipelago that still exist from prehuman contact (Table 5). Historically, we can assume there were more bodies of open water than at present, since Maciolek (1982) considered Ālia pa'akai "Salt Lake" and Ka'elepulu Pond on the island of O'ahu, and Mānā Plain on the island of Kaua'i to be extinct. Therefore, for this section we simply state that most of the wetlands and open water bodies used in this analysis existed prior to human contact and likely in greater numbers.

With the assumption that wetlands and open water bodies were present and functioning throughout the Hawaiian archipelago as defined in Table 1, the habitat for native animals was present (Table 2). Therefore, with the lack of genetic dating for all native species, we assume all native species were present in wetlands prior to human contact and likely in greater numbers.

Montane Bog

Though absent on Ni'ihau and Lāna'i, these bogs were scattered throughout the higher elevations of the other main Hawaiian islands (Table 3). These bogs were characterized by irregular, hummocky cushions of low-growing native sedges, and grasses, in addition to a diversity of unique bog tolerant plants (Table 4). The most unusual aspect was the presence of dwarf individuals (often less than about 10 cm high) of *Metrosideros polymorpha* var. *pumila* ('ōhi'a) and *Vaccinium reticulatum* (ohelo 'ai, Hawaiian blueberry). A widespread Northern Hemisphere bog species of insect-eating *Drosera anglica* (mikinalo, or Sundew) also naturally colonized certain Kaua'i bogs (Cuddihy, 1989 in Stone and Stone, 1989; Ziegler, 2002).

Each bog is distinct and contains a unique assemblage of native plants. The windward slopes of Mauna Kea on the island of Hawai'i contain large expanse of a very wet 'ōhi'a community that has been described as "bog-formation dieback." In such systems on water-soaked soils, stands of 'ōhi'a trees undergo dieback and are replaced by sedges and 'ōhi'a shrubs (Mueller-Dombois, 1986). The botanically rich bogs of east Maui were comprehensively detailed by Loope et al. in 1991. An east Maui montane bog, surrounded by *Deschampsia* grassland was characterized as "alpine" by Vogl and Henrickson (1971) but still has much in common with those found at lower-elevations.

Kaua'i's Kanaele Bog is the State's only lowland (640 m) bog community. Among the rare and endangered plant species found at Kanaele are a species of 'ōhā wai, *Dubautia herbstobatae* (na'ena'e), kāmakahala, a native bog violet, and a native thistle (The Nature Conservancy of Hawai'i, 2019).

Upland Marshes and Swamps

Upland marshes were less common than upland bogs and dominated by hydrophytes (Table 4). A major distinguishing feature was the absence of trees and shrubs. Marshes in the upper Ko'olau Mountains such as Ka'au Crater (O'ahu) fall into this category.

Upland swamps occurred on all the main Hawaiian islands except for Lāna'i. The major feature separating upland swamps from upland bogs and marshes is the presence of trees (Table 4).

Lowland Freshwater Marshes

Lowland freshwater marshes were among the most extensive lowland wetland ecosystems in the main Hawaiian islands, although they tended to occur to the greatest extent on the older islands of O'ahu and Kaua'i. Growing in these wetland sites and forming a dense sod around the margins are *Schoenoplectus lacustris* subsp. *validus* ('aka'akai), *Paspalum vaginatum* (seashore paspalum), and *Bacopa monnieri* (water hyssop) (Gagne and Cuddihy, 1999). An extensive list of wetland plants found in the State of Hawai'i can be found in Lichvar et al., 2016.

Lowland Saline Marshes and Estuaries

This wetland sub-type was believed to be extensively represented in the main Hawaiian islands, especially on Maui, Moloka'i, O'ahu, and Kaua'i. Examples of marshes included: Ninole Springs, Hilea, and Honu'apo, on the island of Hawai'i; Kanahā Pond and Keālia Pond, on the island of Maui; Pala'au, on the island of Moloka'i; Pearl Harbor and Waikiki on the island of O'ahu; and Hule'ia Marsh, on the island of Kaua'i. Vegetation commonly found in these wetlands include grass, *Paspalum distichum*, *Sporobolus virginicus*, sedges such as *Cyperus javanicus*, *C. Laevigatus*, *eleocharis* spp., *Fimbristylis cymosa* and others (Stemmermann, 1981).

Some examples of estuary ecosystems in Hawai'i included: Waipi'o Bay and Waiakea Pond (island of Hawai'i), Keālia Ponds (island of Maui), Maui; Kāne'ohe Bay (island of O'ahu), O'ahu; and Wainiha Bay (island of Kaua'i).

Table 1 Definitions of wetlands and water bodies included in this assessment.**Wetlands**

High elevation or montane bogs—Generally form above 460 m elevation on the northeastern flanks of mountains exposed to prevailing wind and rainfall averaging from 300 to 1000 cm. Small, self-contained bodies of open water found in flat, mid- to upland areas with high persistent rainfall (>500 cm a year). Precipitation also includes fog drip and snow melt on the island of Hawai'i and Maui. The water is acidic, clear, cool, very low in dissolved minerals, and yellow to brownish in color. Saturated soils sit atop a layer of peat which have a layer of clay beneath which inhibits drainage (Polhemus et al., 1992) and a hard iron precipitate within the top 60 m of the soil surface that increases ponding and saturation above that layer (Gagne and Cuddihy, 1999). Bogs have few or no trees or hydrophytes (aquatic plants) and are dominated by mosses and grasses

Upland marshes—Perennial to seasonally intermittent non-forested wetlands in upland areas (100–1200 m) of moderate to high rainfall, but better drained than bogs. Water is clear, sometimes yellowish, with low to moderate dissolved mineral content (Polhemus et al., 1992). Upland marshes are dominated by hydrophytes

Upland swamps—Perennial to seasonally intermittent forested wetlands in upland areas (100–1200 m) with moderate to high rainfall. Water is non-acidic, with characteristics similar to those of upland marshes (Polhemus et al., 1992)

Lowland freshwater marshes—Generally, at low elevation, <100 m that is not immediately adjacent to the coastline. They are maintained either by stream inflows or by exposure of the natural water table. Salinity <0.5‰. Marshes located on windward sides of the islands are less saline than those on leeward sides because of higher rainfall. Perennial lowland wetlands lacking trees but with abundant emergent vegetation (Polhemus et al., 1992). This also includes playa lakes, shallow wetlands found in flat central basins with slopes of 0.2 m per km and where evaporation greatly exceeds inflow of water (Baker, 2016)

Lowland saline marshes and estuaries—Also called coastal wetlands, are areas with perennial, tidal, or seasonal brackish water, often resulting from underground saltwater intrusion (Polhemus et al., 1992). Estuaries are stream segments between the coastline and 1 m elevation (Parham and Lapp 2006 in Parham, 2008) that completely or partially enclosed water bodies typically found where sea mixes with fresh water from rivers and streams. They are maintained by perennial stream runoff and fresh water springs and their inland extent is determined by measurable tidal fluctuation and topography. The physical make-up of estuaries that represent the transition area between the inland waters and the sea can vary widely. The inland margins of bays, harbors, inlets, and lagoons can all be considered estuaries

Open water bodies

Ponds—A body of standing water usually smaller than a lake (Merriam-Webster, 2018). Water depth is shallow, allowing sun to reach the bottom of the water body (euphotic zone). Although shallow, ponds are often thermally stratified (change in temperature at different depths) and have abundant rooted and floating macrophytes (aquatic plants growing in or near water) (Horne and Goldman, 1994). Ponds can be ephemeral (only holding water at certain times of years)

Fresh and saline lakes—Fresh water lakes can be found at all elevations. While saline lakes are generally found near the shorelines. A lake is a body of water of natural origin with surface area >0.1 ha; maximum water depth >2 m, and the absence of a natural oceanic connection (Maciolek, 1982). Freshwater lakes have a salinity of <0.5‰ and saline lakes usually have a salinity >0.5‰ (Polhemus et al., 1992). Lowland freshwater lakes characteristically lacked a natural oceanic connection (surface or subsurface) of a magnitude sufficient to cause demonstrable tidal fluctuations. Saline lakes were usually, but not always, fed by seawater seepage and may have been diluted by rainwater, overland runoff, or groundwater, or concentrated by evaporation

Anchialine pools—A body of water with mixed salinity within a geological formation (coastal lava flows or limestone exposures) that exposes the underlying water table. They include typical small bodies of water as well as water in lava fields, tubes, cracks, and under rock overhangs, and open wells, and may occur singly or in groups (Maciolek and Brock, 1974). Pools display tidal dampening with some pools only having water at high tide. Water flows underground and the pools have no regular surface connection to the sea. Water chemistry is highly variable with salinities ranging from 0 to 41 parts per thousand and surface temperatures ranging from 17 to 36°C (Yamamoto et al., 2015).

Occur singly or in groups and vary in size and depth ranging from a 30 cm or less in surface area to multiple square m and from a couple of cm to over a 30 m in depth (Yamamoto et al., 2015). Depths are variable depending on tidal stage, with certain very shallow pools appearing only at high tide (Polhemus et al., 1992)

Artificial reservoirs—Any human-created body of water constructed depression that holds water with input usually from natural precipitation. Usually used for for agriculture (irrigation or milling operations), other socioeconomic purposes, or created by warfare (e.g., reservoirs, domestic water supply, bomb craters, wastewater treatment plants, stock ponds, aquaculture, golf course hazards) (Polhemus et al., 1992).

Stock ponds: Usually small bodies of water that do not require a boat to cross, are used for providing water to livestock across ranch lands and can be found on most of the main Hawaiian islands.

Settling ponds: Original settling ponds were created in conjunction with milling of sugar. Sugar milling required large volumes of water and many mills were located near wetlands, streams, or rivers. Continue to be built for different industries in Hawai'i.

Wastewater treatment plant: Usually open water impoundments with a polyurethane lining. With enough the buildup of sludge natural wetland vegetation and aquatic invertebrate composition can develop.

Golf course water features: Can vary in depth and size, may be aerated, and have shoreline vegetation

Ponds

Wetlands with vegetation dominated by 'aka'akai, kaluhā, and *Cyperus laevigatus* (makaloa) can be found bordering small spring-fed ponds in areas near the coast on the islands of Moloka'i, Maui, and Hawai'i. Water hyssop is prominent in very shallow water on the edges of these ponds and can exceed the coverage of the dominant sedges at some sites (Gagne and Cuddihy, 1999).

Fresh and Saline Lakes

Fresh and saline lakes occur at all elevations throughout the archipelago. In general, upland lakes are freshwater while those near the coastline are saline to hypersaline (Table 5).

Table 2 List of animal that can be found in Hawai'i wetlands.

Scientific	Hawaiian, English common	ESA listing status	Native, nonnative, or migratory
<i>Waterbirds</i>			
<i>Gallinula chloropus sandvicensis</i>	'Alae 'ula, Hawaiian Gallinule	E	Native
<i>Fulica alai</i>	'Alae ke'o ke'o, Hawaiian coot	E	Native
<i>Himantopus mexicanus knudseni</i>	Ae'o, Hawaiian stilt	E	Native
<i>Shorebirds</i>			
<i>Nycticorax nycticorax</i>	'Auku'u, Black-crowned night heron		Native
<i>Pluvialis fulva</i>	Kōlea, Pacific Golden Plover		Migratory
<i>Arenaria interpres</i>	'Akekeke, Ruddy turnstone		Migratory
<i>Calidris alba</i>	Hunakai, Sanderling		Migratory
<i>Heteroscelus incanus</i>	'Ulili, Wandering tattler		Migratory
<i>Numenius tahitensis</i>	Kioea, Bristled-thighed curlew		Migratory
<i>Waterfowl</i>			
<i>Branta sandvicensis</i>	Nēnē, Hawaiian goose	T	Native
<i>Anas wyvilliana</i>	Koloa, Hawaiian duck	E	Native
<i>Anas clypeata</i>	Koloa mohā, Northern shoveler		Migratory
<i>Anas acuta</i>	Koloa māpu, Northern pintail		Migratory
<i>Anas platyhynchos</i>	Mallard		Nonnative/migratory
<i>Aythya affinis</i>	Lesser scaup		Migratory
<i>Reptile</i>			
<i>Rana catesbeiana</i>	North American bullfrog		Nonnative
<i>Bufo marinus</i>	Cane toad		Nonnative
<i>Fish</i>			
<i>Stenogobius hawaiiensis</i>	'O'opu naniha		Native
<i>Eleotris sandwicensis</i>	'O'opu akupu or 'O'opu ōkuhe		Native
<i>Gambusia affinis</i>	Mosquito fish		Nonnative
<i>Poecilia reticulata</i>	Rainbow fish		Nonnative
<i>Limia vittata</i>	Cuban Molly		Nonnative
<i>Xiphophorus helleri</i>	Green swordtail		Nonnative
<i>Oreochromis mossambicus</i>	Mozambique tilapia		Nonnative
<i>Sarotherodon melanothron</i>	Black-chined tilapia		Nonnative
<i>Tilapia zillii</i>	Redbelly tilapia		Nonnative
<i>Pisodonophis cancrivorus</i>	Rice-paddy eel		Nonnative
<i>Misgurnus anguillicaudatus</i>	Dojo, or Oriental weatherfish		Nonnative
<i>Crustaceans</i>			
<i>Macrobrachium grandimanus</i>	'Ōpae 'oeha'a		Native
<i>Molluscs</i>			
<i>Neritina vespertina</i>	Hapawai		Native
<i>Theodoxus cariosus</i>	Pipiwai		Native
<i>Thiaridae</i> sp.	Malaysian live-bearing snails		Nonnative
<i>Pomacea</i> spp.	Apple snail		Nonnative
<i>Pomacea canaliculata</i>	Apple snail		Nonnative
<i>Pila conica</i>	Apple snail		Nonnative
<i>Corbicula fluminea</i>	Asiatic freshwater clam		Nonnative
<i>Insects</i>			
<i>Megalagrion</i> spp.			Native and nonnative
<i>Anax</i> spp.			Native and nonnative
<i>Nesogonia</i> spp.			Native and nonnative
<i>Pantala flavescens</i>	Globeskimmer		Nonnative
<i>Micracanthia humilis</i>			Nonnative
<i>Mesovelia mulsanti</i>	Water treader		Nonnative
<i>Saldula</i> spp.			Nonnative
<i>Microvelia vagans</i>	Waterbug		Nonnative
<i>Polypedilum nubiferum</i>	Spotted winged midge		Nonnative
<i>Aedes</i> spp.	Mosquito		Nonnative
<i>Culex</i> spp.	Mosquito		Nonnative
<i>Toxorhynchites</i> sp.	Mosquito		Nonnative
<i>Cricotopus bicinctus</i>			Native
<i>Ochthera circularis</i>			Nonnative
<i>Odontomyia ochropa</i>			Nonnative
<i>Chironomus esakii</i>	Large midge		Nonnative
<i>Coleoptera</i> spp.	Water beetle		Native and nonnative

Table 3 Bog sub-type on the main Hawaiian islands.

Island	Bog description/location
Hawai'i	Windward slopes of the Kohala Mountains, Mauna Kea, and Mauna Loa (Jacobi, 1990 in Cuddihy and Stone, 1990)
Hawai'i and Maui	Two bogs are believed to have formed in former small lakes, one along the Wailuku River, Hawai'i (Treeless bog), the other a subalpine bog on East Maui (Flat Top bog)
Maui	High-rainfall windward slopes of east Maui (Loope et al., 1991 in Cuddihy and Stone, 1990)
West Maui, Moloka'i, O'ahu, and Kaua'i	Very wet, poorly drained areas, near mountain summits (Selling, 1948 and Carlquist, 1980 in Cuddihy and Stone, 1990)
Kaua'i	A few sloping bogs also occurred on steeper terrain where precipitation was extremely high, such as in North Bog in the Wai'ale'ale summit region
Kaua'i	The one low-elevation bog on Kaua'i (Kanaele) occurs on shallow, poorly drained acidic peat (Cuddihy and Stone, 1990)

Table 4 Plants characteristically found in wetland sub-types.

Subtype	Characteristic plants
Bog	<i>Oreobolus furcatus</i> , <i>Carex</i> spp., <i>Rhynchospora</i> spp., <i>Dicanthelium</i> spp., <i>Dubautia</i> spp. [na'ena'e] and a diversity of unusual bog-tolerant plants such as <i>Argyroxiphium grayanum</i> (green swords), <i>Plantago</i> spp. (laukāhi), the daisy-like <i>Lagenophora viridis</i> , the fleshy-trunked lobelias of Maui and Kaua'i (<i>Lobelia gloria-montis</i> , <i>L. kauaensis</i> , <i>L. villosa</i>), and fragile clubmoss (<i>Selaginella deflexa</i>), and endemic violets (<i>Viola maviensis</i> , <i>V. chamissoniana</i> var. <i>robusta</i> , and others) (Cuddihy and Stone, 1990)
Upland Marsh	Hydrophytes—reeds and sedges, submerged or floating macrophytes, pondweeds and waterlilies
Upland Swamps	Trees, shrubs, and variety of aquatic macrophytes in open sunlit areas
Lowland freshwater marshes	See Lichvar et al. (2016)
Lowland saline marshes and estuaries	Shrubs and trees such as <i>Pritchardia</i> spp. (loulou), <i>Chamaesyce olowaluana</i> ('akoko), <i>Columbrina</i> spp. (kauila), and <i>Kanaloa kahoowawensis</i> (kanaloa) (Athens, 1997; Athens et al., 2002)

Table 5 Six lakes historically identified from the Hawaiian archipelago (Maciolek, 1982).

Lake name	Island	Elevation	Salinity level	Basin origin
Waiau	Hawai'i	3969 m—Alpine	Fresh	Glacier
Wai'e'ele	Maui	3040 m—High	Fresh	Volcanic (crater)
Nōmilu	Kaua'i	Sea level	Euhaline	Crater
Kauhakō	Moloka'i	Sea level	Saline	Volcanic (Crater)
Green (Wai a Pele) ^a	Hawai'i	Sea level	Fresh/Saline	Volcanic
Laysan	Kamole (Laysan)	Sea level	Hypersaline	Coraline

^aGreen Lake filled with lava on June 2, 2018.

Lake Waiau, an alpine lake formed during the post-Pleistocene melting of glaciers that once occurred on the summit of Mauna Ke'a (Massey, 1978). It is the shallowest freshwater lake at 3 m deep (Maciolek, 1982). Wentworth and Powers (1941) suggest that when frozen, water trapped by fine grained sediments creates an impermeable layer (Woodcock, 1980) keeping water from draining out of the basin, allowing the lake to persist.

Lake Kauhakō differs slightly from the other lakes. Formed during the late Pleistocene, it occupies a precipitous crater 250 m deep within the Kalaupapa peninsula (Stearns and Macdonald, 1947; Macdonald and Abbott, 1970). Unlike other lakes in Hawai'i, sea water intrudes from the basal water table, although there is no evidence of a connection to the ocean (Maciolek, 1982).

Lake Laysan (40 ha) is the only lake in the Hawaiian archipelago that does not occupy a basin primarily formed by volcanic origin. This shallow, central lake is 2.4 m above sea level and is perched on a layer of upraised nonporous coral on a secondarily raised atoll (Rauzon, 2001). This lake was fed by precipitation and washover by seawater. Due to continuous evaporation, the lake water is hypersaline, having a salinity approximately three times greater than the ocean (Schauinsland, 1899; Elschner, 1915; Warner, 1963; Caspers, 1981). Laysan Lake and the fresh seeps currently found along its shores and inland are thought to have been more numerous prior to human contact.

Anchialine Pools

Anchialine pools supported unique plants and animals and Hawai'i may have had the highest biological diversity of any such pools in the world (Maciolek, 1986). Crustaceans and mollusks were the most abundant animals in these ecosystems, although certain rare insects such as the damselfly *Megalagrion xanthomelas* were also present. Waterbird and shorebirds were also present in these ecosystems. Tiny, herbivorous shrimp or 'ōpae 'ula (*Halocaridina rubra*) were the most characteristic species. Algae and bacteria of different forms were present in anchialine pools and many served as food for aquatic animals. The indigenous aquatic vascular plant, tassel pondweed or widgeon grass (*Ruppia maritima*), was likely characteristic of leeward pools on the island of Hawai'i (Stone, 1989).

Historical Range

Estimations of pre-settlement wetlands range from 20,963 ha (USFWS, 1990) to 126,300 ha (van Rees and Reed, 2014). van Rees and Reed (2014) point out that the Hawai'i data included in the 1990 USFWS report (sometimes cited as Dahl, 1990) primarily relied upon a review letter (Kosaka, 1990, *in litt.*) that cited an old Hawai'i wetland assessment that no longer exists and the summary provided no information regarding sources of data or methods used. Kosaka's (1990) analysis started in 1780 while van Rees and Reed went back a 1000 years (plus or minus) to pre-human contact. It should be noted that the 1990 estimate was made before significant advances in Geographic Information Systems (GIS) and computer technology (van Rees and Reed, 2014).

There are no known wetland range estimates for the NWHI.

Viability

Ecosystems sustain through resiliency, redundancy, and representation. The viability of wetlands and open water bodies depends on maintaining multiple and distributed types (redundant) of sufficient quality and size (resilient) with species richness and genetic range (representative) to survive across its ecological environment over time. The phrase "ecologically healthy" refers to functions affecting biodiversity, productivity, biochemical cycles, and evolutionary processes that are linked to the climatic and geologic conditions in the region (Karr et al., 1986 and Karr, 1991 in Naiman et al., 1992). The ecologically healthy, or viable, wetlands that existed throughout the islands of Hawai'i prior to human contact likely maintained natural connections between system components. Native biota that was historically characteristic of Hawaiian wetlands filled environmental niches necessary to sustain the ecosystem.

Resilience is defined as the amount of disturbance that the system can absorb without a change in structure and composition (Holling, 1973; Carpenter et al., 2001). Disturbance in wetlands and water bodies include natural forces such as floods and droughts. Due to hydrogeomorphological characteristics (water easily replaced via rain/groundwater), early stages of succession (lack of trees, pioneer species easily replaced) and highly adapted flora and fauna (avian dispersal, floating seeds, and root systems), "healthy" wetland and water bodies have an increased capacity (high resiliency) to be able to recover from such stochastic and natural events.

Redundancy refers to the extent and range across a given landscape. Redundancy from having multiple resilient wetlands and water bodies can decrease the risk of loss. Wetland sub-types with few occurrences across the islands are less resilient to catastrophic events that might otherwise have a relatively minor impact on those that are widely-distributed (Stacey and Taper, 1992). Hawai'i has limited wetland resources due to its unique hydrogeomorphological characteristics. However, it can be assumed that there were more wetlands spread across the islands before humans arrived, resulting in a higher level of redundancy.

Although historical data are lacking, representation of wetlands and mid to low elevation water bodies in their historical state (pre-human contact) likely entailed a high level of diversity that was duplicated from unit to unit. Compared to lower elevation open water bodies and wetlands, high elevation open water bodies in their historical state likely maintained a lower level of floral and faunal diversity. It can be assumed that adaptation related to the high diversity of native wetland and water body biota that evolved specifically in the tropical environment increased the ability to persist.

The primary driving factor for maintaining a high level of representation for wetlands is related to dispersal and connectivity. Connectivity refers to the ability of plants and animals to move between habitat patches on the landscape (Hanski, 1998; Tischen-dorf and Fahrig, 2000). Wetland and open water body connectivity (both structural and biological) is a dynamic process involving wetting and drying cycles that result in a varied frequency of habitat patches being connected by water (Morris, 2012). Floods are particularly important for dispersal of vegetative propagules (plant structures such as fragmented runners or seeds) into streams, which may then be dispersed in floodwaters to distant sites. Buoyant propagules are usually dispersed farther than those that sink. Biological connectivity is maintained through dispersal and considers whether species can move to similar or other suitable habitat. Species mobility varies and results in different rates, patterns and scales of biological connectivity on the landscape (Taylor et al., 1993).

Wind, water, and birds are the most important natural dispersal vectors in aquatic systems. Wind-mediated seed dispersal is more effective in connecting wetlands that are close together and aligned with the direction of the prevailing winds (Morris,

Table 6 Levels of resiliency, redundancy, and representation for wetland and open water bodies that existed in the Hawaiian archipelago prior to human contact.

<i>Sub-type</i>	<i>Resiliency</i>	<i>Redundancy</i>	<i>Representation</i>
<i>Wetland</i>			
Upland Bogs, Marshes, and Swamps	High	Low	High
Lowland freshwater and saline marshes and estuaries	High	Medium	High
<i>Open water bodies</i>			
Fresh and saline lakes	High	Low	High
Anchialine pools	High	High	Low

2012). Waterbirds are capable of dispersing propagules and eggs of invertebrates that become attached to the feet, feathers or bill, or are consumed and survive passage through the gut. Aquatic invertebrates with wings can also disperse to and populate similar wetland habitats. Water moving between existing water bodies via surface or underground flow can also carry propagules, eggs, and flightless adult and larval forms of aquatic invertebrates.

Table 6, provides a summary of the viability of wetlands and open water bodies in their historical state. These values are assumed based on what is known about them in their native state. For instance bogs and lakes likely recovered quickly from storms and were well-represented via species and genetic diversity. However, there were relatively few bogs and lakes spread across the archipelago and therefore had low redundancy. In contrast, anchialine pools were fairly widespread and well-connected, but contained less biological diversity and thus had lower representation.

Change From Historical Condition

Around 800 AD Polynesians first colonized the Hawaiian islands (Vitousek et al., 2004) and altered wetlands and open water bodies that could be best used for agriculture and fishing (Armstrong, 1983). Despite these habitat modifications by early Hawaiians, many areas of extensive wetlands remained intact and were still utilized by the native fauna (USFWS, 2011).

Fishponds were built to control water flow for the purposes of growing and harvesting fishes, algae, crabs, and shrimp (Table 7). Over 350 fishponds of various kinds have been identified on the eight major Islands. (Apple and Kikuchi, 1977 in Stone, 1989). Fishponds were apparently not developed by other pre-contact cultures of the Pacific but were used especially from the 14th to 19th centuries in Hawai'i (Kikuchi, 1976). At the peak of the pre-European contact era, in approximately 1600 AD, almost all sizable saline and brackish water bodies in the main Hawaiian islands were being used as fishponds (Kikuchi, 1976).

Many low-to-mid elevation freshwater wetlands, upslope from these fishponds, were used for agricultural production of *Colocasia esculenta* (kalo, taro). Valeros and O'Neil (2019) describes the Hawaiian irrigated farming systems which started around the 15th century. Forests above these wetlands such as Kawai Nui Marsh and Kahana Bay (island of O'ahu), Hanalei Valley (island of Kaua'i), and Waipi'o Valley (island of Hawai'i) may have been removed partly to encourage erosion of upland soils into lowland wetland areas used for kalo cultivation (Spriggs, 1985; Stone, 1989). By 1778, kalo was cultivated in nearly every valley in the main Hawaiian islands that contained a stream (Handy and Handy, 1972; Kirch, 1982). As such, it has been proposed that Polynesians actually increased the extent of wetland ecotype in the islands (Stone, 1989). Some of these sites, such as Ke'anae (island of Maui) and Waipi'o (island of Hawai'i), still cultivate kalo today.

The arrival of Westerners starting with British Captain James Cook's expedition in 1778 triggered drastic changes for the Hawaiian culture. Around 1835, plantation sugarcane cultivation led to more extensive stream diversions by transferring large volumes of water out of natural watercourses and into complex systems of ditches, tunnels, flumes, and reservoirs (Wilcox, 1996). The last sugar mill closed in 2016 on the island of Maui (Keany, 2016).

Table 7 Types of Hawaiian fishponds (Kikuchi, 1976).

<i>Fishpond type</i>	<i>Description</i>
Shore ponds or salt water ponds (<i>loko kuapa</i> and <i>loko 'umeiki</i>)	Kuapa were made either by extending a semicircular wall from the shore into the sea and hack to shore, or by walling off the narrowest part of an entrance to a small bay or inlet. <i>Loko 'umeiki</i> were "surrounded by a low wall that is submerged at high tide and has openings walled on each side like lanes, leading in or out of the pond."
Inland ponds or brackish and freshwater ponds were divided into three categories: <i>loko pu'uone</i> (not fresh water), <i>loko i'a kalo</i> , and <i>loko wai</i> (fresh water)	<i>Loko pu'uone</i> were usually connected to the sea by a ditch or stream. <i>Loko i'a kalo</i> were the "taro fish ponds," and <i>loko wai</i> were natural ponds (Summers, 1964 in Stone, 1989)

During this time, many kalo lo'i were converted to rice paddies as a result of a predominately Asian plantation workforce. In 1899, Hawai'i was the third-largest producer of rice in the United States. In 1907, rice plantings covered 3804 watery hectares and produced 42 million pounds of rice. By 1930 most of the Hawaiian fishponds and kalo lo'i had been abandoned (Kikuchi, 1976), drained and filled for dryland agriculture (Stone, 1989; Meier et al., 1993). The last rice mill in Hawai'i, Haraguchi Mill, closed in 1960 (Adams, 2005).

Starting in the early 1900s, the most extensive lowland wetland and open water body subtypes, such as fresh and saline marshes (USFWS, 2010) (Table 8) along the coast were filled or otherwise modified. Areas such as Wai Momi "Waters of Pearl, Pearl Harbor" (island of O'ahu) is said to have had the most fishponds along its shores throughout the State before development in the early 1900s began of what is now Joint Base Pearl Harbor-Hickam (NPS, 2019). In the early 1900s, Waikiki was still a vast lowland marshland encompassing >809 ha which was used for kalo lo'i, fishponds, rice paddies, and duck ponds (Young, 2013). By 1920, Waikiki was drained and filled with dredge material from the Ala Wai Drainage Canal creating dry land for today's Waikiki.

Rapid population growth and urban development after World War II resulted in additional demands for water and land (van Rees and Reed, 2014; Stone, 1989).

A significant amount of what were previously wetlands across the State are now occupied by hotels, housing developments, golf courses, shopping centers, landfills, military installations, highways, former sugarcane fields and settling ponds, and industrial sites.

Lowland wetlands and open water body subtypes have also been hydrologically altered to control flooding in urban areas. Modifications such as stream channelization redirect flow and prohibits this water source from infiltrating lower-elevation wetland and open water body subtypes. Lowland wetlands subtypes are among the most vegetatively degraded of all wetlands habitat types. A few small areas still persist and mostly consist of invasive *Brachiaria mutica* (California grass) and a few patches of native *Schoenoplectus californicus* (kaluhā or bulrush). Kawai Nui is the State's largest remaining marsh (336 ha).

Nonnative mammals have greatly impacted the native vegetation in wetland and open water body subtypes. The first introductions of nonnative mammals arrived with Polynesians around 400 A.D consisting of pigs (*Sus scrofa*), dogs (*Canis familiaris*), and rats (*Rattus* spp.) (Kirch, 1982). The Cook expedition and subsequent explorers traveled with livestock such as pigs, goats, and cattle to serve as food sources for seagoing explorers (Tomich, 1986; Loope, 1998). They were also offerings to Hawaiian Royalty. The mild climate of the islands, combined with the lack of competitors or predators including hunting restrictions by Hawaiian law, led to the successful establishment of large populations of these invasive mammals, to the detriment of all native Hawaiian species and their habitats.

Lake Laysan has varied in depth over the last century. Impacts of guano mining starting in 1891 and extreme defoliation of the island by rabbits released in 1903 caused drifting sand to fill in portions of the hypersaline lake and its proximal freshwater seeps (Ely and Clapp, 1973). In the 1860s, the lake was at most 9.1 m deep, but by the 1920 it averaged 0.91–1.52 m deep, because of the buildup of sand that had been blown in by sand storms (Rauzon, 2001). Professor William Alanson Bryan estimated 10 million seabirds on Laysan in 1903, but 8 years later, the estimation was at little more than a million. In those 8 years, the Pritchardia palms, unique to Laysan, and the island's *Santalum ellipticum* (sandalwood trees) both became extinct. By 1918, the rabbits had eaten so much that the remaining vegetation was only enough to sustain 100 rabbits. Twenty-six plant species had been eradicated, and the Laysan millerbird (*Acrocephalus familiaris familiaris*) gone extinct (Rauzon, 2001).

The USFWS has been working towards eliminating invasive species on the island of Laysan. The vegetation including native bunchgrass has rebounded and native sedges grow thick around the lake's edge. The island is now home to 15 species of endemic insects, the Laysan duck (*Anas laysanensis*), the rarest duck in the world (Liittschwager and Middleton, 2005), the Laysan finch (*Telespiza cantans*), the Laysan millerbird (since translocated by USFWS in 2011 and 2012), and 18 other bird species that nest here and use Lake Laysan, the only lake in the NWHI. Once extirpated from Laysan, many native plant species, such as *Eragrostis variabilis* (kawelu or lovegrass), were reintroduced from other leeward islands (Liittschwager and Middleton, 2005).

Due to their upland, remote locations, montane bogs, upland marshes and swamps have maintained a relatively intact native vegetation community. Being more abundant than bogs, some upland marshes and swamps are transitioning from a native to a nonnative dominated vegetation community (Table 9). Lowland saline marshes are now represented by a rather thickly-growing, species-poor plant community, dominated by *Batis maritima* (pickleweed) and occur in muddy lowland wetland and open water body subtypes periodically flooded by saltwater. Pickleweed was first reported in the Hawaiian islands in 1859 by Hill-ebbrand (1888) and has since spread widely, likely displacing native communities (Gagne and Cuddihy, 1999). Examples occur at Kealia and Kanahā ponds on Maui.

Due to the remote location of Wai'ele'ele and Kauhakō, the terrestrial flora and fauna around the lakes and the aquatic flora and fauna inside the lakes have maintained a relatively intact native community. Although remote, changes at these lakes are being studied and monitored at Lake Waiau by U.S. Geological Survey and Lake Kauhako (cycling process) by NPS. Nōmilu, near the

Table 8 Examples of lowland freshwater marshes in the Hawaiian islands.

Island	Place names
Hawai'i	Pololū, Waimanu, and Waipi'o valleys
O'ahu	Kawai Nui, He'eia, (including Ki'i, Punamanō, and Punaho'olapa), and 'Uko'a Marsh
Kaua'i	Hanalei and Mānā

Table 9 Upland swamps in the Hawaiian islands (Polhemus, 2015).

Location	Description of upland swamp
Windward Mauna Kea, Hawai'i	This area contains closed canopy forest, with a sphagnum moss understory. Some areas have been degraded by cattle grazing, leading to development of artificial upland marsh zones dominated by introduced grasses
Pu'u o Umi, Hawai'i	Located at the summit area of the Kohala Mountains, this swamp exists at a lower elevation than is typical for such ecosystems in Hawai'i
Windward Haleakalā (uluhe swamp), Maui	This is a large area of discontinuous hydric soils thickly overgrown by <i>Dicraopteris linearis</i> (uluhe fern) and scattered with 'ōhi'a and <i>Acacia koa</i> (koa)
Mt. Ka'ala, O'ahu	The flat summit of Mt. Ka'ala supports a swamp formation dominated by low stature 'ōhi'a and <i>Cheirodendron trigynum</i> ('olapa). The largest dragonfly species in the United States, pinao, (<i>Anax strenuus</i> var. <i>kaenana</i>), and several species of native tree snails can also be found here
Ka'au Crater, O'ahu	Appears to have once held a lake that has subsequently been disturbed by human activity and weed invasion. The currently dominated by the indigenous sedge, <i>Cladium jamaicense</i> ('uki), mixed with <i>Schoenoplectus lacustris</i> ('aka'akai), and <i>Commelina diffusa</i> (honohono) and has no open water (Gagne and Cuddihy, 1999; Polhemus, 2015)
Alaka'i Swamp, Kaua'i	The Alaka'i Plateau in the central interior of Kaua'i contains an extensive upland swamp at elevations ranging from 1288 to 1585 m. Rainfall on the plateau is in excess of 5000 mm per year (one of the wettest spots on earth) (Giambelluca et al., 2013), and accumulates in various irregularities amid the terrain and in pockets at the bases of tree roots. The Alaka'i Swamp suffered a significant loss of canopy cover during Hurricane Iniki in 1992, and has only partially recovered. The opening of the canopy has allowed a certain amount of drying to occur, and there seems to be a general consensus among researchers familiar with the area that the overall character is not as wet and saturated as previously. Some classify the swamp as a montane wet forest containing extensive shallow bogs

seashore, shares similar terrestrial plant composition from transition from a native to a nonnative community as lowland fresh and saline marshes and estuaries.

Other currently known open water bodies that are not considered a lake by definition includes: Halulu Lake on the island of Ni'ihau; Violet Lake, Wai'anapanapa, and Kanahā Pond on the island of Maui; Meyer Lake on the island of Moloka'i; and Waiakea Pond and 'Aimakapā on the island of Hawai'i (Maciolek, 1982). All of these have features that are considered to represent wetland subtypes (Table 1).

There are currently an estimated 700 or so anchialine pools found throughout the archipelago, although they are most abundant on the islands of Hawai'i and Maui (Yamamoto et al., 2015). Prior to arrival of Westerners, Hawaiians used anchialine pools as potable water sources, bathing pools, and fishponds. As a result, many of the anchialine pools show evidence of cultural modification, by either Polynesians or modern humans (Maciolek and Brock, 1974). Anchialine pools throughout the State of Hawai'i have steadily become susceptible to degradation from human-induced factors. A majority of these pools have become ecologically degraded and their native biota drastically altered from its pristine conditions (Brock, 1985). Approximately one-third of the anchialine pools in the district of South Kohala on the island of Hawai'i have been destroyed by hotel development (Stone, 1989).

Artificial reservoirs often duplicate the processes and function occurring in natural wetlands and can be complex systems in which water, plants, animals, microorganisms and the environment (sun, soil and air) interact. These bodies of water can attract plant growth and wildlife while also being used for recreational purposes such as boating and fishing. Reservoirs in Hawai'i are usually created by damming the downstream end of a drainage basin. These dams and reservoirs frequently interrupt normal sediment transport processes in rivers and stream systems and affect water temperature and quality (i.e., dissolved oxygen, acidity, salinity, turbidity, temperature). Transport and assimilation of nutrients, amount of in-stream organic matter and related decomposition, channel morphology, habitat quality for native aquatic species, and riparian vegetation recruitment and survival are also affected. Water quality can range from good to poor, with water levels ranging from stable to fluctuation. In Hawai'i, the first reservoirs were constructed on sugar plantations for irrigation and domestic uses by plantation workers. Reservoirs are still used today in Hawai'i for many different purposes (Table 10).

Current Extent and Range

The last comprehensive wetland inventory for all of the islands in the State of Hawai'i was completed in 1979 by the USFWS (Cowardin et al., 1979). To this day, there is no completely accurate map available for Hawai'i's wetlands although various attempts have been made.

Kosaka (1990 *in litt.*) and van Rees and Reed (2014) have made estimates to determine the amount of wetland and open water bodies that have been lost from pre-Polynesian contact and the mid 1900s. These studies indicate the highest wetland loss occurring in the lowland wetland subtypes (at or below approximately 300 m elevation) with majority of it occurring on O'ahu.

Table 10 Use of artificial reservoirs in the Hawaiian islands.

<i>Artificial reservoirs</i>	<i>Impacts</i>
Stockponds	As the number of ranches decreased over the years and agriculturally zoned land changed over to urban zoning, it can be assumed that a number of these stock ponds have been drained and filled in for development. Such ponds often provide habitat for non-native aquatic insect species
Settling ponds (agriculture)	Prior to releasing the “used” water, it was sent to settling ponds before being discharged. The ponds at James Campbell National Wildlife Refuge (NWR) sit on a former wetland that was converted to settling ponds. Today, James Campbell NWR manages these settling ponds to assist in the recovery of threatened and endangered waterbirds and provide protected habitat for migratory shorebirds and waterfowl
Wastewater treatment ponds	May not provided similar vegetative composition and density to other wetlands as a result of a polyurethane lining. However, with the buildup of enough sludge material and algae, aquatic plants can become established
Golf course water feature	If the golf course is near a stream or wetland, water features can flow directly into the stream or wetland carrying high nutrient loads and other contaminants. Even so, certain golf course water features, such as those in upland Lanai, can provide documented habitat for rare native damselfly species
Cultivation of aquatic foods	This started Hawai'i started with the native Hawaiians for kalo loi and fish ponds. Since then, food harvest has expanded to include taro, rice, lotus, prawns, shrimp, and other fish species. Many of these fields/ponds were in or near the outskirts of urban areas. The majority of these wetlands occur on O'ahu, particularly in the area near Kahuku. The industry reached its peak in the mid-1980s, then declined, but is currently increasing again in volume (Mencher, <i>in litt.</i> 2005)
Bomb crater	Sailor's Hat is an artificially created anchialine pool on the south coast of the island of Kaho'olawe. In 1965, the Navy bombed the area and it left a crater 50 m in diameter with a 5-m-deep pool at the bottom (Brock and Bailey-Brock, 1998)

Reeves and Amidon (2018a,b) looked at present distribution of the following wetland subtypes: bogs, upland marshes and swamps, lowland fresh water and saline marshes, estuarine, and open (fresh and saline) water inland of the sea shoreline in the main Hawaiian islands (Figs. 1–4 and Table 11).

The largest wetlands lost over the past century were on O'ahu and include: Waikīkī, Pearl Harbor, Ka'elepulu (now Enchanted Lake), and Ālia pa'akai (Salt Lake). The 1.2 ha Ka'elepulu Wetland Preserve is a small, privately-owned, preserve set aside in 1955, is a remnant of the once expansive Ka'elepulu wetland. The Mānā Plains on Kaua'i, once the largest wetland in Hawai'i at over 650 ha (c. 1910), was reduced to only 80 ha by 2006 primarily due to water diversions for sugarcane (Shallenberger, 1977; Erickson and Puttock, 2006). Within these last 80 ha, 14 ha are designated the Mānā Plain Forest Reserve (formerly the Kawai'ele Waterbird Sanctuary). The greater Mānā Plains area is also an important wetland area due to remaining scattered ephemeral (temporary) wetlands and a Navy wastewater treatment facility (Nadig, 2017, pers. comm.).

Four hundred-year-old Green Lake, located at the bottom of a crater in the Kapoho area on the island of Hawai'i, was considered the largest freshwater lake in Hawai'i (Macdonald and Abbott, 1970). On June 2, 2018, volcanic activity along the East Rift Zone of the active Kilauea volcano fed a channelized lava flow that entered Green Lake, boiling and evaporating the water. Within 5 h of lava entering Green Lake, lava filled the lake and no water remained (USGS, 2018).

Stressors

In the Hawaiian archipelago, wetlands and open water bodies experience a multitude of stressors including those related to human presence and abundance, and climate (Table 12).

Development and Altered Hydrology

Alterations in ground and or surface water due to development (residential, commercial, agricultural, and military) has resulted in wetland subtype losses. In Hawai'i, this ranges from water diversions, discharging fill, building dams, channelizing, pumping, grubbing, grading, deep ripping, and other agricultural or military land use practices (Erickson and Puttock, 2006). Urbanization of many of Hawai'i's lowland wetland subtypes occurring in coastal areas are highly valued for development, especially on the islands of O'ahu and Maui, but is increasing on all islands (Kane, 2014).

The primary demand for surface water over the past two centuries has changed overtime from agricultural to commercial and residential usage. The Hawai'i streams manuscript has a more extension write up on the impacts to surface flow.

The depletion of freshwater aquifers causes saltwater intrusion into coastal groundwater, altering the salinity levels in associated wetlands subtypes and thus decreasing the amount of available fresh or brackish water. Fluctuations in salinity levels alter the species composition of the vegetation and arthropod communities (M. Silbernagel, pers. com. 2008; [USFWS, 2011](#)).

Surface water is the primary source of water input for many wetland ecotypes, especially in the lowlands. Decrease in surface flow resulting from development can affect the succession rate of a wetland along with changes in the in species compositions. Surface water input from developed areas are also a source of water pollution. Further discussion on surface water can be found in the Hawai'i streams manuscript.

Recreation and Human Access

Due to their remote nature and steep terrain, many of the naturally formed wetlands and open water bodies at higher elevations in Hawai'i are spared from the heavy human access and recreation pressure that those in the lowlands are exposed to. This is likely a contributing factor in the preservation of native-dominated wetland ecosystems. By contrast, most lowland wetlands and open water bodies are significantly impacted by human recreation due to their proximity to urban areas. Natural and artificial lowland wetland and open waterbody subtypes are often used by off-road vehicles and dirt bikes, water sources for domesticated ungulates, golf courses, fishing, and boating. Anchialine pools are often used for bathing, lavatories, and dumping trash.

Water Pollution

The input of pollutants, such as fertilizer, human sewage, animal waste, pesticides and heavy metals can exceed the wetland's natural ability to absorb such pollutants and cause degradation as well as kill invertebrates, fish, birds and mammals. Lowland open water body ecotypes, susceptible to act as sinks for pollutants, which means that pollutants tend to accumulate and potentially increase the toxicity with time. Pollutants can enter the surface and groundwater water through urban and agricultural runoff, air pollution, leakage from landfills and dumps, and boats stirring up pollutants. Urban encroachment has the potential to negatively affect wetlands via flushing of household and industrial products into water-collecting systems (storm drains and roadside ditches) which lead to streams, wetlands, and the ocean. Currently, little is done to survey for toxicants in wetlands except for certain Comprehensive Environmental Response, Compensation, and Liability Act (CERCLA) sites on military bases.

Invasive Animals and Plants

Lowland wetland and many open water bodies ecotypes are mainly dominated by invasive fish which are suspected of degrading the food web by depleting the invertebrate prey base used by native birds ([Wirwa, 2007](#)). Invasive fish are especially problematic for anchialine pools where their waste products plug up water flow preventing proper functioning resulting in the loss of the pool as habitat (Wada, *in litt.* 2018).

Beyond the direct effects of trampling and consuming native plants, feral ungulates contribute significantly to severe erosion of watersheds, increased sediment levels in aquatic systems, and their behavior (i.e., rooting, moving across large expanses) facilitates the spread and establishment of competing, invasive plant species ([Merlin and Juvik, 1992](#)). Bogs are exceptionally vulnerable to destructive root and trampling by feral pigs because of soft, easily dug soils and the succulent plants they contain ([Stone and Stone, 1989](#)). Feral animals also remove riparian plant cover that provide shade, change temperature and light conditions which animals have adapted to, and increase nutrients and soil in water, effectively degrading or destroying habitat for aquatic wildlife ([Stone, 1989](#); [USFWS, 2011](#)).

In 2009, Bantilan-Smith et al. found the composition of plant communities of all wetland types in Hawai'i to be predominantly invasive. Invasive plants outcompete native species and eliminate open water, or shallows ([Griffin et al., 1989](#); [Henry, 2006](#)). The alteration of wetland plant communities due to extensive, blanketing overgrowth of invasive plants can greatly reduce the usefulness of wetland native fauna ([Morin, 1998](#); [Jenkins, 2016, in litt.](#)). *Juncus* species (rush, bog rush) such as *J. effusus* (Japanese mat rush), *J. ensifolius*, and *J. planifolius* are a threat to upland wetland subtypes.

Hawaiian introductions to lowland wetland subtypes included *Hibiscus tiliaceus* (hau), *Thespesia populnea* (milo), *Cocos nucifera* (coconut), and *Ludwigia octovalvis* (primrose willow) ([Athens, 1997](#)). Recent introductions and most frequently observed invasive species include: the non-native pickleweed, *Urochloa* (California grass), *Eichornia crassipes* (water hyacinth), *Pluchea indica* (Indian fleabane), seashore paspalum, and several mangrove species. Invasive grasses such as California grass is found in wet fields, ditches, and gullies between sea level and 700 m. It forms dense monotypic stands by layering from trailing stems. It will overgrow most shrubs and trees in its vicinity.

Mangroves are a group of trees or shrubs that live in the coastal intertidal zone. Five species were introduced to Hawai'i in the early 1900s for the purpose of stabilizing coastal mudflats. *Rhizophora mangle* (American mangrove), *Bruguiera gymnorhiza* (Oriental mangrove), and *Conocarpus erectus* (Silver-leaved Buttonwood) and are now established on nearly all of the major islands ([Allen, 1998](#)). Though considered beneficial in many parts of the world, mangroves have a deleterious effect to wetlands in Hawai'i by forming dense monotypic groves. Many of the anchialine pools along the Kona Coast are overgrown with invasive plants. Humans have brought many plant and invertebrate species to Laysan and other NWHI, notably *Cenchrus echinatus*, an invasive sandbur grass, and ants (family Formicidae).

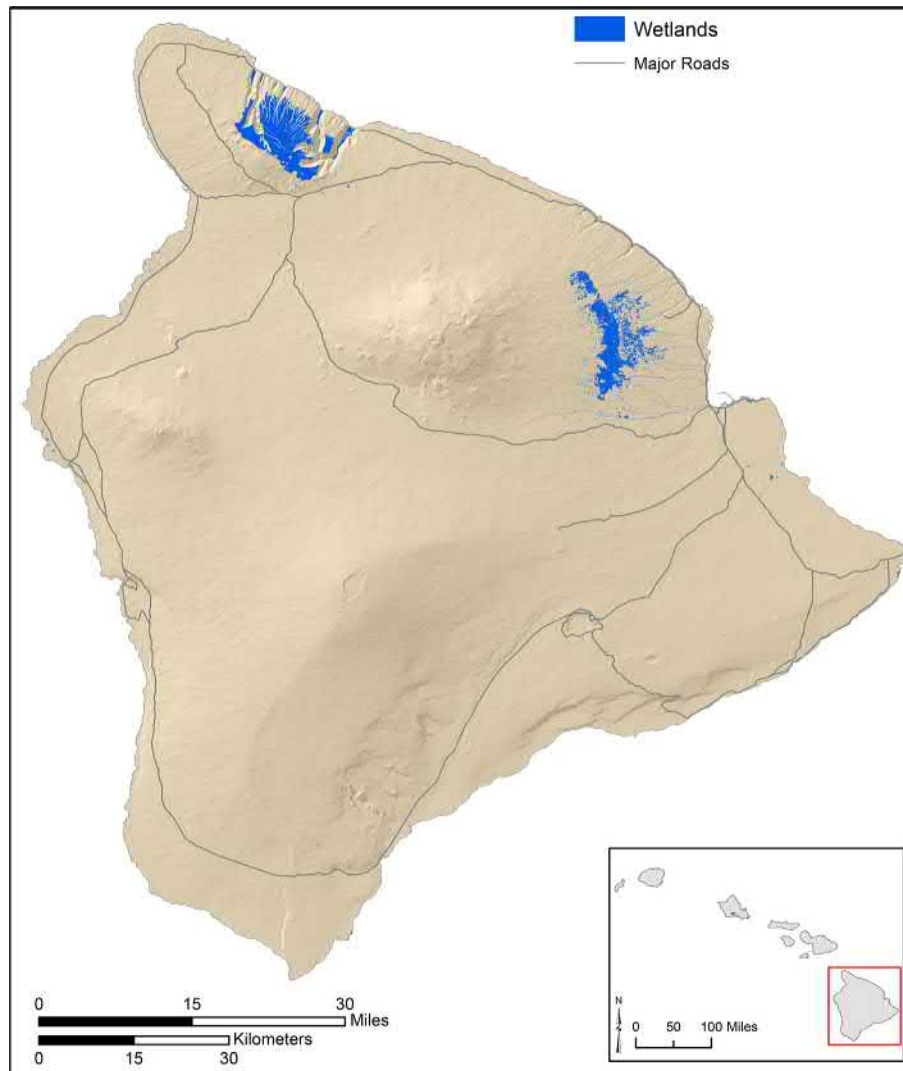


Fig. 1 Representation of wetland and open water body area on the Island of Hawai'i.

Sea Level Rise, Groundwater and Marine Inundation and Flooding

According to global climate models developed by the Intergovernmental Panel on Climate Change, Sea Level Rise (SLR) is occurring globally and is expected to continue into the future. SLR is not expected to be uniform throughout the world, due to factors including, but not limited to (1) variations in oceanographic factors such as circulation patterns; (2) changes in Earth's gravitational field and rotation, and the flexure of the crust and upper mantle, due to melting of land-based ice; and (3) vertical land movement due to glacial isostatic adjustments, sedimentation compaction, groundwater and fossil fuel withdrawals, and other non-climatic factors (Spada et al., 2013 in Kane, 2014; National Oceanic and Atmospheric Administration, 2017). Further, SLR in Hawai'i will not be uniform across the islands due, in part, to vertical land motion resulting from the active growth of the island of Hawai'i (Caccamise et al., 2005 in Kane, 2014; Polhemus, 2015), causing that end of the island chain to become heavier and pushing land below sea level.

Hawai'i's wetlands and a few open water body subtypes, are found just inland of a narrow coastal barrier, are dependent upon ground and marine water sources to maintain water levels and are therefore impacted by SLR in several ways. The size, shape and location of these coastal wetland and open water body subtypes are expected to be modified due to increased flooding inundation. Water chemistry and salinization levels would change due to increased frequency of marine flooding and inundation during storms and high tides. There are several reports that discuss the imminent flooding and inundation of coastal wetlands in Hawai'i due strictly to SLR (Rotzoll and Fletcher, 2012; Kane, 2014; Htun et al., 2016).

The primary source of inundation for lowland wetland subtypes is expected to be from groundwater (Rotzoll and Fletcher, 2012). Rotzoll and Fletcher (2012) define groundwater inundation as "the localized coastal-plain flooding due to the rise of the groundwater table with sea level." As sea level rises, the water table will rise simultaneously, eventually rising above the land surface,

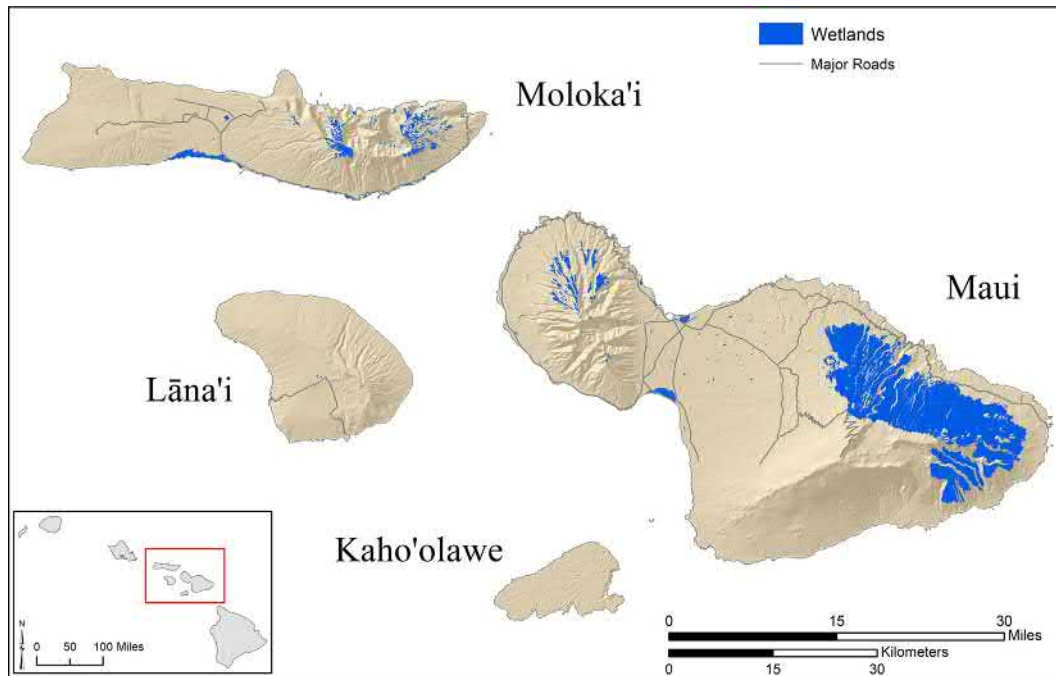


Fig. 2 Representation of wetland and open water body area on the Island of Moloka'i, Lāna'i, Maui, Kaho'olawe.

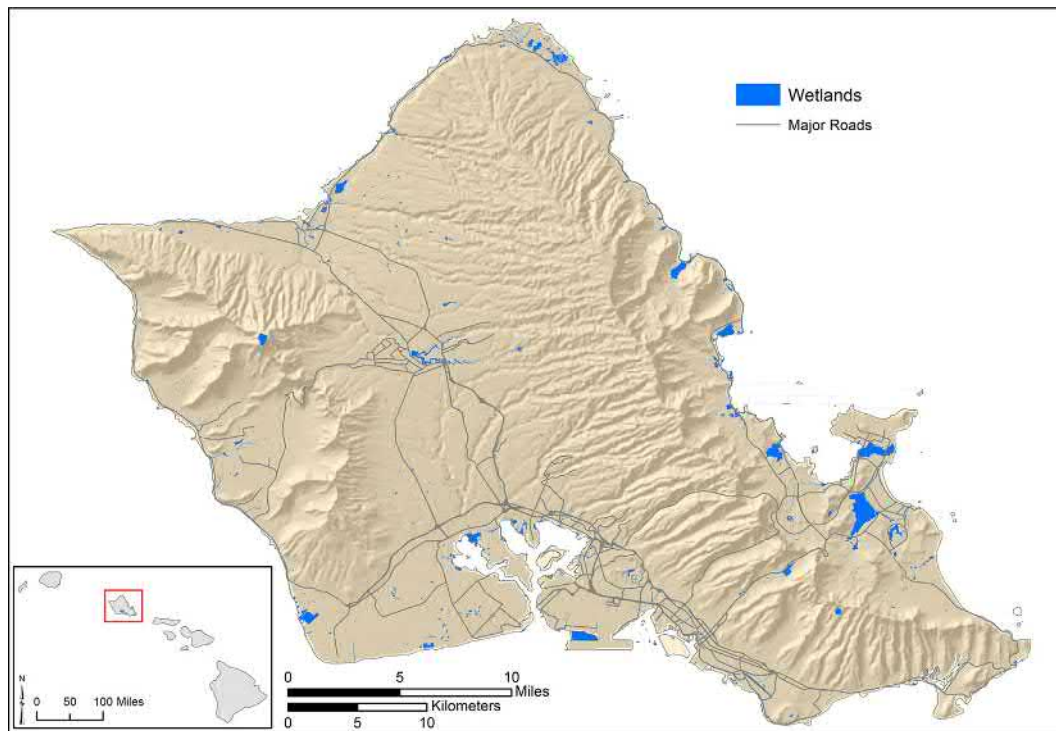


Fig. 3 Representation of wetland and open water body area on the Island of O'ahu.

creating new wetlands, and expanding others, subsequently changing surface drainage, saturate the soil, and inundate land in lower lying areas (Rotzoll and Fletcher, 2012). Groundwater flooding is a faster rate of inundation associated with a sudden rise in the watertable usually as a result of high precipitation rates.

Marine flooding and inundation will constitute a second source of coastal flooding (Kane and Fletcher, 2013). This coastal-plain flooding and inundation is expected to be caused by storm surge (wind driven) and marine overwash (wave driven) resulting from SLR and increases in tropical storm frequency and intensity (Fletcher et al., 1995). This wave action can change coastal

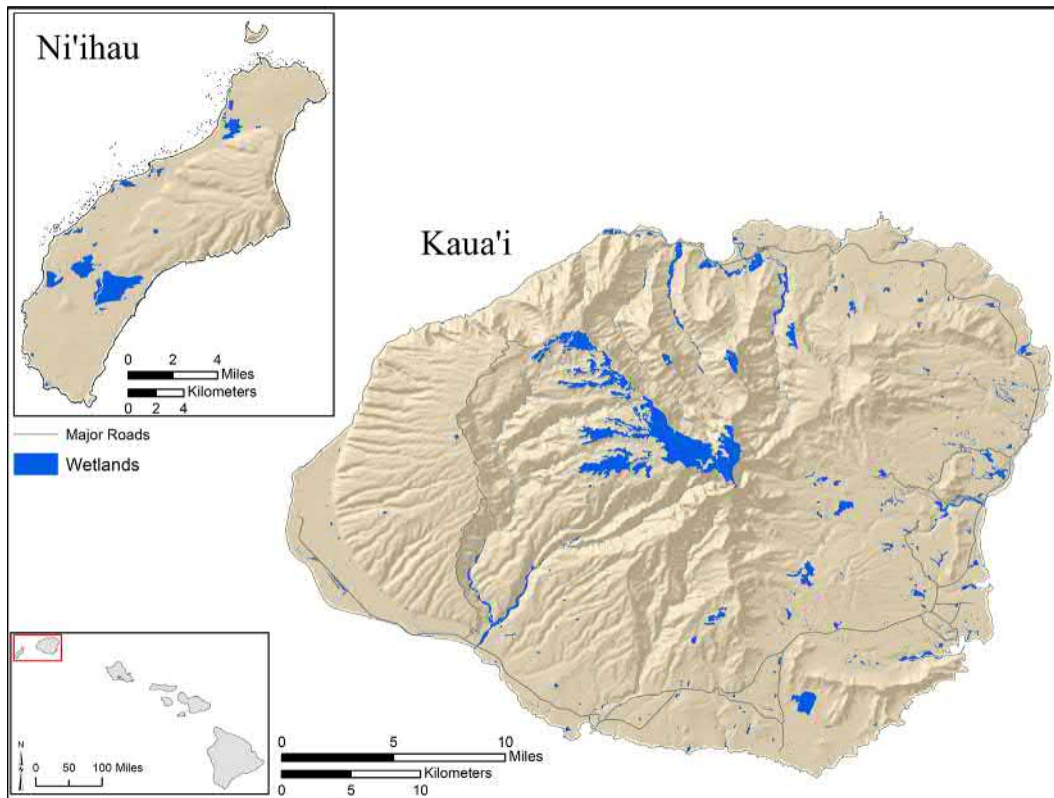


Fig. 4 Representation of wetland and open water body area on the Island of Ni'ihau and Kaua'i.

Table 11 Current distribution of wetland and open water bodies in the main Hawaiian islands (Reeves and Amidon, 2018a,b).

Island	Hectares	Percent of island	Percent of main Hawaiian islands
Hawai'i	478	<1	<1
Maui	736	<1	<1
Lāna'i	18	<1	<1
Moloka'i	468	1	<1
O'ahu	1269	1	<1
Kaua'i	788	1	<1

geomorphology, increasing the flooding risks of the coastal flood-plain (Bernard et al., 2011; Theuerkauf et al., 2014; Lentz et al., 2016, in Sweet et al., 2017).

Once SLR increases beyond 0.74 m, marine inundation will be the dominant source of coastal flooding (Kane and Fletcher, 2013; Polhemus, 2015). Results from recent studies in the main Hawaiian islands suggest estimates on impacts due to SLR have not adequately taken into account the effects of increased frequency and intensity of storm surge and marine overwash which have been grossly underestimated (Storlazzi et al., 2018; Vitousek et al., 2017). In addition to SLR, the islands are projected to experience more severe annual marine overwash flooding events. Increasing SLR, wave intensity, and flooding will continue to contribute significantly coastal erosion increasing the vulnerability of low-lying wetlands to morphological and chemical changes as coastal barriers are eroded. According to a study of the three most populated islands (Maui, O'ahu, and Kaua'i), approximately 70% of all sandy shorelines are chronically eroding (Fletcher et al., 2013).

Some of the most vulnerable lowland wetlands in Hawai'i have no sand dunes or very narrow and low sand dunes, such as Pala'au, south shore on the island of Moloka'i and Keālia National Wildlife Refuge on the island of Maui. Marine inundation is expected to overtake the impacts of groundwater inundation around 2040 (Kane and Fletcher, 2013; L. Jenkins *in litt.* 2016). The critical elevation at Keālia NWR (Maui) at which SLR impacts will rapidly accelerate is 0.2 m and is predicted to be exceeded by year 2028 ± 25. Other lowland wetlands are predicted to experience accelerated inundation at 0.6 m by year 2066 ± 16 (Kānaha State Wildlife Sanctuary on Maui and James Campbell NWR on O'ahu) (Kane, 2014).

Urbanization directly adjacent to coastal wetlands, or surrounding wetlands as is the situation at Kānaha Pond State Wildlife Sanctuary, will limit or prohibit coastal wetlands from a natural landward migration (Clausen and Clausen, 2014 in Kane,

Table 12 Primary stressors affecting wetland and open water bodies.

<i>Human presence/abundance</i>	<i>Climate</i>
Development and altered hydrology	Sea level rise, groundwater and marine inundation and flooding
Recreation and human access	Storms
Water pollution	Drought and increasing air temperature
Invasive animals and plants	

2014). In addition, any managed wetland ecotype near the coast will need to consider the impacts of flooding to surrounding communities and infrastructure such as bordering roads and sewage treatment facilities (Kane, 2014).

Other coastal water bodies, such as anchialine pools, are highly susceptible to the same climate impacts affecting lowland wetland subtypes with no significant barrier from the ocean. Anchialine pools have become tide pools and new pools have been created further inland at Manuka Natural Area Reserve on the island of Hawai'i over the past several years.

Storms and Tsunami

Increased frequency and intensity of tropical storms and hurricanes can impact wetlands and water bodies across all elevations. Tsunamis can impact all ecosystems that occur below the highest recorded runup height, which is currently 122 cm, and potentially higher. A tsunami in 2011 scoured some areas down to bare ground, but large areas of native and nonnative plants also survived the initial onslaught at Kanahā Pond on Maui. Salt water inundation can kill any salt-intolerant plants that survive the initial wave (F. and K. Starr, USGS, pers. comm. 2011).

Drought and Increasing Temperatures

Drought may affect aquatic systems through reduced streamflow, evaporation of standing water, increased water temperature, and the loss of native riparian and wetland plants (Still et al., 1999; Benning et al., 2002). Data on precipitation in Hawai'i, shows a steady and significant decline of about 15% over the last 15–20 years (Diaz et al., 2005; Chu and Chen, 2005). Increased air temperatures will also likely contribute to increased water temperatures. Shifts in vegetative composition, increased risk of forest encroachment, accelerated decomposition rates, and altered peat accumulation are all potential impacts to wetland and open water bodies due to increased temperatures.

Conservation Efforts

In general, the “protection” and active management of invasive species and water resources in wetlands and open water body subtypes are primarily for the management of wildlife conservation, flood control, and protection and usage of cultural sites. This is accomplished through cooperative efforts of State and Federal agencies, watershed partnerships, private organizations, and individual landowners and passive/social management through policies, laws, and other land protection. Wetlands identified as “protected” are those considered secure from development.

Starting in the mid 1900s, lowland wetland and open waterbody subtypes were being protected for the conservation of Hawaiian waterbirds (USFWS, 2011). Conservation and protection involves not only buffering wetlands from direct human pressures, but also maintaining important natural processes that operate on wetlands from outside, which may be altered by human activities. In many cases, active management also does not fully restore or reestablish a wetland to pre-disturbance functions and related physical, chemical and biological characteristics. Management can include invasive (plants and animals) species control or removal and manipulation of water resources to maximize vegetative and open water habitat for different life stages of waterbirds.

Wetlands such as Kawai Nui marsh are recognized by the State as a flood control basin whose water holding capacity continues to decrease as sediments from urban runoff are deposited in the marsh and associated waterways (House Bill 1218 (2017)). Hawaiian renaissance has contributed to an increase in revitalizing old kalo lo'i and fishponds for community and commercial usage. Kaloko-Honokohau National Historical Park is currently undergoing intensive restoration of 16 ha at 'Aimakapā Fish Pond including wetland vegetation (NPS, 2015).

The Wetlands Reserve Program may be one of a few activities to specifically protect, restore, and enhance wetlands. Originally authorized under the 1990 Farm Bill, it was later replaced by the Agricultural Conservation Easement Program in 2014.

Laws and Regulations

Several Federal and State Laws and regulations are in place to protect wetland and open water bodies (Table 13).

Table 13 Federal and State Laws and Regulations impacting wetlands and open water bodies.

<i>Title</i>	<i>Year implemented</i>	<i>Authority</i>	<i>Intent/purpose</i>
Executive Order 1019	1909	Federal	Bird Reserve designation for protection in the NWHI except for Midway (which was under U.S. military jurisdiction)
Presidential Proclamation 2416	1940	Federal	Creation of Hawaiian Islands National Wildlife Refuge
Clean Water Act	1972	Federal	Establishes the basic structure for regulating discharges of pollutants into the waters of the United States and regulating quality standards for surface waters
Endangered Species Act	1973	Federal (USFWS and NMFS)	Protects critically imperiled species and their habitats from extinction
50 CFR 16	1974	Federal	Implements the Lacey Act (18 USC 42), which prohibits importation of injurious species
Convention on International Trade in Endangered Species	1975	International	Ensures that international trade in specimens of wild animals and plants does not threaten the survival of the species in the wild
Executive Order 11987	1977	Federal	Charges Executive agencies with restricting the introduction of exotic species into the natural ecosystems on federal lands; and encourages States to do the same
Executive Order 11988	1977	Federal	Requires federal agencies to avoid to the extent possible the long and short-term adverse impacts associated with the occupancy and modification of flood plains and to avoid direct and indirect support of floodplain development wherever there is a practicable alternative
Hawaii Administrative Rules, Title 4, Subtitle 6, Chapters 68 and 70	1981	Hawaii (Department of Agriculture)	Rules/amendments for noxious weeds, plant and non-domestic animal quarantine, plant import, and bromeliad import
Executive Order 13022	1996	Federal	Creation of Midway Atoll National Wildlife Refuge
Executive Order 13112	1999	Federal	Requires that a Council of Departments dealing with invasive species be created to prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause
HRS 194-2	2002	Hawaii (Department of Land and Natural Resources)	Establishes Hawaii Invasive Species Council (HISC)
Act 85	2003	Hawaii (HISC)	Conveys statutory authority to HISC to continue to coordinate approaches among the various State and Federal initiatives for the prevention and control of invasive species
HRS Chapter 205A for Coastal Zone Management	2006	Hawaii (DLNR)	To preserve, protect, and where possible, to restore the natural resources of the coastal zone of Hawaii
Presidential Proclamation 8112	2006	Federal	Creation of Papahānaumokuākea Marine National Monument. Designated a World Heritage site in 2010
Act 36 (2011) HRS 150A-5.3	2011	Hawaii (DOA)	Imposes a fee for the inspection, quarantine, and eradication of invasive species contained in any freight brought into the State
HB 1568	2011	Hawaii (DOA)	Requires commercial harbors and airports in Hawai'i to provide biosecurity and to facilitate cargo inspections
HRS 174C Hawaii State Water Code	2013	Hawaii (CWRM)	Establishes Commission on Water Resource Management and Water Resource Management Fund
Executive Order 13751	2016	Federal	To prevent the introduction of invasive species and provide for their control, and to minimize the economic, plant, animal, ecological, and human health impacts that invasive species cause (amends EO 13112)
HB 2593 (amendment to HRS 91)	2018	Hawaii	Promotes the humane treatment of feral cats (HRS 91 allows agencies to adopt emergency rules in instances of imminent peril to public health, including livestock and poultry health)
7 CFR 360.200	2018	Federal	Designates certain plants as noxious weeds

- Executive Order 11990—Protection of Wetlands—authorized in 1977; requires federal agencies, in planning their actions, to consider alternatives to wetland sites and limit potential damage if an activity affecting a wetland cannot be avoided.
- 1987 State Water Code—The State of Hawai'i manages the use of surface and groundwater resources through the Commission on Water Resource Management (Water Commission), as mandated by the 1987 State Water Code (State of Hawai'i, 1987; DLNR, 1988a,b). However, in the State Water Code, there are no formal requirements that project proponents or the Water Commission protect the habitats of fish and wildlife prior to issuance of a permit to modify surface or groundwater resources. The State of Hawai'i considers all natural flowing surface water (streams, springs, and seeps) as State property (State of Hawai'i, 1987), and the Department of Land and Natural Resources (DLNR) has management responsibility for the aquatic organisms in these waters (State of Hawai'i, 1992).
- The Endangered Species Act of 1973 (ESA)—Protects critically imperiled species and their habitats from extinction. Wetlands and water bodies in Hawai'i provide habitat for many endangered plant, insect, and water bird species, and as a result receive protection through the ESA, and in particular, the protection of critical habitat for these listed species. Restoration efforts are often centered around these high quality habitats and therefore are not declining as rapidly as surrounding areas that lack these species and associated protections.

Despite the efforts of more than 20 State, Federal, and private agencies, unwanted invasive species are entering the State of Hawai'i at an alarming rate—about 2 million times more rapidly than the natural rate (CGAPS, 2009). In 1993, the Federal Office of Technology Assessment declared the State of Hawai'i's invasive species problem the worst in the nation. The State of Hawai'i's evolutionary isolation from the continents and its modern role as the commercial hub of the Pacific render the islands particularly vulnerable to habitat destruction by invasive species.

Summary of Interactions and Conservation Efforts

The primary stressors to wetlands include habitat loss and destruction caused by development, coastal flooding and inundation, introduction of invasive plants and animals, and contamination (Table 14). These stressors are significant and ongoing, act in concert with other stressors, and are expected to continue or increase in magnitude and intensity into the future without effective management actions to control or eradicate them. Current conservation efforts taken by Federal, State, private, and multiple agency partnerships combined with certain laws and regulations limit some of the effects of the stressors on wetland and open water bodies, but do not eliminate them. The stressors continue to contribute to the further increase of development, loss of species diversity, and loss of water resources. Without heightened levels of intensive and active management, wetlands and open water bodies will continue to be degraded and destroyed.

Of all of the wetland and open water bodies, those in low-elevation locations are most susceptible to major decreases in resiliency and representation due to human and climate-induced stressors. Though it is plausible that some of these habitats could see an increase in redundancy due to climatic stressors (expansion due to flooding and SLR), the plant and animal species found here have experienced reductions in numbers of populations and individuals which in turn reduces their representation. This leads to less resiliency to threats and stochastic events, and makes them vulnerable to future extirpation. The current level of ongoing conservation efforts at lowland wetland and open water body subtypes are not enough to keep them from continuous degradation. The low-lying subtypes near the coastline are also most vulnerable to expansive geomorphological changes caused by increased flooding events and SLR. Anchialine pools adjacent to the coastline could be completely lost. Although huge conservation gains have been made at Laysan Lake, this habitat is incredibly vulnerable to the effects of SLR and increased frequency of storms and flooding (USGS, 2013). There is little mitigation that can be implemented at this point to stop these inevitable impacts.

Table 14 Levels of resiliency, redundancy, and representation for wetland and open water bodies when exposed to current stressors compared to viability in their historic state.

<i>Sub-type</i>	<i>Stressor</i>	<i>Resiliency</i>	<i>Redundancy</i>	<i>Representation</i>
<i>Wetland</i>				
Upland bogs, marshes, and swamps	Human presence/abundance	Slight decrease	No change	Slight decrease
	Climate	Slight decrease	No change	Slight decrease
Lowland freshwater and saline marshes, and estuaries	Human Presence/Abundance	major decrease	decrease	major decrease
	Climate	major decrease	potential increase	major decrease
<i>Open water bodies</i>				
Fresh and saline lakes	Human presence/abundance	Decrease	No change	Decrease
	Climate	Decrease	Little change	Decrease
Anchialine pools	Human presence/abundance	Major decrease	Major decrease	Major decrease
	Climate	Major decrease	Major decrease	Major decrease
Ponds and artificial reservoirs ^a	Human presence/abundance	n/a	Major increase	n/a
	Climate	n/a	n/a	n/a

^aArtificial reservoirs were not historically considered a water body. However, there has been a major increase across the islands since pre-human contact.

Increased levels of restoration and conservation efforts such as fencing, ungulate control, invasive species management, and out-planting at high-elevation wetland subtypes has the potential to maintain the current native status or even reverse any ongoing degradation occurring for these habitats. Ponds and artificial reservoirs are the least susceptible to any of the discussed stressors and are therefore most likely to maintain their current level of viability.

Future Scenarios

The condition of wetlands and open water bodies in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are as follows:

- (1) Conservation values: stakeholder involvement and public opinion determine the formulation, implementation and funding of natural resource conservation within laws and development plans.
- (2) Laws and biosecurity: national, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented. (e.g., hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.).
- (3) Development or conservation planning: national, state, county, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

These conservation management parameters are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The year 2035 is the extent of the “foreseeable future,” and is based on the projected divergence of IPCC Representative Concentration Pathway (RCP) climate change scenarios (van Vuuren et al., 2011a,b; Miller, 2018).

Four foreseeable future scenarios were considered in this wetland and open water body assessment (Table 15). The future condition of wetlands and water bodies in scenario one, the status quo, was characterized from an assessment of change over time in land cover obtained from existing land cover maps. Based on these land cover maps, Reeves and Amidon (2018b) estimated an annual rate of change for wetland and water bodies, and projected little or no change (in area) through the year 2035. A slight increase is shown for Hawai'i and Ni'ihau while a slight decrease is expected for Maui. The sources of the increase are uncertain and may be related to ponds created for grazing. The loss on Maui and increase on Ni'ihau both are associated with reclassification to or from the Coast. These are likely mapping errors and not actual changes. Therefore, wetlands and open water bodies are expected to show little or no change in the foreseeable future. The resulting information on changes in land cover by 2035, as derived from existing land cover change estimates, is the extent of wetlands and water bodies that is expected in the foreseeable future under scenario one, the status quo, where conservation efforts remain unchanged and the current rate of change in land cover is also unchanged.

Due to wetland mapping challenges discussed in previous sections, the future conditions of wetlands and water bodies for scenarios two, three, and four cannot be quantitatively (area) estimated. However, the scenario one estimate can provide a “baseline” for a qualitative characterization of changes in the future condition of wetlands and open water bodies under scenarios two, three, and four.

Changes in human population are captured only by the changes in the “developed” land cover footprint derived from land cover map analysis (Reeves and Amidon, 2018a,b). Impacts from other sources of human activities or human-caused stressors (e.g., plant and animal diseases, wildfires, invasive species, etc.) are not well characterized in the land cover changes, but significantly contribute to increases in the land cover area dominated by non-native vegetation. For an assessment of island-by-island changes in human population, see Reeves and Amidon, (2018a,b).

Also, note that island-wide implementation of the CMPs is unlikely to have a significant effect on climate-related stressors (temperature, precipitation, and severe weather) resulting from global warming by 2035. This lack of CMP climate effects is due to the global lag in climate response to changes in greenhouse gas emissions which occurs on the order of centuries rather than years

Table 15 Four foreseeable future scenarios considered in this wetland and open water body assessment.

<i>Future scenario</i>	<i>Description</i>
Future scenario one	Status quo—The most likely foreseeable future; no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues through the foreseeable future
Future scenario two	A slight increase in natural resource conservation in the CMPs marginally improves conservation management
Future scenario three	A slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management
Future scenario four	A moderate to large increase in conservation actions in the CMPs substantially improves conservation management

(Solomon et al., 2009; Gillett et al., 2011; Jevrejeva et al., 2012). Evidence of climate effects is also confounded by the large annual variation in the Pacific islands climate parameters, which is much greater than projected climate change by 2035. Although impacts from climate-related stressors do not change across the four scenarios, they were included in this analysis because of their overall magnitude of potential importance to future viability.

Wetland and Open Waterbodies Future Scenario One—Status Quo

Scenario one is considered the most likely future scenario, and serves as a “baseline” for comparing among the four future scenarios. There is no change in the implementation of the three CMPs between 2018 and 2035. A continuing current rate of change in land cover through this foreseeable future results in a slow but continuous change in wetlands (Table 16).

Under scenario one, bogs and upland marshes and swamps would remain unchanged in size and distribution, therefore not affecting redundancy. Human-caused stressors will remain the same as there is minimal human interaction in these ecotypes. Ecological function is predicted to be reduced due to the ability of invasive plants and animals to outcompete native plants for water and space, subsequently resulting in a reduction in native biodiversity. Degradation of these native ecotypes will continue to increase, thus slightly reducing their resiliency and representation.

Lowland freshwater and saline marshes, estuaries, and anchialine pools are predicted to decline in size, distribution, ecological function, and quality due to the assumed expansion of the human population and continued development pressures resulting in a major decrease in resiliency, redundancy, and representation.

Fresh and saline lakes would remain unchanged in size and distribution, thereby not affecting redundancy. Lakes at upper elevations would experience the same stressors at corresponding levels as bogs and upland marshes and swamps, resulting in similar resiliency and representation levels.

Artificial reservoirs are expected to increase in distribution due to the assumed expansion of human population and continued development pressures for sewage treatment plants, golf courses resulting in a slight increase in resiliency, redundancy, and representation.

Table 16 Responses of wetland stressors in foreseeable future scenarios.

Conservation management parameters (CMPs)				
Conservation values	Stakeholder involvement and public opinion influence the formulation, implementation, and funding of natural resource conservation and biosecurity (NRC/B) within laws and development or conservation plans			
Laws and biosecurity	National, state, county, and city laws and regulations are the means by which NRC/B are supported and implemented			
Planning for development or conservation	National, state, county, city, and private development plans or conservation plans define actions that result in losses or gains in NRC/B (impacts realized at implementation)			
Foreseeable future scenarios and the resulting wetland conditions				
Use foreseeable future scenario one as a “baseline” to characterize changes in Conservation Actions and Conditions in future scenarios two, three and four	Scenario one: CMPs: Unchanged in support for NRC/B	Scenario two: CMPs: Small increase in support for NRC/B	Scenario three: CMPs: Small to moderate decrease in support for NRC/B	Scenario Four: CMPs: Moderate to large increase in support for NRC/B
	Conservation Actions: No change; current rate of land cover change continues through the foreseeable future. Condition: Area, quality, and sustainability slowly decrease through the foreseeable future.	Conservation Actions: Marginal increase Condition: Area is unchanged through the foreseeable future; quality and sustainability are slightly enhanced through the foreseeable future	Conservation actions: Substantial decrease Condition: Urban and agricultural uses are prioritized over conservation; area, quality, and sustainability substantially decrease through the foreseeable future	Conservation Actions: Substantial increase Condition: Robust, sustained effort to restore, manage, and expand conservation; area, quality, and sustainability substantially increase through the foreseeable future
Stressors	Responses of wetland and water body stressors			
Human presence/abundance				
Development	Small to moderate increase	No change (redevelop)	Moderate to large increase	Small to moderate decrease
Altered hydrology	No change to small increase	No change	Larger increase	Small decrease
Recreation/access	Small increase	Small increase	Larger increase	Larger increase
Water pollution	Small increase	No change	Larger increase	Small decrease
Invasive species	Small increase	Small increase	Larger increase	Small decrease
Climate				
Sea level	Small increase	Small increase	Small increase	Small increase
Storms	Small increase	Small increase	Small increase	Small increase
Drought	Small increase	Small increase	Small increase	Small increase
Air temperature	Small to moderate increase	Small to moderate increase	Small to moderate increase	Small to moderate increase

Future Scenario Two—There Is a Slight Increase in the CMPs That Marginally Improves Conservation Management

Scenario two has Conservation Agencies and stakeholders working with an increased but limited resources to slow or stop the degradation of landscape areas.

Under scenario two, bogs and upland marshes and swamps would remain unchanged in size and distribution, therefore not affecting redundancy. Human-caused stressors are predicted to remain unchanged or increase slightly as there is minimal human interaction in these ecotypes. Ecological function is predicted to be remain unchanged to slightly increase due to less competition with invasive plants and animals, thus slightly increasing their resiliency and representation.

Lowland freshwater and saline marshes, estuaries, and anchialine pools are predicted to decline in size, distribution, ecological function, and quality as the same level as in scenario one. The limited increase in resources to slow the degradation of these ecotypes will not significantly decrease the human and climate-caused stressors resulting in a slight decrease in a slight decrease in resiliency, redundancy, and representation.

Fresh and saline lakes would remain unchanged in size and distribution, thereby not affecting redundancy. Lakes at upper elevations would experience the same stressors at corresponding levels as bogs and upland marshes and swamps, resulting in similar resiliency and representation levels.

Artificial reservoirs would remain unchanged from scenario one because these are directly link with the assumed expansion of human population and development. Thus, this ecotype will retain its form and function, along with resiliency, redundancy, and representation into the foreseeable future.

Future Scenario Three—There Is a Small to Moderate Decrease in Conservation Actions in the CMPs That Substantially Decrease Conservation Management

All natural resource management actions in the CMPs are set aside in deference to land use for economic development. With extensive localized management, some native species may persist in park-like settings or in areas where land development is not possible.

Under scenario three, bogs and upland marshes and swamps, lowland freshwater and saline marshes, estuaries, anchialine pools, and ponds would significantly decline in size, distribution, ecological function and quality due to their reliance on CMPs and conservation resources to address stressors to these wetland ecotypes. Degradation of these ecotypes and human-caused stressors in lowland wetlands will continue to increase as remaining areas become smaller, more fragmented and climate-caused stressors start appearing, thus reducing their resiliency, redundancy, and representation.

Fresh and saline lakes are not expected to decline in size or distribution in the foreseeable future, therefore not affecting redundancy. Human-caused stressors will increase overall and continue to reduce the ecological function and quality of fresh and saline lakes resulting in decreased resiliency, and representation.

Artificial reservoirs are predicted to increase in size and distribution due the to assumed expansion of the human population and continued development pressures from commercial, residential, and recreation, resulting in an increased resiliency, redundancy, and representation.

Future Scenario Four—There Is a Moderate to Large Increase in Conservation Actions in the CMPs That Substantially Improves Conservation Management

Scenario four is an overt and robust, active, ongoing effort is made to engage partners and stakeholders in identifying and prioritizing landscape areas needed for the conservation of native wetlands, and to actively restore and expand them.

Under scenario four, bogs and upland marshes and swamps, lowland freshwater and saline marshes, estuaries, anchialine pools, and ponds would significantly increase in size, distribution, function, and quality from conditions in scenario one due to an overall decrease in wetland degradation and human-caused stressors. These wetland ecotypes are likely to expand as wetlands are protected from development, vegetation and water quality is increased, improved, and or restored, resulting in a significantly increase in resilience, redundancy, and representation.

Fresh and saline lakes are expected to remain unchanged in size and distribution from scenario one. These wetland ecotypes are expected to increase in function and quality due decrease in human-caused stressors resulting in an increase in resiliency and representation.

Summary

Based on our analysis of wetland and water bodies in Hawai'i, all wetlands and water bodies will decline in lieu of intensive management (Table 17). Scenarios one, two, and three are all plausible given the current and potential trajectories of stressors combined with alternate conservation outcomes. It seems unlikely that the substantially improved conditions detailed under scenario four would manifest given the intense effort it would take to reverse or mitigate such forces such as human development (population growth) and climate change.

Table 17 Summary of the expected viability (resiliency, redundancy, and representation combined) for each future scenario for wetland and open water bodies in the Hawaiian archipelago.

<i>Sub-type</i>	<i>Scenario 1: status quo</i>	<i>Scenario 2: slightly improved</i>	<i>Scenario 3: substantially decreased</i>	<i>Scenario 4: substantially improved</i>
Upland bogs, marshes and swamps ^a	No change to slight decline	No change to slight increase	Decrease significantly	Increase significantly
Lowland freshwater and saline marshes, estuaries, and anchialine pools ^a	No change to slight decline	No change to slight decrease	Decrease significantly	Increase significantly
Ponds and fresh and saline lakes ^a	No change or slight decline	Slight increase	Decrease significantly	Increase
Artificial reservoirs	No change	No change to slight increase	No change	Increase

^aFor these wetlands, "no change" is relevant for those areas currently fenced and managed. "Slight decline or increase" relates to those that are currently unmanaged.

See also: Physical Geography of the Hawaiian Islands.

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The Laurentian Great Lakes of North America

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Abstract

The Laurentian Great Lakes of North America are a series of interconnected lakes that, collectively, comprise one of the largest freshwater ecosystems on the earth. Prior to large-scale European settlement, the largely forested watersheds of the Great Lakes Basin delivered few nutrients to the lakes and the lakes themselves maintained a trophic status that ranged from oligo- to mesotrophic conditions. The biotic community of the Great Lakes is relatively depauperate, which reflects the recent geological development of the ecosystem. Historically, there were two main biotic communities in the Great Lakes: those that occupied the biologically less-productive open waters of the upper Great Lakes, and another in nearshore areas and productive embayments. Human activity in the Great Lakes Basin has brought with it a number of stressors, including land use changes, overfishing, altered nutrient loading and invasive species. To help manage these stressors, the management communities of the Great Lakes, which represent two countries, eight states, two provinces, tribal governments, First Nations, and local public agencies have developed a complex patchwork of governance in the Basin.

The Formation and Physical Environment of the Great Lakes

The Laurentian Great Lakes of North America are a series of interconnected lakes that straddle the international border between the United States and Canada (**Fig. 1**). Collectively, these five lakes are the largest freshwater ecosystem on the earth by surface area



Fig. 1 Satellite view of the Laurentian Great Lakes of North America.

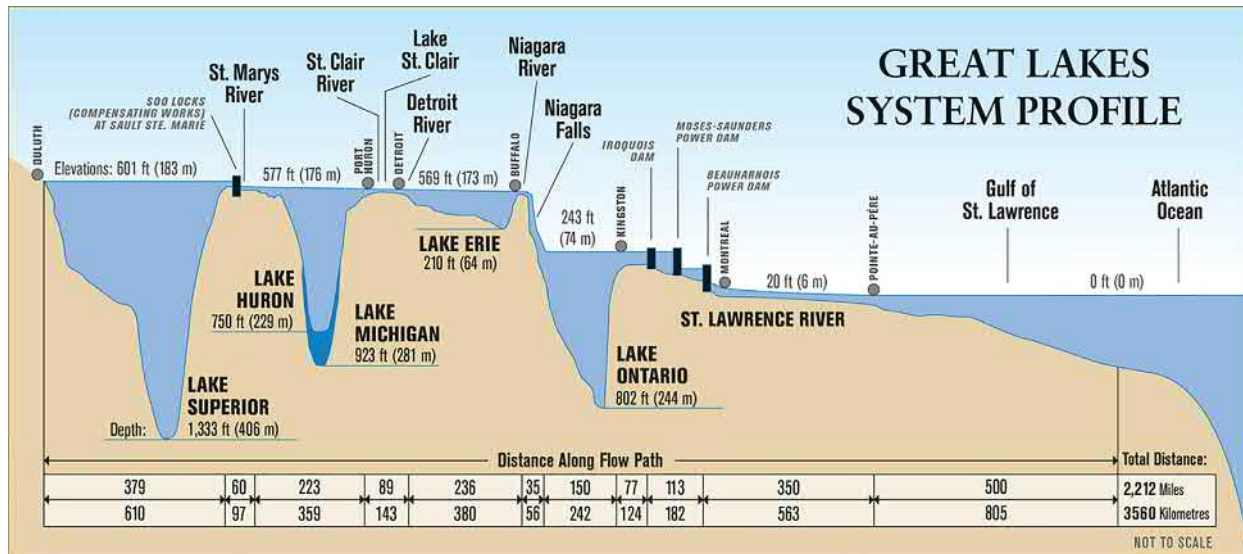


Fig. 2 Map showing the depths of the Great Lakes and major landmarks.

(Lake Baikal is larger by volume) and contain approximately 21% of the surface freshwater on the entire planet. The Great Lakes were formed when the Laurentide Ice Sheet that covered much of North America during the last ice age gradually began melting during the Wisconsin glaciation between 12,000 and 10,000 years ago. Over the course of several thousand years, the ice sheet melted along its southern edge and filled the scoured lake beds, forming a series of proglacial lakes. Around 4000 years ago, the remaining ice dam receded beyond the northern edge of the Basin, establishing a connection between the newly formed Great Lakes and the St. Lawrence Seaway. In its present state, the Great Lakes Basin—an area that includes both the lakes and the watersheds that drain into them—covers an area approximately 240,000 km². In the direction of flow, the Great Lakes are comprised of Lake Superior, Lakes Michigan and Huron, which are separate basins of a single lake that is connected by the Straights of Mackinaw, Lake Erie and Lake Ontario. Retention times vary according to the surface area, depth and predominant current patterns of each lake, with the longest retention time of 191 years in Lake Superior, and Lake Erie having the shortest retention time of 2.6 years. Water flowing through the Great Lakes ultimately drains to the Atlantic Ocean via the St. Lawrence Seaway (Fig. 2).

Prior to European settlement in the Basin, the Great Lakes maintained a trophic status that ranged from oligo- to mesotrophic. The surrounding watersheds of the Basin were largely comprised of forested land prior to settlement and, therefore, delivered few nutrients to the lakes. Coastal wetlands often occupied the space between the land in the watershed and the nearshore waters of the lakes in lower gradient watersheds around the Great Lakes Basin. These wetlands likely further reduced nutrient delivery from the watershed. Within the lakes themselves, cycles of thermal stratification and primary production were tightly linked in an annual cycle. The deeper, open waters of the Lakes Superior, Michigan, Huron, Ontario and the Central and Eastern Basins of Lake Erie can be characterized as dimictic and are prone to stratification during the winter and summer, with periods of turnover and isothermal periods that occur with warming during the spring and cooling during the fall. During isothermal periods, lake temperatures remain near 3–4 °C and intense winds during the fall and early spring promote complete mixing of the water column even in some of the deepest points of the lakes. Shallower areas, such as the Western Basin of Lake Erie and coastal embayments such as Green Bay in Lake Michigan, Saginaw Bay in Lake Huron and Bay of Quinte in Lake Ontario, are among the first areas of the lakes to freeze during winter but lack sufficient depth to experience prolonged summer stratification.

Historical Biological Communities of the Great Lakes

Compared to ecosystems of similar size, the biotic community of the Great Lakes is relatively depauperate, which reflects the recent geological development of the system (Fig. 3). At the base of the food web, the annual cycle of primary productivity throughout the Great Lakes has historically been closely linked with seasonal thermal stratification with a peak of primary production occurring during a spring bloom of mostly centric and pennate diatoms and other green algae. The spring bloom is then followed by a summer clear water phase that often coincides with proliferation of herbivorous zooplankton. During the summer clear water phase, the highest level of primary production may occur deeper in the water column at a point called the deep chlorophyll maximum, which is often at the deepest point where light attenuation, nutrients and thermal stratification can sustain phytoplankton growth. Finally, a second, less-pronounced peak of primary production occurs during the fall. Relatively little is known about primary production in the Great Lakes during the winter, but limited studies have shown that diatom production under the ice can be a significant contributor to annual estimates of algal biomass in some lakes (Revie et al., 2016).

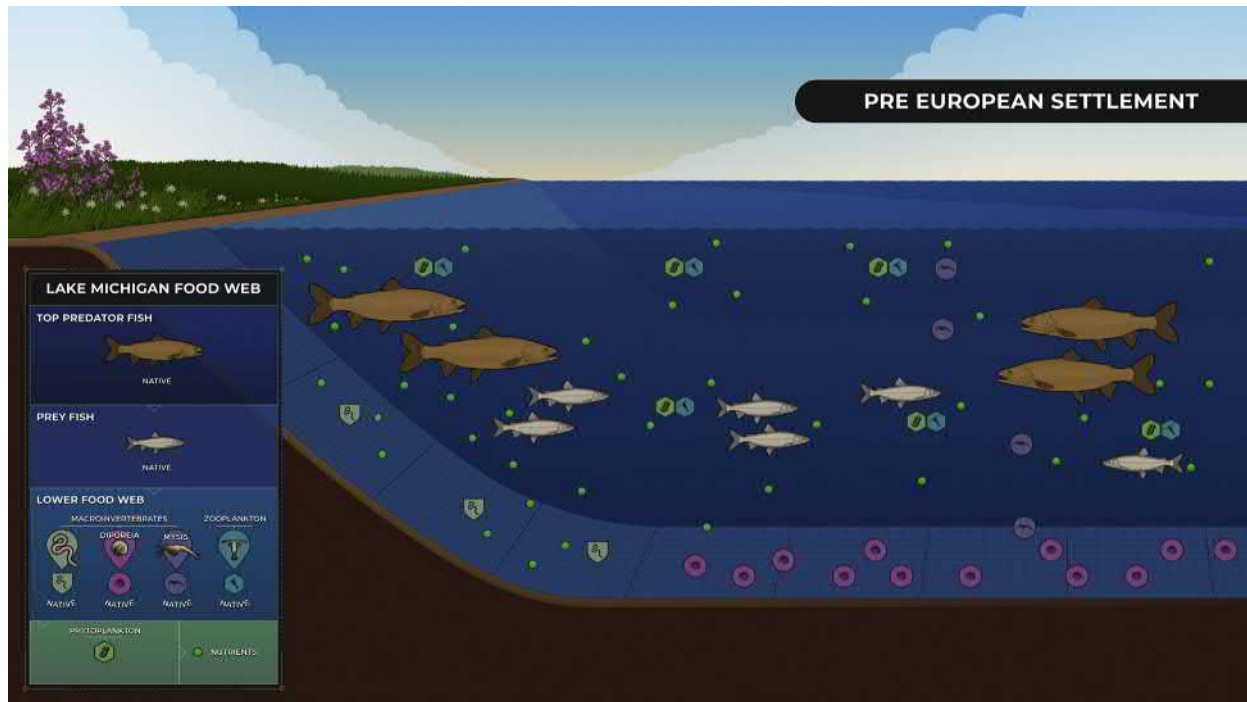


Fig. 3 A representation of the Great Lakes food web prior to European settlement in the basin.

The zooplankton communities in surface waters of the Great Lakes are comprised of three major groups: rotifers, copepods and cladocerans. Rotifers are an important contributor to total zooplankton biomass and their community composition tends to vary according to the trophic state of each particular lake. Some genera, such as *Filinia*, *Brachionus* and *Trichocera*, are more commonly found in highly productive areas like western Lake Erie whereas other genera, such as *Conochilus* and *Kellicottia*, are more common in the oligotrophic waters of the upper Great Lakes (Barbiero and Warren, 2011). Historically, the crustacean zooplankton communities of the Great Lakes display a pattern of seasonal succession that is comparable to many other lentic ecosystems. Calanoid and cyclopoid copepods (common genera include *Limnocalanus*, *Leptodiatomus* and *Mesocyclops*) and their copepodites represent the dominant taxa present during the spring and early summer. As water temperatures and primary production increase through the summer, zooplankton community composition typically shifts towards an increasing relative abundance of cladocerans, including many herbivorous species (*Daphnia*, *Holopedium* and *Bosmina* are common genera) and the predatory cladoceran *Leptodora kindtii*. Beyond seasonal succession, many species of zooplankton in the Great Lakes also undergo pronounced diel vertical migration (DVM), especially during the summer months when stratified conditions are present in the lakes. Species that undergo DVM include many species of *Daphnia*, which spend daylight hours in the deeper waters of the metalimnion, presumably hiding from visual predators near the surface, and migrate upwards to feed near the surface during the night. Other zooplankton taxa, such as *Limnocalanus*, exhibit similar DVM behavior but migrate between the hypolimnion, which they inhabit during daylight hours, and then migrate upwards to the metalimnion during the night, presumably to feed on both algae and smaller zooplankton that are concentrated near the deep chlorophyll layer.

Benthic habitats are typically an understudied component in aquatic ecosystems, and the benthic habitats of the Great Lakes are no exception. However, zoobenthic species can be important contributors to whole-lake secondary production and often play important roles in ecosystem processes, and this is true for the Great Lakes as well. The historical zoobenthic community in the Great Lakes consisted of two main assemblages: one associated with shallow and productive waters, and another associated with deeper, less productive offshore waters. Community diversity was highest in shallow, productive habitats, where many depth-restricted taxa reside, including many species of Oligochaete worms in the family Naididae, as well as common aquatic insect larvae in the families Chironomidae and Ephemeroptera, Hirudinae, Gastropods, and native freshwater mussels in the family Unionidae. In deeper offshore habitats, the zoobenthic community of the Great Lakes was historically dominated by two species of crustaceans, *Diporeia* and *Mysis*, which are important diet items for many different fish species and also represent an important link between benthic production and the pelagic food webs of the upper Great Lakes.

The Great Lakes are home to about 140 native fish species, and the fisheries that the lakes support are an important part of the region's culture and economy. Historically, there were two main types of fish assemblages across the Great Lakes Basin: one typified by the fish community of the open waters of the upper Great Lakes, and another in nearshore areas and productive embayments. In the low productivity waters of Lakes Superior, Michigan, Huron, Ontario and the offshore waters of Eastern Lake Erie, the fish assemblage mainly consisted of salmonines, coregonids and sculpins. Lake Trout (*Salvelinus namaycush*) and Burbot (*Lota lota*)

were the top predators in the offshore food web, and other abundant species included Lake Whitefish (*Coregonus clupeaformis*), Slimy Sculpin (*Cottus cognatus*) and Deepwater Sculpin (*Myoxocephalus thompsonii*). Ciscoes, in both shallow water form (formerly lake herring, *Coregonus artedii*) and the deepwater chubs (*Coregonus* spp.), were an important component of the offshore food web as well (Eshenroder and Burnham-Curtis, 1999). In the shallow and productive areas of the Great Lakes, including the Western Basin of Lake Erie and embayments such as Green Bay in Lake Michigan, Saginaw Bay in Lake Huron, and Bay of Quinte in Lake Ontario, percids, cyprinids and centrarchids were abundant. In these areas, Blue Pike (*Sander vitreus glaucus*) and Walleye (*Sander vitreus*) were the top predators, and other abundant species included Yellow Perch (*Perca flavescens*) and Emerald Shiner (*Notropis atherinoides*) (Eshenroder and Burnham-Curtis, 1999). Lake Sturgeon (*Acipenser fulvescens*) were another important component of the historical nearshore fish assemblage that occupied many of the coastal embayments of the Great Lakes and their tributaries.

Ecosystem Stressors

Human activity in the Great Lakes Basin has brought with it a number of stressors, beginning with the European settlement of the region and the subsequent changing of land-use patterns within the watershed. By the early 18th century, some of the first dams were built in the Great Lakes Basin (Beeton et al., 1999), which blocked access to important spawning habitats for migratory fish species such as Lake Sturgeon and Walleye. The presence of the dams also changed the natural flow regimes of the tributaries and, subsequently, altered nutrient dynamics in the lakes themselves (Hayes, 1999). As more people came to reside in the Great Lakes Basin throughout the early 20th century, human activities in the watersheds related to natural resource extraction, such as timber harvesting and mining, further altered land use patterns in the watersheds. The growing human populations also had a direct effect on land use patterns, as people began converting forests and wetlands into agricultural fields and urbanized areas. Coastal wetlands, which provide important breeding or nursery habitats for many Great Lakes fish species, were dramatically altered throughout this settlement period. For example, over 90% of the coastal wetlands surrounding western Lake Erie and the Detroit River have been removed due to human activity such as draining and diking (Maynard and Wilcox, 1997).

The growing human population in the Great Lakes Basin continued to stress the lake ecosystems beyond the changes occurring in the watershed. By 1829, with the completion of the Erie and Welland canals, the once-isolated Great Lakes became hydraulically connected to the Atlantic Ocean and commercially connected with population centers along the east coast. In particular, the construction of the Welland Canal allowed nonnative species to bypass Niagara Falls, which had served as natural barrier between Lake Erie and Lake Ontario since the initial formation of the lakes, to access the four upper Great Lakes. Two fish species in particular, the parasitic Sea Lamprey (*Petromyzon marinus*) and the planktivorous Alewife (*Alosa pseudoharengus*), entered the upper Great Lakes through the Welland Canal with devastating consequences for the native fish populations. Around this same time period, commercial fisheries were becoming well-established in the Great Lakes, and increasing fishing efforts as well as improvements in fishing technology had already reduced native fish abundance across all five Great Lakes. However, the combined effects of invasive species proliferation and direct fishing mortality had cascading effects on the native fish populations of the Great Lakes. By the 1950s, the combined effects of parasitism by Sea Lamprey and intense fishing pressure led to the collapse of Lake Trout populations in Lakes Michigan, Huron, and Ontario. A similar dynamic was responsible for the extinction of three of the larger morphs of the deepwater chubs in the upper Great Lakes (*Coregonus nigripinnis*, *C. johannae*, and *C. reighardi*). As the combined effects of sea lamprey predation and fishing mortality eliminated the larger morphs of the deepwater chubs, both lamprey and commercial fisheries shifted to focus on smaller species, ultimately reducing the abundance of Lake Whitefish (*Coregonus clupeaformis*) and Ciscoe (*Coregonus artedii*). With the near-elimination of predatory lake trout and native planktivorous fish, alewives became incredibly abundant in the open waters of the Great Lakes and further stressed native fish populations through predation on the planktonic larvae of lake trout, yellow perch, and walleye (Madenjian et al., 2008). By the 1960s, Pacific salmon were being stocked into the Great Lakes in large numbers to help control the booming alewife populations and to provide anglers with sportfishing opportunities (Fig. 4).

Through time, the watersheds of the Great Lakes Basin became increasingly industrialized, which further stressed the ecosystem. Polychlorinated biphenyls (PCBs) are a class of synthetic organic chemicals that were globally manufactured and widely used as insulators with long-term degradation resistance. PCBs can be found in sediments, waters, biological tissues, wastes, air, and certain in-use products due to their high stability (United States and Canada, 2018). Their presence can cause a variety of harmful environmental and human health effects. While Canada and the United States have restricted the manufacturing and importation of PCBs since the 1970s, PCBs still today contribute to fish consumption restrictions in the Great Lakes Basin. By the 1960s, the cultural eutrophication of the Great Lakes due to excessive nutrient loading from both point and non-point sources had become a major concern (Beeton, 1965). Although open waters remained mostly oligotrophic, nearshore areas such as the Western Basin of Lake Erie, and coastal embayments such as Saginaw Bay and Green Bay, commonly experienced negative consequences from excessive nutrient loadings such as harmful algal blooms and severe bottom hypoxia during the summer (Vollenweider et al., 1974). The ships that conduct transoceanic commerce across the waters of the Great Lakes have brought more than just goods to the region; the ballast water that stabilizes these ships also serves as a vector for invasive species from around the globe. Entering through the ballast water of foreign ships, a series of invasions by nonnative species, dreissenid mussels from the Ponto-Caspian region (zebra and quagga mussels, *Dreissena polymorpha* and *D. bugensis*), in particular, have caused major changes in Great Lakes ecosystems (Fig. 5). When dreissenids reach large population sizes, they sequester primary production in nearshore benthic habitats, which acts to constrain nutrients that would otherwise be available to higher trophic levels in offshore areas (Hecky et al., 2004).

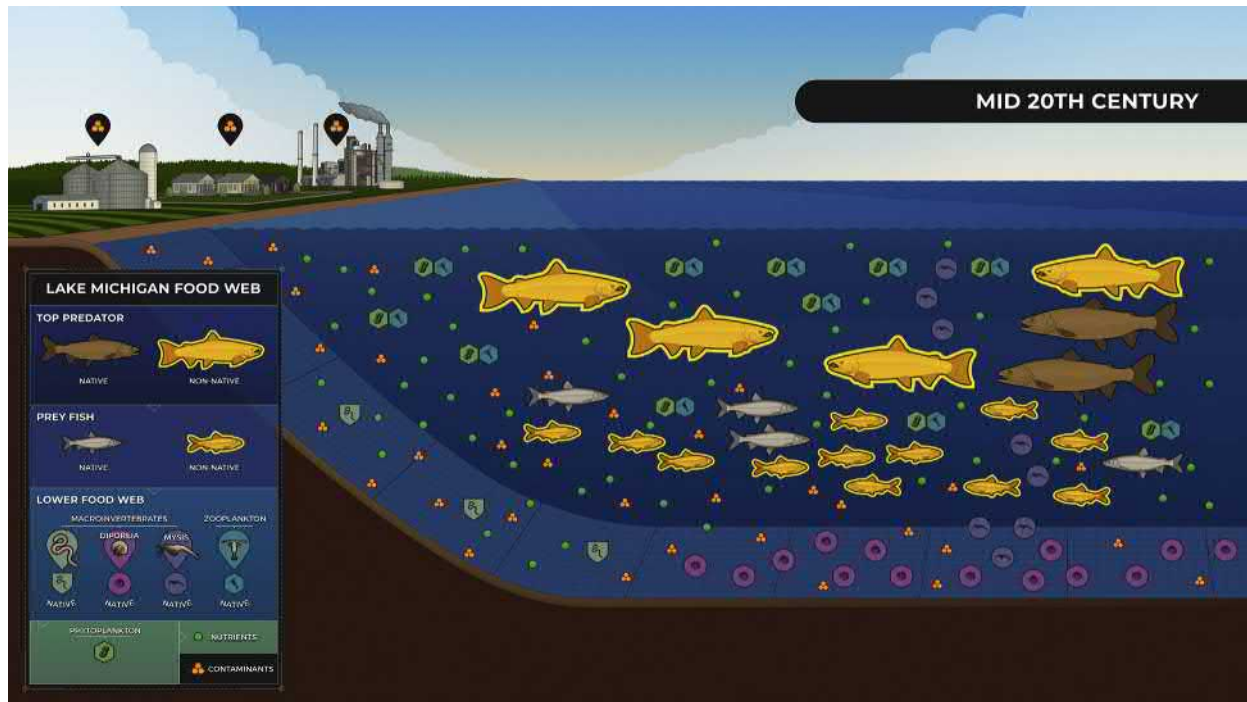


Fig. 4 A representation of the Great Lakes food web in the mid 20th century.

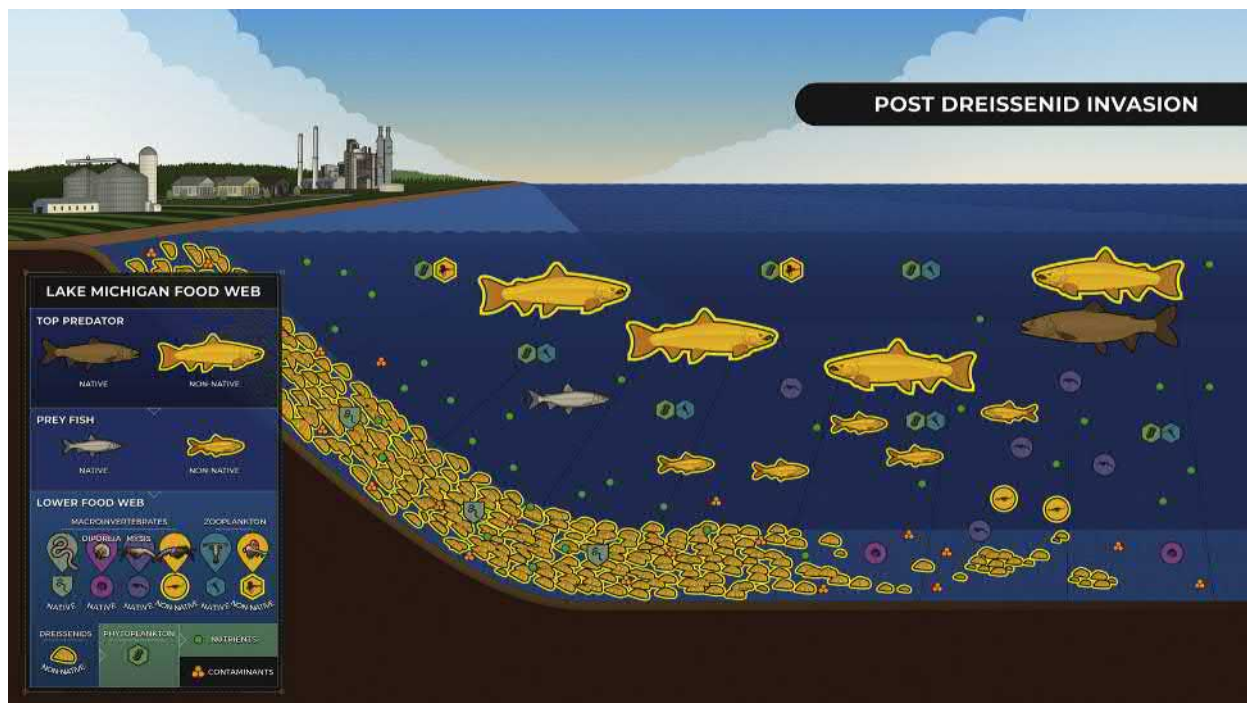


Fig. 5 A representation of the current Great Lakes food web.

Since the 1980s, the physical environment of the Great Lakes has been altered in ways that are consistent with global climate change. Recent documented changes include increases in surface water temperatures (Dobiesz and Lester, 2009), reduced iced cover during the winter, a prolonged stratification period during the summer (Wang et al., 2012), and large fluctuations in water levels (Clites et al., 2014). However, the management communities of the Great Lakes have, thus far, viewed climate change as an interactor with existing ecosystem stressors rather than address the direct effects of climate change (Collingsworth et al., 2017). Surface temperatures in the waters of the upper Great Lakes will increase due to climate change, which may make these areas more

susceptible to the dispersal and colonization of invasive species (Mandrak, 1989). In addition, climate change models consistently forecast increasing precipitation and more pronounced storms during the spring across the upper Midwestern United States. Such changes in seasonal hydrology will influence the presence and severity of harmful algal blooms and seasonal hypoxia in productive areas of the basin such as the Western and Central basins of Lake Erie (Watson et al., 2016). Climate adaptation for the ecosystems of the Great Lakes will rely on the ability of managers to understand and mitigate the interacting effect of these common stressors because they are widespread across the Basin. A recent multi-stressor mapping effort found that many areas important for fisheries, in particular nearshore areas and coastal embayments of Lakes Michigan and Huron, and much of Lakes Erie and Ontario, experienced high cumulative stress (Allan et al., 2013).

Binational Governance of the Great Lakes

The Great Lakes are shared and governed by two countries, eight states, two provinces, and numerous Indian tribes and First Nations, in addition to a multitude of American, Canadian, and international agencies, as well as thousands of local governments (Hall, 2006; Bielecki, 2007). A complex patchwork of governance exists in the Basin, owing to overlapping environmental and natural resources within the Great Lakes system, and similarly overlapping populations concerned with specific resources and functions, as detailed in a review of Great Lakes governance and law by Hall and Houston (2014).

The Great Lakes Basin's two binational treaty organizations are the International Joint Commission (IJC) and the Great Lakes Fishery Commission (GLFC). The IJC was established under the 1909 Boundary Waters Treaty (BWT) and works to prevent and resolve boundary waters disputes between Canada and the United States. The BWT has provided the principles for Canada and the United States to follow in using their shared, or transboundary, waters for over a century (Hall, 2007). The IJC serves as an independent and objective advisor to the two governments related to implementation of the *Great Lakes Water Quality Agreement* (GLWQA). The six politically-appointed IJC Commissioners are advised by more than 20 binational boards and task forces, including the Great Lakes Water Quality Board and the Great Lakes Science Advisory Board, which advise the IJC on policy and scientific matters related to Great Lakes water quality. The IJC also provides oversight of efforts to regulate water levels and flows in some of the Great Lakes and connecting channels. The Great Lakes Fishery Commission (GLFC) facilitates cross-border cooperation of state, provincial, tribal, and federal fishery management agencies for the improvement and preservation of the fisheries under *A Joint Strategic Plan for Great Lakes Fisheries Management* (GLFC, 2007). The Lake Committees of the GLFC are binational committees (except for the Lake Michigan Committee, which does not have Canadian representation) comprised of senior officials from state, provincial, and tribal fishery management agencies. The Lake Committees are tasked with sustainably and cooperatively managing Great Lakes fisheries resources and the fish community, considering issues and problems of common concern to the jurisdictions, developing and coordinating joint state/provincial/federal fisheries programs and research, and making recommendations regarding fisheries management issues affecting the Great Lakes. The Lake Committees also develop and maintain shared fish community objectives, establish appropriate stocking levels and harvest targets, set law enforcement priorities, and formulate management plans. Together, the IJC and the GLFC have facilitated the development of ecosystem-based fisheries management in the Great Lakes, which integrates abiotic, biotic, and social components into decision-making with the goal of improving both natural resources health and ecosystem sustainability (Guthrie et al., 2019).

The original GLWQA, as established in 1972 under the BWT, was signed by U.S. President R. M. Nixon and Canadian Prime Minister P. Trudeau on April 15, 1972, and is recognized as the first multi-national agreement designed to protect and resuscitate a shared environmental resource (Holden, 1972). The 1972 GLWQA set specific water quality objectives for a limited number of parameters, included interim objectives for a wider variety of substances, and called for the control of pollution from industrial sources, shipping and dredging activities, and onshore and offshore facilities, and a reduction in phosphorus loading to the Great Lakes (Barbiero et al., 2018). A significant change in the 1978 amendment to the GLWQA was its stated goal "to re-store and maintain the chemical, physical, and biological integrity of the waters of the Great Lakes Basin Ecosystem"; this shift in emphasis to an "ecosystem approach" adopted a far broader goal than that of its 1972 predecessor, which had focused on the improvement of water quality through pollution control (GLWQB, 1986; Barbiero et al., 2018). The 1978 GLWQA defined the Great Lakes Basin Ecosystem as "the interacting components of air, land, water, and living organisms, including man, within the drainage basin of the St. Lawrence River at or upstream from the point at which this River becomes the International Boundary between the United States and Canada" (GLWQA, 1978), thus recognizing the connection and influence of humans to the structure, function, and processes of the Great Lakes Basin (Guthrie et al., 2019). The GLWQA was further amended in 1983, 1987, and, most recently, in 2012. The 2012 protocol amending the GLWQA reaffirms the United States' and Canada's determination "to protect, restore, and enhance water quality of the Waters of the Great Lakes and their intention to prevent further pollution and degradation of the Great Lakes Basin Ecosystem" (Canada and the United States, 2012).

Another pivotal guiding document in the implementation of ecosystem-based management in Great Lakes was the 1981 *A Joint Strategic Plan for Management of Great Lakes Fisheries* (GLFC, 1981; Guthrie et al., 2019). Signed by the Great Lakes states, the Province of Ontario, and federal agencies, and later amended to include intertribal organizations in the Great Lakes Basin (Gaden, 2007), *A Joint Strategic Plan* transformed the GLFC Lake Committees from information-sharing forums into strategic decision-making entities (Guthrie et al., 2019). This transformation was accomplished by the establishment of jointly-developed fish community objectives for each lake that (1) clarified the fishery management goals, and (2) established environmental objectives needed to support

the fish community objectives (GLFC, 1997; Guthrie et al., 2019). Implementers of the 2012 GLWQA and A *Joint Strategic Plan* are working closely together to implement ecosystem-based management in the Great Lakes.

In addition to federal treaty power, federal environmental lawmaking and natural resources management has been integral in protecting and restoring the Great Lakes ecosystem. The passage of the Clean Water Act in 1972 is recognized as the most significant exercise of federal regulation relevant to the Great Lakes (Hall and Houston, 2014). The Clean Water Act strives to create a partnership between the states and the federal government “to restore and maintain the chemical, physical, and biological integrity of the Nation’s waters” (Federal Water Pollution Control Act Amendments of 1972). To achieve this goal, the Clean Water Act creates several regulatory and funding programs (detailed in Hall and Houston, 2014), including effluent limitations promulgated by the U.S. Environmental Protection Agency. The Coastal Zone Management Act (CZMA) of 1972 provides the basis for protecting, restoring, and responsibly developing U.S. coastal communities and resources. The National Coastal Zone Management Program is a voluntary partnership between the federal government and U.S. coastal and Great Lakes states and territories authorized by the CZMA and administered by NOAA. A wide range of issues are addressed through the program, including coastal development, water quality, public access, habitat protection, energy facility siting, ocean governance and planning, coastal hazards, and climate change.

Local sovereignty of the eight states and the providence of Ontario and interstate governance are also important components of Great Lakes law and policy (Hall and Houston, 2014). Tribal governance and the sovereignty of tribal nations also play a key role in the management of the Great Lakes (Hall and Houston, 2014). Tribes and tribal Great Lakes governance bodies manage tribal water and fishery resources. More recently, the Great Lakes Basin Compact, first signed in 1955, includes each of the eight Great Lakes states as members and creates a Great Lakes Commission comprised of representatives from the member states, with the Canadian provinces of Ontario and Quebec designated as associate members. The Great Lakes governors and premiers negotiated the 2008 Great Lakes–St. Lawrence River Basin Water Resources Compact and the Great Lakes–St. Lawrence River Basin Sustainable Water Resources Agreement to manage new or increased water withdrawals in the Great Lakes Basin. The Agreement is a nonbinding policy between the states and provinces that creates a governance structure to set standards for water use and withdrawals administered primarily under the authority of individual states and provinces (Hall and Houston, 2014).

Management Opportunities

In response to the persistent stressors that negatively impact the Great Lakes, recent management initiatives have been implemented to restore these ecosystems back to their original state. To reverse the cultural re-eutrophication of Lake Erie, along with the growing threat of harmful algal blooms and the expansion of summer hypoxia, the United States and Canada adopted phosphorus reduction targets in 2016. The new targets call for an overall 40% reduction in total phosphorus loads from the Maumee River, and other sources in the western and central portions of the Lake Erie basin. In keeping with the bi-national management strategies of the Great Lakes, each country has developed detailed action plans which outline strategies for meeting the new target phosphorus loads.

In the upper Great Lakes, the proliferation of Dreissenid mussels into deep water habitats has altered the food webs in such ways that they resemble the ecosystems as they existed prior to the industrialization of their watersheds. Productivity is low across all trophic levels, alewife populations have been dramatically reduced and Lake Trout, the top native predator in the ecosystem, has been making a comeback. In this environment, fisheries managers have chosen to promote the reintroduction and stocking of native planktivores, such as ciscoes, in an attempt to promote native species.

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Biogeography: Lakes—African Great Lakes

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Abstract

The African Great Lakes (AGL) are among the most ecologically and economically important aquatic biomes of the world. They are sources of nutritious fish in a region where malnutrition and poverty levels are high, provide employment to fisher communities, and are sources of water for domestic and urban use, hydropower generation, irrigation and wastewater disposal. Some of the lakes have the highest diversity of endemic freshwater fishes and other organisms on earth. The original biogeography of AGL was molded by geological events. Here we examine how the biogeography of AGL has been altered by activities of a rapidly increasing human population whose growth rate is among the fastest in the world through land use change, fishery exploitation, and climate variability and change. Fisheries exploitation was the first to manifest resulting into a decline and in some cases total disappearance especially of some large inshore fish species which, in some lakes led to enhancement of fish production through introduction of new fish species and cage aquaculture. The impacts of conversion of land to agriculture, deforestation, wetland degradation, urban and hydropower developments were cumulative since the turn of the 20th century and their effects on aquatic ecosystems manifested at different rates through changes in physical and chemical conditions, shifts in algal and invertebrate communities and fish stocks, and proliferation of invasive weeds. Some of the lakes with terrestrial game reserves around them were partly shielded from these changes. Climate variability and change, which intensified after the 1970s, triggered further environmental changes, algal communities shifted from large diatoms to smaller diatoms, green algae, and blue green algae, invertebrates from larger to smaller sized groups, and fish stocks became dominated by small pelagic species. These changes have been more severe in shallower lakes or shallow near-shore areas of deep lakes with high human population growth rates and densities. The changes are expected to continue and should be monitored and managed to avoid reaching catastrophic levels. The countries sharing the lakes should network within and between lakes, nationally, regionally, continentally and globally to mobilize and harmonize information and data, and update it regularly to guide management of lakes.

Background

The African Great Lakes, AGL (Malawi, Tanganyika, Kivu, Edward, Albert, Victoria, and Turkana), are in the African Rift Valley region between 14° 40'S–4° 31'N and 28° 50'E–36° 42'E (Fig. 1). The only similar regions of Great Lakes in the world are the Laurentian Great Lakes of North America with five lakes; Superior, Michigan, Huron, Erie and Ontario (Bootsma and Hecky, 2003), but these lie in a single watershed, are shared between the United States of America and Canada, and have a much lower number of fish species (179). The AGL were formed by tectonic activity and hold one-third of the world's surface freshwater. Unlike the Laurentian Great Lakes which are directly joined to each other and lie at almost the same elevation, the AGL are distinct and vary considerably

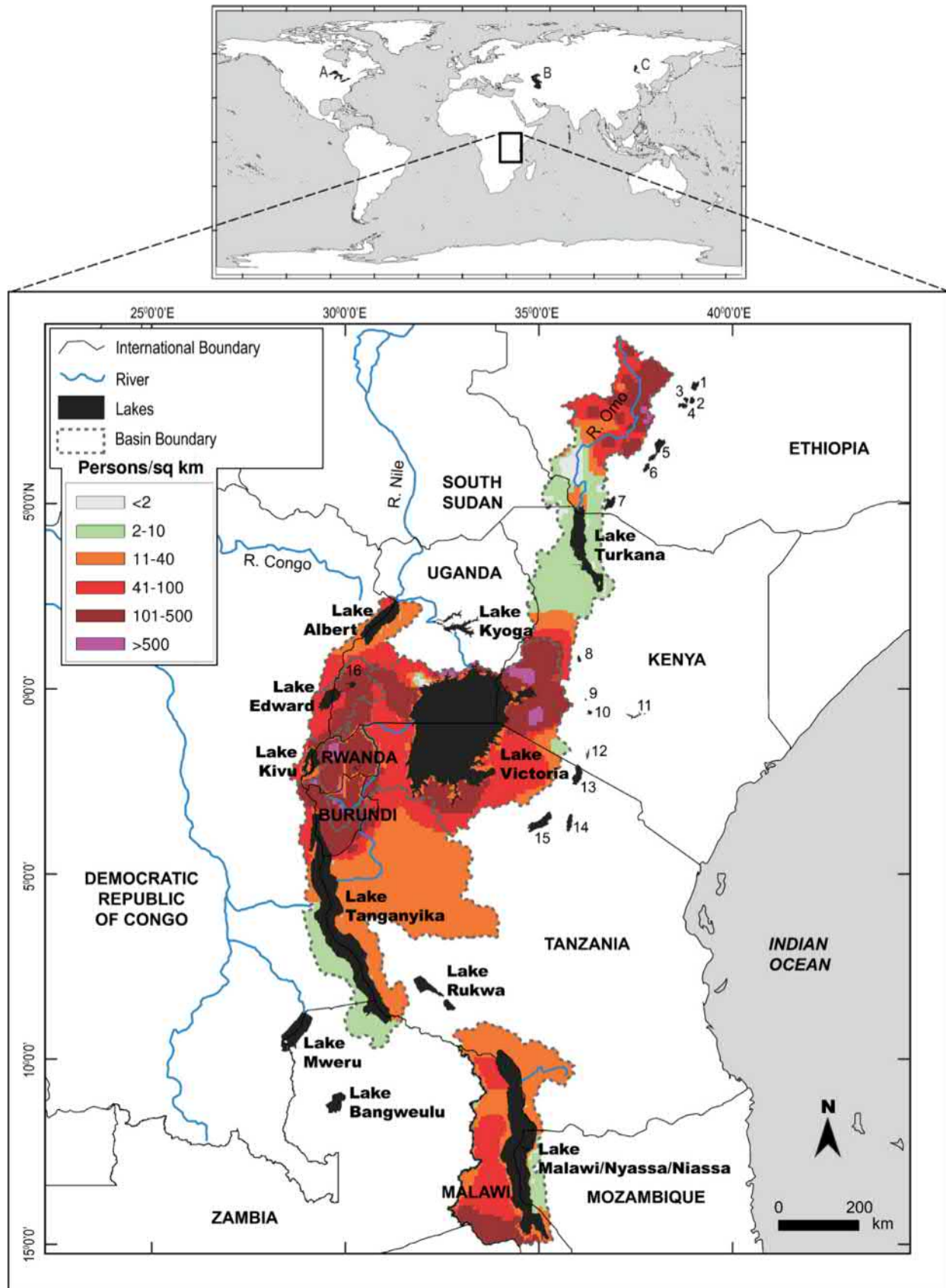


Fig. 1 African Great Lakes and the human population density in their basins. There are over 15 small lakes with internal drainage in the Eastern arm of the rift valley which have been numbered in addition to those labeled. The basin population is from the world population information. The other Great Lakes of the world are the Laurentian Great lakes of North America (A), the Caspian Sea (B), and Lake Baikal (C).

Table 1 Physical features of the different African Great lakes.

Characteristic	Victoria	Malawi	Tanganyika	Kivu	Edward	Albert	Turkana
Age (millions of years)	0.4	2	12	0.1	12	12	4.3
Altitude (m. amsl)	1134	474	773	1460	920	615	360
Catchment area (km ²)	193,000	100,500	223,000	5097	12,100	17,000	130,860
Lake area (km ²)	68,800	29,500	32,600	2370	2325	5300	6405
Shoreline length (km)	3440	1500	1828	860	290	508	820
Average depth (m)	40	264	580	240	17	25	30 m
Maximum depth (m)	80	700	1470	485	112	58	109
Volume (km ³)	2760	7775	18,880	500	40	280	204
Water residence time (years)	23	114	440	193	20		12.5
Flushing time (years)	138	648	7000	88			

Adapted initially from ILEC (International Lake Environment Committee) (2005). Managing Lakes and Their Basins for Sustainable Use: A Report for Lake Basin Managers and Stakeholders, 142pp. Kusatsu, Japan: International Lake Environment Foundation and Herdendorf CE (1982) Large lakes of the world. *Journal of Great Lakes Research* 8(3): 379–412 and improved from different literature sources in the MS.

in their geological characteristics (Table 1; Herdendorf, 1982; ILEC, 2005). They are located in separate sub-basins and the different sub-basins traverse the African continent draining into the Mediterranean in the north, the Indian Ocean in the east and the Atlantic Ocean in the west with one (Lake Turkana) lying in a closed basin. Although regarded as a single lake region, the AGL can be likened to islands and the fauna of even those that are connected is separated by water falls. Their morphometry, age and diverse habitats have enabled them to develop unique, endemic fish faunas and other organisms. An outstanding feature of the AGL compared to the Laurentian Great Lakes is their range of age and morphometry (Table 1), which has not only allowed for evolutionary change but has contributed to the high biodiversity and influenced the impacts of human activities on individual lakes.

The AGL are shared among 10 countries (Mozambique, Malawi, Zambia, Tanzania, Democratic Republic of Congo DRC, Rwanda, Burundi, Uganda, Kenya, and Ethiopia). They are remarkable for being the most species-rich freshwater ecosystems on earth with over 2000 fish species most of them endemic (Eschmeyer and Fong, 2018). They are important sources of highly nutritious fish with high levels of proteins, essential amino acids, vitamins and minerals such as calcium, iron and zinc, which are all important in fighting malnutrition and have health benefits. The fisheries of the lakes provide employment to thousands of people within their basins and many more along the value chain. They are reservoirs of water for domestic, industrial use, and agriculture. There are many urban areas along their shores and in their basins some of which discharge wastes into the lakes. The lake are important transport routes. Many of lakes have hydropower plants on the rivers that flow in or out of them which provide the energy much need for development. Some of the lakes have oil and mineral reserves and developments in the lakes and their basin. Many of the lakes have terrestrial national parks which are important for tourism and which, in some cases shield the lakes from land based degradation. They are also important in modulating local climate.

The way the original biogeography of the AGL was shaped by geological history has been extensively examined (e.g., Beadle, 1962, 1981; Fryer and Iles, 1972; Salzburger et al., 2014) and is, therefore not the focus of this review. The review focuses on how anthropogenic drivers due to economic demands of a rapidly increasing human population, especially in the lake basins, including habitat degradation; resources exploitation; fish species introductions; climate variability and change, and emerging stressors such as cage aquaculture (Musinguzi et al., 2019), have and are expected to continue altering the biogeography of the AGL. We also highlight the information and data needs to guide policies, and the institutional frameworks for management of the lakes. This article contributes to advancement and actualization of the process that was set by the African Great Lakes Conference of May 2017 (Doran et al., 2018) to stimulate action on networking and sharing information and data of the AGL and other lakes of the world. The review, focuses on four key questions:

- (i) What are the main drivers of biogeography of the AGL?
- (ii) What have been the trends in the drivers on the different AGL?
- (iii) How can the drivers be managed to sustain the biogeography of the AGL to enable the lakes provide the desired ecosystem and livelihood services?
- (iv) What institutional arrangements are required to manage the drivers?

The Main Drivers

Chronology of the Main Drivers

At the beginning of the 20th century the biogeography of the AGL and associated small lakes and rivers were in a virtually pristine state shaped by geological events. As the human population has increased, the biogeography has increasingly been altered by the demands of a rapidly increasing human population due to: over-fishing; land use change; and climate variability and change. These have contributed to changes in nutrients, pollutants, algae, invertebrates, fish stocks, and proliferation of invasive species (Table 2).

Table 2 The chronology of events that have contributed to alteration in biogeography of the AGL.

Period	Events and main source of information
Before 1900	Biodiversity and environment of AGL in a pristine state with fish stocks and environment little affected by anthropogenic factors (Hecky et al., 2010)
1900 onwards	Increases in human population intensifies and accelerates land use change due to conversion of land to agriculture, deforestation, wetland degradation, dam constructions, urbanization, and mineral development resulting in nutrient enrichment and pollution (Hecky et al., 2010; Otu et al., 2011)
1900–1950	Fishing effort intensifies with improvement in fishing gear, crafts and access to markets, leading to a decline and collapse of some of some especially larger lake fish species such tilapias and riverine species such as <i>Labeo</i> (Jackson, 1971; Ogutu-Ohwayo, 1990)
Mid 1950s	Non-native fishes (Nile perch, tilapias) are introduced into lakes Victoria, Kyoga and other lakes in their basin, and clupeid into Lake Kivu to improve fish production (Jackson, 1971; Ogutu-Ohwayo, 1990; Ogutu-Ohwayo and Hecky, 1991)
Late 1970s	Trawl fishery is introduced on lakes Victoria and Malawi followed by a decline in haplochromine stocks (Turner, 1977; Ogutu-Ohwayo, 1990)
1970 onwards	Stocks of introduced tilapias especially, Nile tilapia are established in lakes Victoria and Kyoga replacing the native tilapias (Ogutu-Ohwayo, 1990)
1970 onwards	Climate variability and change intensifies contributing to changes in lake levels, and aquatic productivity processes (Ogutu-Ohwayo et al., 2016)
1970–1990	Eutrophication and pollution manifests accompanied by changes in algae, invertebrate, and fish communities, water transparency, and anoxic conditions in Lake Victoria with similar symptoms in other lakes such as Malawi (Hecky et al., 2010; Otu et al., 2011)
Late 1980s	Water hyacinth, <i>Eichhornia crassipes</i> infests lakes Victoria, Albert, Kyoga, and other African lakes (Twongo, 1996)
1980–1990	Stocks of Nile perch in lakes Victoria and Kyoga increase rapidly followed by a contemporaneous rapid decline and disappearance of most haplochromine species and the lakes becomes dominated by the introduced Nile perch and Nile tilapia, and only one native species, <i>Rastrineobola argentea</i> (Ogutu-Ohwayo, 1990)
1990 onwards	Stocks of Nile perch in Victoria decline with increasing fishing effort followed by resurgence of some haplochromine species dominated by pelagic zooplanktivores and detritivores (Kishe-Machumu et al., 2015)
1990 onwards	Fish stocks in lakes Victoria, Albert, Malawi and Kyoga become dominated by pelagic species as in lakes Tanganyika and Kivu (Mangeni-Sande et al., 2019)
2000 onwards	Cage aquaculture is introduced on lakes Malawi, Tanganyika, Kivu, Victoria, Albert, and other African lakes to boost fisheries production (Musinguzi et al., 2019)
2010	The Kariba weed, <i>Salvinia molesta</i> infests Kyoga and Victoria (Wanda pers. com.)

Human Population

The economic demands of an increasing human population have been the main driver of alteration in biogeography of the AGL since the turn of the 20th century (Bootsma and Hecky, 1993). The basins of the AGL have a human population growth rate of 2–5% per year, which is among the highest in the world (PRB, 2014); and a high human population density of up to 500 persons km⁻² which varies between the lake basins (Fig. 1). The highest population density is around Lake Victoria and lowest around Lake Turkana where the population density is also very high in the Omo valley which supplies most of the water to the lake (Fig. 1). About 60–70% of the people in the AGL region depend on agriculture for their livelihood (OECD-FAO, 2016) and there are many economic activities in the lake basins.

Fishery Exploitation

Fishery exploitation was the first driver to manifest changes on the AGL through the decline, and in some cases complete disappearance, especially of the larger native fish species (Graham, 1929; Worthington, 1929; Jackson, 1971; Ogutu-Ohwayo, 1990). Prior to 1910, fisheries of the AGL were exploited for subsistence purposes in near-shore areas using traditional fishing gear such as basket traps, hooks and papyrus seines. The situation changed following introduction of flax and nylon gillnets, improvement in fishing crafts, introduction of outboard engines and improved access to markets. This increased fishing effort (Jackson, 1971; Ogutu-Ohwayo, 1990). The rates of depletion of native fish species have been different depending on habitat, susceptibility, and apparent resilience of individual fish species. The species that were restricted to shallow inshore areas of water bodies or migrated from the lakes to the rivers to breed declined and disappeared first as they were more easily accessible to fishermen.

The decline in native fisheries in some lakes led to introduction of non-native fish species to boost production. In Lake Victoria, this resulted in introduction of a large piscivorous predator, Nile perch (*Lates niloticus*) and four tilapiine species: *Oreochromis niloticus*, *O. leucostictus*, *Coptodon zilli*, and *C. rendalli* during the 1950s following the collapse of the fishery of the native *Oreochromis* species (Ogutu-Ohwayo, 1990). Introduction of the Lake Tanganyika clupeids (*Limnothrissa miodon* and *Stolothrissa tanganyikae*) into Lake Kivu was, however done to improve fish productivity in an impoverished fishery.



Fig. 2 Cages in Napoleon Gulf of Lake Victoria. Note the algal bloom near the cages. Photograph from personal field file.

Cage aquaculture (**Fig. 2**) started on Lake Malawi 2004 to enhance fish production and has expanded rapidly on some AGL and other lakes in Africa (Musinguzi et al., 2019). Most cages are located in shallow areas of aquatic systems and can impact critical biodiversity and breeding areas if not well managed. It can also increase nutrient enrichment and pollution from food wastes, fecal materials, and therapeutics (Gondwe et al., 2011) as well as introduction of invasive species.

Land Use Change

The economic activities of the rapidly increasing human population have been the main driver of alteration in biogeography of the AGL due to conversion of land and degradation of the forest cover as well as critical habitats such as wetlands. This has enhanced siltation and nutrient enrichment of the lakes and exposed the lakes to pollutants and contaminants from land, resulting in loss of critical habitats. The near-shore areas of most of the AGL are increasingly being urbanized, with areas like those around Lake Victoria with the highest human population density, expected to become completely urbanized by 2030 (Seto et al., 2012). Dams have been, and continue to be constructed along the major rivers flowing in and out of the lakes in the AGL region to provide the hydro-power needed for development which affects the environment and biodiversity of rivers and associated lakes (Kano et al., 2016). Oil and gas have been discovered in some of the lakes and their basins (e.g., methane in Kivu and oil in Albert) and exploration and exploitation can degrade the habitats if not properly done. Contaminants from the different human activities have accumulated into aquatic systems overtime further impacting their habitat. This has changed physical, chemical, and biological conditions of aquatic systems.

One of the manifestations of a changing environment was the invasion of the lakes in the AGL region by invasive weeds as the environment of the lakes became altered (**Fig. 3**). Water hyacinth (*Eichhornia crassipes*) infected lakes Victoria and Kyoga in 1980s (Twongo, 1996) and has been reported in the basins of other AGL including Malawi, Tanganyika, and Turkana, and has the potential to disrupt ecosystem services and economic activities. The other problematic plant is the Kariba weed (*Salvinia molesta*), which first occurred on Lake Kariba in the AGL region in the early 1960s following creation of the Kariba dam (Mitchell and Rose, 1979) but has increased in the Kyoga, Victoria and Albert Lake regions since the late 1990s. *Prosopis juliflora* is another weed that was introduced into Lake Turkana with the hope of greening the desert but became invasive and has since spread along inshore waters of the lake disrupting inshore breeding grounds and critical habitats for fish (Avery, 2013). These weeds have mainly altered shorelines, especially of shallow lakes and the nutrient rich shallow near shore areas and bays of deep lakes and rivers, which are areas of high biodiversity and critical breeding and nursery habitats of fishes.

Climate Variability and Change

Climate variability and change intensified in the AGL region with air and lake surface water temperatures increasing since the 1980s (**Fig. 4**). This has increasingly changed the aquatic habitat through fluctuations in lake levels, modification of wind speed,



Fig. 3 Kariba weed on Lake Kyoga (top panel) and water hyacinth on Lake Victoria (bottom panel) showing the influence of the weeds on inshore areas and apparent impact on lake use. Photographs from Fred M. Wanda (top panel) and personal field file (bottom panel).

circulation dynamics, production processes, stratification, loading and recycling of nutrients, and oxygen. This has affected especially those fishes in shallow lakes or shallow near shore areas of deep lakes and contributed to a shift in the composition of organisms to those that can tolerate the changed conditions (FAO, 2010; MacIntyre, 2012; Ogutu-Ohwayo et al., 2016).

Trends of the Drivers in Individual Lakes

The ecosystem drivers discussed above have contributed to alteration of the biogeography of the AGL at different rates depending on age and morphometry of individual lakes, the human population density in their basins, fisheries exploitation, land use change, and climate variability and change, but there are commonalities between the different lakes (Table 3). These have been accompanied by changes in the composition of fishes, fish species introductions and cage aquaculture to boost fish production of some lakes, changes in physical and chemical conditions and other biological factors, and proliferation of invasive weeds.

Lake Victoria

Lake Victoria is shared between Kenya, Uganda and Tanzania. It is the largest, and second youngest among the AGL (~400,000 years) but dried up and refilled about 14,300 years ago (Johnson et al., 1996). The lake has many papyrus-fringed bays in the west and rocky and sandy areas, especially in the south. It has open connection with many large rivers including

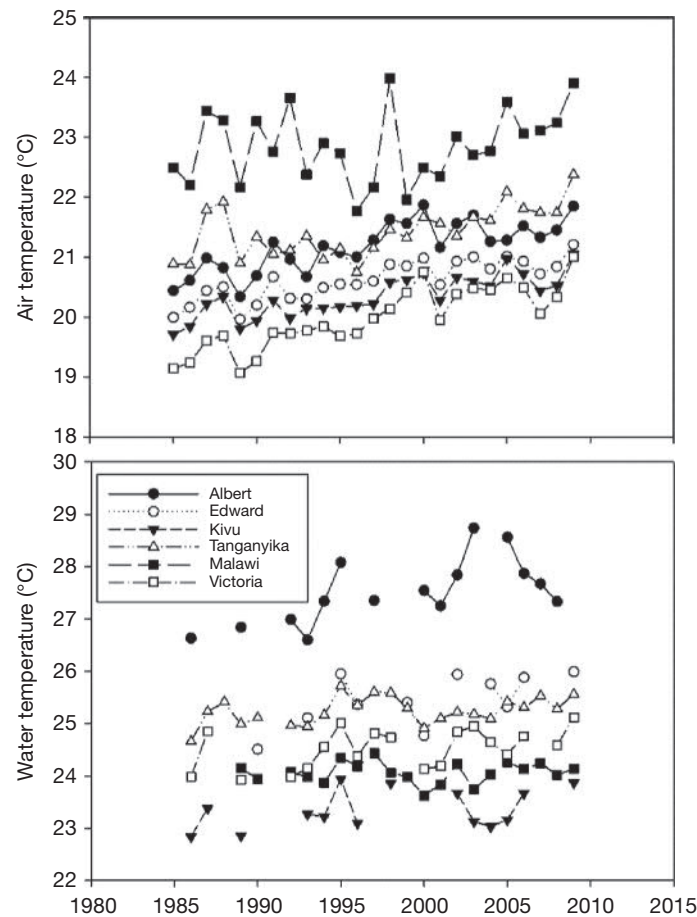


Fig. 4 Changes in air and water temperatures around the AGL between 1985 and 2010. Data adapted from Ogutu-Ohwayo R, Natugonza V, Musinguzi L, Olokokotum M, and Naigaga S (2016) Implications of climate variability and change for African lake ecosystems, fisheries productivity, and livelihoods, *Journal of Great Lakes Research* 42: 498–510, based on data from Sharma S, Gray DK, Read JS, et al. (2015). A global database of lake surface temperatures collected by in situ and satellite methods from 1985 to 2009. *Scientific Data* 2: 150008. <https://doi.org/10.1038/sdata.2015.8>.

Kagera, Katonga, Sio, Yala, Nyando, and Sondu-Miriu. Its outflow is through the Nile, the longest river in Africa, which runs through Lake Kyoga before flowing over Murchison Falls into Lake Albert at an elevation of 615 m amsl and traverses three countries (South and North Sudan, and Egypt) where its waters are highly valuable for irrigation before entering the Mediterranean Sea. The Murchison falls separates the Victoria/Kyoga system and Lake Albert and the fauna of the two systems are distinctly different and have been prevented from mixing by the falls. The Kyoga system has over thirty satellite lakes and shares a similar fish fauna with that of Lake Victoria (Ogutu-Ohwayo et al., 2013). The lake is relatively shallow, has been exposed to most of the ecosystem drivers discussed above, and provides a classical example of how these drivers have, altered the biogeography of the AGL.

The Lake Victoria basin has the highest human population density in the AGL region. It has intensive agricultural activities with high rates of deforestation and wetland degradation, the highest number of urban and peri-urban areas along its shores, and at least five hydropower dams on the Upper Victoria Nile (Table 3). There is extensive deforestation to open up land to agriculture in the lake basin and, in many places, gardens extend up to the edge of the lake (Fig. 5) exposing the lake to contaminants from the catchment area, and enhancing nutrient enrichment, sedimentation and increasing pollution and degrading the lake habitat.

Lake Victoria supports the largest freshwater fishery in the world that produces about one million tons of fish annually but this increased to this level after environmental changes that started in the late 1970s. The fishery directly employs about 200,000 people and up to 700,000 people along the value chain. The lake originally had > 500 haplochromine cichlids and 36 larger lake and riverine fish species (Graham, 1929). The commercial fishery originally comprised about twelve fish species dominated by two endemic tilapias (*O. esculentus* and *O. variabilis*), *Bagrus docmac*, *Clarias gariepinus*, and *Protopterus aethiopicus* while the rivers fisheries comprised *Labeo victorianus*, *Barbus* spp. and Momryrids. The native tilapias mainly inhabited near-shore areas (Graham, 1929) while the riverine species migrated up the rivers to spawn during rainy seasons and returned to the lake to feed (Cadwalladr, 1965). The stocks of the native tilapias and the riverine species were depleted by human exploitation following the introduction of more efficient gears and expansion of markets and their stocks had virtually collapsed by the early 1960s (Fig. 6).

Table 3 A summary of the key ecosystem factors discussed on different AGL and their status generated from literature quoted in this paper.

Key drivers	Victoria	Malawi	Tanganyika	Kivu	Edward	Albert	Turkana
Human population density/km ²	41–>500	11–100	11–500	41–500	41–100	11–100	2–40
Fish species diversity	> 500	~1000	~330	~28	~81	56	50
Changes in large native species	Collapsed	Collapsed	Declined	Had none	Persisting	Declined	Declined
Fish yield (metric tons)	1,000,000	44,000	200,000	10,000	17,000	180,000	9500
Number of fishers	200,000	56,000	45,000	6560	2000	40,000	8160
Number of introduced fish species	5	0	0	2	0	0	0
Cage aquaculture (no of cages)	12,086	53		208			
Land degradation (farming, deforestation, wetlands)	Rampant	Rampant	Moderate	Rampant	Limited	Moderate	High in Omo Delta
Urbanization (municipalities)	At least 9	0	2	1	0	0	0
Number of hydropower dams	> 5	~1	3	3	0	1	5
Status of oil and gas	None	Oil reserves in region	Oil reserves in region	Methane under development	Oil reserves in region	Oil under	development
Oil under development	Much	Little hyacinth	Little hyacinth	None	None	Much	<i>Prosopis juliflora</i> and water hyacinth
Invasive weeds	hyacinth					hyacinth	
Terrestrial game reserves	None	1	4	2	2	1	3
Temperature	Increased	Increased	Increased	Increased	Increased	Increased	Increased
Wind speed	Increased	Decreased	Decreased				
Rainfall	Variable	Increased	Increased				
Lake levels	Decreased	Decreased	Decreased	Decreased	Decreased	Decreased	Decreased
Nutrient loading	Increased	Increasing	Increasing	Increasing			Diminished
Eutrophication	Increased	Increasing		Localized		Localized	
Pollution and sedimentation	Increasing	Increasing	Increasing	Increasing			
Stratification	Shifting	Increased	Increased	Increased			
Anoxia	Increased						
Water transparency	Variable						
Primary productivity/algal biomass	Increased	Decreased	Decreased				
Algal species composition	Shifted						
Invertebrate composition	Shifted						
Contribution of small pelagics to fish yield	45%	35%	65%	60%		80%	

Haplochromine cichlids formed about 80% of the fish biomass in the lake up to the 1980s (Kudhongania and Cordone, 1974). A trawl fishery was then introduced to exploit the smaller predominantly offshore demersal haplochromine species which were still abundant. This too was followed by a decline in catch rates of haplochromines from 1753 kg h⁻¹ in 1976 to 680 kg h⁻¹ in 1982 due to limited resilience of most haplochromine species to exploitation attributed to their limited distribution, as well as specialized breeding and feeding habits of individual species (Ogutu-Ohwayo, 1990).

The collapse of the native fishery led to introduction of Nile perch and four tilapias species to boost fishery production (Ogutu-Ohwayo, 1990). The stocks of the introduced Nile perch increased rapidly from the late 1980s onwards resulting in an increase in fishery yield from about 100,000 tons to about half a million tons annually by the late 1980s (Fig. 7). This was accompanied by a rapid decline in haplochromines which was attributed to predation by Nile perch and is estimated to have exterminated about 200 of the > 500 haplochromine species that inhabited the lake (Witte et al., 1992). During the same period, remnants of the native tilapias whose stocks had been drastically reduced by overfishing collapsed due to competition with the introduced Nile tilapia (Ogutu-Ohwayo, 1990). Although total fishery yield increased, the fishery of the lake became dominated by only three fish species; the two introduced species (Nile perch and Nile tilapia) and one native pelagic cyprinid, *R. argentea* whose importance increased to contribute about 60% to the biomass and 45% to commercial catches from the lake (Mangeni-Sande et al., 2019). Afterwards some haplochromines species especially two pelagic zooplantivorous species, *Yssichromis laparogramma*, and *Yssichromis pyrrhocephalus* increased in abundance (Kishe-Machumu et al., 2015; Fig. 7). These were able to increase through adaptive radiation involving extension of their distribution from offshore to inshore waters and expansion of their zooplankton diet to include insects and other larger prey (Kishe-Machumu et al., 2017).

There were other changes in biogeography of Lake Victoria associated with changes in environment which had been cumulative due to activities of the rapidly increasing human population since the turn of the 20th century (Hecky, 1993) but only manifested after the 1970s. These changes are thought to have been triggered by increasing variability and change in climate which altered wind regimes, circulation dynamics and made accumulated nutrients available to the production processes in the water column (Hecky et al., 2010) and could have been responsible for the increases in fishery yield. The concentration of phosphorus doubled, and silica decreased 10 times, algal productivity increased 5 times, the algal communities shifted from dominance of diatom species *Aulacoseira* spp. to blue green algae, stratification increased, and deep waters became anoxic. The zooplankton community shifted from



Fig. 5 Trees cut to open up land (A) and a garden extending up to the edge of the lake with marginal papyrus burnt (B) in the in the Lake Victoria basin. File photo by the author.

larger calanoid copepods to small cladocerans and cyclopoid copepods and the larger invertebrates by chironomid and chaoborid larvae and the prawn *Caridina nilotica* (Mwebaza-Ndawula, 1994).

It is during the late 1980s, that the water hyacinth (Fig. 3) infested lakes Victoria, Kyoga and Albert covering 60% of the shoreline of Kyoga and 18,000 ha of inshore areas of Lake Victoria (Twongo, 1996) apparently as a consequence of increased nutrient availability. The invertebrate communities under the water hyacinth mats was dominated by low oxygen tolerant types such as chironomids (Wanda et al., 2001), and the fish community by hypoxia-tolerant species, such as the lungfish. Later, the Kariba weed (Fig. 3) increased especially in the shallow Lake Kyoga, but the impact on aquatic biota has not been examined.

Cage aquaculture was introduced on Lake Victoria in 2006 to improve the fish supply deficit to feed the rapidly increasing human population. The highest number of cages in the AGL region is on Lake Victoria (Musinguzi et al., 2019) and will as it expands amplify the changes in biogeography of the lake if not well regulated. The number of hydropower dams along the Victoria Nile has also increased from one to five adding to alteration in biogeography of the river and associated lakes. The lake also has the highest number of urban and peri-urban areas along its shores most of which discharge their waste into the lake and contribute to nutrient enrichment. Other lakes in the region are going through a history similar to that of Victoria and have started manifesting similar symptoms and effects on biogeography of the lakes (Otu et al., 2011). The many changes associated with human activities have made Lake Victoria to be classified among the large lakes most highly impacted by human activities (Dobiesz et al., 2010).

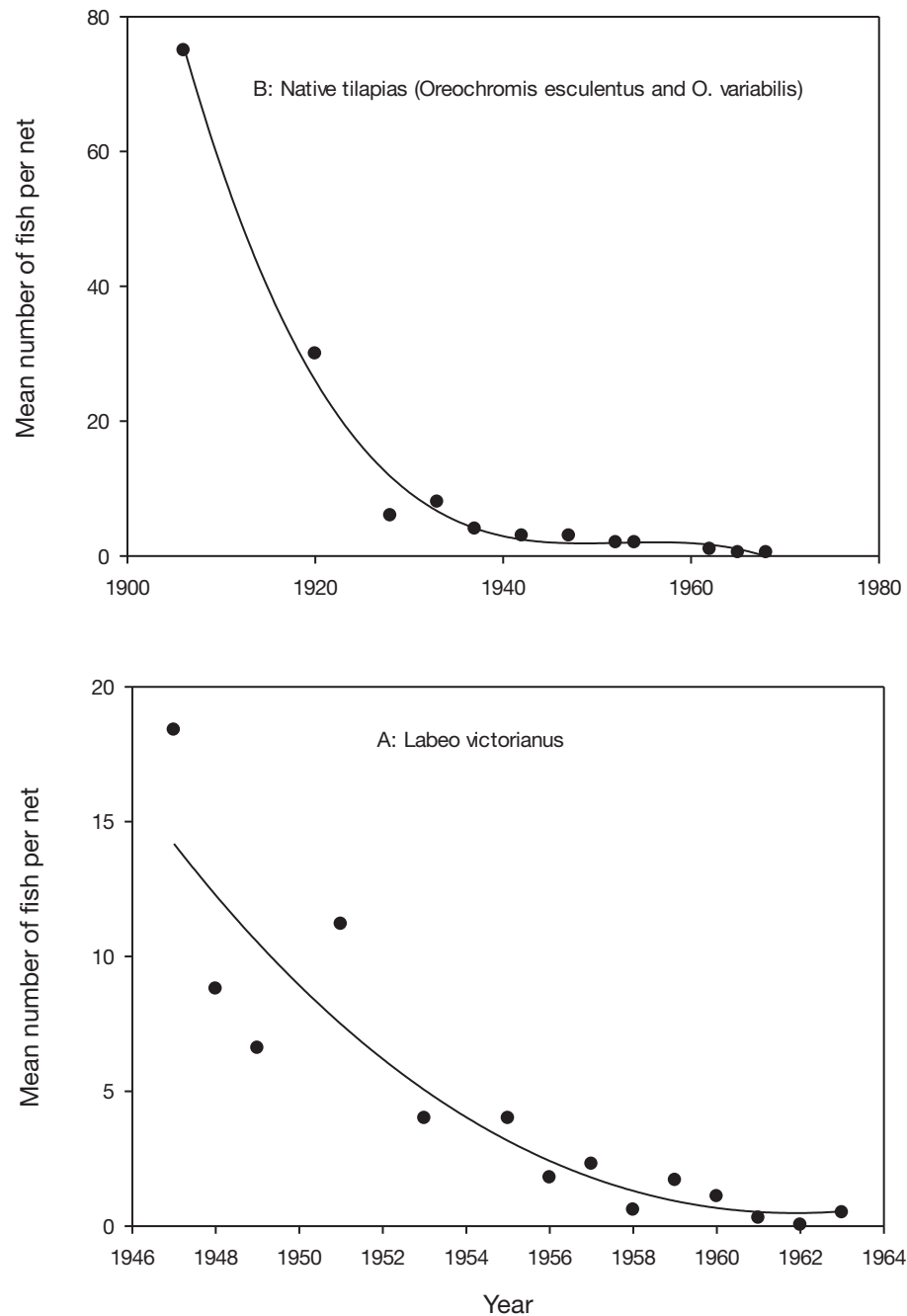


Fig. 6 The decline and subsequent collapse of the originally important lake and riverine fisheries of *Oreochromis esculentus* (B) and, *Labeo victorinus* (A) fisheries of Lake Victoria. Redrawn from Ogutu-Ohwayo R (1990) The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. *Environmental Biology of Fishes* 27: 81–96.

Lake Malawi

Lake Malawi is the southernmost and the third largest of the AGL. It is shared by Malawi, Tanzania and Mozambique. It is the third deepest lake in the world and is meromictic with waters below 200 m permanently deoxygenated (Weyl et al., 2010). The major inflows include rivers Ruhuhu, Rukuru, Songwe, Dwangwa, Lilongwe, and Cobue. The outflow is the Shire River, which flows into the Zambezi that drains into the Indian Ocean. The northern catchment has steep landscape which decreases to the south and deforestation is rampant along the slopes. It has a high diversity of near-shore rocky and sandy habitats that have contributed to evolution of a high diversity of endemic fishes, especially cichlids (Fryer and Iles, 1972).

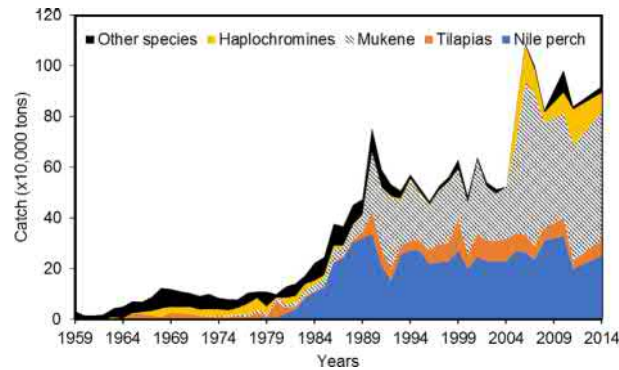


Fig. 7 The changes in commercial catch composition in Lake Victoria between 1959 and 2014 following establishment of Nile perch and Tilapias. Based on Lake Victoria catch statistics in NaFIRRI archives.

Lake Malawi is the most fish species-rich lake in the world with ~1000 fish species mainly cichlids, of which, 90% are endemic. The lake supports a fishery of about 44,000 tons annually, employing about 56,000 fishers and supporting livelihoods of > 1.6 million people (Weyl et al., 2010). Stocks of the three originally commercially important native tilapiine species locally known as chambo were, as for Lake Victoria, depleted through overfishing (Jamu et al., 2011) and the fishery has become dominated by pelagic species mainly *Engraulicypris sardella* which contribute up to 35% of the commercial catches. Introduction of a trawl fishery to exploit open water haplochromines was followed by their rapid decline (Turner, 1977). Nile tilapia, which contributed to displacement of native tilapias from lakes Victoria and Kyoga is used in aquaculture in the Lake Malawi basin and could further affect native tilapias if it gained access to the lake (Genner et al., 2013) and efforts should be made to avoid its entry into the lake. The lake is starting to be threatened by sedimentation, increased nutrient inputs especially phosphorus and the composition of phytoplankton is changing (Otu et al., 2011). The lake is also sensitive to climate change and has experienced a decline in lake levels (Kumambala and Ervine, 2010). Lake Malawi was the first AGL to which cages aquaculture was introduced to boost production and this is contributing to nutrient enrichment (Gondwe et al., 2011) and needs to be well managed.

Lake Tanganyika

Lake Tanganyika is the deepest of the AGL and the second deepest in the world. It is shared between Burundi, Democratic Republic of Congo (DRC), Tanzania and Zambia. It has the longest water residence time and is meromictic like Lake Malawi with water below 150 m having no oxygen (Salzburger et al., 2014). The main river inflows are Ruzizi (from Lake Kivu), Malagarasi and Kalambo, and the main outflow is the Lukuga River which is part of the river Congo system that drains into the Atlantic Ocean. Its entire western shoreline is very steep, which, together with its depth had contributed to it being classified among the large lakes least impacted by human activities (Dobiesz et al., 2010). The fish fauna of lakes Tanganyika and Kivu have with the exception of one species *Barinus mori* been prevented from mixing by rapids along River Ruzizi. The water level of the lake has, during geological times, dropped to levels which have split it into two lakes (Salzburger et al., 2014). This and the high diversity of rocky habitats and sandy near-shore habitats have contributed to evolution of high diversity of fishes including open water pelagic fish species, cichlids fishes and molluscan fauna (Beadle, 1962, 1981).

Lake Tanganyika is the oldest among the AGL and the fish fauna and other organisms that were of a riverine origin have fully become lacustrine with four endemic *Lates* species and two endemic clupeids. In this respect, it's regarded as having the most mature fish fauna and other organisms among the AGL (Coulter, 1988). The lake had 80 non-cichlid species of which 60% were endemic and about 250 cichlid species of which 99% were endemic. The fishery yield from the lake is ~200,000 tons annually, employing 45,000 fishers and providing 25–40% protein to about one million people (FAO, 1999). It has an ornamental fish trade. The native fishery that was originally dominated by four large endemic *Lates* species and two small sardines has changed and is dominated by one pelagic *Lates* species and the two pelagic sardines. The lake had many endemic invertebrate species (83 snail species, 65 endemic), (11 bivalves, 8 endemic), and (200 crustaceans, > 50% endemic) but their current status is not clear.

Climate warming is thought to have affected mixing dynamics of Lake Tanganyika and contributed to a decrease in primary productivity by 20% and fisheries yield by 30% (O'Reilly et al., 2003). Sedimentation is thought to be affecting stocks of inshore haplochromines stocks (Cohen et al., 1996) and development of oil and gas resources which have been discovered in the basin pose additional future threats. There are four terrestrial national parks (Ruzizi, Gombe, Mahale, and Nsumbu) around the lake which partly shield the lake from environmental degradation. Cage fish farming has started on the lake and is expected to grow but given the morphometry of the lake where wastes are expected to accumulate in deep waters, this may have limited impact on biogeography. However, it still needs to be well managed as cages are normally located in shallow near shore areas which are critical fish breeding and biodiversity areas.

Lake Kivu

Lake Kivu is at the highest elevation of 1460 m amsl among the AGL and is shared between DRC and Rwanda. It originally drained northward into the Nile sub-basin but this was reversed following volcanic eruption that formed Virunga Mountains. It flows into Lake Tanganyika over an elevation of 670 m. It is one of the smallest but the third deepest among the AGL. It has a hilly catchment and steep shoreline which is densely populated with high rates of deforestation and a potential source of siltation and localized eutrophication. It is meromictic with a shallow eutrophic zone. The water below 63 m has large quantities of methane and CO₂, and about 99% of the deep water is permanently deoxygenated.

Lake Kivu has the most impoverished fish fauna among the AGL (Salzburger et al., 2014) with 28 species including *Barbus*, *Clarias*, and *Tilapia* species with only 15 haplochromines species, 50% of which are endemic. Consequently, the Lake Tanganyika sardines (*L. miodon* and *S. tanganyikae*) were introduced into the lake in 1959 to enhance fish production. The lake produces about 10,000 tons of fish annually mainly of the sardine fishery supporting about 6600 fishermen (Snoeks et al., 2012). Among the two sardines, it is the predominantly deep water *L. miodon* which became well established and contributes most to the fishery of the lake. The lake has the highest number of fish cages in the AGL region after Victoria and cage fish farming is expected to become a major source of fish on the lake. However, as in the case of Lake Tanganyika, this may not have negative impacts due to the lake's morphometry but should be well planned and managed. The lake has large quantities of methane which is exploited for energy and this needs to be monitored and managed to reduce potential negative impacts. There are also a number of emerging urban areas along its shores and in its basin which will in the long run affect its environment and need to be well managed.

Lake Edward

Lake Edward is located in the Western arm of the rift valley. It is part of the Nile drainage basin draining into Lake Albert. It is the smallest of the AGL and is shared between DRC and Uganda. It has very steep shoreline along the DRC shores. The main river inflows are the Nyamugasani from the southwest and the Ishasha, Rutshuru and Bwindi from the south and is connected to Lake George through a 36 km Kazinga channel. The outflow is via River Semliki to Lake Albert where the fish fauna of two lakes have been prevented from mixing by the Semliki rapids. The lake experiences prolonged stratification and anoxic conditions below 80 m.

Lake Edward has ~81 fish species, of which 60 are cichlids, 92% of them endemic. The fish species composition of the lake has not changed much (Crespi and Ardizzone, 1995) apparently because of its location among national parks (Virunga and Queen Elizabeth) which are protected areas and have partly shielded it from the anthropogenic impact experienced by the other AGL. Similarly, the water quality and productivity of the lake have remained fairly stable over time with no major shifts in nutrient fluxes, phytoplankton species composition or chlorophyll-a. The fishery yield from the lake is about 17,000 tons supporting about 2000 fishers. There are, however, proposals to improve the fishery through exploitation of the abundant pelagic haplochromines. As reported for lakes Victoria and Malawi, haplochromine cichlids are not resilient to heavy commercial exploitation and this could result in a decline in their stocks and needs to be well regulated. There are prospects for cage fish farming and salt mining on the lake which could provide alternative livelihoods of people around the lake whose activities are restricted due to being in a protected game area.

Lake Albert

Lake Albert is the shallowest of the AGL and is shared between Uganda and DRC. It is monomictic, mixing completely once a year. The main inflows are River Semliki from Edward and the Victoria Nile from Lake Victoria via Kyoga and connects to the Albert Nile with which it shares a nilotic fish fauna finally draining into the Mediterranean Sea via the Nile. The water from the Victoria Nile on the north-eastern corner of the lake does not mix much with that of the rest of Lake Albert before exiting to the north but plays an important role of stabilizing the lake water levels.

Lake Albert has relatively low fish species diversity with 56 fish species but with a relatively higher number of non-cichlids compared to other AGL, and unlike other AGL, has only six haplochromine species, two of them endemic (Wandera and Balirwa, 2006). It is the third most productive lake among AGL yielding about 180,000 tons of fish annually supporting about 40,000 fishers. The larger native inshore species such as *Citharinus citharus* and *Distichodus niloticus* were depleted in the early 20th century by the beach seine fishery (Worthington, 1929). Stocks of other large species have, as in other AGL, declined and the fishery has become dominated by two pelagic clupeids (*Neobola bredoi* and *Brycinus nurse*) which contribute about 80% of the commercial catches. Despite this, Lake Albert is the only AGL which has sustained a multi-species fishery, mainly of non-cichlid species and this need to be well managed.

Water temperatures have increased by 0.5 °C and total phosphorus and nitrate have decreased below historical records (Lehman et al., 1997). Murchison Fall National Park that supports tourism is located along its north-eastern borders. Large oil deposits have been discovered in the lake and its basin and exploitation is at an advanced state. This is a major environmental threat to the lake and its biotic communities and should be closely monitored and properly managed to avoid negative impacts on critical habitats of the lake. There are also prospects for cage fish farming which could provide additional sources of fish.

Lake Turkana

Lake Turkana is the northernmost of the AGL, and the world's largest permanent desert and alkaline lake. It is the remotest of the AGL and is shared between Kenya and Ethiopia. It lies at the lowest altitude of 360 m amsl of the AGL in a closed basin in the Eastern Rift Valley. The eastern and southern shores are bounded by rocky margins, and the western and northern shores by sandy sediments.

Lake Turkana has a native nilotic fish fauna similar to that of Albert with ~50 fish species of which 11 are endemic (Beadle, 1981). Its fish stocks and fisheries are similar to that of Albert. The lake has the lowest fish production of ~9500 tons among the AGL supporting about 8160 fishermen (Avery, 2013) but the contribution of small pelagic cyprinid species that contribute most to Lake Albert fishery and are known to occur in Lake Turkana is currently is not known.

Lake Turkana is the most threatened of the AGL partly because of its location in an arid region but more importantly due to construction of dams and planned irrigation schemes along the Omo River which affects the water levels (Avery and Tebbs, 2018; Gownaris et al., 2015). The Omo River provides over 80% of the lake's annual freshwater input and associated nutrients. Development of the dams and irrigation schemes along the Omo River is reducing the flow of water and impacting the water level in a manner similar to what happened on Lake Chad and could turn the lake into the Aral Sea of Africa. For instance, when the Gibe III reservoir was filled in 2015/16, the water level of the lake dropped by 2 m and the irrigation schemes in the Lower Omo are expected to remove an additional 50% of the water. It is predicted that this will cause the lake level to drop by 15 m with enormous consequences on its ecology (Avery and Tebbs, 2018) and need urgent action to avoid it. There are also developments of oil in its western shore which need to be developed in a manner that does not impact negatively on the lake.

Synergy and Lessons From Other Lakes

The changes in biogeography of the AGL have occurred in other lakes in the AGL region, Africa and the world. Lakes such as Kyoga, Mweru and Rukwa which are traditionally not classified among AGL and satellite lakes (e.g., Nabugabo and Wamala in the Lake Victoria basin), about fifteen small lakes in the Eastern arm of the rift valley (Fig. 1) have gone through similar alterations in the lake habitat and fisheries. Lakes Kyoga and Nabugabo have undergone changes in their fisheries and environment similar to that of Lake Victoria (Ogutu-Ohwayo et al., 2013). Lake Chilwa has gone through episodes of drying up with concomitant changes in its fauna and flora associated climate variability and change. Even manmade lakes in the AGL region such as Lake Kariba have experienced similar changes in their environment, biotic communities and fisheries.

Lake Chad in Northern Central Africa which, like Lake Turkana, lies in a closed basin shrunk by 90% between 1960 and 1990 due to dam construction, excess extraction of water for irrigation from the rivers that flow into the lake, and climate change and this was accompanied by a decrease in the number of fish species from about 40 to 15 (Lévêque, 1995). The Aral Sea, in Russia, which was once the fourth largest lake in the world has shrunk by 90% due to diversion of water for irrigation of cotton farms (Whish-Wilson, 2002). Although there are efforts to improve the hydrological conditions of the Aral Sea, the waters are so heavily polluted by the chemicals applied on cotton farms that the fish and the water might never again be suitable for human consumption and use. The resources and environment of the North American Laurentian Great Lakes were also initially shaped by rapid human population growth during the early 19th century due to deforestation and conversion of land to agriculture (Beeton, 1965). The lakes have also gone through periods of nutrient enrichment especially of phosphorus, invasive species especially of the Sea lamprey (*Petromyzon marinus*) which decimated the fish stocks. These alterations have been improved through management efforts and these experiences can be useful to other lakes going through the same history such as those of the AGL region.

Lake Baikal which is the oldest (25–30 million years), the world deepest (1642 m) and probably the world's cleanest lake could have served as a good example of protecting a lake from alterations due to anthropogenic impacts but has started experiencing changes in its environment. Some potential threats to the lake such construction of a paper mill and an oil pipeline, and plans to extract and export water from the lake that were threatening the health of the lake had been prevented. The lake has been designated a UNESCO heritage site. However, it has been invaded by an invasive plant *Elodea canadensis* introduced in the 1950s (Mackay et al., 2002), and is increasingly becoming an important tourist destination and these developments will overtime affect the lake as they intensify and need to be addressed early enough.

Resilience and Persistence

Overall, the impacts of human activities on lakes has been observed to vary with lake morphometry and human population density in their basins (Dobiesz et al., 2010). Large, deep lakes such Tanganyika, Baikal, and Superior, with lower population densities in their basins have been less affected by anthropogenic factors than shallower lakes with high population density and intense agriculture and land use alterations such as Victoria, Michigan and Ontario. Endorheic lakes that lie in a closed basins such as Turkana, Chad and the Aral Sea are highly susceptible to human activities and need special attention.

Small, short-lived fish species that inhabit less structured open-water environment are more resilient than those that are restricted to shallow lakes or shallow inshore areas of deep lakes. Examples include the small short lived small pelagic cyprinids (Fig. 8) whose stocks have increased in importance, and contribute the largest quantity of fish landed in most of the AGL (Table 3; Fig. 9). Most of the cichlid have been depleted but a few have adjusted their life history characteristics and persisted. The species that have persisted under anthropogenic stressors are likely to form future fisheries on the AGL under changing anthropogenic stressors.



Fig. 8 Lake Tanganyika sardine on Lake Kivu. Courtesy, Modesta Medard.

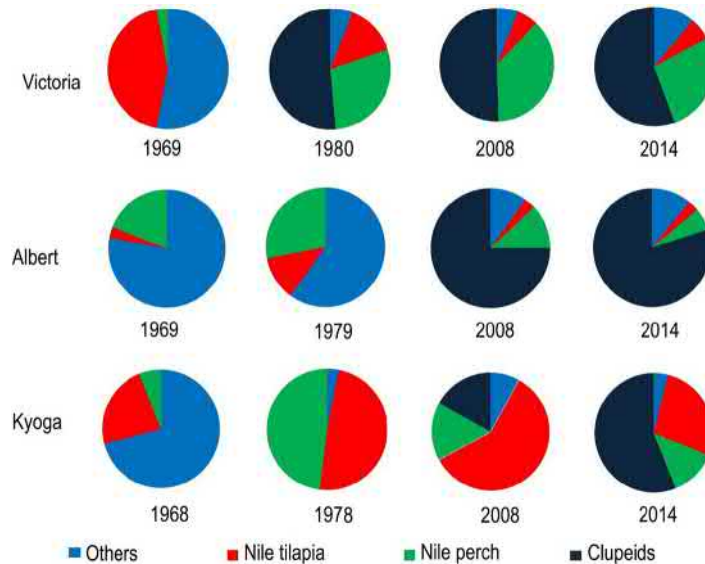


Fig. 9 The changes in contribution of small pelagic clupeids to commercial catches in lakes Victoria, Albert and Kyoga, illustrating the increase in pelagic species in the AGL. The figure is based on fish catch statistics of Uganda.

Understanding the factors that have determined resilience and persistence is important in predicting the future biogeography, especially of fishes under increasing human footprints. Among the tilapia species, it is only the Nile tilapia which has persisted in most of the lakes and even displaced other tilapia species in those lakes to which it has been introduced (Ogutu-Ohwayo, 1990). The success of Nile tilapia is associated to its life history attributes, including early maturation, a broad food spectrum, and a wide habitat range (Fryer and Iles, 1972). It can alter its fecundity under stressful conditions, and can digest blue green algae which have increased in most lakes with eutrophication and can even feed on invertebrates and other fishes when their preferred algal food becomes scarce (Moriarty and Moriarty, 1973; Njiru et al., 2007; Natugonza et al., 2015). These attributes have contributed to the success of Nile tilapia becoming one of the most important commercial fish species in capture fisheries and aquaculture in the AGL region and other parts of the world (Ogutu-Ohwayo et al., 2016). The pelagic fishes, whose populations have increased, have a very fast growth rate, are not habitat restricted and produce pelagic eggs. These small fishes are normally valued less commercially than the larger species. They are, however, be sun dried which has limited impact on the environment and eaten whole, and have high in protein, micronutrients such as calcium, iron and zinc, and vitamins that are essential for healthy living (Hicks et al., 2019). Their nutritional value especially in combating malnutrition among the poor rural communities exceeds their monetary value and should be factored in assessment of their value.

Table 4 A summary of potential management interventions for the different factors that affect biogeography of AGLs and their relative intensity derived by the authors from the information in this review (+++ = high intensity; ++ = moderately intensity; + = little intensity; 0 = not intense).

Management interventions	Victoria	Malawi	Tanganyika	Kivu	Edward	Albert	Turkana
Mobilize and share management data and information	+++	+++	+++	+++	+++	+++	+++
Network institutions to harmonize information and data	+++	+++	+++	+++	+++	+++	+++
Translate harmonize information and data into national policies	+++	+++	+++	+++	+++	+++	+++
Strengthen linkages between research and management institutions	+++	+++	+++	+++	+++	+++	+++
Develop sustainable funding mechanisms	+++	+++	+++	+++	+++	+++	+++
Control human population growth rates	+++	+++	+++	+++	++	+++	+
Promote sustainable land management (SLM) practices, and urban planning	+++	+++	+++	+++	++	+++	+
Reduce deforestation, sedimentation, urban wastes, nutrient enrichment, and pollution and promote afforestation	+++	+++	+++	+++	++	++	+
Incorporate impacts of dams in their planning, design, and operation	+++	+	+	+	+	++	+++
Extract oil and gas in a manner that does not harm aquatic biodiversity and the environment and monitor impacts	+	++	+	+++	+++	+++	++
Control fishing effort, gear types, sizes and numbers, set closed seasons and promote recovery of depleted fishes	+++	+++	+++	+++	+++	+++	++
Develop plans to specifically manage fisheries small pelagics	+++	+++	+++	+++	++	+++	+
Identify and conserve critical habitats for aquatic biodiversity and set up aquatic protected areas	+++	+++	+++	+++	+++	+++	+++
Develop alternative livelihood options specific to fishers	+++	+++	+++	+++	+++	+++	++
Prevent spread of invasive fish species	+	+++	+++	+	+++	+++	+++
Monitor, control and prevent spread of invasive weeds (water hyacinth and Kariba weed)	+++	++	++	++	++	++	+++
Develop best management practices for cage aquaculture through proper planning, siting and production practices	+++	+++	+++	+++	+++	+++	+
Investigate impacts of climate change on aquatic systems, fisheries and livelihoods and develop adaptation and mitigation measures	+++	+++	+++	+++	+++	+++	+++

Management of the Drivers

The above review shows that biogeography of the AGL and other lakes in the world is being altered and is expected to continue to change due to demands of an increasing human population. There is, therefore, need for management measures to regulate the alterations. Some of the initial actions needed based on information discussed in this paper are summarized below and in [Table 4](#) but should be continuously updated with new knowledge and data. Many of the alterations and the required actions are common to the AGL and other lakes in Africa and the world although they differ in intensity between some lakes. Thus, the need to network and share information nationally, regionally, continentally and globally. The key observations and actions which could serve as a baseline in management of the AGL discussed in this article and were also agreed upon during the African Great Lakes Conference of May 2017 ([Doran et al., 2018](#)) are as follows:

- The AGL basins have high human population densities and growth rates, driven primarily by high birth rates. Population growth rates should be moderated through increasing access to family planning and reproductive, maternal and child health services.
- The AGL have increasingly become nutrient enriched from unsustainable land use practices conversion of land to agriculture, deforestation, degradation of wetlands and riparian zones and urban wastes. Sustainable land management (SLM) practices, including protection of forests wetlands and riparian zones, should be promoted to reduce nutrient loading and siltation to protect aquatic ecosystem health. Increase in agricultural productivity should be done through improved and environmentally sustainable farming practices including proper use of fertilizers and pesticides to reduce pressure on bringing poor productivity land into agriculture.
- Most of the shorelines and catchments of the AGL region are becoming urbanized. Urban planning should be applied to minimize pollution of the lakes from industrial and urban wastes. Point and non-point sources of pollution should be identified, and measures taken to manage them.

- (d) Hydropower dams have and continue to be constructed along the rivers flowing into and out of the AGL to provide power required for development but affect the river and lake ecosystems and biodiversity. The impacts of dams on aquatic ecosystems and biodiversity should be determined and mitigation measures included in their design, construction, and operation.
- (e) Oil and methane have been discovered in some lakes and their basins and exploitation is either under way or taking place. Environmental and Social Impact Assessments (ESIAs) should be conducted prior to extraction, and mitigation measures put in place during exploitation.
- (f) There are protected areas on land around some lakes such as national parks but very few lake-based protected areas. Critical habitats for conservation of aquatic biodiversity should be identified and protected.
- (g) Stocks of many fish species of > 20 cm have declined and some completely collapsed due to high fishing pressure, use of destructive fishing gears and methods, invasive species, habitat degradation, and limited resilience. Fishing capacity should be controlled through regulation of gear types, sizes, and numbers, and limiting access. The factors that contribute to decline of some and persistence of other fishes should be determined and incorporated in management measures. Efforts should be made to promote recovery of stocks of depleted large fishes.
- (h) Small pelagic species have increased and dominate fish stocks in many of the AGL amidst multiple stressors. The causes of increase in stocks of small pelagic species should be determined and specific management plans developed for them.
- (i) Fishers have limited livelihood opportunities which contributes to their over-dependency and overexploitation of fisheries. Alternative livelihood options should be developed specifically for fishers to reduce dependency on wild fish stocks.
- (j) Introduction of fish species has, despite in some cases increasing fish production, contributed to depletion of other fishes. Measures should be taken to protect the lakes from introduction of non-native fish species. Restorations should be made only in those lakes with an impoverished fish fauna.
- (k) Cage fish farming has started on many lakes in the AGL region and has potential to reduce the deficit in fish supply due to declining stocks of wild fish stocks, but has socio-economic and environmental challenges. Best management practices for cage fish farming should be developed through spatial planning, site selection, production and market practices, securing the environment, and effective policies.
- (l) Invasive weeds such as water hyacinth (*Eihhornia cresspes*) and the Kariba weed (*Salvinia molesta*) are increasingly becoming a problem in the AGL region. The occurrence, population dynamics, causes of proliferation and impacts of the weeds should be determined and appropriate control measures developed and implemented.
- (m) Temperatures of the AGL region are warming due to human induced climate change, and are affecting aquatic productivity, and shifting aquatic species to those that can adapt to the changed conditions. The impact of climate change on aquatic life, fisheries and livelihoods should be investigated and adaptation and mitigation measures put in place.
- (n) There is considerable information and data for addressing the issues affecting the AGL and their basins but are scattered, sometimes in forms that are not user-friendly, and in many cases not accessible. There is a need to mobilize, package and share information and data and to make it readily accessible in forms that can be used by a wide range of stakeholders.
- (o) All the AGL are shared by more than one country but their management takes place at national levels. Management actions should be developed and harmonized jointly by countries sharing each lake, and adapted for implementation by national governments. Institutions of countries sharing a lake should be networked to harmonize management measures. These should then be translated into national policies for implementations. There should be a network of countries sharing the different AGL to share experiences.
- (p) Many of the research, management, and community institutions working on the AGL are uncoordinated and often donor driven with short life spans. These should similarly be networked to share information to reduce transaction costs. Longer term solutions to coordinate, strengthen, and fund research and management of these critical resources and ecosystem services of the AGL are needed. These should be coordinated through networking of institutions nationally, regionally, continentally, and globally.
- (q) Funding for collection and implementation of management information and data within and across lake basins is inadequate and insufficient to sustain the ecosystem health and services of the AGL. Addressing issues collectively with collaborative funding mechanisms would reduce transaction costs.

Institutional Requirements

Sustainable management of the AGL will require appropriate institutional arrangements to coordinate generation and mobilization of information and data to guide development of policies for management of the lakes and their basins. Management measures are normally taken by national governments at national level. Since most of the AGL are trans-boundary and shared by more than one country, the measures to be implemented at national level need to be harmonized between the countries sharing each lake. The harmonized measures can then be adapted and translated into policies for implementation at national level.

Some of the AGL have formed specific regional institutions to coordinate collection of information and data and harmonizing management measures between the nations sharing a lake such as the Lake Victoria Fisheries Organization (LVFO) and the Lake Victoria Basin Commission (LVBC) on Lake Victoria, The Lake Tanganyika Authority (LTA) on Lake Tanganyika, and The Lake Kivu and Rusizi/Ruzizi River Basin Authority (ABAKIR) on Lake Kivu. Some of the AGL such as Lake Edward, Albert, and Turkana

do not have regional organizations. Since many of the management issues facing the lakes are similar, it will be beneficial to network to develop and share information, data and experience between those organizations with regional institutions. These could then network with institutions around those lakes without such organizations to form an African Great Lakes Network. These arrangements have worked around other shared lakes in Africa such as Lake Chad which has a Lake Chad Basin Commission (LCBC) and at international level such as Great Lakes Fishery Commission and International Joint Commission (IJC) on the Laurentian Great Lakes. Besides many of the issues facing the lakes of the world are similar. It will, therefore, be beneficial to develop networks between the lakes of the world at national, regional, continental and global levels to share information and data, and management experiences. These networks if developed will improve coordination of efforts to mobilize information and data for management of the lakes. Research, management, and community institutions could form similar networks at national, regional, continental and global levels. These arrangements could improve capacity and reduce transaction costs for generation, mobilization of information and data, and implementation of management measures for conservation, development and management of lakes at national, regional, continental and global levels.

Conclusions

The resources of the AGL and their basins are highly valuable for ecosystem health and livelihoods. These resources are changing and will continue to change with the rapidly increasing human population. Most of the lakes are trans-boundary and many of the problems facing them are common among the lakes. There is need to form networks at national, regional, continental and global levels to continually monitor the changes in biogeography and their drivers, and to generate and share information and data to guide policies for development and management of the habitat and resources of the lakes to avoid reaching catastrophic levels and share expertise.

Acknowledgments

We are grateful to colleagues at NaFIRRI who provided input in this article and to Elsevier for inviting us to prepare it and to R.E. Hecky for construction comments on the original draft. This work was particularly inspired by the process set up by the African Great Lakes Conference of May 2017 that was organized by The Nature Conservancy and supported by the African Great Lakes Conservation Fund administered by the Nature Conservancy with funds from John D. and Catherine T. MacArthur Foundation to strengthen collaboration between AGL and by a request by the International Association of Great Lakes Research (IAGLR) to the lead author to develop modalities for strengthening collaboration between the Great Lakes of the world.

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The Biogeography of the Glacier Biome

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Abstract

If nutrients and a carbon source are available, life as we know it can actively reside nearly anywhere liquid water exists—even glacier ice and snow (Zawierucha et al., 2015). Just as with tropical rainforests, temperate grasslands, and polar tundra, the worldwide collection of glacial ecosystems residing on permanent freshwater ice can be considered as a biological biome (Anesio and Laybourn-Parry, 2012). In fact, all kingdoms of life (Ruggiero et al., 2015) have been found living on glacier surfaces, a land cover that extends over $1.6 \times 10^7 \text{ km}^2$ (Williams Jr. and Ferrigno, 2012), or 10% of the Earth's surface. The presence of these organisms living on glaciers leads to melting, and the melt-water they create is necessary for their existence, making the glacier biome important from a global warming perspective (Ganey et al., 2017). While all of the world's glaciers have much microbial life in common, especially single-celled algae, the taxonomic orders of glacier-dwelling macro-invertebrates differ across continents.

Part of Earth's cryosphere, glaciers, icefields, and ice-sheets are freshwater bodies of ice covering mountains and polar regions. Williams Jr. and Ferrigno (2012) report that ice covers most of Antarctica ($1.2 \times 10^5 \text{ km}^2$) and Greenland ($1.8 \times 10^6 \text{ km}^2$) as well as parts of North America ($1.2 \times 10^5 \text{ km}^2$), Asia with its Himalaya ($1.2 \times 10^5 \text{ km}^2$), the Andes of South America ($2.5 \times 10^4 \text{ km}^2$) especially Patagonia ($2.2 \times 10^4 \text{ km}^2$), Iceland ($1.1 \times 10^4 \text{ km}^2$), Europe ($5.8 \times 10^3 \text{ km}^2$), and New Zealand ($1.2 \times 10^3 \text{ km}^2$). These long-lasting bodies of ice form when—on average—the amount of snow that falls exceeds the amount that melts each year (Benn and Evans, 2010).

Glaciologists divide glaciers into three zones based on melt rate relative to snowfall: an upper elevation accumulation zone, where snowfall exceeds melt; a low-elevation ablation zone, where melt exceeds snow accumulation; and the equilibrium line altitude (ELA) between them. This transition zone can be extensive on flat glaciers and icefields. From a biological perspective, the ELA is richest in obligate glacier biota (Takeuchi, 2001, 2013), with both aquatic species (Kaczmarek et al., 2016) found in small, glacier-ice melt pools (Fig. 1) called cryoconite holes (Wharton et al., 1985), and snow and ice dwelling species (Takeuchi, 2001) found on frozen surfaces. The ablation zone is next richest, and includes non-glacier obligate taxa. Although disturbed by extreme rain events (Zawierucha et al., 2019) and rapid melting, the ablation zone is near off-glacier sources of nutrients and life. The upper accumulation zone is a veritable desert despite its snow (Shain et al., 2016) due to lack of melt.

Because liquid water is necessary for life, only where liquid water is present on glaciers can active, respiring life reside (Hodson et al., 2008). This resident, psychrophilic (from the Greek “psukhros” and “phylos” meaning cold-loving) life, usually microbial, may inhabit the glacier's surface (supraglacial), its interior (englacial; Hamilton et al., 2013), or even water between ice and basal bedrock (subglacial), where anaerobic subglacial microbes act as an important source for methane in Antarctica (Wadham et al., 2012) and elsewhere (Boyd et al., 2010). While necessary, liquid water is not sufficient to sustain life. Nutrients, too, such as nitrogen, phosphorous, and potassium (NPK) are needed, as well as a carbon source. Although englacial and subglacial life exists, this biome entry considers only surficial life as seen by a hiker or skier visiting a glacier during the melt season, when liquid water makes life most abundant.

A Glacier Walk

On a sunny late July day, a group of hikers ascends a glacier overlooking the Gulf of Alaska and draining the Harding Icefield (Fig. 2). The hikers leave the world of multicellular plants and warm-blooded animals behind as they step off a terminal moraine, the accumulated rocky debris marking the glacier's toe, and move onto the melting ice and snow of the ablation zone (Benn and Evans, 2010). The abundant blue wavelengths of light from the noon-day sun are not absorbed by water or ice, but instead reflected,

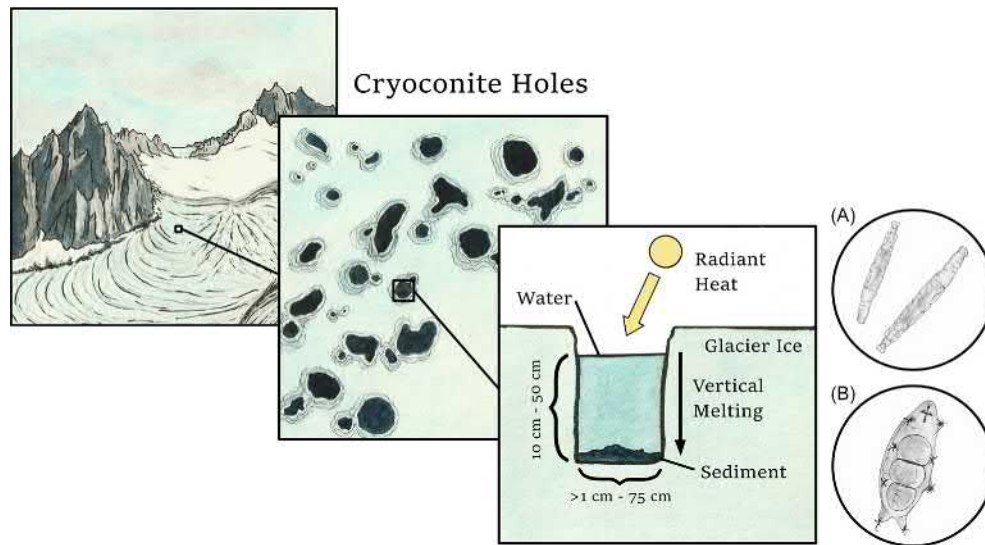


Fig. 1 Cryoconite Holes: (A) Rotifer and (B) Tardigrade.

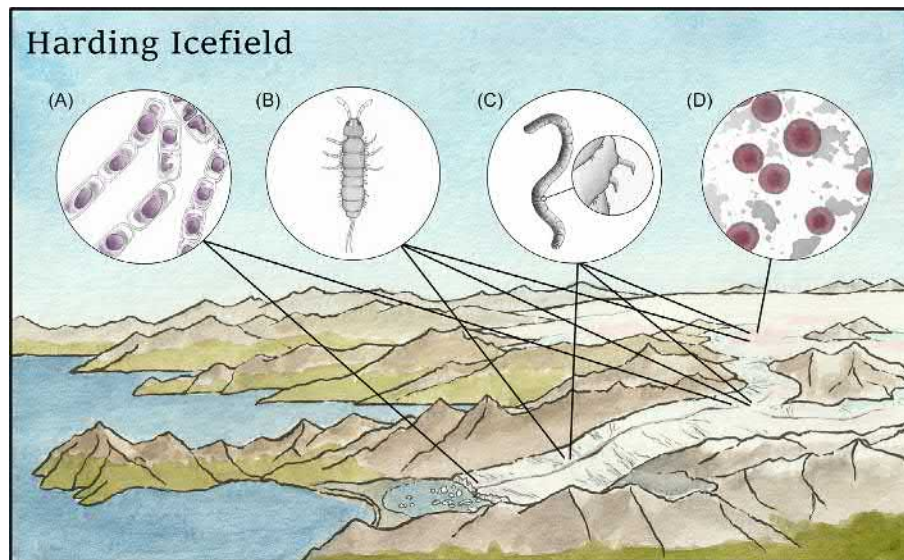


Fig. 2 Coastal Alaskan glacier biota: (A) Ice algae, (B) Collembola, (C) Chugach ice worm showing curved setae, and (D) Snow algae.

giving dense glacier ice (where pressure has removed the air bubbles) its deep blue color. The hikers find the bare ice slippery. To move up-glacier they tread across the natural traction afforded by surfaces dusted in cryoconite (Takeuchi, 2001), a mélange of sediments, wind-blown detritus, and even living and dead microscopic psychrophiles (cold-loving organisms). Stepping past small, meltwater cryoconite holes in the bare ice, the hikers don't realize that each hole is a tiny microcosm of aquatic microbes and microscopic animals (Fig. 1), like rotifers and tardigrades (Zawierucha et al., 2015). Elsewhere, water drains quickly from red-colored snows and purple-tinged rugosities where single-celled algae and cyanobacteria thrive (Takeuchi et al., 2019).

The Ablation Zone

Insolation smooths ablation ice that is clean of debris but roughens the ice when the sun's erosive action is accelerated by dust, mineral particles, and ice algae (Cook et al., 2015). All of these light-absorbing particles darken the glacier's surface, reduce its albedo (reflective value), and so add solar energy to the glacier surface. In fact, most melting on glaciers comes not from warm air temperatures, but from absorbed radiation (Box et al., 2012).

While the tinkle of a thousand tiny rivulets signals melt, even in summer freezing occurs daily and so water, paradoxically, often limits life in this environment literally made of water. The icy nature of glaciers challenges life in other ways, too. Nutrients are sparse and frozen within ice and snow crystals, unavailable to life without melting. And without the microbial equivalent of sunscreen, blinding over-illumination can damage microbes' photosynthetic apparatus as readily as it can snow-blind a hiker without sunglasses.

The ELA

As they approach the snowline marking the ELA, the hikers stop to rope themselves together as protection against crevasse falls. Tying into the safety line, one hiker notices a few thread-like objects a couple centimeters long protruding from the icy walls of a meltwater pool. These “threads” are individuals of the North American glacier ice worm, *Mesenchytraeus solifugus* (Annelida: Oligochaeta: Enchytraeidae), a small, black annelid that looks like an earthworm but lives its life on glacier ice and snow (Shain et al., 2001). Their curved setae along their bodies help them cling to slippery ice.

Roped together, the group clomps over the ice wearing metal crampons. A hiker kicks over a small, flat rock, scraped off a mountain, uncovering hundreds of tiny “snow-fleas” hiding from the sun, but now exploding in all directions like a cloud of dust. These insects of the order Collembola are also called springtails. They can be very abundant on glacier surfaces (Eisenbeis and Meyer, 1999) and cryoconite pools all around the world.

Soon, patches of snow coalesce into snowfields that cover the hard glacier ice. In the hot sun, the snow is wet, and suncups (Vimercati et al., 2019) form with red-colored snow on their sides and bottoms. The hikers stop. One bends over and brings a handful of red snow close to her face to inspect it. The soggy snowball smells fruity.

“That’s watermelon snow,” says a companion. “It’s colored by algae.” Known since the 4th century BCE, watermelon snow was seen under the earliest microscopes to be colored red by living organism. The hikers shuffle through larger and larger patches of red snow, eventually finding themselves surrounded by a vast red snowfield. On glacier-dominated landscape adjacent to the Gulf of Alaska, watermelon snow can cover from tens to hundreds of square kilometers (Takeuchi et al., 2006; Ganey et al., 2017). The Alaskan snow algae living on glaciers of coastal mountains benefit from marine-derived nutrients blown-in from the stormy North Pacific, and in turn the algae feed glacier animals in the billions: ice worms and snow-fleas graze on snow-algae (Goodman, 1971).

The Accumulation Zone

The hikers stop to camp. As the sun drops below the horizon, the temperature cools and the previously wet snow forms a firm crust preventing ice worms that spent the day a meter below the surface protected from the sun from surfacing (Dial et al., 2016). Like other life on the glacier, the campers need water. They light their camp stove and melt snow for hot drinks and dinner. In the morning, the sun spills across the glacier’s surface but the surface crust remains frozen. It will not soften until midmorning, but already algal cells are absorbing sunlight to melt the snow they contact. The hikers continue upward, picking their way past crevasses. Climbing higher into cooler air, the melt-crust thins, then disappears in the accumulation zone. At these higher elevations, the hikers stand in snow virginally white and powder dry: there is no life where perpetual cold prevents the formation or liquid water.

Glacier Life Around the World

This walk could be repeated across glaciers throughout the glacier biome: past cryoconite holes full of microbes and microscopic animals and purple-tinted bare-ice, into red snow and then beyond to the accumulation zone, where no resident life is found. On glaciers of the wetter mountains of the Greater Himalaya (Fig. 3), New Zealand, and South America’s Patagonia (Fig. 4), animals as big as Alaska’s ice worms live. In glacial pools of eastern Nepal, hikers might see larvae of the Himalayan flightless midge (Insecta: Diptera: Chironomidae), *Diamesa de novo* (Kohshima, 1984), a fly that crawls across the bare ice and snow to find mates, or even the rare Tibetan ice worm, *Sinenchytraeus glacialis* (Annelida: Oligochaeta: Enchytraeidae).

In similar habitats on New Zealand’s South Island, keen naturalists could spot a different midge, *Zelandochlus latipalpis*, (Odell, 1956) with flightless males but winged females. In the meltwater pools of South America’s southern Andes, a lucky mountaineer might find a Patagonian dragon, *Andiperla willinki*, (Vera et al., 2012), a flightless stonefly (Insecta: Plecoptera: Gripopterygidae). At the apex of the most complex food-web of all our planet’s glacier ecosystems, the Patagonian dragon feeds on other minuscule animals such as collembola, rotifers, and tardigrades.

Elsewhere on Earth’s icy reaches—Greenland (Fig. 5), Svalbard, the Alps, Siberia, Antarctica—no flightless insects, nor glacier worms, nor other macroinvertebrates have yet been discovered; just microbes using solar energy to melt snow and ice crystals for water and the nutrients bound within. Antarctic and Greenland ice sheets (GrIS) rarely have watermelon-snow, even near the coasts (Williamson et al., 2018). However, a 25,000 km² “dark-zone” covering the west-central GrIS is tinted purple and gray by dense populations of ice-algae (Ryan et al., 2018). Unlike southern Alaska, Greenland experiences relatively light snowfall and a deeper cold, garnering its reputation as a “polar desert.” Similarly, no ice-dwelling annelids or insects larger than collembola have been discovered in Antarctica, Iceland, Europe, or Siberia. Consistent with the ecological principals of island biogeography (MacArthur and Wilson, 1967) and the latitudinal gradient of biodiversity, the small “islands” of European and tropical ice (such as Africa and Papua New Guinea) and the extensive, polar ice-sheets of Greenland and Antarctica have few species. It is the relatively warm, near-freezing glaciers of the temperate latitudes and wet subtropics, where limiting nutrients are blown-in as ocean aerosols, that support the most life. However, as the climate increasingly warms, glaciers, especially small ones, are lost and with them their unique biodiversity (Zawierucha and Shain, 2019).

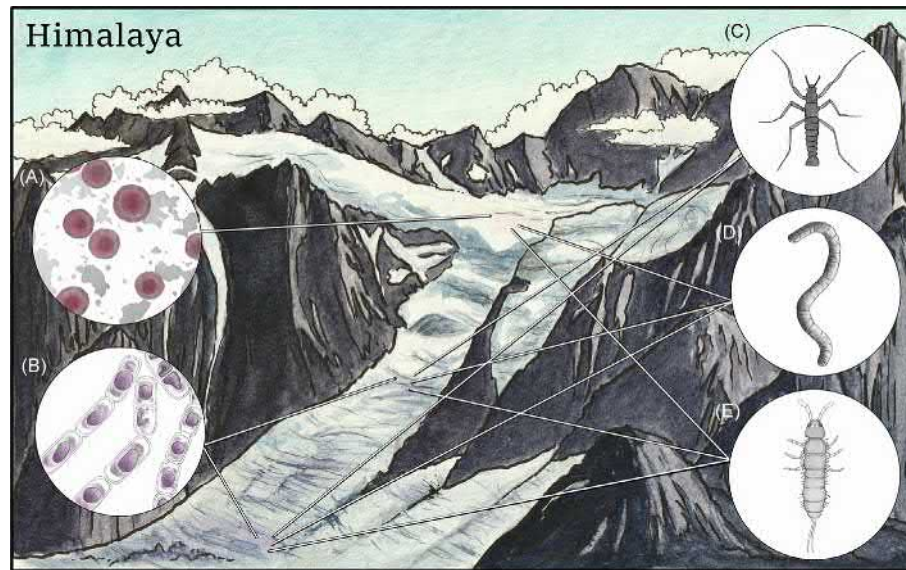


Fig. 3 Tibetan Himalaya glacier biota: (A) Snow algae, (B) Ice algae, (C) Flightless midge, (D) Tibetan ice worm, and (E) Collembola.

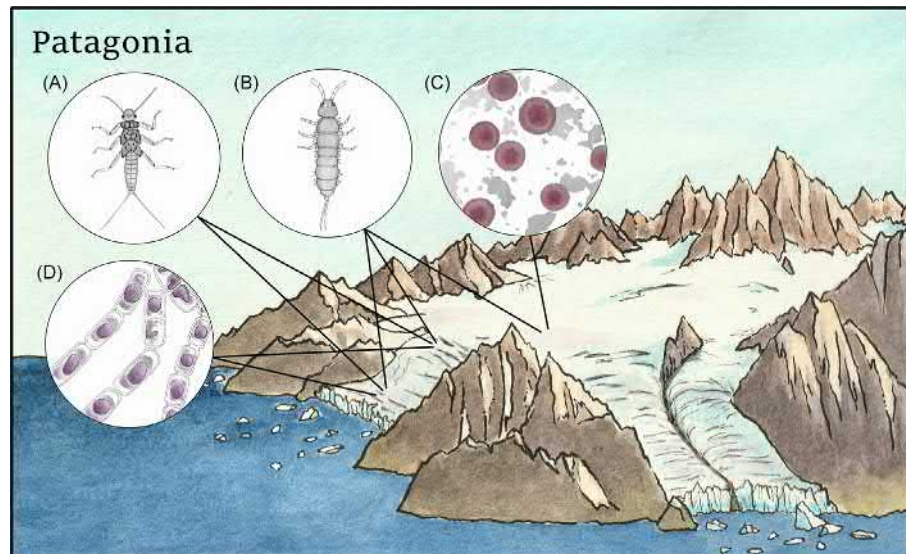


Fig. 4 Patagonian Andes glacier biota: (A) Flightless stonefly, (B) Collembola, (C) Snow algae, and (D) Ice algae.

Glaciers, Icefields, and Ice-sheets as Habitats for Life

Glacier algae solve the problems of frozen water, ice-bound nutrients, and blinding light with pigments. And because these pigments absorb solar radiation, Japanese (Takeuchi et al., 2015), American (Ganey et al., 2017), European (Stibal et al., 2017), and United Kingdom (Cook et al., 2017) scientists working on glaciers from the Arctic to the Antarctic to the high Himalaya increasingly identify microbes as responsible for more melt than any other glacier surface particle, including dust and potent black carbon (Stibal et al., 2017). Unlike the cold geophysics of non-living particles, the biological imperative for living organisms to survive and reproduce leads natural selection to favor those colors most conducive for melt (Dial et al., 2018) while avoiding overheating.

The color we see in an object is determined by the wavelengths of light reflected. The colors unseen in an object are the wavelengths absorbed, with the absorbed radiant energy converted to heat. Purple, blue, green, yellow, orange, and red fill the visible spectrum between damaging ultraviolet and water warming infrared. Sunlight arrives at Earth's surface mostly as blue and green wavelengths. Red and purplish-colored algae absorb these wavelengths, convert them to heat and use the energy to melt ice and survive in a frozen environment.

So why are ice algae one color and snow algae another? The two algal groups are unrelated, having diverged from a common ancestor 800 million to 1 billion years ago (Leliaert et al., 2012). Ice algae belong to the Streptophyta clade, which includes

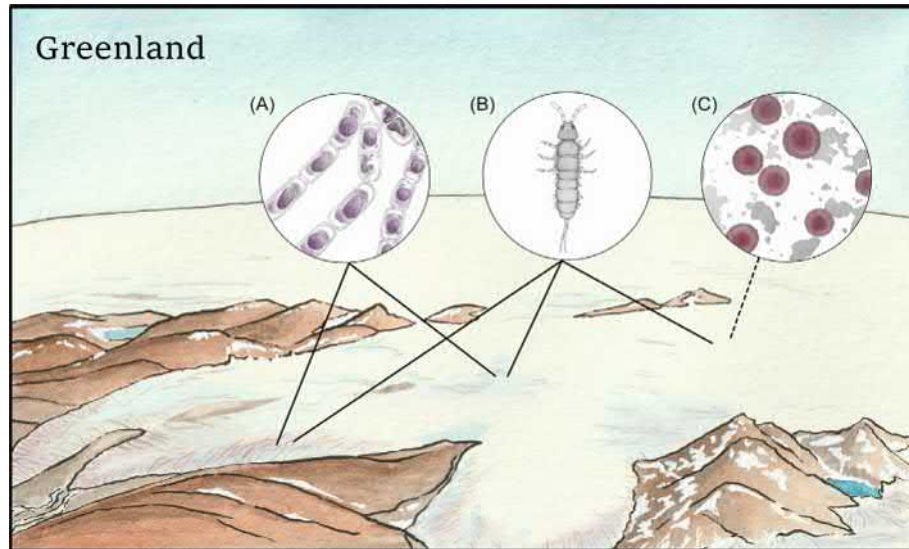


Fig. 5 Greenland Ice-sheet glacier biota: (A) Ice algae, (B) Collembola, and (C) Snow algae.

many uni- and multicellular freshwater algae and land plants. Snow algae are members of the Chlorophyta clade, including diverse marine, freshwater, and terrestrial uni- and multicellular algae. Just as these two taxa independently evolved multicellularity, they similarly arrived at pigment-based solutions to living on ice. The common ice-alga genera (*Mesotaenium*, *Ancylonema* and *Cylindrocapsa*; Kohshima et al., 1993) generally use a phenolic pigment, purpurogallin, to absorb abundant radiation and gives their icy habitat a purplish tint. Common snow-alga genera (*Chlamydomonas*, *Chloromonas* and *Chlainomonas*); (Remias et al., 2016) use a secondary carotenoid, astaxanthin, for the same purpose, coloring the snow they inhabit with their unicellular bodies as red, pink, or even orange. Neither purpurogallin nor astaxanthin is involved in photosynthesis. Instead both pigments block light from photosynthesis, absorbing the wavelengths to generate heat.

Research (Dial et al., 2018) into the melting potential of a red particle reveals that it thaws almost as much as a purple particle, but does so with a lessened heat load on the particle itself; a red particle melts ice both by conduction of absorbed light, and by reflection of red wavelengths, preferentially absorbed by snow and ice. Astaxanthin itself is esterified in fatty deposits filling the cell interior (Bidigare et al., 1993), the likely source of watermelon snow's smell (esters give fruit its distinctive odor). Fatty astaxanthin may also keep an algal cell on the surface of the snow, as oil does on water. Otherwise it might sink into the snow like mineral particles do as they melt into the snow around them.

Glacier travelers often overheat when skiing in black. The same would occur with a black snow alga cell. Ice worms, on the other hand, are black through and through, including their organs. They stay out of the sun, emerge only at night, but likely absorb the purple and blue light that readily penetrates snow. Green is the coolest color in direct sunlight, absorbing the least energy. Dial et al. (2018) conjectures that chlorophyll is green to prevent terrestrial plants from overheating. Green-colored pigments reflect the most abundant wavelength of sunlight to keep cool, the inverse of glacier algae's needs.

Taxa Living on Glacier Ice and Snow

Studies (reviewed by Kaczmarek et al., 2016) of cryoconite holes report ammonia-oxidizing archaea, nitrogen-fixing bacteria, filamentous cyanobacteria (Oscillatoriaceae) which bind with mineral particles, ciliated protozoa, diatoms (Stanish et al., 2013), purple, red, and orange-colored green algae, as well as a variety of snow and ice fungi. Obligate-glacier dwelling animals include cryoconite copepods (Hexanauplia: Copepoda: *Glaciella yalensis* Kohshima, 1987; Kikuchi, 1994; Takeuchi et al., 2000) and flightless midges (Insecta: Diptera: Chironimidae: Diamesinae; Kohshima, 1984) on Himalayan glaciers; semi-flightless midges (Insecta: Diptera: Chironimidae: Podomoninae) on New Zealand glaciers (Odell, 1956; Dumbleton, 1973; Boothroyd and Cranston, 1999); two species of stoneflies (Insecta: Plecoptera: Gripopterygidae) in Patagonia (Kohshima, 1985; Vera et al., 2012; Murakami et al., 2018; Pessacq and Rivera-Pomar, 2019); springtails (Insecta: Collembola; Fjellberg, 2010) worldwide; glacier ice worms (Annelida: Oligochaeta: Enchytraeidae) in North America's Pacific northwest (Wright, 1887; Emery, 1898; Tynen, 1970; Goodman, 1971; Shain et al., 2001; Hartzell et al., 2005; Dial et al., 2012; Dial et al., 2016) and Tibet (Liang, 1979); nematodes in Antarctica (Mueller et al., 2001) and Europe (Azzoni et al., 2015); as well as nearly pan-glacial (Zawierucha et al., 2015) tardigrades (Desmet and Vadrompus, 1994; Zawierucha et al., 2016) and rotifers (Desmet and Vadrompus, 1994; Porazinska et al., 2004; Kaczmarek et al., 2014). Facultative-glacier dwelling organisms include moss and the animals associated with that habitat such as rotifers, tardigrades, mites, and collembola (Hotelling et al., 2019).

Algal Blooms

Because albedo reduction on glaciers and ice-sheets plays an important role in further warming of Earth's atmosphere (Skiles et al., 2018), substantial current research interest focusses on snow and ice-dwelling algae and cyanobacteria: their albedo-reducing properties (Lutz et al., 2016; Stibal et al., 2017; Perini et al., 2019), ecological limitations (Ganey et al., 2017; Hamilton and Havig, 2018), and detection using remote sensing—such as by drones (Ryan et al., 2018), aircraft (Painter et al., 2001), and satellites (Takeuchi et al., 2006; Ganey et al., 2017; Huovinen et al., 2018; Tedstone et al., 2019). Most remote sensing studies use ratios of reflectance bands of onboard camera-like sensors to indicate likely algal blooms. For example, Takeuchi et al. (2006); Ganey et al. (2017) found that the ratio of red-light to green-light intensity as seen reflected from Alaskan glaciers was well-correlated with snow algae abundance there. Tedstone et al. (2019), Ryan et al. (2018) have applied similar approaches to ice algae on GrIS and Huovinen et al. (2018) to snow algae in Antarctica. These remote sensing approaches require ground-based counts of algae with simultaneous spectroscopic reflectance sampling of various densities of algae-covered snow across the wavelengths of light measured by the airborne or satellite-borne sensors.

Two groups of algae from distantly related taxa—the ice algae in the Zygnematophyceae and snow algae in the Chlamydomonadaceae—reduce albedo on glaciers (Anesio and Laybourn-Parry, 2012). Snow algae have a complex life cycle that includes dormant cysts that overwinter, flagellated cells that disperse, and vegetative cells that photosynthesize on the snow surface (Hoham and Duval, 2001). Ice algae have a simple life cycle whereby cells prepare for winter by increasing fatty acid concentration, yet produce no special cells, nor are they motile. Glacier algae (Williamson et al., 2019) prefer to settle on mineral particles (Takeuchi, 2001; Remias et al., 2005; Stibal et al., 2017), perhaps because these provide nutrients, attachment substrates in an unstable habitat or as centers for consortia among microbes (Thomas and Duval, 1995; Remias et al., 2005; Perini et al., 2019).

If algal cells melt frozen surface water by absorbing abundant wavelengths of light, while benefitting from liquid water and nutrients liberated from ice and snow crystals, then algae will increase in abundance, further increasing melt in a positive feedback (Stibal et al., 2012; Benning et al., 2014; Ganey et al., 2017). This hypothesis was tested on an icefield in Alaska by Ganey et al. (2017). To determine if increased algal abundance, increased melt, the scientists applied Nitrogen–Phosphorous–Potassium (NPK) fertilizer to increase algal abundance while simultaneously measuring snowmelt. The experiment showed that addition of NPK increased algal abundance, that increased algal abundance increased melt, and that additional water increased algae, experimentally supporting the feedback hypothesis. Other nutrient studies suggest nitrogen addition from birds (Fujii et al., 2010), iron addition from volcanoes (Harrold et al., 2018), and even inorganic carbon addition (Hamilton and Havig, 2018) can increase snow alga abundance (Ren et al., 2019).

The Biogeography of Macroinvertebrates

Glacial macroinvertebrates are sparse as a group across the world's glacial biome (Table 1). Macroscopic metazoans that are glacially obligate (segmented worms and insects) occur primarily on warm glaciers with high precipitation, such as temperate west coast mountains and the Himalaya with wet summer monsoon. These are west-coast mountain ranges of New Zealand's South Island, North and South America, and the Greater Himalaya at the headwaters of the Ganges and Brahmaputra Rivers. While Scandinavia and Iceland also have west coast mountain ranges, their glaciated regions have been apparently either too small or, more likely, too cold to evolve psychrophilic macroinvertebrates. Based on Bayesian phylogenies of mitochondrial DNA, the North American glacier ice worm (*Mesenchytraeus solifugus*) evolved as three species-level clades (Dial et al., 2016, 2012) on the warm, wet coastal edge of a continental scale ice-sheet located at temperate latitudes. While certainly the most abundant and widespread of all glacial macroinvertebrates, with populations reaching the hundreds of millions or billions on Alaskan glaciers and icefields (Goodman 1971; Shain et al., 2001), the ice worm is sensitive to cold: temperature below about -7°C (25°F) are lethal (Edwards, 1985).

Table 1 Select glacier obligate taxa and their relative abundance distribution across the glacier biome.

Region	Latitude	Plecoptera	Annelida	Diptera	Collembola, Rotifers, Tardigrades	Snow algae	Ice algae
Himalaya	Subtropical		+	+	++	+	++
North America	Temperate		+++		+++	+++	+++
Patagonia	Temperate	+			+++	++	++
New Zealand	Temperate	+			+++	++	++
Europe	Temperate				+++	++	++
Greenland	Polar				++	+	+++
Antarctica	Polar				+	+	+

+: present; ++: abundant; +++: very abundant.

The Biogeography of Glacier Microbes

Like most taxa in most environments, the explosion of advances in technology and computation have revolutionized studies of microbial biogeography. Microbes found on glacier surfaces have been shown to be far more extensive in their distributions than metazoans, as expected from the microbial cosmopolitan dispersion hypothesis: “Everything is everywhere, but the environment selects” (De Wit and Bouvier, 2006). Most studies of the glacier microbiome support this hypothesis in that a few cosmopolitan species dominate glacier ecosystems, but endemism also exists (Segawa et al., 2018; Remias et al., 2018), particularly in gut symbionts of macroinvertebrates (Murakami et al., 2015, 2017, 2018). For example, red snow algae are reported to be not only cosmopolitan across the Arctic (Lutz et al., 2016), but to show DNA haplotypes found in both arctic and Antarctic environments (Segawa et al., 2018). Fungi are less well-known, but studies show that fungi are also a consistent component of algal blooms across the Arctic (Maccario et al., 2014) and Antarctic (Davey et al., 2019). While morphological species seem widespread among all microbial groups residing on glaciers, an observation consistent with genetic studies, unique sequences are present in each region as well. Future studies will reveal more about the complexities of microbial biogeography in the glacier biome.

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Conservation Challenges to Freshwater Ecosystems

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Abstract

Natural freshwater ecosystems represent the terrestrial phases of the global hydrological cycle and include rivers, streams, lakes, ponds, wetlands as well as groundwaters. While fresh waters comprise only 0.01% of the water on Earth and constitute less than one-tenth of the global land surface area, they support >10% of all recorded species including ~30% of all vertebrates. Freshwater ecosystems support the provision of numerous ecosystem services which range from natural flood management, water supply, health, mental well-being to fish nurseries. However, freshwater ecosystems, their biodiversity and the services they provide are being jeopardized by a multitude of anthropogenic (human-mediated) stressors. Some of these threats are generated internally (habitat alteration, fragmentation, overexploitation) while others are external (invasive nonnative species, climate change, atmospheric pollution). Fortunately, many options for freshwater ecosystem conservation exist but require urgent action.

What Are Freshwater Ecosystems?

Natural freshwater ecosystems represent the terrestrial phases of the global hydrological cycle and include permanent rivers, streams, lakes, ponds, wetlands as well as groundwaters. Variations in precipitation, meltwater between seasons and hydrological events also lead to periodic or episodic inundation of floodplains, seasonal wetlands or temporary channels that form transient freshwater ecosystems to which many organisms are adapted. Artificial environments, such as canals, reservoirs, and drainage ditches, also support freshwater species. In contrast with marine and transitional ecosystems (e.g., mangroves, salt marshes, lagoons, estuaries, and open oceans), fresh waters are characterized by lower salt content (fresh water: <5 ppt vs. marine: >30 ppt) and are often subdivided into being “lotic” (flowing) or “lentic” (still) systems (Wetzel, 2001). Fresh waters occur around the world from the poles (e.g., glaciers, ice sheets) through temperate zones to the tropics. Yet, fresh waters comprise only 0.01% of the water on Earth and constitute less than one-tenth of the global land surface area (Lehner and Döll, 2004) while marine systems cover more than 70% of the globe and account for >97% of the Earth’s water (NOAA, 2018). Freshwater drainage basins (i.e., watersheds (North America; used hereafter) or catchments (United Kingdom)) are clearly defined units in terrestrial landscapes, formed where precipitation collects and drains downslope to a common outlet at lower elevation such as an estuary, bay or landlocked wetland (Fig. 1). Being both hydrologically connected and topographically low in the landscape means that fresh waters are open systems that transfer matter, energy and solutes, including pollutants, to and from neighboring ecosystems (Hynes 1975; Brooks et al., 2003). Their connected nature means they are conduits for the longitudinal or lateral movement of organisms, including invasive species, that are now among a wide range of stressors that endanger the disproportionately large biodiversity that inhabit these ecosystems (Reid et al., 2018).

Rivers and Streams

Rivers and streams are lotic systems that connect aquatic and terrestrial environments, circulating precipitation and sediments from the land to lakes, estuaries and oceans. They cover less than 1% of Earth’s nonglaciated land surface (694,000–852,000 km²; Allen and

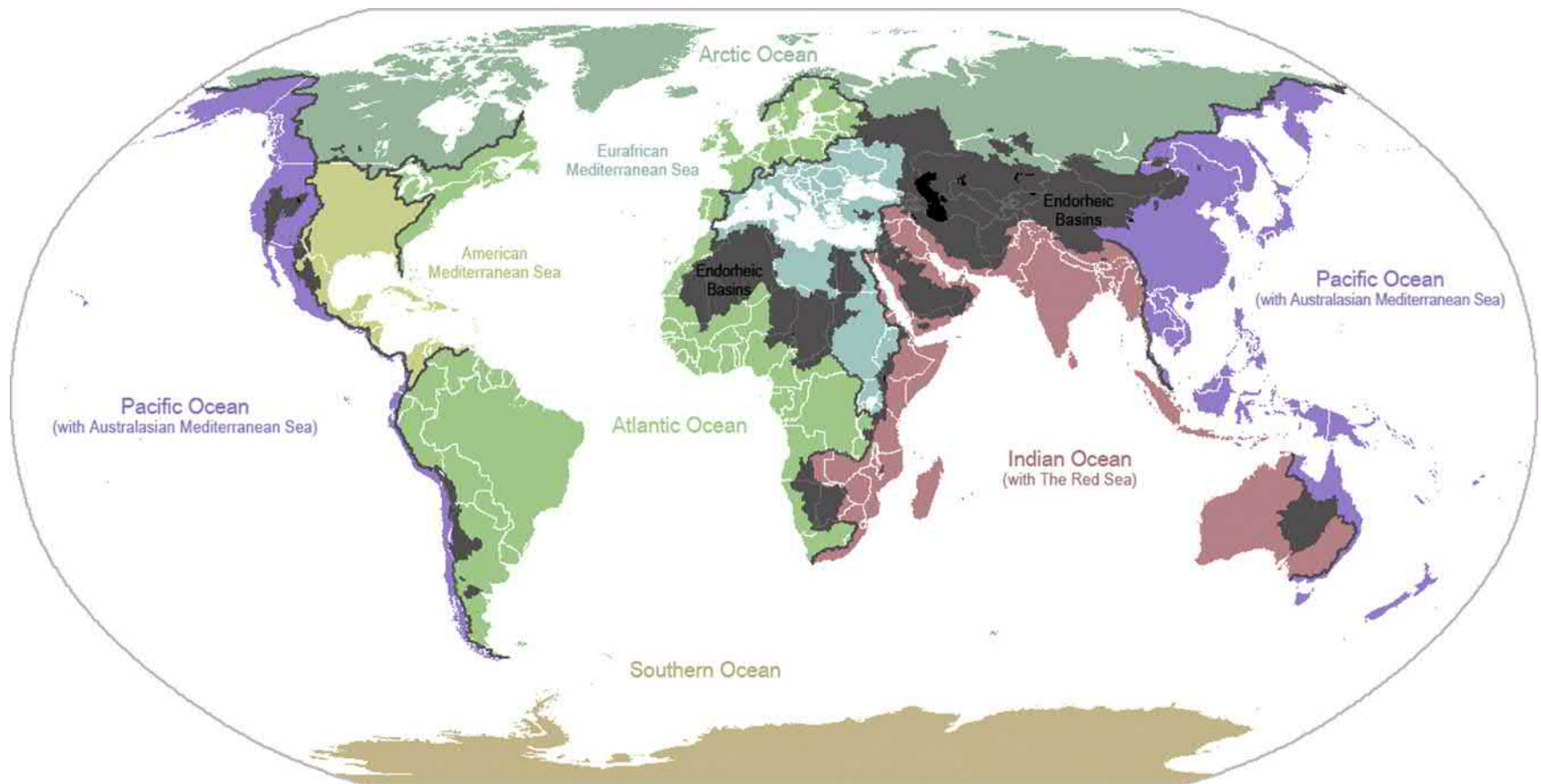


Fig. 1 Major continental divides of the world, showing drainage of fresh waters into the major oceans and seas—gray areas are endorheic (terminal) basins that do not drain into marine ecosystems. Courtesy Public Domain.

Pavelsky, 2018). The world contains a diversity of rivers and streams—distinguished by permanency (e.g., permanent and intermittent), channel shape (e.g., braided and meandering), biodiversity (e.g., algae, invertebrates, fishes), ionic composition (e.g., major ions and macro-nutrients) and other factors—but the vast majority of riverine ecosystems have been altered by humans (Grill et al., 2019).

Lakes and Ponds

Lakes and ponds are lentic systems, many of which are fed and drained by rivers and streams. The world contains at least 304 million natural lakes spanning 4.2 million km² (Downing et al., 2006). However, the majority are small (>91% are 0.001–0.01 km² [0.1–1 ha]) and few are large (0.005% >100 km² [10,000 ha]; Cael and Seekell, 2016). Natural lakes and ponds are found predominantly in mountainous regions, rift zones and areas with ongoing glaciation. Many artificial lakes and reservoirs are constructed for agricultural or industrial purposes (e.g., hydroelectricity; Grill et al., 2019).

Freshwater Wetlands

Wetlands (e.g., swamps, marshes, bogs, and fens), which are either permanently or seasonally inundated by water, are among the most productive habitat types in the world. They cover an estimated 5.4–6.8% of the Earth's land surface area (Lehner and Döll, 2004). Wetlands are found on every continent and can be characterized as being saltwater, brackish (intermediate salinity) or freshwater. Artificial wetlands are also built for wastewater treatment and stormwater runoff.

The Immense Biodiversity of Fresh Waters

To many, freshwater biodiversity means “fish.” Yet, freshwater fish are but one of many organisms that live in fresh waters or depend upon freshwater ecosystems for nourishment or reproduction. While fresh waters comprise just a fraction of the water on Earth, they support >10% of all recorded species (Dijkstra et al., 2014; Mittermeier et al., 2010), estimated at ~126,000 freshwater-dependent species (IUCN, 2019). In fact, ~30% of all vertebrates live in freshwater ecosystems or are entirely dependent upon them—from the amphibians (which exceed 4300 species) and freshwater snakes and turtles to many aquatic birds and even some freshwater-dependent mammals (such as platypus and freshwater dolphins). If one considers just fish, the numbers are also impressive. Of the nearly 30,000 fish species identified to date, well over 10,000 of them are considered to be freshwater—with estimates of around 45% of all fish residing in freshwater at some point during their lives. Beyond the vertebrates, freshwater is also home to many plants and invertebrates. For example, according to the International Union for Conservation of Nature (IUCN, 2019), 5600 Odonata (dragonflies and damselflies), and 5000 mollusk species depend on freshwater habitats (Strong et al., 2007). Even freshwater crabs are incredibly abundant with nearly 1500 species (Yeo et al., 2007). Fresh water clearly has disproportionately high biodiversity. Freshwater wetlands as well as rivers and littoral zones of lentic systems are also home to many plant and algae species albeit they have not been well inventoried from a biodiversity perspective (Denny, 1994; Spence, 1982).

Freshwater Ecosystem Services

Freshwater ecosystems support the provision of numerous ecosystem services—the diverse benefits, both material and nonmaterial, that people obtain from ecosystems (MEA, 2005). Another way to think of ecosystem services is as the contributions nature makes to people (Díaz et al., 2018). Examples of the benefits people derive from freshwater ecosystems vary from having clean water to drink, to feeling a spiritual connection to rivers, lakes and wetlands, to avoiding flooding events and the associated consequences. Freshwater systems also support numerous important ecosystem processes, such as nutrient cycling, which are sometimes referred to as “supporting services” (Carpenter et al., 2009).

The concept of ecosystem services is useful to help freshwater researchers and practitioners consider the diverse ways these systems interact with, and contribute to, human well-being. It encourages a holistic approach to thinking about ecosystems in terms of both social and ecological dimensions (MEA, 2005), with numerous interacting components that vary across space and time (Rodríguez et al., 2006). An associated challenge with employing the ecosystem services concept, however, is how to accurately assess and quantify services. Although there is no single standard method that can be broadly applied to assess freshwater ecosystem services, and ultimately, the appropriate method depends on the purpose of assessment, there are fortunately a growing number of ways this is being achieved in freshwater ecosystems (Table 1) and robust recommendations for how to conduct holistic assessments considering freshwater specific features such as connectivity (Hanna et al., 2018).

Freshwater Biodiversity in Crisis

Despite the importance of fresh waters and their flora and fauna to human needs and wellbeing, freshwater biodiversity is in crisis (Harrison et al., 2018). Global estimates show that freshwater species populations have declined on average by 83% over the last

Table 1 Examples of freshwater ecosystem services and methods that can be used to assess them.

<i>Selected freshwater ecosystem services</i>	<i>Example methods that can be used to quantify freshwater ecosystem services</i>
Drinking water	Water samples collected from a water source used for drinking and analyzed for nutrient concentrations, bacteria, and trace-metals to assess the quality of water for drinking A web-based survey sent to residents of a watershed asking them where they source their drinking water and how satisfied they are the quality and quantity of water they have access to
Sense of place	Interviews with people living within X kilometers of a stream asking them to describe if and how that stream contributes to their sense of place Interviews with people living within X kilometers of a stream asking them what monetary value they would be willing to pay to maintain their access to that stream
Recreation (e.g., paddling)	Distribution of a survey to park visitors determining if recreational paddling was one of the activities they conducted during their visit Classification of rapids along a river in terms of their recreational value for recreational white-water paddling
Food provision (e.g., fish)	Participatory mapping assessing locations visited by relevant community members to catch fish and the amount and species of fish caught Assessment of locally relevant fish contaminant concentrations (e.g., mercury, chromium) to assess the quality of fish for consumption
Flood mitigation	The percent of wetland coverage in a watershed, used as a proxy for the relative capacity for flood mitigation The amount of people found in a floodplain and the financial values of their assets as a means to assess the importance of flood mitigation

Before assessing freshwater ecosystem services researcher or practitioners have to make decisions concerning which ecosystem services are relevant for quantification, the appropriate spatial and temporal scales of assessments, the aspect of ecosystem services that is of interest—that is, do they want to quantify the capacity of a system to provide a service, the actual provision of a service, or the demand for a service, the best indicators that can be used to represent the services they are trying to quantify and establish who are the appropriate stakeholders or individuals that should be involved with quantification.

four decades (Fig. 2; WWF, 2018). Knowledge of the conservation status and distribution of freshwater taxa is limited relative to terrestrial species (Darwall et al., 2011), yet there is growing evidence that extinction risk in fresh waters is exceptionally high. Currently, almost one in three freshwater species is threatened with extinction worldwide, exceeding the risk of extinction compared to their terrestrial counterparts (Collen et al., 2014). Reptiles are potentially the most threatened freshwater taxa, with nearly half of species threatened or near threatened (Collen et al., 2014). Moreover, 40% of assessed freshwater bivalves (Lopes-Lima et al., 2018), 32% of all crayfish (Richman et al., 2015), 32% of all amphibian species (Stuart et al., 2004), 32% of assessed crab species (Cumberlidge et al., 2009), 25% of all mammals and fish (Collen et al., 2014), and 10% of assessed dragonflies and damselflies (Clausnitzer et al., 2009) are near threatened, threatened or extinct, according to the IUCN Red List criteria. This lends urgency to the study of diversity and of the relative risk of extinction of species in freshwater ecosystems, yet freshwater species remain a low priority on national and international conservation agendas, such as the United Nations Sustainable Development Goals (SDGs; Lynch et al., 2017; Reid et al., 2017). Conservation of freshwater biodiversity is partly impeded by an inadequate understanding of the economic value of freshwater species (and the services they provide) as well as a robust understanding of how freshwater species are at risk from multiple interacting stresses.

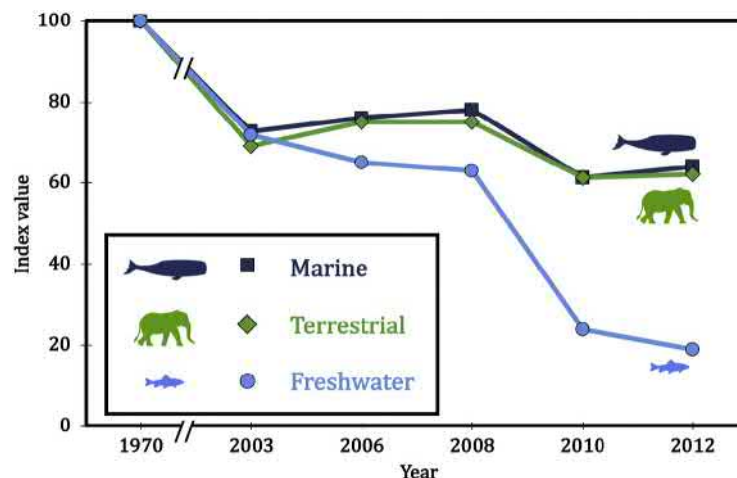


Fig. 2 The World Wide Fund for Nature (WWF) Living Planet Index (LPI) reveals remarkable decreases for freshwater species relative to marine or terrestrial species. These index declines are relative to a benchmark value of 100 in 1970. Dates given here refer to years in which estimates of abundance were made, as LPI reports typically refer to data from 4 years earlier (e.g., the 2016 LPI is based on 2012 data). Data from World Wildlife Foundation (WWF). (2018). Living Planet Report—2018: Aiming higher. In: Gland, Grooten, M. and Almond, R. E. A. (eds.). WWF.

Anthropogenic Stressors

Despite this downward trajectory for freshwater taxa, less than 20% of recent papers deal with aquatic species demonstrating a persistent bias in the conservation literature towards terrestrial organisms (Di Marco et al., 2017). This is problematic for many reasons. Firstly, terrestrial biodiversity indicators are a poor surrogate for freshwater biodiversity (Darwall et al., 2011). Furthermore, while some leading freshwater conservation solutions depend on management at the terrestrial/freshwater interface (e.g., reduced agricultural runoff), many land-based conservation efforts for freshwater biodiversity require implementation over large spatial extents at channel, riparian (relating to river banks) or watershed scales (Darwall et al., 2011). Finally, and as demonstrated above, freshwater ecosystems represent hotspots of endangerment due to the convergence of biological richness and the many forms of human freshwater exploitation. Due to an incurred 'debt' arising from low-viability populations that are in the process of dwindling to extinction, it is likely that freshwater extinction risks will remain high over the forthcoming decades (Strayer and Dudgeon, 2010). Nor will anthropogenic pressures on freshwater ecosystems ease soon, in view of the threats reviewed below.

Why are freshwater species facing such high rates of extirpation and extinction? The answer, in part, was outlined in a seminal review paper by Dudgeon et al. (2006), "Freshwater biodiversity: importance, threats, status and conservation challenges." Here, they identified (i) overexploitation, (ii) water pollution, (iii) flow modification, (iv) destruction or degradation of habitat, and (v) invasion by exotic species as the five leading causes of population declines and range reductions of freshwater organisms worldwide. This authoritative paper has been cited over 1800 times, placing it among the top-cited 1% of papers in the field of Biology and Biochemistry (Web of Science®). However, over the last decade, and as we advance into the epoch now being referred to as "The Anthropocene" (Crutzen, 2006), these threats have escalated and/or evolved, and new or previously unrecognized threats have become more apparent. To address this knowledge gap, Reid et al. (2018) provided a critical update on the status and threats to global freshwater biodiversity. Therein, they identified (i) changing climates, (ii) e-commerce and invasions, (iii) infectious diseases, (iv) harmful algal blooms, (v) expanding hydropower, (vi) emerging contaminants, (vii) engineered nanomaterials, (viii) microplastic pollution, (ix) light and noise, (x) freshwater salinization, (xi) declining calcium, and (xii) cumulative stressors as the most significant contemporary challenges to freshwater conservation (Fig. 3; Table 2; see Reid et al., 2018 for references).

Options for Freshwater Ecosystem Conservation

Protect the best, restore the rest, adapt where pressed.

As revealed throughout this review, pressures and threats to the world's freshwater ecosystems arise at all scales from the local to the global. They are propagated through the aquatic, groundwater, riparian and watershed systems from which lake, rivers and wetlands are formed. Some of these threats are generated internally (habitat alteration, decreased longitudinal or lateral connectivity, pollution, over-exploitation) while others are external (invasive nonnative species, climate change, atmospheric pollution; WWF, 2018). Additional complexity also arises as threats to freshwater ecosystems evolve (Reid et al., 2018). Some of the resulting changes affect freshwater species directly, while alteration in fluxes or exchanges of nutrients, matter and energy affect many ecosystem processes with indirect consequences for populations, species or communities of organisms (Table 2).

Approaches to freshwater ecosystem conservation should ideally be effective in the face of all of these threats and pressures, while also protecting as completely as possible the Earth's diversity of freshwater organisms, freshwater ecosystems and the services they provide. Set against this ideal, however, is the fact that freshwater ecosystems are embedded in terrestrial landscapes whose use and management is seldom focused on conservation, but more on activities such as agriculture, silviculture, extractive industries, urban land or transport that can each cause downstream change or lead to the direct exploitation of water and associated resources. In many freshwater ecosystems, the consequences have developed over decades to centuries—meaning that conservation often has to involve repair or restoration of areas degraded by past impacts as well as the protection of more natural ecosystems.

Boon (1992a,b) developed a hierarchy of options for conserving freshwater ecosystems which ranged from "protection" where systems were relatively pristine; "limitation" or "mitigation" of damage where economic activities were sanctioned in or around freshwater ecosystems; through to "restoration" where past impacts would be reversed. A further option has since been recognized where impacts are considered inevitable—for example from climate change—and involves "adapting" freshwater ecosystems to accommodate or offset the worst effects (Thomas et al., 2016). Hierarchical concepts like these have been the source of the conservation mantra: "protect the best, restore the rest, adapt where pressed."

No matter where in this hierarchy conservation options are applied to freshwater ecosystems, there are two major and related constraints. The first stems from the connections between freshwater ecosystems and their surroundings through which fluxes and flow-paths bring both positive (e.g., resource subsidies) and negative effects (e.g., pollutants; Hynes, 1975; Likens, 2013). The ideal conservation strategy would be to designate, protect, manage or restore entire watersheds as reserves to control such fluxes, but competition with other land-uses often forces compromises so that action can only be localized (Fig. 4). The second major issue is one of scale: where freshwater ecosystems are large—such as in the case of the World's great lakes or river systems—the sheer spatial extent over which conservation problems arise is a challenge in its own right, for example because drainage basins are extensive (often international), while organisms adapted to these systems have endemic character or migratory life cycles that require protection ideally over entire systems such as from source to sea.



Fig. 3 The five major threat categories and their established or potential interactive impacts on freshwater biodiversity from Dudgeon et al. (2006), shown in the inner gray circles. The 12 major threat categories and their established or potential interactive impacts on freshwater biodiversity from Reid et al. (2018), shown in the outer yellow circles.

In non-aquatic ecosystems, the designation of nature reserves is a mainstay of conservation action, and this same approach has been applied to freshwater ecosystems for decades—for example through the specifically aquatic Ramsar Convention (Gardner et al., 2015), through European Natura 2000 Sites under the European Union Habitats Directive (92/43/EEC), or in the United Kingdom as Sites of Special Scientific Interest. In most of these cases, however, designated areas achieve only limited reach, for example from bank-to-bank in rivers, occasionally extending into riparian zones or floodplain wetlands, or to the protection of headwaters often as part of larger terrestrial reserves. In the absence of the protection of freshwater ecosystems at scale, alternative approaches attempt to control or regulate some adverse pressures—a prime example being Europe’s Water Framework Directive (WFD 2000/60/EEC). The WFD simultaneously identifies adverse pressures while encouraging beneficial “programs of measures” to protect or restore freshwaters to “good ecological status”—for example through reduced nutrient inputs or improved wastewater treatment.

Beyond designation or restoration, other potential instruments to encourage freshwater conservation include government financial incentives to replace “income foregone”—for example as part of agri-environment schemes where land-owners are funded to provide sensitive land-management in place of intensification. Voluntary “codes of practice,” for example in the production forestry, extractive or building industries, also set standards by reducing damaging practice. Large-scale demonstration activities sometimes illustrate how freshwaters can be protected in freshwater ecosystems where Indigenous peoples, governments or nongovernmental organizations can influence land management at scale. Increasingly, also, market mechanisms are being explored to protect or restore freshwater through “natural capital” or “markets for ecosystem services” that account more fully for the benefits provided by high quality freshwater ecosystems—for example reduced treatment costs in water supply, natural flood management, health and mental being, or nurseries for important fish stocks (Ormerod, 2014). Key needs in applying such market mechanisms are in identifying providers and users of ecosystem services, ensuring that payments and benefits flow accordingly, and in sourcing investments to fund schemes equitably and sustainably.

Table 2 Characteristics of long-standing (indicated by 'a' superscript) and emerging ('b' superscript) threats to freshwater biodiversity: their geographical extent (and focal regions); the severity of their effects; examples of attendant ecological changes; our degree of understanding; and potential options for mitigating threat effects.

<i>Emerging threat (regions)</i>	<i>Severity of effects</i>	<i>Ecological changes</i>	<i>Degree of understanding</i>	<i>Mitigation options</i>
Over-exploitation (global) ^a	Already causing extinctions; likely to cause more	Alters species size, range, and survival (target + bycatch)	Well understood, but interactive stressor effects unclear	Global commitments; expand freshwater protected areas
Water pollution (global) ^a	Already causing extinctions; likely to cause more	Alters species survival, with clear ecosystem effects	Increasingly well understood but high unpredictability	Improve surveillance; management to favor ecosystem controls
Habitat degradation (global) ^a	Already causing extinctions; likely to cause more	Alters species survival, with clear ecosystem effects	Well understood, but interactive stressor effects unclear	Global commitments; expand freshwater protected areas
Species invasion (global) ^a	Already causing extinctions; likely to cause more	Alters species survival, with clear ecosystem effects	Increasingly well understood but high unpredictability	Improve surveillance; management to favor ecosystem controls
Flow modification (global) ^a	Already causing extinctions; likely to cause more	Fragments river systems, inhibiting species movement	Well understood, but interactive stressor effects unclear	Ameliorate passage infrastructure; assess all project impacts
Changing climates (global) ^b	Already causing extinctions; likely to cause more	Alters species size, range, phenology, and survival	Moderately well understood but high unpredictability	Global commitments; expand protected areas; restore refugia
E-commerce and invasions (global) ^b	Significant role in trade of nonnative plants and animals	Creates novel modes of long-distance dispersal	Largely unregulated activities that are poorly understood	Online consumer accountability tools; awareness campaigns
Infectious diseases (tropics) ^b	Already causing extinctions; likely to cause more	Alters species survival, with clear ecosystem effects	Increasingly well understood but high unpredictability	Improve surveillance; management to favor ecosystem controls
Harmful algal blooms (nutrient-rich, warm) ^b	Linked to species losses; likely to cause more	Reduces species growth, survival, and reproduction	Increasingly well understood, some unpredictability	Improve surveillance; management to favor ecosystem controls
Hydropower (emerging markets) ^b	Already causing extinctions; likely to cause more	Fragments river systems, inhibiting species movement	Well understood, but interactive stressor effects unclear	Ameliorate passage infrastructure; assess all project impacts
Contaminants (developed markets) ^b	Unclear how biodiversity will be changed	Alters some species health, abundance and reproduction	Largely understudied and thus poorly understood	Improve medication disposal; advance wastewater treatment
Nanomaterials (developed markets) ^b	Unclear how biodiversity will be changed	Causes minimal acute toxicity in some species	Considerable uncertainty around long-term effects	Improve detection and characterization; create targeted formulations
Microplastics (developed markets) ^b	Unclear how biodiversity will be changed	Potentially detrimental effects on species health	Considerable uncertainty around long-term effects	Reduce plastic usage; legislation to curb use of specific products
Light and noise (developed markets) ^b	Linked to species disturbance; likely to continue	Alters behavior and physiology of some species	Well understood, but ecosystem-level effects unclear	Identify less harmful types; reduce usage; educate users
Salinization (coastal lowlands) ^b	Linked to species losses; likely to cause more	Reduces species growth, survival, and reproduction	Increasingly well studied and understood	Control point sources; strategic release of freshening flow
Declining calcium (softwater lakes) ^b	Linked to species declines; likely affecting foodwebs	Causes shifts in lake invertebrate assemblages	Increasingly well understood; solutions unevaluated	Further reduce acidic precipitation; replenish calcium in watersheds
Cumulative stressors (global) ^b	Contributing to extinctions; likely to cause more	Magnifies impacts; create ecological surprises	Poorly understood with high levels of unpredictability	Identify multipurpose solutions that protect biodiversity hotspots

^aInformation derived from Dudgeon et al. (2006).

^bModified from Reid, A. J., Carlson, A. K., Creed, I. F. et al. (2018). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews* **94**, 849–873.

Modified from Reid, A. J., Carlson, A. K., Creed, I. F. et al. (2018). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews* **94**, 849–873.

Socio-Political Dimensions of Freshwater Conservation

Fresh water is distributed across the terrestrial landscape as river, lake, and wetland systems, typically arranged as watersheds whereby water flows from upland areas to lowland areas (Figs. 1 and 3). Watersheds have long been recognized as logical planning and management units given that they inherently link land and water (Hynes, 1975) and transcend geopolitical boundaries. This has been amplified in recent years given that watersheds are an example of a coupled social-ecological system and should be managed accordingly (Nguyen et al., 2016). For centuries humans have settled on or near freshwaters for transportation, irrigation,

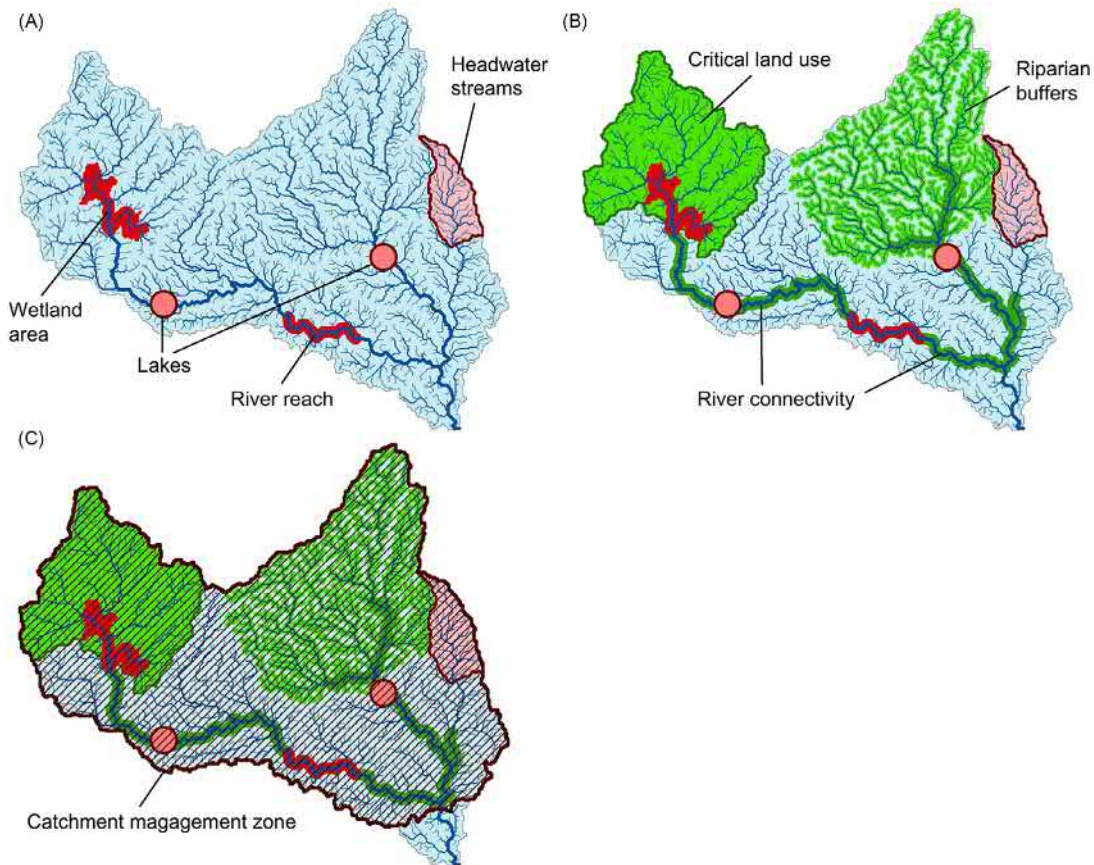


Fig. 4 Options for the conservation of key features affecting freshwater ecosystems. Schematics of freshwater protected area zones include: (A) freshwater focal areas (e.g., particular river reaches, lakes, headwater streams, or wetlands supporting focal species, populations, or communities); (B) critical management zones, such as river reaches connecting key habitats or upstream riparian areas; and (C) a catchment management zone, covering the entire catchment upstream of the most downstream freshwater focal area or critical management zone. Modified from Abell, R., Allan, J. D. and Lehner, B. (2007). Unlocking the potential of protected areas for freshwaters. *Biological Conservation* **134**, 48–63.

power (initially for mills and now for electricity), drinking water, and food (fish) yet humans have also altered the lands that drain and contribute flow to freshwater systems. Given human dependence on contemporary land-use change (e.g., roads, dams, agriculture, forestry, and urbanization), conservation of freshwater biodiversity is remarkably challenging (Crist et al., 2017). Indeed, it is generally understood that the most profitable path toward the conservation of freshwater biodiversity requires engaging with sectors that use water or otherwise alter upland areas that indirectly contribute to biodiversity loss via habitat alteration (e.g., water quality impairments, loss of spawning habitats) as demonstrated above. In the marine realm, one of the biggest drivers of biodiversity loss is overfishing which can most easily be solved by working directly with resource users rather than in freshwater where the industries and actors that negatively influence freshwater biodiversity (e.g., farmers) may be very disconnected and lack the incentives to do so (Beard et al., 2011).

Freshwater biodiversity loss is often considered to be a hidden crisis in that much freshwater biodiversity is unobserved beneath the water surface (Reid et al., 2018). As such, it has been difficult to generate the public and political will to enable meaningful investments or behavioral change needed to protect and restore freshwater biodiversity (Cooke et al., 2013). Grassroots, community-driven actions and stewardship are often heralded as the path forward for freshwater conservation (Silk and Ciruna, 2013) yet that alone fails to account for the broad-scale threats facing such systems. The so-called “food-energy-water nexus” (Smajgl et al., 2016) emphasizes the inherent interconnections of these major issues. Should we prioritize biodiversity preservation over stable energy sources or food for people in some of the most impoverished regions of the globe? Clearly there are difficult ethical, socio-economic and political discussions needed to chart a responsible path forward that represents a win-win-win scenario where freshwater biodiversity is both valued and protected. Global policy instruments often fail to consider freshwater biodiversity (summarized in Darwall et al., 2018) as it is considered a “domestic issue” yet there is a need for elevating freshwater biodiversity to one that is of common global concern (Harrison et al., 2018). Working from both bottom-up and top-down is essential for valuing freshwater biodiversity and committing to a future where we not only respect and conserve freshwater biodiversity but work to actively restore it.

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Conservation of Temporary Wetlands

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This contribution was updated and modified for the *Encyclopedia* from a work published by Elsevier in 2017: Calhoun AJK, Mushet DM, Bell KP, Boix D, Fitzsimons JA, Isselin-Nondedeu F. 2017. Temporary wetlands: Challenges and solutions for protecting a 'disappearing' ecosystem. *Biological Conservation* 211, 3–11.

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Abstract

Temporary wetlands are characterized by frequent drying resulting in a unique, highly specialized assemblage of often rare or specialized plant and animal species. They are found on all continents and in a variety of landscape settings. Although accurate estimates of the abundance of temporary wetlands are available in only a few countries, global estimations identify a decline in number and quality. The key environmental factors driving the structure of ecological communities in temporary wetlands are the duration, timing, frequency and predictability of the aquatic and dry phases, which varies greatly with region and hydrogeomorphic setting. Temporary wetlands have been historically neglected, but improved social awareness of the functions and values of, and increases in scientific interest, suggest that this is changing. They play an ecological role in both global cycles (i.e., CO₂ emissions) and biodiversity (in proportion to their size, they contribute disproportionately to regional and global biodiversity). Moreover, they provide valuable ecosystem services including wildlife habitat, nutrient flux to adjacent ecosystems, flood control, water filtration, and cultural services. Effective conservation of temporary wetlands requires addressing threats (i.e., inconsistent and inadequate regulatory protections; climate change; changes in land use) and management challenges (i.e., management at both local and landscape scales; incomplete understanding of the ecosystem services provided by them; the need to enhance inventories). The most suitable approaches for conserving temporary wetlands include (1) regulations or other forms of protection; (2) sustainable management; (3) restoration and creation; and (4) collaborative conservation.

What Are Temporary Wetlands?

Temporary wetlands are wetlands characterized by frequent drying (normally they dry completely, at least, once a year) resulting in a unique, highly specialized assemblage of often rare plant and animal species (Calhoun et al., 2017). Their defining feature is hydroregime (duration, timing, frequency and predictability of the aquatic phase; Vanschoenwinkel et al., 2009; Sim et al., 2013), and, in some regions, the cyclical nature of droughts, as some permanent water bodies may dry in exceptional

years (Williams, 2006). While throughout our discussion we refer to these landscape features as “temporary wetlands,” it is only the ponded water in the wetland that is temporary in nature. The wetlands themselves are persistent features of a landscape that exist unless drained or filled (Van der Kamp et al., 2016). Usually the water turnover rate is considered the primary environmental cue used to identify the different types of freshwater ecosystems (Margalef, 1983; Wetzel, 2001). Thus, wetlands with short turnover periods (i.e., lotic environments; streams and rivers) differ in both function and community structure than those with longer turnover periods (i.e., lentic environments; wetlands). Hydroregime is the main environmental indicator of gradients in lentic environments (Schneider and Frost, 1996; Wellborn et al., 1996). Hydroregime not only implies physical and biogeochemical changes (especially carbon cycling) in the habitat, but also drives ecological interactions by shaping food webs and altering the composition of potential competitors and predators of species previously adapted to temporary water regimes (Williams, 2006; Lake, 2011).

Where Are Temporary Wetlands Found?

Temporary wetlands are found on all continents, even in Antarctica (Antarctic melt-water ponds), and in a variety of landscape settings, although temporary wetlands exhibit regional differences because different typologies are especially abundant in some areas (Fig. 1) (Zedler, 2003; Williams, 2006; Calhoun et al., 2017). Temporary wetlands are important features in landscapes where permanent water sources are rare (i.e., semiarid and arid areas; Williams, 1985). Many of these wetland features were recognized by ancient cultures and are still considered a valuable part of regional heritage. For example, Aristotle described the biological functioning of one Mediterranean temporary wetland in his “History of Animals” (Boix et al., 2016); Australian Aboriginal people shared knowledge passed down from generation to generation with Europeans about the temporary “gnamma” holes, which were one of their main sources of water (they even elaborated a technique to deepen them) (Bayly, 1999). In addition, temporary wetlands have been created in Europe by humans at least since Roman and Gallo-Roman times as agricultural ponds (Derex, 2001; Delhoofs et al., 2010). Deliberate wetland creation (for runoff and flooding abatement or as incidental features from forestry or development practices) are still common today (Calhoun et al., 2014a).

Estimates of the location, surface area, abundance, and relative importance of temporary wetlands are available in only a few countries and often only for some regions. However, a global estimation shows that in a contemporary timeframe (i.e., 2015), seasonal water covered 0.81 million km², and in the last three decades the transition from permanent to seasonal waters was higher than the reverse transition (72,000 km² and 29,000 km², respectively) (Pekel et al., 2016). In some areas, shifts to more permanent water regimes have occurred, either through the drainage of many smaller wetlands into fewer larger wetlands, which is known as “consolidation drainage” (McCauley et al., 2015); through the construction of dugouts or dikes in wetland basins (Euliss and Mushet, 2004); or through increases in timing and intensity of rainfall events as a result of changing climate regimes (McKenna et al., 2017).

Because they are temporary and generally small, temporary wetlands can be challenging to identify using remote-sensing techniques. Advances in technology, including light detection and ranging (LiDAR), can improve global inventories of temporary wetlands (e.g., Gómez-Rodríguez et al., 2010; Rhazi et al., 2012; Tulbure et al., 2014; Wu et al., 2014). This knowledge is crucial for evaluating their number, distribution, and perhaps increasing their value to society (small waterbodies have been poorly inventoried and undervalued; Downing et al., 2006); and to track widely reported losses (e.g., Brown, 1998; Euliss and Mushet, 1999; Rhazi et al., 2012). Although auditing the numbers and size of wetlands remains a challenge (Jeffries et al., 2016), global estimations identify a negative trend. Since the beginning of the 18th century, wetland loss (mainly inland, temporary wetlands) could have been greater than 80% and wetland loss in the 20th century was almost four times faster (Davidson, 2014). For this reason, the functions and values of temporary wetlands need to be acknowledged and better understood.

Diversity of Temporary Wetland Physical Attributes

Most lentic temporary environments can be considered temporary wetlands, with the exception of some unique habitats (e.g., phytotelmata, a small water-filled cavity in a terrestrial plant). Temporary wetlands are globally distributed and shaped by distinct climate conditions in a variety of biomes and thus encompass a wide range of attributes (Williams, 1985; Williams et al., 2010). For example, although temporary wetlands are generally shallow and relatively small, they vary in (1) size (from a few square centimeters of some rock-pools to hundreds of square kilometers of North American “playas” or thousands of square kilometers of ephemeral Australian lakes), (2) substrate (rock, sand, clay), (3) hydroregime (from ephemeral water bodies in arid regions to seasonal ponds in temperate zones), and (4) sources of water input (rain, snowmelt, stream flow, subterranean). Thus, although rain provides the main water input to temporary wetlands in a great number of regions, in others snowmelt or subterranean waters can play this role (e.g., Irish “turloughs”) and be a determinant of long-term changes in wetland permanence (LaBaugh et al., 2018). Therefore, temporary wetlands comprise a wide range of worldwide waterbody types (Fig. 1), resulting in diverse names to describe them (Williams, 2006; Williams et al., 2010; Calhoun et al., 2017).



Fig. 1 Examples of temporary wetlands (clockwise from top left): Gilgais amongst Plains Grassy Woodland, Monea North Nature Conservation Reserve, Victoria, Australia (photo: J. Fitzsimons); Alpine seasonal pools, Val Thorens, alt. 2520 m, French Alps (photo: F. Isselin-Nondedeu); small rock pool, Massif Central alt. 1500 m, Parc Naturel Régional des Volcans d'Auvergne, France (photo: F. Isselin-Nondedeu); Mediterranean temporary pond, Albera piedmont, Catalonia, Spain (photo: A. Ruhi); dry vernal pool, Acadia National Park, Maine, United States (photo: A. Calhoun); Great Plains prairie pothole, North Dakota, United States (photo: D. Mushet).

Key Environmental Variables and Classification of Temporary Wetlands

The key environmental factor driving the structure of ecological communities in temporary wetlands is hydroregime. Hydroperiod length or pond duration is the most studied hydrologic component, in large part due to its influence over community dynamics and structure (Sim et al., 2013; Boix and Batzer, 2016). However, other aspects of hydroperiod also play a key role, such as predictability (Comín and Williams, 1994) or inundation timing (Kneitel, 2014). Interactions between hydroregime and various biological factors (i.e., predation pressure, strategies to resist desiccation or to recolonize rapidly) have been

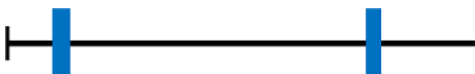
documented (Wellborn et al., 1996; Jeffries et al., 2016). These interactions can be complex and difficult to predict, complicating identification of general patterns of how organisms will respond to hydroregimes (Batzler, 2013), a fact that contributes to the diversity of temporary wetlands.

Pond size is also considered a determinant factor for many features of temporary wetlands although this varies by region (e.g., Ebert and Balko, 1987; March and Bass, 1995; Meintjes, 1996; Spencer et al., 1999). Overall, indirect effects of pond size on community structure (i.e., larger ponds have different environmental characteristics than smaller ponds) seems to be weak in temporary ponds (Ballón et al., 2016). However, in forests, pond size may be correlated with tree canopy closure in some regions, which influences quantity of photosynthetic active radiation and inputs of organic matter consequently structuring part of ecosystem functioning (Mokany et al., 2008; Skelly et al., 2014). Moreover, the interaction of both factors, hydroregime and pool size, has been related to some ecological traits such as the dispersion of the taxa (Vanschoenwinkel et al., 2009).

Several methods for classifying temporary wetlands have been attempted including classification by the biome in which they are present (e.g., tundra, temperate grassland, Mediterranean scrub, tropical savanna), size (i.e., micro-, meso-, macro-habitats), hydrological character (i.e., intermittent, episodic), salinity (i.e., freshwater, saline), origin (natural, artificial; and the latter can be classified according to human use), indicator species, or a combination of several of these factors (Williams, 1985, 2006; Rheinhardt et al., 2008). Classifications based on hydrology, including duration and predictability of the hydroperiod, are frequently used (Comín and Williams 1994; Keeley and Zedler 1998). This includes the most widely accepted classification of temporary wetlands, proposed by Boulton and Brock (1999), which has been adapted and reproduced in several ecology textbooks (e.g., Boulton et al. 2014; Grillas et al., 2004; Williams, 2006; Boix et al., 2016). The classification distinguishes five types of temporary lentic waters (Table 1). These temporary wetlands types are related by potential future changes of hydroregime. Thus, trends of precipitation variation (increases or decreases, which are regionally dependent) and increase of extreme events (such as heavy precipitation events or long dry periods) predicted in accordance with climate change (Brooks 2009; Stocker et al., 2013) imply possible transitions among the separate types of temporary wetlands (Fig. 2).

The relevance of hydrology in shaping ecological function of temporary wetlands is also the core of the conceptual framework of the "Wetland Continuum" (Euliss et al., 2004). This conceptual framework is more comprehensive than the scenarios illustrated in Fig. 2 because it includes not only precipitation but also groundwater recharge or discharge, facilitating the interpretation of biological studies of wetland ecosystems (Mushet et al., 2018). The objective of the Wetland Continuum framework is "to provide

Table 1 Classification of temporary wetlands (TW) according to their hydroregime with some comments of the characteristics of the organisms living in them.

TW type	Flooding regime	Hydroregime	Organisms
<i>Ephemeral</i>		Filled only after unpredictable rain and by run-off. The flooded area dries out during the days following the flooding	Supports low numbers of macroscopic aquatic species compared to pools with longer hydroperiods
<i>Episodic</i>		Dries in 9 out of 10 years, with rare and irregular flooding (or wet periods) which may last for a few months	Terrestrial flora with few aquatic species. Fauna characteristic of temporary waters, dominated by species with highest dispersion capacity or drought resistant strategies
<i>Intermittent</i>		Alternating wet and dry periods, but a more irregular frequency of filling than seasonal wetlands. Flooding may persist for months or years	Aquatic flora restricted to the inner belt. Fauna characteristic of temporary waters, but also species that use waterbody as breeding or feeding site
<i>Seasonal</i>		Alternating wet and dry periods annually, in accordance with the season. Usually fill during the wet season of the year, and dry out in a predictable way every year	Since flooding lasts for several months, macroscopic animals and plants are able to complete their life cycles
<i>Near-permanent</i>		Predictable flooding, though water levels may vary. The annual input of water is greater than the losses (does not dry out) in 9 out of 10 years	The majority of organisms living here cannot tolerate desiccation

Adapted from Boulton, A.J. and Brock M.A. (1999). *Australian freshwater ecology: Processes and management*. Canberra, Cooperative Research Center for Freshwater Ecology.

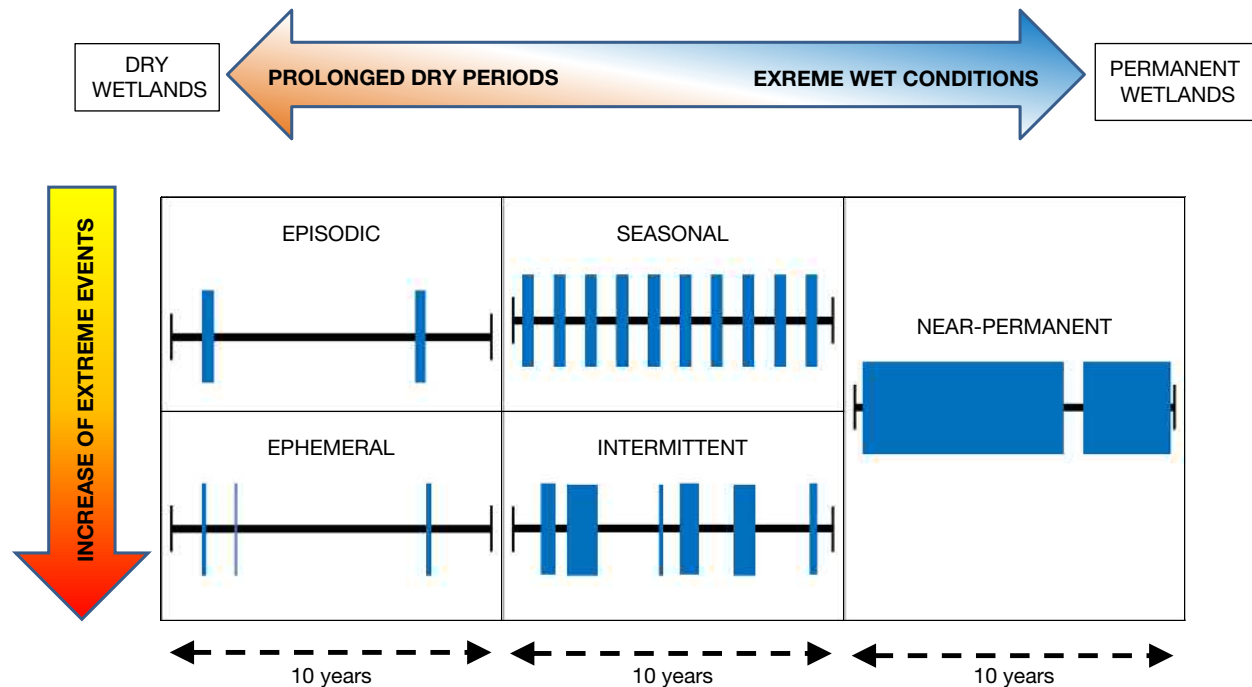


Fig. 2 Changes among temporary wetland types (according their hydroregime, see Table 1) in some future climate scenarios (Stocker et al., 2013) taking into account two aspects: variation in precipitation and increase of extreme events (i.e., heavy precipitation events or long dry periods).

a method that can be used to complement existing classification systems by placing dynamic shifts in wetland class and function within an ecological context to improve interpretation among biological studies conducted in different locales and times." This method is also a powerful tool for analyzing future changes in ecological functioning due to periods of wet or dry conditions (Mushet et al., 2018). Exemplary situations to which the Wetland Continuum framework may be applied include the Prairie Pothole Region of North America, which has been subjected to an extended period of extreme wet conditions (McKenna et al., 2017); or the substantial decline of annual rainfall observed since 1900 in several Mediterranean regions owing to climate change (IPCC, 2007) with markedly prolonged dry periods in wetlands. These hydrological changes imply potential modifications in the populations and metacommunities dynamics, and different patterns between organisms with different dispersion mode or ability are expected (Pyke, 2005; Sim et al., 2013; Boix et al., 2016).

The Age of Enlightenment for Temporary Wetlands? From Negative Perception to Valued Resource

The conservation status of many temporary wetlands around the world is attributable to a long-held negative perception of temporary wetlands. As mentioned earlier, while some ancient cultures in arid and semiarid regions had historic knowledge of temporary wetlands and valued them as part of their heritage, in modern societies these same wetlands are generally viewed more as wasteland or a liability (e.g., as sources of diseases or undesirable animals such as mosquitoes, or a loss of agriculture or developable land) than as valuable assets (Batzer and Boix, 2016; Jeffries et al., 2016). Moreover, the ecological value of individual temporary wetlands has increased as conversion of wetlands to other land uses has increased their rarity in the landscape. Additionally, temporary wetlands have historically received limited scientific attention and, even in some cases, perceptions of the ecology of these habitats are incorrect as conclusions were not evidence-based but rather were extrapolated from studies on permanent wetlands and wetlands in other climates, or were directly compared to permanent wetlands. Despite this, evidence to date suggests that temporary wetlands, by nature of their unique environmental conditions, contribute to beta and gamma diversity (Williams, 2000; Boix et al., 2008; Calhoun et al., 2017). To further complicate our understanding of this system, some scientific ideas on how temporary wetlands function had been established without direct documentation. Results from direct study of temporary wetlands open the door to a different perspective: predation could be an important biotic driver for community structure (Brendonck et al., 2002; Boix et al., 2006; McLean et al., 2016); drought is not a determinant environmental filter in all temporary wetlands because many species are adapted to drought (Biggs et al., 1994; Williams, 1996); and hydroperiod duration is not always the main hydrological factor to explain community composition, because in Mediterranean regions flooding timing could play a more determinant role (Kneitel, 2014; Boix et al., 2016).

Peer-reviewed literature on temporary wetlands is limited prior to the mid-twentieth century (Williams, 2006; Grillas et al., 2010; Jeffries et al., 2016). Using the words of Prof. William D. Williams (1985), "Despite the obvious ubiquity, ecological

importance and limnological interest of temporary waters, most limnological texts have little to say about them". In fact, for this reason Prof. D. Dudley Williams named temporary wetlands as "the Cinderellas of aquatic science"—in other words, the ugly and neglected little sister of the more charismatic, larger wetlands (Williams, 2006). However, an increase in scientific interest of temporary wetlands is evident for the following reasons (Blaustein and Schwartz, 2001; Williams, 2006):

- temporary wetlands are ubiquitous and many of them small, making them ideal subjects for pure and applied research studies;
- temporary wetlands can support a wide range of studies because they can be more readily manipulated for experiments, and their abundance allows for replication;
- temporary wetlands contribute to general understanding of "ephemerality" phenomena in terms of ecosystem functioning, community structure, and population dynamics of biological adaptations;
- temporary wetlands are inland environments characterized by high physical variability, and this variability drives both molecular and morphological evolution;
- temporary wetlands harbor disease vectors;
- temporary wetlands significantly contribute to aquatic biodiversity;
- temporary wetlands contain an important proportion of land-water ecotone;
- temporary wetlands have played a key role in biogeographical processes, because they served as postglacial dispersal routes.

Other investigators have noted additional wetland contributions of scientific importance, which include the following:

- temporary wetlands could be important study systems for explaining the origins of life, as earliest life forms may have arisen in shallow ponds (Ranjan et al., 2019);
- temporary wetlands represent an example of faunal complexes persisting over millennia with locally adapted endemic species (Keeley and Zedler, 1998);
- temporary wetlands are characterized by a unique combination of isolation and connectedness at different spatial scales, which can result in the evolution of endemic species (Zedler, 2003);
- temporary wetlands play a significant role in global cycles (Downing, 2010; Obrador et al., 2018), especially in C cycling through C storage and through emitting CO₂ (Holgerson, 2015; Holgerson and Raymond, 2016; Marcé et al., 2019); and
- temporary wetlands are an ideal habitat to study metacommunity dynamics because they configure networks of aquatic patches inside a terrestrial matrix with a reduced time window for species dispersal (Jeffries et al., 2016; Tornero et al., 2018; Cunillera-Montcusí et al., 2019).

Improved social awareness of the functions and values of and increases in scientific interest in temporary wetlands suggest perceptions of this resource are changing (Angeler, 2009; Brock, 2009; Calhoun et al., 2014b). The latter is demonstrated by the rising number of publications as journal articles (Fig. 3), monographs or proceedings of workshops or symposia (e.g., Diget and Rioux, 1998; Witham, 1998; Blaustein and Schwartz, 2001; Fraga, 2009; Bagella et al., 2016), and textbooks or chapters on temporary

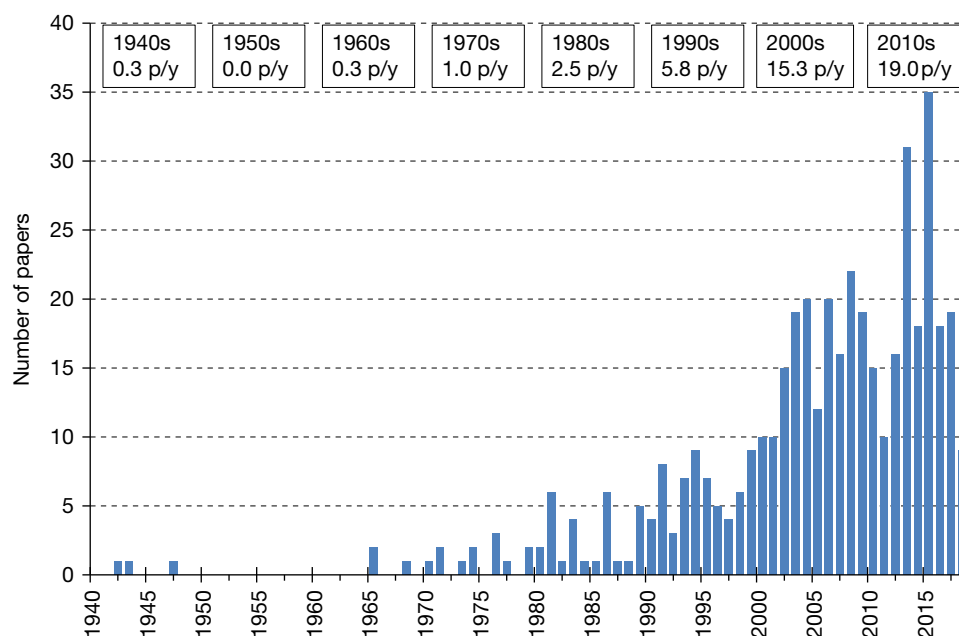


Fig. 3 Number of papers published every year (p/y) from 1940 to 2019 in which the following terms are included in the title: "temporary wetlands," "temporary ponds," "temporary pools," "ephemeral wetlands," "ephemeral ponds," "ephemeral pools," "vernal ponds," and "vernal pools". Data extracted in July 2019 from the data base "Web of Science" (Clarivate Analytics). The top boxes show the mean number of publications per year for each decade.

wetland ecology (e.g., Williams, 2006; Alfonso et al., 2011; Lake, 2011; Boix et al., 2016; Jeffries et al., 2016) or conservation (e.g., Grillas et al., 2004; Calhoun and deMaynadier, 2004, 2008; Fraga et al., 2010; Sancho and Lacomba, 2010; Díaz-Paniagua, 2015).

Why Are Temporary Wetlands Ecologically and Socially Important?

Biogeochemistry and Hydrology

Gaps in our knowledge about the distribution and abundance of small waterbodies, or temporary wetlands, have been long neglected (Downing et al., 2006), and not surprisingly, so has the role of these wetlands in global cycling of matter (Downing, 2010; Hunter et al., 2017; Golden et al. 2019). Part of this can be explained by the relatively small size of most temporary wetlands, but their neglect can also be explained by the temporary nature of their ponds, making the wetlands themselves perceived as being temporary landscape features (Grillas et al., 2004; Boix et al., 2016; Van der Kamp et al., 2016). Ironically, it is this very characteristic of alternation between dry and wet phases of temporary wetlands that makes them crucial biogeochemical hotspots compared to surrounding upland systems. For example, dry wetlands substantially contribute to CO₂ emissions and have long been known as sources of CO₂, whereas inundated wetlands acted either as a source or a sink of atmospheric CO₂ (Catalán et al., 2014; Holgerson, 2015; Obrador et al., 2018). These CO₂ emissions have only recently been included in global estimates of CO₂; the first published estimates reveal a significant contribution of temporary systems (Marcé et al., 2019). Other biogeochemical functions of temporary wetlands include denitrification, sediment retention, pesticide transformation, and absorption of phosphorus and other aquatic pollutants (Zeng and Arnold, 2013). Temporary wetlands provide a disproportionately large fraction of wetland edges, and biogeochemical and other wetland functions tend to be enhanced in areas of wetland-edge (Cohen et al., 2016). Temporary wetlands also have a relevant role in some processes at a landscape or even a regional scale. For example, vernal pools in central Maine, United States, function as hotspots of leaf litter decomposition, denitrification and enzyme activity compared to adjacent upland forest sites (Capps et al., 2014).

In terms of their hydrology, temporary wetlands are known to be “nodes in hydrologic networks connecting landscapes in four dimensions—longitudinal, lateral, vertical, and through time” (Rains et al., 2016). Networks of temporary wetlands exist along a continuum of hydrologic connectivity from relative hydrologic isolation to predicted connectivity (Leibowitz et al., 2008; McLaughlin et al., 2014). Many temporary wetlands reduce peak floodwater flows, contributing to groundwater recharge or discharge (Euliss et al., 2004; Ganesan et al., 2016) and providing stream base flow. Temporary wetlands also provide lag, sink, and source (contribution) functions (as summarized by Rains et al., 2016) and “spill and fill” and “spill and merge” functions (Leibowitz et al., 2016) that have effects on the physical, chemical, and biological status of downstream waters.

Biodiversity

Temporary wetlands support a unique assemblage of biota adapted to living in temporary waters and hence contribute disproportionately to the biodiversity of both aquatic and semi-aquatic animals and plants (Williams, 2000; Herault and Thoen, 2009; Pinto-Cruz et al., 2009) by harboring rare and endemic taxa (Collinson et al. 1995; Marsh and Trenham, 2001; Calhoun et al., 2017; Mushet et al., 2019). In France, for example, vernal pools represent 0.05% of the natural habitats but hold around 35% of rare species and 5% of the protected plant species (Sajaloli and Limoges, 2001). The European Habitats Directive (European Directive 92/43/CEE) considers “Mediterranean temporary ponds” a priority habitat to conserve, but the Directive defines this wetland type strictly by the presence of particular plant species (European Commission 2003; Bagella et al. 2007). Moreover, obligate temporary species (i.e., some branchiopods) are examples of extremely rare species only known from selected ponds around the world (Alonso and García-de-Lomas, 2009; Cottarelli et al., 2010).

In addition to supporting rare and exclusive species, temporary wetlands also maintain metapopulation structure of many faunal groups, due to their importance as a foraging resource or breeding habitat (Griffiths, 1997; Wissinger, 1997). Many terrestrial mammals, amphibians, reptiles, and birds use the abundant resources in pools (i.e., egg masses, amphibian larvae and adults, invertebrates, algae and plants) to supplement their diets, especially following winter in temperate and boreal regions (Paton, 2005). Further, the absence in temporary wetlands of biotic groups not well adapted to drought allows the success of other biotic organisms susceptible to predation or competition (Wellborn et al., 1996). For example, the absence of fish (with few exceptions fish are not adapted to temporary waters; but see Pazin et al., 2006; Laufer et al., 2009; Lanés et al., 2014) in temporary wetlands increases the abundance and richness of invertebrate and amphibian specialists groups (Jeppesen et al., 2001). Fish predation may be a key factor in the structuring of communities (e.g., Brooks and Dodson, 1965; Brucet et al., 2010; Compte et al., 2011) and the flora and fauna of temporary wetlands in the absence of fish illustrates this well. Lastly, temporary wetlands also support biota that are terrestrial (Lott, 2010), or neither fully terrestrial nor fully aquatic (Jeffries et al., 2016). These additions to biodiversity are often overlooked in freshwater ecological studies (Mushet et al., 2019).

At landscape scales, temporary wetlands increase biodiversity through the addition of an aquatic feature (ephemeral to semi-permanent) in a terrestrial matrix that otherwise might include only permanent aquatic features. Temporary wetlands serve as aquatic stepping stones in an upland matrix and provide foraging and resting habitat for facultative species migrating to other resources. For example, in Europe, the agile frog (*Rana dalmatina*) can breed in different temporary ponds depending on the year (Guyétant, 1997), similarly the palmate newt (*Lissotriton helveticus*) can disperse across a network of temporary wetlands within a forest matrix (Isselin-Nondedeu et al., 2017). In the United States, the northern leopard frog (*Lithobates pipiens*) and bullfrog

(*Lithobates catesbeianus*) overwinter in deep-water habitats, migrate to temporary wetlands for reproduction or feeding, and then return to deep-water habitats to hibernate (Mushet et al., 2013). Additionally, Mushet et al. (2019) found that over long temporal periods, the number of taxa accumulate and therefore contribute to biodiversity at a greater rate in wetlands with temporary ponds compared to those with more permanent water regimes.

Socioeconomic

Temporary wetlands provide valuable ecosystem services including wildlife habitat, nutrient flux to adjacent ecosystems, flood control, water filtration, and cultural services (e.g., Turner et al., 2008; Gascoigne et al., 2011; TSSC, 2012). For example, prairie potholes provide breeding habitat for over 50% of all North American duck populations, despite covering only a tiny portion of the area of their range (Baldassarre and Bolen, 2006), and support extensive recreational and educational opportunities. Gilgais are used by grazers to graze seasonally stock in areas that lack permanent water (Lachlan Riverine Working Group, 2016). Soaks associated with rocky outcrops, gnamma holes and gilgais were an important source of water for indigenous communities as they enabled people to forage seasonally over areas that lacked permanent water (see Fitzsimons and Michael, 2017). Given the connections between social, economic, and ecological importance of temporary wetlands, scientific advances documenting the range of ecological functions provided by these resources create opportunities for enhanced understanding and documentation of their socioeconomic importance (Bauer et al., 2017).

What Are the Current Threats and Management Challenges?

Inconsistent and Inadequate Regulatory Protections

The lack of rigor and consistency in regulatory protections for small aquatic resources is a global phenomenon (Acuña et al., 2017). For example, in Europe, Canada, and the United States many wetlands are exempt from regulation based on size or size of impact or are not regulated at all (see the European Water Framework Directive; Clean Water Act and Food, Conservation, and Energy Act of 2008 in the US; Mushet et al., 2014; Creed et al., 2017). In addition, wetland regulations typically target the wetland depression with little regard to adjacent terrestrial ecosystems or connectivity to other critical wetland resources (Cohen et al., 2016). Some small aquatic resources do receive enhanced protections, but such protections are afforded to a small subset of the resources (Bagella et al., 2007; Zacharias and Zamparas, 2010; Mushet et al., 2014; Levesque et al., 2019). The cumulative, landscape scale impacts of loss of small, temporary wetlands are not currently addressed in regulatory frameworks (Jansujwicz and Calhoun, 2017).

Climate Change

The tight relationship between hydrology and temporary wetlands makes them extremely vulnerable to changes in climate. By virtue of their small size (high watershed to surface area or volume ratio) and temporary hydroperiods, temporary wetlands are very responsive to changes in temperature and precipitation patterns (Fig. 2). The International Panel on Climate Change's predictions for the next 100 years suggest that temperature increases will be greatest in high latitudes, precipitation amounts and patterns will change, frequency of extreme storm events will increase, and sea levels will potentially rise 20–60 cm (Junk et al., 2013). Responses to climate change will vary across a gradient from arid to boreal regions, from individual wetlands and types, and across species (Calhoun et al., 2017). For example, temporary ponds and their biota in Mediterranean climates are more threatened by reduced precipitation, increased salinity, and extended droughts than temperate or boreal temporary wetlands (Boix et al., 2016). Precipitation events may become more extreme in some areas coupled with seasonal changes in distribution (Junk et al., 2013). Repeated droughts will increase decomposition rates of soil organic matter and change the composition of the vegetation that may contribute to carbon storage (Hervé et al., 2019). Extreme shifts in aquatic invertebrate biodiversity (Sim et al., 2013; Renton et al., 2015) and plant species composition (Ghosn et al., 2010; Bagella and Caria, 2013) may occur in all temporary systems as a result of changes in climate patterns (wetlands and waterways).

Changes in Land Use

Temporary wetlands are small, dynamic, and vulnerable to land-use changes. Moreover, temporary wetlands are threatened by ecosystem loss and degradation associated with land change and land management activities, pollution, resource extraction, and invasive species. For example, conversion and use of lands for urbanization, agriculture, and livestock (switching temporary wetlands to permanent pools; Beja and Alcazar, 2003; Euliss and Mushet, 2004); water extraction; other human-mediated impacts to biodiversity, including sedimentation (Grillas et al., 2004); and toxic pollution (Collins et al., 2014) can result in the modification or destruction of temporary wetlands. In every continent, invasive species are a major threat to wetland biodiversity (Brinson and Malvarez, 2002; Zedler, 2004). Although the period of time without water impedes the colonization by exotic fishes, many exotic and specially adapted species have invaded temporary waters, including plants (Collinge et al., 2011; TSSC, 2012; Brundu, 2015), crayfishes (Carreira et al., 2014; Rodríguez-Pérez et al., 2014), and amphibians (Escoriza et al., 2014; Meilink et al., 2015). These invaders have contributed to the loss of species, wetland functions, food web dynamics, and habitat structure.

Management Challenges

Ecological

Temporary wetlands require management at both local and landscape scales; they are active biological, physicochemical, and ecological nodes in a terrestrial matrix (Grillas et al., 2004; Amis et al., 2009; Mushet et al., 2014; Golden et al., 2019). Since temporary wetlands are defined by hydroperiod, they are extremely susceptible to changes in land-use patterns and activities beyond the wetland footprint that alter hydrologic patterns. Because most temporary wetlands have high perimeter to surface area ratios and relative low volume with limited inlet and outlets, if present at all, they are also quite sensitive to alteration in chemistry from sediments and pollutants. In addition, many temporary wetlands support wildlife with biphasic or complex life histories involving annual migrations of hundreds of meters, making the adjacent terrestrial habitat an integral part of conserving their functions (Semlitsch, 2002; Bird and Day, 2014; Groff et al., 2017). Direct losses or fragmentation of wetlands, particularly ephemeral ponds, decreases wetland density increasing travel distances for biota, particularly those organized in metapopulations, using multiple aquatic resources (Gibbs, 1993).

Conservation of temporary wetlands ecosystems is made difficult by trends in conservation priorities, funding, and research that discount these resources (Martín-López et al., 2011) and therefore undercut scientific understanding of multi-scale processes. One major challenge is then to manage, conserve, or restore by integrating spatial scales from wetland to landscape, taking into account all fluxes of energy, materials and organisms. Clearly, one will not be able to manage for all things, but being aware of the implications of management is important at any scale.

Social

Limited public awareness of, incomplete understanding of the ecosystem services provided by, and cost:benefit issues associated with the conservation of temporary wetlands can complicate their management. For many temporary wetlands, public understanding of their functions is limited, diminishing support for public conservation actions (Mushet et al., 2014; Marton et al., 2015; Cohen et al., 2016). Two exceptions provide inspiration for addressing the challenge of limited public awareness. The importance of temporary wetlands in supporting breeding waterfowl in the Prairie Pothole Region is widely recognized and led to the region becoming known as the “duck factory of North America” (Lynch, 1984; Batt et al., 1989). Educational outreach has also helped to reverse some forestry practices detrimental to temporary ponds in the region of Chiron in France where it has been estimated that 90% of temporary wetlands were destroyed after intensive tree plantation and drainage (Couderc, 1979; Isselin-Nondedeu et al., 2013). Less visible ecosystem functions, however, such as biogeochemical and stream base flow support, are often not well-documented and are easily underappreciated or devalued (Millennium Ecosystem Assessment, 2005). Ecosystem services of temporary wetlands will have to be better quantified and explained to change perceptions of value and support for different management structures. The spatial mismatch between conservation benefits and costs can also challenge management of temporary wetlands. While the social importance of temporary wetlands can be quite significant (because they are the summation of many values held by society), temporary wetlands may offer individual landowners only limited private value relative to competing uses of lands. Management approaches that recognize the spatial distribution of benefits and costs and full extent of conservation costs are more likely to navigate these challenges successfully (Shogren et al., 2003; Bauer et al., 2010, 2017; Jansujwicz et al., 2013; Sunding and Terhorst, 2014; Levesque et al., 2016).

Public valuing of temporary wetlands could lead to enhanced inventories. To effectively manage temporary wetlands, it is essential to have a spatially explicit inventory and assessment of their ecological status and the context of the terrestrial matrix (Van Meter et al., 2008; Van den Broeck et al., 2015). Still, detailed wetland inventories are lacking in large sections of the world (e.g., China, South America, Russia), and small wetlands are often disregarded or not captured in places where inventories are conducted (Robertson and Fitzsimons, 2004; Junk et al., 2013). In addition, information may be available but poorly accessible and dispersed across agencies or private entities. If wetlands are mapped remotely, the ability to identify these features will vary greatly depending on the nature of the matrix. For example, in forested landscapes containing vernal pools in midwestern and northeastern North America, remote detection is problematic, often missing as much as 30% of pools (Tiner et al., 2015; Dibello et al., 2016). Even in open areas, remote detection of small wetland features can be limited by atmospheric conditions or spatial resolution of the sensor being used (Rover and Mushet, 2015). However, as technologies continue to improve (e.g., Wu and Lane, 2017), the ability to remotely detect and map small wetland features will continue to improve, especially with 3-D digital technology and high resolution LiDAR and Synthetic-Aperture Radar (SAR) approaches (Tiner et al., 2015; Wu and Lane, 2017).

Approaches for Conserving Temporary Wetlands

The most suitable approaches for conserving temporary wetlands include regulations or other forms of protection; sustainable management; collaborative conservation; and restoration and creation. Regulations or other forms of protection range from restrictive local protections conserving temporary wetlands and adjacent habitat to broader national regulations (e.g., the listing of the “Seasonal Herbaceous Wetlands [Freshwater] of the Temperate Lowland Plains” ecological community as critically endangered under national threatened species/communities legislation in Australia). Top-down regulation (at any government level)

has the advantage of setting clear rules but may suffer from lack of enforcement or “buy in” from the stakeholders being regulated. Protection may also result from crisis management of increasing threatened or rare temporary wetlands. For example, in southeastern Australia, ephemeral wetlands such as gilgais typically occur on fertile country which was privatized and suffered from conversion to more intensive agricultural activities. Efforts to increase the representativeness of Australia’s reserve system has seen the acquisition of a number of significant properties containing temporary wetlands (e.g., [Fitzsimons and Ashe, 2003](#); [Fitzsimons et al., 2004](#)).

Small natural features, including temporary wetlands, are arguably best managed using the meso-filter approach ([Hunter, 2005](#)), where features that may be small ecosystems in their own right or ecological elements within larger ecosystems can, by nature of their small size, open the door to sustainable management. Management approaches (including landowner incentives) will range from practices specific to land uses adjacent to temporary wetlands to landscape-scale approaches that recognize the functions of temporary wetlands as wetland complexes embedded in, and likely integral to, other ecosystems. For example, in arid and semi-arid Australian rangelands, gilgai conservation was considered a key feature in market-based incentives for landholders to better manage grazing ([Smyth et al., 2007](#)). In southeastern Australia, market-based auctions for conservation actions have been in place for the past decade and would prioritize ephemeral wetland communities due to their conservation status based on past loss and ongoing threats. Integration of vernal pools as a component of forest biodiversity is a way to manage sustainably both terrestrial and aquatic habitats. In many national forests in France and commercial forests in the northeastern United States, the application of best management procedures includes reducing disturbance immediately adjacent to pools by implementing management zones around the pools and implementing standards for maintaining uneven aged forest stands ([Calhoun and deMaynadier, 2004](#); [Guittet et al., 2015](#)).

Similarly, a market-based approach has been developed in New England, United States, to manage vernal pools in developing landscapes. A creative, voluntary, hybrid approach—a community based collaborative effort that draws from both top-down (a regulatory “stick” or incentive) and bottom-up regulatory restrictions—has generated great interest as a new conservation tool ([Freeman et al., 2012](#); [Calhoun et al., 2014b](#); [Levesque et al., 2016, 2019](#); [McGreavy et al. 2016](#)). In this program, impacts to pools in developing areas generate fees from developers to conserve vernal pool landscapes in rural areas in the same town (Special Area Management Plan for Vernal Pools in US Army Corps of Engineers Region 1; [Levesque et al., 2016, 2019](#)).

Collaborative voluntary approaches may evolve without the regulatory “stick.” For example, in Australia, collaborative landscape-scale arrangements such as Conservation Management Networks (biophysical networks of remnant vegetation sites across a variety of tenures and a social network of managers, owners, and interested people) have also been applied in fragmented landscapes containing temporary wetlands ([Edwards and Fox, 2013](#); [Fitzsimons et al., 2013](#)). These arrangements seek to (a) increase the protection status of sites; (b) maintain, enhance and re-establish remnants across private and public land; (c) bring together owners and managers of vegetation remnants; (d) connect and buffer remnant patches; and (e) develop consistent and complementary management across sites, and are across tenures.

Sustainable management in the face of climate change necessitates approaches that, as [Beier et al. \(2015\)](#) recommend, conserve “nature’s stage.” This approach moves conservation away from focusing on dynamic targets such as community types, e.g., spruce-fir forests or wood frog breeding pools, to capturing the physical features that support the array of defining characteristics of any given ecosystem target. For temporary wetlands, this would mean conserving an array of hydrogeomorphic settings (ones that support short to long hydroperiods in different physical settings) to allow a range of biogeochemical and water quality functions as well as support of diverse biota ([Marton et al., 2015](#)); this approach increases the chances that species and processes can evolve with changes in climate. In addition, the importance of allowing for gene flow among diverse temporary pool communities is highlighted by [Rice and Emery \(2003\)](#) and others who advocate for maintaining or restoring microevolutionary processes to meet the challenges of a shifting climate.

Restoration or creation of temporary wetlands ([Fig. 4](#)) may result from legal restrictions on impacts that require mitigation for wetland losses or from voluntary efforts to ameliorate losses. An inability to recreate hydrology is often the cause of a failure in restoring or creating temporary wetlands, particularly for pool-breeding amphibians and invertebrates ([Petranka et al., 2007](#); [Calhoun et al., 2014a](#); [Drayer and Richter, 2016](#)). In the North American Prairie Pothole Region, efforts to restore plant communities of temporary wetlands typically result in communities of lower floristic quality compared to plant communities of undisturbed wetlands ([Mushet et al., 2001](#), [Salaria et al., 2019](#)), but successes in plant restoration have been reported in other regions of the United States ([Ferren and Hubbard, 1998](#)). In gilgai depressions in southeastern Australia, increased floristic biodiversity occurred with removal of grazing, while gilgai microrelief homogenized by cultivation showed some recovery after release from cultivation ([Nolan et al. 2018](#)). In addition, landscape setting and condition and location with respect to other aquatic resources is important to wetland functions. It is challenging to recreate natural wetland functions in off-site areas that might not be conducive to natural wetland conditions.

In situations where wetland losses are high, wetland restoration or creation may be a good option. For example, efforts to restore vernal pools in France and Spain have attempted to create short hydroperiods by digging shallow pools that are very dependent on precipitation. Initial results concerning abiotic functions and amphibian colonization are promising ([Ruhí et al., 2012](#); [Isselin-Nondedeu et al., 2013](#)). However, even after relatively long periods post restoration, communities and ecological functions in many temporary wetlands are often not entirely restored ([Ruhí et al., 2009](#); [Matthews and Spyreas, 2010](#); [Moreno-Mateos et al., 2012](#); [Ruhí et al., 2016](#), [Salaria et al., 2019](#)). Creating temporary wetlands where they previously did not exist is an even greater challenge.



Fig. 4 Examples of temporary wetland restoration projects developed in NE of Iberian Peninsula. Left side, creation of temporary ponds to reinforce amphibian populations in Esplet, La Selva, Spain (photos: A. Ruhí). Right side, restoration of the “Bassa del Pla dels Rosers” in Albera, Alt Empordà, Spain (photos: M. Pascual and J. Montaner).

Acknowledgments

This research was supported by National Science Foundation award EPS-0904155 conferred to Maine EPSCOR. We thank Eduardo Gonzalez, Vincenc Acuña, Maria Felipe Lucia, and Malcolm Hunter for providing early reviews of the manuscript from which this chapter was based (i.e., Calhoun et al., 2017). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Wetlands of the Mariana Islands

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Published by Elsevier Inc.

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Abstract

This article represents an assessment of Mariana Island Wetlands that includes the current status, stressors, and future viability. Wetlands in the Mariana Islands are comprised of the following categories: estuarine wetlands, forest wetland/swamps, freshwater marshes, lakes, and artificial wetlands. Wetlands have been significantly impacted by human habitation in the islands, with many degraded, fragmented, or lost due to development, invasive species, fire, erosion, altered hydrology, agriculture, and pollution. Hydrophytic vegetation is primarily composed of species of grasses, reeds, ferns, and trees. Wetlands provide habitat for some species listed as endangered, while a couple of species reliant on wetlands have been extirpated. Variables considered in analyzing current condition and future scenarios include stressors as well as conservation efforts. Considering the vulnerability of the wetlands and limited representation across the islands, as well as climate-related changes, it is anticipated that these habitats will continue to degrade in the absence of intensive or consistent management into the future.

Introduction

This document is an overview of wetlands that occur in the Mariana archipelago and describes the ecological factors that influenced them over time. Wetlands do not occur on all the islands: Guam contains the largest number and hectares of wetlands in the Marianas but wetlands also occur on Rota, Tinian, Saipan, Anatahan, and Pagan (Figs. 1 and 2; Table 1). All the islands are volcanic in

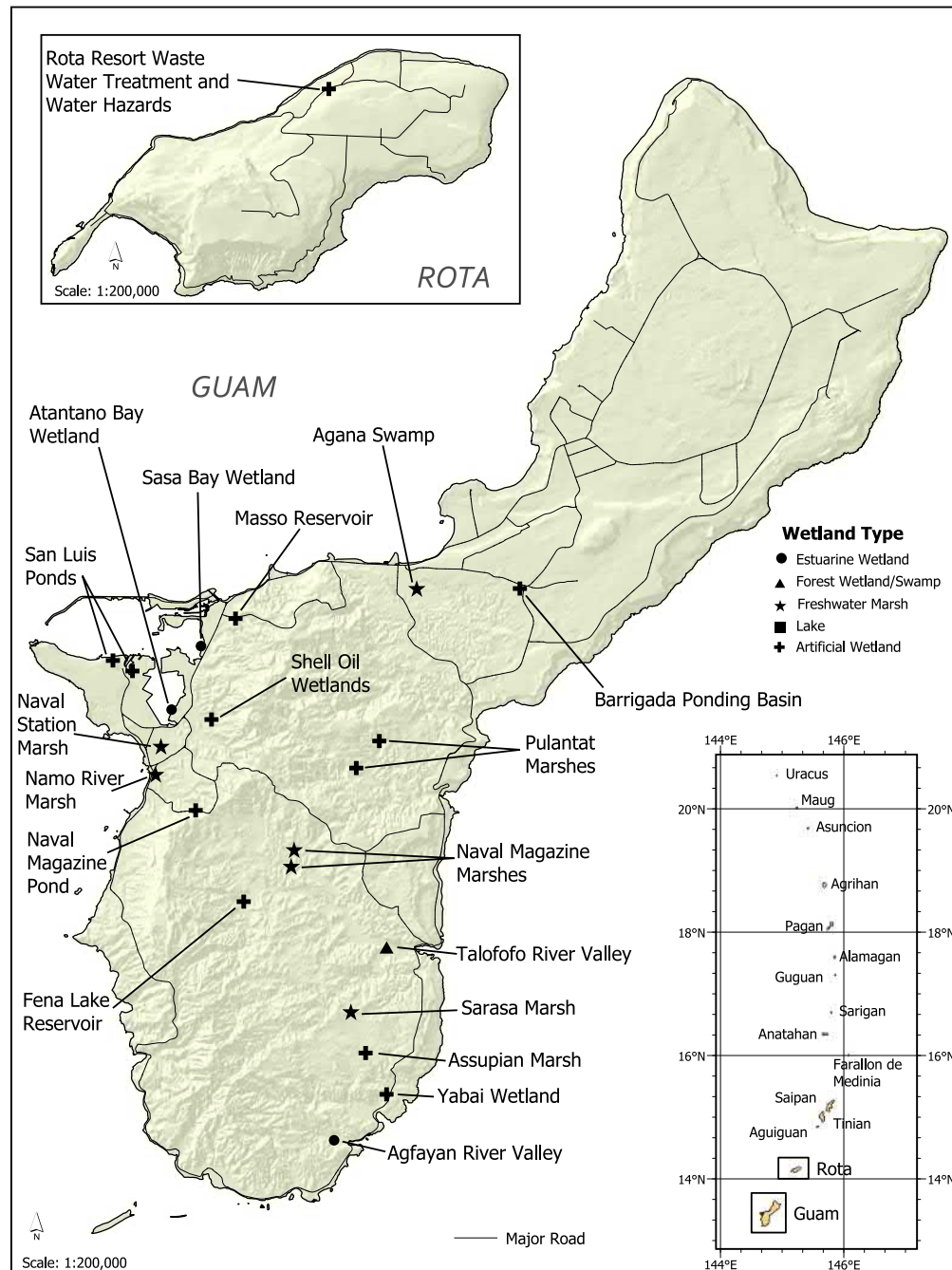


Fig. 1 Approximate locations of wetlands by type on the islands of Guam and Rota, Mariana Islands (see Table 4).

origin. The older islands in the south (Guam, Rota, Tinian, and Saipan) are primarily elevated coral limestone and weathered basalt (Mueller-Dombois and Fosberg, 1998), while the younger northern islands, including Anatahan and Pagan, are primarily volcanic and some have active volcanos (Ohba, 1994). An introduction to the Mariana archipelago including geography, hydrology, island names and descriptions, and climate can be found in Harrington et al. (2019). Another biome publication that references wetlands in the Mariana Islands is "Mariana Islands Coastal Ecotype" (Plentovich et al., 2019).

Wetland Description

Wetlands are lands that are permanently or periodically saturated with water, which impacts the nature of soil development and what animals and plant communities live in the soil and on its surface (Cowardin et al., 1979). Wetlands in the Mariana Islands function similarly to wetlands in other locations, for example, as flood storage, groundwater recharge, nutrient cycling, and buffer

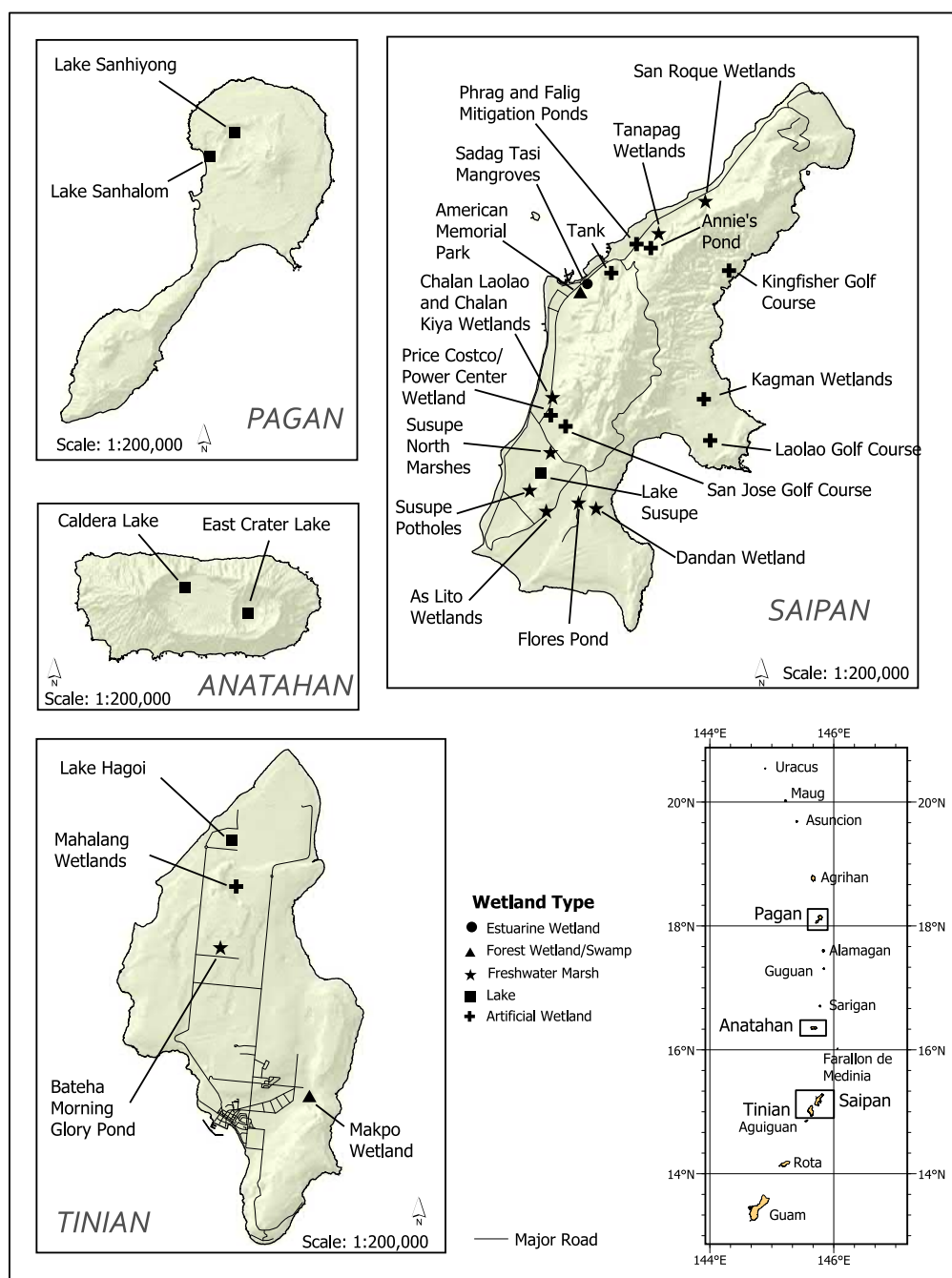


Fig. 2 Approximate locations of wetlands by type on the islands of Tinian, Saipan, Anatahan, and Pagan in the Mariana Islands (see Table 4).

Table 1 Estimated wetland habitat and percentage of land cover in the Mariana Islands (Reeves and Amidon, 2018).

Island	Area in hectares	Area (% of Island)	Area (% Archipelago)
Guam	443	1	<1
Rota	4	<1	<1
Tinian	14	<1	<1
Saipan	182	2	<1
Anatahan	101	3	<1
Pagan	24	<1	<1

areas. Wetlands are also one of the most productive ecosystems in nature (Guam Coastal Management Program, 1991). In the Mariana Islands, wetlands are also crucial for the conservation and recovery of the Mariana Common Moorhen (*Gallinula chloropus guami*), locally known as pulattat. This endemic subspecies was listed as endangered in 1984 mainly due to the drainage/loss of suitable habitat (USFWS, 1984). The nganga' or Mariana Mallard (*Anas platyrhynchos oustaleti*), another endangered subspecies endemic to the Mariana Islands, was also reliant on wetlands, and is now extinct (USFWS, 1977, 2004). The bako or White-browed Crake (*Porzana cinerea*) was also apparently restricted to marshy areas on Guam and has also been extirpated, disappearing around the same time as the draining and development of much of the freshwater habitat on the island (Baker, 1951; Jenkins, 1983). Another species, the endangered ga'ga karisu or Nightingale Reed-warbler (*Acrocephalus lusincia*), while not an obligate wetland species, is typically found in most wetlands on Saipan (Marshall and Worthington, 1996) and has been extirpated from Guam, where it was primarily restricted to wetlands (Baker, 1951; Reichel et al., 1992).

Wetland determination is made on the basis of three factors, vegetation, soil, and hydrology (Cowardin et al., 1979; DEQ, 1997). Under this classification system, a wetland must have one of three attributes: (1) the land predominantly supports hydrophytes (a plant growing in water or on substrate that is periodically deficient in oxygen resulting from excessive water content) at least periodically; (2) the substrate is primarily undrained hydric soil (soil that is wet long enough to periodically result in anaerobic conditions, influencing the growth of plants); and (3) the substrate is non-soil and is saturated with water or covered by shallow water at some time during the growing season each year (Cowardin et al., 1979).

The vegetation found in the different types of wetlands in the Mariana Islands varies, and may depend on for example, saltwater influences, local disturbances, cultivation of crops, and whether they are permanent or ephemeral. In the Mariana Islands hydrophytic vegetation is primarily composed of species of grasses, reeds, ferns, and trees (Liske-Clark, 2015). Though not a complete list, Table 2 lists plant species commonly found in wetlands in the Mariana Islands. On Guam, wetlands have the lowest proportion of endemic species of all the major plant habitats, with widespread natives and a high proportion of nonnative species (Lee, 1974). Lee (1974) postulates this may be due to the fact that the wetlands on Guam are generally small and have a patchy distribution. Table 3 lists animals commonly found utilizing wetlands in the Mariana Islands.

Prehuman Condition

There are no known wetland range estimates for the Mariana Islands. Information on wetlands across the Mariana archipelago prior to human settlement is very limited. It has been generally believed that people arrived in the Mariana Islands between 3500 and 4000 years ago, but more recent information indicated they arrived as early as 4300 (Athens and Ward, 2004; Athens et al., 2004; ERCE, 1990). For example, pollen samples acquired from core sample taken from a small coastal wetland on the west side of Guam showed an entirely forested area (Athens and Ward, 2004; Athens et al., 2004). A core from a sinkhole in a site on Saipan (Kagman) that was a wetland during prehuman times shows that the vegetation prior to 4520 was characterized by mixed

Table 2 Common plant species found in wetlands in the Mariana Islands (ERCE, 1990; Fosberg, 1960; GDAWR, 2006; Moore et al., 1977; Raulerson and Rinehart, 1992; Stemmermann, 1981; Stinson, 1993; Stone, 1970; Vogt and Williams, 2004; Wiles and Ritter, 1993).

Scientific name	Chamorro, common name	Vegetation type	Wetland category ^a	Native or nonnative
<i>Acrostichum aureum</i>	Langayao, Swamp fern	Fern	Obligate	Native
<i>Avicennia marina</i>	Gray mangrove	Mangrove	Obligate	Native
<i>Barringtonia racemosa</i>	Langasat, Fishkill	Tree	Facultative ^b	Native
<i>Bruguiera gymnorhiza</i>	Mangle lahe, Oriental mangrove	Mangrove Tree	Obligate	Native
<i>Ceratopteris thalictroides</i>	Water fern	Fern	Obligate	Native
<i>Cocos nucifera</i>	Niyog, Coconut Palm	Tree	Facultative ^c	Nonnative
<i>Cyperus</i> spp. (<i>C. javanicus</i> , <i>C. odoratus</i> , <i>C. polystachyos</i>)	Cyperus	Sedge	Obligate?	Native
<i>Eleocharis ochrostachys</i>	Spike rush	Sedge	Obligate	Nonnative
<i>Hibiscus tiliaceus</i>	Pago, Beach Hibiscus	Tree	Facultative ^b	Native
<i>Hydrilla verticillata</i>	Waterweed	Herb	Obligate	Nonnative
<i>Ipomea aquatica</i>	Kangkun, Swamp morning glory	Vine	Obligate	Nonnative
<i>Ludwigia octovalvis</i>	Titmo, Primrose willow	Forb/Herb	Obligate	Nonnative
<i>Panicum purpurascens</i>	Para grass	Grass	Facultative	Nonnative
<i>Paspalum vaginatum</i>	Seashore paspalum	Grass	Obligate	Nonnative?
<i>Phragmites karka</i>	Karisu, Phragmites	Reed grass	Obligate	Native
<i>Polygonum minus</i>	Mamaka, Smartweed	Herb	Obligate	Native
<i>Rhizophora mucronata</i>	Mangle hembra, Red mangrove	Mangrove	Obligate	Native
<i>Rhizophora apiculata</i>	Mangle	Mangrove	Obligate	Native
<i>Scirpus littoralis</i>	Bulrush	Sedge	Obligate	Nonnative

?, not entirely clear that this species was introduced.

^aObligate—A plant that occurs in wetlands 99% of the time. Facultative—A plant equally likely to be found in wetlands as nonwetlands.

^bFacultative—A plant that occurs in wetlands between 67% and 99% of the time.

^cFacultative—A plant usually found in nonwetland conditions, but 1%–3% of the time is found in wetlands.

Table 3 List of animals that are commonly found in Mariana Island wetlands (Englund, 2011; Jenkins, 1983; Marshall Jr., 1949; Polhemus and Richardson, 2019; Pratt et al., 1987; Reichel and Glass, 1991; Richardson et al., 2009; Stinson, 1993; Vogt and Williams, 2004; Wiles and Ritter, 1993; A. Marshall, pers. obs.).

Scientific name	Chamorro name, common name	ESA listing status	Native, nonnative, or migratory
Herons/egrets/bitterns			
<i>Ixobrychus sinensis</i>	Kakkak, Yellow Bittern		Native
<i>Egretta sacra</i>	Chuchuko atilong, Pacific Reef Heron		Native
<i>Bubulcus ibis</i>	Chuchuko a'pak, Cattle Egret		Migratory
Waterfowl			
<i>Anas oustaleti</i>	Nganga', Mariana Mallard	Extinct	Native
<i>Anas acuta</i>	Northern Pintail		Migratory
<i>Aythya fuligula</i>	Tufted Duck		Migratory
Water birds			
<i>Porzana cinerea</i>	Bako, White-browed Crake	Extirpated	Native
<i>Gallinula chloropus guami</i>	Pulattat, Mariana Common Moorhen	Endangered	Native
Shorebirds			
<i>Pluvialis fulva</i>	Dulili, Pacific Golden Plover		Migratory
<i>Heteroscelus incanus</i>	Dulili, Wandering Tattler		Migratory
<i>Heteroscelus brevipes</i>	Dulili, Siberian (Gray-tailed) Tattler		Migratory
<i>Actitis hypoleucos</i>	Dulili, Common Sandpiper		Migratory
<i>Numenius phaeopus</i>	Kalalang, Whimbrel		Migratory
<i>Arenaria interpres</i>	Dulili, Ruddy Turnstone		Migratory
Other birds			
<i>Acrocephalus luscini</i>	Ga'ga Karisu, Nightingale Reed-warbler	Endangered	Native
Mammals			
<i>Rattus</i> spp.	Rats		Nonnative
Reptiles and amphibians			
<i>Varanus indicus</i>	Hilitai, Monitor (Mangrove) lizard		Nonnative
<i>Littoria fallax</i>	Kairo', Eastern dwarf tree frog		Nonnative
<i>Bufo marinus</i>	Kairo', Marine toad		Nonnative
<i>Trachemys scripta</i>	Red-eared slider		Nonnative
<i>Boiga irregularis</i>	Brown treesnake		Nonnative
Fish			
<i>Awaous guamensis</i>	Atot, Mariana goby		Native
<i>Stiphodon elegans</i>	Atot, Green riffle goby		Native
<i>Gambusia affinis</i>	Mosquito fish		Nonnative
<i>Oreochromis mossambicus</i>	Mozambique tilapia		Nonnative
<i>Clarius macrocephalus</i>	Itot, Catfish		Nonnative
<i>Poecilia reticulata</i>	Guppy		Nonnative
<i>Cichla ocellaris</i>	Tucanare		Nonnative
Insects			
<i>Limnogonus fossarium skusei</i>	Water-strider		Native?
<i>Anax guttatus</i>	Pale-spotted emperor dragonfly		Native
<i>Orthetrum sabina</i>	Slender skimmer dragonfly		Native
<i>Plantala flavescens</i>	Globe skimmer dragonfly		Native
<i>Tramea transmarina</i>	Red glider dragonfly		Native
<i>Agriocnemis femina femina</i>	Variable wisp damselfly		Native

?, not entirely clear that this species is native.

grassland and forest (Athens et al., 2004). These data show a change in vegetation with forest disappearing and grasses predominating on Saipan and with savanna and grassland pollen increasing on Guam at the time of the presumed appearance of humans (Athens and Ward, 2004; Athens et al., 2004). Cores obtained at American Memorial Park on Saipan included *Acrostichum* spores indicative of marsh conditions and which currently occur there today (Jarzen and Dilcher, 2009). Other species that commonly occur in various Mariana Islands wetlands today and that occurred in the cores, were *Bruguiera gymnorhiza*, *Cyperus* spp., and pollen from a *Hibiscus* comparable to *Hibiscus tiliaceus* (Jarzen and Dilcher, 2009; Table 2). Cloud Jr. et al. (1956) suggest that geologically, Lake Susupe and the surrounding marshes are barred-off lagoon remnants created by limestone sand deposits. The brackish lake is about 1066.8 m inland from the Philippine Sea (Wong et al., 1990). Cultural evidence suggests that Lake Susupe and/or its associated marsh areas may have been more extensive in the past (Thomas and Price, 1980). Paleohabitat evidence from Guam also shows changes in coastal habitat associated with changes in sea level and human use of the areas, and changes in sea level also affected the growth of mangrove forests, sedge-dominated wetlands and other coastal and low-elevation habitats (Carson, 2011). In the Marianas, measurements indicate a 1.8 m higher sea level dated 3400 through 1050 BCE that was followed by a draw-down over several centuries (Dickinson, 2000, 2003; Kayanne et al., 1993).

There is also little information on the effects of stochastic events for the Mariana Islands prior to human contact. There is evidence of sea level changes in the Mariana Islands (Carson, 2011) and on Rota there is evidence that there was a wetland prehistorically (Becker and Butler, 1988; Stinson et al., 1991), but the extent of prehistoric impacts are not known. Prior disturbances due to typhoons or floods may have been minimal as the species and habitats adapted to those conditions.

Habitat Viability of Prehuman Wetlands: Resiliency, Representation, and Redundancy

Habitats sustain through resiliency, redundancy, and representation. The viability of wetland habitat depends on maintaining multiple and distributed habitat types (redundant) of sufficient quality and size (resilient) with species richness and genetic range (representative) to survive across its ecological environment over time. The phrase “ecologically healthy” refers to functions affecting biodiversity, productivity, biochemical cycles, and evolutionary processes that are linked to the climatic and geologic conditions in the region (Karr, 1991 and Karr et al., 1986 in Naiman et al., 1992). The ecologically healthy, or viable, wetland habitat that existed prior to human contact likely maintained natural connections between system components. Native biota that was historically characteristic of wetlands in the Mariana Islands filled environmental niches necessary to sustain the habitat.

Resilience is defined as the amount of disturbance that the system can absorb without a change in structure and composition (Carpenter et al., 2001; Holling, 1973). Disturbance in wetland habitat include natural forces such as typhoons, floods, drought, and sea level change. Due to hydric soils and highly adapted flora and fauna in the wetlands, “healthy” wetlands would have had an increased capacity (high resiliency) to be able to recover from such stochastic and natural events.

Redundancy refers to the extent and range of a habitat across a given landscape. Redundancy from having multiple resilient wetlands can decrease the risk of loss. Habitats with few occurrences across the islands are less resilient to catastrophic events that might otherwise have a relatively minor impact on widely-distributed habitats (Stacey and Taper, 1992). It can be assumed that throughout the Marianas, wetlands were limited by both the presence of hydric soils and hydrology and therefore were on only found on the few islands which contained hydric soils, sufficient rainfall, and topography suitable for ponding water. Therefore, it is likely wetlands were only found on Guam, Tinian, Saipan, Pagan, and possibly Rota, before human contact.

The primary driving factor for maintaining a high level of representation for wetlands is related to dispersal and connectivity. Connectivity refers to the ability of plants and animals to move between habitat patches on the landscape (Hanski, 1998; Tischen-dorf and Fahrig, 2000). Wind, water, and birds are the most important natural dispersal vectors in the Marianas. Wind and ocean currents are particularly important for dispersal of vegetative propagules (plant structures such as fragmented runners or seeds) to disperse to distant sites. Biological connectivity is maintained through dispersal and considers whether species can move to similar or other suitable habitat. Migratory birds contribute to connectivity between wetlands at small to large scales (i.e., regional to inter-continental) while transiting between feeding, breeding, and nonbreeding areas (Buelow and Sheaves, 2015). Species mobility varies and results in different rates, patterns and scales of biological connectivity on the landscape (Taylor et al., 1993).

Table 4 summarizes the viability of wetlands in their historical state. These values are assumed based on what is known about these habitats in their native state. For instance, lakes likely recovered quickly from storms. However, there were relatively few lakes found across the archipelago and therefore had low redundancy and low representation. In contrast, marshes may have also had high resiliency, but also had higher redundancy and therefore higher representation.

Change from Prehuman Condition

The islands have been greatly altered due to the long history of human habitation. The prehistoric human impacts on the natural environment include the development of a savanna landscape in the interior upland areas of Guam and the decline in pollen of Guam’s native forest species (Athens and Ward, 2004). The data indicate a significant change in the appearance and natural history of Guam in around 2000 years due to early human settlement (Athens and Ward, 2004). There is limited direct pollen evidence for prehistorical agriculture, but taro, *Colocasia esculenta*, pollen was documented in a core suggesting it was likely grown in coastal wetlands around 1100 years ago (Athens and Ward, 2004). Additionally, sedimentary evidence indicates that there was an increase in coastal deposition resulting from erosion from the surrounding hillsides after 2400 cal. B.P. implying intensive use of the landscape, presumable for agriculture (Athens and Ward, 2004).

After Guam was “discovered” by Magellan in 1521, the islands have been administered by the Spanish, Germans, Japanese, and Americans, each culture importing crops and ornamental plants, as well as animals (Moore et al., 1977). Wetlands were used for rice

Table 4 Levels of resiliency, redundancy, and representation for wetlands that existed in the Mariana Islands prior to human contact.

Habitat type	Resiliency	Redundancy	Representation
Estuarine wetland	High	Low	Medium
Forest wetland/swamp	Medium	Low	Medium
Marsh	High	High	High
Lake	High	Low	Low

and taro cultivation, uplands were subjected to slash and burn agriculture, and during World War II, the southern islands were variously impacted by battles, runway construction, increased human population, and bombs (Engbring et al., 1986; ERC Environmental and Energy Services (ERCE), 1990; Moore et al., 1977; Stinson, 1993). After the war, large military installations were built on Guam and *Leucaena leucocephala* was seeded by the US military on Guam, Saipan, and Tinian (Engbring et al., 1986; Fosberg, 1960).

There are very few comprehensive studies of wetlands in the Marianas and much of the published information is included in vegetation or ornithological surveys across the archipelago (Fosberg, 1960; Moore et al., 1977; Tenorio and Associates, Inc., 1979). Two of the most detailed reviews of the wetlands on Guam and the CNMI were written by Wiles and Ritter (1993) and Stinson (1993) respectively. According to Wiles and Ritter (1993), significant losses of wetlands occurred historically on Guam, though they wrote that the extent of losses is difficult to quantify. For example, there was extensive destruction and alteration of wetlands by the US military in the Apra Harbor area between 1945 and 1950 when the Navy expanded port facilities there (Mueller-Dombois and Fosberg, 1998; Wiles and Ritter, 1993). As a result, mangrove communities along the eastern harbor and freshwater wetlands along the Sasa, Atantano, and Namo Rivers were destroyed (Wiles and Ritter, 1993). A coastal highway built around the southern half of Guam resulted in roadbeds built across wetlands and likely altered natural drainage patterns (Wiles and Ritter, 1993).

Current Condition

Based on the above, it is not likely that the original character of wetlands in the Marianas is preserved on any of the islands. The vegetation of the islands is so altered by humans that its original character has only been preserved in a few restricted locations, such as along cliffs (Spoehr, 1957). Clearly, the quantity of natural wetlands has significantly decreased. The area of wetlands totals 443 ha on Guam and 260 ha in the CNMI, which includes the area for a number of artificial wetlands (Table 5; Guam EPA, 2008; Reeves and Amidon, 2018). Natural wetlands in the Mariana Islands are mainly located in low elevation areas. Following are descriptions of the types of wetlands currently on each of the six islands.

Guam

Within the Mariana archipelago, Guam contains the largest number of wetlands (Guam Division of Aquatics and Wildlife Resources (GDAWR), 2006; USFWS, 1991; Wiles and Ritter, 1993). The majority of wetlands occur in the southern and central areas of the island (Fosberg, 1960; Fig. 1). In these areas, the clay or argillaceous limestone soils retard the percolation of waters, allowing surface waters to accumulate while the northern limestone plateau allows rapid water seepage such that few marshy areas occur in the north (Wiles and Ritter, 1993). Many of the wetlands in the interior are located along the upper drainages of river and small tributaries (Wiles and Ritter, 1993).

As noted, there have been significant losses of wetland on Guam historically, though the extent of losses has not been well quantified (USFWS, 1991, 2009; Wiles and Ritter, 1993). The 1983 National Wetland Inventory maps for Guam indicate there were around 2023 ha (5000 acres) of wetlands at that time, while current estimates are 443 ha (1094 acres) (Table 5; Guam EPA, 2008; Reeves and Amidon, 2018). Some of the losses were due to extensive destruction and alteration of wetlands by the US military around Apra Harbor due to the expansion of port facilities, some resulted due to the building of the coastal highway around the southern part of the island, and in the mid-1970s to mid-1980s, several sets of aquaculture ponds were constructed in wetlands along the Talofof, Agfayan, and Ajayan Rivers (Wiles and Ritter, 1993). Much of Agana Swamp was infilled to expand Agana

Table 5 Landownership and acreage of wetland habitat in the Mariana Islands (Reeves and Amidon, 2018).

Island	Land ownership ^a	Area in hectares
Guam	DoD	125
	NPS	0.4
	Private	167
	Public	35
	Unknown	113
Rota	Public	3
Tinian	DoD (leased)	13
	Unknown	0.4
Saipan	Private	76
	Public	105
Anatahan	Public	100
Pagan	Public	23

^aPublic land includes village or agricultural homesteads and lands in the CNMI leased to developers. Department of Defense (DOD) lands include lands owned by DOD on Guam and lands leased by DOD and leased back to farmers and ranchers on Tinian. NPS lands include lands leased by the National Park Service on Saipan. Unknown areas are those where ownership data is unavailable.

Village, including a shopping center built in 1978 (Ayers and Clayshulte, 1983; Wiles and Ritter, 1993). Other land development projects have increased resulting in additional wetland fills, however, regulatory agencies have been successful in reducing the number of wetland fills since then and protective regulations have improved (Wiles and Ritter, 1993). Wetlands have also been affected by pollution, agriculture, fires, and erosion. In addition, although karisu (*Phragmites karka*) is indigenous, it has infilled many wetlands, and reduced the ability to support a diversity of flora and fauna. Wiles and Ritter (1993) speculate that this indigenous species has been impacted by disturbances to the wetlands, increasing its abundance.

Estuarine wetlands are found in areas of tidal intrusion or brackish waters and consist primarily of mangroves. Mangroves on Guam are the most extensive and diverse in the Mariana Islands, although they total only around 2.25 ha (GDAWR, 2006). The largest areas of mangroves occur along the eastern shores of Apra Harbor (GDAWR, 2006; Wiles and Ritter, 1993). Atantano wetland is one of the largest wetlands on Guam and has freshwater as well as estuarine areas (Table 6; Wiles and Ritter, 1993). This large natural coastal wetland is located on the southeast side of Apra Harbor and has the most developed mangroves in the Mariana Islands (Wiles and Ritter, 1993).

Forest wetland/swamps occur along the edges of marshes, rivers, and in wet depressions in forests (Wiles and Ritter, 1993). This wetland type is dominated by woody vegetation, typically *Hibiscus tiliaceus*, however, the Taloforo River Valley is dominated by *Baringtonia racemosa* (Fosberg, 1960; Wiles and Ritter, 1993). This Forest wetland/swamp is the largest contiguous wetland on Guam located in the riparian areas along the Taloforo Valley and lower Ugam Rivers, and is unique for being the primary area used by the endangered Mariana Gray Swiftlet (*Aerodramus vanikorensis bartschi*) for foraging (Wiles and Ritter, 1993).

Freshwater wetlands are characterized by emergent, herbaceous vegetation (Stemmermann, 1981). There are a number of natural freshwater marshes on Guam (Table 6). They range in size from around 96 ha of marshland (Agana Swamp) to some that are less

Table 6 Wetland types found in the Mariana Islands (DEQ 1997; ERCE 1990; GVP 2019; Marshall and Worthington, 1996; Ritter, 1997; Stinson, 1993; Takano, 2003; Wiles and Ritter, 1993, USFWS 1991, 1996).

Island	Wetland-type				
	Estuarine wetland	Forest wetland/swamp	Freshwater marsh	Lake	Artificial wetlands
Guam	- Sasa Bay Wetland - Atantano Bay Wetland - Agfayan River Valley (forest wetland/swamp)	- Taloforo River Valley	- Agana Swamp - Naval Station Marsh - Namo River Marsh - Naval Magazine Marshes (3 marshes) - Sarasa Marsh		- Barrigada Ponding Basin - Masso Reservoir - Shell Oil Wetlands (4 ponds) - San Luis Ponds (2 estuarine ponds) - Pulantat Marshes (2 marshes) - Naval Magazine Pond - Fena Lake Reservoir - Assupian Marsh (ephemeral) - Yabai wetland (ephemeral)
Rota					- Rota Resort golf course waste water treatment ponds and water hazards
Tinian		- Marpo (also called Makpo) Wetland (no longer extant)	- Bateha Morning Glory Pond (seasonal)	- Lake Hagoi	- Mahalang Wetlands (bomb craters filled with water)
Saipan	- Sadag Tasi Mangroves	- American Memorial Park	- Susupe North Marshes - Susupe Potholes - Flores Pond (ephemeral) - San Roque Wetlands - Tanapag Wetlands - Chalan Kiya Wetland - Chalan Laolao Wetland - DanDan Wetland - As Lito Wetlands	- Lake Susupe	- Kagman Wetlands - LaoLao Golf Course - San Jose Golf Course - Price Costco/Power Center Wetland - Falig Mitigation Pond - Phrag Mitigation Pond - Annie's Pond (ephemeral) - Tank - Kingfisher Golf Course
Anatahan				- Caldera Lake - East Crater Lake	
Pagan				- Lake Sanhiyong (Lower Lake-brackish) - Lake Sanhalom (Upper or Inner Lake-freshwater)	

than 0.5 ha (Wiles and Ritter, 1993). These freshwater marshes tend to be dominated by very dense stands of karisu, but other types of vegetation occur, including other grasses, as well as sedges, and the fern *Acrostichum aureum* (Fosberg, 1960; GDAWR, 2006; Wiles and Ritter, 1993). Agana Swamp is the largest natural freshwater wetland on the island, but it is surrounded by development and the thick beds of karisu prevent other favorable plants from becoming established, reducing its attractiveness to wildlife, including the endangered pulattat (Wiles and Ritter, 1993).

Artificial wetlands on Guam were originally created as water impoundments for use by humans, cattle, and crops, including Fena Lake, Masso Reservoir (Fig. 3), and Pulantat Marsh, or to eliminate flooding in the surrounding area, such as Barrigada Ponding Basin (Table 6; Wiles and Ritter, 1993). Some of the sites are no longer used for their original purpose, but serve as important habitat for conserving the pulattat (Wiles and Ritter, 1993). The vegetation in these areas is variable, but karisu and pogo are usually minor components (GDAWR, 2006). Many of these sites are considered important in the conservation of the pulattat (Stinson et al., 1991).

Rota

Currently, there are no natural wetlands on Rota. The pulattat currently occurs at wetlands on Guam, Tinian, and Saipan, but has not been recorded historically on Rota (Baker, 1951; Engbring et al., 1986). In 1992, construction began on an 18-hole golf resort, that included a wastewater treatment plant and water features on the golf course (Fig. 1; Table 6). Wiles and Worthington (1996) noted that a variety of migratory birds were attracted to the site since its creation, and in 1995, adult and juvenile pulattat, were observed using the site (Worthington, 1998). Prehistoric evidence indicates that the pulattat once occurred on Rota (Steadman, 1992; Becker and Butler, 1988 cited in Steadman, 1992). Since the pulattat is an obligate wetland species, it is thought that wetlands occurred at one time on Rota but were lost due to human-related wetland loss or elimination of wetlands due to sea-level changes (Steadman, 1992; Stinson et al., 1991). Pulattat continued to be observed at the Rota Resort sites on occasion (Takano, 2003).

Tinian

Tinian has several wetland areas, Hagoi Marsh, Bateha Morning Glory Pond, Mahalang Wetlands, and Marpo Swamp (Fig. 2; Table 6). Historical literature indicates that Marpo Swamp was formerly open water used by a variety of waterfowl (Barratt, 1988; Northern Islands Company, 1989; cited in Stinson, 1993). Currently, Marpo is used a water source for the island and is heavily overgrown with *Hibiscus tiliaceus*, and no longer has open water (Engbring et al., 1986; A. Marshall, pers. obs). Batea Pond is a very small and seasonal marsh and Mahalang Wetlands are bomb craters filled with water (USFWS, 1996; A. Marshall, pers. obs). Lake Hagoi is a freshwater marsh about 15 ha in extent, but the amount of open water varies quite a lot depending on rainfall and it occasionally dries up during droughts (Engbring et al., 1986; Stinson, 1993; USFWS, 1996). Lake Hagoi is important habitat for the endangered pulattat (USFWS, 1996). The number of pulattat using Hagoi varies considerably with water level both being higher in the wet season (USFWS, 1996). Pulattat have been observed sporadically at Bateha and Mahalang Wetlands (USFWS, 1996). Ducks and other migratory species were frequently observed at Lake Hagoi and migratory species were occasionally observed at Bateha and Mahalang wetlands (USFWS, 1996).

Saipan

Wetland loss on Saipan has occurred through filling, cultivation of rice and sugar cane, and development, and the introduction of nonnative fish is believed to have altered the aquatic environment (Stinson, 1993; USFWS, 1991). There are numerous natural wetlands of various sizes mainly on the west coast of the island (Fig. 2).

American Memorial Park, administered by the National Park Service, is primarily forest wetland/swamp (Stinson, 1993). There are mangroves (*Bruguiera gymnorhiza*) and *Hibiscus tiliaceus* in the wetland, but this area has been heavily impacted by fill and waste



Fig. 3 Masso Reservoir, Guam. Photo credit: Greg Koob.

oil (Stinson, 1993). The wetland is a mosaic of marshy areas with *Acrostichum aureum*, open areas with emergent wetland vegetation, and mixed wet forest of *Hibiscus tiliaceus*, *Bruguiera gymnorrhiza*, and ironwood (*Casuarina equisetifolia*) (Johnson, 2003). There are also mudflats adjacent to the park and migratory shorebirds may be observed there (A. Marshall, pers. obs.). The forest/wetland area is utilized by the ga'ga karisu (Johnson, 2003; Mosher, 2006; Rauzon, 2010; Williams, 2007). Pulattat may also be observed in the wetland on occasion, though they not very common (Johnson, 2003; Rauzon, 2010; Williams, 2007; A. Marshall, pers. obs.). Fig. 4 shows an example of a *Hibiscus tiliaceus* dominated swamp on Saipan.

There are a number of freshwater marshes on the island, for example, Susupe Marsh Wetlands, Chalan Kiya (Fig. 5), DanDan Wetland (Fig. 6) and Flores Pond (Table 6). Many of these wetlands are predominantly karisu marsh areas and several are important for providing flood storage (DEQ, 1997). Some of the ephemeral wetlands, such as Flores Pond, are important to the pulattat because they don't have the invasive tilapia, which likely compete for food resources (Stinson et al., 1991).

Lake Susupe (Fig. 7) is the largest wetland in the Commonwealth of the Northern Mariana Islands (CNMI) and the lake and surrounding wetlands comprise over 60% of freshwater wetlands in the CNMI (Engbring et al., 1986; Stinson, 1993). Susupe Lake is believed to have been a coastal lagoon that was formed when sand blocked it off from the ocean (DEQ, 1997; Stinson, 1993). The lake occupies around 17 ha and is important for flood control and groundwater recharge (DEQ, 1997; Stinson, 1993).



Fig. 4 Photo of typical *Hibiscus tiliaceus* dominated swamp in Tanapag, Saipan. Photo credit: Tyler Willsey.



Fig. 5 Photo of a marsh in Chalan Kiya Saipan. Photo credit: Tyler Willsey.



Fig. 6 DanDan Wetland, Saipan. Photo credit: Greg Koob.



Fig. 7 Susupe Lake, Saipan. Photo credit: Greg Koob.

Many of the artificial wetlands on Saipan, such as Kagman and the Price Costco wetlands (**Fig. 8**), have been created as mitigation due to fill of other wetlands resulting in habitat loss for the pulattat (DEQ, 1997; A. Marshall, pers. obs., 1996). In addition, there are also a number of ponds created by golf courses on the island, such as Kingfisher and LaoLao Bay Golf Course Ponds (**Fig. 9**), which are also used by pulattat and some migratory birds.



Fig. 8 Price Costco Wetland, Saipan, choked with *Phragmites karka*. Photo credit: Greg Koob.



Fig. 9 Photo of an artificial wetland at Lao Lao Golf Course in Kagman, Saipan. Photo credit: Tyler Willsey.

Anatahan

Anatahan is a stratovolcano (volcano built up of alternate layers of lava and ash) with an elongate caldera running 5 km east to west and 2.5 km north-south (Fig. 2, Rowland et al., 2005). There are two volcanic craters in the caldera, the western portion is an older center crater that had a vegetated central basin and a smaller eastern pit crater with steep sides, some vegetation, and bubbling mud pits at the base that were sometimes submerged in a shallow lake (Division of Fish and Wildlife (DFW), 2000; Kessler, 2011; Rowland et al., 2005). The island's volcano erupted in May 2003, its first historical eruption, followed by eruptions in 2004, 2006, and 2007 (Global Volcanism Program (GVP), 2019). The final eruption ended in 2008 (GVP, 2019). At some point following the eruptions, two lakes were observed in the caldera; the western Caldera Lake and the East Crater Lake (Table 6; Mapcarta, 2019). There are currently no known observations of vegetation or animals utilizing either lake.

Pagan

There are two lakes on Pagan, Lake Sanhiyong (Lower Lake or Lagoon Lake) which is brackish, and Lake Sanhalom (Upper or Inner Lake) which is freshwater (Table 6). The lakes are both located on the northern section of the island (Fig. 2). Lake Sanhiyong is on the west coast, separated from the ocean by a cinder beach, such that tidal influence is small, but waves sometimes wash over the beach during storms raising the level of the lake (Stinson, 1993). Lake Sanhalom is located on the western foot of Mount Pagan and had warm springs that emptied into the lake on the southeast shore (Stinson, 1993). Both lakes are considered geologically young and do not have developed marshes (Stinson, 1993). Wetland habitat has been drastically altered and reduced on Pagan (Reichel et al., 1992). Most of the vegetation that occurred around the lakes was destroyed in the 1960 and 1970s by introduced feral ungulates and in 1981, Mount Pagan erupted depositing thick layer of volcanic ash and cinders, and buried much of the vegetation that remained in and around the lakes (Stinson, 1993). Another factor that affected the ecology of the lakes was the introduction of the nonnative Mozambique tilapia (*Oreochromis mossambicus*) in the 1950s (Stinson et al., 1991). The fish occur in both lakes having survived the eruptions (Stinson, 1993). Both lakes have sparse emergent vegetation and are mainly surrounded by nonnative vegetation (A. Marshall, pers. obs.).

Primary Wetlands Stressors (Table 7)

Development and Altered Hydrology

Stinson (1993) states that development and drawdown for water use are the greatest threats to wetlands. Development can result in small- and large-scale filling of wetlands, bisecting sections of a wetland, run-off of polluted water, soil run-off, changes in vegetation, increased human access, increased access of feral cats (*Felis catus*) and dogs (*Canis familiaris*), and modified drainage patterns (Wiles and Ritter, 1993; Stinson, 1993; Stinson et al., 1991). Development has impacted most of the wetlands in the Mariana Islands. For example, Highway 1 (built around 200 years ago) on Guam divides Sasa Bay and Atantano wetlands into two areas

Table 7 Primary stressors affecting wetlands in the Mariana Islands.

<i>Human presence/abundance</i>	<i>Climate change</i>
Development and altered hydrology	Sea level rise, groundwater and marine inundation and flooding
Invasive plants and animals	
Water pollution	Typhoons
Recreation and human access	Drought
Erosion	Temperature
Fire	

acting as a dike and altering drainage patterns and likely salinity (Wiles and Ritter, 1993). Marpo wetland on Tinian is a prime example of a wetland extant in 1957 that no longer exists due to pumping of the water since the 1930s (Spoehr, 1957; Stinson, 1993; Stinson et al., 1991).

The populations in Guam and the CNMI have increased dramatically from 62,641 (1955) to 167,294 (2019) on Guam and from 7985 (1955) to 57,216 (2019) in the CNMI (Worldometers, 2019a, 2019b). The increase in population and increasing reliance on tourism (Wiles and Ritter, 1993; Stinson, 1993) has resulted in construction beyond just residential housing; roads, hotels, shopping malls, commercial buildings, parks as well as the facilities needed for support, including water, sewage treatment plants, landfill, seawalls, etc. Guam and the CNMI have been identified as two of 13 of the most developed small island international destinations characterized by visitor density (McElroy, 2003).

Invasive Plants and Animals

Table 8 lists the primary invasive species that impact wetlands and the species that utilize wetlands in the Mariana Islands. Islands are particularly susceptible to introductions of non-native species (Vitousek, 1988). The impacts of these species in wetlands varies considerably, for example, invasive rodents can directly alter the distribution, diversity and abundance of plants, and indirectly impact seed dispersers such as birds and invertebrates (Steadman, 1999; Wiewel et al., 2009; Wilson Rankin et al., 2018). Monitor lizards, however, are most likely to mainly impact birds, such as the pulattat. The species mostly likely to impact the wetland itself include invasive plants, which can reduce cover resulting in changes in water temperature, outcompete native species, or invade the wetlands reducing

Table 8 Primary invasive species that occur in Mariana Island wetlands.

<i>Common name</i>	<i>Scientific name</i>	<i>Primary species affected</i>	<i>How the species impacts the habitat</i>	<i>Where present</i>	<i>References</i>
Scarlet (Ivy) gourd	<i>Coccinia grandis</i>	Native vegetation	Blocks sunlight and smothers native plants	Guam, Tinian, Saipan	PIER (2019)
Bitter melon	<i>Momordica charantia</i>	Native vegetation	Blocks sunlight and smothers native plants	Guam, Tinian, Saipan	PIER (2019)
Chain of love	<i>Antigonon leptopus</i>	Native vegetation	Blocks sunlight and smothers native plants	Guam	PIER (2019)
Elephant grass	<i>Pennisetum purpureum</i>	Native vegetation	Reduces native habitat	Guam, Rota, Tinian, Saipan, Anatahan, Pagan	PIER (2019)
Mosquito fish	<i>Gambusia affinis</i>	Native invertebrates	Altered aquatic ecosystem	Guam, Tinian, Saipan	Stinson (1993)
Tilapia	<i>Oreochromis mossambicus</i>	Native vegetation, pulattat	Reduces native habitat, competes with pulattat for food, and may prey on chicks	Guam, Tinian, Saipan, Pagan	Wiles and Ritter (1993), Stinson (1993), Stinson et al. (1991)
Monitor lizard (Mangrove monitor)	<i>Varanus indicus</i>	Preys on birds and eggs	Reduces bird dispersers which affects vegetation dispersal	Guam, Rota, Tinian, Saipan, Pagan	Reed et al. (2010), Stinson (1993), USFWS, (1996, 2009)
Brown treesnake	<i>Boiga irregularis</i>	Preys on birds and reptiles	Reduces bird dispersers which affects vegetation dispersal	Guam	USFWS (1991)
Rodents	<i>Rattus</i> sp.	Native vegetation and birds	Depredates native flora and fauna	All islands	USFWS (1996)
Ungulates (pigs, goats, deer, carabao, cattle)	(<i>Sus scrofa</i> , <i>Capra hircus</i> , <i>Rusa marianna</i> , <i>Bubalus bubalis</i> , <i>Bos taurus</i>)	Native vegetation, birds	Depredates native fauna, impacts quality of wetlands through erosion, sedimentation, and input of waste	Guam, Rota, Tinian, Saipan, Pagan	Wiles and Ritter (1993), Stinson (1993), USFWS (1996)

the amount of open water, as well as feral ungulates, which can affect the quality of the water itself through sedimentation, waste products, trampling, foraging, and changes in water temperature, (Griffin et al., 1989; Henry, 2006; Merlin and Juvik, 1992; Morin, 1998; Stone, 1989; USFWS, 2015). One of the most impactful introduced species in the Mariana Islands is the brown treesnake (BTS, *Boiga irregularis*). The BTS was accidentally introduced to Guam shortly after WWII (Rodda et al., 1992). The BTS spread across Guam resulting in multiple impacts, including devastating the island's terrestrial fauna, as well as socioeconomic and human health impacts (BTTWG, 2015). The BTS caused the extinction or serious reduction of most of the islands resident bird species, including the ga'ga karisu (extirpated from Guam) and the Yellow Bitter, the latter which has apparently altered its breeding habitat from wetlands in the late 1970s to urban areas and islets by mid-1990 (Jenkins, 1983; Reichel et al., 1992; Wiles et al., 2003).

Water Pollution

Pollutants, for example, fertilizer, animal waste, pesticides, and heavy metals, can exceed the ability of a wetland to absorb such pollutants, leading to degradation, and may result in the death of invertebrates, fish, and birds using the wetland. Lowland wetlands may be susceptible to act as sinks for pollutants, meaning that pollutants tend to accumulate and potentially increase the toxicity with time. Pollutants can be deposited through urban and agricultural runoff, non-native ungulates, air pollution, and leakage from landfills and dumps. Wetlands in urban areas may be particularly susceptible as storm drains and roadside ditches may lead to streams and wetlands.

An oil spill at the mouth of the Laguas drainage of the Sasa Bay wetland in June 1980 occurred when oil leaked from a pipeline buried along Highway 1 that killed or damaged about 1.8 ha of mangroves (Wiles and Ritter, 1993). Currently, little is done to survey for toxicants in wetlands in the Mariana Islands.

Recreation and Human Access

Most of the wetlands in the Marianas are significantly impacted by human recreation due to their proximity to urban areas. Natural and artificial wetlands are often used as water sources for domesticated ungulates, golf courses, and for stocking nonnative fish, as well as areas to dump trash, and harvest vegetation such as kangkun (*Ipomea aquatica*) for consumption.

Erosion

Erosion may be caused by poorly planned development, clearing vegetation, careless construction practices, rooting, trampling, and overgrazing by ungulates, agriculture, fire, and building roads. In turn, erosion can result in excess sediment deposition, changes in native plant and animal communities by destabilizing substrates, damaging or destroying individual plants, altering hydrological patterns, and the shrinkage or loss of wetlands. Erosion is noted to have impacted a number of wetlands on Guam (Wiles and Ritter, 1993).

Fire

Fires caused by humans either intentionally (clearing of land or for hunting) or unintentionally (improper disposal of ignition sources) is relatively common. Fires remove vegetation from the landscape creating loose soils and ash, which after rain events, can cause large amounts of sediment to wash into rivers increasing turbidity and ultimately depositing it into wetlands. This infilling allows the encroachment of karisu and other grasses, and result in the decrease of open water habitat (Wiles and Ritter, 1993). Fires were noted to impact at least 9 of the wetlands on Guam listed in Table 4 (Wiles and Ritter, 1993). Reichel and Glass (1991) indicate the fires may have played a role in the decline of the ga'ga karisu at Agana Swamp.

Sea Level Rise, Groundwater and Marine Inundation and Flooding

Climate change is expected to result in changes in rainfall, storm intensity and frequency, temperature, and sea level rise. In fact, some of these changes are already occurring, including sea level rise and increasing surface air temperatures, and the impacts from these changes to various habitats are already being observed (Keener et al., 2012). Lowland areas are vulnerable to sea level rise, wave-over wash and saltwater intrusion (Keener et al., 2012) and the majority of wetlands in the Marianas Islands occur in lowland areas. As a result of increased inundation from high waves, coastal wetlands and mangrove areas are becoming more saline over time (Gilman et al., 2008). The increased salinity is expected to impacts the plants and animals that rely on freshwater resources (Keener et al., 2012). Seawater intrusion and flooding is also expected to negatively impact wetlands as well as contaminating aquifers and wells and damaging agriculture (Keener et al., 2012).

Typhoons

Typhoons are common in the region of the Pacific that includes the Mariana archipelago (Engbring et al., 1986). The impacts of typhoons include downed, damaged, and defoliated vegetation from intense wind, heavy rain and salt spray and mortality by salt water inundation in low-lying areas (Fosberg, 1960; Kerr, 2000). Salt water inundation can also have a negative impact on animal species that rely on freshwater wetlands, for example the pulattat which prefers freshwater wetlands (USFWS, 1991).

Drought and Increasing Temperature

Drought may result in reduced streamflow, evaporation of standing water, increased water temperature, and the loss of native riparian and wetland plants (Benning et al., 2002; Still et al., 1999). Guam and the CNMI have had fewer extreme one-day rainfall events in the past 60 years (Keener et al., 2012).

In the Western North Pacific, maximum and minimum air temperatures have shown upward trends in the past 60 years, though the variability is high (Keener et al., 2012). Increased temperatures may result in changes in vegetation composition, increased risk of forest encroachment, and accelerated decomposition rates, that have the potential to impact wetland habitats. Increased air temperatures are likely to result in increased water temperatures as well that would impact wetland reliant species.

Conservation Efforts

The impacts from stressors can be mitigated through laws and regulations, land protection, outreach, as well as restoration/management efforts, such as control of predators and invasive species, establishing buffers, and water management regimes. Land ownership of wetlands in the Marianas varies considerably by island (Table 5). For example, Lake Hagoi, the main wetland on Tinian, is located in the area leased by the U.S. Department of Defense (DOD). Under their Integrated Natural Resources Management Plan (INRMP), the pulattat is monitored annually at Lake Hagoi and Bateha wetlands to examine long-term population trends and changes in the wetland habitat (Naval Facilities Engineering Command (NAVFAC), 2019). A buffer zone and fire suppression measures may be added at a later date. The DOD also owns around 125.45 ha of wetlands on Guam and plans to eradicate feral pigs at the Camp Covington wetlands (Naval Facilities Engineering Command (NAVFAC), 2019).

The U.S. National Park Service (NPS) manages roughly 20.23 ha of hibiscus dominated swamp on Saipan as well as a small constructed marsh at American Memorial Park (Willsey, pers. obs. 2019). The CNMI Department of Land and Natural Resources (DLNR) purchased a 4.49 ha section of Lake Susupe in 1981 for the protection, restoration, and preservation of freshwater wetlands, habitat, and species. On Saipan, some artificial wetlands were created as mitigation for the loss of wetlands in other areas, for example, the Price Costco Wetland and Annie's Pond.

One of the main conservation efforts that occurs in the Mariana Islands is aimed at preventing the spread of the brown treesnake from Guam to the CNMI. To that end, the Brown Treesnake Technical Working Group (BTTWG) has written a biosecurity plan with objectives to prevent the BTS from getting off Guam, suppressing BTS numbers, and eradication from Guam (BTTWG, 2015).

Conservation efforts are also undertaken by both the CNMI DFW and the GDAWR. For example, DFW conducts surveys and research on the ga'ga karisu and GDAWR is working to preserve habitat for the pulattat. Both agencies conduct surveys and research on several species in order to better understand conservation needs. The University of Guam and the Northern Mariana Islands are also actively involved in research on invasive species as well as native species.

Laws and Regulations

Table 9 indicates a number of Federal and State Laws and regulations that protect wetlands in the Mariana Islands. These laws and regulations are vital in helping to minimize the impacts of the stressors on these wetlands. While Federal regulations apply across all jurisdictions, local laws differ between Guam and the CNMI. Biosecurity laws are widespread and are important due to the economic damage caused by invasive species, such as the brown treesnake.

Summary of Interactions and Conservation Efforts

The most significant stressors for wetlands are development and altered hydrology and the impacts of invasive species. At this time, conservation efforts and laws and regulations have not prevented declines in the quality or quantity of wetlands across the archipelago. For example, the Price Costco mitigation wetland on Saipan is currently not being managed as agreed on and the wetland has become overgrown with karisu, such that there is little open water remaining.

The need for increased levels of protection and restoration is significant, particularly with an increasing human population. The work of the local agencies and Universities may be expected to improve conservation efforts in the future.

Future Scenarios

The wetland habitat's response to four foreseeable future scenarios (Table 10) was evaluated out to the year 2035 (see Miller (2019) for the determination of foreseeable future). The condition of wetlands in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The CMPs are as follows:

Table 9 Federal and State laws and regulations impacting wetlands in the Mariana Islands.

<i>Title</i>	<i>Year implemented</i>	<i>Authority</i>	<i>Intent/purpose</i>
Fish and Wildlife Coordination Act of 1958	1958	Federal	Enacted to protect fish and wildlife when federal actions result in the control or modification of a natural stream or body of water. 1958 amendment includes a requirement that other federal agencies coordinate with the USFWS about proposals that have an impact on wetlands.
Sikes Act and the Integrated Natural Resources Management Plan	1960	Federal	Directs the U.S. Department of Defense to carry out conservation and natural resources rehabilitation on military installations in coordination with local and federal fish and wildlife agencies. Amendments to the Act required installations to create an Integrated Natural Resources Management Plan (INRMP) to describe future and ongoing conservation projects on military lands.
Land and Water Conservation Fund Act	1965	Federal	Federal program established to provide funds and matching grants to federal, state and local governments for the acquisition of land and water, and easements on land and water, for the benefit of all Americans.
Clean Water Act	1972	Federal	Establishes the basic structure for regulating discharges of pollutants into the waters of the United States and regulating quality standards for surface waters.
Endangered Species Act	1973	Federal (USFWS and NMFS)	Protects critically imperiled species and their habitats from extinction.
50 CFR 16	1974	Federal	Implements the Lacey Act (18 USC 42), which prohibits importation of injurious species.
Convention on International Trade in Endangered Species	1975	International	Ensures that international trade in specimens of wild animals and plants does not threaten the survival of the species in the wild.
Executive Order (EO) 11987	1977	Federal	Charges Executive agencies with restricting the introduction of exotic species into the natural ecosystems on federal lands; and encourages States to do the same.
Executive Order 11988	1977	Federal	Requires federal agencies to avoid to the extent possible the long and short-term adverse impacts associated with the occupancy and modification of flood plains and to avoid direct and indirect support of floodplain development wherever there is a practicable alternative.
Executive Order 11990	1977	Federal	Issued to “minimize the destruction, loss or degradation of wetlands and to preserve and enhance the natural and beneficial values of wetlands.” To meet these objectives, this EO requires federal agencies, in planning their actions, to consider alternatives to wetland sites and limit potential damage if an activity affecting a wetland cannot be avoided.
Fish, Game, and Endangered Species Act, Public Law (PL) 3–47	1981	CNMI	Authorizes the designation of endangered species and critical habitat and established the Division of Fish and Wildlife and contains fish and wildlife regulations.
Commonwealth Environmental Protection Act, PL 3–23	1982	CNMI	Established the Division of Environmental Quality (DEQ) and includes regulations for water quality certification, waste water discharge, as well as earth-moving permit systems.
Coastal Resources Management Act, PL 3–47	1983	CNMI	Established the Coastal Resources Management Office and contains regulations and standards for activities permitted in “Wetland and Shoreline Areas of Particular Concern” (APCs).
Emergency Wetlands Resources Act	1986	Federal	Authorizes the use of money from the Land and Water Conservation Fund for the purchase of wetland habitat by the Secretary of the Interior. Prior to this Act, the purchase of wetlands by the Federal Government had been prohibited.
Public Land Exchange Act, PL 5–33	1987	CNMI	Includes the framework for the acquisition of land for public purposes, including wetland protection, through exchange for public land.
Executive Order 13112	1999	Federal	Requires that a Council of Departments dealing with invasive species be created to prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause.

Table 9 Federal and State laws and regulations impacting wetlands in the Mariana Islands.—cont'd

<i>Title</i>	<i>Year implemented</i>	<i>Authority</i>	<i>Intent/purpose</i>
An Act to Amend the Guam Environmental Protection Agency Guam Soil and Erosion and Sedimentation Control Regulations, PL 25–152	2000	Guam EPA	The purpose of these regulations is to control accelerated soil erosion, thereby preventing the pollution of Guam's waters (wetlands, streams, and rivers) from fertilizers, pesticides, sediments and other polluting substances carried by sediment, and to protect property and to promote the public health, safety and welfare by regulating grading, clearing, grubbing and stockpiling, and by setting minimum standards for erosion and sedimentation control for the island of Guam.
Northern Mariana Islands Administrative Code Chapter 65–30, § 65–30-005	2014 Amendment	CNMI DEQ	The purpose of the regulations and technical provisions in this chapter is to establish certain minimum standards and requirements as determined by the Division to be necessary for control of nonpoint source runoff from human-related activities. Specifically, these regulations are designed to: (1) Protect marine and fresh water quality; (2) Maintain and enhance beneficial uses of marine and fresh waters; (3) Promote public awareness of the importance of protecting the CNMI's marine and fresh water resources from siltation, and bacteriological, and chemical contamination; and (4) Protect public health by protecting and enhancing the quality of marine and fresh water recreational and traditional fishing sites.
Executive Order 13751	2016	Federal	To prevent the introduction of invasive species and provide for their control, and to minimize the economic, plant, animal, ecological, and human health impacts that invasive species cause (amends EO 13112).
7 CFR 360.200	2018	Federal	Designates certain plants as noxious weeds.

Table 10 Four foreseeable future scenarios considered in this Mariana Islands wetland assessment.

<i>Future scenario</i>	<i>Description</i>
Future scenario one	Status Quo—The most likely foreseeable future, no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues through the foreseeable future
Future scenario two	A slight increase in natural resource conservation in the CMPs marginally improves conservation management
Future scenario three	A slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management
Future scenario four	A moderate to large increase in conservation actions in the CMPs substantially improves conservation management

- (1) *Conservation Values*: stakeholder involvement and public opinion determine the formulation, implementation and funding of natural resource conservation within laws and development plans.
- (2) *Laws and Biosecurity*: national, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented (e.g. hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.).
- (3) *Development or Conservation Planning*: national, state, county, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

Scenario 1: Status Quo

This scenario is considered the most likely future scenario, and serves as a “baseline” for comparing among the four future scenarios. Under this scenario, there would be no change to implementation of the three CMPs between 2019 and 2035 (Table 11). An increasing human population and increased development, land, and water use is expected on the inhabited islands and therefore habitat stressors are expected to increase at a small annual rate. Development is likely to continue to result in direct fill of small scale

Table 11 Responses of stressors on wetlands in the Mariana Islands in foreseeable future scenarios.

Conservation Management Parameters (CMPs)				
Conservation Values	Stakeholder involvement and public opinion influence the formulation, implementation, and funding of <i>natural resource conservation and biosecurity</i> (NRC/B) within laws and development or conservation plans.			
Laws and Biosecurity	National, state, county, and city laws and regulations are the means by which NRC/B are supported and implemented.			
Planning for Development or Conservation	National, state, county, city, and private development plans or conservation plans define actions that result in losses or gains in NRC/B (impacts realized at implementation).			
Foreseeable future scenarios and the resulting wetland conditions				
Use Foreseeable Future	Scenario One	Scenario Two	Scenario Three	Scenario Four
Scenario One as a “baseline” to characterize changes in	CMPs: unchanged in support for NRC/B.	CMPs: small increase in support for NRC/B.	CMPs: small to moderate decrease in support for NRC/B.	CMPs: moderate to large increase in support for NRC/B.
Conservation Actions and Habitat Conditions in Future Scenarios Two, Three and Four.	Conservation Actions: no change; current rate of land cover change continues through the foreseeable future. Habitat Condition: habitat area, quality, and sustainability slowly decrease through the foreseeable future.	Conservation Actions: marginal increase. Habitat Condition: habitat area is unchanged through the foreseeable future; habitat quality and sustainability are slightly enhanced through the foreseeable future.	Conservation Actions: substantial decrease. Habitat Condition: urban and agricultural uses are prioritized over conservation; habitat area, quality, and sustainability substantially decrease through the foreseeable future.	Conservation Actions: substantial increase. Habitat Condition: robust, sustained effort to restore, manage, and expand conservation; habitat area, quality, and sustainability substantially increase through the foreseeable future.
Habitat Stressors				
Human Presence/Abundance	Responses of wetland stressors			
Development	Small to moderate increase	No change (redevelop)	Moderate to large increase	Small to moderate decrease
Altered hydrology	No change to small increase	No change	Larger increase	Small decrease
Recreation/access	Small increase	Small increase	Larger increase	Larger increase
Water pollution	Small increase	No change	Larger increase	Small decrease
Invasive species	Small increase	Small increase	Larger increase	Small decrease
Fire	Small to moderate increase	Small increase	Larger increase	No change to small decrease
Erosion	Small increase	No change	Larger increase	Small decrease
Climate				
Temperature	Small to moderate increase	Small to moderate increase	Small to moderate increase	Small to moderate increase
Precipitation	Small decrease	Small decrease	Small decrease	Small decrease
Sea Level	Small increase	Small increase	Small increase	Small increase
Storms	Small increase	Small increase	Small increase	Small increase

wetlands, increased fires, and erosion. Laws and biosecurity CMPs are expected to remain unchanged while human development continues to grow, resulting in the potential for new invasive species while existing invasive species will likely continue to spread. A slight decline in the quality and quantity of natural wetlands may be expected, while artificial wetlands may slightly increase due to increased need for water for new developments, including golf courses and sewage treatment plants.

We envision the increased fill of wetlands will facilitate the encroachment of karisu decreasing open water habitat. Drought will also continue to allow for the encroachment of karisu by decreasing open water habitat. Overall, this scenario will likely result in continued degradation of natural wetlands that will negatively impact the species that rely on them.

Scenario 2: There Is a Slight Increase in the CMPs that Marginally Improves Conservation Management

Under this scenario, conservation agencies and stakeholders work with increased but limited resources to slow or stop the degradation of landscape areas. This scenario may be considered status quo but with minor improvements in the CMPs (Table 11). While human populations increase, development would not increase substantially, however, increased water needs could still impact the hydrology of wetlands on inhabited islands. With improved biosecurity, the risk of new introduced species arriving will be slightly reduced, but the extant species on the islands might still be expected to increase in number and range. For example, feral pigs and deer would continue to contribute to erosion on Guam by impacting vegetation in the watershed through rooting and grazing of bank stabilizing plants increasing soil erosion and wetland fill. We envision if significant damages to the watershed are occurring, natural resource agencies will attempt to reduce or eliminate the cause whether it be reducing ungulate numbers in key areas or increasing awareness of the impacts of fire. Feral ungulates are not currently in high enough numbers to cause significant impacts to wetlands on Saipan, but it could become an issue in the future, and could have impacts on Tinian and Pagan.

Even with improved natural resource conservation, this scenario could still result in a slight decline in the quality and quantity of natural wetlands but to a lesser extent than scenario one. The status of artificial wetlands may remain unchanged from Scenario 1.

Scenario 3: There Is a Small to Moderate Decrease in Conservation Actions in the CMPs that Substantially Decrease Conservation Management

Under this scenario, all natural resource management actions in the CMP are set aside in deference to land use of economic development. While localized management may allow some wetlands to continue to exist, a significant decline in the quality, quantity, and ecological function of wetlands and the species that rely on them would be expected. An expanded human population will further require increased land and water use to the detriment of wetlands. Weakened biosecurity measures in this scenario are expected to result in increased invasive species as well as an increase in the number of invasive species that currently occur on the islands.

Under this scenario, feral ungulates will increase in numbers in the CNMI and will begin having impacts to wetlands similar to those seen in Guam. The incidence of fire will increase and will result in significant effects to wetlands by increasing the amounts of loose soil vulnerable to erosion during rain events. There would be no planning or management to try and address climate-related changes, further adding to the negative impacts on wetlands.

Scenario 4: There Is a Moderate to Large Increase in Conservation Actions in the CNMPs that Substantially Improves Conservation Management

Scenario four is an overt and robust, active, ongoing effort is made to engage partners and stakeholders in identifying and prioritizing landscape areas needed for the conservation of natural wetlands, and to actively restore and expand them. Under this scenario, increased support and emphasis on natural resource conservation would result in management to restore these habitats. Development would no longer be expected to result in the direct fill of wetlands as responsible urban planning would leave these areas undeveloped and increasingly rely on re-development instead. Improved implementation of biosecurity regulations and removal of invasive species from habitats that are negatively impacted would improve the habitats.

Fire, as a significant contributor to erosion in the Marianas, would be the focus of a robust effort by regulatory agencies. Outreach campaigns informing the public of the damage fires may cause and monitoring of high risk areas by law enforcement and regulatory agencies would greatly reduce the frequency and intensity of fires in the Marianas. Under this scenario existing artificial wetlands may be modified and vegetated to more closely resemble natural wetlands, providing higher quality habitat for wildlife. In addition, the creation or enhancement of wetland systems in the lower reaches of key watersheds for water quality and coral reef enhancement are likely to occur under this scenario.

Summary

Based on this analysis, it is likely that wetlands in the Mariana Islands will decline without intensive conservation management efforts (Table 11). Scenarios one, two, and three are likely to result in fragmentation, degradation, and loss of natural wetlands as well as in declines of species due to the stressors. Under scenario four, improved and more robust sustained conservation efforts will help mitigate the impacts of stressors, but climate-related changes may be expected to continue. Additional exploration will likely be needed to determine how to best mitigate climate-related changes.

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Lentic Freshwater: Ponds—Aquaculture Ponds

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Abstract

Capture fisheries production is no longer increasing, and production of fish, shrimp, and molluscs by aquaculture is necessary to meet the global demand for aquatic food animals. Aquaculture is conducted in freshwater areas, brackishwater areas, and in the ocean. Most fish production from aquaculture is in freshwater areas, and freshwater fish are reared mainly in ponds. The global, freshwater pond surface area was estimated at 8.8 million ha in 2004. Since 2004, freshwater aquaculture production has doubled; but, because the intensity of production has increased, the global pond area in 2016 was estimated to only be around 11 million ha. Nevertheless, the freshwater pond aquaculture area and volume is great enough for it to be included in the freshwater biome. The impact of aquaculture on the freshwater biome appears mostly negative, because aquaculture ponds tend to be eutrophic and of low biodiversity. Aquaculture pond effluents also are enriched in nutrients and organic matter and can cause eutrophication in receiving water bodies. As with agricultural production, which also has many negative environmental impacts, aquaculture production is necessary to supply the human population with food. Efforts to make food production more resource-use efficient and less harmful to the environment are critical to society.

Introduction

Fish, shrimp, and other aquatic animals are an important source of food and especially of animal protein for humans. According to the Food and Agriculture Organization (FAO) of the United Nations (FAO, 2018), 20.2 kg (live weight equivalent) capita⁻¹ of aquatic animals were consumed globally in 2015. While the average consumption of 21.6–25 kg capita⁻¹ of fisheries products was similar among North America, Europe, Asia, and Oceania (Australia and South Pacific Islands), the average annual consumption in Africa was only 9.9 kg capita⁻¹. By economic status, average annual consumption was 7.7 kg capita⁻¹ in low-income, food-deficient countries, 20.5 kg capita⁻¹ in other developing countries, and 24.9 kg capita⁻¹ in developed countries. At present, aquatic animals provide 17% of animal protein for human consumption (FAO, 2018).

Fish culture in ponds was possibly practiced as many as 4000 years ago in China and Egypt. The earliest known document on the topic is from China and dated 475 BCE; it was written by Fan Li and entitled *Fish Breeding* (Stickney, 2000). Fish and shrimp culture has been practiced for many centuries in China, Japan, and other Asian countries, and carp culture in Europe apparently began with the Romans and spread into central and eastern Europe where carp farms have been common since the 1600s and 1700s (Balon, 1995; Stickney, 2000).

The prospects for aquaculture were vastly improved by development of hatchery methods for producing fish and shrimp for stocking in ponds. It also was discovered that primary productivity and fish production in ponds could be increased by applying fertilizers to promote the growth of natural food organisms for culture animals. Acidic ponds could be limed to enhance response to fertilizers. Manufactured feeds were developed that allowed greater production of aquaculture animals than possible in fertilized ponds. Finally, it was also discovered that more feed could be applied (and greater fish and shrimp production realized) if mechanical aerators were used to aerate pond water and prevent low dissolved oxygen concentrations. Much of this knowledge about pond aquaculture management was developed between 1900 and 1980. Nevertheless, aquaculture did not contribute much to global fisheries production until the capture fisheries reached or possibly exceeded its sustainable limit in the late 1980s. The stagnation of capture fisheries has led to further improvement in aquaculture technology and a trend of increasing aquaculture production (Fig. 1).

Global Aquaculture Production

Capture fisheries production is somewhat greater than aquaculture production (Fig. 1), but roughly 20 million tonnes (Mt) of the capture fisheries are used annually for nonfood purposes; mainly for fish meal and oil production. Aquaculture production, which

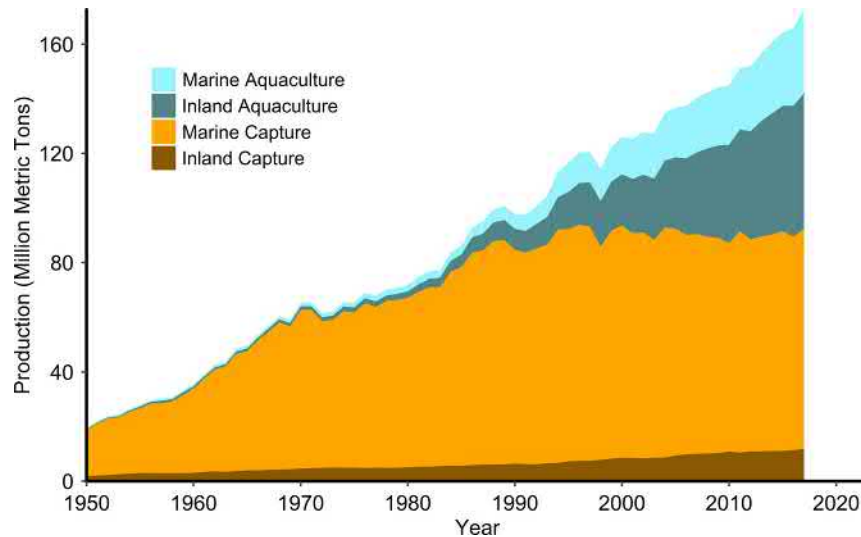


Fig. 1 Global fisheries and aquaculture production. Data from FAO FishStat (www.fao.org/fishery/nems/38200/en).

is used almost exclusively for human consumption, accounted for 53% of fisheries products for human consumption in 2016 (FAO, 2018). Some question the reliability of the FAO fisheries statistics and claim that capture fisheries still produces more food for human consumption than does aquaculture (Edwards et al., 2019), however it is not disputed that aquaculture makes a major contribution to global fisheries production and that future increases in fisheries production must come from aquaculture. The FAO fisheries statistics, for better or for worse, are the most comprehensive dataset available and often the only data available for a particular assessment of aquaculture production.

The global production and utilization of aquatic food animals by capture fisheries and aquaculture are summarized (Table 1). In 2016, freshwater bodies provided only 12.8% of capture fisheries production, while 64.2% of aquaculture production was from inland (mostly freshwater) culture systems. Aquaculture production in 2016 consisted of 54.1 Mt. of finfish (mostly from freshwater), 17.1 Mt. of molluscs (mostly from the ocean), and 7.9 Mt. of crustaceans (mostly from brackish or ocean waters). There also was 0.94 Mt. of other aquatic animals to include sea cucumbers, turtles, sea urchins, jellyfish, etc., which came mostly from marine waters. In addition, 30.1 Mt. of aquatic plants were farmed mainly in the ocean (FAO, 2018). Total aquaculture production was 110.2 Mt. of which 80.0 Mt. were fish, molluscs, and crustaceans.

The amount of aquaculture varies greatly by continent, by country, by region within a country, and within a region. Asia is the leading aquaculture continent with 89.40% of global production in 2016. Percentage of production by other continents were Europe, 3.67%; South America, 3.38%; Africa, 2.48%; North America, 0.81%; Oceania 0.26%. Production was reported for a total of 192 countries in 2016 (FAO, 2018), but 10 countries produced 94% of inland global production (Table 2). Much of the production in several of these countries was not freshwater production or was not done in ponds.

Several hundred species of fish and other aquatic organisms are produced by aquaculture, but relatively few species make up most of the production. The major species produced by pond aquaculture and their 2016 production are given in Table 3. Most of the whiteleg shrimp and milkfish production is from coastal ponds filled with seawater or brackishwater. While the FAO database does not report aquaculture production from ponds separately, FAO (2018) emphasizes that ponds are the main freshwater aquaculture production method. According to data presented by Verdegem and Bosma (2009), 92.6% of freshwater aquaculture

Table 1 Global production by capture fisheries and aquaculture of fish, crustaceans and molluscs in 2016.

<i>Production category</i>	<i>Live weight quantity (million tonnes)</i>
Inland capture fisheries	11.6
Marine capture fisheries	79.3
Total capture fisheries	90.9
Inland aquaculture	51.4
Marine aquaculture	28.7
Total aquaculture	80.0
Total fisheries and aquaculture	170.9
Human consumption	151.2
Nonfood uses	19.7

FAO (2018). *The state of world fisheries and aquaculture*. Rome: Department of Fisheries, Food and Agriculture Organization of the United Nations.

Table 2 Top 10 freshwater aquaculture countries in 2016 and the major types and amounts of production.

Country	Group	Production (t)	Inland production (% by country)
China	Carps and goldfishes	21,846,726	68.7
	Tilapia	1,866,381	5.9
	<i>Total</i>	31,783,782	
India	Carps and goldfishes	4,204,000	82.8
	<i>Total</i>	5,076,131	
Indonesia	Catfishes ^a	1,307,278	38.0
	Tilapias	1,103,812	32.1
	Carps and goldfishes	578,579	16.8
	<i>Total</i>	3,439,892	
Vietnam	Catfishes ^a	1,207,654	50.3
	Carps and goldfishes	478,840	19.9
	Tilapias	183,817	7.7
	<i>Total</i>	2,401,113	
Bangladesh	Carps and goldfishes	990,486	49.6
	Catfishes ^b	502,527	25.2
	Tilapias	342,567	17.1
	<i>Total</i>	1,997,645	
Egypt	Tilapias	940,309	68.6
	Carps and goldfishes	200,909	14.7
	<i>Total</i>	1,370,660	
Myanmar	Carps and goldfishes	820,312	85.5
	Catfishes ^a	42,601	4.4
	<i>Total</i>	959,768	
Brazil	Tilapia	239,131	47.1
	Characins	212,310	41.8
	Other species	35,759	7.0
	<i>Total</i>	507,500	
Thailand	Tilapia	208,144	49.8
	Catfishes ^a	131,634	31.5
	<i>Total</i>	418,023	
Iran	Carps and goldfishes	201,096	54.8
	Trout and salmon	163,325	44.5
	<i>Total</i>	366,636	

^a*Pangasius* and *Clarias* combined.^b*Pangasius*, *Clarias*, and silurids.FAO FishStat (www.fao.org/fishery/nems/38200/en).

production was from ponds, and at least 90% of the 2016 production also is likely from ponds. Some inland aquaculture production is done in ponds filled with low-salinity surface water or with saline groundwater from wells (Roy et al., 2010). This production is not great, but it is not completely separated from the freshwater production in the FAO database.

Freshwater Pond Area

Records of aquaculture pond areas are not maintained by some governments, and most governments that maintain such records seldom update the data. The most reliable estimate of the global aquaculture pond area is probably that of Verdegem and Bosma (2009). They placed the total water surface areas of freshwater and coastal, brackishwater aquaculture ponds in 2004 at 8,750,509 ha and 2,332,737 ha, respectively. Their data suggested that 92.6% of freshwater aquaculture production and 17.5% of marine aquaculture production (including brackishwater) was derived from ponds, and annual production intensity was 2.89 and 1.42 t ha⁻¹ for freshwater and brackishwater ponds, respectively.

Table 3 Major species produced by pond aquaculture and global production of each in 2016.

Species	Production (million tonnes)
Grass carp, <i>Ctenopharyngodon idellus</i>	6,068,000
Tilapia spp.	5,377,000
Silver carp, <i>Hypophthalmichthys molitrix</i>	5,301,000
Common carp, <i>Cyprinus carpio</i>	4,557,000
Bighead carp, <i>Hypophthalmichthys nobilis</i>	3,527,000
Carassius spp.	3,006,000
Catla, <i>Catla catla</i>	2,961,000
Freshwater fishes nei, <i>Osteichthyes</i>	2,362,000
Roho labeo, <i>Labeo rohita</i>	1,843,000
Pangas catfishes nei, <i>Pangasius</i> spp.	1,741,000
Milkfish, <i>Chanos chanos</i>	1,188,000
Torpedo-shaped catfishes nei, <i>Clarias</i> spp.	979,000
Wuchang bream, <i>Megalobrama amblycephala</i>	826,000
Cyprinidae	670,000

FAO FishStat (www.fao.org/fishery/nems/38200/en).

Freshwater (inland) production in 2016 was 51.37 Mt. of which at least 90% was from ponds. The amount of area necessary for this production at the estimated 2004 production intensity of 2.89 Mt. ha⁻¹ would be 16.00 Mha. However, aquaculture production in ponds is becoming more intensive. For example, statistics collected by the US Department of Agriculture (https://www.nass.usda.gov/Surveys/Guide_to_NASS_Surveys/Catfish_Production/index.php), revealed that between 2004 and 2016, the intensity of ictalurid catfish production in the United States roughly doubled increasing from 3.86 to 7.91 t ha⁻¹. Production of other species also is increasing, and there may have been much less increase in the global aquaculture pond water surface area since 2004 than suggested by the straight-line interpolation above.

Fairly reliable data on the coastal shrimp farm area are available because of the environmental controversy concerning the conversion of mangrove forest areas to shrimp ponds. Aquacultured shrimp production is exclusively from ponds; it increased by 106.2% between 2004 and 2016, but the global shrimp pond area increased by only 18.6% (Boyd and McNevin, 2015). The intensity of shrimp production in ponds increased from 1.31 t ha⁻¹ in 2004 to 2.28 t ha⁻¹ in 2016. The production of freshwater aquaculture increased by 89.0% between 2004 and 2016. Assuming the intensity of freshwater production increased at a rate similar to marine shrimp production, the increase in freshwater pond aquaculture area would not have exceeded 25% and the 2016 area likely was around 11.0 Mha.

Ponds require more land than the land covered by the water impounded in them. Embankment ponds require land beyond water edges, canals may be used to convey water from other water bodies into embankment ponds, some farms may have reservoirs in which source water is held before introduction to ponds, and settling basins may be necessary to assure compliance of farm discharge with effluent quality standards. Aquaculture farms also require land for buildings, roads, parking, and staging areas.

The amount of land that is necessary for embankments and other farm-level earthen infrastructure increases the land required on aquaculture farms. The ratio of the total area devoted to aquaculture on a farm to the production pond water surface area is called the land to water ratio (LWR). A satellite imagery study of 100 aquaculture farms (2783 production ponds) in 26 countries (Jescovitch et al., 2016) revealed that the LWR was on average 1.48, i.e., each 1-ha increment of production water surface area required 0.48 ha of additional land at the farm level. The LWR may be calculated with the following equation:

$$\text{LWR} = 1.5583X^{-0.102}$$

where X = the average area of the production ponds on an aquaculture farm (ha).

Based on the average LWR and a global freshwater pond water surface of 11 Mha, the total area devoted to freshwater pond aquaculture would be 16.3 Mha. This area is roughly equal to the areas of Suriname or Tunisia or the states of Florida or Wisconsin in the United States.

Types of Aquaculture Ponds

Aquaculture ponds usually are of one of three types. The most common type is made by building embankments around an area in which water is confined. Soil usually is removed from the area to become the pond bottom and used as earthfill for the embankments. Embankments normally are 2–3 m high, 2–5 m wide at the top, and side slopes of embankments are 1:1 (vertical:horizontal) to 1:3 depending upon soil characteristics (Fig. 2). Embankments and pond bottoms are thoroughly compacted to minimize the potential for seepage, and pipes or various types of concrete water gates with dam boards installed to convey water into and out of ponds. Pond bottoms are gently sloped toward the water exit structure to facilitate complete draining at harvest. Embankment ponds are ideal for aquaculture because their water levels may be maintained and controlled. Embankment ponds usually can be drained and refilled as needed to fit the management schedule.

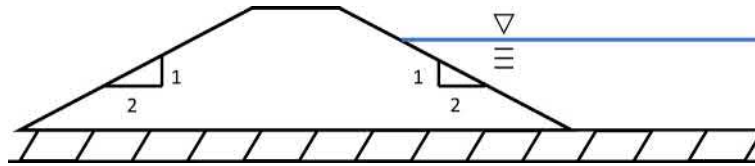


Fig. 2 Cross-section of an aquaculture pond embankment.

A watershed pond is constructed by building an embankment (dam) across a watershed to retain stream flow, overland flow, or both. Watershed ponds typically have a standpipe and a drain pipe extending through the bottom of the dam for establishing the water level and discharging excess inflow. A spillway with its bottom at a slightly higher elevation than the top of the stand pipe usually is included at one end of the dam to avoid water overtopping the dam after periods of unusually large inflow. In dry weather, water levels may decline drastically in watershed ponds—particularly in those without stream inflow.

Excavated ponds are constructed by digging a basin which is usually filled by rainfall and surface storm flow. Some excavated ponds may extend below the top of the water table and fill partially by groundwater inflow. The soil excavated to produce such ponds is either piled around the pond or disposed in another area. These ponds typically fill in the rainy season, but their water levels may be very low at the end of the dry season. Excavated ponds usually are small (≤ 0.1 ha), and they cannot be drained at harvest.

The average depth of aquaculture ponds may range from 1 to 4 m, but most ponds have average depths of 1.25–2.0 m. Maximum depths of embankment and excavated ponds usually are not more than 0.5–1.0 m greater than average depth. Some watershed ponds may have maximum depths two to three times greater than average depths.

In extensive culture, ponds usually are fertilized and feed is not applied. Production typically is $< 0.5 \text{ t ha}^{-1} \text{ crop}^{-1}$. In semi-intensive culture, feeds are applied, but mechanical aeration is not used. Production usually is $1\text{--}2 \text{ t ha}^{-1} \text{ crop}^{-1}$. Both feeding and mechanical aeration are applied in intensive culture and production will typically be $> 3 \text{ t ha}^{-1} \text{ crop}^{-1}$. Extensive and semi-intensive ponds sometimes have areas in excess of 100 ha, but they usually are not greater than 10 ha in area. Ponds for intensive production seldom exceed 1 ha in water surface area and highly intensive culture ($> 20 \text{ Mt. ha}^{-1} \text{ crop}^{-1}$) is normally done in ponds with surface areas < 0.25 ha.

Water Use

Aquaculture farms often take large amounts of freshwater from streams or other water bodies. The amount of water required per tonne of aquaculture production varies with the type of water management used on a farm. Some farms use water only to fill ponds and maintain water levels, some use water exchange in which water is flushed through ponds daily, most pond aquaculture facilities drain ponds completely for harvest, while some retain pond water for reuse and only drain ponds at intervals of 5–10 years. Despite the method used, aquaculture farms discharge water, and they usually release it back into the same water body from which it was taken. Nevertheless, ponds reduce downstream flow, because of evaporation and seepage losses. There are cases where water use by aquaculture farms have reduced downstream flow causing conflicts with downstream water users. Also, when groundwater from wells is used in ponds, there can be competition for groundwater use.

Boyd (2005) suggested that water use in aquaculture be defined as the amount of reduction in downstream flow plus the removal of groundwater for use in ponds. This is similar to the way water consumption has traditionally been defined for irrigated agriculture, because irrigation water is from surface water bodies and groundwater sources (Wisser et al., 2008). In water footprint methodology in common use today, soil moisture replenished by precipitation and transpired by agricultural crops is called green water (Hoekstra and Mekonnen, 2012). Blue water is the term given to surface or groundwater used for irrigation of agricultural crops, and the volume of freshwater necessary to dilute the pollution from agricultural or other production process is termed gray water. This practice is used despite the fact that rain falling on terrestrial ecosystems evaporates whether land cover is crops, natural vegetation or other cover (Boyd and McNevin, 2015).

According to Verdegem and Bosma (2009) freshwater removal for aquaculture totals $16,900 \text{ m}^3 \text{ t}^{-1}$ production, but this estimate included green water and embodied water resulting from freshwater necessary to make feed ingredients. Tucker et al. (2017) estimated water use (including embodied water in feed) for channel catfish production in Mississippi as $2700 \text{ m}^3 \text{ t}^{-1}$. Boyd and McNevin (2015) calculated that $4088 \text{ m}^3 \text{ t}^{-1}$ were necessary to produce fish in ponds drained after each crop. Assuming that 46.2 Mt. of aquatic animals were produced in inland ponds in 2016, about 235 km^3 of freshwater would have been required. This quantity is larger than the storage volume of ponds which is around 165 km^3 based on pond area and average pond depth discussed previously. Additional freshwater was used in other inland aquaculture systems, but the volume was no doubt considerably less than that used in ponds.

In 2016, about 39.9 Mt. of aquaculture feed were produced (Alltech, 2017), and around 70% of the feed was used in inland, pond aquaculture. Chatvijitkul et al. (2017) found that embodied freshwater in feeds for freshwater species averaged $1370 \text{ m}^3 \text{ t feed}^{-1}$ and the land embodied in feed ingredient production was $0.239 \text{ ha t feed}^{-1}$. The use of embodied freshwater and land

in feed for freshwater aquaculture is therefore about 38.3 km³ and 6.7 Mha, respectively. Embodied freshwater accounts for only 16.2% of freshwater use in aquaculture production, and embodied land represents 28.3% of the total area devoted to inland farms.

Pond Management

The following is a list of the major management practices of which some or all may be applied in a particular type of pond aquaculture: ponds may be filled by rainwater and overland flow, or they are filled from streams, lakes, or wells; larger aquatic plants and animals are excluded by management practices; one or more selected species of fish or shrimp are stocked; fertilizers, liming materials, feed and other amendments are applied to promote production of the culture species; mechanical aeration may be applied; in the culture of some species, from 10% to 400% of the pond volume may be flushed from ponds by intentional input of water from the water source; some ponds have partial or complete plastic liners to avoid erosion of earthwork by aerator-generated water currents; ponds usually are drained to facilitate harvest and allow pond bottom soil treatments.

Aquaculture ponds receive inputs of nitrogen and phosphorus in organic fertilizers such as manures and other agricultural wastes, chemical fertilizers and feed. A low fertilizer application rate would be equivalent to around 0.25 kg nitrogen and 0.05 kg phosphorus ha⁻¹ day⁻¹, while some ponds may receive as much as 4 kg nitrogen and 1 kg phosphorus ha⁻¹ day⁻¹.

Usually 20–40% of nitrogen and phosphorus applied in fertilizers and feed to aquaculture ponds is recovered in fish at harvest (Boyd and Tucker, 1998; Boyd and Li, 2012). In crustacean farming, nitrogen recovery is similar, but only around 10% of phosphorus is recovered. Aquaculture feeds usually contain 4.5–7.0% nitrogen and 1.0–1.5% phosphorus (Chatvijitkul et al., 2018). At a daily input of 100 kg ha⁻¹ of a feed containing 5% N and 1% P and assuming 30% recovery of nitrogen and phosphorus in fish biomass at harvest, the daily nitrogen and phosphorus inputs to the water in feeding wastes would be about 3.5 kg N ha⁻¹ day⁻¹ and 0.7 kg P ha⁻¹ day⁻¹. Feeding rates in some ponds may be two to three times greater than in this example. Of course, ponds have a great ability to assimilate waste through microbial decomposition, ammonia diffusion, nitrification, denitrification, and phosphorus adsorption by sediment. No more than 10% of organic carbon and phosphorus and 30–40% of nitrogen added to ponds in feed and fertilizer are usually discharged in pond effluents (Boyd and Tucker, 1998).

High nutrient inputs make aquaculture ponds highly eutrophic. Typical rates of gross primary productivity range from 1 to 6 g carbon m⁻² day⁻¹ and values above 10 g C m⁻² day⁻¹ have been reported (Boyd and Tucker, 1998). Dense plankton blooms suppress light penetration and aquatic macrophytes usually are not abundant in aquaculture ponds. Moreover, the primary producers consist mainly of cyanobacteria. Of course, a large zooplankton community also develops in ponds, and bottom soils contain an abundance of benthic animals. Several studies have documented benthic insects, annelids, bivalves, gastropods, in the benthic environments of aquaculture ponds (e.g., Correia et al., 2002; Martinez-Cordova et al., 1998; Riise and Roos, 1997). It is likely that these contribute in some way to the feeding of cultured shrimp and fish species in those ponds.

Environmental Impacts

While the physiochemical and biological principles that operate to determine water quality and biological productivity are the same in aquaculture ponds as in natural water bodies, the two types of aquatic environments are structurally and hydrologically much different. Moreover, in aquaculture ponds, physiochemical, and biological processes are subjected to a high degree of management. Fertilized ponds are analogous to fertilized pastures for livestock, and ponds receiving feed are analogous to livestock production where feeds are used. Highly intensive pond aquaculture are similar to concentrated animal production facilities (feed lots).

The amount of land devoted to aquaculture in an area, and the manner in which the ponds are superimposed into the landscape varies. In some aquaculture areas, there are huge expanses of farms with ponds located very close together, and the main feature of the landscape is aquaculture ponds (Fig. 3). There also are single aquaculture farms widely separated from others and imposed into various landscapes (Fig. 4).

One environmental complaint about aquaculture is that it may result in conversion of large areas into ponds or it may cause disruption of terrestrial habitats by fragmentation of other land uses. The most serious ecological damage occurs when wetlands are converted to ponds and large areas of ponds are installed on flood plains. Additionally, aquaculture has been blamed for much of the conversion of mangrove habitats. Aquaculture has been estimated to account for roughly 544,000 ha of mangrove conversion (Hamilton, 2013). However, the topic of land conversion by aquaculture and the consequences of the conversions are not as well researched in freshwater systems.

Intensification of aquaculture can lessen the area of land and water use for aquaculture per tonne of production. The amount of embodied freshwater and land in feed depends on the efficiency with which the feed is used. Feed use efficiency often is calculated as the weight of feed needed to produce a unit weight of live aquaculture biomass at harvest. This ratio is called the feed conversion efficiency (FCR) which ranges from 1.2 to 2.5 depending upon the culture species and the effectiveness of pond management. A typical FCR for most pond culture species is 1.5–1.7.

There is a large input of organic matter to pond bottoms from organic fertilizers, feeding wastes, and dead plankton resulting in organic matter accumulation in sediment. Boyd et al. (2010) measured organic matter accumulation rates in 233 aquaculture ponds at 25 locations in nine countries; the accumulation rates ranged from 28 to 333 g C m⁻² year⁻¹ with an average of 150 g C m⁻² year⁻¹. Global carbon burial in aquaculture ponds was estimated to be 16.6 Mt. year⁻¹. By comparison large



Fig. 3 An aquaculture pond dominated landscape. Courtesy of Google Images (<https://www.pexels.com/photo/aerial-aquaculture-buildings-canals-1467519/>).



Fig. 4 A small aquaculture pond on a small-holder farm in the ponds. Courtesy of Google Images ([https://commons.wikimedia.org/wiki/File:USAID_Measuring_Impact_Conservation_Enterprise_Retrospective_\(Philippines;_Kalahan_Educational_Foundation\)_38482292350.jpg](https://commons.wikimedia.org/wiki/File:USAID_Measuring_Impact_Conservation_Enterprise_Retrospective_(Philippines;_Kalahan_Educational_Foundation)_38482292350.jpg)).

reservoirs on the world's rivers are estimated to sequester $160 \text{ Mt. C year}^{-1}$. Carbon sequestration in ponds offset a portion of the carbon dioxide emissions of aquaculture production. However, aquaculture farms are not carbon dioxide emission neutral, and they also result in emissions of methane and nitrous oxide which also are greenhouse gases (Ma et al., 2018; Rutegwa et al., 2019).

As previously discussed, the fish and crustacean populations in aquaculture ponds consist mainly of the species stocked. Ponds may be in monoculture, but many ponds in Asian countries are in carp or other polycultures (e.g., Costa-Pierce et al., 1984). Outside of the culture species, biodiversity is usually low in ponds. Plankton blooms normally consist of phytoplankton and zooplankton like cladocerans, copepods, and rotifers (e.g., Burke et al., 1986). The composition of plankton communities stimulated by fertilization in aquaculture ponds often consists of dense blooms of cyanobacteria. These organisms excrete odorous compounds into the water that can be absorbed by the culture animal resulting in an off-flavor in fish flesh (Tucker, 2010). Off-flavor has been particularly troublesome to the United States channel catfish industry, and it also has been observed in other fish and crustacean species. Pond bottoms usually are disinfected by lime treatment after ponds are drained (Boyd and Tucker, 1998). Although, this kills many

of the benthic organisms, the benthic community quickly recovers and aquaculture pond bottoms contain an abundance of annelids, chironomid larvae, and other worms (e.g., Tidwell et al., 1997). It has been suggested that benthic invertebrates play a role in nutrient cycling in aquaculture ponds (Adamek and Marsalek, 2013) and therefore may be important, even if they are often not considered so during production. In coastal areas in Southeast Asia, low intensity systems sometimes referred to as “silvo-fisheries” or “integrated mangrove aquaculture” exist where mangrove trees are grown in the ponds (Clough et al., 2002). These systems are primarily used for growing Black tiger shrimp (*Penaeus monodon*) and increase mangrove cover, however farmers typically allow some more valuable species like mud crabs (Family Portunidae) and milkfish (Family Chanidae) to remain in the ponds when the water is exchanged with the tidal flow. These wild fish and crustaceans are subsequently harvested with the shrimp periodically (Joffre et al., 2015), and therefore the practice is extractive from the local fish communities.

Because of the eutrophic nature of most aquaculture ponds, water discharged from ponds usually has higher concentrations of suspended solids and nutrients such as nitrate, ammonia nitrogen, and phosphate than found in receiving waters (Sarà, 2007a; Tucker and Hargreaves, 2008). Pond effluents also may have elevated bacterial abundance and contain aquatic animal pathogens (Sarà, 2007b). If many ponds discharge into the same water body, it can have a negative additive effect on the receiving waterbody, spread disease, and decrease the water quality of water used for intake in ponds downstream. Additionally, some ponds introduce chemicals such as antibiotics into the environment during culturing which are discharged into the environment (Holmstrom et al., 2003; Rico et al., 2012; Binh et al., 2018).

Aquaculture can have negative impacts on fish assemblages and other aspects of biodiversity in local streams, although the degree of this impact depends on the nature and quality of the receiving waters. Local predators may also interact with aquaculture ponds. Pond managers go to great lengths to prevent piscivorous birds from preying in ponds by using techniques such as complex netting systems and acoustic deterrents (Bevan et al., 2002), as well as lethal control methods (Blackwell et al., 2000). While typically not thought of when discussing aquaculture on a global scale, small-scale aquaculture facilities are managed to produce fish for stocking into natural waters to restore native fish populations. Fish population restoration is most common in North America and Europe. Aquaculture for restoration efforts is such a small fraction of the total global production that the production is often not counted in global aquaculture statistics like the FAO FishStat database. The one exception is the rearing and stocking of salmonid juveniles in the Pacific Northwest, the North Atlantic and elsewhere.

Conclusion

Pond aquaculture is an important source of animal protein for human diets, especially in Asia where most of aquaculture production occurs. Aquaculture has become as important as capture fisheries in producing aquatic food animals, and most freshwater aquaculture is conducted in ponds. Their combined water surface area and water volume is great enough to make ponds a small but significant component of the freshwater biome. Ponds have caused conversion of terrestrial to freshwater habitat, but the biodiversity of aquaculture ponds is low and likely does not add to the local biodiversity in many locations. Moreover, pond effluents can cause water quality deterioration in water bodies into which they are discharged. With the continued growth of aquaculture, the minimization of the impacts caused by production will be important in protecting local biodiversity. Ultimately, this means aquaculture needs to become more resource efficient, and will likely depend on responsibly increasing intensification, and not relying on an increase in new pond area for production.

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Microplastics in Freshwater Environments

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Abstract

The constantly increasing production and use of synthetic plastic materials are responsible for the global increase in plastic debris in freshwater environments. Microplastics (MPs) have been found in the water and sediments of lakes and rivers worldwide, with concentrations correlated with human population density. Wastewater treatment plants have been identified as one of the main point sources for MP release, including microbeads and clothing fibers. Synthetic polymers are identified by their chemical composition using Fourier Transform Infrared and Raman spectroscopies. In freshwaters, the primary synthetic polymers that have been detected are polyethylene, polypropylene, polyester, and polystyrene. Field studies show that MPs are ingested by a variety of freshwater organisms, including clams, insects, and fish, but are retained at relatively low densities. Laboratory experiments document the effects that MPs can have on the metabolism, growth, survival, and reproduction of aquatic organisms, but usually at plastic particle concentrations that are orders of magnitude higher than those currently found in nature. The increased surface area of the small MP particles allows them to concentrate persistent organics pollutants from the aquatic environment. At this time there is limited information available on the concentration of toxic chemicals on freshwater MPs or the kinetics of the release of these compounds to organisms upon ingestion. Because MPs do not readily degrade, it is important for humans to reduce our reliance on plastic materials before their concentration in freshwater biomes reaches critical levels.

Introduction

The extensive use of plastic items worldwide can be attributed to plastics' flexible properties and low costs of production. For example, the physical characteristics of polyethylene and polypropylene give plastic items high resistance to aging and prevent deterioration (Derraik, 2002). Worldwide, plastic production has increased dramatically since the 1950s, reaching the current rate of 359 million metric tons per year (Plastics Europe, 2019). The cumulative production of plastic from 1950 to date has been calculated as over 8300 million metric tons (Blair et al., 2019). This excess production and use of plastic items have resulted in the designation of this era as the *Plasticene Age* or *Age of Plastics* (Reed, 2015). The production of plastic materials is expected to double in the next 20 years. With less than 25% of plastic items being recycled (Alimi et al., 2018), the potential for environmental pollution by plastic debris is intensifying. The fact that most plastics are not biodegradable on any reasonable human time scale increases the threat of environmental impact from plastic. Although plastics can photodegrade (UV-B degradation) and be broken down by mechanical abrasion, these processes end up producing massive amounts of small particles of microplastics (MPs) that continue to persist in the environment. An estimated eight million tons of plastic debris enters the oceans every year (Jambeck et al., 2015), but there is currently little information on the total amount of plastic accumulating in freshwater biomes.

MPs are small particles of synthetic polymers derived from petroleum and are produced intentionally (e.g. preproduction pellets) and unintentionally (e.g. fragmentation of larger plastic debris). MPs are a relatively new type of environmental contaminant whose impacts on ecosystems are very poorly understood. While MPs have received substantial attention in the marine environment, in freshwater biomes these particles have only been documented and studied during the last decade. MP particles have now been reported from freshwaters worldwide and an increasing number of studies are being conducted to explore the adverse effects that MP may have on aquatic organisms and ultimately on human health.

MPs are ubiquitous anthropogenic stressors affecting all of the world's biomes. MPs are found in the air (Panko et al., 2013; Sommer et al., 2018), water, and soil, and can easily be ingested by organisms (Browne et al., 2011). Due to their small sizes, MPs

can concentrate toxic compounds from the environment (Rodrigues et al., 2019). Additionally, some of the chemical additives used during plastic production are endocrine disruptors (Monneret, 2017). There is concern that MPs may also affect humans through ingestion, inhalation, or dermal contact (Prata et al., 2019b).

Classification and Types of MPs

Currently, there is no consensus on the definition of MPs based on size that is congruent with SI (System International) units. To distinguish macro and micro plastic particles, 5 mm was proposed as the maximum size limit for MPs (Arthur et al., 2009; Barnes et al., 2009; Ryan et al., 2009; Thompson et al., 2009). However, some researchers have used different size classifications for macro (1–100 cm), meso (1–25 mm), micro (1–5000 µm) and nanoplastics (1–100 nm or 1–20 µm) (e.g. Hartmann et al., 2019). Frias and Nash (2019) recently defined MPs as “any synthetic solid particle or polymeric matrix, with regular or irregular shape and with size ranging from 1 µm to 5 mm in maximum dimension, of either primary or secondary manufacturing origin, which are insoluble in water.” Whereas, the Group of Experts on the Scientific Aspects of Marine Environmental Protection (GESAMP, 2015) has noted the lack of international agreement on MP definitions, they currently recommend the use of MPs for all particles <5 mm in diameter. For this paper, we are only including reports of MP particles ranging from 1 to 5000 µm.

There are more than 5000 types of commercial plastic polymers (Wagner and Lambert, 2018), however, six polymers make up approximately 80% of plastic production: polypropylene (PP), polyethylene (PE), polyvinyl chloride (PVC), polyethylene terephthalate (PET, also known as polyester PES), polystyrene (PS), and polyurethane (PU), Table 1 (Utracki, 2003; Plastics Europe, 2019). Plastics with a density less than 1.0 g mL⁻¹ will float in freshwaters, while those with higher densities tend to sink (Andrady, 2011).

MPs are found in a variety of shapes in aquatic biomes including filaments/fibers, films, fragments, spheres/pellets and foams and occur in a range of colors including clear, white, red, brown, yellow, green, blue and black (Rodríguez-Seijo and Pereira, 2017). MP fibers are increasingly reported as one of the most common forms of MPs in samples from freshwater environments (Eerkes-Medrano and Thompson, 2018). Figs. 1 and 2 are showing MPs found in samples from environmental and cosmetic products.

MP Sources

MPs can be produced in two distinct ways. Primary MPs are plastic particles that are initially manufactured in small sizes, including virgin resin pellets or flakes and preproduction plastics. Synthetic microbeads are used in personal care products (facial cleansers,

Table 1 Some main types of plastics and their uses.

Name	Abbreviation	Density (g mL ⁻¹) ^a	Uses
<i>Thermoplastics</i>			
Polypropylene	PP	0.90	Food packing, snack wrappers, automotive parts, bank notes
High density polyethylene	HDPE	0.96	Toys, milk bottles, shampoo bottles, houseware, pipes
Low density polyethylene	LDPE	0.92	Bags, trays, containers, agricultural films
Polyvinyl chloride	PVC	1.40	Windows frames, floor and wall covering, pipes, cables
Polyethylene terephthalate ^b	PET/PETE/PEST	1.55	Soda and water bottles, clothing
Polystyrene	PS/PST	<1.05	Expanded foam, eyeglasses frames, egg trays, insulation, cups
Polyamides (nylons)	PA	1.02–1.14	Adhesives, fibers, films, clothing
Polycarbonate	PC	1.36	Electrical connectors, insulators, medical tubing, instrument covers
Polymethylmethacrylate	PMMA	1.18	Lightweight sheets or Plexiglass™
<i>Thermosets</i>			
Polyurethane	PU/PUR	1.052	Building insulation, pillows and mattresses, fridge insulations
Epoxy resins	EP	1.82	Adhesives, glass reinforced, paints and coatings
Polyvinyl ester	PVE	1.80	Paints, transportation, buildings, aerospace,
Cellulose acetate	CA	1.30	Containers, tools, packaging, fibers
Silicone		1.5	Seals, O-rings, linings, insulations
Phenol formaldehyde	PF	1.21	Bakelite™, billiard balls, paints, plywood
Urea formaldehyde	UF	1.5	Decorative laminates, textiles, cotton blends, electrical appliances
Phenolic resins	PH	1.28	Laboratory countertops, coating, adhesives, billiard balls
Acrylic resins	AC	1.19	Automotive, architectural, coating

^aSea water density 1.02–1.03 g mL⁻¹, freshwater density ~1.0 g mL⁻¹.

^bPolyethylene terephthalate is also known as polyester (PES).

Data from Utracki, L. A. (2003). *Polymer blends handbook*. USA: Kluwer Academic Publishers; Plastics Europe. (2019). *Plastics-the facts*. An analysis of European plastics production, demand and waste data. Plastics Europe: Association of Plastic Manufacturers.

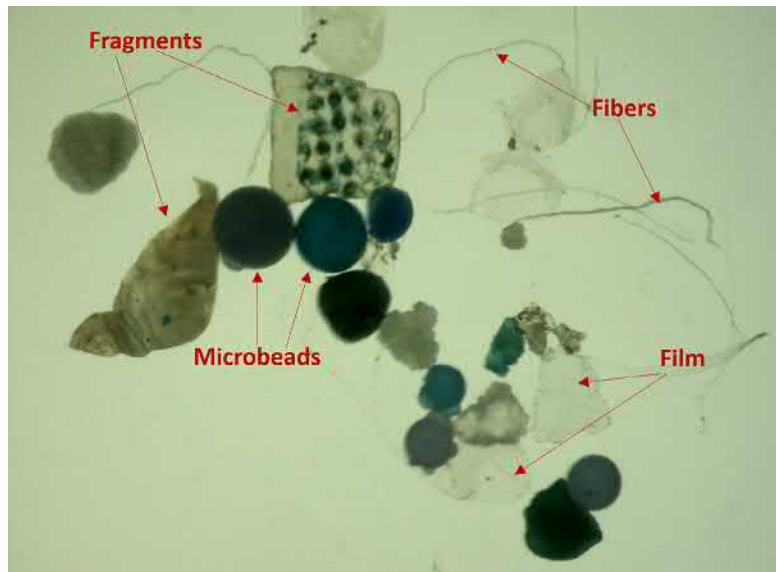


Fig. 1 Sample from St. Louis River Estuary, Duluth, MN showing MP types.



Fig. 2 Microplastics from (A) cosmetic products with microbeads (bar size 670 μm), (B) freshwater environment (pellet size 4988 μm , Lake Superior) and (C) marine environment (fragment size 2149 μm , Mediterranean Sea).

tooth pastes, shower gels, makeup, insect repellents and sunscreens) and as carriers for certain types of medicine. They occur in powders used for injection molding and in ink for 3D printers. Primary MPs are frequently used as industrial abrasives for cleaning using air/water-blasting, and are found in drilling fluids employed in oil and gas exploration (Duis and Coors, 2016).

Secondary MPs are produced by fragmentation of larger plastic items as a result of photodegradation (UV radiation) and physical abrasion which produce small particles that fall into the micro- or even nanoparticle size ranges. Sources of MP fragments include the breakdown of plastic bags, bottles, cups, food wraps, plastic films used to cover agricultural soil and crops, foam insulation materials, and even from automobile tires (Duis and Coors, 2016; Wagner and Lambert, 2018). Synthetic microfibers are created from degradation of clothing and textile products containing blends of polyester, polyacrylic, and nylon (Browne et al., 2011).

Plastic materials can enter aquatic systems from accidental industrial spills, runoff from agricultural fields that use plastic mulches, inadequate recycling, discharges from municipal wastewater treatment plants, and individual littering. Microbeads that are used in cosmetics and toothpastes often end up in domestic wastewater. Kalčíková et al. (2017) reported the daily release of an average of 15.2 mg of microbeads per person to the sewage system in Ljubljana, Slovenia. MP fibers produced from laundering textiles are another major source of MP pollution. Washing a normal 6 kg load of polyester-cotton blend clothing can release 138,000 fibers, while 496,000 fibers can be produced from a load of polyester clothing, and 729,000 fibers from a load of acrylic materials (Napper and Thompson, 2016). The initial washing of fabrics releases the largest amount of fibers, but fibers continue to be released even after ten washings (De Falco et al., 2019).

While there are many sources of MPs in freshwater systems, wastewater treatment plants (WWTPs) are one of the most important point sources for microfibers and microbeads (Carr et al., 2016; Dris et al., 2018; Ou and Zang, 2018). WWTPs were developed with the objective of treating human and industrial wastes to remove organic matter, nutrients, and harmful bacteria so that treated effluents could be discharged into marine and freshwater systems without compromising human health or causing environmental

damage (Vijayan and Mohan, 2013). The plants are not specifically designed to remove MPs and during treatment can actually form additional MP sized particles when larger particles are abraded as the plastic debris moves through the plant.

Studies have examined the effectiveness of plants with primary, secondary, and tertiary treatment methods in removing MPs (Table 2). Influent waters often contain between 12 and 7000 plastic particles (pp) L⁻¹ (Gündoğdu et al., 2018; Simon et al., 2018). Tertiary WWTPs are able to remove up to 98% of the microliter (natural and synthetic) during treatment which includes screening, grit removal, and chemically enhanced settling (Talvitie et al., 2017). Smaller MP fragments as well as natural (cotton, linen and wool) and synthetic textile fibers may pass through the screens used for sewage treatment. Michielssen et al. (2016) reported that fibers were the predominant form of microliter released from WWTPs and could account for 80% of the material in the final effluent. Confirmation of the composition of the fibers is important when determining the amount of MP material actually discharged to the environment (Ziajahromi et al., 2017b). Talvitie et al. (2017) found that up to 66% of the textile fibers that were released in treated effluent samples were natural and not synthetic.

While effectively treated effluents from WWTP can contain very low concentrations of MPs (0.3×10^{-6} pp L⁻¹ (Carr et al., 2016), due to the large volumes of water treated, this can still result in the release of several thousand MP particles to the aquatic environment each day. A WWTP in Detroit, MI (USA) was estimated to discharge approximately 9 billion fibers (natural and synthetic) per day in its effluent, representing the release of 3800 fibers per person per day into the Detroit River (Michielssen et al., 2016). Improved treatment plant designs can reduce this discharge load.

MP fragments and fibers that are retained by the WWTPs usually end up in the sewage sludge. Mahon et al. (2017) found that sludge contained 4200–15,400 MP particles kg⁻¹ dry weight. The most common form of MP found in the sludge was fibers (Mahon et al., 2017; Talvitie et al., 2017). Treated sludge, known as biosolids, is often applied to farmland as fertilizers. In the United Kingdom, approximately 80% of sewage sludge is applied to agricultural soils (Horton et al., 2017). Runoff from the fields can resuspend the fibers and transport them to rivers and lakes, or to the ocean.

MP Collection and Identification

MP particles have been found in freshwater ecosystems throughout the world, floating at the water's surface, suspended in the water column, intermixed with beach and bottom sediments, and even in the digestive tracts of aquatic organisms. The methods used to collect MPs in freshwaters are similar to those used in marine environments (Wang and Wang, 2018). MPs can be collected from the water using nets, trawls, pumps and grab samples. The mesh that is used to collect and concentrate the samples varies considerably (20–500 µm), with smaller meshes clogging faster, but retaining smaller sized MPs. Metallic grabs or corers are used to collect samples of bottom sediments, while the top five cm of beach sediments are generally collected by hand and sieved. A variety of techniques are used to collect biota, depending on the study design. The distribution of MPs in freshwaters has not been documented as well as that of marine ecosystems. The diverse hydrological patterns of inland lakes and rivers that receive runoff from urban and agricultural areas leads to large variations in MP concentrations within the water bodies and requires a large number of samples to adequately describe the distribution pattern of the particles (Horton et al., 2018).

MP particles must be sorted from the other material in the water or sediment samples prior to enumeration and identification. Some researchers use density separation, which involves adding solutions with a high specific gravity (ZnCl₂, NaCl, NaBr, NaI, CaCl₂, ZnBr₂, or Na₂WO₄) to the sample and then collecting the MPs that float to the top of the sample. Samples are often sieved to isolate materials of different sizes for analysis. If a lot of plankton is present in the samples, chemicals (KOH, H₂O₂, Fe²⁺, acids, and enzymes) may be added to digest the organic matter. MPs are then examined qualitatively or quantitatively (Fig. 3). Qualitative analyses involve visually or microscopically sorting and counting particles that resemble plastic materials, while qualitative analyses include additional steps to confirm the identity of the plastic polymers. Microscopy generally cannot differentiate MP particles less than 50 µm (Alam et al., 2019) and it is critical to use quantitative techniques to avoid counting paint chips, natural cellulose fibers or fly ash as MPs (Eriksen et al., 2013). On the other hand, due the large numbers of particles in samples, fluorescent dyes (Maes et al., 2017) and Nile Red (Andrady, 2011) are being used during sorting in qualitative analyses to rapidly distinguish the stained MPs from the background material. However, some synthetic polymers do not stain and this can affect the identification and quantification of MP particles and fibers (Prata et al., 2019a).

Hyper-Spectral Imaging (HSI) in the Short-Wave Infrared (SWIR) range is another technique used to detect plastic by differentiation of absorption bands in the spectra region and vibration of C–H molecular bonds. Serranti et al. (2018) found that this technique can identify plastic debris floating in the ocean (PP, PE and PS) in a size range of 1–5 mm. Elemental analysis using Scanning Electron Microscopy with energy dispersive X-ray spectroscopy (SED/EDX) has been used to differentiate particles with high organic content from plastic (Girão et al., 2016; Wagner et al., 2017).

In order to advance MP research, the correct identification of MP particles is essential and Fourier Transform Infrared (FTIR) and Raman spectroscopies are the main quantitative techniques used to identify synthetic polymers of plastics. These vibration spectroscopy techniques detect the chemical bonds in the samples and can differentiate between the different types of synthetic polymers and natural debris. These instruments use their own libraries to identify the polymers. Micro-FTIR with Attenuated Total Reflection (ATR) and micro-Raman can analyze particles as small as 5–10 µm (Käppler et al., 2016). Pyrolysis-gas chromatography-mass spectrometry (Pyr-GC-MS) is another technique used to obtain information about plastic polymers. This technique is based on thermal degradation and pyrolysis of polymer fragments which are separated by GC and characterized by MS (Mintenig et al., 2018). Thermal extraction desorption gas chromatography mass spectrometry (TED-GC-MS) permits the identification of MPs without requiring any sample treatment (Dümichen et al., 2017).

Table 2 Worldwide distribution of MPs in freshwater biomes.

Year of publication	Location	Matrix analyzed	Size range of MPs analyzed (μm)	Methods for counting and identifying MPs	Main fingerprinting and morphology of MPs	Concentration of MPs (plastic particles per unit volume or area)	References
<i>Africa</i>							
2018	Bloukrans River Systems (South Africa)	Sediment	63–5000	Dried, sieved, density separation, filtered, microscopic examination		Summer 6.3 ± 4.3 pp kg^{-1} dw; Winter 160 ± 139 pp kg^{-1} dw	Nel et al. (2018)
2019	Streams near Bizerte Lagoon (Tunisia)	Sediment	200–5000	Dried, density separation, filtered, microscopic examination, FTIR-ATR	98.7% fibers, PP, PE	2340 ± 227 to 6920 ± 396 pp kg^{-1} dw	Toumi et al. (2019)
<i>Asia</i>							
2014	Lake Hoysgol (Mongolia)	Surface water	355–4750	Net sample, sieved, digested, density separation, microscopic examination	Fragments, films, lines/fibers	0.020 pp m^{-2}	Free et al. (2014)
2015	Three Gorges Reservoir and tributaries (China)	Surface water	112–5000	Net sample, sieved, settled, supernatant collected, microscopic examination, FTIR-ATR	PE, PP	$0.192\text{--}13.6$ pp m^{-3}	Zhang et al. (2015)
2016	Taihu Lake (China)	Surface water	5–5000	Grab sample, filtered, digested, microscopic examination, μFTIR , SEM/EDS	Fibers, Cellophane, PET, PES, Terephthalic acid, PP	$3.4\text{--}25.8$ pp L^{-1}	Su et al. (2016)
2016	Taihu Lake (China)	Surface water	333–5000	Net sample, filtered, digested, microscopic examination, μFTIR , SEM/EDS	Fibers, Cellophane, PET, PES, Terephthalic acid, PP	$0.01\text{--}6.8$ pp m^{-2}	Su et al. (2016)
2016	Taihu Lake (China)	Sediment	5–5000	Grab sample, density separation, filtered, digested, microscopic examination, μFTIR , SEM/EDS	Fibers and fragments Cellophane, PET, PES, Terephthalic acid, PP	$11\text{--}234.6$ pp kg^{-1} dw	Su et al. (2016)
2016	Tibet Plateau Lakes (China)	Shoreline sediment	1000–5000	Dried, sieved, density separation, filtered, microscopic examination, μRaman , SEM	PE, PP	8 ± 14 to 563 ± 1219 pp m^{-2}	Zhang et al. (2016)
2017	Vembanad Lake (Kerala, India)	Sediment	<5000	Sieved, dried, digested, density separation, filtered, microscopic examination, μRaman	Films, foams common, PE, PS, PP	$96\text{--}496$ pp m^{-2} (252.8 ± 25.8 pp m^{-2})	Sruthy and Ramasamy (2017)
2017a	Urban Lakes and Rivers (China)	Surface water	50–5000	Pump sample, sieved, digested, filtered, microscopic examination, SEM, FTIR	Fibers PET, PP, PE	1660 ± 639.1 to 8925 ± 1591 pp m^{-3}	Wang et al. (2017a)
2017b	Beijiang River (China)	Littoral zone sediment	<5000	Dried, density separation, ultrasound, filtration, microscopic examination, SEM, FTIR	PE, PP	178 ± 69 to 544 ± 107 pp kg^{-1} dw	Wang et al. (2017b)
2018	Three Gorges Reservoir (China)	Surface water	48–5000	Pump sample, sieved, digested, filtered, microscopic examination, μRAMAN , SEM	Fibers PP, PE, PS	$1597\text{--}12,611$ pp m^{-3} (4703 ± 2816 pp m^{-3})	Di and Wang (2018)
2018	Three Gorges Reservoir (China)	Sediment	48–5000	Grab sample, density separation, sieved, digested, filtered, microscopic examination, μRAMAN , SEM	Fibers PS, PP, PE	$25\text{--}300$ pp kg^{-1} ww (82 ± 60 pp kg^{-1} ww)	Di and Wang (2018)
2018	West and South Dongting Lake (China)	Surface water	45–5000	Pump, filtration, digestion, density separation, filtration, microscopic examination, Raman	Fibers PS, PET, PP, PE	$367\text{--}2317$ pp m^{-3}	Jiang et al. (2018)

(Continued)

Table 2 (Continued)

<i>Year of publication</i>	<i>Location</i>	<i>Matrix analyzed</i>	<i>Size range of MPs analyzed (μm)</i>	<i>Methods for counting and identifying MPs</i>	<i>Main fingerprinting and morphology of MPs</i>	<i>Concentration of MPs (plastic particles per unit volume or area)</i>	<i>References</i>
2018	West and South Dongting Lake (China)	Shoreline sediment	<5000	Dried, density separation, digestion, density separation, filtration, microscopic examination, Raman	Fibers PET, PE, PS, PP, PVC	200–1150 pp kg ⁻¹ dw	Jiang et al. (2018)
2018	Saigon River (Vietnam)	Surface water	50–4850	Grab samples, digested, density separation, filtered, microscopic examination, FTIR	PES fibers,	172–519 pp L ⁻¹ (fibers)	Lahens et al. (2018)
2018	Saigon River (Vietnam)	Surface water	50–4850	Net samples, digested, density separation, filtered, microscopic examination, FTIR	PE, PP fragments	10–223 pp m ⁻³ (fragments)	Lahens et al. (2018)
2018	Pearl River (China)	Sediment	20–5000	Grab sample, dried, density separation, filtration, digested, microscopic examination, μFTIR	55% fibers, 43% fragments PE, PP	80–9597 pp kg ⁻¹	Lin et al. (2018)
2018	Pearl River (China)	Surface water	20–5000	Bulk water sample sieved, digested, density separation, filtered, microscopic examination, μFTIR	80% fibers, 19 % fragments PP, PE, PET	379–7924 pp m ⁻³	Lin et al. (2018)
2018	Rivers near Shanghai (China)	Shoreline sediment	100–5000	Dried, density separation, filtered, microscopic examination, μFTIR	89% spheres, 8% fibers, 4% fragments, PP, PES, rayon	802 $\pm$ 594 pp kg ⁻¹ dw	Peng et al. (2018)
2018	Taihu Lake, (China)	Surface water	20–5000	Bulk water sample, sieved, digested, filtered, microscopic examination, μFTIR	Fibers	0.5–3.1 pp L ⁻¹	Su et al. (2018)
2018	Taihu Lake, (China)	Sediment	20–5000	Dried, density separation, sieved, digested, filtered, microscopic examination, μFTIR	Fibers	15–160 pp kg ⁻¹	Su et al. (2018)
2018	Dongting and Hong Lakes (China)	Surface water	50–5000	Bulk water sample, sieved, digested, filtered, microscopic examination, SEM, μRaman	Fibers, PE, PP	900–4650 pp m ⁻³	Wang et al. (2018)
2019	Ciwalengke River (Indonesia)	Surface water	50–2000	Grab sample, filtration, density separation, filtration, microscopic examination, Raman	65% fibers, PES, nylon	5.85 $\pm$ 3.28 pp L ⁻¹	Alam et al. (2019)
2019	Ciwalengke River (Indonesia)	Sediment	50–2000	Density separation, filtration, microscopic examination, Raman	91% fibers, PES, nylon	30.3 $\pm$ 15.9 pp kg ⁻¹ dw	Alam et al. (2019)
2019	Selenga River Basin (Mongolia)	Shoreline debris	<5000	Visual collection, digestion, filtration, microscopic examination, μFTIR	99% PS foam	1.20 $\pm$ 1.21 pp m ⁻²	Battulga et al. (2019)
2019	Rivers, Tibet Plateau (China)	Surface water	45–5000	Pump, filtration, digestion, density separation, filtration, microscopic examination, Raman	69–93% fibers, PE	483–967 pp m ⁻³	Jiang et al. (2019)
2019	Rivers, Tibet Plateau (China)	Shoreline sediment	<2000	Dried, sieved, density separation, digestion, density separation, filtration, microscopic examination, Raman	54–81% fibers, PET	50–195 pp kg ⁻¹ dw	Jiang et al. (2019)
2019	Rice and fish culture ponds (China)	Water	20–5000	Filtration, digestion, microscopic exam, μFTIR	Fibers, films PP and PE	0.4 $\pm$ 0.1 pp L ⁻¹	Lv et al. (2019)
2019	Rice and fish culture ponds (China)	Sediment	20–5000	Density separation, filtration, digestion, microscopic exam, μFTIR	Fibers, PE, PP, PVC	10.3 $\pm$ 2.2 pp kg ⁻¹	Lv et al. (2019)

2019	Feilaixia Reservoir (China)	Surface water	112–5000	Net sample, sieved, filtered, dried, smaller particles microscopic examination, larger particles picked out for μ FTIR	Foams, films, fragments and fibers PP and PE	$0.56 \pm 0.45 \text{ pp m}^{-3}$	Tan et al. (2019)
2019	Lake Ulansuhai (China)	Surface water	48–5000	Pump, sieved, digestion, filtration, microscopic examination, FTIR, SEM, EDS	Fibers PE, PST, PET	$1760 \pm 710 \text{ to } 10,120 \pm 4090 \text{ pp m}^{-3}$	Wang et al. (2019b)
2019	Urban Lakes, Changsha (China)	Surface water	50–5000	Filtered, digested, microscopic inspection, SEM, Raman	PP, PE, PET, PA fibers (lines), also PP, PE, PS fragments, films, foam	$2425 \pm 248 \text{ to } 7050 \pm 1061 \text{ pp m}^{-3}$	Yin et al. (2019)
2019	Yongjiang River (China)	Surface water	50–5000	Pump, sieved, digestion, filtration, microscopic examination, Raman	73–92% fibers, 14% fragments, PET, nylon, PE	$2345 \pm 1858 \text{ pp m}^{-3}$ (500–7700)	Zhang et al. (2019b)
2019	Yongjiang River (China)	Sediment	48–5000	Density separation, filtration, digestion, microscopic examination, Raman	60% fibers, 30% fragments, PE, PP, PET	$285 \pm 110 \text{ pp kg}^{-1} \text{ ww}$ (90–550)	Zhang et al. (2019b)
<i>Australia</i>							
2019	Urban wetlands (Melbourne)	Sediment	35–1000	Sieved, dried, density separation, filtered, microscopic examination	Fragments, beads, fibers	$2\text{--}147 \text{ pp kg}^{-1} \text{ dw}$	Townsend et al. (2019)
<i>Europe</i>							
2012	Lake Geneva (Switzerland)	Surface water	300–5000	Net sample, sieved, dried, microscopic examination	Primary and secondary particles	0.048 pp m^{-2}	Faure et al. (2012)
2013	Lake Garda (Italy)	Beach Sediment	<5000	Density separation, microscopic examination, Raman	Fragments 46% PS, 43% PE, 10% PP	$108\text{--}1108 \text{ pp m}^{-2}$	Imhof et al. (2013)
2015	River Seine (France)	Surface water	100–5000	Net sample, filtered, microscopic examination	Fibers	$3\text{--}108 \text{ pp m}^{-3}$	Dris et al. (2015)
2015	River Seine (France)	Surface water	330–5000	Net sample, filtered, microscopic examination	Fibers, fragments, spheres	$0.28\text{--}0.47 \text{ pp m}^{-3}$	Dris et al. (2015)
2015	6 Lakes (Switzerland)	Surface waters	300–5000	Net sample, sieved, digestion, microscopic examination, FTIR	Fragments, films, foams PE, PP, PS	0.091 pp m^{-2} (0.026 mg m^{-2})	Faure et al. (2015)
2015	5 Rivers (Switzerland)	Surface waters	300–5000	Net sample, sieved, digestion, microscopic examination, FTIR	Fragments, foams PE, PP, PS	$7 \pm 0.2 \text{ pp m}^{-3}$ ($1.4 \pm 3.4 \text{ mg m}^{-3}$)	Faure et al. (2015)
2015	6 Lakes (Switzerland)	Beach sediment	300–5000	Density separation, sieved, microscopic examination, smaller fraction digested before examination, FTIR	Foams, fragments PE, PP, PS	$1300 \pm 2000 \text{ pp m}^{-2}$ ($920 \pm 1500 \text{ mg m}^{-2}$)	Faure et al. (2015)
2015	River Rhine (Germany)	Beach sediment	63–5000	Dried, sieved, density separation, digestion, filtration, microscopic examination, FTIR	Fragments, spheres PE, PP, PS	$228\text{--}3763 \text{ pp kg}^{-1} \text{ dw}$ ($21.8\text{--}932 \text{ mg kg}^{-1} \text{ dw}$)	Klein et al. (2015)
2015	River Main (Germany)	Beach sediment	63–5000	Dried, sieved, density separation,	Fragments, spheres	$786\text{--}1368 \text{ pp kg}^{-1} \text{ dw}$	Klein et al. (2015)
2015	Rhine River (Basel to Rotterdam)	Surface water	300–5000	digestion, filtration, microscopic examination, FTIR Net samples, sieved, digestion, sieved, density separation, microscopic examination, FTIR	PE, PP, PS Spheres, fragments PS, PP	$43.5\text{--}459 \text{ mg kg}^{-1} \text{ dw}$ 0.89 pp m^{-2}	Mani et al. (2015)
2016	Lakes Bolsena and Chiusi (Italy)	Beach sediment	300–5000	Sieved, dried, density separation, digestion, dyed, filtered, UV microscopic examination, SEM	Fragments, fibers	$1922\text{--}2117 \text{ pp m}^{-2}$ ($112\text{--}234 \text{ pp kg}^{-1} \text{ dw}$)	Fischer et al. (2016)
2016	Lakes Bolsena and Chiusi (Italy)	Surface water	300–5000	Net sample, sieved, density separation, dyed, filtered, UV microscopic examination, SEM	Fragments, fibers	$0.8\text{--}4.4 \text{ pp m}^{-3}$	Fischer et al. (2016)
2017	River Thames (United Kingdom)	Sediment	1000–4000	Sieved, dried, microscopic examination, density separation, filtration, dried, microscopic examination, Raman	Fibers, fragments	$185 \pm 42 \text{ to } 660 \pm 77 \text{ pp kg}^{-1} \text{ dw}$	Horton et al. (2017)

(Continued)

Table 2 (Continued)

<i>Year of publication</i>	<i>Location</i>	<i>Matrix analyzed</i>	<i>Size range of MPs analyzed (μm)</i>	<i>Methods for counting and identifying MPs</i>	<i>Main fingerprinting and morphology of MPs</i>	<i>Concentration of MPs (plastic particles per unit volume or area)</i>	<i>References</i>
2018	Rivers Marne and Seine (France)	Surface water	>80	Net sample, digestion, density separation, filtered, microscopic examination, FTIR	Fibers rayon, PET, PP, PA	Site averages of 22.1 ± 25.3 to 100.6 ± 99.9 pp m^{-3}	Dris et al. (2018)
2018	Mersey and Irwell Rivers (England)	Sediment	63–5000	Cylindrical sampler, sieving, dried, density separation, filtration, microscopic examination, FTIR	Fibers, fragments, beads	Pre flood average 6350 pp kg^{-1} ; post flood average 2812 pp kg^{-1}	Hurley et al. (2018)
2018	Antua River Basin (Portugal)	Shoreline sediment	55–5000	Grab sample, dried, sieved, digested, density separation, filtration, microscopic examination, FTIR	PE, PP, PS, PET Fragments, fibers, films	18–629 pp kg^{-1} dw; 2.6–71.4 mg kg^{-1} dw	Rodrigues et al. (2018)
2018	Antua River Basin (Portugal)	Surface and bottom water	55–5000	Pump sample, sieved, digested, density separation, filtration, microscopic examination, FTIR	PE, PP, PS, PET Fragments, films, foams, fibers	58–1265 pp m^{-3} ; 5–51.7 mg m^{-3}	Rodrigues et al. (2018)
2018	Teltow Canal (Germany)	Surface water	450–5000	Grab sample, sieved, dried, digested, filtered, SWIR imaging, microscopic check	PE, PP	0.01–95.8 pp L^{-1}	Schmidt et al. (2018)
2018	Subalpine Lakes (Italy)	Surface water	1000–5000	Net sample, sieved, digested, microscopic examination, FTIR	74% Fragments, PE, EPS, PP	0.004–0.057 pp m^{-2}	Sighicelli et al. (2018)
2018	River Tame and Tributaries (United Kingdom)	Sediment	63–4000	Wet sieved, dried, density separation, microscopic examination, FTIR	49% Fragments 22% fibers PE, PVC, PMMA	110 kg^{-1} dw	Tibbetts et al. (2018)
2019	River Kelvin (Scotland)	Shoreline sediment	11–2800	Dried, sieved, density separation, filtration, microscopic examination, SEM- EDS	88–95% fibers	161–432 pp kg^{-1} dw	Blair (2019)
2019	Rivers, reservoirs and fish ponds (Hungary)	Surface water	100–2000	Pump sample, sieved, density separation, digested, filtration, μFTIR -ATR	PP, PE, PES, PS,	3.52–32.05 pp m^{-3}	Bordós et al. (2019)
2019	Rivers, reservoirs and fish ponds (Hungary)	Sediments		Grab sample, density separation, digestion, filtration, μFTIR -ATR	PP, PS, PES	0.46–1.62 pp kg^{-1} 0.8 ± 0.37 pp kg^{-1}	Bordós et al. (2019)
2019	Stormwater retention ponds (Denmark)	Surface water	10–2000	Pump sample, filtration, digestion, density separation, FTIR imaging	17 polymers, mainly PP	490–23,000 pp m^{-3} (85–1143 $\mu\text{g m}^{-3}$)	Liu et al. (2019)
2019	Viborg stormwater retention pond (Denmark)	Surface water	10–500	Grab sample, filtered, digested, FPA- μFTIR imaging	PEST, PP, Acrylic	270 pp L^{-1} (4.2 $\mu\text{g L}^{-1}$)	Olesen et al. (2019)
2019	Viborg stormwater retention pond (Denmark)	Sediment	10–500	Core sample, sieved, dried, density separation, digestion, FPA- μFTIR imaging	PP	950,000 pp kg^{-1} dw (0.4 g kg^{-1} dw)	Olesen et al. (2019)
<i>North America</i>							
2011	California Rivers (USA)	Surface water	1000–4750	Net tow, sieved, microscopic examination	Foam, pellets, fragments, films, lines	<1–153 pp m^{-3}	Moore et al. (2011)

2011	Lake Huron (Canada)	Beach sample	Pellets <5000 Fragments >5000	Visual collection, sonication, μ FTIR- ATR, SEM	PE pellets, PP fragments, PS foams	0–408 pp m ⁻² ; mean 37.8 pp m ⁻²	Zbyszewski and Corcoran (2011)
2013	Laurentian Great Lakes (USA)	Surface water	355–4750	Net samples, density separation, sieved, microscopic examination and SEM/EDS of smaller particles	Pellets, fragments	0–0.466 pp m ⁻² ; average 0.43 pp m ⁻²	Eriksen et al. (2013)
2014	St. Lawrence River (Canada)	Sediment	>500	Grab sample, sieved, microscopic examination, scanning calorimeter	Microbeads	0–136,926 pp m ⁻² ; 13,832 $\pm$ 13,677 pp m ⁻²	Castaneda et al. (2014)
2014	Lakes Erie and St Clair (Canada/ USA)	Beach sample	<2000	Visual collection, cleaned, dried, hand sorted, FTIR, SEM	Fragments, foams PE and PP	0.18–8.38 pp m ⁻²	Zbyszewski et al. (2014)
2015	Lake Ontario (Canada)	Beach sediment	<1000, 1000–5000, >5000	Visual collection, sorting, enumeration, Raman	PS foam, industrial pellets, fragments	21.8 pp m ⁻² (excluding PS)	Corcoran et al. (2015)
2015	Lake Ontario (Canada)	Bottom sediment	<0.500, 500–710, 710–850, 850–1000, >1000	Core sample, dried, sieved, density separation, microscopic examination, FTIR	74% PE	0.087–0.62 pp g ⁻¹ dw	Corcoran et al. (2015)
2016	Great Lakes Tributaries (USA)	Surface water	333–4750	Net samples, sieved, digested, filtered, microscopic examination	Fibers, fragments	0.05–32 pp m ⁻³	Baldwin et al. (2016)
2016	Lake Ontario	Nearshore sediment	>63	Grab, core or sediment trap samples, dried, sieved, sorted, density separation of smaller fraction, microscopic examination, Raman, FTIR	Fibers, fragments	980 pp kg ⁻¹ dw	Ballent et al. (2016)
2016	Lake Ontario	Tributary sediment	>63	Grab samples, dried, sieved, sorted, density separation of smaller fraction, microscopic examination, Raman, FTIR	Fragments, fibers	610 pp kg ⁻¹ dw	Ballent et al. (2016)
2016	Lake Ontario	Beach sediment	>63	Core samples, dried, sieved, sorted, density separation of smaller fraction, microscopic examination, Raman, FTIR	Fragments, fibers	140 pp kg ⁻¹ dw	Ballent et al. (2016)
2016	Raritan River (USA)	Surface water	125–2000	Net tows, sieved, dried, digested, density separation, microscopic examination,		Upstream WWTP 24 $\pm$ 11.4 pp m ⁻³ Downstream WWTP 71.7 $\pm$ 60.2 pp m ⁻³	Estahbanati and Fahnenfeld (2016)
2016b	Lake Michigan (USA)	Surface water	355–999 1000–4749 >4750	Net tow, sieved, digested, filtered, microscopic examination, SEM/EDS,	79% fragments, 14% fibers	Average 0.017 pp m ⁻²	Mason et al. (2016b)
2016	North Shore Channel (USA)	Surface water	333–2000	Net tows, sieved, dried, digested, density separation, filtered, microscopic examination	Fibers, fragments	1.94–17.93 pp m ⁻³	McCormick et al. (2016)
2017	Lake Winnipeg, (Canada)	Surface water	333–5000	Net sample, sieved, digested, filtered, microscopic examination, SEM	Fibers	0.053–0.75 pp m ⁻²	Anderson et al. (2016)
2017	Waucana Creek (Canada)	Surface water	80–4750	Net tow, sieved, digested, microscopic examination, hot needle	Fibers, fragments	0.9–7.7 pp m ⁻³	Campbell et al. (2017)
2017	Hudson River (USA)	Surface water	>100	Grab sample, filtered, microscopic examination, μ FTIR	Fibers 43% cotton, 22% PET, 22% fluoro-polymer/Teflon, 7% PP, 7% nitrocellulose /clay	Median 0.98 pp L ⁻¹ (fibers) Estimate 50% plastic	Miller et al. (2017)

(Continued)

Table 2 (Continued)

<i>Year of publication</i>	<i>Location</i>	<i>Matrix analyzed</i>	<i>Size range of MPs analyzed (μm)</i>	<i>Methods for counting and identifying MPs</i>	<i>Main fingerprinting and morphology of MPs</i>	<i>Concentration of MPs (plastic particles per unit volume or area)</i>	<i>References</i>
2017	Ottawa River (Canada)	Sediment	300–5000	Grab sample, dried, sieved, digested, density separation, microscopic examination	Fibers	220 pp kg ⁻¹ dw	Vermaire et al. (2017)
2017	Ottawa River (Canada)	Surface water	100–5000	Grab sample, sieved, digested, filtered, microscopic examination	Fibers	0.1 L ⁻¹	Vermaire et al. (2017)
2017	Ottawa River (Canada)	Surface water	100–5000	Net sample, digested, filtered, microscopic examination	Fibers, some fragments, beads	1.35 pp m ⁻³	Vermaire et al. (2017)
2018	Gallatin River Watershed (USA)	Surface water	100–9600	Grab samples, filtered, dried, microscopic exam, hot needle, FTIR	80% fibers, 19.7% fragments, PE, PET, rayon	57% samples had pp, average 1.2 pp L ⁻¹	Barrows et al. (2018)
2018	Lake Superior (USA)	Surface water	333–5000	Net tows, sieved, digested, density separation, filtration, microscopic examination, Pyr-GC/MS, ATP-FTIR	Fibers, fragments, films PVC, PP, PE, PET	0.037 $\pm$ 0.027 pp m ⁻² 0.0012 mg m ⁻²	Hendrickson et al. (2018)
2018	Snake and Columbia Rivers (USA)	Surface water	100–5000	Grab samples, filtered, dried, microscopic examination, hot needle test, Raman	58% fibers	75% samples had pp, 0.91 $\pm$ 1.14 pp L ⁻¹	Kapp and Yeatman (2018)
2018	Snake and Columbia Rivers (USA)	Surface water	100–5000	Net samples, filtered, digested, density separation, microscopic examination, hot needle test, Raman	48% fibers	92% samples had pp, 2.57 $\pm$ 2.95 pp m ⁻³	Kapp and Yeatman (2018)
2019	Atoyac River Basin (Mexico)	Sediment		Trowel or grab samples, dried, digested, density separation, filtration, microscopic examination, SEM/EDX	26% films, 22% fragment 15% fibers, 11% pellets	4500 $\pm$ 702 pp kg ⁻¹ dw	Shruti et al. (2019)
<i>South America</i>							
2017	Sebutal Lake (Argentina)	Beach sediment	350–5000	Dried, sieved, digested, density separation, microscopic examination, FTIR	Fragments, fibers, foams	704 pp m ⁻²	Blettler et al. (2017)
2019	Pantanal wetlands and rivers (Brazil)	Surface water	68–5000	Net tow, filtered, microscopic examination	50% fibers, 19% fragments, 22% pellets, 9% foam	9.6 $\pm$ 8.3 pp 100 L ⁻¹	de Faria et al. (2019)

Data sources: See References.

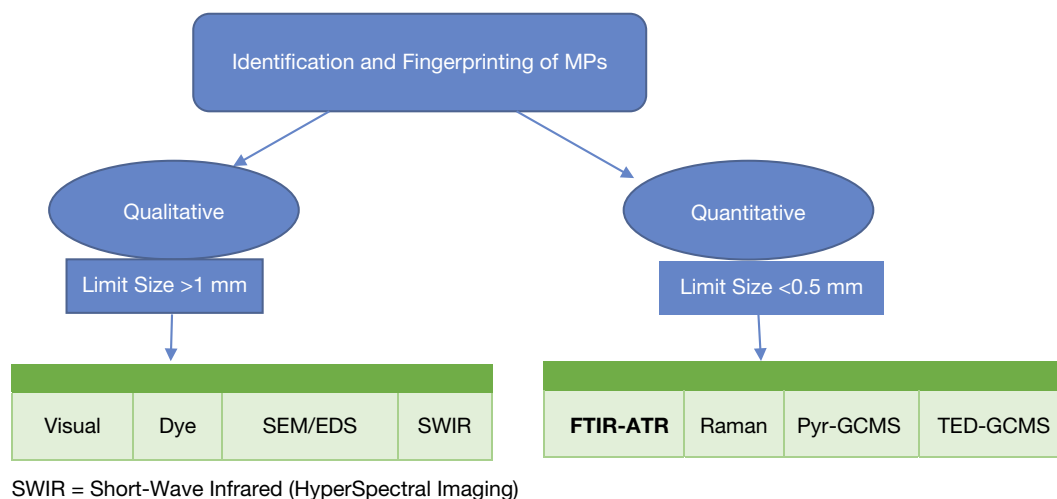


Fig. 3 Analytical techniques to identify MPs in freshwater environmental samples.

Distribution of MPs in Freshwaters

The number of reports of MPs from freshwater lakes and rivers has increased dramatically from 2012 through 2019 (Table 3). Research has been concentrated in Europe, Asia, and North America, but studies of the inland waters of Africa, South America, and Australia have begun in the last few years. The data from various authors is not directly comparable due to the use of different collection and processing methods and a lack of standardization of reporting units (Rios Mendoza and Balcer, 2019a). MP concentrations in surface waters ranged from 0–270 pp L⁻¹ by volume and 0–563 pp m⁻² by surface area. In bottom sediments the concentrations range from 0–10 pp g⁻¹ sediment, while on beaches densities varied from 0–0.8 pp g⁻¹ or 0–2117 pp m⁻² (Table 3).

In spite of the lack of harmonization of sampling techniques, certain trends are evident. China has the highest plastic production in the world (Plastics Europe, 2019), including textiles, and makes extensive use of plastic films as mulch for agricultural use (Lv et al., 2019; Wang et al., 2019b). Surface waters of lakes and rivers in China contain some of the highest MP concentrations, often over 1000 pp m⁻³ (Table 3). Worldwide, urban areas generally contain higher concentrations of MPs than rural areas (Table 3), and stormwater retention ponds tend to concentrate MPs, with levels reaching 23–270 pp L⁻¹ in water and 9.5×10^5 pp kg⁻¹ dw sediment (Liu et al., 2019; Olesen et al., 2019).

With regards to MP morphology, the most common forms were fibers > fragments > pellets or microbeads. The presence of sewage plants increases the concentration of MPs in the water, especially of fibers (Browne et al., 2011; McCormick et al., 2014; Wang et al., 2017a, b).

MPs and Toxic Compounds

MPs contain a mixture of chemicals that are introduced during their manufacture, including additives, stabilizers, flame-retardants, antibacterial and antioxidant agents, pigments, fillers, and plasticizers including phthalates (Hahladakis et al., 2018). These chemicals can be released when MPs enter aquatic environments, leading to the suggestion that plastic be classified as a hazardous material (Rochman et al., 2013a). While information on the interaction of toxic compounds with MPs in freshwater systems is limited at this time, it is an important factor in understanding the adverse effects of environmental pollution on aquatic organisms.

Macro, micro and nanoplastic debris can concentrate and transport toxic compounds in the environment (Mato et al., 2001; Rios et al., 2007) and assessing the abundance of the MP particles and measuring their sizes is essential to determining the real risk of these plastic particles. Smaller particles (Fig. 2) have larger surface areas and can concentrate higher amounts of toxic compounds on their surfaces. MPs adsorb persistent organic pollutants (POPs), semipersistent polycyclic aromatic hydrocarbons (PAHs), heavy metals and pharmaceutical chemicals from the aquatic environment.

The main mechanisms for chemical adsorption on plastics are through hydrophobic (Wang et al., 2019a; Guo and Wang, 2019), electrostatic (Guo and Wang, 2019), van der Waals (Xu et al., 2018), or double bonds interactions (Hüffer and Hofmann, 2016). Rios and collaborators have studied the toxic compounds adsorbed on the surfaces of MPs collected from the Laurentian Great Lakes. They detected PAH concentrations ranging from 0.47–20.26 µg g⁻¹ on MPs from the Great Lakes and from the St Louis River Estuary (SLRE). PCBs ranged from nondetectable to 9.86 µg g⁻¹ in samples from the Great Lakes and from 0.40–3.46 ng g⁻¹ in SLRE. Organochlorine pesticide concentrations varied from 4.3–63.9 ng g⁻¹ (Rios Mendoza and Balcer, 2019b; Rios Mendoza, 2019). Faure et al. (2015) reported toxic compounds on MPs from Swiss Lakes with PAHs ranging from 0.086–5.714 µg g⁻¹, PCBs from 0.4–548 ng g⁻¹, and organochlorine pesticides from 1.4–2715 ng g⁻¹.

Table 3 Microplastic concentrations in Wastewater Treatment Plants and efficiency of removal.

Year of publication	Location	Methods for counting and identifying MPs	Size range of MPs analyzed (μm)	Concentration of MPs (plastic particles per unit volume or area)	Percent Removal	Dominant particle morphology and polymer	References
2016	8 facilities Los Angeles (USA)	Filtered, microscopic examination, FTIR	45–400	Secondary effluent $1.76 \times 10^{-5} \text{ pp L}^{-1}$ Tertiary effluent $0.3\text{--}2.4 \times 10^{-6} \text{ pp L}^{-1}$	99%	PE fragments	Carr et al. (2016)
2016a	17 facilities USA	Filtered, microscopic examination	125–>355	Effluents $0.004\text{--}0.195 \text{ pp L}^{-1}$ Avg. 0.050 pp L^{-1}		59% fibers and 33% fragments	Mason et al. (2016a)
2016	1 facility River Clyde Glasgow, Scotland	Filtered, microscopic examination, FTIR	>65	Influent 15.7 pp L^{-1} Effluent 0.25 pp L^{-1}	98%	67% flakes and 18% fibers in effluent. 28% PE, 20% PA, 12% PP, 12% Acrylic	Murphy et al. (2016)
2017	7 facilities Rhine and Meuse Rivers, Netherlands	Grab sample, filtration, density separation, microscopic examination, μFTIR	10–5000	Influent $68\text{--}910 \text{ pp L}^{-1}$ Effluent $5\text{--}81 \text{ pp L}^{-1}$ Sludge $510\text{--}760 \text{ pp kg}^{-1} \text{ ww}$	72%	Fibers dominant	Leslie et al. (2017)
2017	7 facilities Ireland	Grab sample, elutriation, density separation, filtration, microscopic examination, FTIR	<45–250	Sludge $4196\text{--}15,385 \text{ pp kg}^{-1} \text{ dw}$		78% fiber, 7 polymers	Mahon et al. (2017)
2017	12 facilities Oldenburg-East-Frisian (Germany)	Filtration, digestion, density separation, microscopic examination, μFTIR	20–>500	Effluent $0\text{--}50 \text{ pp } >500 \mu\text{m m}^{-3}$ $10\text{--}9000 \text{ pp } <500 \mu\text{m m}^{-3}$ Sludge $1000\text{--}24000 \text{ pp kg}^{-1} \text{ dw}$	97%	14 polymers, PE fibers dominant	Mintenig et al. (2017)
2017b	3 facilities Sydney, Australia	Filtration, digestion, density separation, stained, microscopic examination, FTIR-ATR	25–500	Tertiary treatment effluent 0.28 pp L^{-1}	90–98%	PET fibers	Ziajahromi et al. (2017b)
2018	2 facilities Turkey	Filtered, digested, density separation, microscopic examination, μRaman	55–5000	Influent $12,000\text{--}36,000 \text{ pp m}^{-3}$ Effluent $2700\text{--}8700 \text{ pp m}^{-3}$	73–79%	60% fibers 7 polymers, 51% PET, 29% PE, 14% PP	Gündoğdu et al. (2018)
2018	1 facility Mikkeli (Finland)	Grab sample, filtered, digested, digital optical microscopy, μFTIR , μRaman	250–5000	Influent 57.6 pp L^{-1} Effluent 1.0 pp L^{-1} Sludge $8.2\text{--}301.4 \text{ pp g}^{-1} \text{ dw}$	98.4%	79% PET fibers, 4% Nylon fibers, 11% PE particles	Lares et al. (2018)
2018	10 facilities Denmark	Grab sample, filtered digested, Focal Plane Array (FPA) and FTIR imaging	10–500	Median Influent 7216 pp L^{-1} Effluent 54 pp L^{-1}		Mainly particles/fragments, PES, PE, PP, acrylates	Simon et al. (2018)

Data sources: See References.

Interactions of Aquatic Organisms with MPs

MPs as a Habitat for Microbes

Plastic debris can be colonized by a variety of microbes and develop into a unique aquatic community known as the “plastisphere” (Zettler et al., 2013). These diverse floating colonies can be transported long distances across the water surface. As the biofilm grows and increases in density, the plastic material and its associated microbial community can sink, thus serving as a vector for the spread of potentially harmful bacteria and other organisms throughout the water column (McCormick et al., 2014).

McCormick et al. (2014) found that microplastic pellets and fragments collected near a WWTP in the North Shore Channel of Chicago IL developed an extensive biofilm of prokaryotic organisms with a density up to $0.3 \text{ cells } \mu\text{m}^{-2}$ of surface area. DNA sequencing revealed that the bacterial community on the MP particles was distinct from that of the water column or on natural

organic material from the same area and contained a high abundance of *Pseudomonas*, which may be able to degrade MPs. Several genera of bacteria that contain pathogenic strains were also found at elevated levels on MP particles (McCormick et al., 2014).

By serving as a substrate, MPs enable bacteria to grow in close contact with each other, potentially allowing for increased horizontal gene transfer (HGT) or exchange of genetic information via plasmid transfer. This exchange could lead to the formation of more antibiotic resistant strains of bacteria. Arias-Andres et al. (2018) studied this hypothesis using a strain of *Escherichia coli* with a plasmid that encodes for trimethoprim resistance. They found a large increase in the HGT rate in bacteria grown in water from Lake Stechlin, Germany that contained microplastic particles versus controls without microplastic.

Field Studies on Ingestion and Other Interactions

MP particles that enter freshwater environments may be consumed by a variety of aquatic organisms including clams, worms, crayfish, insects, tadpoles, and fish (Table 4). The ability to detect small MPs in aquatic organisms is affected by the analytical procedures that are used to extract and identify the possible MP particles. Some researchers dissected the digestive tracts and examined the contents microscopically, while others chemically dissolved the digestive tract or the entire organism to remove organic material and then separated the MP particles by flotation or filtration prior to microscopic examination.

Recent studies have included the use of FTIR spectroscopy to confirm that the microparticles are actually MPs and not other natural materials such as cellulose, cotton, wood, or sand grains. The most commonly ingested form of MPs was fibers comprised of PES, PE/PET, PE, and PP (Table 4). The percentage of examined organisms that contained MPs varied considerably (Table 4), ranging from 20% or less (Sanchez et al., 2014; Faure et al., 2015; Phillips and Bonner, 2015; Biginagwa et al., 2016; Roch and Brinker, 2017; Roch et al., 2019; Su et al., 2019) to over 75% (Jabeen et al., 2017; Silva-Cavalcanti et al., 2017; Campbell et al., 2017; Nel et al., 2018; Xiong et al., 2018). While MP particles were commonly found in aquatic organisms, the density of MP per individual was generally quite low (<3 pp ind⁻¹, Table 4). Higher densities of MPs were found in bottom feeding fish and those from urban locations with more environmental contamination (Zheng et al., 2019; Silva-Cavalcanti et al., 2017; Peters and Bratton, 2016; Sanchez et al., 2014; Phillips and Bonner, 2015).

While field studies have concentrated on determining the number of MPs ingested by aquatic animals, organisms can interact with plastic debris in other ways. Caddisfly larvae build external cases or tubes from sand and other materials that they find in the environment (Fig. 4) and can incorporate MPs if they are present. MP particles were found in 7% of the cases of caddisfly larva collected from an urban section of the River Tame, United Kingdom (Tibbetts et al., 2018) and in 58% of the cases of the species *Lepidostoma basale* from a stream in Germany (Ehlers et al., 2019).

Laboratory Studies

Several laboratory experiments have investigated the interactions of MPs with aquatic organisms ranging from microbes to fish under more controlled conditions (Table 5). Organisms have been exposed to MPs via water, sediment, or through their diets. The test concentrations of MPs have been reported using a variety of units, including number or weight of plastic particles per unit weight of sediment, or per volume of test medium. Due to the wide variation in size and weights of the MP particles, some authors have begun to report test concentrations both by weight and number of particles. Experimental exposures of MP concentrations have ranged from 0.5–2570 pp g⁻¹ or 2–20 mg g⁻¹ dry weight in sediment, and from 50– 1×10^{10} pp L⁻¹ or 0.01– 1×10^4 mg L⁻¹ in water. The most commonly tested forms of MP have been PE and PS spheres and fragments and PES/PET fibers (Table 5).

Initial studies were designed to determine whether or not MPs of various shapes and sizes could be ingested and to what degree the particles would accumulate in the guts of the test organisms (Imhof et al., 2013; Rochman et al., 2017; Murphy and Quinn, 2018; Li et al., 2019; Cuthbert et al., 2019). While plastic particles are readily ingested by a variety of organisms (Table 5), they are also egested fairly rapidly, resulting in a low body burden in most test organisms (<15 pp ind⁻¹, or <4.1 pp g⁻¹). Some size selectivity was observed, with *Gammarus* ingesting smaller MP fragments (32–63 μ m) at the highest rates (Straub et al., 2017; Weber et al., 2018). Li et al. (2019) found that the number of fibers ingested by Asian clams was related to the flexibility of the plastic polymer (Table 5), with PET fibers favored over PEA and AC. The more rigid PA, RA and PVA fibers were not ingested as readily.

Ingested MP materials can be retained in an organism's digestive tract or passed through the body to be egested in the feces. Smaller sized particles may move from the gut into other body tissues by crossing the epithelial lining. To determine the concentration of MP in various parts of an organism, researchers may dissect or dissolve the specific organs to extract and count the individual plastic particles. When exposing organisms to smaller particles, the practice has been to use MPs labeled with fluorescent dyes and then use imaging to detect the dye and particles in various locations in the organism. The strength of the fluorescent signal is correlated to the number of particles ingested. Organisms can be damaged during sample preparation (Guilhermino et al., 2018), allowing particles to appear in other tissues besides the gut. While MPs have primarily been found in the digestive tracts of organisms (Table 5), small MPs (1–5 μ m) have been reported from various tissues of Asian clams (Guilhermino et al., 2018), zebra mussels (Magni et al., 2018), *Daphnia* (Rosenkranz et al., 2009) and zebrafish (Lu et al., 2016). Schür et al. (2019) questioned the ability of fluorescent microbeads to move from the gut of *Daphnia* through the peritrophic membrane (which coats the food pellets in cladocerans), and then through the gut epithelium into lipid droplets. They found that fluorescent dyes can leach from plastic particles and end up in lipids, even when MP particles were not visible. Catarino et al. (2019)

Table 4 Ingestion of MPs by freshwater organisms in natural environments.

Organism	Location	Processing procedure	% Organisms with MPs	Average number of pp ind ⁻¹ or weight ⁻¹ of organism ^a	Dominant particle morphology and polymer	References
Asian clam <i>Corbicula fluminea</i>	Taihu Lake, China	Soft tissue extracted, digested, filtered 100 µm mesh, microscopic examination, FTIR or SEM/EDS		0.2–12.5 pp g ⁻¹ ww	Fibers	Su et al. (2016)
Asian clam <i>Corbicula fluminea</i>	Yangtze River Basin, China	Soft tissue extracted, digested, filtered, microscopic examination, FTIR		0.4–5.0 pp ind ⁻¹ 0.3–4.9 pp g ⁻¹ ww	Fibers	Su et al. (2018)
Annelid worm <i>Tubifex tubifex</i>	Salford Quays, Manchester, UK	Organisms rinsed, 24 h depuration, tissue digested, microscopic examination, hot needle test, FTIR	48	0.8 ± 1.01 pp ind ⁻¹ 129 ± 65.4 pp g ⁻¹ ww	87% PE/PET, AC, and PP fibers 14% PST, PE, PP fragments	Hurley et al. (2017)
Crayfish <i>Procambarus clarkii</i>	Rice and fish culture ponds, China	Digestive tract removed, digested, filtered, microscopic examination, FTIR		2.5 ± 0.6 pp ind ⁻¹	Fibers PE and PP	Lv et al. (2019)
Mayflies Heptageniidae and Baetidae Caddisflies Hydropsychidae	Rivers in South Wales, UK	Field collection, half preserved, half allowed to depurate. Organisms rinsed, homogenized, digested, microscopic examination, dark field spectroscopy for particles from 0.5–5 mm	≈ 50	Maximum 0.14 pp mg ⁻¹ dw Depurated organisms ≈ 0.65 pp ind ⁻¹ preserved specimens 1.15 pp ind ⁻¹		Windsor et al. (2019)
Chironomid larvae <i>Chironomus</i> sp.	Bloukrans River System, South Africa	Collected, preserved, weighed, digested, filtered, microscopic examination	75–98	0.37 ± 0.44 pp mg ⁻¹ ww summer 1.12 ± 1.19 pp mg ⁻¹ ww winter		Nel et al. (2018)
Tadpoles	Small waterbodies, Yangtze River Delta, China	Samples pooled, digested, filtered, microscopic examination, µFTIR-ATR		0–2.73 pp ind ⁻¹ 0–168 pp g ⁻¹ ww	68% PES fibers, 7% PP fibers	Hu et al. (2018)
Fish Bleak <i>Alburnus alburnus</i> , Common dace <i>Leuciscus leuciscus</i> European perch <i>Perca fluviatilis</i> , Roach <i>Rutilus rutilus</i>	Lake Geneva, Switzerland	Preserved specimens, GI tract dissected and examined microscopically	7.5	1 Bleak had 31 fibers 2 Dace contained fragments No items in other species		Faure et al. (2015)
Fish—Gudgeon <i>Gobio gobio</i>	Rivers in France	GI tract dissected, microscopic examination,	12 (range 9.5–42% by site)			Sanchez et al. (2014)
Fish—Composite sample of 44 species from 12 families	Rivers in Texas near Gulf of Mexico, USA	Stomach and upper GI tract dissected, microscopic exam, FTIR	8.2 (range 5–29% by drainage)		1.3% had filaments 2.7% fragments and 3.1% films PP, PES, PA, PS, nylon	Phillips and Bonner (2015)
Fish—Bluegill, <i>Lepomis macrochirus</i>	Brazos River Basin, Texas, USA	Stomach contents removed, washed through filters, microscopic exam	45	0.34–1.33 pp ind ⁻¹ of different size classes	96% threads	Peters and Bratton (2016)
Longear sunfish, <i>L. megalotis</i>	Lake Victoria, Tanzania	Entire GI tract removed, digested, 250 µm sieve, microscopic examination, FTIR	44		PE, PU, PES, PE/PP, silicone rubber	Biginagwa et al. (2016)
Nile Tilapia <i>Oreochromis niloticus</i>			20			

Fish—6 species	Taihu Lake, China	Entire GI tract removed, digested, floatation, 5 µm filter, microscopic examination, FTIR.	95.7 with MPs (43.5% also contained mesoplastics ^b)		57–88% fibers	Jabeen et al. (2017)
<i>Cyprinus carpio</i>				2.5 ± 1.3 pp ind ⁻¹		
<i>Carassius auratus</i>				1.9 ± 1.0 pp ind ⁻¹		
<i>Hypophthalmichthys molitrix</i>				3.8 ± 2.0 pp ind ⁻¹		
<i>Pseudorasbora parva</i>				2.5 ± 1.8 pp ind ⁻¹		
<i>Megalobrama amblycephala</i>				1.8 ± 1.7 pp ind ⁻¹		
<i>Hemiculter bleekeri</i>				2.1 ± 1.1 pp ind ⁻¹		
Fish—Round goby <i>Neogobius melanostomus</i>	Rhine River, border of France and Germany	Entire GI tract dissected, digested, density separation, filtered, microscopic examination, hot needle,	27	1.25 pp ind ⁻¹		Roch and Brinker (2017)
Fish—common barbel <i>Barbus barbus</i>			20	1.0 pp ind ⁻¹		
Fish—catfish <i>Hoplosternum littorale</i>	Pajeu River, Brazil	GI tract dissected, rinsed in 63 µm sieve, visual examination	83	3.6 pp ind ⁻¹ Range 1–24	Size range <1–12 mm 88.6% of items <5 mm 46.6% fibers, Remainder hard and soft particles	Silva-Cavalcanti et al. (2017)
Fish—5 species	Waucana Creek, Canada	Entire GI tract removed and digested, 5 µm filter, microscopic examination	73.5 overall	3.28 pp ind ⁻¹ range 1–20	48% fibers, 43% fragments	Campbell et al. (2017)
Northern Pike- <i>Esox lucius</i>			83		15% contained balls of clear fibers (not enumerated)	
White Sucker <i>Catostomus commersoni</i>			72			
Emerald Shiner <i>Notropis atherinoides</i>			71			
Fathead minnow <i>Pimephales promelas</i>			50			
Five-spine stickleback <i>Eucalia inconstans</i>			70			
Fish—13 species	Three Gorges Reservoir, China	GI tract digested, filtered, microscopic examination, Raman microscopy	25.7	0.33 ± 0.58 to 1.5 ± 1.38 pp ind ⁻¹ for different species	Fibers, sheets, fragments PE and nylon	Zhang et al. (2017)
Fish—roach, <i>Rutilus rutilus</i>	River Thames, UK	Entire GI tract opened, contents removed, examined microscopically, Raman	32.8	0.69 pp ind ⁻¹ ,	75% fibers PE, PP, PES	Horton et al. (2018)
Fish—11 species	Lake Michigan tributaries, USA	GI tract dissected, dried, digested, filtered, microscopic examination	85	10 ± 2.3 to 13 ± 1.6 pp ind ⁻¹ at three sites	97–100% fibers	McNeish et al. (2018)
Fish—cyprinid <i>Gymnocypris przewalskii</i>	Qinghai Lake	GI tract dissected, digested, filtered, microscopic examination, Raman	100	5.4 pp ind ⁻¹ (2–15 pp ind ⁻¹)	Fibers in all, sheets in half, PE, PS, nylon, and PP	Xiong et al. (2018)
Fish—16 species in family Serrasalminidae (pacu and piranhas)	Xingu River Basin, Brazil	Stomachs dissected, rinsed, microscopic examination, FTIR	26.7		29.2% MP 70.8% MesoP ^b 53% filaments, 47% fragments 8 polymers	Andrade et al. (2019)

(Continued)

Table 4 (Continued)

Organism	Location	Processing procedure	% Organisms with MPs	Average number of pp ind ⁻¹ or weight ⁻¹ of organism	Dominant particle morphology and polymer	References
Fish—Eel <i>Monopterus albus</i>	Rice and Fish culture ponds, China	Digestive tract dissected, digested, filtered, microscopic examination, FTIR		3.3 ± 0.5 pp ind ⁻¹	Fibers, PE, PP	Lv et al. (2019)
Fish—Loach <i>Misgurnus anguillicaudatus</i>	Rice and Fish culture ponds, China	Digestive tract dissected, digested, filtered, microscopic examination, FTIR		1.8 ± 0.5 pp ind ⁻¹	Fibers, PE, PP	
Fish—three spine stickleback <i>Gasterosteus aculeatus</i> and amphibians—Newts <i>Triturus vulgaris</i>	Viborg stormwater retention pond, Denmark	Organisms freeze dried, pooled, digested, filtered, FTIR imaging		65 pp ind ⁻¹ 3 µg ind ⁻¹	41% polyester, also PP, PA, PE	Olesen et al. (2019)
Fish—22 species	11 rivers and 6 lakes in Germany	GI tract dissected, digested, density separation, filtered, microscopic examination, hot needle test, only 20–5000 µm particles included	20.6% in rivers 16.5% in lakes	1–4 pp ind ⁻¹	54% fragments, 39% fibers	Roch et al. (2019)
Fish—Gudgeon <i>Gobio gobio</i>	Rivers in Belgium	GI tract dissected, dried, ground, density separation, digestion, microscopic exam, FTIR or Raman	9		Only 8 particles confirmed as MP, 7 different polymers	Slootmaekers et al. (2019)
Fish— <i>Gambusia holbrooki</i>	Wetlands, Australia	Separated heads and bodies, digested separately, filtered, microscopic examination, µFTIR-ATR	19.4 in body 7.2 % in heads	0.60 ± 1.33 pp body ⁻¹ 0.11 ± 0.44 pp head ⁻¹	62–100% fibers 11 polymers, PES, rayon, polyamide, P dominant.	Su et al. (2019)
Fish—9 species	Pearl River Catchment, China	GI tract removed, freeze-dried, digested, filtered, density separation, microscopic examination, µFTIR	50% overall 45	7.0 ± 23.8 pp ind ⁻¹ 2.7 ± 4.0 pp ind ⁻¹	Fibers, fragments, films common PET, PE, PP, PE/PP	Zheng et al. (2019)
Silver carp <i>Hypophthalmichthys molitrix</i>						
Grass carp <i>Ctenopharyngodon idella</i>			37.5	2.8 ± 3.9 pp ind ⁻¹		
Guangdong black bream <i>Megalobrama hoffmanni</i>			61.4	6.0 ± 11.3 pp ind ⁻¹		
Barbel chub <i>Squaliobarbus curriculus</i>			50.0	3.0 ± 6.0 pp ind ⁻¹		
Mud carp <i>Cirrhinus molitorella</i>			48.8	4.1 ± 7.5 pp ind ⁻¹		
Common carp <i>Cyprinus carpio</i>			15.8	0.2 ± 0.4 pp ind ⁻¹		
Prussian carp <i>Carrasius gibel</i>			43.6	1.6 ± 2.8 pp ind ⁻¹		
Redbelly tilapia <i>Coptodon zillii</i>			75.0	27.4 ± 54.0 pp ind ⁻¹		
Blotched snakehead <i>Channa maculata</i>			25.0	0.4 ± 0.8 pp ind ⁻¹		
Birds—Grey heron <i>Ardea cinerea</i> , Mute swan— <i>Cygnus olor</i> Mallard <i>Anas platyrhynchos</i>	Lake Geneva, Switzerland	Digestive tract removed, examined	89	4.3 ± 2.6 pp ind ⁻¹ 4.8 ± 8.9 mg ind ⁻¹	Fragments dominant, foam, film, beads, fiber also observed	Faure et al. (2015)

^app: plastic particle; ind: individual; dw: dry weight; ww: wet weight.

^bMesoplastics ranged from 5.1 to 25 mm in length.

Data sources: See References.

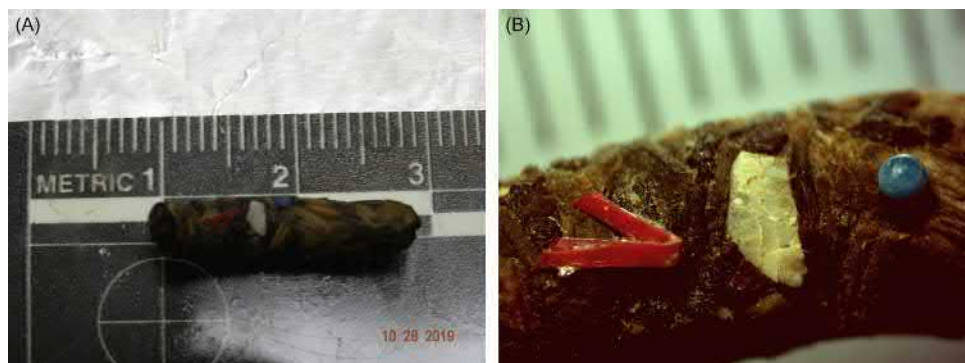


Fig. 4 Limnephilidae caddisfly case with MPs added by authors to show sizes of natural debris with plastic particles.

also reported that the use of fluorescence alone is not sufficient to prove that MP particles have moved from the gut into other organs, especially for particles $>1\ \mu\text{m}$ in size.

MPs can affect aquatic organisms in a variety of ways. Canniff and Hoang (2018) found that algal growth increased in the presence of PE beads which may have served as a substrate for the algae. On the other hand, Lagarde et al. (2016) reported that algal growth was reduced after 78 days of exposure to PP and HDPE fragments, hypothesizing that algal colonization and aggregation of the MPs increased the density of the fragments which settled out of the water column.

Many scientists have employed standardized toxicity test methods to examine the effects of MP on amphipods, water fleas, and fish. These experiments exposed test organisms to a range of MP concentrations under controlled conditions and then determined the highest concentration that had no effect of the organisms (NOEC), the lowest concentration that initiated an observed effect (LOEC), and the concentrations that caused an effect or were lethal to 50% of the test organisms (EC50 and LC50 respectively). Effects can include reduced feeding rates, motility, growth, reproduction, or survival.

Redondo Hasselerharm et al. (2018) reported that only one of six benthic invertebrate species they tested were affected by MPs when exposed to PS fragments in sediments at concentrations up to 40% of the sediment dry weight (Table 5). The amphipod *Hyalella azteca* was more sensitive to PP fibers (10-day LC50 = $71\ \text{pp mL}^{-1}$) than to PE particles (10-day LC50 = $46,400\ \text{pp mL}^{-1}$, Au et al., 2015). Ziajahromi et al. (2018) found that growth and survival of the midge *Chironomus* was affected by MP at environmentally realistic concentrations ($0.5\ \text{pp g}^{-1}$) in sediments.

MP can interfere with some organisms' ability to swim or feed by becoming entangled in their appendages or filling their guts (Table 5). Eltemsah and Bøhn (2019) reported a 5-day EC50 mobility of $35\text{--}52\ \text{mg L}^{-1}$, for the waterflea, *Daphnia*, exposed to $6\ \mu\text{m}$ PE beads. PE fragments affected *Daphnia* reproduction more than PE beads (21-day EC50 = $8.6 \times 10^4\ \text{pp mL}^{-1}$ versus $2.8 \times 10^5\ \text{pp mL}^{-1}$, Ogonowski et al., 2016). *Ceriodaphnia* are more sensitive than *Daphnia* to MP pollution (Ziajahromi et al., 2017a) and showed greatest sensitivity to PES fibers than to other forms. Although the fibers were not ingested, they interfered with *Ceriodaphnia* swimming and led to a 48-h LC50 of $1.5\ \text{mg L}^{-1}$ or $1.3 \times 10^4\ \text{pp L}^{-1}$. In chronic 21-day tests, Jaikumar et al. (2019) found that MP concentrations as low as $100\ \text{pp mL}^{-1}$ decreased at least one component of reproduction in three species of water fleas.

More sensitive biological tests have been used to detect evidence of physiological effects (Table 5) including oxidative stress, neurotoxicity, and immune responses in model organisms including fish (Karami et al., 2016; Lu et al., 2016; Haghi and Banaee, 2017; Jin et al., 2018; Lei et al., 2018; Wen et al., 2017).

Adverse effects in the environment can be caused by exposure of organisms to MP particles themselves or to pollutants that have been absorbed by the MPs. Laboratory studies have been conducted to examine the combined effects of MPs and a variety of chemical contaminants (Table 6). Wardrop et al. (2016) and (Rochman et al., 2013b) fed fish a diet that contained MP particles that had been exposed to PBDE, PAHs, and PCBs in the environment. Bioaccumulation of the contaminants in the test organisms was enhanced for some of the congeners. In experiments where organisms were exposed to MP and chemical contaminants in the same test solution, the MPs often increased the uptake and toxicity of the chemicals (Guilhermino et al., 2018; Frydkjær et al., 2017; Karami et al., 2016; Haghi and Banaee, 2017) or the effects were additive (Ma et al., 2016).

Ziajahromi (2018) found that MPs may decrease the toxicity of insecticides to midge larvae in lab water, but did not see the same effect in river water where higher organic carbon levels may have had a greater affinity for the insecticide. Understanding the chemical partitioning rates between chemical contaminants and plastics versus natural organic carbon is critical for predicting the effects of MP on chemical transfer in aquatic ecosystems. Frydkjær et al. (2017) found that PE fragments absorbed phenanthrene at a rate 8–35 times lower than natural plankton under laboratory conditions and they concluded that since the abundance of plastic in aquatic environments is much less than that of plankton, plastic may not be significant route of enhanced chemical exposure to organisms in the food chain.

Table 5 Laboratory experiments on effects of MPs on freshwater organisms.

Organism	Exposure conditions		Results	References
	Particle type ^a and size (μm)	Plastic concentration		
<i>Bacteria</i> Microbial community	PE spheres 212–250	2 and 20 mg g ⁻¹ sediment $\approx$ 257 and 2570 pp g ⁻¹ sediment	Reduced diversity of microbial community in clean sediment in 14 days	Kleinteich et al. (2018)
<i>Algae</i> <i>Chlamydomonas reinhardtii</i>	PP and HDPE fragments 400–1000	100 mg in 100 mL media	NEF on growth in 60 days, aggregates of algae and pp developed, increased settling rate of algae, may account for reduced growth in 78 days	Lagarde et al. (2016)
<i>Raphidocellis subcapitata</i>	PE beads 63–75	130 mg L ⁻¹ $\approx$ 9.9 $\times$ 10 ⁶ pp L ⁻¹	Increased algal growth, possibly served as substrate	Canniff and Hoang (2018)
<i>Plant</i> <i>Lemna minor</i>	PE spheres 10–45	5.0 $\times$ 10 ⁴ pp mL ⁻¹	MP adhered to <i>Lemna</i> surfaces-maximum 7 pp mm ⁻² or 42 pp dried colony ⁻¹ . NEF photosynthesis or growth in 30 days	Mateos-Cárdenas et al. (2019)
<i>Cnidaria</i> <i>Hydra attenuata</i>	PE flakes <400	0.01–0.08 g mL ⁻¹ $\sim$ 800–6400 pp mL ⁻¹	Particles were ingested, reduced feeding rates, increased egestion rates Predicted NOEC 2800 pp mL ⁻¹	Murphy and Quinn (2018)
<i>Mollusca</i> Asian clam <i>Corbicula fluminea</i>	PET fragments 12–704 PE fragments 14–704 PVC fragments 80–704 PS fragments 68–704 Fluorescent polymer spheres 1–5 PEA fibers	4.1 mg L ⁻¹ 2.8 mg L ⁻¹ 4.2 mg L ⁻¹ 3.2 mg L ⁻¹ 0.2 and 0.7 mg L ⁻¹ $\approx$ 3.67 $\times$ 10 ⁷ –1.28 $\times$ 10 ⁸ pp L ⁻¹ 100 and 1000 pp L ⁻¹	Accumulated 5 $\pm$ 6 pp ind ⁻¹ in 3 days Accumulated 8 $\pm$ 6 pp ind ⁻¹ in 3 days Accumulated 3 $\pm$ 3 pp ind ⁻¹ in 3 days Accumulated 4 $\pm$ 3 pp ind ⁻¹ in 3 days MP found in digestive tract, digestive gland, connective tissues, hemolymphatic sinuses and on gills. Inhibition of enzyme activity 0.3 pp g ⁻¹ ingested at 100 and 1000 pp L ⁻¹ Fibers arched Ingested at 1000 pp L ⁻¹ 0.1 pp g ⁻¹ ingested at 1000 pp L ⁻¹ Not ingested Not ingested Ingested 0.5 pp g ⁻¹ at 100 pp L ⁻¹ and 4.1 pp g ⁻¹ at 1000 pp L ⁻¹ Ingested fibers were curved and bent into loops Ingested 1.7 pp g ⁻¹ at 1000 pp L ⁻¹ Ingested 0.2 pp g ⁻¹ at 1000 pp L ⁻¹	Rochman et al. (2017) Guilhermino et al. (2018) Li et al. (2019)
Zebra mussel <i>Dreissena polymorpha</i>	AC fibers PA fibers RA fibers PVA fibers PET fibers PET fibers 100–250 PET fibers 1000–5000 PS beads 1 and 10	100 and 1000 pp L ⁻¹ 100 and 1000 pp L ⁻¹ 100 and 1000 pp L ⁻¹ 100 and 1000 pp L ⁻¹ 100 and 1000 pp L ⁻¹ 100 and 1000 pp L ⁻¹ 100 and 1000 pp L ⁻¹ 5 $\times$ 10 ⁵ pp L ⁻¹ of each size and 2 $\times$ 10 ⁶ pp L ⁻¹ of each size	MP found in gut lumen, tissues, and hemolymph. Increased level of dopamine, did not produce oxidative stress or genetic damage.	Magni et al. (2018)
Mud snail <i>Potamopyrgus antipodarium</i>	Polymethyl methacrylate fragments 29.5	1:10 ratio of plastic to food	MP ingested, 87.8% of feces contained MPs	Imhof et al. (2013)
European fingernail clam <i>Sphaerium corneum</i>	PS fragments 20–500	0.1–40% of sediment dw	NEF survival or growth in 28 days	Redondo Hasselerharm et al. (2018)

<i>Annelida</i> <i>Lumbriculus variegatus</i>	Polymethyl methacrylate fragments 29.5	1:10 ratio of plastic to food	93% ingested MPs	Imhof et al. (2013)
	PS fragments 20–500	0.1–40% of sediment dw	NEF growth or reproduction in 28 days	Redondo Hasselerharm et al. (2018)
<i>Tubifex</i> spp.	PS fragments 20–500	0.1–40% of sediment dw	NEF survival or growth in 28 days	Redondo Hasselerharm et al. (2018)
<i>Nematoda</i> <i>Caenorhabditis elegans</i>	PA fragments 70	0.5–10.0 mg m ⁻²	Decreased survival, growth, reproduction, and intestinal calcium levels. Oxidative stress noted. LOEC = 0.5 mg m ⁻²	Lei et al. (2018)
	PE fragments 70	0.5–10.0 mg m ⁻²	Decreased survival, growth, reproduction, and intestinal calcium levels. Oxidative stress noted. LOEC = 0.5 mg m ⁻²	
	PP fragments 70	0.5–10.0 mg m ⁻²	Decreased survival, growth, reproduction, and intestinal calcium levels. Oxidative stress noted. LOEC = 0.5 mg m ⁻²	
	PVC fragments 70	0.5–10.0 mg m ⁻²	Decreased survival, growth, reproduction, and intestinal calcium levels. Oxidative stress noted. LOEC = 1.0 mg m ⁻²	
	PS spheres 0.1, 1.0, 5.0	0.5–10.0 mg m ⁻²	PP accumulated in digestive system. Caused oxidative stress, decreased survival, growth, reproduction, and intestinal calcium levels. 1.0 µm particles most lethal. LOEC = 0.5 mg m ⁻²	
<i>Crustaceans</i> Ostracod <i>Notodromas monacha</i>	Polymethyl methacrylate fragments 29.5	1:1 ratio of plastic to food	32.4% ingested MPs	Imhof et al. (2013)
Isopod <i>Asellus aquaticus</i>	PS fragments 20–500	0.1–40% of sediment dw	NEF survival or growth in 28 days	Redondo Hasselerharm et al. (2018)
Amphipod <i>Gammarus duebeni</i>	PE spheres 10–45	Fed <i>Lemna minor</i> with adsorbed MP	29% contained pp after 24 h depuration period, NEF survival in 48 h exposure	Mateos-Cárdenas et al. (2019)
Amphipod <i>Gammarus fossarum</i>	PA fibers 500 × 20	100–1.3 × 10 ⁴ fibers cm ⁻² basal area of chamber	Ingested and egested rapidly. NEF feeding rate. Decreased assimilation efficiency at 2680 fibers cm ⁻²	Blarer and Burkhardt-Holm (2016)
	PS beads 1.6	500–6 × 10 ⁴ pp mL ⁻¹	PP ingested, found in gut but not in midgut glands or epithelial cells of gut. NEF feeding rate or assimilation efficiency at 12,500 beads mL ⁻¹	Straub et al. (2017)
	PHB fragments (biodegradable) 32–250	10–1 × 10 ⁵ pp ind ⁻¹	32–63 µm particles ingested in highest amounts, NEF feeding rate or assimilation efficiency. Decreased weight gain	
Amphipod <i>Gammarus pulex</i>	PMMA fragments 32–250	10–1 × 10 ⁵ pp ind ⁻¹	32–63 µm particles ingested in highest amounts, decreased assimilation efficiency and weight gain	Imhof et al. (2013)
	Polymethyl methacrylate 29.5	1:10 ratio of plastic to food	Ingested, 96% of feces contained MPs	
	PS fragments 20–500	0.1–40% of sediment dw	16–165 µm MPs were ingested. Ingestion rate proportional to sediment dose. NEF survival or feeding rate in 28 days. EC10 growth = 1.07% EC50 growth = 3.57%	Redondo Hasselerharm et al. (2018)

(Continued)

Table 5 (Continued)

Organism	Exposure conditions		Results	References
	Particle type and size (μm)	Plastic concentration		
Amphipod <i>Hyalella azteca</i>	PET fragments 10–150	0.4–4000 pp mL ⁻¹	High ingestion of fragments <53 μm , up to 6600 pp ind ⁻¹ NEF survival, metabolism or feeding in 48 days	Weber et al. (2018)
	PE particles 10–27	10 - 1 $\times$ 10 ⁵ pp mL ⁻¹ acute exposure 5 $\times$ 10 ³ – 2 $\times$ 10 ⁴ pp mL ⁻¹ chronic exposure	MP ingested, but did not translocate out of gut. NEF growth in acute exposure. Decreased reproduction and growth in chronic exposure. 10-day LC50 = 46,400 pp mL ⁻¹	Au et al. (2015)
	PP fibers diameter 20 length 20–75	22.5–90 pp mL ⁻¹	MP ingested, but did not translocate out of gut. Increased egestion time. Decreased growth. 10-day LC50 = 71.43 pp mL ⁻¹	
	PS fragments 20–500	0.1–40% of sediment dw	No MP ingestion. NEF survival, feeding rate or growth in 28 days.	Redondo Hasselerharm et al. (2018)
Water flea <i>Ceriodaphnia dubia</i>	PE beads 1–4	0.5–16 mg L ⁻¹ $\approx$ 1.7 $\times$ 10 ⁴ –5.4 $\times$ 10 ⁵ pp L ⁻¹	Beads ingested, gut full at 4 mg L ⁻¹ and higher 48-h LC50 = 2.2 mg L ⁻¹ (7.4 $\times$ 10 ⁴ pp L ⁻¹)	Ziajahromi et al. (2017a)
	PE beads 1–4	62.5–2000 μg L ⁻¹ $\approx$ 2.1 $\times$ 10 ³ –6.7 $\times$ 10 ⁴ pp L ⁻¹	8-day EC50 reproduction = 958 μg L ⁻¹ (3.2 $\times$ 10 ³ pp L ⁻¹)	
	PES fibers 26–1150 long average 280	0.125–4 mg L ⁻¹ $\approx$ 1.1 $\times$ 10 ³ –3.4 $\times$ 10 ⁴ pp L ⁻¹	No fibers ingested, but bubbles noted under carapace, antennal and carapace deformities, fibers affected swimming behavior 48-h LC50 = 1.5 mg L ⁻¹ (1.3 $\times$ 10 ³ pp L ⁻¹)	
	PES fibers 26–1150 long average 280	31.25–1000 μg L ⁻¹ $\approx$ 272–8600 pp L ⁻¹	8-day EC50 reproduction = 429 μg L ⁻¹ (3.5 $\times$ 10 ³ pp L)	
Water flea <i>Daphnia magna</i>	PE spheres 1–5	1 $\times$ 10 ³ –1 $\times$ 10 ⁷ pp mL ⁻¹	18 °C 96-h NOEC = 5.0 $\times$ 10 ³ pp mL ⁻¹ Little change at higher temperatures	Jaikumar et al. (2018)
	PE fragments 1–10	1 $\times$ 10 ³ –1 $\times$ 10 ⁷ pp mL ⁻¹	18 °C 96-h NOEC = 1.0 $\times$ 10 ⁵ pp mL ⁻¹ Little change at higher temperatures	
	PE spheres 1–5	100–1 $\times$ 10 ⁵ pp mL ⁻¹	21-day LOEC reproduction = 100 pp mL ⁻¹	Jaikumar et al. (2019)
	PE fragments 1–10	100–1 $\times$ 10 ⁵ pp mL ⁻¹	21-day LOEC reproduction = 100 pp mL ⁻¹	
	Fluorescent PS beads 0.02 and 1.00	2 μg L ⁻¹	Both sizes ingested. Fluorescence appeared in gut and lipid storage droplets. Depuration rate faster for the larger MP beads	Rosenkranz et al. (2009)
	PMA fragments 29.5	1:10 ratio of plastic to food	100% ingested MP	Imhof et al. (2013)
	PET fibers 60–1400 long, 30–530 wide, 2–21.5 thick	12.5–100 mg L ⁻¹ $\approx$ 6.64 $\times$ 10 ⁴ –5.3 $\times$ 10 ⁵ fibers L ⁻¹	MP uptake and depuration noted, increased mortality in 48 h in unfed organisms- not dose dependent.	Jemec et al. (2016)
	PS 0.05–10	1–50 mg L ⁻¹	Uptake and depuration of MP and NP observed. NEF from larger particles. 0.05 μm NP most toxic. 48-h EC50 immobilization = 15.13 mg L ⁻¹ , damaged swimming/feeding appendages.	Ma et al. (2016)
	PE beads 4.1 $\pm$ 1.0	100–2.25 $\times$ 10 ⁵ pp mL ⁻¹	Decreased feeding rate, and growth, increased mortality. 21-day EC50 reproduction = 2.8 $\times$ 10 ⁵ pp mL ⁻¹	Ogonowski et al. (2016)
	PE fragments 2.6 $\pm$ 1.8	100–2.25 $\times$ 10 ⁵ pp mL ⁻¹	Decreased feeding rate, and growth, increased mortality. 21-day EC50 reproduction = 8.6 $\times$ 10 ⁴ pp mL ⁻¹	Rehse et al. (2016)
	PE spheres 1–4	12.5–400 mg L ⁻¹	Ingestion and egestion noted, caused immobilization 96-h EC50 = 57.43 mg L ⁻¹	
	PE spheres 90–106	12.5–400 mg L ⁻¹	MP accumulated on water surface, not ingested, NEF	

<i>Daphnia pulex</i>	PS beads 2	$0.1\text{--}1 \text{ mg L}^{-1} \approx 1.4 \times 10^6\text{--}1.4 \times 10^7 \text{ pp mL}^{-1}$	Ingested up to $1.24 \times 10^6 \text{ pp ind}^{-1}$ or $0.89 \mu\text{g ind}^{-1}$ in 24 h. In 21 days, body burden up to $3.0 \times 10^5 \text{ pp ind}^{-1}$ or $2.43 \mu\text{g ind}^{-1}$ NEF survival or reproduction	Rist et al. (2017)
	PE beads 10–106 and PE fragments 10–75	$0.0001\text{--}10 \text{ g L}^{-1}$	24 h ingestion related to dose $33\text{--}50 \text{ pp ind}^{-1}$ in 24 h, Beads egested at higher rate than fibers 48-h EC50 mobility = 0.065 g L^{-1} for fragments	Frydkjær et al. (2017)
	PE beads 63–75	$25\text{--}100 \text{ mg L}^{-1} \approx 1.9 \times 10^6\text{--}7.6 \times 10^6 \text{ pp L}^{-1}$	Ingested $3.81\text{--}15.06 \text{ pp ind}^{-1}$ NEF survival or reproduction	Canniff and Hoang (2018)
	PE spheres 1–5	$1 \times 10^3\text{--}1 \times 10^7 \text{ pp mL}^{-1}$	18 °C 96-h NEC = $1 \times 10^5 \text{ pp mL}^{-1}$ More toxic at higher temperatures	Jaikumar et al. (2018)
	PE fragments 1–10	$1 \times 10^3\text{--}1 \times 10^7 \text{ pp mL}^{-1}$	18 °C 96-h NEC = $5.01 \times 10^4 \text{ pp mL}^{-1}$ More toxic at higher temperatures	Eltemsah and Bøhn (2019)
	PS beads 6	$5\text{--}300 \text{ mg L}^{-1}$	MP ingested and adhered to body surfaces and appendages. Decreased growth. 120-h EC50 immobilization = $35\text{--}52 \text{ mg L}^{-1}$	Jaikumar et al. (2019)
	PE spheres 1–5	$100\text{--}1 \times 10^5 \text{ pp mL}^{-1}$	21-day LOEC reproduction = 100 pp mL^{-1}	Schür et al. (2019)
	PE fragments 1–10	$100\text{--}1 \times 10^5 \text{ pp mL}^{-1}$	21-day LOEC reproduction = 100 pp mL^{-1}	
	PS beads 0.02 and 1.0	$2 \mu\text{g L}^{-1}$	Did not detect smaller fluorescent particles in Daphnia. Larger particles clearly visible in digestive tract. No fluorescence outside of gut.	
		2 mg L^{-1}	Fluorescence observed in lipid droplets and gut of Daphnia for both sizes of MP. Larger beads observed in gut. Fluorescence of lipids due to movement of dye, not pp.	
<i>Daphnia pulex</i>	PS 1	$0.1\text{--}600 \text{ mg L}^{-1}$	48-h EC50 immobilization = 66.97 mg L^{-1} 48-h LC50 = 87.83 mg L^{-1}	Zhang et al. (2019a)
	PS 10	$0.005\text{--}40 \text{ mg L}^{-1}$	48-h EC50 immobilization = $19\text{--}9.94 \text{ mg L}^{-1}$ 48-h LC50 = 291.69 mg L^{-1}	
	PET/PA fibers 10×2	10 pp mL^{-1}	31.7% mortality in 168 h Aggregates of MP and algae noted on antennae and carapace	Zocchi and Sommaruga (2019)
	PE beads 1–10	$0.01 \text{ mg mL}^{-1} \approx 2.2 \times 10^6 \text{ pp mL}^{-1}$	38% mortality in 168 h Aggregates of MP and algae noted on antennae and carapace	Jaikumar et al. (2018)
	PE spheres 1–5	$1 \times 10^3\text{--}1 \times 10^7 \text{ pp mL}^{-1}$	18 °C 96-h NOEC = $1 \times 10^5 \text{ pp mL}^{-1}$ More toxic at higher temperatures	Jaikumar et al. (2019)
	PE fragments 1–10	$1 \times 10^3\text{--}1 \times 10^7 \text{ pp mL}^{-1}$	18 °C 96-h NOEC = $1 \times 10^5 \text{ pp mL}^{-1}$ More toxic at higher temperatures	
	PE spheres 1–5	$100\text{--}1 \times 10^5 \text{ pp mL}^{-1}$	21-day LOEC reproduction = 100 pp mL^{-1}	
	PE Fragments 1–10	$100\text{--}1 \times 10^5 \text{ pp mL}^{-1}$	21-day LOEC reproduction = 100 pp mL^{-1}	
<i>Insects</i>				
Mosquito	PS beads 2 and 15	$50\text{--}200 \text{ pp L}^{-1}$	Larvae ingested MP—up to $256 \text{ pp larva}^{-1}$. MP transferred to pupal and adult stages. NEF survival or growth	Al-Jaibachi et al. (2019)
<i>Culex pipiens</i>	PS 2	100 pp mL^{-1}	MP ingested, average 5.8 pp ind^{-1}	Cuthbert et al. (2019)
Mosquito	PS 2	Fed <i>C. pipiens</i> that had been exposed to MP	MP found in predators, amount related to consumption rate	
<i>Culex pipiens</i>				
Phantom midge				
<i>Chaoborus flavicans</i>				
Midge	PE spheres 1–4, 10–27, 43–54, 100–126	500 pp kg^{-1} sediment ww	NEF on survival or growth with $100\text{--}126 \mu\text{m}$ MP. Decreased survival and growth in three smaller size classes, effects greatest for $10\text{--}27 \mu\text{m}$ MP. Emergence of adults decreased for all MP sizes	Ziajahromi et al. (2018)
<i>Chironomus tepperi</i>				
<i>Fish</i>				
African catfish	LDPE fragments < 60	$50 \text{ and } 500 \mu\text{g L}^{-1} \approx 1.4 \times 10^3 \text{ and } 1.4 \times 10^4$	MP not found in gill or liver tissues but gill and liver tissues were damaged. Altered levels of lipids and proteins in blood plasma	Karami et al. (2016)
<i>Clarias gariepinus</i>			Decreased gene transcription in brain tissue	
Common carp	PE	$1\text{--}2 \text{ mg L}^{-1}$	Changes in blood biochemistry indicating physiological stress and organ damage	Haghi and Banaee (2017)
<i>Cyprinus carpio</i>				

(Continued)

Table 5 (Continued)

Organism	Exposure conditions		Results	References
	Particle type and size (μm)	Plastic concentration		
Zebrafish <i>Danio rerio</i>	PS beads 5	20 mg L ⁻¹ 2.9 × 10 ⁵ pp mL ⁻¹	MP accumulated in gills, liver, and gut	Lu et al. (2016)
	PS beads 20 PS beads 0.07, 5	20 mg L ⁻¹ 4500 pp mL ⁻¹ 20–2000 $\mu\text{g mL}^{-1}$	MP accumulated in gills and gut High doses caused inflammation and signs of oxidative stress in the liver. Lipid profile and liver metabolites affected	
	PS beads 0.5 and 50	100 and 1000 $\mu\text{g L}^{-1}$	At higher concentrations MP caused inflammation and increased production of mucous in gut and resulted in changes in gut microbiota	Jin et al. (2018)
	PA fragments 70	0.001–10.0 mg L ⁻¹	NEF survival, caused intestinal damage	Lei et al. (2018)
	PE fragments 70	0.001–10.0 mg L ⁻¹	NEF survival, caused intestinal damage	
	PP fragments 70	0.001–10.0 mg L ⁻¹	27% decrease survival at highest concentration, caused intestinal damage	
	PVC fragments 70	0.001–10.0 mg L ⁻¹	NEF survival, caused intestinal damage	
Discus fish <i>Symphysodon aequifasciatus</i>	PS spheres 0.1, 1.0, 5.0	0.001–10.0 mg L ⁻¹	NEF survival or intestine	Wen et al. (2017)
	PE spheres 70–88	200 $\mu\text{g L}^{-1}$	NOEF on growth or survival in 30 days at temperatures of 28 °C or 31 °C. Greater accumulation of MP in tissue at higher temperature. MP affected predation rates at lower temp. Digestive and metabolic enzyme activities altered by presence of MP	

^aPolymer types: PE: polyethylene; PEA: polyester amide; PES: polyester; PHB: polyhydroxybutyrate (biodegradable bioMP); PMA: Polymethyl acrylate; PVA: polyvinyl alcohol; RA: rayon.

Data sources: See References.

Table 6 Interactions of MP with chemical contaminants in laboratory exposures.

Species	MP exposure		Chemical contaminant ^b and exposure concentration	Results	Reference
	Particle type ^a and size μm	Plastic concentration			
Microbial community	PE spheres 212–250	1 mg g ⁻¹ sediment 257 pp g ⁻¹ sediment	Phenanthrene 30.2 $\mu\text{g g}^{-1}$ on MP Anthracene 29.5 $\mu\text{g g}^{-1}$ on MP Florfenicol 1.8 and 7.1 mg L ⁻¹ in test solution	Observed change in sediment microbial community structure exposed to contaminants on MPs was different than response to contaminant alone No change in microbial community structure, but MP decreased rate of anthracene degradation. MP increased uptake of florfenicol. Decreased feeding and cholinesterase activity, showed neurotoxicity, oxidative damage	Kleinteich et al. (2018)
Asian clam <i>Corbicula fluminea</i>	Fluorescent polymer spheres 1–5	0.2 and 0.7 mg L ⁻¹ 3.67 $\times 10^7$ to 1.28 $\times 10^8$ pp L ⁻¹			Guilhermino et al. (2018)
Water flea <i>Daphnia magna</i>	PS 0.05–10	2.5–50 mg L ⁻¹	Phenanthrene 0.05–1.2 mg L ⁻¹ in test solution	Joint effects of MP and phenanthrene were additive. MP increased immobilization of <i>Daphnia</i> . Increased bioaccumulation of phenanthrene, and slowed degradation rate. MP did not bioaccumulate or affect toxicity of phenanthrene.	Ma et al. (2016)
	PE fragments 10–75	0.05 g L ⁻¹	Phenanthrene 0.008–5 mg L ⁻¹ in test solution	MP increased toxicity Phenanthrene EC50 = 0.47 mg L ⁻¹ w/o MP and 0.14 mg L ⁻¹ w/MP	Frydkjær et al. (2017)
	PA fragments 15–20	200 mg L ⁻¹	BPA 5–15 mg L ⁻¹ on MP	MPs adsorbed BPA and were ingested, MPs reduced rate of immobilization from BPA.	Rehse et al. (2018)
	PS 1	0.1 mg L ⁻¹ 1.82 $\times 10^8$ pp mL ⁻¹	Roxithromycin 0.01 mg L ⁻¹ in test solution	MP increased oxidative stress, decreased antioxidant enzyme activity	Zhang et al. (2019a)
	PS 10	0.1 mg L ⁻¹ 1.82 $\times 10^5$ pp mL ⁻¹		MP reduced oxidative stress, Increased antioxidant enzyme activity	
	PET/PA fibers 10 $\times$ 2	10 pp mL ⁻¹	Glyphosate acid 2.5 mg L ⁻¹ in test solution Roundup gran 2.5 mg L ⁻¹ in test solution Glyphosate-IPA 2.5 mg L ⁻¹ in test solution	Increased Mortality in 168 h Increased mortality in 168 h Decreased mortality in 168 h	Zocchi and Sommaruga (2019)
	PE beads 1–10	2,200,000 pp mL ⁻¹ 0.01 mg mL ⁻¹	Glyphosate acid 2.5 mg L ⁻¹ in test solution Roundup gran 2.5 mg L ⁻¹ in test solution Glyphosate-IPA 2.5 mg L ⁻¹ in test solution	Increased mortality in 168 h Increased mortality in 168 h Decreased mortality in 168 h	
Midge <i>Chironomus tepperi</i>	PE beads 10–27	1600 pp L ⁻¹ 5 mg L ⁻¹	Bifenthrin 0.1–3.2 $\mu\text{g L}^{-1}$ in test solution	Decreased toxicity of bifenthrin in lab media, but not in river water. 48-h LC50 = 1.3 $\mu\text{g L}^{-1}$ with MP vs. 0.5 $\mu\text{g L}^{-1}$ w/o MP	Ziajahromi (2018)
Zebrafish <i>Danio rerio</i>	PE 10–106 PE 10–106	10–1000 pp mL ⁻¹ 1000 pp mL ⁻¹	Silver 1 $\mu\text{g L}^{-1}$ in test solution Silver Beads incubated with 1 μg L ⁻¹ Ag prior to exposure to 1 $\mu\text{g L}^{-1}$ in test solution	MP did not affect uptake of Ag in 24 h exposure MP reduced total uptake of Ag in 24 h, but increased proportion in intestine	Khan et al. (2015)
	PVC 200–250	400 mg L ⁻¹	Phenanthrene 0.5 mg L ⁻¹ in test solution 17 α -ethinylestradiol 1 $\mu\text{g L}^{-1}$ in test solution	MP addition reduced gene expression indicating reduced phenanthrene availability MP addition reduced gene expression indicating reduced ethinylestradiol availability	Sleight et al. (2017)

(Continued)

Table 6 (Continued)

Species	MP exposure		Chemical contaminant and exposure concentration	Results	Reference
	Particle type and size μm	Plastic concentration			
Japanese medaka <i>Oryzias latipes</i>	PE Virgin and exposed/ aged pellets <500	10% by weight of diet Fed 6 mg food with 0.6 mg MP fish ⁻¹ day ⁻¹	PAHs, 24–58 ng g ⁻¹ diet PCBs 0.3–5.3 ng g ⁻¹ diet PBDEs 1.1–3.1 ng g ⁻¹ diet	Body burden in exposures with contaminated MP similar to controls except for elevated chrysene, PCB28, and PBDE levels. Liver damage noted indicating glycogen depletion	Rochman et al. (2013b)
African catfish <i>Clarias gariepinus</i>	LDPE fragments <60	50 and 500 $\mu\text{g L}^{-1}$ (1400 and 14,000 PP L ⁻¹)	Phenanthrene Nominal concentrations 10 and 100 $\mu\text{g L}^{-1}$ on MP	MP may have changed bioavailability of phenanthrene. Increased degree of gill damage, changes in lipids and proteins in blood plasma and gene transcription rates in brain compared to phenanthrene alone.	Karami et al. (2016)
Common carp <i>Cyprinus carpio</i>	PE	1–2 mg L ⁻¹	Paraquat 0.2–0.4 mg L ⁻¹ in test solution	Changes in blood biochemistry indicating physiological stress and organ damage. Increased toxicity of Paraquat	Haghi and Banaee (2017)
Rainbow fish <i>Melanotaenia fluviatilis</i>	PE 10–700	10 mg day ⁻¹ in food	PBDE 200 ng g ⁻¹ day ⁻¹ diet on MP	MP ingested, PBDE bioaccumulated in fish tissues over 63 days, amount varied by PBDE congener	Wardrop (2016)

^aPE, polyethylene^bBPA, bisphenol A; PAH, polycyclic aromatic hydrocarbon; PBDE, polybrominated diphenyl ethers; PCB, polychlorinated biphenyl.

Data sources: See References.

Summary

The increased use of plastic materials by humans has led to the contamination of freshwater biomes with MP debris. MP particles are now found in the water column and sediments of lakes and rivers worldwide. While concentrations of MPs are generally fairly low <1 pp L⁻¹ in surface waters and <10 pp g⁻¹ sediment, higher concentrations are observed near urban areas, sewage plants and retention ponds where materials can settle. With the use of finer nets and sieves for sample collection, researchers are finding that fibers are more widespread and numerous than fragments or microbeads and pellets.

Although freshwater organisms do ingest MPs, the density of plastic in individual organisms in nature is generally quite low due to the ability of the organisms to depurate the plastic materials. Laboratory studies have found that MPs can adversely affect the metabolism, growth, reproduction, and survival of aquatic organisms, but generally at concentrations much higher than those found in nature.

Few studies have been done on the ability of MPs to accumulate toxic chemicals from freshwater environments and the kinetics of the release of these compounds to organisms upon ingestion is generally unknown under environmental conditions. Koelmans et al. (2016) found that MPs adsorb POPs in lower concentrations than natural media in the oceans. However, it should be noted that MPs are not biodegradable in a reasonable human time scale, and will be continuously concentrating toxic compounds from the aquatic environment.

Because MP pollution is an anthropogenic issue, we need to develop a way to decrease this environmental problem by enacting one of the UN's sustainable development goals "responsible consumption and production" (United Nations, 2015). By promoting education to raise the awareness of the general public to the negative effects of the indiscriminate use of everyday plastic items, we can produce a change in behavior regarding the consumption and uses of plastics.

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The Springs Biome, with an Emphasis on Arid Regions

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Abstract

Springs ecosystems occur where groundwater reaches the Earth's surface, and are physically and biologically significant, complex, and highly socio-ecologically interactive ecosystems, particularly in arid regions. However, springs are threatened by intensifying human appropriation, contamination of groundwater, and surface habitat destruction. I review the literature and conceptual underpinnings of ecosystem ecology, springs distribution, typology, eco-evolutionary, and socio-cultural characteristics and processes in arid versus mesic/humid landscapes, and identify conceptual and data gaps. I estimate that the world's at least 2.3 million terrestrial springs produce at least 10.7 km³ of water/year. Most ecohydrogeological characteristics and processes discussed apply to all terrestrial springs across latitude and elevation; however, aridland springs differentially or more often have: (1) steeper environmental moisture and nutrient gradients between adjacent uplands, (2) distinctively different biotic assemblages; (3) higher occurrence of endemism and rare species in evolutionarily significant paleorefugia; (4) interrupted, losing-stream springbrooks, disconnectivity that retards non-native species colonization; (5) lower levels of flow and increased ephemeral flow; (6) reduced resiliency and more dynamism in vegetation development following disturbance; (7) greater susceptibility to anthropogenic impacts that leads to (8) loss of springs habitat and increased probability and incidence of extinction of springs-dependent species. These differences and greater conservation urgency elevate the need for improved stewardship of aridland springs. The study of aridland springs reveals much about the ecohydrology, distribution, ecological development and function, biogeography, ecological roles, and importance to humanity of springs everywhere, and the need and opportunities for enhanced stewardship of this highly endangered biome.

Introduction

Springs ecosystems are places influenced by the exposure and often the flow of groundwater onto the Earth's surface. Springs are widely recognized as being biologically productive, diverse, and socio-ecologically highly interactive ecosystems that supply high-quality water with spiritual and therapeutic qualities (Stevens and Meretsky, 2008; Cantonati et al., 2012; Glazier, 2014; Kreamer et al., 2015; Cantonati et al., 2020). Arid conditions prevail across about 29% of the Earth's surface, with deserts occurring in characteristic peri-equatorial as well as high latitude and high elevation settings (Kottek et al., 2006). While the values and significance of springs are widely recognized in arid regions, many of those same properties, processes, and values occur in springs everywhere on Earth, from profundal seafloor vents to tropical and high elevation environments. In part, the widely recognized

uniqueness and values of springs ecosystems is related to their internal constancy: individual springs often have remarkably constant or consistent flow, geochemistry, and temperature. However, springs across the Earth vary enormously in those characteristics, as well as in type, size, isolation, density within landscapes, biota, ecological processes, and human uses and values. Integration of these many physical, biological, ecological, and socio-cultural attributes and processes within and among springs makes their study a compelling and highly interdisciplinary field of ecohydrological study, one on which the pace of research is accelerating (Cantonati et al., 2020). Unfortunately, for all of their recognized value, springs are among the most threatened ecosystems, particularly in arid regions, with estimates of ecological impairment and loss commonly exceeding 70% in many landscapes (Stevens and Meretsky, 2008).

Below, I briefly review the growing literature on springs ecology and contribute data, illustrations, and examples to describe the conceptual underpinnings, distribution, typology, physical, biotic, eco-evolutionary, and socio-cultural characteristics and processes of springs, emphasizing those in arid regions. I use a “bottom-up” ecosystem approach to describe the physical and biological characteristics and processes, and anthropogenic uses of springs as ecosystems. I distinguish between those traits and processes in arid- and semi-arid regions as compared to those in more mesic humidity provinces. I primarily use examples from the arid American Southwest, but reference relevant studies from around the world. Aridland springs provide textbook cases of springs distribution, ecological development and function, biogeography, ecological roles, importance to humanity, and how stewardship can be improved. However, most of those ecohydrogeological underpinnings apply to all springs, both terrestrial and subaqueous (e.g., marine seafloor vent), and ranging from superarid (e.g., the Atacama Desert of northern Chile) to superhumid tropical rainforest regions. Thus, while the focus of this paper is on springs in arid regions, the processes, characteristics, and lessons to be learned apply to springs everywhere on Earth. Springs ecosystems have not previously been clearly recognized as an Earth biome; however, their globally distinctive characteristics across water quality and lentic vs. lotic gradients merit consideration of that designation.

Background Literature

Ecohydrogeological consideration of springs has a history rivaling that of humanity itself. Among the early recorded observations on springs, Aristotle (ca. 330 BCE) hypothesized on the source(s) of groundwater in Greece. Pliny the Elder (77 AD) related springs flow and geochemistry to vegetation production and structure throughout the Mediterranean region. Agricola and Perrault established the basic premises and laid the historical foundation for the science of hydrology (Perrault, 1674; Harter, 2003). Intensive research during the 20th Century was conducted on springs hydrogeology by Fuller (1904, 1910), Keilhack (1912), Steinmann (1915), Bryan (1919), Meinzer and Hare (1915), Meinzer (1923, 1927), Clarke (1924), Thienemann (1922), and Stiny (1933). On a parallel track in the 19th and 20th Centuries, the science of community ecology arose from the writing of Forbes (1887), Cowles (1911), Gleason (1926), Tansley (1935), and Lindeman (1942), with work on aridland hanging garden springs ecology by Woodbury (1939) and the codification of ecosystem ecology at Silver Springs Florida by Odum (1957). Reviews of springs ecohydrology have been presented by Alfaro and Wallace (1994), Williams and Danks (1991), and Botosaneanu (1998). In the present century, much additional review and new research on springs ecosystems has been conducted (e.g., Cantonati et al., 2007; Springer et al., 2008; Stevens and Meretsky, 2008; Springer and Stevens, 2009; Kresic and Stevanovic, 2010; Glazier, 2014; Kreamer et al., 2015; Stevens et al., in press). Among those studies, Glazier (2014) provided a detailed synopsis of available literature, information, and insights on the lexicon and approaches to classification of springs. Considerable recent focus also has been placed on springs ecosystem inventory, assessment, and management (e.g., Patterson and Cooper, 2007; Abele, 2011; US Forest Service, 2012; Knight, 2015; Stevens et al., 2016a,b). This research and new, innovative ecological tools, such as the use of eDNA to study springs biodiversity (e.g., Emerson et al., 2015) are expanding insight into springs ecosystem distribution and ecology, and stewardship needs, challenges, and solutions.

A Conceptual Ecosystem Model

Based on the above literature, springs are becoming increasingly recognized as important, physically-based, groundwater-dependent ecosystems (GDEs), occurring because of the exposure or emergence of groundwater (Eamus and Freund, 2006). Consequently, springs are regarded as “bottom-up” ecosystems, deriving their existence and structure from physical processes. Robust, “top-down” trophic cascades can develop at some springs (e.g., the highly endemized predatory invertebrate food chain at warm, stenothermic, mineralized and fishless Montezuma Well in Arizona; Blinn, 2008); nonetheless, physical interactions govern nearly all ecosystem dynamics in and around most springs.

Understanding the role of physical interactions affecting biological and anthropogenic interactions at springs is most easily envisioned through a springs conceptual ecosystem model (Stevens et al., in press; Fig. 1). In this model, bedrock and geologic structure, regional and long-term climate, and aquifer characteristics and processes set the stage for groundwater emergence. Springs sources emerge in a particular geomorphic setting (Meinzer, 1923; Alfaro and Wallace, 1994; Springer and Stevens, 2009), subject to a site-specific microclimate, and influenced by interactions between disturbance and productivity (e.g., Connell, 1978; Huston, 1994). These processes cumulatively create a landscape template, including soils and microhabitats, and generate “site hospitality” (sensu Stevens et al., in press) to potential colonizing populations. That habitat template is colonized through passive and active

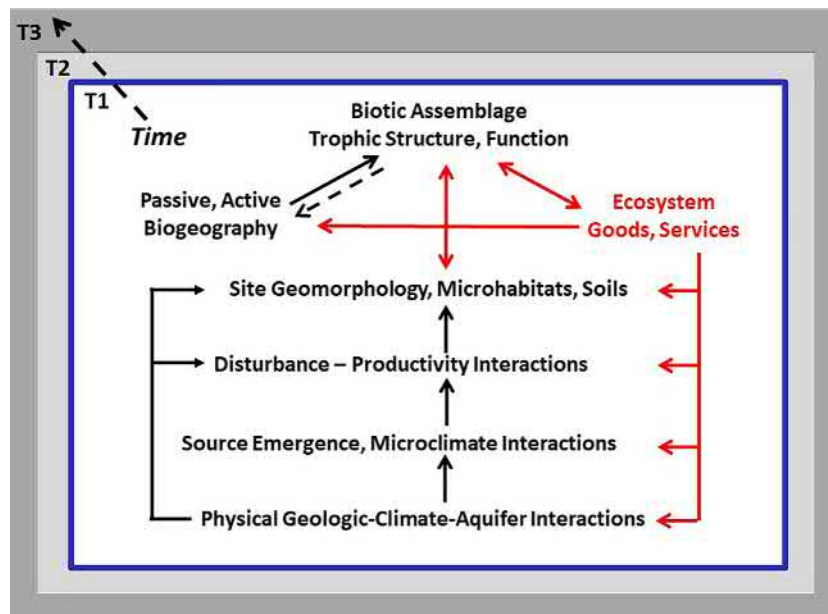


Fig. 1 General conceptual model of springs ecosystems (simplified and redrawn from Stevens et al., in press). Black lines indicate natural interactions, while red lines indicate anthropogenic influences.

biogeographic processes and develops and changes over time, supporting species that interact to varying extent through competitive and feeding relationships, and generating up-trophic matter and energy transfers. Based on hydrogeologically-mediated geographic isolation and the intraecosystem intensity of biotic interactions, springs trophic structure in both arid and mesic regions can vary from simple systems that support a few widespread species to remarkably complex productive and dynamic systems (Odum, 1957; Blinn, 2008). Springs provide essential ecosystem goods and services, particularly fresh water in arid regions, and have exerted powerful influences on human evolution, and cultural and socio-economic well-being through time (e.g., Broad, 2006; Haynes, 2008; Gleick, 2010; Cuthbert and Ashley, 2014). However, all characteristics and processes of springs ecosystems can be appropriated, altered, eliminated, or created by indirect and direct anthropogenic activities. I use this conceptual model to organize the following sections in relation to the physical, biological, ecosystem process, human impacts, and stewardship of springs.

Hydrogeology and Geography

Source Waters

Groundwater expressed at springs sources is almost entirely derived from exogenic meteoric (atmospheric) precipitation (Figs. 1 and 2). Groundwater catchment basins develop in the context of regional and continental tectonics, which affect geologic structure and directs groundwater residence and flowpaths, and commonly range in area from < 1 to hundreds or thousands of km². Although generally mirroring surface catchment basins (Springer et al., 2017), notable exceptions exist in the Australian Great Artesian Basin (e.g., Ponder, 1986) and the North American Great Basin Desert. In the latter region, groundwater in the White River drainage in eastern Nevada, United States flows beneath at least three surface catchment basins before emerging in the Moapa River in the lower reach of this drainage system and then into the Virgin and Colorado River drainages (Thomas et al., 1996).

In temperate and high-elevation landscapes, snowmelt often is a primary source of groundwater, infiltrating and recharging local and regional aquifers (Fig. 2). In arid, lower latitude, and/or low-headwater settings, such as parts of North Africa, Australia, the North American Southwest, the Atacama Desert in central western South America, and elsewhere, groundwater is sourced from rainfall, with much recharge taking place in geologically structurally controlled stream channels, or exists in relictual paleo-groundwater aquifers that developed during Pleistocene or prior wet climate regimes. Depending on the region and setting, synoptic geology and structure, regional climate, and surface ecosystem characteristics, surface waters infiltrate into soils and subsurface strata. In arid and superarid environments, most precipitation is lost to evapotranspiration and only a small percent is available for groundwater recharge: Iorns et al. (1965) estimated that < 3% of precipitation was captured in aquifers in the arid Upper Colorado River basin in southwestern United States. Also contributing to groundwater supplies, a miniscule but geochemically informative quantity of connate (endogenic) water containing helium, carbon dioxide, and other compounds is derived from crustal degassing, and emerges from deep-aquifer springs (e.g., Crossey et al., 2009).

Limestone-dominated landscapes are renowned as settings in which groundwater moves through complicated pathways in the faults and fractures of karstic terrains, often with variable but short-duration residence times. Karstic terrain covers 12% of the Earth's surface, with many examples of highly productive aridlands karst springs (e.g., Huntton, 2000; Tobin et al., 2017;

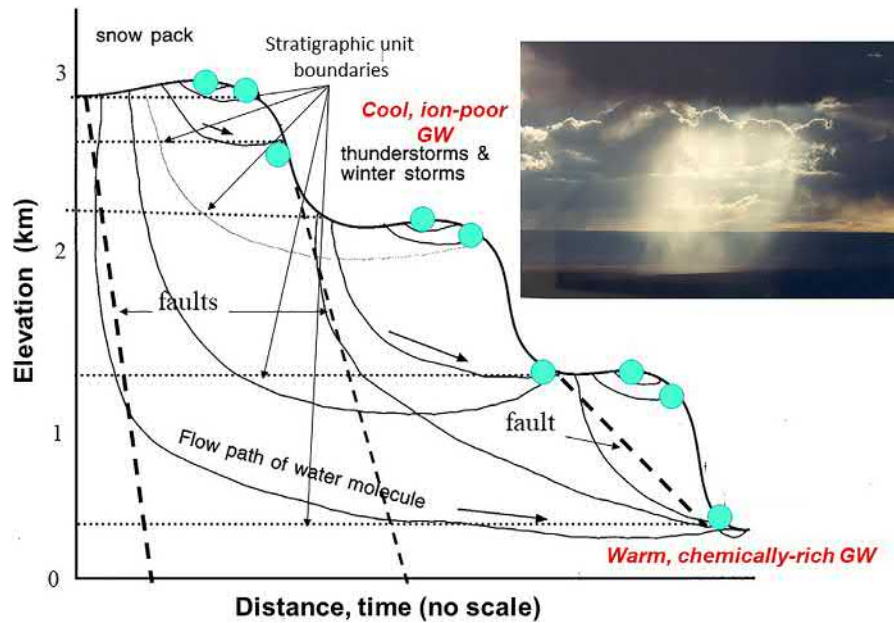


Fig. 2 A general illustration of groundwater infiltration and flowpaths. Springs (filled circles) can emerge wherever gravity and stratigraphic tilt causes groundwater to reach the surface.

Chen et al., 2017). Worthington (2007) opined that karstic aquifers were characterized by “triple porosity”, with contrasting flow and storage properties in the matrix, structural fractures, and channels. His triple porosity karst aquifer model differs from other models that emphasize a range of flow from conduit to diffuse storage. Additional modeling complexity arises in karstic terrains with stacked aquifers and varying porosity and infiltration in relation to geologic structure. In such settings, normal concentration-overburden-precipitation groundwater modeling is improved by incorporating geographic information on non-randomly distributed, point-sources of infiltration, such as sinkholes and estavelles (Jones et al., 2019).

Ecosystem Structure and Classification

Springs emerge in a diverse array of forms and settings, a complexity that despite much excellent research on springs hydrogeology has long-eluded comprehensive classification (Stevens et al., in press). Steinmann (1915) and Thienemann (1922) recognized three types of springs by the velocity of water emerging from the source: lentic pool-forming limnocrenes, lotic flowing rheocrenes, and wet meadow or marshy helocrenes. These three “spheres of discharge” (sensu Meinzer, 1923) describe how springs flow emerges (the realm of interest of most hydrologists), but do not incorporate the surface linkage and related landforms and habitats that constitute the full subsurface-surface linked springs ecosystem (the realm of interest of ecologists; Cantonati et al., 2020). As a consequence, the lexicon used to describe springs has been largely based on physical hydrogeological properties or societal uses, rather than on the principles of ecosystem ecology, and have failed to provide unambiguous classification of the great array of springs ecosystem types that exist on Earth.

Springer and Stevens (2009) and Stevens et al. (in press) used source and outflow geomorphology and ecosystem ecology to propose 13 major types of terrestrial springs. Their classification, illustration, and dichotomous key distinguishes among these springs ecosystems, including: simple exposure of the groundwater table; cave springs; geysers; gushets (madicolous flow cascading down cliff faces); fluvial, upland, and blister wetland wet meadow helocrenes; ice hill (i.e., pingos), organic, and carbonate mound forms; floodplain and upland hillslope springs; artesian fountains; hanging gardens (Welsh, 1989); hypocrenic expressions of groundwater through wetland vegetation; pool-forming springs (limnocrenes); springs emerging in stream channels (rheocrenes); as well as no-longer-flowing paleocrenes. Those authors note that many springs have dominant and also subdominant typology (e.g., a gushet emerging in a hanging garden), and that English adjectival attribution of secondary and sometimes tertiary types was appropriate (e.g., a natural pond in a wet meadow spring is a limnocrenic helocene), but they recognize that such linguistic subtleties may be more awkward in other languages.

Nearly all of the springs types mentioned above exist in aridland and mesic environments, perhaps excepting natural geysers, nearly all of which occur in mesic environments, such as Yellowstone National Park in Wyoming and New Zealand (e.g., the Rotorua geothermal field). Another exception, hanging gardens are perhaps best represented in arid, largely geologically undeformed sandstone-dominated landscapes, such as those in southern Utah and northern Arizona. Biotic analyses among springs types reveal characteristic patterns of vegetation habitat structure and composition, as well as human uses (e.g., Sinclair, 2018). The geomorphic configuration of springs ecosystems at and downstream from the point of emergence results in ecological

differentiation of their biotic assemblages and their human uses and impacts, and much research is needed to more clearly distinguish these characteristics and processes to improve springs stewardship in both arid and mesic environments.

The above authors also note that any springs type can be created or altered through anthropogenic manipulation of flow or of site geomorphology. Abandoned artesian well bores can produce fountains or even geysers (e.g., the Tecopa Bore in California, [Wamalwa et al., 2011](#); Crystal Geyser in central Utah, [Han et al., 2013](#)). Another common anthropogenic springs manipulation throughout the world involves excavation of ponds for livestock watering in wet meadows, creating anthropogenic limnocrenic helocrenes. Sewage effluent-fed streams have become common urban features (e.g., Las Vegas Wash in southern Nevada), often functioning as hillslope or rheocrene springs. Also, the release of water from a dammed stream or river can be regarded as an anthropogenic rheocrene, ecological alterations that exert potentially large impacts on downstream ecosystem ecology (e.g., [Ward and Stanford, 1983](#)). A cave-like excavation into a cliff-emerging springs source to focus flow is called a “qanat”, a common feature throughout the world. In relation to springs classification, [Stevens et al. \(in press\)](#) recommended that human-created springs be classified based on their ecological function, with the modifying term “anthropogenic” applied as a secondary or tertiary adjective.

Geomorphic Microhabitats

Adding to their geomorphic and biological diversity, springs ecosystems often are composed of complex mosaics of microhabitats. Springs ecosystems, such as large hanging gardens or gushets may support a dozen microhabitats, each of which support discrete, sometimes interacting assemblages of flora and fauna ([Stevens et al., in press](#)). Common microhabitat types encountered include channels and terraces, pools, wet walls, and source caves. While different suites of these geomorphic microhabitat landforms are characteristic of specific springs types, each microhabitat has properties that influence its biological colonization and development, and each can undergo microhabitat-specific changes over time, such as the development of travertine dams. The colonization history and variation in the microhabitat array contribute to the high levels of individuality recognized for these generally small, but often complex ecosystems. However, insufficient within-springs inventory data exist at present to determine differences between microhabitat arrays in arid versus mesic landscapes.

[Stevens et al. \(2016b\)](#) proposed calculating springs geomorphic complexity using the Shannon-Weiner diversity metric ([Shannon, 1948](#)) based on the number and relative area of springs-associated microhabitats, and [Springer et al. \(2015\)](#) and [Sinclair \(2018\)](#) demonstrated positive correlations between geomorphic diversity and plant species richness at springs in both arid and semi-arid landscapes in mesic and arid portions of western North America, respectively. Additional analyses are needed to clarify the relationships between geomorphic and biological diversity within and among springs types.

Springbrooks (springs runout channels) are among the most prominent springs microhabitats. Usually driven by gravity, groundwater is exposed at the Earth’s surface at springs, often flowing across the land and merging with other aquatic ecosystems. Springbrooks and their associated riparian and peripheral environments are defined as springfed stream channels that are more strongly influenced by springs flow than by surface flow. The length of the springbrook can be defined as the point at which surface processes begin to dominate over the springs influences on the channel geomorphology and habitat, and as the point at which a “zero order” springs channel becomes a first order stream (sensu [Strahler, 1957](#)). Springbrooks typically are linear-erratic, slightly incised channels ([Griffiths et al., 2008](#)), extending downstream to where surface flow-influenced channel meandering, terrace formation, and other characteristic stream geomorphic landforms become apparent, along with changes in biodiversity ([Stevens et al., 2005](#); [Dumnicka et al., 2013](#); [Morrison et al., 2013](#)).

Geography: Abundance and Density

Springs are abundant on Earth, occurring both on land and in submarine settings, but the absolute number and density of springs varies enormously among countries and continents ([Fig. 3](#)). Close examination of distribution maps indicates that springs emerge in greater density in topographically complex landscapes. In the case of the United States, springs density is high in the major mountain ranges (Appalachian, Ozark, Sierra Nevada, and Rocky Mountain Ranges), but relatively low in flatlands, such as the southern Great Plains. This is intuitive, because springs are more likely to emerge where strata are tiled and aquifer edges are exposed in escarpments and mountain ranges ([Stevens and Meretsky, 2008](#)).

Estimates of springs abundance on Earth have ranged up to 50 million, but systematic mapping data are not available for most regions and continents (e.g., particularly Asia, Africa, and South America). [Glazier \(2014\)](#) presented data on terrestrial springs density from around the world that can be used to crudely estimate overall density and test whether springs density/km² varies between arid and semi-arid, versus mesic and humid landscapes. His data indicate that springs density is generally low but is spatially highly variable (median = 0.01 springs/km², $N = 42$ landscapes, 1 sd = 0.79 springs/km²). Due to the high variance among landscapes and the 30-fold difference between median and average density (0.30/km²), global springs density values, tripling the estimated grand median value to 0.03 springs/km² produces a conservative prediction of 2.5 million terrestrial springs on Earth (planview land area = 1.48×10^8 km²). Although a large number, it is more than an order of magnitude lower than some previous estimates of springs abundance on Earth.

Much of the reason for the large uncertainty in springs density involves variation in the accuracy of mapping data, which often are incomplete and inaccurate, even in developed nations such as the United States, and which is abundantly apparent between regions and nations ([Fig. 3](#)). For example, previously published data on the abundance of springs in Nevada, the US’s driest state,

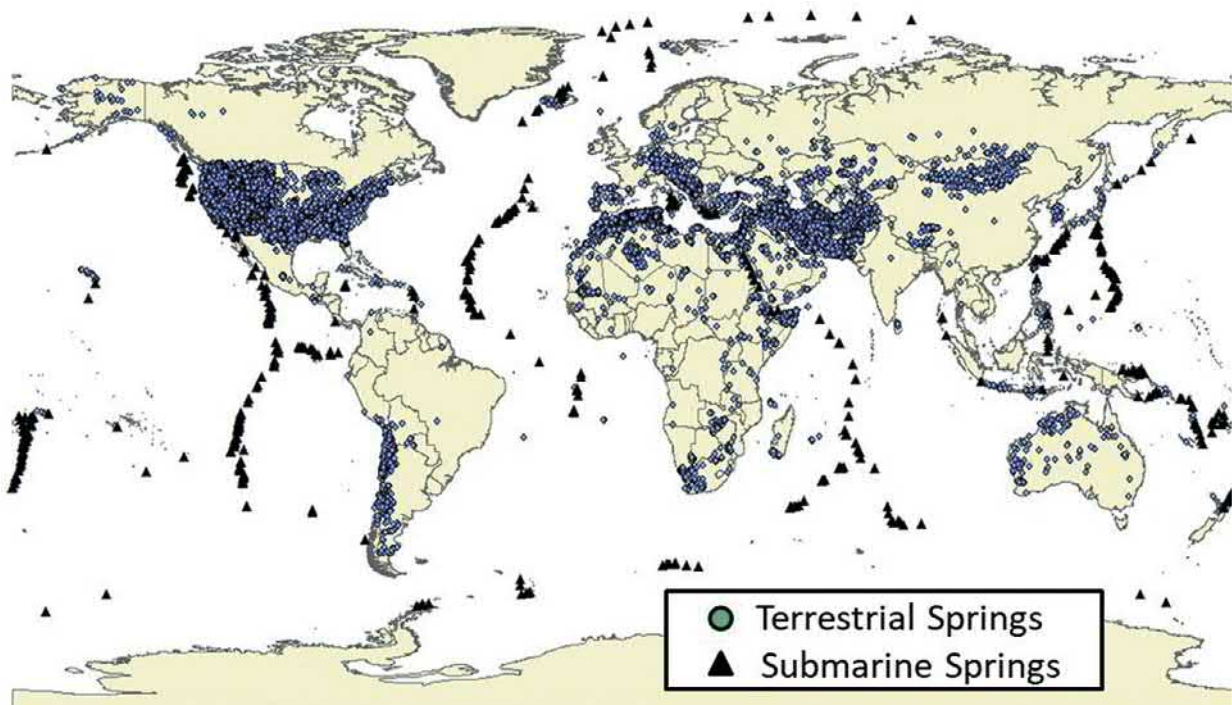


Fig. 3 A preliminary map of global springs distribution. Differences among countries are largely due to the quality and availability of mapping data.

indicated that 4179 springs existed there (Glazier, 2014). Over the past decade, the Museum of Northern Arizona's Springs Stewardship Institute (SSI 2019) mapped and inventoried many Nevada springs, and now reports an estimated 27,000 Nevada springs, a density of 0.095 springs/km² and 6.5-fold more than previously reported (Fig. 4). Nevada presently has the highest density of springs in the United States (SSI 2019), a result of the many hundreds of Basin and Range Geologic Province mountain ranges with likely thousands of small aquifers that characterize the state. Intensive springs inventory programs elsewhere in the Great Basin similarly have greatly increased the number and density of springs in large landscapes (e.g., Junghans et al., 2016). Profundal seafloor springs are primarily distributed along tectonic spreading ridges, although coldwater submarine seeps also have been

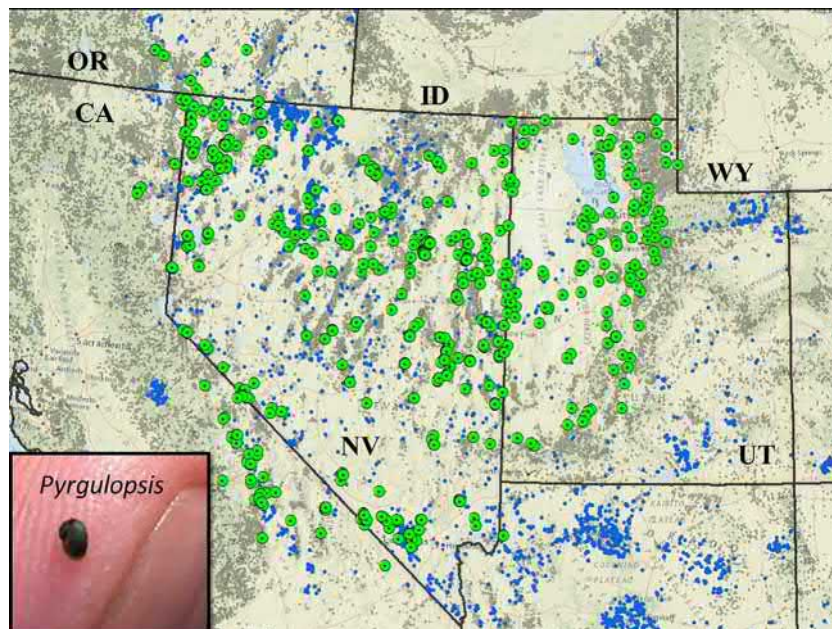


Fig. 4 Springs of the Great Basin, United States, including those known to support tiny but often highly locally endemized springsnail species, such as *Pyrgulopsis* (inset), more than 120 species of which exist, primarily in one or only a few North American springs (Hershler and Liu, 2017).

identified (Joseph, 2017). In contrast, springs density estimates decrease by an order of magnitude or more in tectonically quiescent regions, such as the American Great Plains (Stevens and Meretsky, 2008), although prairie pothole exposure springs are abundant in the central and northern Great Plains (Van der Valk, 1989).

Springs density can be expected to be greater in more humid regions. Glazier's (2014) data indicate a trend supporting this premise: springs density in mesic regions (median = $0.019/\text{km}^2$, $N = 24$, 1 sd = 1.007) was 2.5-fold greater than that in arid and semi-arid regions (median = $0.007/\text{km}^2$, $N = 18$, 1 sd = 0.042). However and again, high levels of spatial variability and inconsistent mapping data obscure the significance of this pattern, and more accurate regional and national springs inventories are needed for a more complete test of this basic assumption.

Discharge

Springs and seeps are abundant in many landscapes and contribute substantially to local and national water budgets throughout the world (Glazier, 2014). Some of the Earth's largest terrestrial springs include: mesic New Zealand's South Island Te Waikoropupū Spring (average discharge = 1.4×10^4 L/s); and large aridland Northern Hemisphere springs, such as Syria's Ra-El-Ain Spring (average discharge, $Q = 3.63 \times 10^4$ L/s) and Turkey's Dumanli Spring (average $Q = 5.03 \times 10^4$ L/s; Karanjac and Günay, 1980; Alfaro and Wallace, 1994). At least five large European and African cities rely virtually exclusively on large springs for urban water supplies (Stevanovic, 2010; Glazier, 2014; Stevens et al., in press); and other large springs are described in Meinzer (1927) and Stevanovic (2010). However, most springs produce little flow, generally between 0.1 and 1.0 L/s, and many desert springs are ephemeral, flowing only seasonally or only after wet periods. The following examples illustrate these patterns. (1) A recent inventory of 97 springs in Nevada reported that the mean Q was 0.2 L/s, with a maximum Q of 186 L/s at one site (SSI 2019). (2) In one of the few comprehensive national analyses, Pérez (1996) summarized the flow of springs in Spain, reporting a grand median Q from more than 25,000 springs of 0.7 L/s and a grand mean $Q = 12$ L/s. Those data indicated that 24,500 (98%) of the springs had flows < 35 L/s but those springs produced only 45% of the cumulative discharge, while the remaining 2% of springs contributed more than half of that nation's springs flow. (3) Stevens et al. (2016a) examined springs discharge in Arizona, reporting a grand median Q of 0.14 L/s and a grand mean of 19.8 L/s among 1342 springs. Extrapolating from those flow data to the state's estimated 10,300 reported springs suggested that springs produce 17,176 L/s ($542 \text{ km}^3/\text{year}$) of discharge, roughly 6% of the 2012 state water budget. Arizona springs are used to support wildlife, livestock production and other agricultural activities, as well as providing domestic and some urban water supplies. (4) The single, small Wittmer Spring on the arid Galápagos Island of Floreana (ca. 0.5 L/s) has been the primary source of freshwater and social intrigue since its discovery in the late 18th Century (e.g., Treherne, 2002). (5) Many springs, large and small, are ephemeral, a flow pattern recognized by Glazier (2014) as "sipeocrenic". For example, La Fontaine Spring flows seasonally and erratically, providing baseflow for the La Morgue River in France (Stevens et al., in press). Thus, large springs (median $Q > 500$ L/s) make up far fewer than 1% of the total global population of springs, but those springs are unquestionably important water sources. However, the vast number of much smaller springs provide critically important local sources of water for biodiversity and for many human populations, particularly in arid regions.

At present global terrestrial springs discharge estimates are extremely crude. However, if 98% of the Earth's estimated 2.3 million terrestrial springs have a median discharge of 0.1 L/s, they would produce approximately 7.1 km^3 of water/year. If that is half of the Earth's total terrestrial springflow, and 2% of the springs are large and contribute half again as much flow, I very conservatively estimate that terrestrial springs produce at least $10.7 \text{ km}^3/\text{year}$ of freshwater discharge; however, I recognize that the total global discharge could easily be twice that estimate. Clearly, many more data are needed to provide a more accurate estimate.

Water Quality

Water quality (temperature and geochemistry) changes as water infiltrates through the soil and passes into the subsurface environment, where it is affected by latitude, elevation, bedrock geology, infiltration pathways, aquifer geology, emergence forcing mechanisms, and flowpath duration. Variation in the quality of groundwater emerging from springs is generally low, while variation among springs is enormous, and much variation in water quality can exist within individual aquifers, such as the large Coconino aquifer in northern Arizona (Bills and Flynn, 2003). Springs water quality can affect the source geomorphology (e.g., at mineral-depositing springs, or through channel formation), its biotic assemblage composition and diversity (e.g., Sinclair, 2018), as well as human uses and the impacts we exert upon them (Figs. 1 and 2).

Springs water temperature characteristics have been described and summarized primarily in relation to mean annual air temperature, ecology, or human sensation, and range from near freezing to hyper-thermal sea floor vent springs (e.g., Waring, 1965; Alfaro and Wallace, 1994; Springer et al., 2008; Glazier, 2014; Stevens et al., in press). Groundwater temperatures in non-thermal and warm springs generally reflect residence time and flowpath length (Fig. 2), and influence food chain length (Glazier, 2012). Shallow, high elevation aquifers in both arid and mesic landscapes generally express cool to cold, low ion content water temperatures, reflecting cooler ambient conditions and short flowpaths and residence times. Low elevation aridland springs generally express warmer, mineralized water temperatures due to ambient climate, often longer flowpaths, and protracted duration of flow travel times (e.g., Thomas et al., 1996; Johnson et al., 2012). However, karstic terrains across latitude and elevation often are characterized by rapid passage of infiltrating water and delivery of cooler waters to lower elevations, such as occurs in springs emerging from the Redwall Aquifer in northern Arizona (Tobin et al., 2017). In contrast, geothermal conditions reflect groundwater interaction with magmatism, and potentially rapid, pressurized movement of groundwater through aquifers. Many thousands of

geothermal springs have been developed globally for recreational and therapeutic uses, making it increasingly difficult to find undeveloped sites at which to study hot springs ecosystem ecology (but see Brock, 1978; Morrison et al., 2013).

Springs geochemistry studies have identified a wide array of important ion constituents and water quality variables that characterize springs water quality, including borate, calcium, carbonate, chloride, dissolved oxygen, magnesium, methane, potassium, rare earth elements, silica dioxide, sodium, stable isotopes, sulfate and sulfide, nutrients, and combinations thereof, as well as alkalinity, bacteriology, biological oxygen demand, nutrients, pH, turbidity, water color (Peale, 1886; Palmer, 1911; Clarke, 1924; Fitch, 1927; Meinzer, 1927; Futak and Langguth, 1996). Futak and Langguth (1996) classified Greek springs as: normal earth alkaline hydrogen-carbonatic; normal earth alkaline, hydrogen-carbonatic-sulfatic waters; and enriched alkali earth alkaline hydrogen-carbonatic waters. Geochemical analyses have been successfully used to describe aridland karstic springs (e.g., Shuster and White, 1971; Bonacci, 1993; Huntoon, 2000; Crossey et al., 2009; Hershey et al., 2010; Springer et al., 2017), but those studies do not illuminate differences among humidity provinces. The factors that affect springs water temperature (above) also generally affect geochemistry, so that lowland aridland springs are more likely to be mineralized than those at higher elevations (e.g., Ledbetter et al., 2016); however, global characterization of geochemical differences between arid and mesic regions remains outstanding due to complex interactions in relation to tectonism, geologic province, as well as latitude, landscape position, regional geology and climate, springs type, and a host of other locally important variables.

Although groundwater passage results in geochemical alteration of the water, the oxygen and hydrogen isotopes of the original surface precipitation are conserved, allowing groundwater age and residence time to be estimated. However, springs flow is typically comprised of both longer-distance, as well as locally-recharged groundwater, complicating the dating of the emerging water. Nonetheless, groundwater age analyses show that groundwater flowpath duration ranges from <0.01 to 10^6 year, with long flowpaths of paleowater noted in arid regions (e.g., Ponder, 1986 in the Great Artesian Basin of Australia; Thomas et al., 1996 in the North American Great Basin Desert).

Habitat and Area

Springs habitat area includes the area of open water, wetlands, and riparian lands directly influenced by springs. Open water pool, stream, and cascading habitats each can support discrete biotic assemblages, which also transition downstream to the point that surface flow begins to dominate stream processes (e.g., Morrison et al., 2013). Open water habitat often makes up only a small percentage of the overall landscape influenced by groundwater emergence in springs ecosystems, the exceptions being limnocrenes and some rheocrenes and mound springs. Most springs habitat area is dominated by saturated or moist soils, generating some to much wetland and riparian habitat. The percent of open water habitat is likely somewhat less at aridland springs due to higher productivity, vigorous emergent plant growth, and greater evapotranspiration rate; however, thorough analyses of such microhabitat relationships require far more data than currently are available. Nonetheless, springs-supported wetland and riparian habitats are of primary importance as habitat for both springs-dependent and upland species as sources of habitat and food, particularly in water-limited arid regions. Depending on springs type, riparian plant zonation (and likely that of other biota) occurs in a radiating pattern, changing outwards from the source from aquatic to wetland to peripheral riparian to upland species composition (likely tightly related to xylem water potential characteristics of the plant species present; Merigliano, 2005). Vegetation structure, and function also are strongly dependent on springs type (Sinclair, 2018). For example, (1) marshy helocrenes tend to be dominated by wetland graminoids, and riparian herbs and shrub species in both arid and mesic regions; (2) hanging gardens are occupied by a distinctive flora of tightly adapted and endemic species; and (3) arid regions support helocrenic palm oases, but not swamp forests.

Individual springs occupy a median area of approximately 0.05 ha in Nevada, cumulatively occupying up to a maximum of 0.004% of the land area of that state (SSI 2019), and likely no more than 0.005% of the entire coterminous US land surface area. Thus, despite their considerable influence on local ecology across the terrestrial world, the total habitat area of springs is extremely small. However, few data are available to determine whether springs area differs in mesic as compared to arid regions. Overall, springs make up only a tiny fraction of the planet's arid as well as mesic surface area, but as described below, they exert a disproportionately large influence on the world's bio-cultural ecology than would otherwise be predicted based on their generally small flow and habitat area.

Springs Biology

Biogeography

Springs function as insular patches of habitat, and therefore are natural laboratories in which to examine the role of passive and active biogeographic processes. Assemblage comparisons of passively dispersing biota at springs indicate that some taxa are prone to orderly biogeographic patterns of colonization, while others are not. For example, Kodric-Brown and Brown (1993) and Ríos-Arana et al. (2018) reported highly structured Australian fish and Chihuahua Mexico rotifer assemblages, respectively, with strong patterns of assemblage nestedness. Nielson et al. (2019) reported analogous patterns of nestedness in non-native weedy plant colonization of springs in Alberta, Canada. In contrast, Weissinger et al. (2012) reported only weak nestedness among macroinvertebrates in Utah sandstone springs. Thus, at least in some cases, interactions between isolation and patch size influence species richness and assemblage characteristics.

In contrast to passively-dispersing organisms, larger volant and non-volant invertebrates and vertebrates engage in non-random habitat selection of springs. This is readily apparent among predators ranging from aquatic beetles to large predators and humans using springs as ambush sites (e.g., Haynes, 2008). For example, I found 10 species of aquatic predaceous beetles in an extremely isolated, 1 m² *Canis latrans*-excavated exposure springs (a “coyote pozo”) at the head of the Gulf of California. Many aquatic predatory insects actively search for rare freshwater habitats in arid regions, arriving singly or in large flocks (e.g., Stevens et al., 2007). Additionally, migrating avifauna and other volant and non-volant terrestrial organisms in arid regions may preferentially use lacustrine, palustrine, stream, and springs habitats as stop-over or stepping stone habitats, and are at risk under a drying climate in landscapes such as the arid Great Basin in western North America (Haig et al., 2019). Also, the role of springs water quality in larval fish imprinting and spawning migration is recognized and exploited among salmonids (Ueda, 2011), and may be widespread among other freshwater and anadromous fish taxa. Understanding such processes may increase appreciation of the role of springs within watersheds.

Springs-Dependent Biodiversity

Springs are widely regarded as hotspots of biodiversity that support rare, endemic, and often critically endangered springs-dependent (crenobiontic) species (e.g., Williams and Danks, 1991; Botosaneanu, 1998; Ponder, 1986; Fensham and Fairfax, 2003; Unmack, 2001; Cantonati et al., 2007; Unmack and Minckley, 2008; Martens et al., 2010; Rossini et al., 2018; Stevens et al., in press). Endemism within aridland springs is particularly renowned, including that of diatoms, invertebrates (e.g., truncatelloidean springsnails; Hershler et al., 2014), and fish (e.g., Unmack, 2001; Minckley and Unmack, 2008; Rossini et al., 2018). For example, the Great Basin White/Moapa River drainage with its long, slow deep-aquifer springs sourcing, collectively supports at least 30 endemic and rare invertebrate and fish species (e.g., Hershler and Liu, 2017; Southern Nevada Water Authority, 2019).

Phylogenetic research has revealed the hydrobiid aquatic springsnail assemblage of Death Valley, California has arisen due to periodic post-Miocene habitat connectivity stemming from repeated endorheic lake expansion and contraction, coupled with erratic dispersal events (Hershler and Liu, 2008). Such studies demonstrate the extent of environmental change over geologic time that results in high levels of endemism in aridland springs.

While an exhaustive list of the world’s springs-dependent and endemic species remains outstanding, several regional studies indicate the existence of hundreds to thousands of springs-dependent taxa globally, with a disproportionately high percentage of those species found in aridland springs. Among existing literature, the following taxa and examples have been shown to be reliant on springs, particularly in arid regions:

- Plants
 - Diatoms (e.g., Lai et al., 2019)
 - Vascular plants (e.g., Texas Wild Rice (Poaceae: *Zizania texana*), endemic to the San Marco River); flowering shrub (*Flaveria mcdougallii* (Asteraceae), endemic to alkaline springs in central Grand Canyon, Arizona); Australian endemic springs plants and assemblages (Rossini et al., 2018; Australian Biological Resources Study, 2020)
- Platyhelminthes flatworms (Schockaert et al., 2008)
- Gastropoda (e.g., Hydrobiidae springsnails; Ponder, 1986; Hershler and Liu, 2017)
- Arthropoda
 - Crustaceans—subterranean freshwater Isopoda, surface-dwelling Anostraca, Amphipoda (e.g., *Hyaella* spp.), and microcrustaceans (e.g., Ríos-Arana et al., 2018)
 - Chelicerata—aquatic mites, spiders (e.g., Gerecke and Di Sabatino, 2007)
 - Insecta—Odonata (Stevens and Bailowitz, 2009), Ephemeroptera, Plecoptera, Hemiptera (e.g., Belostomatidae, Naucoridae, Nepidae; Stevens and Polhemus, 2008), Coleoptera (e.g., Dryopoidea; Shepard, 1993), Diptera, Trichoptera
- Fish—Goodeidae, Cyprinodontidae, and Cyprinidae in the United States (Minckley, 1973; Sigler and Sigler, 1986); Plotosidae, Gobiidae, Eleotridae, and Atherinidae in Australia (Unmack, 2001; Rossini et al., 2018)
- Amphibians—e.g., Barton Springs Salamander (*Eurycea sosorum*) in Texas, Relict Leopard Frog *Lithobates onca* in Nevada
- Reptiles—several southwestern US *Thamnophis* garter snakes (Brennan and Holycross, 2006)
- Mammals—Preble’s meadow jumping mouse (*Zapus hudsonius preblei*; Trainor et al., 2012), Amargosa vole (*Microtus californicus scirpensis*)
- Birds—American Dipper (*Cinclus mexicanus unicolor*), which commonly nests behind springfed waterfalls in the Southwest (Stevens et al., in press).

Springs Assemblages

Depending on springs type, location, landscape context, and adjacent biome interactions, springs biotic assemblages can be highly dynamic, or can be remarkably constant habitats, supporting closely adapted and highly endemized faunal assemblages. Nekola (1999) distinguished between weedy species-dominated neorefugia versus long-term stable paleorefugia, which exist for evolutionarily significant time periods and support relict assemblages. Paleorefugial springs include many stable, deep-aquifer springs in arid regions that support high concentrations of unique and rare species (e.g., Montezuma Well in Arizona, Blinn, 2008; Ash Meadows

in Nevada, [Patton et al., 2008](#); Cuatro Ciénegas in northern Mexico, [Unmack and Minckley, 2008](#); Dalhousie and other mound springs in Australia, [Ponder, 1986](#)).

Deep-aquifer/long flowpath paleoregional springs have sufficient stability over evolutionary time to allow the interaction and evolution of complex assemblages of highly endemized taxa. Montezuma Well in central Arizona is a 17 m-deep, 120 m-wide, highly mineralized, fishless, collapsed carbonate mound spring pool. It supports high algal primary productivity, and an endemic amphipod, *Hyalella montezuma* ([Blinn, 2008](#)). During the daylight hours the amphipod serves as prey for three taxa of predatory insects (including one endemic water scorpion), which occupy the vegetated margins of the pool. To avoid these visually-feeding insects the amphipod population moves out to the center of the pool during the day. At night, four species of leeches (including the endemic genus *Motobdella*) swim up from a zone of benthic floc to feed on amphipods they detect in the water column, chasing the amphipods back to safety of the margin vegetation. Thus, predation pressures cause the planktonic amphipods to undertake a remarkable daily migration. With at least six endemic species, Montezuma Well has the highest concentration of unique species in any single springs ecosystem in North America, to my knowledge. Naturally high concentrations of arsenic there may facilitate the evolution of endemism, a process that warrants further study ([Compton-O'Brien et al., 2002](#)). However, all of that ecosystem's endemic species are invertebrate animals, and except for a single diatom species, no endemic plant taxa exist there. The pattern of substantially greater levels of localized endemism among springs invertebrates than among vascular plants is apparent throughout North America, Europe, and Australia, and points to substantial differences in gene flow patterns and evolutionary processes between plants and animals.

Although the composition and structure of springs vegetation has been widely accepted as a monitoring metric, vegetation dynamics are largely a function of springs type ([Sinclair, 2018](#)). Slope angle, flow perenniality, and scour frequency all vary with springs type, limiting the utility of vegetation as a metric of ecological integrity in some hillslope and gusset springs, and most rheocrenes. For example, wetland vegetation cover at one gusset I studied in Grand Canyon varied from 20% to 90% over a three-year period due to rockfall and flood scour ([Grand Canyon Wildlands Council, 2004](#)). Such variation is perhaps more likely to exist in aridland springs, where storm intensity and frequency are highly variable. Therefore, while useful for less disturbed sites, springs vegetation cover may not be universally useful as a monitoring metric.

Non-native species are commonly encountered at springs and have been the subject of considerable concern in the conservation and restoration of springs and native endemic SDS. Intuitively, one would expect that springs habitats that are strongly dominated by native vegetation would be resilient to invasion by non-native plant species; however, the great dispersal capacity of many weed species means that even slight natural or anthropogenic disturbances at springs that expose moist soil provide habitat for non-native plant establishment. Thus, non-native plant species like several grasses (Poaceae), salt-cedar (*Tamarix* spp), Russian olive (*Elaeagnus angustifolia*), proliferate at springs, and non-native plant species richness often appears to be positively correlated with the richness of native species (e.g., [Stevens and Ayers, 2002](#)). Non-native fauna that may negatively affect native faunal SDS in the American Southwest include: *Potamopyrgus antipodarum* New Zealand Mudsnails, *Melanoides tuberculata* Red-rimmed Melania freshwater snails, cambarid crayfish (e.g., *Procambarus clarkii*), *Lithobates catesbeiana* American Bullfrogs, a large assemblage of non-native aquarium and game fish species ([Sada, 2008](#)), as well as managed and feral livestock. Oftentimes, environmentally eurytolerant non-native species are able to colonize habitat occupied by steno-adapted SDS, making the invaded springs habitat far more competitive for the native species. But in contrast, non-native species are not always necessarily detrimental to endemic SDS. For example, growing evidence indicates a positive relationship between native, highly endemized truncatelloidean springsnails and non-native watercress (*Nasturtium officinale*) throughout the United States.

Ecosystem Ecology

Ecological Roles of Springs

Springs play important ecological roles in many of the landscapes in which they exist, including providing critical flow, water quality and other habitat components, and ecosystem goods and services, all of which are of elevated importance in arid regions. Our studies indicate that every natural stream in non-ice-dominated landscapes on Earth, and particularly those in arid and low-headwater regions, is sourced by springs, helocrenes, or from lakes, many of which also are limnocrenic ([Junghans et al., 2016](#); [Miller et al., 2016](#)). [Gomi et al. \(2002\)](#) and [Stevens et al. \(in press\)](#) recognize that springs are fundamentally important in stream networks, with the latter authors recommending that springs be considered as “zero order” streams (sensu [Strahler, 1957](#)), playing an essential sourcing role in surface water ecology. However, aridland springbrooks often are losing systems, flowing for limited, potentially seasonally varying distances before sinking back into the ground. Disconnection from downstream waters can protect desert springs from invasion by non-native aquatic species, such as exotic crayfishes, amphibians, and released aquarium and game fishes. Thus, from a conservation standpoint, interrupted habitat connectivity may be a highly advantageous, natural characteristic of aridland springs.

Despite their generally small discharge, springs ecological function and habitats constitute an enormous but largely overlooked role in synoptic upland and stream ecology in both arid and mesic environments. Springs have been described as keystone ecosystems, small but highly ecologically interactive ecosystems, without which both internal (allochthonous) and synoptic upland (allochthonous) ecological activity and processes are reduced or lost ([Perla and Stevens, 2008](#)). Their study revealed high levels of inter-ecosystem interactivity around Seaman Spring in arid southern Utah. That ecologically attractive and interactive aridland habitat patch generated extensive autochthonous carbon while also providing habitat and food resources for upland biota. While

such measurements are rare, I predict that the keystone ecosystem function is a much more prominent characteristic of arid land springs than it is in regions with higher levels of humidity, where water is less of a limiting resource. Strong differences in the ecological roles of springs likely exist in arid versus mesic environments, and in the role of springs in relation to uplands across climate zones and under changing climates. Of particular interest, climate change adaptation requires recognition of the role of springs as potential refugia, and whether and how these ecosystems will respond to increasing environmental stress (Cartwright et al., 2020).

Trophic Complexity

Lindeman's (1942) concepts of ecosystem ecology were ground-truthed at Silver Springs in Florida (Odum, 1957), but springs ecosystem ecology has been tested at relatively few other sites, which typically are limnocrone, mound, or geothermal springs. If sunlight is not obstructed by cliff walls, overhanging rocks, or tree cover, the net annual primary productivity (NAPP) of the aquatic domain of a springs ecosystem can exceed $5 \text{ kg C/m}^2/\text{year}$, equal to or exceeding the gross annual primary productivity of adjacent wetlands (Odum, 1957; Blinn, 2008; Threvis et al., 2007). Terrestrial geothermal springs, and even chemautotroph-driven seafloor vent springs also show remarkably high levels of NAPP (e.g., Brock, 1978; Morrison et al., 2013; McNichol et al., 2018). In contrast, NAPP in arid lands is commonly 2–3 orders of magnitude lower, and in harsh, virtually rainless settings, such as the Chilean Atacama Desert, may be virtually zero. Thus, a key defining feature of aridland springs is the steepness of the moisture gradient from the springs into the adjacent uplands. A linear distance of less than a meter and an elevation rise of only a few centimeters above the water surface may be sufficient to transform: NAPP, soil temperature, quality, and nutrient availability; vegetation composition, zonation, structure, and function; faunal composition; and springs-upland eco-interactivity across the aquatic to xeric moisture gradient.

Although poorly studied, springs in humid regions are expected to demonstrate much shallower environmental gradient slopes, with only gradual upslope transitions in those variables, relatively low dissimilarity between springs riparian and upland vegetation characteristics, and lower faunistic differences and springs-uplands interactivity. Springs ecological interactivity overall, and whether the springs-to-uplands environmental gradient steepness is continuous or is subject to thresholds in arid versus humid landscapes remain important research topics, particularly in the face of changing climate.

Subsidy Exchange

Subsidy exchange in springs involves consideration of all matter and energy interactions and NAPP across space and time, of which the carbon budget can serve as a suitable surrogate (e.g., Foley et al., 1996; Figs. 1 and 5). With solar energy as the primary source of energy, terrestrial springs receive allochthonous organic carbon and nutrients through atmospheric, gravity and animal-transported (including invertebrate and vertebrate) sources from adjacent upslope, lateral, atmospheric, and upwelling groundwater sources. Springs internally produce aquatic and riparian autochthonous carbon, recycling it, and potentially exporting it laterally, downstream through the springbrook, vertically into the atmosphere, into adjacent riparian soils, and into the hyporheic zone, as

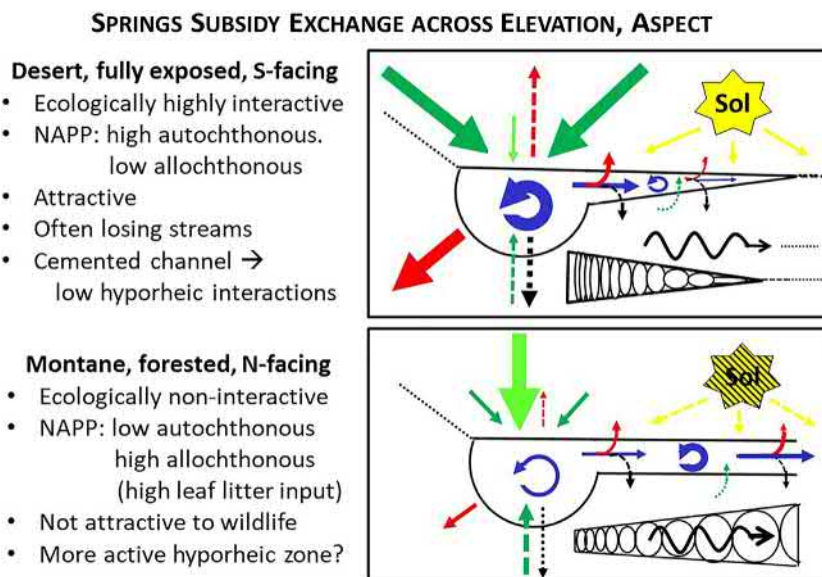


Fig. 5 A conceptual model of ecological subsidy exchange in aridland springs. (Upper graph) a low-elevation or south-facing upland hillslope springs ecosystem that is not shaded by cliffs or forest canopy. (Lower graph) a high elevation or north-facing upland hillslope springs ecosystem that is heavily shaded by forest canopy or by adjacent cliffs. Line widths indicate relative strength of effect, and diagonal lines represent lateral subsidy exchange, whereas vertical lines indicate atmospheric or hyporheic exchange.

well as a tiny fraction that may be returned into the aquifer. As mentioned above, the steepness of the moisture gradient in aridland springs distinguishes them from the gradient slopes in humid regions; however, aridland springs occur in a wide array of geologic, geomorphic, elevation, and climate settings, in open as well as heavily shaded environments. While upland allochthonous NAPP and C inputs may be relatively low in arid regions, unshaded aridland springs in unforested, open settings with unobstructed direct solar radiation have increased autochthonous NAPP and nutrient spiraling, extending downstream through the springbrook (Fig. 5A). However, desert springbrooks often are truncated as losing streams, with decreasing aquatic NAPP and trophic exchange over distance, and also often with carbonate-cemented channel floors that limit hyporheic interactivity (Fig. 5, upper graph).

In considerable contrast, sunlight-limited, shaded, north-facing, forested springs at higher elevations have reduced growing season length and consequently relative autochthonous carbon exchange and NAPP may be greatly reduced. In such springs, nutrient spiraling and productivity of the springbrook may remain equal or increase over distance downstream, and hyporheic zones may often remain interactive due to the general absence of channel floor cementation (Fig. 5, lower graph). Aquatic macro-invertebrate and wetland plant species richness, springs-upland wildlife interactivity, and endemic species presence often are low in such springs, with all but the latter increasing over distance downstream through the springbrook (e.g., Glazier, 2014). Thus, considerable ecological variance exists in relation to shading as well as other constraints on productivity. Conceptual modeling of those differences in the context of subsidy exchange can provide the foundation for future study and predictive modeling.

Humans and Springs

Uses

Anthropogenic preemption of ecosystem goods and services, and well as regional and global environmental alteration can alter all of the above hydrogeological, climatic, and ecological characteristics and processes of springs, resetting the ecosystem trajectory of ecosystem development (Fig. 1). Human evolution is uniquely tied to springs, as demonstrated in the paleohydrological reconstruction of the Olduvai Gorge in Kenya (Cuthbert and Ashley, 2014). During times of drought, early hominins there likely retreated to springs, which served as refugia buffered to some extent from climate change. However, springs also serve as ecological ambush sites for both human and non-human predators, which may account for the association of human remains with those paleosprings, and Pleistocene megafaunal kill sites at North American springs (e.g., Haynes, 2008). However, and perhaps due to the high rates of organic production and decomposition, there appears to be a general paucity of fossil remains from paleosprings prior to the Neogene.

Springs have been widely and actively used, and revered by humans throughout recent pre-historic and historic time. The Greek Oracle Springs at Delphi played a central role in world politics for nearly a millennium (Broad, 2006), and Peirene Fountain in Corinth was used for several thousand years for religious purposes and therapy (Robinson, 2011). Gihon Springs in Jerusalem, the many springs described by Pliny the Elder, European springs appropriated for Roman aqueducts, and many more examples exist of springs being intensively used by humans throughout history (e.g., Kreamer et al., 2015). In arid North America, multiple indigenous tribes regard individual springs as the place of emergence of their culture, including the Hopi Sipapu, the Zuni Ribbon Falls Springs, the Hualapai Peach Springs in the Southwest, and Gabrielino Tongva (Kuruvungna) Springs in Los Angeles, California, and others. Nabhan (2008) and Rea (2008), and other authors document indigenous reverence for and use of springs.

Unfortunately, for all the reverence in which they are held, springs stewardship has remained remarkably under-informed. In recent times, the intensification of appropriation of springs ecosystem goods and services has accelerated to the point that springs and springs-dependent species in many regions are threatened by both regional and local human activities. Groundwater depletion is a major, coarse-scale threat to the continued existence of springs in many developing regions, particularly where there is little concern for, or regulation of groundwater extraction. Such regulation is regarded as a states' right issue in the United States, and has contributed to the overdraft or dewatering of many large, important aquifers, such as those around large southwestern US cities like Las Vegas (Deacon et al., 2007), and the Ogallala Aquifer in the central southern Great Plains (McGuire, 2007). In addition, widespread contamination of groundwater may occur through hydraulic fracturing (e.g., Burton et al., 2016). More localized threats include: geomorphic alteration or obliteration of springs sources through agricultural and livestock management practices; spring box housing required by the US Environmental Protection Agency to protect drinking water sources; surface water pollution by livestock; inappropriate fencing; single-species management efforts; alteration of adjacent landscapes (e.g., upland grazing or forest management; flow regulation of rheocrene springs on river floodplains, etc.); as well as many other impacts. Specific springs types, such as southwestern ciénegas have a lengthy history of appropriation, loss and impairment, making them now among the rarest springs types in the American Southwest (e.g., Hendrickson and Minckley, 1985). However, not all anthropogenic impacts on springs negatively affect ecological properties. For example, Zawal et al. (2018) reported that flow regulation of Krąpiel River in Poland prevented flood scour of floodplain springs and enhanced the diversity of springs-dependent mites and other invertebrates.

Few regional studies of springs economics have been conducted, but those that have indicate that springs can have enormous impacts on local economies and societal well-being (e.g., Griebler and Avramov, 2015; Mueller et al., 2017). Gleick (2010) emphasized that water bottling operations also have become a multi-billion dollar worldwide industry that is having severe impacts on groundwater supplies.

Springs Ecosystem Conservation

Springs and the aquifers that support them are globally threatened by human activities, and many recently reported extinctions have been of springs-dependent species. Groundwater pumping, livestock and other agricultural uses and pollution, mining impacts, urbanization, and the introduction of non-native species have altered many springs on Earth, and nearly 20% of submarine springs appear to be threatened by sea-floor mining. The extent of ecological impairment of springs often exceeds 70% among many landscapes in Europe, North and Central America, and Australia, and urbanization of arid regions often depletes local groundwater, eliminating springs altogether. Nearly every study of springs ecosystems indicates the need for better conservation of springs and springs-dependent species (e.g., Minckley and Deacon, 1991). However, the only springs type currently recognized by the European Union (2014) as worthy of conservation are petrifying springs (Cantonati et al., 2016), and only a few countries in the world have national springs protection programs. Given the great biological, cultural, and socioeconomic value of springs, and the crucial role of sustainable groundwater for continued human existence, springs warrant far more conservation attention than they previously have received (Cantonati et al., 2020).

Several organizations have begun to promote improved springs management, among which are the US Forest Service (2012), the Howard T. Odum Florida Springs Institute (floridaspringsinstitute.org), and the Museum of Northern Arizona Springs Stewardship Institute (SSI) in Flagstaff, Arizona (<http://SpringStewardshipInstitute.org>, <http://SpringsData.org>; Ledbetter et al., 2014). The missions of the latter two organizations are to improve scientific understanding and management of springs in Florida and throughout the world, respectively. SSI provides protocols, free on-line information and education on management through trainings in springs inventory, ecological assessment, information management, planning, implementation, and monitoring.

If the supporting aquifer is relatively intact and functioning, aridland springs ecosystem rehabilitation efforts can be highly successful (Davis et al., 2011; Lehosmaa et al., 2017). For example, Burke et al. (2015) documented a well-planned restoration plan for Pakoon Ranch Springs in northwestern Arizona, and over a five-year period transformed a heavily degraded former cattle and ostrich ranch into a well-functioning restored springs complex. Cole and Cole (2015) reviewed the distribution and status of aridland ciénegas, recommending rehabilitation actions for stewards of those springs. Rehabilitation recommendations multiple springs types are presented in Stevens et al. (2016c), who conclude that best management practices for springs often can easily and inexpensively be successful, even on severely degraded springs, provided the aquifer is at least moderately intact. Among the actions, simple rehabilitation actions can include: protection of the often biologically distinctive source area by fencing; installation of a flow splitter to provide water for human uses while still maintaining flow at the source; and constructing a trail to the source to reduce hillslope erosion (Stevens and Meretsky, 2008).

Conclusions

I describe and discuss the global springs biome, including conceptual, physical, biological, ecosystem ecology, and anthropogenic interactions, and I distinguish, where relevant, differences between aridland springs and those in humid regions. The background literature and information presented indicate that springs in both aridlands and mesic environments broadly overlap in ecosystem characteristics and processes. However, aridland springs differentially or more often appear to have: (1) steeper environmental gradients of moisture and nutrient availability between the springs and the adjacent uplands habitats, creating (2) more discrete and distinctively different assemblages; (3) higher levels of endemism and rare species occurrences, with some springs functioning as evolutionarily significant paleorefugia; (4) interrupted, losing-stream springbrook habitat disconnectivity, which may thwart or delay colonization by aquatic non-native species; (5) a tendency towards lower levels of flow, with an increased propensity for ephemeral flow; (6) reduced resiliency and a tendency towards more dynamism in vegetation development, and likely faunal assemblage development, following disturbance; (7) greater susceptibility to anthropogenic impacts, particularly appropriation of water resources, and (8) consequent loss of springs habitat and increased probability and incidence of extinction of springs-dependent species.

With their diverse geomorphology, ecology, and biotic assemblages, springs ecosystems constitute a distinctive global biome, one that differs strongly in physical derivation, ecological processes, and assemblage composition from those in immediately adjacent uplands. Where the springs biome exists in arid lands, it becomes highly distinctive and critically important, providing point source biodiversity and ecological, cultural and socio-economic influence and interactivity. The sensitivity of aridland springs to anthropogenic alteration cannot be overstated, making them the “canary’s canary in the coal mine,” and whose degraded ecological condition portends long-term threats to groundwater supplies and quality, landscape ecological integrity, and societal sustainability.

The loss and impairment of springs ecosystems constitutes a global crisis that, despite much recent research, is still and ever more rapidly increasing in severity. Averting this crisis requires scientific agreement about the springs lexicon and classification (Thompson et al., 2002; Stevens et al., *in press*), as well as far more public discussion, support and political will to invest in basic mapping, inventory and status evaluation, and implementation of often simple, inexpensive rehabilitation measures. Although environmental foresight has yet to become a conspicuous trait of human society, more education and outreach is needed to shift cultural perceptions and improve environmental stewardship. Such a paradigm transition is desperately needed to reduce our impacts to these remarkable, irreplaceable ecosystems. The global demise of springs is a challenge humanity can overcome if only we can muster the individual and collective societal will to do so.

Acknowledgments

I thank the Museum of Northern Arizona (MNA) and its administrative staff for support of my work. I thank Marco Cantonati, Rod Fensham, Doug Glazier, Robert Knight, Don Sada, Ed Schenk, and Abe Springer for conceptual discussions on springs ecosystem ecohydrology. The MNA Springs Stewardship Institute staff provided much-appreciated assistance in information management and map production, particularly Jeri Ledbetter, Marguerite Henrie, and Jeff Jenness. I thank the *World Biomes* editor and anonymous reviewers for insightful and much-appreciated comments on earlier versions of the text.

See also: Desert Oasis Springs: Ecohydrology, Biocultural Diversity, Mythology, and Societal Implications

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Headwater Streams

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Abstract

Headwater streams are the source streams at the initiation points of all river networks. These source streams may make up almost 80% of total stream length, but because of their small size and water volumes are extremely sensitive to the surrounding landscapes. Headwaters contribute to the characteristics of the downstream network in terms of water quality (nutrients, other solutes and temperature), sediment transport, and organic matter supply. These streams represent a distinct ecosystem as they support organisms that require relatively constant physical conditions, enemy-free spaces, or specific resources typical of source streams. The species found there are often unique to headwaters, and the key ecosystem functions usually differ from downstream in terms of being more dependent on organic matter sources from the surrounding terrestrial landscape, rather than instream primary production. Headwaters are also very sensitive to land use as they are strongly regulated by their surroundings, and often not protected.

Introduction

In common language, headwaters may refer to all source waters upstream of the point at which the observer is standing, meaning it could be an enormous area contributing to the flow at a given point. However, in the scientific literature headwaters are the smallest of what we consider small streams, that is the most headward of channels, but there is no consensus on a definition. Definitions based on stream order are problematic as the order system is typically based on a 1:50000 (Strahler, 1952) or 1:100,000 map scale, and even "first order" streams (first blue lines on such a map) could be relatively large at that scale. Meyer et al. (2007), Wohl (2017) and others define headwaters as first- and second-order streams, and Meyer et al. (2007) specifies a 1:24000 scale, which is still potentially large. We define headwaters as those streams without perennial tributaries, distinguishing them from other small streams (Gomi et al., 2002; Moore and Richardson, 2003; Richardson, 2019). That is, in the context of a network, they are the uppermost link with no other links (branches) until the node (tributary junction) at the base of the headwater. Another way of defining headwater streams is the intensity of the interaction between the stream and its surrounding landscape, i.e. the degree of coupling, which is difficult to measure (Church, 2015). One approach to this is whether coupled hillslope-stream processes, such as mass-movement, dominates sediment supply (Gomi et al., 2002). Hence, definitions differ across the literature. Our definition is based on headwaters being first-order streams based on field observations, which we have tried to differentiate from other small streams (second order and higher). Headwater streams can be ephemeral, intermittent or perennial (Feminella, 1996), and may even change between these classes from year-to-year based on precipitation patterns in any year. Regardless of a firm definition, they are the smallest of streams in a river network.

Leopold et al. (1964) estimated at least 73% of stream channel length in fluvial networks are 1st and 2nd order streams based on 1:24000 scale maps. Some estimates suggest that only 21% (Hansen, 2001) to 43% (Meyer and Wallace, 2001) of actual stream channel lengths even show up on the map scale of 1:24000. Hence, however headwaters are defined, they likely account for much more stream length than other channel sizes in any river network.

Initiation points of streams occur at the point of concentrated water flow leading to clear evidence of fluvial processes, such as sediment movements (Montgomery and Dietrich, 1992). Headwaters may also originate from glaciers, snow packs, springs, or other sources. In some cases the first stream in a network might be from a wetland or lake, and this may be considered a headwater by some scientists.

Headwaters can occur anywhere that surface flow is initiated from alpine areas to sea level, and in rainforests through to prairies and near desert. Thus, many of their properties will be very dependent on the nature of the watershed they drain, including climate, vegetation, geology and hydrology.

Given that headwaters typically drain small areas, they can be sensitive to periods of low precipitation inputs and gradually diminished flows that in some years may leave them without visible surface water for periods of time. The loss of surface flow may begin at the initiation point, or further downstream, which is often referred to as the variable source area concept, but there may be other variants on how types of source areas for flow actually influence discharge (e.g. [Dahlke et al., 2012](#)).

Properties of Headwaters

Hydrology

Headwaters gather water from a relatively small contributing area or catchment, and thus they can be individually quite “flashy”, i.e. instantaneous stream discharge can change quickly. Some estimates of the contribution of headwaters to the mean annual flow of entire river networks are ~41% for a drainage in Colorado ([Caruso and Haynes, 2011](#)) to ~70% in the northeastern USA ([Alexander et al., 2007](#)). However, as small systems, the peak discharges may still be relatively small. Their small catchment areas also often mean that there is limited groundwater storage and at times of year surface flow may retreat to a few lengths of contributing area, that is, they have a variable source area. These periods of low flows can be a strong influence on the biology as water availability disappears from the surface and any moisture may be subsurface, that is, hyporheic. Many headwater streams go through periods when surface flows disappear and they become intermittent annually or during years of lower than average precipitation ([Fig. 1](#)).

The discharge rates of headwaters can be highly variable across the landscape and through time in terms of discharge at any given moment due to the variation in inputs of precipitation, storage capacity, and the flowpaths through which shallow groundwater moves. The timing of discharge depends on when precipitation arrives, and in what form, as snow storage can result in low winter discharge coupled with a spring freshet as snow melts. In some regions, rain-on-snow events result in large peak flows as the input of warmer rain adds melted snow to the discharge generation (e.g. [Moore and Wondzell, 2005](#)). The relation between precipitation and discharge also depends on the characteristics of the soils and geology of the shallow groundwater zone, where coarse soils in glaciated or volcanic landscapes may be highly permeable, whereas clays may be more slowly draining, or even lead to overland flows. The storage capacity of headwater basins can be overwhelmed if the antecedent conditions leads to saturated soils and precipitation flows directly into streams, often leading to greater peak flows during periods of regular and intense precipitation.

Geomorphology

In some landscapes with large parent materials in the soils, headwaters may be colluvial ([Montgomery and Buffington, 1997](#)), i.e. their peak flows are unable to move the largest particles, and the channel works its way around those larger rocks and pieces of wood. As headwaters are usually directly connected to the hillslopes and there is no stored alluvium or floodplain, therefore slope failures often end in the channel. Much of the sediment supply entering stream networks comes from mass wasting events along the hillslopes connected to headwaters, as well as from erosion of slopes and streambanks.

Headwaters are sometimes steeper than downstream reaches, but this is not necessarily so. [Church \(2015\)](#) suggests that volume and timing of discharge, sediment caliber and volume, the bank (including slope of the bank) and bed structures, and channel gradient are four of the dominant processes influencing morphology of headwater streams. This influences structure as fine-grained materials can be easily moved by most flows, deposited on the banks, and deeply rooted, riparian vegetation can strongly influence structure and lead to deep, narrow channels. However, in very low-gradient channels, even this bed material may remain dominant ([Church, 2015](#)). Headwaters can express step-pool morphologies when the caliber of bed materials are large and channels are steep, through to deeper, meandering channels when finer materials dominate the sediment supply in lower gradient channels. Nevertheless, the majority of high roughness channels in a network are headwaters ([Church, 2015](#)).

Headwaters are often the source of sediment supplies to downstream, shaping the possible configurations of downstream channel structures ([Church, 2015](#)), depending in part on the transport capacity of the source streams, grain-size distributions and slopes, as above. The balance of sediment supply and transport are dynamic, and vary through time and space, creating heterogeneity in morphology and rates of transport downstream (e.g. [Fritz et al., 2018](#)). Large wood can be important as a channel-structuring element ([Gomi and Sidle, 2003](#)), but often spans headwater channels for a considerable period before falling into the channel when it is in advanced states of decomposition and more easily broken and transported.

Water Chemistry

Inputs of water are characteristic of shallow groundwater and precipitation, and thus water chemistry bears a signature of local groundwater inputs. Often it is suggested that headwater streams are relatively nutrient poor, as it depends on the subsurface, geological composition through which groundwater flows, and also the residence time of the water. Some transformations, e.g. nitrogen and other solutes, can occur at higher rates in headwaters than larger streams and thereby reduce the nitrogen concentrations delivered downstream ([Peterson et al., 2001](#)). One estimate suggests 65% of nitrogen flux to downstream networks comes from headwaters ([Alexander et al., 2007](#)).



Fig. 1 Three examples of headwater streams. (A) A headwater stream in New Zealand's south island, showing a step-pool morphology as can occur in steeper landscapes with large rock elements. (B) A headwater in a boreal forest in Finland. (C) A headwater in the tundra-like landscape of western Iceland.

Influence of Surroundings on Local Stream Properties

The very high ratio of edge to area in headwaters means that streamsidelines have a very large influence on these small streams, through shading, inputs of organic matter (e.g. leaves, wood, seeds), etc. As stream width increases, the amount of organic matter inputs per unit area, particularly leaf litter, decrease, so the surrounding vegetation has less and less influence (e.g. [Naiman and Sedell, 1979](#)). Headwater streams are often heavily shaded, but that depends on the nature of the surrounding vegetation and the local topography. Forest streams are typically shaded, but in low-relief landscapes, the water table may restrict forest trees and support shrub and herb-level vegetation, such as willows and sedges, which offer little shade. Likewise, headwaters in prairie or alpine situations are unlikely to be shaded by vegetation to any great extent.

The pattern of shading of headwaters by forests depends on the successional state of the forest (more, but patchy, light through older forests), and some amount of patchy light may contribute to the overall productivity of a stream ([Heaston et al., 2018](#)). The

surrounding riparian forest can also have a large influence on flows during low-flow periods as vegetation may extract water for transpiration from subsurface (e.g. [Moore and Wondzell, 2005](#)).

Disturbance Regimes

Headwaters experience a number of disturbance regimes. Often these disturbances are intense, but infrequent, such as mass wasting events that accompany high precipitation events. Wet soils can lead to slope failures which run into headwaters. Moreover, sediments (rock and wood) stored in headwaters can be mobilized during higher flows and lead to debris torrents of materials down the small channels to where the material is deposited where gradients are lower (creating fans) or continues down larger streams into which materials are delivered. Examples of such events have been described for streams in Oregon (e.g. [Lamberti et al., 1991](#); [Swanson et al., 1998](#)).

Headwaters are also subject to the impacts of fire, volcanic eruptions, etc. [Nitschke \(2005\)](#) compared the impacts of fire on headwater streams to that of forest harvesting, and found fire resulted in larger increases in nutrient and other solute fluxes, increased sedimentation, and lower concentrations of dissolved organic carbon than occurred following forest harvesting.

Food Resources

Biologically available energy sources (resources at the base of headwater communities) are often divided into green (primary production) and brown (detrital) pathways, that is, autotrophic and heterotrophic production, respectively. Headwaters are often heterotrophic in forested settings, such that inputs of organic matter from vegetation contribute the largest fraction of available energy for stream organisms (e.g. [Fisher and Likens, 1973](#)). This, coupled with shading that can limit primary production, means that allochthonous (from outside the stream) sources provide most of the biologically available energy. However, headwaters can arise in any landscape and the dependence on organic matter from vegetation may not be true in alpine, tundra and prairie regions.

Organic materials occur in headwaters in two primary forms, particulate and dissolved. Dissolved organic carbon (DOC) is not strictly speaking dissolved, as it is operationally defined as carbon-based molecules passing through a standard filter paper with nominal pore size of $\sim 0.7 \mu\text{m}$. DOC is typically available to bacteria that can use it as an energy source. Particulate organic carbon (also referred to as detritus) is divided into coarse ($> 1 \text{ mm}$ diameter) and fine ($< 1 \text{ mm}$ diameter, but larger than DOC), largely as coarser particles are decomposed more commonly by fungi and smaller particles processed by bacteria. The size of these particles also influence which consumers eat the particles and associated microbes. DOC enters headwaters in groundwater, and also from the leaching of soluble organic compounds from particulates, which are primarily delivered from vegetation, such as leaf litter and wood, in the area surrounding headwater streams.

Organic matter inputs occur seasonally and can lead to periods of limiting supply for consumer populations in headwaters (e.g. [Richardson, 1991](#); [Wallace et al., 1999](#)). The nutritional quality of organic matter depends on the species, lignin content (e.g. wood is a low-quality resource compared to leaves), and nutrient regime (e.g. [Rosemond et al., 2015](#)). Other organic inputs include terrestrial invertebrates from the surrounding vegetation, which can contribute considerably to the production of small fishes and other predators (e.g. [Wipfli, 1997](#); [Sato et al., 2016](#)).

Autochthonous (primary) production can include photosynthesis by algae (including cyanobacteria), which contribute to biofilms growing on most surfaces (rock, wood, invertebrates, other plants, etc.). Mosses can also be significant contributors to primary production in headwater streams ([Fritz et al., 2009](#)). Infrequently, in headwaters draining iron-rich geologies the growth of iron-reducing bacteria can contribute to biofilm production in small streams as an additional source of biologically available basal resources (e.g. [Hildrew and Townsend, 1976](#)).

Biological Diversity

Reviews on the biological diversity of headwaters have been published by [Meyer et al. \(2007\)](#), [Richardson and Danehy \(2007\)](#), and [Richardson \(2019\)](#). Headwaters are key habitats to many organisms, some of which are found nowhere else in stream networks. Some of the reasons for these organisms to use headwaters are summarized in [Table 1](#). However, the relative importance of some of these functions are yet to be tested, as one requires well-designed experiments to separate the individual contributions of each of these processes.

Many species depend on particulate organic matter as a food source, and these organisms are referred to as detritivores, or by a description of the way they eat, known as functional feeding groups ([Cummins, 1974](#)). Species feeding on large particles are often known as shredders as they break down larger particles, and species feeding on fine particles are called collectors, which can be further broken down into filterers (some kind of filtering mechanism to catch particles) or gatherers (collect particles from the stream bottom). Detritivores, particularly shredders, are frequently more abundant in headwater streams than in larger streams as a consequence of the abundance of these inputs. However, it is clear that this is not globally the case and in many tropical streams there may not be specialist detritivores as there are in more temperate and subtropical systems. This dependence on coarse particulate organic carbon is one reason for species to be found primarily or exclusively in headwater streams.

Given their small size, headwaters rarely support larger-bodied predators, or only small numbers. This provides other species with a refuge from larger-bodied predators. In many cases the top predators might be small fish or amphibians. Some species appear

Table 1 Some of the putative mechanisms for the particular use of headwaters by species.

Mechanism	Explanation
Dependence on organic matter	Often shaded by vegetation, which contributes organic matter and limits primary production. Dependence on groundwater inputs also leads to higher concentrations of dissolved organic carbon contributing to microbial growth
Thermal conditions	Groundwater inputs tend to predominate flow generation and results in moderated temperature regimes
Enemy-free space	In headwaters the small spaces do not support many or any larger predatory species, and thereby provides a refuge for some species
Reduced competition	Some species find relaxation of competitive interactions in headwaters
Breeding and rearing	This may entail some degree of predator avoidance or other specific resources
Flow conditions	Discharge can be very “flashy”, i.e. rapid responses to precipitation. Discharge can also be very low due to small contributing areas during times of limited precipitation
Water quality	Often considered to be nutrient poor, and reflects the signal of the groundwater that contributes to flow
Physical structure and size	Small habitat spaces restrict potential for large-bodied species, limits population sizes for other species. Often colluvial, depending on geology and gradient
Disturbance regimes	In some landscapes, channelized debris flows may be rare but large magnitude. Punctuated changes in discharge due to large inputs can lead to flood disturbance. Fire and drought can also be important disturbance events

This table builds on summaries in Meyer et al. (2007), Richardson and Danehy (2007), and Richardson (2019).

to use headwaters seasonally for particular life stages, especially for young (small) individuals avoiding predators. Seasonal use of headwaters might also provide for use of a thermal preference for a narrow range of temperatures.

There are many species found in headwaters. The best studied headwater stream in the world is arguably the Breitenbach in Germany in which over 1800 species have been found, including over 1000 insect species (Wagner et al., 2011). Other studies in headwaters have documented similar levels of diversity in subsets of taxonomic groups, i.e. characterization of invertebrates or algae, but not the entire community. The diversity of headwater communities includes all kingdoms of life. The best characterized groups are the animals, algae, and fungi. Even some invertebrate groups may be less well known, such as Nematoda (Majdi and Traunsperger, 2015). Protists, bacteria, and viruses are probably more speciose than currently understood and there is a great opportunity to add to knowledge of these groups in headwaters.

Ecosystem Processes

As the first channels in a stream network, headwaters are at the endpoints and have only one connection to the rest of the network, in contrast to larger streams which have many nodes connecting them. Fagan (2002) has demonstrated how this is likely to influence local population dynamics in headwaters where isolation by distance along the stream network, as well as the relatively small habitats they provide results in low colonization rates to headwaters. Moreover, the small spaces of headwaters also implies relatively small populations, with a higher potential rate of local extinction (population extinction at a site). The balance of colonization relative to extinction also imply headwater populations are more vulnerable to disturbance than species that also occur in larger streams (Fagan, 2002). This also suggests that headwater communities operate as meta-communities, linked by colonization, even if the rates of colonization might be low (Datry et al., 2017). Given that materials, nutrients and organisms potentially move between adjacent and downstream ecosystems, headwaters function as meta-ecosystems (Datry et al., 2017; Harvey and Altermatt, 2019).

Headwater streams contribute to, and form, connections to downstream waters through supply of water, nutrients, other solutes, sediments (of a range of sizes), and biological materials (Fritz et al., 2018). These connections are critical to supplying organic materials to downstream in the form of particulate and dissolved carbon (Wipfli et al., 2007). Organic materials that fall into headwater streams are processed (i.e. broken down to smaller particles or incorporated into animal biomass) in situ or exported downstream (Webster et al., 1999). Headwaters are considered leaky ecosystems, and studies have demonstrated that most of the process of creating smaller, easily transported particles is done by invertebrates. For instance, when densities of invertebrates were reduced through insecticide application over 3 years, the flow of fine organic particles was reduced by ~56% relative to control streams (Wallace et al., 1991). In that study of three headwater streams in North Carolina, the average export of fine particles per year was in the range of 221 to 369 kg ash-free dry mass year⁻¹ (Wallace et al., 1991) to downstream reaches. Wipfli and Gregovich (2002) concluded that export of organic materials, including invertebrates, from headwaters could support a large portion of the fish production in the larger receiving streams.

Connectivity can be defined as the degree to which ecosystems functionally and structurally interact (Leibowitz et al., 2018), and headwaters are considered to be strongly connected to downstream reaches. Inputs to headwaters can also come from downstream and riparian areas, and this interconnectedness is referred to a meta-ecosystems to recognize the contributions of adjacent ecosystems (Datry et al., 2017).

Given the contributions of headwaters to water quality (e.g. solutes, temperature) and quantity, organic matter supplies, and value as habitats, it is evident that alterations to headwaters through disturbance and land use can have large cumulative effects.

However, the individual effects of modifications are hard to trace downstream, in part due to the dilution effects as networks increase in size (discharge) downstream.

Management and Threats

Small streams are easily threatened by land use, and often converted to ditches and buried in pipes to make way for development (Elmore and Kaushal, 2008). Developed landscapes have been referred to as “stream deserts” due to their lack of surface stream reaches due to stream burial in storm drain systems (Napieralski et al., 2015). Incorporation of headwater streams into pipes often leads to rapid downstream changes in discharge in response to precipitation given there is little resistance to flow movement through pipes, which can lead to downstream flooding where the storm drain system flows into larger streams. Burial of headwater streams also reduces nitrogen mineralization and leads to higher export rates of nitrogen to downstream areas contributing to additional eutrophication where drainage pipes drain to rivers (e.g. Peterson et al., 2001; Beaulieu et al., 2015). One of the most destructive of land-use impacts on headwater streams is associated with mountaintop mining, in which overburden is bulldozed directly into headwater streams, filling the valley and eliminating the stream (Palmer et al., 2010).

Forestry, agriculture, urbanization, and other land-uses can have profound impacts on headwater streams, even if they are not buried or channelized as mentioned above. In general, a suite of changes occurs that has been referred to as the urban stream syndrome for urban headwaters (Booth et al., 2016) and similarly for forestry landscapes (Richardson, 2008). These changes include higher peak flows (runoff over pavement, pipes or compressed soils, lack of uptake by vegetation), higher erosion and nutrient transport, warmer water in summer, and channel simplification. There can also be higher concentrations of contaminants such as pesticides and other organic compounds.

Legislative provisions for protection of headwaters is often lacking (Kuglerová et al., 2017). In the USA headwaters are a point of contention for whether the Clean Water Act applies (Fritz et al., 2009). Protection of headwaters from forestry activities varies from a great deal of protection in states like Washington (buffers at initiation points, junctions, upstream of extent of fish), to little more than a machine-free zone in adjacent British Columbia.

Although headwaters are rarely impounded for water supplies in most places, in regions with subsistence agriculture, even headwaters may provide irrigation and drinking water supplies. However, impoundments for power production, flood control, and other uses still impact headwater streams by flooding them and turning them into parts of the resulting reservoirs.

Stream restoration is a widespread practice in an attempt to repair damage due to past land use. Most of these activities are applied to streams larger than headwaters, and not particularly successfully (Palmer et al., 2014). However, in places efforts at bank stabilization, exclusion of livestock, and planting of riparian trees for shade have had success in bringing back some of the functions of headwater streams (Beechie et al., 2010). In some rare instances the loss of headwater streams is being reversed by a practice known as daylighting of buried streams, that is, returning them to surface flows (Wild et al., 2011).

Many streams around the world now receive some amount of streamside protection, but this is rarely the case for headwaters (Richardson et al., 2012). Streamside management often has the aim of providing shade, streambank stability to reduce erosion, nutrient uptake and organic matter inputs (including wood). This management often takes the form of leaving some amount of vegetation, a buffer, along streams. Buffers are now commonly applied in forestry, agriculture and urban settings (Richardson et al. 2012). The amount of vegetation retained varies considerably by jurisdiction and for the particular kind of land use (Blinn and Kilgore, 2001). Small streams may need forested buffers of 30 m or more to retain their functions in terms of erosion control and sediment storage, channel structure, temperature regimes, nutrient processing and community structure (Sweeney and Newbold, 2014). However, most headwaters are unlikely to receive anything close to this amount of protection from adjacent land use. Clearly, headwater streams deserve greater protection than currently afforded in most jurisdictions.

Headwater streams are increasingly recognized for the critical roles they play in contributing to productivity and integrity of downstream ecosystems (e.g. Nadeau and Rains, 2007; Colvin et al., 2019; Kuglerová et al., 2019). These functions include moderating peak flows and provision of cool, clean water. Intact headwaters also limit the degree of erosion which mitigates sediment supply to downstream. Headwaters also process organic matter and critically supply organic materials that support the productivity of downstream foodwebs (Wallace et al., 1991; Wipfli and Gregovich, 2002). Headwater streams can provide breeding and rearing sites for species that eventually form part of downstream biological communities. Nutrient mineralization in headwaters also reduces the potential nutrient supplies to downstream (Peterson et al., 2001). In fact, an extrapolation of estimates of some ecosystem services (water supply, water purification, and carbon sequestration) from headwater streams for the entire USA suggests headwaters may provide value of \$US 15.7 trillion per year (Nadeau and Rains, 2007; Hill et al., 2014; Creed et al., 2017). Headwaters serve a large role in determining the characteristics of downstream ecosystems, and those functions are easily disturbed by land use.

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Hawaiian Islands Streams

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Published by Elsevier Inc.

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Abstract

A Habitat Status Assessment (HSA) was completed for streams, including rivers and seeps, for the state of Hawai'i. This stream HSA defines what Hawaiian streams are, what the ideal stream conditions were prior to human arrival, the current stream condition based on human and climatic stressors, and what streams may become from an analysis of four future scenarios. Hawai'i currently has 376 perennial streams and less than 15% of those streams are classified as pristine, typically having clear, cold water, and a strong flow all year round (U.S. Fish and Wildlife Service, 1978a,b). Rainfall is the primary source that feeds the streams from the headwaters beginning in the mountains and flowing toward the sea. With the lack of references and descriptions available, we are only able to infer how Hawaiian streams functioned under ideal conditions prior to human contact approximately 1500 years ago. Stream viability from pre-human contact to current condition was assessed based on the resiliency of a stream to withstand stochastic environmental events, redundancy to withstand a catastrophic event, and the representation of streams to adapt to a changing environment over time. Current condition of Hawai'i streams was assessed

from when the first Polynesians arrived up to 2018. Streams were important to Hawaiian Society as land divisions called Ahupua'a were established based on local watershed boundaries from mountains to the sea. Within each Ahupua'a, streams were utilized by Native Hawaiians for agriculture and aquaculture (CWRM, 1993). Presently, about 50% of all Hawaiian streams are diverted and highly altered through agricultural use and urban developments (U.S. Fish and Wildlife Service, 1978a,b; Oki, 2003). Hawaiian streams continue to degrade due to pressures from anthropogenic, stochastic, and climatic events. These include development, channelization, water diversion, human recreation, pollution, climatic events such as drought, erosion and sedimentation, and invasive species. Current conservation efforts for restoration and management, policy and laws, education and outreach, and creation of protected natural reserves are ongoing, and these efforts aid in continuing the protection of Hawaiian streams from further decline in functionality from listed stressors. This HSA for Hawaiian streams analyzed four future scenarios all differing in their levels of natural resource management from 2018 to the foreseeable future of 2035. The three variable conservation management parameters for each future scenario are conservation values, laws and biosecurity, and development or conservation planning. The four future scenarios analyzed for Hawaiian streams are status quo, slightly improved conservation measures, substantially decreased conservation measures, and substantially improved conservation measures which are all based on varying degrees of conservation management. Based on these analyses, we anticipate that stream habitats will continue to decline unless there is a significant increase in the conservation management parameters.

Introduction

The Hawaiian archipelago is the most isolated landmass in the world with extreme variations in elevation, wind, rain, topography, substrate, and hydrology. These variations coupled with the remoteness of the archipelago within the Pacific Ocean, create unique biomes on each of the islands and atolls. We provide an overview of the coastal system in Hawai'i and describe the ecological factors that have influenced the system over time and into the future. Please see the chapter by Harrington on the Physical Geography of the Hawaiian Islands included in this work for a full description of the unique geography, geology, climate, hydrology and descriptions of the islands in the Hawaiian archipelago.

Description

Perennial streams in Hawaii are characterized by clear, cold water, with strong flow all year long. Rainfall is the primary source of water for Hawai'i's streams, although snow melt may provide some minor contribution on the higher mountains. Once rain infiltrates into the soil, the water flows down slope below the surface, often resurfacing as an existing stream bed or by creating a headwater spring source for an entirely new stream. From the streams' headwaters in the rainforest and mountain zones, they flow toward the sea. During this travel, they carve gulches, gullies, and narrow canyons. They also flow over rocky cliffs creating waterfalls and can have sufficient velocity to move boulders and trees from their banks during storms. Farther downstream, these mountain streams can form canyons, valleys, and coastal floodplains (CWRM, 1993). The windward sides of islands are usually the wettest and contain the majority of perennial rainforest streams that support numerous aquatic flora and fauna (Parham et al., 2008). Many streams flow into valleys in the form of waterfalls. As a stream flows, softer material in a streambed erodes relatively quickly until a harder substrate is reached. The stream will continue to flow across this substrate until it reaches and flows over an exposed edge, creating a waterfall. The softer material beneath the falling water continues to erode away until the harder substrate is exposed, and the process is repeated. Sometimes a deep plunge pool is formed where the falling water meets the substrate. These pools often can't be seen from the bottom of the valley (Ziegler, 2002).

Only five of the Hawaiian islands (Kaua'i, O'ahu, Moloka'i, Maui, and Hawai'i) have enough elevation to capture the rain clouds brought to the islands by the prevailing trade winds, and for the resulting orographic rainfall to generate perennial streams. Ni'ihau and Lāna'i are lower in elevation and have ephemeral streams, meaning they are intermittent and may only occur following large rain events. Kaho'olawe, Nihoa, Mokumanamana, Mokupapapa, and Puhahonu are lower and only have seeps (a small leak or flow through porous material or small holes) and ephemeral seeps (a seep that only leaks/flows during and following a period of heavy rainfall).

Hawaiian streams generally are defined by the following characteristics:

1. They are small in length compared to many of the larger streams on the United States mainland. Only 28%, or 7.4%, of the streams in Hawai'i are 10 miles or longer (DAR Hawaiian Streams, 2018a). Larger streams are typically called rivers. The Wailuku River on the island of Hawai'i is 28 miles long and is the longest river in Hawai'i.
2. Many Hawaiian streams are characterized by waterfalls. This feature is due to the steep profile of Hawai'i's mountains, which are composed of successive layers of lava with varying hardness, and is especially evident in the geologically younger islands, such as the island of Hawai'i.
3. Rainfall is the primary water source for stream habitats. Localized heavy rainfall and storms may cause flooding. These flood events, often lasting only a couple of days contribute to the flashy (as in flash flood) discharge patterns characteristic of Hawaiian streams (DAR Hawaiian Streams, 2018a). Streams in Hawai'i are prone to flash floods because rainfall is intense, drainage basins are small, basins and stream profiles are steep, and channel storage is limited (Oki, 2003).

- a. Storm events passing through the islands are especially important in regard to generating runoff on islands of lower elevation, since such islands are unable to capture orographic rainfall. As such, the major surface water features on lower elevation islands are seeps and ephemeral seeps. These stream habitats heavily rely on storms passing through the Hawaiian islands for groundwater recharge. Without heavy rain events, seeps would dry out (Figs. 1–4).

Geology and Water Availability

The form and functions of Hawai'i's streams are created and maintained through frequent high flow events. However, low-flow and base-flow events are equally important, especially during periods of drought. Rivers, streams, and seeps fed by basal ground water exhibit permanent, stable low flows (U.S. Fish and Wildlife Service, 2010).

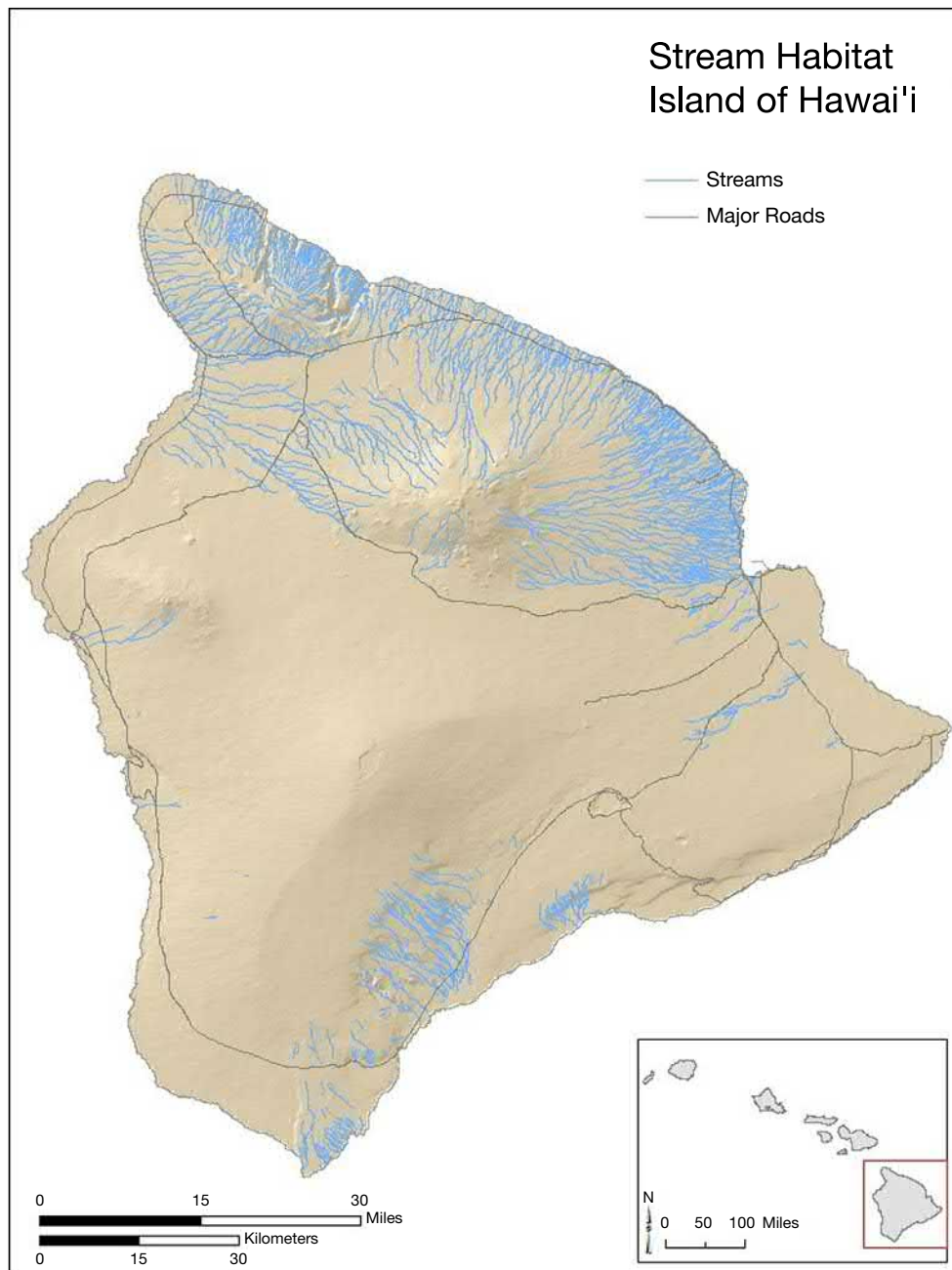


Fig. 1 Map displaying stream habitat for Island of Hawai'i.

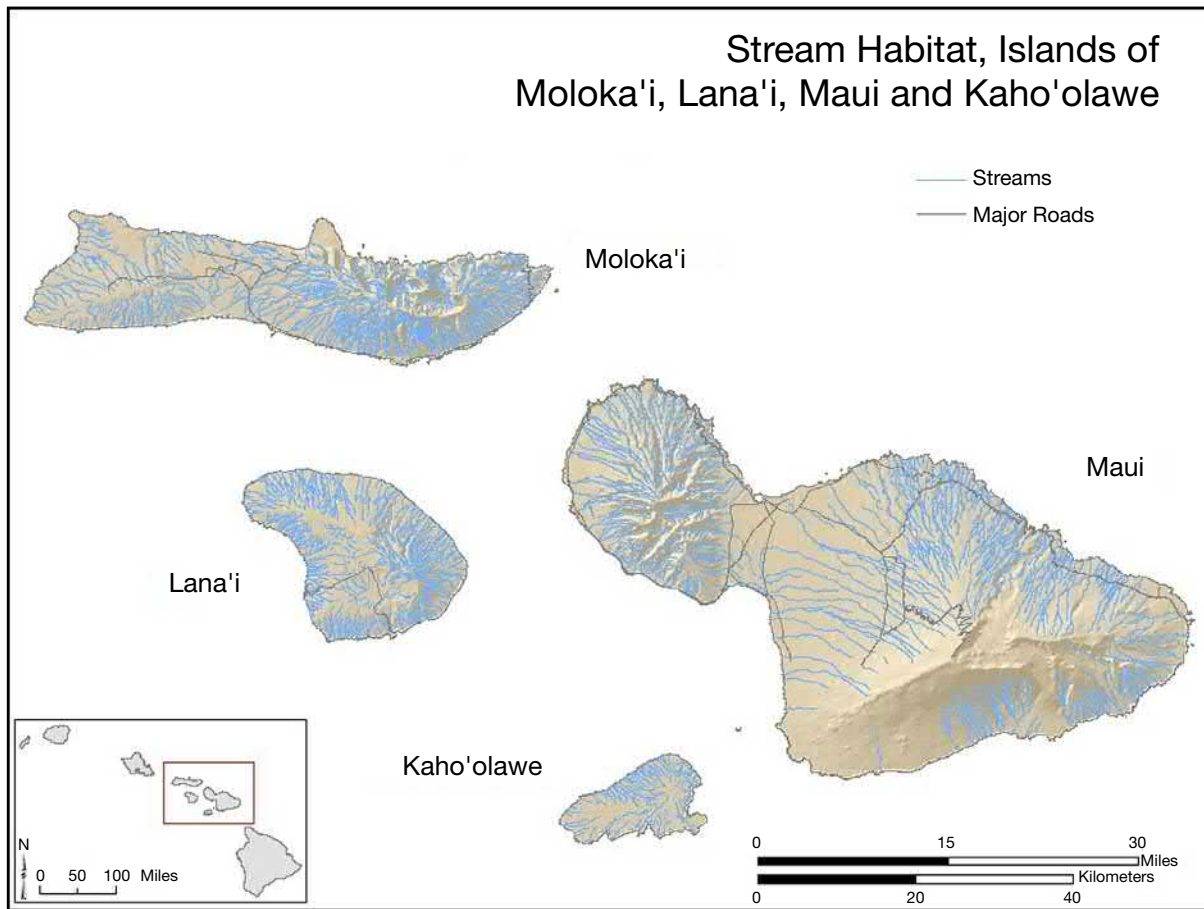


Fig. 2 Map displaying stream habitat for islands of Moloka'i, Lāna'i, Maui and Kaho'olawe.

Streams in Hawai'i gain water along some reaches and lose water along other reaches depending on local geohydrologic conditions. Some streams can lose water if the streambed is above the water table in an area, while others do not flow continuously to the coast because water enters through the streambed and becomes groundwater. The hydraulic properties of the rocks near the stream affect the rate of flow between the stream and groundwater body. When stream channels are lined with concrete to channelize the water to certain areas, this makes it almost impossible for surface water to percolate through and add to the underlying groundwater levels (Oki, 2003).

The upper reaches of many Hawaiian streams are within or near the area where volcanic dikes crop out. Factors that affect water levels in streams and groundwater bodies can control the interaction between surface water and groundwater. These factors include rainfall, groundwater withdrawals, and ocean tides. Rainfall may cause dry, intermittent streams to flow, which can lead to discharge from a stream to the groundwater body or to the ocean. Long periods of rainfall may lead to increased groundwater recharge over a region and a rise in groundwater levels. Rising groundwater levels may lead to increased groundwater discharge to streams or reduced surface-water discharge to the groundwater body. At lower elevations, water levels in streams and groundwater bodies may be affected by ocean tides. Thus, streams in coastal areas may either gain or lose water during the day depending on the effects of the tides on streams and groundwater levels (Oki, 2003).

Natural and Physical Boundaries

A reach classification system (Parham, 2008) was developed by Bishop Museum researchers in collaboration with the State of Hawai'i's Division of Aquatic Resources (DAR) biologists to provide a general classification of stream reaches that could be applied systematically to all streams on all islands. The reach types are based on elevation and the presence and size of waterfalls in the stream.

- *Estuary*: All stream segments between the coastline and 3 feet (ft) (1 meter (m)) elevation.
- *Lower reach*: Stream segments lying between 3 ft. (1 m) and 65 ft. (20 m) elevation and below any barrier of at least 32 ft. (10 m) high.

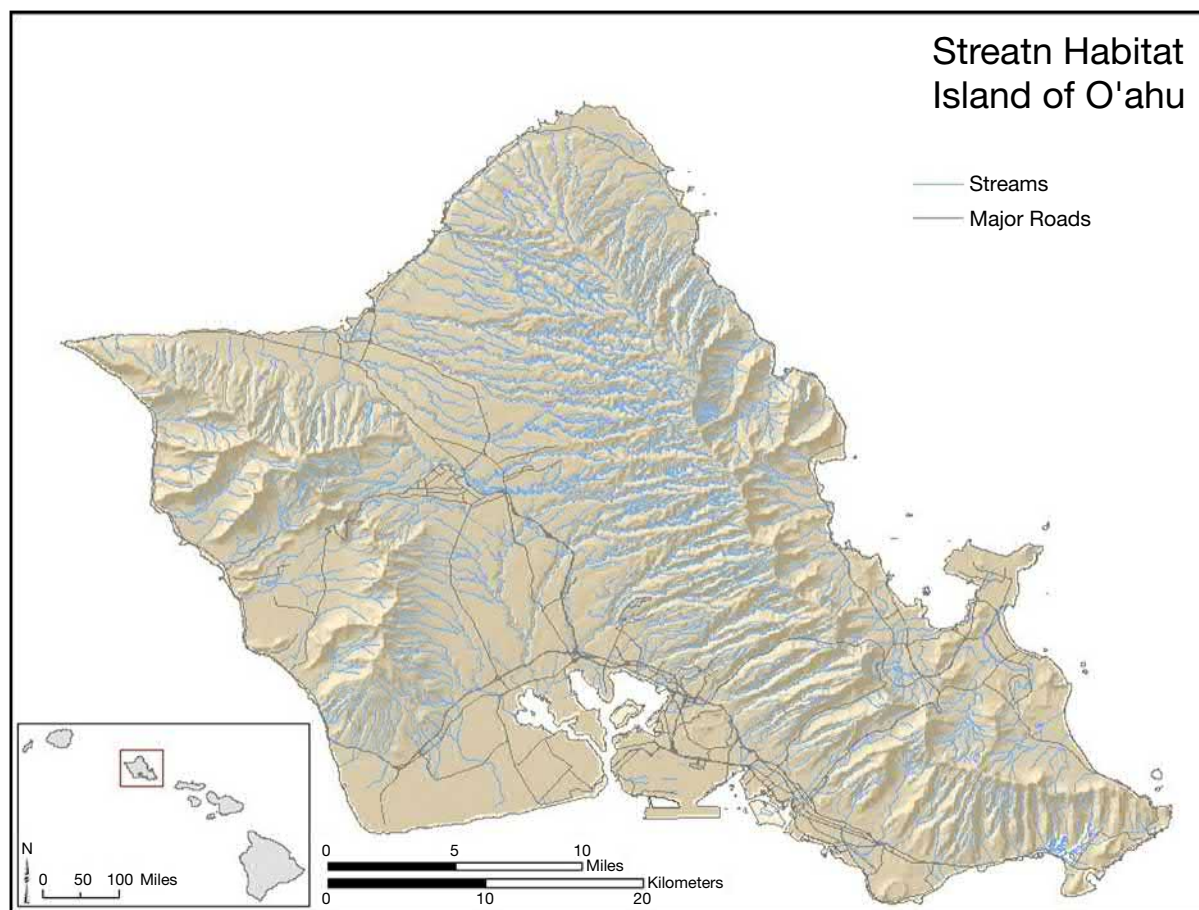


Fig. 3 Map displaying stream habitat for Island of O'ahu.

- *Middle reach*: Stream segments lying at greater than 65 ft. (20 m) elevation or above the first 32 ft. (10 m) barrier and less than 656 ft. (200 m) elevation or below the first 65 ft. (20 m) high barrier.
- *Upper reach*: Stream segments lying at greater than 656 ft. (200 m) elevation or above the first 65 ft. (20 m) barrier and less than 2460 ft. (750 m) elevation.
- *Headwaters*: Stream segments lying at greater than 2460 ft. (750 m) elevation.

Biotic Components

In strongly flowing streams, there is little accumulation of sediment, leaf litter, and other loose debris due to continuous flow and flash flooding caused by heavy rains in the mountains or strong weather fronts. Storms can occur any time of the year but are most frequent during the winter months between February and April (Fitzsimons et al., 2008). Because of frequent flash floods, mountain streams remain in a constant state of recovery from the most recent freshet.

Flash floods flush away debris that contribute to oxygen depletion during periods of low water, remove sediments that can smother the eggs of stream animals, and open up the stream mouth where it flows into the sea (DAR Geology, 2018b).

Vegetation Composition and Structure

Generally, streams contain less than 25% canopy cover. Streams can flow through varied landscapes including rainforests, deciduous forests, and high altitude grasslands. Canopy cover is important because it keeps water cool and limits the growth of algae. Cool water has a greater oxygen holding capacity than does warm water. Streams without canopy cover are exposed to the warming effects of the sun, which can change plant and animal species composition and abundance. Streams that are exposed to too much sunlight may have thick algae attached to the rocks, floating algal mats, surface scum, and/or a microbial sheen. These are all

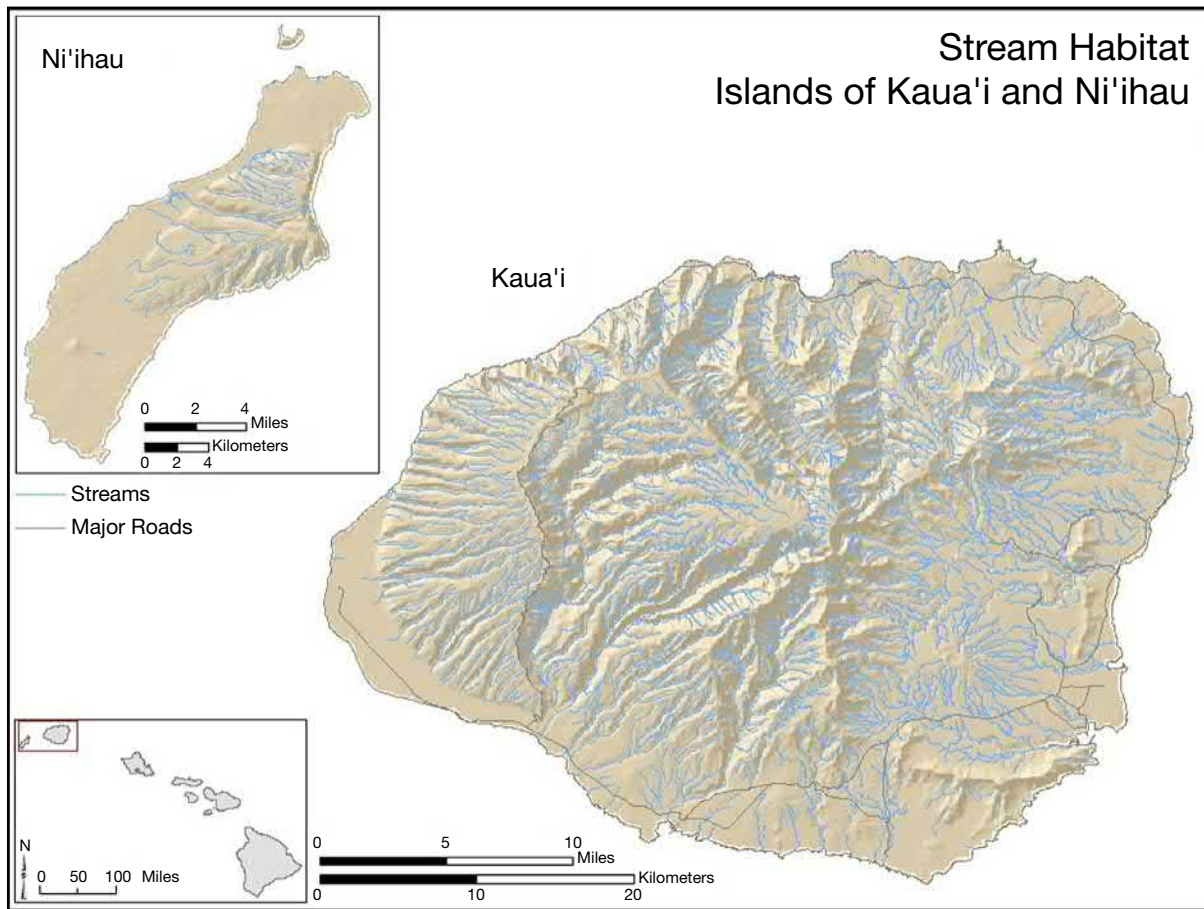


Fig. 4 Map displaying stream habitat for islands of Ni'ihau and Kaua'i.

indicators of eutrophication, an excessive richness of nutrients due to runoff which causes a dense growth of aquatic plant life (Natural Resources Conservation Service, 2001).

Habitat Viability

Resiliency (the ability to withstand environmental stochasticity), redundancy (the ability to withstand catastrophic events), and representation (the ability to adapt to a changing environment over time) will be discussed in the following sections as to how viable stream habitats were/are/expected to be (historically, currently, and in the future).

Prehuman Condition

Prior to the arrival of Polynesians approximately 1500 years ago, streams in the Hawaiian archipelago likely looked much different than they do today. Although no references or descriptions are available for this prehuman time period, we can infer what it may have looked like from existing stream systems and our knowledge of the ecological processes that affect stream form and function.

Prior to human arrival, we can assume that Hawaiian streams functioned under ideal conditions. The Natural Resources Conservation Service has described what ideal stream conditions might look like (Natural Resources Conservation Service, 2001).

Mixed (Open and Closed) Canopy

Canopy is an indicator of shade. Considering prehuman conditions involved no invasive plant or animal species, it is likely that canopy conditions let enough sunlight in for some algal growth that fed native aquatic species, but not enough to make the stream eutrophic. A mixed canopy increases the resiliency of the stream habitat by keeping the water cool during periods of drought, and by keeping the surrounding soil moist which reduces erosion.

Riparian Zones and High Bank Stability

Riparian area is the width of the natural vegetation zone from the edge of the active channel (or normal water line) out onto the floodplain. Considering prehuman conditions involved optimal canopy, and diverse understory, shrub, and groundcover species, it is likely that riparian zone conditions were good. A good riparian zone has high resiliency—reduces surface runoff, controls erosion, provides shade, and dissipates energy during flood events. Bank stability is the potential for erosion from the stream banks into the stream. High bank stability indicates the bank is not bare or erodible. Although, some bank erosion is normal in a healthy stream. Excessive bank erosion occurs where riparian zones are degraded. Considering prehuman conditions involved good riparian zones, it is likely that most stream banks were highly stable.

Low Turbidity

Turbidity is an indicator of erosion. Considering prehuman conditions involved optimal canopy, good riparian zones, high bank stability, and no invasive ungulates, it is likely that most streams were minimally turbid (because of high resiliency). In the rare event of flooding, it is likely that a stream habitat would become turbid for a short period of time, but would likely recover quickly once the surrounding riparian/bank area stabilizes. This high redundancy is attributed to rainfall. Surrounding riparian/bank areas on the windward side of higher islands were more redundant than those on the leeward side of lower islands because higher rainfall would help to regenerate vegetation and stabilize banks, which would in turn, limit erosion.

Low Plant Growth

Plant growth is an indicator of eutrophication. Considering prehuman conditions likely involved mostly shaded, nonturbid conditions, it is also likely that few streams were ever eutrophic. In the rare even of a fire, where surrounding vegetation and canopy cover were destroyed, it is possible that a stream habitat would experience higher than average plant growth because of over exposure to the sun. However, on higher islands that generate orographic rainfall, riparian vegetation and canopy would reestablish and prevent the stream from eutrophication. Stream habitats on higher islands are more likely to exhibit this type of redundancy than lower islands because of their ability to generate orographic rainfall.

Habitat Available for Native Species

The potential for stream biota to live, thrive, and recover from disturbance is dependent on the variety and abundance of suitable habitat available. Stream habitats on windward sides of higher islands were more likely to have higher representation than stream habitats on leeward sides of high and low islands because of the ability to generate orographic rainfall on windward sides. Considering prehuman conditions didn't involve stream alterations such as diversions, withdrawals, or channelization, it is likely that most of the larger streams on the windward sides of higher islands contained five main habitat types (streams on windward sides of lower islands possibly had five main habitat types, but they probably had less diversity):

1. *Seeps and springs*—Areas in the riparian zone where there is groundwater input.
2. *Pools*—Areas characterized by smooth undisturbed surface, slow current, and deep water. Included in this habitat would be deep plunge pools at the bases of cascades or waterfalls.
3. *Runs*—Areas characterized by moving water, but no broken water surface or whitewater.
4. *Riffles*—Areas characterized by broken water surface, rocky or firm substrate, moderate or swift current, and relatively shallow depth (less than 18 in.). Generally, the flow is fast and shallow.
5. *Cascades*—Waterfalls, or steep riffles with greater than 3% gradient.

Habitat Viability

Prior to human contact stream habitat likely exhibited high resiliency. For example, in the event of drought, there was likely enough canopy to keep the water cool and keep it from evaporating quickly. Similarly, the canopy was likely able to keep the soil in the riparian and buffer zones moist enough to support vegetation and prevent excessive erosion. In the event of lava, streams likely rerouted around the flow (or over time, over or through the lava rock, depending on how big the flow was). In the event of fire, if riparian vegetation was affected, the stream would likely have been susceptible to erosion until the vegetation was reestablished. However, since surrounding riparian habitat likely had high representation, affected areas would have been able to be reestablished relatively quickly due to the proximity of appropriate source material.

Prior to human contact stream habitat likely exhibited high redundancy. Due to the range of stream habitats found on higher islands (Kaua'i, O'ahu, Maui, island of Hawai'i) compared to lower islands (Ni'ihau, Lāna'i, Kaho'olawe), it is likely that streams on higher islands were able to withstand catastrophic events, like drought, better than streams on lower islands. This is likely due to the higher islands being able to generate orographic rainfall which helped those streams recover more quickly than streams and seeps on lower islands that are more ephemeral and have a higher reliance on climatic events that bring heavy rainstorms.

Historically, the level of stream habitat diversity depended on if the mountains were high enough to generate orographic rainfall and which side of the island the stream was located (windward or leeward). Typically, stream habitats exhibited high representation on higher islands, with more diversity on windward sides of the islands; and low representation on lower islands likely with lower diversity.

Current Condition

Stressors

Fresh water on oceanic islands is important for agricultural, industrial, and individual use. Diversion, channelization, and withdrawals of stream water by humans for these purposes or for flood control is a continual threat to stream habitat quality, even in lowland areas. One-fifth of Hawai'i's streams, mostly on O'ahu, have been channelized, lined, or straightened in order to carry floodwaters away from people and property, stabilize stream banks, or increase the amount of land for development (CWRM, 1993; U.S. Fish and Wildlife Service, 1978a,b). Agricultural chemicals, sedimentation, municipal wastes, invasive species, and changes in turbidity, oxygen content, flow, and water temperature can all lower the quality of the habitat. Feral animals or livestock, and urbanization or land use practices that remove streamside canopy cover, can increase water temperatures and cause eutrophication (Stone, 1989). Furthermore, as climate change causes higher temperatures and longer dry seasons or drought, stream discharge can be reduced significantly, causing irreversible changes.

Channelization and Water Diversion

Streams played an important role in indigenous Hawaiian Culture. Ahupua'a were land divisions which served as political, traditional, economic, and social units of Hawaiian Society based on local watersheds with boundaries running from the mountain summits to the sea. Within each division, native Hawaiians developed agriculture and aquaculture systems that utilized many of the islands' streams to supply the water (CWRM, 1993). Diversion of streamflow for agricultural use was an ancient Hawaiian practice and engineering achievement. Excavations and radio carbon dating suggest these irrigated farming systems started around the 15th century. Typically, these systems dam perennial streams with large rocks, divert the water into ditches, distribute the water to terraced pond fields that were used to grow primarily taro (*Colocasia esculenta*), then divert water back to the stream where it empties into fishponds, estuaries, or the ocean. The sugarcane industry expanded on this ancient Hawaiian practice by diverting streamflow from headwaters and transporting it by ditches and tunnels to distant areas, which were usually dry lowland areas. In 1856, the first ditch diversion for sugarcane irrigation took place on Kaua'i. Since then, complex networks of diversion and transport were used to move water throughout Hawai'i (Lau and Mink, 2006).

About 50% of all streams throughout Hawai'i are diverted for agricultural use of water, and urban streams are highly altered by channelization and straightening for flood control (U.S. Fish and Wildlife Service, 1978a,b; Oki, 2003). About 40 of these are larger stream systems that form stream-mouth estuaries.

Channelizing streams can be detrimental to riparian ecosystems by quickly removing fish and wildlife habitat, destroying streambank vegetation and changing stream depth, velocity and temperature. It can also alter stormwater discharges into wetlands, estuaries, and the ocean. Interrupting stream continuity can also impede migrating native freshwater fish, snails, and shrimp (CWRM, 1993). Stream diversions for development and agriculture can also reduce habitat availability around streams by decreasing flows and water depths (Brasher, 2003).

Channelization and water diversion decrease resiliency of stream habitat. By removing surrounding vegetation, erosion and turbidity increase. Fewer habitat types are available for species, which lowers representation. In the event of drought, water temperature increases which in turn increases plant growth and eutrophication.

Urbanization

Urban development increases the area covered by impervious surfaces. It directly lowers the resiliency of stream habitat by increasing the amount of polluted runoff into the stream. Many urban streams serve as conduits for excess storm drain runoff and over-stressed sewage systems, as well as illegal dumpsites for garbage (CWRM, 1993). All of these are negative impacts to the stream habitat and lower its representation, making it uninhabitable to native species. As urbanization continues to increase, so will stream modification (Brasher, 2003). The removal of canopy will lower the resiliency of the stream habitat, and with the addition of polluted runoff, more streams will become eutrophic.

Recreation

Hiking, swimming, fishing, and/or picnicking along Hawai'i's streams can inadvertently cause harm by trampling vegetation, disturbing terrestrial and aquatic species, and polluting the streams (CWRM, 1993). An increase in human disturbance, for example—trespassing and damage from recreational motorbike riding, can create openings (loss of vegetation and canopy) in the forest near streams. These openings can lower resiliency, which increases stream bank erosion and water temperature, which may eventually cause eutrophication if recreation persists (West Maui Mountains Watershed Partnership, 2018).

Storms, Flash Floods, Erosion, and Sedimentation

A severe flash flood carrying a large debris load of boulders and large tree limbs is capable of pushing adult animals completely out of a stream (as happened with Hurricane 'Iniki in 1992) (Fitzsimons et al., 2008; Parham et al., 2008). Flash flooding events can cause mudslides, stream erosion, push heavy boulders and large vegetation downstream, thus destroying ungulate fencing, bridges, and other manmade channelization/diversion structures. Not only do storms and flash floods cause immediate damage to stream banks (i.e., erosion), but they also wipe out the vegetation that provides canopy cover and bank stabilization, both of which help to prevent erosion.

One such flash flood event occurred on Maui in September 2016, destroying numerous fences in West Maui. 'Iao Valley State Park, located in Wailuku on Maui, closed for months due to severe damage. Damage included an eroded streambed, damage to ungulate-proof fences due to the heavy debris load of boulders and tree limbs, and loss of the stream flow gauge. Other physical structures including the parking lot and associated outbuildings were also destroyed. Another event occurred on Kaua'i in April 2018 when flooding west of Hanalei completely cutoff access to Wainiha and Hā'ena communities for excess of a year.

As mentioned in the Description section, streams in Hawai'i are prone to flash floods because rainfall is intense, drainage basins are small, basins and stream profiles are steep, and channel storage is limited (Oki, 2003). Historically, stream habitats exhibited ideal conditions and could "weather the storm." However, currently, with added stressors such as flooding, streams are much less resilient (reduced riparian area and bank stabilization). Furthermore, redundancy is lowered as development increases, which makes it hard for streams to maintain habitat diversity (low representation) and support native species.

Drought and Wildfire

Severe periods of drought have the potential to negatively impact stream flow for Hawaiian streams by converting perennial streams to intermittent streams, and current intermittent streams and seeps to dry out. With these stream flow conversions, native and nonnative plants will die and dry out from the lack of water, which will also be detrimental to the aquatic flora and fauna. This will cause severe erosion of the streambed and remove canopy cover causing water, if flowing, to be in full sun thus increasing the water temperature and eutrophication. As noted above in the Storms section, an especially severe flash flood can carry a large debris load of boulders and large tree limbs capable of pushing adult animals completely out of a stream (as happened with Hurricane 'Iniki in 1992) (Fitzsimons et al., 2008; Parham et al., 2008). The effect of catastrophic events is exacerbated by other stressors as it changes the quality of the surrounding vegetation making it more susceptible to windfall and erosion. As dry biomass accumulates near streams and surrounding habitats, wildfire has the propensity to occur more frequently and spread faster over greater distances due to the quick burning nature of flashy fuels like dead grass and plant material that can cause the stream temperature to increase.

Drought decreases stream habitat resiliency by decreasing canopy cover, which increases water temperature. During long periods of drought, high temperatures can cause the soil to dry out and erode, and also cause eutrophication. Drought also decreases redundancy. Without orographic rainfall, streams cannot support communities of native species. This would also result in a decrease in representation because without rainfall, stream diversity decreases.

Invasive Species

Early immigrants and settlers brought domestic animals and plants to Hawai'i. Over time, some of these pigs (*Sus scrofa*), deer (*Axis axis*), goats (*Capra hircus*), sheep (*Ovis orientalis*), and cattle (*Bos taurus*) ran wild, trampling and eating native plants, spreading seeds and spores from nonnative vegetation, increasing erosion and siltation due to trampling through streambeds, causing streambank alterations, and leaving feces on stream banks that lead to elevated bacterial and nutrient levels (CWRM, 1993). The long list of invasive species includes terrestrial and aquatic plants and animals. Some introduced species have not proliferated, and a few appear to be harmless. However, many of these species have become invasive and have exerted negative effects on the islands' flora and fauna, especially at stream habitats. Entire streams and estuaries have become choked with nonnative vegetation to the point that native plants are crowded out, egg-laying sites for stream fishes and invertebrates are buried beneath vegetation, mud, and silt, and the water no longer has sufficient dissolved oxygen to support most aquatic animals. Nonnative and invasive vegetation decrease stream bank stabilization due to shallow root systems, which leads to erosion, and adds sediment to the stream that eventually is discharged into the ocean. Nonnative freshwater fish species currently outnumber native stream species, and the number of introduced species is likely to increase in spite of efforts to protect native species.

Invasive species lower resiliency by dominating riparian areas. Invasive plant species have shallow root systems that are ineffective at stabilizing streambanks. This results in erosion and turbidity, following normal rainfall. Invasive species also lower representation by dominating stream habitats. They outcompete native vegetation, which results in low habitat diversity. Native plant and animal species cannot compete in a stream habitat dominated by invasive species (Figs. 5–13).

Conservation Efforts

Protection of streamside vegetation to preserve natural aquatic temperature and light conditions and sources of food for stream organisms is important. Feral ungulates such as pigs, deer, goats, sheep, and cattle should be removed from watersheds drained

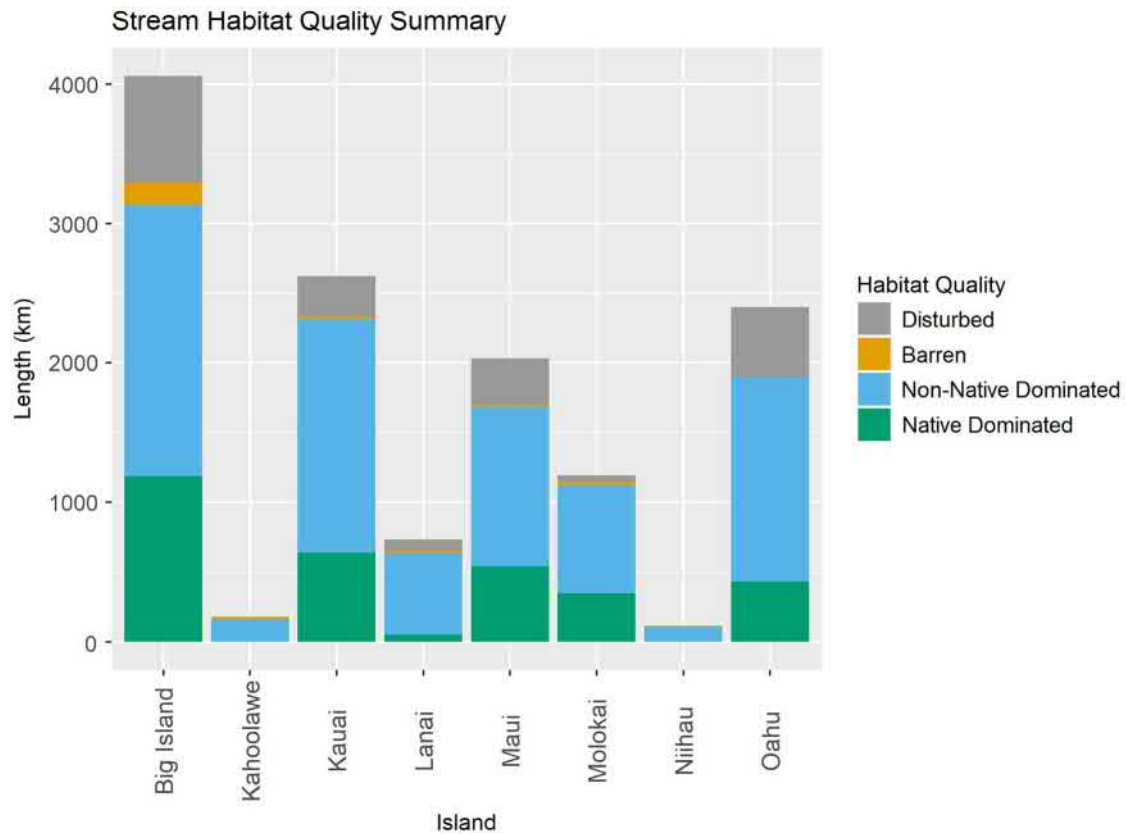


Fig. 5 Summary of stream length through four different habitat quality types. From: Reeves, M. K. and Amidon, F. (2018). *Habitat status assessment methods – Hawaii, current condition summaries*, pp. 439. Technical report from the U.S. Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, Hawaii.

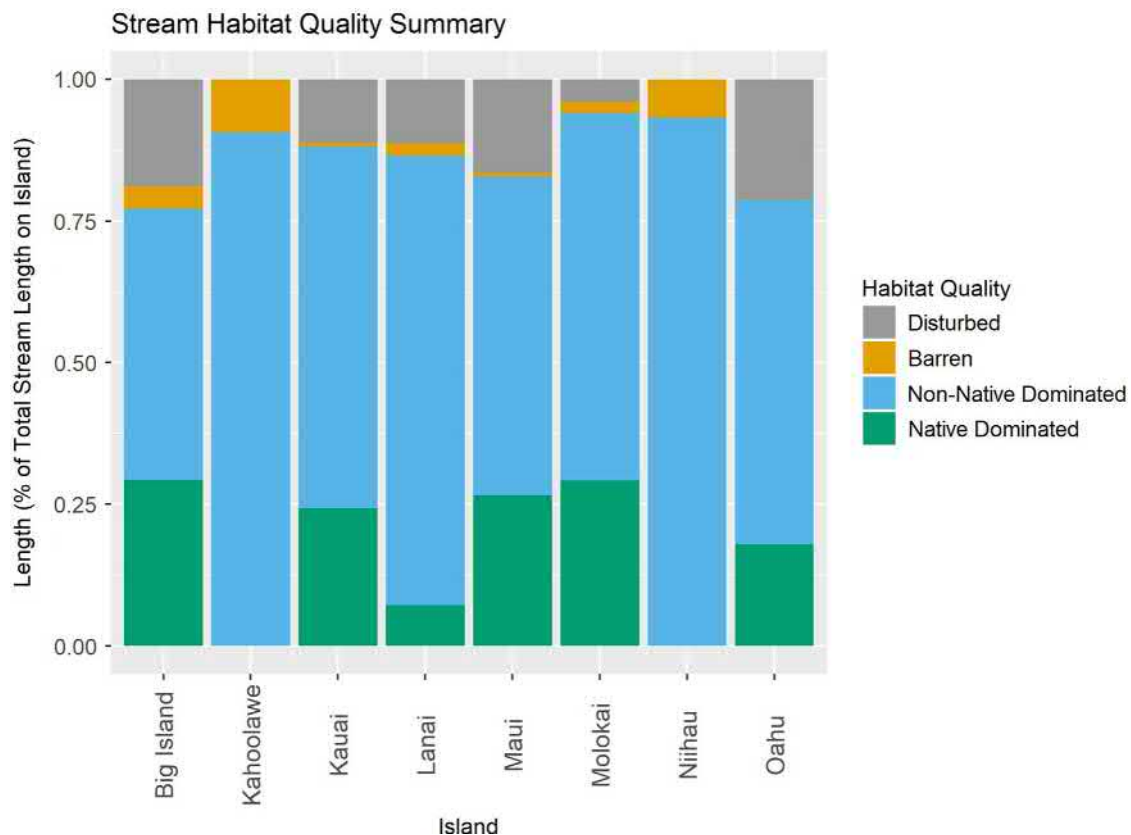


Fig. 6 Percent of total stream length through four different habitat quality types. From: Reeves and Amidon, 2018.

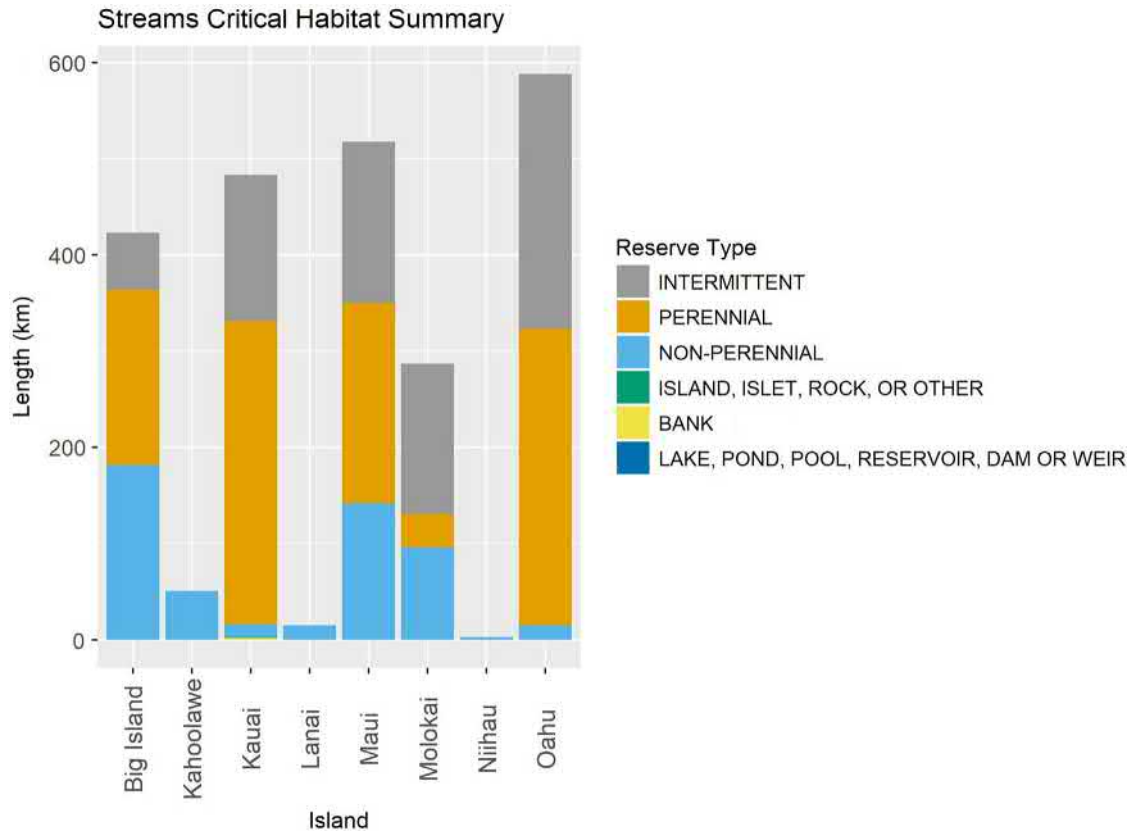


Fig. 7 Length of stream reserve type in delineated critical habitat. From: Reeves and Amidon, 2018.

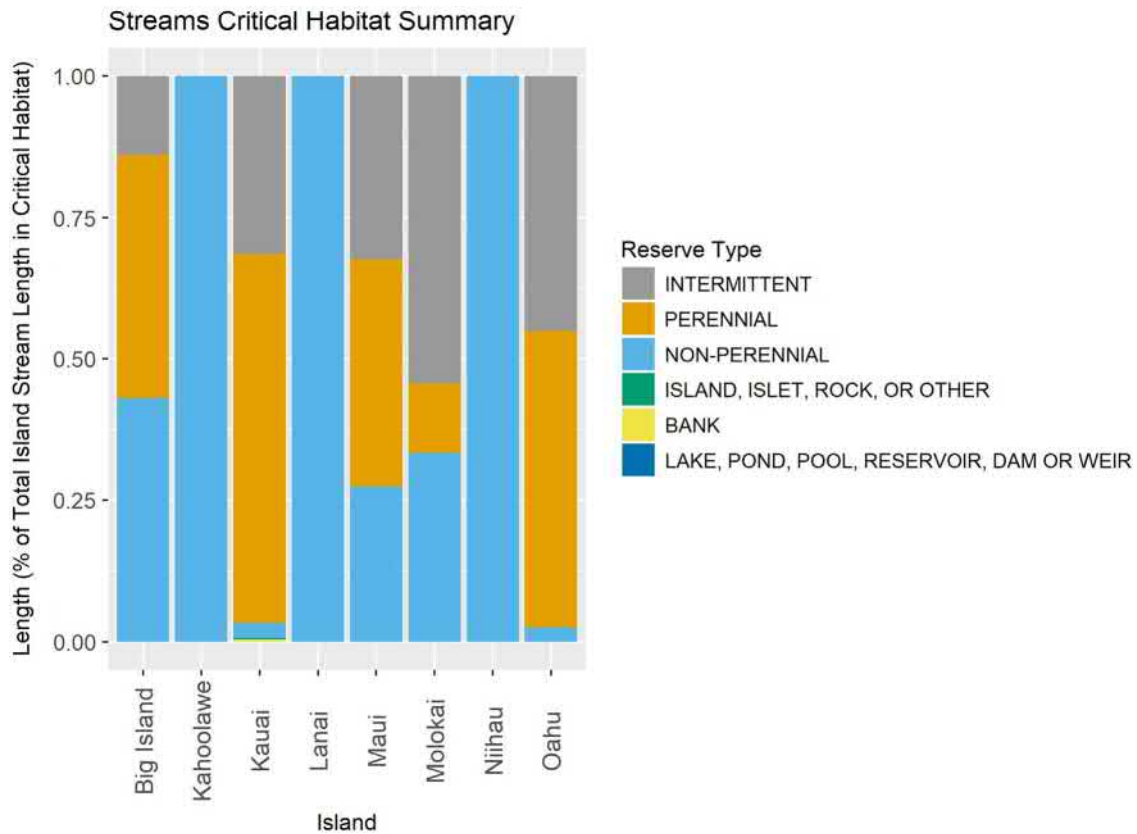


Fig. 8 Percent of total island stream length in critical habitat. From: Reeves and Amidon, 2018.

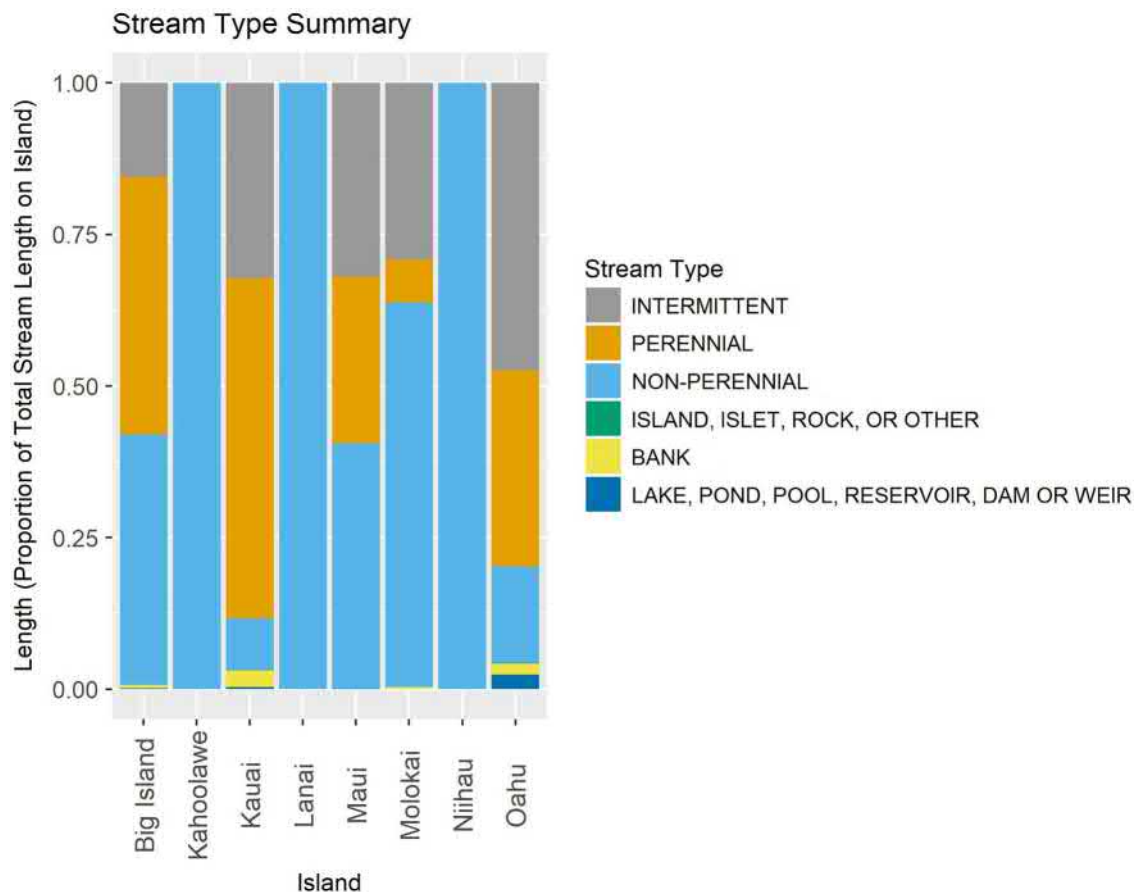


Fig. 9 The proportion of stream types by total length on Hawai'i. From: Reeves and Amidon, 2018.

by nearly pristine streams, and prevention of pollution from development and agriculture in these areas should be emphasized. Watershed partnerships, government agencies, and nonprofit groups protect streams and entire watersheds by fencing areas to keep ungulates out, removing ungulates within the fenced areas if required, removing invasive plant species to promote native plant growth, and organizing education and outreach events focused on the importance of protecting Hawaiian streams and watersheds. Channelization projects that result in replacement of natural substrate with artificial bottom material, reduction of stream channel length, and vegetation removal should be avoided where feasible. Active conservation education about the value of Hawaiian streams is necessary along with educational materials available from environmental groups that help inform the public about conservation issues (Stone, 1989). Watershed groups, government agencies, and nonprofit groups are playing a critical role in restoring stream functions through watershed plans and restoration activities. As a result, their efforts generally increase resiliency, redundancy and representation.

Management

Management actions to address stressors can help to improve stream habitat conditions. Implementing feral ungulate control and invasive plant control will promote growth of native vegetation along riparian areas, which will decrease erosion and increase resiliency of stream habitats during flood events. Restoring and enhancing populations of native pollinators and plants can increase canopy cover over streams, which will keep them cooler and increase redundancy of stream habitats during drought events. Educating the community and implementing monitoring programs can keep communities aware and get them involved in actively working to conserve stream habitats. Over time, this will increase representation of stream habitats in their ability to adapt to changing environmental conditions.

Nonnative animal control

Feral ungulates have a serious effect on native ecosystems—particularly on the ground layer of vegetation. Native plants evolved without the need to defend themselves against large animals; most have no thorns or toxins to keep animals from grazing on them. Very few native plants have deep root systems, and cannot survive when the soil around them has been trampled and compacted. Impacts to the streambanks due to trampling from ungulates can cause erosion and stream incision. Small mammals, such

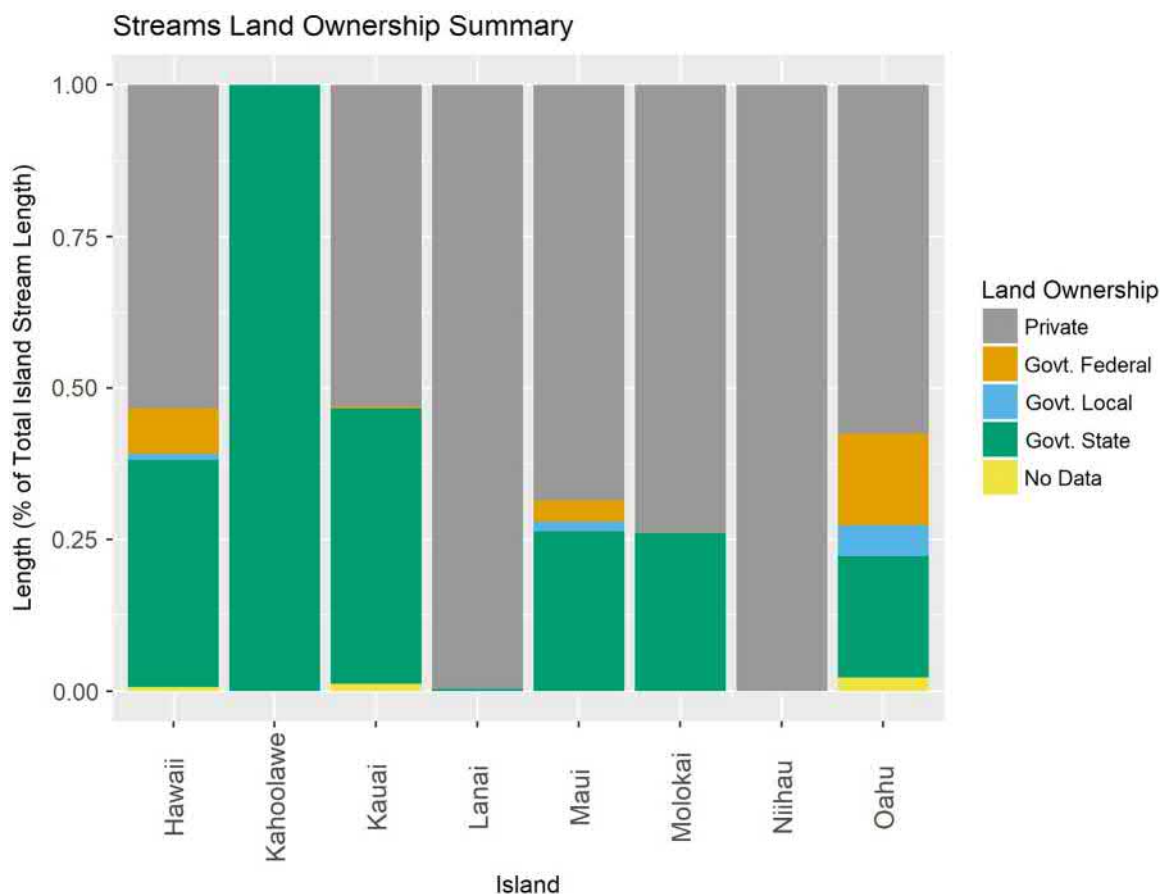


Fig. 10 Percent of total island stream length based on land ownership. From: Reeves and Amidon, 2018.

as mongoose (*Herpestes javanicus*), rats (*Rattus rattus*), and mice (*Mus musculus*), can also be a serious threat. They prey on native birds and nests, feed on the seeds and seedlings of native plants, and carry diseases such as leptospirosis which can harm humans as well as animals when it gets into stream systems. Actively removing animals is often required to limit their effects. Public hunting and staff control, fencing, one-way gates, and other innovative actions are components of successful animal control efforts attempted throughout Hawai'i.

Nonnative plant control

Nonnative and invasive plants can pose serious threats to the native Hawaiian ecosystems including streams. Certain weeds have the ability to spread quickly, establish themselves in many types of forest habitats, and take over large areas. They do this by out-competing the native plants, particularly at the seedling stage. Control of these weeds requires a variety of measures, including mechanical removal (machines or hand), applying herbicides, or biological control methods.

Restoration and habitat enhancement

Management of native ecosystems may also require restoring or enhancing existing populations of native pollinators (birds and insects) or plants. Increasing the number of existing individuals of rare plants through propagation and out-planting programs or increasing the number of rare birds through captive breeding and release are among the tools available. Maintaining or restoring the dynamic natural processes is the goal of native ecosystem protection and restoration programs. Outplanting native species near streams can aid in lessening streambank erosion and provide canopy cover keeping the streams cooler.

Monitoring

A comprehensive monitoring program that helps managers understand what resources are present in each specific area, their health and abundance, and what threats are present can help to inform management for different streams and along different stream reaches. Monitoring actions include periodic surveys to gather information on the status and condition of resources, the status and extent of threats to those resources, and the success or failure of management actions.

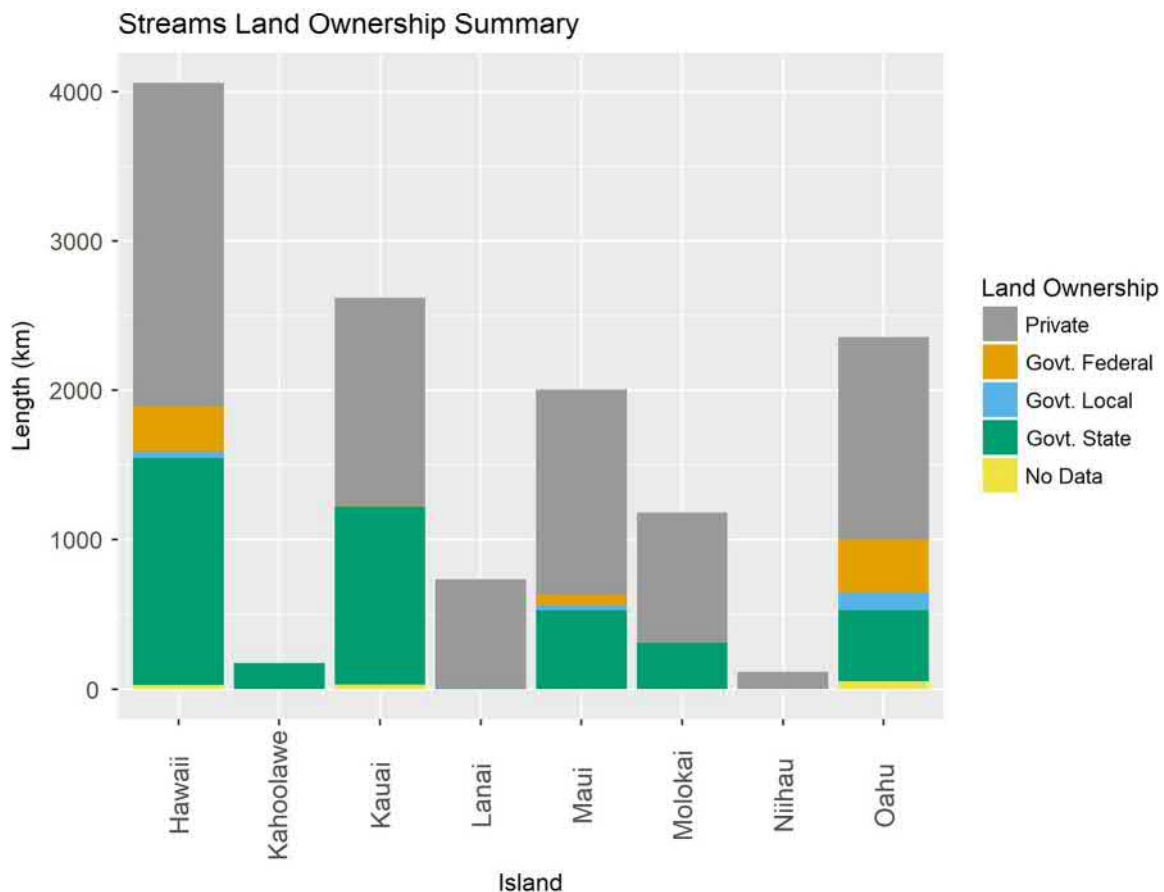


Fig. 11 Total length of streams based on land ownership. From: Reeves and Amidon, 2018.

Education and outreach

Without a clear understanding of what native ecosystem management involves and why it is needed, public support for these programs will be difficult to obtain. Information and education are incorporated into protection efforts whenever possible. To obtain public support for management, an education program that includes products such as informational brochures, video productions, speakers to address schools and community groups, and active outreach and volunteer programs are all important conservation strategies utilized by Hawaiian conservation groups and agencies.

Land Protections

The State of Hawai'i has statewide the Natural Area Reserves System (NARS) that was established to preserve in perpetuity specific Hawaiian land and water areas that support assemblages, as relatively unmodified as possible, of the natural flora and fauna, or notable geological sites. The system presently consists of 21 reserves on five islands, encompassing 123,810 acres of the State's most unique ecosystems. The diverse areas found in the NARS range from marine and coastal environments to lava flows, tropical rainforests, and even an alpine desert.

Many of these NARS encompass numerous streams and the surrounding habitat. One of the statutory responsibilities of the NARS Commission is to conduct studies of areas for possible inclusion and recommend to the governor and the department areas suitable for inclusion within the reserves system (HRS § 195-7). Other reserves that protect and actively manage Hawai'i's native ecosystems including streams (Figs. 9 and 10) are the National Park Service, The Nature Conservancy of Hawai'i, USFWS National Wildlife Refuges, State of Hawai'i Wilderness Parks, and National Historic Parks.

Laws and Regulations

The United States Army Corps of Engineers' (USACE) regulatory efforts authorized by the Clean Water Act and the Rivers and Harbors Act protect a wide variety of aquatic resources, including wetlands, rivers, streams, tidal waters, coral reefs, shellfish

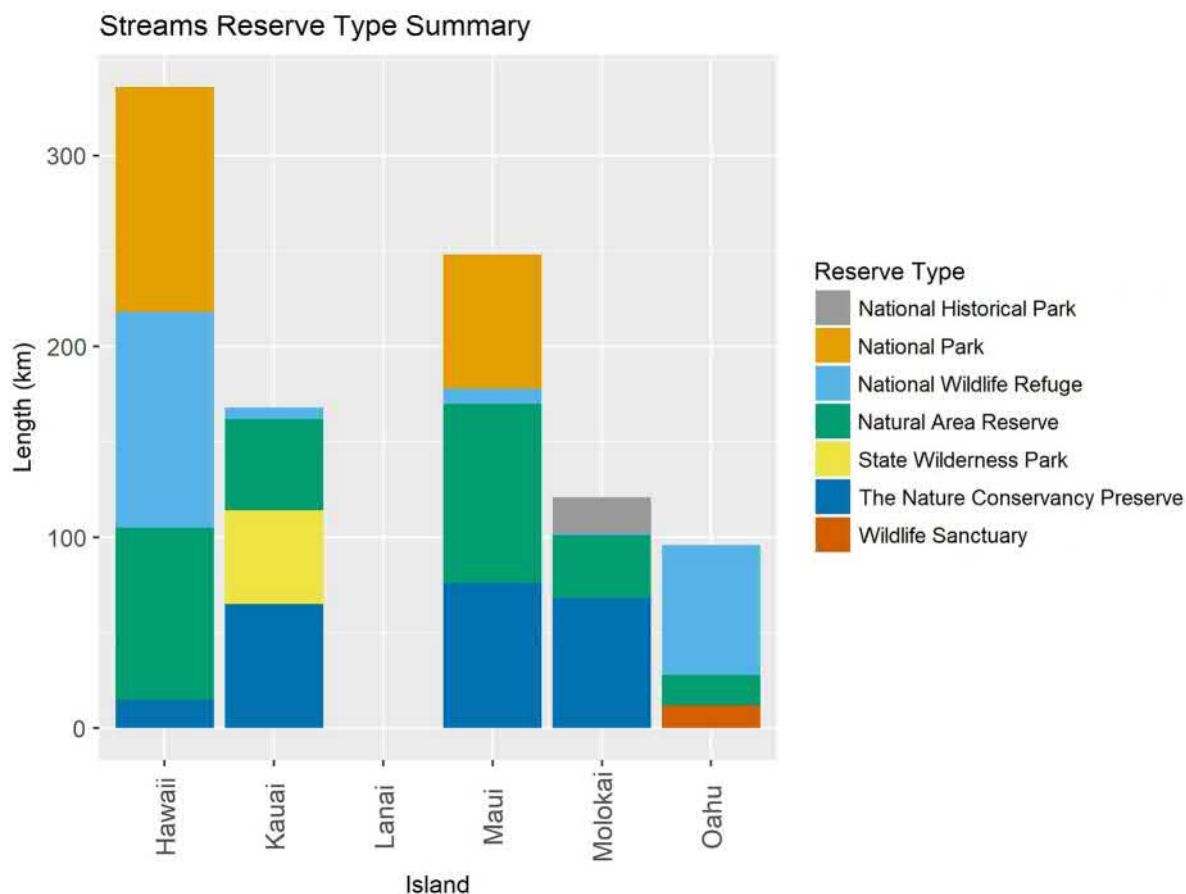


Fig. 12 Length of streams through different reserve types. From: Reeves and Amidon, 2018.

beds, and the oceans. The permit process is designed to minimize environmental impacts of construction and dredging activities in U.S. waters and to ensure such efforts are thoughtful and coordinated. The Corps Regulatory Program provides oversight of discharges of dredged or fill material into waters of the United States, and construction or other work in navigable waters of the United States, under Section 404 of the Clean Water Act and Section 10 of the Rivers and Harbors Act of 1899. A proposed project's impacts to these areas will determine what permit type is required. The USACE Regulatory Program is committed to protecting the Nation's aquatic resources and navigation capacity, while allowing reasonable development through fair and balanced decisions. The USACE evaluates permit applications for essentially all construction activities that occur in the Nation's waters, including streams and wetlands. The Honolulu District evaluates about 300 permit applications each year under its regulatory program. The Corps authorizes permits under Section 10 and 404 permits throughout Hawai'i.

The Hawaii State Water Code (HRS 174C) provides a Commission on Water Resources Management (CWRM) with authority to establish minimum instream flow standards to protect stream habitats for fish and wildlife. Specifically, the Code mandates that public trust uses such as minimum instream flows for ecological integrity and traditional cultural practices must be fully addressed before off-stream allocations can be granted. In 1988, legislators also asked the State Commission on Water Resources to set up a Wild and Scenic Rivers System, although only limited progress has been made in this regard. Streams proposed for such designation include Kahana Stream on O'ahu; Kahakuloa and Hanawi on Maui; Waimanu on Hawai'i; Kilauea, Hanalei, and Lumaha'i on Kaua'i; and Wailau and Pelekunu on Moloka'i (Stone, 1989).

The CWRM has recently implemented Interim Instream Flow Standards (IIFS) for numerous streams on Maui, and is in the process of additional designations on that island. For over 100 years, the majority of the perennial streams on Maui had been diverted to the island's central isthmus for sugarcane irrigation. On April 24, 2014, the CWRM settled a contested case involving West Maui streams by restoring flows in four major windward catchments (Waikapu, Wailuku, Wai'ehu and Waihe'e). Even after the closure of the last Maui sugarcane plantation in 2016, however, water from streams on the windward coast of East Maui continued to be diverted from this sector for other uses (KHON2, 2018), over the objections of various stakeholder groups. On June 20, 2018, the CWRM issued the largest water rights decision in state history. The decision involved 27 streams on East Maui, restoring flows to many of these diverted systems and requiring all future diversions to be fully justified. The direction of these recent legal decisions means many streams on Maui and elsewhere in Hawai'i may now have the opportunity to gradually return to

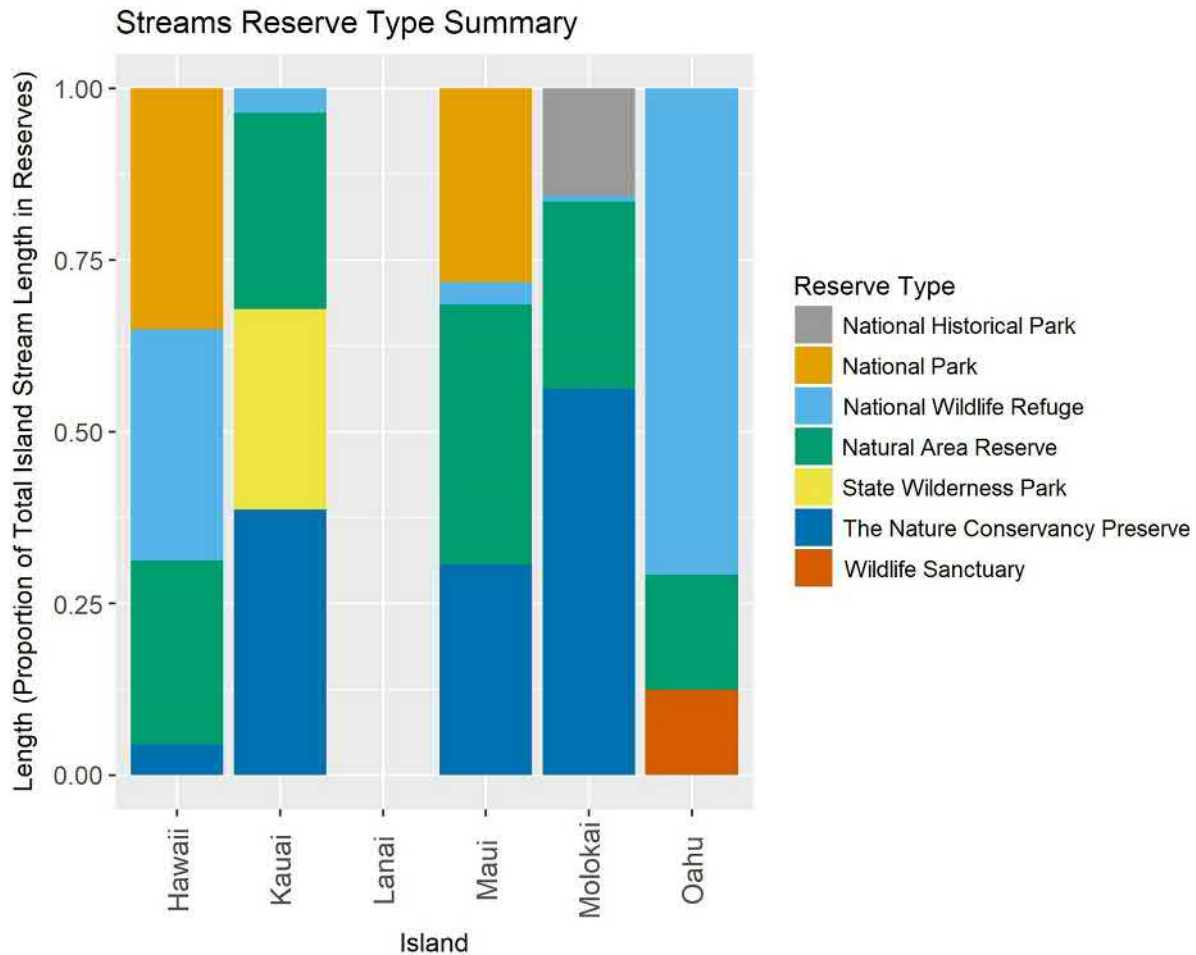


Fig. 13 The proportion of total island stream length in reserves. From: Reeves and Amidon, 2018.

more natural flow regimes similar to those that prevailed when the first Polynesians arrived in the islands, which will benefit native aquatic biodiversity.

Habitat Viability

Stream habitat currently exhibits relatively low resiliency compared to historical stream habitats. Many stream habitats no longer have native canopy to keep the water cool in the event of a drought. Similarly, many stream habitats don't have a canopy to keep the soil moist for riparian and buffer zone vegetation that prevents erosion during drought. In the event of a fire, if riparian vegetation is affected, the stream will likely be susceptible to erosion, eutrophication, and also to reestablishment by invasive species, since native riparian vegetation is often poorly represented.

Currently, stream habitat redundancy is still greater on higher islands compared to lower islands. However, redundancy overall is reduced across the Hawaiian islands due to stressors such as channelization, water withdrawals, development, invasive species, etc. For example, most O'ahu streams, despite being in or near highly developed areas, will likely recover from drought more quickly than seeps on Lāna'i, which were severely impacted by agriculture and feral ungulates. Both types of stream habitats, however, will now recover at a slower rate overall compared to how they would have recovered historically. These added stressors lower redundancy across the board by decreasing the overall number of flowing stream systems across the islands, but higher islands will still recover faster because of their ability to capture orographic rainfall.

Stream habitat on higher islands currently still have higher representation than stream habitat on lower islands because of their ability to generate orographic rainfall. However, compared to historical stream habitat, representation is lower across all islands. Urbanization and invasive species are a couple of the main stressors that lower representation and diversity of stream habitat to the point to where no native species can compete.

Future Scenarios

The condition of stream habitat in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are as follows:

- (1) *Conservation values*: Stakeholder involvement and public opinion determine the formulation, implementation and funding of natural resource conservation within laws and development plans.
- (2) *Laws and biosecurity*: National, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented. (e.g., hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.).
- (3) *Development or conservation planning*: National, state, county, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

These conservation management parameters are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The year 2035 is the extent of the “foreseeable future,” and is based on the projected divergence of IPCC Representative Concentration Pathway (RCP) climate change scenarios.

The four foreseeable future scenarios considered in this habitat assessment are:

Future Scenario One, Status Quo—The most likely foreseeable future; no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues through the foreseeable future.

Future Scenario Two—A slight increase in natural resource conservation in the CMPs marginally improves conservation management.

Future Scenario Three—A slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management.

Future Scenario Four—A moderate to large increase in conservation actions in the CMPs substantially improves conservation management.

The future condition of stream habitat in Scenario One, the status quo, was characterized from an assessment of change over time in stream land cover obtained from existing land cover maps (Amidon and Reeves, 2018a,b). Based on these land cover maps, an annual rate of change for Stream habitat was estimated, and a projected change (in acres/hectares) was calculated for the year 2035. The resulting information on changes in land cover by 2035, as derived from existing land cover change estimates, is the extent of the Stream habitat that is expected in the foreseeable future under Scenario One, the status quo, where conservation efforts remain unchanged and the current rate of change in land cover is also unchanged.

The future conditions of stream habitat for Scenarios Two, Three, and Four cannot be quantitatively (acres/hectares) estimated. However, the Scenario One estimate can provide a “baseline” for a qualitative characterization of changes in the future condition of Stream habitat under Scenarios Two, Three, and Four.

Changes in human population are captured only by the changes in the “developed” land cover footprint derived from land cover map analysis (Amidon and Reeves, 2018a,b). Impacts from other sources of human activities or human-caused habitat stressors (e.g., plant and animal diseases, wildfires, invasive species, etc.) are not well characterized in the land cover changes, but significantly contribute to increases in the land cover area dominated by nonnative vegetation.

Also, note that island-wide implementation of the CMPs is unlikely to have a significant effect on climate-related stressors (temperature, precipitation, and severe weather) resulting from global warming by 2035. This lack of CMP climate effects is due to the global lag in climate response to changes in greenhouse gas emissions, which occurs on the order of centuries rather than years. Evidence of climate effects is also confounded by the large annual variation in the Pacific islands climate parameters, which is much greater than projected climate change by 2035. Although impacts from climate-related habitat stressors do not change across the four scenarios, they were included in this analysis because of their overall magnitude of potential importance to future habitat viability.

Future Scenario One, Status Quo

Summary: Scenario One is considered the most likely future scenario, and serves as a “baseline” for comparing among the four future scenarios. There is no change in the implementation of the three CMPs between 2018 and 2035. A continuing current rate of change in land cover through this foreseeable future results in a slow but continuous change in the habitat as described below.

Description: Using the current rate of change, the land cover for stream habitat was calculated for the year 2035. The projected change in land cover by 2035 is the only future scenario with quantitative values (acres or hectares). The anticipated changes, under Scenario One, for each of the habitat stressors affecting stream habitat are given in Table 1.

An expanding human population and increased development and general land use on all inhabited islands is anticipated, and therefore habitat stressors are expected to increase at a small annual rate. Exceptions are a small to moderate annual rate of increase for development, wild fires, and surface air temperature, and a small annual rate of decrease for precipitation. Development of land for residential, commercial, and agricultural purposes will continue.

Because the Scenario One biosecurity CMP remains unchanged while the population and development continue to grow, an increased potential for new invasive species and new diseases (particularly those affecting native plants) exists. The introduction of additional plant diseases and invasive species may enhance the conditions that support wildfires.

Under this scenario, rivers, streams, and seeps will likely show a decrease in condition and abundance compared to current conditions. This decrease in representation is attributed to increase in human population and development that will decrease water availability of rivers and streams since more water will be diverted for human and agricultural uses. Redundancy will likely decrease, compared to the current condition, especially on lower islands because of their inability to generate orographic rainfall. Current streams that are year-round will increasingly become intermittent. Streams that are currently intermittent may become eliminated, especially those on leeward sides of the Hawaiian islands. Seeps on high elevation islands may increasingly become intermittent, while seeps on lower elevation islands may increasingly become eliminated. Without updating laws to accommodate increases in recreation human presence/abundance-related stressors, there is the potential for rivers and streams to be utilized more frequently, which will slightly increase the spread of invasive species, transforming native streambanks to nonnative vegetation. Root systems and resource requirements of these invasive plant species may likely increase erosion and sedimentation of stream habitats. Increase in these stressors will likely lower resiliency of stream habitats, compared to the current condition. For example, a slight decrease in bank stability is likely to occur due to invasive ungulates and humans trampling the edges of the rivers and streams. So in the event of a storm, flooding will likely have an increased negative effect on riparian and stream bank areas because of a decrease in riparian quality and bank stability caused by ungulates and human recreation. Erosion and sedimentation will increase, and riparian vegetation may be decreased. Decrease in riparian vegetation will likely decrease canopy cover, which may increasingly lead to eutrophication.

Overall, based on this analysis, it is anticipated that under this scenario, rivers streams and seeps will decrease, relative to current condition, in condition and abundance, and will have a lower likelihood of supporting native ecological communities that depend on rivers and streams. By 2035, it is anticipated that rivers, streams and seeps will likely have lower redundancy and representation across the Hawaiian islands, and be less resilient to stochastic events.

Table 1 Responses of Stream habitat stressors in foreseeable future scenarios.

Conservation management parameters (CMPs)				
Conservation values	Stakeholder involvement and public opinion influence the formulation, implementation, and funding of natural resource conservation and biosecurity (NRC/B) within laws and development or conservation plans			
Laws and biosecurity	National, state, county, and city laws and regulations are the means by which NRC/B are supported and implemented			
Planning for development or conservation	National, state, county, city, and private development plans or conservation plans define actions that result in losses or gains in NRC/B (impacts realized at implementation)			
Foreseeable future scenarios and the resulting stream habitat conditions				
Use foreseeable future	Scenario One: CMPs:	Scenario Two: CMPs: small	Scenario Three: CMPs: small	Scenario Four: CMPs:
Scenario One as a “baseline” to	unchanged in support for	increase in support for	to moderate decrease in	moderate to large increase
characterize changes in	NRC/B	NRC/B	support for NRC/B	in support for NRC/B
Conservation actions and	Conservation actions: no	Conservation actions:	Conservation actions:	Conservation actions:
habitat conditions in future	change; current rate of	marginal increase	substantial decrease	substantial increase
Scenarios Two, Three, and	land cover change	Habitat condition: habitat	Habitat condition: urban and	Habitat condition: robust,
Four	continues through the	area is unchanged through	agricultural uses are	sustained effort to restore,
	foreseeable future	the foreseeable future;	prioritized over	manage, and expand
	Habitat condition: habitat	habitat quality and	conservation; habitat area,	conservation; habitat area,
	area, quality, and	sustainability are slightly	quality, and sustainability	quality, and sustainability
	sustainability slowly	enhanced through the	substantially decrease	substantially increase
	decrease through the	foreseeable future	through the foreseeable	through the foreseeable
	foreseeable future		future	future
Habitat stressors	Responses of stream habitat stressors			
Development	Small to moderate increase	No change (redevelop)	Moderate to large increase	Small to moderate decrease
Altered hydrology	No change to small increase	No change	Larger increase	Small decrease
Recreation/access	Small increase	Small increase	Larger increase	Larger increase
Water pollution	Small increase	No change	Larger increase	Small decrease
Invasive species	Small increase	Small increase	Larger increase	Small decrease
Plant diseases	Small increase	Small increase	Larger increase	No change to small decrease
Fire	Small increase	Small increase	Larger increase	No change to small increase
Erosion	Small increase	No change	Larger increase	Small decrease
Climate				
Temperature	Small to moderate increase	Small to moderate increase	Small to moderate increase	Small to moderate increase
Precipitation	Small decrease	Small decrease	Small decrease	Small decrease
Storms	Small increase	Small increase	Small increase	Small increase

Future Scenario Two

There is a slight increase in the CMPs that marginally improves conservation management.

Summary: Conservation Agencies and stakeholders work with increased but limited resources to slow or stop the degradation of landscape areas.

Description: Scenario Two is essentially “status quo” with minor improvements in the three CMPs. The anticipated changes, under Scenario Two, for each of important habitat stressors for (habitat name) habitat are given in [Table 1](#).

Though there is an expanding human population in Scenario Two, development is not expected to substantially increase. A slightly improved biosecurity effort should help reduce invasive species and plant diseases but increases are still expected. The small increased support of natural resource management in the CMPs is not expected to greatly alter wildfire frequency and intensity, but these might (lower slightly) compared to Scenario One. The CMP supported conservation will not prevent, mitigate, or reverse the impacts of climate change-related stressors.

Under this scenario, rivers and streams are predicted to slightly increase, relative to status quo, in condition and abundance. Although seeps will also experience a slight improvement in conservation actions, it will not be enough to significantly change the declining trend described in Scenario 1. Instead, we anticipate that the rate of decline of seeps will likely begin to plateau, relative to status quo, in condition and abundance. The slight increase in representation of rivers and streams is based on assumptions that there are slightly better conservation values and laws protecting stream habitats from further degradation. In areas with population increase, there may be stricter policies that require an increase in stream habitat restoration. However, these efforts will likely have little to no effect on seeps, as their representation plateaus at status quo, because there will be no change in hydrology, despite the needs of an increasing population. Conservation values and laws should slightly increase in stream habitats where human recreation increases in order to mitigate erosion, sedimentation, bank alteration, water pollution, and the spread of invasive species. Conservation values and laws should also slightly increase to mitigate the increase in climate related stressors like temperature and flooding. Removing invasive species and outplanting native species will be key in maintaining bank stability and canopy cover, which will minimize sedimentation and eutrophication. Redundancy of rivers, streams and seeps will likely plateau at the status quo across the Hawaiian islands, with higher islands being able to recover faster because of their ability to capture orographic rainfall. Although some stressors are projected to slightly increase, laws and values are also projected to slightly increase in order to balance out and mitigate negative effects of those stressors. Resiliency of rivers and streams will likely increase slightly as a result of slight increase in conservation values and laws. Those conservation values and laws will likely have no effect on seeps; therefore, resilience of seeps will likely plateau at the status quo. Stricter policy will need to occur in order to allow an increase in groundwater recharge before we see an increase in seep resiliency.

Overall, based on this analysis, it is anticipated that under this scenario, rivers and streams will slightly increase, relative to status quo, in condition and abundance, and will have a slightly higher likelihood of supporting native ecological communities that depend on rivers and streams. The rate of decline of seeps is anticipated to plateau (stay similar to the condition described in the Current section, above), likely and will therefore have a slightly increased likelihood of being able to support native ecological communities that depend on seeps, relative to the condition of the habitat described in Scenario 1. By 2035, it is anticipated that rivers and streams will likely have slightly higher representation and resiliency across the Hawaiian islands. Redundancy of rivers and streams will likely plateau across the Hawaiian islands. Representation, redundancy and resiliency of seeps will likely plateau at current levels.

Future Scenario Three

There is a small to moderate decrease in conservation actions in the CMPs that substantially decreases conservation management.

Summary: All natural resource management actions in the CMPs are set aside in deference to land use for economic development. With extensive localized management, some native species may persist in park-like settings or in areas where land development is not possible.

Description: Scenario Three has substantial declines in natural resource conservation within the three CMPs. An increasing human population is supported in its use of land for economic development over the conservation of native habitats. Areas that cannot support development become the only areas of free-living native species. The anticipated changes, under Scenario Three, for each of habitat stressors important to (habitat name) habitat are given in [Table 1](#).

An expanding human population requires increased land use for agriculture and development. Biosecurity controls are significantly weakened in this Scenario leading to an increase in invasive species problems and new plant diseases. Combined together, these factors will result in substantial increases of wildfire frequency and extent. The substantial loss of CMP supported conservation may locally aggravate the impacts of climate change-related stressors.

Under this scenario, rivers and streams are predicted to severely decrease, relative to status quo, in condition and abundance. Seeps on higher elevation islands are predicted to severely decrease in condition and abundance, some becoming ephemeral; while seeps on lower elevation islands are expected to become ephemeral or eliminated. This decrease in representation is based on assumptions that development in watersheds will increase so much that rivers and streams will become channelized, seeps will be lost, and hydrology will be altered so severely that it will drastically lower water availability of streams. Increase in temperatures and longer periods of drought will eliminate water resources, and as a result likely dry out these stream habitats. Long periods of

drought will also dry out riparian areas and make them susceptible to fire. Increased fire events will eliminate riparian vegetation and prevent regrowth, decreasing bank stabilization. A high increase in flood events will likely wipe out riparian areas further increasing erosion and sedimentation. Resiliency will be drastically reduced with no canopy to keep the water and soil cool, leaving the stream susceptible to sedimentation and eutrophication. Redundancy will be drastically lowered across the Hawaiian islands; however, higher islands will likely retain some level of resiliency and water flow for a longer time period because of their ability to capture orographic rainfall. Lower islands that only have seeps may likely only see seeps after storm events, if at all. In this scenario, conservation values and associated laws are minimal, so there will likely be little to no funding allocated to watershed or stream restoration and maintenance.

Overall, based on this analysis, it is anticipated that under this scenario, stream habitats will severely decrease, relative to status quo, in condition and abundance, and will have a much lower likelihood of supporting native ecological communities that depend on stream habitats. By 2035, it is anticipated that stream habitats will likely have lower representation and redundancy across the Hawaiian islands, and be less resilient to stochastic events.

Future Scenario Four

There is a moderate to large increase in conservation actions in the CMPs that substantially improves conservation management.

Summary: An overt and robust, active, ongoing effort is made to engage partners and stakeholders in identifying and prioritizing landscape areas needed for the conservation of native habitats and ecosystems, and to actively restore and expand these habitats and ecosystems.

Description: A substantial emphasis on natural resource conservation is present in the three CMPs, reflecting increased societal concern for declines in natural habitats and biodiversity. Active and well-supported natural resource management begins to restore these habitats and ecosystems and expand their landscape areas. The anticipated changes, under Scenario Four, for each of habitat stressors important for (habitat name) habitat are given in [Table 1](#).

The needs of an expanding human population are addressed through more efficient land use governance based on redevelopment rather than development of undeveloped areas. Modern and novel agricultural practices focus on those that do not affect existing natural areas or areas needed for native habitat restoration. Substantially improved biosecurity regulations decrease introductions of invasive species and plant diseases. These improved land management actions result in decreased wildfire frequency and extent. The substantial increase in CMP supported conservation may locally mitigate the effects of climate change-related stressors, but climate change is expected to continue.

Under this scenario, rivers, streams and seeps are predicted to increase, relative to status quo, in condition and abundance. This increase in representation is based on assumptions that all human presence/abundance-related stressors will decrease. Decrease in these stressors (i.e., stricter regulations limiting water diversions and withdrawals) will likely increase water availability of stream habitats across the Hawaiian islands. Decrease in these stressors along with an increase in conservation values and associated laws will likely improve riparian areas, further increasing bank stabilization and decreasing erosion. Funding will likely be allocated to stream restoration and maintenance along entire watersheds, increasing the value of the ecosystem services stream habitats provide. As the ecosystem services provided by stream habitats are so highly valued by the public, it is anticipated volunteer efforts and community involvement will increase to restore stream and riparian habitats to historically high levels. Resiliency will likely increase since restored riparian areas will provide canopy cover to keep the water and soil cool, preventing eutrophication and erosion of stream banks during periods of drought. Redundancy will also increase across the Hawaiian islands at all elevations. It is likely stream habitats on the higher islands will recover/rebound more quickly because of their ability to capture orographic rainfall. Lower islands with ephemeral seeps will likely now have seeps that occur year-round. Lower islands with seeps that occur year-round will likely now see these seeps turning into ephemeral streams, especially following storm events. Ground water recharge will likely increase, which will increase overall water availability, even on lower islands that don't capture orographic rainfall. Seeps on higher islands will also increase in condition and abundance, relative to status quo, because of overall increase in ground water recharge.

Overall, based on this analysis, it is anticipated that under this scenario, stream habitats will increase, relative to status quo, in condition and abundance, and will have a higher likelihood of supporting native ecological communities that depend on stream habitats. By 2035, it is anticipated that stream habitats will likely have higher representation and redundancy across the Hawaiian islands, and be more resilient to stochastic events.

See also: Physical Geography of the Hawaiian Islands.

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Streams of the Mariana Islands

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Published by Elsevier Inc.

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Abstract

This article provides a review of the flowing water, or lotic, ecosystems found in the Mariana Islands, with a particular emphasis on perennial streams. The geology, hydrology, and biota of these streams is discussed for the islands of Guam, Rota and Saipan, the only islands in the archipelago which possess perennial stream ecosystems. Current integrity and future conservation of these ecosystems is also evaluated in the context of human-mediated stressors such as wildland fire, aquatic invasive species and climate change. A provisional assessment is provided as to how the condition of such streams may change over time based on future climate scenarios.

Introduction

The current article provides a review of the flowing water, or lotic, ecosystems found in the United States Territory of Guam and the Commonwealth of the Northern Mariana Islands (collectively referred to hereafter as the “Mariana Islands” or “Marianas”), with a particular emphasis on perennial streams. The Mariana Islands consist of an island arc in the northwest Pacific to the east of the Philippines, containing 15 islands of volcanic origin, all lying in tropical latitudes (for a general contextual overview of geography and ecology of the Mariana Islands as a whole see other chapters in this work). The geology, hydrology, and biota of these streams is discussed, and their current condition evaluated in the context of human-mediated stressors, including wildland fire, aquatic invasive species and climate change.

Of the approximately 102 perennial streams currently recognized within the Mariana Islands, including tributaries to larger systems, nearly all occur on Guam (Taboroši et al., 2005), with the exception of one perennial stream system each on the islands of Rota and Saipan. No perennial streams occur on any of the other 12 islands in the archipelago. Consequently, the larger portion of the following discussion regarding stream ecosystems within the Mariana Islands concerns the island of Guam, with secondary emphasis on Rota and Saipan.

Overall, streams in the Mariana Islands are similar to those elsewhere in the tropical insular Pacific in exhibiting the following characteristics:

1. They are prone to exhibit rapid, flash flood-like discharge patterns (Fig. 1) due to their relatively small catchment sizes, steep channel profiles, and limited capacity for stream channel storage (defined as the overall capacity for water within the boundary of a given stream’s banks). The rainfall events feeding into these catchments are also often intense and episodic, frequently as a result of tropical cyclones in the latter half of any given calendar year, leading to rapid increases in stream discharge volume over short periods of time.
2. They are short in length compared to streams on the continents or larger land masses. For example, streams on Guam range from 1 to 7 miles (1.6 to 11.3 km) in length, with shorter and more linear catchments on the south and west flanks of the island, and longer, more integrated catchments draining eastward from the island’s center (Figs. 5 and 6). Stream systems on Rota and Saipan are even shorter, with the only perennial stream on Saipan being <1.5 miles (2.4 km) long, and the only perennial stream on Rota being a mere 0.87 mile (1.4 km) in length (Camacho et al., 1997).
3. They possess stair-step bed profiles containing one or more waterfalls, defined as a cascading feature with a gradient of 40% or greater, somewhere along their length (Figs. 6 and 7). Such breaks in the bed profile occur due to steep island topography, coupled with an underlying petrology consisting of successive layers of limestone, lava and lateritic or saprolitic soils that exhibit varying degrees of resistance to erosion. Such waterfalls can also represent barriers to the upstream migration of certain aquatic organisms.

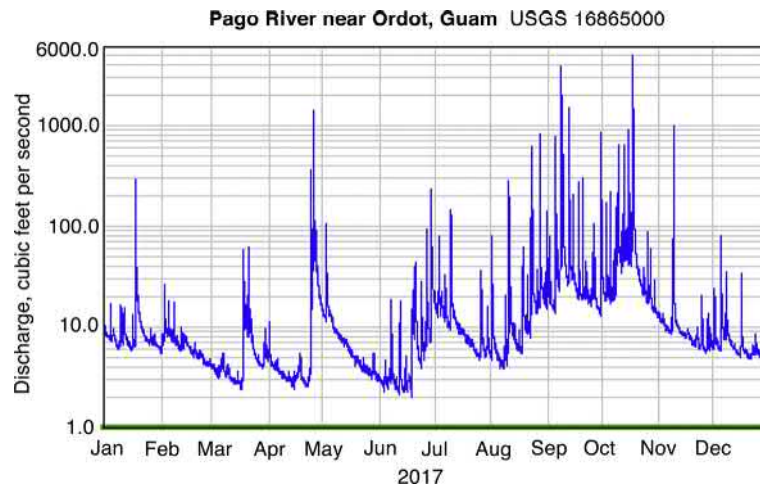


Fig. 1 An annual hydrograph for the Pago River on Guam for the year 2017, illustrating the flashy nature of discharge in this catchment, and the significant clustering of periodic flood peaks during the typical typhoon season of the year from July to December, both patterns being typical of Marianas Streams. The system reverts to base flow only at certain points in the dry season from January to June. Data from US Geological Survey.

4. Due to the locations of these streams on oceanic islands that have never possessed connections to larger continental areas, their biotas are limited and disharmonic, lacking many groups of fishes and aquatic insects typically encountered in continental settings. For example, there are no primary freshwater fishes, defined as those that complete their entire life cycle in fresh water. In addition, there is an absence or very low species richness of certain aquatic insect groups such as mayflies, caddisflies, and stoneflies that are important components of stream food webs on the continents. Instead, the biota of Marianas streams consists of a limited suite of fishes, shrimps, mollusks and insects specifically adapted to exploit the particular habitats offered by these systems, often through amphidromous life cycles, meaning that they possess a marine planktonic larval stage, with the post-larvae migrating back into freshwaters, where the adult stages live and reproduce.

These characteristics render streams in the Mariana Islands, and the Pacific islands in general, hydrologically and biologically distinctive in comparison to those elsewhere in the world.

Stream Ecosystem Classification

An ecosystem classification scheme for the inland waters of the insular Pacific, including both streams and wetlands, was proposed by Polhemus et al. (1992). Under this system, three classes of streams were recognized: (1) Intermittent Streams, consisting of channels that lack permanent surface flow, but may contain flowing water after heavy rains, and sometimes retain permanent pools at exposed bedrock sills or in other areas of low substrate permeability; (2) Interrupted Streams, which support perennial flow in their upper reaches, but become dry as this flow sinks into the bed further downstream, so that there is no continuous flow all the way to the sea except during the wet season or after major rainstorms; and (3) Perennial Streams, which maintain flow throughout their entire length and discharge continuously to the ocean during all seasons, irrespective of seasonal variations in precipitation. All of these stream types occur in the Mariana Islands, but the current article concentrates primarily on perennial streams, which support the richest and most persistent biota. Due to a lack of established definitions in the scientific literature, we make no attempt to draw a formal distinction between "rivers" and "streams", although both terms are used for features in the Marianas, with the Talofofo River on Guam being the largest and longest stream in the archipelago.

It should also be noted that man-made diversions may convert perennial streams into interrupted streams by dewatering certain reaches, although in this case they are considered as a separate, Artificially Interrupted Streams ecosystem class. The waters diverted from such streams are in turn often fed into another flowing water ecosystem class, Artificial Ditches and Flumes, consisting of man-made channels which carry flow laterally across natural drainage divides. Such anthropogenic systems tend to have limited biota, often consisting of introduced species. Although widespread in the Hawaiian Islands, such artificial aquatic ecosystems are of relatively limited extent in the Mariana Islands. Examples on southern Guam include the diversions from the Almagosa and Bona springs, which are conveyed to the Fena Valley Reservoir storage system (Ward et al., 1965).

Along the length of any given perennial stream, Polhemus et al. (1992) also recognized three discrete divisions: (1) the Headwater Reach, lying above 800 m elevation or having a gradient of >30%, or both, and often exhibiting a significant amount of bedrock exposure in the channel (Fig. 3); (2) the midreach, lying between 800 m and 50 m elevation, with a more moderate gradient, and a bed substrate consisting of mixed rocks, cobble and gravel, with limited representation of bedrock or fine sediment; and (3) the Terminal Reach, generally lying below 50 m elevation, with a low gradient, and a bed substrate containing large amounts of gravel and fine sediment. The boundary between the midreach and the terminal reach is often marked by the first significant barrier in the stream bed, such as a waterfall, that bars the upstream migration of itinerant marine fishes (Fig. 7).

Stream terminal reaches in many cases transition into estuaries, where limnetic stream waters (those with 0 ppt of salinity) intergrade with euhaline marine waters (32–36 ppt salinity) through an intermediate mixohaline estuary zone (1–31 ppt salinity). Such estuaries are tidally influenced, and provide corridors for the entry of certain transient marine biota into stream terminal reaches, as well as the transit of larval and juvenile amphidromous species which spend portions of their life cycles in both freshwater and marine environments. The upper extent of such estuaries is generally defined by the presence of some degree of salinity, coupled with the upper limit of measurable tidal fluctuation. In many cases such estuaries are often vertically stratified in terms of water chemistry, with a fresher, nearly limnetic layer at the surface, and a denser, more saline layer on the bottom. Such stratified layers may also exhibit dichotomous current regimes, with low salinity waters flowing out at or near the surface, while higher salinity waters flow in at or near the bottom.

A final flowing water ecosystem class in the Marianas consists of Rheocrenes, which are flowing springs, often emerging from and passing over bedrock faces. Small rheocrenes are present on most of the islands in the Marianas, irrespective of island size, although they often have small discharge volumes and flow for only short distances. Although generally insufficient to support fishes or crustaceans, they may provide habitat for native aquatic insects.

Hydrology

The ultimate source of water for all perennial streams in the Mariana Islands is seasonal and orographic rainfall. Such precipitation inputs can be substantial in the Mariana Islands, with the average rainfall on the entire island of Guam, averaged across the wet and dry seasons of the year, amounting to approximately one billion gallons per day (Ward et al., 1965). Some of this is recycled to the atmosphere as evapotranspiration, with 4 inches (10 cm) of rainfall per month being necessary to meet such demands in the river basins of southern Guam. Below this amount, the vegetation becomes drought-stressed, while above this amount excess runoff and spring discharge will increase stream flow (Ward et al., 1965). In certain areas with favorable geology, such as southern Guam and a few small areas on both Rota and Saipan, a certain proportion of the precipitation may also be captured subsurface as perched groundwater lying up to several hundred feet above sea level, where it is trapped between a porous overlying limestone caprock formation and less permeable underlying basalts (Gingerich, 2003). Such perched groundwater emerges at the contact between the limestone and the basalt, forming permanent seeps and springs that produce continuous base flows in stream headwaters. The remaining rainfall that is not lost to evapotranspiration or captured as groundwater runs off directly into the sea. Because the proportion of rainfall that runs off is high on these islands, especially in those areas of impermeable volcanic terrain where most stream channels form, the discharge rates of even their perennial streams are subject to notable variations between the wet and dry seasons, and dry spells of only a few weeks can lead to significantly diminished stream flows (Ward et al., 1965).

Outside of Guam, Rota and Saipan, the remaining 12 islands within the Mariana Archipelago lack flowing streams altogether, due to their small sizes coupled with porous limestone or recently erupted volcanic substrates that allow rapid percolation of rainfall into aquifers. These groundwaters discharge as basal springs along the coasts, thus precluding the formation of perennial streams at higher elevations. Despite a dearth of perennial streams within the Mariana Archipelago as a whole, nearly all of the islands do possess perennial seeps, which can be important habitat for certain aquatic insect species. During the wetter months of the year the various intermittent streams on Rota and Saipan will also exhibit some degree of surface flow, although the biota of such transient aquatic ecosystems is often limited to dispersive and opportunistic aquatic insect species such as dragonflies.

In perennially flowing Marianas streams, there is limited accumulation of sediment, leaf litter, and other loose debris, due to continuous flow coupled with periodic strong flushing by flash floods, which are triggered by convectional rains in the mountains or strong weather events such as tropical cyclones (Fig. 1). While storms in the Mariana Islands can occur any time of the year, the typical typhoon season runs from late June through December, with the peak occurring between late August and mid-November (Lander, 1994). During this period, mountain streams may experience repetitive high discharge peaks over a short period, and remain in a near-constant state of recovery from the most recent flood. Although potentially destructive, flash floods may also produce positive effects by flushing away debris that might otherwise contribute to oxygen depletion during periods of low water; removing sediments that can smother the eggs of stream animals; and opening up stream mouths where they flow into the sea, thereby allowing for biotic interchange through estuaries.

Except in the few areas of remaining intact native forest, such as those tributaries above the Fena Valley Reservoir in the upper Talafofo River basin of Guam, canopy cover above Marianas streams is often 25% or less, depending upon the immediately surrounding habitat. Perennial streams on Guam flow for most of their lengths through a variety of anthropogenically transformed landscapes (Fig. 2), including altered native or non-native forests of variable density, often dominated by coconut or betel nut palms; low stature *tangan-tangan* (*Leucaena leucocephala*) woodland; ironwood (*Casuarina equisetifolia*) savanna; fire-mediated grasslands dominated by swordgrass (*Miscanthus floridulus*); fern banks; marshy areas with reeds (*Phragmites karka*); and even urban channelization (Muller-Dombois and Fosberg, 1998). As such, it is difficult to make generalizations regarding a “typical” riparian zone for streams in the Marianas (Boyer et al., 2009), except to note that shading on Guam is often low due to destruction of surrounding vegetation by wildland fire (Fig. 3), whereas those few stream reaches on Saipan that harbor permanent water are heavily shaded (McCagan et al., 2008).

The amount of canopy cover is important as it relates to water temperature and the formation or absence of algal growth. Cool water has a greater capacity to hold oxygen, an important factor for supporting stream fauna. Conversely, streams without canopy cover are more exposed to the warming effects of the sun, which can affect plant and animal species composition and abundance.

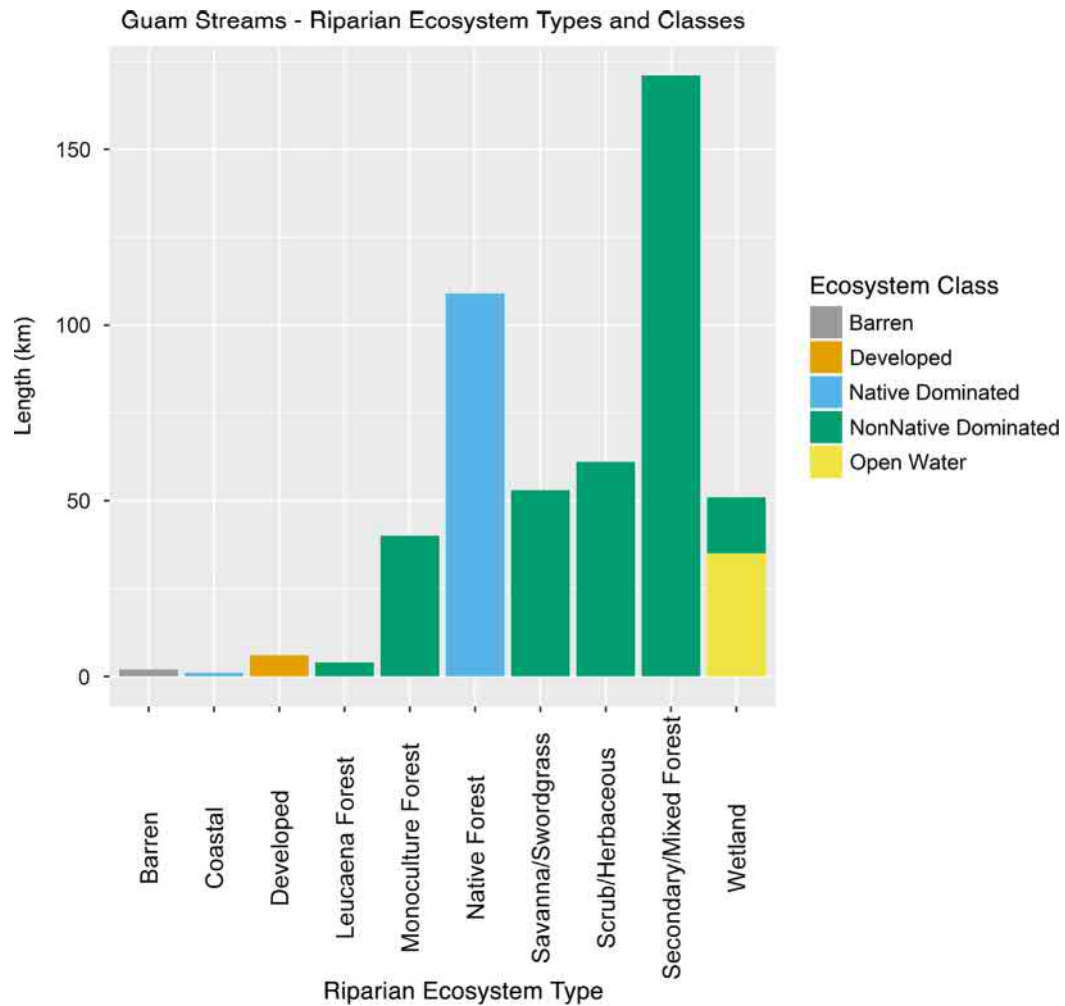


Fig. 2 Riparian ecosystems of Guam.



Fig. 3 The headwater reach of the Ylig River on southern Guam, illustrating significant bedrock exposures in the channel, and relatively low shading due to the absence of an overtopping riparian canopy. Photo: Dan A. Polhemus.

Streams over-exposed to sunlight may develop thick mats of algae attached to the rocks, floating algal mats, surface scum, and a microbial sheen. These are all indicators of eutrophication, an excessive richness of nutrients due to runoff which causes a dense growth of aquatic plant life (NRCS, 2001) but is deleterious to other organisms.

Island of Guam

The island of Guam lies at 13°27'N, 144°47'E, and is the most populous of the Mariana Islands, with 162,000 residents. The island is of hybrid geological origin, consisting of volcanic uplands on the southern half and an elevated, cliff-bound limestone plateau in the north (Figs. 4 and 5), with these two geologic units being separated by the Pago-Adelup fault, which cuts transversely across the

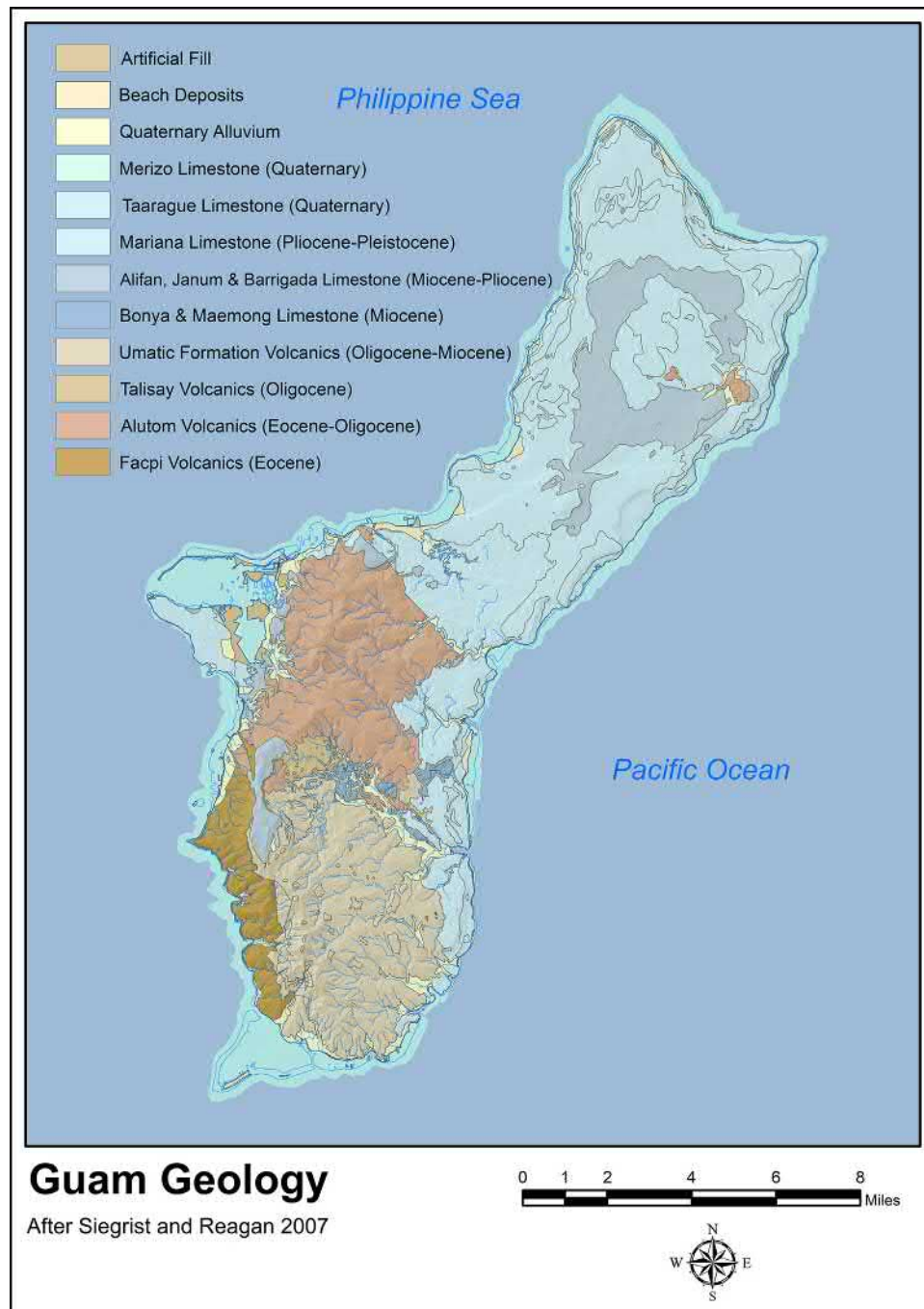


Fig. 4 The surface geology of Guam, as simplified from the geological map of Siegrist and Reagan (2007).



Fig. 5 The topography of Guam, illustrating the relatively flat-lying limestone plateau in the north of the island which is devoid of streams, and the more heavily dissected volcanic terrain in the southern half of the island, which contains the majority of the perennial streams in the Marianas.

island (Taboroši et al., 2005). Despite consisting of only a single island, the Territory of Guam has a total land area of 212 miles² (549 km²), which is larger than the combined land area of all the islands within the remainder of the Mariana Island chain. The highest point on the island is Mt. Lamlam, in the southern highlands, which reaches 1334 ft. (407 m.). The coastlines of Guam are for the most part steeply dropping, although there are extensive beach areas on the western side at Tumon and Agana bays, and a reef-fringed lagoon in the south at Merizo. Native forest cover on Guam was extensively damaged during World War II, but has regenerated in many areas of the north, which are under military control, while continuing to suffer regular damage from poorly controlled wildland fires in the south. In contrast to the remainder of the Mariana Islands, Guam harbors a large number of perennial streams (Taboroši, 2013), all of which occur in the volcanic southern portion of the island (Fig. 5). These include 46 stream catchments of greatly varying sizes (Best and Davidson, 1981), which can be grouped into 19 major watershed units (Fig. 6).



Fig. 6 The major watershed units of Guam, also showing the locations of major waterfalls, which represent barriers to the upstream migration of many euryhaline fish species.

Guam exhibits a pattern of alternating annual wet and dry seasons similar to the rest of the Marianas, with a wet season from July to December, during which two-thirds of the annual rainfall occurs in a typical year (Lander, 1994), and a drier season from January to June, during which mean monthly rainfall is < 8 inches (Johnson, 2012). It is estimated that somewhere between 12 and 30% of Guam's wet season rainfall is produced by the passage of tropical cyclones within 180 nautical miles, with the remainder arising through convection (Lander, 1994; Johnson, 2012). Although rainfall data has been collected from over 60 sites on the island since 1906, most of these gauges have short periods of record, so understanding of long-term rainfall climatology from 1950 to the present is largely based on records from a limited number of gauges at Umatac, Ylig River, the former NWS meteorological observatory at Taguac, Anderson Air Force Base, and Naval Air Station Tiyan (Fig. 3), the latter two stations having the longest periods of record (Lander and Guard, 2003). Mean annual rainfall at the various locations gauged on Guam ranges from 84 to 116 inches (213–295 cm) per year (Johnson, 2012), with the wettest areas in the southern mountains, and the driest areas at

scattered points along the west coast (Lander and Guard, 2003). Inter-annual rainfall on Guam is strongly influenced by ENSO cycles, with droughts tending to occur in the winter and spring seasons following an El Niño event (Lander, 1994).

As noted, Guam is divided into two discrete petrological and geomorphological units (Figs. 4 and 5): (1) southern Guam, which has low permeability volcanic terrain drained by numerous perennial streams and (2) northern Guam, which is an elevated limestone plateau of high permeability that lacks flowing surface watercourses but contains large subsurface aquifers (Johnson, 2012). In this regard, the island functions as two disparate units in regard to its hydrological response to precipitation inputs, with volcanic southern Guam being a surface water sector, and limestone northern Guam being a groundwater sector.

In southern Guam, streamflow data are available from 19 USGS stream gauging stations with periods of record extending from 1951 to the present, although none of these gauges have continuous records for this entire period, and only two of the gauges that have >35 years of record are not affected by upstream diversions (Keener et al., 2012; Heitz and Khosrowpanah, 2015). This gauging data indicates a strong correlation and in-phase tracking between annual rainfall and stream discharge in southern Guam, although the relationship is not strictly linear. Maximum streamflow peaks in an average year strongly match maximum median rainfall, which occurs in September, whereas minimum stream flows have a lag, occurring in April, about 1 month after the normal annual rainfall minimum (Lander, 1994). This data clearly demonstrates a relationship between meteorological and hydrological drought on Guam, and also suggests that the average return interval for severe droughts may be close to 10 years, with severe droughts and correspondingly reduced stream flows having occurred in 1966, 1979, 1983 and 1998 (van der Brug, 1986; Polhemus, 2017).

Recharge rates for Guam's aquifers were investigated by Johnson (2012), who found that under drought conditions the recharge rate was 32% lower than mean baseline recharge. Based on analysis of monitoring well data, water levels in the aquifer during a typical year run 180 degrees out of phase with annual precipitation cycle (Lander, 1994), usually peaking in February, 6 months after the average maximum rainfall is received in September. There is thus a significant lag time between when rainfall occurs and when it actually enters the water table, indicating that it may take up to half a year to initiate aquifer recovery following a period of drought or over-utilization. Therefore, although stream total flows (which include surface runoff) closely track the temporal variation in rainfall, perennial stream base flows (which consist only of aquifer discharge) may run out of phase with precipitation inputs by several months.

The volcanic southern portion of Guam has 17 major watershed units (Fig. 6) containing 100 freshwater streams (if named tributaries are counted) within 46 catchments, constituting the vast majority of the streams found in the Mariana Islands. The constituent watersheds vary greatly in size, from the large and well-integrated Talofoto catchment that drains 28 miles² (73 km²) in the center of southern Guam, to the numerous short, relatively linear catchments such as Cette, Umatac and Geus along the southwest coast, which drain the steep seaward slopes of the southern mountains. In addition, the flat northern limestone plateau of Guam has no defined surface drainage channels, with water percolating into caves and emerging as springs near the coast.

Guam's native stream biota includes a moderately diverse array of fishes, prawns, molluscs and insects, although many of these groups are still inadequately studied. Information regarding Guam's freshwater fishes is fragmented, and no good compendium of records regarding their distribution or ecology has been published. Information is similarly fragmentary for freshwater molluscs and insects. By contrast, the local freshwater crustacean assemblage is well characterized, and has been the subject of ecological study (Leberer and Nelson, 2001).

Based on the checklist of Meyers and Donaldson (2003), supplemented by data from Walsh et al. (2014) and unpublished data supplied by the Guam Division of Aquatic and Wildlife Resources (Tibbatts, in litt.), a total of 32 species of native fishes are known to occur in stream habitats on Guam. The majority of these, consisting of 22 species, are itinerant marine-breeding taxa which enter estuaries, and may also penetrate a short distance up slow-moving stream terminal reaches to varying degrees, usually stopping when they encounter swifter water flowing over rocky substrates. This euryhaline assemblage includes taxa such as the Indo-Pacific tarpon (*Megalops cyprinoides*), mangrove red snapper (*Lutjanus argentimaculatus*), and several species of mullet (*Crenimugil seheli*, *Ellechlone vaigiensis*, *Moolgarda engeli*, and *Neomyxus leuciscus*) which are important food and sport fishes. Also present are certain morphologically specialized fishes, such as the narrow-lined pufferfish (*Arothron manilensis*), the bearded eel goby (*Taenioides limicola*), the feathered river garfish (*Zenarchopterus dispar*), and several species of pipefishes (*Microphis brachyurus*, *Microphis leiaspis*). Species in a few of these marine genera, notably flagtails (*Kuhlia* sp.) and eels (*Anguilla* sp.) may penetrate upstream well beyond the estuaries, dispersing through rocky midreaches until being stopped by the first major waterfall (Figs. 6 and 7). Anguillid eels in particular often preferentially inhabit deep plunge pools at the bases of waterfalls.

In addition, there are 10 additional species of gobies (Gobiidae) and sleepers (Eleotridae) on Guam whose adults live and breed in freshwater (Walsh et al., 2014). All of these species are amphidromous, with a marine planktonic larval stage and post-larvae migrating back into freshwaters, where the adult stages live and reproduce; as such, their life cycle still requires a link to marine habitats (Watson, 1991, 1992). Among the 8 goby species represented, 4 are largely confined to estuaries and lower-gradient stream terminal reaches, including the bandfin mangrove goby (*Mugilogobius cavifrons*), the speckled goby (*Redigobius bikolanus*), the spotfin river goby (*Awaous ocellaris*) and an apparently undescribed species of *Stenogobius*. The remaining 4 goby species can be found further upstream through more swiftly flowing midreach habitats with rocky beds. The upstream limit for the Mariana goby (*Awaous guamensis*) generally occurs at the first major waterfall barrier, but the red-tailed goby (*Sicyopterus lagocephalus*), the dwarf goby (*Stiphodon percnopterygionus*), and a potentially undescribed belted goby in the genus *Sicyopus* are capable of surmounting such barriers to enter headwater reaches. These latter species in the subfamily Sicydiinae can form their pelvic fins into a "pelvic disk," which functions as the equivalent of a suction cup, allowing them to inch up wet vertical rock faces, and thus reach considerable elevations above the sea (Keith et al., 1999). Among the sleepers, the dusky sleeper (*Eleotris fusca*) is a species of



Fig. 7 Tarzan Falls, on the upper Ylig River, is typical of the numerous waterfalls that interrupt stream profiles on Guam. Such falls represent the upper limit of habitat for itinerant marine fishes, but can be surmounted by certain gobies and shrimps which are adapted to exploit headwater reaches. The wet rock faces also provide specialized habitat for certain aquatic insects. Photo: Dan A. Polhemus.

estuaries and slow terminal reaches with muddy bottoms, in which they partially bury themselves. Another, currently undescribed species of cavernicolous sleeper is also known from water caves in the northern portion of Guam (Larson, 2001; Meyers and Donaldson, 2003).

As currently interpreted, the freshwater decapod crustacean fauna of Guam includes 7 species of small detritivorous shrimps in the family Atyidae (*Antecaridina lauensis*, *Atyoida pilipes*, *Atyopsis spinipes*, *Caridina brachydactyla*, *Caridina mertoni*, *Caridina typus*, *Halocaridinides trigonophthalma*), 2 larger species of omnivorous prawns in the family Palaemonidae (*Macrobrachium equidens*, *Macrobrachium lar*), and 3 species of crabs in the family Varunidae (*Orocvitta mollitia*, *Varuna litterata*, *Ptychognathus* sp.) (Leberer and Nelson, 2001; Leberer and Cai, 2003; Walsh et al., 2014; Tibbatts, 2017 in litt.). There is, however, lingering taxonomic uncertainty regarding the proper identification of some of these species, and the above list should thus be considered provisional. As with the gobiid fishes discussed previously, all of these crustaceans are amphidromous, with a freshwater adult stage and a marine pelagic larval stage, and the atyids can also climb waterfalls, just like sicydiine gobies, to colonize headwater reaches. The atyid genera appear to segregate on the basis of habitat, with *Atyoida pilipes* in swift, shallow riffles, and the assemblage of *Caridina* species inhabiting deeper water runs and pools. Flagtail fishes in the genus *Kuhlia* seem to exert significant predation pressure on these atyid shrimps, with lower densities and smaller sizes of shrimps in stream reaches where *Kuhlia* are present (Leberer and Nelson, 2001). In addition to these stream-dwelling species, an apparently undescribed *Halocaridinides* species has been reported from caves in northern Guam (Leberer and Cai, 2003).

The streams of Guam also support at least 16 species of freshwater prosobranch mollusks (Smith, 2003; Walsh et al., 2014), although the aquatic mollusk biota as a whole seems to be undersampled. This assemblage includes 11 species of amphidromous Neritidae in the genera *Clithon*, *Neritina*, *Neritodryas* and *Septaria*, all of which are herbivorous and widespread in the western Pacific. Adults of these species cling to midstream rocks and can often be found in swiftly flowing water. The remaining 5 species are obligate freshwater members of the Thiaridae, which are omnivorous and occur on sand or other softer substrates in standing or gently flowing water.

The aquatic insect biota of Guam is insufficiently investigated, and relatively comprehensive faunal assessments are available for only a few orders. The best-studied group are the dragonflies and damselflies (Odonata), with 14 species, including 1 archipelagic endemic species (*Anax piraticus*) and two endemic subspecies (*Agrionoptera insignis guamensis* and *Rhyothemis phyllis vitellina*), all of these also occurring on Saipan and Tinian. These local endemics tend to breed in standing water habitats rather than streams. The remaining dragonflies consist of widespread species that will exploit both stream pool habitats and ponds. Interestingly, Guam supports no endemic damselfly species (suborder Zygoptera), despite the fact that locally endemic species in this group are typical of a typical feature of islands as large and well-watered as Guam elsewhere in the Pacific. This anomaly is further highlighted by the presence of an endemic damselfly species on adjacent Rota (Polhemus et al., 2000).

A checklist of Guam's aquatic true bug (Heteroptera) biota has also been generated (Polhemus in litt.), and contains 13 species, of which a water strider (*Limnogonus lundbladi*), a shore bug (*Saldula guamensis*) and a toad bug (*Nerthra nervosa*) are currently considered endemic. Except for the above two orders, no other aquatic insect groups have been comprehensively tabulated for the island or are known to harbor endemic species there. Based on recent survey work across 12 sites representing varied habitats,

Englund (2011) reported 35 species of freshwater aquatic insects from Guam representing 6 orders. These included 11 species of Odonata, 9 species of Heteroptera, 10 species of flies (Diptera), and one species each of mayfly (Ephemeroptera), caddis fly (Trichoptera) and aquatic moth (Lepidoptera). A widespread diving beetle (*Eretes griseus*) has also been reported from the island (Miller, 2002). Based on all of the above information, it thus appears that the current stream insect biota of Guam consists of at least 41 species representing 7 orders, with 6 endemic taxa.

Island of Rota

Rota lies at 14°09'N, 145°13'E, and is the second largest island in the Marianas. Its western end of is dominated by the Sabana Plateau, or "Mt. Sabana," consisting of an irregular plateau measuring approximately 1300 ft. (400 m) in height and 4 miles² (10.4 km²) in area, rising to a highest summit at 1612 ft. (491 m) Mt. Manira. Largely comprised of limestone with some older volcanic outcrops, the plateau contains numerous caverns and is very porous in general. There are no long-term rainfall gauging records for the island, thus its hydrology is inadequately understood, but annual precipitation is likely to be about 80 inches, similar to adjacent Guam and Saipan. As on those latter islands, spring discharges exhibit a direct response to precipitation deficits, with the Matan Hanum and As Onan springs that constitute the major water supplies for Rota both exhibiting reduced flow volumes from April through June of the 1998 drought year (Carruth, 2005).

Rota is similar to northern Guam in possessing very few stream channels, intermittent or otherwise, due to the high permeability of its limestone bedrock (Davis, 1958). As a result, most rain falling at the upper elevations filters quickly into the substrate, leaving only ephemeral streams along its slopes. While the east, north and west sides of the plateau gradually drop off in a series of natural terraces, the southern slopes of the plateau are particularly steep, with vertical cliffs dropping precipitously to an area known as the Talakaya region, (Keel et al., 2007). Comprised of older volcanic substrate, the Talakaya region (Fig. 8) protrudes between two limestone formations lying both above and below (Randall, 1989). Spring water emerges at the limestone-basalt interface below the highly permeable Sabana Plateau (Fig. 8), providing the source for a set of perennial streams in this limited part of the island (Polhemus et al., 2000; Keel et al., 2007).

According to Camacho et al. (1997), stream flow is intermittent in most of the streams in this region, occurring primarily during periods of heavy rainfall. The one exception is Okgok Stream system (Fig. 8), which is considered the only true perennial stream on Rota. This catchment drains approximately 40% the Talakaya region, where highly weathered volcanic soils are exposed at the

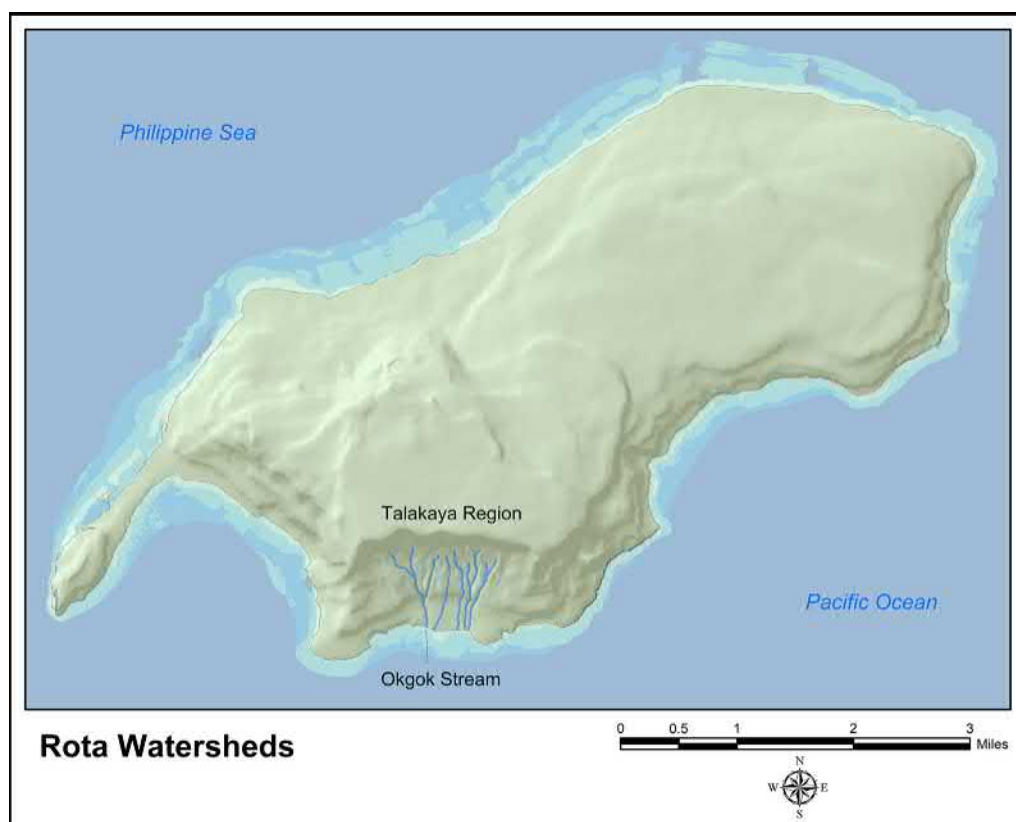


Fig. 8 The watersheds of Rota, illustrating how stream channels are confined to the Talakaya region in the far south of the island. Only the Okgok Stream is perennial, with all the other channels shown supporting only intermittent flow during the wet season or after heavy rains.



Fig. 9 Sonson Water Cave, the primary source for the Okgok Stream system on Rota. Photo: Mike Richardson.

surface (Camacho et al., 1997). Approximately 0.87 mile (1.4 km) in length, Okgok Stream originates at a large artesian spring known as the Sonson Water Cave (Fig. 9), located at approximately 820 ft. (250 m) elevation. The vegetation along the headwater and midreach of Okgok stream consists primarily of mature, tall-canopied, native forest on limestone (Keel et al., 2007; US Forest Service, in litt.), which provides an extensive canopy cover and shading. The terminal reach has riparian vegetation consisting largely of cultivars such as banana, breadfruit, bamboo and coconut (Camacho et al., 1997).

Several of the Talakaya springs are used as the primary domestic water source for Rota, including Matan Hanum Spring, As Onon Spring, and most significantly the Sonson Water Cave (Polhemus et al., 2000; Berger et al., 2005; Keel et al., 2007). A concrete collection structure with associated piping has been built into the entrance of Sonson Water Cave (Fig. 9), and delivers approximately 2.7–3.8 million liters-per-day of water (1.8 Mgal/day) to Rota's municipal system (Stafford et al., 2005; Keel et al., 2007). At present, water captured from these springs exceeds demand, although periodic drought conditions can reduce the discharge from these springs in certain years. Under such conditions, dewatering of the Okgok Stream is entirely plausible without concomitant changes to water use and conservation (Keel et al., 2007). Indeed, (Berger et al., 2005) reported that water extraction from the springs other than the Sonson Water Cave already leaves many of the streams in the Talakaya region dry most of the year.

The most comprehensive study of Okgok Stream to date remains the work of Camacho et al. (1997), funded by the US Fish and Wildlife Service. This study characterized the aquatic macrofauna of the perennial Okgok Stream as well as several other intermittent streams found within the Talakaya region, and also assessed other biotic factors including canopy cover. These investigators reported the presence of four native fish species, consisting of the marine itinerant flagtail (*Kuhlia rupestris*) in the terminal reach below the first waterfall, with an eel (*Anguilla marmorata*), and two gobies (*Stiphodon elegans*, *Sicyopus leprurus*) inhabiting the swifter midreach waters further upstream. Three native species of shrimps were also recorded, consisting of one large palaemonid (*Macrobrachium lar*) and two much smaller atyids (*Atyoida pilipes*, *Caridina typus*), all of these again in faster flowing midreaches with rocky or gravel substrates, and lying above the first waterfall, which blocks the upstream migration of the predaceous flagtails. The native freshwater mollusk assemblage at Okgok Stream contained two species of thiarids (*Melanoides tuberculata*, *Thiara scabra*), but exhibited a surprising absence of amphidromous neritids, which are common and diverse on adjacent Guam.

The aquatic insect biota of Rota remains poorly known, and was not addressed by the surveys of Camacho et al. (1997). Subsequently, surveys by US Fish and Wildlife Service biologists determined that the Okgok Stream and its tributaries are the single known locality in the world for the Rota blue damselfly (*Ischnura luta*), the only single-island endemic stream-breeding invertebrate species in the Mariana Islands (Polhemus et al., 2000). In addition to *I. luta*, one further widespread damselfly, *Ischnura aurora*, is also recorded from Rota (Liefstinck, 1962), although this species is also capable of breeding in ponds and wetlands, unlike *I. luta* which appears to be an obligate stream-breeder, and due to its limited range has been protected under the US Endangered Species Act. Other species of aquatic insects are undoubtedly present on Rota, but further survey work is needed to characterize this biota.

Although the study of Camacho et al. (1997) concluded that the aquatic fauna of Rota was less diverse than that of many other areas studied within the Western Pacific, including Guam, the overall assemblage in the Okgok Stream is in fact considerably richer than that reported from Saipan, the only other island in the Marianas with a perennial stream. This further highlights the relatively impoverished faunal assemblage present in Mariana Island streams as a whole, due to their limited spatial extent and isolation from source areas.

Island of Saipan

Saipan lies at 15°11'N, 145°45'E, and represents a formerly submerged and secondarily uplifted volcanic island formed at the margin the Pacific Plate. Approximately 95% of the island's surface geology consists of limestone, overlying thinner layers of sandstone, conglomerate and breccia sitting atop an andesitic volcanic core (Izuka and Ewart, 1995). A ridge of limestone runs through the middle of the northern two-thirds of the island, forming large stretches of mostly east-facing cliff line, with 1556 ft. (474 m) Mount Tagpochau, the highest point on the island, occurring within this ridgeline near the island's center. Similar to Guam and Rota, annual rainfall on Saipan averages approximately 80 inches (203 cm) per year, with 67% of this arriving during the wet season which extends from July to November (Carruth, 2003; Lander, 2004). Intra-island variation in rainfall appears to span a relatively narrow range, from 75 inches (190 cm) annually at the airport to 90 inches (229 cm) annually at Capitol Hill (Lander, 2004), with no pronounced leeward versus windward dichotomy. The preceding numbers must be treated as approximations, because there is ambiguity as to the locations of the rain gauges involved over time, and their data are thus not precisely representative of any particular site. In addition, no single location has a 30-year record generally deemed necessary to establish an accurate rainfall climatology. Despite its abundant rainfall, Saipan exhibits relatively few stream channels due to the high permeability of its limestone surface, and most of the streams present are intermittent (Davis, 1958), although some in the Achugao and Kagman watershed units (Fig. 10) may retain nearly permanent pools (McCagan et al., 2008). In this regard it is similar to Rota and the northern portion of Guam.

Talufofo Stream, on the northeast side of Saipan (Fig. 10), is the only stream with true perennially flowing reaches on the island (Izuka and Ewart, 1995), having a drainage basin that encompasses a roughly triangular-shaped area of approximately 1.6 miles² (4.1 km²). The Talufofo Stream catchment is branching and dendritic, with three principal tributaries, consisting of the North, Middle, and South Forks. Like many streams on southern Guam and the Okgok Stream on Rota, base flow in the Talufofo basin headwaters originates as perennial groundwater discharging from springs which emerge at points where a contact between the porous limestone formations and less permeable underlying volcanic formations is exposed, generally at elevations between 400 and 500 ft. (122 and 152 m) (Izuka and Ewart, 1995). These small headwater reach channels are surrounded by grass-covered savanna slopes, while the lower half of the basin along the midreaches and terminal reach is covered by a mixed-secondary forest (Fig. 11). The three forks converge at a point about 0.4 mile (0.64 km) from the coast, where the underlying substrate transitions to highly permeable limestone, causing streamflow to become seasonally intermittent from this point to the coast (Izuka and Ewart, 1995). As such, the Talufofo may be considered a naturally interrupted stream according to the ecosystem classification of Polhemus et al. (1992). According to measurements taken in the mid-1990s, the sum of the average flows at the Middle Fork and South Fork gaging stations, plus an estimate of the average flow at a point along the lower midreach of the North Fork, was equivalent to about 1.91 million gallons of water per day (MPG), or 7.2 million liters per day (MLD) (Izuka and Ewart, 1995).

The most comprehensive hydrological study of Talufofo Stream to date remains the work of Izuka and Ewart (1995), conducted during the mid-1990s and commissioned by the CNMI government to assess the feasibility of using the stream's water to supplement Saipan's municipal water supply. The island of Saipan has, since the drought of 1983, endured persistent water supply problems, with the shallow wells which supply most domestic uses becoming brackish due to the island's porous geology and shallow freshwater lens (van der Brug, 1986; Carruth, 2003, 2005). During their analysis, Izuka and Ewart (1995), examined flow characteristics of Talufofo stream, its chemistry, and the stream's origin and interaction with the underlying geology. Based upon streamflow and water-chemistry data, the study indicated that discharge from springs was in hydraulic connection with the limestone aquifer near the headwaters of the Talufofo Stream basin. Most pertinently at the time of the study, this meant that pumping from wells in the limestone substrate at the headwaters of Talufofo Stream catchment would likely decrease spring flow into Talufofo Stream itself—essentially negating the rationale for taking water out of the stream if pumping at the aquifer source were conducted concurrently. The study provided very little other information regarding the health or condition of Talufofo Stream, and there seem to be no subsequent studies assessing its condition.

On Saipan, there are also numerous other small springs originating from elevated limestone aquifers in the central uplands of the island, but few are monitored. Discharge was measured at Donni Spring from 1952 to 1954, and again from 1969 to 1983 using a continuous-recording gauge. During the drought of 1982–1983, flow at this spring registered only 69% of normal (van der Brug, 1986), clearly demonstrating the close coupling between precipitation inputs and groundwater discharge, similar to that seen on southern Guam. Based on the current fragmentary data, it is not possible to quantitatively evaluate the effects of the subsequent 1998 or 2016 El Niño droughts on Saipan's surface hydrology.

Very little work has been done on the freshwater biota of Saipan or the other Mariana Islands outside of Guam and Rota (James et al., 2010), and no endemic freshwater species are known to occur on the island. Based on collections made from a limited number of sites on Saipan, with identifications validated through use of molecular techniques (James et al., 2010), 8 species of native freshwater fishes occur (McCagan et al., 2008), including the estuarine Indo-Pacific tarpon (*Megalops cyprinoides*), and the amphidromous green riffle goby (*Stiphodon elegans*) and spine cheek gudgeon (*Eleotris acanthopoma*), the latter two inhabiting limnetic waters. Both the *Stiphodon* and *Eleotris* species are not recorded in current lists from nearby Guam, and it is possible that some taxonomic confusion exists regarding the identities currently assigned to species in these genera across the Marianas as a whole.

In regard to native aquatic invertebrates, Saipan's inland waters harbor 3 native shrimps (*Caridina typus*, *Palaemon concinnus*, *Macrobrachium lar*), and 9 widespread damselfly and dragonfly species (*Ischnura aurora*, *Agriocnemis femina*, *Anaciaeschna jaspidea*, *Diplacodes bipunctata*, *Tholymis tillarga*, *Pantala flavescens*, *Rhythemis regia*, *Chalcoptilon*, *Tramea transmarina*, *euryhale*, *Macrodiplax cora*), as well as the two archipelagic endemic dragonfly taxa, the species *Anax piraticus* and subspecies *Agrioptera insignis guamensis*,



Fig. 10 The major watershed units of Saipan. Only the labeled Talafofo Stream is perennial (although naturally interrupted), with all the other channels shown supporting only intermittent flow during the wet season or after heavy rain events.

which also occur on Guam (McCagan et al., 2008; Lieftinck, 1962). Although some of the shrimp and dragonfly species will breed in streams, many of the latter are more typically found associated with ponds or small wetlands. Other stream-associated shrimps, molluscs and aquatic insect species undoubtedly occur on Saipan, but proper surveys have not been undertaken to characterize this biota.

Conservation

Based on radiocarbon dates from archeological sites in Saipan, it appears that human habitation in the Mariana Islands dates back at least 3500 years (Spoehr, 1955; Fitzpatrick, 2018), this being the oldest evidence for prehistoric settlement in all of Micronesia.

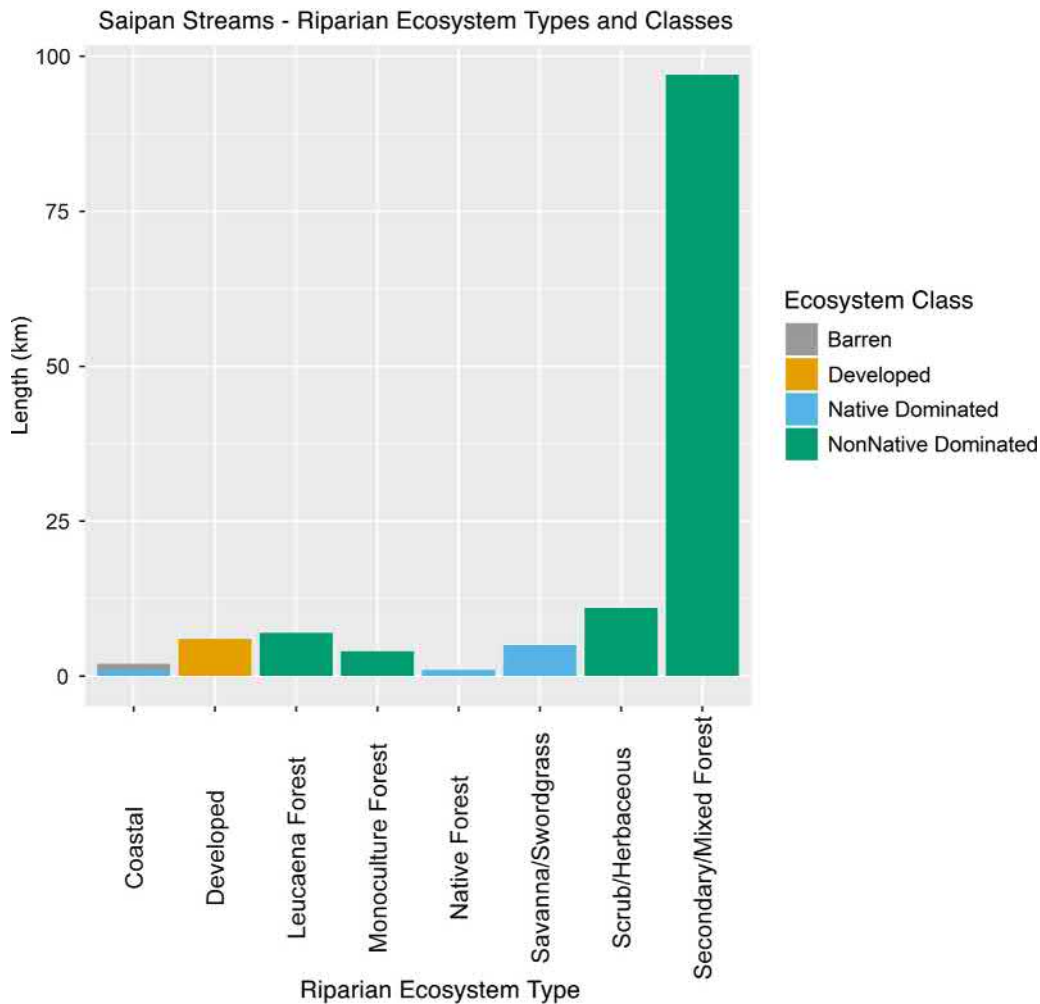


Fig. 11 Riparian ecosystems of Saipan.

These early inhabitants had a significant effect on the native vegetation of the islands over three millennia through the agencies of fire and forest clearing for agriculture (Muller-Dombois and Fosberg, 1998), particularly after A.D. 900 when the population appears to have increased substantially (Fitzpatrick, 2018), and this in turn undoubtedly had some impact on runoff patterns and stream flow regimes. No records exist of this, however, and only fragmentary descriptions are available of the nature of the landscape even at the time of Spanish colonization (Muller-Dombois and Fosberg, 1998), which produced additional ecological disruption from European-introduced crops and ungulates. In the 20th century, forest clearing and combat during World War II further served to disrupt the landscape, obscuring its original patterns of vegetation, and creating denuded badlands in areas such as southern Guam.

As such, it is possible to make only tentative inferences as to how Marianas streams functioned under their original, intact condition prior to the arrival of the Chamorro people. Based on more intact systems elsewhere in the insular Pacific, it is likely that in their original state Marianas streams may have been bordered by closed canopy riparian forests in their headwaters, trending to mixed open canopy forest at lower elevations, possibly dominated by betel nut palms (*Areca catechu*) (Muller-Dombois and Fosberg, 1998). The stream channels probably exhibited high bank stability, waters flowing in them had lower turbidity, and there was a lesser degree of in-stream algal growth, allowing better oxygenation and more favorable habitat for native aquatic species.

Streams were used by the early Chamorro as sources of fresh drinking water and to a limited extent for irrigation of various traditional crops such as taro, rice, ginger, yams, breadfruit, and bananas, although there is little evidence of extensive ditching or rice terracing (Hunter-Anderson et al., 1995). Later, during the Spanish colonial period from the 1565 to 1898, stream waters continued to be used for the irrigation of newly introduced crops including corn and sugar, and during the period of Japanese occupation during World War II rice cultivation expanded to support the military presence (Rogers, 1995). Even so, stream diversions on Guam have historically been limited, due to the absence of a plantation economy, with most of these diversions taking small volumes of water and occurring near headwater springs (Ward et al., 1965). At the present time, Guam derives 80% of its municipal drinking water from about 180 groundwater wells, predominantly located in the northern half of the island (Gingerich, 2003). The remaining 20% of water supplies are derived from reservoirs in southern Guam, primarily the Fena Valley

Reservoir, the largest on the island, which also incorporates diversions from the Almagosa and Bona springs (Ward et al., 1965; Gingerich, 2003). As such, many of Guam's perennial streams still flow unimpeded to the sea.

Current threats to watershed integrity on Guam, and elsewhere in the Marianas, include chronic wildland fire and feral ungulate disturbance in the headwater areas, associated sedimentation from lands degraded by fire or ungulates, channelization near the coast in areas of urban or suburban development, and pollution from scattered small point sources such as carelessly discarded paints or oil. The most obvious and recurrent of these disturbances is wildland fire. The frequency of fires on Guam was analyzed by Minton (2006) for the period from 1979 to 2000, with the island averaging 730 fires per year over this period, burning an annual average of 4800 acres (1942 ha). On both Guam and the islands of the CNMI, fires were concentrated in the dry season months, with over 95% of ignitions occurring between January and June. Annual fire variability was also strongly correlated with rainfall, in regard to both the number of fires and fire sizes (Minton, 2006). Years immediately following ENSO events displayed a significantly higher incidence of fire, with the number of fires more than doubling and the number of acres burned more than tripling in comparison to non-ENSO years, illustrating a link between El Niño-mediated droughts and subsequent fire frequency and size. The translated ecological effects of increased wildland fire on Guam include spread of invasive, non-native grasses which promote additional fire and loss of remaining forests, as well as higher rates of erosion from the burned areas, resulting in increased sediment influx into stream channels. In particular, Minton (2006) documented a six-fold increase in erosion rates from recently burned savannahs in the Piti-Asan watershed. Such effects are also persistent, with the same study noting a two-fold increase in sedimentation 2 years later in comparison to unburned areas, despite a certain degree of vegetative recovery. Drought and fire thus work in tandem to alter watershed vegetative cover and increase stream channel sedimentation. Because nearly all wildland fires in the Marianas are anthropogenic in origin, as a result of arson, carelessly discarded cigarettes, or hunters seeking to provide new grass shoots for introduced deer or to drive out pigs, this source of watershed stress is potentially amenable to socially-based management solutions, although these have to date had little success.

Another significant threat to the biological integrity of Mariana Islands streams is the continuing introduction and establishment of invasive, non-native aquatic species (Walsh et al., 2014). Freshwater ecosystems on Guam now support at least 13 invasive fishes (Walsh et al., 2014; Tibbatts, in litt.), including large predators such as striped snakehead (*Channa striata*), Mozambique tilapia (*Oreochromis mossambicus*), and other cichlids such as the oscar (*Astronotus ocellatus*) and butterfly peacock bass (*Cichla ocellaris*) that consume native fish species; various mosquitofish, guppies and swordtails (*Gambusia affinis*, *Poecilia reticulata*, *Xiphophorus helleri*) that have adverse effects on native aquatic insect species; and common carp (*Cyprinus carpio*) that overturn substrate and degrade water quality. Eight of these species, including the Mozambique tilapia, the mosquitofish, and the sailfin molly, have been confirmed on Saipan as well (McCagan et al., 2008; James et al., 2010).

In addition, at least 20 species of non-native amphibians and reptiles are now established in the inland waters of the Guam (Walsh et al., 2014; Tibbatts, 2017 in litt.), including the cane toad (*Rhinella marina*), 7 frog species that can potentially breed in flowing streams (*Fejervarya cancrivora*, *Fejervarya limnocharis*, *Hylarana guentheri*, *Kaloula pulchra*, *Litoria fallax*, *Pelophylax nigromaculatus*, *Pseudacris regilla*), the Chinese softshell turtle (*Pelodiscus sinensis*), and the red-eared slider turtle (*Trachemys scripta elegans*), the first and last listed species having also reached Saipan. At least 4 introduced aquatic mollusk species are also present on Guam or Saipan (McCagan et al., 2008; Tibbatts, 2017 in litt.), including two large-sized apple snail species (*Pila conica*, *Pomacea canaliculata*) that are considered agricultural pests impacting traditional taro cultivation. Finally, at least 8 invasive aquatic plants have become established on Guam (Tibbatts, 2017 in litt.), including major aquatic weeds such as water hyacinth (*Eichornia crassipes*), water lettuce (*Pistia stratiotes*), and duckweed (*Lemna minor*) which can rapidly cover the surfaces of stream pools or other slow-flowing reaches, significantly affecting sunlight penetration and nutrient cycling.

Most of these non-native species are capable of establishing themselves in the limnetic terminal reaches or midreaches of streams, and some such as tilapia will also invade mixohaline estuaries, although their distribution on the islands is variable since their dispersal across drainage divides requires human assistance. Certain watersheds on Guam, such as Agana and Talafofo (Fig. 6), now contain large numbers of such species, while in other smaller, more remote watersheds they are still essentially absent (Tibbatts, in litt.). Such aquatic invasive species also do not appear to be as well-established in the few streams on Rota and Saipan, and measures should be taken to prevent their future importation, establishment or spread.

Future Scenarios

Given the strong linkages between precipitation and Marianas stream discharges previously described, any future assessment of the integrity of these ecosystems must take projected climate change into account. As an ancillary product to the National Climate Assessment effort, a Pacific Islands Regional Climate Assessment (PIRCA) was produced in 2012 (Keener et al., 2012). This document, incorporating the contributions of nearly 100 independent experts, evaluated the state of knowledge related to climate drivers, impacts, and adaptive capacity within three sub-regions of the Pacific, including the Western North Pacific which includes the Mariana Islands. The findings bearing on freshwater systems are summarized below, and those wishing greater detail should consult the PIRCA, which treats these subjects in greater depth.

Depending on representative concentration pathway (RCP) model employed, CO₂ concentrations are projected to reach levels between 420 and 935 parts per million (ppm) by the end of the century (IPCC, 2014). As of May 2019 atmospheric CO₂ stood at 413 ppm, an increase of over 93 ppm from when standardized readings first began to be collected in the late 1950s at the Mauna Loa Observatory in Hawaii. The accumulation of carbon dioxide and other greenhouse gases in the atmosphere has led to warming

of both the atmosphere and the oceans due to the enhanced greenhouse effect. Temperature projections from both the Intergovernmental Panel on Climate Change's (IPCC) Fourth Assessment Report (Parry et al., 2007) and the second national assessment (US Global Change Research Program, 2014) indicate continued warming into the foreseeable future, with global average surface temperature projected to increase 1.2–6.4°C by 2100, with best recent estimates placing the range between 1.2 and 3.2°C (IPCC, 2014; Gattuso et al., 2015). Average tropical sea surface temperature (SST) is expected to increase by 50–80% of the average rate of atmospheric change (Guinotte et al., 2003). Therefore, average sea temperatures in the Marianas will probably increase by 1–2°C over the course of this century, providing additional atmospheric water vapor. Such increases in ocean and air temperature are related to changes in atmospheric circulation patterns that may result in more severe periods of drought and more markedly episodic high precipitation events, a trend already observed in Hawaii (Chu et al., 2009) where long-term stream and precipitation gauging records depict clear declines in precipitation and stream base flow over the past century, but high variations in stream total flow (Oki, 2004).

Global circulation models have projected that under a global warming regime fewer tropical storms will form, due to increased propensity for wind shear in high SST environments (Nolan and Rappin, 2008), but that those storms which do form will be more intense (Bengtsson et al., 2007), a prediction that has been borne out by recent storms of record intensity, such as Typhoon Yutu, that have affected the Marianas (and many other tropical areas of the world) in recent years. Modeling of the hydrological cycle under a regime of warming climate results in a projection of a 27% increase in atmospheric water vapor in the tropics over the next 100 years. Because this is also coupled with a longer residence time of water in the atmosphere, this increase in atmospheric water vapor does not necessarily result a marked increase in precipitation; instead, the moister atmosphere simply becomes capable of retaining greater heat content, thereby spawning stronger storms (Bengtsson et al., 2007). Global circulation models therefore project an increase in the proportion of extreme weather events in the most severe categories (Webster et al., 2005; IPCC, 2014), with the associated potential for extreme precipitation events, and thus higher and more acute discharge peaks, and more severe flash flooding in Marianas stream catchments.

The intensity and frequency of days of extreme heat are also projected with high confidence to increase over the course of the 21st century across the Mariana Islands. The CMIP3 model ensemble under several emissions scenarios produced projections that annual surface air temperatures (SATs) for the Western North Pacific sector containing the Mariana Islands, will range from 1.1 to 1.3°F higher by 2030, 1.9 to 2.6°F higher by 2055, and 2.7 to 5.1°F higher by 2090 (Australian Bureau of Meteorology and CSIRO, 2011). A subsequent analysis using the CMIP4 model ensemble further supported these projections (Parry et al., 2007). More recently, Polhemus (2017) presented model runs from the new CMIP5 ensemble under RCP 8.5, which generated somewhat revised projections, with SATs in the Western North Pacific ranging from 0.4 to 2.0°F higher by 2030, 2.0 to 3.5°F higher by 2055, and 4.8 to 6.4°F higher by 2090. Although there is some variability in the results of these different model suites, the underlying conclusion of steadily rising future temperatures is consistently the same (see Appendix 1).

For precipitation, projections of future trends are less well constrained than those for mean annual temperature. Although some initial approaches to climate model downscaling are being undertaken for the Marianas, such efforts are still incipient, and the results provisional. Any projections therefore have considerable uncertainty, which can only be reduced by future improvements in regional model input parameters. An initial run with the current CMIP5 ensemble under RCP 8.5 presented by Polhemus (2017) produces projections that indicate average daily precipitation will exhibit a 12–13% increase in the Marianas sector as a whole by 2100 (see Appendix 1). These projections do not, however, provide any information as to potential changes in the temporal distribution of rainfall within any given year.

These projected changes in ocean and atmospheric temperature, precipitation patterns, and tropical storm intensity over the coming decades all have significant implications for the future state of perennial stream ecosystems in the Marianas. The warming projected during the next 50 to 100 years will create heat-related stress for human communities and agriculture, putting additional loads on water supply systems. The increased heat will also further promote wildland fire, thereby further degrading stream catchments and increasing sedimentation, and creating increased extinction risk for native plant and animal species (Urban, 2015). Seasonal changes in precipitation patterns, coupled with increased temperature and evapotranspiration, also have the potential for widespread and significant impacts to water resources and agriculture, which will create both societal and ecological challenges. Based on historical and projected patterns of land-cover change in the Marianas, often associated with fire during drier periods, impacts from invasive species and human development are likely to amplify the adverse effects of climate change on freshwater habitats and their associated species, unless informed policy and adequate management strategies are proactively implemented.

A limited suite of conservation efforts are currently underway in the form of evolving policy and laws, restoration and management, education and outreach, and creation of protected natural reserves, but all these have to date had only a modest impact as far as shielding Marianas streams from further declines in functionality (Englund, 2011). As such, perennial streams Mariana Islands currently continue to suffer from degradation of surrounding habitats, and will continue to do so in the absence of more effective land management practices, particularly on Guam (Taborosi, 2013).

Appendix 1

Supporting climate model data for future scenarios (from Polhemus, 2017).

The data provided below represent preliminary outputs from the CMIP5 ensemble of 36 dynamical climate models. Each CMIP5 model was interpolated horizontally to 1 degree by 1 degree grids, over a time series beginning in 2010 and ending at 2099. Those

regridged data were then interpolated to each island point using the bilinear interpolation method. Ten years are chosen as the time slice to represent the specific year, e.g., the mean value from 2025 to 2034 to represent the value of 2030, the mean value from 2050 to 2059 to represent the value of 2055, and the mean value from 2090 to 2099 to represent the value of 2100.

Minimum and maximum projected air temperature envelope bounds of each of the above time steps were calculated from data representing a subset of the CMIP5 ensemble, using only those models that project t-min and t-max over the three time windows indicated above. These data represent the average value of t-min and t-max taken over the sampling windows, and thus are not strictly the t-min and t-max of the daily average temperature, and will have a slightly broader variance from central tendency, but are sufficient to indicate approximate envelopes of uncertainty.

The present-day reference values were calculated as averages for period 1995–2004, using the full CMIP5 model ensemble.

	<i>Guam</i>	<i>Saipan</i>	<i>Rota</i>	<i>Tinian</i>
CMIP5 Air Temperatures (°C)				
36 model ensemble				
<i>Average</i>				
Daily Temp. Average Current	27.1514	26.9380	27.0635	26.9602
Daily Temp. Average 2030	27.6959	27.4789	27.6060	27.5011
Daily Temp. Average 2055	28.5346	28.3185	28.4444	28.3404
Daily Temp. Average 2099	30.1406	29.9203	30.0498	29.9430
<i>Minimum range</i>				
Daily Temp. Min. Current Av.	26.7807	26.5623	26.6923	26.5850
Daily Temp. Min. 2030	27.4638	27.2553	27.3763	27.2769
Daily Temp. Min. 2055	28.3640	28.1559	28.2762	28.1775
Daily Temp. Min. 2099	29.9273	29.7067	29.8348	29.7299
<i>Maximum range</i>				
Daily Temp. Max. Current Av.	27.4726	27.2652	27.3860	27.2864
Daily Temp. Max. 2030	28.1615	27.9792	28.0841	27.9981
Daily Temp. Max. 2055	29.0484	28.8559	28.9669	28.8759
Daily Temp. Max. 2099	30.6311	30.4235	30.5439	30.4455
CMIP5 Precipitation (mm)				
36 model ensemble				
<i>Average</i>				
Daily Precip. Average Current	5.5791	4.8443	5.2325	4.9000
Daily Precip. Average 2030	5.6430	4.9158	5.3049	4.9765
Daily Precip. Average 2055	5.9328	5.1068	5.5665	5.1781
Daily Precip. Average 2099	6.3260	5.4502	5.9364	5.5235
<i>Minimum range</i>				
Daily Precip. Min. Current	2.5840	1.9550	2.3180	2.0020
Daily Precip. Min. 2030	2.7180	2.0240	2.4600	2.0870
Daily Precip. Min. 2055	2.9870	2.1490	2.6370	2.2150
Daily Precip. Min. 2099	2.9780	2.1350	2.6180	2.1970
<i>Maximum range</i>				
Daily Precip. Max. Current	9.8770	8.0190	8.7060	8.1160
Daily Precip. Max. 2030	9.2680	7.6350	8.3740	7.7500
Daily Precip. Max. 2055	9.2580	7.3810	8.4870	7.5650
Daily Precip. Max. 2099	10.0540	8.3730	9.3320	8.5300

See also: Wetlands of the Mariana Islands; Physical Geography of the Mariana Archipelago; Developed Systems in the Mariana Islands Archipelago; Coastal Strand and Mangrove Swamps of the Mariana Islands; Savannas of the Mariana Islands Archipelago; Mariana Islands Forest.

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Intermittent Rivers and Ephemeral Streams: A Unique Biome With Important Contributions to Biodiversity and Ecosystem Services

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Abstract

The majority of flowing waterbodies throughout the world can be considered intermittent rivers or ephemeral streams (IRES) because at some point in time and space they stop flowing or dry. Despite their global abundance, less is known about this biome compared to perennial—permanently flowing—rivers. However, a recent surge in research has dramatically improved our understanding of how IRES function and what types of biodiversity and ecosystem services they support. A cycle of terrestrial-aquatic habitat conditions caused by the periodic drying and rewetting creates a high temporal dynamic in the biogeochemistry, biodiversity, and ecosystem services of IRES. Vast amounts of accumulated sediment, organic matter and organisms can be transported from IRES downstream to larger rivers or lakes, contributing to the global C cycle. The mosaic of aquatic and terrestrial habitats along IRES hosts high biodiversity including microorganisms, plants, invertebrates, reptiles, and mammals, with specialized strategies to resist to or recover from changes in habitat conditions. Although IRES provide a broad range of ecosystem services including provision of fresh water and cultural enrichment, there is a continued struggle to protect this dynamic and threatened biome.

What Are Intermittent Rivers and Ephemeral Streams?

Hydrologically Diverse and Globally Abundant

Intermittent rivers and ephemeral streams (IRES) refer to all flowing waters that cease flow and/or dry completely at some point along their course (Datry et al., 2017, Fig. 1). Arguably the world's most widespread type of flowing water (Larned et al., 2010; Datry et al., 2018a), IRES range from small ephemeral streams that flow for a few days after heavy rain to large intermittent rivers that recede to isolated pools but might not dry completely. Many local names for IRES exist throughout the world such as temporary rivers, winterbournes, wadis, arroyos and ramblas (e.g., Steward et al., 2012), highlighting the diversity and cultural importance of this biome to people living in their catchments.

IRES occur on all continents, including Antarctica (Larned et al., 2010; Steward et al., 2012). IRES are dominant features of hyper-arid, arid, semi-arid, and dry-subhumid regions, which represent a third to half of the Earth's land surfaces (Tooth, 2000; Whitford, 2002; Millennial Ecosystem Assessment, 2005, Fig. 1). As examples of their abundance, 70% of rivers are classified as intermittent in Australia (Sheldon et al., 2010), 66–94% of river lengths in Southwestern United States (i.e., Arizona, New Mexico, Utah, Nevada, Colorado, California; Levick et al., 2008) are IRES, and they are found across Mediterranean, temperate, humid, boreal, alpine and polar regions (Sabater and Tockner, 2009; Bonada and Resh, 2013; Leigh et al., 2015). Virtually every river network includes IRES, notably because the dense network of headwaters, which can make up >70% of the total river network length, is typically intermittent (Lowe and Likens, 2005; Meyer et al., 2007; Fritz et al., 2013; Grill et al., 2019).

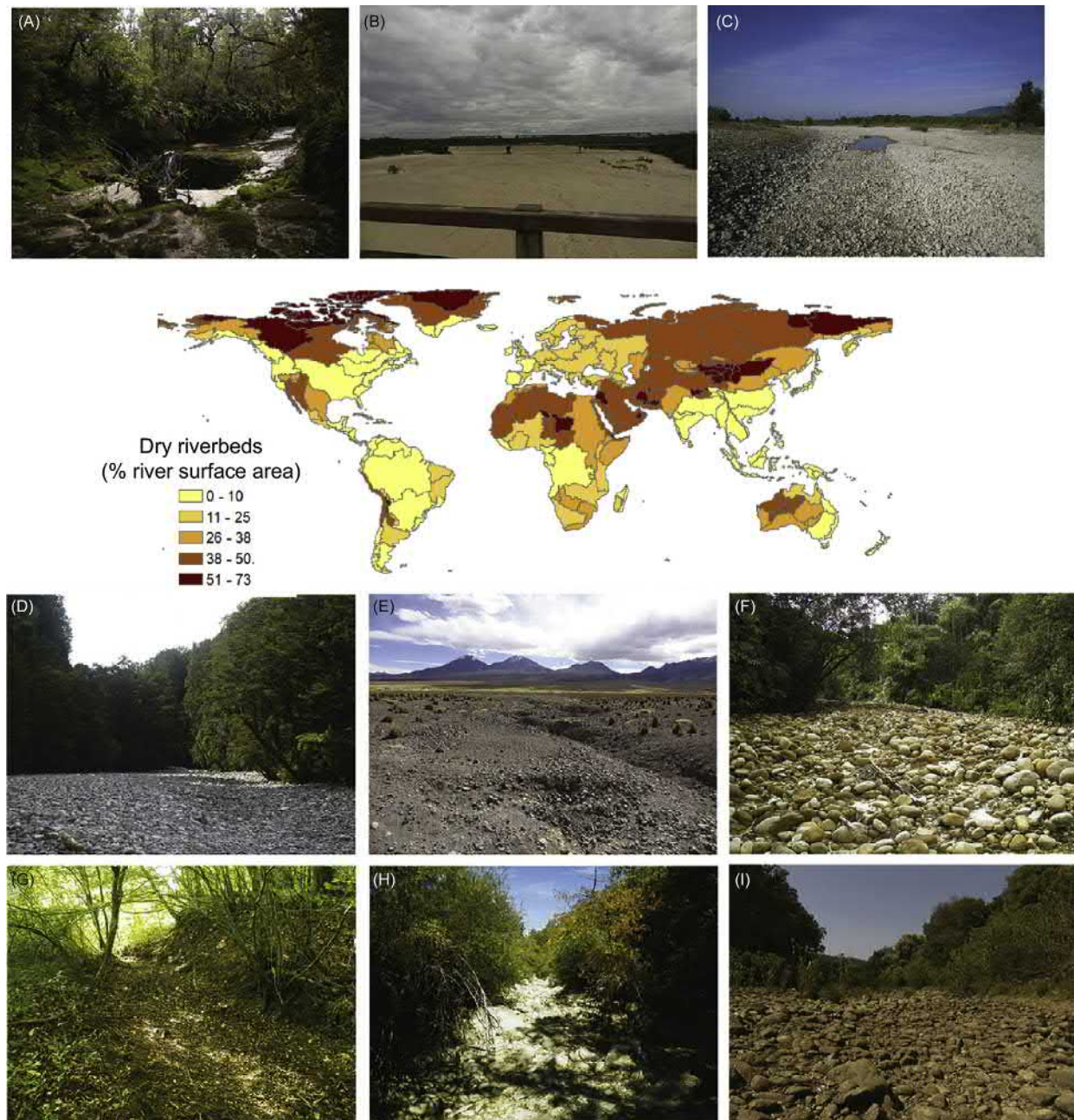


Fig. 1 Different types of IRES from across the world: (A) unnamed karstic stream, West Coast, South Island, New Zealand, (B) Río Seco, Chaco, Bolivia, (C) Asse River, Provence, France, (D) unnamed gravel-bed stream, West Coast, South Island, New Zealand, (E) unnamed stream, Altiplano, Bolivia, (F) Chaki Mayu, Amazonia, Bolivia, (G) Clauge, Jura, France, (H) Calavon River, Provence, France, and (I) Hozgarganta River, Andalucía, Spain. The map represents five categories of the percentage of dry riverbeds over the total river surface per COSCAT (a global segmentation scheme of coasts and river catchments; [Meybeck et al., 2006](#)). Dry riverbeds have been estimated as the river surface area dry all year long from models developed in [Raymond et al. \(2013\)](#). These estimates represent the only available global estimates and may over-represent dry riverbeds at higher latitudes. Photo credits: Thibault Datry (A–F), Bertrand Launay (G and H), and Núria Bonada (I).

Three-in-One: IRES Contribute to Lotic, Lentic, and Terrestrial Dynamics

IRES are dynamic shifting habitat mosaics of flowing, non-flowing and dry patches ([Fig. 2](#)), the extent and connectivity of which constantly vary across drainage basins in response to river discharge and groundwater levels ([Stanley et al., 1997](#); [Jaeger et al., 2014](#); [Datry et al., 2016a](#)). To account for this dynamism in habitat types, concepts from lotic (aquatic flowing), lentic (aquatic non-flowing) and terrestrial ecology are used to understand these ecosystems ([Datry et al., 2014b](#)). In general, river networks are an aquatic continuum in a terrestrial matrix and therefore meta-ecosystems linked by lateral (terrestrial to aquatic), vertical (from

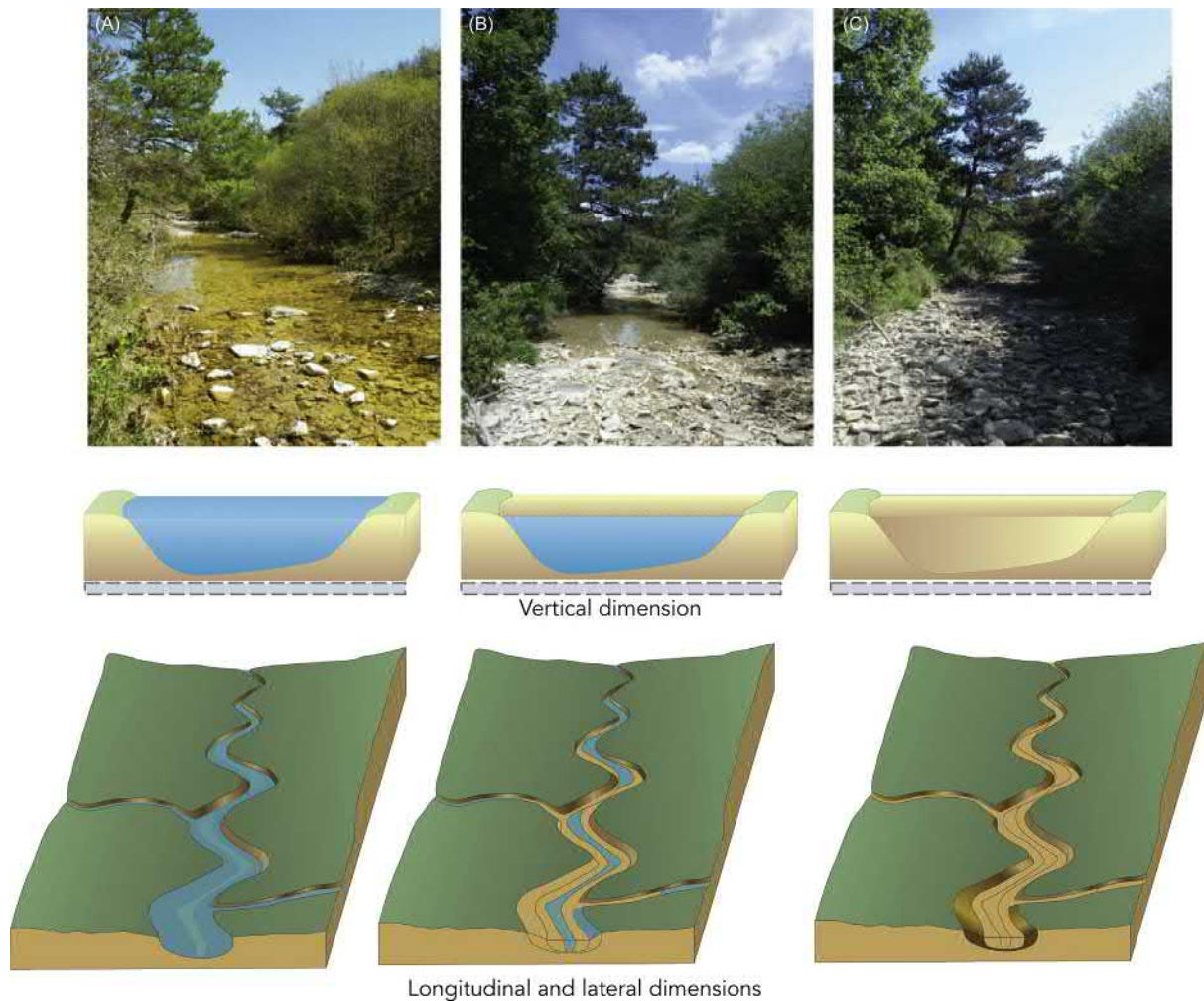


Fig. 2 Alternating lotic (flowing) (A), lentic (non-flowing) (B) and terrestrial (dry) phases (C) in an intermittent river of France (Calavon River). Below each photo is a graphical depiction of the likely vertical and longitudinal and lateral dimensions of each flow-state. Gray box below stream channel (vertical dimension) represents the hyporheic zone that may remain saturated even during surface drying events. Photo credits: Bertrand Launay.

the surface to the subsurface) and longitudinal (from upstream to downstream) flow of matter and energy (Battin et al., 2009). In IRES, the mosaic of lotic, lentic, and terrestrial environments creates patches of sub-ecosystems that interact differently among each other and with the terrestrial matrix. The flows of matter and energy, which affect biogeochemical cycles and ecosystem functioning, change with alternating dry and wet phases and depending on network position (Datry et al., 2017; von Schiller et al., 2017). Lateral flows of organisms and resources with the surrounding terrestrial habitat are likely to be enhanced during the dry phase when terrestrial organisms colonize dry riverbeds. However, little is known about the spatiotemporal variability of these flows and their effect on biogeochemical cycles and ecosystem functioning at the entire river network scale.

Biogeochemical Dynamics in Intermittent Rivers and Ephemeral Streams

Streams and rivers transport a variety of dissolved and particulate compounds, such as nutrients (e.g., nitrogen, phosphorus) and organic matter, which constitute bases for stream food webs and ecosystem functioning (Meybeck, 1982). The biogeochemical cycles, resulting from the input, removal, transformation, production, and export of these compounds, are generally controlled by factors such as humidity, temperature, flow velocity (Shumilova et al., 2019). In response to alternating lotic, lentic, and terrestrial phases over time and geographic location, IRES have temporally and spatially discontinuous biogeochemical processes with pulsed nutrient and OM inputs, processing, and transport events (von Schiller et al., 2017).

Organic matter processing (i.e., decomposition) and transport are typically halted while riverbeds are dry due to reduced activity of microorganisms (Corti et al., 2011; Sabater et al., 2016) and loss of hydrological connectivity, respectively. However, stream

biofilms associated with dry sediments may continue processing organic matter (Timoner et al., 2012) and the activity of some anaerobic microbes may lead to changing levels of stream nutrients, such as nitrogen (Austin and Strauss, 2011; Merbt et al., 2016) on dry riverbeds. Colonization of the dry riverbed by terrestrial animals (e.g., insects, mammals) and plants may also modify organic matter and nutrients dynamics through imports of terrestrial compounds or utilization of the instream resources.

In pools that may remain along the dry riverbed matrix, the accumulation of organic matter combined with high respiration rates and the lack of oxygen when air temperature rises can create anaerobic or hypoxic conditions. Organic matter usually accumulates in the form of leaf litter from riparian trees, as algae growth in pools with low canopy cover, or both, and rates of decomposition are low (Corti et al., 2011). The nutrient balance is also modified due to denitrification processes, with nitrates usually decreasing and phosphate and ammonium contents increasing (von Schiller et al., 2011). Very low oxygenation at the later stages of pool drying may also lead to methane production (Gómez-Gener et al., 2016).

Flow resumption usually leads to pulses of organic matter and nutrients that are imported from the riparian zone into the stream and from upstream to downstream as the lateral and longitudinal hydrological connectivity is restored. Pulses of decomposition may then occur downstream where massive amounts of organic matter accumulates (Corti and Datry, 2012; Datry et al., 2018b).

Organic matter decomposition and microbial activity are the main drivers of carbon dioxide emissions from river ecosystems. CO₂ emissions from IRES are similar to those of their perennial counterparts during the flowing phase, globally estimated to be 1.75 g CO₂ m⁻² day⁻¹ (Raymond et al., 2013). However, these estimates do not take into account the rewetting and dry phases during which CO₂ emissions may greatly exceed those during flowing phases. Whereas dry sediments can release up to 67.5 g CO₂ m⁻² day⁻¹ (Gómez-Gener et al., 2016), pulses of decomposition and sediment respiration during rewetting events may emit up to 13.7 g CO₂ m⁻² day⁻¹ (Datry et al., 2018b, Box 1) and 21.1 g CO₂ m⁻² day⁻¹ (Gallo et al., 2014), respectively. Annual contributions of IRES to global CO₂ emissions may therefore be much greater and more important than those of perennial rivers, magnified by the spatial abundance and ubiquity of IRES across the Earth's surface.

Biodiversity in Intermittent Rivers and Ephemeral Streams

From Microbes to Elephants, IRES Support High Biodiversity

Microbiota, including bacteria, archaea, protozoa, fungi, cyanobacteria, and algae grow both in benthic habitats as well as in the water column itself and comprise the base of aquatic foodwebs (Pusch et al., 1998; Weitere and Arndt, 2003; Battin et al., 2016). Flow intermittence can cause differences between environmental conditions in IRES and perennial rivers, such as water temperature, dissolved oxygen, dissolved organic matter, inorganic nutrients, flow velocity, and light. These differences in environmental conditions likely drive differences in the composition of microbiota between IRES and perennial biomes (Romaní et al., 2017). Microbes are known to play a key role in biogeochemical processes in rivers, such as organic matter decomposition, and our understanding of microbial biodiversity continues to advance as molecular approaches make it easier and more affordable to quantify microbial diversity. For example, pyrosequencing uncovered compositional differences in bacterial communities on cobbles during flowing, non-flowing, and rewetting stages of flow intermittence in a Mediterranean IRES (Timoner et al., 2014).

Plant communities that inhabit IRES are influenced by the dynamic hydrologic conditions which create favorable environmental conditions for both vascular aquatic and riparian plants (Sand-Jensen and Frost-Christensen, 1998; De Wilde et al., 2014). Plants comprised of various functional groups, including emergent and submerged, respond differently to flow intermittence (Brock and Casanova, 1997). Some emergent helophytes, such as Cyperaceae and Juncaceae, can tolerate complete drying of above and below-ground biomass. Submerged plants usually die during drying conditions except for desiccation-resistant seeds that can germinate upon rewetting (Brock et al., 2003). Thus, the availability of "seed banks" is an important attribute of plant communities allowing persistence in IRES.

Aquatic and terrestrial invertebrates are arguably the most well-studied organisms inhabiting IRES (Leigh and Datry, 2016). The dynamic environmental conditions and habitat types found within IRES influence the composition, abundance, and diversity of invertebrates (Datry et al., 2016a), often driving differences in community composition and richness between IRES and perennial rivers. In general, taxonomic richness of aquatic invertebrates in IRES is lower than that of equivalent-sized perennial rivers (Datry et al., 2014a; Soria et al., 2017). However, when the terrestrial phase of IRES is considered, total invertebrate richness, accounting for aquatic and terrestrial taxa, may be similar or even higher in IRES. Typically, community composition of invertebrates changes along a gradient of flow intermittence, with IRES communities being subsets of the species found within sites with more permanent flow (Datry et al., 2014a). IRES invertebrate community composition shifts in response to timing, duration, and frequency of lotic phases, often with distinct invertebrate communities within each hydrologic phase. For example, mayflies, stoneflies and caddisflies can typify aquatic invertebrate communities during the flowing phase, whereas odonates (dragonflies and damselflies), aquatic beetles, and true bugs may dominate during the lentic phase (Bonada et al., 2007). During the terrestrial phase, both terrestrial and semiaquatic invertebrates colonize IRES, including insects (mainly ground beetles), arachnids, centipedes, crustaceans, millipedes, snails, springtails, and worms (Steward et al., 2017).

Fishes inhabit intermittent rivers, including those in arid regions of Africa and Australia (Lévêque, 1997; Allen et al., 2002). Generally, fish diversity is lower in IRES compared to equivalent-sized perennial systems because relatively few species can cope with flow intermittence. However, some fish are adapted to breathing oxygen from the atmosphere (e.g., African sharptooth catfish [*Clarias gariepinus*]). Persistence of most fishes within IRES is facilitated more by movements into and out of drying habitats than by their ability to resist desiccation, although pools can be an important refuge for stream fishes (Magoulick and Kobza, 2003).

Box 1 The 1000 intermittent river network: measuring the importance of IRES to global carbon and CO₂ emission. The “1000 Intermittent River Project”: Measuring the Importance of IRES to Global Carbon and CO₂ Emissions

Drastic changes in flow regime and IRES distribution prompt fundamental questions: how are the biogeochemistry and biodiversity of river networks affected by these changes? How do these alterations vary across climatic and biogeographic regions?

To address these questions, an international group of researchers started a multidisciplinary effort called the “1000 Intermittent Rivers Project” (#1000IRP on Twitter). The project’s main goal is to merge individual knowledge, forces, and passions through simple, consistent, and comparable joint experiments in IRES worldwide.

Since its 2016 inception, the project has grown to over 120 participants from 28 countries (Datry et al., 2016b). Although some regions, including Africa and Asia, remain poorly represented in this collaborative effort, the group continues to recruit new participants for future experiments.

The first coordinated experiment done by #1000IRP is recognized for contributing to the understanding of global C cycle and CO₂ emissions (Datry et al., 2018b; Shumilova et al., 2019). In this global experiment, researchers collected leaf litter and other organic matter and sediments from 212 dry riverbeds across the globe. Samples were then sent to a single laboratory for further processing.

One major finding from this experiment was that rewetting events in IRES contribute up to 10% of daily CO₂ emissions from all rivers and streams. During rewetting, dissolved organic carbon, phenolics, and nitrate are leached from sediments and organic matter are washed downstream. This indicates that rewetting phases in IRES are “hot moments” of biogeochemical activities that likely play an important role in how rivers function.

As more rivers begin to dry as a result of climate change and increased water demands, there will be a continued need to study IRES at the global scale through collaborative experiments.



Photo credits: Petr Pařil.

Swimming allows fish to disperse to access food and habitat resources within IRES during their lotic hydrological phases (Kingsford et al., 2006; Wardle et al., 2013). IRES provide an important habitat type for some fish species during their life cycle. For example, IRES constitute a key spawning and juvenile rearing habitat for the federally endangered coho salmon (*Oncorhynchus kisutch*) along the US Pacific Coast (Wigington et al., 2006). IRES likely provide abundant food resources through terrestrial subsidies and fish may experience lower levels of competition and predation compared to perennial rivers (Courtwright and May, 2013; Kerezszy et al., 2013).

Other wildlife, such as amphibians, reptiles, birds, and mammals use IRES for a variety of reasons, especially in arid and semiarid regions where water is limited. Most amphibians are well-suited to inhabit IRES because of their life cycles which constitute both aquatic and terrestrial stages (Wells, 2010). Many reptiles are attracted to IRES because of higher humidity compared to terrestrial habitats. Bird species that are not dependent on water often congregate in riparian areas of IRES to roost and reproduce (Shine and

Brown, 2008). Mammals ranging in size from rodents (Gibson and Olden, 2014) to elephants (Elephantidae) and hippopotamuses (*Hippopotamus amphibius*) (Kok and Nel, 1996; Lakshminarayanan et al., 2016) are also commonly found in and around IRES (Kerezesy et al., 2013). Although IRES likely attract wildlife during lotic and lentic hydrologic phases, dry riverbeds are movement corridors for all types of terrestrial vertebrates including lizards, birds, rodents, lagomorphs, carnivores, and ungulates (Sánchez-Montoya et al., 2016).

Strategies for Persistence in IRES

To persist in the dynamic conditions of IRES systems, organisms have a variety of adaptations that are often categorized into traits of either resistance or resilience to flow intermittence (Bonada et al., 2007; Robertson and Wood, 2010; Robson et al., 2011; Datry et al., 2014a). Traits are broadly characterized into physiological, morphological and life-history features of organisms. Resistance can be defined as the capacity of a species, a community, or an ecosystem to persist unchanged by and during a disturbance (Stanley et al., 1994; Vander Vorste, 2015) and includes diapause, desiccation-resistant eggs, cocoons or cells, body armoring and aerial respiration (Bonada et al., 2007; Robson et al., 2011). Resilience, or the capacity to recover from disturbance, is favored by traits such as short lifespans with early maturity, asexual reproduction, and strong aerial or aquatic dispersal ability (Bonada et al., 2007; Datry et al., 2014a; Vander Vorste, 2015). Typically, there are several sources of colonization of IRES by taxa with either resistant or resilient strategies (Fig. 3).

Organization of Metacommunities Within IRES

A metacommunity is a set of local communities connected by dispersal (Leibold et al., 2004). In a metacommunity, community assembly is determined by the capacity of species to tolerate and develop under local environmental conditions (environmental sorting) and to reach the community through dispersal (i.e., spatial connectivity and organism dispersal ability). IRES support dynamic metacommunities in which local communities experience alternating aquatic and dry phases as well as changes in

Biotic community resistance and resilience to river drying

Resistance strategies

allow organisms to survive flow cessation and persist within a stream reach

Sources of resistance in IRES

Remnant pools

As stream riffles dry, organisms can survive in remnant pools if environmental conditions remain favorable

Hyporheic zones

Once surface water is lost, some organisms can survive in saturated hyporheic zones (saturated interstitial sediments below and adjacent to the streambed).

Desiccation-resistant stages

Eggs, larvae, pupae or adult life stages that can resist desiccation for up to many years before becoming active again upon stream rewetting.

Resilience strategies

allow organisms to recolonize a previously dry stream reach from elsewhere

Sources of resilience in IRES

Dispersal by drift

Organisms entrained in water flowing downstream or on floating detritus

Crawling and swimming

Crawling and swimming upstream or downstream

Aerial dispersal

Aerial adult life stages of aquatic insects

Fig. 3 Examples of traits that enhance the resistance and resilience of aquatic invertebrates to surface water drying Adapted from Vander Vorste, R. (2015). The hyporheic zone as a primary source of invertebrate community resilience in intermittent alluvial rivers: Evidence from field and mesocosm experiments. PhD Thesis. University of Lyon 1: Lyon, France. 210 pp.

hydrological connectivity, forming a mosaic of habitats that usually connect and disconnect each year (Datry et al., 2016a). These spatiotemporal dynamics leads to recurrent changes in community assembly mechanisms (Datry et al., 2016a; Sarremejane et al., 2017).

Environmental sorting is the main driver of aquatic organism assembly during flow recession phases because drying creates a strong filter eliminating the least adapted species. On the other hand, dispersal processes should be more important when flow resumes as organisms recolonise from surrounding habitats (Datry et al., 2016a, Sarremejane et al., 2017). However, the interplay of these mechanisms is likely to differ for species adapted to lotic, lentic, and terrestrial habitats, for example, dispersal-related processes likely being more important for lotic and terrestrial species as flow recedes. More research is needed to determine which local conditions (e.g., drying frequency, flow state and water chemistry) and connectivity features (e.g., distance to perennial reaches and isolation within the river network) drive community assembly where and when in the river metacommunity. Understanding this will allow better characterization of community assembly in response to flow intermittence.

Management of Intermittent Rivers and Ephemeral Streams

Ecosystem Services Provided by IRES

IRES provide important cultural, regulating, and provisioning ecosystem services, varying between aquatic and dry phases (Datry et al., 2018a; Koundouri et al., 2017). IRES bring spiritual and inspirational enrichment and are also widely appreciated for recreational opportunities and aesthetic values. Regulating ecosystem services provided by IRES include flood protection and water purification. As discussed previously, IRES support an important role in riverine nutrient cycling and contribute to global CO₂ emissions. Provisioning ecosystem services provided by many IRES include fresh water and food. The dynamic flow regime of IRES also influences provision and types of these various ecosystem services. For example, IRES can support recreational fishing during wet phases but be used as a path by walkers or as foraging areas for livestock during dry phases.

Protection and Management of IRES

Relatively little attention has been given to IRES protection and management, perhaps because dry channels have, until recently, been perceived as lifeless symbols of human impacts or poorly functioning river systems. In many countries, IRES are not legally recognized as part of the river network (Acuña et al., 2014), and although their recognition has increased in the past decade, their status as waterways that are worth protecting is still debated by authorities in the United States (Marshall et al., 2018, Box 2). In Europe, IRES protection status depends on how “waterbodies” are classified by regional authorities or each river basin, with differences in the ways that IRES are perceived and protected across countries (Fritz et al., 2017). In Australia where IRES are prevalent, they are included in most management plans and legislation. Nevertheless, IRES are sometimes included within protected areas and, when this is so, their conservation focuses on maintaining their natural flow regime and the connectivity to aquatic refuges (e.g., pools, Leigh et al., 2015). Ephemeral streams, i.e., those dry most of the time, are typically prone to being dismissed from management plans, and limited knowledge about their ecosystem services often hinders their conservation (Boulton, 2014).

IRES are often omitted from ecological monitoring programs implemented to characterize the ecological quality of rivers. Most biomonitoring techniques have been developed for perennial rivers and often perform poorly in IRES, particularly because reference communities (i.e., under those experiencing little or no human impact) usually have fewer taxa than those in their perennial counterparts (Stubbington et al., 2018a). Typically, biomonitoring index scores decrease with flow intermittence as well as with human impacts (Wilding et al., 2018). Biomonitoring tools therefore need modification to account for the natural variability of IRES communities and to efficiently disentangle the effect of flow intermittence from human impacts (Stubbington et al., 2018a). However, characterization of communities across the range of aquatic and terrestrial conditions that occur in IRES—including responses to natural hydrological variability and to human stressors is still needed. Such research will enable the development of effective biomonitoring strategies, which include terrestrial and lentic phases, therefore recognizing the dynamism of these ecosystems (Stubbington et al., 2018b).

Future of IRES and Global Change

In IRES, flow cessation and drying can have natural and non-natural causes. Disentangling these causes is rarely easy (Gallart et al., 2017), and often, multiple causes interact. Different processes generate natural drying in IRES: transmission losses (e.g., infiltration of surface water into porous streambeds), evapotranspiration, downward shifts in groundwater tables, hillslope runoff recession, and freeze-up (Larned et al., 2010). Anthropogenic drying can be due to one or more of the following human activities: alteration of land-use patterns, flow regulation, surface or groundwater extraction, and reduced precipitation and increased evaporation resulting from climate change (Palmer et al., 2008; Steward et al., 2012).

The flow regimes of streams and rivers are prone to severe alterations worldwide, mainly in response to drying climates across much of the globe coupled with rapidly increasing human demands. Consequently, the occurrence and spatial and temporal extent of IRES are both increasing over time (Larned et al., 2010; Datry et al., 2018a). Shifts from perennial to intermittent flow regimes are projected by the 2050s for streams and rivers across much of the globe, including north-eastern and south-western Australia, Brazil, California, the Caribbean, southern Africa, West Africa and around the Mediterranean Basin (Döll and Schmied, 2012). Conversely,

Box 2 Case study of current environmental protection of IRES systems in the United States. Does Environmental Policy Protect Intermittent and Ephemeral Streams?

Case Study: Waters of the United States (WOTUS)

In the United States, the Clean Water Act (CWA) provides legal protection of the ecological health of rivers. However, a debate over whether intermittent and ephemeral streams should be included in these protections was sparked in 2006 in the U.S. Supreme Court. Guidance by the Supreme Court decision stated that rivers with permanent or seasonal hydrologic connections to Traditionally Navigable Waters should be protected. Without a relatively permanent hydrologic connection, streams with a connection through hydrological and ecological factors that affect the chemical, physical, and biological health of navigable waters should also be protected.

Following the Supreme Court decision, inclusion of intermittent and ephemeral streams in the CWA by the US Environmental Protection Agency (USEPA) has wavered. Freshwater scientists have been in favor of including intermittent streams within the jurisdiction of waters of the United States, in part, due to the recognition that these streams provide “many ecosystem services, including water provision and purification, that contribute substantially to securing water quantity and quality” as stated in [Marshall et al. \(2018\)](#). Following an independent review of > 1200 scientific publications, USEPA's Science Advisory Board informed a Clean Water Rule in 2015 aiming to recodify the waters of the United States to include intermittent streams. As of 2019, the US federal government has failed to implement the Clean Water Rule despite direct advice from freshwater scientists ([Acuña et al., 2014](#); [Marshall et al., 2018](#); [Sullivan et al., 2019](#)). Without adequate protection, the US puts 58% of all waterways in the contiguous US at risk of degradation ([Marshall et al., 2018](#)).



Photo credits: Ross Vander Vorste.

some natural IRES are predicted to become perennial in Siberia and parts of Canada and Alaska due to warmer winters ([Döll and Schmied, 2012](#)). Similarly, many natural IRES are becoming more intermittent and dry periods are getting longer ([Larned et al., 2011](#)). However, trends of increasing drying are not universal and controlled releases from dams and weirs, discharge of agricultural, industrial and urban effluents, inter-basin transfers and snow melt can contribute to decreased intermittence of many IRES, turning some of them artificially perennial ([Hassan and Egozi, 2001](#); [Steward et al., 2012](#)). In some water-scarce areas, the baseflow of urban rivers is maintained by wastewater effluents ([Luthy et al., 2015](#)). Reversal of seasonal patterns of drying are observed in other areas, where channels are used to carry irrigation flows released from upstream dams: peak flows from dam releases occur when flows in the channel used to cease whereas dams retain water, sometimes causing flow to cease at a time when the downstream river historically flowed ([Barnett and Pierce, 2009](#)).

Summary

Intermittent rivers and ephemeral streams contribute substantially to global biogeochemical processes and help sustain biodiversity. In many regions of the world, this biome dominates as the main freshwater ecosystem type compared to their perennially flowing counterparts. A dynamic flow regime is what sets IRES apart from other aquatic ecosystems; creating opportunities for lotic, lentic, and terrestrial organisms. Many of these organisms have specific trait adaptations that allow them to persist through phases of flowing water, pooling, and completely dry channels. Across the landscape, biotic communities can change quickly from phase to phase because they are connected by dispersal forming metacommunities. IRES likely play a major role in how metacommunities

are organized because of their dynamic nature. Although IRES are becoming more widely recognized for their importance in providing ecosystem services, they are increasingly under threat by global change. Under future climate change, many more perennial rivers are expected to become intermittent or ephemeral and drying may become more severe. Protection of this biome, which is currently limited compared to perennial rivers, continues to be an issue to be resolved.

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Restoration of Riparian Habitats

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Abstract

Riparian areas are the terrestrial interface between freshwater and upland environments, encompassing important ecotones where aquatic and terrestrial biophysical processes intersect to create unique and dynamic habitats. Diverse riparian habitats support organisms adapted to variable hydrologic conditions associated with seasonal precipitation patterns and cycles of erosion and deposition. Riparian ecosystems encompass habitats for both aquatic and terrestrial species, making these areas biodiversity hotspots across river networks. Riparian restoration is an effective conservation practice that can benefit terrestrial and aquatic organisms as well as promote water quality. Owing to their high conservation value, the protection and restoration of riparian areas has become a primary objective of land-management interests globally. Restoration practices include adjusting or targeting land- and water- management activities to meet conservation goals. Effective riparian restoration strategies will vary across biomes in response to distinct biophysical and social considerations at stream corridor, catchment, and regional scales.

Characteristics of Riparian Habitats

Riparian areas are semiterrestrial systems extending from water's edge to the uplands, their spatial extent controlled by surface and groundwater hydrology (Naiman et al., 2005). Riparian areas include floodplain and streambank landforms which exhibit unique soil and vegetation characteristics resulting from periodic inundation. Across biomes, riparian areas and the biogeochemical systems they represent vary based on climate, lithology, and elevation, as well as land use, cultural, and political contexts. Riparian habitats extend from mountain headwaters to coastal lowland streams and thus encompass a wide variety of habitats and vegetative communities.

The structure, function, and maintenance of riparian habitat derive from both lateral and longitudinal processes. Riparian areas are gradients where transitions and exchanges occur between freshwater and upland ecosystems. They also function as corridors where organisms and materials flow in linear paths along streambanks. Hydrological, biological, and geochemical processes affect the lateral and longitudinal characteristics of riparian systems. Numerous feedbacks connect riparian systems to both upland and freshwater ecosystems. Processes that influence riparian systems include deposition and erosion of streambanks (sediment transport), variations in the timing and magnitude of streamflow, and nutrient transfers from stream to streambank and back. Freshwater flows can control local habitat, leading to riparian communities uniquely cued to predictable seasonal patterns of discharge. Terrestrial and aquatic disturbance events affect the flow of materials both across the riparian gradient from freshwater to upland, as well as along riparian corridors from drainage divide to sea. Long-distance seed dispersal is facilitated by streamflows and flood events and creates natural riparian vegetation patterns across hydrologically connected river networks (Bourgeois et al., 2016).

Ecosystem Services Provided by Riparian Systems

Riparian areas provide a suite of valuable ecosystem services that make them a focus of conservation efforts around the world (Dufour et al., 2011; Bagstad et al., 2013; Penaluna et al., 2017, 2018). Intact riparian vegetation and hydro-geomorphic processes directly affect streamflow and water temperature, instream habitat complexity, water quality, and biodiversity that contribute to economic values. These regions also provide significant social and cultural value to human communities around the world.

Streamflow and Water Temperature: Streamside vegetation increases water infiltration rates, potentially mediating high flows associated with precipitation patterns, and enhancing groundwater recharge that supports baseflow conditions during dry periods (Caissie, 2006). Riparian areas can also store cool water from spring flood events, releasing stored waters into stream channels through subsurface flows during the summer season, effectively increasing baseflow volumes and regulating stream temperatures (Elmore et al., 2003). Shading of stream channels by intact riparian forests and vegetation regulates stream temperature, which in turn supports aquatic ecosystems and cold-water dependent fishes (Beschta et al., 1987). Vegetation can contribute to cool thermal regimes in off-channel habitats (i.e., alcoves, side channels) by enhanced subsurface flow from floodplain springbrooks and lateral seeps (Poole and Berman, 2001; Ebersole et al., 2003). Riparian areas also help maintain streamside thermal microclimates by altering wind speed, humidity, and local air temperature (Olson et al., 2007).

Instream Habitat Complexity: Woody vegetation in riparian areas is an important source of large wood recruitment to streams. Instream large wood reroutes water to transform stream-channel morphology, creating complex instream habitat important for native aquatic species (Bilby and Bisson, 1998). The root structures of streamside vegetation stabilize streambanks, minimize erosion, and benefit stream habitat quality.

Water Quality: Intact riparian vegetation enhances water quality by protecting streams from detrimental effects of upslope land uses by absorbing flood flows, increasing evapotranspiration, and limiting downstream sedimentation (Naiman et al., 2005). Riparian vegetation filters nutrients from agricultural chemical treatments or urbanized areas as runoff drains into stream channels during storm events (Vidon et al., 2010). Sediments, nutrients, and toxic materials are filtered from floodwaters or runoff by particulate trapping and the binding of materials to leaf litter and soils in these areas (Correll, 1999). For example, concentrations of nitrate in shallow groundwater decline as the groundwater moves through riparian zones before reaching stream channels (Davis et al., 2007).

Biodiversity: Riparian habitats can support a large proportion of a region's biodiversity, including numerous riparian-obligate organisms (Naiman and Decamps, 1997; Sabo et al., 2005; Olson et al., 2007). Other species use riparian habitats to complete their life cycle, particularly migrating birds, butterflies, and mammals. Networks of riparian areas along stream channels provide important habitat and dispersal corridors. Further, because riparian areas provide cool, moist microclimates, they may be particularly important for conservation prioritization as climates change in the future (Seavy et al., 2009; Beier, 2012; Capon et al., 2013; Krosby et al., 2018).

Cultural and Social Value: In addition to their services supporting ecosystems and water quality, riparian areas are also culturally and socially important. The value of riparian systems can be seen across rural and urban societies around the world. Along the Oueme and Okpara Rivers of Central Benin, West Africa, riparian forests are an integral element of *ibu odo*, or sacred pools of cultural importance (Ceperly et al., 2010). Riparian systems are additionally valued for their function as windbreaks and hunting grounds, supporting hunting and fishing activities of cultural and economic importance. In a study along a river in Indonesia, Vollmer et al. (2015) found that riparian corridors provide high value non- or indirect-use cultural services to low-income urban residents. Riparian areas can function as greenspaces and parks, providing sources of recreation and tourism and thus having passive economic value (Johnson and Carothers, 1982). Private property also benefit economically from riparian vegetation, as studies have shown a positive relationship between property values and distance to riparian areas in the USA (Qui et al., 2006; Bin et al., 2009).

Degradation of Riparian Habitats

Owing to their location next to vital waterways, riparian ecosystems are subject to severe degradation by human land and water usage (Fig. 1). The many detrimental impacts on riparian habitat, stream habitat, and water quality are well documented in the literature (Mensing et al., 1998; Feld et al., 2011). Forestry, agriculture, urbanization, and other human land uses have reduced or eliminated riparian areas around the world. Deforestation is a significant driver of riparian habitat degradation. Swift (1984) found that riparian area has been reduced by more than 66% by development, with more than an 80% reduction in riparian vegetation in arid areas of the western and midwestern USA. In Europe, floodplain forests have shrunk by an estimated 88% as a result of land-clearing (UNEP-World Conservation Monitoring Centre, 2000). Common alterations to riparian systems include simplification of stream channels and floodplain drainage to support infrastructure development. Stream channelization can result in floodplains being entirely cut-off from river channels, reducing the area of slow-water habitats and wetlands vital to both biotic and hydrological functions. Existing riparian systems are further compromised by pollution (both point- and non-point source), timber harvest and extraction, invasive species, and erosion from agricultural practices and roads (Naiman and Turner, 2000).

Just as land-management actions can greatly reduce or destroy riparian habitat, water management decisions involving water diversion, impoundment, or withdrawal can alter hydrologic processes, reduce inundation of riparian floodplains, and change riparian ecosystems. Floodplain regions can be intensely simplified for flood control purposes, and water withdrawals for agricultural uses can result in floodplain regions being cut-off entirely from river channels. Altered hydrologic regimes can reduce or eliminate riparian habitats throughout the river network. Vegetation patterns can be significantly affected as upland species encroach into riparian areas, causing shifts in vegetation community structure and function.

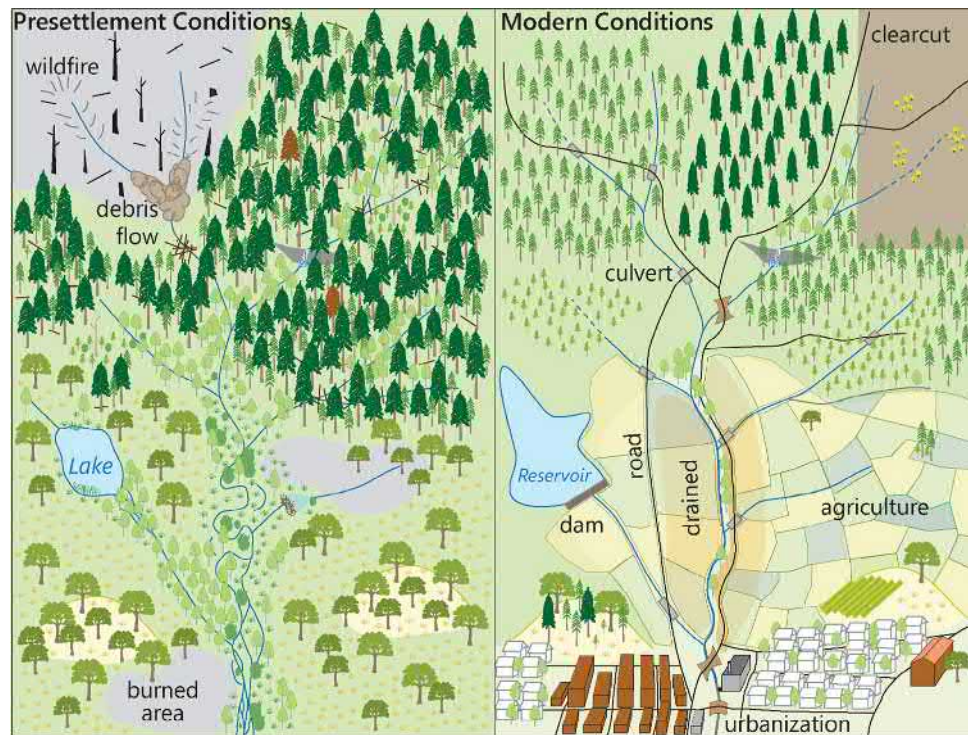


Fig. 1 Anthropogenic alterations to riparian ecosystems across a watershed may be due to changes in natural disturbance processes, draining and in-filling of floodplains for development and road construction, agriculture, timber harvest, or urbanization. All of these changes result in modifications to the functional processes embedded in riparian systems that support productive aquatic-terrestrial ecosystems. Kathryn Ronnenberg, US Forest Service, Pacific Northwest Research Station.

Restoration Policies and Practices: Tools in the Toolbox

Riparian restoration policies and practices aim to recover degraded or destroyed riparian systems. These efforts focus on land- and water-management activities that can help restore or improve riparian condition based on target criteria. Restoration efforts can include land-management decisions, protective policy measures to govern riparian corridors, and timing of water releases to more closely match natural flow regimes, along with on-the-ground actions directed at physically restoring riparian biota, structure, and function.

Land Management

Restoration of degraded riparian habitat can be implemented at site scales (for individual projects) or across broader extents encompassing multiple land uses or ownerships. Site-scale projects can include active restoration actions intended to improve site condition (e.g., tree-planting or seeding, vegetation thinning, channel grading, invasive species removal). Relinking disconnected floodplains to their river, particularly where channels have downcut or have been simplified, may include grading or excavation to restore sinuosity, restructure channels, and sculpt topographic conditions capable of supporting riparian vegetation (Manci, 1989). For example, active restoration measures including channel widening and sediment addition have been used to restore a section of the Tama River near Tokyo from a single-thread incised channel into a braided gravel-bed river (Nakamura et al., 2006).

Other restoration actions rely on passive actions intended to reduce environmental stress. Passive restoration relies on natural processes to guide the recovery process. These efforts can be site-specific, reducing factors or causes of degradation at specific site. A common example in the USA is the use of riparian fencing to exclude cattle grazing (Fig. 2). Excluding cattle grazing from riparian areas can result in an increase in riparian vegetation, greater streambank stability, and shifts in stream channel profile from wide and shallow to narrow and deepened channels.

At larger spatial extents, one way to protect or improve riparian systems is through policy that prescribes or recommends limitations in actions that can adversely affect riparian systems or have detrimental impacts on stream water quality. To meet water quality and aquatic habitat goals, policy-prescribed standards generally establish a target condition for riparian areas and limit land uses in order to promote riparian vegetation. Worldwide, riparian-management policies enacted by local, regional or national governments vary considerably based on land use and ownership and by whether they are voluntary or mandated policies (Cashore and McDermott, 2004; Lee et al., 2004). One common strategy is the adoption of fixed-width stream-adjacent buffers where certain



Fig. 2 Response in riparian condition following passive restoration actions in Spawn Creek near Logan, Utah, USA. Prior to restoration, the riparian area was frequently grazed by cattle, resulting in reduced riparian vegetation and alterations to stream banks. Livestock exclusions were set up at the site in 2006. Vegetation response is clearly seen in the post-restoration photo from 2015 (A1) compared with conditions in 2004 prior to restoration action (A2). Within the restoration period, an increase in riparian vegetation is observed in 2015 (B1) compared with photos from 2 years earlier (B2). The increase in vegetation has stabilized stream banks and reduced erosion. Photographs provided by PACFISH/INFISH Biological Opinion Effectiveness Monitoring Program (United States Forest Service, Fish and Aquatic Ecology Unit, Logan, Utah).

management actions are prohibited (Richardson et al., 2012). For example, the Ibrahim River in Lebanon is protected by 500 m buffers due to the rivers historical and cultural significance (Makhzoumi and Abboud, 2005).

Voluntary restoration or conservation actions often include incentive-based programs for landowners to maintain or restore riparian vegetation. These approaches are particularly necessary in landownerships where policy protection may be minimal or absent, and where land uses are focused on economic gain and resource extraction. Technical assistance from agencies and institutions, such as the Soil & Water Conservation Districts in the USA, can provide important capacity to individual landowners seeking to adopt innovative riparian-management practices. These programs can be crucial for targeting riparian restoration in areas where restoration action may be most effective, for example restoring riparian areas in agricultural regions to remove nonpoint source pollutants from surface waters.

Water Management

Characteristics of annual discharge, including the timing, magnitude, and frequency of peak flows, are crucial to maintaining and connecting riparian habitat (Poff et al., 1997). Simplification and alteration of flow regimes contribute to riparian ecosystem degradation. Streamflow restoration, implemented through water-management policies and practices, can improve riparian condition and function. Tools for restoring streamflow include changing the timing and quantity of water releases to mimic natural inundation patterns and the reallocation of water rights from extractive uses to instream purposes.

González et al. (2015) reviewed riparian restoration projects from around the world and found that hydro-geomorphic approaches (e.g. dam operations, controlled floods) were the most frequently adopted riparian restoration practice based on their review. Flood pulsing is a significant driver of riparian function (Junk et al., 1989; Tockner et al., 2000). High flow or flood events

that are a characteristic of the natural flow regime (Poff et al., 1997) allow for seed dispersal of riparian plants, the creation of complex stream bars and channels, and the maintenance of dynamic riparian systems. Water flows may be managed to allow for natural pulses or high-flow events that aid in riparian vegetation development (Rood et al., 2005; Merritt et al., 2010).

Scientists and engineers have collaborated to investigate and model the effects of dam removal or adjustments to water-release schedules on sediment transport and riparian structure and function. In the Colorado River basin of Mexico and USA, experiments have been conducted to examine effects of high flows on sand bar development and riparian seed dispersal (Ralston, 2010; Melis et al., 2015). In the northeastern United States, The Nature Conservancy has partnered with the Army Corps of Engineers to better understand linkages between surface elevation and riparian vegetation to better manage flows for environmental purposes (Marks et al., 2014). However, many challenges remain to restore hydrologic connectivity to maintain processes important to riparian ecosystems at watershed-scales.

Developing environmental flow thresholds (often called “e flows”) to meet multiple ecosystem needs is an increasing priority for water managers. In many societies, water has traditionally been allocated for human uses such as industry, irrigation, and municipal uses before considering ecosystem water needs. Water may be diverted from streams, reducing streamflow volumes or even drying the stream entirely, reducing or destroying available riparian habitats. To alleviate this problem, environmental flow transactions, agreements under which water-right holders commit to a reduction in water use to serve environmental purposes (Aylward, 2013), have become a major focus of restoration efforts around the world. For example, in the Columbia River Basin of the Canada and USA, the Columbia Basin Water Transaction Program transfers water rights to instream purposes to support functioning riparian and riverine ecosystems across the 674,000 km² watershed. Over a 14-year period, the program has supported projects that restore flows to over 2414 km of streams within the Columbia River Basin, protecting over 12 million megaliters of water over the next 100 years (McCoy et al., 2018).

In arid regions, where water resources are scarce, innovative approaches showcase the benefits of allocating limited water supplies to promote streamside vegetation. One example is the short-term water use agreements developed by the Arizona Land and Water Trust in Arizona, USA, under which water users agree not to pump groundwater or divert surface waters over a pre-determined period of time in order to meet short-term ecological goals or test the efficacy of certain restoration actions. Water use agreements offer a flexible tool that allows for innovations and partnerships in landscapes where economic and conservation goals need to be carefully balanced. This pragmatic approach to restoring riparian corridors acknowledges that in some places, it may not be feasible for entire landscapes to be managed as biodiversity reserves (Citron, 2010).

The Managed Aquifer Recharge site (MAR5) of the Gila River Indian Community is another example of an environmental water transaction that seeks to balance multiple needs and provide ecological, social, and cultural benefits. Colorado River water is delivered to central Arizona through the Central Arizona Project aqueduct, which spans 336 miles and requires pumping water up-gradient. The MAR5 restoration project directs a portion of the Gila River Indian tribe’s water right toward groundwater recharge. This allows farmers of the Gila River Indian Community to access less expensive groundwater, provides community members the ability to visit a flowing stretch of river, and returns riparian vegetation to a previously dewatered river section (GRIC, 2015). The community vision of promoting multiple goals is an example of the many innovations in managing water to support riparian systems around the world.

Riparian Restoration Strategies

The numerous tools available for both land and water management require a clear strategy to articulate project goals and guide the planning, coordination, implementation, and monitoring of riparian restoration actions. The spatial and temporal scope of riparian restoration can be a significant driver of the restoration strategy. For example, restoration of small stream reaches may promote a direct approach (e.g., tree planting, terrace grading, or large-wood placement). These projects often have very specific goals focused on the stream reach, for example local habitat restoration, or enhancing stream-side shade or filtration of diffuse pollutants from an adjacent land use, and involve a short timeline for planning and implementation. A large-scale, long-term restoration strategy may coordinate a variety of targeted riparian restoration practices at a watershed or corridor scale to promote multiple conservation objectives. A process-based strategy can focus on restoring riparian functions that create and form diverse habitat conditions across an entire river system. Emerging strategies for riparian restoration have focused on scaling up restoration efforts, coordinating management actions, proactively planning restoration under climate change, and developing new tools and sampling designs to monitor restoration efficacy and before- and after- effects.

Scaling Up Restoration Efforts

Riparian areas provide important ecosystem services from headwater to estuary. Over time, as tools and approaches to riparian restoration have developed, the focus of work has begun to shift from reach-scale projects affecting local riparian habitat to strategies designed to restore or improve riparian function at the scale of the river-basin (Stella et al., 2013). Lorenz and Feld (2013) found that degraded riparian areas upstream can effectively neutralize the benefits of site-scale restoration downstream. Rather than opportunistically pursuing riparian restoration practices on a case-by-case basis, targeted approaches to riparian restoration consider restoration actions in the context of broader watershed processes (Boudell et al., 2015). There is an increasing focus on restoration strategies to maintain ecological functions within the context of natural disturbance regimes (Poff et al., 1997; Reeves et al., 1995).

Such a management approach is intended to support species of concern and their habitat by maintaining key ecological linkages, while balancing human consumption, cultural, and recreation needs.

Watershed-scale restoration planning is complicated by landownership and jurisdictional oversight, as well as the complex network structure of river systems. Watersheds encompass multiple jurisdictions, and thus large-scale riparian restoration requires coordination across institutions and individuals with diverse land- and water-management goals that operate under different standards depending on ownership and land use. The management of riparian areas is particularly complicated as these areas encompass private property rights associated with land use as well as public interests in the protection of waterways (Boisjolie et al., 2017). This results in a wide range of variability in protective standards which fragments riparian management at the watershed scale, creates gaps in protective efforts along the river corridor, and results in complex patchworks of protective measures within and across watersheds (Boisjolie et al., 2019).

Integrated Watershed Management

Considerable coordination is necessary to develop restoration strategies at the watershed scale. Integrated watershed management is emerging as a means for coordinating planning to effectively implement riparian restoration from a multi-ownership perspective. Ideally, integrated watershed management provides a holistic framework to understand the biophysical and social landscape of the river and its valley: evaluating the basin hydrology, understanding land and water uses, engaging local communities, and applying appropriate science to guide the adoption of protective and restorative measures. The approach is simultaneously research-driven and applied, considering both economic and ecological sustainability when developing land-use goals (Naiman et al., 2005). It has been adopted by managing entities and collaborative efforts around the globe, with multiple examples of approaches based on regional considerations (Flitcroft et al., 2018). Steps involved in an integrated watershed plan may include social and technical actions. Developing partnerships with key stakeholders, facilitating the involvement and input of these stakeholders, and implementing educational outreach are all steps to developing a successful management plan. Technical approaches may include the gathering of data to characterize the watershed, the creation of monitoring plans, the identification of issues and risks, and the development and implementation of catchment management plans (Ireland Environmental Protection Agency, n.d.).

An integrated watershed-management approach for riparian restoration encompasses riparian zones throughout the river network. As outlined by González et al. (2017), integrated conservation of riparian zones is most effective when clear restoration goals are developed that can be properly evaluated. Goals and planning should encompass multiple spatial and temporal scales. Conserving riparian regions across a watershed scale also necessitates pursuing numerous approaches to restoration and protection, including technical, socio-economic, and legal avenues.

Effective riparian restoration is difficult owing to the multi-disciplinary knowledge necessary to plan, implement, and monitor practices. Depending on the location, a restoration strategy may require expertise in forest management, land-use policy, restoration ecology, geomorphology, aquatic ecology, fisheries, and hydrology (Dufour et al., 2018), as well as input from sources of local and cultural knowledge (Flitcroft et al., 2018). A key factor for the efficacy of integrated watershed management is the development of a basin-wide knowledge network allowing for collaboration. Coordination across watersheds and landownerships supports knowledge networks or social infrastructure that incorporates diverse perspectives to aid in effective planning, implementation, and monitoring (Flitcroft et al., 2009). In many parts of the USA, watershed councils provide for coordination of riparian restoration activities through collaborative processes. New technical tools such as Lidar or satellite imagery also enhance and enable large-scale modeling that can aid in holistic planning and large-scale management. Just as restoration design and planning is attempting to “scale-up”, so are efforts to educate, communicate, and collaborate on science and management elements central to large-scale restoration.

Pro-Active Restoration Planning Under Climate Change

Riparian areas are a special conservation focus under a changing climate because of their importance in supporting biodiversity. Perry et al. (2015) describes the multiple potential effects of climate change on riparian ecosystems, including both direct effects on wildlife and vegetation, and indirect effects on streamflow, temperature, and precipitation. To respond to anticipated changes in conditions across watersheds, more attention is being paid to pro-active restoration planning and design that considers potential climate-change effects (Flitcroft and Giannico, 2013; Perry et al., 2015; Tonkin et al., 2019). More forecasting tools may be needed to effectively plan for alternative futures and adaptively manage river corridors under a changing climate (Tonkin et al., 2019). Advances in geospatial data have led to the emergence of tools to identify priority riparian areas for climate adaptation that can help better target restoration actions (Krosby et al., 2018).

Effectiveness Monitoring

As riparian restoration strategies expand to consider watershed-scale processes and target natural ecological processes, monitoring long-term restoration effects becomes increasingly important. Monitoring may focus on the ecological effectiveness of a restoration project, or simply on compliance of the project in implementing the project plan (i.e., was the planned amount of soil moved, trees planted, etc.). An emerging focus of restoration design includes developing methods to evaluate the efficacy of riparian restoration at broader spatial and temporal scales than previously explored (Hausner et al., 2018). In a review of scientific literature focused on

riparian restoration monitoring, González et al. (2015) found that monitoring occurred predominantly for single projects with narrow goals at small spatial scales (reach-scale or smaller) over short time frames (< 6 years). Funding for effectiveness monitoring can be scarce, particularly for long-term processes like disturbance regimes, ecological succession, and community changes. Regional assessments of riparian condition and recovery actions are rare. To enhance the effectiveness of applied riparian restoration efforts, there is a need to implement rigorous long-term experimental designs, with projects that offer comparisons among methods to identify failures or successes (González et al., 2015).

New tools are being developed that use fine-scale spatial data and analyses over a long time-scale to help inform and guide riparian restoration planning (Salo and Theobald, 2016; Macfarlane et al., 2017a,b; Hausner et al., 2018). Recent advances allow mapping of changes in riparian vegetation composition, structure, and spatial extent at new scales (Dufour et al., 2013). Extensive databases for data sharing are being developed for large areas, such as the Colorado River Basin (Woodward et al., 2018). New approaches to quantify land-use effects on riparian vegetation structure are also being developed (Wasser et al., 2015). These emerging research frontiers can guide restoration efforts to support riparian function from a holistic watershed-scale perspective that incorporates both ecological and social needs.

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Implications of Climate Change to Groundwater

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Abstract

Groundwater is an essential life-sustaining resource for billions of people worldwide. It is also a critical backstop during drought when surface water supplies are reduced. But unsustainable depletion of groundwater is now documented on both local and global scales. Climate change will exacerbate these problems. Higher temperatures and more extreme droughts will alter the timing and availability of surface water increasing reliance on groundwater. At the same time groundwater recharge will be reduced limiting supplies for consumptive use and for ecosystems. The net effect of climate change on groundwater depends not only on changing climatic conditions or the physical attributes of a region, but also on human actions and management decisions. Researchers, managers and policy makers involved with and responsible for groundwater stewardship are attempting to develop robust and innovative modeling tools, policies and management strategies to develop the capacity of individuals, groups, or organizations to adapt to the physical and social changes anticipated under climate change. Examples include: the development of modeling tools, an increase artificial recharge and recycled water, incentives to reduce demand, and the development of local drought reserves.

Introduction

Groundwater is an essential life-sustaining resource for billions of people worldwide ([Giordano, 2009](#)). It is also a critical backstop during drought when surface water supplies are reduced. Where extraction rates exceed natural recharge rates the problem is unsustainable depletion of groundwater, now documented on both regional ([Rodell et al., 2009](#)) and global scales ([Wada et al., 2012](#)).

Climate change will exacerbate these problems. Scientists project higher temperatures and more extreme droughts by the end of the 21st century that will alter the timing and availability of surface water, and more individuals and sectors will look to groundwater as a source of supply ([Foster and MacDonald, 2014](#)). At the same time groundwater recharge will be reduced limiting supplies for consumptive use and for ecosystems. Important issues are how the more extreme droughts projected under climate change will

interact with the hydrogeophysical characteristics of a groundwater basin to affect groundwater storage, and what management practices are being used to support groundwater sustainability and security.

The Groundwater Resource

Groundwater represents about 30% of available freshwater on the planet, and it is critical in regions with limited or no surface water supplies (Bovolo et al., 2009). It frequently has a higher storage capacity and is of higher quality than surface water (Kundzewicz and Döll, 2009). It is also less subject to seasonal or interannual variation, making it more reliable than surface water sources. Groundwater also sustains wetlands and riparian ecosystems in humid regions, and unique aquatic ecosystems in more arid and coastal environments.

Groundwater is stored in the sediment pores and fractures beneath the land surface in unconfined, confined and semi-confined aquifers. Between the land surface—including the soil, and the water table—the top level of groundwater, is the vadose or unsaturated zone. Rainfall and applied water infiltrate through the vadose zone down to the water table, and they ultimately recharge groundwater (Fig. 1). A physical definition of groundwater includes soil water, deeper vadose zone water, and unconfined and confined aquifer water.

Precipitation that falls onto the land can infiltrate into the ground to become groundwater. If the water meets the water table it can move both vertically and horizontally. Water moving downward can also meet more dense and water-resistant nonporous rock and soil, which causes it to flow in a more horizontal fashion, generally toward streams, the ocean, or deeper into the ground.

The characteristics of aquifers and confining layers of subsurface rocks (which water has a difficult time penetrating) determine the directions and speed of groundwater movement. Subsurface geologic formations and their arrangements both influence aquifer interconnections and the patterns of hydraulic conductivity that shape aquifer flows (Fogg, 1986). Groundwater movement (Fig. 2) is driven by pressure and occurs in the zone of saturation.

As unconfined aquifers are nearer to the land surface than other formations, they can be recharged by the infiltration of precipitation or other surface water. Confined aquifers are often layered between geologic formations called *aquicludes*, which almost completely obstruct flow, or *aquitards*, which are less permeable and restrict but still allow flow (Harter, 2003).

Recharging aquifers is critical to avoiding the depletion of aquifers over time where groundwater is withdrawn for consumptive use. While precipitation is the major source of groundwater replenishment, recharge is a complex process that is affected by the properties of land, climate, and human activities such as irrigation and pumping (Meixner et al., 2016). Geology and geomorphology (topography, soil, and vegetation) of an area can affect the location and timing of recharge. For example, crystalline metamorphic and igneous rock formations have very small permeability so that any recharge water flows mostly through fractures and faults (Davis and DeWiest, 1966). Basaltic and volcanic formations have more porous zones between lava flows or in lava tubes that can receive direct recharge from precipitation and snowmelt (Fram and Shelton, 2015). Finally, water temperatures can also affect recharge infiltration.

Groundwater Withdrawal Impacts

Groundwater use has frequently resulted in extraction rates exceeding natural recharge rates affecting groundwater flow and storage (Fig. 3).

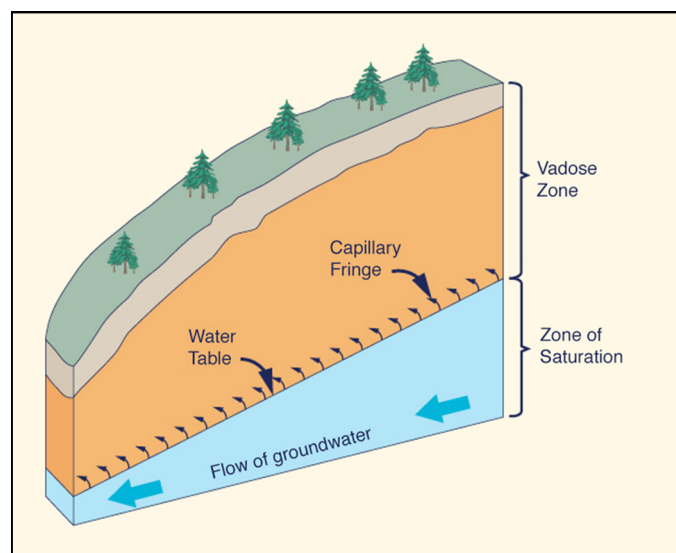


Fig. 1 Groundwater. USGS.

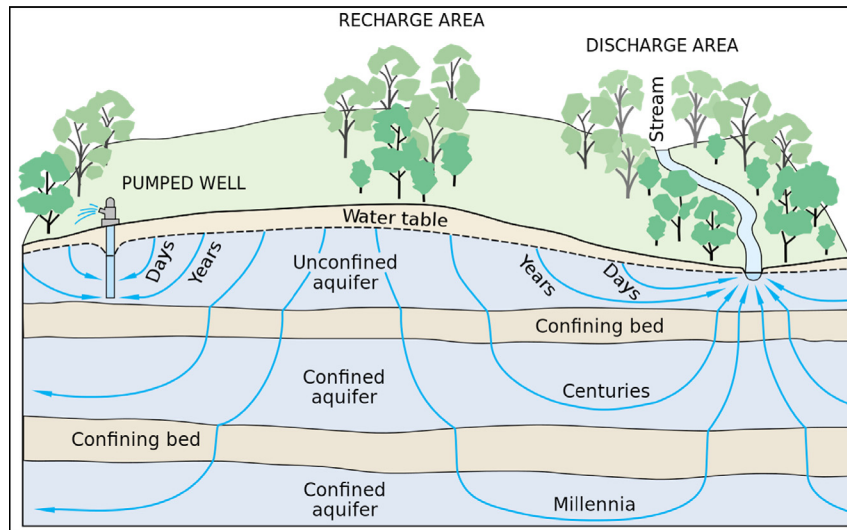


Fig. 2 Groundwater flow. USGS.

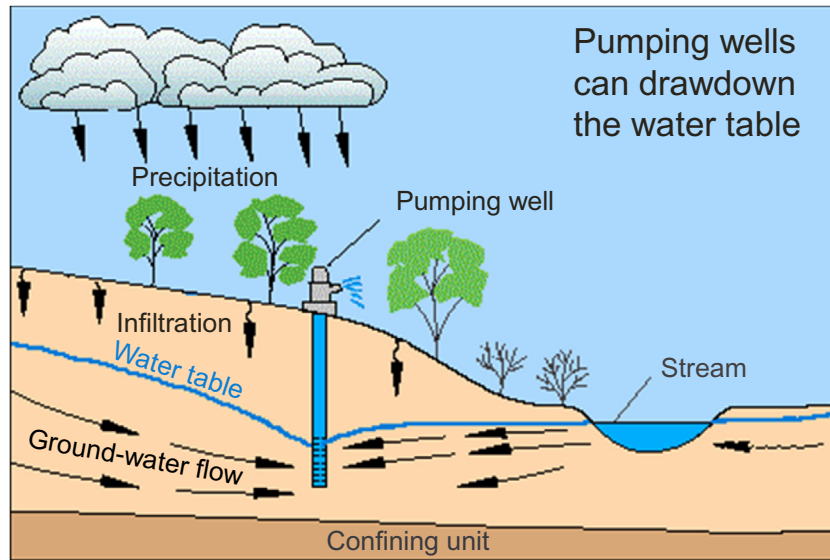


Fig. 3 Pumping effects on groundwater flow. USGS.

When pumping exceeds recharge, basins can become significantly overdrafted and exhibit long-term groundwater depletion and loss of storage (Gleeson et al., 2010). Satellite data shows that several of the world's largest aquifers are in overdraft and nearing depletion. Fig. 4 illustrates groundwater storage trends for Earth's 37 largest aquifers from a UCI-led study using NASA GRACE data (2003–13). Of these, 21 have exceeded sustainability tipping points and are being depleted, with 13 considered significantly distressed, threatening regional water security and resilience. An estimate of groundwater depletion for most of the globe showed that West Asia, the central United States, northwestern India and northeastern China are among the areas showing the most serious loss of storage (Siebert et al., 2010; Wada et al., 2010a,b).

Groundwater depletion can lead to subsidence, seawater intrusion and depletions of interconnected surface water.

Subsidence

Subsidence is defined as a decline in the elevation of the land surface. In parts of California and south-central Arizona, subsidence of land damages buildings, pipelines, canals, highways, and other facilities. Subsidence results from the force of gravity operating with the lowering of the water level or the potentiometric surface of water in a confined aquifer. Subsidence may deprive the aquifer of the ability to recharge, even when water is forcibly injected into wells, thus permanently limiting the capacity of the ground to store water for future.

limits of groundwater that can be withdrawn without unacceptable impacts (Ostrom et al., 1999). CPRs create specific governance challenges. Establishing groundwater rights is complex, with groundwater being extracted by widely dispersed and numerous pumps overlying an aquifer. Moreover, different actors drawing from the same basin may have competing interests, opinions, aspirations, and power positions (Bouarfa and Kuper, 2012). Empirical studies found that interdependence, trust, reciprocity, cooperation and connectedness of individual actors are key in sustaining CPR institutions (Ostrom, 1990, 2010). Other important institutional factors include transparency and accountability, financial viability, and strong commitment by government (Ostrom, 2010; Meinzen-Dick et al., 1997; Megdal et al., 2015). But inclusion and representation can be limited and contested (Cleaver and De Koning, 2015).

These governance challenges have led to inadequate reductions in groundwater extractions in most countries despite attempts to regulate groundwater use (Shah, 2009; Giordano, 2009; De Stefano and Lopez-Gunn, 2012; Frija et al., 2015). In many semi-arid and arid latitudes, where persistent groundwater depletion is driven by competition over limited and ever-decreasing water resources, there can be accelerated water loss and economic disparities (Famiglietti, 2014a,b). Some governance frameworks have been proposed that address imbalances in groundwater access, as well as who defines the rules that determine access and use, but research on whether and how inequities in access are affected by climate change and drought needs more attention.

Climate Change

Anthropogenic climate change depends on the accumulation of carbon dioxide and other heat-trapping gases (GHGs) emitted from human activities in the atmosphere. Climate changes can be projected under different emission scenarios, or representative concentration pathways (RCPs), and global climate models (GCMs) use different RCPs to project future climate conditions.

Climate change has the potential to produce anomalies in temperature and precipitation that will alter atmospheric features of the global hydrologic cycle through greater evaporation, sea-level rise, melting glaciers and ice caps, changing rainfall patterns, and extreme weather events (IPCC, 2014). Already observable effects of global climate change on the environment include shrinking glaciers, earlier break up of ice on rivers and lakes and shifts in plant and animal ranges (NASA, 2019).

Temperature

Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millennia.

IPCC (2014)

Each of the last three decades has been successively warmer at the Earth's surface than any preceding decade since 1850 (Fig. 5). Continued emissions of greenhouse gases will cause further warming and changes in all components of the climate system. It is virtually certain that there will be more frequent hot and fewer cold temperature extremes over most land areas on daily and seasonal timescales as global mean temperatures increase. Heat waves are very likely to occur with a higher frequency and duration, as will occasional cold winter extremes (Bates et al., 2008; IPCC, 2014). In the United States, what have been once-in-20-year extreme heat days (1-day events) are projected to occur every 2 or 3 years over most of the nation (NASA, 2019).

Extreme Events

Incidents of extreme weather, including flood and drought frequency, are projected to increase as a result of climate change. With rising temperatures, many locations will see a substantial increase in the number of heat waves per year and a likely decrease in episodes of severe cold. Precipitation events are expected to become less frequent but more intense in many areas, and droughts are projected to be more frequent and severe in the 21st century in some seasons and areas due to reduced precipitation and/or increased evapotranspiration as temperatures rise (NOAA, 2018).

While defining an extreme drought is challenging as the effects of drought accumulate slowly over a considerable period of time and may also linger for years after it is over, projections are that globally by the 2090s drought-affected areas are likely to increase. The proportion of the land surface in extreme drought at any one time is also predicted to increase 10-fold from the present (Kundzewicz et al., 2008). Regions such as the U.S. Southwest will see more frequent and intense droughts due to increased heat and changing rainfall patterns, already visible in the Mediterranean, southwestern USA and southern African regions. In 2011, Texas experienced its driest 12 months ever. At the peak of the 2012 drought, 81% of the contiguous United States was under at least abnormally dry conditions. Globally, drought struck several major breadbasket regions simultaneously in 2012, adding to food price instability. In countries already facing food insecurity, cost spikes can lead to social unrest, migration, and famine (Center for Climate and Energy Solutions can be found at: <https://www.c2es.org/content/extreme-precipitation-and-climate-change/>).

Flood frequency and magnitude are also projected to rise by the end of this century in regions experiencing increases in precipitation intensity. The proportion of total rainfall from heavy precipitation events in the mid-latitude land masses and over wet tropical regions are also very likely to become more intense and frequent by the end of this century as global mean surface temperatures increase (IPCC, 2014). There are already statistically significant trends in the number of heavy precipitation events in some regions including the United States, where the Midwest and Northeast saw strong increases in these events. Changes in the near-term, and

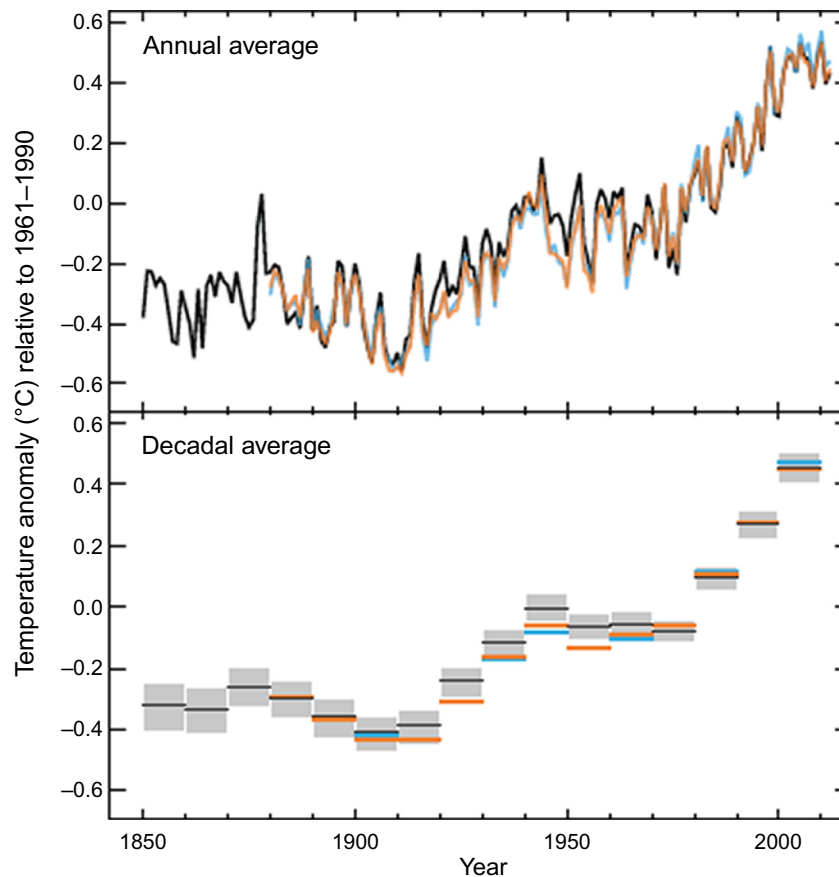


Fig. 5 Observed globally averaged combined land and ocean surface temperature anomaly 1850–2012. IPCC (2014). Climate Change 2014: Synthesis Report. *Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Core Writing Team, R. K. Pachauri and L. A. Meyer (eds.). IPCC: Geneva, 151 pp.

at the regional scale will be strongly influenced by natural internal variability. These trends are likely to continue as the planet continues to warm. For each degree of warming, the air's capacity for water vapor goes up by about 7%. An atmosphere with more moisture can produce more intense precipitation events, which is what has been observed (Center for Energy and Climate Solutions, 2019).

Groundwater and Climate Change

Impacts of Climate Change on Groundwater

Climate change, including projected changes in temperature and precipitation, will impact surface water availability and consequently groundwater through changes to runoff and baseflow, and then to recharge (Hatchett and McEvoy, 2017). Higher temperatures under climate change will result in warmer and shorter winters that can increase surface drying and lead to a loss of soil moisture that will affect groundwater recharge. Temperature increases will also lead to more precipitation falling as rain instead of snow in many regions, resulting in an increase in short-term high flows and faster runoff that will also affect groundwater recharge (IPCC, 2014; DWR, 2017). Additionally, the increasing co-occurrence of dry years with warm years will raise the risk of more extreme droughts (IPCC, 2014) that will also reduce groundwater recharge and consequently groundwater storage (Table 1).

Challenges to addressing groundwater impacts under climate change include:

- A mismatch between large-scale global or regional climate models and small- or medium-scale hydrological processes.
- Limited long-term groundwater data and information that impairs investigations of the responses of groundwater systems to climate change (Zhang, 2015).

Managing Groundwater Under Climate Change

The net effect of climate change on groundwater depends not just on changing climatic conditions or the physical attributes of a region, but also on a wide range of human actions and management decisions. Researchers, managers and policy makers involved

Table 1 Climate impacts to groundwater.

<i>Climate changes</i>	<i>Climate impacts</i>	<i>Impacts to groundwater</i>
Temperature increases	Surface drying-loss of soil moisture	Recharge reduced
Precipitation	More rain and less snow with more short-term high flows and faster runoff	Recharge reduced
More frequent and intense droughts	Reduced surface supplies increased groundwater withdrawals	Storage reduced
Sea level rise	Seawater intrusion	Storage reduced

with and responsible for groundwater stewardship are attempting to develop robust and innovative modeling tools, policies and groundwater management strategies by building the capacity of individuals, groups, or organizations to adapt to the physical and social changes anticipated under climate change (Huntjens et al., 2011).

Modeling tools

Modeling tools for groundwater planning and policy evaluation under climate change are essential for assuring that groundwater levels do not experience long-term declines.

To incorporate the social and physical complexity of groundwater management under climate change, researchers are integrating modern simulation methods with management tools based on physical, institutional, environmental, and economic metrics that reflect decision-making objectives (Gorelick and Zheng, 2015). Examples include optimal groundwater pumping strategies that can control a shallow water table (Barlow et al., 1996); optimal cropping, reservoir release, and groundwater management policies can be used to maximize profit Schoups et al. (2006); and a complex agricultural hydro-economic model that can be used to maximize annual farming benefits subject to hydrologic relations (Maneta et al., 2009). Agent-based models (ABM) can be a versatile approach to represent a coupled human-natural system to define the relationships between simple individual behaviors, collective structures, and interactions with the environment (Macy and Willer, 2002).

Determining sustainable thresholds for groundwater aquifers

A minimum threshold can be defined as the quantitative value that represents the groundwater conditions that when exceeded may cause long-term groundwater depletion and concomitant undesirable impacts in a basin. To establish a minimum threshold it is necessary to first determine a basin's inflows and outflows and then determine a threshold that will avoid long-term groundwater declines. This is generally called the sustainable yield of the basin. While the earlier concept of safe yield emphasized aquifer dynamics (Bredehoeft, 1997; Kalf and Woolley, 2005), sustainable yield also incorporates societal inputs regarding what are considered unacceptable (Alley and Leake, 2004; Gleeson et al., 2010). Both determining a water budget and calculating the sustainable yield of a basin are complex and challenging processes that can require modeling studies and fieldwork, along with a definition of unacceptable impacts from pumping (Rudestan and Langridge, 2014).

To establish a minimum threshold for groundwater levels under climate change, it is necessary to determine the protective groundwater levels necessary to avoid defined unacceptable impacts. Protective levels are often averaged over a reasonable time period to try to accommodate variability in precipitation. It is also necessary to calculate an amount needed in storage to avoid declining groundwater levels during a prolonged and/or intensive drought that are not likely to recover over the long term. To do this, it is first necessary to specify the degree of drought risk. Combining a range of drought lengths in years with a range of drought intensities can provide metrics for potential target droughts. Additionally, the identification of past historical droughts can be used to determine risk for a specific location. The effect of future climate change on any increase in drought severity or frequency of a similar future drought also needs to be considered (Langridge and Daniels, 2017).

Recharging aquifers

Water in aquifers is the most effective strategic weapon against drought.

Army Corps of Engineers (1993)

Recharging aquifers is essential to sustaining a groundwater aquifer over time and to having a groundwater reserve that can be used during drought when surface supplies are limited. It can occur naturally through precipitation that infiltrates into the ground. Recharge can also happen when water is pumped or injected into wells or spread over a land surface to allow it to seep into the aquifer. The term managed aquifer recharge (MAR), also known as aquifer storage and recovery (ASR), is defined as "intentional storing and treatment of water in aquifers' frequently for later recovery or environmental purposes" (Gale and Dillon, 2005). MAR/ASR techniques include surface spreading basins, vadose zone dry wells, and direct injection to recharge aquifers using wells. This approach can be utilized to meet municipal and agricultural water demands in water-scarce regions, as well as assist in the reuse of wastewater. Importantly groundwater in recharged basins can serve as a buffer during periods of drought and changing or variable climate.

Multidisciplinary approaches that incorporate the necessary geophysical and hydrological information, and information on stakeholder/community engagement in program implementation and success, as well as economic and financial analysis are important components for MAR/ASR success (see [Megdal and Dillon, 2015](#)). These include market price, alternative cost, marginal product value, damage cost avoided, contingent value methods, defensive (insurance) value, and environmental value of in situ groundwater. [Maliva \(2014\)](#) notes that costs for drinking water supplies that are typically half the costs of brackish water desalination.

Additionally, implementing MAR/ASR programs requires obtaining water for active recharge. Approaches include supply-side—where groundwater managers attempt to search for new water supplies including from recycled water, desalinated water and rainwater capture, and demand side—where the focus is on controlling groundwater withdrawals.

Increasing supply

Current management approaches to increase supply frequently involve surface storage infrastructure including large multi-purpose dams, small-scale dams, weirs, irrigation systems, rainwater harvesting cisterns, or interbasin transfer schemes. Large reservoirs were built around the world for the storage of surface water. Along with social and environmental concerns, the impact of increasing temperatures and more extreme events will reduce water inputs into these large storage facilities under climate change.

Supply side approaches can also include new wells, the deepening of existing wells and increased groundwater withdrawals, but this approach can negatively affect long-term groundwater storage that could be available during drought.

Additionally, while conservation and water use efficiency are frequently promoted as a demand reduction approach, with suggestions for adequate financial investment in water-saving technology and economic instruments to encourage reduced water consumption ([Foster and Garduño, 2013](#)), it can also increase demand in the future if be saved water is primarily used for new development.

Supply side approaches

- Expand recycled water facilities and use
 - Develop aquifer storage and recovery systems (ASR/MAR) using recycled water
 - Increase storage capacity by building reservoirs and dams
 - Desalinate seawater
 - Expand rainwater capture and storage
 - Remove invasive nonnative vegetation from riparian areas
 - Develop strategies to avoid groundwater loss from contamination
-

Reducing demand

While most groundwater management strategies focus on increasing supply, demand management is also critical to preventing groundwater overdraft and assuring that groundwater is available during drought. It has become an important global policy element for sustainable groundwater management under climate change, and is acknowledged by the World Bank, Asian Development Bank, USAID, GTZ and other international as well as national organizations. However, demand reduction, including limiting withdrawals, is less employed, frequently contested ([Hoogesteger and Wester, 2017](#); [Langridge et al., 2016a,b](#)), and can be difficult to implement with considerable legal and administrative issues.

Demand side approaches

- Establish permit systems or other regulatory or adjudicative restrictions on withdrawals
 - Expand use of economic incentives (e.g., water replenishment fees, metering, and pricing) to encourage reduced withdrawals
 - Reduce water demand for irrigation by changing the cropping calendar, crop mix, irrigation method and area planted
 - Increase incentives to reduce water demands for landscaping
-

Quantitative restrictions are frequently employed to control or influence the amount of water used. Mechanisms and strategies can be developmental, technical, distributive, or financial and market based. Examples include withdrawal and use permits, drilling bans, establishing a water rights system with assigned volumes, electricity pricing, replenishment fees and pumping taxes, and the regulation of drilling companies. Market mechanisms for water trading and sales are also utilized. These can have varying degrees of success in reducing drought vulnerability. This is particularly the case where groundwater use is intensive, and there has been mixed success in using demand management to reduce groundwater extractions ([Shah, 2009](#)).

Conjunctive use of surface and groundwater

Conjunctive use programs typically involve either substitution of surface water in lieu of groundwater pumping, or underground storage of surplus surface water in wet periods for subsequent withdrawal in times of scarcity. The aquifer provides storage for surface water that can be drawn on depending on need. Conjunctive use of surface water and groundwater can enable aquifers to recharge and help to mitigate the water supply stress in responding to climate change and drought.

Optimization models have been proposed for conjunctive use of surface water and groundwater primarily for planning cropping patterns and irrigation water management (Zhang, 2015). Earlier models failed to consider the impacts of future climate change, but recent research is attempting to incorporate climate change impacts into the planning and management of conjunctive water use (Hanson et al., 2012; Hoekema and Sridhar, 2013; Pingale et al., 2014).

Creating a groundwater drought reserve

Establishing a local groundwater drought reserve can mitigate the risk of water shortfalls during an extreme drought under climate change. This can be done by estimating the water shortfall under a range of potential droughts as well as how much water can actually be extracted without unacceptable impacts. Additionally, water demands during a drought generally increase, but some water usage curtailment may also be instituted. Subtracting anticipated water demands during a drought from likely supplies provides the shortfall for specified drought years. The sum of these shortfalls across the duration of the target drought provides the total drought water shortfall. A drought reserve would need to accommodate this quantity to protect against unacceptable impacts for a specified target drought (Fig. 6: Langridge and Daniels, 2017).

Water markets, water transfers, and groundwater banking

Water markets enable the temporary, long-term, or permanent transfer of the rights to use water in exchange for compensation. Water transfers can enable the movement of water to places of critical need, especially during a drought. Because most water is used for irrigation globally and in California, water is frequently leased or sold by farmers or irrigation districts, who transfer/market water to other farmers with scarce supplies and higher value crops, to growing cities or to water providers that supply cities, and to environmental programs. Transfers are often used for “conjunctive use” of groundwater and surface water.

While often a market transaction between a willing buyer and a willing seller, it is also a negotiation with a number of parties with important and legitimate interests in the water that need to be accommodated. Transfers require an appreciation of the complexities of water as a public resource that render it distinctive from other commodities, including the issue of distributive equity. If climate change influences the distribution of water then, indirectly, the rules regarding groundwater access and ownership may influence the impacts of climate change and drought on humans.

Groundwater information systems

Recent developments in studying groundwater under climate change include using satellite measurements of groundwater storage and levels (Famiglietti, 2014a,b; Van Loon et al., 2017; Rodell et al., 2018; Massoud et al., 2018). The Gravity Recovery and Climate Experiment (GRACE) is one such 15-year satellite mission to monitor and study changes in the earth’s water system, of which groundwater is a component (Famiglietti, 2014a,b; Rodell et al., 2018). Scientists also use it to highlight regions where continued monitoring is essential for quantifying impacts to the hydrologic cycle from climate change. Where monitoring wells are absent,

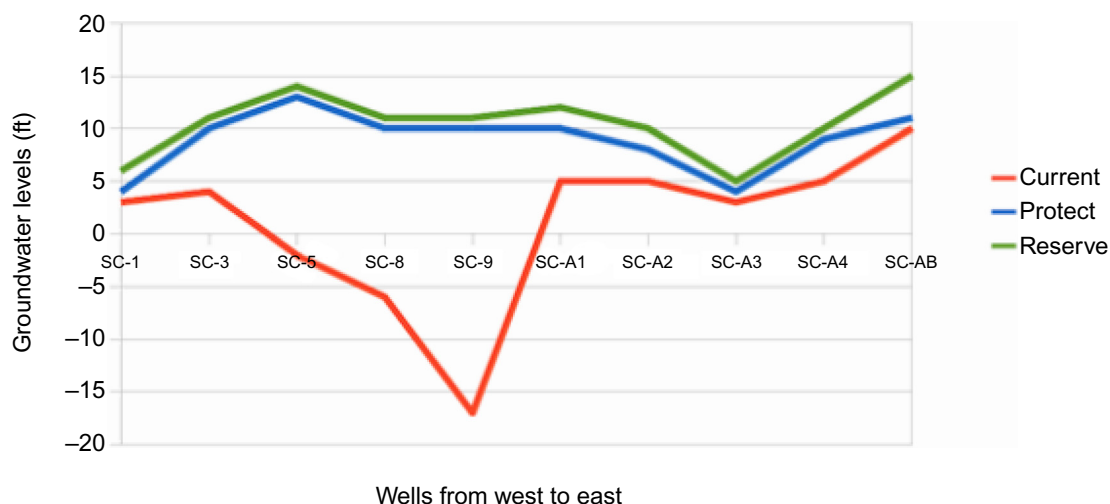


Fig. 6 Example of Protective and Reserve Levels Compared to Current Levels—Data from Soquel Creek Water District 2009. Langridge, R., and Daniels, B. (2017). Accounting for climate change and drought in implementing sustainable groundwater management. *Water Resources Management* 31(11), 3287–3298.

and/or data are missing, the deployment of these and other additional geophysical methods offer an avenue to support evidence-based groundwater management and decision-making.

Climate Change and Groundwater in California

California exemplifies the increasing global water supply crisis, exacerbated by rapid population growth in some of the driest regions and limitations of an energy-demanding and over-allocated water system.

Temperatures vary depending on latitude, elevation, and proximity to the coast. The coastal regions, Sierra Nevada foothills, and much of the Central Valley have a Mediterranean climate, with warmer, dry weather in summer and cooler, wetter weather in winter (Fig. 7). Coastal areas have substantially cooler summers, moderated by the influence of the ocean. California also has high annual variability in rainfall with more rain in the north than in the south, almost no rain in the summer, and periodic droughts. Tree-ring studies show that in the past there were often long periods of dryness sometimes followed by several wet years (Griffin and Anchukaitis, 2014) (Fig. 8).

During drought, groundwater is an essential component of California's water supply providing ~60% of the state's demand. The problem is that groundwater pumping increases during drought and exceeds replenishment in many basins resulting in long-term groundwater level declines (Fig. 9). Moreover, there is no permit system to withdraw groundwater in the state and landowners overlying a groundwater basin have a right to pump with limited restrictions, contributing to the overdraft and concomitant negative impacts including overdraft, seawater intrusion, land subsidence and water quality degradation. Since 2010, some areas of the state already see "alarming declines in groundwater levels," with negative impacts that include irreversible land subsidence, poor water quality, reduced surface flows, ecosystem impacts, and the permanent loss of capacity to store water as groundwater (DWR, 2015a,b). Additionally, many overdrafted aquifers contain high levels of contamination (DWR, 2015a,b).

Climate change will exacerbate these issues. Projections are that temperatures will rise throughout the state during the 21st century (Cayan et al., 2008:21), and the 2014 temperatures were the warmest on record for the state (Office of Environmental Health Hazard Assessment, California Environmental Protection Agency, 2018). This will exacerbate drought conditions in the future and increase groundwater storage deficits.



Fig. 7 Shaded relief map of California. National Atlas.

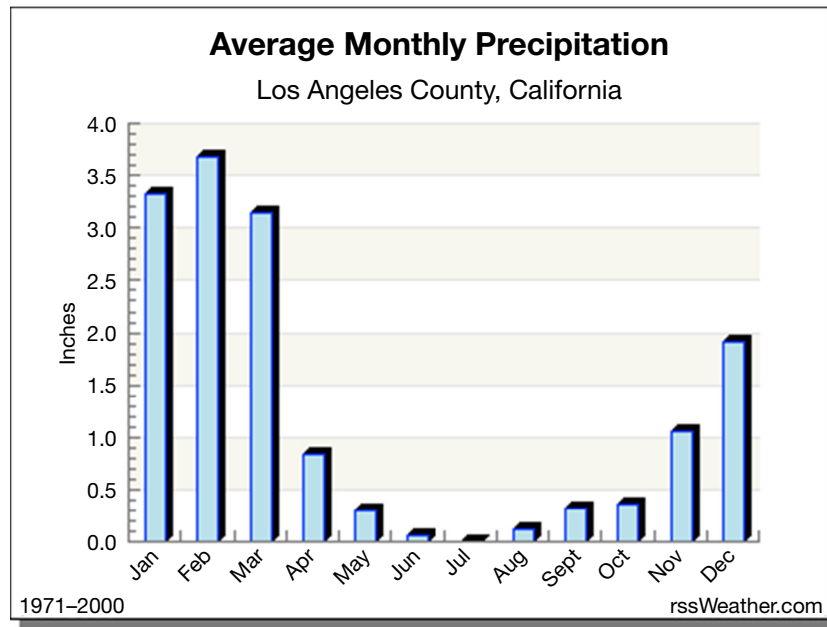


Fig. 8 Seasonal rainfall in Los Angeles, California. rssWeather.com.

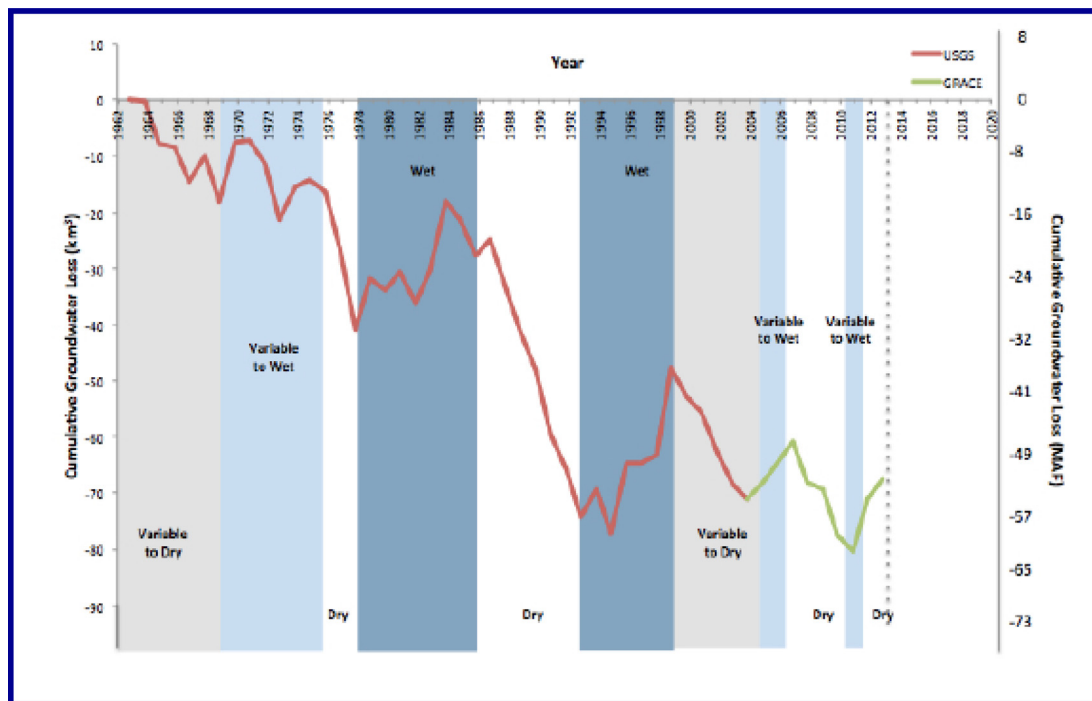


Fig. 9 California Drought and Groundwater. Famiglietti, J. S. (2014a). Epic California drought and groundwater: Where do we go from here? National Geographic <https://blog.nationalgeographic.org/2014/02/04/epic-california-drought-and-groundwater-where-do-we-go-from-here/>; Famiglietti, J. S. (2014b). The global groundwater crisis. *Nature Climate Change* 4(11), 945–948.

The state is also heavily reliant on snowmelt from the Sierra Nevada and Trinity mountains that is captured, stored and then imported primarily to areas of Southern California via two large water projects, the Central Valley Project (CVP) and the State Water Project (SWP). Projections of warmer and shorter winters with more precipitation falling as rain instead of snow and more short-term high flows and faster runoff, will reduce this surface water storage (DWR, 2017) thereby affecting the reliability of the imported water that is used for active and in-lieu groundwater recharge by many basins. Under end-of-century business-as-usual warming, in a major drought, the Sierra Nevada is projected to lose 85% of its snow, and even in a wet year it is likely to lose 2/3rds of its snow

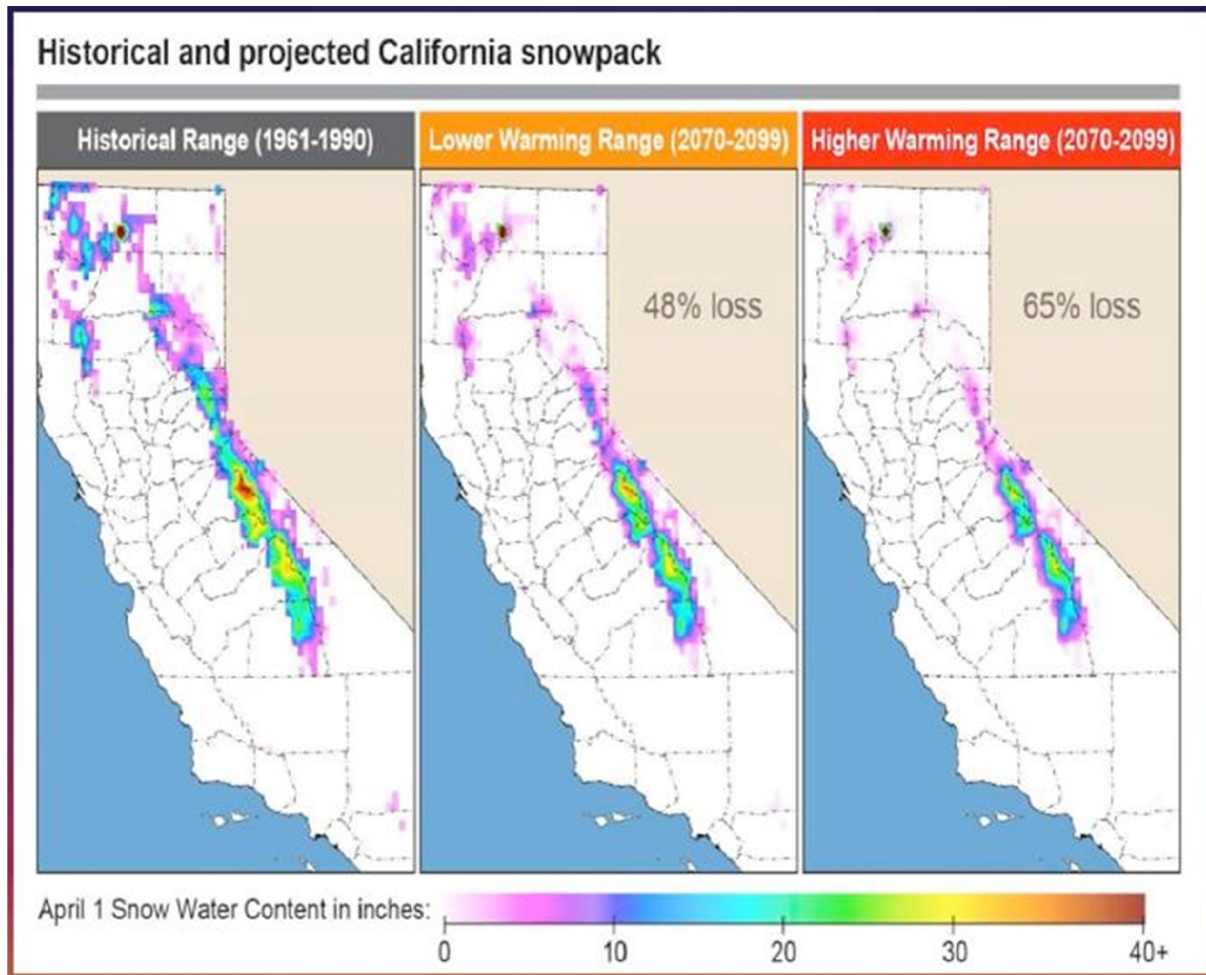


Fig. 10 Historical and projected snowpack under two different climate change futures, from the California Water Plan Update 2013.

(Berg and Hall, 2015). Under these conditions, State Water Project (SWP) deliveries will decrease and will be more costly in the future (Fig. 10) (Tanaka et al., 2006; Harou et al., 2010).

In 2012–16, California experienced the most severe drought in the last century with accumulated moisture deficits worse than any previous continuous span of dry years. Record high temperatures and long-term warming trend intensified the impacts of limited precipitation (Berg and Hall, 2015; Diffenbaugh et al., 2015), and groundwater levels in many basins decreased significantly (DWR, 2017).

The Sustainable Groundwater Management Act (SGMA)

To address these problems, in 2014 the California legislature passed the Sustainable Groundwater Management Act (SGMA) (AB 1739, SB 1168 and SB 1319) that for the first time established new mandatory rules for 127 high and medium priority groundwater basins with declining groundwater levels. Groundwater users in these basins were required to form groundwater sustainability agencies (GSAs) and to develop groundwater sustainability plans (GSPs) with the state evaluating local GSPs and their implementation.

The SGMA defines “sustainable groundwater management” as: “The management and use of groundwater in a manner that can be maintained during the planning and implementation horizon without causing undesirable results,” defined as:

- Chronic lowering of groundwater levels indicating a significant and unreasonable depletion of supply and reduction of groundwater storage.
- Significant and unreasonable seawater intrusion, degraded water quality, and land subsidence that substantially interferes with surface land uses.
- Surface water depletions that have significant and unreasonable adverse impacts on the beneficial uses of surface water.

SGMA requires the incorporation of climate change assumptions into the development of projected water budgets, and GSAs are including traditional approaches to manage groundwater basins in their GSPs.

New Approaches and Management Trends

Although SGMA does not include explicit incentives for proactive management of groundwater to address the more extreme droughts projected under climate change, GSAs are developing new ways of providing recharge and establishing drought reserves to address future climate change. New approaches to recharge include using flood flows to both irrigate agriculture as well as to recharge groundwater basins, illustrated in [Fig. 11](#) ([Kocis and Dahlke, 2017](#)).

The use of, recycled water continues to increase ([Pezzetti and Balgobin, 2015](#)), and there has been an increase in desalination and stormwater capture projects ([Langridge et al., 2018](#)). The SGMA allows for charging fees for pumping in excess of allocations, and approaches to reduce pumping are being incorporated into many GSPs. Several basins have developed local groundwater drought reserves ([Langridge and Fencil, 2019](#)) ([Table 2](#)).

Notably, California became the first state in the country to adopt a Human Right to Water. It states that: “every human being has the right to safe, clean, affordable and accessible water adequate for human consumption, cooking and sanitary purposes, and state agencies have a duty to consider this as they establish policies and regulations.”

Final Thoughts

Given the world’s reliance on groundwater and threats posed by drought, there is an increasing need to understand the barriers and opportunities to managing groundwater sustainably under future climatic changes and ever present drought conditions. Vulnerability to drought and climate change is not geographically bounded by the groundwater basin, for example, but is affected by choices and conditions on multiple scales ([Adger et al., 2009](#)). This is especially true in California, where melting snowpack is captured in reservoirs and transmitted throughout the state. But what renders any region’s groundwater vulnerable to climate change and drought in a given geography are both physical teleconnections such as ENSO events, Arctic Sea ice, and ocean surface temperatures that can alter the experiences and severity of drought; and social teleconnections including global economic forces, education and knowledge flows, and legal and governance structures that shape capacities and barriers to adaptation to a future climate ([Moser and Hart, 2015](#)).



Fig. 11 A flooded field at Terranova Ranch near Kings River. Don Cameron.

Table 2 Management trends.

Strategies	Management trends
Conservation	1976 drought—Voluntary conservation 2007–09 drought—Mandated conservation SBX-7-20x20x20 2012–14 drought—EOB-29-15: mandatory 25% reduction for urban users. Rescinded in 2017 New bills (AB 1668 and SB 606) in 2019 will direct water agencies to limit customers' indoor water use to an average of 55 gal per person each day. The goal is reduced to 52.5 gal by 2025 and 50 gal by 2030
Recycled water use ~190,000 AF	Recycled water use 1970: ~175,000 AF 1987: ~267,000 AF 2009: ~669,000 AF 2015: ~714,000 AF
Financial incentives to limit withdrawals	Increasing use to comply with SGMA
Planning	Move from voluntary sustainable groundwater management to mandatory sustainable groundwater management plans
Local drought reserves	Increasing use of local groundwater drought reserves

Source for the information on recycled water use: Pezzetti, T., and Balgobin, D. (2015). California recycled water use in 2015, https://water.ca.gov/LegacyFiles/recycling/docs/2015RecycledWaterSurveySummary_Slunits.pdfhttps://www.water.ca.gov/LegacyFiles/recycling/docs/2015RecycledWaterSurveySummary_Slunits.pdf.

According to the IPCC (2014), the array of potential adaptive responses available to human societies is very large, including technological, behavioral, and managerial strategies. While traditional drought adaptation strategies are known and developed, the effectiveness of various options to fully reduce risks for vulnerable groundwater-stressed areas during extended and intense drought periods nevertheless remains an ongoing challenge for the future.

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Glaciers and Ancient Carbon

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Abstract

Glaciers participate in the global carbon cycle. They collect, produce, transform, store and release carbon. A part of this carbon is ancient and is “captured” by the glacier in two ways. Firstly, a growing glacier may override an ecosystem and lock organic matter long enough to become ancient. Secondly, the surface of even remote glaciers “collect” aerosols containing ancient carbon. These aerosols are combustion products of fossil fuels such as coal, oil or gas. Sooner or later, compounds containing ancient carbon are released from the glacier, and these compounds can be bioavailable. It has been shown that ancient carbon can be assimilated into food webs in glacier forelands, in glacial rivers, and in marine environments. Living invertebrates may achieve a radiocarbon age of several thousand years. Increased glacier melting due to climate change will increase the flow of ancient carbon to various food webs and may disturb radiocarbon dating of sediments.

Introduction: Glaciers Matter

Glaciers and permanent snowfields are “cold deserts” with little biological activity. Still, their presence and dynamics have several ecological effects. Containing about 70% of the Earth’s freshwater, they contribute substantially to the global hydrological cycle. During the last decades, it has been clear that glaciers also play a role in the global carbon cycle. Ice and permanent snowfields cover as much as 11% of the terrestrial areas (National Snow & Ice Data Center), and this large surface accumulates short- and long-transported (windblown) carbon, organic as well as inorganic. Glacier surfaces may also produce organic matter through photosynthetic activity in so-called cryoconite holes. Organic material collected, produced or transformed on the glacier surface can be preserved within the ice for a long time. Furthermore, glaciers may contain overridden soil and vegetation. Sooner or later, glacier-locked carbon is released by melting water at the glacier front and transported away in glacier rivers. In other words, glaciers collect, produce, transform, store and released carbon. They are ecosystems housing unique life adaptations of cold-adapted and cold-loving microorganisms, both autotrophs and heterotrophs (Hodson et al., 2008; Stibal et al., 2012; Hood et al., 2015). Glaciers are now recognized as a biome—the cryospheric biome (Anesio and Laybourn-Parry, 2012).

Glaciers are “climate trackers” (Fig. 1): As climate changes, so do glaciers (Lowell, 2000; Oerlemans, 2005). Increased glacier melting will increase carbon release via glacial river systems. In a review paper, Hood et al. (2015) estimated that across five continents, mountain and polar glaciers contain about 6 petagrams (Pg) of organic carbon. Most of this is stored within the Antarctic ice sheet. However, the annual release of ice-locked organic carbon occurs mainly from the Greenland ice sheet (especially particulate organic carbon) and from mountain glaciers (especially dissolved organic carbon). Due to climate change, glaciers are shrinking, and glacier mass loss is responsible for about 13% of the annual release of dissolved organic carbon from glaciers. Based on an assumed accelerated melting rate, the cumulative loss of glacial dissolved carbon by 2050 might amount to half of the annual release of dissolved organic carbon from the Amazon river. Glaciers link terrestrial and aquatic carbon transport, including land-to-ocean fluxes.



Fig. 1 Glaciers matter in the global carbon cycle. They collect, produce, transform, store and release carbon. A part of this carbon may be ancient. Glaciers are also “climate trackers”, releasing increased amounts of water and carbon. This glacier snout is part of the Hardangerjøkulen glacier in South Norway. During 12 years, from 2005 to 2017, the glacier front receded 155 m, leaving the barren area seen on the picture. Photo: Sigmund Hågvær.

A somewhat surprising discovery during the last decades is that carbon released by glaciers may be very old, up to several thousand years. After release, this ancient carbon can be assimilated by microorganisms and invertebrates in the glacier foreland and support early colonization of life on newly deglaciated areas. Ancient carbon is also transported away and assimilated by various organisms in glacial river systems—and even in the ocean (Bardgett et al., 2007; Hood et al., 2009; Stubbins et al., 2012; Singer et al., 2012; Hågvær and Ohlson, 2013; Spencer et al., 2014a,b; Fellman et al., 2015a,b; Hågvær et al., 2016).

Assimilation of ancient carbon results in a paradox: Living organisms, for instance insects, can achieve a radiocarbon age of several thousand years (Hågvær and Ohlson, 2013; Hågvær et al., 2016).

This review will discuss the sources of ancient carbon, how is it captured and stored by glaciers, and the ecological role of ancient carbon after being released.

Two Main Sources of Ancient Carbon

There are two main ways in which a glacier may become a store of ancient carbon. The first is easy to conceive: If the glacier grows and overruns vegetation and soil, the carbon in the captured ecosystem may be locked up beneath the glacier long enough to become ancient. The second is cryptic but important: The glacier surface may receive tiny aerosol particles which are the result of incomplete combustion of fossil fuels like coal, oil or gas. These particles are “ ^{14}C -dead”, which means that they contain mainly the ^{12}C isotope and has a very high radiocarbon age.

Overriding Vegetation and Soil

During the 8–10,000 year period after the termination of the last ice age, the size of individual glaciers has varied according to climate changes. For instance, the present Norwegian glaciers are not remnants of the large “ice age glacier”, which once covered the whole country, as today's glaciers have been periodically absent (Nesje et al., 2008). The latest growth period for Norwegian glaciers terminated around 1750, at the end of a cold period called “the little ice age”. Characteristic “1750-moraines” are common, and there is documentation from around 1750 that certain mountain farms were abandoned or even destroyed due to the advancing glacier front (Foss, 1802).

The ice mass of glaciers is to a certain degree plastic, and organic matter held by the glacier is finally expelled at the edge. For instance, during the last decades, Norwegian glaciers have receded strongly and released woody items like bow and arrows from thousands of years old hunting cultures. These items are perfectly preserved and seem freshly made.

Capturing Air-Borne Aerosols

While only certain glaciers contain subglacial, relict soil or vegetation, all glaciers have the ability to capture ancient carbon on their surface. Fine-particulate aerosols can remain airborne for up to 3 months (Druffel, 2004) and are able to contaminate ice sheets in

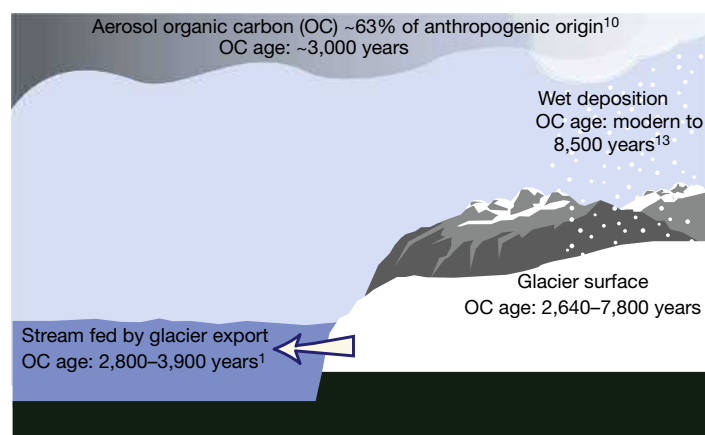


Fig. 2 Aerosols containing ancient carbon of anthropogenic origin can be deposited on glacier surfaces even in remote areas. The Figure illustrates the glacial organic carbon cycle, including some examples on radiocarbon age. From Stubbins, A., Hood, E., Raymond, P. A., et al. (2012). Anthropogenic aerosols as a source of ancient dissolved organic matter in glaciers. *Nature Geoscience* 5, 198–201.

remote areas (Fig. 2). For instance, in the Juneau Icefield in Southeast Alaska, dissolved organic carbon deposited on snow surfaces consisted mainly of fossil fuel combustion products (Fellman et al., 2015a). Since the industrial revolution, the global atmosphere has been gradually contaminated with aerosol particles carrying ancient carbon. An ice core from an alpine glacier in Switzerland revealed that almost half of the organic carbon deposited in 1940 originated from combustion of fossil fuels, while deeper ice from before 1850 contained virtually nothing of this element (Jenk et al., 2006). Studies of the air quality in Zurich showed that about 30% of the organic carbon in the air was of anthropogenic origin (Szidat et al., 2006). Unsurprisingly, this carbon may be washed out from the air during rain, as shown by Raymond (2005) who found ancient carbon from fossil fuels in rainwater in the Northeastern United States.

Ancient Carbon Beneath, Upon or Within Glaciers: Case Studies

Ancient Carbon Beneath Glaciers

A direct way of dating overridden organic material is to bore through the ice and collect organic matter beneath the glacier. Two case studies from Svalbard illustrate this. Frozen soil and vegetation were found 30–35 m below the present-day surface of the Longyear glacier. Interestingly, this soil system contained microbes which had survived more than 1100 years in a subglacial, permafrozen state. Before that, the actual area was ice-free for at least 800 years, but then overrun by a growing glacier (Humlum et al., 2005). The microbial community structure and ecology was also studied in subglacial sediments of two other Svalbard glaciers (Kastovska et al., 2007). Even here, viable bacteria, cyanobacteria and microalgae were detected. Newly deglaciated soils were similar in microbial structure but different from vegetated sites. These results suggested that subglacial microorganisms retained the ability to proliferate if conditions improved. A diverse microbial life beneath a high Arctic glacier was also documented on Ellesmere Island, Canada (Skidmore et al., 2000). Clearly, organic compounds in overrun vegetation and soil may not only be stored for a long time but can be slowly modified by cold-tolerant microorganisms, although temperature is close to zero.

Surface-Collected Ancient Carbon and Supraglacial Processes

Glacier surfaces often appear dirty. They receive both ancient carbon via aerosols and modern carbon via wind-blown debris. Stibal et al. (2010) studied organic matter content and quality in debris on the surface of the Greenland ice sheet. Three key processes influenced the carbon cycling here: eolian (wind) input of microbial inoculum and nutrients, in situ biological carbon transformation (photosynthesis and decomposition), and the wash-away of supraglacial debris by meltwaters. Glacier surfaces are to a varying degree a habitat for biological production. On a Svalbard glacier, Stibal et al. (2008) found that microbial primary production was insignificant in comparison with allochthonous organic carbon input. However, from Greenland, Bhatia et al. (2010) concluded that the majority of supraglacial dissolved organic matter originated from autochthonous microbial processes on the ice sheet surface. A considerable proportion of protein-like compounds were observed in the supraglacial samples.

Glacier surfaces may have a surprisingly high microbial activity which influences the global carbon cycle (Anesio et al., 2009; Hodson et al., 2010). Algae, bacteria and viruses may thrive in so-called cryoconite holes, which can cover 0.1–10% of the glacier surface. These are small, water-filled depressions in the ice (usually less than 1 m in diameter and less than 0.5 m deep). They are created when solar-heated inorganic and organic debris—including dark aerosols—melts into the ice and gradually aggregate. Studies on cryoconite holes in Svalbard, Greenland and the European Alps revealed a high microbial activity, although temperatures were close to 0°C. It was estimated that cryoconite holes in glaciers outside Antarctica could fix as much as 64 Gg of carbon per year.

In cryoconite holes, aerosol particles containing ancient carbon are mixed with new organic matter produced by chlorophyll-containing algae and cyanobacteria. Aerosols can also be chemically transformed by microorganisms and included in new organic compounds. The collective chemical products from these “cryoconite hole ecosystems” can either be stored within the glacier or washed off the glacier surface. In the last case, they can end up within glacier cracks, or be transported away via glacial rivers.

When finally released through melting water, ancient carbon from aerosol particles can be more or less transformed, more or less mixed with other products created in cryoconite holes, and further mixed with rather unchanged in-blown organic material of recent origin. The radiocarbon age of this final mix depends on the relative proportion between ancient and recent carbon and is not “the age of this sample”. We can only say that the higher the radiocarbon age, the more ancient carbon does the actual sample contain. In contrast, if a distinct piece of a plant released from overridden vegetation is analyzed separately (for instance a twig or a tree stem), its radiocarbon age will be true.

Glaciers With Both Overridden and Surface-Collected Ancient Carbon

The following case studies from Greenland illustrate the combined release of ancient carbon from overridden soil/vegetation, and from airborne, surface-trapped particles (Bhatia et al., 2010, 2013). During the early melting season in spring, the release of organic carbon via melt water was considered to stem mainly from the surface of the glacier. A considerable proportion of protein-like compounds probably originated from autochthonous processes on the ice sheet surface. Later in the melting season, there was an increase in lignin-like and other material that probably derived from underlying vegetation and soil. We see that supra- and sub-glacier organic matter can give different signals in the discharged melt water. However, here it must be added that microbial oxidation, which occurred under the glacier, contributed to the release of metabolic products.

Thus, the release of ancient carbon from the Greenland glacier fed not only the foreland and glacier rivers, but was also discharged into marine environments.

Release and Biological Use of Ancient Carbon

Bioavailable compounds released from glaciers may contain ancient carbon. When these compounds are assimilated, for instance by microorganisms, ancient carbon can end up in food chains, either in the glacier foreland, downstream in glacial rivers, or in marine environments. Some examples will illustrate these alternatives.

Occurrence and Use of Ancient Carbon in Glacier Foreland, Supporting Early Succession

In newly exposed glacial “soil”, heterotrophic microbial communities may use ancient carbon before autotrophic succession starts. This was demonstrated in an Austrian glacial foreland, where microbes used both ancient and modern carbon as an energy use during the first 50 years of succession (Bardgett et al., 2007). Also in Svalbard, ancient organic carbon has been documented in glacier foreland soil (Yoshitake et al., 2011).

In front of a melting Norwegian glacier, freshly produced sand and silt contained organic material with a radiocarbon age of 5160 years (Hågvær et al., 2016). This organic material tended to aggregate in depressions, including the bottom of newly created ponds of varying size, some of them less than a square meter large. These ponds turned out to function as “biological oases” (Fig. 3). Sediments of 8-year-old ponds contained dense populations of tube-living chironomid larvae, which had a radiocarbon age up to 3270 years when analyzed with intact gut content. Tipulid larvae collected from the same pond sediments, analyzed after the gut content had been removed, had a radiocarbon age of 1610 years, proving that ancient carbon had been assimilated into their tissue. Larvae may either have digested directly organic compounds containing ancient carbon, or eaten bacteria that had assimilated ancient carbon. These ponds even contained diving beetles, of which both larvae and adults were assumed to feed on chironomid or tipulid larvae. Larvae and adults of diving beetles had radiocarbon ages of 1200, and 1130 years, respectively. The use of ancient carbon in ponds lasted for several decades, since larvae in a 80 year old pond was 350 year “old”.

It has long been recognized that predator invertebrates like spiders and carabid beetles colonize virgin ground like glacier forelands before a visible vegetation is present (Hågvær, 2012; Hågvær et al., 2017). This has been called “the predator first paradox” (Hodkinson et al., 2002). According to ecological theory, a new ecosystem must start with plants, followed by herbivores, and then predators. The paradox has been explained by aerial transport of prey like midges and flies to the virgin ground. Such transport occurs (Coulson et al., 2003; Flø and Hågvær, 2013) but it is only part of the story. Hågvær and Ohlson (2013) and Hågvær et al. (2016) documented another possibility: Local production of prey based on the use of ancient carbon released from the glacier. Following up the case mentioned above, they showed that adult chironomid midges hatching from young ponds had a radiocarbon age of 1040 years. Microscopic studies of gut contents from predatory carabid beetles and harvestmen (Opiliones) revealed that chironomid midges that had fallen to the ground made up a substantial part of their diet (Hågvær and Pedersen, 2015). This transport of ancient carbon from aquatic to terrestrial habitats explained why terrestrial predators among beetles, harvestmen and wolf spiders had radiocarbon ages between 340 and 1100 years (Fig. 4).

The pioneer ecosystem on a newly deglaciated area was supported by three “invisible” food sources (Fig. 5): (1) Ancient carbon assimilated by chironomid larvae in young ponds and transported to terrestrial predators via adult midges. (2) A terrestrial biofilm



Fig. 3 These insects from 7 to 9-year-old ponds contained ancient carbon released by the glacier. (A) In the sediment surface, numerous tubes can be seen, in which chironomid larvae were living. (B) Chironomid larvae, here partly freed from their tubes, had a radiocarbon age of 3270 years. (C) Two predacious larvae of the diving beetle *Agabus bipustulatus* (radiocarbon age 1200 years), and three cylindrical Tipulidae larvae (Diptera) (radiocarbon age 1610 years). (D) Adult predacious diving beetles, *Agabus bipustulatus*, had a radiocarbon age of 1130 years. From Hågvar, S., Ohlson, M. and Brittain, J. E. (2016). A melting glacier feeds aquatic and terrestrial invertebrates with ancient carbon and supports early succession. *Arctic, Antarctic, and Alpine Research* **48**, 551–562.

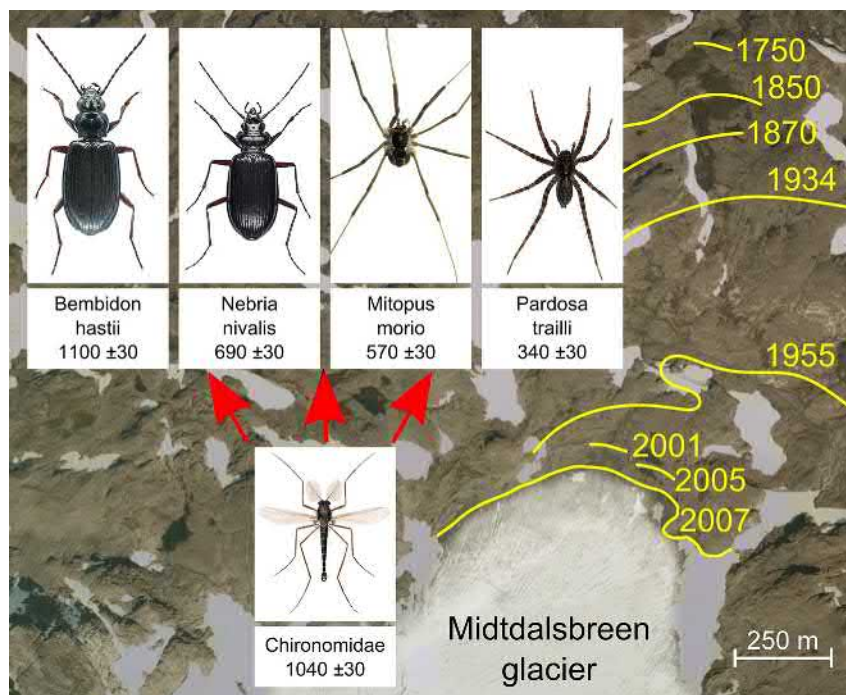


Fig. 4 Living, but “old”. Four predatory invertebrates living on barren pioneer ground had radiocarbon ages between 340 and 1100 years. Gut contents revealed that they had eaten adult chironomid midges. As larvae, midges had assimilated ancient carbon in young ponds. Some moraines back to 1750 are shown. From Hågvar, S. and Ohlson, M. (2013). Ancient carbon from a melting glacier gives high ^{14}C age in living pioneer invertebrates. *Scientific Reports* **3**, 2820.

containing diatom algae, on which certain pioneer Collembola grazed. (3) Tiny pioneer mosses grazed upon by certain Collembola and beetles. Collembola was not an important food source for predators in the actual site.

Transport and Use of Ancient Carbon in Glacial Rivers

Hood et al. (2009) showed that heavily glaciated watersheds in Alaska transported ancient dissolved organic matter with a radiocarbon age up to 3900 years, all the way to the Gulf of Alaska. The bioavailability to marine microorganisms was highest for the oldest organic matter.

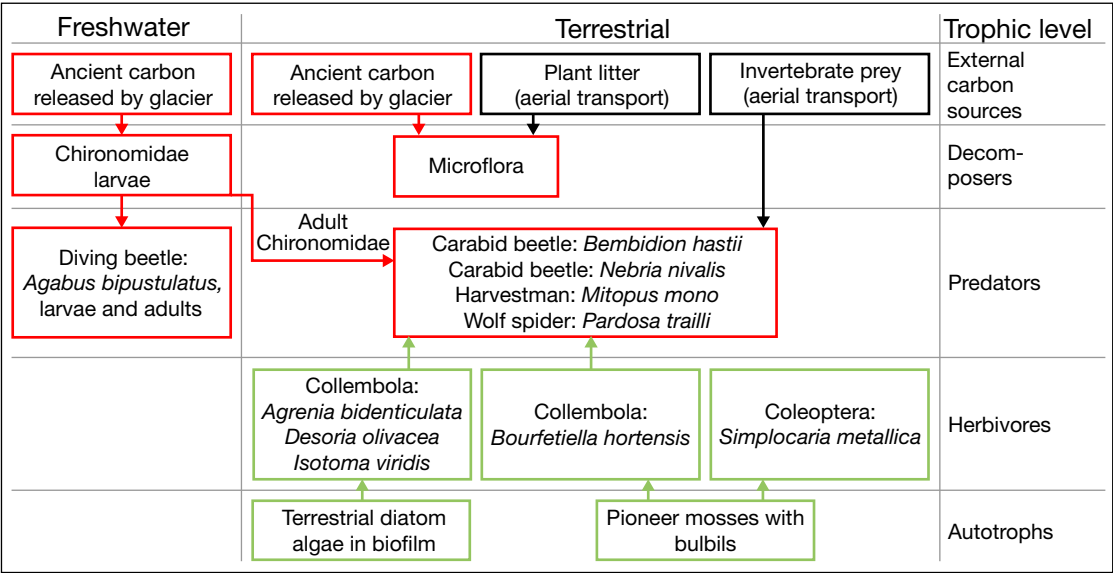


Fig. 5 Ancient carbon (red boxes and arrows) contributes to a pioneer food web on 3–7 year old ground. The flow of chlorophyll-produced carbon is illustrated in green, and the contribution of aerial transported carbon in black. Trophic levels are shown for both freshwater and terrestrial habitats. Chironomid midges hatching from young ponds transported ancient carbon to terrestrial pioneer predators. From Hågvar, S. and Ohlson, M. (2013). Ancient carbon from a melting glacier gives high ^{14}C age in living pioneer invertebrates. *Scientific Reports* 3, 2820.

In 26 glaciers within the European Alps, [Singer et al. \(2012\)](#) studied the molecular composition of ice-locked organic matter, sampled 0.5 m below the glacier surface. Among several molecular clusters, two contained ancient carbon. One molecular group was humic-like with polyphenols from lignin and could represent overridden soil and vegetation. The other molecular group could be combustion products deposited on the glacier surface. The ancient carbon compounds had radiocarbon ages between 600 and 8500 years. They were biodegradable and assimilated in inoculum experiments, indicating that ancient carbon contributed to downstream carbon cycling.

In Southern Norway, a river fed by a receding glacier transported bioavailable ancient carbon ([Hågvar et al., 2016](#)). Chironomid larvae were sampled 0.8, 1.4 and 4.0 km downstream. Their radiocarbon age was 1190, 1260, and 290 years, respectively. In order to avoid possible contamination from nonassimilated matter, their gut content was removed before the analysis. Guts contained few signs of algae, but a lot of small mineral particles. There is a possibility that these might have been ingested during grazing on bacterial biofilm.

[Fellman et al. \(2015b\)](#) showed that dissolved ancient carbon in an Alaskan proglacial stream was assimilated into a food chain, probably starting with an epilithic bacterial biofilm. Second level was grazing chironomid larvae, whose gut content contained fine rock fragments. Third level was predatory, juvenile salmonids.

It should be mentioned that also nonglacial rivers may carry bioavailable ancient carbon. In that case, the ancient carbon is typically derived from peat and captured by the river through erosion. Two cases of eroding tundra rivers can illustrate this, one from Siberia ([Vonk et al., 2013](#)) and one from Alaska ([Schell, 1983](#)). In the Siberian case, bioavailable dissolved organic carbon of more than 21,000 years age was transported downstream and all the way to the coast. In the Alaskan case, old peat particles were assimilated by aquatic invertebrates. Old squaw ducks (*Clangula hyemalis*) feeding on these invertebrates had only 85% modern ^{14}C content, corresponding to an “age” of 1300 years. There are even rivers that contain ancient carbon from both glacier and eroded soils or peat, like the Yukon River basin ([Aiken et al., 2014](#)). [Caraco et al. \(2010\)](#) reported bioavailable ancient carbon in Hudson river, due to erosion in agricultural lands and sewage inputs. Crustacean plankton ingested small-particulate ancient carbon and became highly ^{14}C depleted.

Marine Environments Receiving Ancient Carbon From Glaciers

The Gulf of Alaska is fed by several glacial rivers. They expel dissolved organic matter containing ancient carbon into the marine environment. The ancient carbon is derived mainly from combustion aerosols that have been deposited on the glacier surfaces. The most heavily glaciated watersheds carry the oldest carbon, which is also the most bioavailable. Near-shore marine environments respond with increased growth of bacterioplankton. Due to rapid glacier melting, the delivery of relic carbon to the Gulf is increasing, and this may affect the function and productivity of coastal ecosystems ([Hood and Scott, 2008](#); [Hood et al., 2009](#); [Fellman et al., 2010, 2015a](#)).

Another marine locality receiving considerable amounts of ancient carbon is the coastal waters of Greenland. ^{14}C -depleted organic matter is released by the receding glacier, transported downstream to the coast or washed directly into the ocean ([Bhatia et al., 2013](#)).

Perspectives

Combustion-Derived Black Carbon Accelerate Glacier Melting

Black carbon aerosols deposited on glacier surfaces in Himalaya accelerate ice melting, which in the long run threatens the water supply for billions of people. A study of carbon isotopes in aerosols and snowpit samples showed that about half of the carbon was ancient and derived from fossil fuels, while the other half was due to biomass combustion (Li et al., 2016). Clearly, the human use of fossil fuels has a double effect on glacier melting, both by increasing the global temperature, and by spreading black carbon that absorbs solar heat on glacier surfaces.

Ancient Carbon Enter Contemporary Food Webs

The human combustion of fossil fuels leads to a global spread of ancient carbon through far-reaching aerosols. A part of this ancient carbon is bioavailable and is gradually incorporated in contemporary food webs of various ecosystems. This is especially evident in aquatic environments, both freshwater and marine. A review by Guillemette et al. (2017) stresses that this change in resource utilization may alter food web stability, structure and dynamics of ecosystems. As shown above, ancient carbon may also find the way to terrestrial ecosystems, for instance by midges with aquatic larvae (Hågvar and Ohlson, 2013).

Primary succession on virgin ground in a glacier foreland is fascinating ecology, and still more if ancient carbon can support the process. The presence of young ponds in which chironomid larvae can assimilate ancient carbon was a key factor in the referred example, but more case studies are welcome.

Since ancient carbon released by glaciers can be “pumped” into both aquatic and terrestrial food webs via chironomids, these midges deserve closer ecological studies. It remains to clarify whether bacteria in ponds or rivers represent the first step in the assimilation of bioavailable ancient carbon, or whether chironomid larvae can digest the ancient carbon directly. More studies should also be performed on the possible assimilation of ancient carbon in vertebrate predators like fish or insect-feeding birds along glacial rivers.

A simple way to document release and biological use of glacier-derived ancient carbon is to sample chironomid larvae in glacial rivers and measure their radiocarbon age. Gut contents should be removed before analysis to avoid contamination from nonassimilated matter.

Ancient Carbon Disturbs Radiocarbon Dating

If organisms that have assimilated ancient carbon are included in sediments, for instance as slowly decomposable insect chitin in lake sediments, a future radiocarbon aging of the actual sediment layer will achieve a too high age. Since glacier surfaces are efficient collectors of ancient aerosol carbon and since organisms in glacial rivers are able to assimilate this carbon, lakes and wetlands which belong to glacial watersheds are especially vulnerable to be contaminated by sediments with “too high age”.

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Relevant Website

nsidc.org—National Snow & Ice Data Center.

Freshwater: A Glossary of Terminology Used in Freshwater Biology and Management

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Abstract

A glossary of more than 220 terms used in reference to freshwater is provided to establish a common base of understanding among workers in this discipline.

Introduction

The Freshwater Biome is rich in concepts and associated terminology. The Biome includes many forms, uses, and distributions of freshwater (Suring, 2020). The usage of the terminology to describe these forms, uses, and distributions may vary over time, geographically, and by discipline. Different meanings of the same words may cause misunderstandings, especially by students in the various fields associated with freshwater and by specialists from other disciplines who may not be familiar with specific uses of terms. As such, it is useful to provide a glossary of current definitions of freshwater terminology to accompany the chapters describing the Freshwater Biome and its management.

The glossary does not intend to provide a review or history of all uses of particular terms, nor how they may be used in fields other than those associated with the ecology and management of freshwater. The glossary excludes terminology specific to the names of species and higher taxa associated with freshwater ecosystems, place names, taxonomy, legal and regulatory terms, and acronyms.

A Glossary of Terminology Used in Freshwater Biology and Management

Term	Definition	References
Ablation	The loss of ice and snow from a glacier system. This occurs through a variety of processes including melting and runoff, sublimation, evaporation, calving, and wind transportation of snow out of a glacier basin.	Molnia (2004)
Acid precipitation	Rainwater or snow containing sulfur and nitrogen compounds and other pollutants associated with industrialization.	Freshwater Information Platform (2019)
Aeolian	Pertaining to the action or effect of wind.	Lincoln et al. (1998)
Allochthonous	Describes material that comes into freshwater systems from outside the system (e.g., organic matter entering freshwater systems from trees).	Maitland and Morgan (1997)
Alluvial deposits (alluvium)	Material such as clay, silt, sand, and gravel deposited by modern rivers and streams.	Freshwater Information Platform (2019)
Amictic lakes	Lakes that do not have a period of overturn because they are perennially frozen.	Lincoln et al. (1998)
Amphidromous	Migration of organisms downstream to an estuary to feed or for growth during short periods, followed by upstream migration.	Lucas and Baras (2008)
Anadromous	Migration by organisms from marine systems to upstream freshwater spawning systems.	Lucas and Baras (2008)
Anchialine	Haline water, usually with restricted exposure to open air, and always with subterranean connections to the sea.	Culver and Pipan (2013)
Ancient carbon	Carbon pulled out of the atmosphere and stored in the bodies of plants hundreds or thousands of years ago.	Dean et al. (2018)
Aphotic	Without light, generally interpreted limnologically as receiving less than 1% of solar irradiance reaching a lake surface.	Lewis (2009)
Aquaculture	Farming of plants and animals that live in water, such as fish, shellfish, and algae.	United States Geological Survey (2019)
Aquatic ecosystem	A community of organisms together with their physical environment organized around a body of water.	Texas Aquatic Science (2013)
Aquatic macroinvertebrates	Macroscopic animals without backbones ("invertebrates") that are large enough to be seen with the naked eye ("macro," e.g., >0.5 mm).	Freshwater Information Platform (2019)
Aquiclude	A barrier that is almost impermeable to water flow between aquifers.	Harter (2003)

(Continued)

<i>Term</i>	<i>Definition</i>	<i>References</i>
Aquifer	A water-bearing layer of soil, sand, gravel, or rock that will yield usable quantities of water to a well.	Freshwater Information Platform (2019)
Aquitard	A geological layer or formation which limits the flow of groundwater between aquifers.	Harter (2003)
Autochthonous inputs	Organic matter from within a freshwater system's primary production from algae or periphyton.	McManamay and Jager (2020)
Autotrophy	Self-sustained production of organic matter from inorganic substances.	Schmidt and Hahn (2012)
Bacterioplankton	Bacterial component of the plankton that drifts in the water column of both seawater and freshwater ecosystems.	Pommier (2011)
Benthic	The zone of a lake extending a few centimeters above and below the bottom of the lake.	Lewis (2009)
Benthos	The community of organisms living around surfaces (e.g., sediments, plants) in aquatic ecosystems.	Strayer (2009)
Biome	A major ecological community characterized by distinctive life forms.	Lincoln et al. (1998)
Bioturbation	Sediment mixing caused by the activities of organisms.	Strayer (2009)
Blackwater rivers	Rivers that are rich in humic acids and with low nutrient concentrations.	Lincoln et al. (1998)
Blue water	Fresh surface and groundwater; in other words, the water in freshwater lakes, rivers, and aquifers.	Hoekstra et al. (2011)
Braided river	A braided river channel consists of a network of smaller channels separated by small and often temporary islands called braid bars.	Freshwater Information Platform (2019)
Capture fishery	Capture fishery refers to all kinds of harvesting of naturally occurring living resources in both marine and freshwater environments. On a broad level, capture fisheries can be classified as industrial, small-scale/artisanal, and recreational.	GreenFacts Digests (2019)
Catadromous	Organisms that are reared in freshwater and migrate to the marine environment to spawn.	Lucas and Baras (2008)
Catchment	A natural drainage basin which channels rainfall into a single outflow.	Lincoln et al. (1998)
Cienega	Wetland systems unique to the American Southwest that are wet meadows with shallow-gradient and permanently saturated soils in otherwise arid landscapes.	Hendrickson and Minkley (1984)
Collectors	Organisms that filter and collect smaller particles of organic matter found in the water column and bottom sediments. This organic matter can range in size from 0.01 to 1.0 mm and usually arrives in water columns and benthic sediments as a result of organic matter being broken up by shredder species.	Stumpf et al. (2015)
Colluvial	Colluvial material or colluvial soil is a general name for loose, unconsolidated sediments that have been deposited at the base of hillslopes by rainwash, sheetwash, slow continuous downslope creep, or a variable combination of these processes.	Leopold and Völkel (2007)
Crenobiology	The study of the biology of springs.	Sada et al. (2001)
Crenobionts	Species largely restricted to springs.	Glazier (2009)
Crenophiles	Species that commonly occur in spring habitats but also occur elsewhere.	Glazier (2009)
Crenoxenes	Species that occasionally occur in springs.	Glazier (2009)
Cryoconite	A mélange of sediments, wind-blown detritus, and even living and dead microscopic psychrophiles on a glacier's surface.	Takeuchi et al. (2015)
Cryoconite holes	Small, glacier-ice melt pools.	Wharton et al. (1985)
Cyanobacteria	Cyanobacteria are one of the largest and most important groups of bacteria on Earth. They live in water, and are photosynthetic. This means that they convert the carbon dioxide in the atmosphere into oxygen. Cyanobacteria are mainly responsible for generating the oxygen that is found in the Earth's atmosphere today. Although their common name is "blue-green algae," the cyanobacteria are bacteria, and are not related to algae.	GreenFacts Digests (2019)
Detritivore	Animals that feed primarily on fragments of organic matter (detritus) found in soil and bottom sediments.	Freshwater Information Platform (2019)
Detritus	Particulate organic matter.	Lincoln et al. (1998)
Dimictic	Lakes with a pattern of two mixing periods (spring turnover–summer stratification–fall turnover–winter stratification).	LakeAccess (2006)
Dissolved organic carbon	Dissolved organic carbon is generally defined as organic matter that is able to pass through a filter which removes material between 0.70 and 0.22 µm in size.	Strack et al. (2008)
Dissolved oxygen	Oxygen gas absorbed by and mixed into water.	Texas Aquatic Science (2013)
Domestic water use	Water used for household purposes, such as drinking, food preparation, bathing, washing clothes, dishes, and dogs, flushing toilets, and watering lawns and gardens.	United States Geological Survey (2019)
Drainage basin	The land area that contributes water to a stream or lake system or directly to the ocean; also referred to as a catchment basin.	Freshwater Information Platform (2019)
Drought	An extended period of below normal rainfall or other deficiency in water supply.	Texas Aquatic Science (2013)
Ecosystem services	Resources and processes that are supplied by ecosystems, generally grouped into four broad categories: provisioning, such as the production of food and water; regulating, such as the control of climate and disease; supporting, such as nutrient cycles and crop pollination; and cultural, such as spiritual and recreational benefits.	Texas Aquatic Science (2013)

<i>Term</i>	<i>Definition</i>	<i>References</i>
Ecotopes	The smallest ecologically distinct landscape features in a landscape mapping and classification system. As such, they represent relatively homogeneous, spatially explicit landscape functional units that are useful for stratifying landscapes into ecologically distinct features for the measurement and mapping of landscape structure, function and change.	Runhaar and Udo de Haes (1994)
Ectothermic	Having a body temperature determined primarily by the temperature of the environment (i.e., cold-blooded).	Lincoln et al. (1998)
Embodied water	Embodied (or virtual) water is a measure of the total water used in production of a good or service.	Hoekstra and Chapagain (2011)
Emergent plant	A plant rooted in shallow water with much of the stem and most of the leaves above water.	Freshwater Information Platform (2019)
Englacial	Interior of a glacier.	Hamilton et al. (2013)
Ephemeral streams	All flowing waters that cease flow and/or dry completely at some point along their course.	Datry et al. (2017)
Epilimnion	The uppermost and warmest layer (also called the mixed layer) of a lake that experiences density stratification induced by seasonal warming at the lake surface.	Lewis (2009)
Equilibrium line altitude	An upper elevation accumulation zone exists on glaciers, where snowfall exceeds melt; a low-elevation ablation zone exists, where melt exceeds snow accumulation. The equilibrium line altitude is the transition area between the two zones.	Dial and Ditto (2020)
Euphotic	That portion of a lake receiving sufficient solar irradiance to support photosynthesis (typically more than 1% of full solar irradiance).	Lewis (2009)
Eutrophic	Rich in basic nutrients.	Maitland and Morgan (1997)
Eutrophication	Enhanced primary productivity caused by nitrogen and phosphorous, organic pollution, intense catchment land use, and habitat degradation.	Freshwater Information Platform (2019)
Evaporation	The process of liquid water becoming water vapor, including vaporization from water surfaces, land surfaces, and snow fields, but not from leaf surfaces.	United States Geological Survey (2019)
Feed conversion efficiency	The efficiency with which the bodies of livestock convert animal feed into the desired output.	Fry et al. (2018)
Filter feeders	Any animal that feeds by filtering suspended particulate organic matter from water.	Lincoln et al. (1998)
Firn	An intermediate stage in the transformation of snow to glacier ice. Snow becomes firn when it has been compressed so that no pore space remains between flakes or crystals, a process that takes less than a year.	Molnia (2004)
Flood	An overflow of water onto lands that are used or usable by humans and not normally covered by water. Floods have two essential characteristics: the inundation of land is temporary; and the land is adjacent to and inundated by overflow from a river, stream, lake, or ocean.	United States Geological Survey (2019)
Floodplain	The land bordering a stream, built up of sediments from stream overflow and subject to inundation when the stream floods.	Freshwater Information Platform (2019)
Fluvial	Pertaining to rivers.	Freshwater Information Platform (2019)
Fluvial deposits	All sediments, past and present, deposited by flowing water.	Freshwater Information Platform (2019)
Freshwater fishes	Those that complete their entire life cycle in freshwater.	Polhemus and Richardson (2020)
Freshwater, fresh water	Water that contains less than 1000 mg per liter (mg/L) of dissolved solids; generally, more than 500 mg/L of dissolved solids is undesirable for drinking and many industrial uses.	United States Geological Survey (2019)
Glacier	A huge mass of ice, formed on land by the compaction and recrystallization of snow that moves very slowly downslope or outward due to its own weight.	United States Geological Survey (2019)
Gray water	Wastewater from clothes washing machines, showers, bathtubs, hand washing, lavatories and sinks.	United States Geological Survey (2019)
Green water	The precipitation on land that does not run off or recharge the groundwater but is stored in the soil or temporarily stays on top of the soil or vegetation.	Hoekstra et al. (2011)
Groundwater	Water in the zone of saturation where all open spaces in sediment and rock are completely filled with water.	Freshwater Information Platform (2019)
Groundwater recharge	Inflow of water to a groundwater reservoir from the surface. Infiltration of precipitation and its movement to the water table is one form of natural recharge. Also, the volume of water added by this process.	United States Geological Survey (2019)
Headwater streams	Headwater streams are the smaller tributaries that carry water from the upper reaches of the watershed to the main channel of the river.	Richardson (2019)
Helocrenes	A spring that results in a marshy bog.	Hynes (1970)
Helophyte	A perennial plant with renewal buds, commonly on rhizomes, buried in soil or mud below water level.	Lincoln et al. (1998)
Heterotrophic	Organisms that obtain nourishment from exogenous organic matter.	Lincoln et al. (1998)
Holomictic	Lakes having complete free circulation throughout the water column at the time of winter cooling.	Lincoln et al. (1998)
Homopycnal inflows	Incoming water and lake water of same density resulting in thorough mixing of the two.	Timms (2009)
Hydric soil	Soil that is wet long enough to periodically result in anaerobic conditions, influencing the growth of plants.	Cowardin et al. (1979)

(Continued)

<i>Term</i>	<i>Definition</i>	<i>References</i>
Hydrochory	Life history traits that depend on dispersal of seeds, fruits, and spores by water.	McManamay and Jager (2020)
Hydrogeology	The study of groundwater.	Mudd (2020)
Hydrogeomorphic	An interdisciplinary science that focuses on the interaction and linkage of hydrologic processes with landforms or earth materials and the interaction of geomorphic processes with surface and subsurface water in temporal and spatial dimensions.	Sidle and Onda (2004)
Hydrography	The study of investigating bodies of water.	Eckhardt (2019)
Hydrologic cycle	The cyclic transfer of water vapor from the Earth's surface via evapotranspiration into the atmosphere, from the atmosphere via precipitation back to earth, and through runoff into streams, rivers, and lakes, and ultimately into the oceans.	United States Geological Survey (2019)
Hydrology	The science of the properties, distribution, and effects of water.	Freshwater Information Platform (2019)
Hydroperiod	The duration of inundation by water over a year	Crane et al. (2013)
Hydrophyte	Plant growing in water or on substrate that is periodically deficient in oxygen resulting from excessive water content.	Cowardin et al. (1979)
Hydrophytic	Thriving in wet or aquatic situations.	Lincoln et al. (1998)
Hydropower	Electrical energy produced by falling water.	Eckhardt (2019)
Hydroregime	A system made up of water and the associated aquatic environments within a delimited geographical entity.	Greenberg et al. (2015)
Hyperpycnal inflows	Incoming water more dense than lake water, so it flows along the bottom of the lake.	Timms (2009)
Hypolimnetic	Cold bottom water below the thermocline in a lake.	Lincoln et al. (1998)
Hypolimnion	The most dense, deepest, and coolest layer of a thermally stratified lake. The hypolimnion does not support photosynthesis, because it lacks solar irradiance, and in many cases shows partial or complete depletion of dissolved oxygen.	Lewis (2009)
Hypopycnal inflows	Incoming water less dense than lake water, so it flows on the surface of the lake.	Timms (2009)
Hyporheic zone	Where groundwater intermixes with surface water.	McManamay and Jager (2020)
Hypoxia	A deficiency of oxygen; water having dissolved oxygen concentrations <2 mg/L.	Roman et al. (2019)
Industrial water use	Water used for industrial purposes in such industries as steel, chemical, paper, and petroleum refining.	United States Geological Survey (2019)
Infiltration	Flow of water from the land surface into the subsurface.	United States Geological Survey (2019)
Inselberg	Isolated rock outcrops that stand out abruptly from surrounding plains.	Potembski and Barthlott (2012)
Insulosity	The percentage of the lake area occupied by islands.	Lincoln et al. (1998)
Intermittent rivers	All flowing waters that cease flow and/or dry completely at some point along their course	Datry et al. (2017)
Interrupted streams	Streams which support perennial flow in their upper reaches, but become dry as this flow sinks into the bed further downstream, so that there is not continuous flow all the way to their mouth except during the wet season or after major rainstorms.	Polhemus et al. (1992)
Irrigation	The controlled application of water for agricultural purposes through constructed systems to supply water requirements not satisfied by rainfall.	United States Geological Survey (2019)
Irrigation water use	Water application on lands to assist in the growing of crops and pastures or to maintain vegetative growth in recreational lands, such as parks and golf courses.	United States Geological Survey (2019)
Jökulhlaup	A glacier outburst flood resulting from the failure of a glacier-ice-dam, glacier-sediment-dam, or from the melting of glacier ice by a volcanic eruption (Icelandic).	Molnia (2004)
Karst topography	A landscape typical of gypsum and limestone areas, where sinkholes have formed as a result of the dissolution of rocks by rainwater; narrow, crumbling ridges separate the sinkholes.	Freshwater Information Platform (2019)
Lacustrine deposits	Material deposited by or settled out of lake waters and exposed by the lowering of water levels or the elevation of land. These sediments range in texture from sand to clay and are usually varied (layered annual deposits).	Freshwater Information Platform (2019)
Lake	A large body of standing water.	Texas Aquatic Science (2013)
Lentic	Related to slow-moving water, such as in lakes and bogs.	Freshwater Information Platform (2019)
Limnetic	Pertaining to the open water of a lake away from the bottom.	Lincoln et al. (1998)
Limnetic zone	The part of a lake that is too deep to support rooted aquatic plants.	Texas Aquatic Science (2013)
Limnocrenes	A spring that results in a large, deep pool.	Hynes (1970)
Limnology	Scientific study of physical, chemical, and biological conditions in lakes, ponds, and streams.	Eckhardt (2019)
Limnophilous	Living in ponds or marshes.	Eckhardt (2019)
Lithophils	Aquatic species that protect eggs by depositing, burying, or hiding them within crevices of substrates.	McManamay and Jager (2020)
Littoral	Near the shore of a waterbody, where irradiance reaching the bottom is >1% of solar irradiance at the water surface.	Lewis (2009)
Littoral zone	The part of a lake that is shallow enough to support rooted aquatic plants.	Texas Aquatic Science (2013)
Livestock water use	Water used for livestock watering, feed lots, dairy operations, fish farming, and other on-farm needs.	United States Geological Survey (2019)

<i>Term</i>	<i>Definition</i>	<i>References</i>
Lotic	Related to fast-moving water, such as in most streams and rivers.	Freshwater Information Platform (2019)
Macrobenthos	Benthic animals large enough to be retained on a coarse (usually 0.5-mm mesh) sieve.	Strayer (2009)
Macrophyte	All aquatic higher plants, mosses and characean algae, but excluding single celled phytoplankton or diatoms.	Freshwater Information Platform (2019)
Marsh	A wetland dominated by reeds and other grass-like plants.	Texas Aquatic Science (2013)
Meander	A loop-like bend in a stream or river that develops when a watercourse flows through level land and erodes its floodplain.	Freshwater Information Platform (2019)
Meiobenthos	Benthic animals too small to be retained on a coarse (usually 0.5-mm mesh) sieve, but large enough to be retained on a fine (usually 0.05-mm mesh) sieve.	Strayer (2009)
Meromictic lakes	Lakes that are permanently stratified due to a density gradient resulting from chemical stratification.	Lincoln et al. (1998)
Metacommunity	A set of local communities connected by dispersal of organisms.	Leibold et al. (2004)
Metalimnion	A layer of transitional density and temperature that connects the epilimnion to the hypolimnion.	Lewis (2009)
Mining water use	Water use during quarrying rocks and extracting minerals from the land.	United States Geological Survey (2019)
Monomictic	Lakes and reservoirs that are relatively deep, do not freeze over during winter, and undergo a single stratification and mixing cycle during the year (usually in the fall).	Eckhardt (2019)
Moulin	A narrow, tubular chute or crevasse through which water enters a glacier from the surface.	Molnia (2004)
Mud	Loose slushy fine sediment consisting of clay, silt, fine sand, and organic material. Often water-formed and deposited on the bottom of lakes and rivers.	Freshwater Information Platform (2019)
Nekton	The assemblage of swimming organisms in a body of water.	Eckhardt (2019)
Nilotic	Relating to the Nile River or to the Nile region of Africa.	Bender (2019)
Nitrogen	An inorganic nutrient essential for plant growth and reproduction when in oxidized forms (nitrate, nitrite, ammonia); excess can cause eutrophication; problems are usually associated with agricultural runoff and sewage.	Chesapeake Bay Foundation (2019)
Non-point source	A pollution source that cannot be defined as originating from discrete points such as pipe discharge. Areas of fertilizer and pesticide applications, atmospheric deposition, manure, and natural inputs from plants and trees are types of non-point source pollution.	Freshwater Information Platform (2019)
Nye or N-channels	Channelized systems in glaciers that involve water flow through channels incised into the underlying bedrock or subglacial sediments.	DeBeer et al. (2020)
Oligomictic lakes	Lakes having a relatively stable stratification with only rare periods of circulation.	Lincoln et al. (1998)
Oligotrophic	Having a low supply of plant nutrients.	Eckhardt (2019)
Organic matter	Plant and animal residues, or substances made by living organisms. All are based upon carbon compounds.	United States Geological Survey (2019)
Orographic rainfall	Rainfall produced by supersaturation of an air mass forced upward by a mountain range.	Lincoln et al. (1998)
Oxbow lake	A lake formed when river meanders are cut off from the main channel.	Freshwater Information Platform (2019)
Psychrophiles	Literally meaning cold-loving; these are organisms adapted to growth at low temperatures, having an optimum growth temperature of <15 °C and a maximum growth temperature of <20 °C.	Scherer and Neuhaus (2006)
Peak glacier water	Annual runoff of water from glaciers continues to rise until a maximum ("peak water") is reached, beyond which runoff steadily declines.	Huss and Hock (2018)
Pelagic	Living and feeding in the water column, as opposed to living associated with a sea or lake bottom, see also benthic.	Freshwater Information Platform (2019)
Percolation	The movement of water through the subsurface soil layers, usually continuing downward to the groundwater or water table reservoirs.	Eckhardt (2019)
Perennial streams	Streams which maintain flow throughout their entire length and discharge continuously to their mouth during all seasons, irrespective of seasonal variations in precipitation.	Polhemus et al. (1992)
Phosphorous	An inorganic nutrient essential for plant growth and reproduction; excess can cause eutrophication; problems are usually associated with farmland runoff, sewage, and detergents.	Chesapeake Bay Foundation (2019)
Phreatic water	Permanent groundwater that has very slow flow rates and consequently longer residence times—decades or even centuries.	Culver and Pipan (2013)
Phytolithophils	Aquatic species that protect eggs by depositing them on plants.	McManamay and Jager (2020)
Phytoplankton	Microscopic plants that float or drift almost passively in oceans, lakes, or rivers.	Freshwater Information Platform (2019)
Phytotelmata	Small pools of water within or upon plants.	Lincoln et al. (1998)
Phytotelmic	Organisms that inhabit small pools of water within or upon plants.	Lincoln et al. (1998)
Planktivores	Organisms that feed on planktonic organisms.	Lincoln et al. (1998)
Plankton	Microscopic free-floating living organisms not attached to the bottom or able to swim effectively against most currents.	Texas Aquatic Science (2013)

(Continued)

<i>Term</i>	<i>Definition</i>	<i>References</i>
Point source	A source at a discrete location such as a discharge pipe, drainage ditches, well, or concentrated livestock operation. Point source pollution arises from a discrete source, e.g., the discharge from a sewage treatment works. See also non-point source.	Freshwater Information Platform (2019)
Pollutant	A substance that contaminates the water, air, or soil.	Texas Aquatic Science (2013)
Polymictic lakes	Lakes without a persistent thermal stratification and which circulate continuously with brief periods of stability.	Lincoln et al. (1998)
Pond	A body of standing water small enough that sunlight can reach the bottom across the entire diameter.	Texas Aquatic Science (2013)
Pondscape	A network of ponds with ecological interactions.	Lemmens and Pinceel (2020)
Pool	Part of a stream where the water slows down, often with water deeper than the surrounding areas, which is usable by fish for resting and cover.	Texas Aquatic Science (2013)
Pool/riffle ratio	The ratio of surface area or length of pools to the surface area or length of riffles in a given stream reach; frequently expressed as a relative percentage of each category. Used to describe fish habitat rearing quality.	Texas Parks and Wildlife Department (2019)
Potable	Water suitable, safe, or prepared for drinking.	Eckhardt (2019)
Potamodromous	Within river migration.	Lucas and Baras (2008)
Precipitation	Rain, snow, hail, sleet, dew, and frost.	United States Geological Survey (2019)
Primary consumer	Organisms that consume primary producers.	Chaloner et al. (2009)
Primary producer	Organisms that generate organic compounds from inorganic nutrients.	Chaloner et al. (2009)
Profundal zone	A lake's deep-water region that is not penetrated by sunlight.	Eckhardt (2019)
Psychrophilic	Cold-loving life (usually microbial).	Dial and Ditto (2020)
Rain	Water drops which fall to the Earth from the air.	Eckhardt (2019)
Reach	In general, a length of stream with relatively homogenous characteristics.	Eckhardt (2019)
Recharge	Water added to an aquifer. For instance, rainfall that seeps into the ground.	United States Geological Survey (2019)
Reoligotrophication	Lakes and similar water bodies that are poor in nutrients and plant life and rich in oxygen.	Gerdeaux (2004)
Resilience	The capacity to recover from disturbance.	Datry et al. (2014)
Resistance	The capacity of a species, a community, or an ecosystem to persist unchanged by and during a disturbance.	Stanley et al. (1994)
Restoration	The return of an ecosystem to a close approximation of its condition prior to disturbance.	Texas Parks and Wildlife Department (2019)
Return flow	Surface water that returns to the natural environment after diversion for beneficial uses, such as for irrigation.	Eckhardt (2019)
Rheocrenes	Flowing springs, often emerging from and passing over bedrock faces.	Hynes (1970)
Riffle	A shallow section in a river or stream where the water flows swiftly; may be less turbulent than rapids.	Freshwater Information Platform (2019)
Riffle-pool section	Regular alternation of shallow (riffle) areas with higher current velocities and gravel-cobble substrates followed by deeper slow-flowing pool areas with finer substrates. Mountain streams often have a fixed riffle-pool sequence.	Freshwater Information Platform (2019)
Riparian (area)	The area adjacent to a stream or river with a high density, diversity, and productivity of plant and animal species relative to nearby uplands.	Freshwater Information Platform (2019)
River	A natural stream of water of considerable volume, larger than a brook or creek.	United States Geological Survey (2019)
River basin	The whole river system including all tributaries and springs from the source to the mouth (sea).	Freshwater Information Platform (2019)
Riverine	Relating to, formed by, or resembling a river including tributaries, streams, and brooks.	Texas Parks and Wildlife Department (2019)
Röthlisberger or R-channels	Channelized systems in glaciers that involve water flow through ice-walled conduits that are kept open where the rate of wall melting exceeds the rate of conduit closure due to ice creep.	DeBeer et al. (2020)
Runoff	The part of rain and snowmelt that runs over the ground and into a stream or other water body.	Freshwater Information Platform (2019)
Scour(ing)	Removal of sediment from the streambed by flowing water.	Freshwater Information Platform (2019)
Sediment	Soil particles, sand, and minerals washed from the land into aquatic systems as a result of natural and human activities.	Eckhardt (2019)
Seep	A spot where water contained in the ground oozes slowly to the surface and often forms a pool; a small spring.	Eckhardt (2019)
Sewage	The waste and wastewater produced by residential and commercial sources and discharged into sewers.	Eckhardt (2019)

<i>Term</i>	<i>Definition</i>	<i>References</i>
Shredders	Organisms that feed off of coarse particulate organic material such as small sections of leaves. They ingest the organic matter along with volunteer organisms (fungi, microorganisms) attached to the source.	Benfield and Webster (1985)
Siltation	The deposition of finely divided soil and rock particles upon the bottom of stream and river beds and reservoirs.	Eckhardt (2019)
Snow	Precipitation in the form of branched hexagonal crystals often mixed with simple ice crystals, which fall more or less continuously from a solid cloud sheet. These crystals may fall either separately or in cohesive clusters forming snowflakes.	Eckhardt (2019)
Spring	A defined area where a natural discharge of groundwater returns to the surface.	van Everdingen (1991) and White (2019)
Stagnicolous	Living in stagnant water.	Eckhardt (2019)
Step-pool	A step-pool system is a geomorphologic phenomenon occurring in high-gradient mountain streams >3% with alternating steps and pools having a stair like appearance.	Chin (1999)
Stream	A general term for a body of flowing water; natural water course containing water at least part of the year. In hydrology, it is generally applied to the water flowing in a natural channel as distinct from a canal.	United States Geological Survey (2019)
Stream bed	The stream bottom.	Freshwater Information Platform (2019)
Stream order	A hydrologic system of stream classification. Each small unbranched tributary is a first-order stream. Two first-order streams join to make a second-order stream. A third-order stream has only first and second-order tributaries, and so forth.	Texas Parks and Wildlife Department (2019)
Stream reach	An individual segment of stream that has beginning and ending points defined by identifiable features such as where a tributary confluence changes the channel character or order.	Texas Parks and Wildlife Department (2019)
Stygobites	Stygobites are obligate inhabitants of groundwater systems.	Humphreys (2006)
Subglacial	Area between glacial ice and basal bedrock.	Hamilton et al. (2013)
Sublimation	The transition of water directly from the solid state to the gaseous state, without passing through the liquid state; or vice versa.	Eckhardt (2019)
Subsidence	Sinking down of part of the earth's crust due to underground excavation, such as removal of groundwater.	Eckhardt (2019)
Supraglacial	Surface of a glacier.	Hamilton et al. (2013)
Surface water	All moving and standing water naturally open to the atmosphere.	Freshwater Information Platform (2019)
Suspended solids	The small solid particles in water that cause turbidity. Particles of suspended sediment tend to settle at the channel bottom, but upward currents in turbulent flow counteract gravitational settling.	Eckhardt (2019)
Swamp	A wetland in which trees or woody shrubs predominate.	Texas Aquatic Science (2013)
Thermocline	Fairly thin zone in a lake that separates an upper warmer zone (epilimnion) from a lower colder zone (hypolimnion).	Eckhardt (2019)
Thermokarst	A land surface characterized by very irregular surfaces of marshy hollows and small hummocks formed as ice-rich permafrost thaws; it commonly occurs in Arctic areas, and on a smaller scale in mountainous areas.	Pollard (2018)
Transpiration	Process by which water that is absorbed by plants, usually through the roots, is evaporated into the atmosphere from the plant surface, such as leaf pores.	United States Geological Survey (2019)
Tributary	A stream that feeds into a larger stream. Also called a feeder stream.	Freshwater Information Platform (2019)
Vadose	Water in the Earth's crust above the level of permanent ground water.	Lincoln et al. (1998)
Virtual water	Virtual (or embodied) water is a measure of the total water used in production of a good or service.	Hoekstra and Chapagain (2011)
Water quality	A term used to describe the chemical, physical, and biological characteristics of water, usually in respect to its suitability for a particular purpose.	United States Geological Survey (2019)
Water table	Level below the earth's surface at which the ground becomes saturated with water. The surface of an unconfined aquifer which fluctuates due to seasonal precipitation.	Eckhardt (2019)
Water year	A continuous 12-month period for which hydrologic records are compiled and summarized.	Texas Parks and Wildlife Department (2019)
Waterfall	A cascading feature with a gradient of 40% or greater.	Polhemus and Richardson (2020)
Watershed	A planning term that refers to the area from which surface water drains into a common lake or river system or directly into the ocean; also referred to as a drainage basin or catchment basin.	Freshwater Information Platform (2019)
Wetland	Wetlands are lands that are permanently or periodically saturated with water, which impacts the nature of soil development and what animals and plant communities live in the soil and on its surface.	Cowardin et al. (1979)
Zoobenthos	The community of animals living around surfaces (e.g., sediments, plants) in aquatic ecosystems.	Strayer (2009)

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A Glossary of Terminology Used in Marine Biology, Ecology, and Geology

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Glossary

Abiotic Without life.

Abyss The great depths of the oceans, usually considered to be depths of 2000–6000 m, a region of low temperatures, high pressure, and an absence of sunlight.

Abyssal hills Tract, sometimes extensive, of low (100–500 m) elevations on the deep sea floor.

Abyssal plain An extensive, flat, gently sloping or nearly level region at abyssal depths.

Abyssopelagic Open water habitat of the abyss. Distinct from the benthic (seabed) habitat.

Accretion Process of sediment build-up.

Acoustic backscatter A method of detecting discontinuities in the water, often used for current and turbidity measurements and for detecting changes in the character of the seafloor.

Adaptation A process by which species evolve, and by which individuals adapt, their growth and/or behavior to better survive and grow in a particular environment.

Adaptive radiation Process of new species evolving to adapt to different environmental conditions.

Advection The horizontal movement of water, or a property of water through such movement (e.g., temperature change through the movement of water).

Aggradation Reworking of the sediment by waves and currents.

Aggregate The collective term for sand, gravel and crushed rock typically used by the building industry. They can be compacted to firmly fill a space and are often bound together with cement (to make concrete) or bitumen (for road surfacing).

Aggregation A collection of animals or plants gathered or clustered together.

Algae The simplest plants; maybe single-celled (such as diatoms) or quite large (such as seaweeds). Live in salt or fresh water and on land.

Allopatric speciation The process through which species arise while separated geographically.

Alpha-diversity The number of species in a sample.

Aphotic zone The part of the water column where light does not penetrate.

Apron Gently dipping seabed surface comprised of sediment found at the base of a slope; commonly the product of slumping (sediment failure) of a steep slope.

Archaeology The study of historic and prehistoric communities.

Archipelago A group of adjacent islands.

Assemblage A neutral substitute for “community” but implying no necessary interrelationships among species; also called species assemblage.

Atoll An annular reef enclosing a lagoon in which there are no promontories other than reefs and islets composed of reef material.

Bank Elevation of the seabed over which the depth of water is relatively shallow. Sand banks are sedimentary features longitudinal to the current.

Barrier Islands Elongate offshore islands or sandbanks oriented parallel to the coastline which may form a lagoon between the island and the coast and which protect the coast from prevailing wave action.

Basin Depression, characteristically in the deep sea floor, more or less equidimensional in shape and of variable extent.

Bathyal Deep-sea, variously attributed to range from 200 to 2000 m or 4000 m depth.

Bathymetry Seafloor elevations and the variations in water depth; the topography of the seafloor.

Bathypelagic The zone of open water below the euphotic (well-lit) and mesopelagic (poorly lit) but above the abyssopelagic.

Bay, embayment A body of water partly enclosed by land.

Beach draw down Removal of sediment deposits from a beach by waves and currents.

Beach recharge Placement of aggregates on beaches to replace that lost by erosion (beach nourishment) or to protect coastal resources.

- Bedform** Sedimentary features of the seabed oriented transverse to flow direction; ripples, dunes, and sand waves.
- Bedload transport** The transport of sediments by currents, rolling or hopping along the seabed.
- Bejerrnick's Law** "Everything is everywhere, the environment selects." This means that species have the potential to be everywhere over time but that the environment selects which species live in a place. While strictly untrue, there is evidence that it applies relatively more to microscopic than larger organisms.
- Benthic boundary layer** A zone of the water column close to the seabed within which sediment (bedload) transport occurs.
- Benthic ecology** The nature and distribution of organisms on or within the seabed and the interactions between them and their environment.
- Benthic fauna** Animals that live on or within the seabed.
- Benthic** Associated with the seafloor.
- Benthos** The collection of organisms living on or within the seabed.
- Berm** A narrow shelf, bank, or ledge at the top or bottom of a slope; in coastal geomorphology a sedimentary feature (ridge) built along the coast, above the level of high tide, by storm wave action.
- Beta-diversity** The turnover of species composition between samples in a geographic area.
- Biocoenosis** The "living community"; formulated in 1877 by Karl Möbius; describes the organisms living in the same habitat, and is a now used synonymously with the term "community."
- Biodiversity** The Convention of Biological Diversity definition encompasses the variation within species (genetic, phenotypic), between species, and of ecosystems (habitats, productivity, processes). Most commonly used to describe variation between species.
- Biogenic habitat** Physical habitat created by living organisms, such as coral reefs, oyster beds, tubeworm reefs, kelp beds, seagrass beds.
- Biogeographic boundary** The area across which species composition changes more rapidly than within a biogeographic region. Not to be confused with habitat boundaries and ecotones.
- Bioherm** Mound-shaped deposits of rock and sediment produced by marine organisms. Coral reefs and *Halimeda* banks are well-known examples.
- Biomass** The mass of organisms in a sample measured as weight.
- Biome** A large geographic area dominated by a plant life-form that provides physical habitat for other species. Used on land for deciduous forests, tundra, grasslands. Comparable marine biomes are seagrass beds, kelp and mangrove forests, and coral reefs with symbiotic algae.
- Bioregionalisation** A spatial representation depicting the boundaries of hierarchical geographic areas considered useful for environmental management.
- Biota** All living organisms, including fauna and flora, within a defined area.
- Biotone** A zone of transition between core provinces used in an Australian bioregionalisation scheme. Biotones are not simply "fuzzy" boundaries but represent unique transition zones between the core provinces.
- Biotope** A habitat with a characteristic community. Also called facies.
- Boulder** Sediment grains >256 mm diameter.
- Boundary-layer currents** Currents at the sediment-water interface.
- Brackish** Neither freshwater nor full-salinity seawater. Typically with 1–20 ppt salinity. See "Estuarine."
- Burrowing** Organisms that burrow in the substratum, be it sediments or rocks.
- Canyon** A relatively narrow, deep depression with steep sides, the bottom of which generally has a continuous slope, developed characteristically on some continental slopes.
- Cay** A small, low elevation sandy island formed on the surface of a coral reef.
- Channel** A narrow sea area, often with strong currents, between island and mainland, between two major islands, or created by currents in seafloor sediment (e.g., deep-sea channel).
- Chemoautotroph** Organisms that create energy from chemical reactions, as distinct from phototrophs which use sunlight.
- Circalittoral** Seabed on the Continental Shelf dominated by animals, where benthic algae are rare or absent. It is usually seasonally stratified, and the effect of wave action is limited to storms. Typically considered between 50 and 200 m depth range.
- Clay** Particles of between 0.00024 and 0.0039 mm in size, or all particles <0.004 mm in diameter. Smaller than silt. In contrast to silt, clay has colloidal properties (i.e., particles unlikely to settle when floating in a liquid). Mud is comprised of clay and silt.
- Cline** A geographic gradient in some variable, such as a species attribute (e.g., color).
- Cobble** Sediment grains 64–256 mm in diameter.
- Cold seep** Area of seafloor where gases and fluids are released but not hot water (hydrothermal vent).
- Colonial** Animals that live as a part of one physically connected colony, such as corals, bryozoans and some tubeworms and tunicates.
- Colonization** Process of organisms establishing themselves in an environment where they were not already present.

Commensal Organisms of different species that live together, sharing space or food, whereby at least one partner benefits from the association and neither have detrimental effects on the other (i.e., not parasitic).

Community A group of species that are assumed to be interdependent (though this is often not demonstrated). The term can be used in a variety of hierarchies. Communities at larger scales can be progressively subdivided, such as spatially, taxonomically and trophically, to finer scales.

Competitive exclusion One species excludes another due to being a superior competitor for a resource.

Competitive release The absence of a competitor allows a species to increase in abundance and/or distribution.

Continental margin The submerged prolongation of continental landmass consisting of the seabed and subsoil of the continental shelf, slope and rise but not the deep ocean floor.

Continental rise A gentle slope rising from the oceanic depths toward the foot of a continental slope of between 1 and 2 degrees slope.

Continental shelf Seafloor that is the submerged part of a continent, extending from the low water line to a depth at which there is usually a marked increase of slope toward oceanic depths; often generalized to about 200 m depth.

Continental slope Surface dipping seaward from the continental shelf edge typically with a slope of >2 degrees and extending to the upper limit of the continental rise, or the point where there is a general decrease in steepness.

Convection The vertical movement of water as part of its stirring caused by differences in density.

Coral reef platform The flat or nearly flat area of considerable extent, dropping off abruptly on one or more sides, extending around a coral reef in the photic sea surface waters and composed of live and/or dead coral reef.

Coral reef (see also "Reef") Reefs developed through biotic processes dominated by corals. In geology, sedimentary features, comprised of macroscopic skeletal framework, built by the interaction of organisms and their environment, that have synoptic relief and whose biotic composition differs from that found on and beneath the surrounding sea floor.

Corridor Narrow geographic areas considered to facilitate the dispersal of species from one area to another across an otherwise unsuitable environment.

Deep In oceanography, an obsolete term which was generally restricted to depths greater than 6000 m.

Delta Seaward prograding sediment body deposited at the mouth of a river.

Demersal A species living on or near the seabed. Commonly used for near-seabed living fish.

Deposit feeding Animals that feed on sediments and other material deposited on the seabed.

Digital terrain model (DTM) Also digital elevation model (DEM). A three-dimensional grid representation of the shape of the earth (seafloor or land) surface.

Diversity Biological or ecological diversity is most commonly measured as the number of species, also called species richness. Many other indices of diversity include the relative abundance of species as well as species richness in their calculation. These indices may emphasize the dominance or evenness of the abundance of species in a sample. See Alpha, beta, gamma diversity, and biodiversity.

Dominant species A species that dominates a sample or area by virtue of its abundance, biomass, size, or conspicuousness.

Downwelling The process by which surface waters sink to greater depths in the ocean. Important mechanisms are cooling of surface waters and/or addition of salt through the production of sea ice in polar seas.

Dune Sedimentary bedforms larger than ripples, greater than 0.6 m in wavelength and greater than around 10 cm in height. Dunes are mostly asymmetrical in profile, with a gentle upcurrent stoss slope and a steeper down-current lee slope which may be at the angle of repose of the sediment. Dune crestlines may be either linear (two-dimensional) or nonlinear (three-dimensional, barchan-shape) in plain view. Large dunes may have smaller dunes superimposed upon them (see also "Sand waves").

Dysphotic zone The part of the water column, below the euphotic zone, that receives low levels of sunlight but insufficient to support plant growth; see also "Mesopelagic."

Ecosystem The combination of species, their interactions, and the physical and chemical processes in their environment in a defined area.

Ecotone A transition zone between two ecologically distinct areas such as habitats, biotopes or ecosystems.

Encrusting Form of growth of animals and plants with a tough or hard texture (the crust), over rocks, and other materials.

Endemic Species only known to occur at one location or area of defined extent, such as a country or sea area.

Epibenthos The collection of organisms living upon the seabed, including animals (epifauna) and plants (epiflora) living on the surface of the seabed or on other animals and plants that live there.

Epibiota Animals, plants and microbes living on the seabed.

Epipelagic The collection of organisms living in well-lit (euphotic) surface waters of the open ocean; above the mesopelagic.

Errant Animals that can wander, are mobile. As distinct from sessile and sedentary.

Escarpment Elongated and comparatively steep (sometimes vertical) slope separating flat or gently sloping areas at different average depth.

Estuary The seaward portion of a drowned valley system which receives sediment and water from both fluvial and marine sources giving rise to a unique sedimentary regime and areas of variable salinity.

- Eulittoral** The area between the low and high tide marks, and the supralittoral and sublittoral fringe. Also called mediolittoral, tidal flat, and hydrolittoral.
- Euphotic zone** The upper part of the water column that receives sufficient light to allow plant growth.
- Euryhaline** Organisms that can live in a wide range of salinities.
- Eutrophication** The environmental problem of excessive plant growth (e.g., Planktonic or benthic alga) leading to oxygen fluctuations (hypoxia, anoxia, and supersaturation), and where dead and rotting plants create a public nuisance. Typically results from the release of nutrients from human activities.
- Evenness** Also called equitability, refers to how the abundance of species is distributed in a sample or group of samples. If all species have equal abundance then evenness is maximized. The inverse of evenness is dominance.
- Extinction** The disappearance of a species from Earth.
- Extirpation** The disappearance of a species from a defined geographic area.
- Fan** Relatively smooth, fan-like, depositional feature normally sloping away from the outer termination of a canyon or canyon system.
- Fauna** Animals; covering both invertebrates and vertebrates.
- Fetch** The unobstructed distance of ocean over which wind has blown to create observed surface waves.
- Fines** Small particles such as sand and silt.
- Fjord** A long, narrow, deep inlet of the sea between steep slopes, formed by glacial erosion. Sometimes spelt "fiord."
- Floodplain** A strip of relatively flat and normally dry land alongside a stream, river, or lake that is covered by water during a flood.
- Food web** A term used to describe the food relationships between members of a community.
- Founder effects** The consequence of founding parents genes for their progeny. With only a few founders, the species may be considered to have gone through a genetic "bottleneck."
- Fragmentation** The breakup of an area of habitat such that what was one population of a species is now several disconnected populations which may consequently be at greater risk of extirpation.
- Frequency range (Hz)** The wavelength of sound measured in cycles (wavelengths) per second; one Hertz (Hz) is a sound wave that travels at one cycle per second.
- Front** In oceanography, a vertical hydrographic boundary between two water masses which are distinguished by their temperature, salinity, and/or productivity.
- Gamma-diversity** The total number of species in a large geographic area. See Alpha- and beta-diversity.
- Gene flow** Exchange of genes within a population or between populations that reduces genetic diversity.
- Genetic drift** Accumulation of random mutations of alleles over time with a consequent change in genetic make-up.
- Geodiversity** The natural range (diversity) of geological (rocks, minerals, and fossils), geomorphological (landforms and processes), and soil (sediment) features. It includes their assemblages, relationships, properties, interpretations, and systems.
- Geophysical anomaly** An abrupt change in the geophysical features of the seabed, potentially associated with wrecks and archaeological sites.
- Geophysics** The study of the physics of the earth. Geophysical survey techniques use physical properties themselves (e.g., magnetism) or apply properties to see how the earth affects them (e.g., radar), to determine something about the earth's structure.
- Glacial outwash** Deposits of material washed out from glaciers by rivers.
- Glaciation** The formation, movement, and recession of glaciers.
- Granulometry** Determination of particle size composition of sediments.
- Gravel** Sediment grains 2–4 mm in diameter.
- Gregarious** The behavior of animals that live in groups, but can survive singly.
- Groynes** Breakwaters used to reduce the rate of transport of beach deposits.
- Guild** An association or classification for a group of species, often not taxonomically related, that share or use a resource in a similar way (e.g., sediment living macrofauna, gelatinous zooplankton), or live in the same part of the environment (e.g., plankton, benthos).
- Gullies** Narrow channels of one to tens of meters in width, created by moving water.
- Guyot** Seamount having a comparatively smooth flat top formed by wave erosion, coral reef growth, or aerial erosion and subsequent subsidence below the sea level.
- Habitat** The environment where an individual, species or group of species live that can be repeatedly found in nature.
- Hadal** Pertaining to depths of the ocean greater than 6000 m.
- Hadopelagic** Open water habitat of the hadal region. Below the abyssal.
- Harbor** Inlet with a port facility.
- Haul-out site** A site where seals come onto the shore or sandbanks.
- Hole** Local circular depression, often steep-sided, of the seafloor.
- Holocene** Epoch of geologic time spanning the last 11,700 years from the end of the Pleistocene Epoch (and the end of the last ice age) to the present.
- Hydrocarbon seep** Feature of the seafloor where hydrocarbons are being released through the seabed sediments.

Hydrodynamic processes Processes associated with waves, tides, and currents.

Hydrothermal vent A hot water spring on the ocean floor.

Hyperbenthos Animals that live close to the seabed but are not usually on it (i.e., epibenthos, epifauna) or in it (i.e., endobenthos, infauna). Typically used for crustaceans but in theory could include other taxa. The term demersal is used for fish.

Immigration The arrival of organisms to a place, which may result in their establishment (colonization).

Infauna Animals living within sediments.

Infralittoral Always submerged, below the low-tide within the euphotic zone. Seabed often dominated by algae, with variable water column temperatures.

Inlet Semi-enclosed area of the coast. Related terms include sea lough (Ireland), sealoch (Scotland), fjord, fiard, ria, voe.

Inquiline Animals that live within other organisms but are not considered parasitic. Similar to commensal ("living with") but usually used where the relationship has yet to be determined.

Inshore Generally within 5 km of the coastline and <50 m depth. Same as coastal seas. In the United Kingdom, the term "Inshore" applies specifically to the area within 6 nm of the coast where marine activities are managed at a local or regional scale.

Interstitial Organisms living in the space between grains of sediments. See also "Meiofauna."

Intertidal zone The area between the high-water mark and low-water mark that is submerged at high tide and exposed at low tide. Often used synonymously with seashore.

Island Land surrounded by water.

Island biogeographic theory Holds that the number of species in a location is a result of the interaction between the number colonizing and going extinct, such that islands that are larger and near a mainland source for colonist will have more species than smaller and more remote or isolated islands. This balance between colonization and extinction is also termed "Species equilibrium theory."

Knoll Relatively small (500–1000 m tall) isolated elevation of a rounded shape; a small seamount. Larger than a sea-hill.

Knot A speed of one nautical mile (nm) per hour.

Lagoon A shallow marine (sometimes brackish to hypersaline) coastal water body, receiving little—if any—fluvial input, separated from the sea by a restricted inlet usually having a sill.

Landform Geomorphological feature.

Latitudinal gradients Changes in the number (richness) of species with latitude.

Littoral drift The net movement of material along the shore under the influence of prevailing waves and currents.

Littoral Between upper and lower tidemarks, exposed to air at the lowest tides. In marine ecology is equivalent to intertidal and seashore. In wider literature may refer to coastal land and subtidal areas down to 200 m.

Macro-ecology Ecological patterns across geographic areas.

Macrofauna Fauna typically retained on a 1 mm sieve, visible but not usually identifiable to species level by eye.

Magnetometer Also known as a fluxgate gradiometer. A remote sensing instrument capable of identifying subsurface archaeological features by measuring the difference in their magnetic properties against the surrounding soils.

Managed retreat Areas where the sea is allowed to inundate sites formerly protected by sea defenses.

Marine protected area (MPA) Defined by the IUCN as "any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment." See IUCN for updates.

Megafauna Large animals easily identified by eye without magnification; e.g., Mammals, birds, fish, sharks, turtles, lobsters, starfish. Larger than macrofauna.

Meiofauna Fauna retained on a 0.1 mm sieve but that pass through a 1 mm sieve. Smaller than macrofauna.

Mesolithic Middle stone age period ("middle stone age").

Mesopelagic Referring to the poorly lit open water habitat below the epipelagic (euphotic) and above the bathypelagic. Also called the twilight zone.

Metapopulation A population that exists in a connected complex of spatially discrete populations, such as in habitat fragments.

Microfauna Bacteria and small unicellular organisms not visible to the naked eye or retained on standard sieves.

Mid-domain effect The proposition that the environment constrains species ranges such that more ranges will overlap in the tropics, and thus more species will occur there.

Mitigation Measures to minimize, reduce or eliminate impacts.

Mud Sediment grains <0.063 mm diameter. Includes silt and clay.

Multibeam data Bathymetric and backscattered data derived from multibeam echo sounder.

Narrows Narrow channels of water forming the entrance to inlets, often with shallow sills and called Rapids.

Neap tide The minimum amplitude of the astronomical tide (every 14 days between the full and new moon).

Nekton An aquatic organism, such as whales, turtles, fish, squid, and krill (euphausiids) that can swim powerfully enough to move against currents.

Neolithic Later stone age period ("new stone age").

Neritic Pertaining to the water column overlying the continental shelf.

Net transport The residual movement of sediment after its oscillatory movement on tidal currents, or under the influence of waves.

Neuston The collection of organisms living on the sea surface (epineuston) or within the top 20 cm of the surface (hyponeuston).

Niche The range of environmental conditions (such as temperature, salinity, nutrients) within which a species can exist and reproduce. Sometimes defined as everything a species is or does. The preferred (or fundamental) niche is the one in which the species performs best in the absence of competition or interference from extraneous factors.

Noise Defined as unwanted sound and is usually measured in decibels (dB) referenced to an acoustic source frequency dB(A).

Nursery ground An area of importance for juvenile animals and plants.

Oceanic Referring to the open ocean, away from coastal waters.

Offshore Open ocean distant from land, typically with stable water column characteristics (stenothermal, stenohaline), permanently stratified, beyond freshwater influence, without benthic algae. Generally >5 km from the coastline.

Omnivore An animal that eats both animal and plant food.

Open coast Any part of coast not an island or inlet.

Overburden Sediment (often sand) deposited on top of local sediments OR deposits of soil and rock that are removed to gain access to ore deposits at open cast mines.

Overfalls Areas of rough water (relatively higher surface waves) generated by sudden changes in seabed topography, such as sandbanks and deeps.

Oxygen minimum zone Area of the ocean with seasonal or permanently low oxygen conditions.

Palaeolithic Earlier stone age period ("old stone age").

Palimpsest Sediment that exhibits attributes of a previous depositional environment, but also attributes of the modern environment.

Parasitic Organisms that feed on a host but do not normally lead to its death.

Parthenogenic Female animals that can produce fertile eggs without fertilization from sperm.

Pebble Sediment grains 4–64 mm diameter based on the Cailleux and Wentworth classification.

Pelagic Organisms, relating to or living in the water column of seas and oceans (as distinct from benthic). Includes nekton and plankton.

Phanerogam meadow Extended or patchy areas of seagrass in the Mediterranean Sea colonized by *Posidonia oceanica* (L.), and/or *Cymodocea nodosa* (Ucria). In other areas formed by the seagrasses *Posidonia*, *Zostera*, or related species.

Phototrophic Organisms (chemoautotrophs) that generate energy using sunlight. See "Chemoautotroph."

Physiognomy The apparent characteristics, outward features, or appearance of ecological communities often characterized by dominant species.

Physiography The physical geography of the land and seabed. See "Terrain," "Topography."

Phytoplankton Microscopic free-floating plants that drift in sunlit surface waters.

Pinnacle High tower or spire-shaped pillar of rock or coral, alone or cresting a summit. It may extend above the surface of the water. It may or may not be a hazard to surface navigation.

Plankton The collection of organisms, often microscopic, that are suspended freely in the water column.

Plateau Flat or nearly flat area of considerable extent, dropping off abruptly on one or more sides.

Pleistocene Epoch of geologic time during the Quaternary period extending from the end of Pliocene epoch around 2.6 million years ago up to the beginning of the Holocene epoch, 11,700 years ago.

Pleuston The collection of organisms that live on the ocean surface.

Pockmarks Small (1–10's m) circular depressions in the seafloor caused by the release of a gas or liquid (e.g., hydrocarbon seeps).

Polynya From the Russian word for "lake," an area of open water surrounded by sea ice.

Primary production Production of organic matter by converting light or chemical energy from primary materials, such as photosynthesis and chemosynthesis.

Progradation Reworking of the sediment by waves and currents toward deeper ocean due to sea level fall.

Quaternary Period of geologic time extending from the end of Pliocene epoch around 2.6 million years ago up to the present; a collective term for the Holocene and Pleistocene epochs.

Rapoport's rule The proposition that species geographic ranges increase with latitude and elevation (and perhaps depth), and thus there are more species in the tropics.

Realm A biogeographic region defined by an assemblage of species distinct from other regions, with characteristic endemic (geographically rare or localized) species. Distinct from habitat which is characterized by its dominant species (often common species), and biome (see above).

Recolonization The reestablishment of marine populations in an area from which they had been lost.

Recruitment The influx of new members into a population by either reproduction or immigration.

Reef ridge Long, narrow elevation with steep sides composed of live or dead coral.

Reef(s) Hard substrata raised from the seabed that provide a substratum and/or cover for marine life. May be formed by rocks, coral, shells, tube-worms, and other organisms. Also, used in hydrography to refer to hard substrata that may be a hazard to safe navigation.

Relaxation effect The consequence of habitat fragmentation that splits populations such that some are extirpated, and thus the species richness declines following fragmentation. Island Biogeographic Theory predicts a loss of species richness due to a decreased habitat area.

Relaxation time The time required for species and populations to adjust to changed environmental conditions.

Relict Sediments that were originally deposited under different environmental conditions than those occurring today. See also "palimpsest." The term is also used for relict populations of a species "trapped" in an environment that is a refuge of former more widespread environmental conditions that allowed the species a wider distribution range.

Relief The variation in the elevation (or depth) of the seafloor.

Ridge (A) Long, narrow elevation with steep sides. (B) Long, narrow elevation often separating ocean basins. (C) Linked major mid-oceanic mountain systems of global extent.

Ripple Sedimentary bedforms smaller than dunes (see "Dune").

Rock Ecologically is a "hard substratum" with an epibiota but where infauna is absent or rare.

Rough ground Areas of seabed where there are boulders or biogenic reefs.

Rugosity The roughness or irregular texture of the seabed.

Saddle Broad pass, resembling in shape a riding saddle, on a ridge or between contiguous seamounts.

Sand dunes See "Dune."

Sand waves Replaced by the term "dune" in modern usage. Undersea "sand dunes" that may be static or move under the influence of waves and tides and are subperpendicular to the current.

Sand Sediment grains 0.063–2 mm diameter.

Scavenger Animals that feed on dead animal material, and sometimes also drift algae.

Sea-hill A seabed feature elevated more than 100 m from the surrounding seabed. Smaller than a knoll and seamount.

Seamount An underwater mountain greater than 1000 m in relief above the sea floor, characteristically of volcanic origin and conical form.

Seascapes Undersea landscapes. Topographic features that reoccur geographically (e.g., seamounts, estuaries, canyons, and plains).

Sedentary Animals that do not normally move, but can if required (e.g., sea anemones, mussels).

Sediment Ecologically are so-called "soft substrata" with infauna, and usually some epibiota.

Sediment processes Processes that affect the creation, erosion, transport and deposition of sediments.

Sediment sink A site where there is a net accumulation of sediment.

Sediment transport Movement of sediment in the water column or on the seabed.

Seismic data Acoustic data derived from a low frequency (less than 12 kHz) seismic sound source, typically using compressed air or electric pulses, that produce an image of sediment layers comprising the seabed.

Seismic waves Pressure waves generated by volcanic eruptions, earthquakes or explosions that propagate through the earth's crust; waves that are detected and recorded by seismographs.

Sessile Animals attached to the substratum.

Shoal Offshore hazard to surface navigation that is composed of unconsolidated material such as gravel or shell.

Side scan sonar An acoustic remote-sensing method of identifying seabed features using a sonar two-fish that emits sound waves at a low angle of incidence to the seabed.

Sill Seafloor barrier of relatively shallow depth restricting water movement between adjacent basins. In oceanography, the sill depth signifies the depth of water that a water mass must achieve in order to pass between basins.

Silt Particles of between 0.0039 and 0.0625 mm in diameter. Larger than clay, smaller than sand. Mud is comprised of clay and silt.

Sonar Derived from the phrase "sound navigation and ranging"; method or equipment for determining the water depth by underwater sound (echolocation).

Sound A deep embayment located between offshore islands and the mainland or between islands.

Speciation Process of a species being formed from other species.

Species richness The number of species that occurs in an area or collection of samples.

Species saturation The idea from Island Biogeography Theory that the number of species in an area has a maximum determined by the rate of local colonization and extinction; such that if a new species becomes established then an existing species will go extinct.

Species turnover The change in species composition over time and/or space. See "Beta-diversity."

Splash or spray zone Area of upper seashore not submerged at high tide but sprayed at high tide by breaking waves.

Spring tide The maximum amplitude of the astronomical tide (every 14 days corresponding with the new and full moon)

Stenohaline Organisms limited to a narrow range of salinities. The opposite of euryhaline.

Stepping stones Small areas of habitat that enable a species to disperse across otherwise unsuitable environment.

Storm surge A major rise in sea level above the normal range due to episodic events such as low atmospheric pressure and high winds.

Strait A channel or gap between an island and the mainland, or two headlands.

Strandline Area of upper seashore where loose seaweed and other floating debris is deposited by the falling tide.

Stratified In water, where one or more horizontally extended water masses lie on top of each other. They are separated by boundaries based on differences in temperature (thermocline), density (pycnocline), and/or salinity (halocline). See also "Front."

Subduction zone Adjacent to active plate margins, a place where ocean crust collides with and is subducted beneath continental crust or another ocean to create a ridge and ocean trench complex.

Sublittoral Below the littoral, never exposed to air. Same as subtidal. Includes the infra- and circa-littoral.

Sublittoral fringe Transition zone where littoral and sublittoral species occur, sometimes determined by differences in neap and spring low tides.

Substrate A substance used as a food source by organisms or enzymes. This usage has been extended to any surface a plant or animal lives upon, whether biotic or abiotic materials. Ecological use favors use of substratum (singular) and substrata (plural) where the surface is for attachment rather than a food source.

Substratum(a) Surface (singular) to which an organism grows on or amongst. Substrata is plural.

Supralittoral Uppermost part of shore affected by wave splash but not regularly submerged by the sea. Also called the supratidal, epilittoral, splashzone, spray zone, littoral fringe, and strandline.

Surrogate A measurable entity that is used to represent, or substitutes for, a more complex element of biodiversity that is more difficult to measure.

Suspension feeding Animals that feed on water-borne particulate material, which may include plankton.

Swale A low lying marshy area, such as between sand dunes.

Symbiotic Organisms that both benefit from their association.

Sympatric speciation Species that evolve within the same geographic area, perhaps due to specialization on different food resources or seasonal differences in growth or reproduction.

Taxon (Taxa) A distinct category of organism at any level in the taxonomic hierarchy from species to family to kingdom. Taxa is plural.

Terrace Relatively flat horizontal or gently inclined surface, sometimes long and narrow, which is bounded by a steeper ascending slope on one side and by a steeper descending slope on the opposite side.

Terrain The physical land surface and seabed.

Terrigenous Derived from the land, as in terrigenous sediment. Usually siliciclastic rather than calcareous or calciclastic.

Tidal range The amplitude of the tides in a particular area due to astronomical (gravitational forces of the sun and moon) forcing.

Topography The form, relief, shape and texture of the earth's surface, including the seabed.

Trench Long, narrow, characteristically "V"-shaped in section, very deep and asymmetrical depression of the sea floor, with relatively steep sides.

Trophic level The position of an organism in the food chain or "food pyramid," determined by the number of transfers of energy that occur between the non-living energy source and that level.

Trough Long depression of the sea floor characteristically flat bottomed and steep sided and normally shallower than a trench.

Tsunami A very fast moving oceanic wave, initiated by an underwater disturbance, such as an earthquake, volcanic eruption or slumping (Japanese for "harbor wave").

Tubicolous Animals that live in tubes.

Turbidity current A dense mixture of suspended sediment and water that flows downslope under the influence of gravity. Normally constrained to the continental slope and attributed to the formation of submarine canyons.

Upwelling An oceanographic process by which water rises from the lower depths upwards into shallow surface waters.

Vagile Animals that move around.

Vagrant Animals outside of their normal habitat or environment. They may be searching for new habitats or mates.

Valley Relatively shallow, wide depression, the bottom of which usually has a continuous gradient. This term is generally not used for features that have canyon-like characteristics for a significant portion of their extent.

Vicariance The geographic separation of a population or biota by climatic and/or geological events, typically resulting in the formation of new species.

Water mass A volume of water that has defined salinity and/or temperature characteristics.

Wave refraction Modification of the angle of waves by seabed features.

Wave rose A method of showing the size and direction of waves based on the frequency of occurrence in different quadrants of the compass.

Winnowing Removal of fine material from coarse ones by winds or currents.

Zones Horizontal areas of vertical height above, and depth below, sea level which has a characteristic fauna and flora. Also called étage.

Zooplankton Planktonic animals; i.e., Animals that live in the plankton and which are unable to move against regional currents.

Abstract

The natural sciences are rich in concepts. The usage of the terminology to name these concepts may change over time and due to mistaken or extended use of terms. Some are adopted from a particular vernacular language where the word may have a different meaning than its use in science (e.g., endemic) and some scientific terms may become used in wider society (e.g., ecosystems). Alternative meanings of the same words can cause confusion, especially among students and nonspecialists not familiar with the nuances of usage. It is thus useful to provide a glossary of how a community defines its terminology at the present time. Here we provide definitions of about 300 terms commonly used in marine ecology, oceanography and geology.

Introduction

The natural sciences are rich in concepts. The usage of the terminology to name these concepts may change over time and due to mistaken or extended use of terms. Some are adopted from a particular vernacular language where the word may have a different meaning than its use in science (e.g., endemic) and some scientific terms may become used in wider society (e.g., ecosystems). Alternative meanings of the same words can cause confusion, especially among students and nonspecialists not familiar with the nuances of usage. It is thus useful to provide a glossary of how a community defines its terminology at the present time. This glossary was developed as a collaboration between the scientists of the GEOHAB (Marine Geological and Biological Habitat Mapping) and WoRMS (World Register of Marine Species) communities. It was published online on WoRMS from 2010 and comments by users led to additions and corrections.

The glossary does not intend to provide a review or history of all uses of particular terms, nor how they may be used in other fields of research. The definitions are those recommended for use in marine biology, ecology, oceanography, and geology. The glossary excludes terminology specific to the following areas: names of marine species and higher taxa (see WoRMS); place names (see gazetteers at MarineRegions.org and GEBCO); taxonomy; physiology; archaeology; fisheries; legal and regulatory terms; acronyms.

Further Reading

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World Maps of Ocean Environment Variables

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Abstract

Understanding the ocean environment at a global scale has never been so important due to the need to predict the effects of climate change and its consequences for biodiversity, including the ecosystems and species which are influenced by, and in turn alter, their environment. Here we present world maps of long-term (annual and decadal) averages of the following ocean environment variables: seabed depth and slope; sea surface and near seabed temperatures; current velocity and wind speed; wave and tide height; dissolved, saturated and utilized oxygen; effects of water transparency on photosynthetic radiation and depth; phytoplankton productivity and calcite; nutrients; salinity, pH, and suspended particulates; and summer and winter ice cover. We point out some of their key geographic features, correlations between variables, and interrelationships.

Introduction

The ocean, covering 71% of the planet (Costello et al., 2010), plays an important role in regulating the global climate through the interaction of water with the atmosphere. While in the oceanic environment, a number of environmental conditions affect the mobility, growth, survival, and productivity of biological organisms. Among these variables, the depth, availability of light, oxygen, water current, salinity, temperature, and nutrients influence species distributions across the ocean. Moreover, the three-dimensional nature of the oceanic environment makes the environmental conditions vary from location to location both horizontally and vertically (Sayre et al., 2017). Animal life occurs throughout the oceans, from the ice-covered polar regions to hot hydrothermal vents, and deepest trenches (Rothschild and Mancinelli, 2001; Zeppilli et al., 2018). To characterize the ocean environment we need to understand how different environmental parameters interact between each other.

Typically, marine environmental data have been gathered from combinations of observations and modeled values of ocean surface (e.g., wave height), water column (e.g., temperature, salinity, oxygen), seafloor measurements (e.g., depth) (Valavanis et al., 2008), in situ observations (e.g., survey cruise, AUV and Argo floats), and remotely sensed satellite data (e.g., chlorophyll-a, surface temperature) (Costello et al., 2017). In this article, we discuss the environmental characteristics of the world ocean based on an interpretation of selected publicly available global environmental data (Basher et al., 2018).

Statistics

The color gradients on the maps show the relative high and low values of each environmental variable (Figs. 1 and 3–6). The actual average, maximum, minimum and variation are provided in Tables 1 and 2, and positive and negative correlations between them in Table 3. Because the standard deviation and error are dependent on the mean, we also provide the coefficient of variation. It is important to note that these values are dependent on the spatial resolution of the underlying data. The maps are at a spatial resolution of 5 arc minute (about 9.2 km in the equator). Thus, local areas may have more extreme maxima and minima than stated in the Tables. For example, areas with cliffs will have higher slopes, narrow channels higher currents, and enclosed sheltered shallow bays may have higher temperatures.

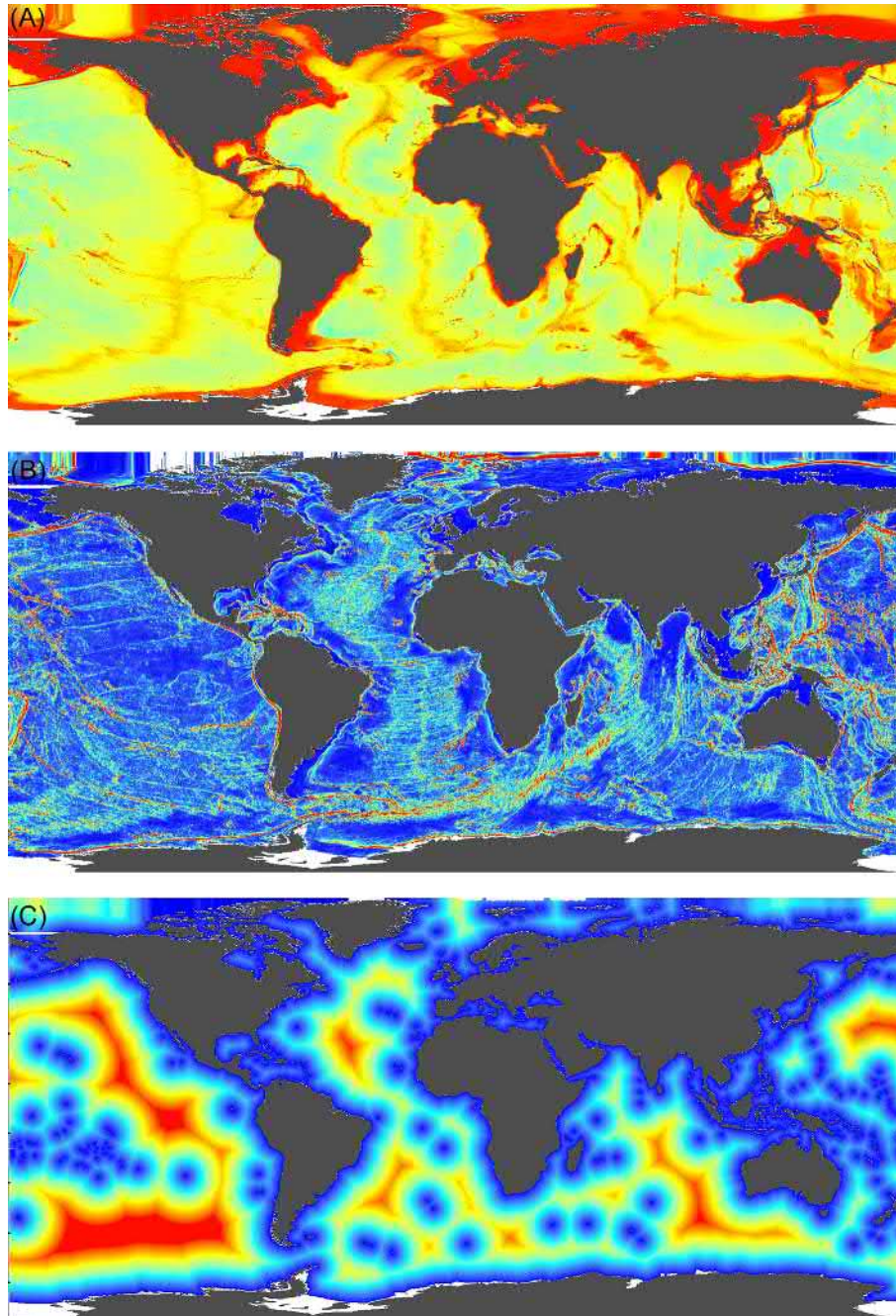


Fig. 1 World maps of (A) bathymetry, (B) slope and (C) distance to land. Color scales from *red to blue* indicate (A) shallow to deep, (B) high to low slope, (C) far to near coast. See **Table 1** for range of values of each variable. Data from Basher, Z., Bowden, D. A. and Costello, M. J. (2018). Global Marine Environment Datasets (GMED). World Wide Web electronic publication. Version 2.0 (Rev.02.2018). Available at <http://gmed.auckland.ac.nz> (Accessed 2 March 2019).

Bathymetry

Depth is one of the most important environmental variables because it correlates with almost all other environmental parameters in the ocean. The deepest depth is 10,294 m (**Table 1**). The northern hemisphere has a larger area of continental shelves, and more ocean close to land compared to the southern hemisphere (**Fig. 1**). Light penetration, temperature, and nutrient availability in the water column decline with depth at any particular point (**Fig. 1, Table 3**). In addition, the variability of environmental variables declines with depth, for example for temperature (**Fig. 2A**) (**Costello et al., 2018**). Most of the ocean is remarkably flat, with a slope of less than one degree (**Table 1**), and areas with relatively high slope indicate the presence of mid-ocean ridges, underwater volcanic

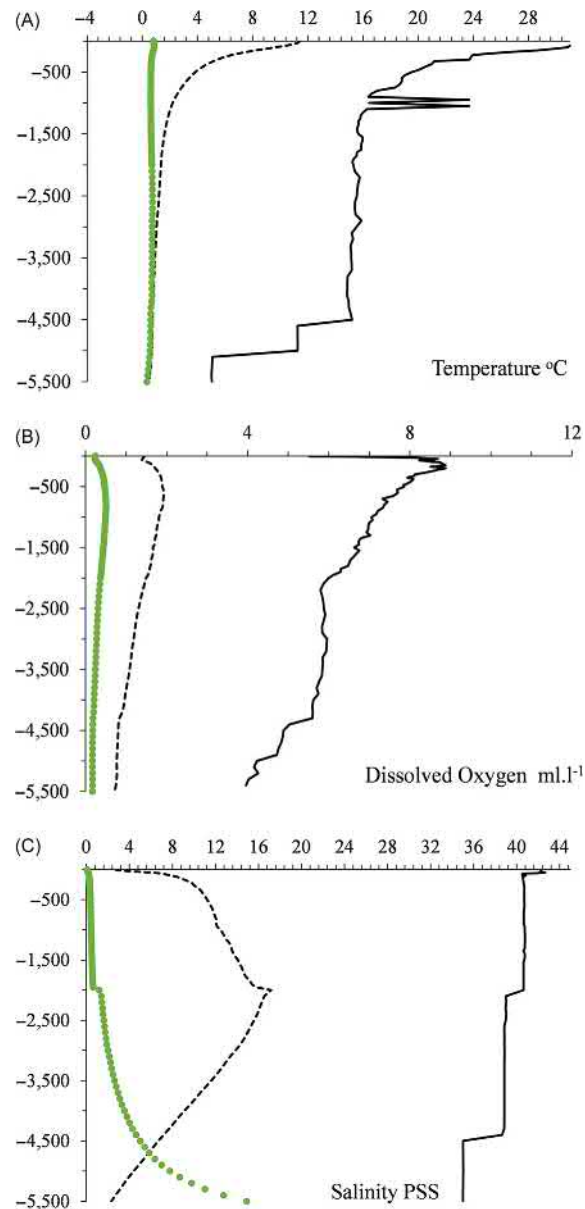


Fig. 2 Depth gradients of (A) temperature, (B) oxygen, and (C) salinity, shown as standard deviation (*dotted line*), coefficient of variation (*green*) and average (*solid line*). Modified from Costello, M. J., Basher, Z., Sayre, R., Breyer, S., and Wright, D. J. (2018). Stratifying Ocean sampling globally and with depth to account for environmental variability. *Scientific Reports* 8(1), 11259.

activity, and seamounts. There are over 1 million sea-hills, and some 70,000 seamounts, that is hills rising over 1 km from the seabed (Costello et al., 2010).

Temperature

The temperature of the ocean depends on the amount of solar energy absorbed by the ocean surface. Through its direct effect on biochemistry and physiology, and indirect effect on environmental conditions, temperature regulates biological processes and diversity in the ocean. Tropical oceans receive a lot of direct sunlight for much of the year, while polar regions only receive sunlight in summer. Tropical temperatures are about 25 °C to 30 °C and polar -2 °C to $+2$ °C. With depth, temperature rapidly drops until about 1000 m and then remains relatively consistent all the way to the seabed (Fig. 2A). Thus, the warmest waters are near the equator and coldest waters are near the poles (Fig. 3), while the deep sea is as dark and cold as a domestic fridge (<4 °C).

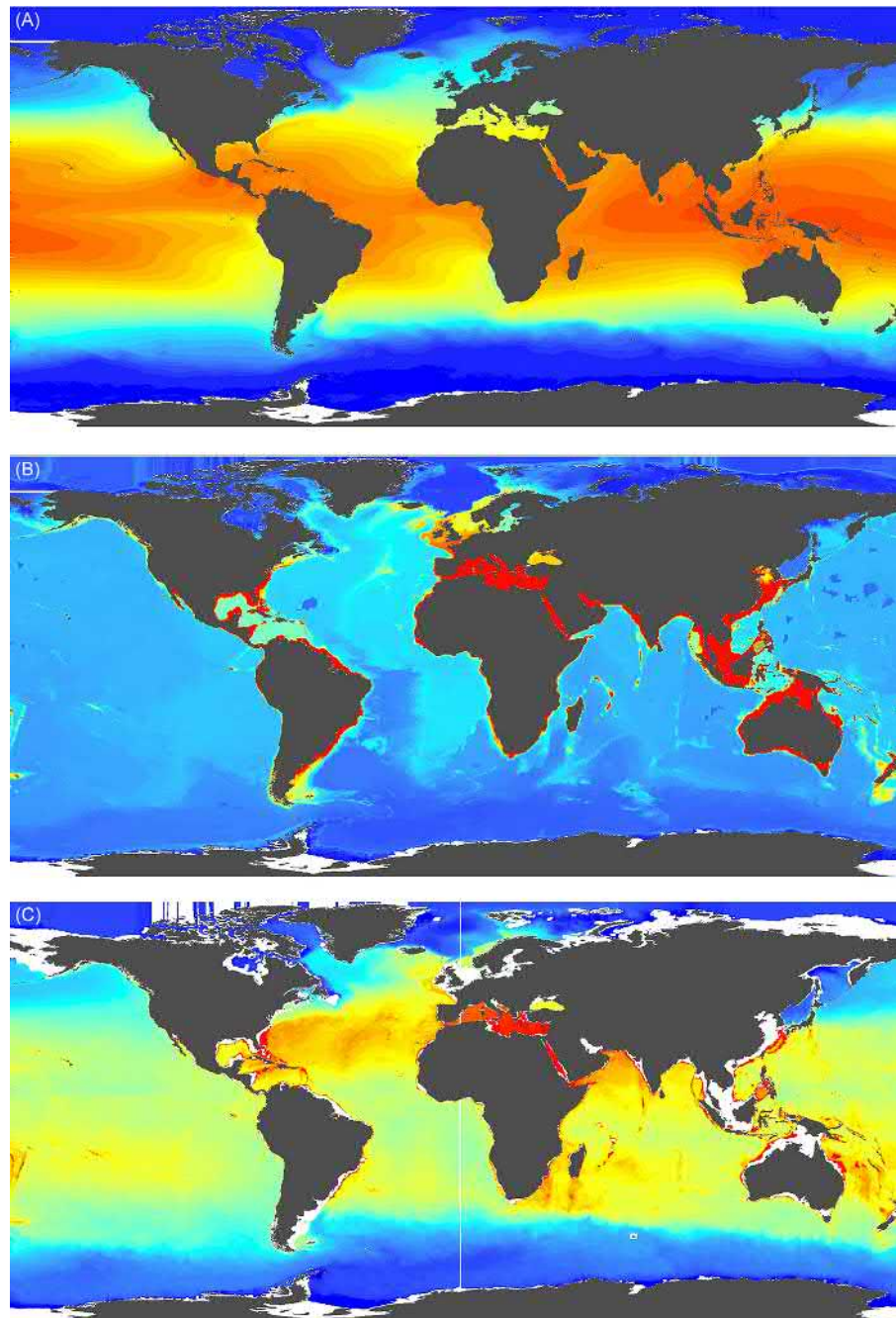


Fig. 3 World maps of long-term average sea temperature at the (A) surface, (B) seabed and (C) water column average (from surface to seabed). Color scale from *red to blue* indicates warm to low temperature. See [Table 1](#) for values of each variable. Data from Basher, Z., Bowden, D. A. and Costello, M. J. (2019). GMED: Global marine environment datasets for environment visualisation and species distribution modelling. *PeerJ* (In Review).

Water movement

Global winds drag on the water's surface ([Fig. 4A](#)). As a result of the Coriolis Effect (due to the Earth's rotation) circulating air and ocean currents are deflected toward the right in the Northern Hemisphere and toward the left in the Southern Hemisphere. The major surface ocean currents deflect in a clockwise spiral in the Northern Hemisphere and anti-clockwise in the Southern Hemisphere. These major spirals of ocean-circling currents are called gyres and occur north and south of the equator.

Currents are largely driven by wind, tides and the global circulation of water ([Fig. 4B](#)). As water is denser than air, it has more momentum and once in sets in motion, it easily keeps flowing. Surface currents of the ocean are driven by global wind systems that

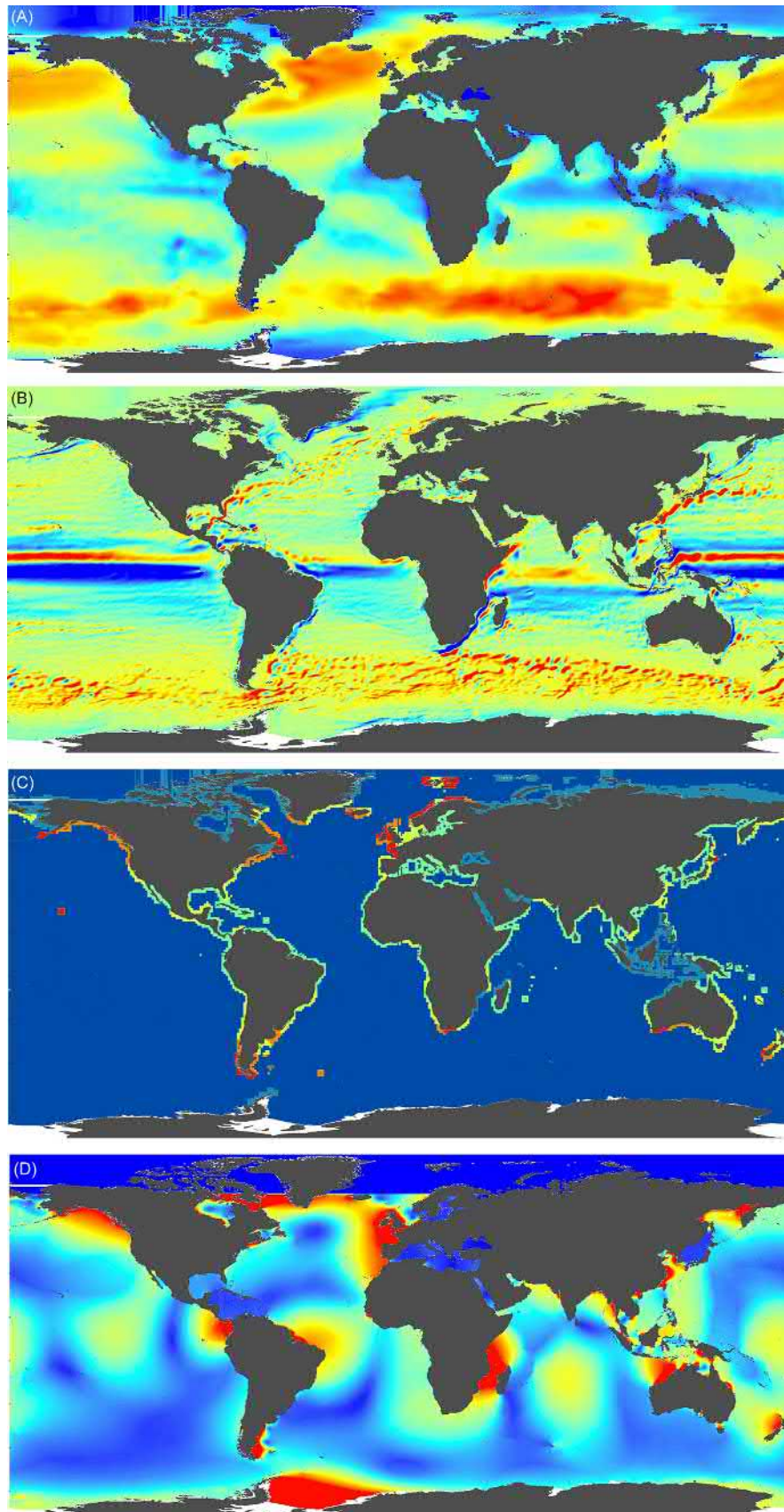


Fig. 4 World map of (A) wind speed, (B) surface currents, (C) wave height, and (D) tide height. Color gradients from red to blue indicate fast and slow for (A) and (B), and high to low for (C) and (D). See [Table 1](#) for range of values of each variable. Data from Basher, Z., Bowden, D. A. and Costello, M. J. (2019). GMED: Global marine environment datasets for environment visualisation and species distribution modelling. *PeerJ* (In Review).

are fueled by the energy from the sun. Currents play an important role in moving water between the poles and the tropics. Currents also move food and nutrients from the coast further out into the sea. Currents flowing along the western side of ocean basins (e.g., Gulf Stream) are typically stronger, deeper, and narrower due to the rotation of the Earth, which piles water along the western edge of land masses, while currents flowing along the eastern side of ocean basins are weaker, wider, and slower. This phenomenon is known as the western intensification of currents (Thurman et al., 2013). These effects can be seen as currents move along the north-west Atlantic and Pacific oceans (Fig. 4B). Long-term positions of major currents in the ocean have changed over millennia due to plate tectonics, climate, and periodic astronomical events such as asteroid impacts. These factors influenced the shape of ocean basins and defined the path and location of modern-day currents.

Unimpeded by land masses, the strongest winds and currents are in the Southern Ocean and known as the Antarctic Circumpolar Current (Fig. 4B) (Rintoul et al., 2001). Strong winds also prevail in the northern latitudes, but are weaker in the Arctic and equatorial latitudes. The equator is bounded by latitudes with very high and low currents. The region where Pacific waters pass through the islands of Papua New Guinea and Indonesia to the Indian Ocean has the highest diversity of marine species in the world, and is part of the Coral Triangle region (Asaad et al., 2018a,b, 2019).

Vertical movements of the ocean include those due to waves and tide. Together with the current, wave action is one of the most significant environmental conditions affecting life in the sea. Waves are higher in coastal waters due to the effect of shallowing depths, and the high waves due to strong winds in the northern and southern latitudes can be seen in Fig. 4C. The impact of waves generally reduces with depth (Fig. 4C). In contrast, tidal movements are a function of the Earth's rotation and currents, and tend to be higher where they are forced by current movements (e.g., north-east Atlantic and Pacific oceans) and are constrained by narrowing land barriers (e.g., seas in the west north Pacific) (Fig. 4D). Tidal height is highest on the eastern northern hemisphere oceans (Fig. 4D).

Oxygen

Dissolved oxygen in seawater is absorbed from the atmosphere and is a byproduct of photosynthesis. As a result, most oxygen-rich water is found near the surface in the sunlit (also called the photic and epipelagic) zone, which where all plants and most marine organisms live (Costello and Chaudhary, 2017). Dissolved oxygen has a strong relationship with temperature (Garcia et al., 2005; Table 3), which is reflected in polar oceans having high concentrations of dissolved oxygen compared to the tropics (Fig. 5A). Below the photic zone there is no photosynthesis or absorption from air, and the respiration of animals and microbes consumes oxygen. Thus, oxygen declines with depth (Table 3, Fig. 2B), and large areas of deep water in the eastern Pacific and Indo-Pacific region are low in oxygen (i.e., hypoxic) (Fig. 5C). The near seabed hypoxic regions have high "utilized oxygen" (Fig. 5D), mirroring the areas of low oxygen.

The high phytoplankton productivity of the Arctic results in high oxygen saturation, and the relatively high consumption of oxygen in the warm tropics leads to lower saturation (Fig. 5C).

Light Transparency

The euphotic depth is where the amount of light (irradiation) sufficient for photosynthesis, called photosynthetically active radiation (PAR), is 1% of its surface value (Morel and Berthon, 1989). This depth is measured by satellite as a function of water clarity, and thus its depth depends on the concentration of particles suspended in the water column (Table 3). These particles are highest near the coast (Fig. 6A). Phytoplankton biomass tends to be lower in the tropics because growth is nutrient (rather than light) limited, and thus water clarity (or light transparency) and PAR are highest in offshore tropical latitudes (Fig. 6B). Thus, productivity was positively correlated with the salinity, Particulate Organic Carbon (POC), and diffuse attenuation coefficient (DAC) (Fig. 6, Table 3). When more suspended particulate matter is present (i.e., coastal waters), the depth of this photic zone will be shallow, only a few meters. In offshore waters, where coastal landscape influences are negligible and concentrations of plankton are sparse, the photic zone is as deep 142 m (Table 1) (Fig. 6C), but locally may extend to 200 m. Polar regions generally have shallower euphotic depths value due to the presence of sea ice. Furthermore, the nutrients (nitrate, phosphate, and silicate) showed negative correlation with temperature and depth, which may indicate why photosynthetically active radiation (PAR) was greater in warmer waters (Table 3).

Productivity

Plant growth depends not only on sufficient light, but also sufficient macro-nutrients, primarily oxidized nitrogen and phosphorous. Nitrogen is comprised of two oxidized forms, nitrate and nitrite, of which nitrate dominates, and ammonia. Ammonia is highly volatile and rapidly utilized by plants and thus of low concentration in unpolluted seawater. Thus nitrate is the primary indicator of nitrogen available to plants. In contrast to freshwaters where phosphorous limits plant growth, in seawater plant growth is generally nitrogen limited. Thus plant productivity, in this case phytoplankton because the data are derived from satellite observations of changes on ocean color, is highest near the coasts where freshwater runoff (including rivers) contributes nitrogen (Fig. 6D). Upwellings of seawater from deep nutrient rich waters to shallow depths also contribute to productivity. In addition, diatoms, one of the primary groups of phytoplankton, require silica to build their cell walls, and thus silica is essential for their growth.

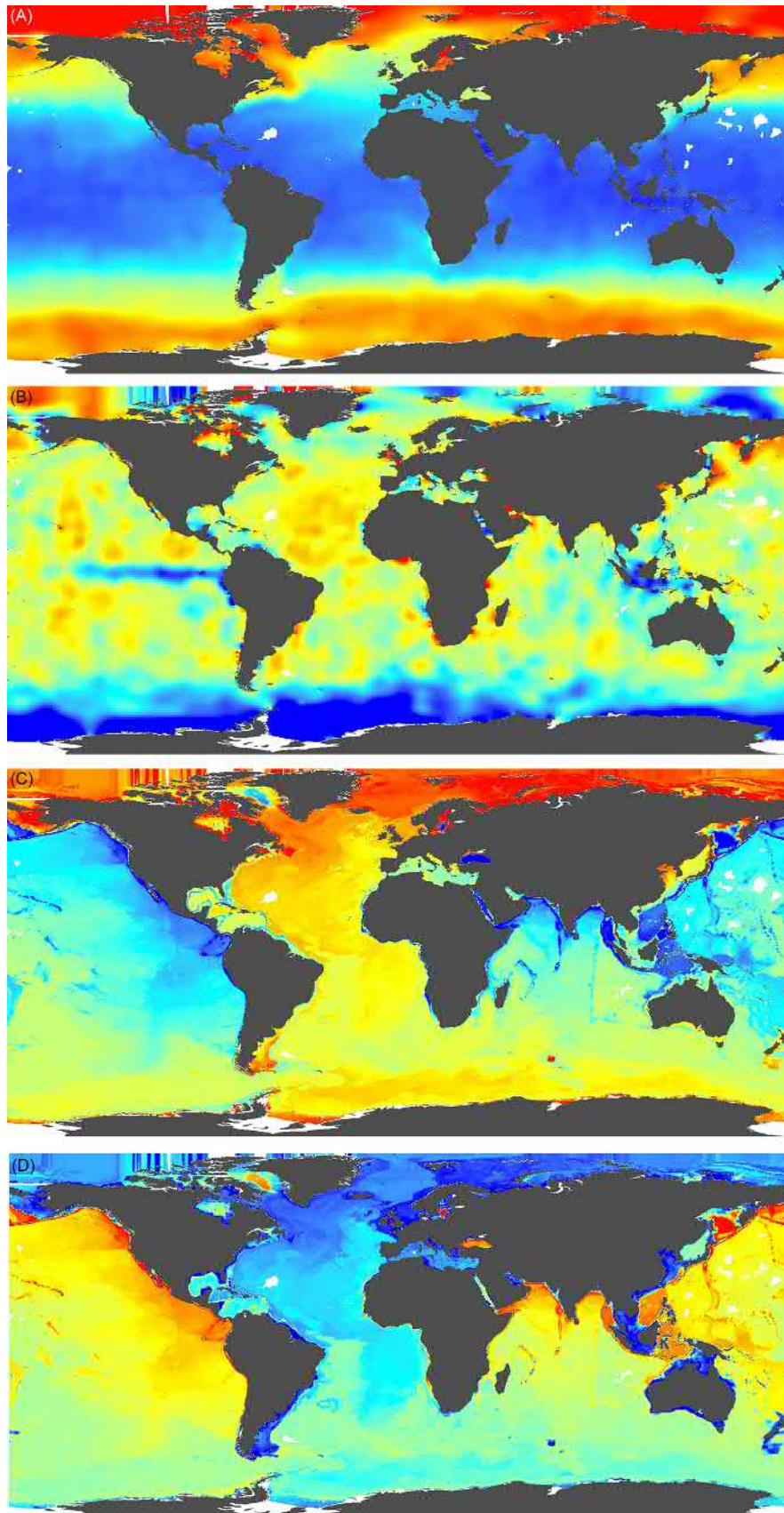


Fig. 5 World maps of oxygen as (A) surface concentration, (B) surface saturation, (C) seabed concentration, and (D) utilized at the seabed. Color gradients from *red* to *blue* indicate more to less. See [Table 1](#) for range of values of each variable. Data from Basher, Z., Bowden, D. A., and Costello, M. J. (2019). GMED: Global marine environment datasets for environment visualisation and species distribution modelling. *PeerJ* (In Review).

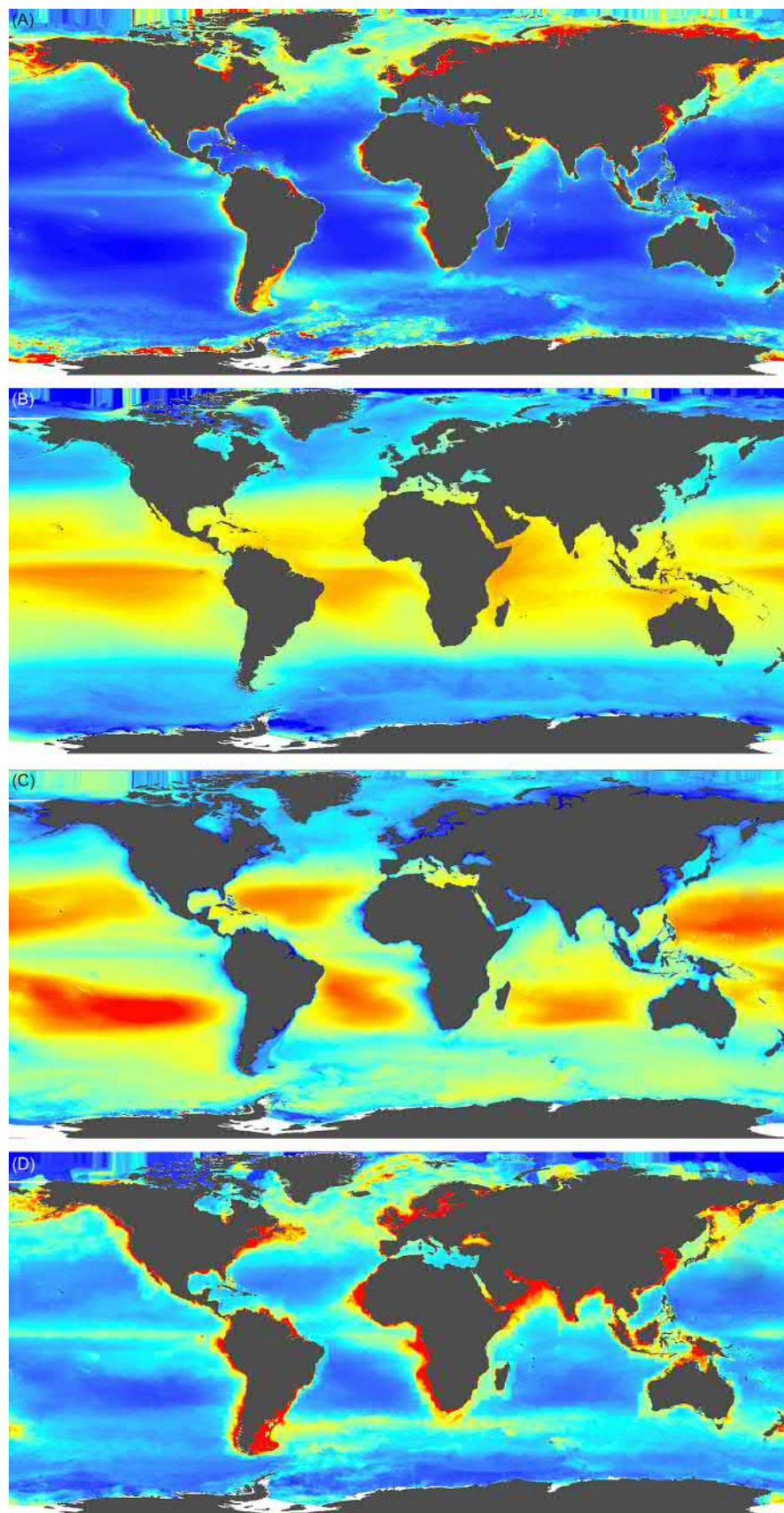


Fig. 6 World maps of the effects of light transparency in the ocean, expressed as the (A) diffuse attenuation coefficient, (B) photosynthetically active radiation, (C) Euphotic layer depth, and (D) phytoplankton productivity. Color gradients of from *red to blue* indicate more to less. See [Table 1](#) for range of values of each variable. Data from Basher, Z., Bowden, D. A., and Costello, M. J. (2019). GMED: Global marine environment datasets for environment visualisation and species distribution modelling. *PeerJ* (In Review).

Table 1 Descriptive statistics for the physical environmental layers.

Layers	Minimum	Maximum	Mean	Standard deviation	Standard error	Coefficient of variation
Physical						
Depth (m)	10,294	0	3440	1739	0.72	0.5
Slope (degree)	0	21.65	0.98	1.22	0	1.2
Land distance (km)	1	2774	666	554	0	0.8
Ice cover (annual) (% 0–1)	0	1	0.12	0.27	0	2.18
Ice cover (May–October)	0	1	0.12	0.28	0	2.29
Ice cover (November–April)	0	1	0.11	0.28	0	2.56
Wave height (m)	0	7	0.28	0.99	0	3.51
Wind speed (m.s ⁻¹)	0	12	7	1.96	0	0.27
Tide average (m)	0	6.4	0.5	0.45	0	0.97
Current (m.s ⁻¹)	−0.9	1	0	0.1	0	16.16
Euphotic layer bottom depth (m)	7	142	72	24	0.01	0.33
Diffuse attenuation coefficient (m ⁻¹)	0.02	0.89	0.06	0.04	0	0.79
Temperature (°C)	−1.0	31.5	14.4	10.94	0	0.76
Temperature maximum	−1.0	35.2	16.8	11.18	0	0.66
Temperature minimum	−2.0	30.8	12.5	10.68	0	0.86
Temperature range	0	27.8	4.1	3.02	0	0.74
Temperature (May–October)	−2.1	30.7	14.4	11.33	0	0.78
Temperature (November–April)	−2.1	30.7	14.4	11.12	0	0.77
Average water column temperature	−2.3	26.0	5.6	3.63	0	0.65
Seabed temperature	−2.08	29.5	2.0	3.86	0	1.97
Salinity (PSS)	0	41	33.6	2.5	0	0.07
Average water column salinity	6.3	40.6	34.5	1.91	0	0.06
Photosynthetically active radiation (Einstein.m ⁻² .day ⁻¹)	0	64.82	34.13	9.06	0	0.27

All values are in annual means and refer to the ocean surface unless noted otherwise. The Standard Deviation (SD) is used to quantify the amount of variation in the data. The Standard Error adjusts the SD for the number of samples taken. The Coefficient of Variation (CV) is the SD as a percentage of the sample mean and is thus independent of the mean and units in which the measurement has been taken.

Data from Basher, Z., Bowden, D. A. and Costello, M. J. (2019). GMED: Global marine environment datasets for environment visualisation and species distribution modelling. *PeerJ* (In Review).

Table 2 Descriptive statistics for the environmental layers related to plant productivity.

Layers	Minimum	Maximum	Mean	Standard deviation	Standard error	Coefficient of variation
Chemical						
Chlorophyll-a (mg.m ⁻³)	0	60.38	0.19	1.31	0	6.94
Chlorophyll-a maximum	0	64.00	0.47	2.23	0	4.75
Chlorophyll-a minimum	0	57.80	0.08	0.82	0	10.77
Chlorophyll-a range	0	62.16	0.33	1.67	0	5.01
Chlorophyll-a (May–October) maximum	0.03	64.57	0.67	2.08	0	3.12
Chlorophyll-a (November–April) maximum	0.02	64.57	0.42	1.31	0	3.16
Primary productivity (mgC.m ⁻² .day ⁻¹ .cell ⁻¹)	0	4875	370	278	0.11	0.75
pH	6.73	8.62	8.19	0.06	0	0.01
total suspended matter (g.m ⁻³)	0.03	48.49	0.93	2.37	0	2.54
Nutrient						
Calcite (mol.m ⁻³)	0	9	2.7	3.14	0	1.17
Nitrate (μmol.L ⁻¹)	0	46	5.2	5.91	0	1.13
Seabed nitrate (μmol.L ⁻¹)	0	56	28.6	9.85	0	0.34
Phosphate (μmol.L ⁻¹)	0	2.4	0.7	0.6	0	0.91
Seabed phosphate	0	4.5	2.01	0.65	0	0.32
Silicate (μmol.L ⁻¹)	0	69	9.6	13.3	0.01	1.38
Seabed silicate	0	268	98	52.51	0.02	0.53
Dissolved O ₂ (mL.L ⁻¹)	2	9.9	5.5	1.45	0	0.26
Seabed dissolved O ₂	0	10.2	4.8	1.27	0	0.26
Saturated O ₂ (mL.L ⁻¹)	76.05	113	100	3.25	0	0.03
Seabed Utilized O ₂	−2.4	7.7	2.9	1.21	0	0.42
Particulate organic carbon (mol.m ⁻³) (POC)	18.5	12,898	89	119	0.05	1.33
Particulate in-organic carbon (mol.m ⁻³) (PIC)	0	10,808	143	213	0.09	1.49

All values are in annual means and refer to the ocean surface unless noted otherwise. Details as in Table 1.

Data from Basher, Z., Bowden, D. A., and Costello, M. J. (2019). GMED: Global marine environment datasets for environment visualisation and species distribution modelling. *PeerJ* (In Review).

Table 3 The Pearson correlation matrix of selected data layers.

	<i>Depth</i>	<i>Temperature</i>	<i>Salinity</i>	<i>Current</i>	<i>Dissolved O₂</i>	<i>POC</i>	<i>PIC</i>	<i>Euphotic depth</i>	<i>Primary productivity</i>	<i>PAR</i>	<i>DAC</i>	<i>Ice</i>	<i>Nitrate</i>	<i>Phosphate</i>
Temperature	−0.31	–												
Salinity	−0.41	0.50	–											
Current	−0.01	−0.28	−0.06	–										
Dissolved O ₂	0.37	− 0.97	− 0.58	0.25	–									
POC	0.45	−0.24	− 0.53	0.01	0.29	–								
PIC	0.31	−0.38	−0.41	−0.01	0.40	0.12	–							
Euphotic depth	− 0.56	0.59	0.46	−0.11	− 0.64	− 0.59	−0.32	–						
Primary productivity	0.34	0.11	−0.11	−0.02	−0.09	0.55	−0.13	−0.49	–					
Photosynthetically active radiation	−0.23	0.91	0.46	−0.36	− 0.88	−0.17	−0.41	0.52	0.14	–				
Diffuse attenuation coefficient	0.55	−0.35	−0.5	0.01	0.39	0.81	0.15	− 0.72	0.57	−0.26	–			
Ice	0.45	− 0.62	− 0.61	−0.03	0.66	0.22	0.66	−0.45	−0.23	− 0.56	0.33	–		
Nitrate	−0.05	− 0.70	−0.07	0.27	0.62	0.01	0.07	−0.28	−0.13	− 0.60	0.09	0.22	–	
Phosphate	0.03	− 0.75	−0.17	0.24	0.68	0.04	0.13	−0.37	−0.10	− 0.64	0.13	0.28	0.93	–
Silicate	0.06	−0.64	−0.17	0.15	0.60	0.09	0.21	−0.30	−0.14	−0.53	0.18	0.45	0.86	0.83

Layers with significant correlations ($r^2 > \pm 0.5$) are highlighted in *bold*.

Basher, Z., Bowden, D. A. and Costello, M. J. (2019). GMED: Global marine environment datasets for environment visualisation and species distribution modelling. *PeerJ* (In Review).

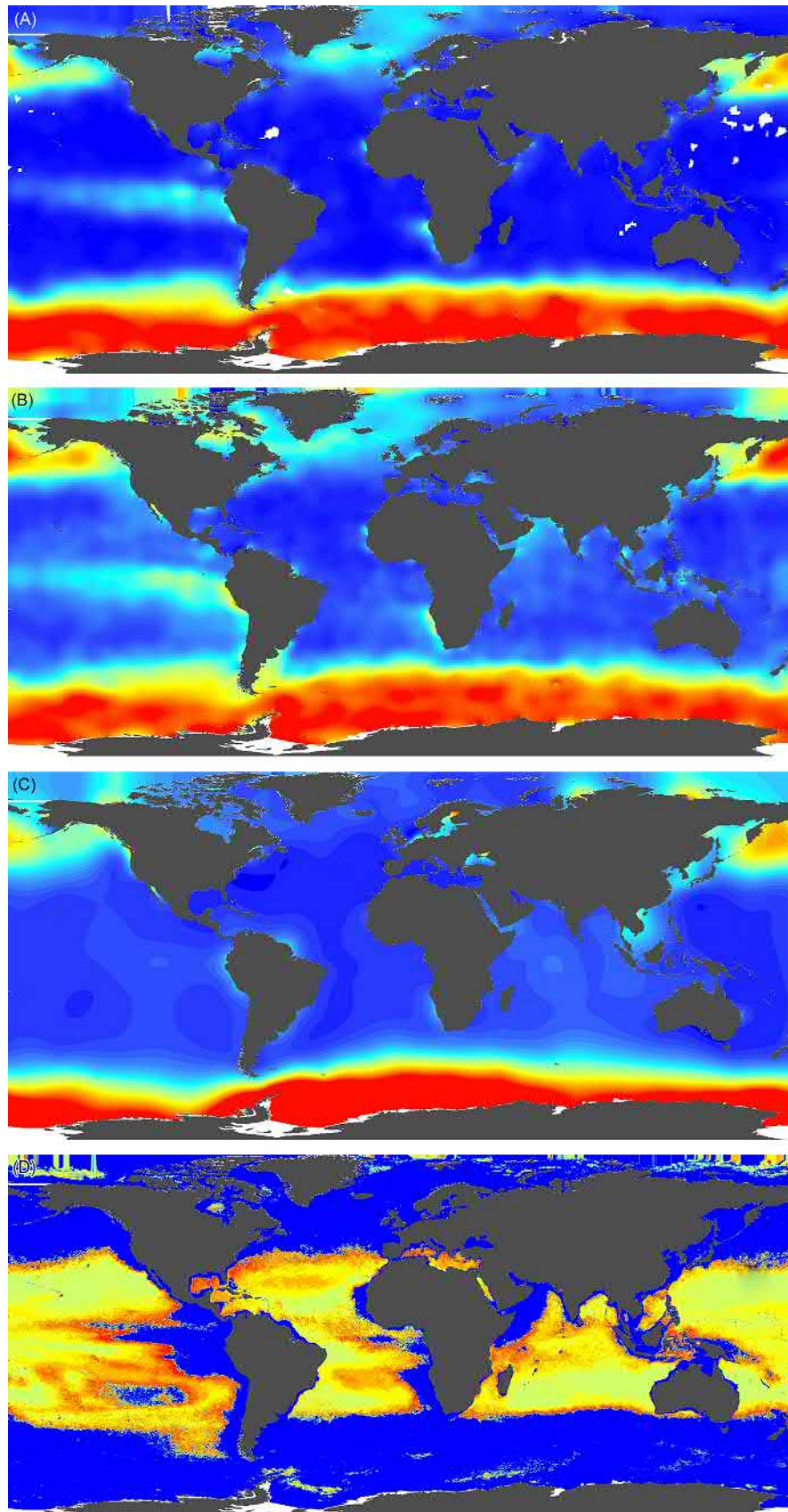


Fig. 7 World maps of the plant nutrients (A) nitrate, (B) phosphate, and (C) silicate. The mineral (D) calcite is from the shells of plankton. Color gradients from *red* to *blue* indicate more to less. See [Table 2](#) for ranges of values of each variable. Data from Basher, Z., Bowden, D. A., and Costello, M. J. (2019). GMED: Global marine environment datasets for environment visualisation and species distribution modelling. *PeerJ* (In Review).

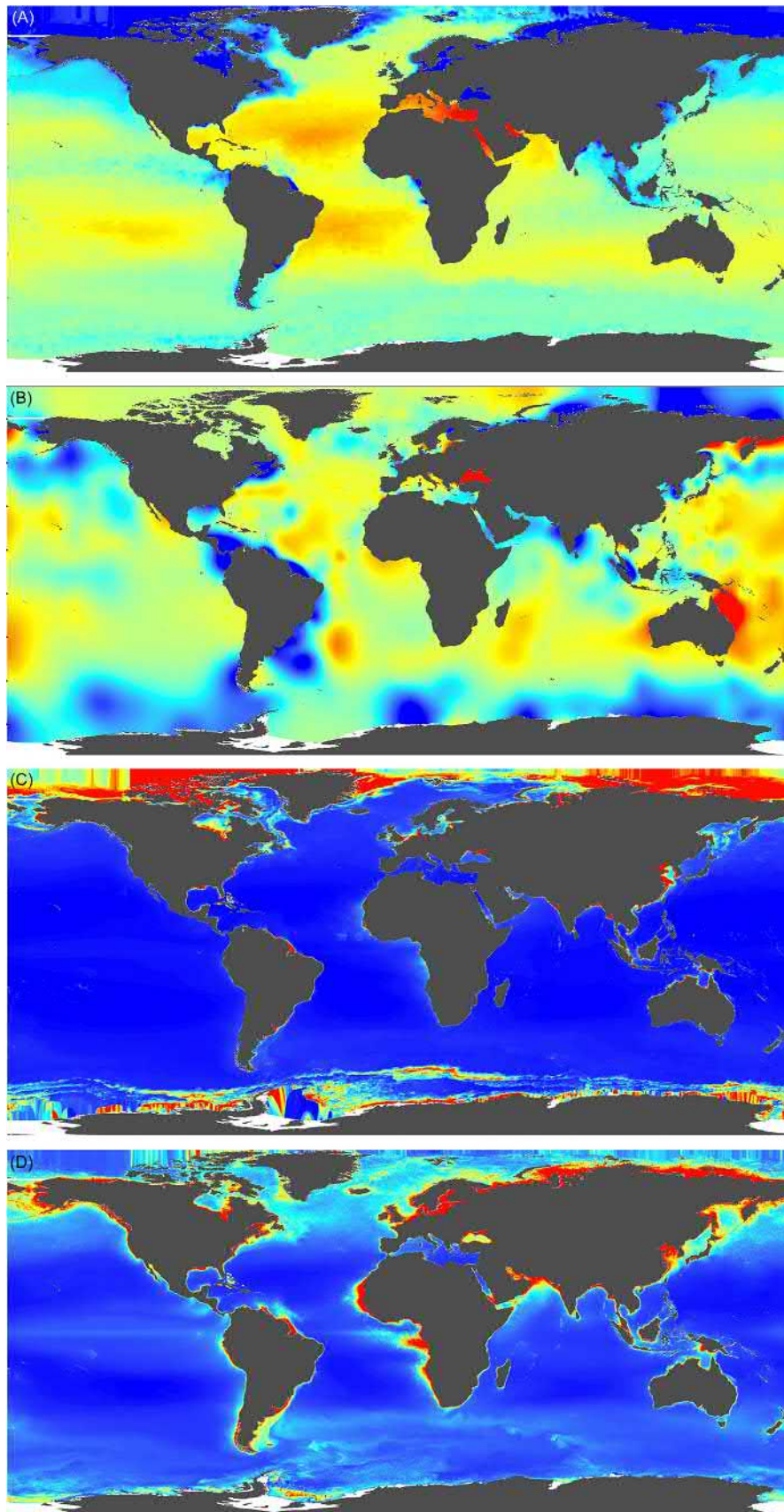


Fig. 8 World maps of (A) salinity, (B) pH, (C) total suspended (particulate) matter, and (D) particulate organic carbon (an indicator of particulate biological material) in the ocean. Color gradients from *red to blue* indicate more to less. See [Tables 1 and 2](#) for ranges of values of each variable. Data from Basher, Z., Bowden, D. A. and Costello, M. J. (2019). GMED: Global marine environment datasets for environment visualisation and species distribution modelling. *PeerJ* (In Review).

In the Southern Ocean and parts of the north Pacific, nutrients are exceptionally high (Fig. 7A–C), this is because a micronutrient, iron, is limiting plant growth. In these locations iron derived from land runoff, including oceanic islands, and brought to the surface in feces of marine mammals, may increase productivity at local spatial scales (Frey et al., 2014).

Calcite is an indicator of the growth of plankton that have calcified shells, notably coccolithophore phytoplankton and foraminifera (protozoan animals). Their growth is highest in the tropics (Fig. 7D). It is lower in temperate latitudes and regions of upwelling due to these taxa being outcompeted by the faster growing diatoms (Culver and Buzas, 2000; Sarmiento et al., 2004; Gregg and Casey, 2007).

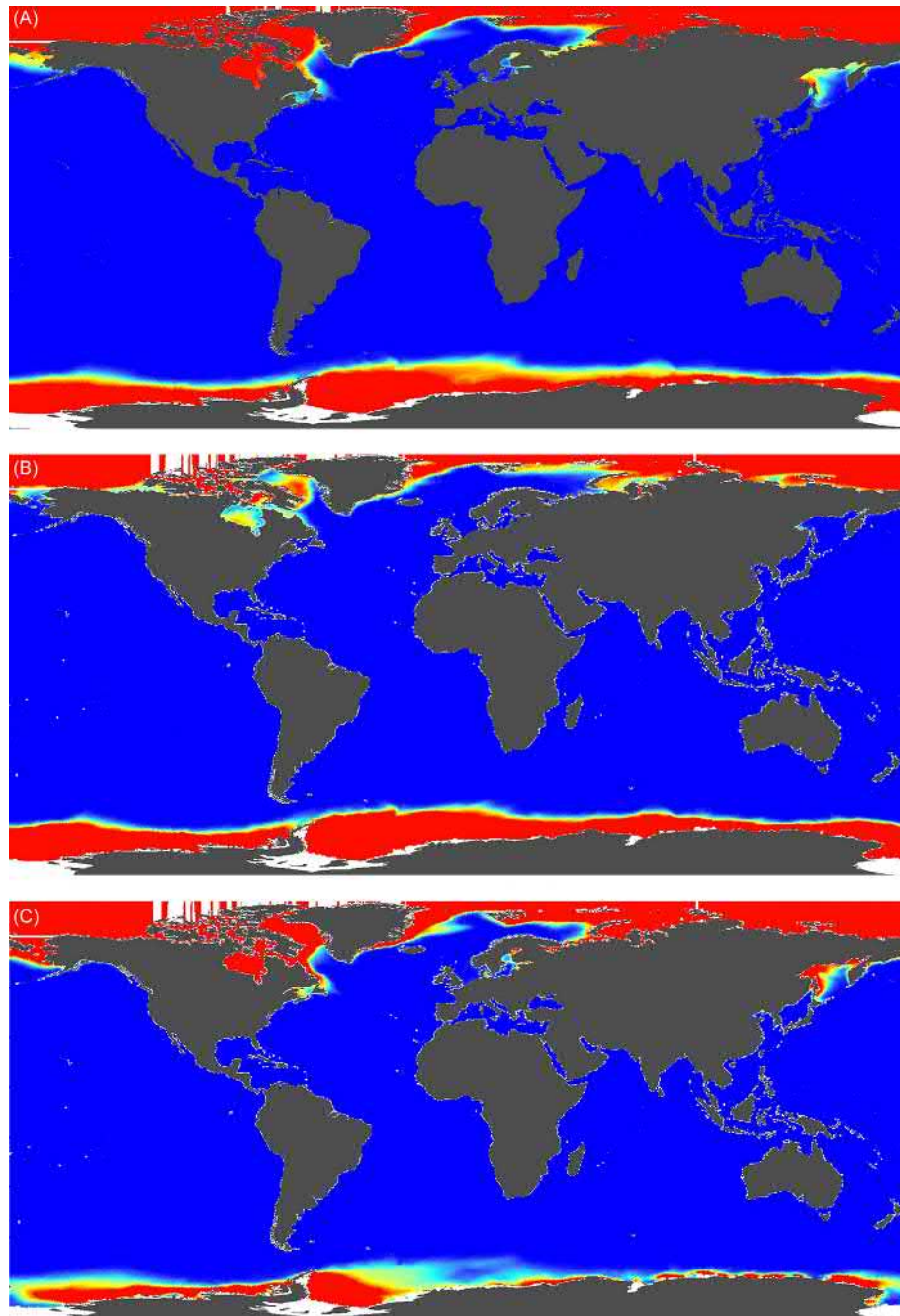


Fig. 9 World maps of ice cover as (A) annual average, (B) northern summer (May–October) and (C) southern summer (November–April) in the ocean. Color gradients *red to blue* indicate more to less cover. See Table 1 for range of values of each variable. Data from Basher, Z., Bowden, D. A. and Costello, M. J. (2019). GMED: Global marine environment datasets for environment visualisation and species distribution modelling. *PeerJ* (In Review).

Salts, pH, and Particulates

The salinity (or saltiness) of seawater refers to the amount of inorganic salts dissolved in the water. Although most seawater has a salinity of ~ 35 , it can reach up to almost 40 in some areas such as the Mediterranean and Red Sea (Fig. 8A). The units of salinity measurement have changed over time, including g/kg, ppt (parts per thousand), ‰, and PSU (practical salinity units), but it is now preferred to use the PSS (practical salinity scale) and just state the numerical value.

In estuaries, salinity is typically low, as there is regular input of freshwater, typically from a river. Salinity is higher around the tropics of Cancer and Capricorn, where the evaporation rate is high and precipitation (rainfall) is low. It is lower in high latitudes due to low evaporation rates combined with high precipitation and runoff as well due to the melting of icebergs. In the tropics, surface salinity is higher and rapidly decreases from ~ 200 to 1000 m where it stabilizes at around 35 (Thurman et al., 2013). At high latitudes the pattern is inverted: surface salinity is lower at the surface than at depth (Figs. 2C and 8A).

pH varies very little in seawater (Table 2) compared to freshwaters. It is relatively stable in open ocean, and varies most where freshwater runoff meets the ocean (i.e., estuaries) (Hofmann et al., 2011). The world map shows pH is generally higher in the Pacific compared to other oceans (Fig. 8B).

The concentration of particulate matter in seawater, presented as total suspended solids, is higher near land reflecting freshwater inputs (Fig. 8C). Similarly, Particulate Organic Carbon (POC) indicates organic carbon is highest near where estuaries or rivers enter the ocean (Fig. 8D). This is due to high phytoplankton growth and productivity increasing organic carbon concentrations (Harrison and Cota, 1991).

Ice

Sea ice is frozen seawater that floats on the ocean surface. It forms in both the Arctic and the Antarctic in each hemisphere's winter and retreats in the summer but does not completely disappear (Fig. 9). Floating ice caps have a profound influence on the polar environment, influencing ocean circulation, weather, and regional climate. The influence of sea ice coverage is not just regional, it's global. As ice crystals form in the surface ocean they expel salt which increases the salinity of water under the ice. This creates cold dense (higher salinity), oxygen-rich, water which sinks to the ocean floor and flows toward the equator. This flow drives the formation of the ocean circulation system, also called the global ocean conveyor belt (Broecker, 1991): a mechanism which maintains the global heat balance.

Conclusions

Here we have mapped a wide range of ocean environmental variables and shown how they vary quantitatively and correlate with each other (Tables 1–3). Comparing the maps show how they relate to each other geographically. These facts, and knowing their interrelationships, are essential to predict the effects of climate change on our oceans, and the effects of human activities on biodiversity. Understanding these spatial relationships, including the effects of plant growth on nutrients, oxygen and calcite, within the water masses created by the forces of energy (currents, wind, tides, temperature) and water density (salinity), within the confines of depth and topographic gradients and distance to land, has never been so important.

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Relevant Website

<http://gmed.auckland.ac.nz>—Global Marine Environment Dataset (GMED).

The Biology, Ecology, and Societal Importance of Razor Clams

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Abstract

Razor clams (Pharidae and Solenidae, Mollusca) are ecologically and economically important deep-burrowing bivalves. They are distributed in shallow waters of the tropical, subtropical, and temperate seas. The North-West and the Indo-West Pacific has the highest species richness (about 85% of all species) mostly in the Sea of Japan, China Sea, the Gulf of Thailand, and the Andaman Sea. Their species composition forms 16 biogeographic regions which concur with existing marine biogeographic hypotheses. More than half of the species are endemic to these biogeographic regions. This is an exceptionally high rate of endemism in the oceans and suggests little gene flow between populations. Species richness increases from the cold temperate to intermediate latitudes and dips near the equator following the mean sea surface temperature. Species richness decreases with temperature range, chlorophyll-*a* concentration, and primary productivity over all latitudes, but increases with ocean area in the Northern Hemisphere. Most species are predicted to shift their distribution ranges poleward in the future due to global warming. Thus the mid-latitude peaks of species richness will move further apart, increasing the dip in richness near the equator.

Biology and Ecology

Systematics and Taxonomy

The Solenidae family of razor clams has three genera, *Solen* Linnaeus, 1758, with more than 65 species, *Solena* Mörch, 1853 with two species, and *Neosolen* Ghosh, 1920 with one species *Neosolen aquaedulcioris* (Ghosh, 1920), within the superfamily Solenoidea in Subclass Heterodonta, and Class Bivalvia (Cosel, 1990; Bouchet et al., 2010; MolluscaBase, 2018). At first, *Solena* Browne was classified as a subgenus of *Solen* Linné Cosel (1990). Later, Ghosh (1920) included nine genera in the Solenidae, namely *Solen* Linné, 1758; *Solena* Browne, 1756; *Neosolen* Ghosh, 1920; *Ensis* Schumacher, 1817; *Ceratisolen* Forbes and Hanley, 1848 (= *Pharus*); *Subcultellus* Ghosh, 1920 (= *Phaxas*); *Cultellus* Schumacher, 1817; *Pharella* Gray, 1854; and *Siliqua* Mühlfeld, 1811 (Cosel, 1990). Later, Cosel (1990) included two genera *Solen* Linnaeus, 1758 and *Solena* Mörch, 1853 within the Solenidae, and he classified *Ensisolen* Habe, 1977 and *Neosolen* Ghosh, 1920 (with only one species *aquaedulcioris*) as subgenera of *Solen*. He also classified the now extinct subgenera *Eosolen* Stewar, 1930 and *Plectosolen* Conrad, 1866 under *Solena* from fossil records. The fossil records of Solenidae are rare because of their fragile shells, but there are some records from the late Eocene about 40–42 million years ago (Mya) (Cosel, 1990).

Shell Morphology and Anatomy

Solen shells range from 50 to 120 mm in length, can be thin and translucent to opaque, straight to slightly curved, and short to narrow. In cross-section they can be oval to tubular, truncated or with rounded anterior and posterior ends. The shells have thin elongate valves with a wide gape at each end. Each valve has one cardinal tooth, an external ligament, and a glossy periostracum (Fig. 1) (Cosel, 1989, 1990; Saeedi et al., 2013).

Solenid shells do not close completely, so posterior and anterior ends of the shells are always open (Saeedi et al., 2009). A long, powerful foot and elongate shell enables razor clams to rapidly burrow into substratum (Saeedi et al., 2009). They have two fleshy siphons which extend into the water column to pull in water to feed on plankton. These have an autonomy function which is an anti-predator adaptation. This means they can lose their siphons when attacked by predators, and then the siphon can regrow (Saeedi et al., 2009, 2013).

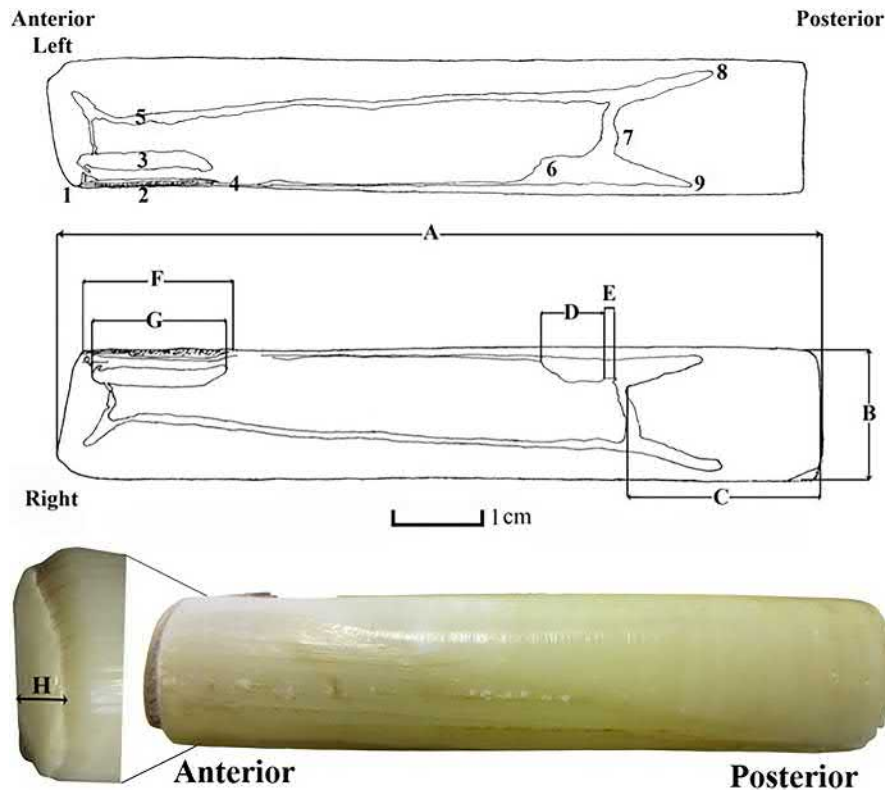


Fig. 1 Internal view of both valves of *Solen dactylus*, half-schematic drawing. 1: hinge; 2: ligament; 3: anterior adductor muscle scar; 4: anterior retractor muscle scar; 5: pallial muscle scar; 6: posterior adductor muscle scar; 7: pallial sinus; 8: ventral limb of pallial sinus; 9: dorsal limb of pallial sinus. (A) Total shell length; (B) Greatest width of shell; (C) Distance of the innermost point of the pallial sinus to the posterior margin; (D) Length of posterior adductor scar; (E) Distance between posterior adductor scar and pallial sinus; (F) Ligament length; (G) Length of anterior adductor scar; (H) Anterior furrow shell length. Presence of anterior shell furrow was also recorded.

Growth and Reproduction

Growth rate in Solenidae has been measured in *Solen dactylus* and *Solen cylindraceus*, which grow 20–30 mm and 23 mm per year, respectively depending on their age (Saeedi et al., 2009; Nel et al., 2013). Growth rate in Solenidae after the first year of age becomes increasingly slower as the clams become reproductive.

The sexes are separate in Solenidae and the species *Solen strictus*, from Hong Kong, *S. marginatus* from Spain, and *S. dactylus* from Iran spawn only once a year (Gribben, 2005; Remacha-Trivino and Anadon, 2006; Saeedi et al., 2009). They release large volumes of gametes that lead to synchronized external fertilization and subsequent recruitment (Saeedi et al., 2009).

Solen marginatus has a planktonic larval period of less than 2 weeks and requires sandy and muddy substrata for juveniles to settle into (da Costa et al., 2011). In at least this species, the relatively large eggs have high levels of stored nutrients and a short larval development time of only 8 days (da Costa et al., 2011).

Habitat

Solenidae inhabit the lower portions of sandy-muddy intertidal zones down to a depth of 110 m (Saeedi et al., 2013, 2017). However, most species are found in shallow waters (0–30 m) where they can constitute an important component of in-faunal soft-bottom communities (Cosel, 1990). Annelids, crabs, gastropods, and other borrowing bivalves are the most common cohabitants of these soft-bottom communities (Lassuy and Simons, 1989). Only two species, *Solen annandalei* and *Solen kemp* are known to tolerate low salinity conditions, namely in Chilka Lake, India, with 0.5 to 30 ppt salinity at an average depth of <5 m (Cosel, 1990; Nayak et al., 2004).

Biogeography

Members of Solenidae are distributed worldwide with the exception of the polar regions and some oceanic islands such as New Zealand (Saeedi et al., 2017; Cosel, 1990) (Fig. 2). About 45 *Solen* species are distributed in the tropical western Pacific Ocean from Japan and China to the Indian Ocean and Australia (Cosel, 1989, 1990; Saeedi et al., 2009, 2013; Guerra et al., 2011). New species

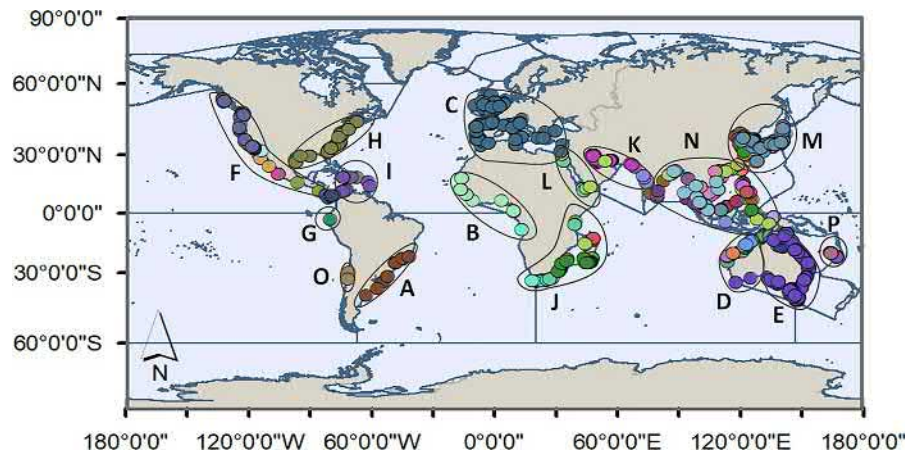


Fig. 2 Distribution of Solenidae species showing 16 biogeographic regions (solid black lines) derived from sample locations (colored points, each color represents one species). South-west Atlantic (A); west Africa (B); north-east Atlantic and Mediterranean (C); western Australia (D); eastern Australia (E); north-east Pacific (F); central-east Pacific (G); north-west Atlantic (H); Caribbean Sea (I); south-west Indian Ocean (J); north-west Indian Ocean (K); Red Sea and Gulf of Aden (L); north-west Pacific (M); Indo-West Pacific (N); south-east Pacific (O); New Caledonia (P).

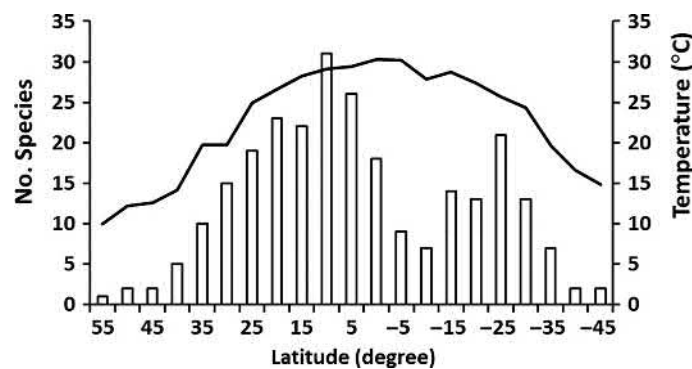


Fig. 3 Number of total Solenidae species (plus one) (hollow bars) versus mean sea surface temperature (solid line) in 5 degree latitudinal bands.

are still to be expected in the Indian Ocean and the western Pacific, the Coral Triangle (mainly Indonesia, Philippines, Papua-New Guinea), and northern Australia (Cosel, 1990). Saeedi et al. (2017) studied the global biodiversity and biogeography of Solenidae and she discovered a bimodal global latitudinal species richness for the first time in Solenidae (Fig. 3) and later in all marine species (Chaudhary et al., 2016; Saeedi et al., 2017). Global patterns of Solenidae species richness increased from the poles to intermediate latitudes and dipped near the equator, exhibiting a strongly bimodal pattern that is likely to be temperature driven (Saeedi et al., 2017) (Fig. 3). A non-linear relationship between species richness and mean sea-surface temperature was compatible with this bimodal pattern (Saeedi et al., 2017). Cluster analysis of similarity patterns of species composition (i.e., presence of Solenidae species) for 5 degree latitudinal-longitudinal grid cells showed 16 significant biogeographical regions that concurred with existing marine biogeographical hypotheses (Fig. 2). More than half of the species were endemic to specific biogeographical regions (Saeedi et al., 2017).

Comparison with models of future temperatures scenarios found that most Solenidae species were predicted to shift their distribution ranges poleward due to climate warming; that is, species in the northern hemisphere would shift northward and southern species southward (Saeedi et al., 2016). Model results predicted that the mid-latitude peaks of species richness will move further apart, increasing the dip in richness near the equator, due to global climate change (Saeedi et al., 2016).

Ecological Importance

Of the 242,954 accepted marine species, 48,048 are marine molluscs (Bouchet, 2006; WoRMS, 2018). Molluscs significantly contribute to the food web as herbivores and predators. The filter-feeding of bivalves, such as razor clams, can improve water quality (Dumbauld et al., 2009). Razor clams' are also prey to crabs, sea birds, and demersal fish especially on newly recruited razor clams

when they have the highest mortality rates (Guerra et al., 2011; Lassuy and Simons, 1989). However, razor clam deep-burrowing behavior (about 30 cm into the substrate) hides them from many predators. The average density and biomass reported for Pharidae is about 60–80 individuals m^{-2} and 1–3 kg m^{-2} respectively (Guerra et al., 2011), but biomass in Solenidae has not been reported so far. They can also play a role in the nitrogen cycles of surface waters by excreting ammonium which is used by algal populations as a nitrogen source (Lewin et al., 1979).

Razor clams can be bio-indicators of heavy metals such as Mg, Fe, Cu, and especially Zn in their environment (Saeedi et al., 2012). However, *Solen brevis* (in Pahang, Malaysia), *S. dactylus* (in Bandar Abbas, Iran), and *S. regularis* (in Moyan and Serpan, Sarawak) remained safe for human consumption because metal concentrations were under the limits established by national and international health standards (Kanakaraju et al., 2008; Kamaruzzaman et al., 2010; Saeedi et al., 2012). Only one species, *Neosolen aquaedulcoris*, is assessed in the IUCN Red List of Threatened Species, and it was considered to be of “Least Concern” status (Bogan, 2012).

Societal Importance

Approximately 11% (6.6 million tonnes) of all marine species exploited by the fishing and aquaculture industry were molluscs (Yearbook, 2018; FAO, 2011). In 2009, molluscs accounted for 38% (13 million tons) of the total harvest of the global mariculture industry (FAO, 2011, #274), most of which were mussels and clams. Although the contribution of Pharidae and Solenidae to this is likely minor, they are relatively high value per unit weight. Members of Solenidae are mostly consumed as seafood in Europe, North America, East Asia, and South Asia (Saeedi et al., 2013; Guerra et al., 2011). In some countries like Iran people harvest Solenidae species as bait for fishing and as a food source in shrimp culture (Saeedi et al., 2009).

In an economic context, the sharp rise in price of razor clam meat as a source of nutrition for humans, particularly for Pharidae and Solenidae, exemplifies the increased importance of bivalves on global commercial markets (Fernández-Tajes and Méndez, 2007). The import value of razor clams in central and northern European markets reached EUR550 million in 2004 (Fernández-Tajes and Méndez, 2007; da Costa and Martínez-Patino, 2009; da Costa et al., 2011). In the European Union, Spain alone accounts for approximately 43% of the total volume of imported razor clams (Fernández-Tajes and Méndez, 2007).

There are different harvesting methods to collect razor clams such as digging, dredging, electric fishing, salting, and using fishing tools with a hook in the end (Saeedi et al., 2009; Guerra et al., 2011). Razor clams have been over-harvested around the world especially in Europe (Fernández-Tajes and Méndez, 2007) and southeastern Asia where there are no regulations in place to protect their populations (Saeedi et al., 2009).

A better understanding of the reproductive biology of razor clams could assist fisheries managers in reducing harvesting pressure at specific locations. For example, *Solen regularis* (Sarawak) (Rinyod and Rahim, 2011), *S. dactylus* (Iran) (Saeedi et al., 2009), and *S. marginatus* (Spain) (Remacha-Trivino and Anadon, 2006), spawn in winter and rest in early spring and summer. Established spawning behaviors of these species have shaped regulations that limit harvesting to nonspawning seasons (Saeedi et al., 2009). Similar knowledge contributed to more sustainable management of razor clam fisheries and potential species for aquaculture in Europe (da Costa et al., 2011). Fisheries need to take care not to deplete populations of razor clams because their high degree of endemism makes them susceptible to over-fishing and suggests little recruitment from distant populations.

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The Biology, Ecology and Societal Importance of Marine Bryozoa

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Abstract

Bryozoans are common animals in marine benthic (seabed) ecosystems, and also occur in freshwater rivers, with 6063 and 108 extant species in each environment respectively. There are 17,867 fossil species described. They are distributed across the oceans with a relatively high diversity on the Antarctic shelf. They are colonial suspension filter feeders with a calcified skeleton, a wide variety of life cycles and growth forms, and are well represented in the fossil record.

Biology

Taxonomy and Systematics

Bryozoans are a phylum of aquatic invertebrates containing around 24,000 extant and fossil described species (Bock and Gordon, 2013; Pagès-Escolà et al., 2019a) (Table 1). They are one of the most common invertebrates on benthic substrata, with 6063 marine and 108 freshwater extant species, most of them found in rivers and rarely in lakes (Bock, 1982; Ryland, 2005; Ballesteros, 2006; Wood et al., 2012; Pagès-Escolà et al., 2019a). They are also well-preserved in the fossil record due to their calcified skeleton, with 17,867 bryozoan species in the fossil record (Taylor and Waeschenbach, 2015; Pagès-Escolà et al., 2019a). An estimated 1350 extant and 2430 fossil species remain to be described by the final of this century (Pagès-Escolà et al., 2019a).

There are three classes of Bryozoa (Table 1). The Gymnolaemata are mostly marine species. It is the most species rich bryozoan group, and includes the order Cheilostomatida that has the most genera, over 600 (Table 1). They are characterized by body walls which range from entirely organic to rigidly calcified (Ryland, 2005). They originated in the Upper Ordovician (450 Myr ago). During the Late Jurassic (about 164–145 Myr ago) the order Cheilostomatida had evolved to have most of the complex skeletal structures seen today (Canu and Bassler, 1927; Taylor, 1990).

The Stenolaemata have only marine species, and most are fossil, except for those in the Order Cyclostomatida (Ryland, 2005). They are characterized by calcified body walls. The earliest fossil records were from the Lower Ordovician (500–430 Myr ago) (Ernst and Schafer, 2006). The Phylactolaemata are exclusively freshwater species, with membranous and gelatinous skeletons. They originated during the Upper Ordovician (Ryland, 2005).

Morphology

Bryozoan colonies vary in size and form from small colonies that create crusts a few centimeters across, such as the Mediterranean *Chorizopora brognartii*, *Puellina hincksi* and *Disporella hispida*, to large and rigid colonies of *Pentapora* species that can reach 1 m in diameter (Zabala, 1986; Cocito, 2004; Pagès-Escolà, 2019) (Fig. 1). In most species, the skeleton is external and calcified (Ryland, 2005).

Bryozoans do not have respiratory, circulatory or excretory systems (Bock, 1982; Zabala, 1986; Ryland, 2005). They have a nervous system that enables retraction and extension of their tentacles (see below) (Zabala, 1986; Ryland, 2005).

Table 1 Number of class, orders, families, genus and species for extant marine and freshwater bryozoans.

Class	Order	Habitat	Family	Genus	Species
<i>Gymnolaemata</i>	All	Marine	162	654	5206
	<i>Ctenostomatida</i>	Marine	33	63	325
	<i>Cheilostomatida</i>	Marine	130	592	4821
<i>Stenolaemata</i> ^a	<i>Cyclostomatida</i>	Mostly marine	51	138	835
<i>Phylactolaemata</i>	<i>Plumatellida</i>	Freshwater	7	13	94

Extinct orders not included.

^aMostly fossil species.

Data obtained from WoRMS database.

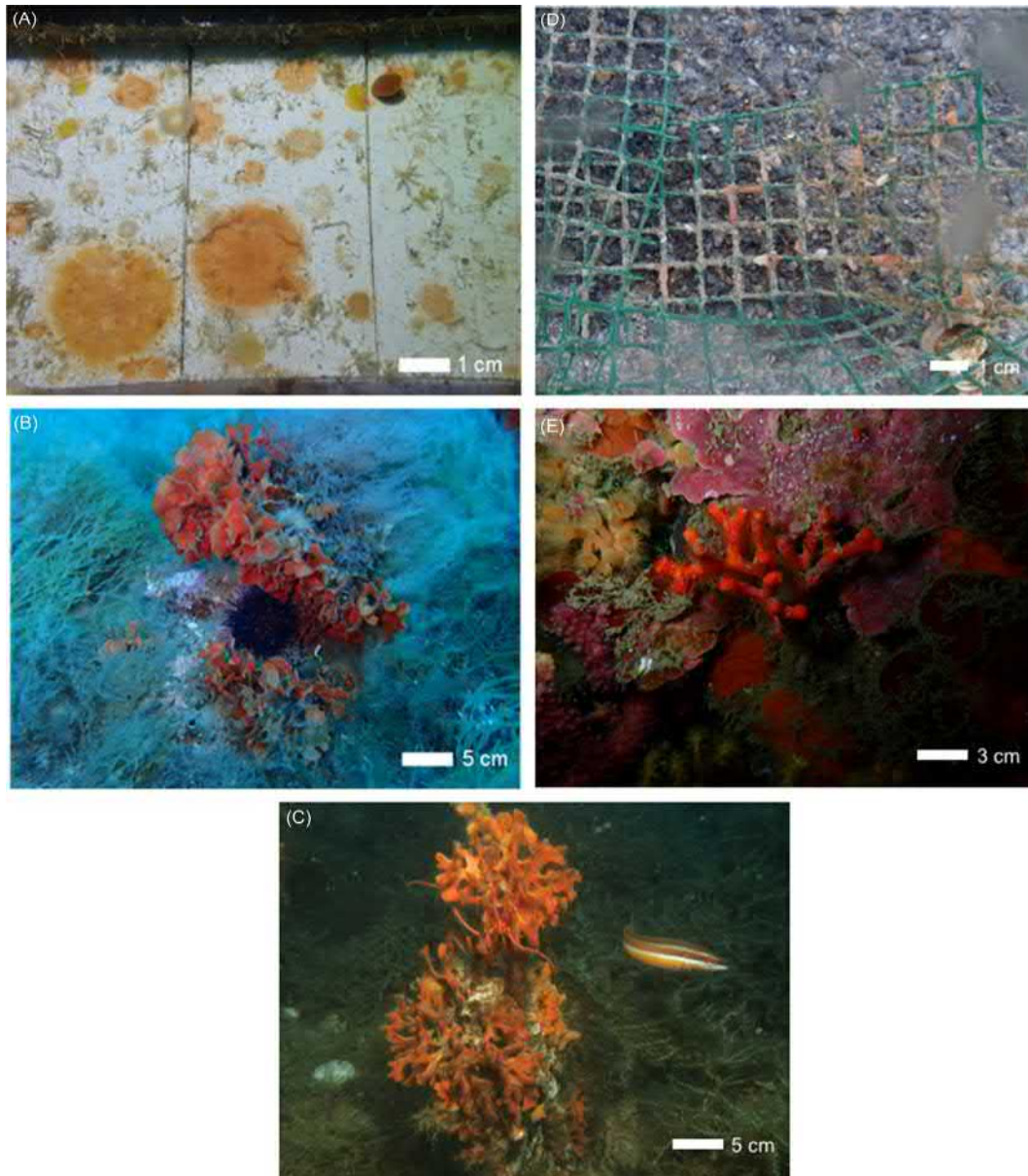


Fig. 1 Examples of bryozoan species forms and habitats. (A) Small colonies of Mediterranean bryozoan species that form crusts such as *Chorizopora brogniartii*, *Puellina hincksi* and *Disporella hispida*. (B) Large colonies of the Mediterranean bryozoan *Pentapora fascialis*. (C) Large epibiotic colonies of *Pentapora fascialis*. (D) Crust and recruits of different bryozoan species such as *Pentapora fascialis* and *Turbicellepora avicularis* found on a plastic mesh. (E). Colony of the Mediterranean bryozoan *Myriapora truncata* in a cave. Photographs by Pagès-Escolà. Modified from Pagès-Escolà M (2019) *New insights into the ecology and conservation of bryozoans: from global diversity patterns to the responses to anthropogenic stressors in the Mediterranean Sea*. Doctoral dissertation University of Barcelona.

Zooids

The functional units of bryozoan colonies are called zooids, which generally are enclosed in a case, the zooecium, that in many species secretes a rigid skeleton of calcium carbonate. The zooids are separated from each other by body walls with a system of pores which connect the zooids (Bock, 1982; Ryland, 2005). Zooids differentiate functionally and structurally. The most abundant zooids are feeding “autozooids” characterized by a ring of tentacles (lophophore) at their distal extreme, with cilia that create a flow of food particles to the mouth. Other zooids, called avicularias, are thought to be involved in the defense of the colony (Zabala, 1986; McKinney and Jackson, 1991; Ryland, 2005).

During the growth of the colony, some zooids sexually differentiate to have reproductive organs producing eggs or spermatozooids. The majority of bryozoan species have hermaphroditic zooids with simultaneous ovaries and testes. In some species, mature sexual zooids specialize as reproductive “gonozooids,” which are enlarged zooids with a chamber (oecium) and a body wall (ovicell) where internal fertilization occurs (Zabala, 1986; Ryland, 2005; Pagès-Escolà, 2019).

Fertilization can be external (in the sea), or internal in the gonozooids (Bock, 1982; Zabala, 1986). In addition, asexual reproduction processes can occur by fragmentation of the colonies (Zabala, 1986; McKinney and Jackson, 1991; Ryland, 2005).

The bryozoan life cycle is characterized by two phases. The first is characterized by sexual reproduction which produces a pelagic larva, and then a second phase of asexual growth or budding, which starts with settlement of the larvae (Ryland, 2005) and growth by budding of the colony. Fragmentation processes can also create new colonies and recruits (Linacre and Keough, 2003; O’Dea, 2006).

Ecology

Habitat

Most marine bryozoan species inhabit shallow waters, and some range as deep as 8000 m in the Indian and Pacific Ocean (Hayward, 1981). Bryozoans feed on planktonic particles captured by ciliated lophophore tentacles, which they can beat to create a current to the mouth (Ryland, 2005). Thus they are found in locations where the water current is sufficient to deliver food particles (Zabala, 1986).

Small species can create crusts on species, such as on the seagrass *Posidonia oceanica*, corals and seaweeds (Casola et al., 1987; Zabala et al., 1993; Manriquez and Cancino, 1996). Large bryozoans can be found attached to rocky seabed and walls, occupying exposed or epibiotic positions, such as the case of *Pentapora fascialis*, and inside caves, such as *Myriapora truncata*. Bryozoans such as *Pentapora fascialis* and *Turbicellepora avicularis*, have been found growing on plastic mesh and lost fishing lines lying on the seabed (Pagès-Escolà et al., 2019b) (Fig. 1).

Damage to bryozoan skeletons has been used as an indicator of impacts due to severe storms (Cocito et al., 2001) and scuba divers (Sala et al., 1996; Garrabou et al., 1998; Teixidó et al., 2013; De la Nuez-Hernández et al., 2014).

Biogeography

Bryozoans are widely distributed across the globe (Fig. 2), with a notably high diversity in the Southern Ocean (Barnes and Griffiths, 2008; Tittensor et al., 2010). This suggests that their latitudinal gradient in species richness may differ from the commonly accepted pattern that posits most diversity in the tropics (Chaudhary et al., 2016, 2017; Saeedi et al., 2017). However, despite their wide distribution, there has been no analysis of bryozoan biogeography at a global scale.

Due to the high abundance and diversity of bryozoans in the fossil record, they have been used to study paleoclimatic conditions (Berning, 2007), and are thus of scientific importance in understanding the Earth’s history.

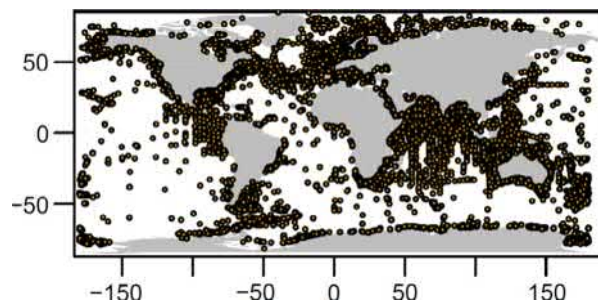


Fig. 2 Recorded global distribution of bryozoans (GBIF, 2017; OBIS, 2017). Data from OBIS and GBIF Databases.

Social Importance

Economic

Although most bryozoan species have no known economic value, some species produce bioactive compounds or metabolites which have pharmacological applications. For example, bryostatins in *Bugula neritica* have potential anti-carcinogenic benefits (Jha and Zhi-Rong, 2004).

Ecological

Large bryozoan skeletons form habitats for other species that enhance associated diversity (Cocito, 2004; Lombardi et al., 2014). Most of these bryozoan skeletons are found in temperate regions, where the environmental conditions benefit the formation and persistence of these structures, even after they die (Wood et al., 2012). Their ecological benefits include providing additional available surfaces and crevices that protect other species from predation, and shelter from physical disturbances such as waves and light irradiance (Buss and Jackson, 1979; Bradstock and Gordon, 1983; Cocito, 2004; Wood et al., 2012; Lombardi et al., 2014). The presence of a bryozoan can also facilitate colonization by other bryozoan species (Cocito, 2004; Lombardi et al., 2014).

Invasive Species

There are around 86 bryozoan species recorded as invasive in the World Register of Introduced Marine Species (Ahyong et al., 2019). Most invasive species have been introduced through accidental transport as fouling on commercial ships or recreational boating (Kipp et al., 2010; Murray et al., 2011; Brine et al., 2013), with some examples of cosmopolitan invaders such as *Watersipora subtorquata* and *Bugula neritina* (Floerl and Inglis, 2005). The effects of introduced bryozoans include changes to the abundance and structure of kelp forests due to the effects of encrustation of some bryozoan species such as *Membranipora membranacea* (Scheibling and Gagnon, 2009; Krumhansl et al., 2011).

Climate Change

Previous studies showed that some species, such as the Mediterranean species *Pentapora fascialis* is sensitive to ocean warming and recurrent heat waves (Pagès-Escalà et al., 2018), making it susceptible to the effects of climate change. However, this has been only studied in the Mediterranean Sea and remains to be studied on other species and regions. Moreover, because bryozoan skeletons are calcified by calcite or aragonite they sequester carbon (Cocito et al., 2001; Wood, 2014) and may be vulnerable to ocean acidification (Smith, 2014).

Conservation

Because they provide biogenic habitat, conserving bryozoans benefits a wider variety of associated species. For this reason, it may be desirable to actively restore damaged populations (Pagès-Escalà et al., 2019b). Yet, despite their wide distribution, abundance and diversity, there is a lack of knowledge of many aspects of bryozoan biology and ecology, such as population dynamics, life cycles, and biochemistry.

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Seagrass Biome

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Abstract

Similar to terrestrial biomes the marine domain has large areas with similar plant life forms. One of these is the seagrass biome. Seagrasses are flowering plants adapted to live in submerged coastal areas of tropical and temperate regions. Analogous to terrestrial biomes, seagrass provides feeding, breeding, and nesting habitats to associated fauna. It plays an important role in coastal environmental and ecological stability. However, the disturbance from human activities and natural disasters can accelerate seagrass loss. With the current awareness of the importance of seagrass biome, many conservation measures have been taken to protect it.

Introduction

The seagrass biome consists of meadows of plants similar to terrestrial grasslands distributed in tropical, subtropical, and temperate coastal areas (Green and Short, 2003). These angiosperm monocots have a well-developed root system to anchor to the seabed. Not only roots but rhizomes anchor seagrasses to the seabed and form underground biomass (Short et al., 2007). They have well-built mechanisms to survive in saline conditions in estuaries, lagoons and open seawater on the continental shelf and nowhere else. Seagrasses live their life in a submerged environment and have specialized pollen for underwater pollination (Green and Short, 2003; den Hartog and Kuo, 2006; Short et al., 2007).

Taxonomy

Phylogenetically, the seagrass biome is a functional group of four not necessarily closely related aquatic monocot families, namely the Zosteraceae, Cymodoceaceae, Posidoniaceae, and Hydrocharitaceae. They have 11 genera and 60–70 species (Green and Short, 2003; den Hartog and Kuo, 2006; Horton et al., 2018) (Table 1). The Zosteraceae has two genera; *Phyllospadix* and *Zostera*. The Cymodoceaceae has five genera *Amphibolis*, *Cymodocea*, *Halodule*, *Syringodium*, and *Thalassodendron*, family Hydrocharitaceae has three genera; *Enhalus*, *Halophila*, and *Thalassia* and family Posidoniaceae has one genus, genus *Posidonia*. All species in the families Zosteraceae, Cymodoceaceae, and Posidoniaceae are seagrasses. The family Hydrocharitaceae has only 3 out of 17 genera that are exclusively marine (den Hartog and Kuo, 2006).

A few monocot species in the families Ruppiaceae and Zannichelliaceae, which are primarily freshwater taxa, can live in brackish and marine conditions. They may occur in seagrass meadows among true seagrasses. Thus the seagrass biome is not comprised exclusively of certain plant families. *Ruppia tuberosa* from the family Ruppiaceae and *Lepilaena marina* from the family Zannichelliaceae are exclusively marine whereas *Ruppia maritima* forms meadows in both marine and freshwaters (den Hartog and Kuo, 2006). Molecular studies may reveal how seagrass evolved from marine algae to terrestrial plants and transitioned back to sea and clarify uncertainties of taxonomic relationships of seagrass species (Les et al., 1997). The genome of *Zostera marina* has been fully sequenced to identify the genomic losses and gains involved in adapting in the marine environment (Olson et al., 2016).

Environment

Physical variables such as depth, wave height, water clarity (a measure of light attenuation), temperature, salinity and photosynthetically active radiation and chemical parameters such as pH, and nutrients such as phosphate, nitrate and dissolved oxygen concentration, control the distribution of seagrasses (Short et al., 2001; Jayatilake and Costello, 2018). Depth is a proxy for light penetration through the water column and controls the vertical distribution of seagrass (Dennison, 1987; Duarte, 1991; Short et al., 2001; Duarte et al., 2007). The lower depth limit of seagrass distribution is known as the compensation depth (Gallegos and

Table 1 The seagrass species and their families

Cymodoceaceae	Hydrocharitaceae
<i>Amphibolis antarctica</i>	<i>Enhalus acoroides</i>
<i>Amphibolis griffithii</i>	<i>Halophila australis</i>
<i>Cymodocea angustata</i>	<i>Halophila baillonii</i>
<i>Cymodocea nodosa</i>	<i>Halophila beccarii</i>
<i>Cymodocea rotundata</i>	<i>Halophila capricorni</i>
<i>Cymodocea serrulata</i>	<i>Halophila decipiens</i>
<i>Halodule beaudettei</i>	<i>Halophila engelmanni</i>
<i>Halodule bermudensis</i>	<i>Halophila hawaiiiana</i>
<i>Halodule emarginata</i>	<i>Halophila johnsonii</i>
<i>Halodule pinnifolia</i>	<i>Halophila minor</i>
<i>Halodule uninervis</i>	<i>Halophila ovalis</i>
<i>Halodule wrightii</i>	<i>Halophila ovata</i>
<i>Syringodium filiforme</i>	<i>Halophila spinulosa</i>
<i>Syringodium isoetifolium</i>	<i>Halophila stipulacea</i>
<i>Thalassodendron ciliatum</i>	<i>Halophila tricostata</i>
<i>Thalassodendron pachyrhizum</i>	<i>Thalassia hemprichii</i>
	<i>Thalassia testudinum</i>
Posidoniaceae	Zosteraceae
<i>Posidonia oceanica</i>	<i>Heterozostera tasmanica</i>
<i>Posidonia australis</i>	<i>Phyllospadix iwatensis</i>
<i>Posidonia sinuosa</i>	<i>Phyllospadix japonicus</i>
<i>Posidonia angustifolia</i>	<i>Phyllospadix scouleri</i>
<i>Posidonia ostenfeldii</i>	<i>Phyllospadix serrulatus</i>
<i>Posidonia robertsoniae</i>	<i>Phyllospadix torreyi</i>
<i>Posidonia coriacea</i>	<i>Zostera angustifolia</i>
<i>Posidonia denhartogii</i>	<i>Zostera asiatica</i>
<i>Posidonia kirkmanii</i>	<i>Zostera caespitosa</i>
	<i>Zostera capensis</i>
	<i>Zostera capricorni</i>
	<i>Zostera caulescens</i>
	<i>Zostera japonica</i>
	<i>Zostera marina</i>
	<i>Zostera mucronata</i>
	<i>Zostera muelleri</i>
	<i>Zostera noltii</i>
	<i>Zostera novazelandica</i>
	<i>Zostera tasmanica</i>

From Jayatilake, D. R. M. and Costello, M. J. (2018). A modelled global distribution of the seagrass biome. *Biological Conservation* **226**, 120–126. <https://doi.org/10.1016/j.biocon.2018.07.009>.

Kenworthy, 1996; Hemminga and Duarte, 2000). At this level of depth, the amount of light reaching the seagrass plant is sufficient for photosynthesis and is equal to the plant respiration. The distribution of seagrasses may vary from 1 to 90 m (Duarte, 1991). The amount of light required for photosynthesis differs from seagrass species to species. The minimum light requirement for seagrass photosynthesis is identified as 10%–20% of sea surface light (Duarte, 1991).

Different seagrass species prefer a different level of salinity from brackish water to hypersaline seawater (Hemminga and Duarte, 2000; Hogarth, 2007). However, temperature is the primary environmental factor responsible for the global biogeography of seagrasses (Short et al., 2001; Jayatilake and Costello, 2018; Larkum et al., 2018). Temperature controls plant physiological activities such as photosynthesis, respiration, the seasonal cycle of growth, flowering and seed germination (Lee and Dunton, 1999; Short et al., 2001; Kaldy et al., 2015; Shimba and Jonah, 2017). Many studies have been focused on only one or a few species and how a few abiotic factors contributing to the distribution of seagrasses. A full study on how comprehensive all seagrass species response to all possible abiotic variables is yet to be done.

Biogeography

The composition of seagrass species varies from region to region. In 2003, Green and Short mapped the global distribution of seagrass species and identified 24 different regions each with different combinations of seagrass species (Green and Short, 2003). Short et al. (2007) identified six seagrass bioregions, namely: (1) Temperate North Atlantic (North Carolina, United States to Portugal); (2) Tropical Atlantic (including the Caribbean Sea, Gulf of Mexico, Bermuda, the Bahamas, and both tropical coasts of

the Atlantic); (3) Mediterranean (including the Mediterranean Sea, the Black, Caspian and Aral Seas and northwest Africa); (4) Temperate North Pacific (Korea to Baja, Mexico); (5) Tropical Indo-Pacific (East Africa, South Asia and tropical Australia to the eastern Pacific); and (6) Temperate Southern Oceans (New Zealand and temperate Australia, South America, and South Africa). The Tropical Indo-Pacific region had the highest species diversity with 24 species of seagrass (Short et al., 2007).

Seagrass distribution has been mapped with remote sensing and satellite imagery, aerial survey and photography, multispectral scanning, underwater video, permanent transects, occurrence records from herbariums, online database depositories, and modern computerized modeling methods (Kirkman, 1990; Green and Short, 2003; Jayathilake and Costello, 2018). Recently, the world maps of seagrass have been updated by combining over 43,000 field data records with 13 environmental variables in species distribution models (Fig. 1). The map has 30 arc sec resolution (c. 1 km at the equator) (Jayathilake and Costello, 2018) and is available at <http://data.unep-wcmc.org/datasets/46>. However, this map predicts the potential distribution of seagrass and not its abundance. Whether seagrass occurs and how much occurs at any location requires local-scale observations. Such studies can find seagrass has been lost due to human impacts (see below).

Role in Ecosystems

The seagrass biome has a three-dimensional structure analogous to terrestrial biomes. It has a vertical and horizontal distribution which provides shelter, feeding, breeding, nesting habitats for diversity animals (Beck et al., 2001; Orth et al., 2006; Jayathilake and Costello, 2018). This biome has high primary and secondary productivity and provides a home to many threatened species including dugong (*Dugong dugon*), fan mussel (*Pinna nobilis*), dwarf seahorse (*Hippocampus zosterae*), and green sea turtle (*Chelonia mydas*) (Preen and Marsh, 1995; Orth et al., 2006; Short et al., 2007; Hughes et al., 2009). As a nursery habitat for juvenile fish, it provides a significant contribution to fisheries (Lilley and Unsworth, 2014). Seagrasses are considered ecosystem engineers as they can control and maintain suitable habitat for other species by improving water quality, light availability, sediment stability, and increasing carbon and other nutrient availability (Hemminga and Duarte, 2000; Duarte, 2002; Orth et al., 2006; Bos et al., 2007; McGlathery et al., 2012).

Seagrass meadows are an important feeding ground for many marine herbivores and these secondary producers support higher trophic levels in the foodwebs (Hemminga and Duarte, 2000; Duarte, 2002; Cullen-Unsworth and Unsworth, 2013). Seagrasses capture and store carbon dioxide in their above ground and underground body mass known as blue carbon (Nellemann et al., 2009; Macreadie et al., 2014). Indeed a recent mapping of the seagrass biome (Fig. 1) has doubled previous estimates of the area it covers (Jayathilake and Costello, 2018). This means its global contribution to carbon sequestration may be higher than the current prediction. In addition to the above ecological benefits, the seagrass biome has nonconsumptive value in tourism, research, education, religion, and culture (Cullen-Unsworth and Unsworth, 2013).



Fig. 1 The MaxEnt model predicted environmental range for the seagrass biome. From Jayathilake, D. R. M. and Costello, M. J. (2018). A modelled global distribution of the seagrass biome. *Biological Conservation* **226**, 120–126. <https://doi.org/10.1016/j.biocon.2018.07.009>.

Conservation

Seagrass cover has been declining globally at a rate of 0.9% per year before 1940 and 7% per year after 1990 (Waycott et al., 2009). For the last 125 years, more than 51,000 km² area of seagrass meadows has been lost due to natural and anthropogenic disturbances (Orth et al., 2006; Waycott et al., 2009). These are also vulnerable to natural disasters at both regional (storms, cyclones, floods, hurricanes, earthquakes, disease, grazing by herbivores) and global (warming) scales (Short and Wyllie-Echeverria, 1996; Short and Neckles, 1999; Marbà and Duarte, 2010). Human-induced disturbance such as dredging, sedimentation, eutrophication, habitat fragmentation, boat anchoring and propeller scars accelerate seagrass loss (Short and Wyllie-Echeverria, 1996; Montefalcone et al., 2010). Because of their ecological importance as one of the most productive coastal vegetation, it is essential to understand in the local and global distribution, uses, threats, management and conservation values. Thus, in some areas active seagrass restoration has been undertaken. For example, fishermen in Japan created a Marine Protected Area where they banned dredging and replanted seagrass to help restore fisheries (Tsurita et al., 2017). Similar active seagrass restoration has been used to help coastal ecosystems recover from eutrophication, pollution, and dredging (van Katwijk et al., 2016).

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The Kelp Biome

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Abstract

The kelp biome is an assemblage of forest forming seaweeds of the order Laminariales (macroalgae). They occur in cool waters in shallow temperate and deep tropical seas. Similar to terrestrial forests, the kelp biome has a three-dimensional structure which provides habitats for a diversity of associated fauna and flora. Sea surface temperature, water motion, light penetration and nutrient availability control the distribution of kelp forests. Factors such as violent storms, diseases, environmental fluctuations, overgrazing, pollution, and sediment influx from land can cause loss of kelp forests. Establishing marine reserves and improving water clarity by reducing sediment inputs can restore and protect kelp forests.

Introduction

The kelp biome consists of species from the order Laminariales (brown algae) (Smale and Moore, 2017). They attached to rocky sea beds in the lower intertidal and shallow subtidal zones in temperate and subpolar region (Teagle et al., 2017). Similar to terrestrial biomes and other marine biomes (seagrass, mangrove, and zooxanthellate corals), the kelp biome has a three-dimensional (3-d) structure with plants attached to the rocky seafloor with a holdfast (Smith, 2000). These giant underwater primary producers exhibit a high diversity in growth forms and many of them grow above 30 m in length (Wernberg et al., 2019).

Morphology

As kelp members are brown algae, the plant is known as a thallus and in plural thalli. The thallus has a holdfast, stipe and blades or frond (Dayton, 1985; Wernberg et al., 2019). Similar to the angiosperm roots, the holdfast attaches the thallus to the rocky substratum. The stipe is analogous to the stem of plants and fronds function as leaves. The arrangement of stipe and fronds are the primary morphological characters to identify different species of kelp (Wernberg et al., 2019). These algae have the ability to change their morphology according to environmental conditions such as high wave action and turbulence, and population density (Fowler-Walker et al., 2006; Arenas and Fernandez, 2000).

Kelp can form three morphological groups according to the canopy height and the length of the blade, namely, "canopy," "stipitate," and "prostrate" (Dayton, 1985; Duggins, 1988; Steneck et al., 2002; Alongi, 2018). *Macrocystis* spp. form massive common canopies on the west coasts of North and South America, eastern and southern Pacific region, southern Australia and New Zealand. They are, known as giant kelp, whose fronds can grow up to 45 m (Steneck et al., 2002; Wernberg et al., 2019). The kelp species *Alaria fistulosa*, *Ecklonia maxima*, and *Nereocystis leutkeana* form canopy forests up to 10 m in height (Dayton, 1975, 1985; Steneck et al., 2002). Stipitate kelps are shorter than small canopy-forming kelps and have rigid upright stipes (Dayton, 1985). Most of the *Laminaria* species are stipitate kelps, as are some species of *Ecklonia*, *Lessonia*, *Pterygophora*, *Eisenia*, *Pleurophyucus*, and *Thalassiphyllum*. Prostrate kelps lack an erect stipe and lie on the seabed at low tide (Steneck et al., 2002). Several species of *Laminaria* form prostrate kelp forests (Steneck et al., 2002).

Taxonomy

The word "kelp" is a common term for the members of the order Laminariales. Molecular studies have clarified the familial and generic relationships in the order Laminariales (Bolton, 2010). Currently, kelp comprise 9 accepted families, 59 genera, and 144 species (Guiry and Guiry, 2018). Most of the species are in the three most common families: Alariaceae, Laminariaceae, and

Lessoniaceae. The most species rich genera are *Alaria*, *Laminaria*, *Saccharina*, *Ecklonia*, and *Lessonia* (Teagle et al., 2017). The genus *Laminaria* has 29 species and genus *Alaria* has 15 species (Guiry and Guiry, 2018) (Table 1).

Geographic Distribution

There are two to three times more kelp species present in the northern than southern hemisphere (Wernberg et al., 2019). In general, kelps are cold water adapted species (Fig. 1). However, there are deep water kelp forests in the tropics in both hemispheres comprised of *Eisenia galapagensis*, *Laminaria brasiliensis*, and *L. abyssalis* (Graham et al., 2007; Santelices, 2007; Smale and Moore, 2017). *Lessonia* is widespread in the southern hemisphere and is the only genus not present in the northern hemisphere.

Abiotic Control

The distribution of kelp forests is controlled by many environmental variables such as substratum, wave action, sea temperature, light penetration through the water, and nutrients (Steneck et al., 2002). Kelp typically anchors its holdfast to rock, boulders or cobbles (Wernberg et al., 2019). The lowest temperatures kelp occur in are 5°C in the Arctic. In the tropics, although the sea surface temperature is 23–24°C, they live at depths where the temperature is 20°C (Žuljević et al., 2016; Wernberg et al., 2019). High sea surface temperature can cause physiological stress to kelp (Gerard, 1997), and consequently range contractions and reduction of kelp cover (Voerman et al., 2013; Wernberg et al., 2016; Smale and Moore, 2017).

Like all marine plants, kelps restrict their distribution to the photic zone. Their depth distribution is limited by light, and they often grow down to 40 m depth (Wernberg et al., 2019). Some deep water tropical kelps such as *Eisenia*, *Laminaria*, and *Ecklonia* can grow down to 260 m in the Indian Ocean and Mediterranean Sea where the water column is clear enough for light penetration

Table 1 List of families and genera belonging to kelp biome (Guiry and Guiry, 2018)

Family and subordinate genera	No of species	Family and subordinate genera	No of species
Agaraceae	11	Akkesiphycaceae	1
<i>Agarum</i>	4	<i>Akkesiphycus</i>	1
<i>Costaria</i>	2		
<i>Dictyoneurum</i>	2		
<i>Neogagarum</i>	2		
<i>Thalassiophyllum</i>	1		
Aureophycaceae	1	Alariaceae	25
<i>Aureophycus</i>	1	<i>Alaria</i>	15
		<i>Eualaria</i>	1
		<i>Lessoniopsis</i>	1
		<i>Orgyia</i>	1
		<i>Pleurophycus</i>	1
		<i>Pterygophora</i>	1
		<i>Undaria</i>	4
		<i>Undariella</i>	1
Chordaceae	6	Laminariales familia incertae sedis	3
<i>Chorda</i>	6	<i>Costulariella</i>	1
		<i>Feditia</i>	1
		<i>Phyllariella</i>	1
Laminariaceae	63	Lessoniaceae	32
<i>Arthrothamnus</i>	2	<i>Ecklonia</i>	13
<i>Cymathere</i>	2	<i>Egregia</i>	3
<i>Laminaria</i>	29	<i>Eisenia</i>	5
<i>Macrocystis</i>	1	<i>Lessonia</i>	11
<i>Nereocystis</i>	1		
<i>Pelagophycus</i>	1		
<i>Polyschidea</i>	1		
<i>Postelsia</i>	1		
<i>Pseudolessonia</i>	1		
<i>Saccharina</i>	22		
<i>Streptophylloopsis</i>	1		
<i>Tauya</i>	1		
Pseudochordaceae	2		
<i>Pseudochorda</i>	2		

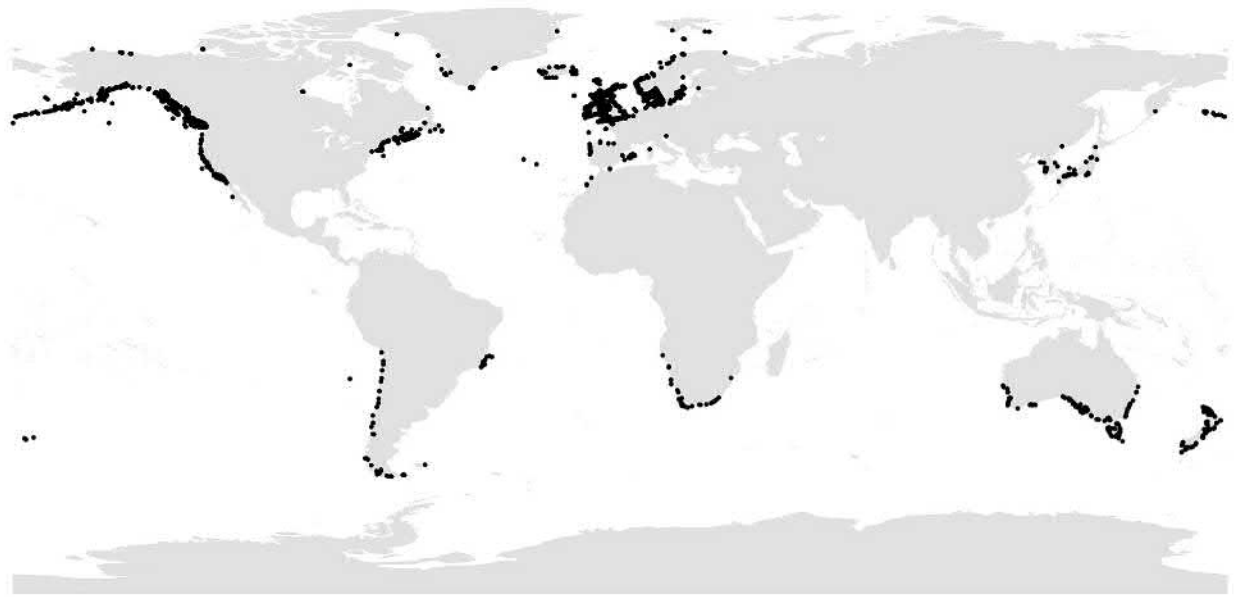


Fig. 1 The global distribution of kelp based on data from the Global Biodiversity Information Facility (2017), and the Ocean Biogeographic Information System (2017) (Jayatilake and Costello unpublished data).

(Graham et al., 2007; Žuljević et al., 2016). Kelp grows well in turbulent water. Wave action or water currents are important to supply nutrients, disperse propagules, and remove mucus and fouling organisms from the frond (Hurd, 2000; Gaylord et al., 2002).

Role in Ecosystems

Because kelp forms a major habitat, it is recognized as a keystone species and “ecosystem engineer” (Jones et al., 1994; Teagle et al., 2017). Its three-dimensional forest structure increases volume, heterogeneity and complexity (Teagle et al., 2017). Kelp can make environmental conditions more favorable for marine organisms by altering light penetration, water flow, physical disturbances and sedimentation (Eckman et al., 1989; Wernberg et al., 2005; Rosman et al., 2007; Smale et al., 2013). It provides feeding, breeding, and nesting habitats for a vast array of associated fauna and flora including fish, urchins, crustaceans, polychaetes, and mammals. Over 10 phyla live in kelp forests (Steneck et al., 2002). Through this support of biodiversity, kelp facilitates coastal fisheries and tourism.

Kelp is used as a fertilizer, food for farmed species, and food for people (Wernberg et al., 2019). Kelp and other macroalgae are cultivated commercially in Japan, Korea and China as human food (Correa et al., 2014). However, new uses are emerging. Kelp is a well-known source for three hydrocolloids: agar, alginates, and carrageenans. These are key ingredients for a range of products such as nutritional supplements, food flavors, food colors, texturing agents and stabilizers, agarose and bacteriological agar for microbiological and electrophoresis media, textile printing, and paper coating (Bixler and Porse, 2011). Kelp is the major food source in abalone and sea urchin farms (Correa et al., 2014). *Saccharina latissima* is a source of sugar, alginate, mannitol, and glucan. As kelp does not contain a lignin wall, it is easy to extract sugar by simple operations such as milling or crushing (Wargacki et al., 2012).

Kelp Deforestation

Natural factors such as storms, herbivory, pathogens, turbidity and temperature affect the distribution of kelp (Steneck et al., 2002). Natural deforestation events tend to be seasonal and/or transient. However, human activities can directly and indirectly affect kelp forest density and range and may be more persistent unless the causes are mitigated. Direct impacts occur due to kelp harvesting and high turbidity due to sediment runoff from land reducing light penetration (Wernberg et al., 2019). Indirect impacts are due to fisheries and climate change. Sea urchin populations increase when their predators, such as lobsters, crayfish, fish and otters, are removed by fishing (Smale et al., 2013; Costello, 2014). The natural “trophic cascade,” and thus kelp cover, is naturally restored in marine reserves when predator populations recover (Leleu et al., 2012). Climate change is affecting the intensity and frequency of storms (Steneck et al., 2002) which may impact kelp abundance. Ocean warming will result in kelp shifting its distribution to areas with suitable temperatures (Teagle et al., 2017) as has kelp and other seaweeds around Australia (Wernberg et al., 2011, 2016) and

Spain (Voerman et al., 2013; Piñeiro-Corbeira et al., 2016). In addition, herbivorous fish can move into higher latitudes from the subtropics and consume kelp (Vergés et al., 2016; Hobday et al., 2018).

Conservation

As mentioned previously, kelp forests are being fragmented due to the direct and indirect effects of climate change and fishing (Wernberg et al., 2013, 2019). A global map of the kelp biome would help conservation by indicating areas potentially suitable for kelp and improve quantification of the significance of kelp in the carbon cycle ("blue carbon"). In its absence, it is difficult to quantify the loss of kelp. However, studies using remote sensing are mapping kelp at local and regional scales (Bennion et al., 2018; Nijland et al., 2019).

Kelp is the most significant 3-d habitat in shallow cold temperate latitudes in terms of its spatial cover and height from the seabed. Other 3-d habitats are more limited in extent: seagrass occurs on sediments in a shallower depth range; cold-water coral reefs are deeper (e.g., Costello et al., 2005); and mangroves and shallow water coral reefs are largely absent outside the tropics and subtropics. The loss of kelp is thus of conservation significance because it provides a unique and extensive 3-d habitat, including shelter and food, for many species. It thereby contributes to the healthy functioning of ecosystems and fisheries. Recognizing this, Australian giant kelp forests have been listed as endangered under the Environmental Protection and Biodiversity Conservation Act in 2012 (Bennett et al., 2015; Teagle et al., 2017), and some Mediterranean kelp forests were listed as endangered under the IUCN Red List for the Adriatic (Žuljević et al., 2016). The loss of kelp due to fishery-induced trophic cascades, only recently discovered through observations in marine reserves (e.g., Leleu et al., 2012), is likely to be more globally widespread than presently appreciated. This adds to the loss of coastal kelp due to increased turbidity due to land-runoff from agriculture, forestry and urban development. Reducing such runoff, and creating marine reserves with no fishing of top predators will help kelp forests naturally recover.

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Marine Ecosystems of the World

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Abstract

The concept “ecosystem” is here defined as a geographic area (of any size), comprised of communities of organisms and their environment, where biological and energy interactions are greater within than with adjacent ecosystems. It has been loosely used with regard to the oceans, in part because of the difficulty in determining the spatial boundaries of an ecosystem. At least 25 marine classifications have been developed for the purpose of fisheries, and environment and conservation management, and some used the term “ecosystem.” Most were based on expert opinion or ad hoc management areas, but recent studies have used data analysis to map ecosystems at a global scale. Thus, there are now global ocean ecosystem classifications that distinguish up to 28 “units” based on environmental data analysis to a depth of 5500 m. However, whether these units have unique species communities remains to be determined. It is possible that animals move between these units vertically (diel migrations) and horizontally. The increased availability of data on species distributions will enable such questions to be answered.

The concept “ecosystem” was originally used in a publication by [Tansley \(1935\)](#). He indicated that the organism should not be regarded without its ambient environment. Afterward [Lindeman \(1942\)](#) introduced the transfer of energy between the parts of an ecosystem within this concept. Moreover, [Odum \(1953\)](#) argued that the most important contribution of the concept “ecosystem” to ecological understanding was to incorporate causal relationships among the factors in an area. Later, [Odum \(1964\)](#) developed the field of “systems ecology”, which concerned “the structure and function of levels of organization beyond that of the individual and species.” In addition, [Odum \(1968\)](#) further concluded that the core of ecosystem analysis is “eco-energetic.” Dynamic ecology, including the laws of thermodynamics, had been gradually viewed as fundamental to ecosystem theory, such as the definition of productivity as a flow of energy ([Odum, 1968](#); [Patten, 1966](#); [Watt, 1968](#)). Afterwards, with the application of computers and mathematics for modeling, the emphasis of ecosystem studies changed from description to prediction ([Cherrett and Bradshaw, 1989](#)). By synthesizing previous works, [Willis \(1997\)](#) refined the definition of ecosystem as “a unit comprising a community (or communities) of organisms and their physical and chemical environment, at any scale, desirably specified, in which there are continuous fluxes of matter and energy in an interactive open system.” Ecosystem definitions include the concepts of a spatial area delimited by physical, chemical and biological energy fluxes and interactions that are stable over years ([Odum, 1968](#); [Society et al., 1989](#); [Blew, 1996](#); [Rowe, 1997](#); [Willis, 1997](#)). Here, we also define an ecosystem as an enduring, spatially bounded environment where biological and energy interactions are greater within than with other ecosystems.

Environmental classifications help distinguish marine ecosystems, and environmental conditions determine the abundance and distribution of biological species, including fisheries ([NRC, 1999](#); [Watson et al., 2003](#)). These conditions also influence variation in oxygen concentration, absorption and release of carbon dioxide, release of water vapor and aerosols ([Schimel, 2013](#)), and atmospheric concentrations of greenhouse gases ([Doney and Schimel, 2007](#); [Archer, 2010](#)). Thus knowing how many marine ecosystems exist and their distribution could contribute to understanding biogeography, managing natural resources, and modeling sea-air interactions that influence climate.

Marine environmental classifications have been developed at different scales for the purpose of fisheries, environment and conservation management ([Table 1](#)). Twelve of these maps of marine “regions” were limited to geographic zones such as the coast, continental shelves, deep sea and open oceans. They were all limited to using only a few variables or features in their design, such as ocean color and/or previous literature. Furthermore, many of them were either adjusted by or based on expert opinion ([Table 1](#)).

Some classifications were based on geography, bathymetry and/or topography ([International Hydrographic Organization, 1953](#); [Menard and Smith, 1966](#); [Smith and Sandwell, 1997](#); [Becker et al., 2009](#); [Harris et al., 2014](#)). Others used remote sensed and/or oceanographic data ([Hayden et al., 1984](#); [Longhurst, 1995, 1998, 2007](#); [Oliver et al., 2004](#); [Irwin and Oliver, 2009](#); [Silvia De et al., 2013](#); [Bailey, 2014](#)). Only [Harris and Whiteway \(2009\)](#) used both seabed and water column variables in their classification.

Species distribution data have been less used, in part because of their limited availability at global scales. However, the distribution of pelagic species has been mapped ([Rohde and Hayward, 2000](#); [van der Spoel, 1994](#); [Rytter Hasle, 1976](#); [Banse, 1964](#)), and expert workshops ([UNESCO, 2009](#)) mapped regions based on reviews of knowledge of species and environmental conditions to propose regions for conservation management for coastal ([Spalding et al., 2007](#)), open ocean pelagos ([Spalding et al., 2012](#)), and the deep-sea ([Watling et al., 2013](#)). [Costello et al. \(2017\)](#) provided the first global scale classification across all pelagic and benthic taxa, identifying 28 “realms” based on species endemism. The boundaries between some realms are only generally known because of the lack of sufficient field data in some areas, and it is likely that seasonal variation will widen the boundaries in mid-latitudes.

Perhaps the most comprehensive and objective classifications were those based on unsupervised cluster analyses. These produced the 37 three-dimensional “Ecological Marine Units” defined to 5500 m depth by [Sayre et al. \(2017a, b\)](#), 13 three-dimensional mesopelagic units by [Reygondeau et al. \(2017\)](#), 28 biological realms by [Costello et al. \(2017\)](#), and 7 ecosystems distinguished by

Table 1 Previous global marine geographic classification mapping

<i>Publication</i>	<i>Utilized Data and Information</i>	<i>Methodology</i>	<i>Product</i>
International Hydrographic Organization (1953)	Geographic distribution of marine areas	Usage of place names	Limits of all Oceans and Seas
Banse (1964)	Physical environmental factors and species movement	Relationship examination	Vertical distribution of zooplankton
Menard and Smith (1966)	Bathymetric oceanographic charts	Hypsometric calculation	Ocean basin provinces
Rytter Hasle (1976)	Plankton from literature and additional samples	Interpolation data from phytoplankton net samples	Biogeography of some marine planktonic diatoms
Hayden et al. (1984)	Criteria based on surface currents	Oceanographic classification by surface currents (Dietrich, 1963)	A classification of marine and coastal areas
Sherman and Alexander (1986)	Maritime information in coastal regions	Experts' opinion	Large Marine Ecosystems, coastal only
van der Spoel (1994)	Previous literature	Expert opinion	Pelagic boundaries
Smith and Sandwell (1997)	Previous depth soundings and marine gravity information from spacecraft	Satellite altimetry and ship depth soundings	Sea Floor Topography
Longhurst (1995, 1998, 2007)	Ocean color and physio-chemical data	Expert opinion	Surface pelagic, not coastal
Rohde and Hayward (2000)	Distribution of scombroid fishes and their parasites	Species level analysis	Oceanic barriers
Watson et al. (2003)	LME and Longhurst publications	Synthesizing previous work	Fisheries regions
Oliver et al. (2004)	Sea surface temperature and remote sensing reflectance (chlorophyll) from AVHRR and SeaWiFS	Multivariate cluster analysis	Water masses on continental shelves
Spalding et al. (2007)	Reviewed previous regional coastal mapping	Experts' opinion	Coastal Marine Ecoregions of the World (MEOW)
Hardman-Mountford et al. (2008)	Monthly chlorophyll-a mean	Hierarchical cluster analysis	Classification of biomes based on chlorophyll-a
Oliver and Irwin (2008) and Irwin and Oliver (2009)	Sea surface temperature and ocean color data derived from MODIS/Aqua	Multivariate cluster analysis of ocean color	Biogeochemical provinces; their variation in 2007
UNESCO (2009)	Review of previous studies	Experts' opinion (Delphi method)	Global Open Oceans and Deep Seabed (GOODS) classification
Becker et al. (2009)	Ships carrying echo sounders	Ship samples and satellite derived gravitational anomaly data	Marine topography
Harris and Whiteway (2009)	Depth, slope, NPP, sediment thickness, bottom temperature, bottom DO	Multivariate analysis	Global seascapes in high seas
Spalding et al. (2012)	Previous biogeographic works	Expert opinion	Pelagic provinces globally
Watling et al. (2013)	Physical and chemical variables indicating organism distribution at the deep-sea floor	Experts' opinions based on discussions	Deep ocean floor (> 800 m)
Silvia De et al. (2013)	Remote sensing of ocean color	Shannon entropy	Oceanic phytoplankton regions
Bailey (2014)	Ocean currents, including temperature, salinity, upwellings	Dietrich (1963)'s surface currents classification	Ecoregions of ocean
Harris et al. (2014)	Bathymetry from satellite derived gravitational anomaly data	Algorithm-assisted manual digitisation	Geomorphic features on seafloor
Costello et al. (2017)	Pelagic and benthic species distribution data	Standardized cluster analysis of species occurrence data	Biogeographic realms
Sayre et al. (2017b)	3-dimensional environmental variables of temperature, salinity, oxygen, nitrate, phosphate, and silicate	K-means Clustering analysis	Ecological Marine Units
Reygondeau et al. (2017)	3-dimensional mesopelagic environmental data from Wold Ocean Atlas	Multivariate cluster analysis and boundary frequency	Mesopelagic BioGeoChemical Provinces
Zhao et al. (2018)	21 environmental variables from GMED (2014)	K-means clustering analysis using cosine similarity as distance function	7 marine ecosystems of the world ocean

analysis of 20 environmental variables by Zhao et al. (2018). The latter comes closest to representing the strict definition of ecosystems because of the more comprehensive set of data analyzed and its comparison to other classifications.

Three fully global classifications of the ocean based on quantitative environmental data analysis have been published. Oliver and Irwin (2008) applied a method which used hierarchical and k-means clustering on sea surface temperature and radiance to map 81

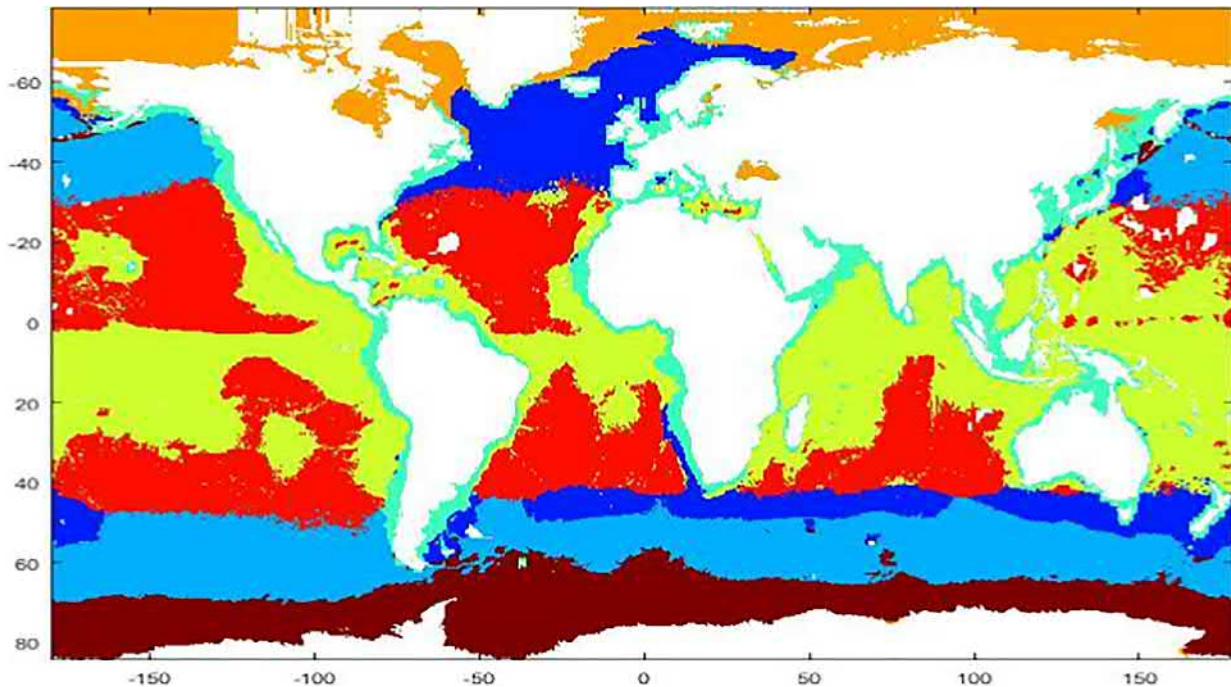


Fig. 1 Map of the 7-clusters marine ecosystem classification based on the 20 environmental variables. Different color zones present different marine ecosystems, while the white zones represent terrestrial regions and areas with no data.

“provinces.” Sayre et al. (2017b) used k-means clustering on six variables (temperature, salinity, oxygen, nitrate, phosphate, and silicate) to a depth of 5500 m. They distinguished 37 three dimensional regions named “Ecological Marine Units” (EMU), of which 22 comprised 99% of the ocean volume. However, there have been 20 environmental variables available for ocean surface waters at a global scale (Basher et al., 2014). These variables are derived from models incorporating satellite and in-situ sampling over one or more decades. They indicate epipelagic conditions to 200 m depth which is where most ocean productivity, variability and species occur (Costello and Breyer, 2017; Costello and Chaudhary, 2017; Costello et al., 2018). Thus, Zhao et al. (2018) used these 20 physical, biochemical and nutrient variables to distinguish seven global marine ecosystems by cluster analysis (Fig. 1). They also compared these ecosystems to the classifications of EMU and Realms to show where they coincided, and the location of environmental boundaries that may be significant in limiting species distributions, and/or be areas of ecological interest (ecotones).

There is thus a range of classifications of the oceans available. Strictly speaking only those classifications that comprise spatially bounded areas where energetic and ecological interactions are likely to be greater within that with adjacent areas, can be considered ecosystems. The best indications of such boundaries are derived from multivariate analyses of environmental data and species distributions. The increasing availability of globally modeled environmental data, and empirical species distribution data (Costello et al., 2015), are enabling more accurate and objective classifications.

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The Biological, Ecological, and Ecosystem Roles of Marine Amphipoda

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Glossary

- Amplexus** A type of mating behavior in which the male grasps the female about the back and they move around together.
- Biofouling** The unfavorable accumulation of microorganisms, plants, algae, and animals on submerged structures or wetted surfaces.
- Burrower** Amphipoda that excavate holes in substrata, such as sediments.
- Carpochelate** Immovable finger of gnathopods occurring on the 5th article (carpus) in some families such as Leucothoidae, Anamixidae, and Ischyroceridae.
- Dioecious** Individuals are either male or female during their life.
- Ecdysis** The molting (shedding) of an outer skin layer.
- Ectoparasite** A parasite that lives on the exterior surface of its host such as the skin.
- Filter feeders** Amphipoda that feed by filtering suspended matter and food particles from water using setose antennae or gnathopods. They may occur on soft or on hard substrates at a variety of depths.
- First maxillae** Paired structures of the mouth used for tasting and manipulating food.
- Grazers** Amphipoda which scrape and/or pluck from the substratum to consume microorganisms, diatoms, bacteria, ciliates, and/or algae.
- Infestation** Multiple parasites living on one host.
- Inquiline** Amphipoda that are commensal or parasitic in invertebrates such as sponges and tunicates.
- Lobe** A small rounded or angular process.
- Lower lip** A bilaterally symmetrical complex forming a partition behind the mouth.
- Mandibles** The pair of jaws on the sides of the mouth.
- Maxillipeds** One pair of appendages posterior to the maxillae as the rearmost structure in the mouth part field.
- Nestler** Amphipoda that hide among algae, epifauna or in crevices.
- Parthenogenesis** A form of asexual reproduction where the gamete develops into a new individual from an unfertilized egg cell.
- Predators** Amphipoda that prey upon other organisms.
- Rostrum** A small, spine-like triangular process on the front of the head.
- Scavengers** Amphipoda that feed on [material](#) such as carrion.
- Second maxillae** Pair of lobate structures posterior to the first maxillae.
- Sessile eye** Eye without a stalk.
- Setose** Covered or have some setae, bristles, spines, barbs or quills.
- Tubicolous** Amphipoda that live in a tube.
- Upper lip** A single lobe, anterior to the mouth.
- Vermiform** Long and cylindrical, worm-like.

Abstract

The order Amphipoda are commonly known as beach-hoppers, sand-hoppers, side-swimmers, scuds, or land hoppers. Previously, they consisted of four suborders with distinct habitats, namely: Gammaridea (benthic in marine to freshwater environments); Caprellidea (marine skeleton shrimps); Hyperiidea (marine pelagic parasites of gelatinous zooplankton); and Ingolfiellidea (mainly living in interstices of aquatic gravel and sediments). However, they were recently re-classified into six suborders: Amphilochidea, Colomastigidea, Hyperiidea, Hyperipsidea, Pseudogolfiellidea, and Senticaudata (includes species formerly part of Gammaridea and Caprellidea). There are almost 10,000 described species of 221 families, 444 subfamilies, and 1664 genera of Amphipoda. Around 300 terrestrial, 1900 freshwater, and 7800 marine species exist, and most are benthic. In the sea, Amphipoda inhabit coastal, tropical, polar, deep-sea, and hydrothermal vents. Eighteen fossil species have been discovered, and all are Gammaridae and Pontogammaridae, which are mostly from the freshwater environment.

Introduction

The order Amphipoda are commonly known as beach-hoppers, sand-hoppers, side-swimmers, scuds, or land hoppers. Previously, they consisted of four suborders with distinct habitats, namely: Gammaridea (benthic in marine to freshwater environments); Caprellidea (marine skeleton shrimps); Hyperiidea (marine pelagic parasites of gelatinous zooplankton); and Ingolfiellidea (mainly living in interstices of aquatic gravel and sediments (Brusca and Brusca, 1990; Lowry and Poore, 1989; Martin and Davis, 2001). However, they were recently re-classified into six suborders: Amphilochidea, Colomastigidea, Hyperiidea, Hyperipsidea, Pseudogolfiellidea, and Senticaudata (includes species formerly part of Gammaridea and Caprellidea) (Lowry and Myers, 2013). There are almost 10,000 described species of 221 families, 444 subfamilies, and 1664 genera of Amphipoda. Around 300 terrestrial, 1900 freshwater, and 7800 marine species exist, and most are benthic. In the sea, Amphipoda inhabit coastal, tropical, polar, deep-sea, and hydrothermal vents. Eighteen fossil species have been discovered, and all are Gammaridae and Pontogammaridae, which are mostly from the freshwater environment (Horton et al., 2018).

General Biology

Morphology

The body of Amphipoda is characteristically laterally compressed and held in a curved position (Fig. 1). Other body shapes are depressed, vermiform, and cylindrical as in Phliantidae, Eopliantidae, and Caprellidae, respectively (Fig. 2). Beach Amphipoda in the family Talitridae are called sand-hoppers because they can jump by rapidly extending their bodies. Most species are <2 cm in length. Some members have bright sometimes patterned body colors of red, green, and/or blue which may resemble and provide camouflage in their habitat (Lincoln, 1979).

Amphipoda have a distinct head which often curves downward and bears two pairs of antennae that are commonly long and hairy. Some Amphipoda species have a robust rostrum on the margin between the bases of antenna one. The shape of the rostrum is a useful characteristic for recognizing the family groups such as in Oedicerotidae and Synopiidae (Fig. 3A and B). Occasionally, we

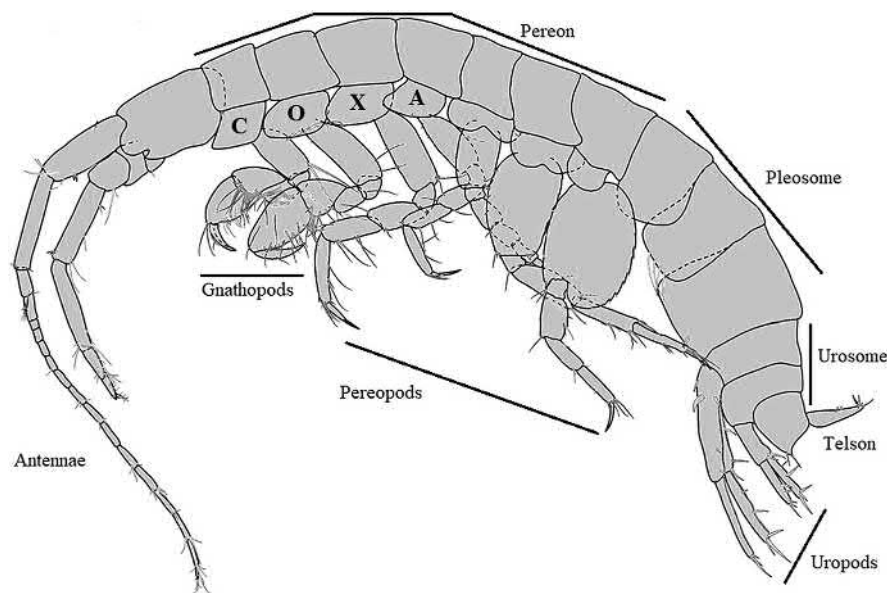


Fig. 1 Appendages of *Victorioripisa bantenensis* Arfianti and Wongkamhaeng, 2017, an eyeless marine amphipod crustacean, notes: pleopods are missing.

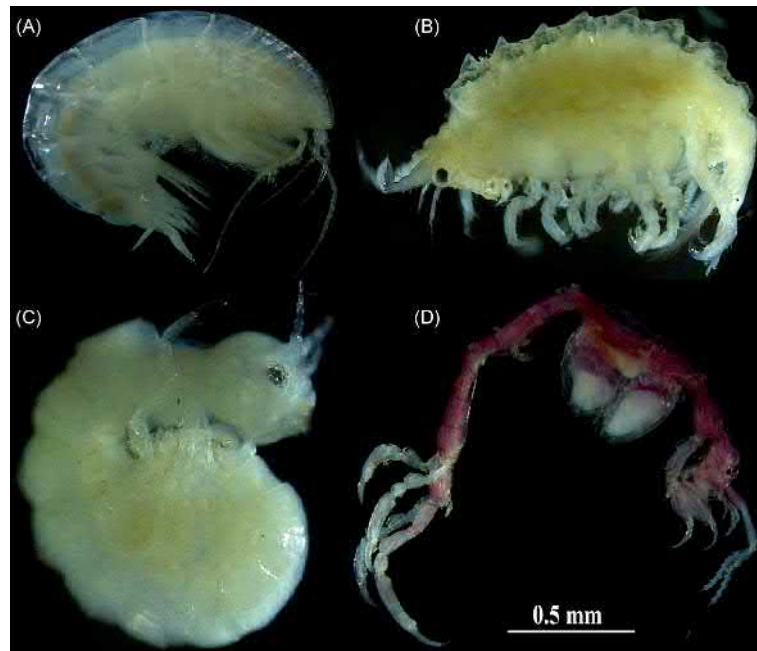


Fig. 2 The variety of body shape in Amphipoda (A) laterally compressed, (B) depressed, (C) vermiform, and (D) cylindrical.



Fig. 3 The distinct rostrum shape in Oedicerotidae and Synopiidae (A and B) and eye size in pelagic Hyperiididae (C and D).

see a lobe in the anterior part of the head which is useful for identifying some genera (Lincoln, 1979). Their eyes are sessile (not on stalks as in crabs, prawns, and lobsters) and generally well-developed. However, they vary considerably in size from tiny or absent (eyeless) as in subterranean or deep-water species, to massive in pelagic species (Fig. 3C and D). Their eyes are on the lateral surface of the head with some variations, such as where eyes are situated high on top of the enormous rostrum (e.g., Oedicerotidae) or well forward on a lateral lobe as in the Corophiidae. The mouth is on the ventral side of the head, with movable upper and lower lips, mandibles, two pairs of maxillae, and maxillipeds (Barnard and Karaman, 1991; Coleman, 2007; Lincoln, 1979).

The thoracic region of Amphipoda bears seven pairs of walking legs. The first two pairs have claws used in feeding called gnathopods, distinctively shaped in many species, such as in Leucothoidae (Fig. 4A and B). The five remaining pairs are for walking, climbing, and cleaning the anterior appendages, called pereopods. The next three pairs called pleopods are for swimming. Three pairs of uropods at the end of the abdomen are used for jumping or anchoring, can be very distinct in size, as in Platyischnopidae (Fig. 4C) (Barnard and Karaman, 1991).

The part of an amphipod's leg near the body is called the coxa. The gills attach on each side of the coxae 2–7. The shape of coxae can be very large as in Cyproideidae and Lysianassidae (Fig. 4D and E). In some species of Atylidae, the gills have a distinctive pleated shape (Fig. 4F). Above the anus or at the posterior end of the animal, there is a telson that can be cleft (Barnard and Karaman, 1991).

Sexual Dimorphism

The sexes in Amphipoda are separate and frequently show sexual dimorphism in their antennae, body size, and/or gnathopods. In many families, male Amphipoda (Fig. 5B) have longer antennae, and larger gnathopods and/or body size than females (McLaughlin, 1980; Iyengar and Starks, 2008). In Gammaridae, the enlarged gnathopods of males function for clasping the female during pairing for mating (Borowsky, 1984). The elongated antennae are for tactile detection (Steele, 1995) during mate searching and enhancing chemosensing ability (Kaufmann, 1994).

Reproduction

Sexual maturity in female Amphipoda is characterized by the presence of brood plates or oostegites, and in males by the enlargement of the second pair of gnathopods or the presence of genital papillae that occur as a small pair of projections in the seventh pereonal sternite. Marine Amphipoda are generally dioecious with external fertilization. Males and females pair up, such as by sharing tubes in tubicolous species or amplexus in gammarids (Borowsky, 1990; Strong, 1973). In at least one species, *Crassikorophium bonellii* (H. Milne Edwards, 1830), the fact that the male has never been seen indicates parthenogenic reproduction (Costello and Myers, 1989).

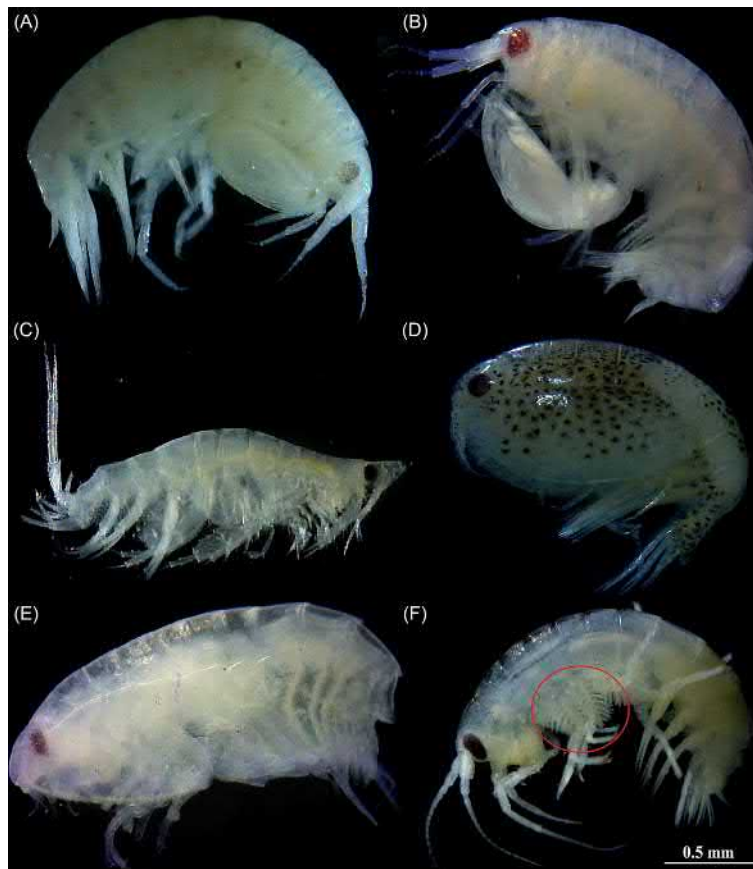


Fig. 4 The distinct gnathopods in Leucothoidae (A and B), uropod in Platyischnopidae (C), coxae in Cyproideidae and Lysianassidae (D and E), and pleated gills in Atylidae (F).

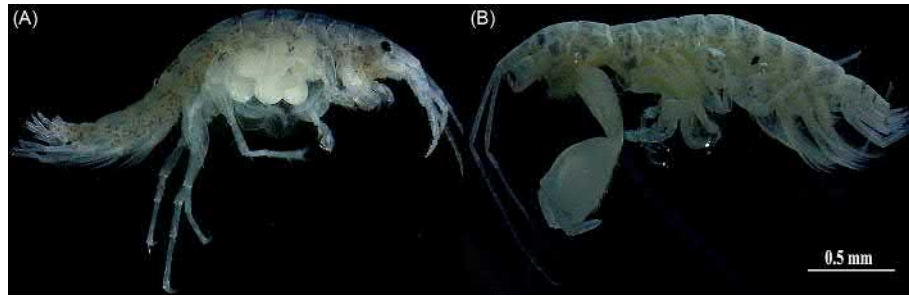


Fig. 5 Female Aoridae carrying eggs in a brood pouch (A) and male Aoridae showing enlarged gnathopods (B).

Typically, in gammarids the male will begin to pair with a female by grasping and mounting the dorsal side of a female by using the second pair of gnathopods before mating. Then, the male releases spermatophores from the ventral side of his seventh pereon into the brood lamellae (Borowsky, 1984). The embryos are deposited in a brood pouch on the underside of adult females (Fig. 5A) and will hatch into juveniles within 1–3 weeks. Juveniles remain in the pouch for some days before they are released. They have successive molts to reach maturity without metamorphosis.

Reproduction and life history are influenced by environmental factors such as food supply and temperature. Thus, Amphipoda in the low latitude areas tend to have a small body and shorter generation times than those in colder high latitudes (Aravind et al., 2007; Barnard and Karaman, 1991; Sainte-Marie, 1991).

Ecology and Behavior

Amphipoda are a crucial component in the energy flow of food webs. They link higher trophic levels, primary to secondary production, and benthic-pelagic communities. Among other vagile invertebrates in the seagrass ecosystems, Amphipoda are one of the dominant groups. Fish, birds, cnidarians, and animals such as seals prey on Amphipoda for their food (Griffiths et al., 2017; Green and Burton, 1987; Michel et al., 2016).

Amphipoda are sensitive to a broad range of aquatic pollutants. Because they live well in laboratory conditions, have a short direct life cycle, and are easy to handle and culture, they are popular organisms for ecotoxicology (Costa and Costa, 2000; Mann et al., 2010). In an experimental study, Caprellidae were considered as food for fish in aquaculture (Baeza-Rojano et al., 2014).

Amphipoda utilize diverse food resources and species may be filter, deposit, and suspension feeders; as well as grazers, predators, scavengers, parasites, and commensals (Bousfield, 1987; LeCroy et al., 2009; Watling, 1993). Most Amphipoda species are free-living, but some species are parasitic (Table 1). Studies on pelagic Amphipoda reported their vertical migration toward the sea surface during the night (Brusca, 1967, 1973; Waterman et al., 1939).

Species of the Suborder Hyperiidea are pelagic but also recognized as parasites in gelatinous zooplankton. A family from this suborder, that is, Cystisomatidae is distinct among other pelagic Amphipoda due to their large size (>100 mm in length) and transparent body, permitting us to see the internal organs (Brusca, 1981). The family Phronimidae have a unique behavior. They excavate the internal tissue of their prey such as salps, doliolids, and pyrosomes to form a transparent barrel-shaped house (Harbison et al., 1977; Hirose et al., 2005; Laval, 1978; Zeidler, 2004).

The family Cyamidae are all parasitic, known as whale lice, and are ectoparasites that crawl on the skin of cetaceans. This parasitic family is little known due to its specialized natural habitat—whales that are constantly moving and difficult to study. It is believed that infestations of Cyamidae are only possible during cetacean mating or from cetacean mother to calf, as they cannot swim well freely. Cyamidae will die if they lose their grip on their host (Iwasa-Arai and Serejo, 2018; Pfeiffer, 2009).

Calliopiella michaelsoni Schellenberg, 1925, a species from the family Calliopiidae, lives in a commensal association with gastropod molluscs (snails) to protect them from desiccation and solar irradiation. *Cardiophilus baeri* G.O. Sars, 1896, of the family Behningiellidae, lives in the mantle cavity of bivalve molluscs and gets protection and food from their host's feeding activities (Brattegard, 1963; Pirlot, 1932; Vader, 1972). Leucothoidae are also commensal Amphipoda living inside the body cavities of sessile invertebrates, particularly sea squirts and sponges (Thomas and Barnard, 1983; Thomas and Klebba, 2007).

Species of *Dyopodes*, a genus from the family Dulichiidae, secrete threads of mucus and a solid spinning thread from their specialized setae and pereopods 3–4, to construct a mast-like structure that indicates their territory and from which they capture food using their setose antennae (Mattson and Cedhagen, 1989). When a predator approaches, they move down the mast and clutch it lengthwise to make them less accessible to the predator. The amphipod family Cyphocarididae are predators of other amphipods, cladocerans, ostracods, and copepods (Yamada and Ikeda, 2000; Haro-Garay, 2003). Their body can glow (bioluminescent) as a feeding strategy to catch prey in their deep-sea habitats (Bowman, 1967; Dahl, 1979; Hessler et al., 1972).

Caprellidae are clinging Amphipoda that mostly prey on small invertebrates. The 2nd gnathopods of males have a poison tooth. The males use it for fighting other males until the death of the opponent (Takeshita and Wada, 2012). While expecting to ambush the prey, they will patiently sit and motionless for long periods with praying-mantis style body posturing. Thus, Caprellidae are also known as praying mantis crustaceans (Guerra-García and Lowry, 2009; Lowry and Stoddart, 2003).

Table 1 Variety of lifestyles, habitats, and environments of the order Amphipoda

Suborder	Superfamily	Free-living	Parasitic	Benthic	Pelagic	Marine	Brackish	Fresh-water	Terrestrial
Amphilocheia	Alicelloidea Lowry & De Broyer, 2008	+	—	+	—	+	—	—	—
	Amphilocheia Boeck, 1871	+	—	+	—	+	—	—	—
	Aristioidea Lowry & Stoddart, 1997	+	+	+	+	+	—	—	—
	Dexaminoidea Leach, 1814	+	—	+	—	+	—	—	—
	Eusiroidea Stebbing, 1888	+	—	+	—	+	—	—	—
	Haustorioidea Stebbing, 1906	+	—	+	—	+	+	+	—
	Iphimedioidea Boeck, 1871	+	—	+	—	+	—	—	—
	Leucothoidea Dana, 1852	+	—	+	—	+	—	—	—
	Liljeborgioidea Stebbing, 1899	+	—	+	—	+	—	—	—
	Lysianassoidea Dana, 1849	+	—	+	—	+	—	—	—
	Maxillipioidea Ledoyer, 1973	+	—	+	—	+	—	—	—
	Oedicerotoidea Lilljeborg, 1865	+	—	+	—	+	—	—	—
	Stegocephaloidea Dana, 1852	+	—	+	—	+	—	—	—
	Synopioidea Dana, 1852	+	—	+	—	+	—	—	—
Colomastigidea	Colomastigidea Chevreux, 1899	+	—	+	—	+	—	—	—
	Pagetinoidea K.H. Barnard, 1931	+	—	+	—	+	—	—	—
Hyperidea	Lanceoloidea Bovallius, 1887	—	+	—	+	+	—	—	—
	Phronimoidea Rafinesque, 1815	—	+	—	+	+	—	—	—
	Platysceloidea Spence Bate, 1862	—	+	—	+	+	—	—	—
	Scinoidea Stebbing, 1888	—	+	—	+	+	—	—	—
	Vibilioidea Dana, 1852	—	+	—	+	+	—	—	—
Hyperopsidea	Hyperopsidea Bovallius, 1886	+	—	+	—	+	—	—	—
	Podosiroidea Lowry & Myers, 2012	+	—	+	—	+	—	—	—
Pseudogolfiellidea	Pseudogolfielloidea Lowry & Myers, 2012	+	—	+	—	—	—	+	—
Senticaudata	Aetiopedesidea Myers & Lowry, 2003	+	—	+	—	+	—	—	—
	Alloccrangonyctoidea Holsinger, 1989	+	—	+	—	+	+	+	—
	Aoroidea Stebbing, 1899	+	—	+	—	+	+	+	—
	Ampithoidae Boeck, 1871	+	—	+	—	+	—	—	—
	Bogidielloidea Hertzog, 1936	+	—	+	—	+	+	+	—
	Calliopoidea Sars, 1895	+	—	+	—	+	—	+	—
	Caprelloidea Leach, 1814	+	+	+	—	+	—	—	—
	Carangoliopsoidea Bousfield, 1977	+	—	+	—	+	—	—	—
	Caspicoidea Birstein, 1945	+	—	+	—	+	+	+	—
	Cheluroidea Allman, 1847	+	—	+	—	+	—	—	—
	Chevalioidea Myers & Lowry, 2003	+	—	+	—	+	—	—	—
	Corophioidea Leach, 1814	+	—	+	—	+	+	+	—
	Crangonyctoidea Bousfield, 1973	+	—	+	—	—	+	+	—
	Gammaroidea Latreille, 1802	+	—	+	—	+	+	+	—
	(Bousfield, 1977)								
	Hadzioidea S. Karaman, 1943	+	—	+	—	+	+	+	—
	(Bousfield, 1983)								
	Isaeoidea Dana, 1852	+	—	+	—	+	—	—	—
	Kurioidea Barnard, 1964	+	—	+	—	+	—	—	—
	Microprotopoidea Myers & Lowry, 2003	+	—	+	—	+	—	+	—
	Neomegamphoidea Myers, 1981	+	—	+	—	+	—	—	—
	Photoidea Boeck, 1871	+	—	+	—	+	—	—	—
	Rakiroidea Myers & Lowry, 2003	+	—	+	—	+	—	—	—
	Talitroidea Rafinesque, 1815	+	—	+	—	+	+	+	+

(+) indicates present, (—) indicates absent.

As do all Aoridae, *Microdeutopus gryllotalpa* Costa, 1853 builds and inhabits individual tubes on solid substrata. They grab food resources that pass by the tube entrance. The food can be consumed directly or can be stored by gluing it to the tube for later use. Inside the tubes may be occupied by a male and female adult, or after copulation, only a brooding female. After copulation and the female having molted, the male will leave the tube voluntarily (Borowsky, 1980; Myers, 1971).

The genus *Jassa* from the family Ischyroceridae are well known as biofouling organisms and can be an initial colonizer and dominate marine biofouling systems (Barnard, 1958). As tubicolous Amphipoda, they construct tubes on floating, solid and artificial surfaces (rafts, the hulls of ship, shipwrecks), among hydrozoans, or algae (Lincoln, 1979), using a silk produced by spinning glands in pereopods 3 and 4 (Lowry, 1981; Beermann and Franke, 2012). Their tubes can attach to each other forming

thick mats with detritus, attached to various hard substrata, and they can cover clean substrata at high densities (Barnard, 1958; Dixon and Moore, 1997).

Introduced and Invasive Amphipoda

Species that are transported by human activities outside their native distributional range are termed introduced species. If they spread and/or cause harm to the environment, economy or human health, they are called invasive species. Around 5%–20% of introduced species are invasive and have negative impacts (IUCN, 2018).

At present, 58 marine, brackish, freshwater, and terrestrial Amphipoda are categorized as introduced by the World Register on Introduced Marine Species (WRiMS, Ahyong et al., 2018). Once invasive, Amphipoda can disturb the stability of an ecosystem by rapidly dominating the community and displacing native species. They also reduce biodiversity in the system through competition and predation (Cohen and Carlton, 1998; Kennish, 2002). Most introduced species are aquatic, however, some terrestrial amphipods such as *Arcitalitrus dorrieni* (Hunt, 1925) was introduced to Europe among plants imported from Australia (Costello, 1993).

Marine

Introduced Amphipoda are mainly marine and from the family Corophiidae (Ahyong et al., 2018). *Monocorophium sextonae* (Crawford, 1937) may have been introduced to Britain and Ireland among fouling on ships from New Zealand (Costello, 1993). Other introduced species in marine environments are *Elasmopus pecteniscus* (Spence Bate, 1862) and *Stenothoe gallensis* Walker, 1904. These species were introduced to the Mediterranean Sea through the Suez Canal. Due to the high number of introduced species detected, the Mediterranean Sea is the sea most affected by biological invasion (Costello et al., 2010; Strefaris et al., 2005; Zenetos et al., 2010). Two species of *Aoroides*, *A. semicurvatus* Ariyama, 2004 and *A. curvipes* Ariyama, 2004, native to Asia, were introduced into European seas through oyster transfers and shipping (Gouillieux et al., 2016).

Freshwater

Invasive Amphipoda are mostly reported from the freshwater environment. In Europe, introduced freshwater Amphipoda have led to the displacement of native Amphipoda (Costello, 1993; Dick, 1996). The displacement is through differential aggression, mutual predation, shorter generation times or higher fecundity, and different environmental tolerances (Dennert, 1974; Dick et al., 1993, 1995).

The Ponto-Caspian (Black Sea, Caspian Sea, and Sea of Azov) species *Dikerogammarus haemobaphes* Eichwald, 1841 (demon shrimp) and *Dikerogammarus villosus* Sowinsky, 1894 (killer shrimp) have invaded European freshwaters and are predicted to invade North America and worldwide in the future (Bovy et al., 2015; Rewicz et al., 2014). Other freshwater gammarids that have been introduced and are invasive in European waters are *Gammarus pulex* (Linnaeus, 1758) (to Ireland from Britain), *Gammarus tigrinus* Sexton, 1939 and *Crangonyx pseudogracilis* Bousfield, 1958 from North America to Europe.

The expansion of invasive species was accelerated by the interconnectivity of waterways through canals in Europe, ship ballasts, and bilge waters of international transportation (Nunes et al., 2015; Jazdzewski and Konopacka, 2002). Their success to out-compete resident species is aided by early sexual maturation, rapid growth rates, high fecundity, strong predatory behavior, opportunistic feeding habits, and high adaptability to wide ranges of temperature and salinity (Grabowski et al., 2007; Kinzler et al., 2009; Rewicz et al., 2014).

Conclusion

In summary, Amphipoda are small, shrimp-like crustaceans without a planktonic larval phase. They have a variety of behaviors, including mate guarding, and tube-building. As suspension and deposit feeders, and predators, they provide an important link between primary producers and predators in ecosystems. The majority are free-living, but some are parasites or commensals. Globalization and human activities have led to the arrival of several species outside their native range, some of which have become invasive in freshwaters.

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Conservation of Giant Clams (Bivalvia: Cardiidae)

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Abstract

Giant clams are conspicuous bottom-dwellers of the tropical Indo-Pacific coral reefs. To date, there are 12 recognized species divided into two genera (*Hippopus* and *Tridacna*) in the subfamily Tridacninae. Because of their large body sizes and shallow distributions, giant clams are readily found and collected, and have been a reliable traditional coastal resource (food and shells) throughout their geographic range. Unfortunately, the unsustainable levels of exploitation, coupled with loss of habitats, pollution and climate change, have threatened the survival of wild giant clam populations. Due to the nature of their reproduction (e.g., late reproductive maturity and broadcast spawning), giant clam populations are highly sensitive to stock depletion, which reduces fertilization success and subsequently, recruitment rates. To better safeguard the remaining giant clam populations, conservation actions such as listing in the CITES Appendix II and the IUCN Red List of Threatened Species have contributed to stemming further declines, and local laws have helped to manage subsistence fishing practices and curtail illegal fishing. Mariculture also has a complementary role in the conservation of giant clams, as it can produce large numbers of individuals to assist in the restoration of depleted populations. In addition to these existing measures, it is important to meaningfully engage with all stakeholders (e.g., fishers, traders, and public) on the ecological value of giant clams and consequences of overexploitation to bring about changes in attitude and lead to sustainable fishing practices.

Introduction

Giant Clams (Subfamily Tridacninae)

Giant clams are large marine bivalve molluscs that live in close association with the tropical coral reefs (Neo et al., 2017). The biggest species, *Tridacna gigas* (also known as the true giant clam) could grow over 1-m long (Rosewater, 1965) and weigh more than 250 kg (Lucas, 1994). While the smallest species of giant clams, *Tridacna crocea* (also known as the burrowing giant clam) can reach up to 15-cm long (Rosewater, 1965), it is still larger than most bivalves. These conspicuous shelled animals are readily recognizable by their large body sizes, colorful outer mantle tissues, and heavy fan-shaped shells. Unlike other bivalves, giant clams cannot fully close their shells. A common sedentary inhabitant on the Indo-Pacific coral reefs, the giant clam provides physical habitat structure and filters phytoplankton (Neo et al., 2015a), and is considered an indicator of reef health by Reef Check (Hodgson, 2001). Being a long-lived marine species, giant clams are sentinels on the reefs that may provide indications of long-term reef health and conditions.

The giant clams are scientifically classified in the order Veneroida, family Cardiidae, subfamily Tridacninae, consisting of two genera: *Hippopus* and *Tridacna* (Schneider, 2002). This means that the true cockles are their closest relatives. Currently, the 12 recognized species (Fig. 1) are mainly distributed along the shallow coasts and coral reefs from South Africa to the Pitcairn Islands, and from southern Japan to Western Australia (Neo et al., 2017). Geographically, *T. maxima* and *T. squamosa* are the most widespread, followed by the intermediate-range species, *Hippopus hippopus*, *T. gigas*, *T. derasa*, *T. noae*, and *T. crocea*, and

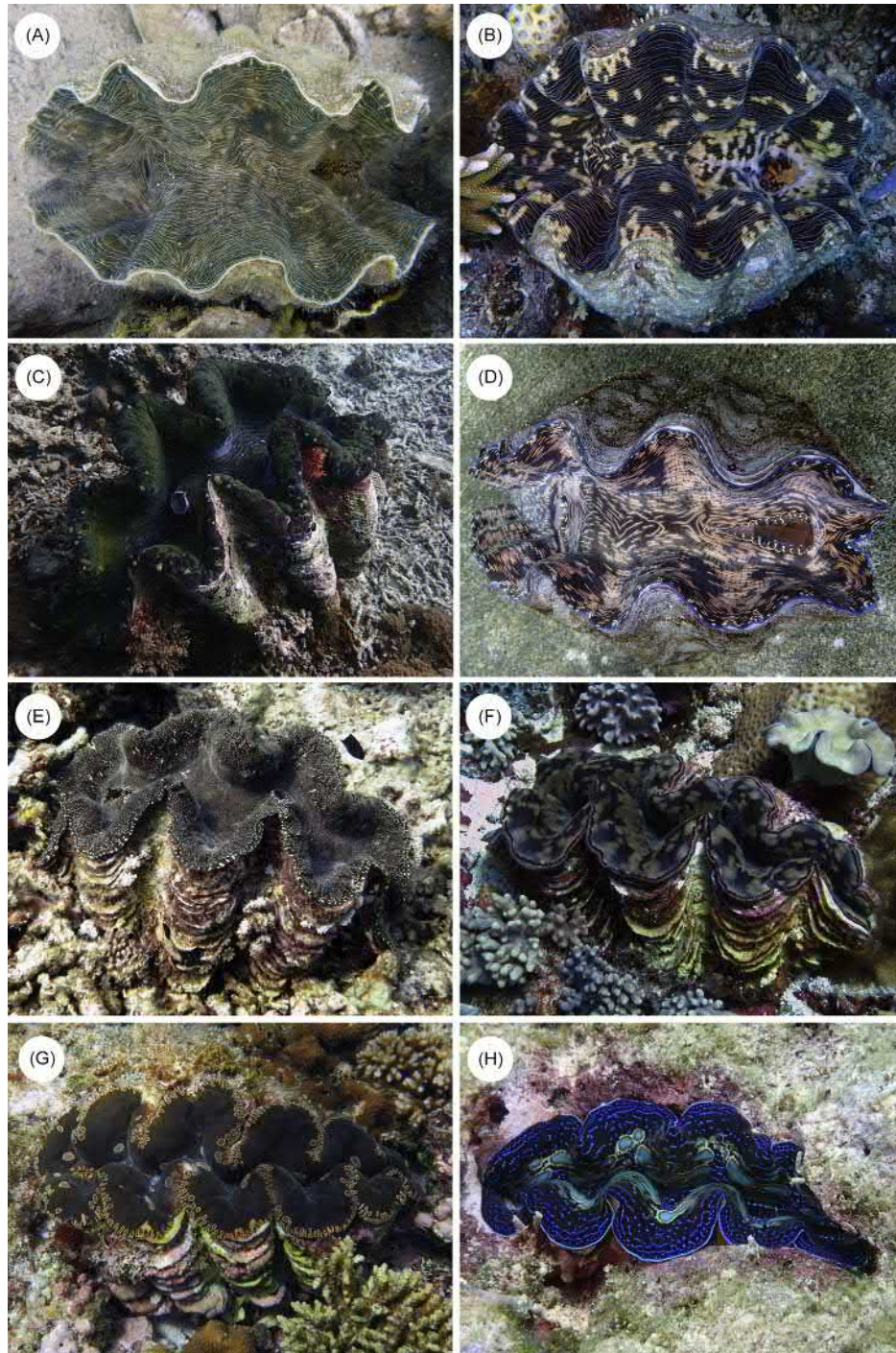


Fig. 1 Giant clam species: (A) *Hippopus hippopus*, (B) *Hippopus porcellanus*, (C) *Tridacna gigas*, (D) *Tridacna derasa*, (E) *Tridacna squamosa*, (F) *Tridacna maxima*, (G) *Tridacna noae*, (H) *Tridacna crocea*.

restricted-range species, *H. porcellanus*, *T. mbalavuana* (formerly known as *T. tevoroa*), *T. squamosina* (formerly known as *T. costata*), *T. rosewateri*, and *T. lorenzi* (Neo et al., 2017).

Biology of Giant Clams

Giant clams are simultaneous hermaphrodites: maturing first as males between 2 and 6 years of age, and later developing functional hermaphroditic gonads that produce both mature sperm and eggs (Lucas, 2014). During spawning, the release of sperm before eggs is assumed to prevent self-fertilization (Ellis, 1998), and depending on an individual's size, the number of eggs released varies from

tens of thousands (Neo et al., 2011) to hundreds of millions (Lucas, 1988). Their larval life cycle (Fig. 2) lasts for approximately 9 days prior to settlement (Crawford et al., 1987; Ellis, 1998). Fertilized eggs first develop into trochophores within 12–24 h and into shelled swimming veligers within 36 h of fertilization (Ellis, 1998). The older pediveligers (7- to 8-days old) then develop a foot that is capable of actively searching and settling onto suitable substrata (Neo et al., 2009, 2015b). Pediveligers then continue to metamorphose into juvenile spats, where they thicken and enlarge their shells and overall body size. Juvenile giant clams remain motile using their foot for locomotion (Huang et al., 2007), and search for suitable substrata (Neo et al., 2009, 2015b) or conspecifics (Sim et al., 2018) before attaching themselves on the seabed with byssal threads. Despite their high fecundity, size distributions of giant clams suggest that recruitment of juvenile clams is low, implying that mortality of early pelagic or postmetamorphic stages is high (Yamaguchi, 1977).

Like most bivalves, giant clams are filter feeders. Larvae, juveniles and adults capture suspended particulate food such as phytoplankton, zooxanthellae, micronutrients, and trace metals via their ctenidia (gills) (Fitt, 1993; Klumpp et al., 1992). In addition, giant clams obtain food from their symbiosis with zooxanthellae that live within their tissues (Belda and Yellowlees, 1995). In their early life history, eggs and larvae (called veligers) are free of symbiotic zooxanthellae (Mies et al., 2017a; Waters et al., 2016), and only in the adults will zooxanthellae be present in dense masses (Griffiths and Klumpp, 1996). The highly motile veliger larvae acquire their symbiotic microalgae via ingestion at an early stage, manifesting within their guts and selectively not digested (Nakayama et al., 1998; Waters et al., 2016). Unlike in corals, the zooxanthellae are extracellular in giant clams, occupying a tubular system within the mantle tissues (Norton et al., 1992). They serve a similar symbiotic function of using the host's waste products to produce the bulk of photosynthates (e.g., glucose, amino acids) taken up by host giant clams (Goreau et al., 1973; Ishikura et al., 1999). The steady and continuous supply of nutrients from zooxanthellae afforded the giant clams a nutritional advantage over nonsymbiotic bivalves (Hawkins and Klumpp, 1995).

In early larval stages, the free-swimming trochophores and veligers can alter their depth distribution and actively select settlement sites (Neo et al., 2015b). Subsequently, veligers metamorphose into pediveligers, which have a foot used for crawling on the seabed. The foot is also covered in cilia that allows the giant clam larva to sense and orientate to its surroundings in search of shelter (Dumas et al., 2014; Neo et al., 2009). The pediveligers, over time, become increasingly sedentary but remain mobile as they grow into juveniles and adults (Huang et al., 2007; Suzuki, 1998). Interestingly, juvenile clams have been shown to move more at night, potentially an adaptation to avoid visual predators (Soo and Todd, 2014; Suzuki, 1998). Juveniles were also observed to move nonrandomly and clump towards conspecifics (Huang et al., 2007), and further experiments have found that aggregative behavior have trade-offs between predator defense and conspecific competition (Sim et al., 2018). Some notable behavior in adult giant clams include self-righting (Fankboner, 1971), shadow responses (Stasek, 1965), and squirting reflexes (Neo and Todd, 2011), which can aid as antipredatory defenses.

Ongoing Threats and Challenges

Utilization of Giant Clams

Giant clams have benefitted people for millennia (Richter et al., 2008), and have long been an important component of fisheries in the Indo-Pacific region. Their shallow distribution, conspicuous appearance, and sessile nature make them easy to harvest with simple fishing gear. During reef gleaning, nonspecific fishing, and free-diving (Hviding, 1993), giant clams are usually opportunistically collected, or their flesh excised from the shells with knives and/or wooden sticks (Kinch and Teitelbaum, 2010). SCUBA

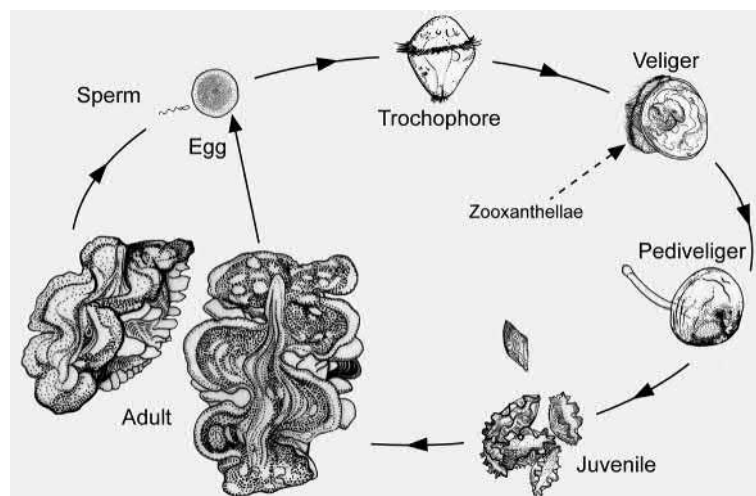


Fig. 2 Life cycle of the giant clam.

and improvised diving apparatus such as the hookah gear (a simple surface air feed) have also been used to extract clam meat underwater, hence obviating the need to retrieve the heavy shells.

Food

The giant clam forms a significant part of the diet of people living in Oceania and Southeast Asia (Munro, 1983). The entire clam, except for its kidneys, can be eaten (Hviding, 1993), and their adductor muscles are highly valuable food in Southeast Asia (Pearson, 1977). Almost all species of giant clams have been extensively used, and greater domestic needs led to an increase in subsistence fishery during the early 1970s (Juinio et al., 1989; Wells, 1982). The demand of clam meat for commercial sale had also caused rapid stock reductions across their range in the Indo-Pacific region (Dawson and Philipson, 1989; Kinch and Teitelbaum, 2010). Substantial markets for giant clams as food existed in Okinawa and Taiwan when surveyed between the 1970s and 1990s (Dawson and Philipson, 1989). In Okinawa, clam meat is considered a delicacy and remains an important element in traditional Japanese food (Anne Claus, 2017). In Taiwan, the adductor muscles once fetched prices up to US\$30 per kilogram (Shang et al., 1991). Wild populations in the Pacific Ocean were also threatened by illegal poaching carried out by Taiwanese clam vessels in foreign waters from 1969 to 1976 (Hirschberger, 1980; Pearson, 1977). Large-scale poaching continues to be a major persistent threat, as various countries (Australia, Cambodia, Malaysia, and the Philippines) have reported an increase in illegal clam fishing boats within the last 5 years (Neo et al., 2017). Commercial harvesting of wild stocks is now banned in most countries, but poorly regulated subsistence fishing can still threaten existing stocks.

Shells

There is a long history of their calcified shells being used as materials and ornament, and Table 1 provides an overview of the various uses of giant clam shells. Previously, giant clams were collected in large quantities for the ornamental shell trade, mostly exported to Japan, Australia, the United States, and Europe (Tisdell, 1994a). It was perceived that the commercial value for shells was greater than meat and adductor muscle (Juinio et al., 1987; Tisdell, 1994a). Shells were traded for decorative and utilitarian purposes, from high-value products such as jewelry to low-value uses such as aggregate in building materials (Heslinga, 1996). Also, species with colorful and large shells (e.g., *H. hippopus*, *H. porcellanus*, *T. gigas*, and *T. squamosa*) typically fetched higher prices than the smaller *T. maxima* and *T. crocea* (Juinio et al., 1987). Consequently, the supplies of shells became severely limited due to overexploitation of natural stocks (Juinio et al., 1989) or export bans (i.e., the Philippines; Neo et al., 2017). While the international trade in giant clam shells (and meat) are closely regulated by international legislation (such as CITES), the sale of shells within domestic markets remains open and popular among tourists and shell collectors (Fig. 3A and B). An example of the largest *Tridacna* shell markets today is found in China, where large fossilized shells are made into handicrafts (Larson, 2016; Fig. 3C and D).

Table 1 A summary of the various uses of giant clam shells

Use(s) of giant clam shells	Where?	Information source(s)
● Artifacts used as tools and burial ornament ● <i>Tridacna crocea</i> shells used to weigh down fishing nets ● <i>Tridacna squamosa</i> shells used as talismans against evil influences ● <i>Tridacna</i> adzes—prehistoric culture of Southern Ryukyu ● Fossilized giant clam shells made into carvings and sculptures ● Body ornament (necklace and bangles) used in traditional costumes and worn during festive seasons or weddings ● Terrazzo tiles	Ryukyu Archipelago	Asato (1991), Kinoshita (1992), and Nishihara (2004)
● Accessories, carvings, and sculptures ● Clam shell rings—traditional exchange currency and ceremonial objects ● Sacred containers—holy water font ● <i>Tridacna</i> adzes—a tool used for smoothing rough-cut wood in handicraft ● <i>Tridacna</i> shell plaques—associated with burials ● Weaponry—to throw down on approaching enemies ● Axe heads	Hainan Island, China Kedat, northern Sabah, Malaysia Karimun Java, Pulau Seribu, Indonesia Solomon Islands (Melanesia)	Larson (2016) Albert et al. (2017) Brown and Muskanofola (1985) Hocart (1931), Hviding (1993), Miller (1979), Richards and Roga (2004), Waite (1983), and Willey (1896)
● <i>Tridacna</i> adzes—a tool used for smoothing rough-cut wood in handicraft ● Domestic tools—water troughs for pigs ● Engraved <i>Tridacna</i> shell discs—cosmetic palette, decorative ornament	Manus Islands, Papua New Guinea (Melanesia) Pohnpei, Eastern Caroline Islands (Micronesia) Tuvalu (Polynesia) Libya, Iran, Iraq, Israel, Italy, Jordan	Dawson and Philipson (1989) Ayers and Mauricio (1987) Dawson and Philipson (1989) Brandl (1984, 2001), Reese (1988), and Reese and Sease (1993)



Fig. 3 Giant clam shells are sold as tourist souvenirs (A) and intricate carvings (B). The raw materials for large carvings are often the fossilized shells (C and D) that were collected from dredging of seabed.

Live aquarium industry

Growing in popularity, the aquarium trade for giant clams has become increasingly significant in the last three decades (Mies et al., 2017b). Around the early 1990s, feasibility studies were conducted in Australia and the United States to explore potential markets for giant clams as aquarium specimens (Shang et al., 1991; Tisdell, 1994b). Aquarium retailers showed interest in selling the colorful invertebrates, but expressed concerns over the lack of knowledge of aquarium care, transportation, and availability of stocks. Over time, the build-up of knowledge (e.g., Bell et al., 1997a,b) boost retailers' confidence in selling giant clams as aquarium pets. In 2001 alone, more than 100,000 live giant clams were internationally traded for the aquarium industry (Wabnitz et al., 2003) and that number has since been growing. The major countries presently exporting for the aquarium trade are Viet Nam, French Polynesia, and Palau (Mies et al., 2017b). Based on the CITES Trade Database, approximately 50% of traded specimens are cultured (CITES, 2018). However, Mies et al. (2017b) highlighted discrepancies in data reporting, pointing out the lack of traceability (i.e., whether a specimen is wild or aquacultured) and underestimated numbers of traded clams in the CITES database.

Deterioration and Loss of Habitats

The pressure of human-induced activities threatens the health of coral reef environments and hence the survival and growth of giant clams that live in them. A global meta-analysis for *T. maxima* revealed that, except for areas with very low human population density (<20 inhabitants per 10,000 m² of reef), densities of giant clams decreased with increased human presence (Van Wynsberge et al., 2016). In the northern Red Sea, abundance of giant clams was higher at sites further away from anthropogenic sources and implied that the main stressors were degraded habitats, tourism, and water pollution (Mekawy and Madkour, 2012). Environmental stressors such as reduced salinities (e.g., attributed to extended periods of heavy rainfall) could also significantly lower the survival, growth and photosynthetic performance of giant clams (Maboloc et al., 2015). Urbanization of coastal areas has been shown to negatively impact giant clam population numbers. For example, many of the reefs in Singapore where giant clams were previously found have been buried as a result of large-scale land reclamation projects (Neo and Todd, 2012). Sediment stress, a consequence of coastal development, may reduce photosynthesis and increase respiratory demands in giant clams (Elfving et al., 2001).

Climate Change

Giant clam's unique symbiotic relationship with zooxanthellae makes them particularly susceptible to the effects of warming oceans. Extremes in either temperature or ultraviolet irradiation due to climate change can lead to poor growth, bleaching (Fig. 4), and higher mortality in giant clams (Andréfouët et al., 2013; Leggat et al., 2003). Ocean acidification has also been demonstrated to exert detrimental effects in juvenile giant clams, where experimental evidence showed that they exhibit negative shell growth (Waters, 2008) and lower survival rates (Watson et al., 2012), when exposed to increasing carbon dioxide levels (~600–1000 µatm

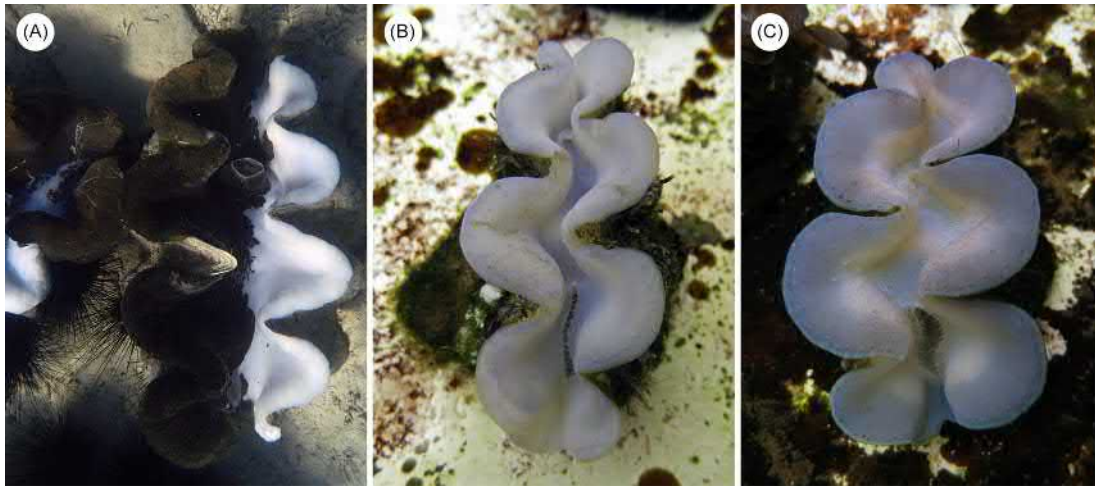


Fig. 4 Like corals, the giant clams may become thermally stressed and expel their photosynthetic symbionts. This causes their tissues to turn white, and the extent of bleaching may differ between species. During the 2016 bleaching event, some individuals of *Tridacna gigas* showed partial bleaching at the Bolinao Marine Laboratory (Bolinao, Pangasinan) in the Philippines (A), but most *Tridacna maxima* showed full bleaching at the hatchery in Singapore (B and C).

$p\text{CO}_2$). Responses of early life-history stages to the effects of climate change stressors are generally poorly understood; with only a single combined effects study demonstrating that salinities at 27 and 32 PSU had no significant effect on larvae survival but mortality increased at the higher of two temperatures tested, namely 22.5°C and 29.5°C (Neo et al., 2013a). Climate warming and acidification can lead to bleaching of stocks in hatcheries, and cause problems of algal overgrowth, poor shell precipitation, and possibly premature spawning patterns, which are all undesirable for spawning and rearing of larvae and juveniles. Thus, climate change effects may lead to lower productivity and/or survival of clams (Wilkinson and Buddemeier, 1994), raising costs for mariculture.

Consequences of Declining or Depleted Giant Clam Populations

Giant clam populations are highly sensitive to stock depletion because their reproductive success in nature requires the synchronized broadcast spawning among conspecific clams (Lucas, 1988). Synchronous spawning in giant clams is dependent on the chemical cues found on the eggs (Munro et al., 1983), although it is not understood how a clam “decides” to release which gamete type during reproduction. Upon dispersal of eggs by water currents, the chemical cues present then induce other neighboring clams to release sperm, thus allowing fertilization of eggs by sperm from different clams (Braley, 1984). Sadly, as threats aforementioned still persist today, the number of viable spawning individuals is rapidly declining. Giant clam populations consequently face imminent decline due to poor reproductive success, especially when densities in nature fall below certain (as yet undefined) levels (Beckvar, 1981; Gwyther and Munro, 1981). In areas with low densities, it has been proposed that collecting and aggregating mature giant clams in close vicinity of each other could assure greater success in fertilization (Gwyther and Munro, 1981; Huang et al., 2007). Wild stocks may also recover via the dispersal of planktonic larvae from other reefs brought in by prevailing currents (Neo et al., 2013b). Such recovery, however, may take decades if coral reefs are isolated and/or currents are unfavorable. So, methods for restocking giant clams have been developed (e.g., Waters et al., 2013).

Conservation Measures

Legislation and Regulations

Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)

Giant clams were identified as species to be included in CITES due to rapid exploitation of their wild populations in the early 1980s (Wells, 1982, 1997). All giant clam species are listed in the Appendix II of CITES, which consists of species that are not necessarily now threatened with extinction but may become so unless trade is closely controlled. All living or dead specimens, including all readily distinguishable parts and derivatives, are subject to the Treaty’s provisions for Appendix II species. CITES also states that the international trade in giant clams is permitted only if the relevant export and import certifications are issued by Parties. While dated, an earlier assessment of CITES role highlighted its shortcomings in the management of giant clams (Wells, 1997), which remains relevant for discussion. First, the effectiveness of enforcing CITES is largely dependent on whether countries involved in the trade are signatories to the Treaty, or if a nonsignatory is trading with the signatories (i.e., to trade, an equivalent of

CITES permit documentation is required from nonsignatory). Second, the scope of CITES Treaty does not manage domestic trade of giant clams within countries, regardless of their status as a Party member. Despite these limitations, the Animals Committee of CITES holds regular meetings to review trade levels of listed species and provides updates to Parties such as the animal's taxonomy and nomenclature (UNEP-WCMC, 2018).

International Union for Conservation of Nature (IUCN) Red List of Threatened Species

Giant clams were included in the first volume of the IUCN Invertebrate Red Data Book (Wells et al., 1983), which highlighted the urgency to better manage their levels of exploitation. Of the 12 recognized giant clam species, nine of them have been assessed and listed on the IUCN Red List of Threatened Species (IUCN, 2018). Four species are listed as Vulnerable: *T. gigas*, *T. derasa*, and *T. rosewateri*, based on the rate of decline of remaining wild stocks; *T. mbalavuana*, on the basis of its small and declining "area of occupancy" (Wells, 1997). *Hippopus hippopus*, *H. porcellanus*, *T. maxima*, and *T. squamosa* are listed as Lower Risk: Conservation Dependent on the basis of decline and disappearance of many populations. *Tridacna crocea* was initially excluded in the earlier assessments due to insufficient data (Wells, 1997), but was reinstated in the 1996 Red List and now listed as Lower Risk: Least Concern. *Tridacna noae*, *T. squamosina*, and *T. lorenzi* are not yet on the Red List as these species were recent rediscoveries, where data on wild stocks are limited. Also, the current Red Listings for giant clams are dated (i.e., 1996) and thus, require urgent updating to reflect current status quo of species.

Local management and enforcement efforts

Across the Indo-Pacific region, efforts to reintroduce giant clam species in places where they have been extirpated or for culturing purposes have been on-going but overall, these programs have met with limited successes (e.g., Teitelbaum and Friedman, 2008). At national level, the focus of giant clam management is lowering exploitation (see Neo et al., 2017 for detailed conservation efforts implemented throughout Indo-Pacific). For instance, some coastal communities in the South Pacific have placed stricter measures to alleviate fishing pressures, such as banning clam fishing for commercial use, setting minimum size limits for subsistence harvesting, imposing harvesting quotas or bag limits, restricting clam fishing to free diving only, and banning the use of mechanical fishing equipment (Andréfouët et al., 2013; Kinch and Teitelbaum, 2010). Results of these implemented measures vary among these South Pacific nations as it depends on the levels of exploitation (i.e., a highly exploited population will take a longer recovery time) and willingness to adopt these practices (Lucas, 1997). In addition to these measures, several countries have specific laws to protect their giant clam stocks, and Table 2 shows the level of protection given to these endangered invertebrates. Despite these collective efforts, illegal clam fishing by coastal communities still remains prevalent in many of the mentioned countries, probably due to its traditional importance as a coastal resource, coupled with the lack of manpower and funding to support monitoring, surveillance and law enforcement (Neo et al., 2017).

Mariculture of Giant Clams

The development of mariculture techniques for giant clams was spurred on by the rapid decline in natural populations due to overexploitation throughout much of their distribution (see Ongoing Threats and Challenges). Compared to other marine molluscs, the mariculture of giant clams is a relatively recent development, but has experienced rapid progress since its initiation in the 1980s (e.g., Bell et al., 1997a; Braley et al., 2018; Crawford et al., 1987; Ellis, 1998; Fitt, 1993; Heslinga, 2012, 2013; Lucas, 1994; Mies et al., 2017b). Like other aquaculture farming, most giant clam farms operate on a commercial (or semicommercial) basis, with the goal of efficient production of primary products (meat and shells) for various markets (Lucas, 1997; Mies et al., 2017b). While the mariculture of giant clams is not necessarily for conservation or sustainable exploitation of resources, it can provide cultured juveniles for restoring or enhancing wild populations (e.g., Kinch and Teitelbaum, 2010; Waters et al., 2013). Thus, supporting conservation and facilitating sustainable harvest (Lucas, 1997; Heslinga, 2012; Waters et al., 2013; Moorhead, 2018).

Restocking reefs with cultured giant clams

Mariculture and restocking of giant clam populations have proven to be effective (e.g., Gomez and Mingoa-Licuanan, 2006), although these efforts require long-term commitment and monitoring. There exist examples in Micronesia, the Philippines (Fig. 5), and Japan where mariculture and restocking have maintained momentum for over 20 years (Bell, 1999; Gomez and Mingoa-Licuanan, 2006; Kakuma and Kamimura, 2011). In addition, many of the cultured juvenile clams were shipped around the Indo-Pacific region in 1980s and 1990s, matured in ocean nurseries at the destination countries, and then used as breeding stock in local hatcheries. Aside from boosting giant clam numbers via restocking, another desired outcome is the production of local recruits by these restocked clams. There is firm evidence of this from Yap (Federated States of Micronesia) and the Philippines from restocked *T. derasa* and *T. gigas*, respectively (Cabaitan and Conaco, 2017; Neo et al., 2017). These examples are encouraging as they confirm that restocking programs can achieve reproductive sustainability, and eventually provide viable breeding stock to support local hatchery programs. Restocking is not without its challenges (e.g., Benzie and Williams, 1996; Lucas, 1997), but four decades of experience in this endeavor have shown that the most reliable approach is to implement well-managed, financially sustainable giant clam hatcheries and well-defended ocean nurseries (Heslinga, 2013).

Table 2 A brief overview of existing legislations pertaining to the in-situ protection of giant clams

Country	Law and regulation
Australia	The harvest and trade of giant clams managed under the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act)
China	Protected under the Marine Environment Protection Law of the People's Republic of China (Li, 2013). <i>Tridacna gigas</i> is the only species listed as Category 1 protection at national level, which is the highest protection afforded in China under their Wild Animal Protection Act
Cook Islands ^a	Gathering of giant clams for export and sale is prohibited under several by-laws such as the Aitutaki Fisheries Protection By-Laws (1990) and Penrhyn (Prohibition on Exportation of Pasua) By-Laws (2007)
Federated States of Micronesia	Only Yap and Kosrae states have laws regarding use of giant clams (Smith, 1992). The Yap State Code (Title 18, Section 1006, Protection of clams) prohibits harvest of giant clams for commercial sale, but not enforced. Under the Kosrae State Code Section 13.523, a sanctuary area is declared for the purpose of protecting giant clams
Fiji ^a	Under the Fisheries Act of 1942 (Cap 158), the export of giant clam meat from Fiji of the following species (<i>Tridacna derasa</i> , <i>T. squamosa</i> , <i>T. maxima</i>) is prohibited
French Polynesia ^a	The Délibération n° 2007–98 APF (2007) regulates activities relating to collection, breeding and repopulation of giant clams
Guam ^a	No commercial harvesting of giant clams allowed under the Fishing Regulations (Cap 12)
India	Of the species inhabiting Indian waters, <i>Hippopus hippopus</i> , <i>Tridacna maxima</i> , and <i>T. squamosa</i> , except <i>T. crocea</i> , are legally protected as Schedule I species under the Wildlife Protection Act of India (1972) (Apte et al., 2010)
Indonesia	Seven species inhabiting Indonesian waters included on the national list of protected species since 1987 under the Surat Keputusan Menteri Kehutanan No. 12/Kpts/II/1987 (Nijman et al., 2015). Now consolidated under the Conservation of Living Resources and their Ecosystems Act, 5/1990, specifically the Government Regulation No. 7/1999 on Preserving Flora and Fauna Species that provides the criteria for specifying protected species (Ezekiel, 2018)
Japan	Prohibits recreational fishing of giant clams under the Okinawa Prefectural Fisheries Regulations. Failing to observe the rules is an infringement of the Japanese Fisheries Law (Okinawa Prefectural Government, n.d.)
Malaysia	Protected under the main Fisheries Act No. 317 (1985), specifically defined by the Fisheries (Control of Endangered Species of Fish) Regulation (1999), where it is an offense to capture giant clams (Ezekiel, 2018). The latter lists four species: <i>Tridacna gigas</i> , <i>T. squamosa</i> , <i>T. maxima</i> , and <i>T. crocea</i> (Gomez, 2015)
Mauritius	Protected under the Fisheries and Marine Resources Act 2007 and it is considered illegal to possess them (Ramah et al., 2018)
Myanmar	The Department of Fisheries Notification for Control of Endangered Fish Species lists protected species, including giant clams (Ezekiel, 2018). It is an offense to capture giant clams as specified in this regulation
New Caledonia ^a	Regulations exist in the Northern and Southern Provinces to manage local harvest of giant clams
Niue ^a	Under the Domestic Fishing Act (1995), gathering of giant clams whose size is less than indicated in the Domestic Fishing Regulations (1996) is not allowed
Palau	Under the Domestic Fishing Laws of Palau (Ref. 27 PNCA 1204), it is against the law to export any of the seven species present in Palau waters, or part thereof, regardless where the species may have originated, except cultured ones (SPC/BMR, 2012)
Papua New Guinea	Managed by National Fisheries Authority under the Fisheries Management Act (1998) and Fisheries Management Regulation (2000) (Yaman, 2009)
Philippines	Protected under The Philippine Fisheries Code of 1998 (Republic Act No. 8550). Under this law, all species listed on CITES (including giant clams) are considered “endangered” and may not be taken without a special permit from the Bureau of Fisheries and Aquatic Resources (Gomez, 2015)
Republic of Kiribati	Management and protection of endangered species under the Fisheries Act, Section 22 and the Environment Act, Section 24 (Kinch and Teitelbaum, 2010)
Samoa	The Fisheries Management Act 2016 prescribes measures for the protection of giant clams (Moorhead, 2018)
Solomon Islands	General management and regulation of giant clam fishery under the Fisheries Act 1998 and the Fisheries Regulation 1998 (Kinch and Teitelbaum, 2010). The latter includes banning the harvesting of wild giant clams for commercial sale
Thailand	Protected under the current Royal Ordinance on Fisheries B.E. 2558 (2015) (previously known as the Fisheries Act 1947) that prohibits fishing of giant clams (Knight et al., 2010). Giant clams given “protected” status under ministerial regulations issued under Section 6 of Wild Animal Reservation and Protection Act No. 3 (2003) (Ezekiel, 2018)
Tonga	Protected under the Fisheries Act 1989, while their harvest is managed under the Fisheries Management Regulation 2008, which prohibits the sale of giant clams in local market without its shells to ensure the clam meets the size limit for each species (Kinch and Teitelbaum, 2010)
Vanuatu ^a	Under the Fisheries Act 2005 (Cap 315), specifically the Fisheries Regulations Order No. 28 (2009), the harvesting of wild giant clams for export is not permitted
Viet Nam	The Ministry of Agriculture and Rural Development Decision No. 82/2008/QĐ-BNN listed three species of giant clams, based on IUCN criteria v2.2 and 2007 Red Book for Viet Nam (Ezekiel, 2018)

^aInformation retrieved from Coastal Fisheries Species Regulations, Management Plans and Legislation in Pacific Island Countries and Territories, SPC Coastal Fisheries Programme. [Online] <http://www.spc.int/CoastalFisheries/CFM/LegalText/ByJurisdiction> (Accessed on 17 December 2018).



Fig. 5 The Bolinao Marine Laboratory, which is part of the University of the Philippines's Marine Science Institute, is one of the longest standing giant clam mariculture programs. The program's focus has been on *Tridacna gigas* (inset), but has bred and farmed other species over the years. The laboratory also runs training courses on handling and culturing giant clams.

Conclusions

Giant clams are endangered in many parts of their geographic distribution. The biggest driver of decline is probably overharvesting for human use (food and materials). Habitat loss, coastal development, pollution and climate change are additional factors that can negatively impact their survival. To highlight the plight of giant clams, conservation measures such as the CITES listings and IUCN Red List of Threatened Species raised awareness of the threats, as well as the enforcement of existing local laws regulates (or bans) both subsistence and commercial fishing. In addition, mariculture and restocking to help maintain population numbers have had some success. Scientific research on giant clams over the years has also helped to reinforce the case for protecting these charismatic molluscs. Moving forward, modern conservation approaches such as biophysical modeling and molecular genetics can help solve basic questions such as larval dispersal and connectivity, fishery projections, and population genetics. Besides science-based conservation and management, it is critical to involve all stakeholders and improve conservation literacy through education, outreach, and capacity building. Highlighting the ecological benefits of giant clams and consequences of overexploitation can help bring about changes in attitude and lead to improved fishing practices.

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The Coral Triangle: The Most Species Rich Marine Region on Earth

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Abstract

The Coral Triangle encompasses parts of South-East Asia and the Western Pacific and is a priority for marine biodiversity conservation because it has the highest species richness, and endemism, of any marine region globally. Considered to be the region with the world's highest shallow-water reef-building coral species, reef fishes and mangrove biodiversity, this region also comprises important habitats for threatened species. Areas of high biodiversity importance are clustered along the southern part of the Philippines, the north-eastern part of Malaysian Sabah, central to eastern part of Indonesia, the eastern part of Papua New Guinea and the Solomon Islands. Yet, the marine resources in this region are threatened by various human-induced factors and climate change-induced impacts.

Biodiversity Significance of the Coral Triangle Region

The Coral Triangle (CT) region is a marine area situated along the equator between the Indian and the Pacific Oceans. It encompasses parts of South East Asia and Melanesia and includes the Exclusive Economic Zone (EEZ) of six countries: Indonesia, Malaysia, The Philippines, Papua New Guinea, Timor-Leste, and Solomon Islands, as well as the EEZs of two adjacent nations: Brunei Darussalam and Singapore (Fig. 1). This region has been referred to as the "Indo-Malayan Triangle" (Burke et al., 2002), the Indo-Malay-Philippines Archipelago (Carpenter and Springer, 2005), the "East Indies Triangle" (Briggs, 2005), and by many other names reviewed by Hoeksema (2007). Scientists have proposed an ecological boundary of the CT based upon the 500 species isopleth for reef-building coral species richness (e.g., Green and Mous, 2008; Veron et al., 2009).

The Coral Triangle has been known as the global epicenter of shallow marine biodiversity. The main reef types found in the region are fringing, patch, and barrier reefs, with total coverage of 43,577 km² (UNEP-WCMC et al., 2010). In terms of coral diversity, the CT region contains more than 605 zooxanthellate corals, including 15 regional endemics (Veron et al., 2009), with the center of diversity spanning from the Philippines to the eastern part of Indonesia (Hoeksema, 2007). The highest diversity has been found in the Birds Head Seascape of Papua-Indonesia, which hosts up to 577 species of scleractinian corals (Mangubhai et al., 2012). This region also has many deep-sea scleractinian corals with more than 110 species of azooxanthellate scleractinian corals in the deep-water between the Philippines and New Caledonia (Cairns, 2007).

Considered to be the area with the world's highest mangrove biodiversity, 36–46 species out of the world's 70 mangrove species have been found in the region (Polidoro et al., 2010). Of these, 15% have been classified as threatened species. The mangrove forests cover an area of 41,318 km² (Giri et al., 2011a, 2011b) and over 65% of them are distributed in the coastal area of Indonesia (Fig. 2).

Seagrass meadows cover an area of 3263 km² of the CT (Beger et al., 2013). Sixteen out of 60 of the world's seagrass species have been found in the Coral Triangle, mainly on the reef flats (Wilkinson, 2008; Short et al., 2011). The highest diversity was found in the Philippines (14 species), followed by Papua New Guinea and Indonesia (12 species) (Fig. 2) (Green and Short, 2003).

Allen (2008) highlighted that the world's center of reef fish species richness extended from Indonesia to Papua New Guinea and the Solomon Islands, and northward to the Philippines. The Indonesian archipelago contains more than 2122 species of reef fishes (Allen, 2008), and the central Philippines is the world's reef fish epicenter (Carpenter and Springer, 2005). In total, the CT region supports more than 3250 species of reef fishes (Sanciangco et al., 2013) which comprise 52% of Indo-Pacific reef fish (37% of the world's reef fish) (Allen, 2008). The CT is also a center of fish species endemism, with endemism concentrated around Raja Ampat in the Bird's Head Seascape of Indonesian Papua (Fig. 3).

This region also comprises important habitats for threatened species. Six out of seven of the world's sea turtle species inhabit the Coral Triangle's marine and coastal areas as their nesting beaches, feeding grounds, and migratory routes. These turtle species are *Eretmochelys imbricate* (hawksbill), *Dermochelys coriacea* (leatherback), *Chelonia mydas* (green), *Caretta caretta* (loggerhead), *Lepidochelys olivacea* (Olive Ridley), and *Natator depressus* (flatback) (MoF-MoMAF, 2010). The Papuan Beach of Jamursba

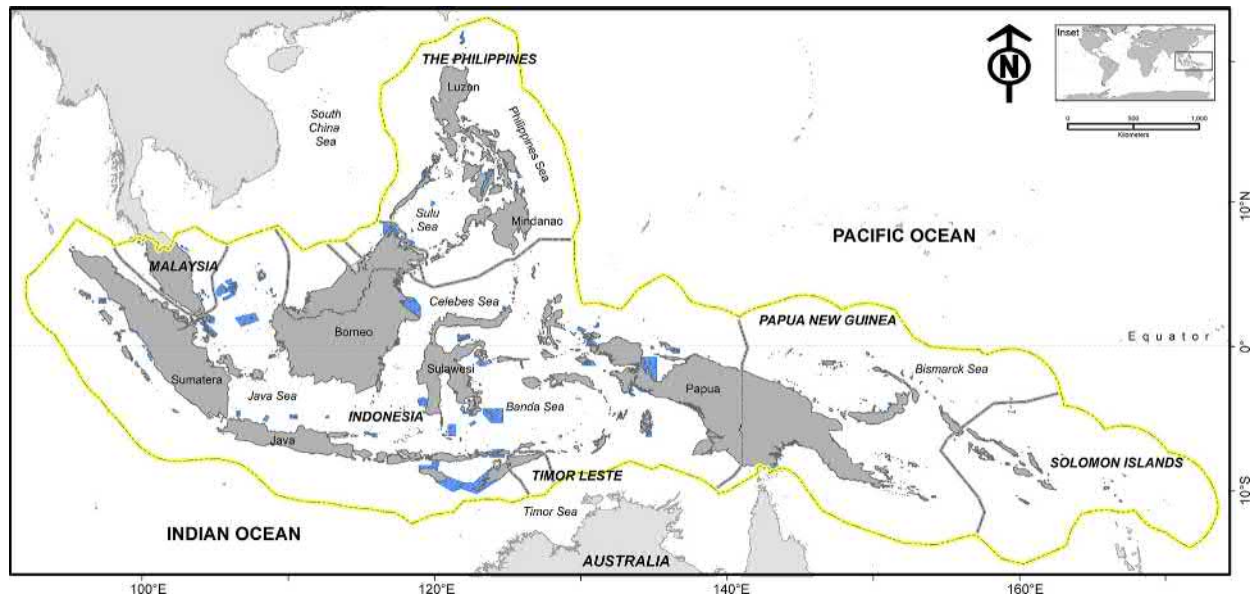


Fig. 1 Map of the Coral Triangle, showing Coral Triangle countries EEZ outer boundaries (yellow-dashed line) and distributions of nearly 2000 units of Marine Protected Areas (blue). Country boundaries are indicated by a gray-dashed line.

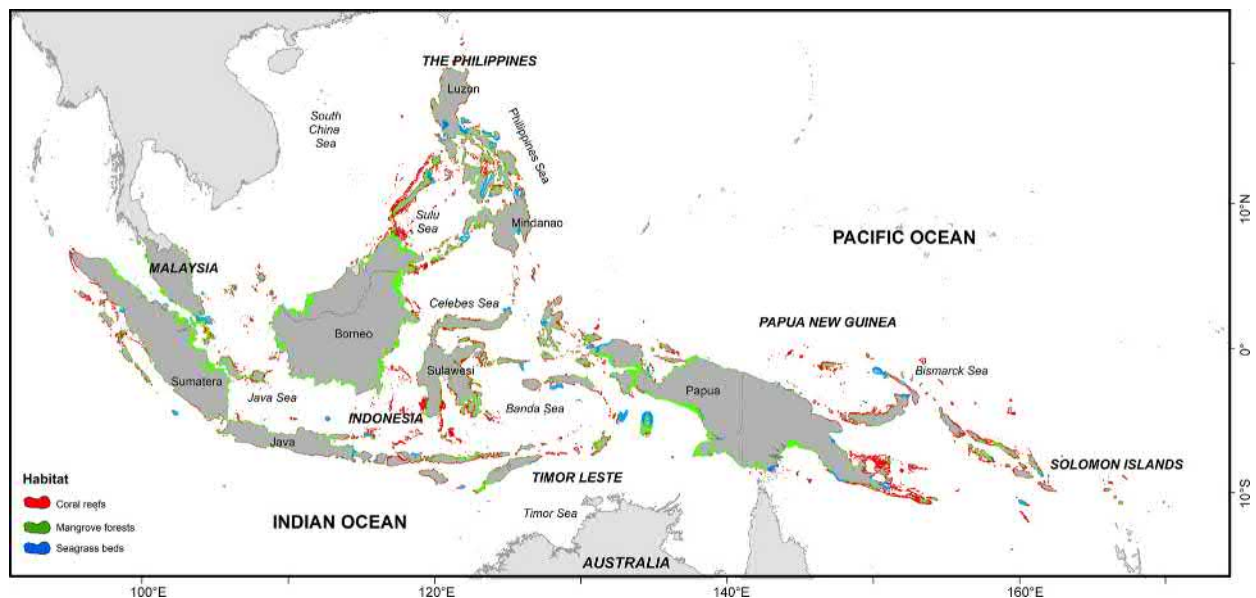


Fig. 2 Distribution of three biogenic habitat within the Coral Triangle: Coral reefs (red), mangrove forests (green) and seagrass beds (blue). The largest coverage of biogenic habitat was coral reefs followed by mangrove forests and seagrass beds (UNEP-WCMC et al., 2010; UNEP-WCMC and Short FT, 2005; Giri et al., 2011a,b). Adapted from Asaad, I., Lundquist, C. J., Erdmann, M. V., and Costello, M. J. (2018a). Delineating priority areas for marine biodiversity conservation in the Coral Triangle. *Biological Conservation* 222, 198–211. <https://doi.org/10.1016/j.biocon.2018.03.037>.

Medy-Wormon is one of the most significant rookeries for leatherback turtles (Hitipeuw et al., 2007; Mangubhai et al., 2012). It comprises 75% of the total leatherback nesting in the western Pacific and represents the last important nesting population in the entire Pacific (Tapilatu and Tiwari, 2009).

Several species of marine mammals are also found in this region, ranging from cetaceans (whales, dolphins, and porpoises), and sirineans (dugongs). More than 31 species of cetaceans have been found in Indonesian waters (Rudolph et al., 1997). Approximately 15 species have been sighted in the Bird's Head Papua region include Bryde's whales, False killer whales, sperm whales, Indo-Pacific humpback whales, Pan-tropical spotted dolphins and Fraser's dolphins (Kahn, 2007; Mangubhai et al., 2012).

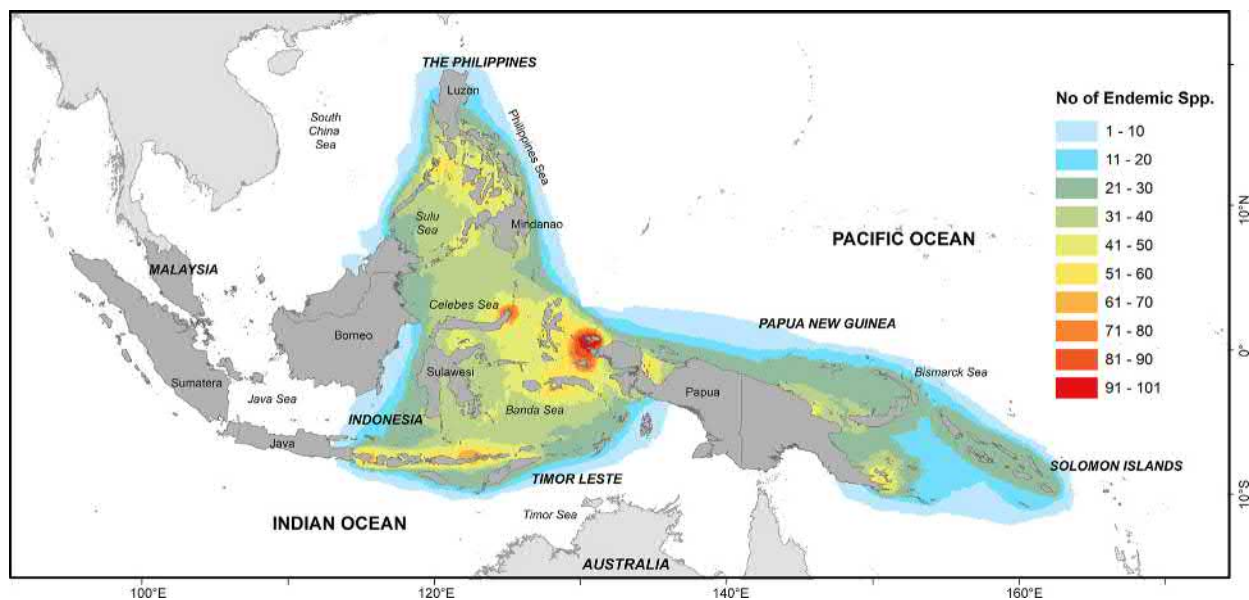


Fig. 3 Distribution of 373 endemic reef fishes within the Coral Triangle. The highest concentration (red) was found in the Raja Ampat Archipelago of Indonesian Papua with over 100 endemic species (Allen and Erdmann, 2013). Adapted from Asaad, I., Lundquist, C. J., Erdmann, M. V., and Costello, M. J. (2018a). Delineating priority areas for marine biodiversity conservation in the Coral Triangle. *Biological Conservation* 222, 198–211. <https://doi.org/10.1016/j.biocon.2018.03.037>.

Areas of Biodiversity Importance

Because the Coral Triangle is the global rich-spot of marine biodiversity, there is a great interest to understand the spatial pattern and distributions of marine biodiversity in the region. Asaad et al. (2018a) identified areas of highest importance for biodiversity protection in the Coral Triangle based on ecological criteria derived from a critical review of international conservation policies (Asaad et al., 2016). The data used for the criteria were: (1) sensitive biogenic habitat was analyzed based on the spatial distribution mangrove forests, seagrass meadows and coral reefs; (2) modeled geographic distributions and occurrence records of species to evaluate the criterion of species richness; (3) distributions of species of special conservation concern; (4) distributions of endemic reef fish species; and (5) distribution of nesting sites and migratory routes of sea turtle species.

Asaad et al. (2018a) found that the areas of the high biodiversity importance (*biodiversity rich spots*) were along the southern part of the Philippines, the north-eastern part of Malaysian Sabah, central to eastern part of Indonesia, the eastern part of Papua New Guinea and the Solomon Islands (Fig. 4). These included seven sites with the richest biodiversity: three sites in the Philippines (i.e., the Verde Island Passage, the southern part of Negros Island and Cebu Island) and four sites in Indonesia (i.e., the northern tip of Sulawesi, Ambon Island, Kei Islands, and Raja Ampat Archipelago) (Fig. 3). These sites contained the full range of biogenic habitat, and were predicted to be inhabited by more 4000 marine species. Three sites (i.e., northern tip of Sulawesi, Kei Island, and the southern part of Negros Island) were also identified as important habitat for three species of sea turtle. The Raja Ampat Archipelago hosted more than 100 species of restricted-range reef fishes, which was the highest number in the Coral Triangle region and probably for all oceans (Fig. 5).

Threats to Biodiversity

The marine resources in the Coral Triangle region are threatened by various indirect and direct human-induced factors including destructive fishing practices, overfishing, pollution and coastal development (Burke et al., 2012; Green et al., 2014). In addition, climate change-induced impacts such as rising sea-level, increasing sea-surface temperature, and ocean acidification are likely to add to these threats (Hoegh-Guldberg et al., 2009; McLeod et al., 2010).

Burke et al. (2012) found that the most destructive threats to the coral reefs in the Coral Triangle region are unsustainable and damaging fishing practices. Indonesia has banned trawling throughout its Exclusive Economic Zone (MoMAF, 2016) and imposed a heavy penalty to the illegal fishing activities. Other destructive fishing methods such as the use of dynamite (blast fishing) and poisonous fishing, although prohibited by law, are still practiced along the coasts of the region (Table 2) (Burke et al., 2012; Bacalso and Wolff, 2014; De Alessi, 2014). In addition, an excess of land-based run-off and sedimentation has led to declines in coral cover, reduced coral diversity, and increased bioerosion along the coasts of Indonesia and the Philippines (Fabricius, 2005).

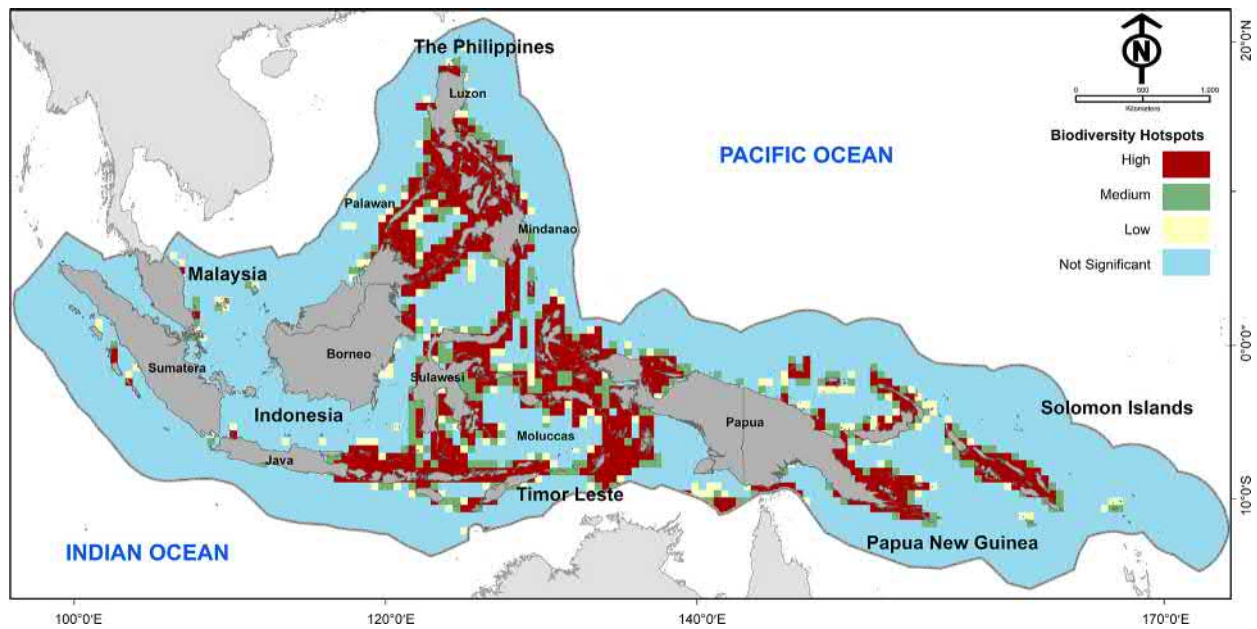


Fig. 4 Map of clusters of cells of biodiversity importance in the Coral Triangle. Areas of the high biodiversity importance were clustered along the southern part of the Philippines, the north-eastern part of Malaysian Sabah, central to eastern part of Indonesia, the eastern part of Papua New Guinea and the Solomon Islands. Adapted from Asaad, I., Lundquist, C. J., Erdmann, M. V., and Costello, M. J. (2018a). Delineating priority areas for marine biodiversity conservation in the Coral Triangle. *Biological Conservation* 222, 198–211. <https://doi.org/10.1016/j.biocon.2018.03.037>.

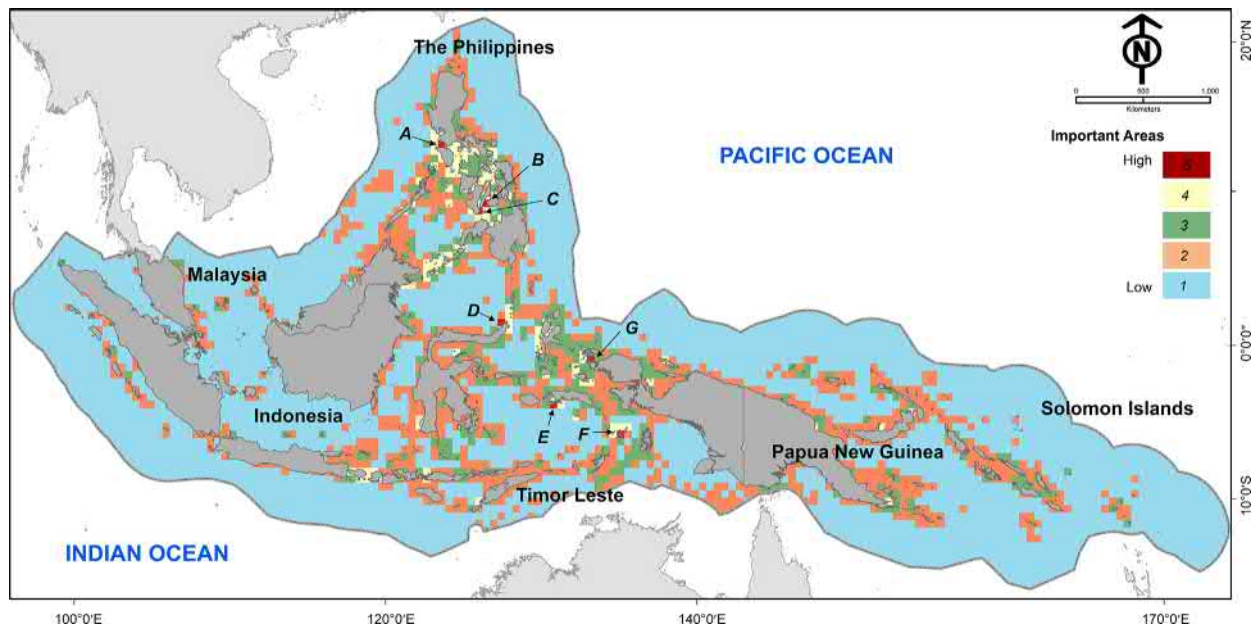


Fig. 5 Map showing sites of biodiversity importance in the Coral Triangle. The most significant sites included: (A) Verde Island Passage (between Luzon and Mindoro Island), (B) Negros Island, (C) Cebu Island, (D) Northern tip of Sulawesi, (E) Ambon Island, (F) Kei Islands, and (G) Raja Ampat Archipelago of Indonesian Papua. Adapted from Asaad, I., Lundquist, C. J., Erdmann, M. V., and Costello, M. J. (2018a). Delineating priority areas for marine biodiversity conservation in the Coral Triangle. *Biological Conservation* 222, 198–211. <https://doi.org/10.1016/j.biocon.2018.03.037>.

The Coral Triangle region has also experienced a high rate of mangrove forest loss caused mainly by habitat conversion to aquaculture, human settlements, infrastructure and timber logging (Table 1) (Wilkinson, 2008; Primavera, 2000). In Indonesia, mangrove forests were categorized as 31% in good condition, 27% moderately destroyed and 42% heavily destroyed (Kusmana, 2014).

Large marine species are also experiencing threats of extinction (Polidoro et al., 2008). In the Coral Triangle region, shark fisheries increased during the last decade due to growing demand for shark products, including fins, flesh, oils, and skins (Lack and Sant, 2011; Lack and Sant, 2012).

Table 1 Known threats and impacts to marine biodiversity elements in the Coral Triangle

<i>Habitat and species</i>	<i>Threat</i>	<i>Impact</i>	<i>References</i>
Coral reefs	Anthropogenic (Coral Triangle region)	85% under pressure	Burke et al. (2012)
	Terrestrial run-off (Indonesia)	Reduction of 30%–60% coral diversity	Edinger et al. (1998)
	Blast fishing	Net loss of community equal to US\$ 306,800 per km ² of coral reef	Pet-Soede et al. (1999)
	Coral Bleaching (Tubbataha NP, Philippines, 1998)	22% declined life coral cover	Burke et al. (2012)
Mangrove forests	Conversion to aquaculture ponds, settlements and port developments, harvesting for pulp productions (South East Asia, 1998)	Loss of >50%	Wilkinson (2008)
	Conversion to aquaculture ponds (Philippines, 1950–1998)	Loss of >50%	Primavera (2000)
Seagrass beds	Coastal development	Loss of 30%–60%	Unsworth and Cullen (2010)
	Infrastructure development (Indonesia)	Reduction of >26% seagrass habitat	UNEP (2004)
Sharks	Persistent siltation due to deforestation (Sabah-Malaysia)	Significant decline	Freeman et al. (2008)
	Shark fisheries (Indonesia)	Annual catch = 109,924 t (first world's largest shark harvest)	Lack and Sant (2012)
Sea turtles	Shark fisheries (Malaysia)	Annual catch 23,808 t (10th world's largest shark harvest)	Lack and Sant (2012)
	Fisheries by-catch (Indonesia)	7700 killed every year	Dirhamsyah et al. (2014)
	Legal catch (Papua New Guinea)	> 15,217 turtles per year	Humber et al. (2014)

Further climate change related stressors that may affect marine resources include the raising of sea-surface temperatures. In the year of 1998 (Wilkinson, 2008) and repeatedly in 2010 (Maynard et al., 2012), coral reefs in several locations in this region were severely impacted by mass coral bleaching and mortality events. The severity of bleaching increased between the events in 1998 and 2010 (Heron et al., 2012). In the Philippines, the 1998 coral bleaching was found in the Tubbataha Reef National Park (Table 1) (Burke et al., 2012), while in Indonesia, the 2010 coral reef bleaching was spread-over Indonesian reefs. Severe bleaching was found in the Sumatera and Sulawesi reefs, and minor bleaching was reported in Java, Bali, Moluccas and Papuan reefs (Tun et al., 2010). These bleaching events are become more common, and possibly their frequency is exceeding the time required for recovery in between bleaching events (Heron et al., 2016; Hughes et al., 2018).

Marine Protected Areas

Marine Protected Areas (MPA) have been recognized as the primary mechanism to protect biodiversity and are widely advocated as an effective tool for conserving and managing biodiversity (Brooks, 2010; Costello 2014; Costello and Ballantine, 2015; Venter et al., 2014). MPA have been defined as “a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve a long-term conservation of nature with associated ecosystem services and cultural values” (Dudley 2008). This broad MPA definition has been applied to various types of MPAs worldwide including MPAs in the CT region. MPAs have been established since the mid-1970s and 1980s in several parts of the Philippines, Malaysia, and Indonesia, followed by Papua New Guinea and Solomon Islands in the late 1990s and Timor Leste in 2007 (Green et al., 2011). They include no-take reserves, sanctuaries, recreation parks, protected landscapes and seascapes, national parks and marine managed areas (Weeks et al., 2014; White et al., 2014). However, contrary to expectations that MPA aim to protect biodiversity in a natural condition, over 90% allow fishing and thus population structures and food webs are altered (Costello and Ballantine, 2015). The Coral Triangle is not exception to this, and thus we consider only <5% of the MPA are fully protected.

Currently, there are 1972 MPA in the Coral Triangle region, covering an area of 200,881 km² (Cros et al., 2014) that are focused on protecting ecological, fisheries, and other essential socioeconomic and cultural values (Table 2) (Walton et al., 2014). Different MPA archetypes are found in different countries (White et al., 2014) due to differences in the science behind the MPA design and the characteristics of social, economic, and governance of each country (Christie and White, 1997; Weeks et al., 2014). Some countries, such as Indonesia, tend to establish large, multiple zone MPAs, while other countries such as the Philippines, Papua New Guinea, and the Solomon Islands prefer to develop small sanctuary areas supported through local government or community-based MPAs (Green et al., 2011; Walton et al., 2014). However, underrepresentation of ecological and biodiversity coverage of marine protected areas occurs in the region, where it was estimated that the current coverage equates to <2% of the Coral Triangle countries EEZ, predominantly located in coastal waters and the average representation of biodiversity features within the existing MPA network was about 5% (Asaad et al., 2018b).

Table 2 The distribution, number, coverage and habitat representation on MPA in the Coral Triangle

Marine protected areas	Indonesia	Malaysia	Philippines	Papua New Guinea	Solomon Islands	Timor-Leste	Region
MPA							
Number ^a	108	51	1653	59	100	1	1972
Total area (km ²) ^a	157,841	15,661	20,940	4558	1325	556	200,881
MPA size (km²)^a							
Maximum	35,211	10,200	2789	2334	823	—	35,211
Minimum	0.9	11.8	0.02	0.04	0.02	—	0.02
Mean	1461.5	270.4	12.7	130.2	16	—	407.8
EEZ coverage							
Surface (km ²) ^b	5,923,493	468,167	1,809,462	2,388,742	1598,119	38,990	12,226,973
MPAs in EEZ (%) ^a	2.7	3.5	1.1	0.2	0.1	1.3	
Habitats							
Coral reef							
Total Area (km ²) ^c	19,938	1585	12,057	7145	2817	35	43,577
% in MPA ^c	23.5	32.5	5.5	3.6	3	5.9	21.4
Seagrass							
Total Area (km ²) ^d	1598	125	1270	153	80	25	3251
% in MPA ^c	18.8	32	3.9	14.4	0.25	1	12.7
Mangrove							
Total Area (km ²) ^e	27,914	5591	2590	4746	466	11	41,318
% in MPA ^c	7.9	1.2	2.5	0.02	0.5	0	5.7

^aWhite et al. (2014)^bCostello et al. (2010)^cBeger et al. (2013)^dUNEP-WCMC et al. (2010)^eGiri et al. (2011a, b)

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Defining Marine Spatial Units: Realms, Biomes, Ecosystems, Seascapes, Habitats, Biotopes, Communities and Guilds

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Abstract

We distinguish between concepts used to classify and map geographic areas, with examples from the marine environment. Biomes are large areas dominated by long-lived plants providing habitat for other species. Ecosystems are areas where biological interactions and energy fluxes are greater within the area than with adjacent ecosystems. Realms are defined by their geographically rare (endemic) species whereas habitats, communities, whereas biotopes are characterized by the most abundant and/or conspicuous species. While ecosystems and biomes contain guilds of species, they are not defined by them, so their species composition varies geographically. Seascapes, like landscapes, are defined by their physical geography (topography, physiography) alone. However, depth zones are distinguished by environmental conditions, notably light, temperature, oxygen, and nutrients. The term regions is applied to areas with varying ad hoc criteria for their delimitation, including geographic, environmental, biological, and management suitability. Alternative terms for, and examples of, these concepts are provided. Classifications can show relationships within concepts (e.g., habitats, realms) but different concepts (e.g., seascapes and habitats) should not be forced into simple hierarchical systems. The spatial relationships of world realms, biomes, and ecosystems are mapped. Authors are encouraged to apply concepts appropriately and minimize jargon so as not to confuse or alienate readers.

Introduction

This article distinguishes among different concepts used in ecology to classify and map geographic areas, with examples of how they apply to the marine environment (Table 1). It is necessary because terms get loosely used by both scientists and outside ecology, creating confusion into the underlying concepts and about what people are trying to communicate. Many terms are highly context dependent, such as habitat. In some cases, multiple terms apply to the same concept and leave one wondering whether some authors use this jargon to impress readers. Instead, we advocate using the least amount of jargon possible and restricting use to the core concepts reviewed here.

Concepts in ecology may borrow words from vernacular use and contribute words to popular use. For example, the words ecosystems, habitat and ecology are used in socio-political settings. However, the meaning of the word may vary and drift. Habitat is sometimes incorrectly used as an alternative to place, but while every habitat has a place, every place does not have the same habitat. A habitat is not a geographic location. Neither should habitat and ecosystem be used interchangeably, but they often are, even in scientific settings. Another example is where the term endemic in ecology and biogeography refers to a species whose geographic range is limited to a particular area. Popular usage can mean that a species occurs in an area and is not necessarily unique to it, e.g., a disease may be endemic to a country. When people migrate, they move from one place to another, but in ecology, migration means the regular movement of individuals to and from, for example, breeding and feeding grounds. The term substrate is used for the food source that a microbe or enzyme may consume, and has tended to replace the term substratum (plural substrata) used to describe the surface on which an organism lives in or on (but does not necessarily feed on), probably by writers overlooking the subtle difference in spelling and then perpetuating it. However, the context always makes the meaning clear. A glossary of marine ecological terminology has been published as part of this work.

In addition to the different applications of the same words by scientists and the public, some scientists use terms casually, thereby creating or perpetuating confusion in concepts (Jax, 2006; Faber-Langendoen et al., 2020). Here, we distinguish several concepts widely used in ecology to define geographic areas (Table 1). They differ not only in their meaning, but their purpose and how they are measured. These terms are context dependant but not always dependent on the geographic scale. However, several schemes have been proposed to classify regions, seascapes, and habitats based on area (reviewed in Costello, 2009). These use terms like mega-, meso-, macro-, and micro-habitat; or province, region, formation or zone. However, because different schemes apply different scales and units to these terms, such as the variety of definitions of depth zones, it seems better to state the dimensions

Table 1 A summary of the definitions and examples of marine geographic concepts.

<i>Concept</i>	<i>Definition</i>	<i>How measured</i>	<i>Examples</i>
Realm	Geographic area distinguished by a high proportion of endemic species arising from evolutionary history	Geographic distribution of species	Marine realms (Costello et al., 2017, 2018a,b). See Table 3 and Fig. 2
Biome	A large region characterized by similar habitat-forming plant growth forms enduring over years		Kelp forest, mangrove forest, seagrass meadow, salt-marsh, shallow coral reefs
Ecosystem	A large area of similar environmental conditions where it is considered that biological interactions and energy fluxes are greater within the ecosystem than across its boundaries to adjacent ecosystems	Cluster analysis of environmental variables that would define a water mass and be related to ecological conditions, such as nutrients, salinity, light, and temperature	The 3D “Ecological Marine Units” of Sayre et al. (2017a, b.) and the 2D photic zone marine ecosystems (Fig. 2)
Seascape (geoform, hydroform, physiotope)	A topographic or physiographic area defined by the shape of the coastline, bathymetry, and/or hydrography	May be defined visually, by acoustic seabed mapping, aerial photography, spectrophotometric sensing (ocean color), temperature, salinity	Fjord, bay, estuary (if variable salinity), lagoon, banks, straits, sounds, canyon, trench, ridge, shelf, slope, rise, seamount, basin, plain, gyre, upwelling, depth zones (Table 4)
Habitat	A physical environment inhabited by a named species or community over a timescale of years and replicated spatially	Depends on the species or community of interest. The habitat for a marine mammal, seabird, and fish may be very different in size and physical environment	Examples in Table 2 and Fig. 3
Biogenic habitat	A three-dimensional habitat created by a species or group of species, and occurring over a timescale of years and replicated spatially		Biomes at a local scale where the species are named, e.g., <i>Zostera marina</i> meadow. Examples in Table 2, Fig. 3
Assemblage	A group of species found together. Whether they interact or not is not known or assumed		In practice conflated with community
Community (bio-, phyto-, zoo-, micro- coensis)	An assemblage of interacting species in a particular habitat occurring over a timescale of years and replicated spatially	Visual observation, photography, samples of substrata and biota	Examples in Table 2 and Fig. 3
Biotope (ecounit, facies, biofacies)	A combination of a distinct community of species in a defined physical habitat		Examples in Table 2 and Fig. 3.
Ecotones	Boundaries between ecologically defined areas, such as habitats		Pycocline, Thermocline, Sea surface
Region (bio- eco- region, province, zone, section)	Expert opinion and/or based on ad hoc use of biogeographic, oceanographic or management criteria	Variously defined depending on the context of the study. Bioregions may be defined by environmental conditions and selected species distributions	Administrative environmental management areas for fisheries, conservation. Reviewed in Costello (2009) and Zhao and Costello (2019b)

Alternative but less widely used terms, or synonyms, and in parentheses. Keywords are in bold.

of the spatial areas and depth zones than assume a reader knows what is meant by, for example, “deep sea” (Costello and Breyer, 2017; Costello et al., 2018a).

The meaning of terms can also change with usage. For example, the term biotope was first used over 100 years ago to mean the physical habitat of a biocenosis (community) but is now used as the unique combination of a community and habitat (Olenin and Ducrotoy, 2006). The term biotope is useful because different communities may occur the same physical habitat, such as due to successional change and ecological interactions. For example, on rocky habitat, kelp forest replaced “sea urchin barrens” following the restoration of natural food web relationships, called trophic cascades, in a marine reserve (Leleu et al., 2012).

Mapping

Maps are spatial models that illustrate the distribution of environmental features. Their scale and resolution vary, and where areas are mapped, the lines separating them may be more or less a true reflection of natural conditions. Thus, in the present context, the boundaries between areas may be narrower or broader than the lines suggest. The boundaries and areas of marine ecosystems are

relatively stable at low latitudes but vary with seasons in high latitudes, reflecting seasonal changes in temperature, phytoplankton dynamics and nutrient cycles (Zhao and Costello, 2019a). Ecological boundaries separating ecosystems, habitats, and biotopes are termed ecotones (Risser, 1995).

In practice, all spatial units have an implicit size, with realms, biomes, and ecosystems being large, sometimes continental, in area. In contrast habitats, communities and biotopes may occur at scales of centimetres to kilometres. A minimum area of 5 m² is commonly used as a guide for the minimum mapping unit for marine benthos (Costello and Emblow, 2005). Microhabitats within this area, such as rockpools on a seashore, or boulders on a sediment seabed, would be recorded as features of the habitat or biotope as they may significantly affect its species composition and diversity.

Seashores may be also mapped at an entire seashore level based on the dominant substratum and wave exposure conditions, such as achieved for some countries (e.g., Ireland, Neilson and Costello, 1999) and the world (Sayre et al., 2018). The BioMar benthic biotope classification recognizes upper level substratum-based “major habitats” (e.g., Littoral Rock) and second level wave exposure “habitat complexes” within a hierarchical classification (Table 2). The BioMar classification forms the marine component of the European Union Nature Information System (EUNIS) standard classification of habitats for environmental management (Galparsoro et al., 2012).

Biomes are large areas with long-lived plants that provide three-dimensional habitat for other species. The terrestrial biome classification is accordingly primarily based on plant cover and growth forms (Faber-Langendoen et al., 2020). Marine equivalents are mangroves, seagrass meadows, kelp and other seaweed forests, and shallow tropical reef-building corals that host symbiotic algae (Jayatilake and Costello, 2018, 2020). In the absence of true biomes in the open (pelagic) ocean, the term biome has been sometimes used to describe areas defined by satellite derived ocean color indicative of phytoplankton abundance (Reygondeau and Dunn, 2018) and groups of pelagic provinces (Spalding et al., 2012). Other authors may refer to such areas of ocean color as epipelagic ecosystems if they assume biological interactions and energy fluxes are greater within the water mass than with adjacent areas.

A new classification of the terrestrial environment combines layers of vegetation (biomes), with landforms (landscape features), and climate, to create a world map of terrestrial “ecosystems” (Sayre et al., 2020). The same approach is not possible in the oceans because only the ocean fringe has biomes, and most of the ocean seabed lacks plants (Costello et al., 2018a). In contrast, on land, the term habitat usually refers to some form of plant cover.

Areas may also be classified by ad hoc combinations of environmental and biological knowledge, using expert opinion and field observations, and be adjusted to fit administrative needs. Here, we group these under the term regions. Some are management units for countries (e.g., Exclusive Economic Zones), fisheries (Food and Agriculture Organization and International Council for the Exploration of the Sea fisheries management regions), and environmental studies (“Large Marine Ecosystems”) (reviewed in Zhao and Costello, 2019b). Conservation prioritization may define biodiversity hotspots based on their richness of biogenic habitat (e.g., coral reefs), species and endemic species, as conducted for the Coral Triangle by Asaad et al. (2017, 2018, 2020), and for the world ocean (Zhao et al., 2020). However, biodiversity hotspots may also be places with high fish abundance and human impacts (reviewed in Jefferson and Costello, 2020), and the term “hotspots” has been used for areas of high pollution or heat events. Thus the term “regions” is used here to cover the numerous management orientated nomenclature applied to geographic areas in the ocean.

Classification

Because the terms in Table 1 are different concepts they cannot be forced into any linear or hierarchical relationship. Thus, a biome may cross several biogeographic realms (Fig. 1). However, ecosystem boundaries may align with boundaries of biomes and realms because they represent areas with contrasting environmental conditions and these conditions may affect the dispersal of species and hence endemism (Fig. 2). Indeed, all four major marine biomes (Fig. 1) fall within one coastal ecosystem (Fig. 2), and several realm boundaries (only accurate to $\pm 5^\circ$ latitude longitude) approximately align with ecosystem boundaries (e.g., Southern Ocean).

Classifications are our attempt to organize concepts. They can have predictive value when one level in a classification is known to be regularly associated with its neighbors and other levels. For example, species classifications inform how one species is related to others. However, the true relationships between the geographic concepts in Table 1 are more likely to be multi-dimensional than linear. Nevertheless, it can thus be informative to show how habitats and communities form biotopes in a two-dimensional matrix (Fig. 3). When concepts are independent it does not necessarily help to force them into hierarchical relationships, some with 10 levels in the hierarchy (e.g., Last et al., 2010).

Any classification of habitats invariably must make some arbitrary decisions which means it is likely to differ from classifications developed for other geographic regions and environments. A physical habitat may occur in several ecosystems, seascapes, or realms; such as a wave exposed rocky seashore. Thus, to try to form a hierarchical relationship (for example) of habitats within seascapes is misleading because it may suggest a habitat may only occur within that seascape whereas it may occur in several (Costello, 2009). Instead, habitats and seascapes, like biomes and realms, should be mapped and reported separately as they are different concepts; neither is a subset nor superset of another.

The basic units of habitat classifications as observed in the field can be reconciled between studies, enabling comparison of maps of habitats and biotopes across decades (Leleu et al., 2012; Remy-Zephir et al., 2012). In addition, methods of assigning certainty to marine benthic habitat maps developed in Europe can be applied internationally, including in New Zealand (Lee et al., 2015).

Table 2 A checklist of the upper three levels (major habitat, habitat complex, biotope complex) of the BioMar marine biotope classification of Connor et al. (1997a,b) illustrated in two-dimensions in Fig. 3.

<i>Littoral rock</i>	<i>Cirralittoral rock</i>
Lichens or algal crusts (9)	Exposed
Exposed (mussel/barnacle shores)	Faunal crusts or short turfs (3)
<i>Mytilus</i> (mussels) and barnacles (7)	<i>Alcyonium</i> -dominated communities (tide-swept/vertical) (4)
Robust fucoids and red seaweeds (3)	Barnacle, cushion sponge and Tubularia communities (very tide-swept/sheltered) (5)
Moderately exposed (barnacle/fucoid shores)	Moderately exposed mixed faunal turfs (4)
Barnacles and fucoids (7)	Bryozoan/hydroid turfs (sand-influenced) (9)
Red seaweeds (5)	Cirralittoral <i>Sabellaria</i> reefs (1)
Ephemeral green or red seaweeds (freshwater or sand-influenced) (3)	Mussel beds (open coast cirralittoral rock mixed substrata) (3)
<i>Mytilus</i> (mussels) and fucoids (3)	Brittlestar beds (2)
<i>Sabellaria</i> (honeycomb worm) reefs (1)	Grazed fauna (moderately exposed or sheltered rock) (2)
Sheltered (fucoid shores)	Ascidian communities (silt-influenced) (3)
Dense fucoids (stable rock) (10)	Soft rock communities (2)
Fucoids, barnacles or ephemeral seaweeds (mixed substrata) (8)	Sheltered
<i>Mytilus</i> (mussel) beds (mixed substrata) (1)	Brachiopod and solitary ascidian communities (8)
Rockpools (9)	Sheltered <i>Modiolus</i> (horse-mussel) beds (2)
Overhangs and caves (3)	Faunal turfs (deep vertical rock) (2)
	Caves and overhangs (deep) (1)
<i>Littoral sediments</i>	<i>Cirralittoral offshore rock</i>
Littoral gravels and sands	<i>Lophelia</i> (cold-water coral) reefs (1)
Shingle (pebble) and gravel shores (2)	
Sand shores (7)	<i>Sublittoral sediments</i>
Estuarine coarse sediment shores (1)	Infralittoral gravels and sands
Littoral muddy sands	Maerl beds (open coast/clean sediments) (4)
Muddy sand shores (4)	Shallow gravel faunal communities (2)
Littoral <i>Zostera</i> (seagrass) beds (1)	Shallow sand faunal communities (5)
Littoral muds	Estuarine sublittoral gravels and sands (3)
Saltmarsh (26 +)	Cirralittoral gravels and sands (3)
Sandy mud shores (4)	Infralittoral muddy sands
Soft mud shores (3)	Seagrass beds (2)
Littoral mixed sediments (2)	Shallow muddy sand faunal communities (4)
	Cirralittoral muddy sands (5)
<i>Infralittoral rock</i>	Infralittoral muds
Exposed	Angiosperm communities (lagoons) (2)
Kelp with cushion fauna, foliose red seaweeds or coralline crusts (13)	Shallow marine mud communities (4)
Robust faunal cushions and crusts (surge gullies & caves) (10)	Estuarine sublittoral muds (7)
Moderately exposed	Cirralittoral muds (3)
Kelp with red seaweeds (11)	Infralittoral mixed sediments
Grazed kelp with algal crusts (3)	<i>Laminaria saccharina</i> (sugar kelp) and filamentous seaweeds (4)
Sand or gravel-affected or disturbed kelp and seaweed communities (7)	Maerl beds (muddy mixed sediments) (3)
Sheltered	Oyster beds (1)
Silted kelp (stable rock) (14)	Shallow mixed sediment faunal communities (3)
Estuarine faunal communities (shallow rock/mixed substrata) (3)	Estuarine sublittoral mixed sediments (3)
Submerged fucoids, green and red seaweeds (lagoonal rock) (4)	Cirralittoral mixed sediments (3)
Other fauna and seaweeds (shallow vertical rock) (3)	Cirralittoral offshore sediments (3)

The species on rock may also occur on other hard substrata (e.g. shells, piers, and shipwrecks). The number of biotopes and sub-biotopes described in Connor et al. (1997a,b) is indicated in parentheses.

A common area of confusion is where ecosystems, seascapes, and habitats are conflated because all comprise a geographic area with distinct environmental conditions and are inhabited by some species. While species occur in ecosystems, they do not define them. In contrast, species composition defines a habitat. Seascapes are agnostic to what species occur within their area. For example, there are about 70,000 seamounts (submerged mountains more than 1 km high from the seabed), and over one million sea-hills (Costello et al., 2010). A seamount is a seascape defined by the seabed topography, and it may be a habitat for some large mobile species, like a bay may be a habitat for mammals or birds. However, it will contain a variety of habitats for benthic species depending on depth, substrata, wave and current exposures, and the same habitats will occur elsewhere. The seamount may even form a distinct oceanographic ecosystem due to its effects on water movements and the pelagic-benthic interactions, as suggested by

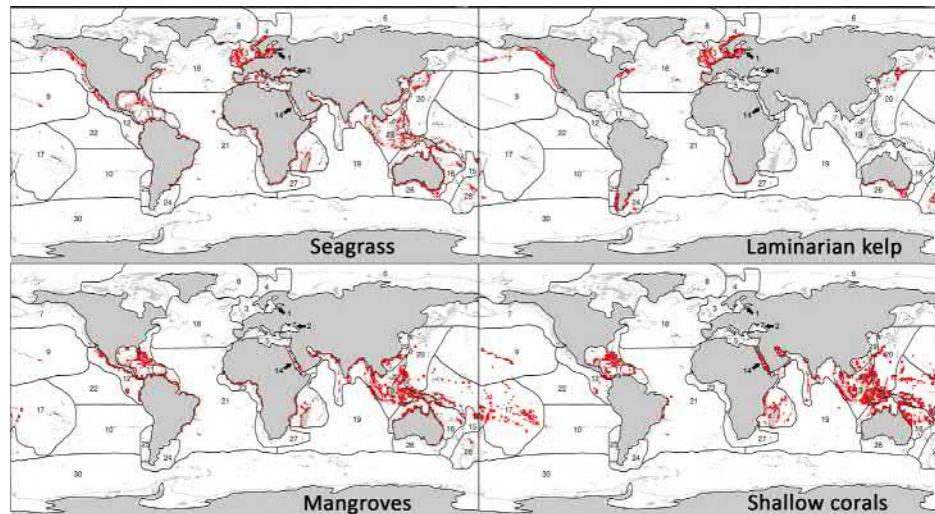


Fig. 1 World maps showing how one biome (in red), seagrass, is distributed across all except the polar realms (Table 3) (Jayatilake and Costello, 2018, 2020). Two biomes, mangroves and shallow reef-building corals, are limited to tropical and sub-tropical realms, while the fourth, laminarian kelp biome is distributed in cold temperate high latitudes (Jayatilake and Costello, 2020). The areas occupied are 1,646,788 km² for seagrass, 1,469,900 km² for laminarian kelp, 151,390 km² for shallow water corals, and 136,850 km² for mangroves. Each biome consists of tens of species, but varying species composition in each realm.

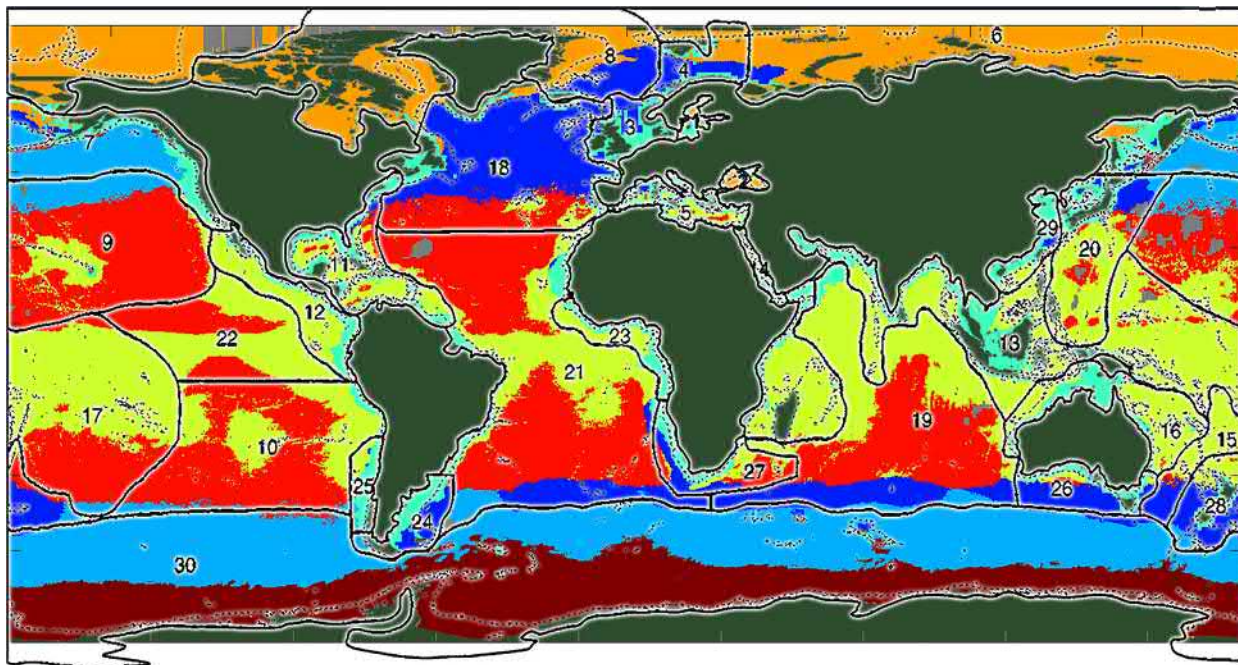


Fig. 2 The Zhao epipelagic marine ecosystems of the world (Zhao and Costello, 2019a,b; Zhao et al., 2019) overlaid by the boundaries of the biogeographic realms. Note the biomes (Fig. 1) occur in the coastal ecosystem which is most visible around continents, and also in small coastal ecosystems around oceanic islands which are difficult to see due to the map resolution.

some of the distinct ecosystems around ocean islands (Zhao et al., 2019). In fact, the mapping of seascapes is more the domain of physical geography than ecology, and regional and global maps of seabed geomorphological units have been published (e.g., Greene et al., 1999; Heap and Harris, 2008; Harris and Whiteway, 2009; Last et al., 2010; Harris et al., 2014). Specialist classifications of coastal seascapes based on tides and salinity (Tagliapietra et al., 2009) and sediments (Boyd et al., 1992) have also been proposed. While seascapes are analogous to landscapes on land, they may also be physically defined by water body conditions and termed pelagic seascapes (Kavanaugh et al., 2016).

Substratum → Zonation ↓ Wave exposure →	ROCK			Mixed sediment	SEDIMENT		
	Exposed	Moderate	Sheltered		Gravel, Coarse sand	Sand, fine to medium	Mud (> 30 % silt)
Littoral	Lichens				SALT MARSH		
	Ephemeral green & red seaweeds (low salinity)			Gammaridae (low salinity)	Barren		
	Barnacles & <i>Mytilus</i> (mussel)	<i>Fucus</i> , limpet, barnacles	<i>Ascophyllum</i>	Sugar kelp & filamentous seaweeds	Burrowing amphipods, bivalves rare	Polychaetes & bivalves, burrowing amphipods rare	Polychaetes, <i>Corophium</i> , <i>Hydrobia</i>
	Red seaweeds & <i>Corallina</i>	<i>Sabellaria</i> reefs	Mussel beds				
Sub-littoral	Sponges & bryozoa under kelp	Grazed rock under kelp	Silted under kelp	Submerged fucoids	<i>Zostera</i> spp.		
	anemones, sponges & colonial ascidians (wave surge tolerant)		fauna		Maerl		
	coralline algae & calcareous tubeworms (scour tolerant)	Brittlestar beds	Modiolus (mussel) beds			Burrowing megafauna <i>Nephrops</i> ,	
			Serpulid (tube-worm) reefs	Hydroid-bryozoan (current swept)	<i>Amphura</i> spp. polychaetes	seapens	
	<i>Flustra</i> , hydroids, <i>Alcyonium</i> (current tolerant)	<i>Sabellaria</i> reefs Rich faunal turfs	Axinellid sponges & brachiopods	Solitary ascidians (silt tolerant)	<i>Neopentadactyla</i> , <i>Venerupidae</i>	<i>Abra</i> , <i>Nucula</i> , <i>Corbula</i> , spionid polychaetes	<i>Beggiatoa</i>

Fig. 3 Example of a marine seabed biotope matrix showing the spatial relationships between the communities (colored boxes) and their physical habitat defined by height (intertidal = littoral), depth (subtidal = sublittoral), substratum and wave exposure for benthos in Irish and British seas. These factors distinguish biotopes at the upper levels of the European marine biotope classification developed by the BioMar project (Table 2). Within the matrix the characteristic species of the communities occurring in the habitats are indicated (see classification for full definitions and details). Based on Costello MJ, Emblow, C (2005) A classification of inshore marine biotopes. In: Wilson JG (ed.) *The Intertidal Ecosystem: The Value of Ireland's Shores*. pp. 25–35. Dublin: Royal Irish Academy.

In contrast to habitats, ecosystems are usually considered over larger areas. What makes the concept of ecosystem unique is that it is a geographic area where ecological exchange of energy and matter is stronger within than across a boundary to adjacent ecosystems. This is difficult to measure but can be approximated by measures of temperature and biologically influenced variables (e.g., nitrogen, phosphorous, silicate, oxygen) as conducted for the world ocean by Sayre et al. (2017a,b), Costello et al. (2018a,b) and Zhao et al. (2019) (reviewed in Zhao and Costello, 2019a,b), and increasingly available at global scales (e.g., Basher and Costello, 2019; Basher et al., 2020).

The concept of coral reef ecosystems is widely applied to shallow subtropical areas that include coral reefs. They include varying areas of sandy and rocky habitats, and seagrass meadows. Whether coral reefs form truly closed ecosystems is doubtful but yet the term is useful because “coral reefs” alone may only refer to the living corals which are a small part of a reef “ecosystem” (Hatcher, 1997). Similarly, the same corals can extend into deeper water where they are called mesophotic corals (Laverick and Rogers, 2020). These are sometimes called mesophotic coral ecosystems, although habitats or biotopes may be more appropriate (Tables 2–4).

Species Guilds and Traits

In addition to terms used to map geographic areas, ecological guilds are groups of species that are similar in size and role in an ecosystem (Costello, 2009). For example, the pelagos and benthos refer to organisms living in open water and associated with the seabed respectively. The first can be subdivided by whether they live on the ocean surface (pleuston), in the tens of centimetres under the surface (neuston), are too small to control their horizontal distribution (plankton, although they may adjust their depth), are large and swim effectively against the current (nekton), or are animals (e.g., zooplankton) or plants (e.g., phytoplankton). Benthic guilds may live within the seabed (infauna), upon the seabed (epibiota, epifauna, epiflora), in the water above but associated with the seabed (i.e., demersal = hyperbenthos = benthopelagic), and interstitially nested within epibiota or sediments (Costello et al., 2020).

Guilds may also be distinguished by body size, or as a consequence of the net or sieve used to sample or process samples. The terms macro- and meio- benthos, pico- and nano-plankton, and mega-fauna are common in marine ecology, but intermediate micro- and meso- size groups are also used (Costello et al., 2015, 2016, 2020).

Taxa may also be grouped into groups based on their diet and comprise: predator, scavenger, omnivore, herbivore, parasite, plant (photoautotroph), grazer, suspension feeder, filter feeder, deposit feeder, detritivore, decomposer, and chemoautotroph. In addition, taxa may be grouped by their “habit”: sessile, sedentary, tubicolous, burrowing, drifting, solitary, gregarious, social, colonial, encrusting, inquiline, symbiotic, mobile (vagile), and natant (swimming). For definitions of these and other ecological terminology see Costello et al. (2020). These attributes may also be considered as species traits (Costello et al., 2015).

Table 3 The marine biogeographic realms (Fig. 2).

Realm level 1	Sub-realm level 2	Sub-realm level 3	Realm
Inner Baltic Sea			1
Black Sea			2
NE & NW Atlantic & Mediterranean, Arctic & North Pacific	NE Atlantic & Mediterranean	NE Atlantic	3
		Arctic Europe	4
		Mediterranean	5
	Arctic & N Pacific	Arctic	6
		North Pacific	7
		N Atlantic boreal & sub-Arctic from Canada to Greenland Sea	8
Mid-tropical North Pacific Ocean			9
South-east Pacific			10
Mid-Atlantic, Pacific & Indian Oceans including coastal tropics & warm-temperate areas	Tropical W Atlantic & Tropical E Pacific	Tropical W Atlantic	11
		Tropical E Pacific	12
	Coastal Indian Ocean, W Pacific, Arabian Gulf to New Caledonia, S Pacific tropical islands, & N, W & E Australia.	Tropical Indo-Pacific & coastal Indian Ocean	13
		Red Sea	14
		Tasman Sea to SW Pacific	15
		Tropical Australia & Coral Sea	16
	Open Atlantic, Indian, & Pacific oceans	Mid South Tropical Pacific	17
		Offshore & NW North Atlantic	18
		Offshore Indian Ocean	19
		Offshore W Pacific	20
		Offshore S Atlantic	21
		Offshore mid-E Pacific	22
		Tropical E Atlantic	23
	S South America	Argentina	24
		Chile	25
	S Africa, S Australia, & New Zealand	S Australia	26
		S Africa	27
		New Zealand	28
North West Pacific			29
Southern Ocean			30

The classification hierarchy is based on overlap in species composition. Note the Inner Baltic and Black Seas were distinct because they included freshwater species and may thus not be considered as marine as the other realms. N = north, S = south, E = east, W = west.

Following Costello MJ, Tsai P, Wong PS, Cheung A, Basher Z, Chaudhary C (2017) Marine biogeographic realms and species endemism. *Nature Communications* 8(1057).

Table 4 Depth zones and associated nomenclature in the ocean.

Depth (m)	Environment	Pelagos	Benthos	Ecosystem function
0	Tidal air exposure	Epipelagic (phytoplankton)	Littoral	Photosynthesis and respiration. Variable nutrients and oxygen.
200	Photic zone		Infralittoral (seaweeds)	
1000	Twilight zone < 1% light	Mesopelagic	Circalittoral	
2000	Aphotic zone < 4 °C	Bathypelagic	Deep-sea	Respiration low. Higher nutrients. Low oxygen.
4000		Abyssopelagic Hadopelagic	Abyss	

Changes in the air and light exposure of the environment with depth are reflected in changes in dominance of plants in both the pelagos (the water-column biota, including phytoplankton) and benthos (the seabed biota including seaweeds, seagrass, and corals with symbiotic microalgae). These biota then determine the ecosystem function, including concentrations of oxygen, carbon dioxide and available nutrients. Environmental variability declines with depth, and there are no "Ecological Marine Units" unique to depths below 4000 m (Costello et al., 2018a,b).

Adapted from Costello MJ, Breyer S (2017) Ocean depths: The mesopelagic and implications for global warming. *Current Biology* 27(1): R36–R38. 10.1016/j.cub.2016.11.042.

Conclusions

The concepts reviewed here are useful for understanding how biodiversity exists where it does, and how it functions. Realms reflect past evolutionary conditions, including continental drift. The geographic distributions of ecosystems and biomes reflect current environmental and ecological conditions over large areas, while habitats, communities, and biotopes reflect local conditions. Realms are defined by the presence of geographically rare endemic species whereas habitats and communities are defined by the most abundant or otherwise dominant species. Seascapes are defined by physiography and not biology, while ecosystems are defined by ecological interactions and energy fluxes, not particular species. Consistent and accurate uses of these concepts will improve the clarity of scientific communication.

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The Biology, Ecology and Societal Importance of Marine Parasites

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Abstract

Although marine parasites are often small cryptic organisms that are difficult to study, they are a highly adapted, diverse group of organisms playing important roles within ecosystems. Parasites have complex lifecycles that involve a single host or a number of intermediate hosts. Parasites have been shown to act as ecosystem engineers, sometimes changing the behaviour of one host in order to enable their transition to the next host. The many modifications that individual parasites make have implications for the structure of food webs and the functioning of ecosystems. Their ubiquitous presence can be used to understand the structure of and pressures on host species and food webs. While it is tempting to assume that parasites have similar biogeographic patterns as their hosts, studies have shown that external parasites have different spatial distribution trends, trends which have implications with regards to climate change. Although marine species are generally expected to decline as climate change increases, current research indicates that climate change may be favorable for parasite pathogenicity and distribution. This could have economic impacts on fisheries and aquaculture and biological impacts on the function and structure of marine ecosystems. This article reviews our current biological and ecological knowledge of parasites, discusses how parasites have been used as a tool to understand other aspects of the marine realm, and outlines current predictions regarding the response of parasites to climate change.

Introduction

Parasitic organisms are typically small cryptic animals concealed on or within their hosts and are often noticed only when their presence causes pathogenicity (illness) in commercially relevant species or pets. In addition to the direct effects they cause to their hosts, ecologists are discovering the indirect roles that parasites play in structuring the marine environment. This article introduces the diversity of marine parasites, the interactions with their hosts, and the consequent effects they have on marine food webs and ecosystems.

Defining Parasites

Definitions of what constitutes a parasite vary from field to field. The study of parasites is approached from a number of disciplines, including physiology, ecology, epidemiology, veterinary, economics and evolutionary biology. For this article, parasitism is understood to be a close association of two organisms, in which one (the parasite), during at least one life-history stage, depends on the other (the host) and directly derives some nourishment and/or shelter from it but does not intentionally kill the host. The direct benefit to the parasite is almost always in the form of food, but other benefits have been noted including habitat, shelter and transport. Microbiologists have focussed on fungi, viruses and bacteria and have considered some of these as parasitic, but for the purposes of this article, we will only consider animal parasites which infest other animals (see Table 1 for specific taxa). Specifically,

Table 1 Major groups of metazoan taxa where parasitism has transitioned, the predicted number of these transitions and the number of extant parasitic species within these taxa

		Minimum number of	
Marine parasitic taxa		Parasitic transitions	Parasitic species
<i>Crustaceans</i>			
Phylum Arthropoda			
SubPhylum Crustacea			
Class Branchiura	Arguloida	1	32
Class Hexanauplia			
SubClass	Monstrilloida, Siphonostomatoida	6	2302
Copepoda			
SubClass	Ascothoracida, Cirripedia (Rhizocephala, Thoracica)	2	811
Thecostraca			
Class Malacostraca			
Order Amphipoda	Hyperidea, Cyamidae	2	72
Order Isopoda	Cymothoidea, Cryptoniscoidea, Bopyroidea	3	414
Class Maxillopoda			
SubClass		1	37
Pentastomida			
SubClass		1	37
Tantulocardia			
<i>Molluscs</i>			
Phylum Mollusca			
Class Bivalvia	Unionida	1	–
Class Gastropoda	Triviidae, Ovulidae, Eulimidae, Epitoniidae, Pyramidellidae, Architectonicidae, Cypraeidae	9	6104
<i>Helminths</i>			
Phylum Acanthocephala			
		1	416
Phylum Annelida			
	Hirudinea	1	47
Phylum Nematoda			
	Chromadoria (Rhabditida, Monhysterida), Dorylamia (Trichinellida, Dioctophymatida)	15 +	1921
Phylum Platyhelminthes			
SubPhylum Neodermata			
		1	
Class Cestoda			2254
Class Monogenea			2498
Class Trematoda			5085
TOTAL		44 +	21,165
<i>Terrestrial Parasitic Taxa</i>			
Phylum Arthropoda			
SubPhylum Chelicerata			
Class Arachnida			
SubClass Acari	Mesostigmata, Sarcoptiformes, Trombidiformes, Ixodida, Phoxichilidiidae	31	13,838
SubPhylum Hexapoda			
Class Insecta			
Order Psocodea		2	10,988
Order Siphonoptera		1	2047
Order Strepsiptera		1	613
Order Diptera	Ceratopogonidae, Culicidae, Tabanoidea, Hippoboscidae, Simuliidae	60	16,610
<i>Helminths</i>			
Phylum Acanthocephala			
		1	723
Phylum Annelida			
	Hirudinea	1	123
Phylum Nematoda			
	Chromadoria (Rhabditida, Monhysterida), Dorylamia (Trichinellida, Dioctophymatida), Ironina	15 +	4497
Phylum Platyhelminthes			
SubPhylum Neodermata			
		1	
Class Cestoda			2388
Class Trematoda			2752
TOTAL		113 +	54,869

Updated and adapted from Poulin, R. and Morand, S. (2004) *Parasite Biodiversity*. Washington, DC: Smithsonian Institution Press; Blaxter, M. and Koutsovolous, G. (2014). The evolution of parasitism in Nematoda. *Parasitology* **142**, S26–S39. doi: 10.1017/S0031182014000791; Costello, M.J. (2016). Parasite rates of discovery, global species richness and host specificity, *Integrative and Comparative Biology* **56**(4), pp. 1–12. DOI: 10.1093/icb/icw084; Weinstein, S. B. and Kuris, A. M. (2016). Independent origins of parasitism in Animalia, *Biology Letters* **12**, p. 20160324. DOI: 10.1098/rsbl.2016.0324. Parasite numbers synthesized from Catalog of Life (Roskov, Y., et al. (2018). *Species 2000 & ITIS Catalogue of Life, 2018 Annual Checklist. Species 2000: Naturalis*. The Netherlands: Leiden. ISSN 2405-884X: Digital resource at www.catalogueoflife.org/annual-checklist/2018.) and Global Biodiversity Information Framework (GBIF) Backbone Taxonomy (GBIF: The Global Biodiversity Information Facility. (2019). *What is GBIF?*. Available from <https://www.gbif.org/what-is-gbif>).

we exclude animals that feed off plants, such as the many species of plant-feeding insects and roundworms, as these are considered herbivores, and we exclude parasitoid insects because they intentionally kill their host and are therefore considered predators (Costello, 2016; Lucius and Poulin, 2017).

Parasite Diversity

Parasitism has evolved at least 223 times in 15 of 35 recognized animal phyla (Weinstein and Kuris, 2016). It is believed that parasitism evolved through a variety of opportunistic circumstances: from using larger animals for food, shelter, increasing dispersal potential, and maintaining more consistent environmental conditions by living in close proximity (Poulin and Morand, 2004). There are also cases of parasites that are closely related to their hosts—even within the same species. For example, ceratoid angler fish have adopted parasitism to solve the problem of reproduction in the darkness of the ocean depths. In some species, once the male locates the female, he latches on to her and eventually fuses to her, providing sperm to fertilize her eggs. As he is then permanently attached, he derives nutrients from the female (Pietsch, 2005).

Hosts may have one to many species of parasites. For example, *Thyrstites atun*, a predatory species of snake mackerel that occurs in the southern hemisphere, has been found to host 16 species of parasites (Nunkoo et al., 2016). Such data have led researchers to the conclusion that there are more parasitic species than host species (Toft, 1986; Poulin, 2014). Even so, of all described animal species, it is estimated that only 5% are parasitic (Costello, 2016). There have been many discussions about why there is this lack of described parasitic species, particularly referencing; their cryptic lifestyle and the difficulty in locating and identifying parasitic species; the lack of research in large geographic regions, for example, the deep ocean; the predicted hyper diversity; a paucity of parasite taxonomists; the use of as yet unrecognized synonyms; and under-sampling even within well studied taxa (e.g., birds and elasmobranchs) (Rohde, 2002; Caira and Jensen, 2014; Chaudhary et al., 2016; Poulin and Presswell, 2016; Jorge and Poulin, 2018).

With the introduction of data-centred science (Kelling et al., 2009) and a renewed effort to determine how many species there are in the world, analyses by some researchers have concluded that most species on earth have been named (Costello et al., 2012, 2013a; Costello and Chaudhary, 2017). Costello et al. (2015) analyzed the trends in rates of description for 32,000 fish species globally. They discovered that the species to be first described tended to be more widespread and larger in size and occurred in shallower depths and near more developed countries (e.g., northern hemisphere). In analyzing trends in rates of description for parasites in both marine and terrestrial ecosystems, Costello (2016) found that most molluscs, crustaceans, ticks, fleas, and insects had decreasing rates of description since the year 2000, with the peak discovery period for helminths and microsporidians occurring in the 1970s. This suggests that most parasites have been named and that further surveys for parasitic diversity will demonstrate that parasitic species discoveries may not yield as many species as non-parasitic taxa (Costello, 2016), challenging current predictions (Poulin, 2014).

Adaptations to the Parasitic Lifestyle

Parasites have evolved complex defensive strategies and developed intricate life cycles to improve their survival. Some parasites have developed simple or direct life cycles that involve active transmission via free living larval stages that attach to passing hosts (e.g., Rhizocephala, Ascothoracica, Copepoda, and Monogenea). For example, parasites of the class Monogenea have adapted to living on the skin, fins and gill filaments of fresh water and marine fish (Rohde, 2005). The hermaphroditic adults release eggs into the water column. When the eggs hatch, they release a heavily ciliated larval stage known as an oncomiracidium. These oncomiracidium have numerous posterior hooks and opportunistically latch onto passing hosts, completing their lifecycle. The larval hooks develop into complex holdfast organs or “haptors,” which are specifically adapted to maintain attachment to their preferred host (see Fig. 1 for examples).

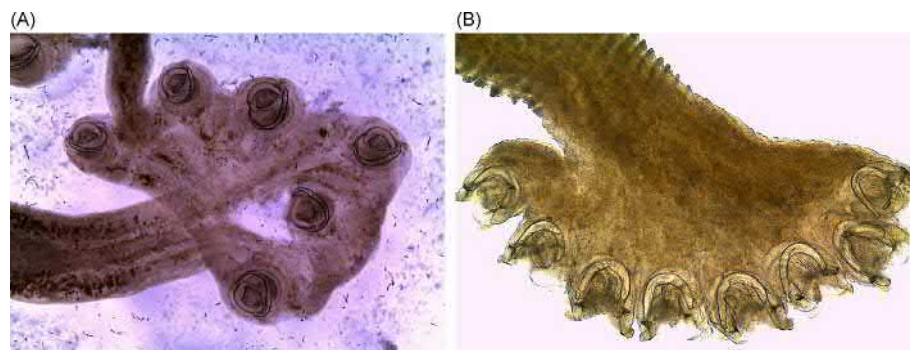


Fig. 1 Showing haptors of *Callorhynchicola multitesticulatus* and *Callorhynchicotyle callorhynchi* found infecting gill filaments of *Callorhinchus capensis* in South Africa (40x magnification). (Photo's by TM).

In contrast to the simple and direct life cycle of Monogenea, other parasites have developed complex or indirect lifecycles where sexual reproduction occurs in the definitive host and various stages of development and/or asexual reproduction occur in one or more intermediate hosts (e.g., Cestoda, Trematoda, Acanthocephala, Nematoda) (Table 2). For example, *Curtuteria australis*, a digenean trematode off the New Zealand coast (Allison, 1979; Fig. 2) has two intermediate hosts. Its eggs are released in the droppings of oystercatchers (*Haematopus* spp.), its definitive host. These eggs are ingested by the whelk *Cominella glandiformis*, a marine gastropod snail, where they develop into larvae (called redia) in the digestive gland. Once temperatures reach 20°C, the redia release free swimming larvae (called cercaria) into the surrounding water, which infect the cockle *Austrovenus stutchburyi*. In heavily infected cockles, not only is foot tissue replaced by the metacercaria cysts, but the size of the foot relative to that of the shell is reduced, leading to the diminished ability of the cockle to bury itself in the sand (Thomas and Poulin, 1998). This alteration in behaviour makes the cockle seven times more susceptible to predation by shorebirds (Thomas and Poulin, 1998). Once consumed by the oystercatcher, the parasite infects the digestive tract, completing its life cycle.

Whether their lifecycles are simple or complex, parasites in both categories have evolved the ability to infect a range of potential micro habitats that the host's body may provide. Like the monogenean example above, parasites can infect specific regions of their hosts, including musculature, various organs and cavities and externally in gill chambers, fins, mouth, skin, and scales. The traits parasites have developed to survive these micro habitats include: a reduction in size compared to related non-parasitic species; a reduction or complete loss of sensory and/or locomotory structures; the development of attachment organs so as not to be carried away or cleaned from the host; resistance to host immune systems and/or protection against hostile environments (e.g., cuticles); and specialized reproductive strategies with high reproductive potential.

Parasite-Host Coevolution

Due to the antagonistic nature of the host-parasite interaction, unique selection pressures are exerted on both the parasite and the host, resulting in parasites that are highly specialized to infect particular hosts. However, there are exceptions, like trypanorhynch cestodes that can infect multiple intermediate host species. This parasite-host interaction creates an evolutionary tension that allows for a delicate equilibrium to be created between the host and the parasite (Hudson, 2005). This evolutionary equilibrium is known as the Red Queen Hypothesis; namely that both parasite and host must continuously adapt to keep up with each other's adaptations (Morand and Krasnov, 2010). However, creating a defensive strategy against every potential parasitic species would be a costly endeavor for the host. Therefore, it is less costly to allow a moderate level of defense at the expense of slight infection. For a parasite, it is worth having a lower level of pathogenicity within a host, so as to not activate the host's full defenses which allows for improved transmission. It is within these moves and counter moves that we get a glimpse of just how parasites may structure entire ecosystems through their effects on host abundance and/or behaviour.

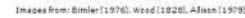
Ecology of Parasites

Effects of Parasites on Ecosystems

If we continue with the example of *Curtuteria australis*, this parasite controls how energy is transferred through the ecosystem by directly effecting predator-prey interactions. This is done by limiting the natural behaviour of the whelk to a riskier behaviour. This small change alters the food web dynamics and community structure in the ecosystem. A parasite's impact on reducing host fitness and modifying competitive and trophic interactions among species have effects on the abundance of different species and the strength of interactions between them. Therefore, the parasite impacts the way that energy flows through the ecosystem directly.

Table 2 Parasitic taxa of marine organisms, their type of life cycle, mode of transmission to the next host and general habitat on host

Main parasitic taxa	Direct/indirect life cycle	Mode of transmission	Habitat
<i>Crustaceans</i>			
Branchiura	Direct	Active—Attachment	External—body surface
Copepoda	Direct and indirect	Active—Attachment	External—body surface, oral cavity, eye
Ascothoracida	Direct	Active—Attachment	External—anchored within and on body surface
Rhizocephala	Direct	Active—Attachment	External—body surface
Thoracica	Direct	Active—Attachment	External—body surface
Amphipoda	Direct	Active—Attachment	External—body surface
Isopoda	Direct	Active—Attachment	External—body surface, oral cavity
<i>Helminths</i>			
Acanthocephala	Indirect	Passive—Ingestion	Internal—gut
Cestoda	Direct and indirect	Passive—Ingestion	Internal—body cavity, gut
Monogenea	Direct	Active—Attachment	External—body surface, gills, oral cavity
Nematoda	Indirect	Passive—Ingestion	Internal—body cavity, gut
Trematoda	Direct and Indirect	Active and Passive—penetration or ingestion	Internal—gut and many internal organs



Within the marine realm, one of the clearest and well documented geographic patterns is the latitudinal diversity gradient (Hillebrand, 2004). Latitude is a surrogate for temperature and solar radiation (including day length and seasonality), which in turn influences primary and secondary productivity (Chaudhary et al., 2016). Chaudhary et al. (2016, 2017) reviewed the literature and available global data for 65,000 marine species and concluded that species diversity increased with decreasing latitude. This

translates to a diversity gradient with low levels of diversity at the poles and a gradual increase through the temperate zone toward the tropics.

This increase in diversity is observed in internal parasites, particularly helminths of marine fish (Rohde, 2002, 2010, 2016; Jorge and Poulin, 2018). Jorge and Poulin (2018) tested the expected spatial similarity between host and parasite diversity for helminth parasites of vertebrate hosts across the globe, including marine fish. Their results show that although associations were weak, there was a significant positive covariation between host species richness and the number of parasite species reported in the same latitude, supporting the observed latitudinal trends for endo parasites. These results show that as host diversity increases, there is a similar increase in endoparasitic diversity.

Ectoparasites, however, amplify this latitudinal gradient and show an increase in relative diversity compared to their endoparasitic counterparts, with comparatively higher species diversity of monogenean flukes per species diversity of hosts, as latitude decreases (Rohde, 2002, 2016). The most likely explanation, according to Rohde (2002), for this relative increase in ectoparasitic diversity compared to other parasitic species is due to temperature. Decreasing latitude results in a general increase in temperature and genetic studies have shown that with increasing relative temperature, there is an increase in evolutionary speciation rates in plants and animals (Rohde, 2002; Gillman et al., 2014).

Longitudinal gradients

Longitudinal gradients of diversity have not been as well documented as latitudinal gradients, but centres for high diversity compared to other areas around the globe have been recorded (Morand and Krasnov, 2010). A primary area is within the Coral Triangle of the Western Pacific Ocean (Asaad et al., 2019). A secondary area is the Caribbean, although this area is not as diverse as the Coral Triangle (Rohde, 2010).

It has become clear that there are barriers to longitudinal dispersal in the oceans, which inhibit the movement of species across the globe. The most effective barrier appears to be the Eastern Pacific Barrier which, due to a lack of islands and a deepening of the thermocline toward the east, reduces the dispersal potential of many species, including parasites, from the western to the eastern parts of the Pacific (Morand and Krasnov, 2010). The “New World Barrier,” represented by the North and South American continents, prevents longitudinal species movement between the eastern Pacific and the Atlantic (Costello et al., 2017). These phenomena have been documented for monogenean and copepod parasites of tuna and mackerel species (Rohde and Hayward, 2000).

Depth gradients

Reviews of marine diversity show an exponential decrease in diversity with depth with a suggested peak at approximately 400–500 m (Costello and Chaudhary, 2017). Rohde (1984) reviewed data of vertical gradients for parasitic species from several authors and concluded that parasite diversity and prevalence becomes poorer with depth. Inshore and open ocean surface fishes have more species of parasite and a greater abundance of parasites than midwater species (Marcogliese, 2002). However, bottom dwelling (benthic) fishes had more species and greater numbers of parasites than midwater (pelagic) species. This is probably due to their food including more infected intermediate hosts, being larger in body size and with a longer life span than mid water species (Rohde, 2010).

There is little knowledge of parasites of the deep oceans. The deep ocean (depths deeper than the continental margin, approximately 200 m) is a hostile environment with low temperatures (2°C average), no light penetration which makes photosynthesis practically impossible and a food supply that is dependent on detritus from the upper levels of the ocean (Costello and Breyer, 2017). This environment is not conducive to high diversity. However, there are exceptions, particularly around hydrothermal vents, whale falls and cold seeps that have an incredible abundance of animals for such hostile environments. Whether parasite abundance is also high in these habitats remains to be studied (De Buron and Morand, 2004).

The latitudinal, longitudinal and depth gradients in marine parasites remain to be analyzed at global scales and across all marine parasite taxa. At present it appears they follow the same biogeographic patterns as other species, but confirmation across a broader scale is desirable. Furthermore, the species richness and endemism of parasites and their hosts are not necessarily linearly correlated. For example, there may be thresholds of host population density where parasites become more or less pathogenic due to dispersal success.

Societal Importance of Marine Parasites

Humanity’s dependence on the ocean for food and ecosystem services is well documented. Almost 80% of commercially relevant marine species are being fully exploited or over exploited (FAO, 2016). As a result, the 21st century has seen unprecedented developments of aquaculture initiatives, currently contributing over 40% of total marine resources for human consumption (FAO, 2016). With humankind’s dependence on these resources in mind and the established knowledge of how ingrained parasitic organisms are within these ecosystems, we’ll discuss how marine parasites impact human society. We consider this impact both directly, in the sense of infection, and indirectly, in their impact that is of commercial relevance.

Public Health

Most parasitic organisms infect the portions of the fish that humans don't eat, particularly the visceral organs that are removed before consumption. There are parasitic organisms that infect the flesh of fish (usually intermediate stages of helminth parasites), and of these, only a few have health impacts on humans. Fortunately, most of these parasites are killed after cooking for 1 min at 60°C or frozen to -20°C for 24 h (Olsen, 1986). However, with the increasing popularity of consuming raw, smoked and/or undercooked fish, the occurrence of human infections from this source has increased (Olsen, 1986; Macpherson, 2005). Parasite infection from raw marine fish involves only two kinds of helminth parasites; from the *Anisakidae* family (e.g., round worms, Nematoda) and the *Diphylllobothrium* genus (e.g., tape worms, Cestoda).

Anisakid worms use marine mammals or piscivorous birds as definitive hosts, with aquatic invertebrates and fish as intermediate hosts (Chai et al., 2005). The intermediate phase of these round worms encyst within the musculature of their hosts and are pervasive in their choice of host, having been found in anchovies in Italy, salmon in Norway and Japan, and in herring, cod, tuna and sardine species globally, just to name a few.

Anisakiasis is the infection of these encysted round worm larvae specifically from species in the *Anisakis* and *Pseudoterranova* genus. These larvae are ingested and attempt, unsuccessfully, to develop within the gastrointestinal tract of humans. Typically, the worm elicits an immune response in human immune systems that causes severe pain, nausea and vomiting. *Anisakis* species are also known to cause allergic reactions in humans due to a biochemical release as a defensive strategy against the host immune system. Within fish processing factories, asthma, conjunctivitis and contact dermatitis have been observed in workers who work in direct contact with fish that are infected with these parasites (Nieuwenhuizen et al., 2006).

Diphylllobothriasis is an infection caused by species from the *Diphylllobothrium* genus. This parasite's life cycle is highly complex, with two intermediate hosts and fish-eating mammals or birds as its definitive host. Infection is usually obtained through the eating of the developmental stages of the parasite present in anadromous fish musculature, particularly salmonid species. Most infections are asymptomatic with rare symptoms including abdominal discomfort, diarrhea, vomiting and weight loss (Olsen, 1986; Chai et al., 2005).

Fisheries and Aquaculture

Parasites can significantly contribute to financial losses for the fisheries industry (Lafferty et al., 2015). Regardless of whether they pose an actual health risk, the appearance of parasites in fish and the presence in the musculature can lower the value of fish products and can prevent them from being sold on local and international markets. It is difficult to measure the impacts of parasites on wild caught fish, as the prevalence on wild caught fish is comparatively lower than fish sold from aquaculture (Costello, 1993; Shinn et al., 2015).

Aquaculture is predicted to contribute 65% of our fish needs by 2030 (FAO, 2016). Therefore, there is an expected increase in aquaculture production to meet this demand. As parasitic infestations threaten the sustainability of the industry, environment and food security for a growing global population, the development and implementation of measures to lessen parasitic diseases and improve the farmed organisms' health have important social, economic, environmental and political implications.

Parasites with direct host to host transmission tend to thrive when their hosts are at a high density, as in intensive fish farming. The most significant parasites in salmon farming are species of copepods called sea lice (Family Caligidae). In the north Atlantic and Pacific oceans, two louse species, *Lepeophtheirus salmonis* (which is specific to salmon) and *Caligus elongatus* which is not host specific, cause significant costs to salmon farms (Costello, 1993, 2006). For both these species, lice from wild fish colonize fish farms. Once established within these farms, they become parasitic reservoirs and act as year round sources of lice that cross-infest surrounding wild fish populations, causing significant mortality in Ireland, Scotland, Norway, Canada, and Chile (Costello, 2009a).

Various methods are employed to control lice infestations. These include biological control methods (e.g., vaccines against bacteria, cleaner-fish to remove salmon lice), chemical treatments (e.g., pesticides and disinfectants) and changes in nutrition to strengthen fish immune systems (Costello et al., 2001). The most effective methods are to prevent or delay parasite infestation by not having overlapping generations of fish on the same farm and having 'fallow' periods when no host fish are on the farm site (Costello 2006). Apart from the monetary costs of incorporating these treatments, the environmental costs can also be substantial, particularly the aforementioned impact on wild fish populations.

Shinn et al. (2015) provided a review of global marine and brackish water aquaculture industries and used examples from these industries to try and predict the economic losses associated with the infection of key parasitic disease events within the industry. As an example, *Salmo salar* (Atlantic salmon) constitutes one of the most established aquaculture industries to date with over 40 years of experience. Globally, the farmed salmon industry is worth over \$15.4 billion USD (FAO, 2016). In 2006, caligid copepod ectoparasites, particularly *Lepeophtheirus salmonis*, added 6% to the global production cost (Costello, 2009b). This is a major constraint to a global industry and has consequences all the way down the supply chain to the consumer.

Parasites represent a key constraint to production, sustainability and economic viability in aquaculture (Timi and Mackenzie, 2015). Although some infections are predictable due to experience within the aquaculture industry, there are substantial costs associated with the control and management of outbreaks that have consequences throughout the supply chain (Costello, 2006, 2009b).

Parasites in Applied Research

Although parasites have a bad reputation and are considered “reprehensible citizens,” they have been shown to be important in contributing to understanding how ecosystems function (Poulin, 2007). This section will discuss the usefulness of marine parasites in applied research, from providing unique perspectives on how pollution is impacting biota to providing information on the structure of their host populations. Finally, we address the potential impact that climate change may have on parasitic species and the potential consequences on their hosts.

Biological Indicators

Fish parasites have been used as biological indicators to provide information on aspects of hosts’ feeding ecology and behaviour, including in remote areas such as Antarctica (Palm et al., 2007). As most fish parasites with complex life cycles are transmitted through the food chain, they can provide information on food web interactions that may not be seen through traditional stomach content analyses (Lafferty et al., 2008). For example, researchers creating a food web in the Baltic Sea found that using known parasitic infections through the food web provided more information on the food web structure than looking at the observed diet alone (Valtonen et al., 2010). A secondary benefit to this research is to discover the intermediate hosts of the parasite species and, as a result, clarify parasitic life cycles (Marcogliese, 2002). This research has been extended to provide information to fisheries managers on fish population structure during stock assessments (Timi and Mackenzie, 2015).

Fisheries stock assessments are conducted to assess the biological status of fisheries and inform managers as to the state of that fishery (Catalano et al., 2014). For example, Reed et al. (2012) identified that a “tetracotyle” type metacercaria (digenetic trematode) infecting the eyes of sardines was a useful biological tag because of its site specificity, ease of detection and probable long life span in its sardine host. By collecting, analyzing and modeling over 5,000 sardines-worth of parasite prevalence, infection intensity and abundance, Weston et al. (2015) found that there were two separate stocks of sardine. This information has allowed South African fisheries managers to better manage this fishery.

As parasites can be specific to a host family, genus and/or species, they can also be used in host identification. For example, diphyllidean cestodes assist in confirming identification of species of rays around Britain (Williams, 1964). Other parasites have been used in clarifying phylogeny, particularly in determining the host’s and parasites taxonomic positions. Olson et al. (2010) found that trypanorhynch cestodes formed two primary lineages and were monophyletic. This split provided independent support for rejecting the notion that rays are derived from sharks and supported the most recent molecular phylogenetics of the Neoselachii in which modern sharks are considered a sister group of skates, rays and saw fish.

Environmental Indicators

Parasites have been used as indicators of environmental change in two distinct ways, as effect indicators and as accumulation indicators (MacKenzie, 1999; Williams and MacKenzie, 2003; Sures et al., 2017). Effect indicators are parasites that are either positively or negatively impacted by changing environmental variables, and it is this change in population structure that is measured. Blonar et al. (2009) provides a meta-analysis of the effects of various sources of pollution (e.g., pesticides, metals, eutrophication, and sewage) on parasite populations, and they identify which parasite taxa and pollution sources effect these populations. They conclude that communities of digenean (trematode) and monogenean helminths are negatively impacted by changes in their environment, particularly heavy metals, eutrophication and sewage. The researchers conclude that by monitoring population-level changes in these taxa, parasites can provide information on the relative health of polluted areas.

Accumulation indicators are species that accumulate substances, such as toxins, from their surroundings and concentrate these substances within their tissues and organs. Historically, free living organisms, predominantly mussel species (Zuykov et al., 2013), have been used in pollution studies. Helminth parasites, particularly Acanthocephala, Cestoda and Nematoda, are susceptible to heavy metal accumulation due to their site of infection within the stomachs of their hosts. Parasites that have been identified as potential indicators have been measured with heavy metal concentrations orders of magnitude higher than the surrounding host tissues (Morris et al., 2016; Nachev and Sures, 2016).

Compared to mussels and other free-living sentinel species, parasites are small, cryptic and difficult to retrieve from their environment. This makes them unattractive to include in accumulation studies. However, as parasites occur throughout marine food webs and reside within hosts for extended periods of time, the monitoring of metals in their tissues can deliver information about the spatial and trophic distribution of pollutants, information traditional benthic sentinels cannot provide (Sures et al., 2017).

Parasites’ Potential Response to Climate Change

Local studies on warming events indicate that global climate warming may impact parasite biology and ecology. Changes that have been recorded in the protozoan parasite *Perkinsus marinus* include an increased pathogenicity in oysters along the east coast of North America during uncharacteristic winter warming events (Harvell et al., 2002). Similarly, warmer winters have led to increased invasions by copepod parasite species on aquaculture farms (Callaway et al., 2012). In some cases, it is the duration of low winter

temperatures, rather than the minimum temperature, that is most important for maturation, mortality, and re-infection within some parasite populations (Marcogliese, 2001). An increase in average winter sea surface temperatures will allow parasites to survive through the winter and consequently allow for increased survival and earlier maturation in the spring.

As temperature increases and biochemical reactions speed up, this increased metabolism is limited by the amount of fuel an organism has access to (Lafferty, 2009). As parasitic organisms depend on their host for food, an increase in temperature has the ability to increase the parasites pathogenicity on the host. Therefore, not only does the host have to deal with their own increased thermal stress, but also an increase in parasite pathogenicity (Marcogliese, 2001). For example, with increases in temperature, dissolved oxygen levels in the water decrease, which increases stress to the fish. Concurrently, a rise in temperature may shorten generation time and increase growth rates of gill parasites (such as monogeneans). The combination of decreased oxygen and increased parasite burden can cause respiratory problems for fish, often resulting in mortality (Marcogliese, 2001).

More importantly, though, increasing temperatures have been shown to alter the seasonality and biogeographical range of many species (Hillebrand et al., 2018). These range shifts will undoubtedly affect their associated parasites. This could potentially result in parasitic organisms discovering new hosts and may cause unprecedented pathogenic outbreaks in naïve host populations. In addition, these range shifts could cause local extinctions of parasitic species (in the case of host specialist species) and consequent indirect effects to ecosystems (Strona, 2015).

Conclusions

This article demonstrates the biology, ecology and societal importance of marine parasites. As evidenced by the examples of parasites in food web studies, these organisms have contributed significantly to our understanding of the direct and indirect impacts of parasites in controlling host populations (Marcogliese, 2004; Lafferty et al., 2008). In their use as biological and environmental indicators, parasites have not only allowed researchers to understand the trophic structure of ecosystems but have shown their ability to be used as sentinels within environments to provide information on host population structure and the impact that pollution may be having on an ecosystem (MacKenzie and Abaunza, 1998; Palm, 2011; Nachev and Sures, 2016).

As technology advances, with respect to genetic analysis and general taxonomic methodology, researchers are still discovering hundreds of species annually due to efforts in parasitic description being at their highest rate ever (Costello et al., 2013b; Poulin and Presswell, 2016). While perhaps most parasites have been named (Costello 2016), this is only the first step in understanding their biology and ecology (Rohde, 2002; Chaudhary et al., 2016; Poulin and Presswell, 2016; Jorge and Poulin, 2018).

Poulin et al. (2016) provide their perspective on the current state of marine parasitology and its collaboration with marine ecology and identify challenges to inter-field collaboration. These challenges include: a need for greater awareness of parasitology in general ecological journals; keeping parasitology relevant with current trends in general ecological theory; maintaining or improving current discovery rates of parasitic species and their life cycles; increasing our footprint of research into more geographic areas (e.g., open and deep oceans); and finally developing models to understand transmission dynamics of parasites. What their article highlights is that parasitology as a discipline can and should depend on more established disciplines such as marine ecology to guide its future endeavors.

Climate change is likely to impact parasite communities directly through changes in environmental conditions and indirectly through changes in host species. Therefore, the current challenge for parasitologists and conservationists is to understand the ecological roles played by parasites so as to predict how and which ecosystem functions may be altered as climate changes.

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The Biology, Ecology, and Societal Importance of Marine Isopods

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Abstract

The Isopoda are a large and morphologically diverse group of crustaceans. Roughly 6250 of the 10,300 described species are marine or estuarine. The taxonomic description of isopods started in 1840 and shows two strong phases of discovery and although the discovery rate has slowed down since the 1990s, the Isopoda are a promising group for more new species discoveries in the future. The order has a worldwide distribution occurring in terrestrial, freshwater, and marine habitats. Marine isopods can be found from pole to pole in each of the worlds' oceans. The majority of the known species occurs in shallow-water habitats, but isopods are also widely distributed in the deep sea with the Asellota as the dominant group at these depths. Some isopod families have evolved a parasitic life-style, displaying different life histories and often a highly modified appearance. Those parasites do not only infest wild host populations, but also frequently cause problems in fish farming and commercial fisheries. As marine woodborers some species, too, cause considerable damage to man-made marine infrastructure.

Systematics and Taxonomy

The order Isopoda is one of the largest orders of crustaceans with about 10,300 described species, of which roughly 6250 are marine or estuarine (Poore and Bruce, 2012). Just like so many other animals and plants the first isopods were named by Linnaeus (1707–78). However, for marine isopods the history of discovery started in 1840 when Milne Edwards' paper on Crustacea was published (Poore and Bruce, 2012). In the beginning important contributions to the taxonomy of the Isopoda were made particularly by experts from Europe and North America. History shows clearly two strong phases in the discovery of new marine isopod species. The first phase stretched from the 1880s to the 1930s and the second was during 1980s–2000 (Poore and Bruce, 2012). In the modern era new sampling methods made the sampling of very small size classes and so far unsampled habitats possible, which led to a series of new discoveries. Since the 1990s the rate of species discovery has slowed down. During that decade about 20% of all known species and 10% of the known genera were described (Poore and Bruce, 2012). Although a lot of isopod species are already scientifically described, there still remain many to be discovered in the future.

Scientists agree on the Isopoda being a monophyletic group. Such a consensus does not exist when it comes to the relationship of the group to other peracarid orders. Peracarida is the superorder which comprises the Isopoda and 11 other orders of crustaceans. Several cladistic analyses have been made; some of them stating the isopods are a sister taxon to Tanaidacea, others see them more closely related to Amphipoda (Poore and Bruce, 2012). Even on genus and species level the taxonomy is constantly changing. Over the years many species names have been revealed to be synonymies, as have some genera. For example Smit et al. (2014) mentioned in their review on the global diversity of the fish-parasitic family Cymothoidae that 16 of its genera and 83 species are in synonymy. Seven additional species therein were regarded as *Nomina dubia*, where it was doubted that they were valid species names.

Morphology

As crustaceans isopods have a segmented, chitinous exoskeleton with jointed appendages. The overlapping, articulated tergites (dorsal plates of each body segment) provide protection as well as flexibility. Isopoda have a dorsoventrally flattened body, which can be divided into three regions: the head (cephalon), thorax (pereon), and abdomen (pleon). Each body segment bears a pair of appendages. The segments of the head are fused and the respective appendages from anterior to posterior are the first pair of antennae (or antennules), second antennae, mandibles, maxillules, and maxillae (Poore and Bruce, 2012). The first thoracic segment (and sometimes the second) is fused to the head and its appendages are modified into maxillipeds which help processing food (Barnes, 1980). The head also bears a pair of well-developed compound eyes, which are always sessile in isopods. The pereon

consists of seven free segments, each bearing a pair of pereopods, which are uniramous (unbranched) and usually adapted as walking legs. The pleon has six segments, of which the last one is fused with the telson forming a pleotelson (Poore and Bruce, 2012). The abdominal appendages are called pleopods and are biramous and lamellar. The last segment of the abdomen bears a pair of biramous uropods, which can be either fan-shaped or styliform (slender and pointed) (Barnes, 1980). In contrast to most other crustaceans the Isopoda are lacking a carapace, which usually forms a branchial chamber to protect the gills (Barnes, 1980). Probably as a response to the reduction of the carapace the respiratory structures have shifted from the thorax to the abdomen. In isopods the pleopods function as gills (Brusca et al., 2016). Female isopods have a special ventral brood pouch, the marsupium, formed by oostegites (cuticular lobes extending from pereopodal coxae). The juveniles hatch inside the marsupium and are actively released by the female as manca larvae. The manca stage lacks the last pair of pereopods, but otherwise resembles an adult isopod (Poore and Bruce, 2012). The missing pair of appendages appears when the juveniles molt into adults. A synapomorphy, in other words a characteristic all groups of isopods share and which is derived from their last common ancestor, of the Isopoda is the biphasic molting. When the old cuticle is shed to enable an increase in body size, isopods first shed the posterior part of the body and later they molt the anterior part (Brusca et al., 2016). The period between the successive molts, the so called interecdysis, can take from several hours up to a few days (Kaïm-Malka, 1997).

The size range spans from 0.5 mm to as big as 500 mm in the giant isopod *Bathynomus giganteus* A. Milne-Edwards, 1879. The majority range between 3 and 20 mm (Poore and Bruce, 2012). Isopods are mostly cryptically colored or patterned. Some may show a certain degree of ornamentation or spines across their body surface. They usually have separate sexes, although there are some hermaphroditic species. While in most isopods there is none to very little sexual dimorphism, in parasitic species it may be marked (see Fig. 1I and J for sexual dimorphism in Gnathiidae) up to dwarf males and large and highly modified females. Isopods are a morphologically very diverse group (see Fig. 1). Sometimes some body segments are fused and some appendages lacking or



Fig. 1 Diverse forms of isopods. (A) Arcturidae: *Neastacilla tuberculata* AIM MA76468, with long antennae and an elongated body; (B) Paranthuridae: *Paranthura punctata* AIM MA80474; (C) Bopyridae AIM MA31344; (D) Cirolanidae: *Cirolana* sp. AIM MA124551, ventral view, displaying the typical elliptical body shape of an isopod; (E) Idoteidae: *Idotea metallica* AIM MA4568; (F) Serolidae: *Serolis polita* AIM MA31576, trilobite-like appearance; (G) Scyphacidae: *Scyphax ornatus* AIM MA100630; (H) Plakarthriidae: *Plakarthrium typicum* AIM MA75430, ventral view, extensions of coxae and peduncular articles of antennae forming oval outline; (I) Gnathiidae: *Gnathia* sp., male with distinctive protruding mandibles, scale bar: 1 mm; (J) Gnathiidae: *Gnathia* sp., gravid female carrying about 30 eggs, scale bar: 1 mm; (K) Munnopsidae: *Munna neozelanica* AIM MA76473.

reduced. A few groups have a rather elongate and cylindrical body shape compared to the more elliptical form of the typical isopod. Parasitic isopods probably are the most modified ones. Whereas male parasites often are easily identified as isopods, female parasites are sometimes scarcely recognizable as such. Some have lost all segmentation, being only sac-like forms, not at all resembling an isopod anymore (Williams and Boyko, 2012).

Biogeography

Isopods have a worldwide distribution. They occur virtually in every habitat on earth (except in terrestrial Antarctica) and are the most successful group of terrestrial crustaceans. In fact, land-living Isopoda are the only truly terrestrial crustaceans having evolved to be completely independent of water. Marine isopods can be found in all of the world's oceans from pole to pole. Since they form such a diverse group, biogeographical studies have focused more on specific taxa or regions (e.g., Borges et al., 2014 for Limnoriidae in Europe; Brusca, 1987 for the Galapagos region) than on the global picture involving all marine isopods. Poore and Bruce (2012) did a comprehensive study on the global diversity of marine isopods, but they excluded the suborder Asellota and crustacean symbionts from it. About half of all coastal, shelf and upper bathyal species occur in temperate waters, 40% in the tropics and the remainder in polar seas (Poore and Bruce, 2012). The greatest concentration of temperate species is found in Australasia, while for the tropical regions the Central Indo-Pacific is richest in species. The fish-parasitic family Cymothoidae are most diverse in tropical waters, also with the Central Indo-Pacific holding twice as many species than other tropical regions (Smit et al., 2014). The Antarctic holds nearly four times as many species as the Arctic. Temperate species show an asymmetry in latitudinal distribution with 1.35 times as many species in the Southern Hemisphere than within the same latitudes on the Northern Hemisphere (Poore and Bruce, 2012). Parasitic isopods associated with crustacean hosts exhibit highest diversities in the North West Pacific, East Asian Sea, and Central Indian Ocean, as well as in the North East Atlantic, Antarctic, Arctic, and Mediterranean (Williams and Boyko, 2012). The distribution patterns of parasitic species are, of course, influenced by host distributions.

Habitat

Members of the Isopoda can be found in every marine habitat. Their bathymetric range stretches from the intertidal zone to the dark and cold depths of the world's oceans. Although the deepest ever recorded species (6435–7280 m) is a member of the family Antarcturidae within the suborder Valvifera (Poore and Bruce, 2012), the most diverse and species rich group inhabiting the deep-sea floors is the suborder Asellota. However, the majority of species occur in shallow-water habitats on rocky shores, muddy environments, and sandy beaches (Poore and Bruce, 2012). Isopods can be found burrowed in sand, dead wood or algal holdfasts; inhabiting worm tubes, sponges, crevices or the shells of dead molluscs; or living beneath rubble or rocks. Some species of marine isopods are also able to tolerate low salinities and are frequently found in brackish waters, like estuaries or mangroves.

Ecology and Life History

Since marine isopods are benthic animals (Barnes, 1980) without a pelagic larval phase and also not exactly long-distance swimmers, their dispersal abilities are somewhat restricted. As for many other marine invertebrates, rafting on floating objects may be considered as a common dispersal mechanism, although *Idotea metallica* Bosc, 1802 (Fig. 1E) is probably the only obligate rafter within the Isopoda (Gutow et al., 2006; Tully and Ceidigh, 1986).

Isopods display a variety of feeding methods. They are scavengers, predators, parasites, detritus feeders, and filter feeders. Their diet is herbivorous, carnivorous, or omnivorous.

When it comes to reproduction the most notable aspect, which separates isopods from other crustaceans, is that they do not produce the typical nauplius larva. Instead isopods have a larval stage called manca, which lacks the last pair of pereopods (see "Morphology"). An isopod life-cycle begins with the female laying previously fertilized eggs into a special brood pouch, the marsupium. Egg size and number of eggs are correlated with female body size (Poore and Bruce, 2012). The eggs hatch inside the marsupium and the female continues to carry the larvae. At some point the young are actively released by the female as mancas. The number of manca larvae, which are released from one female, varies with the size of the female and ranges from 10 to 1600 individuals (Poore and Bruce, 2012). The juvenile isopods undergo a series of successive molts until they reach the size of adults and sexual maturity. For an individual of *Natatolana borealis* (Lilljeborg, 1851) it may take 9–11 molts to grow from 4–5 mm to 19–20 mm in length (Kaïm-Malka, 1997).

Parasites

Only a few isopod families are parasitic, but those may be very species-rich. For example the family Bopyridae contains 605 species in 167 genera in 10 subfamilies (Williams and Boyko, 2012; WoRMS, 2018). Bopyrids (Fig. 1C) parasitize other crustaceans like hermit crabs or shrimps, whereas other isopods are fish-parasitic (Smit et al., 2014). Not only teleost fishes are suitable hosts.

Elasmobranchs are also parasitized by isopods (Smit and Basson, 2002). Even other isopods end up being hosts for their parasitic relatives. Some species of Cabiropidae can be found in the brood chambers of bopyrids, which is termed hyperparasitism (Williams and Boyko, 2012). Within the Isopoda both ecto- and endoparasitic species can be found. Usually the parasites have a specific site of attachment, either somewhere on the host's body surface or in the branchial chamber or the mouth of the host. In cymothoids, for instance, the attachment site is species specific or sometimes even specific for a certain genus (Smit et al., 2014). Cymothoidae infest only one host during their life cycle. The larvae are released as a free-swimming manca stage and are immediately infective to suitable hosts (Adlard and Lester, 1995), even though they can remain free-swimming for several days while feeding on their yolk stores (Smit et al., 2014). The larvae seek a suitable host and attach to it, then they undergo successive molts into the adult stage. The juvenile first becomes a male in case there's already a female present. If no female is present, the male will transform into a larger female, which is then referred to as an adult (Smit et al., 2014). Other parasitic isopods associated with crustacean hosts infest two hosts during their life cycle, the intermediate host being a pelagic copepod (Williams and Boyko, 2012). After the larva has molted into the infective stage for the definite host, it detaches from the copepod and seeks a suitable crustacean host like some kind of crab or shrimp. It transforms into a juvenile and moves to the final attachment site. Sex determination in parasitic isopods is not fully known, but in many cases the first isopod that settles on a host becomes a female and subsequent individuals develop into males (Williams and Boyko, 2012). Females feed on the hemolymph or ovarian fluids of the host, whereas males are not known to do so. In contrast to other obligate parasites members of the family Gnathiidae are only parasitic during their larval stages. The adults (see Fig. 11 and J) are free-living forms, do not feed at all and form harems within the substrate or sponges (for a review on gnathiid isopods see Smit and Davies, 2004).

One parasitic isopod that managed to get at least some attention from a nonscientific audience is the tongue-replacing isopod, *Cymothoa exigua* Antarcturidae and Meinert, 1884. Brusca and Gilligan (1983) report on the not only structural but also functional replacement of the hosts' tongue. *C. exigua* infests fish hosts. Females attach in the mouth, while males attach to the gills. The blood-feeding of the female parasite leads to a decrease in blood circulation in the tongue and results in the degeneration of the organ. At that stage the isopod is found attached to the remaining tongue stub replacing the degenerated host structure. Parasitized fish seem to be in a good condition (Brusca and Gilligan, 1983) and there is evidence that the host uses the isopod as a kind of artificial tongue during food processing.

It is not uncommon that isopod parasites act as parasitic castrators. Parasitic castration is defined as an intensity-independent prevention or blockade of host reproduction by taking up the host's whole reproductive energy (Lafferty and Kuris, 2009). In their review on parasitic castrators Lafferty and Kuris (2009) note that the parasites may range in body mass from 3% up to 50% of their host's body mass and that some parasites, like bopyrid isopods, castrate their hosts without specifically targeting reproductive tissues. Fogelman et al. (2009) report on the effects of the cymothoid isopod *Anilocra apogonae* Bruce, 1987 on a cardinalfish. In accordance with the principle of parasitic castration the intensity of parasite infestation was always limited to one adult per parasitized fish. Parasites were also relatively large, weighing about 3.8% of the host's weight (Fogelman et al., 2009). Infested fish had significantly smaller gonads than unparasitized individuals. Moreover, parasitized female cardinal fish produced significantly fewer ova, of which only a few were mature. Male fish seemed to lose their ability of mouthbrooding. They also had a negative impact on the growth rate of their vertebrate hosts.

Economic and Environmental Impact

During the glory days of seafarers it wasn't huge and terrifying sea monsters which posed the biggest threat to ships built out of wood. Marine woodborers (shipworms, pill bugs, and gribbles) caused extensive damage to wooden vessels and marine infrastructure throughout the centuries. An estimation of the global damage caused by woodborers in the early 2000s was stated at US\$1 billion per year (Raya et al., 2015). However, the biggest amount of the damage is caused by shipworms, which are bivalves of the family Teredinidae. Woodboring crustaceans are species belonging to the isopod families Sphaeromatidae and Limnoriidae, commonly referred to as pill bugs and gribbles, respectively. Unlike members of the Limnoriidae sphaeromatids do not ingest wood as a food source, but rather simply excavate burrows utilized for shelter (Si et al., 2002). The greatest diversity of marine woodborers is found in tropical coastal water bodies (Raya et al., 2015). This pattern is consistent with the natural distribution of mangrove forests, which represent the natural habitat of marine wood-boring organisms. Along the southwestern coast of Florida the wood-boring isopod *Sphaeroma terebrans* Bate, 1866 caused a gradual shrinking of the mangrove forest area during the mid-20th century (Rehm and Humm, 1973). Woodborers also caused problems in communication technology by attacking submarine cables. In 1916, for example, the isopod *Limnoria lignorum* (Rathke, 1799) was identified as the cause of a break in the Cook Strait Cable, one of six telegraph cables connecting New Zealand's North and South Island (Raya et al., 2015).

Parasitic isopods can cause great losses in commercial fisheries and fish farming. Stepien and Brusca (1985), for instance reported nocturnal attacks of cirrolanid isopods on caged giant kelpfish *Heterostichus rostratus* at the coast of California. It was observed that the fish showed great distress once specimens of *Cirrolana diminuta* Menzies, 1962 were present. The isopods inflicted major damage to the gill filaments, as well as to the gonads and livers of fish, causing high mortality. In India cultured catfish *Mystus gulio* suffered serious lesions and anorexia from infections with *Cymothoa indica* Schioedte and Meinert, 1884 leading to mass mortality (Rajkumar et al., 2005). Within 10 days 100% of the fish stock died. Even when infections are not as severe and do not cause parasitized fishes to die, the resulting smaller sizes, lower weights, lesions, and/or deformations make the product unattractive to customers (Čolak et al., 2018). Often the cultured hosts are not the same host species which are known to be infected by the

respective parasites in the wild (Rajkumar et al., 2005; Smit et al., 2014). Methods against isopod infections in aquaculture (other than manual removal) include chemical treatments (see Costello, 1993), of which deltamethrin and diflubenzuron have been shown to decrease parasite prevalence with low toxicity for the fish in Mediterranean fish cultures (Athanasopoulou et al., 2009). Not only teleost fishes but also commercially important crustaceans like shrimp, king crabs, and brachyuran crabs are parasitized by isopods, negatively affecting the salability of infected hosts (Williams and Boyko, 2012). On the other hand isopods can be the good guys, when they—in their role as scavengers—remove waste feed from tuna farms in South Australia, diminishing the ecological impact of aquaculture on the ecosystem (Svane and Barnett, 2008).

Although humans do not rank among typical hosts for parasitic isopods, there are records of attacks on humans. Garzón-Ferreira (1990) reports being bitten numerous times by the usually fish-parasitic isopod *Rocinela signata* Schioedte and Meinert, 1879 during snorkeling at the coast of Colombia. The isopod began to feed immediately after attachment and sometimes it attached itself so firmly to the skin that it was necessary to kill it in order to remove it. Of course this case is rather an exception than the general rule.

In July 2017 a human body was retrieved from Australian waters, which showed extensive postmortem predation of the skin and subcutaneous tissues (Tiemensma et al., 2017). From the affected sites five isopod specimens were removed and identified as two different species of the family Cirolanidae, well-known marine scavengers.

Summing it up one can note that even though isopods are only very small creatures, they can cause severe problems. Also, since they are distributed worldwide, these problems are not locally restricted. So far a lot of effort has been put into isopod taxonomy, but still many more species remain to be discovered and named. The life histories of many groups and species are often poorly studied and very little is known about the ecology of deep-sea isopods and their role in this remote environment. These and other research gaps remain to be filled.

Acknowledgments

Thanks to the Auckland War Memorial Museum, Auckland, New Zealand (AIM) for the permission to take photographs of some museum specimens out of their collection.

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Mesophotic Coral Ecosystems

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Abstract

Mesophotic coral ecosystems have been studied for almost as long as researchers have studied shallow coral reefs. This may be surprising, given that the term mesophotic was coined as recently as 2008. At their shallowest, most agree, mesophotic reefs are found between depths of 30 and 40 m. This reef zone then extends to the limit of photosynthetic activity in hard corals, a maximum depth of about 165 m. The mesophotic zone has been further divided into an upper and lower mesophotic zone either side of a global 60 m depth boundary. The lower mesophotic harbors a biota distinct from shallow reefs, while the upper mesophotic is a transitional zone between the two. The mesophotic environment can be characterized as low in light, temperature, and wave action in comparison to shallow reefs.

Background

Marine biology as a field has always faced challenges of access. Utilizing newly developed SCUBA and submersible technologies in the 20th century opened the marine environment to detailed study by scientists. SCUBA allowed taxonomists to document new taxa otherwise missed in complex 3D habitats and to adopt experimental approaches to subtidal ecology (Eschmeyer et al., 2010). Despite this, SCUBA studies have been largely limited to depths shallower than 30 m so as to remain within recreational dive regulations. Meanwhile advances in video techniques with submersibles and remotely-operated vehicles (ROVs) allowed the study of deep-water ecosystems hundreds and thousands of meters beneath the surface (Costello et al., 2005; Roberts et al., 2008). However, submersibles, are expensive to hire and operate, historically lacked dexterity, and may miss small taxa. The large ROVs necessary for taking biological samples face operational difficulties in shallow waters (e.g. overheating of cables). Typically, submersible and ROV studies have focussed on ecosystems below the ranges of zooxanthellate corals (for some exceptions see Fricke and Meischner, 1985; Fricke and Knauer, 1986). The different limitations of these methods permitted an understudied depth zone to form. A 2008 review (Menza et al.) reported 90% of all publications mentioning coral failed to report data deeper than 30 m. On the other hand, research has shown that photosynthetic hard corals regularly occur far deeper than 30 m. The current depth record stands at 165 m at Johnston Atoll (Maragos and Jokiel, 1986). This is not a globally unusual case, with further depth records set for the Bahamas, Red Sea, and Great Barrier Reef past depths of 100 m (Englebert et al., 2014; Reed, 1985; Schlichter et al., 1986), as reviewed by Kahng et al. (2010).

In 2008 a workshop was hosted by the National Oceanic and Atmospheric Administration (NOAA, USA) to bring together researchers interested in studying the hard to access “middlingly deep” coral reefs. These were the reefs found below recreational dive limits, but not the “deep” cold water coral reefs found usually beneath the photic zone formed by azooxanthellate or facultatively zooxanthellate corals (Roberts et al., 2008). They coined the term Mesophotic Coral Ecosystem (MCE), to help coordinate research and define shared research interests (Puglise et al., 2009). MCEs were meant to be recognized by their distinct ecology,

as the low light areas of reefs containing photosynthetic hard corals (Baker et al., 2016a). In practice, the term mesophotic has been applied to studies deeper than the 30 m limit of recreational diving (Laverick et al., 2018).

As hard corals typically rely on photosynthesis to satisfy their calorific demand, and light energy decreases exponentially with increasing depth (Fricke and Knauer, 1986), we would expect MCEs to be subject to a differing ecology to shallow reefs. Research on MCEs, plugging the knowledge gap reported by Menza et al. (2008), has become increasingly common as a result of advances in diving technology, autonomous exploration (Pyle, 1998), and the realization MCEs significantly increase global reef area (Harris et al., 2012).

Despite increasing research effort, how to recognize an MCE is still open for discussion. An absolute upper depth limit of 30 m fails to capture the variability of environmental conditions responsible for changing rates of reef transition between sites (Laverick et al., 2017). A number of site descriptions discuss changing richness with depth and identify clusters of deep and shallow species (Bridge et al., 2012; Muir et al., 2015), yet very few attempt to define reef structure in terms of indicator taxa (Bejarano et al., 2014). Following the second international MCE workshop in 2014 the need to address such issues was acknowledged (Loya et al., 2016).

As well as background on how the field of mesophotic research came to be, this article aims to give the reader an introduction to the evolving use of key terminology and existing research foci. The field already has a number of excellent reviews, technical reports, and recently a book (Loya et al., 2019). These resources are listed at the end of this article for those interested in reading more thoroughly about MCEs.

Key Terms

Mesophotic Coral Ecosystems (MCEs)

[MCEs] are characterized by the presence of light-dependent corals and associated communities typically found at depths ranging from 30–40 m and extending to over 150 m in tropical and subtropical regions. The dominant communities providing structural habitat in the mesophotic zone can be comprised of coral, sponge, and algal species.

(Puglise et al., 2009, pV)

MCEs are defined by their ecology, not their absolute depth range.

(Baker et al., 2016a, p12)

Initially, the term ‘Mesophotic Coral Ecosystem’ was coined to bring together researchers with an interest in studying a difficult to access system. Though the original definition published states a range that MCEs can begin from (30–40 m), there is little to no guidance on how to apply this range. Consequently, most researchers use 30 m as a static depth limit (Laverick et al., 2018). This is despite later clarification that MCEs are defined by their ecology and not a depth limit (Baker et al., 2016a,b). How to recognize an MCE in the absence of depth information, is therefore an active area of research (Laverick et al., 2017; Loya et al., 2016; Tamir et al., 2019). Additionally, it is worth noting that Scleractinia may comprise only a minor component of benthic diversity by area. In spite of whether a reef is dominated by sponge, algae, or other groups instead, the term MCE is currently used to refer to these reefs as well (Puglise et al., 2009).

Upper and Lower Mesophotic

...The upper mesophotic is home to many shallow-water marine organisms and represents a transition zone between shallow-water and lower mesophotic communities. The lower mesophotic represents a distinct community with some species exhibiting special physiological adaptations.

(Kahng et al., 2014, p72)

Many MCEs within the Caribbean Sea exhibit a clear demarcation between the upper mesophotic community (30–60 m), with biodiversity that overlaps with the shallow coral reefs, and the ecologically distinct lower mesophotic community (60–100 m).

(Lesser et al., 2018, p62)

Shortly after the term mesophotic entered the literature, a distinction was made between the upper and lower mesophotic (Kahng et al., 2014). The upper mesophotic represented an area of overlap, containing some shallow species, while the lower mesophotic contained its own taxa. Kahng et al. (2010) initially reviewed a number of ecological papers reporting a split in community structure in the mesophotic zone. As would be expected, the depth these boundaries occurred at was variable by region and taxon. However, researchers have settled on a ‘60 m rule’ to currently divide MCEs (Lesser et al., 2018). The 60 m rule has been validated with a global meta-analysis, showing the upper- lower mesophotic boundary can be detected as the loss of shallow taxa (Lesser et al., n.d.).

Temperate Mesophotic Ecosystem

As a notable number of researchers understood the word mesophotic to mean a depth zone below 30 m (Fig. 1A), it did not take long before it was used to refer to ecosystems other than tropical and sub-tropical MCEs (Bo et al., 2011). In order to reflect the growing use of the term mesophotic in temperate regions, the term temperate mesophotic ecosystem (TME) was used in a workshop at the European Coral Reef Symposium in 2017. TMEs have now worked their way into the categorization process of the research depository [Mesophotic.org](https://mesophotic.org) (Bongaerts et al., n.d.), and the recent mesophotic coral ecosystems book (Loya et al., 2019). The current use of the term TME follows Fig. 1A for MCEs, but at temperate latitudes.

Mesophotic

Though MCEs were defined in the 2009 research strategy, use of the term mesophotic (literally meaning middle light) as an adjective has been more fluid. Initially, researchers used the word mesophotic as a short-hand for reefs deeper than 30 m (Fig. 2A; Laverick et al., 2018). It was this behavior which caused TMEs to enter our vocabulary, as discussed above. Introducing the upper and lower mesophotic (Fig. 2B) advanced the term towards ecological features, as agreed during collaborative exercises (Baker et al., 2016a; Puglise et al., 2009). However, why is it the upper mesophotic, instead of the lower shallows? The upper mesophotic is agreed as the area of community overlap between shallow and mesophotic taxa. As such, mesophotic has also been used to describe communities distinct from shallow reefs (Semmler et al., 2016; Laverick et al., 2017; Baldwin et al., 2018; Rocha et al., 2018; Fig. 2c). Shallow and mesophotic communities may overlap at the limits of their depth ranges, but crucially, these depth limits are site-specific. Identifying groups of taxa as either shallow or mesophotic is a more flexible approach, which permits the investigation of community level processes and can help avoid comparing apples and oranges. We raise these points now, as the use of language can cause confusion when discussing reef recovery processes later.

Biodiversity

Our knowledge of the biodiversity on MCEs has improved greatly. The number of publications considering MCEs has trebled (Laverick et al., 2018) since Menza et al. (2008) quantified the knowledge gap. Yet, there are notable biases any reader should be aware of before the discussion of broad patterns. Almost 80% of publications come from the western Atlantic or the Hawaiian archipelago, as opposed to the Red Sea, Indian Ocean, the Coral Triangle, and the Great Barrier Reef (Fig. 3; Turner et al., 2017; Laverick et al., 2018). Our knowledge base is also heavily skewed taxonomically. Both systematic reviews by Turner et al and Laverick et al. estimate the number of species from different taxa present deeper than 30 m. Both reviews found the majority of studies considered fish or Scleractinia. Turner used 43 studies of these two groups, with an additional eight studies found for algae, and 14 studies for sponges. Laverick used 30 studies of fish and Scleractinia, and estimated richness values with four studies for different algal taxa, three studies of octocorals, and two of antipatharians. Taxa represented by a single study, such as brachyuran crabs (Hurley et al., 2015), were excluded by Laverick et al.

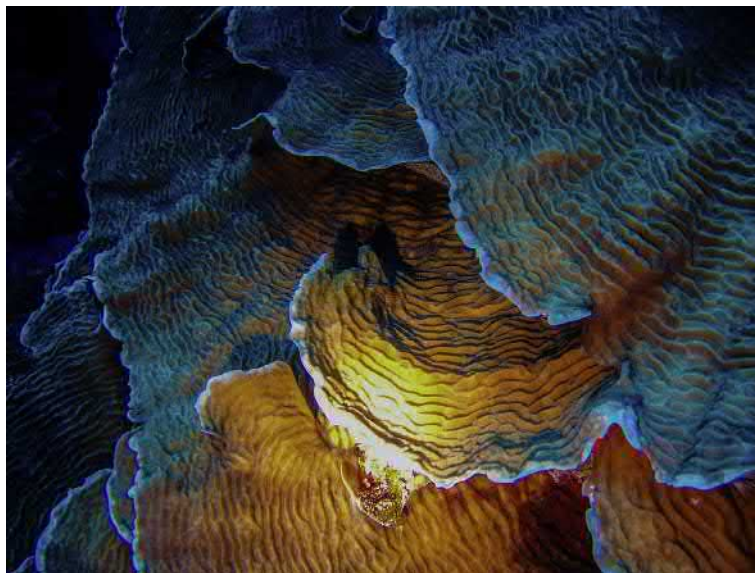


Fig. 1 Mesophotic Coral Ecosystems contain coral species specially adapted to low light environments, scleractinian species found on these reefs often have gracile growth forms which maximize the available surface area for light capture, but are more sensitive to changes in sedimentation or physical disturbance. Image by Jack Laverick from Utila, Honduras.

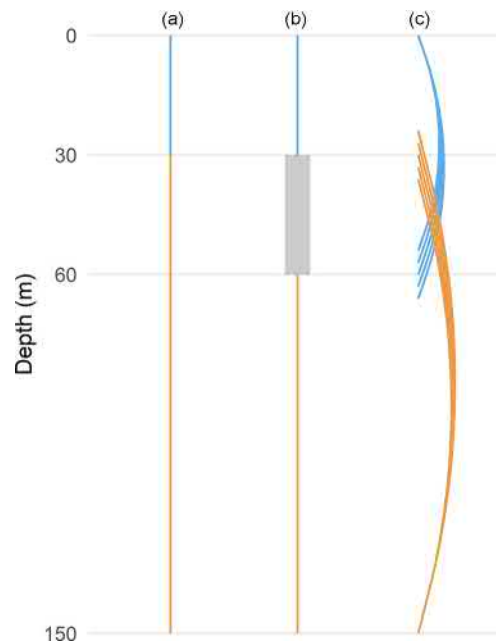


Fig. 2 A schematic representation of key mesophotic terms. *Blue lines* represent the shallow zones/species/depths. *Orange* indicates the mesophotic. The *gray box* in (b) is the area of community overlap (the upper mesophotic). *Curved lines* in (c) represent distributions of identified communities instead of depth limits. (a) Mesophotic, a difficult to access reef zone. A static depth limit is a simplification of (Puglise et al., 2009). (b) Upper Mesophotic, area of community overlap. Lower Mesophotic, distinct species below the ‘60 m rule’ (Kahng et al., 2014). (c) Shallow and mesophotic communities can be identified as assemblages of species with site-specific depth distributions. (Laverick et al., 2017) as indicated by (Baker et al., 2016a).

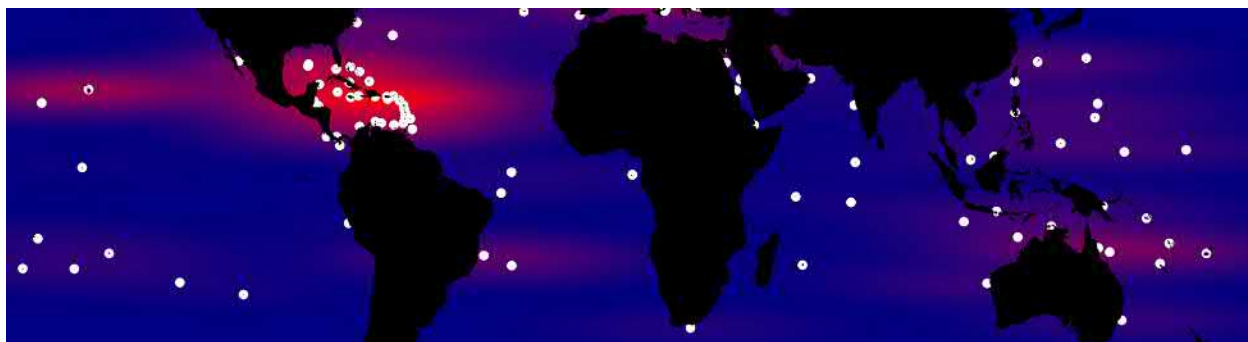


Fig. 3 A heatmap of study effort in the mesophotic zone, limited to the tropics and subtropics. *White dots* indicate study locations, colors indicate the density of publications, with *red areas* more often studied than *blue*. This map was generated from the [Mesophotic.org](https://mesophotic.org) databank.

In general, the geographical patterns in mesophotic scleractinian biodiversity appear to mirror those on shallow reefs. Areas with a large number of shallow coral species, such as the Great Barrier Reef and Coral Triangle, also have a large number of mesophotic taxa when thoroughly surveyed (Muir et al., 2018). Low diversity reefs in the Caribbean similarly have lower levels of diversity on mesophotic reefs. It is important to note the taxonomy of deeper species is not as refined as for shallow reefs (Luck et al., 2013), but there is currently no reason to suspect this has a geographical bias. Along depth gradients, the number of scleractinian species tends to decline monotonically, however, such patterns are affected by declining survey effort with depth (Laverick et al., 2018). This is in contrast to the abundance of corals, which may peak at intermediate depths (Tamir et al., 2019; Rooney et al., 2010). The combination of these two features means that mesophotic coral distributions can appear more patchy, with small areas of high coral cover with a low number of species (Hoeksema et al., 2016).

In contrast, the number of sponges increases with decreasing depth. A Caribbean-wide synthesis revealed that sponge densities quadruple over depth gradients of 100 m (Lesser and Slattery, 2018). This increase was not offset by decreasing colony sizes, with percent benthic cover consistently found to increase to a similar degree.

Seagrasses and algae can occur surprisingly deep, given that they are photosynthetic. Kelp beds have been found at tropical latitudes at depths of 70 m (Graham et al., 2007; Joly and De Oliveira Filho, 1967). Underwater footage has suggested crustose coral-line algae occurs as deep as 301 m in Bermuda (Stefanoudis et al., n.d.-a) and 312 off the Pitcairn islands (Friedlander et al., 2014).

Along the Great Barrier Reef seagrass beds have been found to extend to 61 m, containing up to five species. These beds became rarer with increasing depth (Coles et al., 2009). Calcareous rhodolith beds dominate MCEs of the Abrolhos Bank, Brazil (Brasileiro et al., 2015). Species richness and abundance remains fairly constant until a decline after 60 m depth. While Scleractinia, seagrass, and rhodoliths decline with depth, and sponges increase, in the Hawaiian archipelago algal taxa exhibit a peak in species richness. At around 85 m depth there are 50% more algal species than at 40 m (Pyle et al., 2016). Off the coast of Florida the peak in algal richness was between 30 and 50 m, also with an increase of 50% in comparison to shallow reefs (Hanisak and Blair, 1988). Off Bermuda, macroalgal abundance and biodiversity peaks around 60 m (Stefanoudis et al., n.d.-a; Stefanoudis et al., n.d.-b). At mesophotic depths in the Caribbean, it is not uncommon for algae to be the most abundant benthic group (Laverick et al., 2017). In the Bahamas, the limit on the abundance of the brown alga *Lobophora variegata* on MCEs appears to be grazing pressure as opposed to intrinsic physiology (Slattery and Lesser, 2014). As such, when grazing pressure is reduced, phase shifts to an algal dominated state on MCEs are possible. After the introduction of invasive lionfish, which predated grazing fish species, *L. variegata* abundance increased by 50% (Lesser and Slattery, 2011) (Fig. 4).

We know very little about octocorals and black corals (Antipatharia) on MCEs. Wagner (2015a) reported eight black coral species shallower than 150 m in the Hawaiian archipelago. These eight species had overlapping depth ranges, and as a group were most abundant around 50 m depth (Wagner, 2015b). Similarly, of seven species identified off Bermuda from 0 to 300 m depth, five were found shallower than 150 m (Wagner and Shuler, 2017). On the Flower Garden Banks, USA, black corals were observed between 48 and 115 m. Black corals appear to constitute a minor component of benthic diversity, at up to 4.5% benthic cover (Clark et al., 2014), leaving them vulnerable to overexploitation (Gress and Andradi-Brown, 2018). There are typically more octocoral species reported from mesophotic surveys than black corals. On the Great Barrier Reef peak octocoral richness at the genus level occurred at depths greater than 60 m, with rarefaction curves estimating about 37 genera (Bridge et al., 2012). In the gulf of Eilat, species richness of octocorals was higher at upper mesophotic depths, with 21 of the total 31 species recorded. Only 16% of the species were common across shallow and mesophotic depths, indicating distinct communities. This is in parallel to research finding distinct communities across depth gradients in Scleractinia (Laverick et al., 2017), and fish (Baldwin et al., 2018).

In comparison to sessile taxa, it might be expected that patterns with depth for fish may be less pronounced. The ability to move offers a route to avoid environmental fluctuations. In reality, fish communities are also structured by depth (Stefanoudis et al., n.d.-a, n.d.-b; Baldwin et al., 2018), with high rates of species discovery reported during surveys of new regions (Baker et al., 2016b). Further, a global meta-analysis revealed the shallow to mesophotic transition occurs 12 m shallower for fish than benthic taxa (Lesser et al., n.d.). Fish populations on mesophotic reefs have increased rates of geographical endemism (Kosaki et al., 2017; Pyle et al., 2016), and can be found at higher population densities (Fukunaga et al., 2016). High fish densities could be explained by comparatively high levels of exploitation on shallow reefs (Kadison et al., 2017; Lindfield et al., 2015), but not all mesophotic fish populations show higher levels of abundance (Andradi-Brown et al., 2016a). Beyond abundance, biomass may shift to different feeding guilds with increasing depth (Andradi-Brown et al., 2016a; Bejarano et al., 2011; Fukunaga et al., 2016; Stefanoudis et al., n.d.-a, n.d.-b) (Table 1).



Fig. 4 Jack Laverick pictured diving a closed circuit rebreather with a large, multispecies, stand of *Agaricia* off the island of Utila, Honduras. Photo courtesy Brian J. Sullivan.

Table 1 Example benthic taxa found on Mesophotic Coral Ecosystems around the world (Brasileiro et al., 2015; Bridge et al., 2012; Gress and Andradi-Brown, 2018; Laverick et al., 2017; Pyle et al., 2016; Shoham and Benayahu, 2016; Tamir et al., 2019; Wagner, 2015a; Wagner and Shuler, 2017)

Benthic group	Examples
Scleractinia	<i>Agaricia lamarcki</i> , <i>Agaricia undata</i> , <i>Leptoseris hawaiiensis</i> , <i>Madracis</i> spp., <i>Montastraea cavernosa</i> , <i>Montipora millepora</i> , <i>Pachyseris speciosa</i> , <i>Stylophora pistillata</i>
Octocorallia	<i>Ellisella barbadensis</i> , <i>Muricella</i> spp., <i>Rhytisma f. fulvum</i> , <i>Sinularia vrijmoethi</i> , <i>Siphonogorgia</i> spp.
Antipatharia	<i>Acanthopathes undulata</i> , <i>Antipathes atlantica</i> , <i>Antipathes caribbeana</i> , <i>Myriopathes</i> cf. <i>ulex</i> , <i>Plumapathes pennacea</i> , <i>Tanacetipathes tanacetum</i>
Algae	<i>Caulerpa</i> spp., <i>Cladophora brasiliensis</i> , <i>Dictyopteris</i> spp., <i>Dictyota</i> spp., <i>Halimeda</i> spp., <i>Lithothamnion crispatum</i> , <i>Lobophora variegata</i> , <i>Microdictyon</i> spp.

Adaptations

For the light-dependent biodiversity of the mesophotic zone, satisfying energy demands poses a significant challenge. Photosynthetically active radiation declines exponentially with depth, necessitating physiological adaptation. Here we focus on Scleractinia. To acknowledge research on other groups, we will highlight one non-coral example of adaptation to the mesophotic environment. The sponge *Plakortis angulospiculatus* has a plastic defense strategy which changes down a depth gradient (Slattery et al., 2016). In the shallows the sponge uses high levels of a chemical deterrent against spongivorous fish. With increasing depth these chemicals are present at a reduced concentration. Instead, more energy is invested in wound regeneration and protein synthesis. This trade-off exists as there is a gradient of decreasing grazing pressure with depth. Interestingly, when sponges are transplanted to different depths, they are able to alter their defenses.

Skeletal Adaptations

Perhaps the most apparent adaptation to the low-light environment is the modification of coral growth forms. As depth increases, flatter growth forms become more prevalent (Video 1 in the online version at <https://doi.org/10.1016/B978-0-12-409548-9.11904-9>). This trend is not only driven by an increase in the abundance of plating species, such as agariciid corals (Hoeksema et al., 2016), but also by plastic responses in other taxa. In the Gulf of Eilat, the branching coral *Stylophora pistillata* shifts from thick to thin branches to a plating form with depth (Einbinder et al., 2009; Nir et al., 2011). In the Coral Sea and the Great Barrier reef, corals of the genera *Isopora* and *Acropora* flatten their branches while increasing their spacing and fragility (Muir et al., 2015). In the Caribbean, mounds of *Orbicella annularis* (Dustan, 1975), *Montastraea cavernosa* (Lesser et al., 2010), and *Stephanocoenia intersepta* (pers. obs.) become flatter in low-light environments. These changes have been interpreted as increasing surface area to volume ratios of the coral holobiont for efficient light capture. A trade-off exists across depth gradients, between the need for robust growth forms in the shallows to withstand water movement, and fragile growth forms at depths for light capture.

In addition to macro-scale changes to coral skeletons, taxa common on MCEs are known to have skeletal patterns at the micron-level (Kahng et al., 2012). Kahng et al. placed fragments of *Leptoseris* spp. from Hawaiian MCEs under a scanning electron microscope, revealing repeated channels approximately 100 μ m wide. The presence of channels in the skeleton is typical of agariciid corals more generally. These structures were not present in shallow water *Porites* spp. and are suggested to help with the efficient harvesting of light by increasing internal photon scattering. This hypothesis is supported by aquaria trials showing corals which scatter light with their skeleton to a high degree are more easily bleached (expel their endosymbionts, Swain et al., 2016).

Pigmentation

Kahng et al. (2012) discuss the skeletal adaptations of *Leptoseris* spp. in the context of lower light reflectance, despite lower pigmentation concentrations than shallow *Porites*. However within a species, corals on MCEs may contain higher levels of pigment (Lesser et al., 2010). This can be achieved by increasing the density of zooxanthellae within the coral host (Bongaerts et al., 2011), and/or the chlorophyll content of each cell (Cohen and Dubinsky, 2015). These physiological changes are useful to a limit, as eventually self-shading will offset any benefit from further pigment increases (Smith et al., 2017). Nuanced changes in pigmentation are also possible, with the ratios of different forms of chlorophyll changing with depth for *S. pistillata* in the Red Sea (Nir et al., 2011). Research from the same area describes the widespread expression of fluorescent pigments by mesophotic corals (Eyal et al., 2015). Eyal et al. (2015) noted that the depths with high levels of fluorescence coincide with peaks in the abundance of mesophotic coral species. Exactly how fluorescent pigments help mesophotic corals is still a topic of discussion. Earlier in the same year Roth et al. (2015) described coral fluorescence from Hawaiian mesophotic reefs, and concluded the pigments unlikely enhance symbiont photosynthesis. This was following assessments of photosynthetic parameters of fluorescent and non-fluorescent coral colonies.

Long term aquaria trials have since shown that fluorescent proteins can improve the survival of coral colonies under mesophotic light conditions, and that this may be linked to improving the penetration of light to deeper tissues layers (Smith et al., 2017).

Discussion of the variation in *Symbiodinium* (symbiotic zooxanthellae) clades harbored by corals are closely related to those of pigmentation in corals. *Symbiodinium* clades may be stratified by depth both within and between species (Bongaerts et al., 2015). The degree of symbiont stratification observed by Bongaerts et al. (2015) correlated with their reproductive strategy. Brooding coral species tend to inherit their symbionts maternally. Broadcasting taxa instead acquire their symbionts from the environment as planulae (Kirk et al., 2013). This allows broadcasting species to be more flexible in their symbioses. Though symbiont switching within a coral colony has been recorded by shallow studies (Jones et al., 2008; Kemp et al., 2014), manipulative experiments relocating *S. pistillata* across depths have repeatedly failed to induce change in *Symbiodinium* communities (Bongaerts et al., 2011; Borell et al., 2016; Einbinder et al., 2016). Despite this, it has been suggested a more gradual acclimation period could allow for symbiont-switching to occur in this species (Cohen and Dubinsky, 2015). In the absence of evidence for symbiont switching (as opposed to zonation) on MCEs, it seems likely symbiont-zonation results from selection acting on holobionts (coral-symbiont combinations). This is rather than corals acquiring the appropriate symbiont for their location post-settlement. This will have implications for reef recoveries under shifting environments, as recruitment and growth of new colonies will be slower than changing the symbionts of established corals.

Mixotrophy

Scleractinian coral species can all be placed on a spectrum of energy acquisition between autotrophy (photosynthesis) and heterotrophy (filter-feeding). As the energy available from sunlight is lower on MCEs, it is possible that corals could increase their rates of heterotrophic feeding to compensate (Palardy et al., 2005). Heterotrophic subsidy, therefore, has been studied as a possible mechanism permitting mesophotic hard corals to thrive in low-light environments (Alamaru et al., 2009; Crandall et al., 2016; Lesser et al., 2010). Stable isotope analyses have been conducted on a variety of mesophotic species, as the relative importance of heterotrophy and photosynthesis can be inferred from isotopic signatures in tissue carbon and nitrogen (Peterson and Fry, 1987). As is to be expected, the relationship between the importance of heterotrophy and depth is species-specific. In the Caribbean *Agaricia lamarcki* derives nutrients from heterotrophy through the entire depth range, with a photosynthetic signal only apparent in the shallows (Crandall et al., 2016). Meanwhile *M. cavernosa* (Crandall et al., 2016; Lesser et al., 2010) relies increasingly on heterotrophy as depth increases.

In the Red Sea, Alamaru et al. (2009) asked similar questions of *Favia fava* and *S. pistillata*. Though the heterotrophic capacity of both species remained constant with depth, whether lipids were synthesized from heterotrophically or photosynthetically acquired carbon differed. *Stylophora pistillata* relied on photosynthesis for lipid precursors in the shallowest 15 m, below this heterotrophy becomes increasingly important. Meanwhile, *F. fava* relies on heterotrophy to synthesize lipids across its entire depth range. This is an important distinction when viewed alongside trends in the ratio of carbon to nitrogen (C/N) in coral tissue. Higher C/N values are considered a sign of good condition as key energy compounds, such as lipids and carbohydrates, become more abundant in comparison to the protein machinery of the organism. With increasing depth the C/N ratios of *F. fava* remained constant, but declined for *S. pistillata*. This suggests the higher levels of heterotrophy in *F. fava* was advantageous for life in the mesophotic zone, in comparison to *S. pistillata* which has lower energy reserves when light levels decline.

Conservation and Refuges

A sizeable portion of recent research on MCEs was inspired by a conservation angle. In 1996, when writing about coral bleaching, Peter Glynn suggested:

Possible refuge habitats that would be protected from rapid temperature rise might be found at moderate depths, in upwelling centres, on oceanic banks or island shores exposed to vigorous circulation, and at some high latitude sites.

(Glynn, 1996, p505)

From this the Deep Reef Refugia Hypothesis (DRRH) was formalized (first reviewed for the Caribbean by Bongaerts et al., 2010), positing deeper reefs may be protected from climate pressures threatening shallow reefs. If deeper reefs survived a disturbance event, they may provide recruits which contribute to shallow reef recovery. Consequently, reefs deeper than 30 m (Mesophotic sensu Fig. 2A) became an area of conservation interest. This interest only grew as threats to shallow water reefs appeared to become increasingly severe (Hughes et al., 2017). Glynn's (1996) original suggestion focussed on fluctuations in temperature and resulting coral bleaching, but the refuge potential of MCEs was recognized to apply to a wider range of impacts and stressors (Bridge et al., 2013). Physical damage associated with water movement during storms is expected to decline with depth. Similarly, deeper reefs are often also further from shore. As such MCEs may also avoid stresses associated with sedimentation, coastal development, and fishing. When discussing areas which only avoid single, short term (i.e., not on a decadal time scale) pressures such as these, one should strictly talk about deep reef refuges (singular refuge). Refugia (singular refugium), meanwhile, provide long term

buffering against multiple stressors over many decades (Kavousi and Keppel, 2017). Current studies of mesophotic reefs and the DRRH have therefore tended to consider refuges, as long time series are rare.

Directly testing whether mesophotic reefs contribute to deep reef refuges is difficult. It would require damaging multiple shallow reefs and waiting for potentially lengthy regeneration times, which could then be linked to MCEs. There are a number of assumptions, however, which must be true in order for recovery dynamics to occur on a given reef. These assumptions closely match core elements of meta-population models from other fields.

Firstly, we assume community overlap between shallow and mesophotic reefs. Only depth-generalist taxa will be able to contribute to shallow reef recovery after a shallow disturbance. We would not expect mesophotic specialist taxa to contribute to a direct replacement of shallow biodiversity, nor would we expect shallow specialist taxa to occur in the refuge in the first place. Research into community overlap deeper than 30 m on reefs has therefore been framed as a conservation question (Laverick et al., 2018; Muir et al., 2018; Rocha et al., 2018). Globally we expect 2/3 species occurring on shallow reefs to appear at depths greater than 30 m (Laverick et al., 2018). This suggests MCEs (sensu Fig. 2A) could be a significant, but not comprehensive, store of shallow reef biodiversity.

Secondly, we assume that deeper populations are not sink populations, but are reproductively active and capable of contributing to shallow recruitment. Multiple studies exist addressing the issues of fecundity with increasing depth (Eyal-Shaham et al., 2016; Feldman et al., 2017; Holstein et al., 2015, 2016; Liberman et al., 2018; Prasetya et al., 2015; Shlesinger et al., 2018), and vertical connectivity (Slattery et al., 2011; Brazeau et al., 2013; Serrano et al., 2014; Goodbody-Gringley et al., 2015; Bongaerts et al., 2017). It remains unclear how often reproduction at depth is sufficient to support shallow reef recovery; especially as this may be a balance between population size, depth dependent fecundity, and settlement probabilities (Holstein et al., 2016; Kramer et al., 2019). Never the less, the above studies document the production of propagules, and settlement, on MCEs.

Finally (though there may be more barriers), reduced mortality with depth is still simply assumed for most sites. Lower levels of damage have been observed with increasing depth after thermal anomalies (Sinniger et al., 2012; Smith et al., 2014; Muir et al., 2017; Frade et al., 2018; Laverick and Rogers, 2018). However, different stresses and disturbances have differing frequencies and intensities between sites. The Red Sea for instance is known for its high water temperatures, however, it also has a local pool of species capable of tolerating these levels (Osman et al., 2018). In Palau, shifting thermoclines can transport thermal stress from the shallows onto MCEs (Schramek et al., 2018). Taxa on mesophotic reefs may still be vulnerable because of increased sensitivities. Hard corals from more stable environments may be less tolerant of changes in ambient conditions as a result of reduced phenotypic plasticity (Oliver and Palumbi, 2011). Bleaching has been observed on MCEs (Nir et al., 2014) and in some instances the thermal susceptibility of mesophotic hard corals has been shown to be higher than shallow species (Smith et al., 2015). In addition to bleaching pressures, disease (Smith et al., 2010), and storm damage (White et al., 2013) has been observed. The fragile nature of mesophotic hard corals leaves them particularly susceptible to physical disturbance (Bongaerts et al., 2013), while the typically large plating growth forms at mesophotic depths are more vulnerable to the negative effects of sedimentation (Rogers, 1990).

It is important to note that MCEs should not be considered synonymous with deep reef refuges. Though early on it was convenient to reduce 'mesophotic' to a depth (Fig. 2A), and so the area of interest for the DRRH, this way of thinking can run into difficulties when considering the shallows and mesophotic as different communities (Fig. 2C; Laverick et al., 2016, 2017, 2018). By using a community-based definition, mesophotic reefs cannot protect shallow communities during a period of disturbance. This is relevant when interpreting the research on community overlap with depth, discussed above. Instead, deep reef refuges occur in the mismatch between the lower depth ranges of taxa, and the relationship between stressors, impacts and depth (Fig. 5-DRRH). Environmental damage is therefore a function of the vertical extent and intensity of the event, and the vertical distribution and depth-dependent susceptibilities of taxa. Though shallow taxa may extend deeper than 30 m, depth refuges may also operate over much smaller depths. In Panama, susceptibilities, depth gradients, and two coral bleaching events resulted in the extirpation of a hydrocoral only in the very shallowest portions of the reef (< 11 m; Smith et al., 2014).

Separating out mesophotic communities from the main discussions of deep reef refuges not only increases clarity, but also allows us to investigate the rather neglected issue of mesophotic conservation. MCEs face a variety of threats themselves and require protection in their own right (Andradi-Brown et al., 2016b). Though there may be realizations of deep reef refuges for mesophotic communities, not just shallow taxa, we may expect the primary threats to MCEs to behave differently to those on shallow reefs (Fig. 5-MCE Threats).

The damage to unique biodiversity on MCEs may be more severe with increasing depth in a variety of cases (Fig. 5-MCE Threats). As mentioned earlier, mesophotic taxa may be less resilient to thermal stress because of increased sensitivities (Smith et al., 2015). The invasive lionfish (*Pterois volitans*) has been implicated in phase shifts to an algal dominated state at mesophotic depths in the Caribbean (Lesser and Slattery, 2011; Slattery and Lesser, 2014). The efficacy of management options for lionfish declines with depth (Andradi-Brown et al., 2017a; Andradi-Brown et al., 2017b), resulting in high numbers on MCEs (Aguilar-Perera et al., 2017; Gress et al., 2017; Nuttall et al., 2014; Pinheiro et al., 2015). As mesophotic taxa live at the extreme end of photosynthetic performance, any events which modify the underwater light field are likely to have a greater effect than on shallow taxa. Examples of such processes could include shading induced by sediment resuspension after storms or coastal development. Similarly changes to algal blooms, either from coastal run off or climate-related drivers, could also have consequences for mesophotic taxa (Tamir et al., 2019). In this case, periods of net photosynthesis and seasonal bleaching of *Stylophora pistilata* on MCEs coincide with phases in the annual algal bloom in the gulf of Eilat/Aqaba (Nir et al., 2014). It is likely eutrophication events in this

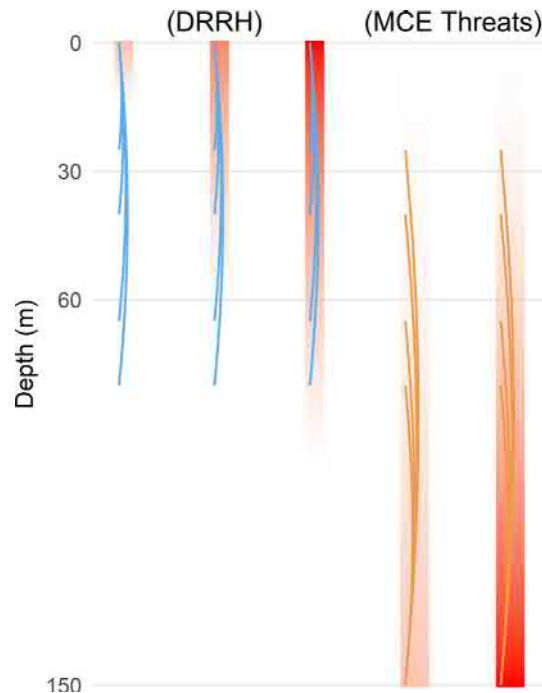


Fig. 5 A schematic representation of threats to coral reef ecosystems, and which ones we may expect to be relevant to the conservation of shallow or mesophotic reefs. The deep reef refugia hypothesis (DRRH) considers whether shallow taxa (*blue*) can avoid shallow disturbances (*red*). As depth increases the strength of these threats is expected to decrease. The mismatch between the species depth range and the maximum impacted depth determines the size of the refuge area. Threats (*red*) more likely to affect mesophotic taxa (*orange*) are those which accumulate with increasing depth i.e. shading from suspended sediments or algal blooms. In this case the shallowest mesophotic taxa may be protected, with conservation risks being determined by how rapidly the impact strengthens with depth.

location during the 1990s (Loya, 2004) had notable effects on mesophotic communities. Only now are we able to monitor these events and call for the protection of MCEs.

Further Reading

For those interested in reading on MCEs in more detail, there are a number of excellent sources of further information. We will not provide a list of every review of the mesophotic literature. Instead, the following are the products of significant collaboration between most of the active researchers in the field at the time of publication.

- 1) The Mesophotic research strategy arising from NOAA's 2008 workshop (Puglise et al., 2009).
- 2) Released at the International Coral Reef Symposium in 2016, members of the mesophotic community worked together to publish a report explicitly considering the deep reef refugia hypothesis. The topics covered include mesophotic biodiversity, the ecosystem services it provides, and the threats it faces (Baker et al., 2016b).
- 3) Recently the state of the field was synthesized as part of Springer's coral reefs of the world book series. Chapters touch on regions, concepts, and knowledge gaps in the field; and is side by side with [Mesophotic.org](http://mesophotic.org) as one of the largest single sources of information on MCEs (Loya et al., 2019).

List of Relevant Websites

<http://mesophotic.org> is listed as one of the accomplishments of the 2008 meeting (Puglise et al., 2009). Though it has gone through a couple of different formats, its most recent incarnation is as a repository of publications and an address book of the mesophotic community (Bongaerts et al., n.d.).

Acknowledgment

We would like to thank Pim Bongaerts for providing us with the GPS points of studies in mesophotic.org.

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Hotspots of Marine Biodiversity

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Abstract

First used to prioritize terrestrial sites with exceptional concentrations of species, exceptional levels of endemism, under exceptional degrees of threat, the term biodiversity hotspots was extended to the marine realm in 2002. Since then there have been 18 global scale studies of marine biodiversity hotspots. The data and criteria used to identify hotspots varies within the literature. However, most research highlighted the same areas as hotspots of marine biodiversity. Species richness generally peaked in Australia, South East Asia through to Japan, South Asia, South East Africa, the Caribbean and South East United States. Centers of endemism are identified in South Africa, the East and West Coasts of Australia and isolated areas such as Hawaii, Easter Island, New Zealand, and Antarctica. Hotspots of both high species richness and high species endemism are located in the West Caribbean, South Madagascar, Chagos Islands, Maldives, Lakshadweep, Sri Lanka, South Japan, East China Sea including Taiwan, Coral Triangle, New Caledonia, Vanuatu and North East and North West Australia. Although protecting marine hotspots should be prioritized in order to protect ocean biodiversity, the distribution of species richness varies between taxa, and many centers of endemism are distinct from areas of high species richness. Therefore, protecting marine biodiversity hotspots does not represent a comprehensive strategy to represent and protect all marine life. Moreover, only four studies acknowledge the importance of protecting IUCN threatened species, yet those species are at the highest risk of extinction. Only by protecting hotspots of species richness, hotspots of endemism and threatened species can we reduce the risk of species extinction, support the recovery of marine species and protect marine biodiversity.

Introduction

Hotspots is an approach used to prioritize sites in need of conservation (Myers, 1988; Roberts et al., 2002; Briscoe et al., 2016). It was first used by Myers in 1988 to identify areas of tropical forest that featured exceptional concentrations of species with exceptional levels of endemism, under exceptional degrees of threat. Since then, the term “Hot Spots” has become synonymous with terrestrial biodiversity conservation spatial planning (Medail and Quezel, 1997; Reid, 1998; Myers et al., 2000; Ceballos and Ehrlich, 2006; Mittermeier et al., 2011). Initially extended to the marine realm and tropical reefs by Roberts et al. (2002), identifying hotspots of marine biodiversity has likewise been promoted in marine conservation (Allen, 2008; Morato et al., 2010; Lascelles et al., 2012), particularly given the emerging crisis for ocean biodiversity (Myers and Worm, 2003; Bellwood et al., 2004; Payne et al., 2016). More recently, identifying freshwater biodiversity hotspots has also utilized Myers’ approach (Oberdorff et al., 2011; Grant et al., 2012; Tedesco et al., 2012; Collen et al., 2014). Overall, the growing number of terrestrial, freshwater and marine species facing extinction far outweigh the conservation resources designated to protect them (Myers et al., 2000). Consequently, mapping and protecting biodiversity hotspots represents a cost-effective use of resources to protect planetary biota (Pimm and Raven, 2000; Roberts et al., 2002; Mittermeier et al., 2011; Marchese, 2015).

Since its inception, the term marine biodiversity hotspots has been used to describe a variety of distribution patterns. From areas with high species richness, diversity and abundance (Renema et al., 2008; Bennison and Jessopp, 2015; Descombes et al., 2015; Laptikhovsky et al., 2017), to those with high productivity, endemism, threatened species, taxonomic distinctiveness, and high threat intensity (e.g., Valavanis et al., 2004; Davidson et al., 2012; Lewison et al., 2014; Schuyler et al., 2016; Briscoe et al., 2016; Friedlander et al., 2016). However, the majority of scientific literature designates marine biodiversity hotspots as a combination of high species richness, endemism or threat, as shown by Roberts et al. (2002), Bellwood and Meyer (2009), O’Loughlin et al. (2011), Selig et al. (2014), Dulvy et al. (2014), Jenkins and Van Houtan (2016), and Ramírez et al. (2017) among others. Consequently, research has helped to define and map marine biodiversity hotspots in order to focus conservation efforts (Olson and Dinerstein, 2002; Tittensor et al., 2010; Ramírez et al., 2017).

Designating Marine Hotspots

There have been numerous small-scale studies focusing on individual taxonomic groups and species. For example, studies on biodiversity hotspots of Australian sponges in tropical and subtropical Australia (Hooper et al., 2002), cyclostome bryozoans in

Spirits Bay, New Zealand (Taylor and Gordon, 2003), and hotspots of sea cucumber biodiversity in the Antarctic (O'Loughlin et al., 2011). To date there have been 18 global scale studies of marine biodiversity hotspots (Table 1). Roberts et al. (2002) were the first to identify marine biodiversity hotspots on a global scale. They analyzed species richness and endemism of reef fish, corals, snails and lobsters, as well as threats to coral reefs from human impacts, based on coastal development, overexploitation and pollution. They designated 18 centers of endemism, from areas as small as Easter Island to areas as large as the Great Barrier Reef (Veron et al., 2011), of which 10 were deemed threatened by human impacts and subsequently defined as marine biodiversity hotspots (Roberts et al., 2002) (Table 1). Additional global scale studies have concentrated on specific groups of taxa, e.g., marine mammals (Pompa et al., 2011), sharks (Lucifora et al., 2011; Dulvy et al., 2014), and fish (Stuart-Smith et al., 2013), as well as across taxonomic groups (e.g., Tittensor et al., 2010, Selig et al., 2014, Jenkins and Van Houtan, 2016; Ramírez et al., 2017).

Marine biodiversity hotspots studies had large variations in the number of species included in each study, ranging from 121 to 12,796 (Table 1). The most detailed studies, by Molinos et al. (2016) and Selig et al. (2014), included 12,796 and 12,497 species, while studies concentrating solely on marine mammals included just 115, 123, and 121 species respectively (Kaschner et al., 2011; Pompa et al., 2011; Albouy et al., 2017). However, Worm et al. (2005) showed that species richness of tuna and billfish corresponded with other pelagic taxa across trophic levels, acting as an indicator of overall pelagic species richness (Worm et al., 2005; Tittensor et al., 2010; Trebilco et al., 2011). While 17 of the 18 studies reviewed used species richness, some based hotspots solely on species richness ($n = 9$), but others combined this with endemism or threats ($n = 8$, Table 1). Regardless of the number of species and criteria used for assessment, most previous research highlighted the same key regions as hotspots of marine biodiversity (Fig. 1).

The Coral Triangle (CT) is widely acknowledged as the center of marine biodiversity (Hoeksema, 2007; Barber, 2009; Bellwood and Meyer, 2009; Asaad et al., 2017) and was designated as a hotspot by the majority of reviewed literature ($n = 12$). It encompasses the seas around The Philippines, Indonesia, Papua New Guinea, Malaysia, The Solomon Islands, and Timor-Leste (Walton et al., 2014; Asaad et al., 2017). The CT harbors 76% of the world's zooxanthellate coral species (Veron et al., 2009a, b), more than 3250 reef fish species (Sanciango et al., 2013), six species of sea turtles (Asaad et al., 2018), more than 22 dolphin species (WWF, 2007), the highest richness of seagrass species (Spalding et al., 2003), and the largest mangrove forest in the world (Polidoro et al., 2010; Walton et al., 2014). As well as extraordinary levels of biodiversity, 225 million people live in the region (Veron et al., 2011) depending on the local marine ecosystems, habitats and species for their food and livelihood. Consequently, the human impacts on this region are likely severe (Veron et al., 2011) and given that Indo-Pacific reefs are declining each year (Bruno and Selig, 2007), make this a key marine biodiversity hotspot.

Geographically close to the Coral Triangle, another frequently stated hotspot from the literature ($n = 16$) are the waters of Japan, Taiwan and China. The upwelling of currents and variation in ocean temperatures make this hotspot highly biodiverse (Veron et al., 2011; Huang et al., 2015). The species richness of the region is influenced by the Kuroshio Current which increases larval dispersal from the CT northward as far as Japan (Veron et al., 2011). The literature shows that the waters of Japan and China are a global hotspot for cetacean species richness with >30 species, at least seven endemic, (Pompa et al., 2011). The South China Sea also has extraordinary coral diversity (571 known species Wu and Zhang, 2012; Huang et al., 2015). Additionally, Roberts et al. (2002) observed that South Japan harbored the highest levels of species endemism in their tropical study, highlighting the biological importance of this hotspot. The area is heavily impacted, with heavy fishing pressure, pollution, and dense human populations continuing to threaten the remaining marine biodiversity (Watson and Pauly, 2001; Daoji and Daler, 2004; Albouy et al., 2017).

Thirteen of the global studies reviewed included South Africa or the Eastern African region (countries including, South Africa, Mozambique, Madagascar, Kenya, Tanzania, Seychelles, and the South Mascarene Islands) as marine biodiversity hotspots. Eastern South Africa has particularly high species endemism (Roberts et al., 2002), while overall South Africa is a biodiversity hotspot for cetaceans (Pompa et al., 2011; Albouy et al., 2017) and sharks (Lucifora et al., 2011; Dulvy et al. 2014). Global studies show that the East African region has high species richness of reef fish (Stuart-Smith et al., 2013) and marine mammals (Albouy et al., 2017). Unfortunately, the marine biodiversity of Kenya, Tanzania, Mozambique and the Mascarene Islands is heavily impacted by overfishing and habitat degradation (Halpern et al., 2008), making it a hotspot for conservation.

Eleven studies located marine biodiversity hotspots in the Caribbean, Gulf of Mexico and South-Eastern United States (Table 1), regions that often showed overlap within the literature. Caribbean corals exhibit low coral species diversity, with the Mesoamerican barrier reef system home to just 65 species of scleractinian corals (Mission Blue, 2013), compared with the ≥ 600 species present in the CT (DeVantier and Turak, 2017). However, the high endemism of marine species (Roberts et al., 2002; Lucifora et al., 2011; Selig et al., 2014), increasing anthropogenic pressure on marine ecosystems (Hughes 1994; Hawkins and Roberts, 2004; Govers et al., 2014), historical and current large-scale coral bleaching events (Goreau, 1992; Wilkinson and Souter, 2008; Alemu and Clement, 2014), and a phase shift from coral dominated to macroalgal dominated reefs (Bruno et al., 2009; Arias-González et al., 2017), make the Caribbean an important hotspot for marine biodiversity and conservation efforts. Neighboring the Caribbean, the Gulf of Mexico is highly biodiverse (Costello et al., 2010). In addition to high species richness, the gulf is home to a variety of IUCN threatened species such as bluefin tuna (Endangered), which are known to spawn in the warm waters of the gulf (Teo et al. 2007); whale sharks (Endangered), which aggregate annually in their hundreds (Hueter et al., 2013), and five species of sea turtle (Valverde and Holzwart, 2017). The Gulf of Mexico is heavily impacted by overfishing, pollution and habitat loss, and biodiversity in the region is the second highest threatened globally after the Mediterranean (Costello et al., 2010). Adjacent to the gulf and the Caribbean, South-Eastern United States harbors high biodiversity of all taxa (Molinos et al., 2016), specifically high shark species richness and endemism (Lucifora et al., 2011), and fish species richness (Worm and Branch, 2012). This hotspot is also subject to overfishing and habitat loss and in need of prioritizing to protect marine biodiversity (Costello et al., 2010).

Table 1 Review of literature on global marine biodiversity hotspots.

<i>Author(s)</i>	<i>Species</i>	<i>Criteria</i>	<i>Hotspots</i>
Rutherford et al. (1999)	33 Species foraminifera	Species richness	Middle latitudes in all oceans
Roberts et al. (2002)	3235 species Reef fish, corals, snails, lobster	Species richness, endemism, human threats	Philippines; Gulf of Guinea; Sunda Islands; South Mascarene Islands; Eastern South Africa; North Indian Ocean; South Japan; Cape Verde Islands; West Caribbean; Red Sea
Worm et al. (2005)	15 Species ^a Tuna and billfish	Species richness	Clustered mostly in the subtropics: U.S. and Australian East Coasts; South of the Hawaiian Islands chain; East of Sri Lanka; most prominently in the South Eastern Pacific
Tittensor et al. (2010)	11,567 Species across 13 taxonomic groups ^b	Species richness	Philippines; Japan; China; Indonesia; Australia; India and Sri Lanka; South Africa; Caribbean and South West United States
Kaschner et al. (2011)	115 Species ^b Marine mammals	Species richness	New Zealand; Japan; Baja California; Galapagos Islands; the South East Pacific; the Southern Ocean
Lucifora et al. (2011)	507 Species ^b Sharks	Species richness, functional diversity, endemism	Japan; Taiwan; the East and West Coasts of Australia; South East Africa; South East Brazil; South East United States
Pompa et al. (2011)	123 Species ^b Marine mammals	Species richness, endemism, IUCN threat status	Baja California; Peru; North East America; Argentina; North West Africa; South Africa; Japan; Australia; New Zealand. Key marine endemism sites: Hawaiian Islands; Galápagos Islands; San Felix and Fernandez Islands; Mediterranean Sea, Kerguelen Island
Trebilco et al. (2011)	15 Species ^b Tuna and billfish	Species richness, human threats	US East Coast; South East Sri Lanka; Mauritius; Easter Island; Australia; Brazil; China; Costa Rica; El Salvador; India; Japan; Kenya; Nicaragua; Somalia; Tanzania
Worm and Branch (2012)	>4000 Species Fish	Species richness	Caribbean and South East United States; Western Central America; North East South America; Brazilian South East; North West Africa (Morocco, Western Sahara, Mauritania, Senegal); South Africa, Mozambique (Inc. Channel); Madagascar; Arabian Sea (Inc. Red Sea, Persian Gulf); Yellow Sea; East China Sea; South Japan; Taiwan; South China Sea; Indonesia; Philippines; Malaysia; North and East Australia
Jablonski et al. (2013)	5726 Species Bivalves	Species richness	Tropical West Pacific (Northern Australia, Indonesia, Malaysia, Philippines, Taiwan, China, Vietnam, Cambodia, Thailand)
Stuart-Smith et al. (2013)	2473 Species Reef fish	Species density, species evenness, functional group richness, functional diversity	West Indian Ocean (Mozambique, Tanzania Kenya, Madagascar, Seychelles, Mauritius, Reunion); Central Indian Ocean (Maldives, Chagos Archipelago); East Indian Ocean (Andaman Islands, Burma, Thailand); Central-Western Pacific Ocean (Indonesia, Malaysia, Philippines, New Guinea, Taiwan and south of Japan); North-East/West Australia; Central Pacific Ocean; India and Sri Lanka; Red Sea
Dulvy et al. (2014)	1041 Species ^b Chondrichthyans	Species richness, IUCN threat status, endemism	Indo-Pacific Biodiversity Triangle; Red Sea; Mediterranean Sea; Northern South America from Ecuador to Brazil including Panama; South East Brazil to South East Argentina; Togo, Benin, Nigeria, Cameroon, Equatorial Guinea and Northern Gabon; South Africa, Mozambique and East Madagascar; East Yemen and West Oman; Northern Persian Gulf; Northern Bay of Bengal and Andaman Sea; China, Taiwan, Vietnam and the Gulf of Thailand; North Australia; South and South East Australia; New Caledonia
Selig et al. (2014)	12,497 Species >21 phyla and 966 families ^b	Species richness, endemism, human threats	Australia; Indonesia; Antarctica; Russia; Japan; Philippines; Canada; Greece; Vietnam; Papua New Guinea; China; Taiwan; Egypt; Brazil; United States; Malaysia; Turkey; Mexico; Bahamas
Jenkins and Van Houtan (2016)	4352 Species	Species richness, endemism, human threats, IUCN threat status	Coral triangle, East Melanesia, Micronesia, Ryuku Archipelago, Caribbean, Sri Lanka, Red Sea, region of Madagascar
Molinos et al. (2016)	12,796 Species ^b	Species richness	Caribbean; Gulf of Mexico; South East United States; Mozambique; Tanzania; Kenya; Madagascar; India and Sri Lanka; Maldives; Chagos Archipelago; Andaman Islands; Burma; Thailand; Indonesia; Malaysia; Philippines; New Guinea; Taiwan; South Japan; Northern Australia; Central Pacific Ocean
Albouy et al. (2017)	121 Species ^b Marine mammals	Species richness, human threats	Baja California; Peru; Patagonian waters of Chile and Argentina; Uruguay; South East Brazil; Western Sahara; South Africa; Southern Mozambique; South Japan; Gulf of Thailand; Java Sea; Southern Australia, Tasman Sea; New Zealand

(Continued)

Table 1 (Continued)

Author(s)	Species	Criteria	Hotspots
Davidson and Dulvy (2017)	1007 Species ^b Chondrichthyans	Endemism, IUCN threat status	Argentina, Brazil, Uruguay, Chile, Colombia, South Africa, Mozambique, Indonesia, Philippines Taiwan China, Japan, Australia
Ramírez et al. (2017)	2183 Species ^b Fish, marine mammals, seabirds	Species richness	Peru and the Galápagos Archipelago; Patagonian waters of Argentina and Uruguay; West Indian Ocean (South Africa, Mozambique, Tanzania Kenya and Madagascar); Central-western Pacific Ocean (Indonesia, Malaysia, Philippines, New Guinea, Taiwan and south of Japan); New Zealand and East and South Australia; Oceania and central Pacific Ocean

Note the species analyzed in each study, the criteria used to assess sites and the designated hotspots.

^aValidated against total predator richness (145 species) from independent scientific observer data from the Atlantic and Pacific Ocean.

^bIndicates geographic scope is whole ocean.

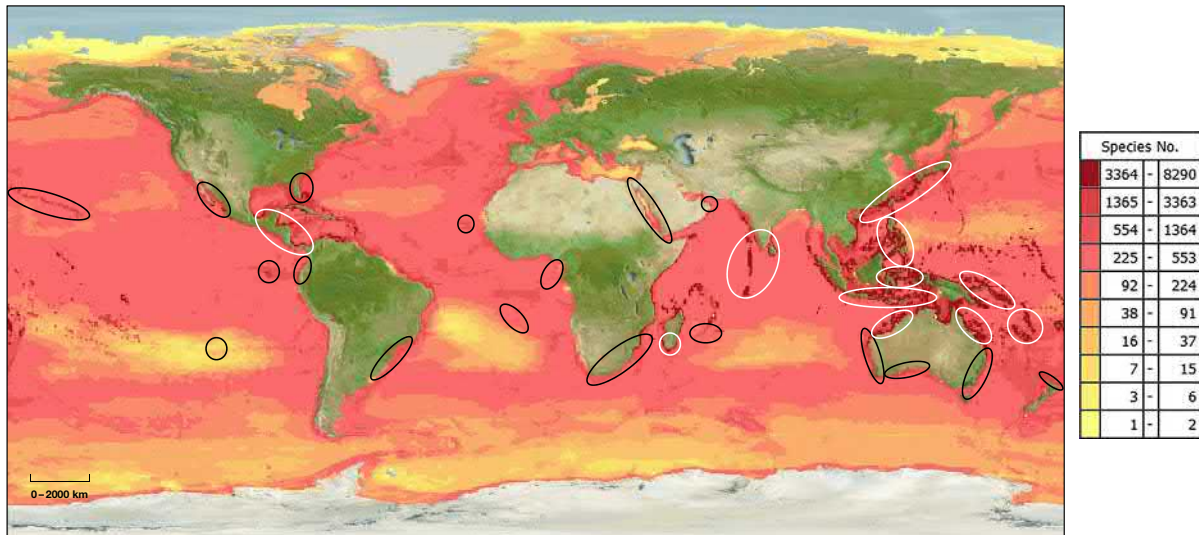


Fig. 1 Centers of endemism as defined by the reviewed literature (circled) overlaid on species richness derived from modeled geographic ranges of 25,000 marine species from AquaMaps (Kaschner et al., 2016). Hotspots of both endemism and species richness are circled white.

In total, the literature lists more than 70 discrete marine biodiversity hotspots in the EEZs of more than 71 countries (Table 1), as well as in the High Seas (also called Areas Beyond National Jurisdiction, ABNJ). Species richness varied depending on the taxa studied, but generally peaked in Australia, South East Asia though to Japan, South Asia (India, Sri Lanka, Lakshadweep, Maldives, Chagos Archipelago), South East Africa, the Caribbean and South East United States (e.g., Tittensor et al., 2010; Worm and Branch, 2012; Stuart-Smith et al., 2013; Molinos et al., 2016). Endemism is higher in areas isolated by distance, notably Hawaii (Pompa et al., 2011), Easter Island (Roberts et al., 2002), and Antarctica (45% species endemic) and New Zealand (51%) (Costello et al., 2010). Endemism is also higher in areas with currents moving water from tropical to temperate regions, e.g., east and west coasts of Australia (Roberts et al., 2002; Selig et al., 2014; Davidson and Dulvy, 2017), South Africa (Pompa et al., 2011; Dulvy et al., 2014; Selig et al., 2014) and Japan (Lucifora et al., 2011; Selig et al., 2014; Davidson and Dulvy, 2017).

The literature that included human threats as an assessment criteria for hotspots ($n = 5$) used threats and human impacts derived from either Halpern et al. (2008), a synthesis of 17 anthropogenic drivers of change; or Bryant et al. (1998), a map based indicator of threats to coral reefs based on coastal development, overexploitation, and pollution. Halpern et al. (2008) showed medium to high impact in all areas designated by the literature as areas of high species richness, while Bryant et al. (1998) assigned a local threat level for coral reefs as either high or very high for the majority of Caribbean and CT reef systems. In addition to human threat and risk indicators, the literature has used IUCN species status to determine at risk species (e.g., Pompa et al., 2011; Dulvy et al., 2014; Jenkins and Van Houtan, 2016; Davidson and Dulvy, 2017), with threatened species richness and endemism mapped in order to prioritize the protection of imperiled species (Dulvy et al., 2014). Three of the four studies that included threatened endemic species, showed hotspots overlapping with those of global species richness and endemism. The remaining study (Pompa et al., 2011) focussed solely on marine mammals, which have high species richness in the southern hemisphere and contrasting distributions to other marine taxa (Kaschner et al., 2011; Albouy et al., 2017).

Fig. 1 shows that areas of high species richness often correspond with high species endemism, but areas of high endemism are also often distinct to areas of high species richness. Examples of high endemism and low species richness include the Gulf of California, South East Brazil, South Africa, Southern Mozambique and the Red Sea, among others, as well as islands and archipelagos such as Hawaii, Easter Island, St Helena and Ascension Islands, Cape Verde Islands, the Mascarene Islands and New Zealand, which typically have lower species richness and higher species endemism due to isolation (Costello et al., 2017). Although Antarctica has high endemism, it is generally excluded as a hotspot because it is relatively species poor when compared to the tropics (Costello et al., 2010) and was only included by one study (Selig et al., 2014). The “hottest” hotspots, areas of high endemism and species richness, are in the West Caribbean, South Madagascar, Chagos Islands, Maldives, Lakshadweep, Sri Lanka, South Japan, East China Sea including Taiwan, Coral Triangle, New Caledonia, Vanuatu and North East and North West Australia (Fig. 1).

Methods of Mapping Hotspots

The literature has used a variety of data sources to map global marine species distributions and threats to biodiversity (Table 2). Studies have compiled extensive data from previous research, opinion sources, fishing records and site surveys, as well as using

Table 2 Data used to determine marine biodiversity hotspots.

Author(s)	Primary data	Supplementary data
Rutherford et al. (1999)	Planktonic foraminifera database—from surface-sediment samples	Sea surface temperature satellite data
Roberts et al. (2002)	Expert opinion, museum records, literature sources, monographs, loan specimens, and extensive personal observations by author(s)	Bryant et al. (1998)—threats to coral reefs based on observational and objective data
Worm et al. (2005)	Fishery records—Japanese longline data (1990–99) ^a	Independent scientific observer data from Atlantic and Pacific longline fisheries
Tittensor et al. (2010)	Ocean Biogeographic Information System (OBIS)	Expert verified range maps and empirical occurrence data
Kaschner et al. (2011)	Relative Environmental Suitability (RES) model—based on expert knowledge, literature and occurrence data	
Lucifora et al. (2011)	Expert knowledge from literature sources and fishery reports	Global Biodiversity Information Facility (GBIF) occurrence records—where supported by literature
Pompa et al. (2011)	Literature sources—objective and observational data	International Union for Conservation of Nature (IUCN)—threat status
Trebilco et al. (2011)	Fishery records—Japanese longline data (1990–99) ^a	Halpern et al. (2008)—Human impacts based on observational and objective data
Worm and Branch (2012)	FishBase—based on objective and observational data, expert opinion and literature sources	Sea Around Us Project data, based on fishery records, numerous other databases and literature
Jablonski et al. (2013)	Literature, museum specimens, expert opinion, and occurrence data	
Stuart-Smith et al. (2013)	Reef Life Survey data—based on observational occurrence records	FishBase and authors' expert knowledge of species
Dulvy et al. (2014)	Expert opinion, literature sources, observational occurrence records	IUCN threat status, Food and Agriculture Organization (FAO) landing records
Selig et al. (2014)	Expert opinion, AquaMaps—predicted distributions based on occurrence data and expert opinion, BirdLife International—distributions based on objective and observational data	Halpern et al. (2008)—Human impacts
Jenkins and Van Houtan (2016)	IUCN species range maps—based on objective expert opinion and literature, BirdLife International, NatureServe and State of the World's Sea Turtles—both based on observational occurrence records and expert opinion	Halpern et al. (2008)—Human impacts, IUCN threat status
Molinos et al. (2016)	AquaMaps	
Albouy et al. (2017)	IUCN species range maps	Halpern et al. (2008)—Human impacts
Davidson and Dulvy (2017)	Expert opinion, literature sources, observational occurrence records	IUCN threat status
Ramírez et al. (2017)	IUCN species range maps, BirdLife International species distributions	FAO—FishStatJ

Data sources show variation within the literature, with studies using objective and observational data as the primary basis for species distribution analyses.

^aValidated against total predator richness (145 species) from independent scientific observer data from the Atlantic and Pacific Ocean.

environmental envelopes, derived from occurrence data and known habitat use, to model distributions for species groups and individual taxa (Kaschner et al., 2011; Selig et al., 2014; Molinos et al., 2016). This data has then been used to assess a variety of criteria for measuring “diversity,” including species richness (all but Davidson and Dulvy, 2017), functional diversity (Lucifora et al., 2011; Stuart-Smith et al., 2013; Albouy et al., 2017), phylogenetic diversity (Albouy et al., 2017), functional richness (Lucifora et al., 2011; Stuart-Smith et al., 2013; Albouy et al., 2017), and how evenly distributed individual abundances were between species (Stuart-Smith et al., 2013). The chosen species diversity criteria were then mapped, along with any further data such as threat level and endemism, and those mapped cells that represented the highest proportions of the selected criteria were deemed hotspots of marine biodiversity. Worm et al. (2005) and Trebilco et al. (2011) selected the 50 cells with the highest values for species richness and/or diversity. Albouy et al. (2017) defined hotspots as “all grid cells with values in the upper 2.5 % and 5 % of the biodiversity facet and human threat value distributions,” while Ramírez et al. (2017) highlighted hotspots as those cells with species richness above the upper 95th percentile.

Of the seven studies to include endemism, Jenkins and Van Houtan (2016) defined endemic species as those species classed as “small-ranged” by the IUCN, species with ranges smaller than the global median for that taxon (Jenkins et al., 2015). All other studies used their own metrics of endemism. Roberts et al. (2002) defined marine biodiversity hotspots as centers of endemism with a medium to high level of threat from human activities, as defined by Bryant et al. (1998). They calculated areas of high species richness by mapping the geographic ranges of species and plotting the top 10% of cells with most species for each taxon. To assess endemism, they calculated range rarity as the reciprocal of range size, summed across species present (Roberts et al., 2002), and mapped the top scoring 10% of cells for each taxon. Cells in the top 10% for at least two taxa, added with any adjacent cells in the top 5% for any single taxa, were defined as multitaxon centers of endemism. Additionally, centers of endemism, cells with the top 5% for 1 taxon and 20% for two or more taxa were also included, resulting in 18 centers of endemism. They then calculated the number of restricted-range species, range ≤ 10 cells (500,000 km²), within each center of endemism and ranked sites according to the number of restricted-range species present. Although this method of defining marine biodiversity hotspots does not use species richness, range-rarity and species richness were shown to be closely coupled for corals (Roberts et al., 2002). This means that prioritizing hotspots as defined by Roberts et al. (2002) would benefit coral diversity, but may prove less beneficial for noncoral associated taxa (Roberts et al., 2002). However, their strategy was effective for species representation, with the 18 centers of tropical endemism including 74–96% of all species studied (Roberts et al., 2002).

Selig et al. (2014) used two measures of endemism, range rarity, areas with the greatest concentrations of relatively rare or range-restricted species, and proportional range rarity, areas with restricted range species, regardless of the number of species (range rarity/species richness). For diversity metrics (species richness, rarity and proportional range rarity) they identified the 5% of grid cells within the total area of EEZs and ABNJ that had the highest values. Using an area threshold ensured that each diversity metric contributed an equal area to the assignment of priorities (Selig et al., 2014). A 10% area threshold for human impacts was used because a 5% area was deemed too restrictive for overlap with other metrics and 10% was deemed beneficial for assessing broad scale management impacts (Selig et al., 2014). Consequently, 10% of the highest and lowest impacted EEZs and ABNJ were identified. Priority areas were then defined based on overlap between these diversity metrics and areas of high or low human impact. This technique ensures that areas with high endemism and species richness that are both heavily impacted and relatively pristine will be deemed as hotspots.

Pompa et al. (2011) used political endemism, that is species with a range restricted to a single country. They compiled species richness of marine mammals by mapping geographic range, and created a presence and absence matrix to tally the number of species present in each cell. Key conservation sites were then determined as either the 2.5% of cells with the highest species richness or as those with endemic species. This method of analyzing endemism was efficient at targeting single species such as the Hawaiian monk seal, Australian sea lion and vaquita, species that their respective country's may take an active interest in conserving (Pompa et al., 2011). However, many marine mammals are highly mobile, migratory, and do not observe state boundaries. Consequently, species endemic to ecosystems, regions and biogeographic realms, such as the finless porpoise, endemic to the waters of southern Japan and eastern China, will not be deemed priority species through this assessment.

Lucifora et al. (2011) defined marine biodiversity hotspots as those cells with at least the 95th percentile of shark species richness or endemism. Endemism was estimated for each cell as the sum of the inverse of the range of the species present in that cell (as in Roberts et al., 2002), with range defined as the number of cells a species occurred in. Cells were grouped according to their similarity of shark species composition, resulting in 93 biogeographic units. These units varied in size from 2 to 9645 1-degree latitude-longitude cells with similar assemblages (Lucifora et al., 2011). The cells with the highest number of species and highest number of endemic species were then identified in each unit, resulting in priority areas for all shark communities. Hotspots of shark species richness and endemism were shown in Indonesia, China, and Sri Lanka (Lucifora et al., 2011). These countries have the largest shark harvests in the world (Lack and Sant, 2011; Davidson et al., 2016), but the study did not include a threat index, and consequently did not prioritize shark biodiversity hotspots for protection.

Dulvy et al. (2014) defined endemic chondrichthyans (cartilaginous sharks, rays and their relatives) as those species with an extent of occurrence less than 500,000 km². The cells containing the highest number of IUCN threatened endemic species were called “Irreplaceability Hotspots.” Irreplaceability was calculated as the sum of the inverse of the geographic range of all threatened endemic species in a cell. Consequently, a cell value of 0.1 would represent 10% of a threatened endemic species' total global range. In total this resulted in 15 Irreplaceability Hotspots that harbored 66 threatened and endemic chondrichthyans (Dulvy et al., 2014). They also mapped species richness and threats, finding that areas of greatest species richness coincided with areas of most threatened

species (Dulvy et al., 2014). In addition to using IUCN species classifications, threatened species were categorized by habitat, enabling a comparison of species from coastal and continental shelf, neritic and epipelagic, deep-water and mesopelagic habitats.

Davidson and Dulvy (2017) determined endemism as those species with range areas less than or equal to the 50th percentile (595,749 km²) of extent of their geographic range, resulting in 99 imperiled and endemic chondrichthyan species. Hotspots were then defined by counting the number of imperiled endemic species in each hexagonal grid cell (23,322 km²) within each EEZ. This analysis resulted in the majority of hotspots being located in EEZs, with only five hotspot cells in ABNJ.

Application in Marine and Terrestrial Environments

The concepts used to define marine biodiversity hotspots are similar to those used in terrestrial environments. Myers et al. (2000) designated 25 terrestrial biodiversity hotspots driven by two criteria, endemic species, and threats. They based endemism principally on species of vascular plants, as their presence is critical to almost all forms of animal life (Myers et al., 2000), with an area needing to contain at least 1500 of the world's 300,000 species (0.5%) as endemics. The second basis, threats, necessitates that a hotspot of endemism should have lost $\geq 70\%$ of its primary vegetation. A similar approach was followed by Roberts et al. (2002) who identified tropical reefs as the most important areas for marine biodiversity, and used endemism and threats as the principle criteria for hotspot selection.

As in the marine realm, there have been numerous terrestrial studies focusing on individual taxa. Ceballos and Ehrlich (2006) mapped terrestrial mammal biodiversity hotspots using species richness, endemism and threat to extinction. They mapped species geographic ranges, counting the number of species present in each cell to attain species richness, a technique used in marine studies by Lucifora et al. (2011) and Pompa et al. (2011) among others. Endemic species were classified as those in each cell with a range $\leq 250,000$ km², and threatened species were those within each cell considered to be threatened, endangered or critically endangered by the IUCN. They then deemed cells to be hotspots by combining the top 2.5% and 5% of each category. Orme et al. (2005) identified bird breeding hotspots based on species richness, endemism, and threat. As in other terrestrial and marine studies, species richness was a count of the total number of species in each grid cell based on known ranges, threat was determined as those species in each cell that were deemed as threatened (BirdLife International, 2000), and endemism was defined as those species with restricted ranges, in this case those with a range of < 30 grid cells. Hotspots were then defined as the richest 2.5% of cells for each criterion. Finally, the congruence of hotspot cells were measured, resulting in 32 grid cells common to all hotspot types (Orme et al., 2005). Although this method analyzed the congruence of hotspots, the methods used to delineate biodiversity hotspots are conceptually the same as those used for various terrestrial and marine assessments (Myers et al., 2000; Roberts et al., 2002; Trebilco et al., 2011; Albouy et al., 2017).

The methods used for defining marine and terrestrial biodiversity hotspots have also been used in freshwater biodiversity hotspot analyses (Groombridge and Jenkins, 1998; Oberdorff et al., 2011; Tedesco et al., 2012; Collen et al., 2014). Species richness was calculated as the number of species per cell (Collen et al., 2014), endemism as species inhabiting a single drainage basin (Tedesco et al., 2012; Abell et al., 2008) or those with geographically restricted ranges, e.g., ranges in the lower quartile of a taxon (Collen et al., 2014). Threat was based on the distribution of IUCN threatened species (Collen et al., 2014), or analysis using Vörösmarty et al.'s (2010) global map of threats to freshwater biodiversity, a synthesis of 23 environmental impact stressors. Typically the 5% highest scoring cells of each parameter (Collen et al., 2014), or countries with the highest total counts (Tedesco et al., 2012), were then used to prioritize areas as hotspots of freshwater biodiversity (Collen et al., 2014). Whether in the marine, terrestrial or freshwater environment, the methods used to delineate sites are comparable between species groups, diversity indices and environments, providing a logical, universal approach to prioritize and subsequently protect biodiversity hotspots.

Discussion

The criteria outlined by Myers (1988) and used in the subsequent literature to designate marine biodiversity hotspots have been used both as single indices (Rutherford et al., 1999; Worm and Branch 2012; Ramírez et al., 2017) and collectively (Lucifora et al., 2011; Trebilco et al., 2011; Dulvy et al., 2014) to prioritize more than 70 sites for conservation (Table 1). When analyzing the distribution of marine species, endemic species and threats, it is clear that protecting hotspots of marine biodiversity should be viewed as the first step to ensuring the ecological integrity of our oceans, but will not be an effective strategy to represent and protect all marine life. Despite similarities, the distribution of marine species richness shows variations between taxa (Tittensor et al., 2010). Marine mammals display higher species richness in mid-southern latitudes (Pompa et al., 2011; Kaschner et al., 2011; Albouy et al., 2017), sharks, skates, rays and chimaeras have higher species richness along continental shelves (Lucifora et al., 2011; Dulvy et al., 2014), and some pelagic species show higher species richness in the open ocean (Worm et al., 2005). Moreover, fishes are one of the most intensively studied marine taxonomic groups (Eschmeyer et al., 2010), making up 24% (5877) of the 25,000 marine species with modeled distributions on AquaMaps (Kaschner et al., 2016). Considering that marine mammal and chondrichthyan species combined represent 1136 (Pompa et al., 2011; Davidson and Dulvy, 2017) of the 240,000 described marine species (Costello et al., 2013), and that reef fish alone outnumber these groups, ~ 4500 species (Froese and Pauly, 2014), identifying and protecting marine hotspots using species richness will not represent all marine taxa. How representative hotspots based on vertebrates are of all marine species is not yet known.

In addition to variations in marine taxa distributions, many centers of endemism are distinct from areas of high species richness (Fig. 1). Thus prioritizing hotspots of biodiversity based on Myers' criteria alone will leave centers of high endemism but low species richness unprotected. Endemic species contribute significantly to global biodiversity (Kosaki et al., 2017), but are more vulnerable to extinction due to their restricted ranges (Roberts et al., 2002). Furthermore, the distribution of endemic species is not always congruent between taxa, with shark (Lucifora et al., 2011; Dulvy et al., 2014), marine mammal (Pompa et al., 2011), and seabird species (Croxall et al., 2012) known to have discrete distributions, as well as overlapping areas of endemism. In the terrestrial realm, areas of high species richness often correlate with areas of high species endemism (Caldecott et al., 1996; Myers et al., 2000). However, as in the marine realm, there are also centers of endemism in isolated terrestrial areas that have low species richness (Caldecott et al., 1996; Kier et al., 2009). For example, islands are recognized as global centers of endemism (Kier et al., 2009) despite island species richness being generally lower than mainland sites (Whittaker and Fernández-Palacios, 2007; Kreft et al., 2008). Additionally, terrestrial areas of endemism differ between taxa, as shown by Kier et al. (2009) who found that when comparing the top 30 regions of plant endemism richness, amphibian endemism shared 49% of range equivalents but mammals only 32%. In freshwater environments, areas of high species richness are congruent with areas of high numbers of endemic species. However, the percentage of freshwater endemic species is greater in isolated areas, showing substantial centers of endemism in areas inside and outside the tropics (Tedesco et al., 2012; Abell et al., 2008). Patterns of freshwater endemism and species richness also lack congruence among taxa, as shown by Collen et al. (2014) who compared the distribution of freshwater amphibians, reptiles, mammals, crabs, fishes, and crayfish.

From global assessments of species endemism in marine, freshwater and terrestrial environments, it is clear that hotspots of endemism are both congruent with, and distinct from areas of high species richness. The IUCN use endemism as a criterion to identify conservation areas instead of species richness (Asaad et al., 2017). By doing so they aim to protect the ranges of endemic species as well as more common species that may have overlapping distributions. Regardless of the criteria preferred, in order to effectively prioritize and protect marine biodiversity, both global and regional scale assessments of endemism between groups and individual species are necessary.

Myers' criteria for designating hotspots requires that areas be under exceptional degrees of threat. This criterion enables biodiverse areas to be urgently prioritized before they are lost to exploitation and destructive practices, and is defined as areas that have lost $\geq 70\%$ of primary vegetation (Myers, 1988). In the marine realm, habitat loss is difficult to quantify, requiring well planned monitoring (Airolidi et al., 2008) and the extent of some habitats, such as mesophotic coral reefs, is only now beginning to emerge (Lesser et al., 2009; Bridge et al., 2013; Laverick and Rogers, 2019). Five studies used threats as a parameter for designating areas as marine biodiversity hotspots (Table 1). However, by using threat analyses to define marine biodiversity hotspots, we may exclude high biodiversity areas that are unthreatened or no longer threatened. Coral reefs harbor one third of all described marine species (Reaka-Kudla, 2001; Costello, 2015) and cover just 0.2% of the marine environment (Veron et al., 2009a,b), but coral reefs worldwide are under varying degrees of threat (Carpenter et al., 2008). Rather than only deeming threatened coral reef ecosystems as marine biodiversity hotspots, all areas with the richest and most unique biodiversity should be prioritized. Moreover, due to the increasing global scale impact of anthropogenic stressors, such as climate change induced ocean warming and acidification (Costello et al., 2013; Rodgers et al., 2018), as well as continued unsustainable and destructive fishing practices (Petrossian, 2015; Rhodes et al., 2018), it could be argued that all marine habitats and species are under threat. Consequently, designating hotspots based on species richness and endemism alone represents a more efficient approach to target and conserve marine biodiversity.

The aim of Myers' (1988) hotspot analysis was to enable a 'silver bullet' strategy to combat biodiversity loss and target conservation resources where they were needed most. It garnered worldwide interest, generating more than \$ 750 million USD of funding support, the largest sum ever assigned to a conservation strategy (Myers and Worm, 2003), and has since been used extensively in marine, terrestrial and freshwater conservation planning. Defining biodiversity hotspots has helped lead to the protection of 15% of terrestrial environments (Gray et al., 2016; Jones et al., 2018), but to date less than 5% of the world's oceans are afforded some form of protection. Additionally, just 2% of the ocean is designated as no-take marine reserves (Marine Conservation Institute, 2019), the most effective type of marine protected area (Lester and Halpern, 2008; Costello and Ballantine, 2015). Myers' approach has been used extensively, and over the last 30 years the term hotspots has evolved to pertain to areas of high species richness, or areas of high endemism, that may or may not be under high threat. The data used to underpin hotspot analyses has also evolved from objective and observational data to modeled and observational data sources, enabling the prediction of species distributions under altering climatic variables and threats (Kaschner et al., 2011; Molinos et al., 2016; Ramírez et al., 2017).

Threatened species, which may have reduced genetic diversity (Phillips et al., 2011; Evans et al., 2014), may be subject to higher human exploitation and habitat loss (Dulvy et al., 2014), and frequently have restricted ranges (Gales and Fletcher, 1999; Hawkins et al., 2000). Due to their increased vulnerability they must be prioritized for protection, yet these species are not necessarily included in global scale hotspot analyses. In total the IUCN has assessed 987 marine species as threatened (IUCN, 2019) (i.e., Critically Endangered, Endangered or Vulnerable), but many more are data deficient (DD) and likely threatened (Dulvy et al., 2014; Jarić et al., 2016; Jenkins and Van Houtan, 2016; Roberts et al., 2016) (Fig. 2). Just four studies acknowledge the importance of protecting IUCN threatened species by including IUCN status in their biodiversity hotspot assessments (Pompa et al., 2011; Dulvy et al., 2014; Jenkins and Van Houtan, 2016; Davidson and Dulvy, 2017). Only by protecting biodiversity hotspots of species richness, centers of endemism and threatened species can we reduce the global risk of species extinction, support species recovery (Ardron et al., 2009) and protect marine biodiversity.

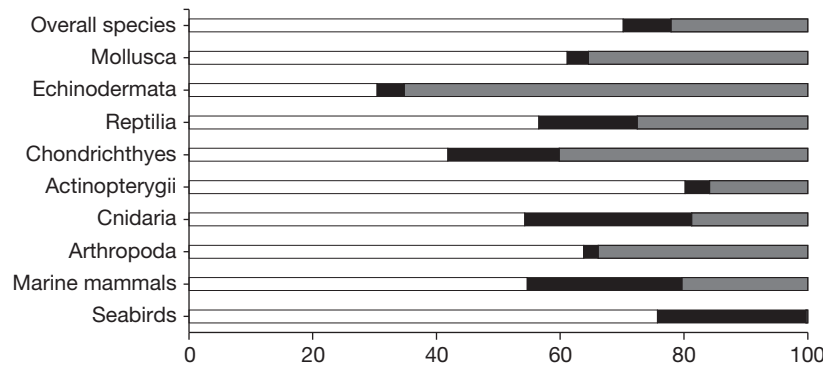


Fig. 2 Percentages of marine species groups assessed as not threatened (white bar), Threatened (black), and data deficient (gray) by the IUCN. Overall species (12,748), Mollusca (1374), Echinodermata (362), Reptilia (69), Chondrichthyes (1083), Actinopterygii (7957), Cnidaria (879), Arthropoda (254), Marine mammals (128), and Seabirds (346). All data from the IUCN Red List (IUCN, 2019), correct on 01/05/19.

Acknowledgments

Tamlin Jefferson is very grateful to be the recipient of the Commonwealth Scholarship, and the Stanley Wishart Low Memorial Scholarship in Marine Science.

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The Classification, Diversity and Ecology of Shallow Water Octocorals

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Glossary

Ancestral gene order To date six different mitochondrial gene orders have been found in the subclass Octocorallia. The mitochondrial gene arrangement shared by the octocoral common ancestor is considered the ancestral one.

Anthocodia The distal part of a polyp, bearing the mouth and the tentacles; in many cases it can be retracted within the calyx, the stem, the branch or within the cortex.

Apomorphy A character derived/changed from the form found in the ancestor.

Aragonite skeleton Aragonite is a carbonate mineral, one of the three most common naturally occurring crystal forms of calcium carbonate (CaCO_3), the other forms are the minerals calcite and vaterite.

Autozoid Autozooids are one of the five polyp types in octocorals, and the main function of autozooids is to gather food with their tentacles and make sure it gets to the mouth of the autozoid polyp.

Clade Characters or traits that are derived from ancestral characters over evolutionary history or organisms which share a common ancestor are grouped into the same clade. A clade is monophyletic by definition.

Dynamite fishing Also known as blast fishing is the practice of using explosives to stun or kill schools of fish for easy collection. This is often illegal and can be extremely destructive to the surrounding ecosystem, as the explosion often destroys the underlying habitat (such as coral reefs).

Epibiont An epibiont (from the ancient Greek meaning "living on top of") is an organism that lives on the surface of another living organism and is harmless to its host.

Exon loci Specific traits of a gene at certain positions on the chromosome.

Gastrovascular or gastric cavity Also, coelenteron, the interior space of a polyp.

Gene order The arrangement of the genes into a given genome.

High-throughput sequencing In molecular biology, a technology which allows to sequence on large scales and simultaneously multiple DNA molecules.

Indel-rich In molecular biology, INDELs refer to mutation/recombination events that occur in the genome of a given organism. Such mutations can be either insertions or deletions.

Marine Natural Products (MNP) Natural compounds produced by marine organisms which have potential economic and commercial value.

Mitogenome Small fraction of the total DNA that is contained in the mitochondria. Animal mitogenomes typically harbor 13 protein-coding genes, two ribosomal RNA genes and 22 transfer RNA genes. Variations in terms of gene content and genome size may occur in some non-bilaterian metazoans.

Monogeneric In taxonomy monogeneric refers to a group that includes a single genus.

Monophyletic group In phylogenetics a group of organisms that share the most recent common ancestor.

Ovulids (Ovulidae) A common name for members of the family Ovulidae, other common names are cowry allies or false cowries. Ovulidae is a family of small to large predatory or parasitic sea snails, marine gastropod molluscs.

Paraphyletic group In phylogenetics is a group of organisms which include the most recent common ancestor but a few of its descendant.

Pharynx Tubular passageway between the mouth and the gastric cavity in octocoral polyps.

Pinnule The lateral processes of a tentacle.

Polyp leaves The flattened expansions bearing the secondary polyps in some Pennatulacea.

Polyphyletic group In phylogenetics a group of organisms derived from more than one ancestor.

Predator An organism that preys upon other organisms.

Prostaglandines A group of physiologically active lipid compounds that have various hormone-like functions (regulating inflammation, blood flow, etc.).

RAD-Seq Restriction site Associated DNA Sequencing (RAD-Seq) is a fractional genome sequencing strategy. By digesting the genome with a restriction nuclease and attaching a series of adapters to the resulting DNA fragments, large numbers of genetic variations such as SNPs can be readily identified from analysis of next generation DNA sequence data.

Sanger sequencing Method of DNA sequencing based on selective incorporation of chain-terminating dideoxynucleotides by DNA polymerase during in vitro DNA replication.

Sclerite A calcareous element, irrespective of form, in the mesoglea. Also occurring in the axis of Scleraxonia. There are many different forms of sclerites (Fig. 2B).

Siphonoglyph (sulcus) The strongly ciliated groove extending down one side of the pharynx.

Stolon Rounded or flattened elongate or membranous coenenchyma expansion growing over or into the substrate and peripherally producing new polyps.

Stolonifera A subordinal grouping within the Alcyonacea, characterized by the colony growth form of polyps connected through stolons.

Subordinal group Taxonomic entity just below the order rank; this rank is not recognized by some taxonomists.

Synapomorphy Refers to derived characters of a clade. A synapomorphy is a shared apomorphy that distinguishes a clade from other organisms.

Topological incongruences When phylogenetic relationships among taxa are not consistent in the phylogenetic trees obtained using different methods.

Ultra-conserved elements Portion of the DNA regions that are highly conserved among different species/lineages.

Vagile Free to move about.

Abstract

Shallow water tropical and subtropical coral reef communities are among the most species rich habitats of the world. Among these coral reefs, octocorals are common members of invertebrate reef fauna. The ecological importance of octocorals can be seen through their use as microhabitats by marine vertebrates and invertebrates (e.g., shrimp, fish, ovulids); acting as important spawning, nursery, breeding and feeding areas for a variety of other organisms, and additionally providing refuge from predators. Therefore, their three-dimensional structures contribute to the structural complexity and biodiversity of reefs, facilitating niche diversification, and speciation. Despite their importance to reef ecology and biodiversity, octocorals have received relatively little attention, compared to other anthozoan groups such as scleractinian corals, and thus remain a poorly known and little-studied group. However, as their abundances increase due to the decline of scleractinian corals worldwide, octocorals are likely to play a growing role in future reefs. The purpose of this review is thus to gather existing knowledge on their biology, ecology and societal importance in order to provide a comprehensive information source for future research efforts.

Systematics and Taxonomy

Octocorallia Haeckel, 1866 is a subclass within Anthozoa Ehrenberg, 1834, phylum Cnidaria Verrill, 1865, and its members have been reported worldwide (Van de Water et al., 2018). Octocorals are found in many marine environments and are most diverse and conspicuous on tropical and subtropical shallow reefs and in deep-sea environments, where they are often dominant space-occupiers and important structural components of the benthic community (McFadden et al., 2010). There are approximately 3500 species of soft corals, gorgonians, and sea pens described, which belong to ca. 378 octocoral genera from 55 families (Daly et al., 2007; McFadden et al., 2010; Williams and Cairns, 2018), with new species, genera (e.g., Benayahu et al., 2017a,b; Conti-Jerpe and Freshwater, 2017; Lau et al., 2018, 2019; Lau and Reimer, 2019) and even families (McFadden and van Ofwegen, 2012; Breedy et al., 2012) continuing to be described. This is especially true for environments in deep-sea and in the shallow coral reefs of the Indo-Pacific, where the highest diversity of octocorals is observed (Pérez et al., 2016). Octocorallia currently has three orders (Alcyonacea, Helioporacea and Pennatulacea). Helioporacea (blue corals) and Pennatulacea (sea pens) are the only orders with well-defined synapomorphies; blue corals due to their massive aragonite skeleton, and sea pens for the presence of a proximal peduncle used for anchorage in the substrate (McFadden et al., 2010; Goffredo and Dubinsky, 2016). Bayer (1981) merged the remaining four orders into Alcyonacea, which comprises stoloniferous forms, soft corals, and gorgonians, and this scheme is

currently followed by most taxonomists. However, Alcyonacea is still considered unstable along with many family-level classifications (McFadden et al., 2006, 2010).

The sea pens, order Pennatulacea Verrill, 1865, comprise 14 families, 37 genera, and over 200 species (Williams, 2011; McFadden et al., 2010; García-Cárdenas et al., 2019; Kushida and Reimer, 2019) (Fig. 1A). Two suborders, Sessiliflorae Kükenthal, 1915 and Subsessiliflorae Kükenthal, 1915, were established in the early 20th Century, which some classification systems still use in the present day (Cordeiro et al., 2019a). Sessiliflorae have autozooids arising directly from the rachis, whereas Subsessiliflorae have polyps connected on polyp leaves (Kükenthal and Broch, 1911, Kükenthal, 1915, Imahara et al., 2014, Cordeiro et al. 2019). Further morphological and cladistical investigations into the classification system of Pennatulacea proposed by Kükenthal and Broch (1911) and Kükenthal (1915) highlighted the paraphyly of Sessiliflorae and monophyly of Subsessiliflorae (Williams, 1995; Kushida and Reimer, 2019). The difficulties encountered so far are most likely due to sampling efforts, the paucity of morphological characters, and high intraspecific variability (Williams, 1992). To date molecular phylogenetic reconstructions by Dolan et al. (2013) and Kushida and Reimer (2019) strongly reject the monophyly of the two suborders. Most recently, Hogan et al. (2019) sequenced the complete mitogenome of deep-sea sea pens and found at least three different mitogenome arrangements within Pennatulacea, including one novel gene order. Besides from the ancestral gene order (Beagley et al., 1995; Brockman and McFadden, 2012) that is the most common among octocorals, the bamboo coral genus *Acanella* and a member of family Keratoisidinae have differing mitochondrial gene orders (Brugler and France, 2008). As well, the sea pen *Umbellula* has been reported to have a novel gene arrangement for octocorals (Hogan et al., 2019).

The order Helioporacea Bock, 1938 comprises only two families, Helioporidae Moseley, 1876 and Lithotelestidae Bayer & Musik, 1977. Members of Helioporacea produce a solid matrix forming a crystalline aragonite skeleton, which is considered a unique feature among octocorals (McFadden et al., 2010). The family Helioporidae is monogeneric, represented by two valid species within the extant genus *Heliopora* Blainville, 1830, (Fig. 1B and D) and it is most well-known for the blue coral *Heliopora coerulea* (Pallas, 1766). Recently, a second valid species, *Heliopora hiberniana* Richards et al., 2018 was described from northern Western Australia. Unlike *H. coerulea*, some individuals of *H. hiberniana* feature a white skeleton, thus displacing the most diagnostic and conserved character within the genus *Heliopora*—the blue skeleton (Richards et al., 2018). The family Lithotelestidae includes only two genera, *Epiphaxum* Lonsdale, 1850 (Bayer, 1992), with two extant species reported from the deep seas of the western Atlantic and the western Indian Oceans (50–400 m), and *Nanipora* Miyazaki & Reimer, 2015, found from several shallow locations in the western Pacific, including Thailand, Okinawa, and Dongsha Atoll (Miyazaki and Reimer, 2015; Miyazaki et al., 2016; Plaza et al., 2017; Reimer et al., 2017). Unexpectedly, *Nanipora* has been found in seagrass beds along the northwestern coast of Dongsha Island with unusual colony forms; either forming hollow rounded mounds, unattached to any other organism, or encrusting other organisms, such as seagrass stem bases, sponges, and dead scleractinian corals (Reimer et al., 2017) (Fig. 1E).

All other remaining octocoral species belong to the order Alcyonacea Lamouroux, 1816, which is thus the most diverse order in terms of species number. This order includes ~31 families of soft corals and sea fans (Fig. 1C and F–J), and lacks any defining synapomorphies (Daly et al., 2007; McFadden et al., 2010). Members of this order have been divided into sub-ordinal groups Alcyoniina, Calcaxonia, Holaxonia, Protoalcyonaria, Scleraxonia, and Stolonifera, however this classification is not supported by molecular analyses and is acknowledged to reflect morphological categories rather than clades (Bernston et al., 2001; McFadden et al., 2006, 2010; Cordeiro et al., 2019b).

Despite their high diversity, only about 25% of the described octocoral species are found in waters shallower than 50 m (Williams and Cairns, 2015; Pérez et al., 2016). Each subordinal group includes shallow water octocorals, yet most of the species inhabiting coral reef communities are alcyoniids. *Lobophytum* Marenzeller, 1886, *Sinularia* May 1898 and *Sarcophyton* Lesson, 1834 are considered among the most important contributors to the total biomass of Indo-Pacific reefs, covering up to a quarter of the reef surface (Dinesen, 1983; Fabricius and Alderslade, 2001). Members of Calcaxonia, Holaxonia and Scleraxonia, also known as gorgonians, are commonly distributed in worldwide coral reefs, and are particularly diverse and abundant in the Caribbean (Bayer, 1961). Similar to soft corals and sea fans, stoloniferans can be found at various depths and latitudes (Daly et al., 2007; McFadden and van Ofwegen, 2012). Among them, *Tubipora musica*, the only known reef-building alcyonarian species (Fig. 1I and J), contributes to the benthic coverage of Indo-Pacific reefs, and can reach relatively high coverages (up to 28%) at some Western Australia locations (Richards et al., 2013).

Biology and Morphology

As the name octocoral suggests (from Latin “octo”), the sessile, mostly colonial Octocorallia are composed of polyps with eight tentacles (almost always pinnate) and eight mesenteries (divisions in the body cavity), characters that are invariant within the clade (Daly et al., 2007).

In octocorals, the polyp is the individual zooid and together the polyps are responsible for all the vital functions of the colony (e.g., growth, food capture, transport of nutrients, irrigation with seawater, defense and reproduction). Most octocoral species have a single type of polyp (the autozooid) and are monomorphic. Species in some groups, such as sea pens, have a second type of polyp (the siphonozooid), and thus are dimorphic. The siphonozooid may either have one rudimentary tentacle or none at all and their function is to transport water, supporting the hydroskeletal system of the colony. In general, the term “polyp” refers to sexual individuals, the autozooids (Bayer, 1973; Fabricius and Alderslade, 2001; Samimi-Nami and Ofwegen, 2012). Oozooids, which are single primary polyps located at the center of the colony, are exclusively known from sea pens. However, other types of polyps

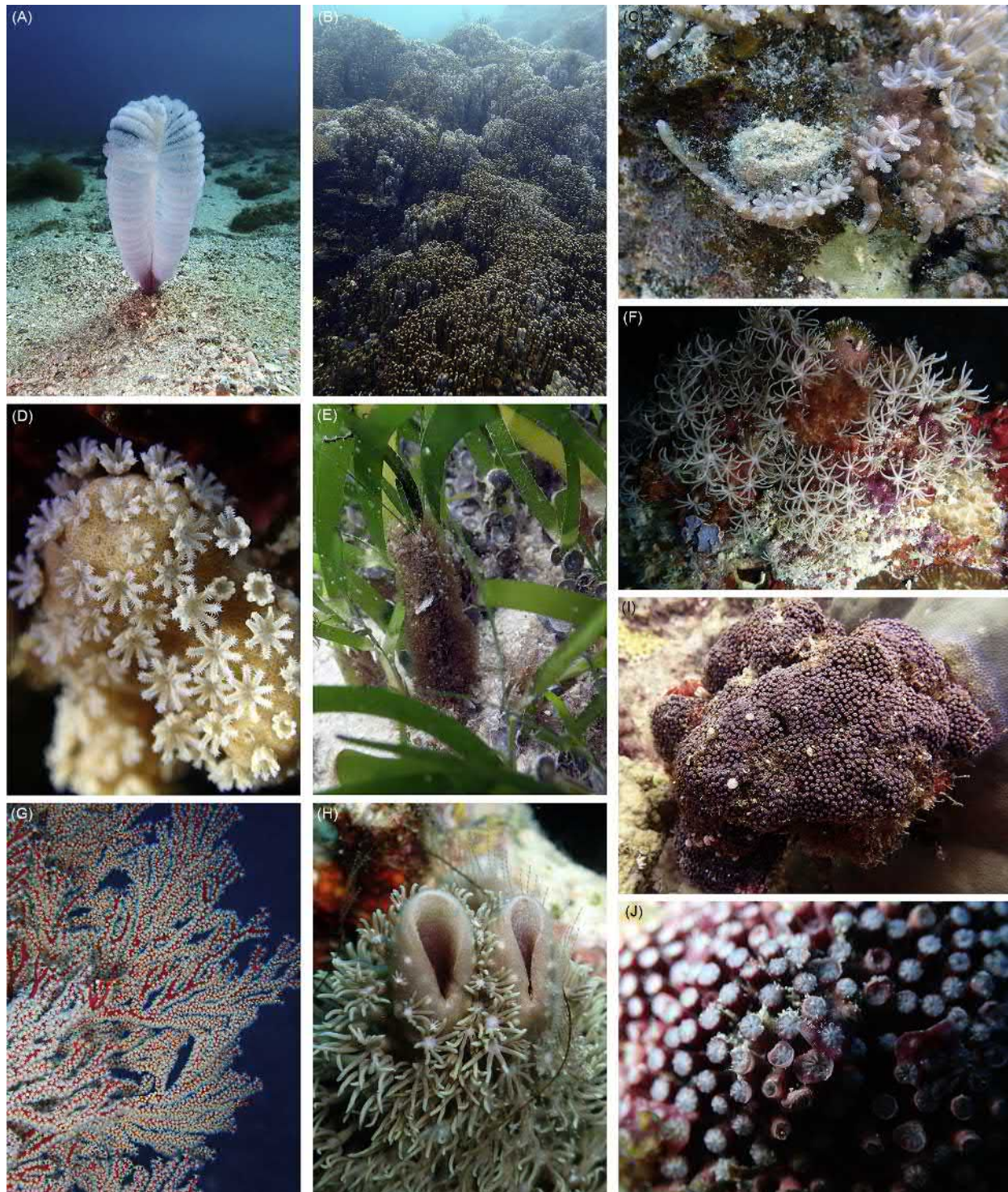


Fig. 1 Diversity of octocoral growth forms (A) sea pen *Virgularia* sp. Photograph: JD Reimer. (B) Blue coral *Heliopora* sp. Photograph: JD Reimer. (C) Stoloniferous octocoral *Clavularia* sp. Photograph: YW Lau. (D) Close-up of blue coral polyps. Photograph: YW Lau. (E) Lithotelestid octocoral *Nanipora* sp. Photograph: YW Lau. (F) Encrusting octocoral *Briareum* sp. Photograph: YW Lau. (G) Sea fan *Anella* sp. Photograph: JD Reimer. (H) Soft coral *Sarcophyton* sp. Photograph: YW Lau. (I) Reef building octocoral *Tubipora* sp. Photograph: GY Soong. (J) Close-up of *Tubipora* sp. Photograph: YW Lau.

such as mesozooids or acrozooids can also be observed in some Pennatulaceans (Williams, 2011; Williams et al., 2012). Recently, a fifth type of polyp, the acrozooid, was described in two *Pteroeides* species from the tropical western Pacific coral reef regions (Williams et al., 2012).

The polyp is a tubular structure, consisting of two main parts. The upper end (anthocodia) is contractile, extends above the colony surface and has a central mouth opening surrounded by eight tentacles. The tentacles have finger-like extensions (pinnules) along each side, which enhance the surface area of the polyp. The contractile tentacles contain sensory cells and stinging capsules. The mouth extends into a gastrovascular or gastric cavity through a short tubular pharynx, which has a modified sidewall that is called the siphonoglyph or sulcus. This serves to drive water into the gastric cavity and from there to the rest of the colony through the canal system. The gastrovascular cavity has eight protruding radially arranged tissue plates (the mesenteries), which have an important function in the polyp hydraulic system, contain digestive gland cells and in most genera, produce the gonads. The lower part of the polyp is embedded in common tissue, the coenenchyme. The coenenchyme is penetrated by a complex system of tubes (solenia) that enable communication among all polyps in a colony (Bayer, 1973; Fabricius and Alderslade, 2001; Samimi-Nami and Ofwegen, 2012).

Octocorals are suspension feeders and their access to food depends on environmental conditions, relying on water currents (Gili and Coma, 1998). Octocoral polyps can filter small organic particles ($< 20 \mu\text{m}$) from the water column, or capture larger particles, intercepting, for example, zooplankton and larvae with their tentacles. The nematocysts (stinging cells) of octocorals are simple, and therefore, their food is limited to small and weakly swimming plankton (Samimi-Nami and Ofwegen, 2012).

Reproduction

Comparable to scleractinians, sexuality in octocorals is highly conserved. Gonochorism, in which mature colonies exhibit male or female reproductive tissues exclusively, predominates in octocorals, with 89% of investigated species exhibiting this form of sexuality (Kahng et al., 2011). In contrast to scleractinians, hermaphroditism, in which both male (spermaries) and female (oocytes) gonads co-occur in the same colony, is relatively rare among octocorals. Octocoral species can also be mixed or parthenogenetic; mixed species have a regular incidence of gonochoric and hermaphroditic colonies and in parthenogenetic species, oocytes produced by female colonies develop into viable planula larvae without fertilization (Kahng et al., 2011).

Similar to many other species of Anthozoa, octocorals are able to reproduce both sexually and asexually. Colony growth of octocorals is a mode of asexual reproduction via budding of polyps. In addition, octocorals exhibit various mechanisms of vegetative propagation (e.g., fission, fragmentation, polyp detachment, branching growth, and stolonal growth), and for some species this asexual proliferation can support high population growth rates (Lasker, 1988; Kahng et al., 2011). These forms of asexual reproduction occur frequently in many shallow-water octocoral species, however, they have yet to be observed among deep-sea octocorals, as knowledge about reproductive processes in deep-sea octocorals is scarce in general (Watling et al., 2011).

There are two basic types of sexual reproduction in octocorals; broadcast spawning and brooding. In broadcast spawning, colonies release gametes into the water column, and fertilization and planktonic development take place in the water column. Two pathways can occur in brooding, either (1) fertilization of eggs occurring in the maternal colony and embryos developing internally in autozooids, siphonozooids or specialized brood chambers (internal brooding) (Kahng et al., 2011; Watling et al., 2011), or (2) eggs or zygotes are released by the polyps but attach on the adult colony surface where they then further develop prior to release (external surface brooding) (Benayahu and Loya, 1983; Kahng et al., 2011; Watling et al., 2011).

In general, studies on shallow-water octocoral species demonstrate that the frequency of broadcast spawning versus brooding varies within Octocorallia by taxonomic order (Watling et al., 2011). Sea pens reproduce exclusively by means of broadcast spawning, whereas shallow water soft coral and gorgonian species appear to be more flexible concerning reproductive strategies, exhibiting broadcast spawning and brooding (Watling et al., 2011), sometimes even within the same genus, as seen in *Alcyonium* (McFadden et al., 2001).

Octocoral Identification

Unlike reef-building stony corals (Scleractinia), the large majority of octocorals do not produce a massive skeleton (but see Fig. 2A), and instead most species produce calcium carbonate skeletal structures consisting of numerous separated microscopic components called sclerites (Fig. 2B). Sclerites provide support and defense from predators and demonstrate a high variability in shape, coloration, surface morphology, and size. These small skeletal elements are formed by poly-crystalline calcite aggregates (a type of calcium carbonate, CaCO_3) deposited on a fine horny fibrous matrix constructed of proteins. Many taxa have an axial skeleton that consists of a dense brown calcified, horn-like substance, gorgonin (a form of collagen) (Jeyasuria and Lewis, 1987), or of sclerites that are densely packed together. This axial structure is what distinguishes the gorgonians from other octocorals (Samimi-Nami and Ofwegen, 2012), and is the main support structure of the gorgonian polyp colony (Jeyasuria and Lewis, 1987).

Octocoral taxonomy has traditionally been based on the study of the shape of the colonies, and the color, size and form of sclerites (Bertson et al., 2001). The relative proportions of the different sclerite types are used as an identification method and have constituted the main criteria for the delimitation of species (Aharonovich and Benayahu, 2012).

The important role of sclerites in octocoral taxonomy was not recognized until the late 1800s and early 1900s, as microscopes were much less advanced at the time. Subsequently, early species descriptions did not include sclerite illustrations, or included only minimal details, hampering the present-day taxonomy and systematics of Octocorallia, as many of these earlier species descriptions often fit multiple species within a specific genus or family.

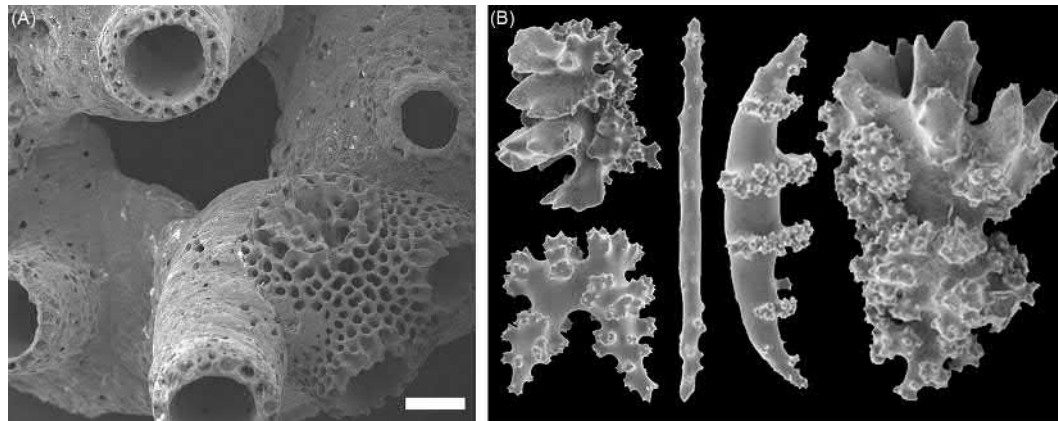


Fig. 2 Scanning electron microscope images of (A) *Nanipora kamurai* aragonite skeleton from Dongsha Atoll (Taiwan), scale bar 0.5 mm. Photograph: YW Lau. (B) Some sclerite types seen in plexaurid species, from left to right: foliate spheroid (top left), butterfly (bottom left), rod, scaphoid, unilaterally foliate club (sclerites not to scale). Photographs: FR Stokvis.

However, recent papers have shown that octocoral species without sclerites are not rarities, and to date, the absence of sclerites or other calciferous skeletal parts have been found within seven octocoral families: Acanthoaxiidae, Acrossotidae, Cornulariidae, Dendrobrachiidae, Alcyoniidae, Clavulariidae, and Xenidiidae (Alderslade and McFadden, 2007, 2011; López-González et al., 1995; Benayahu et al., 2017a; Lau and Reimer, 2019). The lack of sclerites has important implications for future studies, as they currently represent one of the major diagnostic features of the group (Alderslade and McFadden, 2011; Benayahu et al., 2017a; Lau and Reimer, 2019). Despite a long history of research, it is clear more work on morphological diagnostic features is needed.

Molecular Markers and Phylogenetic Analyses

The classification of many morphologically difficult to identify octocoral groups requires detailed species descriptions and identification keys. However, identification of octocorals at fine taxonomic levels (e.g., genus, species) is usually hampered by the lack of diagnostic characters (Bayer, 1961; Sánchez, 2007). Since 1855, when Valenciennes first investigated octocoral sclerites, the comparative assessment of sclerite diversity has represented the preferred strategy among octocoral taxonomists. However, in recent years, the use of DNA sequences and phylogenetic analyses has become an alternative and important method for the identification and systematics of these organisms.

The monophyly of Octocorallia and its sister relationship to Hexacorallia was confirmed by early molecular phylogenetic studies, which used partial or complete 18S ribosomal DNA sequences (Bridge et al., 1995; Song and Won, 1997; Berntson et al., 1999; Kim et al., 1999; Won et al., 2001; McFadden et al., 2010), partial (Chen et al., 1995) or complete 28S rDNA sequences (McFadden et al., 2010), and partial mitochondrial 16S rDNA sequences (France et al., 1996; McFadden et al., 2010). A short fragment of the mitochondrial gene cytochrome *c* oxidase subunit 1 (Cox1) has been proposed as standard molecular marker for metazoans (Hebert et al., 2003). Although this marker is still widely considered for molecular analyses, its use has shown limitations for anthozoans in general (Shearer et al., 2002; Huang et al., 2008) and specifically for octocorals (McFadden et al., 2011), making Cox1 generally unsuitable as a species-specific marker. On the other hand, the octocoral specific mitochondrial MutS-like protein (mtMutS) has been extensively used for molecular and phylogenetic analyses, providing significant insights into the systematics of the subclass; the unique protein-coding gene provides a synapomorphy for the Octocorallia (McFadden et al., 2010), as it has not been found in the mitochondrial genomes of other metazoans (Culligan et al., 2000; McFadden et al., 2010). Besides mitochondrial DNA, Chen et al. (2009) showed that the nuclear genome of some anthozoans may evolve up to five times faster than the mitochondrial genome, suggesting therefore the need of exploring the nuclear and mitochondrial DNA regions. Nuclear markers such as ATP Synthetase Subunit α (ATPS α), Internal Transcribed Spacers (ITSs) and 28S ribosomal DNA (28S rDNA) have been recently considered for biodiversity assessments and taxonomic surveys of different octocoral taxa (Haverkort-Yeh et al., 2013; McFadden et al., 2014).

The phylogenetic trees published so far, which are mainly based on a handful of mitochondrial and nuclear loci, have shown some topological incongruences. For instance, Berntson et al. (2001), using 18S rRNA, recovered Pennatulacea as polyphyletic, whereas McFadden et al. (2006), with two mitochondrial protein-coding genes (Nad2 and mtMutS), found Pennatulacea monophyletic and placed within alcyonaceans. In the same study, the authors recovered most of the alcyonacean subordinal groups as polyphyletic. Recently, studies on South African stoloniferans (McFadden and van Ofwegen, 2012), deep-sea calcaxonians (Pante et al., 2012) and shallow water scleraxonians (Cairns and Wirshing, 2015; Conti-Jerpe and Freshwater, 2017) have corroborated McFadden et al.'s results, and it is clear that many octocoral groups need taxonomic revisions based on molecular results.

Besides the standard molecular markers, recently, the sequencing of complete mitochondrial genomes has allowed exploration of gene arrangements and/or gene novelty (Brockman and McFadden, 2012; Hogan et al., 2019), testing the use of indel-rich regions

and variable traits as alternative DNA barcodes (Poliseno et al., 2017a), and inferring robust phylogenies using extended coding-protein gene datasets.

Although molecular analyses are now considered standard procedures in taxonomy, technologies such as Sanger sequencing are being quickly replaced by high-throughput sequencing applications, which allow generation of much larger datasets in a short time and with reduced costs. Next generation sequencing applications in octocoral taxonomy include the use of RAD-Seq for species delimitation (Pante et al., 2015; Herrera and Shank, 2016), the recovery of mitogenomes for evolutionary studies (Figueroa and Baco, 2015; Poliseno et al., 2016, 2017b), and, as recently tested by Quattrini et al. (2018), the use of hundreds of ultra-conserved elements and exon loci for deep phylogenomic analyses.

Future octocoral taxonomy will undoubtedly build upon a combination of molecular and more traditional morphological techniques (Conti-Jerpe and Freshwater, 2017). However, the lack of important morphological features, such as sclerites, hold implications for future studies, and thus emphasizes the need for new molecular techniques. For octocorals in particular, the development of reliable species-specific molecular markers is needed. Additionally, the use of extended datasets including mitochondrial and nuclear traits as well as hyper-variable regions could provide better resolution, allowing more reliance on molecular data when morphological information is scarce.

Marine Biogeography, Ecology and Symbioses

Octocorals have been recorded across a wide range of depths, from littoral waters down to deep-sea abyssal depths (deepest octocoral reported *Thouarella vitjaz* Zapata-Guardiola & López-González, 2012 at 6400 m), as well as from the tropics to the arctic regions and from all oceans worldwide (Van de Water et al., 2018). The highest diversity of octocorals has been observed in the shallow coral reefs of the Indo-Pacific (Pérez et al., 2016; Van de Water et al., 2018). In the deep sea, pennatulaceans and gorgonians are the predominant octocoral groups and their biogeography has been recently reviewed by Watling et al. (2011).

Octocorals are such a large and diverse group that marine biogeographical studies have often focused on either specific taxa or regions. For instance, Williams (1992) investigated the octocorallian fauna of South Africa, reporting on the diversity, bathymetric and geographic distribution and abundance of different groups (i.e., soft corals, gorgonians and sea pens) in the Atlantic and Indo-Pacific waters. Vargas et al. (2008) analyzed the distribution patterns of a widespread and species-rich eastern Pacific octocoral genus (*Pacifigorgia*) and reconstructed the geographical distribution, using the data available from museum collections, of most of the species until then described. Recently, the use of DNA sequences allowed reconstruction of the historical biogeography of the genus *Paramuricea* in eastern Atlantic and Mediterranean (Poliseno et al., 2017a), and to estimate the geographical ranges and regional endemism of Indo-Pacific members of the family Xenidiidae (McFadden et al., 2019). Octocoral distribution is often influenced by various environmental parameters (Yesson et al., 2012). However, the conspicuous presence of octocorals in nearly all benthic marine habitats is an indication of the adaptive nature of this taxonomic group (Van de Water et al., 2018). Octocorals play a crucial role in shallow water coral reef communities, as many sessile marine organisms contribute to the high marine biodiversity by acting as host for associated organisms (Hoeksema, 2017; Reijnen et al., 2011). Octocoral communities create three-dimensional networks, providing critical habitat and shelter for associated organisms and other reef dwellers (Wirshing et al., 2005; Sánchez et al., 2003; McFadden et al., 2006; Reijnen et al., 2010), fostering total reef biodiversity. Sea pens, in particular, provide habitat in sandy and muddy locations from shallow to deep waters. Soft corals, gorgonians (including sea fans) act as hosts for organisms such as fish, molluscs and crustaceans. These organisms can use their hosts, for example, as food sources or simply as shelter against predators. An example is the slender filefish, *Monacanthus tockeri*, which can be seen in between the branches of octocorals in the Caribbean, using them as background camouflage for protection (Ben-David and Kritzer, 2005; Sánchez, 2017) (Fig. 3A and B). Octocorals have potentially vulnerable soft tissue yet they appear to be largely free from predation (Pawlik and Fenical, 1992). Sclerites in the soft tissue seem to be the main contributor to defense. In addition to skeletal support, sclerites fulfill a second role as structural defense against predators (West, 1997). However, the bearded fireworm, *Hermodice carunculata*, is an exception and also feeds on soft corals (as well as hard corals, zoantharians, anemones and hydrocorals) by engulfing entire polyps or on entire branch endings by removing the soft tissue (Lewis and Crooks, 1996; Souza et al., 2007). Additionally, gastropods such as ovulid snails (Pawlik and Fenical, 1992) and coralliophilid snails (Meulens, 2012; Del Monaco et al., 2010) can cause tissue damage (West, 1997); rather than killing their host, small quantities of tissue are removed. Colonial invertebrates are only rarely killed by their predators and, due to their modular body plan and capacity for regeneration, they may be little impaired by attacking predators. It should be noted that the wounds resulting from consistent tissue removal, which bares the underlying axial skeleton, can be colonized by algae, causing inhibition of tissue regeneration (Harvell and Suchanek, 1987).

Epibiont appearance and life history are often very well adapted to their specific octocoral host and allow them to live in symbiosis (Reijnen et al., 2011, 2014). Relationships are often so complex that octocorals and their symbionts can act as model organisms to study the evolution of defense strategies (Reijnen et al., 2010, 2011, 2014). Some host-symbiont relationships can be very intricate and one such example are diminutive seahorses (*Hippocampus* spp.), collectively called pygmy seahorses (Lourie and Kuitert, 2008; Reijnen et al., 2011). Some species of the miniature tropical fish, *Syngnathi*, can live in very close association with specific octocorals, mainly sea fans (e.g., *Muricella*, *Annella*, *Acanthogorgia* spp.). For instance, pygmy seahorse species have adapted their coloration and body ornamentation in the form of tubercles to exactly match the shape of the polyps of their gorgonian hosts (Lourie and Randall, 2003) (Fig. 3C and D). The small sizes of pygmy seahorses (the smallest species is around 13.3 mm in length,



Fig. 3 In situ photographs of (A and B) the slender filefish *Monacanthus tuckeri* seeking shelter in the branches of *Plexaurella* sp. Photographs: YW Lau. (C) The pygmy seahorse *Hippocampus barganti* on *Muricella* sp. Photograph: FR Stokvis. (D) *Hippocampus* sp. on *Anella* sp. Photograph: FR Stokvis. (E) The ovulid snail *Pseudosimnia culmen* on *Dendronephthya* sp. Photograph: BT Reijnen. (F) The ovulid snail *Prosomnina draconis* on *Melithaea* sp. Photograph: BT Reijnen.

Hippocampus denise Lourie & Randall, 2003) combined with their excellent camouflage suggests that these animals are easily overlooked and therefore poorly observed, as finding them is usually challenging (Lourie and Randall, 2003; Lourie and Kuitert, 2008).

Little information is available on host specificity and possible intermittent occurrence on octocoral hosts for most pygmy seahorse species (Goh et al., 1999; Reijnen et al., 2011). In addition, host gorgonians are often difficult to identify due to a lack of clear morphological diagnostic characters (e.g., *Annella* spp.). Therefore, to fully understand the intricate relationships between host and symbiont, future studies on pygmy seahorses should also emphasize attention on their octocoral host (Reijnen et al., 2011).

Ovulid snails are another example of obligate associations with cnidarians, with most examples occurring associated with octocorals (Reijnen et al., 2010). Ovulid snails are one of the few parasitic organisms that feed on octocorals and are commonly found on soft corals. Ovulid species have a mantle that covers the shell and are well camouflaged. Like the pygmy seahorse, the mantle of the snails can have bright colors and structures that resemble the branches of their octocoral host (Reijnen et al., 2011) (Fig. 3E and F).

Octocorals do not only host organisms on their surface, but also act as host to organisms that find a home within their tissues. Many octocorals host unicellular algae, dinoflagellates of the family Symbiodiniaceae, which are also called zooxanthellae (Van Oppen et al., 2005). Previous studies investigating the diversity of octocoral-associated zooxanthellae, have found that octocorals harbor five of the seven recently revised genera (*Symbiodinium* Freudenthal, 1962 (formerly "Clade A"), *Breviolum* J.E. Parkinson &

Lajeunesse, 2018 (former “Clade B”), *Cladocopium* Lajeunesse & H.J. Jeong, 2018 (former “Clade C”), *Durusdinium* Lajeunesse, 2018 (former “Clade D”), *Gerakladium* Lajeunesse, 2018 (former “Clade G”) (Franklin et al., 2012; Lajeunesse et al., 2018; Van de Water et al., 2018). The majority of investigated octocorals harbored only a single genus, indicating geographical patterns; *Cladocopium* being dominant in the Pacific Ocean and the Red Sea (Van Oppen et al., 2005; Goulet et al., 2008a,b), *Durusdinium* in Caribbean octocorals (Goulet and Coffroth, 2004; Goulet et al., 2008a,b) and *Symbiodinium* in Mediterranean octocorals (Forcioli et al., 2011). Octocoral-Symbiodiniaceae relationships have received far less attention than those of scleractinian corals and thus there are critical gaps that remain in the understanding of the functional and ecological significance of these symbioses (Van de Water et al., 2018). These obligate mutualistic symbioses play an important role in extending available energy resources and thus potentially influence biodiversity on reefs (Van Oppen et al., 2005; Fabricius and De’ath, 2008).

Economic and Environmental Importance

The majority of taxa from which recent new marine natural products (MNPs) have been reported since 1990 belong to the phyla Porifera (49%) and Cnidaria (28.6%) (Leal et al., 2012). Approximately 99% of the new marine natural products from Cnidaria come from anthozoan species. One of the main sources of these new marine natural products in Anthozoa are octocorals (Leal et al., 2012). Approximately 60% of their extracts are bioactive molecules with medicinal potential (Coll, 1992; Khalesi, 2008), and octocorals can therefore be considered as a promising group for pharmacological uses. Many octocoral species have biologically active metabolites; they can have antibacterial, anticoagulant, antifungal, anti-inflammatory, antimalarial, antiprotozoal, antituberculosis and antiviral properties (Mayer et al., 2010, 2011). These metabolites can be precursors for potential medicines, which has been proven for prostaglandins (Gerhart, 1986; Sammarco and Coll, 1992; Stanley-Samuelson, 1994; Almeida et al., 2014; Weil et al., 2016).

The soft coral *Sinularia flexibilis* (Quoy & Gaimard, 1833) contains highly potent bioactive compounds (secondary metabolites), many of which have important ecological roles in the defense against predation and competition for space (Khalesi, 2008), but have been proposed to be of potential use in the development of antibiotics (Clark, 2000), natural sunscreen and cosmetic products (Volkman, 1999), or even promising anticancer drugs (Weinheimer et al., 1977; Yates and Carlson, 1992). *Antillogorgia elisabethae* (previously assigned to *Pseudopterogorgia*) is one of the few octocoral species that currently has commercial use as it is harvested from the Little Bahama Bank in the Bahamas (Lasker and Porto-Hannes, 2015; Williams and Chen, 2012). Annual harvest data are not publicly available, but the value of the fishery has been estimated to be \$3–4 million (Bruckner, 2002) and the demand for pseudopterogins is estimated at 30–45 t per year (Puyana et al., 2004). Sometimes, the economic benefits from such developments are more productive than local fishing industries (Fabricius and Alderslade, 2001).

Additionally, some octocorals are commercial resources, with some of these well-known since antiquity. For example, the red skeleton of the precious coral genera *Corallium* and *Paracorallium* are very much sought after and have been extensively used for crafts (Ascione, 1993). The history of the utilization of red coral *Corallium rubrum* goes back as early as 30,000 years ago, in which peoples used the skeleton for jewelry, as currency, and as religious talismans (Tescione, 1973; Tsounis et al., 2007). Commercial harvesting of red corals began in the 19th Century (Tsounis et al., 2007) and has a history of heavy overexploitation, raising concerns about the sustainability of collecting precious corals (Tsounis et al., 2013). The regeneration rate of red coral colonies is slow as they are long-lived and slow-growing apex marine organisms (Bramanti et al., 2014). Therefore, Corallidae species are fragile resources vulnerable to human influences (Tsounis et al., 2010). Now, *C. rubrum* is still threatened and has been assigned an endangered status by IUCN (Garrabou et al., 2015). As well, the trade of *C. elatius*, *C. japonicum*, *C. konojoi*, *C. secundum* are controlled legally by annex III of CITES (Convention of International Trade of Endangered Species), are Helioporidae spp. and Tubiporidae spp. Besides from precious corals, members from families Primnoidae and bamboo corals from the family Isididae are also commonly used in the jewelry industry (Tsounis et al., 2010).

Coral reef related tourism is a fast-growing industry and the beauty of octocorals has become a main attraction in scuba diving, and in particular octocorals can form wide “gardens” and beautiful scenery, attracting divers from all around the world. However, tourism on and close to coral reefs can also have negative impacts and cause both direct and indirect pressures on these same reef communities and threaten reef communities (Coma et al., 2004): e.g., degradation and lots of marine life (Hasler and Ott, 2008; Albuquerque et al., 2014; Lamb et al., 2014; Spalding et al., 2017), as well as indirect risks due to poorly planned coastal development, including dredging, building on intertidal spaces, and increases in pollution and solid waste (Davenport and Davenport, 2006; Wongthong and Harvey, 2014; Liu et al., 2012; Spalding et al., 2017). However, the risks from coral reef related tourism are thought to be less than those of fishing, land-based run-off, or coral bleaching (Harriott, 2004; Spalding et al., 2017). In some cases, tourism may even be helpful in reducing certain threats, by offering financial or social incentives for sustainable management (Cater and Cater, 2007; Cruz-Trinidad et al., 2009; Arizpe and Covarrubias, 2010; Spalding et al., 2017), raising environmental awareness (Ong and Musa, 2012), as well as encouragement of coral reef restoration (Dearden et al., 2007).

Octocoral Disease

Under rapid climate change and increasing human pressure, coral reefs are facing dramatic increases in coral-bleaching and disease occurrence leading to unprecedented mortality events (Precht et al., 2016) across a large spectrum of reef organisms (Harvell et al.,

1999), including octocorals. Among the cnidarians, scleractinians and octocorals appear to be among the most disease-impacted groups (Weil and Rogers, 2011).

The first case of an octocoral disease was documented by Morse et al. (1977) in Bonaire and Trinidad in the Caribbean. Populations of the sea fan *Gorgonia ventalina* showed tumor-like growths leading to tissue death and erosion of the affected colony. An alga was identified as the causative agent and it was mentioned that all the observations of tumors occurred on impacted reefs exposed to environmental stress (Morse et al., 1977). However, recently, these purple spots have been shown to be caused by parasitic copepods (Ivanenko et al., 2017). Subsequently, in 1982, the first mass-mortality event involving a Caribbean octocoral, *Gorgonia flabellum*, was reported along the coast of Costa Rica (Guzman and Cortes, 1984); this was the first epizootic in a long series of disease outbreaks. In the 1990s, reports of new coral diseases and devastating disease outbreaks proliferated in the literature. In the Caribbean, thousands of sea fan coral colonies died from the fungal disease *Aspergilliosis* (Smith et al., 1996). Later, in the late 1990s, disease outbreaks affected octocorals in the Great Barrier Reef (Willis et al., 2004). Temperate populations have not been spared and disease outbreaks have been documented in the Mediterranean Sea (Cerrano et al., 2000) and in the cold waters of the English Channel (Hall-Spencer et al., 2007). The last two decades have seen the Eastern Pacific (Sánchez et al., 2014) and the subtropical Atlantic Ocean (Cassola et al., 2016) added to the long list of geographical areas where octocoral diseases seem to thrive.

The latest review on octocorals diseases reports at least 19 known diseases affecting around 42 species worldwide (Weil et al., 2016). In Weil et al.'s (2016) review, disease was defined as any impairment of the normal structure or function of an organism and includes responses to biotic agents such as viruses, fungi or bacteria or environmental factors (Work and Aeby, 2006; Weil et al., 2016).

Investigating marine diseases is not an easy task. Knowledge of marine bacteria is very limited and marine bacteria are very difficult if not impossible to culture in the laboratory (Joint et al., 2010). As a consequence, to date causative agents have been identified for only eight octocoral diseases and these include bacteria, cyanobacteria, virus, fungi, filamentous algae, and parasitic copepods (Weil et al., 2016). The terrestrial fungus *Aspergillus* spp. and the bacterium *Vibrio* spp. are infamous for the death of millions of octocoral colonies in the Caribbean (Smith et al., 1996; Geiser et al., 1998) and the Mediterranean Sea (Bally and Garrabou, 2007), respectively. One major driver common to all diseases affecting octocorals appears to be high seawater temperatures (Van de Water et al., 2018), which have been positively associated with all major massive mortality events. However, whether high temperatures increase pathogen virulence or decreases host resistance, or a combination of both, remains to be determined.

Bleaching, i.e., the loss of coloration due to the loss of endosymbiotic Symbiodiniaceae in response to elevated temperature, falls within the definition of disease (Weil et al., 2016). Mass bleaching and mortality events have been reported worldwide in octocoral communities, and as with zooxanthellate scleractinian corals are due mostly to sustained periods of extreme heat, in the Caribbean and the Pacific during El Niño events in 1998, 2005, and 2010 (Loya et al., 2001; Strychar et al., 2005; Goulet et al., 2008a,b; Slattery et al., 2019), and in the Mediterranean Sea during the 2003 heat wave (Garrabou et al., 2009). In addition, bleaching is known to impair anthozoan physiology and thus increase vulnerability to microbial diseases (McClanahan et al., 2009).

Compared to scleractinians, octocorals appear to have higher resistance to bleaching due to their lower dependency on dinoflagellate symbionts (Fabricius and Klumpp, 1995). However, a recent study by Baker et al. (2015) demonstrated that not all octocoral species can afford to lose their symbionts. There have already been cases in which reef ecosystems have undergone a so-called phase shift from a hard coral-dominated state toward a higher abundance of soft corals (Van de Water et al., 2018). However, additional studies are necessary to investigate the energetic needs of octocorals and their resilience and recovery subsequent to bleaching events (Van de Water et al., 2018).

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Among all octocorals, gorgonians are clearly the most affected by abnormal health conditions, but they have also been observed on soft corals. There have been no records of diseases affecting Pennatulacea, *Heliopora* or the suborder Stolonifera thus far. In the Caribbean, the relative abundance of octocorals has increased over the years as a consequence of the decline of scleractinian species (Edmunds and Lasker, 2016), and in several places, a gradual transition from scleractinian to soft corals has occurred (Lenz et al., 2015). Therefore, in the context of climate change, the increasing susceptibility to disease of octocoral populations may have important consequences in terms of community composition structure and function, and in terms of biodiversity, and therefore also with regards to economic and ecological services. Despite the mass mortality events recorded in the past, the consequences of such losses are still poorly understood. However, recent studies conducted in the Mediterranean Sea have demonstrated that gorgonians can influence the composition and abundance of vagile assemblages (Ponti et al., 2016). In Okinawa, Loya et al. (2001) reported drastic changes in soft coral community structures following coral bleaching, including a notable decrease in soft coral cover as well as a shift in species dominance due to differential susceptibilities of bleaching. In the Mediterranean Sea, the disappearance of gorgonians may also cause a shift from important bio-constructors such as crustose coralline algae to filamentous algae assemblages (Ponti et al., 2014). This would in turn impair the complexity and resilience of these fundamental bio-constructions and their ecosystems (Ponti et al., 2014).

Conclusions and Future Directions

Although octocorals are affected by pollution, diseases and global climate change (Van de Water et al., 2018) and their ecological importance and role in coral reef communities is increasingly being emphasized (Ruzicka et al., 2013; Tsounis and Edmunds, 2017), the research attention they have received is still significantly less when compared to that of scleractinian corals (Prada et al., 2010; Van de Water et al., 2018).

A better knowledge of octocorals becomes especially relevant in light of the phase-shifts that coral communities are facing under increased climate change and global warming and other anthropogenic influences. Basic knowledge about octocoral taxonomy and their systematics have yet to be unraveled, and the development of novel methods to achieve this goal are yet to be accomplished. Taxonomic documentation is key to communicating biological information and establishing biodiversity. Combining it with ecology and knowledge on the functional roles of octocorals on coral reefs could contribute in the development of strategies in building resilience in coral reef communities (Van de Water et al., 2018).

Acknowledgments

We would like to thank Frank R. Stokvis (Naturalis Biodiversity Center) for providing scanning electron microscope (SEM) images of sclerites of plexaurids and in situ photographs of pygmy sea horses on octocorals. We thank Dr. Bastian T. Reijnen for permission to use in situ photographs of ovulid snails on octocorals.

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Marine DNA Metabarcoding

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Abstract

DNA metabarcoding is now a well-established method that uses DNA sequencing techniques and bioinformatics to identify a wide variety of species from mixed samples, such as gut content and sea water samples. A major benefit of this method is its sensitivity, which allows the detection of the presence of animals in the sampled environment, without having to collect or kill specimens. It is thus a great biomonitoring tool to assist in marine conservation and management. This article provides a brief overview of DNA metabarcoding touching on the essential elements that should be considered when using this method (e.g., marker regions and DNA database coverage) and how it is being incorporated into marine research (e.g., detecting invasive species).

What Is DNA Metabarcoding?

DNA metabarcoding uses high-throughput DNA sequencing (HTS) for the taxonomic identification of multiple species from a mixed sample. It is an extension of the highly popular “DNA barcoding” approach, which has been used very successfully to identify individual specimens to species level ([Kress and Erickson, 2008, 2012](#); [Kress et al., 2015](#)). DNA metabarcoding can have considerable advantages over traditional morphological identification, as it can be more rapid, accurate, sensitive, and cost-effective. The types of mixed samples that can be analyzed using this method include seawater, fecal matter, mucus, sediment, and gut content. DNA metabarcoding thus allows for detection of a species without directly sampling it. Mixed samples are dealt with in two ways: either in a targeted approach whereby organisms, or tissues, of interest, are isolated from the mixed sample prior to DNA extraction; or in a nontargeted approach whereby all DNA is extracted from the entire mixed sample ([Fig. 1](#); [Deiner et al., 2017](#); [Nielsen et al., 2018](#); [Taberlet et al., 2018](#)).

The laboratory analysis portion (e.g., sample dissection, DNA extraction and DNA amplification) of DNA metabarcoding can have a great influence on the end results, and each step (starting from sample collection and preservation) that leads to the final identifications should be considered critical and be undertaken in a uniform manner. DNA extraction is the first molecular step in the DNA metabarcoding process and, although not essential, specialized DNA extraction kits can be very beneficial, as they have been developed to suit different source material (e.g., seawater or fecal matter; [Hermans et al., 2018](#); [Jeunen et al., 2019](#)). DNA degradation is highly likely in environmental samples and thus extracting high molecular weight DNA from these samples is generally unlikely. This means that targeting a 300 base pair (bp) portion of a marker (barcode) region is likely to be more successful than targeting a 1000 bp portion of the same marker region. Thus, choices of marker regions and primers are critical ([Alberdi et al., 2018](#)). Marker regions selected for DNA barcoding are generally housekeeping genes, such as mitochondrial DNA cytochrome oxidase I (COI) or 16S/18S ribosomal RNA (rRNA) genes. These gene regions have been largely conserved in many species over time, but also have intervening regions where the DNA sequences have diversified sufficiently to enable discrimination among closely related species. Thus, these regions can be seen as a unique code for identifying species and are known as DNA barcodes. These regions are targeted during DNA amplification in a process known as polymerase chain reaction (PCR) and when mixed samples are used, such as in DNA metabarcoding, a pair of universal primers needs to be used in order to amplify the targeted gene region from a wide variety of species that may be present in the sample.

Primers are DNA oligonucleotides, which are short nucleic acid sequences that are synthesized in the laboratory. They each anneal to a specific location on the DNA during PCR, and provide a consistent starting point for DNA replication. Universal primers have been designed to amplify the same DNA region from diverse species in a single PCR. Because the most common current methods of HTS (e.g., Illumina MiSeq™ platform) provide shorter DNA sequence reads (currently 2×300 bp length) than traditional Sanger sequencing methods (up to 1000 bp), specialized PCR primers are required for DNA metabarcoding that amplify much shorter DNA fragments than the traditional barcoding genes. Although this brief overview of DNA metabarcoding describes PCR-based methods, it should be noted that PCR-free methods can also be used (e.g., shotgun sequencing

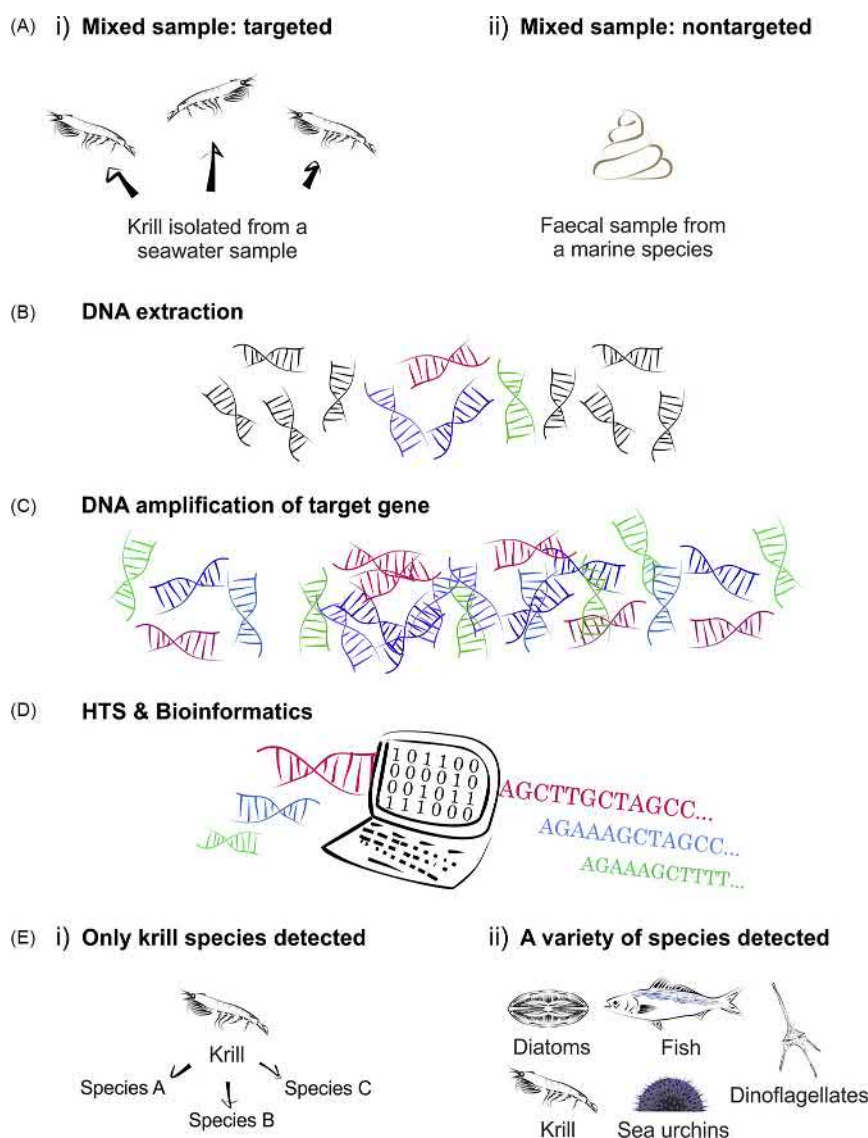


Fig. 1 An illustration of a targeted and nontargeted DNA metabarcoding approach. (A) Targeted DNA metabarcoding (i) is a process whereby organisms of interest (e.g., krill) are first isolated from the mixed samples (e.g., seawater), whereas in nontargeted DNA metabarcoding (ii) there is no selection from the raw samples (e.g., feces). (B) DNA extractions isolate the available DNA in the mixed samples. (C) Polymerase chain reactions (PCRs) amplify only the DNA from the marker region of interest (e.g., COI). (D) High-throughput DNA sequencing (HTS) provides the raw DNA sequences of the PCR products. The raw sequencing data is filtered using a bioinformatics pipeline (e.g., Qiime 2). Only the most reliable sequences are retained and are generally clustered into highly similar groups of sequences (molecular operational taxonomic units; MOTUs or OTUs). Each OTU's consensus sequence is then matched to a reference sequence from a chosen DNA database (e.g., Genbank or Midori), thus assigning taxonomic identities to the OTUs. (E) In a targeted approach it is expected to only identify species relevant to the organisms that were selected (i), but from a nontargeted approach it is expected that a wide variety of organisms may be identified (ii).

and mitochondrial enrichment; Zhou et al., 2013; Tedersoo et al., 2015; Liu et al., 2016; Kimmerling et al., 2018; Mariac et al., 2018; Jo et al., 2019; Stat et al., 2019).

Once DNA amplification has been undertaken for the specific marker region/s of interest, then the PCR products are sequenced on a next-generation sequencing platform (e.g., Illumina MiSeq™). The raw HTS data undergoes analyses where the sequences are filtered for quality, and highly similar filtered sequences are clustered together and consensus sequences are derived. The different consensus sequences are known as molecular operational taxonomic units (MOTUs or OTUs) and are compared to reference DNA databases in order to assign taxonomic identity to the OTUs. The quality filtering and clustering is undertaken using bioinformatic pipelines; open-source pipelines include Qiime 2 (Bolyen et al., 2019), Mothur (Schloss et al., 2009), and Obitoools (Boyer et al., 2016). Amplicon sequence variant (ASV) methods can also be used, instead of using OTU methods, and may be the preferred method in future, but detailed discussion of this topic falls outside the scope of this brief overview (Callahan et al., 2017).

The DNA sequence reference databases may be noncurated, i.e., a public repository with little taxonomic quality control, such as the National Center for Biotechnology Information (NCBI) Genbank database (Benson et al., 2013). Alternatively, it may be curated with only selected sequences that meet various taxonomic quality controls, such as Midori (Machida et al., 2017) which is a COI database, and SILVA (Quast et al., 2013) which is a small and large subunit rRNA database. Marker choice for studies is usually influenced by database coverage of target organisms and the resolution that it may provide (Alberdi et al., 2018; Nielsen et al., 2018). For example, many large metazoans are best discriminated using the mitochondrial DNA COI barcode region, whereas rRNA regions are often best suited to microorganisms (van der Reis et al., 2018).

Generally, multiple DNA extractions, multiple PCRs of those DNA extractions, and multiple DNA markers are all beneficial when wanting to identify the most complete set of taxa possible from a mixed sample. The cost can be minimized for sequencing by pooling (equimolar concentrations) across PCR replicates for a single sample per gene and then pooling again across different genes for a single sample. However, this strategy is dependent on the question of interest, the diversity within the sample, and the time and financial constraints of the study at hand. Overall, DNA metabarcoding is applicable in multiple areas of research involving community ecology and can provide sensitive biodiversity data that was previously inaccessible.

Applications of Marine DNA Metabarcoding

Many of the deepest parts of the oceans are yet to be explored and those areas that have been explored are still poorly understood. This is largely due to the difficulties of observing marine life directly in its natural environment, compared to the more easily observed terrestrial life, thus making the task of understanding marine ecological communities more complex.

Marine biodiversity characterization using DNA metabarcoding, over a period of time, can assist in biomonitoring (Valentini et al., 2016; Stat et al., 2017; Cahill et al., 2018; Cristescu and Hebert, 2018; Siegenthaler et al., 2018; Taberlet et al., 2018). Biomonitoring is mainly used in two types of applications which are very closely linked, the theoretical understanding of ecological processes and the practical application to marine conservation and management. This information can indicate the health of a community and if it may be under threat, such as the absence of species of conservation interest, or the presence of invasive species. There is potential to assess relative abundance of species using DNA metabarcoding, although the way to determine abundance should be approached with caution (Pompanon et al., 2012; Thomas et al., 2016; Taberlet et al., 2018; Deagle et al., 2019; Lamb et al., 2019; Piñol et al., 2019). One of the most beneficial aspects of incorporating the use of DNA metabarcoding as a biomonitoring tool is that more detailed diversity information is gained at each time point, and thus when repeated over time changes can be much more accurately assessed (Jarman et al., 2018). These changes may relate to the progress of restoration of marine areas, monitoring fluctuations in marine protected areas or marine areas that are thought to be affected by human activities, such as oil drilling.

Some examples of the use of DNA metabarcoding in ecological processes would include how ocean warming and climate change may be affecting pelagic food webs. In addition to detecting the presence of species in the environment, DNA metabarcoding can also be used on animal gut contents to provide information on prey composition (Young et al., 2015). It can also be used in understanding what impacts invasive species may have on native species, by identifying and monitoring the invasive species' diet to see how it may impact the native community in future (Harms-Tuohy et al., 2016). The management of fisheries includes both ecological processes and marine conservation and management. The reconstruction of food webs and thus identifying trophic levels and keystone predators (e.g., using DNA metabarcoding on gut content or water samples) is critical for sustainable fisheries management (Riccioni et al., 2018) and pathogenic microorganisms detected may even indicate the health of the community and threats to commercial species. Moreover, DNA metabarcoding could be coupled with more traditional fisheries management (e.g., traditional net surveying) and marine monitoring in general, to assess species distribution (Malviya et al., 2016; Bakker et al., 2017; Cahill et al., 2018; Deiner et al., 2017; Lobo et al., 2017; McInnes et al., 2017; Grey et al., 2018; Siegenthaler et al., 2018). Siegenthaler et al. (2018) demonstrated how DNA metabarcoding can complement traditional net surveys, by using a marine benthic generalist's gut contents to detect twice as many fish species when compared to traditional net surveys. It has also been used to assess the biological impacts that offshore activities, such as gas or oil drilling, may have on the biodiversity in that area and to identify potential taxa that could be utilized for assessing environmental health (bioindicators) (Laroche et al., 2018; Cordier et al., 2019).

Another major application of DNA metabarcoding is in biosecurity for the detection of toxic, pathogenic, and invasive species (Viard and Comtet, 2015; Zaiko et al., 2015, 2018; Xiong et al., 2016). DNA metabarcoding can also be applied to wildlife forensics, and the monitoring of rare, endangered and/or threatened species (Staats et al., 2016; Pikitch, 2018). A major benefit of using DNA metabarcoding for biomonitoring (e.g., biosecurity, rare/invasive species or wildlife forensics) is that it can be extremely sensitive to the presence of low numbers of such organisms or low concentrations of DNA, and can be immediately applied to the detection of a wide range of such species. This is in contrast to more targeted, species-specific monitoring such as DNA probe approaches, which may take a long period to optimize for monitoring.

DNA metabarcoding is also particularly useful in applications such as determining diet, where often no morphological features remain for taxonomic identification. Such dietary information provides insight into the broader biodiversity and food web structure that is present in the predator's surroundings. Through such diet analyses, it has been proposed to use abundant benthic marine generalists as natural biomonitors for ecosystems; individuals can be sampled regularly and thus allow an ecosystem's inhabitants to be identified and monitored (Siegenthaler et al., 2018).

DNA Metabarcoding Limitations

DNA metabarcoding is useful for assessing taxonomic composition of mixed samples within a short time and with little effort per sample. It requires little taxonomic expertise for fast, reliable and accurate taxonomic assignment, and even fully digested material can be used. However, the accuracy of this type of taxonomic identification is largely dependent on the reference databases available. At present, these are still incomplete, but the DNA metabarcoding approach has the benefit that identifications may be improved to a finer taxonomic resolution with time, as the sequence data can be reanalyzed with ease when the databases are updated (Leray et al., 2013; Aylagas et al., 2018; Devloo-Delva et al., 2018; Nielsen et al., 2018). There are currently substantial efforts being made to sequence reference organisms from species in a wide range of taxa and thus it is expected that the databases will improve dramatically in a short time-frame. Marker region and primer selection also play a role in the efficiency and accuracy of taxon detection, as this will determine how fine the taxonomic resolution is and ultimately what database would be best suited for the selected marker region and targeted organisms.

Ultimately, taxonomic expertise will still be needed to compile accurate and complete sets of reference specimens for DNA sequencing. However, traditional taxonomic methods have been shown to be poorer in detecting and identifying taxa in mixed samples than modern DNA metabarcoding methods (Jakubavičiūtė et al., 2017; Granquist et al., 2018; Siegenthaler et al., 2018). Some studies still benefit from coupling traditional taxonomic assignment methods with modern taxonomic assignment; generally this is best for quantitative analyses. However, a major goal of many DNA metabarcoding studies has been to not only identify the range of species present, but also estimate their relative abundance in the sample. As the range of potential quantitative biases became better understood, the consensus opinion became that DNA metabarcoding should be used cautiously for quantitative analyses (e.g., Lamb et al., 2019). Recent advances provide some hope in this endeavor, particularly in well-understood systems, and where quantitative controls can be used (e.g., Thomas et al., 2016). Alternatively, PCR-free approaches may offer the most promising way forward (e.g., Mariac et al., 2018).

Small differences among species in DNA sequence at the primer annealing sites can result in differences in the rate of PCR amplification. This “amplification bias” among species means that the number of DNA fragments sequenced from each species is not likely to accurately reflect the true relative abundance of individuals of those species in the original sample. Such “quantitative” DNA metabarcoding is feasible, but requires strict comparative controls (Alberdi et al., 2018). At the extreme, amplification bias can result in some divergent taxonomic groups being very poorly amplified by a specific PCR primer set, and thus not detected at all in the final analysis. It is not yet possible to design a single primer set that is truly universal, and this is why the use of either multiple primers for the same gene region and/or different marker regions is encouraged, in order to minimize amplification bias and increase the taxonomic diversity detected (Deagle et al., 2013; Clare, 2014; Leal and Ferrier-Pagès, 2016; Alberdi et al., 2018; van der Reis et al., 2018; Corse et al., 2019). This is especially critical when target communities are highly diverse or even unknown (e.g., in the case of gut contents). Having multiple primers for a single marker region and the use of multiple gene regions increases the possibility of detecting different taxa, and provides a more comprehensive picture of the community.

PCR inhibition, another potential PCR amplification bias, is common when trying to amplify the DNA extracted from many environmental samples containing inhibitory compounds, resulting in a lowering of biodiversity detection. To combat this, systematic PCR optimization (including trialing different PCR reagents and the use of quantitative PCR on serially-diluted DNA templates) can be extremely useful (van der Reis et al., 2018). The DNA used in a PCR should be in a homogenous state before PCR amplification. However, this does not ensure that DNA from all taxa is present, due to the small volume of DNA used in a single PCR, and the varied concentrations of extracted DNA from different taxa (causing PCR amplification stochasticity). Thus, replicate PCRs for the same sample should be undertaken in order to increase the chances of amplifying DNA from majority, if not all, taxa that are present in the mixed sample. This increases the chances for detection of rare species and reducing false negatives. PCR replicates are generally pooled together by sample before sequencing in order to minimize costs. These methods will allow the maximum proportion of the true diversity to be detected (O’Rourke et al., 2012; Schrader et al., 2012; Leray and Knowlton, 2015; Murray et al., 2015; Laroche et al., 2017; Alberdi et al., 2018, 2019). While DNA metabarcoding has been found to detect more of the taxa present than when using traditional methods, it is always advisable to undertake a preliminary study to identify potential weaknesses. For example, assessing which primer sets are beneficial to the study—how complete and reliable is their taxonomic resolution?

Finally, the great sensitivity of PCR is one of the strengths of DNA metabarcoding, but it can also be a problem, in terms of false positives. These can arise from sources such as traces of contaminating DNA (including human) during sampling, transport, storage, and laboratory analysis. Thus, great care needs to be taken in the interpretation of OTUs represented by a small number of sequences. These can be controlled to some degree by (i) employing minimum limits on the number of sequence copies required for the inclusion of an OTU in the final list of confirmed species present in each sample, (ii) investigating which species are present in the controls and/or (iii) relying on consistent presence of a species in all PCR sample replicates. However, this will not remove all false positives or artefactual sequences and likely could remove false negatives or true sequences that originated from low DNA concentrations. Therefore, one can take many different DNA sequence filtering approaches in order to provide more confidence in identifications. These include being more stringent in regards to OTU clustering and applying a minimum sequence copy number needed for each OTU to be retained. However, if this approach is too conservative the chance is high that rare taxa are removed from the dataset (potential loss in biodiversity due to the removal of false negatives). However, the taxa that remain have a higher probability of accurately representing the mixed sample, e.g., through removal of secondary PCR products such as chimeric sequences—false positives (Burgar et al., 2014; Clare et al., 2016).

Conclusion

There are many benefits that DNA metabarcoding brings to ecological studies, such as noninvasive environmental sampling and the detection of a species recent presence, and these have accelerated progress in our understanding of marine ecological processes. It has the potential to be incorporated with traditional marine biomonitoring, assisting with species identification of entire communities. The sensitivity of DNA metabarcoding requires that great care be taken during sampling and laboratory work to avoid sample contamination, as well as during computer analyses to have an accurate interpretation of the data. However, it is clear that this technique is now a powerful tool for marine ecological understanding and management.

Further Reading

We have used the most recent DNA metabarcoding articles as references. We encourage anybody new to the topic to start with the very helpful book, “Environmental DNA: For biodiversity research and monitoring,” by [Taberlet et al. \(2018\)](#). Included in the reference list are many insightful DNA metabarcoding review articles that go into depth about topics we have touched on, such as [Deagle et al. \(2019\)](#) “Counting with DNA in metabarcoding studies: How should we convert sequence reads to dietary data?” and [Alberdi et al. \(2018\)](#) “Scrutinizing key steps for reliable metabarcoding of environmental samples.”

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Biology and Ecology of Zoantharians (Cnidaria: Hexacorallia: Zoantharia)

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Abstract

Zoantharians (Cnidaria: Hexacorallia: Zoantharia) are sessile animals found from the intertidal zone to the abyssal ocean in a variety of marine ecosystems such as coral reefs and sandy seafloors. Although some Zoantharia species produce toxic secondary metabolites, their colonies serve as food sources and shelter to many organisms. The metabolites produced by zoantharians have shown promising results in the pharmacognosy industry. Additionally, some species are popular in the aquarium hobby or as jewelry. The order Zoantharia, with 9 families and 28 genera, has representatives occurring worldwide. Zoantharia are thought to have unique distribution patterns for marine anthozoans. For example, the group appears to have relatively low rates of endemism, with some species having very wide distributions inside each ocean basin. As well, there are several pairs of sibling species between the Atlantic and Indo-Pacific oceans. Due to the importance of the order Zoantharia, additional research in the systematics and distribution of species will help achieve a better understanding of evolution in marine ecosystems. In this article we provide an overview of the group and comment on possible future research trends.

Introduction

Morphology

Zoantharians (Anthozoa: Hexacorallia) are an order of benthic cnidarians with polyps that have a central mouth in the oral disk with one ciliated groove, which creates water currents towards the gastric cavity (Haddon and Shackleton, 1891, Fig. 1). The main external morphological characters used for identification are the color, shape, and size of the polyps and the number of tentacles, which are always in two rows around the oral disk. Additionally, characters of the internal anatomy including the types and number of mesenteries, arrangement of the marginal musculature, and the types and sizes of stinging cells (=cnidae) are also useful in identifying species (Carlgren, 1900; Pax, 1910; Lwowsky, 1913; Ryland et al., 2000; Low et al., 2016).

Most species are colonial, with individual polyps connected by a common tissue. However, species in the genera *Abyssoanthus* and *Sphenopus*, for example, have solitary polyps (Steenstrup, 1856; Reimer et al., 2007a,b). Although zoantharians do not produce a carbonate skeleton, most species are able to aggregate sediment into their tissue, such as sand grains and sponge spicules. This contributes to polyp formation, and some species can have up to 45% of their wet tissue weight being sediment (Haywick and Mueller, 1997). However, representatives of the family Zoanthidae (genera *Acrozoanthus*, *Isaurus*, and *Zoanthus*) and the genus *Kulamanamana* (in family Parazoanthidae) are exceptions with sediment-free polyps (Rafinesque, 1815; Sinniger et al., 2013). Furthermore, some zoantharian genera are able to produce a scleroprotein layer (e.g., *Kulamanamana* and *Savalia*; Ocaña and Brito, 2003; Sinniger et al., 2013).

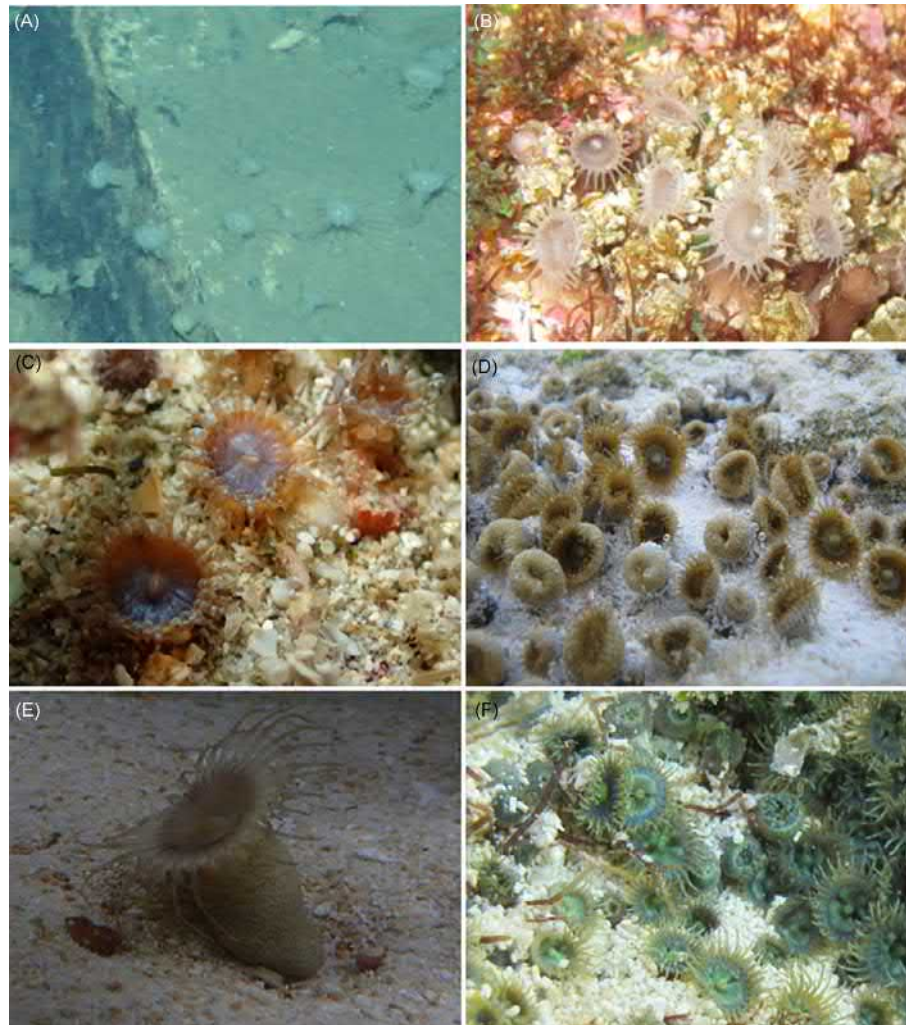


Fig. 1 Representatives of the order Zoantharia. Species shown are *Abysssoanthus convallis* (A), *Isaurus tuberculatus* (B), *Neozoanthus uchina* (C), *Palythoa grandiflora* (D), *Sphenopus marsupialis* (E), and *Zoanthus sociatus* (F). Images credits: JD Reimer (A and E), I Kawamura (B), and MEA Santos (C, D, and F).

Systematics

The order Zoantharia is divided into two suborders according to mesentery arrangement; Brachyknemina and Macroknemina (Haddon and Shackleton, 1891). Mesenteries are internal tissues that are sheet-like partitions extending from the polyp wall into the gastrovascular cavity. A mesentery is complete when the tissue connects the polyp wall and the gastrovascular cavity, while an incomplete mesentery does not reach all the way until the cavity. These two suborders are delineated based on the character of the fifth mesentery pair, either being complete (macroknemic, species of the suborder Macroknemina) or incomplete (brachyknemic, species of the suborder Brachyknemina). Although this division is still accepted (Low et al., 2016), molecular studies have shown that Macroknemina is not monophyletic as these species do not share a common recent ancestor (Sinniger et al., 2005; Swain, 2010, 2018). Therefore, the classification at the suborder level of the order Zoantharia requires revision.

Taxonomic research of zoantharians has a history of being neglected, mostly due to species' simple body plans, with relatively few diagnostic characters, and a high rate of intra-specific morphological plasticity (Burnett et al., 1997; Ryland and Lancaster, 2004; Kamezaki et al., 2013). For example, the size and color of polyps of the same species can have a high amount of variation depending on hydrodynamic regime or on the amount of shading or sunlight (Ong et al., 2013).

Molecular studies of the diversity of Zoantharia started with Burnett et al. (1995, 1997) using proteins, and from the early 2000s researchers have used fragments of mitochondrial and nuclear DNA markers (e.g., Reimer et al., 2004, 2006, 2007a,b; Sinniger et al., 2005, 2008; Risi and MacDonald, 2016). These molecular studies have improved our knowledge about the phylogenetic positioning of Zoantharia clades and have also clarified which characters are more useful to delineate species, in addition to leading to more knowledge of the zoantharian diversity of many locations around the globe (Reimer et al., 2008; Koupaei et al., 2014; Santos et al., 2016).

Table 1 Systematics of the order Zoantharia (Low et al., 2016; Horton et al., 2019).

Suborder	Family	Genera
Brachycnemina	Neozoanthidae	<i>Neozoanthus</i>
	Sphenopidae	<i>Palythoa</i> <i>Sphenopus</i>
	Zoanthidae	<i>Acrozoanthus</i> <i>Isaurus</i> <i>Zoanthus</i>
Macrocnemina	Epizoanthidae	<i>Epizoanthus</i> <i>Paleozoanthus</i> <i>Thoracactis</i>
		<i>Aenigmanthus</i> <i>Hydrozoanthus</i> <i>Terrazoanthus</i>
		<i>Antipathozoanthus</i> <i>Bergia</i> <i>Bullagummizoanthus</i> <i>Corallizoanthus</i> <i>Hurlizoanthus</i> <i>Isozoanthus</i> <i>Kauluzoanthus</i> <i>Kulamanamana</i> <i>Mesozoanthus</i> <i>Paleozoanthus</i> <i>Parazoanthus</i> <i>Savalia</i> <i>Umimayanthus</i> <i>Zibrowius</i>
	Hydrozoanthidae	<i>Microzoanthus</i> <i>Nanozoanthus</i> <i>Abyssozoanthus</i>
	Parazoanthidae	
	Microzoanthidae	
	Nanozoanthidae	
	Abyssozoanthidae	
Incertae sedis		

The order Zoantharia currently has 9 valid families and 28 genera (Table 1). However, the total species richness of Zoantharia is not clear due to the recognition of a high number of potential species synonyms (Burnett et al., 1995, 1997; Reimer et al., 2010; Risi and MacDonald, 2016; Santos et al., 2019) combined with large numbers of undescribed specimens at species or higher taxonomic levels (Reimer et al., 2012, 2017a,b; Kise and Reimer, 2016; Santos et al., 2016, 2019).

Ecological Interactions

There are three main types of ecological interactions reported for species of Zoantharia: (1) hosting microalgae (Class Dinoflagellata, Family Symbiodiniaceae) inside their tissues (i.e., endosymbionts); (2) growing attached to another benthic marine invertebrate group; and (3) serving as shelter and prey for other animals.

Symbiotic Algae

Zoantharian and associated endosymbionts are able to exchange nutrients and these microalgae provide carbon-based photosynthates to their host (Muscatine and Hand, 1958). Apart from representatives of the genus *Sphenopus* (Steenstrup, 1856) and three *Palythoa* species (*P. mizigama*, *P. umbrosa*, and *P. macmurrichi*; Haddon and Shackleton, 1891; Irei et al., 2011), all brachycnemic species host these symbionts. Likewise, some macrocnemic species also have obligatory or facultative endosymbiosis. The identity of Symbiodiniaceae genera (Lajeunesse et al., 2018) associated to zoantharians has primarily been investigated using DNA sequences of the molecular nuclear internal transcribed spacer 2 region, and species of Zoantharia are known to be associated with genera *Breviolum*, *Cladocypium*, *Durusdinium*, and *Symbiodinium* (former *Symbiodinium* “clades” B, C, D, and A, respectively; reviewed in Santos, 2019).

Marine Invertebrates as Substrata

Many Zoantharia lineages have symbioses with other benthic invertebrates (Fig. 2), in which the zoantharian polyps grow attached to animals such as Annelida, Arthropoda, Cnidaria, Echinodermata and Porifera. Most macrocnemic lineages have evolved

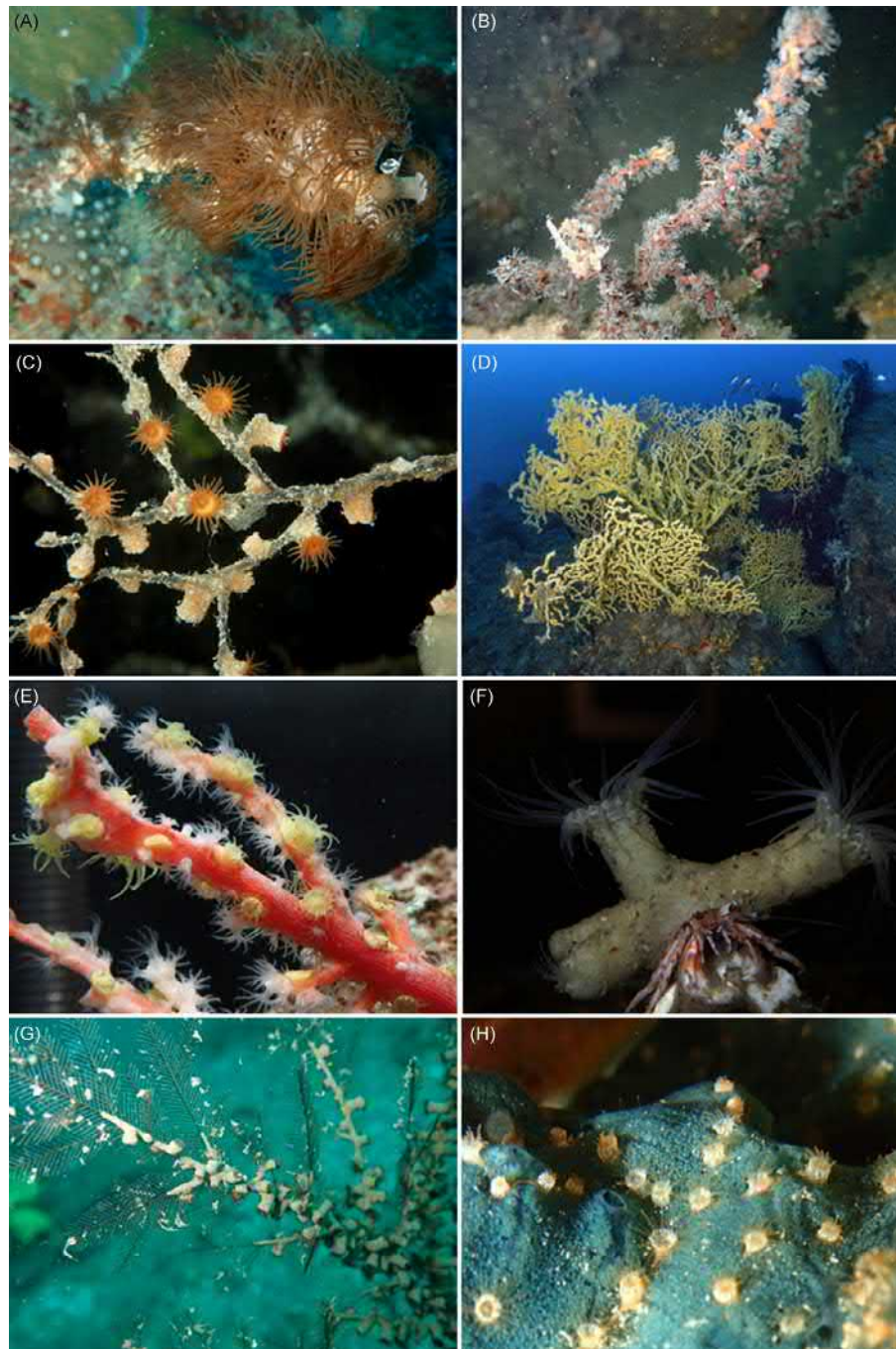


Fig. 2 Zoantharian symbioses with marine invertebrates. *Acrozoanthus australiae* and *Epizoanthus inazuma* with eunicid worms (A and B, respectively), *Antipathozoanthus remengesau* and *Savalia savaglia* with antipatharians (C and D, respectively), *Corallizoanthus tsukaharai* with octocoral (precious coral) (E), *Epizoanthus* cf. *paguricola* with hermit crab (F), *Hydrozoanthus gracilis* with hydrozoan (G), and *Umimayanthus chanpuru* with sponge (H). Images credits: MEA Santos (A, B, G and H), JD Reimer (C), E Trinito (D), S Nakachi (E), and T Moritaki (F).

facultative or obligatory symbiotic relationships, such as the genera *Bergia* and *Umimayanthus* with sponges (West, 1979; Montenegro et al., 2016) and the genus *Hydrozoanthus* with hydrozoans (Sinniger et al., 2010). Additionally, one brachycnemic genus has obligatory associations with Eunicidae worms and their polyps are only observed growing attached to the worm tubes (genus *Acrozoanthus*, Saville-Kent, 1893; Reimer et al., 2011).

Although Zoantharia-invertebrate interactions have not been comprehensively studied, research has indicated that the associations can range from mutualism to parasitism. For example, the zoantharian *Zibrowius primnoides* kills the tissue of their octocoral host to use their hard axis as attachment substratum (Carreiro-Silva et al., 2011, 2017). On the other hand, some

Zoantharia species do not seem to harm some sponge and worm hosts (West, 1979; Montenegro et al., 2015; Kise and Reimer, 2016). The influence of zoantharians on their sponge hosts in the Caribbean finds both positive and negative interaction outcomes (Lewis, 1982; Lewis and Finelli, 2015; Swain and Wulff, 2007; Swain, 2012). Furthermore, it is possible that zoantharians give advantages to hermit crab partners, as metabolites of their polyps could provide protection against predators. In addition, some of these zoantharians excrete a chitin layer that may enable the crab to grow a large shell (Ates, 2003). Likewise, the hydroid *Plumularia habereri* reaches its largest colony sizes when the zoantharian *Hydrozoanthus gracilis* is associated with it, indicating a possible beneficial interaction (Di Camillo et al., 2010). Nevertheless, the large majority of these potential interaction outcomes have not been tested. Many of these zoantharian symbioses are not limited to shallow waters but also reported from mesophotic reefs and the deep-sea (e.g., Carlgren, 1927; Sinniger et al., 2013; Ryland and Ward, 2016; Carreiro-Silva et al., 2017; Reimer et al., 2019).

Habitat Forming

Zoantharians are used for housing and protection by organisms that live upon, under, or even inside their colonies (Fig. 3). Among associated fauna are small crabs, worms and flatworms, as well as larvae of invertebrates and nudibranch juveniles (Den Hartog and Holthuis, 1984; Den Hartog and Turkay, 1991; Pérez et al., 2005; Trivedi and Vachhrajani, 2014; Biondi et al., 2019; Bee Yan and Ng, 2019). Most of these associations have been observed on the zoantharian genera *Palythoa* and *Zoanthus* (but see *Parazoanthus* reported in Den Hartog and Holthuis, 1984).

Predators

Despite many zoantharian species having sediment in their tissue, as well as stinging cells and toxic metabolites, some animals are able to eat zoantharian polyps. Zoantharia are known to be food sources for echinoderms (Obuchi and Reimer, 2011), fireworms (Ott and Lewis, 1972; Suchanek and Green, 1982; Sebens, 1982; Gleibs and Mebs, 1995; De Assis et al., 2017), fishes (Randall and Hartman, 1968; Sebens, 1982; Bonaldo et al., 2005; Francini-Filho et al., 2010; Longo et al., 2012), nudibranchs (Gosliner, 1985; Bertsch et al., 2009; Kumari et al., 2019), prosobranch gastropods (Robertson, 1967, 1980), and sea turtles (Stampar et al., 2007; Hart et al., 2013; von Brandis et al., 2014; Proietti et al., 2015; Spier and Gerum, 2017). Zoantharia feed on plankton and particles suspended in the water column, and some *Palythoa* species are known to have relatively high plankton feeding rates compared to other anthozoans (Sebens, 1977; Fabricius and Metzner, 2004; de Santana et al., 2015). Thus, such zoantharians are important trophic links, and in addition some zoantharians can also transfer metabolites to higher trophic levels (Gleibs and Mebs, 1999).

Similar to studies of associated fauna, predation records are mainly of the most common zoantharians in shallow-waters, the genera *Palythoa* and *Zoanthus*. For example, adult and juvenile nudibranchs that live on colonies of *P. mutuki* can eat the zoantharian mucus (Kumari et al., 2019). Additionally, field observations have noted the predation of *P. caribaeorum* and *Z. sociatus* by hawksbill turtles in Brazil (Stampar et al., 2007; Proietti et al., 2015), while the gastric content of this turtle species in Caribbean can be up to 86% *Z. sociatus* (Hart et al., 2013). The fact that *Zoanthus* tissues are sediment-free might make them easier to digest compared to *Palythoa* species with high sand content.

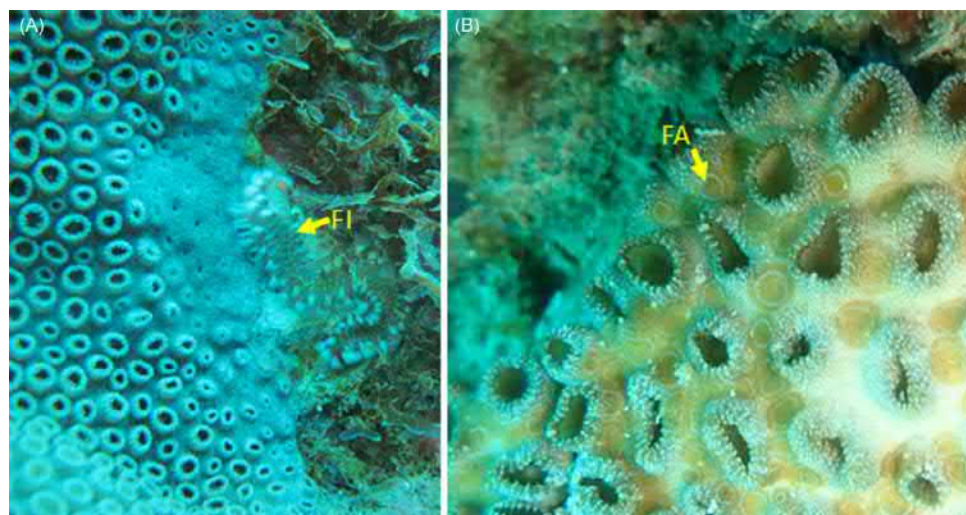


Fig. 3 *Palythoa caribaeorum* with a fireworm ("FI" arrow) predator in Brazil (A) and *P. tuberculosa* hosting flatworms ("FA" arrow) inside the tissue in Indonesia (B). Images credits: MEA Santos.

Distribution

Reproduction and Dispersal

As most species of Zoantharia are sessile, dispersal is primarily through the larval phase. There is little information about larval development, but aquarium experiments have revealed that the larvae of *Palythoa tuberculosa* are able to survive more than 3 months (Polak et al., 2011). The few published studies about sexual reproduction of zoantharians have been conducted mostly with shallow water species occurring in < 50 m depths. Overall, brachyncemic species appear to be generally hermaphroditic, while macrocnemic species are not (Ryland et al., 2000). For example, brachyncemic *P. caribaeorum* and *P. variabilis* were reported as sequential protogynic hermaphrodites in Brazil (Boscolo and Silveira, 2005), whereas macrocnemic *Epizoanthus couchii*, *Parazoanthus anguicomus*, *P. axinellae*, and *Savalia savaglia* were shown to be gonochoric (Ryland et al., 2000; Previati et al., 2010).

Asexual reproduction is common in sessile invertebrates and can improve their dispersal and survival at local and regional scales (Foster et al., 2007; Harrison, 2011; Capel et al., 2017). Accordingly, zoantharians can disperse via asexual reproduction and many modes are known for the genera *Acrozoanthus*, *Palythoa*, *Parazoanthus*, *Savalia*, and *Zoanthus* (Karlson, 1983; Ryland, 1995; Acosta et al., 2001, 2005; Previati et al., 2010; González-Muñoz et al., 2019). Common asexual reproduction mechanisms are edge fissions or release of polyp balls or clusters (Acosta et al., 2005; Previati et al., 2010; González-Muñoz et al., 2019). Edge fission occurs when a parent colony segregates a polyp group at the colony edge, and this is often observed under competition for space with other species. On the other hand, polyp balls are usually produced and detach in the center of large colonies with substrate irregularities such as shells (Acosta et al., 2005). The polyp balls can roll on the substrate and be dispersed by waves and storms, allowing these colonies clones to escape local selective factors and environmental stress (Acosta et al., 2005).

Furthermore, dispersal through rafting has been observed in groups closely related to zoantharians. Hydrocorals, scleractinian corals, and sea anemones can travel long distances attached to floating volcanic sea-rafting pumice (Jokiel, 1989, 1990; Bryan et al., 2004, 2012) or man-made objects (Hoeksema et al., 2012, 2015). Likewise, brachyncemic and macrocnemic zoantharians are able to attach to different structures, including anthropogenic objects made of glass, nylon and metal that can float. Thus, it is possible that rafting plays a role in the distribution of Zoantharia (Santos and Reimer, 2018). In addition, some species of *Palythoa* and *Zoanthus* are hermaphrodites (Fadlallah et al., 1984), resilient against desiccation (Sebens, 1982; Rabelo et al., 2013), and have fertile polyps throughout the year (Boscolo and Silveira, 2005), indicating that these groups can have a high success as rafting riders (Santos and Reimer, 2018).

Zoogeography

Different species of Zoantharia occur across the world's oceans from the intertidal zone down to abyssal depths (Pax and Mueller, 1956; Burnett et al., 1997; Reimer et al., 2007a,b; Santos et al., 2019). Brachyncemic species are distributed in shallow waters of tropical to warm temperate seas (< 50 m for zooxanthellate species; Duerden, 1898, 1900; Carlgren, 1941; Reimer et al., 2007a,b, 2017a,b; while azooxanthellate *Sphenopus* is known until ~ 100 m depth; Kise et al., 2019). On the other hand, macrocnemic zoantharians have a more extensive distribution range as they also occur in temperate and polar oceans (e.g., Carlgren, 1927; Swain, 2010), and to greater depths (Carlgren, 1913; Carreiro-Silva et al., 2017; Reimer et al., 2019). Additionally, representatives of the family Abyssoanthidae have been reported down to ~ 5300 m depth (*Abyssoanthus convallis*; Reimer and Sinniger, 2010).

Although brachyncemic zoantharians are ubiquitous to shallow coral reef ecosystems, their zoogeographical patterns are poorly known. A recent study in the Atlantic Ocean revealed that these zoantharians have lower endemic rates than other common reef animals, as well as exceptionally wide distribution ranges (Santos et al., 2019). Likewise, some *Palythoa* and *Zoanthus* species in the Indian and Pacific oceans have extensive distributions (Hibino et al., 2013; Reimer et al., 2017a). Different than hydrocorals and scleractinian corals, which have generally deep genetic divergences between lineages of the Atlantic and Indian/Pacific oceans (Fukami et al., 2004; Arrigoni et al., 2018), there are sibling zoantharian species pairs between these two ocean regions (Reimer et al., 2012; Santos et al., 2016; Santos, 2019).

Furthermore, eight of the nine Zoantharia families are cosmopolitan, with the exception of Neozoanthidae that has so far been only reported from the Indian and Pacific region (Santos, 2019). Zoantharia have higher genera-level diversity in the Indian and Pacific compared to the Atlantic Ocean. Out of 28 total genera, 24 are found in the Indian and Pacific oceans, of which eight are endemic to this region (Santos, 2019).

Economic Importance

The pharmacognosy industry actively investigates Zoantharia, and has mainly focused on species of *Epizoanthus*, *Palythoa*, *Parazoanthus* and *Zoanthus* (Cariello et al., 1974; Moore and Bartolini, 1981; D'Ambrosio et al., 1997; Kuramoto et al., 1998; Miyashita et al., 2004; Cachet et al., 2009; Wilke et al., 2009; Ramos and Vasconcelos, 2010; Genji et al., 2010; Yoshimura et al., 2012; Rocha, 2013; Cen-Pacheco et al., 2014; Guarnieri et al., 2018; Guillen et al., 2018; Matsumura et al., 2018). For instance, bioprospecting research has isolated molecules from zoantharians that show promising results in the treatment of osteoporosis (Kuramoto et al., 1998; Genji et al., 2010) and snakebites (Guarnieri et al., 2018).

Zoantharia species are also common in the aquarium hobby industry, in particular brightly colored morphotypes of *Palythoa* and *Zoanthus*, which can reach prices of up to 100 USD or more for single polyps. Additionally, some lineages of the family Parazoanthidae (e.g., *Kulamanamana haumeae*) are popular in the jewelry business and are commonly known as “gold coral” (Waller and Baco, 2007).

Research Trends

This article has highlighted the economical relevance and ecological importance of the order Zoantharia. Moreover, some zoantharian species have high dispersal potential and generalist strategies to survive in varying environments. Such attributes have enabled these zoantharians to have exceptionally extensive distributions at large geographical scales, and overall Zoantharia show low endemism rates compared to other common animals in reef ecosystems. Nonetheless, there is still a lack of zoantharian studies following research lines such as genomics and population genetics. Future studies should examine the connectivity of zoantharian populations across ocean basins. The identification of environmental barriers to gene flow of such a widespread group will increase the knowledge of adaptation in marine ecosystems, and this is also relevant to management strategies.

Acknowledgments

We thank I Kawamura, E Trinito, S Nakachi, and T Moritaki (Toba Aquarium) for kindly providing images used in Figs. 1B, 2D–F, respectively. The chapter editor MJ Costello is also thanked for comments that improved an earlier version of this article.

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The Anthropogenic Biosphere: Lines of Evidence for Sustained Direct Interactions Between Humans and the Environment

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Abstract

The field of ecology has shifted from a relatively narrow focus on plant and animal populations and communities to more broadly understanding ecological patterns, processes and changes, including those shaped by interactions with human societies. This trend is embodied by the growth of research and scholarship investigating direct interactions between humans and environments: the science of coupled human and natural systems. Understanding global ecology and its modification through land use as the emergence of an anthropogenic biosphere composed of anthromes (anthropogenic biomes) allows for a synthesis of human-related ecological topics from local to global scales. In this article we introduce the section that shifts the perspective from biomes to anthromes, soundscapes, changing aquatic systems, and pressures of energy development on land cover.

Introduction

The global patterns of life on Earth have been described in relation to variations in climate, terrain and soils since at least the time of Alexander von Humboldt's work in the late 18th century (Schrodt et al., 2019). In 1939, Richard Carpenter wrote in "The Biome" about Clements' 1916 paper proposing the term biome itself as "a biotic community consisting of both plants and animals." More than 50 years after Clements, in 1962, Robert Whittaker published his "Classification of Natural Communities" framing global vegetation patterns and biomes as a function of temperature and precipitation, providing a framework still widely used to understand the global patterns of terrestrial ecology. Just over 40 years later, anthropogenic biomes or anthromes were conceptualized by Ellis and Ramankutty (2008) to characterize the global patterns of ecology shaped by human societies.

In conceptualizing anthromes, Ellis and Ramankutty, like Whittaker, used an empirical approach to assess ecological patterns at global scale. Unlike both Clements and Whittaker, they recognized and incorporated direct and sustained human interactions with the biotic communities and more broadly human interactions with ecosystems. Thus they shifted the framework for ecology from the classic model of vegetation patterns shaped by climate to the model of an anthropogenic biosphere in which human societies shape heterogeneous and multifunctional landscape mosaics of used, remnant and novel habitats that vary in response to land-use system, land use intensity and population density (Ellis et al., 2010; Ellis, 2015). As a consequence, researchers, students, and practitioners can now visualize and interact with maps and data quantifying how more than three-quarters of Earth's ice-free land surface has been transformed into dense settlements, villages, croplands, rangelands, and seminatural lands as well as the wildlands still remaining without intensive use. Though fragments of ecosystems and habitat representing the classic biomes are still embedded within most anthromes, and nearly one quarter of Earth's land remains as wildlands, the multifunctional mosaic landscapes of anthromes have largely transformed or replaced the biomes and ecosystems described in the other volumes in this Encyclopedia.

This reframing of global ecology to incorporate the realities of an increasingly human world has created an intellectual space for linking broader concepts across ecology, conservation, and sustainability science (Martin et al., 2014). Indeed, during these last 10 years, anthrome frameworks have been used or cited across a diversity of disciplines (Fig. 1). Building on this collection of manuscripts in this volume we see these connections via chapters focused on the intensively used, seminatural, and wild anthromes. The thread of direct human interaction with the environment is maintained across subsequent chapters extending to marine and aquatic systems, the acoustic spaces we are all embedded within, and lastly, specific applications and local case studies of coupled human and natural systems (Quinn and Quinn, 2020a) that shape and are shaped by the landscape.

The first four chapters present either a global summary or application of anthromes. Ellis 2020 provides a summary of the development of anthromes and challenges the reader to consider or reconsider the focus of earth stewardship in the Anthropocene. With a historical perspective and an updated anthrome dataset, Goldewijk (2020) provides a review of how the anthrome classifications provide a valuable lens on historical patterns. The article provides a reconstruction of global changes in anthrome distribution from 10,000 BCE to 2015 CE and evidence of temporal and regional heterogeneity in land cover change. Land-use intensity is one important input for the anthrome classification. Andersen and Quinn (2020) provides a review of Human Appropriation of Net Primary Production (HANPP), focusing on global, regional, and watershed scale patterns of land-use intensity via HANPP. In addition,



Fig. 1 Journal classifications and citation counts, via 2019 Web of Science search, of papers that cite anthromes and associated literature.

he begins to explore spatial correlations between HANPP and anthromes. Lastly, [Cook and Quinn \(2020\)](#) review plant and vertebrate biodiversity patterns across anthromes, highlighting overlooked conservation spaces in used anthromes.

The subsequent four chapters review natural and human systems of dense settlements, villages, and seminatural (in particular residential and populated woodlands) anthromes. These anthromes are home to the greatest number of people (an average population density of 258 persons km^{-2}) and over 40% habitat loss on only 17% of ice-free surface ([Ellis et al., 2010](#)). Thus, the relationship and interactions between human and natural systems here are close and complex. Vogt provides a trio of chapters about urban systems ([Vogt, 2020a,bc](#)) and specifically forests across urban, mixed settlements and semi-natural woodland anthromes. Vogt also addresses the biophysical ([Vogt, 2020b](#)) aspects of urban forest characteristics and how they may be similar or different from our naive assumptions of what a forest is. Building on this description she reviews the benefits of ecosystem services of urban forests and tools to estimate their value. However, because these forests are embedded in anthromes, Vogt provides a review of urban forests and social-ecological systems ([Vogt, 2020a](#)), in particular discussing actors (e.g., residents; stormwater management districts; real estate developers and builders; property management companies, among others), ownership, distribution of the benefits discussed in the previous chapter, costs of their maintenance, and perhaps more importantly, how there is heterogeneity and often a lack of spatial (and perhaps temporal connection) between benefits and costs of trees and forests in these used and seminatural anthromes. [Unnikrishnan and Nagendra \(2020\)](#) use Bangalore, India as a case study to demonstrate how nature and society have “shaped, transformed, and influenced each other’s trajectories of development” in dense settlements and villages with a particular focus on the role of urban water bodies, colonization, and the urban commons. They conclude, much like Vogt, that as we look forward that the future is equitable and just. Shifting towards more traditional urban ecology, [Parsons and Backe \(2019\)](#) review trophic interactions between trees, herbivores, and natural enemies in used and seminatural anthromes. In their consideration of arthropod invasion dynamics, biotic homogenization, and urban species distributions they highlight the dynamic nature of ecology in used anthromes.

Cropland and rangeland anthromes are globally extensive anthromes, together encompassing almost 50% of ice-free surface ([Ellis et al., 2010](#)), though generally with lower population densities than the anthromes discussed above. Rangeland, the most extensive anthrome, is addressed by [Schallner et al. \(2020\)](#). In particular, they review the capacity of rangelands to provide ecosystem goods and services in the face of increasing demand on these lands. With a focus on global arable land, [Quinn \(2020\)](#) uses the anthrome data set to describe patterns of cropland anthromes and the importance of cropland to global and regional biodiversity conservation. Given the frequency of trees in cropland anthromes, [Gold \(2020\)](#) provides a valuable review of the patterns and value of agroforestry; farming and food systems where trees and agriculture are integrated to optimize multiple ecological and economic functions, for both temperate and tropical regions. More regionally focused, [Ricard et al. \(2019\)](#) provide a case study of agroecology in the Pampas of Argentina, calling for adaptive, science-based management to help maintain agricultural productivity while maintaining biotic and abiotic ecological processes. [Ferrara et al. \(2019\)](#) highlight the importance of heterogeneous agricultural landscapes for both ecosystem function and cultural ecosystem services. The call for place-based and practice-based stewardship in the future that is reflective of heterogeneous cultural landscapes. Lastly [Hölting et al. \(2019\)](#) define and discuss the importance of multifunctionality across working landscapes highlighting how a better sense of the valuation of multifunctionality could improve how we manage landscapes.

Moving away from the anthromes with the greatest direct impact of humans, [Allan et al. \(2020\)](#) review global wildlands including discussions of definitions, origins, and applications of the term. They link and build upon recent mapping efforts of wilderness defined as “pressure free lands with a contiguous area > 10,000 km² for the years 1993 and 2009” with the spatial classification of anthromes by [Ellis et al. \(2010\)](#). They find, perhaps not surprisingly, a high level of spatial congruence between the defined wilderness areas of [Allan et al., 2017](#) and the statistically defined wilderness of anthromes; though a clear difference is evident in the rangelands of Australia and Mongolia. In addition, for readers interested more broadly in wildlands and wilderness, it is worth noting the discussion wilderness provided by [Speitz \(2019\)](#) in the following section on the complexity of our definitions and application of wilderness. Building on traditional ideas of wilderness and conservation and more recent discussions on conserving half the earth for conservation, [Boyle \(2019\)](#) discusses how anthromes vary within and across protected areas, highlighting the frequency of used anthromes embedded in many protected areas.

Moving beyond the specific framework of anthromes, subsequent chapters review other ways that humans’ direct and sustained interactions with the biosphere have shaped the environment. [Hanks \(2020\)](#) provides a comprehensive assessment of the impacts of dams on river structure and function and consequently human systems. The heterogeneity in placement and value of the over 16 million dams adds complexity to their management and sustainability. Moving from freshwater to marine systems, [Roark \(2020\)](#) and [Boonstra et al. \(2019\)](#) review two interactions that result in direct sustained impacts on marine systems. [Boonstra et al. \(2019\)](#) focus on the coupled human-natural system of small-scale fisheries in the Global North and South. In their review, they point out how small-scale fishing systems are shrinking under multiple pressures and may serve as an essential biocultural refugium. [Roark \(2020\)](#) reviews the drivers of and sustained impacts of endocrine disruptors in marine systems, focusing on how these persistent environmental contaminants can result in reproductive, developmental, metabolic, or behavioral dysfunction in marine organisms.

Capturing an emerging space in how humans interact with and shape the environment, [Happel and Happel \(2019\)](#) review the field of soundscape ecology. In particular, they document the development of the field, key concepts including biophony, geophony, and anthrophony, and the impacts of human noise on the ecosystem and species health. In a more focused review, [Oden et al. \(2019\)](#) discuss the pervasive impacts of roads on avian vocalizations. An expanding energy portfolio to include renewable sources has resulted in a broader scale direct impact of energy on land use and land cover. Addressing this emerging driver of change, [Pereira et al. \(2019\)](#) and [Basudde \(2020\)](#) link the development of energy and land-use policies. Given the global and growing footprint of energy development, their local case studies in Brazil and Uganda serve as a good starting point for future scenarios and discussion. The section ends with two focused case studies from the US National Park Services. [Spies et al. \(2019\)](#) and [Phillipson et al. \(2019\)](#) each provide a status assessment from island regions (Hawai’i and the Mariana Islands Archipelago) shaped by development. In particular, they consider the impacts of the regions current ecological status, key stressors, conservation efforts, and future viability in the region.

Conclusion

This section captures some of the ways that human interactions shape terrestrial and aquatic environments. Pollution and runoff, desertification, invasive species, road networks, agriculture, and many other factors are all impactful and pervasive. But as a collection, these chapters help us understand the environments we live and work within. Moreover, by emphasizing the links and feedbacks between natural and human systems ([Quinn and Quinn, 2020a](#)), they suggest that anthromes serve as a bridge in this Encyclopedia and more broadly in scholarship and practice between biomes and sustainability science and human systems ([Quinn and Quinn, 2020b](#)).

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Anthromes

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Abstract

Human societies and their use of land have transformed ecology across this planet for thousands of years. As a result, the global patterns of life on Earth, the biomes, can no longer be understood without considering how humans have altered them. Anthromes, or anthropogenic biomes, characterize the globally significant ecological patterns created by sustained direct human interactions with ecosystems, including agriculture, urbanization, and other land uses. Anthromes now cover more than three quarters of Earth's ice-free land surface, including dense settlements, villages, croplands, rangelands, and seminatural lands; wildlands untransformed by agriculture and settlements cover the remaining area.

Introduction

Human societies and their use of land have transformed ecology across this planet for thousands of years (Ellis, 2015; Stephens et al., 2019). As a result, the global patterns of life on Earth, the biomes, can no longer be understood without considering how humans have altered them. Anthromes, or anthropogenic biomes, characterize the globally significant ecological patterns created by sustained direct human interactions with ecosystems, including agriculture, urbanization, and other land uses (Ellis and Ramankutty, 2008). Anthromes now cover more than three quarters of Earth's ice-free land surface, including dense settlements, villages, croplands, rangelands, and seminatural lands; wildlands untransformed by agriculture and settlements cover the remaining area.

Look out of any airplane window or at imagery from any Earth satellite and the signs of human transformation are everywhere. From the farms, grazing lands, plantations and managed forests that sustain our societies to the settlements and cities where we live and the roads, railroads and paths that crisscross the continents and connect us all together. Using spatial data from remote sensing, government statistics, and other sources, these global fingerprints of human societies, including human-altered vegetation cover, built structures, crops, livestock grazing, irrigation, roads and the varying densities of human populations can be brought together, characterized, and mapped using Geographic Information Systems (GIS). The first such effort in this direction, the Human Footprint, used these data to assess human influences on ecology as a single number varying from high to low (Sanderson et al., 2002). But is it truly possible to capture the rich diversity of human transformation of ecology across this entire planet using a single number?

In 2008, Ellis and Ramankutty set out to map the globally significant patterns of human altered and managed ecosystems through a statistical approach called cluster analysis (Ellis and Ramankutty, 2008). Using this approach, the globally significant patterns of human shaped ecosystems could be mapped from data on human populations, land use and vegetation cover, just as the natural biomes, in all their rich diversity from tundra to tropical rainforests, are mapped relation to the globally significant patterns of climate, terrain, and other natural environmental conditions. In 2010, this approach was updated to allow anthromes to be mapped globally over time, from 1700 to 2000 (Ellis et al., 2010). Anthrome maps based on this system of classification are now used widely in teaching, research and conservation (e.g. Chapin III et al., 2012; Martin et al., 2014; Merritts et al., 2014; National Geographic Society, 2014; Freeman et al., 2016; Miraldo et al., 2016; Dinerstein et al., 2017; Smith et al., 2019). Using this system of anthrome classification, five "levels" of are recognized and mapped globally, as described in Table 1 and illustrated in Fig. 1.

Anthromes and the Anthropogenic Biosphere

Urban and other dense settlement anthromes are the most highly transformed anthromes on Earth and sustain population densities well over 1000 persons per square kilometer in landscapes largely converted into settlements and other residential and industrial infrastructure. Village anthromes are also highly transformed and densely populated (above 100 persons per square kilometer), but their mostly agricultural landscapes sustain largely rural populations, often in regions inhabited and farmed since ancient times.

Table 1 Anthrome classes within five anthrome levels, with global areas for 2015 CE in square kilometers (percent in parentheses; based on Ellis et al., 2020; Fig. 1).

Area (%)	Name	Description
2,237,074 (1.7%)	Dense settlements: Urban and other nonagricultural dense settlements	
723,555 (0.5%)	Urban	Densely built-up environments with very high populations
1,513,519 (1.1%)	Mixed settlements	Suburbs, towns and rural settlements with high but fragmented populations
9,365,333 (7.1%)	Villages: Densely populated agricultural settlements	
1,078,848 (0.8%)	Rice villages	Villages characterized by paddy rice
1,974,819 (1.5%)	Irrigated villages	Villages characterized by irrigated crops
5,436,990 (4.1%)	Rainfed villages	Villages characterized by rainfed agriculture
874,677 (0.7%)	Pastoral villages	Villages characterized by pasture and rangeland
19,379,053 (14.7%)	Croplands: Lands used mainly for annual crops	
1,048,619 (0.8%)	Residential irrigated croplands	Irrigated croplands with substantial human populations
9,998,304 (7.6%)	Residential rainfed croplands	Rainfed croplands with substantial human populations
5,550,446 (4.2%)	Populated rainfed croplands	Croplands with significant human populations
2,781,684 (2.1%)	Remote croplands	Croplands without significant populations (irrigated and rainfed)
34,900,571 (26.5%)	Rangelands: Lands used for pasture and livestock grazing	
6,905,141 (5.2%)	Residential rangelands	Rangelands with substantial human populations
10,656,903 (8.1%)	Populated rangelands	Rangelands with significant human populations
17,338,527 (13.2%)	Remote rangelands	Rangelands without significant human populations
31,963,461 (24.3%)	Seminatural lands: Inhabited lands with minor use for permanent agriculture and settlements	
4,302,009 (3.3%)	Residential woodlands	Forest biome regions with minor land use and substantial populations
7,342,981 (5.6%)	Populated woodlands	Forest biome regions with minor land use and significant populations
8,749,492 (6.6%)	Remote woodlands	Forest biome regions with minor land use without significant populations
11,568,978 (8.8%)	Inhabited treeless and barren lands	Regions without natural tree cover having only minor land use and a range of populations
33,958,547 (25.8%)	Wildlands: Lands without human populations or substantial land use	
15,399,162 (11.7%)	Wild woodlands	Forests and savanna
16,001,211 (12.1%)	Wild treeless and barren lands	Regions without natural tree cover (grasslands, shrublands, tundra, desert and barren lands)
2,558,174 (1.9%)	Ice, uninhabited	Regions covered by permanent ice
131,804,039 (100%)	Global land	

While these urban and village anthromes covered only about 8% of Earth's ice-free land in 2000 CE, more than 80% of Earth's human populations lived in them. Moreover, ongoing migrations from rural areas into cities are making urban anthromes even denser as human populations continue to concentrate into and expand Earth's relatively small but dynamic area of urban anthromes.

The farm fields that produce most of our food are mostly found in croplands anthromes. In some croplands, crops cover the land almost completely. More common though, are croplands formed of a complex mix of crops, settlements, and patches of tree cover and other less intensively managed habitats. Rangeland anthromes sustain grazing livestock and are the most extensive of the used anthromes. While these cover nearly one third of Earth's ice-free land, they also tend to be lower productivity areas that sustain relatively low population densities and are usually less transformed by human use. Seminatural anthromes are relatively lightly populated and used landscapes, with a majority of their areas composed of remnant and recovering habitats.

Wildlands without human populations or intensive use of land still cover nearly one quarter of Earth's ice-free land. Yet only about 20% of Earth's tree cover is in wildlands and more than one third of wildlands are in relatively barren regions, like deserts and tundra. As a result, wildlands account for only about 10% of Earth's terrestrial net primary productivity (NPP)—the photosynthetic production of plants that supports the rest of life on Earth—even less than one would expect based on their area. Remarkably, in 2000, the total area of wild forests remaining on Earth was less than the total area of densely populated village and urban anthromes. The same holds for NPP, with more net primary production occurring within the densely populated anthromes than in Earth's last remaining wild forests. More remarkable still, more than 25% of Earth's tree cover is embedded within cropland anthromes, a greater extent than the total area of forests remaining in wildlands. Clearly, the intensively used anthromes deserve serious attention in understanding Earth's ecology, and their global area and ecological importance are vast and growing.

Anthromes Are Mosaics of Used and Novel Ecosystems

While about 40% of Earth's land is used directly for crops, pastures and settlements, a nearly equivalent area is neither used directly for agriculture and settlements nor left behind in large wild areas without these uses. What is the ecology of these areas? The answer requires a deeper understanding of the way landscapes tend to be transformed and managed by human societies.

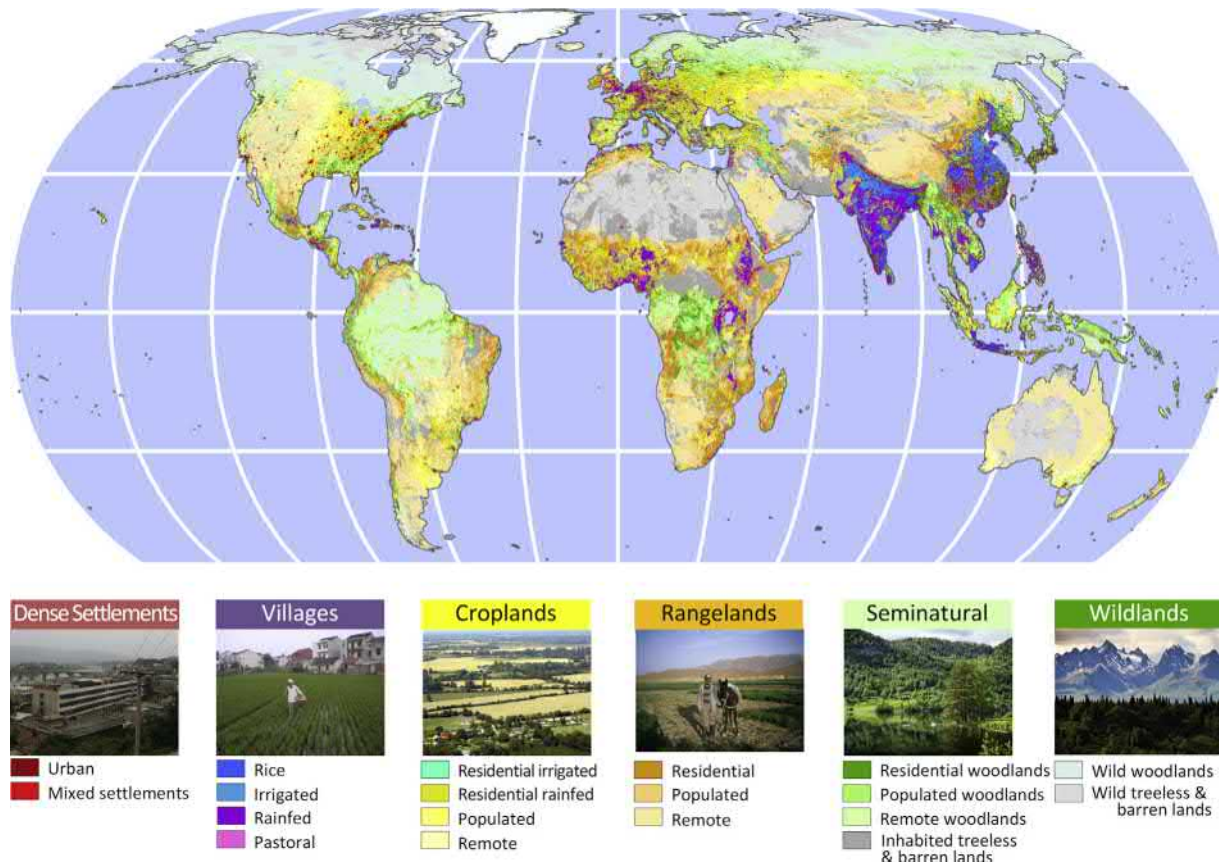


Fig. 1 Global map of anthromes in 2015 CE. Eckert Equal Area projection (Ellis et al., 2020).

Even within the most densely populated and intensively used anthromes, including urban areas and ancient village landscapes, humans rarely convert all land into agricultural and residential uses, but rather, selectively concentrate these uses in areas where they will be most productive, while also planting and retaining trees and other green spaces in association with settlements and infrastructure. When viewed from high above, we see urban areas and settlements embedded within seas of agricultural land, with patches of trees interspersed within and among croplands and residential areas, and managed vegetation is mixed with natural and seminatural vegetation. For this reason, anthrome landscapes tend to be more complex than those of the classic biomes, and are best characterized as heterogeneous multifunctional mosaics of different land uses and land covers, especially where terrain is complex and populations area dense.

Productive level terrain is generally the focus of agriculture and settlements, while hillier, drier, mountainous, and remote terrain tends to be left unused or less used, even when surrounding areas are used intensively. Patches of used land are often abandoned and left to recover within used anthromes, and even remnant patches of habitat within anthromes that have never been managed for production tend to become transformed by human influences ranging from more frequent fires and fire suppression, to harvests of fuelwood, timber and other natural resources, hunting, foraging, increased exposure to exotic species, pollution, and other human influences. Even the isolation of remnant patches from other habitat patches within the used landscape can alter rates of species extinctions and invasions. As a result of these pervasive human influences, even the least disturbed areas of anthrome landscapes generally have biotic communities and ecosystem processes that differ substantially and potentially irreversibly from their prior historical state, broadly fitting the definition of novel ecosystems (Hobbs et al., 2009; Ellis et al., 2010).

Thus considered at a landscape scale, the used and seminatural anthromes are multifunctional mosaics of ecosystems used for production, within which islands of remnant, recovering, and lightly used novel ecosystems are embedded (Fig. 2). For this reason, anthromes are far more than just the used areas of the planet. In fact, they retain a greater global area of lightly used habitats, about 37%, than the total area remaining as wildlands (around 23%). Moreover, these areas tend to be both ecologically productive and highly biodiverse, even though their habitats show clear legacies of human influence and their biological communities tend to be composed of novel assemblages of native, introduced and invading species (Ellis, 2013). The novel ecological patterns and process of anthromes, which now cover more than three quarters of Earth's terrestrial surface, represent the biosphere in its current, human-altered form, and provide the basis for an ecology of the anthropogenic biosphere (Ellis, 2015).

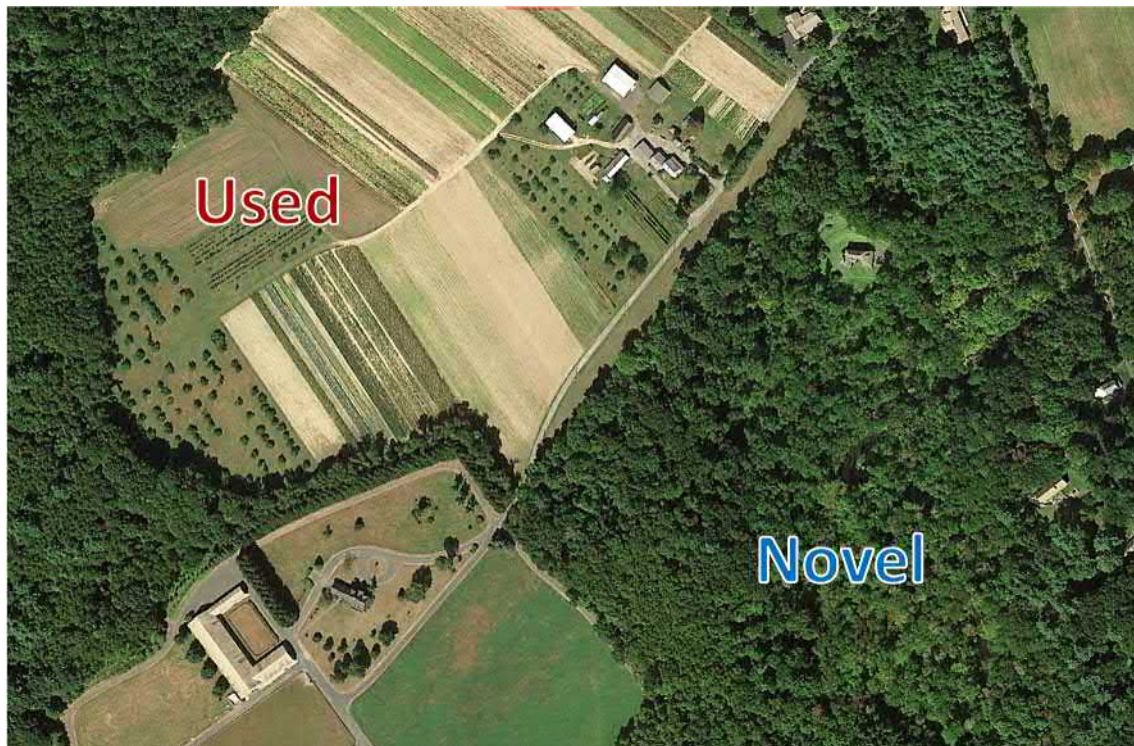


Fig. 2 Anthromes are heterogeneous landscape mosaics composed of used lands and novel ecosystems.

Ecological Science, Theory, and Education in an Anthropogenic Biosphere

Biomes are introduced as the fundamental units of the biosphere in nearly every introductory biology, Earth science, and environmental science textbook. While anthromes should not be thought of as a replacement for existing biome systems based on vegetation and climate, anthromes offer a more objective view of the terrestrial biosphere in its contemporary anthropogenic state. This new model of the biosphere moves us away from an outdated view of the world as “natural ecosystems with humans disturbing them” and towards a vision of “human systems with natural ecosystems embedded within them” (also known as social-ecological systems or coupled human and natural systems). This is a major change in paradigm for most natural scientists concerned with ecology and environments, but it remains a critical advance in efforts to better understand the biosphere as it exists today, and even in the deeper past. Increasingly, anthrome maps and global data on human transformation of ecology are helping to accomplish this, as part of basic curriculum in biology and ecology textbooks (Chapin III et al., 2012; Merritts et al., 2014; Freeman et al., 2016). Anthromes have also been called “human biomes,” a less precise term, and a related term, “indoor biomes” is also increasingly used (Martin et al., 2015).

From the basic theoretical view, the anthrome model of ecological pattern and process has implications for understanding the fundamentals of ecological science from global to regional and even local scales. This general understanding has been integrated within the theory of anthroecology which aims to investigate, understand, and address the ultimate causes of anthropogenic ecological change that shape the emergence of anthromes at global scale, and the ecological patterns, processes and dynamics within anthromes over time and under different social and ecological conditions (Ellis, 2015). Fig. 3 illustrates the different conditions of population density and land use under which the different anthromes form, and how these conditions in turn shape the patterns and processes of net primary production (NPP), carbon storage or emissions from soils and vegetation, reactive nitrogen (from both natural, agricultural and industrial processes), and the patterns of biodiversity in terms of species richness of both native and introduced species.

Efforts to deepen scientific understanding of the ecological patterns and processes shaped and sustained by human societies are ongoing at global, regional and local scales, including recent efforts to define a new “human age” of geologic time, the Anthropocene epoch (Ellis, 2011, 2015, 2018; Waters et al., 2016). Though the Anthropocene remains an informal term and a work in progress (Ellis, 2018), interest in better understanding human transformation of the biosphere is growing almost as fast as human societies are transforming the planet.

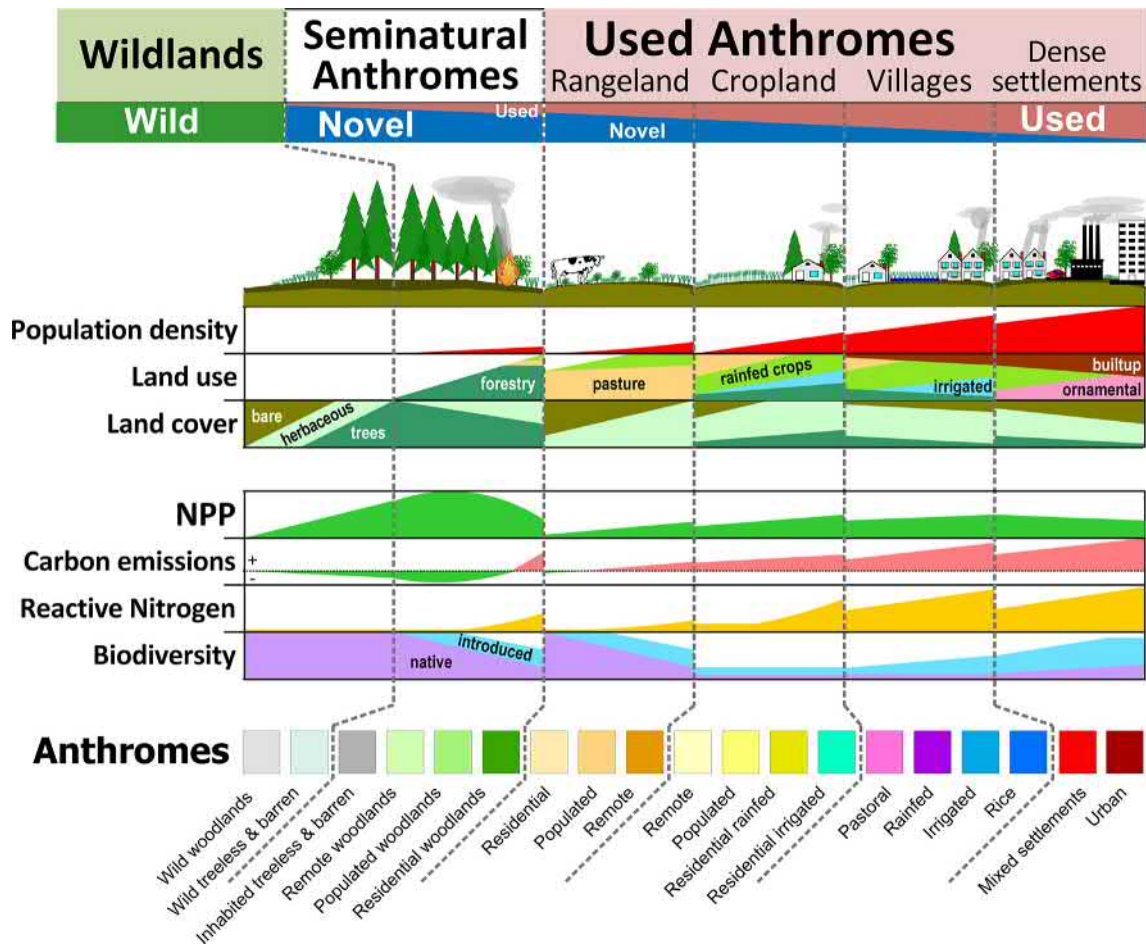


Fig. 3 Conceptual diagram illustrating patterns of populations, land use, novel habitats and biotic communities and ecosystem properties within and across anthromes.

Earth Stewardship in the Anthropocene

Human transformation of this planet is causing unprecedented and accelerating changes in Earth's ecology, from climate change to the massive losses of habitat that are causing species extinctions at alarming rates. While focusing on the negative consequences of human transformation of Earth can help to eliminate some of these, it is equally, if not more important, to focus on efforts to guide the unprecedented powers of contemporary human societies towards creating a better future for both people and nonhuman nature on the only planet we share; the vision of Earth stewardship (Chapin III et al., 2011; DeFries et al., 2012).

Now that humans have reshaped more than three quarters of the terrestrial biosphere into anthromes, the need to conserve biodiversity and nonhuman habitats in the working landscapes of anthromes is increasingly recognized as critical (Martin et al., 2014). Though wildlands are critical habitats for biodiversity conservation in large-scale protected areas, anthromes have largely replaced wildlands in Earth's most biodiverse and productive regions; the novel ecosystems embedded within anthrome landscapes now cover nearly twice the global area of wildlands. Even though many species are poorly adapted to living in close proximity with human societies (and vice versa), recent studies indicate that under appropriate conditions, most native taxa may be sustainable within anthromes, even while increasing anthrome productivity in support of human populations (Ellis, 2013; Quinn et al., 2014).

One key principle of sustainable ecosystem management in the anthropogenic biosphere of the Anthropocene is to develop and sustain beneficial or at least nonharmful interactions between human and nonhuman species and habitats, because avoiding these interactions entirely is simply not a practical strategy in most areas. In working towards more effective environmental governance strategies, anthromes can play a key role in moving conservation discussions beyond the outdated paradigm that human use of ecosystems merely "destroys" them. While there are certainly many examples of human degradation of ecosystems without any long-term benefits to anyone or any being, the conversion of natural habitats into farms, settlements and other infrastructure, creating anthromes, is the basis for sustaining human societies. There are better and worse ways to manage Earth's ecology, but the notion of "going back to nature" to sustain human populations is no longer an option.

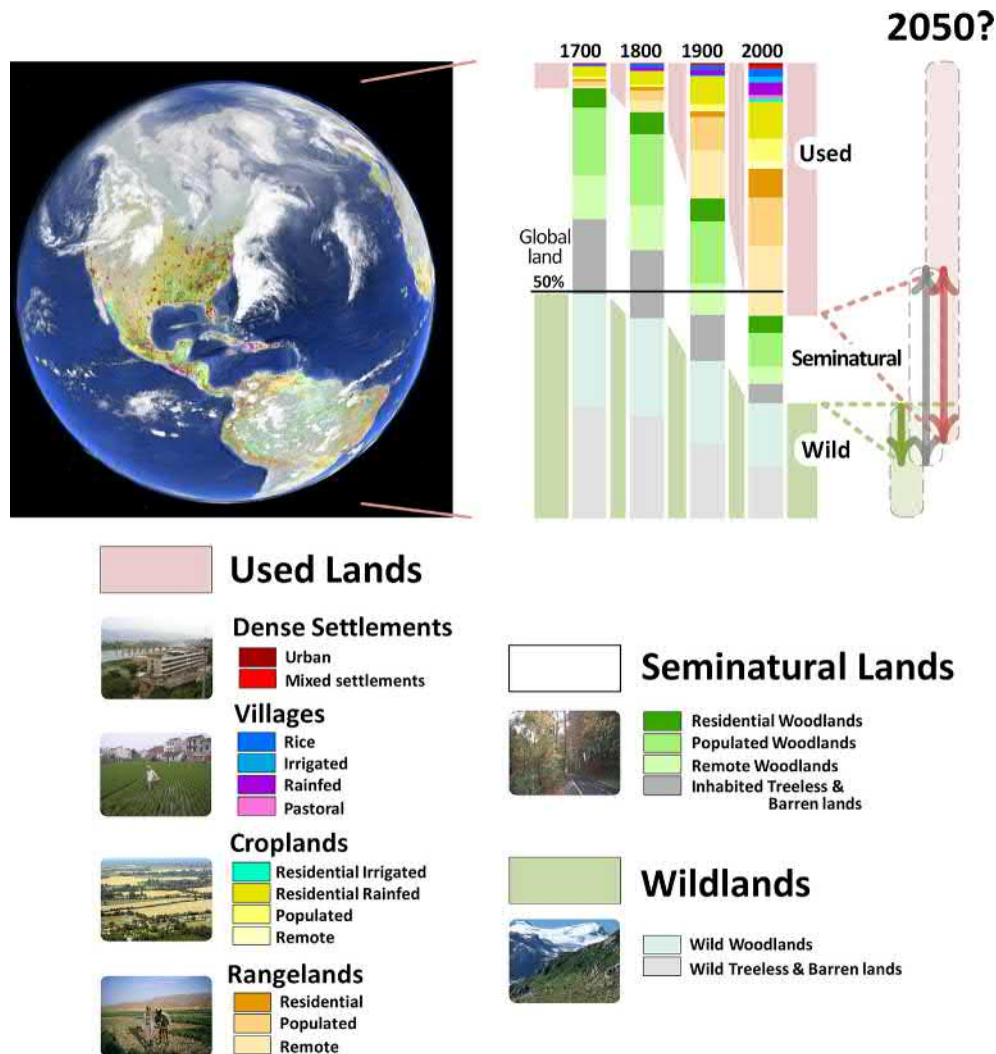


Fig. 4 Earth stewardship in an anthropogenic biosphere. What kind of biosphere do “we” want?

Earth stewardship in the Anthropocene has to be about much more than just “preventing humans from destroying the planet.” The way forward will depend on visions of the future “we” want and strategies to get there: a future where people and nature can thrive together over the long term (Fig. 4). Yet there is no “we,” no singular “humanity” working the levers of planetary governance in the cockpit of spaceship Earth. Making this better future possible will require negotiations across our diverse populations of stakeholders, the “we,” who must work together towards these better futures—from farmers ranchers, urbanists and conservationists, to Indigenous Peoples and governments, nongovernmental organizations and international corporations. The challenges of creating a better future will require multi-level governance solutions that bring people together to negotiate productively across the global supply chains, producers, consumers and conservationists that are now shaping the biosphere (Ellis, 2019).

Do “we” want a sprawling world of human infrastructure that consumes most of Earth’s land, or a dense urban world that leaves plenty of shared and wild spaces to sustain the rest of life? The answer will come from all of us, and it will require much more than saving nature in places far away. Earth stewardship in the Anthropocene will mean governing anthromes to more effectively serve human needs while making space to sustain the rest of nature in an increasingly anthropogenic biosphere.

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Relevant Website

<http://anthrome.org>—link to anthromes project web site hosted by the author, including educational materials, maps, and downloadable datasets.

Historical Change in Anthromes

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Abstract

Since mankind began clearing land and domesticating favored plants and animals at the start of the Holocene, the terrestrial biosphere has been transformed into anthropogenic biomes or anthromes. A first attempt to reconstruct global changes in anthrome distribution from 10,000 BCE to 2015 CE (the Anthromes12K dataset) was derived by using human population density and land use from the History of the Global Environment (HYDE) database (version 3.2), in combination with alternate anthromes classification schemes. At the beginning of the Holocene almost 40% of the Earth's land surface was classified as completely wild, without human settlement or agriculture. The remaining 60% was classified as seminatural with only minor areas of agriculture and settlements, where 33% of the seminatural class was classified as inhabited treeless and barren lands and 26% as remote woodlands.

The first significant areas of cropland and rangeland anthromes emerged around 1 CE (2%) slowly increasing to 5% in 1000 CE. Villages and dense settlements still occupied hardly any space that time (0.2%). The global extent of croplands and rangelands increased by agricultural expansion into wildlands and intensification of land use to 9.4% in 1700 CE and this process accelerated to the end of the 20th century to a share of almost 42%. Villages and dense settlements occupying 8% of the global land surface. All this happened at the expense of seminatural lands who decreased in area by 35.5% and wildlands who lost 14.5% of their original area. This transformation took not place evenly distributed over the Earth and over time, but varied greatly across regions and biomes, depicting large differences in the onset of agriculture.

Introduction

Humans have altered the face of the Earth's landscapes for thousands of years. The first hunter-gatherer cleared land through burning, then the emergence and spread of agriculture took place, leading eventually to the rise of large-scale urban industrial societies (Ellis, 2015; Ellis et al., 2013; Kirch, 2005; Smith and Zeder, 2013). Although the role of recent global populations and land use change in transforming Earth's climate received much attention lately (Foley et al., 2005), we cannot understand these processes without assessing their long-term dynamics in transforming the biosphere (Ellis et al., 2013).

These long-term dynamics can be assessed directly by applying existing historical reconstructions of land use and population, e.g. (Kaplan et al., 2011; Newbold et al., 2015; Ramankutty and Foley, 1999), or by emerging new datasets, such as charcoal and pollen, although these have not (yet) a globally coverage. One recently developed method of assessing the human transformation of the terrestrial biosphere is by mapping the transformation of the "natural vegetation patterns as shaped by climate, terrain and other biogeographic factors" (or classic biomes), into anthropogenic biomes (or anthromes). The idea is that human interactions with ecosystems shaped the global patterns of ecology (Ellis et al., 2010; Ellis and Ramankutty, 2008).

A rule-based classification system, first developed by Ellis et al. (2010), is used to map anthromes by integrating global datasets of human population and land use. In this study, the most recent version of the HYDE database version 3.2 was used (Klein Goldewijk et al., 2011). HYDE provides estimates for population, built-up area, cropland (irrigated and non-irrigated), rice, pastures and rangeland on a 5-arcminute resolution (85 km² at the equator).

Methodology

The potential natural vegetation map of [Prentice et al. \(1992\)](#) formed the basis of the pristine start situation, assuming no human interference at all. Then, an updated and modified rule-based anthrome classification model of [Ellis and Ramankutty \(2008\)](#) upon the new HYDE 3.2 global dataset of human land use was applied.

HYDE

HYDE is an internally consistent spatially explicit database describing the long-term development of human population and land use. Population is represented by 5' resolution maps of total, urban and rural population, as well as built-up area and population density, for the period 10 000 BCE to 2015 CE. The land use categories include croplands, with a distinction between irrigated and rain-fed crops (other than rice) and irrigated and rain-fed rice. Also, land used for livestock grazing is separated into two categories; more intensively used and managed pasture, and less intensively used rangeland. This was done in a two-fold manner to satisfy climate modelers which act upon these classification labels whether to convert the ecosystems or not. A more elaborate description is provided in [Ellis et al. \(2020\)](#).

The starting point for allocation of population and land use are reference maps for the year 2010 CE. The reference map for population was derived from [LandScan \(2014\)](#). The United Nations World Population Prospects ([UN, 2009](#)) provided population statistics for the post-1950 CE, and various country specific sources were applied, if available. The reference maps for cropland and grazing land were derived from the European Space Agency (ESA) consortium ([ESA, 2016](#)). See [Klein Goldewijk et al. \(2017\)](#) for an elaborate description of the selection criteria. The reference map for rice was created by combining data from the MIRCA database ([Siebert, 2008](#); [Siebert et al., 2015](#)), [Ricepedia \(2015\)](#) and maps from [You et al. \(2014\)](#).

The influence of these satellite-based reference maps for allocation weakens when modeling into the past, and some simple allocation rules take over. These rules combine a set of normalized maps of population density, soil quality, distance to water, slope and climate for croplands, and a combination of climate, potential biomes favorable for grazing (e.g. natural grasslands, savanna), net primary production and population density for grazing lands. Irrigation and rice are allocated default within the total cropland area.

Classification System

Anthromes version 2.1 basically replicates the original anthromes 2.0 approach of [Ellis et al. \(2010\)](#) by using grazing land (=pasture + rangeland) together as a direct substitute for the original, combined, "pasture" variable of the original HYDE 3.1 dataset. Anthromes v2.1 classification distinguishes 20 detailed anthrome classes grouped into five major categories: Dense settlements, Villages, Croplands, Rangelands, Seminalural lands and Wildlands (see [Table 1](#)).

Results and Discussion

The Global Scale

Humans started influencing their natural environment already thousands of years ago by using fire as a tool to open natural savannas and grasslands for hunting and early forms of agriculture. Slowly, people evolved to a more sedentary existence by domesticating crops and animals. This process took place over a long time, roughly 12000–6000 BCE and in several places in the world, for example, the Levant region, northern China and India, and Central America. This transition from hunters/gatherers to sedentary farming is often referred to as the Neolithic Revolution ([Goudsblom, 2002](#)). Until 5000 BCE, roughly 60% of the Earth consisted of seminalural land, while the remaining 40% can be classified as wildlands. However, large parts of the seminalural class consist of remote woodlands and inhabited treeless and barren land with very low population densities indeed ([Fig. 1](#)).

The first noticeable agricultural lands seem to appear roughly around 2000 BCE, still occupying a very modest 1% of the total global land area. At 1 CE, the Mayans flourished in Central America, the Han dynasty reigned in China, India went through its Middle Period and the Roman Empire emerged in Europe, which resulted in a more widespread of croplands and rangelands all over the world, but still occupying < 6% of the total land area ([Fig. 1](#)).

In the centuries that followed, apparently not much expansion of agricultural area took place. Notably, large parts of Europe were depopulated as result of the Black Plague and subsequently many rural areas were abandoned and left for regrowth of the original forests ([Bork and Lang, 2003](#)). A process that also took place in the Americas after the Europeans arrived in 1492 CE. Introducing not only livestock and different agricultural practices but also diseases such as smallpox and the flu, which resulted in a decimation of the native population in many regions. This must have had a large impact on the native ecosystems such as a large regrowth of native forests ([Nevle and Bird, 2008](#)).

The pace of agricultural expansion really increased in the early 18th century, roughly at the start of the Industrial Revolution. It was a time of worldwide exploration and colonization, and establishment of plantations in many regions. Mechanization in the first half of the 20th century replaced horsepower and boosted rapid clearing of large areas of natural ecosystems such as for example the Great Plains in the US. A major boost of agricultural growth happened after WWII driven by the mass application of artificial fertilizer and genetic improvement of crops, also referred to as the Green Revolution or the Great Acceleration. All this is manifested by

Table 1 Anthrome version 2.1 classification scheme.

Dense settlements: Urban and other dense settlements

11 Urban Dense built environments with very high populations

12 Mixed settlements Suburbs, towns and rural settlements with high but fragmented populations

Villages: Dense agricultural settlements

21 Rice villages. Villages dominated by paddy rice

22 Irrigated villages. Villages dominated by irrigated crops

23 Rainfed villages. Villages dominated by rainfed agriculture

24 Pastoral villages. Villages dominated by rangeland

Croplands: Lands used mainly for annual crops

31 Residential irrigated croplands. Irrigated cropland with substantial human populations

32 Residential rainfed croplands. Rainfed croplands with substantial human populations

33 Populated rainfed croplands. Croplands with significant human populations, a mix of irrigated and rainfed crops

34 Remote croplands. Croplands without significant populations

Rangelands: Lands used mainly for livestock grazing

41 Residential rangelands. Rangelands with substantial human populations

42 Populated rangelands. Rangelands with significant human populations

43 Remote rangelands. Rangelands without significant human populations

Seminatural lands: Inhabited lands with minor use for permanent agriculture and settlements

51 Residential woodlands. Forest regions with minor land use and substantial populations

52 Populated woodlands. Forest regions with minor land use and significant populations

53 Remote woodlands. Forest regions with minor land use without significant populations

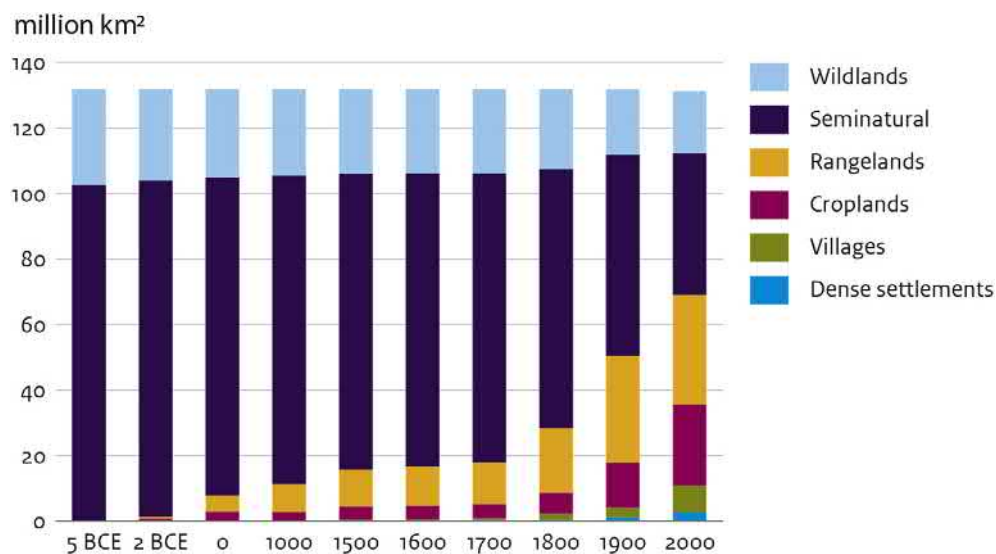
54 Inhabited treeless and barren lands. Regions without natural tree cover having only minor land use and a range of populations

Wildlands: Lands without human populations or substantial land use

61 Wild woodlands. Forests and savanna

62 Wild treeless and barren lands Regions without natural tree cover (grasslands, shrublands, tundra, desert and barren lands)

63 Wild, remote, ice

**Fig. 1** Transformation of anthromes over time.

the increase of the cropland and rangeland anthromes, at the cost of mostly the semi natural lands, and to a lesser extent the Wildlands (see Fig. 2).

After the Second World War the world's population increased exponentially. More and more people started to live in cities and towns, in 2008 CE more people on the planet lived in villages, towns and cities than on the countryside (UN, 2018). However, the share of Villages and Dense settlements is still very modest, it occupies around 0.5% of the Earth's total land area, although there are some places with higher levels (NW Europe, parts of India, China; Figs. 2 and 3).

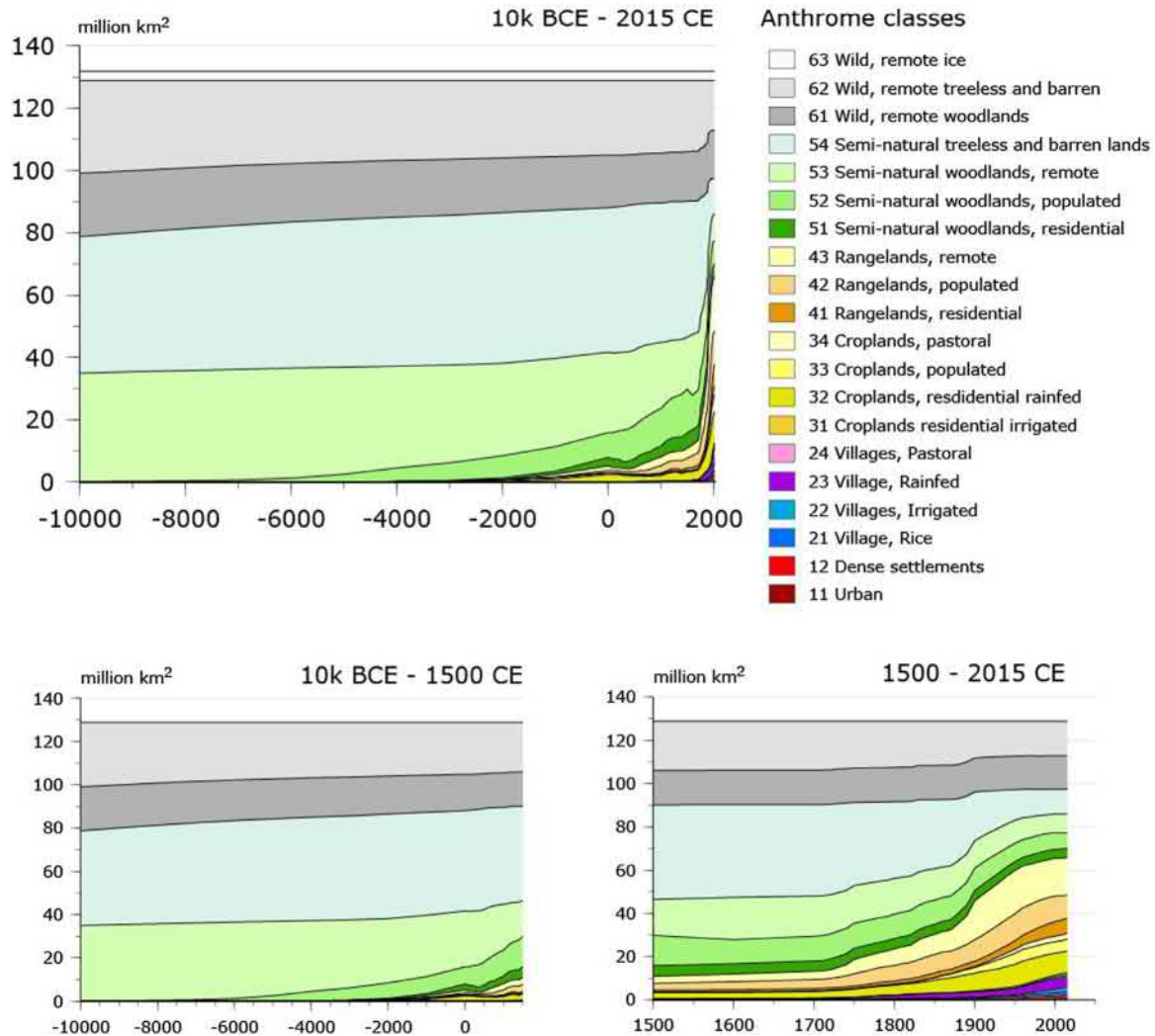


Fig. 2 Anthromes v2.1 development over the 12k period, with two snapshots for the 10k BCE–1500 CE and 1500–2015 CE period.

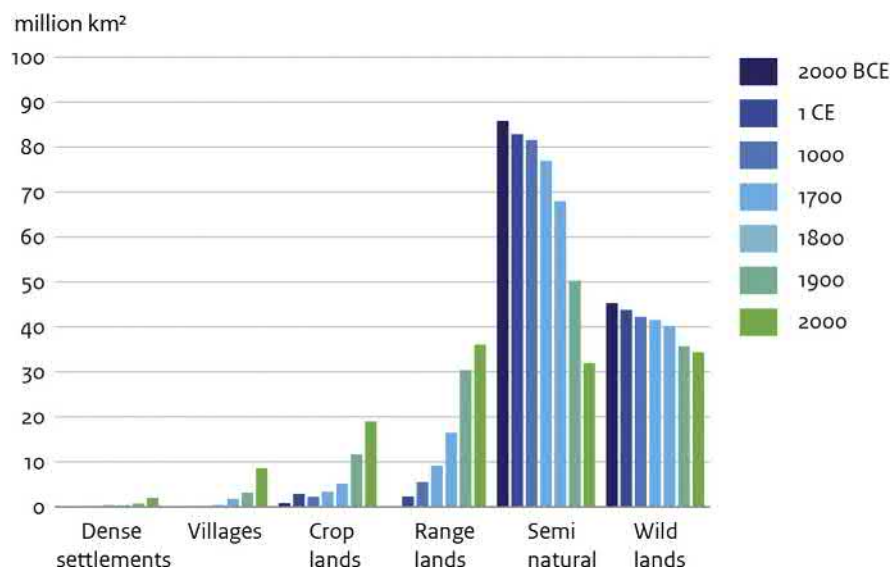


Fig. 3 Anthromes v2.1 development in selected time slices showing the transformation of the different anthromes classes into each other. A clear increase of human dominated classes Dense settlements, Villages, Croplands and Rangelands at the costs of Seminatural lands and Wildlands.

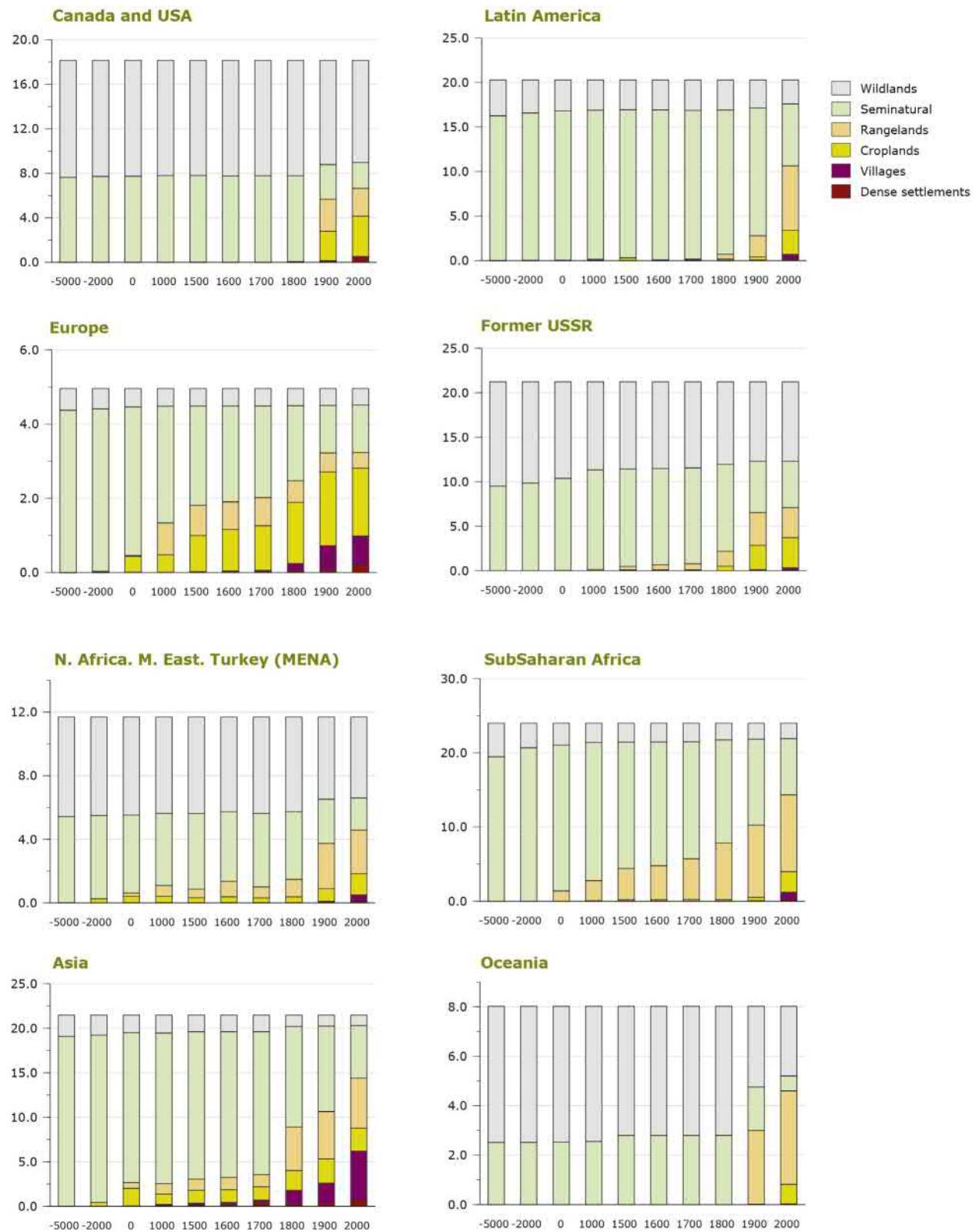
Regional aggregated Anthromes (in million km²)

Fig. 4 Regional anthromes development over time (note the different Y-axes).

The Regional Scale

The transformation of biomes was not evenly distributed over time and space. Some regions transformed earlier than others, and some biomes were converted much more than others. All regions had quite a share of wildlands at the start of the Holocene, but some more than others. Oceania still had 65% wildlands back then, comparable to the 60% of former USSR, Canada and the United States, and the Middle East, North Africa and Turkey (MENAT) region, the rest was seminatural. Latin America and sub-Saharan Africa had less wildlands left (around 20%), Asia and Europe (~10%), the rest was already seminatural, but not densely populated. Canada and the United States and the former USSR still have a fair share of wildlands left (~60%), mainly boreal forest and arctic tundra, comparable with MENAT and Oceania, mainly barren and hot deserts.

Also, the start of agricultural development is not evenly distributed around the world. It was much earlier in MENAT, Asia, and Europe, where domestication of plants and animals took place as early as 9000–6000 BCE. The share in cropland dominated Europe from 1 CE onwards, while in Asia the increase in cropland and rangelands developed simultaneously until the onset of the 18th century, when rangelands expanded faster than croplands. Both regions saw an early growth of villages and dense settlements then other anthromes.

Developments were much different in the so-called New world. The regions of Oceania, Canada and the United States and Latin America experienced relative recently, that is, over the past two centuries, a significant increase in croplands and rangelands. Although native populations in those regions, especially in the Americas, already for a long time had practiced agriculture, it apparently was on such a modest scale that is hardly does shows up in analysis such as [Klein Goldewijk et al. \(2017\)](#). Recent evidence suggests that those studies might have severely underestimated the number of people and their agricultural presence in the pre-Columbus period. In Oceania the Aborigines did not practice sedentary agriculture, they were hunters and gatherers. In Sub-Saharan Africa Rangeland existed since 1 CE and occupies at present a relatively large share of the total anthromes scheme (ca. 50%), comparable with Oceania ([Fig. 4](#)).

Spatially, the anthromes wildlands category resides predominantly the higher latitudes such as the arctic and Antarctic regions, but also the hot desert areas such as the Sahara, Namibian and Australian deserts. The reminder of the world was at the beginning of the Holocene in a Seminatural state, either treeless and barren (fUSSR, MENAT), remote populated (fUSSR, Latin America) or populated at various levels (Europe, India, China). Around 1700 CE rangelands had established themselves in sub-Saharan Africa, Europe, and parts of (central) Asia, e.g. Western China and Mongolia. The most people living in Villages and Dense settlements were prominent in large parts of Europe and in the large river basins in India and China, see [Fig. 5](#).

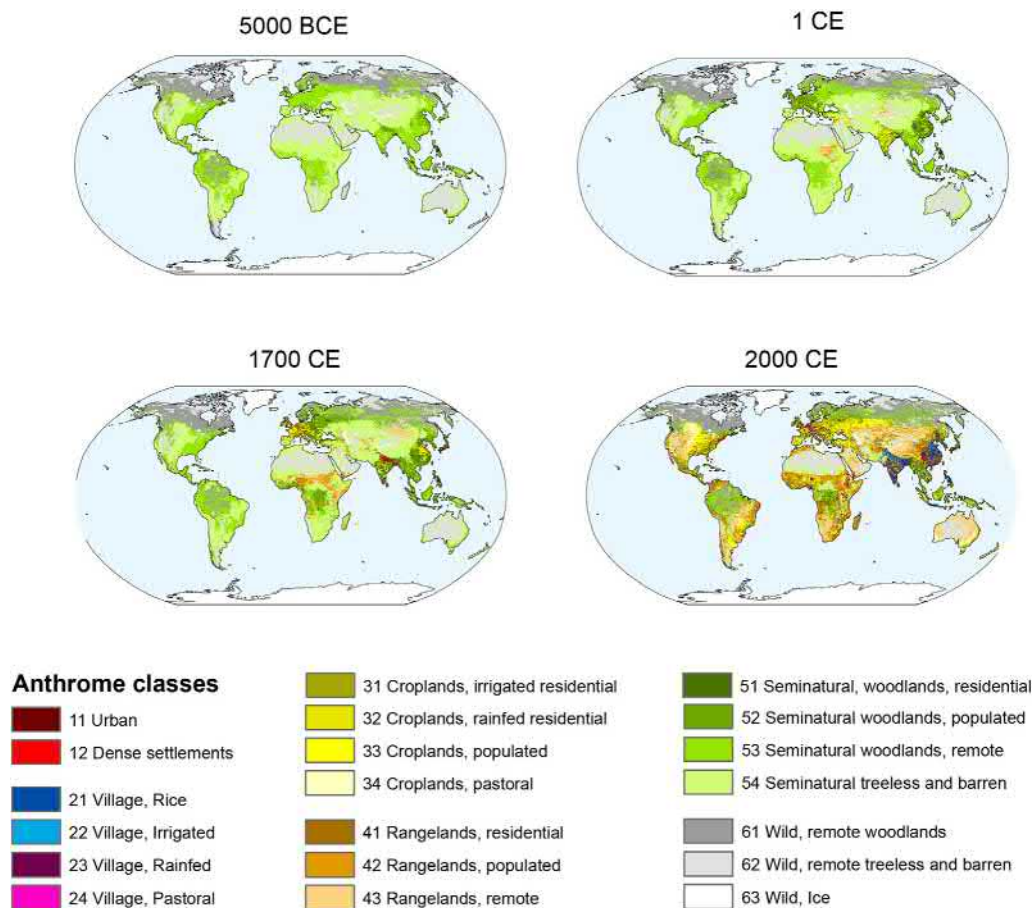


Fig. 5 Anthrome maps over the Holocene, selected years.

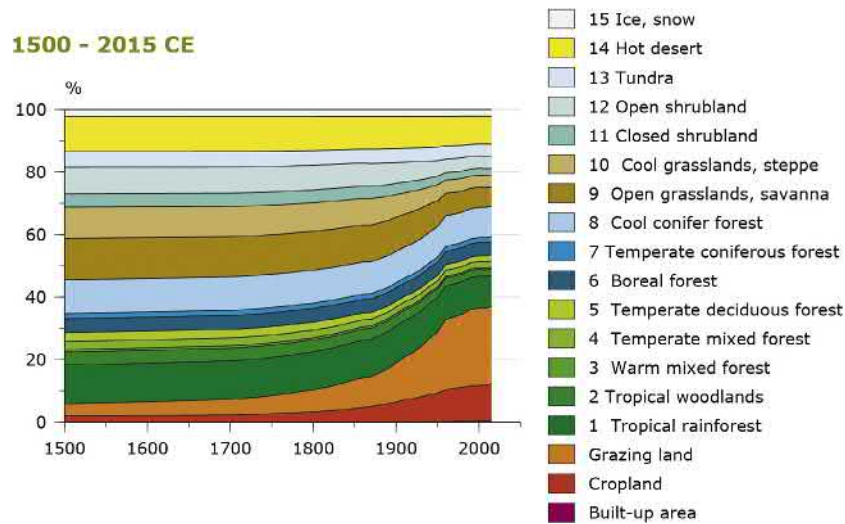


Fig. 6 Percentage change of natural and anthropogenic biomes over time.

The Biome Scale

All these expansions of human influence must have had an impact on the natural ecosystems. One way of dealing with this is looking at biomes. Biomes are defined as a large naturally occurring community of flora and fauna occupying a major habitat, e.g. forest or tundra. As we look at the largest change we see that this mostly happened in the last five centuries, and especially in the open grasslands and savanna class (no. 9) which occupied 14.5% of the total land area in 10k BCE and 5.9% in 2015 CE, a loss of 8.6%. The second largest loss occurred in cool grasslands & steppe class (no. 10) which went from 10.8% to 3.2%, a loss of 7.6%. Open shrublands (class 12) lost 5%, Closed shrublands (class 11), Hot deserts (class 14), Tropical rainforests (class 1) and Tropical woodlands (class 2) all lost 2 to 3% of their original area. The other categories lost <2%. If we translate this to forest versus non-forest it yields a 9.8% loss in forests, and 27.6% in non-forested area, so surprisingly to some most of the transformations took place not in forests but in grasslands. The transformation of the natural biomes is depicted in Fig. 6.

Nevertheless, some regions still suffered a considerable loss of forest area. Europe, Asia and MENAT lost 40% or more of their original forest biomes during the Holocene. SSA, Oceania and Latin America lost between 22% and 30%, while the United States and Canada in North America and fUSSR lost less than 13% from their (large) original forest area, see Table 2. One has to be aware that the overall number can be a bit misleading. For example, the number does not reflect the large deforestation and reforestation waves in the United States during the 19th and 20th centuries. The change in the non-forested biomes is even larger in all regions except MENAT (dominated by the Sahara Desert). In the rest of the world's regions more than half of the original biomes has been transformed to other types of use, mostly the natural grasslands and savannas. They were often converted into croplands or rangelands. In some regions the deforestation trends have been reversed recently, the so-called forest transition. Coupled to a relative high standard of living, income, GDP some countries could afford to abandon prime agricultural area and let them regrowth or replanted to forest again. Examples are the United States, Japan, and Europe.

Conclusion

To conclude, a long term anthromes dataset for the Holocene has been produced. It shows a slow but steady development over time of human encroachment towards the wild, uninhabited regions of the world. This expansion of anthropogenic land use resulted first

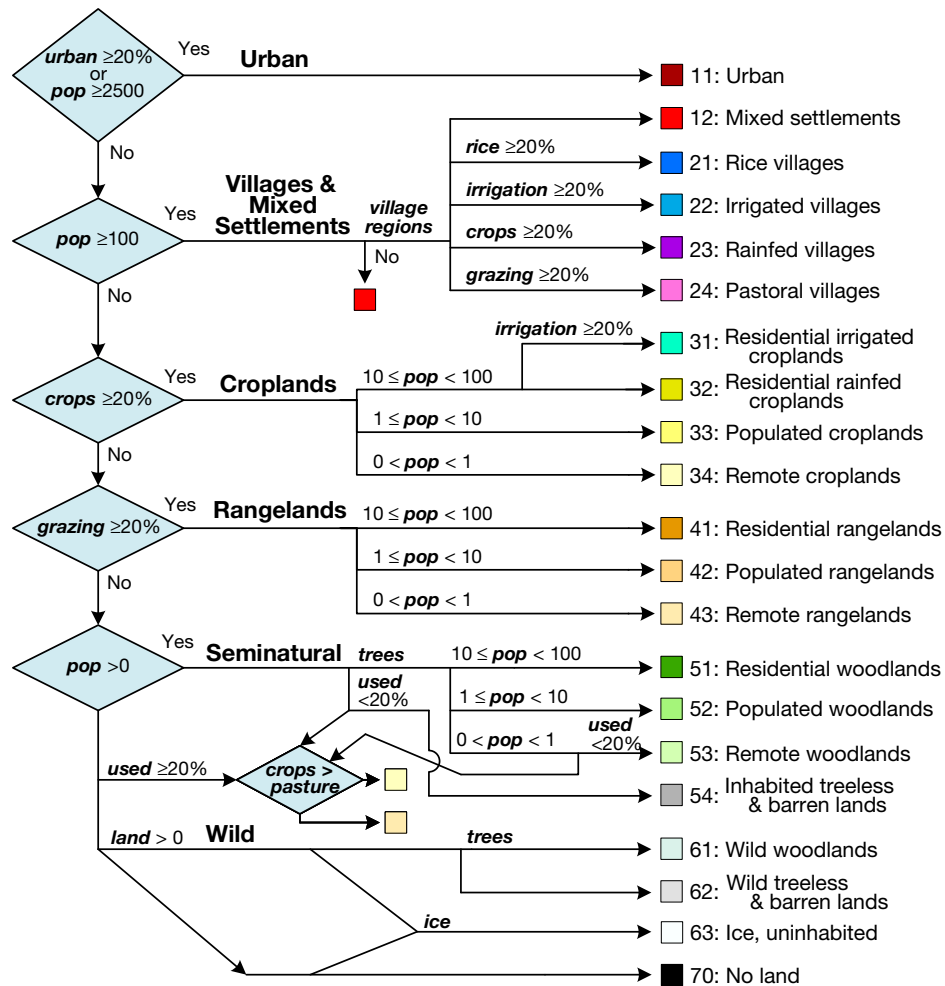
Table 2 Forest and Non-forest transformation 10k BCE–2015 CE.

	Forest	Non-forest
Canada and USA	–13%	–45%
Latin America	–22%	–57%
Europe	–40%	–46%
fUSSR	–9%	–51%
N. Africa, M. East, Turkey	–45%	–31%
Sub-Saharan Africa	–30%	–50%
Asia	–40%	–59%
Oceania	–29%	–51%

in conversion of natural ecosystems, mainly natural grasslands, savannas and forests. The expansion of agriculture happened at a rather slow pace, varying per region in magnitude and timing. It accelerated in the past three hundred years but seem to slow down recently. At the same time, we also witnessed in the more densely populated areas more and more intensification of human land use activities.

Appendix A: Anthromes Classification Flowchart

Anthromes v2.1 classification algorithm. Same as Anthromes 2.0, with four changes. First, the grazing variable is substituted for the HYDE 3.1 pasture variable, because HYDE 3.2 now separates the HYDE 3.1 pasture variable into separate pasture = % area covered by intensively managed pastures) and rangeland = extensively managed grazing areas; grazing = pasture + rangeland. Second, land variable classifies cells with land area > 0 (anthromes v2.0 did not include cells without land). Third, a new anthrome class = 63 = ice, uninhabited is added; anthromes 2.0 included only ice-free land. Fourth, a no data anthrome class is added = 70 (used only as a placeholder for no data values after classification).



Appendix B: Regional Breakdown

Since HYDE is used as one of the inputs for the Integrated Model to Assess the Global Environment; IMAGE (Stehfest et al., 2014), all computations have been performed following the IMAGE regional breakdown. For simplification we aggregated the IMAGE regions into nine Anthromes regions.

Reg. no	Anthrome region	IMAGE regions	Land area (km ²)	% of total land area
1	North America	Canada	8,918,000	6.8
		USA	9,078,798	7.0
2	Latin America	Mexico	1,943,090	1.5
		Rest Central America	735,115	0.6
		Brazil	8,442,870	6.5
		Rest South America	9,184,572	7.0
3	Europe	Western Europe	3,625,136	2.8
		Central Europe	1,337,584	1.0
4	M. East, N. Africa and Turkey (MENAT)	Middle East	5,173,031	4.0
		Northern Africa	6,014,386	4.6
		Turkey	775,569	0.6
5	sub-Saharan Africa (SSA)	Western Africa	11,350,296	8.7
		Eastern Africa	5,849,409	4.5
		South Africa	1,219,090	0.9
		Rest Southern Africa	5,600,266	4.3
6	former USSR	Ukraine +	824,610	0.6
		Asia-Stan countries	3,888,675	3.0
		Russia +	16,517,548	12.7
7	Asia	India	3,164,144	2.4
		Korea	236,430	0.2
		China +	10,886,215	8.4
		Southeastern Asia	2,576,856	2.0
		Indonesia +	2,415,585	1.9
		Japan	421,313	0.3
		Rest of South Asia	184,3407	1.4
8	Oceania	Oceania	8,034,489	6.2
9	Greenland	Greenland	312,914	0.2
	World (without Antarctica)		130,369,398	100.0

Acknowledgments

Klein Goldewijk contributions were supported by NWO VENI grant no. 016.158.021. This study was also undertaken as part of the Past Global Changes (PAGES) LandCover6K working group project, which in turn received support from the US National Science Foundation and the Swiss Academy of Sciences.

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Human Appropriation of Net Primary Production

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Abstract

Human transformation of the planetary landscape is extensive and may have exceeded the land system change planetary boundary. The human appropriation of net primary production (HANPP) method models the intensity of human pressure on the landscape at different scales. Globally, HANPP has doubled since 1900 and currently humans appropriate about 25% of the total net primary production of the planet. HANPP spatially correlates well with anthropogenic biomes, as “used” anthropogenic biomes generally correlate with high HANPP. In addition to the global scale, the HANPP method can also be used at regional, national, and local scales, though extrapolation of datasets from one scale to the next should be carefully considered. Embodied HANPP is used to better understand the effect of imports and exports, and shows that HANPP generally is transferred from rural to urban populations. As a model, HANPP does have a relatively high level of uncertainty, but appears to be an important measure of land transformation.

Introduction

Although scientific concern regarding human alteration of the landscape has a long history, the extraordinary scale of environmental change became very apparent only in the last 25 years. Vitousek et al. (1997) showed the transformation of the planetary surface for the benefit of humans (e.g., Kareiva et al., 2007) was spatially extensive and had major impacts on global systems such as biodiversity and biogeochemical cycles. Later, Foley et al. (2005), Ramankutty et al. (2008) and others showed that row crop and pasture covered nearly 40% of the ice free planet. The subsequent delineation of the planetary landscape into anthropogenic biomes (anthromes) showed that over 58% of the planet is “used,” much of the rest is semi-natural, and less than 20% wild. Most of the “used” anthromes are directly associated with producing food via the village, row crop, and rangeland anthromes (Ellis, 2011). About 30% of the used anthromes of the planet are utterly transformed landscapes—high density settlements, villages, and croplands. The recent planetary boundary concept (Rockström et al., 2009; Steffen et al., 2015a) indicates that land use change has likely surpassed their definition of the boundary, though the choice of forest cover for the of the boundary by Steffen et al. (2015a) is somewhat controversial.

Regardless of the definition of the land-system change boundary, human conversion of the landscape typically reduces net primary production, the uptake of carbon by plants and other autotrophs minus energy lost via respiration, metabolism, and maintenance. As anthromes reflect human use of potential vegetation and land use intensity, a correlation between anthrome classification and change of net primary production seems likely. To address the uncertainty in the land-system boundary, Running (2012) proposed that the human appropriation of net primary production (HANPP) method could be used as a planetary boundary as it integrates the land-system change, freshwater use, biosphere integrity, and biogeochemical flow boundaries. But what is HANPP and how does it link to anthromes and land-use change?

The HANPP Method

Human appropriation of net primary production or HANPP is a measure of land use *intensity*. In effect, it is a measure of how humans transform the landscape to provide food, shelter, and transport. The domestication of the landscape, however, requires a

trade-off in that humans replace the vegetation that could potentially grow with different vegetation that can be harvested and grazed or with infrastructures such as buildings and roads. In effect, humans *appropriate* net primary production of the landscape because of land use change, harvest of biomass (crops, timber, forage, animals), and sometimes fire. Haberl et al. (2014) suggest HANPP is an “integrated socio-ecological indicator quantifying effects of human-induced changes in productivity and harvest on ecological biomass flows.” They suggest that HANPP is a valuable quantitative socioecological indicator that captures in a measurable and comparable way how humans transform and domesticate the landscape to meet our needs. The consideration of land use intensity also suggests anthromes and HANPP may have a close spatial association.

In general, HANPP is calculated by comparing the potential NPP of the defined landscape’s potential vegetation at a given time to the actual NPP of the landscape while accounting for harvest of crops and grazing of pastures and rangelands (Haberl et al., 2007, 2014). The basic equation for calculating HANPP is the following (Eq. 1, Fig. 1):

$$\text{HANPP} = \text{NPP}_{\text{pot}} - (\text{NPP}_{\text{act}} - \text{HANPP}_{\text{harv}}) \quad (1)$$

In this equation, NPP_{pot} is the potential net primary production of the landscape, NPP_{act} is the estimated NPP of the landscape as it exists, and $\text{HANPP}_{\text{harv}}$ is the NPP appropriated by harvesting of crops and timber and grazing by animals. $\text{HANPP}_{\text{harv}}$ includes “used extraction” (HANPP_{uc}) and the unused fractions associated with harvest such as residues left on the fields, roots of trees and crops left behind, and human induced fires. The difference between NPP_{pot} and NPP_{act} is $\text{HANPP}_{\text{luc}}$, or how much NPP is appropriated by land use change. NPP in each part of the equation can refer to either above ground NPP or to total NPP (above ground growth plus growth of roots below ground), and thus above ground or total HANPP. Generally, HANPP is reported as a percentage of NPP_{pot} , though it is also reported in mass of carbon per year appropriated (Haberl et al., 2007). These variables used in calculating HANPP (Haberl et al., 2014) are explained below in an introductory manner. Haberl et al. (2014) contains an excellent history of the development of the HANPP concept. A full discussion of methods and their limits are contained in Haberl et al. (2007), Erb et al. (2009), and Haberl et al. (2014).

Potential Net Primary Production: NPP_{pot}

The estimated net primary production of the landscape under a given climate condition in the absence of human land use is called the *potential* net primary production. Numerous methods exist for estimating potential net primary production, including large scale computer simulation models that account for multiple variables to simpler models that account for only rainfall and temperature (see Haberl et al., 2007, 2014; Andersen et al., 2015). These models are calibrated against actual measured net primary production of vegetation in various biomes reflecting potential vegetation. The choice of model depends on the nature and scale of the research problem. For example, at the global scale, the LPJ model is typically used (Haberl et al., 2007; Krausmann et al., 2013). In contrast, Andersen et al. (2015) in a study of HANPP at the watershed scale chose a very simple model to calculate NPP_{pot} based on temperature and rainfall. At each scale, data is lost when simplifying the spatial heterogeneity of potential vegetation. The model chosen should reflect the scale of the analysis and the availability of local data on net primary production.

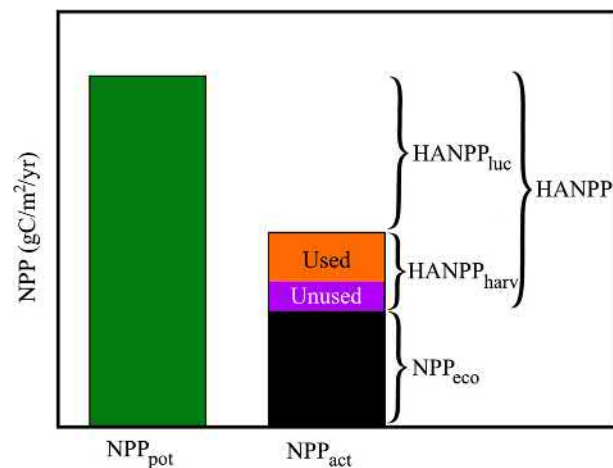


Fig. 1 A conceptual model of the human appropriation of net primary production (HANPP). NPP_{pot} is the model estimate of potential net primary production (NPP), NPP_{act} is actual NPP of land cover types in the landscape, NPP_{luc} is NPP loss caused by land use change, NPP_{harv} is NPP of harvested timber and vegetation for crops and grazing, and NPP_{eco} is the NPP remaining in the landscape ecosystem postharvest. Modified from Haberl H, Erb KH, and Krausmann F (2014) Human appropriation of net primary production: Patterns, trends, and planetary boundaries. *Annual Review of Environment and Resources* <https://doi.org/10.1146/annurev-environ-121912-094620>.

Actual Net Primary Production: NPP_{act}

The actual NPP of the landscape is more difficult to estimate because real landscapes typically are a mosaic of different land uses. For example, a region can be a complex mixture of forest, low-density housing with turf grass and sparse trees, and row crop. Estimating NPP_{act} at finer grains requires knowledge of (1) the area of different land use and cover types, and (2) the NPP of the vegetation of the different land use and cover types.

At smaller scales, the land use and land cover of an area are typically classified using data from either satellite imagery or air photos depending on the scale of the research problem. For example, a global scale study of HANPP done at the 5' scale would require satellite imagery, but a watershed scale study could use airphotos or satellite imagery with a smaller grain (e.g., 30 m Landsat data). GIS databases, such as the USDA Cropscape or the US National Land Cover Database, can be used to get the area of a particular land cover rather than classifying oneself, but smaller land cover elements including single trees or smaller roads may be lost at this resolution. As Haberl et al. (2014) notes, the derivation of land cover datasets is difficult and time consuming because of the need for the areas for each pixel in the area of interest must total 100% and the total of all the pixels should align with that for the known land cover of the area of interest (this works primarily for state or national level where land cover data is available).

Once the land cover is classified, calculating the NPP_{act} for an area is difficult as it requires the use of data from the literature regarding ecologically similar landscapes or models (e.g., the LPJ model, Haberl et al., 2014). For forests and grasslands, data can be extrapolated from the literature or derived from vegetation models. Ideally, these data come from as similar an ecoregion as possible, but when local data is not available, regional is preferred to global. Vegetation models such as the LPJ model can also account for soil degradation and irrigation. For croplands, NPP_{act} is derived from crop harvest data typically collected and or made available at the national, state, or county level (e.g., Haberl et al., 2007; Andersen et al., 2015) using a variety of crop and harvest indices. More difficult are residential and urban lands that have complex mosaics of shrubs, trees, turf grass, and impervious surface. Such a mosaic has a complex mixture of NPP ranging from impervious surface at $0 \text{ g C m}^{-2} \text{ yr}^{-1}$ to turfgrass at $1000 \text{ g C m}^{-2} \text{ yr}^{-1}$ to forested areas of over $1000 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Andersen et al., 2015). On a global scale, or even national scale, the problem of urban mosaics is not as critical because urban land cover tends to be a low percentage of the total area. However, at smaller regional or watershed scales, urban land cover can be a significant percentage of the total. When total HANPP (above + below ground NPP) is calculated, root:shoot ratios are needed for forests, grasslands, and croplands and the root:shoot data are derived from the literature (e.g., Haberl et al., 2007).

Harvested Net Primary Production: $HANPP_{harv}$

$HANPP_{harv}$ is the amount of net primary production from row and fodder crops, timber, and grazing animals that are appropriated by humans (Haberl et al., 2014). Row crop and timber harvests are available at the national level from a variety of sources such as FAOstat. In the US, county level data for crop harvests are available for 5 years increments from the US Department of Agriculture. Assumptions need to be made for losses and residual crop carbon left behind (e.g., Haberl et al., 2007). Access to timber harvest data below the national level can be more problematic but is available for some regions (e.g., US Forest Service in the United States as used in Andersen et al. (2015)). Grazing harvest requires knowledge of the type and number of animals, amount of grazing land, and assumptions of the return flow of carbon to the soil via manure (see Haberl et al., 2007).

Net Primary Production Lost by Land Use Change: $HANPP_{luc}$

$HANPP_{luc}$ is the amount of net primary production appropriated by land transformation from one land use to another. The HANPP of land use change (luc), then, is the difference between the potential net primary production (NPP_{pot}) and the actual net primary production (NPP_{act}) of the landscape (Fig. 1). In nearly all cases, NPP_{act} is lower than NPP_{pot} . For example, converting forest cover with an above ground NPP of $1000 \text{ g C m}^{-2} \text{ yr}^{-1}$ to row crop with an above ground NPP of $500 \text{ g C m}^{-2} \text{ yr}^{-1}$ would be an above ground HANPP of 50% before harvest. The only exception to this rule would be where groundwater is used to convert desert into row crop, which results in an NPP greater than NPP_{pot} and an HANPP of greater than 100% (e.g., Haberl et al., 2007). Only a few locations at the global scale have HANPP greater than 100%, and all are in arid regions. Urban areas are the most extreme example of $HANPP_{luc}$ as impervious surface has an $HANPP_{luc}$ of 100% as NPP is effectively reduced to $0 \text{ g C m}^{-2} \text{ yr}^{-1}$.

Estimation of HANPP requires a number of assumptions (often unique to a given scale), extrapolation of datasets within and across different scales, and the use of computer models. As a consequence, there is always a level of uncertainty associated with each part of the HANPP calculation and the final estimations. Researchers interested in calculating HANPP for their region of interest should take the necessary time to consider these assumptions and the type of data available.

Global Patterns of HANPP

At the global scale, HANPP is calculated both in terms of mass of carbon per year (e.g., Pg C yr^{-1}) and as a percentage of the potential net primary production, NPP_{pot} . Global HANPP has been calculated using a number of methods over the years (see Haberl et al., 2014 for a history). Haberl et al. (2007) calculated that, for the year 2000, the global above ground HANPP was about 29% and global total HANPP was about 24%. This is significant in that the results indicate that nearly one third of the potential

global net primary production on an annual basis is appropriated by a single species—humans. Global mapping by Haberl et al. (2007) shows that HANPP is unequally distributed, with the highest appropriation percentages in India, eastern China, Europe, and the midwest of the United States (Fig. 2A), areas that classify as cropland and village anthromes. A few areas have high HANPP, such as southern Australia and western Africa but are smaller in spatial extent.

Similar to heterogeneity in spatial distribution, drivers of HANPP vary. Row crop harvest contributes nearly 50% of the global total HANPP, grazing on rangeland contributes nearly 29%, and timber harvest contributes almost 11% (Haberl et al., 2007). Thus, human food, fiber, and timber harvest account for 89% of the global total HANPP of $15.6 \text{ Pg C yr}^{-1}$. Not all HANPP_{harv} is used in a final form by humans, such as consumption of food (Krausmann et al., 2008). Indeed, about $\frac{2}{3}$ of HANPP_{harv} is used. The other $\frac{1}{3}$ of HANPP_{harv} is not used by humans, including crop residues and roots left behind or vegetation burned in fires.

Since 1900, global total HANPP has doubled to about 25% of potential net primary production (Krausmann et al., 2013). Compared to other indicators of global change this result is somewhat stunning given the exponential growth in the human population and consumption of resources, particularly post WWII (Steffen et al., 2011, 2015b; Krausmann et al., 2013). For comparison, affluence (measured as GDP) has increased over 20 fold and population has increased more than 3 fold during this time period (Steffen et al., 2011). This relative decoupling is a direct outcome of the agricultural intensification of the Green Revolution, as fertilizer, high-yield crop varieties, irrigation, mechanization, and pesticides have dramatically increased the yield of croplands (Foley et al., 2005, 2011). Thus, increasing yields associated with the Green Revolution dramatically slowed the expansion of cropland, even allowing reforestation in some parts of North American and Europe. The Green Revolution, particularly nitrogen fertilizer produced by the Haber-Bosch process, has allowed the population to grow far greater than the planet could otherwise support, but also led to a number of unintended consequences (Erismann et al., 2013). Although agricultural intensification reduced demand for arable land and thus limited the growth in HANPP, the trade-off associated with an exponential rise in nitrogen fertilizer use is an exponential rise in the greenhouse gas N_2O and a dramatic increase in hypoxic coastal zones (Steffen et al., 2015b). Additionally, much of the intensification of agriculture is driven by irrigation, which has led to falling groundwater tables around the world (Famiglietti, 2014).

The Potential Correlation of HANPP and Anthropogenic Biomes

Ellis and Ramankutty (2008), Ellis et al. (2010), and Ellis (2011) have developed the concept of anthropogenic biomes as a way to better show that the global ecological system is now essentially a human system that has semi-natural ecosystems embedded within it. In effect, they find that over 55% of the ice-free land surface is “used.” Used landscapes are those dominated by urban, village, row crop, and rangeland anthropogenic biomes. Urban land cover is relatively small ($\sim 3\%$) showing the primary importance of agriculture for land transformation. A comparison of the global distribution of anthromes (Fig. 2B) with that of global total HANPP (Fig. 2A) shows a distinct overlap of used anthromes with high total HANPP. Village anthromes in India and China, row crop anthromes in the midwestern United States, urban/row crop/village anthromes in Europe, cropland/rangeland anthromes in southeastern South America, and village/cropland anthromes in west Africa correlate with high HANPP. Perhaps the most striking example of all of these is India, with 60–100% HANPP and nearly 100% village anthrome. These patterns make sense, as anthromes are defined in part by population density (Ellis and Ramankutty, 2008) and population density has been found to have a strong correlation to HANPP (Krausmann et al., 2009). Additional research is required to fully understand the relationship, but on a broad scale, used anthromes with high land use intensity have the highest HANPP.

HANPP efficiency ($\text{HANPP}_{\text{harv}}/\text{HANPP}$) is typically highest in cropland anthromes associated with industrial agriculture (Haberl et al., 2014) or in village anthromes of Southeast Asia (Haberl et al., 2014) with high population densities. In contrast, regions with low HANPP efficiency are found in where there is low population densities. Additionally, areas with high HANPP_{luc} relative to HANPP_{harv} suffer from yield gaps. Yield gaps occur where NPP_{act} is well below the potential NPP for crops, often because of soil degradation or a lack of nutrients in cropland anthromes. Such areas would have low HANPP efficiency, such as sub-Saharan Africa (Haberl et al., 2014).

Local and Regional HANPP

Numerous studies have focused on HANPP at subglobal scales. Reviews of regional and national scale studies can be found in Haberl et al. (2014) and Andersen et al. (2015). These reviews show HANPP at the national level in the early 21st century ranged from about 20% to about 75% and is dominated by row crop and pasture. In summary, three main concepts emerge from these studies conducted at the national and regional scale. First, agriculture dominates estimates of HANPP at the regional and national scale. Second, HANPP exhibited considerable spatial heterogeneity. Third, even where trends emerge, such as declining HANPP, the trends include exceptions and show considerable temporal variability. These three concepts suggest local scale studies could increase our understanding of how human interaction with the landscape over time affects HANPP.

Studies conducted below the regional or national scale, such as the watershed scale, face multiple methodological hurdles. Largely, the problem is one of scaling datasets collected at one spatial and temporal scale to a spatial and temporal different scale. For example, Andersen et al. (2015) used county level data from the United States Department of Agriculture to calculate HANPP_{harv}. The method faced three significant challenges. First, they had to assume that the distribution of animals and crops at

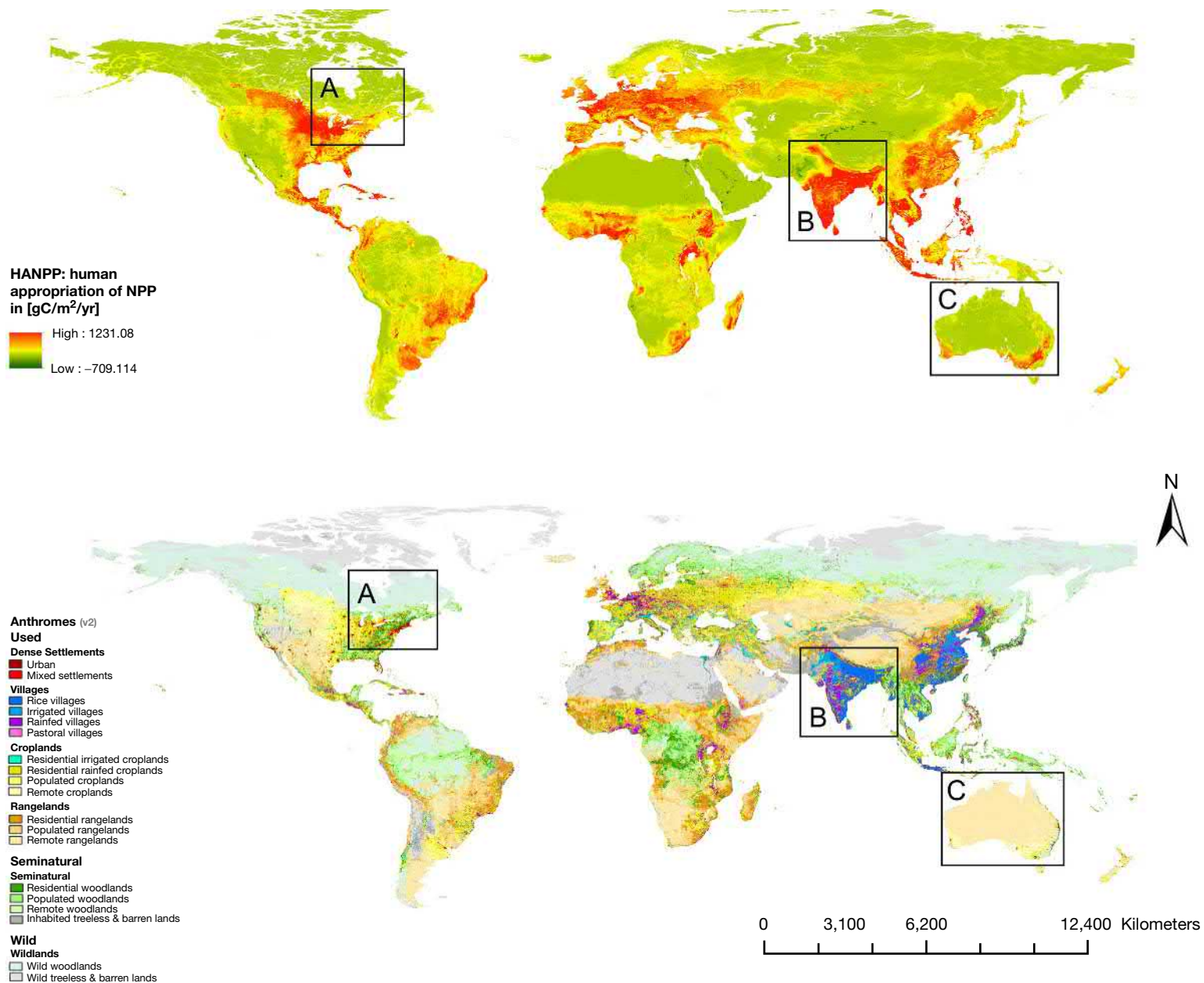


Fig. 2 (A) Global map of the human appropriation of net primary production (HANPP) Data from Haberl et al. (2007). (B) Global map of anthropogenic biomes. Data from Ellis et al. (2010) Insets highlight similar patterns in three locations between HANPP and anthrome type.

the county scale held for the watershed scale. Second, the USDA farm level data is only collected every 5 years, and the agricultural data was collected in 1969 and 2007, which didn't match the aerial photos (1968) or satellite data (2011) year. This leads to uncertainties in the analyses, but probably less than the difference between the 2 years. Third they had to digitize aerial photos to have comparable spatial data for land use and land cover and for sufficient accuracy for the analysis. This is similar to the challenges faced by Krausmann et al. (2013) when attempting to calculate global HANPP back to 1900.

Embodied HANPP

Calculation of HANPP national, regional, state, and local scales needs to consider how energy flows are impacted by or impact other near or distant regions. The material footprint of humanity has expanded dramatically with the great acceleration, tripling since 1970 (Wiedmann et al., 2013). The material footprint, of which biomass is a part, provides a measure of the consumption of resources by nations and accounts for both domestic use and imported/exported material associated with global trade. The concept of embodied HANPP (Erb et al., 2009) is similar to the biomass part of the material footprint. Embodied HANPP, or eHANPP, demonstrates the pressure exerted on ecosystems associated with the imports and exports of biomass, thereby connecting regions that are net producers (exporters) of biomass to net consumers (importers) of biomass (Haberl et al., 2009, 2014). Erb et al. (2009) completed a detailed analysis of embodied HANPP on a global scale. Not surprisingly, urban regions had the highest eHANPP consumption. Thus, eHANPP shows a transfer from rural (cropland and village) anthromes to urban anthromes. The eHANPP also represents the impact of globalization, with trade of eHANPP between countries. However, relatively few countries as of 2000 were involved in this imbalance (Erb et al., 2009; Haberl et al., 2014). Only 10 countries, mainly in the Americas and Oceania, were major net exporters and only 10 countries, mainly in East Asia and Europe were major net importers. Trade of eHANPP could certainly increase as population grows and as the affluence of less developed countries increases.

Critiques of the HANPP Method

The HANPP method is, above all, a model. As with any other model, HANPP relies on a variety of assumptions and simplifications of the real world. For example, the NPP_{pot} of a given watershed, nation, or region is a model based on local empirical data that subsequent extrapolation relies on assumptions of how plants might grow in response to heterogeneous climate and soil conditions. Perhaps the most thorough critique of the HANPP method is in Smil (2011). Smil's primary critique was that many of the variables are poorly quantified and have large margins of error, largely because the numbers are from national scale datasets that have to be extrapolated to smaller scales. Additionally, the model is based on land use classification at the $5' \times 5'$ scale, which can be difficult to resolve because of landscape heterogeneity. Reflective of the maturation of the concept, many of the issues brought up by Smil (2011) have been addressed by Running (2012) and Haberl et al. (2014), among others.

Perhaps the most important critique is that HANPP does not consider the *qualities* of the affected land area. For example, converting the current rainforest to cattle pasture or soy production today is far more damaging to biodiversity and ecosystem function at this moment than rice production in Southeast Asia that may have been cultivated for centuries (Smil, 2011). HANPP also is *lowered* by intensifying agriculture, so there is the trade-off of lower HANPP for higher environmental impact beyond a given region, as noted above. Although the latter are valid critiques, HANPP remains a valuable measure of the human impact on the landscape caused by land use change and biomass harvest and aligns well with anthropogenic biomes.

Summary

HANPP is a model that estimates how much net primary production humans appropriate, or co-opt (Running, 2012), by land use change, harvest, and fire (Haberl et al., 2007). The model may have a relatively high uncertainty and not account for the environmental trade-offs of intensive agriculture which lowers HANPP. However, the global scale results suggest that humans are appropriating approximately one-third of aboveground net primary production and one-quarter of total (above + below ground) NPP (Haberl et al., 2007, 2014; Krausmann et al., 2013), suggesting HANPP is a clear quantitative measure of global change. In addition, and valuably for global synthesis, global HANPP patterns correlate well with anthropogenic biomes, suggesting that HANPP is an important and scalable measure of human impact on the terrestrial environment.

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Patterns of Vertebrate Richness Across Global Anthromes

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Abstract

Biodiversity conservation is traditionally presented in the context of biomes and ecoregions. However, these frameworks fail to incorporate the extent to which humans have shaped ecosystems on local and global scales and may provide an inaccurate representation of ecological associations in many landscapes. In this article, we review global biodiversity within the context of anthromes; a global classification of land use and land cover patterns that reflects population density and land use intensity. We review species richness data for birds, mammals, and amphibians as a factor of anthrome classification and compare our results with existing plant richness data. Plant, bird, mammal, and amphibian richness is greater in anthromes with higher population density and moderate land use intensity. Village and rangeland anthromes are frequently the most species rich. Richness of threatened species is also highest in village anthromes. There is a positive correlation between total richness and threatened species richness for birds and mammals, but not for amphibians. These data suggest that conservation programs can and should work to prioritize conservation in ecosystems with higher population density and land use change. Future work should consider different biogeographical extents to improve understanding of biodiversity patterns in anthromes.

Introduction

Spatial patterns of global biodiversity, prioritization, and protection are most often associated with biomes and ecoregions, which are ecological classifications reflecting temperature, precipitation, elevation, and latitude. Studies of biodiversity and conservation through this traditional lens have revealed global patterns and changes in biodiversity. For example, [Tedesco et al. \(2014\)](#) examined fungal diversity by biome and biogeographic region and [Pimm et al. \(2014\)](#) ranked richness of plants and fish by ecoregion and analyzed distributions of mammals, birds, and amphibians. [Chape et al. \(2005\)](#) reviewed the number, extent, and effectiveness of current global protected areas in relation to biomes; [Hoekstra et al. \(2005\)](#) mapped protection and habitat loss, ranking rates of change by biome and ecoregion; and [Joppa and Pfaff \(2009\)](#) mapped protected area by ecoregion and assessed the effectiveness of their placement. Biome and ecoregion frameworks have also been used to model and anticipate future changes; for example, [Sala et al. \(2000\)](#) provided a ranking of biomes with respect to expected ecosystem changes across varying scenarios for the year 2100.

Given the extent of human influence on the landscape, global narratives based strictly on biotic and abiotic factors may not provide the most realistic representation of biodiversity distributions and change ([Martin et al., 2014](#)). Agricultural lands, including cropland and rangeland, cities, and peri-urban landscapes, continue to expand in scale and impact. Land for the production of food, fiber, and fuels encompasses at least 39% of Earth's ice-free surface ([Foley et al., 2005](#)), and while cities only cover approximately three percent of the world's surface area, their impact extends far beyond municipal boundaries (e.g., [Brown and Quinn, 2018](#)). It is understood that land use and land cover change shifts species diversity patterns, but the extent, impact, and permanence of these anthropogenic land use and land cover types necessitates research to understand how biodiversity varies within and between anthropogenic ecosystems like farms, cities, and villages.

Anthromes (anthropogenic biomes) build on the existing biome classification system and incorporate land use intensity and human population density ([Ellis et al., 2010](#)) to reflect the extent to which humans have shaped the Earth's surface. With now over 55% of the terrestrial biosphere being anthropogenic and less than 45% remaining wild or seminatural, it is crucial to integrate human influence into the framework with which we consider biodiversity and conservation ([Ellis et al., 2010](#)). [Ellis et al. \(2012\)](#) applied the anthrome framework at a global extent to map plant diversity and found that plant richness was greatest in seminatural remote woodlands (Fig. 1; Anthrome 53), dense mixed settlements (Anthrome 12), and pastoral villages (Anthrome 24) and lowest in wild woodlands (Anthrome 61), seminatural inhabited treeless and barren lands (Anthrome 54), and wild treeless and barren lands (Anthrome 62). Anthromes have also been used to frame biodiversity patterns at local extents for birds (e.g., [Quinn et al., 2014](#); [Quinn et al., 2017](#)) and for mammals ([Gómez et al., 2018](#)), but vertebrate biodiversity has not yet been analyzed by anthrome at a global scale. Building on both biome and anthrome-focused studies, and considering how vertebrate species may differ in their distributions within and across anthromes, we review global spatial patterns of vertebrate richness (birds, mammals, and amphibians) as a function of anthrome type.

For this review we obtained global anthrome classification and distribution data for the year 2000 from the Anthromes version 2.0 ESRI Binary Grid ([Ellis et al., 2010](#)). We obtained species richness data for birds, mammals, and amphibians from

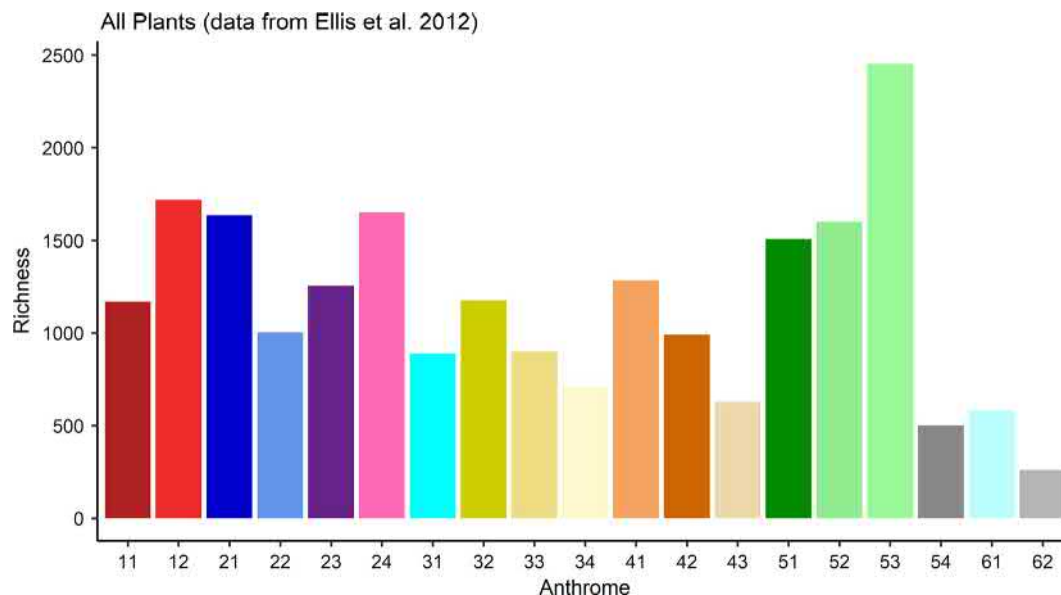


Fig. 1 Patterns of median plant richness across anthromes. Data from Ellis EC, Antill EC, and Kreft H (2012) All is not lost: Plant biodiversity in the anthropocene. *PLoS One* 7(1): e30535. <https://doi.org/10.1371/journal.pone.0030535>.

BiodiversityMapping.org (Jenkins et al., 2013; Pimm et al., 2014) that incorporates breeding bird ranges from BirdLife International and range data for mammals and amphibians from the International Union for the Conservation of Nature (IUCN). Threatened species classifications were determined by Jenkins et al. (2013) and Pimm et al. (2014) based on species considered vulnerable, endangered, or critically-endangered on the IUCN Red List. The above data were created at a global extent with input data from IUCN, BirdLife International, NatureServe, and USGS.

We re-projected the species richness data to align with the projection of anthrome data using ArcMap version 10.5.1 (ESRI) and rescaled it using the resample tool in ArcGIS to match the cell size of the anthrome data (5 arc-minute grid cell (km^{-2})). Using raster calculator, we created a new raster containing anthrome classification and species richness within each cell. This produced count data indicating the number of cells of a particular anthrome classification with particular species richness (0 through n). We calculated richness by anthrome at a global extent. We used the package “splitstackshape” (Mahto, 2018) to expand the data obtained from ArcGIS. We created plots using the “ggplot2” package (Wickham, 2016). Subsequent correlations (significance set to an alpha value of 0.05) and all data processing were done using R version 3.4.3.

Results and Discussion

Among all bird species (Table 1 and Fig. 2), median richness is the highest in rice villages ($n = 289$), followed by residential rangelands (275), pastoral villages (267) and residential woodlands (256). The total median richness is lowest in wild (38) and seminatural (93) barren lands. The median number of threatened birds is the greatest in villages. The median richness for threatened bird species is highest in rice villages (9), irrigated villages (6), rainfed villages (6), and pastoral villages (6). The lowest median richness for threatened birds is in wildlands (1), barren lands (1), and remote rangelands (1). There is a strong positive correlation ($r = 0.781$, $p\text{-value} = 0.000$) between median richness of total and threatened bird species (Fig. 3). There is also a strong positive correlation ($r = 0.749$, $p\text{-value} = 0.0002$) between mean richness of total and threatened species (Fig. 3B).

The median richness of all mammals (Table 1 and Fig. 2) is highest in pastoral villages ($n = 74$), residential rangelands (72), and residential woodlands (66). Total mammal richness is lowest in wild (15) and seminatural (28) barren lands, wild woodlands (33), and remote rangelands (33). The greatest richness of threatened mammals is in seminatural remote woodlands (6) followed by rice villages (5). Richness for threatened mammals is relatively low across all anthromes (min = 1, max = 6), however richness was lowest in barren lands (1), wildlands (1), residential (2) and remote (2) rangelands, all cropland anthromes (2), and dense urban (2) and mixed (2) settlements. There is a positive correlation ($r = 0.510$, $p\text{-value} = 0.026$) between median richness of total and threatened mammal species (Fig. 3) and a strong positive correlation ($r = 0.787$, $p\text{-value} = 0.0000$) between mean richness of total and threatened mammal species (Fig. 3B).

The median value of total species richness of amphibians (Table 1 and Fig. 2) is highest in residential woodlands (18), rice villages (17), residential rangelands (16), pastoral villages (16), and mixed settlements (16). The lowest richness is in wild barren lands (1), wild woodlands (2), and seminatural barren lands (3). Median species richness of threatened amphibians is low across all anthromes (min = 1, max = 2), but highest amongst rainfed (2) and pastoral (2) villages. There is no correlation between median total and threatened richness ($r = 0.244$, $p\text{-value} = 0.314$; Fig. 3) or between mean total and threatened richness ($r = 0.299$, $p\text{-value} = 0.213$; Fig. 3B).

Table 1 Summary of minimum, median, mean, and maximum richness for total and threatened bird, mammal, and amphibian richness.

		Bird								Mammals								Amphibians							
Anthrome		Total				Threatened				Total				Threatened				Total				Threatened			
Class	Label	Min.	Med.	Mean	Max.	Min.	Med.	Mean	Max.	Min.	Med.	Mean	Max.	Min.	Med.	Mean	Max.	Min.	Med.	Mean	Max.	Min.	Med.	Mean	Max.
11	Urban	6	173	199	609	1	4	5	29	1	47	52	194	1	2	3	31	1	14	16	131	1	1	2	18
12	Mixed settlements	8	185	234	663	1	4	6	28	1	51	63	212	1	2	4	30	1	16	19	131	1	1	2	23
21	Rice villages	86	289	287	518	1	9	10	24	3	59	65	154	1	5	6	27	1	17	18	68	1	1	2	18
22	Irrigated villages	30	188	204	573	1	6	7	23	2	43	47	183	1	3	3	24	1	9	10	100	1	1	2	19
23	Rainfed villages	6	218	244	663	1	6	7	23	1	57	65	214	1	3	4	33	1	12	15	124	1	2	2	28
24	Pastoral villages	8	267	273	652	1	6	6	22	2	74	82	216	1	3	4	21	1	16	19	133	1	2	2	24
31	Residential irrigated croplands	5	168	182	585	1	5	5	22	1	47	51	189	1	2	3	27	1	8	10	100	1	1	2	20
32	Residential rainfed croplands	6	187	225	661	1	4	6	27	1	54	64	217	1	2	3	36	1	12	15	127	1	1	2	28
33	Populated croplands	5	183	207	651	1	5	5	28	1	47	56	207	1	2	3	36	1	8	12	121	1	1	2	17
34	Remote croplands	2	169	185	620	1	3	4	30	1	44	46	201	1	2	4	33	1	7	9	115	1	1	1	17
41	Residential rangelands	5	275	266	661	1	5	6	29	1	72	80	214	1	2	3	25	1	16	20	133	1	1	2	22
42	Populated rangelands	4	198	229	650	1	5	5	29	1	53	68	203	1	3	3	27	1	9	17	131	1	1	2	27
43	Remote rangelands	2	146	157	650	1	2	3	30	1	33	41	202	1	2	2	22	1	6	10	123	1	1	1	26
51	Residential woodlands	8	256	261	666	1	4	5	27	1	66	76	215	1	3	5	33	1	18	21	130	1	1	2	25
52	Populated woodlands	4	195	252	644	1	3	5	28	1	53	75	201	1	3	5	35	1	13	21	135	1	1	2	22
53	Remote woodlands	3	192	276	642	1	4	5	28	1	53	87	205	1	6	6	32	1	11	33	135	1	1	1	15
54	Inhabited treeless and barren lands	2	93	114	666	1	3	3	27	1	28	34	217	1	1	2	28	1	3	6	103	1	1	2	32
61	Wild woodlands	2	120	147	643	1	2	3	30	1	33	44	204	1	1	3	31	1	2	9	128	1	1	1	11
62	Wild treeless and barren lands	1	38	50	583	1	1	2	30	1	15	18	184	1	1	1	19	1	1	2	85	1	1	1	15

Richness data from Jenkins CN, Pimm SL, Joppa LN (2013) Global patterns of terrestrial vertebrate diversity and conservation. *PNAS* 110(28): E2602–E2610; Pimm SL, Jenkins CN, Abell R (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344(6187): 1246752.

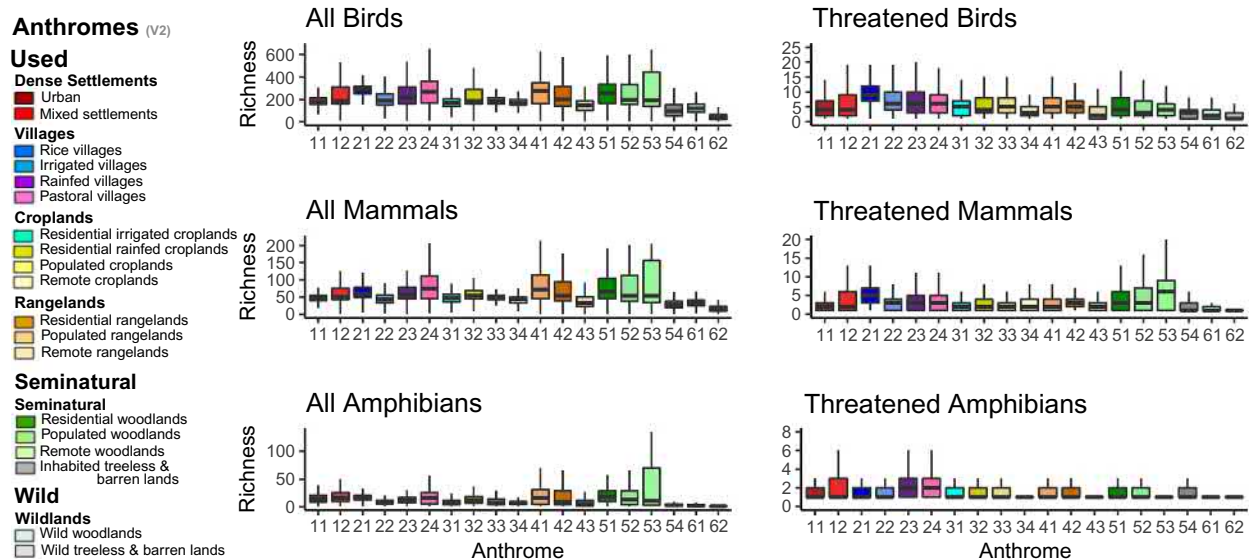


Fig. 2 Median total richness and threatened richness of birds, mammals, and amphibians by anthrome type. Richness data from Jenkins CN, Pimm SL, and Joppa LN (2013) Global patterns of terrestrial vertebrate diversity and conservation. *PNAS* 110(28): E2602–E2610; Pimm SL, Jenkins CN, and Abell R (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344(6187): 1246752.

The results show high variation in vertebrate species richness by anthrome, low species richness in barren and wildlands, and higher richness in villages and rangelands. These results are consistent with the findings of the Ellis et al. (2012) analysis of plant richness. Upon further analysis of the distribution of vertebrate richness by anthrome, several significant patterns emerged. Village anthromes exhibit high median total richness and threatened richness, specifically among rice and pastoral villages. This pattern may be a result of the distribution of village anthromes in tropical systems where historical biodiversity patterns were shaped by temperature and precipitation that resulted in higher potential species richness. High threatened species richness in villages is consistent with high rates of decline of biodiversity in tropical regions and rapid land use change. Residential rangelands and seminatural residential woodlands also have high total richness across taxa, while remote rangelands have among the lowest richness of threatened birds and mammals. The low threatened species richness in rangelands may be attributable to effective and sustainable management resulting from a history of multifunctional land use (e.g., Havstad et al., 2007) where grazing and conservation have gone hand in hand. Richness, both total and threatened, is consistently low among wild treeless and barren lands, seminatural inhabited treeless and barren lands, and remote rangelands. These patterns of low richness despite low human interference is likely a consequence of broader biogeographical and evolutionary patterns that make these regions less hospitable to wildlife.

Overlap in anthromes of high richness between taxa presents opportunities for conservation. Three anthromes (pastoral villages, residential rangelands, and residential woodlands) have among the highest richness for both birds and mammals. Although the anthrome with the highest total bird richness (rice villages) was not among the highest richness for mammals, the overlap between the two taxa reveals an opportunity for prioritization of conservation efforts across multiple taxa. This also suggests that anthrome classifications could be used to target specific anthrome types for conservation efforts. Beyond these three anthromes, the correlations between total and threatened richness for birds and mammals presents an opportunity for conservation action both broadly and for targeted species to be complementary. The correlation between median total and threatened richness was not as strong for mammals as it was for birds though the correlation values of the means were similar. Both associations are positive, again suggesting complementary efforts are possible. Moving forward, there is a need to analyze richness by anthrome type at varying spatial extents to more fully understand these patterns of richness, both within and between anthromes, and their implications.

Conclusion

This work builds on a deep foundation of research focused on biomes and ecoregions. However, by considering spatial biodiversity patterns as a function of anthromes, we can begin to understand and create conservation solutions that integrate human and natural systems. This shift in global frameworks offers new opportunities for improvement in conservation research and implementation. While most conservation research has focused on lands classified as “natural,” despite the extent and permanence of human land use types (e.g., urban, cropland, rangeland), this review highlights the value of focusing research and prioritization on inhabited and seminatural lands. The global patterns of species richness described in this review can help identify and prioritize conservation efforts beyond wildlands and protected areas. This focus on anthromes does not suggest that natural or protected areas are unimportant, rather it emphasizes the need to consider lands beyond the boundaries of protected areas which are often deprioritized or overlooked in the broader context of conservation prioritization. This review reveals a clear overlap in anthromes of high

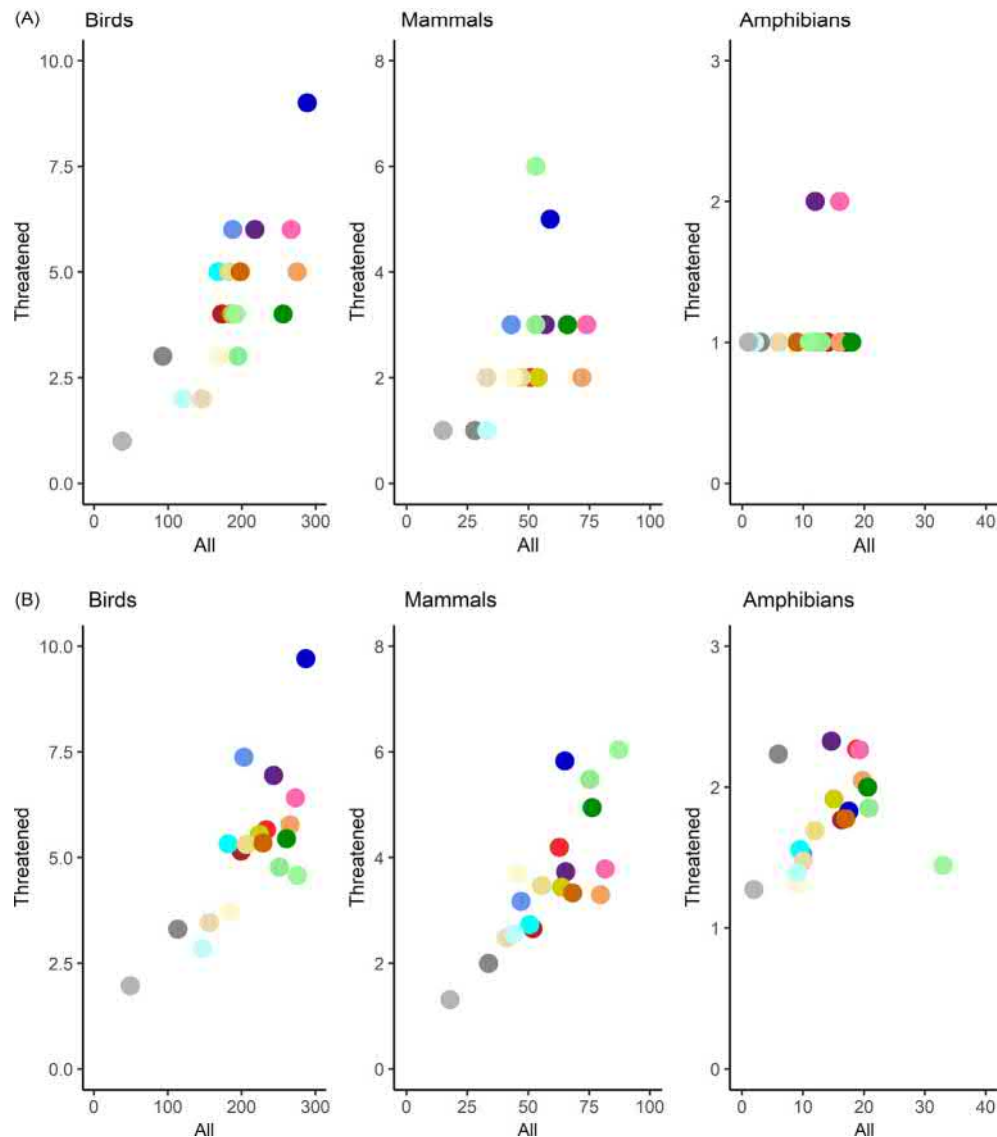


Fig. 3 (A) Correlation between median total richness and threatened richness of birds, mammals, and amphibians for each anthrome type. (B) Correlation between mean total richness and threatened richness of birds, mammals, and amphibians for each anthrome type. (A and B) Ellis EC, Goldewijk KK, Siebert S, Lightman D, and Ramankutty, N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* 19(5): 589–606; Jenkins CN, Pimm SL, Joppa LN (2013) Global patterns of terrestrial vertebrate diversity and conservation. *PNAS* 110(28): E2602–E2610; Pimm SL, Jenkins CN, and Abell R (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344(6187): 1246752.

population density, moderate land use intensity, and high richness across multiple taxonomic groups. This overlap, along with the positive correlation between threatened and total species for birds and mammals, indicates a significant opportunity for congruent conservation action across anthromes. Further spatial analyses at varying biogeographical extents are needed for a deeper understanding of species distribution within the anthrome framework.

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Urban Social-Ecological Systems

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Abstract

The world’s population has gone from 30% urban in 1950 to 55% urban in 2018, and will be 60% urban by 2030 (United Nations Population Division, 2019b). Urban areas are the most intensely and densely settled places human inhabit on the planet. Though they comprise less than 3% of Earth’s land surface area, they account for an estimated 78% of global carbon emissions, 60% of residential freshwater use, and 76% of wood use (Grimm et al., 2008). In this article, we discuss the concepts crucial to understanding urban social-ecological systems, including articulating some of the dialogue around defining some key terms, comparing frameworks used to research urban systems, and briefly discuss the related discipline of urban ecology.

Urban Social-Ecological Systems

The extent of human impact on the planet is such that several scholars have articulated the need for alternative conceptualizations of the classic human-nature dichotomy. For instance, Ellis and Ramankutty (2008) proposed the concept of “anthropogenic biomes” or “anthromes” to capture the global impact of humans on all ecosystems. Meanwhile, geologists (e.g., Zalasiewicz et al., 2015; Waters et al., 2016) and sustainability scientists (Steffen et al., 2015) have argued that the current widespread human alteration of Earth system processes warrants designating an entirely new geologic period the “Anthropocene.” Increasingly, humans and nature cannot be separated, no matter where you are on the planet. Urban areas, as home to a majority of the world’s population (United Nations Population Division, 2019a), are arguably front and center in this new world. Though urban areas comprise less than 3% of Earth’s land surface area, they account for an estimated 78% of global carbon emissions, 60% of residential freshwater use, and 76% of wood use (Grimm et al., 2008). Thus, it is crucial to understand the social and ecological mechanisms driving the structure and dynamics within urban areas, as well as how urban areas impact surrounding ecosystems and global Earth systems processes.

Urban areas are the most intensely and densely settled places human inhabit on the planet. They have extensive so-called “gray infrastructure” above and below ground (often called the “built environment”). Urban areas have more “natural” elements like trees and parks (often called “green infrastructure”), as well as natural or constructed bodies of water (called “blue infrastructure”; Table 1 and Fig. 1). The infrastructures of cities are cohabitated not just by people, but also by wildlife, both more desirable (e.g., birds, butterflies, sometimes rabbits and squirrels) and less desirable (e.g., rats, raccoons, monkeys, coyotes, any number of insect pests such as cockroaches, fire ants; cf., Nyhus, 2016) from a human standpoint, and any number of relatively invisible types of biodiversity such as insects and microbes that live in the soil, trees, yards/gardens, greenroofs, and every corner of the built environment. Beyond the physical and ecological elements of urban areas, there are innumerable social elements: politics and political systems; formal and informal economic activities; social norms of appropriate behaviors; demographic patterns related to living, working, and moving about the city; concerns about inequality, inequity, and participation in city life; and numerous other issues connected to housing, education, crime and violence, jobs and employment, transportation, etc. Furthermore, these social issues have significant impact on the quality of and access to gray, green, and blue infrastructure (cf., Taylor, 2009).

In this article, we discuss the concepts crucial to understanding urban social-ecological systems, including articulating some of the dialogue around defining some key terms, comparing frameworks used to research urban systems, and briefly discuss the related discipline of urban ecology.

Table 1 The biophysical elements of urban social-ecological systems include all types of gray, green, and blue infrastructures, some of which are listed below, as well as the living things—human and non-human—inhabiting these infrastructures.

<i>Gray infrastructure</i>	<i>Green infrastructure</i>	<i>Blue infrastructure</i>
Water management systems: Sanitary sewers and septic tank systems, potable water delivery systems, stormwater drains and pipes and underwater storage tanks, seawalls, levees, etc.	Trees (in parks, along streets, sidewalks, alleys, on vacant lots, adjacent to railroad or light rail tracks, in yards, in parking lots, etc.)	Natural or remnant bodies of water: Lakes, rivers, streams, bays, wetlands
Electrical power and cable/internet lines	Public and private gardens and yards	Constructed bodies of water: Canals, reservoirs, retention ponds for stormwater runoff, harbors and marinas
Energy infrastructure: Conventional power plants (coal, natural gas, nuclear, etc.), Solar panels, etc.	Parks, large and small	
Paved impervious surfaces: Roads and highways, plazas, sidewalks and walking paths, parking lots, driveways, piers	Nature preserves or reserves (remnants of the surrounding native ecosystem such as forest or prairie, or of a constructed or restored type, e.g., a constructed wetland)	
Transportation infrastructure: Bridges, tunnels, street car tracks, light rail and elevated train tracks, subway systems, gondola lifts	Sports and recreation fields (<i>when covered in living grass as turf rather than astro-turf</i>): Golf courses, baseball diamonds, football fields, etc.	
Buildings, large and small, ranging from the smallest, stand-alone houses, sheds, and garages, to extensive conference or hotel centers occupying land equivalent to several city blocks, to tall skyscrapers with dozens of stories above ground and sometimes several basements and subbasements below	Cemeteries	
	Green areas at institutions, like school campuses, hospitals, business or industrial parks	
	Other landscaped areas, sometimes called “greenspaces”	

Key Definitions

In order to understand urban social-ecological systems as an anthropogenic biome, we need to unpack the concept of “social-ecological system” and the meaning of “urban.”

What Is a “Social-Ecological System”?

Social-ecological systems (SESs) are those where there are both human and natural components interacting to produce observed system-level outcomes. [Colding and Barthel \(2019\)](#) review the discourse on SESs over the past several decades. They note that the term “social-ecological system” was first defined in 1988 in the context of epidemiology by Cherkasskii, who spoke of the “biological” and “social and economic conditions” as “two interacting subsystems” where the social subsystem “acts as the internal regulator” of the biological subsystem processes and mediates interactions between the social and biological (1988; as quoted in [Colding and Barthel, 2019](#)). In the context of human impacts on ecosystems, the term was expanded upon in 1998 by [Folke and Berkes \(1998\)](#), who viewed the social-ecological system as a complex, dynamic, open system whose properties are influenced by the surrounding ecological and social systems. [Folke and Berkes \(1998\)](#) also developed the first framework for SESs, which posited a language and analytical structure for examining natural resource systems and the fit of management institutions (rules, strategies) with ecological dynamics. Subsequently and in-part based on the [Folke and Berkes \(1998\)](#) work, [Ostrom \(2007, 2009\)](#) also proposed a SES framework for examining the sustainability of natural resource use in common property settings. Ostrom’s SES framework—called the “most comprehensive conceptual framework for diagnosing interactions and outcomes” in SESs ([Partelow, 2018](#)) (Ostrom won the Nobel Prize in Economics in 2009)—comprises nested sets of variables related to the social components (governance system, users of the resource) and biophysical components (properties of the resource system, i.e., a forest, and individual resource units, i.e., trees or other forest products) of the system interacting with one another to produce outcomes ([Partelow, 2018](#)). (For more on frameworks in the context of urban systems, see the section below on “Frameworks for Understanding Urban SESs.”)

The origins of the SES concept as described above are in rural natural resource management systems where there is some type of resource being harvested or used by the managing community—e.g., forests being managed for timber, fisheries for fishing, irrigation systems for watering crops. Resource use happens differently in urban areas. For example, timber products needed for building are not (usually) harvested from within a city, but rather brought in from outside forests, while the resources generated by cities are things like the ecosystem services provided by green infrastructure ([Jerome et al., 2019](#)), innovation ([Florida, 2011](#)), economic activities ([Pain et al., 2016](#)), or even human social capital or community connections (e.g., [Sampson and Graif, 2009](#)). Nonetheless, cities are perhaps the most quintessential SESs. In urban areas, the “social” part of SESs is arguably most dominant to the average urban dweller. Social elements include all those constructs of human society, ranging from the often-intangible social and political dynamics of urban dwellers (working, shopping, going to school, engaging in community and leisure activities like going to religious services, volunteering, recreating, socializing, etc.) to the more tangible impacts resulting from the way people move about and act on urban areas (through, for example, walking, driving cars, planting and maintaining trees and landscaping, growing food or flowers, constructing roads and buildings, and even littering). The “ecological” part of urban SESs is perhaps better



Fig. 1 Examples of gray, green, and blue infrastructure in urban social-ecological systems described in Table 1 from the authors' home city of Chicago, IL (A–D), Venice, Italy (E), and Shenyang, China (F). (A) Buildings, roads, sidewalks and other gray infrastructure in Chicago's downtown. (B) A restored riparian area (in the foreground) along the South Branch of the Chicago River (blue infrastructure) in Ping Tom Memorial Park (green infrastructure) in Chinatown on Chicago's south side. (C) The entrance to Diversey Harbor on Lake Michigan (blue infrastructure) on Chicago's north side with the downtown skyline visible in the background. (D) Tree tops and buildings (green and gray infrastructure, respectively) in Chicago's Lincoln Park neighborhood with Lake Michigan (blue infrastructure) visible in the background. (E) Perhaps one of the best known constructed blue infrastructures is the network of canals in Venice, Italy. (F) A man fishes along a waterway (blue infrastructure) adjacent to a park in Shenyang, China. Residential buildings of identical height (gray infrastructure) are visible in the skyline in the background. All photos by author J. Vogt.

conceptualized as “biophysical,” that is, all of the biological/ecological and physical elements in the city, inclusive of the built environment and green and blue infrastructures described in Table 1.

What Is “Urban”?

An understanding of what is “urban” means is crucial for a complete understanding of urban SESs. Generally, there are three ways of defining urban relevant to studying urban areas: by population size or density, by physical or ecological features (geographic definition), by jurisdiction or administrative unit (governance definition). Each of these three are described below, as well as their implications for understanding urban SESs.

Population-based definitions of urban

Technically, “urban” is defined by each individual country or region, but most countries use as at least part of their definition the total number of people or the density of people living in a contiguously developed area (UN Population Division, 2019a). For example, in the United States, “urbanized areas” refer to those with more than 50,000 people (U.S. Census Bureau, 2018). A related term, “urban clusters,” refers to areas with 2500–50,000 people, and “rural” encapsulates all non-urban areas (U.S. Census Bureau, 2018). The Canadian definition of urban includes slightly smaller communities, defined as population centers of more than 1000 people, but also adds a population density threshold of more than 400 people per square kilometer (Statistics Canada, 2017). Across the world, localities or towns with 2000 or more people appears to be a common threshold population size that makes an area classified urban, though the most recent edition of the United Nations’ *World Urbanization Prospects* report notes that this threshold varies widely from 200 to 50,000 people (United Nations Population Division, 2019a). In Africa, areas defined as urban vary from a minimum size of 2000 people (in Ethiopia, Kenya) to 5000 (Zambia) to 10,000 (Senegal) (Francis and Chadwick, 2013, after United Nations Statistics Division, 2017).

Because of this variability, the European Commission has undertaken an effort to standardize the definitions for urban in order to more consistently track urbanization. The European Commission considers an “urban center” to be an area with “a minimum of 50,000 inhabitants *plus* a population density of at least 1,500 people per square kilometer (km²) or density of build-up area greater than 50 percent” and an “urban cluster” to be an area with “a minimum of 5,000 inhabitants *plus* a population density of at least 300 people per square kilometer (km²)” (Ritchie, 2018, *emphasis in original*). The total population and population density of an urban area are not related; that is, larger cities are not necessarily denser (Fig. 2).

Using the UN’s country-defined concept of “urban,” 55% of the global population lives in urban areas as of 2018 (United Nations Population Division, 2019a). Using the European Commission’s standardized definition, 85% of the global population lives in urban areas (52% in urban centers and another 33% in urban clusters) as of 2015 (Ritchie, 2018).

Biophysical definitions of urban

Beyond defining urban areas based on population, there are definitions based on physical or ecological aspects of urban areas that use geographical data. Although most country-specific definitions of urban utilize population or population density as summarized above, occasionally they will use a more biophysical definition. Algeria, for example, uses how many “constructions” (presumably, buildings) are in a geographical area, and there must be 100 or more constructions spaced 200 m or less apart for an “urban” area (United Nations Statistics Division, 2017, as quoted in Francis and Chadwick, 2013).

Researchers interested in determining how much land area on Earth is “urban” are most concerned with physical and ecological definitions of the term. For instance, Schneider et al. (2009), in their analysis of global urban extent based on remote sensing data, eschew population-based definitions entirely and use a spatial definition that,

...define urban area based on the physical attributes and composition of the Earth’s land cover: urban areas are places dominated by the built environment. The “built environment” includes all non-vegetative, human-constructed elements, such as roads, buildings, runways, etc. (i.e., human-made surfaces), and “dominated” implies coverage greater than 50% of a given landscape unit (the pixel). (Schneider et al., 2009, p. 2)

Using this definition, Schneider et al. (2009) report that only 0.5% of Earth’s land surface area is urban. This is one of the smallest reported percentages in the literature. Their definition of urban is crucial to understanding why. Because these authors are conducting a pixel-by-pixel analysis of urban area using data at 500-m spatial resolution, they must decide what to do with pixels that are not majority “built environment” per the definition above, but may still be located within the conventional boundaries of a city. Schneider et al. (2009) continue, “When vegetation (e.g., a park) dominates a pixel, these areas are not considered urban, even though in terms of land use, they may function as urban space” (p. 2–3). They further clarify that “urban areas are contiguous patches of built-up land greater than 1 km²” (Schneider et al. (2009), p. 3). Other geographical analyses of urban land area extent using satellite-based data have estimated as low as 0.2% urban area and as high as 2.4% as of 2000 satellite data (Potere and Schneider, 2007). The higher of these estimates is data from the Global Rural-Urban Mapping Project (GRUMP), which is the source of the oft-cited statistic that urban areas comprise “<3%” of global land area (e.g., Grimm et al., 2008).

Urban extent analyses based on ecological character might define urban areas very differently. For instance, Ellis and Ramankutty (2008) in their classification of global land area into levels anthropogenic biomes (“anthromes”) use population density in combination with land use and land cover data to define two relevant classes of highly-settled biomes. “Dense settlements” are defined as those “with substantial urban area” inclusive of “urban” (“dense built environments with very high populations”) and

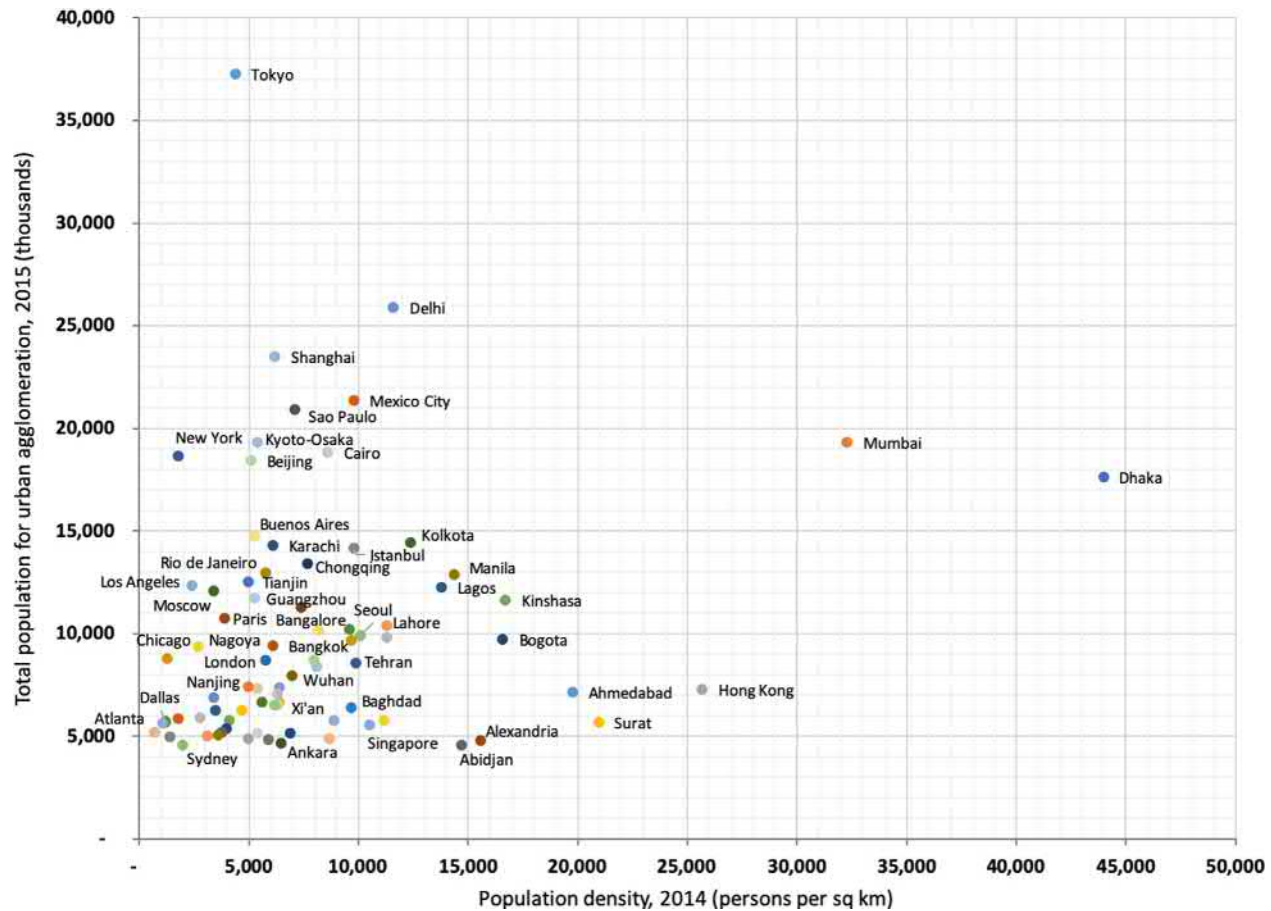


Fig. 2 Population density by total population for the 100 largest cities (by total population). Data sources: *Population density data* downloaded from: Our World in Data (2014) “Population Density by City, 2014.” Available from: <https://ourworldindata.org/grapher/population-density-by-city> (Accessed 13 Dec 2019). Originally from: United Nations, Department of Economic and Social Affairs, Population Division (2014) *World Urbanization Prospects: The 2014 Revision*, CD-ROM Edition. <http://urbandata.unhabitat.org/>; *Total population data* downloaded from: United Nations, Department of Economic and Social Affairs, Population Dynamics (2018) *World Urbanization Prospects 2018, File 12: Population of Urban Agglomerations with 300,000 Inhabitants or More in 2018, by country, 1950–2035 (Thousands)*. Available from: <https://population.un.org/wup/Download/> (Accessed 13 Dec 2019).

“dense settlements” (“dense mix of rural and urban populations, including both suburbs and villages”) biomes (Ellis and Ramankutty (2008), p. 442). The “villages” biome is “dense agricultural settlements” inclusive of several different types of agricultural village biomes (e.g., rice villages, pastoral villages; Ellis and Ramankutty (2008)). According to these definitions, Ellis and Ramankutty (2008) classify 1.1% and 5.9% of ice-free land area in “dense settlement” and “village” anthromes respectively, and state that 80% of the total global population lives in these densely settled area. However, because of the composite use of population density, land use, and land cover data with which the anthromes are specified, not all land use with these densely settled anthromes is urban: 57% of land use within the dense settlements biome is urban, while 35% of villages biome land use is urban (WebTable 2 in Ellis and Ramankutty, 2008).

Governance-based definitions

From an urban governance perspective, there are three additional terms relevant to a discussion of what is urban from an urban SES point of view and used by the United Nations and others in defining, describing, and studying cities. The first is “city proper,” which refers to the administrative or jurisdictional boundary of a municipality (i.e., a city, town, village, etc.; United Nations Population Division, 2019b). This definition is in contrast to that of “metropolitan area,” which includes a larger geography around the city proper “according to the degree of economic and social interconnectedness of nearby areas” (United Nations Population Division, 2019b). The final, perhaps most meaningful for urban SESs, is “urban agglomeration,” which is defined as

...the population contained within the contours of a contiguous territory inhabited at urban density levels without regard to administrative boundaries. It usually incorporates the population in a city or town plus that in the suburban areas lying outside of, but being adjacent to, the city boundaries (United Nations Population Division, 2019c).

These terms are important from the perspective of urban social-ecological dynamics: What a city itself considers its jurisdictional or functional boundary impacts land use, land cover, and other ecological and social patterns and processes. For instance, commuters coming by car, bus, or train into the city creates a social and economic connection between the city proper and the surrounding metropolitan area or urban agglomeration, but also has an ecological impact in terms of the carbon emissions and land cover of different forms of transportation.

Clearly, the definition of urban is complicated at best. For a SESs view of “urban,” total population size, population density, built-up area, ecological characteristics, and governance/administrative boundaries all impact the social-ecological nature of a city. Fig. 3 describes some of the social and ecological considerations for cities with different total populations and population densities.

It is an open question which type of definition of “urban” is most useful from an urban SES perspective. Within the field of urban ecology, there is a debate on what constitutes “urban” for the sake of research. MacGregor-Fors (2011) in a classic article from the urban ecology field entitled, “Misconceptions or misunderstandings? On the standardization of basic terms and definitions in urban ecology,” argues that the lack of standard definitions obfuscates the ability of urban ecological research to be fully comparable across studies. He further encourages urban scholars to specify the following seven pieces of information for their study:

(1) the geographical location of the study area in lat/long format to facilitate comparisons (reporting the location of the geographical center of the urban study site), (2) total number of inhabitants at the time when the study was conducted, (3) updated human population growth rate (in a percentage scale to allow comparisons), (4) size of the urban area (in square kilometers. . .), (5) main urban land uses (even though the study may not explore them), (6) the biogeographic (e.g., zoogeographic, phytogeographic) region in which the urban area is settled, (7) type of habitats present prior to the establishment of the urban area, and (8) principle habitats and land uses currently surrounding the urban area (MacGregor-Fors, 2011: p. 348).

This approach would certainly help with consistency and allow for better comparison across studies of urban systems of different types and sizes and across multiple locations, climates, etc.

Urbanization

Regardless of how urban areas are defined—whether by population size or density, by built-up area, or by biome—throughout the history of human civilization, urbanization has increased. Urbanization is the process through which people and geographies become more urban—that is, more built-up, more densely settled, of larger geographic dimensions, etc. (United Nations Population Division, 2019a). By the UN’s country-specified definitions, the world’s population has gone from 30% urban in 1950 (United Nations Population Division, 2019a), to 55% urban in 2018, and will be 60% urban by 2030 (United Nations Population Division, 2019b). In 2018, one in eight urban residents lives in megacities of more than 10 million people, 23% live in cities of 1 million or more, and half of the global urban population lives in cities of less than 500,000 people (United Nations Population Division, 2019b). By 2030, 706 cities of more than 1 million will house 28% of the global population (United Nations Population Division, 2019b). According to Seto et al. (2011)’s geographic analysis of urbanization, by 2030 global urban land extent will be nearly three times what it was in 2000, with 1.2 million km² of new urban land. In their words, “the first 30 [years] of the 21st century is highly likely to experience more urban land expansion than all of history” (Seto et al., 2011; p.16088). Together, these analyses indicate that while the urban population will increase by only 22% (from 4.2 billion to 5.2 billion; United Nations Population Division, 2019b), these people will be occupying three times the land area occupied by cities at present (Seto et al., 2011).

Urbanization will have significant negative impacts on global ecosystems (cf., Johnson, 2013). Seto et al. (2012) projected that future urban expansion (to three times current urban extent) will result in substantial biodiversity loss, particularly in regions of the world that were relatively unimpacted by urbanization prior to 2000 such as the biodiversity hotspots in the mountains of eastern Africa, the Western Ghats (a mountain range on the southern Indian peninsula), and Sri Lanka. Carbon emissions due to urbanization will also be substantial: “loss of vegetation biomass. . . [will be] equal to ~5% of emissions from tropical deforestation and land-use change” (Seto et al., 2012).

Clearly, urbanization is not occurring equally in all regions of the planet. China, for instance, is urbanizing rapidly, from 18% in 1978 to 55% in 2014 (Huang et al., 2016). Annual regional urbanization rates—that is, the rate of increase in urban populations—for the period from 1995 to 2015 range from 3.44% to 2.78% in Africa and Asia respectively to just 0.31% in Europe and 1.24% in North America (UN-Habitat, 2016).

Frameworks for Understanding Urban SESs

Given that both urban areas (Seto et al., 2011) and the number of people living in them (United Nations Population Division, 2019a) will continue to steadily increase through the first half of the 21st century, and that urban areas constitute the vast majority of global demand for natural resources (water, materials, energy, etc.; Grimm et al., 2008), understanding the social and ecological patterns and processes at work in cities is crucial to creating cities that are livable and sustainable. Urban SESs are complex, dynamic systems with both human and natural components.

One of the more useful ways of studying and describing SESs is through the use of a framework, or a structured set of variables organized in a way that describes the potential interactions among them. Ostrom (2010), in the version of her 2009 Nobel Prize in Economics speech printed in the *American Economic Review*, expounded on the utility of frameworks for research:

Type	Description		Select social & ecological considerations
Dense megacities <i>HIGH total population, HIGH population density</i>	Urban agglomerations of more than 10 million people are often called 'megacities' (United Nations Population Division 2019b). In addition, megacities are geographically large and often quite dense. There were 29 megacities as of 2015 (Figure 1), 33 in 2018, and will be 43 megacities by 2030 (<i>ibid.</i>). But not all of these are densely populated: The Tokyo metropolitan area, for instance, comprises more than 37 million people, yet hosts only 4,400 people per square kilometer. Population densities of more than 5,400 people per kilometer mile earn a city a place on the list of the top 50 most dense urban areas. Dhaka is a megacity of 17.6 million and is the most densely-settled city in the world at 44,000 people per square kilometer. Mumbai, the world's 6th largest city with 19.3 million people, is also its 2nd densest, at 32,300 people per square kilometer.	 Mumbai is one of the world's largest and densest cities, with striking inequality, as visible in this drone image. <i>Photo by Johnny Miller.</i>	- Large geographic extent, sometimes forming 'megaregions' of hundreds of thousands of square kilometers of built-up area - Dense built-up area of impervious surfaces creates stormwater and urban heat island problems - Megacities often have tremendous inequality, housing some of the richest and most impoverished people in close proximity (e.g., Mumbai in (A)) - Large populations often mean high burdens on infrastructure: grey (freshwater distribution systems and electrical grids struggle to deliver adequate water and power; transportation of all types is overcrowded, etc.), green (parks can be overused and soils heavily compacted, urban forests can be inadequate), and blue (waterways are polluted and/or overused for recreation, bathing, irrigation) - Multiple, potentially overlapping or conflicting layers of governance in megacities and megaregions can complicate coordination of services, land use planning, etc.
Sprawling metropolis <i>HIGH total population, LOW population density</i>	Not all cities are densely populated. In many parts of the world (Canada, United States, Australia, Japan), cities sprawl across large metropolitan areas and have relatively low or middling population densities (compared to other similarly-sized cities). Of the 80 most populous cities in the world, the cities with the lowest densities (under 2,500 people per square kilometer) are all in the U.S. or Australia. For instance, Chicago and Hong Kong have relatively similar total populations (8.8 and 7.2 million, respectively), but while Hong Kong is the third most dense city in the world (at 25,700 people per square kilometer, in a total geography of 1,1073 km²), Chicago is ranked 95th in density with just 1,300 people per square kilometer in a much larger geography (over 28,000 km²). Atlanta is the least dense of the world's largest cities, with a population of 5.2 million spread over more than 21,000 km² resulting in a density of just 700 people per square kilometer.	 Chicago's Lake Michigan shoreline and sprawling north side at night. <i>Photo by Jess Vogt.</i>	- Large geographic extent and low population density may result in an inefficient use of space and resources (e.g., in transportation as people move around a relatively dispersed city) - Lower population density can afford opportunities for both large greenspaces such as parks, nature preserves, etc., as well as smaller patches such as yards, gardens, boulevards, etc. - (For some cities) Higher rates of home ownership due to lower population densities and the greater relative availability of single-family residential housing (e.g., Philadelphia; Taylor 2009) - The legacies of social and ecological patterns are visible in these cities, e.g., historical (and sometimes modern) racial discrimination in home mortgage practices creating inequalities in home ownership and clustering of racial groups into neighborhoods

Fig. 3 Characterization of urban areas by total population and population density. Total population data downloaded from: United Nations, Department of Economic and Social Affairs, Population Dynamics (2018) *World Urbanization Prospects 2018, File 12: Population of Urban Agglomerations with 300,000 Inhabitants or More in 2018, by country, 1950–2035 (Thousands)*. Available from: <https://population.un.org/wup/Download/> (Accessed 13 Dec 2019); *Population density data downloaded from: Our World in Data (2014) "Population Density by City, 2014."* Available from: <https://ourworldindata.org/grapher/population-density-by-city> (Accessed 13 Dec 2019). Originally from: United Nations, Department of Economic and Social Affairs, Population Division (2014) *World Urbanization Prospects: The 2014 Revision*, CD-ROM edn. <http://urbandata.unhabitat.org/>. Mumbai: Photo by Johnny Miller, from Rao S (2018, Sept 21) Drone photos capture the staggering inequality in Mumbai *Quartz India*. Available from: <https://qz.com/india/1396785/drone-photos-capture-the-staggering-inequality-in-mumbai/> (Accessed 13 December 2019). Chicago: Photo by author J. Vogt. Liaocheng: Photo by Justin Jin from: Johnson I (2013, June 15) China's Great Uprooting: Moving 250 Million into cities. *The New York Times*. Available from: <https://www.nytimes.com/2013/06/16/world/asia/chinas-great-uprooting-moving-250-million-into-cities.html> (Accessed 14 Dec 2019). Detroit: Photo by author J. Vogt.

Continued

Planned, new city <i>LOW total population, HIGH population density</i>	Rarely, cities may have relatively high population densities but a low total population size. Many smaller cities in China meet these criteria. In newer, planned cities that have been built very rapidly by the Chinese government in an effort to move more than 250 million people into cities, dense high-rise residential housing is replacing traditional, less dense housing in new agricultural and industrial centers, to create places for workers to live (Johnson 2013). However, because of the way administrative boundaries work in China, this high density in and near city centers is not reflected in calculations from country-reported total population and municipal area. Chinese municipalities are called county-level cities, and the complex of cities within a province exhaustively cover the entire area, meaning that sometimes large rural and agricultural areas are included in municipal limits and thus calculations of city population densities.	 High density residential buildings being constructed in Liaocheng, China, a city of just 677,000 residents – relatively small by global standards – as of 2015. Photo by Justin Jin.	- High density can mean large impervious surface areas, but proper planning can also yield large greenspaces - Rapid development may result in high resource use and throughput (waste) - In China, many of these cities displace people from traditional communities as they replace farmland and rural dwellings with impervious pavement and high rises, and replace farmland work with factory jobs and high unemployment, causing significant social and emotional impacts on the newly-urban residents (Johnson 2013)
Small- and medium-sized cities and towns <i>LOW total population, LOW population density</i>	The vast majority of the cities, towns, and communities that people reside in have relatively low total population sizes and low population densities. The UN reports that, “In 2018, there were 467 cities with between 1 and 5 million inhabitants and an additional 598 cities with between 500,000 and 1 million inhabitants” (United Nations Population Division 2019b, p. 2). And yet globally half of urban residents live in cities of less than 500,000 people (United Nations Population Division 2018). Small towns and cities may be growing rapidly in total population, density, and/or geographic extent, which is the case for many smaller cities in Africa, which is currently the most rural continent (United Nations Population Division, 2019b). In other parts of the world, such as the United States, these smaller cities are actually decreasing in population and density. Detroit, for instance, was once a city of over 1.8 million people (in the city proper) in the 1950s when it was a peak manufacturing hub in the United States. However, as of 2018, its population is just under 700,000 (though the urban agglomeration contains 3.6 million).	 Detroit's population decline has resulted in extensive vacant houses which have been demolished in the past decade yielding acres of vacant land inside Detroit city proper, as seen while flying over Detroit. Photo by Jess Vogt.	- Highly varied social and ecological dynamics depending on country, geography, climate, configuration, social and political dynamics, - The large number of small and medium cities and towns with low populations and population densities can offer lots of opportunities for innovation in planning, management, development, etc., in order to optimize outcomes for unique local social and ecological conditions - The variation in social and ecological dynamics makes it difficult to generalize or transfer results of urban social-ecological research from one urban area to another - In cities in the post-industrial “Rust Belt” in the United States (e.g., Detroit, at left), urban centers are often decreasing in population and density, as people (often Caucasian in race in the so-called “white flight”) leave cities for the surrounding suburbs, which then sprawl out across a region. This can deepen racial disparities in access to urban amenities and services.

Fig. 3, Cont'd

While the terms frameworks, theories, and models are used interchangeably by many scholars, we use these concepts in a nested manner to range from the most general to the most precise set of assumptions made by a scholar. . . . [A] *framework* is intended to contain the most general set of variables. . . . It provides a metatheoretical language to enable scholars to discuss any particular theory or to compare theories. A specific *theory* is used by an analyst to specify which working parts of a framework are considered useful to explain diverse outcomes and how they relate to one another. . . . *Models* make precise assumptions about a limited number of variables in a theory that scholars use to examine the formal consequences of these specific assumptions about the motivation of actors and the structure of the situation they face (Ostrom, 2010: 646; emphasis added).

From the standpoint of SES research, frameworks do two things: First, they provide a common language for scholars and practitioners examining a system or set of problems through multiple disciplinary lenses. Urban SES research requires the integration of multiple disciplines in order to account for the complexity of modern environmental problems. Interdisciplinary research is challenging and frameworks help define and redefine terms for cohesive and widely applicable conceptual analysis. A good framework's generalizable language usable in subsequent models and theory for explaining urban phenomena. Furthermore, for a holistic understanding of urban SESs, it is necessary to acknowledge the myriad decisionmakers, the constant changes in human and natural elements over time, the presence of feedbacks between ecological and social subsystems, and the uncertainty in drivers, interactions, and outcomes in cities (Alberti, 1999). Frameworks can help organize and describe these properties.

Second, frameworks provide a structure enabling scientific inquiry and diagnosis, helping researchers and managers figure out how the components in urban areas interact and thereby help understand what is guiding observed outcomes (Cox, 2011; Partelow, 2018). Frameworks with nested components in particular can help researchers unpack complex systems (Cox, 2011). SESs tend to be nested—that is, specific social and ecological elements are nested within larger social or ecological subsystems, which are—for urban systems—nested within urban areas as a whole. For instance, on the ecological side, trees might be in a small forested area that is within a city public park that is located adjacent to and within a river's catchment basin that drains into a regional watershed. On the social side, a single individual is part of a household that may live in a larger apartment building that may be part of a housing project that is located within a neighborhood that is part of one of many political wards that together make up the administrative units of a city. Frameworks can help conceptualize the nested nature of urban SESs as well as the interactions between social and ecological components within and across levels of nestedness (see also Cash et al., 2006 for an excellent discussion of the levels of SESs).

Comparing Frameworks in Urban SES Research

In part because of the interdisciplinarity required for studying urban areas (see also the next section on “Urban Ecosystems—A Related Concept”), there is no single framework universally used. Therefore, three frameworks are described below—the Human Ecosystem Framework (Pickett et al., 1997), the Ecosystem Dynamics Framework (Grimm et al., 2000), and the Urban Ecology Framework (Alberti et al., 2003). Fig. 4 displays the graphical representations of each framework, while Table 2 compares how the frameworks conceptualize the social and ecological elements of urban SESs. (Title Case is used in Table 2 and through this section to identify the language and terms used by the original authors to describe the subsystems and components of their framework.)

The Human Ecosystem framework (Fig. 4A) was first applied to cities by Pickett et al. (1997), who adapted the framework proposed by Machlis et al. (1997) for ecological research more broadly. The framework separates social and ecological subsystems, using a hierarchical approach to identify a set of nested components for each subsystem. The framework is comprised of four variable tiers with three major subsystems: the Human Social System, and Resource System, within which is nested Ecosystem Resources (Machlis et al. (1997)). The framework uses the ecosystem concept from traditional ecology, seeking to use the framework as a tool to instruct how humans might be added to ecosystems in urban areas (Machlis et al. (1997)). Intended for researchers with a stronger background in ecology and natural phenomenon, Pickett et al. (1997) provide ample detail in the nested social system, and theories of spatial heterogeneity and hierarchy have a strong emphasis in the framework (the idea of Patch Mosaics appears in the Ecological Processes box of the framework in Fig. 4A).

The Ecosystem Dynamics framework (Grimm et al., 2000; Fig. 4B) was influenced by Pickett et al. (1997) but is more rooted in the social, cultural, and economic sciences and focuses on understanding the influence human activities have on biophysical properties of urban systems. According to these authors, “Human perception, choice, and action are often the phenomena that drive political, economic, or cultural decisions that lead to or respond to change in ecological systems” (Grimm et al., 2000, p. 572). Following this idea, the framework prioritizes human actions as drivers of executing policy, ultimately leading to change in ecological systems (Grimm et al., 2000). Uniquely, the Ecosystem Dynamics framework identifies urban Land Use as a central component mediating the impact of Environmental Context and Societal Patterns on Ecological Patterns (which then feedback on Environmental Context and Societal Patterns via Ecological Conditions and Human Perceptions and Attitudes, respectively; Pickett et al. (1997)).

The Urban Ecology framework (Alberti et al., 2003; Fig. 4C) views cities as emergent phenomena with dynamic interactions among socioeconomic and biophysical forces. The highly integrated framework organizes all human and ecological elements in urban systems into four subsystems: Drivers, Patterns, Processes, and Effects/Changes (Alberti et al., 2003). Unlike Pickett et al. (1997), Grimm et al. (2000), and Alberti et al. (2003) lacks an explicit distinction between social and ecological elements highlighting the intractable connections between social and ecological subsystems in cities. The absence of explicitly defined social and ecological systems in the headings of components necessitates an interdisciplinary approach to studying urban systems.

All three frameworks facilitate the integration multiple disciplines to assist in hypothesis testing for interactions in urban SESs, but represent urban social-ecological system slightly differently, in part due to the different applications, goals, and intended users of the frameworks. While they differ in their portrayal of social and ecological subsystems, the nestedness of components, as well as how interactions and feedbacks are represented, they all have been widely used by the original authors as well as subsequent scholars to structure analyses of urban SESs.

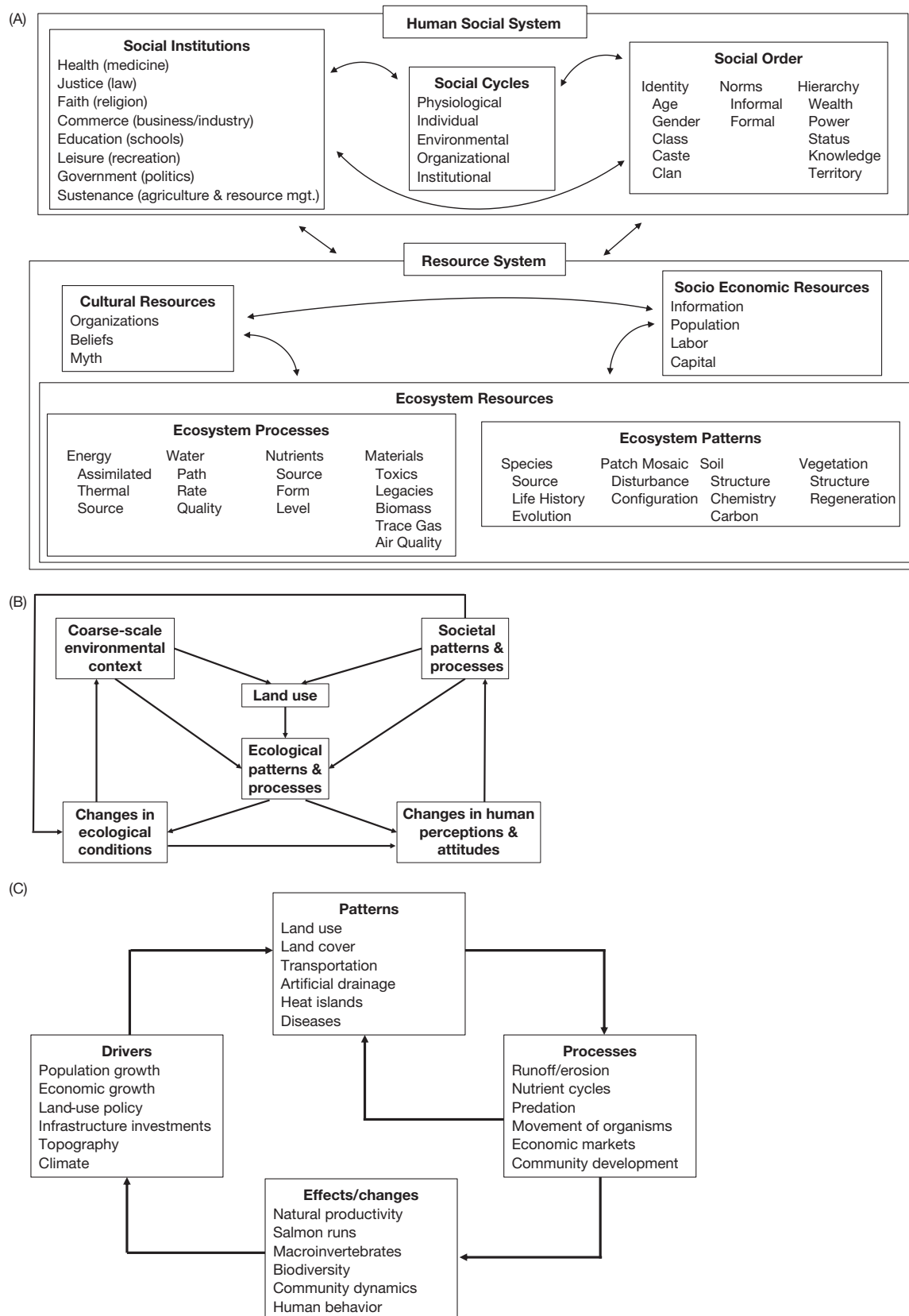


Fig. 4 Three widely-cited frameworks for describing urban systems: (A) The Human Ecosystem Framework, (B) The Ecosystem Dynamics Framework, and (C) The Urban Ecology Framework. (A) Pickett STA, Burch Jr. WR, Dalton SE, Foresman TW, Grove JM, and Rowntree R (1997) A conceptual framework for the study of human ecosystems in urban areas. *Urban Ecosystems* 1: 185–199. <https://doi.org/10.1023/A:1018531712889>; (B) Grimm NB, Grove JM, Pickett STA, Redman CL (2000) Integrated approaches to long-term studies of urban ecological systems. *Bioscience* 50(7): 571–584. [https://doi.org/10.1641/0006-3568\(2000\)050\[0571:IATLT0\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0571:IATLT0]2.0.CO;2); (C) Alberti M (1999) Modeling the urban ecosystem: A conceptual framework. *Environment and Planning B: Planning and Design* 26(4): 605–630.

Table 2 A comparison of selected frameworks for studying urban social-ecological systems.

Framework	Social elements	Ecological elements	Integration
Human ecosystem (Pickett et al., 1997)	Divides up the social subsystem into Social Institutions, Social Cycles, and Social Order, with nested social elements within each, since ecologists are less familiar with social dynamics. Considers Cultural and Socio-Economic Resources in Resource System along with Ecosystem Resources	Ecological subsystem details are surface level due to ecologists' presumed familiarity with Ecological Processes (Energy, Water, Nutrients, Materials) and Patterns (Species, Soil, Vegetation)	Some parts of social systems in urban areas not considered independent from ecological phenomena (e.g., Cultural and Socio Economic Resources are considered together with Ecosystem Resources). Graphically, subsystem components are depicted as interacting with one another and then the Human Social and Resource System interact at a higher level
Ecosystem dynamics (Grimm et al., 2000)	Humans are connected to Ecological Patterns and Processes primarily through Land Use. Human Perceptions impact Societal Patterns and Processes (which impact Land use)	Land Use is a mediator for the influence of Societal and Environmental Context on Ecological Processes, which then feedback on Human perceptions and Ecological conditions	Coarse-Scale (climate, geology, and history) Environmental Context and Societal Patterns and Processes (culture, demography, and social institutions) are linked through their effects on Land Use, but Societal Patterns also directly influence Ecological Conditions
Urban ecology (Alberti et al., 2003)	A focus on the higher-level urban Drivers, Patterns, Processes, and Effects/Changes eschews separation of urban components into social and ecological subsystems. Urban dynamics visualized as a single feedback loop where both social and ecological Drivers (e.g., Population Growth, Climate) affect observed Patterns (e.g., of Land Use and Land Cover), which influence ecological and social processes (e.g., Runoff, Community Development). Processes in turn influence both Patterns as well as the Effects/Changes observed in cities (e.g., Biodiversity, Human Behavior)		

Sources of information on the frameworks from Pickett STA, Burch Jr. WR, Dalton SE, Foresman TW, Grove JM, and Rowntree R (1997) A conceptual framework for the study of human ecosystems in urban areas. *Urban Ecosystems* 1: 185–199. <https://doi.org/10.1023/A:1018531712889>; Grimm, NB, Grove JM, Pickett STA, and Redman CL (2000) Integrated approaches to long-term studies of urban ecological systems. *Bioscience* 50(7): 571–584. [https://doi.org/10.1641/0006-3568\(2000\)050\[0571:ATLTQ\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0571:ATLTQ]2.0.CO;2); Alberti M (1999) Modeling the urban ecosystem: A conceptual framework. *Environment and Planning B: Planning and Design* 26(4): 605–630.

Urban Ecosystems—A Related Concept

An article on urban social-ecological systems would not be complete without a brief discussion of the related concept of urban ecosystems and field of urban ecology. To be fair, most studies of urban SESs would likely be classified as urban ecology. Indeed, the phrases “urban social-ecological systems” or “urban social-ecological system” appear in a fraction of the academic search results as “urban ecology,” “urban ecosystems,” or “social-ecological systems” (Table 3). Urban ecology is the study of cities as ecosystems. In a review of the history of the field, McDonnell (2011) defined the field as follows: “Urban ecology integrates both basic (i.e., fundamental) and applied (i.e., problem oriented) natural and social science research to explore and elucidate the multiple dimensions of urban ecosystems” (p. 9).

As a field of scholarship, urban ecology has really come into its own since the late 1990s, when ecologists truly began to dedicate themselves to the study of cities (McDonnell, 2011). Yet, sociologists, political scientists, planners, geographers and other social scientists had been studying urban dynamics for decades, and the “Chicago School” of sociology in particular began using ecological ideas to describe how cities functioned for people in the 1940s (McDonnell, 2011). These social scientists generally used the theories, frameworks, and methods from their own disciplines in studying urban systems, however. Modern urban ecology as a field is more interdisciplinary and even transdisciplinary (interdisciplinary research that involves stakeholders and practitioners). The three frameworks for understanding urban SESs discussed in the previous section are all rooted in the field of urban ecology. And out of this research has emerged 13 “principles” of urban ecology (Pickett and Cadenasso, 2017; Table 4).

One of the most common way of conceptualizing urban ecology is as ecology “in,” “of,” and “for” cities. Broadly, the “ecology in cities” approach examines classical ecological questions of ecological functioning, nutrient cycling, species diversity, and patterns of

Table 3 Number of search results for phrases related to urban social-ecological system research in three major academic search engines. Search conducted on January 11, 2020.

Search	Google Scholar	Web of Science	EBSCOhost Academic Search Complete
“urban social-ecological system” OR “urban social-ecological systems”	757	33	13
“urban ecology”	About 106,000	1541	4917
“urban ecosystem” OR “urban ecosystems”	About 17,400	1659	2416
“social-ecological system” OR “social-ecological systems”	About 17,500	3629	1561

Table 4 Thirteen principles of urban ecology.

1. Cities and urban areas are human ecosystems in which social-economic and ecological processes feedback to one another
2. Urban areas contain remnant or newly emerging vegetated and stream patches that exhibit ecological functions
3. Urban flora and fauna are diverse, and this diversity has multiple dimensions (e.g., taxonomy, phylogenetics, function, geographic origin)
4. Human values and perceptions are a key link mediating the feedbacks between social and ecological components of human ecosystems
5. Ecological processes are differentially distributed across the metropolis and the limitation of services and excess of hazards is often associated with the location of human communities that are poor, discriminated against, or otherwise disempowered
6. Urban form is heterogeneous on many scales, and fine-scale heterogeneity is especially notable in cities and older suburbs
7. Urban form reflects planning, incidental, and indirect effects of social and environmental decisions
8. Urban form is a dynamic phenomenon and exhibits contrasts through time and across regions that express different cultural and economic contexts of urbanization
9. Urban designs and development projects at various scales can be treated as experiments, and used to expose the ecological effects of different design and management strategies
10. Definition of the boundaries and content of an urban system model is set by the researchers based on their research questions or the spatial scope of its intended application
11. Urban comparisons can be framed as linear transects or as abstract gradients, and the abstract comparisons acknowledge the spatial complexity of urban heterogeneity
12. Urban land covers and land uses extend into and interdigitate with rural or wild land covers and uses
13. The flux of water, including both clean water supply, waste, and stormwater management, is of concern to urban and urbanizing areas worldwide, and connects them explicitly to larger regions

"Principle" in this treatment means components of a potential theory or framework.

Principles from Pickett STA, Cadenasso ML (2017) How many principles of urban ecology are there? *Landscape Ecology* 32: 699–705. <https://doi.org/10.1007/s10980-017-0492-0>.

competition, predation, etc., as they are applied to the ecological elements of cities (see also the discussion in McPhearson et al., 2016). The "ecology of cities" approach, on the other hand, considers the entire city itself as an ecosystem and examines human drivers of (and how human systems are impacted by) ecological patterns and processes. Finally, the "ecology for cities" approach has recently emerged as a transdisciplinary approach that seeks to apply research and understanding of urban social-ecological systems to practical policy and decision making for the sustainability of cities (Childers et al., 2015; Grove et al., 2016; Schwarz and Herrman, 2016).

Conclusion

This article has reviewed definitions of social-ecological systems, urban, and urbanization; described and compared frameworks for studying urban areas as social-ecological systems; and discussed the related concept of urban ecosystems and urban ecology. Urban social-ecological systems research is an emerging field building on at least three decades of urban ecological research since the 1990s but with no single unifying conceptual framework or theories to date. However, given that a majority and growing proportion of the human population lives in urban areas, understanding the social and ecological patterns and processes at work in cities will play an important role in making sure that cities are both livable for people and environmentally sustainable.

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Urban Forests: Biophysical Features and Benefits

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Abstract

Urban forests are all the trees, forests, associated vegetation growing in or very near the cities, towns, and communities where people live, work, and play. What makes urban forests different from forests outside urban areas is their existence in dense areas of human settlement—cities, towns, suburbs, etc. What qualifies as urban from the standpoint of urban forestry includes a range of population sizes or densities (parallel to the Ellis et al. (2010) mapping of anthropogenic biomes, or anthromes, to human population densities): There is no minimum threshold for how many people must live in a community for it to have an urban forest, and the term urban forestry is applied to the management of populations of trees in communities of all sizes. This article discusses the definitions of urban, urban forests, and urban forestry, describes the biophysical characteristics of urban forests and what makes urban forests different from non-urban forests, and details the ecosystem services and disservices provided by urban forests.

Urban Forests and Urban Forestry

Urban forests are all the trees, forests, and associated vegetation and ecosystem components growing in or very near the cities, towns, and communities where people live, work, and play. These “dense settlements”—inclusive of large urban areas and their suburbs, but also towns, etc.—are one of the levels of anthropogenic biomes, or “anthromes,” that has the highest human population density and intensity of impact (Ellis et al., 2010), and urban forests can help mitigate negative impacts. Urban forests can include trees planted in many different types of growing spaces: in the parkways (i.e., boulevards, tree lawns) along streets and next to sidewalks in cities (called “street trees”); in public parks or cemeteries; trees in front or back yards (i.e., private gardens) on residential property; on institutional properties such as school or hospital campuses or business or industrial parks; along highways; growing spontaneously in vacant lots and along alleys; trees in remnant natural areas or planted woodlands; and more (Fig. 1). Because they are co-located in places inhabited by people, urban forests include not only the trees and soil and other abiotic and biotic features in the surrounding growing environment, but also the people living in cities who impact the urban forest.

The science and practice of planting, maintaining, monitoring, and managing the populations of trees in urban areas in order to ensure the provision of the benefits these trees and forest produce for people is called “urban forestry.” Urban forestry—sometimes also called “urban forest management”—consists of a suite of activities, including but not limited to planting, maintaining (pruning, watering, mulching, staking, etc.), and removing trees, but also tree inventory, pest monitoring and plant health care, tree risk assessment, planning for future tree planting and management, and even educating the general public on the benefits and care of trees and advocating on behalf of the urban forest. Performed under ideal circumstances—that is, when experienced urban forest managers have access to complete data on their urban forest, as well as adequate time, labor, and sufficient monetary and quality material resources—urban forest management ensures the net benefits provided by the entire urban forest are maximized (see the section below on “The Benefits and Values of Urban Forests”). Urban forestry is closely connected to the field of *arboriculture*, or the “practice and study of the care of trees and other woody plants in the landscape” (ISA, 2019). Whereas urban forestry deals with entire populations of trees in cities, arboriculture is more often concerned with the care and maintenance of single trees.

In the sections that follow, I describe the biophysical aspects of urban forests, what makes urban forest different from non-urban forests, and the ecosystem services and disservices provided by urban forests.



Fig. 1 The many types of trees in the urban forest. All photos taken by the author.

Biophysical Aspects of Urban Forests

What Is “Urban”?

What makes urban forests distinctly different from forests outside urban areas is their existence in areas of human settlement. In the anthromes terminology, this includes “dense settlements” (urban and mixed settlements) and populated “seminatural lands” such as residential woodlands and populated woodlands (Ellis et al., 2010). In order to understand urban forests as a central component of these anthromes, it is crucial to understand what “urban” means in this context. What is considered urban for the sake of urban forests varies around the world and even from community to community within a single country, but generally means the

communities where people live. Sometimes, the term “urban” is defined by the number of people living in a community or population center, sometimes also with respect to the density of people living in an area. For instance, the US Census Bureau defines the term “urbanized areas” as those having 50,000 or more people, while “urban clusters” have between 2500 and 50,000 people; “rural,” then, is a term inclusive of all areas that do not qualify as urban ([US Census Bureau, 2018](#)). This definition of urban is not consistent across the entire world, or even all of North America: Statistics Canada, responsible for the Canadian census, for instance, defines urban as all population centers of greater than 1000 people with a density of greater 400 people per square kilometer (1036 people per square mile) ([Statistics Canada, 2017](#)). And in Africa, for example, urban definitions range considerably—containing more than 2000 inhabitants (Ethiopia, Kenya), more than 5000 inhabitants (Zambia), or more than 10,000 inhabitants (Senegal)—or, in Algeria, are defined instead by the number of “constructions” (100+, spaced 200 m or less apart; [United Nations Statistics Division, 2011](#), as summarized in [Francis and Chadwick, 2013](#)).

What qualifies as urban from the standpoint of urban forestry can actually include a range of population sizes or densities. Generally, there is no minimum threshold for how many people must live in a community for the it to have an urban forest, and the term urban forestry is applied to the management of populations of trees in communities of all sizes. Because of this, sometimes the term “community forestry” is preferred by smaller towns for which the term “urban” may not resonate. The US Forest Service, for instance, uses the phrase “urban and community forestry” to refer to the program within the Forest Service that administers to urban forests. However, “community forestry” and “urban forestry” are not interchangeable in all parts of the world. In Canada for instance, “community forestry” refers to communities that have a significant economic dependency on forest resources and the forestry industry (i.e., forest-dependent communities; [Duinker et al., 1994](#)). In Europe also, the term “community forestry” was also initially linked not to modern concepts of “urban forestry” but instead to heritage woodlands in smaller towns or more rural areas that are managed by the local community ([Konijnendijk et al., 2006](#)).

Urban Forest Characteristics

Most readers will be more familiar with the idea of a “forest” than with an “urban forest,” despite the fact that more than 50% of the global population lives in some type of city or town, and 29% live in so-called urban anthromes ([Ellis et al., 2010](#)). City dwellers may experience the urban forest on a more regular basis than “natural” forests outside cities. Urban forests differ from non-urban forests in several essential ways. First, the image of a “forest” may conjure expansive stands of trees, shrubs, and other vegetation with a closed canopy of leaves overhead letting little light through to the forest floor, which may be dense with leaf litter and ground vegetation. Some parts of the urban forest may look similar to non-urban forests, for instance, if there are remnant patches of native forest that have been enclosed by urban development and set aside as parks, nature preserves, or backyard woodlands. There may also be areas of planted (non-remnant) forest within a city that share this more traditional forested character. Whether planted or remnant, these areas are sometimes called urban forest natural areas, naturalized areas, forest patches, urban woodlands or woodlots, or forested parks. These areas likely include more than just trees, but also shrubs and herbs as ground cover, and depending on quality, may contain habitat for urban wildlife including small mammals, insects, and birds. Urban forest natural areas may about bodies of water that are near or within urban areas, such as streams, rivers, ponds, lakes, or canals. The growing conditions for trees in these types of areas are more likely to mimic those for trees in natural areas outside of cities, and the soils, hydrology, nutrient flows, microclimate, and ecology may be more similar to natural areas.

However, urban forests also include trees growing outside of more natural or naturalized areas within cities—in parks, the front or back yards of residential properties, along streets, etc. These types of growing conditions are much different from the semi-natural conditions of urban forest natural areas. Both above and belowground growing space may be more constrained, especially for trees highly constructed spaces. For instance, trees growing in a tree pit are especially constrained: tree pits are small growing spaces with perhaps only a couple square meters of growing substrate (soil, sometimes mixed with gravel or other medium), often found along streets, in plazas, parking lots. The base of a tree in a tree pit is likely surrounded on all four sides by concrete paving impervious to water, and the area immediately adjacent to the tree trunk may be covered with a metal grate that, if not properly sized, may interfere with the root flare and healthy trunk growth. Belowground, tree roots must compete with urban infrastructure such as buried power and cable lines, storm and sanitary sewer pipes, gas lines, building and road foundations, etc., not to mention cope with high levels of soil compaction, soil nutrient imbalance, and inadequate soil drainage (or conversely, poor water retention). Aboveground, these trees may be heavily pruned so that they do not interfere with urban infrastructure such as buildings, fences, signage, street lights, above ground power and cable lines, etc., or may have limited exposure to light due to shading by tall urban buildings. Because of this suite of constraints, trees in constrained urban areas may be in poor condition, of small size and sub-optimal form, and experience high mortality rates and short life spans.

Yet other trees in some urban spaces may experience more favorable growing conditions. For instance, trees in high-quality urban parks may have relatively unlimited growing space, be well-cared for (through regular pruning and watering, pest management, etc.), and even may have access to additional nutrients (either through direct fertilizing of the tree, or as a byproduct of fertilizing the nearby turf grass). They may be growing in a wide-open area free of competition with other trees or other urban infrastructure. These high-quality growing conditions may lead to long-lived trees that grow large and provide significant benefits.

The Benefits and Values of Urban Forests—Ecosystem Services

Urban forests are important for cities because trees provide benefits that have substantial value for the people who live in those cities. This section will discuss how urban forests produce benefits, how these benefits are valued, and how this value is calculated.

Structure, Function, Benefits, and Value

The mechanism through which urban trees and forests provide value to people can be conceptualized as the structure-function-benefits relationship (Fig. 2). The structural characteristics of urban trees—such as tree size, species, etc.—and urban forests—such as the extent of urban tree canopy cover across all or a portion of an urban area—contribute to the ecosystem functions provided by those trees and forests. Trees and forests, whether in urban or non-urban areas, perform a variety of ecosystem functions, including regulating functions such as climate management through shading and evapotranspiration; biodiversity functions such as providing nesting habitat for urban wildlife; production functions such as producing edible fruits and nuts; and “information functions” (c.f., de Groot et al., 2002) such as the aesthetic and scientific opportunities afforded by the existence of urban trees (Table 1). These ecosystem functions, when viewed through an anthropocentric lens, translate into benefits and value for people, often termed ecosystem services. (In urban forestry, “benefits” is often used synonymously with “ecosystem services”. In the broader ecosystem services literature, *ecosystem services* are “the benefits humans obtain from ecosystems” (Millennium Ecosystem Assessment, 2005, p. v). However, urban forest discourses more frequently use the more general “benefits” term in both the scholarly literature as well as in communications with the general public.) For instance, the water regulating functions of trees benefit people when trees are used as part of green infrastructure-based solutions for managing stormwater in urban areas.

Urban forest structure and function are biocentric ways of conceptualizing the importance of the urban forest. *Biocentric*, in this context, refers to the intrinsic value of trees and forests—that is, nature for nature’s sake; the urban forest will have these functions regardless of what if any value humans place on them. All of the functions listed in Table 1 (with the exception of information functions) can be considered biocentric. Urban forest benefits and value, on the other hand, are anthropocentric concepts. *Anthropocentric* refers to the value of trees and forests explicitly for human benefit and use; that is, the functions of urban forests would have no benefits or value without that which humans place on them. Urban forestry and urban forest management are mostly anthropocentric, which makes sense given the explicit consideration of urban forests as trees located in the places where people live and work.

The structure-function-benefits relationship has implications for how people think about and manage urban forests. Urban forests may be managed according to goals that align with the biocentric, intrinsic value that structure and function has. For instance, managers may have goals for species composition (e.g., a single species can account for no greater than 10% of all public trees) or size distribution (e.g., have more small, young trees than large, mature trees in the urban forest) of their urban forest. These types of biocentric goals often imply a rationale related to urban forest function (e.g., a diverse species composition decreases vulnerability of the urban forest to taxa-specific pest or disease outbreak). On the other hand, anthropocentric urban forest management goals related to the benefits and values of trees might consider management of the urban forest in order to provide a specific level of benefits (e.g., gallons of stormwater diverted from runoff in order to prevent the city from needing to issue capital improvement funds to allow the public works department to install larger pipes when updating stormwater infrastructure).

The list of particular benefits provided by urban forests is extensive, and the benefits of trees is one of the more well-researched areas of urban forestry as a scholarly discipline. Urban forest benefits can generally be thought of as falling into three categories: environmental benefits, including those related to urban environmental quality issues such as air quality, water quality, and microclimate, as well as biodiversity and conservation benefits such as wildlife habitat; social benefits such as human quality of life,

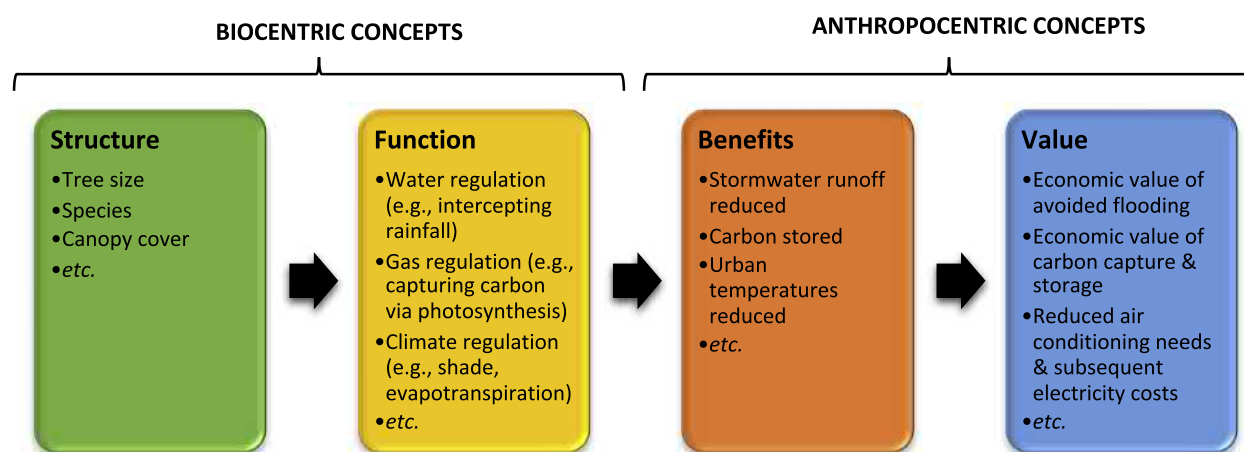


Fig. 2 Urban forest structure such as tree size and species impact how urban trees and forests perform key ecosystem functions such as climate regulation (through shading and evapotranspiration), which in turn impacts the production of benefits such as reducing urban temperatures. Since these benefits often have real value to people living in urban areas, they are often translated to economic terms, such as the decreased electricity costs resulting from reduced need for air conditioning. Note that urban forest structure and function are “biocentric” concepts while benefits and value are “anthropocentric” concepts. See main text for a more detailed discussion of structure, function, benefits, and value in the context of biocentric and anthropocentric ideas of the urban forest.

Table 1 Select ecosystem functions performed by trees and forests in cities.^a

Function	Explanation
<i>Regulation functions</i>	<i>The “maintenance of essential ecological processes and life support systems” (de Groot et al., 2002, p. 396)</i>
Gas regulation	Trees photosynthesize, taking in carbon dioxide and releasing oxygen.
Climate regulation	Through shading and evapotranspiration trees have a cooling effect on the local microclimate, while larger groups of trees or forested areas such as parks contribute to the urban breeze cycle, whereby as the hot air over paved areas and buildings rises, drawing in the cooler air from adjacent vegetated areas.
Water regulation	Tree canopy and roots slow the infiltration of stormwater and help manage runoff in urban areas, as well as filter, retain, and store fresh water (e.g., in retention ponds or local bodies of freshwater).
Soil retention	Tree roots make sure that soil is not eroded, particularly along steep slopes (e.g., next to highways).
Waste treatment	The leaf surface area provided by tree canopies filters the air of particulate matter and pollutants.
Biological control	A diverse species composition within the urban forest helps reduce vulnerability to infestation by a taxa-specific pest or disease.
<i>Habitat functions</i>	<i>The function urban trees of urban forests have of providing habitat for plant and animal species.</i>
Refuge	Trees and forests provide living spaces and foraging resources for wildlife.
Nursery	Trees and forests provide habitat for wildlife to use to reproduce (e.g., nesting locations for birds, squirrels).
<i>Production functions</i>	<i>Trees and urban forest can, in certain cases, provide natural resources for human use.</i>
Food	Trees produce edible fruits, nuts, and seeds.
Raw materials	As they grow and mature, trees have increased wood volume, which can be used for human purposes at the end of their urban life.
<i>Information resources*</i>	<i>Trees and urban forests can “provide opportunities for cognitive development” (de Groot et al., 2002, p. 396)</i>
Aesthetic*	Trees and urban forests produce greenery and flowers that have aesthetic appeal for humans in urban areas.
Recreation*	Trees and urban forests in cities are physical spaces for—as well as encourage individuals to—exercise and recreate outside in cities.
Scientific and education*	Trees and urban forests can provide opportunities for scientists and the general public alike to study and learn about nature.

Ecosystem functions list borrowed in part from de Groot et al. (2002) typology of ecosystem functions. An * indicates an ecosystem function that is dependent on the presence and values of humans in order to be a function (anthropocentric).

^aSome readers may be familiar with the Millennium Ecosystem Assessment (2005) categories for ecosystem services (provisioning, regulating, cultural, and supporting). The above table does not use these categories here because the table presents a list of ecosystem functions, which are slightly different from services: ecosystem functions are about what an ecosystem does as a system of biotic and abiotic components, while ecosystem services are about what an ecosystem provides to people. Ecosystem functions can be translated into ecosystem services by applying an anthropocentric filter to examine how the functions of an ecosystem benefit humans. See main text for a more detailed description of the translation of urban forest structure and function into benefits and values for people.

human health, and community social capital; and economic benefits such as those related to property values, utilities expenditures and investments such as electricity and water and associated infrastructure, and economic development. Table 2 provides a semi-comprehensive but non-exhaustive list of the benefits of urban forests, since researchers are constantly investigating new benefits. In particular, significant new research on the social and human health benefits of urban forests is emerging through the work of several dedicated communities of scholars.

Calculating Urban Forest Economic Value

Urban forest benefits are sometimes translated into dollars or monetary terms to express the value that urban forests have in economic terms. Using methods from the field of ecological economics, urban forest researchers have monetized benefits such as stormwater management, air pollution, reduced energy costs, aesthetic benefits manifesting as property value increases, and even improvements in physical and mental aspects of human health. Table 3 describes select studies that have used scientific research to empirically examine the connection between urban forest structure, function, benefits, and, for select studies, economic value.

i-Tree: A case study of calculating urban forest value

One of the most dedicated and long-term efforts to translate urban forest structure and into benefits and economic value for people is the effort by researchers with the US Forest Service and Davey Resource Group to develop i-Tree (www.itreetools.org). i-Tree is a suite of online software tools into which an urban forest researcher or manager can enter data about the structure of a tree population (either by uploading a spreadsheet of a tree inventory or by accessing existing tree canopy cover data, where available) and get back data about some of the most commonly-valued benefits (stormwater, aesthetics/property value, energy, air quality, and carbon dioxide) produced annually by a tree population as well as the dollar value of these benefits. (Note that because the i-Tree software automatically quantifies both the benefits (e.g., kilowatt hours of electricity conserved due to the cooling benefits of trees) as well as the economic value of this benefit (e.g., dollars saved on electricity), the term “benefits” when used by i-Tree means both benefits and value.) A simple version of i-Tree built for entering data for just a single tree can be found at the National Tree Benefits Calculator (<http://www.treebenefits.com/calculator/>). Fig. 3 shows the results from the National Tree Benefits Calculator for the benefits provided by a 12-in. (30 cm) diameter red maple (*Acer rubrum*)—a common urban street tree planted across the world—growing on a single-family residential property in Chicago, Illinois.

Table 2 A semi-comprehensive list of the benefits of urban trees.

<i>Environmental</i>	<i>Social</i>	<i>Economic</i>
<i>Air quality</i>	<i>Urban quality of life</i>	<i>Property value</i>
Produce oxygen	Enhance urban quality of life	Increase property, land value
Filter air	Provide outdoor recreation/leisure opportunities	Increase neighboring property value
Remove ozone	Provide nature in the city	Reduce time to sale for property sales
Remove carbon monoxide	Reduce noise and apparent loudness	Increase rental price for properties
Remove nitrogen dioxide	Decreased incidences of some types of crime	Increase property taxes
Remove particulate matter	<i>Human health</i>	<i>Utility benefits</i>
Remove smog	Create relaxed psychological states	Reduce expenditures on stormwater infrastructure
<i>Stormwater</i>	Averted premature death (e.g., decrease mortality from cardiovascular disease and upper respiratory illness)	Avoid investments in new power infrastructure
Reduce rate and volume of stormwater runoff	Decreased length of hospital stays following surgery	Provide potential for future carbon offsets
Reduce flooding damage	Improve mental health (e.g., decrease ADHD symptoms, reduce stress)	Save on annual heating/cooling costs
Reduce water quality problems	Improve physical health (e.g., decrease asthma rates, cardiovascular disease, and low birth weight)	Save on electricity costs
Recharge groundwater	<i>Community/social capital</i>	Save on fuel expenditures
<i>Carbon related</i>	Build a sense of community (stronger neighborhood ties)	<i>Economic development</i>
Reduce carbon dioxide emissions	Enhance a community's social identity and self esteem	Increased tourism revenue
Store/sequester carbon	Provide a sense of place	Increased business activity
<i>Energy related</i>	Provide settings for significant emotional and spiritual experiences	Contribute to the economic vitality of the community
Reduce annual energy use	<i>Individual human capital</i>	Provide returns on municipal investments
Reduce summer time energy use	Provide opportunities for inner city children to experience nature	<i>Pollution abatement</i>
Reduce seasonal cooling energy	Build skills associated with green trades	Reduce expenditures on air pollution removal
Reduce carbon dioxide emissions from power plants	Promote individual environmental responsibility	
<i>Microclimate</i>	<i>Aesthetic benefits</i>	
Provide shade	More pleasant urban environments	
Reduce solar radiation	Improve scenic quality	
Modify microclimate	Provide privacy	
Reduce relative humidity	Create seasonal interest and highlighting seasonal changes	
Reduce air temperature		
Reduce urban heat island effect		
Reduce glare/reflection		
Control wind		
<i>Biodiversity and conservation</i>		
Provide wildlife habitat		
Enhance biodiversity		
Provide stability to urban ecosystems		

Re-classified from a list presented by Roy et al. (2012) in their literature review of 115 studies, with additions from more recent literature as necessary.

Table 3 Examples of scientific studies that have provided evidence for select environmental, economic and social benefits of urban trees and forests.

<i>Benefit</i>	<i>Description of scientific study</i>	<i>Source</i>
<i>Environmental</i>		
Oxygen production	Used data on tree biomass from field plots in 16 cities across the continental US to extrapolate oxygen production by trees in US urban forests to be 61 million metric tons, but because of the large amount of oxygen already in the atmosphere, notes that the value of oxygen production by urban forests to society is negligible.	Nowak et al. (2007)
Air pollution removal*	Used data from field plots in 10 US cities to model particulate matter (PM _{2.5}) removal by urban forests and observed average air quality improvements in each city ranging from 0.05% to 0.24%, with an annual value to society ranging from \$1.1 million to \$60.1 million (2012 USD).	Nowak et al. (2013)
Cooling/temperature regulation	Used bicycle-sensed microclimate and weather data in combination with tree canopy cover data from Madison, Wisconsin, and observed that daytime air temperatures were inversely linearly correlated with tree canopy cover, and that temperatures were substantially lower for neighborhood blocks with canopy cover greater than 40%, and that the air temperature increases caused by high amounts of impervious surface cover can be offset by the cooling effects of trees.	Ziter et al. (2019)

(Continued)

Table 3 Examples of scientific studies that have provided evidence for select environmental, economic and social benefits of urban trees and forests.—cont'd

Benefit	Description of scientific study	Source
Stormwater management	Compared structure of street tree populations in 9 communities around Cincinnati, Ohio, and used i-Tree software to model stormwater benefits and observed greater stormwater benefits for those communities with greater tree canopy cover, and for those communities meeting the urban forest management standards of the Tree City USA program.	Berland and Hopton (2014)
<i>Social</i>		
Increased opportunities for recreation	Conducted surveys of park visitors and gathered data about urban forest structure in public parks in Berlin, Germany, and Salzburg, Austria, and found that visitors engaged in both active and passive forms of recreation and rated shaded (treed) areas as most important to passive relaxation activities.	Voigt et al. (2014)
Decreased mortality	Compared county-level mortality rates from 1990 to 2007 across 15 states impacted by emerald ash borer (EAB), and observed a decrease in cardiovascular- and lower-respiratory-tract illness-related mortality rates in counties not invested with EAB compared to counties with EAB infestations (which had thus experienced a significant loss of tree canopy in a short period of time).	Donovan et al. (2013)
Stronger community ties	Compared “greener” and “less green” areas of public housing complexes in Chicago in a number of studies conducted in the late 1990s, and observed greater social interaction among residents in greener areas, greater incidence of adult-child interactions, stronger social ties among neighbors, and a reported stronger feeling of belonging for residents in greener areas.	Kuo (2003)
<i>Economic</i>		
Increased business district retail sales*	Conducted surveys of residents in small and large towns and observed that for both size communities, shopping area streetscapes with trees were not only perceived as more pleasant and desirable by patrons but that patrons were willing to pay more for goods purchased in treed shopping areas compared to those without trees.	Wolf (2005)
Increased residential property value*	Compared 600 recently-sold single-family residential properties across six communities around Cincinnati, Ohio, and observed higher property sales prices for properties with higher urban tree canopy cover in the amount of \$780 (2012 USD) per every 1% increase in tree cover.	Dimke et al. (2013)

An * next to the benefit indicates that the study measured the economic value of the benefit.

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Benefits of your tree

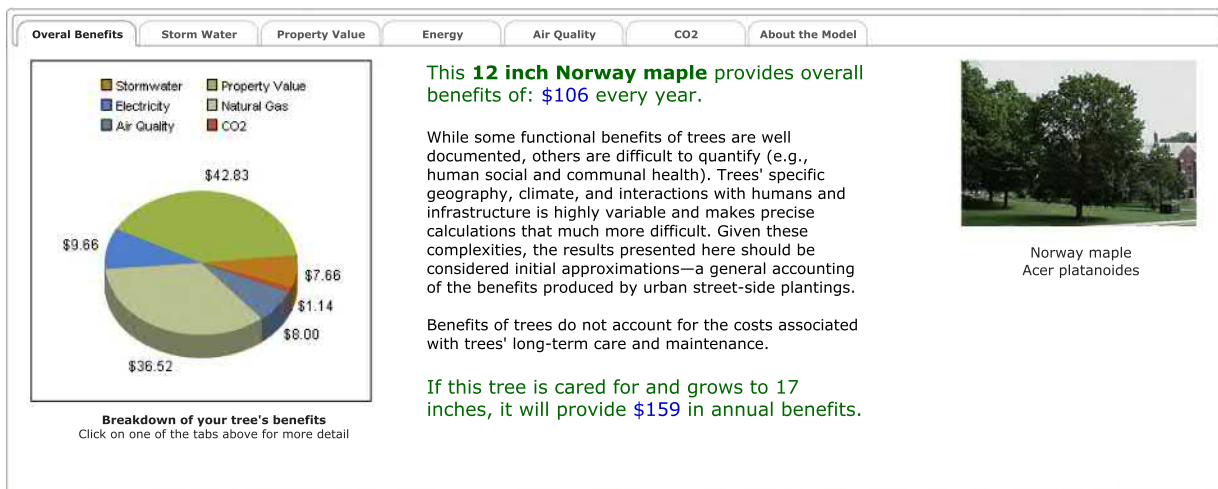


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National Tree Benefit Calculator

Beta



The National Tree Benefit Calculator was conceived and developed by
Casey Trees and Davey Tree Expert Co.



Fig. 3 The results of translating the structure of a 12" Norway maple (*Acer platanoides*) growing in a single-family residential land use area in Chicago, Illinois into urban forest benefits and value. Using the National Tree Benefits Calculator (<http://www.treebenefits.com/calculator/>).

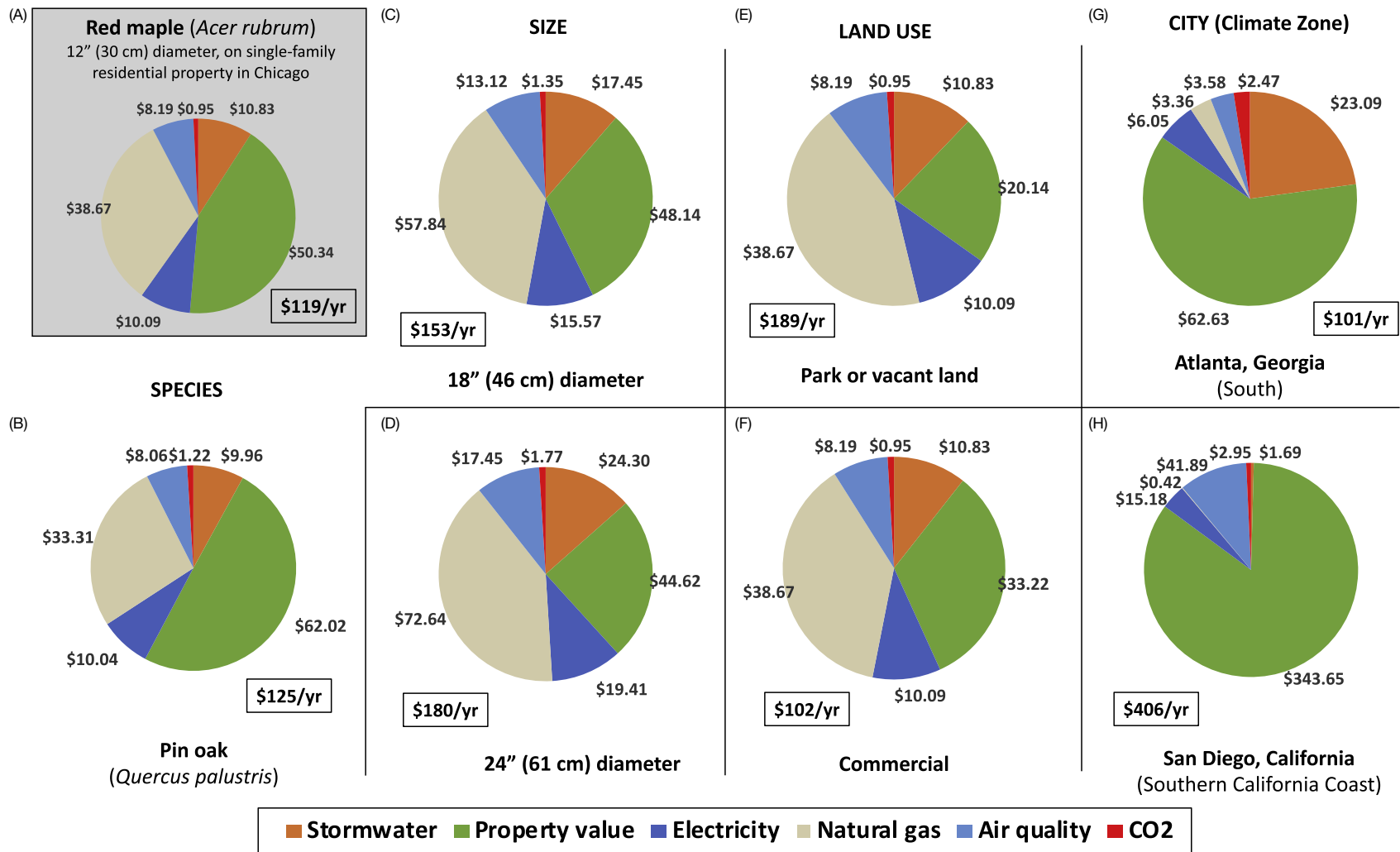


Fig. 4 Comparing urban tree benefits for a 12-in. (30 cm) diameter red maple (*Acer rubrum*, a) grown on single-family residential land use in Chicago, Illinois, to a similarly grown pin oak (*Quercus palustris*, b), 18- and 24-in. (46- and 61-cm) red maples (c and d), the same 12-in. red maple grown on park or commercial land (e and f), or on single-family residential property in Atlanta or San Diego (g and h). Based on results from the National Tree Benefits Calculator (<http://www.treebenefits.com/calculator/>). Specifications used in the calculator are as follows: (a) Red maple (*Acer rubrum*), 12" diameter, Single-family residential, Chicago, Illinois (Northeast climate zone). (b) Pin oak (*Quercus palustris*), 12" diameter, Single-family residential, Chicago, Illinois (Northeast climate zone). (c) Red maple (*Acer rubrum*), 18" diameter, Single-family residential, Chicago, Illinois (Northeast climate zone). (d) Red maple (*Acer rubrum*), 24" diameter, Single-family residential, Chicago, Illinois (Northeast climate zone). (e) Red maple (*Acer rubrum*), 12" diameter, Park or other vacant land, Chicago, Illinois (Northeast climate zone). (f) Red maple (*Acer rubrum*), 12" diameter, Small commercial business, Chicago, Illinois (Northeast climate zone). (g) Red maple (*Acer rubrum*), 12" diameter, Single-family residential, Atlanta, Georgia (Southern climate zone). (h) Red maple (*Acer rubrum*), 12" diameter, Single-family residential, San Diego, California (Southern California Coastal climate zone).

The structure, function, benefits, and value provided by a tree are impacted by countless factors related to the tree itself, where it is growing, maintenance performed, and any number of additional variables in the surrounding community that might impact a tree's structure. The key factors considered by i-Tree calculations include species, size, land-use type, and the climate in which the tree is growing. Comparing the value of benefits for similar trees that vary only on one of these dimensions can be instructive towards understanding the connection between tree structure and benefits (Fig. 4). For instance, climate impacts not only how a tree grows but also the value of benefits such as heating and cooling energy savings. Of the major benefits valued by i-Tree (and the National Tree Benefits Calculator), for a 12-in. red maple tree growing in Chicago, Illinois, located in i-Tree's Northeast climate zone, the largest portion of a tree's value comes from property value benefits, followed by energy savings due to decreased consumption of natural gas. However, for the same 12-in. red maple tree growing in warmer climates, such as Atlanta, Georgia (located in the Southern climate zone) or San Diego, California (in the Southern California Coastal climate zone), while property values are still important (especially for San Diego where the housing market is highly competitive and residential real estate prices are high), natural gas energy savings from reduced heating needs are negligible (compare panels a, g, and h of Fig. 4).

The five major benefits (stormwater, property value, energy, air quality, and carbon dioxide) considered in i-Tree-based analyses are not the only benefits of urban trees (as illustrated by the extensive list in Table 2), nor are they the only benefits researchers have translated to economic values. Thus, the calculation of tree value provided by i-Tree and applications like the National Tree Benefits Calculator is a conservative estimate of the true value of an urban tree or forest. Researchers with the i-Tree team are currently working to expand the ability of this software tool—widely used by urban forest managers—to integrate value calculations for a larger list of tree benefits, including human health. For instance, a recent study considered four major human health-related benefits (birth weight, attention deficit hyperactivity disorder [ADHD], cardiovascular disease, and Alzheimer's disease) plus two additional urban quality-of-life benefits (school performance, crime), and found that the potential total annual value of urban trees and forests in the United States is between \$2.7 and \$6.8 billion (2012 USD) (Wolf et al., 2015). Incorporating this new research into tree benefits calculations will improve researchers' and managers' abilities to communicate the benefits of urban trees and forests to the general public and, importantly, urban policy makers. Additionally, researchers are working to expand the ability of i-Tree for use in a greater variety of locations around the world (currently i-Tree is most accurate in calculating benefits and values for urban trees and forests in the United States).

Externalities of Urban Forests—Ecosystem Disservices

The functions of urban trees and forest produce not only benefits or ecosystem services for people, but also “ecosystem disservices,” or negative consequences for people from nature (c.f., Lyytimäki and Sipilä, 2009). These “externalities” are public costs—that is, not captured in the private cost of a good or service. Externality-related costs are not paid for by any particular individual as part of the costs of the urban forest. Urban trees produce many types of ecosystem disservices that can be classified as either environmental or social (Table 4). Ecosystem disservices that might be classified as economic are better conceptualized as direct costs, though it

Table 4 Environmental and social ecosystem disservices produced by urban trees and forests.

<i>Environmental</i>	<i>Social</i>
<i>Water-related problems</i>	<i>Health problems</i>
Increased water consumption (especially in drought-plagued regions)	Allergies due to release of plant pollen
Drainage problems from tree root-sewer conflict	Attacks by insects/animals associated with urban forests (e.g., mosquito habitat)
<i>Debris/waste issues</i>	Increase of insects/animals acting as vectors for disease
Disposal of green waste generated during tree pruning/removal	<i>Safety concerns</i>
Disposal of debris/clutter from leaves and nuts/fruits/seeds	Obscured views/decreased traffic visibility
Disposal of debris during infrastructure repair due to tree conflicts	Risk to human safety from falling limbs
<i>Air pollution-related</i>	Actual increases in crime
Release of biogenic volatile organic compounds (BVOCs; air pollution)	<i>Aesthetic concerns</i> Darkness
Release of carbon dioxide during maintenance due to use of fossil-fuel powered equipment	Debris/clutter of leaves and nuts/fruits/seeds
Release of carbon dioxide during decomposition of tree or tree debris	Sap dripping on parked cars
<i>Ecosystem integrity</i>	Improper maintenance leads to displeasing form (e.g., topped trees, weed-filled vacant lots, excessive sprouting)
Displacing native species/escape of invasive species from urban forests	<i>Negative perceptions of trees/forests</i>
<i>Energy-related</i>	Fear of crime
Increased energy consumption due to improperly placed trees	Fear of disease
Increased energy consumption due to tree maintenance	Fear of insects or other animals
Loss of solar panel capacity due to shading by trees	Fears of forests and trees

Re-classified from a list presented by Roy et al. (2012) in their literature review of 115 studies, with additions from literature focused explicitly on ecosystem disservices (Lyytimäki and Sipilä, 2009; Dobbs et al., 2011; Lyytimäki, 2014). (Note that ecosystem disservices of trees in Roy et al. (2012) that might be considered economic costs are better conceptualized as either direct costs (cost of planting and irrigation, trees falling across power lines, etc.) rather than externalities or ecosystem disservices.)

should be noted that many of the disservices listed in Table 4 may be translated into economic value the same way the benefits listed in Table 2 may be translated into economic value. However, these values most of the time are not explicitly paid for by any particular actor associated with the urban forest, and thus are external (i.e., “externalities”) to the decision-making of individuals or groups with respect to urban forest management.

Conclusion

This article has described urban forests as all the trees, forests, and associated vegetation and ecosystem components growing in or very near the cities, towns, and communities where people live, work, and play. This includes trees planted along streets and boulevards, in parks, on private property, in vacant lots, and even those trees that spring up in unmanaged alleys or along transportation corridors. Urban forests produce significant benefits, or ecosystem services, for urban residents, but also have externalities, or ecosystem disservices. While this article has focused on the biophysical, or ecological, elements, there are also significant human influences on urban trees and forests.

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Urban Forests as Social-Ecological Systems

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Abstract

Urban forests are all the trees, forests, associated vegetation growing in anthromes with higher levels of population density (e.g., dense settlements and populated woodlands). This chapter describes the important human elements of urban forest ecosystems, including actors, ownership regimes, and management, the distribution of urban forest benefits, the direct costs of urban forests, and current conceptions of urban forest sustainability. The chapter concludes by presenting a comprehensive framework for understanding the many factors that shape urban forests as social-ecological systems of inseparable natural and human components.

Urban forests are by their very nature systems of both natural components (i.e., trees, etc.) and human components (i.e., people living in urban areas) found in anthromes (cf., [Ellis et al., 2010](#)) ranging from dense settlements to populated woodlands. Thus, in addition to considering the biophysical characteristics of the trees and forested areas that make up urban forests, it is also necessary to consider the human elements of the urban forest.

This article examines how the human elements of urban forests produce observed outcomes, in particular, urban forest benefits and costs. These human elements include the actors (people and groups) who interact with the urban forest, patterns of urban land ownership (e.g., whether urban forests are located on public or private property), and the management undertaken by these actors on different property types. Actors, ownership, and management impact the distribution of the benefits of urban forests as well as the direct costs of urban forests. The article concludes by presenting a comprehensive framework, synthesized from the literature, for understanding and studying urban forests as social-ecological systems.

Actors in the Urban Forest

The biophysical and ecological character of forests and trees in urban areas are extensively influenced by human actions. There are a number of different actors—individuals and groups—interacting in various capacities. The list of actors influencing the urban forest includes municipalities; privately-owned tree care companies; power companies managing utility rights-of-way; nonprofit organizations with missions connected to urban greening; residents’ or neighborhood associations; business associations; storm-water management districts; real estate developers and builders; property management companies; large institutional landowners (e.g., colleges and universities, hospitals, schools); homeowners, landowners, and other urban residents; and more. Each of these actors has a different jurisdiction and area of influence, as well as goals and capacities related to the urban forest. For instance, real estate developers looking to develop or redevelop single properties or large parcels of land may or may not value the urban forest as an important part of residential or commercial building projects, and they may or may not possess the skill, knowledge, or interest to design developments with infrastructure that promotes a healthy urban forest (e.g., by protecting large trees, preserving patches of existing forest, or designing adequate spaces for planting new trees). Utility companies manage trees along a utility corridor in which electricity infrastructure (power lines, etc.) is located; as such, utility foresters are concerned with maintaining the necessary clearance around power lines to as to avoid electrical service disruptions caused by trees.

Even within a single actor type, involvement with and capacity for urban forest management may vary across cities. For municipalities, resources (expertise, budget, etc.) available for urban forest management at the municipal level also impact the urban forest. In some cities, authority for urban forest and tree management is designated to the department of public works, while in others this authority may be held by parks and recreation, or in rare cases, a stand-alone urban forestry department. Some municipalities have certified arborists on staff—highly skilled, certified professionals trained in the care of trees—while other cities contract out tree work to private companies, or rely on untrained city staff to perform tree care (though the latter is not advisable). Additionally, the budget for municipal management of the urban forest can vary significantly from city to city, and some cities may even lack a dedicated urban forestry budget entirely, relegating urban forest management to crisis-response only (e.g., removal of hazardous trees, cleaning up debris from storms).

Actors may interact with one another on urban forest management. For instance, municipalities may be legally obligated to maintain the trees located along streets in the public right-of-way, but may contract the planting, maintenance, and/or removal of street trees to a private tree care company staffed by certified arborists or even to a local nonprofit organization that may in turn engage neighborhood residents as un-trained or semi-trained volunteer tree stewards in simple tree care tasks (e.g., watering recently-planted trees). Or, a local urban forestry nonprofit organization may collaborate with residents' associations and homeowners to plant trees in a new housing development with low canopy cover. Or stormwater management districts may collaborate with the local municipality on a tree giveaway program to encourage more planting of trees on private property.

Ownership: Public Versus Private Urban Trees

As alluded to above, different actors may be responsible—formally (legally) or informally—for taking care of different parts of the urban forest. The urban forest in cities is frequently described in terms of existing on either public property or private property (The concepts of ownership and property discussed in this section are biased towards Western European (colonial) ideas of private property. For better or worse, this is consistent with the majority of the urban forest discourses *writ large*. While the study of urban forestry in developing and non-Western countries is growing, future discourse and scholarship would benefit from being more inclusive of other land management regimes). *Public property* includes land owned or managed by a public entity, such as a municipality (village, town, city, or county government), public utility or other public authority (such as a state or national highway department), or the *public right-of-way* (area extending from the edge of a public street a certain distance onto adjacent private property, to which one or more public authorities have limited rights of access and use and sometimes also maintenance responsibilities over). Public trees include park trees and any additional trees on public land (a golf course, town square, publicly-managed cemetery, etc.), but also all trees in the public right-of-way (street trees, trees along a publicly-owned and managed trail, etc.).

Across an entire city, the public urban forest accounts for only a small percentage of the urban forest (though it should be noted that in some parts of a city, e.g., a city center business district, all of the urban forest may exist on public land or in the public right-of-way such as boulevards, parks, and public plazas). Private trees are the remainder of the urban forest not on public property, accounting for as much as an estimated 90% of “urban tree canopy cover” (the geographic extent of tree canopy covering an urban area, as measured through use of aerial or remote sensing imagery) (e.g., for Baltimore, MD, USA: [Troy et al., 2007](#)). This means that the vast majority of urban trees exist outside of direct public control or management, despite the fact that the benefits produced by the urban forest are largely benefits to the general public. And though a large scholarly discourse and practitioner community exist centered on municipal urban forest management (including even a specific certification for “Municipal Specialist” that supplements the International Society of Arboriculture [ISA] Certified Arborist credential; [ISA, 2019](#)), the portion of the urban forest existing on public land is minimal. Thus, collaboration among actors responsible for the public urban forest (i.e., municipal—staff and contracted—foresters and arborists) and those responsible for the private urban forest (e.g., individual homeowners, businesses, institutions with large tracts of land such as colleges, hospitals, etc.), is necessary for the urban forest as a whole to produce optimal benefits to all.

The Complexity of Urban Forest Management

All of these different actors all influencing urban forest outcomes in different ways creates a complicated and “polycentric” urban forest management situation. *Polycentric* refers to the many overlapping yet independent centers of decision making that exist in urban areas ([Ostrom et al., 1961](#): p. 831). Also called urban forest “governance” (e.g., [Lawrence et al., 2013](#); [Krajter Ostoić and Konijnendink van den Bosch, 2015](#)), this polycentric situation contributes to the sustainability and resilience of urban forests by creating redundancies in the management of urban forests: if one of these actors is unable to act on behalf of the urban forest (e.g., a recession causes municipal budget cuts that eliminate an entire urban forestry program or department), the others may be able to pick up the slack (e.g., adjacent homeowners may be able to pay for tree planting and maintenance in the public right-of-way).

Given this polycentric urban forest management, the specific level (or intensity) of management for a group of trees within the urban forest is connected to a number of factors, including whether the trees are planted or grew up spontaneously, what type of land use or property ownership the tree is growing on, and the party (or parties) responsible for or engaging in the management of the trees. The configuration of factors that impact urban forest management creates a gradient of management levels ([Fig. 1](#)),

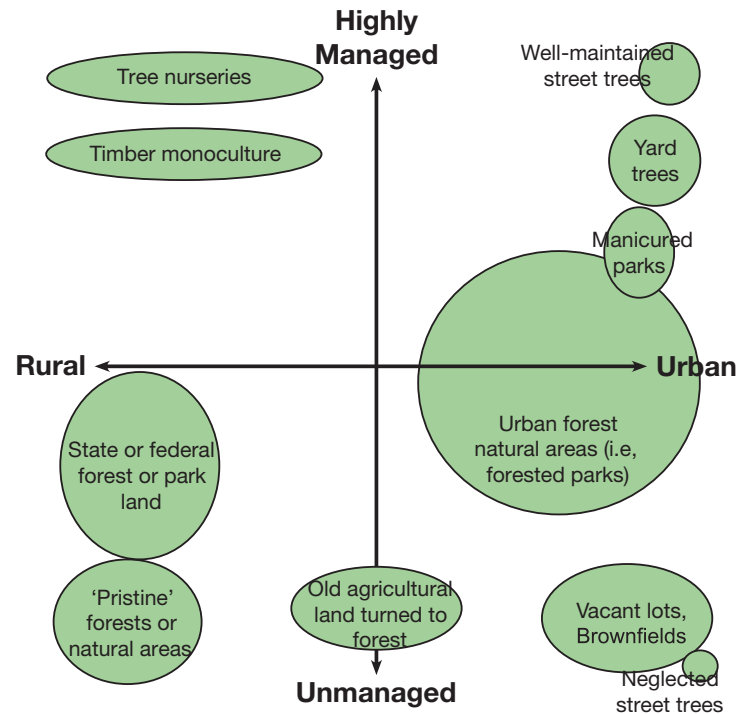


Fig. 1 Examples of the types of trees and forests in and around urban areas, presented by where they likely exist along an urbanization and management gradient.

ranging from the completely unmanaged trees (e.g., such as those that have spontaneously grown up in vacant lots that are completely neglected by humans) to the most highly managed trees (e.g., street trees in narrow boulevards or tree pits adjacent high traffic streets, or in plazas in urban centers, where they need to be regularly watered, pruned, and monitored for pest/disease damage in order to maintain the appropriate and safe tree form). Fig. 1 shows how this gradient intersects with the urbanization (i.e., urban-to-rural) gradient for different types of forests.

The Distribution of Urban Forest Benefits across Urban Areas

The complexities of urban forest management in combination with the social and ecological heterogeneity of urban landscapes result in an unevenness of urban forest structure, which in turn creates disparities in who benefits from urban forests. Additionally, the people and groups who receive benefits from the urban forest may have different experiences of what those benefits are depending on how they interact with the urban forest and what their personal values, preferences, and experiences with nature are. This section describes these two issues and demonstrates that discussions of the benefits of trees are more complicated than just listing the many benefits and calculating an economic value.

Research has demonstrated that the urban forest is distributed unequally across urban areas. This results in environmental justice and equity issues since people are also not distributed equally across urban areas. Two recent meta-analyses (systematic, quantitative analyses of existing literature) have examined the relationship between urban tree canopy cover and income (Gerrish and Watkins, 2018) or race (Watkins and Gerrish, 2018), finding evidence for inequitable distribution of tree canopy by both demographic variables. Gerrish and Watkins (2018) synthesized 61 studies that researched the relationship between urban forests and income in urban areas and discovered that urban forests are inequitably distributed across income groups, with tree canopy cover (on both public and private lands) disproportionately lower in low-income areas. Watkins and Gerrish (2018) find a similar pattern for race: in their synthesis of 40 studies, they observe lower urban forest cover in areas of high minority populations (Watkins and Gerrish (2018) note that since low income and minority populations are often co-located in urban areas, the relationship between race and tree canopy cover is tightly connected to income, and thus recommend that any policies to address systemic inequities should consider both race- and income-based inequalities). They observe especially lower forest cover on public land in non-humid climates for African American residents (Watkins and Gerrish 2018). These findings have important implications for urban forest practice, particularly for efforts to address urban forest inequities. The actors engaged in urban forest management—including municipalities, nonprofit groups, professional urban foresters and arborists, and urban residents—have different responsibilities, capacities, and goals. For instance, research conducted in the Toronto, Canada, area by Conway et al. (2011) examined the urban forestry activities (e.g., conducting a tree inventory, planting or maintaining vegetation, stated importance of vegetation-related

issues) of business improvement associations and neighborhood residents' associations. Their findings suggest that residents' associations in particular engage in uneven levels of urban forest activities, leading to inequities in urban forest structure across neighborhoods that differ by racial, ethnic, and income characteristics (Conway et al., 2011).

Furthermore, urban forest benefits are experienced differentially by different people and groups within urban areas. Westphal (2003) developed a typology of understanding urban forest benefits—particularly social and economic benefits—that considers, on one dimension, whether benefits are accrued through passive experience of versus active involvement the urban forest and, on a second dimension, to whom the urban forest benefits accrue (on a scale of single individuals to an entire community). Westphal (2003) defines “passive experience” of the urban forest as simply being in the presence of urban trees, forests, and greenspace, while “active involvement” is defined as participation in an activity to green the urban environment such as planting trees or gardening. Fig. 2 maps select social and economic benefits of urban forests along these two dimensions. Both dimensions help answer the question of how urban forest benefits accrue to people. Some types of benefits are only experienced by those who actively engage with the urban forest. For instance, individuals who actively participate in tree planting, care, and management—either as professionals or as volunteer stewards of the urban forest—build skills associated with green trades. The benefit of skill building is only experienced by individuals engaged in active greening activities but not to the community at large. Another benefit that only results through active engagement is the stronger ties to other groups that organizations may experience as a byproduct of participation in collaborative urban forest management (e.g., city-wide tree planting initiatives). On the other hand, some benefits accrue to all people regardless of their level of engagement with the urban forest, simply due to the presence of trees. Individuals engaged in either active or passive forms of engagement with the urban forest may experience relaxed psychological states. The entire community benefits from a more pleasant urban environment due to the presence of trees.

A final issue in determining who benefits from the urban forest stems from the fact that the values of trees often calculated in tree benefits analyses (e.g., i-Tree or Tree Benefits Calculator, which produce a monetary figure for the economic benefit of the urban forest or single urban tree, respectively) are overly simplified. Valuations of the urban forest by necessity homogenize the preferences and values of people and groups in urban areas with respect to trees. In reality, the values of trees are heterogeneous not only across the spatial dimensions an urban landscape, but also across human communities. Different types of people, groups, and communities may value trees for different benefits. People's landscape preferences vary (e.g., a manicured lawn versus xeriscaped yard; trees and forests versus wide open spaces). The objectives of groups and organizations differ (e.g., a tree planting organization interested in planting large shade trees in a park that would produce lots of urban forest benefits versus an urban gardening group interested in planting only small fruit bearing trees and leaving sunny open spaces for gardening). Another example is the stormwater management benefits of trees and green infrastructure, which may be a primary concern for the municipal authority and stormwater utility coping with combined sewer overflows in a particular neighborhood; however, individual homeowners who do not experiencing flooding on their property may place a much higher value the shade and property value benefits of trees, or may even dislike trees due to needing to clean-up their leaves or because trees shade and reduce the efficacy of rooftop solar panels (see Opportunity costs in the section “The Costs of Urban Forests” below). Ultimately, the heterogeneity and complexity of urban environments and people complicate assessments of the benefits and value of urban trees and forests to human communities.

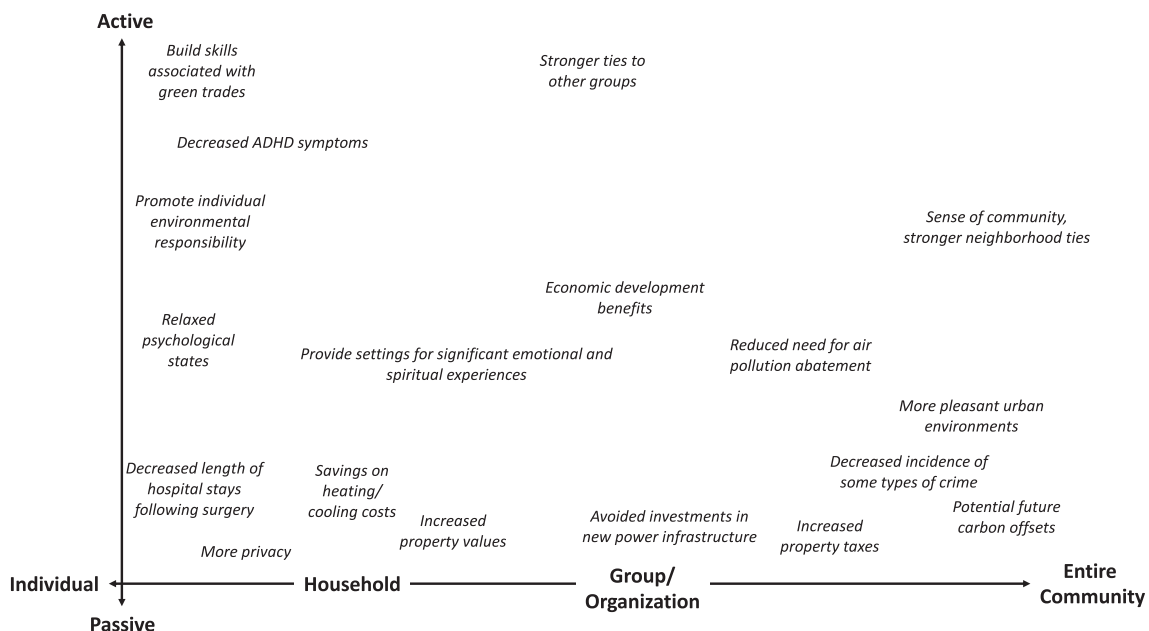


Fig. 2 The social and economic benefits of urban forests can be mapped along two dimensions: passive vs. active engagement with the urban forest; and, whether the benefit accrues on the level of a single individual to an entire community. Dimensions of social benefits of urban greening after Westphal, L. M. (2003). Social aspects of urban forestry: Urban greening and social benefits: A study of empowerment outcomes. *Journal of Arboriculture* 29(3), 137–147.

The Costs of Urban Forests

Another factor that complicates discussions of how urban forest management impacts urban forest benefits to people is that urban forests do not only have benefits; they also have substantial costs—both to individuals and groups, as well as to the public and the environment as a whole.

In order to understand how costs impact urban forest management and decision-making (and vice versa), it is helpful to review how urban forest professionals conceptualize tree benefits and costs in practice. Urban foresters often speak of trees and forests as one of the few types of physical infrastructure in urban areas that appreciate in value after installation, in contrast to the gray infrastructure such as streets, sidewalks, sewers, and other hardscape that begin depreciating the day they are completed. It is true that because trees grow after being planted in urban areas, a tree should theoretically provide an increasing level of benefits throughout its lifetime until being removed (Fig. 3). However, urban trees only appreciate if they are healthy and able to survive and grow to a large size where they provide substantial benefits. Research has found that if a cohort of trees (group of trees planted at the same time) do not survive at sufficiently high rates, the benefits produced by the cohort of trees does not increase over time—that is, the appreciation of benefits resulting from the growth of surviving trees does not outweigh the loss of benefits resulting from high tree mortality (Widney et al., 2016). Thus, for the benefits of the urban forest to increase over time, planted trees must survive. For planted urban trees, the establishment period—or the first 1–3 years after being transplanted, sometimes into a potentially harsh growing environment—can be a particularly vulnerable time where mortality rates are high. In order to survive and grow, planted trees must be cared for by people and, in particular, watered during the establishment period. Thus, though surviving trees do appreciate and provide benefits to people, they also require significant investment from people.

Investment, or maintenance costs incurred during a tree's early life, may be quite high (Fig. 3). Early costs include the costs of planting (purchasing high-quality tree stock from a nursery, plus labor and materials to put the tree in the ground, including tree workers, shovels for small trees or heavier equipment for large trees, any soil amendments used, mulch, water, etc.) as well as the costs of early essential maintenance for recently planted trees (watering during the first 2–3 growing seasons after planting, formative pruning to create appropriate tree form for urban areas, etc.). If a tree is optimally maintained early in life, the maintenance costs during the mature phase then go way down and are limited to occasional pruning, pest monitoring, and other types of routine mature tree maintenance.

For the urban forest as whole, there are two major categories of costs: “private costs” and “public costs” (Table 1; modified from a typology presented in Vogt et al., 2015b). *Private costs* are costs borne by a particular actor (group or individual) as part of expenditures on or because of the urban forest. Private costs include the direct costs incurred during management of the urban forest and costs resulting from tree conflicts (infrastructure repair and liability costs). *Public costs* are costs incurred because of the urban forest but not paid for by any particular actor and instead borne by society at large. Public costs include externality-related costs (also called ecosystem disservices) and opportunity costs. Direct costs, costs from tree conflicts, liability costs, and opportunity costs are discussed in greater detail below.

Direct Costs—Management and Maintenance

Direct costs incurred during the provisioning and maintaining of trees and the urban forest are private costs. These costs—i.e., management costs—include expenditures on labor and materials required to plant trees (the trees, tools, mulch, soil amendments, water and water equipment, etc.). Direct costs are paid by actors performing specific actions in order to manage the urban forests, for

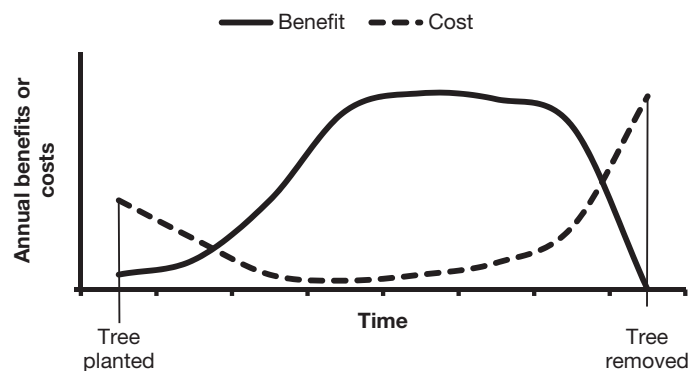


Fig. 3 Generalized (hypothetical) profile of the annual benefits provided by and costs incurred from over the entire lifetime of a single tree from planting to removal. The net benefits provided over the entire tree's life can be conceptualized as the area in between the benefits (solid line) and costs (dashed line). Modified from Vogt, J. M., and Fischer, B. C. (2014). A protocol for citizen science monitoring of recently-planted urban trees. *Cities and the Environment* 7(2), art. 4. Available at: <http://digitalcommons.lmu.edu/cate/vol7/iss2/4> and Vogt, J., Hauer, R. J., and Fischer, B. C. (2015b). The costs of maintaining and not maintaining the urban forest: A review of the urban forestry and arboriculture literature. *Arboriculture & Urban Forestry* 41(6), 293–323.

Table 1 Types of costs associated with urban forests.

	Type of cost	Explanation/examples
Private costs	Direct costs (i.e., maintenance and management costs)	Dollars expended to purchase labor and materials involved in the planting, pruning, watering, and other types of maintenance of trees in the urban forest
	Infrastructure interference costs (i.e., repair costs)	Pavement and sewer repair costs; removal of tree limbs or debris blocking signage, power lines, storm drains, etc.; costs from tree-initiated power outages; or other costs incurred when trees damage or interfere with infrastructure
	Liability costs	Damages paid from a lawsuit or settlement awarded when trees or parts of trees cause injury to persons or property, such as an improperly cared for tree falling on a house, vehicle, or person
Public costs	Externality-related costs (aka, “ecosystem disservices”)	Emissions of biogenic volatile organic compounds (VOCs) by trees; allergies due to tree pollen; release of carbon dioxide during decomposition of trees or tree debris or by maintenance equipment (gas-powered chain saws, lift trucks used to access tree canopy during maintenance, etc.); leaf/debris clean-up
	Opportunity costs	Space where trees are planted cannot be allocated to other competing uses, such as parking, bike lanes, sidewalk cafés, etc.; shade from trees may preclude use of sunny areas for installation of solar panels or for gardening

Modified from Vogt, J., Hauer, R.J., and Fischer, B.C. (2015b). The costs of maintaining and not maintaining the urban forest: A review of the urban forestry and arboriculture literature. *Arboriculture & Urban Forestry* 41(6), 293–323.

instance, municipal budget outlays for the pruning of street trees. In order to better understand the magnitude of the direct costs of urban forests, it is helpful to understand the types of maintenance required by urban trees and forests, and how maintenance and management impact urban forest outcomes.

A note on terminology: The terms “maintenance” and “management” are often used interchangeably with respect to the urban forest, though they mean slightly different things. For the purposes of the following discussion, *maintenance* will refer to activities undertaken with the intent of caring for individual trees, while *management* will refer to activities to care for urban trees in the aggregate (so, maintenance of trees, but management of the urban forest).

There are a number of activities commonly undertaken to maintain urban trees, including transplanting, various types of pruning (e.g., formative pruning of young trees and structural pruning of mature trees to create appropriate form for urban spaces, pruning to remove dead or broken branches after storms); watering (during establishment after transplanting, or during periods of drought); mulching (ideally, seasonally, to hold in soil moisture and minimize competition between tree roots and grass, weeds, and other plants); amending soils (if needed, through fertilization or inoculation with mycorrhizae), inspecting and treating for pests and diseases (also called “plant health care”), installing tree support or lightning protection systems (generally only for old, mature, or particularly significant trees), and, finally, removing trees and tree stumps (either due to conflict with other infrastructure, during construction, as a result of natural or pest/disease-related mortality, etc.).

The cost of the labor and materials necessary to performing these maintenance tasks may be paid for by one or more actors in the urban forest: municipal urban forestry programs; individual homeowners, business-owners, or institutional landowners maintaining trees on private property; nonprofit urban forestry organizations; or any other party taking fiscal responsibility for the maintenance of public or private trees. The data that exists on the relative costs of different types of tree maintenance activities is limited (Vogt et al., 2015b), but a recently conducted census of municipal tree care activities in the United States revealed that tree pruning and tree removal are the costliest tree care expenditures as a percent of total municipal urban forestry budget (Hauer and Peterson, 2016). Fig. 4 shows the relative costs of other specific maintenance and management activities included in municipal tree care (from Hauer and Peterson, 2016).

One of the ways trees are maintained is by being planted in cities in the first place. However, researchers have estimated that only approximately one-third of trees in North American cities are planted (Nowak, 2012), leaving a substantial number of trees within urban areas that emerge spontaneously. This spontaneous tree generation has led to a significant invasive species problem for some cities. For instance, in Chicago area, it has been estimated that over one-quarter (28.2%) of the trees in the region (by count) are the invasive European buckthorn (Nowak et al., 2013). Since buckthorn is a small-stature species that does not provide a large number of benefits, this can yield substantial pressure on urban forest managers to remove this and other invasive species in the urban forest, particularly in the more naturalized, less highly managed areas of the urban forest where buckthorn may compromise the quality and integrity of urban forest ecosystems.

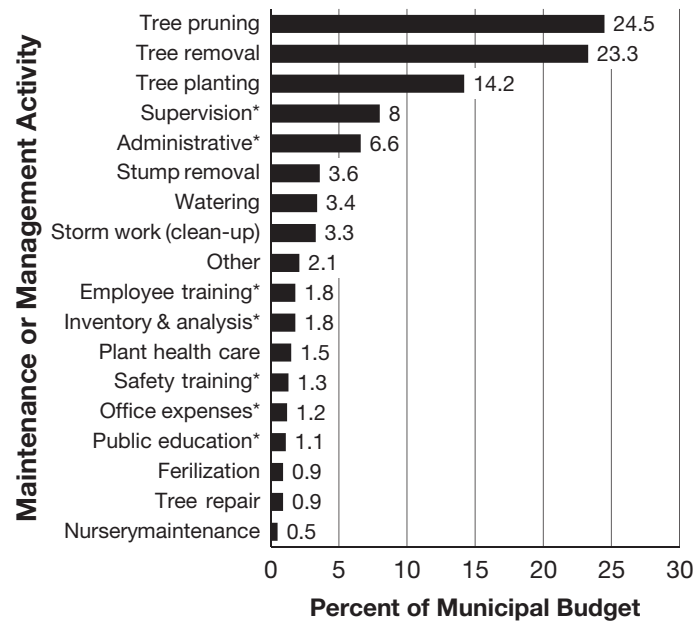


Fig. 4 The average percent of municipal urban forestry program budgets spent on particular tree maintenance and management activities, based on a 2014 survey of municipal urban forestry programs in the United States. An * indicates an activity that is management, while other activities are maintenance. Data used with permission from Hauer, R., and Peterson, W. (2016). *Municipal Tree Care and Management in the United States: A 2014 Urban & Community Forestry Census of Tree Activities*. 16–1. Stevens Point, WI. Available at: <https://www.uwsp.edu/cnr/Pages/Forestry—MTCUS.aspx>.

In examining how maintenance impact urban forest outcomes, the language of ecologists when discussing the impact of ecological disturbances (cf., Walker and Willig, 1999) is useful. Urban forest structure is influenced not only by the type of maintenance, but also the party performing the maintenance as well as intensity (how much maintenance is performed), frequency (how often maintenance is performed), duration (for how long maintenance is performed), and extent (on what part of a tree, or which trees within the urban forest). Just like when considered for ecological disturbances are called a “disturbance regime” (e.g., Hobbs and Hueneke, 1992), these factors together make up a “maintenance regime,” which impacts the structure of each urban tree individually as well as the urban forest in the aggregate.

In addition to the maintenance performed on urban trees, additional urban forest management activities are also part of the direct costs of urban forests. Management activities consider the entire urban forest—or a significant aggregation of trees such as those in a park or park system, all the trees in a neighborhood or along a corridor, etc.—and generally involve higher-level planning, advocacy, and even policy-making activities. This includes urban tree inventory and analysis, generating master and strategic plans for the urban forest, engaging in public education, outreach, and awareness building, lobbying for or creating tree policy at the municipal or even state or national level, plus the generic administrative and office expenses of running any type of program. These costs are more likely paid for by groups engaging in stewardship of the urban forest for a city such as municipal urban forestry programs or urban greening nonprofits, rather than by particular individuals such as homeowners. However, large private or institutional landholders such as colleges and universities, or neighborhood/residents’ associations or business associations may also engage in management activities that have costs.

Costs Resulting from Tree Conflicts—Infrastructure Repair and Liability Costs

In addition to the direct costs of urban forest maintenance and management, there are also private costs that result from tree conflicts in the urban environment including infrastructure interference and liability costs. Infrastructure repair costs are incurred due to above- and belowground conflicts. Above ground conflicts include tree branches growing into fences, signage, or—most commonly—above ground power and cable lines. In particular and most costly, when trees sufficiently conflict with power lines such as during or after a storm or high-wind event, they can cause power outages that result in costly tree debris cleanup and power infrastructure repair, as well as loss of revenue to the power company for the duration of the service outages. Belowground conflicts result when tree roots grow into storm sewer drains or water supply pipes or underneath sidewalks or curbs causing buckling of the concrete. The cost of repairing damaged infrastructure are generally paid by the actor responsible for management of the infrastructure needing repair (electric utility companies, water management authorities, or public works departments managing streets and sidewalks).

In almost all cases, conflict between trees and infrastructure results from improperly planted and/or maintained trees, not from inherent or unavoidable tendency for trees to cause damage. For instance, it is a common misconception that tree roots will always interfere with a storm sewer or water supply pipe if the two share the same underground space. However, in reality existing small cracks or inadequately sealed joints in aging pipes leak moisture or nutrients that attract small tree roots, which then expand small cracks into large cracks or roots grow into the pipes contributing to clogs. Similarly, a tree with a large mature size planted under a power line will become an interference, while a tree with a small mature size planted in the same place will cause no problems with above ground power infrastructure. This is why there is a popular maxim among urban foresters: “right tree, right place, right time,” meaning that when planting trees, urban foresters must consider the proper tree (species, size at maturity, etc.) for the proper place (planting area type, soil and environmental quality, etc.) and plant the tree at the right time (at the right time of year for seasonal climate, or after a major construction project not before, etc.).

In the worst cases, improperly planted and maintained trees can cause serious damage to property or injury to people. If the person whose property or person is injured decides to pursue legal remedy, a lawsuit can result in the assigning of liability for the tree causing injury and paying of monetary damages to the victim. Thus, liability costs are incurred and paid as legal settlements by the actor taking responsibility for (or deemed responsible in a court of law) the tree that caused the damage. In the case of trees on private property, this is usually the property owner, but for trees in the public right-of-way, assigning legal responsibility for the damage caused by the tree can get more complicated. For instance, the physical land in the right-of-way is owned by the adjacent property owner but the city generally has access rights for certain purposes such as maintaining the sidewalk or accessing buried sewer pipes. Responsibility for mowing the grass or maintaining any non-tree vegetation in the right-of-way boulevard between the street and the sidewalk may fall to the adjacent homeowner, yet legal responsibility for planting, maintaining, and removing any trees in the right-of-way may be either held by the city or may also be the duty of the adjacent homeowner. If legal responsibility over a tree is unclear due to the lack of clear delegation of responsibility of tree care and maintenance or lack of clear ownership of the property on which the tree itself is located, who has liability for the tree in the event of partial or entire tree failure is murky and will need to be determined in a court of law. Whoever is liable for the tree will then be responsible for paying any monetary damages awarded to the victim. Municipalities that take responsibility over the trees in the public right-of-way may even budget for paying liability claims (in or out of court), although it is obviously preferable for any party in charge of part of the urban forest to monitor and maintain trees in order to proactively assess tree risk and avoid any tree failures that cause injury to persons or property.

Opportunity Costs—A Public Cost of Urban Forests

The private costs described above—maintenance and costs resulting from tree conflicts—are paid for by someone. The public costs of urban trees and forests, on the other hand, are those costs borne by no particular individual or group but instead by urban residents as a whole. These include ecosystem disservices and “opportunity costs.” Ecosystem disservices are the negative externalities produced by urban trees and forests, such as pollen that causes allergies. *Opportunity costs* are the costs of undertaking one particular action or decision and foregoing another. In the context of urban trees and forests, opportunity costs refer to the activities or land uses that cannot be engaged in if urban trees and forests are planted, managed, etc. For instance, there is limited space in the public right-of-way and many competing possible uses for this space such as parking, bicycle lanes, sidewalks, a grassy boulevard, bench, bike racks, waste receptacle, sidewalk café, raised flower bed, trees, etc. Since not all of these uses can happen simultaneously, whenever one particular use is chosen for a given space, the cost of forgoing the other types of uses for the space is considered the opportunity cost of a particular use. If trees are planted in the public right-of-way, the space cannot be used for a sidewalk café by an adjacent restaurant. On other types of public land such as parks or public squares, opportunity costs are similar: for instance, if there is a forested area in a portion of a park, this area cannot be used for a parking lot, picnic area, public pool, or other use. The opportunity costs of trees are not just relevant on public lands. Private landowners can face opportunity costs as well. Trees that cast too much shade may preclude installation of solar panels on the roof or use of a yard space for gardening of vegetables that require sunlight.

Urban Forest Sustainability

Whatever the configuration of individual trees and patches of forest and actors managing the urban forest, in the end, when the costs of urban forests are subtracted from the benefits—either as a formal, mathematical calculation, or an informal comparison of the benefits and costs—ideally, net benefits are positive. And in the optimal scenario, the net benefits of the urban forest are not just positive at a given point in time, but they are sustained (or increase) over time.

What Does “Sustainability” Mean for Urban Forests?

There are two different angles from which scientists and practitioners have conceptualized sustainability as related to the urban forest. The first and most common way of conceptualizing urban forest sustainability considers primarily the persistence of the urban forest resource itself—that is, the trees—over time, and thus, by proxy, the net benefits provided by the urban forest in the

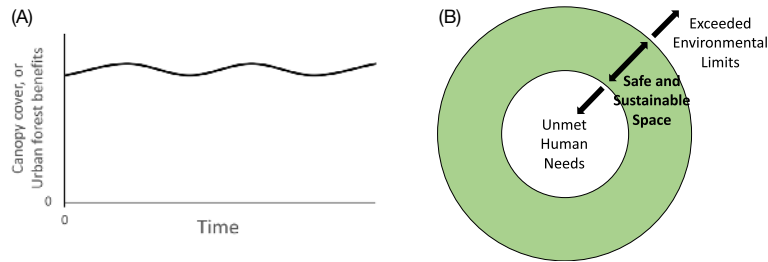


Fig. 5 Two different ways of conceptualizing urban forest sustainability: (A) As an approximately sustained level of a particular urban forest structural parameter such as canopy cover (or level of net benefits) over time; or, (B) As part of meeting human needs while making sure that Earth's environmental limits are not exceeded. (B) After Raworth, K. (2017). *Doughnut economics: 7 ways to think like a 21st century economist*. White River Junction, Vermont: Chelsea Green Publishing, as adapted for urban forests by Vogt, J., and Hauer, R. (2017). Sustainability science for urban foresters and arborists. *Arborist News* 26(4), 28–34.

aggregate. A “sustainable urban forest” in this context refers to maintaining an approximately consistent level (or increasing level) of a particular structural parameter such as canopy cover, stocking level or number of trees (Fig. 5A), or of the urban forest benefits provided (cf. Clark et al., 1997; Dwyer et al., 2003). Because of the way tree structure is connected to function and benefits, the largest trees in the urban forest provide the most benefits and since tree mortality is highest for planted trees during the establishment period just after transplanting, sustaining an optimized level of urban forest benefits through time involves maintaining a diverse species assemblage and appropriate distribution of trees of different sizes and ages (Fig. 6; after Richards, 1983).

The second way to conceptualize urban forest sustainability involves a more holistic assessment of how urban forests might fit into larger efforts for community or urban sustainability (or even global sustainability). In this context, sustainability is defined as meeting human needs (food, housing, energy needs, etc.) while making sure that the environmental limits of the Earth (for processes such as climate change, freshwater use, land system change, etc.) are not exceeded (cf., the definition of sustainability used by Steffen et al. (2015) and Raworth (2017)) (Fig. 5B). So the quest for the sustainable urban forest then is how can urban forests contribute to meeting human needs without exceeding Earth's environmental limits (cf., Vogt and Hauer, 2017)? For instance, in hot dry climates, properly placed drought-tolerant trees can provide shade and decrease urban temperatures help mitigate the impacts of climate change without requiring excessive amounts of freshwater for irrigation. Another example is the planting of fruit trees, which provide fresh food in urban food deserts and contribute to meeting human needs.

These two conceptualizations of urban forest sustainability are not necessarily incompatible. The former (Fig. 5A) is a much more specific idea of what sustainability of the urban forest is and to be satisfied requires only that the urban forest (i.e., the trees as a natural resource) be maintained. The latter (Fig. 5B) requires consideration of multiple urban forest benefits and costs in the context of the trade-offs between environmental- and human-related sustainability goals, which can contribute to the maintenance of the urban forest (that is, the persistence of urban forest structure over time, as in Fig. 5A). Depending on the existing urban forest situation (structure, actors, etc.), one or the other means of operationalizing sustainability may be more desirable.

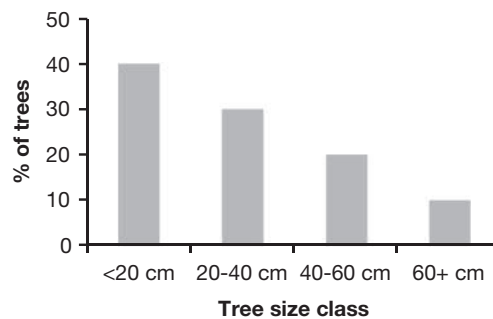


Fig. 6 Size class distribution of trees in an urban forest that sustains a constant level of net benefits over time. Figure created from a text description of the appropriate “age distribution”—where tree size is a proxy for age—for a “stable” urban forest, as described in Richards, N. A. (1983). Diversity and stability in a street tree population. *Urban Ecology* 7(2), 159–171.

Table 2 Components and criteria of a sustainable urban forest. Optimal performance levels, as well as the key objective that performance level is designated to achieve as defined by Kenney et al. (2011) are shown. Performance levels for each criteria can be found in the Appendix of Kenney et al. (2011).

Component	Criteria
Vegetative resource	Relative canopy cover
	Age distribution of trees in the community
	Species suitability
	Species distribution
	Condition of publicly owned trees
	Publicly owned natural areas
	Native vegetation
Community support	Public agency cooperation
	Involvement of large private and institutional land holders
	Green industry cooperation
	Neighborhood action
	Citizen-municipality-business interaction
	General awareness of trees as a community resources
Resource management	Regional cooperation
	Tree inventory
	Canopy cover inventory
	Citywide management plan
	Municipality-wide funding
	City staffing
	Tree establishment planning and implementation
	Tree habitat suitability
	Maintenance of publicly owned, intensively managed trees
	Tree risk management
	Tree protection policy development and enforcement
	Publicly owned natural areas management planning and implementation

Components and criteria listed from: Clark, J. R., Matheny, N. P., Cross, G., and Wake, V. (1997). A model of urban forest sustainability. *Journal of Arboriculture* 23(1), 17–30.

Criteria for Evaluating Urban Forest Sustainability

Within the field of urban forestry one of the first to consider urban forest sustainability was Clark et al. (1997), who presented an approach for evaluating urban forest sustainability. They consider the characteristics of the urban forest and urban forestry activity within a single municipality that are crucial to sustaining the urban forest resource over time. For these authors, a “sustainable urban forest” refers to an urban forest system that persists “over time in a way that provides maximum benefits from the functioning of that forest” (Clark et al., 1997: p. 17). To this end, they describe the three core components of a sustainable urban forest—a healthy vegetative resource, comprehensive management, and a supportive community—as well as a set of criteria that if achieved should yield a sustainable level of urban forest benefits over time (Clark et al., 1997; Table 2). The framework was updated and clarified by Kenney et al. (2011), who added detailed performance indicators to each of the criteria in the Clark et al. (1997) three core components, in order that managers or others might actually measure the sustainability of a particular urban forest according to the framework by assessing the level of performance for each of the sustainability criteria.

What Shapes Urban Forest as Social-Ecological Systems?

As illustrated in this chapter, a confluence of complex factors shape the trees and forests in urban areas. Observed characteristics of urban forests—such as urban forest structure, benefits, ecosystem disservices, and sustainability—are ultimately shaped by both human and biophysical factors. Because of this urban forest ecosystems can be best understood as “social-ecological systems.” A *system* is a group of components interacting in a self-organizing capacity to generate some type of outcome or function that would not be intuitive based on the sum of the components. More simply, systems are “a set of things ... interconnected in such a way that they produce their own pattern of behavior over time” (Meadows, 2008). *Social-ecological systems*—sometimes also called “socio-environmental systems” or “coupled human-natural systems”—are systems of both human and natural subsystems, where the inter-workings of each subsystem are inseparable from one another and the entire system cannot be fully understood without looking at the system as a whole (c.f., Ostrom, 2009; Epstein et al., 2013; Vogt et al., 2015a). Urban forests—with their interlinked

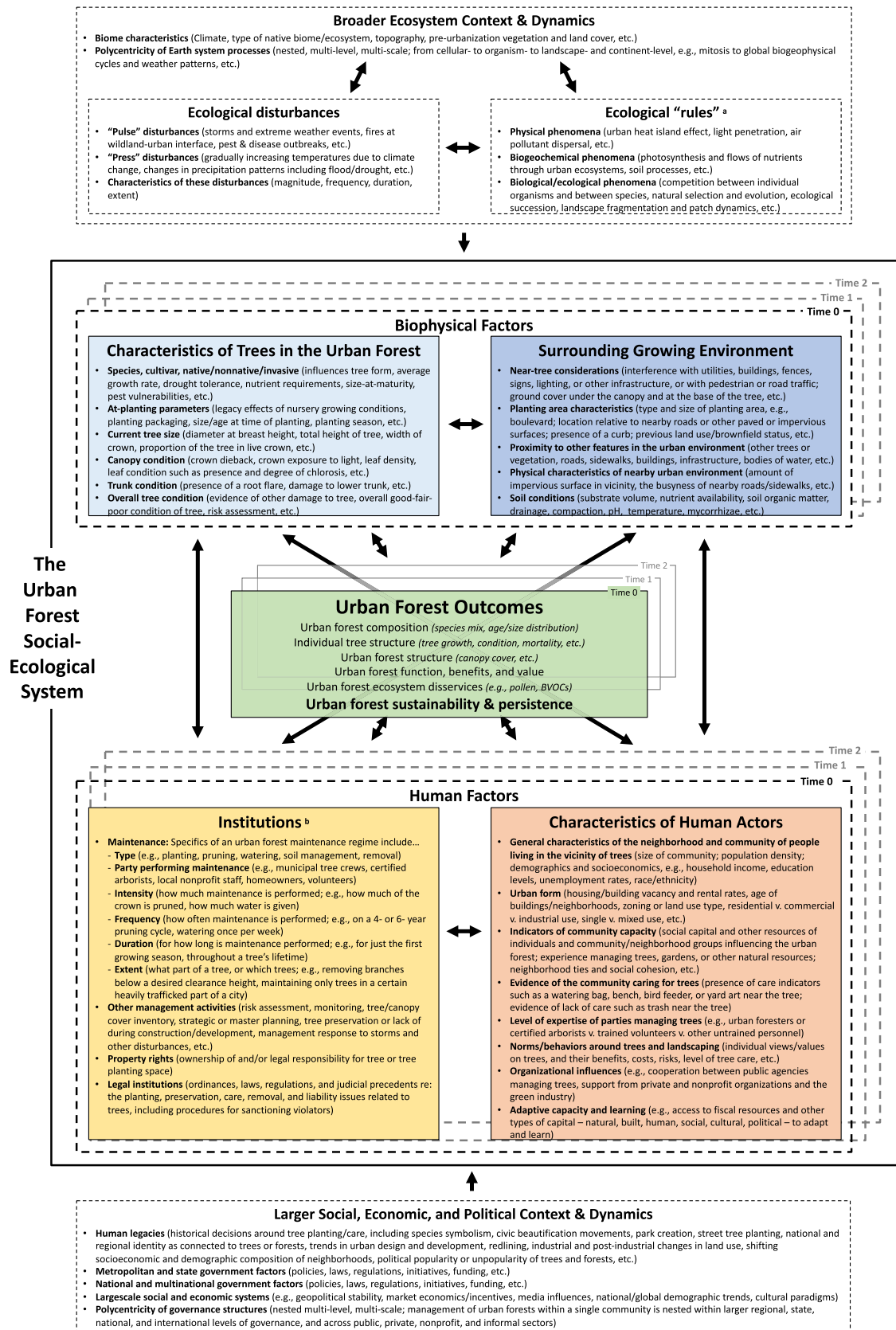


Fig. 7 A comprehensive framework for understanding and examining observed outcomes in urban forests as social-ecological systems. There are four core sets of endogenous variables relating to characteristics of the tree, the surrounding growing environment, institutions, and the characteristics of the human community, which interact to produce observed urban forest outcomes. Core sets of variables, interactions, and observed outcomes are dynamic and may change over time. Additionally, core sets of variables are influenced by the context and dynamics of the

systems of trees and the people and groups who interact with those trees to produce the character of the urban forest—are social-ecological systems (Vogt and Fischer, 2014; Vogt et al., 2015c).

In seeking to understand how any system functions, it is often of interest to examine the sets of components within the system and the relationships between components, in order to elucidate how interactions lead to observed outcomes. A framework is useful to this end. A framework contains general sets of variables that may be related to one another in order to “[provide] a metatheoretical language to enable scholars to discuss any particular theory or to compare theories” (Ostrom, 2010). Frameworks can be particularly useful for fields such as urban forestry that are *transdisciplinary*—that is, that combine knowledge and methods from multiple academic disciplines and from research and practice and integrate both researchers as well as non-researcher stakeholders from across multiple sectors—and can help provide a common language for communicating.

For urban forests, a comprehensive framework for understanding and examining urban forests as social-ecological systems is presented in Fig. 7 (based on an unpublished manuscript-in-progress by the author; synthesized from existing urban forestry frameworks by Clark et al. (1997), Mincey et al. (2013), Vogt and Fischer (2014), Vogt et al. (2015b,c), Steenberg et al. (2016), Roman et al. (2018), and Hilbert et al. (2019); and the social-ecological systems framework by Ostrom (2009); as updated by Epstein et al. (2013) and Vogt et al. (2015a)). In the framework, the factors that shape urban forest outcomes are numerous, but can be broadly grouped into four core sets of variables: the characteristics of the tree; the surrounding growing environment; *institutions* (the rules and strategies governing interactions between humans and between humans and the environment, in this case, the maintenance and management of the urban forest); and the characteristics of the human community. These core sets of variables interact with one another, but are also influenced by broader ecosystem dynamics, as well as the larger social, economic, and political systems within which urban forests exist. All of these factors must be considered in order understand the complex outcomes observed in urban forest ecosystems and in efforts to study urban forest dynamics.

Conclusion

Urban forests are all the trees and vegetation existing in close concert with humans in some of the most densely settled places on the planet. As such, in order to understand the biophysical and ecological character of urban forests, we must examine how the various actors, from professional urban foresters to homeowners to urban greening nonprofits, maintain and manage the urban forest on both public and private property. This management (or, sometimes, such as on vacant lots, lack thereof) results in urban forest benefits or ecosystem services (such as aesthetic beauty, shade, and stormwater management). But trees, forests, and the management they require also has costs, including direct, private costs for maintenance (such as pruning, watering) or to deal with tree conflict with infrastructure (e.g., heaving up sidewalks), as well as public costs in the form of ecosystem disservices (e.g., tree pollen producing allergies) and opportunity costs (space for trees in the public right-of-way cannot also be used for a bike lane). Because of these interactions between humans and the vegetation in cities, the urban forest can be best understood as a social-ecological system.

broader ecosystem and social, economic, and political systems within which urban forest exist. ^a“Ecological rules” language after Epstein et al. (2013) and Vogt et al. (2015a). ^b“Institutions” refers to the formal and informal rules and strategies that structure interactions between people and between people and the environment, after Ostrom (2005). Unpublished manuscript-in-progress by the author. Synthesized from the many existing frameworks for understanding urban forests outcomes (Clark, J. R., Matheny, N. P., Cross, G., and Wake, V. (1997). A model of urban forest sustainability. *Journal of Arboriculture* 23(1), 17–30; Mincey, S. K., Hutten, M., Fischer, B. C., Evans, T. P., Stewart, S. I., and Vogt, J. M. (2013). Structuring institutional analysis for urban ecosystems: A key to sustainable urban forest management. *Urban Ecosystem* 16(3), 553–571. <https://doi.org/10.1007/s11252-013-0286-3>; Vogt, J. M. and Fischer, B. C. (2014). A protocol for citizen science monitoring of recently-planted urban trees. *Cities and the Environment* 7(2), art. 4. Available at: <http://digitalcommons.lmu.edu/cate/vol7/iss2/4>; Vogt, J.M., Watkins, S. L., Mincey, S. K., Patterson, M. S., and Fischer, B. C. (2015c). Explaining planted-tree survival and growth in urban neighborhoods: A social-ecological approach to studying recently-planted trees in Indianapolis. *Landscape and Urban Planning* 136, 130–143. <https://doi.org/10.1016/j.landurbplan.2014.11.021>; Vogt, J., Hauer, R. J., and Fischer, B. C. (2015b). The costs of maintaining and not maintaining the urban forest: A review of the urban forestry and arboriculture literature. *Arboriculture & Urban Forestry* 41(6), 293–323; Steenberg, J. W. N., Millward, A. A., Nowak, D. J., and Robinson, P.J. (2016). A conceptual framework of urban forest ecosystem vulnerability. *Environmental Reviews* 1–12. <https://doi.org/10.1139/er-2016-0022>; Roman, L. A., Pearsall, H., Eisenman, T. S., Conway, T. M., Fahey, R. T., Landry, S., Vogt, J. M., van Doorn, N. S., Grove, J. M., Locke, D. H., Bardekjian, A. C., Battles, J. J., Cadenasso, M. L., Konijnendijk van den Bosch, C. C., Avolio, M., Berland, A., Jenerette, G. D., Mincey, S. K., Pataki, D. E., and Staudhammer, C. (2018). Human and biophysical legacies shape contemporary urban forests: A literature synthesis. *Urban Forestry & Urban Greening* 31, 157–168. <https://doi.org/10.1016/j.ufug.2018.03.004>; Hilbert, D. R., Roman, L. A., Koester, A. K., Vogt, J., and van Doorn, N.S. (2019). Urban tree mortality: A literature review. *Arboriculture & Urban Forestry* 45(5), 167–200) and the social-ecological systems framework (Ostrom, E. (2009). A general framework for analyzing sustainability of social-ecological systems. *Science* 325(5939), 419–422. <https://doi.org/10.1126/science.1172133>; Epstein, G., Vogt, J. M., Mincey, S. K., Cox, M., and Fischer, B. (2013). Missing ecology: Integrating ecological perspectives with the social-ecological system framework. *International Journal of the Commons* 7 (2), 432–453. Retrieved from <http://www.thecommonsjournal.org/index.php/ijc/article/view/371/331>; Vogt, J.M., Epstein, G. B., Mincey, S. K., Fischer, B.C., McCord, P. (2015) Putting the “E” in SES: Unpacking the ecology in the Ostrom social- ecological system framework. *Ecology and Society* 20(1), art. 55. Available at: <http://www.ecologyandsociety.org/vol20/iss1/art55/>).

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Quenching a City's Thirst: The Shifting Waters of Bangalore

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Abstract

This article posits the idea that while the idea of an anthrome may be relatively new, several cities of the global south with histories of settlement spanning several millennia are indeed examples of long standing anthromes. They have been shaped by and in turn influence human society creating a co-evolved, tightly coupled social ecological system. Using the case of the waterscape within the south Indian city of Bangalore, we demonstrate how nature and society have shaped, transformed, and influenced each other's trajectories of development over several millennia. These coupled with today's conditions of uncertainty caused by the Anthropocene, have created unique challenges of equity, justice, and sustainability—all of which need to be considered in the new age urban planning discourse.

A Peopled Planet

We live in the era proposed as the Anthropocene—an era synonymous with the pervasiveness of the human footprint. An era where human actions and behavior have not just shaped societies and cultures, but also transformed the non-human and non-living components of the biosphere. Cities are examples of such transformations—they are landscapes that are constantly increasing in number, and evolving to represent predominant trends in economies, lifestyles, and associated global connections. Over 55% of the global population today live in cities, with that number projected to reach about 75% by 2050. Given the dense concentration of people in cities, it is only expected that these spaces be modified, transformed, and shaped to represent the greatest utility to people who live there.

Cities are social-ecological systems—with complex coupled interlinkages between people and nature, influenced and being influenced by each other. Thus contemporary expressions of the urban space are essentially productions of complex interactions between people and nature—both those which have occurred in the city's past, and are ongoing in various forms today. Not surprisingly, then cities also represent “novel ecosystems”—ecosystems that have been significantly altered and reshaped in structure and process by human influence, and that are further managed in ways that espouse specific human purposes. Further, the reach and pervasiveness of human influence within these ecosystems means that local ecologies and biodiversity become altered in ways and abundances that were not originally a part of the landscape. For example, the creation of agrarian landscapes and their transformations (such as the example of Bangalore that follows), were sustained through the creation of novel ecosystems characterized by populating barren land or replacing native vegetation with domesticated plant or animal species in order to further human life and productivity. These transitions and associated creation of novel ecosystems relate explicitly to the idea of the Anthropocene—the new proposed geological epoch characterized by rapid changes in global social-ecological conditions that have been brought about primarily by the scale and reach of human activity on the planet. Within urban settings, these transitions into novel ecosystems may have occurred across long time scales, governed by multiple resource regimes (each with their own priorities and urban visions), interacting with each other and building upon prior regimes, it is highly unlikely that one can envision a future that returns these ecosystems to their original form and function. Urban ecosystems thus have to be managed bearing in mind their unique historical trajectory of transformation in form, function and imagination, and with attention to the social and ecological roles they play in the contemporary and future city.

The south Indian city of Bangalore represents a classic example of these novel ecosystems. Old inscriptional records attest to the pervasive role that humans have played in shaping and modifying the social-ecological systems in the landscape surrounding Bengaluru, from as far back as the 6th century CE. This is especially visible when one focuses upon transformation of urban commons—lakes, village forests, village pastures and other ecosystems—across regimes of governance imposed by successive dynasties of the precolonial era (before CE 1799), the British colonial regime (CE 1799–1947) and the modern Indian independent state (CE 1947–present). Conceptualized and built to support a predominantly agrarian lifestyle, the lakes, orchards and pastures created by village communities have transformed the landscape, and co-evolved with the growth of human settlements over multiple centuries. In this article, we provide a detailed account of these transformations, making the case for this city as a novel ecosystem that gives us a deep insight into processes of urbanization in parts of the global south, that are rapidly urbanizing yet continue to represent a major knowledge gap in research on Anthromes.

Setting the Context: Bangalore

Bangalore, once called India's "Garden City," was well known for its green spaces and its pleasant weather, owing to its location on the elevated Deccan Plateau. In recent years, it has become synonymous with the outsourcing of the global information technology industry, becoming called the "Silicon Valley of India." Bangalore has since colonial times been a strong player in the global scenario, because of its strategic location for colonial civil and military establishments, and its continued economic importance within independent India. The colonial state of Mysore (of which Bangalore was a part) was a site of experimentation with modernity, thus making Bangalore one of the first cities in India to receive electricity, telephone connections and centralized piped water and sewerage networks. In part, these innovations fuelled the rapid urban growth of the city, attracting greater densities of people, paving the way for its current-day reputation as one of independent India's major metropolitan cities.

At the same time, Bangalore has also had a trajectory of dramatic landscape transformation as evidenced by its blue and green infrastructure. Geographically, the city lies in the rain shadow of the Deccan Hills, and as such lacks a major perennial water source, making it prone to aridity and drought. Despite the constant challenges of water availability, the city has been occupied since prehistoric times, and has been inhabited by settlements since at least the 6th century CE. The expansion of human settlement in this landscape is owed in part to the creation of networked reservoirs designed to capture and harness rainwater across the elevation gradient characterizing the city. Designed for meeting the needs of the primarily agrarian precolonial societies, these reservoirs (tanks or lakes as they are known today) operated in tandem with a selection of other urban commons including village forests, cemeteries, temple tanks, and large open wells (that tapped into shallow aquifers recharged by the tanks). Today, however, several of these commons have disappeared from the cityscape, or have been repurposed for meeting other urban demands (such as those of residential space or public infrastructure), while the remaining ones are rendered vulnerable by pollution, encroachments, and general neglect (Fig. 1).

The two main uses for which this system was engineered have either disappeared or taken on new forms—the former, which is now restricted to small urban pockets, and the latter, which is obtained through a system of long distance transfer—rendering the social fabric upon which the system operated redundant. At the same time, these spaces, the urban commons, continue to perform valuable ecosystem services (such as attracting local biodiversity, regulating the urban microclimate, and groundwater recharge among others), that make them ecologically indispensable. Urban commons within these contexts refer to (formerly) collectively managed resources such as lakes and associated village forests, grazing lands, and other spaces. They also represent spaces from which it is difficult to exclude people from while at the same time the total amount of available resources decreases, the more benefits are extracted from them. They thus represent both integral yet highly vulnerable ecosystem resources within cities.

As such the story of these spaces represent both the creation and co-evolution of a novel ecosystem as well as illustrates the challenges involved in their governance and management. In the following sections, we will attempt to trace the coevolution of Bangalore's urban commons through processes of urbanization from precolonial times to the present. In doing so, we will also demonstrate how through centuries of anthropogenic transformation, the city represents a "novel ecosystem" that encapsulates and presents multiple, power laden, conflicting visions and thus associated challenges for ecosystem management.

Engineering Flows of Water and Culture—Bangalore's Precolonial History

The earliest records available for the landscape around the contemporary boundaries of the city of Bangalore are in the form of copper plate and stone inscriptions (that date back to about the 6th century CE). These provide a record of the presence of varying local chieftains and rulers. They describe various events such as the grant of land, battles, the creation of lakes, and the grants of revenues from agriculture to temples. Inscriptional records also provide valuable insight into the geophysical landscape of the time, both in terms of their content as well as in terms of their chronology and spatial locations.

Geographically, Bangalore consists of both elevated regions (known locally as *malnad*) as well as plains (known locally as *maidan*). Our research has shown that settlements in this city spread from the plains (where the earliest inscriptions have been found) to the hills. In order to support agriculture, early settlers made use of the natural elevation gradient and undulating terrain to build reservoirs to harvest rain water. Connected by means of channels, and designed to harness rainwater, a system was created whereby water overflowed from one reservoir into the other, providing water to the city. The building of these tanks continued for

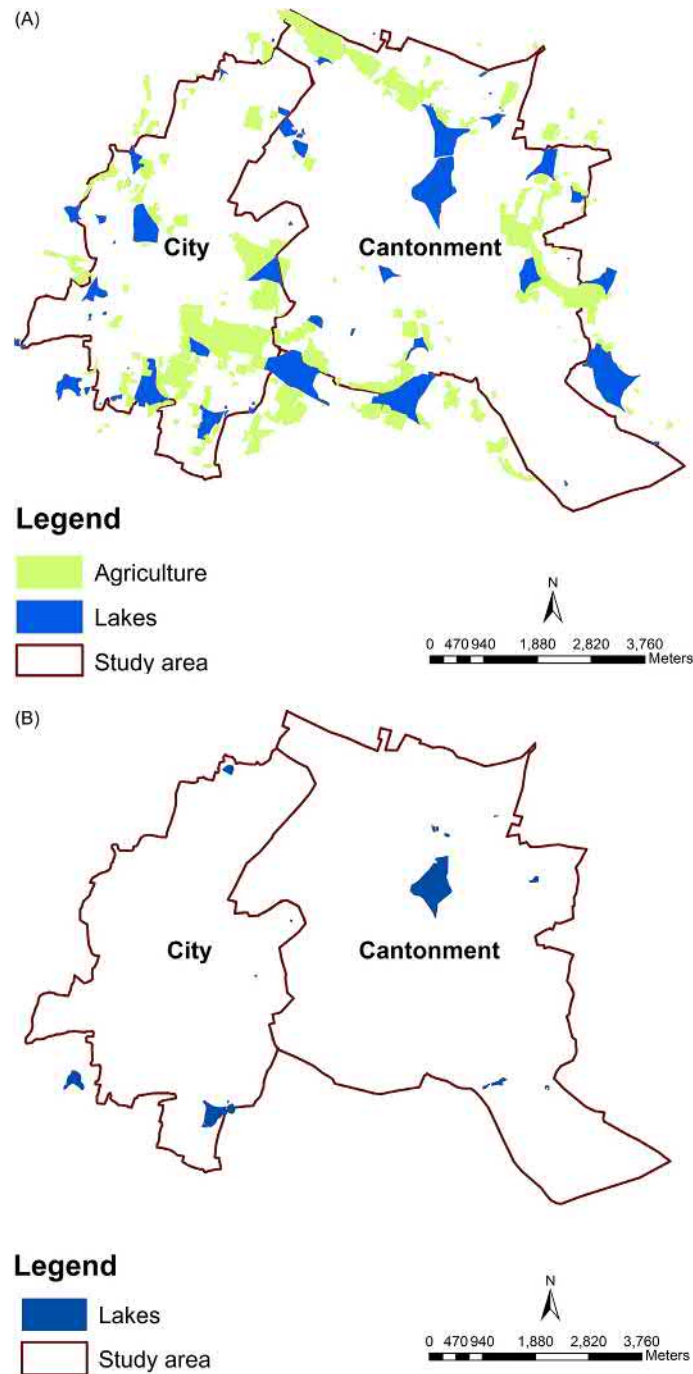


Fig. 1 (A) Map showing the distribution of lakes in colonial Bangalore—CE 1885. (B) Map showing the distribution of lakes within the formerly colonial spread of Bangalore city—2014. *Note:* Both of these figures were previously published in an Arcadia article by the authors titled “The lost lakes of Bangalore,” available at <http://www.environmentandsociety.org/arcadia/lost-lakes-bangalore>. Copyright: Hita Unnikrishnan.

several centuries, supported by local residents, communities and chieftains owing allegiance to multiple regional dynasties. Along with these seasonal surface water sources, people made use of open wells associated with each lake as a secondary source of water, ensuring water availability throughout the year. Open wells drew on groundwater in shallow aquifers that were recharged by the tanks.

By re-engineering the waterscape, this process of tank building irreversibly transformed a semi-arid landscape devoid of trees into a fertile landscape conducive for agriculture, horticulture, fishing and grazing. Over the centuries, the city transformed into a space that not just provided for agrarian livelihoods, but also into a rich biodiverse landscape with forests and wooded groves, populated by wildlife and birds—in other words, an engineered urban commons. British colonial interventions continued to shape this novel

ecosystem, via technological and engineering interventions to the city's waterscape that reshaped human activities and livelihoods centered around these ecosystems.

Engineering Modernity: The Colonial Tryst With Bangalore

The advent of colonial rule in India and more specifically into the city of Bangalore (starting at the end of the 18th century) brought transformative changes to the landscape. These changes had impacted people and biodiversity, and were driven in part by rapidly changing demographics of the city, notions of health, hygiene and sanitation, advent of technology that enabled modernization of infrastructure, leading to associated changes in the meanings ascribed to resources formerly important for utilitarian purposes, as well as a form of urban planning that was reflective of these important transitions.

Colonization and Changing Demographics of Bangalore City

Bangalore, as noted earlier, was particularly well placed to support the colonial enterprise not least because of its high elevation and resulting mild weather conditions. This attractiveness of the city drew large numbers of European settlers, so much so that by the middle of the 19th century, Bangalore was being referred to as the "Pensioner's Paradise." It was also a very strategic place within the Deccan plateau for the setting up of one of many British Cantonments in south India. In addition to attracting large European populations, these events also attracted large numbers of native migrant populations in search of labor from neighboring towns and states. This influx of people meant increased requirement of land and water to meet the requirements of the population. On the one hand, between the late 1880s and until the country became independent in 1947, this demand for land meant the creation of several new residential extensions and public infrastructure such roads, railways, and recreational amenities. Several of these new settlements were facilitated by repurposing existing water infrastructure—the rain water channels and lakes.

The increased demand for water also came at a time when the city received electricity, and began to be supplied by a networked and piped water supply systems connecting every household. Beginning from the late 19th century, water began to be pumped from increasingly longer distances outside the city, settling finally upon the river Cauvery over a 100 km upstream of the city. The formerly important tank system, now unable to meet the needs of an expanding population (among other factors) fell into gradual disuse, or became repurposed in various ways—converted into buildings, drained for use as playgrounds, parks and exhibition grounds, and used to store waste and sewage.

Colonial Notions of Health, Hygiene, and Sanitation

An increase in population was not the only factor that brought about transformations within this waterscape. The advent of colonialism into the city also brought with it lived experiences of the Europeans with epidemics such as bubonic plague and malaria, both within their native homelands as well as within the colonies they established. These experiences shaped the creation, reproduction, and perpetuation of discourses on what constituted healthy and hygienic urban spaces. European experiences with the prevention and control of disease in one part of the world (such as bubonic plague in England, or plague, malaria and cholera in India) were further transplanted into other parts of the Empire, reacting and often conflicting with local social and ecological contexts, producing distinctive cityscapes.

It was in India that the idea of racially segregated zonation of urban centers was developed, ostensibly to keep British soldiers free from diseases (e.g., cholera, plague, malaria, and typhoid), perceived as prevalent in designated "native towns." The British Raj created the institution of British Cantonments—military outposts in several Indian towns, that were physically separated from the native city. The Cantonment in Bangalore, which operated between 1798 and 1947 was one of the largest and most prominent.

Bangalore served as an example for the larger colonial enterprise in terms of experimenting with infrastructure and town planning (the city for instance pioneered networked water infrastructure projects and was also the first city to receive electricity in South Asia). For the 1902 Nobel Laureate, Sir Ronald Ross, then stationed in Bangalore as a Surgeon Major, the city became an experimental site for his path-breaking work on malaria. Further, Ross's encounters with epidemics of cholera, plague, and typhoid in Bangalore, led him to propose and influence the implementation of centralized, networked systems of sanitation, conservancy, and water supply to increase health and life expectancy. The model of town planning that emerged from these experiments emerged as the signature of British colonial establishments across the global south, indeed forming the foundation upon which infrastructure and urban planning in these cities continue to rest upon.

What did these ideas mean for the tank infrastructure that was characteristic of this town? First, the idea of a water resource began to shift from collectively managed, open reservoirs to those contained within hygienic, enclosed spaces. This necessitated the construction of enclosed, covered reservoirs, into which water would be pumped in by an equally enclosed, reticulate system of pipes. Concomitantly, open reservoirs (such as tanks and their associated channels) began to be perceived as unhygienic and therefore carriers of disease, filth, and other hazards. People dependent upon such reservoirs (such as native communities of washer folk—the *dhobies* as they were locally known, farmers, and fishermen) began to be perceived also as being unsanitary and prone to disease. People were on the one hand actively discouraged from depending upon these formerly important infrastructure, and on the other, the idea of racial segregation between European and native populations was perpetuated along lines of health and

hygiene. The tanks, in keeping with this line of thinking, began to be seen as conduits for the city's sewage—transforming what was essentially a seasonal fresh water resource designed to capture rainwater, into perennial bodies associated with the city's refuse. These ideas further accelerated the decline and conversion of Bangalore's many water bodies and associated channels, rendering them polluted, and thus allowing them to be repurposed keeping in line with the prevalent ideas of sanitary urban planning. Accordingly, several prominent lakes such as the Miller's tank series of central Bangalore were drained as part of large scale epidemic prevention programs, further, and irrevocably transforming the waterscape. In a sense, therefore, the urban commons was replaced by a centralized vision of what infrastructure provision was meant to look like.

Colonial Ideas of Modernity and Technological Advancement

In addition to these new notions of health and hygiene, colonization of the city also brought with it its own ideas of modernity and the role of technology in enabling those ideas. If the notions of health and hygiene served to bring about a separation between native and European populations, colonial beliefs of the superiority of western technology and modernity served to further reinforce that divide. The colonial idea of modernity was built upon the promise of large infrastructural projects and the power of the engineer as a vehicle for delivering that promise. Accordingly, the construction of large dams, the creation of large interconnected systems designed to provide water into the city and transport sewage away from it, and the enabling of connectivity across large swathes of land—through roads, railways, electricity, and telephones.

Such interventions, while aimed at making the city more economically productive and resilient to disease, were based upon western understandings of the cityscape, and transplanted into colonies without consideration of the specific contexts within which they were being implemented. They also furthered the divide between the native and European populations in terms of differences in lifestyles and technologies they used. Native technologies were seen as inferior to those brought into the colonies by the west and as such this served to perpetuate the notion that these technologies needed to be replaced by superior modern ones. Accordingly, the role of engineers and large scale interventions in resource governance and management superseded the more decentralized infrastructure that was characteristic of precolonial tank management. This change in perception of the urban as a space supporting lives and livelihoods through localized resource systems into one driven by global economic concerns and supported by large scale infrastructural interventions further served to increase the disconnect between urban residents and the resources that once supported them.

Changes in Meanings Ascribed to the Utility of Resources

Changes effected from the top also brought with it associated changes within people who interacted directly with the waterscape. The interplay between increasing demands placed on land and water resources, associated rise of real estate and property values, changing notions of health, hygiene, sanitation, technology, and modernity resulted in shifting attitudes of resource users and dependents towards the waterscape of Bangalore. Water contained within the tanks began to be associated less with the sustenance of lives and livelihoods and more with their value as aesthetic or recreational adornments enhancing the beauty of the city. Over time, these ideals became more powerful, influencing decisions made over resource management and governance. At the same time, it resulted in the marginalization of those communities for whom the water body represented something other than these ideas of aesthetic or recreational utility. Our research on lost tanks of Bangalore (the Sampangi, today repurposed into the Sri Kanteerava Indoor and Outdoor Stadium, the Dharmambudhi—today the city's central bus station, and the Millers tanks—today an agglomeration of various residential neighborhoods and public infrastructure) shows that their decline was caused due to the interplay between changing urban imaginaries of resource utility, progressive marginalization of the communities of grazers, fishers, and farmers most dependent upon them and their resultant alienation from the resource, rendering the water body vulnerable to threats such as pollution, encroachment, and reclamation. The repurposing of these former water bodies reflects the dominant ideals that governed colonial urban planning—those of aesthetics and recreation (stadium), public infrastructure (Millers tanks in central Bangalore), and the desire for large interconnected hubs of transport (bus station).

Co-evolution of Novel Ecosystems in Colonial Bangalore

These changes had multiple consequences for the ecosystems of Bangalore, and the social-ecological connections they embodied. The connectivity between the lakes was lost, cutting off the flows of water characteristic to the city in its precolonial form. Livelihoods dependent on these water bodies such as agriculture, pottery, and fishing became increasingly marginalized and often relegated to the peripheral regions of the city. Livelihood commons associated with the water bodies such as grazing lands and village forests were destroyed, giving way to public infrastructure, educational institutions, and residential complexes that were constructed in their place.

In the colonial city, now distinctly urban in form and character, a divide began to emerge between spaces of human habitation and nature. Urban wildlife of the city became seen as a threat to human habitation, and the conquest of wildlife was seen as an achievement. Rewards were offered for the culling of wildlife, commensurate with the potential human hazard involved. Bears, tigers, cheetahs, snakes, scorpions, and elephants were systematically hunted to rid human habitation off "vermin." Organized hunts were set up often to the exasperation of villagers who objected to the thundering of horses across their fields and the worrying of livestock by the hunting dogs participating in these hunts.

Focus also shifted to improving the aesthetics and recreational utility of the urban form. Thus the creation of large gardens landscaped in the European manner with fountains and walkways, the incorporation of menageries in some of them (in which wildlife could be experienced), and the opening of these spaces at specific times of the day for recreation. Native plants and trees began to be replaced by imported species of vegetables, fruits and ornamental trees—with substantial investment into research to enable their cultivation on in India.

The novel ecosystem engineered by the precolonial inhabitants of Bangalore thus coevolved with the changing aspirations of the city. A change that was reflected through a flowing waterscape worshipped as sacred, now transformed into perennial sewage fed semi-stagnant and eutrophic water bodies, considered a health hazard. Through the relegation of urban wildlife to areas separate from human habitation, and the introduction and sustained propagation of those forms of biodiversity deemed to enhance the human experience of the urban. It was also a change that manifested through homogenizing societies as being aspirational of the dominant urban vision—and one that marginalized and slowly excluded livelihood-dependent communities or groups of people for whom the social-ecological system represented utilitarian benefits.

Engineering Urban Futures: Independent India, Technocracies, and Their Influence

The Independent State and Its Vision

Independent India continued to build on its colonially inherited infrastructure and retained focus on large scale technologies and infrastructural projects for the provision of water and other utilities. At the same time, there was a new emphasis on first expanding the public sector (from the 1950s into the 1990s) and later neoliberalizing the economy (from the 1990s onwards). Both of these events served to expand the boundaries of the city, while at the same time accelerating the repurposing of water bodies, associated channels, and other commons into further built structures. Accordingly, several additional lakes of the city were transformed into residential communities, malls, sports stadiums and public infrastructure. Surviving lakes further continued to act as a sink for the massive volumes of sewage discharged by the city as it grew and expanded beyond its colonial boundaries. Further, lifestyles dependent upon resource provisioning from water bodies (such as fishing) began to be regulated by centralized institutions, which oversaw the introduction of commercially viable exotic fish species into the ecosystem.

Ecological manifestations of system in response to the large scale changes wrought by these developments occurred gradually over time. One of the most noticeable effects of these changes was that of seasonal flash flooding in areas formerly occupied by water bodies or their channels, especially during the monsoons. Given that several of these areas are also occupied by the most vulnerable and marginalized of the city's population, these events have posed further challenges in terms of equity and justice within the social ecological system. There has been a decline in migratory water birds as a consequence of the loss of the city's lakes, wetlands and green cover. The depletion of ground water (owing to the loss of recharge function provided by lakes and a massive increase in borewells), and changes in rainfall, increasing prevalence of urban heat islands and other changes local microclimatic conditions have emerged as a consequence of ecosystem transformation.

Challenges posed by these changing social ecological system conditions have evoked multiple responses in recent years with calls and attempts to restore or rejuvenate the lost waterscape of the city. One of the earliest attempts to draw attention to the scale of the issue came in the form of a government report in 1987, which drew attention to individual lakes and their status. This was followed by documentations of bird diversity by naturalist groups who sought to spotlight the loss of lakes. Sporadic, but mostly unsuccessful attempts towards rejuvenating water bodies began in the 1990s, and by the early 2000s, there was a short-lived attempt to use Public Private Partnerships for restoring water bodies. Focus within these mechanisms however retained colonial notions of increasing the aesthetic, recreational, and real estate value of the water bodies. Little thought was devoted to the social-ecological system—thus these attempts converted the natural slope of lakes into “fishbowls,” lit up lakes at night with artificial light, replaced native vegetation with exotic ornamentals, and provided playgrounds, fountains and boating facilities for the urban recreationalist. Conversely, livestock owners, farmers, or commercial washer folk were denied access to these water bodies. Commercializing the water bodies meant the uninterrupted requirement of water within individual lakes that were mostly devoid of connectivity with others in the network—this necessitated tapping into deep groundwater aquifers to pump up water into the lake during summer or other periods of drought.

Community Collectives and the Promise of Coproduction

Beginning in the early 2000s, an increasing engagement with both the social and ecological components of the system led to the rise of citizen action, networking with state to rejuvenate their urban water commons. Two of the best known examples are those of the Kaikondrahalli lake in southwest Bangalore and Jakkur lake in the northern part of the city. In both of these cases, local resident groups have worked with the Government to rejuvenate these lakes while keeping ecological and social contexts in mind. Accordingly, while aesthetic and recreational benefits have been promoted through landscaping and the creation of jogging tracks, these are also used by livestock grazers and fishers. Local varieties of plants and trees have been encouraged, while fountains and night lights have been minimized as disruptive to biodiversity. Some open wells have been restored. These activities have been planned in conjunction with local vulnerable populations such as livestock grazers in ways that they can benefit from the arrangement. For example, in Jakkur lake, gardens include local medicinal plants that can be harvested by peri-urban village communities. Such efforts are not without their own challenges including those of networking effectively across diverse user groups and with local

bureaucracies, and systemic challenges such as dealing with large scale sewage inflow into the water bodies, and preventing encroachments by powerful land mafia.

Though localized, these efforts have succeeded in improving local social ecological system dynamics. For example, around both lakes, a number of nesting water birds can be spotted, including cormorants, pelicans, painted storks and other migratory water birds that had disappeared for some years but that have slowly started to return. Water quality within some of these lakes have been shown to have improved, also positively affecting the quality and catch of fish harvested from them. Socially, a sense of community cohesiveness (though still challenged by social inequities and power imbalances) has been brought about through these collective efforts lending hope for equitable and just urban futures within the city. These efforts have also proven inspirational to emergent collective action around other water bodies of the city, while at the same time, diversifying and scaling up into other sectors such as finding solutions to the city's traffic woes.

Conclusion: Quenching Urban Thirsts Within a Changing Waterscape

The story of Bangalore's shifting waterscape is one that is characterized by dramatic social and ecological transformations over time. It is a story of changes in the values of nature, the ideas of what constitutes the urban space, and the role that urban nature plays within the predominant vision of the city at a given point in time. For example, the creation of the originally engineered systems of interconnected water bodies was a reflection of the need for dependable sources of water in conditions of semi aridity, in order to sustain lives and agrarian or associated livelihoods. Its subsequent transformation, however, was dictated by changing visions of urbanity (for example colonial ideas of modernity and sanitation intertwined with the idea of an urban water body as being more aesthetic and recreational in utility). Adaptive management by communities in response to context specific challenges and associated positive and negative feedback loops have also played a major role in the production of this waterscape.

The city of Bangalore, is thus highly representative of an anthrome—a novel ecosystem—but one that has been so for several millennia. Changes within the anthrome are visible over large periods of time and reflect the co-evolution of nature with human society and processes of urbanization. These transformations have been a very integral part of the city's evolution over time, so much so, that the initial roots of the city are mostly forgotten by the vast majority of urban dwellers in Bangalore. Indeed, many residents of Bangalore remain unaware of the fact that the water bodies they now call "lakes" were manmade or that they were instrumental in the creation of Bangalore's identity as a Garden City.

While the idea of an anthrome is relatively new, the case of Bangalore as illustrated here is reflective of the fact the creation of an anthrome itself is not a new phenomenon. Bangalore is not unique either in being an anthrome of such long standing—these large scale human mediated transformations are an important character of urban spaces in many south Asian landscapes that have had long histories of human settlement. Indian cities such as Chennai or Mumbai, as well as other cities of the global south such as the Peruvian city of Lima or the Indonesian city of Jakarta have all recorded large scale human mediated landscape transformations in the form of water and irrigation works (some of which remain in use even today).

However, in today's age of the Anthropocene, the scale and intensity of human influence has increased greatly, leading to more pervasive and dramatic landscape changes. We now deal with newer challenges brought on by changing lifestyles (for example an increased dependence on plastics leading to the widely publicized problem of marine and coastal plastic accumulations). This in turns creates a need to find new ways of managing social and ecological systems in ways that pay attention to the fragility, finitude, and fairness of both the social and ecological components of the system.

For example, in the case of Bangalore, one of the ways traditionally used to manage sewage pollution in lakes was what was referred to as "natural sewage treatment." It consisted of making use of natural vegetation and wetlands in and around the water body to filter incoming loads of sewage, while at the same time diluting its concentration through the seasonal monsoons of the region. This coupled with annual desilting programs was sufficient to maintain these lakes. Unfortunately, this approach proved incapable of dealing with the 21st century city, which receives large volumes of sewage and diverse sources of polluted water. Systemic changes in response to these have already been developed and are being widely implemented—sewage treated through Sewage Treatment Plants is now being directed into the water bodies. In other words, seasonal monsoons have a reduced role in filling up the water bodies—instead they are continually being replenished by treated sewage. Many lakes have thus transformed from seasonal, rain filled, to perennial and sewage filled, impacting their ecological processes and biodiversity. However, policy and institutional arrangements have not kept pace with these developments, a situation that can have long lasting impacts on the region.

On the social front too, while today there are still livelihood groups such as farmers and fishermen dependent upon the water bodies, their numbers are constantly declining with newer generations opting towards more "urban" livelihoods and occupations that are not dependent on ecosystems. The importance of lakes as sacred spaces, important to sustaining resource dependent occupations is also waning. It is unlikely that the system can revert into its older form that was aimed at sustaining an earlier form of socio-cultural engagement with ecology—what is more likely is that urban water commons will continue to gain more traction as aesthetic and recreational utilities. Indeed, the history of the urban water commons of Bangalore, that we have illustrated earlier, shows that this change is already well underway.

Consideration of these aspects is very important in the larger contexts of the Indian city (as also other cities of the global south) that on the one hand are struggling to meet their burgeoning demands of development, and on the other dealing with issues of sustainability. These issues are further compounded by the increasingly visible effects of climate change—an increase in extreme

events (floods, earthquakes, and heatwaves among others), leading to an exponential increase in the number of climate migrants finding their way into more urban spaces. What is needed therefore in this new era, is consideration of whether these changes can be made equitable and just. Can the new age urban planning regime foster a sense of inclusivity within the planning process itself—one that pays attention to the many ways in which urban commons—the anthromes—are ecologically and socially relevant in the production of the urban space?

Acknowledgments

Funding for this study was obtained through a Newton International Fellowship awarded to Hita Unnikrishnan by the British Academy, and from Azim Premji University.

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Tree, Herbivore, and Natural Enemy Relationships in Cities Now and in the Future

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Abstract

Cities are dominated by impervious surfaces and by vegetation planted and managed by people. These urban features affect arthropod abundance, distribution, and phenology and can influence how arthropods interact with each other and with their host plants. In this article we first explore the mechanisms by which the features of urban anthromes affect arthropod herbivores and their natural enemies. We then consider how cities shape, at regional and global scales, arthropod invasion dynamics, biotic homogenization, and overall species distributions and how these patterns are affected by background climate. Lastly, we look to the future and consider how insect ecology on urban trees may continue to change as the world becomes warmer and more urbanized. We highlight how changes in abiotic conditions and biotic interactions may influence arthropods and their response to urbanization. Cities are as complex as the humans that plan them and the biota that occupy them. Regarding cities as dynamic systems will help us design landscapes and management strategies that protect urban trees and the organisms that depend on them.

Introduction

Humans can shape ecological processes in cities by altering the physical environment and by directly and indirectly affecting plants and animals (Frankie and Ehler, 1978; Raupp et al., 2010; Dale and Frank, 2018). For example, when planners choose the location and size of green spaces, their decisions affect local temperature patterns and habitat connectivity for mobile organisms (Burkman and Gardiner, 2014). When residents determine how many and which plants to install in their yards, these choices influence how attractive the yard is to certain animals (Burghardt et al., 2009). Arthropods are widespread in cities, respond strongly to the features of human-dominated environments, and have the potential to both contribute to and reduce the benefits provided by wildlife in urban areas (Raupp et al., 2010). However, people often make decisions about urban landscapes without consideration for how arthropods might be affected.

In cities, herbivores (e.g., aphids, caterpillars) and arthropods in higher trophic levels (e.g., spiders, parasitoid wasps) may rely directly and indirectly on managed plants for oviposition sites, shelter, food resources, or refuge from predators (Frankie and Ehler, 1978; Raupp et al., 2010). Trees, in particular, often provide key habitat for arthropods in urban areas (Raupp et al., 2010). Many of the arthropods living on urban trees are considered beneficial from the human perspective, such as pollinators and arthropods that support charismatic animals (e.g., songbirds) at higher trophic levels (Narango et al., 2017). However, urban trees can also support herbivore pests, which can damage trees and reduce tree benefits or even directly cause harm to humans (Dale and Frank, 2018). For

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example, oak processionary caterpillars (*Thaumetopoea processionea*), which release hair-like structures that cause allergic reactions in people and pets, live on planted urban trees in London, England (Tomlinson et al., 2013). Regardless of whether people explicitly consider arthropods—both beneficial and harmful—when making management decisions, human choices in urban landscapes influence arthropods.

In this article we will discuss how urban environments affect arthropods and their interactions with other organisms. We will focus specifically on temperate “dense settlement” anthromes (Ellis et al., 2010) that have high human population densities and are dominated by urban land cover (Fig. 1). In the first section we will discuss how human choices about land cover, especially managed vegetation and impervious surfaces like roads and buildings, can directly and indirectly affect arthropods on a local scale. We focus primarily on herbivores, which are essential for urban food webs but are also frequent pests on managed plants. We also focus on the natural enemies, such as predatory beetles and parasitoid wasps, that help to control herbivore populations. Herbivore and natural enemy responses to urban features at a small, local scale can also drive larger patterns. Therefore, in the second section we will consider how cities shape, at regional and global scales, arthropod species distributions and invasion dynamics and furthermore how these patterns are affected by background climate. In our last section, we look to the future and consider how insect ecology on urban trees may continue to change as the world becomes warmer and more urbanized.

Arthropod Responses to Urban Features

Vegetation and Arthropods in the City

Vegetation diversity and complexity

Human choices about trees in cities, especially about which species to plant and where to plant them, affect herbivores and their natural enemies. Both on individual city blocks and in the city as a whole, the diversity and homogeneity of tree species are the product of many individual human choices. Overreliance on a single tree species can facilitate the rapid spread of some pests, such as the emerald ash borer (*Agrilus planipennis*), which has caused significant tree losses as it has invaded North American cities that have high densities of green ash (*Fraxinus pennsylvanica*) (Raupp et al., 2006). To safeguard against disease and pest risk, practitioners and researchers have recommended increasing urban tree diversity, and some cities have even created rules for the proportion of trees of a given taxon that can be planted along city streets (Paap et al., 2017; Raupp et al., 2006; Santamour Jr., 1990). In addition to being at lower risk of catastrophic tree loss due to invasive herbivores, urban landscapes with high plant diversity and habitat complexity may also have fewer chronic pests (Fig. 2). For example, pine needle scale insects (*Chionaspis pinifoliae*) were more abundant on pines in simple “impoverished” landscapes, such as roadsides and parking lots, compared to pines in more complex wooded habitats (Tooker and Hanks, 2000). Natural enemies may contribute to these patterns, as habitats with greater complexity provide predatory and parasitic arthropods with alternative prey and carbohydrate resources, cooler microclimates, and refugia from predators (Gardiner et al., 2009; Landis et al., 2000). However, not all natural enemies respond equally to changes in vegetation or habitat complexity in urban areas, and additional mechanistic studies could inform the design and management of urban areas to promote natural enemies and pest control services on city trees (Burkman and Gardiner, 2014).

Tree species selection

Tree species selection in urban areas depends on many factors. A resident may attempt to simultaneously support animal biodiversity, avoid pests, and provide shade to reduce energy costs. Recommendations based on one of these criteria, for example to plant native plants to support arthropod biodiversity (Burghardt and Tallamy, 2013), may conflict with recommendations for the other criteria. In addition, it is not clear whether patterns observed on trees in suburban and rural areas apply in densely urbanized areas where features like habitat connectivity, plant stress, and temperature play important roles in structuring arthropod communities.

People’s choices about which tree species to plant in cities may be guided by aesthetic or maintenance priorities, ecosystem services (e.g., stormwater reduction), or the desire to support biodiversity, including herbivorous arthropods (e.g., caterpillars) that support higher trophic levels (e.g., birds). To date, the discussion about selecting plant species that support arthropod biodiversity in ornamental landscapes has focused on a distinction between “native” and “non-native” plant species. Native trees are generally described as those that evolved in the geographic area of interest, while non-native species are those that evolved elsewhere and were introduced to the new area, such as through the ornamental plant trade. Due to a coevolutionary history, native herbivores may have an easier time locating native plants and avoiding or tolerating these native plants’ defenses (e.g., defensive chemicals) compared to plants with which they share no coevolutionary history (Ehrlich and Raven, 1964). As a result, native plants may host a greater diversity and abundance of some insect herbivores, which may support fauna at higher trophic levels (Burghardt et al., 2009; Burghardt and Tallamy, 2013; Frank et al., 2019). This is frequently considered a positive attribute of native plants. For example, in Maryland, United States, residential yards planted with native plants supported more caterpillars and birds than yards planted with non-native plants (Burghardt et al., 2009). However, native herbivores may also reach injurious levels on native plants in cities, requiring management action and/or reducing tree health (Dale and Frank, 2014; Meineke et al., 2013; Raupp et al., 2010).

Because arthropods in higher trophic levels do not feed directly on plants, they may be less sensitive to plant origin than herbivores (Procheş et al., 2008). In a study conducted in Raleigh, North Carolina, United States, scale insect abundance was higher on native maple (*Acer*) and oak (*Quercus*) trees than on non-native congeners, but predator and parasitoid abundance, diversity, and community composition were similar between the native and non-native trees (Frank et al., 2019). In contrast, Greenstone et al. (2017) found more spiders consuming brown marmorated stink bug (*Halyomorpha halys*) egg masses in native ornamental

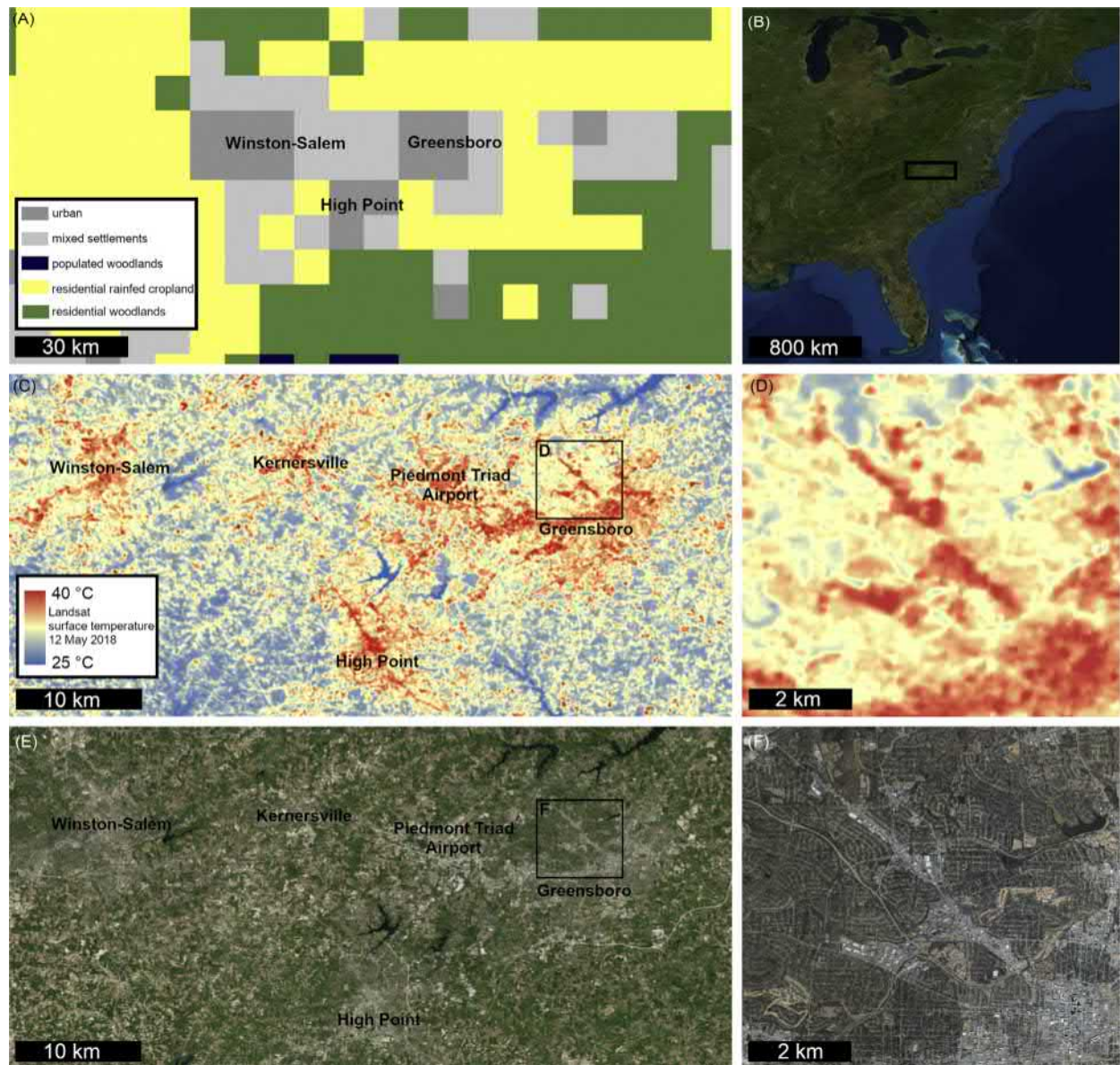


Fig. 1 Anthrome classification, surface temperature, and land cover of the Piedmont Triad region in North Carolina, United States. (A) Anthrome classification at 10 km resolution from Ellis et al., 2010. “Urban” and “mixed settlements” are classified by Ellis et al., 2010 as “dense settlements,” the focus of this article. (B) East coast of North America, with box indicating the location of the Piedmont Triad region that is depicted in other panels. (C) Landsat thermal map of surface temperature at 30 m resolution showing that cities are warmer than non-urban areas. (D) Landsat thermal map of surface temperature at 30 m resolution within Greensboro, NC, indicating variation in surface temperature within a single city. (E) Land cover image showing impervious surface (gray) concentrated in cities. (F) Land cover image showing impervious surface (gray) and woody vegetation (green) within Greensboro, NC. For panels (E) and (F), note that areas of impervious surface correspond to warm (red) areas in panels (C) and (D). Image sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo.

landscapes than in non-native ornamental landscapes. Overall, the effects of plant origin on arthropods in higher trophic levels are understudied in cities, and more research is needed to determine how human decisions about native and non-native plant species affect natural enemies and their capacity to control pest populations in urban areas.

Temperature and Arthropods in the City

Arthropods are ectotherms and are sensitive to changes in temperature. Cities are often several degrees warmer than surrounding rural areas, a phenomenon known as the urban heat island effect (Oke, 1973) (Fig. 1). Even within a city, an arthropod can encounter both hot and cold spots (Fig. 1). Some pest species reach higher densities, have faster development rates, and/or achieve higher fecundity in areas with elevated temperatures (Dale and Frank, 2017; Zvereva and Kozlov, 2006). In metropolitan Seoul,



Fig. 2 Variation in local landscape around urban trees. Trees are planted in many different urban conditions and habitats. The picture to the left depicts a tree surrounded by dense amounts of vegetation and higher habitat complexity, which may provide habitat for natural enemies that can control tree pests. The two pictures on the right depict trees planted in areas with high amounts of impervious cover and little vegetation. These trees may be more likely to have hotter tree canopies and fewer natural enemies.

South Korea, cicada population densities increase with temperature (Nguyen et al., 2018). In Raleigh, NC, United States, oak lecanium scales (*Parthenolecanium quercifex*) are more abundant in hot parts of the city due to acclimatization or adaptation to high temperatures as well as reduced control by natural enemies caused by a phenological mismatch (Meineke et al., 2013, 2014). Understanding which herbivores have higher fitness in warmer areas and how plant damage by herbivores may change with urbanization will ultimately help landscape managers better prioritize pest targets in urban areas that pose the most risk to trees.

Impervious Surface and Arthropods in the City

Impervious surfaces, such as buildings and roads, often replace vegetation in urban environments (McKinney, 2008) (Fig. 1). The addition of impervious surfaces, which absorb and reradiate heat, coupled with the loss of cooling vegetation, result in higher temperatures in cities compared to outlying areas (Oke, 1973). Some insect species respond positively to environments dominated by impervious surface. Impervious surface cover is the best predictor of both egg density of horse chestnut scale (*Pulvinaria regalis*) in Oxford, United Kingdom (Speight et al., 1998), and presence of Asian citrus psyllid (*Diaphorina citri*) in California, United States (Thomas et al., 2017). Other arthropod species, especially those with sensitive habitat requirements, may have lower fitness or survival in areas with high impervious surface cover. For example, native Lepidoptera species richness declined with the replacement of habitat with impervious surfaces in San Francisco, CA, United States (Hafernik and Reinhard, 1995).

Impervious surface cover may affect arthropods through plant-driven effects like changes in plant water and nutrient availability. Some arthropod species thrive in areas where trees are water stressed, potentially due to their ability to capitalize on changes in plant defense and nutrient allocation that sometimes occur when plants are water stressed (Dale and Frank, 2017; Speight et al., 1998). In Raleigh, NC, United States, gloomy scale (*Melanaspis tenebricosa*), which feeds on parenchyma cells, reaches higher densities on red maples (*Acer rubrum*) surrounded by impervious surface due to additive effects of warmer temperatures and higher plant water stress (Dale and Frank, 2017). In contrast, aphids, which feed on plant phloem, have lower abundance on water stressed plants, a phenomenon attributed to reduced turgor pressure in plant tissues that makes phloem harder to access (Huberty and Denno, 2004).

Within a city, the abundance of vegetation in an area is typically inversely related to impervious surface cover (Blair and Launer, 1997; McKinney, 2008) (Figs. 1 and 2), which can result in less habitat for natural enemies and fewer natural enemies that control pests. Hanks and Denno (1993) attributed greater scale abundance on mulberry trees in urban landscaped planting beds to reduced habitat complexity and fewer generalist predators when compared to mulberry trees in urban forest areas. Impervious surface can also indirectly affect top down control of tree pests by fragmenting habitat and reducing the ability of some natural enemies to travel among patches and control plant pests (Burkman and Gardiner, 2014; Niemelä and Kotze, 2009). For example, ground beetles (Carabidae), many species of which are predaceous and are sensitive to ground cover changes, are less abundant and diverse in urban areas where impervious cover is high (Niemelä and Kotze, 2009).

Overall, changes in herbivore communities associated with changes in impervious cover can mean that herbivore damage on urban plants is affected as well. For example, chewing damage was lower on seven species of broadleaf trees in urban areas with

more impervious cover when compared to natural areas (Nuckols and Connor, 1995), potentially a result of fewer chewing herbivores in urban areas. Alternatively piercing-sucking herbivores are often abundant in urban areas (Hanks and Denno, 1993; Just et al., 2018; Meineke et al., 2013; Raupp et al., 2010), which may mean more piercing-sucking damage on plants in areas with high impervious cover.

Regional and Global Patterns: Scaling Up From the City Block

Individual arthropods respond to small scale changes in their local environment. Within a single city block of a dense settlement anthrome, insects are navigating different microclimates, encountering different food plants and prey resources, and interacting with plants that may be stressed by harsh urban conditions. The specific responses of arthropods to these local conditions shape distributions of arthropods within a single city. Some patterns of arthropod responses to urban features are replicated across cities, but others are unique due to the environmental or social context in which a city is embedded.

Effects of Background Climate on Arthropods in Cities

Certain features of cities, such as impervious surfaces and the urban heat island effect, are common to many urban areas around the world (McKinney, 2006). However, cities are embedded in landscapes with a wide range of climates, which may affect arthropod responses to urbanization. Arthropods in tropical areas tend to tolerate a narrower range of thermal conditions and live closer to their thermal optima than arthropods at high latitudes (Addo-Bediako et al., 2000). As a result, urban warming may push arthropods in tropical areas beyond their thermal optima, reducing their fitness, but benefit arthropods living at high, colder latitudes (Diamond et al., 2015; Youngsteadt et al., 2017). In mid-latitude cities, responses are expected to be highly variable (Youngsteadt et al., 2017). In a study of four temperate North American cities spanning 6.6° of latitude, Youngsteadt et al. (2017) found that at the highest studied latitude, insects on urban trees tended to benefit from warm urban temperatures. In mid-latitude cities, there was not an overall positive or negative response because of large variation, with populations of some taxa increasing and others decreasing with urban warming (Youngsteadt et al., 2017).

In some cases, factors associated with urbanization may be more important than background climate for predicting arthropod responses. In Europe, herbivory was lower on woody plants in cities than in adjacent rural areas, a pattern which was independent of latitude but was stronger for cities with a larger human population (Kozlov et al., 2017). The abundance of gloomy scale (*Melanaspis tenebricosa*), a key pest of red maple (*Acer rubrum*) in urban areas in the southeast United States, increased with urbanization in eight cities independent of latitude, likely due to combined effects of temperature and water stress on trees surrounded by impervious surface (Just et al., 2019; Dale and Frank, 2017). In their study of insect communities on urban trees in four cities, Youngsteadt et al. (2017) found that, in contrast to expectations based on latitude, insects declined with urban warming where urbanization was most intense (Queens, New York, United States), possibly because of factors like habitat fragmentation and isolation that were more important than temperature. These studies and others demonstrate that cities may disrupt theoretical ecological patterns related to climate and arthropods in non-urban settings, which complicates predictions about how to manage plants and arthropods in cities throughout the world.

Effects of Vegetation Distribution on Arthropods in Cities

On a global scale, climate is among the most important drivers of vegetation structure and diversity, but human activity can disrupt natural patterns in plant distribution (Ellis et al., 2012). For example, though the native ecosystem in Los Angeles, CA, United States, is drought-deciduous shrubland, non-native trees with high water requirements (e.g., sweetgum, *Liquidambar styraciflua*) are grown in the city with help from landscape irrigation systems (Pataki et al., 2013). In naturally forested regions, urban plant communities differ from forest communities due to the routine planting of non-native tree species in cities and filtering out of species that cannot survive in urban conditions (McPherson et al., 1997; Raupp et al., 2006).

A single ornamental plant species may be grown in cities both on and off its continent of origin, resulting in overlapping tree species compositions in geographically distant cities (Kendal et al., 2012). Many non-native insects are introduced in cities as a result of the ornamental plant trade, the trade of other goods, or through intentional introduction by humans (Paap et al., 2017). Combined, the introductions of plant and arthropod species contribute to the homogenization of arthropod communities in cities that are geographically distant (McKinney, 2006). Homogenization of arthropod fauna in cities can involve both specialist and generalist insects. When specialist insects are transported with their host plants to regions with favorable abiotic and biotic conditions, they can establish populations outside their native range. Crape myrtle (*Lagerstroemia indica*) is planted on several continents besides its native Asia, and its specialist aphid, the crape myrtle aphid (*Tinocallis kahawaluokalani*), is also found in many of these locations which are geographically far apart (e.g., North America and Africa) (Mizell et al., 2006). Generalist arthropods are typically more successful in urban areas than specialists, in part because urban features or scarce host/prey resources may filter out species with sensitive habitat requirements (Burkman and Gardiner, 2014). Since features like impervious surface, pollutants, and habitat fragmentation are common to many cities around the world, a generalist insect that thrives in one city may thrive in others if introduced.

Arthropod Invasion Dynamics in Cities

When an arthropod is introduced and establishes in an urban area, it can potentially invade non-urban areas. Because of this, cities are sometimes called “beachheads” or “bridgeheads” for invasion (Cadotte et al., 2017; Paap et al., 2017). Cities are good beachheads because rates of introduction of non-native species are high and because they provide environments where some invasive species are likely to thrive and establish populations (Cadotte et al., 2017). For organisms that are limited by cold, the urban heat island effect or human infrastructure may contribute to higher winter survival. For example, at the northern end of its range in the US, the mimosa webworm (*Homadaula anisocentra*) has higher survival when it overwinters on heated buildings, allowing it to survive in the city at latitudes that would otherwise be too cold (Hart et al., 1986).

In addition to tolerating the abiotic conditions, an organism invading a new area must also interact with other organisms. For herbivores, establishment is only possible where suitable host plants are available. Because cities have different plant compositions than natural areas, they may offer host plants for invasive arthropods that are not available or are limited outside the city. The crape myrtle bark scale (*Eriococcus lagerstroemiae*), detected in the United States in 2004, attacks crape myrtle (*Lagerstroemia indica*) trees, which occur predominantly as ornamental trees in their introduced North American range (Wang et al., 2016). An introduced organism may experience less pressure from natural enemies, especially specialist natural enemies, in its introduced range (Bauer et al., 2005) and encounter lower competition in the city than it would encounter outside the city (Cadotte et al., 2017). These biotic factors increase the likelihood that a species can establish once it is introduced. Once established, there is potential for the species to invade new areas. Global insect invasions continue without saturation (Seebens et al., 2017), suggesting that the challenges of managing insect pests on urban trees will only continue to grow.

Looking Forward: Managing Arthropods on Urban Trees

Plant-arthropod interactions in cities are dynamic and are affected by evolutionary processes, environmental change, and human decisions. The drivers of plant-arthropod interactions we have discussed thus far, such as responses to urban and background temperatures and human choices about native and non-native plants, are all happening at the same time. In this final section, we will highlight some key considerations and main ideas about managing urban trees and arthropods while major global changes like urbanization and climate change continue to interact.

Plant Effects

Plants are already responding to anthropogenic climate change and will continue to be affected by climatic changes in future decades (Lobell and Gourdji, 2012). The combination of elevated temperatures and atmospheric carbon dioxide is expected to alter plant nitrogen content and defense compounds in ways that affect herbivores’ performance on their host plants (Zvereva and Kozlov, 2006). Ultimately, both herbivores feeding directly on plants and arthropods in higher trophic levels are likely to respond to changes in the abiotic and biotic environments.

Changes in plant water stress may be a particularly important consideration for landscape practitioners managing pests on urban trees in the future, as many urban trees are already growing in hot and dry conditions. Additive effects of elevated temperature and plant water stress caused by impervious surfaces in urban environments and worsened by climate change may mean higher densities of some pest species (Dale and Frank, 2017). Wood borer attacks typically increase with plant water stress (Huberty and Denno, 2004; Koricheva et al., 1998) and some species, such as southern pine beetle (*Dendroctonus frontalis*) and mountain pine beetle (*D. ponderosae*) are also already responding to elevated temperatures caused by climate change (Cudmore et al., 2010; Lesk et al., 2017). Thus wood borers may be important priority pest targets for landscape managers, particularly in light of recent outbreaks of mountain pine bark beetle (*D. ponderosae*), emerald ash borer (*Agrilus planipennis*), and others outside of their native ranges (Cudmore et al., 2010; Raupp et al., 2006). However, as highlighted in this article, not all pests respond similarly to plant water stress (Huberty and Denno, 2004; Koricheva et al., 1998). Ultimately, better understanding of which pests may be most affected by water stress and warming temperatures will help managers identify pests of greatest concern on urban trees.

Natural Enemy Control

Not all arthropods are expected to respond to climate change and urbanization in the same way. Fragmentation of habitat for some natural enemies created by the addition of impervious surfaces may mean fewer natural enemies to control pests on city plants in a more urban future (Burkman and Gardiner, 2014). Phenological mismatches are another possible mechanism for reduced natural enemy control of pests in cities in the future. In Raleigh, NC, United States, oak lecanium scales (*Parthenolecanium quercifex*) at hot urban sites produced eggs earlier than those at cold urban sites, but parasitoid wasps did not similarly advance their phenology at the warmer sites (Meineke et al., 2014). Though the parasitoid wasps attacked scales at similar rates at hot and cold sites, the scale insects at hot sites had a head start on egg production that allowed them to escape control by the parasitoid wasps. Phenological mismatches like these between pests and their natural enemies could have negative implications for pest control and ultimately may be a priority area of concern for managers of urban trees, particularly for those pests that respond positively to urban warming.

Cities as Sentinels of Climate Change

Climate change experiments are expensive and logistically difficult. Present day cities, which are often 2–3 °C warmer than surrounding areas, can serve as living laboratories to explore questions about how organisms may respond to future climate changes (Lahr et al., 2018). Using a comparison of scale insects on present-day urban and rural forest trees, as well as historical herbarium specimens collected from forests, Youngsteadt et al. (2015) found that herbivores' responses to urbanization provide useful clues about their responses to background climate warming. In particular, scale insect abundance was higher on trees in warmer areas of the present-day city, on historical specimens collected during warm periods, and in present-day (warmer) rural forests compared to the same forests historically. From a management perspective, a correlation between arthropod responses to urban and global warming introduces the possibility of using cities to make informed predictions about which pests may be of growing concern in the future. However, cities will not work as sentinels in all cases. Some arthropods may respond more strongly to urban features like pollutants, frequent disturbance, or impervious surfaces than to temperature. Long-lived organisms, like trees, which are difficult to grow and study for warming experiments, organisms with life history traits which are highly sensitive to warming, and organisms with low dispersal capability to move beyond city limits may be the best candidates for studies attempting to link responses to urban and global warming (Lahr et al., 2018). Continued studies of arthropod communities across urbanization gradients will make it possible to distinguish shared patterns in responses of certain taxa or feeding guilds to urban and global warming and further inform management.

Interacting Effects of Urbanization and Climate Change on Arthropods

Organisms' responses to urbanization may interact with responses to climate change, for example if climate change affects individuals within and outside cities differently. Interactions between urbanization and background temperature are apparent in present-day studies of the effects of urbanization along latitudinal gradients. For example, organisms often advance their phenology in response to warmer urban or warmer background temperatures, but in a study of butterflies at 83 sites in Ohio, United States, ranging from undeveloped to urban, Diamond et al. (2014) found that butterfly phenology was delayed for seven of twenty species when urban warming was combined with latitudinal (i.e., background) warming. Exploitative species, including those that can feed on many different host plants or have multiple generations per year, had smaller delays in phenology. These results suggest that organisms may show idiosyncratic responses to climate change in urban areas, where urban heat may push some organisms beyond their thermal optima but move other organisms closer to their optima. In some cases, arthropods that are currently pests in cities may be unable to tolerate the additional warming caused by climate change and management activity could be reduced. However, if species benefit from the combination of urban and background climate warming, pest problems in cities are likely to increase in the future, particularly for exploitative species that are already causing problems in urban areas, such as invasive or generalist insect pests.

As the climate continues to change, cities may affect arthropods' geographic ranges. Many non-native arthropod species are initially detected in urban areas, where trade activity introduces new species and warm urban conditions may facilitate their establishment (Paap et al., 2017). For arthropod species that are expanding their ranges due to climate change, movement of individuals to cities may effectively increase their expansion rate. The northern boundary of the range of the pine processionary moth (*Thaumetopoea pityocampa*), native to northern Africa and southern Europe, has been expanding northward for decades due to increases in minimum winter temperatures (Battisti et al., 2005). In the 2000s, the species was moved by people (via ornamental plants) beyond the northern edge of its range to the Paris, France, area, where warmer urban temperatures buffered cold winter temperatures in this location (Robinet et al., 2012). At the southern end of the range, survival is not limited by cold, and thus the warmer temperatures in cities may not benefit the organism and could even be detrimental. As this example highlights, cities may play an important role in shaping organisms' distributions as the climate continues to change.

Managing Arthropods in the City and Beyond

The amount of Earth's surface classified as dense settlements is expected to increase in coming decades. Because humans control the planning of our cities, there will be opportunities to manipulate landscape plantings, set aside land for greenspace, and reduce impervious surfaces in ways that may reduce pests on urban trees, support tree health, and promote biodiversity. Cities can provide places where landscape managers can experiment and design solutions to mitigate the potential negative effects of global change and to make cities healthier for people and other organisms. The lessons learned from these management experiments and decisions can be used to guide management beyond city limits too.

Ecological relationships, including those on urban trees, are often non-linear, and arthropods' responses to a warmer climate and warmer cities will likely be complex. Cities can act as an ecological filter for certain species and types of traits, such as effective dispersal, and drive eco-evolutionary feedbacks (Alberti, 2015; Niemelä and Kotze, 2009). As a result, management strategies developed for present-day arthropods may become less effective as species living in urban areas continue to evolve. Despite these challenges, planners, managers, and designers have many tools they can currently use to minimize pest risk on urban trees. By considering a few key trends and studies, such as those highlighted in this article, planners and designers may be able to identify priority pest targets and explore management strategies that can protect the health of urban trees in a warming climate and a changing world. For example, selecting trees that are more drought-resistant and better adapted to urban conditions may help

reduce the risk of pest outbreaks and promote the long-term health of trees. Implementing regular watering regimens for urban trees could also be another strategy to help prevent water stress and reduce pest densities and damage. Furthermore, tree planting is often suggested as both a mitigation and adaptation strategy for climate change because trees sequester and store carbon and also have a cooling effect on their surrounding environment (Meineke et al., 2016; Nowak and Dwyer, 2007). Because pest problems are often reduced in parts of a city with high tree canopy cover, this strategy may help to reduce or avoid emerging pest problems as the global climate continues to warm. Planting a diversity of trees in urban forests and a diversity of plants around trees could also be a strategy to promote habitat for natural enemies that control tree pests and reduce overall risk of pest outbreaks.

Strategies that reduce pests on trees in cities may also reduce pests in surrounding areas. As described in this article, many non-native pests are introduced to novel environments for the first time through cities, so reducing the spread of pests on city trees may prevent infestation of forests and other habitats in surrounding areas. Cooling cities through strategic tree plantings may also reduce the use of cities as overwintering sites for some pests that may spread to other areas. Lastly, lessons learned about strategies to control pests in one city may be informative for other cities with a similar climate, as biotic homogenization of flora has made cities more similar across the globe.

Arthropods will continue to play an important role in cities as climate change, globalization, and urbanization continue. The choices we make today about managing plants and arthropods in cities will inform the solutions of tomorrow and promote the health of people and ecosystems in urban areas and beyond.

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Global and Regional Cropland Anthromes

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Abstract

Global farming and food systems drive at least 39% of land use. Cropland, an intensive and extensive land use, drives almost 15% of land use. However, the distribution of this land-use type and historical land cover change is heterogeneous. Clear clusters of cropland anthromes exist globally (e.g., the Midwestern United States), in grassland and Mediterranean biomes, and in Indomalaya and Oceania biogeographic realms. However, the spatial alignment of these clusters varies historically. Agriculture, and in particular cropland, has clear impacts on ecosystem structure and function. However, biodiversity conservation is a priority in many regions with an active debate in the literature as to the best pathways forward. In part, this reflects the unique characteristics of cropland anthromes including frequent tree cover and multifunctional land use.

Global Patterns in Cropland

Land dedicated to farming and food systems is estimated to cover at least 39% of the world's ice-free surface (Foley et al., 2005). While rangeland covers a greater percent, cropland is more intensive as a consequence of regular cultivation and frequent increasing applications of chemical inputs. In the global classification system of anthromes, farming systems are embedded in three anthrome types; rangeland, village, and cropland (Ellis et al., 2010). Our focus here, cropland anthromes, hold just over half of the world's arable cropland (Ellis and Ramankutty, 2008). Cropland anthromes are a heterogeneous landscape with patches of trees and pasture embedded in the arable farmland matrix. As such, this anthrome should be viewed as a multifunctional landscape with the potential for combining food, fiber, and fuel production with other landscape goals including biodiversity conservation, recreation, and a diversity of other valued states and functions (Allen et al., 2018).

Though there were initially five cropland anthrome sub-classifications (Ellis and Ramankutty, 2008), the subsequent analysis processes applied in Anthromes V2 (Ellis et al., 2010) reduced the number of cropland anthromes types or sub-classifications to four; placing populated irrigated and populated rainfed croplands together. The four additional types are residential irrigated cropland, residential rainfed croplands, populated croplands, and remote croplands. The four types of cropland anthrome vary most clearly as a function of population density and source of water. Irrigated and rainfed residential croplands have a population density (persons km⁻²) of 74 and 68, respectively. The population density in populated croplands density is 12 and is less than 2 people per km⁻² remote in remote croplands.

In 2000, cropland anthromes were 15% of anthromes globally (Fig. 1). Residential irrigated croplands and remote croplands were classified as one and 2% of global anthromes respectively, populated cropland, 5%, and residential rainfed cropland 7%.

Qualitatively, cropland anthromes have the greatest concentration in temperate regions including central North America and western Eurasia with clear clusters in sub-Saharan Africa, southern Australia, and South America, and Indonesia (Fig. 2). Residential Rainfed Cropland has the greatest concentration in Western Eurasia, Populated Croplands are most frequent in the east-central United States. Remote cropland anthrome is clear in the Great Plains of north-central North America and in Australia. Residential Irrigated anthrome is scattered within California (NA) and the Mississippi Alluvial Valley in North America, Mexico, the Middle East, France, southern Patagonia.

Cropland anthromes are most frequent in temperate regions broadly (> 80%) and specifically within grassland (51%), Mediterranean (45%), temperate broadleaf (40%), and tropical forest (30%) biomes (Fig. 3). Strikingly, over 50% of temperate grassland biome would be classified as cropland anthrome. This pattern of change closely parallels the top four biomes ranked by habitat converted in Hoekstra et al. (2005), though the tropical forest subtypes differ.

If we sort percent change by biogeographic region (Fig. 4) we see that Oceania and Indomalaya have the greatest percent of the region as cropland anthromes (> 20%), though all regions are over 11%. Within biogeographic regions, types of cropland anthrome vary (Fig. 5). For example, in Australasia, which has the lowest percent change overall, is dominated by remote croplands, Indo Malay and Afrotropic by residential croplands, and the Nearctic the most even.

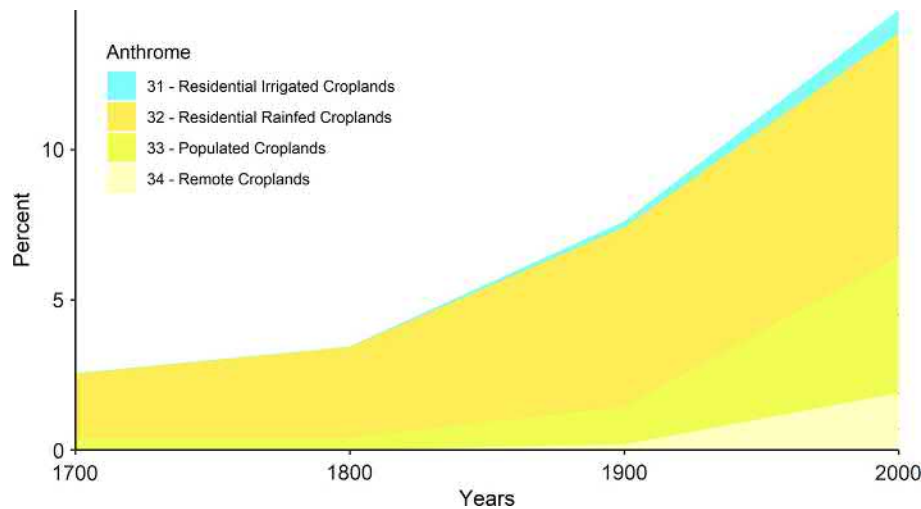


Fig. 1 Change in percent global coverage of each cropland anthrome between 1700 and 2000.

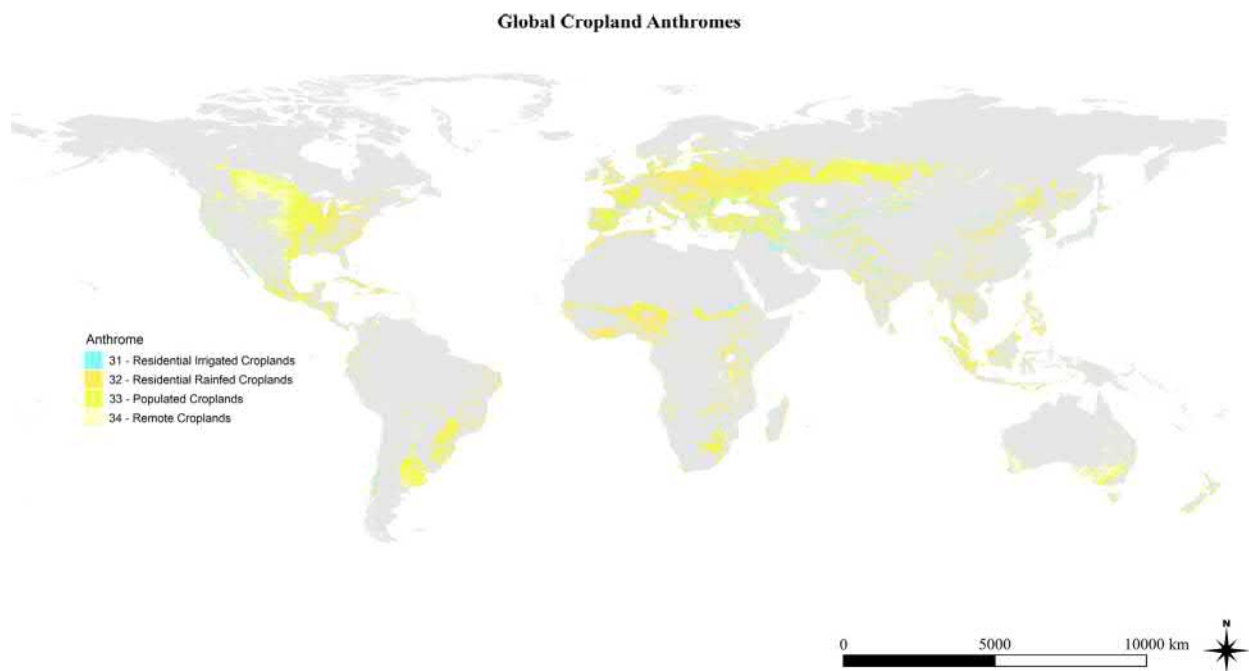


Fig. 2 Global extent of cropland anthromes. Data from Ellis EC, Klein Goldewijk K, Siebert S, Lightman D, and Ramankutty N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* 19: 589–606.

Unique Traits of Cropland Anthromes

In addition to extensive arable land, cropland anthromes have a number of other unique traits. For example, 15% of people live in these four anthromes. The human population of cropland anthromes is lower than that of the Villages and Dense Settlements but is still a significant portion of the global population. However, most of the people benefiting from arable croplands do not live in croplands, suggesting that telecoupling, or a connection across longer spatial distances, is key to consider. Trees are also common in these landscapes. Indeed, cropland anthromes contain about a quarter of global tree cover (Ellis and Ramankutty, 2008). As a consequence of trees, frequent pastures, and intensive plant growth of selective crops (e.g., corn, soybean, wheat, cotton, Fig. 7), cropland anthromes have a greater share of net primary productivity (NPP) than the entire wild forests biome (Ellis and Ramankutty, 2008). However, it is interesting to note, that a significant portion of this NPP is appropriated for human consumption, a process discussed in the article in this volume on Human Appropriation of Net Primary Productivity (HANPP).

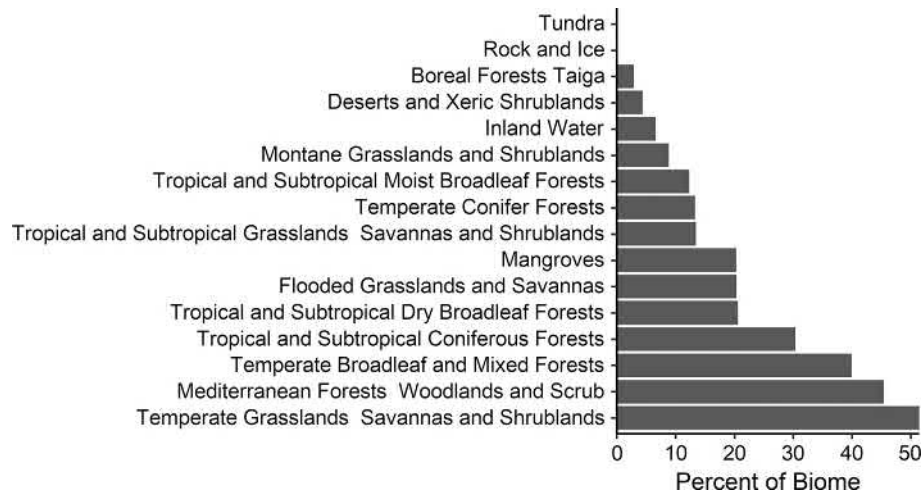


Fig. 3 Percent of each biome type classified as a cropland anthrome. Data from Ellis EC, Klein Goldewijk K, Siebert S, Lightman D, and Ramankutty N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* 19: 589–606.

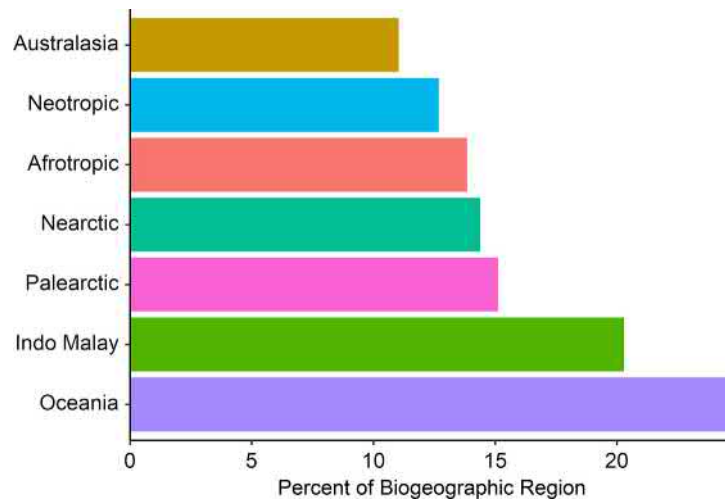


Fig. 4 Percent of each biogeographic region classified as cropland anthrome. Data from Ellis EC, Klein Goldewijk K, Siebert S, Lightman D, and Ramankutty N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* 19: 589–606.

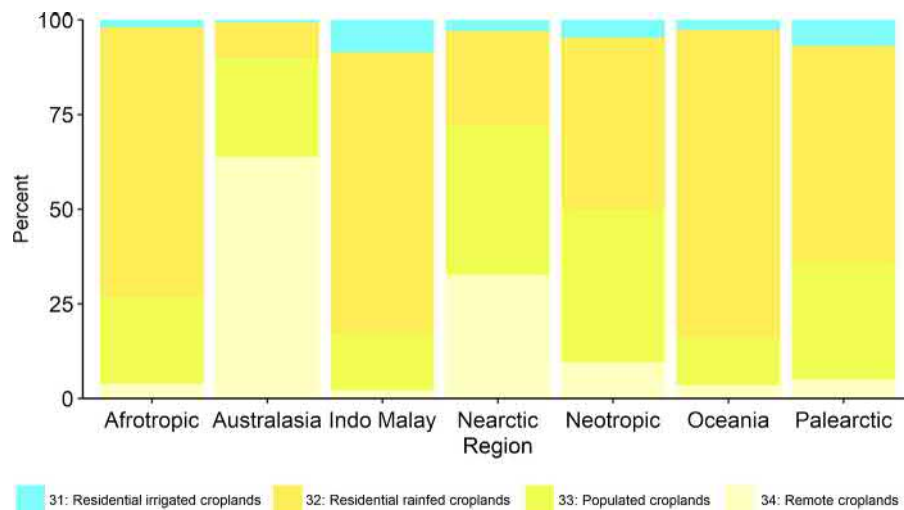


Fig. 5 Percent of each cropland anthrome type within each biogeographic region. Data from Ellis EC, Klein Goldewijk K, Siebert S, Lightman D, and Ramankutty N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* 19: 589–606.

An Expanding Anthrome

The spatial extent of cropland has increased over the last 300 years (Fig. 1) but at a slower rate in the last 60 years (Fig. 6, FAOstat from Food and Agriculture Organization of the United Nations, 2019). Globally, cropland anthromes increased from 2.6% to 14.7% of global cover between 1700 and 2000 datasets (Fig. 1). This growth is not evenly distributed, with only Europe remaining relatively constant (further discussion below). Residential Rainfed cropland was the most extensive throughout (~2%–7%). Residential irrigated croplands remain under 1% of global anthrome cover across each anthrome century. But undoubtedly their impact is broader given that the water they use is drawn from beyond the extent of the croplands. Tilman et al. (2002) show how the footprint of irrigation increased globally between 1960 and 2000. The anthrome data (Figs. 2 and 5) provides one data point on how intensification via irrigation has spread heterogeneously but in key locations, as discussed below. Importantly, during this time use of chemical fertilizers and pesticides also increased globally (Tilman et al., 2002) magnifying the ecological impact of agricultural expansion on biodiversity (discussed below). Cereals have long been the most abundant crop (Fig. 7, FAOstat from Food and Agriculture Organization of the United Nations, 2019) with oil crops increasing most rapidly in the last 60 years. Importantly, the continued increase in yields has not slowed the expansion of cropland (Rudel et al., 2009).

Regional Heterogeneity in Spatial and Temporal Patterns of Croplands

There is clear regional variation in both spatial and temporal patterns of cropland anthromes. For example, cropland anthromes were already dominant in western Europe and the Middle East by 1700 but expanded in eastern Europe between 1800 and 2000 (Fig. 8). The footprint of irrigated cropland is most obvious in 2000, particularly in the Middle East and western Europe.

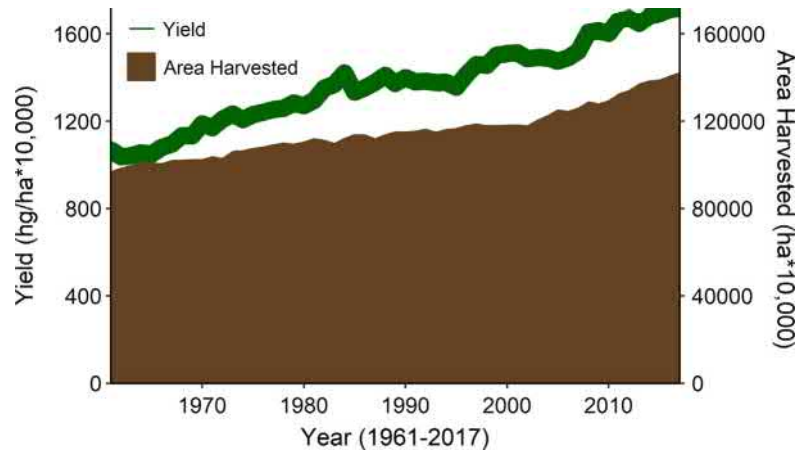


Fig. 6 Global yield and area harvested (1960–2017). Data from FAOstat.

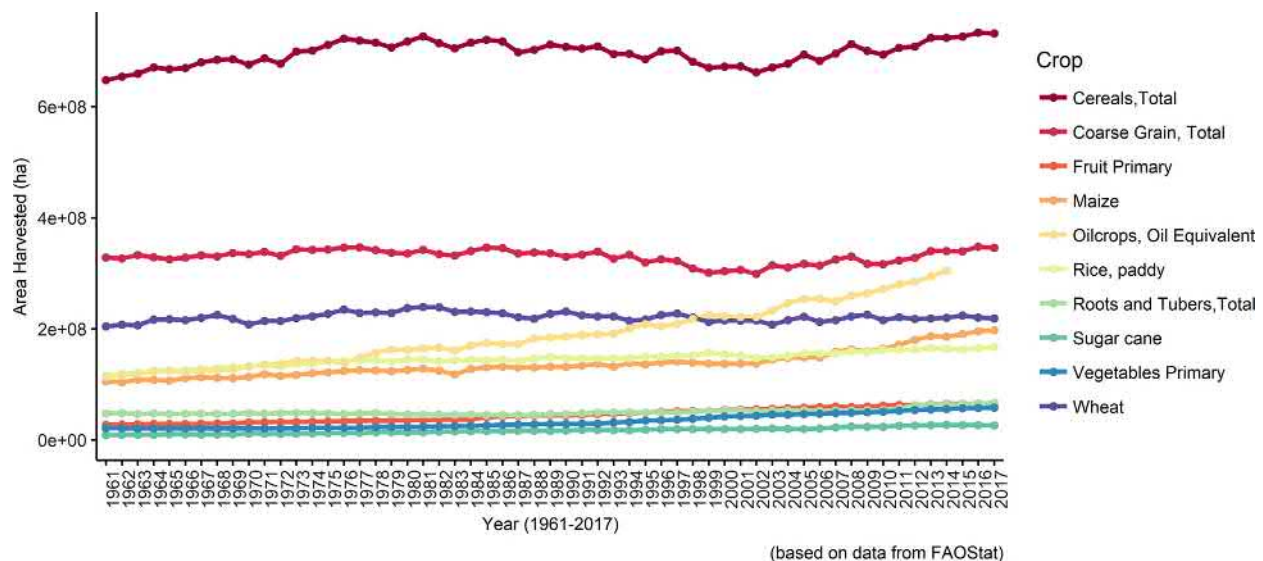


Fig. 7 Global area harvested of 10 key global crops. Data from FAOstat.

In contrast, in North America, cropland anthromes were largely absent in 1700, and even 1800. Indeed, the greatest change in the extent of cropland occurred between 1800 and 1900 (Fig. 9). The northern Great Plains have most recently increased in cropland, likely shifting from rangeland between 1900 and 2000. Since 1900, intensification via increased irrigation has occurred in the south-central and western parts of the region. Like western Europe, clusters of cropland anthromes were already evident in southeast Asia in 1700 (Fig. 10A). Interestingly, the extent of cropland declined in southeast Asia. However, the extent of village anthromes is much more extensive in the 2000 dataset (Fig. 10B).

Threats to Cropland

Despite the global extent and historical expansion of cropland, recent spatial data analyses suggest that key croplands may be lost to other land-use types. For example, d'Amour et al. (2017) suggest that we could lose 1.8–2.4% of global cropland by 2030. These are not marginally productive agricultural lands either, as their data suggest, this could result in a 3.4–4.2% loss of production. Given the expected increases in global population and consumption, loss of cropland is an essential conservation question. Indeed, van Vliet et al. (2017) project continued loss, particularly as a consequence of the expansion of urban land use and land cover disproportionately on land that is ideally suited to farming and food systems. This suggests a more complex narrative around croplands and conservation where patterns of interaction between agriculture and other institutions or systems are regional and context-specific.

Biodiversity Conservation Within Cropland Anthromes

Given the extent of cropland globally, much research has been focused on how to best protect biodiversity in cropland anthromes given the demand for food, fiber, and fuel (e.g., Krebs et al., 1999; Batáry et al., 2010; Meehan et al., 2010; Fahrig et al., 2011; Quinn et al., 2017). Agriculture is frequently faulted for habitat loss and species decline. The current economic efficiency of replacing a diversity of perennial plant communities with a limited number of annual monocrops, coupled with government subsidies, has resulted in agriculture being the dominant matrix of many landscapes worldwide. Unlike ranching and forestry, conservation efforts within the agricultural matrix are discounted because of the low expectations of farmland as a source of ecological stability and biodiversity. However, because agriculture is a dominant land-use, conservation efforts need to consider how this matrix can be managed to enhance associated wild biodiversity.

In a conservation context, it is helpful to have a sense of patterns of richness across anthromes (Martin et al., 2014). At a global extent, the median richness per pixel of plant (Ellis et al., 2012) bird, amphibian, and mammal communities is greatest in residential rainfed cropland (Fig. 11; data from Jenkins et al., 2013 and Pimm et al., 2014). Relatively there are the fewest number of threatened birds and amphibians in remote croplands and the fewest threatened mammals in residential irrigated croplands (Fig. 11). A broader review of richness by anthrome type is available in Cook and Quinn, this volume.

Much of the debate on biodiversity conservation in cropland anthromes has focused on the spectrum of conservation actions between land sparing and land sharing (or wildlife-friendly farming) (Green et al., 2005; Fischer et al., 2008). More recently this discussion has moved from considering the extremes of these options to reflecting how they can be incorporated together appropriately at a given scale and in a given location (Quinn et al., 2014; Fischer et al., 2014).

It is interesting to compare the focus of conservation in cropland anthromes between different areas. The contrast between systems is best demonstrated between Europe and North America. From a research perspective, Europe has gone so far as to define a group of wild species that have a specific relationship with agriculture. In particular, the United Kingdom, as part of its nationwide health assessment, has included a group of birds classified as “farmland birds”. These species may or may not have been present in the same relative abundances 100 or 1000 years ago, but have adapted to the dominant agricultural land use in the region, though threats to these species exist as agriculture intensifies. Across Europe, birds and farming have a long history. These species likely did not thrive in the historical wooded land cover of the region but adapted to thrive under the low-intensity agriculture. More recently, as a result of farmland intensification, the status of these populations has declined, leading to calls to protect farmland species. In contrast, in North America there remains a focus on species classified by biome or ecosystem type; for example grassland birds. And conservation research and practice focus more on cropland expansion versus intensification. However, we have seen many species decline precipitously over the last 50 years, corresponding to the intensification of cropland (Quinn et al., 2017). Future research should consider how these differences drive conservation and farming policy. The anthromes data provides one way to give spatial context to this observation. In comparison to the extensive history of complex interaction and co-evolution between agriculture and biodiversity in Europe seen across the historical anthrome data the relationship between the two in North America, particularly in the Great Plains is recent and impactful. Thus birds and farming in North America have a much shorter relationship, with little time for species to adapt in response to land cover change. There is also value in examining tropical agroecosystems, which have been home to many efforts to balance production and conservation. A combined focus is arguably needed to address the response of biodiversity to agriculture.

Organic farm management has been shown to aid species conservation efforts in croplands. When compared to similar non-organic farm systems, organic farms frequently demonstrate greater richness and abundance of multiple taxa (Hole et al., 2005). As a result, organic farm management is frequently classified as wildlife-friendly farming rather than as land sparing (Green

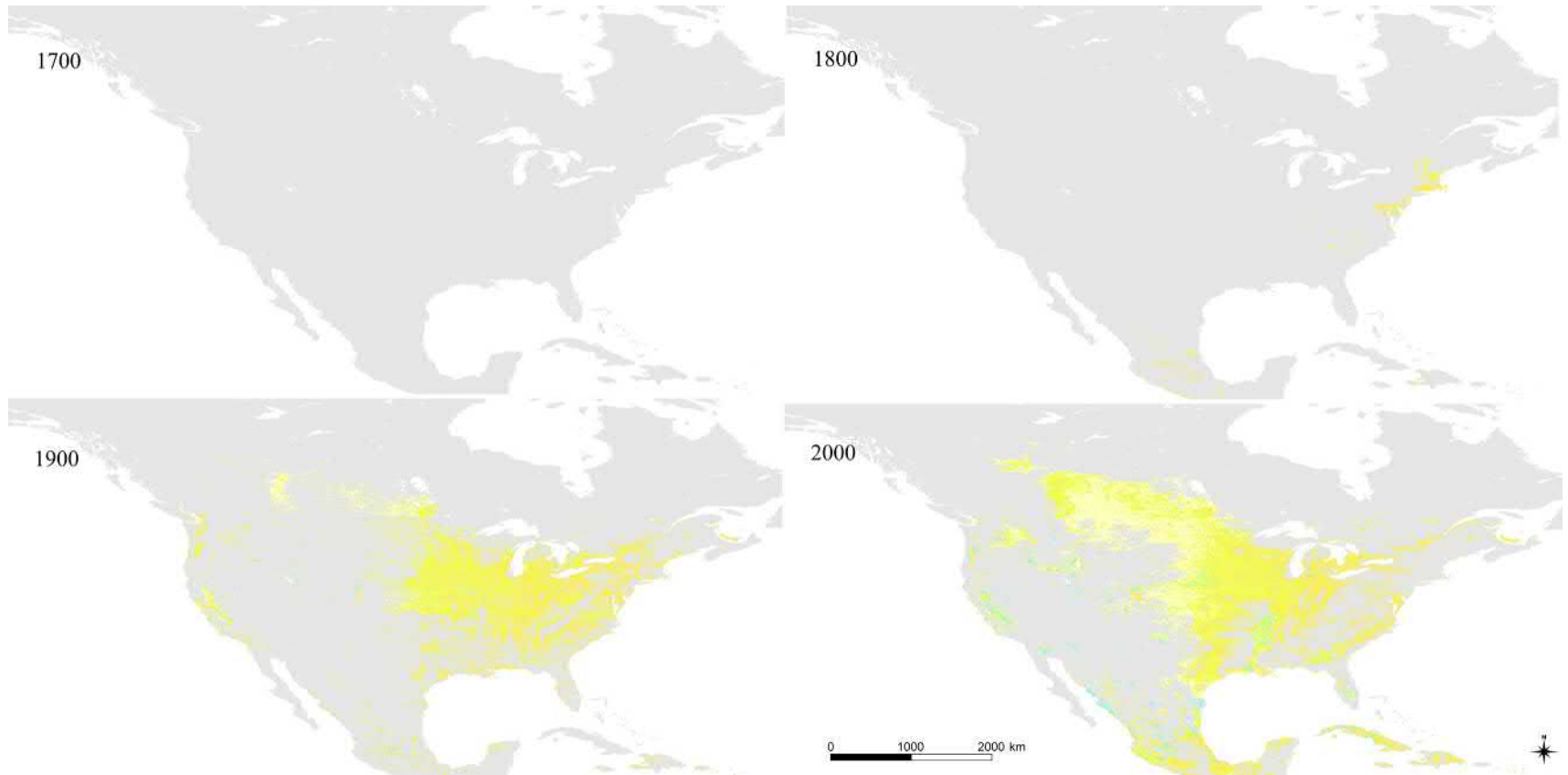


Fig. 9 Spatial and temporal (1700–2000) variation in cropland anthromes within North America. Data from Ellis EC, Klein Goldewijk K, Siebert S, Lightman D, and Ramankutty N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* 19: 589–606.

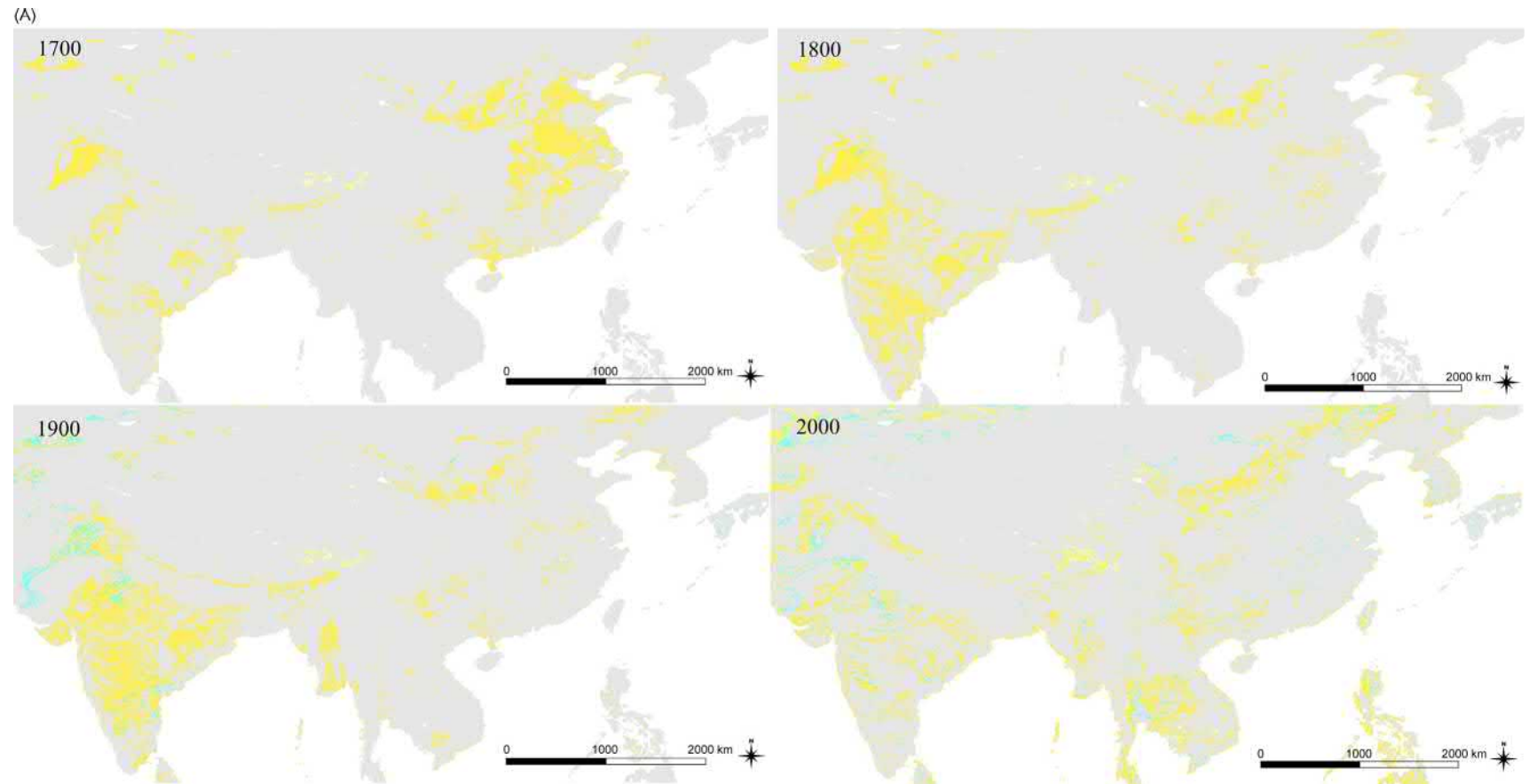


Fig. 10 (A) Spatial and temporal (1700–2000) variation in cropland anthromes within southeast Asia. (B) Anthromes of southeast Asia. Note the high frequency of village anthromes in blue and purple. Data from Ellis EC, Klein Goldewijk K, Siebert S, Lightman D, and Ramankutty N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* 19: 589–606.

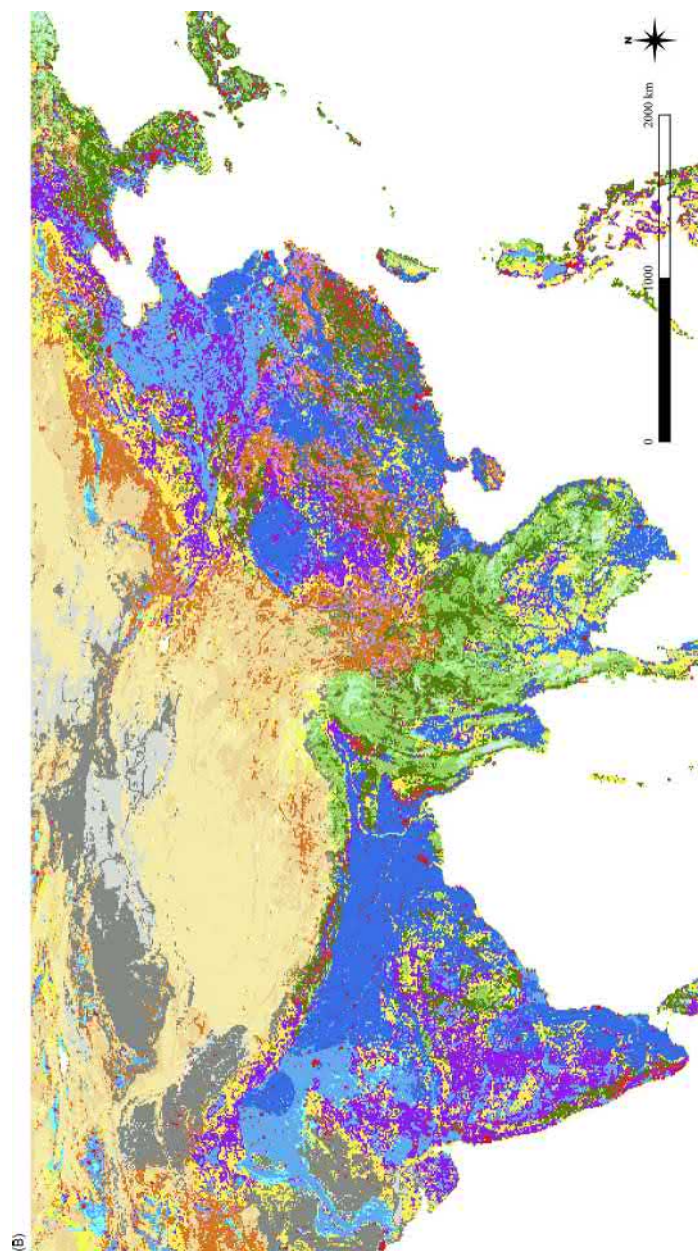


Fig. 10 (continued).

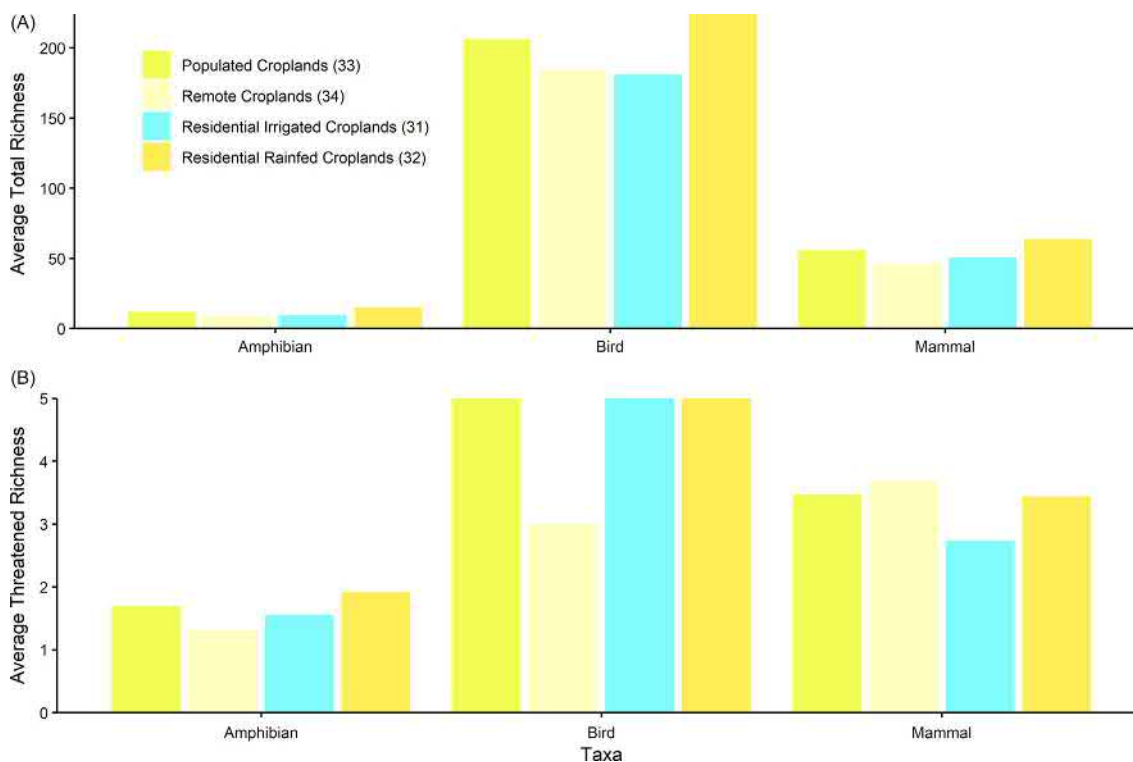


Fig. 11 Total richness (A) and threatened richness (B) of amphibians, birds, and mammals by anthrome type. Richness data from Jenkins CN, Pimm SL, and Joppa LN (2013). Global patterns of terrestrial vertebrate diversity and conservation. *PNAS* **110**(28), E2602–E2610; Pimm SL, Jenkins CN, and Abell R (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**(6187), 1246752.

et al., 2005; Fischer et al., 2008). However, because organic regulations vary by country and often stipulate only what practices cannot be used, the adoption of species-friendly practices and associated land use and land cover patterns can vary greatly between and within farms (Gabriel et al., 2010). Organic agriculture is among the most rapidly growing sectors of agriculture. In 2006, farmland was certified organic in over 135 countries, totaling over 30 million ha and 0.65% of worldwide agricultural area (Willer et al., 2009). Almost a quarter (24%) of organic land is found in Europe, 16% in Latin America, and 7% in the United States. Within each region, the share of total agricultural land that is certified organic is 1.62% in Europe, 0.68% in Latin America and 0.57% in North America (Willer et al., 2009). Despite its small footprint, organic farming has frequently been evaluated for its contribution to biodiversity conservation.

Conclusion

In summary, cropland anthromes are a dynamic, multifunctional, and linked global and regional systems. The extent of this anthrome has increased globally in the last 400 years as has the intensification of cropping systems. In addition to their local footprint, cropland anthromes are connected to populations globally via our current farming and food system. Cropland anthromes however are more than just farmland. They are important population hubs, contain significant tree cover, and are central to current and future conservation efforts.

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Measuring Land Potential and Human Impacts in Rangelands

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Abstract

Humans and rangelands have a complex and intertwined history. Rangelands provide many goods and services to humans, and humans have altered rangelands through their activities. Land potential describes the capacity for production of ecosystem services utilizing the inherent properties, resistance, and resilience of a location. The alteration of land potential by humans has led to changes in how these landscapes function and the ecosystem services they provide. Understanding current and future human needs along with the history of a landscape allows for land potential to act as a filter for management decisions. By combining inherent properties of a site with resistance and resilience along with knowledge about past management activities, land potential can help managers identify not only limitations but also opportunities for investment of resources that are both ecologically and economically positive on the landscape.

Rangelands and human beings have a complex relationship where rangelands provide many goods and services necessary for human sustenance, and humans undoubtedly influence the production of these goods and services. Food, fiber, water, and energy are fundamental human necessities produced by these systems. Being the most extensive human influenced biome, the rangeland anthrome covers nearly one third of the Earth's ice-free surface but only accounts for 5% of the world's population (Ellis and Ramankutty, 2008). Among the many variable definitions of rangeland, most incorporate a land cover type (e.g., "land on which the indigenous vegetation is predominantly grasses, grass-like plants, forbs, or shrubs and is managed as a natural ecosystem" (SRM Glossary of Terms, 1998)) combined with a land use that typically emphasizes grazing or pastoralism (Lund, 2007). Rangelands support 50% of global livestock production (Millennium Ecosystem Assessment (MEA), 2005) although they account for less than 15% of terrestrial net primary production (Ellis and Ramankutty, 2008). There is no doubt that provisioning services (i.e., meat and fiber production) are important contributions of rangelands, however there are numerous additional ecosystem services (supporting, regulating, and cultural) that are receiving increased attention (Briske et al., 2017a,b).

Anthropogenic pressure on rangelands has increased with human population and the associated demands for food and shelter (Millennium Ecosystem Assessment (MEA), 2005). Following European settlement and expansion of railroad infrastructure, United States rangelands were primarily used for livestock production (Holechek, 1981) and the exploitation of natural resources led to significant changes in many rangeland systems (Sayre et al., 2012). Anthropogenic impacts often altered the potential of rangelands to produce the goods and services required for our continued existence, and the level of anthropogenic pressure determined the degree to which rangeland potential was impacted. This historic overutilization of rangeland resources left a legacy of degradation, and current land management must account for these constraints.

Describing these heterogeneous and expansive landscapes can be difficult, especially when considering anthropogenic impacts and uses. The concept of land potential, however, provides a practical approach to contextualize opportunities and limitations of a given piece of land. Land potential is composed of three distinct elements: potential production of one or more ecosystem services, resistance of the land to degradation, and resilience following disturbance (Herrick et al., 2013). This concept utilizes the inherent properties of a site along with anthropogenic influences to determine the capacity of that site to produce goods and services (Fig. 1). This framework effectively represents pertinent rangeland processes and functions, because it factors in the history of human interaction with this complex landscape.

In this article, we provide a framework for addressing rangelands and the anthropogenic pressures they are facing through the lens of land potential. First, we discuss the inherent properties that govern land potential, followed by the concepts of resistance and resilience within the land potential definition, and then the ecosystem services that humans rely on rangelands to provide. After establishing the land potential concept and framework, we discuss how humankind has altered and continues to alter land potential

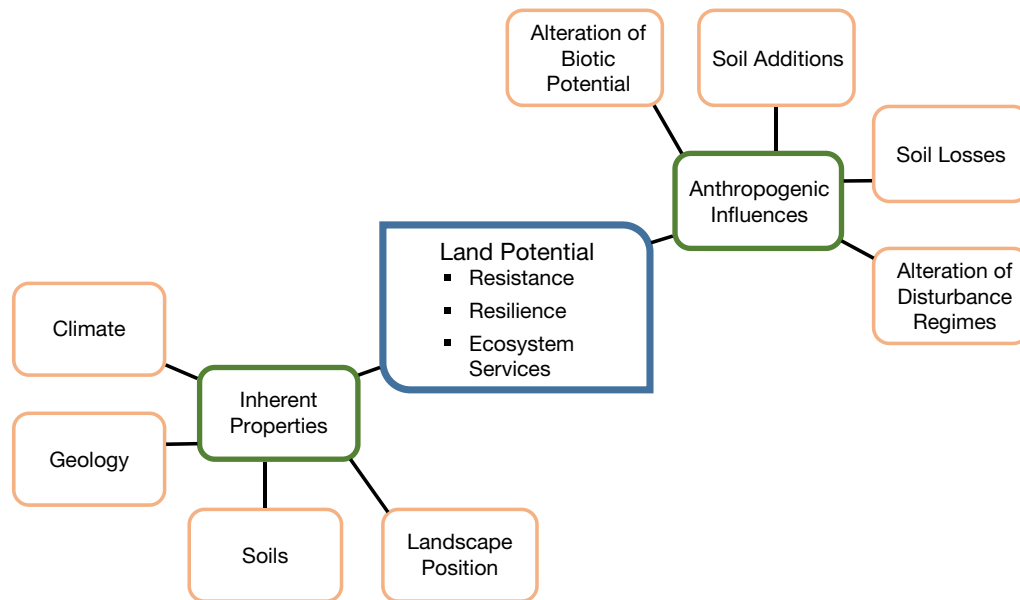


Fig. 1 Elements of and anthropogenic influences on land potential.

across a variety of rangelands using examples mostly from the United States. We conclude with a discussion of land potential assessment and how this framework could be used to make sustainable rangeland management decisions concerning ecosystem service provisioning.

Fundamentals of Land Potential

The capacity of a rangeland to sustain ecosystem services, resist degradation, and recover following disturbance can be captured in the concept of land potential (Herrick et al., 2017). Within the land potential framework, climate, soils, and landscape position determine the potential plant and soil biological communities and ecosystem processes. Together, these properties and processes determine an inherent range of ecosystem services produced by the landscape. Any alteration to these components leads to a corresponding change in ecosystem services. Land potential, much like soil, is a malleable characteristic that is determined first by inherent properties that can be both static (e.g., soil physical properties, parent material, etc.) and dynamic (e.g., plant and soil biological communities, etc.), which can change naturally over millennia or through anthropogenic influence at much shorter time scales.

Inherent and Dynamic Properties

Inherent, or relatively static, properties of a system, like climate, soils, resident plant community, etc., and the functions they facilitate define land potential within an area. Climate is fundamental to our understanding of how landscapes develop. Temperature and precipitation regimes favor certain plant and soil biological communities in specific areas, and soils develop at different rates under different climatic patterns. Rangelands developed where combinations of temperature and precipitation regimes favor grass and shrub species on a wide range of soils. Climate, both historical and present, influences biological community dynamics and soil formation, and given that climate impacts the inherent properties of a location, climate along with disturbance regimes will also drive land potential when viewed at broader spatial scales.

Disturbances are events that place pressure on ecological systems leading to partial alteration of natural ecosystem function (Nimmo et al., 2015), and are usually categorized by the type of pressure that is placed on an ecosystem (Lake, 2000). Pulse disturbances, like wildfire and flood, are discrete events that impact an area on a limited time scale and allow time for natural recovery following the event. Ramp disturbances, like drought, begin by putting slight pressure on the system, which is then exacerbated as the disturbance continues. Lastly, press disturbances are often anthropogenic, like urbanization and land development, and place long-term pressure put on an ecosystem that are never alleviated and can, therefore, force complete alteration of ecosystem function. Historic disturbance regimes, like wildfire, flood, and drought (Lake, 2000; Nimmo et al., 2015) are typically characterized by the frequency, intensity, and duration of naturally-occurring disturbances and determine how an ecosystem would normally respond to any such event.

Climate, geology, and geomorphology are broad-scale properties of an area that heavily influence how the disturbance regime affects the development of other finer-scale characteristics, like soil physical properties and resident plant community. Soil physical properties include relatively dynamic properties such as available water holding capacity (AWC), infiltration capacity, bulk density, and physical crusts, and shape land potential through impacts to rangeland processes (Herrick and Brown, 2016). They also include relatively static soil properties such as texture (i.e., soil particle size distribution) and mineralogy (as influenced by parent material), which affect some ecological functions (e.g., erosion control and nutrient cycling) both directly, and through their effects on the relatively dynamic properties. Soil texture correlates strongly with AWC and infiltration, and is a major influence on soil stability, all key indicators of land potential. Mineralogy affects soil chemical properties, like pH, electrical conductivity, and sodium adsorption ratio (SAR), which impacts soil stability as well. Soil aggregate stability is a metric for soil surface resistance to degradation, and often, a change in this is linked to a related change in soil texture or soil chemistry and can be indicative of soil loss or deposition, which directly impacts land potential on the landscape. Rangeland soils have highly variable physical and chemical properties, can be especially complex when considering the wide range of climate, precipitation, and disturbance regimes (Briske et al., 2017a,b).

High variability in rangeland soils is compounded by the almost equally variable landforms. Landscape position (i.e., where the site is on the landscape) and soil erosion are strongly related to one another as well as the inherent soil physical properties. For example, soils that are found in depositional, lowland areas are often vastly different from upland soils occurring within the same landscape, resulting in very different inherent potential of the system (Herrick et al., 2017). Landscape position is also generally related to soil depth and nutrient availability, and other factors such as degree of incline and slope contour influence how water flows over the soil surface along with erosion potential. Landscape position and soil stability can also have significant influence on the vegetation types we can expect to see and even affect soil biological communities.

Plant community composition is a dynamic property that determines the short-term potential of land to sustain ecosystem services (e.g., erosion and climate control, pollination, food, fiber, etc.) and influences historic disturbance regimes of that area. Thus, changes in plant community composition or function can reflect alteration of land potential due to modification of rangeland processes. In rangeland systems, vegetation communities are often identified by a combination of resident plant community (i.e., what species are expected to be present and in what assemblages), as well as plant functional groups represented (e.g., blue grama grassland, sagebrush shrubland). Describing plant communities based on functional traits is useful for rapid biological and ecological characterizations of rangelands, but may not fully describe the land potential due to omission of many important soil properties (McGill et al., 2006; Walker, 1992).

Although plant communities are comparatively easy to describe, soil biological communities are often much more difficult to characterize. Soil bacterial and fungal community diversity, richness, activity, and relative abundance are also very dynamic, and can have a significant impact on short-term land potential as they have large impacts on soil nutrient cycling and availability, as well as soil aggregate stability. Changes in these communities following disturbance can therefore indicate alterations in ecosystem process and function (Seaton et al., 2019; Landgenheder et al., 2010). Biological soil crusts are a component of the soil biological community that play a key role in landscape function and land potential. Biological soil crust communities include cyanobacteria, fungi, eukaryotic algae, lichens, and moss and are restricted to the first few centimeters of the soil surface. These communities are characteristic of arid and semi-arid rangelands and are often associated with interspace regions devoid of vegetation. Measurements of relative abundance and diversity of soil biological communities can indicate biological stressors within the soil as some community members are more tolerant of harsh conditions (Seaton et al., 2019; An et al., 2013). Soil biological crust communities can also influence characteristics related to soil erosion such as runoff extent and velocity. Knowledge of soil biological communities adds to the overall understanding of land potential, and can help inform estimates of soil resistance to degradation or ability to recover following disturbance.

Resistance and Resilience

Resistance and resilience are two additional components of ecosystems that define land potential. Both concepts were born from the ecological resilience theory developed in the 1970s at population and community scales (Holling, 1973) and have since evolved in usage at the landscape scale (Carpenter et al., 2001; Nimmo et al., 2015; Briske et al., 2017a,b). The two concepts of resistance and resilience are specific to each ecosystem and are determined by the inherent abiotic and biotic characteristics of that system along with the historic disturbance regime. Ecological resilience theory describes how a system acts in the face of disturbances, natural and anthropogenic (Holling, 1973). Resistance is the capacity of a natural system to withstand disturbance and retain its function, whereas resilience is the capability of an ecological system to return to previous stability or to reorganize itself with renewed functionality (Seybold et al., 1999). Abiotic and biotic components of ecosystems interact within natural disturbance regimes to determine how that system reacts and responds to the disturbances present during its development. Because resistance and resilience are process-based characteristics of a landscape, they are applicable at almost any scale of observation (both temporal and spatial), and coarser-scale usage is needed to understand the impacts to land potential. Although natural events have shaped resistance and resilience of all ecosystems, many systems have lost some of their natural capacity to withstand external influence due to anthropogenic alteration of historic disturbance regimes and subsequent impacts to the inherent characteristics of a landscape.

Utilizing resistance and resilience with the land potential framework can provide some guidance when trying to predict how ecosystems will function under altered disturbance regimes (Lake, 2013). The scale and scope of human interactions with rangeland systems requires consideration of natural ecosystem response when faced with anthropogenic disturbance. By acknowledging and understanding how a system naturally responds, these natural responses can provide guidance for land management decisions in the face of continued human pressures.

Resistance and resilience are also key to the production of ecosystem services on rangelands throughout the world. When ecosystem function is maintained or improved, rangelands provide many important ecosystem services. Resistance and resilience help determine the capacity of an ecosystem to withstand disturbance while maintaining functionality, which directly contributes to the sustained production of many key ecosystem services.

Land Potential and Ecosystem Services

The supply of rangeland ecosystem services, or the benefits humans receive from rangeland ecosystems (Millennium Ecosystem Assessment (MEA), 2005), are directly dependent on the various aspects of land potential, which is driven by inherent biophysical properties as well as anthropogenic influences on ecosystem properties (Fig. 1) (Brown and MacLeod, 2011). Rangelands are often characterized as having highly heterogeneous biophysical properties. When coupled with diverse land use histories, the resulting land potential and associated ecosystem services on a landscape are frequently diverse.

The Millennium Ecosystem Assessment (MEA) placed ecosystem services into four broad categories representing provisioning, regulating, supporting, and cultural services (Table 1) (Millennium Ecosystem Assessment (MEA), 2005). Given the anthropocentric nature of ecosystem services, the values placed on them vary across user communities (e.g., producer, conservation, recreation, cultural), socioeconomic status, and gender, to name a few (Martín-López et al., 2012). Demand also drives emphasis placed on certain ecosystem services. For example, in U.S. rangelands emphasis has generally been placed on provisioning services or those that could directly be harvested by humans (e.g., food, fiber, energy, or water). Over the last 150 years the primary provisioning resources produced on these rangelands have evolved in direct response to demand shifting from predominantly sheep to cattle production and the expansion of fossil fuel based energy resources to clean energy resources such as wind and solar (Yahdjian et al., 2015).

Table 1 Potential anthropogenic influences on production of select ecosystem services.

<i>Ecosystem services</i>		<i>Range management examples of anthropogenic influences on sustainable production of ecosystem services</i>	
<i>Class</i>	<i>Example</i>	<i>Positive</i>	<i>Negative</i>
<i>Supporting</i>			
Primary production		Land management decisions (e.g., timing, frequency, intensity of disturbances) and restoration of degraded plant communities to maximize primary production.	Land management decisions that reduce primary productivity.
<i>Provisioning</i>			
Food		Technological advances and improved techniques for livestock production.	Overutilization of grazing resources, competing land uses (housing developments, energy, etc.)
Water		Ground and surface water allocations/use based on known or projected availability.	Unsustainable use of ground and surface water for production purposes.
Energy		Allocation of rangeland for energy production.	Policy restrictions limiting the use of rangelands for oil, gas, wind, or solar production.
<i>Regulating</i>			
Air quality		Restoration activities that promote soil stabilization, proper timing of prescribed fire, proper fuels management to reduce wildfires probability outside of historical regimes.	Increased particulate matter due to degraded/destabilized plant and soil biological communities eolian erosion of soil and natural/prescribed fire outside of the historical range of variability.
Erosion control		Restoration activities that promote soil stabilization (e.g., revegetation, grazing strategies, placement of roads and fences).	Increased loss of soil due to degraded/destabilized plant communities.
<i>Cultural</i>			
Recreation		Policies to promote multiple use of public lands.	Loss or degradation of land available for recreation purposes (e.g., hiking, biking, camping, bird watching).
Spiritual values		Protection for areas used for spiritual purposes.	Loss of culturally important plants, soil, rocks, and minerals restricting their availability for spiritual purposes.

Examples of Anthropogenic Influence on Land Potential

Effects of forage overutilization arise from stocking grazing animals at a rate in excess of the carrying capacity of land for an extended amount of time (Derner et al., 2017). Human-induced changes to the land from this process may result in either positive or negative changes in land potential. Positive human impacts include land improvement through implementation of sustainable land use practices (e.g., conservative stocking, drought monitoring, timing of grazing, periods of rest) with the goal of increasing resistance and resilience to future degradation. Negative human impacts resulting from overutilization include the unsustainable removal of biomass, soil compaction, increased erosion potential, and even increased albedo, which could lead to reduced evapotranspiration and rainfall (Millennium Ecosystem Assessment (MEA), 2005; Sala et al., 2017). The overutilization of grazing resources following settlement of the American west has weakened resident above- and belowground biological communities in many areas, which has had drastic impacts on land potential. Overgrazing in conjunction with drought only intensifies the negative impacts on ground-cover, diminishing the possibility for full recovery (Treydte et al., 2017). Globally, this “human-induced” driver of change is often credited with being the reason for rangeland abandonment and the relocation of pastoralists and rural populations (Millennium Ecosystem Assessment (MEA), 2005). The emphasis on livestock production has decreased the value of the landscape to provide wildlife habitat, control erosion, and effectively cycle nutrients, all resulting from unsustainable grazing practices (Sayre et al., 2012).

The effects of human activities on land potential have been documented in many other parts of the world including east Africa. In Kenya, rangelands are primarily used for traditional livestock raising by nomadic pastoralists (Fratkin, 2001). Additionally, African rangelands provide habitat that supports many native wildlife species (Georgiadis et al., 2007). Communal use of the landscape has led to large areas of degraded rangeland due to the overutilization of grazing resources, similar to the American west. Accelerated erosion and soil loss have led to reductions in numerous ecosystem services, including providing wildlife habitat, and the demand for resources provided by the land has increased rapidly over the past few decades (Millennium Ecosystem Assessment (MEA), 2005). To combat this reduction in land potential, many international programs (IRP, 2019) have focused on restoration and rehabilitation of soil resources throughout the region (see Kimiti et al., 2017). By improving resistance and resilience through restoration and rehabilitation of the landscape, land potential can be increased to support increased ecosystem services.

The prairie ecosystems of the North American Great Plains were historically among the most productive rangelands in the world. Given their high land potential associated with productive soils, favorable climate, and gentle terrain, it is no surprise that much of its extent has been altered via cultivation following European settlement (Sampson and Knopf, 1994). Historically, indigenous peoples predominantly used the region for hunting and gathering resources due to the large populations of wildlife and diversity of native flora throughout the area, and utilized areas along waterways for small-scale crop production. The conversion of these prairie systems to intensive crop production by European settlers reshaped key ecosystem services provided by this landscape as well. Due to intensive management and introduction of significant external inputs such as fertilizer, one specific ecosystem service has been augmented at the expense of many others. Current management in this region is for crop production, and provisioning services (food and ethanol production, in this case) far exceed what the landscape naturally provided. Although provisioning services have increased, the capability of the system to provide regulating and cultural services has been significantly impaired. External inputs of fertilizer impact nutrient cycling and water quality, and traditional cultivation increases soil loss by inhibiting erosion control. The implications of widespread conversion to croplands to wildlife are mixed, favoring habitat generalists like robins and pheasants at the expense of native grassland specialists such as prairie chickens and horned larks (Knopf, 1994; Askins et al., 2007). Additionally, this habitat loss impacts many species of butterfly and other important pollinators (Moranz et al., 2012). From the relics of this system that still exist, we are still learning how significantly the conversion has altered the services provided. Although many services have been changed, the benefits to human society via increased production and revenue overall outweigh most of the negative impacts, and new cultivation techniques are developing that help to restore some of these services.

Assessing Land Potential

With an understanding of how historic land potential has been altered by anthropogenic influences, the question remains: How do we gauge land potential? Many assessments rely on historic accounts and records to describe the potential natural vegetation of an area (Udvardy, 1975; Olson et al., 2001). These classifications are typically based on climatic characteristics along with plant physiology and soil properties to estimate the potential productivity of the area (Prentice et al., 1992). These groupings allow managers to understand what plant communities would historically have been present on sites and the related ecosystem services provided. Others attempt to describe the dynamics of a site with an emphasis on state and transition models that include process-based thresholds that dictate disturbance response, which influences resistance and resilience (Bestelmeyer et al., 2003; Stringham et al., 2003; Briske et al., 2005). Spatial and temporal scale is also a key consideration when determining how to assess land potential and new tools are emerging to facilitate this.

Advances in quality and accessibility of remote sensing data along with increases in computing power have allowed for the integration of machine learning and artificial intelligence systems to estimate land potential through determination of potential natural vegetation along with human influence at global scales (Ellis et al., 2010; Hengl et al., 2018). At more local scales, LandPKS, a mobile phone application, was developed for site-specific determination of land potential (Fig. 2) (Herrick et al., 2013, 2017). This tool predicts the available water holding capacity and infiltration rate for an area based on inherent site characteristics



Fig. 2 Using LandPKS to evaluate land potential.

such as slope, rock content of the soil, and soil texture by depth, while allowing the user to adjust these numbers based on soil organic matter, which is a relatively dynamic property that can be affected by management. Available water holding capacity serves as an ideal measurement of production potential because it integrates many other site characteristics in its calculation (e.g., soil texture, rock fragments, organic matter). Along with a measurement of land potential, LandPKS also offers users a way to monitor trends on the landscape through plant community measurements that facilitate flexible management strategies (Herrick et al., 2017).

Managing Within a Rangeland Potential Framework

When land potential has been adequately characterized, land managers can use this concept to evaluate their ability to achieve management goals on a given piece of land. Although understanding land potential alone will not guarantee a positive outcome, it can be used to develop a more complete understanding of the opportunities and limitations that exist for a given piece of land. Land potential can be used to prioritize restoration treatment (e.g., revegetation, herbicide) locations for favorable responses and avoid some locations where there would be a high probability for a negative response like soil erosion (UNEP, 2016). Making ill-informed management decisions can translate into economic loss, environmental degradation of biotic and abiotic resources, and depending on the land's resilience, lasting negative impacts to the ecosystem services that land supports.

Selection of treatment locations for brush control provides an example of how land potential could be used in management decisions. In this scenario, there are two locations within a management unit undergoing woody plant encroachment that are candidates for treatment. Using the land potential concept to evaluate both sites, managers determine that, although both sites are visually similar, inherent soil properties are quite different. One site has a shallow soil with a root-restricting layer of caliche at 20 cm depth, and the other is on a deeper soil without any restrictive layer. The available water capacity (as measured by LandPKS) on the former site is less than 2 cm and on the latter site is ~5 cm. With the filter of land potential, the latter site would be identified as the more appropriate location for brush control treatment due to a higher likelihood of positive response. By understanding the fundamentals of land potential within a management context, one can make effective and efficient decisions regarding implementation of management activities.

Land potential provides a meaningful filter for the evaluation of landscapes at all spatial and temporal scales. By combining inherent properties of a site with resistance and resilience along with past management activities, land potential can help managers identify not only limitations but also opportunities for investment that are both ecologically and economically positive on the landscape. Land potential can and should be used in concert with other tools available to land managers that describe the processes occurring on the landscape (e.g., Ecological Site Descriptions, State and Transition Models, etc.). Utilizing land potential in conjunction with other tools allows for the optimization of land management strategies to fulfill specific objectives and represents an underlying framework that can be used for decision-making across scales and locations.

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Anthromes—Temperate and Tropical Agroforestry

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Abstract

The proposed designation of the Anthropocene suggests a triple challenge of preventing biodiversity loss, mitigating and adapting to climate change, and sustainably providing resources for a growing human population. Anthromes often take the form of multifunctional mosaics of perennials and annuals (e.g., agroforestry systems). Biodiversity-based land management of working lands has been practiced since ancient times and their value has been recognized, updated and promoted across our global biomes over the past forty years. Analogous agroforestry systems are found in common biomes across the globe. Agroforestry incorporates an array of successful strategies, historic and modern, that have relevance for achievement of multiple Sustainable Development Goals (e.g., biodiversity, climate change, poverty alleviation). Four agroforestry biomes are described, both historic and modern, that will play an important role in helping to achieve global Sustainable Development Goals. These include: (1) Mediterranean anthrome (dehesa/savanna with livestock); (2) Highland/lowland/island tropical anthrome (homegardens and multi-strata systems); (3) Temperate zone anthrome (silvopasture, alley cropping—silvoarable); and (4) Arid/semi-arid tropical anthrome (improved fallows, farmer-managed natural regeneration, evergreen agriculture).

Introduction

More than three quarters of the terrestrial biosphere have been reshaped by humans into anthropogenic biomes (anthromes), embedding substantial areas of remnant and recovering novel ecosystems within the agricultural and settled landscapes that sustain human populations (Ellis and Ramankutty, 2008). Anthromes often take the form of multifunctional mosaics (e.g., agroforestry systems) within which substantial remnant and less intensively managed ecosystems are often left embedded, especially where terrain is heterogeneous (Ellis, 2013; Van Noordwijk et al., 2019b).

The proposed designation of the Anthropocene suggests a triple challenge of preventing biodiversity loss, mitigating and adapting to climate change, and sustainably providing resources for a growing human population. Proper management of “working lands” (i.e., farms, forests and rangelands) is needed in order to address this triple change. These working lands must be managed both to complement the biodiversity conservation goals of protected areas and to maintain the diverse communities of organisms, from microbes to mammals, that contribute to producing food, materials, clean water, and healthy soils; sequestering greenhouse gases; and buffering extreme weather events, functions that are essential for all life on Earth. Temperate and tropical agroforestry systems are directly connected with Sustainable Development Goals (SDGs), goals which are needed to be reached address the loss of biodiversity, climate change and regenerative farming (e.g., soil health) at both large and small scales (Van Noordwijk et al., 2018; Van Noordwijk et al., 2019b). The creation of SDGs has enabled multifunctional land uses, including agroforestry, to gain wider support. An integrated landscape approach, with increased functionality per unit of land, appears to be the best way of coherently targeting the SDGs (Van Noordwijk et al., 2018).

Agroforestry focuses on the role of trees on farms and in agricultural landscapes to meet the triple bottom line of economic, social and ecological needs in today's world. Across the globe, the science and practice of agroforestry can contribute to many of the SDG key challenges: (1) Hunger eradication based on agroforestry methods of soil fertility and land regeneration; (2) Market driven, locally focused tree cultivation systems that generate income and build assets to lift more rural poor from poverty; (3) Advance the health and nutrition of the rural poor through increased use of plant diversity; (4) Conservation of biodiversity through

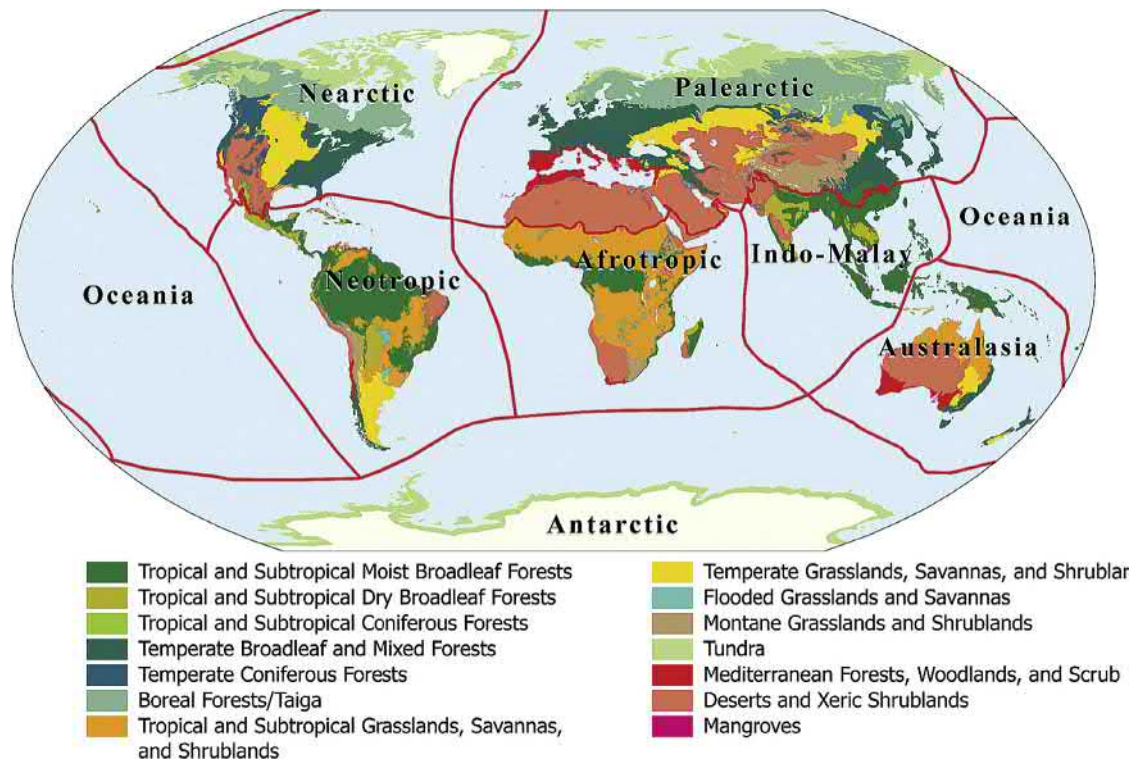


Fig. 1 Ecoregions categorized within 14 biomes and eight biogeographic realms (Olson et al. 2001). Similar temperate and tropical agroforestry anthromes correspond to similarities across ecoregional biomes.

integrated conservation solutions using agroforestry technologies; (5) Protecting watersheds and water quality through agroforestry-based solutions; and (6) Assisting rural poor to better adapt to climate change through intentional cultivation of a diverse array of tree/shrub crops (Garrity, 2004; Nair et al., 2017).

An important dimension of biodiversity for agroforestry is the representation of trees in local knowledge and the degree of specificity of ethnobotanical knowledge, linked to culture, language and ethnicity. Across a wide range of settings and agroforestry anthromes, total tree diversity ranges from 10 to 1000 species. For example: (1) 100 indigenous species were located in tree diversity surveys in 16 villages in Burkina Faso, Mali, Niger and Senegal (Cámara-Leret et al., 2019); (2) A total of 127 species were identified with acknowledged local use value in homegardens plus coffee agroforestry systems in Southwestern Ethiopia (Jemal et al., 2018); (3) A total of 190 tree species were noted in coffee-based multi-strata agroforestry systems on the slopes of Mount Kenya (Carsan et al., 2013); (4) and hundreds of native tree species are currently found in agroforestry ecosystems in the Peruvian Amazon (Dawson et al., 2008), forming an important reservoir of biodiversity.

These multifunctional land management strategies, found throughout the world across temperate and tropical biomes (Fig. 1), represent a major opportunity to ensure sustainable production of food and fiber along with the ecological heritage of the planet (Ellis, 2013; Nair et al., 2017; Kremen and Merelender, 2018; Udawatta et al., 2019). Four major global agroforestry anthromes, rooted in history and currently under active use, will be covered including:

1. Mediterranean anthrome (dehesa/savanna with livestock).
2. Highland/lowland/island tropical anthrome (homegardens and multi-strata systems).
3. Temperate zone anthrome (silvopasture, alley cropping—silvoarable).
4. Arid/semi-arid tropical anthrome (Improved fallows, farmer-managed natural regeneration, evergreen agriculture).

Mediterranean Anthrome (Dehesa, Silvopasture)

The Mediterranean basin anthrome is dominated by silvopasture systems which include the Spanish *dehesa* “La Dehesa”, also known as “*Montado*” in Portuguese. The term “*dehesa*” comes from Spanish and refers to land in Southeast Spain set aside as free pastures for roving shepherds and herds belonging to the “*mesta*.” The *dehesa* is a human influenced agroecosystem in continuous use for centuries (Martín-Vicente and Fernández-Alés, 2006).

Climate is the primary identifying characteristic of the Mediterranean *dehesa* biome, defined by marked variation of seasons, a hot and dry summer (from 3-11 months), with a period of limited rain during the relatively cold season that extends from autumn

to spring. Rain is erratic and therefore its distribution throughout the year is as important as its total value. In addition to the Mediterranean basin, this type of climate also exists in California, along the Pacific coast of South America (Chile), in South Africa, and in Southeast Australia (Le Houérou, 1993).

The Mediterranean dehesa, a traditional agroforestry system, includes more than 3 million hectares of the Iberian Peninsula. Similar systems are found in northern Greece, Crete and Corsica (Eichhorn et al., 2006). Dehesas average 500 ha but there are systems that are as large as 5000 ha. The hot, dry summer climate of the Dehesa requires a relatively large area to support enough pasture for livestock, and rotational grazing is practiced as a key to management approach in order to be ecologically and economically viable (Moreno and Pulido, 2009).

The dehesa is a savanna-based silvopasture system, where livestock, disbursed trees and shrubs, pasture and crops all have important roles. Dispersed trees are combined with crops, pasture and shrubs as a result of the different management practices focused on agriculture, livestock, forestry and game. Dehesas are used for extensive livestock raising (sheep, cattle and pig) and cereal cultivation in long rotations. The trees have a direct value as fodder crop, providing acorns and leafy branches in autumn and winter, when the herbage production is low, and an indirect value as shelter for cold in winter and heat in summer. As a consequence, the trees are planted, managed and regularly pruned with the aim of maximizing acorn production (Martín-Vicente and Fernández-Alés, 2006).

Components of the System

The dehesa anthrome is not only characterized by diversity in species (fauna and flora), but also by structure and production. The system consists of an open tree layer (50 trees ha⁻¹) and an annual grass layer, whose composition and functioning largely depend upon the tree layer. The tree layer is typically composed primarily of evergreen species of *Quercus* (*Q. rotundifolia*, *Q. suber* L., *Q. faginea*), although other deciduous *Quercus* are also common (*Q. pyrenaica*, *Q. pubescens* Willd., *Q. canariensis* Willd.) (Martín-Vicente and Fernández-Alés, 2006).

Domestic livestock are the primary product of the dehesa and as such the tree and forage components of the system are based on the nutritional needs of the livestock. At its most basic form, the dehesa contains a two-strata structure, herbaceous and arboreal. The herbaceous forage layer typically consists of natural pasture, however crops and improved pasture are also used. The arboreal layer includes low density disbursed trees, typically ranging from 20 to 40 trees per hectare (10–50% canopy ground cover). Trees are maintained to provide diverse products to the system (fruits, fuel wood, cork, fodder) as well as for protection of the soil and herbaceous layers (Moreno and Pulido, 2009).

The Holm oak (*Quercus rotundifolia*) and cork oak (*Q. suber*) are the most frequently used tree species in the Iberian Peninsula. The holm oaks are found in the interior regions and the cork oaks are present in the more temperate and humid regions, with more Atlantic influence. Holm oak are excellent producers of sweet acorn, while the cork oak is valued for cork production. Other species present in the more humid dehesas include other oaks (*Q. faginea* and *Q. pyrenaica*). These tree species are valued for fodder since branches can be pruned for food in periods of pasture scarcity (Moreno and Pulido, 2009).

A highly diverse layer with a half dozen of shrub species is common in dehesas including *Cistus* sp., *Retama* sp., *Erica* sp., *Arbutus unedo*, and *Viburnum tinus*. The shrub layer includes species that have a high nutritional content for domestic livestock and for game species (Hajer et al., 2004).

Intentional establishment of trees within dehesas is a traditional practice. The predominance of *Quercus ilex* subsp. *ballota*, which produces a sweeter acorn than other oaks, is attributed to the active role of humans in the tree establishment within the dehesa (Martín-Vicente and Fernández-Alés, 2006).

Highland/Lowland/Island Tropical Anthrome (Homegardens and Multi-Strata Systems)

Tropical homegardens, found across the globe in fertile, moist tropical lowlands and highlands, are intimate, multi-strata combinations of various trees and crops, sometimes in association with domestic animals, around homesteads. In terms of ecological distribution, the highest concentrations of homegardens are in the humid and subhumid tropics including tropical islands of the Pacific, but they are also common in other ecological regions, especially the tropical highlands of Asia, Africa, and Mesoamerica (Nair, 1989). Excellent examples of multistory tropical homegardens with similar structure, function and species analogs are found on Java (Indonesia) (e.g., Talun-Kebun, Pekarangan), India (Kerala) in East Africa (e.g., Shamba, Chagga), and in Central America (e.g., Huertos Familiares) (Nair and Kumar, 2006) (Fig. 2).

Species complexity in homegardens is anthropogenic, a result of deliberate attempts and meticulous selection and management by farmers to provide the products they consider are important for their subsistence and livelihood (Nair, 2006). Homegardens are reputed among the oldest forms of land use activity (next only to shifting cultivation) that has evolved through generations of gradual intensification of cropping in response to increasing human pressure and the corresponding shortage of arable lands. The Javanese homegardens of Indonesia and the Kerala homegardens of India have evolved over centuries of cultural and biological transformations and represent the accrued wisdom and insights of farmers who have interacted with environment, without access to exogenous inputs, capital, or scientific skills (Wiersum, 2006).

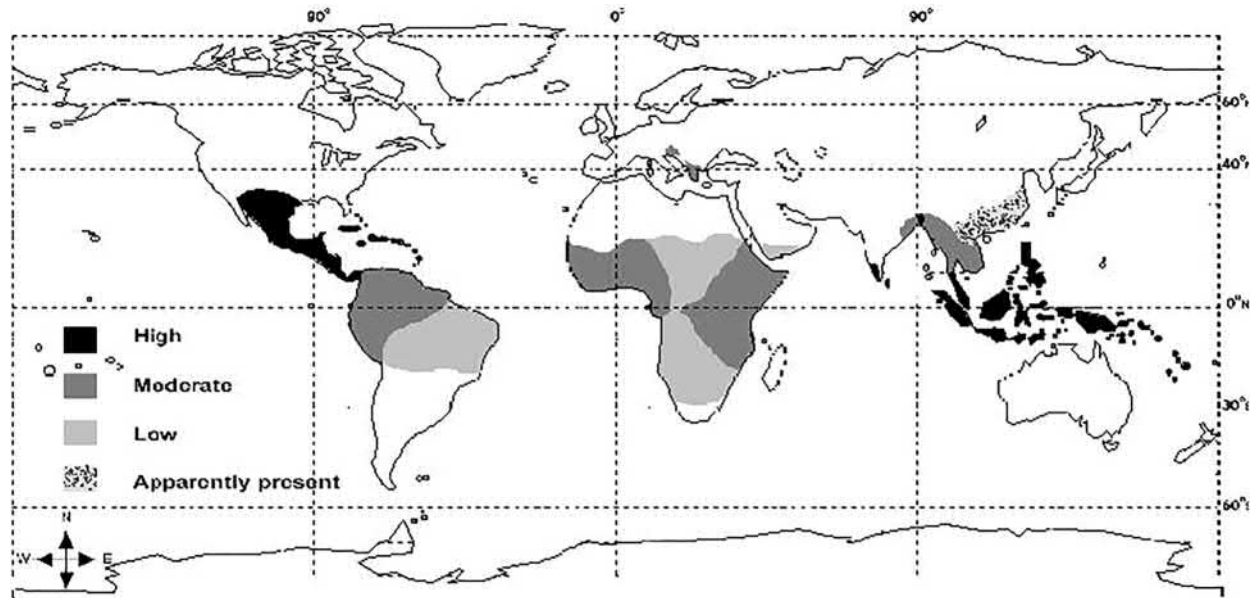


Fig. 2 Global distribution of homegardens (Nair and Kumar, 2006).

In most high-rainfall areas of the Americas and Asia, trees are an integral part of the agroecosystem and they form the key physical feature of the local natural environment (Ewel, 1986; Perfecto and Vandermeer, 2008). Coffee and cacao have long been produced under the shade of trees in Mesoamerica and South America and consequently traditional coffee and cacao farms are indistinguishable from native forest when viewed from a satellite (Götz and Harvey, 2007).

Components of the System

Homegardens contain a mix of annual food crops with frequently harvestable tree crops that provide food and sometimes cash income. They represent a confluence of human ingenuity with ecological ambience, offered by year-round growing seasons and the amenability of the various species to grow under shade in mixed stands. In the most widely studied homegarden systems in South—and Southeast Asia, homegardens are used to produce products with high nutritional value (proteins, vitamins, minerals), medicinal plants and spices, firewood, and sometimes also forage crops and construction wood (Wiersum, 2006).

High levels of species diversity are common to all homegardens. Food plants (food crops and fruit trees) are the most common species in most homegardens throughout the world. This underscores the fact that food- and nutritional security is the primary role of homegardens—a point noted throughout homegarden literature (Brownrigg, 1985; Fernandes and Nair, 1986). Next in importance to food crops are cash crops, and with increasing trend toward commercialization, the interest in such crops is likely to only increase.

Deliberate selection and management of trees (domestication) by humans that has been going on for millennia in agroforestry systems (Simons and Leakey, 2004). Leakey et al. (2005) present evidence that subsistence farmers have domesticated locally popular indigenous fruits (*Dacryodes edulis* and *Irvingia gabonensis*) in Cameroon and Nigeria. Much of this in situ domestication has taken place in homegardens. Similar patterns of domestication have happened for other plant species in homegardens around the world, especially in those with long history as in South- and Southeast Asia (Wiersum, 2004). The global extent of homegardens is reported to include 5 million ha of land in Indonesia, 0.5 million ha in Bangladesh, 1 million ha in Sri Lanka, and 1.4 million ha in Kerala, India (Kumar and Nair, 2004).

Over the past forty years, traditional homegardens have been subjected to further scientific development throughout the globe and are currently referred to as multi-strata agroforestry. Coffee (*Coffea* spp.) cultivation covers 11 million hectares, involves 10 million farmers yielding 22 million tons of green coffee annually. Coffee production impacts the livelihoods of 125 million people. Cocoa (*Theobroma cacao*) cultivation covers 10.2 million hectares, includes 10 million cocoa farmers who produce 4.5 million tons annually. Cocoa production impacts the livelihoods of 40–50 million people. Globally, almost 50% of coffee and 30% of cocoa is cultivated under shade in multi-strata agroforestry systems by smallholder farmers (Somarriba and Lopez-Sampson, 2018). In addition to these crops, many other well-known perennials, such as black pepper (*Piper nigrum*), vanilla (*Vanilla fragrans*), along with lesser-known crops including Yerba mate (*Ilex paraguariensis*) and cupuazú (*Theobroma grandiflorum*) are typically grown under shade trees in multi-strata agroforestry systems (Somarriba et al., 2001). Multi-strata agroforestry systems help to address SDGs by providing environmental integrity, carbon sequestration, biodiversity conservation, economic valuation of intangible benefits, and social equity. In terms of complexity and species diversity, homegardens and multi-strata agroforestry systems represent

a unique set of ecological sustainability characteristics of natural systems as well as production benefits of agricultural systems. Nutrient cycling within multi-strata systems, a consequence of species diversity, further benefits ecological sustainability (Nair and Kumar, 2006).

Temperate Zone Anthrome (Silvopasture, Alley Cropping—Silvoarable)

Large parts of North America and Eurasia have similar biomes. All of these areas share similarities in precipitation, temperature, elevation and latitude. The Eastern USA along with parts of Eastern Canada, Western Europe, a large part of Eastern China, Korea and Japan contain large areas of the temperate broadleaf and mixed forest biome (Whittaker, 1975). In addition, the temperate broadleaf and mixed forest biome is found in Australia, New Zealand, Chile and Argentina. These biomes are dominated by broad leaved deciduous trees but also containing conifers. The temperate broadleaf and mixed forest biomes Temperature deciduous forests occur in mid-latitudes where cool winters, warm summers, and high year-round precipitation occurs. These regions have long growing seasons (4 to 6 frost free months) and precipitation either distributed evenly throughout the year or peaking in the summer (Walter, 1985) (Fig. 2).

China has practiced agroforestry for many centuries (You, 1991; Zhu et al., 1991). Orchards and mixed farming agroforestry practices were widely utilized throughout many parts of Europe from Roman times up to World War II (Lelle and Gold, 1994; Eichhorn et al., 2006). Historically, Native Americans, across what is now the United States and Canada, have been practicing indigenous forms of what could be termed landscape-scale agroforestry for millennia (Rossier and Lake, 2014). In Europe and elsewhere, specific differences arise due to a patchwork of many countries, each with different land use practices and traditions in agriculture, forestry, and agroforestry (Eichhorn et al., 2006; Dupraz et al., 2018).

Five agroforestry systems are commonly found in the USA and Canada, and of these five, two are commonly found across most regions of the temperate zone. Due to climatic similarities across temperate regions, combined with related economic infrastructure, alley cropping (silvoarable) and silvopasture practices are common throughout the temperate zone (Gordon et al., 2018). Temperate zone agroforestry is defined as: intensive land-use management that optimizes the benefits (physical, biological, ecological, economic, and social) from biophysical interactions created when trees and/or shrubs are deliberately combined with crops and/or livestock (Gold and Garrett, 2020).

As mentioned, two agroforestry systems in particular, silvopasture and alley cropping (silvoarable) are common to all areas of the temperate zone (Gold and Hanover, 1987).

Alley Cropping (Silvoarable)

A key advantage of food-producing agroforestry systems is that they are more resilient to climate stressors than are annual cropping systems. Compared to temperate zone annual crop monoculture production practices, integrated tree and crop practices, that is, alley cropping, can increase land use efficiency through improved overall yields compared to separate production of trees and crops in monocultures (Wolz et al., 2017). Agroforestry systems can diversify farm portfolios, spread risk and increase both the economic and environmental resilience of farms (Krebs and Bach, 2018). In addition, alley cropping can increase ecosystem resiliency by buffering against weather extremes, diversifying income as a hedge against financial risk, increasing biodiversity, reducing soil erosion and improving nutrient- and water-use efficiency (USDA-FS, 2017).

Alley cropping (silvoarable) systems consist primarily of timber, nut or fruit trees intercropped with arable crops. Alley cropping systems combine trees planted in single or multiple rows with agricultural or horticultural crops cultivated in the alleyways between the tree rows. When specialty crops such as herbs, fruits, vegetables, nursery stock, or flowers are grown in the alleys, the microclimate created by the trees enables the economic production of these sensitive high-value crops in stressed environments.

In the USA, high-value nut or acorn-producing hardwoods such as walnut (*Juglans* spp.) (Scott and Sullivan, 2007; Cardinael et al., 2015), chestnut (*Castanea* spp.) (Wilson et al., 2018), pecan (*Carya illinoensis* (Wangenh.) K. Koch.) (Kremer and Kussman, 2011), hazelnut (*Corylus* spp.) (Molnar et al., 2013) and oak (*Quercus* spp.) (Eichhorn et al., 2006) are the favored species in alley cropping practices (Gold 2019). Typical intercrops include corn, soybean, winter wheat and oats (Wolz et al., 2017).

In the United Kingdom, silvoarable agroforestry (alley cropping) often takes the form of orchard intercropping with fruit trees or nut trees and involves a horticultural component in either the understory or the overstory. Tree rows provide income from the fruit (e.g., apples, pears, cherry), nuts (walnut, hazelnut, chestnut) and cropped alleys provide annual income. Intercrops include cereal commodity crops along with horticultural and/or root crops (Newman et al., 2018).

Intercropped fruit orchards are found in many parts of Europe. The total area is estimated to be around 1 million hectares in 11 countries stretching from northern France, Switzerland, Austria through Germany and reaching up to northern European countries including Poland and Denmark (Herzog, 2000). In Europe, on the alluvial terraces of the Isère river new walnut plantations are intercropped with maize for the first years. It is sown very close to the trees, which stimulates tree height growth and restricts side-branching. Walnut growers follow the maize with winter wheat or barley for several seasons, which gives more space for the trees and makes it easier to prune them following the nut harvest (Mary et al., 1998).

Historically, in Italy, crops were very commonly planted among trees of various species in fields. Trees included fruit trees or olive plantations, or trees like ash, maple (*Acer* spp.) and elms. They were used as trellis for grapes and would also provide forage

and biofuel for fires and ovens and twigs for basketry. When fields were not sown with cereals or forage crops they would be grazed. At present, olive plantations are intercropped with cereals or forage crops, as olive plantations are long lived wide spacing between trees. Research on modern olive alley cropping systems combines olives with other crops, and uses chickens to weed and fertilize the trees and the crop (Rosati et al., 2009).

In the temperate region of China, alley cropping systems based on paulownia (*Paulownia* spp.) intercropped with grains (e.g., winter wheat), oil crops, vegetables, medicinal herbs and melons are the most commonly practiced agroforestry systems. In addition, Chinese date (*Ziziphus jujuba*) intercropped with agricultural crops has a long history and is widely practiced. Intercropping with apple (*Malus* spp.), peach (*Prunus persica*) and pear (*Pyrus* spp.) has also been widely adopted since the 1970s and intercropping of crops with ginkgo (*Ginkgo biloba*), or maidenhair trees, has also been developed (Chang et al., 2018).

Silvopasture

Silvopasture systems involve the use of timber, nut, or fodder trees with pasture and/or range and livestock (e.g., cattle, sheep, goats) using managed intensive rotational grazing practices. Integrating trees, forage crops, and livestock creates a system that produces a constant flow of marketable products while maintaining long-term productivity. Economic risks are reduced because livestock and forest components require different inputs, share few common diseases and pests, and sell into different markets. In addition, silvopasture systems are visually desirable within rural landscapes. There is evidence that humans have an evolutionary predisposition to prefer savanna-type landscapes to forests (Balling and Falk, 1982). Integrated forest grazing systems often have a normal forest structure and an open grassy understory similar to early successional plant communities of native forests. Rows of pruned pine trees in silvopastures with a well-groomed pasture understory are open and park-like.

Given the widespread co-occurrence of grazing and forestry across North America, intensive and integrated production of livestock and tree products is the most prevalent form of agroforestry found in the United States and Canada. The most commonly practiced forms of silvopasture in North America are integrated forest grazing and silvopastures. Integrated forest grazing uses livestock to harvest native forest plants as part of a planned forest ecosystem management system. Private land holdings in the eastern and central portions of the United States often include woodlots or non-industrial forests which are grazed by livestock. The largest blocks of grazed, privately-owned industrial and non-industrial forests are found in the southern and southeastern United States (Pent et al., 2020).

Silvopasture has been common in Europe since the Neolithic period to graze sheep, goats, pigs and cattle both within forests and on wood pastures outside the forest (Pinhasi et al., 2005). This is still common in many parts of Europe. Historically, a wide range of species were retained in wooded pastures, with species producing edible fruits being most common. Species included oaks (*Quercus* spp.), beech (*Fagus* spp.), lime (*Tilia* spp.), ash (*Fraxinus* spp.), sycamore (*Acer pseudoplatanus*), chestnut (*Castanea sativa*), hornbeam (*Carpinus* spp.) and some fruit trees (pear (*Pyrus* spp.), cherries and plums (*Prunus* spp.), apple (*Malus* spp.)). Trees were often left in pastures and agricultural fields, where they did not interfere with manual cultivation techniques and provided shelter and feed for animals (Hartel et al., 2015).

The southern beech, (*Nothofagus antarctica*) one of the main deciduous native species in Patagonia, Argentina, covers ~750,000 hectares. This region is where much of the silvopastoral activity is concentrated. Roughly 70% of native southern beech forest in Patagonia has been used as silvopasture systems. Sheep and cattle are the primary livestock species grazed under the southern beech (Peri et al., 2018).

Components of the System

Similar to the situation in tropical biomes, temperate agroforestry systems share “key agroforestry ideotype combinations” where functional attributes of the components (i.e. mixtures of deep- and shallow-rooted tree species, legumes and non-legumes, etc.) are similar across the temperate zone.

Alley Cropping

Alley cropping can be viewed as recreating the structure of a savanna in an agroforestry system with multiple canopy layers consisting of a design that contains an overstory of nut trees, mid-layer of fruiting small trees and shrubs, and a groundcover of annual crops or perennial grass groundcover. In nut-based agroforestry systems, crops grown in the alleys between tree rows provide annual income while the longer-term nut crop matures. Primary agroforestry and alley cropping design criteria include imitation of the structure and function of natural ecosystems with species that generate an economic yield to support the farmer (Krebs and Bach, 2018).

Growers planning to farm between tree rows need to think about the width of their alleyways. Between-row spacing is primarily determined by machinery width, mature size of nut tree species, with secondary considerations for sunlight requirements of the alley crop. With closer spacing, the intercrop grown in the alley will encounter light competition at an earlier age, requiring a more rapid change to shade-tolerant intercrops (Wilson et al., 2018). Wider spacing makes intercropping easier but delays the fullest realization of economically viable nut crop yields.

Recommended principles for designing the cropping system based on this approach include selecting species for complementary functional traits, developing complex trophic levels and reproducing ecological succession (Malézieux, 2012). Trait-based agroecology has emerged as one of the dominant paradigms in terrestrial ecology (Martin and Isaac, 2018). Studies that evaluate the complex linkages between functional traits, functional diversity and ecosystem functioning have recently begun to explore concepts surrounding “multifunctionality,” the idea that multiple ecosystem functions should be considered as a management goal. Multifunctionality has clear implications for trait-based agroecology and for agroforestry, where land managers manipulate on-farm diversity to enhance ecosystem services beyond yield alone (Finney and Kaye, 2017).

Silvopasture

Silvopasture is an agroforestry practice that intentionally integrates trees, forage crops, and livestock into a structural system of mutually supportive planned interactions. These interactions are managed intensively to simultaneously produce wood or non-timber forest products, high quality forage, and livestock on the same land unit in an environmentally sustainable manner. The forage component may be either native forage plants or introduced species managed as an improved pasture. This more intensive approach to land use provides the foundation for integrated commercial timber and livestock production systems (Pent et al., 2020).

While alley cropping combines two components, trees and crops, silvopasture deliberately integrates three components: trees, understory vegetation, and domestic livestock. Trees and livestock are combined with improved pasture plants to form carefully designed systems that integrate intensive animal husbandry, silviculture, and forage agronomy. Livestock become tools for managing forest trees and their understory plant communities for multiple outputs or outcomes, including timber, forage, wildlife habitat, fire fuels reduction, and improved water quantity and quality. Skillful selection of forage plants and manipulation of micro-environments within silvopastures can result in high quality green feed available for livestock, while providing them with shelter during inclement weather (Pent et al., 2020).

Most ruminant livestock species are viable candidates for temperate zone silvopasture including cattle, sheep and goats. Chickens are also an option. Pigs must be very carefully monitored to avoid damage to trees and understory forages. There are two main approaches to silvopasture systems: (1) Establishing trees within existing pasture lands; (2) Thinning native forest stands to support the growth of pasture for forage (Gold and Garrett, 2020).

Understanding the phenology and morphology of tree and grass species, or their growth over time, can aid in the selection of complementary components of a silvopasture system and the proper management of competitive tree-forage interactions. Silvopasture influences ecosystem processes of hydrology, nutrient cycling, energy flow, and succession primarily through manipulation of community structure. The basic strategy combines trees, forages, and livestock such that each component produces usable products and contributes to stability and conservation of land resources. These systems also can contribute to enhanced aesthetics and outdoor activities. While management intensity may be high, silvopasture systems require lower external inputs of nutrients or pesticides than open pastures (Pent et al., 2020).

Arid/Semi-Arid Tropical Anthrome (Improved Fallows, Farmer-Managed Natural Regeneration, Evergreen Agriculture)

In the semi-arid and sub-humid zones of West Africa, known also as the savanna woodland biome, farmers have for many generations maintained a traditional land-use system, known as the agroforestry parklands system, which is characterized by the deliberate retention of trees on cultivated or recently fallowed land. Trees are an integral part of the system, providing food, fuel, fodder, medicinal products, building materials and saleable commodities, as well as contributing to the maintenance of soil fertility, water conservation and environmental protection (Boffa, 1999).

The savanna woodland biome occurs widely in tropical and subtropical regions including some Caribbean islands, Brazil and northern Argentina, east and central Africa, portions of India and China, northern and eastern Australia. Compared to the more mesic tropics, it is found where the dry period is more prolonged and the annual rainfall is less than in true closed forest. Trees are widely scattered, usually leafless during dry season and vegetation is usually rich in herbs (especially grasses). Trees are commonly stunted to the size of tall shrubs, usually less than 60 feet high at best with flattened crowns. Many of the trees belong to the legume family (Fabaceae) (Boffa, 1999).

Improved fallows and farmer-managed natural regeneration (FMNR) are practiced widely across sub Saharan and other semi-arid regions of Africa, India, the Caribbean, Mexico and Central America. In particular, in many parts of Sub Saharan Africa, farmers use improved fallows as a strategy for improving soil fertility within a shorter time-period, compared with natural fallow. Improved fallows are an agroforestry technology consisting of planting legume tree and/or shrub species in rotation with cultivated crops. These improved fallows contribute to food security, climate change mitigation and adaptation, and sustainable conservation of natural resources (Partey et al. 2017). When the fallow period ends, trees, shrubs, and/or herbaceous legumes are cut down or coppiced and the resultant biomass (leaves, twigs, branches) is incorporated into the soil while the land is prepared for the following crop. Legume species improve the soil through biological nitrogen fixation in which recycled nutrients are deposited through litter or when biomass is harvested at the end of the fallow period and incorporated into the soil. Improved fallows are

recognized as cost-effective and a viable alternative to inorganic fertilizers. Evidence of improved soil fertility and increased crop productivity with improved fallows have been observed across sub-Saharan Africa (Partey et al. 2017).

The most well described and widely promoted agroforestry practice in Sub Saharan Africa centers on *Faidherbia albida*. Over 60 years ago scientists observed that farmers throughout the Sahelian region of Africa were retaining their *Faidherbia* trees in their sorghum and millet fields (Barnes and Fagg, 2003). The species has long been an integral part of Sahelian agriculture, where farmers have nurtured and protected the trees growing in their fields for centuries. The trees are a frequent component of the farming systems of Senegal, Mali, Burkina Faso, Niger, Chad, Sudan, and Ethiopia, and in parts of northern Ghana, northern Nigeria, and northern Cameroon (Boffa, 1999). There are many reports of substantial increases in the grain yield of unfertilized millet grown under *Faidherbia* in West Africa (Barnes and Fagg, 2003). Increases in yield have also been reported for sorghum grown under *Faidherbia* in various parts of Ethiopia, other parts of Africa, and in India. The deliberate expansion and promotion of the traditional *Faidherbia* agroforestry system is currently known as Evergreen Agriculture, defined as the integration of selected tree species into annual food crop systems (Garrity et al., 2010).

The use of farmer-managed natural regeneration (FMNR) has enabled a major “regreening” to take place in the Sahel in recent decades. In southern Niger alone, following two decades of drought and famine in the 1970s and 1980s with massive losses of crops and livestock, human outmigration and mortality, over 5 million hectares of farmlands have “regreened” (Pye-Smith, 2013). This has improved crop and livestock productivity and enhanced the resilience of these agricultural systems to drought and temperature extremes in the face of climate change. The practice of FMNR of trees on farmlands is accelerating across the Sahel. At present, trees occupy 16% of the total area of croplands in the semi-arid and subhumid zones of the Sahel (Brandt et al., 2018), and 23% in the West Africa savannas. Nearly 100% of this tree cover is a result of the practice of FMNR by the millions of small-scale farmers of the region. FMNR has also gained in popularity in many dryland areas in western, eastern and southern Africa (Brandt et al., 2018).

Components of the System

Incorporating improved fallows includes the addition of fertilizer trees into the agricultural landscape. The term “fertilizer trees” is commonly used to refer to the utilization of N-fixing leguminous trees in cereal production systems to improve the availability of N to crops. Included among the widely used fertilizer trees in Sub-Sahara are acacia (*Acacia* spp.), albizia (*Albizia* spp.), calliandra (*Calliandra calothyrsus*), erythrina (*Erythrina* spp.), faidherbia (*Faidherbia albida*), flemingia (*Flemingia* spp.), gliricidia (*Gliricidia sepium*), inga (*Inga edulis*), leucaena (*Leucaena* spp.), and sesbania (*Sesbania* spp.) (Sileshi et al., 2014). Impacts include restoration of soil fertility and promotion of the biological processes and ecological functions that, taken together, rehabilitate degraded land and increase crop yields. In terms of increased crop yields, synergistic effects of synthetic fertilizer and fertilizer trees have been documented. Substantial yield increases from fertilizer trees have been demonstrated with many crops including maize, millet and sorghum even at 25–50% of the recommended dosages of synthetic fertilizer. Key to the success of improved fallows are nutrient cycling, increased availability of macronutrients (extractable N, P, and K), cations and improvement in soil pH, increased organic matter (SOM), enhanced biological activity, improved soil physical properties, and better water relations (Sileshi et al., 2014).

In Evergreen Agriculture, vegetative soil cover is maintained throughout the year by the deliberate intercropping of trees in order to sustain a green cover on the land throughout the year. This approach increases nutrient supply through nitrogen fixation and nutrient cycling, generates increased quantities of organic matter in soil surface residues, improves soil structure and water infiltration, enhances carbon storage both above- and below-ground, induces more effective conservation of above and below-ground biodiversity and increases the direct production of food, fodder, fuel, fiber and income from products produced by the intercropped trees (Garrity et al., 2010).

Farmer-managed natural regeneration (FMNR) involves identifying and protecting the naturally regenerating seedlings of trees and shrubs that establish themselves on farmlands. It is dependent upon the presence of living root systems and seeds. Shoots from existing roots grow more rapidly than saplings from seed because of better- and well-established root systems, and make up the bulk of the protected woody stems on farms in southern Niger. Farmers generally choose one to five of the strongest stems from stumps they wish to retain on their land and pruning away the remainder. These stems are managed to grow into full canopy trees that can be harvested to provide fruits, medicine, gum, oil, firewood, timber. In addition, they provide foliage used as fodder for meat and milk production, tree nectar for honey, and tree leaves as biofertilizers for improved soil health and crop production. Favored species vary from place to place along with the density of the trees in the crop fields with densities ranging from 40 to 150 trees per hectare (Garrity and Bayala, 2019).

Species commonly found in FMNR in the African drylands include the baobab tree (*Adansonia digitata*), which provides nutritious fruits and leaves; the shea tree (*Vitellaria paradoxa*) that provides butter used in cooking, in chocolate and cosmetics; gum arabic (*Acacia senegalensis*) that provides a gum used in many food items; and as previously mentioned, *Faidherbia albida*, which enriches soils and provides valuable pods and foliage for fodder (Garrity et al., 2010). Trees on farmlands provide another significant stream of benefits including soil and water conservation and a more favorable microclimate for crops to withstand wind and heat and drought stress (Bayala et al., 2014).

Summary

Agroforestry incorporates an array of successful strategies that already exist across the globe spanning many biomes (Nair et al., 2017; Van Noordwijk et al., 2019a). Biodiversity-based management of working lands, including agroforestry, has been practiced since ancient times and their value has been recognized, updated and promoted across our global biomes over the past forty years. Some of these management systems, such as home gardens, indigenous use of fire, selective retention of array of trees, shrubs, food and medicinal crops no longer exist in their original form, whereas others, such as silvopasture and multi-strata farming systems, persist in many different biomes. These biodiversity-based working land management practices are knowledge, rather than technology, intensive (Wiersum, 2004). Agroforestry systems, multifunctional land management strategies found throughout the world across temperate and tropical biomes, represent a major opportunity to ensure sustainable production of food and fiber along with the ecological heritage of the planet (Ellis, 2013; Nair et al., 2017; Kremen and Merelender, 2018; Udawatta et al., 2019).

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The Argentine Pampas: A Novel Ecosystem at the Crossroad

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Abstract

The Pampas plains were originally covered by grassland communities modulated through the millennia by a combination of rainfall, temperature and small topographic gradients. The anthropic intervention historically modified pristine structures and functions giving rise to a novel ecosystem that was reoriented to produce food, fiber and bio-energy. From the beginning of the 20th century, the quick expansion of agriculture on natural lands and the intensification of agricultural practices triggered big ecological changes that altered the stocks and fluxes of carbon and the hydrological processes as well. Carbon and water were closely linked to the provision of habitat for biodiversity and the supply of regulation ecosystem service. Inevitably, ecological functions associated with carbon and water were profoundly modified the anthropic intervention, but conservation practices and technology incorporation in the last decades smoothed and even reversed the most outstanding negative trends. It is well known today that a return to the pristine condition will no longer be possible in the Argentine Pampas because of social and economic reasons, but an adaptive, science-based management helps maintaining the agricultural productivity preserving at the same time novel biodiversity assemblages and new configurations of ecosystem service provision.

Should the Pampas Be Considered a Novel Ecosystem?

Human activities have deeply altered land cover patterns through conversion to croplands and pastures (Tilman et al., 2001; Foley et al., 2005; Ellis et al., 2010) particularly affecting temperate grasslands worldwide (Ramankutty et al., 2008). The Argentinean Pampas biome has not escaped this conversion. In 1774 Thomas Falkner described the Pampa as “One immense sea of grasslands, with scattered forest islands...” (Ghera and León, 2001). With this statement he transmitted the perception of the native inhabitants and the reasons why this landscape is named “Pampas” (in the natives’ language Quechua “Pampa” means “uniform extensive plain”). Since then, Pampean grasslands have been severely modified by human activities.

Taking advantage of the diversity of soils, climates and landscape, these transformations of the vegetation and the use of land occurring in the Pampas biome were extended to the bordering biomes. In this sense, it is convenient to distinguish those changes of wide geographical distribution such as deforestation and establishment of agricultural crops in dry forests of the Chaco and Espinal along with the progress of livestock. This plays an important role on the services provided by their ecosystems (Jobbagy, 2011). Only small corridors of remnant grassland survive within the matrix (Bilenca and Miñarro, 2004). Hence, grassland fragmentation (Baldi et al., 2006), plant invasions (Poggio and Mollard, 2010) and reductions in area of remnant grassland (Burkart et al., 2011) may lead to the generation of novel ecosystems (Hobbs et al., 2013). This diversity of ecological land cover patterns created and sustained by human populations also links human and natural systems (Ellis and Ramankutty, 2008). This is most relevant in novel ecosystems, like the Pampas agro-ecosystem where new combinations of species and abiotic conditions make the outcome of management even less predictable (Hobbs et al., 2013).

The Pampas biome is a 60 Mha plain located in the center of Argentina between 57°W and 68°W and 28°S and 40°S (Fig. 1). Several subunits are recognized based on geomorphology, drainage, geology, physiography, soils and vegetation (Cabrera, 1951; Soriano et al., 1991).

The Pampas are climatically considered as a warm temperate region, with a mean temperature ranging from 14 °C in the South and the isotherm of 18 °C delimiting the North, and humid, with annual rainfall ranging from 500 mm in the West to 1200 mm in the East (FAO, 2006). This region has shown a significant change in precipitation in the last century (Giorgi, 2002) with an increase

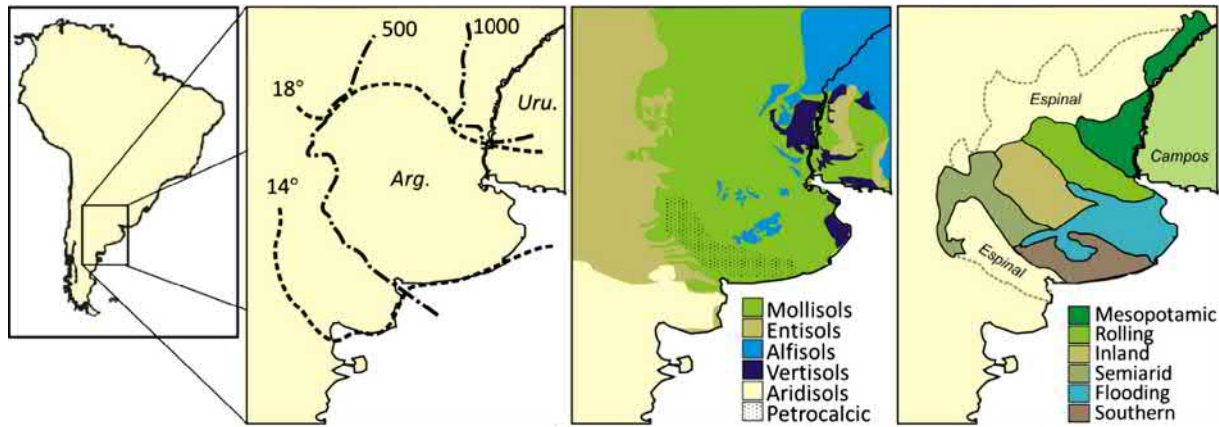


Fig. 1 Climatic and edaphic characteristics and sub-regions of the Pampean biome. Own elaboration with data from FAO (Food and Agriculture Organization). (2006). *LocClim local climate estimator version 1.10*. Rome: FAO/SDRN; Moscatelli, G. (1991). Los suelos de la Región Pampeana. In Barsky, O. (ed.) *El desarrollo agropecuario pampeano*, 1st edn., pp. 1–76. Buenos Aires: INDEC-INTA-IICA; Berhongaray, G. (2010). *Carbono en suelos pampeanos: efectos de la vegetación y el uso*. M.Sc. Thesis. 113 p.; Cabrera, A. L. (1951). Territorios fitogeográficos de la República Argentina. *Boletín de la Sociedad Argentina de Botánica* 4, 21–65.

in annual values from the 1960s (Minetti et al., 2009). Furthermore, the increase has been particularly marked near the western margin of the Pampas, displacing westward the transition to semi-arid regions that represent the boundary of rainfed agriculture (Viglizzo et al., 1995). Nevertheless, there is still a considerable uncertainty about the future climatic conditions.

The region is considered a hyperplane (Jobbagy et al., 2008), a flat or slightly rolling with Mollisols as predominant soils (Moscatelli, 1991), formed on loess-like materials (Alvarez and Lavado, 1998). Because of the eolian origin of sediments from Southwest to Northeast and the climatic rainfall gradient from West-East, the depth and texture of soils varies from shallow and sandy in the West to deep and clayed in the East (Alvarez and Lavado, 1998; Berhongaray et al., 2013). The predominant clay mineral in the region is illite (Alvarez and Lavado, 1998). Within the upper 1 m of the soil profile a petrocalcic horizon appears in many soils along the West and the South ends of the region (Teruggi, 1957). Soil organic carbon is strongly associated to rainfall (Berhongaray et al., 2013). Conversely, soil pH is not climate regulated, with a range from 6 to 9, and no signals of acidification by cultivation have been detected (Berhongaray et al., 2013). High pH values are usually associated to hydromorphic lands (Hall et al., 1992).

This anthrome supports one of the largest temperate grasslands on the globe and has undergone major changes since the 16th century on it (Matteucci, 2012). A traditional plant vegetation approach defined the Pampas as a vast of humid and sub-humid grassland (Baldi and Paruelo, 2008) in which graminaceous species predominate, with some minor areas occupied by natural forest that cover 7% of the total surface (Cabrera, 1994). Ecologically, the Pampas is limited in the northern and western margin with the eco-region of Espinal. The Espinal portion extends irregularly from the center of province of Santa Fe, northeastern Córdoba and northern Entre Ríos and supports remnant xerophilic woodlands dominated by *Prosopis*. These woodland remnants are isolated and immersed in an agricultural matrix.

Originally, only small groups of indigenous nomadic people inhabited the area before Europeans brought horses and cattle by the mid-16th century. While the indigenous people had probably used fire to facilitate hunting, it is assumed that both the fire and grazing regimes would have changed greatly since the introduction of livestock as well as the use of fires to herd the cattle and horses around 1600 (Soriano et al., 1991). The Pampas grasslands have experienced an especially high increase in agricultural production (Baldi and Paruelo, 2008), particularly of soybean since the 1990s, bolstering Argentina's role as a world-leading agricultural producer (Baumann et al., 2016). Today, the largest areas are sown with soybean as summer crop and wheat as winter crop followed by oats, corn, sunflower and natural or semi-natural grassland under cattle grazing (Lara and Gandini, 2014). Around 90% of the national grain production is carried out in this region.

While croplands occupy about 85% of the mosaic area, anthropic elements such as fencerows, roadsides, and woodlots, homesteads, water bodies and abandoned land, each one covering less than 1% of the remaining surface, which sustain most of plant diversity in agro-ecosystems, particularly native plants (Ghersa et al., 2012; Poggio et al., 2015). Water bodies and woodlots of foreign trees, a novel element introduced 150 years ago in the Pampas, are used as wind barriers occupying 0.2% of the area and are important drivers of bird and arthropods richness and abundance (Ghersa et al., 2012; Poggio et al., 2015). At the same time, this has triggered widespread loss and fragmentation of natural vegetation (Viglizzo et al., 2010) and an increasingly replacement of grazing land cropland (Gavier-Pizarro et al., 2012).

Historical Drivers of Landscape Change

The change in land use and cover through agricultural expansion (Goldewijk et al., 2017) and intensification through the increasing use of technology and external inputs, such as high yield crop varieties, fertilization, irrigation or pesticides (Adhikari et al., 2018),

have been the main historical drivers of changes in the world's biomes. Lands with agricultural aptitude in Argentina were no exception to this global trend. Regional change occurred both in terms of conversion of land for cultivation, as in the gradual intensification of agriculture (Viglizzo et al., 2011; Piquer-Rodríguez et al., 2018).

The Pampas, originally characterized by a treeless grassland where vegetation heterogeneity was determined by topographic and climate gradients, has a longer land-use history. Cattle ranching started in the 16th century with the arrival of the first European settlers (Giberti, 1954) and grazing became the main regulator of the structure and functioning of the native grasslands (Soriano et al., 1991). Due to the lack of fences protecting crops from grazers, workers and transportation, during the first centuries of colonization crops were cultivated only at small scales near villages (Sbarra, 1964). According to official records, the cropped area expanded since the end of the 19th century (Fig. 2, see Multimedia Video 1 in the online version at <https://doi.org/10.1016/B978-0-12-409548-9.12060-3> annexed) in response to the massive immigration, the spread of wired fences and the expansion of the railway network (Hall et al., 1992). Nowadays, the Pampas were mostly converted to cropping and pasture-based grazing areas. The modification of the landscape and the introduction of new organisms caused the creation of novel ecosystems (Viglizzo et al., 2001; Satorre, 2005).

Agricultural expansion was fast in the humid areas and slow in the sub-humid and semiarid ones. Rainfed crops were cultivated where annual rainfall is above 600 mm, on well-drained soils. Hydromorphic soils were used for grazing. The cultivated area increased 45% between 1990 and 2006, then expanding outside the Pampas regions. One-half of the cultivated lands was allocated to genetically modified soybean crops (Leguizamón, 2016). Currently 60% of the Pampas is under annual crop production, with soybean (*Glycine max* (L.) Merr.), wheat (*Triticum aestivum* L.), and maize (*Zea mays* L.) as major crops (Viglizzo et al., 2011).

The Pampas represented a large scale, long-term, and non-controlled experiment of low input farming (Viglizzo et al., 2001) until the 1990s, referring to systems that use reduced quantities of inputs such as fertilizers, agro-chemicals, irrigation, machinery, etc. (Matson et al., 1997). Nevertheless, since the beginning of the 1990s, the spread of an increasingly soybean-dominated agriculture was supported by no-tillage (Nocelli Pac, 2018), double soybean-wheat cropping, cover crops, and the increasing use the low-cost fertilizer and pesticide inputs (Gavier-Pizarro et al., 2012; Andrade et al., 2017; FAOSTAT, 2019), which allowed intensified cultivation schemes. As a result, the production of the main crop commodities in the region was quadrupled during the last 50 years (Fig. 3) (Secretaría de Agroindustria, 2019), allowing a more efficient use of water and nutrients in comparison to cultivation before the 1960s (Andrade et al., 2017; Piquer-Rodríguez et al., 2018). In particular, no-till gained ground quickly, and was an effective solution to the problem of soil organic matter loss due to erosion as it leaves a greater percentage of soil covered with plant residues (Fu et al., 2006). It meant to keep soil in its place and mainly keep the top layer which is the most fertile fraction. In line, because of fossil-fuel savings, no-till adoption drastically reduced greenhouse gases (GHGs) emissions (Neufeldt et al., 2015). The combined effects of those technologies explained yield increases in main crops (Fig. 4) reflected in the patterns of crop yield growth, stagnation, and collapse (Ray et al., 2012).

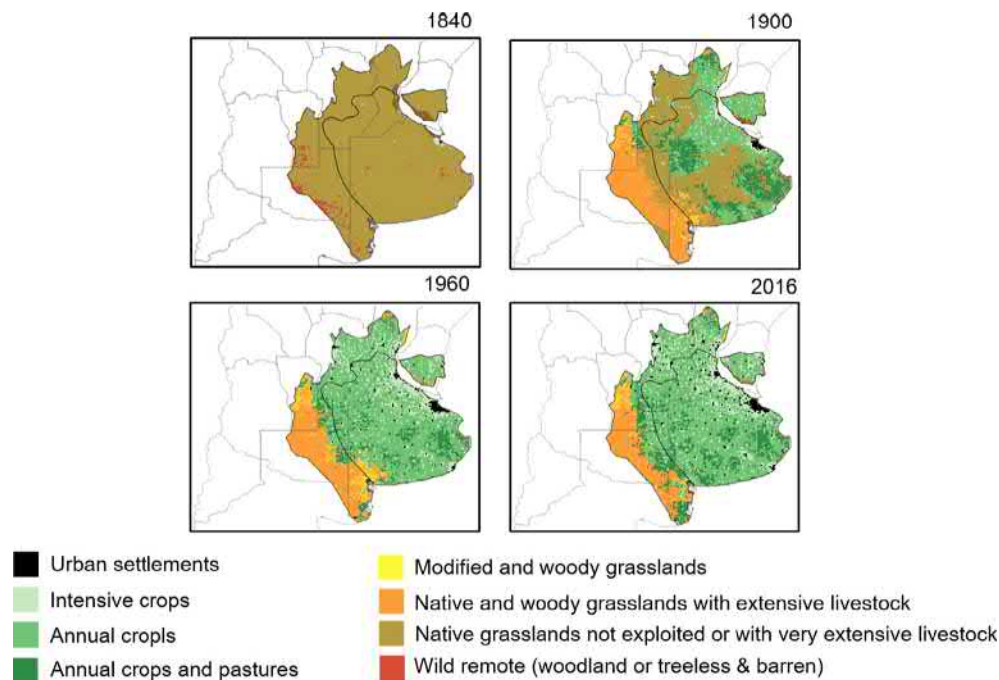


Fig. 2 Pampas anthromes evolution since the mid-nineteenth century. Own elaboration from Goldewijk, K. K., Beusen, A., Doelman, J., and Stehfest, E. (2017). Anthropogenic land use estimates for the Holocene—HYDE 3.2. *Earth System Science Data* 9, 927–953.

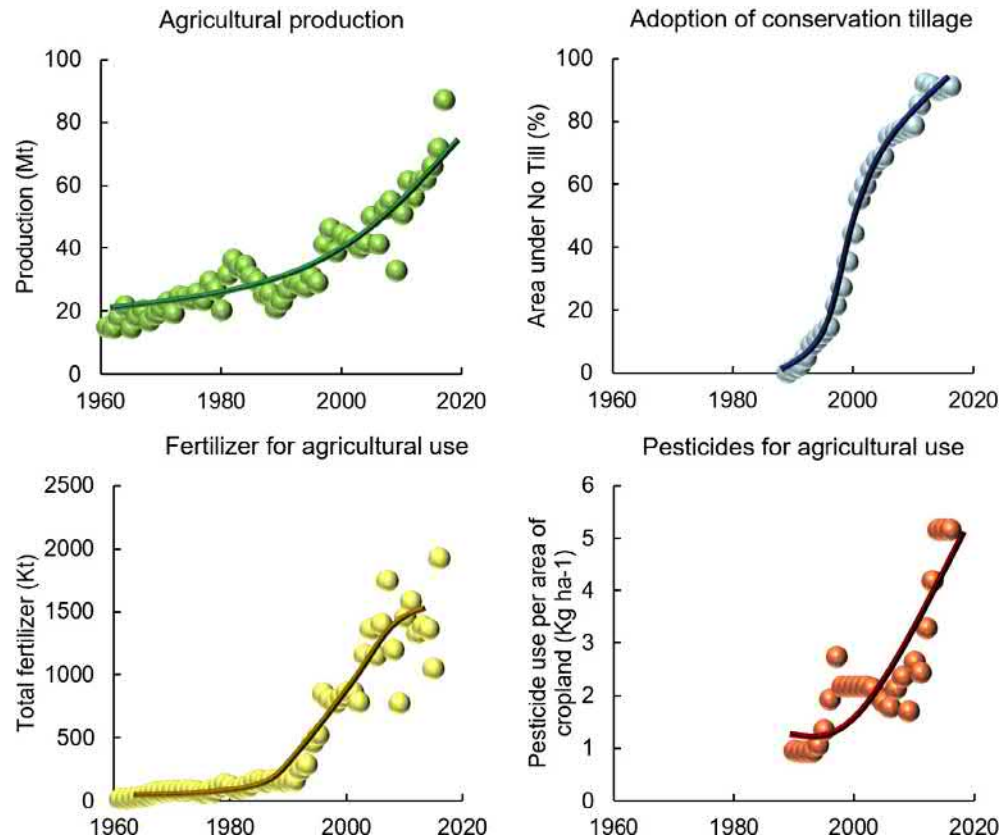


Fig. 3 Technological drivers of landscape change in the Pampas for half a century. Agricultural production represents values for the principal commodities produced in the Pampas region (maize, sunflower, soybean and wheat). Cultivation techniques represent the change from conventional tillage to no-till system. Fertilizer (all Nitrogen (N) and phosphate (P_2O_5) nutrients) and pesticides inputs are referred to national agricultural use. Own elaboration from Secretaría de Agroindustria. (2019). *Estimaciones Agrícolas*. Dataset. <<https://datos.agroindustria.gob.ar/dataset/estimaciones-agricolas>> Accessed: 22 July 2019; Nocelli Pac, S. (2018). *Update! Evolution of no till adoption in Argentina*. Buenos Aires: Aapresid; FAOSTAT. (2019). *Food and Agriculture Organization of United Nations Datasets*. <<http://www.fao.org/faostat/en/#data>> Accessed: 22 July 2019.

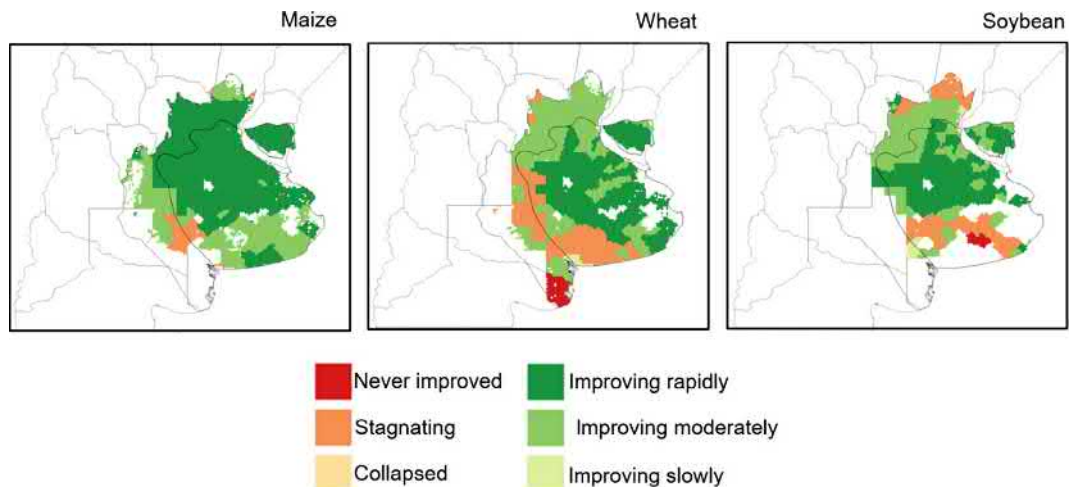


Fig. 4 Crop yield trends over the period 1961–2008. The trends were divided into the six categories and color coded. Maps show only those areas in the political unit where the crop was harvested. Own elaboration from Ray, D. K., Ramankutty, N., Mueller, N. D., West, P. C., and Foley, J. A. (2012). Recent patterns of crop yield growth, stagnation, and collapse. *Nature Communications*, 3, 1293.

The expansion of wheat, corn and sunflower in the 20th century, and the expansion of soybeans in 1990s displaced most ranching activities into the Espinal biome (Modemel et al., 2016; Viglizzo et al., 2011). Thus, large portions of natural lands historically used for cattle grazing were converted to row-crop production (Baldi and Paruelo, 2008). That conversion was probably strengthened by the outstanding adoption of technology innovations in crop production in contrast to technology incorporation in livestock production, which still remained relatively stagnant.

Carbon and Water Dynamics in the Pampas

GHGs Emissions and Carbon Balance

The rapid conversion of land affected bio-geochemical processes in general and the balance of GHGs in particular. The carbon balance can vary strongly when the analysis is scaled down from the region and the country to the agricultural system. For a comparative purpose, Figs. 5 and 6 show average estimates of carbon balance (emission minus sequestration) in livestock and crop production activities.

There are great variations between the compared systems. With the exception of extensive production schemes, livestock systems clearly tend to show higher emission rates per hectare than the crop production ones. Then, while the carbon balance tends to be positive in extensive, and negative in intensive cattle production systems, the negative balance tends to predominate in crop production systems with a probable exception in the case of high-yielding maize. However, setting aside the irrigated rice production (which shows high rates of carbon emission), it should be noted that the negative balance of crops is significantly less important than that of intensive livestock systems.

The carbon balance of the whole agricultural system will depend on the combination and proportion of land allocated to different farming activities. In the case of soybean, its rotation with agricultural activities that show higher capacity to sequester carbon will generate integrated systems with GHG emission levels that are lower than those of soybean monocultures. This notion may become relevant when farmers try to evaluate and certify production activities in terms of their carbon balance. A diversified production scheme where crops rotate may benefit the production system as a whole.

Carbon Losses and Gains in the Pampas Soils

When the natural vegetation is removed for cultivation, there is a decrease in the soil organic carbon content, which was observed in the soils of the Pampas. That loss of soil carbon was greater in early years and was greater in the soils of the humid portion, with high original soil carbon content, than in the soils of the semiarid portion, with less soil carbon content (Fig. 7). The causes of the decrease in the soil carbon levels were the soil erosion and the negative carbon balance between the carbon inputs from crop residues and the loss of carbon as CO_2 from soil organic matter decomposition. In recent years it was observed that this tendency

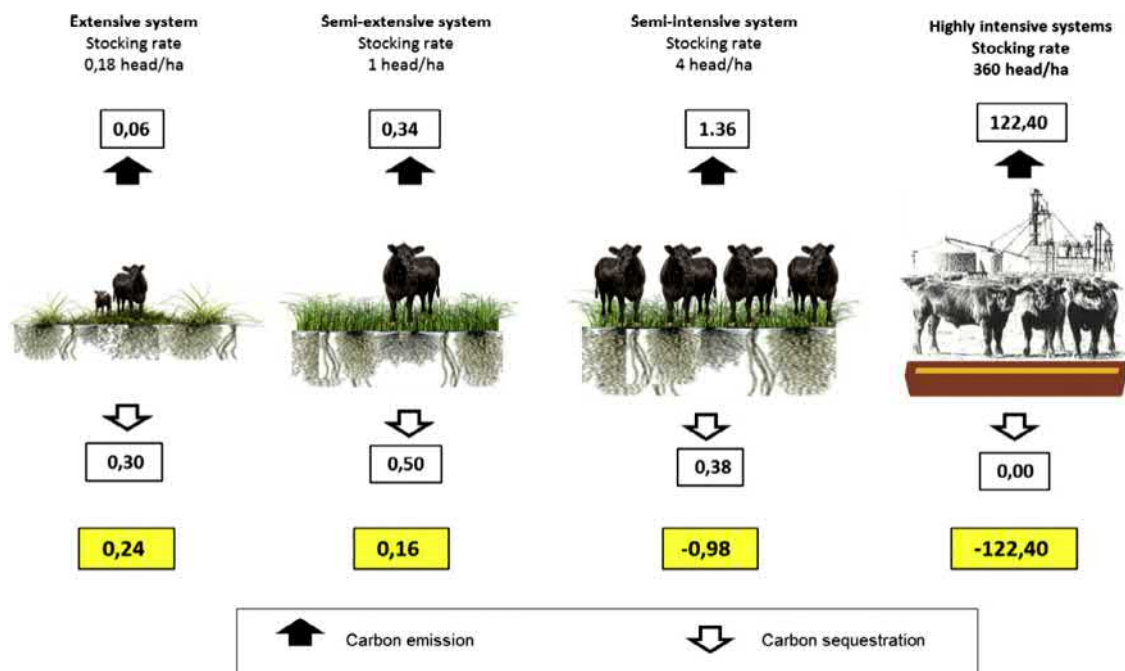


Fig. 5 Estimated figures show the difference of carbon emissions, soil carbon sequestration and carbon balance ($\text{ton ha}^{-1} \text{ year}^{-1}$) between four beef production systems that differ in their intensification level. Negative figures indicate that carbon emission is greater than carbon sequestration.

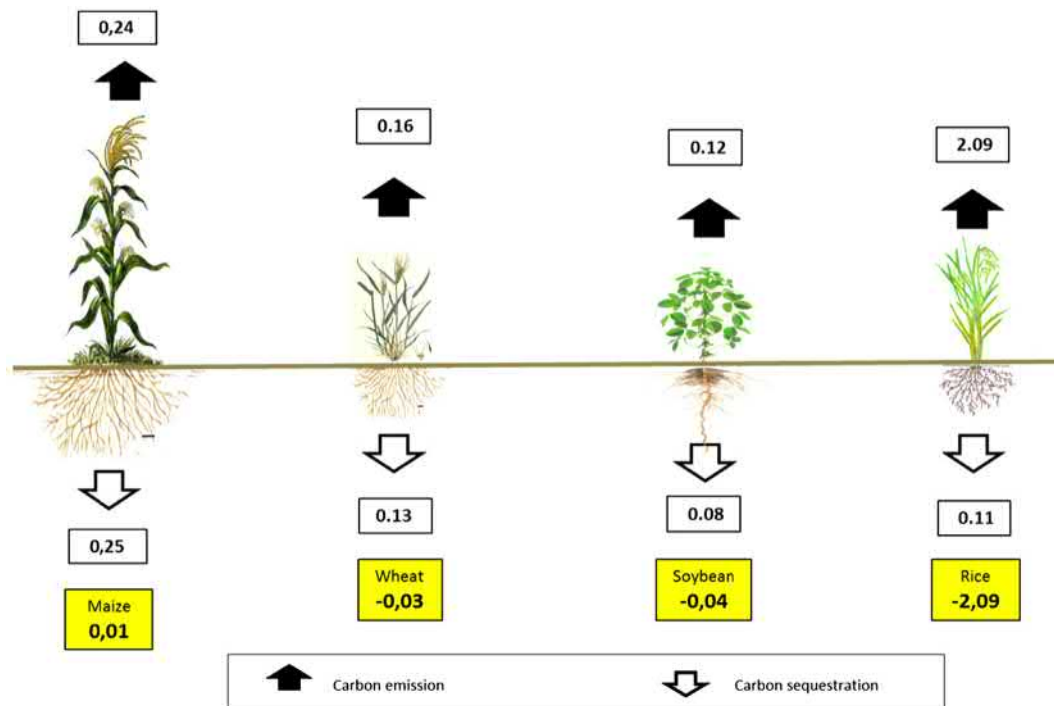


Fig. 6 Estimated figures show the difference in carbon emissions, soil carbon sequestration and carbon balance (ton ha⁻¹ year⁻¹) between four crop production systems that are spread in South America. Negative figures indicate that carbon emission is greater than carbon sequestration.

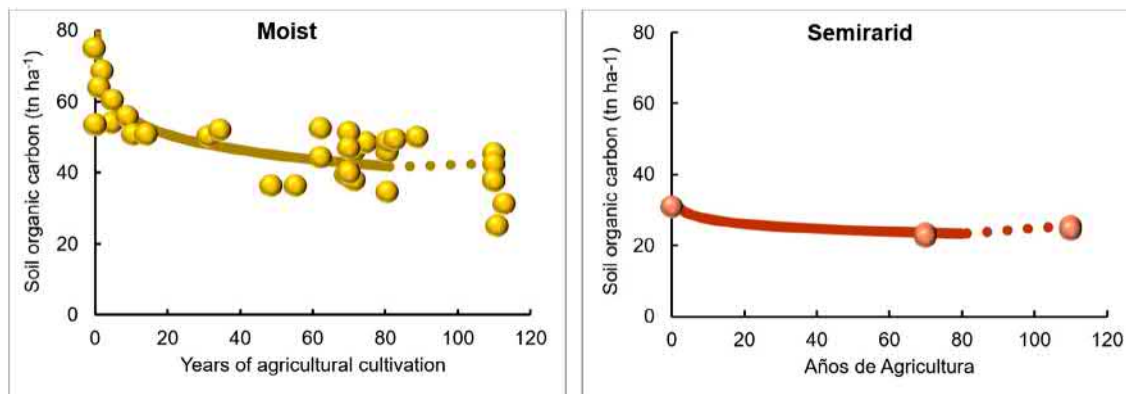


Fig. 7 Soil organic carbon loss in the Pampas during 120 years of agricultural crops. References: *Full line* represents the changes occurred in systems under conventional tillage. *Dotted line* represents the changes due to agriculture into no-till system. Own elaboration from Andriulo, A. and Cordone, G. (1998). Impacto de labranzas y rotaciones sobre la materia orgánica de suelos de la región pampeana húmeda. In Panigatti, J.L., Marelli, H., Buschiazzi, D. and Gil, R. (eds.) *Siembra directa*, 1st edn, pp. 65–96. Buenos Aires: INTA y Hemisferio Sur SA; Berhongaray, G., Alvarez, R., de Paepe, J. L., Caride, C. and Cantet, R. J. C. (2013). Land use effects on soil carbon in the Argentine Pampas. *Geoderma* **192**, 97–110; Alvarez, R., Steinbach, H., and de Paepe, J. L. (2015). Carbono Orgánico. In Alvarez, R. (ed.) *Fertilidad de suelos y fertilización en la Región Pampeana*. 1st edn, pp. 47–91. Buenos Aires: Editorial Facultad de Agronomía.

was attenuated or reversed in the Pampas through the adoption of technology and good agronomic practices (Alvarez et al., 2015; Andriulo and Cordone, 1998). Those soils with an initial high level of soil carbon are slowing down their loss, and those with initial low levels of soil carbon are even increasing its level. Despite of the gradual reduction of perennial pasture and the higher proportion of soybean in crop rotations, the carbon inputs increased by increases in the crop yields (genetic improvement and fertilization) and due to the incorporation of the no-till as a generalized practice. Additionally, in the last decades an increase in rainfall also contributed to higher yields and carbon inputs, especially in the semiarid lands.

Soil carbon losses were similar in most sub-regions, 27%–28% reduction in soil carbon stock, except for the Southern and Flooding Pampas where losses were much lower (Fig. 8) (Berhongaray, 2010). The Flooding Pampa is a large sub-region for livestock production, where the production system is based on the use of natural grasslands. Few croplands are found in this sub-region,

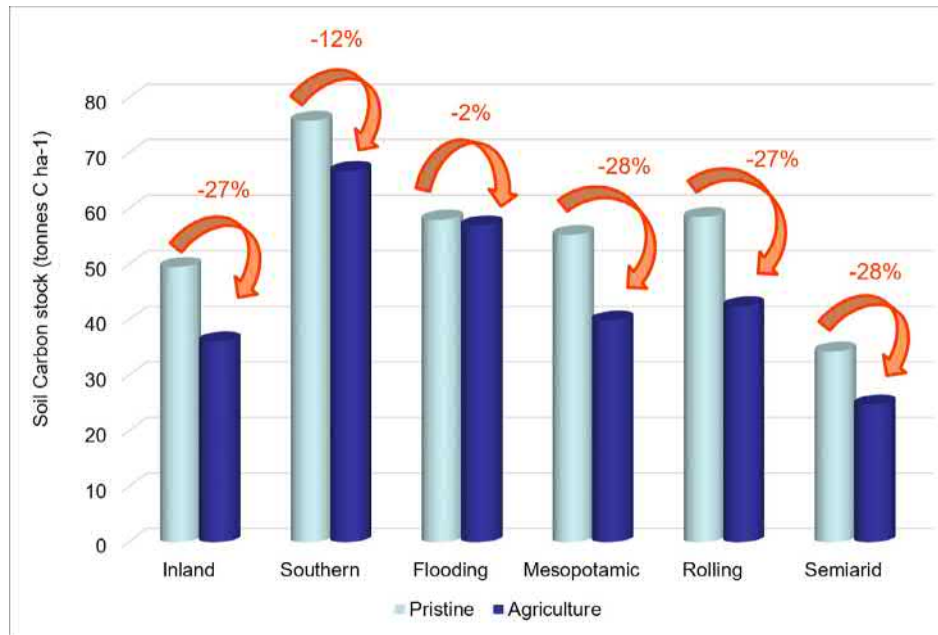


Fig. 8 Soil carbon stock in natural remnants and croplands (equivalent soil mass of 3000 t ha^{-1}) of different sub-regions of the Pampa biome. Own elaboration from Berhongaray, G. (2010). *Carbono en suelos pampeanos: efectos de la vegetación y el uso*. M.Sc. Thesis. 113 p.

and land use conversion was less significant than that of the rest of the Pampas. Therefore, this sub-region remained almost isolated from annual crops expansion and this explains its small reduction in soil carbon stocks. On the other hand, despite the Southern Pampas had a land-conversion history that was similar to most sub-regions in the Pampas, its colder climate has probably prevented a higher carbon loss from soil organic matter decomposition.

When soils are converted from cultivated to permanent perennial vegetation, i.e. from crop to pasture, the soil carbon loss can be reverse (Studdert et al., 1997). Soil carbon content significantly increase after the conversion from cropland to pasture (Fig. 9). Unlike annual crops, cultivated pastures maintain a permanent cover of vegetation on the soil, reducing soil temperatures, and adding higher amount of organic matter, particularly from belowground, to the soil (Guo and Gifford, 2002). A diversified production system, with frequent conversions to pasture, could partially or fully recover the amount of carbon lost from soil during the cultivation process.

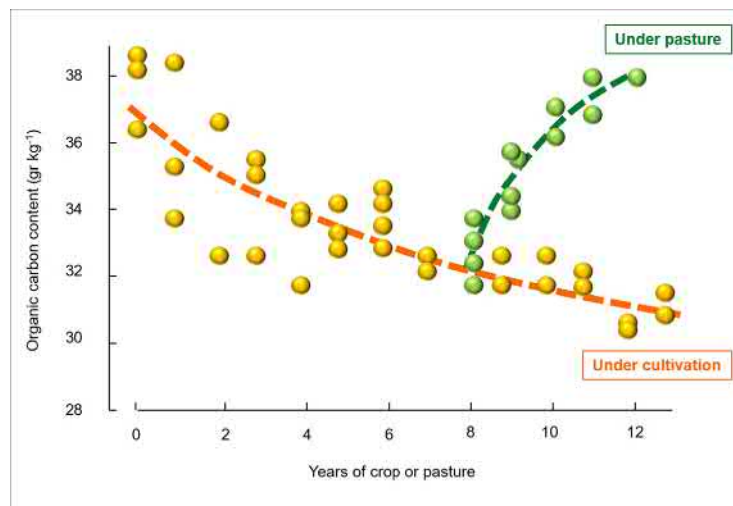


Fig. 9 Evolution of organic carbon content in soil under agriculture and in response to the inclusion of a grass-based perennial pasture. Own elaboration from Studdert, G. A., Echeverría, H. E. and Casanovas, E. M. (1997). Crop-pasture rotation for sustaining the quality and productivity of a Typic Argiudoll. *Soil Science Society of America Journal* **61**, 1466–1472.

Hydrological Processes in the Pampas Novel Ecosystems

As evapotranspiration decreased because of the replacement of perennial vegetation by annual crops, water runoff and water infiltration increased and the water table rose and approached the soil surface (Bertram and Chiacchiera, 2017). Annual crops were associated with the water-table rise (Fig. 10) because they remove less water by transpiration than trees and pastures. This has been a common phenomenon that occurs today in central Argentina mainly due to the expansion of annual crops over natural and grazing lands (Viglizzo et al., 2011; Bertram and Chiacchiera, 2017). Frequent floods in croplands of the Pampas are more associated with water-table rise and less with the increase of precipitation. In few words, floods in the Pampas are primarily explained by the water table rise and secondarily by rains. The severity of the problem increased in flat terrains with little drainage capacity.

Common sense indicates that an adaptive measure consists on working on the configuration of the system. Different species and farming activities have different potentials to remove water from the subsoil and to maintain the phreatic level at different depths. For example, wheat has a low evapotranspiration potential but alfalfa and forests show a high evapotranspiration potential. Therefore, the combination of activities with different potential to remove groundwater may play an important role to face the challenge of managing the hydrological balance of the ecosystem (Frank and Viglizzo, 2012).

The impact of the system configuration on water table depth in the Pampas was assessed between 1974 and 2008 through a model simulation process that was supported by field measurements (Nosetto et al., 2015). The authors found that the water table tends to accompany the rainfall variability, but its depth varied with farming activities. In the case of soybean monoculture, the phreatic depth tends to be close to the zero level (soil surface), but when two annual crops were introduced into the system the water table tended to move to deeper layers. When a rotation scheme with perennial pastures was incorporated into the system, the phreatic depth tended to move even deeper. This is an interesting example that shows how humans can handle the water table by modifying the configuration of the farming system.

So, looking ahead for practical lessons to ameliorate the flooding risk, the role of pasture-based livestock activities should be revalued, as well as crops and forest activities with high transpiration potential. The strategy should aim at strengthening the role of some regulatory ecosystem services that are associated with the dynamics of carbon and water in ecosystems.

Carbon, Water and Ecosystem Services

The characterization of ecosystem functioning is significant for different purposes such as biodiversity conservation and ecosystem service provision. Paruelo et al. (2001) showed that land-use influences carbon variability (in soil and biomass) throughout different seasons in the year. The amount of support, provision and regulation ecosystem services (MEA, 2005) may be decreased by decreases in net primary productivity, or C exported out of the system. Given that carbon and water interact for ecosystem functioning, a change in the carbon stocks and the carbon flows can modify the economy of water and the related ecosystem service provision (Viglizzo et al., 2016). A highly simplified picture (Fig. 11) can help understanding how water pathways were modified as humans replaced the grassy biomes in the Pampas by human-modified configurations, mostly cultivated pastures and annual crops.

In a general functional picture, part of the rainfall that follows the transpiration and evaporation pathways feed backs to clouds and rainfall. The fraction of water reaching the ground that was not evaporated nor transpired is normally known as water yield. Water yield may be divided between runoff and infiltration, providing water to the maintenance of surface streams (rivers), water bodies (lagoons, lakes) and underground aquifers. This simple functional scheme has been deeply modified by land-use/land-cover change. For example, most of the water that is reaching the ecosystem from rainfall is diverted to the evaporation pathway in

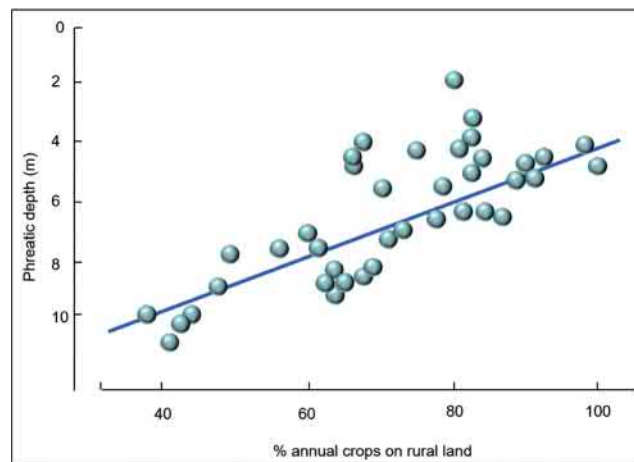


Fig. 10 Relationships between the percentage of annual crops and the water table depth in a soybean-cropping area of Central Argentina. Own elaboration from Bertram, N. and Chiacchiera, S. (2017). Ascenso de napas en la Región Pampeana: ¿Consecuencia de los cambios en el uso de la tierra?. Argentina: INTA EEA Marcos Juárez. <https://inta.gob.ar/sites/default/files/script-tmp-inta_napas_mjz_13.pdf>.

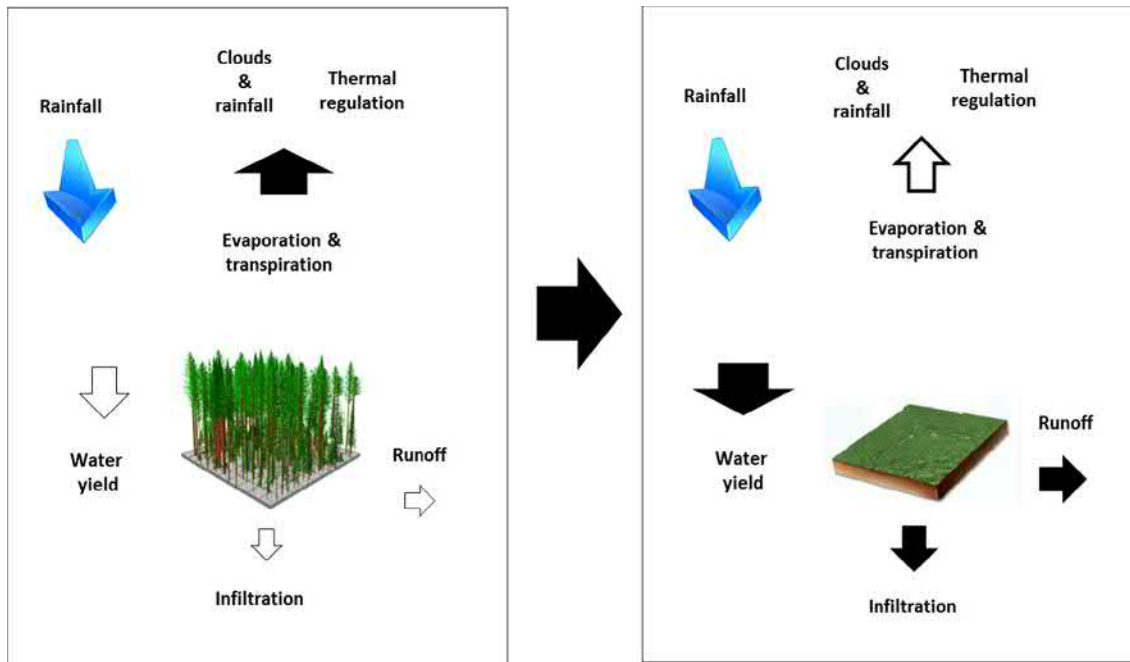


Fig. 11 The modification of carbon- and water-related processes by land-use/land-cover change can drastically modify both basic ecological functions and the provision of essential ecosystem services. Own elaboration from Viglizzo, E. F., Jobbágy, E. G., Ricard, M. F., and Paruelo, J. M. (2016). Partition of some key regulating services in terrestrial ecosystems: Meta-analysis and review. *Science of the Total Environment* **562**, 47–60.

a tall-grass perennial biome that had a high biomass carbon stock and was typical of the pristine Pampas. When such biome was converted into a cultivated land or simply in a bare soil with minimum plant coverage, carbon and water circuits were deeply modified, and runoff and infiltration pathways were privileged at the expense of evapotranspiration. So, trade-offs among ecosystem services were inevitable when land use and land cover were modified by anthropic interventions. Some of them such as those related to thermal and rainfall regulation were weakened in benefit of others like stream and water body maintenance and groundwater recharge (Viglizzo et al., 2016).

Concluding Remarks

Historical land-use and management change in the Pampas has irreversibly modified the biological structure and the ecological functionality of pristine ecosystems. This is the reason because the Pampas is essentially an anthrome and novel ecosystem where a restoration to the original condition is unthinkable. Driven by economic and social forces, some provisioning ecosystem services like food, fiber and bio-energy production were privileged and maximized at the expense of support and regulation services like soil formation, carbon sequestration, water regulation, soil protection and habitat provision. The replacement of the pristine by a novel agricultural ecosystem was inevitable in a fertile plain like that of the Pampas because agriculture was the basis to sustain the economy and the social development in Argentina during the last one and a half century.

Grasslands, one of the most transformed biomes of the world (Ellis and Ramankutty, 2008), have been considered highly relevant to global carbon sequestration (Viglizzo et al., 2019). As Norton (2018) argued, a science-based adaptive management is necessary to harmonize production and conservation in novel ecosystems. Various knowledge-based technologies and agronomic practices were applied to maintain novel ecosystems in the Pampas in a long-term sustainable condition: (i) spatial and temporal diversification of activities (agro-diversity), (ii) crop-crop and (iii) crop-pasture rotations, (iv) crops sequence, (v) conservation and zero tillage, (vi) cover crops (or “service crops”), (vii) fertilization and (viii) groundwater management were important to increase productivity and control carbon and water pathways. So, beyond agriculture, they were essential to maintain the habitat, the biodiversity, and the provision of ecosystem services under a novel ecological format.

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Multifunctional Landscapes

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Abstract

Multifunctional landscapes are typically characterized by diversified land use and complex landscape structure, thereby potentially covering many, often competing interests of different stakeholder groups. Central to the concept of multifunctionality is the assumption that this supply of a more diverse set of (market and non-market) goods leads to a number of environmental, social and economic benefits. Management strategies that increase the multifunctional use of landscapes, while sustaining natural resources for future generations, are therefore needed. Managing for landscape multifunctionality, however, requires some deep system changes, such as the collaboration between stakeholders across spatial scales and sectors as well as the transition toward more sustainable land management practices. Recently, assessments of landscape multifunctionality applying the ecosystem services framework (i.e., benefits that people obtain from nature) have emerged. In this article, we outline how such assessments have advanced our understanding of land use, which uncertainties and challenges remain to assess multifunctionality and how the valuation of multifunctionality could be used to make better informed management decisions.

Multifunctionality of Landscapes—Understanding the Concept

Multifunctionality is commonly understood as the supply of multiple ecosystem functions, services or goods within the same area (Hölting et al., 2019; Manning et al., 2018). Central to the concept of multifunctionality is the assumption that the supply of a more diverse set of (market and non-market) goods leads to a number of environmental, social and economic benefits (Foley et al., 2005). Addressing the different needs of society is essential if we are to develop sustainable and resilient landscapes that ensure the long-term protection of biodiversity and ecosystem services (O'Farrell and Anderson, 2010). In the last decades, the societal demands for achieving higher levels of landscape multifunctionality have therefore increased, in particular in connection with efforts to develop more sustainable land management strategies and to achieve increased socio-ecological resilience.

From Multifunctional to Uniform Landscapes—and Back Again?

While discussions on multifunctionality recently gained increased attention in the scientific community as well as in political agendas, multifunctionality of landscapes is not a novel concept. It has its origin in agricultural production systems which have traditionally been established and maintained to produce a multitude of different goods (Vos and Meekes, 1999). The first agricultural systems developed around settlements, where people used their environment and natural resources in manifold ways. They cultivated crops, grazed animals and used individual trees or forests in a small-scale, self-sufficient manner. Such

integrated farming-forestry systems were highly adapted to regional environmental and climatic conditions. They slowly formed characteristic landscapes throughout Europe and other human-dominated landscapes around the world, supplying location-specific sets of goods and services (Vos and Meekes, 1999).

With increasing population growth, however, the management and use of agricultural land intensified (Foley et al., 2005). Agricultural production per unit area increased substantially in the past decades due to higher inputs of land, labor, fertilizer, pesticides and feed (IPBES et al., 2018). At the same time, farms increased in size, while the diversity of cultivated crops decreased. Rural agricultural landscapes eventually transformed from multifunctional landscapes into highly specialized and rather uniform landscapes (Vos and Meekes, 1999). Due to landscape homogenization and land use intensification, interactions between ecological processes were increasingly decoupled, with severe impacts on ecosystem functions and services (Foley et al., 2005). For example, pollination rates continue to be rapidly declining due to the limited temporal and spatial availability of natural floral resources for wild pollinators and the growing use of pesticides. Likewise, soil erosion and water run-off rates are increasing due to the removal of hedgerows and other landscape elements, as a result of agricultural expansion and intensification.

In the course of these major land use changes, landscape management has become an issue of governmental planning processes and we have experienced a growing disconnection between humans and their local environment (IPBES et al., 2018). A large extent of agricultural products is nowadays part of globalized markets and decisions on what is being produced and sold at which price are made at the supra-local level, reinforcing this disconnection. Many rural areas worldwide are experiencing population declines. Smaller revenues or harder life conditions have contributed to the abandonment of these areas, leading to a continuous loss of local knowledge and place attachment (Foley et al., 2005; IPBES et al., 2018). Relational values, such as place attachment, cultural identity and moral responsibility, must be promoted again within conservation policies to strengthen the connection between humans and the environment and to contribute to the maintenance of multifunctional landscapes (Allen et al., 2018). While in many parts of the world there are virtually no landscapes left that are not shaped by humans, notions toward “multifunctional landscapes” and similar concepts such as “nature-based solutions” and “integrated agro-ecosystems,” have been picked up again, steering discussions toward increased sustainability and socio-ecological resilience (see “The Capacity of a Landscape to Supply Multiple Functions and Services: Interactions at the Landscape Scale” section) (Fischer et al., 2017; O’Farrell and Anderson, 2010).

Recent Applications and Conceptual Advancements

Linked to the idea of multifunctional landscapes, the role of interacting ecological processes and functions has always been a focal study object in ecology. In the last years, studies on multifunctionality have evolved tremendously in many fields of environmental sciences. Multifunctionality has been assessed within a broad spectrum of spatial scales and land use systems, including agricultural landscapes, urban areas, soil ecosystems, farms, forests, coastal areas, and water bodies (Hölting et al., 2019). Studies range from microbiological studies (e.g., studying the relationship between microbial diversity and functions such as nutrient cycling or organic matter decomposition; Delgado-Baquerizo et al., 2016) to the field of landscape planning, where landscape structures and functions are analyzed to better design multifunctional landscapes (Lovell and Johnston, 2009). Different methods have been developed to quantify ecosystem multifunctionality (Byrnes et al., 2014; Hölting et al., 2019) and the concept has become highly relevant in many regional planning strategies, in international legislation (e.g., Common Agricultural Policy of the European Union) and in intergovernmental organizations (e.g., World Trade Organization) (O’Farrell and Anderson, 2010). The increased use of the multifunctionality concept is certainly linked to the expected benefits in terms of biodiversity conservation, sustainability and socio-ecological resilience (see “The Capacity of a Landscape to Supply Multiple Functions and Services: Interactions at the Landscape Scale” section).

To quantify the level of multifunctionality, studies use a range of different methods to aggregate ecosystem function or service indicators into a single metric (Byrnes et al., 2014). Some studies assess multifunctionality by taking the sum or the average of all functions or services recorded. In this approach, all functions or services obtain equal weights. Other studies argue that functions or services only account to multifunctionality if they exceed a certain threshold value (Byrnes et al., 2014). These studies count the number of functions or services that are supplied above this specific threshold. Another widely-used approach is to define different weights for different functions or services, or to quantify the diversity of functions or services instead of their supply levels only (Stürck and Verburg, 2017). There is no consensus about when to use which method, as each approach has its own advantages and constraints (summarized in Hölting et al., 2019). While these conceptual and methodological ambiguities in the application of the multifunctionality concept may have potentially jeopardized its practical use in land management, recent works (Manning et al., 2018) have made substantial progress to disentangle the existing confusion in terminology.

Ecosystem multifunctionality has recently been “redefined” and two major strands of research have been characterized (Manning et al., 2018). The first strand of research quantifies multifunctionality based on ecosystem functions, typically at small spatial scales such as plots. It largely deals with the relationship between biodiversity and the number of ecosystem functions that are supplied within a particular land use type. Numerous studies have proven that high levels of biodiversity at multiple trophic levels are needed to sustain ecosystem multifunctionality (Soliveres et al., 2016). As different species provide different functions, this relationship depends on the functional diversity and redundancy in an ecosystem. Nevertheless, these studies generally underpin the important role of biodiversity for ecosystem functioning (Byrnes et al., 2014). Other studies belonging to this strand of research have analyzed the impacts of land use regimes on multifunctionality, as well as dependencies between forest structure and multifunctionality (Felipe-Lucia et al., 2018).

The second strand of research focuses mainly on larger spatial scales, often on landscapes being composed of different land use types. These studies define multifunctionality as the supply of multiple ecosystem services (including provisioning, regulating and cultural ecosystem services) across the landscape, and aim to evaluate the multifunctionality of a landscape by accounting for all ecosystem services used by people (Manning et al., 2018). Focusing on ecosystem services allows to shed a new light on the use of landscapes (Stürck and Verburg, 2017): instead of representing land use/land cover information, such studies aim to capture the complexity of social-ecological systems by making the difference between service provider units (i.e., potential ecosystem service supply) and beneficiaries (i.e., actual ecosystem service use). The foreground of this strand of research includes studies investigating the level of the use of these services, people's demand for ecosystem services, its distribution among different stakeholders (Mastrangelo et al., 2014; Plieninger et al., 2019) and different components of human well-being.

The two conceptual ways to define multifunctionality outlined here (ecosystem function-focused multifunctionality with a plot-based, ecological perspective vs. ecosystem service-focused multifunctionality with a landscape-scale, human-centered perspective) can help us understand the approaches used in existing studies regarding multifunctionality (Hölting et al., 2019). In the following sections, we reflect on the concept of multifunctionality from the latter, the landscape-scale, ecosystem service perspective.

The Capacity of a Landscape to Supply Multiple Functions and Services: Interactions at the Landscape Scale

This section describes the interrelations between human land use, biodiversity, ecosystem functions and services in multifunctional landscapes (Fig. 1) for biomes that are classified as “human biomes” or “anthromes” (Ellis and Ramankutty, 2008): (1) Humans shape landscapes through land use and management practices. (2) Landscapes contribute to a specific set of ecosystem functions, i.e. processes that maintain the internal functioning of the ecosystem, such as energy cycles or nutrient fluxes. Land use and management decisions also affect biodiversity, i.e., the diversity of genes, species and ecosystems, (3) either directly (e.g., through pest control or wildlife management) or (4) indirectly through changes in the landscape (e.g., through modification of forage opportunities or habitat quality). Biodiversity, on the other hand, also influences landscape structures (e.g., through grazing or creation of habitats). (5) Species and their functional traits influence and control ecological processes and functions (Byrnes et al., 2014). (6) Ecosystem functions eventually provide ecosystem services, in case they lead to the provision of specific goods and benefits to people, thereby (7) contributing to various components of human well-being (i.e., health, safety, material needs) (de Groot, 2006; MEA, 2005). (8) Finally, the production and consumption of ecosystem services is shaped by the location-specific demand for ecosystem services by people.

Since ecosystem functions and services interact, either enhancing or reducing each other, human land use and management decisions do never affect only single functions or services, but always multifunctionality as a whole. In addition to human activities, there are other important non-anthropogenic factors and drivers—such as climate, soils, landforms, biotic processes and natural

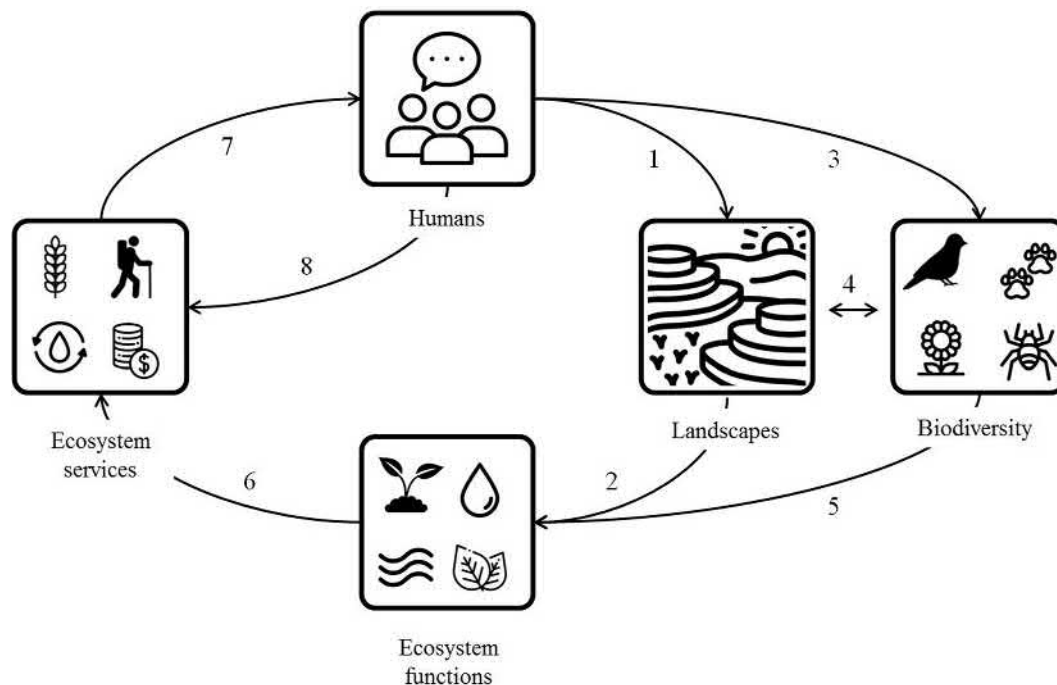


Fig. 1 Interactions between human land use, biodiversity, ecosystem functions and ecosystem services: (1) land use and management practices affecting landscapes, (2) contribution to ecosystem functions by landscapes, (3) direct effects on biodiversity, (4) interactions between biodiversity and landscape structures, (5) contribution to ecosystem functions by species, (6) supply of ecosystem services, (7) contribution to human well-being, (8) demand for ecosystem services. Icons designed by Freepik.

disturbances—that influence the potential capacity of a landscape to supply specific functions or services. However, it is humans who directly influence this capacity through land management practices and strategies that are often specifically tailored to promote or reduce certain functions or services. For example, pollination is promoted through beekeeping; soil erosion is reduced by targeted reforestation measures. Against this background, land use and management can be considered the most influential driver of landscape multifunctionality in human-dominated landscapes or “anthromes.” “Conventional biome systems” that do not take into account the impacts of human activities are considered less accurate than models that describe “human biomes” (Ellis and Ramankutty, 2008).

Multifunctional Landscapes—An Ecosystem Service Perspective

Why Adopting an Ecosystem Service Perspective on Multifunctionality?

First, translating ecosystem functions into ecosystem services is important to better understand land use interests and decisions

While studying ecosystem functions and their dynamics within landscapes is fundamental to understand the processes within ecosystems, the ecosystem service concept is embedded in a broad and inclusive framework that gives us the opportunity to translate this ecological complexity into a limited number of ecosystem services of interest for human well-being (de Groot, 2006; Turkelboom et al., 2018; see also Fig. 1). By assessing the value of ecosystem services that are most relevant to the people within a study area, we step from an exploratory lens on landscapes to a normative, anthropogenic perspective. This step is needed to better understand what people demand within a landscape, how they depend on certain ecosystem services and how they prioritize land use decisions for or against certain ecosystem services.

Second, including marketable and non-marketable goods can help steering management decisions toward increased sustainability

We typically manage landscapes for the supply of a few, mostly marketable goods and services such as food or timber (de Groot, 2006; Turkelboom et al., 2018). However, it is necessary to better understand the impacts of land use decisions for a wide range of ecosystem services. Besides these marketable goods, we demand and depend on ecosystem services that are non-marketable, such as many cultural and regulating services. Many of these non-marketable ecosystem services are heavily affected when landscapes are managed for the supply of one or a few ecosystem services only. On the other hand, non-marketable ecosystem services may be of key importance for steering management decision toward sustainability. For example, cultural ecosystem services, often closely related with the attachment of people to their landscape, can be crucial for long-term conservation: People who value their landscape are typically more willing to take stewardship for it and to invest in sustainable management (Fischer et al., 2017). While non-marketable ecosystem services are often intangible and therefore not included in conventional market-based analyses (de Groot, 2006), the ecosystem service framework provides methods to better account for the value of such goods and services (Turkelboom et al., 2018). Regulating services are often measured in biophysical terms, such as differences in air temperature, amounts of carbon stored in trees and soils, and nutrient content in soils. Cultural ecosystem services can also be assessed using direct measures (e.g., number of spots for recreation, educational visits, or artistic publications). In all cases, ecosystem services can be assessed using social valuation methods (e.g., structured surveys, participatory mapping and stated preferences) or econometric methods. The ecosystem service framework thereby helps quantifying multiple aspects of multifunctional land use, which eventually results in a more integral way of understanding land management.

Third, the ecosystem service concept can ease the communication of scientific findings to decision-makers

The ecosystem service concept has been designed to better communicate “wicked” (interlinked and complex) problems of environmental degradation, associated effects on social inequity and economic interests to a broad range of audiences, including decision-makers. It has been picked up by science-policy platforms ranging from local to global level, such as the UK National Ecosystem Assessment (UK NEA), the international TEEB initiative “The Economics of Ecosystems and Biodiversity,” or the Millennium Ecosystem Assessment called for by the United Nations in 2000. The ecosystem service concept further is an integral part of the Nature’s Contribution to People (NCP) concept recently developed by the Intergovernmental Platform for Biodiversity and Ecosystem Services (IPBES) and has been promoted as a tool to effectively illustrate trade-offs between different land use-decisions (Turkelboom et al., 2018). Different methods have been used to convey this information to policy makers, ranging from policy briefs and ecosystem service maps to public meetings with invited stakeholders, proposed action plans and guidelines. Moreover, the integration of long-term environmental costs (through payments for ecosystem services, PES) and the involvement of stakeholders in ecosystem service assessments can provide additional support to policy decisions that stimulate reflections upon landscape multifunctionality (de Groot, 2006).

Links to Sustainability and Resilience

The concept of landscape multifunctionality is strongly linked to the concepts of sustainability and resilience (O’Farrell and Anderson, 2010). Landscapes that offer a diverse and interlinked set of ecosystem functions generally have a higher capacity to withstand disturbances and to adapt to environmental changes (Byrnes et al., 2014; Foley et al., 2005). From an ecological point of view, such landscapes have long been considered as more resilient than those providing only a small number of ecosystem functions.

More recently, the resilience concept has been extended beyond its ecological meaning, in order to include human-nature interactions. Also from a socio-ecological perspective, a landscape supplying a more diverse set of goods and services has the potential to satisfy the demands of many different groups of people; hence, it can be considered more multifunctional. Such a landscape will also be more resilient to fluctuations in market prices of individual products and might eventually help mitigating conflicts that evolve from competing demands. Multifunctional landscapes are further associated with relational values, such as higher levels of place attachment, local knowledge and stewardship of the landscape by its inhabitants (Fischer et al., 2017). Thus, socio-ecological resilience relates to both the adaptive capacity of society to react to changes in the environment, as well as to the capacity of ecosystems to adapt to or withstand changes posed by humans (Mastrangelo et al., 2014).

Landscapes that are managed under the multifunctionality paradigm are further considered to be environmentally sound, socially equitable and economically feasible—the elements embedded in the sustainability concept. As resources are limited, land management needs to hold on to these three criteria in order to conserve natural resources, generate welfare and promote equity for current and future generations. Losing important ecosystem services in non-multifunctional systems can, on the other hand, have severe impacts for certain stakeholder groups and may lead to environmental degradation processes. The prevention of any kind of degradation processes through sustainable land management practices, on the other hand, has tremendous potential to reduce future costs of environmental restoration efforts (IPBES et al., 2018).

Toward Increased Multifunctionality of Landscapes

Remaining Challenges to Assess Landscape Multifunctionality

Selecting relevant ecosystem services and their indicators

Characterizing multifunctional landscapes via ecosystem service-based multifunctionality assessments remains challenging, as it is associated with a number of assumptions made in ecosystem service assessments and resulting uncertainties. The first crucial step is the identification and quantification of all relevant (i.e., representative) ecosystem services within the study area. The quantification and mapping of these services can be based on direct measurements (e.g., field observations and surveys), indirect measurements (e.g., remotely sensed proxies), look-up tables, models, or expert knowledge (Hölting et al., 2019). The increasingly inter- and transdisciplinary research on ecosystem services, together with the growing availability of ecological, social and remotely sensed data is promising to allow advances (Cord et al., 2017). However, limited temporal and spatial resolution of available data oftentimes poses constraints to landscape-scale ecosystem service assessments and produce uncertainties. To increase representability and legitimacy, the services and the indicators chosen to quantify each ecosystem service are best identified together with experts and relevant stakeholders of the study area (Mastrangelo et al., 2014; Turkelboom et al., 2018). The selected ecosystem services should further include all ecosystem service categories and be assessed following different approaches (i.e., ecological, economic and social), to minimize potential bias related to the valuation method (Martín-López et al., 2014).

Assessing the actual use of and demand for ecosystem services

Another major challenge is to assess the actual use of ecosystem services or the actual benefit that people obtain from nature. Studies predominantly assess the (potential) supply of ecosystem services, which is not directly linked to the actual use or the benefits derived from ecosystem services (O'Farrell and Anderson, 2010; Turkelboom et al., 2018). In the case of provisioning services, for example, a high supply can benefit the local population only if the product is consumed locally or the revenues remain in the area. In reality, however, this is most often not the case, as farms might be owned by external companies and the products are often exported to national or international markets. In the case of cultural services, on the other hand, a low service supply might be sufficiently contributing to people's well-being, if the level of supply meets their demand (e.g., opportunities for recreation). Assessing the demand for services or their actual use and benefits is therefore more useful to inform management and hence a currently fast developing field of research (Pleninger et al., 2019).

This is also closely linked to the challenge of obtaining a differentiated view on the beneficiaries of ecosystem services. Most studies do not differentiate between different groups of stakeholders and rather generalize that the supply of ecosystem services is contributing to the quality of life and human well-being in general. Especially in multifunctionality assessments, hotspots of ecosystem service supplies are often equated with hotspots of increased human well-being (Stürck and Verburg, 2017). This bears two main risks: (i) first, the risk that management recommendations are based on such hotspot analyses instead of the location-specific supplies and demands for ecosystem services and (ii) second, the risk of overlooking the demands of vulnerable stakeholders placed outside the assessment and decision-making processes. Research advances should therefore not only differentiate between demand, supply and actual use of ecosystem services, but also between different groups of stakeholders.

Assessing multifunctionality at the right scale

The capacity of a landscape to supply ecosystem services, as well as the demand of people for certain ecosystem services vary within and across landscapes: while a small patch can in most cases only produce one or a limited number of ecosystem services (e.g., field scale), a larger amount of different ecosystem services are being produced within a larger scale (e.g., landscape scale). Similar to the land sharing/sparing debate (Ekroos et al., 2016), it is important to consider where and at which scale (extent) increasing multifunctionality is needed. It is for example debatable, whether multifunctionality needs to be implemented at the plot scale, or whether patches with lower multifunctionality are acceptable, providing that management strategies promote a high level of

multifunctionality at the landscape scale (Felipe-Lucia et al., 2018). In order to orient multifunctionality assessments toward the development of specific management strategies, it is important to assess multifunctionality at the spatial scales relevant for implementation (Turkelboom et al., 2018). In practice, the choice of spatial scale for ecosystem service assessments, however, often depends on the availability of data, the resolution of underlying field or modeled data, or on administrative scales relevant for their management (Stürck and Verburg, 2017).

Despite the remaining challenges to assess multifunctionality, such analyses can provide highly valuable, area- and context-specific information for policy-makers. In particular, the identification of priority ecosystem services for assessment and of relevant stakeholders needs to be a transparent and recurrent process that will vary depending on the study area.

Governance Across Sectors and Scales

Landscape management is influenced by a network of administrative bodies, institutional arrangements, individuals and stakeholder groups on different scales of governance (MEA, 2005; Nagendra and Ostrom, 2012). A transition toward multifunctional landscapes therefore requires deep system changes. First of all, multifunctionality needs to be the common goal across socio-economic sectors and administrative levels. Stakeholders of different sectors should formulate joint objectives to increase multifunctionality and work collaboratively to reach their goals (O'Farrell and Anderson, 2010). Relevant stakeholders include governmental bodies (e.g., provincial and municipal administration), "influential" land users (e.g., companies, land owners, farmers, foresters) and "non-influential" land users (e.g., recreationists, citizens) (Turkelboom et al., 2018). Cross-sectoral work, however, is a major challenge in countries which are predominantly sectorally organized.

Besides the different sectors, there are different scales of governance that influence land use and landscape management, from the international agreements to their implementation at the local level. In practice, countries follow these international agreements, but apply their policy instruments at the national level. In turn, countries dictate decisions on regional or provincial levels and design regional management plans to support municipalities and rural communities. In many cases, management practices locally framed and implemented will potentially have the strongest impact on ecosystems and the services they supply. While multifunctionality is often defined as a management aim at the landscape level, policies on multifunctionality have to be formulated at all scales of the decision-making process (Nagendra and Ostrom, 2012) to achieve a coherent strategy.

Implementing a Strategy for Multifunctional Landscapes

Increasing the multifunctionality of landscapes typically requires multiple changes in landscape management that are often not straightforward. For example, diversifying local agricultural production requires changes in market structures, commercialization channels, education, financial and policy instruments. While such systemic changes need time, other smaller-scale and practical viable solutions toward increased multifunctionality can be achieved in the meantime. We argue that a step-by-step adaption of current management systems is most promising to increase the multifunctionality of landscapes. It goes without saying that, for example, the introduction of landscape elements that increase landscape heterogeneity (e.g., ponds, hedgerows, trees, flower strips) and offer key habitats, forage and nesting opportunities (Foley et al., 2005; Mastrangelo et al., 2014) can substantially increase multifunctionality. Such elements further affect multiple ecosystem functions (e.g., nutrient cycles, photosynthesis or evapotranspiration) and eventually increase multiple ecosystem services (e.g., aesthetic value, buffer capacities or climate regulation) (de Groot, 2006) (Fig. 1). Other management practices that can be adapted to foster multiple ecosystem services in human-dominated landscapes include a reduction in the use of pesticides and fertilizers, which should be extremely precise and species-specific, a focus on diversity and self-sufficiency instead of crop yield, and sustainable soil and water management practices. On the other hand, changes in the social system toward a polycentric governance can contribute to adapting global and national policies to local needs while engaging a more diversified set of stakeholders in the decision-making processes of landscape management (Nagendra and Ostrom, 2012). In general, it is crucial to look at the landscape in a more integral way in order to increase multifunctionality and to achieve a more equal distribution of their services. Still, we need a better understanding of the interrelations between management practices and their effects on ecosystem functions and services at the landscape scale. In turn, how such landscape management policies affect different sectors of society is crucial to promote sustainable livelihoods and to reduce social and environmental conflicts. Context-specific solutions are required to design multifunctional landscapes. Therefore, it is also crucial to integrate local knowledge holders in decision-making processes.

Conclusions

While we are facing a number of environmental crises, a more integral way of land management is required to achieve multifunctionality at the landscape scale. Global population growth and changing consumption patterns have led to a growing demand for food, land, water and energy. At the same time, intensive land use affects water quantity and quality, soil fertility and air quality in many parts of the world. On top of that and exacerbated by climate change, the loss of biodiversity is predicted to increase, which will have unpredictable consequences for ecosystem functioning and ecosystem service supply at the landscape scale. In essence, land is a limited resource that is subject to a lot of pressures. The multifunctional use of landscapes has been advocated as a way to manage land in a sustainable way that maintains ecosystem functioning and conserves natural resources for future generations.

It means promoting multiple ecosystem services instead of focusing on the supply of a few. Spatial planning must therefore aim to change human-dominated landscapes into more multifunctional systems. The design of such multifunctional landscapes is always area- and context-specific, as different sets of functions and services can be provided and are required in different landscapes. Additionally, the demand for ecosystem services depends on local stakeholders, who need to be involved in regional management plans. While it is challenging to find “optimal” multifunctional landscape solutions, there are already a few promising examples (e.g., increase of green space in urban areas, employment of agroforestry and sustainable intensification practices, and financial support systems to increase landscape structure and biodiversity; Foley et al., 2005).

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Biocultural Heritage in Sicilian Olive Groves; The Importance of Heterogeneous Landscapes over the Long Term

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Abstract

Low-intense agroecosystems may be key for mitigation of vulnerability to climate change, as to build ecological and social resilience of local communities.

As an example of low-intensity systems, the article will focus on olive land use dynamics occurring at different temporal and spatial scales in the island of Sicily. Sicilian olive intercropping systems have resulted in the formation of heterogeneous cultural landscapes and heritage that supports place-based and practice-based know-how, drawing on transmitted and new knowledge—what we call Biocultural Heritage. The domestication and continuous careful management of these trees by locals have been a crucial element for their longevity: they can thus be seen as stabilities in a changing landscape along time and space.

The article crosscuts history and spatiality at different scales to allow the olive trees of Sicily to “talk” about their millennial entanglements with the other elements of local ecosystems, man included. Considered biocultural refugia able to preserve both agricultural biodiversity and traditional ecological knowledge, their social and ecological history is explored through the identification of breaking points in time and spatial nodes of connection.

Such enduring landscapes are increasingly under threat due to climate change and intense land abandonment; their progressive fragmentation represents a huge threat for their ecological complexity, agricultural practices, biocultural heritage and socio-economic conditions of local communities. We conclude the article advancing suggestions for their future stewardship.

Introduction

Accelerating climate change, as rapid socioecological modifications of land use, calls for new deeper transdisciplinary knowledge on agro-ecosystems. Land use has influenced many aspects of the environment and is also interlinked with regional and global climate. Quantifying land use changes and their effects on past and present environment is a challenge; nonetheless, such knowledge is needed if we want to develop land management strategies for climate warming mitigation. The recognition of the ecological function of agricultural societies is fundamental to inform and inspire sustainability research (Bird and Nimmo, 2018) and low-intensity farming areas are excellent study cases to investigate and find evidence for landscape effects on ecological and farming systems. Ancient olive groves, agro-sylvo-pastoral systems, traditional vineyards agro-economic systems are a few examples, today recognized as Globally Important Agricultural Heritage Systems since they play a crucial role for agrobiodiversity conservation and livelihood (FAO, 2018). In rural landscapes, “natural” ecosystems have a long history of coexistence with agricultural land use systems as evidenced by the spatial extent of cropland, rangeland, and village anthromes overtime (Ellis et al., 2010). The functionality of these landscapes depends on the interactions among natural ecosystems, agroecosystems, and the social and cultural characteristics of the people that create and manage them (López-Pintor et al., 2018); low-intense agrosystems may be key for mitigation of vulnerability and to build ecological and social resilience (Schermer et al., 2018).

The Mediterranean environment, and its dynamics over time, particularly in relation to agriculture, have been the topic of an animated debate. There is a Mediterranean “problem” to solve: does the Mediterranean represent an environment which has

been able to support agricultural way of life (based, among other crops, on olive and mixed agricultural cultivation) for more than eight millennia and can this continuity be thus defined as “sustainable”? Or has the Mediterranean been the place of environmental and devastation due to climatic anomalies, mismanagement, exploitation of natural resources and destruction of primeval forests? These questions represent different ways of viewing Mediterranean agricultural and semi-natural anthromes (Emanuelsson, 2009).

Regardless, we witness today the alarming disappearance of both farmed areas and connected local agro-ecological knowledge. The few land users remaining face a quite pressing dilemma: agricultural practices are considered to be responsible for habitats fragmentation and destruction (Campbell et al., 2017) while, on the other hand, decline in traditional low-intense farming has often had negative effects on biodiversity and high species richness at local scale (Beilin et al., 2014). Simplistic generalizations have led to low-intense agrosystems being seen as almost immune to climate change, soil degradation, loss of biodiversity, and reduction of resilience (see critical discussion in Iuga et al., 2017). Knowledge co-created with local communities have shown instead how these areas are not only affected by such problems but, even worse, they suffer from serious economic and social marginalization, as land degradation (Biasi et al., 2017; López-Pintor et al., 2018).

Among low-intensity agroecosystems, our contribution focuses on Mediterranean intercropping systems, with special attention to land use dynamics in olive cultivation occurring at different temporal and spatial scales in the island of Sicily. Mediterranean islands are characterized by the high level of diversity in biotic and environmental conditions. Their complex historical biogeography makes them important ecological reservoirs, informing us about the long-term entanglements between human and environment and their crucial role in the preservation of such biocultural heritage (Médail, 2017). Landscape persistence should be given the same attention as landscape change (Lieskovský and Bürgi, 2018) and this is the starting point of our analytical approach: here we use vegetation stability and its different spatial patterns displayed in the landscape as indicators of diverse land uses, management strategies and adaptive dynamics. Olive land use systems are of extreme longevity as olive trees can be even several thousand years old. Their peculiar manifold spatial configurations, shaped by the millenary interplay between humans and nature, provide a unique opportunity to study long-term adaptability processes, map land use relative temporalities and understand the logics behind them. Using olive trees as both spatial control points and as historical “archives”, we will here embark on a journey through the spatiotemporal land use variations in Sicily, while exploring historical trajectories, the formation of culture and socio-ecological adaptation. After a brief geographical background, the article will delve into the biogeography of Sicilian woody vegetation, looking at olive patch matrix interactions within a millennial perspective through the analysis of breaking points in time and spatial nodes of connections. Reclaiming the endurance of olive biocultural heritage in Sicily, we conclude the article providing suggestions for its future stewardship.

Geographical Background

Mediterranean islands, with a wide range of sizes, altitude and remoteness, are reservoirs of unique genetic lineages, mainly for most endemic plants, in other words “current refugia” which ensure the conservation of plant biodiversity. They are also key entities to disentangle the role of environmental versus human pressures in the long-term preservation of these biodiversity hotspots and their cultural heritage (Médail, 2017) (Fig. 1).

The island of Sicily itself has an overall surface of c. 25,703 km² and includes also five smaller archipelagos. Geomorphological features have been crucial for the development of its flora and fauna, since most of the surface is made of hills (62%) and mountains (24%) overlooked by Mount Etna, the highest active volcano in Europe. The entire island is quite geologically heterogeneous, also for micro-climates, vegetation and land use. Sicily has approximately 2700 vascular-plant species, 11% endemic and a wide diversity of cultivated species, with most of the territory covered by “cultivated lands and temporary fallow lands” (846,470 ha), “olive groves and other dry crops” (336,528 ha), “citrus groves and irrigated orchards” (158,592 ha), “vineyards” (142,558 ha), “greenhouses” (15,608 ha) and “hazel groves” (12,411 ha). The natural wood communities occupy about the 6.78% of the total island, limited to relatively small biotopes living in protected areas. Other widespread features are Mediterranean grassland (12.84%), used for grazing and regularly affected by wildfires, and azonal vegetation as shrubs, maquis and garrigues in rocky cliffs, lava fields, riverbeds, sandy coastal stations and brackish marshes (Benedetto and Giordano, 2008; Gianguzzi et al., 2015). Urbanized areas represent only the 4.86% of the regional surface; the overall population is around 5 million (ISTAT, 2019).

Talking With the Trees

Ecosystems and their specific set of land use practices are a result of repeated feedback between land use as an ecological process and the response of the ecosystem itself: they co-evolve, producing in complex adaptive systems characterized by multiple timelines with different rates of change and persistence (Sinclair et al., 2017). To understand such living dynamic systems we can interpret their relationships with the environment, while recognizing them as fully agents in the spatial and temporal evolving dynamics of the landscape; what we here refer to as “talking with the trees”. Thus, here we will explore the ecological and social history of olive trees by crosscutting time and space at different scales. Through the identification of historical breaking points (significant events in time which could have affected olive trees dynamics in the island) and spatial nodes of connections (olive trees patterns at various spatial scales) occurring over the long term in Sicily, we reveal how such hybrid and heterogeneous temporal entanglements have a spatial dimension displayed in the landscape. The result is a holistic approach to complexity which merges many kinds of evidence

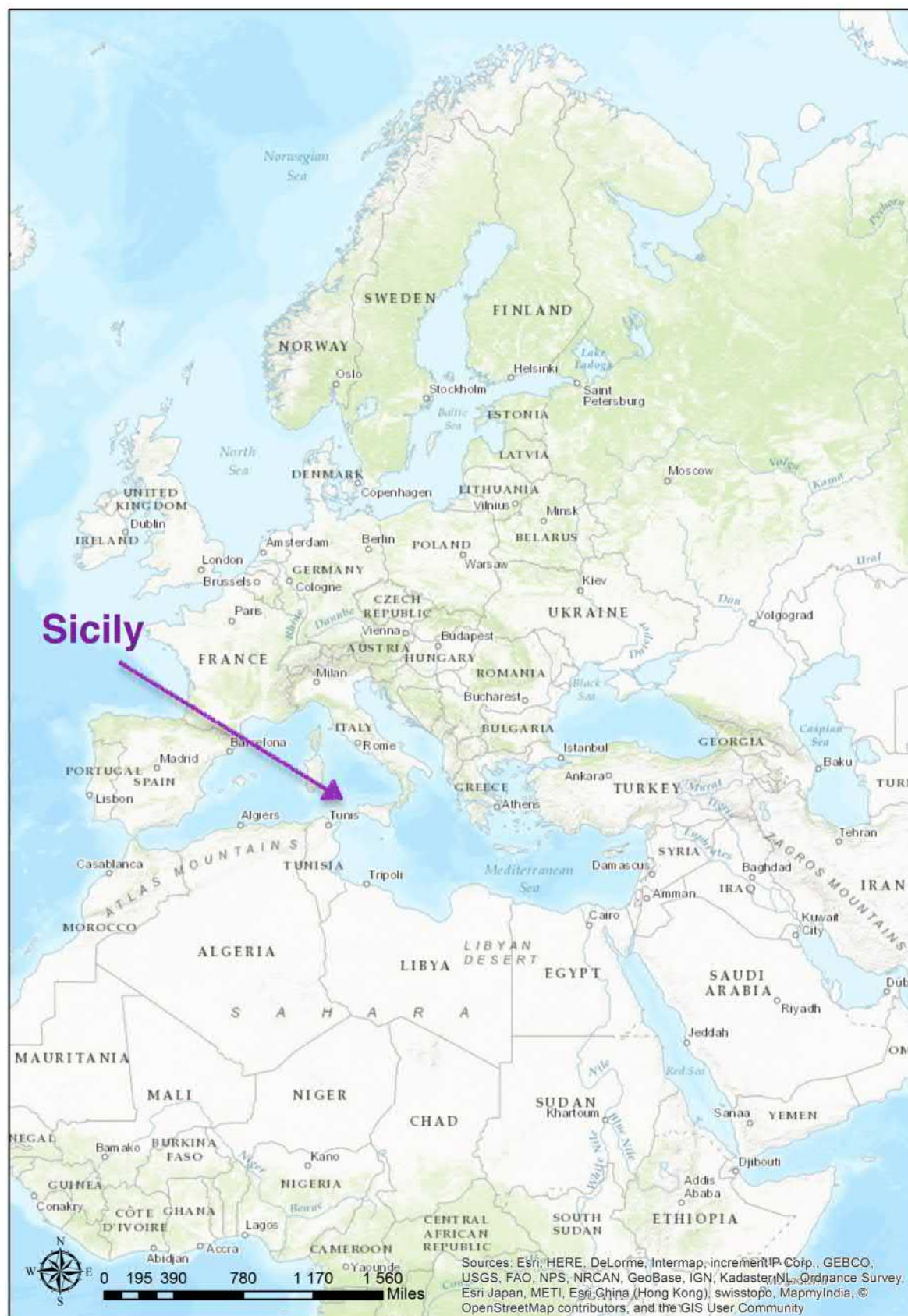


Fig. 1 Location of sicily in the Mediterranean sea and Europe (Ferrara, 2016 on dataset provided by ESRI).

to reach new understandings about human- environment relationships over long-term historical transformation dynamics and multiple spatial scales.

Biogeography of Woody Vegetation in Sicily

With a rich biodiversity and long history of human-environmental interactions, the Mediterranean region is characterized by a high degree of spatiotemporal heterogeneity in vegetation patterns. Published syntheses of multiple modern and fossil pollen records have revealed subclimax vegetation communities, the long-standing evidence of vegetation turnover and the complex interactions between plant assemblages, disturbance and climate, as the evergreen shrub dominated by Oleaceae (Sadori et al., 2016; Woodbridge et al., 2018). Peculiar to the central Mediterranean is the ability of vegetation to rapidly respond to climate change, being developed in a complex physiographic system that enhances high diversity and assemblages, often located in ecological niches close to each other, coexisted throughout the glacial–interglacial cycles of the Quaternary, ready to alternately develop following climate oscillations. The vegetation history of the central Mediterranean is further characterized by a long-lasting and intense human impact on the landscape through agropastoral and silvicultural practices, forest clearance, fires, and demographic increase (Di Rita and Magri, 2019).

Woody Mediterranean vegetation has been dramatically influenced by human activities for thousands of years. Since the Neolithic, human influence on ecosystems, especially on forests, have been intense and the profound transformations of natural into cultural landscapes are the result of millennia of human activities. With the exploitation of resources provided by tree species, humans interfered with their natural distribution, gathering or cultivating some of them (e.g. olive, walnut and chestnut trees) since ancient times. Olive (*Olea europaea* L.) was one of the most important fruit trees in the ancient Mediterranean region and a founder species of horticulture in the Mediterranean Basin, considered the most prominent and economically important fruit tree, providing edible fruits and, more importantly, storable oil used since antiquity for cooking, lighting, cultic and medical purposes. In the wild, olive (*Olea europaea* L. subsp. *europaea* var. *sylvestris*) grows in habitats characterized by a typical Mediterranean climate, usually hilly areas as part of the garrigue and maquis. Whereas the wild olive is considered a sensitive bioindicator for the Mediterranean bioclimatic zone, cultivation has caused the species (*Olea europaea* subsp. *europaea* var. *sativa*) to surpass its natural bioclimatic limits and to be grown at higher altitudes and latitudes as well as in areas more arid than its wild habitats (Langgut et al., 2019). Today, the olive tree is also appreciated for its multi-functionality: hydrogeological safeguarding of mountains and hills, climate mitigation actions, landscape enhancement (Brunori et al., 2017).

Patch Matrix Interactions Within a Millennia Perspective

Rural landscapes reveal a complex system of human-environment interactions across extended temporal trajectories. Vertically, through time stratifications there is a diachronic accumulation of changes occurring through dynamic interactions between human interventions and climatic, geomorphological and ecological changes. Horizontally, we have the formation of heterogeneous mosaics of spaces created by both temporal dynamics (historical stratification as explained above) and a series of heterarchical relationship between climatic conditions, landforms, soils, vegetation and human activities (Bazan et al., 2019). Ecosystems, and their specific set of land use practices, are the result of repeated feedbacks between land use as an ecological process and the response of the ecosystem itself: they co-evolve, producing biocultural diversity, in complex adaptive systems characterized by multiple time-lines with different rates of change and persistence (Crumley et al., 2017).

Sicily is considered a special historical-naturalistic laboratory: shaping vegetation through land use over millennia, humans have been the geodesigners of the Sicilian landscape. Olive trees, living in the same place for centuries, are keystone biocultural elements that preserve both biodiversity (Prevedello et al., 2018) and related traditional agro-ecological practices (Calvet-Mir et al., 2018). They are an extremely unique case of persistence; as a perennial crop, they represent long-term investment, still producing for both self-consumption and trade markets. Even if abandoned, trees always remain on the field and survive, being able to adapt to specific climatic, topographical and soil characters, while exhibiting high plasticity (particularly for the native varieties) and optimizing the genotype-environment relationship (Marchi et al., 2018).

As a result of the interaction between natural and anthropogenic factors, distinct patterns of olive groves can be found in the rural landscape of Sicily today: scattered old- century olive trees, ancient olive orchards, mixed crops, olive trees in terraces and pocket terraces, olives as boundary markers, small- scale geometric plantations as exemplified above (Ferrara, 2016). In other words, olive different patterns in spatiality represent different biocultural timescapes since each of them is expression of specific cultivation modalities related to cultural negotiations with nature (Huebener, 2018) occurred at different temporalities in Sicilian history (Figs. 2 and 3).

The different spatial patterns of olive trees can be considered as different ecogeographic units, defined by the physical environment, the multiple land uses, management strategies and production practices. Their spatial configuration has a great importance for landscape function: the gain or loss of a land-use has different consequences depending on where it takes place because it can affect biodiversity, modifying individual patch size and connectivity with similar patches, acting as ecological barriers or corridors for species dispersal, thus potentially increasing or decreasing biological diversity.



Fig. 2 Patch matrix interactions between different olive historical and spatial patterns in the same landscape, example 1.



Fig. 3 Patch matrix interactions between different olive historical and spatial patterns in the same landscape, example 2.

Breaking Points in Time

Sicily was part of the natural distribution area of *Olea europaea* pollen rain during the Pleistocene and served as areas of refugia during the Last Glacial Maximum (Langgut et al., 2019). Sicily, being an island, played a large role as a shelter of a significant number of endemic trees (Médail et al., 2019): evidence of *Olea europaea* var. *sylvestris* during the Preboreal have been found in several paleosites of the island, suggesting an early colonization of the species and its adaptation to local ecological conditions (Sadori et al., 2016). Reconstructions of the Holocene vegetational dynamics and regional fire history in the evergreen vegetation belt of coastal areas of Sicily has shown that there was a fire-prone open grassland until ca. 8050 BC, when an increase in *Olea* percentages is registered; such rapid afforestation was climatically induced (due to higher moisture levels) and affected the intensive early Neolithic agriculture, in the sense that the rise could have reduced the harvest success and thus forced people to migrate in search of new agricultural land, from the coast to the hilly country of central Sicily. Vegetational conditions remained almost stable for several millennia, suggesting that the landscape was still open, probably comparable to the present-day *Olea*–*Pistacia* maquis, even during periods with highest *Olea* occurrences. The fire frequency remained rather low until ca. 800 BC, as frequent anthropogenic burning began, causing a collapse of the coastal forest (Langgut et al., 2019; Sadori et al., 2016).

Dating the beginning of olive cultivation in Sicily remains quite difficult. Being *Olea* dominant in the local natural forest (so its pollen values significantly high in humid phases), such marker cannot be a clear temporal indicator of the date for domesticated olive cultivation. Some chemical signatures of olive oil have been instead identified in three Early Bronze pottery vessels from southern Sicily, dated to the 5th and the beginning of the 4th millennium BP (Tanasi et al., 2018); we could then infer olive cultivation and oil production from that period onwards. The cultivation of olive trees was in any case a process mediated by sociocultural adaptation; probably the first domestication started very experimentally, originating as part of more mixed cultivations with the purpose to increase fruit size and improve their quality, as well as to produce oil (Forbes and Foxhall, 1978).

With the domestication of the oleaster started a new era in land use, the tree crops or “wooden crops” (Emanuelsson, 2009) system, which has persisted in several forms until today. Near-East human migrations to the West Mediterranean Basin brought new olive cultivation methods into the island. After the Roman conquest of Sicily in the 3rd century, the impact on the environment increased and Romans implanted an extensive agrarian system (the *latifundum*) based on wheat and vineyards, accompanied by the presence of scattered olives. During the final centuries of the Roman period (4th–6th centuries) the agrarian economy in Sicily reached its peak, favored by a period of increased humidity which made it easier to expand cultivation. Such fortunate climatic conditions allowed the late Roman-Byzantine society to continue into the early Medieval Period without major interruptions.

Sicily's early-Medieval era of prosperity seems to have come to an end around AD 750, when a sudden climatic shift toward aridity caused a change in the local hydrological conditions crucial to agriculture. Agriculture had to deal with a changed climate (the beginning of the dry period is dated AD 750–850), as well as a general socio-economic decline, could have weakened the Byzantine communities in Sicily, making them vulnerable to Islamic invaders, who completed their conquest of the island between AD 827 and 878 (Sadori et al., 2016). With the arrival of the Arabs on the island, an authentic agrarian revolution began: introduction of new crops, innovative soil improvement techniques and hydraulic systems which contributed to a better use of water resources, a temporal and spatial differentiation of production and a more integrated view of the agricultural system in all its components (irrigation, energy, micro-climate and aesthetic functions): a completely different approach to agriculture which, for its holistic nature, could be indeed defined as agroecology. Such structural revolution marked deeply the Sicilian agrarian landscape; it was the beginning of the *coltura promiscua* system, based on an authentic intercropping of the fruit trees (olive included) (Barbera and Cullotta, 2016).

During Late Middle Ages the first forms of feudal system were introduced in Sicily, even though based on the old structure of the Roman *latifundia*. Olive trees were not yet considered systematically as a crop by themselves, but just an integration to the main cereal production of extremely large estates owned by noble families, or by bishops, and managed locally by tenants. Late Medieval was also the period when several oil-mills started to be hidden and thus realized underground, testifying late Medieval fears of the Turkish pirates' incursions in the island (von Falkenhausen, 2013; Tyerman, 2005).

In the 17th–19th centuries, together with the rest of Europe, Sicily was affected by the Little Ice Age. Several clusters of climatic extreme events occurred around 1691–1694, 1713–1714 and 1812–1814, which affected the island olive crops remarkably, due to heavy snowfalls and frosts. A frost of -13°C kills the olive to the ground; its base survives, but it needs to be re-grafted and takes several years to produce olives again. Ancient olives still alive today, as multi-stemmed trees, contain quite interesting records of historic frost damages (Grove and Rackham, 2001).

Deforestation and early agriculture mechanization started in Sicily in the 20th century, following the overall European trend of intensification and standardization. Immediately after World War I, the Fascist regime revived the old Roman concept of Sicily as the “granary of Italy”, but the cultivation of cereals on a large scale was not well managed and impoverished the soils (Martini et al., 2016). The *latifundia* system was officially dismantled after World War II, but the new land system (based on small-scale private properties) was not able to provide peasants with enough means; moreover, even though legally dismantled, the effects of that land structure are still dominant in Sicily today through the influence of rural forms of mafia (Lupo, 1993); olive cultivation has become a mean of resistance for small-scale land users, within a system devoted mainly to cereal cultivation and husbandry.

In the last 50 years, the implementation of measures under the European Union Common Agricultural Policy (CAP) has brought an increase in crop productivity through the massive use of mechanization and pesticides: intensive olive plantations have appeared in coastal areas and inland hills, while the most rural and inaccessible locations have been characterized by a high degree of abandonment. From the 1970s, the old *coltura promiscua* of the island (together with its biodiversity and agroecological measures to contrast soil erosion and habitats degradation), started to disappear, while new modern terracing and hydraulic systems, stone-clearing and stone-made artifacts have become the protagonists of the agricultural landscape transformation (Barbera and Cullotta, 2016).

Nowadays, despite their huge ecological and cultural importance, olive trees (both old-century trees and younger ones) covers a total surface which is no more than 6.23% of the island (our elaboration on data from ISTAT, 2016). A number of EU programmes have been tackling rural abandonment since 1994, trying to ensure the survival of the olive intercropping systems, but so far they have had little effect (Ferrara, 2016).

Spatial Nodes of Connection

Space is intertwined with time in simultaneities ongoing of histories and geographies (Massey, 2006). In this sense the landscape has always the nature of “work in progress” (Ingold, 1993, p. 162), in which we can read spatiality and temporality.

Focusing on the occurrence of the olive trees as a single plant species and on the typology of their spatial connectivity, we will here discuss the high level of heterogeneity in their spatial and temporal patterns.

Terraces

There are several old and hand- built terraces in the mountains and hilly areas of Sicily (Figs. 4 and 5).

The terraces system has permitted cultivation on slopes with an inclination of even up to 75% (Blondel, 2006) and they have always been a way to fight soil erosion. Built with stone walls, they run horizontally across slopes, while pocket terraces surround individual trees on very steep slopes, where it was impossible to realize proper terraces (Foxhall, 2013). Unfortunately, there are no detailed data and information about all the terraced areas in Sicily since, due to their marginal position, they have always been the first places to be abandoned. Terraces are also very difficult to date, but from the ancient trees standing on them we could infer their age. Today many of them are affected by soil erosion and degradation, thus in many cases they are hidden by overgrown vegetation (La Mantia et al., 2011). Olive trees have always been a traditional crop suitable for terraced areas, and in fact many ancient trees could be found on them.

The agroecological value of terraces is huge. As a land management system, they are not only able to produce value from steep slopes, transforming them into productive areas; they also protect or slow down potential erosion and sloping processes, improving the moisture level and consequently the micro- climate. Terraces are often located between woody areas and open field crops, so they also prevent fires from propagating. Finally, their role in biodiversity conservation is crucial since in a terraced system it is possible to find a wide group of different habitats and ecosystems (Barbera and Cullotta, 2016).

Coltura promiscua

Coltura promiscua (tree species intercropping, in combination with pasture or grain cultivation), is one of the most ancient land use patterns in Sicily (Fig. 6).

Originally, the aim of mixed agriculture was the minimization of crops loss; on the island, *coltura promiscua* landscapes are located mainly in complex and transitional geomorphological contexts as between hills and high mountains. Mixed cropping, often close to urban settlements and agro-forestry systems, creates closed landscapes characterized by traditional and highly patch-intensive cultivation mosaics, with the olive tree as a significantly constituent. In addition to its economic importance and peculiar historical identity, the olive tree in a *coltura promiscua* setting plays a very important role in preventing soil erosion. This is particularly significant in more marginal and degraded areas, that are often semi-abandoned nowadays. The fuzziness of the boundaries in a *coltura promiscua* system makes it difficult, in some cases, to locate different crops, or to differentiate between pastures, Mediterranean scrubs, or cultivated and native trees, as the gradient of combinations may vary (Barbera and Cullotta, 2016).

Olea europaea woods remains and trees outside forest

In the island there are some remains of ancient *Olea europaea* woods, including the Mimiani olive wood and some abandoned woods in the Hyblaean Plateau; *olea* semi-woods today could be also the signs of ancient abandoned orchards (Ruhl et al., 2011).

Scattered olive trees, or trees outside forest, are quite often present in the Mediterranean cereal open fields interplanted with typical Mediterranean woody crops such as olive, grapevine, almond and carob. In the inner areas of the island this spatial pattern could be often found, since such open fields are in many cases what remains of more and less ancient *latifundia*. It is also possible to find lines of old-century olive trees planted as boarder markers and protection against wind for citrus groves.

The multifunctional role of the trees outside forests in the Mediterranean agricultural landscapes is huge, since they play the key role of ecological corridors in those areas characterized by intense and mono-culture land use (Marchetti et al., 2002).



Fig. 4 Remains of ancient terrace systems.



Fig. 5 Pocket terrace covered by overgrown vegetation.



Fig. 6 Example of coltura promiscua (intercropping system) with olive and several other tree species.

Contemporary olive groves

Contemporary olive groves are characterized by a typical straight geometric structure. They may be found in hilly and plain areas of the island and their extension usually does not exceed the 3–4 ha, unless in the case of highly intensive plantations. Trees in such groves are usually very young (from 1 to 60 years old approximately). This type of spatial pattern emerged as a result of the 20th century agriculture intensification, even though some types of specialized olive groves could also be found in ancient large estates. Nonetheless, strictly geometric olive groves are mostly the result of the CAP implementation in Sicily, since several subsidies have been granted to farmers in order to allow them to plant new orchards according to spatial rationalization logics over the short-term (Ferrara, 2016).

The Endurance of Olive Biocultural Heritage in Sicily

Worldwide, many of the most biodiverse landscapes have been produced by long-term, anthropogenic management practices. In places where local management has been discontinued, or cultural landscapes have become relict, historical-ecological research has

demonstrated that the absence of humans can lead to a decline in species diversity, landscape heterogeneity, and threats to livelihood, also in relationship to the cultural significance of the social practices embedded in the landscapes they produce. Local ecological knowledge, traditions, social norms, and languages are intimately linked with the landscape, and crucial for both biological and agro-ecological diversity.

In Mediterranean agro-ecosystems, old-century olive trees are a unique example of the long-term stewardship relationship between people and nature (Allen et al., 2018; Chan et al., 2016). The domestication and continuous careful management of olive trees by locals have been crucial for their longevity; they can thus be seen as stabilities in a changing landscape along time and space and as living biocultural refugia (Barthel et al., 2013), preserving biodiversity and the extraordinary “melting pot” of traditional local agro-practices and different ecological knowledges that have crossed the island of Sicily for millennia.

Local land use practices and traditional agro-ecological knowledge has brought a high endurance and adaptability of these social- ecological systems, which are linked both with biodiversity, rural identity and heritage (cf. Lindholm and Ekblom, 2019). We consider Sicilian ancient olive trees as continuities in the historical landscape. Their quite unique longevity and resilience, together with their special spatial configurations, offer the unprecedented opportunity to study long-term adaptability processes, mapping land use relative temporalities and understanding the logics behind them.

Conclusion: From Carving up to Transformative Stewardship

In complex Mediterranean agro-ecosystems is imperative to counteract soil and land degradation, water depletion, rural area depopulation, as well as the loss of local ecological knowledge. A better understanding of the multiple use and functions of tree crop landscapes will contribute to improve food security, land quality and conservation of natural resources.

Biocultural Heritage is a new and enabling concept in terms of supporting local advocacy groups, legal frameworks and agricultural innovation by and for local communities. Importantly, practices related to Biocultural Heritage are closely linked to the construction and confirmation of identities and social cohesion that are place-based and drawing on heritage (Lindholm and Ekblom, 2019).

A long-term ecological model on how traditional systems evolved to cope with vulnerability is needed to build resilient communities. Through the identification of landscape transformations, insights may be gained into important issues such as their responses to anthropogenic and environmental pressure, enabling researchers to predict the impact of future global changes. These enduring landscapes are in fact increasingly under threat due to climate change and intense land abandonment; their progressive fragmentation represents a huge threat for the ecological complexity of rural landscapes, their agricultural practices, cultural heritage, and socio-economic conditions of local communities (Biasi et al., 2017).

Tracing Sicilian olive land use across different spatial and time scales may consequently allow for an exploration in the local engagement processes with vulnerability and the related socio-ecological adaptation strategies. Land use play a crucial role because on one hand it is affected by climate change but, on the other hand, it has the potential to mitigate climate change (Schermer et al., 2018). Paradoxically low-intense agroecosystems could play today a strategic role in tackling the effects of climate change, while maintaining ecological diversity, improving adaptability and putting into practice a sustainable model of land use which may go beyond business-as-usual logics. The historical role of agriculture in creating semi-natural anthromes (Ellis et al., 2010) is still not fully appreciated by many; nor is the fact that for many European high nature value areas the only practicable, socially acceptable and sustainable management involves the continuation of low-intensity farming. Ecologists and conservationists should think less of “remnants of habitat being left amongst farmland” (Signal and McCracken, 1996, p. 413) and more of farmland anthromes for which optimum management practices need to be co-developed with local communities; while, at the same time, emphasis on site-based conservation should be complemented by strategic initiatives promoting a broader management approach at the landscape scale. Within a transformative perspective pursuing a new meaningful re-coupling between ecosystems and social systems, land use and local conditions should be understood in their dynamic relationship, in which agrosystems resilience must be always considered in a critical perspective, and where the simplistic reintroduction or maintenance of traditional farming could not be the panacea because these systems may be poorly equipped to cope with new environmental conditions. If agroecosystems, included the traditional ones, are a constantly changing heterogeneous patchwork of relations between people, plants, animals, other organisms and the environment happening at different temporal and spatial scales, how can this dynamism and these relations be maintained?

The problem is general, but the solutions cannot be generalized, because they need to be tailored to different local contexts and co-developed with locals, within an overall framework that consider farmlands as biotopes having ecological value by themselves. It is within this framework that transformative stewardship promotes different ways of understanding the environment and human-nature relationships, based on the knowledge of ecological and social interdependencies organized in networks of interactions reconnecting people to the biosphere, changing human behaviors at the individual level but also promoting collective actions, emphasizing relationships between people about nature, including their emotional and cultural dimensions.

Such type of stewardship emphasizes the diversity of values and responsibilities but also the need for fundamental social change in order to ensure that conservation efforts would not exacerbate social, democratic and ecological vulnerabilities. Based on adaptive co-management, transformative stewardship considers that we can increase the resilience of a system by using science and social learning, building dialogues based on a form of ecological solidarity that allows for a plurality of perspectives.

Acknowledgements

We are grateful to Tommaso La Mantia (Agriculture and Forestry Science Department, University of Palermo) for his valuable contribution to this article.

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Protected Areas and Anthromes

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Abstract

Protected areas cover about 15% of the Earth's terrestrial land, and there are current efforts in place (e.g., Aichi Target 11) to increase the extent of protected areas globally. Although some protected areas have shown to slow the loss of natural habitats and biodiversity loss, there is great variability in the extent to which protected areas are directly impacted by humans. Anthropogenic biomes, or anthromes, can vary within and across protected areas, as some protected areas have little human impact while other protected areas have intense human impact. However, these anthromes have changed over time within and outside of the protected areas. Given the calls to increase the extent of protected areas globally, it is important to take anthromes into consideration as a factor in determining where protected areas will best serve biodiversity conservation.

Protected Areas

Globally, ~15% of terrestrial land and 4% of marine areas are protected in more than 240,000 protected areas (Fig. 1: Protected areas). The United Nations Environment World Conservation Monitoring Centre (UNEP-WCMC) has quantified the extent of protected areas in all countries and territories that are classified as UN Environment Regions. As of July 2019, the percentage of

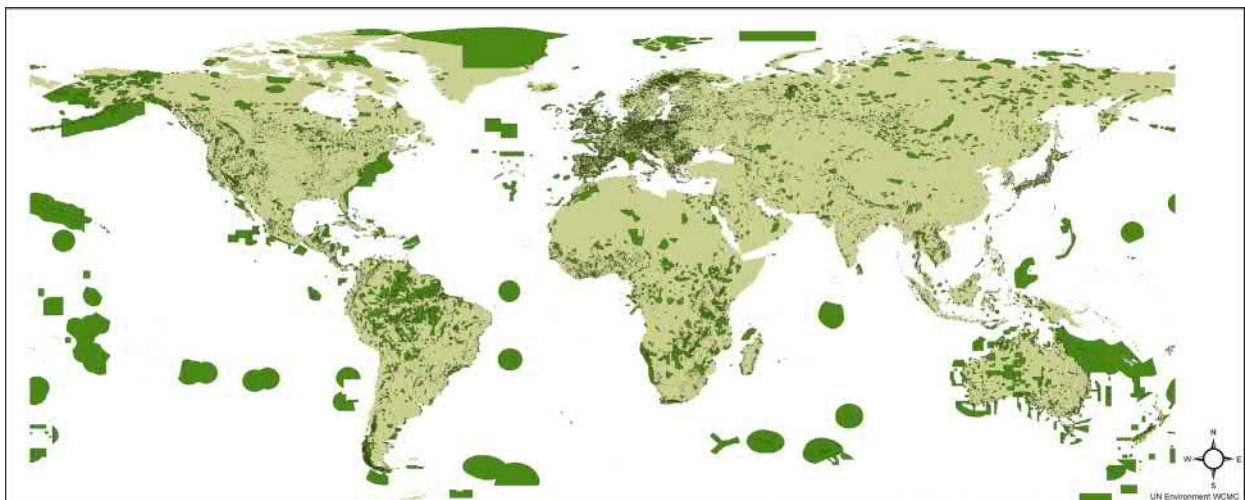


Fig. 1 Protected areas (terrestrial and marine) across the globe. Data source: UN Environment WCMC.

Table 1 Protected areas (PAs) by Region^a.

Region	Number of PAs	% of area protected		IUCN management category (% of PAs) ^b							Governance type (% of PAs) ^b				
		Terrestrial	Marine	I	II	III	IV	V	VI	Other ^c	Government	Private	Shared	Indigenous people and local communities	Not reported
Africa	8507	17	4	1	4	<1	4	1	3	88	50	12	3	3	33
Asia and Pacific	29,527	19	12	13	6	24	34	7	8	9	76	5	9	2	8
Europe	152,774	20	10	5	<1	12	29	9	1	44	87	<1	<1	<1	12
Latin America and Caribbean	8588	23	13	3	10	3	14	7	21	42	47	10	2	9	32
North America	42,237	9	15	7	4	6	11	68	2	2	65	21	9	<1	4
Polar	35	86	34	29	3	9	6	3	3	49	49	0	0	0	51
West Asia	358	7	5	5	4	2	16	6	10	58	43	1	8	3	46

^aUNEP-WCMC (2019). Protected Area Profile from the World Database of Protected Areas, July 2019. Available at: www.protectedplanet.net.

^bPercentages do not always add to 100 due to rounding.

^cOther consists of three categories: not reported, not assigned, and not applicable.

terrestrial area that is protected varies by geographical region, ranging from 7% and 9% in West Asia and North America, respectively, to 86% in the polar region (Table 1). For marine areas, these values range from 4% and 5% protected in Africa and West Asia, respectively, to 34% protected in the polar region.

The International Union for Conservation of Nature (IUCN) has defined main categories for protected areas, and these categories define the objectives of the reserves in the category, have distinguishing features based on the level of human activities, and have specific roles in the landscape or seascape. The IUCN categories are: Ia (strict nature reserve), Ib (wilderness area), II (national park), III (natural monument or feature), IV (habitat/species management area), V (protected landscape/seascape), and VI (protected area with sustainable use of natural resources). Some protected areas have strict protection laws (IUCN management category I), while others permit a variety of human activities (IUCN management category VI), and others have no IUCN ranking (Table 1). The percentage of protected areas under the various IUCN categories varies geographically: 31% of the protected areas in the polar areas are in either the IUCN category I or II, while 5% of the protected areas in Africa and Europe are designated in IUCN categories I or II.

The governance of the protected areas is primarily based on government protected areas (79% of protected areas), followed by private (5%), shared (3%), and indigenous peoples and local communities (<1%); 12% of the protected areas do not report their governance structure. The governance of the protected areas also varies geographically (Table 1). For example, governance in 87% of the protected areas in Europe is by government, while in West Asia and Polar regions these percentages drop to 43% and 49%, respectively. Private governance is greatest in North America (21% of protected areas), while the highest percentages for shared governance (8–9%) are in Asia and the Pacific, North America, and West Asia. Governance by indigenous people and local communities is greatest in Latin America and the Caribbean (9%), with all other regions having 0–3% of their protected areas falling into this category. Although these governance data are informative, it is important to note that in four regions, more than 30% of the protected areas did not have governance information reported (Polar: 51% of protected areas, West Asia: 46%, Africa: 33%, and Latin America and the Caribbean: 32%).

Biodiversity Conservation

The percentage of terrestrial land and marine areas that have been designated as protected has increased during the past several decades. Although multiple studies have shown that protected areas often aid in biodiversity conservation, the global rate of species declines has consistently increased and almost half of terrestrial tropical protected areas have experienced biodiversity loss during the past couple of decades (Laurance et al., 2012). Therefore, there remains a great need to expand, improve upon, and complement the current protected areas, with an eye to conserving biodiversity.

In October 2010, the Convention on Biological Diversity's Conference of the Parties set forth the Aichi Biodiversity Targets as part of the Strategic Plan for Biodiversity 2011–20. These 20 targets address five strategic goals associated with reducing biodiversity loss. These targets range from increasing people's awareness as to why biodiversity is important, and how people can work on conserving biodiversity and use biodiversity sustainably (Target 1) to mobilizing financial resources to carry out the plan (Target 20). Aichi Target 11 specifically addresses protected areas: this target is to protect 17% of terrestrial land and inland waters, and 10% of coastal and marine areas by 2020 (<https://www.cbd.int/sp/targets/>).

However, some argue that Aichi Target 11 is not sufficient for biodiversity conservation (Dinerstein et al., 2017). Venter et al. (2014) found that only 15% of threatened vertebrates have adequate coverage from protected areas: 17% of threatened vertebrates

were not located within a protected area, and overall, 85% of threatened vertebrates are not covered by protected areas to an extent great enough to provide future protection. Marine protected areas can positively impact biodiversity conservation, but staff and budgetary limits can negatively impact conservation measures (Gill et al., 2017). Therefore, the expansion and creation of new protected areas must be strategically done so that biodiversity is protected to a greater extent (Gill et al., 2017; Venter et al., 2014). Although protected areas can be terrestrial or marine, this current encyclopedia article focuses on terrestrial protected areas and the relationship between them and terrestrial anthromes.

Anthromes

Ecologists typically classify regions into biomes, based on vegetation and climate patterns. However, these biome classifications rarely take into consideration the impact that humans have on ecosystems and biodiversity, specifically the alterations that humans have made to biomes. Human behavior can be an important factor in species distribution patterns; for example, Brum et al. (2013) found that land use was a better predictor than climate for amphibian distribution.

The concept of anthromes, or anthropogenic biomes, was introduced by Ellis and Ramankutty (2008). Anthromes are determined by factors such as human population, land cover, and land use. To date, anthromes primarily have focused on terrestrial regions. During the past decade, researchers have used anthromes to address questions related to how humans impact global ecosystems, and the connections between ecosystems and humans. Overall, protected land has a smaller human footprint than non-protected land, but almost 60% of protected land experiences some extent of human pressure (Jones et al., 2018). Furthermore, more than 50% of protected areas consist solely of land that is under intense human pressure; only 10% of protected areas are free of human pressure (Jones et al., 2018). Therefore, it is important to examine protected areas in light of the human presence and pressure on these protected areas.

The anthrome categories may vary in number, depending on the analysis. The data presented in this overview follow the second version of the anthrome data set (Anthromes V2; Ellis et al. 2010). Anthrome classes provide a different view of a geographic area, when comparing these anthromes to biomes (Fig. 2). This is not to say that one data set is superior to the other; using a combination of data sets can help further discern patterns in species distributions, biodiversity, and conservation, especially in the context of the role that humans have played in shaping and being shaped by the local environment.

Protected Areas and Anthromes

Anthromes are not equally protected: remote woodlands, wild treeless and barren, and wild woodlands have the largest percent of their areas protected, while irrigated villages, rice villages, and residential irrigated croplands have the least protection (Martin et al., 2014), and areas that are not as populated by humans typically have greater protection than anthromes that are more populated (Martin et al., 2014). Furthermore, anthromes have not received equal attention when it comes to research studies; urban, mixed settlements, and residential woodlands have been the focus of the most studies, while rice villages, remote rangelands, and irrigated villages have been studied the least. When Martin et al. (2014) examined the prioritization of protection for an area (based on biodiversity hotspots), they found that anthromes that had a higher prioritization had less protection.

Anthrome Change: 1700–2000

As human population has increased, the pressures that humans put on their environment have intensified. By mapping data from Ellis et al. (2010), one can see that in 1700, the most prevalent anthromes at a global scale were wild woodlands (29% of terrestrial areas), wild treeless and barren lands (27%), inhabited treeless and barren lands (14%), and populated woodlands (13%). By 2000, the most prevalent anthromes at a global scale were relatively similar, with the two most-prevalent anthromes being the same as in 1700. However, the percentage of area making up wild woodlands and wild treeless and barren lands was approximately half of the 1700 values: wild woodlands (19%), wild treeless and barren lands (15%), remote rangelands (13%), and populated rangelands (9%). The similarities in most-prevalent anthromes are due to the large land masses in the high latitudinal regions and the Sahara Desert in Africa where the extent of direct human influence on the land has not been as great as it has been in other regions. The differences between 1700 and 2000 are much more evident when examining areas in mid- and low-latitude regions (Fig. 3A and B).

The extent to which anthromes have changed in mid- and low-latitude regions is evident when examining the global data, as well as in areas inside and outside of protected areas. Protected areas often are subjected to less land cover change than nonprotected areas, and this pattern is illustrated in the case of some, but not all, protected areas. For example, in an area of central and eastern Brazil, covering areas that include the Amazon and the Atlantic Forest, some of the indigenous areas in the Amazon have not encountered as large a change in anthromes as areas outside of these protected areas, or compared with protected areas in the Atlantic Forest region (Fig. 3C and D). These differences can be seen visibly, even before the differences are quantified. However, as evident from these examples (Fig. 3D), current protected areas in Brazil represent a range of anthromes, including ones that have been moderately-to-intensely used by humans.

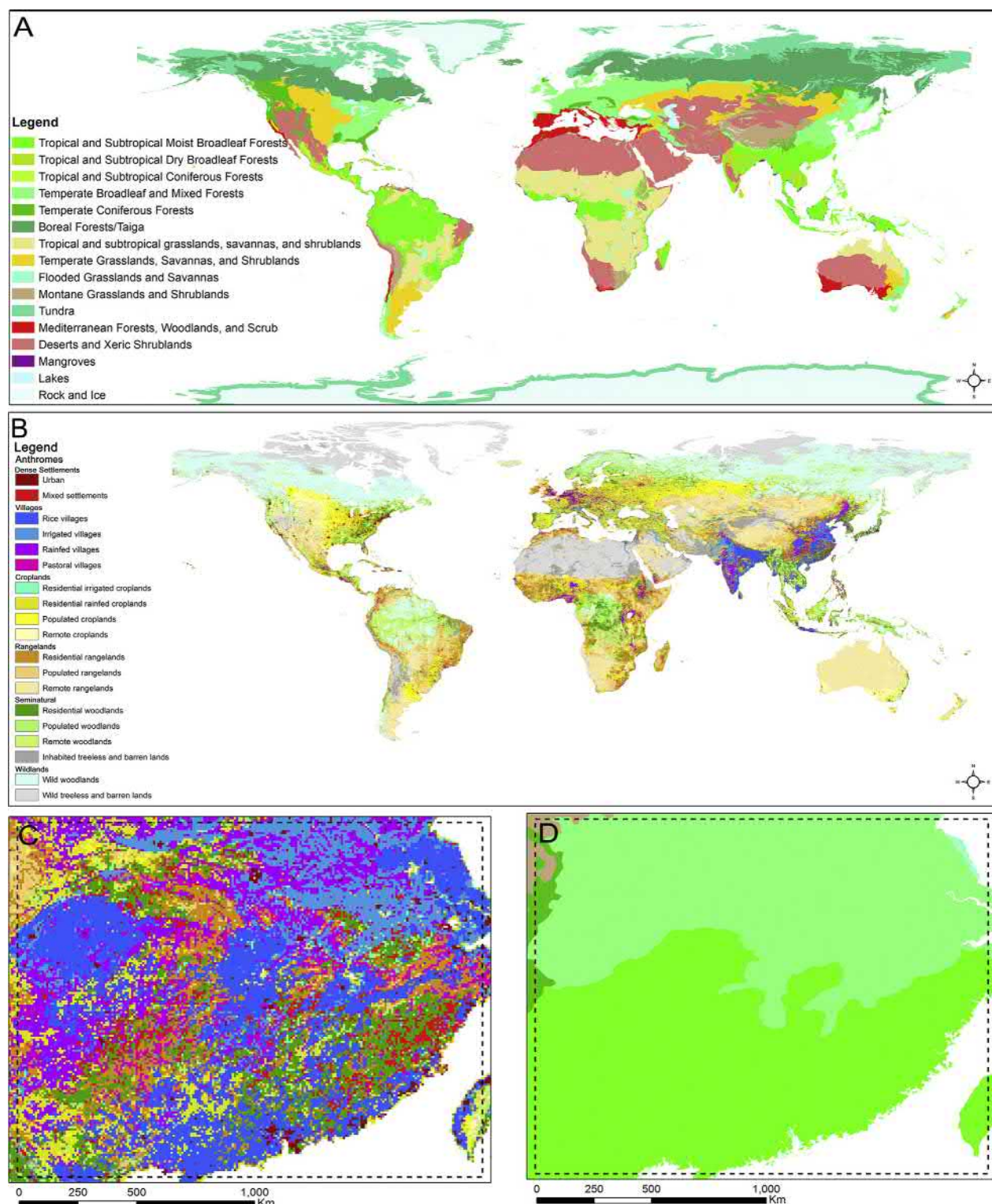


Fig. 2 Terrestrial biomes (A) and terrestrial anthromes (B) differ in the data they provide. In an areas of East Asia (*dashed box*), there are close to 10 anthromes noted (C) while the same geographic region is noted by three biome types (D). Consider having one large map to show the global patterns, but then subset boxes to show what a small area looks like when using biome data, anthrome data, and satellite imagery. Data sources: World Wildlife Fund; Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D., and Ramankutty, N. (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* **19**, 589–606.

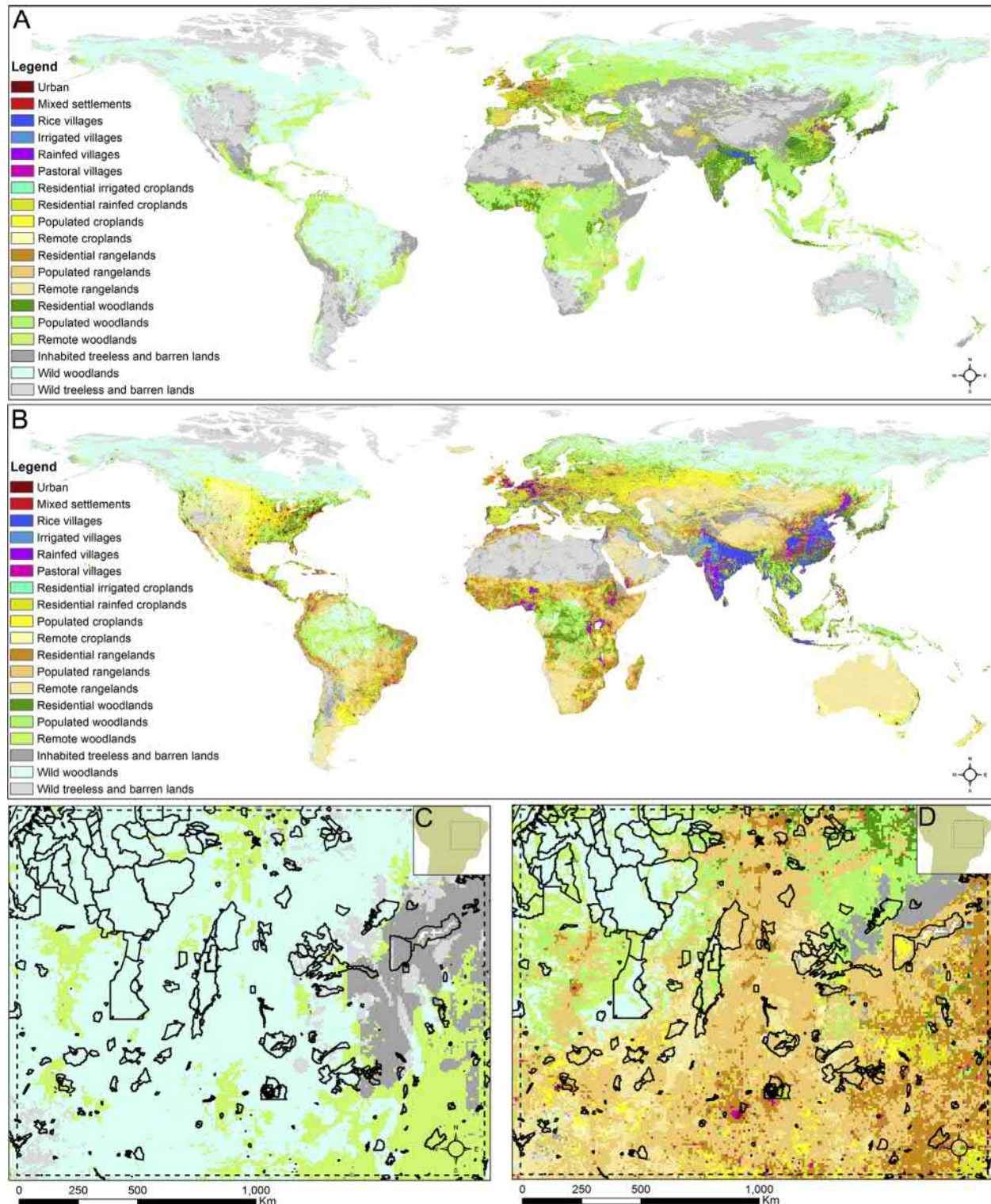


Fig. 3 Terrestrial anthromes have changed from 1700 (A) to 2000 (B), especially in mid- and low-latitude regions. These changes are evident inside and outside of protected areas, including in a subset (C and D) of the Amazon and Atlantic Forest regions in Brazil. In 1700, wild woodlands (67% of the geographic area mapped; C) and remote woodlands (18%) dominated the landscape, including in areas that eventually became protected areas (delineated by the *black polygons*). By 2000 (D), much of the wild woodlands and remote woodlands, especially outside of the protected areas located in the northwestern area of the sample (in the Amazon), had been converted to populated rangelands (39%) and residential rangelands (12%), with wild woodlands (11%) and remote woodlands (7%) representing a much smaller area than in 1700. These areas where the anthromes changed from 1700 include localities that are currently designated as protected areas. Data sources: Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D., and Ramankutty, N. (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* **19**, 589–606; UN Environment WCMC.

Roads

Another variable to consider when studying the extent to which biomes are impacted by humans is the presence of roads: although ~80% of the terrestrial regions of Earth do not have roads, the roads that do exist split the land cover into many patches, and more than 92% of these patches are $\geq 100 \text{ km}^2$ (Ibisch et al. 2016). These findings have implications for the protection and conservation of anthromes. For example, Ibisch et al. (2016) found that remote rangelands (16.7%), wild woodlands (16.7%), and wild treeless and barren lands (14.2%) had the highest percentage of roadless areas (defined as roads and the 1-km buffer surrounding the roads), while urban (0.05%), mixed settlements (0.4%), pastoral villages (0.5%), and residential irrigated croplands (0.6%) had the smallest percentage of roadless areas in their anthromes.

In summary, about two-thirds of the roadless areas were represented by remote and unmodified anthromes, but anthromes with a heavier human influence, such as rangelands, also attained a relatively high percentage of roadless areas in some geographic locations (Ibisch et al. 2016). When examining the results on a country basis, continental United States, southern Canada, western Europe, and Japan had the smallest percentage of their areas considered roadless. On a continent-level, Africa, South America, Australia, and Asia all had more than 87% of their land as roadless, while Europe (41.6%), North America (61.4%), and Oceania (63.9%) had a notably smaller percentage of their areas considered as roadless.

Green List of Protected and Conserved Areas

The IUCN Green List of Protected and Conserved Areas highlights 45 sites in 14 countries that have been deemed to be strong positive examples in the management and governance of protected areas and conserved areas. Of these 45 sites, 32 were terrestrial sites with geographical extents delineated in the World Database of Protected Areas and with anthrome data covering the extent of the protected areas (Table 2).

When the most-common anthrome in each protected area was noted, there was quite a range of anthromes listed: 12 anthromes were the most-common anthromes in at least one of these 32 sites. Of these 12 anthromes, residential rainfed croplands (19% of these 32 protected areas) was the most-common anthrome for the greatest percentage of the protected areas on the IUCN Green List of Protected and Conserved Areas (Table 2; Fig. 4). Following residential rainfed croplands were residential woodlands (13%), urban (9%), remote rangelands (9%), populated rangelands (9%), populated woodlands (9%), residential rangelands (6%), remote woodlands (6%), rainfed villages (6%), inhabited treeless and barren lands (6%), wild treeless and barren land (3%), and populated croplands (3%). Some of the protected areas from the IUCN Green List of Protected and Conserved Areas were relatively small, so the resolution of the anthrome data (Ellis et al. 2010) did not account for the small areas or heterogenous areas within a small protected area. Furthermore, some terrestrial protected areas were on islands, and the geographical extent was not covered in the Ellis et al. (2010) anthrome data set.

Of these 32 terrestrial protected areas from the Green List of Protected and Conserved Areas, the IUCN categories for the reserves included Ia (3% of the 32 terrestrial reserves), II (31%), IV (19%), V (16%), and VI (3%). There were no protected areas in the IUCN categories Ib or III, and 28% of the protected areas did not have an IUCN category listed (because it was considered not applicable or the category was not reported to the World Database of Protected Areas). When the anthromes were ranked by the extent of human impact (lowest: inhabited treeless and barren lands; greatest: urban; see Fig. 2B legend for the anthrome categories), there was no a relationship between IUCN category and anthrome type (Pearson's Correlation: $P = .21$, $n = 23$, $P = .34$) for the 23 protected areas with an IUCN ranking. For example, the only protected area with an IUCN category Ia classification had residential rainfed cropland as its most-prevalent anthrome, while the only protected area with an IUCN category of VI had remote woodlands as its most-prevalent anthrome.

Of the 32 protected areas included on the Green List of Protected and Conserved Areas, 72% are governed by governments, 3% are joint governance, 9% are nonprofit governed, and 16% have no information reported regarding governance. All three of the nonprofit-governed protected areas represented on the list have residential rangelands or residential rainfed croplands as the primary anthrome represented. The one joint-governed protected area is primarily urban. The government protected areas range from inhabited treeless and barren lands as the primary anthrome (lowest human influence) to rainfed villages (greatest human influence for the current data set) as the primary anthrome.

Half Earth, Nature Needs Half, and Other 50% Proposals

A recent set of proposals have been made that focus on increasing the area of protected areas to 50% or more of Earth (terrestrial as well as marine ecosystems). These proposals include Half Earth (<https://www.half-earthproject.org/>) and Nature Needs Half (<https://www.half-earthproject.org/>), but there have been scientifically-based calls for 50% protection of ecosystems by a number of studies dating back several decades (see review in Dinerstein et al. 2017). Overall these proposals address the challenge of conserving biodiversity while meeting human demands (e.g., food, shelter).

Is it feasible to protect 50%? In an analysis of 846 terrestrial ecosystems on Earth, Dinerstein et al. (2017) found that 12% of the ecosystems were more than 50% protected, 37% were less than 50% protected but had the potential to reach 50%, and 24% are in danger of being destroyed. Therefore, if these 37% were upgraded to 50% protected, the goal could be reached. However, a goal of 50% protected is not necessarily simple in order to maximize biodiversity, as one needs to consider which areas should be protected

Table 2 IUCN green list of protected and conserved areas as of July 2019^a.

Country	Site name	WDPA designation	IUCN category	Governance	Primary anthromes ^b	
					Most common	Second-most
Australia	Arakwal National Park and Cape Byron State Conservation Area	National Park	V	Joint governance	Urban	Residential woodlands
	Montague Island Nature Reserve	Nature Reserve	IV	Government	—	—
China	Eastern Dongting Lake National Nature Reserve ^a	—	—	—	—	—
	Longwanqun National Forest Park ^a	—	—	—	—	—
	Mount Huangshan Scenic Area	World Heritage Site	Not applicable	Not reported	Residential woodlands	Populated woodlands
	Shaanxi Changqing National Nature Reserve ^a	—	—	—	—	—
	Sichuan Tangjiahe National Nature Reserve ^a	—	—	—	—	—
	Wudalianchi Geological Park	UNESCO-MAB Biosphere Reserve	Not applicable	Not reported	Rainfed villages	Residential rangelands
	Galeras Fauna and Flora Sanctuary	Fauna and Flora Sanctuary	V	Government	Populated rangelands	Residential rainfed croplands
Colombia	Gorgona Natural National Park	Natural National Park	II	Government	—	—
	Tatamá Natural National Park	Natural National Park	II	Government	Residential rangelands	Populated rangelands
Egypt	Ras Mohammed	National Park	II	Government	Inhabited treeless and barren lands	Wild treeless and barren land
	Wadi Al-Hitan	World Heritage Site	Not applicable	Not reported	Wild treeless and barren lands	—
France	Bois du Loc'h	Forest Integral Biological Reserve	Ia	Government	Residential rainfed croplands ^c	—
	Cerbère-Banyuls Marine Natural Reserve	National Nature Reserve	IV	Government	—	—
	Champ du Feu Managed Biological Reserve	Forest Managed Biological Reserve	IV	Government	Residential woodlands	—
	Côte Bleue Marine Park	Specially Protected Areas of Mediterranean Importance	Not assigned	Government	Urban ^d	Rainfed villages ^d
	Donzère Mondragon Hunting and Wildlife Reserve ^e	—	—	—	—	—
	Écrins National Park	National Park—Core Area	II	Government	Remote rangelands	Populated rangelands
	French Southern and Antarctic Lands National Nature Reserve	National Nature Reserve	Ib	Government	—	—
	Guadeloupe National Park	National Park—Core Area	II	Government	Populated rangelands	Residential rainfed croplands
	Hochfeld Managed Biological Reserve	Forest Managed Biological Reserve	IV	Government	Residential woodlands	—
	Iroise Marine Nature Park	Marine Nature Park	V	Government	—	—
	Marais d'Episy Sensitive Natural Area	Biotope Protection Order	IV	Government	Residential rainfed croplands	—
	Orlu National Hunting and Wildlife Reserve	National Hunting and Wildlife Reserve	IV	Government	Remote rangelands	Populated woodlands
Italy	Pyrénées National Park	National Park—Core Area	II	Government	Remote rangelands	Populated woodlands
	Vosges du Nord Regional Nature Park	Regional Nature Park	V	Government	Residential woodlands	Residential rainfed croplands
	Gran Paradiso National Park	National Park	II	Government	Populated rangelands	Residential rangelands
Jordan	Ajloun Forest Reserve	Forest Reserve	IV	Government	Rainfed villages	—
	Azraq Wetland Reserve	Wetland Reserve	IV	Government	Inhabited treeless and barren lands	Mixed settlements

Table 2 IUCN green list of protected and conserved areas as of July 2019^a.—cont'd

Country	Site name	WDPA designation	IUCN category	Governance	Primary anthromes ^b	
					Most common	Second-most
Kenya	Lewa Wildlife Conservancy	Community Conservancy	Not reported	Nonprofit organizations	Residential rainfed croplands	Residential rangelands
	Oi Kinyei Conservancy	Community Conservancy	Not reported	Nonprofit organizations	Residential rainfed croplands	—
	Oi Pejeta Conservancy	Community Conservancy	Not reported	Nonprofit organizations	Residential rangelands	Pastoral villages
Korea	Jirisan National Park	National Park	II	Government	Remote woodlands	Populated woodlands
	Odaesan National Park	National Park	II	Government	Populated woodlands	Residential woodlands
	Seoraksan National Park	National Park	II	Government	Populated woodlands	Residential woodlands
Lebanon	Al Shouf Cedar Nature Reserve	UNESCO-MAB Biosphere Reserve	Not applicable	Not reported	Residential rainfed croplands	Rainfed villages
Mexico	Espíritu Santo Marine Archipelago National Park	National Park	Ia	Government	—	—
	Isla San Pedro Mártir Biosphere Reserve	Biosphere	Ia	Government	—	—
Peru	Amarakaeri Communal Reserve	Communal Reserve	VI	Government	Remote woodlands	Wild woodlands
	Cordillera Azul National Park	National Park	II	Government	Populated woodlands	Wild woodlands
Spain	Doñana Natural Park	Natural Park	V	Government	Residential rainfed croplands	Residential irrigated croplands
	Sierra Nevada Natural Park	Natural Park	V	Government	Populated croplands	Residential rainfed croplands
United Arab Emirates	Al-Wathba Wetland Reserve	Ramsar Site, Wetland of International Importance	Not reported	Not reported	Urban	Inhabited treeless and barren lands

^aIUCN green list of protected and conserved areas: <https://www.iucn.org/theme/protected-areas/our-work/iucn-green-list-protected-and-conserved-areas/iucn-green-list-areas> and World Database of Protected Areas (WDPA; <https://www.protectedplanet.net/>). Four reserves in China are not included in the WDPA data set.

^bAnthromes are designated for terrestrial areas, so marine areas do not have anthrome data listed here. Some island reserves also do not have anthrome data available. When only one anthrome is listed for a site, the site consists 100% of the listed anthrome. Data source: Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D. and Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* **19**, 589–606.

^cDue to the small size of the reserve (0.7 km²), the anthrome data set's resolution did not classify the area as being forested.

^dOnly a small percentage of this protected area is terrestrial; most of the protected area is marine.

^eThis site was listed in 2019 and as of July 2019 there are no accompanying data available on the IUCN or Protected Plant websites.

(and where), as results could vary based on which regions are protected (Ellis and Mehrabi, 2019). In addition, there are questions as to how the protected areas are governed, to what extent the protected areas allow for movement between reserves (which is important for migrating species as well as species that are impacted by climate change), the extent to which there multi-use areas in the protected area, to what extent agriculture is displaced, who has sovereignty over the land, and how to cover the operating costs of the protected areas (Ellis and Mehrabi, 2019).

How Are We Doing?

The majority of the current protected areas were created during the 20th century. The extent of terrestrial ecosystems has approximately doubled since the early 1990s, and continues to increase. There have been conservation successes through these protected areas, with overall global patterns indicating that species richness and abundance are higher inside protected areas, compared to outside of these areas (Gray et al., 2016). However, there can be great variability in the success of a protected area, and many protected areas have minimal funding.

Distribution and Management

Protected areas are not always representative of global ecosystems. Often these reserves are geographically remote or represent areas that humans have not wanted to use for commercial purposes, and they are typically not located in areas with high concentrations of threatened vertebrate species (Venter et al. 2017). The location of reserves does not always match with areas with high phylogenetic diversity (Daru et al., 2019). Furthermore, the locations of protected areas do not often match with the areas that are used by species

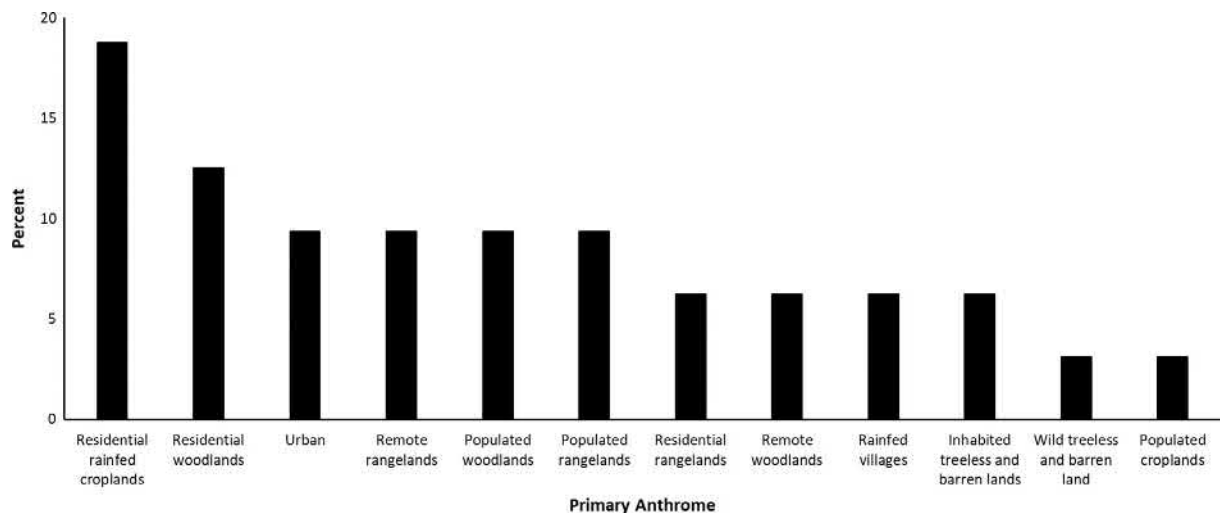


Fig. 4 Twelve anthromes were the most-common anthrome for at least 1 of the 32 terrestrial sites from the IUCN Green List of Protected and Conserved Areas as of July 2019. Of these 32 sites, residential rainfed croplands represented the greatest percentage of sites: 19%. Data sources: IUCN Green List of Protected and Conserved Areas: <https://www.iucn.org/theme/protected-areas/our-work/iucn-green-list-protected-and-conserved-areas/iucn-green-list-areas> and World Database of Protected Areas (WDPA); <https://www.protectedplanet.net/>; Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D. and Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* **19**, 589–606.

that migrate; for example, less than 10% of migratory bird species are covered by protected areas throughout their range (Runge et al., 2015). It is important to strategically place new protected areas in locations where biodiversity conservation may be maximized.

Protected areas also do not have equal protection, even on paper. Although protected areas are distributed across the globe, and in many cases having protection makes it more likely that the land cover will not be modified, more often than not these protected areas are found in areas that are less likely to be subjected to land cover change than other areas. For example, Joppa and Pfaff (2009) found that most national protected areas often are located in areas with higher elevation, increased slopes, and farther from roads and cities; Venter et al. (2014) found that protected areas are often areas that are less expensive to protect, and they are not necessarily areas of high priority for biodiversity protection (as priority areas tend to be more expensive to protect). As a result, there are concerns that protected areas often protect more marginal lands. Furthermore, reasons for the placement of the current protected areas vary greatly based on location.

Furthermore, many protected areas do not receive adequate funding, and they can be hampered by poor management of the areas (Pringle, 2017). Strong management of the protected areas, including having people present in the protected reserve to provide protection of the reserve, was found to be a predictor of a successful reserve (Laurance et al., 2012). One may learn more about management effectiveness, by accessing the Protected Areas Management Effectiveness (PAME) data and reports. The framework for assessment includes taking into consideration management design and planning, management adequacy and appropriateness, and management delivery such as outputs and outcomes.

Biodiversity Conservation

Although one of the primary goals of protected areas is to conserve biodiversity, the rate of species declines has consistently increased. Furthermore, human pressure on protected areas increased over a 15-year period in the 1990s and 2000s, particularly in Southeast Asia, Latin America, Sub-Saharan Africa, and Euro-Asia (Geldmann et al., 2014). Protected areas without an IUCN ranking had greater increases in human pressure, followed by protected areas in category IV. Jones et al. (2018) found that approximately one-third of protected areas are impacted by human pressure; since 1992, 55% of the protected areas have had an increase in human pressure. They found that large protected areas with strict protections had the least amount of human pressure.

There are several examples of protected areas that represent ecosystems that had been degraded and restored (Pringle, 2017), highlighting the importance of considering protected areas and human activities together. Furthermore, Gray et al. (2016) found that species richness and abundance was higher inside even some of the protected areas that had been impacted by human land use (e.g., plantation and cropland). Therefore, understanding the impacts of protected areas on anthromes can be important. Furthermore, given the amount of land that is impacted by humans, taking anthromes into consideration can be important in determining the overall conservation situation.

Pringle (2017) highlights “eight pillars of upgrading protected areas”: (1) “Protect remaining refuges and harness nature’s resilience”—allow natural processes to work, and realize that the restored ecosystem may differ from the original ecosystem;

(2) “Upsize and interconnect”—consider expanding protected areas by increasing their boundaries; (3) “Be long-term and local”—the importance of having a core, local team that can work to improve the protected area; (4) “Pay the opportunity costs”—work with constituencies to increase support for the protected areas; (5) “Develop creative financial strategies”—consider varied financial strategies, such as public-private partnerships; (6) “Know thy biodiversity”—the importance of knowing which species are located within the protected area; (7) “Be adaptable”—realize that some plans may work better under certain situations, and goals may differ depending on the constituents; and (8) “Involve young people”—get children involved and invested in nature.

Socioeconomic Considerations

As outlined above, humans have played a significant role in shaping the anthromes, as well as in the establishment, management, support, and, in some cases, degradation, of protected areas. The earlier sections mention the various roles that humans play in shaping protected areas and anthromes, but it is important to specifically consider how social objectives and economics have shaped (and will shape) protected areas and anthromes. Sometimes the studies of protected areas have a sole focus on biodiversity metrics, excluding any considerations of socioeconomics. Many scholars have argued that it's very important to take economic and social issues into consideration when establishing and managing a protected area. Protected areas should benefit biodiversity conservation and humans. Several of the pillars highlighted by [Pringle \(2017\)](#) specifically address the role that various constituents can play in sustaining a successful protected area; these pillars also stress the importance of understanding that the effort in sustaining a successful protected area will be a long-term investment by people. As the number of protected areas increase, it is very important to ensure that humans, as well as biodiversity, benefit ([Ellis and Mehrabi, 2019](#)).

Moving Forward

As discussed earlier, the type of management that a protected area is under is often related to the success of the reserve. In fact, [Adams et al. \(2019\)](#) found that using funding for management provided increased benefits compared to using the funds to expand the extent of the protected areas. With the call for an increase of the percentage of the Earth that is under protection, some argue that it's increasingly important to focus on the management of the current protected areas, as well as consider the management of soon-to-be created reserves, in order to reap the maximum benefits of the reserve. In other words, simply expanding the number and size of protected areas is not necessarily going to help reach the goal of conserving biodiversity and ensuring that human needs are met. Without investment into management, biodiversity benefits may not meet their potential. Therefore, some propose that protected area expansion, although important, should be accompanied by appropriate management in the already-established protected areas, as well as those protected areas that are being designated in the near future to meet specific targets.

To meet the 17% goal of Aichi Target 11, almost 2 million km² (representing 190 terrestrial ecoregions in 114 nations) will need restoration ([Mappin et al., 2019](#)). Although restoration of land that has been slightly modified is seen to be possible, there are ecoregions that have been so heavily modified that restoration will take great effort. Therefore, there needs to be a concentrated effort to evaluate the potential of restoration for particular ecoregions, and identify specific ecoregions in specific locations where there is a higher likelihood of success.

[Ellis and Mehrabi \(2019\)](#) recommend that people consider the Half Earth concept as a Whole Earth project, that people should be encouraged to work to protect biodiversity at multiple scales (local, regional, and global) instead of thinking about protection as two halves: “nature’s half” and “human half.” This argument is supported by the fact that, as discussed above, humans have impacted a majority of the terrestrial surface of Earth already. By including anthromes in analyses, one can better understand what the primary actions of humans are (and have been) based on geographical location. For example, it could be helpful in tracing the history of the geographical location, noting to what extent the anthromes have changed in particular locations. Furthermore, analyses could reveal if there are geographical patterns in regards to the spatial distribution of anthromes, the history of the current anthromes, and the distribution of particular species. Such considerations can be important when thinking about biodiversity conservation overall, but particularly when certain species are of conservation focus. Species have a range of habitat requirements, and some are more sensitive to particular types of human activities than to other human activities. By having a better understanding of the anthromes in a protected area, as well as outside a protected area, could help with plans to conserve biodiversity.

Conclusion

Given that the majority of the land on Earth has been impacted to some extent by humans, it is important for there to be more widespread consideration of how humans and the natural systems in which humans have evolved are interconnected. Solely

designating areas as protected areas will not necessarily conserve biodiversity for the future; the protected areas need to be ecologically relevant in order to maximize biodiversity conservation. Because the percentage of land that is considered pristine, with little to no human impacts, is minimal when compared to all terrestrial areas on Earth, and the majority of protected areas also are impacted by humans, addressing conservation issues such as biodiversity decline, as well as understanding current and future impacts of climate change on biodiversity, will require natural scientists, social scientists, policy makers, lawmakers, educators, and humans in general to take a look at the natural system in which we live, and truly think about how our behaviors and actions impact the rest of the system, as well as how the natural system impacts our lives.

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The Extraordinary Value of Wilderness Areas in the Anthropocene

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Abstract

Humans have altered the majority of Earth's terrestrial surface, yet some places still remain relatively undisturbed by modern society. These wilderness areas contain the most intact ecosystems on Earth. Here, we review the emerging evidence that wilderness areas are exceptionally important relative to more degraded ecosystems for biodiversity conservation (e.g. halving species extinction risk), Earth system functioning (e.g. supporting continental scale hydrological cycles), and for supporting the cultural integrity of many indigenous communities worldwide. We then describe the current state of wilderness conservation and mapping. Despite their immense value, wilderness areas are being rapidly lost, are under protected, and are almost completely overlooked in global environmental policy. Our window of opportunity to safeguard Earth's last wilderness areas and their unique values is closing fast, but through a combination of smart policy changes and immediate large-scale conservation efforts, we can still secure them for future generations.

"If future generations are to remember us with gratitude rather than contempt, we must leave them something more than the miracles of technology. We must leave them a glimpse of the world as it was in the beginning"

—Lyndon B. Johnson

Wilderness Defined

Humans have significantly altered the majority of Earth's terrestrial area (Ellis and Ramankutty, 2008; Venter et al., 2016b). Land uses such as pasture and cropping are now extensive (Ramankutty et al., 2008; Alkemade et al., 2013), industrial infrastructure, forestry, road networks and urban areas are proliferating (Seto et al., 2012; Ibisch et al., 2016), and activities such as the harvesting and hunting of wild plants and animals are highly unsustainable (Ripple et al., 2016). The increase in these "human pressures" has come at the expense of previously wild places, causing biodiversity and the condition of ecosystems to decline worldwide (Ellis et al., 2010; Barnosky et al., 2012; Ceballos et al., 2017). However, human pressure varies across Earth's surface, and some corners of the planet remain undisturbed by the impacts of modern society. These places can be considered wilderness, and contain the most intact ecosystems on Earth (Lesslie et al., 1988; Mackey et al., 1998; Watson et al., 2016).

Wilderness does not mean "pristine" or "untouched" because nowhere meets this standard in an era of human forced climate change and global pollution (Barnes et al., 2009; Scheffers et al., 2016). Wilderness areas are also not exclusive of people, as human presence can and does occur within them, provided human impacts are minimal and do not compromise the ecological integrity of the area (Mackey and Claudie, 2015; Larsen and Jaeger, 2017). Human societies have occupied all continents except Antarctica and influenced the environment much more than previously thought. For example, prehistoric humans farming domesticated plants shaped tree communities in some of the remotest parts of the Amazon rainforest (Levis et al., 2017). However, the ecological

footprint of these societies is challenging to measure and is likely minimal compared to the environmental impacts of modern industrial land-uses (Klein et al., 2009; Newbold et al., 2016).

There is room for debate as to what truly constitutes wilderness, and a variety of definitions have been developed by governments, non-government organizations and researchers, but there is no global consensus on the definition (Hawes et al., 2018). Most prominent definitions have several attributes in common; they identify wilderness by setting minimum thresholds of naturalness (the extent to which an area is unaffected by human pressures or to which it retains its ecological integrity), remoteness (from infrastructure and landscape disturbance), and size (e.g. a minimum contiguous area) (Lesslie et al., 1988; Mackey et al., 1998; Hawes et al., 2018). Here, we follow these definitions and consider wilderness areas as “large, ecologically intact landscapes”, and when mapping wilderness areas, set minimum thresholds on their size and naturalness to provide a precise definition (Allan et al., 2017).

There have also been deliberations about whether the term wilderness is still relevant given humanity’s ubiquitous fingerprint (Cronon, 1996). However, regardless of how wilderness is defined, it is clear that large intact ecosystems hold an exceptional range of environmental and cultural values that are being lost in more human modified, fragmented, and ecologically degraded landscapes (Freudenberger et al., 2012; Lovejoy, 2017; Watson et al., 2018a). We now describe these values, and their important contribution to human well-being and the health of the planet, demonstrating that protecting wilderness is critical for averting the biodiversity crisis, addressing anthropogenic climate change, ensuring ecosystem service provisioning, and maintaining the world’s human cultural diversity.

The Exceptional Values of Wilderness

Biodiversity Conservation

Humans are currently driving a biodiversity extinction crisis. Species populations are declining, their ranges contracting, and extinction rates are 1000 times higher than background levels (Pimm et al., 2014; Ceballos et al., 2015, 2017). When it comes to averting this crisis, protecting wilderness areas is critical because they still support high levels of species richness and endemism, and contain large populations of common but declining species (Mittermeier et al., 2003; D’agata et al., 2016; Watson et al., 2016). Wilderness areas are the only places that still contain species assemblages at near natural levels of abundance, especially for large mega-fauna (Mittermeier et al., 2003; Ripple et al., 2015), and wide ranging and migratory species (Klein et al., 2009; Bauer and Hoyer, 2014; Lamb et al., 2018; Photopoulou, 2018). They also support the ecological processes that sustain biodiversity over evolutionary time-scales such as trophic relations at regional scales and animal dispersal and migration (Soule et al., 2004).

Perhaps the best quantification of the value of wilderness for biodiversity is a recent study by Di Marco et al. (2019), who showed that species in wilderness communities are—on average—half as likely to go extinct as those in non-wilderness communities. This demonstrates how wilderness areas buffer species against extinction. Ensuring large wilderness areas are protected is also essential because smaller patches of habitat tend to lose many of their species over time (MacArthur and Wilson, 1967; Soule et al., 2004). This is especially true for top predators; whose populations frequently collapse in isolated habitat patches that are too small or suffer hunting from humans along the periphery. As such, wilderness areas are key refuges for species that are sensitive to exploitation by, or conflict with humans, which includes many charismatic carnivore species (Gibson et al., 2011; Ripple et al., 2014). As disturbance sensitive species disappear from human dominated landscapes, wilderness areas are rapidly becoming their last strongholds. These wilderness refugia serve as important reservoirs of genetic information, and sources of populations and propagules for restoration and rewilding efforts (Ceaşu et al., 2015b). They are also places where nature can be studied free from human disturbance, serving as important baseline references of ecological and evolutionary function.

Notably, wilderness areas are not safe from all possible threats to biodiversity. For example, invasive species can spread into wilderness areas jeopardizing biodiversity in these places. Wilderness areas will not necessarily protect species from climate change, and conditions in many of the most remote intact areas globally are changing rapidly. However, wilderness areas do confer many benefits to species in the face of climate change that other more degraded areas do not. Wilderness refuges are especially important given rapid climate change, because they allow species to adapt by housing large populations (allowing for local genetic adaptation), and enabling species to disperse to favorable climates without having to cross human barriers (Scheffers et al., 2016; Tucker et al., 2018). There is also evidence that the impacts of climate change on ecological communities are felt more severely in degraded and fragmented landscapes than intact ones, and this holds for many ecosystems, including rapidly changing ones such as the arctic (Hansen et al., 2001; Djoghla, 2008; Mantyka-Pringle et al., 2012; Watson et al., 2018a). As such, proactively securing the remaining wilderness is increasingly seen as fundamental to global efforts to avert the biodiversity extinction crisis (Watson and Venter, 2017).

Ecosystem Services

Unimpeded by human activity, wilderness areas continue to support the natural evolutionary and ecological processes that underpin life on Earth, providing a suite of high value ecosystem services (Klein et al., 2009; Watson et al., 2009; IPCC, 2014). For example, wilderness areas regulate climate regimes and hydrological cycles at multiple scales (Salati et al., 1979; Furniss et al., 2010). This includes generating rainfall, for example air that passes over ecologically intact tropical forests produces twice as much rain as degraded forests or converted land (Sheil and Murdiyarso, 2009). Evapotranspiration also has a cooling effect

that buffers the temperatures of local climates during heatwaves (Deo et al., 2009; Ahlström et al., 2015). The quantity of ecosystem services provided also increases with the size of a wilderness area (Wright et al., 1999; Chagnon and Bras, 2005), and in many cases is a direct result of that size because it allows wilderness areas to act as complete self-organizing systems (Sanderson et al., 2002). This has major implications for conserving wilderness areas because damage in one part of the system can affect the functioning of the entire system (Laurance, 2005; Peres, 2005). For example, it is estimated that the Amazon requires at least 75–80% of its forest cover to retain its hydrological cycle (Sampaio et al., 2007; Lovejoy and Nobre, 2018), and therefore must be conserved almost in its entirety (Laurance, 2005).

Proactively protecting carbon rich wilderness also makes a significant contribution to stabilizing atmospheric CO₂ levels, and achieving global climate mitigation goals. This is because ecologically intact ecosystems have a greater capacity to sequester and store carbon than degraded ecosystems (Mackey et al., 2013; Avitabile et al., 2016). For example, one third of the total global stock of forest biomass carbon is stored in the boreal forest biome, the most intact ecosystem on the planet (Pan et al., 2011), and the Amazon region stores nearly 38% of the above ground carbon stored in woody vegetation in tropical America, Africa and Asia combined (Walker et al., 2014). Beyond forests, intact coastal systems including mangroves, salt marshes, and seagrasses have an exceptional capacity to sequester and store carbon (Fourqurean et al., 2012). However, when degraded, they quickly change from carbon sinks to major carbon sources (Howard et al., 2017). The same applies for other intact ecosystems, for example, slight degradation of intact forests can cause substantial carbon release (Houghton, 2012; Chaplin-Kramer et al., 2015; Watson et al., 2018a; Maxwell et al., 2019).

Wilderness areas have an important role to play in the fight against anthropogenic climate change beyond storing and sequestering carbon. In many situations they provide humanity with a direct defense against extreme climatic events such as floods, sea level rise and cyclones (The World Bank, 2009). For example, intact mangroves, grasslands, coral reefs, wetlands and forests are humanity's best protection against floods and storms (Bradshaw et al., 2007; Ferrario et al., 2014), with highly intact ecosystems providing stronger protection than degraded ones (Alila et al., 2009; Brookhuis and Hein, 2016). The intact mangroves of the Tamil Nadu coast in India, for instance, significantly reduced damage to human structures following the tragic Indian Ocean Tsunami of December 26th 2004 (Alongi, 2008).

Securing intact ecosystems is also recognized as humanity's most cost-effective defense against climate change (The World Bank, 2009; Martin and Watson, 2016), and is often orders of magnitude cheaper than engineered solutions such as building sea walls instead of protecting intact reefs, salt marshes and mangroves (Shepard et al., 2011; Jones et al., 2012). Recent analyses estimated that coral reefs save Indonesia, the Philippines, Malaysia, Mexico and Cuba over 400 million USD annually through flood avoidance (Beck et al., 2018), and that wetlands saved the United States over 625 million USD in flood damages following hurricane Sandy in 2012 (Narayan et al., 2017). Perversely, ecosystems such as coral reefs are often destroyed or degraded in the process of building sea walls and protective infrastructure (Grantham et al., 2011; Maxwell et al., 2015).

Human Cultural Diversity

Wilderness areas are home to many of the most politically and economically marginalized indigenous communities on Earth (Gorenflo et al., 2012; Schwartzman et al., 2013). These peoples number in the hundreds of millions and are reliant on the ecosystem services provided by intact marine and terrestrial ecosystems for essential resources such as food, water, and fiber (MEA, 2005). Securing wilderness is central to reducing poverty and marginalization of these people's, and for achieving many United Nations Sustainable Development Goals (SDG's) such as human well-being, clean water, reduced inequalities, peace and justice, as well as the biodiversity and climate goals (United Nations, 2015). Many indigenous peoples have inhabited wilderness areas for millennia, developing strong bio-cultural connections to the land (Larsen and Jaeger, 2017). In these cases, securing wilderness is critical for securing their long-term cultural integrity.

There have previously been conflicts between the people living in wilderness areas and conservationists, with wilderness debates historically framed as mutually exclusive choices between conservation and development. However, wilderness conservation thinking has evolved, and it is increasingly recognized that there are common interests between conservationists and local communities in light of growing human pressure on the natural environment (Venter et al., 2016b; Larsen and Jaeger, 2017). The sustainable livelihoods and cultural integrity of many indigenous communities are often threatened by the same industrialized development pressures that threaten biodiversity and wilderness areas (Boff, 2002; Sutherland, 2003). For example, human cultural and language diversity, which co-occurs with biodiversity, is declining outside of wilderness areas (Gorenflo et al., 2012; Amano et al., 2014). There are also cases of violent conflict between economic development and indigenous peoples (Simmons, 2002; Finer et al., 2008), including the mass-murder of uncontacted Amazonian tribes by gold miners (Darlington, 2017), and inter-tribal warfare spurred on by oil exploration in Ecuador (The Economist, 2013). Protected areas, indigenous protected areas, and other land-use designations preventing industrial development can act as important buffers protecting indigenous people and ensuring they have the wild spaces required to maintain their cultures. As such, there are opportunities to integrate both nature and culture in the conservation of large wilderness areas.

The State of Wilderness Conservation

Even though most definitions of wilderness lack precision, the broad concept of wilderness as still proved valuable, motivating conservation efforts for centuries. For example, wilderness inspired the writings of Audubon, Muir, Leopold and others, whose

works form the moral foundations of our field. Leopold in particular recognized that landscapes are systems, which if functioning properly, support the processes that generate soil, water, and life. Leopold compellingly articulated this ethical philosophy in his 1949 classic *A Sand County Almanac*, popularizing the idea that wilderness areas have value if preserved in their wild state, and inspiring generations of conservationists. Wilderness protection was also the inspiration for Yellowstone, the world's first national park, designated in 1872 in the United States. The national park model spread worldwide and still forms the backbone of conservation efforts today.

Despite the historical importance of wilderness, and the emerging scientific consensus showing that intact ecosystems have exceptional ecological values compared to more degraded ecosystems, wilderness areas have been overlooked as conservation priorities in the last few decades (Myers et al., 2000; Brooks et al., 2006). This is partly because the concept of wilderness has come under heavy scrutiny, being described as a human construct, and criticized for promoting a dualistic vision which separates people from nature (Cronon, 1996; Sarkar, 1999). Wilderness conservationists have also been criticized for protecting wilderness from the people who live there, or at their expense, although modern wilderness conservation is now moving beyond this (Mackey and Clau die, 2015; Larsen and Jaeger, 2017). As a result of this criticism, the term wilderness has become controversial and even unmentionable in some circles (Hawes et al., 2018). However, it is important to note that these are not criticisms of wild places and their values, but rather how the term wilderness is defined and used, and how wilderness conservation is carried out (Cronon, 1996).

There is often an implicit assumption amongst conservationists that wilderness areas are free from human impact due to their size, remoteness, and historically limited human presence. As a result, there is a notion that they do not require conservation action, and that conservation resources would be better spent on places that contain high concentrations of threatened species and are thought to be under more imminent threat (Margules and Pressey, 2000; Ricketts et al., 2005). Some conservationists have argued that such reactive approaches to conservation should take precedence over proactive efforts to conserve wilderness (Ricketts et al., 2005; Kareiva and Marvier, 2012; Pressey et al., 2017). However, it is increasingly acknowledged that this is a false dichotomy and conservation requires a balance of both reactive and proactive approaches (Brooks et al., 2006; Cardador et al., 2015; Watson and Venter, 2017; Sacre et al., 2019). Furthermore, until very recently, there were no global analyses of changes in the extent of wilderness areas over time, making it challenging to ascertain how threatened they were.

Information on the condition, threat and protection status of wilderness areas globally was limited because they were not monitored in any regular fashion (Lovejoy, 2017), and the best available maps of global wilderness extent dated back to the early 2000's (Hannah et al., 1994; Sanderson et al., 2002; Mittermeier et al., 2003). Although these maps had proved useful for numerous ecological and conservation analyses (Di Marco and Santini, 2015; Inostroza et al., 2016; Kormos et al., 2016; Payne and Bro-Jørgensen, 2016), they provided a temporally static and much outdated view of wilderness extent (Watson et al., 2009; Laurance et al., 2012, 2014). More recent mapping efforts include global roadless areas (Ibisch et al., 2016), which do not capture many human activities that degrade wilderness areas, and maps of intact forest landscapes (Potapov et al., 2017), which utilize satellite imagery data to assess direct human induced forest structural alterations and fragmentation within forest ecosystems (Potapov et al., 2017).

Despite this lack of up-to-date information, concerns for the safety of wilderness areas were valid considering the widespread pressure humanity is exerting on the natural environment (Steffen et al., 2015; Venter et al., 2016b). Wilderness values can be lost long before habitat has been completely cleared, making wilderness areas particularly vulnerable to pressures such as roads that can have extensive indirect or 'offsite' impacts (Raiter et al., 2014, 2018). These can include the isolation and fragmentation of species populations, increased access for hunting and logging, and increased risk of anthropogenic fire ignition (Mackey et al., 1998; Laurance et al., 2017). In light of growing human pressure globally, there were calls within the conservation community for updated maps of wilderness areas, which would make global assessments of their threat and protection status possible (Bertzky et al., 2013; Kormos et al., 2016).

Recognizing that the lack of up-to-date information on wilderness extent constituted a major impediment to wilderness conservation, we developed new global maps of terrestrial wilderness areas for the years 1993 and 2009 (Fig. 1) (Allan et al., 2017). Utilizing global maps of cumulative human pressure (Venter et al., 2016a), we identified wilderness as all pressure free lands with a contiguous area > 10,000 km² for the years 1993 and 2009. These places represent the most intact ecosystems globally, and are likely to be operating with natural levels of species abundance, community structure and disturbance regimes. We compared the maps of pressure free lands with maps of Earth's Anthropogenic Biomes (Fig. 2), a categorization of Earth's ecosystems based on patterns of sustained direct human interactions (Ellis et al., 2010), and found high congruence between areas identified as wilderness or wild lands in the two approaches (Fig. 3).

The updated wilderness maps enabled an analysis of changes in wilderness extent between 1993 and 2009, which highlighted the catastrophic loss of 3.3 million km² of wilderness (Watson et al., 2016). This is an area greater in size than India, which amounts to a 10% decline in total global wilderness extent over 16 years. To give this context, wilderness loss is occurring four times faster than forest loss globally (Keenan et al., 2015), making wilderness areas some of the most threatened ecosystems on Earth. Only 30 million km² of Earth's terrestrial wilderness remains (23%) and it is rapidly diminishing.

These results highlighted the importance of wilderness conservation, and challenge the widely held perception that wilderness areas are relatively safe from human impacts. Many of the greatest wilderness declines occurred in the Amazon and Central Africa, which are some of the most biodiverse regions on Earth. Furthermore, efforts to conserve wilderness within protected areas between 1993 and 2009 lagged well behind the rate of loss, which was double the rate of protection globally (Watson et al., 2016). Similar mapping has since been carried out for the marine realm (Jones et al., 2018), showing that marine wilderness has almost completely retracted to the polar regions, with only 13% of the ocean still pressure free.

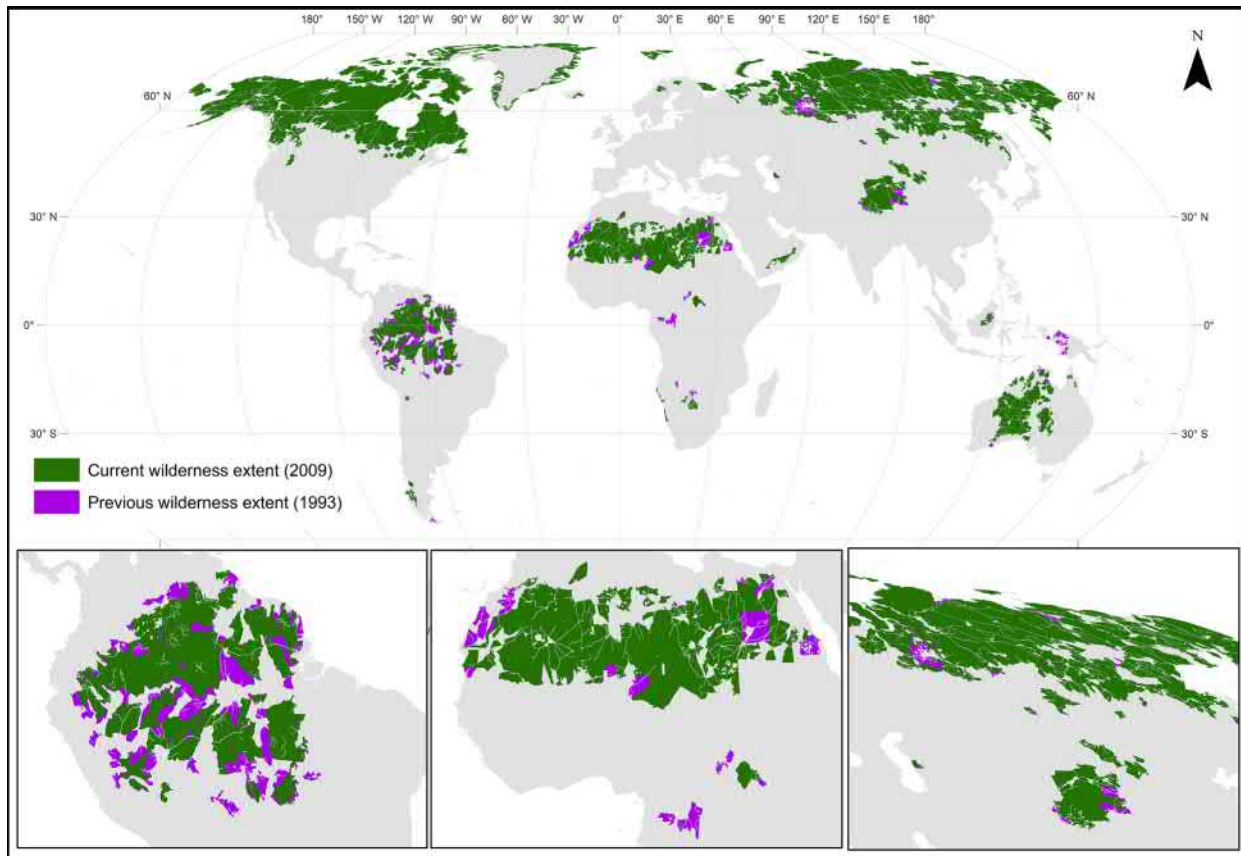


Fig. 1 The 1993 (purple) and 2009 (green) extent of wilderness areas. Data obtained from [Allan et al. \(2017\)](#). Over 3.3 million km² (>10%) of wilderness was lost during this time period ([Watson et al., 2016](#)).

It is also evident that wilderness conservation has received insufficient attention in international environmental agreements and policy deliberations to date ([Watson et al., 2016](#); [Maxwell et al., 2019](#)). Global efforts to achieve ambitious sustainable development and environmental targets have almost completely overlooked the contributions of wilderness areas and their outstanding values ([Watson et al., 2018b](#)). At the international level, there is no formal recognition of the importance of wilderness areas, and no explicit targets for wilderness protection in many of the most powerful multilateral environmental agreements. This includes in the Convention on Biological Diversity ([CBD, 2011](#)), a platform which attempts to coordinate international action to halt or reverse biodiversity loss ([CBD, 2011](#)), and the World Heritage Convention, which aims to protect the world's most valuable natural and cultural sites ([UNESCO, 1972](#)). It is also surprising that the United Nations Framework on Climate Change (UNFCCC) Paris Agreement ignores the important role that wilderness areas play in the fight against climate change ([Maxwell et al., 2019](#)).

The little recognition that wilderness areas have received in policy includes the United States Wilderness Act of 1964 which established standards for protection of wilderness on federal land. A small number of countries including Canada, Australia, Finland and South Africa have followed suit, implementing similar legislation to protect wilderness ([Mittermeier et al., 2003](#)). The International Union for the Conservation of Nature (IUCN) recognizes specific protected areas worldwide that contain wilderness, and includes criteria on size and intactness (Criterion C) in its recently published Global Standards for identifying Key Biodiversity Areas ([IUCN, 2016](#)). Although Criterion C was purposefully designed to protect wilderness, only two sites per ecoregion can qualify based on Criterion C, meaning that only a limited number, albeit a representative sample, of wilderness areas will be captured. Secondly, KBA status does not confer any formal protection for an area—they are conservation priorities that may warrant formal protection ([Smith et al., 2019](#)).

The lack of strong international policy recognition for wilderness areas has significant ramifications for national environmental strategies. The tendency for national biodiversity conservation plans is to focus on remnant habitats and endangered populations of species living in degraded, fragmented and altered ecosystems, with very few nations clearly articulating conservation goals for wilderness areas ([Klein et al., 2009](#); [Watson et al., 2009](#); [Ceașu et al., 2015a](#)). Some wilderness areas are protected under national legislation such as the 1964 United States Wilderness Act, which formally defines and protects wilderness on federal land. However, in most countries, wilderness areas are not formally defined, mapped or protected, and there is nothing to stop them being exploited by national and local governments, private business, and civil society.

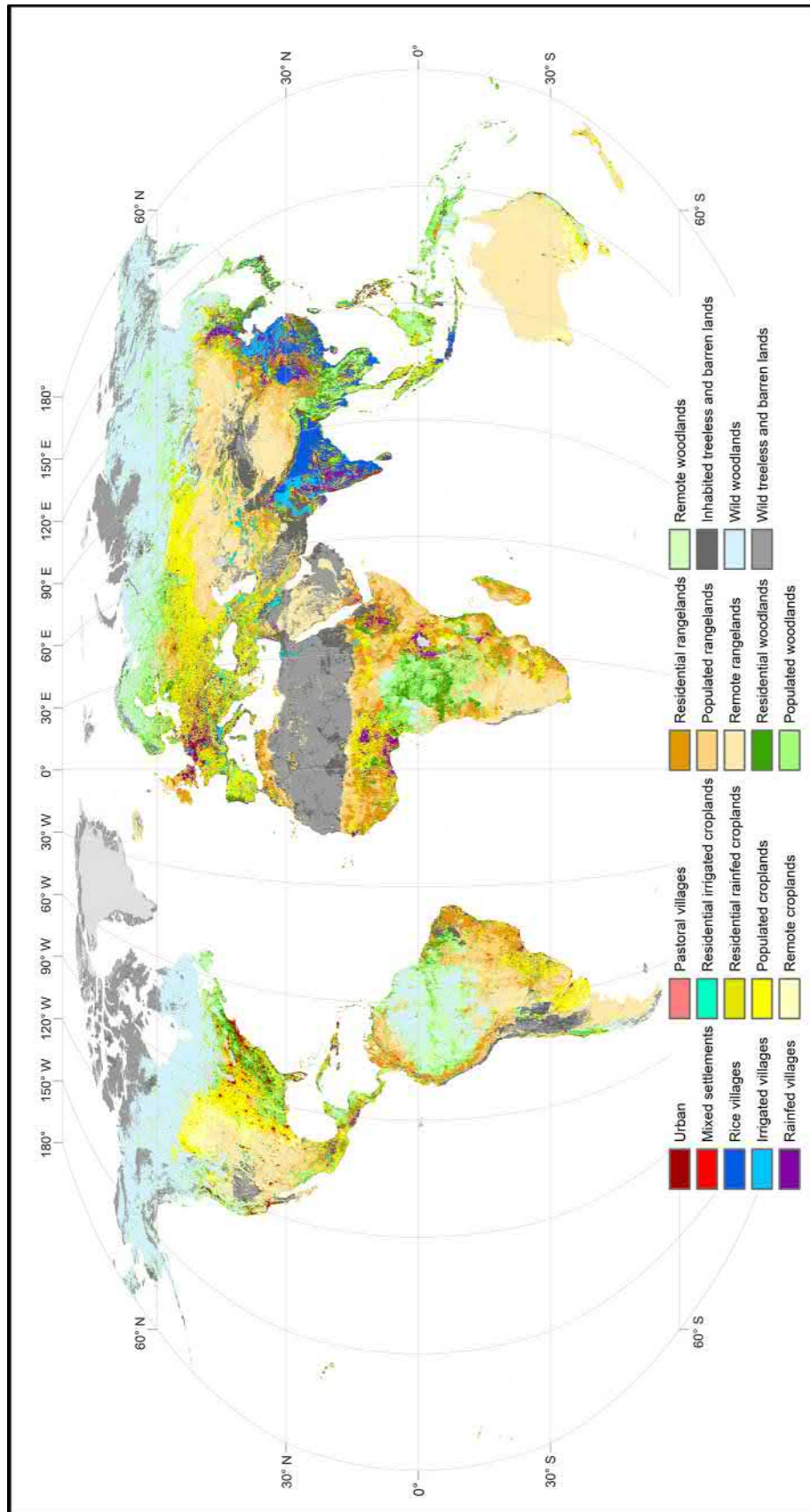


Fig. 2 Earth's anthropogenic biomes. Data from Ellis et al. (2010).

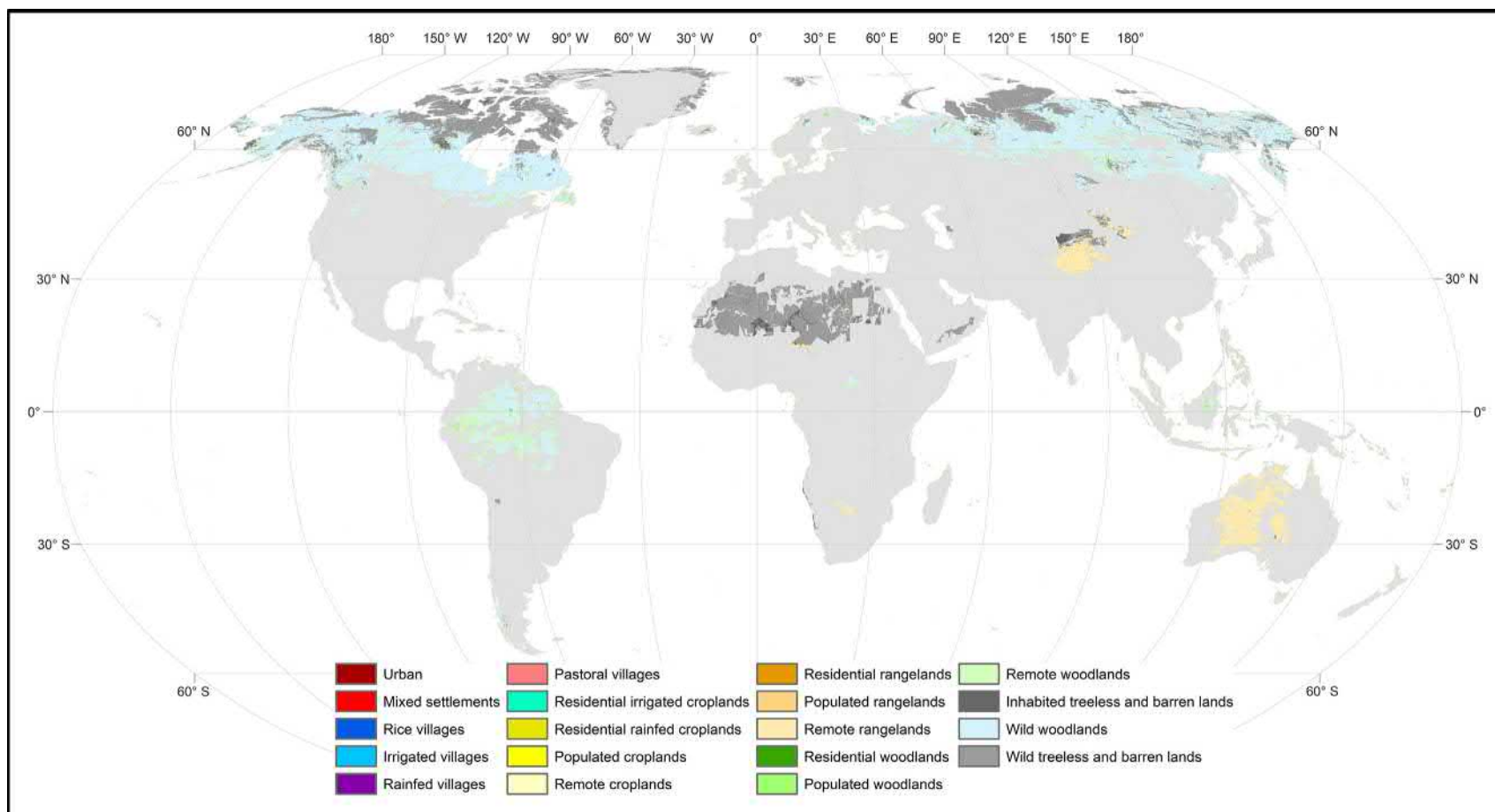


Fig. 3 Distribution of Anthropogenic biomes within wilderness areas. Wilderness areas primarily consist of wild woodlands (46%), wild treeless and barren lands (33%), remote rangelands (10%), and remote woodlands (6%).

The implications of the lack of policy recognition for wilderness areas has been noticed, leading to recent and timely calls for international environmental agreements to take a more central role in wilderness conservation (Martin and Watson, 2016; Watson et al., 2016; Watson and Venter, 2017; Barnes et al., 2018; Maron et al., 2018). In particular, there have been calls for the World Heritage Convention, one of the most powerful conservation instruments, to become more engaged in wilderness conservation (Kormos et al., 2016). The role that the World Heritage Convention could play in wilderness conservation is clear (Allan et al., 2018), and represents a substantial conservation opportunity moving forward. It is also in the World Heritage Conventions interests to protect wilderness areas, since the unique values of wilderness are closely aligned with those outlined in the criteria for World Heritage status.

Perhaps the most immediate opportunity to recognize wilderness in policy and set targets for its protection lies with the CBD. The CBD, is a platform that attempts to coordinate international action to halt or reverse biodiversity loss (CBD, 2011), and is one of the most important international agreements relating to biodiversity conservation, with 196 countries currently working towards commitments outlined in the 2020 Strategic Plan. These targets shape the behaviors of individuals, governments and non-government organizations, who appear to take their commitments seriously. The CBD's next Strategic Plan for Biodiversity will take effect in 2020 and run until 2030, representing a crucial opportunity for the conservation community to learn from past mistakes and develop smarter, more ambitious targets (Butchart et al., 2016).

A step towards this could be to radically increase protection coverage targets (i.e. post Aichi Target 11) to a point where they are sufficient to achieve environmental outcomes such as averting the biodiversity crisis and ensuring wilderness areas remain intact (Di Marco et al., 2016; Lovejoy, 2017). Beyond targets for the expansion of protected areas, a new target could also be established for the complete retention of intact natural ecosystems (Maron et al., 2018) (i.e. post Aichi Target 5). This would have to be part of a multi-pronged global strategy with a parallel focus in already degraded landscapes on preventing immediate extinctions and species declines, either via protection or restoration efforts (Allan et al., 2019), and in highly human dominated areas retaining human-nature interactions (Maron et al., 2018).

Conclusion

Human pressure on planet earth will only increase as our population climbs and technology continues its relentless advance. Our window of opportunity to safeguard human well-being and the health of our planet is closing fast. Securing wilderness is an essential step towards this, as these areas house exceptional biodiversity, cultural, and climate regulation values. Wilderness values can only be conserved in their current, naturally functioning state. Once they are degraded, full restoration is near impossible. As President Lyndon B. Johnson observed when he signed the United States Wilderness Act in 1964 "If future generations are to remember us with gratitude rather than contempt, we must leave them something more than the miracles of technology. We must leave them a glimpse of the world as it was in the beginning, not just after we got through with it". "Once our natural splendour is destroyed, it can never be recaptured. And once man can no longer walk with beauty or wonder at nature, his spirit will wither and his sustenance be wasted". Given we have already lost so much, we must grasp this opportunity to secure wilderness before it disappears forever.

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Dams: Anthrome Enablers

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Abstract

Dams have been altering riverine ecosystems for as long as humans have been constructing them. In contrast to the river continuum concept that conceptualized rivers as long continuous entities, the serial discontinuity concept (SDC) was developed as a framework for the study of dammed aquatic ecosystems and has proved to be useful in this way. Dams are globally ubiquitous but not evenly distributed geographically, with some countries having far more dams than others, nor within the anthropogenic biomes of the world. The GRanD database reports 6862 large dams worldwide; however, large dams comprise a small portion of dams on the landscape. Many smaller dams can be difficult to account for and in fact one study estimates there to be 16.7 million dams worldwide. In the United States alone, the national inventory of dams reports >90,000 dams. Dams have been demonstrated to have positive impacts on human civilization through their various designed purposes, of which irrigation is the dominant form (38% of large dams). However, dams also have detrimentally affected humans in many ways. For example, dams have displaced an estimated 40–80 million people and are known to increase the incidence of vector borne diseases. In addition to their impact on humans, their influence on ecosystems has been intensely studied and documented, with the results indicating dams are not in the best interests of those systems. Well documented and highly publicized are dams impact on migratory fishes (e.g., salmon species). The heightened awareness by the general public in dams being harmful to aquatic ecosystems and their aging infrastructure has lead to increased interest in their demolition and removal. While dam removal projects are generally considered a boon for ecosystems, their removal can have disadvantageous effects on humans (e.g., economic loss) and therefore all known impacts of dam removals should be considered during this process.

Man-Made Rivers

Lotic ecosystems are often viewed and studied within the context of the River Continuum Concept (Vannote et al., 1980) which conceptualizes them as continuous entities, with ever changing physical and chemical variables that result in predictable physico-chemical attributes and subsequent biological communities along this gradient. This perception is somewhat scale dependent and is applicable at large scales; however, at smaller scales physicochemical and biological patterns may seem random (Stanford and Ward, 2001). These riverine ecosystems are largely products of their watershed, where chemical, geophysical, and biological processes are determined by the river's longitudinal and lateral interconnectedness. Within a watershed, the river's flow is determined by the surrounding hill-slopes; which, through overland and groundwater flow, direct sediments, nutrients, organic matter, and pollutants into the stream channel. The ability for aquatic fauna to move up- and downstream is due to both locomotory ability of the organism and stream morphology (e.g., waterfalls, flow velocity, etc.). Despite this useful and overarching conceptualization, most riverine systems are subject to a variety of discontinuities, most of which are anthropogenic in nature and of which dams are the likely the most ubiquitous and impactful. As such, Ward and Stanford (1983) developed the Serial Discontinuity Concept (SDC) as a theoretical framework for evaluating the influence of dams on lotic systems. Depending on location of dams along a stream's gradient, dams differentially modify physicochemical and biological attributes resulting in conditions that appear more similar to stream reaches some distance up- or downstream of the dam.

Man as the dominant species in ecosystem earth, who by building dams adds to his long-demonstrated capacity for technological change, and who seeks beneficially to integrate that skill with an ongoing process of interaction among human and other elements of the ecosystem. With inspiration and skill, he may mould a better world for his descendants.

SCOPE (1972).

The construction of dams has historically been a socio-economically acceptable practice due to the view that they are necessitated by the need for development of the urban, industrial, and agricultural complex. As human populations have grown so too has the need for increased access to good and services. Dams, with their ability to store water for a variety of reasons but particularly for agricultural irrigation, have acted to facilitate development, which has led to a vast transition of the landscape by increasing human capacity for urbanization, industrialization, and agriculturalization, away from a *natural* landscape and towards anthropogenic

biomes. While dams have arguably improved the human condition for centuries and have certainly been instrumental in guiding the direction of the human condition, they have also been detrimental in many socio-ecological contexts. As such, they are quite likely the most ubiquitous, anthrome enabling human creation.

The number of large dams (Dam with height >15 m or height between 5 and 15 m with a storage capacity of ≥ 3 million m^3) globally as reported by the Global Reservoir and Dam Database (GRaND) (Lehner et al., 2011b) is 6862 and they vary across space (Fig. 1A). Of those dams, the numbers are dominated by structures built for irrigation purposes (ICLD) (Fig. 2A). Furthermore, half of all large single purpose dams serve to irrigate the land (Fig. 2B). And while the purpose of dam use is more evenly distributed for multipurpose dams, still 24% of these dams are for irrigation purposes (Fig. 2C). The geographic distribution of dams is not even, as there is a lot of regional variation in the density of dams around the globe (Fig. 1A). When considering dams in the framework of Anthropogenic Biomes (or Anthromes) (Ellis and Ramankutty, 2008), the distribution is also quite variable (Fig. 3A and B). Of the dams listed in the GRaND database (Lehner et al., 2011a), there are 2095 large dams or 30.5% of the total number of large dams globally that can be found in the residential irrigated mosaic biome whereas the next highest number of dams (736 large dams or 10.7%) is found in the populated forests biome. Six of the 21 anthropogenic biomes each have $<1\%$ of the large dams worldwide within their boundaries (Fig. 3B).

Dam construction and impoundment of waterways has been carried out by humans for thousands of years for reasons that include hydropower, flood control, irrigation, water supply, navigation, and recreation among others (WCD, 2000). While it is likely that earlier dams exist, the Jawa dam in modern day Jordan is the first dam known to exist (ca. ~ 3000 BC). The dam was developed for domestic and agricultural water supply for the short-lived development of Jawa. Early dams, like the Jawa dam and the equally famous Sadd el-Kafara (ca. 2950–2750 BC) in Egypt were gravity dams where the enormous weight of the structure kept the dam in place (Fahlbusch, 2009). These early dams were built to sustain life in regions that are characterized by extreme droughts and wet periods, where dams could store rain waters during the wet periods for future use when conditions were dry. Dams that were successfully built for these purposes allowed civilization to progress. This progress resulted in better crop yields, higher survival rates, higher reproductive rates, and thus increased development. In turn, increased development resulted in greater consumption of resources and the need for advances in technology. Technological advances in dam construction continued around the globe with the Roman Empire building a plethora of dams and also the first arch dam, followed by the middle ages where dam construction showed little advancement. Beginning in the 1850s dam construction entered the modern age, as engineers began to embark on a three-dimensional understanding of the stresses on dams. Within the last 100 years the most technologically advanced dams have been built for supply water, flood control, recreation, and hydropower (White, 2016).

Dam construction in the United States saw a boom between 1950 and 1979 when there were 45,759 dams constructed (Fig. 4). The National Inventory of Dams (2019) reports that as of 2018 there are $>91,000$ dams in the United States and its territories that meet at least one of four size criteria (Fig. 1B). Just as in the global distribution of dams (Fig. 1A), the distribution of dams in the United States is also not evenly distributed (Fig. 1B). Those dams create a surface area of 18,670,124 ha and store 128,027,735 ha meters of water (National Inventory of Dams, 2019). In the U.S. alone between 500,000–600,000 miles of river (14–17% of the total river miles in the Continental U.S.) are impounded and only 312 “significant” streams are free flowing along their entirety. None of the 15 large river systems in the U.S. are free from anthropogenic impoundment (Agents of Watershed Change). Dams continue to be built around the world, largely for the production of hydropower. At the global scale there was a lull in dam construction from 1990s to 2000s, which has recently given way to a global boom. In 2014 there were 3700 major dams being constructed worldwide, each able to produce at least 1 Megawatt of power (UNEP, 2013). Through time, dams have continually gotten larger (i.e., height), yet from the 1960s to the 1980s there was a period where dam size was relatively stable, but since that period, dams have trended towards larger size (Lehner et al., 2011a,b) (Fig. 5). While records for large dams are more easily attained, the total number of dams worldwide is much more difficult to assess and is largely incomplete. Lehner et al. (2011b) estimated worldwide there to be 16.7 million dams, with reservoirs >0.01 ha.

As demand for energy around the globe continues to grow, particularly in areas such as sub-Saharan Africa and South Asia, due to increasing population and coupled economic development, a push to connect the 1.4 billion people that are disconnected from electricity supply, and continued efforts to decrease carbon emissions, the impetus to construct more dams will only continue to increase (Zarfl et al., 2015; Boyé and de Vivo, 2016). Additionally, investment in hydropower will be important as countries seek to meet their energy demands in Kyoto-compliant ways (Zarfl et al., 2015). As the world pursues the worthy goal of reducing greenhouse gas emissions, well thought out hydroelectric dams will play an important role. Along with hydropower and due mostly to human population growth and economic development, dams will continue to be seen as solutions for other water related purposes such as irrigation, development, technological change, income distribution, and life style change (WCD, 2000). As Goodland (1996) suggests, these infrastructure projects should be environmentally sound and socially equitable.

Dams and Humans

Dams have been viewed as symbols of human achievement and societal advancement as humankind has endeavored to harness natural resources for their own purposes. As such, dams have, undoubtedly, contributed to the improvement of the human condition throughout history. Water storage for irrigation, domestic, industrial, and municipal use, flood control and mitigation, and hydropower have contributed to improved human health, increased food security, created economic opportunities, and alleviated the threat of loss of life and resources. This has been particularly important in arid regions of the world (Richter et al.,

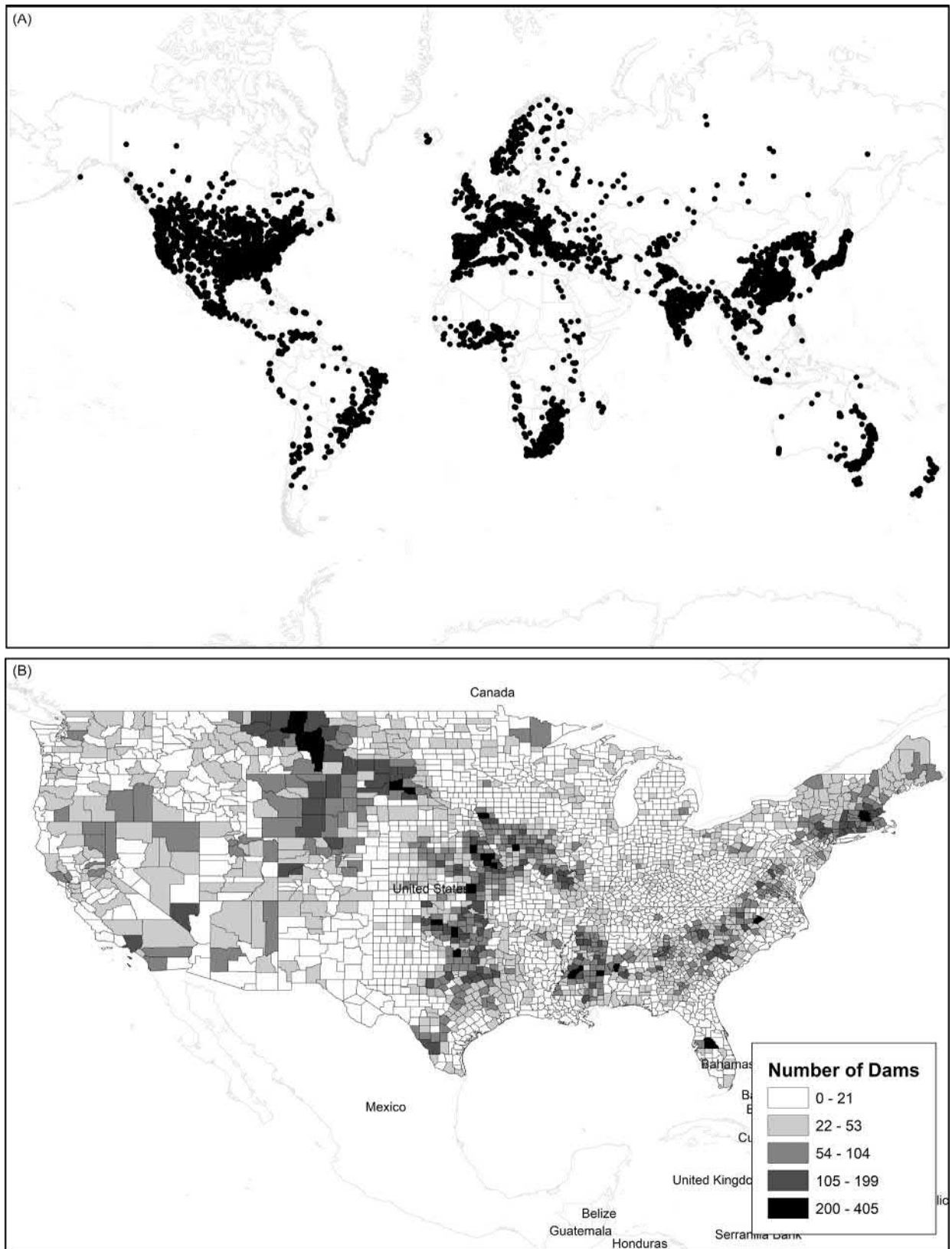


Fig. 1 (A) Global distribution of large dams based on the GRaND database. (B) Number NID listed dams within each United States county.

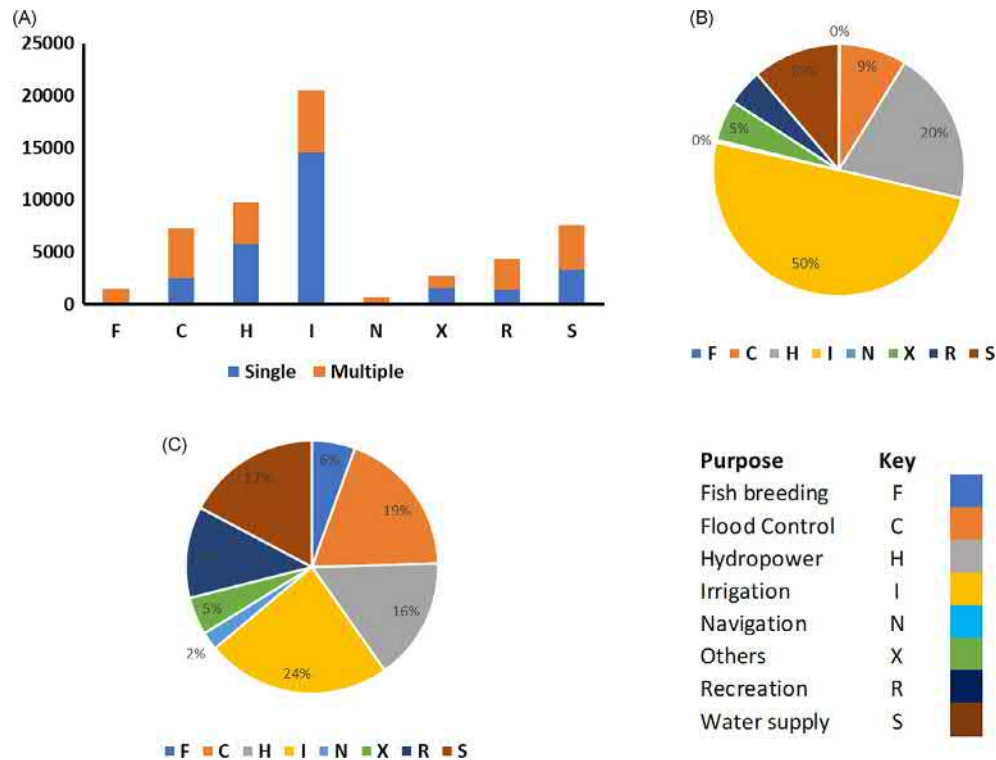


Fig. 2 (A) Dam purpose and single or multiple use status for large dams worldwide. (B) Percentage of use for single purpose dams worldwide. (C) Percentage of use for multipurpose dams worldwide. Source: International Commission on Large Dams (ICOLD). Available at: https://www.icold-cigb.org/GB/world_register/general_synthesis.asp (Accessed: 12 March 2019).

2010). Increasingly, dams serve multiple purposes but there is a lot of continent-to-continent variation in the function dams serve. For example, in Asia 65% of large dams function for irrigation purposes, whereas in North American only 11% of large dams serve this purpose (WCD, 2000).

If the misery of the poor be caused not by the laws of nature, but by our institutions, great is our sin.

Charles Darwin in *Voyage of the Beagle*.

While it is true that dams have had positive influences on humans, they have also had negative social and environmental impacts that tend to affect the poor, indigenous, and vulnerable groups disproportionately (Lerer and Scudder, 1999). This has largely been through the diversion of water which limits access, but construction of dams has also displaced many (WCD, 2000). For example, construction of the Three Gorges Dam in China, which produces 22,500 MW of electric power, displaced 1.2 million people (Boyé and de Vivo, 2016). Worldwide, in the 10 years between 1985 and 1995, The World Bank (1996) reported that 40 million people were involuntarily displaced by dams and a total of 40–80 million people have been displaced by dam construction (WCD, 2000). As many watersheds cross political boundaries, modification of riverine flow by dams can involve local, state, regional, and federal agencies and court battles with high stake regional environmental implications. This type of scenario is not relegated to arid regions and as an example can be seen in the “Tri-State Water Wars” of Alabama, Georgia, and Florida, USA, an area with seemingly ample rainfall and water storage but where conflict over water rights and water access arose (Tri-State Water Wars). With increased demand on water resources, coupled with the fact that nearly half of the world’s 106 primary watersheds are influenced by a major dam (WCD, 2000), cross-boundary conflicts like these are likely to increase through time and at multiple spatial scales.

Dams, particularly those that are large and used for irrigation purposes, have been found to increase the presence of vector-borne diseases (Hunter, Rey and Scotts, 1982; Lerer and Scudder, 1999) but even small impoundments have been associated with increased prevalence of vector-borne diseases (McCann et al., 2018). They have been implicated with increases in the prevalence for a variety of human health related diseases that includes encephalitis, filariasis, gastroenteritis, hemorrhagic fevers, intestinal parasites, malaria, and schistosomiasis; thereby, having important public health implications at regional or national scales (Hunter, Rey and Scotts, 1982; Lerer and Scudder, 1999; Zhu et al., 2008; McCann et al., 2018). In addition to human diseases, dams have also been found to influence animal health. For example, increases in river fluke and trypanosomiasis have been found to be associated with dam construction (Stanley et al., 2007). Dams have increased navigability, allowed for more dense human population, altered hydrological regimes and riverine ecology, and increased local agricultural practices, which has allowed vector-borne diseases to flourish (Lerer and Scudder, 1999).

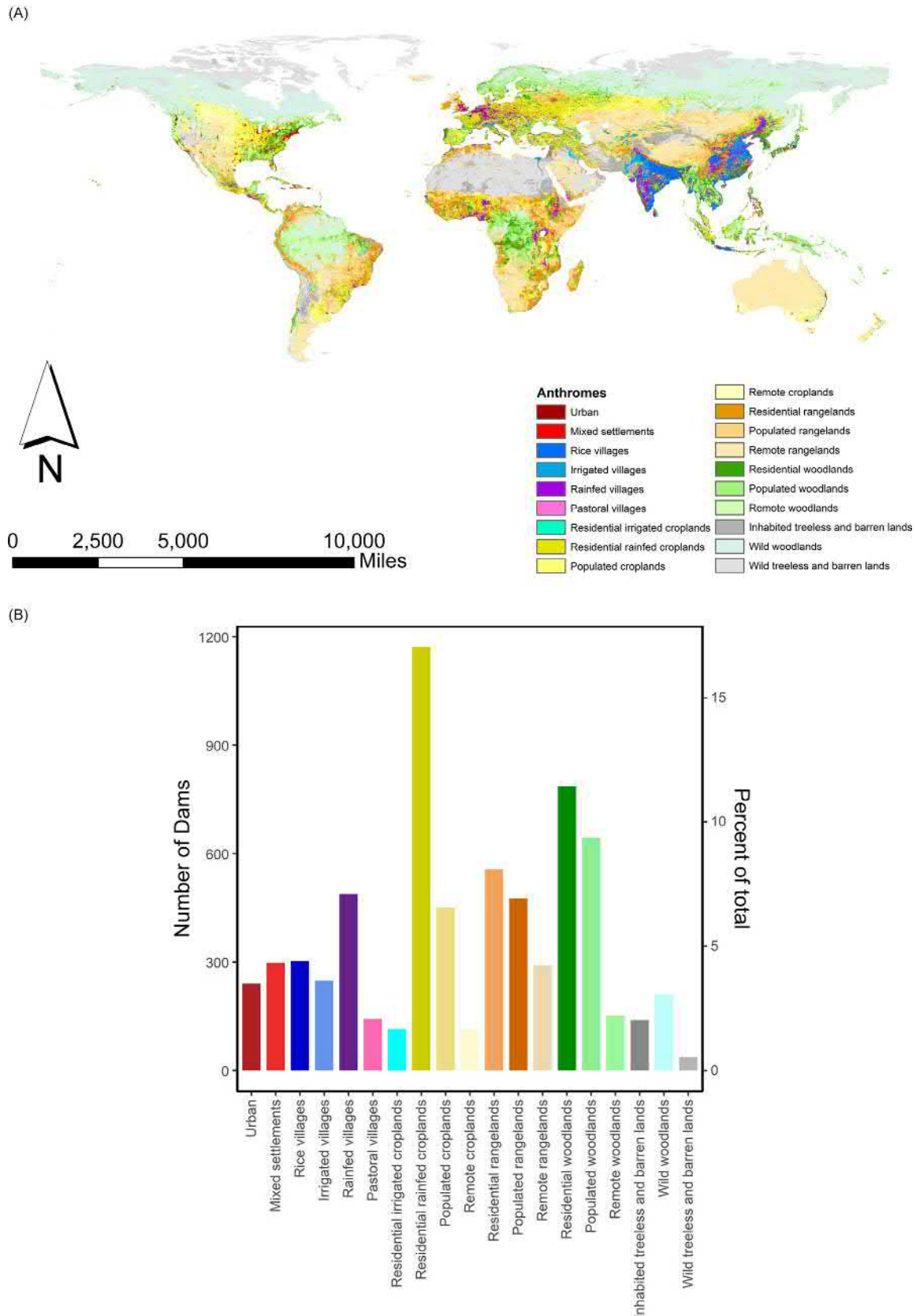


Fig. 3 (A) Map of anthropogenic biomes (anthromes) of the world. (B) Figure showing the number of dams and percentage of the total number of dams within each anthropogenic biome. (A) Data from Ellis, E. C. and Ramankutty, N. (2008) 'Putting people in the map: Anthropogenic biomes of the world', *Frontiers in Ecology and the Environment* 6(8), 439–447. <https://doi.org/10.1890/070062>. (B) Source: International Commission on Large Dams (ICOLD). Available at: https://www.icold-cigb.org/GB/world_register/general_synthesis.asp (Accessed: 12 March 2019).

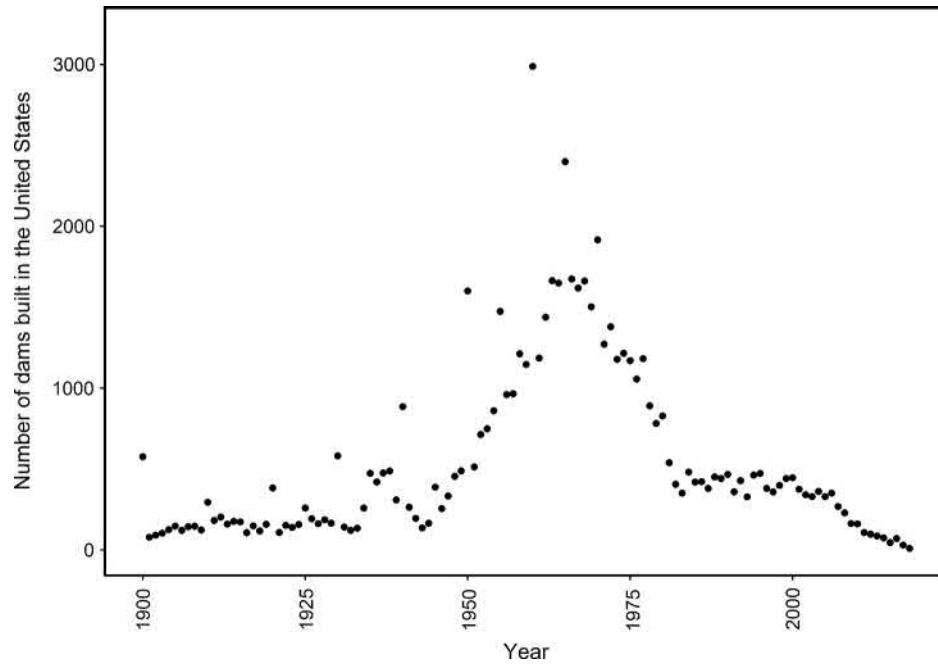


Fig. 4 Number of dams in the United States constructed annually from 1900 to 2010. Source: National Inventory of Dams.

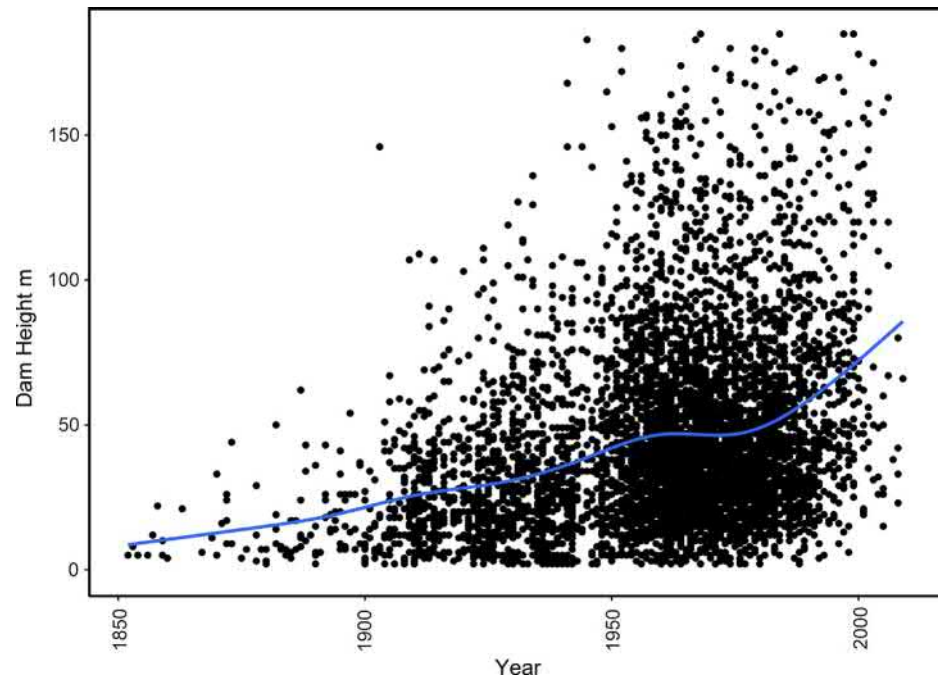


Fig. 5 Dam size through time (1850–2010) globally. Source: International Commission on Large Dams (ICOLD). Available at: https://www.icold-cigb.org/GB/world_register/general_synthesis.asp (Accessed: 12 March 2019).

Dams and Ecosystems

There is no shortage of water in the desert but exactly the right amount.

Edward Abby in Desert Solitaire: A Season in the Wilderness.

In addition to the influences dams have on human systems, dams have been shown to alter hydrologic, physicochemical, and biological systems in both the upstream and downstream direction (Katano et al., 2009; Thompson et al., 2011; Ellis and Jones,

2016; Guzy et al., 2018; Hanks and Hartman, 2018). Most studies of dam influences on ecological systems have been in general agreement with the theoretical construct of the SDC (Ward and Stanford, 1983). In fact, Stanford and Ward (2001) found only one river out of nine that they studied did not fit the SDC. Various animal taxa, including fish, aquatic macroinvertebrates, and anurans, have been shown to respond along recovery gradients below dams in a similar fashion (Ellis and Jones, 2016; Guzy et al., 2018; Hanks and Hartman, 2018) and presumably in response to altered instream and riparian habitat.

Possibly the most notable and obvious disturbance of biota by dams is that of disruption of fish migrations and specifically those of diadromous species (Petts, 1984). Of particular noteworthiness are dams that act as barriers for salmon migration in the western United States. Dams have been found to act as barriers for adult salmon swimming upstream as they return to spawn in their natal streams and juvenile salmon swimming downstream as they make their way to nursery grounds and eventually to the Pacific Ocean to mature into adults. The importance and noteworthiness of the influence of dams on salmon migration is due, in large part, to the economic value of the salmon industry. For example, in 2013 the commercial salmon industry in California alone was estimated at \$244 million U.S. dollars and the recreational salmon industry at \$105 million. The economic impact for California caught salmon was \$1176 per fish (recreational riverine salmon) and \$151 per fish (commercial ocean salmon) (Salmon economic impact: What is a fish worth?, n.d.). The Columbia River (U.S.A.) once supported vast salmon migrations to >80% of the watershed; however, due to main-stem dams, migratory habitat by 1978 had been reduced to <30% for sea-run spawning populations (Robinson, 1978).

The influence of dams on habitat (e.g., instream, riparian, and in up- and downstream directions) has been demonstrated through a variety of studies (Harvey, 1987; Katano et al., 2009; Thompson et al., 2011; Hanks and Hartman, 2018). Much emphasis has been placed on the ability of dams to disrupt sediment transport. The ability of dams to trap sediments in reservoirs has two important considerations: (1) reduction of sediment transport to downstream sections of the river and (2) loss of reservoir storage capacity due to sedimentation. The reduction of downstream sediment loads modifies sediment composition, armors stream beds, and erodes stream banks (Jones, 2010). Additionally, dams alter substrate size and velocity at sites in close proximity to dams resulting in abnormally larger substrate and higher velocities than would be expected were dams absent (Cortes et al., 2002; Poff and Hart, 2002; Katano et al., 2009; Freedman et al., 2013; Hanks and Hartman, 2018). The World Commission on Dams (2000) reports that reservoirs around the globe are losing storage capacity due to sedimentation at a rate estimated to be between 0.5% and 1% per year. This implies that without vast monetary investment in sediment removal, the reservoirs will lose 12–25% of their storage capacity every 25 years. As sedimentation fills reservoirs, their useable capacity will be reduced and there is the potential for outlet and turbine operation to be impacted, as well as increases in marshland in backwater regions (Wang et al., 2005; Zhu et al., 2008). For example, Zhang et al. (2000) predicted that within 100 years after completion of the Three Gorges Dam, 27 large-scale marshlands will emerge with a total area of 34 km². Additionally, the trapping of sedimentation in reservoirs has resulted in loss of river delta land area in places like the iconic Mississippi River Delta, where there is a >25% reduction in deltaic wetlands over the last few decades as the rate of oceanic erosion has outstripped that of sediment accretion. Sea level rise only acts to exacerbate these situations (Blum and Roberts, 2009).

In addition to the instream, longitudinal habitat modification through disrupted sediment transportation, many dams function to reduce water reaching downstream floodplains thereby decoupling an essential component of functional riverine ecosystems (Junk, Bayley and Sparks, 1989). Many rich and productive agricultural soils can be found in floodplains, where for millennia these “flood-pulses” have deposited nutrient rich sediment in river floodplains. Without this link between the aquatic and terrestrial realms, lotic system productivity is reduced and community composition and nutrient dynamics are modified (Junk et al., 1989; Bayley, 1991). The intensity of the disruption of sediment transport is variable and dependent upon the dam location and type. Run of the river dams tend to have shorter reservoir resident times and thus reduced impact on sediment transport; whereas, large dams that function for irrigation, flood-control, and hydropower typically act as effective traps for sediment (Yeager, 1993).

Riverine thermal regimes are often shifted due to dams and the magnitude of change is dependent on whether water releases are of epilimnetic or hypolimnetic origin. As aquatic species have strong phenological adaptations to water temperature (Bunn and Arthington, 2002), such disturbances can have important consequences for the timing in individuals’ life histories (Hauer and Stanford, 1982; Crowder and Magnuson, 1983; Bunn and Arthington, 2002; Williams, 2008). Waters released epilimnetically are typically well oxygenated with near ambient temperatures; however, temperatures can be elevated in the summer and winter and delay warming and cooling in downstream waters (Fraleigh, 1979). Where water is released hypolimnetically, stratified reservoirs can result in a reduction of water discharges that are 13–18 °C (TVA, 1978). Regardless of whether waters are released hypolimnetically or epilimnetically, there has been shown to be a negative impact on aquatic fauna (Yeager, 1993; Hanks and Hartman, 2018). The rate at which temperature changes as the distance from dam increases is a function of many variables (Rice et al., 2001) but the distance to recovery from thermal impacts has been found to be as much as 113 km downstream of the dam (Lehmkuhl, 1972).

Dam as Creators of Socio-Ecological Alternate Stable States

Many of the modifications described above result in long-term socio-ecological system changes and result in alternate stable states above and below dams (Bascompte et al., 2012; Collins et al., 2012; Wohl and Beckman, 2014; Skalak et al., 2017). Stable states are maintained by positive feedback mechanisms, where once the system has passed some critical point, an alternate state is imminent (Angeli, Ferrell and Sontag, 2003). Dams have the potential to break positive feedback mechanisms that maintain a stable state, whether that be in ecosystems or social systems, and the disruption of feedback mechanisms in complex systems can be the result of

abrupt external shock to the system or gradual shifts that push the system closer to a “tipping point,” where in either case, the result is a self-propagating regime shift (Bascompte et al., 2012). Skalak et al. (2017) determined that the presence of dams in the Upper Missouri River drove changes that lead to alternate geomorphic conditions and thereby resulted in an alternate stable ecological state. They concluded that this was in large part due to modified flow and sediment transport dynamics. While the findings of the Skalak et al. (2017) study that evaluated the Upper Missouri River hold true across much larger geographies, then and understanding of the global implications of modified flow and sediment transport dynamics needs a great deal of attention. As an example, Lehner et al. (2011b) found flow disruption by dams, as measured by cumulative upstream reservoir capacity that exceeds 2% of annual flow, to be greatest for large rivers (i.e., average flow >1000 m/s) where 76.7% were affected. >60% of rivers worldwide are affected by dams or diversions (WCD, 2000). While the impact dams have on flow regimes is typically considered detrimental to the riverine ecosystem, low flows, as controlled by dams, may act to restrict or prevent invasive species encroachment into stream sections upstream of dams (Acreman et al., 2009). Dams have long been agents for changing not only riverine landscapes but also social and cultural landscapes, thus resulting in a variety of socio-ecological alternate stable states. Their longevity and extent of spatial impact has enabled many dams to act as socio-ecological system modifiers, for better or worse, which has resulted in a suite of alternate stable states that have driven the transition towards anthropogenic biomes.

Dams are typically viewed as water control devices that impound lotic systems to various extents but due in large part to the difficulties of identifying small scale water control devices there are many small dams that are unaccounted for. The extent to which these small, unaccounted for dams act to modify socioecological systems is an area of research with rich questions to be asked. As an example, rice fields in the Coastal Plain of the southeastern United States and specifically along the coast of southern North Carolina, South Carolina, and Georgia have extensive dam structures that impound water at varying levels, even today (Fig. 6). South Carolina was the epicenter for rice cultivation in the southeastern U.S. and at the apogee of rice farming in the region (1860s) there was an area impounded that was approximately 60,703 ha (Ferguson, 2004). Of this vast coastal land area, Colleton County contains an estimated 20,000 ha of historic rice fields and 10 NID registered dams, yet only one dam from the NID is associated with any of these historic features (National Inventory of Dams, 2019). The vast number of dam structures (dikes) associated with these historic landscape features is unaccounted for. The interconnected, complex nature of the rice field dike systems (outer and inner dike systems) (Fig. 6C) make it difficult to account for them in dam registries such as the NID; however, ignoring a feature that has reshaped water resources across such a vast region is impertinent to their historic and contemporary impact on the socio-ecological systems within the region and the globe. Much of the impounded areas are floodplains, and while they are inundated during portions of the year, they would have been, and still are to a large extent, inundated for periods longer than they would be without these control devices.

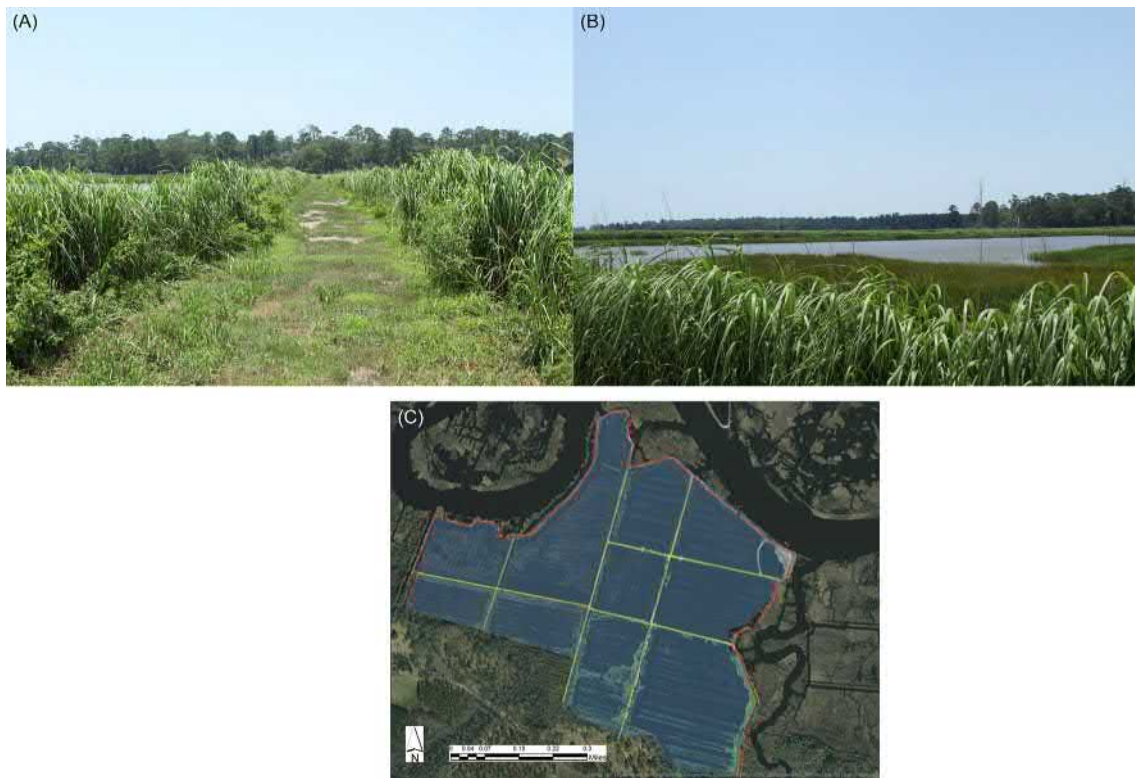


Fig. 6 Historic rice fields in coastal South Carolina. (A) Image of a rice field dam (dike), (B) image of a rice field impoundment, and (C) areal photograph of rice fields showing in red the outer dam (dike) system, in yellow the inner dike system, and the blue polygon is the impounded rice field. Image credit: Daniel Hanks (A and B).

The enormous undertaking of creating these small impoundments was the product of the socio-economic period that was driven by slave labor and a technical knowledge system that was developed through time in western Africa. As slavery in the United States ended after the American Civil War and a new socio-economic norm developed, rice cultivation and its economic benefits also collapsed. The socio-economic-ecological system that exists within a given time frame results in a stable state that is self-correcting through a variety of positive feedback mechanisms that include social, economic, and ecological components and once one of these is broken (e.g., abolishment of slavery as a social construct) the entire system changes and may result in an alternate stable state.

Dam Removal

Records of dam removals in the United States go back to 1916 with the first recorded incident being the removal of a dam in Pennsylvania on Big Spring Run. In the United States dam removals were uncommon until the mid-1970s when environmental awareness became more mainstream and the impacts of dams were more widely known (Petts, 1984). Dam removal continued to gain momentum for the next 25 years, while dam construction saw a precipitous drop across the United States but until the year 2000, dam construction still outpaced dam removals. However, since 2000 the number of dams removed has been greater each year than the number of dams constructed (National Inventory of Dams, 2019; Duda et al., 2016) (Fig. 7). Coupled with increased knowledge of the ill effects of dams combined with continued concerns about their aging infrastructure and costs to maintain them, interest in dam removals continues to increase (Stanley and Doyle, 2003). The increased interest in dam removals has been further amplified through highly publicized dam removals such as those on the Elwha River in Washington, U.S. (Elwha and Glines Canyon Dams), which, until removed, blocked salmon migrations. Of the dams removed in the U.S. 65% have been <5 m tall and 85% have been <10 m tall. The largest dam to have been removed in the U. S. to date is the Glines Canyon Dam at 64 m tall. The Condit Dam on the White Salmon River is the next tallest dam to have been removed in the U.S. at 38 m (Duda et al., 2016).

As noted above, the negative effects of dams have been well studied and documented, yet with increased emphasis on dam removals, there has been less interest and study of the effects of dam removals. While dam removals are seen as a powerful tool to restore lotic habitats, the removal of dams can have socio-ecological impacts that should be further studied and given full consideration when dam removal is sought as a restorative measure. Ecologically, dam removal can impact downstream spawning grounds, food supply, and community composition (Sethi et al., 2004; Burdick and Hightower, 2006; Stanley et al., 2007; Orr et al., 2008). Cost-benefit analyses are often used to evaluate whether a dam should be removed but costs and benefits of socio-ecological systems (e.g., dam removal projects) are often difficult to measure, for example placing a monetary value on an endangered species and ecosystem services may be difficult in many regards as they are variable in space and time and differ among stakeholders (Daily et al., 2000; Whitelaw and Macmullen, 2006; Fisher and Turner, 2008). Regardless of these limitations, decisions by policymakers and stakeholders to remove dams are often based on cost-benefit analyses (Whitelaw and Macmullen, 2006). Whitelaw and Macmullen (2006) highlight six principles they suggest should be considered when dams are potentially being removed; however,

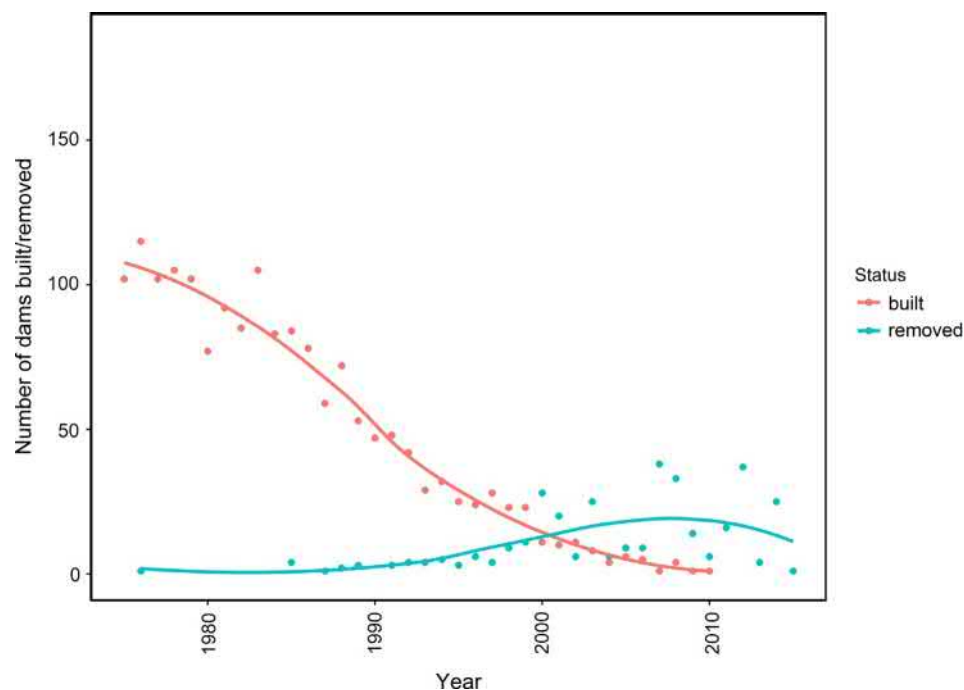


Fig. 7 Comparison of the number of dams constructed and the number of dams removed in the United States since 1975.

these principles are derived from an anthropocentric economic perspective and do not consider the full suite of consequences for keeping or removing a dam. As Fisher and Turner (2008) point out, there are “benefits” that extend beyond services ecosystems provide, which include recreation opportunities, aesthetics, cultural contentment, among others. All of which relate to human welfare. While extremely difficult and complicated by human interests, a full accounting of the known socio-ecological factors associated with any given dam removal project should be considered.

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From Anthrome to Refugium? A Short History of Small-Scale Fisheries in the Anthropocene

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Glossary

Anthromes Parts of the terrestrial and aquatic biosphere considered not as pristine but as human-altered ecosystems, thereby accounting for globally significant patterns of social-ecological interaction that (re)produce these ecosystems and the various types of value they represent.

Biocultural refugia Anthromes where primary producers find refuge from pressures that are invoked by social and ecological change.

Enclosure of small-scale fisheries A process whereby small-scale fishers lose access to and control over aquatic and marine environments to industrial fishers, industries, business, or states.

Small-scale fisheries Fishing practices that are not industrialized, and which can have one or more of the following qualifications: technologically simple; low operating costs; labor-intensive; capital-extensive; different target species; artisanal; short trips; small catches; family business; diversified livelihoods; subsistence; traditional; low profitability.

Abstract

Names can be confounding. Small-scale fisheries (SSF) refer to a wide variety of fishing practices that are distinctive not only for their scale of operation. From a global perspective, small-scale fisheries include fisheries that are often (but not always) performed with artisanal gear; rely on family labor; take place in coastal environments, lakes and lagoons; and have diverse catch portfolios. In this article we investigate SSF—its characteristics and values—by considering explicitly the type of aquatic and marine environments in the Global North and South that they exploit and change. We assume that with the modernization and industrialization of fisheries these environments have acquired a more pronounced profile because SSF is becoming enclosed. To explore and discuss this assumption we use the literature on (small-scale) fisheries and our own work, and start by considering the contribution of fisheries to the transformation of aquatic and marine environments into anthromes. From here we argue that the anthromes where small-scale fishers currently operate are shrinking under the pressures from a globalizing and urbanizing world, and as such come to function as biocultural refugia. We conclude with a discussion of the implications of this trend for the overall resilience of small-scale fisheries worldwide, and the qualities and values that these types of fishery represent as alternatives to industrially organized food production that depends on growth-based economies.

Introduction

Simple gear; low operating costs; labor-intensive; capital-extensive; different target species; artisanal; short trips; small catches; family business; diversified livelihoods; subsistence; traditional; low profitability; and, of course, small. These are some of the qualifications used to demarcate small-scale fisheries (SSF) from more industrialized fishing practices (Berkes et al., 2001).

It is important to emphasize that while SSF is thought to share one essential common feature (scale), SSF practices—especially from a global perspective—are connected by several overlapping similarities, none of these common to all (Brandt, 1972; Johnson,

2006). How SSF manifests empirically is highly contingent and dependent on particular social and ecological conditions. As SSF entails such a broad variety of practices it is often complicated and problematic to make general statements about what SSF is and does.

In this article, we will investigate if the development of SSF—its characteristics and values—can be understood through the type of aquatic and marine environments in the Global North and South that they exploit and change. We assume that with the modernization and industrialization of fisheries these environments become more distinctive as anthromes because SSF is becoming enclosed. Industrial fisheries are now capable of catching fish far and deep at sea. Practices of SSF, on the other hand, are more and more limited to environments that are not suited from an economic or ecological perspective for modern fisheries. These environments might be too shallow, too difficult to navigate, or have too small stocks or species to be profitable for industrial fisheries. Such environments typically include lakes, estuaries, lagoons, wetlands, archipelagos, but even urban waterscapes. What can a focus on the shared features of the natural environments in which small-scale fishers work—lakes, lagoons, archipelagos, and coastal waters—teach us about the global characteristics, development and benefits of SSF?

To answer this question, we first conceptualize the environments that SSF exploit as anthropogenic biomes, so-called “anthromes.” The term anthrome makes explicit how human activity interacts and reproduces ecosystems. It highlights the terrestrial and aquatic biosphere not as pristine but as human-altered ecosystems, thereby accounting for globally significant patterns of social-ecological interaction that (re)produce these ecosystems and the various types of value they represent (Ellis and Ramankutty, 2008). With this definition in place we will next consider the anthromes of SSF in more detail, and argue that SSF, in the global North and South, struggle with a number of general problems, which together contribute to the enclosure of SSF. In response to enclosure, small-scale fishers worldwide face the dilemma of industrializing their business and expanding their ecological range, quit fishing, or taking refuge to marine or aquatic environments that are not particularly suited for industrialized fishing techniques. As a result of this development, the SSF that remains today is often practiced in shrinking anthromes. We conclude with a discussion of the implications of this trend for the overall resilience and sustainability of small-scale fisheries worldwide, and explore if the anthromes of SSF should be considered as “biocultural refugia” (Barthel et al., 2013), anthromes where small-scale fishers find refuge from pressures that are invoked by social and ecological change.

Anthromes in Aquatic and Marine Environments

Marine and aquatic environments have played a crucial role in human history (Fagan, 2017); its ecologies provisioned people with a varied menu of fish, sea- and water birds, shellfish, turtles, and mammals such as otters or seals. Archeological evidence points out that the earliest large and fixed human settlements around 6500 BCE sprang up in wetlands, such as the Mesopotamian alluvium. Wetlands provided people with a breadth of ecological opportunities for hunting, fishing, foraging, and gathering (Erlandson and Rick, 2010).

For a long time, it was thought that prehistoric fisheries only had a limited impact on the biology and ecology of marine and aquatic environments. Especially marine environments were considered mostly inaccessible for early fishers, and above all, inexhaustible (Roberts, 2007). But historical research has refuted the assumption that aquatic and marine environments transformed into anthromes only after the onset of fisheries industrialization (Vickers, 2004; McCauley et al., 2015). Between stone-age and fossil-fuel fisheries lies a long and varied history of innovation, acceleration and geographical expansion of fishing effort that goes hand in hand with both gradual and rapid environmental change (Pitcher and Lam, 2015; Fagan, 2017).

A telling example of the long-term environmental history of fisheries comes from Medieval Europe, where—around the year 1050—people began to include more fish in their diet. It was the urban centers with their growing populations that needed increasing bulks of protein. Fish formed a relatively easy source for this. Moreover, fish provided an important source for religious obligation (Fagan, 2008) and even prestige consumption on urban markets (Fagan, 2017). However, at the same time as urban demand for fish increased, freshwater and migratory fish stocks dwindled because stocks had problems to spawn due to the construction of numerous mills and dams, and agriculture induced siltation and sedimentation. The crisis in the freshwater fish supply in 11th and 12th century Europe made fishers turn to the sea in search of pristine stocks (Hoffmann, 2001; Fagan, 2017). A change in the urban diet followed, and people now started eating more marine instead of the freshwater and migratory fish that had traditionally been served (Roberts, 2007).

This example, along with others (see Roberts, 2007; Pitcher and Lam, 2015; Fagan, 2017), makes clear that fisheries from an early age have importantly influenced and shaped marine and aquatic environments. Some of these fisheries grew very large in terms of their manpower, financial investments, fishing capacity and geographical reach. The medieval cod and herring fisheries in Europe or the whaling industry of the 18th and 19th centuries were global, commercial fisheries that traded products over long distances. For some of these fisheries the influence was deep, long and extensive enough to transform pristine ecologies into anthromes (Roberts, 2007; Barrett, 2019).

Yet, during pre-industrial fisheries some pristine ecosystems continued to exist. These were found in inaccessible environments, such as deep offshore waters, that stayed out of human reach. Only recently these environments have turned into anthromes, when fishing boats were equipped with modern fishing technology, such as fish finders; freezers; nylon nets, and powered with steam or fossil fuel (Pitcher and Lam, 2015). Supported by these technological innovations and driven by commercial trade across the globe, fisheries quickly expanded its geographical reach to become a major global force causing irreversible changes in marine and aquatic ecological interactions (Fagan, 2017). So much so that the development of fisheries after the 1950s is documented as a sequential

depletion of stocks (Berkes et al., 2006) and trophic levels (Pauly et al., 1998) that turned aquatic and marine environments everywhere in the world into anthromes (Pitcher and Cheung, 2013).

The Creation of SSF

Although fisheries expanded its geographical reach and environmental impact since long, it was during the decades following the Second World War that fisheries development revolutionized globally through the introduction of several low-cost technological innovations, such as nylon nets (Bavinck, 2011). During these decades, a need develops especially for governments to distinguish between industrial fisheries that operate at a larger scale (e.g., larger boats, catch volumes, and longer trips) and traditional fishing practices. This is how the denotation SSF for the first time comes in use (McGoodwin, 1995). The term singles out fishers and fishing practices that somehow fail to industrialize with the purpose to target these for subsidies or loans that are supposed to enable modernization (Berkes et al., 2001).

But with the growing recognition and understanding of the environmental impact of industrial fisheries, SSF gradually gains another connotation. It becomes used to single out a type of fisheries that is believed to be relatively ecologically sustainable in comparison to industrial fishing. In this interpretation SSF has low emissions of carbon dioxide; low by-catch and discards due to the use of selective gear; high quality of the catch; low overall environmental impact on bottom sediments; and, perhaps most importantly, it is geographically bound, which means that there is an incentive to sustain fish stocks in a long-term perspective (McGoodwin, 1995). Because of these qualities SSF seems better able to meet the requirements of ecosystem-based management and post-carbon society than industrial fishing. Caution is warranted though. It is clear that SSF practices can also degrade marine environments, as exemplified with some of environmental histories of preindustrial fisheries (Vickers, 2004). Moreover, SSF practices that target a particular vulnerable key-stone species, such as eel or sharks can be ecologically unsustainable (see Björkvik et al. (2019a) for the example of eel).

Both interpretations of SSF continue to be used to justify interventions that aim to strengthen the development of rural and coastal livelihoods and communities. In the global South, the label SSF is used to signal the need for further economic development through improved technologies, access to markets, licensing, etc. (Béné et al., 2010). In the global North, it is used to suggest policies that aim to protect small-scale fishers from global economic competition (Björkvik et al., 2019a,b).

These interventions signal that SSF is under pressure in many places in the world (Kittinger et al., 2013). In the global North, its economic profitability went down; the resilience of stocks has declined due to overfishing, climate change, and pollution; and fisheries regulation has increased substantially (Björkvik et al., 2019a,b). Moreover, the competition over marine resources has intensified between SSF and protected predatory species, like seals, but also between SSF and other social groups that want to use marine environments for economic development, alternative energy production, housing, or nature recreation and conservation (Kerr et al., 2018). Small-scale fishers in the global South likewise struggle with declining resilience and productivity of marine environments due to pollution, overfishing, and climate change, and here too regulation is increasing and becoming stricter (Boonstra and Dang, 2010). Unlike in the global North, small-scale fishers in the global South also suffer from competition with other small-scale fishers, as there so many of them (Hanh and Boonstra, 2018).

Shrinking Anthromes

A number of scholars qualify these pressures as the “enclosure of the commons” (Murray et al., 2010; Pinkerton and Davis, 2015) or “ocean grabbing” (Bennett et al., 2015). Such labels highlight that small-scale fishers lose access to and control over aquatic and marine environments to industrial fishers, industries, business, or states (Bavinck et al., 2018), which consequently means that the anthromes in which SSF operates are shrinking in size. It is clear that this process impacts the development of SSF negatively, but it can also have a positive impact on aquatic and marine environments if SSF negatively impacts the resilience and sustainability of these environments. As we made clear in the foregoing, the impact of SSF on environmental sustainability is equivocal. Attention therefore needs to be paid to the social and ecological characteristics of SSF rather than assuming its practices are inherently sustainable (Björkvik et al., 2019a,b).

Small-scale fishers seek out different ways to find relief from the closure of the commons. The most straightforward response is to exit fisheries. Fishers in the global North can sometimes enable their exit through subsidies for boat scrapping or selling their fishing quotas. In the global South, this type of support is mostly non-existent, which means that many fishers have no option but to continue fishing. Exiting fisheries under these circumstances can only be done through finding alternative means and incomes to sustain livelihoods. For many fishers in the global South this means migrating to cities in search for new types of income (Hanh and Boonstra, 2018).

Another coping strategy is to expand the fishing business, through increasing the rates of return. It is important to realize that expanding fishing effort involves a qualitative change in the style of fishing. It requires considerable investments in technology to upgrade vessels and gear, perhaps to buy fishing quota and/or licenses, but also a willingness and capacity to take risk with investments and to expand fishing beyond the local environments to target new and larger fishing grounds.

Some small-scale fishers can or are not prepared to make such changes. This group applies a number of strategies to remain fishing but without scaling up their businesses (Salmi, 2015; Boonstra et al., 2018). A first strategy is to reduce operation costs

by maximizing use of local social and natural capital (Boonstra and Hentati-Sundberg, 2016). Examples include reliance on family labor, non-monetized economic exchange, repairing rather than replacing gear and vessels, and using own skills and knowledge or from family/friends to do repairs. A second strategy is to diversify fishing livelihoods. Diversification can relate to the fishing practice itself, when fishers target a broad spectrum of species, e.g., freshwater and marine species, but it also relates to their livelihoods when they obtain income from various other activities, which can include farming, trading, or manual labor (Allison and Ellis, 2001; Salmi, 2005). A third strategy is to innovate small-scale fisheries by gearing it to (urban) markets for local and niche food. Examples here include the selling of local fish through fisher-owned shops and restaurants, but also the marketing and processing of fish as an exclusive product (Björkvik et al., 2019a,b). Below we present two vignettes of SSF in the global North and South which illustrate various ways in which fishers cope with the enclosure of the commons, but also the continuous development of SSF.

Vignette From the Global South: The Tam Giang Lagoon

The Tam Giang Lagoon is located in Thua Thien Hue province, in the centre of Vietnam. With an area of 20,000 ha and length of 70 km, it is the largest lagoon in the Southeast Asia. The lagoon is a brackish water ecosystem with rich biodiversity and biomass and provides livelihoods for 100,000 people via small-scale fishing and aquaculture (Hanh and Boonstra, 2018).

Fishing is a traditional livelihood activity and performed with stationary fishing gear fixed in certain places in the lagoon, e.g., stake traps and bottom nets, and mobile fishing gear that is moved around in the lagoon, e.g., gillnets and steel-framed bottom traps. Although fisheries in the lagoon has been targeted since the 1950s/1960s it continues to operate under a de facto open access regime (van Tuyen et al., 2010). Since the 1980s fishing effort increased, because regulation was not able to pose limits on fishing effort, while so-called Doi Moi policies ("renovation" policies) connected Vietnam to global markets, which promoted seafood exports pushing the price of seafood upwards. Moreover, population in the lagoon grew and improved fishing technology, such as nylon nets but also electric fishing gears and steel-framed traps, became available and affordable (Boonstra and Nhung, 2012). As a result, the number of fishers in the lagoon rose dramatically between 1982 and 1993 from 5575 to 9120. The total fish catch of the lagoon also spiked from 850 ton in 1976 to 2112 ton in 1993. Yet, fish catch per household decreased steadily since the early 1990s (Ho et al., 2016).

By the early 1990s, aquaculture was introduced to the lagoon and expanded rapidly (Boonstra and Nhung, 2012). The Vietnamese government helped to support the establishment of aquaculture through provisioning loans against low interests and giving out areas in the lagoon for tenure. With this support and the high international and national demand for seafood the area in the lagoon used for aquaculture increased from 20 ha in 1990 to 4200 ha in 2006 and developed into an intensive monoculture (Boonstra and Hanh, 2014). The introduction and development of aquaculture deteriorated the lagoon water quality dramatically as it increased waste loads, which contributed to eutrophication, and high levels of coliform density and organochlorine pesticides (van Tuyen et al., 2010). This deterioration in turn impacted the growth and health of aquatic and marine species. Moreover, the expansion of aquaculture through the lagoon also reduced and contaminated nursery and spawning areas as well the fishing grounds for small-scale fishers (Armitage and Marschke, 2013).

As a result, small-scale fishers in the lagoon have been struggling to keep catches sufficiently high (Hanh and Boonstra, 2018). They do so primarily by increasing their exploitation efforts as they lack the capacity and alternative opportunities to earn income outside fisheries (Armitage and Marschke, 2013; Hanh and Boonstra, 2019). It goes without saying that this response only accelerates a deterioration of the lagoon resources and thus in the long run local fishers' livelihood.

Since the middle of the 2000s, alarmed by the deteriorating sustainability of the lagoon, the provincial government has implemented a number of measures to improve the lagoon resources as well as the users' livelihoods (Armitage et al., 2011). Fisheries regulation has been enforced more stringently, and several types of gear are now prohibited, while other more artisanal, benign types are encouraged to be reused, such as bamboo traps. The government also started allocating territorial user rights for fisheries to user groups as a way to limit access and improve the monitoring and enforcement of fisheries regulation. The construction of new aquaculture ponds is prohibited, and existing ponds are encouraged to contain more extensive polycultures to minimize waste load and the spread of diseases (Hanh and Boonstra, 2018). Moreover, the government installed 26 nursery and spawning areas (equivalent to 2.8% of the lagoon area) to improve species reproduction and survivals. In addition, the lagoon now houses 400 artificial reefs where a total of 400,000 juvenile fish, shrimp and crab are introduced. Finally, the reduced catches from the lagoon are of much less interest to global markets where buyers want to purchase large quantities. As a result, fishers and aquaculturists in the lagoon are nowadays returning to supplying local markets with freshly caught fish.

Vignette From the Global North: The Stockholm Archipelago

The Stockholm archipelago is the second largest archipelago in the Baltic Sea, consisting of over 24,000 islands. It covers an area of 1700 km² from Vaddö island in the North to Öja island in the South around 150 km, and extends from Stockholm city 80 km eastward (Hedenstierna, 1989).

Fisheries has been a primary livelihood activity for the inhabitants of the archipelago for many centuries. It used to be one of the activities that local peasant communities engaged in, next to farming and forestry (Thornström, 1978; Löfgren, 1979; Selling, 2010). This peasant lifestyle disappeared after the Second World War with the introduction of new catch methods, such as pound nets for

catching eel introduced in the 1960s, and the demand for work in urban centres (Selling and Holmer, 2007; Björkvik et al., 2019a,b), such as Stockholm City. From then onwards the style of fishers in the archipelago became more distinct as a small-scale operation because it differed considerably from other fisheries that industrialized and expanded their operations financially and geographically (Boonstra and Hentati-Sundberg, 2016).

The remaining professional fisheries in the Stockholm archipelago is predominantly a mixed-species fishery that targets cod, herring, flounder, eel, whitefish, perch, pike and pikeperch. Fishers own boats that are often smaller than 12 m, and combine a number of gear types, including mostly traps and gillnets. Since the 1970s most of the fishers in the archipelago stopped or retired. At the moment, there are approximately 30 professional fishers left (Andersson and Sjöberg, 2012).

A number of changes has made it more difficult to provide oneself a livelihood based on fishery in the archipelago. The economic profitability of the fishery has been in decline the recent decades (Waldo et al., 2013). At the same time, the resilience of Baltic fish stocks is impaired due to overfishing, climate change, and eutrophication (Blenckner et al., 2015). As a consequence of these changes fisheries regulation has increased substantially (Hentati-Sundberg and Hjelm, 2014). Moreover, fishers also face increased competition over fish and marine resources from growing seal and cormorant populations (Königson, 2011) as well as other stakeholders that aim to use the archipelago for economic or leisure purposes.

Historically, fishing used to be a very important livelihood strategy in Stockholm innercity as well (Ericson Wolke, 2001). With its currents, its brackish and sweet water Stockholm offered lots of opportunities for catching a wide variety of fish. It currently still has around 30 different species, making the city one of the most species-rich fishing locations in Sweden (Stockholm City, 2019). The most common way of fishing in the Stockholm inner city has traditionally been seine fishing and fishing with hand nets. This way of professional small-scale fishing disappeared during the second half of the 20th century (Ericson Wolke, 2001).

With industrialization and modernisation, the character and role of fishing in Stockholm City changed. Industry and untreated sewage discharge deteriorated the health of the water and the health of the fish stocks. Moreover, with the development of modern trade and retail, city folk increasingly purchased fish from elsewhere in supermarkets supplied by global production networks. In fact, it has become difficult nowadays to find and purchase fish from the region in Stockholm (Andersson and Sjöberg, 2012). Yet, fishing in the city never completely ceased. The efforts for the improvement of the water quality towards the end of the 20th century (Ericson Wolke, 2001), and the yearly release of around 35,000 salmon and trout in the inner-city, maintain a fishing stock that currently attracts a culturally diverse group of anglers. In a remarkable contrast with professional fisheries in the wider archipelago, fishing in Stockholm's innercity has recently reinvigorated after a long time of decline. Some of these fishers fish purely for recreation using catch and release, but there are also others who fish in the city for providing themselves and others with food. In any case, it seems that the (mostly) free access and improved ecologies of urban waters in Stockholm City has reinvigorated a small-scale fishery that provides a culturally and economically diverse group of urban dwellers with opportunities for leisure and food.

Discussion: From Anthrome to Refugium?

As exemplified in the two vignettes, small-scale fishers globally are pressured from various social and ecological changes, which include the deterioration of aquatic and marine natural resources as well as intensified economic competition and stricter government regulations. For many small-scale fishers worldwide it is becoming increasingly difficult to maintain their business and livelihood (but there are of course exceptions, i.e., places where small-scale fishers are doing well, see e.g., Boonstra et al., 2018 for the example of the vendace fishery in Northern Sweden).

Despite global differences small-scale fishers generally are losing access to and control over aquatic and marine environments. As a consequence, they are becoming more dependent on environments that, for various reasons, are not targeted by industrial fisheries, other businesses or governments. Sometimes, small-scale fishers are forced to operate in these areas due to government restrictions or exploitation of marine and aquatic environments by other economic actors. In other cases, small-scale fishers might choose themselves to focus on and operate in these environments because it enables them to avoid competition with more powerful actors, or to access a niche market (based on a certain species or locality) from which to improve profits.

What unites these environments is that they currently lie outside of the interest of industrial fishers or other larger-scale economic businesses operating in the marine and aquatic economy. They can be economically unattractive for a number of reasons: the environments may be inaccessible for industrial fishers, e.g., too shallow and therefore only allowing small vessels (Murawski, 2000); they may be habitats for fish that are not in high demand on the markets the industrial fishers target; or they may not allow a uniform catch in terms of volume and species composition because of seasonal variability and/or species, thus complicating a constant and large market supply (Johnson et al., 2005).

We suggest that the marine and aquatic environments that continue to allow the establishment and sustenance of SSF can be defined and further explored as a specific anthrome, namely an anthrome that is shrinking due to the further enclosure of marine and aquatic commons under the pressure of competition over access to and control over natural resources. Can such shrinking anthromes of SSF be characterized and understood as biocultural refugia? Biocultural refugia accommodate small-scale fisheries that represent various forms of capitals that otherwise would be outcompeted and made redundant.

As we demonstrated with the enclosure of SSF, and the two vignettes, SSF in the global North and South are currently undergoing major changes. With ongoing urbanization and globalization many small-scale fisher livelihoods are discontinued. The small-scale fishers that continue their businesses often have to compete with a growing interest in aquatic and marine environments coming from corporations, environmental conservation, or states. Under these pressures small-scale fishers are seeking out places and

species that are relatively underexploited and/or which exploitation can only accommodate a knowledge and labor-intense operation. Surely not all SSF can be characterized in this way, but we expect that in the future the remaining small-scale fishers will find refuge in anthromes that have these characteristics.

As such these refugia maintain working alternatives to industrially organized food production that is inherently tied to economies that are based on continuous growth of output (Roelvink et al., 2015). From a resilience perspective, the existence of biocultural refugia that enable small-scale fisheries represents a valuable resource because they contribute to response diversity needed for transitions towards more sustainable societies (Boonstra and Joosse, 2013).

At the same time as the anthromes of SSF are shrinking, we also perceive the (re)establishment of anthromes especially in urban settings. As the vignette of Stockholm city illustrates, SSF in different forms may return as soon as new opportunities develop. The presence, development and (re)establishment of fisheries in urban waters in both the global North and South is currently an undervalued and forgotten manifestation of SSF. We foresee that the importance of urban SSF will continue to grow in a quickly urbanizing planet and therefore demands (scientific) attention and management.

The example of urban SSF also nicely illustrates the unique polymorphous nature of SSF stemming from the ability of small-scale fishers to respond differently to changing circumstances through improvisation and make-do with the resources at hand (Baker and Nelson, 2005). A characteristic that also makes capturing SSF—its qualities and benefits - in generic or quintessential definitions impossible and perhaps not useful. Based on the analysis offered here, we argue that SSF can be understood and valued as highly diverse practices that can offer alternatives to industrialized, monetized and expansive fisheries. But, the social and ecological benefits and opportunities of its various local manifestations need to be assessed time and again, because SSF is inherently variable and diverse.

Moreover, the existence of refugia for SSF, and the resilience of small-scale fishers, does in itself not guarantee the preservation of knowledge and skill important for a transition to sustainable exploitation of marine and aquatic resources. Several challenges continue to threaten the livelihoods of small-scale fishers. One challenge is generic regulations that fail to distinguish between different types of fisheries. Previous studies have shown that regulations often disfavor SSF because they impede the maintenance of a diversified fishing (Hentati-Sundberg et al., 2015). Another challenge is the lack of recruitment and succession of young fishers. There are few examples of new entrants into SSF, and the number of sons and daughters continuing their family's small-scale fishing operation is decreasing, among others because the economic pay-off from small-scale fishing is low (Blomqvist et al., 2016). A final challenge concerns changes that are induced from global inter- and teleconnections (Hull and Liu, 2018) from which even refugia are not exempt. Indeed, research indicates that the health and size of local fish stocks is impacted by activities that take place in far-removed locations (Drouineau et al., 2018), such as off-shore fishing (Sumaila et al., 2015), or pollution from industry.

Conclusion

In the late Anthropocene fishers started to power their boats with fossil fuels and adopted technologies that allowed them to scale up their fishing range and effort. The fishers that lagged behind this development, either by choice or from necessity, are nowadays known as small-scale fishers. Defined originally foremost by what they were not, namely industrialized and modernized SSF, houses a great number of different fishing styles whose diversity is impossible to cover in a quintessential definition.

Despite the tremendous global diversity of this type of fisheries, there are a number of common threats to their existence and development. Based on an overview of these threats, and our knowledge of their specific and local manifestation in the global North and South, we have argued that the anthromes that continue to host SSF could be characterized as biocultural refugia. These refugia represent valuable storehouses of knowledge and skills that have potential to contribute to post-growth societies that use and preserve aquatic and marine environments sustainably.

To be sure, we are not suggesting in this article to turn back the clock, but rather to utilize the unique skill and capabilities of small-scale fishers to enable a transition to a post-growth and renewable energy use of aquatic and marine environments. Such a transition would involve the retro-innovation (Stuiver, 2006) rather than re-establishment of SSF to benefit sustainable development.

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Endocrine Disruptors and Marine Systems

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Abstract

Environmental contaminants known as endocrine disruptors (or endocrine-disrupting chemicals, EDCs) are increasingly detected in marine systems. EDCs are structurally diverse compounds including steroids, phenols, phthalates, organochlorines, and organotins; these compounds are found in pharmaceuticals, pesticides, personal care products, plastics, and a variety of other products. EDCs in the marine environment wind up in the water column, in organisms, and adsorbed to sediments, especially in the shallow neritic zone and in bodies of water that experience limited water exchange. The fate of marine EDCs is determined by a combination of abiotic and biotic processes. Some EDCs are susceptible to degradation but are nonetheless perpetually present in marine systems due to continuous replenishment and are therefore considered pseudo-persistent. Others are remarkably stable and resist degradation and thus are considered persistent. Persistent EDCs are often lipophilic and thus tend to bioaccumulate and biomagnify. EDCs interact with the endocrine systems of animals by interfering with the concentrations or activities of hormones or their receptors, thereby leading to reproductive, developmental, metabolic, or behavioral dysfunction. Many EDCs agonize or antagonize hormone receptors, while others modulate the activities of enzymes involved in synthesis or metabolism of hormones or alter the expression of genes that encode receptors or protein hormones. Much has been learned in the last several decades about the presence of EDCs in marine systems and the effects of EDCs on some marine organisms. However, existing knowledge gaps must be addressed if we are to understand the scope of human impacts on marine systems. In addition, priority must be given to developing remediation strategies that both reduce the inputs of anthropogenic EDCs into marine systems and mitigate the effects of these chemicals in marine organisms.

Introduction to Endocrine Disruptors

Many human impacts on coastal and marine ecosystems are obvious and well documented; these impacts include habitat alteration or destruction, introduction of invasive species, extinction of native species, overfishing, and pollution. Other human impacts are not as well recognized though certainly no less troubling. For example, environmental contaminants known as endocrine disruptors (or endocrine-disrupting chemicals, EDCs) are increasingly detected in coastal and marine systems. An EDC is defined by the US EPA as “an exogenous agent that interferes with the production, release, transport, metabolism, binding, action or elimination of natural hormones in the body responsible for the maintenance of homeostasis and the regulation of developmental processes” (Kavlock et al., 1996). EDCs are structurally diverse compounds that can be found in pharmaceuticals, pesticides, personal care products, plastics, and a variety of other commercial and industrial products. These compounds interact with the endocrine systems of animals by mimicking, blocking, or altering the metabolism of hormones or their receptors, leading to reproductive, developmental, metabolic, or behavioral dysfunction. The most well studied hormones that are susceptible to disruption by EDCs include sex steroids (e.g., estrogens, androgens, or progestins), thyroid hormones, protein hormones (e.g., gonadotropins and glucoregulatory hormones such as insulin and growth hormone), and molting hormones, though other signaling pathways (e.g., those involving nitric oxide, heat shock proteins, and immune mediators) are also susceptible. While many natural compounds (such as phytosterols and pheromones) can be considered EDCs, this article focuses on anthropogenic EDCs as they relate to human impacts in estuarine and marine systems.

Sources and Fates of Endocrine Disruptors in the Marine Environment

Anthropogenic EDCs are produced and primarily used in terrestrial systems, but they readily enter the aquatic environment by way of sewage or wastewater effluent, landfill leaching, industrial discharge, and surface water runoff from urban and agricultural areas.

EDCs in ground and surface waters eventually make their way to the ocean. EDCs can also enter the marine environment directly from mariculture facilities and marine vessels. Regardless of source, EDCs in the marine environment wind up in the water column, in organisms, and adsorbed to sediments.

The ultimate fate of a marine EDC is determined by a combination of abiotic processes such as photolysis, hydrolysis, volatilization, ionization, and sediment sorption as well as biotic processes such as absorption, metabolism (or biotransformation), and elimination. Within organisms, metabolism of EDCs occurs via one or both of two phases. In phase I metabolism, xenobiotics including EDCs are oxidized, reduced, or hydrolyzed, typically by enzymes in the cytochrome P-450 (CYP) protein family. In phase II metabolism, xenobiotics are converted into more hydrophilic metabolites, which are easier to excrete, via the conjugation of polar functional groups including glucuronic acid, sulfate, glutathione, and acetyl groups. Aspects of water chemistry, such as pH and osmolarity as well as temperature, also dictate the fate of marine EDCs, as these factors can affect solubility as well as rates of degradation and uptake. Some EDCs, including many pharmaceutical compounds, are susceptible to abiotic and biotic degradation but are nonetheless perpetually present in marine systems due to continuous replenishment (e.g., via wastewater inputs) and are therefore known as *pseudo-persistent organic pollutants*. Others, notably the very stable organochlorine compounds such as polychlorinated biphenyls (PCBs) and dichlorodiphenyltrichloroethane (DDT), resist biotic and abiotic degradation and thus are known as *persistent organic pollutants* (POPs).

The stability of POPs such as PCBs and DDT allows them to accumulate for long periods of time, thereby increasing the chance that their concentrations in the marine environment will reach or exceed observable adverse effect levels. The persistence of POPs also allows them to remain intact through repeated cycles of vaporization and condensation. On a global scale, the process by which such chemicals vaporize, travel via air currents to cooler locations, and then condense is known as global distillation (or *the grasshopper effect*). Over the course of many years, global distillation slowly transports POPs from warmer to cooler locations and thus from lower to higher latitudes and altitudes, causing POPs to accumulate on mountaintops and around the poles (Fig. 1; Wania and Mackay, 1996). In this way, the regions of the globe farthest from human industry and agriculture are becoming some of the most contaminated with POPs, many of which are EDCs.

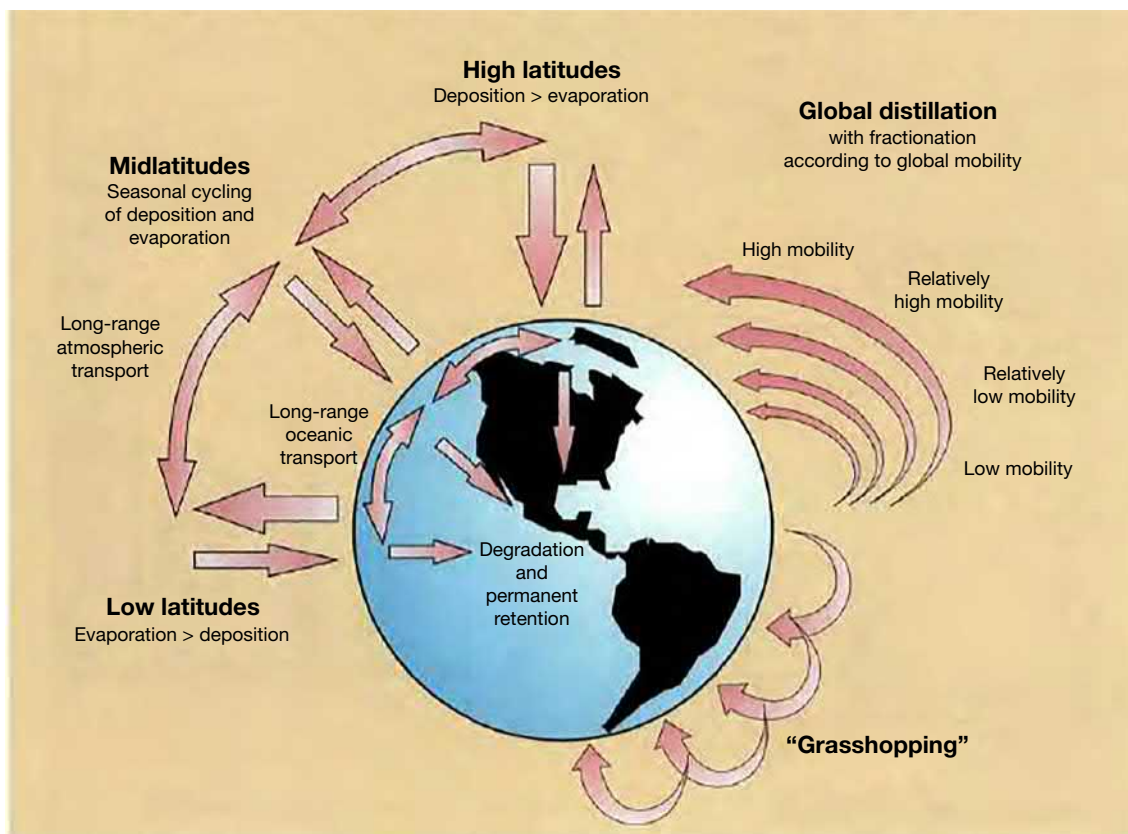


Fig. 1 Mechanisms responsible for the migration of chemicals around the globe. In the tropics, the rate of evaporation exceeds the rate of condensation or deposition; at the poles, the opposite is true. The process by which stable, persistent organic pollutants (POPs) vaporize, travel via air currents to cooler locations, and then condense is known as global distillation (or “grasshopping”). Over the course of many years, global distillation transports POPs from warmer to cooler locations and thus from lower to higher latitudes and altitudes, causing POPs to accumulate on mountaintops and around the poles. Figure reprinted with permission from Wania F and Mackay D (1996) Tracking the distribution of persistent organic pollutants. *Environmental Science and Technology* 30: A390–A396.

The majority of POPs are problematic not only because they can act as EDCs and disrupt hormonal pathways in animals but also because they are lipophilic (or “fat-loving”). Lipophilic chemicals readily distribute into fatty tissues such as brain and adipose tissue, from which they can be remobilized during periods of weight loss. This remobilization process liberates POPs from fat stores in lactating mammals, such that males often have higher total body burdens of POPs compared to females in their reproductive years. However, this pattern comes at a hefty cost, as POPs liberated from maternal fat stores are directly transferred to neonates via milk. POPs also tend to bioaccumulate and biomagnify due to their lipophilic properties. For this reason, the concentration of POPs measured in marine primary producers (e.g., algae) exceeds that of the water (due to bioaccumulation), and the concentration measured in consumers often exceeds that of producers (due to biomagnification). Top predators including large, migratory fish and marine mammals may be especially vulnerable to the effects of POPs given their terminal positions in the food web. For example, organochlorine levels in top predators like odontocetes (e.g., striped dolphins and beluga whales) can be an order of magnitude higher than in planktivores such as mysticetes (e.g., fin whales; [Fossi et al., 2003](#)). Terminal predators that live near the poles experience the combined effects of biomagnification and global distillation, causing animals such as polar bears, seals, and whales (as well as the indigenous humans who consume them) to have incredibly high body burdens of these toxic chemicals.

Concentrations of EDCs in estuarine and marine systems also depend heavily on hydrodynamics. For instance, EDCs tend to be more concentrated in the neritic zone, which overlies the continental shelf and is located near the coastline, than in the deeper oceanic zone. This pattern is likely explained by higher rates of dispersion and dilution that occur in offshore, oceanic environments than in shallower, nearshore areas. Not surprisingly, concentrations of EDCs are especially high in shallow coastal waters near major human population centers. Estuaries, which are important nursery grounds for many coastal organisms, are particularly vulnerable to EDC contamination, especially when agricultural run-off or effluent from sewage or wastewater treatment plants or from other industrial activities enters upstream waters. As rivers drain into estuaries and water velocity slows, particulate matter settles in a process known as sedimentation. Organic matter in sediments acts as a sorbent for nonpolar (i.e., lipophilic) compounds, whereas minerals in sediments act as a sorbent for polar and amphiphilic compounds. Contaminants bound to particulate matter thereby concentrate in estuarine sediments. For this reason, demersal (or bottom-feeding) estuarine animals that consume benthic prey often demonstrate higher contaminant loads than animals that feed higher in the water column. Sediment-bound contaminants can be liberated by flood tides, dredging, or other processes that disturb the estuary floor, such that concentrations of EDCs vary both spatially and temporally.

Marine contaminants such as EDCs also tend to accumulate in water bodies that experience limited water exchange. For example, organisms in the Mediterranean Sea often demonstrate contaminant loads an order of magnitude (or more) greater than those measured in Atlantic or Pacific organisms ([Aguilar et al., 2002](#)) due to the fact that the Mediterranean is surrounded by some of the most populous countries in the world and experiences only minimal exchange with the Atlantic Ocean. The Baltic Sea also participates in limited exchange with the North Sea and thus accumulates contaminants originating from industrial operations in the Rhine River basin.

Hydrodynamics also determine the fate of marine litter plastics and microplastics, which contain endocrine-disrupting additives like alkylphenols, plasticizers like alkyl or aryl esters of 1,2-benzene-dicarboxylic acid (also known as phthalates), monomers like bisphenol A (BPA), and stabilizers like tributyltin (TBT). The world's oceans receive plastic particles of various sizes at a rate of approximately 8 million metric tons per year, the majority of which end up on the sea floor ([Gallo et al., 2018](#)). Plastics also accumulate in floating patches in all five of the world's major ocean gyres, in bodies of water with limited exchange, and in polar areas. Plastics of all sizes can serve as both sources of and sinks for marine EDCs, as contaminants can both leach out of and adsorb into the pores within plastics. Migration of chemicals out of plastics is highest for small additives leaching out of polymer matrices with large pores. Typically, the chemicals that leach out of plastics are unreacted components left over from the manufacturing process, as these components are not covalently bonded to the polymer matrix. In addition, lower molecular weight compounds such as dimethyl phthalate and alkylphenols with short alkyl chains are more water-soluble and thus leach out of plastics more quickly than higher molecular weight compounds like di-2-ethylhexyl phthalate and alkylphenols with long alkyl chains. While plastics leach EDCs into marine systems, they can also concentrate other organic contaminants because of their lipophilic (i.e., hydrophobic) properties. Polyethylene plastics have a particularly high affinity for hydrophobic compounds and therefore sorb and concentrate more organic contaminants than other plastics such as polyvinylchloride (PVC) and polypropylene. Contaminants adsorbed onto marine plastics can travel long distances, protected from degradation by encapsulation within the matrix of plastic polymers. Aided by low temperatures, high salinity, and low light conditions, this molecular encapsulation increases the half-lives of adsorbed contaminants and thereby contributes to their pseudo-persistence in marine environments.

Effects of Exposure to Endocrine Disruptors in Marine Organisms

EDCs can be taken up into marine organisms by absorption across the skin or gills, inhalation, or ingestion. Given that most EDCs are at least moderately lipophilic, they are often readily absorbed across epithelial membranes (e.g., in the skin, gills, or lungs) into body fluids by simple diffusion. In the special case of contaminant-laden plastics, EDCs can be transferred out of the plastics and into organisms after ingestion of either plastic particles, which are often mistaken for food, or prey items that previously consumed plastics. Within the digestive tract, where organic materials and natural surfactants such as amphiphilic bile salts accumulate, contaminants may be especially likely to desorb from plastics into digestive fluid, from which they can be absorbed into body fluids. Once absorbed into circulation, EDCs can then exert a variety of effects on development, reproduction, and homeostasis. Unlike

typical toxicants, for which the magnitude of detrimental endpoints often demonstrates a linear or exponential relationship with dose, many EDCs are associated with nonmonotonic (i.e., U-shaped or inverted U-shaped) dose-response curves. EDCs are especially problematic because they are bioactive at extremely low doses (on the order of ng L^{-1}), which often correspond to environmentally relevant concentrations. In addition, many EDCs exhibit trans-generational effects that are mediated by epigenetic responses to exposure, such that the impacts are experienced one or more generations after exposure.

The pathways associated with steroid hormones, including estrogens and androgens, are major targets of EDCs. When exposure to EDCs is associated with responses similar to those induced by endogenous estrogens or androgens, those EDCs are said to have *estrogenic* or *androgenic* effects, respectively. Conversely, when EDCs inhibit the activity of endogenous estrogens or androgens, those EDCs are said to have *anti-estrogenic* or *anti-androgenic* effects, respectively. The majority of EDCs elicit such effects either by binding to the extracellular face of membrane-bound receptors or by diffusing across cell membranes and binding to intracellular receptors located in the cytoplasm or nucleus. Chemicals that bind to receptors and activate them are known as *agonists*, whereas chemicals that bind to receptors and inactivate them are known as *antagonists*. Many EDCs are either agonists or antagonists of hormone receptors such as estrogen or androgen receptors. The estrogen receptor in particular is implicated in responses to a number of EDCs, as this receptor is notoriously “promiscuous,” meaning that it demonstrates an affinity for a variety of compounds other than its endogenous ligands (estradiol, estrone, and estriol). Natural and synthetic compounds found in the environment that are able to agonize the estrogen receptor are collectively termed *environmental estrogens* or *xenoestrogens*.

Other EDCs stimulate or inhibit enzymes involved in synthesis, metabolism, or excretion of hormones or their receptors. For example, several known EDCs modulate the activity of CYP enzymes involved in steroid synthesis and phase I metabolism or conjugating enzymes involved in phase II metabolism, thereby altering the production of endogenous hormones or the clearance of both hormones and xenobiotics. Still other EDCs alter the expression of genes that encode hormone receptors or protein hormones. The mechanisms by which several classes of the better studied EDCs exert their effects are described below.

Pharmaceutical Estrogens

Pharmaceuticals constitute approximately a quarter of global chemical production (Murmans, 2003) and are used worldwide for both medicinal and agricultural purposes. Pharmaceuticals with substantial endocrine-disrupting capabilities include steroidal estrogens such as estrone (E1), 17β -estradiol (E2), and estriol (E3) as well as 17α -ethinylestradiol (EE2), the synthetic estrogen commonly found in birth control pills. Municipal sewage treatment plants do not remove or degrade most pharmaceutical compounds, so medications (including steroids) that are discarded or excreted into sewer systems are released unchanged into the environment by way of sewage treatment plant effluent. Steroidal estrogens are also used in high density livestock production facilities and thus are found in higher levels in marine systems impacted by agricultural runoff. Steroidal estrogens have been detected in marine systems globally, but their concentrations are often higher in estuaries than in the open ocean. Estuarine sediments in particular seem to be a sink for steroidal estrogens.

In vertebrate animals, natural and synthetic steroidal estrogens bind to and agonize both intracellular and membrane-bound estrogen receptors. Vertebrates express two isoforms of intracellular estrogen receptors (ESRs), termed estrogen receptor 1 (ESR1, formerly ER α) and estrogen receptor 2 (ESR2, formerly ER β). Due to a teleost-specific whole genome duplication, teleost fish express two versions of ESR2 (ESR2a and ESR2b). Upon activation by steroidal estrogens, ESRs dimerize and function as transcription factors, thereby regulating expression of estrogen-sensitive genes. Membrane-bound (or G protein-linked) estrogen receptors (GPERs) also bind steroidal estrogens, although the pathway downstream of ligand binding differs from the pathway involved in ESR signaling.

Exposure to steroidal estrogens at inappropriate concentrations or during inappropriate developmental windows alters gene expression and is associated with a variety of effects in vertebrates including feminization of males. For example, males of oviparous (or egg-laying) fish species that are exposed to exogenous estrogens often express vitellogenin, a female-specific protein produced in response to estrogens by the liver for subsequent incorporation into yolk. Exposed male fish also commonly develop ovotestes, or male gonads containing oocytes (or eggs), and they suffer impaired spermatogenesis, decreased sperm motility, and decreased sperm counts. In both male and female fish, exposure to exogenous steroidal estrogens leads to additional detrimental outcomes such as decreased fertility, increased incidence of certain cancers, and increased mortality. Invertebrates are also affected by exogenous steroidal estrogens, which are associated with developmental delays and female-biased sex ratios in marine invertebrates such as polychaete worms, molluscs, and crustaceans (Forget-Leray et al., 2005; García-Alonso et al., 2011; Ruiz-Velázquez et al., 2018).

Phenols

Phenols are aromatic organic compounds that consist of a phenyl group covalently bonded to a hydroxyl (or alcohol) group (collectively called a phenol group). The most common phenols in the marine environment include bisphenols like bisphenol A (BPA), which contains two phenols connected by an alkyl group, as well as alkylphenols (APs) and their derivatives, alkylphenol ethoxylates (APEOs), which both contain a phenol group covalently joined to an alkyl chain. BPA and its relative, bisphenol S (BPS), are used in the production of polycarbonate plastics, which can be found in food and beverage containers, electronic devices, plastic lenses, and automotive products. Bisphenols are also components of epoxy resins that are used in thermal paper and as linings of

food and beverage containers as well as water pipes. APs and APEOs are used as surfactants, detergents, emulsifiers, dispersants, and stabilizers in products such as paints, adhesives, lubricants, phenolic resins, fire retardants, pesticides, textiles, personal care products (including fragrances), and a variety of plastic goods.

The primary inputs of phenols into marine systems occur by way of sewage and wastewater treatment plant effluent and industrial discharge. Thus, marine phenols reach their highest concentrations in coastal areas near human population centers. Because BPA, BPS, and APs are used as building blocks in a variety of plastic goods, marine litter plastics can also leach phenols into seawater directly, though APs with longer alkyl chains are less likely to leach than APs with shorter alkyl chains (Teuten et al., 2009). Microbes residing in shallow sediments transform less toxic APEOs into more toxic APs including nonylphenol (NP) and octylphenol (OP). The length of alkyl chains determines the rate of transformation of APEOs into APs, as APEOs with long alkyl chains resist degradation and therefore persist in the environment for longer periods of time than APEOs with short alkyl chains (David et al., 2009).

Although APEOs are not typically considered EDCs, APs as well as BPA and BPS are estrogenic, meaning that they bind to and agonize ESRs (and are thus considered environmental estrogens). In addition, APs are also anti-androgenic, meaning that they bind to and antagonize androgen receptors (Bonefeld-Jørgensen et al., 2007). Thus, as with steroidal estrogens, exposure to bisphenols and APs is associated with feminization in males and resulting decreased fertility. Also like steroidal estrogens, phenols associate with particulate matter and are found at their highest concentrations in sediments of coastal areas including estuaries, lagoons, and harbors. Because phenols are amphiphilic, they can adsorb to both sorbent organic matter and minerals in sediments. As a result, bottom feeders and sediment-dwelling organisms (including demersal filter feeders) accumulate higher concentrations of phenols than marine organisms that live higher in the water column (David et al., 2009).

Plasticizers

Plasticizers are additives used in the production of plastics to reduce the attraction between polymer chains, thereby increasing the flexibility and durability of the resulting plastic. The most common plasticizers are phthalate esters, which are used primarily in the manufacturing of products made from PVC, including shower curtains, upholstery, flooring, and food containers. Phthalates are also used as dispersants, binders, and emulsifiers in personal care products, adhesives, detergents, paints, and pharmaceuticals. When used as plasticizers, phthalates are not covalently bonded to the polymer matrix and thus readily leach from plastics, especially when the plastics are exposed to elevated temperatures, low pH, or ultraviolet light. Lower molecular weight phthalates such as dimethylphthalate (DMP) are less hydrophobic and thus leach more readily from plastics than higher molecular weight phthalates like diethylhexylphthalate (DEHP). Landfill leachate and marine plastic litter, along with industrial discharge, are the primary sources of marine phthalates. For this reason, marine phthalates, like phenols, reach their highest concentrations in coastal environments near human population centers.

Unlike pharmaceutical estrogens and phenols, phthalates are anti-androgenic (Grady and Sathyanarayana, 2012), meaning that they interfere with the activity of androgens such as testosterone and dihydrotestosterone. Specifically, phthalates inhibit enzymes involved in steroidogenesis, thereby decreasing circulating levels of androgens. Exposure to phthalates is associated with a number of detrimental effects in male vertebrates, including malformations of the reproductive tract, decreased phallus size, impaired sperm production, and decreased sperm count. In essence, exposure to phthalates during the period of sex determination causes demasculinization (or feminization) of developing male vertebrate animals.

Organochlorines

Organochlorines (OCs) are organic compounds that contain at least one covalently bonded chlorine atom. Synthetic OCs include a number of EDCs such as polychlorinated biphenyls (PCBs) and dichlorodiphenyltrichloroethane (DDT) along with its metabolites (especially dichlorodiphenyldichloroethylene or DDE). Although the use of many OCs has been outlawed or restricted in most countries for several decades, OCs are generally stable molecules that bioaccumulate within organisms and biomagnify through food webs. They are therefore classified as persistent organic pollutants (POPs) and can still be detected at appreciable concentrations both in the environment and in organisms, especially at high latitudes and high elevations (due to the grasshopper effect, discussed above). The number of chlorine atoms in an OC molecule is positively correlated to its half-life and thus inversely correlated to its rate of metabolism or degradation, such that highly chlorinated compounds are more likely to persist in the environment than OCs with fewer chlorines. Conversely, less chlorinated compounds are selectively depleted as OCs travel toward the poles and through food webs.

DDT was widely employed in the 1940s and 1950s as an insecticide that was effective against hundreds of different pest species, including the vectors responsible for transmitting malaria and other deadly diseases. This OC achieved notoriety in Rachel Carson's book *Silent Spring*, which implicated DDT and other insecticides in the poisoning deaths of birds, fish, and other wildlife species in the years after World War II. Like many other EDCs, DDT is estrogenic. Specifically, it agonizes estrogen receptors and also increases expression of enzymes involved in estrogen synthesis. The primary DDT metabolite, DDE, antagonizes androgen receptors and thus is anti-androgenic. Due to their estrogenic and anti-androgenic effects, exposure to DDT or DDE at environmentally relevant concentrations is associated with feminizing and demasculinizing effects such as increased incidence of intersex, decreased sperm quality, and decreased fertility in male fish (Sun et al., 2016).

Until the late 1970s, over 200 congeners of PCBs were produced (primarily in the US but also in Europe) for use in capacitors, transformers, hydraulic fluids, and lubricants. PCBs resist degradation and are stable even at extreme pHs and temperatures. They typically enter the environment by leakage from or improper disposal of aging electrical equipment, and their resistance to degradation allows them to persist in the environment. Like other POPs, PCBs are lipophilic and thus bioaccumulate and biomagnify. For example, PCBs biomagnify by one or more orders of magnitude as they move through the polar food web from fish to seals to polar bears (Letcher et al., 1998). Although PCBs have not been extensively produced or used in manufacturing for several decades, they continue to be detected in the fatty tissues of marine organisms, especially those living and feeding in polar waters or in bodies of water that experience limited exchange.

The various PCB congeners exert their endocrine-disrupting effects by interfering with several hormone signaling pathways. For example, PCBs with fewer chlorine atoms weakly agonize estrogen receptors, whereas PCBs with more chlorine atoms weakly antagonize estrogen receptors. Most PCB congeners also antagonize androgen receptors. Multiple PCB congeners also interfere with the activities of thyroid hormone transporting proteins (known as transthyretins) and the activities of enzymes involved in steroid synthesis and metabolism. Thus, various PCBs can be considered estrogenic, anti-estrogenic, anti-androgenic, and/or thyroid-disrupting EDCs. Effects of exposure to PCBs can include anemia, immune suppression, hypothyroidism, and reduced fertility, especially in apex predators with high PCB body burdens, such as many marine mammals (Reijnders, 1986; Schwacke et al., 2012).

Organotins

Organotins (OTs) are organometallic compounds that contain at least one covalently bonded tin atom. Historically, OTs were extensively employed as antifouling additives in paints used on marine vessels and in mariculture facilities. Although OTs were banned from use in marine paints in 2008 by the International Convention on the Control of Harmful Anti-fouling Systems on Ships, developing countries that are not members of the International Maritime Organization can still use OTs for this purpose. In addition, OTs are still used globally as industrial and agricultural biocides, industrial catalysts for the production of polyurethane foams and silicone, and PVC stabilizers. OTs, especially those that are trisubstituted (i.e., they contain three tin atoms), are more toxic than inorganic tin to living organisms. In fact, OTs are among the most toxic anthropogenic chemicals that impact marine systems, as exposure of marine organisms to OTs is associated not only with endocrine disruption but also with dysfunction of the immune system, the nervous system, and metabolism. OTs exert their toxic effects through a number of mechanisms, including inhibiting CYP enzymes such as aromatase (the enzyme that converts androgens to estrogens) that are involved in steroid synthesis, inhibiting phase I and phase II metabolizing enzymes (thereby interfering with detoxification pathways), inhibiting steroid excretion, and agonizing the retinoid X or ultraspiracle receptors, which normally interact with other nuclear receptors such as peroxisome proliferator-activated receptor (PPAR- γ) and the arthropod ecdysone receptor. As a result of the myriad effects of OTs on synthesis and metabolism of steroids and activity of nuclear receptors, exposure of marine organisms to OTs is associated with altered gonad morphology and thus reproductive dysfunction; increased adipogenesis, lipid accumulation, and weight gain; and molting problems, especially in marine crustaceans (Yi et al., 2012; Berto-Júnior et al., 2018; Vogt et al., 2018).

OTs are susceptible to photolysis, which involves stepwise dealkylation of OTs to less toxic inorganic tin; however, this process is slower in sediments than in the water column and OTs have a strong affinity for sediments. As a result, OTs accumulate in benthic sediments; the sediments found in harbors, estuaries, marinas, and other coastal waterways have especially high concentrations of OTs given their proximity to shipping activities. Because they are hydrophobic, OTs bioaccumulate. In particular, they bind to sulfhydryl groups like those found in glutathione and proteins; thus, OTs accumulate in glutathione- and protein-rich tissues such as the liver and kidneys. Interestingly, OTs also bind to the protein keratin, which is found in hair and feathers; thus, birds and mammals are able to excrete OTs better and may therefore be less susceptible to the toxic effects of these chemicals than other marine organisms. OTs are also poorly biotransformed, in part due to their ability to inhibit detoxification pathways, and thus biomagnify as they move through food webs.

Of the OTs, tributyltin (TBT) is the most well studied and is arguably the most well known EDC that impacts invertebrate animals. The notoriety of TBT stems from its detrimental effects on reproduction in marine gastropod molluscs such as whelks. Specifically, exposure to TBT, even at low doses, induces a form of metabolic androgenization known as imposex, or the development of a vas deferens and penis, in female gastropods. This finding has been confirmed in over 200 species of marine gastropods and likely results from the effects of TBT on steroid synthesis and metabolism in these animals, although other mechanisms may also be responsible.

Future Directions and Final Comments

This article focused on the sources, fates, and effects of the most well studied anthropogenic chemicals that are found in marine systems and are known to interfere with the endocrine systems of animals. The list of such chemicals is long and growing, and a number of confirmed EDCs were not discussed here. For example, many insecticides (such as the juvenile hormone analogue, methoprene) target the processes of molting and metamorphosis to prevent maturation of larval arthropod “pests.” These insecticides can have detrimental effects on non-target species such as marine crustaceans, which employ the same pathways used by “pest”

species to regulate growth and development. Indeed, these unintended consequences of exposure to anthropogenic chemicals make the increasing prevalence of insecticides and other EDCs in marine systems especially concerning.

While much has been learned in the last several decades about the presence of EDCs in marine systems and the effects of EDCs on some marine organisms, many knowledge gaps still exist. For example, concentrations of most EDCs in deep, oceanic waters are rarely measured, and how these concentrations differ spatially and temporally is largely unknown. Furthermore, the fates of most EDCs in marine systems are not well understood, particularly for chemicals that partition into sediments or other compartments that are logistically challenging to study. The effects of EDCs on most marine organisms are also not well known, particularly for marine invertebrates. Although invertebrates represent 95% of the animals on the planet, we know very little about how environmental contaminants affect performance in these animals. This deficiency likely stems from a general lack of knowledge about invertebrate endocrine systems, which are more dependent on peptide hormones and less dependent on steroid hormones (with the notable exception of ecdysteroids) compared to the analogous systems of vertebrate animals. To better understand the scope of human impacts on marine systems, these knowledge gaps must be addressed. In addition, priority must be given to developing remediation strategies that both reduce the inputs of anthropogenic EDCs into marine systems and mitigate the effects of these chemicals in marine organisms.

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Soundscape Ecology

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Abstract

Soundscapes represent the sum of biotic, abiotic, and human generated sound in the landscape. Monitoring sounds can lead to insights both on habitat integrity and an early warning of threats to them. Where soundscapes are endangered, technology has made soundscape recording and analysis more accessible and affordable, resulting in the ability to continuously monitor wide areas for habitat health and human activity. Coupled with global communications and computing platforms, soundscape monitoring and analysis permits low cost and continuous monitoring of natural habitats. This is important because as climate change and human activity disrupt more and more habitats it provides a rigorous but cost-effective way to quantify and monitor changes to minimize habitat loss and extinctions.

Introduction

The field of soundscape ecology combines elements of bioacoustics, the study of animal vocalizations, with environmental acoustics, the scientific study of how sound is carried through the landscape (Krause, 2017). Every place in the world has a unique audio signature. This is composed of a combination of several types of sounds. Biophony includes biological sounds, the voices of animals. Geophony refers to geophysical or abiotic noise. For many places, for much of the year, the only natural sounds may be geophysical, including wind, storms, and water such as rivers or oceans. Anthrophony are the sounds made by people, including both the voices of people along with everything manmade, which now can be heard in even the most remote corners of the world with the sound of engines and planes. Increasingly it is hard to escape man-made noise anywhere in the world. For example when recording in the California mountains we have had recordings of biological sounds dominated by the sound of loggers with chainsaws on adjoining land, and in remote regions of the Amazon rainforest boat engines may be heard miles away (Fig. 1).

Soundscape ecology can be seen as a specialized branch of landscape ecology. As with the study of habitats, soundscapes can be classified based on geography, looking at the way ecology shapes them according to both physical factors and the influence of people (Pijanowski et al., 2011). As discussed elsewhere in this encyclopedia, anthromes are biomes shaped by how people interact with ecosystems, and need to be considered to fully understand biogeography (Martin et al., 2014).

Just as disturbance shapes biomes, it also influences the integrity of natural voices. As a pragmatic science, it seeks both to understand how human disturbance interferes with the functioning of soundscapes, and how measuring this can help both predict, measure and remedy these disruptions.

Anyone who has enjoyed a dawn chorus of birds in the spring time, or a night chorus of insects, can appreciate that animal sounds can be a striking part of a soundscape. While they may be viewed as a relaxing accompaniment to a natural setting or even just background noise, to the animals they serve a very serious purpose justifying the energy expenditure to make loud and repetitive sounds.

The rich soundscape of a tropical rain forest or spring in a temperate forest represents the complexity of communication in an environment with many competing species. Abundant spring peepers, for example, can be almost deafening in a temperate North American wetland in the spring. Like any other part of a habitat, the ability of a sound to carry far enough to be effective is a resource that can be as important as food or shelter for an animal. If a species cannot deter intruders or find mates in a habitat it will eventually become locally extinct. For this reason, animals have evolved strategies that differ from each other to make sure their specific vocalization can both get through and be understood by the intended recipient. As is often the case in nature, this simple need leads to marvelously complex and rich soundscapes where different species vocalize in different frequencies, at different times, and with different harmonics and rhythms (Fig. 2).

In the most ecologically diverse habitats, animals should be seen to occupy most spaces of the audio niche both temporally and spatially. In other words, there should always be an animal calling, at each frequency. In a sonically saturated habitat such as

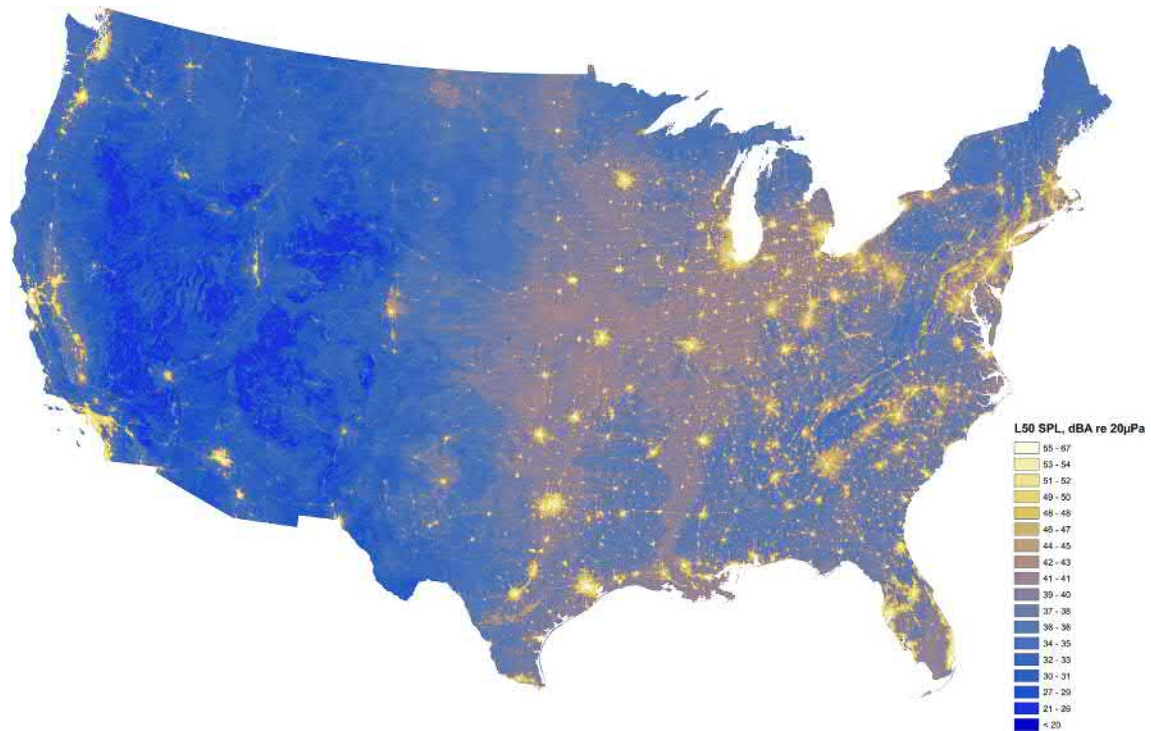


Fig. 1 NPS sound data map.

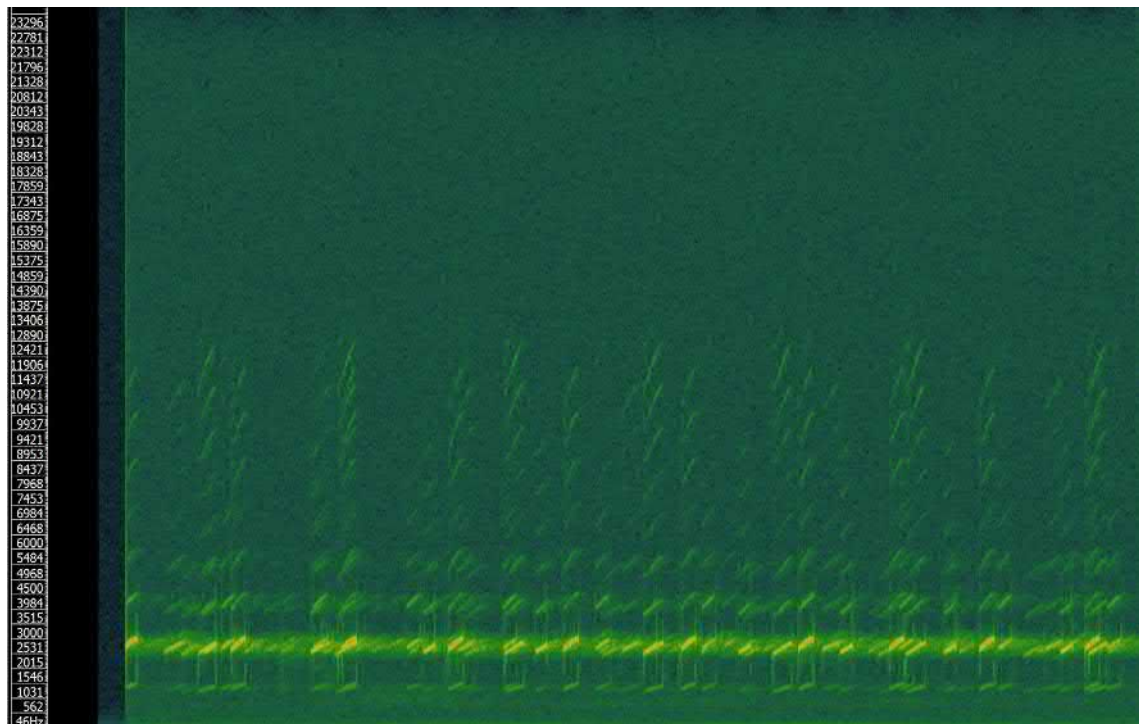


Fig. 2 Peeper Spectrograph.

a tropical rainforest at dawn, all the sound niches may be so fully occupied that animal species may take turns, for example a bird of one species calling briefly and another calling at the same frequency when the first bird stops.

Animal vocalizations are a critical part of their survival and reproductive strategies. As a result, animals have evolved to develop distinctive vocalizations that carry as far as possible. The ability to transmit sounds to reach the maximum number of potential

mates or deter the most rivals conveys clear selective advantages. Using sound takes less energy than physically patrolling a territory so is a good adaptive strategy.

This paper discusses how animals divide the sound niche into acoustic habitats, and how these sonic patterns can be used to study and predict the health of animals and their biomes. Techniques are described to use soundscapes as a tool to protect species and their habitats.

Acoustic Niche Hypothesis

During field trips to a variety of tropical habitats in North, Central and South America, Asia and Africa, Bernie Krause and Ruth Happel developed an acoustic niche hypothesis viewing sound space like any other ecological niche, in which animals divide up available resources. With his background in music, and hers in ecology, they hybridized their knowledge and focused on how animals fill all the space available in a soundscape, much as musicians fill a musical staff with notes.

Over time, each species evolves its own acoustic bandwidth based both on the specific frequency and time of day to defend a sonic territory, to minimize being drowned out by other species or ambient noise.

As with any other ecological niche, animals compete for space, in this case acoustically. Looking at sonograms of animals in undisturbed and biologically rich habitats, there are no gaps in the sound spectrum. Every organism has its own place, either in time or frequency pitch, to avoid competing with the sounds of other species.

As Bernie Krause ([Krause, 2012](#)) refers to it, the ‘Animal Orchestra’ is a rich and unique ensemble that is never the same in two locations. This is the essence of why soundscapes are important and worthy of study—they are the living representation of complex animal interactions that have developed over millennia to help animals survive in a locality.

The most vibrant and diverse biological soundscapes are in the tropical rainforest. Almost every part of the temporal and spatial sound spectrum is filled with insect, bird, and other sounds. Tropical rainforests can be loud and some tropical rainforest animals—for example howler monkeys and gibbons—have vocalizations that can travel for miles.

At the opposite extreme there are deserts in the western United States that actively absorb sound. They are very quiet, sometimes disturbingly so. In between are many soundscapes in temperate and tropical regions that may vary widely in the volume and variety of biological sounds seasonally. Wet seasons, spring/summer, and migrations may cause a normally depauperate soundscape to become very active for a short period as insects hatch and mammals and birds come to feed.

Spectrographs and Recording Technology

While soundscapes have clear value in biological study, it is a relatively new field of study due to the reliance on technology to collect and analyze soundscapes. There has been a clear relationship between new technologies and soundscape studies. Prior to the ability to accurately record soundscapes and bring them back to the lab for analysis, soundscape analysis was more craft than science, limited to individual experiences in identifying sounds in natural settings.

Technology to record sounds was only developed in the late 19th century. While occasional attempts to record natural sounds on location were undertaken for movies and other artistic purposes, the expense and complexity of recording good quality sound in the wild limited this for most of the 19th and 20th centuries.

Ornithologists have long used bird song and bird calls as ways to identify and find birds, and they were pioneers in recording animal vocalizations in the wild. Much of their focus was on capturing individual bird calls, to assist in identification. They generally used parabolic or shotgun microphones that could capture the specific vocalization of the animal. Such microphones are good at a distance and were necessary with older recording technology such as magnetic tape and cassette recordings due to limited dynamic and frequency range of the recordings.

One of the initial reasons for this approach to animal sound recording was limitations in the ability to record sounds in the field. Until very late in the 20th century, field recording involved the use of analog magnetic tape—either reel-to-reel or cassette recorders. Analog recordings have the disadvantage of losing data every time they are copied, and depending upon the type of tape used some frequencies are recorded more effectively than others. In the early days of wildlife sound recording this bias in frequency and sound loss during copying of tapes made the focus animal sound identification instead of soundscape analysis. While someone with a high-quality reel-to-reel tape recorder could get good quality sound recordings, it was only a partial representation of the amount of sound present in the soundscape.

Only in the 1990s did portable digital tape recorders become widely available. Digital recordings also for the first time allowed full fidelity copies to be made of the original recording. Bernie Krause and Ruth Happel pioneered the use of digital recordings in the tropics during this period, and the recordings still provide a historical record of habitats that often no longer exist. This kind of longitudinal historical perspective is much easier with digital recording technology. These techniques have greatly advanced comparative analysis of sounds collected by different people in different locations at different times.

By the early 21st century flash memory in relatively inexpensive digital recorders and smartphones replaced digital tape. This lowered the cost and complexity, and made the recording process less subject to environmental issues like humidity. Along with the growth of the Internet and cloud storage, digital sound archives became more accessible to researchers.

With the ability to record a full sound spectrum without bias toward certain frequencies and with lossless copies, it is possible to get high quality recordings of the overall soundscape without focusing on a specific animal or call. Use of a shotgun or parabolic microphones usually requires the presence of a person to point the microphone at the desired animal or sound, while soundscape recording can be better automated for continuous or remote recording with omnidirectional microphones.

One additional emerging technology in soundscape ecology is passive acoustic monitoring (PAM). PAM has previously been used to monitor whales, as well as for terrestrial studies (Rodi and Herbst, 2012; Towsey et al., 2014). Although technologies differ between applications, PAM is increasingly used in ways that minimize human intervention, and use passive arrays rather than human observers. Such automated recording systems are still evolving, but show tremendous promise for a variety of scientific and conservation applications.

In recent years, with advances in batteries, solar power, and energy efficient digital electronics, automated recording has come increasingly into use worldwide. Automated recording devices generally work best with omnidirectional stereo microphones. Stereo (recording with two channels) permits movement of sound to be tracked in a soundscape and recording in all directions permits a wider area to be monitored. With increasing sensitivity of microphones and better noise filtering and higher resolution recording, specialized microphones have become less important.

Relying on trained observers to conduct biological surveys requires both a select group of individuals to conduct the surveys, and also leads to potentially unreliable comparison between data sets. Collecting recordings can provide more consistent results.

Automated recording technologies have been used since the early days of soundscape recording. When Ruth Happel was recording habitats in the southern US, she would frequently record the dawn chorus of natural sounds using automatic timers and pre-set microphones and digital recorders. This technique not only was less labor intensive, but also less disruptive of the natural soundscape. Many of the most common vocalizations heard by humans are alarm calls due to the presence of humans. Having automated or remote recording without a human present is often a much better way to capture an undisturbed natural soundscape.

In addition to recording technologies, techniques to visualize sound have also evolved over the years. Many recordings of soundscapes are represented by a spectrogram, a visual representation of sounds, in two or three dimensions depending on how it is displayed. When reading a spectrogram, it is not unlike reading music. The song moves from left to right in time, and the high-pitched notes are higher than the lower pitched notes. The width of each note shows the duration, rather than in musical notation having quarter, half and whole notes (Fig. 3).

One axis is time, the second axis is frequency, and sometimes loudness of sounds is represented through color, with intense colors showing the loudest vocalizations. The axis with sound is usually shown in seconds, though of course this might vary depending on the unit of time being represented. The ordinate shows the frequency or pitch, with higher pitched sounds representing higher frequencies. The frequency is measured in Hertz (Hz).

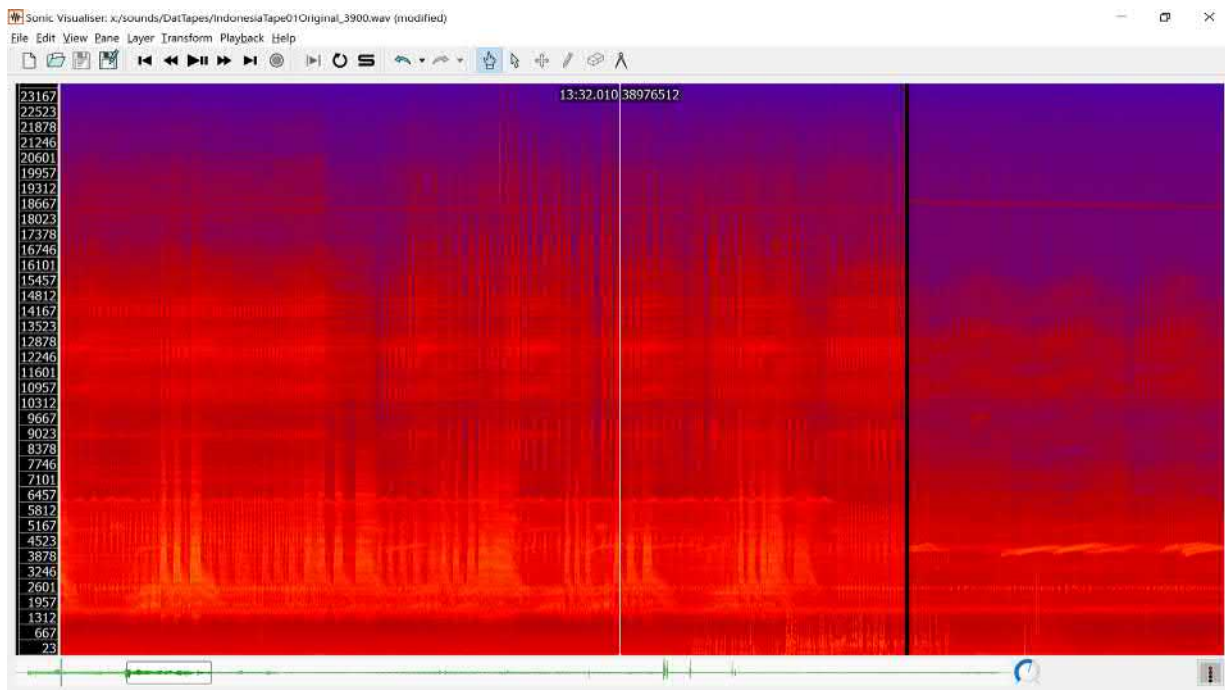


Fig. 3 Spectrogram of an Indonesian rain forest soundscape.

Patterns of vocalizations often vary widely by time of day and year. Dawn and dusk are favored by many species for acoustic properties aiding in transmitting sounds. Cooler air temperatures make the air denser, permitting sounds to travel farther. Certain times of year are also noisier, especially in temperate habitats, when spring through fall tend to have more species calling than in winter, often to declare territory or attract a mate. A wide range of variables affect soundscapes, including weather, plant phenology, vegetation structure and complexity, temperature, solar radiation, and humidity, habitat alteration, climate change, introduction of toxins, and spread of invasive species.

It's not necessary to have working knowledge of all recording or spectrograph techniques to appreciate the significance of acoustic niches. However, it is worth noting that the limits of such technology have historically meant that disruptions within the wild soundscape went widely unnoticed. It is only as recording technology evolves that we will gain the full picture of what we have already lost.

Habitat and Soundscape Degradation

Traditional biological surveys and research in both temperate and tropical regions reveals that soundscape diversity is related to habitat quality, with decreasing acoustic diversity in urban and agricultural locations, as well as disturbed forests. The biodiversity of sounds can be closely correlated with biological diversity.

People shape soundscapes, both directly with planes, trains and automobiles, along with indirectly altering the structure of the habitat with deforestation and similar activities that intrude on natural soundscapes, and continue to shape the sounds long after the human sounds are gone.

This evolutionary importance of animal vocalizations for survival and reproduction means that sounds themselves are a reliable indicator of the presence or absence of animals. Soundscapes become a way to measure relative, and sometimes absolute animal abundance and behavior. Soundscapes are not only worth preserving for their own sake—they are also a way to assess health of a habitat and a low-cost way to inventory animal populations that can be conducted and compared over extended periods. Acoustic monitoring can serve as an aural canary, with soundscape changes serving as a bellwether for deeper environmental problems, warning of current or developing issues with endangered habitats and species. Changes in animal sounds over time and space can help show underlying changes to habitats as a result of climate change, pollution, and ecological disruption such as deforestation.

A striking example of animals shaping their calls directly to avoid competing with human sounds is the research of [Ernstes and Quinn \(2016\)](#). A study of brown-headed nuthatches and other birds in South Carolina observed they shifted their vocalizations higher to avoid being masked by vehicle traffic. Traffic noise that carries farthest is usually low frequency, so the movement of vocalizations up to a less contested frequency would be a reasonable adaptive response. A similar change in animal behavior in response to traffic noise is seen in Australian frogs. They are observed to shift their calls to a higher frequency when in the presence of traffic noise ([Parris et al., 2009](#)).

In addition to effects on land, people are creating difficulties for communication of marine animals. In oceans, commercial shipping has led to increasing background noise over the last 150 years. Right whales adjust their calls in response to these changes, using a higher fundamental frequency and calling less often in high noise habitats, due to the low frequency noise that can interfere with their vocalizations. This study shows that the shift has occurred with whales in their lifetimes, so is not being created by evolutionary selection ([Parks et al., 2007](#)).

Notably, seismic surveying, ship noise, and other anthropogenic factors seem to disrupt the acoustic niche of both whales and dolphins, as recent studies ([Guarino, 2018](#)) have shown that dolphins become louder and whales become quieter with increased ambient noise. Potentially, as scientists become more aware of the ways in which anthropophony causes shifts in the acoustic ecosystem, soundscape studies will increasingly be consulted in both court cases and policy making.

Seismic surveying—the process of using reflected sound waves, such as from air guns fired into the sea floor, to search for oil and gas reserves—is potentially deadly for whales and other marine mammals. This practice has been linked to stranding events ([Mcgeady et al., 2016](#)), decreased concentration of zooplankton ([McCauley et al., 2017](#)), potentially disrupted polar bear denning ([Amstrup, 2018](#)), and other significant ecosystem shifts. For this reason, seismic surveying is emerging as one of the most litigated forms of anthropophony in recent years, with numerous environmental law firms filing suit to stop not simply offshore drilling, but the noise pollution accompanying it. The Sierra Club recently lobbied ([Moffitt, 2019](#)) to stop SAExploration from conducting seismic surveying in the Arctic Refuge, as just one example of soundscape ecology becoming increasingly relevant in energy policy and law. The Gullah/Geechee Nation's ([Cooper, 2018](#)) campaign against offshore drilling also emphasizes the potentially deadly impacts of such surveys on whales and dolphins. Around the world, numerous coastal stakeholders are increasingly concerned not simply by the risk of oil spills from offshore rigs, but also by noise pollution, and more overlooked ways in which such practices disrupt the coastal soundscape.

Whatever the normal level of diversity when human generated sounds enter a soundscape, they can represent a challenge to existing occupants of a sound spectrum. For example, if a road is built through any of the habitats mentioned above, it has the potential to disrupt the animals living there who depend upon sound to defend territories and find mates. Disturbances from human activity to a soundscape can disrupt animal survival strategies, change animal behavior, and cause animals to become less abundant or even go locally extinct.

Soundscapes as a Conservation Tool

In order to use recordings as a tool to understand habitats and their associated sounds, and how they are changing due to human influence, there must be better ways to standardize measurement. One means of doing this is to set up arrays of recorders around the world, to continuously monitor a variety of habitats. This is faster and more effective than assessing biodiversity with visual surveys, or by relying on trained teams of experts.

As passive acoustic monitoring, or PAM, becomes more advanced, such technologies will likely become increasingly prominent, and play a larger role in environmental law and enforcement mechanisms as noted. Already, PAM is used by marine mammal observers at night, or in other adverse conditions when visual monitoring is not possible. By listening for whale calls, observers can help seismic surveying companies comply with the Endangered Species Act, the Marine Mammal Protection Act, and other such statutes that regulate the take of whales and other protected species. Passive acoustic monitoring has additionally been used to monitor various terrestrial ecosystems, and has been used in bird and other animal studies (Pieretti et al., 2015; Towsey et al., 2014). Typically, such studies are less tightly regulated than PAM for marine mammals, which may be subject to Bureau of Ocean Energy Management regulations and other restrictions. As PAM becomes more widely implemented, however, it may become more commonly used as an enforcement tool in terrestrial ecosystems, and aid in the detection of poaching or illegal logging.

Systematic collection of recordings allows analysis of sonic patterns, both to determine a baseline and to understand what makes a healthy habitat. Sounds can be classified as biological, geophysical, and associated with people. In studying sounds and their association with habitat health, it should be possible to both assess biodiversity, and map out changes over time to see what impacts affect biodiversity most. Conservation efforts can use bioacoustics both to understand and protect wildlife habitats (Kocsis, 2017).

Longitudinal studies, looking at how sounds differ from seconds to hours, extending to time of day, season, and yearly, it may be possible to observe how soundscapes are changing in response to people on both a small scale locally, and longer-term impacts of climate change, to understand through sound how changes to habitats are affecting species.

At the present time organizations like Rainforest Connection are pioneering real time recording and transmission of sounds for analysis using cellular connections. While cellular connections can be used for this purpose, it is expected that soon low earth orbit satellites will make real time transmission of sounds to cloud based sound archives available over much wider areas than are currently possible (Weitering, 2019). Already Rainforest Connection uses their cloud platform for real time monitoring of forests where they work, with better connectivity using satellites, this should be possible over a much wider area with inexpensive solar or battery powered devices (Nunez, 2017).

Satellite images and drones can observe and measure deforestation, but may miss equally important ecological factors like hunting, fires, and invasive species. Field studies and surveys can pick these up but are usually limited in time and location. Recording devices can capture animal vocalizations from several hundred meters away, day and night. They can record at set times, or continuously, if there is solar power or a cellular network signal. While sound recordings can be large in size, they are relatively straightforward to analyze compared to image or video files and are not subject to changes in light in order to collect usable data. Sound analytic techniques have progressed quickly with advances in computer technology, and sophisticated audio analysis is now possible with even handheld devices.

If companies have a program that requires legal compliance with no deforestation, they can be monitored by bioacoustics to determine how much forest remains. Audio monitoring can catch hunting, habitat degradation, and fires below the canopy that might be missed by satellites or other visual data collection and help with action against activities like illegal logging and poaching (Burivalova et al., 2019).

Soundscape Monitoring—Progress and Potential

An analytical platform for global soundscape monitoring would advance research in a number of areas, along with providing a baseline that could be used for environmental improvement and conservation enforcement. An ideal platform would provide capabilities for secure transfer of sounds from any location to a repository where they can be analyzed and compared with previous recordings in the same location and with similar habitats in other localities.

In order to effectively study and compare soundscapes and use this data to monitor and understand habitats, significant amounts of data must be collected and analyzed. Recorders can now be set up in remote areas and run by either battery arrays or solar power, so they can be collected continuously. Automated recording equipment is already being used in conservation and research (Palminteri, 2016; Jahn et al., 2017; Brandes, 2008). Software is being developed to measure the diversity of soundscapes (Kocsis, 2017).

Potential dimensions of analysis include spectral analysis, which can be used to determine how much of the sound spectrum is being used by wildlife. It should also include temporal analysis to investigate patterns of animal sounds throughout each day and throughout the year. If simultaneous recordings are done at different locations, animal abundance can be estimated by triangulation of the different animals on overlapping recordings. Once baselines have been established, it would be straightforward to identify specific species at different localities, and to often estimate their abundance. This would lead to identifying marker species for specific types of habitat change and lead to definitions of the soundscape of a healthy habitat, and to permit diagnosis of unhealthy habitats (Palminteri, 2016). Using machine learning and statistical analysis it would be able to characterize specific habitats patterns and find similarities between soundscapes in both time and space.

With adequate refinement even single species abundance could be monitored across different soundscapes in some cases (Zwart et al., 2014). Software has been used successfully to identify the calls of a single species in a series of thousands of daily recordings (Jahn et al., 2017) to research behavior of birds in the Pantanal of Brazil. Automated recording technology coupled with automated analytics and species identification could be extended and expanded. Once the software is developed to identify a single species it could potentially be reused indefinitely on new recordings to extend species ranges or monitor trends in species abundance in a variety of habitats.

If multiple recorders are set up in an area at intervals, it would also be possible to record movement of vocalizing animals through the forest by comparing simultaneous recordings. The amount of data that could be extracted from continuous recording is mainly limited by the number of animals vocalizing, and how much interest and effort there is in analysis.

If records are kept of what remediation steps can achieve results, then those same steps can be applied to different locales with similar soundscapes. Soundscape analysis would allow a quantifiable measure of environmental health with a minimum amount of personnel at a locale. As noted in Burivalova et al. (2019) it would be ideal for monitoring compliance of industries that are regulated to meet environmental standards, in addition to providing valuable research information on a global scale.

A new and important tool is the development of acoustic indices, to measure acoustic energy in field recordings. Standard tools to quantify 24 h recordings will allow systematic comparisons of data across habitats and research studies. This can be used to estimate biodiversity in a controlled and comparable way. Research suggests there are optimal ways to collect and analyze recordings to maximize information (Pieretti et al., 2015).

Acoustic indices can measure and predict species diversity in a broad view of both space and time, which is especially important in biodiversity hotspots where rapid development and habitat loss, in association with climate change, threatens a broad range of biomes and species (Buxton et al., 2018). This provides a quick and accurate means of assessing biodiversity often more accurate than more costly and time intensive methods of traditional ecological assessment.

Conclusions

Soundscapes, and the unique habitats they represent, may be changing and in some cases endangered, but advances in technology permit them to also be used to help save biodiversity. While soundscape recording used to be an expensive and time-consuming activity, it is now possible to use sound and soundscapes as a way to document and monitor a wide array of habitats.

Soundscapes represent not only a unique resource and signature of a habitat, they also provide a way to record an essential characteristic of a habitat through time. This can serve as a historical record and also be used as a monitoring tool with minimal environmental disruption. In association with other developing technical resources, including camera traps and drones, continual audio recordings can assist in alerting and locating disruptions to habitats and species through hunting, logging, mining, and other threats. A library of sound recordings can be used to document and correlate with biological data, to determine patterns of biodiversity in association with sonic signatures. Recordings can also be used in real time to alert local wildlife managers to immediate habitat threats, so they can act on them before the animal or habitat is lost. This is a valuable resource that should be fully leveraged in the effort to preserve wildlife and habitats.

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Soundscapes and Anthromes: A Review of Proximate Effects of Traffic Noise on Avian Vocalization and Communication

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Abstract

Across anthromes there has been an increase in the number and miles of roadways with a corresponding increase in vehicle traffic. Roads and associated traffic and traffic noise has been shown to affect avian abundance, breeding success, density and species diversity. An expanding body of literature has demonstrated that many bird species alter the way they vocalize in order to be heard by conspecifics and other species in response to the noise generated by traffic and other human activity. This review summarizes the literature that describes the effects of traffic noise on birds across anthromes. Documented changes in vocalizations due to traffic noise include shifts in amplitude, frequency, rate, timing, and duration of vocalizations along with a number of behavioral adaptations. Costs of altering vocalizations include the inability to attract a mate, poor vocal performance, not sounding like conspecifics, and being more easily heard by predators. Outstanding research needs in this area include (1) controlling variables that might affect negative impacts on birds along roadways, (2) analyzing vocal communication during the non-breeding season, (3) identifying consequences of and responses to acoustic masking (e.g., inability to protect a territory or faulty parent-offspring communication), and (4) applying research to mitigation efforts.

Introduction

Anthromes are geographical categories that represent globally significant ecological patterns created by sustained direct human interactions with ecosystems (Ellis and Ramankutty, 2008). Much like global land use and land cover change, humans have altered much of the world's acoustic characteristics with anthropogenic sounds; sustained sounds that are different in pitch, amplitude, acoustic structure, distribution, and often more continuous than sounds produced in natural environments (Nemeth et al., 2013; Pijanowski et al., 2011; Slabbekoorn and Ripmeester, 2008). Roads and associated traffic in particular have a broad acoustic impact, affecting nearly one-fifth of the total land area in the United States (Forman et al., 2002). The resulting acoustic impacts from roads and associated traffic may be broad, extending outwards as far as 450 m into the landscape adjacent to roadways (McClure et al., 2013; Slabbekoorn and Ripmeester, 2008; Summers et al., 2011). Aspects of traffic effects, volume and noise, as well as urban noise disturbance effects on avian species have been a focus for studies in the past 20 years; with a trend towards studying the disturbance effects of traffic noise specifically (Fig. 1).

Birds have among the most elaborate and complex acoustic signals in the animal kingdom (Marler, 2004), communicating primarily through songs and calls. These vocalizations occupy nearly all available acoustic niches (Farina et al., 2011). Calls are simpler and shorter than songs and can convey a variety of messages (Marler, 2004). Songs are longer, more melodic, and are mainly used for attracting females and deterring rivals (Marler, 2004). Most songs and calls produced by birds range between 1 and 9 kHz (Rheindt, 2003; Zollinger et al., 2012). Since traffic noise is generally characterized by a low frequency band of noise between 0 and 4 kHz (Nemeth et al., 2013; Nemeth and Brumm, 2010; Patricelli and Blickley, 2006; Pieretti and Farina, 2013), the lower frequencies of bird vocalizations may overlap with traffic noise resulting in acoustic masking. This concept can be seen in Fig. 2 where the lower-pitched portion of the Blue Jay's (*Cyanocitta cristata*) vocalization is drowned within the low frequency traffic noise.

Acoustic masking occurs when one sound masks, or interferes with, another sound (Fig. 2). Species with lower-frequency vocalizations (1–2 kHz) will have greater acoustic interference, or masking, than those with higher-frequency vocalizations (higher than 4 kHz) that are above typical traffic noise levels (Templeton et al., 2016; Halfwerk et al., 2011a; Luther and Baptista, 2010; Parris and Schneider, 2008; Polak et al., 2013). Different species of birds have different sensitivities to traffic noise. Any acoustic masking of their vocalizations presents the possibility of negatively affecting their communication and reproductive fitness, as verbal

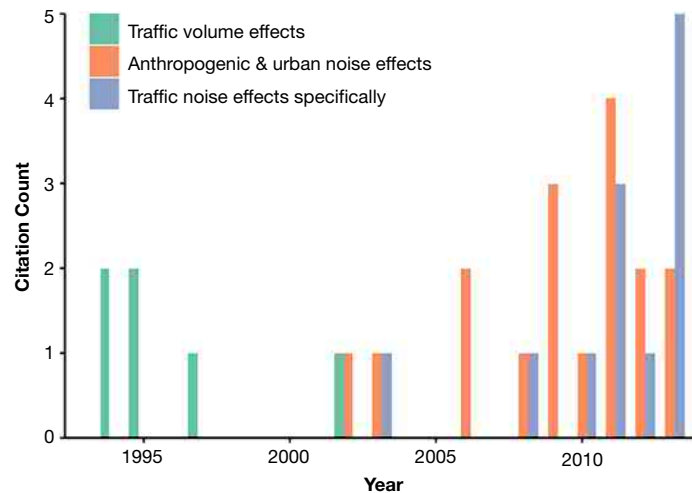


Fig. 1 Years of publications for studies show a trend over time of studying traffic effects on avian species, to urban and anthropogenic noise effects, to specifically traffic noise effects on avian species. Papers obtained from the Web of Science following a key word search for the terms avian, communication, vocalization, traffic, roads, and noise.

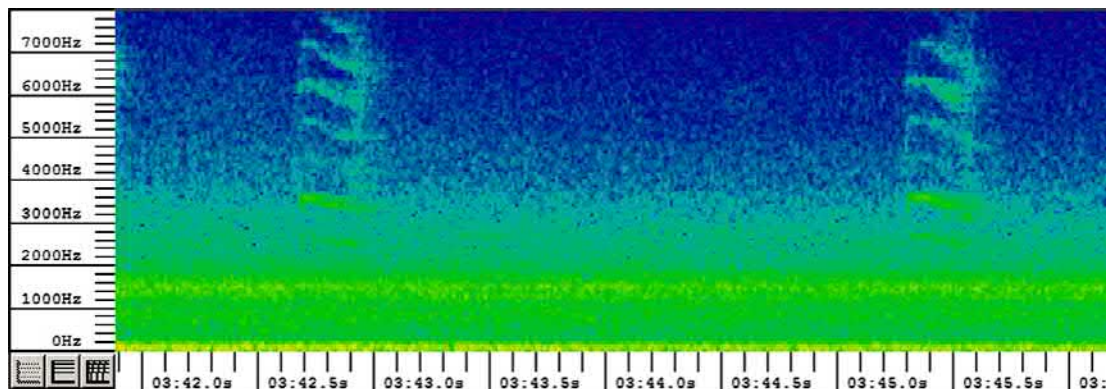


Fig. 2 The low frequency, constant traffic noise, as seen across the bottom of the sonogram, drowns out the lower frequency portions of a Blue Jay's call.

communications can only be beneficial if the receiver detects the vocalization. Thus acoustic masking of vocalizations by traffic noise has proximate and ultimate implications (Templeton et al., 2016; Ryan and Brenowitz, 1985; Rheindt, 2003) and it is essential that we recognize the impacts of increased traffic noise on avian communication. In this review we summarize the growing body of literature that focuses on impacts of traffic noise on bird vocalizations and identify key gaps in knowledge.

Methods

We searched Google Scholar (<http://scholar.google.com/>) for combinations of the following key words: avian, communication, vocalization, traffic, roads, and noise. The identified articles were divided into two major themes: proximate and ultimate responses to traffic noise. We summarized research on proximate responses into six categories: changes in frequency, amplitude, timing, structure, learning, behavior, and mechanisms of response to change. We also touch on an ultimate response of divergence between urban and nonurban songs due to acoustic masking by traffic noise.

Proximate Outcomes of Acoustic Masking

Frequency shifts. The most common response of birds to traffic noise is to vocalize at a higher frequency, or pitch, which includes: increasing the minimum frequency (Ernstes and Quinn, 2016; Oden et al., 2015; Dowling et al., 2011; Luther and Baptista, 2010; Luther and Derryberry, 2012; McLaughlin and Kunc, 2013; Slabbekoorn and den Boer-Visser, 2006) changing the maximum frequency (Dowling et al., 2011), shifting the entire vocalization to a higher frequency (Francis et al., 2011; Goodwin and Podos, 2013; Halfwerk et al., 2011a; Parris and Schneider, 2008; Rheindt, 2003), or increasing the frequency of peak notes (Nemeth et al.,

2013). Shifting all, or parts, of a vocalization up in pitch allows for fewer, lower-pitched notes that could potentially be masked by anthropogenic noise (Pieretti and Farina, 2013; Slabbekoorn and den Boer-Visser, 2006).

Species with lower-pitched calls are more likely to shift their vocalizations. Parris and Schneider (2008) showed that the lower-pitched Gray Shrike-thrush (*Colluricincla harmonica*) sang at a higher frequency (pitch) when near traffic noise. In contrast, the higher-pitched Gray Fantail (*Rhipidura fuliginosa*) did not change its song in the presence of traffic noise. The differences in type of shift are demonstrated by both Great Tits (*Parus major*) and Common Blackbirds (*Turdus merula*). While both species sing at higher pitches in urban areas, Common Blackbirds shift their whole song upwards in frequency while Great Tits only increase their minimum frequency (Nemeth and Brumm, 2010; Slabbekoorn and Peet, 2003). Males that adjust the frequency of their songs in order to exploit a spectrally favorable frequency could possibly reduce the attractiveness of the song (Halfwerk et al., 2011a). For example, female Great Tits may cheat on their mates if the male does not sing a low pitch song (Halfwerk et al., 2011a).

Amplitude increases. Birds adjust and adapt the amplitude (volume) of their vocalizations daily to compete with ambient noise (Brumm and Todt, 2002; Brumm, 2004; Nemeth and Brumm, 2010; Zollinger and Brumm, 2015). For example, the Noisy Miner (*Manorina melanocephala*) will call more loudly at noisier locations near busy roads than near quieter residential streets (Lowry et al., 2012). Increasing amplitude in response to an increase in ambient noise is known as the Lombard effect (Lombard, 1911). The Lombard effect is usually accompanied by a change in pitch of all or part of a vocalization since lower frequency vocalizations (1–4 kHz) tend to have less energy (Nemeth and Brumm, 2010). It has been suggested that amplitude is the key factor in exchanging verbal information and that amplitude has a larger, stronger effect on communication distance than frequency (Nemeth and Brumm, 2010). For example, Great Tits that increased their amplitude could communicate further distances, even in the presence of high traffic noise (Nemeth and Brumm, 2010).

Timing adjustments. Birds can change the timing of their vocalizations to avoid competing with their neighbors, to take advantage of small gaps in ambient noise, or to not sing when predators are more active or a mate is not near (Brumm, 2007; Ficken et al., 1974). Least Flycatchers (*Empidonax minimus*) will sing between the songs of Red-eyed Vireos (*Vireo olivaceus*) so as to not have overlap of the two species' songs (Ficken et al., 1974). In response to traffic, European Robins (*Erithacus rubecula*), have been shown to change the time of day they vocalize by singing at night when traffic noise levels are low (Fuller et al., 2007). Spotless Starlings (*Sturnus unicolor*) and House Sparrows (*Passer domesticus*) have an earlier start to their dawn singing near high traffic noise (Arroyo-Solís et al., 2013).

Vocalization structure modifications. Species may vary vocalization structure by changing rate or rhythm, increasing the length of all or parts of the vocalization, or increasing redundancy in one song or call before switching to another (Brumm and Slater, 2006; LaZerte et al., 2017). Changing the rate and/or rhythm of a song or call can include temporal structures, note timing, or syllable timing within the vocalization (Patricelli and Blickley, 2006). Chaffinches (*Fringilla coelebs*) use serial redundancy to ensure their message is received while in noisy areas (Brumm and Slater, 2006). Pacific Wrens (*Troglodytes pacificus*) will decrease the length of their vocalizations (Gough et al., 2014) while European Robins will decrease both the length and complexity of their vocalizations near high levels of noise in order to send a clear message (McLaughlin and Kunc, 2013). While making a change may allow a bird to be heard, it could also increase the risk of having a poorer vocal performance that may not be as attractive to females (Byers, 2007).

Learning constraints. Vocalizations that are masked may be copied incorrectly or never learned (Slabbekoorn and Ripmeester, 2008). Copying imprecision may result from a bird hearing, and therefore only learning, part of a song. Those bird species that are able to learn multiple songs may be at an advantage in areas of high traffic noise. If a certain song does not elicit a response, those birds with multiple songs in their repertoire are able to drop that song and still have others to choose from (Slabbekoorn and Ripmeester, 2008).

Behavior alterations. Birds may also alter behaviors associated with vocalizations in order to have their vocalizations heard. Birds may turn their heads in order to send their vocalization in the direction of the receiver (Dooling, 2005) and it has been found that European Robins will move away from the source of noise before vocalizing (McLaughlin and Kunc, 2013).

Mechanism of Response to Change

Vocalization Plasticity. Some avian species are born with innate vocalizations and are unable to modify them during their life (Kroodsma, 1984). These species, mainly non-passerines, require no auditory examples for vocal development (Kroodsma and Konishi, 1991). However, there's a large group, composed of mainly passerines, which must learn their songs and calls from listening to others of their own species: their parents, neighbors, or members of their flock or social group. Within these vocal learned species, some are able to modify their songs multiple times throughout their life, while others stop developing that ability early in life. This is due to a plastic period of vocal development where learning after a certain developmental landmark is reached cannot occur (Ríos-Chelén et al., 2012; Slabbekoorn and Peet, 2003). Song Sparrows could be age-limited song learners since the songs in their repertoire are identical year after year (Nordby et al., 2002). Noisy territories do not hinder birds with innately higher-pitched vocalizations or birds that learn to restrict vocal output to a frequency range that overcomes the masking effect of ambient noise. Those species without vocal plasticity may not be able to avoid acoustic masking and may have to search for more suitable, quiet habitats.

Anatomical limits. Some birds may have anatomical or physiological limits in their ability to vocalize at higher frequency ranges to be heard over traffic noise. This could include the angle they can hold their head, how wide they can open their beak, their beak shape, and their body size. Typically, the frequencies that birds are able to produce are related to their body size. The larger the body size, the lower the frequency of the bird's songs or call; and, the smaller the body size, the higher the frequency of their vocalizations

(Ryan and Brenowitz, 1985). There is also an association between body size and amplitude (Brumm, 2004). The larger the body is, the greater the amplitude and vice versa. A bird cannot change the vocal mechanisms in their throats that allow for certain characteristics of a song to be produced (Podos et al., 2004). Having an anatomical or physiological limit for making a vocalization could cause birds to avoid areas with high levels of traffic noise.

Ultimate Outcomes of Acoustic Masking

Bird vocalizations, like all attributes of living organisms, can evolve due to a changing environment. The acoustic properties of the environment, and their masking effects, can influence the evolution of vocal signals (Brumm, 2004; Goodwin and Podos, 2013; LaZerte et al., 2017; Pijanowski et al., 2011; Slabbekoorn and den Boer-Visser, 2006). Song learning altered by traffic noise is at least partly responsible for the song divergence between populations of species living in cities and forests (Nemeth et al., 2013; Slabbekoorn and den Boer-Visser, 2006). Copying imprecision can lead to variation in songs which can then lead to the development of dialects that are easier to detect over the noise (Luther and Baptista, 2010; Podos et al., 2004; Slabbekoorn and den Boer-Visser, 2006). Reproductive isolation of species can be due to divergence between urban and nonurban songs, urban songs being higher pitched than nonurban songs (Slabbekoorn and Ripmeester, 2008).

Is a Focus on Noise Drowning Out Other Factors?

While the focus of this review is on the impacts of traffic noise on avian vocalizations, there are other issues that should be considered. Roads and road noise also impacts avian density, richness, abundance, distribution, diversity, breeding success, reproductive success, and stress (Halfwerk et al., 2011b; McClure et al., 2013; McLaughlin and Kunc, 2013; Polak et al., 2013; Reijnen and Foppen, 1995; Reijnen et al., 1995). It is suggested by many authors that it is the actual noise from traffic that has the greatest negative impact on birds (Forman et al., 2002; Halfwerk et al., 2011b; McClure et al., 2013; Parris and Schneider, 2008; Polak et al., 2013; Reijnen and Foppen, 1994, 1997; Reijnen et al., 1995). However, others suggest the most negative impacts on birds in habitats adjoining roads may be due to factors other than traffic noise (Crino et al., 2013; Fernandez-Juricic, 2001; Foppen and Reijnen, 1994; Forman et al., 2002; Francis et al., 2009; Goodwin and Shriver, 2010; Halfwerk et al., 2011b; Herrera-Montes and Aide, 2011; Miller et al., 2003; Reijnen and Foppen, 1994, 1995; Reijnen et al., 1995; Rheindt, 2003; Summers et al., 2011). These negative impacts of roadways include: air pollutants, microclimatic modification, visibility of cars, road kill, and predators attracted to road vicinity.

Needs for Future Research: Proximate and Ultimate Outcomes of Acoustic Masking

Territory guarding. Male birds changing their territorial songs to overcome acoustic masking is a predicted response to traffic noise that has not yet been tested. If a male near traffic noise sings normally he risks the possibility of not having his song heard. If he alters his song, the message may not be received correctly. If the song is not heard or understood, it could lead to having to fight off intruding males to keep them from encroaching into his territory, which would detract from the time spent singing to attract females (Slabbekoorn and den Boer-Visser, 2006). There are studies on traffic noise affecting mate fidelity and choice, but information is needed to see if traffic noise could cause males that have changed their songs to lose their territory during the breeding season or to suffer reduced fitness.

Inter- and intra-flock communication. Changes in communications between and among species are another predicted response of traffic noise whose effects remain understudied. Vocalizations can inform the receiver of the whereabouts, identity, and distance of the sender in order to keep in contact with a mate, a flock mate, or a social group (Halfwerk et al., 2012; Slabbekoorn and Halfwerk, 2009). Parents and their offspring use acoustic signals to recognize and communicate with each other (Kilner, 1999). Young birds beg for food and attention from their parents with distinguishable vocal sounds (Marler, 2004). If the vocalizations are not heard, or the sender has made the vocalization sound different, information may not be transferred correctly. It has been found that noise causes Tree Swallow (*Tachycineta bicolor*) nestlings to fail to respond to parental cues (Leonard and Horn, 2012). However, the consequences of this failed connection are unknown. Studies are needed on how traffic noise could potentially interrupt conspecific communications, intra-flock communications, or inter-species communications and the consequences of those interruptions.

Winter. Migratory birds have four parts of their migration cycle: spring migration, summer breeding, fall migration, and overwintering. Research and management for birds has largely focused on the breeding season and their migration patterns (Faaborg et al., 2010). There is a lack of information and research during the wintering season. Winter months are important for migrating birds as they build nutrient reserves for the spring migration (Faaborg et al., 2010) and breeding season. For non-migrating birds, the winter season provides security and time to acclimate to the resources and hiding places in a bird's home range. More information is needed on how traffic noise interrupts birds' communication in the winter when the focus is not on mating and territory but rather food location, predators, and contact calls (e.g., Oden et al., 2015). Interruption of winter vocalizations can cause identity confusion, disrupt food information transfer, and cause predator warnings to be misinterpreted or not heard.

Traffic noise vs traffic volume. Research that better controls other stimuli associated with noise such as physical alteration of habitat or visual disturbance presented by moving traffic is needed (Francis et al., 2009; Nemeth and Brumm, 2010; Slabbekoorn and Ripmeester, 2008; Summers et al., 2011). To suggest traffic noise is the only factor contributing to negative effects on birds, researchers must design a study that blocks visual disturbances from traffic, keeps birds from colliding with traffic, have no pollution or food

Table 1 List of different mitigation efforts to reduce the impacts of traffic and traffic noise on avian species.

	Mitigation techniques	Source
On cars	Better engine features	Forman et al. (2002)
	Quieter mufflers	Forman et al. (2002)
	Quieter vehicle aerodynamics	Forman et al. (2002)
	Different tires or brake systems	Forman et al. (2002)
On roadways	Road barriers	Slabbekoorn and Ripmeester (2008)
	Depressed highways	Forman et al. (2002) and Maekawa (2004)
	Underground tunnels	Maekawa (2004)
	Speed limitations and restrictions	Forman et al. (2002) and Halfwerk et al. (2011b)
	Alternate road routes	Halfwerk et al. (2011b)
	Key road closures during breeding season	Halfwerk et al. (2011b)
Near roadways	Screens to keep birds away from roads	Summers et al. (2011)
	Barriers to force birds to fly over roads	Summers et al. (2011)
	Land buffers next to roads	Miller et al. (2003)
	Soil berms	Forman et al. (2002)
Planning	Better urban planning on roads	Reijnen et al. (1995)
	Noise tax based on season, type of car, tires, and speed	Halfwerk et al. (2011b)

coming from the cars, and find a way to not have a habitat edge near the traffic noise. Or, researchers can bring traffic noise into an area with no previous anthropogenic noise. In order to show that variables besides traffic noise contribute most to the negative effects on birds, a roadway with all of its pollution and flashing lights must be used, but it must be silent. Also, more specific information on why certain species thrive near traffic is needed.

Conclusion

The effects of traffic and traffic noise on birds and their vocalizations are not fully understood. Many methods have been proposed to reduce the impacts of traffic and traffic noise on avian communities (Table 1). Although many have suggested mitigation methods, there is a need for additional studies to test their efficacy in reducing the negative impacts on birds. Finding cost-efficient mitigation techniques for traffic noise may help decrease noise pollution and therefore reduce the consequences of acoustic masking. Along with mitigation efforts, research is needed to determine predicted responses of traffic noise and their effects on male territory guarding, on inter- and intra-flock communication, and during non-breeding times of the year. Despite gaps in our knowledge, we can conclude that traffic is having a negative impact on certain avian species and we need to begin implementing mitigation measures to prevent this problem from worsening.

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Scarcity and Abundance in the Brazilian Semi-arid: The Strategies for Harnessing the Renewable Energy Potential of the Region (Re)Differentiating the Territory

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Abstract

The union of strategies of inequality reduction and promotion of renewable energy may have a greater impact on the decrease of social needs, promoting the appropriation of benefits by local communities. In this context, there is a need for the participation of local communities in the scope of public policies for the establishment of priorities that potentiate these strategies, particularly energy landscape and social acceptance. According to [Stiglitz \(2016\)](#), the greatest danger in the world is inequality, which overcomes all other dangers. It is therefore reinforced that the reduction of inequality should be a priority for all.

This way the aim of this article is to evaluate the impact of the advance of the use of renewable energy resources in the Brazilian semi-arid region in the historical context of scarcity and poverty in the region and, secondly, considering the abundance of energy resources. It seeks to understand the way in which the benefits derived from the exploitation of these resources are appropriate, based on a “built consensus” of imposition that is conceptually considered as a promoter of sustainability.

Introduction

Brazil is a country of recognized vocation for energy production and supply, with an emphasis on abundant renewable sources, which account for 43% of all energy offered in the country and 80.4% of all electricity consumed ([EPE, 2019](#)). In the energy context, the Brazilian Semi-arid is today the central stage of attention to the development of its high wind and solar potential. Of all installed wind power capacity in Brazil, 17.2 GW in 2019, 85.7% is in the northeastern semi-arid ([Brannstrom et al., 2018](#)). Together, considering the pace of solar expansion and the fact that the areas located in the Brazilian semi-arid region have the best solar potential in the entire territory, where average annual radiation values are comparable to the best regions in the world ([Pereira et al., 2017](#); [Constantino et al., 2018](#)), this technology will be intensely present modifying the territory.

Contrary to energy abundance, this same semi-arid area in an area close to three times the size of Germany, comprising 1133 municipalities in nine states of Brazil, with 82% of them registering a Human Development Index (HDI) of <0.65, houses a population in which 50% have no income or have as their sole source of income government benefits, mostly (59.5%) women ([de Araújo, 2011](#)).

The region is characterized by periodic natural irregularities configured by critical and prolonged periods of drought and has high temperatures, low thermal amplitudes, strong insolation and high rates of evapotranspiration and low rainfall, making its rivers provide low water availability. This unfavorable picture has historically marked its population and shaped a reality of scarcity and penury.

The condition of low development of the Brazilian Semi-arid does not result from a recent conjuncture. Water scarcity and stress in the region is a natural determination that holds. The unfavorable picture assumes such a historical and cultural breadth that the experienced poverty shaped the stereotype of the “sertanejo man”, the one that the drought literature tried to shape as a fort, highlights the drought and its shortage as a result of a natural fact. The adversity of the climate guides the life of its population, then

resigned to the natural rain cycle, reducing all employment and income generation alternatives that are linked to the annual rainfall regime. With this, agriculture and livestock strongly focus on subsistence.

The low level of development of the region is the result of discriminatory investment processes between Brazilian regions promoted by the central government. The South-Southeast axis received the full attention of the State to the detriment of the North and Northeast. These asymmetries in the allocation of resources, added to their natural characteristics and historical factors conditioned the local economy to be structured in a fragile manner, based on reduced social and economic sustainability activities. To get an idea of the gap that separates the northeastern semi-arid from the rest of the country, one can illustrate its per capita Gross Domestic Product (GDP), which in 2015 reached less than the US\$ 2000 per year, well below the Brazilian GDP per capita, which is US\$ 8500 (Cavalcante Júnior et al., 2019).

The Semi-arid region comprises 1262 municipalities, distributed over 1,128,697 km² and with a population of 27,870,241 inhabitants (SUDENE, 2017). Most of its territory is covered by Caatinga, a Brazilian biome considered as the more sensitive to human interference and global climate change. (The Caatinga originally covered an area of approximately 1 million km². Currently, its remaining area is 734,478 km², with < 1% being protected by protected areas. Deforestation for firewood is one of the main activities that contribute to desertification, drought and loss of Brazilian biodiversity (ASA, 2019).) About 1.5 million farming families (28.82% of all Brazilian family farming) occupy only 4.2% of the Semi-arid arable land, while 38% of the land belongs to rural settlements in the hands of a small elite (ASA, 2019).

The region continues to be neglected due to the lack of investments oriented to human coexistence with the natural reality of drought and drought regime (Cavalcante Júnior et al., 2019), where it is observed:

- Migration as an escape;
- Naturalization of the social and economic problems of the semi-arid region, making it possible to sustain a cloud that underpins the political pending issues of the power maintenance game, creating barriers to the region's development and coexistence with climate variability;
- Establishment of a development process strongly marked by the emigration of productive capital towards the Center-South of the country;
- In the 1930s, emergency projects aimed at the Semi-arid were implemented vertically, without appreciating the potential that these populations have historically built to cope with the natural drought condition;
- In the 1970s, the variability takes on even more dramatic contours and the "Drought Industry" is established.

The "good news" announced for the Semi-arid is its transformation into a renewable energy-producing space. However, the central issue to be discussed is not limited to the use of energy resources, but also to point out and understand to whom this energy is being produced, and what its purpose is (Harjanne and Korhonen, 2019).

The set of technologies that harness renewable energy allows us to look for a window of opportunity to associate the expansion of electricity supply, from the perspective of distributed generation, in vulnerable communities in the Northeastern Semi-arid region, particularly in places of extreme poverty, which enable the disruption of local populations to the cycle of poverty and scarcity. So, that social inequalities and opportunities for development are not limited between countries, but also intraregional.

In this atmosphere of reflection, it is valid to bring up local social demands, as there is a "world" of abundance as opposed to a "world" of scarcity. On the side of scarcity, it is possible to meet social demands through the Municipal Human Development Index (HDI-M), considering that there are still gaps in individual freedoms and choices. According to (UNDP, 2016), the idea of Human Development seeks to shift efforts beyond the economic sphere. The purpose of the HDI was to provide a counterpoint to another widely used indicator, the Gross Domestic Product (GDP) per capita, which considers only the economic dimension of development.

The combination of strategies to reduce inequalities, as well as the promotion of renewable technologies, both national and local, can have a considerable impact in reducing the heterogeneities of social conditions, promoting the appropriation of gains by local communities. In this context, the need arises for the participation of local communities in the context of public policies to establish priorities that enhance these strategies. According to Stiglitz (2016), the greatest danger in the world today is inequality, which overcomes all other dangers. This reinforces the view that reducing inequality must be a priority for all. In this context, Stiglitz (2016) states: "Inequality is very expensive. The price of inequality is the deterioration of the economy, which becomes less stable and less efficient, with less growth, and with the subversion of democracy. The large and growing divide between the richest 1% and 'the other 99%' is not just one of many concerns, but the defining feature of a completely sick economy."

The chapter, therefore, aims to evaluate the repercussions of the advancement of the use of renewable energy resources in the Brazilian Semi-arid in the historical context of scarcity and poverty of the region, and on the other hand, considering the abundance of energy resources. Thus, we seek to understand the appropriation of the benefits arising from the exploitation of these resources, based on a "built consensus" of imposition that is conceptually considered as a promoter of sustainability.

Brazilian Semi-arid: A Development Model to Be Overcome

It is observed that there is ambiguity in the development of renewable energy in the Semi-arid region, since, on the one hand, the land is fertile for the reproduction of wealth via energy production, while on the other hand, it does not represent a significant

benefit to the local populations. For Ahlborg (2018), this contradiction is the result of the unequal social order that generates unequal results of power and produces growing feelings of disappointment and frustration among the actors involved.

In the Northeast Semiarid, the scarcity of rain, accompanied by high temperatures and evapotranspiration, triggers a real competition for water and, consequently, a water crisis is potentially more serious in rural areas. Water deficiency affects the poorest groups, especially small farmers, who face and live with the risk of food insecurity. All these impacts add to the crisis in the availability of clean water in the 21st century, which is seen more as a management problem, as well as technological and financial support, rather than a crisis determined by scarcity and lack (Tundisi, 2010).

In the semiarid region, rainfall irregularity defined policies to mitigate the impacts of drought. Historically, policies prioritized the construction of reservoirs that answered to assistance actions, and permanent and structured interventions. Reservoirs, better known as weir, have changed the landscape and provided productive activities. However, the supply of the rural population, dispersed, and small communities that live far from the springs, which continue to depend on water trucks, which can travel up to 250 km/day, was not resolved (ANA, 2017). (A truck equipped with a large tank, or reservoir, used to transport water <https://www.google.com.br/search?q=Dicion%C3%A1rio>.) This is the solution for locations with chronic scarcity that live with the poor spatial and temporal distribution of water resources (Schroeder and Conti, 2013).

In Brazil, the average water consumption is 153.6 L/inhabitant/day. In 2017, the consumption varied regionally, being discrepant between the Southeast, with 180.3 L/inhabitant/day and the Northeast regions, with 113.6 L/inhabitant/day (ANA, 2018). With the effects credited to climate change on water resources, the per capita water availability is insufficient in the states of Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, and Sergipe. The situation is becoming unsustainable for the populations of these states affected by water stress (Marengo et al., 2011).

With water deficit at least 70% of the year, according to Marengo et al. (2011), increasing scarcity and resource constraints increase water vulnerability and, as a result, socioeconomic conditions deteriorate and may compromise food production in the countryside. In turn, the population becomes impoverished, and their escape to the cities may be inevitable, signifying their uprooting of the rural space, and thus the maintenance of the cycle of poverty in the urban space.

On the other hand, the favorable weather conditions in the region led to the implementation of large agroindustrial complexes for the production of tropical fruits. The main centers are located in the Mossoró region, in the states of Rio Grande do Norte and Ceará, and the region of Petrolina and Juazeiro, in the states of Pernambuco and Bahia. These are irrigated crops that use high technological intensity in the various stages of the production chain and account for the occupation of labor at the poles. Table 1 shows the production data of the main crops in the region for 2017. It is noticed that some products such as cashews, melons, mangoes, and papaya account for >50% of national production. In turn, cashews, melons, mangoes, papayas, grapes, watermelons, and lemons are exported, with important participation in the country's trade balance (Kist et al., 2018).

Considering the significant numbers of agricultural and renewable energy production, especially from solar and wind sources, when confronted with the socio-environmental reality in the Semiarid region, that is, the low social indicators and the environmental weaknesses represented by water scarcity and the permanent threat of desertification, it is clear that the development model put in place requires a strong adjustment in its policies. The abundance expressed in the results of the region's production system, with the production of electricity for large consuming centers through renewable sources, and fruits with the quality demanded by the developed markets, contrast with the reality experienced by the majority of the population that resides in the Semiarid. An enclave effect has thus been constructed, where the benefits help few, but the negative effects and cultural impacts are extensive (Ioris, 2011).

Table 1 Output quantity and exported from the main fruits in Northeastern Brazil in 2017.

<i>Fruit</i>	<i>Output quantity (t)</i>	<i>Share of the national production (%)</i>	<i>Export quantity (t)</i>	<i>Export share in production (%)</i>	<i>Main producing state</i>	<i>State share in export (%)</i>
Cashew	131,906	99%	11,522,688	9%	CE	79%
Melon	514,276	95%	233,299,436	45%	RN	70%
Mango	812,275	75%	167,262,032	21%	BA	50%
Papaya	628,404	59%	24,496,417	4%	RN	45%
Grape	681,272	36%	44,073,010	6%	PE	72%
Watermelon	663,458	29%	69,220,416	10%	RN	70%
Lemon	88,781	7%	36,647,323	41%	BA	59%
Northeast output	9,447,969	25%	598,993,799	6%		

Adapted from IBGE (2017). Pesquisa Pecuária Municipal—PPM 2017. Available at: <https://sidra.ibge.gov.br/pesquisa/ppm/quadros/brasil/2017> (Acessado: 2 de fevereiro de 2019); Kist, B. B., et al. (2018). *Anuário da Fruticultura Brasileira 2018*. Santa Cruz do Sul: Editora Gazeta Santa Cruz; MAPA—Ministério da Agricultura, Pecuária e Abastecimento (2019). AGROSTAT—Estatísticas de comércio exterior do agronegócio brasileiro, AGROSTAT. Available at: <http://indicadores.agricultura.gov.br/agrostat/index.htm>.

The Emergence of Modernization of the Northeastern Semi-arid and the Permanence of Poverty in the Abundance

The images of the Brazilian Northeast are marked by poverty and misery, under the cloak of economic backwardness and climatic conditions present in the conception of drought region, generated by political projects that were thought from superficial propositions. However, this conception denotes the reality of the regional semi-arid space, when its definition disregarded its socio-environmental complexity and considered the regional phenomenon of droughts as the main reason for the Northeast's economic doldrums (de Castro, 1984). As a result, the region received special attention during the first decades of the 20th century, resulting in emergency policies and projects involving, above all, the semi-arid space.

This issue served as the basis for the development of regional development policies, in particular, the creation of the Northeast Development Superintendence (SUDENE), which began to make efforts to boost the economy of stagnant regions and promote their integration with the national territory, resulting in the diversification of economic activities after 1960.

From this decade, with the State's support, the Northeast was the object of investments to meet the new planning model that, on the one hand, modernized it, giving it a new economic dynamism, and on the other, maintaining the traditional structures. of resistance to modernization, as happened in territorial patches of sugarcane, cacao and semi-arid backlands (de Araújo, 2015).

In the context of economic modernization, the developmental industrial model has strengthened the region's link with the country's southeast, and the poles of irrigated agriculture with national and international markets. However, such dynamism has not reached everywhere, leading to large interregional economic imbalances and increasing social inequalities. The coexistence of imbalances and inequalities did not inhibit the actions of the state and monopoly capital, which prioritized the diffusion of new technologies for the use of water, even scarce, to attract investment in the wetter areas of the semi-arid backlands. This region has received large irrigation programs to benefit large economic groups to the detriment of the rural, poor and landless population (de Andrade, 2005).

Thus, the geographically uneven development in the Northeast was consolidated, as it is what matters and guarantees the gains with its location, production, and consumption (Silva et al., 2008). In this way, it was perceived that greater participation of the Northeast in the new globalized economy, embodied as an engine of change, was passively combined with the multinationalized economic and corporate interests that were accelerating (Becker, 2003). Thus, the territory gains new content and imposes new behaviors and, consequently, generates possibilities for production, circulation of inputs, products, money, ideas, information, orders and men (Santos and Silveira, 2006).

New strategies of accumulation and reproduction for the semi-arid region of Brazil, once sentenced to failure, were created with a view to its internationalization. Today, this economic dynamic gives it a new historical configuration. However, the construction of this new regional image did not break with the social drama, remaining in the country as the region with the lowest record of development indicators. Thus, and based on this reason, we consider that globalization, even appropriating or even producing differentiation to expand the inherent mercantile logic, becomes a diffuser of inequalities (da Costa and Porto-Gonçalves, 2006).

Since the threshold of this century, the Northeast has been an alternative for investments in renewable potentials for electric power generation. A new paradigm? From scarcity space to abundance space, the Semi-arid is the jewel of the time, while wind and sun become the adornments lacking to solve the severe problems concentrated mainly in the countryside. Contrary to and frustrating this possibility, water pollution and contamination by pesticides and industrial waste aggravate social and environmental conditions, and circumstances indicate that we are against what needs to be done (UN, 2018).

Semi-arid climatic conditions, water scarcity and the physical nature of soils restrict land use and exploitation, and limit agricultural activities. In this environment, a mass of small farmers end up producing activities with little economic impact or even leaving the field. Contradicting these conditions, this space attracts energy companies that seek intense solar radiation and constant winds of great commercial value for conversion to electricity, confirmed by harnessing the solar and wind energy potential in Fig. 1.

There are 1.5 GWp in solar photovoltaic energy and 12.2 GW in wind energy in installed capacity in the Semi-arid, with the highlight of a total of 17 municipalities distributed in 08 states with photovoltaic solar energy installations, while wind energy is present in 71 municipalities distributed in 06 states.

As for power generation from biomass-fired thermoelectric power plants, a total of 14.8 GW of installed capacity in Brazil was registered on June 2019, using the following sources: sugarcane bagasse; biogas; elephant grass; charcoal; rice husk; ethanol; blast furnace gas from biomass; firewood; black liquor; vegetable oils and forest residues. The Northeast region operates an installed capacity of 1.7 GW from this technology, being 53% of sugarcane bagasse; 41% black liquor; and the remaining 6% from elephant grass biogas, forest residues, and charcoal. However, considering the Semi-arid range, the installed capacity is only 101.12 MW, 94% from sugarcane bagasse, and the remaining forest residues. This discrepancy is justified because most of the sugarcane plantations are located on the coast and, therefore, the use of sugarcane bagasse occurs in this territorial range (ANEEL, 2019).

Water and energy are inextricably linked and fundamental to food production, especially in areas of regional water vulnerability. Water, in particular, is essential to life and the environment, and its scarcity arouses global interest. For Cavalcante Júnior et al. (2019), in the semi-arid region the resources of wind and solar renewables, in addition to the availability of water, have particular characteristics and connect themselves to the scarcity and irregularity of rainfall.

However, such links are not yet unveiled in the Brazilian reality, since renewable energy projects, especially the wind source, prioritize the macroeconomics, marginalizing the local dimension (Riva et al., 2018). A consensus, like renewable energy, as it is being harnessed, is a priority in electricity generation, but it is not intended directly for the welfare of those living in rural areas with which they share the same territory.

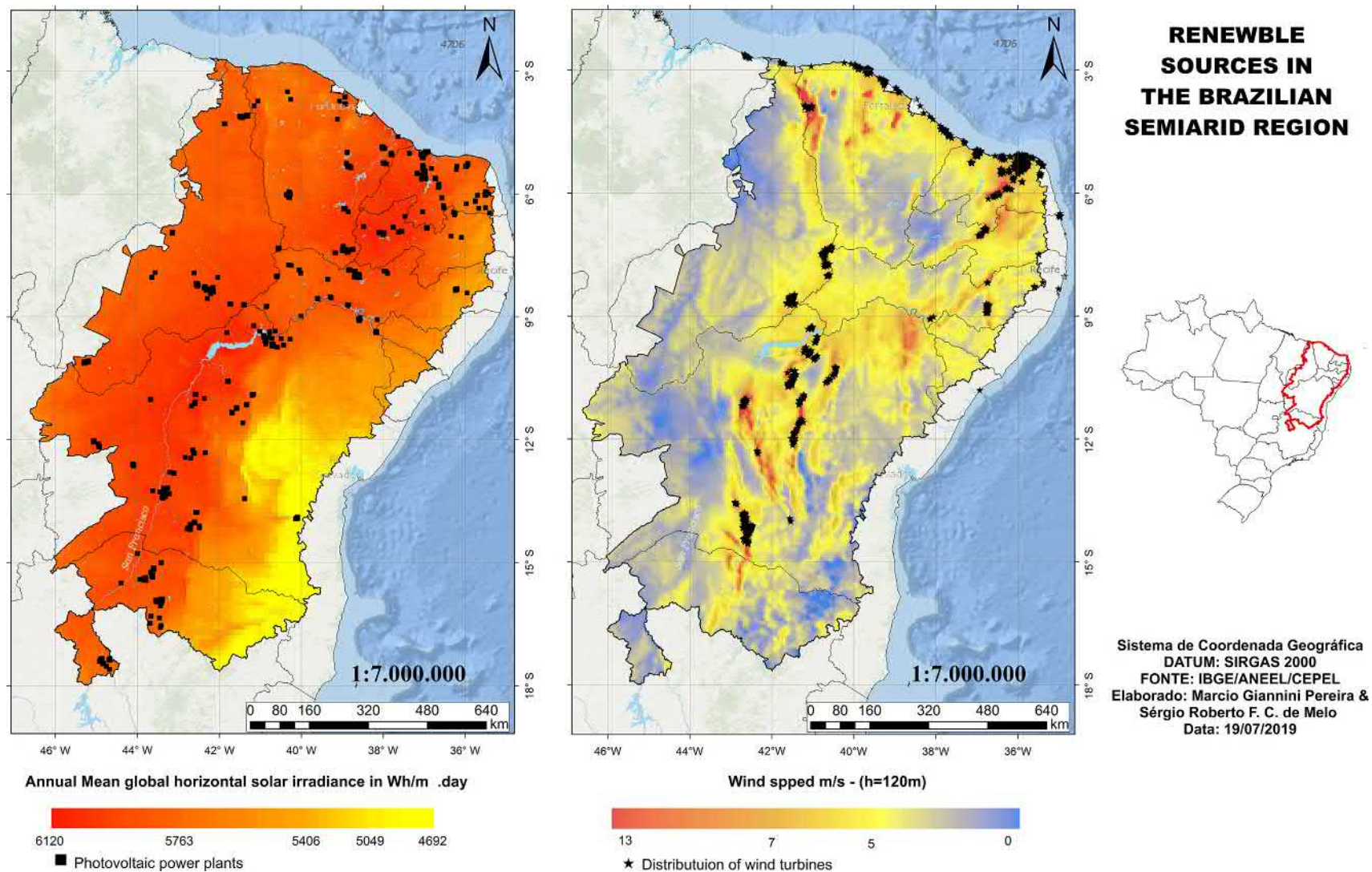


Fig. 1 Distribution of Solar and Wind Energy Potential in Brazil's Semi-arid. Adapted from INPE (2019). LABREN. Available at: http://labren.ccst.inpe.br/atlas_2017.html#; INSA (2019). SIGSAB. Available at: <http://sigsab.insa.gov.br/acervoDigital>; ANEEL (2019). BIG—Banco de Informações de Geração. Available at: <http://www2.aneel.gov.br/aplicacoes/capacidadebrasil/capacidadebrasil.cfm>; IBGE (2019a). Mapas—Bases e referenciais. Available at: <https://mapas.ibge.gov.br/bases-e-referenciais/bases-cartograficas/malhas-digitais>; IBGE (2019b). SIDRA—Banco de tabelas estatísticas. Available at: <https://sidra.ibge.gov.br/home/pimpfrg/nordeste>.

Final Considerations

In the Semi-arid Northeast, water requires political, academic and social commitment. It demands full responsibility because the water crisis is everyone's problem and not just a regional one. The crisis and scarcity were determinant for structural changes, but the effects of droughts still fall on a large part of the rural population facing difficulties in agricultural activities (Maciel and Pontes, 2016). Even so, the crisis and the scarcity gain importance to speed up the ways to follow, through new institutional arrangements, including the adoption of renewable energy sources in the regional economy, which must be oriented to overcome social inequalities.

There are reasonable reasons to rethink about the way we produce energy in Brazil or in World. The energy geography shows that there are no limits or borders in the results of the way we treat to the planet considering the persistence of poverty or climates changes. The spatio-temporal characteristics of energy production, chains and use should be revisited under context of scarcity and abundance and this has to be done using many and different scales both for international to regional scale (Brazilian semi-arid).

The Brazilian semi-arid contributes positively to the Brazilian electricity matrix, highlighting the presence of renewable hydroelectric, solar and wind energy sources. The São Francisco River hydroelectric use in the region amounts to 10 GW of installed capacity, where the 09 plants account for 10% of the national hydroelectric generation. Photovoltaic solar energy has 1.53 GW of installed capacity, present in 08 states and 22 municipalities of the Semi-arid, corresponding to 79% of the existing in the Northeast, 73% of the national. And as for wind power, there are 12.2 GW installed in the Semi-arid, present in 71 municipalities and 08 states, which corresponds to 81% of national capacity.

In the hydroelectric case, for the region, the expansion potential is practically exhausted. Photovoltaic solar energy is predominant when considering the national context. However, there is a potential for exploration in the semi-arid region yet to be explored, and there is a prospect of expansion. And as for wind power, there is already an important installed base with potential for further use, as the expected potential for the region has not yet reached 50%. Thus, the semi-arid with 23.7 GW of installed capacity in hydroelectric, solar and wind sources, makes up 20% of the national total for these sources. The current scenario and the future perspective show the region as strategic for the constitution of a strongly renewable national electric matrix.

Thus, despite the water scarcity that characterizes it and negative impacts on socioeconomic and environmental levels, the Brazilian semi-arid region that hosts Caatinga responds to some contemporary economic demands consistently. Irrigated fruit at its exploration centers and the presence of renewable energy exploration, with the prospect of expansion, position the region within the scope of the most recent developments. It should be emphasized that this model that favors accumulation in certain sectors, cannot disseminate this development to its population, which still resents public policies that contemplate it and that try to point out ways for its full development.

Water scarcity in the same space of energy abundance determines that it is necessary to establish a balance in the form of harnessing natural resources, to generate benefits that can make possible the dignified existence of the population that inhabits this space. Achieving this balance requires state bodies responsible for water management to put in place appropriate policies and legal framework to allocate and manage available water resources (GWA, 2003). Hence the importance of following paths for new learning about the limits, potentialities, and unpredictability of long periods of drought. Drought should be addressed as part of climate characterization. However, their intensification may be added as a consequence of climate change. Already its confrontation must be dealt with in the field of public policies, where the role of renewable energies can be crucial in generating local employment, income, and citizenship.

The environmental movement and promotion of renewable sources of energy are meritorious, but when captured by the restricted interests of capital reproduction, it loses its purpose. In this sense, this approach reinforces the idea of the consensus built on renewable energy sources as inducing local development when it is separated from the social dimension.

The sustainability discourse associated with the promotion of renewable sources of energy tends to be an instrument of persuasion and social conviction of technologies when the perspective of the appropriation of gains by the local community is not incorporated. (Chomsky (2013a, 2013b)) states that in more developed societies coercion and force are no longer working tools. In this sense the established power structure seeks instruments of coercion to impose their thinking, ultimately seeking behavior control. In the context of the built consensus, Chomsky (2013a) points out that the image of the world that is presented to society has only a pale relationship with reality.) This issue takes shape in particular in regions of extreme economic and social need, such as the Northeastern Semi-arid. Bauman and Donskis (2014) point out that societies should not fall into adiabaticization, where the established standard model is limited to the consumer-commodity relationship, i.e., technological advancement is not exempt from the ethical and moral issue.

The combination of strategies to reduce inequalities as well as the promotion of renewable technologies can have a considerable impact on reducing the heterogeneities of social conditions, promoting the appropriation of gains by local communities.

Finally, nature has endowed the region with plenty of sun and wind and has deprived it of water and fertile land. This unequal impact requires efforts to link these natural resources through technological progress, which has enabled the development of hydraulic and energy systems. However, the connection between development and technological progress goes *pari passu* with monopoly capital, but still indifferent to the prevailing conditions of poverty and misery of most semi-arid rural families.

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Promoting the Transfer and Development of Climate-Smart Energy Technologies in Uganda

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Abstract

Uganda has strong opportunity for Climate Smart Energy Technologies (CSET) trade expansion with 89 out of 96 countries in the scope of this article. The contributory cost of technologies to ensuring access to electricity for all Ugandans by 2030 ranges between \$0.63 billion and \$1.24 billion. The assumed level of electricity demand per household in each settlement, is an important factor determining which technology offers the lowest cost. At the lowest consumption levels, most settlements will find that stand-alone systems are the most economical option (with solar PV technology a highly viable option). At this low level of consumption, mini-grid wind technology plays only a minor role. Assuming higher consumption levels implies that mini-grid solar PV becomes an economically attractive option and replaces stand-alone solar PV technologies in many settlements.

Introduction

The United Nations Framework Convention on Climate Change defines climate change as a shift of temperature and/or precipitation that is observed over comparable periods of time, attributed directly or indirectly to human activity, above that caused by natural climate variability (United Nations, 1992). The Intergovernmental Panel on Climate Change (IPCC) finds with 95% certainty that human activity, by increasing concentrations of greenhouse gases in the atmosphere, has been the dominant cause of the observed warming since the mid-20th century. According to a 2014 *Overseas Development Institute (ODI) publication*, the primary sources of emissions are fossil fuel emissions and changes in land use.

To address these drivers of climate change, are climate-smart energy technologies which are an important subset of climate-smart goods and technologies (UNESCAP, 2011). UNESCAP (2011) mentions four categories of climate smart energy technologies; clean coal technologies, wind power, solar technology, and energy-efficient lighting. The World Trade Organization (WTO) provided a list of 153 environmental goods as a result of The Doha Ministerial Declaration. The World Bank identified 43 climate-friendly products that had been derived from the previously submitted WTO 153-product list. In addition, UNESCAP proposed a list of an additional 21 products that appeared on one of the International Centre for Trade and Sustainable Development (ICTSD) lists and also on one of the Asia-Pacific Economic Cooperation (APEC), Organization for Economic Co-operation and Development (OECD) or WTO lists. In total, the list comprises 64 Climate-smart goods and technologies (CSGTs) classified by the Harmonized Commodity Description and Coding System (HS) 2002 codes at the 6-digit level of the Harmonized System.

Technology transfer, the act of conveying knowledge from one organization or sub-unit to another, is necessary if the above technologies and goods are going to adopted broadly. Teece (1977) identified four stages of technology transfer: (1) pre-engineering technological exchanges, (2) transfer of process design and associated process engineering for process innovation; product design and production engineering for product innovation, (3) use of research and development to adapt and troubleshoot the technology, and (4) pre-startup training and process debugging costs.

Most of the previous studies have attempted to answer the question: "Is there any trade opportunity for climate smart energy technologies to mitigate climate change?" For example, the research work includes Anbumozhi et al. (2016); as well as World Bank (2008). Haselip et al. (2011) aim to share different views about enabling frameworks and best practices for technology transfer in the area of climate change. Notable, quantitative analysis using gravity modeling has been widely used to describe trends in trade in climate smart energy technologies, as well as identifying opportunities for expanding trade and investment in climate smart energy technologies. Furthermore, energy system modeling with the integration of geographic information system (GIS) has

been used to help identify the most effective electrification strategy on a geospatial basis. In addition, liberalization and facilitation of trade in climate smart energy technologies is also popularly examined in order to ensure access by all countries as seen in [UNESCAP \(2011\)](#).

Among a number of studies applying the gravity model in international trade, many scholars focus on predicting the trade potentials and examining determinants affecting trade relations, such as [Nguyen and Kalirajan \(2016\)](#). In addition, the gravity model has been extensively used to analyze the effects of common Free Trade Areas (FTAs) using the dummy variables on common borders. Noticeable studies include [Jafari et al. \(2011\)](#); as well as [Binh et al. \(2011\)](#).

Among a number of studies applying the electrification planning methodologies, drawing on geographic information system (GIS) tools, many scholars focus on categorizing zones into areas that are more appropriate for either conventional or renewable technologies based on techno-economic criteria, e.g. [Amador and Domínguez \(2005\)](#) and [Szabó et al. \(2011\)](#) investigated energy solutions in rural Africa.

Uganda Case Study

Uganda's National Development Plan (2010–15) recognized climate change action as crucial for the country to become a competitive, upper middle-income country by 2040 ([Bickersteth, 2015](#)). As part of the review, this case study investigates the transfer potential of climate smart energy technologies to Uganda to answer the main question: "How can climate smart energy technology transfer be fostered to a developing country like Uganda at affordable prices without undermining entrepreneurship and investor confidence, and consequently, innovation and economic welfare?"

The case study demonstrates the gravity model to measure the trade potential of Climate Smart Energy Technologies (CSET) for Uganda. In addition, the geographic information system (GIS) based, Open Source Spatial Electrification Tool (OnSSET), is used to estimate energy demand and the most cost-effective supply option for a particular location.

Methodology

Gravity Model

The gravity model has been used extensively in empirical international trade since it was introduced by [Tinbergen \(1962\)](#), who pointed out that empirically trade between two countries was determined by their relative masses and their distance from each other. The gravity model employed within this study for estimation and analysis purposes is considered as the following equation, in which all continuous variables are expressed in logarithms:

$$\ln T_{ij}^t = a_{ij} + a_1 \ln GDP_i^t + a_2 \ln POP_i^t + a_3 \ln DISTANCE_{ij} + a_4 \ln REER_{ij}^t + a_5 \ln INFR_i^t + a_6 \ln INFR_j^t + a_7 BORDER_{ij} + a_8 TA_{ij} + e_{ij} \quad (1)$$

In which:

$i = 1, 2, \dots, 96$ (trade partner countries); $j = 1$ (Uganda); t implies years from 2007 to 2016.

e_{ij}^t : error term.

T_{ij}^t denotes country (i) trade value in Climate Smart energy technologies with country (j) in year (t).

GDP_i^t and POP_i^t describe the gross domestic product (GDP) and population of country (i) in year (t), respectively.

$DISTANCE_{ij}$ measures the geographic distance between country (i) and country (j). $REER_{ij}^t$ is the real effective exchange rate between country (i) and country (j) in year (t). $INFR_i^t$ and $INFR_j^t$ indicate the quality of infrastructure score index of country (i) and country (j) in year (t), respectively.

$BORDER_{ij}$ is the dummy variable for common border, which take the value of 1 if the two countries share the same border and 0 otherwise.

TA_{ij} represents the dummy variable, which is equal to 1 if country (i) has the trade agreement with Uganda, otherwise 0.

Gravity Model Data

This case study follows [UNESCAP \(2011\)](#), to identify the list of 64 climate-smart goods and technologies (CSGTs) classified by the Harmonized Commodity Description and Coding System. Uganda's trade data on climate smart energy technologies is taken from the UN Comtrade database (<http://comtrade.un.org/>). The countries of consideration are the main trading partners of Uganda for climate smart energy technologies. GDP and population data is taken from the World Bank Development Indicators (<https://data.worldbank.org/>). Data on exchange rates is obtained from the official website of World Bank. Data on distance and borders employed within this study is drawn from the website of Centre d'Etudes Prospectives et d'Informations Internationales (CEPII) at http://www.cepii.fr/CEPII/en/bdd_modele/bdd_modele.asp. The distance is geographic distance between Uganda and its main trading partners. The quality of infrastructure scores of both Uganda and her trading partners are taken from the Global Competitiveness Report released annually by the World Economic Forum. This index covers the quality of the transport and

communications infrastructure network. General infrastructure in the country is ranked for all selected countries in this study, ranging from 1 for underdeveloped to 7 for extensive and efficient ones. Trade agreement participation including both multilateral and bilateral ones is collected from the website of Uganda's Ministry of Trade, Industry and Cooperatives.

Jakab et al. (2001) propose the concept of speed of convergence to calculate potential trade. The average speed of convergence is defined as the average growth rate of potential trade divided by average growth rate of actual trade between the years of observation:

$$\text{Speed of convergence (SC)} = (\text{Average growth rate of potential trade} / \text{average growth rate of actual trade}) \times 100 - 100 \quad (2)$$

Accordingly, we suggest convergence if growth rate of potential trade is lower than that of actual trade and the computed speed of convergence is negative with the divergence in the opposite case. The argument for the prominent efficiency of this method over the point estimated method is that the speed of convergence exploits the dynamic structure of the data during the estimation, which offers a more reliable analysis than the point estimates.

This case study computes trade potential with the help of following formula:

$$\Delta T = \text{Predicted} - \text{Actual trade flows} \quad (3)$$

For our analysis, in particular, we denote convergence if SC and ΔT turn out with the opposite signs, and we posit divergence in the opposite case.

The OnSSET model and its main accompanying steps pursued in this study are summarized in the flow chart below (see Fig. 1).

It is based on the Open Source Spatial Electrification Tool by KTH-dESA (2018). Uganda's Energy Sector GIS Working Group data is used to determine the existing and planned transmission network as well as power plant location. Additional costs are assigned to the electricity grid expansion process based on the topology of the entire country. In order to develop energy demand scenarios, "tiers" of access are incorporated. A mini and small hydro potential dataset is one of several datasets used for this study. Moreover, night-time light datasets are used in combination with the population distribution, the transmission and road network in order to identify the presently electrified populations. In this analysis, the costing of each technology considers the topological characteristics of the country, e.g. areas on higher elevation would indicate an additional investment cost due to higher construction and transportation costs. Likewise, proximity to the road network, land cover, slope gradient and distance from substations affect the initial investment cost. The modular approach (indicated in Fig. 1 above) allows for data sets to simply be replaced when more accurate or updated information is available.

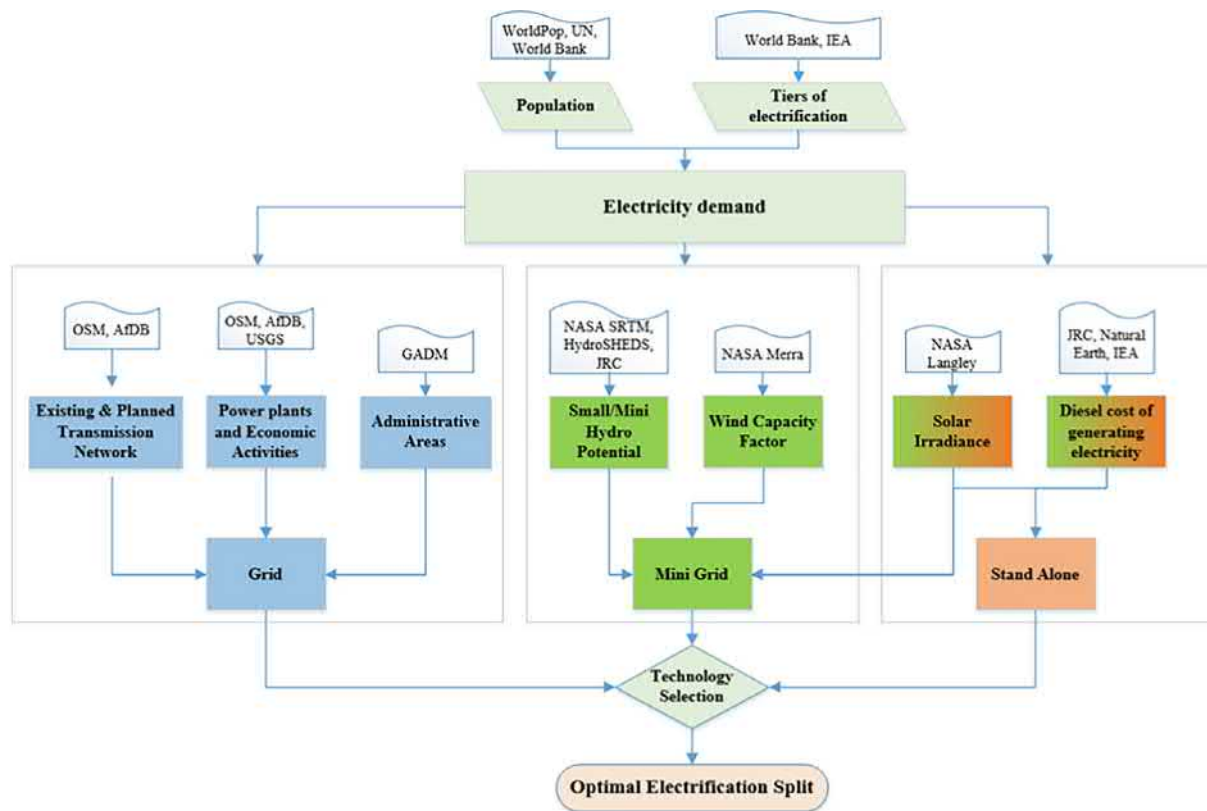


Fig. 1 Framework of OnSSET and principal data sources.

Energy Demand

Geospatial data entailing the administrative boundary of Uganda, population density which is “assigned” to point locations of 1 km by 1 km, hereinafter called settlements, existing infrastructure (transmission lines) and national access to electricity is processed to derive information about the current electrification status of Uganda. Thereafter, the transmission grid is assumed to expand to connect with planned power plants. The population is adjusted to reflect the population projected for 2030 by the Uganda Bureau of Statistics. Population combined with different tiers of electrification leads to future electricity demand scenarios—a crucial input to the cost-optimal allocation of electrification options. Each tier represents different levels of electricity services provided, starting from basic lighting to services that provide comfort, such as air conditioning as captured in **Table 1** below.

The various tiers are assessed for all given grid points in order to capture different specificities of energy demand levels per region. In reality, significant income differences across the country would imply different energy demand levels and all five tiers are likely to co-exist in the country.

Assigning Costs

The energy options analyzed include categories of renewables among them mini-grid systems and stand-alone systems. For every GIS cell, the levelized cost of generating electricity (LCOE) of these options are evaluated. The resulting LCOE information is fed into the GIS model to determine the most economical option for each grid cell given its geospatial characteristics. In this analysis, diesel prices are considered in order to assess how increasing oil prices influence the least cost energy mix.

Results and Discussion

The independent variables (GDP_i^t , $POPI_i^t$, $REER_{ij}^t$, $INFR_i^t$, $INFR_{ij}^t$) explain approximately 17% variations of trade values of Climate Smart Energy Technologies between Uganda and its 96 trading partners. This value is due to the omission of “DISTANCE_{ij}”, “BORDER” and “TA” variables because of collinearity (**Table 2**).

Uganda’s trade of Climate Smart Energy Technologies is positively correlated with the economic size of its trading partners. Larger economies tend to have a higher supply of exporting Climate Smart Energy Technologies to Uganda. Also, the increase in GDP reveals that these countries are able to produce larger amounts of Climate Smart Energy Technologies for export to Uganda. This positive relation is in line with higher incomes allowing for more resources being available for cleaner technologies, as well as higher Research and Development for clean technologies. Accordingly, larger economies mean higher promotion of cleaner technology development, and a better marketing system for supplying those technologies.

Foreign Labor force, positively influences trade in Climate Smart Energy Technologies. This positive correlation can be explained by the fact that as population grows, the trading partners may increase technological output for export while utilizing more skilled and/or cheaper labor. Over the years, the challenges in transportation have affected the transportation cost and hindered the inflow of technologies to Uganda.

The exchange rate variable, linked to the impacts of price variations due to exchange rate volatility on trade flows of Climate Smart Energy Technologies, is negatively associated with technology transfer. In particular, the appreciation of the Uganda Shilling against the currencies of trading partners results in an increase in import value of Climate Smart Energy Technologies to Uganda. The negative impact on the trade value can be explained by the fact that Uganda’s imports of Climate Smart Energy Technologies are capital-intensive climate components. As a result, an increase in exchange rate leads to a decrease in the trade value of climate smart energy technologies.

An increase by 1 unit in exchange rate means the Uganda Shilling appreciation would reduce trade in Climate Smart Energy Technologies by Uganda to the tune of 0.08 units. The estimated coefficient value also reveals a negative long run relationship between the real effective exchange rate and trade value. Therefore, the management of the exchange rate plays a major role in promoting trade of Climate Smart Energy Technologies especially with regard to the fact that Uganda is a net importer of those

Table 1 Mapping of tiers of electricity to indicative services.

Access level	Tier 1	Tier 2	Tier 3	Tier 4	Tier 5
Indicative appliances powered	Task lighting + phone charging or radio	Tier 1 + general lighting + air circulation + television	Tier 2 + light appliances	Tier 3 + medium or continuous appliances (i.e. water heating, ironing, water pumping, rice cooking, micro wave)	Tier 4 + heavy or continuous appliances
Consumption per capita per year for a certain efficiency level (kWh)	8	44	160	423	598

Table 2 Estimated results using fixed effects regression.

note: lnDISTANCE omitted because of collinearity

note: BORDER omitted because of collinearity

note: TA omitted because of collinearity

Fixed-effects (within) regression	Number of obs	=	452
Group variable: countrysum	Number of groups	=	89
R-sq: within = 0.0398	Obs per group: min	=	1
between = 0.1593	avg	=	5.1
overall = 0.1652	max	=	10
	F(5, 358)	=	2.97
corr(u_i, Xb) = -0.9772	Prob > F	=	0.0121

LnTRADE	Coef.	Std. Err.	t	P> t	[95% Conf. Interval]	
LnGDP	.190614	.1894855	1.01	0.315	-.1820306	.5632587
lnPOP	7.24565	2.470604	2.93	0.004	2.38693	12.10437
lnDISTANCE	0	(omitted)				
lnREER	-.0840715	1.291129	-0.07	0.948	-2.623222	2.455079
lnINFRj	-2.059183	.7875008	-2.61	0.009	-3.607892	-.5104744
lnINFRi	-.3770492	.6285372	-0.60	0.549	-1.613138	.8590399
BORDER	0	(omitted)				
TA	0	(omitted)				
_cons	-115.4375	39.90825	-2.89	0.004	-193.9215	-36.95342
sigma_u	12.112433					
sigma_e	1.731459					
rho	.97997481	(fraction of variance due to u_i)				
F test that all u_i=0: F(88, 358) = 8.23 Prob > F = 0.0000						

Source: Author's calculation in STATA.

goods. The two variables reflecting the overall quality of infrastructure of Uganda and its trading partners are both found to have negative coefficients as per the result of the model.

The overall infrastructure scores included in the model reflect the modes of transport—including high-quality roads, railroads, ports, and air transport—which enable entrepreneurs to get their goods and services to market in a secure and timely manner and facilitate the movement of workers to the most suitable jobs.

Estimation indicates that the quality of infrastructure of both Uganda and her trading partners are important determinants of Uganda's trade performance in Climate Smart Energy Technologies. In particular, a unit improvement in the scores of Uganda and 89 countries leads to a 2.06 and 0.38 unit decrease respectively in the trade value of Climate Smart Energy Technologies to Uganda. Also, it is clear that the improvement of the infrastructure index of Uganda's trading partners has a relatively larger impact on the trade value compared to that of Uganda. Extensive and efficient infrastructure is critical for ensuring the effective functioning of the economy. Additionally, a well-developed infrastructure system is essential for attracting foreign direct investment in cleaner technologies and production which are crucial for promoting trade of climate smart energy technologies in Uganda. Therefore, a better infrastructure is not only strongly associated with the expansion of Climate Smart Energy technology trade but also with Uganda's trade in other commodities and economic growth in general.

According to [UNESCAP \(2011\)](#), among the most important barriers to climate-smart foreign direct investment are technical/infrastructure (including grid-related) barriers.

Trade potential of Climate Smart Energy Technologies for Uganda.

Considering only statistically significant coefficients, the estimated trade of Climate Smart Energy Technologies for Uganda is as follows:

$$\text{LnT}_{ijt} = -115.438 + 0.191 \times \text{LnGDP}_{it} + 7.246 \times \text{lnPOP}_{it} - 0.084 \times \text{lnREER}_{ijt} - 0.377 \times \text{lnINFR}_{it} - 2.059 \times \text{INFR}_{it} \quad (4)$$

The regression results from Eq. (2) are employed to estimate the speed of convergence (SC) and the difference between potential and actual trade value of Climate Smart Energy Technologies (ΔT). The calculation of trade potential of Climate Smart Energy Technologies for Uganda is presented in Table 3 below.

The bilateral trade situations in Climate Smart Energy Technologies between Uganda and its 96 trading partners are divided into two separate groups, i.e. convergence and divergence. Trade opportunity of Climate Smart Energy Technologies denoted by the convergence situation implies that there is a scope to increase Uganda's trade value of products with its particular partners.

Considering both Speed of Convergence (SC) and trade potential (ΔT) for each particular market, this study is able to identify that Uganda had convergence with 89 out of 96 countries in the scope of the research for this article. In this regard, Uganda has not exploited full potentials in trading of Climate Smart Energy Technologies with 89 countries. In other words, there is a large scope for trade expansion between Uganda and those countries in the next period.

Geospatial Electrification Analysis for Renewable Energy Technology

In total, four scenarios focusing on wind power and solar photovoltaic (PV) technologies were created for Uganda using OnSSET. These scenarios clearly show that the assumed level of electricity demand per household in the settlements is an important factor determining which renewable energy technology offers the lowest cost (Figs. 2–5).

At the low consumption level, most settlements will find that stand-alone systems are the most economical option (i.e. solar PV technology). At this low level of consumption, mini-grids, more so wind technology mini-grids plays only a minor role. A mini-grid is a set of small-scale electricity generators and possibly energy storage systems interconnected to a distribution network that supplies electricity to a small, localized group of customers and operates independently from the national transmission grid. Mini-grids range in a size from a few kilowatts up to 10 MW (Introduction to Mini-grids, n.d.). Higher energy consumption levels imply that mini-grids more so solar photo voltaic technology mini-grids become an economically attractive option and replace stand-alone solar photo voltaic technologies in many settlements hence increasing their overall contribution to achieving access to electricity for all Ugandans by the year 2030.

The contributory cost of the solar photo voltaic and wind renewable technologies in ensuring access to electricity for all Ugandans by 2030, ranges between \$0.63 billion and \$1.24 billion by the year 2030. The lower a household's electricity consumption, the lower the overall investment needed to achieve access to electricity for all by the year 2030 though this can peak at a certain high consumption (as captured in Fig. 5) and thereafter dip.

Considering the solar PV and wind renewable energy technologies, the lowest-cost investment ticket for achieving access to electricity for all Ugandans by the year 2030 corresponds to scenario 4 below where consumption is assumed to be at tier 5 for urban, and tier 4 for rural. The highest investment cost on renewable energy technologies corresponds to the household consumption (tier 4 for urban, and tier 3 for rural) in scenario 3 below. When the consumption levels are low, the considered renewable energy sources will be used to provide electricity to an average of 16% of the population. However, increasing the energy consumption level to tier 5 for urban and tier 4 for rural (scenario 3) reduces the average contribution of the considered renewable sources to 10% of the population (Figs. 6–9).

Case Study Conclusion

The case study shows there is huge room for trade expansion with 89 out of 96 trading partners in the scope of this article. There appears to be a great urgency for Uganda to pursue consumption of Climate Smart Energy Technologies which not only will contribute to economic growth but also will reduce the impacts of climate change in Uganda. Taking advantage of opportunities at hand will require several fundamental policy interventions.

Conclusion

Many pertinent considerations arise for siting a renewable energy resource. For example, does the site allow for interconnection to the electrical grid and transmission of the energy generated? How suitable is the land where the facility will be physically located? What impacts should be expected on surrounding land, water, and wildlife? How will the facility affect the local community? A wide range of legitimate concerns give rise to local opposition to new energy infrastructure of whatever kind, from the local environmental and health effects of a facility, to environmental justice in site selection, to perceived impacts on surrounding property values and esthetic considerations. The answers to these questions are inevitably both resource and site specific.

Despite work in technology transfer, there remains difficulty in developing countries to recruit individuals that understand and can interpret the science of climate variability. The ability to understand and effectively communicate potential future climate-based scenarios to decision makers are thus critical success factors for adaptation and mitigation strategies (Noe et al., 2007). This capacity resides with human resources. It is impossible to adapt to climate change without linking the process up with people who take the decision that impairs or makes the environment.

Table 3 Trade potential of Climate Smart Energy Technologies for Uganda.

Country	Group	Speed of convergence (SC)	Difference between potential and actual trade (ΔT) in USD	Situation ^a
Australia	I	-96.55884055	1,633,363,638	1
Belgium	I	-99.69590993	797,280,072	1
Brazil	I	-99.96448166	14,457,026,853	1
Canada	I	-59.09686745	2,504,358,732	1
China	I	-99.11825893	97,524,257,622	1
Denmark	I	-99.98836441	403,259,636	1
Egypt	I	-97.64907368	6,316,452,409	1
Germany	I	-99.16929136	5,889,288,756	1
India	I	-97.59404133	90,793,718,158	1
Japan	I	-100.0986463	9,248,707,349	1
Kenya	I	-56.34141495	3,112,175,268	1
Netherlands	I	-98.27122292	1,206,182,363	1
South Africa	I	-97.25931543	3,812,244,157	1
Sweden	I	-99.94855981	686,723,703	1
Switzerland	I	-99.67349549	575,749,971	1
Thailand	I	-86.7809283	4,898,939,742	1
United Arab Emirates	I	-53.67132451	589,490,472	1
United Kingdom	I	-98.06931269	4,591,128,434	1
United Rep. of Tanzania	I	-99.93677017	3,513,456,318	1
United States	I	-95.18818015	22,643,084,164	1
Rwanda	II	-102.660479	772,701,301	1
South Sudan	II	-103.6529329	767,678,296	1
Austria	III	-99.58776032	612,110,009	1
Bulgaria	III	-98.33925205	531,183,302	1
Croatia	III	-99.33084855	312,568,205	1
Cyprus	III	-102.7160146	81,461,359	1
Czechia	III	-99.83765506	759,077,449	1
Estonia	III		96,063,652	
Finland	III	-99.66304625	390,988,676	1
France	III	-99.72773559	4,738,450,640	1
Greece	III	-99.06070095	796,293,321	1
Hungary	III	-100.0172559	720,424,752	1
Ireland	III	-99.98073003	331,470,375	1
Italy	III	-99.45872772	4,321,899,616	1
Latvia	III	-98.72139645	149,656,815	1
Lithuania	III		220,051,121	
Luxembourg	III	-102.2160119	38,164,333	1
Poland	III	-100.0565882	2,757,106,966	1
Portugal	III	-100.0018503	759,157,217	1
Romania	III	-99.35448394	1,461,005,237	1
Slovakia	III	-100.180092	391,338,546	1
Slovenia	III	-100.2560155	148,444,132	1
Spain	III	-99.98153182	3,358,542,572	1
Bolivia (Plurinational State of)	IV	-101.5964177	736,267,771	1
Colombia	IV		3,376,017,629	
Mexico	IV	-102.9024267	8,683,819,226	1
Panama	IV		271,138,358	
Angola	V	-103.5784596	1,793,977,558	1
Botswana	V	-118.7203547	150,372,308	1
Dem. Rep. of the Congo	V	-103.3721217	4,937,302,250	1
Ethiopia	V	-102.6393968	6,625,181,285	1
Gabon	V	-103.2149558	125,422,762	1
Ghana	V	-102.4426116	1,843,149,193	1
Jamaica	V	-100.4169091	205,234,040	1
Lesotho	V	-101.6444885	150,805,024	1
Mauritius	V	-99.84672646	90,022,661	1
Mozambique	V	-102.9519482	1,839,635,234	1
Namibia	V		163,528,779	
Niger	V	-103.8862508	1,268,605,943	1
Nigeria	V	-99.98380572	11,994,848,229	1

Table 3 Trade potential of Climate Smart Energy Technologies for Uganda.—cont'd

Country	Group	Speed of convergence (SC)	Difference between potential and actual trade (ΔT) in USD	Situation ^a
Senegal	V	–102.9402951	982,585,648	1
Seychelles	V	–101.2125216	6,477,774	1
Sierra Leone	V		485,205,452	
Sudan	V	–102.2899945	2,588,585,231	1
Swaziland	V	–101.8539486	89,724,707	1
Zambia	V	–103.2071387	1,054,622,376	1
Zimbabwe	V	–102.1557494	1,059,920,192	1
Azerbaijan	VI	–101.4384801	667,890,662	1
Georgia	VI	–98.9726722	280,094,468	1
Iceland	VI	–100.8254476	23,347,366	1
Norway	VI	–98.96866596	360,834,346	1
Russian Federation	VI	–100.1190829	10,384,318,355	1
Serbia	VI	–99.50373742	523,344,597	1
Turkey	VI	–99.99855446	5,372,589,262	1
Ukraine	VI	–99.63530156	3,310,746,096	1
Bangladesh	VII		11,226,348,204	
Indonesia	VII	–99.99489609	17,911,950,369	1
Iran	VII	–99.66933632	5,510,873,878	1
Israel	VII	–99.72990242	568,161,586	1
Jordan	VII	–104.8167573	565,849,432	1
Kuwait	VII	–105.5045216	238,599,335	1
Lebanon	VII	–99.99876618	353,972,023	1
Malaysia	VII	–99.21411133	2,094,590,191	1
Nepal	VII	–101.1215592	1,995,340,779	1
Pakistan	VII	–163.1107041	12,778,441,700	1
Philippines	VII	–102.0337769	6,968,878,597	1
Qatar	VII	–99.85455335	142,410,995	1
Rep. of Korea	VII	–102.0171838	3,623,504,924	1
Saudi Arabia	VII	–99.58644627	2,080,748,701	1
Singapore	VII	–96.65587599	376,193,858	1
Sri Lanka	VII	–100.7576486	1,480,310,748	1
Syria	VII	–99.32641961	1,443,849,360	1
Viet Nam	VII	–99.96733798	6,526,293,286	1
Br. Virgin Isds	VIII	–102.4202754	1,958,383	1
New Zealand	VIII	–101.1790888	320,051,993	1
Tunisia	VIII	–99.96681642	785,007,791	1

^aNote: 1 and 0 denote convergence and divergence respectively. Group I includes the main trading partners of Climate Smart Energy Technologies of Uganda, Group II includes East African Community (EAC) countries, Group III includes members of the European Union (EU), Group IV includes American countries, Group V includes countries in African, Caribbean and Pacific (ACP) membership, Group VI includes Non-EU European countries, Group VII includes Asian countries while Group VIII is classified as other countries.

Source: Author's calculation.

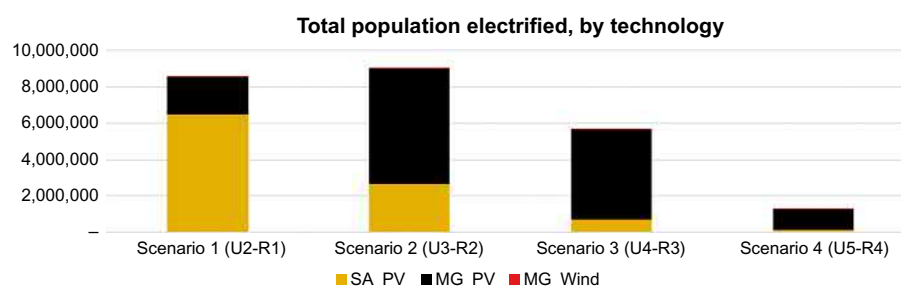


Fig. 2 Total population electrified, by technology. *Note:* Ux–Rx refers to the electrification tier for urban and rural settlements, respectively (Table 1). Source: Author's simulation.

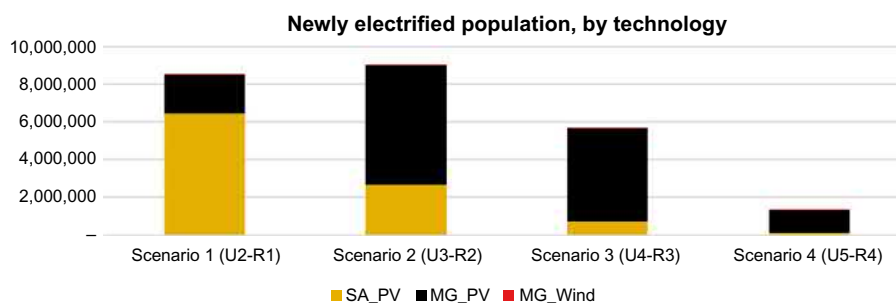


Fig. 3 Newly electrified population, by technology. *Note:* Ux–Rx refers to the electrification tier for urban and rural settlements, respectively (Table 1). Source: Author's simulation.

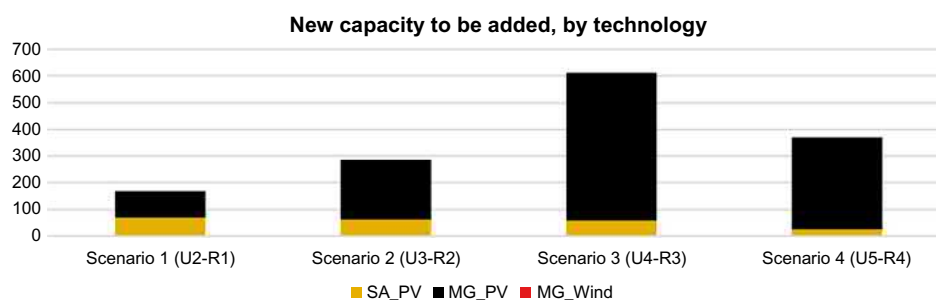


Fig. 4 New capacity (in Megawatts) to be added, by technology. *Note:* Ux–Rx refers to the electrification tier for urban and rural settlements, respectively (Table 1). Source: Author's simulation.

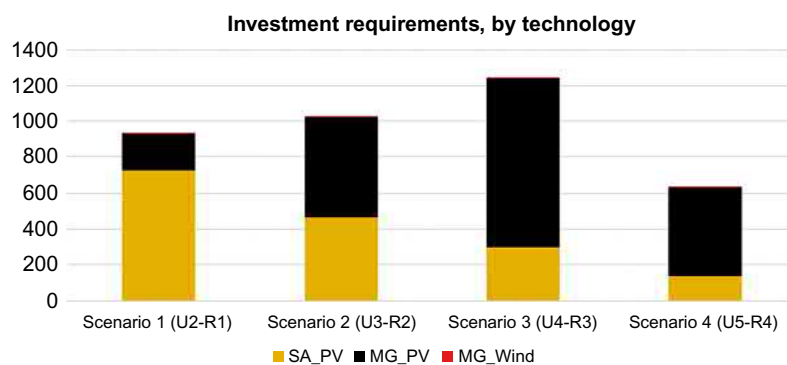


Fig. 5 Investment requirements (in million US Dollars), by technology. *Note:* Ux–Rx refers to the electrification tier for urban and rural settlements, respectively (Table 1). Source: Author's simulation.

To train people for climate change adaptation and mitigation is critical to the success of the campaign on environmental sustainability with climate change. Although the training should be goal-driven, the output is largely determined by the input of the trainee. Awareness and educational capacity reflect on the expected input of the trainee. Therefore, one should be exposed to challenges and allowed a robust level of latitude to contribute toward dealing with the problems. The robustness makes for creativity. However, the capacity building approach to climate change adaptation and mitigation has a long gestation period as a setback.

Legislation alone cannot offer all the solutions of climate change adaptation and mitigation. There is need to focus on the attitude and commitment of people who operate the policies. The future challenge for the educational and energy technology policies perhaps is implementation. The more the implementation is devoid of corrupt tendency the farther the project of advancing climate change resilience will be on its road to success.

SCENARIO 1: U2 - R1

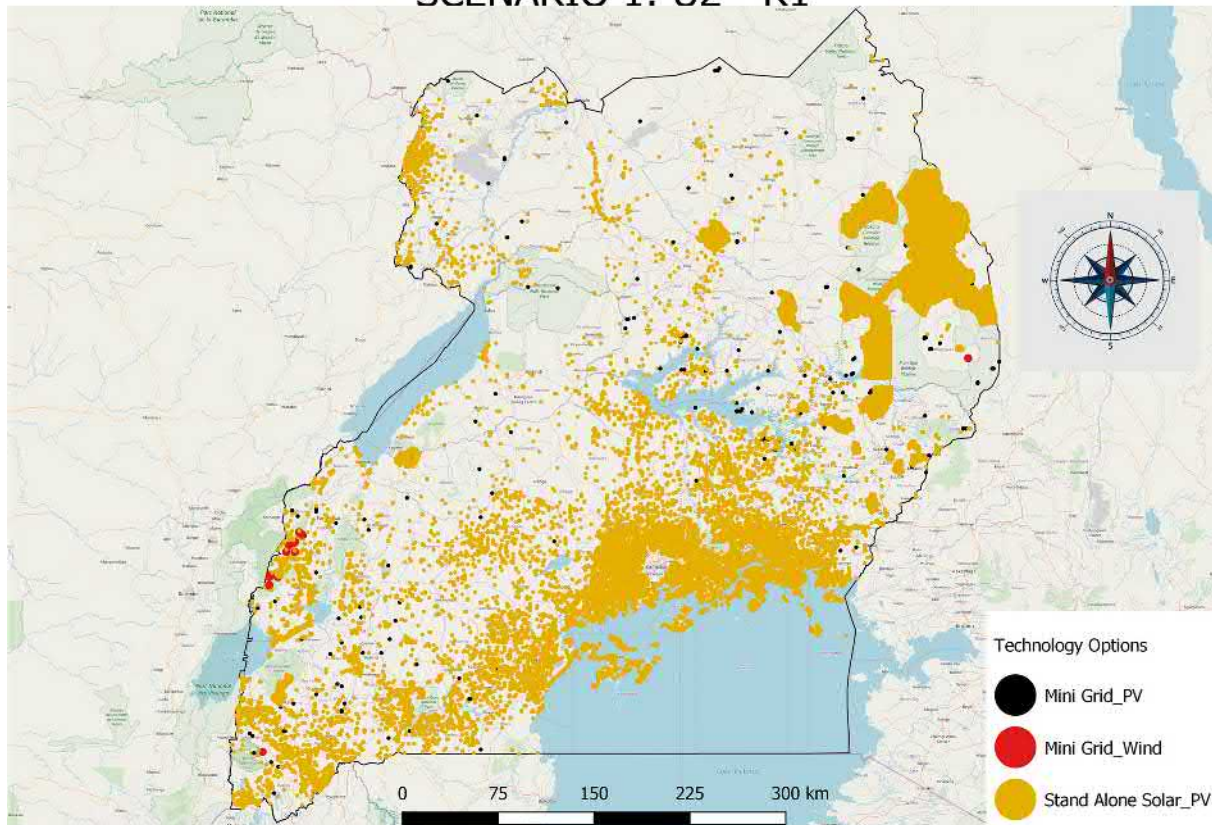


Fig. 6 Scenario 1 (U2-R1).

SCENARIO 2: U3 - R2

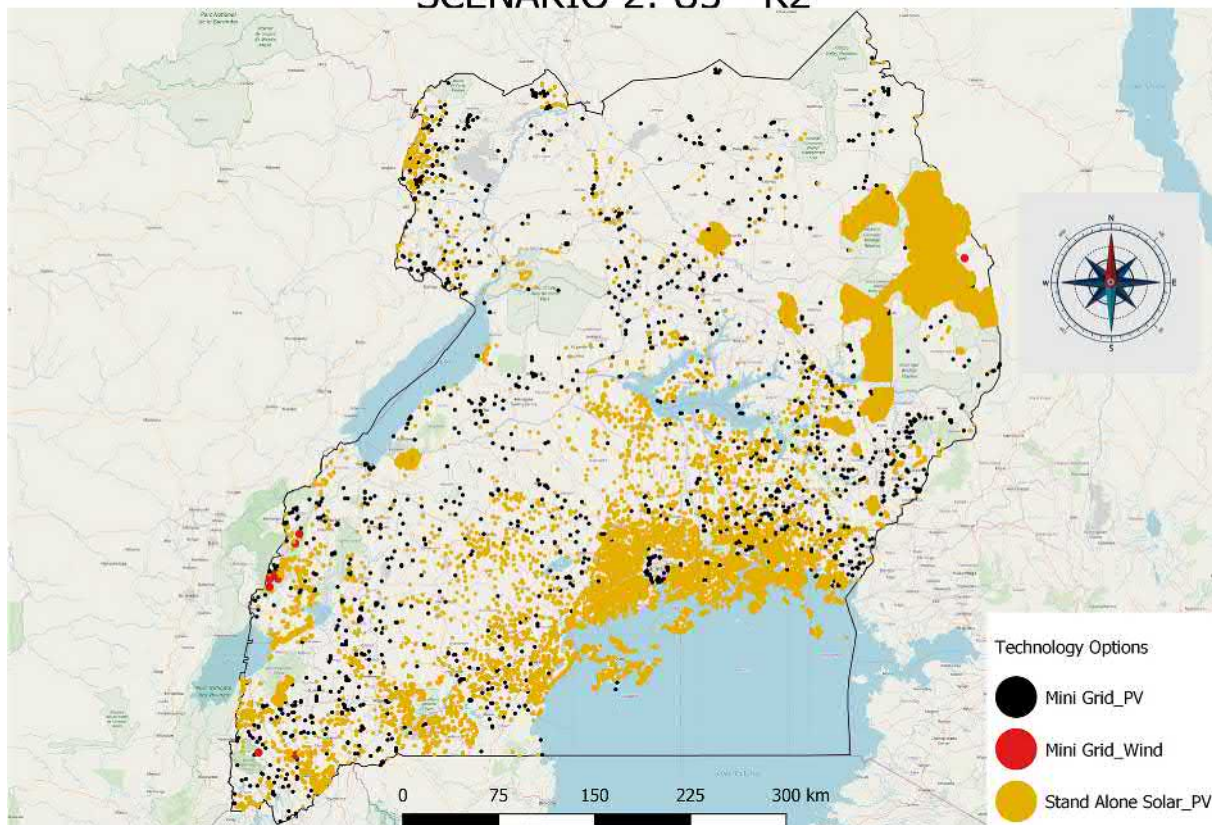


Fig. 7 Scenario 2 (U3-R2).

SCENARIO 3: U4 - R3

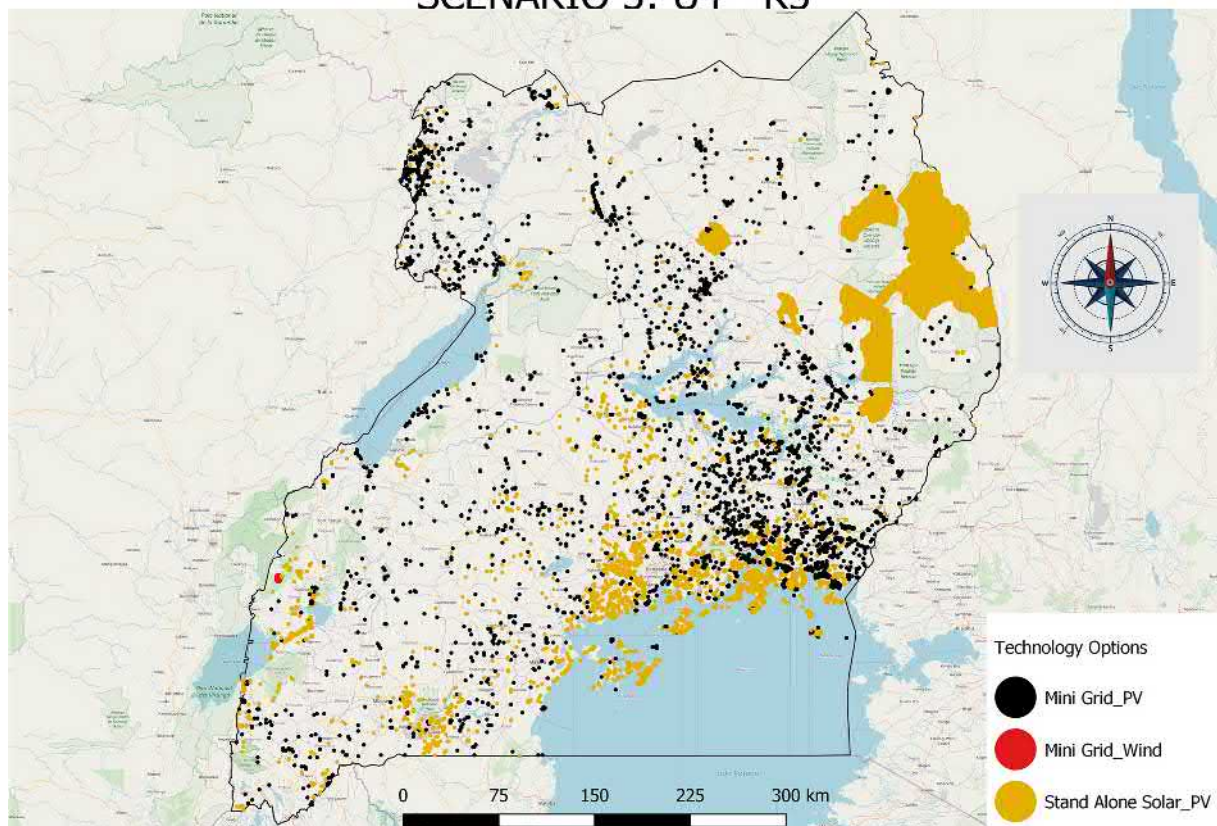


Fig. 8 Scenario 3 (electrification results under the scenario are defined by urban demand at tier 4 and rural demand at tier 3).

SCENARIO 4: U5 - R4

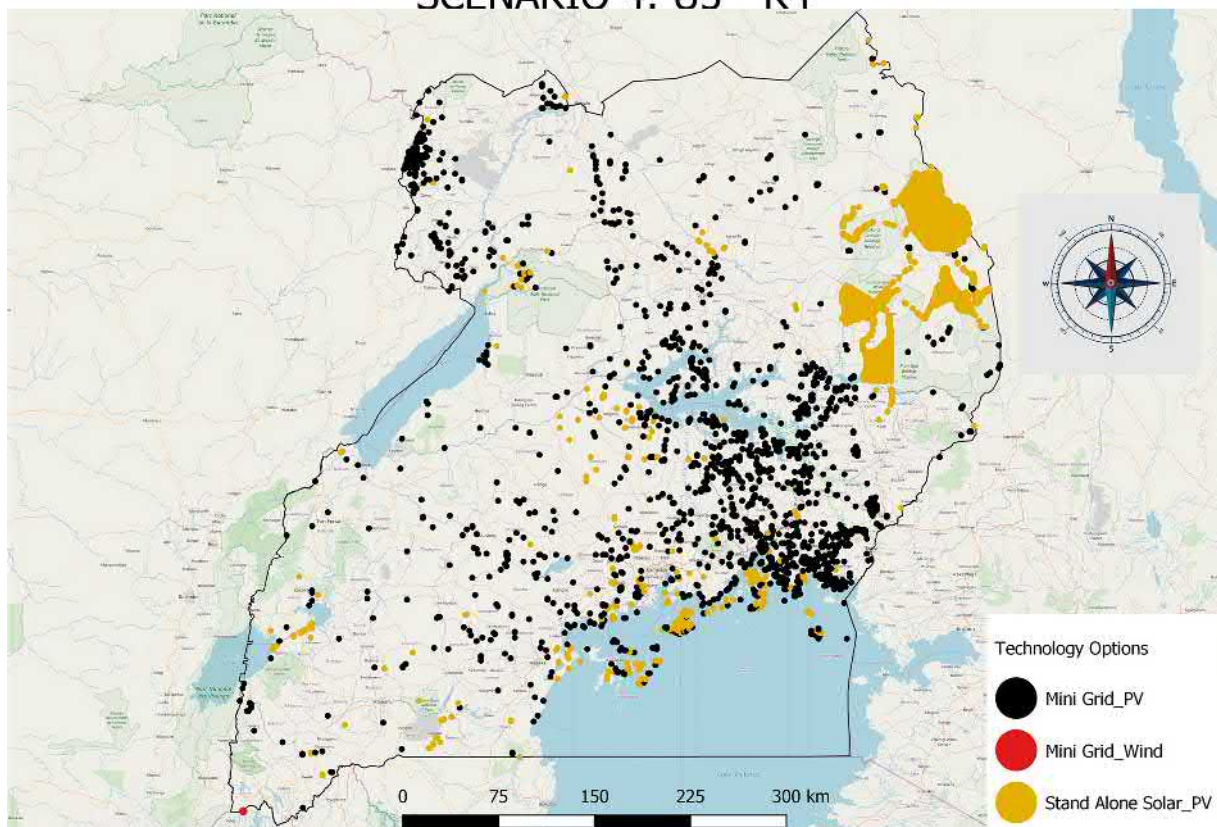


Fig. 9 Scenario 4 (U5-R4).

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Developed Systems in the Mariana Islands Archipelago

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Published by Elsevier Inc.

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Abstract

This article represents a status assessment of the Mariana Islands developed system, including the current status, stressors, and future viability. Developed systems within the Marianas Archipelago exist where there are human populations, primarily focused on the coasts of Guam, Saipan, Rota, and Tinian Islands. The quality of the developed system is largely composed of a mixture of nonnative vegetation types, and predominantly nonnative wildlife. Our assessment of the developed system viability, defined as the likelihood of persistence over the long term, is based on the concepts of representation, redundancy, and resiliency. The main stressors to developed systems are effects of climate change, additional development, typhoons, pollution and invasive species. Ongoing conservation efforts are helping to protect plants and wildlife within developed systems, and the conservation depends largely on combined efforts of State, Federal, multiagency organizations, nonprofit organizations, and the voluntary support of private landowners. The Marianas developed system represents a unique land use type, whose composition is dynamic across its range. Due to growing human population numbers, the developed system is likely to decrease in size over the coming years, as development increases. Projections for the persistence of developed systems in the Marianas largely depends on the conservation actions taken, which should be implemented to safeguard pockets of biodiversity found within these systems.

Introduction

The geography, geology, climate, hydrology and descriptions of the islands in the Marianas archipelago are described in the Physical Geography of the Mariana Archipelago by Harrington included in this work. However, what the above factors lack is how land use and land cover change also reflect the role of human population density and land use intensity. Across the Marianas archipelago increasing population and land use intensity has resulted in a shift in the landscape towards dense settlement and populated anthromes (Ellis et al., 2010).

This document provides an overview of the developed system in the Mariana Islands Archipelago (Marianas) and describes the ecological factors that have influenced this system over time and into the future. It provides an assessment of the system, its current status, stressors, conservation efforts, and future viability. Developed systems can occur in any location on the islands but, are primarily located in coastal areas where the majority of the human population resides. This system type displays varying amounts

of vegetation, impermeable surfaces (e.g., roads, parking lots, buildings), and permeable surfaces, and can range from small farms to homes, and dense commercial development. Developed systems are generally dominated by nonnative and, often, invasive species. The vegetation is actively managed and generally maintained through planting, irrigation/artificial watering, and/or mowing.

The Marianas archipelago consists of the island of Guam in the south, and the remaining islands stretching northward in the archipelago are the Commonwealth of the Northern Mariana Islands (CNMI). The island of Guam is an unincorporated territory of the United States and the CNMI is an insular area and commonwealth of the United States. The majority of the human population currently resides on the southern islands of Guam, Rota, Tinian, and Saipan (Fig. 1A–C).

The amount of developed area is associated with human populations found on each of the islands across the Marianas. Due to the population sizes, Guam and Saipan have the largest amount of developed area both, in absolute size, and relative to land mass, followed by Rota and Tinian (Figs. 1 and 2). The remaining islands have less than one acre of developed area. The developed system is defined as the ecological area within developed areas, and is comprised of planted landscape, farmland and agricultural areas, and remnant grass and forest patches distributed throughout the landscape. The developed system is defined as containing impermeable man-made surfaces, landscaped areas, active cropland areas, roads, towns, parks, golf courses, airstrips, quarries, and military facilities, being highly influenced by ongoing human activities, typically with < 10% vegetative cover. While much of the developed system is comprised of nonnative vegetation, small remnant areas of native vegetation may exist. Our assessment of developed system viability, defined as the likelihood of persistence over the long term, is based on the concepts of representation, redundancy, and resilience.

Stressors to developed systems reduce the quantity and quality of vegetation, but also may result in an expansion of the system, especially to the currently unoccupied islands. Naturally occurring stressors including typhoons and drought have and will continue to impact the developed systems. Remnant forest areas that have not been developed, are dispersed throughout the landscape. There are also many planted landscapes that are primarily comprised of nonnative vegetation. The primary stressor in the developed system is the construction of impermeable surfaces and buildings which reduce the quantity of vegetation. The conservation of these systems depends on combined efforts of Territory, Commonwealth, Federal, multiagency organizations, private landowners, and passive/social management through policies, laws, and land protections.

We developed four plausible future scenarios, each differing in their levels of natural resource management, to evaluate the status of developed systems into the future. The future scenarios are based on analyses of land cover changes documented in geospatial layers for the time period until 2035. Scenario one is essentially “status quo” continuing for the foreseeable future, which means we envision no change in the three conservation management parameters: conservation values, conservation and biosecurity-related laws, and Territorial/civic planning for development to the year 2035. Scenario two is essentially “status quo” with minor improvements in the three conservation management parameters. In scenario three, all actions of conserving native habitats and their ecosystems are set aside in deference of economic development, and small areas are maintained as conservation parcels. Scenario four envisions a foreseeable future with substantial declines in the three conservation management parameters. Scenario four

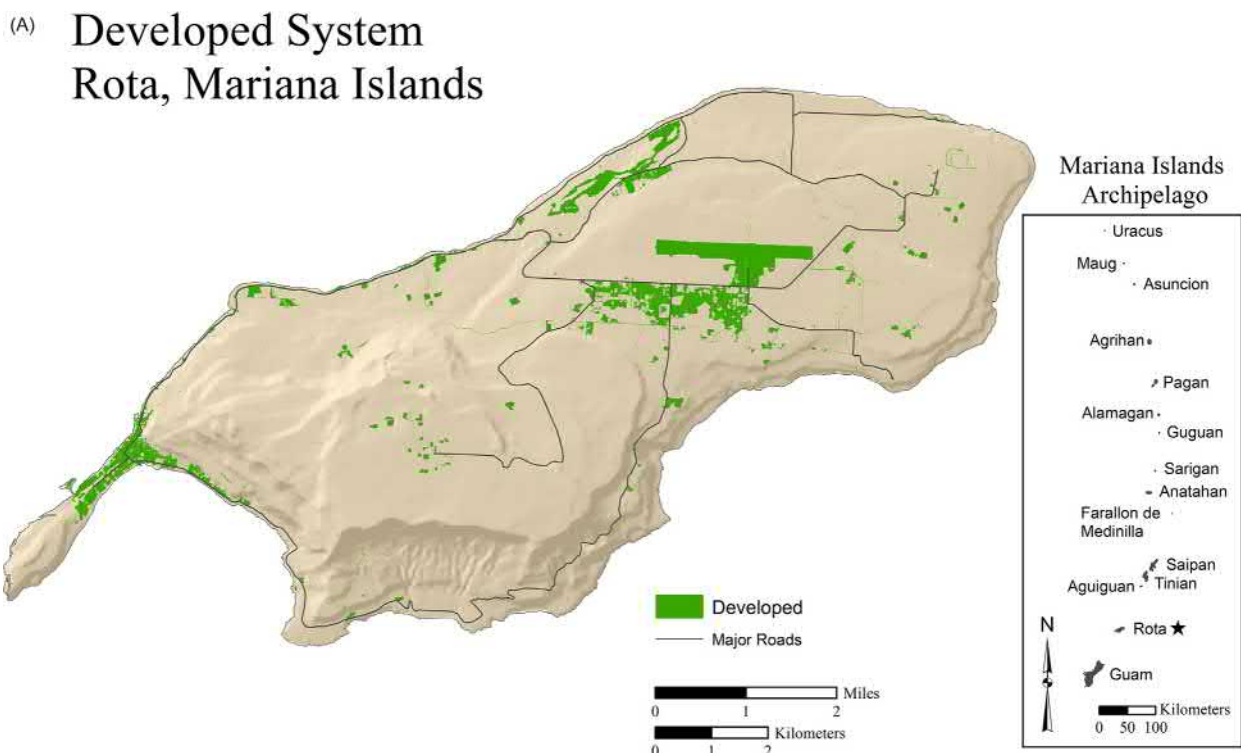


Fig. 1 Developed system across the Marianas on the islands of (A) Rota, (B) Tinian and Saipan, and (C) Guam (Reeves and Amidon, 2018).

(B)

Developed System Tinian and Saipan, Mariana Islands

Developed
Major Roads



Mariana Islands Archipelago



Fig. 1 (continued).

(C) Developed System
Guam, Mariana Islands

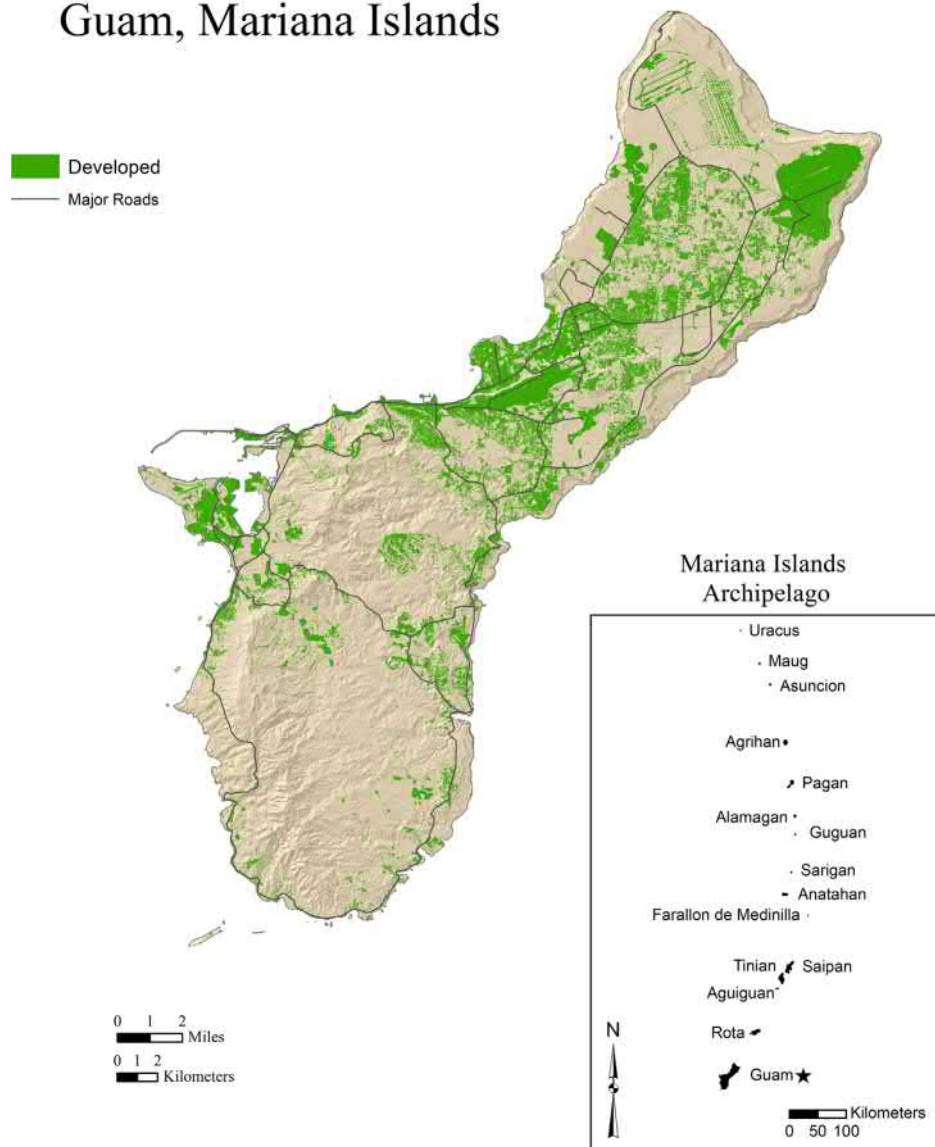


Fig. 1 (continued).

represents an overt and robust, active, ongoing conservation effort (seeking moderate to major resources) to (a) identify and prioritize, with partners and stakeholders, the habitats and ecosystems needed for conservation, and (b) actively restore and expand these habitats and ecosystems. Scenario four envisions a foreseeable future with substantial improvement to the three conservation management parameters.

Developed System Description

The vegetation included in developed systems may consist of a wide variety of trees, shrubs, grasses and other vegetation that is primarily nonnative. This vegetation is present in urban or residential areas that are generally adjacent to impervious surfaces and trail corridors, grown in spaces beside houses and buildings and as part of landscaped, open space areas. Developed systems also include actively managed cropland and fields that are generally maintained through planting, irrigation or mowing such as golf courses and landscaped businesses and residences.

In addition to natural rainfall patterns, vegetation in developed systems is often highly supplemented by artificial irrigation. Both rainfall and artificial watering have the potential to increase runoff and ponding areas along impervious surfaces throughout

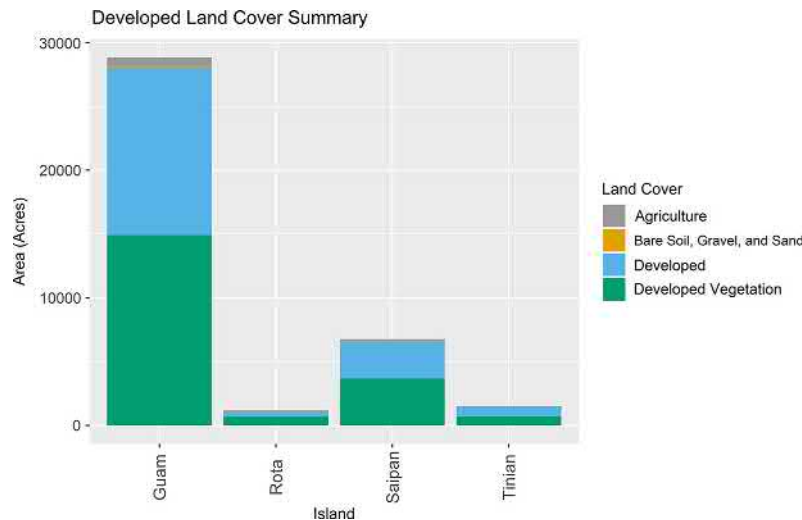


Fig. 2 Land cover types within developed systems across the Marianas on the islands of Guam, Rota, Saipan and Tinian (Reeves and Amidon, 2018).

developed and urban areas. The amount of water available and retained can vary based on the substratum. The developed system has the potential to exist in any type of substratum across the volcanic or limestone areas of the archipelago. Some examples of these soil types include shallow, well drained, moderately rapidly permeable soils in limestone whereas other volcanic soils can be very deep, somewhat poorly drained, moderately slowly permeable soil with moderate to very high water holding capacity (College of Natural and Applied Sciences (CNAS), 2018).

Categories of Developed Systems

Developed systems include the following four landcover types: (1) developed, (2) developed vegetation, (3) bare soil/gravel/rock, and (4) cropland (Table 1). Developed areas include buildings and impervious surfaces (Amidon et al., 2017). Developed vegetation includes manicured lawns, golf courses, parks, and ornamental vegetation. Bare soil and gravel habitats are primarily comprised of quarries and consolidated formations. Croplands include all irrigated plots of land that were cleared for the production of various crops, as well as fallow agriculture fields. Vegetation in developed systems includes a wide variety of species including various well-pruned native and nonnative trees, grasses, and shrubs. Since the majority of vegetation in this system was intentionally planted either for agricultural or ornamental purposes, developed systems tend to be dominated by nonnative species.

Vegetation Composition and Biodiversity

Cropland areas within developed systems may be limited to one vegetation type as a commercial crop or small family farms with a variety of crops including vegetables, melons, root crops, fruits, nuts, coconuts, and nursery crops. Many of these crop types are cultivated in lateritic soils on Guam, which are rich in iron oxide and derived from a wide variety of rocks weathering under strongly oxidizing and leaching conditions (Moore and McMakin, 1979). These various types of agriculture are not necessarily represented by consistency in structure since production on small family farms varies widely. The most common types of crops grown in cultivated lands are tomatoes, bananas, sorghum, watermelons, green onions, eggplants, and cucumbers (United States Department of Agriculture (USDA), 2006; Wiles et al., 1990). The warm year-round climate in the Marianas combined with high levels of humidity, make these islands hospitable for a number of native and nonnative plant species. For example, the island of Guam is home to over 600 species of vascular plants, and more than 100 different tree species (United States Department of Agriculture (USDA), 2006).

The vegetation composition of developed systems usually ranges from barren areas to vegetated areas, and may be very low in species diversity, with limited canopy cover, if any (GIS GAP, <https://gapanalysis.usgs.gov/gaplandcover/data/>). In addition, species composition changes in urban environments such that the number of nonnative species increases and native species decreases (McKinney, 2002). The species most affected by invasion of nonnative species are the endemic species, likely because they have evolved on islands and show the least competitive ability (Lee, 1974). Palm trees are commonly cultivated in urban areas, due to their relatively low maintenance and small footprint. Grassed areas such as golf courses and soccer fields are also common in developed areas. Due to developed areas resulting from modern human modification, no prehuman condition exists for developed system areas.

Table 1 Developed system categories (Amidon et al., 2017).

Category	Description
Developed	All buildings (concrete and other materials), paved surfaces, and roads. Gravel roads are generally included in this category as well.
Developed vegetation	Includes lawns and mowed areas as well as ornamental and shade trees and shrubs. Parks, golf courses, and residential open spaces are also included.
Bare soil/gravel/rock	All consolidated formations such as rock and quarries.
Cropland	All agriculture fields and sites planted for agriculture, including recently cleared or planted lands, as well as managed fallow fields. Agricultural trees and shrubs planted in rows are also included.

Vegetation in developed systems is primarily planted and maintained with human influence. However, there are a variety of sources of natural recruitment and dispersal. Pockets of remnant forest exist in urban areas, providing a source of seeds. Wind plays a major role in spreading prolific seeds of invasive plants throughout the islands, as does wildlife that traverses the area. Invasive plants such as ivy gourd (*Coccinia grandis*) are presumably spread throughout the developed systems by birds and invasive mammals.

Fauna found in developed systems may consist of many of the same species found in more natural areas (birds, insects, bats) but are limited by availability of foraging and nesting resources and by the effects of habitat fragmentation in the large spaces created between individuals and populations. For example, roads favor species with expanded dispersal abilities in disturbed habitats at the expense of species with limited mobility. Research has shown that development and urbanization has the ability to alter ecological processes (Moll et al., 2019). Habitat fragmentation may pose barriers to animal movement, while increasing the connectivity of disturbed sites promoting the spread of nonnative weeds, pests, and pathogens (Noss et al., 2006). The fauna in developed systems within the Marianas consists primarily of nonnative mammals, including pigs (*Sus scrofa*), deer (*Rusa marianna*), shrews (*Suncus murinus*), snakes (*Boiga irregularis*), domestic cats (*Felis catus*), and dogs (*Canis lupus familiaris*), and rats (*Rattus* spp.) (Wiles et al., 1990), and birds, including Eurasian tree sparrow (*Passer montanus*), black drongo (*Dicrurus macrocercus*), and Philippine turtle-dove (*Streptopelia bitorquata*; Engbring and Ramsey, 1984; Engbring et al., 1986). Among the plant species recommended by the CNMI government for disturbed areas in developed systems, are sumac (*Aidia cochinchinensis*), Niyoron (*Cordia subcordata*), Alum (*Melanolepis multiglandulosa* var. *glabrata*), Lada (*Morinda citrifolia*), Amahadyan (*Pipturus argenteus*), and Ahgoa (*Premna obtusifolia*) (Zarones, 2014).

Current Condition

There is a wide range of development across the Marianas which is primarily correlated with human population. Guam and Saipan are the most populated islands across the island chain and thus have the largest percentage (21% and 23% respectively) of developed area (Figs. 1 and 2; Tables 2 and 3) relative to their size. On Guam developed areas are largely concentrated in the northern

Table 2 Amount of developed areas in the Marianas represented by absolute area per island (acres), percentage of developed area relative to island size and percentage of developed area relative to the entire archipelago (Reeves and Amidon, 2018).

Island	Categories	Area (Acres)	Area (% of Island)	Area (% of Archipelago)
Alamagan	Developed	<1	<1	<1
Agrihan	Developed	<1	<1	<1
Rota	Agriculture	108	1	<1
	Bare soil/gravel	21	<1	<1
	Developed	365	2	<1
	Developed vegetation	687	3	<1
Tinian	Agriculture	77	<1	<1
	Bare soil/gravel	9	<1	<1
	Developed	749	3	<1
	Developed vegetation	707	3	<1
Saipan	Agriculture	131	<1	<1
	Bare soil/gravel	64	<1	<1
	Developed	2908	10	1
	Developed vegetation	3684	13	1
Guam	Agriculture	672	<1	<1
	Bare soil/gravel	144	<1	<1
	Developed	13,125	10	5
	Developed vegetation	14,909	11	6

Table 3 Census estimates of the human population on the islands on Guam, Rota, Tinian, Saipan, and the Northern Islands of the CNMI.

Year	Guam	CNMI				CNMI total
		Rota	Tinian	Saipan	Northern Islands	
1920	13,275 ^a	—	—	—	—	5159 ^b
1925	—	—	—	—	—	8800 ^b
1930	18,509 ^c	—	—	—	—	19,496 ^b
1935	—	—	—	—	—	44,043 ^b
1940	22,290 ^c	—	—	—	—	—
1950	59,498 ^c	—	—	—	—	6286
1958	—	969 ^d	405 ^d	7321 ^d	262 ^d	8290
1960	67,044 ^c	—	—	—	—	—
1970	84,996 ^c	895 ^d	710 ^d	7967 ^d	68 ^d	9640
1980	105,979 ^c	1261 ^d	866 ^d	14,549 ^d	104 ^d	16,780
1990	133,152 ^e	2295 ^f	2118 ^f	38,896 ^f	6 ^f	43,315
2000	154,805 ^g	3283 ^h	3540 ^h	62,392 ^h	6 ^h	69,221
2010	159,358 ^g	2527 ^h	3136 ^h	48,220 ^h	0 ^h	53,883

References for population estimates are noted and totals for the CNMI without a reference are the sum of the estimates from Rota, Tinian, Saipan, and the Northern Islands.

^aU.S. Census Bureau (1932).

^bUnknown (n.d.).

^cU.S. Census Bureau (1982a).

^dU.S. Census Bureau (1982b).

^eU.S. Census Bureau (1992a).

^fU.S. Census Bureau (1992b).

^gU.S. Census Bureau (2010a).

^hU.S. Census Bureau (2010b).

portion of the island, while on Saipan developed areas are concentrated on the southern portion of the island. The islands of Rota and Tinian are much less developed with approximately 5–6% developed habitat on each island (**Table 2**). On Rota the developed area is largely limited to Songsong and Sinapalu, and on Tinian development is limited to San Jose. Development, as a result of population increases, has led to pockets of dense tree vegetation in some urban areas, open grassy areas in parks and yards, and numerous palm trees and shrubs along coastal areas. Agriculture makes up <1% of total island area on any of the Marianas (**Table 2**).

System Viability

Systems sustain their existence through resiliency, redundancy, and representation. The viability of developed systems depends on maintaining multiple, distributed system types (redundant) of sufficient quality and size (resilient) with species richness and genetic range (representative) to survive across its ecological range over time. Representative systems are those not restricted to particular locations but are scattered throughout the islands. Resilience is defined as the amount of disturbance that the system can absorb without a lasting change in structure and composition ([Holling, 1973](#); [Carpenter et al., 2001](#)). Redundancy refers to the extent and range of a system across a given landscape, and redundancy of multiple resilient systems can decrease the risk of loss. Developed system disturbances include forces such as typhoons and sea level rise, as well as anthropogenic stressors. Constrained or limited areas, with less representation across the islands, are less resilient to catastrophic events that might otherwise have a relatively minor impact on widely-distributed systems ([Stacey and Taper, 1992](#)).

Stressors

Development

Economic development and associated construction has, and continues to impact, the vegetation within developed systems across the Marianas. The construction of buildings and facilities associated with public infrastructure (e.g., fresh water, sewage treatment, etc.) have the potential to convert developed vegetation, bare soil, and croplands to developed impervious surfaces and structures. Development across the Marianas is primarily correlated with human population size. Developed land areas are currently most prevalent in the southern, more populated islands whose local economies depend on construction and real estate, both privately and associated with the US military ([ICF International, 2009](#); [PEGS, 2018](#)). At least a third of the island of Guam is occupied by the United States military, which includes a variety of land use types including many developed and developed vegetation areas ([Owen, 2010](#)). The military buildup on both Guam and Tinian also increases the likelihood of introducing invasive species, and the

development of additional land areas throughout the Marianas (Marler, 2013). Creating more developed habitat and importing of equipment increases the likelihood of invasive species being introduced, or spreading among islands in the archipelago. Brown tree snakes (*Boiga irregularis*) were introduced to Guam around 1949 as a result of movement of military assets among islands, and continue to have devastating long-term effects on ecosystems and biological composition on the island (Rodda and Savidge, 2007). A loss of pollinators due to brown tree snake predation, has the ability to affect the resiliency and representation of developed vegetation across Guam.

Invasive Species

Many invasive species are established in the Marianas and impact both developed systems, as well as the organisms that utilize the developed vegetation within these systems (Table 4). Urban areas are hotspots for biological invasions, and while additional invasive species may be present, their range and effects have not yet been fully investigated. Many common invasive plants (e.g., *Bidens alba* and *Antigonon leptopus*) thrive in developed habitats across the Marianas because they can survive harsh urban climates, while collecting water from impervious surfaces. Brown tree snakes are prevalent throughout the developed habitats of Guam, and their invasion has led to the near extirpation of a number of native bird, bat, and invertebrate species (Rodda and Savidge, 2007). The Coconut Rhinoceros Beetle (CRB) (*Oryctes rhinoceros*) has had devastating effects on coconut palm trees (*Cocos nucifera*) in developed areas on Guam and Rota, and was likely introduced to Guam with construction materials arriving from Asia (USDA, 2008). Their persistence in the environment may have been driven by the absence of insectivorous birds and mammals, as a result of their predation by brown tree snakes (Moore et al., 2015). The near extirpation of insectivorous birds on the island of Guam has led to a disproportionate number of spiders, with an average of 18.37 spider webs per 10 m on Guam, compared to 0.45 webs per 10 m on nearby developed islands with birds (Rodgers et al., 2012). Invasive ungulates such as pigs and goats graze many islands in the Marianas archipelago, including unfenced croplands in developed systems. They have a notable effect on the abundance and diversity of native plant species within these areas. Their eradication from the islands of Sarigan and Anatahan led to an increase in tree species richness and density, with a composition changing towards a more native and diverse ecosystem (Kessler, 2011). Following ungulate removal, open grass areas were filled with saplings and small trees, leading to 100% ground cover and dense closed canopy. The overall density of tree species increase from 1.48 trees/100 m² to 13.70 trees/100 m² in just 7 years.

Typhoons

The Marianas lie in a region with a high propensity for tropical cyclones (aka Pacific Typhoon Belt) and are therefore, regularly exposed to typhoons. Typhoons cause a variety of impacts to the environment including pruned or downed vegetation from intense wind, defoliation, heavy rain, flooding, and saltwater inundation in low-lying areas (Kerr, 2000). Mortality of any vegetation across

Table 4 Primary invasive species in the Marianas developed systems.

Common name(s)	Scientific name(s)	Primary species affected	How invasive affects the system	Where present	References
Coconut rhinoceros beetle (CRB)	<i>Oryctes rhinoceros</i>	Coconut palms	Loss of vegetation	Guam, Rota	Marshall and Moore (2016)
Invasive ungulates (goats, pigs, Philippine deer)	<i>Capra hircus</i> , <i>Sus scrofa</i> , <i>Rusa marianna</i>	Native vegetation	Soil disruption, increased sedimentation input, compete with native species, deplete natural resources	Guam, Aguiguan, Tinian, Rota, Anatahan, Pagan, Agrigan	Liske-Clark (2015) and Wiles et al. (1990)
Rodents (roof rats, Polynesian rats, Norway rats)	<i>Rattus rattus</i> , <i>Rattus exulans</i> , <i>Rattus norvegicus</i>	Native vegetation, prey on native and nonnative fauna, including birds.	Prevent tree regrowth, damage to crops, compete with forest birds for seeds	All Islands	U.S. Fish and Wildlife Service (USFWS) (2007), Liske-Clark (2015), and Wiles et al. (1990)
Pests (little fire ant, white flies, aphids)	<i>Wasmannia auropunctata</i> , <i>Trialeurodes vaporariorum</i> , <i>Aphis</i> spp.	Agricultural crops and some forestry trees, native vegetation.	Reducing plant vigor	Guam, Rota, Saipan and Tinian	Smith (2004)
Brown tree snake	<i>Boiga irregularis</i>	Birds, bats, lizards, pets	Extirpation of most birds, loss of forest trees due to absence of seed dispersers and pollinators	Guam, Saipan	Rodda and Savidge (2007)

the islands due to a typhoon reduces the quality and resilience of vegetation in developed systems. Typhoons also damage infrastructure and buildings throughout the developed system. Damage from typhoons can open areas for more intense development causing the loss of open space developed vegetation and cropland areas. Additionally, emergency response to typhoons increases the risk of spreading invasive species. Typhoons have the ability to disrupt ongoing conservation efforts to protect endangered species such as the Mariana crow (aka, *Corvus kubaryi*), as was evident when Typhoon Mangkhut, a powerful category 2 storm, hit the island of Rota in September of 2018. The typhoon coincided with the reproductive season for the crow, and severely disrupted the habitat and recovery progress for that species (San Diego Zoo, 2018). In October of 2018 Tinian and Saipan were hit by an extremely powerful category 5 storm, super Typhoon Yutu, which caused widespread damage across the Marianas. The majority of developed structures on Tinian were destroyed, and much of the low-lying vegetation on the island was shredded or uprooted by powerful winds measuring up to 180 mph (295 km/h) (National Hurricane Center (NHC); Hurricane Research Division; Atlantic Oceanographic and Meteorological Laboratory, 2018). The destruction of developed vegetation subunits, which are already fragmented as a result of development, decrease the redundancy and representation of system. The destruction of developed structures and fragmented forest areas may lead to additional development as a result of land being denuded, decreasing the resiliency of the system. Super Typhoon Yutu devastated much of Tinian, including habitat for the Tinian monarch (*Monarcha takatsukasae*), an endemic bird that was removed from the federal list of endangered and threatened wildlife in 2004 (USFWS, 2004). An analysis of vegetation on the island of Tinian following Yutu showed that it caused severe damage and defoliation of vegetation, in habitats utilized by the Tinian monarch (Amidon et al., 2018). The frequency and severity of typhoons in the Marianas are expected to increase as the effects of climate change continue to manifest (Holland and Bruyere, 2014).

Climate Change

According to the Intergovernmental Panel on Climate Change (IPCC), human activities have caused a 1°C increase in temperature above preindustrial levels, and if the current rate of warming remains constant, we could reach an increase of 1.5°C by the year 2030 (IPCC, 2018). Both the size and intensity of large-scale storms are expected to increase in coming years, and recent data demonstrates category 4 and 5 hurricanes have increased at a rate of 25–30% per °C increase in global warming (Holland and Bruyere, 2014). Additionally, ocean warming is causing an increase in recurrent regional coral bleaching events, which have increased fivefold in the last 35 years (Hughes et al., 2018). Combined with ocean acidification, these more frequent bleaching events are expected intensify and lead to mass coral bleaching events, disease, and coral mortality (Hoegh-Guldberg et al., 2007). A decline in coral reef cover is expected to impact fisheries and tourism, and increase bioerosion, leading to a decrease in coastal protection. A decrease in coastal protection combined with sea level rise could lead to erosion of the shoreline, particularly in developed coastal areas. The intrusion of saltwater into the freshwater aquifer as a result of sea level rise may lead to the contamination of resources used to sustain vegetation, resulting in habitat migration and a possible disruption in ecological services (Craft et al., 2008). Variation in temperature has the potential to alter key biological processes such as metabolism and reproduction, potentially altering the biological composition of habitats (Stenson et al., 2002).

Wildfires

A growing threat to developed areas in the Marianas is destruction of habitat due to wildfires. Intentionally set wildfires are common, particularly during on Guam during the dry season (January–June). Many of the intentionally set fires adjacent to developed system or in developed vegetation are the result of hunters attempting to drive invasive ungulates out into the open, where they can be easily pursued. Recent data suggests that the creation and expansion of savannas is a direct result of human wildfire activity, and that this has facilitated the spread of invasive species across southern Guam (Athens and Ward, 2004). Between 1979 and 2000 there were an average of 730 fires per year on Guam, which burned a total of 1942 ha (4800 acres), or 4% of the total land area (Minton, 2006). While the wildfires themselves may not occur within the developed system, the denuding of vegetation can lead to erosion and sediment runoff, which can impact coastal, stream, and urban areas within the developed system. The expansion of development into areas burned by wildfires puts developed areas and developed vegetation at risk for future wildfire events.

Point Source and Nonpoint Source Pollution

One aspect of the developed system is the increase in abundance of impervious surfaces, as well as the channelization of waterways, which act as conduits for the movement of pollutants in the environment. Point source pollution is any single identifiable source from which pollutants are discharged, such as large farm outfalls and sewage pipes (Environmental Protection Agency (EPA), 2005). Nonpoint source pollution is the collective result of runoff from multiple sources, both large and small. Examples of nonpoint source pollution includes dirt from construction sites, oil from parking lots, residual pesticides, and septic tank leaching. Pesticide and herbicide use is among the highest in developed systems compared to other system types based on heavy cultivation and agricultural use. There have been demonstrated negative effects to arthropod communities as a result of pesticide runoff, at both the lethal and sublethal levels (Stark and Banks, 2003). Honeybees are an important pollinator of many plant species, and exposure to neonicotinoid pesticides decreases both foraging success and survival, leading to colony failure (Henry et al., 2012). Sublethal effects associated with some pesticides has a negative effect on immune responses, and increases oxidative stress for arthropods

(James and Xu, 2012). Impervious surfaces in developed systems increase the amount of water transported to waterways, and channelized waterways act as conduits for pollutants, which can have deleterious effects on nearshore marine animals and ecosystems (Richmond et al., 2018, 2019).

Conservation Efforts

There are various groups engaged in on-the-ground management of invasive species or loss of vegetation. Management activities are coordinated through cooperative efforts of territorial agencies, Federal agencies, watershed partnerships, private organizations, and individual landowners and passive/social management of developed systems through policies, laws, and land protections.

Invasive Species Management and Control Activities

In general, terrestrial invasive species on small oceanic islands establish and impact most developed system categories. It is often more practical to apply biosecurity and management efforts across the island rather than attempting to focus efforts on specific systems. The level of specificity applied to any control and management effort, however, will vary by location, species, and the suite of associated impacts anticipated or occurring. One factor that may be utilized in developed systems is the potential for rapid detection of invasive species, due to the presence of people in these areas. Several invasive species management programs are reliant upon public engagement and education, in order to detect new invasive species, and their impacts in developed systems. Successful public awareness and citizen science campaigns include the CNMI Brown Bree Snake Interdiction Program to prevent the spread of brown tree snakes, as well as the Humatak Project, a program that protects watersheds by tackling bioerosion issues caused by invasive ungulates (Shelton and Richmond, 2016; Richmond et al., 2019).

Prevention of invasive species through biosecurity (e.g., the management of the risks to animal, plant, human, and environmental health posed by pests and diseases) measures is essential in limiting risk to habitats and species of the Marianas, and preventing the spread of invasive species throughout the islands. Both the CNMI and Guam have biosecurity mechanisms as part of their overall seaport and airport programs. The University of Guam and the Northern Marianas College provide research and extension services to support invasive species management. Activities include CRB monitoring, management, and research programs. Similarly, both the CNMI and Guam have government offices and staff that support management of various established pest species and provide extensive natural resource management, conservation, and restoration efforts.

Local and Federal Management

In Guam, public law 25-152 was put in place to ensure all development projects are reviewed by the local environmental protection agencies and do not result in negative impacts to the human environment. This regulation allows for the Guam Department of Agriculture, Division of Aquatic and Wildlife Resources to review all development projects which will involve the clearing of habitat prior to the start of project activities to ensure that there are no negative impacts to protected species, and to reduce impacts from soil erosion. The Northern Mariana Islands Administrative Code Chapter 65-30, § 65-30-101 details the permit requirements for any land clearing activities. This mechanism was put in place to ensure no unauthorized clearing of habitat occurs in the CNMI. The US Fish and Wildlife Service (USFWS) administers the Endangered Species Act, and consults on federally funded projects in the Marianas to conserve federally listed species and designated critical habitat. The Sikes Act was originally passed in 1960 to direct the US Department of Defense (DoD) to carry out conservation and natural resource rehabilitation projects on military installations in coordination with local agencies and the USFWS. Installations are required to create an Integrated Natural Resources Management Plan which describes ongoing and future conservation projects on military lands. In the Marianas, DoD manages large tracts of lands on Guam, Tinian, Pagan, and Farallon de Medinilla.

Future Scenarios

The condition of developed systems in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out, and their effects on developed systems. In the following sections we will analyze future scenarios and their possible impacts for conservation in the Marianas. The CMPs are as follows:

- (1) *Conservation values*: stakeholder involvement and public opinion determine the formulation, implementation and funding of natural resource conservation within laws and development plans.
- (2) *Laws and biosecurity*: national, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented. (e.g., hunting regulations, Clean Water Act, Endangered Species Act, and local laws, etc.).

- (3) *Development or conservation planning*: national, territorial, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

These conservation management parameters are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The year 2035 is the extent of the “foreseeable future,” and is based on the projected divergence of IPCC Representative Concentration Pathway climate change scenarios (van Vuuren et al., 2011a,b).

The four foreseeable future scenarios considered in this assessment are:

Future Scenario One, Status Quo—the most likely foreseeable future; no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues through the foreseeable future.

Future Scenario Two—a slight increase in natural resource conservation in the CMPs marginally improves conservation management.

Future Scenario Three—a slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management.

Future Scenario Four—a moderate to high increase in conservation actions in the CMPs substantially improves conservation management.

The future condition of developed systems in scenario one, the status quo, was characterized from an assessment of change over time in developed, developed vegetation, bare soil, and cropland land cover obtained from existing land cover maps (see Amidon and Reeves, 2018 for a description of land cover change assessment methodology). Based on these land cover maps, an annual rate of change for developed systems was estimated, and a projected change (in acres/ha) was calculated for the year 2035. The resulting information on changes in land cover by 2035, as derived from existing land cover change estimates, is the extent of the developed system that is expected in the foreseeable future under scenario one, the status quo, where conservation efforts remain unchanged and the current rate of change in land cover is also unchanged. The future condition of developed systems for scenarios two, three, and four cannot be quantitatively estimated. However, the Scenario One estimate can provide a “baseline” for a qualitative characterization of changes in the future condition of developed systems under scenarios two, three, and four.

Changes in human population are captured only by the changes in the developed land cover footprint derived from land cover map analysis (Amidon and Reeves, 2018). Impacts from other sources of human activities or human-caused stressors (e.g., plant and animal diseases, wildfires, invasive species, etc.) are not well characterized in the land cover changes, but significantly contribute to increases in the land cover area dominated by nonnative vegetation.

The island-wide implementation of the CMPs is unlikely to have a significant effect on climate-related stressors (temperature, precipitation, and severe weather) resulting from global climate change by 2035. This lack of CMP climate effects is due to the global lag in climate response to changes in greenhouse gas emissions, whose full effects may take decades or centuries to manifest (Solomon et al., 2009; Jevrejeva et al., 2012). Although impacts from climate-related habitat stressors do not change across the four scenarios, they were included in this analysis because of their overall magnitude of potential importance to future system viability.

Future Scenario One, Status Quo

Summary: Scenario one is considered the most likely future scenario, and serves as a “baseline” for comparing among the four future scenarios. There is no change in the implementation of the three CMPs between 2018 and 2035. A continuing current rate of change in land cover through this foreseeable future results in a slow but continuous change in the system as described below.

Description: Using the current rate of change, the acreage of developed land on the inhabited islands is expected to increase by 30% by the year 2035, reflecting generally increasing trends in human populations on these islands (Table 3; Amidon and Reeves, 2018). This expected increase in development will likely result from the conversion of native and nonnative forests to this land cover type. The anticipated changes, under scenario one, for each of the stressors affecting the developed system are given in Table 5. An expanding human population and increased development and general land use on all inhabited islands is anticipated, and therefore stressors are expected to increase at a low annual rate. Exceptions are a low to moderate annual rate of increase for development and surface air temperature, and a low annual rate of decrease for precipitation. Development of land for residential, commercial, and agricultural purposes will continue at an annual rate of 25%. This will likely lead to a decrease in developed vegetation, as developed areas increase. Because scenario one biosecurity CMPs remain unchanged while the human population and development continue to grow, an increased potential for new invasive species and new diseases (particularly those affecting native plants) exists. The introduction of additional plant diseases and invasive species, has the potential to alter the biological composition of developed vegetation, and reduce the resiliency, redundancy, and representation of this developed system type. Altered hydrology, combined with a reduction in rainfall, may enhance the conditions that support wildfires. Wildfires clear vegetation and lead to erosion, which can decrease water quality, leading to small increases the amount of pollution entering waterways.

Table 5 Responses of developed system stressors in foreseeable future scenarios.

Conservation management parameters (CMPs)				
Conservation values	Stakeholder involvement and public opinion influence the formulation, implementation, and funding of natural resource conservation and biosecurity (NRC/B) within laws and development or conservation plans.			
Laws and biosecurity	National, state, county, and city laws and regulations are the means by which NRC/B are supported and implemented.			
Planning for development or conservation	National, state, county, city, and private development plans or conservation plans define actions that result in losses or gains in NRC/B (impacts realized at implementation).			
Foreseeable future scenarios and the resulting developed (urban and agricultural) conditions				
Use foreseeable future scenario one as a “baseline” to characterize changes in Conservation Actions and Conditions in future scenarios two, three, and four.	Scenario One: CMPs: unchanged in support for NRC/B. Conservation Actions: no change; current rate of land cover change continues through the foreseeable future. Condition: habitat area, quality, and sustainability slowly decrease through the foreseeable future.	Scenario Two: CMPs: small increase in support for NRC/B. Conservation Actions: marginal increase. Condition: habitat area is unchanged through the foreseeable future; habitat quality and sustainability are slightly enhanced through the foreseeable future.	Scenario Three: CMPs: small to moderate decrease in support for NRC/B. Conservation Actions: substantial decrease. Condition: urban and agricultural uses are prioritized over conservation; habitat area, quality, and sustainability substantially decrease through the foreseeable future.	Scenario Four: CMPs: moderate to high increase in support for NRC/B. Conservation Actions: substantial increase. Condition: robust, sustained effort to restore, manage, and expand conservation; habitat area, quality, and sustainability substantially increase through the foreseeable future.
Developed system stressors	Responses of developed system stressors			
Development	Small to moderate increase	No change (redevelop)	Moderate to high increase	Small to moderate decrease
Altered Hydrology	No change to small increase	No change	Larger increase	Small decrease
Recreation/access	Small increase	Small increase	Larger increase	Larger increase
Water pollution	Small increase	No change	Larger increase	Small decrease
Invasive species	Small increase	Small increase	Larger increase	Small decrease
Plant diseases	Small increase	Small increase	Larger increase	No change to small decrease
Fire	Small to moderate increase	Small increase	Larger increase	No change to small increase
Erosion	Small increase	No change	Larger increase	Small decrease
Climate				
Temperature	Small to moderate increase	Small to moderate increase	Small to moderate increase	Small to moderate increase
Precipitation	Small decrease	Small decrease	Small decrease	Small decrease
Sea level rise	Small increase	Small increase	Small increase	Small increase
Storms	Small increase	Small increase	Small increase	Small increase

Future Scenario Two

There is a slight increase in the CMPs that marginally improves conservation management.

Summary: Conservation agencies and stakeholders work with increased but limited resources to slow or stop the degradation of landscape areas. There is no change in development, with areas currently occupied by development are redeveloped rather than opening new areas.

Description: Scenario two is essentially “status quo” with minor improvements in the three CMPs. The anticipated changes, under scenario two, for each of important stressors for the developed system are given in [Table 5](#). Though there is an expanding human population ([Table 3](#)) in scenario two, development is not expected to substantially increase due to redevelopment of currently developed areas (e.g., higher density housing, conversion of urban vegetated areas to impervious). A slightly improved biosecurity effort should help reduce the current rate of invasive species and plant disease invasion, but slight increases are still expected. The small increased support of natural resource management in the CMPs is not expected to greatly alter wildfire frequency and intensity, but these might lower slightly compared to scenario one. The CMPs supported conservation will not prevent, mitigate, or reverse the impacts of climate change-related stressors.

Future Scenario Three

There is a low to moderate decrease in conservation actions in the CMPs that substantially decreases conservation management.

Summary: All natural resource management actions in the CMPs are set aside in deference to land use for economic development. With extensive localized management, some native species may persist in park-like settings or in areas where land development is not possible.

Description: Scenario three has substantial declines in natural resource conservation within the three CMPs. An increasing human population (**Table 3**) is supported in its use of land for economic development over the conservation of native habitats. Remnant developed vegetation and bare soil areas that cannot support development become the only areas of free-living native species within the developed system. A larger increase in invasive species and plant diseases have the potential to alter biological composition of developed system types, decreasing the resiliency, redundancy, and representation of developed systems. A larger increase in altered hydrology combined with an expected small decrease in precipitation due to climate change, are expected to lead to an increased risk of wildfires, erosion, and pollution. The anticipated changes, under scenario three, for each of the stressors relevant to the developed system are given in **Table 5**.

Future Scenario Four

There is a moderate to high increase in conservation actions in the CMPs that substantially improves conservation management.

Summary: An overt, robust, active, and ongoing effort is made to engage partners and stakeholders in identifying and prioritizing landscape areas needed for the conservation of native dominated developed systems, and to actively restore and expand these ecosystems.

Description: A substantial emphasis on natural resource conservation is present in the three CMPs, reflecting increased societal concern for declines in natural habitats and biodiversity. Active and well-supported natural resource management begins to restore developed systems and ecosystems and expand their landscape areas. The anticipated changes, under scenario four, for each of the stressors important for the developed systems are given in **Table 5**. The needs of an expanding human population (**Table 3**) are addressed through more efficient land use governance based on redevelopment rather than further development of undeveloped areas. Modern and novel agricultural practices focus on methods that do not affect existing natural areas, or areas needed for native wildlife restoration, and increase the productivity and resiliency on existing croplands. Substantially improved biosecurity regulations decrease introductions of invasive species and plant diseases, and prevent the spread of unestablished introduced species. These improved land management actions result in decreased wildfire frequency and extent, preventing runoff and decreasing water pollution. The substantial increase in CMPs supported conservation may locally mitigate some effects of climate change-related stressors, but climate change effects are expected to persist.

Conclusion

The primary stressor to developed systems is vegetation loss and destruction caused by development. Threats from development are significant and ongoing and are expected to continue or increase in magnitude and intensity into the future unless there are effective management actions. Current conservation efforts taken by Federal, Territorial, private, and agency partnerships combined with certain laws and regulations limit some of the effects of the stressors on the habitat, but do not eliminate them. The stressors continue to contribute to the further increase of development and loss of vegetation.

In summary, developed systems are resilient (**Table 5**), in part due to the increased capacity to recover from stochastic and natural events. However, they remain threatened by fragmentation as a result of further development, as well as the presence of nonnative vegetation. The nature of invasive plants, which are commonly found in developed and urban areas, is to create self-sustaining populations which become dominant or disruptive to native systems. The developed system is less defined by typical species across the archipelago than it is by anthropogenic influence and a dominance of nonnative species, so this land use type is considered representative due to the distribution across the islands.

The Marianas developed systems represent a unique ecosystem type, whose composition is dynamic across its range. Due to growing human population numbers, the developed system is likely to shrink in size over the coming years, as development increases. The persistence of developed systems, and reduction of overall vegetation in the archipelago means that stressors are likely to increase and biological components within the system will decrease, should substantial increases in conservation actions not be implemented. Effects from climate change are likely to occur regardless of conservation measures in place, which will increase the likelihood of compounded effects from other stressors such as erosion, wildfire, plant diseases, and invasive species. The long-term survival of biodiversity in developed systems remains under threat, so long as nonnative species dominate the landscape. The implementation of strong conservation actions are needed to address the true impacts of these stressors on the long-term viability of developed systems across the Marianas.

See also: Physical Geography of the Mariana Archipelago.

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Hawai'i: Anthropogenic Changes—The Developed System of Hawai'i

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Abstract

The following analysis represents the results of a status assessment for the developed system in the Hawaiian Islands including its current status, stressors, conservation efforts, and future viability. The developed system occurs primarily in lowland areas with some in mid- and high elevation areas. There are five categories with varying amounts of vegetation, impermeable surfaces (e.g., roads, buildings), and permeable surfaces. Biodiversity within the developed system is lower compared to the other systems and is generally dominated by nonnative species. Currently, the developed system in Hawai'i occurs on each of the eight main Hawaiian Islands with Ni'ihau, Kaho'olawe, and the Northwestern Hawaiian Islands (NWHI) comparatively containing very little. Our assessment of developed system viability, defined as the likelihood of persistence over the long term, is based on the concepts of representation, redundancy, and resiliency. The main stressors on the developed system are insects and disease, axis deer, fire and drought, altered hydrology, pollutants, and land use changes. Ongoing conservation efforts are helping to address each stressor. The conservation of the developed system depends on combined efforts of State, Federal, and multi-agency organizations, watershed partnerships, private landowners, and passive/social management through policies, laws, and land protection.

Developed System Description

In the Hawaiian Islands, increasing population and land use intensity has resulted in a shift in the landscape towards dense settlement and cropland anthromes (Ellis et al., 2010). Within these anthromes, developed habitat could be classified as one of five categories: open space, low-, medium-, and high-intensity development, and areas of agriculture/cultivated lands. The future scenarios viability assessment was conducted to evaluate how variations in management actions and policy decision making will likely affect the viability of these habitat types. Determination of the most likely scenario to occur in the foreseeable future will aid in determining the best course of action to maintain status quo or possibly lead to an improvement in systems functions (Gibson and Quinn, 2017).

Vegetation Structure

Developed system vegetation ranges from impermeable surfaces (e.g., roads, buildings) to permeable surfaces of regularly tilled agricultural areas, fallow agricultural and open areas, areas modified by minimal development, or areas with higher intensity use with little to no vegetation remaining (Cuddihy and Stone, 1990). Agricultural areas may be limited to one vegetation type as a commercial crop. Open areas that are fallow (untilled agricultural areas, parks, golf courses) could contain some taller vegetation providing some canopy cover (Gagne and Cuddihy, 1999). Vegetation structure of low-intensity developed habitat within untilled fields and cleared land would tend to be composed of native species that existed prior to development consisting of low-statured herbaceous plants to higher-statured woody plants (Cuddihy, 1989; Gagne and Cuddihy, 1999). Vegetation structure of a medium-intensity developed system demonstrates a range of structure from completely herbaceous to woody plants providing some canopy. Vegetation structure of a high-intensity developed system includes those with a limited range of structure depending on available space (Gagne and Cuddihy, 1999).

Vegetation Composition and Biodiversity

The vegetation composition of the developed system usually ranges from barren areas to vegetated areas, which may be very low in species diversity, with limited canopy cover, if any (GIS GAP, 2018). Studies have shown that the diversity of species declines in areas of higher intensity development (McKinney, 2002; Sax and Gaines, 2003). In addition, species composition changes in urban environments such that the number of nonnative species increases and native species decreases (McKinney, 2002). Open areas that are fallow could contain the highest levels of biodiversity; however, the flora and fauna are dominated by nonnative species (Gagne and Cuddihy, 1999). Vegetation communities of a low-intensity developed system is composed of native and nonnative species. Vegetation communities of a medium-intensity developed system include mostly nonnative species for lawns, cleared land, and small parks and gardens. Vegetation communities of a high-intensity developed system include only those left in place or planted as horticultural features as part of the development (e.g., street trees, hedges) (Gagne and Cuddihy, 1999). In summary, the vegetation composition of developed habitat is characterized by the dominance of nonnative species (Cabin et al., 2002). Fauna found in a developed system may consist of many of the same species found in more undisturbed areas (birds, insects, bats) but are limited by availability of foraging and nesting resources and by the effects of habitat fragmentation in the large spaces created between individuals and populations. For example, roads favor species with good dispersal abilities in disturbed habitats at the expense of species with limited mobility. Habitat fragmentation may pose barriers to animal movement, while increasing the connectivity of disturbed sites promoting the spread of nonnative plants, pests, and pathogens (e.g., transported by vehicles) (Noss et al., 2006).

Physical and Life History Components

Geology—Most coastal and lowland developed systems in Hawai'i overlay areas of reef, beach, and lagoon deposits, alluvium, young and old dune deposits, and basalt lava (pāhoehoe and 'a'ā) (Street, 1992; Walker, 1999; Landfire, 2016, unpublished data). Developed systems in mid- to high-elevations overlay old to young basaltic lava (GIS GAP, 2018; Landfire, 2016, unpublished data).

Water availability—The majority of the developed system occurs at lower elevations and is typically dry, with annual rainfall of < 20 in (50 cm); however, windward rainfall may be high enough (up to 40 in (100 cm)) to support mesic-associated and sometimes wet-associated vegetation (Price and Carlquist, 1999). The developed system, including impervious areas and tilled and fallow fields, overlays natural and manmade groundwater features (Mink and Bauer, 1998). Polynesian settlers used perennial streams and springs as the main sources of water and built elaborate diversions for agricultural use. Tunnel and ditch systems were constructed to transport water on every island except Kaho'olawe and Ni'ihau. More recently, drilled wells, infiltration galleries, and drainage tunnels are the most common ways used to access groundwater (Mink and Bauer, 1998).

Natural and Physical Boundaries—The developed system is bounded by the ocean and by steep cliffs or slopes that are not suitable for construction, agriculture, or other modification.

Inclusions—The developed system may also contain anchialine pools, emergent wetlands, ponds, pools, and streams with coexisting faunal species such as wetland birds, fish, anchialine pool shrimp, and damselflies (GIS GAP, 2018; Landfire, 2016, unpublished data).

Pre-Human Condition

The developed system did not occur in Hawai'i before human colonization.

Current Condition

The developed system is predominantly found on six of eight Hawaiian islands: Kaua'i, O'ahu, Moloka'i, Lāna'i, Maui, and Hawai'i. Ni'ihau is inhabited but is privately owned with no general public access to be able to obtain current data; however, satellite views

show there are no paved roads and very few small buildings and homes. Kaho'olawe has no permanent habitation, although there are a few unpaved roads and small buildings and structures for use during restoration activities. No analyses are available regarding developed habitat on the Northwestern Hawaiian Islands (Landfire, 2016, unpublished data). Pihemanu (Midway Atoll) consists of two land areas totaling 26 mi² (66 km²), one of which has unused runways and a second that is more developed with an active runway, roads and impervious surfaces, buildings to support permanent residents, and a walled harbor. Lalo (French Frigate Shoals) and Hōlanikū (Kure Atoll) both have runways in disrepair. The remaining atolls and islands: Nihoa, Mokumanamana (Necker), and 'Ōnūnui (Gardner Pinnacles) have no developed areas.

The developed system first appeared in Hawai'i when Polynesians settled the islands >1000 years ago, and their success depended upon availability of water resources, mostly for cultivation of taro and other crops (Mink and Bauer, 1998). They modified the landscape by building extensive hydraulic works to support needed agriculture. Introduced plants replaced native vegetation in succession on fallow and abandoned fields (Cuddihy and Stone, 1990). Crops (sugarcane, pineapple, and rice) were grown commercially beginning about 1835 (Ziegler, 2002). By the late 1870s, the first well was drilled on southwestern O'ahu, supplying artesian water and allowing for the great increase in numbers of residents and development. Modification of the landscape on the Hawaiian Islands continued with the onset of long-distance passenger aircraft, the end of the plantation system for sugarcane and pineapple, and a growing population with the concurrent increase in residential areas, apartment complexes, highways, and military bases (Fung Associates, Inc., 2011). In 1980, there were 18 sugar and pineapple plantations totaling >300,000 acres (ac) (121,406 hectares (ha)), but as of 2017, only 5000 ac (2023 ha) of these crops remained (Lyte, 2017, unpublished data). Currently, agriculture is dominated by small farms averaging 160 ac (65 ha) in size for production of nursery and greenhouse crops and some livestock, poultry, and their products (HDBEDT, 2017). Urban residential and commercial development in Hawai'i is more prevalent at lower elevations along the coast, although some developed areas may be at higher elevations suitable for development to occur (e.g., astronomical telescopes). Current developed system areas for each island is shown in Figs. 1–4.

Categories of the Developed System

The developed system of the Hawaiian Islands falls into five categories: (1) open space, (2) low-intensity developed, (3) medium-intensity developed, (4) high-intensity developed, and (5) agriculture/cultivation. Descriptions and examples of each category are provided in Table 1.

The five categories of developed habitat occur in different proportions on each Hawaiian island as represented in Fig. 5 (Reeves and Amidon, 2018, unpublished data). A large portion of the land area of Midway in the NWHI is developed (for access by aviation with an active runway and support facilities, and was determined by satellite imagery).

O'ahu has the largest percentage of land area within the developed system (33%), followed by Maui at 22%, Kaua'i at 18%, Hawai'i Island at 7%, Moloka'i at 6%, Lāna'i at 4%, and Ni'ihau and Kaho'olawe at 1% (as shown in Fig. 6).

Flora and Fauna Composition and Biodiversity

Species that occur in the developed system may be one of three types and can be native or nonnative. The first type, urban avoiders, consists of plant species that are sensitive to human activities and includes late successional (old growth) and wetland plants. The second type, urban adapters, consists of plant species that do well in managed lands and ruderal areas such as cultivated turfgrass, ornamental shrubs and trees, wind-dispersed lawn weeds such as dandelions and crabgrass, and bird-dispersed shrubs, trees, and weeds. Some animal species in the developed system are those that can exploit human foods and garbage, and that also benefit from fewer predators in these areas. This also includes bird species that are ground feeders, omnivores, seedeaters, and aerial sweepers. Tilled areas used for crops, and nurseries or small parks and gardens may be considered as urban adapters, but can only persist when being actively managed. The third type, urban exploiters, depends on human resources and not on the amount or types of vegetation. These are mostly animal species including house sparrows, Norway rats, mice, cats, mongoose, and insects such as cockroaches. Plants that are urban exploiters include those species that can tolerate disturbance (mostly grasses and annuals) and that have wind-dispersed seeds, a tolerance of pollution, trampling, and alkaline compacted soils (McKinney, 2002). Species are sustained through their redundancy, resiliency, and representation. These terms can also describe the viability of different systems, including the developed system. System viability depends on maintenance of multiple and distributed populations (redundancy) of sufficient quality and size (resiliency) with biological richness and genetic range (representation) to persist over time.

Landownership

One of the NWHI, Midway Atoll (an Unincorporated Territory administered by the U.S. Fish & Wildlife Service as a National Wildlife Refuge), consists of three islets, one of which (Sand Island) is almost entirely developed habitat (actively used runways and buildings). Of the remaining Hawaiian islands, O'ahu has the greatest land area of developed habitat, 32%, consisting of 122,313 ac (49,498 ha) with the largest portion (over 82,000 ac; 33,184 ha) privately owned. Maui is the second most developed island (over 21%), consisting of 99,478 ac (40,257 ha) of developed habitat with the largest portion (over 89,000 ac; 36,017 ha) privately owned. Kaua'i consists of almost 18% developed habitat (almost 64,000 ac; 25,900 ha) with the largest portion (almost 39,600 ac; 16,026 ha) privately owned. The island of Hawai'i consists of nearly 7% developed habitat (almost 173,000 ac; 70,010 ha) with the largest portion (almost 138,000 ac; 55,845 ha) privately owned. Moloka'i consists of about 6% developed

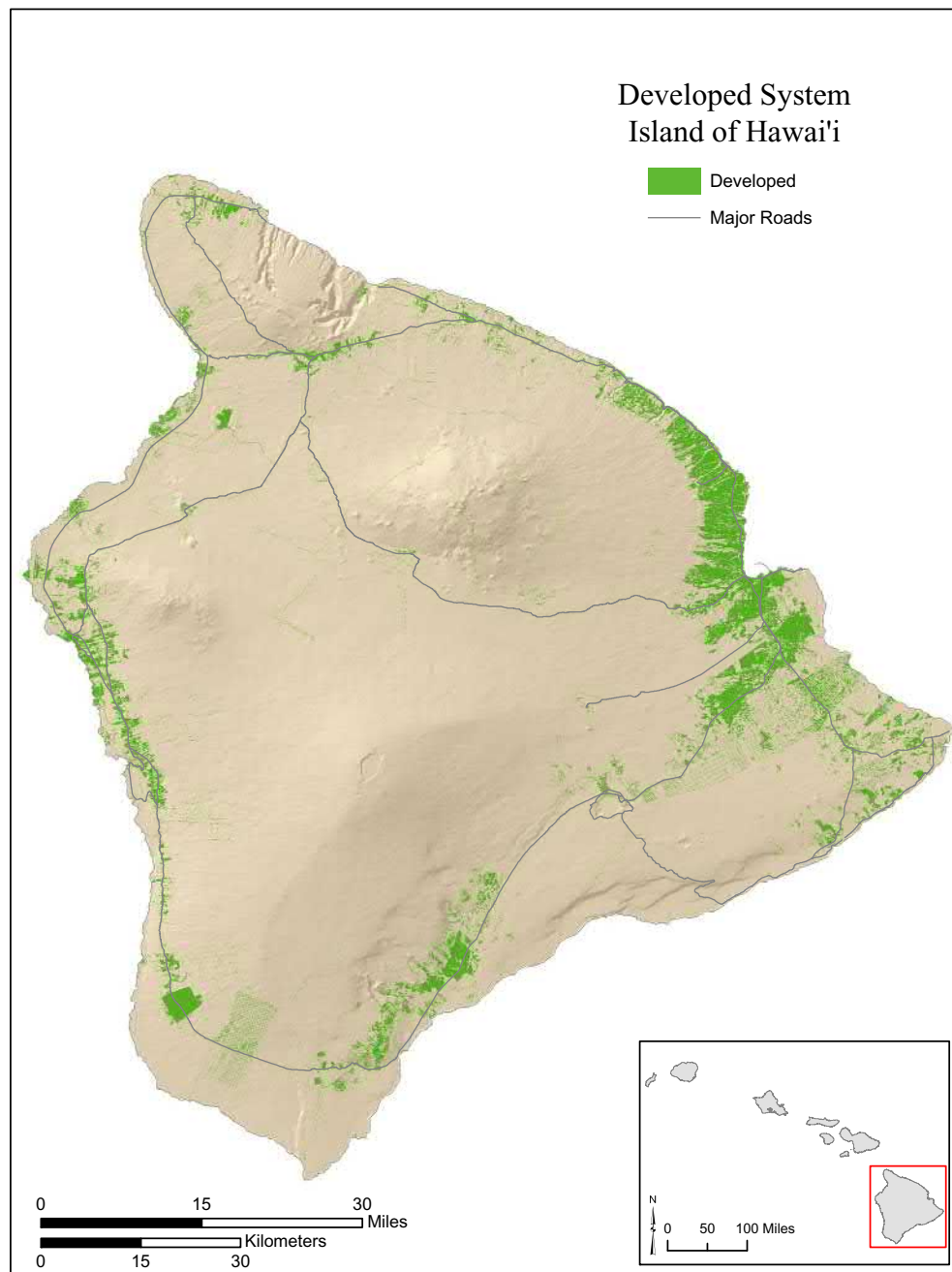


Fig. 1 Map of current extent of the developed system in the island of Hawai'i. From Reeves, M. K. and Amidon, F. (2018). *Habitat status assessment methods—Hawai'i, current condition summaries*. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI.

habitat (10,420 ac; 4217 ha) with a little over 6000 ac (2428 ha) privately owned. Lāna'i consists of almost 4% developed habitat (almost 3400 ac; 1376 ha) with nearly all being privately owned, Ni'ihau consists of <1% developed habitat all of which is privately owned. Kaho'olawe consists of <1% developed habitat all of which is state-owned ([Hawaii State Office of Planning, 2017](#)). This information is summarized in [Table 2](#).

Stressors

Insects and disease, axis deer, fire and drought, altered hydrology, pollutants, and land use changes are stressors that affect the developed system. Below are descriptions of the most significant stressors and their impacts on the developed system.

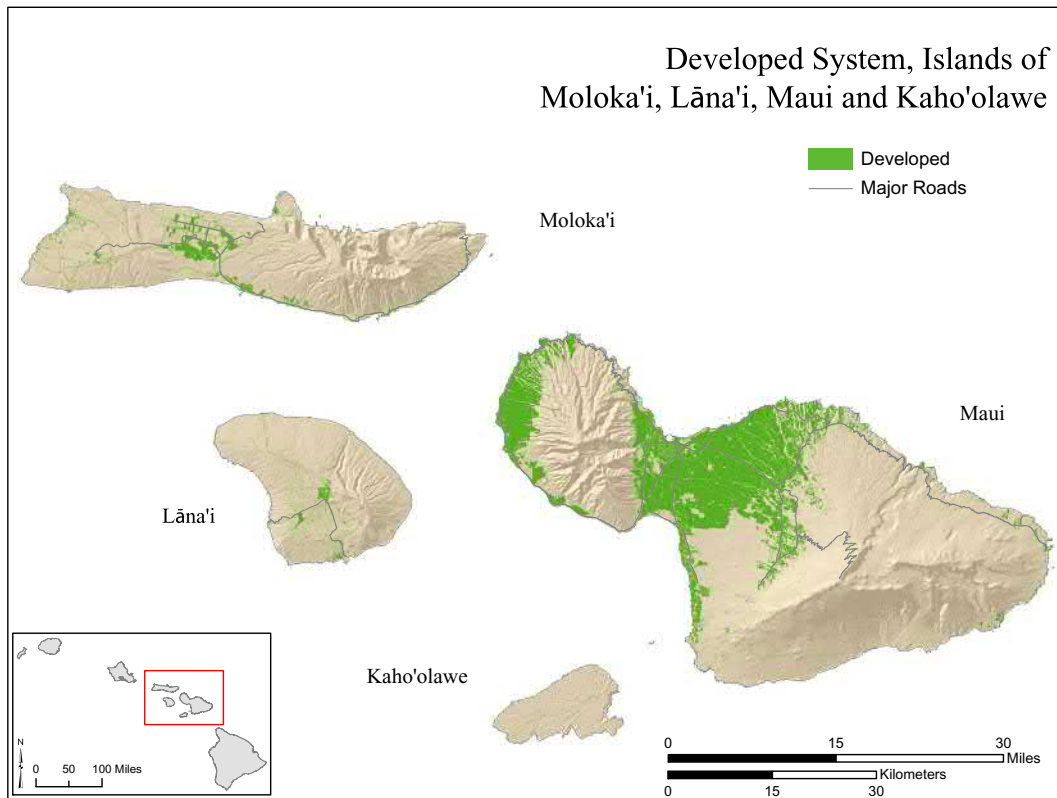


Fig. 2 Map of current extent of the developed system in the islands of Moloka'i, Lāna'i, Maui, and Kaho'olawe. From Reeves, M. K. and Amidon, F. (2018). *Habitat status assessment methods—Hawai'i, current condition summaries*. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI.

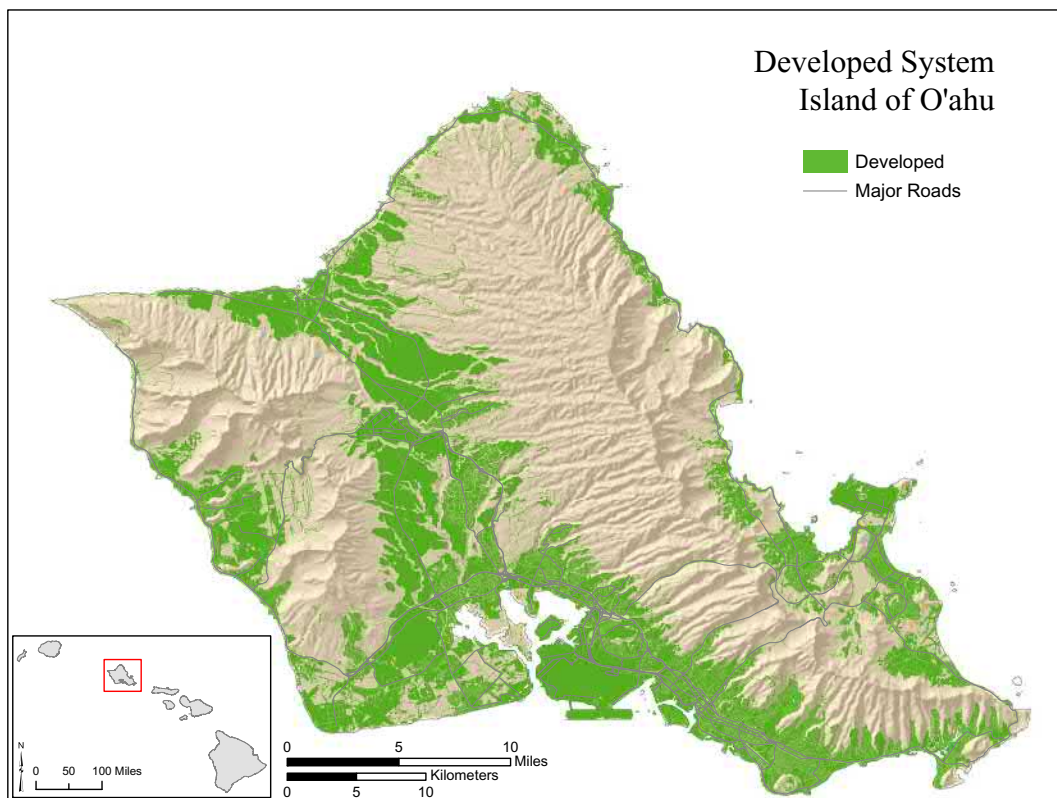


Fig. 3 Map of current extent of the developed system in the island of O'ahu. From Reeves, M. K. and Amidon, F. (2018). *Habitat status assessment methods—Hawai'i, current condition summaries*. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI.

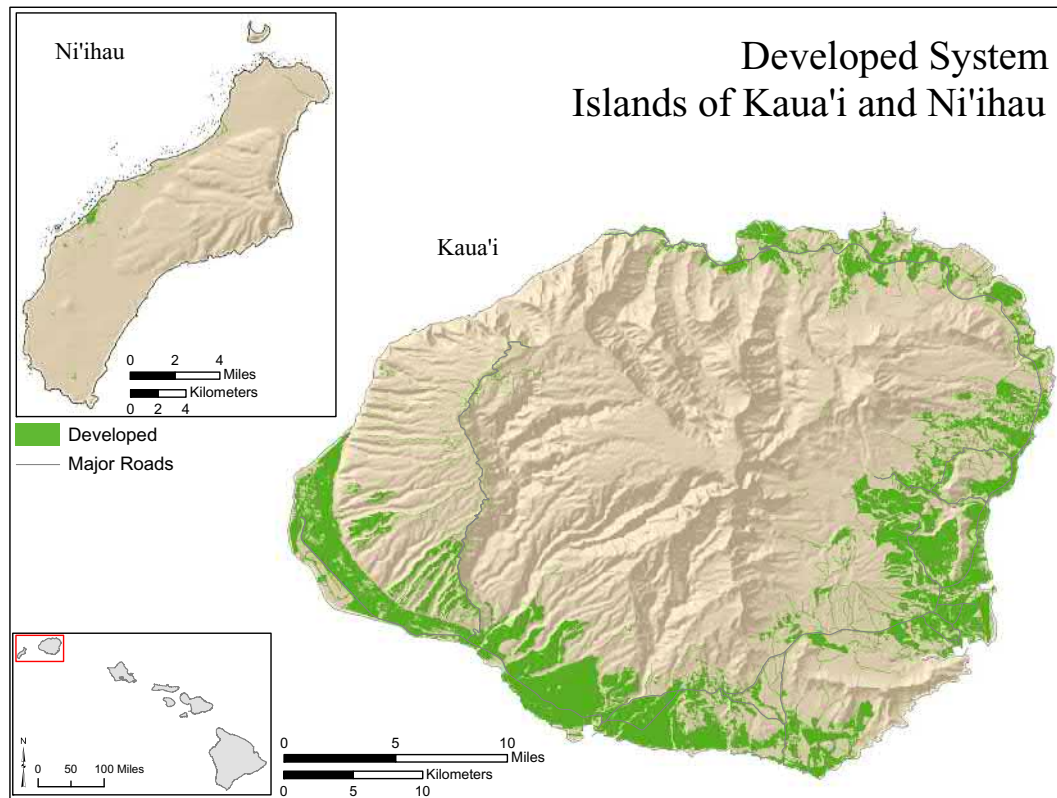


Fig. 4 Map of current extent of the developed system in the islands of Kaua'i and Ni'ihau. From Reeves, M. K. and Amidon, F. (2018). *Habitat status assessment methods—Hawai'i, current condition summaries*. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI.

Table 1 Developed system categories.

Category	Description	Examples
Open space	Mostly vegetated, primarily lawn grass, some construction materials, < 20% impervious surfaces	Large-lot single-family housing units, parks, golf courses, and vegetation planted for erosion control, aesthetic purposes, or recreation areas
Low-intensity	Mixture of constructed materials and vegetation and 20–49% impervious surfaces	Single-family housing units
Medium-intensity	Mixture of constructed materials and vegetation and 50–79% impervious surfaces	Single-family housing units
High-intensity	Highly developed areas where people reside or work in high numbers and 80–100% impervious surfaces	Apartment complexes, row houses, and commercial/industrial use
Agriculture	Planted lands of variable physiognomy	May include ordered rows of plantings in agricultural-zoned lowland mesic and wet settings with a wide variety of dominants of taller-statured plants (e.g., banana and papaya), and shorter-statured crops (e.g., vegetable crops) and fallow fields

From: Landfire. (2016), unpublished data, Landfire/GAP land cover map unit descriptions, based on NatureServe Ecological Systems. 1398 pp.

Insects and diseases—Pest species such as nonnative insects and diseases can be introduced to Hawai'i through import of cargo and plants through ports and then move from one island to another by inter-island transport. Existing State and Federal regulatory mechanisms do not adequately prevent the introduction of these pests and diseases (HDLNR DAR, 2003). Below we provide examples of two insect pests recently introduced to Hawai'i that affect the developed system and the consequences of their introduction.

The coconut rhinoceros beetle (CRB) (*Oryctes rhinoceros*) is native to tropical and subtropical southeastern Asia and is one of the most damaging insects to coconut and African oil palm trees (Bedford, 2015, unpublished data). Adult beetles bore their way into the crown of healthy palms or plants and then bore outward through the base of a central palm frond (Molet, 2013). It is unknown

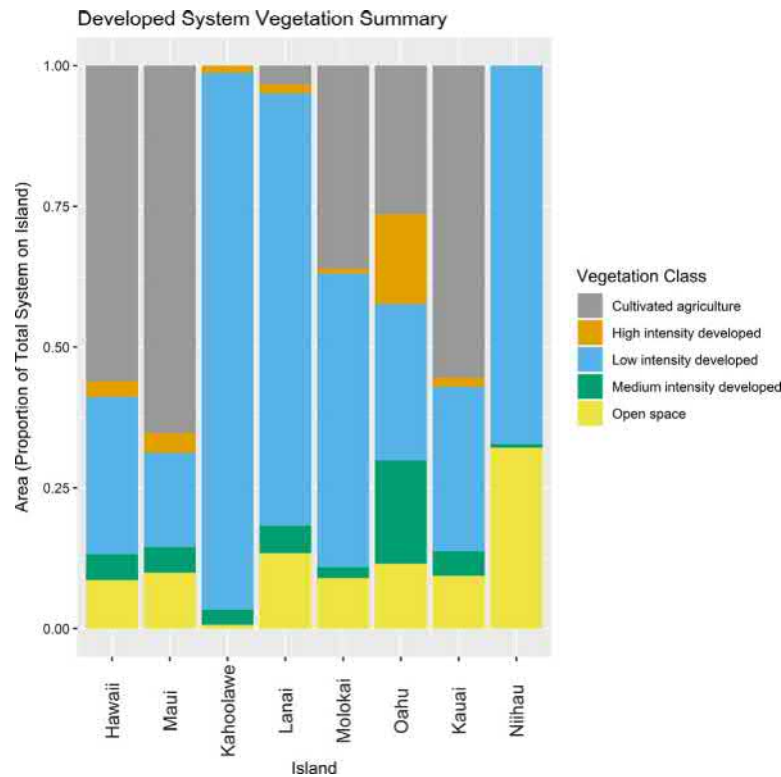


Fig. 5 Distribution of the developed system vegetation in the main Hawaiian Islands. From Reeves, M. K. and Amidon, F. (2018). *Habitat status assessment methods—Hawai'i, current conditions summaries*. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI.

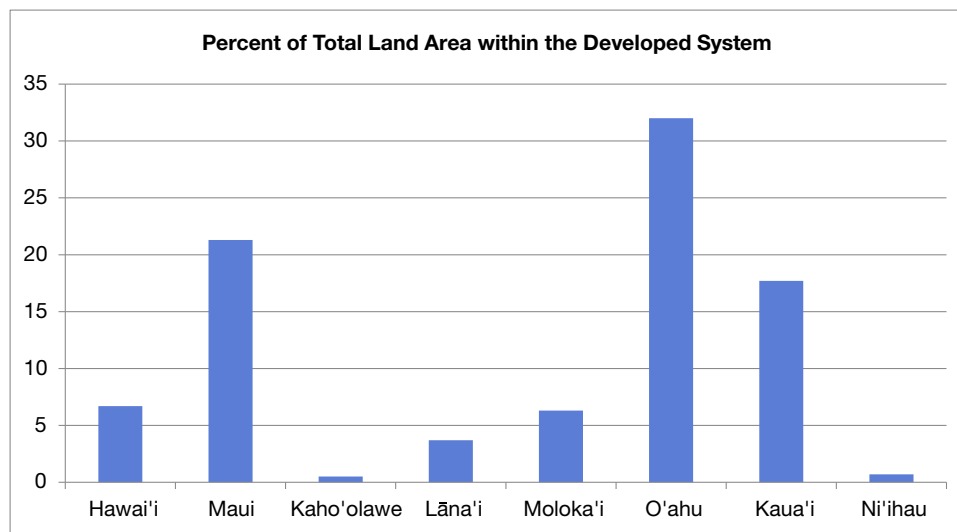


Fig. 6 Total land area within the developed system for each of the main Hawaiian Islands. From Reeves, M. K. and Amidon, F. (2018). *Habitat status assessment methods—Hawai'i, current conditions summaries*. Technical report from United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office, Honolulu, HI.

when it was introduced to Hawai'i, but it was first detected on O'ahu in December 2013 at Pearl Harbor-Hickam Joint Base (USDA-APHIS, 2015, unpublished data). This insect quickly spread across the southwest portion of O'ahu within a few months after detection (USDA-HDOA, 2014, unpublished data). The CRB has the potential to devastate populations of native and nonnative palms and agricultural crops in Hawai'i including pandanus, banana, and pineapple by damaging and killing individual trees, reducing crop yields, and by increasing costs to implement control measures and replacing plants (HISC, 2018a, unpublished data).

Table 2 Developed system landownership (acres, hectares).

<i>Island</i>	<i>Federal</i>	<i>State</i>	<i>County</i>	<i>Private</i>	<i>Other</i>	<i>Total developed</i>	<i>Percent developed</i>
Hawai'i	1649	25,970	939	137,727	6635	172,920	6.7
	667	10,510	380	55,736	2685	69,978	
Maui	304	7406	2188	89,571	9	99,478	21.3
	123	2997	885	36,248	4	40,257	
Kaho'olawe	0	149	0	0	0	149	0.5
	0	60	0	0	0	60	
Lāna'i	<1	192	46	3099	0	3337	3.7
	<1	78	19	1254	0	1350	
Moloka'i	54	4140	97	6129	0	10,420	6.3
	22	1675	39	2480	0	4217	
O'ahu	20,890	11,679	5313	82,224	2207	122,313	33
	8454	4726	2150	33,275	893	49,498	
Kauai	1211	19,664	518	39,569	2765	63,727	17.7
	490	7958	210	16,013	1119	25,605	
Ni'ihau	0	0	0	333	0	333	0.7
	0	0	0	135	0	135	

The *Erythrina* gall wasp (*Quadrastichus erythrinae*) is native to Africa and was first discovered on O'ahu in April 2005 in native wiliwili trees (*Erythrina sanduicensis*) in native forest and in nonnative *Erythrina* trees or coral trees (*E. variegata*) used for landscaping and windbreaks around farmsteads (Rotar et al., 1986). The gall wasp has caused substantial impacts to the native wiliwili trees and to the agricultural industry in Hawai'i (Rubinoff et al., 2010). It quickly spread and by October 2005, it was reported on all of the main Hawaiian islands except Ni'ihau (Heu et al., 2008, unpublished data). Wasps lay their eggs in young leaves and stems and as the larvae develop, galls form in the leaflets and petioles (Heu et al., 2008, unpublished data). Leaves and stems with many galls reduce plant growth and vigor, defoliate trees and cause death of trees (Yang et al., 2004). The gall wasp has almost eliminated Moloka'i's coral tree population; therefore, farmsteads that used coral trees as windbreaks must now manage wind damage to their crops in other ways (Tizon, 2007, unpublished data).

In addition to the insect introductions described above, plant diseases already introduced to Hawai'i such as banana bunchy top, papaya mosaic virus, and powdery mildew (all transmitted by insects) affect agricultural areas of the developed system and move from those areas to other previously unaffected areas, possibly affecting other native and nonnative plant and invertebrate species. These stressors decrease the resiliency of the developed system, leading to less redundancy necessary for continued representation.

Feral ungulates—Axis deer (*Axis axis*) were introduced to Moloka'i (eight animals in 1868, increasing to over 1000 in 20 years), Lāna'i (1920), and Maui (1960), and illegally released on the island of Hawai'i in 2010 (Tomich, 1986; BigIsland.com, 2011, unpublished data). Axis deer browse on a wide variety of trees and shrubs in native forest, fruits and vegetables on agriculture lands as well as plantings in more intensely developed areas. Axis deer have high reproductive rates, and in the absence of predators have population growth rates as high as 20–30% (Hess, 2008). The estimated cost of axis deer damages to farms, ranches, and resorts in Maui County for a two-year period was calculated at over 2 million dollars (The Economic Research Organization at the University of Hawaii (UHERO), 2016). Other feral ungulates such as pigs (*Sus scrofa*), goats (*Capra hircus*), cattle (*Bos taurus*), and mouflon (*Ovis musimon*) may affect the developed system by trampling leading to erosion, and by herbivory of plant species; however, we have no direct evidence of this occurring on a large scale within the developed system.

Fire and drought—In Hawai'i, over 1000 wildfires burn >17,000 acres annually and the amount of area burned each year is increasing (Pacific Fire Exchange, 2014, unpublished data). The majority of wildfires are human caused (arson, fireworks, trash, cooking accidents, vehicle-caused wildfires, agricultural fires) that get out of control (HDLNR-DOFAW, 2016) with the highest density (66%) of ignitions occurring within developed areas (Trauernicht et al., 2015) (Fig. 7).

Wildfires affect the developed system by increasing the amount of fire-prone invasive grasses (e.g., guinea grass (*Megathyrsus maximus*), buffelgrass (*Pennisetum ciliare*), fountain grass (*Cenchrus setaceus*), and molasses grass (*Melinis minutiflora*)), which in turn increases the risk for wildfires, creating a grass-fire cycle. These fire-prone species quickly invade burned areas, creating areas dominated by fine continuous fuel loads that are easily ignitable and carry fire quickly across the landscape (Smith and Tunison, 1992; HDLNR-DOFAW, 2016). Wildfires destroy vegetation and heavy rainfalls following wildfire events increase soil erosion and landslides, leading to increased sedimentation of streams, wetlands, and downstream systems (e.g., coral reefs) (Pacific Fire Exchange, 2014, unpublished data; HDLNR-DOFAW, 2016). Increased sedimentation causes continued degradation of streams, stream flow, and wetlands, and prevents these systems from properly functioning.

Altered hydrology and soil composition—Hawai'i has experienced drought conditions throughout history, with increasing and longer episodes in the past 15 years (Hawaii Civil Defense, 2011). Site clearing, grading, and converting pervious surfaces (e.g., vegetated areas) to impervious surfaces (actions associated with the developed system) alters hydrology by increasing runoff, erosion, and sediment into surface waters (HDBEDT, 1994). The conversion of pervious surfaces to impervious (e.g., rooftops, roads, parking lots, sidewalks) decreases the ability of the ground to filter runoff thereby increasing runoff (HDBEDT, 1994). To address

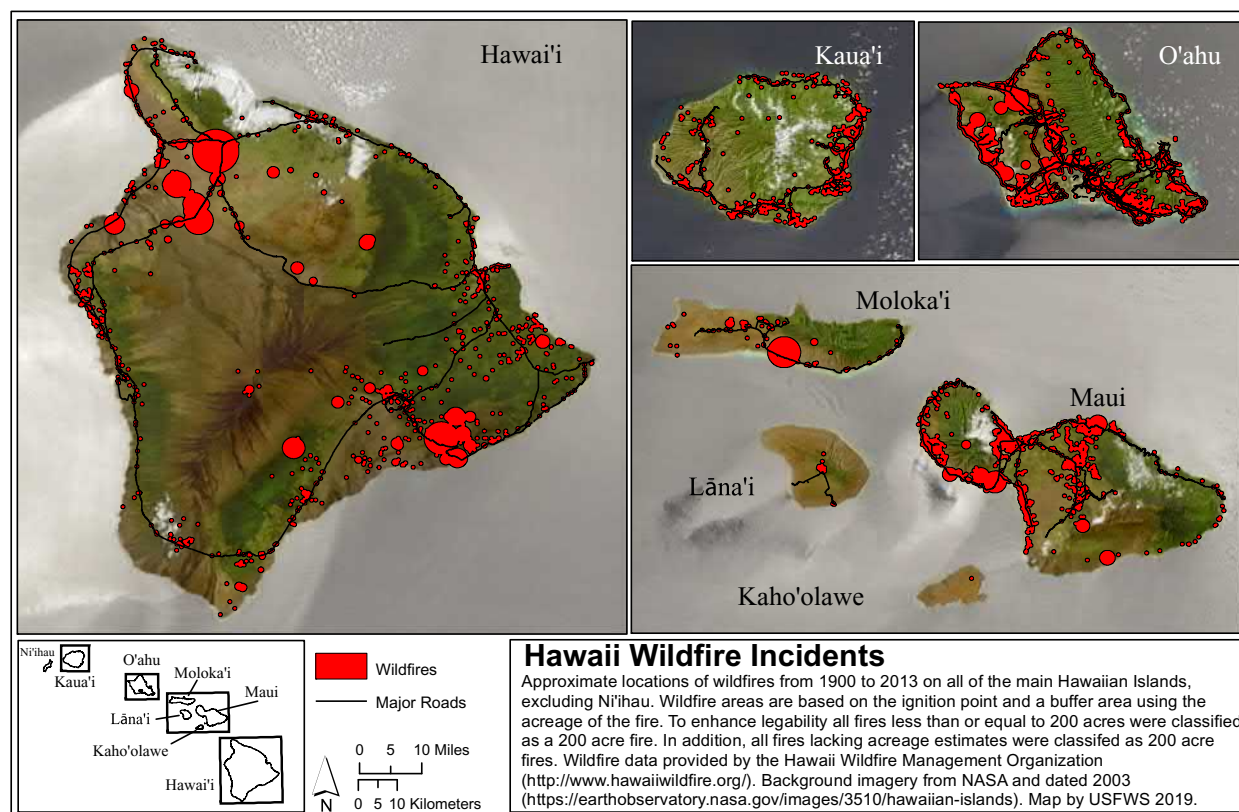


Fig. 7 Recorded wildfire incidents in the main Hawaiian Islands from 1900 to 2013. Map produced by the United States Fish and Wildlife Service, Pacific Islands Fish and Wildlife Office.

elevated flows from increased runoff and to prevent streambank erosion, runoff conveyances are constructed or drainages are modified (HDBEDT, 1994). Other examples of changes to hydrology due to urbanization include higher peak discharges, increased volume of urban runoff during storms, increased frequency and severity of flooding, and reduced streamflow during drought conditions (HDBEDT, 1994). Increased runoff also results in less water being available for consumptive use; therefore less water is available for agricultural uses.

The dominant water source in Hawai'i is groundwater, either as a basal lens floating on seawater, or as high-level water. Perennial streams and springs are important water supplies for large-scale agriculture and most large streams are diverted for irrigation (using tunnel and ditch systems). Some tunnels act as drains for use of high-level groundwater. As of the mid-1990s, groundwater extraction for human and agricultural use remained below sustainable yields (Mink and Bauer, 1998). Potential over-pumping of groundwater is controlled through the Commission on Water Resources Management's defined sustainable yield determinations, and production would be reduced or shifted to other aquifers that are not over the defined yield (Hawai'i Board of Water Supply, 2016). However, the basal water level is currently less than half of its volume of 100 years ago (Mink and Bauer, 1998).

Intensive farming practices in Hawai'i that rely on tillage and synthetic fertilizers tend to decrease the soil's mineralizable N (available nitrogen) pool. Nitrogen mineralization decreases primarily because conventional farming practices decrease organic matter. For both the Hawaiian Waimea (very fine sandy loam) and Waialua (silty clay) series soils, long-term cultivation decreased nitrogen mineralization by a factor of 30. This also indicates low microbial activity and degradation of the biological properties of the soil. Sustained over-use of farmlands without best management practices would continue to degrade soil nutrients and possibly compact the soil making it less water-permeable. Mitigation for this loss would take sustained application of large amounts of organic matter over several years (Deenik, 2006).

Pollutants—Urban and agricultural areas are a source of pollutants (e.g., sediment nutrients, bacteria, toxic chemicals, oil, and trash) that enter into streams, wetlands, coastal areas, and the ocean (HDBEDT, 1994). Roads, buildings, parking lots, and other non-permeable surfaces prevent rainwater from soaking into the ground and increases the volume and speed of water runoff, increasing soil erosion, and flushing pollutants into streams and through storm drains to the ocean.

Land use zoning changes—There are four land use districts in the State of Hawai'i: Agriculture, Conservation, Rural, and Urban. Statewide, the majority of land falls within Conservation or Agriculture districts (both of which do not allow major development), with O'ahu being the exception since a fair amount falls within the Urban district (101,661 ac, 41,141 ha) (HDBEDT, 2017). As areas are reclassified from agriculture to urban, major development within the urban land use district can change the ecological function of the existing system. Undeveloped areas, that were or could be used for agriculture or left as open space, when reclassified

for urban use and developed, exhibit increases in water runoff and sedimentation by surface changes from permeable to non-permeable.

Conservation Efforts for the Developed System

There is active (on-the-ground) management of invasive species, wildfire, and water resources in the developed system through cooperative efforts of State agencies, Federal agencies, watershed partnerships, private organizations, and individual landowners and passive/social management of the developed system through policies, laws, and other land protections.

Invasive Species

The effects of invasive species on the developed system are addressed in several ways. The Hawai'i Invasive Species Council (HISC) established in 2003 was created to implement invasive species management statewide ([HISC, 2018b, unpublished data](#)). Invasive species committees (ISCs) are voluntary partnerships of government, private, and non-profit organizations. Five Hawaiian islands have separate smaller committees to address island-specific issues: Hawai'i (BIISC), Maui (MISC), Moloka'i (MoMISC), O'ahu (OISC), and Kaua'i (KISC). These committees identify and prioritize invasive species (plants and animals) for control or eradication, including recent developed habitat invaders such as the *Erythrina* gall wasp and the coconut rhinoceros beetle discussed in "Insects and Diseases."

Hawai'i's Department of Transportation (HDOT) established the Highway Division's Statewide Noxious and Invasive Pest Program (SNIPP) that has prepared a 10-year strategic plan to steward lands affected by the highway system ([HDOT, 2011](#)). This plan is implemented in cooperation with stakeholders in the public and private sectors. The plan determines funding needs for prevention of invasive species establishment, early detection and response, control and management, restoration, and community and organizational outreach. Funding costs to implement the plan are included as part of construction project work plans and federal funds are available at an 80:20 match for the annual SNIPP budget. The stakeholders include the ISCs, the Department of Land and Natural Resources (DLNR), the Hawai'i Department of Agriculture (DOA), the U.S. Department of Agriculture (USDA), the University of Hawai'i-College of Tropical Agriculture and Human Resources (UH-CTAHR), the U.S. Fish and Wildlife Service (USFWS), The Sierra Club, and The Outdoor Circle. The HDOT also provides guidelines for landscape maintenance and pruning of trees, shrubs, palms, and hedges along roadways ([State of Hawai'i, 2011](#)). The actions require obtaining a contractor's license, insurance, and use of an International Society of Arboriculture Certified Arborist. The HDOT describes pruning techniques, risk assessment, and guidelines for native planting. The Certified Arborist must work in coordination with an HDOT engineer and be aware of all federal, state, and county regulations.

The invasive nonnative ungulate most likely to affect the developed system is the axis deer ([Martin, 2011, unpublished data](#)). Axis deer are provided and maintained by the State as a hunting resource on Maui, Lāna'i, and Moloka'i. The State does not permit their introduction to other Hawaiian islands. In response to axis deer being illegally released on the island of Hawai'i in 2010, the DLNR has developed a response and removal plan, including a partnership with the DOA, the BIISC, Federal agencies, and private landowners ([BigIsland.com, 2011, unpublished data](#)). In addition, the BIISC prepared House Bill 2593 to amend the Hawai'i Revised Statute 91, which allows agencies to adopt emergency rules in instances of imminent peril to public health, including livestock and poultry health ([Martin, 2011, unpublished data](#); [Aila, 2012, unpublished data](#)). The rule was enacted into law in 2012 and allowed for a rapid response and removal of axis deer from the island of Hawai'i ([State of Hawai'i, 2012, unpublished data](#)).

The Hawai'i DOA established a "Noxious Weed List" of plants that are not allowed to be imported into the state; however, this list is not comprehensive and does not prevent importation of all potentially invasive plants (HAR 1981-Title 4, Subtitle 6, Chapter 68). The Department of Homeland Security-Customs and Border Protection (DHS-CBP) is responsible for inspecting commercial, private, and military vessels and aircraft, and related cargo and passengers arriving from foreign locations ([DHS-CBP, 2017, unpublished data](#)). However, CBP focuses on quarantine issues involving non-propagative plant materials; wooden packing materials, timber, and products; internationally regulated commercial species under CITES; and federally listed noxious plants, seeds, soils, and pests of concern to the continental United States, such as pests to mainland U.S. forests and agriculture. In 2011, House Bill 865 amended the statute to increase the fee imposed for inspection, quarantine, and eradication of invasive species contained in freight brought into the State (from 50 cents to 75 cents per 1000 pounds of freight) in an attempt to provide enough funding for enforcement of existing regulations ([HDOA, 2011, unpublished data](#)).

The Agricultural Research Service (ARS) is the chief scientific research agency for the USDA, and conducts research to find solutions for agricultural problems, including biocontrol. Because of the severity of the effects of the *Erythrina* gall wasp on native plants, agriculture and the plant industry, the ARS conducted a search for an effective biocontrol. A wasp from East Africa, *Eurytoma erythrinae*, a known predator of the *Erythrina* gall wasp, was extensively tested and ultimately released to help bring the *Erythrina* gall wasp infestation under control ([HDOA-ARS, 2010, unpublished data](#)). A later study showed that the success of the predatory wasp was dependent on local environmental factors such as drought which contributed to poorer health of the infected plants overall. A higher success of the predatory wasp is expected over the long term as populations of the *Erythrina* gall wasp decline ([Bell et al., 2013](#)).

Fire

Wildfires are most frequent in developed areas (but these are not the largest areas in acres consumed) (see Fig. 7). The Hawai'i Division of Forestry and Wildlife (DOFAW) and Hawai'i Wildfire Management Organization (HWMO) have adapted national fire education resources to local contexts in Hawai'i (Trauernicht et al., 2015). Fuel breaks are expensive to maintain in Hawai'i because of the terrain and year-round plant growth. Hawai'i's fire management community has had to consider alternate fuels management strategies to reduce fuels. The four county fire departments of Hawai'i, Kaua'i, Maui, and O'ahu respond to building, vehicle, wild-land, trash, and marine vessel fires, but are primarily trained and equipped for structural fires. The Hawai'i Division of Forestry and Wildlife (DOFAW) is the primary responder for wildfires on State land; however, DOFAW does not employ full-time firefighters. These agencies have mutual aid agreements, and can assist each other or be assisted by Federal agencies at Hawai'i Volcanoes National Park and the U.S. Army Garrison on Oahu or Hawai'i. Because fires are most frequent in the developed system, reducing these fires require addressing issues such as human behavior, public safety, education, economics, and disaster response.

Watershed and Water Resources Management

With the demise of plantation agriculture in Hawai'i in the 1990s (sugarcane and pineapple), large amounts of agricultural land and irrigation systems were made available. In response, the State plans to strengthen and expand the diversified agriculture industry. The agricultural water use and development plan prepared by the HDOA analyzes the needed capital improvements along with providing estimates of future water usage and agricultural needs (HDOA, 2003).

There are 16 Soil and Water Conservation Districts (SWCDs) in Hawaii, with a board that operates on a voluntary basis in partnership with the USDA-Natural Resources Conservation Service (NRCS). The NRCS enters into agreements (through the Farm Bill) with landowners to maintain their land-use operations according to NRCS standards by managing conservation plans that result in soil savings, reduction of sedimentation, control of invasive species, and reforestation of riparian buffers and declining habitats (HDLNR-DWLM and USDA-NRCS, 2012, unpublished data). Because soil acts as a water "filter" by buffering, degrading, and immobilizing various pollutants (e.g., chemicals, pesticides, nutrients), emphasis is placed on employing practices of conservation and sustainable use of the land (HDLNR-DWLM and USDA-NRCS, 2012, unpublished data).

The State's Commission on Water Resource Management (CWRM) also recognized the need to update the 2008 water resource protection plan; however, interim flow standards remain at status quo (no increase or decrease in the current stream flow rates) (CWRM, 2014, unpublished data). Recently, in-stream flow standards were set for four West Maui streams: Ukumehame Stream, Olowalu Stream, Kaua'ula Stream, and Launiupoko Stream (The Maui News, 2018, unpublished data). The CWRM Initiative report describes management measures, practices, and goals for watershed management in low- to high-intensity developed systems and golf courses, including those for storm water control, erosion prevention, sedimentation, movement of toxic substances. The report details each local agency's responsibilities for implementation of management measures and determines which regulatory and non-regulatory mechanisms are in place (HCZM, 2015).

Watershed partnerships are voluntary alliances of public and private landowners committed to protecting over 2 million acres of watershed lands in Hawai'i (Hawaii Association of Watershed Partnerships (HAWP), 2018, unpublished data). Partnerships are established on five islands: Hawai'i, Maui, Moloka'i, O'ahu, and Kaua'i. Most of the protected areas are in non-developed habitat; however, about 20,000 ac (8000 ha) of the developed system fall within areas of watershed partnership jurisdiction, depending on the water resources. The partners provide funding and other support, such as allowing construction of ungulate enclosure fencing on their properties. They also implement invasive plant removal, create fire buffer areas, and conduct predator control.

Vegetation Management

Landscape maintenance and tree pruning in developed habitat is also regulated by State, county, and federal laws. The City and County of Honolulu has rules and regulations regarding planting and maintenance of street trees with enforcement of penalties for violation of any provision of the rules (City and County of Honolulu, 1971). For example, street trees have other protections, e.g., protections for a seabird, the white tern or manu o kū (*Gygis alba*). The white tern occurs in the Pacific islands, but in Hawai'i is found only on O'ahu in low- to high-intensity developed systems of Honolulu (Pacific Rim Conservation, 2017, unpublished data). The O'ahu population is considered Threatened by the State of Hawai'i, but currently has no federal status. Besides the threat of predation by cats, rats, and barn owls, and egg and chick mortality from strong winds; careless tree trimming can also result in loss of eggs and chicks. Private, county, State, and federal organizations provide information to arborists and the general public regarding tree trimming if the birds are present. State and federal law prohibits disturbance of white terns and their eggs and chicks. Agencies do not allow trimming of trees while white terns are occupying them for nesting, and penalties for disturbance (fines) are in place.

The USDA-NRCS, the National Center for Appropriate Technology (NCAT), and the Hawaii College of Tropical Agriculture and Human Resources (CTAHR) provide recommendations to farmers regarding best farming practices including soil testing (for fertility and quality), erosion prevention, conservation tillage to improve water conservation, planting and harvesting flexibility, and improving soil tilth (condition) (CTAHR, 2018, unpublished data; NCAT, 2015, unpublished data; USDA-NRCS, 2018, unpublished data).

Open Space

There are rules and regulations concerning an “open space requirement” for low-, medium-, and high intensity developed systems. Open space is defined as noncontiguous, unbuilt, and unobstructed spaces at-grade between and adjacent to public and private structures, and must be maintained as a recreational or social facility. For example, the Kaka’ako Community Development District enforced incorporation of 54 ac (22 ha) of public recreation space and 16 ac (6.5 ha) of private recreation space (decks on private property) for any building construction in the Kaka’ako (downtown Honolulu) area ([HCDA, 2013, unpublished data](#)).

Stakeholder Engagement

The HWMO has an on-the-ground wildfire education program and facilitates Community Wildfire Protection Plans across the State. In addition, HWMO collaborates with fire responders, land managers, and the general public to foster environmental and cultural stewardship and implement projects that address land development and planning ([HWMO, 2018, unpublished data](#)).

The Conservation Fund provides partnership opportunities for residents and organizations to protect natural resources while also focusing on community development. >4000 ac (1619 ha) have been preserved on Maui for public use in partnership with the National Park Service. A strategic conservation plan for Kona on the island of Hawai'i includes a framework for guiding future land development and conservation decisions for North and South Kona. This plan includes recommendations to enhance green infrastructure and urban water management with selected areas for growth and for rural watershed lands ([The Conservation Fund, 2018, unpublished data](#)).

The Outdoor Circle is a non-profit organization founded in 1912, with the primary mission of protecting and enhancing the environment of Hawai'i for future generations. Members first established urban green spaces by planting trees, establishing public parks and gardens, and were instrumental in banning placement of advertising billboards. They continue work with each county specific to the needs of the local communities, plant and protect trees and open space, provide environmental education, and promote community beautification ([The Outdoor Circle, 2018, unpublished data](#)).

The USDA-NRCS, in cooperation with State and county agencies, published a booklet for public distribution describing the various ways the public can contribute to resource conservation in the developed system ([USDA-NRCS, 2012, unpublished data](#)). The booklet describes many conservation practices including composting, managing beneficial and harmful insects, managing native and invasive plants (including xeriscaping and soil management), and water conservation and storm water control methods, with references and links to other information resources.

Interactions of Stressors and Conservation Efforts

The developed system in Hawai'i is primarily under private ownership (358,652 ac, 145,141 ha), more than five times as much as under State ownership (69,200 ac, 28,004 ha), therefore, any benefits of conservation actions are primarily accomplished through voluntary measures ([Hawaii State Office of Planning, 2017](#)). Areas of developed systems under State ownership benefit from State conservation and protection rules and regulations as enforced by State agencies or private organizations in partnership with the State.

Invasive species already in Hawai'i require intensive long-term management actions (coconut rhinoceros beetle, *Erythrina* gall wasp). The Invasive Species Committees (ISCs) on each island have a better chance of effective control of invasive plants and animals by using methods for rapid response (detection) and control (eradication). Some recent examples of invasive plant species quickly intercepted and controlled by the ISCs are *Nasella tenuissima* (Mexican feather grass), *Cryptostegia grandiflora* (rubber vine), and *Melinis nerviglumis* (ruby grass) ([HISC, 2018c, unpublished data](#)).

Fire is one of the major threats to the developed system. Implementation of fire management plans by private and State landowners contributes the most to fire prevention, along with efforts to foster educational programs concerning fire and environmental stewardship for private landowners and land managers.

Watershed and water resources management actions are implemented in the developed system by enforcement of state and county laws and regulations. Watershed partnerships play a large part in conservation at the landscape level, and involve cooperation between private, state, county, and agencies.

Vegetation management is conducted at a smaller scale, through both private and State actions, with some contributions at the federal level (USDA-NRCS) regarding best management practices for agriculture.

Provision of open space is part of residential construction requirements (implemented mostly through private landowners).

Stakeholder engagement and cooperation between landowners and State and federal agencies provides benefits of educational programs, conservation planning for community development, and planning for urban green spaces and green infrastructure.

The conservation efforts currently conducted and discussed above limit some of the effects of the stressors on the developed system, but do not eliminate them. The stressors continue to contribute to the further increase in area of the developed system and the increase in loss of species diversity, loss of water resources, and degradation of agricultural land and open areas.

Future Scenarios

The condition of the developed system in the foreseeable future is based on potential changes in three conservation management parameters (CMPs). These conservation parameters capture the social and legal mechanisms under which natural resource conservation is carried out. The CMPs are as follows:

1. *Conservation values*: Stakeholder involvement and public opinion determine the formulation, implementation and funding of natural resource conservation within laws and development plans.
2. *Laws and biosecurity*: National, state, county, and city laws and regulations are the means by which natural resource conservation and biosecurity are supported and implemented (e.g., hunting regulations, Clean Water Act, Endangered Species Act; and local laws, etc.).
3. *Development or conservation planning*: National, state, county, city, and private development plans or conservation plans define specific actions that result in losses or gains in natural resource conservation and biosecurity (impacts are only realized at the time of implementation).

These conservation management parameters are critical factors that drive the direction and magnitude of natural resource conservation, and determine foreseeable future scenarios. The year 2035 is the extent of “foreseeable future,” and is based on the projected divergence of IPCC Representative Concentration Pathway (RCP) climate change scenarios (van Vuuren et al., 2011a, 2011b; Miller, 2018, unpublished data).

The four foreseeable future scenarios considered in this assessment are:

Future Scenario One, Status Quo—The most likely foreseeable future; no change in natural resource conservation in the CMPs, so the current rate of change in land cover continues through the foreseeable future.

Future Scenario Two—A slight increase in natural resource conservation in the CMPs marginally improves conservation management.

Future Scenario Three—A slight to moderate decrease in conservation actions in the CMPs substantially decreases conservation management.

Future Scenario Four—A moderate to large increase in conservation actions in the CMPs substantially improves conservation management.

The future condition of the developed system in Scenario One, the status quo, was characterized from an assessment of change over time in developed land cover obtained from existing land cover maps (Amidon and Reeves, 2018, unpublished data). Based on these land cover maps, an annual rate of change for the developed system was estimated, and a projected change (in acres/hectares) was calculated for the year 2035. The resulting information on changes in land cover by 2035, as derived from existing land cover change estimates, is the extent of the developed system that is expected in the foreseeable future under Scenario One, the status quo, where conservation efforts remain unchanged and the current rate of change in land cover is also unchanged (Table 3).

The future conditions of the developed system for Scenarios Two, Three, and Four cannot be quantitatively (acres/hectares) estimated. However, the Scenario One estimate can provide a “baseline” for a qualitative characterization of changes in the future condition of the developed system under Scenarios Two, Three, and Four.

Changes in human population are captured only by the changes in the developed land cover footprint derived from land cover map analysis (Amidon and Reeves, 2018, unpublished data). Impacts from other sources of human activities or human-caused system stressors (e.g., plant and animal diseases, wildfires, invasive species, etc.) are not well characterized in the land cover changes, but significantly contribute to increases in the land cover area dominated by nonnative vegetation. An assessment of island-by-island changes in human population is described by Miller (2018, unpublished data).

Also note that island-wide implementation of the CMPs is unlikely to have a significant effect on climate-related stressors (temperature, precipitation, and severe weather) resulting from global warming by 2035. This lack of CMP climate effects is due to the global lag in climate response to changes in greenhouse gas emissions that occurs on the order of centuries rather than years (Solomon et al., 2009; Gillett et al., 2011; Jevrejeva et al., 2012). Evidence of climate effects is also confounded by the large annual variation in the Pacific islands climate parameters, which is much greater than projected climate change by 2035. Although impacts from climate-related system stressors do not change across the four scenarios, they were included in this analysis because of their overall magnitude of potential importance to future system viability.

Table 3 Summary of overall condition for the developed system categories in the future scenarios.

<i>Developed habitat category</i>	<i>Scenario 1: Status quo</i>	<i>Scenario 2: Slightly improved</i>	<i>Scenario 3: Substantially decreased</i>	<i>Scenario 4: Substantially improved</i>
Open space	Slight increase	Slight increase	Decrease	Increase
Agriculture and cultivated land	Decrease	Slight increase	Decrease	Slight increase
Low, medium, and high-intensity developed	Increase	Slight increase	Significant increase	Slight to moderate decrease or redevelopment

Future Scenario One, Status Quo

Summary: Scenario One is considered the most likely future scenario, and serves as a “baseline” for comparing among the four future scenarios. There is no change in the implementation of the three CMPs between 2018 and 2035. A continuing current rate of change in land cover through this foreseeable future results in a slow but continuous change in the system, as described below.

Description: Using the current rate of change, the land cover for the developed system was calculated for the year 2035 (Amidon and Reeves, 2018, unpublished data). The projected change in land cover by 2035 is the only future scenario with quantitative values (acres or hectares). An expanding human population and increased development and general land use on all inhabited islands is anticipated, and therefore system stressors are expected to increase at a low annual rate. Scenario One has the greatest likelihood of occurring in the foreseeable future. The anticipated changes, under Scenario One, for each of the stressors affecting each category of the developed system are described below and are given in Table 4.

Developed system-open space: The current amount of open space on each island will see increases at the status quo rate, with proportionally little gain or loss of area (approximately $\pm 2 \text{ mi}^2$, $\pm 5 \text{ km}^2$) (Amidon and Reeves, 2018, unpublished data). Conservation values will stay the same. Government agencies, non-profit organizations, and private landowners will continue to contribute resources to conserve open space. Laws and regulations will be enforced with no changes or only a slight increase in effectiveness. Pollution, invasive plants and animals (axis deer, insects), and the numbers of wildfires, will increase at status-quo rates, and there will be a slight increase in altered hydrology and recreation/human access (land use). Climate change-associated stressors such as drought (and higher temperatures) will be slight to moderate and localized (Table 4). Climate change models are predicting a decrease in rainfall for the remainder of this century (HDLNR-DOFAW, 2016). The decrease in rainfall will worsen drought conditions in the developed system, impacting farmers, cattle ranchers, and individuals who rely on catchment water systems (Hawaii Civil Defense, 2011). Drought also increases thereby increasing the potential for wildfires (Hawaii Civil Defense, 2011). Resiliency of open space will remain at status quo levels, with a slight decrease for the foreseeable future, due to pressure from continued growth of impervious areas and the associated increase of low- to high-intensity development and continued low-level impacts

Table 4 Responses of the developed system stressors in foreseeable future scenarios.

Conservation management parameters (CMPs)				
Conservation values	Stakeholder involvement and public opinion influence the formulation, implementation, and funding of natural resource conservation and biosecurity (NRC/B) within laws and development or conservation plans			
Laws and biosecurity	National, state, county, and city laws and regulations are the means by which NRC/B are supported and implemented			
Planning for development or conservation	National, state, county, city, and private development plans or conservation plans define actions that result in losses or gains in NRC/B (impacts realized at implementation)			
Foreseeable future scenarios and the resulting developed system conditions				
	Scenario One:	Scenario Two:	Scenario Three:	Scenario Four:
Use Foreseeable Future Scenario One as a “baseline” to characterize changes in <i>Conservation Actions</i> and <i>System Conditions</i> in Future Scenarios Two, Three and Four	<i>CMPs:</i> Unchanged in support for NRC/B <i>Conservation actions:</i> No change; current rate of land cover change continues through the foreseeable future <i>System condition:</i> System area, quality, and sustainability slowly decrease through the foreseeable future	<i>CMPs:</i> Small increase in support for NRC/B <i>Conservation actions:</i> Marginal increase. <i>System condition:</i> System area is unchanged through the foreseeable future; habitat quality and sustainability are slightly enhanced through the foreseeable future	<i>CMPs:</i> Small to moderate decrease in support for NRC/B <i>Conservation actions:</i> Substantial decrease <i>System condition:</i> Urban and agricultural uses are prioritized over conservation; system area, quality, and sustainability substantially decrease through the foreseeable future	<i>CMPs:</i> Moderate to high increase in support for NRC/B <i>Conservation actions:</i> Substantial increase <i>System condition:</i> Robust, sustained effort to restore, manage, and expand conservation; system area, quality, and sustainability substantially increase through the foreseeable future
System stressors				
Development	Small to moderate increase	No change (redevelop)	Moderate to large increase	Small to moderate decrease
Altered hydrology	No change to small increase	No change	Larger increase	Small decrease
Recreation access	Small increase	Small increase	Larger increase	Larger increase
Water pollution	Small increase	No change	Larger increase	Small decrease
Invasive species	Small increase	Small increase	Larger increase	Small decrease
Plant diseases	Small increase	Small increase	Larger increase	No change to small decrease
Fire	Small to moderate increase	Small increase	Larger increase	No change to small increase
Climate				
Temperature	Small to moderate increase	Small to moderate increase	Small to moderate increase	Small to moderate increase
Precipitation	Small decrease	Small decrease	Small decrease	Small decrease
Sea level	Small increase	Small increase	Small increase	Small increase

of stressors. Those islands currently with a smaller amount of open space (Moloka'i, O'ahu), relative to the islands of Lāna'i and Ni'ihau, may see more significant effects from stressors because the amount of open space is smaller initially, resulting in less redundancy and representation of this habitat (see Figs. 1–4). Although an analysis was not done specifically for Midway Atoll, we expect the amount of open space to remain the same at status quo levels, keeping in mind the possible rise in sea level (and concurrent loss of open space) at a future time period beyond 2035.

Developed system—Agriculture/Cultivated land: Agricultural/cultivated areas will lose the largest amount of area (almost 10 mi², 26 km²) of all the categories of the developed system (Amidon and Reeves, 2018, unpublished data). Moloka'i will lose 6%, O'ahu will lose 32%, Hawai'i will lose 49%, and Kaua'i will lose 100% (Table 5). There is no calculated change in area for Kaho'olawe, Lāna'i, or Ni'ihau. This loss may contribute to the continued increase in one or more of the other developed system categories: open space, and impervious areas of low- to high-intensity developed system. Conservation values will stay the same. Government agencies, non-profit organizations, and private landowners will continue to contribute resources to conserve agricultural areas. Laws and regulations will be enforced with no changes or only a slight increase in effectiveness. Pollution, invasive plants and animals (axis deer, insects), and the numbers of wildfires, will increase at status-quo rates, and there will be a slight increase in altered hydrology and recreation/human access (open space use). Climate change-associated stressors such as drought (and higher temperatures) will be slight to moderate and localized (Table 4). Resiliency of agriculture/cultivated land will remain at status quo levels, with a slight decrease for the foreseeable future, due to pressure from continued growth of impervious areas associated with low- to high-intensity development and continued low-level impacts of stressors. Those islands currently with a smaller amount of agricultural/cultivated land (Lāna'i, Kaho'olawe), relative to the islands of Kaua'i, Maui, and Hawai'i, may see more significant effects from stressors because the amount of agricultural/cultivated land is smaller to begin with, resulting in less redundancy and representation of this habitat (see Figs. 1–4).

Developed system—Low-intensity developed, medium-intensity developed, and high-intensity developed: Impervious surfaces associated with the three levels of intensely developed habitat will increase slightly at the status quo rate, with proportionally small gains in area (approximately 4 mi², 10 km²) (Amidon and Reeves, 2018, unpublished data). Kaua'i will gain 16% of developed habitat, Hawai'i will gain 14%, Maui will gain 12%, O'ahu will gain 6%, Lāna'i will gain 4%, and Moloka'i will gain 1% (Table 5). There is no calculated change in the amount of developed area for Kaho'olawe and Ni'ihau. Conservation values will stay the same. Government agencies, non-profit organizations, and private landowners will continue to enforce provisions of open space and recreational use areas concurrent with development. Laws and regulations will be enforced with no changes or only a slight increase in effectiveness. Pollution, invasive plants and animals (axis deer, insects), and the numbers of wildfires, will increase at status-quo rates, and there will be a slight increases in altered hydrology and recreation/human access (land use). Climate change-associated stressors such as drought (and higher temperatures) will be slight to moderate and localized (Table 4). Resiliency of low- to high-intensity developed habitat will remain at status quo levels, with an increase for the foreseeable future, due to continued growth of impervious areas associated with this habitat and continued low-level impacts of stressors. Those islands currently with the smallest amounts of low- to high-intensity developed habitat (Ni'ihau, Kaho'olawe) may not see significant increases of this habitat type because of their generally slower growth rate. The islands with a moderate amount of low- to high-intensity developed habitat (Lāna'i, Moloka'i, Hawai'i) may see a more significant increase in the amount of these categories, resulting in more redundancy and representation of this habitat (see Figs. 1–4). Although an analysis was not done specifically for Midway Atoll, we expect the amount of low- to high-intensity developed space to remain the same at status quo levels, keeping in mind the possible rise in sea level (and concurrent loss of low- to high-intensity developed habitat) at a future time period beyond 2035.

Table 5 Estimated acreages and percent of island in developed systems currently (2012) and in the foreseeable future (2035) for the Hawaiian Islands (excluding the Northwestern Hawaiian Islands) (Amidon and Reeves, 2018).

System	Island	Current (2012)		Future (2035)		
		Acres	% of Land	Acres	% of Land	% Change 2012–35
Developed	Hawai'i	76,064	3	87,090	3	14
	Maui	34,550	8	38,528	8	12
	Kaho'olawe	149	1	149	1	0
	Lāna'i	3227	4	3369	4	4
	Moloka'i	6658	4	6743	4	1
	O'ahu	90,052	24	95,053	26	6
	Kaua'i	28,402	8	32,949	9	16
	Ni'ihau	332	1	332	1	0
Cultivated	Hawai'i	96,858	4	96,403	4	0
	Maui	64,928	14	33,328	7	–49
	Kaho'olawe	0	0	0	0	0
	Lāna'i	112	0	112	0	0
	Moloka'i	3760	2	3533	2	–6
	O'ahu	32,261	9	22,031	6	–32
	Kaua'i	35,324	10	0	0	–100
	Ni'ihau	0	0	0	0	0

Future Scenario Two

There is a slight increase in the CMPs that marginally improves conservation management. Scenario 2 has the third most likelihood of occurring in the foreseeable future.

Summary: Conservation agencies and stakeholders work with increased but limited resources to slow or stop the degradation of the developed system.

Description: Scenario Two is essentially “status quo” with minor improvements in the three CMPs. Though there is an expanding human population in Scenario Two, development is not expected to substantially increase. Slightly improved biosecurity efforts should help reduce invasive species and plant diseases but increases are still expected. The small increased support of natural resource management in the CMPs is not expected to greatly alter wildfire frequency and intensity, but these might lower slightly compared to Scenario One. The CMP supported conservation will not prevent, mitigate, or reverse the impacts of climate change-related stressors, as discussed for each category of the developed system, below. The anticipated changes, under Scenario Two, for each of important habitat stressors for the developed system are given in [Table 3](#).

Developed system—Open space: The current amount of open space on each island will see small increases ([Amidon and Reeves, 2018, unpublished data](#)). Conservation values regarding recreation and human access, invasive plants, animals and diseases, and wildfires will increase. Government agencies, non-profit organizations, and private landowners will increase enforcement of laws and regulations to protect open space from these five stressors, and possibly new efforts, laws, and regulations will be implemented. Altered hydrology and pollution and their effects on open space will not change. The effects of climate change-associated stressors such as drought may have a localized decrease because of conservation actions such as vegetation management through ungulate (axis deer) control and nonnative plant removal to improve water retention, even though air temperatures will moderately increase ([Table 4](#)). Resiliency of open space will slightly improve for the foreseeable future, due to lessened pressure from continued growth of impervious areas associated with low- to high-intensity development and some low-level management of stressors. Those islands currently with a smaller amount of open space (Moloka'i, O'ahu), relative to the islands of Lāna'i and Ni'ihau, may see more significant effects from stressors because the amount of open space is smaller initially, resulting in less redundancy and representation of this habitat (see [Figs. 1–4](#)). Although an analysis was not done specifically for Midway Atoll, we expect the amount of open space to remain the same or slightly increase because of better management; however, the possible rise in sea level at a future time period beyond 2035 may negate any increases in open space.

Developed system—Agriculture/cultivated land: Agricultural areas will continue to lose area ([Amidon and Reeves, 2018, unpublished data](#)); however, as conservation values increase, government agencies, non-profit organizations, and private landowners will continue to contribute resources to conserve these areas. Laws and regulations to protect agriculture/cultivated land from recreation and human access, invasive plants, animals and diseases, and wildfires will increase, and possibly new efforts, laws, and regulations will be implemented. Altered hydrology and pollution and its effects to agriculture/cultivated land will not change. The effects of climate change-associated stressors such as drought may have a localized decrease, even though temperatures will moderately increase ([Table 4](#)). Resiliency of agriculture/cultivated land will slightly improve for the foreseeable future, due to lessened pressure from continued growth of low- to high-intensity development and some low-level management of stressors. Those islands currently with a smaller amount of agricultural/cultivated land (Lāna'i, Kaho'olawe), relative to the islands of Kaua'i, Maui, and Hawai'i, may see more significant effects from stressors because the amount of agricultural/cultivated land is smaller initially, resulting in less redundancy and representation of this habitat (see [Figs. 1–4](#)).

Developed system—Low-intensity developed, medium-intensity developed, and high-intensity developed: Some development will occur but not at an increased rate, and there may be some redevelopment rather than newly created developed areas ([Amidon and Reeves, 2018, unpublished data](#)). Conservation values regarding recreation and human access, invasive plants, animals and diseases, and wildfires will increase. Government agencies, non-profit organizations, and private landowners will increase enforcement of laws and regulations to protect low-, medium-, and high-density developed habitat from stressors, and possibly new efforts, laws, and regulations will be implemented. Altered hydrology and pollution and their effects on the high-intensity developed system will not change. The effects of climate change-associated stressors such as drought may have a localized decrease because of conservation actions such as vegetation management through ungulate (axis deer) control and nonnative plant removal to improve water retention, even though air temperatures will moderately increase ([Table 4](#)). Resiliency of low- to high-intensity developed habitat will not change significantly. Those islands currently with the smallest amounts of low- to high-intensity developed habitat (Ni'ihau, Kaho'olawe) may not see significant increases of this habitat type because of their generally slower growth rate. The islands with a moderate amount of low- to high-intensity developed habitat (Lāna'i, Moloka'i, Hawai'i) may see a more significant increase in the amount of these categories, resulting in more redundancy and representation of this habitat (see [Figs. 1–4](#)). Although an analysis was not done specifically for Midway Atoll, we expect the amount of low- to high-intensity developed space to remain the same, keeping in mind the possible rise in sea level (and concurrent loss of low- to high-intensity developed habitat) at a future time period beyond 2035.

Future Scenario Three

There is a low to moderate decrease in conservation actions in the CMPs that substantially decreases the conservation management. Scenario Three has the second highest likelihood of occurring in the foreseeable future.

Summary: All natural resource management actions in the CMPs are set aside in deference to land use for development. With extensive localized management, some native species may persist in park-like settings or in areas where development is not possible.

Description: Scenario Three has substantial declines in natural resource conservation within the three CMPs. An increasing human population is supported in its use of land for development over the conservation of native landscapes. Areas that cannot support development become the only areas of free-living native species. An expanding human population requires increased land use for agriculture and development with no encumbrance from natural resource management. Biosecurity controls are significantly weakened in this Scenario leading to an increase in invasive species and new plant diseases. Combined, these factors will result in substantial increases in wildfire frequency, intensity, and extent. The substantial loss of CMP supported conservation may locally aggravate the impacts of climate change-related stressors. The anticipated changes under Scenario Three for each of the habitat stressors important to each category of the developed system are discussed below and are given in [Table 4](#).

Developed system—Open space: The current amount of open space on each island will decrease as a result of less enforcement of rules and regulations by government agencies, non-profit organizations, and private landowners ([Amidon and Reeves, 2018, unpublished data](#)). Conservation values will decrease resulting in a higher increase in recreation and human access, more invasive plants and animals, and more wildfires. Altered hydrology and pollution will have greater negative effects on open space as the pollutants from human use (construction) and agriculture are added to open space with fewer controls and without remediation. The effects of climate change such as higher temperatures and drought will also increase ([Table 4](#)). Resiliency of open space will decrease for the foreseeable future, due to increased pressure from continued growth of impervious areas associated with low-to high-intensity development and no management of stressors. Those islands currently with a smaller amount of open space (Moloka'i, O'ahu), relative to the islands of Lāna'i and Ni'ihau, will see greater effects of the negative impacts on open space, resulting in less redundancy and representation of this habitat (see [Figs. 1–4](#)). Although an analysis was not done specifically for Midway Atoll, we expect the amount of open space to decrease, resulting from the continued rise in sea level and continued loss of open space at a future time period beyond 2035.

Developed system—Agriculture/cultivated land: The current amount of agriculture/cultivated land on each island will decrease as a result of an increase in low-, medium-, and high-intensity development ([Amidon and Reeves, 2018, unpublished data](#)). Enforcement and creation of new laws and regulations to protect agriculture/cultivated land from recreation and human access, invasive plants, animals and diseases, and wildfires will decrease because of the increase in the effects of these stressors on the developed system with fewer control actions and no remediation. Altered hydrology and pollution and their effects on agriculture/cultivated land will increase. The effects of climate change such as higher temperatures and drought will also increase ([Table 4](#)). Resiliency of agriculture/cultivated land will decrease for the foreseeable future, due to increased pressure from continued growth of low- to high-intensity development and no management of stressors. Those islands currently with a smaller amount of agricultural/cultivated land (Lāna'i, Kaho'olawe), relative to the islands of Kaua'i, Maui, and Hawai'i, may see more significant effects from stressors because the amount of agricultural/cultivated land is smaller initially, resulting in less redundancy and representation of this habitat (see [Figs. 1–4](#)).

Developed system—Low-intensity developed, medium-intensity developed, and high-intensity developed: Low-intensity, medium-intensity, and high-intensity developed systems will increase in area ([Amidon and Reeves, 2018, unpublished data](#)). Conservation values decrease resulting in a higher increase in recreation and human access, more invasive plants and animals, and more wildfires, resulting in greater degradation of the developed system. Laws and biosecurity regulations and enforcement will decrease, exacerbating the effects of the increase of the human use, pollution, invasive species, and wildfires. Diseases carried by invasive plants and animals will also increase. Altered hydrology and pollution will have greater effects on developed habitat such as impacts from water extraction, and impacts from pollutants on the plants and animals in the developed system. The effects of climate change such as higher temperatures and drought will also increase. Changes to community planning will no longer be limited by conservation measures to control these stressors ([Table 4](#)). Resiliency of low- to high-intensity developed habitat will actually increase. Those islands currently with the smallest amounts of low- to high-intensity developed habitat (Ni'ihau, Kaho'olawe) may not see significant increases of this habitat type because of their generally slower growth rate. The islands with a moderate amount of low- to high-intensity developed habitat (Lāna'i, Moloka'i, Hawai'i) will see a significant increase in the amount of these categories, resulting in more redundancy and representation of this habitat (see [Figs. 1–4](#)). Although an analysis was not done specifically for Midway Atoll, we expect the amount of low- to high-intensity developed space to remain the same, resulting from the continued rise in sea level (and concurrent loss of low- to high-intensity developed habitat) at a future time period beyond 2035.

Future Scenario Four

There is a moderate to large increase in conservation actions in the CMPS that substantially improves conservation management.

Summary: An overt and robust, active, ongoing effort using moderate to major resources is made to identify and prioritize, with partners and stakeholders, the systems needed for conservation, and to actively restore and expand these systems. Scenario Four has the fourth most likelihood of occurring in the foreseeable future.

Description: A substantial emphasis on natural resource conservation is present in the three CMPs, reflecting increased societal concern for declines in natural habitats and biodiversity. Active and well-supported natural resource management begins to restore this habitat and ecosystem and expand their landscape areas. The needs of an expanding human population are addressed through more efficient land use governance based on redevelopment rather than development of new areas. Modern and novel agricultural

practices focus on those that do not affect existing natural areas or areas needed for native system restoration. Substantially improved biosecurity regulations decrease introductions of invasive species and plant disease. These improved land management actions result in decreased wildfire intensity, frequency, and extent. The substantial increase in CMP supported conservation may locally mitigate the effects of climate change-related stressors, but climate change is expected to continue. The anticipated changes, under Scenario 4, for each of the habitat stressors for each category of the developed system are discussed below and given in Table 4.

Developed system—Open space: The current amount of open space on each island will increase (Amidon and Reeves, 2018, unpublished data). Conservation values regarding recreation and human access, invasive plants, animals and diseases, and wildfires will be at their highest resulting in greater plant and animal diversity and greater water availability. Government agencies, non-profit organizations, and private landowners will increase enforcement of laws and regulations to protect open space from these five stressors, and new efforts, laws, and regulations will be implemented. Altered hydrology and pollution and their effects on open space will decrease. The effects of climate change-associated stressors such as drought may have a localized decrease, even though temperatures will moderately increase (Table 4). Resiliency of open space will improve for the foreseeable future, due to lessened pressure from growth of impervious areas associated with low-to high-intensity development and active management of stressors. Open space on all islands will see fewer effects from stressors resulting in more redundancy and representation of this system (see Figs. 1–4). Although an analysis was not done specifically for Midway Atoll, we expect the amount of open space to remain the same or slightly increase because of better management; however, the possible rise in sea level at a future time period beyond 2035 may negate any increases in open space.

Developed system—Agriculture/cultivated land: Agricultural areas will remain the same or possibly gain area (Amidon and Reeves, 2018, unpublished data). As conservation values increase, government agencies, non-profit organizations, and private landowners will continue to contribute resources to conserve these areas. Laws and regulations to protect agriculture/cultivated land from recreation and human access, invasive plants, animals and diseases, and wildfires will increase, and possibly new efforts, laws, and regulations will be implemented. Altered hydrology and pollution and its effects to agriculture/cultivated land will decrease. The effects of climate change-associated stressors such as drought may have a localized decrease, even though temperatures will moderately increase (Table 4). Resiliency of agriculture/cultivated land will improve for the foreseeable future, due to lessened pressure from continued growth of low- to high-intensity development and active management of stressors. Those islands currently with a smaller amount of agricultural/cultivated land (Lānaʻi, Kahoʻolawe), relative to the islands of Kauaʻi, Maui, and Hawaiʻi, may see more significant improvement because the amount of agricultural/cultivated land is smaller initially, resulting in more redundancy and representation of this system (see Figs. 1–4).

Developed system—Low-intensity developed, medium-intensity developed, and high-intensity developed: Low-intensity, medium-intensity, and high-intensity developed systems will decrease in area (Amidon and Reeves, 2018, unpublished data). Conservation values will increase resulting in managed recreation and human access, fewer invasive plants and animals, and fewer wildfires. Laws and biosecurity regulations and enforcement will increase, lessening the effects of the increase of human use, pollution, invasive species, and wildfires. Diseases carried by invasive plants and animals will also decrease. Altered hydrology and pollution will be better managed and have lesser effects on developed habitat. The effects of climate change-associated stressors such as drought may have a localized decrease, even though temperatures will moderately increase (Table 4). Changes to community planning will better implement conservation measures to control these stressors (Table 4). Resiliency of low- to high-intensity developed habitat will stay the same. Those islands currently with the smallest amounts of low- to high-intensity developed habitat (Niʻihau, Kahoʻolawe) may not see significant increases of this system type. The islands with a moderate amount of low- to high-intensity developed systems (Lānaʻi, Molokaʻi, Hawaiʻi) will see a more controlled increase in the amount of these categories, resulting in more redundancy and representation of these systems (see Figs. 1–4). Although an analysis was not done specifically for Midway Atoll, we expect the amount of low- to high-intensity developed space to remain the same, keeping in mind the possible rise in sea level (and concurrent loss of low- to high-intensity developed habitat) at a future time period beyond 2035.

Summary

Development, urbanization, and neglect of an ecological system can contribute to further loss of functional capacity of the system including loss of biodiversity. If management of stressors and other conservation actions are conducted, the loss can be kept at status quo, or possibly reversed, leading to an improvement in systems functions. Currently, for the foreseeable future (until 2035), we estimate that changes to the developed system in Hawaii will remain at status quo, with no significant gain or loss in functional capacity.

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Sustainability Science in Concept and Practice: An Introduction to Human and Social Systems

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Abstract

Given the scale of global change, we can fairly conclude that studying the biomes of our Earth must be accompanied by an investigation into why humans interact with biomes the way they do. Sustainability science is an emerging discipline addressing this need with distinct theories and lines of research while remaining deeply connected with related disciplines that link human and natural sciences such as conservation biology, anthropology, ecological economics, and sociology. In this article, we introduce and summarize how researchers from a wide variety of disciplines share work and ways of thinking that are critical for anyone studying human and social systems in both biomes and anthromes.

Introduction

What is the purpose, in an encyclopedia focused on biomes, of 25 articles on sustainability in concept and practice? Articles in the previous section focused on the idea of anthromes, or anthropogenic biomes. Those articles review the multitude of ways that human and social systems have shaped biomes via direct interaction with local, regional, and global landscapes and as a consequence of an increasing human population. Given the scale of these changes to local and global ecosystems, we can fairly conclude that studying the biomes of our Earth must be accompanied by an investigation into how and why humans have changed and used the natural resources within biomes and how our actions threaten the integrity, and perhaps the likelihood of continued persistence, of said biomes. At the same time, we should seek to understand the potential for humans to create positive change, emerge as leaders, and educate future generations.

Importantly, humans are not a monolithic group. Individuals and communities live in different places, have different histories and values, and response to different incentives. To that end, this section introduces you to some of the broader concepts, issues, and discussions that are occurring in disciplines outside of, but related to, scholarship in the natural sciences presented in the other volumes of this encyclopedia. In particular, we introduce you to the field of sustainability science and associated discourses from disciplines closely entwined with the work to create a sustainable society on our planet.

What Is Sustainability Science?

Sustainability science is an emerging discipline with its own theories and lines of research while remaining deeply connected with related disciplines that link human and natural sciences such as conservation biology, anthropology, ecological economics, and sociology (Clark, 2007; Kates, 2011). Sustainability scientists seek to link the study of natural and human systems with the explicit goal to create a world that can provide for all people while protecting natural resources and all species. Given the intimate and diverse connections between human and natural systems, any student or practitioner that seeks to protect biomes and associated flora and fauna must also understand the human and social systems. To understand, and ultimately influence, human behavior, laws and policies, and the paradigms that govern our decisions, we must seek to understand and integrate the knowledge that comes from diverse areas of study. In the articles below, researchers from a wide variety of disciplines share work and ways of thinking that are critical for anyone studying biomes or anthromes.

This section starts with an overview of two key theories that are at the heart of sustainability. Domazet et al. provide an overview of key models utilized by sustainability scientists, including the planetary boundaries and Doughnut Model. This latter model of economics was created by Kate Raworth as a way to visualize “social foundations of development to be achieved and biospheric boundaries not to be crossed.” Next, Quinn and Quinn explain the concept of Coupled Human-Natural Systems, a model that emerged largely from the field of ecology. They offer examples of key dynamics within CHANS that scientists and practitioners should be familiar with to engage in dynamic systems-thinking including: spatial and temporal scale, heterogeneity, and vulnerability within anthromes.

More narrowly focused on valuation theories, the next two articles consider how our current economic paradigms drive decision-making that pushes us past planetary boundaries, while also exploring alternative economic theories that can help create sustainable societies. and economic system evaluations. Domazet et al. overview the concept of degrowth, an economic framework that “re-orient economic activity away from material production” by decoupling capitalist economic growth with social well-being based

on the fundamental idea that there cannot be infinite economic growth on a finite planet. Extending this theme further, Collste challenges the “business as usual” model of economic growth by reviewing four alternative approaches to mainstream economics; Post-Keynesian economics, Critical Institutional Economics, Ecological Economics, and systems dynamics.

Much like current scholarship more broadly (e.g., [Chan et al., 2016](#)), the above authors all note how the value of anthromes, biomes, and natural resources is more than the economic value. Addressing this important theme, three authors help us examine the many different ways humans value the environment and our ever-changing and complicated relationships to nature. Allen provides an overview of how different working definitions of “values” and “valuation” from disciplines such as economics, anthropology, and philosophy have shaped assumptions about human behavior, and consequently, decisions and policies about conservation. Stone examines the role of ethics in deciding how and when to value anthromes by overviewing three ethical frameworks; descriptive moral psychology, traditional ethical theory, and environmental sustainability, that can be used to establish “ethical values for managing anthromes and principles for evaluating the human conduct that creates and modifies them.” Speitz critically examines the very idea of wilderness by looking at how views on the interconnection and/or separation of wilderness and humanity, and the resulting shifting purposes of conservation, has changed in the past century.

Sustainability science is ultimately about helping people create positive change to ensure a safe and healthy planet ([Raworth, 2017](#)). Therefore, much research and consideration are devoted to change-making and change-makers. These subsequent articles examine critical questions of *who* creates change and by looking at the roles of leaders ([Ferdig, 2007](#)). Ferdig disabuses us of the notion that a sustainability leader must be a charismatic visionary individual with global prominence and influence. She offers a definition of a sustainability leader as “anyone – regardless of background, social standing, expertise or positional power – who takes responsibility for understanding and generating workable solutions with others.” She offers 12 keys to practicing sustainability leadership. More narrowly, Burbach and Delozier look at a specific leadership role, the boundary spanner. A boundary spanner is someone who can “reach across organizational borders to build relationships, interconnections, and interdependencies in order to manage complex problems.” They use the increasing challenges within water management to examine the role that boundary spanners play in collaboration. Lastly, Breesawitz looks at how leaders can utilize communication tactics and conflict management to influence behavior among followers. He also looks at the interplay of leadership roles with environmental education. This section also offers three separate papers on educational issues (see below).

As noted above, it is not just who creates change but also how. The following five articles address *how* change is created by looking at the roles of leaders, interconnected disciplines, and organizations including aquariums and zoos, and cooperatives. Derezotes looks at the need for interdisciplinarity in sustainability and provides what he calls an ecobiopsychosocialspiritual approach. This article combines the insights of ecopsychology with social justice values by exploring the links between the well-being of anthromes and biomes with social and human well-being. Mann, Ballantyne, and Packer offer a look at the role of aquariums and zoos in promoting conservation and individual behavior change while also exploring the changing roles served by these essential organizations. Specific case studies of behavior change promotion are included such as; sustainable seafood, domestic cats, and the environmental impact of releasing balloons. Akanji proposes the cooperative as a principle unit for environmental management, arguing that cooperatives provide all members access to information, inclusive participation, and access to justice, which are necessary for holistic and sustainable environmental management. Lastly, an important article examines the need for, and current lack of, diversity and inclusion in conservation science and practice.

Next, three authors provide context for examining *how* change is created as well as barriers to achieving sustainable practices in light of uncertainty and complexity in both human and natural systems. First Bamberg and Schulte overview central questions asked by environmental psychologists and utilize compelling research within another sub-discipline, health psychology, to examine five overarching themes of processes present during behavior change: motives, self-regulation, resources, habits, and environmental/social influences. They also discuss the practical implications of said research for helping people adopt a more sustainable lifestyle. One frequently discussed aspect of behavior change is associated with farming and food systems. Indeed, when individuals begin to consider how to live a more sustainable lifestyle, one of the first things they question is their diet. Bignet et al. review studies on metrics that define and/or assess the health and environmental impacts of different dietary choices. Lastly, the concept of “sense of place” is an important theory utilized by sustainability science researchers. Knapp explores how sense of place shapes and is, in turn, shaped by anthromes. She then examines how sense of place may influence responsiveness to climate change. While sense of place has been primarily considered a positive motivator for environmental conservation, Knapp shows that it is sense of place that may lead to “resistance, slow response, active adaptation or transformed sense of place” when confronting climate change. This is a key point in many topics where our initial perception of an idea may need to change in the face of more information or nuance.

Scientists are often criticized for an inability to effectively communicate research to mass audiences, contributing to low levels of scientific understanding and therefore low levels of support for behavior change and environmental policies by the public ([Lindenfeld et al., 2012](#)). Five authors provide perspectives on different areas where communication of sustainability is important including on social media, by individuals working on conservation projects, and in agriculture. Reilly looks at the application of social media for sustainability communication by individuals, corporations, and public entities. She examines critical concerns of online communication for sustainability including greenwashing and the challenges of measuring sustainability performance. Sklair and Boykoff examine how anthromes have appeared in mass media coverage of climate change and which ideas of anthromes have appeared in mass media coverage of the Anthropocene. They show how media coverage of “anthro” and “climate change” has increased in popular news media in the last decade. The authors then examine how anthromes such as urban cities, croplands, rangelands, and forests are discussed in regards to “the anthropocene”.

Briggs looks at the challenges faced in communicating science to a broad audience including use of jargon and the lack of science literacy among the general populace. She first summarized the history of science communication and then provides an overview of methods used to successfully communicate science and conservation projects. Briese looks specifically at science communication within agriculture and the role of extension scientists and public and private crop advisors play in communicating science to farmers. He examines how individuals in these roles become “trusted partners” to deliver the latest information and research to the men and women working on the farm. Lastly, to address the need for better communication, Bernier explores a deep human instinct that can be used in communicating sustainability: storytelling. He offers specifics on creating a “sustainability story” that is compelling to the reader, communicates knowledge, and inspires action. He concludes with a list of sustainability story examples.

One of the most important topics for understanding how to create a sustainable planet is the role of education (Tilbury, 1995). Below are three unique articles that examine how education can contribute to peoples’ understanding of conservation and sustainability in biomes and anthromes. The first article looks at the broader role for education while the following papers look specifically at those who are training to work in conservation. Powell, Smith, and Brown begin their article that focuses on the importance of training wildlife biologists to work in anthromes and on private lands with a critique of current higher education training that focuses on public lands management. They then offer a case study of a modification to the learning objectives for a fisheries and wildlife degree program at the university level and offer suggestions to enhance efforts to train wildlife biologists to work in the arena of anthromes and private land. Davis shares principles of education for sustainability including: enabling learners to see issues and solutions through critical thinking and developing agency and transformative capabilities. She then offers case studies of how education for sustainability is being applied across a range of educational contexts, from K12 through higher education. Last, Wood provides a personal narrative as a young conservationist training to protect nature in a time of increased and rapid anthropogenic change. She documents three key considerations as conservation moves further into the 21st century; exercising flexibility in where conservation occurs, more openness to what a conservationist may look like, consideration of a wide range of necessary skills for innovative problem-solving, understanding the importance of experiences in influencing behaviors, and engaging non-scientific audiences.

While by no means comprehensive, the articles above provide an overview of intersectionality and interdisciplinary considerations necessary for today and tomorrow’s sustainability scientists, conservation biologists, and practitioners seeking to protect our environment while creating a safe home for humans. Each article can be stand-alone and or supplement biology and ecology classrooms and discussions. Our aim here was to offer a wide range of considerations and discussion points to augment the study of the world’s biomes. Every student, faculty member, and even citizen will need to have a basic understanding of how sustainability functions in theory and practice as we collectively strive to create a sustainable future.

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Coupled Human and Natural Systems: A Review and Anthrome Case Study

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Abstract

Systems thinking is a way of looking at the world to understand how individuals, populations, communities, and institutions interact beyond their distinct boundaries. Coupled human and natural systems (CHANS) has emerged as one framework to better understand the connections within and between systems often looked at separately. Researchers and practitioners are interested in how these couplings function to move along a pathway toward (or away from) a sustainable future. In this article we review key elements of CHANS. These elements are applied to examples from human, natural, and coupled systems including agriculture, conservation, lakes, the human body, fire, and climate change. We end with a case study to link anthromes and CHANS.

Introduction

Systems thinking is a way of looking at the world to understand how individuals, populations, communities, and institutions interact beyond their distinct boundaries. For example, systems thinkers look at how the conservation of wildlife predators affect prey populations (Carter et al., 2014) or how private land owners affect biodiversity conservation (Quinn and Wood, 2017). Coupled human and natural systems (CHANS) has emerged as one framework (alongside social-ecological systems and human-environment systems) to better understand the connections within and between systems often looked at separately. Central to this concept is how human systems and natural systems interact; i.e., how they are coupled. CHANS is the explicit acknowledgment of a two-way interaction where the condition of natural systems are shaped by human decisions and that the condition of human systems is shaped by natural processes (Fig. 1). In addition, researchers and practitioners are interested in how these couplings function to move along a pathway toward (or away from) a sustainable future. For example, systems thinkers using a CHANS concept will ask how the loss of pollinators in agricultural systems is affected by practices farmers use on their farm and, also, how the abundance or absence of pollinators affects the yields that a farmer can produce in a year. Formalized by Liu et al. (2007a,b), the concept of CHANS has been applied by a large and diverse network of scholars (<http://chans-net.org/>) to frame examinations of how humans and the environment interact. Scholarship in CHANS has recently been described as “complex, dynamic, interconnected” (Ferraro et al., 2019). This focus on complexity is in direct contrast to how science is most frequently conducted with a focus on reductionism, isolation, and disciplinary silos.

In this article, we briefly review core elements of coupled human and natural systems (CHANS), providing examples from within and between human and natural systems to discuss how thinking in systems provides a deeper understanding of our current state in the world, how things came to be the way they are, and how we can be intentional in moving forward as we create a sustainable planet. Then as a brief case study, we link CHANS and anthromes to explore the theme of this article as part of the broader theme of Volume 5 of this Encyclopedia.

Identification of Human and Natural Systems

The term system can be applied to a wide variety of organized units. Broadly, a *system* is a collection of similar or interacting parts. Meadows (2008) describes a system as “a set of things interconnected in such a way that they produce their own pattern of behavior over time.” When utilizing a CHANS lens to examine a sustainability issue, it is often helpful to start with a list of individual human and natural systems. In Fig. 2, systems associated with private land conservation such as landowners, migratory bird species, or

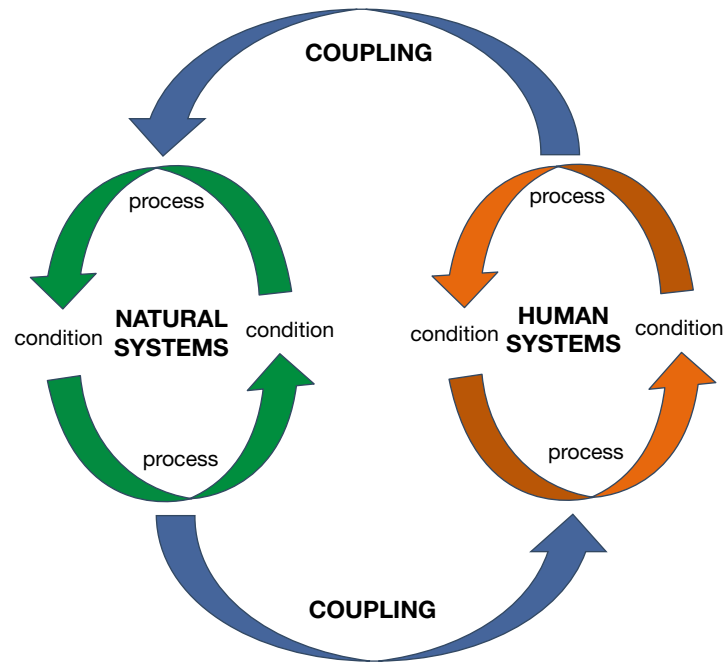


Fig. 1 CHANS model from the US National Science Foundation (NSF). Key elements suggested by NSF are “(1) the dynamics within one or more natural systems (2) the dynamics within one or more human systems (3) the processes through which the natural systems affect human systems (4) the processes through which the human systems affect the natural systems.”

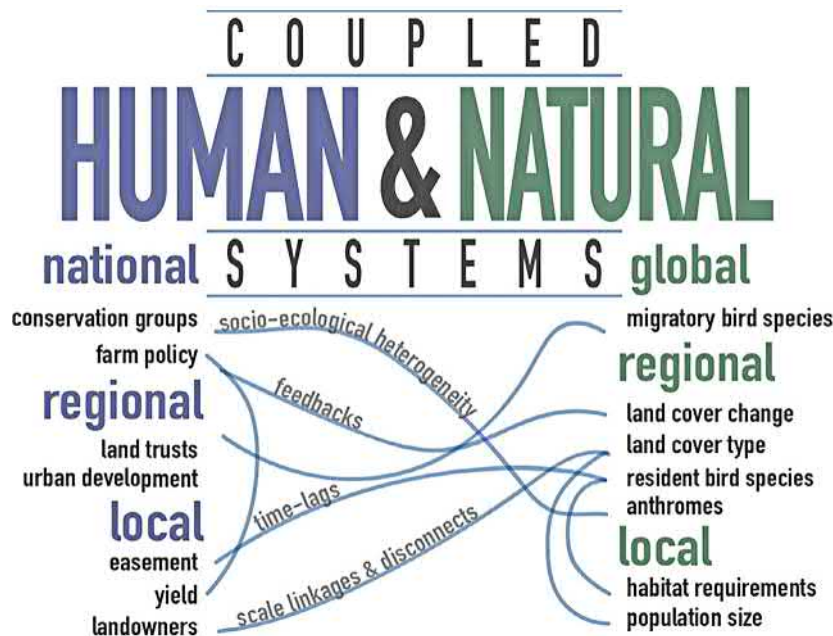


Fig. 2 A list of human and natural systems associated with private land conservation sorted by spatial scale. Reprinted with permission from Quinn JE and Wood JM (2017) Application of a coupled human natural system framework to organize and frame challenges and opportunities for biodiversity conservation on private lands. *Ecology and Society* 22(1): 39.

national farm policy are listed. Then one can examine how each of these systems interact with and impact the others (the focus of the rest of this article). For example, landowners may influence migratory bird species through their choice to provide suitable habitat or not. Whether or not a landowner can afford to, or is willing to, leave habitat available for birds may be influenced by national farm policies. These interactions, among many others not listed here, will determine the health of migratory bird species.

Scale

When you have an assortment of systems identified, one way they can be organized is by different *scales*, including but not limited to, spatial, temporal, biological, and social. Human systems exist from small scale (such as an individual making the decision to recycle) through to large scales (such as international organizations such as the United Nations FAO including global agricultural policy). Natural systems can exist from a declining population of pollinators in a restored Iowa prairie to the Earth's global scale carbon cycle. Considering scale can help organize the complexity of different systems. Indeed, Simon Levin wrote in 1992 that "scale... is the fundamental conceptual problem in ecology if not in all of science... unifying population biology and ecosystem science, and marrying basic and applied ecology."

One helpful way to visualize variations across scale is with a stommel diagram. Stommel diagrams are one tool for organizing systems across scales that has been used in different disciplines (reviewed in [Peterson, 2010](#)). The example of a *stommel diagram* below from [Gordon et al. \(2008\)](#) shows the time and spatial scale over which shifts or patterns occur in different systems. Starting a systems analysis by organizing the relevant systems by scale can be a very effective way to see how different systems relate ([Fig. 3](#)).

Another way that systems are often organized across scales is as *nested systems* ([Liu et al., 2007a,b](#)). The concept of nested systems explains that systems exist within other systems. An easy way to understand this is to consider a smaller system, the human body. Humans have many systems such as digestive, reproductive, respiratory, and circulatory. All of these systems are nested within a larger system; the individual. The same goes for human systems, natural systems, and CHANS. A tree is a system itself but is nested within a population of trees, which is nested in a community that is a forest ecosystem. A university is a system but is nested with the larger system of higher education, which is nested in a broader human community. Likewise, the university campus and all the students living and studying there are also nested in the larger natural ecosystem of the biome the university was built within.

What is key for CHANS is connecting the human and natural systems. For example, people growing food are nested within larger systems of government and economic policy that influence when and how people can access resources. The same farm growing food is nested within broader climate patterns that determine what crops can be grown (e.g., coffee in the tropical anthromes and wheat in temperate cropland anthrome). As noted above, how a person manages land for food production affects the quality of the natural system. For example, excess pollution in a large watershed can impact the fish in a stream nested in that watershed. Other examples include how cities respond to changes in precipitation patterns and flooding due to climate change, how biodiversity conservation in protected areas affects local residents, and how cultural norms around food and fishing impact local fish populations through sustainable management or over-fishing. Indeed, many of these systems are discussed throughout this volume for those interested in learning more.

Similar to how systems are nested, systems can be linked over longer distances. *Telecoupling* refers to links between humans and nature through space; from local to global links. For example, when someone purchases a computer that contains tin or tungsten that was mined in Africa and parts that were assembled in China and shipped to France, that person is linked through space with natural systems that provide these materials from far away as well as to all of the people who were involved in the mining, processing, production, transportation, and retail of said computer. Farming and food systems have many telecoupled elements including distribution of food, sourcing of synthetic inputs, and spread of pollution. For example, [Rey and Huettmann \(2019\)](#) recently modeled the telecoupling of fisheries in Patagonia ([Fig. 4](#)).

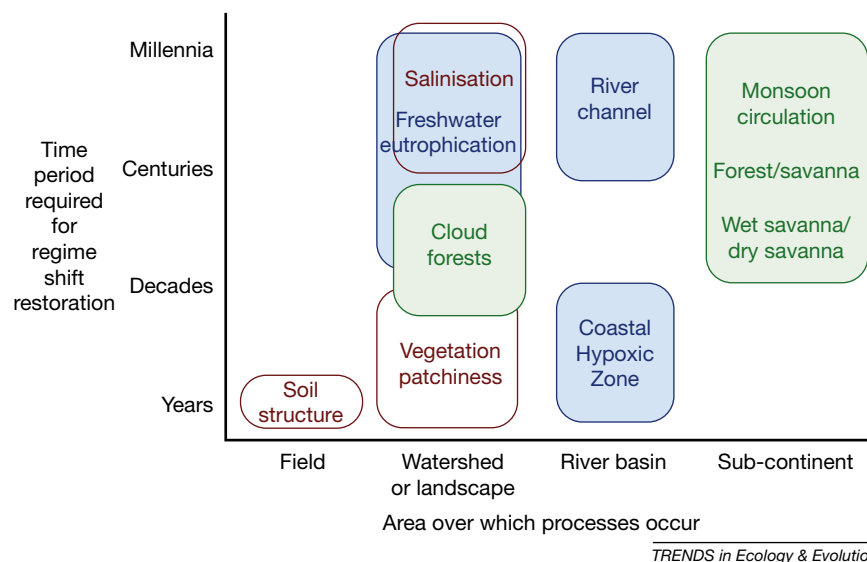


Fig. 3 Stommel diagram of the time and spatial extent over which different shifts occur in different systems. Reprinted with permission from Gordon LJ Peterson GD and Bennett EM (2008) Agricultural modifications of hydrological flows create ecological surprises. *Trends in Ecology & Evolution* 23(4): 211–219.

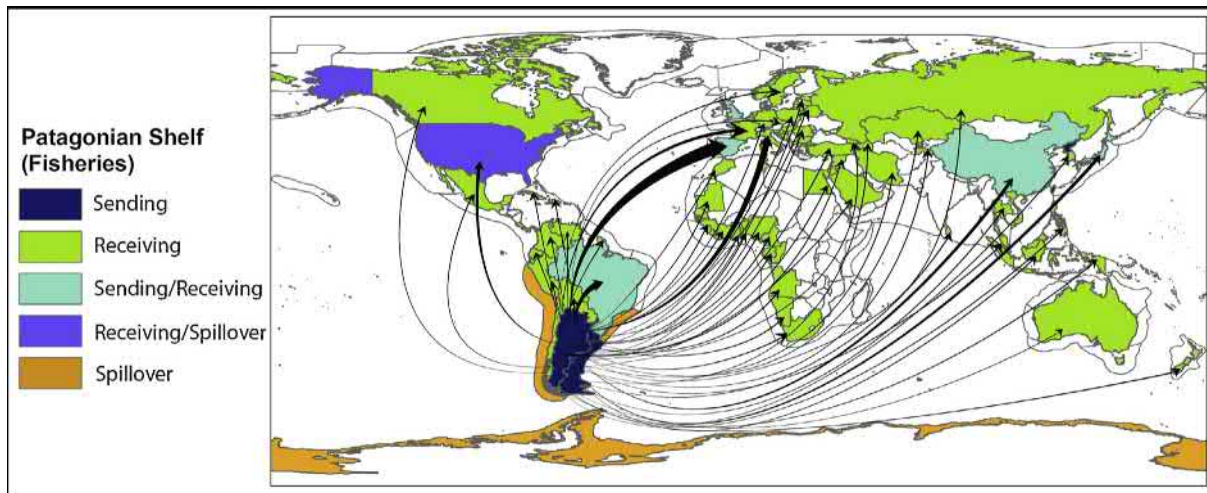


Fig. 4 Telecoupling of fisheries systems from the Patagonian Shelf. Reprinted with permission from Rey AR and Huettmann F (2019) Telecoupling analysis of the Patagonian Shelf: A new approach to study global seabird-fisheries interactions to achieve sustainability. *Journal for Nature Conservation* 125748.

Legacy Effects and Time Lags

Two essential elements of understanding temporal scale within systems are *legacy effects* and *time lags*. The temporal scale recognizes that human and natural systems interact through time. Time lags and legacy effects occur because the feedbacks or couplings between systems are not always immediate. Humans are interacting with an environment billions of years in the making by our use of fossil fuels and our actions today will have consequences far into the future. For example, within human systems, we do not see the results of investment in preschool education until years later when examining well-being and attainment outcomes for children who received early schooling years before. These same children's perception of the value of nature later as adults is influenced by how much time they spent in nature as a child (Holt et al., 2019).

Another example is the impact on current climate patterns from the Industrial Revolution. Manufacturing and industry increased in the late 1700s. As a consequence, the amount of carbon dioxide and other pollutants in the atmosphere increased. One immediate effect of this at a local scale was poor air quality (e.g., the London Fog). However, many of the effects of this pollution were not seen immediately. One of these was climate change. There was a time lag on the impacts of increased carbon dioxide in the atmosphere. Thus the increases in global surface temperature we are seeing today are a legacy effect of historical pollution. Indeed, when we examine the current state of any system, it is the result of all actions that came before; the current state of a system is actually a legacy. The current state of the health of your body is a legacy of all of the choices you have made until today (amount of sleep, the food you ate) as well as factors beyond your personal control (genetics and socioeconomic status). Current low household wealth among African Americans in the United States is a legacy of slavery, segregation, and racist economic policies in deciding who received home loans and who did not. Looking at the legacy of the past can provide important insight and unexpected conclusions about the current state of a system. For example, the Scottish Highlands and English Lake District are celebrated for the grassy slopes and an abundance of sheep. However, this pastoral landscape is heavily modified by human intervention in the past, including but limited to a legacy of timber clearing by the Romans, English land ownership policies, and recent subsidization of grazing (Hobbs, 2009).

We can see that much of the difference between a time lag and legacy effect is based on the time frame that you are referencing from. A coupling is best framed as a legacy if you are looking to the past. A time lag may be more valuable if you are looking forward.

Heterogeneity

Part of the complexity of understanding interactions within and between systems is *heterogeneity*. The prefix "hetero" means "different." Heterogeneity is the idea that couplings between human and natural systems and subsequent outcomes or patterns are different within and across systems, place, or time. Humans affect and are affected by, natural systems in very different ways. For example, people in highly developed countries have a greater indirect effect upon the environment through their creation of carbon emissions than do people in less developed countries. Yet, people in poverty will experience the consequences of high carbon emissions (climate change) in very different ways than wealthier populations. A person who relies upon subsistence crops to feed their family will be more immediately and more seriously impacted by drought than someone who may not be able to purchase blueberries at the grocery store because of seasonal drought in another hemisphere but still has the option to purchase

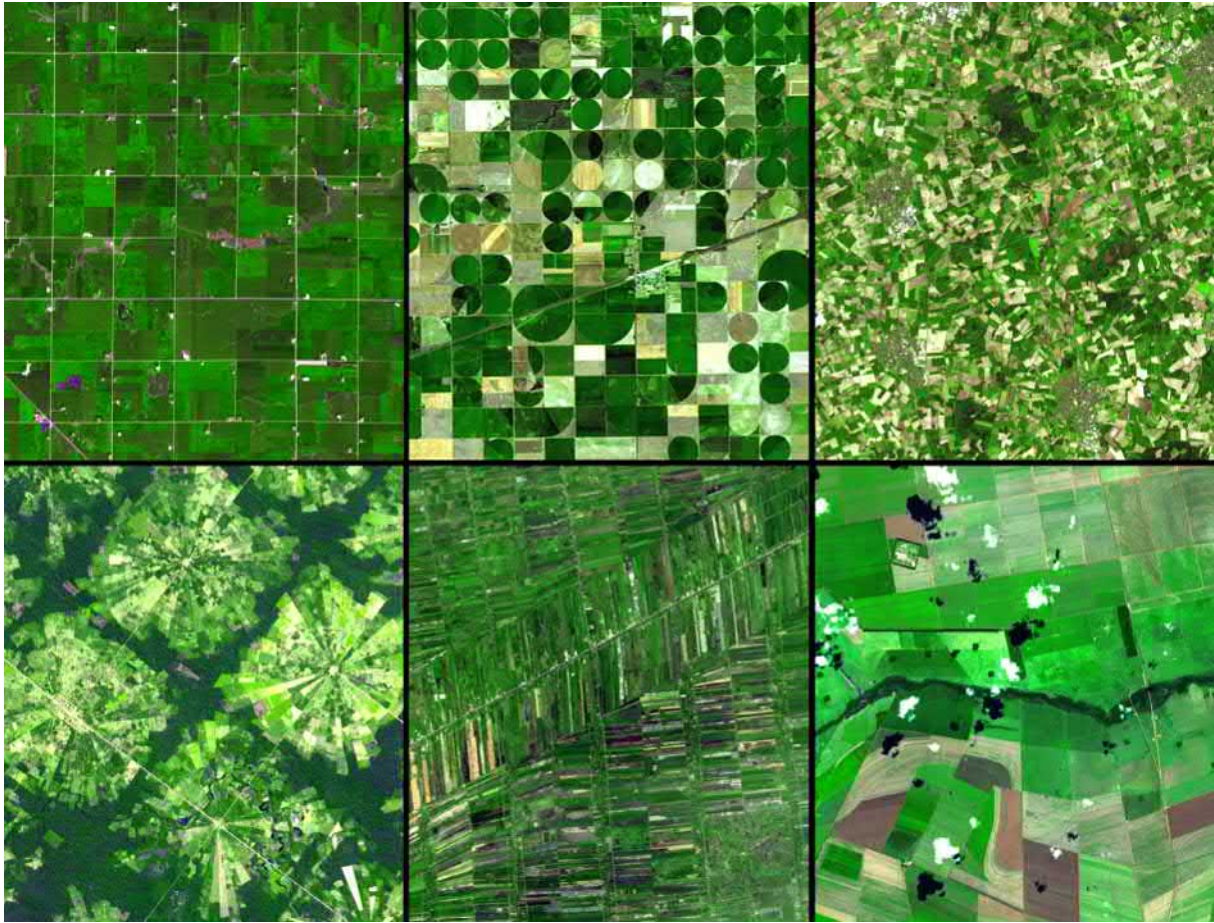


Fig. 5 Heterogeneity in agricultural landscapes. Clockwise from the top left—Minnesota, USA; Kansas USA, northwest Germany, Brazil, Thailand, and Bolivia. Image from NASA. Figure available from: <https://earthobservatory.nasa.gov/images/6605/agricultural-patterns>

strawberries from down the road. Another example is how people living in coastal regions will experience climate change effects such as rising sea levels while people in other areas will be affected by wildfires.

Another way to look at heterogeneity comes from the field of landscape ecology. From this perspective, heterogeneity is described as the variation in the spatial pattern and configuration of different land use and land cover types (e.g., [Fahrig et al., 2011](#)). The patterns of land use and land cover that we see when we look at satellite images show how both natural and human systems create heterogeneity or diversity in land use and land cover. This composite image from NASA ([Fig. 5](#)) of different agricultural landscapes shows heterogeneity within each photo (different size fields, different intensities of green). Between these images of farmland, we also see heterogeneity between different agricultural systems. For example, the image on the top right of cornfields in Minnesota looks very different than the rice fields from Thailand in the bottom middle. These spatial patterns are a combined outcome of both human and natural processes including human drivers of habitat fragmentation, policy, and economic incentives and natural drivers of precipitation, soil type, and potential vegetation.

Nonlinear Dynamics, Thresholds, and Catastrophic Change

Thresholds are transition points between states within a system ([Fig. 6B](#)). When a threshold is reached, a system will change rapidly. This is in contrast to a linear change ([Fig. 6A](#)) where a system state changes gradually as the conditions change (i.e., the metaphor of the frog in the pan with warmed until boiling). Thresholds are important to watch for because of the suddenness of the change and the subsequent impacts on human and natural systems. Imagine a lake system that is catching nitrogen run-off from surrounding urban yards. For a while, perhaps even years, the lake may support plant and animal life despite the increased fertilizer applied to keep yards green. However, there is a limit to the amount of fertilizer that the lake can absorb before an algae bloom occurs. Subsequently, the algae bloom affects the availability of oxygen supplies and, seemingly suddenly, the lake has crossed a threshold from a place that can support life to one that cannot. Although the nitrogen has been building up in the lake for years, it's a sudden shift

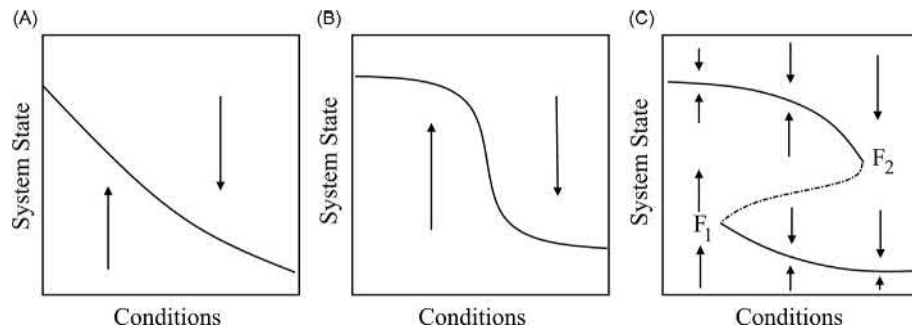


Fig. 6 Models of (A) linear, (B) threshold, and (C) catastrophic change. Modified from Scheffer M, Carpenter S, Foley JA, Folke C, and Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413(supplement 6856): 591–596.

from one state to another (life-supporting to non-life supporting) that seemed to happen quickly. This seemingly-rapid shift is explained because many thresholds are non-linear; i.e., we do not see a gradual and constant change in a system. Instead, we experience rapid change.

Like a threshold change, a *catastrophic* change (Fig. 6C) results in a rapid shift in a system state. However, unlike a simple threshold change, the catastrophic change results in *hysteresis* where multiple system states may exist under the same conditions. As a consequence, for a system to recover to its former state (for example, the life-supporting lake above), the system needs to return to a condition different from the tipping point of the initial change. Most frequently this necessary condition for recovery requires difficult, expensive, and time-consuming restoration to conditions far beyond the last state (i.e., in a lake, it is not enough to merely remove the last ounce of added fertilizer that tipped the system, the lake may have to be completely dredged to remove all pollution) then the tipping point of the threshold of initial change. Another way to think about a catastrophic change is to think of the two alternative states as basins of attraction (Fig. 8). In this figure, the two points lowest points on the lines, or basins of attraction, represent alternative stable states. How difficult it is for a system to cross the threshold can be judged by how steep the walls of the basin are. Specifically, the steeper and taller the basin the more resilient the system is.

Thresholds and phase shifts exist within many coupled human and natural systems. The lake example above is an example of a local scale. On a global scale, the planetary boundaries described by Steffen et al. (2015) are suggested global thresholds for different changes to the planetary earth processes. The difficult part for scientists and policymakers is that there is much *uncertainty* (Fig. 7) in exactly what the threshold is for many systems. When there is uncertainty it is difficult to predict when an event will occur and communicate the need for change when a system appears healthy.

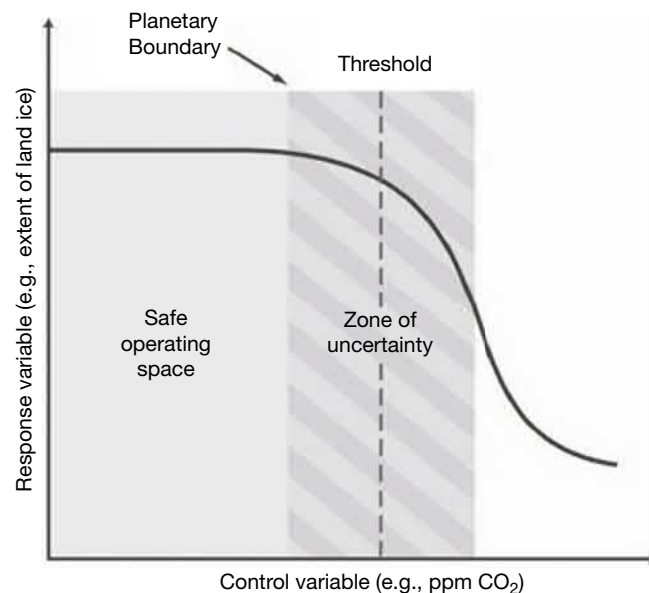


Fig. 7 Uncertainty in exact point of a threshold of change. Reprinted with permission from Rockstrom J et al. Planetary boundaries: Exploring the safe operating space for humanity. *Ecology and Society* 14(2): 32. [online] URL: <http://www.ecologyandsociety.org/vol14/iss2/art32/>.

Vulnerability, Resilience, and Resistance

Liu et al. (2007a,b) define vulnerability in CHANS as “the degree to which systems are likely to experience harm due to changes in internal and external variables.” When a system is *vulnerable*, it is sensitive to being changed. All CHANS systems and subsystems are more or less vulnerable and have the potential to be changed due to human factors, environmental factors, or a combination of both. The opposite of vulnerability is *resiliency*. A system is resilient if it can recover from difficult conditions. Liu et al. (2007a,b) define resilience as “the capability to retain similar structures and functioning after disturbances for continuous development.” *Resistance* is the ability of a system to withstand change. Though resilience and resistance concepts are similar, it is often valuable to differentiate, which we do in the explanation below.

One way to visually represent vulnerability, resilience, and resistance is seen in Fig. 8 as a series of basins of attraction and a rolling ball. Any system can be represented by the ball; this can be a small system such as a lake or a human or a planet-level system such as atmospheric carbon or international governmental treaties. Each system, in its current state, rests in a basin of attraction. Each system has the potential to be moved into a second basin; the location of the dotted circles. If a system experiences “changes in internal or external variables”; a hurricane, a recession, pollution, disease, war, etc. it is being pushed “up” a slope toward a change, potentially rolling into a new basin, which represents a new state.

Vulnerability: If a system is more vulnerable to change, or less resilient, its basin would be drawn as less “deep.” In Fig. 8, System C, is more vulnerable than Systems A and B. Basin C is shallow and therefore System C is more vulnerable to going into a different state. Systems A and B *could* be pushed into a different state, but it would take much larger changes in internal or external variables. The factors that make a system more or less vulnerable will be distinct for each system and each CHANS interaction.

Resilience: The resilience of a system is its ability to *recover* from changes in variables to remain in a stable state. In the figure, this is represented by the depth of the basin of attraction. If the system rests in a deep basin and is pushed by a change in variables up the slope, it will be more likely to “roll” back down into its basin; is more resilient. Systems A and B are more resilient than System C. Of course, it is possible to push any system into a new state given the strength of changes in variables, yet Systems A and B are less likely to be pushed over the *threshold*. We often talk about resilience as a good thing, it is important to note that a system can also be resilient in a poor or unhealthy state.

Resistance: The resistance of a system is its ability to avoid or withstand any change and remain in a stable state. In the figure, this is represented by the steepness of the slope of the basin. System A has the greatest resistance due to the steepness of its slope.

Human systems, natural systems, and CHANS all experience vulnerability, resilience, and resistance. An adult human with a strong immune system is more resistant to catching the flu than a frail elderly person. Even if they do catch the virus, they would be more resilient to recovering from the challenges than an elderly adult with a weakened immune system who would be less resistant to catching the flu and less resilient to recover if they got sick. An ecosystem with greater species richness, which is a greater number of different species, is more resistant to invasive species because more ecological niches are already filled. Tilman et al. (2006) have shown that an ecosystem is more vulnerable to change if it has lower biodiversity. Greater biodiversity provides resilience because it allows an ecosystem to recover if it experiences a change in variables such as disease, drought, fire, deforestation, etc.

It is particularly important for researchers and practitioners to understand these dynamics within CHANS. In the last decade, California, in the United States, and more recently Australia have experienced increasingly strong and deadly forest fires due to changes in internal and external variables in both human and natural elements of the larger system. Human actions and policies have made both human and natural systems more vulnerable to fires. Forest ecosystems have been managed to suppress the fire, resulting in a build-up of flammable biomass which makes forests less resistant to sparks that can start fires. Simultaneously, humans have continued to build homes within and adjacent to fire-vulnerable areas, putting their homes and themselves at

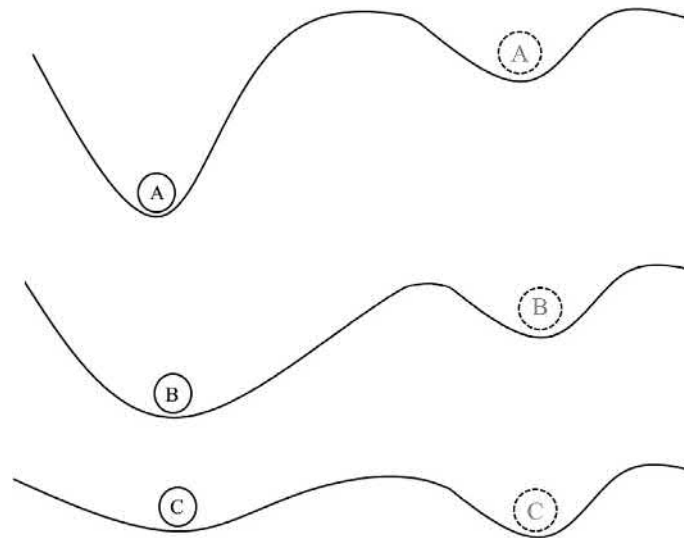


Fig. 8 Model of variation in vulnerability, resilience, and, resistance.

risk. Human and wildlife communities are now more vulnerable to the consequences of forest fires. Forests that burn may recover through ecological succession, but human communities that do not have financial and governmental resources to rebuild are less resilient to recovery and some communities that have burned may never be rebuilt.

Feedback Loops

Feedback loops are ways that systems regulate themselves. Feedback loops can be reinforcing or balancing (sometimes called positive and negative, though those terms often confuse people so we will use reinforcing and balancing here). Reinforcing feedback loops continue to grow a stock within a system or cause something small to increase in size or magnitude. Consider a small ball of snow rolled down a mountain. The snowball (a stock of snow) continues to grow as it rolls. As it gathers more snow and grows, it has a larger surface area that can, in turn, gather even more snow until a giant avalanche is created! An example of a reinforcing feedback loop from human systems is a bank account that gains interest each quarter. As the size of the savings account grows, each quarter it will earn more interest and increase exponentially. Environmentally, increased earth surface temperature increases evaporation from the oceans, resulting in greater water vapor in the atmosphere, increasing greenhouse gasses which then, in turn, again increases the Earth's surface temperature.

CHANS researchers focus on reinforcing loops that influence how human and natural systems interact. Population growth, of humans and all other species, is a key reinforcing feedback loop. Although we may all want a never-ending increase in our savings account due to interest earned, often, if a reinforcing feedback loop is never checked, disaster would quickly ensue. This is where balancing feedback loops come into play. An example from natural systems is the unchecked growth of invasive species. The potential exponential growth of the invasive species allows its population to continue to expand and outcompete native species.

A balancing feedback loop is one in which a system is kept within certain boundaries. Your body temperature is an easy example. If you get too hot, your body has the balancing feedback loop of sweating to cool you down. If you get too cold, your body will shiver to warm you up; thus keeping you within a few acceptable degrees of body temperature. Balancing feedback loops keep a system from crossing a threshold into another state; i.e., in regard to your body temperature it keeps you in the state of being alive. Balancing feedback loops are also in play regarding population growth. Births are a reinforcing feedback loop that, if left unchecked, would never end. Death ensures a balancing feedback that keeps a population within an acceptable range for a given ecosystem. This is why predation by wolves on deer populations is essential to keep deer or any grazer numbers from getting so large that they exhaust their food reserves and starve. Within CHANS, when scientists and policy-makers see reinforcing feedback loops occurring that can damage people or the environment, policies can be implemented to change (or balance) behavior. Indeed, management of large carnivores is a key feedback between human natural systems. [Estes et al. \(2011\)](#) describe how the loss of large predators globally is affecting human and natural systems. However, the complexity of human values associated with predators adds complexity to any suggested simple solution (e.g., [Expósito-Granados et al., 2019](#)).

Surprises

The concept of surprises is important for scientists and practitioners to be aware of even if they cannot be predicted. People and nature do not always react in the way we assume they will. For example, when a major donor gives funds to protect a forest, this can create an unexpected opportunity for conservation in a region. And yet, local residents may be unsupportive of such conservation for seemingly surprising reasons ([Quinn and Wood, 2017](#)). Likewise, a single unpredicted but impactful environmental event can have surprising effects on an ecosystem. For example, [Philpott et al. \(2008\)](#) described how a hurricane damaged areas of coffee plantations and that decreased vegetation complexity on the farm increased impact of landslides after the hurricane. Farmers in certain areas may be prepared for hurricanes, but unprepared and surprised by the after-effects of such events. Therefore, it is essential to recognize and build plans for surprises, good or bad.

Using CHANS to Describe and Better Understand Anthromes

At local, regional, and global scales, land use and land cover change is a clear reflection of the coupling between natural systems and human systems. One global classification of land cover is anthromes. Anthromes, or anthropogenic biomes, characterize at a global scale, ecological patterns of land use and land cover created by sustained direct human interaction with ecosystems ([Ellis and Ramankutty, 2008](#)). Anthromes fall along gradients of land-use intensity and population density, incorporating natural, used, and novel ecosystems to classify areas as Used (including dense settlements, villages, croplands, and rangelands), Seminal, and Wild ([Ellis et al., 2010](#)).

Indeed, anthromes embody many elements of CHANS and can be used to frame conservation actions in anthromes ([Martin et al., 2014](#)). Anthromes are classified at a global spatial *scale*, but can be used to consider regional scale patterns. Anthromes show the *heterogeneity* of land use and land cover patterns missing when we define landscapes as biomes devoid of human interactions. They also show the *feedbacks* between human and natural systems that are an essential component of understanding complex systems. For example, the shifting croplands of the central Great Plains USA ([Fig. 9, Quinn et al., 2017](#)) show how

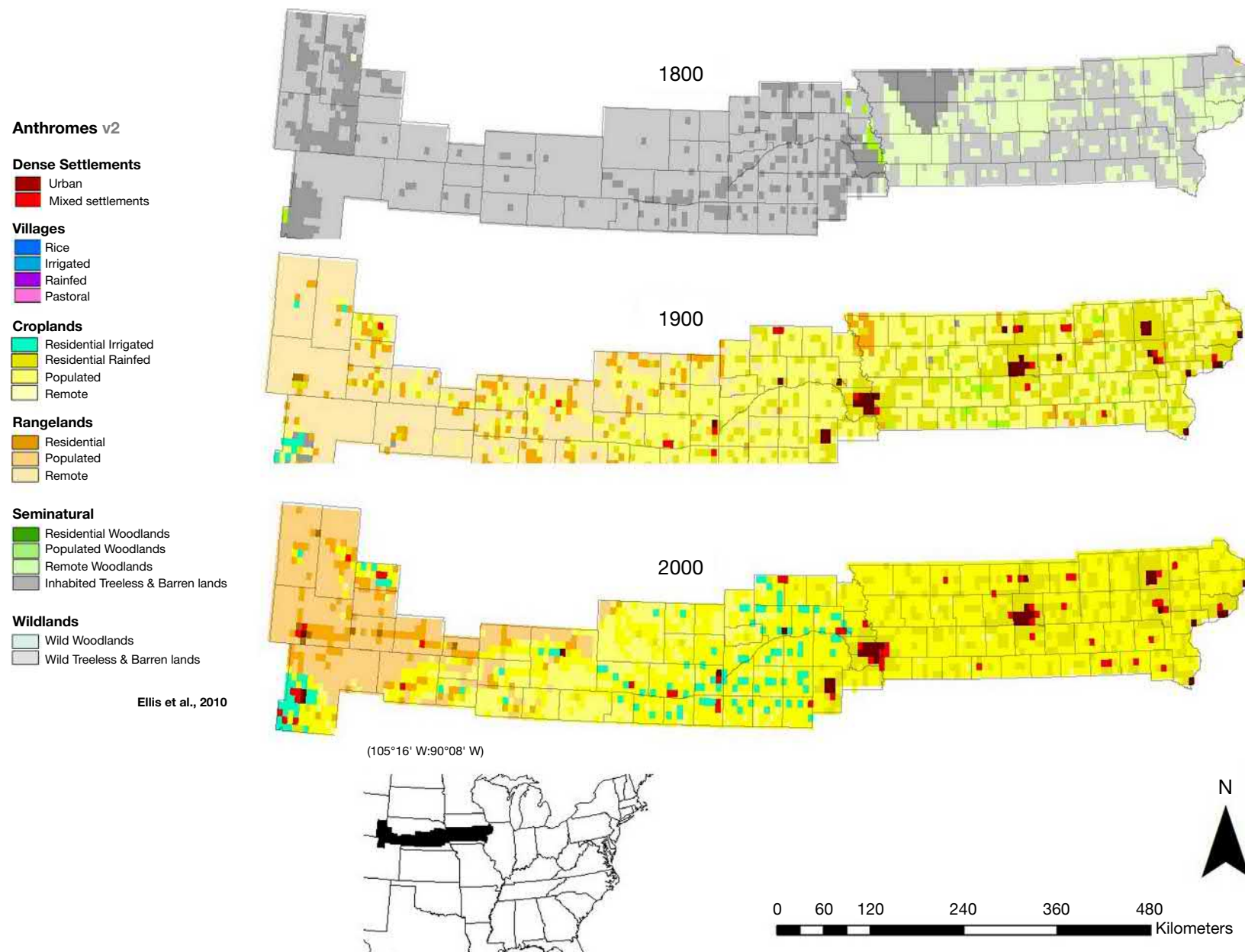


Fig. 9 Threshold shift in extent of cropland and rangeland anthromes in 1900 in the central United States' Great Plains. Reprinted with permission from Quinn JE Awada T Trindade F Fulginiti L and Perrin R (2017) Combining habitat loss and agricultural intensification improves our understanding of drivers of change in avian abundance in a North American cropland anthrome. *Ecology and Evolution* 7(3): 803–814.

expanding farming systems incentivize increased production and subsequent expansion. Historical anthromes provide an opportunity to consider how current systems might be a *legacy* of past decisions. They can also help frame current conservation challenges when a legacy of past land use is considered. For example, the 400-year legacy of agriculture in Europe currently dictates or at least drives many conservation issues, particularly the focus on farmland birds. The change in anthromes over time highlights the *non-linear dynamics* of land use and land cover change. For example, as seen in Fig. 9, the rapid loss of wilderness and subsequent increases in cropland and rangeland across the central United States between 1800 and 1900 (Quinn et al., 2017). In conclusion, both anthromes and coupled human and natural systems provide a way to better describe, model, and understand complex patterns that link human and natural systems.

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Mental Models of Sustainability: The Degrowth Doughnut Model

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Abstract

Due to the concern that achieving human wellbeing through material development is “costing the Earth,” a mental model was developed to show in a single image the aspiration of social foundations of development to be achieved and biospheric boundaries not to be crossed. Anthromes analysis, combined with the cultural imperative of maintenance of global sustainability through coordinated transformation of social metabolism and its environmental impact, makes nation states the immediately available units of sustainability modeling. In this century humans must meet their needs equitably within the biophysical means of the planet. A downscaling of planetary boundaries and social wellbeing foundations (thresholds) to national level through calculations of the impacts and attainments of nation states’ socioeconomic activities makes the doughnut model a conceptual tool bringing sustainability closer to political and organizational impact. To visualize the scale and the possible pathways for the transformation of national and global sociometabolic practices in the 21st century within the “degrowth doughnut” includes the boundaries and thresholds in three domains: cultural, socioeconomic, and biophysical. This way it aims to avoid the conceptually paralyzing trade-off between exclusively biophysical boundaries and exclusively social thresholds of the other doughnut models. Understanding that excesses and shortfalls of current and foreseeable socio-metabolic practices exist in cultural, socioeconomic, and biophysical aspects of nations’ social metabolism allows us to build on nations’ sustainability potentials. The aim of the model and its visual tool is to inform their populations about the direction and scale of the change strategies that they could adopt to contribute to the global effort of maintaining the planetary population within the safe and just operating space of the doughnut under known advantages and constraints of the 21st century.

Planet Earth as a Mosaic of Anthromes

Human influence on the terrestrial biosphere is so pervasive (Barnosky et al., 2012; Kastner et al., 2015; Kolbert, 2014; Steffen et al., 2004; Vitousek et al., 1997; Wilkinson and McElroy, 2007) that the present has been proposed as an entirely new geological epoch, the Anthropocene (Crutzen and Stoermer, 2000). Criticism of the equalizing effect of this term on all human communities (Bonnet and Fresco, 2016; Moore, 2016) warns that this influence is not effected equally by all humans based on their biological and ecological essence, but through human cultural and political institutions (Wainwright and Mann, 2018) with inherent inequalities of benefits and burdens. Anthromes, or “anthropogenic biomes,” present a view of the terrestrial biosphere that takes into account the “sustained direct human interaction with ecosystems” (Ellis and Ramankutty, 2008), providing an alternative global framework for ecological understanding of the terrestrial biosphere as it exists today. The anthromes provide a patchwork of varying intensities of human interaction with the biosphere and denote inequalities in historic and present modifications to the biomes. However, they remain silent about the sustainability of these modifications and their connections to other parts of the patchwork through human culturally constructed institutions.

Anthromes framework recognizes vast differences in human presence in different anthrome types, forming heterogeneous landscape mosaics. This heterogeneity stems primarily from anthropogenic motivations for landscape modification, conditioned by natural geophysical variations of terrestrial biomes. For example, urban activity or agricultural production, in and of themselves, say nothing about the purpose, benefits, and possible future developments of said ecosystem interactions. The anthropogenic motivations, on the other hand, stem from the human cultural constructs that are socio-economic activity and socio-culturally diffused aspirations and values. Strategies for the utilization and modification of the biosphere are, from a planetary perspective, most readily expressed through internationally recognized states (Cudworth et al., 2007).

Anthromes analysis combined with the cultural imperative of maintaining global sustainability makes states the anthromic units of sustainability modeling. Sovereign states become pieces of a heterogeneous global mosaic, and they combine landscape biophysical conditions and the anthropogenic enhancement and re-creation of the said landscape. Furthermore, their social reproduction practices (Bhattacharya, 2017) included in the degrowth doughnut add further understanding of the particular units' contribution to global (un)sustainability. A better understanding of the sustainability potentials and challenges of these states lays the groundwork for an eventual (constructive) understanding of the anthropogenic biomes that will guide interactions between humanity and nature towards preservation, diversity and fecundity rather than extinction. Having taken the political and economic state as a provisional unit of analysis, including ecosystem interactions and social development strategies, the degrowth doughnut model presents a holistic framework in which to view its fair sustainability potential.

Safe and Just Operating Space (SJS) Between Planetary Biophysical Boundaries and Sociometabolic Development Thresholds

In the concern that achieving human wellbeing through material development is “costing the Earth,” a mental model was developed of the tradeoff between the social thresholds to be achieved and the biospheric boundaries not to be crossed (Raworth, 2012). On the inner side of the ring, below the social foundation, lie the shortfalls in providing for average human wellbeing. On the outer side, above the ecological ceiling, lie the excesses of pressure, overshoots, on the planetary life and regenerative systems. Between the two sets of boundaries is the doughnut shaped ecologically safe and socially just abstract space for humanity in the 21st century (Raworth, 2017). Perhaps without meaning to, the SJS model provided a visualization of the *efficiency* of human development (affected also by its outreach, or whom the development was to extend to), whereas we shall be presenting the *sufficiency* of degrowth strategies below.

The biophysical boundaries aspect originates from the planetary boundaries visualization quantifying civilization's impacts on the overall planetary biosphere within a finite circular limit (Rockström et al., 2009; Steffen et al., 2015). These connect to the regions', nations', and communities' unequal contributions to the impacts (and the unequal extraction of the associated benefits) through the estimation of the footprint indicators for different biophysical processes associated with various socio-economic practices (Hoekstra and Wiedmann, 2014). The first step in the construction of the doughnut model, both as a mental model of human interaction with the biosphere and as a visualization, is to combine the boundaries and footprint approaches through the downscaling and calculation of the impacts of socioeconomic activities in national anthromic mosaics (O'Neill et al., 2018).

There are, of course, a variety of ways that the downscaling of planetary boundaries to a unit of nation state can be performed. By, for example, understanding regional environmental limits and the sustainability aspirations of its human population or by distributing a share of each planetary boundary among the states based on some allocation formula. One such allocation formula, simple enough to understand and without discrepancies between climatic specificities, resource availability, and historically differentiated responsibilities (Baer, 2013; Shue, 1999), is the per capita biophysical boundary approach, distributing shares based on current population. The aforementioned discrepancies with the allocation formula, and others like them, are important for resource management and fair responsibility apportionment (O'Neill et al., 2018). However, for the initial conceptualization of a new model and the simplicity of its broad application across orders of magnitude, a straightforward per capita downscaling of boundaries is justified.

As the challenge for a reflective global human population in the 21st century is to meet its needs within the biophysical means of the planet, boundaries along the outer rim are supplemented by the desirable social foundations to be distributed along the inner rim, thus converting the circle of boundaries into a doughnut ring made up of two belts of social foundations and biophysical boundaries (Fig. 2). Again, the definition of the threshold associated with any given foundation, its selection, and its measurement can follow different methodologies, from human needs theory to the politically set Sustainable Development Goals to social and cultural policies associated with degrowth of material throughput (Doyal and Gough, 1991; Kallis, 2018; Raworth, 2017).

Downscaling the fairshare burden of planetary resource use and pollution, and equitable development attainment gives a national doughnut visualization (Fig. 3; O'Neill et al., 2018). One such iteration for individual states presents 11 social objectives (or “foundations”) alongside the nine scaled-down planetary boundaries. A single graphical image quantifies the level of biophysical resource use associated with meeting residents' basic needs. This model modifies the original planetary boundaries structure (Fig. 1) to include ecological footprint and material footprint on the outer rim, along with nine needs satisfiers (nutrition, sanitation, income, access to electricity, education, social support, income equality, quality of democratic institutions, and employment) and two measures of human wellbeing (self-reported life satisfaction and healthy life expectancy) (Fig. 3; O'Neill et al., 2018).

Even in this framework, no direct causal link is implied between the level of resource use and social outcomes, focusing instead on conceptualization of interdependence between social outcomes and “healthy, functioning ecosystems and the resources they provide” (O'Neill et al., 2018) that is deliberately agnostic about specifics of causality (see Einstein on “principle theory approach” below). The comparative analysis resulting from the model's application to over 150 nation states suggests that the sociometabolic practices providing for human wellbeing (development) must be fundamentally restructured to enable basic needs to be met while leaving a much lower material footprint. This work specifically calls for two to six times greater efficiency in universally reaching thresholds for life satisfaction, healthy life expectancy, secondary education, quality of democratic institutions, social support, and income equality (O'Neill et al., 2018). In strategic terms, these statements become a call for sufficiency by recognizing that overconsumption burdens societies with both social and environmental problems as a result of a cultural focus on the pursuit of GDP growth as the key measure of progress (O'Neill et al., 2018). At present, based on the dominant development practices, societies have been given an either-or choice of meeting selected social thresholds by exceeding fairshare of environmental ceilings or failing

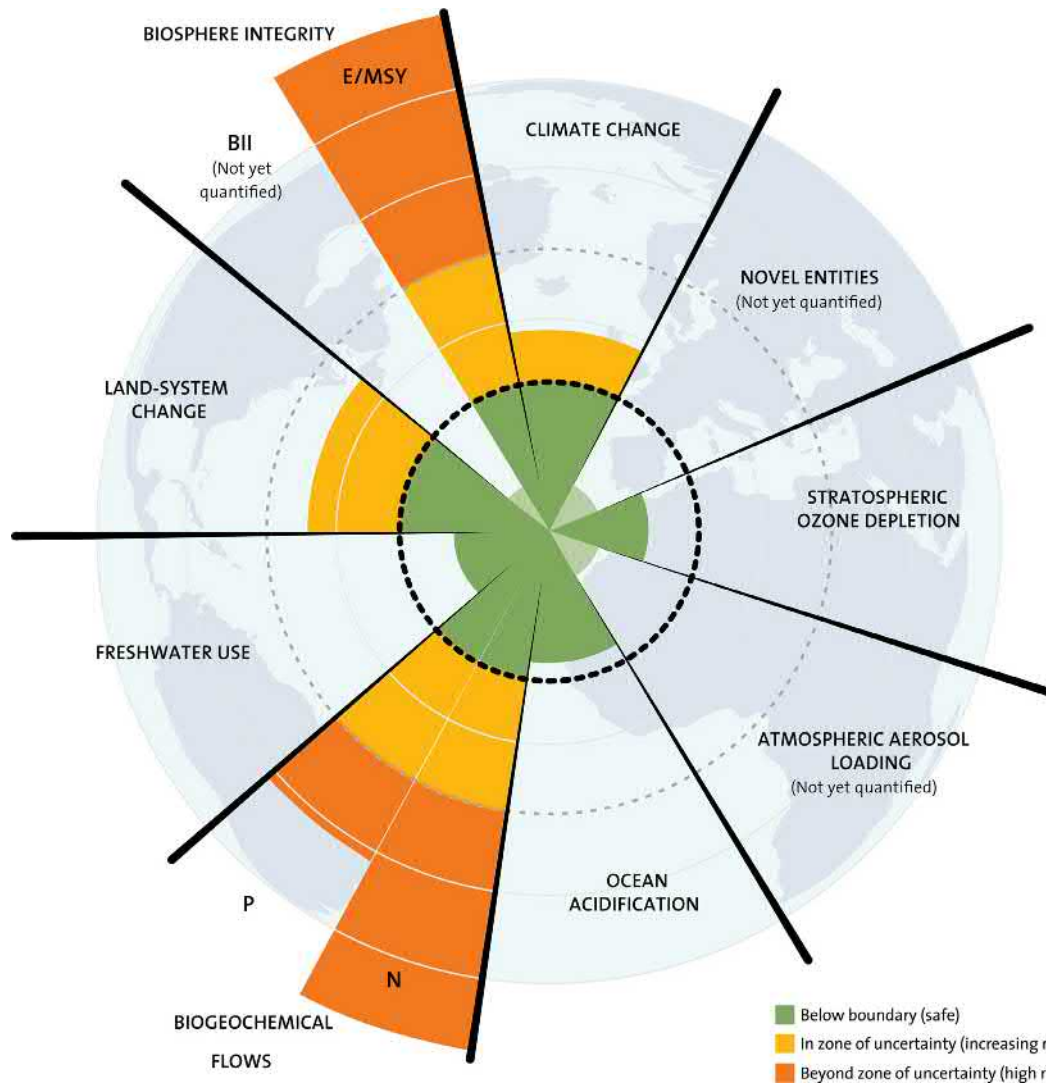


Fig. 1 9 (11) planetary boundaries circular visualization. From J. Lokrantz/Azote based on Steffen, W., Richardson, K., Rockström, J. et al. (2015). Planetary boundaries: Guiding human development on a changing planet. *Science* **347** (6223). 2015 Planetary Boundaries illustration.

to meet the social thresholds by staying beneath them. The SJS framework (Raworth, 2017; O'Neill et al., 2018) with doughnut-shaped visualization of people's basic needs along the inner threshold and the planetary boundaries along the outer rim conceptually locks in this unpalatable choice in treating development and destruction as a necessary strategic trade-off.

The model invites a projection of a desirable future: not exceeding boundaries and not falling short on thresholds. Regional pathways towards this goal can then be developed, incorporating specific cultural adaptations. A broad enough set of indicators will reflect the different contexts in which a given society connects with its immediate and planetary biomes. In economics, qualms about the appropriate theory of value upon which the prices of goods and services in the market should be determined (e.g., whether it is by the labor invested in them or the energy embodied in them) provide a useful conceptual parallel. Rather than settling on a single theory of value through which all worth will be reduced to a market price, we need value-articulating conceptual frameworks and associated processes by which the significance of incommensurable and quantified indicators can be deliberated and compared (Kallis, 2018). This implies that indicators should be qualitatively different, while still permitting clear quantification and boundary/threshold downscaling, and variegated to present a widely understandable model of the multidimensional characteristics of the Earth system, of which humanity is just one component.

The aforementioned analysis of the current situation in 150 nation states (O'Neill et al., 2018) indicates that no long-term balance between material and energy growth aspirations (as the physical costs of development) and infrastructural and socio-structural development attainments can be maintained using the existing conceptualization of development and the awareness of planetary constraints. The doughnut model, thus, warns that the current thermoindustrial social metabolism, predicated on a growth paradigm, cannot continue, because of the unsustainability and injustice of exceeding biophysical limits and achieving social thresholds. The majority of current states provide empirical counterexamples to Western modernity's sustainable

reproduction model of converting energy and material throughput (which are eventually bounded on a planetary scale) into social complexity (which should be fairly available to all if available to any). Those with “good enough” development attainment (achieving social foundations) excessively burden the shared planetary biome, while those who leave no burden exhibit a serious shortfall in social foundations. Any deliberate lowering of expectations of development attainment in order to causally lower its burden on the planetary biome is portrayed as a great individual and social sacrifice (Kish and Quilley, 2017), while individual nations’ partial sacrifices are seen as ineffective globally and the existing “sacrifice distribution” between nation states is seen as unjust. Moreover, historical development of indicators in the classical SJS framework (above) has been to *grow* from 0 or some minimal base to present day values, conceptually expecting the desirable future dynamic to be a simple reversal—less footprint, less development attainment.

Science today suggests that the only feasible way of keeping the average global temperature below its critical tipping point (Steffen et al., 2018) is to actively reduce energy demand and its associated material throughput in the global economy (Alfredsson et al., 2018; Grubler et al., 2018), so as to have a greater technological likelihood of successfully transitioning to renewable energy sources (Hickel, 2019). The associated throughput reduction also promises to directly reduce some of the biogeochemical pressures and transgressions upon the planetary boundaries. Economists conclude that, given available technologies for the conversion of incoming (and short-term stored) solar energy into human wellbeing, this throughput reduction will reduce aggregate economic activity, which is at present most vividly distilled in the measure of GDP. Degrowth thinkers argue that rather than directly causing the reduction of aggregate and average human development along with the additional frustration of aspirations for social wellbeing and emancipation, a planned reduction of this throughput in high-income nations will maintain an abundance of wellbeing through a fairer distribution of available resources, the expansion of public goods, and the associated deconstruction of the cultural components of the growth imperative itself (D’Alisa et al., 2014; Hickel, 2019; Kallis, 2018; Latouche, 2014). This is the conceptual underpinning of the degrowth doughnut visualization presented here.

The Degrowth Doughnut: Specifying a Safe and Just Operating Space for a Historic Conceptual and Metabolic Transformation

The mental model of a safe and just operating space for national and regional anthromic mosaics in a waste and resource constrained 21st century is a visual tool for the conceptual arrangement of an alternative approach that does not prescribe a causal-mechanical model of how to achieve their sustainability. It relies on a visionary understanding in the physical sciences that in crises of paradigms a “principle theory approach” can offer a breakout from a conceptual impasse (Einstein, 1919). This type of explanatory model does not speculate as to the detailed mechanism (think: gears, pulleys and pistons) through which observable variables are connected in the object of its study, but establishes principled and often obvious generalizations about these variables’ change constraints (think: rules, principles, flows) based on self-evident rationalizations of the experiences and axiomatic relationships in the conceptual structure. In our case this means not aggregating causal interactions between selected indicators into projections of future strategies, but constraining the overall abstract space of their possible changes. This is defined by easily understandable principles of the evolution of planetary boundaries, sustainability, democracy, or energy and materials flows. In other words, how far can biophysical changes and social structures go to stay fair and sustainable without specifying at the outset how each of them reflects upon the others. This kind of explanatory conceptualization is in line with a mounting call for solution-oriented transdisciplinary modes of rationalization for human-ecosystems interactions that can achieve global sustainability.

The degrowth doughnut recognizes that contemporary and future national anthromic mosaics’ sustainability connects their biophysical manifolds, socio-economic structures, and cultural attitudes and values in a complex interaction. It deliberately shies away from specifying the causal-mechanical connection between their elements to adhere to the principle methodology and permit a sufficient multiplicity of local and temporal variations in their dynamics. It is constrained by a principled commitment to maintaining whole anthromes within a safe and just operating space. As cautioned generally for doughnut models, “caution must be exercised in considering causative links between the different variables because interactions within and between a social foundation and environment ceiling are likely to be complex, nonlinear and difficult to confirm” (Dearing et al., 2014, p. 233).

Degrowth doughnuts lay the conceptual and analytical groundwork for a paradigm change as barometers of sustainability for policy traction and further strategic empirical studies. The visualization contains biophysical, socio-economic, and cultural segments bearing visual quantification of performance with respect to the scaled-down safe and just operating space concept—the green circular belt of the doughnut. It respects the imperative of the original doughnut (Fig. 2) to visualize necessary changes to current socio-metabolic processes through known excesses and shortfalls which must be reduced, allowing us to progressively eliminate the red bars shown leaking out of the green belt. The red bars along both the inner and outer edges of the doughnut indicate that the current complex interactions between the human population and the local or global biosphere are achieving excesses and shortfalls (quantified by the size of the red bars). It does not imply that any shortcoming in achieving the goals of the inner-ring elicits a cost upon the outer-ring, a trade-off of benefits and burdens.

Biophysically, socio-economically and culturally the degrowth doughnut visualization recognizes that states face excesses that go beyond their fair share of the planetary boundaries and societal discontent, and shortfalls in providing for a fulfilling human life and ecological stability. In the manner of scientific principle theories (Brown and Pooley, 2001) the visualization postulates which key aspects of those practices and descriptions must feature in the transition between the present and the desired future state of the system, between paradigms, quantifying these key aspects for the purpose of a comparative visual representation. For example,

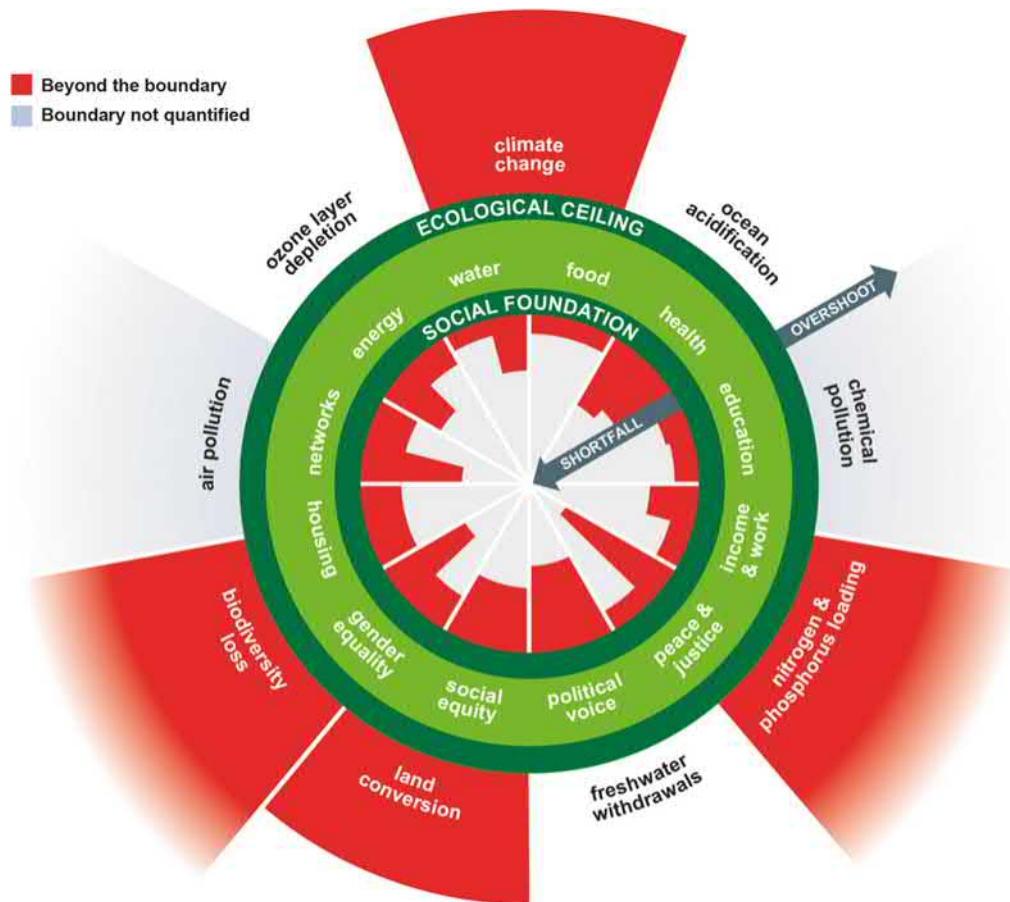


Fig. 2 Doughnut model visualization for the planetary biosphere—outer boundary for ecological ceiling and inner boundary for social foundations. From Raworth, K. (2017). *Doughnut economics: Seven ways to think like a 21st-century economist*. London: Random House. Figure on p. 51: Doughnut model—planetary.

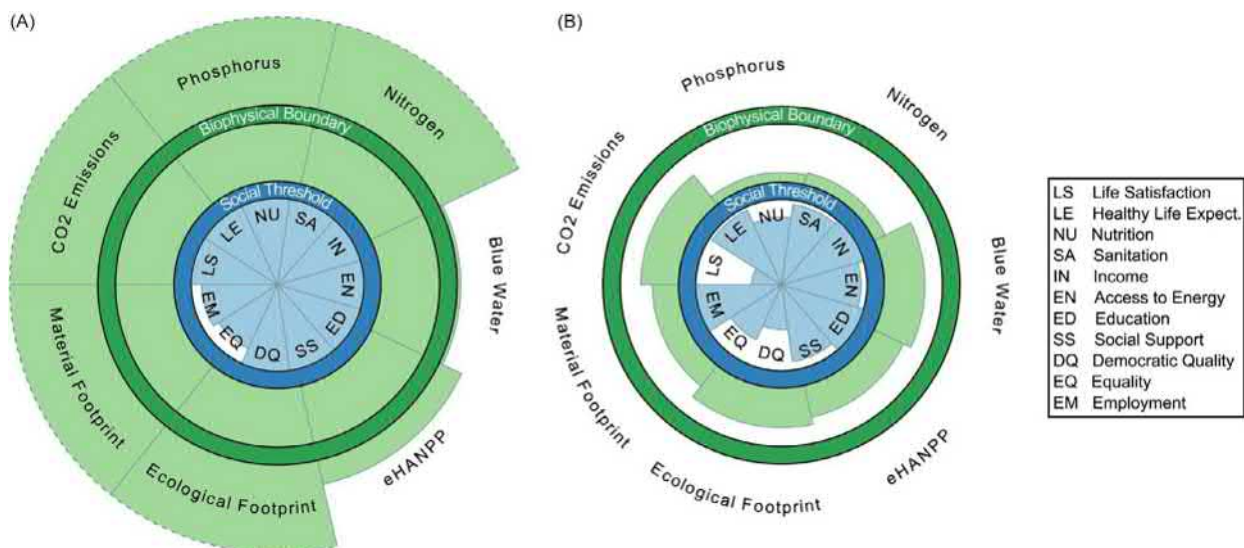


Fig. 3 Doughnut model of safe and just operating space scaled down to nation states (A) United States and (B) Sri Lanka—tradeoff between biophysical boundaries and social thresholds. Blue wedges show social performance relative to the social threshold (blue circle), whereas green wedges show resource use relative to the biophysical boundary (green circle). The blue wedges start at the centre of the plot (which represents the worst score achieved by any country), whereas the green wedges start at the outer edge of the blue circle (which represents zero resource use). From O'Neill, D. W., Fanning, A. L., Lamb, W. F., Steinberger, J. K. (2018). A good life for all within planetary boundaries. *Nature Sustainability* 1, 88-95, Figure 3: Doughnut model—National (including explanatory caption).

climate change is currently characterized by excesses in per capita carbon dioxide emissions, and by shortfalls in terrestrial forest coverage that acts as a sink for emissions. Reducing both the excesses and shortfalls would contribute to a scaled-down safe operating space. This marks a conceptual departure from the visualization of biophysical elements as only the boundaries not to be exceeded and socio-economic elements as only the thresholds to be attained. In such a conceptual structure a zero-sum trade-off is invited, and confirmed through the empirical comparison of existing national anthromes (O'Neill et al., 2018), between planetary ecological stability and human socio-economic development. Such an exclusive trade-off, with empirical support, blocks even the conceptualization of what the needs satisfaction within known planetary boundaries could look like.

Most importantly, a democracy-representing SJS supplements the biophysical and socio-economic segments with a cultural sector, thus recognizing that the attitudes and values prevalent within a given society are inextricably connected to the potential of the given anthrome's human population to adopt reproduction practices (Bhattacharya, 2017) that radically reduce the loading of the externalities of socio-economic practices onto the biosphere and that enhance known restorative properties. Metaphorically, the doughnut visualization can be likened to a human individual seeking a healthy life balance; people try to stay within the green belt of a healthy and morally fulfilling operating space through a supportive habitat and the healthy operation of the mind and body. A mental model is a diagnostic chart which can serve as a strategic departure point rather than a mechanical prescription of actions for a healthy and meaningful life explained through the details of causal interactions between diagnostic indicators. While acknowledging that this interaction exists, the doughnut chooses to remain temporarily agnostic about its details allowing room for contextual specificities within a paradigm shift in envisioning a just and sustainable state.

Understanding that excesses and shortfalls exist in all three segments of nations' reproductive practices allows us to use comparisons between different nation states (which are a mosaic of functional anthromes with some overlap) to inform their populations of the possible change strategies that operate within a fair share of the total planetary population's safe and just operating space. The implied argument is that anthromes' human populations can learn from each other and can make contributions through their actions towards overall planetary stability by developing autonomous mechanisms for reaching biophysical, socio-economic, and cultural aspirations without the unjust burdening of the planetary biosphere. The model implicitly assumes global human cooperation and mutual understanding with localized responsibility for reproduction practices. National doughnut models aim to keep the planetary load manageable and democratically accessible. A circular visualization of finite size deliberately avoids selecting some aspects as "more central," treating for example carbon dioxide emissions, human life expectancy, household debt, and mutual distrust in societies as coequally important. It also prevents a limitless addition of indicators along the ring that would result in the cognitive reaction of conceptually systematizing them into a hierarchy of causal drivers and consequences. It deliberately frames the complexity of the issue within the simple-enough constraints of a safe and just operating space that can resonate with non-experts as well.

Segments, Themes, and Indicators

Ideally, our mental models should be oriented by a set of indicators reflecting the different contexts in which human society is embedded in the anthromes. This does not mean an overburdening myriad of indicators, but a set that is qualitatively different and variegated to depict the complex multidimensional characteristics of the states' anthrome mosaics. Currently, our mental models are guided by the quasi-imposed limited set of concepts, the economic circulation modeling, which severely limits our knowledge horizon (Maria Pulselli et al., 2016). Our strategies to address the ecological and injustice crises of this century are then skewed toward greater consideration of economic output factors at the expense of physical relationship between humanity and non-human nature, and our social relationships between humans within and between communities and states. The symbiosis between the economy, environment, culture and politics must be taken into account in our mental models, strategizing for an integrated system as a whole rather than single parts in isolation from each other. As Maria Pulselli et al. (2016) have advocated that the systemic analysis unites global pressures with local actions, the mental model of the degrowth doughnut should bridge the gap between the "scientific need" for a global systemic transformation and the "governance need" for local action and policy implementation (Maria Pulselli et al., 2016, p. 228).

The principles guiding this conceptual framework include the (i) limited space with constrained properties of an absolutely finite biophysical infrastructure of the planet, (ii) emergence of properties in a "black-box" complex system, (iii) long-term consequences of the short-term transgression of tipping points, (iv) extrapolation of causes and drivers from the tracking of symptoms, (v) inclusion of life-cycle thinking into stocks and flows comparisons, (vi) history of human development as the "common intangible heritage" on a shared planet, and (vii) localized strategic action with fair share of global impact (Maria Pulselli et al., 2016, p. 231).

The degrowth doughnut mental model, as an analytical tool and a visual representation, incorporates these principles to provide a paradigm of democratically "de-growing" the energy and matter throughput of the global economic system and of re-orienting societies' metabolisms toward provisioning to meet the needs of people's well-being by distributing shared wealth through different allocation of resources and ecosystem restoration. Below the degrowth doughnut's foundation lie the shortfalls in democratic activation and wellbeing, education, health, equality, sustainable reproduction and planetary protection. Beyond its outer boundary lie the overshoots of pressure on Earth's life-supporting systems, of resource extraction, exhausting work and junk nutrition, of selfish and uncooperative popular value sets. Between these two boundaries lies the progressive but caring safe and just operating space for humanity in the 21st century metabolic and cultural transformation. The boundaries and the thresholds have broadly cultural, socio-economic and biophysical segments in which sets of indicators are grouped.

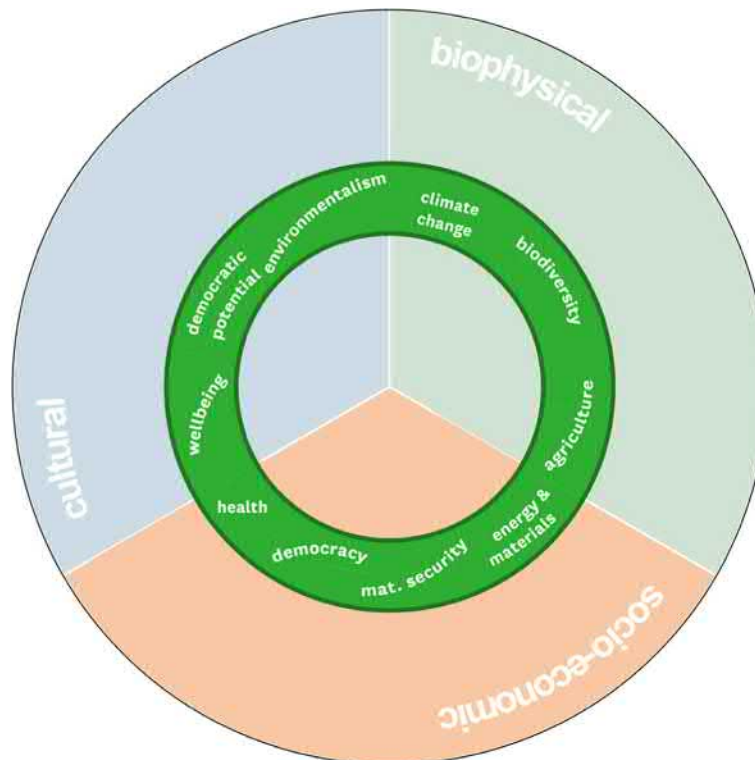


Fig. 4 Degrowth doughnut concepts used to derive the scaled-down quantified visualizations. Boundaries and thresholds exist in all three segments (biophysical, socio-economic and cultural). From Institute for Political Ecology, www.ipe.hr.

Within the cultural segment, three themes are quantified through excesses and shortfalls: planetary-minded environmentalism, democratic potential for desirable socio-metabolic change, and perception of human wellbeing. The indicators track popular attitudes whose overshoots and shortfalls in a nation support a reluctance to engage in democratic activation for reducing the human impact upon local and global biospheres. They also quantify excessive frustration and apathy obstructing design and implementation of the novel social reproduction mechanisms necessary for metabolic change, as well as shortfalls in positive support for degrowth-oriented policies (van den Bergh et al., 2019). It is important for an integrated mental model to keep track of the existing and future life-satisfaction through average self-reported wellbeing (health and satisfaction). Perceptions, though subjective, are important to track as they are the final outcome of the democratically supported metabolic practices among rational reflective members of the human community. They logically connect to the socio-economic segment of the model, to its theme of democratic infrastructure (Fig. 4).

Four themes are included within the socio-economic segment: health, democratic infrastructure, material security of individuals, and material and energy flows of the whole society. Indicators in the theme of material security deliberately do not include a measure of average personal or national income, a cornerstone of current economic tracking of social metabolism which motivates further commodification of public wealth. Current metabolic practices expose citizens to overwork and debt, motivating the externalization of the associated costs by imposing them upon the rest of society and the biosphere (Rosnick and Weisbrot, 2007) while historic attainments in productivity and automation allow for less time to be spent on paid work and for more time to be dedicated to other forms of care and restoration. Conceptually the closest concept to the biophysical segment of indicators is the theme of energy and materials use (Fig. 4), including indicators of per capita energy use, national material footprint and share of renewables within final energy consumption.

The biophysical segment of the doughnut conceptually joins the original circle of planetary boundaries (Fig. 1) with the desirable thresholds of climate change stabilization and ecosystem restoration. It carries with it the themes of human food production (agriculture), biodiversity protection, and climate change (Fig. 4). These are the three crucial biophysical themes for every anthropocene to consider in this century.

Safe and Just Operating Space in Biophysical, Socio-Economic and Cultural Quantification

On the overall doughnut we therefore find external rim boundaries in climate change drivers, pollution, extraction, energy and materials flows, work and debt burdens, inequalities, poor nutrition, the perceived failures of democratic institutions and social cohesion, as well as popular opposition towards action for the preservation of planetary ecological stability. Like the planetary overloading of ecosystems with pollutants and of the atmosphere with climate change-driving greenhouse gases (Fig. 1; Rockström et al.,

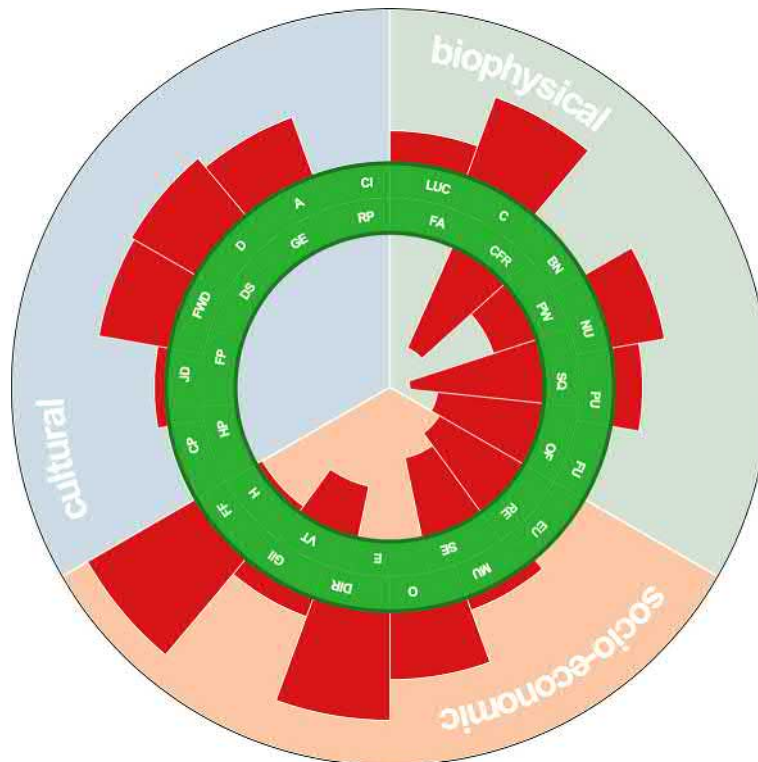


Fig. 5 Degrowth doughnut visualization with 33 indicators for a realistic small European state. *Cultural*: CP, corruption perception; JD, job dissatisfaction; FWD, frustration with democracy in country; D, distrust; A, anthropocentrism; CI, climate change indifference; HP, health perception; FP, flourishing perception; DS, degrowth support; GE, global environmentalism; RP, renewable energy prioritizing. *Socio-economic*: EU, energy use; MU, material use; O, overwork; DIR, debt income ratio; GI, gender inequality; FF, fatty food; RE, renewable energy %; SE, social equality; E, education; VT, voter turnout; H, healthy life expectancy. *Biophysical*: LUC, land use change; C, CO₂; BN, biodiversity neglect; NU, nitrogen use; PU, phosphorus use; FU, freshwater use; FA, forested area; CFR, climate change flood resilience; PW, protected wilderness area; SQ, soil quality; OF, organic farming area. From Institute for Political Ecology, www.ipe.hr.

2009), all these cultural, socio-economic and biophysical factors present excessive burdens on states' fair share of the transformational 21st century social metabolism. They simultaneously hasten the push towards ecosystems collapse and disable societies' cooperation to avert it. Crossing these boundaries moves the states out of a safe and just operating space.

The inner rim lists thresholds for ecosystem restoration, sustainable food and energy provision, social equity, democratic participation, human health, wellbeing, and pro-environmental activation. Shortfalls in reaching these thresholds, like the shortfalls in reaching the goals of development in nature-society doughnut visualizations (Fig. 2), signal insufficiencies in the existing conversion of work and resources into human flourishing and ecosystem stability. The degrowth doughnut's inner ring—its restorative foundation—sets out the basics of 21st century just and sustainable life on which no society should be reneging. The red bars quantify shortfalls within the present organization of an ever-increasing throughput driven by fossil fuels, indicators of what a democratic and just operating space for the climate and extinction constrained 21st century anthromes must strengthen and preserve.

Upon facing the doughnut's themes and indicators, the rationally trained mind gropes for causal mechanisms to be extracted out of the structure: what are the greatest "bads" driving the greatest "goods" and what causal interactions exist between them. Here it is worth bearing in mind Einstein's injunction against premature constructive theory developments (Howard, 2017). Such urges, though understandable, lie in the eye of the reader and are intended by the structure of the doughnut. There is a myriad of logical and empirical connections between the different themes placed around the ring of the doughnut, as well as between the different indicators chosen to quantify them through a globally comparative array. A future sustainability science paradigm should, indeed, determine what these connections are (in particular if there are any feedback loops which drive nonlinear behavior), and seek to discover a fair and effective way to influence their evolutionary dynamics. As a principle theory tool, the doughnut offers a blueprint to transcend the trade-off between development and devastation, to transcend the conceptual paralysis resulting from a lack of mechanism connecting planetary sustainability with the 20th century development. Democratically addressing climate change and biodiversity loss, while providing for people's wellbeing, decent health, nutrition, and material security through a fair and sustainable volume of material and energy flows will all be a part of the safe and just operating space for a redesigned societal reproduction in the 21st century.

In that sense the themes are conceptually more important than the indicators chosen, though the latter must have a realistically broad coverage of different nations or a link to suitably interchangeable proxies to allow for broad enough comparison and

longitudinal temporal tracking from readily available databases. Moreover, while the available comprehensive global statistics are collected on the national scale, most of the themes are open to scaling down to the level of specific metabolically integrated areas rather than politically delineated anthrome mosaics. Likewise, due to changes in energy production and global metabolic flows in the future some indicators could lose significance or sensibility. But an adherence to the principle of seeking a safe and just operating space by scaling down, in a fair way, from known global limits and potentials through concepts of climate stabilization, wellbeing, care for the planet, and fair distribution of its resources, will yield comparable doughnut visualizations.

The usual objection to the quantification of variables within highly complex interactions beyond a simple causal-mechanical model is that it is the quality and not the quantity of the characteristics and phenomena associated with the variables that is really important. This becomes especially pertinent when transdisciplinary assessments, like the doughnut, combine well-known quantitative indicators like carbon and nitrogen pollution with less familiar ones like neglect of biodiversity protection, healthy life expectancy of human population, debt to income ratio of households, or average level of satisfaction of survey respondents with their current job. In the first instance the quality versus quantity objection applies to all indicators, and is usually already addressed within the entrenched scientific disciplines where these indicators are most often used. Indicators do indeed provide descriptions, explanations, and predictions within the standard conceptual frameworks of those disciplines. Their broader discursive acceptance then stems from the popular visibility of respective disciplinary narratives. For example, even the most readily used national carbon emissions data in popular presentation are actually opaque to the debate about short-cycle carbon emissions, the debate about necessary and luxury emissions, and the debate about emissions created outside the specific territory through trade and intercontinental transport.

In the second instance, the quality versus quantity objection renders the transformative role that the principle theory approaches play within scientific paradigms impossible. The tracking of categorical differences in orders of magnitude and coarse-grained trends are the conceptual instruments for reasoning about the possible and impossible changes under constraining principles. This is what allows for workable explanations across a range of otherwise confusing and seemingly disparate phenomena, with a temporary suspension of attention to fine qualitative differences between their constituent elements. A degrowth doughnut is a visual model motivated by the call for a redesign of socio-metabolic interactions to avoid the worst exemplars of environmental degradation and the breakdown of complex modern societies; it is not the fixed mechanism of the causal links between drivers of environmental change and (for example) subjective experiences of poverty.

The consequential objection refers to a strategic action based on the assessments presented in national doughnut visualizations, namely that it is possible to implement courses of action that will reduce the named excesses and shortfalls within the doughnut without seriously improving the quality of life and sustainability of societies and the ecosystems they are in interaction with. In other words, a sort of malicious defeatist short-circuiting of the doughnut themes and indicators without effecting a serious change. This amounts to the objection that the themes and indicators are not well chosen, do not push the right buttons, or even that such indicators cannot be chosen at all because the problem is unfathomable. While short-circuiting is, indeed, a logical possibility, the diverse and widespread nature of the indicators is designed to spot this practice precisely by not fetishizing the crucial few and by maintaining agnosticism about the causal chains between them.

While the questions and samples in the surveys might be engineered to register lower levels of distrust and anthropocentrism, along with higher levels of environmentalism, social equality, and voter participation, a simultaneous action to manipulate the social survey results on a global scale together with reduction in soil erosion of agricultural land and reduction of fresh water and energy use will take at least as much coordinated intellectual and social effort as genuinely attempting to transition to an alternative modernity that will be sustainable by doughnut measures. This answers the final question of the use of the doughnut for anthromes that have no excesses or shortfalls to begin with, or that are capable of removing excesses and shortfalls relatively soon. Such societies and the biomes they inhabit are best positioned to redesign notions of progress and sustainability for the planet; in other words, doughnuts are not designed to be eternal ideological crutches, and the sooner they become uninformative and obsolete because of an end to the practices which fall outside of the safe and just operating space for humanity, the better.

Application of the Model

The doughnut representation with its quantified boundaries and thresholds reminds us that boundary transgressions related to biophysical processes, social justice, and societal commitments to sustainability are already occurring. Shortfalls also already exist in terms of ecosystem restoration, democratic governance, carbon neutral energy provision, and popular support for socio-metabolic transformations that contribute a fair share towards global sustainability. Continuing along the same path by focusing on economic growth as the foundation for an industrial socio-metabolic mechanism to process resources into wellbeing is now creating more problems than it solves. Growth is a maladaptive strategy towards achieving a just sustainability in this century (D'Alisa and Kallis, 2016).

The example doughnut for a peripheral European state in [Fig. 5](#) (based on publicly available data) presents no shortfalls in the average popular perception of personal mental and physical wellbeing (HP, FP) or in the prevalence of values compatible with orientation to new metabolic regimes and globally environmentally beneficial practices (DS, GE, RP). This is the state's cultural potential on which to build transformative strategies. It is, however, hindered by a slight majority of anthropocentrism and a predominantly negative perception of society's current democratic potential and social cohesion (FWD, D).

Building institutions through which collective action on degrowth transition can be fostered to turn its cultural potential into action, together with increasing voter turnout (a shortfall in the socio-economic segment) to enhance representativeness of the existing and new democratic institutions, could lead to desirable outcomes. Mild job dissatisfaction (JD) and overwork (O) present a call for a different organization of work for the economic provision of necessities and wellbeing. At the same time, shortfalls in social equality (SE) and excesses in household debt (DIR) speak to potential instruments for the redistribution of social surplus in the eventual redesign of economy or for public instruction as to the existing burdens of current economic practices.

Gender inequality (GI) must be further reduced to strengthen democratic governance potential, while mean expected educational attainment (E) for contemporary youths is yet another positive area on which there is potential to build. Energy and material flows (in terms of their effect on the planetary boundaries) are already comparatively low and should be maintained, building on the public support for renewable energy provision (RP), which currently exhibits a great shortfall from the perspective of the necessary decarbonization (RE). Carbon emissions and land use change as drivers of climate change need to fall back within the safe operating space, but forest coverage is already optimal. Immediate action is needed in the area of flood protection (CFR) to prepare for increased precipitation already locked-in under climate change. While neglect of biodiversity protection is not excessive, more areas need to be set aside for natural habitats with minimized human impact. Feeding the population with local quality nutrition is a priority, not just because of the excessive loading of the biosphere with artificial fertilizers, but because of the excessive content of lipids in the national diet, poor soil quality, and insufficient organic farming areas (which also carry biodiversity benefits).

Overall, this is a national territory, a political unit governing several anthromes whose primary tasks are securing healthy local nutrition for its population and strengthening its democratic infrastructure for a communal and democratic determination of context-specific sustainability goals. It already has the technological instruments for sufficient social reproduction, which must shift towards renewable energy. Agriculture and renewable energy transformations will help to reduce its contribution to the loading of the planetary biosphere with pollutants, which is something its population is supportive of but also impotent in acting upon because of frustration with the existing democratic infrastructure. Meanwhile, poverty, unsatisfactory work, and debt burden make the existing model of social surplus distribution unsatisfactory despite the fact that its volume (almost) avoids exceeding its fair share of planetary safe operating space. In comparison to other national anthromes with greater biophysical and socio-economic boundary transgressions and existing cultural shortfalls, this state has a more institutional and less material infrastructural change to make.

The doughnut model presents a visual tool for quantifying deviations of social reproduction of the politically determined anthromic mosaics from the safe and just operating space bounded by biophysical, socioeconomic and cultural downscaled indicator values. The doughnut ring contains outer boundaries in climate change drivers, chemical pollution, extraction of renewable limited resources, energy and materials flow, work, debt, gender inequality, overload of insufficient nutrition, residents' perception of democratic institutional failures, social disintegration, and popular opposition towards acting on the preservation of planetary ecological stability—current possible excesses of social metabolism and dominant culture. Its inner boundaries consist of ecosystem restoration, sustainable food and energy production, equality, democratic participation, health, popular perception of personal wellbeing, and pro-environmental values—current possible shortfalls. The model provides a base for guiding strategies of urgent and radical socio-metabolic transformation that human politics must put in practice to achieve a just global sustainability.

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Degrowth

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Abstract

Degrowth is a social movement and a research framework which advocates for a transition to sustainable and just forms of social organization. It proposes to achieve this double objective by “de-growing” the energy and matter throughput of the global economic system and reorienting economic activity away from production of material goods toward provisioning to meet the needs of people’s well-being by distributing shared wealth using different ways of allocating resources (Kallis, 2018). As a “transitional discourse” envisioning alternative societies built on “ecological integrity and social justice” (Escobar, 2015, p. 1), it approaches the transition from a systems-thinking perspective that combines the values of ecology, justice, well-being and democracy (Demaria et al., 2013) with the theoretical foundations of ecological economics, political ecology, post-development, environmentalism of the poor and limits to growth. The proposals in academic literature cluster on (1) reduction of the environmental impact of human activities, (2) redistribution of income and wealth within and between countries, and (3) transition from a materialistic to a convivial and participatory society (Cosme et al., 2017).

Introducing Degrowth

Degrowth emerged as an international movement in the early 2000s from a dissatisfaction with the official responses to climate change and planetary environmental degradation, whose foundations were laid out in the Brundtland Report (1987) and the UN Framework Convention on Climate Change (1992). These documents have explicitly wed the climate action of governments to their commitment to free trade and economic growth, although these two pillars of the capitalist system of production have, since the onset of the industrial revolution and particularly since the Great Acceleration after WWII (Steffen et al., 2011), necessitated a growing appropriation and degradation of planetary ecosystems. The contemporary degrowth movement has three aspects, theoretical, activist and political, which are not rigidly integrated into a common framework but there is a continuous interaction between actors and ideas, especially in the international degrowth conferences (Martínez-Alier et al., 2010). Unlike the ideals of sustainable development, green growth, and green capitalism, degrowth insists that environmental stability and sustainability can only be achieved through a departure from the present growth-oriented global capitalist system.

The term draws its inspiration from *The Limits to Growth* report to the Club of Rome published in 1971 and was coined a year later in French as “décroissance” by French-German philosopher of political ecology André Gorz, only to be confirmed a couple of years later in the translation of a work by Romanian-American economist Nicholas Georgescu-Roegen, the founding figure of ecological economics. The word “officially” entered into English with the first Degrowth Conference held in Paris in 2008 (Demaria et al., 2013, p. 195). Initially the idea of “décroissance” rallied together the grass-roots activists working on issues such as environmental justice, protection of the environment, opposition to extractivism, and infrastructural and energy projects alongside the practitioners of alternative forms of organization of social production and consumption like permaculture, cooperatives, ethical banks, cohousing, squatting, and recycling, gradually consolidating into an international social movement (Demaria et al., 2013, pp. 202–203). Regular international conferences crystallized it also as an activist-led research agenda (Martínez-Alier et al., 2011) and a platform for political advocacy. The research agenda received its provisional manifesto in *Degrowth: A Vocabulary for a New Era* published in 2014, whereas the political advocacy had its first high-profile international foray with the Post-Growth Conference held at the European Parliament in 2018.

The foundational insight of degrowth is that there cannot be endless growth on a finite planet. While the Earth is not an entirely closed-off system, almost no matter enters the atmosphere, and the incoming solar energy is not readily convertible into work that is able to satisfy human needs. Thus, the regeneration of energy stocks and the recycling of matter available for human use can unfold only at a very slow rate. However, the pattern of continuous economic growth inaugurated by capitalism is based on disregard for the overall limits of planetary stocks and flows, counting on substitution of the depleted sources with hitherto untapped ones and simultaneous displacement of ecological impacts to global economic peripheries. Over the last century, global material extraction and primary energy consumption have grown roughly tenfold to 70 Gt/year (Schaffartzik et al., 2014) and 525 EJ/year (Smil, 2016, p. 241) respectively. The world’s ecological footprint currently exceeds the annual bioregenerative capacity of the planet by 70%

(Global Footprint Network, 2013). Human use has significantly altered 75% of global ice-free land (Ellis and Ramankutty, 2008) and 66% of marine environments (IPBES, 2019), and appropriates around one-third of the net primary production of terrestrial systems (Haberl et al., 2014).

This expanding dynamic of extraction has led to a number of negative impacts on Earth's biophysical systems resulting in dangerous climate change, biodiversity loss, acidification of oceans, soil degradation, and land-use change, pushing the planetary systems beyond the limited variability that has provided a safe operating space for human societies to thrive over the last 10,000 years of the Holocene (Rockström et al., 2009). The effects of these disruptions are distributed unequally, hitting both the most economically (Diffenbaugh and Burke, 2019) and environmentally disadvantaged populations and countries the hardest. At present, no country stays within its "fairly apportioned global biophysical boundaries" while also meeting the basic needs of its people (O'Neill et al., 2018). From a degrowth viewpoint, in order to bring societies within the planetary boundaries, the pattern of expanding extraction has to be reversed, and the provisioning systems addressing societal needs must be organized differently.

The patterns of resource-use change throughout history, along with the modes of production and forms of allocation. These patterns define socio-metabolic regimes (Fischer-Kowalski, 2011). The dominant socio-metabolic regime in the contemporary world is defined by a system of industrial production enabled by the high energy intensity of fossil fuels and global free trade. This system is organized around the capitalist separation of workers from the means of subsistence. This separation forces them to work for a wage in order to be able to secure their subsistence by purchasing commodified goods and services in the market, and to work beyond the level that meets their needs in order to generate a surplus. The surplus produced by the workers is appropriated by the owners of capital for private consumption and, fundamental to sustaining the dynamic of growth, for reinvestment into further accumulation of capital. This process of capital accumulation under the conditions of competition is accompanied by an imperative to raise productivity, resulting in growing economic output, i.e., an ever-greater quantity of goods or services produced in a given period of time. This growing economy has a strong historical correlation with the growth of material footprint and CO₂ emissions (1% increase in GDP resulting in 0.6% increase of material footprint (Wiedmann et al., 2015) and 0.5–0.8 increase in emissions (Burke et al., 2015)).

Economic growth at the national level is measured by an increase in the Gross Domestic Product (GDP). Economic policies are drawn up to keep the GDP growing year after year, and GDP growth is a key performance indicator upon which governments stand or fall. The healthy annual growth rate of an advanced economy is considered to be between 2% and 3%, leading to a doubling of economic activity roughly every 24–35 years. The drivers behind this expectation of growth are twofold. On the side of system reproduction, capital is borrowed with the expectation that future growth should repay the debt and interest that will, in the next step, serve as capital for future borrowing. On the side of system justification, the competitive forces of the market tend to reduce wages and create inequalities, whereas growth allows policymakers to promise an increase in wages in the future without needing to redistribute the existing social wealth in the present.

However, researchers on the subject of inequality (Hickel, 2018; Milanović, 2016; Piketty, 2014) have documented that in advanced economies the expected trickle-down effect of wealth has not happened since the 1970s: as wealth has become concentrated at the top, wages have stagnated. Even with the exceptional effect that reduction of absolute poverty in China has had on global poverty, relative poverty in the world has increased since the 1980s (Chen and Ravallion, 2012). Alternative indicators of social progress like the Genuine Progress Indicator (Anielski and Soskione, 2002) reveal that once the negative social and environmental impacts are accounted for, beyond a certain level growth does not bring an increase in objective and subjective well-being and is environmentally disastrous (Kallis, 2018, ch. 4).

While there are hopes that growth can be maintained by making economic processes green and sustainable, empirically there is no evidence that economic growth can be achieved with simultaneous reduction of greenhouse gas emissions (GHG) and material extraction for a sustainably long-term period on a global level (Hickel and Kallis, 2019). This suggests that if the assessment of the Intergovernmental Panel for Climate Change (IPCC, 2018a) warning against runaway climate change, and the assessment of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019) warning against the unprecedented decline of biosystems, are to be taken seriously, human action faces a difficult choice between rapid reduction in throughput or the potential collapse of ecosystems. Without the assumption of near-complete and widespread substitutability of ecosystem services with anthropogenic goods and services, ecosystem collapse would also mean a subsequent economic collapse. Facing this choice, degrowth offers diagnoses and strategies (Demaria et al., 2013, p. 194) that address the major social obstacle to the transformation that is needed in order to make the global social metabolism sustainable: how to prevent that the rapid reduction in throughput does not lead to a widespread and forced reduction in social well-being.

Degrowth Economics: Bringing the Economy Back Into the Biosphere

Degrowth is, in principle, agnostic as to whether the planned reduction of throughput will lead to a reduction in economic output. The goal is not economic depression, but long-term sustainability and societal well-being. However, long-term sustainability might not be feasible without an economic slowdown. The reduction in GHG emissions needed to stay within the Paris Agreement limit of a 1.5 °C or 2 °C increase in average global surface temperature by 2100 compared to pre-industrial levels is achievable only if the world economy rapidly abandons its present pattern of growth driving the expanding use of cheap and polluting sources of energy. The current "business-as-usual" approach with unchecked growth and without rapid and planned decarbonization puts the Earth on a likely pathway of an increase of 4 °C or more. The world would have to cut net emissions to zero by 2050 in order to stay under

1.5 °C or by 2070 to stay under 2 °C (IPCC, 2018b). The necessary annual reductions in GHG emissions to achieve those targets at a zero-growth rate would be 6.8% and 4% respectively, but at a 2% growth rate they would have to be as high as 8.8% and 6% respectively (Hickel and Kallis, 2019, p. 15).

This is, however, far above the most optimistic predictions, which put GHG emissions reductions at a maximum 4% annually—implying that a reduction for a 2 °C increase might be achievable, but only with the rapid deployment of deep decarbonization strategies (transition to 100% renewables, afforestation and soil regeneration, and shift to alternative production processes) and, crucially, a zero-growth rate (Hickel and Kallis, 2019, p. 15). This scenario may still be impossible to implement, requiring the deployment of negative emissions technologies (Gasser et al., 2015). Most prominent among those is bioenergy generation with carbon capture and storage (BeCCS): the combination of planting crops for energy generation and capturing released carbon dioxide in order to store it underground. This combination of technologies is far from maturity, far from the scale of carbon capture needed, in competition for land with agriculture and biodiversity, and risks, in the case of seismic instability, massive carbon leakages from the underground storages (Anderson and Bows, 2011).

The economics of growth is thus at odds with the biophysical realities of climate change mitigation. It is for this reason that degrowth has taken up the task of challenging the economic orthodoxy which underpins climate change policies. However, this undertaking necessitates that degrowth mounts a critique not only of growth but also of the economic science for which it is axiomatic. Namely, the economic models used in the Intergovernmental Panel on Climate Change (IPCC) integrated assessment scenarios that assume, without exception, continued economic growth. These models are built upon the assumption of market equilibrium and are deterministic in a way that cannot account for uncertainties inherent to disequilibrium processes such as climate change, which can trigger unforeseeable changes in social systems over long periods of time, or in the case of the IPCC scenarios until the end of the 21st century (Spangenberg and Polotzek, 2019, p. 199).

Furthermore, they consider growth in GDP as the optimal outcome of decarbonization scenarios, while scenarios leading to a reduction in GDP are considered negative, displaying a bias against substantial changes in societal patterns of production and consumption (Spangenberg and Polotzek, 2019, p. 199). The reason why all economic models assume that growth will occur is that the fields of economics and economic policy are dominated by formal approaches which analyze economic processes in terms of market pricing, exchange values, and money, disregarding substantive determinants of economic processes like the metabolic interactions between society and the environment, politico-institutional structures, and the societal purposes of economic processes (Gerber and Scheidel, 2018).

The dis-embedding of the formal economy from its biophysical, socio-metabolic, and political determinants began historically with the emerging economic science in the 18th century striving to differentiate itself from the political economy and economic history that had dominated its early development. Until the 18th century, economics was no more than a practical art of managing the limited resources of land, estates, and populations. With the work of moral philosophers Adam Smith, David Ricardo, and John Stuart Mill, the definition of political economy gradually shifted away from concerns as to the purposes which guide economic activity to this activity's underlying laws (Raworth, 2017, ch. 1). With the marginalist revolution of the late 19th century, the discipline completed its boundary-work (Gieryn, 1983), succeeding in differentiating itself from neighboring disciplines through the demarcation of its distinct object of inquiry in the form of markets and its methods of formalization in the form of price theory (Gerber and Scheidel, 2018). As the capitalist mode of production emerged and spread across Europe, the focus of economic science shifted from the management of resources to the improvement of productivity, markets, and trade. The consolidation of economics thus proceeded apace with the consolidation of capitalism and the modern state.

The economy as the object of political and institutional governance assumed its present contours in the 1930s and 1940s in response to the Great Depression, ending the period of laissez-faire capitalism. The leading economic nations start to reconceive the national economy as a dynamic system of interactions between economic actors, whose value can be estimated by national accounting, measured by the gross national product and directed by policies which are primarily the responsibility of economic experts who are institutionally safeguarded from direct democratic challenges (Mitchell, 2014). The greater institutional regulation of free markets by national governments accomplished in capitalist economies after WWII then underwent a gradual erosion as international free trade began to intensify, leading to a period of neoliberal globalization during which the global integration of free markets severely limited the capacity of government to plan and direct economic processes and to limit their social and environmental impacts.

During the historical development of economics, substantive concerns of human livelihood and interaction with the environment got pushed into the background. The economy was reconceptualized, as illustrated by the famous circular flow diagram drawn by Samuelson (1948, p. 264), as an isolated system where exchange values circulate between households and firms and no resources are taken from nor waste released into the environment (Daly, 2019, p. 10; Raworth, 2017, Introduction). This is a reductive and distorted image that ecological economics has taken up the task of setting straight. In his foundational contribution to ecological economics *The Entropy Law and the Economic Process* (1971), Nicholas Georgescu-Roegen posited that all economic activity is constrained by thermodynamically irreversible increase of entropy: it takes matter and energy from nature in a condition of higher order and availability for transformations—and returns waste and dissipated heat into nature in a condition of higher disorder and reduced availability. The process of degradation is a necessary byproduct of all value creation, it is irreversible, and recycling can only be achieved with a substantive investment of energy resulting in further degradation.

Georgescu-Roegen thus placed the economic system back inside the biosphere. All value produced in an economy crucially depends on nature's sources of matter and energy, and sinks absorbing waste and dissipated heat. In fact, humans, by drawing on water, food, matter and energy from environments locally and globally, depend for their metabolic reproduction on exosomatic

services of nature—maintenance of biological and social structures that compensate for the inevitable losses due to entropy (Ayres and Kneese, 1969). The basic human endosomatic metabolic rate has been expanded in hunter and gatherer societies through the exosomatic appropriation of food and heat from firewood by a factor of three to four to around 11 GJ/capita annually, in agricultural societies through plant cultivation and animal husbandry to 20–80 GJ/capita, and in industrial societies primarily through fossil fuel burning to 280 GJ/capita (Fischer-Kowalski et al., 2014, pp. 21–22). These expanding patterns of appropriation, alongside increasing complexity and necessary reflexivity of the symbolic or social realm (Ostrom, 2009), have characterized the evolving social metabolism of human societies.

The following energy-materials-culture nexus defines the social metabolism of contemporary growth-oriented capitalist societies. The energy-intensive stocks of fossil fuels are used for energy conversions that increase the productivity of human labor in the transformation of growing quantities of matter into products. Products thus embody the matter and energy that went into producing them. Products sold as commodities can be machines destined to be used in a future production process, or goods and services destined to be irreversibly expended in the consumption process needed for continuous social reproduction (Bhattacharya, 2017). Overall, a section of the human population, the class of capitalists that owns the means of production, employs workers but pays them less than the value of the product of their labor, appropriating the surplus that is left once the wages, machinery, raw materials, energy, and other operating costs have been paid. The greater the ratio of appropriated surplus value to wages, the greater the rate of exploitation of labor. Exploitation happens as an intrinsic and systemic feature of the capitalist organization of social production and indirectly reproduction, as capitalist class must keep drawing as much surplus labor as possible due to systemic commitment to market competition. But capitalists are also able to dictate how the social surplus will be produced and to what ends it will be expended, and thus as a class have more economic power in defining the purposes and priorities of the societal process of production and society's continuous reproduction over time.

Market competition between capitalist enterprises creates a structural imperative that a large part of the surplus must be reinvested into even more productive uses by mobilizing more human labor, more socially reproductive labor that goes into sustaining laboring humans, more resources from nature, more cheap and hard labor from poorer economies to extract those resources, and more knowledge and machines that make that labor more productive. This ultimately leads to the creation of even more surplus, thus engendering a pattern of self-perpetuating growth. However, that growing investment toward productive use also requires growing expenditures on nonproductive consumption in order to absorb the growing amount of product, resulting in an unstable spiral of overaccumulation and underconsumption that unleashes capitalist crises (Kallis, 2018, ch. 2). These are in turn used to reinforce the political imperative of a return to growth, or the current economic system would collapse. The expanding appropriation of resources from nature is thus coextensive with successfully pursuing the imperative of growth, increasing environmental impact through an expansion of social metabolism and socio-economic insecurity through a spur for greater overall exploitation.

Degrowth's critique of the economics of growth—and of the broader dominant “culture of growth” (Latouche, 2009), “growthism” (Daly, 2019) and the “growth paradigm” (Kallis, 2018)—builds upon the insight that, ultimately, the decoupling of the economic system from the throughput of matter and energy is impossible (Parrique et al., 2019). The assumption that all social and environmental challenges can eventually be overcome by maintaining continuous growth ignores the fact that economic processes will always have environmental costs, which on a finite planet only get displaced from one ecosystem to another as the global system of production expands from location to location and replaces one technological process with another. Historical evidence at the global level shows that environmental impacts cannot be substantively diminished in a sustainable way while maintaining economic growth in its present form. Starting from there, degrowth economics pursues the following objectives:

- to reembed the economy into society, and the society into Earth's systems (Raworth, 2017),
- to reconceptualize the economy as “the instituted process of interactions between humans and their environments, involving the use of material means for the satisfaction of human values” (Kallis, 2018, ch. 2),
- to develop policy proposals for the reorganization of the economy and the attendant political system to bring the socio-metabolic processes within the biophysical boundaries,
- to analyze how the growth-oriented capitalist system produces artificial scarcity as coercion to wage labor (Hickel, 2019) and how it “solves” this scarcity through the massive overproduction of material things,
- to analyze how the growth-oriented capitalist system creates dynamics of power, social hierarchies, and oppression through the private appropriation of social surplus (Kallis, 2018, ch. 2), and
- to develop a social system of distribution that would lead to an economy of abundance and human well-being based on sharing.

Degrowth as a New Political Imaginary

Degrowth takes a nonreductivist approach to societal transformation. The transformation that it advocates starts from the understanding that the existing social reality is shaped by an economic system that locks the majority of the world's population into patterns of production and consumption based upon a premise of economic growth and growing throughput. However, as the economic system has coevolved with the political system from which it arose, this lock-in is predicated upon a geopolitical order that is founded on, and legitimizes the subjugation and exploitation of social groups as well as the destruction of nonhuman nature. Therefore, the societal transformation that degrowth advocates requires a reimagining of the political—a repoliticization of

fundamental social questions and antagonisms regarding a common trajectory and alternative visions of the future (D'Alisa et al., 2014a). To maintain the cultural complexity of contemporary life with a biophysically less impactful metabolism, a degrowth transition needs concrete proposals on how each of the processes that maintain high throughput (energy supply, technological infrastructure, financial system, agriculture, manufacture, etc.) could evolve in the desired direction. This is the nonreductivist aspect of degrowth: positing that the future transition has to be conceived of and developed multidimensionally within the boundaries of the Earth's biophysical systems and flourishing cultural emancipation (cf. *Mental Models of Sustainability: The Degrowth Doughnut Model*, this volume).

Degrowth acts as both a provocation and an opening for a new political imaginary, coming amid the burgeoning realization that the imaginary of endless growth on a finite planet can no longer be sustained. The disavowed environmental impacts of the endless growth have become so severe that they are pushing Earth's biophysical systems beyond their limited Holocene variability, presenting a grave threat to the safety and survival of a growing part of the world's population. Therefore, degrowth insists on an unpopular yet realist position that there is no empirical evidence to believe that throughput can be lowered globally and for the foreseeable future without "de-growing" economic output (Hickel and Kallis, 2019). However, acknowledging that the lowering of economic output might adversely affect the well-being of many and particularly of those who are disadvantaged in unequal societies, and acknowledging that people equally fear the loss of socio-economic security as they fear the impacts of the climate crisis (Clayton et al., 2017), degrowth proposes that societies produce less material output while socializing care for the well-being of all. Such an ideal runs counter to the hegemonic common sense that the imaginary of growth instills in governments, experts, and general populations.

After the end of socialism in the countries of Eastern Europe, a social system that prioritized equality but not sustainability as it followed the productivist, extractivist, and growth-oriented trajectory of industrial development, there seemed for decades to be no alternative imaginary of what could supplant the present capitalist social system that prioritizes neither equality nor sustainability. This is where degrowth steps in. It is developing grass-root alternatives and proposals (see the next section) that are both concrete to the extent that they are workable in practice and utopian to the extent that they cannot be aligned with a growth-oriented capitalist society. These real utopias guided by the principles of equality, democracy, and sustainability (Wright, 2013) propose prefigurative practices that show how to organize anything from social production, care provision, financial system, technology, transport, and transit to the collective and convivial expenditure of social surplus on human self-realization. By inserting these practices into the social reality, degrowth practitioners foster new common senses (D'Alisa and Kallis, 2016) rooted in the material organization of the everyday which respond to the looming ecological crisis and demonstrates, practically, that growth is not necessary for human well-being.

These practices are plural and frequently heterogeneous, as they reflect the plural concerns and heterogeneous conditions that exist within and between capitalist societies. They are not axiomatic deductions from a program of transition, because degrowth does not envision transition as the top-down implementation of a societal model, but as an evolutionary process of change which can build momentum, spread, and become generalized at various social scales and across societies as the present capitalist social formation fails to respond to nonlinear disruptions to the environment and to deepening social disparities. However, in this heterogeneity, such practices are the building blocks of a degrowth transition, and share a set of values and orientations beyond the fundamental assumption that they work toward lowering throughput and increasing collective well-being:

First, they require both the dissolution of the capitalist class division which features private appropriation of surplus and the suspension of capital accumulation (Blauwhof, 2012; Kallis, 2018, ch. 6), because the appropriation of surplus gives the power to direct social development while capital accumulation drives the process of economic growth.

Second, they emphasize collective forms of ownership and management of resources like public goods and commons, where the perspective of utility is commensurate with the collective good and its planetarily defined limits. Commoning—practices of creating sustainable systems of provision and peer governance that produce shareable goods as opposed to private accumulation or autocratic allocation (Bollier and Helfrich, 2019)—social and natural resources would shift the emphasis toward sharing and creating collective abundance through the careful maintenance of those resources.

Third, they are guided by environmental justice concerns, starting with the understanding that affluent societies have benefitted from the processes of conquest, imperialism, and "unequal exchange" (Hornborg, 2014; Moore, 2015), and that their economies continue to disproportionately benefit from the historical and present GHG emissions, material extraction, and appropriation of primary production of ecosystems, which have and continue to undermine the ecological and social integrity of less affluent societies. Degrowth thus demands a radical reduction in resource consumption primarily by affluent societies. However, it also acknowledges that not all of the world's population can converge upon the resource-hungry organization of life in affluent societies, as that would require bioregenerative capacities several times greater than what Earth can offer, and collectively following the model of Western development would be detrimental to all. Development has wrought devastation across the Global South and, as a result, these societies ought to be given the opportunity to pursue their own distinct paths of social development based on vernacular forms of sustainable economic organization. However, one precondition is that the Global North first abandons the growth-oriented development which forces those societies to integrate themselves into the capitalist world economy, entering with them into an alliance of de-development (Latouche, 2009, pp. 57–58). This would result in a pluriverse—a different way of understanding existence that permits countless groups of people to create their own distinctive but overlapping cultural realities, a recognition of multiple ways of being in the world.

Fourth, use values in capitalist economies are made commensurate and exchangeable through commodification and prices. This dis-embeds social needs from their social and environmental conditions and places them under the dynamic of self-sustaining

accumulation with a general disregard for any social or environmental damages. Yet the value of needs and damages cannot be made commensurate without the dynamics of economic power working behind the backs of social actors, and are thus, in principle, incommensurable (Martinez-Alier, 1990). In a degrowth society, there would be a reembedding of values within their social and environmental contexts and an institutional and democratic mediation of production and exchange (Polanyi, 2001 (1944)).

Fifth, as degrowth implies a reorientation from the production of commodities to the provision of relational goods, the focus of a degrowth economy would be on care-work, which tends to disproportionately fall upon women and migrants, in turn requiring a fundamental reorganization of social roles along the principles of gender and racial equality (D'Alisa et al., 2014b).

The liberation of the social imaginary from the 20th-century developmental model that degrowth pursues implies an overcoming of the hyperseparation of society from nature (Plumwood, 2005), where expansion to satisfy social needs is seen as mastery over nature that then transgresses the boundaries of nature's biophysical systems—so that social needs and nature seem to stand in opposition. A degrowth society views stability and the ability to thrive, both of society and nature, as mutually reinforcing. It thus avoids the conceptually paralyzing trade-off between biophysical boundaries and social thresholds. Excesses and shortfalls exist in all dimensions of current socio-metabolic patterns: cultural, socio-economic, and biophysical. Understanding this allows us to envision integrated policies to keep the planetary human population within the safe and just operating space defined by known metabolic and cultural constraints of the 21st century (cf. *Mental Models of Sustainability: The Degrowth Doughnut Model*, this volume).

Policy Proposals for Socially Sustainable Economic Degrowth

Degrowth's double objective of achieving sustainable and just societies is primarily aimed at affluent societies. It is the affluent societies that should primarily downscale and redistribute, relieving other societies from the competitive pressures and allowing them to pursue their own different paths leading to that same double objective. If pro-environmental downscaling is implemented along with a redistribution toward greater well-being and equality, a substantial part of the population is likely to perceive it as socially acceptable (Ančić and Domazet, 2015). In affluent societies, it is not a higher level of income, but a lower level of inequality which leads to higher life expectancy and better educational attainment (Wilkinson and Pickett, 2011), and lower disparities in power and income lead to greater environmental protection (Boyce et al., 1999; Raworth, 2017, ch. 3). Therefore, a downscaling of the throughput must necessarily be accompanied by a monumental redistribution of resources and power—requiring all-encompassing democratic control.

In order to achieve this reduction in throughput with a parallel increase in well-being, degrowth proposes these policy measures:

1. *Economy and economics*: The economy has to be made substantive by capping resource use based on the limits imposed by the planet's biophysical boundaries, while human needs have to be democratically planned and equitably allocated to reflect those limits (Gerber and Scheidel, 2018). Sourcing of resources and products should be maximally localized. Economic production should focus on human livelihood and social reproduction, prioritizing relational goods over material goods, and placing sufficiency before efficiency and productivity. Advertising should be reduced and restricted.
Fractional reserve banking, the creation of money by private banks, and debt above what is needed for intergenerational redistribution should be abolished to limit the financial rents that drive the dynamics of growth. Concurrently, the state should take control over the issuing of "public money" (Mellor, 2010) to finance "a basic income or a job guarantee or to subsidize cooperatives, care services, environmental conservation or renewable energy" (Kallis et al., 2014, p. 13).
GDP as a measure should be abolished and replaced with indicators that measure social and environmental integrity through a multidimensional perspective of safe and just operating space (cf. *Mental Models of Sustainability: The Degrowth Doughnut Model*, this volume).
2. *Employment*: Lowering of economic output can lead to unemployment; however, the replacement of energy-rich fossil fuels might require more human labor (Sorman and Giampietro, 2013). Labor should be redirected toward care-work and social reproduction. Working hours should be reduced, work shared (Shor, 2014), and jobs guaranteed to anyone who seeks employment (Unti, 2014).
3. *Investment*: Investments should be redirected away from unnecessary and harmful activities such as military, fossil fuel, and polluting industries and toward achieving environmental sustainability in agriculture, technology, the built environment and infrastructure, financing public services, and supporting the development of a solidarity economy (Johanisova et al., 2014).
4. *Income and taxation*: Societies should establish a universal unconditional autonomy allowance (Liegey et al., 2013) and safe and complete access to basic goods such as food, housing, and care to meet the basic needs of all its members, while also placing a cap on maximum income and taxing wealth to limit disparities. Taxes should shift from taxation of labor to taxation of resources and pollution.
5. *Technologies*: Green technologies should replace polluting technologies to the degree that is feasible for the level of needs of a degrowth society. Gains in efficiency and productivity should be translated into caps on resources and reduction in working hours to prevent a rebound effect or the expansion of production. Technologies should be developed under open license arrangements and should be manufactured locally, while research and development should be done through a global collaborative effort (Medak, 2018).

6. *Restoration of ecosystems*: Downscaling the global throughput of energy and matter will not be enough to ensure planetary ecological stability—halting Earth’s sixth mass extinction as well as arresting anthropogenic climate change. Wherever they have been damaged, ecosystems need to be restored in order to effectively counter the destructive mechanisms already unleashed by the growth imperative. Expanding nature’s protected areas, afforestation, and replacing industrial agriculture with agroecological farming practices, are just some of the methods that can be used to serve this goal. Important as they are in and of themselves, these efforts also have the added benefit of shifting the social imaginary away from the current common sense of *Homo sapiens* as an inherently destructive species, to one that sees humans as inextricably tied to nature and capable of positive interactions with the nonhuman environment, in terms of fostering diversity and fecundity.
7. *Democracy*: Degrowth advocates for developing institutions of real democracy that extend and supersede the nominal democratic control that is prevalent in republican nation-states today. For instance, one vision of “direct democracy” that is gaining more traction within degrowth scholarship (Kallis, 2018; Vansintjan, 2018) is that of libertarian municipalism and communalism that was developed by Bookchin (2007) and Bookchin and Ursula (2015). Libertarian municipalism envisions a system of assemblies within differently scaled local areas, joining in a confederation of free municipalities. The broad consensus is that democratic practices and institutions need to be further developed and deepened from the currently dominant arrangement (Fraser and Jaeggi, 2018) and that economic democracy within workplaces is necessary (Asara, 2015). Since capitalism in all its forms has historically relied on institutional separations between the economic and political spheres (Cattaneo et al., 2012), a key condition for a degrowth transition is to reembed economic processes within the realm of social needs and political deliberation (Kallis, 2018).

Conclusion

The foundational insight of degrowth can be decomposed into three: there cannot be infinite growth of energy and matter throughput on a finite planet, economic growth cannot be decoupled from that throughput at the level of the global socio-ecological system, and the limits of planetary capacity to regenerate are already breached. Degrowth is a movement and a research framework which advocates for a societal transformation to reduce and stabilize, or “de-grow,” the energy and matter throughput of the global economic system, and to reorient economic activity toward designing structures of provisioning and peer-governance that address people’s shared and individual needs through flourishing of public wealth.

It is critical of the conception of economics and economic policy that disregard substantive determinants of economic processes like the metabolic interactions between society and the environment, politico-institutional structures, and the societal purposes of economic processes. It proposes to cap resource use based on the constraints imposed by Earth’s biophysical boundaries, and to democratically plan and equitably allocate common instruments of human needs satisfaction. Employment should be directed toward care-work and social reproduction, and investment directed toward ecosystems restoration and a solidarity economy. Economic production should place sufficiency before efficiency and productivity, ensuring sharing-driven provision for well-being. Societies should establish an unconditional autonomy allowance for all members based on the locally generated social surplus. Real democracy, where everyone interested has equal potential to participate in a collective process, should be the basis of decision-making, setting of boundaries, enforcement of rules and resolution of conflicts.

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New Economic Paradigms

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Abstract

Human activities are the main drivers of the Earth's ecological overshoot. Due to this overshoot, the actions of today may constrain the well-being of future generations. Simultaneously, despite the great extent and increase in economic activity, human needs are not universally satisfied. There is therefore a search for economic theories that offer answers to how to combine safeguarding of human needs with staying within the planetary boundaries. Here, four alternative economic approaches are reviewed. By combining insights from these, one may start to explore new territory and future pathways out of both ecological overshoot and human injustices.

Economic Growth and the Environmental Threat

The success in human development since the industrial revolution, including decreasing hunger rates, improved health, and scientific advances, gets much praise. This success has sometimes been attributed to the ability of the current civilizations to produce continuous economic growth, powered by free trade and globalization (see Fig. 1 portraying World GDP since year 1700 (Roser, 2013)) (Baumol et al., 2007). Nevertheless, we may still not live in the “best of all possible worlds.” What does it imply that World GDP has grown so tremendously?

The growth in world GDP is part of an unprecedented human expansion on Earth that is referred to as the *Great Acceleration* (Steffen et al., 2015). The notion of the *Great acceleration* suggests that the growth in economic activity is linked to a similar growth in environmental pressures and land system changes. Around 1700, nearly half of the terrestrial biosphere was wild and most of the remainder in the seminatural state. Today, due to land use expansion and intensification of land use, a majority of the land is agriculture and settlements, and only a quarter wild. Therefore, the contemporary forms and processes of terrestrial ecosystems are predominantly anthropogenic (Ellis et al., 2010). The current extent of human activities risks triggering biosphere tipping points across a range of ecosystems and scales (Lenton et al., 2019). Such tipping points threaten to undermine the life-support systems and lead to a less habitable “hothouse” climate state (Steffen et al., 2018). That would undermine any progress towards reaching human needs.

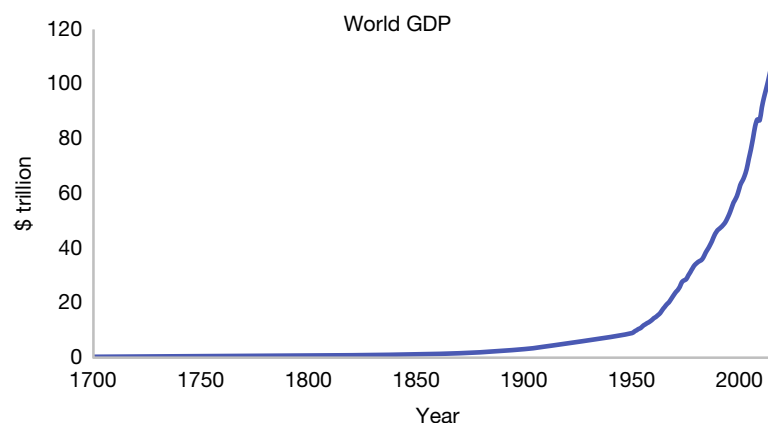


Fig. 1 World GDP from 1700 until today. From Roser M (2013) *Economic Growth*. Our World in Data. <https://ourworldindata.org/economic-growth>.

Furthermore, the needs of the current civilizations are not met. The evidences for this are many: hundreds of millions go hungry and lack the access to basic needs such as clean water (Ritchie and Roser, 2017; Roser and Ritchie, 2013). The inability of present societies to meet the basic needs of many is parallel to an accumulation of wealth in the hands of the few. According to a report from the British charity Oxfam, in 2018, 26 people owned the same wealth as the poorest half of humanity, consisting of 3.8 billion people (Oxfam, 2019). This, while around 800 million people or around 11% of the world population are defined as undernourished (Roser and Ritchie, 2013).

Economics, as a discipline, has set out as a goal to guide societies and this goal has been emphasized within the field. Paul Samuelson, an influential economist who 1970 received The Nobel Memorial Prize in Economic Sciences, has said, “I don’t care who writes the nation’s laws—or crafts its advanced treaties—if I can write its economics textbooks” (Samuelson, 1990). Furthermore, the economist John Maynard Keynes, famously wrote “The ideas of economists and political philosophers, both when they are right and when they are wrong, are more powerful than is commonly understood. Indeed the world is ruled by little else.” (Keynes, 2018, p. 340).

The contemporary economics discipline has been dominated by modern mainstream neoclassical economics, as virtually all university textbooks in economics are written from a neoclassical perspective (Fischer et al., 2018). This domination may be problematic as the same perspective has, combined with the neoliberal discourse, been argued to guide the world towards ever-increasing expansion and is continuing praising the virtue of exponential economic growth (Baumol et al., 2007; Göpel, 2016; Spash, 2017; Weil, 2009). Consequences of the downsides of today’s economies comprise both space and time dimensions of sustainable development. With other words, today’s societies are both failing to meet the needs and aspirations of current generations—and are simultaneously causing ecological problems that risk harming future generations. However, a diverse and growing group of academics is critically reexamining the current economic system and contribute to increased heterogeneity of world views in economics by offering alternative thinking.

The Root of the Problem

The ecological economist E. F. Schumacher argued in his book *Small is Beautiful* (1973) that economists often suffer from normative blindness and assume that economics is a science without presuppositions and is free from values. This is according to Schumacher (1973) a misstep as ideals of modernity, including considering consumption as the purpose of economic activity, influences the discipline. He makes a thought experiment by contrasting views on labor, standards of living, and patterns of consumptions prevalent in the economics discipline, against what they would be like if another point of departure such as Buddhist values would guide the discipline—and argues that these views are vastly different. Economic advises thereby reflect its normative starting points—and these are rarely presented or discussed (Schumacher, 1973).

Four Alternatives and What They Bring

Much of the critique against modern mainstream economics is not new (Daly and Townsend, 1993). Critics have recently, after the 2008/2009 financial crises, focused on inequalities within and between countries—and the increasing ecological crises. In the light of that humanity has entered the Anthropocene, there is a request for alternative economic paradigms that reflect this.

Below, a few more or less encompassing heterodox approaches to economic thinking that all bring different perspectives and tools for guiding the economy in a more sustainable direction, are presented. The four alternatives presented here are Post-Keynesian economics, Critical Institutional economics, Ecological economics, and System Dynamics. These approaches sometimes coincide with assumptions within mainstream neoclassical economics, and as there are many overlaps, there are not always clear distinctions between the different approaches.

This list of four alternative approaches is, of course, by no means exhaustive, and other approaches that deserve attention include Austrian economics, Evolutionary economics, Feminist economics and Marxist economics (see Further Reading).

Post-Keynesian economics

Post-Keynesian economics embarks from the British economist John Maynard Keynes’ ideas in his work *General Theory of Employment, Money and Interest* (Keynes, 2018) that he wrote as a reaction to the great depression. Post-Keynesian economics emphasizes distinct features of Keynes’ ideas, unlike the neoclassical synthesis that sought to incorporate Keynes’ ideas into neoclassical economics.

Post-Keynesian economics includes some assumptions which contrast it to modern mainstream economics and can contribute to the safeguarding of human needs within the safe operating space: it recognizes the contingency upon *historical time* as opposed to *logical time* used within mainstream economics, and it holds *deep uncertainty* as a fundamental building block of the economy, both explained below.

Mainstream neoclassical economics assumes *logical time*. Economic agents act rationally, expect others to act rationally and can thereby estimate the future. The assumption in Post-Keynesian is named *historical time*, according to which the behaviors of the world and individuals are constantly changing, and the past influences subsequent outcomes. Agents are, therefore, unable to figure out what the future is going to be. The past influences the future in unpredictable ways. This uncertainty influences planning and acting. In neoclassical economics, the future is probabilistic and risks can be calculated. Society could use this to insure itself, and by deciding on the risk preference, make an informed choice. According to this assumption, individuals and society can calculate and

plan for all future behavior at once. We can thereby, in line with for example (2018 awarded the Nobel Memorial Prize in Economic Sciences) William Nordhaus' model DICE, calculate and weigh costs and benefits of taking steps to minimize global warming and act rationally following its calculations (Nordhaus, 1992). Such a calculation is, from a Post-Keynesian viewpoint, troublesome as it reduces uncertainty to calculated risk and gives a false depiction of the world. In Post-Keynesian economics, neither the probabilities of, for example, a natural disaster, nor the expected outcomes, in the form of destructed buildings or suffering, can be meaningfully calculated. The world itself is unpredictable and constantly changing—there is *deep uncertainty* (Holt and Spash, 2009).

A consequence of the assumption of *deep uncertainty* in Post-Keynesian economics, is that an individual's behavior may be guided by the behavior of others causing so-called *herd behavior*. As these behaviors can radically transform, the result may be drastic and unpredictable fluctuations on financial markets. One example of this could be the estimations of the future price of a non-renewable resource such as coal. According to a mainstream economic standpoint, prices of coal would reflect its market supply effected by, among other things, its scarcity. As coal mines are being depleted, this would lead to higher mining costs and a lower supply which would drive prices upwards. However, this has not happened. Prices of coal do not reflect their absolute scarcity but rather the, according to Post-Keynesian Economics often irrational, expectations of market actors. A consequence of this is that market-based solutions to environmental degradation, or solutions including putting taxes on non-renewables, may not be effective. Price signals may be important but not sufficient to counteract unsustainable consumption. Instead, from a Post Keynesian perspective, the government has a responsibility to use a multiplicity of tools to counteract irrational fluctuations to limit the societal and ecological harm of an instable economy.

Critical institutional economics

Critical institutional economics (CIE) is another heterodox approach to economics. The main focus of the investigation is institutions in society. Institutions are defined as "systems of embedded social rule" (Hodgson, 2017, p. 45). This definition implies that institutions encompass laws, rules, and praxis as well as more soft norms prevalent in society. Institutional economics incorporates a broad school of thinkers, including those who are closer to mainstream economics as well as those who are more critical to mainstream economics. Those who are closer to mainstream economics typically study what is referred to as *market distortions*. A *market distortion* is when the situation differs from the *ideal market* that is given by perfect competition. The more critical streams of institutional economics bring insights from other disciplines in studying individual and collective behavior. These include insights on the limitations of individuals' rational behavior from psychology (behavior economics) and theories from philosophy, law, history, sociology, and political sciences.

According to CIE, society is shaped by an evolutionary process in which institutions affects the individuals and individuals, in turn, shape the institutions. Markets, which in mainstream economics are typically seen as a default arena that ensures the most efficient outcomes between individuals and for society, are in CIE seen as a result of interactions that can take different forms. The market prices in any economy, therefore, depend on existing regulatory frameworks and norms.

In mainstream neoclassical economics, it is typically assumed that individual preferences are pre-set and stable over time, and an economics investigation departs from individuals' so called *rational choices* between different consumer goods to maximize their expected satisfaction (referred to as utility). Equilibrium outcomes where the individuals' preference satisfaction is greatest are studied and seen as the logical outcome of individuals' behaviors. It is logical as individuals are seen as being always rational and typically narrowly self-interested. Critical institutional economic viewpoints criticize these assumptions for neglecting the specific institutional setting that frames individuals' preferences as well as the structure of the market. Individuals' preferences are also, unlike in neoclassical economics, in CIE not seen as stable but may change over time. CIE sees equilibrium outcomes as only some of many potential outcomes, and they are not necessarily the logical, nor rational, outcomes. CIE applies a more comprehensive view of individual behavior, which is combined with outcomes seen as emerging from interactions.

CIE views individuals' preferences as context-dependent and individuals' preferences, behaviors, and *rationality* may be affected by limited information, cognitive ability, and societal norms. Individuals possess *bounded rationality*, a term coined by Herbert A. Simon but more recently further developed within the subfield of behavioral economics notably by Tversky and Kahneman (awarded the 2002 Nobel Memorial Prize in Economic Sciences) (Kahneman, 2012). The behaviors of individuals affect institutions which feed-back on the individuals' behaviors.

Institutional economists see perceptions, interests, and power as influencing institutions. Power and interest protection are essential when explaining how economic structures like markets and firms are configured (Vatn, 2017). Neoclassical economics typically neglects this role of power.

An institutionalist analysis of the ecological overshoot may include that individuals act within an institutional structure with the norm to continuously strive for increased consumption. There is a conflict between an economic system with growth-demanding institutions and an environment that cannot handle the increased pressure (Vatn, 2017). The strive for increased consumption on an aggregate level, constitutes an unsustainable pressure on the planet. The unsustainable pressures are thus the outcomes of existing institutional structures. CIE policies to limit the ecological footprint do, therefore, not only entail pricing carbon emissions "right," a typical mainstream economics response, but instead seeing the bigger picture of the institutional normative setting and how it can be changed (including notable contributions from Elinor Ostrom (1990) who was awarded the 2009 Nobel Memorial Prize in Economic Sciences). However, we may neither be able to "get institutions right"—as the interdependency between institutions and individuals' behaviors are challenging to predict, and there is no easy way to find out or predict which institutions would be "right."

Also, a society's level of poverty and extent of inequality can, from an institutional perspective, be analyzed as an outcome of its institutions (Acemoglu and Robinson, 2012). Human needs are safeguarded by altering the institutions. The dynamics and evolution of power structures may, depending on the institutions, reinforce existing inequalities and exacerbate poverty. Thus, the fundamental policy issue includes what values and whose interests to protect (Vatn, 2017). Preferences can be deliberated and contrasted to each other, and different institutional structures may reflect or articulate different preferences.

Summing up, institutional economics invites taking a step back in analyzing alternative possible institutional arrangements and their potential effect on individuals' behaviors in line with sustainability. Critical institutional economics provide a perspective that extends the role of governments in providing the right frameworks to carefully analyze changes in norms, laws, and their effect on individual behaviors.

Ecological economics

With roots in ancient Greece and the definition of the world economy as "household," ecological economics focuses on the sustainable management of the world's resources. The current stream of ecological economics, however, took off in the 1960s and 70s when the study of energy and material flows, conceptualized as material throughput of society, came to the center stage of the ecological economists' economic analysis.

Ecological economics describes the economy as embedded in a natural system, see Fig. 2 (adapted from Giddings et al., 2002). Accordingly, the economy has to obey the rules of the biophysical reality within which it exists. Early ecological economists such as Georgescu-Roegen emphasized the need for economics to consider laws of thermodynamics (Georgescu-Roegen, 1993). The first law of thermodynamics includes that matter and energy can never be created nor destroyed within an isolated system. The Earth can be characterized as a closed system as it has a limited exchange of matter with the outside space while it exchanges energy. A consequence of that Earth is seen as a closed system is that the laws of physics constrain the size of humanity's material and energy throughputs.

That the natural system constrains the economy may be seen as undeniable when confronted with the Earth's biophysical limits, but is often overlooked by mainstream economics as well as by many heterodox schools of economics (Spash, 2017). It may be overlooked because the natural system is not considered as core to their analyses. From an ecological economist perspective, omitting this fundamental feature of reality may lead to conclusions and decisions that undermine the regenerative capacity of the biosphere on which the economy depends.

In the much-discussed book from 1972 titled *The Limits to Growth* (Meadows et al., 1972), the authors constructed a computer model to simulate possible futures of the human population. Their results highlighted the critical implications of the exponential growth of the human enterprise and the need to constrain it. One way to conceptualize humanity's aggregate impact on the environment prevalent in ecological economics is the $I = PAT$ equation which calculates the human impact on the planet (I) as a function of the size of the population (P) multiplied by the average affluence (A) and the resource intensity of current technology (T). According to this conceptualization, there are three ways for humanity to limit its footprint: by reducing the size of the population (P), by limiting wealth (A), or by greening the technology or change human behaviors (T). While the equation provides a rule of thumb for calculating the aggregated impact of human activity, it has been criticized for over-simplifying and not accounting for the more complex interrelations between the factors, and to be challenging to measure (Roca, 2002).

Ecological economics also discusses *absolute decoupling*. While some within ecological economics have argued that economic growth can continue while material throughput declines, the definition of absolute decoupling, others argue that it is neither possible nor desirable. The difficulty of decoupling economic growth and material throughput is often attributed to the rebound effect, also referred to as Jevon's paradox. Jevon's paradox states that as technology improves and becomes cleaner, the positive effect of the decreased emissions is counteracted by increased consumption as technology becomes cheaper. An illustrative example

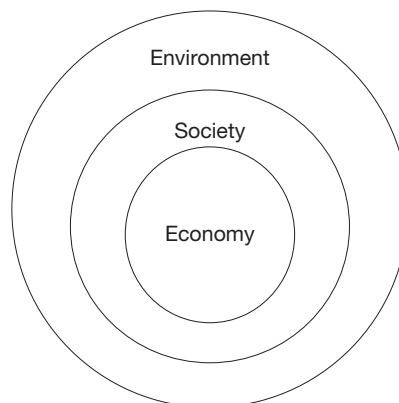


Fig. 2 Conceptualization of nested sustainable development—the economy dependent on society and both dependent on the environment. Adapted from Giddings B, Hopwood B, and O'Brien G (2002) Environment, economy and society: Fitting them together into sustainable development. *Sustainable Development* 10: 187–196. <https://doi.org/10.1002/sd.199>.

relates to energy. Energy production efficiency improvements may initially cause both less environmental harm and lower energy prices. Over time, however, the efficiency gains may be counteracted by the lower energy prices—causing an increase in energy consumption above the initial level. *Relative decoupling* is another concept which denotes that the resource intensity of an economy may decrease per economic output. This concept is, however, not a relevant measurement as the absolute impact on the Earth is what is relevant for sustainability, not its relation to economic output.

The focus on biophysical limits or regenerative capacity of the planet, and the emphasis on constraining consumption for the sake of long-term sustainability, implies a principle of intergenerational justice. Ecological economists have also engaged with concepts of basic human needs to be guaranteed, and Georgescu-Roegen early emphasized the need to limit luxury consumption for the sake of providing basic needs for future generations. While natural scientists and economists have dominated ecological economics, there is a concurrent stream of ecological economics referred to as “social ecological economics,” which adds social and political factors to its analyses. Furthermore, building on ecological economics, the “degrowth critique” has stated that continuous economic growth is not only an environmental problem but also socially unjust as growth is no longer improving humans’ well-being in affluent societies (Spash, 2017).

System dynamics

Other valuable contributions to economic theories that combine the safeguarding of human needs while ensuring staying within the planetary boundaries embark from theories of complex systems. A complexity economics approach typically iterates between the behavior of individuals and the consequences of these for the behavior of social entities (Kirman, 2017). It does, however, rarely portray individuals as having complete information and acting in optimal ways to satisfy their narrowly defined preferences, as is the convention in mainstream economics. Nevertheless, unlike some other heterodox economic approaches that are critical to the use of formalized models, idealizations and reductions (Lawson, 2013)—complexity economics make use of models to simplify and idealize behaviors and explore “what-if” scenarios.

System dynamics is one complex systems approach used to analyze social phenomena that is being used by several schools of economic thought (Radzicki, 2011). It was developed from control theory, cybernetics, and the study of organizations in the 1960s and 1970s by Jay W. Forrester based at Massachusetts Institute of Technology (Forrester, 1961). The system dynamics approach defines a system as a set of things that are interconnected in such a way that they produce a particular pattern of behavior over time (Meadows, 2008). This definition includes three important features that characterize systems: things, interconnections, and time. The way different parts of the system are interrelated is assumed to be the essential factor that explains system behavior. System dynamics interprets these interrelations as causal links between the system components. Causal links are mapped in order to communicate imagined system structures. The system dynamics tradition offers mapping tools (such as causal loop diagrams and stock and flow diagrams) where different assumptions and views can be portrayed and subsequently discussed.

From a system dynamics viewpoint, the ecological overshoot can be attributed to the systems characteristics of the world economy—as it is the causal structure that drives the behavior—and represented by a series of causal chains and loops.

The systems diagram in Fig. 3 portrays a conceptualization of how production depends on a reinforcing loop, and a counteracting loop of social-ecological collapse. Production is at the center of the diagram as it enables the provision of people’s needs required for human well-being. The production also, through the required material throughput, links to pressures on planetary boundaries—with the risk of social-ecological collapse that follows (Collste et al., 2018; Randers et al., 2019).

In Fig. 3, the R1 reinforcing loop causes exponential growth in production through capital accumulation (*production* enables investments in *physical capital* that increases the *production capacity*). This loop is combined with a delayed counteracting loop that risks causing a global social-ecological collapse (an increase in *production* leads to increased *material throughput* that implies *pressures on planetary boundaries*—with the risk of a *social-ecological collapse* undermining further *production*) (Collste et al., 2018). To find alternative futures following the system dynamics approach, one would iterate between model structure and its behavior and analyze different model structure hypotheses and their relationships to reality.

Poverty and inequality are from a system dynamics viewpoint typically seen as the results of a system structure that may lock people in poverty. In this case, the economic success of an individual, family or group of individuals may be self-reinforcing. Lack of economic success can be attributed to the opposite dynamics or a poverty trap perpetuating multidimensional poverty and such system traps exist in various forms and are difficult to escape (Lade et al., 2017).

Meeting Basic Needs and Living Within the Safe Operating Space

The abovementioned heterodox approaches can provide complementary insights to the problems of unmet human needs and ecological overshoot. As Post-Keynesian economics emphasizes that markets often behave irrational and brings the adherence to deep uncertainty, it highlights the need for an active role of governments in directing the economy. This argumentation extends the role of government in promoting human well-being and ecological sustainability, in contrast to narrowly focused market solutions. The Post-Keynesian approach can be combined with the institutionalists’ emphasis on the role of the institutional frameworks in minimizing poverty and human exploitation. Ecological economics provides the ecological guardrails to human development and pinpoints the need to incorporate the biophysical reality in the development of economic institutions. Ecological economics also emphasizes the need to keep conspicuous consumption low not to undermine the living conditions of future generations. It thereby bridges economy and ecology. System dynamics, in turn, offers mapping tools and simulation models that invite to the examining of different hypotheses.

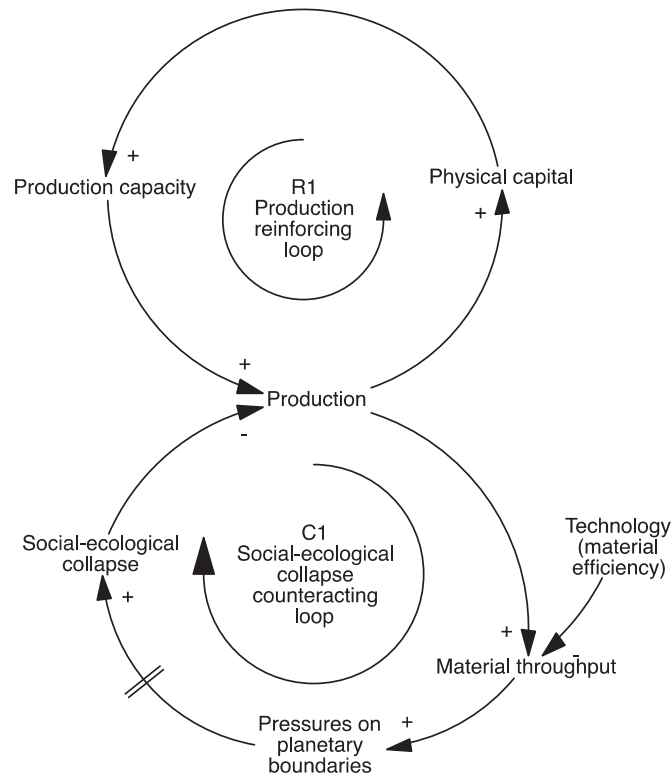


Fig. 3 Conceptual sketch of the Earth3 model used in the [Randers et al. \(2019\)](#) report. From Collste D, Randers J, Goluke U, Stoknes PE, Cornell S, and Rockström J (2018) The empirical bases for the Earth3 model: Technical notes on the sustainable development goals and planetary boundaries [preprint]. *EarthArXiv*. <https://doi.org/10.31223/osf.io/ephfs>.

The future of humanity and its dependence on a flourishing biosphere is at a crossroads. The current way of structuring the economies has resulted in an aggregated size of the world economy that threatens the health of the planet's life-support systems. Simultaneously, human needs are not universally met as many people are hungry and inequalities are extensive. This precarious situation has led to a search for alternative economic paradigms that can provide answers to how to combine the safeguarding of human needs with life within planetary boundaries. This contribution presents four alternative approaches that may contribute to finding ways forward. By combining insights from these, it is possible to explore new territory and future trajectories away from human suffering and ecological overshoot.

Post-Keynesian economics pinpoints the need to consider deep uncertainty and the possibility of governments to intervene to ensure that human needs are met. Ecological economics sets the ecological and biophysical frame within which development has to take place. Institutional economics offers critical analyses to examine how institutions affect human behavior and how human behavior feeds back on institutions. System dynamics, in turn, offers practical tools to critically examine the coherence of different perspectives and explore what-if scenarios by simulation.

To conclude: "There is too much bad news to justify complacency. There is too much good news to justify despair." ([Meadows, 2008](#)). The search for alternatives has just begun.

Further Reading

The critique against modern mainstream economics goes back in history (see *Valuing the Earth*, Ed. [Daly and Townsend \(1993\)](#) for a collection). The critique has gotten renewed attention, see for instance [Trebeck and Williams \(2019\)](#), [Raworth \(2017\)](#), [Jackson \(2011\)](#), [Spash, 2017](#), and [Victor \(2019\)](#).

For a presentation of heterodox schools of economics, see ([Fischer et al., 2018](#)).

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Conservation Values and the Value of Conservation

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Abstract

Values is a central concept to the study of human behavior and conservation policy, but its meaning tends to vary throughout academic literature. This poses a challenge, as scholars operating from different definitions of *values* tend to talk past each other, resulting in widely varying recommendations for effective conservation policy. The purpose of this article is to elucidate the assumptions in academic literature about how values shape human behavior in the context of conservation. The article compares the working definitions of values in economics, anthropology, and philosophy, and how these fields treat the concept of *valuation* or the assessing of values for incorporation into policy. I review how conservation policy historically has been influenced by varying assumptions about how values shape behavior, and I show how this has resulted in conflicting recommendations for how policy should appropriately target human values. Finally, I conclude with a summary of contemporary understanding of conservation values and state of the art recommendations for effective conservation policy design and implementation.

Introduction

David Graeber, in his 2001 book *Towards an Anthropological Understanding of Values* begins with the following passage:

"If one reads a lot of anthropology, it is hard to escape the impression that theories of value are all the rage of late. One certainly sees references to 'value' and 'theories of value' all the time – usually thrown out in such a way as to suggest there is a vast and probably very complicated literature lying behind them. If one tries to track this literature down, however, one quickly runs into problems. In fact, it is extremely difficult to find a systematic 'theory of value' anywhere in the recent literature; and it turns out to be very difficult to figure out what body of theory, if any, that any particular author who uses the term 'value' is drawing on. Sometimes, one suspects it is this very ambiguity that makes the term so attractive" (1).

The same statement seems to apply to the academic publications on conservation policy. Statements about human behavior and the efficacy of policy address values in the abstract, but are often working under varying assumptions of what values are and how they relate to human behavior. The understanding of values is central to the ability to create effective policies, as values shape humans' understandings of the world, and our actions in it. We know people do things for a reason, and values appears to be that reason. Hence, any hope of effective policy mechanisms must engage with, and potentially alter values to be effective.

But, are values concrete or abstract? Are they generally stable or fluid? And how do they interact with conservation policy to alter human behavior in favor of a more sustainable planet? It turns out that these central questions are unresolved in the literature. Nonetheless, numerous studies have been chipping away at the topic from different angles.

This article engages with the various definitions of values as they pertain to conservation policy, and how these definitions have shaped policy historically and into the present. I begin by tracing the definition of "values" across a few principle threads in academic literature—namely psychology, economics, and anthropology, as these fields represent the breadth of the developed literature on *values* and they have been implicitly and explicitly informing conservation policy for decades. Although there are countless other ways to explore the concept of values, the intention here is to provide a general characterization of commonly employed understandings, and not an all-inclusive account of the literatures. I will then proceed to outline various conservation approaches in terms of what each assumes about values, and how related policy mechanisms utilize concepts of values. Finally, I will discuss how policy itself shapes value systems, and the implications of contemporary conservation policy for "conservation values" more broadly speaking.

Values and Valuation

Foundational work by Rokeach (1973) in psychology describes a value as "an enduring belief that a specific mode of conduct or end-state of existence is personally or socially preferable" to an alternative (p. 5). He differentiates these from value systems, which

he describes as “an enduring organization” of these values (p. 5). Though using different terminology, both psychologists and anthropologists have concluded that values are created through culture (Hofstede, 1984; Polanyi, 1957; Schwartz, 1999), with anthropologists highlighting that they are expressed and reproduced by action (Graeber, 2001; Munn, 1986). From this perspective, values guide action and determine human behavior (Rokeach, 1973; Schwartz and Bilsky, 1987).

There is another definition of value, however, that tends to muddle the above understanding. That is the concept of the value of things, or the “qualities inherent in objects” (Schwartz and Bilsky, 1987, p. 550). Much of this confusion stems from economic theory, where theorists argue that human action is motivated by the value of objects, and through self-interested behavior, market efficiency is realized. Market efficiency then maximizes total *value* to society by producing the greatest amount of social good (Jevons, 1866). The value of objects, according to this line of thinking, is reflected in price, or *exchange value*. This conceptualization of values results in a bit of a tautology—an object of high value (price) is valued because it increases societal value (utility), as determined by values (preferences) (see Broome (1991) for an elaboration on this topic)! The murkiness of terminology presents a challenge for conservation praxis when the exchange or economic value of an object or scenario, often the target of a particular policy, becomes conflated with human values (social preferences that guide action) and the two are treated as interchangeable.

If the goal of policy is to maximize social well-being, then implementing policy requires the ability to compare the values of alternative policy scenarios, and make choices based upon these values. In a market setting, economists argue, price is reflective of societal value. Therefore, economists use *valuation*, or estimating the value associated with goods and services, to help predict the impact of different policies. Because environmental goods and services typically are not traded in competitive markets, economists have developed nonmarket valuation techniques to estimate the exchange value of the environment for comparison to market goods. There are a variety of techniques that fall into this category. The indirect techniques of travel cost and hedonic modeling rely on market values that can serve as proxies for environmental goods, such as the amount of money spent to travel to a recreation area, or the price for a house that includes environmental amenities (Champ et al., 2003). Stated preference methods, in contrast, are techniques that rely on surveys that ask individuals to state their willingness to pay (WTP) or willingness to accept (WTA) compensation for changes in environmental services (Adamowicz et al., 1998). Nonmarket valuation allows for subsequent incorporation into cost benefit analysis, which can be used to guide policy. Though nonmarket valuation methods have been critiqued for their inaccuracy (Spangenberg and Settele, 2010), best practices are continually being developed to limit these deficiencies (Carlsson et al., 2007), and economists assert that imperfect valuation is still preferable to no valuation.

The economic understanding of value has heavily influenced conservation science, and conservation scientists have spent the last 20 years trying to precisely measure of the value of nature (Costanza et al., 1997; Daily et al., 2000). Conservation scientists have worked with economists to estimate the value of numerous aspects of environmental management, such as the value of hemlock woolly adelgid management in eastern hemlock forests (Poudyal et al., 2016), or the value of different land management regimes in producing ecosystem services across a watershed (Nelson et al., 2009). Such efforts employ the economic understanding of value, and the techniques of nonmarket valuation, in an attempt to convince policy makers of the value of the environment.

In contrast, anthropologists have tended to argue that values are embedded in social systems (Polanyi, 1957), where they are produced by and reflected in cultural institutions and relationships (Munn, 1986). It follows from this line of logic that economic activity and human decisions cannot be understood as independent from social systems (Dalton, 1961; Sahlins, 1972), and exchange value is only one facet of *value* that has arisen to predominance in a capitalist system (Graeber, 2001). Therefore, any attempt to understand human behavior in an economy needs to understand the entirety of the system within which individuals interact.

The understanding of values as culturally embedded relates to a term that is gaining traction in conservation and environmental circles—that of *relational values*. The idea captured by that term is that values are shifting and context dependent (Pascual et al., 2017). From this perspective, values are constructed in relationships—food might be valuable from a sustenance perspective, but it is also valued for cultural roles, and the social connections fostered through food production, preparation, and sharing (Chan et al., 2016; Klain et al., 2017). This concept mirrors the idea of embedded values in anthropological terms, whereby values cannot be abstracted from the systems within which they are created (Polanyi, 1957). Hence, any attempt at valuation must understand the entirety of the context, and multifaceted approaches to detect multiple value systems are needed (Jacobs et al., 2016).

Those advocating for an understanding of values as relational and embedded have tended to challenge economic valuation. Anthropologists have asserted that economic valuation reduces the multitude of human values to a simplistic, and often ironic, monetary exchange value (Graeber, 2001). Other scholars and conservation activists have raised concerns about placing a monetary value on the environment (Goulder and Kennedy, 2011). The key arguments against such techniques are that they undermine the total value of nature (McCauley, 2006), and that they are inappropriate given the complexity of natural and social systems (Kosoy and Corbera, 2010; Spangenberg and Settele, 2010). For example, many scholars adhere to the idea that environmental values are inherently incommensurable—exchange values do not represent the full complexity of environmental values, such as biodiversity value of species, and aesthetic value of amenities (Martinez-Alier et al., 1998; Norton and Noonan, 2007). Inappropriate valuation may provide a solution to conservation ailments with unforeseen social and ecological consequences because they undermine relational value systems that are crucial for sustainability (Jax et al., 2013; West et al., 2006). Given these challenges to valuation, scholars have suggested that the next step forward should involve understanding the interactions and tensions among values across scales (Díaz et al., 2015), and incorporating a diversity of values into policy (Chan et al., 2017).

How values are understood and “measured” is more than an esoteric discussion, it has real implications for environmental policy design. If values are absolute, and able to be abstracted from social context, then we can hope to effectively identify, target, and design universal policies that people will respond to in predictable ways. Economic valuation would then be critical to

estimating these values for subsequent incorporation into policy, and environmental degradation would require fixing the market via a series of Market Based Conservation Mechanisms or Market Based Incentives. However, if values are relational, then policy must always be context-dependent and nuanced. In this case, policy would need to focus on the establishment and maintenance of effective institutions to mediate environmental behaviors (Dietz et al., 2003). Conservation policy throughout the last 50 years has vacillated among these assumptions about human values, resulting in extreme variation in claims of policy efficacy, as well as varied approaches to conserving the *value* of the environment.

Conservation Policy—A Brief History

Conservation has shifted focus in the last 50 years from the accumulation of protected areas to the sustainable management of multifunctional landscapes (Mace, 2014), and beneath this shift there have been continual battles over appropriate policies and related framing of human values. Prior to the 1980s, conservation was primarily focused on land acquisition—the need to set up protected areas safe from deforestation and environmental degradation (Terborgh, 2004). Protected areas limited human access in favor of the preservation of biodiversity, often forcibly removing humans in their establishment (West et al., 2006). This early conservation endeavor was inspired by the “crisis-driven” nature of conservation, namely that available land needed to be preserved before it was too late (Soulé, 1985). Much of the focus during this phase was on preserving tropical areas and biological hotspots, which were presumed to both house more biodiversity and provide greater return on conservation dollars invested, given the relatively cheaper cost of land in many tropical countries (Myers et al., 2000). Continual developments in ecology, including metapopulation ecology and landscape ecology, identified the need to increase the scale of conservation because biodiversity maintenance required large tracts of connected habitat for population migration (Saunders et al., 1991; Turner et al., 2001). Conservationists recognized that the preservation of isolated protected habitats alone was insufficient to prevent biodiversity loss, and they accordingly shifted focus to landscape scale conservation under the paradigm of biological corridors, mixed-use landscapes, and transboundary protected areas (Townsend and Masters, 2015).

The shift in focus from protected areas to landscape conservation occurred in tandem with an increasing concern among academics and policy makers for human rights. Protected area conservation received extensive criticism from social scientists and human rights activists because park establishment frequently involved the forced removal of humans from within their boundaries, relegating former inhabitants to poverty while denying them access to natural resources necessary for survival (West, 2006). For example, Dan Brockington documented the process through which the creation of the Mkomazi game reserve in Tanzania caused the forced removal of several pastoral tribes from the region, permanently affecting their livelihoods (Brockington, 2002). Scholars further revealed that conservation, though often perceived as solely altruistic, was inherently political and deeply rooted in colonialism—redefining who had access to nature and under what uses (Adams, 2004). Similarly, government officials expressed concern that conservation stymies economic growth because it conflicts with development goals (Malik, 1982). The combination of these voices resulted in a shift in conservation agenda; increasingly, human rights interests became intertwined with global conservation policy (Phillips, 2003).

As human rights and landscape planning moved to the forefront of conservation, the concept of sustainable development arose as the way to meet conservation imperatives while improving human well-being (Bruntland, 1987). Though the term has been critiqued for its vagueness, it addresses the development goal of increasing human well-being across world populations, while emphasizing that environmental resources are finite and integral to the survival of future generations (Lélé, 1991). In practice, sustainable development policies have typically aimed to promote economic growth through encouraging livelihood activities that purportedly operate in harmony with the natural environment. Early sustainable development initiatives promoted nonextractive employment opportunities around parks through the implementation of Integrated Conservation and Development Programs (ICDPs) (Wells et al., 1992), and community control of natural resource management (Brosius et al., 1998). Examples of such initiatives include limiting activities in buffer areas in exchange for development infrastructure (Wagner, 2001), ecotourism within protected areas (Aylward et al., 1996), and community management of sea turtle reproductive sites (including sustainable egg harvest) (Campbell, 1999). Though widely differing in implementation, such initiatives shared in common the philosophy that ecological sustainability depends upon the economic well-being of local populations, and that conservation, if appropriately supported, would ensue under community management (Western and Wright, 1994). Such programs demonstrated mixed results, however, in part due to the complicated nature of communities, and the challenges of scaling ICDPs under the imperative of landscape conservation (Berkes, 2007).

These early initiatives evolved into the contemporary discussion of ecosystem services, whereby the economic sustainability of society is depicted as dependent upon ecosystem health (Costanza et al., 1997; Daily et al., 1997). Ecosystem services classify human benefits, such as water filtration and carbon sequestration, received from ecosystems (Daily et al., 2000). Scholars advocating this concept contend that it will assist in bringing ecosystem values into environmental planning to ensure long-term sustainability (Christie et al., 2012; Engel et al., 2008). The implication is that “win-win” situations can be realized via spatial planning for ecosystem services (Kareiva et al., 2011). However, this requires that values for ecosystem services can be effectively identified and targeted (Wünscher et al., 2008), and that ecosystem services are not in competition with each other across scales (Nelson et al., 2009). Furthermore, effective policy must appropriately target ecosystem service values and adequately alter human behavior across diverse social-ecological contexts.

In the face of continual reduction in biodiversity, bordering on a mass extinction (Ceballos et al., 2015), conservationists seek solutions that are scalable and translatable (Kremen et al., 2000). Market-based Conservation Mechanisms (MBCM) arose to prominence in this context because they purport to offer a cost-effective means of conservation with greater flexibility in implementation than prescriptive policies (Ferraro and Kiss, 2002). These instruments tend to treat ecosystem services as fungible units of value that are transferable across spatial and social scales (Boyd and Banzhaf, 2007). The allure of these approaches is essentially scalar—we can assume that one-size-fits-all will work with enough data to appropriately shape policy. This is seductive for conservation scientists, practitioners, and organizations, who are pressed to find a solution to an ever increasing global environmental crisis.

MBCM commonly refer to any policy mechanism that uses price signals to correct market-failure, in contrast to prescriptive (command-and-control) policies (Pirard, 2012). Though in practice these mechanisms often fall short of establishing actual markets for the trading of environmental goods, they are often deemed “market-based” because they attempt to change behavior by targeting the economic value of ecosystem services (Corbera, 2015; Fletcher and Breitling, 2012). Furthermore, suggestions for improvements on existing market-based instruments frequently point to the need to make them more market-like (Jack et al., 2008). Taken from this perspective, the current state of market-based conservation policies can be seen as an evolution of policies that have been proposed under the explicit goal of becoming increasingly more market-like, thereby providing an efficient means of conservation (Gómez-Baggethun and Muradian, 2015).

MBCM have evolved from taxes and subsidies to trading schemes and payments for ecosystem services (Field and Field, 2002). Popular contemporary MBCM include direct markets, certification schemes, mitigation banking, carbon credits, and payments for ecosystem services (PES). Direct markets and certification schemes use marketing to finance the preservation of environmental goods and services. This includes nature tourism and ecotourism markets (Stronza and Durham, 2008), sustainable tourism certification programs (Honey, 2002), as well as environmentally amenable agricultural practices, such as rainforest alliance coffee (Auld, 2010) and organically produced agriculture (Zanoli et al., 2013). Carbon credits are a cap-and-trade system that allow carbon emitters to trade carbon permits on an open market, thereby maximizing the efficiency of carbon emissions and mitigation (Sorrell and Sijm, 2003). PES programs are a broad category, and perhaps one of the most popular of these mechanisms. These programs attempt to create markets for ecosystem services and identify exchange values for environmental goods so that providers of ecosystem services can receive monetary compensation from ecosystem service users (Wunder, 2005). REDD is a United Nations program that takes the concept of PES and applies it at an international scale, providing international funds to support conservation and carbon sequestration in developing countries (Culas, 2012).

These various conservation policies have occurred in tandem with shifting debates about the relationship between human behavior and value systems. Each of the above conservation approaches has an accompanying argument about human values and human behavior that undergirds its rationale. Unfortunately, these assumptions have typically been implicit, and not subjected to critical review that provides a better understanding of the strengths and shortcomings of each.

Conservation Policy and Conservation Values

Protected area approaches tend to adopt a utilitarian framing of value systems, in which values are fixed, absolute, and humans are subject to “the tragedy of the commons” in their interactions with the natural world (Hardin, 1968). In this framing, those needing natural resources consume and degrade the landscape in a drive to maximize individual utility. Protected areas, monitored by guarded forces, were a logical response to this threat. The only way to stop the public’s innate drive to degrade the land was to separate humans from nature.

Community-centered conservation approaches vary in their framing of value systems, and perhaps have been appealing because those who frame values as utilitarian, and those who consider values as relational in nature can accept them. By using the term “community-centered,” I broadly reference the policy approaches that attempt to include locals in natural resource decision-making, allocation, and management. This would include many ICDPs, Community Based Conservation, Community Based Natural Resource Management, and other grassroots programs. Collectively, they share Elinor Ostrom’s framing of the natural resource allocation problem, whereby institutions can effectively moderate natural resource degradation, as long as they share effective properties (Ostrom et al., 1999). From a utilitarian perspective, communities value natural resources because they are a form of natural capital, whereby they can be converted to other forms of capital to maximize well-being. Through supporting the effective management of these resources by local communities, the conservation movement is supporting their livelihoods, and will therefore garner more support for protected areas, and conservation as a whole (Kareiva and Marvier, 2007). Conversely, a relational values framing also maps onto these approaches—whereby locals’ complexity of knowledge and uses of natural resources, as well as the complexity of relations with the environment, make them potentially *more effective* environmental managers (Brechin et al., 2002). The key from this perspective is that effective community-centered conservation requires engagement with local communities to support complex existing environmental values, and better align these values with conservation efforts (Brosius et al., 1998).

The ambiguity in terms of value framing, however, has turned out to be a weakness of community-centered conservation and has led to its decreasing popularity throughout the start of the 21st century. Those adhering to a relational values framing have tended to argue that programs need to devolve more authority to local communities (Borrini et al., 2004; Campbell and Vainio-Mattila, 2003), while the utilitarian camp tends to advocate for more careful monitoring of resources because locals will tend to over

consume them to support livelihoods (Robinson, 1993; Terborgh, 2004). To complicate this problem, community-centered approaches proved expensive, difficult to monitor, and slow to progress (Berkes, 2004).

Through the ecosystem services framing of environmental values, a utilitarian construct rose to prominence, and community-centered approaches fell out of fashion (Gómez-Baggethun et al., 2010). Economists rooted in neoclassical theory characterize environmental degradation as an example of market failure, where optimal individual decisions do not create optimal social outcomes (Hanley et al., 1997). Market failure exists because the benefits provided by the environment are external to the market and do not factor into private decisions (Gordon, 1954). The solution, from this line of reasoning, has been to propose MBCM that can internalize ecosystem services (externalities), bringing their costs into decision-making. In contrast, numerous scholars have argued that the continual, exponential growth of the market-system itself is the underlying culprit of environmental degradation (Matulis, 2014; McAfee, 1999). These scholars argue that not only will MBCM not work, because they will not appropriately target values, but that through focusing on exchange values they promote a focus on short term-profits that will actually erase the remaining value structures that might be necessary to support conservation into the future (Acheson, 2000).

Conservation Values and Motivational Crowding

This argument speaks to a parallel debate, originating in behavioral economics, concerning the nature of monetary incentives and whether they “crowd-in” or “crowd-out” intrinsic motivation. Frey and Jegen (2001) summarized this literature, demonstrating that monetary incentives either crowd-in (strengthen) or crowd-out (weaken) intrinsic motivation. In other words, monetary incentives themselves appear to change value systems. This literature described case-studies where the nature of the incentive seemed to be particularly important. For example, if altruism was key to the behavior in question, then monetary incentives tended to crowd-out intrinsic motivation because participants began to view the service as something belonging in the economic sphere (Frey and Oberholzer-Gee, 1997). Furthermore, the crowding-out effect became predominant when people recognized a payment as infringing on self-determination. The findings are critical to the role of MBCM, as environmental stewardship is typically undertaken by individuals who are other-regarding, and sense a deep connection to the natural environment (Bramston et al., 2011).

Of MBCM, the most research has been done on motivational crowding in PES programs. Currently, there is a lack of consensus in this literature, though most studies seem to point toward a general caution with the use of economic instruments because of unforeseen interactions with value systems (Neuteleers and Engelen, 2015; Rode et al., 2015). Some studies have found that economic incentives crowd out environmental stewardship (Agrawal et al., 2015; Frey and Oberholzer-Gee, 1997) as they can undermine morality and serve to justify behaviors that might otherwise be unjustifiable (Bowles, 2008). In a review of 50 studies, Bowles and Polania-Reyes (2012) found that when market-like incentives were instituted, in 69% of cases they showed crowding out. They argued that these incentives often trigger a “moral disengagement” and that general social preferences will determine how people respond to economic incentives (p. 390). Further studies have shown that whether an incentive crowds-out or crowds-in intrinsic motivation depends on local context (culture), and individual personality (De Martino et al., 2017; Rode et al., 2015; Van Hecken et al., 2017). Because economic incentives do not result in predictable impacts, the best approach is caution moving forward (Allen and Colson, 2019). If economic incentives run the risk of changing value systems with regards to the environment—they leave “ecosystem services” subject to funding from a volatile market that is accustomed to receiving these services for free (and using them to fuel economic growth). This is particularly challenging, as economic markets do not operate on the same time scale as ecosystems, and policies designed to finance environmental protection might find themselves gutted when markets shift (Allen, 2018).

Though inconclusive, this literature has successfully challenged MBCM to the point that many analysts currently advocate for an integrated approach to policy design and valuation. It seems clear that monetary valuation is not reflective of the complex value systems that inform environmental behavior (Garmendia and Pascual, 2013). Further, despite ample efforts, it is exceedingly difficult to design and support conservation markets—these markets are not as “hands-off” as many once hoped, and they are not clearly increasing ecosystem services (Wunder et al., 2008). As a result, monetary valuation should be a small part of a whole suite of tools used to assess environmental values, and design appropriate policies (Jacobs et al., 2016).

Conclusion: Policy and Value Pluralism

Given the state of conservation as described above, how do we move forward to protect what remains of biodiversity on an increasingly globalized planet? If one thing is salient from the literature examining human values and conservation behavior, it is that context matters. Individuals respond in nonpredictable ways to institutions. Economic incentives may have the intended effects on occasion, but their design rests on assumptions about human value systems that do not necessarily hold outside of the market sphere (Bowles and Polania-Reyes, 2012; Gowdy et al., 2009). On the other hand, mandatory enforcement and government intervention in natural resource use has resulted in human rights violations and continual environmental degradation. So how to move forward?

If people behave in context-dependent ways, uniform policy may be impossible. A diverse suite of policies will be necessary at the local scale to support both heterogeneous multifunctional landscapes and heterogeneous value systems. Increasingly, scholars are finding that perhaps policy has not put enough faith in communities (Gavin et al., 2018). Engaging more effectively with communities might require supporting grassroots initiatives, environmental education, and local markets. Other approaches to

engage with communities might include restructuring PES and REDD programs to meet local needs and inspire collective action (Pfaff et al., 2019). Despite the hopes of one-size-fits-all policies that can easily translate across scales, this review suggests that future policies will need to be flexible so that they can engage communities and mold to local contexts. This might make conservation more challenging, but ultimately, it will likely make it more effective.

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The Role of Ethics in Valuing Anthromes

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Abstract

Human actions have consequences that affect many other species of animals and plants and even nature itself in ways that cause both significant harms and benefits. We must take account of these consequences and evaluate our conduct in light of them by broadening the scope of our ethical thinking. This is especially important in light of the shift in ecological thinking toward an understanding of the terrestrial biosphere in terms of anthropogenic biomes or anthromes. The striking ways in which human beings have changed and continue to modify global ecological patterns into these distinct anthromes calls for a critical understanding of how ethical principles and values apply to them. The purpose of this article is to provide several ethical frameworks that enable us to establish reasonable ethical values for managing anthromes and principles for evaluating the human conduct that creates and modifies them. The article considers in more detail the way in which the scope of ethics has changed in response to concerns about the moral implications of human interactions with the natural environment. It examines the question of what has value and what the source of this value is. The discussion of value leads to a basic understanding of what it means to value anthromes. Finally, the article examines three different ethical frameworks that may be used to value anthromes. These are descriptive moral psychology, traditional ethical theory, and environmental sustainability. As the scope of ethics has enlarged over time, the role of ethics in valuing anthromes has gotten correspondingly more complex.

Introduction

Ethics is the intellectual study of the most fundamental guidelines for human action. Ethics establishes norms for human behavior in all those contexts in which human beings can cause significant benefit or harm to others. It includes virtues such as generosity and justice, rules such as do not cause unnecessary pain or harm, rights such as the right to life, and values such as goodness and happiness. These norms serve both to direct action toward what is good and to evaluate actions as right or wrong, permissible or impermissible, obligatory or forbidden. In the past, it was customary to restrict the scope of ethics to human beings and their individual actions, but that is no longer possible. Human actions have consequences that affect many other species of animals and plants and even nature itself in ways that cause both significant harms and benefits. Consequently, we must take account of these consequences and evaluate our conduct in light of them. Broadening the scope of ethics is especially important in light of the shift in ecological thinking toward an understanding of the terrestrial biosphere in terms of anthropogenic biomes or anthromes. The striking ways in which human beings have changed and continue to modify global ecological patterns into these distinct anthromes calls for a critical understanding of how ethical principles and values apply to them. The purpose of this article is to provide several ethical frameworks that enable us to establish reasonable ethical values for managing anthromes and principles for evaluating the human conduct that creates and modifies them.

The first part of this article considers in more detail the way in which the scope of ethics has changed in response to concerns about the moral implications of human interactions with the natural environment. It examines the question of what has value and what the source of this value is. The discussion of value leads to a basic understanding of what it means to value anthromes. The next sections of the article examine three different ethical frameworks that may be used to value anthromes. In brief, these are descriptive moral psychology, traditional ethical theory, and environmental sustainability. As the scope of ethics has enlarged over time, the role of ethics in valuing anthromes has gotten correspondingly more complex.

Ethics and the Natural Environment

For most of its history ethical discussion has focused only on conduct as it related either directly or indirectly to human beings. From this perspective actions that significantly benefit or harm other persons clearly fall under the purview of ethical thought. Actions that

affect animals, plants, and nature, however, do not unless these actions indirectly benefit or harm other persons. For example, killing an animal for food is not wrong in itself. It would only be wrong if killing the animal for food causes a harm to another person. It is permissible for me to kill my own chickens for food. I could not kill someone else's chickens for food, however, for the same reason that I could not damage their property. This would indirectly be a harm to them. Similarly, polluting a river would not be wrong because of the damage it does to the river and the fish and other animals that depend on it for life. It would be wrong only if this pollution caused harm to human life. The term for this ethical perspective is *anthropocentrism*. According to anthropocentrism ethical principles guide actions that have consequences for human beings. Ethical concerns about anything else are valid only if they can be traced back in some way or other to human concerns.

It is understandable and to a certain extent natural that the scope of ethics should begin with the consideration of human interests. But in light of our affinities with other species it would be surprising if it should end there. Accordingly, many ethicists believe that the scope of ethics must be extended in various ways. Some argue that it should be enlarged to include all sentient beings because they can feel pleasure and pain. Others argue that pain and pleasure are adaptive characteristics of living beings and thus an arbitrary way to limit our ethical deliberations. For them the scope of ethics needs to include all living beings. Yet others who emphasize the interconnections and interdependencies within ecosystems argue that these ought to be included in the scope of ethics as well. These considerations apply generally to the role of ethics in valuing anthromes. From them we may conclude that it is reasonable to speak of the value that anthromes themselves have and of the value of all those beings which inhabit them. There is argument about how to assign appropriate value to those things that fall within the scope of ethics, but it is absolutely important not to begin by excluding things. The role that human beings now have in shaping ecological patterns makes it even more imperative that we extend our awareness of all the ways in which our actions may benefit or harm other things: other human beings, other sentient beings, other living beings, and even the biophysical ecological systems upon which we all depend.

When we do examine the value things have, it is important to distinguish between instrumental value and intrinsic value. Intrinsic value is the value that something has in itself. Instrumental value is the value that a thing has because it leads to something else that has value. When we are sick medicine has instrumental value because it leads to health, which we value. Health has intrinsic value. This distinction relates to the previous discussion in the following way. According to anthropocentrism, only human beings have intrinsic value. Everything else that has value is valuable because it contributes instrumentally to human well-being. Other animals and plants are valuable only because they enable human beings to live well. Similarly, on this view, anthromes have value only because they are the ecological support for human life.

Our dependency upon other animals, plants, and the biomes of which we are a part does mean that these things have instrumental value for us. It does not follow, however, that this is the only value that they have. It is not unreasonable to believe that other living things and even biophysical systems have intrinsic value. What this value is and what it may be based on are important matters that should be decided as part of an ongoing ethical discussion, not excluded from the beginning of it. We need to be open to the possibility that things have value independently of their usefulness to human beings and independently of our judgments about their value.

This openness is especially important with respect to the value of anthromes. Humans have been modifying ecosystems since the discovery of fire, but until recently they were thought of as parts of ecosystems that were largely determined by other factors such as climate, geology, and terrain. Our influence upon the environment, however, has become so pervasive that it is reasonable to think that this relationship has changed, and that human activity itself has become a significant factor in determining the patterns that define an ecosystem. This argument follows the same reasoning for concluding that the current geological period should no longer be called the Holocene. It should instead be named the Anthropocene because of the radical ways in which humans have shaped the climate and environment. Accordingly, biomes that have been permanently modified by human activity may be called anthromes.

This understanding of the significant effects that human activity has on the environment was clearly stated by Rachel Carson in her hugely influential work, *Silent Spring*. Her main concern in this work was the damage that pesticides, especially DDT, were having on the environment. Noting that for most of the history of the earth vegetation and animal life have been determined by the environment, she goes on to claim that "only within the moment of time represented by the present century has one species-man-acquired significant power to alter the nature of his world" (Carson, 2002). Although Carson was concerned about human destruction of the environment, the environmentalist Bill McKibben has written generally about the way humans have left their imprint over the entire globe. He writes about this influence as the end of nature by which he means that nature and its processes no longer exist and function independently of human influence. The clearest example is the way in which human pollution has changed the atmosphere and as a result changed the weather. "By changing the weather," McKibben argues, "we make every spot on earth man-made and artificial. We have deprived nature of its independence, and that is fatal to its meaning" (McKibben, 1989). That, in other words, spells the end of nature.

From this more general perspective, Erle C. Ellis and Navin Ramankutty have argued for the existence of various anthromes, anthropogenic biomes, that range from the most densely populated urban areas to the least populated wilderness areas. They distinguish six types. *Dense settlements* are areas that have high populations with substantial urban areas. *Villages* are areas with dense agricultural settlements. *Croplands* include areas where annual crops are grown along with other land uses. *Rangelands* are characterized by livestock grazing with minimal crops and forests and may have varying levels of human populations. *Forested* areas are those biomes that have forests with human populations and agriculture, but where these populations are minor or inconsequential. Finally, *wildlands* are those biomes without human populations. The shift in perspective that they argue for is a shift from a model of the world as "natural ecosystems with humans disturbing them" to one of "human systems, with natural ecosystems embedded within them" (Ellis and Ramankutty, 2008). This shift, they believe, is necessary for the sustainable management of the biosphere in

the future. It is here that the role of ethics in valuing anthromes will be crucial because ethical principles will be needed to provide guidelines for the decision making involved in this management. Let's look now at three different frameworks for valuing anthromes.

Ethical Frameworks for Valuing Anthromes

The first framework that is useful for valuing anthromes was developed by Richard Shweder and his colleagues (Shweder et al., 1997). It is an ethical framework that psychologists have used to characterize moral reasoning and decision making across cultures. It identifies three distinct ethics that have cross cultural significance: the ethics of autonomy, the ethics of community, and the ethics of divinity. The perspective of this framework may be called *descriptive moral psychology*. It captures the way in which people characterize and understand ethical decision making. The second framework captures three types of moral theories philosophers have used to describe moral judgments about right and wrong and good and bad. They have traditionally distinguished between deontological ethics, consequentialist ethics, and virtue ethics. The perspective of this framework is *traditional ethical theory*. The third framework was developed by Andrew Dobson to describe ways in which environmental writers have approached issues related to environmental sustainability (Dobson, 1998). He distinguishes three different conceptions of environmental sustainability largely understood in terms of what aspects of the environment are most valued and need to be sustained. According to the first conception, environmental sustainability means maintaining critical natural capital because of its value for human welfare. According to the second, sustainability means maintaining natural capital because of its value for human welfare, but it also includes the preservation of irreplaceable natural resources for their intrinsic value. According to the third, sustainability is mainly about preserving nature because it is valuable for its own sake and should be preserved independently of whatever value it may have for human welfare. This framework is described as *conceptions of environmental sustainability*.

These three frameworks are not mutually exclusive. They are best thought of as three different lenses through which we can consider the environment and make judgments about the value different aspects of the environment have. Someone whose ethical perspective draws on an ethics of community may also make judgments that are justified by reasoning that appeals to a deontological ethics and that illustrates a conception of environment sustainability favoring the preservation of natural resources for human welfare. For example, this person may see the natural environment as valuable in the context of family and the local community and justify preserving green spaces within the city by appeal to our duties to provide our children with opportunities to learn about nature. Let's examine the details of each of these different ethical frameworks to understand them better and how they may be used in valuing anthromes.

Ethical Conceptions in Descriptive Moral Psychology

Richard Shweder and his colleagues developed their taxonomy of ethical conceptions by analyzing the ethical discourse of residents of Bhubaneswar, Orissa, India using structured interviews regarding incidents of ethical transgressions (Shweder et al., 1997). We categorize this type of analysis as descriptive psychology since it is an attempt to determine and describe what normative concepts members of a community employed in understanding decision making regarding actions with potential benefits and harms. Analysis of these interviews yielded a list of 16 moral themes which were then organized into three different ethics based on conceptually linked themes: the ethics of autonomy, the ethics of community, and the ethics of divinity.

The normative concepts of the ethics of autonomy are harm, rights, and justice. This understanding of ethics assumes that persons in society are independent from one another and pursue their own interests first and the interests of others or of the society second. Right and wrong are found in the benefits and harms that someone's actions may cause to other agents, and violations of rights are censured. As a result, individual freedom and human choice are central to this conception of ethics.

The normative concepts of the ethics of community are duty and obligation. These are established by a person's role in the family, community, or society. Rather than seeing society as an aggregate of individuals, this conception of ethics situates persons within larger interdependent groups such as family, the local community, and society. Their roles in these groups are frequently established by hierarchies. In the family, for example, the parents have duties to protect and defend their children based on their superior position, and the children have duties to respect and obey their parents based on their inferior position. This conception does not deny the existence of individual desires and interests, but it subordinates these to the good of the larger groups persons are dependent on. Each person is important, but the preservation of family groups, social relationships, and the community is more so.

The normative concepts of an ethics of divinity arise from a sacred or natural order that is established by divine ordinance. The sacred value of persons is derived from their relationship to and participation within this divine order. Duties and obligations toward others are ultimately based on this larger sacred order which is a focus of ultimate concern. Since human action is understood in the context of a sacred order, one that is established by religious tradition, wrong doing is frequently characterized as a sin that degrades the sacredness of a person and of the natural order. Within this conception moral violations of religious obligation established by the natural law lead to impurity and pollution that need to be remedied by sacrifice, punishment, or forgiveness. Each person is important as are human communities, but within this ethics of divinity human beings have a supernatural vocation (Shweder et al., 1997).

Part of the rationale for applying this ethical framework to valuing anthromes is its use in psychological literature related to moral development and moral emotions. For example, Lene Jensen uses the three ethics of this framework to broaden our

understanding of moral development that may be applied across cultures (Jensen, 2011). Paul Rozin and his colleagues use this framework to study and map the moral emotions of contempt, anger, and disgust (Rozin et al., 1999). The other part of the rationale for using this ethical framework is that contemporary philosophers present theories of justice that employ similar categories. Political philosophers who write in the tradition of liberalism typically presuppose a conception of society as an aggregate of individuals in pursuit of various conceptions of the good, which aligns with the ethics of autonomy. By contrast, philosophers who are representative of the communitarianism movement in political thought have emphasized the role of society in determining the nature of a person, and their thought seems to fit within normative concepts of the ethics of community. Other political philosophers draw on a natural law theory that is rooted in the thought of Thomas Aquinas, which would clearly fall within the ethics of divinity.

This framework from descriptive moral psychology creates a suitable perspective for valuing anthromes for at least three reasons. First, these different concepts are drawn from actual conversations about ethical decision making, so they are likely to be realistic ways in which people assign value to human anthromes and include them in their ethical deliberation. Second, they are cross cultural concepts, which is essential for having universal ways of valuing anthromes. Finally, though they describe norms that are already in place among various groups of people, they also roughly correspond to norms that have been carefully established as part of philosophical and political discussions of value.

Ethical Norms of Traditional Moral Theories

The second framework that may be used for valuing anthromes is based on three traditional moral theories. Moral philosophers commonly distinguish between deontological ethics, consequentialist ethics, and virtue ethics. A deontological ethics presents moral agents with fundamental moral rules and obligations for everyone to follow. These rules may be based on conventions which determine that certain actions like breaking promises and injuring innocent people are *prima facie* wrong while others like telling the truth are right. Sometimes the moral rules at the heart of a deontological ethics can be traced back to religious scripture which includes rules like golden rule or the 10 commandments. In the philosophical literature, the German philosopher Immanuel Kant famously proposed a categorical imperative or principle for all rational agents that they should act in ways that their actions could be a universal law for all agents (Kant, 1994). The view that there simply are some fundamental human rights with the understanding that these rights shall not be violated would also be an example of deontological ethics.

A consequentialist ethic bases right and wrong on the good or bad consequences that actions produce. The British philosopher John Stuart Mill's utilitarianism is a good example of a consequentialist ethics. According to Mill, actions that produce the greatest happiness overall are right and actions that lead to unhappiness are wrong. By happiness Mill understands pleasure and the absence of pain and by unhappiness pain and the absence of pleasure (Mill, 2001). Other utilitarians understand happiness in terms of individual satisfactions. For many consequentialist theories of ethics, the nature of the good is defined and then right and wrong are determined by what actions produce this good. This theory of ethics contrasts sharply with a deontological ethics in which what is right is determined independently of what is good or of the consequences of actions. By separating these two, actions that are right in a deontological ethics may lead to consequences that may not be deemed good insofar as the good is identified with human happiness. Since consequentialists define what is right in terms of what produces the good, the same problem does not arise for them.

A virtue ethics bases right and wrong on those actions that contribute to the development of specific virtues and vices as states of a person's character. Most virtue ethics trace their roots back to Aristotle. He defined virtues such as courage and justice as states of character created by actions that are a mean between excess and deficiency with respect to an identifiable moral context. Courageous actions, for example, are a mean between actions that exhibit an excess or a deficiency of fear. In his view the practice of virtues throughout a lifetime would lead to a person's happiness and to the well-being of society (Aristotle, 2000). So the consequences of actions were certainly part of his thinking about ethics. Identifying human virtues, however, and examining how they are cultivated were of central concern. Traditional virtues in Greek society were courage, temperance, justice, and practical wisdom. Later in Medieval philosophy under the influence of Christianity the theological virtues of faith, hope, and love were added to this list. In contemporary philosophy benevolence, charity, generosity, loyalty, and tolerance can be included among the virtues.

These three traditional ethical theories are not exhaustive of possible ethical theories that might be used to value anthromes but they do provide a good starting point. From each of these different theories it is easy to imagine ethical norms and values that can be applied to the human activities that shape biomes around the globe. From the deontological perspective, it would follow that human beings establish rules for human development that can be made into universal laws which include both the way this development affects human beings and the way it affects all the living beings and systems within a biome. From the consequentialist perspective, it would follow that human beings must make decisions by considering as thoroughly and extensively as possible the possible consequences of different actions and policies for humans and other sentient beings in the natural environment. Virtue ethics implies that we should cultivate what might be called environmental virtues that encourage us to be good citizens of the anthromes in which we live. To paraphrase Aldo Leopold, we might think of these virtues as appropriate to humans who no longer think of themselves as conquerors of the land but as plain members and biotic citizens of it.

Ethical Conceptions of Environmental Sustainability

The third framework for examining the ways in which we can value anthromes approaches environmental value from the perspective of environmental sustainability. This framework was developed by Andrew Dobson to classify ways in which thinkers on

environmental sustainability answer questions about what needs to be sustained and why. In contrast to the conception of sustainable development, which has been the focus of much discussion, Dobson makes the concept of environmental sustainability central to his discussion. When we realize that we depend on natural capital to last into the future that cannot be completely or partially replaced by human made capital we have introduced the notion of environmental sustainability. For any theory of sustainability to be about environmental sustainability, he observes, it is essential “that it argue for the sustaining into the future of some aspect of the natural environment” (Dobson, 1998). Dobson distinguishes three conceptions of environmental sustainability. First is a conception that emphasizes the preservation of natural resources for human welfare. Second is a conception that recognizes the preservation of natural resources for both human welfare and non-human welfare, especially those that are irreplaceable. This conception also includes considerations about our duties toward nature independent of human beings. Third is a conception that emphasizes the preservation of nature simply for its own sake rather than for its value for human purposes.

According to the first, what needs to be sustained is critical natural capital. Critical natural capital includes those natural resources and systems that are essential for human survival. It would include water, land, and energy resources, but would also include biological systems and processes. Dobson is happy to include these larger systems within the description while acknowledging that some may think of critical natural capital mainly at a local level as referring to arable land and clean water sources for agriculture. Within this conception of environmental sustainability, the overriding reason for sustaining critical natural capital is to promote human welfare. Since human beings need natural resources in order to live, it is essential that this critical natural capital be sustained indefinitely. Dobson argues that most of the discussions of sustainable development understand and value natural capital in economic terms and argue for its preservation from the anthropocentric perspective that informs this first conception of environmental sustainability. When the question turns to how this sustainability is to be achieved, proponents of this first conception argue for renewing the natural resources that can be renewed, substituting for those which may be endangered or which may simply be running out, and protecting those resources for which there may not be acceptable substitutions. This conception of sustainability emphasizes finding suitable substitutions for critical natural capital that we can depend on in the future. If we could always find such substitutions, then we would not even be looking at a theory of environmental sustainability. But as long as there are some natural resources we can't replace with man-made substitutions, and if we need these resources into the future, Dobson argues, “we are in the presence of a theory of environmental sustainability” (Dobson, 1998). So the first conception of environmental sustainability involves sustaining critical natural capital because it is necessary for human welfare. We sustain critical natural capital by renewing it if possible, substituting human made capital to the extent this is feasible, and protecting the rest.

The second concept of environmental sustainability shifts what needs to be sustained from critical natural capital to resources and other aspects of nature that are being irreversibly lost. The paradigm case of such change is the loss of biodiversity that occurs with the extinction of species. This irreversible natural change can be significant because it means the loss of something that is critical for human welfare, such as the loss of petroleum reserves. But it can also be significant because it means the loss of species that have intrinsic value independent of any use value for human beings. In cases for which irreversible losses to nature have no clear bearing on human welfare, our reasons for avoiding them will gravitate toward arguments that relate to our duties toward nature as such. In Dobson's view this may also involve a sort of weighing of consequences that is common to utilitarian reasoning because we cannot avoid all irreversible losses. As a result, “the benefits from some losses need to be weighed against the gains that might result from the loss.” What is important in this conception is that “the notion of irreversibility needs to be taken into account when calculations of this sort are made” (Dobson, 1998). Since the losses of irreversible nature obviously cannot be renewed the only options for how to handle them are either substitution with something human made that provides the same benefits for human welfare or protection. Protection and preservation, for example, are essential ways to sustain biodiversity and prevent the further extinction of species that are being lost as a result of human development and interference with natural habitats.

The third conception emphasizes the importance of protecting and preserving natural value as such because we have duties to other species and nature or because we believe that they have intrinsic value that must be respected. From this perspective there may be little if any concern about ways in which we can or should develop human-made capital to replace critical natural capital. Of the three conceptions of environmental sustainability, this conception is clearly what we might call the greenest. In literature related to sustainability, it is a version of what Wilfred Beckerman calls “strong sustainability” because it can be understood as the requirement to preserve nature as it is now for future generations for its own sake (Beckerman, 1999). Weaker versions of sustainability advocate preserving nature for the sake of human beings.

At the same time that this framework captures different conceptions of sustainability that have been presented by philosophers and environmental activists over the past few years, it also takes for granted the idea of nature as something separate from human influence. This is especially noticeable in the third conception which argues for sustaining nature as it is now for future generations. Since human activity and development now have a global influence, it is no longer possible to think about a pristine nature that can be preserved and protected from future human influence. It does not follow, however, that we cannot value and protect the beauty of natural spaces for themselves. Consequently, each of these conceptions of sustainability has important implications for valuing anthromes.

The first conception of sustainability emphasizes the importance of conserving, protecting, and preserving those natural resources that essential for human survival and further emphasizes the search for alternative resources that have less environmental impact. The second conception of sustainability pays particular attention to those resources that are irreplaceable, such as petroleum reserves. It also recognizes the intrinsic value that other living beings have and the importance of our taking responsibility for managing and caring for them. This might include a more sustainable agriculture that relies less on chemical fertilizers that are toxic to the land and water as well as kinder provisions for raising animals that are needed for food. The third conception of sustainability

makes room for the recognition that nature in whatever form, from less populated wild areas to urban green spaces has value for human life and intrinsic value. Thinking about any sort of urban or land management benefits from recognizing the instrumental and the intrinsic value of all those aspects of the natural environment that we interact with.

Conclusion

As human development and industrial activity continue to have a significant influence in shaping the ecosystems within which we live, it is especially important to broaden the scope of our ethical thinking and deliberation to include all aspects of the natural environment. There are many goals that have vied for pride of place in the writings of philosophers and environmentalists not the least of which is sustainability. Certainly, valuing the various anthromes that cover the globe must make this one of the important priorities. Others include protecting biodiversity and reducing the current high rate of species extinctions. From a human perspective it is important to preserve green spaces and relatively wild environments for their beauty and capacity to vivify the human spirit. At the same time, it is equally important to create and preserve the sort of social, educational, and economic opportunities that are essential for human happiness. Although the ethical frameworks presented here are not exhaustive, they give a significant variety of perspectives for valuing anthromes that enable us to achieve a sustainable balance between human needs and interests on the one hand and what is needed for other living beings and living systems to thrive on the other. Every anthrome like any other biome is a home to all the living beings that inhabit it. Just as any home has rules to protect the interests of everyone who resides there, we need to draw on the established ethical frameworks that we have at our disposal to guide our behavior toward all members of our anthromes.

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Relevant Website

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Conceptualization of Wilderness

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Abstract

This article tracks the metamorphosis of the idea of wilderness in light of major shifts in thought on conservation strategies and attendant politics. The article opens with a long history of the concept, noting its debts to religious discourses and sublime aesthetics that underwrite ambivalent notions of wilderness as being sacred and terrible, all of which ground notions of wilderness as being necessarily distinct and separate from “civilized” human beings (Garrard, 2012). Next is an overview of geographical associations with the term, such as correlations between wild and west, between wilderness and empty spaces, between uncharted ground and colonial enterprise or even imperializing plunder (Cronon, 1995; Garrard, 2012; Guha, 1998; Miller, 2018; Plumwood, 1998). In so doing, this article’s trajectory sets out to explore wilderness in its seemingly innocent registers that align freedom and power with so-called pristine or pure landscapes. In addition, it details more recent thinking that positions wilderness as a politically- and historically-fraught concept. In terms of the latter understanding, wilderness concepts emphasize polar differences between humanity and nature that ideologically support the spread of an homogenizing, imperializing cultural logic, ultimately spurring human displacements while harming interrelated, interdependent non-human lifeforms and biodiversity in the process (Denevan, 2011). In conclusion the essay introduces nascent branches of alternative wilderness thinking relative to conservation efforts that pertain to both humans and nonhumans and thus transcend typical wilderness dualisms that growing numbers of researchers find to be deeply problematic and detrimental to environmental conservation aims.

Introduction

Where does the wilderness begin or end? How do we know the wild? Answers to such questions tend to be found at the limit of changing definitions of the human if not human culture. For example, a recently published installment of *Nature’s* correspondence section makes clear how ideas of the human, and in turn, how ideas about the inhuman or abhuman shape wilderness thinking as well as wilderness conservation efforts and research. Life sciences specialists joined with forestry researchers to urge readers of *Nature* to once and for all “[a]gree on [the] meaning of wilderness ... [as] a map of valued natural regions [that] should include all wild lands generally judged to be important ... Otherwise, policymakers might wrongly infer that omitted areas are tainted by human presence and no longer worth protecting” (Sheil et al., 2019, 429).

If humans are present, it is assumed that wilderness is not, and thus the impetus for protecting valued wild lands is precisely because they are not (yet) “tainted by human presence” (Sheil et al., 2019, 429). Such urgent pleas for guarding wild spaces by deeming them prized wilderness areas begs the following question: from what do these wild regions need protecting? It might be easy to suggest humanity as the logical and commonplace response, but so-called wild lands might also need protecting from being deemed untouched wilderness, since to certain modern developers wilderness lands are tantamount to storehouses of untapped resources (Sayles, 2015). Ironically perhaps, and as the above example from *Nature* shows, concepts of wilderness long associated with places and states of wild, uncontaminated, or protected nature continue to stage important debates about human culture largely because wilderness concepts so often assume a stark separation between the natural and the cultural (Garrard, 2012). As Timothy Clark puts it in *Nature, Post Nature* “there is nature understood as the other of culture, that which arises of itself without human agency. It may be revered as wilderness or pristine animality, or feared as the bestial and cruelly inhuman. Looser variants of this sense use nature to name the biosphere, or, more casually, a certain idea of the rural as opposed to the urban” (Clark, 2013, 75–6).

While a general consensus might suppose that to study the wilderness is to study biomes remote from humankind, in fact wilderness studies must to some extent examine subsets of the world’s anthromes (Ellis and Ramankutty, 2008; Martin et al., 2014). That is, wilderness researchers necessarily investigate select portions of the world’s anthropogenic, human-influenced biomes, since with anthropogenic “climate change and distribution of pollutants, there is no place on Earth that has not been altered by humans” (Williams et al., 2015, 197; Lieberman et al., 2018). The question then becomes one of determining the extent of human modification to various regions in order to designate areas on the globe as wilderness or wildlands. For example, Conservation International prioritizes and puts particular emphasis on high biodiversity wilderness. According to their agreed upon definitions and markers, high biodiversity wilderness areas must hold a vast majority of their endemic species and be comprised

of at least 70% of their natural habitats (Newbold et al., 2016). Yet to fail to acknowledge the wide array of case-by-case definitions of wilderness, “natural,” wild, or undisturbed lands, or to ignore the sociocultural spectrum of debates framing concepts of wilderness risks gross misunderstandings, as discussed in the following article. Failing to account for shifting definitions of wilderness and the attendant sociocultural problems sparked by narrow wilderness thinking also risks missing altogether the degree to which human definitions of and assumptions about nature inform the various anthromes (wild or not) humanity produces today, not to mention how these divergent wilderness definitions and debates direct conservation policy or any given human value system driving environmental policies.

The following article tracks the metamorphosis of the idea of wilderness, particularly in light of major shifts in thought pertaining to how wilderness environments and wild ecological systems are imagined, or in other words, in light of what could be called the changing terrain of environmental imagination as it relates to wilderness thinking (Purdy, 2015). The article opens with a long history of the concept, noting its debts to religious discourses and sublime aesthetics that underwrite ambivalent notions of wilderness as being sacred and terrible, all of which ground notions of wilderness as being necessarily distinct and separate from “civilized” human beings (Garrard, 2012). Next is an overview of geographical associations with the term, such as correlations between wild and west, between wilderness and empty spaces, between uncharted ground and colonial enterprise or even imperializing plunder (Cronon, 1995; Garrard, 2012; Guha, 1998; Miller, 2018; Plumwood, 1998). In so doing, this article’s trajectory sets out to explore wilderness in its seemingly innocent registers that align freedom and power with so-called pristine or pure landscapes. In addition, it details more recent thinking that positions wilderness as a politically- and historically-fraught concept. In terms of the latter understanding, wilderness concepts emphasize polar differences between humanity and nature that ideologically support the spread of an homogenizing, imperializing cultural logic, ultimately spurring human displacements while harming interrelated, interdependent non-human lifeforms and biodiversity in the process (Denevan, 2011). In conclusion the essay introduces nascent branches of alternative wilderness thinking (Miller, 2018). Such revisionary, non-dichotomous wilderness concepts attempt to afford room for multicultural valuations of wild spaces as well as non-urbanized notions of freedom and liberty.

Blunt Wilderness Binaries

The main trouble with wilderness thinking springs from problems created by its grounding dualisms, or in other words, its blunt and crude binary logics. With its all too easy either-or options, neat this-or-that distinctions, wilderness concepts risk clouding relations and feedback loops existing between and across human and natural systems—relations occurring even in spaces we might call wild (Lieberman et al., 2018). Take for example Thoreau’s famed and paradigmatic expression of the wilderness concept. Thoreau’s grounding assumptions sever the freedoms, agencies, or powers of natural systems from the liberties, license, and rights of humanity’s cultural systems: “I wish to speak a word for Nature, for absolute freedom and wildness, as contrasted with a freedom and culture merely civil” (Thoreau, 1862, 657). The stark contrast between the capitalized, idealized, and universalized version of nature (or ecological communities) that Thoreau aims to speak for, and the relatively smaller, less significant realm of human agency and actions—imagined here as “merely civil”—suggests that human choices, cultures, and histories matter less than the actions and operations of a seemingly omnipotent natural world. Then the depiction of “Nature” as an absolute universal further muddies the waters by making it seem as if ecological systems are timeless and less subject to history, change, or evolution than human systems. In these aspects, Thoreau’s dichotomous wilderness thinking downplays the powerful role that human beings play in any extant natural system’s past, present, or future.

Such dualist misunderstandings of wilderness would later be repatterned, enshrined into law, in effect granting this spurious logic greater currency and staying power by being endorsed by the U.S. federal government and others in following. For instance, in the U.S. the 1964 Wilderness Act (16 U.S.C. 1131–1136) established a preservation system to maintain the “wilderness character” of federally designated areas, offering a definition of wilderness hewing close to Thoreau’s 19th-century account. The document assumes human life to be antithetical to wilderness. Human and natural agencies are not represented as overlapping, interrelated, entangled, or in terms of feedback loops. Rather “earth and its community of life” excludes human beings as well as “human habitation” (Wilderness Act, 1964, 2).

Federally protected wilderness areas welcome humanity only as visitors or researchers, foreclosing the possibility of indigenous human cultures being able to live in these lands regardless of extensive historical, cultural, and ancestral precedents. While it might be tempting to grant that the Wilderness Act does open a backdoor to humanity by allowing intermittent access, its language clearly states that only certain kinds of cultural activities are welcome there, including “opportunities for solitude or primitive and unconfined type of recreation” or the study of “features of scientific, educational, scenic, or historical value” (Wilderness Act, 1964, 2). The dualist language of the law defined wilderness as necessarily separate from everyday human culture or existence, opening protected lands to those solitary itineraries able to afford the occasional leisurely visit, or to those supported by distant if not distinguished research agencies and institutions, while effectively writing out endemic human cultures with long ties to and crucial relationships with their surrounding ecosystems (Dear and Myers Jr., 2005; Garrard, 2012; Guha, 1998; Harmon, 1998; Miller, 2018).

Influential critiques of wilderness discourse find its abiding logic troublesome not only when “anthropocentric-biocentric distinctions [are] accepted as axiomatic” but also when “it quietly expresses and reproduces the very values its devotees seek to reject” (Guha, 1998, 233; Cronon, 1995, 80). William Cronon’s landmark work *The Trouble with Wilderness* grapples with what he calls the “central paradox” of wilderness thinking. Cronon stresses how “wilderness embodies a dualistic vision in which the

human is entirely outside the natural. If we allow ourselves to believe that nature, to be true, must also be wild, then our very presence in nature represents its fall" (Cronon, 1995, 80–81). He goes on to argue that if "this is so—if by definition wilderness leaves no place for human beings, save perhaps as contemplative sojourners enjoying their leisurely reverie in God's natural cathedral—then also by definition it can offer no solution to the environmental and other problems that confront us. ... Worse: to the extent that we live in an urban-industrial civilization but at the same time pretend to ourselves that our real home is in the wilderness, to just that extent we give ourselves permission to evade responsibility for the lives we actually lead. We inhabit civilization while holding some part of ourselves—what we imagine to be the most precious part—aloof from its entanglements" (Cronon, 1995, 81).

For Cronon, at the heart of wilderness thinking is the misleading idea of escape: escape from history and escape from responsibility. Under the rubric of conventional wilderness wisdom, humanity is left off the hook in relation to caring for, managing, or conserving any and all ecological systems that necessarily support human life and culture. Of course, it is important to bear in mind that Cronon emphasizes that his critique is not mounted against those working to protect "wild nature per se, or even to set aside large tracts of wild land" (Cronon, 1995, 81). In contrast, his aim is to expose "specific habits of thinking" spurred by "this complex cultural construction called wilderness" (Cronon, 1995, 81). In Cronon's analysis, the concept of wilderness, be it mentioned in professionally published discourse or common conversation, cannot avoid triggering problematic habits of thinking that ultimately work to undermine anyone's attempts to protect the planet's least human-influenced areas.

Wilderness Roots and Regionalisms

According to Greg Garrard's influential study of the idea of wilderness, such problematic patterns of thought have their roots in cultural geography and religious thought. Garrard's account of wilderness "as the most potent construction of nature available to New World environmentalism," exposes how the concept enjoys a sublime, "almost sacramental value" because of the pivotal role the idea held in relation to "the settler experience in the New Worlds—particularly the United States, Canada, and Australia—with their apparently untamed landscapes and the sharp distinction between forces of nature and culture" (Garrard, 2012, 67). Garrard's research into the sociocultural underpinnings of wilderness logics that assume a fundamental disconnect between ecology and humanity as well as between nature and culture charts how these overlapping dichotomies arise from "a set of distinctions ... based upon a mainly agricultural economy" (Garrard, 2012, 67). Emerging farming communities began to frame notions of home against wilderness and nature due to assumptions that the labors of the farmer are tantamount to a "struggle against nature" equated to Judeo-Christian notions of the curse of toil. The Judeo-Christian model informing most iterations of wilderness concepts in the West "combines connotations of trial and danger with freedom, redemption and purity, meanings that, in varying degrees it still has" (Garrard, 2012, 68).

Thoreau's body of work sheds further light on how the freedom attributed to wilderness not only supported associations between the wild, wilderness, and the West, but also helped to legitimate western expansionism under the banner of Manifest Destiny in United States, a doctrine typified by Jackson Turner's "Frontier Thesis" (Cronon, 1995). In his influential essay penned for the *Atlantic Monthly*, "Walking," Thoreau puts into words and thus helps cement conceptual links between uncharted, "uncivilized" wild spaces with opportunities for individual growth and individual rites of passage that appear to be inseparable from new opportunities to tap untouched natural resources and to access assumedly uninhabited spaces. "When I go out of the house for a walk," Thoreau writes, "uncertain as yet whither I will bend my steps ... I find, strange and whimsical as it may seem, that I finally and inevitably settle southwest, toward some particular wood or meadow or deserted pasture or hill in that direction. My needle is slow to settle, varies a few degrees, and does not always point due southwest, it is true, and it has good authority for this variation, but it always settles between west and south-southwest. The future lies that way to me, and the earth seems more unexhausted and richer on that side" (Thoreau, 1862, 662).

Thoreau's 19th-century coupling of wilderness and a kind of settler colonial logic in line with the doctrine of Manifest Destiny in the United States endures in current wilderness conservation research published across the North America, Europe, and in other regions with large Anglophone populations such as Australia. For example, a highly cited publication with a correspondingly high impact factor holds a title that bears witness to deep and lasting associations between wilderness concepts, colonial and frontier logics, and histories of western expansionism: "The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013" (Potapov et al., 2017, 1). In similar spirit but stated in even more direct terms, another influential study makes synonym out of "wilderness or frontier areas," with wilderness and frontier becoming interchangeable (Laurance et al., 2014, 229). Confirming Cronon's analyses, regardless of whether or not researchers intend to repattern longstanding linkages between nationalist colonial agendas and wilderness concepts, publications on wilderness conservation run the risk of reactivating enduring links not only between wilderness thinking, colonial conquest, and a sense of entitled access to "undeveloped" lands, but also regardless of any existence therein of ancestral human communities. Researchers thus would do well to acknowledge these historical and ideological entanglements.

By explicitly acknowledging the colonial and imperial associations held between "uncharted" or "untouched" wilds and fantasies of a winner-take-all frontier ethos, researchers can begin to better study and more deeply understand the disconnects at play in Thoreau's logic which remain powerfully active today (Sayles, 2015). Thoreau's reverence for and questing after an earthen terrain that "seems more unexhausted and richer" neglects and downgrades the comparatively impoverished, spoilt, and unpromising

grounds that in fact supported his everyday existence, ignores his own part to play in any “spoiling” process, imagines away human livelihoods other than his own, and falsely presumes a seemingly endless reserve of future wild spaces to escape to, or to at least access if not flat out exploit.

Wilderness Conservation and Environmental Colonialism

Postcolonial critiques of wilderness are often at pains to point out how Western philosophy’s sacralization of sublime wilds and pure nature masquerades as valuing nature above all else, but in truth advances dominant regional, national, or imperial goals (Guha, 1998). Environmental colonialism describes the process of forcing a dominant nation, group, or region’s ecological thought and conservation priorities onto other places and peoples, assuming a one-size-fits all approach that routinely fails to respect endemic communities of both human and nonhuman kinds for what they are and for how they work (Guha, 1998). Well known examples include how the United States National Park system forcibly removed indigenous populations out of their ancestral homelands in the name of establishing and protecting the nation’s greatest natural treasures (Guha, 1998; Garrard, 2012; Miller, 2018). Without considering how this process forever changed those environments and their endemic human cultures, this practice has been adopted and repatterned in other countries. Take for example India, where preserves were established to protect animals highly valued by western aesthetics and institutions (Tigers) at the cost of dislocating the area’s often impoverished human residents, in turn causing lasting damaging modifications and disturbances to the newly “protected” area (Guha, 1998). As Cronon reminds us, the “removal of [indigenous communities] to create an “uninhabited wilderness”—uninhabited as never before in the human history of the place—reminds us just how invented, just how constructed, the American wilderness really is. To return to my opening argument: there is nothing natural about the concept of wilderness” (Cronon, 1995, 79).

The faulty dualistic thinking so fundamental to most wilderness constructions proves damning once again, setting up biodiversity conservation as mutually exclusive from supporting human cultures when the opposite has often been the case (Porter-Bolland et al., 2012; Keeling and Sandlos, 2009). The more diverse human cultures that flourish on earth by divergent means of subsistence opposed to the wasteful conventions characteristic of industrial societies in fact help to support, sustain, and preserve biodiversity, with indigenous communities providing important models for protecting and conserving threatened environments within which they live and which they call home (Guha, 1998; Pearce, 2016; Sayles, 2015).

To better fathom the dynamics of environmental deterioration looming over all spaces of the globe, inclusive of its least human influenced areas, it would be a mistake to bracket off wilderness from its relations to other natural and human systems. Mythologized investments in preserving the planet’s remote and so-called pristine areas—flown under the banner of wilderness conservation—cannot bear real fruit without also investigating leading drivers of ecological degradation, such as excessive, uninhibited consumption and wastefulness that has yet to be counterbalanced by cultural shifts toward an ethic of restraint and self-limitation (Guha, 1998; Denevan, 2011). This would balance out the simplistic thinking behind wilderness logic that would suggest that wilderness politics have nothing to do with questions of social justice or equity (Keeling and Sandlos, 2009; Miller, 2018). But since ecologically draining and damaging patterns of overconsumption predominate in the richest, most industrialized countries, it is imperative that the dualist politics of wilderness conservation not be allowed to mistake all human presences in natural areas as being equal or that social justice issues are unrelated to wilderness issues. The key here is that wilderness conservation proponents need to understand how setting aside protected wilderness areas by dislocating and displacing people living in these areas directly transfers resources away from the poor and into the hands of the rich, exacerbating cycles of entitled overconsumption and weakening communities that do least harm to their surroundings, not to mention playing important roles in their home ecosystems (Guha, 1998; Porter-Bolland et al., 2012; Sayles, 2015).

A more tempered and nuanced understanding of wilderness is necessary, where humanity and wilderness are not necessarily contradictory so that conservation practices can help maintain human communities promoting biodiversity and furthermore so that a larger cross section of human cultures are preserved to help counteract wasteful and damaging models of industrial overconsumption predicated upon unchecked expansionism, an expansionism itself reliant upon encroaching into previously “untouched” or “untapped” lands, resources, and communities (Porter-Bolland et al., 2012; Keeling and Sandlos, 2009).

Marking a move in the right direction, rather than only defining wilderness as antithetical to humanity or human culture, we could follow those researchers and scientists who are beginning to distinguish wilderness not against any monolithic concept of humanity or culture, but by a given community’s relationship with and impact on its home environment. Then, for example, we would know wilderness or wildlands by measuring the “degree to which a place is remote from and undisturbed by the influences of modern technological society” rather than simply and crudely by human presence alone (Pärtel et al., 2017).

NatureCultures and Alternative Wilderness Thinking

Can more nuanced, accurate, and responsible alternative wilderness concepts prevail? Can future adopters of the term shake off the concept’s compromising binary logics and reductive dualisms, perhaps instead reactivating “a more richly researched, more imaginatively inclusive” concept that “understood wilderness as a space of liberation that had to be maintained by caring human hands, a place where identity, landscape, community, and memory defined one another? Such would be a creative definition of wilderness that presupposed occupation and laboring, an idea that would have little to do with the notion of the lone, white, male sojourner

coming face-to-face with a sublimely empty nature while on vacation. It would be an equation of wilderness with freedom, with community, with home" (Miller, 2018, 71). So writes wilderness historian Daegan Miller as he reopens the thorny question of "what is wilderness" (Miller, 2018, 52). In his meticulously researched revisionist history of the Adirondack wilderness, Miller pushes back against dichotomized wilderness thinking. He counters patterns of thought conflating wildlands with mythologies of emptiness that erase human and nonhuman histories, and with them their respective work, their respective disturbances, their respective fullnesses, their respective and sometimes overlapping communities. As Miller notes, the "tragedy of wilderness is that all that howling emptiness that many of us now celebrate obscures all that violent history of emptying" (Miller, 2018, 53).

Miller's alternative wilderness accounts offer lines of analyses that hew closely to Donna Haraway's idea of naturecultures, where rather than being mutually exclusive nature is presumed to entail various cultures comprised of both humans and nonhumans (Haraway, 2003). Miller does not fall prey to reductionist oppositional logic. Instead Miller prescribes an understanding of wilderness predicated upon a complicated relationality emblematic of naturecultures, where what qualifies as wilderness might be a "community of trees" and where "unsettled, or untouched, or unbroken" land "didn't mean that it was empty or unpeopled, or even uncleared—it just meant that the predominant view was of forest" or by extension, of any given type of wilderness (Miller, 2018, 88). He embraces wilderness concepts in light of process thinking, striving to account for particular conjunctions and complicating relations. In Miller's detailed research on specific places and particular peoples, we find wilderness alongside work, wilderness with home, wilderness as communal, wilderness as full. Just as humanity is not treated as a monolith in these particular histories of Adirondack wildlands and their human and nonhuman communities, neither is wilderness or wilderness thinking singular or narrowly defined. Rather than falling back on blunt wilderness binaries that mainly perpetuate and reflect concepts linked to histories of settler colonialism and ecological imperialism damaging to both human and natural systems, wildernesses become something both particular and capacious. "Recognizing difference means that many wilderness travelers thought of the woods not as empty, virginal, and waiting to be penetrated by culture—the definition of wilderness that prevails today—but instead as full: full of sound, full of smell, full of health, full of trees and animals. Full of life" (Miller, 2018, 89).

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Using an Ecobiopsychosocialspiritual Approach to Understand and Transform Human Interaction with Anthromes and Biomes

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Abstract

Although our ancestors probably also sensed it, we now know that there is an interconnection between human wellbeing, and the well-being of the anthromes and biomes (A&B) we interact with. Biomes can be thought of as ecological regions characterized by the living things, landforms, and climate in those areas. In addition to the same elements that characterize biomes, anthromes also experience human impact. This interconnection calls for a more interdisciplinary approach to model building and practice in two areas:

First, in addition to traditional biological and geophysical processes, ecological theorists also need to include human cultural, psychological, sociological, and spiritual processes in their model building, in order to investigate, understand, and address the consequences and causes of anthropogenic ecological change (Ellis, 2015).

Second, mental health theorists need to add an ecological perspective to their model building. Since ecological factors influence physical and mental health, professional helpers who serve the mental health needs of individuals and communities need to add an ecological perspective to their practice (Derezotes, 2016).

In this article, an ecobiopsychosocialspiritual (EBPSS) approach to community practice is described, that combines the insights of ecopsychology with social justice values. Then, the reader will be given examples of how to use this EBPSS approach to both understand and transform human interactions with anthromes and biomes.

Introduction

Humanity's advancements in the development of manufacturing, transportation, construction, bio-engineering, energy, and communication technologies continue to outpace the development of conscious and loving relationships with each other, other life forms, and the ecosystems that support all life.

This disparity increasingly intensifies the Global Survival Threats (GSTs) that loom over humanity's future, as well as the future of many other species and the ecosystems that support all life on our planet. These interrelated threats include overpopulation, climate change, preparations for war, and destruction of natural resources (Derezotes, 2005).

Humanity is already experiencing widespread psychological, physical, and social impacts related to GSTs (Doherty and Clayton, 2011). There is evidence that many past societies have disappeared because of local ecological collapse, primarily due to overuse of resources (Moffett, 2018). Today, our individual and collective lack of consciousness about our interconnection with the deteriorating state of our anthromes and biomes has been linked to widespread and increasing depression and anxiety (Macy and Johnstone, 2012) and the distress of "solastalgia" (Albrecht et al., 2007) observed in human populations across the planet. We also know that poor and other minoritized populations tend to experience the greatest impact of ecological change across the globe (Shiva, 2015).

Ecologists and mental health professionals can work together with other disciplines to educate the public about the urgency of ecological GSTs; this chapter is written in the spirit of developing such increasing multidisciplinary cooperation. Because of limited space, this chapter can only be an introduction to this complex and fascinating subject. Some basic concepts, for example, related to

mental health assessment and intervention with clients are offered, but many important details of practice are not included. The phrase “well-being” will be used to include the overall multi-dimensional health of humans and of the A&B we live in.

An Ecobiopsychosocialspiritual Approach to Practice

As the name suggests, the EBPSS approach includes five interrelated dimensions. The “psycho” or psychological dimension is derived from a Greek word for “breath of life” and today is understood to be about the mental construction of a person. “Social” is derived from a Latin word that refers to the relationships between people. “Bio” comes from a Greek word that signifies all life, and “eco” from another Greek word that refers to the connection between life and the environment. Spirituality derives from the Latin word for “breath of life” and today refers to human consciousness and our connection with the Universe. The entire expression suggests that humans are multidimensional beings who are interconnected with the many dimensions of all life and all environments. **Fig. 1** illustrates the interrelatedness of these five dimensions.

A thesis of this chapter is that reconnection with our own inherent multidimensionality, of body, mind, and spirit, can help us also reconnect with other living things and ecosystems, and that such reconnection is a foundation of transformation of human interaction with anthromes and biomes. We cannot connect with nature without connecting also with ourselves, and we cannot connect with ourselves without connecting with nature. The word “healing” is derived from the Latin word for “wholeness”; and the healing of the human race can be conceptualized as the reintegration of all the parts of our EBPSS makeup.

As we heal, and become aware of and express this multidimensionality, our beliefs about and relationship with A&B can also transform. We begin to experience and express what [Wilson \(1986\)](#) called “biophilia,” which is our natural affiliation with all life. There is increasing evidence that spending time in more natural settings, or even interacting with plants and animals, brings measurable physical health benefits to all groups of people; benefits include lowered stress, blood pressure, lowered risk of life-threatening physical and mental illness, and longer life expectancy ([Sheikh, 2019](#)). This biophilia can be experienced and expressed in all five dimensions of development. **Fig. 2** summarizes the discussion of the EBPSS approach.

The Ecological Dimension

In social work and many related disciplines, the terms “ecological” and “environment” have primarily been used to describe human social context, such as family, culture, nationality, and religion ([Derezotes, 2016](#)). In the EBPSS approach, the meaning of the phrase “eco” is expanded to include both human social context as well as the context of urban, village, rangeland, cropland, and other anthromes as well as forest, desert, wetland, tundra, and other biomes ([Wildlife Trusts, 2019](#)).

Humanity is living increasingly separated from the ecosystems that support our lives. A recent study in the United Kingdom for example, revealed that 7 out of 10 people admitted being out of touch with nature; even people living in more rural areas spend increasing time in front of screens, and relatively less time outdoors, than previous generations ([Orr, 2017](#)).

Despite this widespread retreat from nature, human well-being is nevertheless connected with environment. The local environment can strongly influence religious, political, and cultural beliefs and behaviors. Many people have “sacred landscapes,” such as a particular mountain lake, canyon grove, or ocean beach that are especially meaningful to them. A person’s sense of whether she can make a difference in the overall health of his environment is related to their overall well-being, and could be expressed, for example, by her willingness to lobby to have their local or regional government consider A&B in community activities and planning.

The healing of our ecological dimension begins when individuals and communities recognize our interconnectedness with our local and global A&B.



Fig. 1 Interrelated developmental dimensions of individual and collective human well-being.

Dimensions	Theoretical approaches	Central Themes	Examples of evidence of Biophilia
Eco-logical	Community mental/physical health	The community includes not only other humans, but also other life and our ecosystems	Inclusion of A&B in community activities and planning
Bio-logical	Reconnecting with our bodies	Physical health is connected with the health of all life and ecosystem health	Correlations between human well-being and well-being of A&B
Psycho-logical	Eco-Psychology	Mental health is linked with stewardship of other people, other life, and the environment	Beliefs and behaviors that demonstrate commitment to and stewardship of A&B
Socia-logical	Social Justice Perspective	Human well-being is connected with social justice for not only	Beliefs and behaviors that demonstrate commitment
		all humans but also all life and the ecosystems that support us	to social justice of human interaction with A&B
Spiritual	World's wisdom traditions	Development of consciousness (reverent awareness) of human connection with the universe	Beliefs, rituals, and activism that develop and deepen such consciousness

Fig. 2 Constructing an ecobiopsychosocialspiritual (EBPPS) approach.

The Biological Dimension

Over generations, many of us have gradually forgotten that we are animals. In many societies, people tend to believe that humans are the most important species, and that we are the only living things with consciousness, emotions, culture, and morals. The evidence suggests otherwise ([Hogenboom, 2015](#)).

However, we not only increasingly live in separation from other living things, but also live in increasing separation from our own bodies. In fact, most people, especially those of us living in more affluent and “civilized” societies, live in our heads. What does that mean? When I live in my head, most of my awareness is focused on my thoughts, and relatively little awareness is focused on the rest of my body below my neck. I might not, for example, be aware of when my body is hungry or full, needs exercise, or needs rest.

Healing the biological dimension means in part to become reacquainted with the aliveness in my own body, so I can relate to the aliveness all around me as well. That aliveness may include all the sensations, emotions, and energy I may notice in my body from time to time.

The Psychological Dimension

“Ecopsychology explores humans’ psychological interdependence with the rest of nature and the implications for identity, health and well-being” ([Society for Environmental Population and Conservation Psychology, 2014](#)). Ecopsychology has become increasingly recognized and now is represented as Division 34 in the American Psychological Association.

Ecopsychology is an emerging field that is informed by many multidisciplinary and multicultural sources, including Sustainability, Deep ecology, the Green Movement, Biophilia, Shamanism, Transpersonal anthropology, Ecospirituality, Transpersonal ecology, Ecofeminism, Economics [Schroll \(1994\)](#). This ecological perspective has also been recognized in social work and other related disciplines ([Derezotes, 2016](#)).

An important implication of Ecopsychology is the idea that a “mentally healthy” individual, family, organization, or community is connected with and acts as a good steward of local A&B. Conversely, a person may suffer mental health symptoms when she is not aware of her connection with the environment. The [World Health Organization \(2018\)](#) has for many years identified depression and other mental health disorders as among the most serious and widespread global health problems, rooted at least in part in the widespread deterioration of the ecosystems that support all life. In fact, there is increasing evidence that growing numbers of people across the Earth experience “ecological grief” in response to climate change ([Cunsolo and Ellis, 2018](#)). When such grief is ignored, psychological symptoms such as depression and anxiety can emerge.

Depression and anxiety, which often are “comorbid,” or occur together, can be thought of as symptoms of our ongoing attempt to numb painful experiences. Perhaps one of the most painful and globally-widespread experiences today is the realization that climate change is real, that humans have largely contributed to it, and that many experts say that we have less than a few decades to reverse our behavior before even more dire consequences result. When people believe that they are powerless to do anything about this situation, as many do, the numbing can become even more profound. Not all depression and anxiety of course is related to A&B. However, symptoms of depression and anxiety that are related to climate change or other GSTs can be thought of as warning signals from our own human body-mind-spirit, that there is something we need to address, both within ourselves and in the world we live in.

Although the psychological is especially thought of today as having to do with mental activity, humans of course are also emotional beings. Emotions are sometimes understood to be reactions to what the mind thinks, and thus secondary to thought; another perspective is that emotions are primary movers and can drive thought. We do not have enough space in this chapter to further examine this debate, but we can point out that emotions are an important part of the EBPSS nature of a human being.

Healing the psychological dimension means in part that we individually and collectively recognize and address the symptoms that we suffer from as we watch the quality of our living environments steadily decline.

The Sociological Dimension

Most of us are aware of inequities of distribution of wealth and power in our world. Fewer are aware of how different human populations are involved in and affected by destruction of our A&B.

There are in fact significant social justice issues. For example, about 102,000 people currently die annually from human caused fine particulate matter, and People of Color are disproportionately exposed to such pollution and become sick and die more often because of it (Thompson, 2019). In the short term, the physical and emotional costs of GSTs are felt most by the poor and disempowered, who are often most-exposed to changing conditions; in the long term, these costs will be increasing paid by all of our descendants (Shiva, 2015). There will be an estimated 200 million climate refugees by 2050 and the poorest countries, with the exception of Australia, will warm the most (Wallace-Wells, 2019). Costs to more developed nations are not negligible either however; for example extreme weather events cost the United States about 400 billion\$ from 2015 to 2018 (U.S. Global Change Research Program, 2018).

Paralleling our concerns about human diversity is the severe loss of biodiversity in other life forms. About 600 species have gone extinct over the past 250 years because of human activity. Although other life forms are being impacted the most at this point in history, the well-being and existence of human life will be increasingly threatened (Vaughan, 2019).

Sustainability can thus be framed as a social justice issue. The practice of supporting the wellbeing of A&B can be framed as an expression of an "Earth democracy" that includes for example, food democracy (questioning chemicals and genetic engineering) and water democracy (looking at who owns the water) (Shiva, 2015).

Healing of the social dimension begins when we become aware of who is most responsible for destruction of our A&B, and of who (including human populations and other life forms) are most vulnerable to the impact of this destruction.

The Spiritual Dimension

There is arguably a similarity between the way I treat myself, the way I treat other people and the way I treat the A&B in my life. This concept has been recognized by teachers in most of the world's wisdom traditions (Krishnamurti, 2019). For example, from the point of view of a number of religions, consumerism reinforces waste and a false identity based on possessions, promotes harm to A&B, and encourages attachment to materialism (Kaza, 2019).

The dimension of spirituality is not the same as religiosity. Whereas religiosity can be understood as a *social* dimension of human life involving shared rituals, beliefs, and doctrines; spirituality is usually defined as an *individual* dimension of human life involving the person's own search for meaning, purpose, and connectedness. An individual can see themselves as both spiritual and religious, as neither, or as one without the other. Spirituality has become increasingly important in the United States as a 75% majority now see themselves as spiritual, and as a rising number also see themselves as spiritual but not religious (Lipka and Gecewicz, 2017).

Not only do most of us live in our heads, as discussed above, we also typically identify with our thoughts. What does that mean? When I identify with my thoughts, I believe that I am my thoughts and my thoughts are me.

Such identification can be thought of as a function of the ego. The ego is the unexamined (usually unconscious) human mind that identifies with any form, especially mental forms, or beliefs. From a spiritual perspective, ego-identification is a primary cause of disconnection from myself, from other people, and from A&B. This is largely because the ego tends to see itself as special and separate, from other people, other life forms, and from the Universe that is our home (e.g., Tolle, 2005). The healing of ego requires consciousness; consciousness of ego is reverent (friendly) awareness of the power of ego in the present moment.

From a spiritual perspective, when we identify with our own species, we also hold conscious or unconscious negative biases towards other life forms. In a similar way, when human beings identify with nationality, religiosity, or other groupings; such identifications are often exclusive, in that people who are not members are viewed negatively. When people become conscious of their identifications, the power of the identifications tend to decrease. It may be quite possible, for example, to be a patriot and not hate people who live in other countries. Similarly, it might be possible to love humanity, without identifying so much with our species that we view all other life forms as inferior and expendable.

Thus, healing in the spiritual dimension involves consciousness of the ego's identification process, especially identification with beliefs.

Assessing Individuals and Communities with the Ecobiopsychosocialspiritual Approach

The ecology theorist and the mental health practitioner can use the EBPSS approach to understand and assess human behavior towards A&B, and to also assess the impact of those ecosystems on the well-being of individuals and human populations.

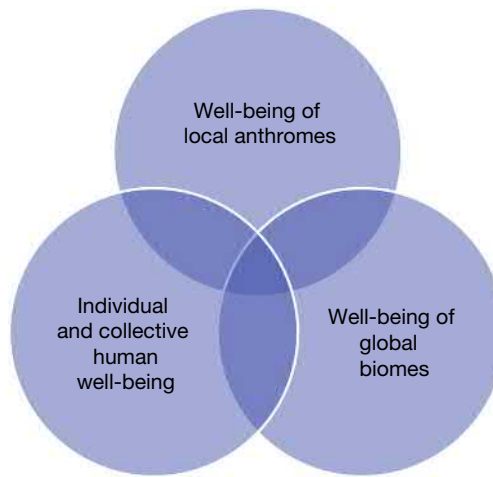


Fig. 3 Interconnected well-being.

From the EBPSS perspective, the well-being of humans is interconnected with the well-being of the A&B we live with. This idea is illustrated in **Fig. 3**. Individual and collective human well-being includes healthy development in all the EBPSS dimensions. Well-being of local anthromes and global biomes is also complex and includes the health of all the living things and of the ecosystems that support all life.

The basic assessment method is to examine each of the five dimensions of EBPSS in the individual and the community we are working with, and look for evidence of biophilia. Biophilia is a term created by [Wilson \(1986\)](#) to describe his theory that humans have a natural affiliation, or connection, with all life, similar to ideas advanced by [Tolle \(2005\)](#) and many other authors writing about the world's great wisdom traditions. The concept of biophilia can be expanded to include all the EBPSS dimensions; in other words, there is ecological, biological, psychological, social, and spiritual biophilia.

Biophilia can be assessed at all dimensions of human development. Biophilia is expressed on the ecological level, for example, when people in a community recognize and advocate for the well-being of the eco-systems they live in or near. One way biological biophilia can be recognized is by examining the awareness people have about how their physical health is connected with the quality of the air they breathe and the water they drink. On the psychological level of biophilia, awareness is directed towards the emotional and cognitive symptoms that are associated with ecological conditions and with the level of commitment to stewardship of A&B. Social justice is an indicator of sociological biophilia; and communities are assessed by the extent to which minoritized populations have access to healthy environmental conditions and resources. Finally, an example of spiritual biophilia is the extent to which our connection with nature is recognized and expressed in local faith communities and other spiritual groups.

When assessing the well-being of an individual; a healthy, whole person is understood to be aware of each of her five dimensions and can express those dimensions effectively and nonviolently. We can define empowerment as this ability to both be aware of and express ourselves in all our dimensions. Healthier people tend to recognize their connection with A&B; more empowered people tend to act to protect and enhance the well-being of A&B.

Case Study A: Assessment

For example, in case study "A" we select a 30 year old woman living in a city in the Midwest, USA. She reports to the social worker that she has been moderately depressed and anxious, with no suicidal ideation, for as long as she can remember. She reports that she lives alone, works full time for a dentist's office, and feels little connection with other people or the anthromes she interacts with. When she was a child she lived in the suburbs with her mother, and they seldom went outdoors. She is unhappy with the way her body looks, and frequently goes on diets that all ultimately fail to help her lose weight.

On the collective (macro) level, the Ecological theorist may want to understand why people in this city continue to vote down proposals to build more sustainable power sources, expand alternative low-energy transportation networks, purchase more urban green spaces, establish tighter emission controls, and regulate pollution into local streams and lakes. The community mental health practitioner may also want to understand how much of the depression and anxiety seen in people living in this urban anthrome is connected with the well-being (e.g., air quality, extent of green space, commuting times, population density, etc.) of the anthrome. Both quantitative and qualitative surveys may provide useful data that helps answer these kinds of questions.

On an individual (micro-mezzo) level, the mental health practitioner may want to assess how much of this young woman's depression and anxiety is related to the deteriorating conditions of her local urban anthrome and global biomes. Such an assessment may have to be largely based upon self-report by the woman during a clinical interview.

Several other ways to assess the possible correlations between anthrome and biome well-being and human well-being include (1) observing what happens when people empower themselves to try to improve their own well-being and the well-being of their

local anthromes and regional biomes, rather than feeling numb and helpless and (2) exposing people to healthier environments and measure any changes in their well-being. The social worker could use both of these strategies in her ongoing assessment of this woman.

Intervening with Individuals and Communities with the Ecobiopsychosocialspiritual Approach

Is it possible to help people empower themselves to transform their relationships with their local anthromes and global biomes? Since current attitudes and behaviors regarding other life and ecosystems appear to be largely learned over the millennia of human civilization, it seems reasonable to assume that these dysfunctional learnings can also be unlearned, and replaced with healthier attitudes and beliefs. Because of the rapid intensification of Global Survival Threats (GSTs) today, such as climate change and preparations for war, such relearning may need to take place relatively quickly, over decades rather than over millennia, and thus effective individual and collective interventions are required.

Multi-dimensional interventions are available on both the micro/mezzo (individual, family, small group) and mezzo (local and global community) levels. Some of these are summarized in Fig. 4. This table organizes interventions along three levels of analysis; (1) micro, mezzo, and macro; (2) indoor and outdoor activities; and (3) EBPSS dimensions. The most effective intervention strategy is viewed as inclusive; in as much as it includes interventions drawn from all of these three levels of analysis. Ecologists and mental health practitioners can partner in developing and utilizing a broad array of interventions that address not only all of the EBPSS dimensions, but also the micro, mezzo, and macro levels of humanity. Brief descriptions of the interventions in Fig. 4 are offered below. The EBPSS approach is not designed to replace more conventional and currently popular approaches to psychotherapy, but is rather designed to be added to such approaches.

Indoor Micro and Mezzo Interventions

Animal assisted therapy helps connect people with their own bodies and with nature, often through interactions with such often human-friendly animals as dogs, cats, and horses. Cognitive-Behavioral work can help people change their beliefs systems about and behaviors towards A&B. Social workers can also use guided visualizations and artistic expressions (such as drawing, music, and dance) to help people examine and express their feelings about life and the ecosystems that support life.

Environmental dialogues are structured conversations on ecological topics. Guidelines for dialogue are utilized in these conversations, and topics might include such controversial issues as urban air pollution regulations, creation of new national monuments, and decisions about energy extraction on public lands. Consumer strategies give people an opportunity to empower themselves to become agents for change by using their purchasing power to, for example, reduce plastic pollution and encourage alternative energy and farming approaches. Finally Transpersonal therapy can help people explore the relationship between their spirituality and the well-being of A&B, and ego-identification work can help us become conscious of our biases about other living things and the ecosystems that support all life.

Outdoor Micro and Mezzo Interventions

Outdoor retreats can be shared experiences for community members who want, for example, to change local attitudes and public policies towards their local anthromes, and such events can target different neighborhoods, age groups, or other populations.

Location	Micro-mezzo levels	Macro level
Indoors	Animal assisted therapy (Bio) Cognitive-Behavioral work (Psych) Guided visualizations (Psych) Artistic expressions (Psych) Environmental dialogue (Soc) Consumer strategies (Soc) Transpersonal therapy (Spir) Ego-identification work (Spir)	Education for children, youth, adults (Eco) Indoor Environmental Quality (Eco) Advocacy for clean air and water (Eco) Population control initiatives (Eco) Voter organization (Soc) Lobbying (Soc) Community dialogues (Soc) Environmental justice work (Soc)
Outdoors	Outdoor retreat (Eco) Identifying sacred landscapes (Eco) Nature walk (Eco) Equine therapy (Bio) Home gardening (Bio) Vision quest (Spir)	Urban planning and architecture (Eco) Community environment projects (Eco) Re-wilding projects (Eco) Outdoor service-learning sites (Eco) Holistic/organic agriculture (Bio) Community gardening (Bio)

Fig. 4 Examples of ecobiopsychosocial approaches in social work practice. Adopted from Derezotes, D. S. (2016). *Ecopsychology: Adding “eco” to the biopsychosocialspiritual perspective*. In Turner, F.J. (Ed.) *Social work treatment: Interlocking theoretical approaches*, 6th edn. Oxford: Oxford University Press.

Individuals can also reconnect with nature by identifying the landscapes that are sacred to them, such as a particular mountain location, river valley, or forest grove and then by visiting these locations. Nature is often a wonderful healing force for people, and nature walks and equine therapy (which could involve simply riding a horse on a trail) are two examples of ways to involve people in natural settings. Interactions with plants can also be healing, and people can become involved in raising their own vegetables and fruits, even in intense urban environments. Finally, a vision quest is usually a solo time spent camping outdoors, during which the individual practices rituals that are spiritually meaningful to her.

Indoor Macro Level Interventions

Ecology and mental health curricula for children, youth, and adults can become required content in public and private school settings. Such content can be both informational (e.g., include climate change data) and self-reflectional (e.g., include exercises designed to encourage self-awareness of connection with nature). Both students and employees can be given opportunities to participate in evaluating and modifying Indoor Environmental Quality as well as to advocate for local clean air and water. Dialogues on, for example, population control initiatives can also be held for community members, during which participants listen to the ideas and concerns of others.

Both students and other community members can be given opportunities to participate in voter organization efforts, during which “Green” (see Wall, 2010) issues are discussed and voted upon. Later, participants can help with lobbying efforts in local, state, and federal settings, in favor of agreed upon issues. Additional community dialogues can be held on a number of Green issues, where people of different political persuasions agree to meet, speak respectfully, and listen for understanding. Finally, community efforts can include environmental justice work, in which people focus upon understanding and changing environmental injustices, such as for example, the plight of local children of poor families who are especially exposed to noisy polluted streets.

Outdoor Macro Level Interventions

Institutions and communities can support Green urban planning and architecture, by implementing new policies, guidelines, and funding opportunities. For example, clean alternative energy projects can be supported financially, rather than penalized, and non-polluting transportation options such as bicycle commuting can be supported through construction of safe community bike lanes and tax incentives.

Communities can also participate in re-wilding projects, in which people help re-create land and water areas where natural living systems can restore themselves. Outdoor service-learning sites can be established in various more-natural areas, where students and others can visit and learn more about the local A&B.

Finally, holistic/organic/regenerative agriculture projects can be developed where local people can volunteer or work to support the production of local healthy food. Within urban areas, community gardening projects give people an opportunity to not only grow their own healthy food, but also to meet other people with similar interests.

Case Study A: Intervention

In follow-up to these brief introductions to these interventions above, we can continue looking at our case study “A” that we began to look at earlier in this chapter. We can now address EBPSS interventions that might be used with the depressed young woman and her community in a city in the Midwest, USA.

The mental health social work practitioner might assess that the young woman has little connection with A&B on any of the EBPSS levels, and that this disconnection is probably a factor related to her depression and anxiety, along with such other factors as her past trauma, relationships, vocational issues, etc. The client’s strongest connection is in the cognitive (psychological) level, because she has above average intellectual intelligence, and understands intellectually, if not emotionally yet, that she is disconnected from her world. The social worker plans to first build on the client’s intellectual strength as she strives to help the client reconnect with her own body, with other people, and with the environment she lives in.

The social worker, or other professional helper, begins by engaging with the woman and forming a helping relationship. She might intervene first by helping the client understand intellectually, and perhaps later also feel, how disconnected she is with her own body, with other people, and with the environments she lives in. She might ask the client if she would like to experience a reconnection with her own body, with other living things, and with the ecosystems that support all life.

The social worker tries to find interventions that fit with the client’s strengths, interests, and cultural context. Since this client is creative and artistic, they agree that she will keep a journal in which she will do some writing and drawings of her experiences. Since the client is especially interested in going outside on a solo experience and has expressed interest in spirituality, they also agree that she will go a vision quest for a night by herself in the closest and safest biome area that is available to her, and do a journal of her experience.

The social worker realizes that the client’s depression and anxiety is not only related to climate change and disconnection with her own body-mind-spirit. She thus also conducts more traditional interventions that help the client address past trauma, current relationships, and work satisfaction, for example.

The social worker, in addition to doing psychotherapy, is also a community organizer and activist. She belongs to a group of local activists that includes ecologists who teach at the local university, students, and other community members. They call

themselves the “Green Giants” and they meet regularly to support each other, identify local and regional issues, and plan responses. Since they realize that a small group of activists cannot take on every issue, they decide to focus this year on the deterioration of the local water and air quality. They start out by hosting a water and air dialogue in a small town 50 miles from the city center, and they invite local farmers and ranchers, city dwellers, and students. They begin the dialogue by setting out guidelines for conversation, especially emphasizing the importance of listening for understanding and speaking respectfully. The conversation is well-attended, and although there is not an agreement on all topics, new relationships are initiated which can lead to further local cooperation around issues that matter to everyone.

Conclusion

In conclusion, the largely human-caused conditions that now threaten the well-being of our A&B also threaten the well-being of all humans on the planet. As these conditions become increasingly serious, we are now seeing a growing recognition that this threat is real, by increasing majorities of people, across cultures, nationalities, and religiosities. This global crisis is thus also becoming an opportunity for global transformation.

In this chapter we looked at how human beings have lost connection with our own bodies, our fellow human beings, other living things, and the ecosystems that support all lives. We examined how this disconnection is related to physical, psychological, and spiritual symptoms that also call to us for recognition and action.

We looked at ways that ecologists and mental health practitioners can work together with multidisciplinary teams to understand and address the root causes of human contributions to the global survival threat of increasing deterioration of our local and global anthromes and biomes.

We offered what we are calling an ecobiopsychosocialspiritual approach to addressing this threat, that starts with the recognition of our own human multidimensionality, of body, mind, and spirit, and that expands upon the idea of biophilia to include the five interrelated EBPSS dimensions. We created a beginning practice model for assessment and intervention across the micro, mezzo, and macro levels of change. We suggest that practitioners and policy makers utilize interventions from all the levels and dimensions, in our efforts to help people transform how we think about and behave towards our A&B.

Much more research can be done to better understand the interconnections between anthrome, biome, and human well-being, and to test the efficacy of the interventions we have looked at, but we already know enough to begin to do more today, to educate, intervene, and transform ourselves and our communities. The well-being of life on our planet is at stake.

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To Explain Behavior Change We Need to Research All Stages of This Process: Where Environmental Psychology Needs to Connect the Dots

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Abstract

Promoting voluntary behavior change is a central research topic in environmental psychology. Thus one would expect to find a huge body of research analyzing the dynamic nature of voluntary behavior change processes as well as their psycho-social drivers. However, reading the existing literature with this expectation is quite disappointing: It is still dominated by cross-sectional studies using psycho-social constructs derived from a limited number of theoretical frameworks to predict behavioral intentions. Thus the central assumption underlying our article is that environmental psychology urgently needs two things: (1) More research analyzing the actual course of behavioral change processes, and (2) newer and more diverse theoretical perspectives for explaining the different stages of behavioral change processes. For this purpose the article systematically adopts in a first step results of health psychology: Here a similar discussion resulted in the identification of five overarching themes representing theoretical explanations for different stages of behavioral change processes: motives, self-regulation, resources, habits, and environmental/social influences. In a second step we present the stage model of self-regulated behavior change (SSBC) as an example for a theoretical framework which integrates different theoretical themes into one testable model. In a third step we summarize the already existing research testing hypotheses derived from the SSBC.

Introduction

Most environmental psychologists view understanding the psychological processes of voluntary behavioral change as a central task of their subdiscipline. Thus one would expect to find a lot of theoretical and empirical work on the phenomenon of how people actually change their behavior. For example, the process displayed by Fig. 1 suggests how the change of a specific behavior might proceed.

The graph describes a fictive person's behavioral change process from the habit to use the car for commuting by bike over a time period of 20 weeks. The grey line indicates the intensity of car use for commuting, the black line the intensity of bike use for commuting. Whereas from week 1–5 the person shows a stable preference for using the car, in week 6 one can observe the initiation of a sudden and drastic behavioral change: Within a few days the previously high car use decreases drastically, whereas the previously low cycling frequency increases drastically. This observable behavioral change is probably the consequence of a longer preceding mental process leading to a fundamental re-evaluation of the two behavioral alternatives 'commuting by car' vs. 'commuting by bike.' For this reason, understanding the mental process which leads to the re-evaluation of competing behavior alternatives is the first central research interest of environmental psychology.

After the initiation in week 7–10 commuting by bike becomes the dominant behavior (area A in Fig. 1). But in week 11 obviously something happens (e.g., longer period of bad weather, illness, work overload, stress within the family) which causes car use to become the person's dominant behavior (area B in Fig. 1) again. Such lapses are typical for behavioral change processes. However, in the present case the person can activate factors and processes which help him or her to overcome this 'crisis' and to install cycling again as dominant behavior for commuting. For this reason, understanding which factors cause these 'crises' and which factors and processes help to reestablish the new behavior after a relapse is a second central research interest of environmental psychology.

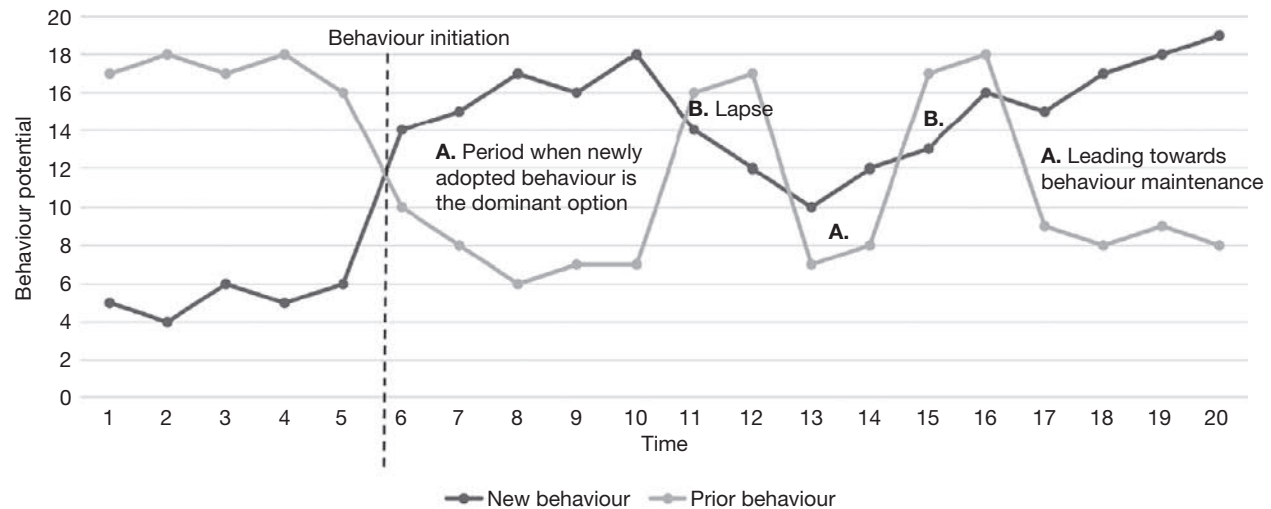


Fig. 1 Dynamic and stages of voluntary a behavior change process. From Kwasnicka, D., Dombrowski, S.U., White, M., and Sniehotta, F. (2016). Theoretical explanations for maintenance of behaviour change: A systematic review of behaviour theories. *Health Psychology Review*, **10**(3), 277–296.

From week 16–20 the person shows a stable preference for cycling which indicates that cycling is likely to be maintained as the dominant behavioral response over a longer time period. For this reason, analyzing the psycho-social factors and processes which influence the long-term maintenance of behavioral change is a central third research interest of environmental psychology. In summary, researching the psycho-social factors and processes underlying behavioral change with the psychological re-evaluation and the successful initiation of behavior, successfully overcoming relapse and maintenance of new behavior are central research interests of environmental psychology.

Aim of the Present Article

The aim of the present article is to review and summarize theoretical approaches and empirical results to answer the three fundamental questions from the previous section. This means investigating the nature of voluntary behavioral change processes in all facets from initiation over successfully overcoming relapses to long-term maintenance. The idea is that empirically supported answers to these questions can provide a good starting point to develop effective interventions which support behavioral change.

A Disappointment

However, approaching the literature with the expectation to find a huge body of research papers discussing and explaining behavioral change processes is disappointing. The field is still dominated by cross-sectional papers applying static predictor models to explain self-reported behavioral change intentions. There are some important papers providing meta-analytical summaries of the effectiveness of behavioral change techniques (e.g., Abrahamse et al., 2005; Osbaldeston and Schott, 2012; Lokhorst et al., 2013; Abrahamse and Steg, 2013). But still, these papers only analyze the (mostly short-time) behavioral effects of intervention techniques without referencing theoretical models of the underlying behavioral change process. We found only one study (Klößner, 2014) which uses a model of behavioral change and analyses the temporal dynamic of the decision-making process to purchase an e-car across 90 days.

Behavioral Change Research Within Health Psychology

Because ending our article here would be a frustrating and less constructive contribution, we looked into the literature of another psychological subdiscipline—health psychology—to find more systematic research on behavioral change processes. Indeed, in the last decades health psychology has invested considerable effort to systematically investigate how to design effective, theory-based behavioral change interventions. For the purpose of our article a systematic literature review conducted by Kwasnicka et al. (2016) provides a good overview which theoretical perspectives may be stimulating for further environmental psychological research. With a systematic data-base search Kwasnicka et al. (2016) identified 100 theories which include factors or processes helpful for describing and understanding the dynamic processes underlying different stages of behavior change. The authors used an elaborated synthesis approach and clustered the 100 theories into five overarching, interconnected themes: Motives, self-regulation, habits,

resources and contextual factors. We are convinced that systematically reviewing these theoretical themes may be stimulating to further develop the behavioral change research within environmental psychology. For this reason the next five sections provide a brief summary of the five theoretically influential themes identified by Kwasnicka et al. (2016).

Theme 1: Motives for Initiating and Maintaining Behavioral Change

Motives are central drivers of the initiation as well as maintenance of voluntary behavioral change: They help establishing priorities and allocating material and psychological resources. Whereas behavior change is often initiated to avoid negative long-term consequences (e.g., stopping ongoing climate change, norm activation model—Schwartz, 1977), the motives to maintain the new pro-environmental behavior are often different from these initiating ones. Motives are particularly facilitating for maintenance if they enable regular gratification from enacting the new behavior: This includes enjoying to do the behavior as such, or enjoying the immediate outcomes of the behavior (theory of planned behavior—Ajzen, 1991). Furthermore, whereas the initiation of behavioral change is often extrinsically motivated, for the maintenance of new behavior intrinsic motivation has to replace extrinsic motivation (i.e., the individual wants to maintain the new behavior itself, self-determination theory—Deci and Ryan, 2000). Especially intrinsically motivating is the perception that the new behavior is in line with central beliefs a person has about him- or herself (self-identity; self-schema theory—Markus, 1977; Van der Werff et al., 2013). Of course self-identity and nested beliefs and values can change as a result of engaging with a new behavior. Such changes in identity positively enhance behavior change maintenance. For instance, a person who cycles to work regularly can develop the self-representation of being an environmentally responsible person. Having a new self-representation of being environmentally responsible, makes it more likely to cycle to work in the future too.

Theme 2. Self-Regulation

Self-regulation includes the processes of self-monitoring, self-evaluation and self-reinforcement as well as dealing with temptations, and hedonistic and impulsive influences that are in conflict with the goals behind behavioral change (Baumeister et al., 1994). Individuals differ in their skill to deal with these situations. In other words, they have a different 'self-regulatory capacity' (temporal self-regulation theory—Hall and Fong, 2007). These differences in self-regulatory capacity are hypothesized to reflect executive control functions (e.g., planning skill, inhibition control, task switching) and they explain the ability to override automated behavioral responses (Nederkooym et al., 2010).

Analyzing the behavior change process with the perspective of active self-regulation it becomes apparent that self-regulation decreases over time: Individuals initiate behavior change when the moment is right, e.g., at times when opportunity costs and goal conflicts are low and motivation and capacity high. However, after initiating behavioral change they are confronted with context-specific cues, changes in options and opportunity costs or varying levels of motivation. These factors may increase the risk of behavioral relapses. In response to situations with a high risk of relapse, individuals may apply effective coping responses. As a result of their self-efficacy they expect more positive outcomes and the probability of future relapse decreases (relapse prevention theory—Marlatt and George, 1984). Nevertheless, individuals may fail to apply effective coping responses in high risk situations. As a result their self-efficacy and positive outcome expectancies decrease. As a consequence individuals often return to their prior behavior and their probability of future relapses increases (Marlatt and George, 1984).

Theme 3. Habits

Dual process models of behavior assume that behavior is governed by the interplay of two regulatory systems: a reflective system, which is based on conscious deliberation, controlled but effortful, and a quicker automatic system that controls habits and impulses (dual-system models—Strack and Deutsch, 2004). To maintain new behavior individuals can do so through ongoing self-regulation via the reflective system. However, self-regulation draws on finite cognitive resources which can be depleted. When cognitive resources are low the 'costly' self-regulation is likely to fail. Thus, the most promising mechanism to maintain a newly adopted behavior is to perform it in a habitual way.

Habits are behavior that has become automated and is triggered by situational cues (Lally et al., 2010; Verplanken and Wood, 2006). They develop over time with repetition and are theorized to be performed outside of conscious awareness (Hofmann et al., 2008; Verplanken and Aarts, 1999). With that said, when trying to create new habits one should not forget the power of 'old' habits. The stronger prior habits are, the more likely an individual is to relapse to the prior behavior. Removing situational cues that may trigger previous behavior therefore can support the maintenance of behavior change with the help of stimulus control (transtheoretical model of change—Prochaska and DiClemente, 1983). In brief, the processes of breaking old habits and developing new ones are likely to act in conjunction for behavior change maintenance.

Theme 4. Resources

Resources are understood as psychological and physical assets that can support the process of behavioral regulation. As maintaining a new behavior is often difficult and requires sustained efforts, resources, which an individual can use in the process, are hypothesized to play an important role. For example, when cognitive resources are limited or depleted due to stress, tiredness, exhaustion and intoxication, an individual's self-regulatory capacity is minimal. Individuals are more likely to initiate behavior change at times when their psychological and physical resources are plentiful and when opportunity costs (effort needed to enact behavior) are low (i.e., resources are not immediately needed for competing demands). Lapse and relapse are thus, associated with low levels of resources.

The dual process models offer an explanation how resources impact behavior change processes. It is hypothesized that resources act as moderators (boundary conditions) on which system generates a behavioral response: Are there enough resources for the resource intensive reflective system or only enough for the resource sparing impulsive system (impulsive versus reflective framework—Hofmann et al., 2008; dual-system models—Strack and Deutsch, 2004)? In short, when cognitive resources are limited effective maintenance of behavior occurs mainly when the behavior is habitually instigated.

Theme 5. Environment and Social Influences

The final theme includes features of the social and environmental context of action. This theme includes aspects of the choice architecture that alter the opportunity costs and accessibility of behavioral options (Thaler and Sunstein, 2009). Many theories emphasize the role of a supportive external environment on behavior change processes. For example, habit theories (Hofmann et al., 2008; Verplanken and Aarts, 1999), hypothesize that environmental cues related to prior and newly adopted behaviors explain whether or not a newly adopted behavior is maintained. A supportive environment facilitates behavior change as it lowers the opportunity costs of the new behavior (with e.g. providing available options, setting incentives and disincentives and influencing opportunity costs and cues). Environmental factors determine the amount of active self-regulation and resource required by the individual. Thus, behavior change is less likely to be maintained in environments which are not conducive of the newly adopted behavior (Mackenbach et al., 2014).

Like environmental factors, social influence affects the choice architecture too. This means that the opportunity costs and incentive structure for behavioral options in a given context is influenced by social interactions too. For example, knowledge and skills can be acquired through social modeling (social cognitive theory—Bandura, 1986). Individuals may follow the guidance of people they trust and they feel connected to (Bandura, 1986). In short, the social influence of peers also impacts one's own maintenance of behavior change. Table 1 again summarizes the five theoretical themes and why they are important for understanding voluntary behavior change.

Table 1 Theoretical themes relevant for the behavioral change process.

Themes	Brief theoretical explanation	Theories included (examples)
(1) Motives	The motive to avoid negative long-term consequences is important for initiating behavioral change. People tend to maintain their new behavior if they have at least one sustained maintenance motive, i.e., they are satisfied with behavioral outcomes, they enjoy engaging in the behavior; if behavior is congruent with their identity, beliefs and values	Norm activation theory (Schwartz, 1977) Theory of planned behavior (Ajzen, 1991) Self-determination theory (Deci and Ryan, 2000) Ecological self-identity (Van der Werff et al., 2013)
(2) Self-regulation	People tend to maintain behavior if they successfully monitor and regulate the newly adopted behavior and have effective strategies to overcome barriers to the performance of the new behavior	Self-regulation theory (Baumeister et al., 1994) Relapse prevention theory (Marlatt and George, 1984) Dual process model of self-control (Hofmann et al., 2008)
(3) Resources	People are successful in initiating and maintaining behavioral change if their psychological and physical resources are plentiful	Reflective and impulsive model (Strack and Deutsch, 2004) Self-control theory (Baumeister, 2002)
(4) Habit	Strong old habits are a central barrier for initiating behavioral change, creating new habit facilitates the maintenance of the new behavior	Habit theory (Verplanken and Aarts, 1999; Verplanken et al., 2008)
(5) Environmental and social influences	A supportive environment and social support are important for initiating and maintaining behavioral change	Social cognitive/learning theory (Bandura, 1986)

Adapted from Kwasnicka, D., Dombrowski, S.U., White, M., and Snihotta, F. (2016). Theoretical explanations for maintenance of behaviour change: A systematic review of behaviour theories. *Health Psychology Review*, 10(3), 277–296.

Stage Models of Behavioral Change as Integrative Conceptual Frameworks

The presented theory themes identified by Kwasnicka et al. (2016) provide a multitude of factors and processes which are potentially relevant to understand behavioral change processes. However, systematic empirical research on behavioral change processes needs an integrative conceptual framework to provide a general understanding of the dynamic and structure of the behavioral change process. Such a conceptual framework is also necessary to systematically derive and empirically test research hypotheses about the behavioral change processes. So-called stage models of behavioral change are becoming increasingly popular as integrative conceptual frameworks of behavioral change processes. Stage models of behavioral change were introduced by Lewin (1952) who stressed the temporal dimension of behavioral change and considered it a process rather than an event. More precisely, he describes behavioral change as a transition through three stages, which he called unfreezing, moving, and refreezing. The transtheoretical model (TTM; Prochaska and DiClemente, 1983) presents an updated version of this idea. The TTM also characterizes behavioral change as a transition through qualitatively distinct stages and additionally formulates that people face stage-specific hindrances. To overcome these, people need stage-specific skills and strategies. The TTM describes the following five stages of change: precontemplation; contemplation; preparation, action, and maintenance. Further the TTM assumes that in most cases behavioral change is not a linear but a cyclical process. Barriers and resistances can keep people fixated at an early stage of change for a long period of time. Frequently, they relapse back to the beginning of the process.

In the literature the TTM has been criticized as a descriptive model that does not provide a convincing theoretical rationale for the postulated five stages as well as the processes triggering stage transition (e.g. West, 2005). The stage model of self-regulated behavioral change (SSBC) developed by Bamberg (2013a,b, see also Klöckner, 2015) provides such a theoretical rationale. For this purpose, the SSBC combines assumptions from the TTM, the model of action phases (Gollwitzer, 1990), the theory of planned behavior (Ajzen, 1991), and the norm activation theory (Schwartz, 1977). The main assumption of the SSBC is that people can change even strongly habitualized behavior, if they are motivated to do so. The SSBC describes this process from abstract motivation to concrete behavior as a series of four stages: (a) predecision stage, (b) preaction stage, (c) action stage, and (d) postaction stage (see Fig. 2).

According to the SSBC, successful behavioral change follows these four stages but setbacks and repetitions may occur between stages. Each stage has its specific challenge, and transitioning from one stage to the next means to cross a threshold of setting a specific intention. First, in the predecision stage, the individual addresses the question why behavioral change is necessary. Drawing upon the example of voluntarily reducing car use, the question in this stage is: "Why is it important to reduce my car use?" The individual has to form a general goal-intention to take action: "In the next few weeks, I intend to reduce my car use". The SSBC predicts, that this intention is influenced by an activated personal norm to reduce car use. This personal norm is defined as a feeling of moral obligation to act. It is triggered by becoming aware of negative consequences of one's behavior (e.g. negative consequences of my car use for the environment and quality of urban life), ascribing responsibility for these consequences to oneself, and the presence of social norms that one is socially expected to reduce car use (e.g. social pressure or support to reduce my car use). The variables and mechanisms determining the goal-intention are derived from the norm activation theory (Schwartz, 1977).

Once the general goal-intention of reducing car use has been set, the individual proceeds to the preaction stage. Before the background of the now existing general car use reduction goal intention, in this second stage of the behavioral change process the relevant question is: "Which action should I take to reduce my car use?" For this purpose the person evaluates his or her attitude towards different alternatives such as walking, using public transportation, cycling, and how easy he or she perceives the implementation of these alternatives (perceived behavioral control, PBC). Attitude and PBC are two constructs taken from the theory of planned behavior (Ajzen, 1991) and they pave the way to the next threshold: developing a behavioral intention.

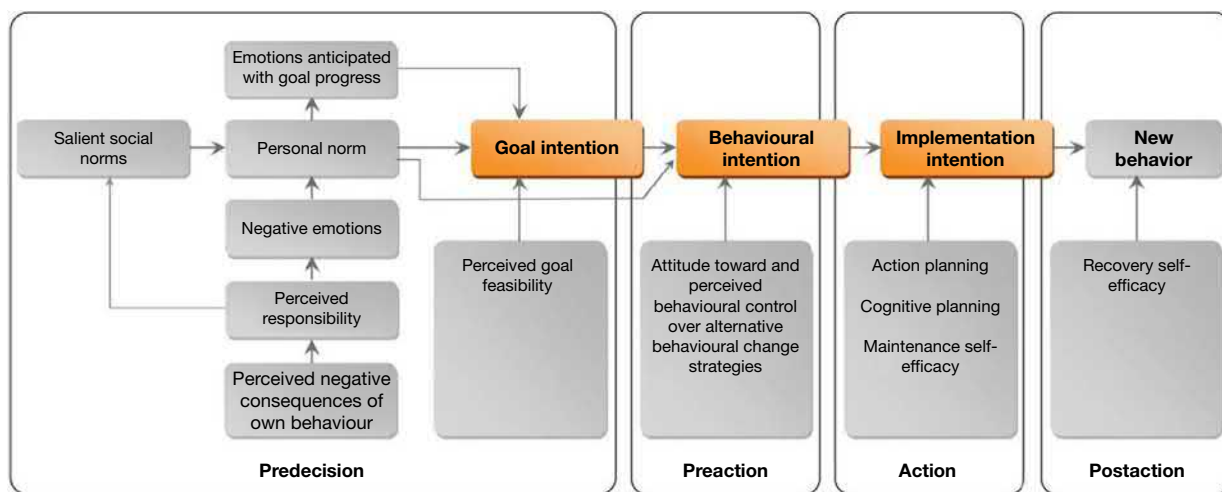


Fig. 2 The stage model of self-regulated behavioral change (SSBC, Bamberg, 2013a).

Here, the person picks a behavior with the best attitude-difficulty-balance for him or herself. Forming this behavioral intention (e.g., “In the next few weeks, I intend on using my bicycle instead of my car to commute to work”) marks the transition from the preaction to the action stage. In this third stage of the behavioral change process the implementation of the chosen behavior needs to be planned. The obstacle to address is: “How do I implement my intended behavioral change?” The ability to plan and remove barriers is the main driving force during this stage. The transition to the last stage is indicated by forming an implementation intention, e.g.: “Tomorrow morning at 7 a.m., I intend to use the Victoria Road for cycling to my company’s building”. In this fourth postaction stage behavioral changes need to be stabilized, and relapses to old behavior have to be dealt with. The ability to recover from a relapse is the main predictor to stabilize a new behavior and to make it a new habit.

Altogether, the model assumes that the transition through the four stages is marked by three critical transition points. Each reflects the successful solution of stage-specific tasks: to form a goal intention, a behavioral intention, and an implementation intention. The greatest strength of the SSBC lies in its detailed description of the task a person has to solve in each of the four stages as well as the specific cognitive ‘mindset’ people need to adopt for solving them.

Implications for Interventions

The ultimate goal of the SSBC is to provide a conceptual framework to systematically develop interventions which support voluntary behavioral change. One practical implication of considering behavioral change as a transition process through different stages is that instead of thinking of one single intervention for all, specific intervention packages have to be developed for meeting the needs and barriers of a specific stage. For instance, interventions targeting people at the predecision stage are more likely to be successful if they concentrate on providing information that can increase both problem awareness and perceived personal responsibility. Also, interventions which activate social and personal norms are likely to be important in this stage. Second, individuals who have set a goal-intention need information concerning the availability and the pros and cons of different behavioral alternatives. Third, individuals who intend on switching to an alternative behavior probably benefit most from interventions supporting the implementation and initiation of this intention, e.g. detailed behavioral planning. Fourth, individuals who already implemented a new behavior profit from intentions which decrease the temptation to relapse. Table 2 presents an overview of stage specific intervention strategies.

Results of Empirical Test of Hypotheses Derived From the SSBC

Valid and reliable measurement instruments are a prerequisite for empirically testing hypotheses derived from the SSBC. In the meantime for all SSBC constructs such measures have been developed and tested in different behavioral contexts (e.g., Bamberg, 2013a,b; Klöckner, 2014). As an example Table 3 presents a short instrument for assessing a person’s current stage of change.

Bamberg (2013a) provides first correlational evidence for the SSBC’s assumptions with regard to the relationships between the various constructs integrated in the model. Klöckner (2014) examined central SSBC premises by studying the decision-making process when purchasing e-cars. For this purpose, 90 participants completed measures of the SSBC constructs 30 times over a period of 60 days. This design allowed for directly testing the chronological dynamics of behavior change processes. Klöckner’s results supported the following SSBC assumptions: (1) In 85% of all transitions observed, participants moved a single stage forward or backward. Only a small number of participants skipped stages when transitioning. (2) Transitions from one stage to the next were preceded by changes in the respective type of intention. The intentions postulated by the model were meaningful predictors for subsequent behavioral changes, lending strong support to their assumed causal relationship. (3) Prior changes in the stage-specific social-cognitive constructs predicted changes of intentions.

To test the effectiveness of SSBC as a guideline to design interventions, Bamberg (2013b) developed and evaluated a SSBC-based social marketing campaign aiming to reduce car use. Based on an initial diagnosis of their current stage membership, participants

Table 2 Stage specific intervention strategies.

<i>Stage of change</i>	<i>Intervention strategies</i>
Predecisional	Make social and personal norms salient (e.g. Goldstein et al., 2008) Enhance problem awareness and self-focus (e.g. Prochaska et al., 2002) Enhance goal setting and goal commitment (e.g. McCalley and Midden, 2002)
Preactional	Provide information about the pros and cons of behavioral alternatives and enhance perceived behavioral control (e.g. Fishbein and Ajzen, 2011)
Actional	Support behavioral planning (e.g. Gollwitzer, 1999)
Postactional	Provide behavioral feedback (e.g. McCalley and Midden, 2002) Prevent the temptation to relapse (e.g. Marlatt and George, 1984)
General strategies	Provide social support (e.g. Hogan et al., 2002) Changes objective context conditions

Table 3 A short instrument for assessing a person's current stage of change concerning car use.

<i>Question: Which of the following statements best describes how you feel about your current level of car use for daily trips (in city X/ to your workplace) and whether you have any plans to try to reduce some or all of these car trips?</i>		<i>Stage allocation</i>
Please choose which statement fits best to your current situation and tick only one box		
At the moment, I use the car for most of my trips. I am happy with my current level of car use and see no reason why I should reduce it	☐ 1	Predecisional
At the moment, I still use the car for most of my trips. I would like to reduce my current level of car use, but, at the moment, I feel it would be impossible for me to do so	☐ 2	
At the moment, I do use the car for most of my trips. I am currently thinking about changing some or all of these trips to noncar modes, but at the moment I am unsure how I can replace these car trips, or when I should do so	☐ 3	Preactional
At the moment, I use the car for most of my trips, but it is my aim to reduce my current level of car use. I already know which trips I will replace and which alternative transport mode I will use, but, as yet, I have not actually put this into practice	☐ 4	Actional
Because I am aware of the many problems associated with car use, I already try to use non car modes as much as possible. I will maintain or even reduce my already low level of car use in the next months	☐ 5	Maintenance
As I do not own/have access to a car, reducing my level of car use is not currently an issue for me	☐ 6	'Captives'

were assigned to the corresponding intervention. The stage-specific intervention elements consisted of personal phone calls and information leaflets, aiming at activating and changing the underlying social-cognitive constructs of the three different intention types. An RCT-design was used for evaluating the campaign's efficacy. The results indicated that participants in the intervention group used public transport significantly more often and used the car significantly less often than the control group. Exhibiting an effect size of $d = .56$, the impact of the SSBC-based intervention on the reduction of car use was about three times stronger than the effects of traditional social marketing campaigns. In addition, there is evidence how the SSBC can be used as a theoretical foundation to construct a behavior change support system, which is web-based, to promote pro-environmental behavior (Bamberg et al., 2015; Mack and Tampe-Mai, 2016; Sunio et al., 2018).

Finally, Keller et al. (2019) published a first systematic review on papers applying the SSBC. They reviewed 10 studies published between 2013 and 2018, six of them were cross-sectional, three were intervention studies and one a correlational longitudinal design (for an overview please see Keller et al., 2019). According to Keller et al. (2019) the cross-sectional and longitudinal studies generally support the SSBC model, although there are some irregularities that warrant further investigation. The intervention studies found stage-tailored information to be more effective in promoting stage progression and behavioral change than nonstage-tailored information. Furthermore, Keller et al. (2019) identified several challenges that researchers may face when applying the SSBC. These include whether and how to analyze multiple, alternative behaviors; how to address the challenge of measuring a comprehensive model while keeping questionnaire length manageable; selecting and defining the role of model constructs in a behavioral context while keeping results comparable; and establishing a validated and reliable tool to diagnose a person's stage of change. Based on these insights, Keller et al. (2019) develop recommendations for researchers to design SSBC studies, which support the advancement of the theory and will then serve both researchers and practitioners for promoting pro-environmental behavior.

Coping Planning and Behavior Change—Research Stimulated by the SSBC

The SSBC also provides a theoretical background for reviewing the existing research on behavioral change processes. This review would indicate that most of this research is currently focusing on the first two stages of behavioral change, namely the predecisional and preactional stages. Research analyzing the factors and processes contributing to the successful implementation as well as maintenance of behavior change (actional and postactional stages) are still rare within environmental research. A recent study by Hsieh et al. (2017, 2019) provides one example for research questions and results which focus on these later stage of behavioral change. More precisely Hsieh et al. (2017, 2019) analyze the role of another volitional construct: Coping planning (Schwarzer, 2008; see also Fig. 2). Coping planning comprises actually enacting and maintaining the intended behavioral change. They assume that both volitional constructs—implementation intention and coping planning—are important in situations with a high risk of relapse. Implementation intention translates a goal into action by a mental link between situational cues and goal-directed responses in the form of “if—then”. In contrast to implementation intention, coping planning involves both anticipation of potential barriers which emerge during performing the actions, and ideas of how to overcome these barriers. As a result, the two planning cognitions may function differently in behavior change: Implementation intention plays an important role in initiating action, whereas coping planning may be more influential in the maintenance of behavior (Sniehotta et al., 2006; Ziegelmann et al., 2006). Supporting this theoretical assumption Hsieh et al. (2017, 2019) found in a randomized experimental intervention study that implementation intention and coping planning independently mediated the effect of behavioral intention on car use reduction. Additionally, coping planning partially mediated the effect of implementation intention on car use reduction. Furthermore, the results also supported the effectiveness of the combined implementation-intention-plus-coping-planning intervention in reducing car use, but not of the implementation intention alone intervention.

Conclusion

If behavioral change constitutes indeed a central environmental psychology topic, environmental psychologists have to invest more effort in researching the dynamic as well as psycho-social drivers of voluntary behavior change processes. Correlational studies with a focus on single psycho-social constructs to statistically predict behavioral intentions are cross-sectional snapshots of a change process and therefore not very helpful. Instead, more experimental longitudinal field studies are urgently needed, to analyze behavioral change processes over a longer time period in a natural setting. Furthermore such studies should be guided by explicit theoretical models of behavior change processes. The presented SSBC provides one empirically supported conceptual framework. The above presented study by Klöckner (2014) provides a good example for this kind of studies. Using the SSBC as a theoretical reference also indicates that research focusing on the later stages of behavioral change—behavioral initiation and maintenance are urgently needed. The presented study by Hsieh et al. (2017, 2019) provides a good reference point for this kind of research. In summary, from our point of view the SSBC provides a starting point for more research on voluntary behavior change processes in environmental psychology. We are convinced that future research will result in more detailed and realistic theoretical and empirical insights.

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Delineating the Plate Boundaries: A Review of Integrated Metrics for Healthy and Environmentally Sustainable Diets

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Abstract

We present the results of an extensive review of studies applying integrated food metrics to assess the health and environmental impacts of food, as well as of studies advancing definitions of the components and boundaries of healthy and sustainable food systems and diet. We review the literature in seven identified categories: assessments of health and environmental impacts of common diets, assessments of the environmental implications of shifting to healthier diets and vice-versa, optimization studies, assessments of the effect of following dietary quality indices on the environment, model diets and guiding frameworks, metrics frameworks for integrated food system impact assessments, and metrics frameworks for integrated dietary impact assessments. We critically discuss the approaches to metrics selection, the nature of metrics, the scale at which they operate, data sources, analytical methods, and target audiences. We conclude that there is a need for more holistic and systematic approaches to defining metrics of healthy and environmentally sustainable diets. Based on identified gaps, we propose a set of 10 criteria to guide the development of more integrated and systematic food metrics for human and environmental health in the future.

Introduction

The global food system currently operates unsustainably both in terms of human and planetary health. Agriculture is responsible for up to 30% of global greenhouse gas emissions (GHGe) (Vermeulen et al., 2012) and 70% of freshwater withdrawals. It is the main source of nutrient overload into aquatic and marine systems, a large chemical polluter, and has expanded like no other land use at the expense of biodiverse carbon storing forests, today covering 40% of ice free land on Earth (Foley et al., 2011; Ellis and Ramankutty, 2008). In addition, 85% of global fish stocks are fully exploited or overfished (FAO, 2015; Deutsch et al., 2011). Food production is thus an essential sector to address in order to achieve overall environmental sustainability (Garnett, 2013). Reciprocally, environmental stewardship is a fundamental determinant of food production: a deteriorated resource base with the loss of key ecosystem services such as pollination and climate regulation, will inevitably undermine system productivity, and consequently have severe repercussions on human health and food security (MEA, 2005; Ramankutty et al., 2006; Myers et al., 2013).

The world also faces a “double burden of malnutrition” (Tirado et al., 2010): while nearly 800 million people still go hungry, more than 2 billion are overweight or obese, and this number is growing rapidly (Ng et al., 2014; Black et al., 2013; FAO, 2015). Hunger and undernutrition remain an acute challenge to global health; the FAO (2015) reported an increase in hunger for the first time in two decades. Simultaneously, the growing obesity trends are linked to the increasing burden of non-communicable diseases (NCDs), such as cancer, cardiovascular disease and type II diabetes. NCDs have now surpassed infectious diseases as the world’s fastest-rising public health problem globally and the largest cause of death in absolute terms, accounting for 63% of global annual deaths (WHO, 2011). Unhealthy diets are a key driver of this epidemic, and in 2010, unhealthy diets surpassed smoking as the leading risk factor for disease worldwide (Lim et al., 2012). Underlying these problems are demographic and socio-economic trends driving changes in dietary patterns worldwide, characterized by an increasing demand for animal products and the consumption of low-diversity and low-quality foods.

To address rising global environmental risks, while creating a nutritionally adequate food future for a world of nearly 10 billion, the global food system needs deep transformation. Despite well-documented linkages and feedbacks between factors underlying public health and sustainability in the context of food, the issues of food production, diet, public health, and environmental and climate change have largely been addressed as separate agendas in science, policy and business—an approach that has proven ineffective (Dora et al., 2015; Johnston et al., 2014; Allen et al., 2014). Consequently, an integrated agenda for healthy diets from sustainable food systems is urgently needed across sectors and academic disciplines.

The Transformative Potential of Integrated Food Strategies

A key requirement to achieve transformative change is to identify and promote “win-win” diets and food production practices that meet both health and environmental goals (Riley and Buttriss, 2011; Macdiarmid et al., 2012). The untapped potential is enormous: Springmann et al. (2016) have estimated that transitioning toward more plant-based diets in line with standard dietary guidelines could reduce global mortality by 6–10% and food related GHGe by 29–70% compared with a reference scenario in 2050.

Identifying and promoting “win-win” diets requires quantitative tools that enable a systematic analysis of the complex relationships between the environmental and health effects associated with the ways in which food is produced and consumed (Fanzo et al., 2012; Riley and Buttriss, 2011; Macdiarmid et al., 2012). Integrated food metrics (IFM) are necessary to quantify what a healthy and sustainable diet entails, and thereby to inform the design of effective food and agricultural policies that promote better sourcing among producers and food industries, to mobilize civil society and the investor community, as well as to encourage better eating habits among consumers (Food Forum, 2014; FCRN, 2016).

A vast body of literature has previously proposed metrics spanning food, environment and health, but the majority considers these in siloes and at varying scales (Fig. 1). For example, some metrics focus on sustainable agricultural practices, some on the water footprint of foods, some on dietary diversity, some on the nutritional quality of a diet with regards to a specific nutritional group, some on ecosystem health and yet some on diet-related population health indicators.

In this paper, we review the advancement of metrics for defining and/or assessing the health and environmental impacts of food and diet. We provide a comprehensive map of existing work that has linked health and environmental metrics into composite indicators, indices and rating systems, as well as initiatives on dietary programs, guidelines and principles for sustainable and healthy eating. Through this review, we investigate what aspects of environment and health (and in what constellations) have hitherto been included in dietary assessments and studies proposing quantitative definitions of healthy and sustainable diets. We discuss the strengths and weaknesses of existing metrics, as well as the challenges in developing metrics that are holistic, understandable and applicable in practice.

Methods

We conducted a literature review of studies proposing and/or applying food metrics that combine both health and environmental aspects, as we consider these two domains to be the ‘hard-wired’ components of diet; a sustainable diet must be produced within planetary boundaries of safe resource use (Steffen et al., 2015) at the same time as fulfilling the nutritional requirements of the human body.

The review was conducted through keyword searching in PubMed, Science Direct, Web Of Science and Google Scholar, as well as upon expert literature recommendation. The following search terms were used in multiple combinations: “food”; “diet”; “health”; “nutrition”; “sustainability”; “environment”; “metrics”; “indicators”; “parameters”; “modeling”; “framework”; “analysis”; “impact”; “scenario”; “life cycle assessment.” We included studies that have proposed and/or applied metrics:

- (1) containing one or more indicators;
- (2) spanning both the environmental and health dimensions of food;
- (3) operating at diet level or other levels that are scalable to diet.

We identify and describe seven categories of studies, providing a structured overview of the state-of-the-art in this young transdisciplinary field. The studies cited throughout the review constitute a nonexhaustive set of examples to illustrate the different categories of studies and underlying methodologies that exist in the literature.

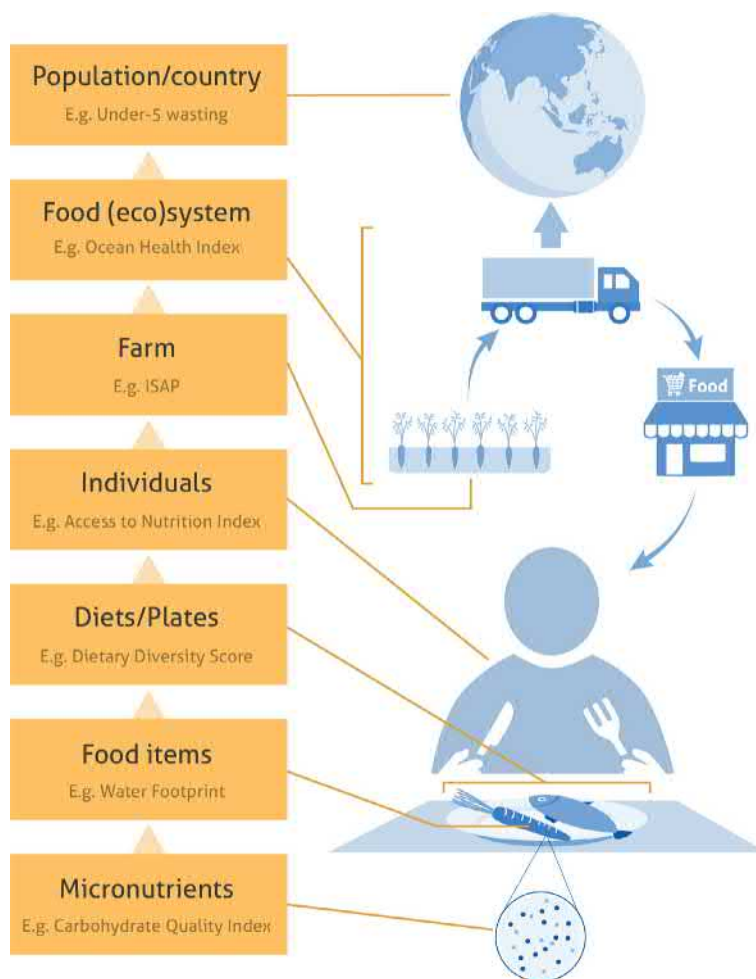


Fig. 1 The multiple dimensions and scales across which food metrics measure health and environmental impacts. From Rigby, D., Woodhouse, P., Young, T., Burton, M. (2001). Constructing a farm level indicator of sustainable agricultural practice. *Ecological Economics*, **39**, 463–478., Halpern, B.S., Longo, C., Hardy, D., McLeod, K.L., Samhoury, J.F., Katona, S.K., Kleisner, K., Lester, S.E., O’Leary, J., Ranelletti, M., Rosenberg, A.A., Scarborough, C., Selig, E.R., Best, B.D., Brumbaugh, D.R., Chapin, F.S., Crowder, L.B., Daly, K.L., Doney, S.C., Elfes, C., Fogarty, M.J., Gaines, S.D., Jacobsen, K.I., Karrer, L.B., Leslie, H.M., Neeley, E., Pauly, D., Polasky, S., Ris, B., St Martin, K., Stone, G.S., Sumaila, U.R., Zeller, D. (2012). An index to assess the health and benefits of the global ocean. *Nature*, **488**, 615–620. Access to Nutrition Foundation (AFN). Access to Nutrition Index. Accessed on 6 March 2019. Source: <https://www.accesstonutrition.org/about-index>, Zazpe, I., Santiago, S., Gea, A., Ruiz-Canela, M., Carlos, S., Bes-Rastrollo, M., Martinez-González, M.A. (2016). Association between a dietary carbohydrate index and cardiovascular disease in the SUN (Seguimiento Universidad de Navarra) project. *Nutrition, Metabolism and Cardiovascular Diseases*, **26**(11), 1048–1056. Hoekstra, A.Y., Mekonnen, M.M. (2011) The water footprint of humanity. *PNAS*, **109**(9), 3232–3237.

Review of Food Studies Integrating Health and Environment

A Growing Demand for Integrated Food Metrics

A legacy of the historical separation of health and environmental issues in the context of food is the persisting lack of integrated dietary guidelines that consider nutrition and environment in tandem (Fig. 2). Still about half of the world’s countries lack national dietary guidelines, and only a few countries have national guidelines that consider both nutrition and the environment: Sweden, the Netherlands, Canada, Qatar and Brazil.

There is, however, a growing realization both within and beyond the research community that an integrated approach to food and diet is paramount to avoid niched strategies that optimize either for environment or health, thereby risking to inflict negative side-effects on one or the other. Integrated strategies toward improving diets would enable to harvest significant economic win-wins which have been estimated to 0.4–13% of global GDP through savings in GHGe and healthcare expenditure (Springmann et al., 2016).

The UN Sustainable Development Goals (SDGs) are an example of the ongoing shift toward a more integrated approach to global sustainability. Notably, out of the 167 proposed SDG targets, about half relate directly to food, which shows how central a theme food is to achieve sustainability overall. Similarly, the UN Standing Committee on Nutrition also recognizes the need for integration, as illustrated in a 2014 technical note on strategies “Towards sustainable, healthy food systems” (Remans et al., 2014). An integrated approach was also recommended by the 2015 United States Dietary Guidelines Advisory Committee, but

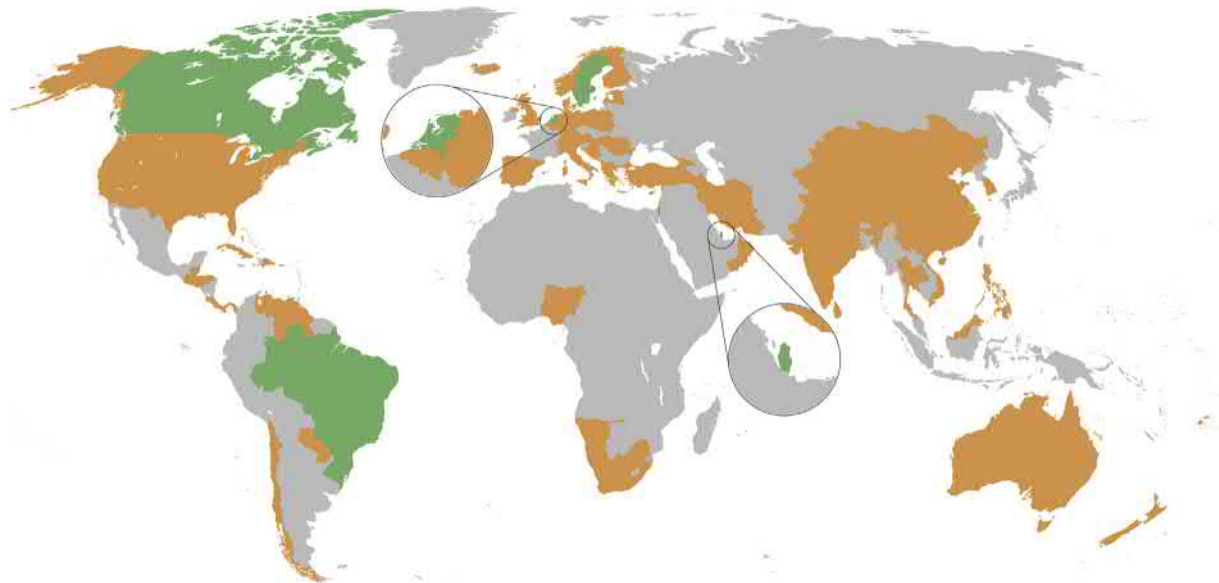


Fig. 2 Global outlook on national dietary guidelines. In orange: countries that have national dietary guidelines in place; in white: countries lacking guidelines; in green: countries that have implemented guidelines integrating both nutrition and environment. Data from Food and Agriculture Organization (FAO) (2019) Food-based dietary guidelines. Source: <http://www.fao.org/nutrition/nutrition-education/food-dietary-guidelines/en/>. Accessed on 2 January 2019.; Gonzalez-Fischer, C., Garnett, T. (2016). Planets, pyramids and the planet: Developments in national healthy and sustainable dietary guidelines: A state of play assessment. Food Climate Research Network (FAO) and Food and Agriculture Organisation (FAO).

was subsequently censored by Congress, which passed a law prohibiting dietary guidelines to mention environmental impacts after intense lobbying from the meat and dairy industry.

A significant number of recent academic studies have also promoted the need for more holistic and standardized assessments of the impacts of diet on health and environment (e.g. Jones et al., 2016; Auestad and Fulgoni, 2015; Demaio and Rockström, 2015; Herforth et al., 2014; Johnston et al., 2014; Allen et al., 2014; Garnett, 2013; Macdiarmid, 2013). They point to the critical need to identify research gaps, clarify and harmonize definitions and concepts, set research priorities, and systematically examine trade-offs.

Studies Proposing and Applying Integrated Food Metrics

In recent years, there has been an upsurge of scientific literature advancing IFM to assess the impacts of food on both health and environment (e.g. Lukas et al., 2015; Tilman and Clark, 2014; Johnston et al., 2014; Allen et al., 2014; Heller et al., 2013). A review by Auestad and Fulgoni (2015) of the sustainable diets literature found that two-thirds of the captured studies were published 2010–2014.

Below we provide a detailed examination of the studies identified in our review of food metrics specifically interlinking health and environment. We identify seven categories of studies based on the diverging ways in which environment and health considerations have been integrated and costudied.

Assessments of health and environmental impacts of common diets

Many studies assess the health and environmental outcomes of common dietary patterns and food groups. These are considered ‘static’ in the analysis, in contrast with scenario-based studies that assume dietary shifts (described below). For example, Van Dooren et al. (2014) compare six dietary patterns in terms of GHGe, land use and 10 nutritional indicators. Tilman and Clark (2014) present a comparative assessment of three global dietary patterns—Mediterranean, pescetarian and vegetarian—against current and future global average diets under a business-as-usual trajectory with regards to GHGe, land-use change and three health outcomes (diabetes, cancer, cardiovascular disease). The combined impacts of diet on climate change and mortality from chronic disease are studied in Scarborough et al. (2012). The land use dimension is added in a similar analysis by Biesbroek et al. (2014). A different health angle is adopted by Rööfs et al. (2015) who assess the adequacy of dietary nutrients alongside GHGe, land use and biodiversity impacts. Similar studies have been conducted on specific food groups, e.g. Aston et al. (2012) or Temme et al. (2013) who assess the combined impacts of consuming red and processed meat.

These studies often consider a narrow set of indicators. In the review by Auestad and Fulgoni (2015), only two studies were found that considered multiple indicators of health and environment. One of them examined the impacts of four dietary patterns using 11 indicators then aggregated to a single score, and the other compared the impacts of habitual diets in the EU27, those recommended by the WHO and the WCRF, and the Mediterranean diet across eight impact categories (Baroni et al., 2007; Wolf et al., 2011).

Assessments of the environmental implications of shifting to healthier diets, and vice-versa

A substantial body of literature investigates the environmental implications of shifting to healthier diets. Heller et al. (2013) have suggested that a dietary shift from the average US diet to national dietary recommendations could lead to a 12% decrease in diet-related GHGe. Hendrie et al. (2014) have demonstrated that red meat and energy dense nutrient poor “non-core” foods are the largest contributors to diet-related GHGe in the average Australian diet. Similarly, Fazeni and Steinmuller (2011) have shown that decreasing meat consumption by 60% and increasing fruit and vegetable consumption as recommended by the German Nutrition Society for Austria would lead to lower energy demand and GHGe, while increasing the availability of land for other forms of production. Macdiarmid et al. (2012) designed a diet including 52 food items, which would meet UK dietary requirements for adult women as well as lead to a 36% decrease in GHGe.

A common problem across these methodologies is that they are health driven, and thus adopt a narrow approach to environmental sustainability, usually only considering GHGe. A limited number of studies concentrate on other environmental variables such as water use (e.g. Hess et al., 2015), land use (e.g. Peters et al., 2016) and nutrient loading (e.g. Westhoek et al., 2014). Only some studies consider several variables combined, such as Behrens et al. (2017) who quantified the impacts on GHGe, eutrophication and land use of adopting nation-specific Nationally Recommended Diets compared with national average diets in 37 countries, showing significant impact reductions in high-income countries but significant increases in lower-middle-income countries.

Some studies have also assessed the environmental implications of reducing specific health risks rather than all-cause mortality, e.g. Downs and Fanzo (2015) examined the carbon, water and ecological footprints of the components of a cardio-protective diet.

The reverse analysis—assessments of the health implications of shifting to environmentally sustainable diets—is far less common. A systematic review by Alexandrowicz et al. (2016) identified 210 diet studies considering GHGe, land use and/or water use, of which only seven reported on health effects, e.g. Milner et al. (2015) who examined the effects on NCD mortality of low-GHGe diets. Alexandrowicz et al. (2016) identified 14 sustainable dietary patterns with reductions of up to 70–80% in GHGe and land use, and 50% in water use compared to baseline diets, for which they also found evidence for reduced risks (albeit modest) of all-cause mortality.

A multi-perspective study by Springmann et al. (2018a) assessed the effects of three dietary-change strategies (environmentally, food security and health driven) on premature mortality, nutritional adequacy and environmental impacts in 150 countries, demonstrating important trade-offs in the two former strategies while the health driven strategy led to the greatest benefits overall.

Optimization studies

A rarer body of work has attempted to optimize the health and environmental outcomes of diet, often adding an economic perspective to the analysis. These studies are using computing methods such as linear programming to optimize the mix of foods to meet specific nutritional and environmental criteria. For example, Wilson et al. (2013) considered the adequacy of dietary nutrients alongside GHGe. A more holistic analysis was provided by Masset et al. (2014) who considered GHGe, nutritional adequacy, energy density and cost.

Assessments of the effect of dietary quality indices on the environment

Some studies have investigated the environmental implications of using different dietary quality indices. For example, Kägi et al. (2012) compared different measures of diet quality to study the relative environmental impacts of different restaurant meals, concluding that using a Nutrient Density Score emphasized vegetable contributions to the diet and hence reduced the environmental impact differences between meals, while using the Nutrient Richness Food Index emphasized meat contributions to the diet, hence highlighting differences. This shows the importance of choosing the appropriate unit of assessment or comparing different ones. Similarly, van Kernebeek et al. (2014) compared the GHGe of different diets using a diet-level nutrient profiling scheme, and suggested that when using nutrient-based criteria, nutrient levels should be capped at 100% of the recommended daily value to prevent “crediting” overconsumption. Vieux et al. (2013) studied the GHGe of French diets while taking into account three measures of nutritional quality: Mean Adequacy Ratio above the median, Mean Excess Ratio below the median, and energy density below the median. They concluded that diets with higher nutritional quality are associated with higher GHGe. These results contradict the broad conclusion in the literature that healthy diets, rich in fruits and vegetables, are also more environmentally sustainable than unhealthy diets. However, this may be explained by the high energy density and relatively low GHGe of low-nutrition foods (in addition to their ease of transport and storage, and low risk of wastage).

Model diets and guiding frameworks

Another set of studies propose ‘model’ diets and guiding frameworks to help consumers improve their nutrition while limiting environmental impacts. Various ideal plates have been suggested, such as the Menus of Change designed by the Harvard School of Public Health in collaboration with the Culinary Institute of America (2014). Other creative forms of outlining healthy and sustainable diets include dietary programs, food score cards and food pyramids, such as the Barilla Centre For Food and Nutrition’s Double Pyramid (2009), which displays foods along health and sustainability gradients. The LiveWell for LIFE initiative outlines a diet that is both healthy and minimizes environmental impacts, taking into account GHGe, obesity prevalence and economic spillovers (WWF-UK, 2012). The FAO has suggested the Mediterranean diet as a prime example of a sustainable diet that takes into account nutrition, biodiversity, local food production and culture (Burlingame and Dernini, 2011), but a challenge is that the Mediterranean diet definition varies between studies (Bach-Faig et al., 2011).

Similarly, a few countries have developed national dietary guidelines that consider both health and environment (Fig. 2). These include emphasizing a plant-based diet, reducing leftovers and waste, consuming locally and regionally produced foods when available, choosing fresh and homemade foods over highly processed and fast foods, conserving water and energy in food preparation, and enjoying meals in good company (Seed, 2014; Brugård Konde et al., 2015; Kromhout et al., 2016; Monteiro et al., 2015).

Metrics frameworks for integrated food system impact assessments

The sparsest set of studies are those that present novel quantitative frameworks for integrated assessment of health and environmental impacts of food systems and diet. Remans et al. (2014) have proposed 10 core principles with associated metrics for measuring the nutritional adequacy and environmental sustainability of food systems. An Institute Of Medicine (IOM) and National Research Council (NRC) (2015) report has advanced an integrated framework for assessing the total impacts of policies across sectors (health, environment and agriculture) in order to equip decision-makers with a tool that enables to test policies for potential negative side-effects on other sectors. A framework has been advanced by Gustafson et al. (2016) to compare the performance of different countries' food systems, employing 25 sustainability indicators across seven domains—nutrition, environment, food affordability and availability, sociocultural well-being, resilience, food safety, and waste. Based on the latter, Chaudary et al. (2018) presented a global-scale analysis quantifying the national food system performance of 156 countries, showing very different patterns of performance between countries. Prosperi et al. (2014) have proposed a food system vulnerability framework comprising 12 indicators measuring exposure, sensitivity, and adaptive capacity of the Mediterranean food system, including nutritional and environmental considerations. A Delphi process was conducted by Allen et al. (2014) to determine a set of key metrics for sustainable food systems, which yielded 15 indicators spanning sustainable production, economic vulnerability and adequate nutrition. Further, Conijn et al. (2018) used the planetary boundaries for land system change, climate change and biogeochemical cycles as benchmarks for analyzing whether different interventions could meet global food demand within planetary boundaries by 2050, showing that shifting to healthier diets (replacing 50% of meat consumption by plants) has a major role to play, but needs to be complemented by significant waste reductions and drastically improved production practices.

A recent report by the EAT-Lancet Commission on Food, Planet, Health (Willett et al., 2019) proposes a “planetarsy health diet” defined by food group-based consumption brackets that together provide the span of a healthy diet, coupled with a quantitative definition of sustainable food production systems based on impact boundaries for water, land, and nutrient use, as well as GHGe and biodiversity loss. The report, as well as a spin-off analysis by Springmann et al. (2018b), confirm the findings of Conijn et al. (2018). The advancement of a comprehensive set of quantitative benchmarks for sustainable food systems is a key contribution of this report, as previously proposed model diets and guidelines were of a broader, qualitative nature and thus lacked the granularity to guide food system actors toward the necessary changes. However, the EAT-Lancet report does not consider environmental impacts postfarmgate, and assumes a decarbonized food system by 2050, making the needed food system changes even greater than the report states. Further, the environmental benchmarks are set at global food system level, causing a scale discrepancy with the health boundaries (set at diet level) and would require downscaling to diet in a regionally adapted manner.

Metrics frameworks for integrated dietary impact assessments

Only a few studies have proposed integrated metrics frameworks that are readily applicable for quantitative dietary assessments. Lukas et al. (2015) introduced the Nutritional Footprint comprising four environmental and four nutritional indicators, and show-cased the framework through a range of meal comparisons. Heller et al. (2013) proposed a conceptual framework for diet-level integration of environmental impacts and nutritional quality assessment which includes a combination of assessment methods, and examples of mid- and end-point indicators. Johnston et al. (2014) offer a descriptive analysis of the determinants of sustainable diets and present a qualitative framework of components and underlying factors and processes to frame what constitutes a holistically sustainable diet. A matrix was proposed by Van Dooren et al. (2014), collapsing land use and GHGe into an environmental axis and 10 nutrient indicators into a health axis, which enables to plot diets and food components against both health and sustainability. Smedman et al. (2010) estimated a composite nutrient density, expressed as percentage of Nordic Nutrition Recommendations for 21 essential nutrients, in relation to cost in GHGe of the production from a life cycle perspective, using an index called the Nutrient Density to Climate Impact index (NDCI). The European project SUSFANS, launched in 2015, is also advancing a definition of ‘SHARP’ diets (Sustainable, Healthy, Affordable, Reliable and Preferred), incorporating metrics of nutrition, environment, economics and food security(SUSFANS, 2017).

A Critique of Existing Food Metrics

As illustrated in this review, a myriad food metrics, guidelines and principles have previously been proposed and applied to various aspects of health and environment, relating to different parts of the food system. This fragmented landscape of metrics demonstrates how diverse food systems analysis is, and at the same time how disconnected studies are. This knowledge can easily be perceived by non-experts as overwhelming. Below we discuss some of the main challenges and gaps associated with previous attempts at developing IFM.

Adopting a Systems Approach to Developing Food Metrics Frameworks

There is an increasing trend toward integrating health and environmental metrics. Still among these more integrated frameworks, there are aspects of health and environment that are rarely represented. A systematic review of studies addressing the measurement of sustainable diets conducted by Jones et al. (2016) identified 30 different metrics of sustainability, among which most studies have evaluated GHGe and to some extent also water and land use, while biodiversity impacts, the disturbance of biogeochemical flows, antibiotics and pesticide use, food waste, and animal welfare are key neglected areas. This pattern of dominance of studies focusing on GHGe was confirmed in the review by Alexandrowicz et al. (2016) as well as in our review. More broadly, metrics related to food production have hitherto favored land-based systems, though productive and extractive marine and freshwater systems are equally important. The great majority of studies are also located in the Global North.

Adopting a systems perspective is essential to identify not only the synergies but also the possible trade-offs between health and environmental goals in the context of food production and diet, which previous studies have already demonstrated exist (Drewnowski, 2014; Ingram, 2011; Macdiarmid, 2013). Hence the importance of food studies encompassing a comprehensive set of metrics. A research priority for studies applying IFM should be to identify scenarios in which sustainable food production aligns with suggested standards for healthy diets similar to the analyses run by the EAT-Lancet Commission (Willett et al., 2019) but at regional scales, for example: how and where could the current under-production of nuts, seeds, fruits and vegetables be carried out so as to minimize environmental impacts? Ironically, foods associated with a healthy diet (e.g. fruits, vegetables and nuts) are to a large extent currently sourced from production systems with low resilience.

Though environmental impacts of food overall are mainly generated at the production stage, that may vary depending on the type of food and supply-chain considered (Viola and Marinelli, 2016). The healthiness of a food is also largely determined by its processing. Diet studies should thus increasingly consider the whole life-cycle of foods, including their preparation. Currently, environmental impact measurements tend to be limited to farmgate and the nutritional quality of foods tends to be evaluated based on their raw form. Ingram (2011) has argued that food metrics should reflect a shift from “what we get” (i.e. the outcomes of food system activities, such as food access and food stability) toward “what we do” (i.e. the activities, such as producing and processing).

Harmonizing Language and Methodology

Not only do the metrics considered vary greatly between studies, the functional units, terminologies, methods and data sources also vary, rendering these studies difficult to compare (Jones et al., 2016; Auestad and Fulgoni, 2015; Hallström et al., 2014). Many authors in the field are calling for streamlined methodologies, as a strong scientific foundation of comparable high-quality studies would support progress in advancing healthy and environmentally sustainable diets.

With regards to functional units, Lukas et al. (2015) base their dietary calculations on *dishes*, whereas Tilman and Clark (2014) construct long-term *dietary patterns* (e.g. Mediterranean or vegetarian) based on meta-data, and Gustafson et al. (2016) make comparisons between *country average diets*. These all differ with regards to time and scale. Each of these approaches has limitations; on the one hand, studying dishes enables a greater level of specificity and accuracy than dietary patterns which require building in a range of assumptions in terms of the foods consumed but on the other hand, studying dietary patterns is more representative of a person's dietary habits than a single dish. Other examples of inconsistency are the discrepancies between studies considering nutritional requirements (e.g. Lukas et al., 2015) versus those considering health outcomes (e.g. Tilman and Clark, 2014), or between studies considering specific health aspects (e.g. Downs and Fanzo, 2015) versus those considering total health (e.g. Springmann et al., 2018a). Beyond the scope of this review are also studies considering specific food groups or products in contrast to studies considering the whole diet.

Studies also demonstrate variations in terminologies used to link food and environment, such as “diet,” “food system,” “value-chain,” “farming,” “agriculture,” or “food consumption” (Auestad and Fulgoni, 2015). The definitional boundaries between these terms is sometimes unclear, for example whether “sustainable diet” considers the sustainability of the whole underlying food system or not. The definition of typical diets such as “Mediterranean” or “vegetarian” diets also vary in terms of the assumed food content and balance.

The approach to selecting metrics in existing IFM frameworks is often poorly specified. More robust, explicit methods for metrics selection will be important in the future, in order to justify why some metrics are included while others are excluded. Criteria for selection could be, for example, data availability, frequency of use in previous studies, importance of the issue represented (in terms of magnitude of current impact), and actionability.

Studies rarely advance or adopt a quantitative definition of a healthy and sustainable diet (Harray et al., 2015), meaning that dietary impact levels are measured but not benchmarked against clearly defined sustainability and health levels. The growing field of dietary assessments based on IFM should look to systematically compare dietary impacts against a standardized set of benchmarks, such as those advanced in the EAT-Lancet Commission (Willett et al., 2019). The FAO (2012) has also advanced an official qualitative definition of sustainable diets, which could provide a good basis for translation into quantitative benchmarks.

Lastly, the data used in previous dietary assessments also vary broadly. On environmental impacts, some studies use primary LCI data, some use secondary LCA data from different platforms such as Agribalyse and Agrifood, and some use non-LCA data describing food impacts at farm-gate (often footprint data). Extensive debate among the scientific community has occurred around the relative strengths and weaknesses of footprinting versus LCA (Hoekstra, 2016; Pfister et al., 2017). Both methods carry the limitation that multiple definitions and system boundaries are used. In the case of LCAs, these sometimes only consider cradle-to-farm

gate impacts whereas others will consider cradle-to-grave impacts (Weidema et al., 2008). LCAs also vary in terms of the functional unit used, characterization factors (coefficients used for converting between units of measurement), and allocation factors (how environmental impacts are being allocated in mixed production systems). This inconsistency makes studies difficult to compare or aggregate, particularly when methods are not thoroughly described (Hallström et al., 2014). LCA data is therefore more useful for comparing the impacts of very different foods or diets, rather than similar ones (i.e. marginal impacts). Cucurachi et al. (2016) mention as a key challenge the fact that LCA tools to quantify marginal impacts are still evolving, and call for a protocol for mining data from diet LCA studies considering completeness, system boundaries and underlying assumptions.

On nutritional intake, data sources vary from clinical trials, 24 h recall surveys, case-control studies, cohort studies, to national nutrition composition tables. Data platforms vary from direct collection, to UN-hosted or other global databases such as FAO, WHO, World Bank, to national health agencies, models and meta-analyses.

Generating and Accessing the Necessary Data

An acute barrier to applying IFM in dietary assessments is the current limitation of data on foodstuffs from specific production systems. A comprehensive body of open-access food environmental data is currently hosted by international organizations such as WHO, FAO and the World Bank, but the data only represents impacts at farmgate and fails to distinguish impact levels based on production practices. The food industry has hitherto been skeptical to disclosing internal supply-chain data. LCA-based data can be found in the literature but is scattered.

Many environmental indicators related to food production also have strong spatial and temporal dependencies, e.g. fluctuations in yield between seasons and regions, which are often not captured in impact studies. Acknowledging these dependencies requires high-resolution datasets and more sophisticated impact assessment methods than used today, for instance basing yield estimates on longer time-series than just one season. In a study of rice farming in Bangladesh, Henriksson et al. (2014) showed substantial variation in environmental impacts between the two to three different farming seasons which are each associated with their own sets of farming practices, intensities of irrigation and yields. Similarly, given that the majority of metrics currently in use for measuring “nutritional quality” rely on a cultural norm by considering food groups, metrics may need to be adapted to local to regional scales. More absolute measures of ecological “nutritional health” that are strongly rooted in epidemiology and applicable universally to human diet are therefore desirable (Heller et al., 2013).

Toward Better Design Criteria for Integrated Food Metrics Frameworks

Drawing from our review, we propose a set of 10 key criteria for future studies advancing IFM frameworks for environmentally sustainable and healthy diets.

1. *Scope*—The framework should represent a holistic set of environmental aspects that, together, regulate the stability of the Earth system, and of nutritional requirements that ensure human health and wellbeing.
2. *Thresholds*—The indicators should carry quantitative thresholds that reflect a sustainable environmental impact and adequate intake for good health. Environmental thresholds should be adapted to the regional context and ecology from which the diet is sourced.
3. *Scientific credibility*—The framework should reflect the scientific evidence on key environmental and nutritional requirements for Earth system stability and good health. The scientific motivations behind the selection of each specific indicator should be specified.
4. *Time scale*—The framework should principally be designed for assessing dietary patterns rather than individual meals, as meals may not be representative of long-term consumption habits. However, meal-based analyses allow for deeper analysis of environmental impacts (see criterion 6 below).
5. *Spatial scale*—The framework should carry flexibility with regards to scale of analysis, given that food consumption data can be gathered at individual, country, regional or global level. Depending on the scale of interest, impact measures could be converted from national-to-global averages down to per-capita measures, and vice-versa.
6. *Life-cycle stages*—Analyses beyond farm gate require detailed information on food’s origins, processing and transport, which is nearly impossible to account for in assessments of longer-term dietary patterns, in addition to post-farm gate data on many highly processed foods being limited. However, if analyzing particular foods where post-farm gate impacts are known to be significant, e.g. fruits and vegetables, these may be important to include.
7. *Production practices*—The framework should, if possible, include a component that captures the production context of food (production mode, animal welfare, embedded ecosystem sensitivity and value) as an ‘add-on’ to the core framework that would be relevant particularly for detailed diet analyses, e.g. individual meals, as it requires detailed information on each food component. Studying production system properties could also be useful in broader food system analyses.
8. *Data sourcing*—For environmental impacts, we recommend the use of footprint or LCA data from peer-reviewed studies that have clearly defined methodologies and use the same system boundaries, allocation factors and characterization factors for comparability. For nutritional intake, we recommend using food nutrition composition tables from governmental agencies or reliable academic sources. For consumption data, we recommend using (sub-)national food surveys from national authorities

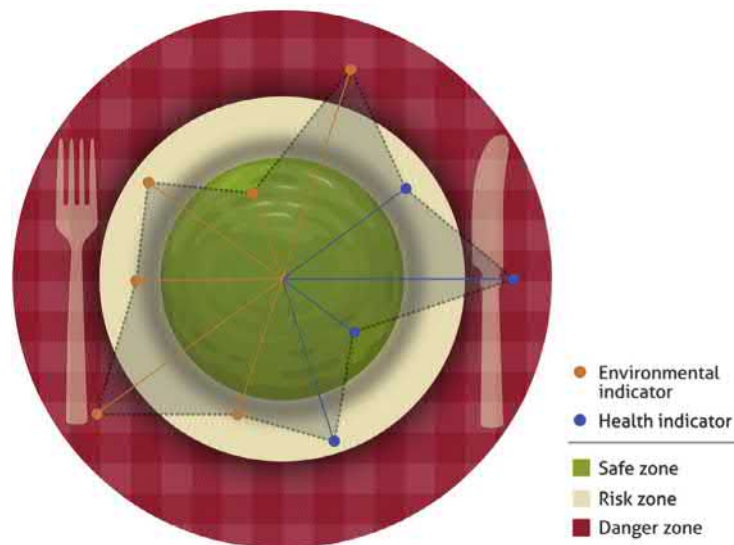


Fig. 3 Prototype of an integrated food metrics framework applied to a fictive diet.

or the peer reviewed literature, or aggregated global data from international organizations (e.g. the United Nations or World Bank), though the scale of interest will to a large extent determine the data source.

9. *Aggregation of results*—It would be useful to develop a method that allows to collapse the framework metrics into a single index or score. This would be useful in making comparisons between, e.g., countries or common dietary patterns.
10. *Practical applicability*—The framework should be designed with the aim to be useful in practice, which requires wrapping a complex set of metrics into a simply communicated message without losing critical information on the way.

Building on previous studies and gaps identified in our literature review, we propose a conceptual prototype for an IFM framework in Fig. 3 to which we have applied a fictive dietary assessment. The blue dots represent health indicators; the orange dots represent environmental indicators. The circular area in green delimits the ‘plate boundaries’ within which impacts on health and environment are considered adequate. The area in orange delimits the ‘risk’ zone, which represents the scientific uncertainty range as well as nutritional flexibility with regards to health effects of food and nutrient intakes. The red zone going outwards is the ‘danger zone’ where impacts on health and environment are scientifically asserted to be harmful. The radial distance from the central black dot to each indicator represents the level of impact measured by each indicator. The fictive diet we plotted falls outside of all plate boundaries except for one health indicator. The area delimited by the black line connecting all indicator levels is used to illustrate a diet’s total dietary impact; this area could also be used to calculate total impacts.

Radial plots have also been used in previous studies (e.g. Lukas et al., 2015; Gustafson et al., 2016) as these enable to easily visualize trade-offs between indicators and identify diets that score within plate boundaries. Represented in this way, results may also become more easily interpretable by non-expert audiences.

Conclusions

The scientific literature contains a wide and fast-growing array of metrics that assess the health and environmental impacts of food. However, most previous studies advancing IFM consider only a few indicators, and thus fail to adopt a systems perspective where health and environmental aspects are interlinked and compared. This puts dietary evaluations at risk of failing to detect potential trade-offs between different environmental and health considerations, or to identify important added benefits.

Some aspects of health and environment have hitherto been well represented by metrics whereas others, although of similar relevance, are frequently neglected. Methodologies, data sources and terminology also vary widely between studies, rendering comparisons of their results difficult.

Future research should seek to consolidate, harmonize and complement existing metrics in order to move toward integrated frameworks that consider a wide range of key health and environmental aspects, that provide quantitative benchmarks for environmentally sustainable and healthy levels of impact, and that are practically useful to food system actors with regards to food choices, production practices or sourcing standards.

We present a prototype for an IFM framework that would allow to conduct absolute assessments of diets’ nutritional adequacy and environmental sustainability, as well as to identify potential trade-offs between objectives. Possible future research applications of such a framework could be, for instance, to assess the environmental implications of shifting food production practices to meet guidelines for healthy diets.

Acknowledgments

We wish to extend our thanks to our colleagues Malin Jonell, Patrik Henriksson, Max Troell and Sarah Cornell at Stockholm Resilience Centre for providing extensive comments and novel perspectives to this paper during the course of its development. Our thanks also go to colleagues at the EAT Foundation for their continuous support to this work.

Funding

This work was funded by the EAT Foundation, Oslo, Norway.

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The Need for Boundary Spanners in Integrated Water Resource Management

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Abstract

Water management is increasingly challenged by climate and technological changes, socioeconomic trends, and aging infrastructure, among myriad others challenges. The traditional top-down, fragmented approach to water management is insufficient to address these challenges. Integrated water resource management, a collaborative and holistic approach, is critical to successful water management. The involvement of those who excel in multi-sector and diverse stakeholder collaboration are required. Boundary spanners are individuals within an organization who can reach across organizational borders to build relationships, interconnections, and interdependencies in order to manage complex problems. Although these individuals may operate on the edge or periphery of an organization, they position themselves as both internal and external communicators. Boundary spanners actively work toward collaboration, attempting to link diverse stakeholders, processes, and information from multiple perspectives in order to influence policies and practices and increase social learning between stakeholders. The multilevel nature of boundary spanning aids the movement and acknowledgement of ideas across various sectors, organizational or geographic boundaries, and political alliances. This article describes the need for, and incorporation of, boundary spanners in integrated water resource management.

Introduction

Water management is increasingly challenged due to changes in availability of water in both quantity and quality. The challenges are being driven by climate change with increasing temperatures and more extreme weather events, rising demand as a result of population growth and other demographic changes (e.g., urbanization), and agricultural and industrial expansion among myriad other drivers. The traditional top-down, fragmented approach to water management is no longer viable. Most water quantity and quality problems are the result of human activity (Rockström et al., 2014; Schultz, 2011); and thus it is more often their social complexity, not their technical complexity, that confront water management. A more holistic, multi-disciplinary, participatory approach is essential. The integrated water resources management (IWRM) approach is considered a preferred way forward “for efficient, equitable and sustainable development and management of the world’s limited water resources and for coping with conflicting demands” (UNDESA, 2014). IWRM is defined as “a process which promotes the coordinated development and management of water, land and related resources, in order to maximize the resultant economic and social welfare in an equitable manner without compromising the sustainability of vital ecosystems” (Hassing et al., 2009, p.3). Introducing boundary spanners into the IWRM process supports collaborative efforts and aids in the development of trust as well as knowledge and perspective sharing while setting the stage for more productive outcomes and future collaboration between parties.

Boundary Spanners

Boundary spanners are individuals within an organization who can reach across organizational borders to build relationships, interconnections, and interdependencies in order to manage complex problems (Williams, 2002). Boundary spanners “manage out,” or across, social and professional ties to influence policies and practices (Austin, 2002; Cash et al., 2006; Klein, 1996). According to

Zhao and Anand (2013), boundary spanners operate on the edge or periphery of an organization positioning themselves as both internal and external communicators. Although boundary spanners typically represent their home organizations, they actively work toward collaboration, attempting to link diverse stakeholders, processes, and information from multiple perspectives (Alexander et al., 2016; van Meerkkerk and Edelenbos, 2014). As representatives of their home organizations boundary spanners operate informally within collaborative endeavors (Safford et al., 2017). By acting as inter-organizational ambassadors, they have an opportunity to influence perceptions and improve knowledge sharing between stakeholders. Creating multiple pathways for stakeholders to learn about each other's values, experiences, and skills is critical to positive collaborative outcomes (Coleman and Stern, 2018).

History of Boundary Spanning

The idea that information exchange from external areas was crucial to continued business development and innovation emerged in the mid-20th century; yet the literature at the time suggested that communication across different spheres within organizational boundaries was not only inefficient, but open to bias and misrepresentation (Dearborn and Simon, 1958; March and Simon, 1958; Wilensky, 1967). Thus, early research on how to manage boundary complexities emphasized the role and development of *gatekeepers* specifically in the area of technology transfer between different departments of an organization (Aldrich and Herker, 1977; Tushman, 1977; Tushman and Scanlan, 1981; Friedman and Podolny, 1992). The notion that boundary spanning could aid the process of innovation by linking an organization's internal network to external sources of information encouraged further investigation as to the usefulness of boundary spanning beyond external information transfer. As institutions and corporations continue to grow in size, they differentiate into specialized areas, each working with specialized tasks or environments. These specialized units develop their own norms, processes, language, and coding schemes, which have the potential to hamper information exchange. Communication across organizational boundaries becomes more and more difficult, thereby harming future development and innovation as well as team cohesiveness. The idea of identifying individuals who have the ability to span networks and encourage knowledge sharing became increasingly important.

Friend et al. (1974) identified a cluster of networking skills as an important characteristic of boundary spanning work and encouraged the development of certain interpersonal relationships, communication, and political skills while also recognizing the interconnectedness of problems and their potential solutions. Webb (1991) refers to certain individuals who possess particular skills within an organization or collaborative effort as those "who are especially sensitive to and skilled in bridging interests, professions and organizations" (p. 231), while Degeling (1995) views these spanners as "entrepreneurs of power" who understand connections, interdependencies, and fractures between stakeholders (Williams, 2002, p. 109). Gradually, the notion that there exists "special" individuals who possess the innate ability to bring people together, break through red tape, and observe the situation in a different way found its way beyond earlier and more simplistic explanations of boundary spanning.

Contemporary Boundary Spanning

Boundary spanning is no longer solely reserved for information transfer within business and political sectors. Individuals who possess interpersonal skills, contextual knowledge, and the ability to unite disparate groups around a common goal are now actively engaged in higher education (Miller, 2008; Pryor and Henley, 2018), public relations (Neill, 2014), social media (Van Osch and Steinfeld, 2016), and healthcare related-fields (Long et al., 2013; Wallace et al., 2018).

Moreover, boundary spanners have been found to play a positive role in both internal and external relationships. Neill (2014) found that internal boundary spanning at the division level of an organization increased informal coalitions. Neill concluded that gathering information across departments can lead to not only improved employee relations, but also better strategic decisions at the administrative level. These findings are similar to boundary spanning involvement in higher education. According to Pryor and Henley (2018), the need for boundary spanners is intensifying as higher education becomes increasingly more complex and dynamic. Leadership both horizontally and vertically is required to strategize new responses to complex external challenges. Those in higher education are seeking individuals who have the ability to manage boundaries, forge common ground, and model collaboration. Pryor and Henley determined that institutions of higher learning are replete with departmental silos and, thus the challenges of building inter-disciplinary alliances and minimizing traditional hierarchical arrangements are critical to opening up effective channels of communication. This is consistent with other research (Floyd and Fung, 2017; Kok and McDonald, 2017) indicating that internal boundaries can reduce inter-organizational coordination interfering with knowledge sharing, innovation, and trust. Thus, a boundary spanner can positively impact relationships with stakeholders external to the organization by improving communication within their home organization.

As the healthcare sector becomes more fragmented, community boundary spanners are being used to connect disparate groups in hopes of improving the flow of information between communities (Long et al., 2013; Wallace et al., 2018). The key challenge is to reduce health disparities by improving relationships across organizations and socio-economic boundaries. Boundary spanning has the potential to facilitate the transfer of specialized knowledge or resources and remove structural holes or barriers that have the potential to isolate communities reducing access to appropriate medical care.

The idea of using boundary spanners to provide effective leadership within a community-based context gained momentum after a 2008 study by Miller focusing on exceptional leadership within university-school-community partnerships. Miller concluded that

individuals with contextual knowledge, interpersonal skills, and high levels of trust could successfully connect dissimilar groups within a community. Furthermore, loyalty to the community and a desire to share knowledge and advocate for those who have been traditionally marginalized increased one's ability to effectively communicate, problem-solve, and increase stakeholder collaboration.

Utilizing boundary spanning as one method of developing informal leadership is valuable to organizations in both Western and Eastern cultures. The evolution of leadership in today's interdependent world requires respect, connection building, intersection of group boundaries, and collaboration toward a common vision. Liu et al. (2018) examined how boundary spanning behavior impacts task performance when mediated by the emergence of informal leadership and hierarchical power inequality (power distance). They discovered that individual boundary spanning is not only an important predictor of leadership emergence, but is positively associated with task performance. In addition, the study revealed that power distance moderates the effects of boundary spanning and has the potential to weaken a boundary spanner's position as an informal leader. Power distance refers to an individual's ability to accept inequality in power; low power distance means individuals expect equality in power and do not accept a leader's authority just because of the leader's position. Researchers have revealed that using boundary spanning activities to improve cooperation, knowledge sharing, and trust between teams at varying levels within an organization increases the likelihood that information exchange across external borders will occur, resulting in better team performance (Choi, 2002; Marrone, 2004). A study done by Liu et al. (2018) demonstrated the multilevel nature of boundary spanning and its usefulness to organizational teams by increasing opportunities to cultivate and improve social networks not only between peers, but also with external stakeholders in order to gather knowledge, share information, and solve problems.

Building Trust Between Stakeholders

Research has found that boundary spanners originate more frequently from private and societal organizations and less from governmental agencies (van Meerkerk and Edelenbos, 2014). The challenge for a government agent acting as a boundary spanner is great, especially when the issue at hand involves numerous scales of governance. Typically, boundary spanners representing public agencies have limited autonomy, which many participants see as undesirable. Studies show that the higher the autonomy of a boundary spanner the more likely she is to develop trust between stakeholders (Williams, 2002; van Meerkerk and Edelenbos, 2014; Thompson et al., 2016). This area, comparing the boundary spanning capacity between private and public actors, however, requires much more study.

Ultimately, boundary spanners attempt to build trust in order to establish solid relationships and improve collaboration between diverse stakeholders. Many are highly sensitive to and skilled in bridging interests and organizations. Numerous studies have shown that trust increases between stakeholders as they participate in the collaborative process (Ostrom, 2003; Davenport et al., 2007; Stern, 2008; van Meerkerk and Edelenbos, 2014). Furthermore, trust has been shown to develop in informal network structures (Edelenbos and van Meerkerk, 2015), and boundary spanners are crucial to creating spaces of interaction so that collaboration can occur. A study done by Coleman and Stern (2018) on three-forest landscape restoration collaborative demonstrated the advantages to using a boundary spanner to help stakeholders agree to rules and procedures, which created a safe place for discussion. This structure allowed participants to express their views and concerns within the participatory process. One boundary spanner from Collaborative A commented, "I like structure; people can trust that they're safeguarded, that there's venues to be heard, there's processes that are supported by the group, whether we like what someone might want to discuss or not, there's a freedom in the structure to allow for, like, a group, like a joint fact finding on an issue if there is a disagreement about it, and we can trust that will happen" (Coleman and Stern, 2018, p. 7).

Increasing Social Learning Capacity

Austin (2002) showed that much of a boundary spanner's work is focused on community practices; that is, on external relations between the organization and its community and on balancing those with internal demands. Boundary spanners devote time to building inter-organizational relationships, as well as pay attention to external issues, build community partnerships, and cultivate a learning organization culture. They create multiple pathways for a community to learn about each other's values, experiences, and skills (Alexander et al., 2016; Coleman and Stern, 2018; van Meerkerk and Edelenbos, 2014). Boundary spanners are critical to "social learning systems" by creating and enacting novel structures of social interaction (Kerson, 2002; Wenger, 2000). Thus, increased social learning ought to enrich the capabilities of IWRM participants.

Power Imbalances

Imbalances of power within the participatory process can leave a boundary spanner struggling to retain and/or engage stakeholders. Stakeholders who feel inadequate because of power or resource imbalances often complain of feelings of exclusion, inequality, and hierarchies. Alexander et al. (2016) revealed that people in governance networks involved with community-based conservation initiatives had to be cognizant of powerful or more influential stakeholders who attempted to control the types and sources of

knowledge. Stakeholders that are more powerful can manipulate social learning and affect the level of trust and collaboration that is formed, thus undermining the participatory process. In these instances, it is critical that boundary spanners find strategies to defuse those behaviors and outcomes. Identifying the core values and interests of a diverse group of stakeholders can be achieved with time (Pretty, 2003); however, key actors need to create the space required for these differences to be deliberated (Lejano et al., 2013; Alexander et al., 2016). Wald et al. (2017) maintain that egocentric behavior within the participatory process of natural resource management must be overcome to establish trust and collaborative behavior.

When control of resources or access is unequal, interventions must occur or those participants with less power will reduce perspective taking and turn away from further collaboration. Previous studies suggest that perspective taking is a key to shared understanding, social bonds, and collaborative behavior (Cialdini et al., 1997), and if stakeholders are unable to develop secure relationships, the collaborative process is at risk. Imbalances exist with not only power or resources, but also ability (Ansell and Gash, 2008). Local stakeholders may not have the skill or expertise to engage in complex or highly technical decision-making deliberations (Yang and Pandey, 2011).

One example of a perceived imbalance of power in the United States occurred during the Platte River Collaborative Watershed Planning Process. Conservation advocates complained that the negotiating table was “uneven and weighted toward development interests” (Ansell and Gash, 2008, p. 551). Since development interests and environmental advocates can have widely diverse capabilities, the collaborative process often favors well-organized and more powerful interests. Some stakeholder groups are spread out and lack the necessary organizational infrastructure placing them at a disadvantage.

Scale Mismatch

Boundary spanners can help overcome inevitable challenges to participants in IWRM related to difference scales of governance and geography. Scale of governance mismatch, experience of the facilitator or project manager, prior conflict between stakeholders, and degree of autonomy of the boundary spanner can add both positive and negative dimensions to the collaborative process. It is important that boundary spanners identify patterns and dimensions of stakeholder group identities early on especially when varying scales of governance are at play (Cheng and Daniels, 2005). Recognizing that watersheds often occur at multiple geographic and jurisdictional scales, boundary spanners need to be cognizant of participants’ unique needs and values. In this way, they can develop a sense of community encouraging stakeholders to connect and identify with others’ concerns about the watershed and community as a whole (Cheng and Daniels, 2005).

Findings by Cash et al. (2006) reinforce the idea that knowledge is perceived differently at various levels or scales, which is a result of individual perceptions as to what is credible, valuable, and legitimate information, and whether or not it is important. This “plurality challenge” (Cash et al., 2006, p. 6) can be addressed by a boundary spanner since this individual acts as an intermediary between the different levels or scales, perceptions, and interests, by assisting in the co-production of knowledge. This type of cross-sector, multi-stakeholder collaboration creates a more comprehensive watershed-based management approach (Enloe et al., 2017), allowing for a variety of discussion and debate.

Autonomy

Results of research on collaborative engagement consistently emphasize the importance and significance of stakeholder perceptions toward other stakeholders, whether stakeholders be from public agencies, nonprofit organizations, or the local community. The notion that stakeholders perceive boundary spanners as somewhat independent or autonomous from their home organization is also significant and the key to successful collaboration. Schotter et al. (2017), whose study was primarily conducted on boundary spanning in global organizations, acknowledged that a boundary spanner’s actions and effectiveness are influenced by both the organizational structure of one’s home institution and that individual person’s capabilities. That being said, boundary spanners can be viewed as direct representatives of their organizations tied to its beliefs and values, lacking autonomy and an unbiased voice. In addition, managerial motivations and one’s business identity can adversely affect their actions and effectiveness. Because a boundary spanner’s role is to cross-organizational borders and make connections, she is more effective when given a certain amount of autonomy to engage constructively with other actors (Williams, 2002).

Conflict

Stakeholders who have experienced a history of conflict with another actor in the IWRM process are more likely to express low levels of trust presenting a challenge to boundary spanners. Tense and conflicted history between participants is likely to result in lack of commitment and participation as well as feelings of suspicion and distrust (Ansell and Gash, 2008). On the other hand, blind trust and unusually high interdependence among groups of stakeholders may discourage collaboration among a wider set of actors. Ansell and Gash (2008) suggest that factions of any kind within the participatory process are less likely to favor collaboration. In those instances, when stakeholders come to the table with predetermined feelings and perceptions, boundary spanners must

work to remediate those low levels of trust and social capital. In fact, when there is a prehistory of conflict among participants, the development of trust becomes the most important aspect of the collaborative process.

Cooperation

The absence of conflict does not always result in cooperation or cohesion within the IWRM process. Participants, for one reason or another, may refuse to acknowledge perspectives different from their own. This may be the result of stakeholders not being given enough time to develop strong relationships, the complexity of the resource issue, feelings of marginalization, or other factors. The boundary spanner's role in this situation is more challenging yet can be overcome with early and transparent communication, continued inclusiveness, and more face-to-face interactions between stakeholders (Megdal et al., 2017). In those situations, where interest conflicts are not a significant factor, boundary spanners can work on improving the efficiency of the IWRM process. For example, a 1-day participatory workshop in Koraro, Ethiopia offered stakeholders an opportunity to share their understanding and perspectives of a water management project that directly impacted them. Agency officials discovered after listening to stakeholder concerns that a one-size-fits-all approach was ineffective and costly, and failed to acknowledge local citizens' preferences (Megdal et al., 2017).

Although boundary spanners strive to promote learning and build competence during the participatory process, the system is not always effective resulting in divided stakeholder relations. Because knowledge sharing is critical to strong cross boundary cooperation, boundary spanners can focus their energies into the quality of the engagement process. Utilizing experts and serious gaming (or role-playing) improves social learning and provides participants the opportunity to explore.

Summarizing Boundary Spanning and Integrated Water Resource Management

The bundle of attributes and abilities that define a boundary spanner is unsettled; nevertheless, an effective combination of the following characteristics is necessary to overcome the barriers needed for long-term stakeholder engagement: demonstration of independent thinking, good listening and communication skills, competence in power management, neutrality, and high integrity (Williams, 2002; Pirson and Malhotra, 2011; Delaine et al., 2015; Coleman and Stern, 2018). In some organizations, upper management chooses boundary spanners because they are well connected within their home organization and are perceived as trustworthy (Schotter et al., 2017). On the other hand, others are individuals who become involved because they want to be an active change agent or cross boundaries and establish lasting relationships (Williams, 2002). Boundary spanners who are perceived by stakeholders as more independent are often considered more trustworthy and viewed as less likely to have a hidden agenda (Thompson et al., 2016).

The specific role of the boundary spanner is critical to a successful IWRM process. The primary objective of a boundary spanner is often to create an environment where diverse stakeholders feel confident to express their opinions, share knowledge, and accept vulnerability thus leading to better collaboration and trust between participants. Boundary spanners who can make the decision-making process more transparent and less contentious encourage more knowledge sharing and participation from stakeholders. Of particular interest to the IWRM process is how boundary spanners can assist with information sharing, which includes both scientific and local knowledge. Grygoruk and Rannow (2017) refer to this as "horizontal interactions" and support the idea of using boundary spanners to help bridge that gap between complex scientific data and stakeholder needs. Sharing scientific and technical information at a level of comprehension, which can be not only understood but also applied, helps facilitate wider stakeholder participation, dialogue, and the associated social learning process that may take place in small group settings. Such information is valuable and should be utilized to aid in decision-making, but as Muñoz-Erickson et al. (2010) point out, disputes over expert knowledge can become a central point of conflict. These debates over issues of fact or information can incapacitate a collaborative process. It is critical that boundary spanners minimize the "us v. them" mentality between groups of stakeholders so that the conflict does not become so deep-seated that participation ceases.

Without a doubt, a primary focus of a boundary spanner is building sustainable relationships. IWRM involves individuals from a variety of professional and organizational backgrounds; thus, these collaborative encounters require boundary spanners to not only recognize but also manage these differences (Williams, 2002). This can be achieved by a boundary spanner maintaining a high degree of contact with her internal organization as well as the external environment. Zhao and Anand (2013) point out that boundary spanners dealing with highly technical or scientific information must often grapple with its complexity, and then must process, filter, and feed that information to external stakeholders. The challenge lies in ensuring that the information is not so distorted or complicated that stakeholders feel excluded and unwilling to negotiate.

As a result of their study on boundary spanning in global organizations, Schotter et al. (2017) realized the advantages to utilizing individuals who can interpret and clearly communicate complex information to others in negotiations. The researchers concluded that boundary spanners' work be modeled after a rubber band allowing for flexibility in mediation. This flexibility permits stakeholders within IWRM to act independently but still change directions when applicable in order to demonstrate alignment with others. Participants benefit from this type of participatory process because they can stretch to accommodate different perspectives yet remain within the confines of their organization's plans and policies. As boundaries become more complex with the addition of more diversity and perspectives, the advantages to the rubber band principle increase.

Even when IWRM stakeholders' interests conflict significantly, research has shown that the presence of a boundary spanner within the participatory process has been positive (Williams, 2002; Klijn et al., 2010; van Meerkkerk and Edelenbos, 2014; Coleman and Stern, 2018). Establishing sustainable and working relationships in complex networks takes on a variety of forms yet the primary goal is the same: cross borders, establish effective connections, facilitate good information exchange, and seek out shared meanings between stakeholders. Although boundary spanners seek to establish personal and lasting relationships between diverse participants and organizations, the danger of creating too tight of a relationship must be recognized. Williams (2002) warns that those networks that are overly reliant on these personal relationships may suffer when the boundary spanner leaves the network.

Conclusion

Although the opportunity to build trust between stakeholders within the IWRM process is crucial to collaboration and policy development, a boundary spanner's role reaches beyond simply trust building and facilitating communication. Today's water managers and political leaders face multiple challenges: climate change, natural events such as flooding and drought, the increasing impacts and risks associated with industrial discharge, urban sprawl and an ever-increasing global population. Those involved with IWRM must consider and engage with multiple actors with diverse perspectives and perceptions in hope of achieving collaboration across various sectors, organizational or geographic boundaries, and political alliances. Reaching across boundaries requires individuals who have the temperament to resist political pressure and provide balanced and accurate information. Environmental policy is often not based solely on scientific evidence, but rather influenced highly by human dimensions. Boundary spanners have the opportunity to work with and educate scientists, policy makers, and citizens on how to engage more effectively in public discourse so that environmental policy decisions are based on accurate and timely data and more readily accepted. (Cvitanovic et al., 2017). A goal of boundary spanning is to reduce the risk that science not meet the needs of decision-makers; the ability to identify contradictory evidence and conflicting perspectives early on in a process may minimize damage to further collaboration. Water management decisions must be seen as legitimate and not a vehicle for pushing particular agendas; scientists and others who have the skills to effectively inform policy at the right moment are needed. Bednarek et al. (2018) identifies these opportunities as "policy windows", and the opportunity to capitalize at these moments increases the likelihood that water policy decisions will be evidence informed and accepted by stakeholders.

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Leadership for Sustainability: Generative Engagement for Change

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Abstract

Countless people are leading the charge toward sustainability thinking and action, and it's not enough. Given the increasing urgency of human-caused climate change and its inevitable destruction, an expanded view of leadership—as generative engagement for change—is more essential than ever before. This article outlines twelve keys for generative engagement which begin with each individual challenging assumptions and beliefs about where humans stand in the complex, interdependent processes of life-as-it's-happening among millions of species within our shared ecosphere. Anyone who cares is called to embrace the role of “leader” and practice engaging—generatively—with others and our shared dilemmas.

My grandson, Sam, was 11 years old when I published my first article outlining the need for an expanded view of leadership for sustainability (Ferdig, 2007). I described sustainability leadership as “an emerging consciousness among people who are choosing to live their lives and lead their organizations in ways that account for their impact on the earth, society, and the health of local and global economies.”

Sam is now 24, working as a civil engineer for a major construction company in Chicago, Illinois. I ask myself, what has changed in the 12 years since I wrote about an emerging consciousness among people who care? I was concerned in 2007 about Sam's future as well as millions of children around the world. I'm no less concerned today as he and other once-children join the “order of grownups” who are presumably doing something to reduce the existential threats to human life on this planet.

“Our leaders are behaving like children!” Greta Thunberg, a Swedish teenager, said to world leaders at the United Nations Climate Change Summit in December 2018 (Holter, 2018). Her words were notable for those of us in the United States who are concerned as we watched our president announce the US withdrawal from the Paris Climate Agreement while eroding environmental protection policies in the United States. It seems we have not yet begun to recognize our interdependence as members of the human species, much less our interdependence among millions of species within our shared ecosphere.

The Past 12 Years

Much has changed in the past 12 years, as things do in complex processes of life happening in and around us moment-to-moment. People grow old as children grow up and economies ebb and flow. National leadership shifts with new elections and changing politics. The drug epidemic reaches crises proportions while scientists continue to conduct knowledge-expanding research, making remarkable advances in the fields of genetics, medicine, technology and neurology to lengthen and enhance the quality human life.

Climate scientists are urgently telling us that human-accelerated climate change is worse than they first thought. CO₂ levels are well beyond acceptable limits for life as we know it on this earth, glaciers are melting and water levels are rising more rapidly than previously estimated. Fresh water supplies continue to dwindle even as desalination research becomes more promising. Destructive storms, flooding and uncontrollable fires are becoming more frequent and intense costing too many human lives and billions of dollars. While the causes of changing climate patterns are many, the burning of fossil fuels and animal agriculture are two of the biggest contributors, along with deforestation according to the United Nations Intergovernmental Panel on Climate Change (IPCC), (2018).

Scientists further estimate that we are now losing species at 1000–10,000 times the natural rate, severely compromising the biodiversity benefits required for healthy ecosystems (Chivian and Bernstein, 2008). Human-accelerated climate change, deforestation, habitat loss, unsustainable agriculture, pollution and pesticides are contributors to rapid extinction (Earth Day Network, 2018). Kolbert describes the sixth mass extinction that is unfolding before our eyes. “There have been five comparable crises in the history of life on Earth,” she writes, “but this one is different: It's being caused by us” (Kinzig, 2014).

Equally dramatic has been the growing trend toward nationalism around the world, an apparently increasing need to distinguish between “them” and “us”, the people or nations we trust and those we can't, don't or won't. People fleeing oppression and violence in search of refuge are increasingly met with resistance wherever they go. Though we haven't yet begun to experience the massive migration to occur as communities along coastlines lose landmass to seawaters (Wallace-Wells, 2019).

Ideological polarities, such as, progressivism vs. conservatism and socialism vs. capitalism appear to be solidifying in the minds of neighbors, acquaintances, and family members who once shared similar enough views they could have thoughtful conversations about differing perspectives. Religious intolerance, growing disparity between the wealthy and poor, institutionalized injustices toward women and people of color, are examples of the complex variables that contribute to the steady hum of dissonance that too often erupts in random displays of hatred and violence.

While much good has happened in the last 12 years; overall, it's hard to say things have gotten better. It's as if the complex, unprecedented challenges of our day have prompted responses within society that are pushing us farther away from understanding ourselves and each other as part of the interrelated and interdependent web of life on earth.

Sam, I welcome you to the ranks of grownups who not only care about people, the natural environment, and finding solutions to the dilemmas we have created for ourselves, but are also willing to explore what it means to be a sustainability leader.

What Does It Mean to Be a Leader for Sustainability?

We learned a long time ago that meaning is in people, not words (Korzybski, 1958). When working with others I've found that tying down concepts according to textbook meanings tends to hamper the thinking processes underneath what it takes to bring a term such as "sustainability" to life in each situation. Though we can ground our thinking about sustainability in the Brundtland and United Nations World Commission on Environment and Development (WCED) (1987)—essentially, living today without compromising the resources needed for others to live in the future.

Numerous writers have adapted the concept of sustainability to fit business (Elkington, 1998) and community planning (Steward and Kuska, 2011) as well as other applications and contexts. Collectively, they tend to feature concern for the natural environment in concert with interrelated concerns for people, profitability, economic and socio-cultural realities, technologies and public policies.

Though whatever the application, for me, sustainability thinking and action becomes meaningful when people begin to consciously shift how they see themselves in relation to one another and the complex processes of life that are occurring in and around them every day (Ferdig and Ludema, 2004).

A "leader," as we use the term at the Sustainability Leadership Institute (SLI), is anyone—regardless of background, social standing, expertise or positional power—who takes responsibility for understanding and generating workable solutions WITH others for the ordinary and overwhelming challenges we encounter day-to-day.

Leadership, in SLI's view, is about the capacity to engage generatively with others to resolve problems, make decisions, and participate in meaningful action. It requires a conscious shift in how we see ourselves in relation to others and how we consciously or unconsciously assume the role of leader in today's society. It means letting go of the idea of leader as the one who knows, who is a visionary, strategist, expert, or the one who provides direction for a pathway forward. It also means letting go of self-certainty and ego that smart, often passionate, people who may think of themselves as leaders, tend to carry along with themselves as they offer their solutions and presume to guide others toward their suggested solutions for success.

There are innumerable books, models and theories of leadership that have direct relevance for sustainability leaders ranging from transformational leadership (Burns, 1978), to transactional leadership (Bass and Avolio, 1994), democratic leadership (Lewin et al., 1939), self-organizing leadership (Knowles, 2002), distributed leadership (Vygotsky, 1978; Spillane et al., 2004), participative leadership (House et al., 2004), resilient leadership (Duggan, 2009; Everly Jr. et al., 2009), regenerative leadership (Hardman, 2011), and collaborative leadership (Chrislip and Larson, 1994). Though none I've studied so far focus specifically on the perspective and practice of generative engagement as highlighted in this chapter, and which, I assert, is a fundamental component of leadership for sustainability.

The human heart longs for the health, safety and well-being for ourselves, our families, colleagues, neighbors, and by extension, people in our communities around the world. We long for a healthy earth, healthy democracies, healthy places to live and work with colleagues, friends and our families that sustain us. This longing surely transcends national identity, political party, economic standing, ethnic origin, and differences in our education.

Sustainability leaders recognize and tap into human longings in themselves and others. They recognize the dissonant undercurrent that appears to be growing stronger, louder, and more menacing each day. They work at becoming informed and aware, inspiring themselves, friends, family and neighbors to participate in meaningful change.

No doubt our ranks are growing. More and more businesspeople, social entrepreneurs, community activists, natural and social scientists, foundation administrators, and everyday neighbors are waking up and talking about the threats we are facing. Universities are embracing interdisciplinary sustainability-related curricula and forming consortiums with other universities for sustainability-minded activity (Hardman, 2011). Even a few politicians are speaking up about the threats of climate change (Hirji, 2019).

However, if we're serious about leading sustainability thinking and action, we must learn what it means to engage generatively, beginning within ourselves and working outwardly to engage with others and our circumstances locally and globally. Below are some keys for getting started (Table 1).

Table 1 Twelve keys to generative engagement as leadership for sustainability.

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1. Discerning the Generative Engagement Difference
 2. Understanding Human Engagement through the Lens of Science
 3. Dancing with Rhythms of Change
 4. Appreciating Institutions as Verbs
 5. Recognizing Unique Lifeviews and Embedded Cultural Paradigms
 6. Practicing Conscious Awareness
 7. Pausing, Reflecting, Meditating
 8. Being Ourselves with Others
 9. Managing Ourselves
 10. Embracing Conflict Fearlessly
 11. Watching our Language
 12. Learning as a Way of Life
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Twelve Keys for Understanding and Practicing Generative Engagement as Leadership for Sustainability

Over a lifetime of observations, experiences and study, I've learned that challenges are best resolved among those who are most immediately impacted by them, and who chose to engage in authentic interaction—whether in workplaces, boardrooms, city council meetings or living rooms. Further, I've learned that the processes for finding workable solutions are significantly enhanced by relational qualities of freedom, inclusion, inquiry, spontaneity and a shared belief in what's possible (Ferdig and Ludema, 2004).

Action research (McNiff, 2017; Reason and Bradbury-Huang, 2001) —systematic learning while doing— coupled with grounded theory development (Strauss and Corbin, 1998) have particular application in social science research in which circumstances call for immediate action, and learning occurs in the processes of participating in the development and practice of alternative actions. My tenure at a Midwestern electric power utility, as well as consultancy in the utility industry, small businesses, government, and nonprofit organizations, not to mention my personal and family relationships, have provided innumerable opportunities for formal and informal action research and learning as well as on-the-ground theory development.

Below, I describe 12 keys for understanding and practicing what I refer to as “generative engagement” developed from my accumulated learnings. I present them as an invitation to consider and begin to experiment with generative practices. Please note the terms “communication” and “human interaction” are used interchangeably with the term “engagement”

1. Discerning the Generative Engagement Difference

Communication—engaging with others and the world around us—is at the center of everything we do. We learned at birth it was an effective means of exercising power and control to get what we want in the form of food and warmth. As we matured we refined our ability to engage strategically: we learned stuff in school, how to have fun, make friends, get dates and ultimately engage with others in our work and personal lives to help make things happen.

Ego and self-interest have a way of creeping into our strategic engagement. Persuading people of our ideas because we believe they will benefit the greater good can be an ego-driven trap. Deception, too, is an engagement strategy for achieving our goals; information can be distorted, withheld, or generalized rendering it misrepresentative or meaningless.

Generative engagement doesn't resort to deception, manipulation or planned strategic advantages to achieve preconceived outcomes. Reciprocal engagement requires an awareness of our interactive and interdependent processes for generating life as it is occurring in the present moment. At the core of generative engagement are humility, a spirit of inquiry and an ethical responsibility to self and other. It means consciously bringing into existence with others what is mutually valued: for example, understanding, trust, good ideas, goodwill, forgiveness, hope, and synergistic energy for finding sustainable solutions.

We choose to engage generatively because we know that our own well-being, and that of those we love, depend on the well-being of the interconnected, interdependent network of life of which we are an inseparable part.

2. Understanding Human Engagement through the Lens of Science

The sciences of physics, biology, chemistry, computer technology and others have given credence to an emerging view of our reality not unlike the view that philosophers and spiritual teachers have been telling us for centuries: everything is interconnected. Not only are matter and energy—living and nonliving—interconnected and interdependent, they are continually moving and changing in response to one another and their circumstances through self-organizing interactions (Kauffman, 1995).

Complexity is simply a term that describes life as it's happening. It reflects the continuous life-giving processes of interaction among entities—atoms, molecules, organs, humans, plants, animals, ecosystems, cities, states, planetary bodies—that create connection, movement and change through relational interdependence. Complexity processes reveal anomalies and paradoxes that appear naturally in ongoing interactions; turbulence can build on itself, sometimes creating major perturbations that result in radical shifts in the interactive patterns, structural form and physical identity (Prigogine, 1996; Lichtenstein, 2000).

Focusing on human processes of interaction from a complexity perspective has profound implications for how we choose to see the world and ourselves in it, and how we choose to think and behave with one another in everyday circumstances.

Everything we do involves interaction in some form whether planting petunias, making a cup of tea or cocreating societies, governments, cities, products, services, wealth, poverty, climate change, other problems and their solutions. We are, right now—every moment—cocreating the world in which we live through our interactions within ourselves, with each other and our environments.

The frequency of interconnectivity among people and ideas, and the speed with which volumes of information can be accessed as a result of the internet, reveal valuable information in new configurations that contribute to previously unimaginable solutions. Though information exposure can also make it difficult to discern that which is valid from that which is wrong-headed, incomplete, obsolete and intentionally deceptive.

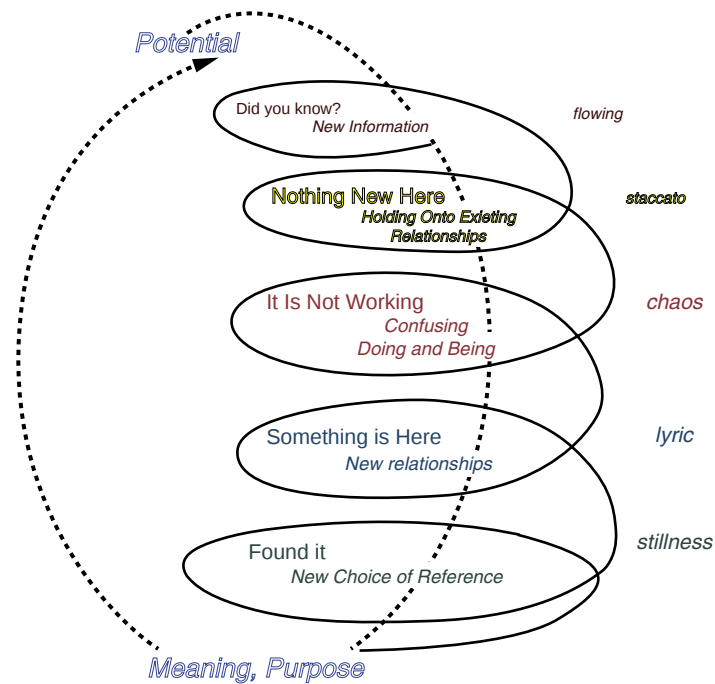
The processes by which we humans engage with one another and circumstances in our individual worlds—all seven billion six hundred million and counting of us—impact our relationships with one another and our natural world wherever we are (Louv, 2012).

3. Dancing With the Rhythms of Change

Learning to understand, accept, and navigate the complexity around us flies in the face of everything we think we know. It asks us to detach ourselves from desired outcomes, to let go of certainty, control and predictability in favor of emerging possibilities. It invites us to rethink the experience of changing.

Moore (2002) drafted a sketch to conceptualize the rhythms of change from a complexity perspective (Table 2).

Table 2 The rhythms of change.



Potential represents infinite possibilities, mostly unimagined; it is complex, unbounded, unquantifiable, unqualifiable.

Flowing is the first rhythm of change as we think conceptually. When energy and information are flowing and we are moving with the flow, our own energy is in sync with what is unfolding. We move along without disruption. Things are as we expect them to be.

Flowing is interrupted by the sensation of *Staccato*, a feeling of being abruptly disconnected. Some complexity writers might call this a perturbation, a subtle indication that something is changing. We may feel startled, surprised, jarred or blocked in some way.

When information continues to be so disconfirming that we literally feel things are breaking apart, we are in the abyss of *Chaos*. Our mental models for making sense of things no longer hold up. We try to control, hang on, leave, dispel our anxiety by doing something ... anything. Nothing seems to work.

When we are learning, we lean into our anxiety. We see that our resistance can teach us about what is important to us and why it is worth saving, or not. In *Lyric*, which is light and graceful, we slow down so we can attend to what has emerged. Our energy is paced, we are able to rest and think more clearly.

When we move into *Stillness*, we see ourselves differently. Our choices of reference—how we refer to ourselves in the new scheme of things—develop and expand. We begin to identify with a larger whole—something outside of ourselves that has value for us. We have a greater sense of relatedness and connection which quiets and replenishes us.

(Moore, 2002)

While Moore's drawing implies a linear progression through change, we know from experience that changing is anything but linear and orderly. Most of us have likely experienced a crisis in some form and found that we did, indeed, know how to recover and adapt to the new situation.

4. Appreciating Human Systems as Verbs

We tend to think of human systems as nouns, a reasonably stable entity with a boundary and identity to which we attribute objective, solid, human-like characteristics. Doing so lets us get away with assuming, when a problem arises, that it's a "systems problem." This way of thinking, speaking and behaving tends to reinforce a belief that "the problem is out of my hands," and, instead, is lurking somewhere in a dark corner of a system (Stacey, 2000a,b). As a result, nothing much changes, if at all.

Similarly, we tend to anthropomorphize a system's workings as if it's a human being. An organization is said to have a vision, mission and human-like values. Systems are often accused of not communicating with one another. The US Supreme Court even passed a ruling that says corporations possess personhood distinct from the individual human beings that comprise them, that is, their owners or stockholders, members of their boards of directors, managers and employees.

Complexity-process thinking reminds us that corporations, institutions, organizations, and other so-called systems comprised of human beings are, in fact, not nouns. They are processes of movement and change among people who are in continuous interaction with one another and their circumstances in relatively close proximity (electronically or physically) within more or less permeable boundaries.

Social theorists (Stacey, 2000a,b; Mead, 1934; Elias, 1989) suggest that an organization, or a collective of individuals, and the respective individuals participating in interactions related to the collective are two aspects of the same moving, changing, self-organizing and evolving processes, each forming and being formed by the other through continuous interaction in relationship as depicted by the Möbius strip below (Fig. 1).

Interdependence among elements of a moving, changing phenomenon suggests each is both enabled and constrained by the other in fluid self-organizing processes of interaction. The phenomenon of enabling constraints within the self-organizing processes of interaction represent a naturally-occurring means of control that inhibits the possibility of "spinning out of control" as more traditional thinkers might worry about.

5. Recognizing Contrasting Lifeviews and Embedded Cultural Paradigms

Each of us processes information through our unique lifeview filters. No two lifeviews are identical any more than our finger prints are identical. Our lifeviews are the result of our unique genetic makeup coupled with our accumulated experiences and influences since birth. Our lifeview filters tend to dictate how we see, interpret and understand what is going on around us, which in turn, inform our communicating actions. Included in our lifeviews are embedded cultural paradigms—worldviews—of which we are mostly unaware (Bois, 1978).

Most of us are familiar with Kuhn's (1997) idea of a "scientific paradigm" as an accepted theoretical framework in any particular discipline; and a "paradigm shift" as a revolutionary phase when discontinuities and anomalies in a particular discipline begin to erode long-held assumptions that prompt conceptual breakthroughs to new ways of understanding the natural world. The transition from Newtonian mechanics to quantum physics is an example.

One can trace elements of a still dominant cultural paradigm—worldview—in Western society today at least to the mid-17th century when empirical positivistic science methods, relying on reductionism, proofs of linear causality, measurement and objective determinations of truth or falsity prevailed.

Discoveries in positivistic science, in turn, fueled an industrial revolution that flourished about a hundred years later in the mid-to late 18th century. As manufacturing became the new driver of progress, scientific management (Taylor, 1911) and organizational structures (Weber, 1983) that featured hierarchy, control, standardization and measurement for organizing people and their work became commonplace in factories, workplaces, the military complex and ultimately educational and public governance institutions. Economic systems favored competition, profitability and accumulated wealth. Exploitation of natural and human resources contributed to the engine of a prospering society.

Generative engagement invites us to examine our ingrained lifeviews and cultural worldviews—assumptions and beliefs to which we've been enculturated and likely can't see them as anything other than "the way things are." Complexity-thinking in science is contributing to emerging conceptual views about how the world works and where humans stand in relation to the processes of life occurring in and around us. On one hand, we know about and espouse these new conceptual views as we go



Fig. 1 A Möbius strip while it appears to have two sides has a surface with only one side and only one boundary. It has the mathematical property of being unorientable. As such, it serves as a metaphor for the inseparable relationship between the individual and the collective, each forming and being formed by the other.

about our business. On the other, if we look closely at ourselves and others in the context of our everyday interactions, we can begin to notice the extent to which we're still mostly stuck in traditional ways of thinking and behaving.

Table 3 illustrates a distinction in embedded worldviews. By now I'm sure you've noticed the inherent flaw in the table as it appears. Presenting information as an either/or dichotomy is itself a reflection of a traditional point of view. While doing so may be a useful device for explaining variations of thinking, it entirely misrepresents the both/and features of our paradoxical reality.

Generative engagement may be best understood from an expanded postpositivistic, complexity point of view; however, there are times when more direct, controlled and predictive thinking and action may be called for. The value of starting from an expanded perspective is that the choice to operate from a traditionalist point of view in a particular set of circumstances involves conscious, self-monitored interaction intended to contribute to the overall generative dynamics for cocreating workable outcomes for a particular challenge.

6. Practicing Conscious Awareness

We all presume to be conscious when we're not in bed, asleep or anesthetized on an operating table. And certainly we're aware of what's going on around us just to make it through a day. So what's the big deal about conscious awareness?

From a generative engagement point of view, conscious awareness is an art to be developed and continually practiced. It mostly means intentionally paying attention to what's less visible in and around the things that grab our attention. It means being sensitive to human energies and values in the present—our own and others—rather than blindly forging ahead doing what we choose to do without considering the impact of our interactions with others (Scharmer, 2009).

Table 3 Traditional worldview of reality and expanding worldview of reality.

<i>Traditional worldview of our reality</i>	<i>Expanding worldview of our reality</i>
Characterized by proven claims of what is so grounded in positivistic, reductionist, empirical observation implying objectivity, certainty and predictability.	Characterized by provisional claims of what is so which acknowledges the <i>paradoxical nature</i> of continually moving, changing, self-organizing processes of life emerging and, therefore, presumes objectivity and subjectivity, certainty and uncertainty, predictability and unpredictability occurring at the same time.
People observe reality from a position outside of the phenomena they observe and, therefore, can make objective claims about the truth or falsity of characteristics of said reality.	People are an inseparable part of the reality they observe; therefore, their observations, interpretations and claims about the truth or falsity of characteristics of said reality are inherently and paradoxically both subjective and objective and cannot be otherwise.
Knowledge is an accumulation of proven truths in the form of aggregated empirical data derived from controlled experiments and studies.	Knowledge is an accumulation of provisional truths in the form of patterns, themes and successive approximations derived from documented participant-observations occurring in a particular situation.
Change occurs in primarily linear and logical pathways forward in time and space leading from cause(s) to effect(s) and, therefore, are presumed to be reasonably predictable. If <i>this</i> happens, then we can expect <i>that</i> result.	Change emerges in linear and nonlinear, logical and nonlogical, pathways in the context of complex, self-moving self-organizing interactions and, therefore, are presumed to be predictably unpredictable and unpredictably predictable.
People can effectively control, manage, and influence outcomes by way of the power (in its various forms) they hold in relation to others.	People have limited ability to control, manage, and influence emerging outcomes given the dynamic power relationships inherent in the complex interactive processes of life happening.
Power can be attained and held by individuals and groups through various means (e.g., knowledge, information, position, physical force, and psychological manipulation) often unequal in relation to others.	Power is relational process that continually moves and changes in the context of complex interactions among individuals and groups in relation to their moving and changing circumstances.
Disagreement and conflict are the result of two or more individuals, and/or the organizations with which they identify, drawing inaccurate conclusions about an objective reality.	The relational and unequal power dynamics create natural tension that both <i>enables</i> and <i>constrains</i> emerging self-organizing outcomes within limits of control.
A paradox is contradictory information creating confusion, misunderstanding and, therefore, is a problem to be solved.	Disagreement and conflict are natural processes among individuals, and/or the organizations with which they identify, as they seek understanding of one another's unique perspective of a moving and changing reality.
Human engagement represents strategic human interaction for accomplishing desired outcomes, i.e., achieving agreement, developing a relationship, managing a work group, or expanding knowledge and understanding needed to fulfill individual, organizational or community objectives.	Paradox is a common feature of complex interactive movement and change creating dissonance that contributes to emerging novelty and change.
	Human engagement represents complex processes of human interaction occurring between and among interrelated, interdependent people engaging in a self-organizing phenomena of life perpetuating itself

Conscious awareness is a meta activity, something for which humans have a distinct advantage over most other life forms (Bois, 1978). For example, we are able to think about our thinking—which is a form of engaging with ourselves. In so doing, we might choose to challenge our long-held assumptions about a belief that may no longer hold water.

Conscious awareness—intentionally noticing—provides information from which we can evaluate and adjust our real-time interactions with an intention of cocreating space for generating understanding and mutually advantageous outcomes with another. Below are areas on which to focus one's awareness.

Being Aware of Oneself—The better you know yourself and the more comfortable you are in your own skin, the easier it is to be your authentic self with others. In addition to observing yourself in action and making real-time adjustments to strengthen a generative dynamic, you might also journal your thoughts before or after the fact. That act of writing can increase your clarity.

Being Aware of Others—This is the time to practice empathy, no matter how far you are from relating to another individual. Acknowledge the whole person: physical, mental, emotional, spiritual. What are they experiencing? thinking? feeling? What might have influenced their lifeview? Listen genuinely. Open yourself to learning. Check out your understanding of what you are hearing and seeing with them.

Being Aware of Immediate Dynamics and the Larger Context—Pay attention to nonverbal communication, that is, tone, expressions, posture, attitudes of people involved. Notice the feeling in the air, the invisible energy in the room. Do your homework to scan the larger environment of things that might affect the immediate circumstances and interactions as well as multiple perspectives related to the challenge at hand.

7. Pausing, Reflecting or Meditating

Stop! Let your practices for enhancing your awareness catch up with you. Find a dark sky and look up at the stars. Or a closet. Breathe slowly and deeply while you're there.

There are no rules for pausing, reflecting or meditating. Though doing so often requires deliberate action in our crazy, busy, high-pressure realities. The benefits, according to testimony by many who have learned to make this a daily practice, are many.

An NYU study of 20 meditators (Buddhist monks and nuns) detected numerous neurological benefits from meditating: (1) cultivates attentional skills, (2) points to an ability of the brain to change and optimize itself, (3) reduces the psychological wall between meditator and his environment, and (4) facilitates naturally-occurring self-reflection (Danzico, 2011).

There are as many ways to pause and meditate as there are people who do so: guided meditation, meditation with music, with others, lying down, standing up, seated a certain way, walking, or enthroned on a mountaintop.

Try closing your eyes and breathing deeply: in 1-2-3-4; hold 1-2-3-4, out 1-2-3-4, hold 1-2-3-4 and repeat for 2 min, then 10 min, working up to longer. Empty your mind of thoughts; when a thought appears, gently push it away. Be patient with yourself. It gets easier with practice.

8. Being Ourselves with Others

To be oneself with others is yet another paradox. We instinctively try to fit in with the crowd, put on our professional selves with clients, or put on our attractive, clever selves when going out on a promising date. We also know the feeling of being our "shoes off" selves when we're at home with trusted friends and family members.

Maybe there are parts of your core self you don't like and want to keep to yourself. Or maybe you think you won't measure up to who you want people to think you are, or what they expect you to be. Who is the real self in these situations? Of course they're all real. And yet, there's a core of who you are that sits at the center of your soul. That's the part that people want to know—and the part you want them to know when you're communicating generatively.

Being ourselves with others is a practice in honesty—first with ourselves (Morgan, 1976). Remind yourself of core integrity questions: Who Am I? What do I stand for? What am I up to? What do I hope to accomplish here? now? before I die? Speak truthfully. Tell it straight. Aim for transparency. But mostly, cut yourself some slack. You are a worthy person as you are. Be that person with others.

9. Managing Ourselves

As practices one through eight above imply, the only person over whom we have any significant control is ourselves and our own thinking and behavior (Stacey, 2000a,b). Others may choose to emulate our orientation and behaviors and, thus, relax into the rhythms and energy of participation, collaboration and co-construction of a shared reality. Or they may not.

Multiple orders of self—A simple way to imagine your capacity to manage yourself in the present moment is to think of multiple orders of yourself occurring simultaneously, each self having slightly more insight and control over the self just below. Your ACTOR self is at the base tier of being, and just above is the OBSERVER self that may have just watched the ACTOR self say something snarky to the difficult person you are negotiating with. The THEORIZER self above OBSERVER self recognizes that the snarky comment is not at all helpful for encouraging the generative dynamic you're hoping to cocreate with this person for finding genuine solutions. The DIRECTOR self, just above the OBSERVER self realizes the ACTOR self needs to act fast, humble itself immediately, and try to say something encouraging to dampen the expressed negativity (Bois, 1978). Most of us probably do some version of managing ourselves as described, but may not consciously direct our attention to do so when we are consumed with our ACTOR self doing its own thing in the dynamic swirl.

Assume personal responsibility—Assuming responsibility for our own thinking and actions that contribute—or not—to generative engagement may seem like a no brainer. Though in the heat of interacting with, say, belligerent or ill-informed people, assuming responsibility for generating understanding (Stacey, 2000a,b) goes a long way toward building relationships and resolving mutual challenges.

Hold ourselves accountable—Veteran Organization Development professionals, Howard and Sue Lamb, once introduced a term—DWYSYWD—to a power plant maintenance crew with whom we were working. The acronym stood for *Do What You Say You Will Do*. The next day the crew plastered a big sign on the power plant wall: DWYSYWD! I've noticed people come up with all kinds of creative tricks for holding themselves and each other accountable, once they acknowledge to themselves their responsibility for doing so.

Seek feedback—Talk to other people, your collaborators, workmates, nemeses and so on. How do they experience you and does it match how you see yourself? Sure their views will be subjective. So is yours. Work with it. It's good information.

Listen to ourselves—Trust your inner voice to give you clues, or maybe a shake down, if you're out of sync with what needs to be happening. Are you pretending you can stand outside the circumstances of which you are a part—judging, analyzing, blaming, intervening, advising or attempting to fix a problem? Or are you participating with a genuine intention to generate understanding and possibilities with people in a situation you probably helped to create?

Move with relational power dynamics—Power, too, moves through interactive processes instead of being held as a possession by some, and not others. While some people are more enabled or constrained than others at any given point thus making the relative distribution of power unequal, in time, people and circumstances inevitably shift and evolve in the dynamic interrelationship (Elias, 1989; Stacey, 2000b). It makes sense to be aware of changing relational power dynamics and move with them.

10. Embracing Conflict Fearlessly, Openly and Respectfully

Conflict is a natural phenomenon of our interactive processes and a fruitful source of learning and change that many of us haven't yet learned to appreciate and fully utilize. In fact, unless we're drawn to exacerbate conflict in what we see as a zero-sum game of COMPETITION seeking to win whatever the cost, we tend to turn ourselves inside out and upside down to ACCOMMODATE others, thereby failing to assert a potentially useful point of view, or to simply AVOID conflict altogether. We're sometimes able to get to a COMPROMISE through constructive interaction, each party giving up some to reach a workable agreement. Though, ideally, we COLLABORATE with the intention of jointly creating new ideas and better solutions than anyone could think up alone (Thomas, 1976).

In the cases of compromise and collaboration, we first have to acknowledge and respectfully confront our disagreements. Why not practice openly embracing conflict? Muster your courage and confront the sense of conflict you're experiencing with another respectfully, with empathy and compassion. Talk with them and listen carefully for understanding without trying to persuade them of anything. Think of the amplified emotional dissonance you and others may be experiencing underneath a conflict as a valuable source of creative energy that needs to be tapped.

11. Watching our Language

We construct our worlds with language and symbols. Yet, in so doing, we tend to forget that our language and symbols are *not* the things they represent, but merely tools we have to work with to generate shared meaning. Further, whatever the words or symbols we use, we can assume our intended meanings are filtered through another's unique lifeview sensory screen and will never be understood exactly as we intend, nor will we understand another's expression exactly as they intend (Bois, 1978).

This is so even when we communicate as carefully and truthfully as we can. Never mind the way we use language and symbols to intentionally or subconsciously misrepresent reality as we know it to be.

Nonetheless, there are practices we can use to help us make our language as accurate as possible as we seek to engage generatively with others (Korzybski, 1958; Bois, 1978).

- Recognize what are referred to as 'over/under-defined' terms, and there are many. Take the words 'sustainability' or 'leadership' as examples. They are under-defined, given that they are abstract terms that are understood uniquely by each who hears and uses them. Yet, they are also over-defined to the extent that would-be experts and writers attempt to nail down with reasonable certainty what the terms mean, and speak of them as if the words-symbols are the things they represent. A sustainability leader practicing generative engagement participates in processes for co-constructing meanings of concepts and terms in the context of their interactions with others in each particular situation.
- Avoid "allness" words when making a claim. For example, avoid words such as "always," "all," "never," and "absolutely" and so on. Be skeptical of others' claims that include all-inclusive words. Omitting such words helps to qualify the pretense of certainty. Rarely is anything always the case.
- Avoid making statements that imply what may have been reasonably true yesterday or a year ago is also true today. For example, "They were resistant to the idea a year ago, though that's not necessarily the case today."
- Avoid making generalized claims about a group of things on the basis of one or a few occurrences within the group that may appear to be the same but are not. Fearing black men wearing hoodies, suspecting police officers of corruption, or distrusting politicians are thought traps in which it's easy to get caught when we read news stories of specific incidents.
- Adding simple qualifiers to your claims can do the trick. State what's true for you without assuming it's true for anyone else. For example, "I have it be that you're entirely overreacting!" Other examples of qualifiers: "In my opinion, ...," "The last time I saw him ...," "From my point of view, ...," "This may be the case, depending on ...," "In this particular situation, ...," "For me,..."

12. Learning as a Way of Life

One can't engage generatively without presuming there is more to learn in any situation. We each naturally filter whatever gets through our mental membrane just to make sense of the infinite stimuli bombarding us every moment. Therefore, we can assume information is left out, maybe really important information (Korzybski, 1958; Bois, 1978). Further, because of our

complex, ever-moving and changing reality, nothing—including what we think we know for certain—stays the same from one moment, year, decade to the next (Stacey, 2000a,b). Information begets information, learning begets learning, new insights and discoveries are generated every day just as misinformation and false truths are generated, and sometimes actively disseminated, daily.

Thinking critically—evaluating the veracity of information we take in—is a very real part of learning as a way of life. Critical thinkers are skeptics—the opposite of a ‘true believer’ described by Hoffer (2010). Critical thinkers question, demand multiple points of view and validation for claims they and others make. Critical thinkers know there is seldom a single right answer to resolve a complex a challenge. Instead, they engage with others to expand their understanding and points of view in the processes of generating possibilities.

Two professors at the University of Washington, USA, designed and cotaught a course entitled, “Calling Bullshit: Data Reasoning in a Digital World.” Their goal is to attract students of every discipline and expose “one specific facet of bullshit” a week, thus enabling students to discern the veracity of information they hear in the news (McWilliam, 2019). This is a great example of learning as a way of life!

Action research and learning, the notion of formally and informally observing and learning while doing, as well as reflecting on what was learned after a situation, has already been mentioned as a key to understanding and practicing sustainability leadership as generative engagement.

Conclusion

My hope is that as you’ve been reading, you’ve been giving consideration to the idea of leadership for sustainability as generative engagement for understanding and responding to the dilemmas before us. Perhaps you’ll experiment with some of the practices. Maybe you’ll share an idea or two with others who care about humanity, the natural environment, and what it is we can do to begin to shift the trends of destruction, exploitation and inequity in our local and global communities. Our ability to engage generatively with ourselves, one another and our environments may be the sole means for evolving ourselves collectively toward a life-giving consciousness and future.

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Conflict and Criticism: The Role of Leaders in Influencing Environmental Behavior

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Abstract

Despite the overwhelming need for humanity to collectively cooperate in engaging in pro-environmental behaviors, there remains a constant and consistent trend of human behaviors which negatively impact environmental systems. Understanding the factors which contribute to environmental behavior and the ways in which this knowledge can be utilized to generate pro-environmental behavioral shifts is critical for the future of a sustainable human existence. In this article, I will evaluate the impacts of leadership on human behavior through communication, conflict, and education. Skillful application of these principles can produce positive results in shifting human environmental behaviors.

As human beings all sharing the same planet, one might assume that preserving the natural systems and processes which sustain our existence would be a commonly shared priority. However, the truth is far more complicated and much less straightforward than one would initially hope for. As a society we have made great strides in advancing our knowledge of how the world around us functions, yet in doing so we have forgotten to pause momentarily to reflect on how our individual behaviors impact these natural systems and how the complexity of the human condition dictates our behaviors. This article examines relevant literature in an effort to explore the roots of environmental behavior and the influence exerted on it through leadership activities such as, communication methodologies, conflict, and education efforts. In doing so, the goal is to broaden the understanding of the factors which serve to dictate human environmental behaviors, providing insight into areas where change can be most readily gained as well as concepts which would benefit from continued research efforts.

Current Situation

Human society, much like any other natural system, is in a state of constant flux. While human society rides a wave of ever-advancing technology and societal interconnectedness, the decades-old problems of understanding and controlling human impact on the world at large has changed and grown as well. Due to science and technology advancement we are able to examine the world around us with ever-increasing precision; uncomfortably so in many ways. This power has provided humanity with the tools to identify and pinpoint the true extent of the torque exerted on this planet's natural resource systems by ever-accelerating natural resource consumption and natural system modification. While this information has become easier to access than ever before, the will and desire from the public to make the changes necessary to halt negative and destabilizing mankind-mediated events has not increased at the same rate as the damage has escalated. Currently, political affiliation, not scientific data, often dictates the beliefs and behaviors of many individuals regarding sustainability and environmental behavior; while debates are waged about the existence of climate change—a step backward if ever there was one.

While environmental behavior is the core of this literature review; behavior itself cannot be examined in a vacuum. More than ever, environmental behavior is increasingly being shaped by external factors in society today. Leadership through communication, conflict, and education can be key in molding the societally accepted behaviors humanity currently demonstrates.

Literature Review

Environmental Behavior

Amel et al. (2017) postulated that human behavior is centrally responsible for the critical conditions of the ecological systems we rely on to sustain human life, and that instilling guilt or fear in people is doing little to shift these behaviors. Worryingly, educating the citizenry—a favorite tactic for decades—still results in the same stagnant and environmentally destructive behaviors occurring

(Amel et al., 2017). Kollmuss and Agyeman (2002) illustrated that the models most often used to address these behaviors center around linear models from the 1970s which have since been proven incorrect. These linear models dictate that environmental knowledge will lead to changes in environmental attitudes; ideally leading to the desired pro-environmental behaviors (Kollmuss and Agyeman, 2002). This simplistic model of understanding behavioral drivers has blossomed and grown into an accepted practice to achieve environmental behavior modification, despite application of these methods resulting in repeated failures. Application of this model can even be observed today in educational initiatives targeting the public in the hope of educating for eventual behavioral change; sadly, these programs too fail to demonstrate consistent measurable outcomes.

From the outside, these behaviors resulting in environmental harm would seem counter intuitive, and the resulting damage to necessary systems would seem obvious. However, that is not the case. Amel et al. (2017) attributes this lack of awareness to the fact that industrialized people are so far removed from natural processes and systems that there exists a disconnect between nature and humankind. It is reasonable to assume that humankind is capable of reacting to direct experiences in immediate proximity, but the capacity to react to indirect experiences is very limited in comparison. Kollmuss and Agyeman (2002) described that immediate and tangible perception of many environmental crises simply does not exist. Kollmuss and Agyeman (2002) furthered this by pointing out examples such as radiation and atmospheric greenhouse gas accumulation as being representative of non-immediate and intangible results of ecological problems, which are often slow to develop and gradual in their increasing intensity—traits which make them harder to perceive for humans who excel at identifying drastic alterations in their immediate environment.

All this serves to further the idea of a behavioral disconnect between humanity's actions and the corresponding reaction in natural systems; reactions which humans are poorly designed to perceive. To understand the roots of human behavior we must understand that social norms act as the underlying driver of all behaviors, pro-environmental or not (Amel et al., 2017). The thought of rejection or indifference from the social group one ascribes to is a far more powerful motivator than an informational pamphlet; rejection is a direct experience with tangible outcomes unlike many environment issues. Due to this factor, continuing psychological research is delineating the ways in which these social norms and constructs can be modified in the future to produce sustainable behavioral actions (Amel et al., 2017). To not pursue the direct connections between psychological sciences and environmental behaviors is ignoring an invaluable explanatory tool for evaluating the mechanisms which dictate our human-nature interactions.

Leadership and Environmental Behavior

Leadership is one of the most powerful factors which shapes human behavior and is recognized as critical for producing a change in behavior as well (Evans et al., 2015). Manolis et al. (2009, p. 881) defined leadership as, "inspiring and mobilizing others to achieve purposeful change." This definition is well suited for the realm of environmental behavior, as the leadership which is sought to create new sustainable and environmentally conscious behaviors will have to act as an adaptive agent for inspiration and mobilization.

Leaders must work to create new values among others; values which provide the motive force to change behaviors (Manolis et al., 2009). Action and reflection cycling will be a key factor of leadership, with the ability to adapt and overcome the change-resistant individuals or social groups whose hesitation lies rooted in fear of unfamiliarity and disruption; albeit without generating direct opposition to the proposed changes (Manolis et al., 2009). This value-changing and value-creation task will be of the utmost value over time, as the values which are prized by groups and individuals alike are more likely to influence attitudes and resulting behaviors (Manolis et al., 2009).

In referencing leadership and behavior, it is important to understand who or what may assume a leadership role. Leadership is often classically associated with a key individual or position, which then performs as a traditional fixed-point of power within an organization or societal group. However, recent research by Evans et al. (2017) suggests that key individuals in a position of authority are not the sole source of leadership and should not be viewed as essential for leadership to take place. Rather, a diverse group of agents can provide a broad and detailed leadership service through the positive and negative influencing of group goals (Evans et al., 2017). With the previously stated definition of leadership referencing the ability to inspire and mobilize, it is important to point out that there is no required position of power or singular skillset that must be possessed to carry out this task—all engaged actants can provide this, it is not only reserved for a charismatic individual occupying a key position of authority (Evans et al., 2017). However, a pluralistic leadership view, one which does not assume that leadership is a singular and unequivocal good, is needed to understand that the sole presence of leadership itself does not automatically equate to positive environmental outcomes (Case et al., 2015). An undercurrent in our nation today being fueled by charismatic leaders opposing pro-environmental behaviors is guided by strong leadership. Regardless of the source of the leadership, the goals and motivations of the leader must be considered when assuming intent when seeking behavioral changes.

Leaders and Communication for Environmental Behavior

Often the communication style and method utilized by leaders is not considered when referencing behavior, but the role they play cannot be understated. In particular, leaders must consider the framing of messages, the succinctness of the statement, and the phrasing of the dispatch which can be formulated to increase the palatability of the concepts being communicated—ideally generating acceptance and value/behavior modification.

Lakoff (2010) pointed out that in today's society there is an overarching political connotation that enters into environmental discussion due to the moral-value tags assigned (or unassigned) to environmental issues which are now closely associated with conservative and/or liberal parties in the United States. While Lakoff (2010) commented that it would be ideal if these political valuations were not associated with environmental issues, this is however the current reality and it is vital that steps are taken to understand how careful framing and communication strategies reinforce these political positions. The conservative party in particular was lauded for the consistent messaging which effectively communicated the central values and views held by the party and its constituents; providing a simple, calculated, and compelling communication methodology to reinforce party values (Lakoff, 2010). Lakoff (2010) cautioned that a thorough understanding of the framing perception system of the human psyche along with careful composition of the messaging that is to be conveyed is critical to avoid potential communication pitfalls. Talking in terms of values while framing issues in a moral valuation context which provides story references that engage emotions and highlight personal values provides a recommended approach to communication with the general public (Lakoff, 2010). Lakoff (2010) also stressed the importance of avoiding jargon and focusing on real/local concerns when attempting to forge bridges of communication and influence behavior.

The phenomenon of motivated reasoning or cultural cognition, a concept which describes the situation which occurs when an individual favors the perception and cognition of information which serves to reinforce their currently held viewpoints and worldviews (Myers et al., 2015), is essential for leaders to understand when crafting messages. This confirmation bias can often result in individuals rebuffing messages targeted at them which run contrary to their personal beliefs or the belief structure of their chosen political or social affiliation group. Myers et al. (2015) went on to posit that simplistic or preferably numeric messages from trusted sources which are perceived to be independent can promote greater receptiveness to information dissemination and may lead to the individual self-identifying their knowledge gap and thusly seeking to fill it independently. However, this is followed later with the assertion that this messaging may backfire with those who automatically have a disbelief in the root of the environmental messaging, i.e., climate change (Myers et al., 2015). This illustrates a problem with messaging and simplicity, the individual may not be receptive or trusting of the source if they are already predisposed against the concept due to a closely held personal belief or value.

Whitmarsh and Corner (2017) further dove into the uniqueness of those having right-leaning views, focusing on the beliefs and communication methodologies that are closely tied with these political views. Perhaps most interestingly, in today's society public climate change engagement is most heavily influenced by the political associations and ideologies a person ascribes to (Whitmarsh and Corner, 2017). While surprising, the partisan nature of many facets of society is more pervasive today than at any time in history. Whitmarsh and Corner (2017) detailed the results of an engagement study targeting right-leaning groups with carefully framed and crafted pro-environmental messages which would typically be met with resistance. After evaluating the response to these targeted messages, the authors deduced that individuals responded better to these framed messages.

Behaviors cannot be changed without communication from dedicated leaders. Therefore, the value of carefully designed and framed messages capable of reaching the target audience cannot be understated. The initiation of constructive dialog with guarded and previously-distanced audiences, coupled with the elimination of senseless and repetitive pandering to those already in agreement, will provide a path toward pro-environmental behavior generation (Whitmarsh and Corner, 2017). The communication methodologies and techniques leaders employ to illicit these behavior shifts are critical, invaluable, and merit further study and research.

Conflict and Environmental Behavior

While conflict may not be considered one of the first primary factors thought of when considering actions which shape behavior, conflict is inevitable during efforts to shift values or behaviors (Manolis et al., 2009). Leaders play a pivotal role in conflict management, working to keep conflict at a level which is necessary for change, but below a threshold which produces direct opposition and resistance (Manolis et al., 2009). This conflict is necessary for change and is a fundamental part of the human condition which occurs when parties assert their interests at the expense of others (Redpath et al., 2013). The complexity of conflict also works to influence human behavior by dictating the ways in which individuals interact with each other, their trust for one another, the weight this trust carries, the depth of the levels of conflict that may exist between parties, the management techniques in conflict mediation this requires, and the realization that there are limitations to what can be done to mitigate conflict; all of these conflict-linked factors influence behaviors in differing ways.

Redpath et al. (2013) described the difficulties in the generation of collaborative efforts due to the deeply-rooted distrust which may be harbored by stakeholders engaged in a conflict. While high quality information, impartial intermediaries, and the need to push parties to identify problems as shared were discussed as integral to the conflict management process; the need for transparency on all parts was repeated time and time again as the most important factor in the process (Redpath et al., 2013). While conflict resolution is more likely if increased levels of trust can be fostered between the involved stakeholders, this trust building needs resources and a great deal of effort to foster the type of power-sharing and assumed vulnerability necessary to develop a long and lasting trust (Young et al., 2016). However, regardless of trust development and resource investment, no conflict will ever be fully resolved and eliminated, it will persist in some form or at some level in perpetuity (Redpath et al., 2013). A similar sentiment was also echoed by Gutierrez et al. (2016, p. 267) when they stated that "conflicts are often not resolved but rather managed," eluding to the amorphous nature of shared solutions and underscoring the limitations of conflict resolution.

Madden and McQuinn (2014) explored the complexities of conservation conflict transformation while expounding on the levels that exist within a conflict. While one may generally consider that the surface dispute is the real crux of the problem, often there is an underlying conflict or deep-rooted conflict below the surface that works to dictate the perceived outward behaviors (Madden and McQuinn, 2014). The evolution of a material or dispute conflict into a deep-rooted conflict over time can result in a simple problem turning into an intractable issue regardless of applied effort and resources. In this manner, conflict has an unparalleled control over behavior, possessing the ability to render any problem unsolvable. To this end, leaders must gain an expanded understanding of conflict and behavior interactions to better manage conflict.

Our natural resource and environmental systems do not naturally engage in conflict in the way humans do, this type of conflict only exists because of the interactions of people (Gutierrez et al., 2016). From a pro-environmental behavior point of view, these conflicts are vital to generate the required behavior changes needed to produce the sustainable outcomes desired. Natural resource and environmental conflicts will only increase in frequency as resource utilization expands and habitats shrink (Gutierrez et al., 2016), putting extra pressure on leaders and stakeholders to seek shared outcomes to manage these conflicts for the long term. While the desired outcome of any environmental conflict is a positive and pro-environmental behavior change, it must be understood that conflict will nearly always generate behavior change but if not handled appropriately it will not benefit the environment. This negative outcome can result in greater distrust and more difficult conflict management in future efforts, serving to further complicate the problem and create a greater hurdle to positive behavior outcomes. As these conflicts dictate current and future behaviors, the nature of new conflicts will change according to those new behaviors—creating a self-sustaining feedback loop which can be either positive or negative depending on leadership and conflict management efforts.

Leadership and the Use of Education for Environmental Behavior

As a leadership initiative, the influence of education on environmental behavior has been a long-term focus of study. Initial linear modeling suggested that the surest method to illicit environmental behavior changes was by educating an individual about natural systems with the belief that they would change attitudes and behavior after coming to the same conclusions as the scientists who collected the initial data (Kollmuss et al., 2002). While this linear: data—attitude—behavior model was later proven to be incorrect, this concept is still applied in many educational and outreach programs with subtle differences that can help to make the behavioral change outcomes a reality. Early childhood education models, undergraduate and graduate-level education programs, and large-scale educational overhaul propositions are all on the table regarding the capacity for education to influence behavior toward a sustainable and equitable outcome. As such, leaders seeking to generate pro-environmental behaviors have focused a great deal of energy and resources on the current and future education system and the power it wields to direct future behavior through capacity building.

Educating in the environment, about the environment, and for the environment are now the looking glass with which environmental education is observed (Davis, 2009). By initiating programs to educate in the environment the goal is to remove the distance between humans and nature at an early age, fostering relationships between children and nature which illustrate that humans are part of nature—not separate (Davis, 2009). Davis (2009) also discussed the ways in which education about the environment is conducted, which is the primary way in which most adult citizens of the United States received environmental education. In this manner teaching centers around the mechanisms and functions of the environment, but no effort is placed on demonstrating the inherent interconnectedness humankind has with the natural world. Education for the environment is the latest direction in environmental education, with the research-guided goal of building capacities in children to respond to future sustainability issues (Davis, 2009). While the engagement level from educators in early childhood environmental education ‘for’ efforts has begun to increase, little research is currently being conducted to understand the dividends and benefits which can be found from early childhood environmental education. This lack of research efforts is a phenomenon Davis (2009, p. 227) described as a “research hole” that is in dire need of being filled. These targeted early childhood efforts will do much to serve as agents for change in overcoming the behavioral driving factors often observed in the general public; while simultaneously addressing the low-level of current environmental education and building an environmentally-literate future population (Carleton-Hug and Hug, 2010).

Similar to the failings observed in the early childhood education system, collegiate-level education systems often fail to build the education “in” and “for,” eschewing it for education “about” instead. Thought, cognitive processes, and most importantly behavior will have to adapt and change if a shift in the methods of human interaction with natural systems is desired or required for future sustainable human—nature interactions (Walsh et al., 2015). From an educational standpoint this will require a fundamental shift in the way we define environmental education and what acceptable outcomes are defined as in the future. While dedicated to an evaluation of a graduate-level sustainability course, Walsh et al. (2015) demonstrated not just the changes in educational methodology required but also described the fundamental thought and behavioral shift associated with learning to work in a multi-disciplinary framework that is the core tenant of educating “for” the environment in a capacity-building education system for sustainability. This skill-building focus which is counter to the standard ‘about’ the environment protocol that is traditionally followed, allowed the students in the graduate program to learn “sustainability in practice” (Walsh et al., 2015:9) which provides for personal behavioral shifts toward positive environmental outcomes—a core focus of this education concept. While the focus on graduate-level students isolates the greater portion of the population from this vital educational experience, the program tenants of

behavioral-shaping capacity-building can be incorporated into other educational systems of varying levels—primary school through high school. By doing so, this allows for an expansion and integration of these ideals at all levels of education.

O'Brien et al. (2013) took the concept of environmental education reform to new heights, proposing that the behaviors needed to address current environmental challenges will require not just differing methodologies for environmental instruction techniques, but rather necessitate a shift in the ways in which problems are defined and solutions are proposed. O'Brien et al. (2013) proposed that viewing current environmental issues as technical problems with currently-known solutions is a disservice to the complexity of the issues and discourages the development of new educational methodologies and capacities. Both of which are necessary to generate the populational behavior shift needed for future sustainability. This focus on moving environmental education systems toward seeing things differently and viewing problems through an altered mental framework will generate friction within the current educational system. Resulting in an exposing of resistance and a lack of desire for change; exactly the sort of values the proposed experiential educational system aims to overcome through educational evolution (O'Brien et al., 2013). As a call to action for educational reform, O'Brien et al. (2013) provides a compelling argument which pokes holes in the current environmental education system and exposes the magnitude of the failures inherent to the current methodology. While not a specific blueprint that details the design and layout of the new systems which must be developed to build these capacities, O'Brien et al. (2013) does list a great many of the specific traits the new system must possess to create the behavior changes so badly needed.

Regardless of the focus of the educational reformation concepts, a common thread in recent environmental education literature is that “business as usual” is not working and environmentally-minded educational leaders are pushing for change. The currently observable behavioral outcomes of education dictate that the education itself needs to change if behaviors are to change. The undercurrents which are allowed to direct the flow of environmental thinking in society today are representative of the educational systems and the capacities they have built within the minds of the population they serve. This does not diminish the influences of other factors on behavior, however the ability to address environmental problems in a different manner and apply sustainability-driven skillsets developed during formative years applies a direct influence on behaviors later in life—environmental leaders know this. Focused development of these skillsets allows for future constructive environmental behavior and internal capacities that increase rationalizing and problem-solving abilities, skills that are vital for future sustainability. However, educational program shifts only address the portion of the population which is engaged in the educational system as a student, parent, or pupil; missing a great percentage of the population who will not benefit from these behavior-changing and capacity building opportunities. This illustrates that while education efforts can generate positive behavioral changes, it cannot be assumed that concentrating on this sector alone will produce the desired global changes needed for future sustainable behaviors; other influence factors will have to be employed to produce the desired positive behavior shifts. Educationally-focused leaders understand these limitations, but push for environmental educational reform as a key facet of influencing human environmental behavior long term through capacity building.

Conclusions and Future Study

Environmental behavior change is an intricate and currently incomplete puzzle that humankind desperately needs to continue to strive to solve. The complexity and staggering number of moving parts that make up behavior (environmental or otherwise) combine to form a confusing and hard to navigate maze littered with good intentions and poor or incomplete research. It would be easy to claim that we already have all the information and we must simply begin to apply it correctly to create positive behavior shift. Unfortunately, this sentiment is untrue and presumes that we fully understand the key drivers of human environmental behavior—when clearly, we do not. This is not to say that we don't have a grasp on several useful, key bits of information that can be applied to generate a positive change in environmental behavior—decision-making is possible despite the uncertainties inherent to this complex system. This is merely to point out that this is not settled science, more research and effort must be directed to exploring the psycho-social and political mechanisms behind environmental behaviors. Continuation of this research coupled with an acknowledgement that behavior is complicated and requires the evaluation and understanding of outside factors and influences will better allow us to determine how environmental behaviors are shaped and reinforced in human society. To this end, dedicated examination of behavior influencing leadership factors such as communication, conflict, and education must be continued to expand our knowledge of what roles each play in influencing individual and group environmental behaviors.

The role of leadership as a factor in behavior reinforcement and change is an area that merits continued research and investigation. It can be seen today that leadership functions can serve to reinforce both positive and negative environmental behaviors. As such, we would be remiss if continued focus on the role played by leadership and study of the composition and source of leadership itself was not performed regarding advancement in the understanding of environmental behavior. As a factor that influences many aspects of human activity, leadership is a powerful tool which will continue to be a focus of study for many years to come.

Leaders must consider communication methodologies and continually evaluate outcomes over time, as the psychological power they possess to change behavior and belief through concept framing and word selection become more valuable in the fight for behavioral change. While commonly shared communication methods call for brash and engaging language, studies have demonstrated that tactical application of communication techniques can serve to reinforce ideas and generate better overall acceptance of concepts and principles which may normally be dismissed immediately. Communication regarding environmental behaviors and supporting concepts without the benefit of these principles will not generate the kind of positive reception and behavior change that

is the ultimate goal. Continued dissemination of these communication concepts and further research into their application to environmental issues needs to be a key focus for researchers seeking to understand the factors to expanding pro-environmental behaviors.

While the focus on leadership and leadership roles expands, the skills that allow for the development and nurturing of conflict needs to be a point of emphasis for environmental behavioral change in the future as well. Studies indicating the value of conflict for the generation of change cannot be understated, highlighting the necessity for positive and progressive conflict development. When environmental leaders act an agent of change, conflict will always be present. The measure of the effectiveness of leadership will be in the ability to control the level of conflict and assure that it is generating progress toward a positive behavioral goal, rather than creating a disconnect and developing a rift which will drive apart critical actants needed to generate these behavioral shifts. This highlights the need for continued research into the complex and critical role of conflict, with a special focus on the behavioral dynamics which it directly impacts. Conflict, like other human sociological constructs, is a vital part of the behavioral puzzle that must continue to be assembled in an effort to broaden the understanding of the interactions between humans and the environment.

Much like the factors which seek to change environmental behaviors in the present, education for the environment and the methods of integrating this into the current educational landscape need to continue to be studied to change behaviors in the future—making education a key long-term focus for leaders. While the motivation for a large-scale overhaul of the entire educational system was advocated by reviewed literature, the possibilities of this type of deconstruction and reconstruction around a sustainability capacity-building system are unlikely to gain traction and acceptance by a public which still debates common core and the existence of climate change. Rather, an integrative solution which merges current practices with leading edge environmental education systems needs to be developed to address the capacity-building needs without gaining disfavor among the population whose children will be on the receiving end of this instruction model. The role which education plays in shaping environmental capacities for sustainability cannot be understated; making the continuation of this research and development of integrated teaching models that much more pressing as a leadership priority.

While many of the roles each individual factor plays in directing human behavior are known, the interconnectedness of each factor and the depth of contribution of leadership through communication, conflict management, and education on environmental behaviors is not yet complete. So, while it can be stated that leadership plays a critical role in determining human behavior, the extent of how effectively leaders utilize communication, conflict, and education is yet unknown. Continued research and study from the point of view of environmental behavioral impact is not just beneficial, but rather of the highest importance for the continued sustainable coexistence of humanity and natural systems. Once we understand how leaders can influence pro-environmental behavior, achieving positive environmental behavior change through the application of research outcomes will become a reality.

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Sense of Place: Shaping and Responding to Anthromes in the Context of Climate Change

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Abstract

Humans interact and are immersed in anthromes. They shape human experience and communities and in turn are shaped by human actions at a variety of scales. We become attached to places because they provide ecosystem services, connect us to community, and provide relative stability in a fast-paced world. Places bound nature-based livelihoods, recreational activities, and our learned aesthetics; shaping both our dependence and our identities. Humans in turn shape physical places to make them more in-line with our values and needs. These complex and shifting relationships form both anthromes and our sense of place. This article seeks to review how sense of place shapes and is shaped by anthromes and then explore how sense of place may influence, and be influenced by our responsiveness to climate change.

Humans interact and are immersed daily in anthromes. They shape human experience and communities and in turn are shaped by human actions at a variety of scales. We become attached to places because they provide ecosystem services, connect us to community, and provide relative stability in a fast-paced world. Places bound nature-based livelihoods, recreational activities, and our learned aesthetics; shaping both our dependence and our identities. Humans in turn shape physical places to make them more in-line with our values and needs. These complex and shifting relationships form both anthromes and our sense of place. This article seeks to review how sense of place shapes and is shaped by anthromes and then explore how sense of place may influence, and be influenced by our responsiveness to climate change.

What Is Sense of Place?

There is increasing awareness of the interlinkages between social and ecological systems, and the importance of understanding the dynamic and complex nature of their relationships to better manage for sustainability (Folke, 2006; Holling, 2001). How humans interact with places is of great interest to many disciplines ranging human geography to psychology and political science to philosophy (Antonsich, 2010; Gifford, 2014; Lewicka, 2011; Williams, 2014). In these various disciplines the sense of place lens varies, including identity (psychology), social process (sociology), culture (anthropology), rootedness (geography), engagement (political science) and stewardship (environmental science) (Ardoin, 2006). Connections also form at various scales from individual to nation states and in different types of places (built environments, natural environments, types of locations). Sense of place has developed as a heterogeneous field encompassing a diversity of concepts to address the relationship between people and place across these domains (Ardoin, 2006).

Most sense of place literature would agree that it is a socially constructed process (Stedman, 2003; Tuan, 1977), based on ongoing and dynamic interaction between people and their environment (Gieryn, 2000) that relies on the biophysical properties of the location (Jorgensen and Stedman, 2001). Common characteristics include the fact that sense of place is contextual, dynamic, interdisciplinary, conscious and/or unconscious and positive or negative. Sense of place is a layered concept, whose elements often include nature, culture and identity. The particular layers and importance of given layers varies by discipline and author. One model, suggested by Scannell and Gifford, includes the person and their experiences and emotions, the process of interaction, including cognition, and behavior, and the biophysical elements of the place itself (Scannell and Gifford, 2010). Concepts affiliated with the personal experience dimension of sense of place include place identity, place dependence, place attachment and place

meaning. These different but overlapping terms describe different components or lenses to consider sense of place, with identity focused on individual internalization of place, dependence focused on reliance on various ecosystem services, attachment based on emotions related to place and meanings related to the descriptors of place.

In this article, I define sense of place broadly as the dynamic collection of meanings, beliefs, symbols, values, and feelings that individuals and groups associate with a particular locality based on human experience, social relationships, and biophysical attributes (Chapin and Knapp, 2015). As we recognize the interdependences between social and ecological systems (described below), and the importance of feedbacks in shaping outcomes for health (human and ecological), sense of place can offer us a concept to consider our linkages to anthromes and how those linkages may change in a context of climate change.

What Are Social-Ecological Systems?

Social-ecological systems are dynamic, interlinked and interdependent systems that include both human and ecological drivers. This concept has gained traction as a framework for understanding the world, as well as generating theories about how the world works. It was popularized by interdisciplinary researchers exploring governance (Ostrom, 1990), as well as system dynamics (Berkes et al., 2002). Informed by ecological theory, Holling proposed a model for how social-ecological systems change over time (Holling, 2001). In this model, systems go through a series of linked stages dependent on levels of potential and connectedness. Within this model, there are a few places where systems can become trapped, including what has been called rigidity (high potential and connectedness) and poverty traps (low potential and connectedness). Rigidity traps are where a system is held in a development stage that is desired by people but increases the rigidity of the system, and therefore it's long-term vulnerability. Poverty traps are when a system gets trapped in a place of low potential and connections and doesn't have the resources to develop and transform.

Associated with social-ecological systems is the idea of panarchy, or how system components are linked across scales (Gunderson and Holling, 2002). Panarchy is a way to describe these linkages and acknowledge feedbacks between levels of organization. For instance, panarchy describes how social-ecological systems operating at different scales are linked by the concepts of revolt, where smaller scales invent, experiment and test potentially influencing larger scales, and remember, where larger scales stabilize and conserve via system memory or legacy (Gunderson and Holling, 2002). Both concepts (poverty/rigidity traps and panarchy) will be useful for considering the interaction between sense of place and anthromes. While beyond the scope of this article, several very helpful books and papers exist that lay out these concepts in more depth (Berkes et al., 2002; Folke, 2006; Gunderson and Holling, 2002). I provide this concise introduction as I think that it is useful to think of sense of place within a social-ecological systems framework.

What Role Does Sense of Place Play in the Development of Anthromes?

Anthromes are shaped and maintained by sense of place, among other drivers, which include economics, power and biophysical components. Sense of place functions at different scales, from the individual to group to region to nation. Over these spatial scales and over time the way we perceive and build meaning in places influences the management decisions we make, and therefore how anthromes develop.

For instance, most of the original wilderness areas in many parts of the United States are "rock and ice" wilderness because their economic value for other uses was low, while the utility they could provide in protecting water supplies was high. The biophysical realities of place led people to ascribe certain values to it, which then became inscribed in laws that extended that use over time. Current hikers, backpackers, climbers, and nature-lovers value the solitude, spirituality and remote recreation opportunities, but these locations are not the only possible places they could have experienced these values. History and meaning-making have made them what people experience today.

Anthromes are heterogeneous partially because of the heterogeneity of ecosystems and natural resources, but also because of sense of place and other factors described above. Heterogeneity in ecosystems can influence the anthromes that develop in place. For instance, in the cropland and rangeland anthromes of the Flint Hills of Kansas the rocky soil allowed the tallgrass prairie to remain intact where other areas were plowed for crops. Within this ecological heterogeneity, smaller ecological niches, the cultural heritage of settlers, and technology led to distinct patterns of sub-anthromes and development of different conceptions of sense of place (Isern, 1985).

As people become more mobile, their sense of place may shift from roots to routes (Chapin and Knapp, 2015). For instance, in the intermountain West there are many small mountain towns surrounded by primarily spruce-fir forests embedded in rangeland, seminatural, and wildland anthromes. These places have a long history of place-making, from summer camps for indigenous people to mining and or ranching communities, and now often as ski resort or summer off-road vehicle (ORV) playgrounds. The legacy of prior use has informed and influenced current development. For instance, mining communities often have a network of roads and trails that now support ORV travel and ski resorts are often surrounded by wilderness areas that protect scenic views. As tourism between places increases, the attraction of ski resort towns has grown, which may lead to the desire to maintain and increase certain types of places. Sparsely populated and naturally vegetated spruce-fir forests function differently than subdivided and managed ski areas in terms of hydrology, natural disturbance regimes such as fire and insects, and habitat. In addition to shifting anthromes, new conceptions of place may lead to the desire to steward or protect different types of places regardless of where they are located

(Chapin and Knapp, 2015). In both scenarios, sense of place influences human values, which in turn shape what a place becomes and therefore the anthromes that are present (Ellis, 2011).

Sense of place is dynamic and can shift based on personal and cultural values and biophysical realities. This in turn can shift the anthromes across a landscape. This is clear when we look at the anthromes that have increased in the last handful of decades and those which have decreased. Places that are valued tend to be reproduced more than those who have low value. For instance, the intermountain West has seen an increase in “ranchettes,” as people have wanted to own land and experience a more rural lifestyle yet in proximity to urban areas (Riebsame et al., 1996). We can also see this in the increase in “walkable” and in-fill developments within cities that attempt to recreate valued attributes of urban living (ability to walk, close commercial districts, interspersed green spaces) within dense settlements and populated woodlands.

What Role Do Anthromes Play in Development of Sense of Place?

Humans interact constantly with anthromes, but they are not always aware of the embedded human element within them. Internalized ideas of human-nature dualism, stemming from Descartes view of subject/object, leads many people to perceive nature as separate and distinct from human communities (Descartes, 1993). Without knowing it, their sense of place is influenced by historical human values and legacies, yet instead of reading them as constructed and interdependent on human behavior, they are perceived as “natural.” This may lead to naïve or unquestioned assumptions about place. For instance, while we now know that indigenous use of fire contributed to pre-European landscapes, they were originally “read” as completely natural systems, devoid of human influence (Stewart, 2002). This reading could lead to inaccurate suggestions about appropriate management for restoration.

Even when unacknowledged, anthromes connect communities of people who have lived in a place across time. This provides a type of system legacy and memory that can either maintain social-ecological systems in similar patterns over time or set them up for either a poverty or rigidity trap. System memory that helps to keep anthromes stable over time can be illustrated by irrigated hay pastures in the rangeland anthromes in the Intermountain West. Over time, these intense green places in semi-arid landscapes have become valued not just for agricultural production (their original intent), but also for wildlife habitat, open spaces, and view-sheds (Ellingson and Seidl, 2009). Agricultural land-trusts have leveraged this shift in value to place conservation easements on these resources which functions to maintain this land use, and social-ecological system, into the future.

A poverty trap can be seen in places that have had a legacy of extraction and where patterns of extraction continue. For example, historical mining communities may have pollution problems that lower the desirability of these places for habitation (at least for those aware of pollution impacts). Historical mining laws may also allow unsustainable ex-urbanization of high alpine locations, leading to the potential for future degradation (erosion, fragmentation, etc.). A rigidity trap can be seen in intensive monocultures in the mid-west that are supplemented with pesticides, fertilizers and ground water. While they produce much of the US food supply, they are protected from collapse by these influxes of resources.

Anthromes influence the ecosystem services produced and therefore the types of livelihoods that can be made in a place. This in turn restricts the types of place identity and place dependence that develops. In the mid-West cropland anthromes, legacies have led to monoculture agricultural fields that over time have homogenized surrounding landscapes and communities. As consolidation of land and specialization of crop has increased, small rural communities have often been transformed (Lobao and Meyer, 2001).

As people interact with different types of anthromes, they become aware of the very different suites of ecosystem services provided by each. This may allow preferences to occur—which can shift how anthromes are valued at different scales. These values are connected to individuals who have different levels of power and resources for impacting landscapes. For instance, scenic and recreational places may be more valued by wealthy “outsiders” for second homes, making it more difficult for traditional livelihoods (ranching or fishing communities) to co-exist based on rising land values and changing culture (Riebsame et al., 1996). It is also possible that over time and with increased mobility, those with power and resources can move to the anthromes that best fit their value set, effectively segmenting people by anthromes. It may also mean that the demographics of anthromes begin to stratify by economic class with those who can afford them able to live in “desirable” anthromes (agrarian landscapes, wooded suburbs) and those unable to afford it relegated to other types of anthromes. This can be seen clearly in home ownership patterns in desirable regions where second homes are more common in recreation centers, with local ownership relegated to less desirable communities (Hall and Müller, 2004).

How Does Climate Change Shift Sense of Place and Anthromes?

Climate change, as both a slow incremental and a fast threshold-inducing driver, will change both anthromes as well as our sense of place. As a slow driver of change, it will create trends in ecosystems and the ecosystem services that are available. This will shift both the livelihoods as well as the qualities and characteristics of places. In addition, climate change will create thresholds and rapid (and potentially unexpected) changes both to ecology, but also to social systems (markets, culture, etc.). These rapid changes will shift the way that human communities interact with ecosystems. It may remove key signifiers of what a place means to people or key relationships developed between people and place.

Human communities will struggle to understand how to live in places that no longer provide a key element of what defined and made meaning for the place. For instance, many agricultural communities in village and cropland anthromes have built social, economic, and ecological systems around the crop or product that they produce. The yearly tasks of cow-calf operators in rangelands of Colorado will be transformed if climate conditions require them to shift to a steer operation, let alone if they transition to growing crops. There will be a mismatch between cultural, social and work activities, a need to acquire new knowledge of production processes, and dislodge seasonal activities that support both the ecosystem, the economy, and the individual health and well-being of operators. A rancher who no longer irrigates in the spring may miss the flow of water, the smell of grass, or the comradery of haying. The same ripple of change will be felt for everything from grape and olive growers to corn and winter wheat producers.

On a larger organizational scale, the way climate change will impact sense of place is also evident in the National Park Service, a US federal agency driven by a place-based mission to preserve distinctive and functional elements of place. What does it mean when there are no glaciers in Glacier National Park or no saguaros in Saguaro National Park? The identity, and the “sense of place” ascribed to specific places will change. This loss of place identity, whether at an organizational or an individual scale, may either lead to feelings of loss, known as solastalgia, although other responses are possible (Albrecht et al., 2007).

Finally, climate change may shift, transform or endanger current anthromes. In this case, although the space still exists, the place will be gone. While place is dynamic and constantly changing, the temporal rate and spatial extent of these changes may be faster and at larger spatial scales than ever experienced before. This could potentially lead to whole social-ecological systems that no longer function, leading to rapid and jarring shifts to both dependence and identity. We are already seeing how climate-induced events are leading to mass displacement. In addition to the physical, emotional, social and psychological impacts to displaced persons, there may also be a shift in sense of place for people in locations receiving migrants, which in turn shifts local community structure.

How Does Sense of Place Influence Our Reaction to Climate Change?

In prior literature, sense of place has been described as a primarily powerful and positive influence in stewardship of places and well-being of people and communities. Only a handful of papers have pointed to the challenge of conflicting sense of place (Yung et al., 2003), NIMBY attitudes (Devine-Wright, 2009), or negative perceptions of place (Tester et al., 2011). There is uncertainty about how sense of place will influence human response to climate change (Devine-Wright, 2013; Masterson et al., 2017). It is possible that sense of place may lead to resistance, slow response, active adaptation or transformed sense of place.

Resisting Change

In response to climate change, residents with a strong sense of place may double down on efforts to keep the place the same. For instance, in one study agriculturalists with a high sense of place were associated with lower levels of transformability (Marshall et al., 2016). This could result in maladaptations that attempt to resist change, creating a rigidity trap. For instance, if climate change is changing climatic envelopes such that saguaros can no longer survive in SNP, one response might be to manipulate the environment so that saguaros can still exist. This may save individual plants but at large expense in keeping the system functioning as it did previously. This type of intervention doesn’t address the driver of climate change, but just one symptom of how it manifests itself. Since it focuses on a symptom (and not the underlying root), it may be maladaptive as it fails to resolve the problem. This response will likely be more common for communities or individuals with the resources to resist.

Slow Response

In addition to maladaptation, high levels of sense of place may slow response to climate change. In Western ranching communities, this might mean that those with longer residence time and dependence (older generation) choose not to take major actions to adapt to climate change or that this older generation retires or becomes unemployed early, leading the younger generation to tackle how their industry will adapt to climate change. It may also mean that the adaptive actions that are chosen are those that are compatible with existing identity and sense of place. This might act to conserve some of the elements of identity and sense of place that can be retained. It may also limit the range of alternatives that people are willing to consider. Since climate change will often manifest in slow or halting and gradual shifts which may reach a threshold or tipping point, it may be easy to ignore when slow or halting. This could result in unexpected transformations driven by tipping points rather than intended and planned transformations.

Active Adaptation

Alternatively, residents with a strong sense of place may be motivated to stay connected to the places that are important to them. This could mean a more active process of adapting and shifting sense of place and identity to climate change. Instead of ignoring or failing to perceive that ecosystems are co-constructed, people may become increasingly aware of how humans have shaped anthromes in the past, how they are doing so currently, and how they might do so in the future. This may lead to more honest and informed discussions of how human values shape ecosystem services, how power influences whose values are embedded in landscapes, and what the decisions of those in the present mean for generations to come. Individuals may begin to recognize the co-produced nature of anthromes and sense of place and actively work to shape both in a way that maintains their values and

important ecosystem services. This more active awareness of how people interact with place may facilitate the questioning of human-nature dualities and a more integrative sense of interconnections.

Transformed Sense of Place

The awareness of interconnection may increase system stewardship and shift conceptions of sense of place from local places that supply local ecosystem services, to a more regional, national or international sense of place where both sense of place and ecosystem services function at a wider scale. This might create different levels of “sense of place” as individuals begin to understand how they are a part of systems at different scales. Since climate change will likely “displace” some of the ecosystem services produced locally, people may gain a better awareness and appreciation for their dependence on services provided elsewhere. For instance, if wildfires in one area remove camping opportunities (at least temporarily) for local residents, they may develop a sense of place with other similar areas that have not experienced severe fires and where they can gain the same experience as in their prior locations. Described as “demos” by one author, this more globalized sense of place may allow better stewardship across scales (Williams, 2014).

Conclusion

Science and policy realms have typically prioritized quantitative and generalizable information in research and decision-making (Adger et al., 2011; Stedman, 2016; Tschakert et al., 2017). Quantitative data collection is relatively direct and the analysis is perceived as less subjective. This results in suggested actions that are often devoid of lived human experience (including attachment, emotion, and values) and are incremental (based on quantities of CO₂) rather than being transformative (Adger et al., 2011). There has also been a desire to produce generalizable or broadly relevant information instead of information related to case and place (Tschakert et al., 2017). Exploring locally-relevant and contextual information may lead to broader changes in behavior and beliefs. This requires more attention to the contextual factors that mediate how sense of place influences climate change response in places undergoing rapid change. It will also require structures to better “hear” and integrate on-the-ground perspectives into climate change adaptation. It also will be critical to think of other “connectors” in social-ecological systems that may play a similar role in response to climate change. These may include empathy, culture and spirituality, among others.

It has been suggested that sense of place could be a useful concept for better understanding social-ecological systems (Masterson et al., 2017; Stedman, 2016). In this article, we have seen how sense of place influences and is influenced by anthromes in a synergistic manner. We have also seen how climate change may influence anthromes and sense of place as well as how sense of place may influence our response to climate change. Current actions to address climate change are inadequate to avoid catastrophic results, including economic and ecological break down (IPCC, 2008). Sense of place, as a linkage between social and ecological realms, may be pivotal for adapting to climate change.

The role of sense of place in response to climate change is uncertain, but it will likely be substantial. If we consider the idea of panarchy, it may function to slow response and maintain systems in current configurations, or it may work to transform systems from the ground up from local to global scales. As a conservative force, it may increase system rigidity and resist change as actors in systems take individual and collective actions to keep the system in the same domain. As a transformative force, personal experience may lead to a paradigm shift in ideas about human-nature connection that influence local-scale adaptation but also how people relate to and interact with nonlocal nature. It is likely that sense of place is and will lead to a range of responses including those discussed within this article.

While urgent action is needed to address the reality of climate change, often touted individual (e.g., changing your lightbulbs), institutional (e.g., installing solar panels), national (e.g., carbon trading systems) and global actions (e.g., carbon reduction commitments) are necessary but not sufficient. Sense of place, by connecting to identity, attachment and dependence, may act internally to influence change at larger levels. While it has been acknowledged that transformation of social-ecological systems may be necessary in the context of climate change (Feola, 2015), current solutions fall short of transforming paradigms. As people wrestle with their connection to specific places, perhaps what they experience will create alchemic shifts that have the potential to transform our relationship with the natural world on multiple scales.

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The Role of Aquariums and Zoos in Encouraging Visitor Conservation Action

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Abstract

The increasing need for people to adopt more environmentally responsible behavior in their everyday lives to secure the future of the planet has given zoos and aquariums both greater relevance and an additional challenge. It is no longer enough to help visitors understand ecosystems and animals and to encourage a love of nature; zoos and aquariums need to go beyond awareness and knowledge, and into the realm of behavior change. Facilities that house animals in human care are being called on to use these animals to engage, inspire and focus visitor attention on the urgent need for action to conserve animals and the physical environments that sustain them. Not surprisingly, therefore, modern zoos and aquariums are passionate about increasing their visitors' pro-conservation knowledge, attitudes and behavior (Ardoin et al., 2015; Ballantyne et al., 2019; Ballantyne and Packer, 2005; Moss et al., 2014; Pearson et al., 2014).

These aspirations regarding visitor conservation behavior require zoos and aquariums to rethink their educational programs and to explore new techniques for visitor interpretation (Gwynne, 2007; Mann et al., 2014a; Ramberg et al., 2002). Accordingly, zoos and aquariums now increasingly draw on social marketing techniques and an understanding of the psychology of conservation, as well as theories of learning and behavior change, to inform the design and presentation of their visitor interpretation and educational programs (MacDonald, 2015; Saunders and Myers, 2003). By complementing their repertoire of educational approaches with the use of behavior change theories and practices, zoos and aquariums are increasingly working towards supporting change in visitor engagement from "knowing" to "caring" to "acting" for animals and nature.

History of Zoo and Aquarium Education

The history of zoo and aquarium informal education has loosely followed the patterns of change over time in theoretical approaches to learning. A behaviorist perspective guided the early days, where the transmission of facts about the animals was paramount. This process occurred either via interpretive signage around the exhibits or through presentations from staff members (often called docents or guides). In both cases the information was presented to the visitor with little consideration for the individual needs of different visitors (Serrell, 1988). More recent approaches to zoo and aquarium education are guided by a constructivist approach to learning, whereby multiple opportunities are provided to visitors to enable them to create their own understanding of animals and ecosystems, building on their past experiences.

Increasingly, progressive zoos and aquariums are basing the design of their education and interpretation programs on behavior change theories such as Ajzen's (1991) Theory of Planned Behavior and Prochaska's (2008) Transtheoretical Model of Change (Wagner et al., 2009). These theories form the foundation of more recent approaches to influencing environmental behavior, such as community based social marketing theory (McKenzie-Mohr and Smith, 1999). The Connect-Understand-Act model proposed by Zoos Victoria is based on contemporary learning theories and uses current behavior change approaches (Lowry, 2009). The model has been used in the formulation of a number of the Zoo's campaigns and programs, and uses the unique advantage of zoos and aquariums—the opportunity to *connect* visitors emotionally to wildlife. Thereafter, the use of educational

resources can build an *understanding* of the threats facing that particular species and what *actions* visitors can take to alleviate the threat (Lowry, 2009).

Today, the relevance of zoo education is being increasingly scrutinized—as William Conway suggested, “Helping New York six-year-olds to learn about African monkeys may not help African monkeys” (Conway, 2007, 14). Zoo and aquarium educators are now more than ever questioning their role and the relevance of their work, to be more effective. The challenge is to ensure that visitors’ needs for animal sightings and information are met, while achieving the broader conservation education goals of the facility. It is clear, therefore, that education in zoos is moving beyond simply helping visitors to learn facts about animals and is increasingly focusing on more relevant outcomes, such as inspiring care for nature and encouraging behavior changes that support conservation and a more sustainable lifestyle (Gusset and Lowry, 2014; Sterling et al., 2007).

It is also interesting to note that there has been a shift in the focus of targeted conservation behaviors, with a new emphasis on actions that can be undertaken locally. Previously, in many cases the only “action” asked of the visitor at a zoo or aquarium was to sign a petition or to donate money to save forests, elephants, pandas or some other charismatic megafauna. This made it difficult for visitors to connect their daily conservation behavior in their local environment with the actions needed to “save the panda” or other animals who lived in remote protected areas or far off countries. Increasingly the links between actions at home and impacts in the wild are being realized, strengthening the message that conservation action can start at home, and that, through appropriate pro-environmental behavior, each visitor can contribute to conservation of animals and the environment. With millions of visitors each year (Gusset and Dick, 2011), the role that zoos and aquariums can play in facilitating such change is now more critical than ever.

Evolution of Interpretation Techniques

As animal exhibits and enclosures have changed to become more representative of natural habitats, so too have the educational techniques used for presenting visitor information within exhibits. Table 1 summarizes process of evolution that has taken place in relation to exhibit types, education techniques, strategies and goals.

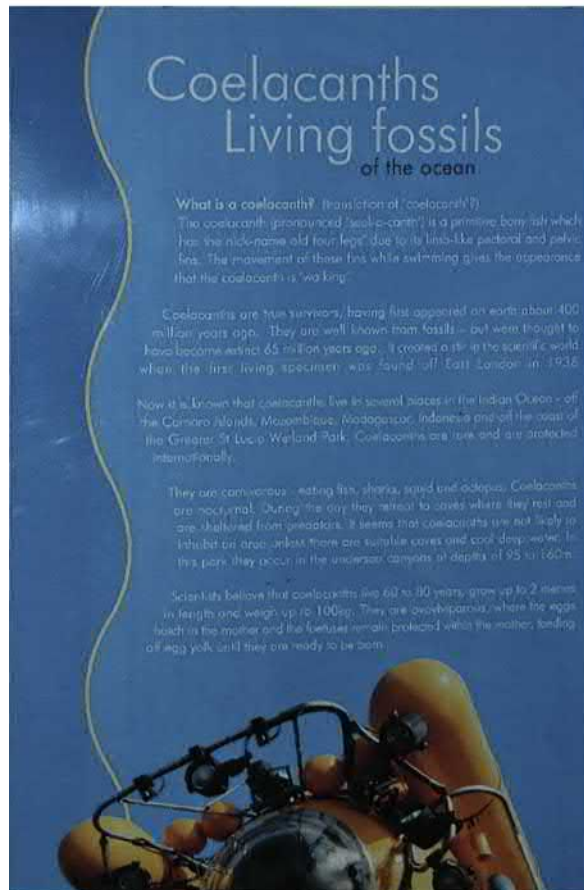
These changes are clearly evident in interpretive signage in zoos and aquariums. Signs have evolved from simple labels displaying the scientific name of an animal, to enormous panels crammed with information, to more recent styles with a minimum of “layered” content arranged around themes and messages and presented in an entertaining and informal manner (Fig. 1) (Moscardo et al., 2007; Serrell, 1988). To facilitate changing educational objectives, techniques for zoo and aquarium interpretation now include better use of technology in the form of touch screens, mobile phone tours and apps (O’Connor, 2010). Recently

Table 1 Evolution of animal exhibits, education techniques, strategies and goals (extended from WAZA, 2005).

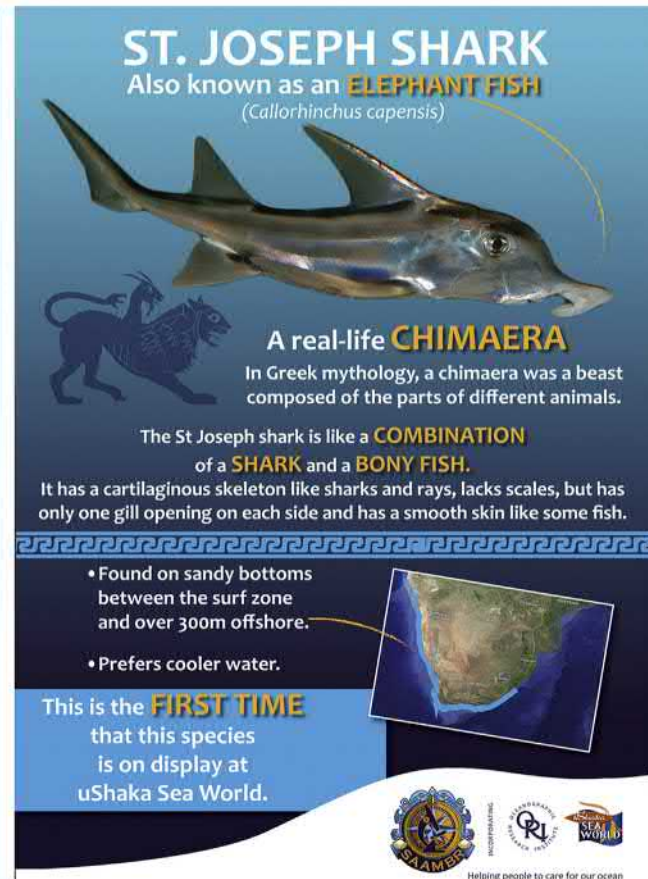
<i>Animal exhibits</i>	<i>Educational techniques</i>	<i>Education strategies</i>	<i>Education goals</i>
1. Cages/tanks 	Taxonomic labels, animal rides	Passive	Inform
2. Naturalistic dioramas 	Animal shows, content rich interpretive signage	Instructional Teacher focused Behaviorist	Teach facts about animals and diversity
3. Ecosystem/Multi-species exhibits 	Interactive activities, videos, minimal interpretation	Learner focused Meaning making	Engage, stimulate and inform visitors about animals and generate concern for animals
4. Immersion exhibits 	Mobile phone tours and apps, touch screens, Websites and animation	Constructivist Conservation psychology	Inspire and empower environmental behavior Issues based content
5. Extending the visit 	Websites, social media	Reflection on action and general call to action	Encourage long term environmentally responsible (conservation) behavior
6. Action campaigns	Targeted media campaigns, focused actions	Social science, behavior change theories	Change specific behaviors amongst visitors and a wider public



(a) Taxonomic label



(b) Text heavy panels



(c) Layered content

Fig. 1 The evolution of interpretive signage in zoos and aquariums. (A) Taxonomic label. (B) Text heavy panels. (C) Layered content.

research has shown that the impact of the visit can be extended beyond the physical time spent at a zoo or aquarium through the provision of post-visit action resources that utilize a range of means to reach visitors after their onsite experience (Ballantyne and Packer, 2011; Ballantyne et al., 2018b; Hughes et al., 2011).

As a further development, an increasing number of zoos and aquariums are now undertaking campaigns to support very specific visitor behavior changes (Dunstan et al., 2016; MacDonald, 2015; Mann et al., 2018; Pearson et al., 2014). In some cases multiple zoos are running campaigns that target similar environmental threats, e.g., palm oil or plastic pollution, and require similar visitor behavioral responses. Such partnerships can then build support at a wider community scale. Collectively these campaigns have potential to reach a tipping point of conservation action with respect to policy, regulatory or market changes (Dunstan et al., 2016; Spring, 2018). For example, the sustainable seafood and palm oil campaigns run by multiple zoos, aquariums and other

partners point to the power of collective action, sometimes called supply-chain activism (Barongi et al., 2015). When visitors across many zoos/aquariums refuse to eat seafood that has been harvested unsustainably or only use products that contain sustainable palm oil, they have a combined significant impact that eventually leads to the legislative and social changes required for long term sustainable business and personal practices.

Zoos and aquariums are well placed to initiate behavior change campaigns or provide support to existing campaigns. As staff in zoos and aquariums are connected to individual animals, species or ecosystems, their passion and knowledge about the threats to those animals gives them a strong motivation to start a campaign. Zoos and aquariums also have easy access to people who specialize in communication—in their education or marketing departments, easy access to thousands of visitors, and the ability to connect people to animals. Feelings of connection to an animal or species have repeatedly been found to influence decisions about behavior (Clayton et al., 2009; Mann et al., 2018; Saunders et al., 2006). The following section provides further details on some of the behavior change campaigns that have been initiated by zoos and aquariums, and some of the results that have been achieved.

Zoos and Aquarium Action Campaigns

Some zoos and aquariums have embarked on ambitious campaigns with clear calls to conservation action in relation to issues such as seafood, palm oil, domestic cats, mobile phones, plastics and climate change—brief examples of these are presented below.

Seafood

Some of the earliest conservation action movements by animal care facilities came from aquariums who launched bold campaigns to change seafood consumption from unsustainable to sustainable species (those better able to survive fishing pressure). The first aquarium-based seafood consumer campaign was initiated by the Monterey Bay Aquarium in 1999 (Fig. 2). Subsequently, over 20 seafood campaigns have been initiated by aquariums, zoos and partnerships between such facilities and other organizations (nonprofit organizations, NGOs, restaurants or retail outlets). Research into the effectiveness of the Monterey Bay Seafood Watch campaign in 2003 and 2004 revealed that over 2 million pocket guides had been given to visitors and that for 76% of the study participants, the pocket guide had influenced their choice of seafood purchased (Kemmerly and Macfarlane, 2009). Recently, the Monterey Bay Aquarium has been able to use its position as a trusted voice for ocean conservation to directly influence the development of ocean policy (Spring, 2018).

The South African Sustainable Seafood Initiative (SASSI) is managed by WWF-SA with local aquarium partners. Research has revealed that 27% of respondents who collected a SASSI card during a visit to uShaka Sea World noted that they were still using the card 6 months after their visit (Mann et al., 2014b). Despite the criticism of seafood awareness campaigns (Barendse et al., 2018; Jacquet and Pauly, 2007), it is clear that collectively these campaigns have changed regional fishing practices and have encouraged increasing numbers of seafood retailers, distributors, food service companies and chefs, to utilize sustainable seafood options (Barendse et al., 2018; De Vos and Bush, 2011; Hallstein and Villas-Boas, 2013; Spring, 2018). The maturation of the sustainable seafood movement, the role of the movement in policy development and the rise of seafood awareness campaigns in Asia should address some of the criticisms that have been leveled against current conservation awareness campaigns (Barendse et al., 2018; Jacquet and Pauly, 2007; Spring, 2018).

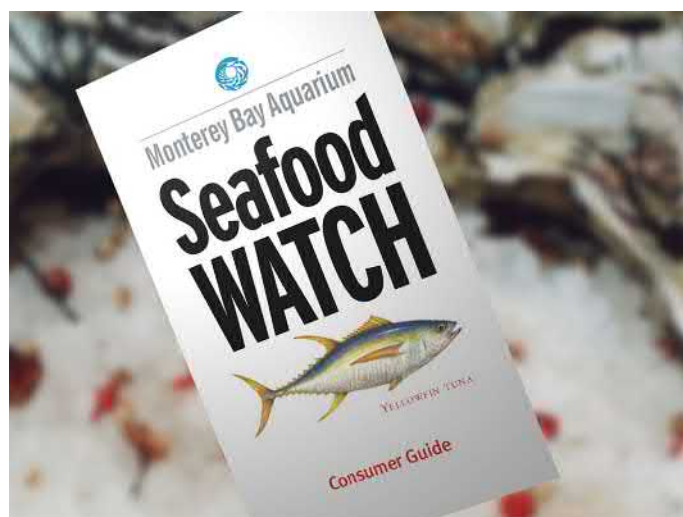


Fig. 2 The Sea Food Watch Campaign prompt card. Monterey Bay Aquarium in the USA was the first aquarium to initiate a seafood campaign.

Palm oil

The clearing of virgin forest for palm oil plantations has had a devastating impact on biodiversity and particularly animals such as orang-utans in many tropical countries. Several zoos have tackled this issue through a range of consumer campaigns. The most robust evidence of the impact of such a campaign comes from Zoos Victoria's 2009 *"Don't Palm Us Off"*—a campaign that sought to raise awareness about the issue of palm oil and galvanize the public into action to reduce future deforestation. Visitors to Melbourne Zoo were engaged in the issue of palm oil both on-site (orang-utan exhibit signage, a 1-min video, wallet cards and petition cards to sign) and off-site (national media, social media, the zoo website, an on-line petition and downloadable fact sheets) (Fig. 3). Over 160,000 people signed a petition for mandatory palm-oil labeling of products, and significant increases were noted in relation to visitors' knowledge, positive attitudes towards orang-utans, and self-reported avoidance of products containing palm oil (Pearson et al., 2014). Importantly, the campaign contributed to changes in palm oil use amongst several major companies and led to changes in Australian legislation with respect to labeling (Banks and Dunstan, 2014). Several other zoos in Australia and New Zealand have adopted the *"Don't palm us off,"* campaign while in other regions, zoos have initiated their own "palm oil" campaigns. In the United Kingdom, Chester Zoo tackled the palm oil issue as a community driven campaign and is on course to help make the city of Chester the world's first sustainable palm oil city. In the United States, Cheyenne Mountain Zoo has designed a mobile application that helps consumers to select products made from sustainable sources of palm oil. Formal evaluation of these latter campaigns on behavior after a visit is not yet available).

Domestic Cats

To address the negative impact of domestic cats on indigenous fauna in New Zealand, Wellington Zoo initiated a campaign (*Cats inside at Night*) that encouraged visitors to keep their cats indoors during the night (MacDonald, 2015). Six weeks after their visit, 70% of respondents reported bringing cats inside at night, with over half attributing this behavior to the zoo messaging (MacDonald, 2015).

Mobile Phone Recycling

To address habitat loss through coltan mining in gorilla habitat, Zoos Victoria's *"They're calling on you"* campaign encouraged visitors to recycle their mobile phones. In less than a year the campaign resulted in more than 10,000 phones being diverted from landfill and raised over \$14,000 (Lowry and Gray, 2009). At least 13 other zoos and 100 community groups have also joined this campaign.

Balloons

After studies showed the enormous impact of balloons and balloon clasps on marine life (Lavers et al., 2014), Zoos Victoria decided to launch a campaign titled *"When balloons fly,"* that calls on the community to commit to "blowing bubbles" at special occasions rather than releasing balloons (Fig. 4). This campaign utilized on-site messaging, special educational programming, off-site partnerships with businesses, councils and festivals, and social media, as well as a highly publicized "World Record" bubble blowing event (McLeod et al., 2018). Over 130,000 visitors pledged to blow bubbles rather than release balloons and over 180 organizations committed to wildlife-friendly alternatives to balloons. Evaluation 12 months after the launch of the campaign revealed a significant decrease in the self-reported likelihood of using balloons (McLeod et al., 2018).



Fig. 3 The orang-utan is the icon associated with many of the palm-oil campaigns.

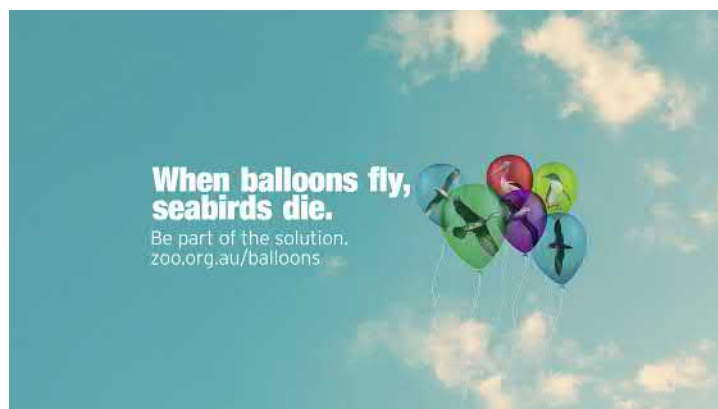


Fig. 4 The “When balloons fly” campaign launched by Zoos Victoria in Melbourne has changed the practices of many celebrations in Australia.

Evaluating Zoo and Aquarium Impacts

It is important for zoos and aquariums to actively measure their impact and identify the factors that influenced the impact. Quantifying the impact of behavior change campaigns can be difficult, because the rapidly increasing levels of public awareness of various environmental issues makes it difficult to tease out the contribution of any one intervention. Zoos and aquariums do not operate in a vacuum but contribute one piece to an enormous puzzle of public awareness-raising. More innovative methods are needed to identify the tipping points to action and to clearly determine which interventions are most effective, and what it is about those interventions that make the greatest impact on the public.

Quantifying the impact of a general visit to a zoo or an aquarium on visitors’ environmental behavior can be even more difficult. Unlike focused campaigns, where the visitor is clearly being asked to do something specific, general zoo or aquarium visits may be targeting a range of environmental behaviors, as well as the knowledge, attitudes and dispositions that act as the precursors to these behaviors. While measuring the ultimate goal (e.g., decreasing a threat to a species or an ecosystem in the wild) is a long term endeavor, steps towards achieving those goals can be measured (Dunstan et al., 2016). Social impact measurements are varied and include:

- counting the number of people taking the target action (e.g., number signing a petition; number of emails sent to companies),
- measuring changes in knowledge and attitudes (e.g., increased understanding of the threats),
- measuring self-reported behaviors after the visit (e.g., post visit evaluation results),
- assessing changes within local or regional communities or markets (e.g., actual number of companies committing to better practices; changes in legislation; and/or growth in market shares for sustainable alternatives), or
- assessing changes at a policy or governance level (e.g., changes in policies or regulations) (Dunstan et al. 2016).

Research by Ballantyne et al. (2011a) in four different wildlife tourism attractions found that four months after a visit, 5% of respondents reported having questioned their values or changed their personal attitudes; and 7% reported some new actions they had taken in support of the environment, as a result of the experience. Interestingly, an analysis of visitors’ memories four months after their visit (Ballantyne et al., 2011b) suggests that while factual information about the animals may have been forgotten, information about the dangers faced by the animals, particularly the threats posed by human actions, were remembered and aroused feelings of protectiveness and concern. This led visitors to think about their role in environmental care and supported a sense of personal responsibility, which in some cases resulted in direct action.

Smith et al. (2008) found that 26 out of 38 people (68%) who were followed up by phone six months after a zoo visit, indicated that they had started an action or increased their commitment to an action to protect birds and their habitats. Vernon et al. (2012) found that 55% of respondents who encountered conservation information or experiences during their visit retained and translated these encounters into personal actions that persisted for up to six months after the visit. Mann et al. (2018) found that more than a year after their visit, 49.4% of respondents could give an example of conservation action that they attributed to their visit. Further, these latter two studies revealed that not only do visitors take action after a visit, but that they communicate with others and inspire them to take action too (48% and 21% of respondents respectively). However, other studies have noted little or no impact on the conservation behavior of visitors after a visit (Adelman et al., 2001, 2000; Ardoin et al., 2015; Dierking et al., 2004).

These somewhat contradictory results highlight the fact that measuring post-visit conservation action is difficult (Stern, 2000), requiring innovative methodology and an open mind (Moss and Esson, 2013). It is often the case that very different estimates of impact are obtained, depending on the way the question is asked. Developing standard techniques for measuring impact, that are shared across sites and repeated across time, may be one way to overcome this problem in the future.

Factors that Lead to Success

The results of several research studies, as well as the application of theory, provide practitioners with some guidance on how to design behavior change campaigns and general visitor experiences that are successful in encouraging and supporting conservation action. In relation to behavior change campaigns, for example, Community-based social marketing theory (McKenzie-Mohr and Smith, 1999) suggests that an effective campaign should:

- select the target behavior with care (have a good understanding of the desired behavior, its impact on the environment, what motivates the behavior, and barriers to the behavior);
- rely on more than simply information (use emotional connections as well as information);
- reinforce the message both during and after the visit (multiple messages about the same behavior, website, downloadable information, fact cards);
- use prompts or triggers (pocket guides, consumer cards, post cards);
- keep visitors involved (post-visit follow-up, information, thank-you messages); and
- mobilize and support early adopters (identify role models who could model desired behavior) (Dunstan et al., 2016; Kemmerly and Macfarlane, 2009; Mann et al., 2018).

Research has demonstrated that the following factors also contribute to the success of a campaign:

- providing opportunities to connect emotionally with an animal;
- ensuring that information is credible and specific, but providing more than just information;
- repeating the same simple message repeatedly;
- having a clear call to action;
- empowering visitors with appropriate tools (cards, petitions, etc.);
- including a prompt to trigger recall;
- providing opportunities to reflect on the requested action;
- reducing barriers to action where possible;
- providing links between the action and daily life;
- understanding that each campaign contributes to a bigger conservation action; and
- being able to change as the situation changes (Dunstan et al., 2016; Kemmerly and Macfarlane, 2009; Mann et al., 2018).

Ballantyne and Packer (2011) conceptualize the factors influencing the impact of general zoo and aquarium visits as an ongoing process of interaction between pre-visit, on-site and post-visit factors.

Pre-visit Factors

Pre-visit factors focus on the previous experiences, beliefs and motivations that visitors bring with them to zoo or aquarium. Understanding visitors' motivations, for example, and their influence on onsite learning and post-visit behavior is critical to an understanding of the process and impact of free-choice learning (Ballantyne et al., 2011a; Falk, 2009). Although it may appear that it is beyond the control of zoos and aquariums to influence pre-visit factors, it has been noted that how a site is marketed can influence visitors' motivations and expectations (Ballantyne et al., 2011a; Mann, 2016). Thus, zoos and aquariums may be able to enhance their impact by promoting themselves as institutions for conservation education.

Another pre-visit factor that has received recent attention is visitor values. Ballantyne et al. (2018a) demonstrated that visitors' personal values influence the extent to which they are able to be reflectively engaged during their visit, with consequences for their post-visit environmental behavior. They concluded that using a values-based approach to visitor interpretation, which acknowledges individual differences in broad life goals and ways of seeing the world, and intentionally builds on and engages with these perspectives, would enhance the impact of a zoo or aquarium visit.

On-site Factors

Some studies have focused on identifying the characteristics of on-site interpretation and visitor experiences that impact on visitors' engagement and behavior change outcomes. The Monterey Bay *Inspiring Ocean Conservation* project (Vernon et al., 2012), for example, found that conservation-focused exhibits and presentations, discussions with a staff member, and taking home a Seafood Watch pocket guide supported an interest in and desire to take action. Similarly, the 'Penguin Promises' program at uShaka Sea World in South Africa (Fig. 5) (Mann et al., 2018) found that allowing visitors to select a "promise to the penguins" from a range of conservation actions was effective in encouraging visitors to increase their engagement in environmentally responsible behaviors. In contrast, many facilities have expended effort in the creation of innovative and attractive exhibits that highlight climate change. However, when these exhibits fail to provide clearly defined calls to action, there is little evidence to support their impact.

Providing visitors with an opportunity to reflect on their experience during their visit has been shown to enhance environmental learning and subsequent environmental behavior (Ballantyne et al., 2011a; Mann, Ballantyne, and Packer, 2017). While having fun with family and friends will always be one of the primary motivations to visit a zoo or aquarium (Ballantyne et al., 2007; Linke and Winter, 2011; Morgan and Hodgkinson, 1999; Packer and Ballantyne, 2002), it is increasingly evident that visitors now see such



Fig. 5 Visitors to uShaka Sea World, Durban, South Africa make a “Promise the Penguin” on a hand-written postcard.

facilities as trusted voices for conservation (Boyle and Mott, 2009) and that they expect zoos and aquariums to provide them with information on how to contribute to conservation efforts (Ballantyne and Packer, 2016; Roe et al., 2014). Since the concept of reflective engagement (cognitive and affective processing of an experience) was introduced in the zoo context (Ballantyne et al., 2011a,b; Packer and Ballantyne, 2013), a number of studies have provided evidence of the importance of reflective engagement in supporting behavior change (Hughes et al., 2011; Pearson et al., 2014).

Post-visit Factors

It has been argued that, in order for zoos and aquariums to really influence the behavior of visitors when they return home, it is essential that conservation messages be reinforced through the provision of post-visit resources (Ballantyne and Packer, 2011; Hughes, 2011; Hughes et al., 2011). Working out how to best reach the visitor after the experience is becoming progressively more important and, as such, research designed to optimize the use of post-visit resources is increasingly being undertaken. These resources could include learning materials in the form of brochures, newsletters, websites, e-mails and social media. Research indicates that the provision of such resources can encourage visitors to participate in environmentally sustainable actions and enhance their attitudes towards wildlife (Ballantyne et al., 2018b; Hughes et al., 2011).

Here are just a few examples of post-visit websites available to support visitors' conservation action at home:

<https://www.zoo.org.au/dont-palm-us-off/>

<https://www.zoo.org.au/balloons/>

<https://www.seafoodwatch.org/>

<https://penguinpromises.com/>

<http://www.cmzoo.org/index.php/conservation-matters/palm-oil-crisis/>

Conclusion

While it is clear that there have been advances in research that evaluates the impact of a visit to a zoo or aquarium on visitors' subsequent conservation action, this field is still new and requires considerable attention (Khalil and Ardoin, 2011; MacDonald, 2015; Mellish et al., 2019). Research has shown that many zoos and aquariums are inspiring their visitors to undertake more environmentally responsible behaviors and that these behaviors can sometimes be sustained during the months if not years after their visit.

However, given the difficulties associated with measuring behavior change, the small number of studies and the many zoos and aquariums undertaking behavior change campaigns there remains great scope for both case studies and theory-based research to provide further evidence of the effectiveness of zoos and aquariums in encouraging conservation action, and to provide guidelines to enhance this impact.

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Cooperatives: An Imperative for a Holistic Environmental Management

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Abstract

In this essay I review perceived beneficiaries of dominant environmental policies versus the losers of such policies. Specifically, a conflict between the conscious environmental bourgeois and the unconscious environmental proletariat. Therefore, I peer review of Karl Popper's piecemeal engineering in relation to the environment; a thought which detects social problems and evaluates public policies in bit and pieces for socially induced transformation, and, in this case, its application to environmental management. Bearing in mind that public institutions, both national and international, are controlled by the environmental bourgeois, I propose that genuine environmental management is imposed on the environmental proletariats, and such duties must be anchored primarily upon the philosophy of cooperatives. Given the foregoing, I advance for a universal piecemeal approach, built on cooperative principles and values for holistic environmental management. This, I defend, is the most significant, radical and realistic mechanism to check-mate further depletion of the earth and serve as a catalyst for the actualization of sustainable development.

Introduction

Our environment is the truest unifying factor available to all of humanity. This is anchored on its readiness to serve humankind irrespective of our divides. We all exercise the freedom to breathe the air, use the water, and explore the land. Though, humans are born free, but everywhere they go, they are also constrained. In other words, the human experience is subject to a variety of forces, which could be social, political, or economic in the environment. Thus, humankind in the bid to improve living conditions have employed some measures that have devastating effects on the environment, for instance, some production or manufacturing processes have triggered ozone depletion and climate change, both of which have contributed to poverty in extreme cases. These environmental challenges further widen the existing divide among the countries of the world particularly in the light of the globalization process.

Divides are a constant feature in the relations that exist in the community of states be it at the regional or sub-regional level although the emphasis gains more publicity in the rather narrow north-south/core-periphery/rich country—poor country classifications. The core substance of divides remain basically within the Marxian “haves, and the have-nots,” bourgeoisie-proletariat divides that are replicate across our universe. The contest between the two has many principal fronts, one of which is the use of the environment; a subject that rears enormous conflict on the economic, social and political fronts. Rising from these is the policy question of “which public policy most appropriately suits the environment, not just for gains, but sustainable development?”. The bourgeois characteristically controls the means of production and consciously influence environmental policies to support their interest. On the contrary, the proletariats, are often pre-occupied with the search for daily bread, thou conscious of their predicament, but not conscious in their drive at influencing policies for remedies.

A way forward is to conceptualize a common ground among environmental activists. Therefore, I will review the ideals of cooperativism that would birth a hybrid of Cooperativism; one that embraces the philosophy of cooperatives, cooperation and solidarity economics, and Karl Popper's philosophical thoughts, especially his concepts of piecemeal social engineering, a thought

which detects social problems and evaluates public policies in bits and pieces for socially induced transformation, in this case, its application to environmental management.

This bears in mind that the bourgeois class, in the present discuss, the environmental bourgeois, controls public institutions across national and international boundaries. Consequently, neither Karl popper's piecemeal social engineering approach, nor cooperativism will be competent in their separate capacities to address contemporary environmental challenges, thus the literature suggest an admixture of both is presented as the most significant and realistic mechanism for environmental management and sustainable development.

Conceptual Clarification

Environmental Management

The 21st century has been of massive industrialization, which entails enormous exploitation of the environment, from massive agriculture to feed the over 7 billion humans currently on earth, to natural resources exploitation with consequences such as gas flaring, and rechanneling of waterways, and further consequences such as water, land and air pollution. The trend has been phenomenal, rarely abated, instead ever increasing, all in response to socio-economic and political dictates across the states of the world. The most pertinent questions appears to be about sustainability, that is, using the environment in a way and manner that future generations are not left at risk.

The interplay of interest between the environmental positivist and their antagonist further brings to fore the importance of the use and management of the environment in relations to sustainable development. While the environmental positivist, which I regard as the environmental bourgeois made up of the world bourgeois class across all the state of the world would continue to canvass for further exploration of the earth, building their position on socio-economic and political exigencies and dictates, the environmental proletariats on the other hand continue to antagonize on the same grounds of socio-economic and political dictates, thou of a different variant, building their position on among others cultural protectionism and sustainable development.

Unbiased observation tells both divides have logical claims to the paths they so vigorously pursue. However, there are needs for a melting point that guarantees not only the best for today, but reserves a much better variant for the future. Thus mankind is faced with the puzzle of which variant offers the most adaptive management to the environment.

Cooperativism and the Environment

Cooperativism is the philosophy of cooperatives, cooperation and solidarity economics, and centers around the cooperatives, which are autonomous association of persons, united voluntarily to meet their common socio-economic needs through jointly owned and democratically controlled enterprises. This is closely linked to Ostrom's idea that common pool resources should be owned and administered by a collective institution. She further views the ownership and control of these resources by the commoners themselves as a better alternative to socialism, that is state control of resources and private enterprise system, both of which are hierarchical in nature and ultimately do not serve the interests of the commoners (Ostrom, 1990). Cooperatives are formed by people who use their products, and services. Though cooperatives vary in types, membership and styles, they all operate for the core objectives of members and the society, at doing these, they have been known to exhibit high level of adaptivity. Cooperative are guided by principles and values.

The Principles are:

- (a) Voluntary and Open Membership
- (b) Democratic Member Control
- (c) Member Economic Participation
- (d) Autonomy and Independence
- (e) Education, Training and Information
- (f) Cooperation among Cooperatives
- (g) Concern for Community.

The values are:

- (a) Self-help
- (b) Self-responsibility
- (c) Democracy
- (d) Equality
- (e) Equity and
- (f) Solidarity

Both principles and values contributed at making cooperatives and the more encompassing philosophy of cooperativism an increasing socio-economic, and political mechanism across the world, with profound applications into government and governance especially the various sub-fields such as trade education, health, agriculture, and infrastructural development. In furtherance to

these, cooperatives, have proved equally relevant in the sphere of environmental management. Wiskerke (2003), conceptualizes this phenomenon in the following words “within the domain of agriculture and rural development, self-organization and self-regulation emerges as a new model of rural governance. Environmental co-operatives are a promising expression characterized by new institutional relations between state agencies and agricultural communities, new social networks of trust at local level and the re-embedding of farming in its local, social and ecological context.”

Although Wiskerke (2003) treats cooperatives in environmental management from the viewpoint of agriculture and rural-urban challenges, the importance of cooperatives to environmental management thou encompasses agriculture and rural-urban challenges, and has a much larger scope. Perhaps in response to the above, Franchini et al. (2017), evaluates cooperatives in environmental management from the viewpoint of challenges of the anthropogenic, having identified international environmental politics and global governance as important pillars in this regards, the authors went ahead to posit “it is necessary to radically modified the institutional structure of cooperation based on international regimes; the transition from environmental politics to global governance.” Both instances affirm the importance of cooperatives in environmental management within the vertical and horizontal structures.

Karl Popper

Sir Karl Raimund Popper was born on the 28th of July 1902 in Vienna, Austria, he was an Austrian-born British philosopher who did many works on the natural and the social sciences. He contributed significantly to science, epistemology, and socio-political philosophy, especially with his antagonism of totalitarianism in all his guises as espoused in his works, specifically the 1945 epoch; His political thought resides squarely within the scope of “enlightenment rationalism and humanism” which buttressed his critique and condemnation of the “Closed Society” in favor of the “Open Society.” Further the condemnation of “Utopian Social Engineering” in favor of “Piecemeal Social Engineering,” and his disposition in favor of Minimalist Democracy as a panacea to defeat the hold of the bourgeoisie class on the modern state places his work in an enduring position for contemporary applications. Karl Popper’s philosophy is relevant to this review as it has proved to detect social and political problems and has shown capabilities to evaluate public policies in bit and pieces for socially induced transformation. Bearing in mind that although cooperatives have played significant role in sustainable development, emerging problems dictates the fortification of cooperative principles and value with other thoughts that have stood the test of time, such is Popperian philosophical thoughts, in this case in application to environmental management.

Main Focus

The gravamen of this work is the actualization of holistic environmental management for sustainable development through the strength of the cooperatives, or more precisely on the wheels of cooperativism. At doing this, the enormity of the bourgeois-proletariat relationship is well emphasized. Bearing in mind the phenomenal of the clash of classes, especially as it relates to the formulation and implementation of environmental policies, the blend of the vertical and horizontal links in the use of the environment, the advantaged position of the beneficiaries of dominant environmental policies and the disadvantaged position of the losers in environmental use and management. It becomes apt, to attempt a hybrid of two largely acceptable developmental philosophies: Cooperativism and Popperism in relation to the environment. From the foregoing a universal piecemeal approach, as discussed by Popper (1945), built on cooperative principles and values is advanced to check-mate not only the further depletion and degradation of the environment, thus achieving the goal of environmental sustainability which is part of achieving sustainable development.

Popperian-Cooperativism and the Environment

The very essence of Popperian-Cooperativism is to supplement the ideas of cooperatives with the thoughts of Karl Popper. It is expected that the hybrid produced will offer a more effective and efficient mechanism for sustainable development through holistic environmental management. Based on this projection, Popperism is related with each of the seven principles of cooperatives, which I review below.

Voluntary and Open Membership

According to the ICA (1995) cooperatives are voluntary organization, open to all persons able to use their services and willing to accept the responsibilities of membership, without gender, social, racial, political or religious discrimination. This principles require membership of cooperatives be made open to all prospective members, and restrictions should be kept at the barest minimum. Chukwu (1990); “the open door advantage of cooperative openness is that the open door policy makes good philosophy, and also promotes the spread of the cooperative movement across countries and the world, thus making the benefits of membership good because of the process of integration.”

Voluntary and open membership principles of cooperatives, examines the voluntariness and openness of organizations that formulates and implements environmental policies. These bodies could be sub-national bodies, national bodies, regional bodies, continental bodies, and international bodies that operates at the inter-continental levels.

These bodies set out to do the following among others:

- (a) assessing the state of the environment
- (b) evaluating the state of the environment
- (c) controlling the environment by various means such as law, regulations, protocols, conventions, incentives, moral persuasion, training, information campaign etc.

In our contemporary world, divides along socio-economics and politics characterizes the membership of such organizations. At the sub-national and national level, non-membership of religious faith, economic standing, educational attainment, non-membership of a particular political party, ethnic affiliation etc. could prevent qualified and willing persons from the membership of relevant institutions that formulate and implement environmental policies. This is a reflection of the realities of existences in many developing countries. There are also versions of this at the regional, continental and inter-continental levels, much as the economic and political giants dictates the pace for less viable states. It is either membership is not "open" or voting patterns are unequal, at other instances, bourgeoisies members "instills" their positions on membership and voting on the sheer strength of their economic and political power.

This bears elements of totalitarianism, as it is against freedom and individualism, it bends toward the Popperian "Closed Society." Popper argued, based on his observation of ancient Greece, that reactionary forces would always be uncomfortable with the rapid changes that characterizes an "Open Society." He posited that closed societies are anti-democratic, marked with rigid class hierarchy, and made no significant contribution to arts and scientific development. Institutions saddled with environmental management should be largely scientific, although their melting point with politics cannot be relegated, but it requires openness, inclusivity and equality. Based on this, they should bear more of the ingredients of the "Open Society." Thus the Popperian "Strain of Civilization" should be encouraged with the utilization of the cooperative principle of Voluntary and Open Membership, while it should be employed for the abolishment of what Popper described as "tribalism" (Open Society Vol. 1).

Democratic Member Control

Cooperatives are democratic in character. They are organizations controlled by their members. These members participate actively in the policy processes. Elected representatives are responsible to the membership. This principle promotes what is otherwise called "economic democracy in action." Since cooperatives were established for the restructuring of the society, especially by way of inclusion, the idea that each person hold a vote regardless of his economic standing goes to support the cooperative values of equality and equity.

According to ICA at its 1966 Congress, Co-operative societies are democratic organizations. Their affairs should be administered by persons elected or appointed in a manner agreed by the members and accountable to them. Members of primary societies should enjoy equal rights of voting (one member, one vote) and participation in decisions affecting their society. Sustainable development, in this case the interest of all in environmental issues are best achieved through meaningful participation of all divides in the policy process.

Democratic politics as espoused with Popper's characterization of the "Open Society" should be the hallmark of environmental management. He argued that societies are more real than the individuals that lives inside of them (Open Society Vol. 180), by consequence he meant that the truest strength or weakness of a society resides in the coming together of her people, preferably on equal yokes. In 2014 the World Resources Institute (WRI) in one of its research works on the viability of democratic principles to environmental management brought back to fore the once proposed five-dam project on the Baker and Pascua Rivers in Patagonia, Chile. WRI posits that while the hydropower was projected to possess the capacity to produce 2650 M watts of electricity, on the contrary the project would flood about 23 mile² of wildlife, with adverse effect on the environment, local culture and economy of the region. The project was successfully opposed by a coalition of over 70 organizations from within and outside Chile. Important is the fact that citizen's agitation was primary in the opposition.

Popper further posits against what he described as "minimalist democracy." He rejected the question of "Who should rule?". Rather he proposed the question of "How can we so organize political institutions that bad or incompetent rulers can be prevented from doing too much damage?". He viewed democracy from a pragmatic angle on a people oriented institutional design. Popper proclaimed that there is nothing intrinsically valuable about democracy until it is built on the sovereignty of the people in a model of democratic member participation.

The Application of Democratic Principles Will Instill Into Environmental Management Fundamental Rights which are Built on the Tripod of:

- (a) Access to Information,
- (b) Public (inclusive) Participation
- (c) Access to Justice.

This can be espoused further with the following assertions:

Firstly, public and private initiatives on environmental exploration should be open to the public forehand. Information; such as development project plans, environmental impact assessment etc. should be readily available for not only public consumption, but to all divides.

Secondly, there should be more discussion at equal pedestrian between governments, governments and communities, government and the business community (communities), companies and communities, communities and communities on environmental use and management.

Thirdly, is access to “real justice” and not justice from the viewpoint of the stronger party. This should include both litigation and Alternative Dispute Resolution mechanism, it should guarantee for all parties quantum of merit and effective means of enforcement.

Member Economic Participation

According to the third principle of cooperatives; members are to contribute equitably, and democratically control the capital of their cooperatives. It spells out the responsibilities of members to their cooperatives, especially as regards finances. Although this principle starts with the emphasis on money management, its core values remain the socio-economic stability and upliftment of members, thus both the cooperative and its finances are structured for the needs of members. Cooperatives are capitalized through the pooling of funds, while this imposes on the association that it exists and operates for the benefit of all members and not just a section of its membership.

Inclusion in environment management is one, participation is another, and perhaps of more importance. Popper’s contention against “utopian social engineering”; a model that seeks to administer the society in accordance with a definite blueprint, where ultimate human ends such as perfect justice, equality, freedom, happiness and fulfillment are fully realized. Rather he argued in favor of the “piecemeal social engineering,” a small scaled model that focuses on one institution at a time and seeks to eradicate sadness, unemployment, poverty, environmental degradation etc. He posits that “utopian social engineering” imposes on the people totalitarianism, as such it must be substituted with another model where men and women are not just pawns in the social system, but are *economic participants* in a new society, (*Poverty of Historicism*, 70).

Institutions involved with environmental management will always have members, but the quality of the participation of members is primary, especially the economic participation of members. On the international stage, non-payment of due has been a major drawback on the activities of such organizations, the revenue aspect of budgetary proposals often fall short of projection due largely to unpaid financial dues on the part of some members. Often, the defaulters lay claim to inability to pay, citing poor financial position or poor standing in the Human Development Index (HDI). However, sub-management of the environment, which is a likely consequence of financial default of such member states, could lead to environmental degradation and consequently disasters which portend further compound economic and financial woes. Non-financial participation on the part of some country under any guise is simply an affirmation to the dominance of the environmental bourgeoisies, as states from the global north have continued to showcase themselves as consistent financial members. Non-financial membership sometimes excludes such members from core decision making roles, thus further widening the gap between divides, ultimately, it confers more economic and political powers to persist in domination on the financial members.

Autonomy and Independence

The fourth principle of cooperatives states “Cooperatives are autonomous, self-help organizations controlled by their members. If they enter into agreements with other organizations, including governments, or raise capital from external sources, they do so on terms that ensure democratic control by their members and maintain their cooperative autonomy.” This principle dwells more on the fundamentals of identity. Cooperatives are to serve their members and not to serve any ideology e.g., politics, religion etc. Institutions saddled with environmental management are to strive toward independence and autonomy, this becomes a task in view of the nature of the support system upon which these institutions were created and currently survive, they are institutions of state(s) and are financed by same.

In Popper’s latter editions of *The Open Society and Its Enemies* he grew more critical of direct state intervention to tackle socioeconomic challenges. Instead the preferred amendments to laws toward less state, but more people oriented approaches. He posits that direct intervention by government is always to the advantage of the state and the elite class, this is to the detriment of those on the other divide. A way out of this, according to Popper is to promote and sustain autonomy and independence in both the policy and legal frameworks.

Most of the institutions involved with environmental management, public or private depends on patronage from either the public or private sectors, and in some cases both to survive. On the other hand, these patronages are a reflection or extension of ideologies, which in turn demand loyalty from institutions they patronize. If this continues, the policy process will continue to be influenced with extraneous interest, which will be inimical to the independence and autonomy of institutions involved with environmental management.

The imperative of avoiding this unpleasant circumstance, is at the core of the humanist value required in the management of the environment. The environment cannot be managed on sectional interest, else it becomes a business from the economic perspective or instrument of domination from the political perspective. Consequently, there arises the strict requirement on environmental management to operate on firm, uncompromising humanist principles, which can only be built on austere approaches that are enshrined in the fourth cooperative principle and the values of cooperatives.

Education, Training and Information

Karl Popper's attempt to critic the "Utopian Social Engineering" concept and in its stead champion the "Piecemeal Social Engineering" theory can only be appreciated in an atmosphere of enlightened minds, according to Corvi (1997) that is in a society with viable and consistent system of education, training and information that is devoid of totalitarianism and centralism. A society, with a social democracy that places education as an integral theme of human rights. Popper posits that "human knowledge grows and changes overtime, and knowledge in turn affects social events" (Internet Encyclopedia of Philosophy, Pg. 8). To Popper, the capacity to gain the knowledge to survive the future is of essence if societies must be kept "Open."

He further contends "change the conditions and the trend may alter or disappear. A trend toward greater knowledge and freedom could be sustained or disrupted, which could facilitate an "Open" or a "Closed" society" (Conjectures and Refutations, 339). The tendency is very high that humans will function better if we understand the theory and practice of issues and circumstances around us, when we appreciate the value behind conflicting theories and practices involved with our daily thoughts and activities. The fifth principle of cooperatives centers around cooperatives as mechanism for improved humanity through education, training and information. It states (ICA, 1995) "cooperatives provides education and training for their members, elected representatives, managers, and employees so they can contribute effectively to the development of their cooperatives. cooperatives inform the general public-particularly young people and opinion leaders about the nature and benefits of cooperation." According to the EPA (2019) environmental education in all its ramification can best be achieved only on the platform of the cooperatives. Environmental education is one, objective utilization of the lessons from the concept for holistic environmental management is another.

Integration of cooperativism into environmental education builds into the various institutions involved with environmental management relationship that raises sustainable achievements through the transformation of such institutions into the appreciation of values in diversity. It instills into the policy process socio-economics and political solidarities, which are essentials for holistic environmental management. Environmental education empowers individuals, groups and institutions to properly explore environmental issues along thoughts and activities for environmental sustainability. It seeks to develop deeper understanding of the environment across divides.

Some of the components of environmental education are:

- (a) Awareness and sensitivity
- (b) Knowledge and understanding
- (c) Promotion of positive attitudes
- (d) Skills development
- (e) Improved inclusion.

Environment education encompasses, both environmental training and information.

Benefits of Environmental Education as the Following:

- (a) Imagination and enthusiasm are heightened
- (b) Learning transcends the formal settings
- (c) Tolerance and understanding are supported
- (d) Integration of sub-national, national and international standards
- (e) Biophobia and nature deficit disorder declines
- (f) Communities are strengthened
- (g) Responsible actions for environmental management becomes more acceptable.

However, all of the above becomes sub-utilized until competent approaches are employed. When member of environmental management institutions are educated, and training and information are in accordance with the cooperative model and Popperian thoughts, personnel saddled with responsibilities become better equipped at contributing effectively at driving such institution toward holistic environmental management.

Cooperation Among Cooperatives

According to (ICA, 1995) "Cooperatives serve their members most effectively and strengthen the cooperative movement by working together through local, national, regional and international structures." The environment is a single unit with broad spectrum, it is segmentalized by human use and projected use. As much as our interest has given us a mental division of our environment, even with the exploration of the earth often carried out from isolatory thoughts about other places, the environment remains a circle. It binds human actions and reactions across different spectrums.

An offshoot of this is the not so robust linkages on environmental management between individuals, groups and institutions. Take for instance in Ibadan, Nigeria; some individuals in their rather uncooperative conception of waste disposal simply go out at night to dump heap of refuse from their home by the roadside, or dump same on waterways during the rainy season with the intention that the rain would wash it away. In similar vein are the activities of some persons in the Niger-Delta region of Nigeria, who in their quest to illegally access crude petroleum burst huge pipelines conveying the product, after obtaining the desired quantity, but leave the remaining to spill into adjacent farmlands, rivers and the natural environment because they lack the capacity

to repair the bursted pipelines. On the larger scale is the shared environmental concern between India and Pakistan, or India and China, some multinationals and host communities etc., all culminates to challenge the environment and its management.

There are always activities on environmental management, with high profile claims of best practices, but there remain a huge vacuum for the redress of environmental degradation, global warming, desert encroachment etc. as support for this assertions. What is lacking is the synergy of activities, or in another word, solidarities among the various activities. Earlier in this work, the importance of solidarities within communities, and institutions involved with environmental management was canvassed. The next frontier canvassed is the solidarity among the various solidarity built initiatives. Each working for itself, for the other and with the other, from the local, national to the international, along horizontal and vertical lines. This is the crust of the sixth principles of cooperatives, "cooperation among cooperatives" in environmental management.

Concern for Community

This is the seventh and last principle of cooperatives, it encompasses all other principle and the values of cooperatives. According to the (ICA, 1995) "Cooperatives work for the sustainable development of the communities through policies approved by their members." Policies aimed at the sustainable development of communities and state should be based on policies agreed to by all the divides present within communities and states. These policies are to be in accordance with the "Piecemeal Social Engineering" as this Popperian philosophy emphasizes the real on small realistic scales with concentration on the truest needs of the community. While promoting the "Piecemeal Social Engineering," Popper introduced a concept he called "Negative Utilitarianism" to proffer answers to the question of "which of the problems of society is most urgent?" he responded that "human misery is the most urgent problem of a rational public policy." Cooperative philosophy has been employed the world over to address human miseries in different facets, e.g., poverty, illiteracy, access to health care, improved agricultural productivity, microfinance and in the instance case environmental challenges.

If the word "community" from the phrase "Concern for Community" is substituted for "environment" toward a better conceptualization of this work, then is safe to conclude that "if cooperative principles and values are agreed upon as management policies for the environment, actualization of sustainable development becomes more realistic."

Conclusion

This review has provided bold conceptualization of holistic environmental management with the use of cooperative principles and values. Bearing in mind the complex nature of man, especially as it involves economic, social and political interest in their various forms, and the different approaches often employed at protecting this interests, there was a further attempt to supplement cooperative principles and values with Karl Popper's philosophical thoughts (Popperism). Based on this, the various human divides, and their strands of input which had taken tolls on environmental management were identified for remedial and improvement to support sustainable development from an admixture of cooperative principles and value on the one hand, and Popperian thoughts on the other. It is hoped that this literature will be of immersed value for environmental management and sustainable development.

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Social Media, Sustainability and Organizations

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Abstract

Communication is a social process affecting human behavior, including both in-person and virtual interaction made possible by advances in technology. Social media communication allows users world-wide to connect with each other, engaging with shared content ranging from personal messages to news to entertainment. Anyone with a device and Internet access may engage with social media, and individuals, businesses, and public organizations are active users. Social media communication is utilized in the important domain of sustainability: Meeting present needs without compromising the ability of future generations to meet their needs. Sustainability activities are broad and include environmental, economic, and social initiatives at multiple levels. This article discusses key elements of social media, its use in organizations, its application within sustainability communication, and future challenges.

Communication is a social process affecting human behavior (Godemann and Michelsen, 2011). Individuals have always communicated with others: first through direct, face-to-face connections, then indirectly through images or the written word, and today through multiple channels and formats made possible by rapid advances in technology. Social media communication allows users world-wide to connect with each other, engaging with shared content ranging from personal messages to news to entertainment. With this shift to digital platforms, anyone with a device and Internet access may engage with social media. This global connectivity, in turn, allows for the creation of virtual networks and communities.

Social media communication covers a broad array of topics, and it is used by individuals, businesses, and public organizations. One steadily-growing domain addressed via social media is sustainability: meeting present needs without compromising the ability of future generations to meet their needs. Sustainability activities are broad and include environmental, economic, and social initiatives at multiple levels. This article discusses key elements of social media, its use in organizations, and its application to sustainability communication.

Background of Social Media

Social media is a broad term that refers to people interacting in online, multidirectional communication. It differs from traditional one-way communication by providing an interactive experience among participants, rather than a transmission outlet broadcasting information with no direct reaction or response (Kaplan and Haenlein, 2010; Joosse and Brydges, 2018; Saxton et al., 2019). Individuals, organizations, businesses, governments, and communities use social media, and the global availability of the Internet has supported this interactive communication. The world's population was about 7.6 billion in 2019, and over half the planet's inhabitants reported using the Internet regularly. Statista data indicate that on average, Internet users across the globe spent 135 min daily on social networks in 2019.

The rise of social media as a powerful communication tool has been rapid, reflecting the explosive increase in information available through major shifts in technology (Godemann and Michelsen, 2011). Kaplan and Haenlein (2010) highlighted the impact of Web 2.0, a term that describes how software developers and end-users have utilized the Internet as a platform to share and modify content in a participatory fashion; see also Fieseler et al. (2010). Social media usage worldwide has contributed to new exchanges of knowledge and different forms of virtual collectives.

The Pew Research Center, a nonprofit, nonpartisan data research center (www.pewresearch.org) began tracking social media engagement in 2005. At that time, some 5% of American adults used at least one social media platform (Pew, 2018); by 2018, 95% of North Americans engaged in social media use, and world-wide social media users reached almost 2.5 billion. This global engagement clearly offers immense potential for communication outreach in multiple domains. Social media market penetration varies by region and reflects the *digital divide*: global inequalities in information access. According to Statista data, North America and Northern Europe reported the highest penetration, at 95%, with significantly fewer users (51% and lower) in Central Asia, the Caribbean, and all regions of Africa.

The broad array of social media formats allows for information transmission, content sharing, and entertainment, and most communication is available instantaneously. Widely and rapidly sharing a social media *post* (text, image, or video) is called *going viral*. From a practical standpoint, social media is easy and inexpensive. While music and video streaming services may charge a subscription fee, the costs for social networking platforms are generally free to users because they are covered by advertiser support. For example, many popular YouTube videos cannot be accessed without first viewing a short advertisement from a corporate sponsor.

User Characteristics

Anyone with access to the Internet and a device (e.g., smartphone, tablet, or computer) can utilize social media, so its reach crosses demographic attributes and geographic boundaries. Social media was first embraced by young participants, but its audience now crosses the age spectrum, although younger users remain the most actively engaged. For example, Pew data (2018) indicated that the Instagram platform achieved 64% market penetration among American young adults (ages 18–29), compared to 21% of middle-aged users (ages 50–64). Younger users may be more likely to embrace social media because of technology expertise. A person brought up after the advent of the Internet and digital technology is considered a *digital native*, while *digital immigrants* have had to learn these skills as adults.

Pew research also indicates differences in social media engagement for other demographic characteristics. People with higher education levels are more likely to report using social media regularly, although variation across user income levels is small. Women are more active users of social media applications compared to men, except for YouTube (with 75% men and 72% women active participants). Platform usage also seems to vary by race, with Facebook most popular among Hispanic users, Instagram used more often by Black users, and Pinterest, by White users (Pew, 2018).

Types of Social Media Applications

Technology developments, coupled with social media's worldwide popularity, has generated an expanding number of applications. Many alternatives are available in content (from news releases to personal blogs), format (text-based transmissions, sound, image, and video), and audience (individuals to groups to organizations). Although social media platforms share many characteristics, they operate in different ways; e.g., the media richness of a virtual game world versus the self-disclosure level of a Facebook post (Kaplan and Haenlein, 2010, p. 62). Joining a social media platform means the user agrees to the platform's terms, giving the site permission to use posted content and allow others to share it. Because individual dialogues rely on original content, such as posting one's own ideas or pictures, they generally circumvent copyright issues. Most platforms typically offer users some control over their activity through privacy and application settings—although some degree of self-disclosure is almost inevitable (Joose and Brydges, 2018). Indeed, the only way to maintain full control over one's personal information on social media is not to share it at all.

Among the earliest social media applications were personal weblogs (*blogs*). Blogs are online publications with brief entries in a narrative style, organized in reverse chronological order, that enable interactive comments. Some blogs are targeted to a small group of like-minded individuals; others have expanded through both social and mass media. An illustration is the "Going Zero Waste" blog (www.goingzerowaste.com) that has been featured by *National Geographic*, *National Public Radio*, *CNN*, *The Guardian*, *CBS*, and *US News and World Report*. Joosse and Brydges (2018) comment that blogs broaden the sources and platforms for environmental communication, making way for new voices—and nonexperts—on the topic. In recent years, many organizations have also become active users of corporate blogs (Fieseler et al., 2010).

Global interconnectivity allowed for the development of social networking. Early social networking sites such as MySpace were developed in the late 1990s, and were followed in 2004 by the establishment of Facebook. Facebook is the most widely-used social media platform in the world. It provides an extensive social networking capacity, also serving its users as a search directory for friends and contacts. The second most popular application is YouTube, which shares videos and music and allows users to upload original content. Other platforms, including Twitter, rely primarily on text, web links, or memes. In general, a social media update is called a *post*, except for Twitter, which calls its short posts *tweets* (up to 280 characters of text). A *meme* is an image plus short text, often meant to be humorous, that is shared on the Internet; an illustration is included in Fig. 2.

Instagram is an image-sharing platform that is very popular for personal activities; it also encourages user interaction through informal questions, quizzes, and polls (e.g., ‘What is your favorite way to recycle?’). The *Pinterest* social network allows participants to visually share interests through posts, primarily images (called *pins*, after a bulletin board). *LinkedIn* is a social networking and search platform focused on professional topics and job opportunities that also includes articles and career-related content. The *WhatsApp* application concentrates on text messaging and voice calls. Several platforms (e.g., Twitter, Instagram, and Facebook) use the *hashtag* concept (# followed by a word or phrase) to organize content, making it easier to access related documentation (Saxton et al., 2019). One illustration is *#sustainability* on Instagram, which had 3.2 million posts in early 2019. Table 1 provides a summary of the seven largest social media applications worldwide. In addition, other popular social media platforms and messaging tools (especially for younger users) include Snapchat, Skype, Tumblr, Reddit and Flickr.

Social Media in Organizations and Communities

Public and Government Organizations

The benefits of global reach, rapid transmission, and low cost encouraged social media communication to extend beyond individual networking to include organizations. Public entities, nonprofits, and governmental agencies (from local to intergovernmental) use social media actively to connect with a wide range of stakeholders. Social media offers high information access and different types of data as well as more interactivity (Joose and Brydges, 2018). Public communication may serve to transmit information (e.g., educating citizens about changes in regulations), and it also provides the opportunity to strengthen stakeholder engagement. For example, social media platforms are an integral part of many public emergency management plans, such as hurricane tracking.

Prior research has reported that civic engagement and political activism are linked with social media use, because it enables direct action as well as knowledge sharing. When citizens gain a voice through social media, industry and government lose their dominance over information (Joose and Brydges, 2018; Saxton et al., 2019). In addition, social media creates social networks that offer opportunities to participate in civic and political actions. Boulianne (2015) found the relationship between social media use and civic/political participation appeared to be positive and correlational.

Business Organizations

Corporate firms, both publicly and privately-owned, are heavy users of social media. Businesses use social media for a variety of purposes (Reilly and Hynan, 2014), such as sharing company information (e.g., on a Facebook page), responding to customer questions (perhaps through Twitter), and recruiting new employees (via LinkedIn). Many large companies maintain multiple

Table 1 Overview of key social media applications.

Social media site	Logo	Established	Primary function	Active users in 2018	Owned by	Users, age 18–29 (%) ^a	Users, college grads (%) ^a
Facebook		2004	Social networking	2.32 billion	Public: NASDAQ	81	77
Twitter		2006	Micro blog	330 million	Public: NYSE	40	32
Instagram		2010	Photo sharing	1.0 billion	Facebook	64	42
YouTube		2005	Video sharing	1.8 billion	Google	91	85
Pinterest		2010	Visually share interests	250 million	Public: NYSE	34	40
LinkedIn		2013	Professional social networking	260 million	Microsoft	29	50
WhatsApp		2009	Text messages and phone calls	1.3 billion	Facebook	27	29

Data sources: Pew Research Center; Statista; company websites.

^aPercentage of American adults as active users (Pew, 2018).

accounts: a parent company presence plus social media sites for their major brands (which may be more active than the parent company account; see Reilly and Larya, 2018), and perhaps other accounts addressing particular topics (Saxton et al., 2019). To illustrate, in 2019 General Motors maintained multiple platforms for each of its automobile brands (e.g., Buick, Cadillac, Chevrolet), a Twitter account addressing diversity (@GM_Diversity), as well as separate Twitter, Facebook, and Instagram accounts for the GM parent company and its Chair and CEO Mary Barra.

Business organizations also engage frequently with the LinkedIn platform. This application emphasizes professional networking and career development, and many firms dedicate resources to LinkedIn as an important part of their job recruitment strategy. LinkedIn also provides a useful search function that targets not only by individuals' names, but also by desired job-related attributes or demographics. This platform claimed 630 million members worldwide in 2019 (www.facebook.com/LinkedIn/).

One of the most important reasons companies use social media is to market their products and services (Reilly and Larya, 2018). As Kaplan and Haenlein (2010) comment, social media allows firms to engage in timely and direct consumer contact efficiently at low cost, and organizations frequently use multiple social media platforms to relay similar marketing content. Making sure the company's message is consistent across all media and outlets is the concept behind integrated marketing communication. Firms also gather data from consumer/company social media interaction that contribute to marketing strategies. Prior research has thus called for social media to be integrated fully within an organization's overall corporate communication strategy (Saxton et al., 2019; Herzig and Schaltegger, 2011).

Savvy organizations also look to social media *influencers* in crafting their communication plans. An influencer has a strong social media presence and established credibility, and his large audience and reputation allow him to influence other users. High-profile influencers impact others not only through direct follower engagement, but also via comments, discussions, *likes* and *shares* by their audience (e.g., *retweets* and *pins*). The sustainability realm offers multiple examples of high-impact social media influencers—including many who are high-profile because of their other roles. Film celebrity and environmentalist Leonardo DiCaprio is an illustration; in May 2019, his Twitter presence included 19 million followers. Another high-impact sustainability influencer is former Microsoft CEO Bill Gates, with 47.2 million Twitter followers in 2019. A sample tweet from his Twitter account is below:

Bill Gates@BillGates 28 March 2019

To prevent the worst effects of climate change, we need to reach near-zero emissions on all the things that drive it—agriculture, electricity, manufacturing, transportation, and buildings—by investing in innovation across all sectors while deploying low cost renewables.

In addition to message content, the freshness of corporate social media communication must be considered. Outdated information and broken links are common, and more serious problems may arise with negative content. Given the broad scope and instantaneous transmission possible with social media, organizations must be vigilant in monitoring for potential information distortion, rumors, and unofficial or unverified sources (Kaplan and Haenlein, 2010; Reilly and Hynan, 2014).

Virtual Groups and Communities

Social media has encouraged virtual groups and communities to form through its online social interaction. Like-minded users may form a public (anyone may join) or private (requires permission) group or community based on shared demographics, backgrounds, or interests: e.g., local neighbors, university alumni, or recycling advocates. Indeed, potential group members may receive an invitation to join a group, based on their network connections and platform activity. These virtual communities vary in complexity and format, and their cohesiveness generally depends on having engaged members plus an organized curator monitoring information flow and the network of connections. One popular example is a Facebook group. These groups provide information sharing and add the social networking dimension of connecting via Facebook profiles. An illustration of a public Facebook group is called 'Sustainability.' This community had over 2000 members in early 2019, and its profile notes,

About This Group: A forum for discussing important sustainability topics and sharing useful or interesting information on the subject. Looking for provocative and even controversial discussions on topics like climate change, water/food shortages, waste and pollution, biodiversity, war and many others.

Other examples of virtual communities include the blogosphere, chat rooms, and virtual worlds. The *blogosphere* generally refers to the collective online network of personal and organizational blogs (Fieseler et al., 2010). A *chat room* operates like synchronous conferencing: group members exchange text information with others in real time. Many social media users participate in *virtual worlds*, in which individuals adopt an *avatar* identity (a figure representing a person) in a fictional computer-based setting—often as part of a game (Kaplan and Haenlein, 2010). For example, *Farmville* (developed by Zynga) lets participants virtually engage in farming by planting and harvesting crops, milking cows, and collecting eggs (www.zynga.com/games/farmville).

Social Media Communication and Sustainability

Individuals and organizations use social media to communicate and interact about an array of topics, including sustainability. Sustainability is a broad construct covering a wide range of issues, ranging from individual recycling behavior to organizational

pollution monitoring to global climate change. Sustainability challenges for organizations are many, and social media applications offer the opportunity to discuss, network, and initiate action about these important issues.

An Overview of the Sustainability Construct

There are multiple approaches to sustainability; the definition used here describes sustainability as development that meets present needs without compromising the ability of future generations to meet their needs (Godemann and Michelsen, 2011). Sustainability considers responsible economic development and social objectives that preserve natural and human resources. A variety of factors underpin the growing engagement with this topic. Examples include shortages of nonrenewable resources (e.g., the rare earth minerals needed for manufacturing computers); regulatory constraints such as carbon emissions standards; consumer demand for organic and fair trade products; and community concern with the future of the planet. Given its broad scope, sustainability is often measured with multiple metrics that use the concept of *net impact*. Net impact refers to the overall impact of a sustainability action or policy when all major aspects are considered. An illustration is the trade-off in tourism development between positive employment growth and negative overcrowding in the local community.

One popular framework for assessing sustainability performance is the *triple bottom line*. This model includes environmental, economic, and social elements (sometimes called the planet, profit, and people dimensions). Fig. 1 presents an overview of this approach to sustainability, with examples of metrics. A similar model is the ESG framework that assesses Environmental, Social, and Governance measures; governance refers to an organization's leadership, controls over issues such as executive pay and audits, and shareholder rights. This framework evolved in capital markets to assess socially responsible funds, an increasingly popular investment option. Global sustainable investment assets under ESG guidelines were \$30.7 trillion in early 2018, up 34% from 2016, according to the nonprofit US SIF (the Forum for Sustainable and Responsible Investment); see www.ussif.org.

A different approach to modeling sustainability uses the *circular economy* framework. Here, the emphasis is on proactively designing a business operation to focus on restoration and regeneration. The circular model moves beyond the linear approach of making, consuming, and discarding products, focusing on three underlying principles: designing out waste and pollution; keeping products and materials in use; and regenerating natural systems. For example, circular economy techniques in a production plant may include new ways of extracting recyclable materials and remanufacturing outputs from these elements (rather than discarding). The circular economy framework is especially relevant for manufacturing firms, as the tweet below from Unilever illustrates.

Environmental sustainability

Factors affecting the physical and natural environment (air, water, land, ecosystems); being 'green'

Metrics include:

- global warming emissions, such as greenhouse gases
- other pollution
- water usage
- hazardous waste
- engagement in recycling

Economic sustainability

Activities concerning the contribution to the ongoing viability of a broader economic system

Metrics include:

- distribution of wealth
- use equitable business practices
- impact on the local economy
- flow of capital among stakeholders
- infrastructure investment.

Social sustainability

Assesses impact on the people and local area in which an organization operates*

Metrics include:

- support human rights
- foster diversity
- provide safe working conditions
- equal opportunity and fair trade
- community development
- produce safe products

*Corporate philanthropy is sometimes coupled with social sustainability

Fig. 1 The sustainability triple bottom line.

Unilever @Unilever. 9 November 2018.

We are working hard to tackle plastic packaging waste in our own operations and beyond, to help us achieve our 2025 sustainable packaging targets. We've just taken another major step forward with three new partnership initiatives #CircularEconomy.

Challenges in Measuring Sustainability Performance

Evaluating sustainability performance is complex, not only due to multiple metrics. As yet, few agencies require monitoring of sustainability measures, and independent third-party assurance (comparable to accounting audits) is not yet in general use. Although European Union rules mandate regular reports (from 2018) on the social and environmental impacts of large company activities (see www.ec.europa.eu/info/business-economy-euro_en), sustainability information is often self-reported data published on a voluntary basis. Some firms do participate in the Global Reporting Initiative (GRI), an independent, international organization established in 1997 that seeks to make sustainability reporting a standard practice (www.globalreporting.org). In addition, some industries do employ self-regulation (Herzig and Schaltegger, 2011). One example is Leadership in Energy and Environmental Design (LEED) certification (Platinum, Gold, Silver, and Certified) awarded for green building construction worldwide (<http://leed.usgbc.org>).

A related issue is the sophisticated nature of many sustainability metrics (Reilly and Hynan, 2014). These may require translation of technical terms not familiar to the community at large: carbon offset trading, the Human Development Index (HDI), and gray water are examples. This challenge is especially relevant in social media, where messaging is brief and often visual. Technical experts in sustainability are needed to translate their expertise to the nonexperts—corporate leaders, politicians, and consumers—who will be making sustainability policy decisions. Further, lack of standardized metrics makes it difficult to compare sustainability performance across industries and organizations (Herzig and Schaltegger, 2011; Reilly and Hynan, 2014). Without required and standardized metrics, many organizations are able to focus their sustainability communication on areas in which they perform well or receive awards. The following is an example from Nestlé's corporate website (www.nestle.com):

We are not driven by awards and recognition. Nonetheless, we are proud to have our sustainability efforts and achievements acknowledged in 2018 by world-leading ratings and rankings agencies. We are also open to working with their suggestions to support continuous improvement.

Greenwashing

With the prevalence of self-reported data, sustainability social media communication is especially prone to *greenwashing*: misrepresenting actual sustainability practices or activities to promote a false image of responsibility (Saxton et al., 2019). Prior research has noted that organizations are reluctant to disclose sustainability 'bad news,' leading to overly positive messaging (Reilly and Hynan, 2014). According to Herzig and Schaltegger, communication about sustainability is often characterized by information asymmetry in which the audience cannot easily access firm sustainability data, leading to low credibility (2011, p. 157). Thus, organizations may be able to portray themselves as sustainability stewards because stakeholders must rely on the companies' own messaging. One greenwashing illustration is Procter and Gamble's announcement of its 2018 introduction of Pampers Pure Diapers:

For parents searching for diaper and wipe options in the "natural" category who don't want to sacrifice performance, the new Pampers Pure Collection offers another choice. It is the first-ever diaper and wipe collection made with premium cotton and other thoughtfully selected materials, stylish prints, and the Pampers protection.

(See Procter and Gamble News Releases: https://news.pg.com/news_releases/all/all/all Thursday, February 22, 2018 11:34 am EST).

Calling disposable diapers and wipes 'pure' and 'natural' ignores that these products require energy to produce, are not recyclable and generally end up in landfills.

Sustainability and Social Media at Multiple Levels

Individual Sustainability and Social Media

The interactive and inexpensive characteristics of social media have contributed to its popularity among individuals engaged in the sustainability domain. Several studies have examined bloggers who actively post about personal choices that support sustainability, such as Joosse and Brydges' (2018) study of green bloggers. According to Joosse and Brydges, these bloggers serve as ordinary nonexperts acting as intermediaries of information about topics including a sustainable lifestyle, beauty products, and food (2018, p. 689). Such sustainability communication may support a process of individual and voluntary behavioral change, such as water conservation or recycling (Godemann and Michelsen, 2011). In addition to tracking their own personal sustainability achievements, many individuals blog about the sustainability progress (or lack thereof) by business and public organizations.

Business Organization Sustainability and Social Media

Business firms regularly use multiple social media platforms to communicate about sustainability (Reilly and Hynan, 2014). As Saxton and his colleagues note (2019), simply creating a related social media account suggests a company is signaling its engagement in the sustainability agenda. Sustainability reporting indicates an organization's willingness to communicate about societal issues, contributing to a positive relationship with its stakeholders (Herzig and Schaltegger, 2011). Stakeholders have become increasingly aware—and often critical—of corporate sustainability performance (Fieseler et al., 2010), so sharing their sustainability activities has become an integral component of many firms' corporate communication (Reilly and Larya, 2018). Below is a Twitter example from McDonalds:

McDonalds Corporation @McDonalds Corp. 9 May 2019.

DYK [Did you know] that we'll be using packaging made from renewable, recycled or certified sources by 2025. So far, we've eliminated more than 300 million pounds of packaging, recycled 1 million tons of corrugated boxes and reduced waste by 30%.

<http://McD.to/6011E9k95> #ScaleForGood.

Some prior research has indicated that a company's sustainability engagement may follow multiple paths. Many initiatives are directed by top management strategy, such as a firm-wide program to reduce solid waste production in manufacturing. But other activities may be grass-roots changes driven by lower-level employees; e.g., an in-house recycling program (Reilly and Hynan, 2014). Herzig and Schaltegger (2011) propose that corporate sustainability communication should consider internal stakeholders (employees and managers) as well as external constituencies (consumers, stockholders, and the media). Whether the messaging is vertical or horizontal and internal or external, social media offers a critical tool for effective sustainability engagement and dialogue (Fieseler et al., 2010). Fig. 2 provides some illustrations of sustainability-related social media messaging.

Public Organization Sustainability and Social Media

The broad sustainability agenda is also relevant for policy makers in public organizations. Indeed, the missions of many public agencies deal directly with sustainability issues, ranging from environmental preservation (e.g., the European Environment Agency) to health (the U.S. Department of Health and Human Services) to workplace conditions (United Nations International Labour Organization). These organizations also have multiple stakeholders—citizens, employees, activists, and the community at large—that hold them accountable for their sustainability performance. Boulianne (2015) found that civic and political engagement correlated positively with social media use, and social media content from companies perceived as socially responsible is more likely to be shared (Saxton et al., 2019, p. 374). Further, the interactive nature of social media allows for an immediate response, which is helpful in implementing sustainability programs or calling for action.

Given the broad reach of international public organizations, they are often expected to provide sustainability leadership because issues such as climate change, water shortages, and social inequity cross national borders. One example is the United Nations' 17 Sustainable Development Goals, adopted by all UN Member States in 2015 as part of the 2030 Agenda for Sustainable Development. The 17 goals seek to provide a shared blueprint and a call for action at the global level, and they address a wide array of environmental, economic, and social sustainability challenges (<https://sustainabledevelopment.un.org/sdgs>). A list of the 17 UN goals is presented in Fig. 3.

Community Sustainability and Social Media

Social media sustainability communication may diverge across various forms of communities. Godemann and Michelsen (2011, p. 6) propose that the task of sustainability communication is to introduce an understanding of the relationship between people and their environment into broader social discourse. Different communities will have diverse interpretations about these elements—and the nature of social discourse itself. Boulianne (2015) points out that social media provides a forum for information and news that is often filtered through a network of trusted others. These networks—and the trusted others in them—will vary, leading to corresponding differences in messaging. Demographics continue to matter: Table 2 shows that platform usage varies by community type, with rural users least active across platforms, perhaps reflecting Internet availability.

Community social media activity may also reflect differences in purpose and location. While some sustainability challenges (e.g., climate change) are global, others may relate specifically to particular users. For example, high-profile sustainability challenges in urban areas may include employment disparity and unequal access to public education, while sustainability concerns in rural and agricultural districts may involve genetically-modified crops and animal welfare. Social media is frequently used to support non-profit activist and social movement actors (Saxton et al., 2019), such as #girlrising, a global movement to educate girls that had 117,000 followers in early 2019. In addition, sustainability messaging also reflects characteristics of the communities involved. The tweets below contrast environmental sustainability posts for a rural wilderness area (Grand Teton National Park in Wyoming) with that of the Sierra Club in urban Chicago.

Grand Teton NPVerified account @GrandTetonNPS 9 May 2019.

Biologists w/the Interagency Grizzly Bear Study Team will conduct grizzly bear research and trapping operations in Grand Teton May 15–Oct 21. This is part of on-going efforts required under the 2016 Conservation Strategy for Grizzly Bear in the GYE.

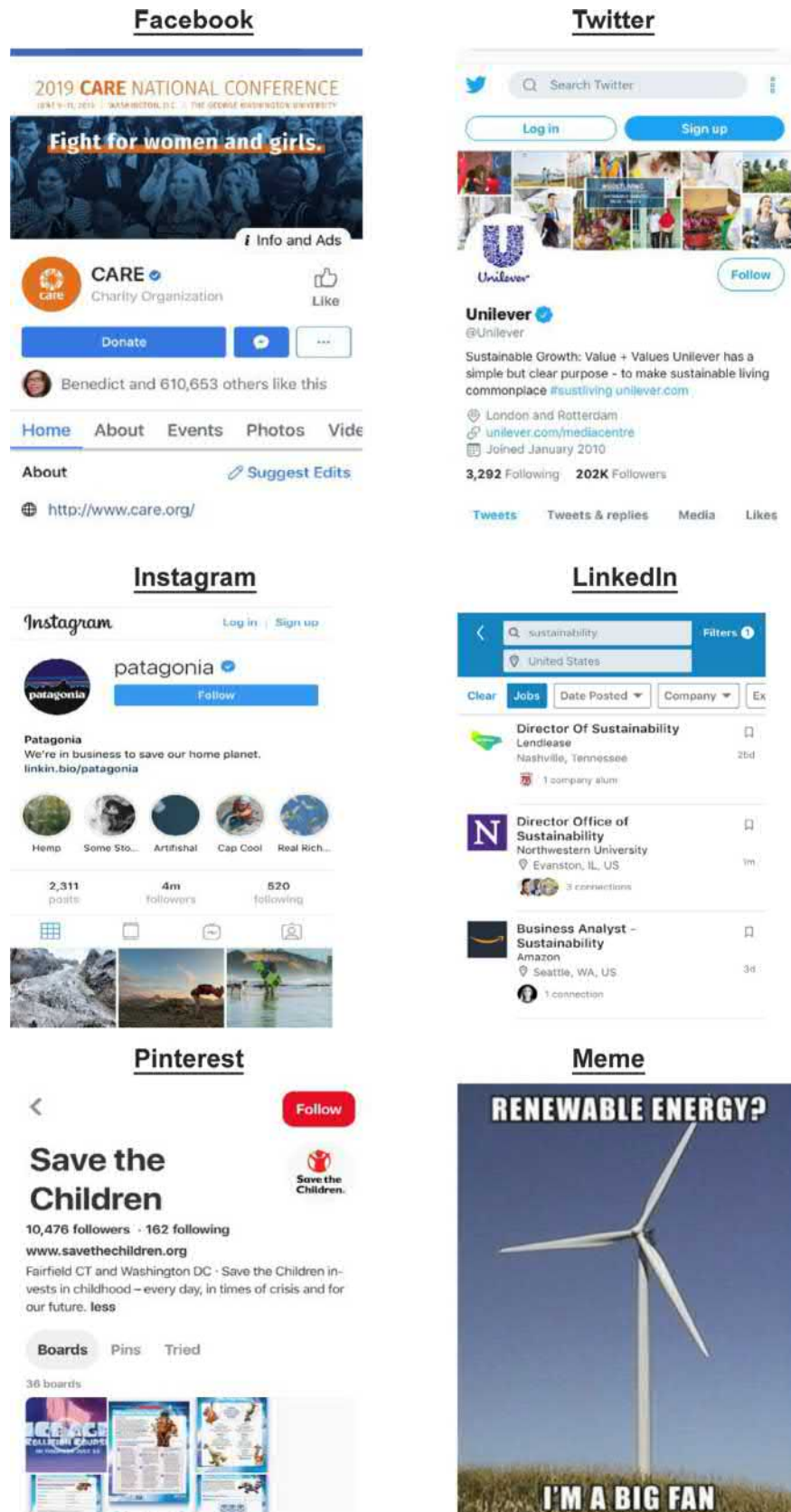


Fig. 2 Illustrations of sustainability-related social media posts.

- 1: No Poverty
- 2: Zero Hunger
- 3: Good Health and Well-being
- 4: Quality Education
- 5: Gender Equality
- 6: Clean Water and Sanitation
- 7: Affordable and Clean Energy
- 8: Decent Work and Economic Growth
- 9: Industry, Innovation and Infrastructure
- 10: Reduced Inequality
- 11: Sustainable Cities and Communities
- 12: Responsible Consumption and Production
- 13: Climate Action
- 14: Life Below Water
- 15: Life on Land
- 16: Peace and Justice Strong Institutions
- 17: Partnerships to achieve the Goal
- 18: Sustainable development

Fig. 3 United Nations sustainable development goals (2015).

Table 2 Adult American active users by community type.

<i>Social media site</i>	<i>Users in urban communities (%)</i>	<i>Users in suburban communities (%)</i>	<i>Users in rural communities (%)</i>
Facebook	75	67	58
Twitter	29	23	17
Instagram	42	34	25
YouTube	80	74	59
Pinterest	29	31	28
LinkedIn	30	27	13
WhatsApp	28	19	9

From Pew Research Center, Social Media Fact Sheet (2018, February 5). Retrieved from www.pewinternet.org/fact-sheet/social-media/.

Sierra Club Chicago @SierraChicago 10 May 2019.

We're very grateful to the musicians of the Civic Orchestra of Chicago for putting together this string quartet program celebrating nature, on Sunday, May 19. Enjoy an afternoon of beautiful music, and help plant seeds in a community garden!

Conclusions

Social media has revolutionized global communication in many realms, including sustainability. Researchers and users alike agree that social media messaging and format will continue to shift, tracking developments in technology. New applications are introduced regularly, often extending current platforms' functionality and user appeal. Social media market penetration is expected to grow, although some countries do monitor or censor online information access and interaction (including China, Iran, and North Korea). While digital sustainability messaging offers many benefits, important challenges remain.

One critical ongoing problem affecting social media communication is source credibility. Limited government monitoring, much self-reported data, and stale information contribute to this problem. Sharing information via social media is simple and (if desired) anonymous, permitting easy transmission of 'fake news.' According to Jooisse and Brydges (2018), social media sources are often viewed as providing low-quality information, frequently serving as 'echo chambers' to confirm already-established opinions. In addition, the tremendous amount of social media information available may lead to information overload (Herzig and Schaltegger, 2011). Kaplan and Haenlein (2010) point out that the growing number of outlets and platforms, coupled with the high volume of messages, make it difficult to analyze social media activity—in any realm—in depth.

Social media users thus may benefit from a healthy skepticism in interpreting messaging. Consider the source: Is the data provided by an organization with stringent ethical reporting guidelines, such as a reputable news organization, an established educational institution, or a respected research agency? Independent fact-checking websites exist, such as FactCheck.org, a project of the Annenberg Public Policy Center of the University of Pennsylvania (www.factcheck.org). Furthermore, reports released on social media may be funded by organizations with ideological agendas, or sponsored by entities with a direct interest in the outcomes. A well-known example is the tobacco industry. Despite the 1964 U.S. Surgeon General's report outlining the health dangers of nicotine, tobacco companies continue to market cigarettes today.

Another fundamental concern is the right to individual privacy for documentation collected and shared over the Internet. High-profile lawsuits involving Facebook and other companies illustrate that social network platforms may track, save, and reveal private information such as personal identification and online browsing histories. According to a Pew survey, about 80% of American social media users reported anxiety about advertisers and businesses accessing data shared on social media platforms; almost two-thirds called for more government regulation (Pew, 2018). While public safety issues are clearly important (such as monitoring threats posted on social media), so also is the privacy of personal information.

Within the sustainability domain, resource scarcity and climate change suggest that global interest in sustainability will continue, supported in part by social media communication. Some intriguing questions here concern underlying values. For example, where does responsibility for sustainability rest—with personal, organizational, or government actions? (see Joosse and Brydges, 2018) Individual decisions contribute to sustainable lifestyle choices, but broader environmental, economic, and social issues arguably demand broader responses. Sustainability policy decisions may also challenge long-held beliefs about individual and organizational behavior. To illustrate, Joosse and Brydges (2018) noted differences in how individual consumption and sustainability preferences varied about 'needing versus wanting' goods. Sustainability choices may also relate to the field of macromarketing, which addresses how society as a whole distributes goods and impacts consumer behavior via marketing strategies. Decisions such as these, coupled with emerging technologies, suggest that social media will continue to impact sustainability actions for the future.

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Mass Media Representations of Anthromes

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Abstract

This article is divided into three sections. The first deals with the ways in which ideas of anthropogenic biomes (anthromes) have appeared in mass media coverage of climate change and global warming. The second section addresses the ways in which ideas of anthromes have appeared in mass media coverage of the Anthropocene. While the precise specifications of anthropogenic biomes have varied somewhat over time, our focus is on the six main categories, namely dense settlements/urban, croplands, rangelands, forests, wildlands, and indoor anthromes. In the third section, we draw out some conclusions from these findings.

Introduction

There are many reasons why it is important to study how scientific concepts are introduced to the public via the mass media. Often this can be a vital process of translating the complexities and nuances of jargon-laden science reports into language that the lay reader can understand. Drew Westen and Celinda Lake have written, “we tend to speak to [citizens] in our language—the language of parts per million, carbon emissions, carbon sequestration, and the like—and expect [the public] to make the translation. We would do well to make that translation ourselves...” (2009). These challenges can be partly attributed to long-standing differences between the ‘Two Cultures’ first explained by CP Snow in the 1950s.

From the invention of the Gutenberg printing press in 1450 and expanded opportunities for communication on a larger scale, books, and pamphlets, ideas, arguments, stories and commentaries began to circulate throughout various segments of society. These seeds of ‘media’ sprouted all over the world in the decades that followed, leading to a growing role in translating (information, concepts, developments, debates) from formal and often insular spaces of scientific research into communities and the public sphere.

Nonetheless, there have been many ongoing challenges of translation. Within language resides the power to effectively (mis) communicate. Differences in language use between science, policy, media and civil society can unavoidably impede efforts to make climate change, the Anthropocene—or any other issue—meaningful in society. Frankly, important research, effective arguments, and interesting insights from science often suffocates under a wet blanket of jargon and complexity. Clinging to nuance has led to alienation of the decision-makers and audiences that the research often seeks to influence in the first place. It is a struggle to translate complicated science into crisp and resonant commentary that is valued in policy communities and in civil society. Yet this is not necessarily a process of ‘dumbing down’ science for public understanding and engagement but can result in ‘smartening up’ communication of the science in order to effectively meet people where they are in the Anthropocene. In reality, scientific findings usually require translation into more colloquial terms in order to be comprehensible and valued in decision-making from the individual to the collective scales. One example of this is anthropogenic biomes or anthromes (defined below). The media, in all its manifestations, has become the main conduit between science and the general public.

The ways that the Anthropocene and anthromes are discussed in the public arena matter. Among many examples, renowned UK science and environmental filmmaker David Attenborough has credited Ralph Cicerone—then president of the US National Academy of Sciences—for delivering a rousing talk in Belgium in 2004. That public talk managed to convince the influential Attenborough of the case for the importance of anthropogenic climate change (Randerson, 2007).

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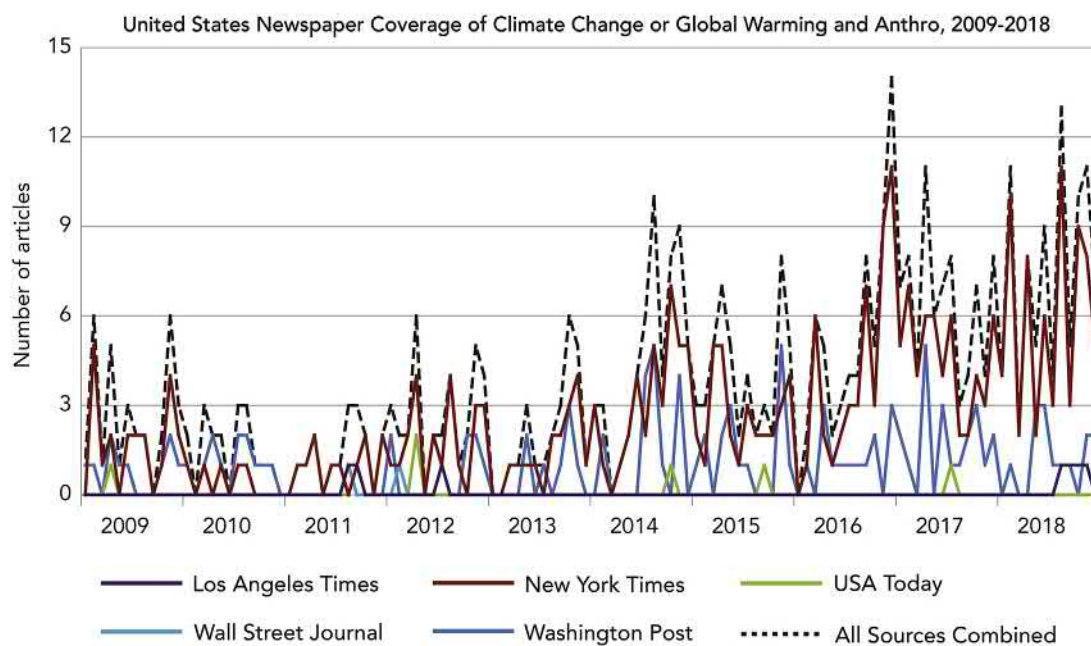
In the public arena, communications through mass media provide a bridge between the formal spaces of science-policy interactions and our everyday lives. In reality, few people spend part of their typical day perusing the latest peer-reviewed research. Instead, citizens more regularly turn to mass media. Mass media play important roles in people's everyday realities and experiences and the ways in which these are discussed at a distance between science, policy and public actors. People throughout civil society rely upon media representations to help interpret and make sense of the many complexities relating to science, governance and society. Furthermore, media messages are critical inputs to what becomes public discourse on today's issues, problems and challenges.

While the precise specifications of anthropogenic biomes, or anthromes, have varied somewhat over time, our focus is on how the main categories, namely dense settlements (urban), croplands, rangelands, and forests (See Ellis and Ramankutty, (2008). On indoor anthromes, a recent addition, see Martin et al., 2015), are represented in the media. In his popular introduction to the Anthropocene, Ellis expands on the original specification of anthromes as follows: 'anthrome landscapes are generally mosaics of used lands interspersed with less used, recovering, and remnant ecosystems transformed by being broken up and embedded within used landscapes' (2018: 121).

Anthromes in the Climate Change Mass Media

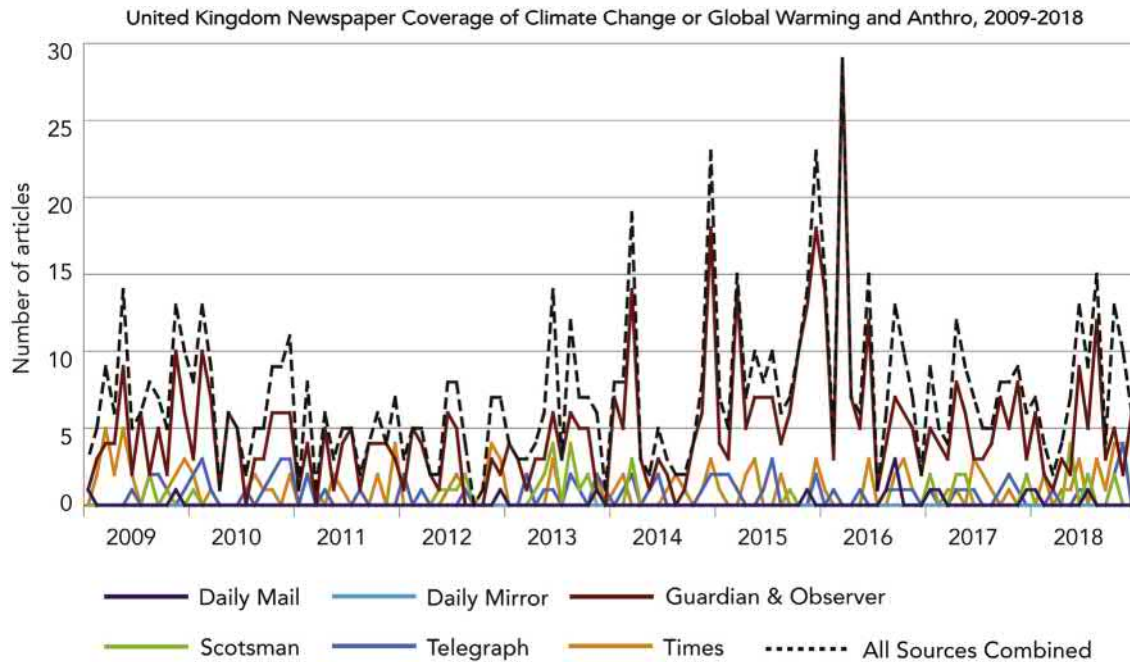
To appraise the presence of the terms climate change, and 'Anthro' (The Boolean we used was 'climate change OR global warming AND anthro'. This approach allowed for the appearance of combinations from the root 'anthro' including Anthropocene, anthromes, anthropogenic and so on. We used the Nexis Uni, Factiva and Proquest databases in order to determine these counts. Secondary checks were also made to validate the returns.) in the media, researchers at the University of Colorado monitored coverage in 12 United Kingdom (UK) and United States (US) newspapers from January 2009 through December 2018. These sources are the *Daily Mail & Mail on Sunday*, *Guardian & Observer*, *The Sun*, *News of the World & Sunday Sun*, the *Telegraph & Sunday Telegraph*, the *Daily Mirror & Sunday Mirror*, the *Scotsman & Scotland on Sunday*, and the *Times & Sunday Times* in the UK (Fig. 1) along with the *Washington Post*, *Wall Street Journal*, *New York Times*, *USA Today*, and *Los Angeles Times* in the US (Fig. 2).

We found that in the US media, coverage steadily increased over this 10-year period. In the first 5 years (2009–13) coverage of climate change and anthro-appeared 123 times, while coverage in the following 5 years (2014–18) was evident 332 times. Of the five sources monitored, the *New York Times* had the most coverage of climate change or global warming and anthro-overall ($N = 319$) followed by the *Washington Post* ($N = 119$). Comparatively, there was scant attention paid to climate change or global warming and anthro-in the *Wall Street Journal* ($N = 2$), *USA Today* ($N = 8$) and the *Los Angeles Times* ($N = 7$) over these 10 years,



This figure tracks newspaper coverage of climate change or global warming and 'anthro' in 5 US newspapers (Washington Post, Wall Street Journal, New York Times, USA Today, and Los Angeles Times), month-to-month from January 2009 - December 2018.

Fig. 1 This figure tracks newspaper coverage of climate change or global warming and 'anthro' in five US newspapers (Washington Post, Wall Street Journal, New York Times, USA Today, and Los Angeles Times), month-to-month from January 2009–December 2018.



This figure tracks newspaper coverage of climate change or global warming and 'anthro' in 7 UK newspapers (Daily Mail & Mail on Sunday; Guardian & Observer; Sun, The News of the World & Sunday Sun; Telegraph & Sunday Telegraph; The Daily Mirror & Sunday Mirror; The Scotsman & Scotland on Sunday; and Times & Sunday Times), month-to-month from January 2009 - December 2018.

Fig. 2 This figure tracks newspaper coverage of climate change or global warming and 'anthro' in seven UK newspapers (Daily Mail & Mail on Sunday; Guardian & Observer; Sun, The News of the World & Sunday Sun; Telegraph & Sunday Telegraph; The Daily Mirror & Sunday Mirror; The Scotsman & Scotland on Sunday; and Times & Sunday Times), month-to-month from January 2009–December 2018.

averaging less than a story a year. Together, the *New York Times* covered climate change or global warming and anthro-more than the other four sources combined over this 10-year period, pointing to possible differences in editorial directives, ownership structures, and story allocations (Boykoff, 2011).

In the UK media, we also found overall increases across this 10-year period. We found that there were 348 stories in the first 5 years (2009–13) that explicitly addressed climate change and anthro-, while 505 stories in the following 5 years (2014–18) included those terms. Of the six UK sources that we studied, the *Guardian/Observer* contained the most coverage of climate change or global warming and anthro-overall ($N = 587$) followed by the *Times and Sunday Times* ($N = 123$). In contrast, the *Daily Mail* ($N = 14$) and the *Daily Mirror* ($N = 1$) largely ignored stories of climate change or global warming and anthro-over this 10-years period. These numbers by media outlet show stark differences that could be linked to newsroom practices and editorial agendas within the newsrooms and ownership as *The Guardian* alone provided more coverage than the other five news organizations combined (Boykoff, 2011).

US and UK coverage combined has shown that coverage including climate change or global warming and anthro- overall has increased over the 10-year period with 183 total stories in 2018 compared to the following high amounts of coverage in 2016 ($N = 177$), 2015 ($N = 171$), and 2017 ($N = 164$). However, while coverage of the US also followed this general pattern of higher coverage in recent years (e.g. the most abundant coverage in 2016–18), coverage in the UK specifically peaked in 2015 ($N = 122$) and 2016 ($N = 115$) when coverage of the Paris climate accord pervaded public discourse. Combined, there were 471 stories on climate change or global warming and anthro-in the first 5 years of study (2009–13) (on average 24.6 per year in the US and 69.6 in the UK) and 837 stories in the second five-year window (2014–18) (on average 66.4 per year in the US and 101 in the UK). These findings also point to more abundant coverage in the UK press ($N = 853$) than the US press ($N = 455$) over this 10-year period overall, even when normalizing for stories per source in each country (as we tracked coverage in five US publications and six UK publications) (Fig. 3).

Evident increases can be seen in media in both the UK and US in similar periods of time. These increases are associated with scientific, ecological/meteorological, political, economic and cultural themes (Boykoff, 2011). For instance, initial increases in 2009 were associated with the United Nations climate talks in Copenhagen, Denmark (COP15), along with news about the hacked emails of scientists from the University of East Anglia (UEA) Climate Research Unit (CRU) in the preceding week, (not so affectionately referred to by many on the ideological right as 'Climategate'). The initial release of the 'Planetary Boundaries' research in the journal of *Ecology & Society* also generated media discussion of these links between climate change or global warming and the

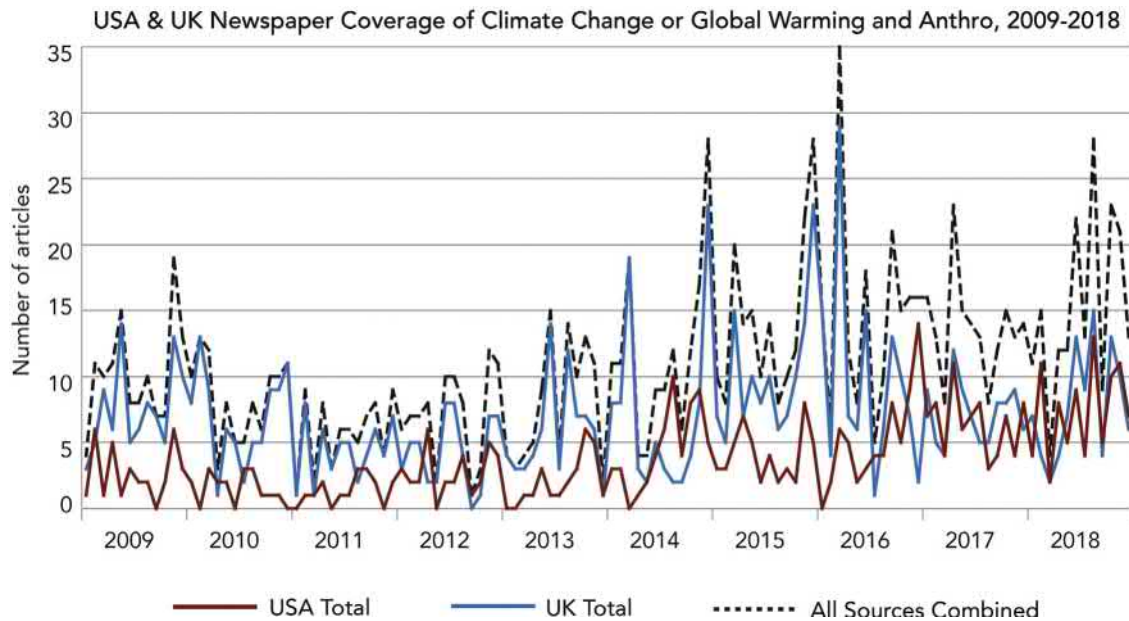


Fig. 3 This figure tracks newspaper coverage of climate change or global warming and ‘anthro’ in US newspapers (*Washington Post*, *Wall Street Journal*, *New York Times*, *USA Today*, and *Los Angeles Times*), UK newspapers (*Daily Mail & Mail on Sunday*; *Guardian & Observer*; *Sun*, *The News of the World & Sunday Sun*; *Telegraph & Sunday Telegraph*; *The Daily Mirror & Sunday Mirror*; *The Scotsman & Scotland on Sunday*; and *Times & Sunday Times*) and all 12 sources together, month-to-month from January 2009–December 2018.

Anthropocene (Rockström et al., 2009). Increases in 2015 and 2016 can be attributed to attention surrounding the Paris round of United Nations climate talks and the resulting Paris Agreement (Boykoff and Lueddecke, 2016).

It is useful to also compare these searches and the wider searches of climate change or global warming through the Media and Climate Change Observatory, where co-author Boykoff is lead Project Investigator. The total US counts of global warming or climate change for across the same five sources—*Washington Post*, *Wall Street Journal*, *New York Times*, *USA Today*, and *Los Angeles Times*—over the 10 year period (2009–18) is 32,006 articles. Compared to the 455 returned through the more specific ‘climate change OR global warming AND anthro’ Boolean string, these articles comprise 1.4% of that wider coverage. Similarly, UK comparisons across the six sources—*Daily Mail & Mail on Sunday*, *Guardian & Observer*, *The Sun*, *News of the World & Sunday Sun*, the *Telegraph & Sunday Telegraph*, the *Daily Mirror & Sunday Mirror*, the *Scotsman & Scotland on Sunday*, and the *Times & Sunday Times*—over the 10 year period (2009–18) returned 62,163 articles. Compared to the 853 articles generated through the more specific ‘climate change OR global warming AND anthro’ Boolean string, these articles also comprise just about 1.4% of that wider coverage. Across these 11 sources in the US and UK, 94,169 articles covered climate change or global warming from 2009 through 2018 (The Boolean used by the Media and Climate Change Observatory (MeCCO) is ‘climate change OR global warming.’ These US and UK newspaper sources comprise a subset of 96 sources (across newspapers, radio and TV) in 43 countries in seven different regions around the world that we monitor monthly through Nexis Uni, Factiva and Proquest databases. Each count is checked by a second counter in order to improve the validity and reliability of our monitoring. This involves a team of eighteen researchers around the world, based primarily at the University of Colorado but also at the National Institute for Environmental Studies (Japan), University of New England (USA), Universidad de Sevilla (Spain), Universidad Complutense de Madrid (Spain), Babson College (USA), and Oslo Metropolitan University (Norway)). Therefore, even though the raw counts in sources in the US and UK have varied over time (see Appendix), the percent coverage across these two countries over this 10 year period (2009–18) is approximately the same (1.4%).

Anthromes in the Anthropocene Mass Media

Interest in the Anthropocene as a potentially new geological epoch has increased rapidly since the term entered the public realm around the start of the new millennium. Though not achieving the volume of coverage of climate change and global warming in the mass media (which began in the 1980s), by the second decade of the 21st century if you were regularly browsing newspapers, magazines, or online sources in many countries in the world for the daily news you might come across mentions of the Anthropocene once or twice a year, more often if you were reading the quality press. However, in a study of coverage of the Anthropocene in the mass media (see Sklair, 2009 ed. forthcoming, hereafter referenced as AMP) (The websites of around 2,000 newspapers, magazines and online news sites were manually searched, finding over 4,000 items that mentioned the term ‘Anthropocene’.), very few items made direct references to anthromes.

The first mass media reference to anthromes found in an item that also mentioned the Anthropocene was by Brandon Keim in the magazine *Wired* (August 27, 2010). 'Maps: How Mankind Remade Nature,' was based on the 2008 article by Ellis and Ramanakutty 'They called their newly-defined areas "anthromes," short for anthropological biomes. It was a map for the *anthropocene*' (Quotes from media sources (translated where necessary) have been edited for clarity. Articles can be accessed by sources and title. Translations from non-English language sources are by researchers from their mother-tongues or translation software, often embedded in media websites. This was often a frustrating task as some languages (notably Japanese) appear to have several terms for the Anthropocene.). In 2011 Andy Revkin in his influential dot.earth blog in the *New York Times*: 'Confronting the Anthropocene' described a presentation by ecologist Erle Ellis 'a mesmerizing tour of the planet's profoundly humanized systems, which he said would be better described as "anthromes" than "biomes."' Ellis said it was important to approach this reality not as a woeful situation, but an opportunity to foster a new appreciation of the lack of separation of people and their planet and a bright prospect for enriching that relationship.' Revkin revisited anthromes several times in subsequent articles in the *Times* and elsewhere (For the influence of Revkin in publicising the idea of the 'good' Anthropocene, see Sklair, 2009 ed. (forthcoming, chapter 4)). In 2015 the *Independent* newspaper (UK) reported: 'The idea of a domesticated Amazonia, the immense diversity of social, cultural and historical processes that shaped Amazonia during the Holocene, situates this vast area in the company of other world anthromes.' The online magazine *The Conversation* (2016) published 'Humans now drive evolution on Earth, both creating and destroying species,' by the prominent Anthropocene researcher Mark Maslin who cites the work of Ellis on Anthromes. Maslin discusses both loss of biodiversity and emergence of new species (for example, the common house mosquito (*Culex pipiens*) which has become 'adapted to London's underground railway,' an unusual shared anthrome. Also in 2016 the Chinese newspaper, *Jing Bao* (Shenzhen) under the heading 'The Beauty of Nature in the Human Age,' reviews Diane Ackerman's popular science book, *The Human Age* in 'Is nature "natural" anymore?,' explaining Ellis's term anthrome as 'global ecological patterns created by sustained direct human interactions with ecosystems.' And in a rare example from the creative arts, in 2018 *Boulder Weekly* reported on an exhibition 'Anthrome' by Jason DeMarte: 'the artist chose a word he came across that means hybrid human-natural systems that now dominate the Earth's surface... It means that in the future everything natural will have some sort of human element in it'. The Anthropocene Media project research turned up more than 600 arts references to the Anthropocene (Sklair, 2009 ed. forthcoming, chapter 13). Despite this paucity of direct references, the idea of anthromes (without citing the term itself), appears very regularly in mass media coverage of the changes in the Earth System that have led to the Anthropocene. Let us now turn to a small selection of articles from a much larger archive on the six major categories of anthromes. This may serve readers as a bridge from everyday experiences of city life, pollution, deforestation, fire, floods and drought, to the idea of the Earth System.

Dense Settlements/Cities/Urban

Anthropocene coverage in the mass media often highlights the connection between urban settlements and anthropogenic biomes. In the Czech mainstream weekly journal *Geoskop* (2013) we find: 'The Anthropocene is not only geologically, but also a cartographically important phenomenon (dense settlements and large infrastructures).' Similarly, *La Hora* (Chile) in 2016, 'The Earth enters a new geological epoch... In the Holocene, human societies increased food production with the development of agriculture, built urban settlements and took advantage of the planet's water, mineral and energy resources' (reprinted in *Ambito Financiero*, Argentina). *The Post* (Athens, Ohio) 'Southeast Sustainability' (2016) is more explicit: 'The Holocene's stability allowed humanity to take advantage of ecosystem services... to develop their settlements. Those settlements, however, have now proliferated... they threaten the stability that initially allowed them to come into being.' From Singapore, the *Straits Times* in 2015, 'Cities power the way into new epoch' tells a different story: 'Cities are efficient users of resources and are best placed to deal with environmental challenges. For Singapore, this brings opportunities... Singapore thus has the opportunity to contribute to global solutions for sustainable urban growth in many areas. Indeed, Singapore was the highest ranked city in the Economist Intelligence Unit's Asian Green City Index' (According to Eco2 Index ratings Singapore was one of the worst ecological performers in the world. <https://www.int-res.com/articles/theme/m530p271.pdf>).

The *Daily Telegraph* (UK) in 2017 goes a little further in a review of *Provisional Cities: Cautionary Tales for the Anthropocene* by Renata Tyszczyk which explores cities as 'exemplary sites for thinking about living in this unsettled time.' Many sources draw attention to the ecological impacts of rapid urbanization. Examples include 'Making a difference' in *The Himalayan* (Nepal) in 2017: 'Once an ecological hot spot, Kathmandu, ten decades ago, was very different from the maze of concrete and buildings it is today. The air was not thick with dust and smoke requiring people to wear a mask; the rivers were not dirty with black slime and there was a decent amount of greenery in the valley. Smog is ever present over cities during the winter months. The drains that are directly empty on the rivers in the capital have wiped out the aquatic life in these rivers. Effects of biodiversity loss through deforestation can be seen in mere years, not in hundreds of years or even decades today. Droughts and massive flooding have increased in duration and magnitude over the past decades.' *Daily Star* (Bangladesh): 'Urbanisation signal detected in evolution' (2017) reports 'changes that were observed in more than 1,600 studies were having an impact on evolution and that human activity, in the form of urbanisation, would have a lasting legacy on life on Earth.'

Croplands

Supporting the idea of anthromes as mosaics, many media references to crops and croplands also engage with other anthromes, as the following items illustrate. *India Today* (2014) 'Ancient Maya activities left lasting impact on environment' reports that researchers

believe that the Maya used water management to adapt to climate change. In studying the wetland systems, we were surprised to find a combination of human and natural contributions (the term Mayacene is used as an early form of Anthropocene); the *Daily Express* (UK) with 'Climate change shock as professor says impact has been GOOD [sic] for wildlife' (2014) reports the research of Professor Chris Thomas who argues that nature is fighting back against human industrialization of the globe... citing the impact of the cane toad on an array of native creatures after it was introduced to Australia from south America to eat beetles on agricultural crops'; and *New Scientist* (2014) in 'Should we upgrade photosynthesis and grow supercrops?' declares: 'Crops with turbocharged photosynthesis will be growing in our fields in a few decades. But there is a danger too.' The *Daily Mail* (UK) in 2015 discussed 'the irreversible transfer of crops and species between the New and Old worlds' (the Columbian Exchange). The *Irish Examiner* (2015) 'Video: Will Humanity be Extinct in 100 Years?' is one of several items to connect water, croplands and potential extinction: 'With no alternative to water not only would millions die of thirst but the ground will be unable to provide us with crops.' Poland's *Krytyka Polityczna* (2015), quoting from an article by George Monbiot first published in the *Guardian*, puts the situation bluntly: 'Without concern for the soil, humanity will not survive. Earth owners around the world are taking part in an orgy of the destruction of the soil on a gigantic scale.' Taking this a little further, the US-based *Scientist* magazine (2016) explains simply 'Speaking of Microbiology... In the Anthropocene, we have lost millions of tons of soil fungi due to conversions of forests to cropland'; *Gazeta po Ukraiński* reported in (2016): 'Could the first farmers cancel the ice age?... The spread of agriculture about seven thousand years ago... to free land for crops and pastures, people burned the forest and, as a result, the amount of carbon dioxide and methane in the atmosphere has increased to such an extent that instead of cooling, there was a warming' (referencing the work of William Ruddiman on the 'early Anthropocene'). *Fox News* (2015) asks: 'Have Humans Caused a New Geological Era?' reporting a scientist who explains: 'when farmers clear-cut forests and plant crops, they change how sediments and runoff wash into the local rivers, often creating a thick layer of silty, sandy clay on the flood plain... But using such geologic clues to date the Anthropocene era runs into a problem: agriculture began at different times around the globe. Some areas, such as certain pockets in Africa, may not have had intensive agriculture until recently' (This connects with debates around start dates for the Anthropocene, a topic often covered in the media.)

Rangelands

In 2008 two articles from the USA discuss rangelands in the context of the Anthropocene. Science journalist Cornelia Dean addresses this as a regional issue in the *New York Times* with 'The Southwest in the Anthropocene,' where she argues, 'Until recently, natural landscapes varied as droughts came and went, warm years were followed by cold years and so on. Now, though, the actions of people have widened the parameters of this natural change, with potentially troubling results in places like the Southwest,' citing William deBuys in the magazine *Rangelands*. In *Mother Jones* 'Us to Earth: We Will Rock You': Soil scientists at Duke University say that these days, even the dirt beneath our feet is man-made, quoting lead researcher Daniel Richter: 'With more than half of all soils on Earth now being cultivated for food crops, grazed, or periodically logged for wood, how to sustain Earth's soils is becoming a major scientific and policy issue.' The popular German weekly *Welt am Sonntag* (2009) puts this issue in starker terms: 'Can we survive the "anthropocene" period?... the methane-producing cattle population has risen to 1.4 billion, contributing to the increasing rate of destruction of tropical rainforests, which releases carbon dioxide and contributes to faster species extinction. Land conversion for grazing (and construction), together with crop tillage, has also caused soil erosion at 15 times its natural rate.'

Forests

Many media articles speak of forests and deforestation. Several items in *News International* (Pakistan) engage with deforestation, for example in 2013 'A forest without trees... One of the ways to fight this menace of environmental destruction is to carry out afforestation at a massive scale and protect the existing trees. But instead of protecting trees, the country seems to be on a tree-cutting spree... Mangroves forest depleting due to man-made mess.' *Gulf News* (2014) assessing Kolbert's book *Field Notes on a Catastrophe* (published in 2006) reports on: 'the extent to which tropical forests in Peru can adapt to rapid change, of habitat fragmentation in the Amazon basin and beyond, and of the consequences of the mass global transference of species from one place to another. It is all pretty grim.' This depressing theme is reinforced in the news website *Guinea Live* in 2015, 'Ebola and Advocacy for the Environment... One of the main causes [of the crisis] is the drastic reduction in the area of forest heritage and wildlife habitat... The natural habitats of wild animals are dangerously reduced'; *Misiones* (Argentina) in 2015 with 'This type of action would reduce the problems we will have in this century to live in the Anthropocene' reports research on 'multiple ways to lessen the alarming disappearance of forests around the world, such as stricter conservation policies, better forest management, and a global framework for climate change policies. Forests are ecological superheroes: they ventilate the planet, nourish the Earth's habitats, regulate the global climate and carbon cycles. From the poles to the equator, our survival depends entirely on healthy forests... this biome is much more threatened by direct anthropogenic contact... it is very possible that humans can curb damage to forests and perhaps even reverse it in some places... it seems suicidal not to consider this option'. We find support for this conclusion in *L'Express* (Canada), 'The environment in 2017: sowing seeds of optimism' reports on the research of Professor Elena Bennett, 'targeting a more positive future with her [Seeds for a Good Anthropocene project](#)... [her] favorite example is a project named Health in Harmony where they work in Borneo, Indonesia to reconnect with forests and healthy people. People receive [health] care at little or no cost in return for the promise to protect local tropical forests and its residents, the orangutans.' *The Independent* (UK) in 2015: 'How we must adjust

our lifestyles to nature: Welcome to the Anthropocene, the human epoch' concludes with a striking anthropogenic image: 'the scrolling text on TV news should show us not only share prices, but data about the size of forests and bogs, about air quality, energy use and bird populations'. Finally, *Sanlian Life Week* (China) in 2012 connects rising populations and anthromes philosophically: '7 billion population—how dangerous is the earth?' arguing 'Glaciers, oceans, forests, once represented certain borders of the world, they were the objects on which human put their fantasy and awe. Now they are precarious under human footprint.'

Conclusion

The science of the Anthropocene and anthromes is very complicated and it is not surprising that journalists do not always report fine detail or the implications of research findings entirely correctly. The complexity is exemplified by a study by Gaffney and Steffen (2017), which mapped out an 'Anthropocene Equation' to clearly articulate human influences on climate change and our life-supporting ecosystem services. This publication was discussed in newspapers all over the world with, understandably, varying degrees of accuracy and attention to detail (for example, in *Gulf Daily*, *India Today*, Indonesia's *Femina*, Iran's *Financial Tribune*, Pakistan's *The Nation* and *Pakistan Today*, Spain's *La Voz de Galicia*, *Al Ghad* in Syria, *The Guardian*, *Star Tribune* from Minneapolis-St. Paul, and *New York Post*). Gaffney and Steffen noted that humans are changing the climate about 170 times faster than natural forces would do alone, which made an eye-catching headline. They concluded that 'the rate of change of the Earth system over the last 40–50 years is purely a function of industrialized societies. Anthropogenic sources contributing to this Anthropocene Equation—affecting the distribution of energy across the planet—include fossil fuel burning (primarily coal, gas and oil) and land use change. This has prompted considerable discussion on how to develop policies to address these developments in the Anthropocene. These processes have been referred to as dimensions of environmental politics (Löwbrand et al., 2015) and have also been dubbed 'Anthropocene Geopolitics' (Dalby, 2007; Clark, 2014).

When reporting on debates among scientists who research anthromes, climate change, and the Anthropocene, journalists are confronted with a heavy responsibility to represent findings accurately, and to draw reasonable conclusions from the evidence in ways that members of the general public (and politicians and corporate executives) will understand and that might help to change behavior to minimize potential risks. In the Anthropocene era, media are powerful and important interpreters of Earth System science and science policy, and journalists have the opportunity of translating what can often be alienating, jargon-laden information into information that all sections of the public could understand. The apparent inability of governments and owners of major industries to take decisive action to deal with what most scientists appear to believe is a series of rapidly accelerating ecological emergencies does not bode well for the future of human life on the planet. Few opinion-formers in the media communicate a sense of urgency. Despite media focus on renewable sources of energy (none of which are carbon neutral) and the need to curb population increases and consumption in richer and poorer societies, research suggests that the media generally neutralize the potential risks of the Anthropocene. This is the message that media reporting of anthromes generally sends.

Acknowledgments

Leslie Sklair thanks the volunteer researchers (about 40 in number) from all over the world who searched media in their mother tongues for articles that mentioned the Anthropocene and, in some cases, analyzed the contents of articles found. They will all be credited by name and specific contributions in the forthcoming book on the project.

Maxwell Boykoff thanks the larger Media and Climate Change Observatory (MeCCO) team from which the climate change or global warming counts have been determined. Team members include Midori Aoyagi-Usui, Andrew Benham, Patrick Chandler, Meaghan Daly, Kaori Doi, Rogelio Fernández-Reyes, Lauren Gifford, Isidro Jiménez Gómez, Jennifer Katzung, Lucy McAllister, Marisa McNatt, Ami Nacu-Schmidt, David Oonk, Jeremiah Osborne-Gowey, Olivia Pearman, Anne Hege Simonsen, and Andreas Ytterstad. Thanks in particular to Andrew Benham for his validity checks on the counts specific to this project. Maxwell Boykoff also thanks the Center for Science and Technology Policy Research, the Cooperative Institute for Research in Environmental Sciences and the University of Colorado who have supported his ongoing MeCCO research endeavors.

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Science Communication: Challenges and Benefits to Conservation Projects

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Abstract

Effective science communication is imperative for successful conservation efforts. Science communication can be improved through the use of personalized frames and digital media. Communicators should be aware of potential roadblocks including jargon and science literacy and should be trained in ways to avoid these problems. By being aware that they are in fact communicating science to an audience that may be different from them in several ways, science communicators can improve their messages and have a greater chance at encouraging a positive change. This article will summarize the history and challenges of science communication and examine successful methods to apply communication tactics to conservation projects.

Introduction

Science communication can be a nebulous term that means different things to different people. As such, it is important to define science communication and related terms. Science communication can be broad: “Sharing science with non-experts” (Rakedzon et al., 2017) or “communicating science to non-technical publics” (Sharon and Baram-Tsabari, 2014). Other researchers and communicators prefer to take a more specific view. Burns et al. (2003) suggested science communication be analyzed and practiced in depth, defining it as “the use of appropriate skills, media, activities, and dialogue to produce one or more of the following personal responses to science: awareness, enjoyment, interest, opinions, and understanding.” At its core, science communication involves providing scientific information to a public that has various levels of understanding.

Ideally, researchers and other science professionals would have the ability to effectively communicate their own research to the public, but intermediate steps are often needed to make sure the message is well presented and received. However, this is often not the case. Therefore, science communication is often carried out by mediators, science communicators, or the media. In this context, mediators can be communicators, educators, or opinion-makers that have a public voice and science communication training (Burns et al., 2003). Challenges to science communication that will be examined include the use of jargon and a lack of science literacy. Both challenges increase the need for intermediate steps to communicate information between scientists and the public.

An overarching goal of science communication is to provide people with the information they need in an understandable way in order to make decisions and possibly promote behavior change (de Bruin and Bostrom, 2013). Identifying what information should be communicated and the best way to do so is essential to ensure effective science communication.

Effective science communication is especially necessary for conservation. A large portion of conservation projects rely not only on researchers, but on the public or practitioners to continue the work after the researcher has gathered data and presented results.

Conservation efforts are often very visual and have the opportunity to tell a story to the public in such a way that a large-scale difference can be made. These stories would not be told without effective conservation communication through various outlets including mainstream media. As scientists address long term issues like climate change and the associated threats to conservation and biodiversity in new and innovative ways, informing the public and garnering large-scale support through communication will be paramount to the success of these projects (Monto and Malhotra, 2011).

This article will summarize the history and challenges of science communication and examine successful methods to apply communication tactics to conservation projects.

History of Science Communication

Science communication has been occurring in a formal setting since the late 1920s and early 1930s. A group of national scientists in the United States took it upon themselves to better educate American citizens about science to enhance the public's capacity to make better decisions, live longer, and create a culture of life-long learning (Logan, 2001). These national scientists saw the proper communication of science as a true calling, believing that "a commitment to the public understanding of science not only provided immediate rewards of improving quality of life and elevating public affairs deliberations but also was perceived as integral to the elevation of democracy, culture, and the evolution of human potential" (Logan, 2001).

Science communication has been studied for almost 100 years. Even so, it was not until 1973 that it was suggested that researchers adjust their communication methods depending on how the public perceived science and their prior knowledge about the topic (Logan, 2001). This change in thinking coincided with the public becoming more involved in conservation as a social movement. The United States experienced a "golden era" of public understanding and respect of science during the Space Race (Nisbet and Scheufele, 2009). On the heels of this public engagement, the United States passed the Clean Water Act, the Endangered Species Act, and saw the social and political outcome of Rachel Carson's *Silent Spring*. This social interest in conservation required researchers to take a closer look at how they were communicating science and related outcomes. This led to jargon and science literacy being identified as primary roadblocks to effective science communication.

Science Communication Challenges: Jargon

Jargon is defined by Sharon and Baram-Tsabari (2014) as "the technical terminology or characteristic idiom of a special activity or group." When the full meaning of a word or concept is not clear, jargon limits the effectiveness of science communication by reducing the number of people who actually understand the message. Sharon and Baram-Tsabari (2014) suggest that people use language differently in different contexts. This different use of a language is called a register. Scientists have developed a scientific register, "used primarily by scientists when communicating about science with their colleagues and students." Jargon can be necessary for scientists to effectively communicate with each other but can be limiting when communicating with the public (Sharon and Baram-Tsabari, 2014). As such, it is important to translate information from a scientific register to speech that is better understood by lay people. To achieve this, scientists can be trained in effective communication with the public and journalists can be trained in effective communication with scientists.

Jargon is deeply embedded in experts and often becomes such a common part of communication that scientists no longer realize they are using it and do not remember a time before they understood the technical aspects of their research (de Bruin and Bostrom, 2013). The easiest suggestion when experts are communicating with nonexperts is to avoid jargon altogether, but this task is often more difficult than it seems. There are few standards as to what level of jargon is acceptable and the baseline understanding the audience generally has, making adjusting messages to avoid jargon very difficult (Rakedzon et al., 2017).

This provides a prime opportunity for mediators. By specially training "science communicators" alongside researchers and journalists in methods of clearly and effectively communicating with the public, the impact of science communication can be improved. Academic writing and popular science writing have different styles and purposes (Rakedzon et al., 2017). There is great potential for scientists who have also been trained in more popular writing or journalists who have a strong understanding of science to be used as science communicators.

Plaxco (2010) suggests a few simple ways to limit the use of jargon in science communications: "First, do not invent new words or phrases if there is already a commonly used word or phrase that accurately fits the bill . . . Second, if at all possible avoid using abbreviations." If jargon in the form of abbreviations is unavoidable, communicators who work in print can easily add footnotes, text boxes, or other easy-to-find methods for the audience to reference what the abbreviation means. This allows the communicator to accurately get the message across without the audience feeling like the information has been "dumbed down" for them to read. Overall, when addressing jargon, science communicators should keep in mind that the audience's understanding should be the top priority.

Science Communication Challenges: Science Literacy

Science literacy is another term that means different things in different fields. For the purpose of this discussion, Koballa et al. (1997) provide a clear definition: "A scientifically literate person is 'one who is aware that science, mathematics, and technology are interdependent human enterprises with strengths and limitations; understands key concepts and principles of science; is familiar with the natural world and recognizes both its diversity and unity; and uses scientific knowledge and scientific ways of thinking for individual and social purposes.'" This definition links back to the scientists of the early 20th century with a call to integrate science into all parts of everyday life as a way to improve society. In terms of conservation, the awareness that the natural world has both diversity and unity is especially important. This comes from an adjustment to the original definition of science literacy, which asked the public to be able to read and comprehend science-related articles. Science literacy in the modern age focuses on creating a lifelong pursuit of science as a part of everyday life (Burns et al., 2003; Koballa et al., 1997).

It is suggested that science literacy follows a continuum, from “fails to recognize words and issues as science-related” to “recognizes that science cannot be separated from the culture in which it is constructed.” This means that people with a high science literacy of key issues in various fields know where these issues came from and why they are or are not widely accepted (Koballa et al., 1997). This allows them to interpret science through the lens of their culture while understanding that the application may be different for people who are different from them. Science communicators are asked to identify where their audience falls along this continuum and change their approach accordingly.

Science literacy is difficult to measure in the general public. Most often, it is implied that compulsory education will provide the science literacy needed to get through life, but even then the standards are not common across all areas. The job ultimately falls to science communicators to ensure their message is being properly interpreted and received by a public that may or may not understand and value science at a base level. Even then, the not so simple act of communicating science may not always lead to an immediate increase in science literacy in the public (Burns et al., 2003).

Much of science literacy is also based on the value individuals place on science as a whole, and those values are often tied up in politics, religion, and other internal systems that take much more than communication to challenge. Generally, people need a base of scientific knowledge to be able to understand media messaging and cultural values surrounding science communication more explicitly and beyond the information being presented (McCaffrey and Rosenau, 2012). Polarization of scientific “beliefs” has been observed along political and religious lines for large-scale issues like climate change and evolution (Drummond and Fischhoff, 2017). There is disagreement among researchers if science literacy levels impact the likelihood of an individual “agreeing” with the science. Most researchers agree that science literacy is not the whole problem. People have predisposed beliefs depending on how they think of themselves in terms of other people and what “their group” is expected to believe in terms of certain issues (Drummond and Fischhoff, 2017). As discussed in the next section, this factor requires science communicators to tailor their message to a specific audience in order to be effective.

Useful Methods to Communicate Science

In most circumstances, people interpret new information in regards to relevant beliefs and positions they already hold (de Bruin and Bostrom, 2013). This means that all forms of science communication are most often considered in terms of whether or not the message aligns with previous opinions and knowledge. de Bruin and Bostrom (2013) suggest that “to develop effective communication materials for members of the general public, scientific experts need to understand what information people need to know”. Communication should be designed to target the most common misconceptions in a way that is easily understood and relevant to the audience (de Bruin and Bostrom, 2013).

Useful Methods: Framing

As different people interpret messages in different ways, the message can be altered to be best received by different groups of people. This broad method is called framing. Nisbet and Mooney (2007) suggest frames can solve many science communication problems: “Frames organize central ideas, defining a controversy to resonate with core values and assumptions. Frames pare down complex issues by giving some aspects greater emphasis. They allow citizens to rapidly identify why an issue matters, who might be responsible, and what should be done.”

It is often difficult for the nonscientific public to understand technical messages because of the large amount of information and media they receive daily. Scientists can fall into the trap of assuming providing technical information will clear up uncertainties within the issue. In reality, most people will not put in the effort to untangle the technical information and will instead compare the message to their preexisting values and make decisions that align with their views (Nisbet and Mooney, 2007). Ultimately, the best tool to properly frame science is to understand the audience receiving the message and adjust accordingly to address issues that matter to them.

Frames are most effective when they address an emotional connection the audience already has (Monto and Malhotra, 2011). Frames often suggest a connection between a concept that is already accepted and a new one, in a way that encourages support of the new concept (Nisbet and Scheufele, 2009; Scheufele and Tewksbury, 2007). Framing is especially useful when addressing conservation. For example, when asking farmers to conserve water, messages should be framed to link water conservation now to higher yields in the future. When asking citizens who live in a city to conserve water, the message should be framed to suggest that everyone else is conserving water so they should too. Both groups may be responsive to framing that suggests water conservation now will provide for future generations, but city residents would be less receptive to framing around higher yields and vice versa. Frames suggest what is at stake for individuals involved in an issue and why that issue matters (Nisbet and Scheufele, 2009; Gamson and Modigliani, 1989). As Nisbet stated, “Scientists and their organizations must learn to focus on framing their messages in ways that activate participation from wider, more diverse and otherwise inattentive publics, while discovering new media platforms for reading these nontraditional audiences.” Frames are extremely audience-specific and must be adjusted frequently to address issues that are current and impactful.

Useful Methods: Digital Media

Science communicators have a great advantage in modern times that was not available to their predecessors. The explosive use of social media and other online news sources has changed how the public receives information and interprets messages. Generally speaking, information still flows from scientists to journalists and then to the public (Logan, 2001). However, digital media encourages the use of informal science education and allows science communication to be included in everyday life. This allows larger portions of society to have access to information that was previously only shared in academic settings (Maier et al., 2014).

In recent years it has become relatively easy to analyze digital trends and apply that data to science communication. Internet usage has replaced traditional surveys as a way to determine the public's interest in conservation topics and encourage successful science communication. One option for science communicators is to use Google trends and similar analytics to determine what frames should be applied to audiences and mitigate the challenges caused by jargon and science literacy (Hghiem et al., 2016).

Case Studies

The following case studies showcase science communication between different communicators and audiences. These project utilized different methods and address the challenges and useful methods to communicate science to their audiences.

Communication Within a Nonprofit

This study considered “how individuals accessed information about a recent science innovation at large non-profits,” specifically The Nature Conservancy (Fisher et al., 2018). The Nature Conservancy is a global conservation nonprofit began in 1951 with a mission to “conserve the lands and waters on which all life depends” (The Nature Conservancy, 2018). This study examined communications between employees at The Nature Conservancy with a specific focus on how communication encouraged the diffusion of innovations, or “the spread and uptake or adoption of new ideas” (Fisher et al., 2018). Online communication and media were the main channels, with email correspondence encouraging employees to visit new information on their website and spread that information to the public. The researchers monitored visits on the new pages of The Nature Conservancy's website and how the type of communication used impacted the number of employees and nonemployees visiting these pages.

The study suggests that simple methods like online newsletters and webinars are effective ways to share knowledge, but a single announcement likely will not gain the maximum attention and diffusion of innovations possible. Persistent and repeated communications in the form of direct and repetitive emails that are framed in different ways to target different audiences within The Nature Conservancy were most effective to increase the views of new information on their website by both employees and the public (Fisher et al., 2018).

The authors also briefly addressed jargon, stating that “the use of common language and methods around evidence based practices can help build legitimacy, shared understanding, and trust needed for sustained collaborations” (Fisher et al., 2018). This was particularly important when encouraging employees to share science with the public. As most of the employees are not trained science communicators, presenting the information in a way that is clear and easy to understand by everyone increased the likelihood of employees being able to share the science effectively.

While most of the research on science communication is focused on communicating science directly to the public, it is also important to consider how scientists and journalists communicate science to their peers in a way that encourages more people to share science with the public. In this case study, using repeated online messages with different frames was the most effective way to increase the traffic on their website and the number of people who saw the new information that was available there (Fisher et al., 2018).

Communication From the Government to the Citizens

This study was done by the Portuguese government to “further enhance public involvement in conservation efforts and improve communication between science and society” (Vieira da Silva et al., 2017). The researchers used focus groups to learn about the general public's cognitive beliefs and normative ethics toward nature and conservation. Cognitive beliefs were observed by discussing people's knowledge and beliefs about nature, biodiversity, species, and conservation. Normative ethics were observed by discussing people's environmental ethics through expressed opinions, values, and actions. The authors found that people were generally concerned about biodiversity loss and other conservation topics but had a poor understanding of the problem, limiting their participation and support in conservation policies (Vieira da Silva et al., 2017).

The researchers used surveys of the public to determine which frames would work best to provide information that people were interested in and would lead to support of new conservation policies. While most framing is done without national surveys, this was an effective method to learn exactly what the people valued and were interested in before trying to build support for new and potentially confusing policies. By learning that people had an interest and value in conservation, the researchers could conclude that effective frames would include basic education about national conservation problems, calling citizens to care for their country and for their future.

Environmental Behavior Change Communication in High Schools

This study was done in Rocky Mountain High School as the administration, staff, and students attempted to shift their culture to sustainable education and energy conservation through behavior changes, education, and a school-wide commitment to sustainability. The researchers found that effective communication tied together the priorities of the school and encouraged success by keeping people aware of the problem and the goal. The communication from the administration to the staff and students was sustained and consistent, providing weekly updates about accomplishments and behavioral expectations to encourage participation in energy conservation efforts and create new social norms (Schelly et al., 2012).

Focus groups comprised of administration, staff, and students were surveyed to determine what communication methods were most impactful to encourage the school as a whole to reach their sustainability goals. They found that environmental leaders with a focus on science communication and framing were important for the project's success. In terms of promoting behavior change, repeated communication through multiple sources was described as the most effective method. These sources included emails to staff, face-to-face encouragement, newsletters, videos, and posters hung around the school. The posters were identified specifically as providing inspirational feedback that created a personal feeling of efficacy in individuals by providing visual updates about energy usage to compare current use with prior use, showing the staff and students that their behavior change was making a difference (Schelly et al., 2012).

Framing was also identified to be important for the success of the project. Since the participants had a wide range of science literacy and interest largely due to the age range between students and teachers, messages about behavioral expectations, knowledge, energy and resource use data, and information about social norms were adjusted for the age group they were addressing. By adjusting for science literacy and age specifically, the administration ensured that all groups felt like their efforts made an impact and they were included in the project (Schelly et al., 2012).

Conclusion

Effective science communication is imperative for successful conservation efforts. Science communication and conservation goals are generally long-term and ask audiences to compare their personal beliefs and values to what is going on in the world around them and how they can choose to make a difference or not (Burns et al., 2003). Especially as researchers address climate change and related conservation problems in new and unique ways, it is especially important to be able to communicate effectively with the public in a way that sparks a positive change (Hoffer, 2014). Science communication can be improved through the use of personalized frames and digital media.

Communicators should be aware of potential roadblocks including jargon and science literacy and should be trained in ways to avoid these problems. Anyone who tells other people about science is a science communicator, including scientists, mediators, the media, and other members of the public. Science is not just communicated from researchers to the public, but also happens peer-to-peer in various fields (Burns et al., 2003). By being aware that they are in fact communicating science to an audience that may be different from them in several ways, science communicators can improve their messages and have a greater chance at encouraging a positive change.

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Science Communication in Agriculture: The Role of the Trusted Adviser

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Abstract

Effective communication of science to end users can be challenging. Misinformation, misunderstanding and mistrust abound. It is imperative that the end user has an understanding and appreciation for science and how it can be applied to solve environmental problems. Scientists have a role to play in this discourse, but here it is argued that they may not be the primary communicator to stakeholders. Agriculture is an important consumer of scientific information and has a long-standing and well-developed relationship with scientists and advisers for obtaining and applying specialized scientific knowledge. Extension scientists and crop advisers are trusted sources of information for farmers. Their partnership leads to better distribution and application of research findings. Professional private crop advisers exist in many countries around the world including Africa, where one example shows how extension has played a key role in developing village residents to take on the role of science delivery. Similar models for partnering extension with community experts to deliver knowledge to residents have been successful in urban settings and provide a model that could be expanded into other disciplines.

Introduction

Despite decades of effort, the science community continues to struggle to clearly communicate scientific facts and elicit citizens to apply science effectively. Echo chambers (Zollo et al., 2017), that reinforce misinformation (Van der Linden et al., 2017), different perceptions of risk (Etkin and Ho, 2007) and political and social beliefs that are not supported by scientific consensus (Benegal and Scruggs, 2018) cloud numerous discussions of science. This confusion leads stakeholders away from actions that benefit them, their communities and the environment (Benegal and Scruggs, 2018). One particularly important current example of this phenomenon is climate change.

Agriculture is recognized as a critical industry that can help reduce carbon dioxide, methane and other greenhouse gas emissions that could prove instrumental in the mitigation of climate change (Robinson et al., 2018; Del Corso et al., 2015; Prokopy et al., 2015). However, changes in farming practices are difficult to implement because new practices often bring unknown risk to an industry that already deals with many uncertainties, including pest pressures, weather variability, and the influence of local and world markets. In developed countries, narrow profit margins mean farmers do not have much room for failure (Del Corso et al., 2015). Thus, narrow margins encourage farmers to stick with proven practices with more predictable risk rather than trying new practices with unknown yield and economic risks (Del Corso et al., 2015). In developing countries crop failure due to unproven techniques could mean starvation for the farmer and her family (Kansiime et al., 2018). Therefore, trust in the input and advice from an adviser is essential to implementing change at the farm level. Building this trust with farmers requires a personal relationship and understanding of the challenges that each farmer faces (Bernacchi and Wulforst, 2017; Coquil et al., 2018).

Discussions of environmental policy often involve two opposing perspectives (Etkin and Ho, 2007; Benegal and Scruggs, 2018). From their perspective policy makers and researchers viewing from the top-down identify what should or needs to be done, but stakeholders and citizens viewing things from the bottom-up identify what can be done or what is practical in light of the perceived financial and social risks involved. Power dynamics along with cultural and philosophical differences often lead to conflict and distrust between these two groups (Gaymer et al., 2014). However, there is a third group in agriculture known as crop advisers,

who currently work to help bridge the gap between researchers and stakeholders. Effective crop advisers and crop consultants are recognized as trusted advisers by farmers, researchers, and university extension (Coquil et al., 2018; Bernacchi and Wulffhorst, 2017; Robinson et al., 2018; Gabel et al., 2018). These privately employed professionals trained in science, directly assist farmers with the application of scientific knowledge and technologies to solve agricultural problems and provide more realistic perspectives on the risks involved (Ates and Sendundar, 2013). This review demonstrates that these professionals and others like them in different industries can provide critical leadership in the implementation of management practices that will benefit the environment and people locally as well as globally.

Top Down Information Dissemination

Another potential source of scientific information available to the citizens is public access journals (PLOS ONE, 2018). However, in many cases obtaining information directly from scientists is not the most efficient, practical or popular method. What are the primary methods by which people access scientific information? Family, friends, university extension and media are all potential sources (Ollerer, 2015). Education about environmental issues emanates from all these sources. Which ones are trust worthy or accurate? Is trust and accuracy the same thing? Ollerer (2015) points out that these sources can perpetuate misinformation and misconceptions even if they are well intentioned. Once again, we are faced with a divide between the top-down (scientists) and bottom-up (citizen/stakeholders). As discussed, agriculture utilizes intermediaries (extension and crop advisers) to deliver science to the end user (farmer). While there are specialists in extension that focus on agriculture, extension is not strictly targeted to support farmers. The charge of extension is to deliver science to all end users, all citizens, rural and urban, young and old alike. However, many scholars have addressed the financial and personnel shortages of extension which are likely to increase in the future (Ates and Sendundar, 2013; Bernacchi and Wulffhorst, 2017; Calvin, 2018; Clyde et al., 2018; Collins and Gaolach, 2018; Coquil et al., 2018; Del Corso et al., 2015; Kansiime et al., 2018; Ollerer, 2015; Robinson et al., 2018; Prokopy et al., 2015; Tyson, 2014).

Trusted Adviser to Practitioner (Middle Down)

Farmers have an inherent connection with plants, animals and soils and depend on healthy biology to support their family and business. Therefore, it is in their best interests to employ management strategies that protect the biological processes that they use to produce a crop. If farmers are so adept at managing biology, why then do we continue to experience large scale environmental problems associated with agricultural practices? The answer to this is at least in part due to the perceptions that management for maximum yield must rely heavily on the use of fertilizers, pesticides and soil tillage and that high yield maximizes economic return. Several of these practices can increase crop yield but are also associated with erosion and nonpoint source pollution. However, there are alternative practices such as no-till, minimum till, cover crops and crop rotation that can balance productivity and environmental risk. Innovative farmers are also experimenting with intercropping, livestock integration and other techniques that could potentially be developed and refined for broader application to address specific agricultural challenges. Difficulty arises because changing production practices involves risk, capital investment, experimentation as well as the precise application of science. Local knowledge of soils, weather, nutrient cycling, and crop adaptation are critical for successful agricultural production. Modification of existing systems that have developed over centuries requires expertise in the science of crop production as it applies locally (Del Corso et al., 2015; Robinson et al., 2018; Kansiime et al., 2018). As mentioned previously, this process also must include a realistic assessment and communication of the risk of change. In addition to traditional knowledge, agriculture continues to embrace advancing digital technology such as satellite and aerial imagery, yield mapping and plant stress indicators such as infrared and near-infrared sensing (Erickson et al., 2018). The ability to obtain and process traditional and precision management information as well as assisting farmers in applying scientifically sound site-specific solutions to solve problems is paramount in implementing on-farm change.

Role of Extension

Delivery of scientific information is the charge of university extension in the United States and many other countries (Calvin, 2018; Clyde et al., 2018; Collins and Gaolach, 2018; Robinson et al., 2018; Del Corso et al., 2015; Prokopy et al., 2015). However, budget cuts, loss of personnel and high demands on staff have led to difficulty of extension carrying out this mission. Increasingly, private advisers are filling the role of information specialists and delivering science directly to farmers (Prokopy et al., 2015; Berti, 2018). For decades extension programs aware of the many challenges they face, the limited resources available to them and the value that farmers place on private advisers have purposely developed programming to increase their influence with crop advisers to assist with this model of science delivery (Roseler et al., 1994; Schmitt et al., 2000). Extension programs have taken on the train-the-trainer philosophy (Bernacchi and Wulffhorst, 2017). Thus, crop advisers and extension have a long history of cooperation and mutual respect. Advisers go to extension specialists to obtain current science and technology training in order to provide this information to their clients (Prokopy et al., 2015; Rickert, 2001). More recently extension is viewing crop advisers as force multipliers to assist in delivering the message. Not only can crop advisers increase the amount of science delivery to farmers, they also have the skills to tailor this information to meet the specific needs of individual farming systems (Bernacchi and Wulffhorst, 2017).

Crop Advisers

Farmers list private crop advisers as one of the four most trusted sources of information (Prokopy et al., 2015). The other three are family, chemical dealers and seed dealers. In North America, the Certified Crop Adviser program (CCA) is one way for advisers to distinguish themselves as reputable purveyors of science. This voluntary certification program is administered by the Agronomy Society of America. To become certified the applicant is required to pass two agronomic knowledge tests (International and local), gain experience in the field providing advice to producers and agree to and sign a code of ethics. The required experience only includes time spent assessing crops and providing advice to farmers and ranges from 2 to 4 years depending on the level of education obtained by the applicant. Once certified, crop advisers need to complete 40 h of preapproved continuous education every 2 years to maintain certification. As of November 2018, there were over 13,000 CCA's in North America (CCA, 2018). This number of CCA's is nowhere near enough to service the needs of each farm, but it provides an existing framework that has proven successful and is quite capable of expanding. The CCA program is also recognized by government agricultural agencies in the United States and Canada as experts in the management of on-farm agricultural challenges. Some federal programs that provide funding for farmers to implement environmentally friendly management practices require the services of technical service providers. The NRCS in the United States recognizes CCA certification as satisfying some of the credentials required to become a technical service provider (NRCS, 2018). One example is comprehensive nutrient management plans. These plans are designed to reduce nutrient losses from agricultural fields and protect the environment from nutrient runoff by using soil tests, knowledge of plant physiology and weather observations to detail when, how and how much manure and other fertilizers are applied to the crop. In sensitive regions such as the Chesapeake Bay, nutrient management plans are required for manure applications (Maryland Department of Agriculture, 2019). This process helps to ensure that the farmers are receiving and applying sound science to improve on-farm and environmental outcomes.

Turkey

The challenges faced by extension are not unique to the United States. High costs and limited resources led the country of Turkey to transition its extension service from a public entity to the private sector (Ates and Sendundar, 2013). Farmers in Turkey still utilize multiple sources for agricultural information, but the private advisers are becoming the primary vehicle. Advisers in Turkey need to pass examinations and earn certificates to practice. All advisers are registered service providers and most continue to attend trainings and educational programs to further their knowledge and education (Ates and Sendundar, 2013). They interact with the remaining extension and research scientists to obtain new information and practices. This system is still being developed, but some important lessons have emerged. Interviews with advisers from the district of Antalya Province identified difficulty in securing payment for services as the most challenging problem faced (Ates and Sendundar, 2013). These advisers also identified that additional agricultural research was needed to support them and the farmers they advise. Political problems have also emerged. The wording of recent government regulations is such that advisers no longer possess prescriptive powers for pesticides. Only government officials in the Ministry of Agriculture and Rural Affairs can perform this duty (MARA, 2009). This change effectively prevents advisers from performing one of their primary duties. Advisers oppose this wording and are working toward change. They also highly recommend that wording be added to create a division between product sales and advisory services (Ates and Sendundar, 2013). Finally, during the transition many growers have been reluctant to pay for advisory services; therefore, advisers are requesting the establishment of incentive payments for farmers that employ crop advisers.

Village Based Advisers

Extension in Tanzania also faces lack of funding and insufficient personnel to service their farmers. On average, there is only one extension worker for every 2300 farmers (Kansiime et al., 2018 Hella, 2013). There is simply no way that extension can function as a primary source of information and assistance to each of these farmers. The limited extension resources are primarily used to support high value crops such as potato while one of the most important staple crops, common bean upon which over 75% of the farmers rely on for daily nourishment goes underserved (Kansiime et al., 2018). In order to address this issue, Tanzania extension has undertaken programs to train village representatives to serve as agricultural information providers (crop advisers) called village-based advisers (VBAs). These VBAs need to live in the village, work on their own and demonstrate good communication skills. The villagers themselves had an integral role in selecting the individuals that were chosen to become VBAs. One person from each of 40 different villages was selected and trained (Kansiime et al., 2018). The training consisted of teaching the VBA's improved techniques for growing common bean such as proper seed spacing and efficient use of fertilizer. They were also given improved seed varieties and tools such as planting strings to facilitate implementation of the new techniques (Kansiime et al., 2018). To test the utility of printed materials, some VBA's were given posters, pamphlets and other educational materials to distribute to other farmers. VBA's did not receive direct compensation for advice given to other farmers, but they did collect a retail markup on the small lots of seed that they sold. The main compensation VBA's received was being the first to receive training and increased status within the community. The goal was for each VBA to educate between 80 and 100 farmers within their community. The study found that VBA's primarily used face to face interactions to distribute the educational information. Techniques used included larger group farmer meetings within the village, small informal meetings and one on one on-farm training (Kansiime et al., 2018).

Village based advisers proved to be highly successful community advocates. On average each VBA connected with almost three times as many farmers as anticipated (282) and traveled great distances (10 km) (Kansiime et al., 2018). The printed materials were found across the study area even where they were not available to the local VBA. The VBA's visited each farm an average of 4.5 times during the season with some as high as seven visits. Surveys indicated that 80% of farmers highly valued the VBA's and resources that they distributed (Kansiime et al., 2018). Using the seed and techniques from the VBA resulted in some farmers doubling their yield of common bean on the same amount of land. Farmers stressed that the most important trait of the VBA's was that they possessed good knowledge that they shared by using the local language in a clear and easy to understand manner. Some farmers identified the VBA's as their primary source of agricultural information. Most of the farmers planned to continue using the techniques they learned from the VBA's as well as the improved seed varieties. Farmers did express a need for greater access to new seed and recommended that additional information on pest management and pesticide usage be provided to VBA's for distribution (Kansiime et al., 2018). The VBA model illustrates the benefits of extension working closely with local crop advisers to reach a larger number of farmers with practical applied scientific knowledge. Knowledge that proves useful to farmers was rapidly and widely adopted and shared from farmer to farmer (Kansiime et al., 2018).

France: Systems Approach

Farmers, crop advisers and research scientists all have a predisposition to manage agriculture as a collection of isolated problems with individual solutions. Research and management tactics are devised to address an individual insect pest, disease or environmental stress (Ates and Sendundar, 2013; Sanya et al., 2018). Singular problem-solving fits well into the typical scientific method of hypothesis testing. Describe the problem, generate a hypothesis that describes a possible cause, design a treatment or solution and test the probability of the hypothesis being true. This process is critically important for evaluating the effectiveness of strategies, products and methods to address individual problems. However, given that we live, work and farm in interconnected ecosystems, this model may not be the most sustainable strategy. Hypothesis testing ignores the interactions of the practice or treatment throughout the ecosystem. Interventions that treat one problem change the balance of the system often resulting in downstream effects that may or may not be predictable.

Systems or holistic management is a strategy that considers the entire ecosystem when addressing problems. For example, pest management systems can include the creation of habitat for organisms that prey on the target pest(s) (Yuksel and Canhilal, 2018). This strategy of pest management called biocontrol has been practiced for centuries and for certain pests can be an important part of the pest management system helping to make the pest control more environmentally friendly and economical. One example is the use of predatory nematodes to control soil insect larvae (Helmberger et al., 2018). The goal is that the nematode predator population will respond to the insect prey population and establish a new equilibrium where the insect no longer reaches crop damaging population levels. In some instances, this works as intended and can result in long term suppression of the pest (UC IPM, 2012). In other cases, secondary organisms respond to the new higher population of the predatory nematode and in turn reduce its population (Helmberger et al., 2018). This interconnected complexity of ecosystems makes biocontrol difficult to study and implement (Coquil et al., 2018). However, there are proven systems-based agricultural practices that provide preventative solutions for individual problems. Long-term management strategies that make use of diverse crop rotations, reduced tillage and cover crops can help to create healthier agro-ecosystems that are more resilient to pests and weather extremes (Coquil et al., 2018).

A study conducted in France of farmers during their transition to a more ecologically based agricultural system revealed the challenges faced by the farmers were more related to the application of knowledge rather than a lack thereof (Coquil et al., 2018). In order to modify the system, the farmers needed to buy, build or modify existing equipment to perform the new tasks. They also needed to adjust their management to facilitate different work periods. For example, adding additional crops or cover crops requires a longer time period of planting, thus changing the work flow and labor needs of the farm. Information needs changed and increased. Farmers needed more observations of biological interactions within specific fields on their farms (Coquil et al., 2018). This is a role where the skills of crop advisers are well suited. Observations of plant growth, plant health, pest populations, beneficial organism populations and the anticipated response of all of these to predicted weather conditions are key skills that crop advisers develop over time. The crop advisers in this study made a distinction between two different types of advice, hot versus cold (Coquil et al., 2018). Hot advice pertains to more traditional immediate discussions to address specific problems. Crop nutrient deficiencies that require corrective action are an example of hot advice. Cold advice refers to long-term systems planning. Encouraging farmers to think about schemes that will reduce soil erosion, or which crops to include in crop rotations are examples of cold advice. Both types of advice have benefits and consequences for the local ecosystem and can be directed to actions that manage not only the problems on the farm but can also have positive environmental effects (Coquil et al., 2018).

Research scientists are the primary source of information that explains our world and the processes in it. We each make personal observations daily with which we evaluate our understanding of the world we live in. Recently, there is a movement of scientists to more directly interact with people via internet blogs and social media such as Facebook, Twitter and YouTube to deliver science to the end user (Ollerer, 2015). Yet this is a minority of scientists and is not yet a major channel for citizens to obtain scientific information.

Trusted Adviser to Researcher/Policy-Maker (Middle Up)

Research is important to provide evidence-based answers to questions and problems facing agricultural production. Identifying questions and clarifying the needs of stakeholders can be challenging for research scientists (Wick, 2018; Gasch, 2019). Extension

is one of the few conduits through which practical research questions originating from farmers can be posed to researchers. Farmers often feel disconnected from researchers because there is no formal interaction between the two. It can be difficult for researchers to identify which problems apply to a broad audience versus those that apply to a vocal minority. Crop advisers bridge this gap by communicating emerging problems and assessment of scale to researchers. This helps to identify research needs which are more likely to benefit a large number of stakeholders. Crop advisers can also help researchers understand the details of practical agricultural production such as the planting, harvest and time management challenges faced by farmers (Desutter, 2018). Crop advisers are also an important source of information for policy makers (NAICC, 2018). First hand knowledge of challenges and research needs of farmers is used to support program funding on national and local levels and help elected officials prioritize funding support for critical research.

Bananas in Uganda: Are Farmers Being Heard?

The development of crop varieties is a critical component of agricultural success. This process requires cooperation of many groups along the way. First, specific challenges need to be identified. Traits that confer drought tolerance, pest resistance, crop quality and increased yield need to be identified and ranked in importance. A high-quality crop that gets wiped out by disease provides no benefit. Similarly, a pesttolerant crop that lacks flavor, nutrition or other desired traits will not be marketable.

Banana was once a significant crop in Uganda; however, the varieties used were susceptible to insect pests and plant diseases that spread throughout the country (Sanya et al., 2018). Recently, efforts to develop new hybrid banana varieties to resist these pests have been undertaken. Sanya et al., 2018, studied the actors involved in the variety development process, their linkages and influences on one another to better understand the relationships between people that ultimately result in the success or failure of adoption of a new variety. The study examined the roles of research, extension, farmers, market representatives, tissue culture and policy agencies including Ugandan government and nongovernment organizations (NGO's). Interviews, surveys and focus group meetings were conducted throughout the process of banana variety development to uncover the interactions between the parties. They found that the farmers role in influencing the final product was limited and primarily peripheral. Given the expense involved and technical nature of plant breeding, it is reasonable that the researchers and national government held a primary role in the development of the varieties. However, the lack of involvement of the farmers is concerning because if their needs and concerns are not addressed, adoption of the new varieties may not occur. One surprising finding of the study was that some NGO's were able to command an influential role in the process. It was not clear if the role of NGO's resulted in the development of successful varieties, but Sanya et al. (2018) argued that this could also result in a disconnect between what is needed on the farm and what is delivered by the variety development program. The influence analysis showed that extension was the most important linkage for farmers. However, extension agents were also largely excluded from the development process. This is yet another example of the disconnect between scientists and farmers that can have important repercussions. If the researchers fail to consider the needs of the farmers, it is possible that their efforts will be wasted on a variety that is not adopted. Once again, the limitation of extension funding and personnel limited their capacity to be involved (Sanya et al., 2018). There were areas in the study region where extension was not available to the farmers, and in some areas where extension was available, they did not have the resources to influence the process. It is encouraging to note that in these areas, community members took up the role that extension would have played (Sanya et al., 2018).

Informing Policy

The distribution of knowledge of science-based and on-farm challenges to policymakers is a critical piece of science communication. Congressional Visits Day is an annual event that is sponsored by the American Society of Agronomy (ASA, 2018). Teams of volunteers consisting of a scientist, a CCA, and a science student are assembled and trained to concisely address the information needs of legislators and their staff in regard to importance of funding for science and agricultural programs. These meetings are conducted in Washington DC at the offices of the legislators and their staff. The team uses this opportunity to communicate the biological, economic and policy challenges faced by scientists and farmers in performing research and developing management strategies. Throughout the year, members of the science and agricultural communities each develop a list of priorities that they feel need to be addressed. The team meets prior to the congressional visit to streamline the message in order to properly articulate the needs of the stakeholders (ASA, 2018).

The National Alliance for Independent Crop Consultants (NAICC) works to build strong relationships with congressional delegates and federal agencies such as EPA and USDA. They are trusted sources of "data, information and clarification for issues relating to [agricultural] businesses" (Goldschmidt, 2018). NAICC members sponsor the Crawfish Boil on the Hill event every year. This time is used to interact with, network and advise policy makers about challenges faced by farmers and agribusinesses. NAICC also closely monitors and informs members of policy discussions and proposed changes. They also provide assistance for members to contact and advise their local representatives on how policy will affect constituent farmers and agricultural businesses (NAICC, 2018).

Certified Crop Advisers and crop consultants from the National Alliance for Independent Crop Consultants (NAICC) also provide expert testimony to the US Environmental Protection Agency (EPA) when it conducts use and needs reviews of labeled crop protection products (Moser, 2019). This information can be vital to preserving pest management technologies. Recently, members testified at hearings for the insecticide chlorpyrifos (Moser, 2019). The testimony informed members of the EPA of the

alternatives available for the management of pests currently controlled with this product. Crop advisers and crop consultants provided direct information about the frequency, abundance and damage to crops caused by these pests as well as their experiential opinions about how removing the product would affect the farmers and environment (Moser, 2019). In this case, there was information that removing the product would place farmers in a position where only one type of insecticide was available, thus severely limiting the farmer and crop adviser from practicing sound IPM principles (Moser, 2019).

Citizen Connections

Citizen science is another opportunity to create connections between scientists, extension and the general public (Clyde et al., 2018). Extension personnel maintain strong connections with research scientists and can serve as the connection for citizens who wish to learn more about and be involved in research projects. Once again extension's expertise in volunteer management, budgeting and science communication and training can benefit both the researchers and citizens. The additional benefit to all is that extension can be an avenue for citizens to initiate, collaborate and help to develop research projects that address their needs (Clyde et al., 2018). An example of this interaction is the Oakland County Lake Monitoring Project in Michigan that has been in existence since 1974 (Lant, 2018). The Huron River Watershed Council trains and provides equipment to volunteers who own boats to sample water quality and screen for invasive species. These volunteers provide much more data than the agency could collect on its own (Lant, 2018). In another example, the American Ornithological Society hosts a website with content specifically for citizens who want to contribute to scientific studies (AOS, 2018). The webpage is designed to connect willing citizens with scientist. Several studies are listed, described and linked so that interested volunteers can contact the researchers and receive training (AOS, 2018). These citizen-to-scientist connections are increasing, but currently, there are few ways for citizens to propose research topics to scientists. Collaboration on citizen science projects could be one important way to accomplish this. Extension's connections with scientists from many disciplines allow them to present citizen ideas to collaborators who have the necessary expertise and interest. Equally, advisers can help citizens refine and articulate their ideas, and act as a conduit to bring their concerns and research needs to extension, scientists, and policy makers.

Hot Shots Program

The delivery of science to citizens can also utilize advisers similar to agriculture. The Hot Shots project in Denver County Colorado is one example of how extension can partner with local experts to deliver science to citizens in a mutually beneficial way. This project differs from traditional extension programs in that it is short-term (weeks-months), utilizes volunteers or part time community experts and is self-supporting. These projects address specific needs of citizens in a particular subject area. Citizen demand for a specific program initiates extension to identify community members with the skills, education and drive to deliver the program. Once vetted, extension enters into an agreement with the individual(s) to provide the training to interested citizens for a fee. Like extension partnering with crop advisers to provide information to farmers, these projects partner extension with local experts to provide the scientific information to citizens. The value of extension is that they have experience in securing funding, preparing budgets, and organizing training and volunteer events. The adviser benefits financially from fees to support the program but also socially by gaining respect and recognition from community members. These aspects mirror the VBA program in Tanzania. The citizens benefit by gaining programing that addresses their needs and interests, and extension benefits by reinforcing their value as a vehicle for the delivery of science to the public.

Filling a Need in the Climate Change Debate

Agriculture is one of the most significant industries in the world and is an important contributor to climate change though greenhouse gas emissions, land use and development and alterations of plants and animals for human needs (Howden et al., 2007). Agriculture is sensitive to changes in climate, for example El Nino/La Nina patterns affecting rainfall and temperature can account for up to 40% of yield variation in staple crops such as grains and oilseeds (Ferris, 1999). Adjustments to farming practices and energy use can provide important mitigation effects for climate change (Bernacchi and Wulfhorst, 2017; Howden et al., 2007) and resource conservation (Gabel et al., 2018).

Fossil fuel use is recognized as a root cause of anthropogenic climate change and needs to be addressed in every industry including agriculture (Robinson et al., 2018). Fossil fuels have allowed us to transport food, goods and people across the globe creating prosperity for many nations, but at the same time, we have been increasing atmospheric carbon dioxide concentration that is changing our climate with the very real possibility that we are making our planet unsuitable for a prosperous human future. Understanding and management of global climate change requires thinking and problem solving on a much higher level (Etkin and Ho, 2007).

The scientific consensus is that climate change is occurring, human activity is a primary cause and there is a need for immediate action to address it (Benegal and Scruggs, 2018). Despite the high degree of agreement among scientists (~97%), nonscientists continue to debate these conclusions (Tyson, 2014; Ollerer, 2015; Benegal and Scruggs, 2018). The distinction between weather and climate for many citizens is blurred and results in misinformation and denial and the subsequent failure to act (Etkin and Ho, 2007; Van der Linden et al., 2017).

Political and philosophical opinions as well as personal experiences and relationships all contribute to an individual's assessment of the true cause and severity of climate change. In the United States, political party affiliation is a strong predictor of agreement with climate change. [Benegal and Scruggs \(2018\)](#) showed Democrats are more likely to agree with climate change than Republicans. They also showed that statements supporting climate change made by a Republican carried more weight with all groups tested (Democrat, Independent and Republican) than if the same statements had been made by a Democrat or scientist. These strong group affiliations are also evident on social media. A study of Facebook users associated with science or conspiracy pages showed high polarization. These users commented, liked and reposted only those ideas that agreed with their existing views. Rarely did they venture out of their echo chambers. The analysis also showed that when users were faced with corrective statements, they largely ignored them ([Benegal and Scruggs, 2018](#)). Even highly compelling well-vetted arguments were dismissed. Users were also more likely to become more convinced in their stance when faced with weak statements that contradict their beliefs. This "inoculation" against differing opinions and facts that do not support preconceived ideas has been illustrated in multiple cases ([Zollo et al., 2017](#); [Van der Linden et al., 2017](#)). Inoculation messages can also be used to steel people against misinformation in public and social media. Presenting people with scientific facts about climate change and warning them that others will try to mislead them on these facts produced a significant protective buffer against misinformation. However, the research did not evaluate the longevity of the protection of these inoculation messages ([Van der Linden et al., 2017](#)). While inoculation messages can be used to protect people from misinformation, they can also be used by nefarious individuals or groups to prevent them from recognizing truth ([Zollo et al., 2017](#)).

Public consensus on climate change that mirrors scientific consensus is viewed by some as a fundamental need in order to enact meaningful change ([Etkin and Ho, 2007](#)). In the realm of national policy, public support is indeed important. The lack of public support leads to time wasted arguing over politics and results in a failure to set funding priorities that could have significant national and global impact.

However, in agriculture this need for climate change consensus is being challenged. [Tyson \(2014\)](#), argues that climate change remains a debate; one that is not likely to be resolved. Nonetheless, sustainable actions and conservation benefits that protect water, biodiversity and environmental quality have immediate and obvious value to all citizens, including climate change deniers. Even [Etkin and Ho \(2007\)](#) state, "...it makes more sense to ask, how can we relate to nature in a more sustainable and functional way...". Indeed, agricultural projects that seek to provide short-term soil and water quality benefits and protection from weather events can have a great positive impact on the environment, e.g. reducing soil erosion or preventing nutrient runoff into rivers, streams and lakes. These projects lead to many of the same actions necessary to mitigate climate change without the need for consensus, assuming responsibility or placing blame on individuals, industries or countries ([Robinson et al., 2018](#); [Tyson, 2014](#); [Gabel et al., 2018](#)). Swiss and French farmers with the help of agricultural advisers have modified their farming techniques to increase habitat to support biodiversity and reduce fertilizer and pesticide inputs without agreement on climate change. They did not agree on anthropogenic climate change, but all farmers surveyed did agree on the environmental and human goals of maintaining soil fertility, producing healthy food, treating animals with respect, using sustainable strategies and providing food security ([Gabel et al., 2018](#)).

The university extension system in the United States is a primary source for continuing education for certified crop advisers (CCA's) and because of this, there is an opportunity for extension to provide information and training directly to CCA's about climate change and practical management strategies that can help mitigate agricultural contributions. Certified Crop Advisers as a group do not show the same level of agreement about climate change as scientists ([Bernacchi and Wulffhorst, 2017](#)), yet this does not mean they cannot be agents for beneficial change. Their work is targeted at helping farmers manage challenges to production, and this includes increasing the production systems resiliency by adapting to changing weather patterns. The adaptive management that CCA's and farmers collaborate on to manage annual weather patterns includes many practices that would be implemented to manage for long-term climate change ([Bernacchi and Wulffhorst, 2017](#)). The CCA's themselves agree with [Tyson \(2014\)](#) that their daily work addresses climate change without the need to sort through the politics and misinformation to convince farmers or coworkers of scientific consensus ([Del Corso et al., 2015](#); [Bernacchi and Wulffhorst, 2017](#)).

Conclusion

Effective science communication is a vital yet difficult task to accomplish. Misinformation, misconceptions and the perpetuation of ideological barriers hamper discourse and utilization of scientific knowledge. Developing trusted advisers to bridge the gap between scientists and citizens can be an important way to deliver knowledge and implement actions that address some of the serious problems that we face, including climate change. These trusted advisers are trained in science and communication, members of the local community and skilled at tailoring scientific knowledge to address local problems. Numerous successes exist in the agricultural industry that demonstrate the importance of trusted advisers as agents of change to improve the management of farming systems. There are also examples of cooperation among scientists, extension and citizens in effectively communicating and utilizing science. These advisers can also facilitate two-way communication between citizens and scientists to establish research priorities and bring research ideas from the citizens/stakeholder to the scientists. There need not be a disconnect between the public and scientists if we amend the concept of top-down and bottom-up communication to include a middle agent, the trusted adviser.

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<https://www.joe.org/>—Journal of Extension.
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<https://naicc.org/>—National Alliance of Independent Crop Consultants.
<https://www.nrcs.usda.gov/>—Natural Resource Conservation Service.
<https://www.plos.org/open-access>—Public Library of Science.
<http://ipm.ucanr.edu/>—University of California Integrated Pest Management.

Sustainability Storytelling Is Not Just Telling Stories About Sustainability

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Abstract

Storytelling is well researched and long recognized to be an intrinsic human instinct, even argued that story has influenced our evolutionary process. But until recently, storytelling diminished from scientific inquiry and presentation, placing precedence on findings. Now that storytelling with sustainability topics is enjoying greater attention in business and creative circles, is traditional narrative structures adequate in depicting modern human interaction with each other and environments? As stories about anthromes and sustainability efforts within them continue to evolve, some argue that typical narrative structures, along with messaging styles like marketing and reporting, don't adequately convey the requisite skills and knowledge needed to realize sustainability change. By increasing focus on place and characters clearly demonstrating sustainability competence in practice, struggle and success, while adopting living systems structure as a model for story structure framing, it is hoped a conscious competence is achieved by a story's audience to then realize sustainability solutions, and stories, in their own time and place. The chapter includes exemplars of sustainability stories and further reading.

Preface

If you are reading this, you are likely already interested in how humans interact and affect the planet, be it through the lens of space and patterns of anthromes, the time of the Anthropocene, the expanding premise of sustainability, or the increasing call for systems thinking and resilience. Or you stumbled upon this chapter digitally or physically, recently after publication or years removed. Either way, you are here, and it is on me as the author to write in a way that keeps you wanting to read beyond the inertia of your initial curiosity, and just like most other humans, you are likely very capable of detecting a bad or boring story or piece of writing right from the start (Cron, 2012), and can easily pass this chapter by. Still, this is an entry to an encyclopedia-style publication, meant to present prior research and knowledge in a straightforward and factual way. So, there is a back and forth of honoring the style and content while satisfying a reader's interest to read on.

If you've already spent time in the other chapters, you've gathered plenty on what we perceive as typical biomes, stretches of our planet that uniquely support life. Much of these biomes now have human fingerprints and footprints upon them, where natural systems have been interrupted and possibly irreversibly altered by human activity, heeding the nomenclature "anthromes" (Ellis and Ramankutty, 2008). As these other chapters have perhaps retained a non-biased scientific approach to human activity, or have lent themselves to explain the harm or benefit done to these corners of the Earth, human actions were driven by a want or need of something of greater perceived value than what the biome was already facilitating. Acting on those wants and needs, and the efforts to correct and remediate the consequences of those actions, is what makes conservation, sustainability, governance and consumption rife with conflict. Where there is conflict there is drama, and where there is drama, there is a story. And for much of the Anthropocene, those who told the most compelling story were often the ones who realized the vision they had for the land and the life upon it (Sachs, 2012).

Introduction

In between jaunts of graduate school and academia, I was a science reporter for a large public radio station. I caught wind of a local man who turned a dilapidated pool in his backyard into a thriving food production system. I was seeking a challenge of a story and thought I could use this as an example to somehow report on closed-loop nutrient cycles, something I was personally interested in. I

visited an open house and found dozens of people in awe of what this man and his family had done. But beyond what was called “Garden Pool,” where water and soil were arranged in a way that supported ample plant and animal food for his family, people were taken and inspired by how this modest family turned their old pool into hundreds of volunteers and an international non-profit building micro-farms in dilapidated spaces locally and in developing countries (Bernier, 2015).

I could have talked exclusively about nitrogen cycling or plant species selection, but I also spoke about this man buying a humble home right when he was laid off from a construction company and wanted an inexpensive way to feed his family. I also included how insistent he was about how many times he messed up, experimented and failed, and is always learning about what he needs to do to make the system better. I’ve interviewed and reported on national laboratories, research university breakthroughs, science policy and space technology, and this man and his pool was one of my most popular stories.

I see this story as a classic sustainability story, a person or persons responding to a challenge regarding typical sustainability concerns (food, water, climate, development, etc.) by developing requisite skills and knowledge to become a sustainability change agent and realize a vision almost anyone can do. In this chapter, I primarily use the term sustainability and less so anthromes or Anthropocene in reference to what we are emphasizing in storytelling. I do so for a couple of reasons. The first is that storytelling has recently gained enormous momentum in the sustainability field, particularly in business and with practitioners (see section: Further Reading), and is also well researched to be a tool frequently used in sustainability efforts for years (Eckstein and Throgmorton, 2003; Grace and Kaufman 2013; Ramondt and Watts, 2005). The second reason is that a story is meant to show us how and why you do what you do. We will cover that premise a bit more in detail later in the chapter, but through the lens of sustainability competence, we adopt an action oriented approach to storytelling, focusing on the capacity or ability to act and sustain a desired behavior or state of being, whereas human affected biomes are the result of action.

Why Story? Are We Wired for It?

In short, a story is “a narrative account of an event or events-true or fictional. The difference between giving an example and telling a story is the addition of emotional content and added sensory details in the telling” (Simmons, 2001, p. 31). By accommodating emotional and sensory detail, it is well researched and argued our brains are hardwired to relate to and be engaged by storytelling (Haven, 2007), where “regions of the brain that process the sights, sounds, tastes, and movement of real life are activated when we’re engrossed in a compelling narrative” (Cron, 2012, p. 4). Response triggers such as emotional engagement, relatability, and entertainment enable stories to convey critical messages simply, which are often missed by reports, news, presentations and lectures, predominant means of communicating science and sustainability (Tyler, 2009). While standard and expected in westernized science, those means often neglect innate human desires and capacities.

Biologist E. O. Wilson describes storytelling as a fundamental human instinct, a means to help convey the meaning of science and inquiry in a way the inquiry process often fails to do, or at least takes too long for the interest of most lay people (Wilson, 2002). He argues that while not every person is an apt storyteller, just about all persons can receive and possibly be persuaded by story. Jonathan Gottschall in *The Storytelling Animal* (2012) presents several social and biological means of which storytelling evolved into the human experience, be it gaudy storytelling to attract a mate, a cognitive exercise, to teach and share experiences vicariously, or to bring groups together, or control them. Gottschall notes that several evolutionists now propose the idea of religion in early human existence made societies work better by groups subscribing to stories shared within a particular church. These stories often praised prioritizing the interests of the group rather than the self, “and what they generally cause people to do is to behave more decently toward members of the group (coreligionists) while vigorously asserting the group’s interests against competitors” (Gottschall, 2012, p. 122).

For as long as we’ve made stories to bring together and distinguish groups and individuals, we’ve also made stories about the land to make sense of natural systems. Familiarity with how to work and manipulate natural systems requires time; indigenous peoples are often those who have the most knowledge and mastery of natural systems in which their people lived for hundreds if not thousands of years. The concept of traditional ecological knowledge (TEK) focuses on the in-depth “understanding that indigenous peoples have on ecosystems and their interconnectedness” (Edwards, 2010, p. 7), with generational knowledge of the land passed down through story.

On several occasions where modern analytical or western science has fallen short of explaining or predicting what ecosystems do, TEK has shown that indigenous understanding of living with seasons, species, and resources is incredibly powerful, useful, and accurate. With examples like the Balinese water temples for sustained rice yield, Tibetan people living in the harsh conditions of the Tibetan plateau and the Inuit sustaining whale hunting for hundreds of years, we have clear examples of how to use TEK and learn from it when building modern resilient communities adaptive to change (Edwards, 2010). While some would argue that reductionist western science and holistic TEK have inherent conflict, Martinez (2010) suggested there can be unity of the two approaches. Martinez argued western science most often quantifies and classifies the natural world, as opposed to listening to it. However, when science takes the time to observe and regard what TEK has been observing and acting with for thousands of years, the two are inherently successful (Martinez, 2010).

Evidence of this recognition and collaboration are emerging. The U.N. Sustainable Development Goals, The Convention on Biological Diversity, and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services recognizes

“indigenous and local knowledge and its contribution to the conservation and sustainable use of biodiversity and ecosystems” (Tengö et al., 2014, p. 580). The result is a multiple evidence base approach to assess biomes and humans’ impact on them “where indigenous, local, and scientific knowledge systems are viewed to generate different manifestations of valid and useful knowledge” (p. 580).

While stories aim to help close the gap between westernized science and TEK, along with tapping into human’s innate penchant for story while not compromising scientific inquiry, the pace of which sustainability challenges are changing is quickening. With unintended consequences emerging from climate change, urban development, and resource mismanagement coupled with active resistance to solutions fostering wicked problems, traditional narrative structures may not serve sustainability efforts to engage, teach, and empower. To demonstrate how acting for sustainability changes both place and people, the next section describes key aspects of sustainability storytelling, an approach embracing complexity and systems structure coupled with sustainability knowledge and skills to stay relevant for as long as sustainability problems exist.

Crafting an Effective Sustainability Story

Whereas telling stories about sustainability follows more traditional methods of storytelling, using narrative structures within a sustainability context, sustainability storytelling intentionally aims to teach, convey, and empower listeners with clear and engaging examples of sustainability in action (Simmons, 2001; Pollock Shea, 2014; Amlani et al., 2016). Not only do these stories demonstrate the skills and knowledge needed to make sustainable change in our communities, but they also empower and motivate an audience member to be a sustainability change agent (Meisner, 2014).

Intent and Audience

When an idea for a story emerges, there is a bit of a vetting process to validate it, as crafting an effective sustainability story takes time. Two renowned storytelling entities, National Geographic and National Public Radio, have a series of questions they ask themselves before delving into story creation.

National Geographic Five Principles of Storytelling (As presented by Susan Goldberg, National Geographic Editor in Chief)

- Does this story make a difference?
- Does this story do what others can’t?
- Can this story be part of the conversation?
- Does this story act urgently?
- Does this story know who you are? (Goldberg, 2017)

NPR Training: Beyond the 5 W’s: What Should You Ask Before Starting A Story?

- What is my story’s driving question?
- What is it not about?
- What are my dream ingredients?
- How will I engage my audience—and hold them?
- How will I ensure the story is fair to the people and the idea it represents?
- What will the audience remember when it’s over? (MacAdam, 2016)

While stories are incredible mechanisms for teaching and having people remember details, customs, life lessons, etc., sustainability stories inherently aim to change behavior and empower an audience, rather than just covering sustainability issues. But before you can consider changing lay audience members into sustainability change agents, if you so desire, storytellers must think of who their audience is. I was in a sustainability communication workshop led by Lee Gutkind, the editor of *Creative Nonfiction* magazine and Distinguished Writer-In-Residence at Arizona State University. In it, one of his initial comments was something like “remember, your audience *wants* to walk away, they *want* to go have a cigarette or beer, they aren’t necessarily interested in what you have to say.” With this, an effective communicator must tell a good story to capture people’s attention. When captivated they will stay and hopefully share your story.

Most sustainability practitioners and academics can likely attest to this; when we give presentations, publish papers and engage the public, we are likely engaging people who are already interested in the topic. While we should not shortchange them of a good story, they are not who we are aiming to captivate (though re-inspiration helps). Rather, the folks who are not interested and didn’t show up are often those most needed to hear the story. To begin reaching those who did not show up, figure out who they are by “listening...finding out what drives them, what their priorities are, and how sustainability fits into the picture” (Pollock Shea, 2014, p. 132). Your opening scene of that picture, and even your opening line, is your only shot to frame the story and engage unaware audiences (Gutkind, 2012; Cron, 2012).

Content

Just about everything that makes a good story still serves as the foundation of what makes an effective sustainability story, particularly the 5 W's: Who, What, Where, When, and Why. The question of 'How' will be addressed a bit later. While simple in premise, many stories fall flat because they fail to adequately address these:

Who: Oftentimes organizations are highlighted in sustainability success stories, as funding for projects can dictate whole organizations. But "stories that feature the organization as the hero tend to be a bit boring or sometimes make us roll our eyes" (Amlani et al., 2016, p. 12). This tends to dilute the resonance of effort with individual audience members who are not part of the organization, and therefore may not share the same values or mission. Rather "position the organization in a facilitating role, in the background supporting the main character(s) or protagonist" (p. 12). You can have empathy for individuals. Individuals are heroes, leaders, followers, and set replicable examples (Humphrey and Adams, 2016).

What: This is two parts. The first is the issue at hand. Clearly identify the problem, first at a small scale then a large scale. Spend little time defining the problem (< 25% of your story time). Try not to put a face on it, rather describing it as the norm, resistance to change, "the way we've always done it." The second is the change you seek and solution you are creating and implementing. Is it strictly local or can it be scaled up? If it can be scaled, briefly describe what it will take to do so.

Where: While honoring bioregionalism, place-based learning, and TEK, stories can move quickly from where they are told, so where stories are set presents an interesting challenge. Stories about drought in the southwest and then stories about urban brown-field reclamation in the northeast will be inherently different. It is onto the storyteller to show and create these places in the audience's mind. It is also important to describe how these places, perhaps biomes and anthromes, affect the issue at hand and to clearly explain when sustainability efforts are unique to a place, and when efforts can happen regardless of place.

When: When can also be tricky, as many of the sustainability issues at hand don't have an end in sight. Or when a conclusion does arrive, we find more unforeseen challenges. When is important to establish not just for the era the story takes place, but how long, such as knowledge gained over generations or simple solutions that take only minutes to do, and if a specific series or sequence of events is needed (Simmons, 2001). Time can also play a central character as the pace of change becomes alarming, such as James Balog's *Chasing Ice* film showing before and after pictures of glacial retreat due to climate change (Howell, 2013; Meisner, 2014). It is also wise to make stories not appear dated as it will extend their longevity and relevance.

Why: What is the value proposition? As in, what does your audience stand to gain from sticking through with the story? Sustainability stories, while they can be entertaining, doesn't exist to entertain. The popular TEDx video and subsequent book *Start with Why* from Simon Sinek (2009) makes it clear that "people don't buy what you do, they buy why you do it." Why are the people in the story waking up and saying, "I am someone to take on this sustainability challenge?" Is it commonly shared values? Agreed upon goals? Incentives? Personal beliefs? To drive the story forward you need motivation and momentum from the characters and the audience. What is your audience's why and how can that resonate with your story's why?

Even if a story about sustainability covers all the W's, it can still fall short of what makes it a sustainability story and a needed call for action. Here are some intentional storytelling approaches that can leave an audience little to work with:

- **Reporting:** In standard reporting and journalism, the primary job is to cover the 5 W's. Having been a science reporter, I mostly had to stay within these bounds. If not, "trying to change people's minds, their lifestyles, or their politics raises ethical questions" (Meisner, 2014, p. 157). In true reporting, you must leave biases out, which means leaving out information that did not originate from the events or from the voices of those involved. A call to action here would violate this.
- **Consciousness raising/raising awareness:** It is often popular to want to raise awareness or consciousness of a topic, which is good and is often what gets an audience interested. However, "people do not change their behavior or their level of civic engagement simply because they are aware of an issue or even because they are knowledgeable about it. Among other factors, they need to feel that it is the right thing to do, and they need to see a clear path" (Meisner, 2014, p. 157). Getting your message out is hard and there are plenty of means to do it (art, videos, canvassing, protesting), but it can sometimes vilify groups or specific people, stifling solutions. In sustainability storytelling, "giving people information on how to be an effective change agent as well as opportunities to participate in actions in combination with consciousness raising is more useful than consciousness raising alone" (p. 157).
- **Marketing:** Along with having a good sense of stories, humans can also be adept sensing when they are being sold something. Stories lend themselves to authenticity through admitting challenges and fault, whereas marketing will often try to keep a more rosy picture of the discussion, though many in business are adopting storytelling (see list of further reading). Below is a dichotomy of marketing of sustainability to sustainability storytelling (Bernier, 2018);

A dichotomy of sustainability marketing to sustainability storytelling

Purpose	Marketing of sustainability	Sustainability storytelling
Who stands to gain?	Entity giving the message to sell a product or service	Individual and group audience members, practitioners
Attention paid to what?	Products or services offered	People overcoming challenges
Tone set and expectation of messaging?	"We have the solution," ease of use, success for you	Conflict, struggle, growth and solution devised and implemented

Conflict, Challenge, and Failure

Challenges serve as conflict, which is what gives drama to any story and keeps an audience engaged as the story moves forward to try and resolve the conflict. Admitting to challenge, and also portraying failure, lends a story and its characters to authenticity, creating further buy-in (Amlani et al., 2016). In typical storytelling, there are four predominant types of conflicts (though there are others):

- Person against person
- Person against self
- Person(s) against nature
- Person against society

Conflict in most stories comes from an us versus them structure, be it heroes and villains, or one story and its morals are pitted against the morals of another story, much like debating religions or political parties (Sachs, 2012, p. 20–29). We often want to deduce stories to a good versus evil scenarios, producing a binary approach to motive and plot, because challenges become easy to interpret. According to professor Tyler Cowen this simplification can typically reduce IQ by 10 points in the moment, often disregarding complexity and conflicting motives (Cowen, 2009). Capturing the challenge of sustainability can often cross each one of the four types of conflict in a single story, fostering complexity in crafting a solution. Even as individuals and groups begin problem solving, “conflicts arise between people as they identify with one another and sections of society. Effective strategies must assume controversy and build on it as a necessary part of social action” (Ramondt and Watts, 2005, p. 4).

Wanting to evoke change ultimately creates conflict, from those who prosper from the status quo, those who are hesitant on making change because of unforeseen consequences, or from those who have a different idea of how to make needed change, although sustainability transitions can be helped by alliances and co-learning between groups (Luederitz et al., 2017). Sharing stories of how one hesitated and struggled through making change invites empathy and understanding as to why you seek change (Humphrey and Adams, 2016). There is a learning curve (a challenge) for all who start making sustainability-oriented changes, and it can serve as the drama needed to overcome in becoming a sustainability change agent. “Story validates the specific circumstances people experience at the same time it invites them to look from another point of view...story invites them to creatively reframe their dilemma” (Simmons, 2001, p. 39).

Show, Don't Tell

It is critical not to tell sustainability stories, but rather show them (Amlani et al., 2016). Instead of covering each significant detail, fact and statistic, which is where presentations, papers and lectures come in, stories are more for showing the experience of the characters. This is done by increasing focus on the setting and the characters, and less on the problem or sustainability issue. This is not a simplification of the content, rather humanize the story first, then legitimize it with well-placed data. Most people have a lay understanding of the challenges sustainability aims to solve, but will likely know little of your characters and places.

This is done because it is the most immediate way your audience can envision themselves in the story. Storytellers can use descriptive but easy to understand adjectives of the environment and the characters, often describing how humans intimately interact with place and each other (Haven, 2014). In these interactions, use multi-sensory language; “I tasted, they felt, it smelled, etc.,” to tease the listener’s senses beyond just listening and watching, reinforcing memory of what to do later because “audience members use the details you provide as a substitute for their own direct sensory observations” (p. 94).

Engaging and influencing an audience, or even peers, friends, and family can be tricky, often devolving into a tell-type messaging and creating the opposite effect of resistance toward sustainable change. Also, modeling desired behavior without providing reason or describing needed knowledge and ability can often fall flat, allowing observers to question what you are doing or even reinforce mental stereotypes (e.g., tree huggers). If met with resistance, it has been shown that stories are better apt to reduce resistance rather than information heavy messaging (Grace and Kaufman, 2013).

In short, tell a story showing the desired behavior and knowledge without telling people what to do. Show competence in practice and in action, demonstrating struggle, learning and successful behavior change. When you do make a call to action, very specific and concise language works best after demonstrating what it can look like for audience members.

“Persuasive communication requires a clear description of the desired outcome and the means to accomplish that objective: Fuzzy generalities are dismissed and forgotten. Requests to take a specific—ideally, measurable—step by a specific date are considerably more powerful” (Pollock Shea, 2014, p. 133).

The How: Sustainability Competence

Clearly exhibiting or explaining how a sustainability problem is a challenge for the characters and how the individual, team, or organization will succeed is critical to sustainability stories, as we are trying to make our audiences *competent* in the topics we tell stories about. To be competent in something is having the necessary ability, knowledge, and/or skill to do something successfully. The specific abilities, skills, knowledge and attitudes for a given field are known as *competencies*, the cognitive abilities and skills an individual has or can learn in order to solve specific problems together with the related motivational, volitional and social willingness to apply the solution in a variety of different situations (Weinert, 2001).

There are many organizations that have lists of sustainability competencies (e.g., UNESCO, International Society of Sustainability Professionals), and often are categorized as:

- Knowledge: Things to know (think nouns),
- Skills: Things one can or should be able to do (think verbs),
- Disposition: The mindset and/or attitude a person should have (Friske and Larson, 2011).

However, competencies are not concepts in isolation, as competency lists tend to present. Rather, it is how well we weave them together “because sustainability problems and challenges have specific characteristics (different from problems addressed in other fields), analyzing and solving sustainability problems requires a particular set of interlinked and interdependent key competencies” (Wiek et al., 2011, p. 204). For instance, one competency for sustainability is “the ability to recognize and understand relationships; to analyze complex systems; to think of how systems are embedded within different domains and different scales; and to deal with uncertainty” (p. 207).

Sustainability stories need to weave together select skills, knowledge and dispositions to be portrayed or exhibited by a sustainability change agent in the story. There shouldn’t be too many, as that becomes unrealistic to replicate, but if an audience member walks away from a sustainability story knowing a concept or two they need to learn more about, and complementary skills on how to act on it, then they are closer to conscious competence, or “becoming aware of what you are doing so that you can adapt what you are doing whenever you need to” (Cabrera and Cabrera, 2015, p. 175).

Perhaps the main drive of sustainability stories is how Derek and Laura Cabrera describe metacognition, where there is “an increase in awareness: awareness of one’s own thoughts, emotions, and motivations, but also an awareness of how one interacts with the outside world” (p. 173). They argue an increased capacity of metacognition leads to an increase in self-awareness of learning processes, cognitive capacity and emotional intelligence. They describe a development of self-awareness on a continuum as follows (p. 175):

- Unconscious Incompetence: We don’t know what we don’t know. The audience who is unaware of sustainability and the impact of their decisions;
- Conscious Incompetence: We realize there is something to learn and are motivated. Perhaps after an audience member is led through a compelling sustainability story;
- Unconscious Competence: Practice of knowledge and skills, but not aware of mastery. This is practice, struggle, failure and growth of sustainability behavior change;
- Conscious Competence: Aware of what you are doing, and you can adapt whenever needed. Mastery of your skills and knowledge that transcends place and challenge.

In conscious competence, the notion of adaptation of your skills and knowledge to new places and challenges speaks to the notion of resiliency, a central tenet of healthy systems. With emphasis on systems thinking and resiliency, we can use systems structure to help organize and tell a sustainability story and demonstrate transformational change.

Sustainability Story Structure: Systems as Story

All stories follow structures, intentionally or not. Examples of story structures include “The Hero’s Journey,” “Nested Loops,” “The Mountain,” “3 Spheres” among others (Sparkol, 2018; Gutkind, 2012). A sustainability story is no different, though sustainability itself follows a systems structure, including elements of connectivity, complexity, emergence, feedback, resilience and other systems aspects. The problems sustainability takes on are complex, but sustainability solutions nor their messaging should be. The goal is to share simple yet strong stories that honor and navigate this complexity by highlighting resilience, revealing unknown connections, and celebrating emergence (the unknown that comes to be when interactive parts come together) as “a story weaves detail, character, and events into a whole that is greater than the sum of its parts” (Simmons, 2001, p. 31).

I teach systems thinking, and in my class I use a lot of quick stories to exemplify how systems manifest in human to human and human to nature interactions. While there are several technical considerations to systems, they are ultimately about relationships, and relationships change based on any number of factors. Stories help to capture and give reason to this, something often lost by a reductionist approach using the scientific method to try and isolate and measure an independent variable.

“A system is an interconnected set of elements that is coherently organized in a way that achieves something” (Meadows, 2008, p. 11). Stories are not much different than systems. Lee Gutkind states that parts of a story are scenes or little stories. Information flows within or in-between scenes and that the pattern scenes are organized is a frame (Gutkind, 2012, p. 218). Frames are malleable, as they “give shape to a story and keeps readers turning pages (or scrolling on screens) to find out what happens from scene to scene” (p. 218). Seeing scenes as elements of a system, and the identification and practice of competencies as the information that flows based on how they are organized, can achieve the desired awareness and empowerment in an audience.

Scenes can be intermixed, or you don’t need to start a story in chronological order, meaning you can drop characters, and audience, right into the middle of rising action to start your story. This helps to break down the typical start to finish linear design of traditional narrative structures. By adopting systems and complexity into story design, we are better able to track “vital deviations: meaningful personal experiences, creative solutions to conflict, and paradoxical truths” (Simmons, 2001, p. 251). While stories can

accommodate tangents or vital deviations, there is a point where it can be too much and exceeds boundaries. “Think of a rubber band—the more you stretch it the tauter it becomes until it breaks. So too with a good story; it can be stretched so that the reader is tantalized with heightening suspense as the writer goes off on related tangents” (Gutkind, 2012, p. 227).

One critical aspect of systems, feedback loops, helps differentiate sustainability stories from more typical stories. As opposed to someone hearing your story and being amused and possibly remembering it for some time, what is the return on telling your story? May it contribute to research? Could it result in a contract? Does it speak directly to the increase or decrease of an action in a community? Are you hoping to develop more sustainability change agents? Sustainability is ultimately an action-based field of work. With a great example of this, Jonah Sachs in *Winning the Story Wars* describes how he worked on the immensely successful viral video *Story of Stuff* with Annie Leonard (see “Examples of Sustainability Stories” section). What went from a near 60 min lecture of facts and figures describing corporate and consumer greed was translated into a 20 min animated short focused on individual empowerment and stick figures depicting everyday choices (Sachs, 2012, pp. 20–29). That video has spun off several other videos, a bestselling book, curriculum guides, a thriving non-profit, and countless speaking engagements giving the space to constantly evolve the story.

The living systems in biomes and anthromes that sustainability aims to sustain should then inform how sustainability stories work. As Annie Leonard found out, her first story was just the start, with its message constantly evolving with the change of the content it contained. But typical story narratives can be too rigid to accommodate needed change. To facilitate this, David Boje refers to living stories as means to have story not stuck to a given time or place. “A living story is all about movement...a founding of story spaces, a networking in the unfolding present, where each story is dialogically relational to another one, and must be told to tell of another social relationship...Living stories are often without beginning, and are never-ending (unlike narrative)” (Boje, 2011, p. 3). Boje then discusses his novel concept of the “antenarrative,” stories that “bridge past narratives stuck in place with emergent living stories. Antenarratives are on the move, founding spaces, whereas narratives have settled into places” (pp. 3–4). Boje describes how narratives turn spaces into places, and that living stories foster spaces where stories can be more dynamic and gives organizations better ability to shape their stories, rather than following narratives that are more linear and static (p. 4).

The systems as story structure approach is emergent, with most conversations happening in creative and business circles and some storytelling academics analyzing its application. Still, healthy systems change and adapt to their environments, as should your story structure. So, as you explore anthromes and their continuous emergence from human intervention, how would you write the story of anthromes? How would your voice and personal narrative impact the message you want to share? And to whom would you intend to share your story with? Below are examples of stories that started small and emerged into bigger, more robust stories that are still changing. While most of them are in video format, know that sustainability stories span across media mediums, and it is up to the storyteller to decide what media they are most comfortable with and what best suits the sustainability story they seek to show.

Examples of Sustainability Stories

An Inconvenient Truth (2006): The documentary film written by and featuring former Vice President Al Gore widely regarded as the film most credited to raising awareness about global warming. While mostly a presentation and talk from Gore, several produced stories were intermixed exhibiting intimate and personal experiences for audiences to resonate with. It has a sequel *An Inconvenient Sequel: Truth to Power* and fostered the launch of the Climate Reality Project organization. Available at <https://www.climateproject.org>.

Story of Stuff (2007): Starting as an acclaimed animated short, the media series *Story of Stuff*, hosted by Annie Leonard, expanded upon the roles we play as consumers and as citizens. She made the case that we are often bombarded by media and companies with the notion that we have more power as shoppers than we do as voters, teachers, parents, students, etc. By using non-identifiable stick figures, she portrayed simple actions as to how we perpetuate and can help reduce cradle to grave consumerism. Available at <https://storyofstuff.org>.

Planet Money Makes A T-Shirt (2013): A 5 part short-video services that described the extensive globalization of making a simple T-shirt and gives personal and in-depth accounts of the people who are on each step of that T-shirt’s journey to you. Available at <https://apps.npr.org/tshirt>.

A Guerilla Gardener in South Central LA (2013): Los Angeles activist Ron Finley presents a powerful and compelling message giving detailed examples of setting, action, setback and solutions for a simple action of planting gardens in blighted urban spaces. One of many effective sustainability stories presented on the TED and TEDx stage. Available at <https://www.ted.com>.

Soil Carbon Cowboys (2019): A series of short videos documenting the lives of ranchers and farmers across the south and northern great plains. Filmmaker Peter Byck of Arizona State University partners with researchers to see how large herds of cattle on open ranges store carbon back into the soil and regenerate soil health. Available at <https://carboncowboys.org>.

Anthropocene Reviewed (2019): John Green, host and writer of the popular podcast *Anthropocene Reviewed* selects two arbitrary facets of the human centered planet on each episode, reviewing them on a five-star scale. For a single person speaking on a subject for 15–20 min with no sound effects, interview subjects or music, it is an exemplar of Simmons’s vital deviations. Available at <https://www.wnycstudios.org/>.

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Creating Change for People and Planet: Education for Sustainability Approaches and Strategies

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Glossary

Education for sustainability (EfS) Education for sustainability develops the knowledge, skills, values and worldviews necessary for people to act in ways that contribute to more sustainable patterns of living. It enables individuals and communities to reflect and act on ways of interpreting and engaging with the world such that social, economic and environmental systems are not diminished for both current and future generations. This is the common form used in Australia.

Education for sustainable development (ESD) See education for sustainability above. ESD is more commonly used in Europe, and in United Nations and UNESCO policies and documents. This terminology is not widely used in Australia.

Embedding change/sustainability In contrast to ad hoc, short-term change that does not last, embedding refers to human/social/educational processes that seek to achieve broad and deep cultural change for sustainability.

Environmental education (EE) Environmental Education is a holistic, lifelong learning process directed at creating responsible citizens who explore and identify environmental issues, engage in problem solving, and take action effectively to improve the environment. Originally, its focus was on learning and teaching about and for the natural environment but is now more like EfS and ESD (below).

Sustainability (see Sustainable development) This is the commonly used term for SD in Australia.

Sustainable development (SD) Sustainable development commonly refers to human development processes that simultaneously meet human needs while also sustaining the ability of natural systems to provide the natural resources and ecosystem services upon which economy and society depend.

Sustainable Development Goals (SDGs) The 17 Sustainable Development Goals offer a blueprint for achieving a better, more sustainable future for all. They address global challenges including poverty, inequality, climate change, and environmental degradation, and how to achieve prosperity, peace and justice.

System thinking/systems change Systems thinking/systems change has emerged as the result of reductionist problem-solving approaches failing to adequately cope with the realities of complexity and uncertainty that cause a system to behave sub-optimally. Instead, it looks for links and synergies to find new ways of framing and overcoming problems, hence it is multidisciplinary and calls on a multiple of agents, relationships and power structures to contribute to a change. As a way of guiding systems change, systems thinking can address root causes of problems and issues and come up with innovative solutions that have the capacity to break through barriers and resistance.

Abstract

The concept of anthromes put humans firmly into “natural” systems. While humans have always shaped and reshaped their environments, recent history illustrates challenges, especially in Australia, this article’s focus. Against the backdrop of Australia, the article calls for effective Education for Sustainability (EfS) to address these challenges. The key role of Education in playing a significant part in the social transformations necessary is explained, along with a short history of Environmental Education (EE), Education for Sustainable Development (ESD), and Education for Sustainability (EfS), and the various international initiatives—mainly developed through the United Nations since the 1970s—that have shaped these sub-fields of Education into contemporary times. Key principals of ESD/EfS include enabling learners to see issues and solutions through the lenses of critique, particularly of our everyday ideas and practices of human development, and to develop agentic and transformative capabilities.

The article then offers an overview of a range of educational contexts—from higher education through to early childhood education—with commentary on how these sectors have responded to the challenges of embedding SD/EfS into their contexts and curricula. A case study for each context is provided to illustrate ways that EfS might be embedded into teaching and learning in order to make positive contributions towards understanding and working with biomes/bioregions for better outcomes for future generations and, indeed, for all living things.

Introduction

There is an Australian poem, “My country” by [Dorothea Mackellar \(1908\)](#), written in 1908 at 19 years of age and visiting England, while pining for Australia. The iconic second verse goes like this:

I love a sunburnt country,
A land of sweeping plains,
Of ragged mountain ranges,
Of droughts and flooding rains.
I love her far horizons,
I love her jewel-sea,
Her beauty and her terror.
The wide brown land for me!

This poem has meaning because it so aptly sums up the Australian continent with its diverse and contrasting landscapes—large inland plains and deserts cut by huge river systems, mountains that are just smallish bumps to snowcapped peaks, over 5000 km of coastline, with hundreds of islands. In this land of extremes, we have regular droughts, wild cyclones with flooding rains that bring heartache and joy in equal measure. On this land live 25 million humans, mostly hugging the coast.

Nevertheless, we need more than love for Australia. The Earth’s ecosystems on which we all depend, are under severe distress, facing unparalleled challenges brought about by disruptions to ecological, social, and economic systems. Recent reports from the Intergovernmental Panel on Climate Change ([IPCC, 2018](#)) and the World Wildlife Fund ([Grooten and Almond, 2018](#)), the Million Species Loss report, confirm that “unsustainable human activity is pushing the planet’s natural systems that support life on Earth to the edge” (2018, para 1).

[Pierrehumbert \(2006\)](#) considers climate change a “catastrophe in slow motion”; we are witnessing the effects of a 1 °C rise in global temperatures through more extreme weather events, rising sea levels and diminishing Arctic sea ice ([IPCC, 2018](#)) with global temperatures expected to rise by a further 0.5 °C to a total warming of 1.5 °C above pre-industrial levels by 2050.

Australia’s Biomes, and Landscapes Under Pressure

The consequences of global warming, especially in Australia, are grave. A temperature rise of 1.5 °C will decimate ecosystems, exacerbating social and economic disruptions and forced migration ([IPCC, 2018](#); [McLeman, 2018](#)). A recent Lancet report ([Watts et al., 2018](#)) predicts a complex and worsening array of climate change health impacts.

Climate disruptions in Australia are already sharply felt. However, it needs to be noted that there has been at least 60,000 years of continuous human settlement in Australia, so ecological change is not new, perhaps better reflecting anthromes ([Ellis and Ramanakutty, 2008](#)) vs. biomes. The first Australians, multiple tribes with distinct nations, territories, languages and cultures, have reshaped landscapes through fire and other farming methods ([Pascoe, 2014](#)) and should be recognized as the first people to reshape its ecological processes and patterns—Australia is not a land of untamed wilderness prior to white colonization. In recent times there has been growing appreciation of and respect for the knowledges, ethics and spiritualities of Indigenous peoples in Australia, who see the world differently to a Western binary between people and place. In Aboriginal and Torres Straits world views, knowledge lives in country and has agency; Indigenous people carry place within themselves; identities are bound to place. Such a fundamentally different worldview has meant very different ways of living on/with the Earth (even though we now know that Indigenous people in Australia were also agriculturists and aquaculturalists, not merely “hapless wanderers across the soil, mere hunter-gathers” (p. 229).

It cannot be disputed that white colonial “settlement/invasion” over the past 220 years has been formidable, deeply reshaping the continent, with increasingly distressing impacts at a rate of change that seems unrelenting. Here, I spell out just two of the anthropogenic challenges arising from human influence on natural ecosystems in Australia in our short 220-year history since colonization.

Sustainability and EfS

Given these challenges to our landscapes and ecosystems, serious questions arise “What is to be done”? Do we give up and leave matters in the hands of our children and grandchildren? What are our responsibilities to future generations and non-human life forms? Ignoring such questions is not an option. A starting point is how we see “development” into the future. Many are critical of the anthropocentric focus of human development especially since the industrial revolution—referred to as the Anthropocene, a proposed epoch when the human species has become dominant, having vastly reshaped the Earth on which we and all other species depend for healthy, vibrant futures. This time is precarious where children are most vulnerable to degrading social, economic and ecological conditions directly impacting their development, wellbeing and even their right to stay alive. The [UNICEF report \(2015\)](#) comments, for example, that “there may be no greater, growing threat facing the world’s children—and their children—than climate change” (p. 7). The dangers from severe weather events, increased risk of disease in unstable environments, water and food insecurities, disrupted livelihood and family displacement, as well as existing inequalities made worse where there are overlaps of high poverty with low access to essential services, become much more pronounced for children than adults.

This contrasts with Sustainability, a multidimensional concept that presents sustainability, not as environment versus people or economy, but as a mix of social, economic and environmental dimensions. Climate change, for example, impacts are environmental i.e. the adverse weather effects such as increased storms and droughts. It is social, in that people are being displaced from their homes leading to short-term disruptions and as well as longer-term effects of climate refugees. It is also economic, causing infrastructure damage and huge insurance payouts.

There are increasingly desperate appeals for radical shifts across all aspects of human development, in particular to Education, to take a more decisive role in transitions to greener, healthier and more just futures. My specific appeal is for greater understanding and implementation of EfS, a sub-field of Education, that has been around for over 40 years but needs far greater attention than is currently the case. Here, I offer a short history and discussion of EfS and its earlier iteration, environmental education. Note, in Europe and some other parts of the world, this is referred to as Education for Sustainable Development (ESD); in Australia, this field is referred to as Education for Sustainability (EfS).

What Is ESD/EfS?

While there is considerable debate about what is ESD/EfS, nevertheless, there is some consensus that.

EfS offers a vision of education that seeks to empower people to assume responsibility for creating sustainable futures. It focuses on interactions between people, and people and environments, requiring a “deep understanding of ourselves, our neighbors, or societal and cultural processes, and how we are connected with ecological systems for life” ([Lang, 2007](#)). EfS is founded on principles of both ecological and socio-political literacy that includes rich understandings of ecology, but also critical inquiry, empowerment, democratic decision making and action taking. It aims for social change that will contribute to sustainable patterns of living, across and between regions, and generations, now and in the future.

According to [Tilbury and Wortman \(2004\)](#), key characteristics of EfS include envisioning, critical thinking and reflection, systems thinking, and building partnerships in decision making. It is futures-oriented, focusing on protecting environments and creating a more ecologically and socially just world through informed action. Other characteristics include inter/transdisciplinary—holistic thinking, transformation, divergent thinking, and having a proactive attitude ([Jickling and Sterling, 2017](#)). While the concepts behind sustainability and EfS continue to evolve, it is transformative education with a focus on ecocitizenship—a concept closely linked to democracy but enriched with an ecological dimension ([Jickling and Sterling, 2017](#)).

A Chronology of ESD/Education for Sustainability

Calls for the environment to be incorporated into education agendas can be traced back to early 1970s resulting in the United Nations Educational, Scientific and Cultural Organization’s Belgrade Charter: A Framework for Environmental Education ([UNESCO, 1975](#)). The goal for environmental education (EE) was to develop:

... a world population that is aware of, and concerned about the environment and its associated problems, and which has the knowledge, skills, attitudes, motivations and commitment to work individually and collectively towards solutions to current problems, and the prevention of new ones (p. 3).

In 1977, UNESCO, together with the United Nations Environment Programme (UNESCO-UNEP, 1977), expanded this definition through the Tbilisi Declaration in recognizing the importance of systems and attention to context as necessary components of EE. The emphasis was on EE being embedded across the whole system of education and adopting a holistic approach to examining social and economic issues through an environmental lens. This Declaration called for environmental educators to be the “priority of priorities”.

Later, the United Nations (UN) World Commission on Environment and Development (UN WCED, 1987) prepared The Brundtland Report (also referred to as Our Common Future) proposing the concept of Sustainable Development (SD). Thus, environmental educators began exploring the implications of this for their education practice. Consequently, there was a shift from a focus on the environment to that of sustainable development.

The United Nations later delivered its action plan for SD, Agenda 21 (United Nations, 1992), further emphasizing a key role for education, awareness and training in sustainable development. Chapter 36 was a specific call for educators to reorient education towards SD, not as an add-on but as a fundamental shift in the purposes and practices of Education.

The next significant development was the UN Decade of Education for Sustainable Development (UN DESD), 2005 to 2014, another effort by UNESCO to encourage EFS in the face of worsening global crises (UNESCO, 2017a). The purpose of the DESD was to further integrate the principles, values and practices of SD into all aspects of education and learning. In Australia, for example, the Sustainable Schools movement was initiated via the DESD to enable and coordinate education initiatives, from early childhood education through to universities, colleges and community education, to scale up their EFS participation.

The most recent global initiative for ESD/Efs is the Global Action Programme (GAP) on ESD, part of a wider UNESCO education agenda to 2030. The GAP’s broad aim is to continue to generate attention and action for ESD across all levels and areas of education (UNESCO, 2018) with ongoing focus on reorienting education and learning to effectively contribute to SD. Action areas include the integration of sustainability into education/training environments using whole-institution approaches and increasing the capacity of educators/trainers. UNESCO’s 2030 agenda also includes 17 interconnected Sustainable Development Goals (SDGs) aimed at securing “a sustainable, peaceful, prosperous and equitable life on Earth for everyone now and into the future” (UNESCO, 2017b, p. 6). Particularly pertinent to educators is Goal 4: Ensure inclusive and equitable education and promote life-long learning opportunities for all.

While progress towards Goal 4 is yet undetermined, it is clear that the program between now and 2030 reconfirms education and educators having a key role in the realization of sustainability (Ferreira et al., 2019). Clearly, Education is seen as a catalyst for change towards the 17 SDGs. As the current Director-General of UNESCO, Irina Bokova, states “Education is key to the global integrated framework of sustainable development goals. Education is at the heart of our efforts both to adapt to change and to transform the world within which we live” (UNESCO, 2015, p. 3). However, this does not mean that educators are wholly responsible for such educational transformation—this all sectors of society must work with educators to reshape and reframe education so that it can fulfill its goal of contributing to sustainable futures.

ESD/Efs Across the Globe

While there has been significant support for ESD/Efs over the decades at the international level through UN/UNESCO initiatives, it is up to individual nations to develop their own responses to environmental/sustainability challenges. How it is implemented in Australia, for example, will be very different from how it looks in China, or in Papua New Guinea, an economically-impooverished nation struggling to emerge from its colonial past. How it is implemented in Japan or Korea where there are different historical and cultural frames for understanding relationships between people and nature—through non-Christian lenses—or how Indigenous ways of understanding human-nature relationships and how these might impact sustainability practices might be enacted, are all aspects of the considerations of Efs in different locale.

Some countries, like Sweden have whole-of-education systems approaches to Efs curriculum and have done so for a long time. Korea has come more recently to EE/Efs/ESD and invested in “green education” across the education spectrum. Australia has had a patchy policy response to Efs—sometimes a leader; sometimes a laggard. Without strong policy impetus, the fortunes of Efs wax and wane within Australian education. Nevertheless, there is a robust practitioner base in the different educational contexts, strong professional associations and networks, and Australian educators are international leaders in Efs researching, theorizing, and publishing, involved in and influencing local and the international efforts. In the next sections, I overview key features of Efs across education sectors, drawing on international and Australian research, and offering some Australian responses.

Efs in Universities

Graduates entering and leaving universities and colleges, even as little as 10 years ago, are moving into a world very different from that encountered by previous generations. Sterling (2014) comments that the future is uncertain, complex and rapidly change manifested by a bewildering array of global issues relating to economic instability, climate change, inequality, loss of biodiversity and migration being just some of the critical changes. While there is acknowledgment of the urgency for learning and teaching about sustainability within universities because of the relevance to students’ future lives, the general consensus is that Efs is far from being

wholly integrated into mainstream university curricula (Ferreira et al., 2019). Although there have been achievements regarding “greening” initiatives such as improving campus transportation, reducing waste, energy and water usage, and cutting-edge “green buildings”, as well as developing sustainability-based research profiles and capabilities, there is a disappointing focus on transforming teaching and learning. I argue that such efforts, while important, fail to harness the essential power of higher education: to inform and engage citizens in the pursuit of more sustainable modes of living.

EfS should be at the heart of higher education’s approach to the “wicked problems” of sustainability (Sterling, 2014; Leal Filho et al., 2017) and must be embedded into every facet of a university’s operations including changes in planning and policy, academic curricula, and research that facilitates environmental and social changes and must be embedded into every discipline area—Law, Engineering, Architecture, Business, Health and, importantly, Education. There is a long way to go before higher education makes the most of its [implied] mandate to educate for societal transformation and displays the leadership in EfS it should be offering. Nevertheless, there are exemplars in higher education leadership as the following case study illustrates.

Case Study: Australasian Campuses Toward Sustainability (ACTS)

ACTS is an Australian and New Zealand higher education organization that “aims to inspire, promote and support change towards best practice sustainability across all types of campuses”. It does this by “building cross-sector partnerships, bringing together sustainability educators, practitioners and change-makers to create a community for positive engagement, capacity building and impact” (<https://www.acts.asn.au/about-us/>). ACTS is focused on supporting higher education campuses to achieve the Sustainable Development Goals (SDGs) through teaching, research and operational practices. A key tenet of ACTS is recognition that education plays a critical role in delivering the global goals by providing “the knowledge, innovations and solutions to address the complex and interconnected societal and environmental challenges that lie behind the SDGs”. It does this via activities including online forums that provide a space for members to share and discuss approaches, challenges and learnings about SDG implementation. It runs annual conferences and the annual Green Gown Awards, an offshoot of the International Green Gown Awards, that cover all aspects of campus life—teaching and research, leadership, facilities and services, to how students can benefit from the quality of life in the communities around them. In July 2019, ACTS joined leading global networks and institutions in Higher Education in declaring a Climate Emergency in recognition of the need for drastic societal shifts to combat the growing threat of climate change.

EfS in Teacher Education—“The Priority of Priorities”

As noted, embedding EE into the teacher education was first identified as critical at the 1971 IUCN Conference on Environmental Conservation Education, and has been reinforced ever since. In Tbilisi in 1977, Education Ministers from around the world identified initial and in-service teacher education in EE as a priority (UNESCO-UNEP, 1977). In 1990, UNESCO-UNEP declared teacher preparation to teach environmental and sustainability education as the “the priority of priorities” (UNESCO-UNEP, 1990, p. 1).

Other important initiatives for teacher education include the UNESCO Chair on Reorienting Teacher Education for Sustainable Development, the UN DESD, and the GAP. UNESCO has supported the integration of ESD/EfS in initial teacher education through Priority Action Area 3: Building capacities of educators and trainers (UNESCO, 2017b). Continuing support by Ministers of Education highlights the important role teacher educators have as powerful agents of change, capable of delivering the global educational response needed to reorient education to achieve the SDGs (United Nations Educational, Scientific and Cultural Organization (UNESCO), 2018).

While the extent to which this recent work has progressed is uncertain, and while UNESCO’s recent reporting highlights many examples of embedding ESD/EfS in teacher education, these tend to be isolated “green patches” driven mostly by the passions and concerns of individual teacher educators who experiment with embedding EfS within their own spheres of influence, rather than wide-scale, systematic approaches (Ferreira et al., 2019). A recent review conducted by Australian researchers (Evans et al., 2017) confirms that the field is characterized by arbitrary, isolated activities such as one-off curriculum development projects, stand-alone EfS modules (UNESCO, 2017a), or mainly integrated into Science and Geography subjects (Van Petegem et al., 2005) rather than through a consistent, more holistic approach (Ferreira et al., 2006). While such efforts are commendable, a systemic approach to embedding sustainability in initial teacher education is called for actioned by EfS becoming an integral part of faculty/departmental policies, core curriculum foci and values, and clearly evident in everyday pedagogies, practices and activities. The following case study offers just one example of how EfS might be embedded into a teacher education program.

Case Study (for More Detail See Ferreira et al., 2019)

EfS has been a part of teacher education at this Australian university situated in tropical Queensland, for about 20 years, though originally as an ad hoc, final-year elective, Environmental Education for the Tropics. Transition to an embedding of sustainability approach began when the whole university underwent a “Curriculum Refresh” initiative, 2009 to 2011, aimed at repositioning itself as a “University of the Tropics” with explicit interest in sustainability, climate change and a focus on impacts on the Great Barrier Reef, literally this university’s backyard. A central aim of Curriculum Refresh was for the university to become a national and

international leader in addressing the critical challenges confronting the tropics. The University employed an integrated approach to improving environmental, cultural, economic and social sustainability via teaching, research, operations and campus management, and community partnerships.

As part of the process, the School of Education adopted a whole-of-school approach to embedding Education for Sustainability (EfS) into its Bachelor of Education (B.Ed). Recognition of sustainability as a cross-curriculum priority in the then newly-developed Australian national school curriculum, helped support this. In addition to revising the original elective, Curriculum Refresh saw two new core sustainability subjects developed as teacher education academics collaborated to embed sustainability concepts, principles, and issues, across courses in early childhood and primary majors. In 2011, at the completion of Curriculum Refresh, there were around 1250 students enrolled in the B. Ed. across two campuses, and in various modes—on campus and off campus/online.

Subsequently, with participation in a nationally-funded Embedding Sustainability in Teacher Education Project commenced in 2009, Education staff further clarified EfS as core. This expanded efforts beyond curriculum development to also be an action research project to document, monitor and study individual and collective efforts in embedding sustainability concepts and values across all Bachelor of Education classes. This led to an integrated EfS-embedded program aimed at providing teaching graduates with understandings of sustainability principles and issues and to confidently and competently engage their future students in sustainability learning.

EfS in School Curriculum

Parallel to what has happened in teacher education around the world, sustainability is also recognized in many school curricula (Buckler and Creech, 2014). For example, it is a requirement in Norway and Sweden that sustainable development be incorporated into education curricula at all levels of schooling as well as in teacher education. In China, the 15th National Congress of the Chinese Communist Party advanced sustainable development as a national strategy with ESD incorporated into China's macro-education policy agenda. China has also explored ESD/EfS practice for more than 10 years including uptake of its Green Schools program. This mirrors the history of such whole-school approaches to EE/ESD/EfS that go back to the 1970s, such as Green Schools, Eco-Schools, and Enviroschools with such movements gaining impetus with the UN Decade of ESD.

In Australia, Sustainability is a cross-curriculum priority (ACARA) and seeks to address the ongoing capacity of Earth to maintain all life. It is recognized that all learning areas such as English, Science, The Arts, Health, and Humanities, have the potential to contribute to the Sustainability priority. As such, Sustainability is included in each learning area in ways consistent with the content and purpose of the study area. Nevertheless, despite this national "mandate", Sustainability is patchily embedded into teaching and learning in schools in Australia. The demise of the national Sustainable Schools initiative, Australia's response to the UNDESD, with loss of personnel, funding and policy push, has meant that contributions to sustainability have been less than satisfactory, though there are some excellent lighthouse schools and committed teachers continuing this good work.

Case Study: The Murray-Darling River Basin and AuSSI-SA

The climate range across the Murray-Darling Basin (MDB) reflects its size, 14% of Australia's land area, and its diverse geography—from rugged mountains to flat semi-arid plains. The Basin is in the south-east of Australia and includes the Australian Capital Territory, parts of Queensland (15%), New South Wales (75%), Victoria (60%) and South Australia (7%). As Australia's most important agricultural region, it produces one third of Australia's food supply and supports over a third of the country's total gross value of agricultural production. Irrigation is the largest user of water from the River Murray system.

Water use is controlled by the MDB Authority with the aim of balancing diverse and multiple demands for water including agriculture, water supply to towns, and ensuring environmental flows for ecosystem services. Little or no flow in the Darling River due to drought and overuse of water has led to fresh water levels falling drastically. In December 2018 and January 2019, massive fish kills occurred in an area called the Menindee lakes where over 1,000,000 fish died. Species affected were predominantly bony herring, but included hundreds of golden and silver perch, as well as dozens of Murray cod, mostly large adults. The largest was 127 cm long.

Towns and cities in South Australia are at the tail end of the problems of the Murray-Darling River system, a source of great contention with severe impacts on water supply and water quality over decades, for drinking, farming and industry in this state.

Supported by the State Education Department and Department of Natural Resources Management (NRM), the South Australian Sustainable School Initiative (AuSSI-SA) provides a framework for schools and preschools to develop a culture of sustainability with their communities, with a focus on water issues. Underpinned by the principles of Education for Sustainability (EfS) discussed earlier, learning for change and developing the knowledge, values and skills needed for leading sustainable lives—over 350 schools and preschools are members of AuSSI-SA. Educational settings sign up and are then supported to plan and manage sustainability initiatives. They are offered technical advice and tailored training sessions for teachers on topics ranging from engaging with nature, food gardens for a dry climate, climate change, air quality, waste and energy matters, mentoring and support for student environment groups, and help in developing site environment management plans, setting sustainability goals and working effectively with the local community.

EfS in Early Childhood Education

As noted, the history of EE/ESD/EfS dates back to the 1970s. However, early education (Birth to the early years of school) efforts were largely missing (Davis and Elliott, 2003) though this is rapidly changing. In Australia, aligned with the more visible school-based initiatives such as the UNDES and Sustainable Schools, a handful of pioneering practitioners and a number of state-based professional networks were established to fill the void and have pushed for recognition and advocacy for ECEfS with the mantra “mainstream not marginal”. Additionally, Australian government early childhood education policy directives launched from 2008 and set against the backdrop of UN DESD initiatives have been instrumental in guiding systemic change across the early childhood education field in relation to EfS. In particular, the national early childhood curriculum guidelines (EYLF) (ACECQA, 2009) emphasizes that “children become socially responsible and show respect for the environment” (p. 32) and that educators “embed sustainability in daily routines and practices” (p. 32).

Internationally, ECEfS was first highlighted by Pramling Samuelsson and Kaga, 2008 in *The Contribution of Early Childhood Education to a Sustainable Society* (2008), and *The Gothenburg Recommendations on Education for Sustainable Development* (2008). This latter noted that “early childhood is a natural starting point for Education for SD” (p. 7) and that young children are both “affected by, and capable of, engaging with complex environmental and social issues” (p. 7). The UN Decade of Education for Sustainable Development (UN DESD 2005–2014) (UNESCO, 2017a) final report further reinforced the unique role of early childhood education in creating sustainable futures for all and outlined the expanding uptake of ECEfS across the globe over the past 15 years or so.

As a result of such state, national and international initiatives, in Australia today, ECEfS is readily visible in programs in childcare services, kindergartens, and preschools. Further, there is renewed focus on outdoor play and nature education that have been an integral part of ECE for well over 150 years. Movements such as Nature Play Australia, and growing interest in forest schools/preschools and their Australian iterations known as bush kindies/beach preschools (see for example, <http://bushkindyexplorers.com.au>) are expanding rapidly. However, while such environmental learning opportunities are to be applauded, I and others assert (and have written elsewhere) that children playing in nature is not enough to combat the unsustainable ideas and practices that reinforce unsustainability. This requires much more ambitious forms of early education. Accordingly, there are a number of ECE services that embrace whole-of-center sustainability and where children’s activist learning for sustainability lies at the heart of the curriculum.

In tandem with Sustainability in the curriculum guidelines for schools and ECE in Australia, another significant impetus for EfS lies with efforts supporting Indigenous Reconciliation and Embedding Indigenous Perspectives into curriculum. Currently EfS and Embedding Indigenous Perspectives have run in parallel rather than being enmeshed; however, this split is changing as both fields begin to appreciate their commonalities. The case study below exemplifies this emerging synergy.

Case Study (See Zerella & Thorpe, 2019 for Further Details)

An example of an ECE service bringing EfS and Indigenous education together is the Bubup Wilam Aboriginal Child and Family Centre in Victoria catering for the education, health and wellbeing of Aboriginal children aged 6 months to 6 years and their families. Here, I have drawn from the center’s website and information provided in a recent “Every Child” article. The Centre’s purpose and philosophy was developed by the local Aboriginal community, for Aboriginal people. Underpinned by Aboriginal, social justice and rights-based pedagogies, the center aims to support children to build strong and proud Aboriginal identities as their foundation for life-long learning, health and wellbeing.

With inequities in health, wellbeing and educational outcomes for Aboriginal people in Australia, Bubup Wilam requires a holistic pedagogical approach, underpinned by Aboriginal perspectives. The Centre recognizes Aboriginal people as the first owners of the land on which they live and learn, and acknowledges and pays respect to the rich history and spiritual connection of their Aboriginal ancestors. In particular, the community recognizes the importance of ongoing learning by respecting the knowledge of Aboriginal people in caring for country for over 1,000,000 years. Likewise, the community acknowledges and mourns the impact of colonization, past and present, on the destruction of the landscapes of the country and the spiritual and sacred sites of Aboriginal peoples.

Of central importance, the center is committed to supporting children in developing skills and knowledge to fight for a more sustainable and respectful future for themselves and future generations, in addressing the environmental challenges and destruction of their land and acknowledges the importance of the children’s voices in fighting for these rights. This unique “connection to country” program supports children’s spiritual connection to their world and respects the interdependence between human, animal and nature. It challenges the children to critically reflect on their custodianship rights and responsibilities. In summary, the center embraces a custodian approach to Sustainability through an Aboriginal lens, underpinned by a pedagogical that challenges Western educational theories and pedagogical approaches, and is in harmony with Indigenous beliefs and practices, and contemporary aspirations.

Conclusion

Humans have a very long history of transforming landscapes and ecosystems. Indeed, we could not have developed without reshaping and exploiting natural elements. Nevertheless, the pace of change and the extent of human impacts on the Earth’s biospheres are unmistakable (Ellis and Ramankutty, 2008) and becoming dangerous. It could be said that humans are “doing

violence” to our Earth. Our current climate emergency, the potential of 1,000,000 species to become extinct, the escalation of environmental refugees, the marginalization of first Nations peoples, and the anticipated mounting negative impacts on children and young people into the future, are nothing short of unconscionable.

While these realities are a result of many factors, education systems are not without blame; Education has contributed to our human failures in delivering societies that are healthy, sustainable, and just for our children and future generations. However, the rise of movements such as “School Strikes for Climate Change” led by Greta Thunberg from Sweden, gives some optimism. Young people are taking action, but what have we come to when it’s our school children who are calling us out? Also, I brightened up recently when I realized that many of these young people have had 15 or more years of education for sustainability, from early childhood through to high school, so perhaps our educational efforts have been more effective than I have been thinking.

Another reason for hope in the Australian context, is that polling conducted in March just prior to the national election in May 2019, shows that Australians see climate change as one of Australia’s most pressing issues (Slezak, 8 May 2019), confirming that Australians were more concerned about climate change at this recent election than at any time since 2007; 61% of voters said climate change was so serious that it should be addressed now. However, responses to the climate change question showed stark generational differences. Among Australians aged 18 to 29, 81% thought Australia should take action on climate change, even if it was expensive. Less than half, 49% of those aged over 45 took the same view. Perhaps, then, the impact of EfS over the past 20–30 years, even if patchy, has had a positive effect. Most of the elderly voters did not have the benefit of EfS.

To conclude, while EfS still has a long way to go before it is universal across the globe, it is making inroads, despite political equivocation and, in some cases, overt political undermining. However, EfS cannot be left to those who are officially recognized as teachers or educators through their qualifications. All of society needs to contribute to EfS—ecologists, botanists, social scientists, artists, technologists, journalists and media in all its forms, medical and health workers, public servants and politicians, children, young people, parents, grandparents and civil society. Particularly those of us living comfortably in richer economies, who have benefited from the practices of exploitative economic growth—be it through cheap clothes made with slave or child labor, exporting e-waste to Vietnam, habitat destruction in the Amazon to supply beef for our middleclass dining tables, or through our everyday contributions to global climate change, we are all in this complex of Anthropocentric-generated emergencies together. Essentially, sustainability is a social justice issue, and EfS is a remedy to such injustices.

Time is fast running out, however, to fix the disrupted biosystems that are our legacy to our children. If we want biomes like the Great Barrier Reef and the mighty waters of the Murray-Darling River, to be viable for all life—human as well as non-human species—for our children, grandchildren and into the next millennium, then EfS must, finally, become “the priority of priorities”. Further, we need to listen to the “the wisdom of our Elders”—our First Nations peoples across the globe who have cared for and been a part of the Earth’s biosystems for thousands of years. We all need to be educators for sustainability in whatever communities we inhabit.

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Training Wildlife Biologists for Work in Anthromes

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Glossary

Anthroscape A human-modified landscape with substantial and permanent alterations associated with management for habitation, commerce, food or fiber production, recreation, or other human activities.

Incentive A payment or concession to stimulate greater output or investment.

Private lands Land under freehold or leasehold by individuals, not including native communal lands, and used for agricultural (subsistence or commercial), industrial, commercial or other income generating purposes.

Role-play A learning exercise designed to promote empathy and understanding of alternate views in which participants act out or perform the part of a person or character.

Wildlife Vertebrate, nondomestic animals.

Wildlife management A human decision and action that affects a wildlife population.

Abstract

Land use and conversion to meet the food and energy demands of an increasing human population is a pervasive threat to global biomes. On private lands, landowners hold the reigns when making decisions about land management. Because private lands supports biodiversity, such decisions have broad implications for biodiversity conservation. However, educational programs training wildlife biologists largely focus on public land management mirroring the public-land focused conservation movement begun in the 20th century in the United States. Wildlife management on private lands has a unique set of challenges, relative to management of public lands. Wildlife biologists working on private lands work in dynamic landscapes with uses that shift with changes in economics, regulatory regimes, and societal and cultural values. Loss of biodiversity in anthromes can be lessened if wildlife and associated habitats are managed appropriately. Yet, despite the importance of private lands for biodiversity, wildlife biologists are often ill equipped to work in these challenging landscapes. To improve preparation of wildlife biologists, we provide a case study of a modification to the learning objectives for a fisheries and wildlife degree program at the university level. Our suggestions are designed to enhance efforts to train wildlife biologists who are ready to work in the arena of private lands. Innovative, effective conservation efforts on private lands have the potential to maintain biodiversity, enhance landscape protection efforts near public lands, and create economic resilience for conservation efforts.

Private Land Conservation in Global Biomes

The wildlife conservation profession began in the United States (U.S.) during the 1900s as a movement to establish laws to protect game species and to develop a series of publicly owned wildlife refuges, parks and forests. Wildlife management has now evolved to include conservation of wildlife and their habitats found on privately owned lands. Here, we define private lands as land under freehold or leasehold by individuals, not including native communal lands (Swift et al., 2003), and used for agricultural (subsistence or commercial), industrial, commercial or other income generating purposes. Because the majority of the arable, inhabitable, usable land in the U.S. is privately owned (approximately 75%, excluding Alaska; Natural Resource Conservation Service, 2001), private lands form an integral component of the conservation landscape in the U.S. At the global scale, private lands

are likely critical for the conservation of wildlife, especially in countries where they constitute a large proportion of the landscape (Powell, 2012).

Certainly, across many parts of the world at-risk species are primarily found on private lands. For example, approximately 75% of the cheetah's (*Acinonyx jubatus*) current global range falls on lands controlled by private individuals or communal/tribal groups (Powell et al., 2017). Similarly, approximately 85% of species listed under the U.S. Endangered Species Act (ESA) spend at least part of their annual lifecycle on private lands (General Accounting Office, 1995). Therefore, it is inevitable and critical that wildlife biologists work on privately owned lands to support conservation planning and implementation. To this end, nongovernmental organizations (NGOs) and government agencies across the world have devoted many positions and money to encourage the management of private lands (MacGowan et al., 2001; Pasquini et al., 2011; U.S. Fish and Wildlife Service, 2014).

Worldwide, management frameworks to incentivize or regulate conservation on private lands vary (Powell, 2012; Kamal et al., 2015). In the U.S., the management of privately owned lands has a unique set of challenges, relative to the management of public lands that are managed in accordance with the public trust doctrine (Ciuzio et al., 2013; Drescher and Brenner, 2018). First, management decisions on private lands are made by a landowner who has invested in the land as means to a livelihood. Therefore, the use of private lands is heavily influenced by commodity prices (e.g., forest products, livestock, crops), and conservation options often lose out to other land use options that provide better economic benefits. In contrast, land use on public land is under the control of government agencies (e.g., Bureau of Land Management [BLM]). Although their decisions are partly driven by state or federal budget constraints, public land managers respond to the mission of the agency that shapes the manner of conservation actions. Therefore, conservation is often the objective on public lands, while profit from investment is often the objective for private landowners. Second, wildlife biologists who engage with private landowners have a very different paradigm for communication than do those who work with public land management teams within a state or federal agency. Third, when species or habitats of concern are found on private lands, wildlife biologists may face problems with access and coordination within the landscape of interest. Landowners may legitimately exercise their private property rights to deny or restrict access, and landowners may opt not to participate in landscape-level conservation planning. In contrast, state and federal agencies often hold access rights to large parcels of public land.

Wildlife biologists in the U.S., and indeed globally, are increasingly required to work in these complex landscapes where culture, society, politics and economics often provide the context for management decisions. Wildlife biologists may operate in supporting roles; they must work in concert with landowners who ultimately make the decision to participate in conservation programs. Given the challenges found in the private lands arena, there is a need to train students and current professionals explicitly to protect and manage the biodiversity on privately owned lands (Norton, 2000; Powell, 2010). Wildlife biologists working in privately owned landscapes need to have training which blends a suite of topics into a set of strategy and decision making skills (Knight, 1999). However, previous assessments of our profession have suggested that academic training programs in wildlife biology often fail to integrate the management techniques, policy, economics, human dimensions, problem solving and communication skills required by wildlife biologists working on private lands (Bleich and Oehler Sr., 2000; Niesenbaum and Lewis, 2003; Newing, 2010). Indeed, in an assessment of nine textbooks for wildlife management published between 1984 and 2013, we found that only three (33%) had explicit sections dedicated to discussions of private land management. Six of the textbooks (67%) provided content on legislation and policy that might affect conservation efforts on private lands, and only five (56%) contained information on economics (e.g., incentive programs or economic value of wildlife). As a result, wildlife biologists may not be adequately trained to work on private lands during the formative stages of their careers.

How might we support the efforts of universities to incorporate learning objectives to bolster training for students who will work as wildlife biologists in private lands? Here, we use selected learning objectives for the Fisheries and Wildlife degree program at the University of Nebraska-Lincoln, Nebraska, U.S. as a case example. We selected this university and program because we contribute to the curriculum committee for the program, and private lands compose 98% of the state of Nebraska (Powell, 2012). In Nebraska the NGO, Pheasants Forever and the state wildlife agency, Nebraska Game and Parks Commission (NGPC), have developed an active partnership to sponsor wildlife biologists working on private lands to assist landowners. In addition, NGPC and the U.S. Fish and Wildlife Service (USFWS) have strong in-house private lands divisions in Nebraska. Despite the private lands emphasis for wildlife management in Nebraska, we demonstrate that the local Fisheries and Wildlife program's learning objectives suffer from the historical bias toward public lands management in the wildlife management profession. We identify the training needs of wildlife biologists working in private landscapes and suggest ways that the University of Nebraska-Lincoln can modify their learning objectives to meet the requirements of private lands biologists (Table 1). In so doing, we provide a case study that can be used to improve or develop existing and future curricula aimed at training wildlife biologists for working on private lands in anthromes (Ellis et al., 2010) or the anthroscape.

What Training Do Wildlife Biologists Need?

Economics and Business

It is true that the conservation profession tends to shy away from the biases inherent in economic decision-making (Soulé, 2013), but we believe that addressing such situational decisions will largely determine the health of our planet in the future. We also know that participation in conservation efforts is strongly influenced by economic tradeoffs (Esseks and Kraft, 1986; Secchi et al., 2008). Thus, wildlife biologists must find ways to work with landowners who manage forestry, livestock, and crop production ventures if conservation on private lands is to be successful.

Table 1 Case examples of modifications that could be made to existing learning objectives for the Fisheries and Wildlife academic program at the University of Nebraska–Lincoln to provide explicit focus on learning experiences related to private lands. Current learning objectives exemplify an historic bias toward professional development for work on public lands.

<i>Area of focus</i>	<i>Current learning objectives</i>	<i>Learning objectives for private lands</i>
Economics and business	• Use mathematical concepts to represent the dynamics of socio–economic data	• Produce a business plan to financially support the conservation of biodiversity on a private forest, ranch, or farm
Human dimensions	• Describe the impact of humans as stewards, managers, and components of natural resource systems	• Describe influences on the values and actions of individuals with regard to conservation of fisheries and wildlife • Propose strategies to address conflicts between private landowners and a resource agency
Entrepreneurship and policy	• Describe the basic requirements of the National Environmental Planning Act • Differentiate the mission and management approaches of the major federal natural resources agencies	• Describe the basic requirements of programs within the current Farm Bill • Contrast approaches to management taken by a state agency, an NGO, and a private landowner who have similar conservation goals • Describe private market incentives for conservation that can be used by private landowners in the US, and compare them to incentives available around the world • Describe the process of developing, implementing and maintaining a conservation easement
Communication	• Give an organized and professional oral presentation that uses appropriate visual aids	• Propose an agenda for a public meeting of a state agency • Develop a script to be used for phone calls to obtain research access to private lands • Produce a pamphlet, radio–message, social media message, or video that summarizes results of research that can be applied on a private forest, farm, or ranch

Private landowners commonly have business plans and strategies for their lands, because their land use ventures typically represent a substantial economic investment. Thus, conservation plans for private lands cannot be developed without consideration of existing business plans, and wildlife biologists must address economic trade–offs in strategies and options. To integrate conservation options into a business plan successfully, it is fundamental that wildlife biologists understand the goals and objectives of the landowner including those associated with production, operations, and marketing, in addition to conservation. They need to be facile with the economic costs and benefits not only of conservation options, but also of all land use options if they are to succeed. This includes having an understanding of federal and state conservation programs that offer direct monetary payments and/or tax incentives and of other business expenses that may influence the willingness of a landowner to include conservation options (e.g., tax incentives for farm expenses, operation costs). Courses should provide opportunities for wildlife biology students to work with students and faculty from business, political science, economics, and marketing departments to construct business plans for private landowners that incorporate conservation options using ‘real–life’ case studies (Table 1). By interacting with private landowners whose livelihoods depend on the land (Fig. 1), wildlife biology students will better appreciate the relevance and importance of their decisions, and gain insight into the skills needed to persuade landowners effectively that conservation can provide economic benefits.

Human Dimensions

In an environment where private landowners are the decision makers, wildlife biologists must be aware of landowner values and behaviors that influence conservation decisions (Kabii and Horwitz, 2006; Selinske et al., 2015) (Fig. 2). They must also appreciate landowner attitudes and opinions that lead to conflicts that interfere with conservation efforts. Landowner attitudes toward wildlife may hinder conservation efforts when wildlife is perceived as a threat (e.g., large carnivores; Davenport et al., 2010), or may encourage conservation when the presence of wildlife may benefit the landowner (e.g., hunting, wildlife viewing; Sims–Castley et al., 2005). Wildlife biologists working with private landowners must also consider social norms in situations in which private landowners value the opinions of their neighbors and friends (Sorice et al., 2011). By understanding opinions and values of private landowners, wildlife biologists can work efficiently and effectively to achieve conservation goals.

We urge universities to include exposure to conflict resolution through challenging role plays based on real–life scenarios. Although university courses that introduce the role of human dimensions in conservation are important, they are no substitution for on–the–ground training. Of specific value would be internship programs with agencies or NGOs that provide opportunities for students to interact with a range of landowners who have different values and intentions; such experiences are fundamental to the success of emerging wildlife biologists destined to work in the anthroscape and across anthromes.



Fig. 1 Interactions between students and private landowners can improve understanding and forge working relationships, such as this conversation between a researcher and a private cattle producer in the Nebraska Sandhills region, USA. Photo by Alan J. Bartels/Nebraska Life Magazine, used with permission.



Fig. 2 U.S. Fish and Wildlife Service Private Lands biologist Nick George talks to a private landowner in a forest about potential restoration efforts. Photo by Mike Budd/USFWS, public domain: USFWS government agency, <https://www.fws.gov/midwest/InsideR3/April18Story5.htm>.

Entrepreneurship and Policy

Successful conservation on private lands requires an understanding of the role of conservation tools such as easements and financial incentives that may be pivotal in protecting wildlife and their habitats. Farm subsidy programs, mitigation techniques, and tax-incentives aimed at individual landowners have been used effectively as incentives to encourage conservation on

private lands (Norton, 2000; Feng et al., 2013; Smith et al., 2018). By combining incentives with education, even more controversial conservation techniques such as prescribed burning can be encouraged (Edwards et al., 2014). Yet, these tools sometimes fail because economic realities (e.g., prices of commodities) force private landowners to opt out of incentive based conservation programs. Therefore, wildlife biologists working in private lands need to diversify their methodology and use other tools (Powell, 2012). Appropriate tools may include incentives provided to the community as a whole that encourage community-level involvement in natural resource management decisions (Bajracharya et al., 2005; Nelson et al., 2010). Landowners can also be encouraged to manage their land to maximize biodiversity and wildlife viewing opportunities in return for economic benefits derived from ecotourism (Stem et al., 2003; Sims-Castley et al., 2005). Similarly, agroforestry schemes that combine agriculture and forestry to create an integrated and sustainable land-use system for the benefit of both landowners and wildlife can be promoted (Bentrup, 2014). Not only do multipurpose systems provide resources for humans (e.g., food, fiber, and energy), but they also provide habitat for wildlife. An understanding of these tools and examples of how they can be implemented through the use of case studies are critical to include in training wildlife biologists destined to operate on private lands (Table 1).

Communication

Perhaps most importantly, students destined for careers as wildlife biologists on private lands must be able to communicate effectively and build solid relationships with a diverse range of private landowners with different needs and values (James, 2002; Jacobson, 2009). Wildlife professionals need working relationships that are based on honesty and trust, especially in situations where landowners feel over-regulated and are concerned that their livelihoods are threatened by bureaucracy. Ultimately, failure to communicate effectively and work cooperatively with private landowners will hinder conservation.

Through effective communication, conservation-based education and outreach, including personal conversations, classroom based teaching, and regional dissemination of information through media (e.g., television, newspapers) can be used to inform, encourage and stress the importance of conservation to private landowners (Horwich, 1990; Lemke et al., 2010). These tools have proven successful in the hands of wildlife biologists working on private lands worldwide, but the applications are site-specific, and each requires knowledge of basic strategies and planning.

We believe that universities are doing a good job at providing opportunities for wildlife biology students to develop basic oral communication skills. However, seldom do they provide opportunities for students to participate in practical communications with landowners and wildlife professionals. We echo the call of Powell et al. (2009) for agencies and NGOs to work with universities to develop training programs for the next generation of wildlife biologists. Students should have an opportunity to interact with landowners during their training (Table 1).

Many of the skills needed for effective education and outreach can be gained through communication courses. However, of additional value would be a course in which students produce outreach materials based on land management practices that promote biodiversity such as rotational grazing or prescribed fire use (Table 1). Opportunities to disseminate materials and receive feedback would allow students to gain firsthand experience with working with private landowners.

Conclusions

Training programs for wildlife biologists should directly address dynamics of private lands in the anthroscape for conservation success across biomes of the world. However, we do not advocate widespread curriculum revision with new courses. The tools for private lands conservation can be taught through modifications to current curriculum, short-courses, continuing education credits, certificate programs, internships, externships, and involvement of government agency and NGO personnel in the classroom.

Wildlife biologists who work on private lands are faced with a seemingly impossible task. The trend of land use changes on private lands and the associated threats to biodiversity will only increase in the future as the human population grows. Underlying economic and political conditions may force increased use of private lands for food production, energy acquisition, industrial output, and human habitation. We can predict that conservation will lose in many of these scenarios, unfortunately. We believe that the basic ingredients for the solution to the problem lies within the private lands landscape; the loss of biodiversity can be lessened if wildlife biologists are better equipped to work in this changing, challenging landscape. Effective conservation efforts on private, working lands have the potential to maintain biodiversity, enhance landscapes surrounding public lands, and create economic sustainability of conservation efforts (Norton, 2000; Powell, 2012). Universities must continue to adapt curricula to provide directed training to students who plan to join the growing ranks of wildlife professionals working in private lands.

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The Future of Conservation in Anthromes: Narrative Analysis From a Millennial Conservationist

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Abstract

Younger generations will face known and unknown challenges in a complex, changing world. Frameworks like anthromes and coupled human and natural systems have helped refocus conservation issues in a way that makes space for human contributions. Young conservationists may find success with not only ecological tools and training, but also with interpersonal and relational skills, such as effective communication. Combining personal narrative inquiry with a literature review, I propose that a promising future in conservation practice involves adaptability (individually and as a field), diversity, and localized grassroots efforts. In particular, I describe: exercising flexibility in where we work (e.g., a focus on populated anthromes and multifunctional landscapes) as well as what a conservationist may look like, considering how different types of skills can contribute to more innovative problem-solving, and considering the role of values and experiences in shaping conservation behaviors and engaging non-scientific audiences.

What does the future of conservation look like? Conservation has deep roots in principles and theory, but is dynamic and innovative. Our world is constantly changing. Our science must shift and keep pace so our actions are based on current understanding. It can take careful scrutiny to recognize we are in the middle of a transition. We develop new methodologies at such a quick rate that it can seem like we barely finish validating current approaches and technology before exploring new ones. The curse and the blessing is that we, as young conservationists, have more and more to catch up on but also a chance to set the tone for the future. Like many, I am comparably new to the field, but have witnessed a transition of themes and jargon. We have moved beyond the view of nature as a separate entity and embraced the interconnection and interdependence between human systems and nature (CHANS; Liu et al., 2007), describing world anthromes (Ellis et al., 2010). The future of conservation is going to be marked by adaptability in how and where we work, heterogeneity and inclusivity in values and skills, and local grassroots engagement.

Adaptability is a strength of this discipline. Structured Decision Making and the new Open Standards for Conservation were not the first conservation planning frameworks, nor will they be the last, but they are key tools that allow for re-evaluation (Schwartz et al., 2018). Science is inherently iterative and embraces change if A leads to C—instead of B, as expected—multiple times. When we behave this way ourselves—adjusting where we work and what we focus on—this is also a strength. Although the wheels of change can be slow to turn, scientists know that we must be flexible when a preponderance of evidence indicates an old framework is no longer adequate. Those of us early in our career may have more mobility to shift our priorities (e.g., to populated anthromes), but we must have the opportunity to do so. Novel problems require innovative solutions, and I think we will see more as younger generations bring forward creative and resourceful ideas.

Diversity is a critical ingredient in resilience, and our conservation will be stronger in conversation with those of different backgrounds. In personal as well as professional settings, being inclusive means valuing those with different career trajectories. One person's skills may be in quantitative or computational analysis, another's in field identification, and another's in public extension, but they may all deserve mentorship and opportunities to practice conservation. STEM initiatives have made significant progress in the US (DeJarnette, 2012) but kids should know that doctor, engineer, and physics teacher are not the only jobs available in science and math. Additionally, conservation groups can focus on common values using relational, human-centric messaging to reach and unite different populations.

Local engagement paired with sound research will have best practical successes. Place-based solutions driven by strong and engaged communities may be of increasing importance in future years. The global reach but localized, context-dependent approach of both the Nature Conservancy and PeaceCorps speaks for itself. Incorporating stakeholders is a method to increase support, and ultimately efficacy, of controversial conservation strategies (Gregory, 2000; Knight et al., 2006). Engaging volunteers for a day of service in their area has merits beyond the work itself—those investments can be transformational and long-lasting. Small, grassroots changes scale up. Intentional regional conservation planning (as in the US's Landscape Conservation Cooperatives framework) can address the specificity of local issues in a way that still allows for coordination between regions. (Examples of such scenario planning are ever more comprehensive; Karner et al., 2019).

These are three broad priorities for the future of conservation research and application. They reflect scholarly and personal experiences: adapting to anthromes as a grounding for effective conservation, embracing heterogeneity in skills and values in conservation training, and engaging stakeholders outside academia, including private landowners and local nonprofits. In each section, I use narrative inquiry to weave together personal reflections and professional lessons into an outlook of millennial conservation.

Adapting to Anthromes: A Conservationist's Evolution

Anthromes are one of our many improved tools for approaching conservation problems (e.g., Gibson and Quinn, 2017). Anthromes organize our thinking around multifaceted and dynamic CHANS and identify solutions for complex problems, “owning” our role as shapes of current and future sustainability challenges (Fuentes and Baynes-Rock, 2017). Societal systems are deeply embedded in directions for conservation science (Sutherland et al., 2009; Fleishman et al., 2011). It is striking that, of the 100 conservation questions of our time (Sutherland et al., 2009), each of the 12 overarching categories is influenced by human inputs, caused by human processes, or directed by human policies. In particular, ecosystem-related questions incorporate anthropogenic effects and ask “what, and where, are significant opportunities” for conservation, including among intensively managed landscapes (Sutherland et al., 2009). The first three priority questions in Fleishman et al. (2011) explicitly consider human needs in relation to conservation goals, and the next five consider how human management activities might be adjusted, but not ceased, to improve biodiversity outcomes. Most of these challenges not only acknowledge human transformation of ecosystems but also ponder how to proceed with conservation objectives without sacrificing human mainstays like agriculture, timber production, and economic growth (Fleishman et al., 2011). Given how deeply ingrained and accepted human needs and activities are in these kinds of guiding documents, it seems clear researchers are working in the Anthropocene.

I had no big picture like global conservation questions or anthromes in mind when I began doing conservation research; I jumped into research because it was fun and I had great mentors. Nonetheless, those experiences shaped my perspective of the discipline, piece by piece building and rearranging a framework of conservation thinking that ultimately does, and *must*, include people. The growth and opportunity that resulted for me individually, and for the field as a whole (e.g., from general biology to applied ecological research on multifunctional landscapes), demonstrates why it is important that conservation remains adaptable and flexible.

In my first year of research I was taught my first lesson in ecology: the whole landscape and community are the keys to understanding a species. To study puma, we studied scat and carcasses of prey, in both choice and poor habitats, but all in what could be classified as wildland anthromes. We were ecological detectives; employing tools and research designs to cobble together life history information. We read trophic cascade books and learned mule-packing, knot-tying, gun-cleaning, and how to survive during long days in rugged, remote wildlands. I fancied myself a kind of renaissance naturalist, a daughter of Aldo Leopold. The Sand County spirit was truly in me—entrancingly so.

I spent three seasons this way. But even working in the beautiful ecosystems of New Mexico, we were not free from the influences of the human population. We learned the perils of discussing the conservation of Mexican gray wolves in public spaces. A challenge of conservation in southwestern states is public and private land grazing rights and the division among stakeholders. As guests, we ought not rub resident ranchers and farmers the wrong way with our ideas of conservation of predators. We worked in human areas, fitting carnivore biology in as well as we could among the regular demands of residents, refuges, and air force bases. These stakeholders had to agree if we wanted to do anything for the big cats other than track them. Even in the land of desert mountains and ponderosa pine forests, nature was both “out there” and in here, with us. I found the proximity of contentious human interests and wild animals to be unwelcome. How do we make the space for conservation efforts within a human world?

I will never stop dreaming about those idyllic landscapes, but I was struck by reality. Literature like *Crow Planet* and *Coyote at the Kitchen Door* and courses in sustainability science and policy diversified my exposure to conservation. I read about the mismatches between biodiversity and where ecologists work (Miller and Hobbs, 2002) and currently protected areas in the United States (Jenkins et al., 2015). I absorbed prioritization papers like “The top 100 questions of importance to the future of global agriculture” (Pretty et al., 2010). Perhaps it was an inevitable result of a liberal arts education that I would be seeking something else besides traditional wildlife biology, or perhaps I simply mirrored changing management attitudes (Manfredo et al., 2018). Regardless of the reason, I came to understand that we cannot all be Yellowstone biologists. What about the nature around us at home? We cannot all travel to pristine “semi-natural” pockets of the globe; in fact, there is a need to study flora and fauna in more populated anthromes (Martin et al., 2012).

Conducting research closer to home, we understood the socioeconomic forces shaping the landscape and had a fuller picture of the environment and its players. To me, like many, urban ecology was not objectively as enticing but I was shown I had a ready-made backdrop for a natural experiment. Our case study was a rapidly developing southeastern city in a temperate forest zone, flanked both by agricultural counties and by a natural escarpment with more land protection activity. We had a spectrum of green spaces to compare, from urban parks to empty lots in suburban neighborhoods, patchy small-scale farms, and finally private conservation easements and nature reserves. With vast structural and compositional differences, which patches represented wildlife habitat? The question I took up then and still have not relinquished is this: what is the value of non-protected or so-called marginal spaces to wildlife? Thinking in terms of anthromes (e.g., Ellis and Ramankutty, 2008) allowed me to incorporate patterns of human land

use into the answers. Temperature forest areas became residential woodlands (Ellis et al., 2010), distinctions which revealed differential conservation potential (Wood and Quinn, 2016).

I learned that study species do not have to be the stuff of dreams. I did not feel the same awe from chickadee songs that I felt handling puma. However, saying I just wanted to count birds was my ticket to conversation with park managers, farmers, and retired property owners. Backyard bird talk is a great equalizer and it granted me access to land, which forged connections between the community and our research. I saw that avian diversity and abundance were outputs, reflecting a number of habitat quality inputs, including the spatial influences of the surrounding human population.

I saw that the habitat patch and matrix were shaped by human decisions into anthromes with conservation potential, and that human activities must be factored into habitat management. That Upstate South Carolina project morphed from traditional bird surveys to audio sampling to anthropogenic effects on bird vocalizations (Ernstes and Quinn, 2015) to a comparison of public versus private land populations (Quinn and Wood, 2017) to—beyond my tenure—socio-economic evaluations of ecosystem services (Quinn et al., 2015) and zoning governance efficacy (Brown and Quinn, 2018). It was intuitive to move from analyzing the ecological context of a forest patch to the socio-environmental context.

I was encouraged by the practicality of studying rapidly developing landscapes because it seemed likely we would have more and more of those. I shifted from studying the urban-to-rural gradient to looking at multi-objective/multi-functional landscapes. I studied avian communities affected by private land management decisions on lands used primarily for timber production. I noticed that the time I spent interacting with landowners was disproportionately greater than the time I spent surveying birds, and that those tree farmers and easement landowners were the ones driving the conservation work. Their willingness to engage was what would really matter for my study. How else would EQIP and other Farm Bill practices I studied be implemented, or conservation acres get protected, but with private citizen actions? I realized outreach and contextual awareness of socioeconomic behaviors are critical to putting conservation into practice beyond protected lands.

I also spent some time in land conservation and stewardship. As I inventoried natural resource values of properties going under permanent protection for a land trust, I faced different strategies of conservation. Of course I believed in promoting large swaths of public parks and national forests; sufficient habitat and connectivity are key to biodiversity conservation (Soulé and Terborgh, 1999; Trombulak and Baldwin, 2010). But what is the influence of private land to regional conservation? In the American southeast, much more of our forestland is privately owned and managed. Surely the decisions that are made daily on all those individual parcels accumulate to affect collective conservation outcomes. That is why my land trust was interested in safeguarding land it believed would serve as buffers for fragile natural communities. I observed firsthand the success of encouraging the small private landowner to make an impact, as well as of regional conservation planning and multi-stakeholder collaboration.

These stepping stones in my development as a conservationist paved the way for a perspective which readily accept that people are relevant to our conservation approach. Most systems we work in are transformed to some extent—not intact, natural communities defined primarily by vegetation and climate but rather changed and novel ecosystems with unexpected dynamics (Ellis and Ramankutty, 2008). Our research priorities must be updated to reflect our reality and practice must catch up with research (Pressey et al., 2007). Humans make up many of these landscapes, and so they must be a part of the study and solution (Knight et al., 2006; Fuentes and Baynes-Rock, 2017). Conservationists of my generation may be able to answer some of these challenges with anthromes in mind. For example, the anthromes approach also adds value to conservation scenario planning involving both biodiversity and ecosystem services, and aids in the identification of strategic trade-offs (Gibson and Quinn, 2017). Anthromes hold potential to facilitate connections between conservation goals and policy, especially in private and working lands (Martin et al., 2014). I have witnessed actionable steps to this effect in multiple anthrome types in the American southeast, including with carbon credit payments and USDA Farm Bill incentive programs. Undoubtedly we will see more.

Embracing More: Inclusion and Diversity

Conservation groups are including people in their mission statements and marketing in intentional ways. From the following examples, it is clear that anthromes are moving from conservation science to practice. In this application, values can be used as tools to connect seemingly disparate ideas and people. In that unity, we will find conservation success.

Enjoying the benefits and services of protected areas is not new, but recent language draws people into the equation perhaps more explicitly than in the past. For example, regional land conservancies highlight the interdependency between nature and people—“wonderful places” are protected because they are where we “live, work, and play” and they “have the power to change our lives” (Conserving Carolina). In rebranding, Conserving Carolina elevated the role of its constituent community by changing their slogan from “Saving the Places You Love” to “For Nature and People. Forever.” Human enjoyment has moved into the Southern Appalachian Highlands Conservancy’s mission statement via the “connecting people to land” initiative. Overall, these trends seem to be a departure from “leave it alone” sentiment of the 20th century, from Wilderness-Act-era restrictions of certain activities on protected land and accusatory imagery like Smokey The Bear and the 1970s “Crying Indian.” Rather than being inaccessible and roped off (for its protection), such organizations envision people interacting with nature (for our enjoyment)—in a respectful and responsible way, of course. Language such as “Find your Park” (Park Service) is invitational, reflecting that personal connections to landscapes are not only acknowledged but encouraged. A similar effort is reflected in academia.

Socio-environmental ties are more notably present in conference themes and keynotes. The 2018 North American Congress for Conservation Biology continued a theme of integration and connections (“Connecting the Urban to the Wild”) from 2012 meeting,

"Bridging the Gap: Connecting People, Nature, and Climate." Others have buzzwords for nature such as "frontiers" or "gateways," and themes of change are recurring (The Wildlife Society, Ecological Society of America, Society for Conservation Biology). The 2019 Ecological Society of America meeting theme is "Bridging Communities and Ecosystems: Inclusion as an Ecological Imperative." The description indicates that ecology must reflect how dynamic and diverse the community is and ought to be, with reference to: transformations, "connect[ing] ... disparate landscapes and subdisciplines," "diverse perspectives," "new techniques," and "interdisciplinary collaborations." The shifting language indicates a potential for connections and experiences—relational and eudaimonic values (Chan et al., 2016)—to improve conservation engagement.

Continuing to integrate principles from other disciplines (e.g., public health in Pullin and Knight, 2001) should help maximize conservation options. In practice, this includes understanding human behavior and decision-making using social science, incorporating the social and economic pillars from sustainability science, and leaning on industry solutions (e.g., improving habitat with "green" and "gray" infrastructure). But this kind of integration and inclusivity should not stop at interdisciplinary efforts.

The gratifying thing about conservation work is that it takes—and indeed will require—all kinds.

Where does a conservationist come from? There is no one way into this field and perhaps no one way forward. Yes, more often than not, conservationists played in the woods and turned over rocks, looking for small life. We had a special place outdoors to explore. But not always. Our trajectories do not all match those of famous naturalists. Sometimes we reach this profession (or passion) because of unexpected opportunities. Could a conservationist not come from another profession with a desire to apply their skills to environmental causes? Someone with a strong chemistry or physical science background may have innovative solutions to offer. Environmental legislation and community organizing takes nonscientific leadership. An ability to teach effectively can be leveraged to instill a wider stewardship ethics and influence far more lives than the standard readership of an academic article. I have learned that conservationists look like many things, and there is room at the table (or in the field) for many people, backgrounds, perspectives, and skill sets.

In deciding what I wanted to be when I grew up, I had a Goldilocks-type meter that indicated which work was not quite right for me. I did not really want to be a veterinarian, I just wanted to work with animals. For a period in my childhood, I vowed to be an escapist "wild girl" who lived in the woods with animals. Like many, I thought of nature as romantically "out there," and at odds with human civilization. It was dichotomous; one or the other, and initially I preferred the one with fewer people. I did not know about wildlife biology—beyond the unbelievable Jane Goodall or TV personalities like Steve Irwin—and ecologists did not frequent high school job fairs. By the time I was in college and had elective courses in my pre-veterinary biology major, I realized some combination of wildlife biology, landscape ecology, and conservation science came close to ticking all my boxes. My inner wild-girl-in-the-woods was almost satisfied when I tracked puma in New Mexican mountains, but it had not all clicked yet—that the field of biodiversity conservation has a lot to do with people and heterogeneity is critical.

What does a conservationist look like? According to the Bureau of Labor Statistics in 2013, 90.5% of environmental scientists were white (The Atlantic, 2013). Women still lag far behind men in total outdoor and wildlife industry employment (Camber Outdoors, 2017; Manfredo et al., 2018). But these facts do not tell the full story of Gen X, millennials, and Gen Z folks who consider themselves conservationists.

As a young generation of conservationists, we do not always reflect the traditional mold of career "-ists" before us: mammalogists, ornithologists, entomologists, ichthyologists. Standing on the shoulders of past ecologists and environmentalists, we have internalized 20th century lessons about the effects of fire suppression, pollution, and overharvesting. We have heard the phrase "novel challenges, novel solutions" for years now and we accepted the need to reframe traditional biomes to include anthropogenic effects earlier in our education. My generation is not made up of only Leopold-esque outdoors folk interested in game management. In graduate school, I witnessed the demand for more diversity and relevance—among faculty, students, and projects—in land-grant agricultural institutions. Many of us did not explicitly want to be trained as deer biologists, but neither did we only want to work with endangered species. We were encouraged to break the habit of introducing ourselves by study taxa and instead lead by conservation issue.

I cannot speak for all my peers, but I see young conservationists as having diverse values and unique motivations. I like working in cause-oriented teams. I believe in community service because I have seen it enhance people's sense of place, belonging, and agency, and seen those be strategically leveraged for conservation (Simon and Wang, 2002). I think a person's connection to the land, something hard to quantify but deeply ingrained, is a key to conservation (Allen et al., 2018). Understanding local contexts is critical to conservation success, even at the level of a family farm. Cruising around properties, hearing landowner's wildlife anecdotes and histories of familial land ownership is my idea of a well-spent field day. I do not think these interpersonal aspects make me less scientific. I also do not think I am alone in wanting to practice conservation in a way that embraces the potential of human contributions rather than disparaging them (e.g., contrast Terborgh's *Requiem for Nature*). As Wendell Berry says, conservationists should care about less glamorous environmental sectors like agriculture because "conservationists eat." Our common denominators are our human experiences which, because they shape our values (Chan et al., 2016), factor highly into the practice of conservation.

Many of us look to the future of conservation and heed the call to work "where humans live." We study marginal habitat, looking for opportunities for urban conservation, education, and outreach. Rather than scoffing at the statistical limitations of citizen science data, we recognize the potential it has for increasing awareness in otherwise isolated populations. We recognize the value of economic arguments to conservation messaging, but we are willing to take a step beyond payment for ecosystem services. We have been taught to be in a more nuanced zone, beyond such instrumental and intrinsic value approaches, and are ready to shift conversations and policy toward relational values (Chan et al., 2016). I have seen many friends engage older folks in conversation

on social media platforms to change their opinions on climate science because they feel it is worth the energy. These efforts require that we recognize how others form values and make decisions differently from us.

As with any problem-solving profession, conservation requires many skills and approaches, which requires many types of people. Conservationists work in academia, NGOs, or state and federal agencies with environmental science, sustainability, biology, ecology, wildlife, or natural resource degrees. But conservationists are also educators, engaging with young school groups about macroinvertebrates in neighborhood streams. They work in courts and statehouses, as environmental attorneys and non-scientist advocates. They are the volunteers who spend weekends improving trails and leading river cleanups. Conservationists are the coders and mathematicians who spend their days on the computer, developing Python scripts in ArcGIS for complex regional habitat analysis. They may not lay hands or eyes on the species or ecosystems they are studying, but they contribute no less than the field technician. Conservationists are the backyard naturalists and birders making notes about unusual patterns in phenology and migration. They are the young couples starting small-footprint but high-intensity farms to promote local agriculture and land sparing. Sometimes, conservationists have to practice in their free time and not as a primary profession. Sadly, this is becoming even more common as graduates struggle to get paid work and break into professional workplaces (Mongabay, 2017). While certainly not always the case in our polarized political climate, young people tend to be accepting of each other's differences (Black, 2010) and I trust we will continue to make space in our field for those with something to offer, even if they do not fit traditional molds.

Throughout various wildlife research projects, I have persistently asked "what else." What else can conservation work entail? I think a conservationist can come from many different places, but we are headed together into the same, though unknown, future. Welcoming a diversity of backgrounds and experiences can only lend us more collective insight, as we tackle more challenges in more places.

Turning Toward Others: Local, Bottom-Up Conservation Efforts

When I think of our conservation challenges for the future, I am not worried about our ability to do good science. We are building bodies of knowledge and advancing our understanding of ecological processes and systems in novel conditions. To me, a looming challenge is effectively practicing conservation. I think we need to focus on our communication—translating our messages and engaging with the right audiences in the right way. This may include some or all of the following:

- improving the public's trust in science,
- communicating well not just with each other but with the public and with policy makers,
- identifying and reaching all stakeholders involved,
- being receptive to new ways of doing things,
- utilizing unconventional but powerful platforms like social media to spread information (infographics, sound bites),
- and doing work that is interdisciplinary.

These all involve interactions with other people and reaching people that are different from us.

I have some ideas about how we might effectively engage others in tackling conservation issues, borne out of work I did at the Southern Appalachian Highlands Conservancy, a regional land trust where I served as an AmeriCorps member. The idea of service was not something advocated for by my academic advisors, but I was drawn to it—affecting change by empowering young leaders in target communities. Environmental conservation is a focus area of The Corporation for National & Community Service's AmeriCorps, although it is not as visible as public school programming or community revitalization (Simon and Wang, 2002). I decided this program would be a humbling way to pass time between college and graduate school and might help me process what I could contribute to conservation. I looked forward to getting out of the theory books and "getting things done" with non-academic folks working in land protection and stewardship. I am not surprised now to learn that AmeriCorps participants show marked changes in values as a result of their service experiences (Simon and Wang, 2002), but I did not expect then for mine to fundamentally change my mindset of conservation.

The service was rewarding and enriching. It taught me more about what various careers in conservation looked like than anything I had been exposed to in school. I learned about non-profit management, the dynamic nature of collaboration with state and federal agencies, and environmental issues specific to a place. I peeked into the legal side of land protection. Above all else, I learned about improving lands for the public good (whether publicly owned or not) and promoting responsible land stewardship. And on a personal level, I was encouraged and impressed by my passionate peers—fellow future conservationists—who lived and breathed their values.

One thing I did repeatedly in my AmeriCorps service was plan, lead, and execute volunteer workdays to improve trails, clean up trash, and control invasive species. These exhausting but exhilarating days came to represent something larger to me: the power and potential of bottom-up conservation.

Leading a good volunteer workday is a parable for practicing conservation. You have to identify your needs and the context, prepare for the work, gather your resources, recruit people, anticipate their needs to keep them happy, and reevaluate the problem at the end of your workday to see if you're going to need to plan another.

The issues behind these workdays involved multiple stakeholders, often with different values and objectives. Take the example of a trail workday on a conservancy-owned tract of land. This particular property was adjacent to National Forest Service land and was

an unintentional gateway for recreationalists. There is an impetus to apply best management practices on such properties, to be a good neighbor and example to others. The land trust would rather protect the water quality of trout streams at all costs by reducing erosion and limiting all impactful recreational activities upstream. But the land trust is subject to board members and the public, so it also experiences some pressure to keep their protected land open for public enjoyment. Also involved in the scenario is the local community—folks who are going to walk, bike, or 4-wheel across the property regardless of signs posted and who may not be aware of how their tread damages the land. Finally, there are the federal and state partners who lent support to the land protection in the first place—USFS and NC Wildlife Commission folks who have a vested interest in collective natural resources. Thus, we had to minimize threats to water quality while maximizing stakeholder satisfaction, and we had to hold a workday to redirect problematic spur trails and improve the grade and sustainability of the main trails.

A number of lessons I learned from coordinating these events can be applied to the future of conservation:

- (1) *Always begin with identifying the problem.* The problem was loose sediment from the unofficial trails washing into high quality trout streams. In conservation science, we have to start with knowledge: making observations, documenting and monitoring, and doing basic science.
- (2) *Plan and prepare.* The observations and knowledge from step 1 help you make a good plan for applying resources toward a particular problem.
- (3) *Have the right tools, or you can't get the work done.* Resources need to be in place before you start. It goes without saying that we need to match conservation problems with the appropriate resources (and this often also means securing sufficient funding). But beyond that, I think the right tools we can have as conservationists in the next generation are communication and critical thinking, on top of a solid foundation of scientific training. In fact, non-disciplinary skills like written/oral communication, leadership, and interpersonal training are desired by employers in multiple sectors (Blickley et al., 2013). Although not all that is required, this broader training will allow us to address varied problems.
- (4) *Success involves people.* None of the planning and preparation mattered unless we had people show up. The jobs were simply too big for the staff alone. Conservation issues have to be made relatable (why should a hiker care about erosion?) and actions/solutions have to be accessible (if you come help us improve a trail, you'll be helping protect water quality). When they arrived, you had to keep them there despite hard, unglamorous work. It was easier when doing a project with visible progress, like pulling invasive plants, but otherwise you needed to get them to learn or experience something new to make the day worthwhile.

Achieving this commitment often takes offering some sort of incentive. This is not unusual for conservation, especially in the private arena; it is a practical approach undertaken by many groups. USDA-NRCS cost-share programs offer assistance for producers to do best management practices that promote soil, water, or wildlife habitat health which may otherwise be prohibitively expensive for them. Land protection is a much easier sell when there are tax incentives, so conservation easement landowners experience an immediate payoff for waiving development rights on their land. Also, the USFWS has several agreements to make it easier on private landowners where threatened and endangered species are concerned. Our volunteers would be given the best experience possible while still getting important work done. Volunteers would be invited to use the trail they helped improve, and I would follow up with them later on with long-term results of their labor.

At the end of these days, people were dripping with sweat and dirt, aching for showers and running toilets. But they would feel they had done something tangible for the issue at hand. That lasting awareness is essential to getting more people committed and making messages stick.

- (5) *The final lesson about workdays was that there were always results I had not anticipated.* These volunteers had totally different backgrounds and day jobs, and sometimes ideologies, but they were unified by a shared love of the region we were working in, or a common value of community service. Sometimes we learn the most when we think we have complete control but we allow ourselves to be surprised by something we could not have predicted.

I believe the work of connecting people to land will be a successful conservation strategy because it transcends other boundaries and constructs. One can hold a land ethic and have various sociopolitical or economic leanings. Owning—or simply enjoying—unique spaces creates solid personal connections which endure because they involve so many senses. For example, hikers completing a trail earn a sense of ownership, hunters and farmers become keen and intuitive naturalists, volunteers invest a piece of themselves in service, and kids treat woods as their own personal playgrounds. Values derived from experiences are powerful (Chan et al., 2016). These authors explain that relational values contribute an important piece to the case for environmental protection—beyond simply intrinsic (for nature's sake) or instrumental (for human's sake) arguments. Such a framework considers the influence of cultural and individual identity, social responsibility and stewardship principles, and additional moral virtues in people's decision-making. Importantly, values are formed because of relationships, experiences, and connections to people and places. I think this is how conservation scales up and effects change: by involving people, keeping them coming back, and counting on them to spread awareness one step further. It is certainly how a group of about 30 AmeriCorps members increases education and awareness about conservation issues in Western North Carolina every year. It is how we could build better trails, establish new wildlife and pollinator habitat, clean up rivers and banks, and make space for native species. And if it takes a volunteer heart, then we ought to be cultivating that more in our peers and children.

Conclusion

Conservation is a broad and complex field that is more about people than I ever thought. It does not happen successfully in a vacuum and it requires innovation, partnership, and communication. We need to recognize that all of us have a worldview shaped by our experiences and we can probably come up with the best ideas if we acknowledge that wealth of diversity. We should listen humbly and be open to being transformed based on conversations with others. And, unfortunately, we cannot do that if we are all just wild girls living in the woods.

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